The Fidelity of Preservation of Insects from the Crato Formation (Lower Cretaceous) of Brazil

Storms break over the Crato Palaeolake, Mark Witton

Nathan Barling

Part-Time Ph.D. Student, 419523

This thesis is submitted in partial fulfilment of the requirement for the award of the degree of Doctor of Palaeontology of the University of Portsmouth.

August, 2018.

First Supervisor: Dr David M. Martill, University of Portsmouth

david.martill@port.ac.uk

Second Supervisor: Dr Sam W. Heads, University of Illinois

swheads@illinois.edu

Abstract:

The Early Cretaceous Nova Olinda Member (Crato Formation) of Brazil boasts the most exceptionally well-preserved non-amber Mesozoic fossil insects. In this project these insect fossils are comprehensively studied. Their fidelity of preservation is investigated, the mechanisms that allowed for it are modelled, and the palaeoenvironments that they lived in are hypothesised.

The Nova Olinda Member fossil insects have a broad range of preservational fidelities. At their lowest-fidelity, they are fragmented low-relief 'scrappy' traces. At their highest-fidelity, they are complete, fully-articulated, high-relief specimens with submicron-scale replication of both external and internal morphology. Cuticular structures (setae, scales, ommatidia, etc.) are sometimes replicated to the submicron-scale via nano-crystalline impregnation of the epicuticle. Internal labile soft-tissues (genitals, guts, tracheal system, etc.) are replicated with high fidelity by globular encrustations and impregnations. The remaining tissues are obliterated by pseudomorphed pseudoframboids (or pseudoframboid-like aggregates), which also protected the carcass from compaction. Globular/granular fabrics generated by decay are proposed based on their consistent occurrence with particularly decay-prone tissues. Artefacts of preparation/curation (cracks, punctures, etc.) are distinguished based on their occurrence without associated mineralogical fabrics.

Statistical analyses are undertaken to quantify the preservational fidelity of the Nova Olinda Member fossil insects and identify taphonomic trends. Although the collection analysed is biased towards members of Orthoptera and Blattodea, results indicate that taxonomy has no control over preservational fidelity. As no other Lagerstätten has been quantitively analysed in this manner, qualitative comparisons are undertaken. Eleven other Lagerstätten are examined, revealing that none yielded fossils as well-preserved as the Nova Olinda Member. In all cases where fossils are examined, they either have their micron-scale morphology obliterated by coarse mineral growth, are compacted to compressions, or are encrusted by irremovable microfossils.

The chemistry and preservational fabrics of the Nova Olinda Member fossil insects are analysed to determine the mechanisms of their exceptional preservation. The fossils are largely preserved in goethite, which pseudomorphs pyrite. The pyrite has two distinct fabrics: a nano-crystalline impregnation of the epicuticle and a coarser pseudoframboidal infill of the remaining carcass. Precipitation of both of these fabrics was stimulated by the metabolic activities of a sulphate reducing microbial mat, with the framboids only forming once pyrite had reached supersaturation. The globular encrustations/impregnations of internal labile soft

tissues are a result of apatite precipitation brought about by ‘minor’ decay. This decay created ‘active sites’ for mineralisation and liberated ions which, combined with dissolved porewater ions, allowed for calcium phosphate precipitation. These fabrics were deposited in a specific order that prevented compaction and allowed for submicron-scale preservation of tissues: Firstly, internal labile tissues were impregnated and encrusted in apatite. Secondly, the epicuticle was impregnated by nano-crystalline pyrite. Thirdly, pyrite overgrew/obliterated the remaining tissues as pseudoframboids. This process is presented in a novel multi-step preservational model.

To understand the biases and controls on the preservation of these fossil insects, their environmental preferences (and modes-of-life where applicable) are comprehensively analysed and compared to modern relatives. The modern environmental preference of each family (or order) reported from the Nova Olinda Member are grouped into simplified environments and tabulated. The data are analysed and three hypothetical regions proposed in a novel palaeoenvironmental reconstruction. These include: an arid scrubland around the palaeolake, a humid fluvio-deltaic region, and a distant forested region. Hypothetical ecological niches are also reconstructed, with xerophytic plants and arthropods, as well as burrowing arthropods, living in the arid scrubland, aquatic/semi-aquatic arthropods living in marginal ‘tongues’ of freshwater at the palaeoshore, and a further fluvial/deltaic freshwater niche inhabited by aquatic/semi-aquatic/riparian plants and arthropods. These reconstructions reveal that the articulated insect fossils were transported to the site of deposition alive or shortly after death by seasonal small-scale flash-floods (caused by seasonal rains). These flash-flood events allowed for insects to be preserved indiscriminate of taxon, size, robustness, or mode-of-life. Finally, a new taxon of fossil wasp is described and its systematics discussed.

Aims:

1. To investigate the fidelity of preservation of the Nova Olinda Member fossil insects by examining which tissues are preserved, quantifying how well-preserved they are, identifying if any taxonomic trends are present (using statistical analyses), and qualitatively comparing them to other Lagerstätten.
2. To determine the replacing minerals and their fabrics through elemental, chemical, and textural analyses, as well as produce a model for the process of fossilisation.
3. To investigate the taxonomic diversity of the Nova Olinda Member insect fauna and present a novel palaeoenvironmental reconstruction based on modern insect preferences.

Scope:

As this project is multidisciplinary, clear boundaries are established for each discipline to maintain achievable goals.

1. *Entomology*: Insects are the most diverse macroscopic organisms and entomology, particularly its systematics, is an *extremely* broad and dynamic topic, and cannot be examined comprehensively in this project. General insect anatomy and the diversity and ecology of several families are examined in this thesis. The systematics of Hymenoptera are explored in more detail during the description of a new taxa.
2. *Taphonomy*: Taphonomic analysis is restricted to controls affecting insects (and other terrestrial arthropods) in laminated limestones and is discussed in generalised terms rather than the specifics of each specimen.
3. *Statistics*: Taphonomic data is subject to explorative cluster and principal coordinate analyses to determine trends between insect groups or ecological roles. Both R-mode and Q-mode cluster analyses are undertaken.
4. *Geochemistry*: Iron sulphide geochemistry is described, including controls and phase pathways, although is restricted to the minerals and fabrics observed in Nova Olinda Member insect fossils.
5. *Sedimentology*: Descriptions of sedimentological features identified during this project are restricted to the laminated limestones of the Nova Olinda Member. Only brief descriptions of other well-known Lagerstätten are otherwise presented here, based on published data.
6. *Palaeontology*: Palaeontology is inherently multidisciplinary, and this project combines several other aspects of palaeontology. Entomological, taphonomic, and sedimentological data are examined to produce palaeoenvironmental and ecological reconstructions.
7. *Energy-dispersive X-ray spectroscopy*: Energy-dispersive X-ray analyses in this project have specific limitations. Prior agreements required most specimens be double Au-Pd coated. In some cases, this results in partially obscured spectra, with C also excluded from most spectra due to the use of a C filament. To preserve insect morphology, no specimens are polished, leading to topographic artefacts in some analyses. Other analyses are undertaken under time constraints, resulting in low counts. Finally, only Nova Olinda Member fossils are subject to energy-dispersive X-ray analysis, as examining the eleven other fossil Lagerstätten is beyond the scope of this project. Instead, mineralogical identifications in other Lagerstätten are based on published data.

Contribution:

Several key contributions to knowledge are made during this project:

1. Recording and presenting examples of exceptional preservation of Nova Olinda Member fossil insects, highlighting the preservation of tissues that are previously unreported on both the macro- and micro-scale. (Published in Cretaceous Research).
2. Recording and explaining the various mineralogical textures that replace Nova Olinda Member fossil insect tissues.
3. Creating a novel six-step taphonomic model for the mineralisation of Nova Olinda Member insects based on chemical analyses, textural observations, and the current understanding of iron sulphide geochemistry.
4. Presenting a novel adaptation of the 'resin-transfer technique', allowing its use for three-dimensional arthropod fossils in semi-porous carbonate sediments.
5. Creating a multi-stage transport model for the Nova Olinda Member insects, including different palaeoenvironments, different starting conditions, and how these affect an insect carcass.
6. Presenting a revised palaeoenvironmental reconstruction of the Nova Olinda Member hinterland, including the identification of multiple environments and seasonal climatic conditions, supported by entomological, taphonomic, and sedimentological data.
7. Describing a new taxon of fossil wasp (Hymenoptera). (Published in Cretaceous Research).

0. 2. Table of contents

0. 3. Word count: 65,545.

0. 4. Tables

0. 5. Figures

0. 6. Abbreviations:

AMNH: American Museum of Natural History. EDX: Energy-dispersive X-ray. EP LC: Department d'Estratigrafia I Paleontologia La Cabrúa. EPDS: Extracellular polymeric diatomatic substances. EPS: Extracellular polymeric substances. FFCLRP/USP, #DBRP: University of São Paulo, Departamento de Biologia. DHG: Nanjing Institute of Geology and Palaeontology, the Chinese Academy of Sciences (Daohugou Formation). FLFO: Florissant Fossil Beds National Monument. FLO: Specimens numbered by Florence Gallien. GR: Green River. HT: Helmut Tischlinger. IEI LC/P: Institut d'Estudis Ilerdencs La Cabrúa/Pedrera. JW: Specimens numbered by Judith Wohlrabe. LC: London Clay. MPV: Museo de Historia Natural Valencia. Mont#$_{\#}$: Montsec. MPZ: Museo de Paleontología de la Universidad de Zaragoza. NBRL#(resi): Residue of a specimen mounted on a separate stub. NBRL: Fossil insect specimens numbered by Nathan Barling. NBSED: Sedimentological specimens numbered by Nathan Barling. NBSTUB: Residue (not from other specimens) or modern insect stubs numbered by Nathan Barling. NHM: Natural History Museum, London. NIGP and DHG: Nanjing Institute of Geology and

Palaeontology, China. NIGP: Nanjing Institute of Geology and Palaeontology. NMVP: National Museum of Victoria (Palaeontology). OM: Organic matter. RdM: Rubielos de Mora. PAST: PAlaeontological STatistics. SEES: School of Earth and Environmental Sciences (at the University of Portsmouth). SEM: Scanning electron microscope. SH: Solnhofen. SMNK PAL: Staatliches Museum für Naturkunde, Karlsruhe (Paleontological). SMNS: Staatliches Museum für Naturkunde, Stuttgart. TEM: Transmission electron microscopy. UnNum: Unnumbered specimens. YPM: Yale Peabody Museum.

0. 7. Acknowledgements:

0. 7. 1. Academic acknowledgements

This thesis is not only the culmination of seven years of work on my part, but also six years of unending support from many amazing people.

Firstly, I'd like to thank my examiners, Philip Wilby, Nic Minter, and Zoe Saynor, for the enormous time and effort invested in reviewing this thesis.

Secondly, I'd like to thank my two supervisors, David Martill and Sam Heads. Not only have they provided a framework of academic support for this project, but also personal guidance throughout easy and difficult times alike. I cannot thank them enough for their time and tolerance in helping me develop from a graduate into an early career scientist.

In addition to David and Sam, several other academic staff have provided academic support and advice. Tony Butcher, David Loydell, Andy Gale, Rob Strachan, Robert Loveridge, Dean Bullen, Mark Witton, Günter Bechly, and Simon Cragg are all thanked sincerely for their help and guidance at various stages throughout this project.

Technical help was provided by members of the University of Portsmouth. Sue Atkins, James Coyne, Joseph Dunlop, Zoe Whittaker, Elaine Dyer, Richard Hing, Geoff Long, and Christine Hughes are all thanked deeply for their help with specimen cleaning, storage, acid digestion, resin transfer, SEM preparation, SEM operation, EDX operation, XRD operation, and overall laboratory guidance.

Several arthropod specimens from other Lagerstätten were required for comparative analysis. Through kindness and generosity, specimens were provided for most of these Lagerstätten. Helmut Tischlinger is thanked deeply for his donation of the only three-dimensional unweathered Nova Olinda Member insect examined in this project (specimen HT001). Susan Butts is thanked for loaning specimen YPM 73015 from the Yale University Peabody Museum of Natural History collection. Enrique Peñalver Mollá is thanked for the loan of specimens MPV-2418-RM and MPV-2419-RM from the Natural Sciences Museum of Valencia collection.

Antoni Lacasa Ruiz is thanked deeply for donating six insect specimens from his personal collection of ‘La Cabrúa’ (Montsec) fossil insects. Günter Schweigert and the Staatliches Museum für Naturkunde, Stuttgart are thanked for the donation of an unnumbered Odonata specimen from the Solnhofen Formation. Finally, Paul Seldon and Claire Mellish are thanked for their assistance and advice in procuring specimens for study.

Many members of administrative staff, especially those in SEES, are warmly thanked for providing help with all manner of tasks. Finally, I’d like to thank Judith Wohlrabe for donating the specimens used in this project, and for sharing her preliminary findings.

0. 7. 2. Personal acknowledgements

The last seven years have been a rollercoaster. While completing this degree, I have moved-house six times, transitioned from being a full-time student to a part-time distance student, had several part-time and full-time jobs, proposed to my (then) girlfriend, organised a wedding, and married my wife. This project has pushed me to the very end of myself, and has taken me to some very dark places. It has been a gruelling uphill battle through academic, personal, and mental health problems. Thankfully, I have had the support of some truly amazing people throughout all of it, without whom I would not be here.

I’d like to start by thanking my parents, Chris and Kay Barling. They have provided unlimited emotional support, encouragement, a place for my partner and I to live, and generously funded the majority of this project. I am immensely thankful for all of this and this project wouldn’t have been possible without their help. They have allowed me to pursue my dream through thick and thin. Thank you so much mum and dad, I love you both.

I would also like to thank the late Thomas and Ruth Barling, my grandparents, who passed on a generous inheritance. Tom was a wonderfully kind and loving man and a true academic to his core. I hope that they would have been proud and happy to see me complete a doctoral thesis and use their inheritance for academic study.

I’d like to also thank my siblings, Joshua and Abigail, for their personal support throughout this project. They provided advice and kinship through all the life-changing events over the last seven years. Along with them has been the continued support (as well as belittling banter) from my friends Zak Dawson, Dimitri Geremezoglu, Steven Brown, Adam White, and *many*, *many* more.

Among those I consider close friends, are dozens of peers (and rivals!), whose own projects have driven me to work harder and strive to be a better scientist. I’d like to deeply thank Luke Hauser, Michael O’Sullivan, Steven Vidovic, Rhian Llewellyn, Benjamin Moon, David Gold, Emily

Roberts, Awwal Bamanga, Sarah Biejat, Sarah Percival-Ridley, Marco Fazio, Emma Hart, Mathias Leidig, Natalia Walasek, Lee White, Georgia Witton-Maclean, Sietske Batenburg, Calum Davies-Brown, Alex Srdic, and many others for creating a nourishing, friendly, and fun working environment as well as pushing me to be the best I can be.

Finally, is the single person who has simultaneously helped and hindered the progress of this thesis the most. To my beautiful, intelligent, and loving wife Annabelle. You are my rock, the foundation of my life. I could never have gotten this far without you and I love you with all my being (she hates it when I'm soppy like this).

0. 8. Declaration:

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

0. 9. Dissemination:

0. 9. 1. Papers:

Barling, N., Martill, D., M., Heads, S., W., and Gallien, F. 2015. High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research*, **52**, 605-622. (This paper was selected as one of the 'best contributions' in Cretaceous Research and presented in their virtual showcase issue. It was the only entomological paper to be selected out of the 39 insect papers published that year, and was also the only paper in the field of taphonomy to be selected.)

Barling, N., Heads, S., W., and Martill, D., M. 2013. A new parasitoid wasp (Hymenoptera: Chalcidoidea) from the Lower Cretaceous Crato Formation of Brazil: The first Mesozoic Pteromalidae. *Cretaceous Research*, **45**, 258-264.

0. 9. 2. Report:

Barling, N. 2015. Taphonomy of dragonflies and damselflies (Insecta: Odonata) from the Crato Formation (Lower Cretaceous) of Brazil. *The Palaeontological Association Newsletter (Sylvester-Bradley Report)*, **88**, 66-69.

0. 9. 3. Presentations and posters:

On April 26th 2016, the findings of this project were presented in a talk at the 7th International conference on fossil Insects, Arthropods, and Amber in Edinburgh, Scotland (International Paleoentomological Society).

In 2013, the findings of this project were presented in an hour-long presentation to an amateur geological society at Southampton University.

In December 2012, the preliminary findings of this project were presented in a poster at the Palaeontological Association's 56th annual meeting in Dublin, demonstrating the potential of the Nova Olinda Member fossils for study.

Two other PowerPoint presentations on the findings of this project were presented at two internal University of Portsmouth conferences.

0. 9. 4. Press and Outreach:

On Boxing Day morning of 2013, I was interviewed by BBC Radio Solent live on air about the significance of *Parviformosus wohlrabeae* (Barling *et al*., 2013).

Chapter 1. Introduction

1. 0. Preamble

Insects are the most diverse and ecologically important macroscopic organisms, constituting a fundamental component of every terrestrial ecosystem since the Lower Devonian (Grimaldi and Engel, 2005). Their importance is derived from their abundance, diversity, wide array of ecological roles, and their intimate relationships with other organisms (particularly angiosperms, i.e. flowering plants) (Grimaldi and Engel, 2005; Mohr *et al*., 2007). To understand, manage, and maintain modern ecosystems, it is essential to establish how these relationships and roles evolved. This can only be achieved by examining and interpreting the insect fossil record.

The Early Cretaceous was a critical period for insect evolution (Grimaldi and Engel, 2005). It saw a major insect radiation, as well as the establishment of their modern faunal composition (in terms of orders and families represented) (Grimaldi and Engel, 2005; Mohr *et al*., 2007; Penney and Jepson, 2014). This period also marked the simultaneous rise and radiation of angiosperms globally, as well as the decline of gymnosperms ('naked-seed' producers, such as conifers) (Mohr *et al*., 2007). Although insect fossils can be found in many Early Cretaceous Lagerstätte (Penney and Jepson, 2014), the Crato Formation (Araripe Basin, north-eastern Brazil) is the only one to preserve insect fossils abundantly with a high-fidelity from South America. It does so because some of its sediments were deposited in a hypersaline palaeolake, located within an arid region of Gondwana (Martill *et al*., 2007a). The depositional setting, and its subsequent geochemical processes, facilitated high-fidelity preservation of numerous and diverse insect carcasses from the surrounding hinterland, offering a unique opportunity to study Gondwanan insect evolution during this critical period. To accurately interpret these fossils, their preservational fidelity must first be investigated. This will determine the degree of carcass alteration by preservational processes and help frame them in a wider ecological context.

Excluding some of the sedimentary observations presented for the Nova Olinda Member (discussed in section 1. 3. 3. 4.), this chapter summarises previous work published on the Crato Formation and other topics relevant to this project.

1. 1. Location

The Crato Formation of north-east Brazil crops out at the borders of the states of Ceará, Pernambuco, and Piauí (Figure 1, A). It is exposed along the north-eastern, eastern, south-eastern, and western flanks of the Chapada do Araripe (a ~150 km east-west by ~50 km north-south plateau), as well as a handful of small outliers to the southeast (Figure 1, B). Outcrops are also reported from the southwest, near Gergelim (Martill pers. comm., 2017). The formation forms a distinctive topography and its composition also results in a distinctive flora (Martill *et al.,* 2007a). Where not overgrown, the outcrop is easily discernible as its laminated limestones are highly distinctive and field brash is markedly slabby (Martill, 2007a).

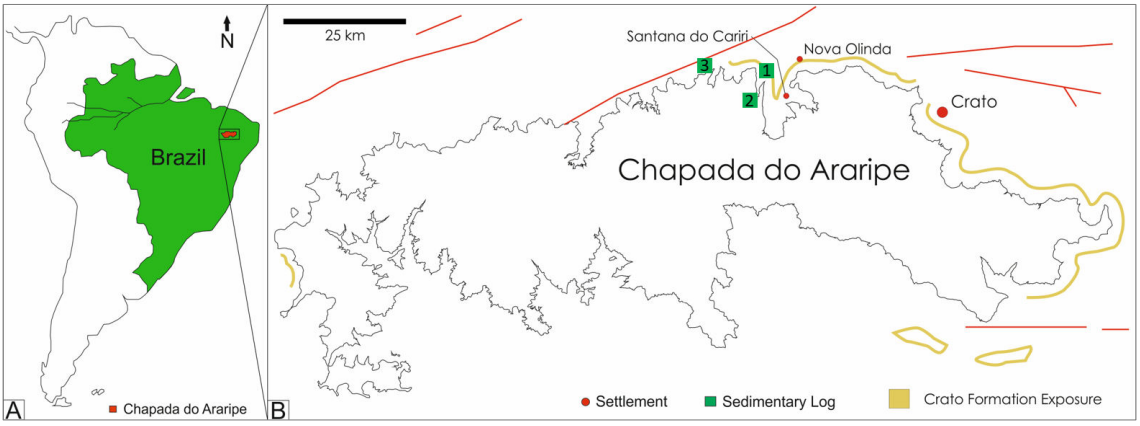


Figure 1. Outcrop locations. A, Map of the location of the Chapada do Araripe. B, The approximate position of Crato Formation outcrops around the Chapada do Araripe, along with the locations of sedimentary logs and the largest settlements. Green squares indicate the locations of logs for composite stratigraphic log for the Crato Formation: 1) Nova Olinda log; 2) Santana do Cariri log; 3) Tatajuba log (see Figure 4). Image adapted from Barling *et al*. (2015). Red lines indicate faults from sigmoidal shears highlighted by Heimhofer *et al*. (2010).

1. 2. Commercial uses

The Crato Formation is quarried commercially for paving slabs (Figure 2) and previously for cement manufacture. This has resulted in a large number of quarries that provide excellent access to the fossiliferous strata, and these are where the fossil specimens are collected. Many specimens are collected by quarry workers who, despite little palaeontological knowledge, find large numbers of well-preserved fossils (Andrade, 2007).

Figure 2. Photograph of the Crato Formation being quarried for paving slabs. Image © D. M. Martill, quarry location near Nova Olinda.

1. 3. Geology

1. 3. 1. The Araripe Basin

The Araripe Basin contains a heterolithic sedimentary sequence (Figure 3) that is exposed along the flanks of the Chapada do Araripe plateau, as well as in numerous stream sections and quarries. The basin is, in part, fault bounded and covers approximately 8,000 km^2 (Assine, 2007; Martill and Heimhofer, 2007). Its geological history is significant for several reasons. Not only does it contain both of the only known Lower Cretaceous terrestrial South American Lagerstätten, but the Crato Formation also coincides with Oceanic Anoxic Event 1b, which is often linked to climate change and extinctions (Alexandre *et al*., 2010). In addition, it is important for the correlation of Brazilian marginal basin development and was deposited during a critical part of the tectono-sedimentary evolution of Brazil: namely, the opening of the south Atlantic Ocean (Ponte, 1992; Martill *et al*., 2007a; Neto *et al.,* 2013). The main phase of basin deposition occurred between the Upper Jurassic (Tithonian) and Lower Cretaceous (Albian) (Neto *et al.,* 2013).

The Araripe Basin sedimentary succession has been divided into several lithologically distinctive formations (Brejo Santo, Missão Velha, Abaiara, Rio da Batateira, Crato, Ipubi, Romualdo, Ararjara, Exu, etc.) (Assine, 1992, 2007; Neumann *et al.,* 2003), however disagreements over the definitions, names, and rankings of several of them persist.

1. 3. 2. Basin age and evolution

The Araripe Basin (Figure 3) is one of several north-east south-west trending half-grabens in the Cariri Valley and was formed when extensional tectonics reactivated a pre-existing sigmoidal shear zone (Figure 1; Heimhofer *et al*., 2010). This period of extensional tectonics was linked to the opening of the northern part of the south Atlantic Ocean during the Late Jurassic to Early Cretaceous (Chang *et al*., 1988; Mattos, 1992, 1999; Neumann *et al.,* 2003; Heimhofer *et al*., 2010). In the Late Jurassic (Tithonian), prior to the extensional tectonics, the Brejo Santo (shales and clay-rich sandstones) and Missão (coarse sandstones) formations were deposited (Neumann *et al*., 2003). This was later followed by the Abaiara Formation (clay-rich sandstones) in the earliest Aptian, during the extensional tectonics (Neumann *et al*., 2003). Together these sediments make up the Cariri Group (Figure 3).

Extensional tectonics ceased during the Aptian (between the Abaiara and Rio da Batateira formations) and a transitional post-rift phase began, resulting in a significant hiatus represented by a major unconformity (Coimbra *et al*., 2002). Above this unconformity lies the Santana Group (Figure 3), which was deposited during a period of reduced subsidence between the Late Aptian and Early Albian. The Santana Group is sedimentologically complex, with a variety of sediment types at its base, including fluvial, lacustrine, deltaic, and shallow marine (Martill pers. comm., 2017). However, the sequence can be simplified to represent the transition from a fluvial-deltaic environment (Rio da Batateira Formation) to a restricted, stratified (with hypersaline lower levels) lake/lagoon with seasonal rains (Crato Formation), and finally to evaporites (Ipubi Formation), which is unconformably (minor) overlain by marginal marine shales (Romualdo and Arajara formations) (Heimhofer *et al*., 2010). This group is unconformably overlain by a massive succession of fluvial siliciclastics (Exu Formation) (Ponte and Appi, 1990; Heimhofer *et al*., 2010).

The Crato Formation is latest Aptian in age, with terrestrial palynological data placing it within the *Sergipea variverrucata* palynozone (Coimbra *et al.,* 2002; Batten, 2007). At this time, it was located 520 km inland from the eastern coast of the newly forming South America, during the breakup of Gondwana. It had a palaeolatitude of 10°–15° south of the equator, placing it within the tropical-equatorial hot arid belt (Chumakov *et al.,* 1995; Heimhofer *et al.,* 2010).

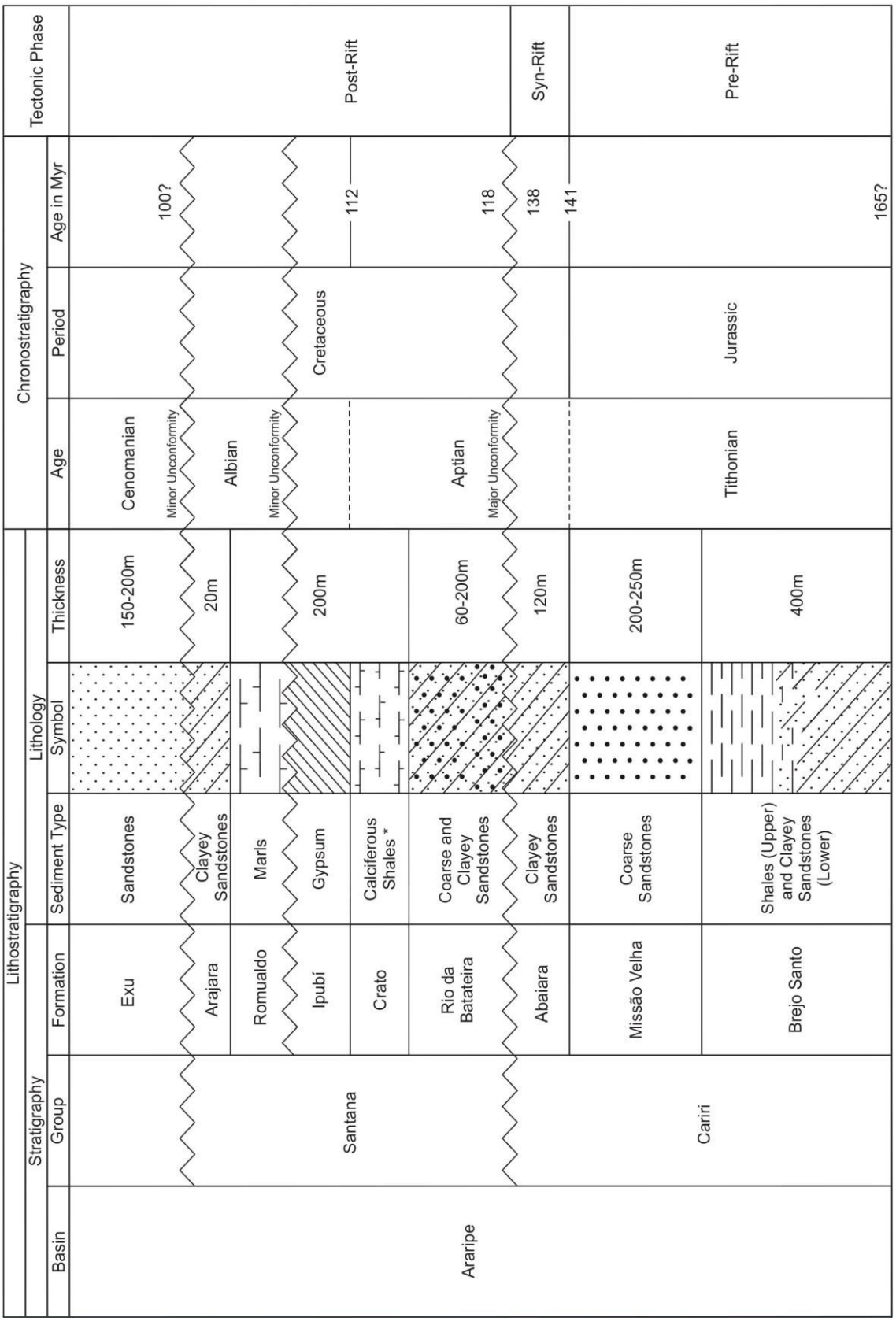


Figure 3. Litho- and Chronostratigraphic log of the Araripe Basin. Figure based on stratigraphic descriptions, names, and rankings presented by Neumann *et al*. (2003). Additional minor unconformity added between Ipubí and Romualdo formations (Martill pers. comm., 2017). Ages are presented in accordance with palynological data provided by Coimbra *et al.* (2002). The sedimentology and sediment type of the Crato Formation (marked with an asterisk) is further described in Figure 4.

The Crato Formation contains alternating clay-carbonate rhythmites (discussed further below), which are believed to represent alternating lake levels (Heimhofer *et al.,* 2010). During periods of high lake-level, the laminated carbonate facies were deposited. Neumann *et al*. (2003) suggested that this was a result of a seasonal climate, however work by Heimhofer *et al*. (2010) alternatively suggests that the lake level change was a result of tectonic activity (as has already been proven for the nearby Codó Formation) (Paz and Rossetti, 2006). During the Early Cretaceous, global eustatic sea-level rise would have episodically established a highly restricted (epeiric) seaway, linking the Araripe Basin with the newly opening south Atlantic Ocean (Arai, 2000). With the information presented above, combined with discussions presented below (section 1. 4. 2.), a marine water influence (albeit with varying salinity) is confirmed for the Crato Formation, as has already been done for the Ipubi and Romualdo formations.

1. 3. 3. Stratigraphy and sedimentology

1. 3. 3. 1. Underlying formations

The Crato Formation is underlain by different lithologies in different areas. In the west, it unconformably overlies Precambrian gneiss basement (Neto *et al*., 2013). In some other areas, it unconformably overlies Jurassic alluvial sediments (Cariri Group) (Neumann *et al*., 2003; Scherer *et al*., 2015). However, in most areas it is underlain by the Rio da Batateiras Formation (Ponte and Appi, 1990), which is rich in microfossils (specifically ostracods and conchostracans) that indicate a non-marine aquatic environment with variable (0-15%) salinity (Syrio and Riso-Netto, 2002).

1. 3. 3. 2. Names and status of the Crato Formation

The Crato Formation takes its name from the town of Crato, a large settlement to the northeast of the Chapada. The formation has a history of controversy with regards to its name. It was originally referred to as the ‘Calacreo do Sant’Anna’ (Small, 1913) and was later included as a member of the Santana (now Romualdo) (Beurlen, 1971; Maisey, 1990, 1991) and Araripina (Silva, 1986) formations. It was first considered a discrete formation by Beurlen (1963), who later referred to it as a member again (Beurlen, 1971). Other publications concerning the nomenclature of the Crato limestones include; Ponte and Appi (1990), Assine (1992), Martill and Wilby (1993), Beurlen (1994), Ponte and Ponte Filho (1996), Assine (2007), and Martill *et al*. (2007a).

Even in recent publications, the Crato Formation is still referred to as a member within the Santana Formation (e.g. Prado *et al*., 2016). This is a result of two conflicting publications from

the same year: Assine (2007) and Martill *et al.* (2007a). Assine (2007) reasserted the Crato limestones as a member of the Santana Formation based on the recommendations of the Brazilian Code of Stratigraphic Nomenclature, whereas Martill *et al.* (2007a) re-established it as a distinct formation for the following reasons:

- The unit can be easily mapped due to its distinctive laminated limestones.
- A basin-wide disconformity separates it and the overlying Ipubi and Santana (Romualdo) formations.
- It has both a distinct palaeobiota and distinct preservational style from the Romualdo Formation, which is also a Konservat-Lagerstätte.

Of these two classifications, Martill *et al.* (2007a) is followed here as it is internationally the most widely accepted nomenclature. This acceptance is partially a result of Assine (2007) being published in Portuguese (and is therefore not as easily accessible to most of the international scientific community), but mostly due to the robust argument presented by Martill *et al*. (2007a).

1. 3. 3. 3. Crato Formation members

There have been numerous discussions over the type section for the Crato Formation. Martill and Wilby (1993) and Berthou (1994) previously outlined type sections (Rio Batateiras log and a Riacho Jacu river log respectively), but these proved inadequate to describe the Crato Formation. Martill *et al.* (2007a) suggested three type sections at Nova Olinda, Santana do Cariri, and Tatajuba (Figure 4, A). Despite the difficulty in identifying a type log, four members were recognised by Martill *et al.* (2007a) (Figure 4, B):

- The Nova Olinda Member
- The Caldas Member (previously named the Barbalha Member by Martill and Wilby, 1993)
- The Jamacaru Member
- The Casa de Pedra Member

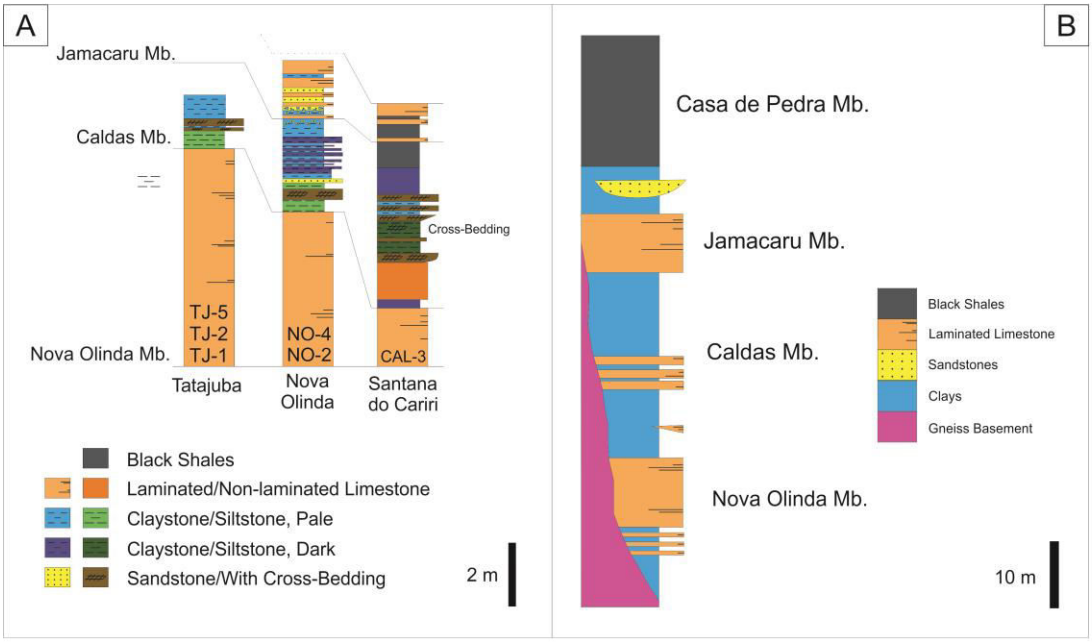


Figure 4. Crato stratigraphy. A, Stratigraphic logs of marked areas in Figure 1. B, Simplified general vertical section (composite log) of the Crato Formation. Logs adapted from Martill and Heimhofer (2007) and Heimhofer *et al*. (2010).

The formation can reach a thickness of up to 60 m and is comprised of the Nova Olinda Member at its base (limestone), overlain by the Caldas Member (silts and clays), then the Jamacaru Member (limestone), and finally the Casa de Pedra Member (silts, clays and black shales in the west). The lowermost Nova Olinda Member is the thickest laminated limestone of the formation and is interbedded at its base with clays. It varies laterally and is reported to differ in thickness and lithology considerably towards the east of the Chapada do Araripe plateau (Martill, 2007a). To the east, the entire formation is dominated by sandstones and some of the most prominent limestone beds are absent, suggesting interdigitation between two distinct formations (Martill, 2007a). Although this hypothesis is supported by the consistent interbedding between laminated limestones, clays, and sandstones throughout the formation, it is yet to be proven. All four members of the Crato Formation are described below. However, this thesis focuses solely on fossils of the Nova Olinda Member and consequently it is examined in greater detail.

1. 3. 3. 4. The Nova Olinda Member

The Nova Olinda Member is up to 13 m thick and has two distinguishable macrofacies and four microfacies (Neumann *et al.,* 2003; Catto *et al*., 2016). The macrofacies are: clay-carbonate rhythmites that are rusty-brown in colour, finely laminated with varying amounts of organic matter, and a laminated limestone facies that resembles a typical ‘plattenkalk’. No samples of the clay-carbonate rhythmites are analysed, as the exceptionally preserved insects are

restricted to the 'plattenkalk' macrofacies. Consequently, further sedimentological descriptions in this section are only of the 'plattenkalk' macrofacies.

The sedimentology of the plattenkalk is macroscopically uniform and typically each limestone bed can be traced laterally over tens of metres (Heimhofer *et al.,* 2010). Samples analysed in this project reveal that the majority sedimentary fabric is that of discrete interlocking rhombohedra (Plate 1; also see EDX Plates 11 and 12), which is typical of recrystallized carbonate sediment and is consistent with previous observations (Heimhofer *et al.,* 2010; Heimhofer pers. comm., 2014). This fabric is superficially similar to that of dolomite, however further alizarin red staining reveals a 99% calcium carbonate content (Figure 5). Dolomite does occur within the member, but is restricted to rare and isolated pipe-like structures (Martill *et al.,* 2008a). The matrix crystals vary in size between 5 and 10 µm (Figure 6). The origin of the calcium carbonate has been debated over the last 24 years (Martill and Wilby, 1993; Heimhofer *et al*., 2010; Catto *et al*., 2016). It was originally considered to be the result of benthic microbial mats (Martill and Wilby, 1993), however a later study (Heimhofer *et al*., 2010) suggested authigenic precipitation in the upper water column ('whitings', possibly by *Micrococcus luteus*). Heimhofer *et al*. (2010) supports this with a consistently negative $\delta^{18}O$ signature for the authigenic calcite, which indicates an ^{18}O-poor meteoric source, such as a freshwater river input. However, the lack of a cyclic stable isotopic pattern could be the result of homogenization of the signal during diagenesis, resulting in a false reading (Heimhofer *et al*., 2010). New research by Catto *et al*. (2016) demonstrates that the limestones were precipitated *in situ* by benthic microbial mats. Observations of low amplitude ripple-like structures and 'tearing' structures (created by halite crystal growth) by Martill *et al*. (2007b) indicates that a benthic microbial mat was present, further supporting this hypothesis (Figure 7; Martill *et al.,* 2007b; Heimhofer *et al.,* 2010). Given the presence of these structures, the fabric of the matrix, and the possibility of false isotopic readings, it is likely that the calcium carbonate was precipitated *in situ* by a microbial mat. The confirmation of a microbial mat does not exclude the possibility of 'soupy' sediment as proposed by Martill (1993b) (discussed later in section 1. 3. 3. 5.), as microbial mats are known to commonly form masses that can float in marine waters (Bender and Phillips, 2004).

Larger calcite crystals occur, but are typically restricted to mineral infills of fossil cavities (Plates 2, 3, and 4). On rare occasions, these larger crystals can reveal moulds of the rhombohedral matrix (Plate 5).

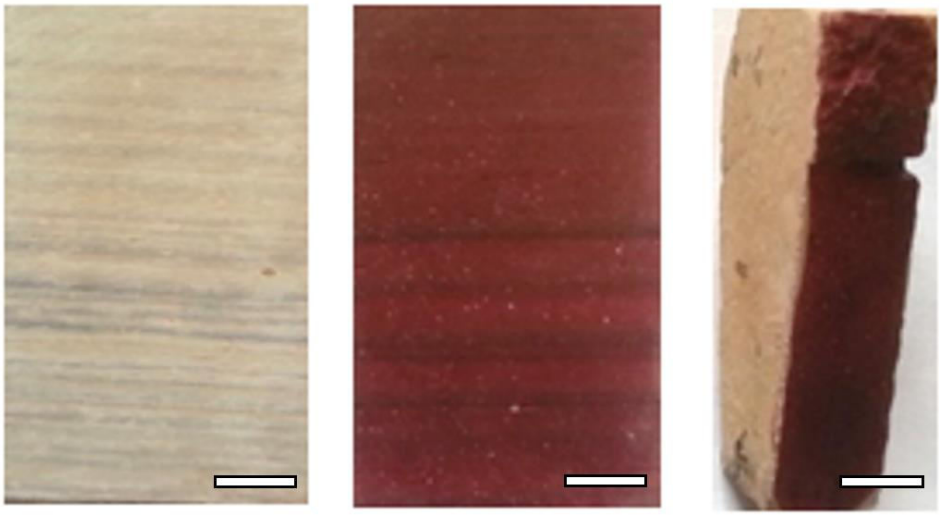


Figure 5. Chemical staining of Nova Olinda Member limestone. Photograph of hand specimen sediment samples. Leftmost is untested 'unweathered' sample. The middle sample is a red alizarin stained 'unweathered' sample. Rightmost is a 'weathered' sample, with the front face red alizarin stained. Dark red colours indicate 99% calcium carbonate content. Scale bars = 1 cm.

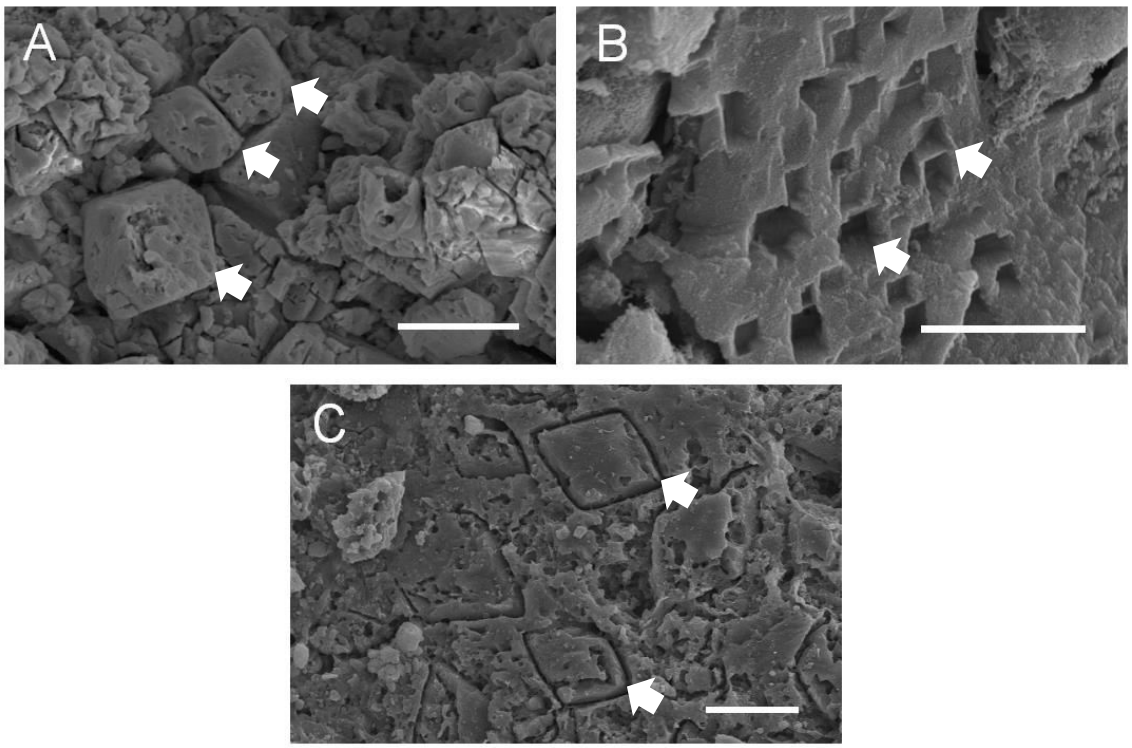


Figure 6. Evidence of discernible matrix crystals in the Nova Olinda Member. A, Acid etched Nova Olinda Member sediment sample showing individual rhombohedral calcium carbonate crystals of varying sizes. B, Rhombohedral termini of calcium carbonate matrix crystals preserved in calcite cement moulds, within posterior abdomen of insect. C, Etched calcite rhombohedra in calcite cement, centre of abdomen. All highlighted by arrows. A, Specimen NBRL11(Stub)-015. B, Specimen FLO36-72. C, Specimen FLO43-55. A and C, Scale bars = 10 µm. B, Scale bar = 5 µm.

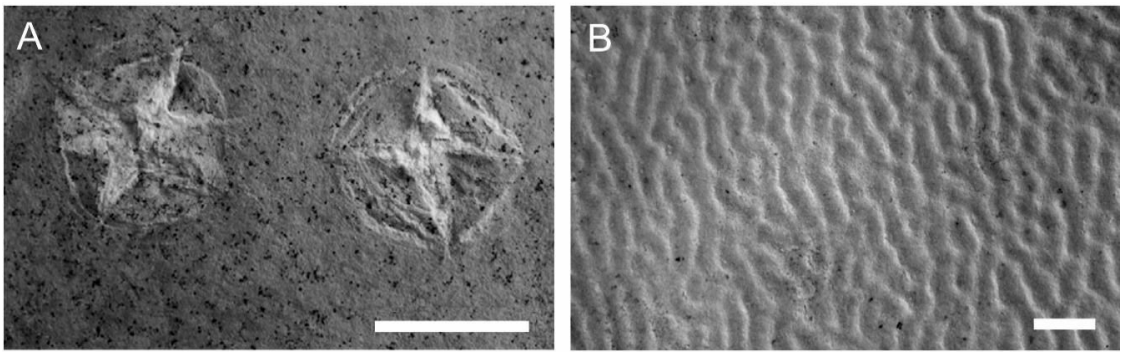


Figure 7. Sedimentary structures of the Nova Olinda Member. A, Halite crystal growths with 'tear' structures ('ghosts') indicating that the sediment was microbially bound together. B, Ripple marks along a single laminae indicating a lithified microbial mat. Images adapted from Heimhofer and Martill (2007). Scale bars = 10 mm.

The laminae examined here have an average thickness of 1 mm, but can be up to 5 mm thick. They alternate between light and dark-blue grey colours when freshly exposed, and between cream buff and rusty-brown colours when weathered (Plate 6). The alternating light and dark colours are probably varves, with the darker laminae representing a wet season with increased microscopic detritus influx (Heimhofer *et al*., 2010).

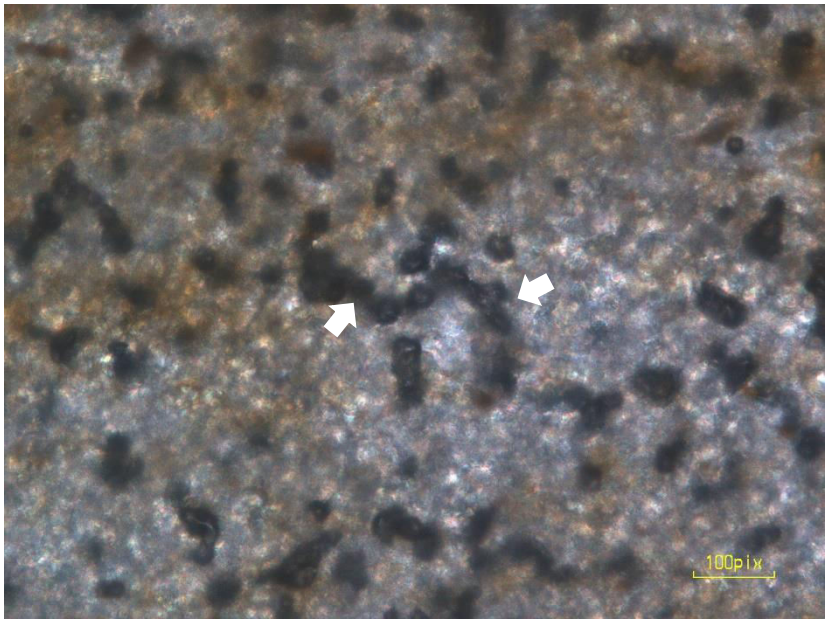


Figure 8. Light microphotograph of a thin section through Nova Olinda Member sediment. Chains of hollow spheres highlighted by arrows, possibly representing chains of algae preserved as iron sulphide fossils. Specimen NBRL017-TS21. Scale bar = 100 pix (~50 µm).

Scanning electron microscopic analyses (SEM, see Chapter 2. 3. 1.) revealed that the sediment, particularly the darker laminae, contain abundant globular and spherical microscopic material, likely representing fossilised microscopic detritus ('organic matter') and microfossils. Where subject to energy dispersive X-ray analyses (EDX, see Chapter 2. 3. 2.), this material was

identified as iron sulphide or its weathering products (EDX Plates 13 and 15-17). The microfossils appear to be photosynthetic algae (possibly *Micrococcus luteus* as noted above) and are often found linked together in chains (Figure 8). The globular material is present as aggregates, often concentrated in abundant 3 – 7 mm bacillus-like structures that coat the surfaces of many laminae (Figure 9; Plates 7, 8, and 9). These structures are predominately made of the globular material, but also contain detrital clay minerals not found elsewhere in the sediment (Figure 10 and Plate 10; also see EDX Plates 13 and 14). This, combined with their size and shape, suggests that they may be from filter-feeding fish, which are known to deposit suspended clay particles in their coprolites (Zhou Y. *et al*., 2014). Juveniles of the abundant fish *Dastilbe* are likely filter-feeders and, as such, these coprolites are attributed to them (Bagarinao, 1994). These structures and *Dastilbe* fossils are discussed further in sections 1. 4. 2. and 1. 5. 4. respectively. No clays were observed outside of the bacillus-like structures.

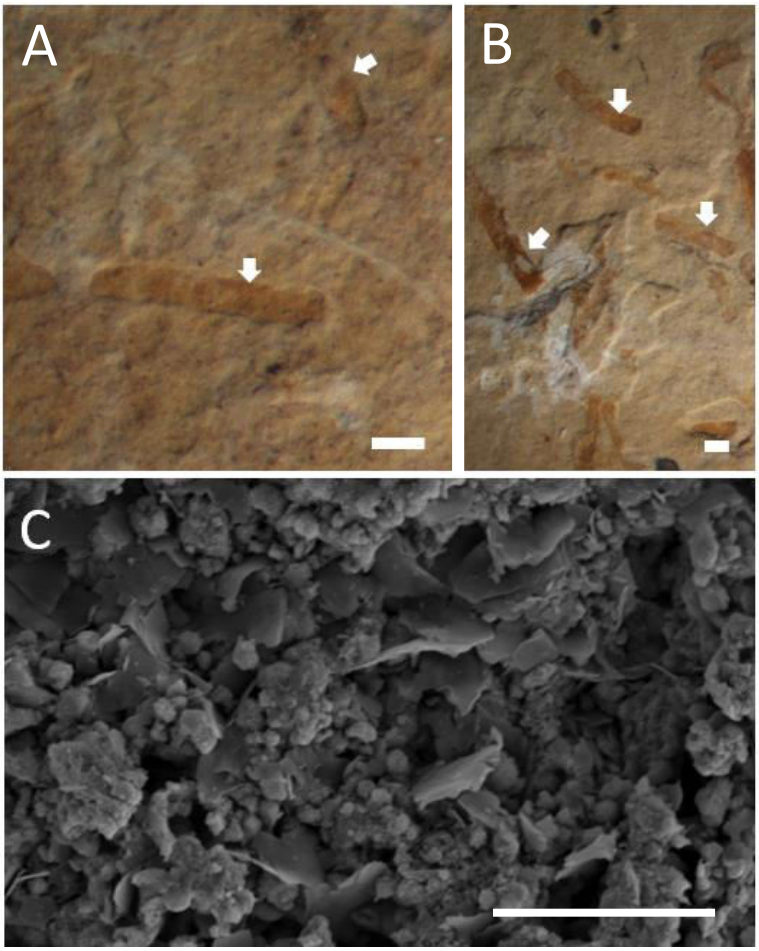


Figure 9. Enigmatic bacillus-like structures that are abundant in the Crato Formation limestones. These structures were previously interpreted as disarticulated Cheirolepidiaceae-like branchlets (Neumann *et al*., 2003) and *Dastilbe* coprolites (Martill *et al*., 2007a). Here the interpretation of fish coprolites is followed and supported with additional evidence. A-B, Arrows highlight bacillus-like structures coating the surface of many laminae. C, Scanning electron micrograph of internal contents of coprolites, displaying globular fabric mixed with blades of clay. A, NBRL015 photo 05. B, NBRL024 photo 01. C, NBRL011(stub)-18. A and B, Scale bars = 1 mm. C, Scale bar = 10 µm.

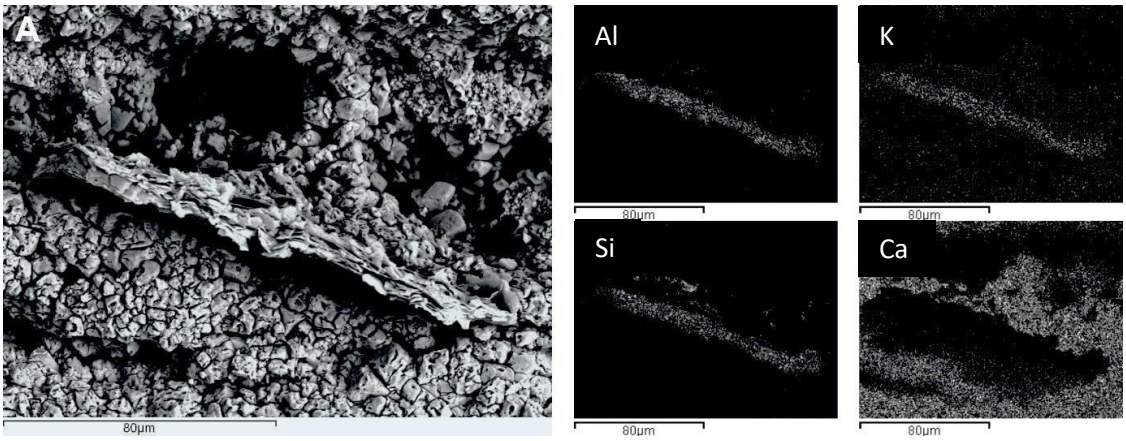


Figure 10. Clay minerals. Scanning electron micrograph of a sediment sample perpendicular to bedding, along with energy dispersive X-ray elemental maps, highlighting clay minerals within *Dastilbe* coprolites in the Nova Olinda Member. The clay minerals are chemically distinct from the surrounding calcium carbonate matrix. A, Scanning electron micrograph. Other images are labelled with their respective elements. EDX Plate 14 also indicates the presence of Mg. Elemental composition and morphology suggests that the clay is likely detrital platy illite. Specimen NBRL011. Number of counts = 15848. Scale bars = 80 µm.

1. 3. 3. 5. Nova Olinda Member microfacies

The Nova Olinda Member was examined microscopically by Catto *et al.* (2016), and its facies re-interpreted as four distinct microfacies: rhythmic, nodular, planar laminated, and crustiform. These are characterised as follows:

- Rhythmic microfacies: 0.5-2 mm long lenses composed of micritic calcite, organic matter, and clay. These also contain a mineralised organic matrix, in the form of microspheres.
- Nodular microfacies: interbedded micritic lenses, organic rich clays, and 1-2 mm spherical/elongate micrite and quartz nodules. The nodules distort laminae and irregular layers are composed of calcite spherulites and peloidal matrix, with some recrystallized euhedral and subhedral calcite. Gypsum and pyrite are also present, along with calcified bacteria.
- Planar laminated microfacies: micrite with planar parallel laminations and dark lenses of organic matter. These lenses are interpreted as *Dastilbe* coprolites here (as outlined in section 1. 3. 3. 4.). Its matrix consists of euhedral to subhedral calcite rhombohedra.
- Crustiform microfacies: prismatic calcite crystals forming palisades, coated in biofilms, and separated by laminites. They also contain dendritic spherical to subspherical calcite clusters.

In this revised scheme, the rhythmic and nodular microfacies correspond to the clay-carbonate rhythmite macrofacies, and the planar laminated and crustiform microfacies correspond to the typical 'plattenkalk' macrofacies. The specimens analysed in this project match descriptions of the planar laminated microfacies. Catto *et al*. (2016) interpreted many of the lenses, nodules, and spherulites in these facies as remnants of bacterial body fossils, bacterial trace fossils (filaments etc.), or, more frequently, extracellular polymeric substances (EPS). They also attributed much of the variation in these structures to differing environmental conditions (e.g. water-level, CO_2 pressure, hydrodynamic energy, pH). They concluded that 90% of the carbonate was generated *in situ* and that, based on well-preserved tetrads and sporomorphs, the terrestrially derived organic matter travelled a short distance from an arid environment to a low-energy site of deposition, with the crustiform microfacies representing a higher-energy aqueous environment. Additionally, they attribute some of the bacterial fossils to shallow-water filamentous benthic bacteria (Catto *et al.*, 2016).

While it is undoubtable that the calcification of EPS and bacterial cells account for some of the spherical calcitic structures (Plate 11), some of the organic material origin and environmental interpretations conflict with previous studies. The descriptions of various clays and organic material lenses (in the rhythmic, nodular, and planar microfacies) do not consider the abundant macrofossils (*Dastilbe*). Here, these structures are interpreted as *Dastilbe* coprolites. Such an interpretation accounts for their size, shape, clay mineral content, and their occurrence with the abundant fish *Dastilbe*. The environmental interpretation by Catto *et al.* (2016) also includes shallow-water bacteria and a high-energy environment. This conflicts with the macro-sedimentological data, as the formation of extensive laminae, in a somewhat soupy sediment (Martill, 1993b; Barling *et al*., 2015), requires deposition below storm wave base and a significant distance from the paleoshore (Heimhofer and Martill, 2007; Nichols, 2009; Heimhofer *et al*., 2010; Martill pers. comm., 2015). Additionally, the extensive gypsum (~30 m thick) of the overlying Ipubi Formation may have required a significantly deep (> 50 m) water body prior to its formation (Silva, 1988; Heimhofer and Martill, 2007; Oliveira *et al.,* 2011; Martill pers. comm., 2015). Although this deep-water requirement could be replaced by a restricted connection to the south Atlantic Ocean (Wilby pers. comm., 2017), the undisturbed laminae still indicate that deposition was below storm wave base. Regardless, the *in situ* model for the origin of the Nova Olinda Member calcium carbonate is well supported and agreed with here.

1. 3. 3. 6. Nova Olinda Member cementation and diagenesis

Despite the relatively uniform nature of the Nova Olinda Member, its diagenesis is complex. Early diagenetic concretions are present in the form of infrequent carbonate concretions and

rarer silicified concretions (Martill *et al.,* 2008a). There are also reports of authigenic barite and pyrite, as well as aggregates of galena and sphalerite (Martill *et al.,* 2008a). While galena and sphalerite are present throughout the Nova Olinda Member, the other minerals are generally restricted to the lower portion, near the basal disconformity (Martill pers. comm., 2016). Additionally, as noted above (section 1. 3. 3. 4.), iron-rich dolomite occurs within the member in the form of a massive brecciated, pipe-like structure reaching 5 – 6 m in height (Martill *et al.,* 2008a). Diagenesis may have also resulted in the homogenisation of the cyclic stable isotope pattern noted by Heimhofer *et al*. (2010).

Further discussions of the complex diagenetic alterations that insect carcasses underwent in the Nova Olinda Member will be presented later in this thesis (throughout Chapters 3 and 4. 2.).

1. 3. 3. 7. Caldas Member

The Caldas Member, originally called the Barbalha Member (Martill and Wilby, 1993), overlies the Nova Olinda Member. The name was proposed original by Martill and Wilby (1993), however the name had previously been used by Assine (1992) for a different range of strata while Martill and Wilby (1993) was in press. As such, Martill and Heimhofer (2007) formally renamed it the Caldas Member. It is a 10 – 30 m thick series of heterolithic siliciclastics and carbonates (Martill and Heimhofer, 2007). The siliciclastics consist of well-bedded thin black shales, silty shales, variegated clays, and sandstones. The carbonates are typically thinly laminated and micritic limestones (Martill and Heimhofer, 2007).

Excluding some horizons particularly rich in ostracods and conchostracans, the member has few fossils, only containing rare and poorly preserved bivalves (Martill and Heimhofer, 2007).

1. 3. 3. 8. Jamacaru Member

The Jamacaru Member (Martill and Wilby, 1993) overlies the Caldas Member and is similar to the Nova Olinda Member in many ways. The sedimentological similarity is such that it can be indistinguishable in small outcrops (Martill and Heimhofer, 2007). It is the first substantial series of laminated limestones above the Nova Olinda Member and is approximately 4 m thick. It consists of a basal < 1 m thick limestone unit, separated from the rest of the limestone by a 0.5 m thick silty shale unit (Martill and Heimhofer, 2007).

The Jamacaru Member can be distinguished from the Nova Olinda Member by its rarity of fossils (rare *Dastilbe*, conchostracans, and wood), abundant halite pseudomorphs, and a silicified stromatolitic top (Martill and Heimhofer, 2007). However, this rarity of fossils could be a result of small outcrop exposure.

1. 3. 3. 9. Casa de Pedra Member

The uppermost member of the Crato Formation is the Casa de Pedra Member (Martill and Heimhofer, 2007). It is estimated to be approximately 10 m thick with no known lateral variation in thickness (Silva, 1988; Martill and Heimhofer, 2007). It consists largely of laminated pyritic black shales, but also contains thin sandy layers (Martill and Heimhofer, 2007). Towards the top of the unit, at least one thin sandstone layer is present with mudcracks. The member is rich in ostracod fossils, with occasional fossils of small fish, typically *Dastilbe* (Martill and Heimhofer, 2007).

1. 3. 3. 10. Overlying formation

The Crato Formation is overlain by the Ipubi Formation, a ~30 m thick sequence of gypsum and rare anhydrite with thin clay partings. This formation represents the evaporation of the water body in which the Crato Formation was deposited (Silva, 1988).

1. 4. Palaeoenvironment

1. 4. 1. Nova Olinda waterbody

The Nova Olinda Member was deposited in a large body of water, approximately 100 km by 50 km in area. The depth of this water body has been disputed, and it has even been suggested that the sediment was sub-aerially exposed (Silva, Unpublished Thesis, 1990). This is widely disregarded as the presence of extensive laminae indicates that deposition occurred below storm wave base, likely exceeding a depth of 50 m (Heimhofer and Martill, 2007).

It has previously been suggested that the Nova Olinda Member was deposited under freshwater conditions (Mabesoone and Tinoco, 1973). However, the current consensus is that the water column was stratified, with relatively oxygen-rich brackish-to-fresh (fluctuating?) upper layers, and anoxic hypersaline lower layers (Heimhofer and Martill, 2007; Heimhofer *et al.,* 2010). There may have been thin, perhaps seasonal, 'tongues' of freshwater at the very top of the water column, originating from rivers (Martill and Wilby, 1993). Recent studies have shown that spider leg flexure can be used as a proxy to measure salinity and spiders from the Nova Olinda Member indicate hypersaline waters (Downen *et al.,* 2016). The water-sediment interface was extremely hostile, with only microbial communities thriving as shown by the complete lack of autochthonous benthic fauna, lack of bioturbation, and the presence of laterally persistent laminae (Martill and Wilby, 1993; Heimhofer *et al.,* 2010). The bottom-water salinity was sufficiently elevated to induce hopper-faced halite crystal growth on the sediment surface (Martill *et al.,* 2007b; Heimhofer *et al.,* 2010). The sediment, sediment-water

interface, and lower water column were anoxic, as demonstrated by the formation of finely disseminated sedimentary pyrite and other iron sulphides (Berner, 1970), as well as the presence of anoxygenic photosynthetic brown 'green' sulphur bacteria (*Chlorobiaceae*) biomarkers (isorenieratene derivatives) (Heimhofer and Martill, 2007).

Heimhofer *et al*. (2010) suggested that the waterbody of the Nova Olinda Member represents a lacustrine environment, and this is supported by stable C and O isotopic signatures. However, there is a lack of a cyclic stable isotope pattern that is perhaps a result of homogenization of the signal during diagenesis (Heimhofer *et al*., 2010). This may have resulted in a false lacustrine reading, as input from seasonal rains and flooding skews results towards a lacustrine setting. The carbon isotopic signature may also suggest equilibration with atmospheric CO_2 (Heimhofer *et al*., 2010).

1. 4. 2. Fish as environmental indicators

As discussed above, the presence of abundant fish fossils and coprolites within the formation indicates that there was a substantial fish community living in the upper water column. *Dastilbe* is a gonorynchiform fish, the juveniles of which are the only abundant fish within the formation (Brito, 2007). Modern gonorynchiformes (e. g. *Chanos chanos*, the 'milkfish') are anadromous and can tolerate varying salinities (Bagarinao, 1994; Davis and Martill, 2003). *Dastilbe* fossils have been found in several other localities in the Lower Cretaceous of Brazil and Africa, suggesting that they were present in the opening south Atlantic Ocean (Davis and Martill, 2003). Additionally, *Dastilbe* are often found in mass mortality events, which were likely the result of algal blooms depleting oxygen (Martill *et al*., 2008b). As such, the Nova Olinda Member water body probably acted as a nursery for *Dastilbe*, with the adults migrating to spawn. These juveniles were the only fish persistently living in the paleolake (Davis and Martill, 2003).

Other taxa (and ontogenetic stages) are present, but are considerably rarer and are believed to represent fish 'washed' into the basin, either from freshwater tributaries or via the restricted connection to the south Atlantic Ocean (Martill pers. comm. 2015). The fish fauna is discussed further in section 1. 5. 4.

In conclusion, the Nova Olinda Member sediments were deposited in a restricted, stratified, largely hostile, lacustrine or lagoonal setting with freshwater input, seasonal rain, and a restricted connection to the south Atlantic Ocean. The precise details of the type of water body and its distance from the newly opening south Atlantic Ocean remain to be established.

1. 5. Fossil diversity

The Nova Olinda Member boasts a remarkable assemblage of palaeo- flora and fauna. It is best known for its well-preserved insects, abundant *Dastilbe*, and pterosaur assemblage (Martill *et al*., 2007a). Although this project focuses on the insect assemblage, many other organisms are important environmental indicators or can directly influence the taphonomy of insects and are therefore discussed below. Due to the large catchment areas of the palaeolake and its tributaries (discussed further in Chapter 5. 1), the Nova Olinda fossil assemblage contains representatives of a variety of environments.

1. 5. 1. Insects

The Nova Olinda Member boasts a high and broad diversity of insects (Grimaldi, 1990; Martill *et al*., 2007a). Over 350 species have been described and at least 55 more are reported, but awaiting description (Figure 11; see Appendices 8. 4.). These are spread across 21 orders, from the primitive Diplura to the derived Diptera and encompass a vast diversity of body-forms. Here, the Nova Olinda Member insect fauna is summarised. Further discussion of the insects, and their environmental preferences will be presented in Chapter 5. 1.

The majority of Nova Olinda Member insect diversity lies within the orders Hemiptera, Neuroptera, Orthoptera, and Odonata. Following this, Coleoptera, Ephemeroptera, and Hymenoptera are also relatively diverse. Many other insect orders are present, but are considerably less diverse.

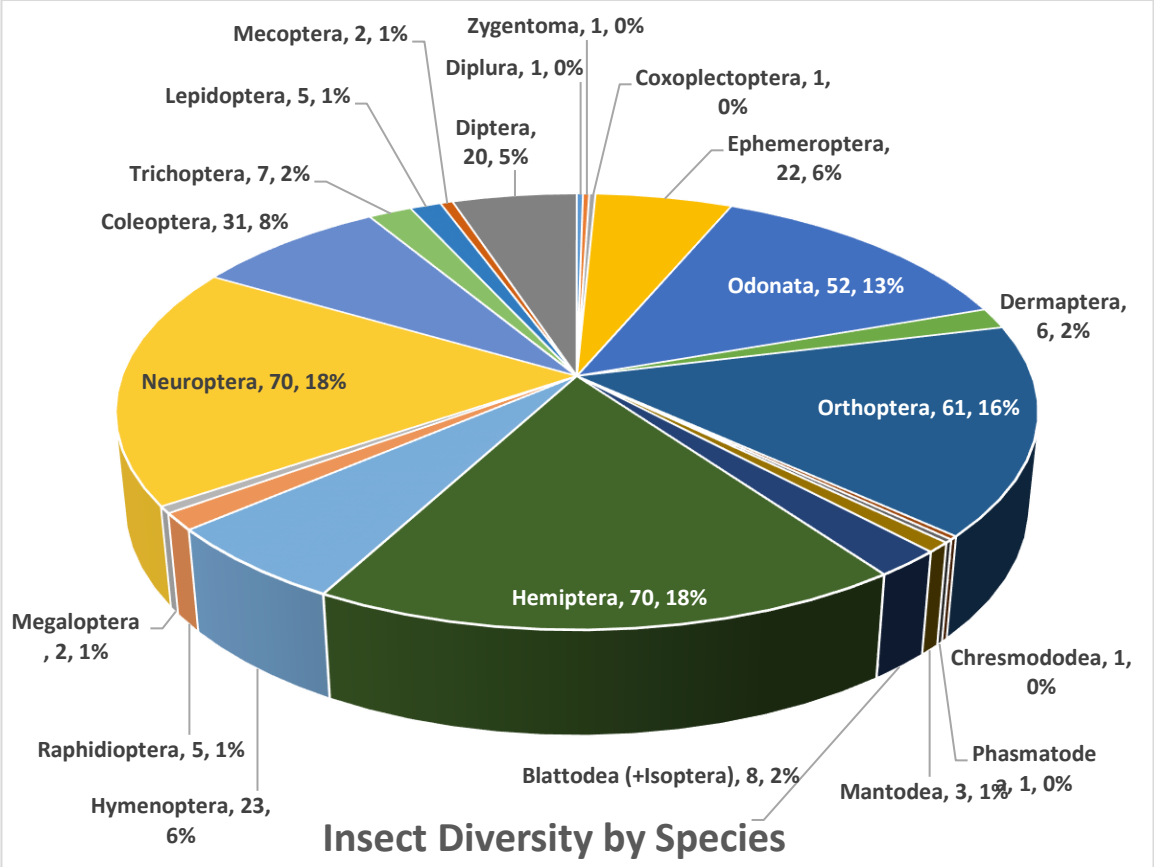


Figure 11. Number of species and percentage of total diversity of Nova Olinda Member insect orders, including undescribed, but distinct species. Includes taxa reported until 2016, see Appendices 8. 4. for full species list. Orders presented from primitive to derived according to Misof *et al*. (2014). n = 392.

In the Nova Olinda Member, insect fossils are allochthonous, thus providing palaeoenvironmental information about the catchment area. To illustrate this, six examples from the Nova Olinda Member were selected from families that are suggestive of specific environments. These include; a family that generally inhabits hot dry climates (Sapygidae); a family of soft-substrate burrowing insects (Gryllotalpidae); a family of insects that live in woody trees (Trogossitidae); a freshwater aquatic family (Dytiscidae); a family that is typically associated with shrubby plants (Rhinotermitidae); and a family that requires rotten and wet decaying substances (Zhangsolvidae) (Figure 12). A comprehensive list of insect orders, or families where appropriate, known from the Nova Olinda Member and their environmental preferences are presented in Chapter 5. 1.

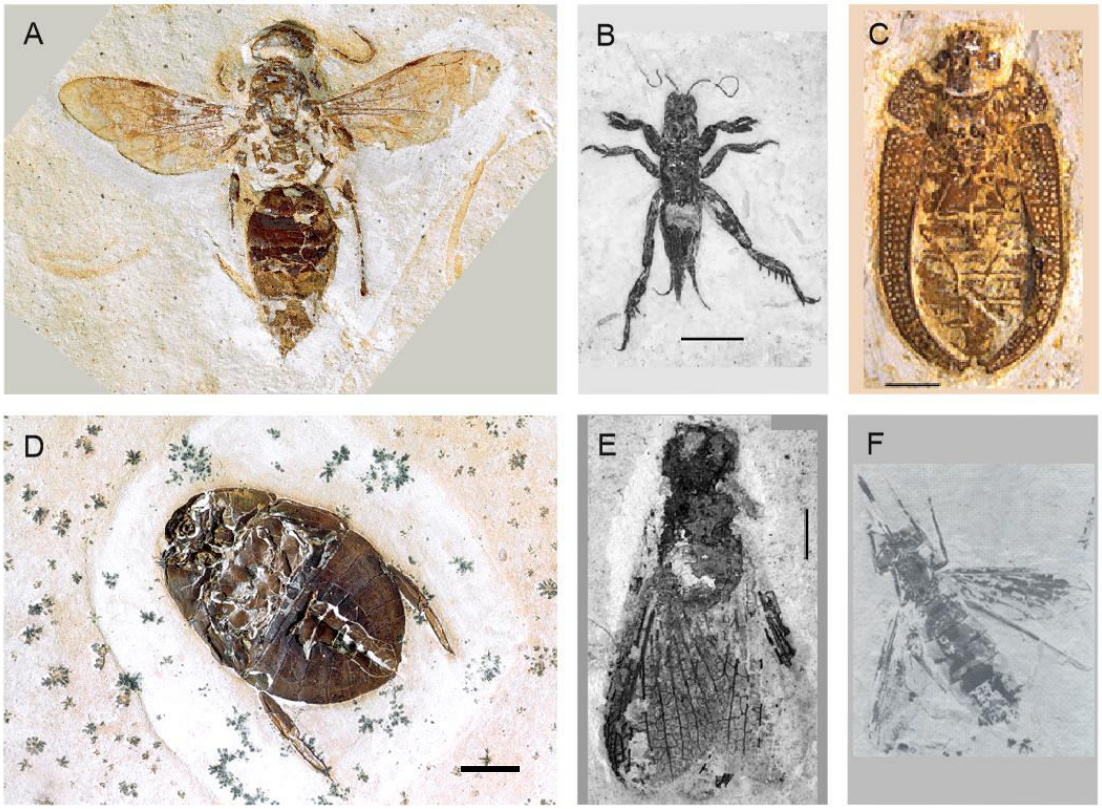


Figure 12. Six fossil insect taxa yielded by the Nova Olinda Member that are suggestive of different environments. A, Sapygidae suggestive of a hot dry climate (*Cretofedtschenkia santanensis* Holotype: SMNS 66594) (Osten, 2007). B, Gryllotalpidae from a cryptic burrowing niche (*Cratotetraspinus fossorius* Holotype: SMNK PAL 5477) (Martins-Neto, 1995b; Heads and Martins-Neto, 2007). C, Trogossitidae which are intimately associated with woody plants (Peltinae, SMNS 66467) (Popov and Bechly, 2007). D, Dytiscidae, an aquatic family of beetles (Unnumbered specimen in University of Portsmouth collection) (Martill pers. comm., 2014). E, Rhinotermitidae suggestive of shrubby plants (*Cretarhinotermes novaolindense* Holotype: SMNS 66196) (Bechly, 2007d). F, Zhangsolvidae associated with rotten plant matter and wet decaying substances [moist environment] (*Cratomyia macrorrhyncha* Holotype: FFCLRP #DBRP-0050) (Mazzarolo and Amorim, 2000). B, Scale bar = 5 mm. C and E, Scale bars = 2 mm. D, Scale bar = 2 mm. Other scales unknown.

The collection donated to this project was selectively weighted to members of Blattoidea and Orthoptera, and so was not used to discuss the taxonomic diversity of the Nova Olinda Member insects. Instead, the collection analysed by Menon and Martill (2007) is considered. Menon and Martill (2007) provided an order-level summary of the diversity of their specimens (Figure 13). The fauna was dominated by Hemiptera (29%), Orthoptera (16%), Ephemeroptera (14%), and Odonata (14%). Neuroptera were also reasonably common (8%). Menon and Martill (2007) also identified insect life strategies (Figure 14), finding that adult aerial and strong fliers accounted for 50% of the arthropod assemblage, with the rest divided between aquatic larvae (14%), mainly terrestrial non-fliers (19%), adult fliers living in proximity to water (7%), aquatic adults (8%), and terrestrial non-insect arthropods (2%).

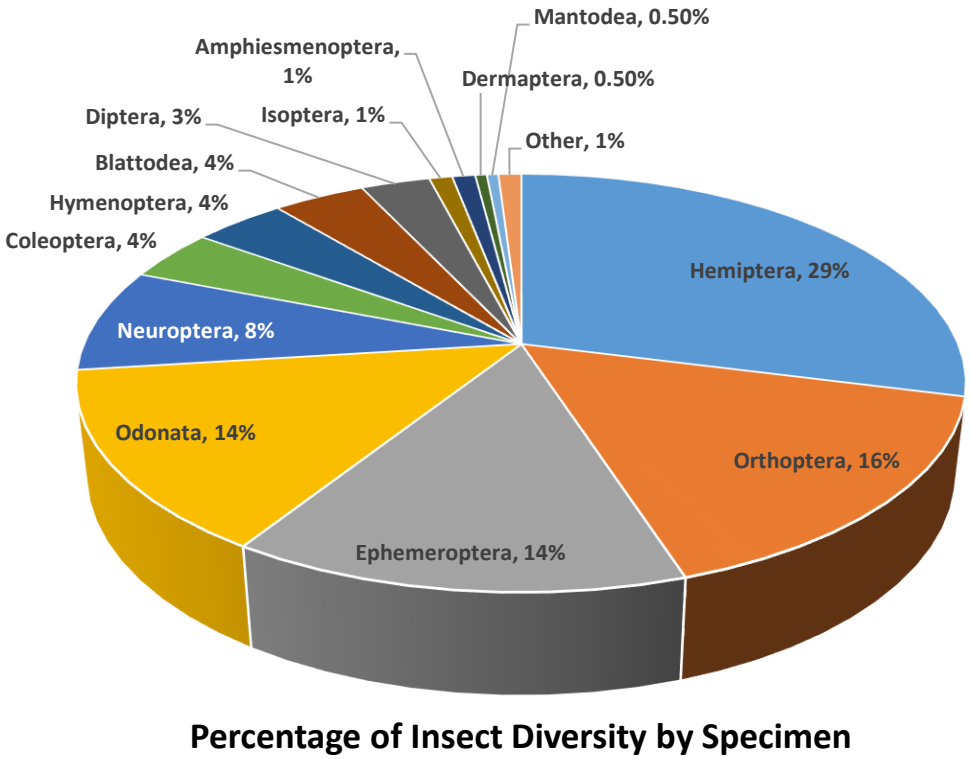


Figure 13. Diversity of Nova Olinda Member insect collection examined by Menon and Martill (2007).

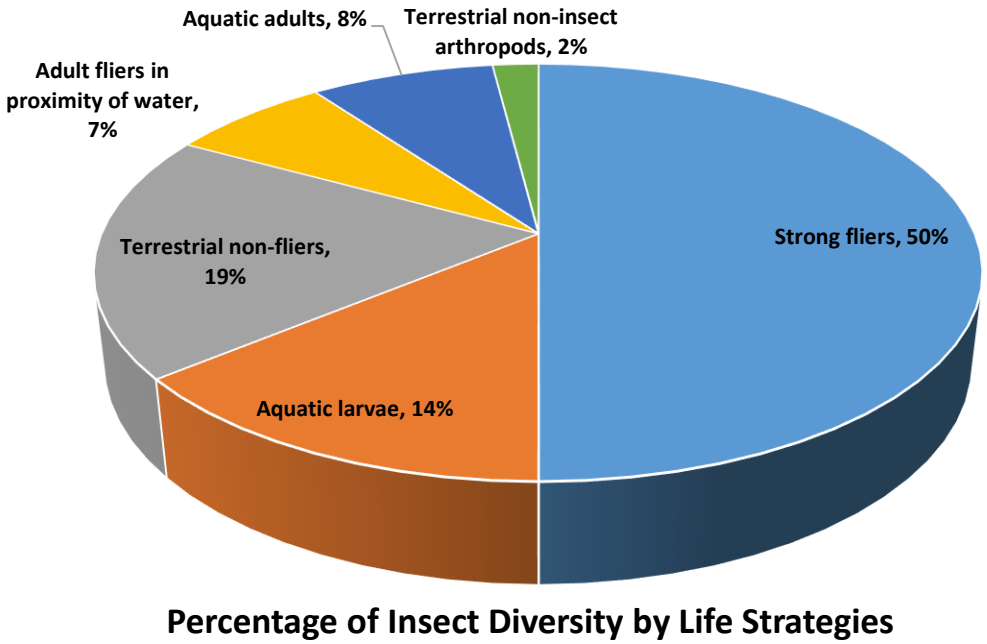


Figure 14. Percentages of insects associated with different life-strategies in the collection examined by Menon and Martill (2007).

1. 5. 2. Arachnids and myriapods

There are several groups of terrestrial non-insect arthropods that share many general taphonomic characteristics with insects and, as such, are also well-preserved in the Nova

Olinda Member. Most notable are the arachnids (spiders, scorpions, harvestmen, mites, and their kin). The Nova Olinda Member is extremely important for the fossil record of arachnids, as it contains a well-preserved, well-sampled, and diverse assemblage of spiders, which is exceptionally rare for non-amber deposits (Selden and Shear, 1996; Selden *et al.,* 2006; Dunlop, 1996, 1998, 2007; Dunlop and Martill, 2002, 2004; Dunlop *et al*., 2007). More recently, many arachnid specimens have been discovered as various amber inclusions and compression fossils in shales (Downen and Selden, 2016). Despite this, the Nova Olinda Member still yields the widest range of arachnid groups of any Mesozoic locality, is one of the only arachnid-bearing formations in the southern hemisphere, and contains the only known Mesozoic camel spiders, whipspiders, and whipscorpions (Dunlop *et al*., 2007).

There are three species of Araneae (spiders) in the Nova Olinda Member and many more yet to be described (Dunlop *et al*., 2007; Downen and Selden, 2016): *Cretaraneus martinsnetoi* (Mesquita, 1996), *Cretadiplura ceara*, and *Dinodiplura ambulacra* (including several specimens of adults and juveniles) (Selden *et al*., 2006).

Scorpiones (scorpions) are considered diverse in the Nova Olinda Member despite only two separate taxa reported (Dunlop *et al*., 2007): *Araripescorpius ligabues* (Campos, 1986; Maisey, 1991; Carvalho and Lourenço, 2001; Dunlop and Martill, 2002; Menon, 2007) and *Protoischnurus axelrodorum* (Carvalho and Lourenço, 2001; Menon, 2007). This 'high' scorpion diversity is usually associated with an arid environment (Dunlop *et al*., 2007). Although much of the hinterland was undoubtedly arid, fossils of *Araripescorpius ligabues* suggest the presence of a more seasonally wet/dry tropical habitat, as modern Chactidae inhabit these settings (Menon, 2007). However, modern Hemiscorpiidae are a diverse group that mostly inhabit arid environments and care should be taken when making this assumption (Monod and Lourenço, 2005). In addition, this is the first Cretaceous record of Hemiscorpiidae.

Acari (mites) occupy a broad range of habitats and lifestyles. There are three putative records of mites or mite activity in the Nova Olinda Member: possible feather mite eggs (Martill and Davis, 1998) that were later suggested to be ostracod eggs (Proctor, 2003), undescribed possible leaf-inhabiting mites (inhabiting Schizaceae), and terrestrial free-living mites (Erythraeoidae) (Dunlop, 2007). These terrestrial mites are remarkably large, and may have filled a more spider-like niche (Dunlop, 2007).

Solifugae (camel spiders or sun spiders) are known from six specimens, all attributed to *Cratosolpuga wunderlichi* (extant family Ceromidae: Selden and Shear, 1996; Dunlop, 1996; Punzo, 1998; Harvey, 2002, 2003; Dunlop and Martill, 2004). Dunlop and Martill (2004) described four specimens of *Cratosolpuga wunderlichi*, despite minor morphological

differences. Modern camel spiders appear to vary in morphology in a way that is taxonomically irrelevant, and so these minor differences did not warrant the erection of a new taxon. They are also typically found in arid environments.

Thelyphonida (whipscorpions) are known from two specimens in the Nova Olinda Member: *Mesoproctus rowlandi* (Dunlop, 1998) and another poorly preserved specimen attributed to *Mesoproctus* sp., but may in fact represent an adult *M. rowlandi* (Dunlop and Martill, 2002; Dunlop *et al.*, 2007). Modern analogues of these taxa tend to desiccate easily and so live underground, only emerging during the night or after periods of heavy rain. Dunlop *et al*. (2007) suggested that the Nova Olinda examples may represent individuals washed into the paleolake during flash floods after heavy rain.

Amblypygi (whipspiders) have an extremely sparse fossil record. Specimens from the Nova Olinda Member represent the majority of their fossils, with the only other specimens described from the Late Carboniferous of Europe and North America, and some undescribed taxa from the Dominican amber. All Nova Olinda specimens are assigned to *Britopygus weygoldti* (Dunlop and Martill, 2002), which is suggested to be a neotropical species. As with whipscorpions, modern whipspiders generally inhabit arid environments but desiccate rapidly (Dunlop *et al*., 2007).

One other fossil arachnid specimen that may represent another arachnid group has been reported, but this is yet to be confirmed (Dunlop *et al*., 2007).

Chilopoda (centipedes) are extremely rare in the fossil record due to the poor sclerotisation of their exoskeleton (Grimaldi and Engel, 2005; Shear and Edgecombe, 2010). At least four species within three genera are known from the Nova Olinda Member: *cf*. *Rhysida* (Dunlop *et al*., 2007), *Cratoraricus oberlii* (Wilson, 2003), *Velocipede bettimari* (Martill and Barker, 1998; Menon *et al*., 2003), and *Fulmenocursor tenax* (Wilson, 2001). Aside from a single Late Jurassic German specimen (Schweigert and Dietl, 1997), these are the only reported Mesozoic centipedes.

1. 5. 3. Crustaceans

A single decapod shrimp is described from the Nova Olinda Member, *Beurlenia araripensis* (Schweigert *et al*., 2007). This taxon was originally described as a palaemonid shrimp (Martins-Neto and Mezzalira, 1991), but is now considered family *incertae sedis* (Maisey and Carvalho, 1995).

Ostracoda (ostracods) are ‘superabundant’ to the point of forming ostracod limestones at several horizons in the Crato Formation (Schweigert *et al*., 2007). However, in the Nova Olinda

Member, their diversity is low with only a few species of smooth-shelled crypridids reported (Silva, 1978a-c, 1979; Depeche *et al*., 1990; Silva-Telles and Viana, 1990), including *Theriosynoecum silvai* (Silva, 1978a-b), *T. munizi* (Silva, 1978a-b), *T. quadrinodosa* (Silva, 1978b), *Harbinia micropapillosa* (Bate, 1972), *H. angulate* (Krömmelbein and Weber, 1971), *Darwinula martinsi* (Silva, 1978a-c), and *Crypridea araripensis* (Silva, 1978a-c). The ostracod assemblage is regarded as non-marine, due to the presence of limnetic taxa (*Candona* sp. see Gobbo-Rodrigues *et al*., 2005) and species that can tolerate a range of salinities (*Darwinula martinsi* see Syrio and Rios-Netto, 2002). Several other taxa are considered in 'open nomenclature': *Harbinia*, *Brasacypris*, *Candona*, and *Zonocypris*(?) (see Carmo *et al*., 2004).

Conchostracans (clam shrimp) of the Nova Olinda Member are understudied, with only three publications briefly discussing them: Martill (1993a), Carvalho and Viana (1993), and Viana and Neumann (1999). Three species of *Cyzicus* are described from the very base of the Nova Olinda Member (possibly not within it). Conchostracans typically inhabit ephemeral water bodies and can tolerate fresh-to-brackish waters, however their occurrence in the Nova Olinda Member is sporadic at best.

Additionally, an isopod specimen has been reported from the Nova Olinda Member, but is yet to be described (Heads pers. comm., 2014).

1. 5. 4. Fish

As discussed in section 1. 4. 2., the gonorynchiform teleost *Dastilbe crandalli* is abundant within the Nova Olinda Member and accounts for the overwhelming majority of fossils (Brito, 2007). Although the genus *Dastilbe* has often been used as a 'waste-basket' taxon for small Cretaceous gonorynchiform fish, it has now been revealed to contain two separate species (*D. crandalli* and *D. moraesi*). Two previous species attributed to the genus have been removed. *D. elongatus* has been synonymised with the type species and *D. batai* likely represents a taxon within the genus *Parachanos* (Dietz, 2007). Other fish taxa are present in the Nova Olinda Member, but are incredibly rare. These include the ophiosid *Placidichthys bidorsalis*, the ichthyodectiform *Cladocyclus gardneri,* a semionotiform *cf*. *Araripelepidotes* sp., the coelacanth *cf*. *Axelrodichthys* sp., an aspidorhynchiform *Vinctifer longirostris*, the tiny ostariophysan *Santanichthys* sp., and the amiiform *Cratoamia gondwanica* (Brito, 2007; Brito *et al*., 2008). A gar, perhaps close to *Atractosteus*, has also been found (Martill pers. comm., 2016).

1. 5. 5. Pterosaurs

Pterosaurs probably represent the most sought-after fossils found in the Nova Olinda Member and have attracted much scientific attention over the years (Martill and Frey, 1998, 1999;

Sayão and Kellner, 1998, 2000, 2006; Unwin and Martill, 2007; Elgin and Frey, 2012). Despite this, the Nova Olinda Member yields a modest number of specimens when compared to similar deposits, even though they are the second most abundant vertebrate group (Martill pers. comm., 2016). For example, the Solnhofen Limestone has yielded thousands of pterosaur fossils, whereas the Nova Olinda Member has only produced hundreds of specimens. This, however, may be an artefact of the relatively recent scientific interest in the Nova Olinda Member fossils (since the 1980s, whereas the Solnhofen Formation has been studied for over 250 years). This assemblage is similar to, albeit smaller than, the younger Romualdo Formation (see: Frey and Martill, 1994; Campos and Kellner, 1996, 1997; Martill and Frey, 1998, 1999; Sayão and Kellner, 1998, 2000, 2006; Frey and Tischlinger, 2000; Nuvens *et al*., 2002; Sayão, 2003; Frey *et al*., 2003a-c). There are 33 species of pterosaur in eight genera described from the Nova Olinda Member (Unwin and Martill, 2007; Elgin and Frey, 2012), of which three genera are unique to the formation: *Arthurdactylus*, *Ludodactylus*, and *Ingridia* (Frey and Martill, 1994; Frey *et al*., 2003b; Unwin and Martill, 2007). In addition, there are at least three new genera awaiting description (Martill pers. comm., 2017). The Nova Olinda Member assemblage is distinct in that it contains few juvenile and perinatal individuals and that there are no small pterosaurs with a wingspan of less than 1.5 m (Unwin and Martill, 2007).

1. 5. 6. Other vertebrates

Anurans (frogs and toads) were first reported in the Nova Olinda Member by Kellner and Campos (1986), and three species have been identified since then (Leal and Brito, 2006; Leal *et al*., 2007; Báez *et al*., 2009). They are extremely rare, but when found are usually complete and fully articulated, often with soft tissue outlines. Originally all specimens were attributed to *Arariphrynus placidoi*, however Báez *et al*. (2009) redescribed two additional species; *Eurycephalella alcinae* and *Cratia gracilis*. Both *A. placidoi* and *E. alcinae* are nested among hylid taxa, whereas *C. gracilis* appears to be a stem neobatrachian. Additionally, one specimen representing a possible pipoid has been reported but is yet to be described (Leal *et al*., 2007; Báez *et al*., 2009).

Testudines (turtles) are neither abundant nor diverse in the Nova Olinda Member (Naish, 2007). Only two species are known from a handful of specimens, both within the genus *Araripemys* (*A. barretoi* (Oliveira and Kellner, 2005) and *A. arturi* (Fielding *et al*., 2005)) and may even be synonymous (Oliveira *et al*., 2011). For a review of Nova Olinda Member turtles, see Naish (2007) and Oliveira *et al*. (2011).

Squamata (lizards) are extremely rare in the Nova Olinda Member (Martill, 2007c; Frey and Salisbury, 2007; Naish *et al*., 2007). Two lizard specimens representing basal terrestrial forms

are known and each is attributed to a separate taxon (*Olindalacerta brasiliensis* and *Tijubina pontei*) (Evans and Yabumoto, 1998; Bonfim, 2002). *Tijubina pontei* was re-described in 2012 to present more diagnostic characters and a clearer demonstration of its validity (Simoes, 2012). Serpentes (snakes) are exceptionally rare within the Nova Olinda Member. In 2015, a remarkable fossil snake was described from the Nova Olinda Member (*Tetrapodophis amplectus*) that retained primitive limbs (Martill *et al*., 2015). This has arguably made the Nova Olinda Member the single most important Lagerstätte for understanding snake evolution.

Four possible Crocodilia (crocodile) fossils are described, with two reported as tentative: *Susisuchus anatoceps*, *cf*. *Araripesuchus*, and *cf. Susisuchus* sp. (with distinct hind-limbs) (Salisbury *et al*., 2003a; Frey and Salisbury, 2007; Figueiredo and Kellner, 2009 respectively). However, these specimens are fragmentary and so their validity is questionable (Figueiredo *et al*., 2009, 2011). One extremely well-preserved, articulated and mostly complete juvenile crocodile has been discovered, but is yet to be described (Martill pers. comm., 2014).

Theropoda (birds and theropod dinosaurs) are extremely rare in the Nova Olinda Member, however isolated feathers are relatively common (Naish *et al*., 2007). Bird and/or non-avian dinosaur feathers were first reported by Martins-Neto and Kellner (1988), later figured by Kellner (1991), and described by Martill and Filgueira (1994). Several other feathers are reported (Kellner *et al*., 1994; Martill and Davis, 2001; Kellner, 2002; Prado *et al*., 2016). The morphology of these feathers matches a flightless animal (either a flightless bird, non-avian theropod, or another feathered archosaur) and they do not fit the morphotype of Tyrannosauroidea, Compsognathidae, Therizinosauroidea, or Dromeosauridae (Sayão *et al*., 2011). The most recently described feathers are attributed to coelurosaurian theropods (Prado *et al*., 2016). Two skeletal remains associated with feathers have been reported, but could not be attributed to any specific taxa (Naish *et al*., 2007). However, in 2015 a remarkable, near complete, bird skeleton (*Cratoavis cearensis*), with feathers and other possible soft tissues was recorded from the Nova Olinda Member (Specimen UFRJ-DG 031 Av., Carvalho, *et al*., 2015).

1. 5. 7. Flora (excluding amber)

The Nova Olinda Member is one of the most important palaeobotanical Cretaceous Lagerstätten as it preserves a large number of diverse terrestrial and aquatic plants during the radiation of angiosperms and global decline of gymnosperms (Mohr *et al.*, 2007). Additionally, fossil plant remains are often preserved intact with roots, stems, leaves, reproductive organs, and even paleosols (Mohr *et al.*, 2007). Early palaeobotanical work on the formation focused on its palynology (Lima, 1978, 1979, 1980, 1989) and this has continued into the 2000s (Pons *et al*., 1996; Arai *et al*., 2001). Studies on the macrofossil flora began in the mid-1980s (Duarte,

1985) and is ongoing (Duarte, 1993; Crane, 1991; Oliveira-Babinsky and Lima, 1991; Bernardes-de-Oliveira *et al*., 1993; Martill, 1993a; Barreto *et al*., 2000; Mohr and Friis, 2000; Mohr and Eklund, 2003; Kunzmann *et al*., 2004; Mohr and Bernardes-de-Oliveira, 2004; Silva *et al*., 2013; Coiffard *et al*., 2013, 2014; de Lima *et al*., 2014). Over 90 species of fossil plant have been described from the Nova Olinda Member, with many more awaiting description.

Apart from a few putative algal groups, all major tracheophyte groups known from the Middle to Lower Cretaceous are present in the Nova Olinda Member. Its assemblage is dominated by gymnosperms (approximating 60% of total diversity), followed by angiosperms (~30%) and, finally, other seed-bearing plants (~10%) (Mohr *et al.*, 2007). Although angiosperm pollen is common, macrophyte angiosperm remains are rare. Several key species provide insights into the hinterland areas around the Nova Olinda paleolake, including *Cariria orbiculiconiformis* and *Schenkeriphyllum glanduliferum*, which both indicate arid environments (Kunzmann *et al*., 2011; Mohr *et al*., 2013). Another species (*Duartenia araripensis*) has growth patterns and leaves characteristic of a seasonally dry climate (Mohr *et al*., 2012). Additionally, *C. orbiculiconiformis* is proposed to fill a niche of rapid reproduction in disturbed habitats (i.e. after floods or fires) (Kunzmann *et al*., 2011). Some examples of *Schenkeriphyllum glanduliferum* are preserved with multi-part flowering structures in differing stages of maturity (Mohr *et al*., 2013).

Other notable taxa include: *Novaolindia dubia*, which displays an unusual combination of characters, possibly indicating an unknown plant group (Kunzmann *et al*., 2007), and *Cearania heterophylla* which has affinities to ephedroid Gnetales, but is also likely a new unknown group (Kunzmann *et al*., 2009). Several specimens of *Friedsellowia gracilifolia* are present at a variety of life stages, including seedlings, young plants, and mature plants (Loewe *et al*., 2012). Many of these specimens also preserve roots, axes, leaves, and reproductive organs (Loewe *et al*., 2012). *Friedsellowia gracilifolia* probably grew in an open sunny habitat, and may have filled a reed-like niche on the edge of the Nova Olinda palaeolake (Loewe *et al*., 2012). *Spixiarum kipea* is a basal monocot that likely had a halophytic ecology (Coiffard *et al*., 2013). *Cratosmilax jacksoni* is the first terrestrial monocot from the member, and all monocots described before 2014 are re-appraised as aquatic taxa (de Lima *et al*., 2014). *Cratosmilax jacksoni* also represents the oldest known member of the family Smilacaceae and the first example from Brazil. Finally, *Hexagyne philippiana* is an 'understorey' plant that thrived in shaded environments (Coiffard *et al*., 2014). It is the first macrofossil piperalean, possibly indicating a Gondwanan origin for this group (Coiffard *et al*., 2014).

1. 5. 8. Amber

Amber is extremely rare in laminated limestones, but does occur very rarely in the Nova Olinda Member (Martill *et al*., 2005; Mohr *et al*., 2007). The amber has been found in association with resin-filled cones, foliage, and palynomorphs that are attributed to the family Araucariaceae (a type of conifer) (*Brachyphyllum* sp., *cf. Wollemi* sp. and *cf. Agathis* sp.). The rarity of amber, combined with the fact that all quarries are believed to be > 1 km distance from the palaeoshoreline, suggests a primary allochthonous deposit, whereby the amber drifted into the site of deposition with plant material, or a re-worked forest soil deposit (Mohr *et al*., 2007; Martill pers. comm., 2015). Amber floats in saline waters, depending on density and gas inclusions (Rasnitsyn and Quicke, 2002). Given that the Nova Olinda Member had hypersaline waters, it is highly likely that the amber floated for a prolonged period of time.

Chemosystemtic biomarkers and the absence of angiosperm triterpenoids and diterpenoids, such as ozic acid, demonstrate that this amber originated from a conifer (Pereira *et al*., 2009). Zhangsolvidae flies and fungal microfossils are known to be preserved as amber inclusions in the Nova Olinda Member (Martill *et al.*, 2005; Wilkommen and Grimaldi, 2007; Arillo *et al*., 2015).

1. 5. 9. Other fossils

A few additional miscellaneous biota are recorded from the Nova Olinda Member by Martill (2007d). Among these are unionid bivalves, viviparid gastropods, and other pulmonate gastropods are reported to occur within the other members of the Crato Formation, suggesting that the basin was periodically filled with freshwater (Martill *et al*., 2005).

1. 6. Catchment area

The Nova Olinda Member catchment area is often considered to represent an arid environment (Grimaldi, 1990; Dunlop, 1998; Dunlop and Martill, 2002; Martill *et al*., 2007a; Heimhofer *et al.,* 2010; Osés *et al*., 2016). This interpretation is supported by an abundance of taxa that typically are associated with arid regions, namely abundant cockroaches, crickets, grasshoppers, and wasps (Grimaldi, 1990; Martill *et al*., 2007; Osés *et al*., 2016). In addition, non-insect terrestrial arthropods have been used as environmental indicators for the Nova Olinda Member catchment area, suggesting that a ‘jigsaw’ of arid habitats were present (Dunlop, 1998; Dunlop and Martill, 2002; Dunlop *et al*., 2007; Heimhofer *et al.,* 2010).

In this project, the insect diversity of the Nova Olinda Member is investigated comprehensively. The purpose of this is to gain a better understanding of the ecology of the

insects present, allowing for a more complete understanding of their taphonomy. In doing so, dozens of families were recognised as suggestive of other environments. Later in this thesis, a novel alternative palaeoenvironmental reconstruction is proposed. Multiple palaeoenvironments are identified and simplified as: 1) an arid scrubby region, 2) a humid riparian/deltaic region, and 3) a forested upstream region. The environmental associations of each family will be presented and discussed in Chapter 5. 1., along with detailed descriptions of the palaeoenvironments.

1. 7. Insect Anatomy

Before the taphonomy of these insects can be analysed, their anatomy must first be outlined. Here, the general anatomy of insects is described, and a simplistic insect body plan is presented highlighting the fundamental components of most insects (Figure 15). The summarised insect anatomy presented below is based on descriptions by Grimaldi and Engel (2005). Insects possess a bewildering diversity of forms and, for each insect anatomical characteristic described here, drastically different variations exist.

1. 7. 1. Body segments

Fundamentally, insects are composed of, or evolved from, the same basic body plan. These are a series of repeated units (metameres) that are organised into three major tagmata: head, thorax, and abdomen. The head consists of one metamere, the thorax three, and the abdomen ancestrally eleven. Typically, the head is adapted for feeding and sensory input, whereas the thorax is primarily used for locomotion, and the abdomen is used for digestion, reproduction, and other visceral bodily functions.

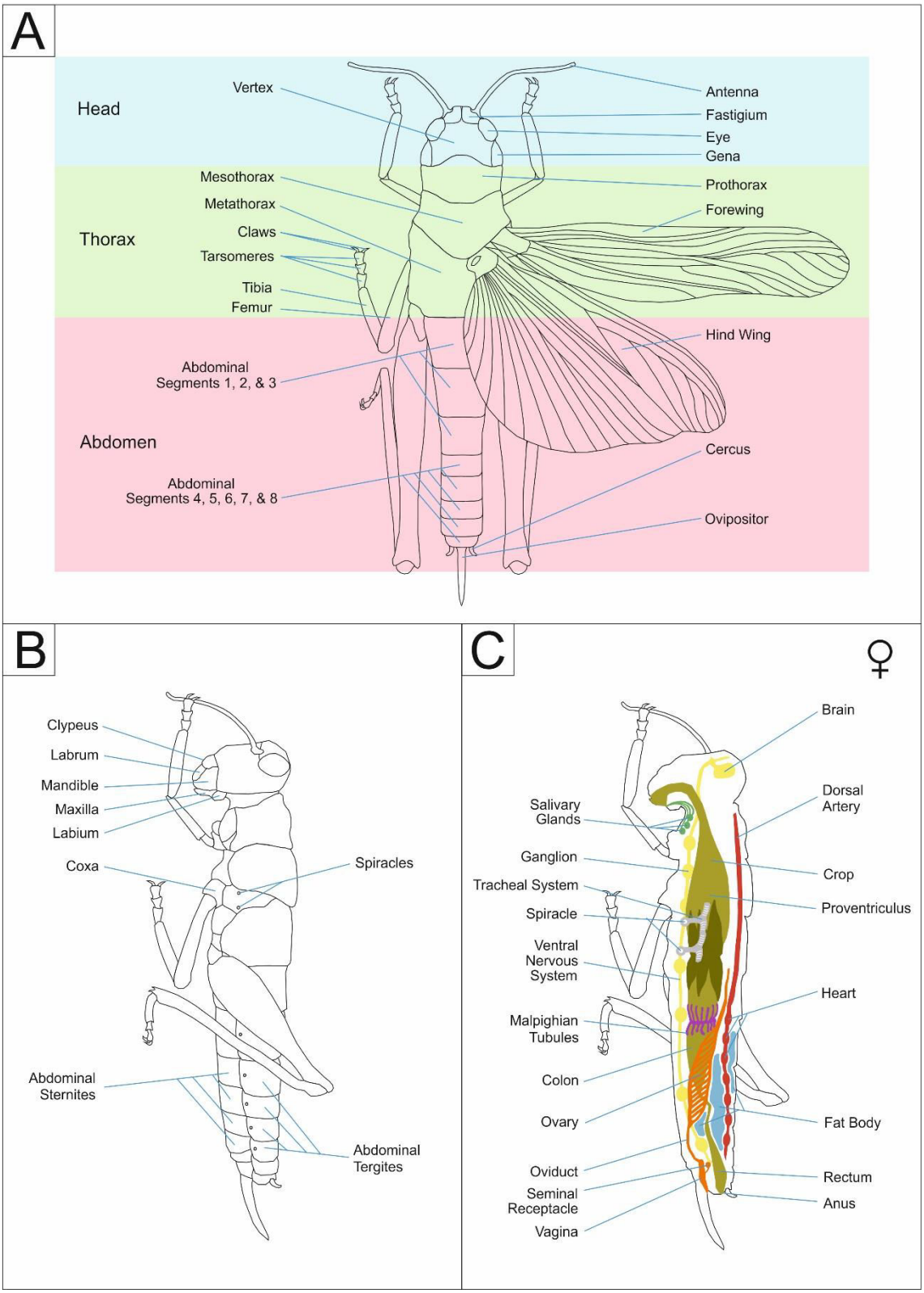


Figure 15. Simplified insect body plan (composite female Orthopteran). Images adapted from Hermann (1966) with information from Grimaldi and Engel (2005). A, Dorsal view highlighting major body segments. B, Lateral view highlighting additional segments. C, Simplified internal organs in lateral view.

1. 7. 2. Limbs and wings

Insects are hexapods and so possess three pairs of limbs. Each limb consists of several segments (coxa, trochanter, femur, tibia, tarsomeres, and claws) and articulate to the thorax via the coxa. Muscles that operate the limb articulation are extrinsic, whereas the other segments are operated by intrinsic muscles. Aside from locomotion, some insect limbs are adapted for burrowing, grasping prey, visual signalling, audial signalling, and many other functions. Several groups have convergently developed raptorial forelimbs for catching prey.

Insects are ancestrally wingless, and several primitive insect orders still are. However, most insects possess two pairs of wings. A few of the more advanced groups can have wingless members (e.g. worker ants do not possess wings, but alates do), or have a reduced number of wings (e.g. Diptera). Wings articulate from the thorax and are powered by powerful flight muscles. Flight muscles rarely act directly on the wing (excluding Odonata) and instead attach to the thoracic wall or cuticular invaginations (phragma). These produce alternating variations in the length and height of the thoracic segments, which create a flapping motion of the wings. Wings consist of two extremely thin, often transparent, fluted epidermal layers supported by a system of veins. The veins not only support the structure of the wing, but also support all metabolic functions of living cells within it. Insect wing venation is also a rich source of characters for systematic studies.

1. 7. 3. Cuticle

Insects are arthropods, and so possess an exoskeleton (cuticle) that covers their body as a series of cuticular plates (sclerites) sutured together (Figure 16). Cuticle serves a myriad array of functions, but is primarily for protection and locomotion. It is a tough flexible material composed of multiple layers (epi- exo- and endocuticle). Chemically, it is a polymer of N-acetylglucosamine (a derivative of glucose). Cuticle can be reinforced to be more rigid (sclerotized) or incorporate heavy metals to make it extremely hard (Gonzalez-Davila and Millero, 1990). To grow, insects periodically moult their cuticle or undergo metamorphosis.

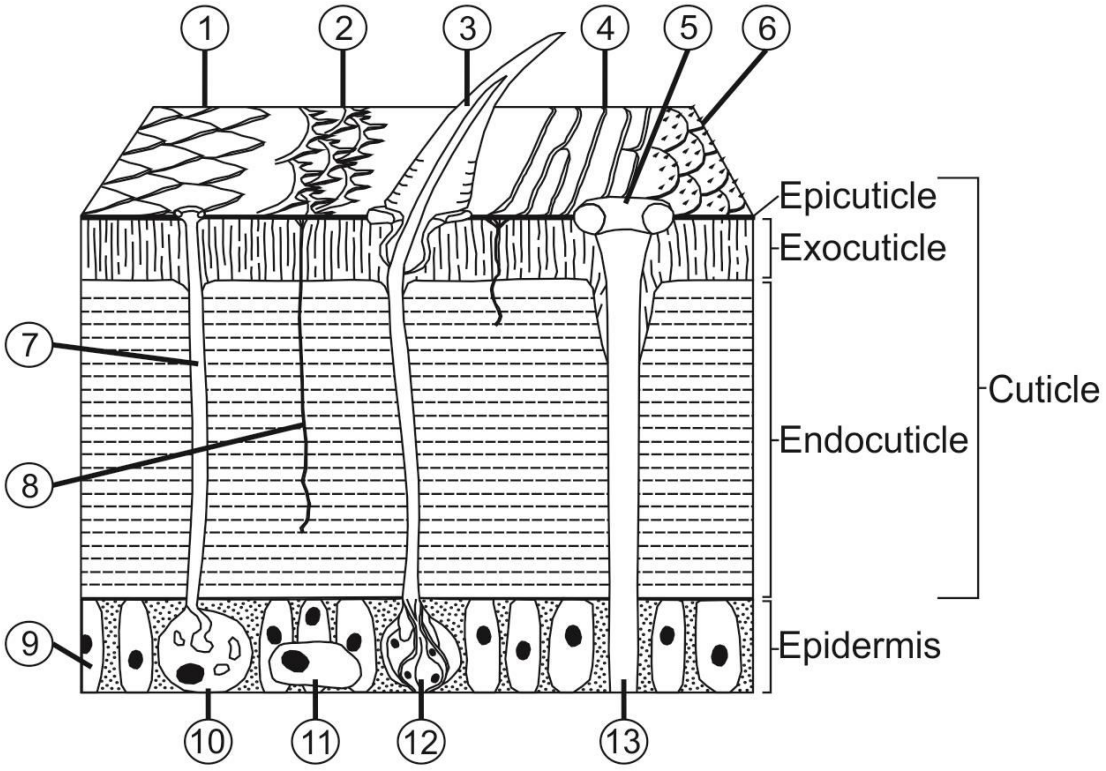


Figure 16. Schematic diagram showing structure of insect cuticle, including several scale morphotypes. 1, Rhombohedral-shaped cuticular scales. 2, Spined cuticular scales. 3, Seta. 4, Long thin cuticular scales. 5, Spiracle. 6, Cuticular scales with 'microspines' (microtrichinum). 7, Dermal gland duct. 8, Pore canal filament. 9, Endodermal cells. 10, Dermal gland cell. 11, Oenocyte. 12, Trichogen cell and cells associated with seta function. 13, Tracheal tube. Figure adapted and expanded from Filshie (1980).

1. 7. 4. Sensory organs

Insects possess an array of sensory organs. Eyes are compound and composed of interlocking repeating hexagonal units (ommatidia), which are in turn composed of a lens (dioptric apparatus) and receptor cells that connect to the brain via an optic nerve. In addition to compound eyes, insects possess multiple simple eyes (ocelli). These are composed of a transparent cornea and can only detect light/dark.

Insects are covered in unicellular projections through their cuticle called setae. These are often mistakenly called 'hairs', as they can give insects a 'bristly' appearance. Although typically rigid, their articulation allows them to move. They are hollow and are frequently associated with hydro-, thermo-, chemo-, and mechano-reception, but can also excrete silk, irritants, or have a variety of other functions (Watling and Thiel, 2013).

Antennae are flexible segmented appendages on the head that can vary greatly in shape, size, and segment number. They are covered in setae, allowing them to function as the primary olfactory and mechanosensory organs. Some insects also possess paired segmented organs on

the posterior of their abdomen (cerci), which may also be covered in setae, allowing them to also function as sensory organs.

1. 7. 5. Internal systems (excluding reproductive)

As with all insect anatomy, their internal structure can vary greatly. Although the fundamental components may be similar, insects from the orders Blattodea, Coleoptera, Dermaptera, Diptera, and Lepidoptera have specially adapted internal systems that may not adhere to the descriptions below.

The insect nervous system consists of a brain, a ventral nerve cord, and multiple ganglia (clusters of nerves cell bodies along the ventral nerve cord). The brain is located in the head and the first three ganglia are fused with it. Several other ganglia are fused above the salivary glands, and the number of ganglia along the nerve cord varies between taxa. These ganglia are also connected by pairs of nerves (interganglionic connectives).

Insects possess an organ called ‘fat body’ that is distributed throughout the entire body, with the majority of it in the abdomen. Its primary roles are essentially the same as a vertebrate liver: energy storage, metabolism, and metabolic regulation. It stores nutrients and synthesises lipids, proteins, and carbohydrates for other tissues. For a detailed description of these processes, see Arrese and Soulages (2011).

The insect respiratory system is composed of a series of relatively simple interconnected internal tubes (trachea), connected to openings in the cuticle (spiracles). This system allows for gases to diffuse throughout the insect body, or to be actively ‘pumped’ in. Trachea branch into finer tracheoles that also act as connective tissue, binding organs together.

As the insect respiratory system allows for the diffusion of gases throughout the body, their circulatory system is ‘open’ and relatively simple. A series of tubes are connected in a one-way dorsal vessel system that is pulsed by a dorsal heart. This pumps hemolymph towards the head, where it enters the body cavity (haemocoel) and flows posteriorly towards the abdomen. Upon reaching the abdomen, it is drawn back into the dorsal vessel through valves (ostia) by the heart. Hemolymph is the arthropod analogue to blood (albeit without red blood cells), which transports hormones, metabolites, and waste. The circulatory system is also important for immunity control, homeostasis, osmoregulation, and moulting.

Connected to the circulatory system is a complex endocrine system, which assists in regulating insect bodily functions. Notably, the prothoracic glands regulate moulting and the corpus allata regulate ‘juvenile hormone’ (which is critical for metamorphosis in holometabolous taxa) and egg production in females.

The insect digestive system (alimentary canal) is composed of three main sections. The foregut is a reinforced canal that allows the movement of food from the mouth to the midgut, while bathing it in saliva to begin digestion. In many taxa, the foregut is also adapted into a food-storing crop. The midgut (mesenteron) is where the majority of digestion and nutrient absorption takes place. Digestive enzymes are secreted by specialised microvilli. Finally, the hindgut is where undigested food is combined with water, salts, waste products, and toxins (via malpighian tubes that extend into the haemocoel) to form faecal pellets. Prior to defecation, water, salts, and some small metabolites are absorbed by the rectum.

1. 7. 6. Reproductive system

Insect reproductive systems are diverse, including laying hundreds of tiny eggs, producing a single tough oothecae, giving birth to live young, and many other strategies. Insects ancestrally lay eggs, and the majority of them still do. In addition, they can receive, store (in the spermatheca), and manipulate sperm from different males. Eggs are made by pairs of ovaries, which consist of a number of egg tubes (ovarioles), depending on species. Accessory glands assist in maintaining sperm, fertilization, and oviposition. Many taxa have specialised accessory glands that also produce venoms or cements. Some taxa also have ovipositors to assist in egg laying, which may in turn be weaponised into ‘stingers’ (especially in Hymenoptera).

Males have testes, usually as a pair. These are connected via seminal vesicles and an ejaculatory duct to external genitals. Males also have accessory glands that assist in protecting and preserving sperm. Some males produce a spermatophore that encapsulates sperm, which can then be transferred to the female during mating. External male genitalia are incredibly diverse and can be exceedingly complex. They are the richest source of morphological characters and are almost universally used as the diagnostic feature for species identification in extant specimens. The penis can be flanked by associated appendages, including the gonoxocae, gonostyli, and parameres. The latter of these are typically used for clasping females.

1. 8. Insect taphonomy

Taphonomy is often portrayed as the study of how an organism decays and fossilises, frequently called the ‘laws of burial’ (Martin, 1999). In reality, taphonomy is much more diverse and encompasses many aspects of ecology and is sometimes extended to include the collection and curation of fossils (Behrensmeyer *et al*., 2000). At its core, taphonomy is an attempt to understand the processes and biases that change or remove information during the

transition of an organism from the biosphere to the lithosphere (Efremov, 1940; Behrensmeyer *et al*., 2000).

Insects are the most speciose macroscopic organisms (May, 1986; Gaston, 1991; Misof *et al.*, 2014). As such, there are no comprehensive studies of insect taphonomy that treat every family. Nevertheless, the taphonomy of insects (and other arthropods) has been studied extensively (Allison, 1986; Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Briggs, 1995a,b, 1999; Aller, 1982; Simon *et al*., 1994; Martínez-Délclòs and Martinell, 1993; Smith, 2000, 2006; Martínez-Delclòs *et al*., 2004; etc.). These studies overcome the issue of high diversity by grouping taxa based on morphological or structural similarities (e.g. high sclerotisation vs low sclerotisation, large vs small, or strong vs weak fliers) (Martínez-Délclòs and Martinell, 1993; Smith, 2006). This allows for certain aspects of their taphonomy to be investigated and, from these studies, a semi-complete picture of insect taphonomy can be created. Below, the major processes that control insect preservation are reviewed briefly, based on published data.

1. 8. 1. Insect decay

Several key controls must be considered when examining insect taphonomy, particularly for the preservation of internal 'soft' tissues. The primary control for the preservation of labile 'soft' tissues is rapid fossilisation (early mineralisation) (Briggs and McMahon, 2016). Any factor that stimulates early mineralisation contributes significantly to the preservation potential of a carcass. One such factor is decay, which, when occurring in small amounts, can stimulate (and in some instances is necessary for) mineralisation (Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Briggs, 1995a,b; Martínez-Délclòs and Martinell, 1993; Duncan *et al*., 2003; Forbes, 2008; Chen *et al*., 2009; Briggs and McMahon, 2016). In these instances, a balance must be achieved whereby enough decay occurs to stimulate mineralisation, but not so much that fidelity is lost (Briggs and McMahon, 2016). Excessive decay will result in carcass destruction and so processes that *slow* decay contribute significantly to the preservation potential of a carcass (Efremov, 1950; Schopf, 1975; Plotnick, 1986; Gall, 1990; Potts, 1994; Wilby *et al*., 1996; Petrovich, 2001; McCoy, 2013; Briggs and McMahon, 2016).

Insect cuticle is decomposed largely by bacteria from the genus *Chitinophaga*, a type of environmental bacteria, which are almost exclusively aerobic (Martínez-Delclòs and Martinell, 1993; Lee *et al*., 2007). In extreme environments (i.e. high temperatures), cuticle can be decomposed by thermophilic bacteria (Suzuki *et al*., 2006). As such, cuticular decomposition is greatly hindered by anoxia and low temperatures (Bunch, 2009). Additionally, actualistic studies have established that the distance an invertebrate carcass travels has little impact on

its state of preservation compared to the duration of travel (Allison, 1986; Duncan *et al*., 2003).

When decay occurs, morphologically similar arthropods generally follow the same sequence of decay stages (Allison, 1988b; Briggs and Kear, 1993a; Briggs, 1995a,b). Additionally, arthropods have decay 'threshold points', whereby structurally critical tissues are lost, often resulting in carcass disintegration (Allison, 1990; Briggs and Kear, 1993a; Briggs, 1995a,b).

For deposition in a lacustrine setting, the transition of an insect from the biosphere to the lithosphere can be separated into four distinct stages. In each stage, there are different controlling factors and decay may affect the carcass differently.

1. 8. 2. Stage One: Transport

An insect carcass (or even a live insect) must be transported rapidly away from predators and scavengers if it is to avoid destruction. Although insects are extremely diverse and occupy a broad range of habitats, the size limitations of their body plan and the similarities between Cretaceous and modern insect communities allows us to hypothesise predatory influences with accuracy (Briggs and Crowther, 2001; Penney and Jepson, 2014). In modern environments, insects are predated upon by small-to-medium terrestrial vertebrates (the largest preying upon colonies of eusocial insects, e.g. anteaters, chimpanzees, and bears), small flying vertebrates (bats and birds), terrestrial invertebrates (including other insects, but especially arachnids), and aquatic vertebrates and invertebrates (predominantly fish and predatory aquatic insects) (Labandeira, 1997). The Early Cretaceous undoubtably had analogues to these groups, perhaps excluding medium-sized terrestrial vertebrates. This is because colonies of eusocial insects were relatively small in the Early Cretaceous (Grimaldi and Engel, 2005). Particularly nimble birds are also able to catch insects on-the-wing (e.g. hirundines, bee eaters, and some raptors), and it is probable that equally nimble fossil taxa, perhaps some pterosaurs, were also able to (Yuan *et al*., 2006; Ősi, 2011; Penney and Jepson, 2014). To preserve an insect carcass, it must avoid these predators and scavengers via rapid transportation.

Immediately after death, slowing/retarding decay is critical for retaining labile tissues (Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Briggs, 1995a,b; Martínez-Délclòs and Martinell, 1993). The general environment in which an insect dies can greatly control its preservation potential (Smith *et al*., 2006). In an arid environment, insect carcasses rapidly desiccate and subsequently disintegrate upon entering water (Smith *et al*., 2006). In a humid environment, bacterial proliferation is favoured and insect carcasses decay rapidly (Martínez-Delclòs and Martinell, 1993; Smith *et al*., 2006). If an insect dies long (days) before being transported to

the site of deposition, labile tissues will not be retained, and the carcass may be preserved only as fragmentary remains (Allison, 1986; Martínez-Delclòs and Martinell, 1993; Duncan *et al*., 2003; Smith *et al*., 2006). In instances of exceptional insect preservation, it is likely that the insect died immediately before or during transport to the site of deposition.

1. 8. 3. Stage Two: Water surface

Most insects tend to float upon contacting water, with only denser wingless insects (e.g. many larvae) or insects with 'covered' wings (e.g. some Coleoptera and most Dermaptera) plummeting through the water surface tension (Martínez-Delclòs and Martinell, 1993; Hass *et al*., 2000). Floatation duration depends on numerous factors, including density, wing size, body size (subsequent tracheal system size), and whether it entered alive or dead (Martínez-Delclòs and Martinell, 1993; Briggs, 1995a,b). Insects that enter water alive actively 'inhale' it through their tracheal system drowning them, as demonstrated with water dyed with black chlorazol indicator by Martínez-Delclòs and Martinell (1993). This rapidly increases their density and reduces floatation time. Larger and more complex tracheal systems have wider channels and more air sacs, resulting in faster flooding, rapid density increase, and ultimately a shorter floatation time (Martínez-Delclòs and Martinell, 1993; Briggs, 1995a,b). An insect that enters a water body dead may remain floating and articulated for up to six months in undisturbed conditions, whereas an insect that enters the water alive will typically sink after four-to-fourteen days (exceptions below) (Martínez-Delclòs and Martinell, 1993).

The ability of an insect to escape from water depends on its wing and body size. A large (5-20 mm) winged insect will attempt to escape the water by raising its wings and flapping vigorously periodically. It will either escape or die of exhaustion after several attempts (Lutz, 1984, 1990). Insects with very large (> 20 mm) wings, such as some Lepidoptera and Orthoptera, will often be unable to move and lie laterally on the water surface. The poorly sclerotized cuticle of Lepidoptera decays rapidly, and they typically disarticulate within two days (Martínez-Delclòs and Martinell, 1993; Etter and Kuhn, 2000). Particularly small winged insects cannot break surface tension and may remain there until carcass disintegration. Consequently, small insects outnumber larger insects on the water surface by as much as 25 times (Martínez-Delclòs and Martinell, 1993). Some Odonata can easily escape water and 'spin dry' themselves (Corbet and Brooks, 2008). Some Blattodea simply crawl out along the water surface (Martínez-Delclòs and Martinell, 1993). Small non-winged insects (e.g. worker ants) can scuttle along the water meniscus, holding their abdomens high above the water surface. This allows them to breathe and escape, or remain alive for a prolonged period (Lutz, 1984, 1990; Martínez-Delclòs and Martinell, 1993). Any process that destabilises the surface tension

of a waterbody (e.g. heavy rain), can cause all insect carcasses to sink (Martínez-Delclòs and Martinell, 1993).

During these varying floatation times, once dead, decay will act rapidly on an insect carcass, obliterating its internal tissues (Allison, 1988b; Briggs and Kear, 1993a; Briggs, 1995a,b). This decay is hindered by hypersalinity, which slows the metabolic processes of decompositional bacteria, essentially 'pickling' the carcass (Ollivier *et al*., 1994; Briggs and Kear, 1994b; Boyero *et al*., 2014). Additionally, the absence of scavenging fish is vital as they are known to remove almost all insect carcasses within hours (Martínez-Delclòs and Martinell, 1993). Small (~ 10 cm) scavenging fish may result in the loss of the softest segments of a carcass (e.g. abdomen), however care should be taken not to confuse this with *in-vivo* interactions (Martínez-Delclòs and Martinell, 1993; Penney and Jepson, 2014).

Carcasses that experience different floatation times can be concentrated at a single site of deposition by gyres, resulting in varying levels of decay among carcasses (Martill pers. comm., 2014). During longer floatation times, a carcass may be 'bound' by a microbial biofilm, protecting it from physical damage, as well as causing it to adhere to any other flotsam it contacts (Gall 1995; Harding and Chant, 2000; Martínez-Delclòs *et al*., 2004).

1. 8. 4. Stage Three: Water column

Insect carcasses sink slowly and vertically, typically completing this stage in minutes to hours depending on water depth and carcass density (Martínez-Delclòs and Martinell, 1993). The presence of a thermocline or halocline can cause a 'second floating', whereby the carcass density is too low to sink through the lower layers, extending the duration in which decay can act (Margalef, 1983). However, in waters where a thermocline or halocline is present, decay is likely hindered by high salinity or low temperatures.

Scavenging fish must also be absent to prevent carcass destruction or fragmentation (Martínez-Delclòs and Martinell, 1993). Despite the relatively short duration of this phase, exceptional preservation requires that these factors are met. Although each carcass has unique fluid dynamics, complete and articulated specimens of the same taxon typically come to rest in similar positions (Martínez-Delclòs and Martinell, 1993).

1. 8. 5. Stage Four: Sediment surface and burial

Upon reaching the sediment surface, carcass articulation will depend largely on the depositional environment (salinity, oxygen levels, sediment composition, and rates of sedimentation), and the robustness of that particular taxon (Martínez-Delclòs and Martinell, 1993). Insect carcasses can remain articulated, but not preserving labile internal tissues, for

almost a year if undisturbed, even if the water is well oxygenated (Martínez-Delclòs and Martinell, 1993). In addition to calm conditions, the absence of benthic scavengers and bioturbators is vital for complete articulation.

Historically, rapid burial has been considered necessary for exceptional preservation (Clarkson, 1998), although it is now known that early mineralisation is the most important factor (Briggs and McMahon, 2016). However, to stimulate mineralisation a carcass typically needs to be entombed, either by sediment or a microbial mat. This can be achieved without rapid burial by the presence of a 'soupy' sediment substrate (Martill, 1993b). Once entombed, the metabolic activities of sedimentary microbes can form sharp geochemical boundaries around the carcass that 'isolate' it, retarding decay, promoting mineralisation, and even concretion formation (Berner 1968; Briggs and Kear, 1993; Gall *et al.,* 1994; Sagemann *et al*., 1999). Alternatively, a carcass could come to rest on a microbial mat and be rapidly over-grown by it. Modern microbial mats only stimulate mineralisation of carcasses in extreme environments, including sabkhas, intertidal flats, anoxic marine sediments, and restricted hypersaline lacustrine settings (Martínez-Delclòs *et al*., 2004).

Following mineralisation, the insect fossil is subject to the same defamatory and destructive factors as most other fossils. These include deep burial, high temperatures, excessive compaction, re-working, dissolution, etc., which must all be absent for exceptional preservation (Clarkson, 1998; Nichols, 2009; Brett and Thomka, 2013). The fossilisation of insect tissues can involve complex geochemistry, particularly so for some of the minerals observed in this project. Below, the most common fossilising minerals and their fabrics are discussed.

1. 9. Fossilising minerals and their fabrics

There is a diverse array of authigenic minerals that can replicate insect soft tissues, some of which form distinctive mineral fabrics. A brief summary of those commonly found in laminated limestones (and relevant to the Nova Olinda Member insects) is presented here. Previous descriptions and identifications of the minerals replacing Nova Olinda Member insects (and their associated fabrics) are reviewed later in section 1. 10. Mineral identifications and fabrics observed in this project are presented in Chapters 3. 3. and 3. 4. respectively.

Some ions will readily bond to organic material (e.g. silica) (Lockley and Rice, 1990). However, they must be present in high concentrations to stimulate mineralisation (Canfield and Raiswell, 1991). The movement of ions in high concentrations results in a geochemical gradient. When

this gradient is in contact with a carcass, the tissues act as a template for mineral growth, replicating them (Berner, 1981; Sorensen and Jorgensen, 1987; Allison, 1988a; Henrichs, 1992; Briggs and Kear, 1993b; Aller, 1982; Simon *et al*., 1994). Some of these gradients are postulated to be intimately associated with the metabolic activities of chemoautotrophic bacterial mats (Briggs and Kear, 1994b; Briggs and McMahon, 2016). The type of mineral precipitated depends on the chemistry of the environment and sometimes the taxa of bacteria present (Efremov, 1950; Allison, 1988b).

1. 9. 1. Calcium carbonate

Calcium carbonates are a common constituent of many fossils. Despite this, they do not usually replace soft tissues. Instead, they tend to fill voids, form cements, and sometimes form nodules (Weeks, 1956; Berner, 1968). Void infills are typically calcite or aragonite, which can be distinguished by their differing crystal structure, with calcite forming trigonal crystals and aragonite forming orthorhombic crystals (Minerals.net, 2018). Calcite void infills and cements are constituted of either very fine grained (1 – 5 μm) crystals (micritic) or larger (20 – 100 μm) crystals (sparry) (Boggs, 2006). These cements can encrust fossils extensively, to the point of obscuring surface detail (Bao *et al*., 1998). Calcium carbonate precipitation does not require bacterial mediation and it precipitates abundantly abiotically (Boggs, 2006). During carcass mineralisation, calcite will cease to precipitate if pH decreases, which occurs when hydrogen sulphide is released by decay (Briggs and Kear, 1994b).

1. 9. 2. Calcium phosphate

Calcium phosphate is commonly known to replicate soft-tissues and it is often associated with Konservat Lagerstätte (e.g. Cerin, Hakel and Hjoula, Monte Bolca, Öland, Santana, Solnhofen) (Martill, 1990; Martill, *et al*., 1992; Wilby and Briggs, 1997; Martínez-Delclòs *et al*., 2004; Eriksson *et al*., 2012). Of these Lagerstätte, Öland ('Orsten'-type) and Santana ('Medusa-effect') preserve soft tissues with the highest fidelity (Martill, 1990; Maas *et al*., 2006). Their preservational fidelity is remarkable, with subcellular ultrastructure retained (Martill, 1990). To achieve this, mineralisation likely occurred very soon after death, although in some laboratory experiments calcium phosphate replacement occurs over weeks-to-months (Martill, 1990; Briggs *et al*., 1993; Maas *et al*., 2006). This preservational fidelity is achieved by calcium phosphate encrustation and impregnation of soft tissues, resulting in distinctive high-fidelity replications that possess a sub-micron granular coating (Figure 17). This type of preservation is attributed to bacterially-mediated calcium phosphate precipitation (Briggs *et al*., 1993; Martínez-Delclòs *et al*., 2004; Maas *et al*., 2006). Although it has been observed that arthropod carcasses can supply enough phosphate for mineralisation of their own tissues (Briggs and

Kear, 1994b), some authors propose that a build-up of phosphates in the sediment, rather than in the carcass, is also required (Briggs *et al*., 1993; Martínez-Delclòs *et al*., 2004). This could be achieved by an abundance of bony fish skeletons in the surrounding sediment (Briggs *et al*., 1993; Martínez-Delclòs *et al*., 2004).

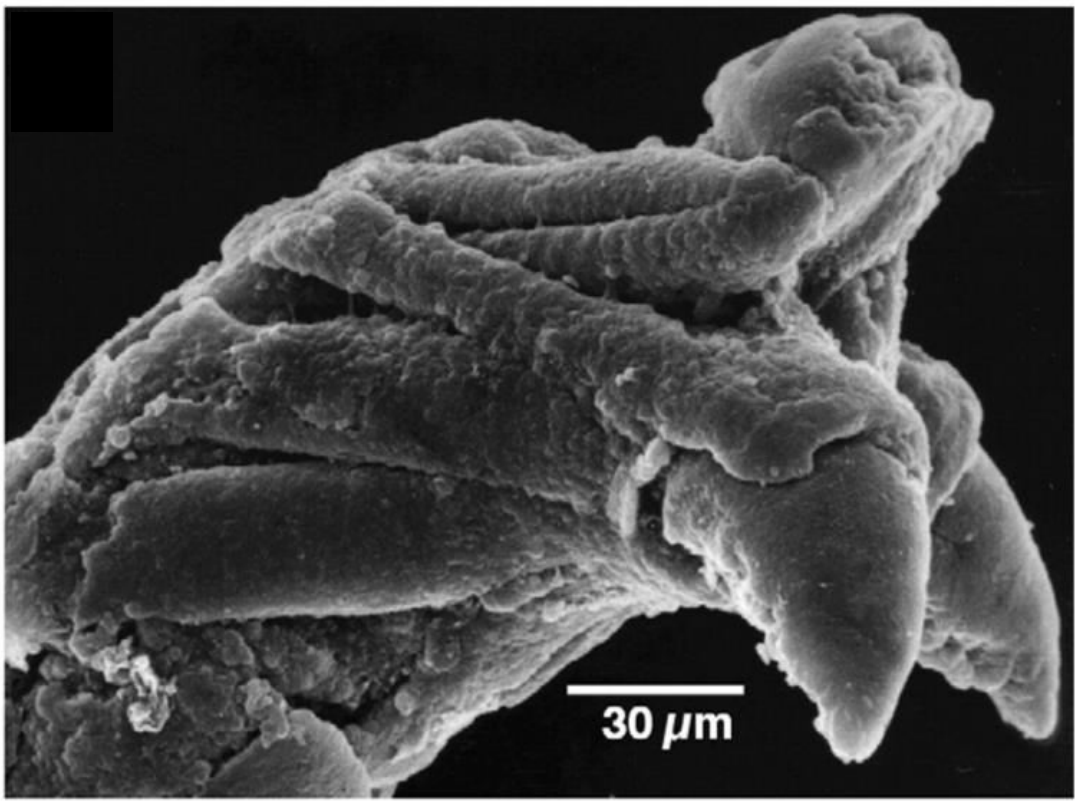


Figure 17. Figure adapted from Mass *et al*. (2006). Phosphatised muscle tissue with distinctive granular surface fabric of a possible immature pentastomid from the Isle of Öland, Sweden. Original image captured by D. Andres, Berlin (Andres, 1989).

1. 9. 3. Silica

Unlike other minerals discussed here, silica (ions) can readily bond to soft tissues without bacterial mediation, if appropriate sedimentological conditions are present (Lockley and Rice, 1990; Butts, 2014). Silica fossilisation occurs as either permineralization, entombment, or replacement, all of which require an abundance of sedimentary silica (Butts, 2014). For replacement to occur, some decay is required to create 'active sites' for silica nucleation (Butts, 2014). Terrestrial Lagerstätten preserving in silica are typically associated with volcanic sediments, whereas in marine settings, silica nodules preserve body and trace fossils abundantly (McCoy, 2013; Butts, 2014).

Taphonomic experimentation demonstrates that sub-cellular structures of metazoans can be preserved readily in silica (Chen *et al*., 2009), however this is reflected rarely in the fossil record (Butts, 2014). More frequently, specimens appear 'perfectly preserved' to the naked

eye, but scanning electron analyses reveal a low-fidelity of micron-scale preservation (Butts, 2014). Large scale (entire fossil) silica replacements can result in beekite ring formation, whereby the fossil contains concentric rings representing fluctuations in silica supply, generating artefacts (Butts, 2014). When a fossil is entombed by silica, the precipitate is cryptocrystalline and can vary in thickness from a thin 'halo' to a large nodule (e.g. chert, flint, and jasper) (Boggs, 2006).

1. 9. 4. Pyrite

Pyrite is a common sedimentary mineral, however it rarely replicates soft tissues (Boggs, 2006). When it does, it can do so exceptionally and many Konservat Lagerstätten have pyrite as the primary preserving mineral (e.g. Beecher's Trilobite Beds, Daohugou Beds, London Clay Formation, Yixian Formation, etc.) (Allison, 1988c; Farrell *et al*., 2009; Wang *et al*., 2012; Zhang and Li, 2012). As pyrite is the dominant mineral replacing Nova Olinda Member insects (now pseudomorphed in goethite), understanding its formation and replacement fabrics are integral to this project (Delgado *et al.*, 2014; Osés *et al*., 2016).

Pyrite possesses a cubic crystal structure and, while abiotic pyrite has been successfully synthesised in laboratory settings (Wang and Morse, 1996; Morse and Wang, 1997), current research indicates that its fossilisation of tissues is intimately associated with sulphate reducing bacteria (Schoonen, 2004; Ohfuji and Rickard, 2005; Briggs and McMahon, 2016). It has many fabrics, but only two have been observed replacing soft-tissues: nano-to-submicro-crystalline replacements, directly replicating soft tissues with a sheet of nanometre-sized crystals, resulting in high-fidelity replications (e.g. Beecher's Trilobite Beds, Farrell *et al*., 2009), and a coarser framboidal replacement fabric that obliterates original micron-scale morphology (e. g. Yixian Formation, Wang *et al*., 2012). These two fabrics can be present within the same fossil. Pyrite can also infill cavities and form concretions around fossils (Allison, 1988c; Boggs, 2006).

1. 9. 4. 1. Pyrite geochemistry

Pyrite geochemistry is complex, polyphase, and extremely oxygen-sensitive (Wolthers *et al*., 2003; Ohfuji and Rickard, 2005). It is typically stable at surface temperatures and pressures but can be metastable depending on the size and nature of its crystals (Berner, 1970; Newman, 1998; Joeckel *et al*., 2005; Ohfuji and Rickard, 2005; Rickard, 2012). It has been established that a series of metastable non-pyritic iron sulphides must precipitate before pyrite can form (Berner, 1964, 1967, 1970; Rickard, 1969; Vaughn and Craig, 1978). These include non-crystalline 'amorphous iron monosulphide' (FeS, sometimes called disordered mackinawite), mackinawite ($(Fe,Ni)S_{0.9}$), and greigite (Fe_3S_4) (Skinner *et al*., 1964; Jeong *et al*., 2008). Of these,

amorphous iron monosulphide is the first phase to precipitate during the reaction between Fe^{2+}_{aq} and S^{-2} under ambient conditions, and does so during early diagenesis just below the sediment surface (Berner, 1970; Lennie and Vaughan, 1996; Wolthers *et al*., 2003). Two different reactions can occur depending on the acidity and temperature of the aqueous solution:

$$pH < 7: Fe^{2+} + H_2S \rightarrow FeS_{amorphous} + 2H^+$$
$$pH > 7: Fe^{2+} + 2HS^- \rightarrow Fe(HS)^2 \rightarrow FeS_{amorphous} + H_2S$$

As these reactions progress in a closed system, the pH of the host solution decreases, eventually causing them to stop (Wolthers *et al*., 2003; Ohfuji and Rickard, 2005). Consequently, time is also a controlling factor in these reactions. These reactions form 'subparticles' (nano-crystals) between 20 – 400 nm in diameter, which are difficult to discern, even under high magnification (Wolthers *et al*., 2003).

After an iron monosulphide phase has precipitated, it reacts with elemental sulphur (S^0), polysulphides (H_2S_n), or hydrogen sulphide (H_2S) to form pyrite (Schoonen, 2004; Wu *et al*., 2012). If elemental sulphur and S^{2-} ions are present, both will react (Ohfuji and Rickard, 2005). Rickard (1997) simplified the typical pyrite formation reaction to:

$$FeS + H_2S_{(aq)} \rightarrow FeS_2 + H_2$$

More recent studies have demonstrated that an intermediate phase of greigite may form during the conversion of mackinawite (disordered or ordered) into pyrite (Hunger and Benning, 2007). Several complex steps occur that can be summarised in the following reaction:

Amorphous Mackinawite | Greigite | Pyrite

$$4Fe^{2+}S^{2-} \xrightarrow[-Fe^{2+}]{-2e^-} Fe_2^{3+}Fe_1^{2+}S_4^{2-} \xrightarrow[-Fe^{2+}]{-2e^-} 2Fe^{2+}S_2^{1-}$$

As shown above, mackinawite can alternatively transform into pyrite via iron loss (as oppose to sulphur gain) (Butler and Rickard, 2000; Hunger and Benning, 2007). Iron loss in this manner results in significant volume shrinkage (up to 41.7% iron loss), which would drastically alter fossil tissues if it occurred in them.

Ultimately, while the reaction pathways and metastability of mackinawite and pyrite are approximately understood, experiments yield drastically varying conclusions regarding Eh, pH, and pressure preferences for all phases (Lennie and Vaughan, 1996; Schoonen, 2004). It is not

certain if greigite is involved at all (Schoonen, 2004). Clearly, more research is necessary, and it appears that sulphate reducing bacteria play a much larger role than simply providing H_2S (Schoonen, 2004; Wu *et al*., 2012; Briggs and McMahon, 2016). Due to these complexities, current models for pyrite framboid formation should only be considered estimations.

1. 9. 4. 2. Pyrite framboids

The description above accounts for nano-to-submicro-crystalline replacement fabrics observed, however pyrite framboid fabrics require further discussion. Pyrite framboid formation has been, and continues to be, an important topic of geochemical investigations (Berner 1969; Farrand, 1970; Sweeney and Kaplan, 1973; Kribek, 1975; Stanton and Goldhaber, 1991; Lennie and Vaughan, 1996; Wang and Morse, 1996; Morse and Wang, 1997; Butler and Rickard, 2000; Wolthers *et al*., 2003; Schoonen, 2004; Ohfuji and Rickard, 2005; Wu *et al*., 2012; Vietti *et al*., 2015). Many palaeontologists refer to globular, grape-like pyrite grains as 'framboids'. However, pyrite true framboids have the distinct definition of 'microscopic spheroidal to sub-spheroidal clusters of equidimensional and equimorphic microcrystals' (Ohfuji and Rickard, 2005). They may have disorganised, partially organised, or regularly organised interiors and range in diameter between 1 – 250 µm, but are typically ~10 µm in diameter and constructed of regularly ordered (or occasionally disordered) equant pyrite crystals (Figure 18) (Ohfuji and Rickard, 2005).

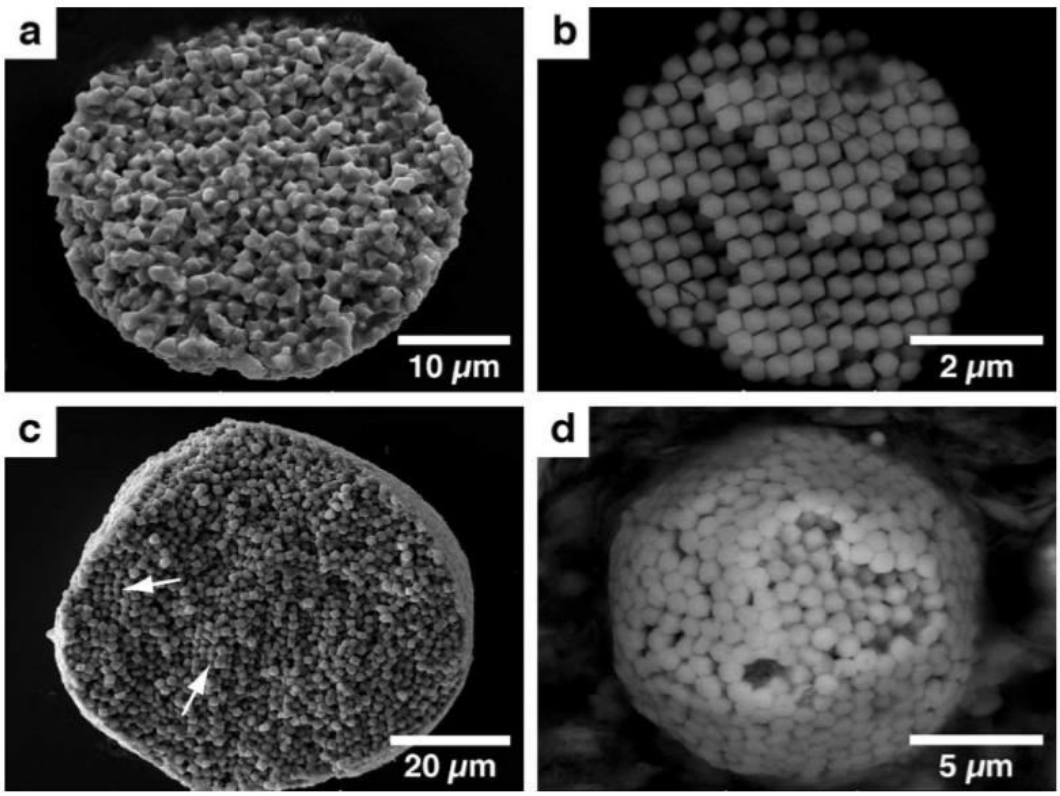


Figure 18. Scanning electron micrographs of different 'natural' pyrite true framboids, showing both internal and external views. A, disorganised. B, organised. C, partially organised. D, external surface. Images from Ohfuji and Rickard (2005).

As with non-framboidal pyrite formation, framboidal pyrite formation below 100°C is complex, polyphase, and inherently difficult to study due to its oxygen-sensitive nature and the difficultly in distinguishing reaction stages (Lennie and Vaughan, 1996; Schoonen, 2004; Hunger and Benning, 2007; Wu *et al*., 2012). Nevertheless, numerous experiments have attempted to characterise its constraints and chemical pathways (Berner 1969; Farrand, 1970; Sweeney and Kaplan, 1973; Kribek, 1975; Stanton and Goldhaber, 1991; Wang and Morse, 1996; Morse and Wang, 1997; Butler and Rickard, 2000; Wolthers *et al*., 2003; Ohfuji and Rickard, 2005; Rickard, 2012). These indicate that pyrite supersaturation is necessary for framboid formation, along with anoxia and abundant sulphate reducing bacteria. However, recent experimentation by Vietti *et al*. (2015) replicated framboid-like structures (interpreted as precursor 'protoframboids') in oxic experimental conditions. This highlights the possibility that the controls for framboid formation occur on the microgeochemical scale, rather than at the overall sedimentary scale.

1. 10. Previous descriptions of Nova Olinda Member preservation and mineralisation

The insects of the Nova Olinda Member Lagerstätte have been studied extensively, and several publications have examined their preservation and mineralisation. Below, these are discussed.

The exceptional preservation of Nova Olinda Member fossil insects was formally highlighted first by Brito (1984) at the 33rd annual Congresso Brasileiro de Geologia, in Rio de Janeiro. Subsequently, Martins-Neto (1987a) described numerous insect species from a collection of 56 specimens and further highlighted their remarkable preservation.

The first in-depth analysis of the preservation of Nova Olinda Member insects was included in the introductory chapter in a comprehensive review of them by Grimaldi and Maisey (1990). Approximately 3000 specimens were analysed, highlighting the unusual diversity, along with SEM and automated X-ray diffraction analyses. High relief and micron-scale details of the cuticle surface, including ommatidia, spines, microtrocia, and setae were reported (Grimaldi and Maisey, 1990). The dominant preserving mineral was identified as goethite and ashing tests revealed no carbon content within the fossils. Matrix analysis revealed a 99% calcium carbonate content, with traces of apatite and pyrolusite (Grimaldi and Maisey, 1990). A preservational model was presented, suggesting replacement of insect tissues by iron minerals in well oxygenated freshwater.

The preservation of Nova Olinda Member fossil insects was discussed later by Bechly (1998c). The entomofauna was introduced as recognisably 'among the greatest even [at] a casual

glance', with an 'unusual taxonomic composition'. This bold statement was supported by examples of preserved micron-scale structures and internal tissues, including stomach and gut tissues, structural colour, and high relief (Bechly, 1998c). The preserving mineral was suggested to be limonite (goethite) and the average preservation was reported to far exceed that of other insect Lagerstätten (Bechly, 1998c).

A comprehensive analysis of the taphonomy of the Nova Olinda Member insects was undertaken by Menon and Martill (2007). Not only did these authors provide further evidence for the exceptional preservation of Nova Olinda Member insects, they also considered the mineralogy of preservation and controlling factors. Two distinct preservational mineralogies were identified: a brown hydrated iron mineral (goethite) and 'black carbonaceous replicas' associated with pyrite. This description of the fossils as 'black carbonaceous replicas' is not reflected in the black specimens examined in this project, and may represent the misinterpretation of iron sulphide preservation. These preserving minerals were correlated with weathering, whereby goethite occurred in weathered (cream) limestone and pyrite occurred in unweathered (blue grey) limestone (Menon and Martill, 2007). The degree of weathering was then correlated with overburden thickness. They concluded that the brown hydrated iron mineral (goethite) represents a weathering product of the 'black carbonaceous replicas' (pyrite). Importantly, it was highlighted that morphological details are often exquisitely preserved in both mineral phases, indicating remarkably little morphological loss during weathering (Menon and Martill, 2007).

Other rarer preservational mineralogies were reported, most notably phosphatised muscle tissues, voids infilled with clear calcite, and rare silicified concretions nucleating on the fossils (Menon and Martill, 2007). It was established that microbial mats played an important role in the preservation of these insects, with sulphate reducing bacteria likely dominating the microbial diversity at the anoxic, sulphur-rich, and hypersaline sediment-water interface (Menon and Martill, 2007). In addition to descriptions of exceptional preservation, Menon and Martill (2007) were the first to highlight the variability in the preservational fidelity of these insects. While compaction is generally minor, rarely, the insect fossils can be restricted to a single lamina (Menon and Martill, 2007). Fragmentary specimens are also rare, only accounting for approximately 6% of specimens (Menon and Martill, 2007). Additionally, there appears to be no control for size or robustness for these insects, as well as no clear evidence for mass mortality events (Menon and Martill, 2007).

Menon and Martill (2007) also noted that strong flying, burrowing, and cryptic insect taxa are common (discussed further in Chapter 5. 1.), along with rarer freshwater insects. This unusual faunal composition was attributed to the periodic influx of insects, either blown into the water

while flying, or flushed in during small-scale floods (Menon and Martill, 2007). Rapid transportation by these processes is hypothesised to bypass most of the normal taphonomic controls for insects, of which scavenging and decay are the most destructive (Menon and Martill, 2007). This, combined with rapid microbial envelopment and early diagenesis of iron minerals and phosphates, allowed for the preservation of labile tissues (Menon and Martill, 2007). Finally, the weathering was identified as deep, slow, and *in situ*, resulting in goethite pseudomorphs of original pyrite fabrics.

1. 10. 2. Delgado *et al.* (2014) and Osés *et al*. (2016)

This project began in 2011. Since then, two additional studies examining the taphonomy and preservational mechanics of the Nova Olinda Member insects have been published (Delgado *et al.*, 2014; Osés *et al*., 2016). Delgado *et al*. (2014) examined Nova Olinda Member insects using diffuse reflectance infrared and energy dispersive X-ray spectroscopy. This elemental analysis indicated the presence of Fe and O, as well as small amounts of P and Mg (Delgado *et al*, 2014). It was also suggested that at least two modes of preservation may have occurred, whereby the external most cuticle was replaced in a different fabric than the internal tissues, albeit in the same mineral phases (a hypothesis which is supported here). A scanning electron microscope figure was also presented, showing what are described as framboidal pyrite pseudomorphs and mineralised EPS (Delgado *et al*, 2014: Fig. 7). Delgado *et al*. (2014) further elaborated that the cuticle-replacing microfabrics are composed of pseudomorphed pyrite framboids, a statement which is not agreed with here. Although pseudomorphed pyrite framboids are present, they replace the internal tissues (and possibly some of the endocuticle), but the external cuticle is not preserved in them. Instead, it is preserved as a nano-crystalline non-framboidal pyrite replacement, and the pseudoframboids are only revealed where the exocuticle is lost (discussed further below and in Chapters 3. 4. and 4. 2., also see Figure 34).

Finally, post (initial-)submission of this thesis, a comprehensive analysis of the mechanism of preservation of the Nova Olinda Member insects was undertaken (Osés *et al*., 2016). This summarised all previous taphonomic work on these fossil insects, confirmed the fabrics of preservation reported by Barling *et al.* (2015) (outlined in Chapter 3. 4.) and presented hypotheses for their mode of preservation (Osés *et al*., 2016). The fossils were subject to numerous microscopic and elemental analyses including energy dispersive X-ray analysis, energy dispersive X-ray fluorescence, soft X-ray spectroscopy, particle induced X-ray emission, and Raman spectroscopy (Osés *et al*., 2016). Iron hydroxides were detected as the primary preserving mineral and proposed to be pseudomorphs of pyrite, based on mineral fabrics. A differing preservational fabric was reported for both external cuticle and internal tissues, with

the external tissues (exoskeleton) replaced by non-framboidal pyrite nanocrystals and the internal tissues replaced by micro-framboidal pyrite (based on the Canfield and Raiswell (1991) and Butler and Rickard (2000) definitions of framboidal pyrite). Osés *et al.* (2016) suggested that sulphate reducing bacteria entombed and infiltrated the carcasses. Their metabolic activities stimulated pyrite precipitation, but the variation in iron and sulphur ion concentrations between the exterior tissues and internal tissues resulted in differing preservational fabrics, including variations in framboid size (Osés *et al*., 2016). Ion diffusion was hypothesised to be controlled by compaction-induced cuticular micro-cracks, as well as the microbial biofilm (Osés *et al*., 2016). The origin of sulphate ions is discussed, and it is noted that sulphate is not present in environments similar to the Nova Olinda palaeolake in sufficiently high concentrations to stimulate mineralisation without associated volcanic sediments (Osés *et al*., 2016). To account for this, Osés *et al*. (2016) suggested that the abundance of sulphate originated from 'evaporites' (presumably referring to the only evaporites in the basin, the overlying Ipubi Formation, which was deposited *after* the fossilisation of these insects).

The most labile soft tissues were identified as preserved in calcium phosphate, rather than pyrite (Osés *et al*., 2016). It was noted that only calcium poor continental waters typically contain phosphate in concentrations high enough to stimulate phosphatisation, and that the Nova Olinda Member is unlikely to have had such an input. Instead, it is proposed that ions liberated by partial decay of the most labile tissues allowed for phosphatisation to occur (Osés *et al*., 2016).

Several fabrics associated with fossilisation were also described. Cuticle-replacing grains were reported to possess dissolution cavities. Web-like structures were reported on many fossils and suggested to be fossilised EPS. However, this identification was based largely on anecdotal evidence and chemical analyses only report a high carbon content. It is probable that these structures instead represent modern fungal contamination (discussed further in Chapter 2. 1. 3.). Both original and templates of euhedral to subhedral or anhedral microcrystals are reported, although only moulds of euhedral microcrystals are figured (Figure 3: C in Osés *et al*., 2016).

Further aspects of Nova Olinda Member insect taphonomy were discussed by Osés *et al.* (2016), including decay-controlling environmental factors and the taxonomic diversity of the assemblage. They noted that many taxa present in the Nova Olinda Member relied on fresh water for reproduction and that the abundance of aquatic taxa may be the result of mass mortality events caused by a periodic increase of H_2S (Osés *et al*., 2016). The prevention of decay is attributed to an euxinic photic zone, which was hypothesised based on previously

published sedimentological data (Heimhofer and Martill, 2007). The importance of anoxia, high salinity, absence of scavengers, and a low concentration of sedimentary organic matter is also noted for this mode of fossilisation (Osés *et al*., 2016).

1. 10. 3. Critique of Osés *et al.* (2016)

The hypotheses presented by Osés *et al*. (2016) are based on a combination of novel analyses and published data. Many (if not most) of the textural descriptions refer to those observed by Barling *et al.* (2015). As Barling *et al.* (2015) is a major component of this thesis, it is natural that there are similarities between the hypotheses presented by Osés *et al*. (2016) and those presented here. However, there are several components of the model proposed by Osés *et al*. (2016) that are disagreed with here. Firstly, although the presence of at least three preservational fabrics (high fidelity non-framboidal pyrite replacements, (pseudo)framboidal pyrite infills/overgrowths, and calcium phosphate impregnations/overgrowths) is agreed with, the relationship between the two types of pyrite preservation is not. Osés *et al*. (2016) follow the interpretation of Delgado *et al.* (2014), whereby the external cuticle is replaced by pseudomorphed framboidal pyrite with the high-fidelity non-framboidal replacement a result of later pyrite overgrowth. They support this with the presence of polygonal lamellae associated with individual framboids (see page 9 of Osés *et al*., 2016). In this thesis, the reverse is proposed, whereby the high-fidelity non-framboidal replacement precipitated first and the pyrite (pseudo)framboids overgrew its internal surface (as well as elsewhere within the carcasses). Secondly, the timing of mineralisation proposed by Osés *et al*. (2016) is ambiguous. They conclude that it occurred during early diagenesis, yet a fundamental component of their model is the presence of cuticular microcracks, allowing for ion movement. Insect cuticle is a relatively flexible material *in vivo* and does not crack in this manner prior to mineralisation (Hopkins and Kramer, 1992). In addition, the requirement for microcracks conflicts with the previously discussed point (i.e. how can cracks in the cuticle control internal mineralisation if the cuticle is yet to be mineralised?). Consequently, they are excluded from the model proposed in this thesis. Finally, the origin of the ions necessary for mineralisation is ambiguous. They are described as originating from ‘evaporites’, with the only evaporites in the basin being the *overlying* Ipubi Formation. It is possible that Osés *et al.* (2016) are instead referring to sedimentary halite growth, as reported by Martill *et al*. (2007b), but this is lost in translation.

In these regards, the model presented later in this thesis differs from that of Osés *et al.* (2016) and this is discussed further in Chapter 4. 2. 1. and 4. 2. 4.

Chapter 2: Materials, preparatory methods, and analyses

2. 0. Preface

In this chapter the number, acquisition, and curation of specimens examined in this project is outlined, followed by descriptions of the preparatory methods implemented. The techniques used to analyse these fossils are then described, along with their equipment and operating parameters. Finally, explorative statistical analyses applied to these fossils to detect taphonomic trends are outlined.

2. 1. Materials

2. 1. 1. Specimens

The specimens used in this project were originally obtained as part of a different Ph.D. project for another student (J. Wohlrabe) at the University of Portsmouth. They were, ironically, donated as 'poor quality', 'unsellable' fossils from an anonymous donor in Germany. Additionally, several specimens were collected by both J. Wohlrabe and D. M. Martill over multiple excursions to the Nova Olinda Member quarries. The project undertaken by J. Wohlrabe focused on the taphonomy of Blattodea (cockroaches) and, as such, the taxonomic diversity of the collection is skewed towards them (as well as Orthoptera, probably as a result of original misidentification). J. Wohlrabe became a distance student several years before this project began, but was unable to complete it for personal reasons. In early 2011, Dr D. M. Martill contacted J. Wohlrabe and arranged for the transfer of the specimens for this project.

2. 1. 2. Prior storage and number of specimens

Originally, over 140 fossil specimens were supplied by J. Wohlrabe, including several that were pre-prepared and mounted for scanning electron analyses. However, many of the specimens were damaged prior to their acquisition for this project. Unmounted specimens had been stored in a large plastic container, stacked in layers separated by newspaper for several years. This meant that lower specimens were not adequately protected from abrasion/compression by overlying specimens. Stub mounted specimens were stored in plastic containers, with typical stub slots to hold them in place. However, some had detached from their slots and abraded against the container walls.

From this collection, a total of 92 unmounted specimens were recovered. These included residues and sedimentological samples that were cut into smaller samples for different

analyses. Several specimens had been damaged heavily and were used as examples of problems faced during curation (described further below in section 2. 1. 3.). From the mounted specimens, 15 were recovered for study, including a new taxon of fossil wasp (SMNS 700902, *Parviformosus wohlrabeae,* described in Chapter 5. 4.). The remaining specimens, most of which were heavily damaged by improper storage, were set aside for future analyses.

Six additional sedimentological specimens were cut from sediment samples collected by D. M. Martill, including examples of 'weathered' and 'unweathered' Nova Olinda Member limestone. Another five specimens of modern insects were mounted for SEM analyses, along with a single sample of pyrite decay. A further 28 additional Nova Olinda Member fossil insect specimens were donated by Florence Gallien from her voluntary work at the University of Portsmouth. Her specimens originated from the collection at the University of Portsmouth and these were mostly pre-prepared and mounted on stubs. Finally, an additional 14 specimens were added during the final stages of this project. One of these was an 'unweathered' Nova Olinda Member insect used for mineralogical analyses (HT001) donated by Helmut Tischlinger, and the remaining were fossils from other comparable Lagerstätten.

In total, 161 specimens were studied in this project (Table 1). Specimen SMNS 70092 (JW614) has been deposited at the Staatliches Museum für Naturkunde, Stuttgart. Specimen YPM 73015 has been returned to Yale Peabody Museum, and specimens MPV-2418-RM and MPV-2419-RM have been returned to E. Peñalver. Excluding these exceptions, all specimens are currently stored at the University of Portsmouth.

Table 1. List of all specimens examined in this project with taxonomic identifications, photograph numbers, coating type, and additional notes. Sputter coating thickness is ~10 nm, due to double coating. (Also see Table 7 in Appendices 8. 7.)

Specimen Number	Taxonomic Identification	Photographs	Sputter Coating	Additional Notes
Judith Wohlrabe Specimens				
NBRL001	Plant Material	NBRL 001 photo 01 - 05	Unmounted	Plant material
NBRL002	Odonata: Epiprocta?	NBRL 002 photo 01 - 04	Uncoated	
NBRL003	Diptera?	NBRL 003 photo 01 - 02	Uncoated	
NBRL004	Orthoptera	NBRL 004 photo 01 - 03	Mounted, uncoated	
NBRL005	Orthoptera	NBRL 005 photo 01 - 03	Uncoated	
NBRL006	Diptera	NBRL 006 photo 01 - 03	Uncoated	
NBRL007	Blattodea	NBRL 007 photo 01 - 03	Uncoated	
NBRL008	Orthoptera or Blattodea	NBRL 008 photo 01 - 04	Au-Pd	Used for sediment analysis
NBRL009	Indeterminate	NBRL 009 photo 01 - 03	Failed Transfer	
NBRL010	Blattodea?	NBRL 010 photo 01 - 04	Uncoated	
NBRL011	Hemiptera: Cicadomorpha?	NBRL 011 photo 01 - 04	Au-Pd	Offcuts used for sediment analysis
NBRL011 (offcut)	Sediment Sample			Chemical staining
NBRL012	Hymenoptera	NBRL 012 photo 01 - 05	Failed Transfer	
NBRL013	Indeterminate	NBRL 013 photo 01 - 06	Unmounted	
NBRL014	Blattodea	NBRL 014 photo 02 - 03	Au-Pd	Interesting cuticular fabrics

NBRL015	Coleoptera/Hemiptera	NBRL 015 photo 01 - 05	Unmounted	
NBRL016	Plant material	NBRL 016 photo 01 - 06	n/a	
NBRL017	Orthoptera	NBRL 017 photo 01 - 04	Unmounted?	
NBRL017 (offcut)	Sediment Sample			Chemical staining
NBRL018	Blattodea	NBRL 018 photo 01 - 23	Au-Pd	High relief, etched
NBRL019	Hemiptera: Cicadomorpha?	NBRL 019 photo 01 - 03	Unmounted?	
NBRL020	Orthoptera	NBRL 020 photo 01 - 04	Transferred	
NBRL021	Blattodea	NBRL 021 photo 01	Unmounted?	
NBRL022	Blattodea	NBRL 022 photo 01	Au-Pd	Replacement fabrics
NBRL023	Blattodea	NBRL 023 photo 01 - 05	Failed Transfer	
NBRL024	Blattodea	NBRL 024 photo 01	Au-Pd	
NBRL025	Blattodea	NBRL 025 photo 01	Recoverable Transfer	
NBRL026	Blattodea	NBRL 026 photo 01 - 04	Au-Pd	500nm microspheres
NBRL026(dupe)			Au-Pd	
NBRL027	Blattodea	NBRL 027 photo 01	Au-Pd	Masked by resin
NBRL028	Blattodea	NBRL 028 photo 01	Failed Transfer	
NBRL029	Orthoptera?	NBRL 029 photo 01	Failed Transfer	
NBRL030	Blattodea	NBRL 030 photo 01	Au-Pd	Extremely scrappy
NBRL031	Blattodea	NBRL 031 photo 01 - 02	Au-Pd	
NBRL031(resi)			Au-Pd	
NBRL032	Blattodea	NBRL 032 photo 01 - 02	Failed Transfer	
NBRL033	Diptera: Culicidae?	NBRL 033 photo 01	Failed Transfer	
NBRL034	Blattodea	NBRL 034 photo 01	Failed Transfer	
NBRL035	Blattodea	NBRL 035 photo 01	Failed Transfer	
NBRL036	Blattodea	NBRL 036 photo 01	Au-Pd	High relief, eyes
NBRL037	Blattodea	NBRL 037 photo 01 - 02	Au-Pd	Highly fractured
NBRL038	Blattodea	NBRL 038 photo 01	Failed Transfer	
NBRL039	Indeterminate	NBRL 039 photo 01	Failed Transfer	
NBRL040	Blattodea	NBRL 040 photo 01	Au-Pd	Scales & preservation fabrics
NBRL041	Diptera	NBRL 041 photo 01 - 02	Unmounted	
NBRL042	Hemiptera: Achilidae?	NBRL 042 photo 01	Recoverable Transfer	
NBRL043	Orthoptera?	NBRL 043 photo 01 - 02	Failed Transfer	
NBRL044	Orthoptera: Elcanidae	NBRL 044 photo 01	Au-Pd	Beautiful ommatidia
NBRL045	Coleoptera	NBRL 045 photo 01	Au-Pd	Micro-setae
NBRL046	Blattodea?		Au-Pd	
NBRL047	Orthoptera?		Failed Transfer	
NBRL048	Coleoptera		Au-Pd	Impression only
NBRL049(dupe)	Orthoptera		Recoverable Transfer	
NBRL050	Orthoptera?		Failed Transfer	
NBRL051	Orthoptera: Elcanidae	NBRL 051 photo 01-05	Au-Pd	Very high relief, complete
NBRL052	Hemiptera?		Recoverable Transfer?	
NBRL053	Neuroptera		Failed Transfer	
NBRL054	Blattodea	NBRL 054 photo 01-05	Au-Pd	Very high relief, complete
NBRL055	Orthoptera	NBRL 055 photo 01-02	Au-Pd	Very high relief, complete
NBRL056	Orthoptera?		Recoverable Transfer?	
NBRL057	Diptera: Tabanidae		Au-Pd	Moderate relief, charging
NBRL058	Odonata			
NBRL059	Orthoptera	NBRL059 photo 01 - 06	Au-Pd	Extremely high relief
NBRL060	Ephemeroptera	NBRL060 photo 01 - 05	Both?	Exceptional gills
NBRL061	Orthoptera	NBRL061 photo 01 - 08	Au-Pd	High relief head only
NBRL062	Orthoptera	NBRL062 photo 01 - 05	Au-Pd	Poor preservation
NBRL063	Orthoptera?	NBRL063 photo 01 - 12	C	

NBRL064	Orthoptera?	(phone _161237, _161242, _161244)		
NBRL065	Orthoptera or Blattodea?	NBRL065 photo 01 - 27	Au-Pd	
NBRL065(scrap)			Au-Pd	Residue stub
NBRL066	Orthoptera	NBRL066 photo 01 - 09	Carbon	Specimen cracked into three parts
NBRL067	Orthoptera	stub mounted after breaking	Au-Pd	
NBRL068	Orthoptera	NBRL068 photo 01 - 17	Au-Pd	
NBRL068(resi)			Au-Pd	Residue stub
NBRL069	Orthoptera	NBRL069 photo 01 - 12	Uncoated	
NBRL070	Orthoptera	NBRL070 photo 01 - 23	Au-Pd	Soft tissues preservation
NBRL071	Blattodea?	NBRL071 photo 01 - 11	Au-Pd	Contamination or EPS?
NBRL072	Orthoptera or Blattodea?	NBRL072 photo 01 - 10	Au-Pd	Extensive charging
NBRL073	Raphidioptera	NBRL073 photo 01 - 05	Au-Pd	Extensive contamination.
NBRL074	Orthoptera	NBRL074 photo 01 - 14	Both?	Poor preservation
NBRL075	Indeterminate	NBRL075 photo 01 - 09	Au-Pd	Charging
NBRL076	Indeterminate	NBRL076 photo 01 - 05	Au-Pd	
NBRL077	Blattodea?	NBRL077 photo 01 - 05	Au-Pd	Hair contamination
NBRL078	Blattodea	NBRL078 photo 01 - 02	Au-Pd	Thin calcite infill
NBRL079	Neuroptera	NBRL079 photo 01 - 03	Au-Pd	Partial resin cover
NBRL080	Indeterminate	NBRL080 photo 01 - 05	Au-Pd	
NBRL081	Hemiptera	NBRL081 photo 01 - 06	Au-Pd	
NBRL082	Blattodea	NBRL082 photo 01 - 06	Au-Pd	
TEST SPECIMEN	Blattodea	Rsn Tst 01 - 29	Au-Pd	
NBNEW001	Orthoptera - DESTROYED	NBNEW01 photo 01-24	Destroyed	Weathered XRD
NBNEW002	Orthoptera, unstudied.	Unstudied	Unstudied	Sample numbered for clay analysis
NBNEW002 (offcut)	Sediment Sample		None	Clay analysis
Pre-mounted by Judith Wohlrabe				
JW078			C	
JW109			C	
JW02#	Indeterminate	SEM only	Prior to acquisition	Wavy fat body
JW291	Blattodea	SEM only	C	
JW339	Blattodea	SEM only	C	
JW456	Indeterminate	SEM only	Prior to acquisition	
JW465	Indeterminate	SEM only	Prior to acquisition	
JW522	Indeterminate	SEM only	Au-Pd	
JW528	Indeterminate	SEM only	Prior to acquisition	
JW614 (SMNS 700902)	Hymenoptera: *Parviformosus wohlrabeae*	SEM only	Au-Pd	
JW614(resi)	Hymenoptera: *Parviformosus wohlrabeae*	SEM only	Au-Pd	Residue stub, ovipositor
JW677	Indeterminate	SEM only	Au-Pd	
JW735	Blattodea?	SEM only	Au-Pd	
JW658			C	
JW999	Indeterminate	SEM only	Prior to acquisition	
Modern Insect Specimens				
NBSTUB01	Antlion wing dorsal view	SEM only	Au-Pd	
NBSTUB02	Antlion wing ventral view	SEM only	Au-Pd	
NBSTUB03	Intact modern insects	SEM only	Au-Pd	Desiccated, multiple taxa

NBSTUB04	Broken modern insects (Diptera & Hymenoptera)	SEM only	Au-Pd	Desiccated, multiple taxa
NBSTUB05	Blattodea: *Periplaneta americana*	SEM only	Au-Pd	
NBSTUB06	Sample of pyrite decay (Crato plant material)	SEM only	Au-Pd	Sampled from NBRL001
Sediment Samples from David Martill				
NBSED01a	Sediment Sample	SEM only	Au-Pd	Numerous offcuts
NBSED01b	Sediment Sample	SEM only	Au-Pd	
NBSED01 (offcut)	Sediment Sample - Ground to powder		Destroyed	Sample used for magnetic separation
NBSED01 (offcut)	Sediment Sample		Unmounted	Chemical Staining
NBSED02a	Sediment Sample	SEM only	Carbon?	Resin Transferred
NBSED02b	Sediment Sample	SEM only	Carbon?	Resin Transferred
Specimens from Florence Gallien				
FLO13	Ephemeroptera	FLO13 photo 01 - 06	Au-Pd	Fungal contamination, etched phosphorous
FLO15	Hemiptera	SEM only	Au-Pd	Outstanding genital preservation
FLO17		SEM only	Au-Pd	
FLO19	Diptera	SEM only	Prior to acquisition	Outstanding genital preservation
FLO26			C	
FLO27	Hemiptera	FLO27 photo 01 - 05	Both	High relief eye
FLO28	Diptera	FLO28 photo 01 - 05	Prior to acquisition	
FLO29	Diptera: Nematocera?	FLO29 photo 01 - 04	Au-Pd	
FLO30			Au-Pd	
FLO31 (a,b)	Diptera?	FLO31 photo 01 - 03	Au-Pd	Fibrous contamination, fossilised microbial mat?
FLO33	Blattodea	FLO33 photo 01 - 11	Au-Pd	unweathered
FLO34			Au-Pd	
FLO35	Blattodea???	FLO35 photo 01 - 08	Au-Pd	
FLO36	Hemiptera: Cicadamorpha: Auchenorrhyncha	FLO36 photo 01 - 05	Au-Pd	Replacement in 200-500nm spheres
FLO37	Indeterminate	FLO37 photo 01 - 04	Au-Pd	Resin Transferred
FLO37(dupe)	Ephemeroptera		Au-Pd	Mayfly Nymph
FLO38	Indeterminate (Hemiptera?)	FLO38 photo 01 - 04	Au-Pd	Well preserved scales
FLO39	Indeterminate		Both?	
FLO41	Indeterminate		Au-Pd	
FLO43	Indeterminate		Au-Pd	Clusters of soft tissue
FLO58	Indeterminate		Au-Pd	
FLO59	Indeterminate		Au-Pd	
FLO63	Indeterminate		Au-Pd	
FLO64	Hemiptera	FLO64 photo 01 - 06	Au-Pd	
FLO68	Indeterminate		Au-Pd	
FLO69	Indeterminate		Au-Pd	
FLO(unnumbered)	Indeterminate		Uncoated	Test, transferred
FLOXX	Diptera		Au-Pd	
Other Lagerstätten Specimens				
HT001	Orthoptera	HT001 photo 01 - 69	C	Unweathered Crato Insects, two orthopterans
SH001	Odonata	SH001 photo 01 – 22	Uncoated	Solnhofen Schernfeld near Eichstätt
GR001	Diptera?	GR001 photo 01 - 09	Uncoated	Green River, multiple fossils inc isolated abdomen
LC001	Decapod Crab	LC001 photo 01 - 22	Uncoated	London Clay, Sheppey

LC002	Decapod Crab	LC002 photo 01 - 24	Uncoated	London Clay, Sheppey DMMC:4b/10
YPM 73015	Trilobite: *Triarthrus eatoni*	BT001 photo 01 - 24	Uncoated	Beecher's Trilobite
MPV 2418 RM	Diptera: Sciaridae: *Sciara* sp.	RdM002 photo 01 - 16	Repaired with resin	Rubielos de Mora Basin
MPV 2419 RM	Diptera: Mycetophilidae	RdM001 photo 01 - 19	Repaired with resin	Rubielos de Mora Basin
Mont001 (A)	Diptera	Mont001 photo 01 - 07	Uncoated	Montsec, 'La Cabrua'
Mont002 (B)	Blattodea	Mont002 photo 01 - 07	Uncoated	Montsec, 'La Cabrua'
Mont003 (C)	Hymenoptera	Mont003 photo 01 - 13	Uncoated	Montsec, 'La Cabrua'
Mont004 (D_1 & D_2)	Coleoptera?	Mont004 photo 01 - 10	Uncoated	Montsec, 'La Cabrua'
Mont005 (E)	?	Mont005 photo 01 - 09	Uncoated	Montsec, 'La Cabrua'
Mont006 (F)	Hemiptera?	Mont006 photo 01 - 16	Uncoated	Montsec, 'La Cabrua'

2. 1. 3. Curation and contamination

The majority of specimens were centred on angular slabs of laminated limestone, approximately 10 – 15 cm in diameter. To aid in storage and SEM viewing, these were cut with a diamond circular rock saw, lubricated with deionised water. Typically, each specimen was cut to a rectangle with approximately 0.5 – 1 cm of limestone matrix remaining around the fossil. This allowed unmounted specimens to be stored closely packed in PELCO® SEM stub containers (with the plastic stub holders removed) and, more importantly, fit in the sputter coaters. Several offcuts were retained for sedimentological analysis (noted in Table 1). The use of PELCO® SEM stub containers allowed for easy access and safely stackable storage that also minimized contamination. Specimens that had been exposed to water during acid digestion or cleaning (discussed later in section 2. 2.) were also stored within desiccators filled with blue-to-pink silica desiccator granules.

Stub mounted specimens were also stored in PELCO® SEM specimen storage holders, or single pin mount storage/mailer tubes where appropriate. Most of these containers were permanently stored in scientific desiccators and, in some cases, under vacuum.

For larger stub mounted specimens (> 6 cm diameter), specialised storage containers were created using Tupperware® containers, an inch-thick layer of foam, and plastic tubing. The foam was pierced with holes and marked with red crosses, allowing stubs to rest on the foam without moving. A central strut was constructed for each container from plastic tubing, providing additional support for the lid and protecting specimens when the containers were stacked.

Improper curation of specimens may result in significant damage. This is especially important for fossils preserved in iron sulphides, many of which are metastable at surface temperatures and pressures, or can act as a substrate for chemotrophic bacteria (Kosman, 2003; Joeckel *et al*., 2005; Andrews *et al*., 2013). Chemical weathering can degrade or destroy specimens if curation is poor (Joeckel *et al*., 2005; Nichols, 2009). When exposed to water, metastable iron

sulphides weather to limonite (a mixture of hydrated iron(III) oxyhydroxides), which may obliterate fossil details, or goethite (an iron oxyhydroxide). The vast majority of specimens examined in this project had already weathered to goethite, luckily with no apparent loss of fidelity. However, even weathered specimens can be damaged by moisture, as it allows for fungal and bacterial growth.

Fungal growth and filamentous bacterial contamination was a particularly pervasive problem in this project. This was mostly due to poor storage of specimens prior to acquisition. In the most extreme cases, fossils could be completely overgrown. Specimen NBRL073 became contaminated with actinomycete bacterial growth during storage and provides an example of extreme contamination (Figure 19; Plates 12 and 13). Contamination like this is extremely difficult to remove without damaging the fossil. Acetone can partially disaggregate the bacterial filaments, but will not restore a specimen as infested as NBRL073. General contamination was also a point of concern, and several specimens were contaminated with dust or lint. In most cases, this was easily removed with a soft-squeeze blower. Nevertheless, the storage techniques used in this project protected the majority of specimens from further contamination similar to that of NBRL073.

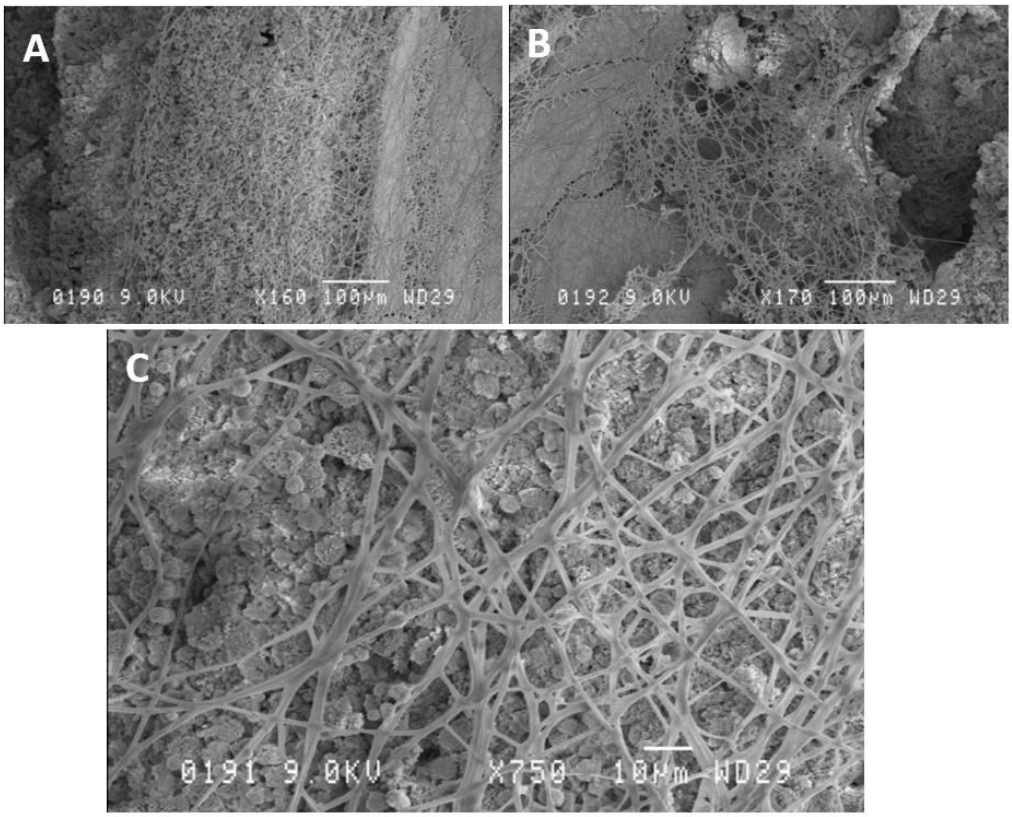


Figure 19. SEM images of specimen NBRL073, showing the extent to which a specimen can be affected by contamination from actinomycete bacteria. A, Filaments overgrowing the eye. B, Filaments overgrowing the thorax. C, Higher magnification image showing the filamentous structure forming a 'mesh'. A, NBRL073-8; B, NBRL073-9; C, NBRL073-10. A-B, Scale bars = 100 µm. C, Scale bar = 10 µm.

2. 1. 4. Light photography

Specimens that were not pre-prepared for SEM viewing, or otherwise damaged, were digitally photographed as part of their curation (photo numbers listed in Table 1). However, some specimens (NBRL046, 047, 048, 049, 050, 052, 053, 056, 057, and 058) were mounted or resin transferred (explained in section 2. 2. 2.) prior to photographs being taken as little-to-no morphological detail was visible. Rock samples were not photographed, unless they were chemically stained. The bulk of the photography was done with a Nikon DS-Fi1 camera with a Nikon Digital Sight attachment, mounted on an Olympus SZ-STS light microscope. Specimen numbers were recorded in the image file name, along with photograph numbers. Images were saved as JPEG files and are either 1280 x 960 or 2560 x 1920 pixels in size. These images provided a record of specimen morphology before acid processing, which was vital for specimens that were later damaged or destroyed.

2. 2. Preparatory methods

2. 2. 1. Chemical preparation

The Nova Olinda Member limestones are readily dissolved by acetic and hydrochloric acid, whereas most of the fossil material is preserved in insoluble iron minerals. Fossil material that is preserved in apatite will be dissolved by hydrochloric acid, but not acetic acid. Consequently, a series of chemical digestions, acid etches, and resin transfers (described in section 2. 2. 2.) were undertaken to further expose the fossils. Most specimens were digested or etched with 10% acetic acid. However, some specimens that were particularly well-cemented, and could not be rapidly exposed by acetic acid, were digested or etched in 5% hydrochloric acid. If a specimen was not at least partially exposed after two days immersion in acetic acid, it was digested in hydrochloric acid. While this undoubtedly damaged any phosphatic preservation, mechanically preparing these fossils risked damaging all of the fossil and would have been too time consuming.

All digestions were carried out under a fume hood and complete digestion usually took two-to-five days, depending on the porosity of the rock, size of the sample, and acid used. At all stages of transfer between liquids, one-to-two drops of 10% Decon 90 were added as a ‘flow aid’ before moving the specimen. This ‘weakens’ the meniscus of the liquid, reducing the chance of damage to the specimen as it breaks surface tension (Green, 2001).

2. 2. 1. 1. Techniques and types of digestion

Most specimens were acid digested after resin transfer (explained in section 2. 2. 2.), and so remained articulated. However, some specimens were completely digested without resin, freeing the fossil from its matrix and forming a 'residue' of fossil material. In all digestions, acid was periodically 'refreshed' by gently decanting and refilling. Once digestion was complete, the remaining residue and acid were poured gently through a 100 µm sieve. The 100 µm sieve was then folded into a half-dumb-bell shape and repeatedly, but carefully, dipped in distilled water (with 10% Decon 90). The remaining digested contents were transferred to a petri dish with 100 ml of distilled water and left to dry. Finally, the material was transferred to an SEM stub for analysis.

Sediment samples that were acid etched were first polished with 100 µm chromium-nickel spheres and distilled water on a glass disk. This provided a smooth surface on which the acid could act, resulting in carbonate-poor areas being highlighted by high relief. Etched specimens were dipped for ten-to-thirty seconds in 10% acetic (for 'weak' etching) or 5% hydrochloric acid (for 'strong' etching). They were then washed with distilled water, and finally immersed in distilled water until effervescence stopped.

2. 2. 1. 2. Problems and cleaning

Decon 90 was introduced as a 'flow aid' after one specimen (NBRL049) revealed intact delicate antennae, protruding several millimetres above the specimen perpendicular to laminae, that disarticulated and fragmented while breaking surface tension.

As specimens were digested, a considerable amount of globular iron hydroxide material, presumably microfossils such as those shown in Figure 8 (in Chapter 1), was released from the sediment. Some of this material floated to the surface and this, combined with CO_2 bubbles released during digestion, formed a thick foamy 'scum' on the water surface. In addition, a 'soupy' mixture of denser particles accumulated at the bottom of the tanks. These residues proved particularly problematic, as any specimen passing through them would be coated in contaminate particles. A combination of techniques were implemented to reduce the amount of globular material coating specimens. Twice daily, the material accumulated on the water surface was carefully removed using plastic spoons. This removed the vast majority of the obstructing material, however an extremely thin film always remained. Plastic tweezers were used to remove specimens from the acid, with minimal disturbance to the 'soupy' denser material.

Digestions were also monitored to prevent excessive evaporation, which results in the growth of calcium acetate crystals around the fossil, obscuring surface details and damaging the specimen (Figure 20: B). Once removed, specimens were gently washed with deionised water, then transferred to triple-deionised water for 24 hours, rather than adding neutralising agents. This was particularly important, as the addition of neutralising agents results in salt formation, creating micron-scale artefacts and obscuring cuticular surface details (Figure 20: A).

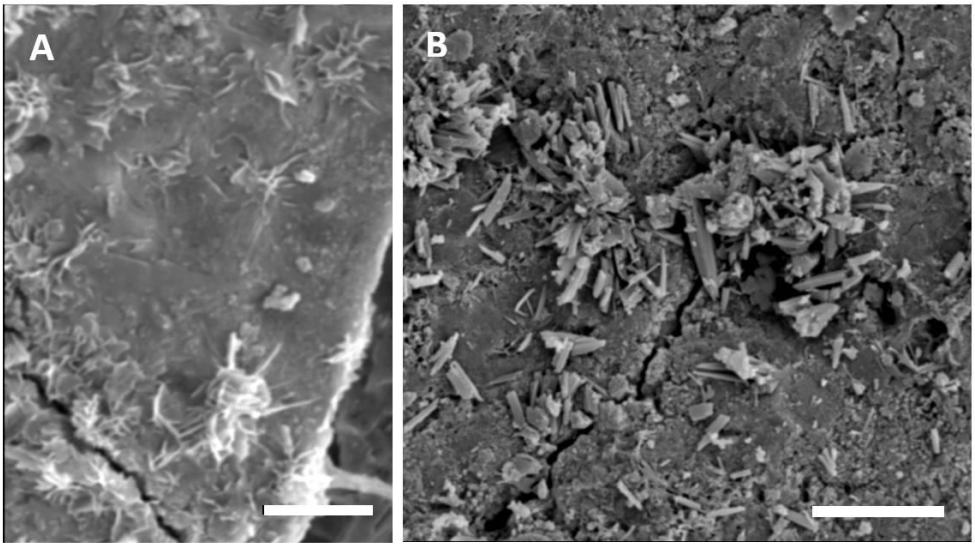


Figure 20. A, Scanning electron micrograph of specimen covered in micro-crystals formed from improper washing and the use of neutralising agents after acid digestion. B, Scanning electron micrograph of crystals formed from acid evaporation. A, JW735-028; B, JW522-013. A, Scale bar = 5 µm. B, Scale Bar = 10 µm.

2. 2. 1. 3. Over-digestion

Several specimens appeared to be damaged during acid digestion. However, due to the limited number of specimens available and the difficulty in procuring new specimens, no control experiments were undertaken to confirm this. Below, a hypothesis for this type of damage is presented, but it remains largely unsubstantiated.

Despite the insolubility of goethite, some specimens that were extensively digested showed signs of damage. Specimens would ‘flake’ (delaminate) in acid, whereby the outer surface of their epicuticle detached in exceedingly thin layers (barely visible, microns thick) (Figure 21; Plates 14, 15, and 16). Eventually, a large portion of the specimen would disintegrate, but the iron minerals would remain undissolved, coming to rest at the bottom of the experimentation tank. It is possible that this damage was a result of pressure exerted by effervescence within the cuticle as calcite cements dissolved, or from abrasion by bubbles created during effervescence.

Prolonged digestion can also result in an unstable contact between different segments or with the host rock/resin/stub (Plate 12: A, and Plate 13: A-D). A partial or unstable contact can

cause further damage to a specimen if viewed under SEM, and can also introduce contamination into the SEM chamber. A specimen that cannot dissipate its charge will be obscured by bright white charging in the micrographs. In the most extreme cases, the charged segment will heat up, vibrate, and eventually dislodge from its mount, potentially contaminating the SEM chamber. For older SEM units (i.e. JEOL JSM-6100 Scanning Microscope), severely charging specimens can also damage the imaging screen. As such, only a few examples of heavily charging specimens were recorded (Figure 22 and Plate 12: A).

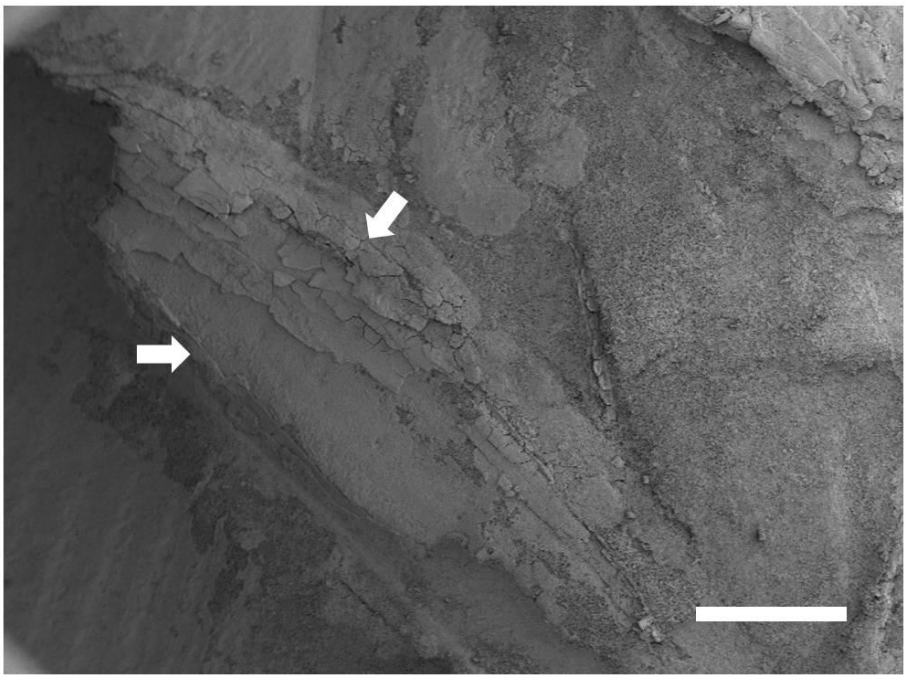


Figure 21. Electron micrograph of delaminating cuticle, highlighted by arrows. NBRL026-05. Scale bar = 1 mm.

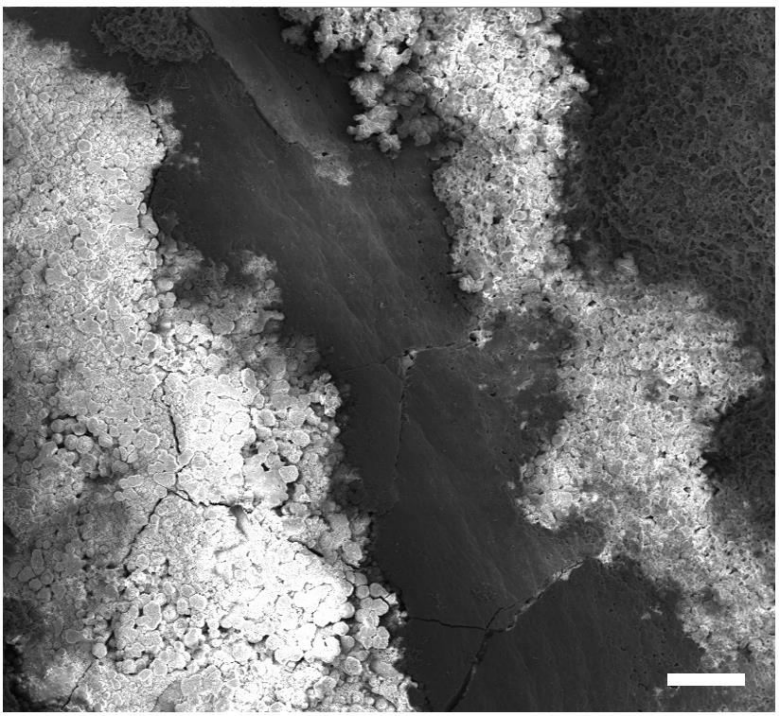


Figure 22. Cuticle unable to dissipate its charge (due to mineralogical fabric), resulting in bright white charging. Specimen NBRL030-12, head. Scale bar = 100 µm.

2. 2. 2. Resin transfer technique

During this project, an adaptation of the 'resin transfer technique' was used (Kühne, 1961; Mayr *et al.,* 2006; Escapa *et al.*, 2010; Graham and Allington-Jones, 2015). The resin transfer technique is used to expose the obscured 'fresh' surface of a fossil, by mounting the already exposed surface into an insoluble resin medium and dissolving away the rock matrix with acid. This reveals the obscured surface of the fossil, while preventing disintegration. This technique was originally developed by Walton (1923) to aid in the study of palaeobotanical specimens and, since then, multiple variations have been adapted (Abbott, 1950; Abbott and Abbott, 1952; Escapa *et al.*, 2010; Larson and Russell, 2014; Graham and Allington-Jones, 2015). However, most of these techniques are used in palaeobotany or the preservation of Messel specimens and are not suitable for this project (Larson and Russell, 2014). The use of thicker polymer resins was first proposed by Cridland and Williams (1966) and, more recently, Escapa *et al*. (2010) proposed adding a second coating to the 'fresh' surface, then exposing the fossil via serial polishing.

Here, a single resin transfer technique was used with two different resins. This technique most closely resembles that of Cridland and Williams (1966), rather than the more recent rendition by Escapa *et al.* (2010). Specimens were typically selected for resin transfer based on high relief, but a damaged or poorly preserved exposed surface. Additional specimens were also selected at random. Initially, a low-viscosity relatively expensive resin was used (Buehler EpoThin Epoxy Resin), however this resulted in several problems. First and foremost was the cost, but the low-viscosity of the resin also allowed it to penetrate past the fossil, masking some of it in an insoluble mix of resin and matrix. The first sample ('Rsn Tst') transferred relatively well, with some masking (Figure 23). Although the extent of masking was moderate, fragile cuticular structures were revealed and so the methodology was not changed. After several other successful tests, approximately 20 specimens were resin transferred at the same time. However, many of these were less successful, and were damaged or destroyed by masking, with the worst cases being NBRL020, 023, 038, and 044, of which NBRL044 is the most extreme example (Figure 24). The extent to which a fossil was damaged in this manner was dependant on the matrix cementation and weathering (matrix porosity), and the three-dimensionality of the fossil itself.

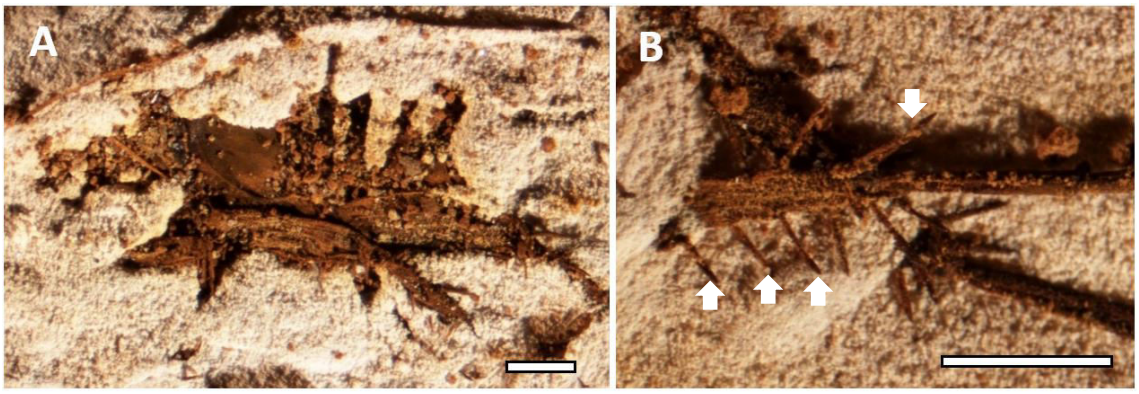


Figure 23. Partial resin masking. A, Resin test specimen (Blattodea) with resin-sediment mix masking head, portion of abdomen, and dorsal thorax. B, Fragile cuticular spines preserved intact and perpendicular to bedding on limbs, highlighted by arrows. A, Rsn Tst-04; B, Rsn Tst-08. Scale bars = 1 mm.

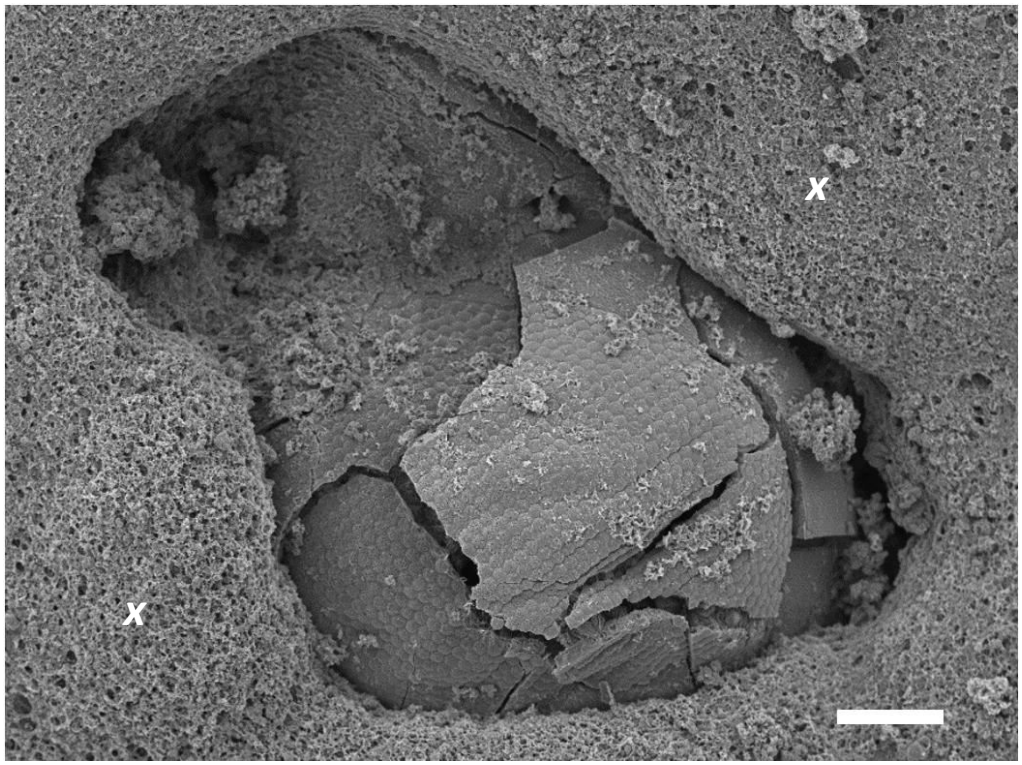


Figure 24. Left eye of specimen NBRL044 (Orthoptera: Elcanidae), showing the extent of resin masking. This eye and the cuticle surrounding it is the only unmasked portion of the specimen. *X*, Insoluble resin-matrix mix. Specimen NBRL044-01. Scale bar = 200 µm.

To combat this problem, a more viscous resin that is less likely to penetrate around the fossil, but still secure it, was sourced. Surprisingly, one of the cheapest resins ('Bisphenol A') met these requirements and was sold by a local homeware shop (Wilkinsons). The downside of this resin is that it does not cure as rigidly as EpoThin, and must be cast in thicker blocks to protect the specimen. The revised resin transfer technique is as follows:

- This process was carried out under a fume hood with appropriate protective clothing, as these chemicals are irritants and dangerous to the environment.
- The specimen was first gently washed with acetone and distilled water to remove any grease or dust.
- A 20 mm high plasticine 'wall' was constructed around the fossil, approximately 5 mm away from it, to create a reservoir for the resin (Figure 25: A). Care was taken to ensure an adequate seal around the specimen so that no resin could escape.
- Bisphenol A and its associated hardener, m-xylylenediamine, were mixed in a glass beaker with a ratio of 1:1 for two minutes. This damaged the glass beaker, but the same beaker could be used multiple times (Figure 25: B).
- The specimen was placed in a disposable container on a level surface, and the resin poured carefully over it until the desired thickness (minimum 10 mm) was achieved (Figure 25: C).
- The specimen was left for two days to cure under a fume hood.
- Once cured, the plasticine was removed with dentistry tools (Figure 25: D).
- Excess rock was then carefully removed using a rock saw or shears (Figure 25: E).
- The specimen could then be subject to acid digestion as described in section 2. 2. 1. Again, importantly the acid was not allowed to evaporate, as this would have resulted in masking by crystal growth.
- Specimen numbers were recorded separately until **after** acid digestion, as even permanent marker would dislodge during digestion and contaminate the specimen.

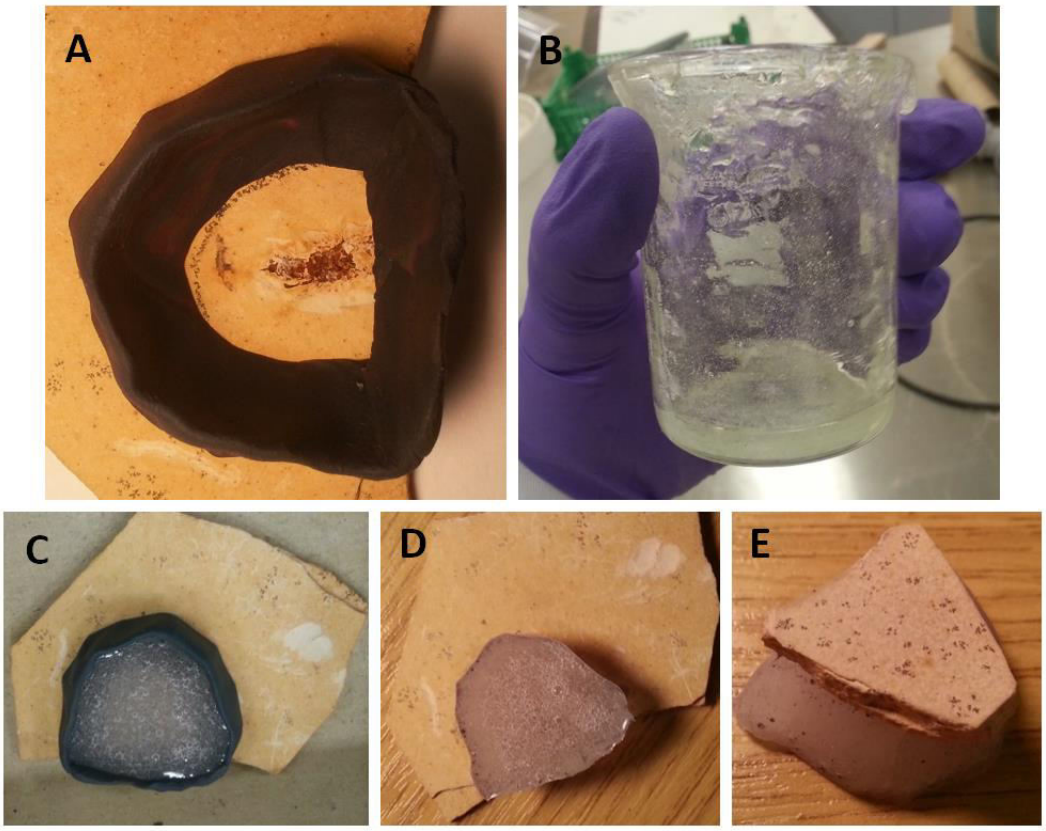


Figure 25. Unnumbered damaged specimen used as an example of resin transfer. A, Specimen surrounded by plasticine reservoir. Right edge is close to fossil due to fracture through sample. B, Damage caused to glass beaker by resin. C, Plasticine reservoir filled with resin over specimen. D, Plasticine cleared from the specimen, leaving only cured resin over the fossil. E, Excess rock removed, leaving specimen ready for acid digestion.

Although this technique may reveal a wealth of additional information, it is not without risk. This technique is irreversible and any fossil must be carefully selected and an extensive record of currently exposed material kept. Fossils that are particularly important (e.g. type specimens) should be avoided, as there is a reasonable chance they will be destroyed. Additionally, there is always the present danger that the specimen may not reveal any detail on its other surface, that the resin will penetrate past the specimen, or that an insoluble micro-nodule or 'halo' may conceal the specimen. Finally, there are questions as to the longevity of transferred specimens and it has been suggested that the resin will degrade over time, preventing future scientists from studying them (Meurgues, 1982). Nevertheless, when the transfer is successful, it frequently reveals fossil material with clarity that would have otherwise remained obscured.

2. 2. 3. Thin sections

Specimens for thin sectioning were cut into rectangular cuboids to fit on a typical microscope glass slide (75 x 26 mm). The standard methodology for creating petrographic thin sections

was followed (Shelley, 1985). Specimens were viewed in both plane polarised and cross polarised light.

2. 2. 4. SEM stub preparation

Specimens were selected for SEM imaging based on preliminary analysis under a light microscope after digestion/transfer. If fine structures or well-preserved cuticle could be seen, the specimen would be prepared for SEM viewing. In some cases, specimens would appear well preserved under light microscopy, but have very low fidelity at the micron scale, or vice versa. As such, some specimens were prepared for SEM viewing regardless of their apparent fidelity. Selected specimens were mounted on a variety of steel stubs using a combination of black carbon pads and carbon cement (conductive carbon cement Leit-C). Stub sizes varied between 12.5 mm, 25 mm, and 32 mm in diameter, with the majority of specimens mounted on 25 mm stubs. Specimens were orientated so that their upper surface was as level as possible, to prevent unnecessary charging or 'shadowing'. Gaps or arches between the specimen and the stub were infilled with carbon cement. Conductive 'bridges' were added, consisting of carbon cement connecting the stub to the upper surface of the specimen, allowing for large specimens to be viewed without excessive coating. The carbon cement was cured in a desiccator overnight. The specimens received a final clean with a soft squeeze blower and acetone before sputter coating to remove any grease or dust acquired during handling.

Most specimens were coated with a gold-palladium alloy in a Quorum Q150RES Sputter Coater, and the rest were carbon coated in a Polaron Equipment Ltd. E5000 SEM Coating Unit (listed in Table 1). Specimens were usually double coated as requested by the operating technicians, resulting in a ~10 nm thick coat. This double coating was part of a non-negotiable agreement to use the JEOL JSM-6060LV Scanning Electron Microscope (Biology Department), as a variable pressure environmental SEM was not available in the initial stages of this project. However, towards the end of this project, one did become available and specimens were examined after a light carbon coating (discussed further below in section 2. 3. 1.).

2. 2. 5. SEM contamination

Contamination is an ever-present issue in SEM analysis. It can create artefacts, obscure important structures, make a specimen look messy (implying poor execution of techniques), and ultimately may lead to false conclusions. Aside from contamination caused by improper storage, specimens can also be contaminated during handling or preparation. With over 160 specimens handled in this project, the majority of which were analysed under a scanning electron microscope, improperly stored prior to acquisition, and prepared in a geochemical

laboratory shared with undergraduates, contamination was inevitable. Figure 26 below provides some examples of contamination that can prove problematic, and Figure 19 above also provides an example of the most extreme contamination.

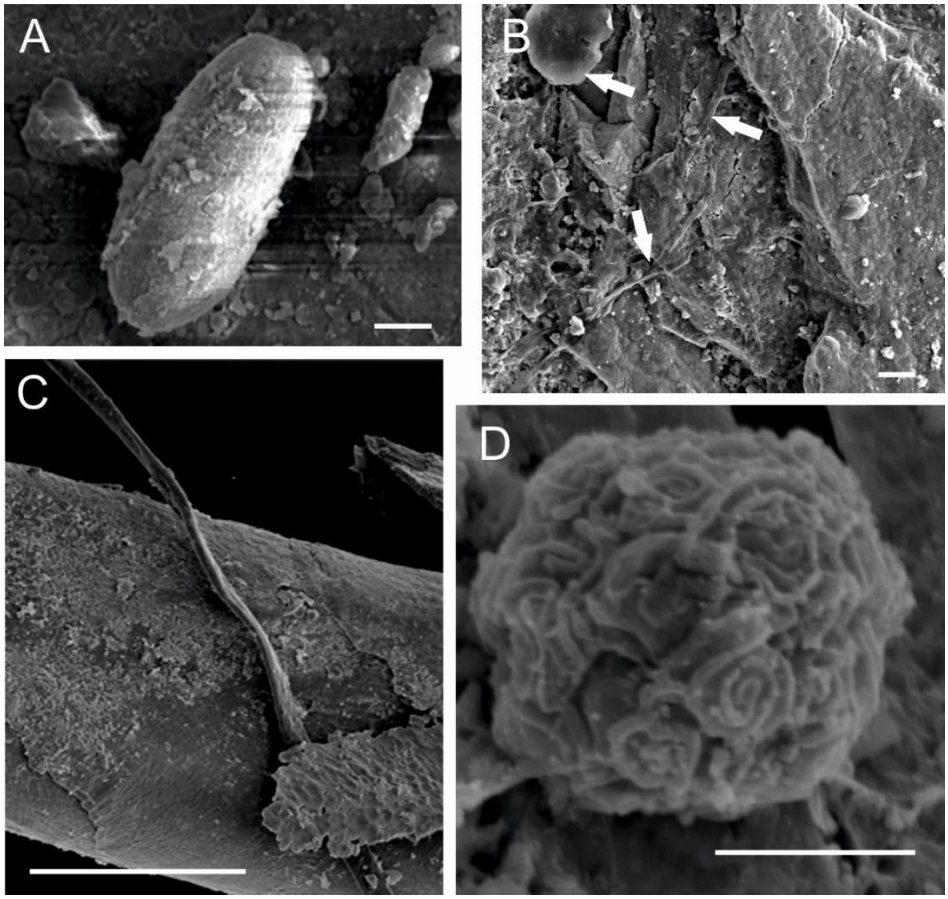


Figure 26. Examples of different contamination encountered in this project. A, Bacillus-like (non-bacterial?) object contaminating specimen. B, Arrows highlight traces of fungal hyphae or bacterial filaments. C, A piece of lint contaminates the disarticulated ovipositor of *Parviformosus wohlrabeae* on the acid residue stub. It has abraded the fragile cuticle, highlighted by arrow, causing it to 'flake away'. D, Modern fungal contaminant, unusually unimploded under vacuum. A, NBRL071-14; B, NBRL057-17; C JW614-020(resi); D, FLO13-25. A, Scale bar = 5 µm. B and D, Scale bars = 10 µm. C, Scale bar = 100 µm.

2. 3. Analyses

2. 3. 1. Scanning electron microscopy (SEM)

A combination of three SEM units were used during this project. The majority of imaging was carried out on a JEOL JSM-6100 Scanning Microscope (within SEES). Further images were also captured on a JEOL JSM-6060LV Scanning Electron Microscope (within the Biology Department) when the SEES SEM was pre-booked or under maintenance. Later (in 2017), several specimens were also viewed with a more advanced EVOMA10 Zeiss Scanning Electron

Microscope with a variable pressure environmental chamber (replacing the JEOL JSM-6100 Scanning Microscope in SEES).

Over 3,500 SEM images were captured. Typically, the first five-to-six images 'mapped out' the specimen, providing a sense of overall preservation and allowing points of interest to be identified. Additionally, if a particularly important or interesting structure was noted, a series of images of increasing magnification towards it were also captured. Images were saved with file names that denoted the specimen number, image number, and a brief summary of the position or structure visible.

Working distances varied between 11 mm and 32 mm, depending on the fragility of the specimen. Due to the extremely high relief of some specimens (up to 5mm), most specimens were studied at approximately 13 mm working distance, as per the recommendation of SEM technicians.

A broad range of voltages (8 – 20 kV) were used in this project, depending on the fragility of the specimen and how effectively it dissipated charge. Only the most durable specimens could be examined at 20 kV, and this was rarely used. Most specimens were examined between 12 kV and 16 kV, and only the most fragile specimens were examined under 10 kV. For most specimens, the spot size (probe diameter) was kept at the default 60 nm.

The analyses undertaken on the EVOMA10 Zeiss SEM were carried out at voltages between 10 – 20 kV. Working distances varied between 11 – 13 mm. I Probe currents varied between 5 pA and 200 pA. These variations allowed for images of uncoated specimens to be captured at high magnifications (up to 85,000 ×). Only newly acquired fossils (to compare other Lagerstätten, discussed in Chapter 4. 1.) were examined uncoated.

Specimens were examined at a range of magnifications. The maximum magnification imaged during this project was 85,500 × magnification, although most sites of interest were easily visible between 1,600 × and 4,000 × magnification.

2. 3. 2. Energy dispersive X-ray (EDX) analysis

Energy dispersive X-ray analysis (EDX) was used in this project to determine the elemental composition of the Nova Olinda Member fossils, their surrounding sediment, and other structures within the sediment (e.g. coprolites). During energy dispersive X-ray analysis, a sample is bombarded by a focused beam of electrons. This excites the bombarded atoms, resulting in the ejection of low-energy shell electrons (Goldstein *et al*., 2007). As an electron from a higher energy shell moves into the lower energy shell of the ejected electron, it releases energy in the form of an X-ray. Each element produces a characteristic X-ray

spectrum, which is treated as photons with specific energies, allowing for localised chemical analysis when detected (Goldstein *et al*., 2007). Analyses can be located on a single 'spot', focusing on one location on the specimen, or the beam can be scanned in a television-like raster, resulting in an elemental distribution 'map' (CFAMM, 2018).

The precision of this technique is limited by statistical error during photon counting (Goldstein *et al*., 2007), and overall accuracy is commonly ± 2% (CFAMM, 2018). Additionally, the resolution of chemical analysis is controlled by beam penetration, which is in turn controlled by beam strength (keV) and sample density. Standard operating energies (20 keV) analysing an 'average' density silicate sample (~ 3 g per cm^3) results in an analysis 'dept' (resolution) of about 2 µm into the sample (CFAMM, 2018).

In addition to statistical errors and low analysis resolution, care must be taken to exclude 'background' readings. 'Background' is a result of the bombarding electrons also producing their own continuous X-ray spectrum. This results in non-present elements being detected in small amounts. 'Background' can be compensated for by long counting times (ideally approximately 20,000 counts) (CFAMM, 2018).

2. 3. 2. 1. Limitations of Energy dispersive X-ray (EDX) analysis in this project

To achieve the best results, specimens should be polished to a flat surface (CFAMM, 2018). In this project, fragile fossil specimens were analysed that could not be polished without obliterating cuticular surface details. Consequently, there is some inherent error due to topographical variations of the samples analysed. Additionally, several analyses were undertaken under strict time constraints, resulting in low counts, and so some samples identify trace elements that are likely part of the 'background'.

Acceleration voltage should, ideally, not be less than half of the highest excitation energy of any elements present (CFAMM, 2018). Iron was the element with the highest excitation energy in the Nova Olinda Member fossils (7.11 keV), and so the acceleration voltage should not have been lower than 14.22 keV (CFAMM, 2018). Some of the fragile fossil material analysed could not withstand high voltage electron bombardment without risking damage, and so some analyses were undertaken at lower than optimal voltages, with some as low as 10 keV. Although this resulted in inadequate intensities and less reliable analyses, it was requested by University of Portsmouth technical staff.

Initially, a JEOL JSM-6060LV Scanning Electron Microscope (Biology Department) with an OXFORD Instruments X-Max EDX attachment was used for EDX analysis. This equipment provided elemental maps of three specimens: FLO15, NBRL011, and NBSED01(a). Later in this

project (in 2017), further specimens were analysed with new EDX equipment. An EVOMA10 Zeiss Scanning Electron Microscope with an Oxford Instruments X-MAX80 EDX attachment was used to provide pin-point and scan analyses. From these analyses, seventeen EDX plates were created (EDX Plates 1-17).

To use the electron equipment in the Biology Department, specimens were required to be double sputter coated and specimens FLO15, NBRL011, and NBSED01(a) were coated with a gold-palladium alloy. This coating allowed for high-magnification images to be captured, but impacted EDX analyses. When plotted on a spectrograph, some peaks for gold alloys overlap with other elements (e.g. rubidium and sulphur), making them difficult to discern (Newbury, 2009). It is possible that these elements are more abundant in these samples than observed in this project.

The later analysis of specimen HT001 was attempted without sputter coating, but no clear images could be resolved at high magnification. Consequently, it was sputter coated with carbon, resulting in carbon being precluded from the EDX analyses of this specimen. Other analyses excluded carbon due to the use of a carbon filament.

2. 3. 3. X-ray diffraction (XRD)

To confirm the exact mineralogy of replacement for both ‘weathered’ and ‘unweathered’ phases, two samples (NBNEW01 and HT001 respectively) were subject to X-ray diffraction (XRD) in a PANalytical X’PERT-3 diffractometer. Samples of cuticle were taken from each specimen, ground to a powder, homogenized, randomly orientated on a glass slide, packed into a sample container, and irradiated with X-rays (Klug and Alexander, 1974). This resulted in constructive interference, which, when Bragg’s Law was met, could be plotted on a X-T intensity plot diffractogram (Klug and Alexander, 1974). This diffractogram was then compared against a database of standard reference patterns, allowing for mineral identifications. Any mineralogies that make up less than two percent of the sample were not detected (Klug and Alexander, 1974). Technical settings, including scan axis, step size, scan time, scanning type, anode material, etc. are available in the appendices (Appendix 8. 6.).

X-ray diffraction was also attempted for clay minerals in a weathered Nova Olinda Member sample (offcuts of specimen NBNEW01). Although clay minerals have been observed concentrated in bacillus-like structures within the sediment (Figures 9 and 10 in Chapter 1), X-ray diffraction analysis could not detect any clays. The sample was repeatedly treated to separate clays, including acid dissolution of the calcium carbonate sediment, centrifugal separation, and orientation on a glass slide to increase basal reflection. However, it appears that they are present in quantities too small to detect. As such, given the depositional

environment, lack of clays in the surrounding sediment, proposed feeding-strategy of *Dastilbe*, and the platy/blade-like nature of the clays, it is likely that they are detrital. EDX Plate 14 (and Figure 10) also confirmed that they consist of Al, K, and Si, suggesting that they may be illite.

2. 3. 4. Transmission electron microscopy (TEM)

The use of transmission electron microscopy (TEM) to reveal the nanometre-scale structure of individual crystals within the Nova Olinda Member fossils was discussed for this project. Professor Simon Cragg, a researcher in the biology department and principle operator of the TEM, refused its use for this project. This was due to the TEM being configured for biological samples, rather than geological samples and the hard-preserving minerals would have damaged its fragile glass cutting blades.

2. 3. 5. Thin section analysis

As discussed above (in section 2. 2. 3.), two specimens (NBRL017 and NBSED02) were selected for thin sectioning with the aims of identifying the mineralogical fabric of the sediment, mineral infills, determining the differences between light and dark laminae, and highlighting the effect of an insect carcass on the surrounding sediment. Specimens were viewed under plane polarised light and cross polarised light. Images were captured using a Nikon DS-Fi1 camera with a Nikon Digital Sight attachment, attached to a MP3502B Petrographic Microscope. Much like the SEM analyses, image file names were saved as the specimen number, image number, and additional information about the examined site.

2. 3. 6. Chemical staining

As some of the matrix crystal morphologies were suggestive of dolomite (EDX Plates 11 and 12; Plates 1 and 5), two specimens (offcuts of NBRL017 and NBRL011) were stained with alizarin red solution to determine their calcium carbonate verses dolomite content (Hobbs, 1954; Evamy, 1963). Before staining, specimens were cleaned with distilled water, then acid etched for ten seconds with 1.5% hydrochloric acid. Finally, the specimens were stained with alizarin red solution for two minutes, producing high-intensity red stains, indicating a 99% calcium carbonate content and little-to-no dolomite (Figure 5 in Chapter 1).

2. 3. 7. Tests for ferromagnetism

To assist in identifying the mineralogy of the unweathered matrix, ferromagnetic separation was undertaken. Offcuts from specimen NBSED01 were cut into 1 cm^3 blocks with a rock saw, then crushed into a fine powder with a rock crusher and tungsten carbide micro-balls. Tungsten carbide is an extremely hard (91 HRA), wear resistant, stiff (a Young Modulus of Elasticity of 98,000,000 pounds per square inch), inert, non-magnetic, and temperature-

resistant (consistent performance up to 427°C) material that is useful as an abrading agent in geological studies (Cardarelli, 2008). The powder was then passed through a magnetic separator.

2. 3. 8. Statistical analyses

2. 3. 8. 1. Taphonomic index

In addition to the specimen numbers and taxonomic identifications, a series of taphonomic characters were also recorded for each specimen (Tables 8a-c in Appendices 8. 7.). The purpose of these was to create a taphonomic dataset, which could be subject to statistical analyses (discussed below in sections 2. 3. 8. 2. and 2. 3. 8. 3.) or from which a taphonomic index could be derived. This taphonomic index represents an average score of taphonomic characters for each specimen and allows for a quick approximate comparison between specimens. The indices could also be compared against taxonomy, ecology, flight strength, trophic level, etc., and allow for taphonomic trends to be identified.

Taphonomic measurements are divided into two categories, based on the type of data collected:

- 'Completeness characters' are characters measuring the presence or absence of tissues. Most of these are divided into percentage ranges of tissues present (0%, 1-24%, 25-49%, etc. (interval answer options)). However, soft tissues are often difficult to discern and so they are measured in simpler categories (well preserved, moderately preserved, poorly preserved, none present (ordinal answer options)).
- 'Non-Completeness characters' measure other aspects of the fossil that relate to its fidelity of preservation. These include whether fragile protruding micro-structures (such as setae) are preserved erect or pressed flat against the fossil (or preserved at all), if cavities are infilled, hollow, or crushed, the highest relief of the specimen, and how extensively each segment is fractured/broken. All 'non-completeness characters' have ordinal answer options (i.e. high/moderate/low).

Only fossils that had not been destroyed or heavily damaged by the resin transfer technique were included, resulting in a total of 64 specimens analysed.

The data are presented in Table 8a, with two additional tables separating completeness (Table 8b) and non-completeness taphonomic characters (Table 8c) (all available in Appendices 8. 7.). The scores for these characters were then normalised, by assigning each answer a value between 0 and 1, depending on how many possible answers there were (i.e. 'none, patchy, extensive' became '0 / 0.5 / 1'). An average was then taken from these normalised characters,

giving the taphonomic index value. This value represents the 'average' preservation of the specimen. The majority of characters measured completeness and only characters that could be observed were included in the calculation of the taphonomic index.

2. 3. 8. 2. Cluster analyses

The data matrix used to generate the taphonomic indices presented above were also subject to several explorative cluster analyses using the software 'PAST' (Hammer and Harper, 2006). Cluster analyses organise specimens into groups based on similarities between their measured characters. The purpose of these analyses is to detect relationships within the data, and cluster specimens accordingly. These clusters could then be compared against taxonomy. Clusters of the same insect family could imply a taphonomic trend within that family, which could then be compared further against their ecology or morphology.

Specimens that had not been coded into the matrices were excluded from the cluster analyses, resulting in a total of 64 specimens analysed. Analyses were undertaken for Table 8a (all taphonomic characters) and Table 8b (completeness characters only). Table 8c (non-completeness characters) was not subject to cluster analyses, as the data relied entirely on simpler ordinal groups, and would have resulted in less robust analyses.

Although the characters analysed were normalised into values between 0 and 1 (as explained above), this was done for the index calculation and not specifically for the cluster analyses. The assigned value is arbitrary, as the data includes ordinal and interval characters. Consequently, the most appropriate algorithm for non-binary ordinal datasets is Paired Grouping (UPGMA) with a Gower similarity index (Hammer and Harper, 2006). However, as the data also include interval characters (and therefore does not correspond to text-book examples for Gower similarity), the 'default' Euclidean similarity index was also undertaken for comparison (Hammer and Harper, 2006).

In addition to the standard R-mode cluster analyses described above, the dataset was also transposed and subject to Q-mode cluster analyses. These investigate the relationship between characters, and produce clusters based on the co-occurrence of characters (e.g. Cullen and Evans, 2016). As some of the characters were only observable in a few specimens, the datamatrix was ill conditioned, resulting in pairs of rows with no common known values, and ultimately the failure of the Q-mode cluster analyses. This was overcome by removing a single abdominal character row that was present only in three specimens: "Other:_____" abdominal segment. This character was added initially to include various external genital structures (e.g. gonoxocae, gonostyli, parameres, etc.) in the taphonomic index, but the rarity

of these structures resulted in the vast majority being un-coded. As with the R-mode analyses, both Gower and Euclidean similarity indices were used with Paired Grouping (UPGMA).

2. 3. 8. 3. Principle coordinate analyses

As will be discussed later (in Chapter 3. 9. 4.), the cluster analyses yielded weak clusters. To corroborate these, principle coordinate analyses were also undertaken in 'PAST' for both datasets (Hammer and Harper, 2006; Minter pers. comm., 2017). In these analyses, only Gower similarity indexes were used (Hammer and Harper, 2006).

A principal coordinate analysis replaces the 'raw' matrix data with a similarity matrix. This multidimensional data can then be condensed into two dimensions by calculating an Eigenvalue for each sample (Gower, 2005). In practicality, these analyses allow for complex multidimensional data to be visualised as simplistic two-dimensional scatter plots, where clusters can be identified easily (Hammer and Harper, 2006).

Chapter 3. Fidelity of preservation

3. 0. Preface

The methodologies outlined in Chapter 2 allowed for the Nova Olinda Member fossil insects to be analysed, revealing their chemical composition, mineralogical replacement fabrics, original morphology, and artefacts created by decay/curation. These revealed several key minerals (pyrite and its weathering products, apatite, and calcite) preserving insect tissues as internal coatings, direct replacements (impregnations), and cavity infills. In this chapter, the fossilising minerals are identified, their mineral fabrics are described, the preserved insect morphology is demonstrated, and artefacts of decay and curation are suggested. Mineral fabrics and preserved insect morphology are discussed separately to prevent the misinterpretation of mineralogical fabrics as original insect morphology.

3. 1. Barling *et al*. (2015)

This chapter incorporates material from Barling *et al.* (2015), including text, figures, and interpretations. As Barling *et al.* (2015) is a multi-author paper, the approximate percentage contribution from each author is outlined: Nathan Barling (75%), David M. Martill (10%), Sam W. Heads (10%), and Florence Gallien (5%).

In addition to its incorporation here, a copy of Barling *et al.* (2015) is included in the appendices of this thesis (Appendix 8. 2. 2).

3. 2. The range of preservational fidelities

Nova Olinda Member fossil insects are known to be exceptionally well-preserved (Bechly, 1998c; Menon and Martill, 2007; Delgado *et al.*, 2014; Barling *et al*., 2015; Osés *et al*., 2016), however some specimens examined in this project were relatively poorly preserved (fragmentary with micron scale original morphology obliterated by mineralogical textures). Consequently, it is more accurate to describe them as having a range of preservational fidelities (or ‘qualities’). Although the insects are commonly complete (abdomen, thorax, head, appendages, and wings articulated) and often appear to be flattened on the bedding plane surface, they are in fact mostly restricted to a single lamina and may exhibit varying degrees of three-dimensionality within it. Infrequently, some appendages, especially limbs, may lie at a high angle to the plane of bedding (discussed further in section 3. 5. 1. 4.; Figure 48: B and C), perhaps indicating submersion in somewhat soupy substrates (*sensu* Martill, 1997).

The specimens examined here were donated due to their relatively poor preservation when viewed in hand specimen. Consequently, they represent relatively poor-quality examples of the Nova Olinda Member fossil insects, giving the collection a below-average fidelity of preservation. Despite this, a broad range of preservational fidelities (both in hand specimen and under SEM) were identified among the specimens. Before demonstrating the exceptional preservation of these fossils, 'exceptional preservation' itself must first be defined.

3. 2. 1. Definition of exceptional preservation

Fossils are widely considered to be exceptionally preserved if they preserve 'volatile non-mineralizing tissues (soft tissues) that are readily degraded by bacteria' (Allison and Briggs, 1991a,b, 1993). As even heavily sclerotized cuticle can be readily degraded by bacteria (*Chitinophaga*) in optimal conditions, many authors consider all insect fossils to represent exceptional preservation (Martínez-Delclòs and Martinell, 1993; Martínez-Delclòs *et al*., 2004; Smith *et al*., 2006; Lee *et al*., 2007; Zhang *et al*., 2010; Ma *et al*., 2012; McNamara, 2013), which does not allow for clarification between insect fossils of varied preservation. Here, a specimen is considered exceptionally well-preserved if it retains fragile morphological structures (e.g. setae, microtrichium), micron-scale cuticular details (e.g. cuticular scales, ommatidia), discernible internal tissues (e.g. organs, muscle fibres, trachea, etc.), or details at or below the cellular level (cells and cell organelles). Consequently, even a fragment of cuticle would be considered well-preserved under this scheme, so long as it retained at least one of the features listed above.

3. 2. 2. Fragmentary specimens

Many Nova Olinda Member insect fossils appear extremely well-preserved in hand specimen and are often complete with appendages intact. As might be expected from a Konservat Lagerstätte, these specimens often show a remarkable amount of detail preserved at the micron scale. There are, of course, exceptions to this and some specimens that appear complete and well-preserved in hand specimen may reveal little or no morphological detail at the micron-scale. Conversely, many specimens preserved as fragmentary remains or isolated segments retain remarkable micron-scale preservation. This suggests that damage to the Nova Olinda Member insects is a result of *in-vivo* activities (perhaps attributable to predation, intra-species competition, or sexual competition) or post-mortem damage (e.g. decay, abrasion, or scavenging) prior to burial, rather than incomplete fossilisation or diagenetic alteration. Consequently, fragmentary specimens analysed here are considered to reflect the taphonomic state of the specimen upon arrival at the site of burial.

3. 3. Replacement mineral identifications

The geochemistry of fossil insect preservation in the Nova Olinda Member has been discussed previously by Grimaldi and Maisey (1990), Menon and Martill (2007), Delgado *et al*. (2014), and Osés *et al*. (2016) (see Chapter 1. 10.). These studies report that the Nova Olinda Member insect fossils are primarily preserved in two minerals: goethite (pseudomorphing pyrite), and calcium phosphate (likely francolite, see Martill, 1998), both of which are corroborated here. In addition to these, calcite has also been observed infilling these fossils (Plates 2 - 4). Other rarer replacement minerals are reported (e.g. silica 'halos', Menon and Martill, 2007), but were not observed in this project and so are not investigated.

Goethite replacements appear as an orange-to-brown globular friable material that can be damaged easily by touching the specimen. This style of preservation is encountered in the weathered, buff coloured limestones (Menon and Martill, 2007). In the unweathered (blue/grey) limestones, the fossils are black and more delicate. The goethite specimens are weathered versions of the black (pyrite) fossils, in which the original replacement mineral has been oxidised *in situ* over a prolonged period, perhaps in the last few thousand years (Menon and Martill, 2007).

To corroborate the presence of previously reported preserving minerals and describe their fabrics (and therefore aid in understanding the processes of mineralisation), the fossils are analysed both chemically and texturally in this project. This allowed for the previously presented preservational models (e.g. Osés *et al*., 2016) to be investigated and improved upon. Below, mineralogical/chemical analyses are presented, followed by descriptions of mineralogical textures. Later in section 3. 5., examples of exceptionally preserved insect tissues are presented, followed by fabrics that are interpreted as artefacts of decay or curation (sections 3. 6. and 3. 7. respectively). These allow for the mineralogical fabrics described here to be discussed without misinterpretation of insect morphology and artefacts.

Various techniques were implemented to identify minerals in not only the Nova Olinda Member insect fossils, but also the surrounding matrix and structures within it. As several of these are constituted of the same minerals as the fossils, the results are presented below separated by technique, rather than by minerals detected.

3. 3. 1. Thin section results

Specimen NBRL017 (Orthoptera) was sectioned through the fossil with the aim of identifying fossil infills and the effect of the fossil on the surrounding sediment. Light microscopy revealed infills with a birefringence typical of calcite (Plate 2: A-B and Plate 6), with most of the cavity infilled by relatively large crystals (sparry calcite cement) (Plate 2: B). Specimen NBRL017 also revealed minor 'soft' sediment deformation around the fossils (Plate 6: A-B), along with 'leaching' of iron

minerals into the surrounding sediment, indicated by diffuse boundaries between rusty-brown fossil material and the pale cream sediment (Plate 6). In some cases, this boundary is sharp and indicates where cements inhibited the diffusion of iron minerals further into the sediment.

Specimen NBSED02 was sectioned, allowing for more aspects of the sedimentology of the Nova Olinda Member to be viewed without the influence of insect body fossils (Plates 7, 9, and 11). Nevertheless, two elliptical structures (probably mineralised EPS or ostracods) were discovered within the sediment. In addition, a vast abundance of spherical microfossils were present throughout the sediment (Figure 8; Plate 7: A-D), forming long chains (Plate 7: B) and rarely preserving evidence of mitosis (Plate 7: D). Numerous *Dastilbe* coprolites were also present, containing a mix of globular goethite, spherical microfossils, and blades of clay (Plate 9).

3. 3. 2. Specimen staining

All sedimentological specimens that were stained with alizarin red solution reacted rapidly, resulting in a deep pink-to-red stain. This is strongly indicative of a > 99% calcium carbonate content and an absence of dolomite (see Figure 5 in Chapter 1).

3. 3. 3. Magnetic Testing

Offcuts from specimen NBSED01 (unweathered) were prepared for magnetic separation. During the separation, attention was paid to the black material (iron sulphide phases), as the pale cream powder represented the calcium carbonate matrix. Both magnetic and non-magnetic black material was detected, indicating a mixture of iron mineral phases, and therefore a more complex geochemistry than previously suggested (Grimaldi and Maisey, 1990; Menon and Martill, 2007; Delgado *et al*., 2014; Osés *et al*., 2016).

Although goethite is known to have some magnetic properties (Barthelmy, 2015b), it can be omitted for several key reasons. Firstly, the magnetic mineral was black, rather than the rusty brown of goethite. More importantly however, goethite is non-magnetic unless heated to 120°C in the presence of a magnetic field (thermoremanent magnetization) (Strangway *et al*., 1968) and the Santana Group is estimated to have reached temperatures of only 100°C prior to weathering (Neto *et al*., 2013). Consequently, the magnetic material could represent greigite (the sulphide analogue to magnetite) or a weakly magnetic form of mackinawite (Rickard, 1974; Kwon *et al*., 2011). The non-magnetic material represents pyrite (explained below).

3. 3. 4. Energy dispersive X-ray spectroscopic analysis (EDX)

Energy dispersive X-ray analyses (EDX) were undertaken to determine the elemental composition of both weathered and unweathered Nova Olinda Member insect fossils, as well as the surrounding matrix. Both pinpoint analyses and elemental maps were implemented. EDX results

are presented across 17 plates (EDX Plates 1-17). Both pinpoint and mapping spectra provide elemental readings of not only the surface elements, but also elements several microns below it. Additionally, due to the use of a carbon filament (and a light carbon coating), carbon has been omitted from several spectra. Elements marked in red had a 1σ error of > 10%, and are less reliable identifications.

EDX Plates 1 and 2 provide an elemental map of a 'weathered' Nova Olinda Member insect fossil, demonstrating Fe and O mineral replacement (goethite) and a stark contrast between the preserving minerals and surrounding Ca- and O-rich (calcium carbonate) sediment (Figure 27; Plates 1 and EDX Plate 2).

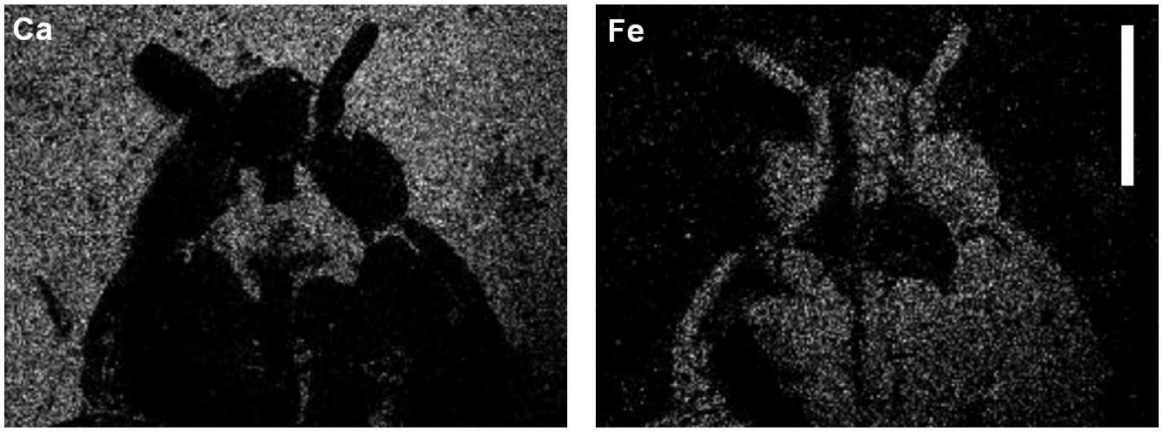


Figure 27. Contrast in elemental composition of Ca and Fe between fossil insect tissues and the sediment in the Nova Olinda Member. Specimen FLO15. Scale bar = 1 mm.

A further EDX map was also captured of an 'unweathered' specimen (EDX Plate 3), highlighting Fe and S (pyrite) as the primary elements preserving cuticle as well as Ca, P, and O (apatite) preserving some internal soft tissues (EDX Plate 3). This analysis also detected an abundance of Sb in the matrix. Sb (Antimony) is known to precipitate with calcium carbonate from copper-containing sulfuric acid solutions, usually during industrial copper purification via electrolysis, but can also occur in nature (Omarov *et al*., 2016). However, Ca is known to be misidentified as Sb by automated elemental spectroscopic software due to their similar peak energies (Calcium Kα 3.690; Antimony Lα 3.604) and, given that no other analyses have detected Sb in the Nova Olinda Member, this is very likely the case here (Newbury, 2009). Further pinpoint analyses of unweathered fossil insect cuticle revealed an assortment of elements (Ca, O, P, S, Fe, Mg), which represent several key diagenetic minerals, including some that may be a result of 'minor weathering' (i.e. gypsum). EDX Plate 4 provides five-point spectra of unweathered wing cuticle. Spectra 8 and 9 were generated from the surrounding matrix, revealing abundant Ca, O, rarer Fe and S, and traces of Si, Mg, and Al. Spectra located on the wing cuticle are dominated by O, S, and Fe, with traces of Mg, Si, P, and Pd (Spectra 5, 6, and 12).

EDX Plate 5 provides three spectra generated from relatively unweathered (i.e. retains pyrite, lacks goethite) insect cuticle (thorax/abdomen) and exposed internally preserved structures. All three spectra reveal Ca, O, S, and Fe at varying levels depending on location, as well as traces of P, Mg, and N. Spectrum 11 reveals a small amount of Fe, despite being located on insect cuticle.

EDX Plate 6 also provides three spectra of unweathered insect body cuticle, focussed on an area of high relief. This area of cuticle is coated in disorganised anhedral grains (Figure 28: A). Spectra of smoother portions of cuticle reveal abundant Fe, O, and S. Spectra that are positioned on the anhedral grains reveal O, S, and Ca (suggesting gypsum).

EDX Plate 7 is the highest magnification analysis of unweathered insect cuticle and provides four spectra. The spectra are located on relatively smooth insect cuticle, or on fragments of disarticulated internal tissues (preserved as amalgamated and intergrown tubular grains, Figure 28: B). Spectra of smooth cuticle reveal a Fe-poor composition, dominated by O and S. The disarticulated fragments of internal preservation are composed of O, Ca, and S, with rare Mg.

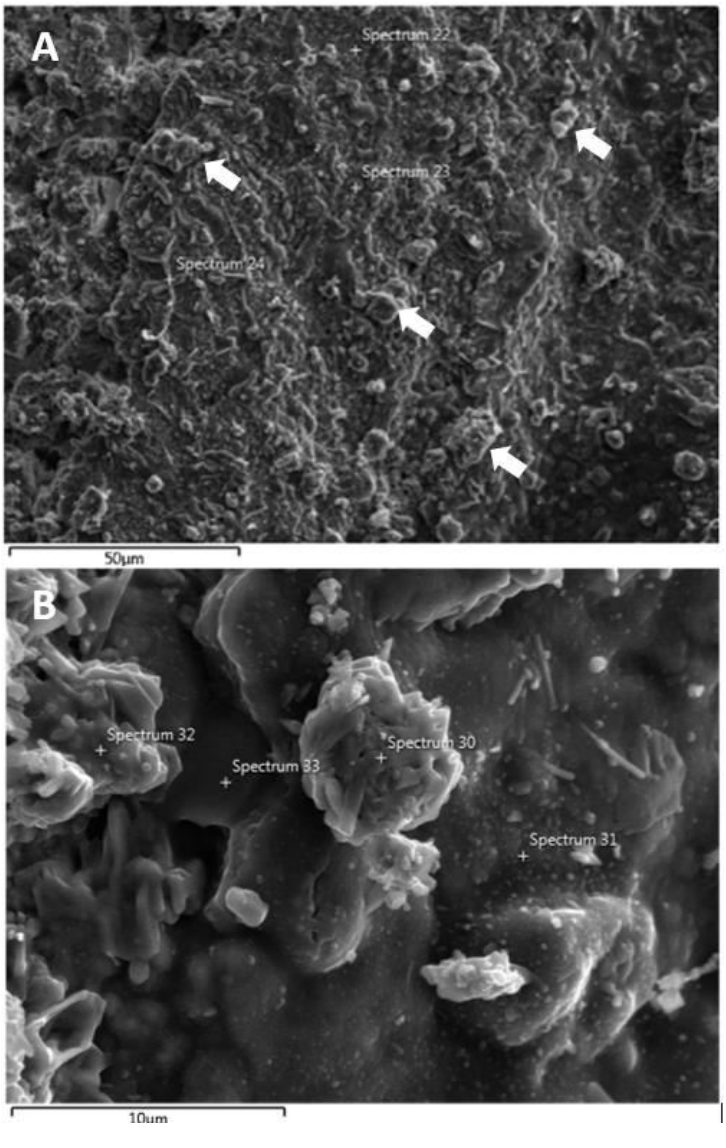


Figure 28. A, Scanning electron micrograph from EDX Plate 6. Arrows highlight disorganised anhedral grains. B, Scanning electron micrograph from EDX Plate 7 displaying relatively smooth insect cuticle (spectra 31 and 33) and fragments of disarticulated grains of internally preserved tissue (spectra 30 and 32). Specimen HT001. A, Scale bar = 50 µm. B, Scale bar = 10 µm.

Specimen HT001, the 'unweathered' fossil insect used in these EDX analyses, frequently displayed needle-like crystals protruding from gaps in otherwise globular cuticle (Figure 29). EDX Plate 8 provides five spectra of these needle-like crystals and the surrounding cuticle. They are composed of O,

S, and Ca. The surrounding cuticle is composed of abundant O, S, and, to a lesser extent, Ca, as well as traces of Fe.

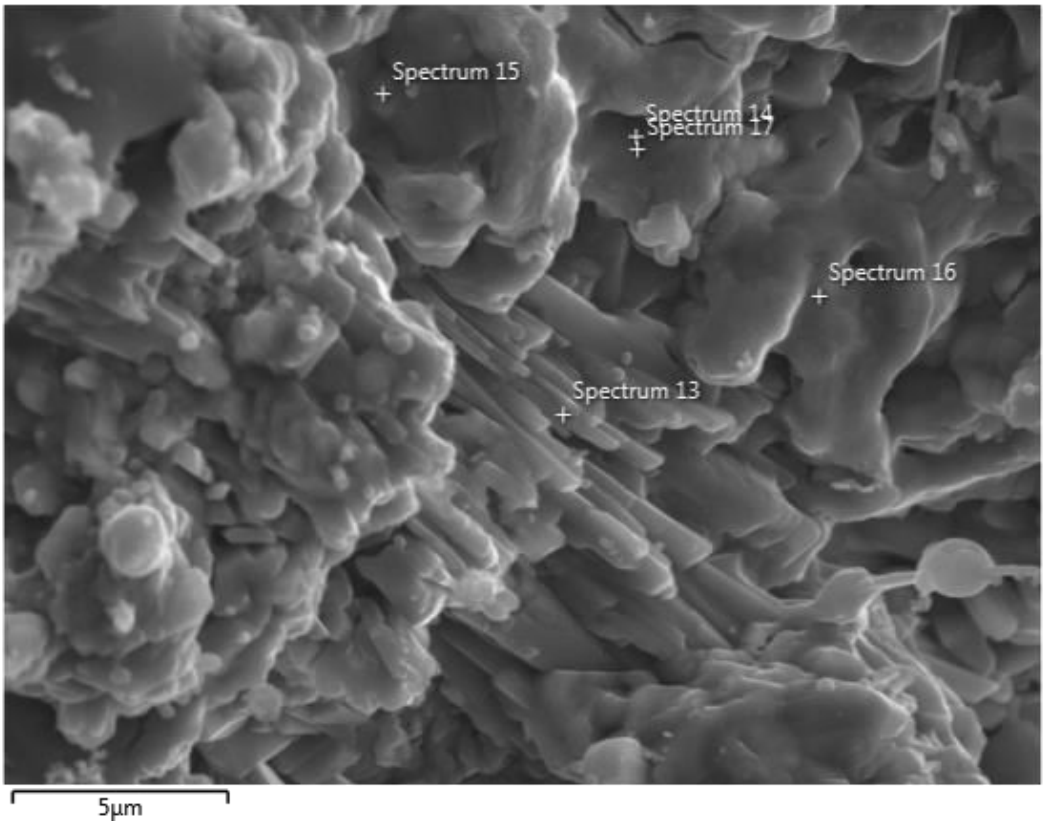


Figure 29. Needle-like crystals, likely gypsum, protruding from unweathered insect cuticle. Spectrum 13 is located on the crystals. Specimen HT001. Scale bar = 5 µm.

Two further analyses were undertaken on a weathered insect specimen. Specimen FLO19 was subject to point EDX analyses, focusing on infilling minerals and the preservation of fibrous material. This specimen was heavily Au sputter-coated, and so Au was detected in abundance in all analyses. Carbon was also excluded. EDX Plate 9 analysed the exposed internal contents of the forelimb. Spectra 1 and 8 revealed that the mineral infills are composed of Ca and O, indicating that they are calcite. Spectra 2 and 4 corroborated reports of Fe and O (the iron oxyhydroxide mineral goethite) preserving cuticle. Spectra 6 and 7 also corroborated the presence of Ca, O, and P, indicating that the fibrous soft-tissues are preserved in calcium phosphate. The presence of P was partially masked by the high Au coating peak, and so it may be more abundant than detected (Gold M 2.120; Phosphorous Kα 2.013) (Newbury, 2009).

EDX Plate 10 analysed the exposed internal genitals (ovaries) of specimen FLO19. The results of this analysis were very similar to EDX Plate 9, with spectra 28 and 29 revealing the mineral infill as calcite, and spectra 32, 34, and 35 also revealing cuticle preservation in goethite. The fibrous soft tissues were not observed to contain P in spectra 30, 31, 33, and 38. However, as noted above, the abundance of a thick Au-Pd coating may be masking the presence of P. In spectrum 30, the large Au peak that may mask the presence of P is highlighted by an arrow. Two spectra (36 and

37) were located on a granular area that preserved fragments of fibrous tissue over a mineral infill. These spectra revealed an abundance of Fe, O, and Ca, as well as trace Si. Again, the presence of P in these spectra was likely masked by abundant Au. All of these analyses were undertaken at optimal settings (Kv = 20, WD = 14.5 mm, I Probe = 200 pA) (CFAMM, 2018).

EDX Plate 11 and 12 provide an elemental map of etched sediment and a single etched calcite rhombohedron from the Nova Olinda Member respectively. Elemental maps reveal an abundance of Ca, O, and C, as well as rarer Fe, Mg, Cl, and Sr. The presence of Cl and Sr is dispersed evenly across the sediment samples in minute amounts, indicating that these are background readings. Peaks for S may have been masked due to an Au-Pd sputter coating.

In addition to examining the elemental composition of the sediment, non-sedimentological structures within the sediment were also analysed. EDX Plate 13 examines a *Dastilbe* coprolite in cross section perpendicular to bedding, revealing not only the distribution of elements within it, but also highlighting its three-dimensionality. The coprolite is composed of Fe, O, Si, Al, Mg, and Cl. The Fe and O are distributed throughout the coprolite in globular grains, whereas Si, Al, and Mg are restricted to blade-like clays. The presence of Cl is likely a background reading. As with EDX Plate 11 and 12, S could not be detected due to an Au-Pd sputter coating.

Associated with one of the coprolites was a particularly large (> 100 µm) aggregate of clay minerals. This aggregate was elementally mapped (EDX Plate 14), revealing Al, Si, K, and rarer Mg. Small clusters of Fe are present as discrete grains around the clays.

The final series of EDX analyses were of unweathered sediment (EDX Plates 15-17). The purpose of these was to map the elemental composition of the unweathered sediment, as well as the unweathered microfossils within it. In EDX Plates 15 and 16, calcium carbonate rhombohedra were not easily discernible. Instead, the matrix consisted of disordered anhedral grains. Despite this, they still mapped as Ca, O, and C, indicating that they too are calcium carbonate. Small amounts of Si were also detected within the sediment as distinct grains, presumably quartz sand or silt. Spherical microfossils were mapped as containing abundant Fe and S across all three analyses (EDX Plates 15-17). Despite the Au-Pd sputter coating, large S peaks were detected and restricted to the spherical microfossils. As such, despite the potential for masking from the sputter coating, it is reasonable to conclude that these microfossils are preserved in an iron sulphide (pyrite).

3. 3. 5. X-ray diffraction (XRD)

Two specimens were analysed with XRD, one (HT001) containing ‘unweathered’ cuticle and the other (NBNEW01) with weathered cuticle. For both samples, a diffractogram (intensity plot) was generated and compared against a database of standard reference patterns (Figures 30 and 32). A

table of corresponding minerals is given, along with their standard intensity patterns (Tables 2 and 3; Figures 31 and 33). The intensity of each diffraction was relatively low (< 2000 counts) due to the extremely small sample size. This does not directly alter mineral identifications as the intensities of characteristic peaks are relative to each other. Instead, it simply makes distinguishing peaks from random background variations ('noise') more difficult. Nevertheless, several minerals were identified.

Specimen HT001 (Figure 30) is dominated by calcium carbonate (80%), but also contains hydrated calcium sulphate (gypsum, 13%) and pyrite (7%) (Table 2). In the diffractogram, calcium carbonate peaks are denoted in blue, pyrite peaks in green, and calcium sulphate peaks in grey, which can all be compared to standard intensity patterns for these minerals (Figure 31). Only one peak (at 17.307, highlighted in Appendices 8. 6.) is unmatched, indicating that another mineral is present and unidentified (partially masked by the other minerals), or that one of the mineral identifications is incorrect. Additionally, any minerals that are below 2% total mass of the sample were not detected. There are many different reference patterns available for these minerals and, interestingly, the pyrite was most closely matched with a synthetic form. As these fossils are certainly not synthetic and an additional unmatched peak is present, the mineralogy is still unresolved. It is extremely likely that the iron sulphide mineral identification is inaccurate and/or that other iron sulphide minerals are present. Consequently, it is probable that the iron sulphide is simply a non-synthetic form of pyrite or a combination of several iron sulphides dominated by pyrite.

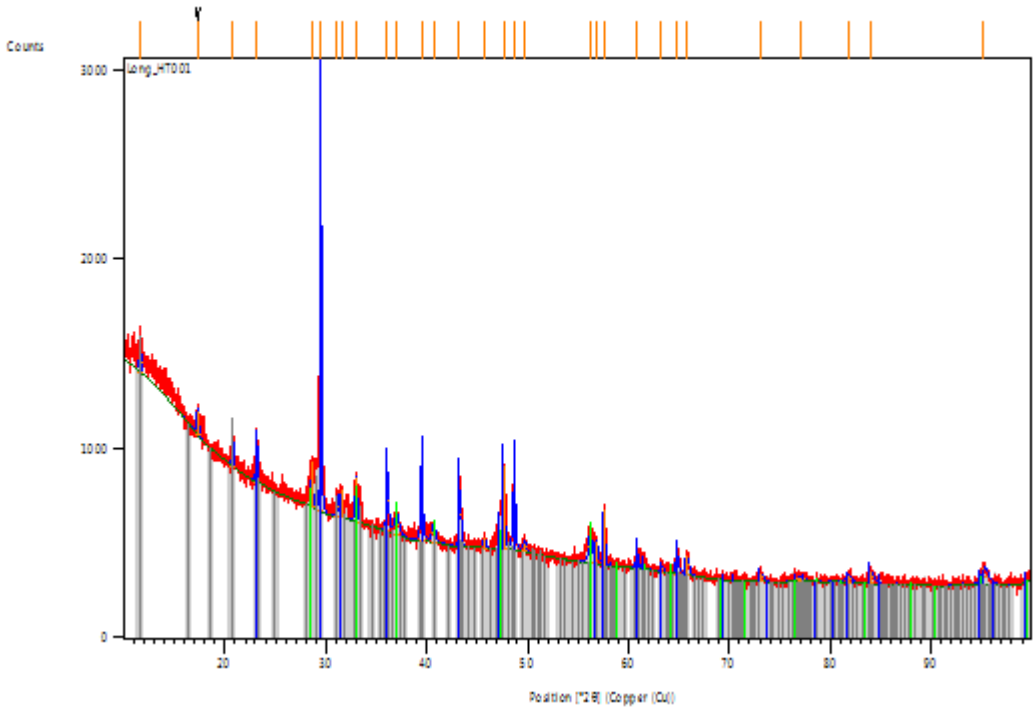


Figure 30. X-ray diffractogram of specimen HT001. Blue peaks correspond to calcium carbonate. Green peaks correspond to pyrite. Grey peaks correspond to hydrated calcium sulphate.

Table 2. Mineral identifications within specimen HT001.

Ref. Code, Name	Compound Name Semi-Quant. (%)	Approximate percent	Scale Fac.	Chemical Formula	Mineral
01-086-2334	Calcium Carbonate	80%	0.970	$Ca(CO_3)$	Calcite
01-079-0617 (synthetic)	Iron Sulphide	7%	0.072	FeS_2	Pyrite
01-070-7008	Calcium Sulphate Hydrate	13%	0.084	$Ca(SO_4) \bullet H_2O$	Gypsum?

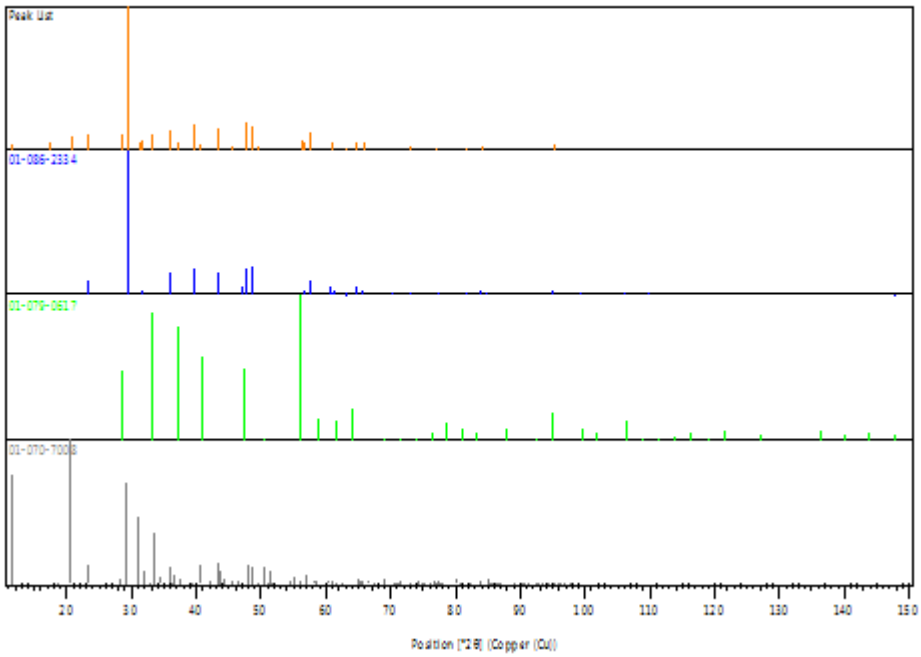


Figure 31. Standard intensity patterns for the minerals identified in the X-ray diffractogram of specimen HT001. No vertical measurement is provided, as mineral identifications are based on relative intensities and peak position (°2θ). Topmost row is copper (anode material, orange). Below that is calcium carbonate (blue), followed by pyrite (green), and finally calcium sulphate (grey).

Specimen NBNEW01 produced a diffractogram (Figure 32) dominated by calcium carbonate, but also containing goethite (Table 3, percentage data not available). In the diffractogram, calcium carbonate peaks are denoted in blue and goethite peaks are denoted in green, which can be compared to standard intensity patterns for these minerals (Figure 33). One peak was not matched with a mineral (at 28.251, highlighted in Figure 32 and Appendices 8. 6.), indicating that the mineralogy is unresolved. Unlike HT001, NBNEW01 contains no iron sulphide minerals and the peak may be a result of the polycrystalline nature of calcium carbonate (Dunlop [James] pers. comm., 2017).

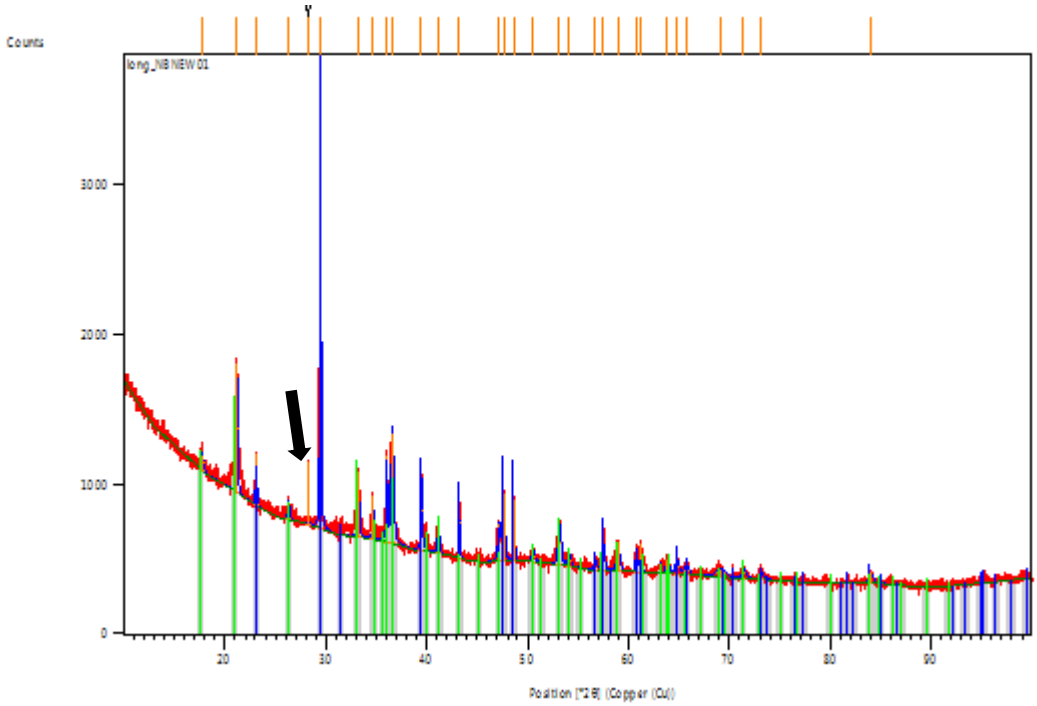


Figure 32. X-ray diffractogram of specimen NBNEW01. Blue peaks correspond to calcium carbonate. Green peaks correspond to goethite. Counts exceed 3,000. Black arrow highlights unmatched peak.

Table 3. Mineral identifications within specimen NBNEW01.

Ref. Code, Name	Compound Name Semi-Quant. (%)	Scale Fac.	Chemical Formula	Mineral
01-072-4582	Calcium Carbonate	0.963	$Ca(CO_3)$	Calcite
00-008-0097	Iron Oxide Hydrate	0.165	$Fe_2O_3 \bullet H_2O$	Goethite

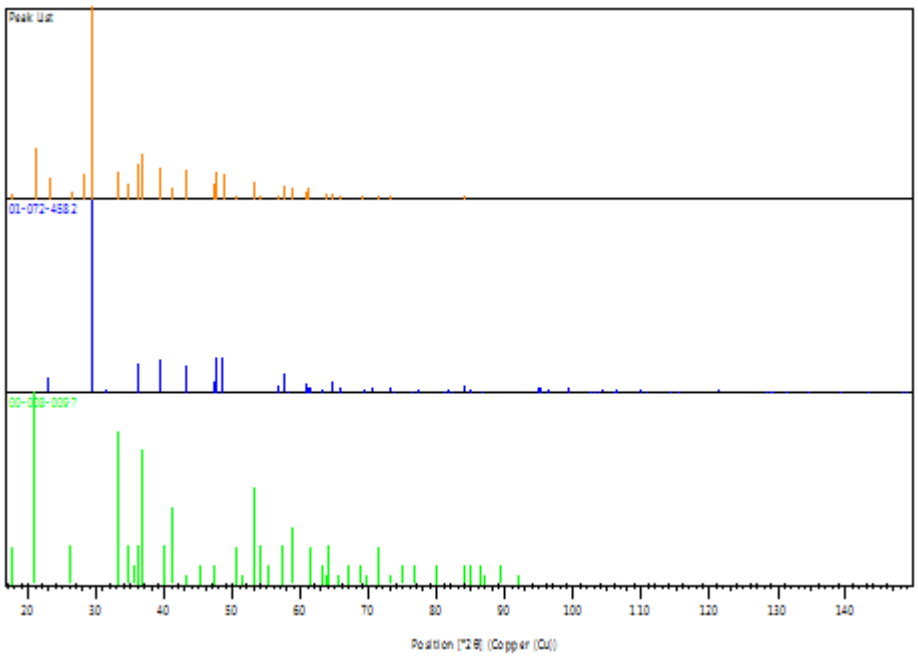


Figure 33. Standard intensity patterns for the minerals identified in the X-ray diffractogram of specimen NBNEW01. No vertical measurement is provided, as mineral identifications are based on relative intensities and peak position (°2θ). Topmost row is copper (anode material, orange). Below that is calcium carbonate (blue), followed by goethite (green).

As noted in Chapter 2, additional technical settings, including scan axis, step size, scan time, scanning type, anode material, etc. are available in the appendices (Appendix 8. 6.).

3. 4. Replacement fabrics

As demonstrated above, Nova Olinda Member fossil insect tissues are preserved in several different minerals, resulting in a variety of preservational fabrics. Here, these fabrics are described and examples provided. Before each fabric is addressed in detail, a schematic summary is presented outlining the major fabrics and some of their variants (Figure 34). These include 1) granular-to-nanocrystalline impregnations, 2) pseudomorphed pseudoframboids, 3) globular impregnations and incrustations, and 4) mineral infills. These different fabrics often correspond to different insect tissue types and so they are presented in three sections below: those that replace external cuticle, those that coat the interior of the cuticle and fill the body cavity, and those that are observed replicating internal labile soft-tissues. The original insect morphology observed in this project (and its fidelity) will be described later in section 3. 5.

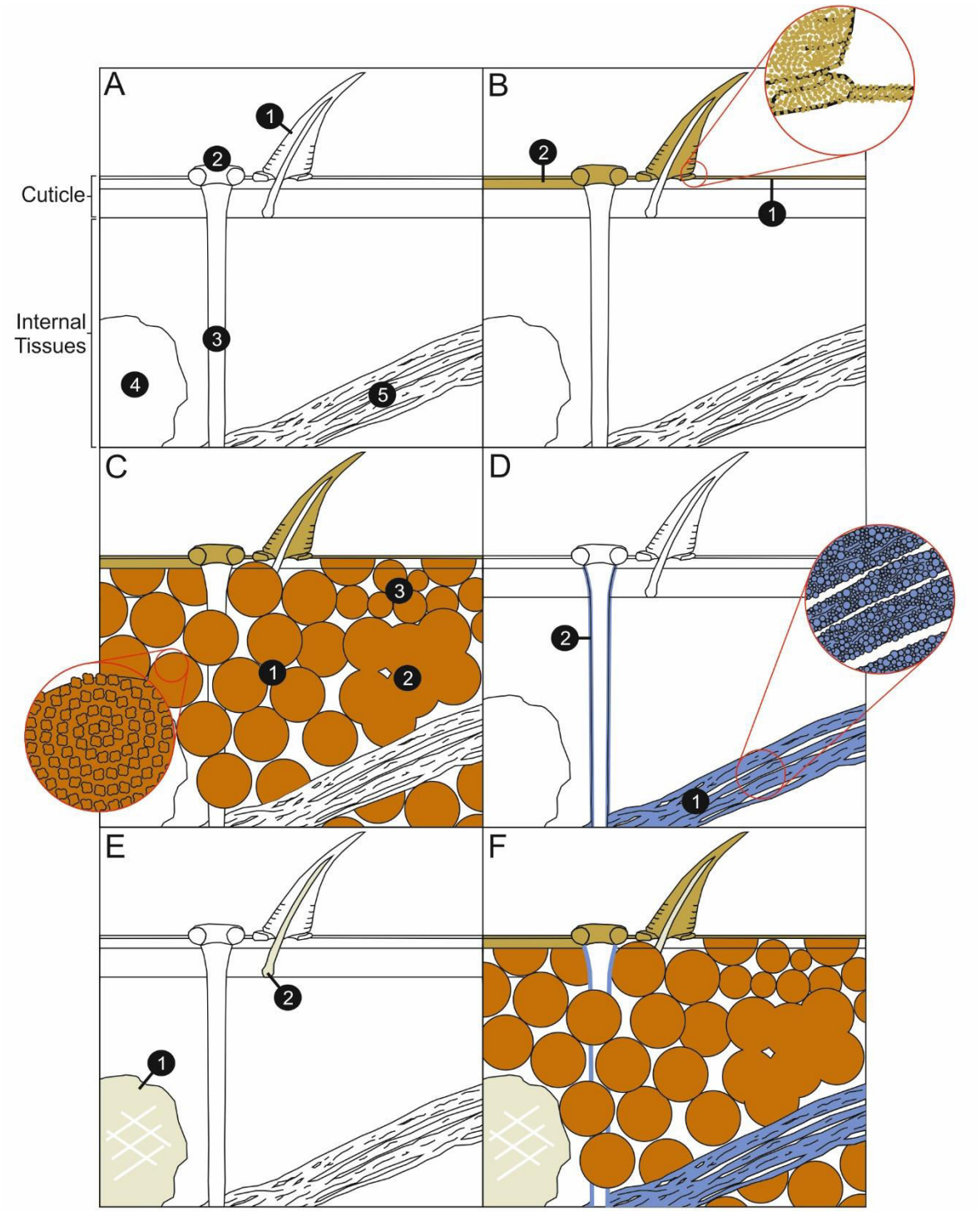


Figure 34. Schematic diagram showing the mineral fabrics observed in Nova Olinda Member insect fossils. A, Schematic cross section of insect tissues: 1, Seta. 2, Spiracle. 3, Tracheal tube. 4, Void. 5, Muscle fibres; B, Nano-crystalline impregnation fabric. Callout highlights nanometre-size of crystals replacing the cuticle, which were indiscernible under SEM. 1, Areas where only the epicuticle are replaced. 2, Areas where both the epicuticle and endocuticle are replaced; C, Pseudomorphed pseudoframboidal pyrite fabric. Callout highlights that the pseudoframboids consist of granules of goethite (pseudomorphing pyrite) arranged in a spiral on a sphere (or hemisphere). 1, Pseudoframboids infilling carcass, obliterating internal tissue morphology. 2, Pseudoframboids that have 'intergrown' or 'merged' and are not easily distinguishable from each other. 3, Pseudoframboids of various sizes; D, Globular impregnation and incrustation of internal soft tissues. Callout highlights the globular replacement fabric. 1, Impregnation and incrustation of fibrous tissues. 2, Incrustation of tracheal system; E, Cavities infilled by calcite. 1, 'Large' (>100 µm) cavities infilled by a single crystal, sometimes with distinct rhombohedral cleavage. 2, Sparry calcite cements infilling remaining voids within the cuticle; F, Schematic summary of all replacement fabrics.

3. 4. 1. Granular-to-nanocrystalline impregnations (of external cuticle)

Much of the external cuticle of weathered Nova Olinda Member insects is replicated with extremely high fidelity due to nanocrystalline impregnation. The fabric of this replacement is so fine-scale that it currently cannot be viewed under SEM in uncoated specimens (Figure 34: B; Figure 35: A). Au-Pd sputter coating allowed for higher magnification images of these fabrics of replacement to be captured (Figure 35: B), but also masked their sub-micron scale structure with Au-Pd clusters (Figure 35: C). The original insect morphology that this nanocrystalline impregnation preserves is discussed in section 3. 5. 1.

Areas of poorer or incomplete preservation reveal a coarser granular mineral fabric of globular/sub-spherical micro-grains (Figure 35: D).

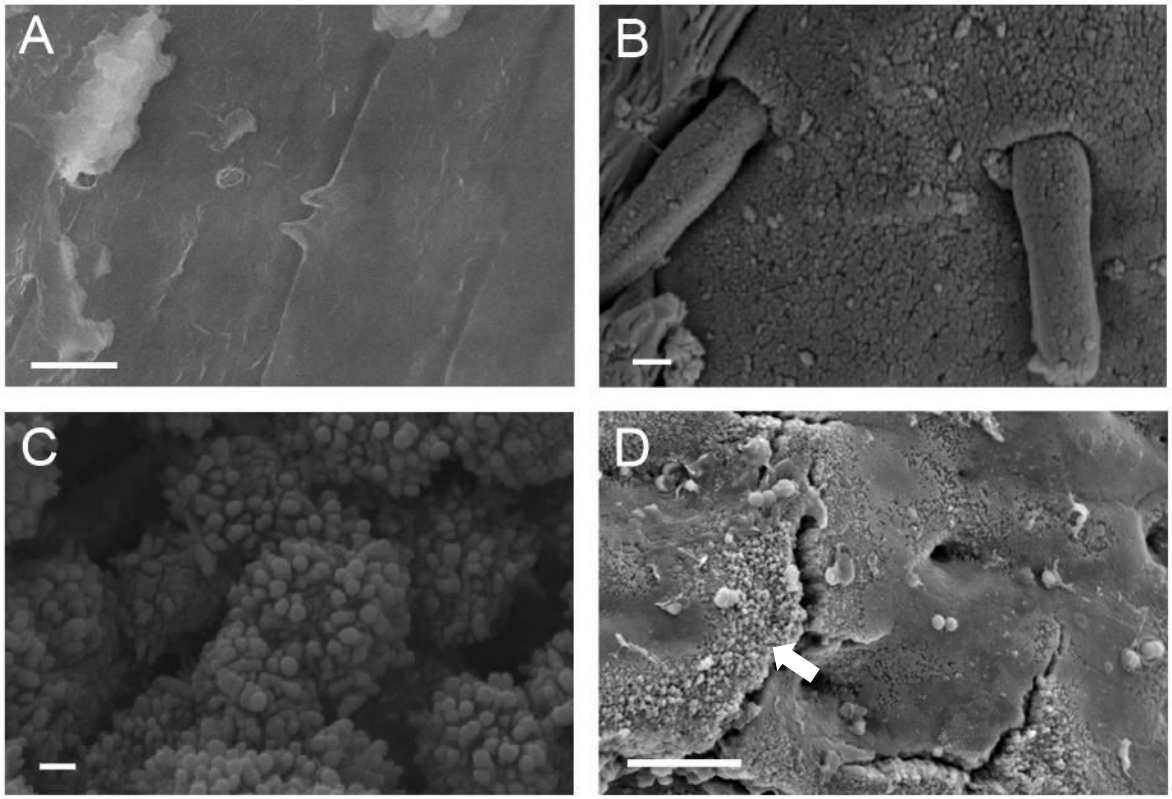


Figure 35. A, SEM image of uncoated Nova Olinda Member insect cuticle (abdomen with cuticular scales) with no discernible replacement grains, suggesting sub-micron scale replacement. B, SEM image of Au-Pd coated Nova Olinda Member insect cuticle, suggesting granular replacement fabric. C, Ultra-high magnification image (85,500 x) of Au-Pd coated Nova Olinda Member insect. Fine-scale globular fabric is a result of sputter coating and obscures replacement fabric. D, Lower magnification SEM of coated Nova Olinda Member insect with poorer preservation, revealing a coarser granular replacement fabric highlighted by arrow. A, Specimen NBRL025-002. B, Specimen JW614 [SMNS 700902– *Parviformosus* holotype] – 079. C, Specimen FLO19 (gold coating). D, Specimen NBRL045-48. A, Scale bar = 2 µm. B, Scale bar = 1 µm. C, Scale bar = 200 nm. D, Scale bar = 10 µm.

Similar to Figure 35: D, some portions of insect cuticle that were incompletely mineralised revealed spherical-to-subspherical granular replacement fabrics. This fabric can directly replace cuticle (Figure 36; Plate 17: D), even where it is surrounded by exceptionally preserved cuticular scales (Figure 36: A-B; Plate 18: A-B), or be scattered across it (Plate 17: A-C and E-H). Where epicuticle is broken away, a tightly packed sheet of micron-scale spheres is sometimes revealed beneath (Figure 36: C). In beetle elytra, a similar texture is present. Two sizes of granular spheroids replace the elytra cuticle with poor fidelity (Figure 36: D; Plate 19), that is perhaps a result of the internal structure of elytra.

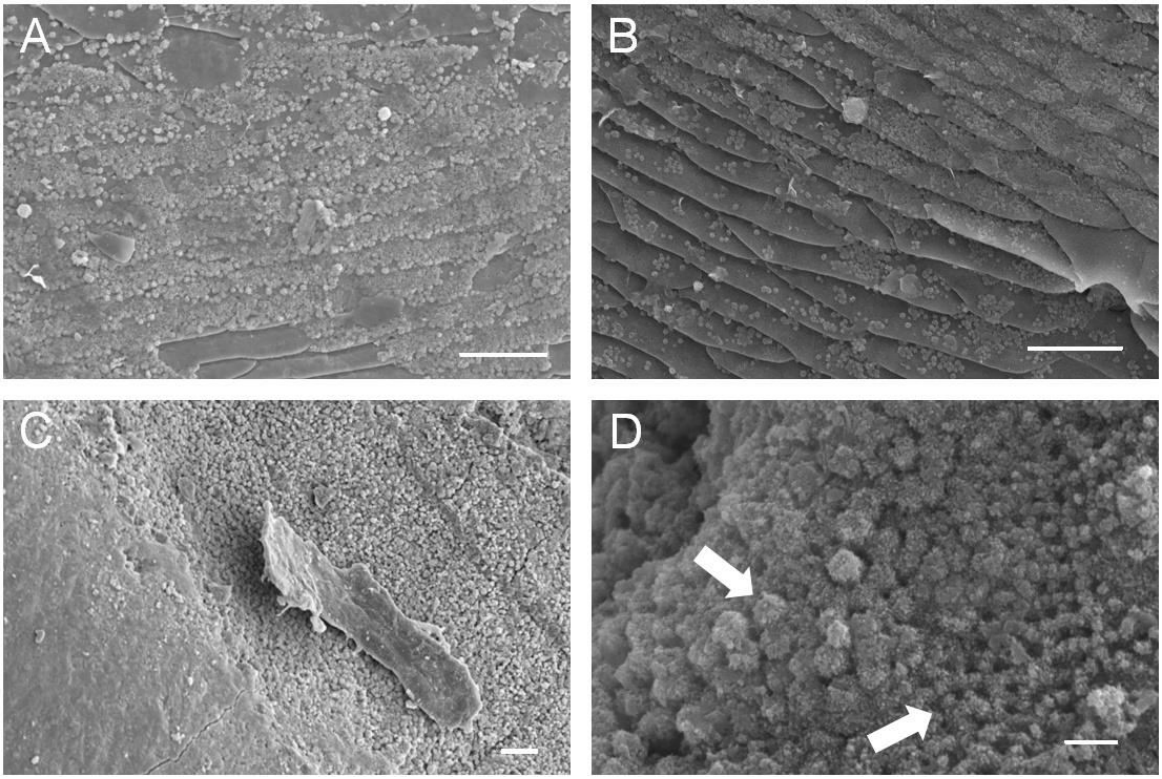


Figure 36. A-B, Spherical and subspherical micro-grains directly replacing insect cuticular scales. C, Damaged and contaminated cockroach cuticle revealing sheet of microspheres beneath cuticle. D, Arrows highlight two sizes of subspherical grains replacing beetle elytra. A, NBRL040-53. D, NBRL045-##31. C, NBRL26-016. B, NBRL040-162. A, Scale bar = 1 µm. B-D, Scale bar = 10 µm.

In unweathered Nova Olinda Member insects, the replacement fabric is mostly smooth, with sub-micron globular aggregates across its surface (Figure 37). Samples sputter coated in C are not masked by globular aggregates in the same manner as those coated by Au-Pd, allowing for the replacement fabric to be observed (as in Figure 37).

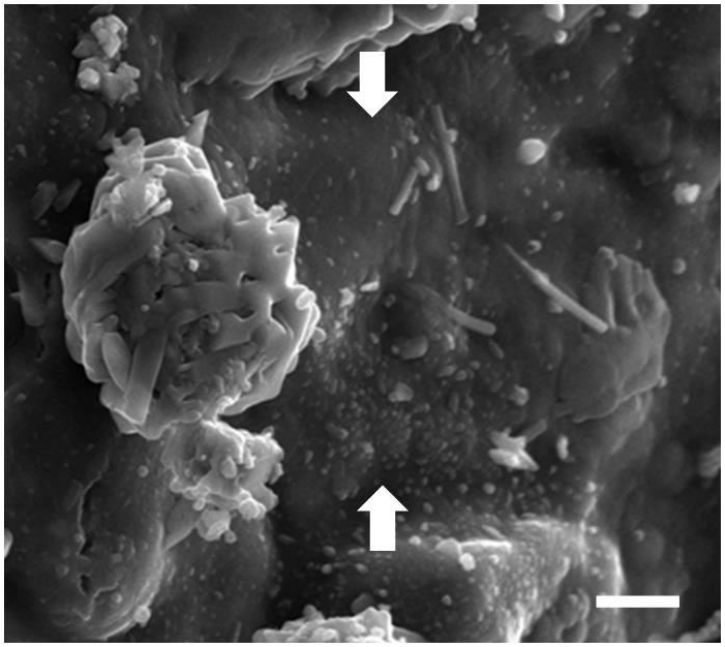


Figure 37. Fabric of unweathered Nova Olinda Member insect wing cuticle, sputter coated with Carbon. Arrows highlight mostly smooth cuticle, with sub-micron globular aggregates across its surface. Specimen HT001. Scale bar = 2 µm.

Very rarely, well-preserved cuticle will rapidly transition into less easily definable preservational fabrics. One example (NBRL014) displays raised isolated fragments of smooth cuticle, held aloft by an irregular lattice of cement over calcite infills (Figure 38: A-B; Plate 20: A-D).

Granular external replacement mineral fabrics can also transition into globular fabrics, typically with increased distance from areas of exceptional preservation (Figure 38: C-D; Plate 21). However, these portions may simply represent the obliteration of external features by calcium phosphate growth.

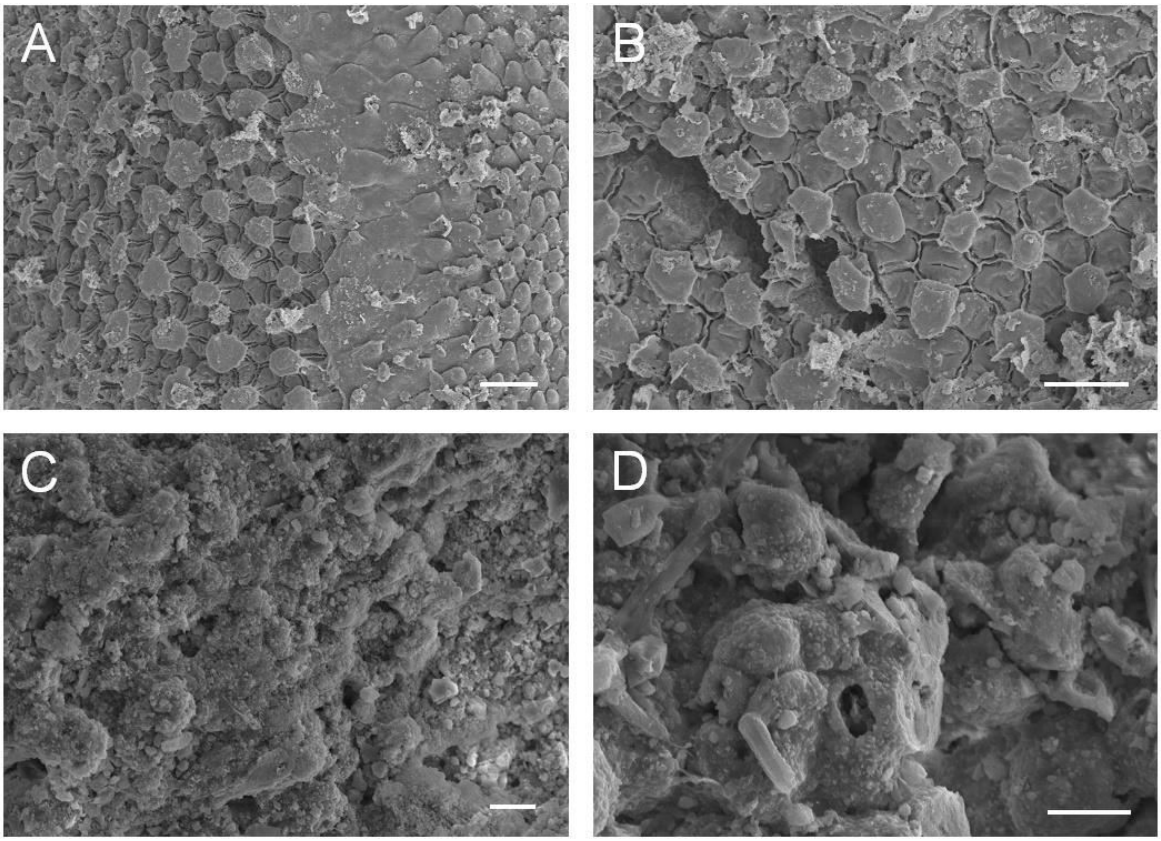


Figure 38. Enigmatic replacement fabrics. A-B, Fabric of isolated sections of smooth cuticle above a latice of cement and infilling calcite crystals. A, Thorax. B, Abdomen. C-D, Globular fabrics of replacement. A, NBRL014-25. B, NBRL014-53. C, FLO13-50. D, FLO13-85. Scale bars = 10 µm.

3. 4. 2. Sub-surface pseudoframboid replacement fabrics (within body cavity)

Although the subsurface tissues of the Nova Olinda Member insects are preserved in a variety of mineral fabrics, one fabric dominates their preservation. Where the epicuticle is lost (either abraded or not preserved) this dominant fabric is often revealed (Figure 39). It consists of spherical or subspherical aggregates of microcrystallites interpreted here as pseudomorphed pseudoframboids (Figure 34: C; Plates 22 and 23). Where these aggregates have grown against a flat surface, or between two surfaces, they may form hemispherical or cylindrical (disc) morphotypes (Figure 39: E-F; Plates 24, 25, and Plate 20: E-F). While these structures are typically ~10 µm in diameter, they can also range in size between 2-15 µm (Figure 39: A; Plates 26 and 27; Plate 28: A-C) and are hollow (Figure 39: C; Plate 25: E and F). Although the microcrystallites show no consistent orientation, they often form small (0.2-1 µm) clusters on the surface of the aggregates (Figure 39: B; Plate 22: C, E and F). These clusters are frequently arranged in a spiral around the aggregate (Figure 39: D; Plate 23: E-D; Plate 24: E-F). In rarer cases, these microcrystallites can be needle-like (Plates 29 and 30: F-H).

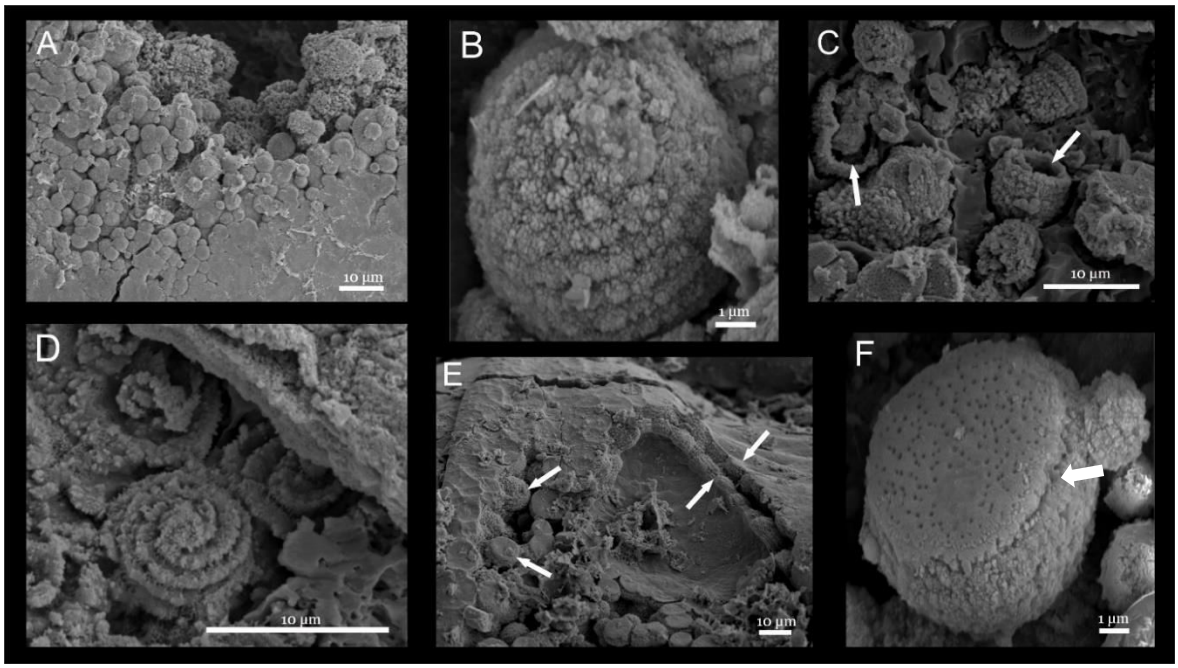


Figure 39. The dominant replacement fabric, and its various forms, of the Nova Olinda Member insects. A, Spherical and subspherical aggregates of varying size replacing insect cuticle, merging to form smooth cuticle replication. B, Spherical aggregate composed of microcrystallites arranged into ~0.5 µm clusters that form rings (or a spiral?) around the aggregate. C, Broken aggregates revealing their hollow interiors, highlighted by arrows. D, Subspherical aggregates beneath cuticle with a spiral morphology. E, Arrows highlight hemispherical aggregates replacing insect cuticle, flat surface replicating the epicuticle with high fidelity. F, Higher magnification image of hemispherical aggregate. Arrow highlights the boundary between replacement fabrics. Scales show in each image.

The spherical and domed portion of the aggregates are interpreted here as a distinct replacement event to the flattened high-fidelity portion (arrow highlights in Figure 39: F). The domed portion is a hemi-spherical pseudoframboid, whereas the flattened portion is an example of the nanocrystalline high-fidelity impregnation of the cuticle (described in sections 3. 4. 1. and 3. 5. 1.). This can be inferred because the domed portion of these aggregates do not replicate original insect morphology in detail. Instead, they occupy the space where the original tissues were. These structures likely grew into voids left by decaying tissues or they obliterated tissues as they grew. The flattened surface upon which these aggregates adhere to replicates the epi/exocuticle of the insect with high fidelity via nano-crystalline impregnation (Figure 40; Plates 23, 24, 26, 28, and 30). Here it is interpreted that the aggregates grew on the interior surface of exo/epicuticle after it had been impregnated by nano-crystalline iron sulphides.

The subspherical/hemispherical aggregates do not replicate original insect morphology with high fidelity. This is because the original crystals were euhedral pyrite, which were later pseudomorphed by globular goethite during weathering. This morphology-obliterating process evidently did not occur where cuticle is well-preserved, demonstrating that two distinct mineral replacement events occurred. Alternatively, the aggregates may have been

globular/cryptocrystalline prior to weathering, possibly as goethite/mackinawite protoframboids rather than pyrite framboids (Vietti *et al*., 2015). This would result in a structure distinct from both pyrite framboids and pseudoframboids. As such, the terms 'pseudoframboid-like aggregates' or 'pseudomorphed pseudoframboids' are used to describe them here. Regardless, the replacement process obliterated original insect micron-scale internal morphology.

Where spherical and subspherical pseudoframboid-like aggregates are located loosely within the insect body cavity (Figure 40: B-C; Plate 22), the same process is presumed to have occurred, albeit away from the pre-mineralised cuticle.

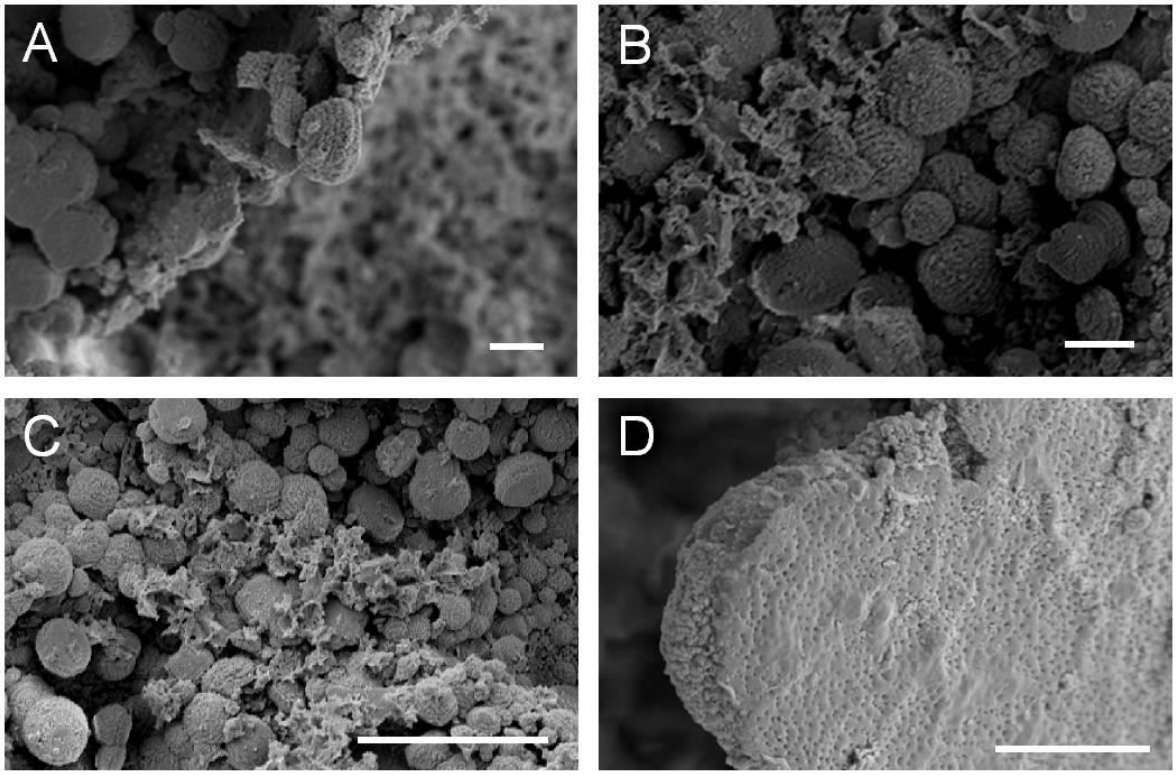


Figure 40. A-C, Hemispherical aggregates throughout the head of specimen JW614 [SMNS 700902– *Parviformosus* holotype]. D, flat surface of hemispherical aggregates, replicating exterior most cuticle. A, JW614-073. B, JW614-004. C, JW614-060. D, JW614-076. A-B and D, Scale bars = 10 μm. C, Scale bar = 50 μm.

3. 4. 3. Globular internal replacement fabric (of internal labile soft-tissues)

Rarely, internal labile 'soft tissues' (i.e. guts, genitals, muscles, etc.) may be replicated with high fidelity, in either subspherical-to-globular grains (Figure 34: D; Figure 41: A-B), or as relatively smooth submicron high-fidelity replacements (Figure 41: C-D). The globular fabric of these internal replacements differs from those described above in that they consist of mostly spherical grains approximately 1 μm in diameter and are composed of calcium phosphate (Figure 41: A). Higher magnification imaging reveals that many of the smooth areas are, in fact, globular at the micron-scale and individual sub-micron grains are still discernible amongst the replacement fabric (Figure 41: D). These fabrics strongly resemble the 'bubble-like growths' and granular fabrics

observed in ‘Orsten’-type soft tissue preservation from the Upper Cambrian Alum shale of Vastergötland and the isle of Öland, Sweden (Maas *et al*., 2006; Eriksson *et al*., 2012). ‘Orsten’-type soft tissue preservation is characterised as phosphate encrustation and impregnation of both external and internal organs during early diagenesis in a limestone medium (either limestone matrix or limestone concretion) (Maas *et al*., 2006; Eriksson *et al*., 2012). Within the Nova Olinda Member insects, this preservational fabric only replicates internal labile soft-tissues.

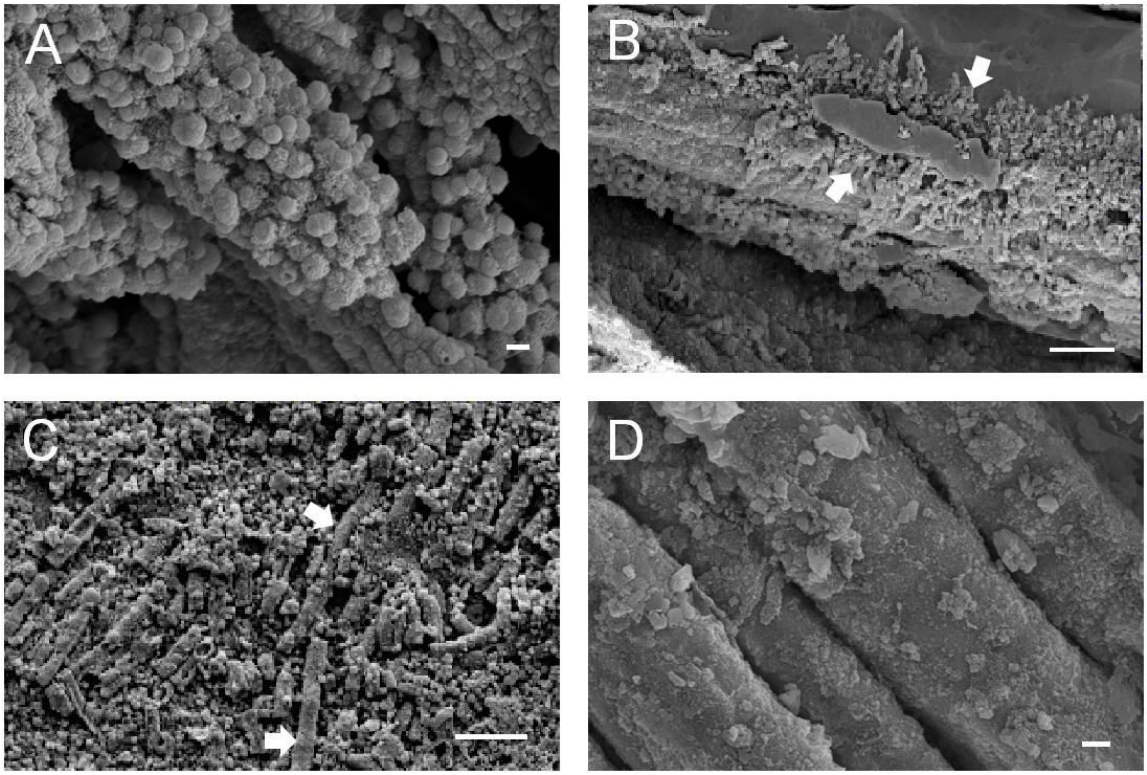


Figure 41. Examples of the fabric of internal soft tissue preservation. A, Replacement of genital muscle fibres/connective tissue by ‘bubble-like growths’. B, ‘Bubble-like’ grains impregnating and coating limb muscle fibres. Arrows highlight clusters/chains of grains. C, Replacement of thoracic (flight) muscle fibres, resulting in a smoother fabric. Arrows highlight muscle fibres. D, Replacement of gill filaments in relatively smooth fabric. A and B, Specimen FLO19. C, Specimen JW291-083. D, Specimen FLO37-24. A and D, Scale bars = 1 μm. B and C, Scale bars = 10 μm.

In the Nova Olinda Member fossil insects, most internal labile soft tissue preservation is found in specimens that also retain well-preserved cuticle with high-relief. Rarely are internal labile soft tissues preserved in low-relief specimens with poorly-preserved cuticle, and only occur as ‘faint traces’ when they are (Figure 42). However, well-preserved cuticle and high-relief specimens do not always retain internal labile soft tissues. As such, it cannot be inferred that the mineralisation of the labile soft tissues assisted (or ‘bolstered’) the preservation of external cuticle. In other words, unlike the pseudoframboid-like aggregates, the ‘Orsten’-type soft tissue preservation occurred independently from the nanocrystalline high-fidelity impregnations.

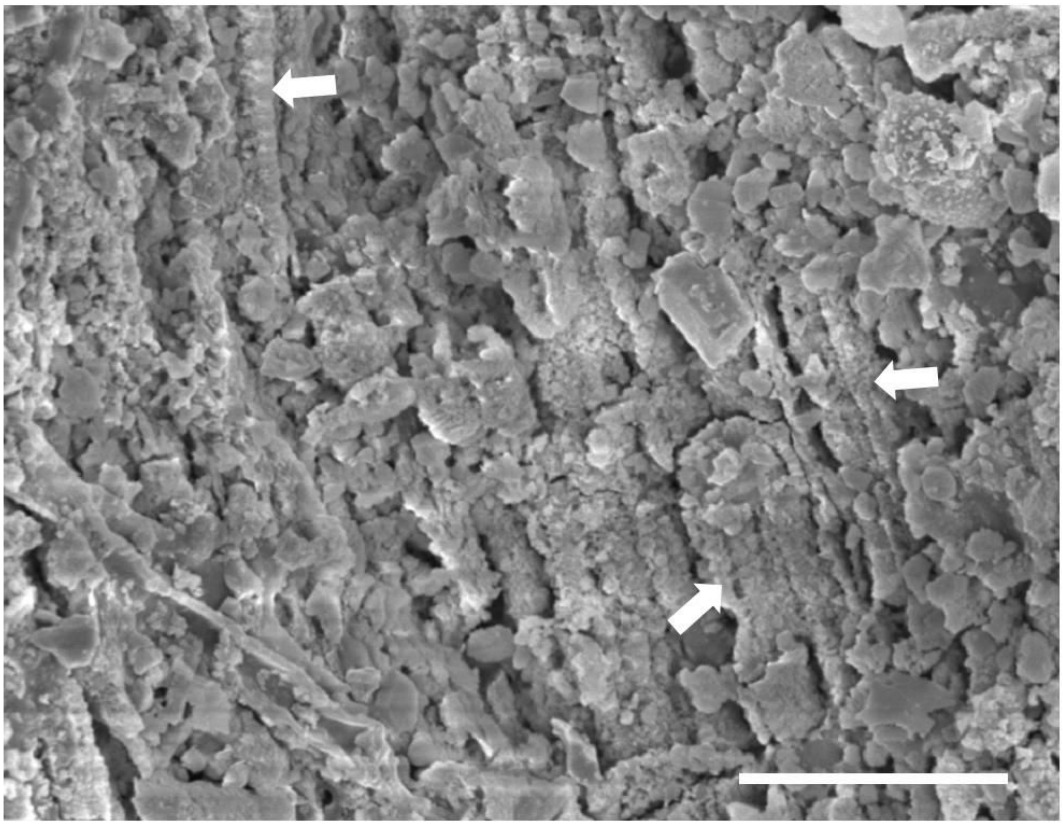


Figure 42. Arrows highlight 'scrappy' traces of poorly-preserved muscle fibres in low-relief, relatively poorly preserved specimen. Specimen NBRL 070-08. Scale bar = 10 μm.

Due to the labile nature of these tissues, it is presumed that either mineralisation occurred extremely quickly (within hours of death, Martill, 1990; Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Briggs, 1995a,b; Maas *et al*., 2006), or that decay was sufficiently retarded to prevent the loss of these structures (Briggs *et al.,* 1993; Maas *et al*., 2006). In reality, it was likely a combination of both of these factors.

3. 4. 4. Mineral Infills

The body cavities of most Nova Olinda Member insect fossils examined were infilled with pseudoframboid-like aggregates (or pseudomorphed pseudoframboids), and only a few were infilled by other mineral phases. This could be an artefact of the preparatory techniques, as acetic acid digestion would have dissolved calcite infills. On the rare occasions that hydrochloric acid was used, any phosphatic infills would have also dissolved.

Where infills were observed, they were calcite (Figure 34: E; Figure 43: A-B). These infills are infrequently associated with areas of exceptionally preserved internal tissues in calcium phosphate (Figure 43: C and D). In extremely rare cases, a single calcite crystal will infill an entire internal organ, replicating its gross morphology (Figure 43: D).

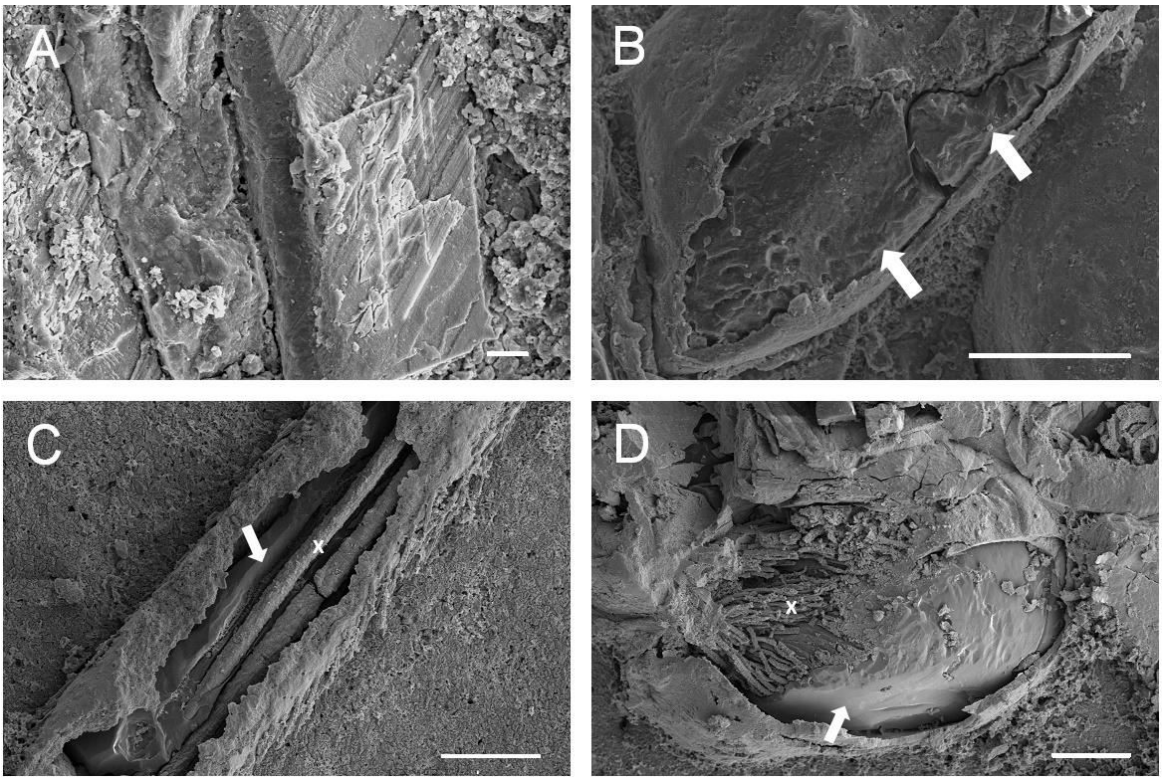


Figure 43. Examples of mineral infills within fossils. A, Calcite with distinct cleavage infilling thorax. B, Two calcite crystals highlighted by arrows, infilling limb cavity. C-D, Calcite infills, highlighted by arrows, associated with exceptional internal preservation of labile 'soft tissues' in calcium phosphate, highlighted by crosses. C, In dipteran forelimb with muscle fibres. D, Calcite crystal infilling dipteran ovary. A, Specimen NBRL057-61. B, Specimen FLO13-55. C-D, Specimen FLO19. A, Scale bar = 10 µm. B-D, Scale bars = 100 µm.

3. 5. Exceptional preservation of insect morphology

Despite the variation in preservational fidelity ('quality') of Nova Olinda Member insect fossils, where preservation is best, both external and internal tissues are preserved remarkably well. In the highest fidelity examples, original insect morphology can be preserved to the sub-micron scale, or extremely labile tissues that typically decay within hours of death may be retained (Briggs 1993). Additionally, some specimens that appear poorly preserved to the naked eye (often fragmentary) reveal exceptionally preserved micron-scale morphology (cuticular scales, setae, ommatidia, etc.) when examined at high magnifications. Despite their poor initial appearance, these specimens are considered exceptionally preserved due to their retention of fine-scale insect morphology. Examples and further descriptions of the most notable and most common exceptionally preserved labile tissue types and structures are presented below.

3. 5. 1. Cuticle

3. 5. 1. 1. Cuticle cross-section

Although insect cuticle is relatively durable and can preserve in many ways in many sedimentary environments, it rarely does so with three-dimensionality except as inclusions in amber (Grimaldi and Engel, 2005; Penney and Jepson, 2014). In the Nova Olinda Member, cuticle appears mostly massive in cross section under SEM, with internal laminae only rarely visible (Figure 34: B: 2; Figure 44; Plate 31). In some cases, fabrics found within the cuticle at high magnification may represent the morphology of the preserving minerals, rather than the ultrastructure of the insect (Figure 39 above). Despite this lack of internal structure, fragile cuticular surface features are frequently exceptionally well-preserved (discussed further below).

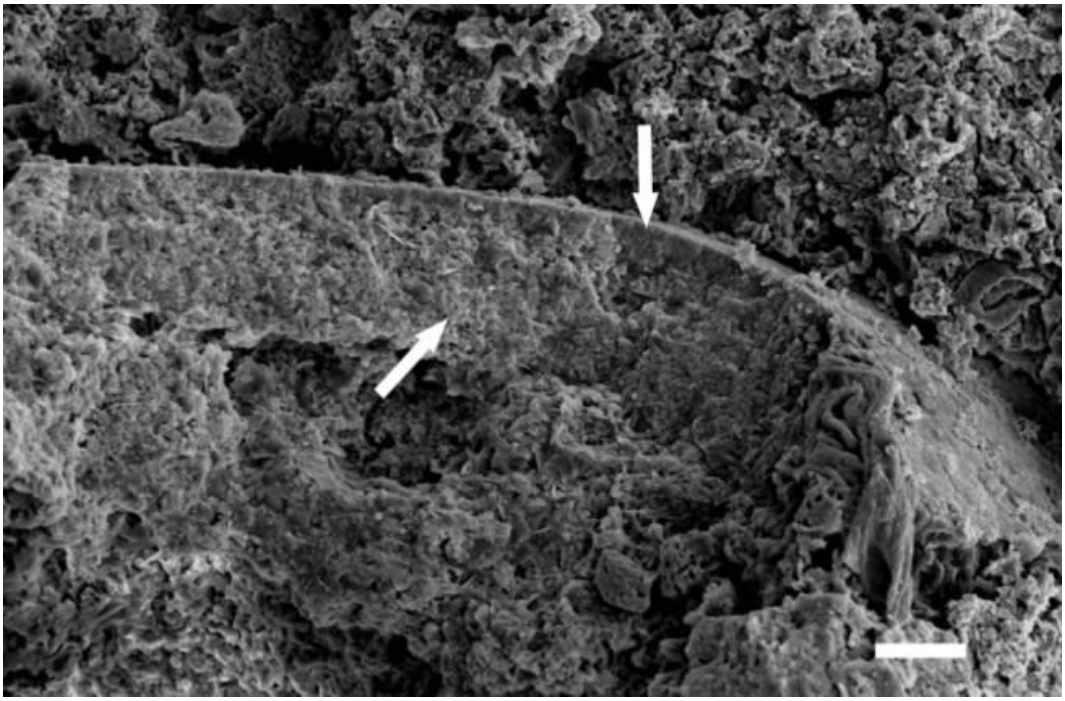


Figure 44. Section through insect cuticle. Upper arrow highlights well-preserved exocuticle, lower arrow highlights poorly-preserved massive endocuticle. Specimen JW735, Blattodea. Scale bar = 10 µm.

In extremely rare cases, structural colour may be preserved in Nova Olinda Member fossil insects (Martill *et al*., 2007a; McNamara, 2013; Barling *et al*., 2015). Structural colour is non-ubiquitous in insects and is generated by constructive inference of light by variations in cuticular nano-structure (McNamara, 2013). Consequently, its preservation is a result of the retention of nano-structural details of the cuticle and represents exceptionally fine-grained replication (impregnation). No specimens examined here retained structural colour (although one specimen from SMNS was figured by Barling *et al*. (2015)) and, consequently, structural colour could not be included in the taphonomic analysis presented here. Nevertheless, the extremely rare occurrence of structural colour demonstrates just how fine-scale the replication of Nova Olinda Member fossil insect cuticle can be.

3. 5. 1. 2. Setae

Setae are fragile filamentous sensory structures ubiquitous in arthropods, covering the majority of the insect body and can even coat their eyes (Figure 45; Rasnitsyn and Quicke, 2002; Garm, 2004; Grimaldi and Engel, 2005). As with most insect cuticular structures, they vary greatly in size, morphology, internal structure, and function (Grimaldi and Engel, 2005).

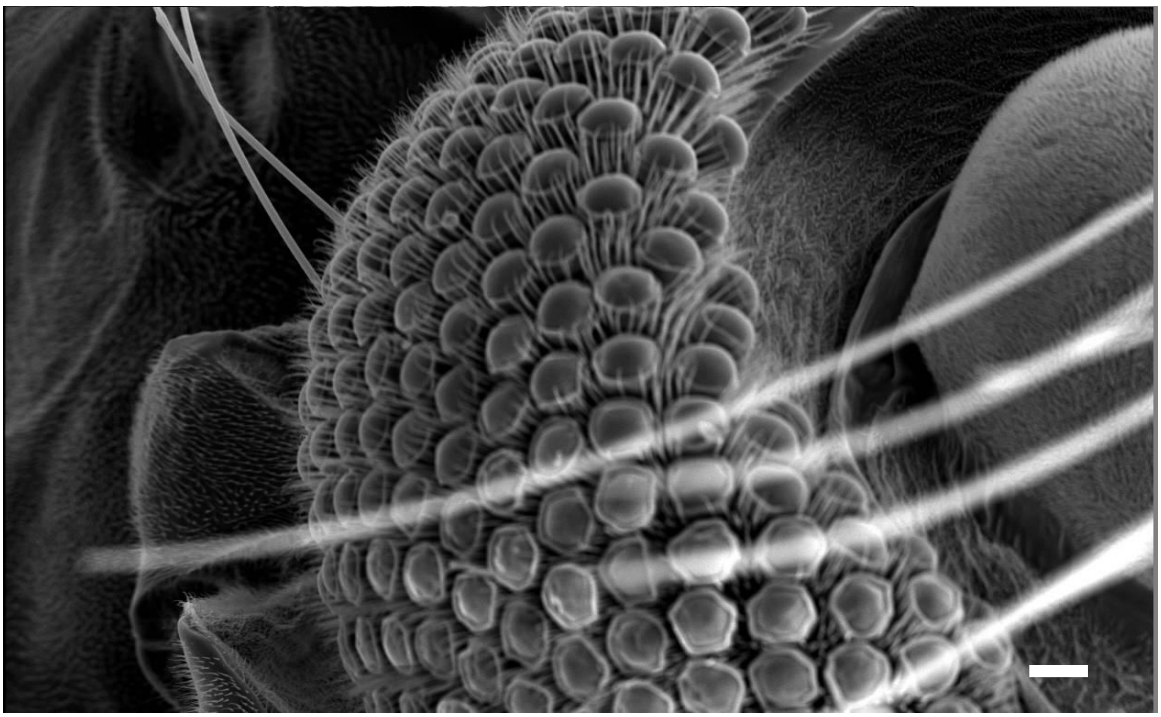


Figure 45. Setae of recent dipteran (Diptera: Culicidae) protruding between separated ommatidia in a compound eye. NBSTUB03-018. Scale = 10 µm.

Several setae 'morphotypes' have been imaged from Nova Olinda Member fossil insects, including setae with ridges (Plate 32), long, curved, and flat setae (Plate 33), cerci and their setae (Plate 34), fine and packed setae (Plate 35), and hollow setae (Plate 36). Despite their fragility, many setae are complete and retain surface details (i.e. ridges, Figure 46; Plates 32 and 34). Smaller (< 1 µm) setae ('micro-setae' or microtrichium) are also present (Plate 37: A), but their minute size renders them extremely fragile and so very few are preserved intact. The majority of micro-setae are preserved only as micro-setal bases (Plate 37: B-D; Plates 38 and 39). Nevertheless, these can reveal interesting morphological details, such as the arrangement of micro-setae into tightly-packed columns (Plate 39: A-B and D).

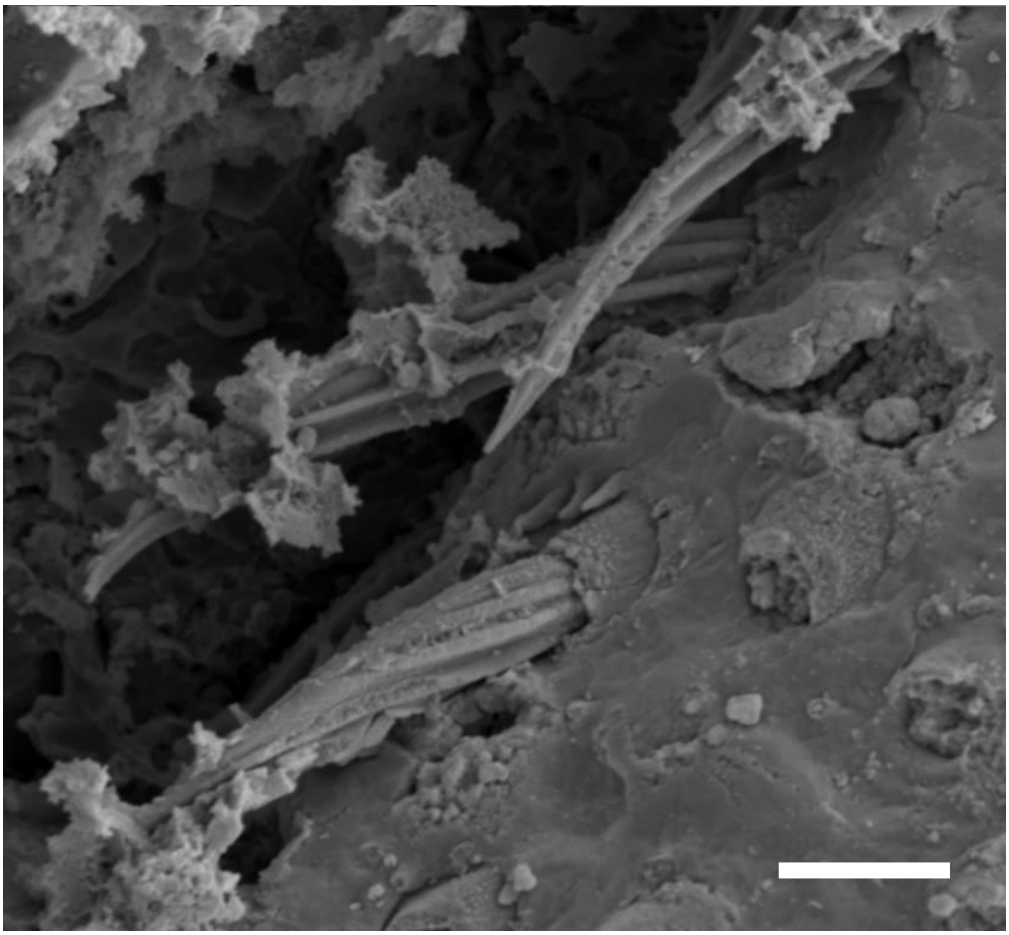


Figure 46. Example of exceptionally preserved small ridged/fluted setae in Nova Olinda Member insect. Specimen FLO19-28. Scale bar = 10 µm.

Due to their protruding nature, setae can be easily damaged (Carlton, 2007). They are frequently fractured or broken (Plate 40), disarticulated (Plate 41), loosely articulated as fragments (Plate 42), be swollen and warped (Plate 43), or only their bases remain (Plates 37 and 44). This makes them useful as a proxy for measuring preservational quality (discussed further in Chapter 6. 4. 4.). Setae that are preserved on exposed cuticular surfaces are generally pressed flat against the cuticle (Plate 32: E; Plate 33: A-F; Plate 36: A-F; Plate 44: A).

3. 5. 1. 3. Scales

Cuticular scales are a non-ubiquitous component of insect cuticle (Grimaldi and Engel, 2005). They are present in the primitive Archaeognatha (bristletails), but are absent in other relatively primitive groups such as Nicoletiidae and Maindroniidae (silverfish and their close relatives) (Grimaldi and Engel, 2005), suggesting that they are a primitive trait. Despite this, they are certainly present in some more derived groups from the Cretaceous including Hemiptera (FLO38) and Blattodea (NBRL018, NBRL036, and NBRL040), but were not observed in Hymenoptera (JW614 [SMNS 700902– *Parviformosus* holotype]). It is unclear if this is a result of damage, incomplete preservation, or taxonomic absence and so their absence cannot be used as a

measure of preservational quality. However, where present they are interpreted as indicating exceptional preservation.

Cuticular scales are an extension of the epicuticle and represent the outermost surface of the insect, excluding protruding structures (e.g. setae or spines) (Plotnick, 1990; Hopkins and Kramer, 1992). They are generally extremely thin (approximately 500 nanometres in thickness, Plate 45: D) and may overlay each other (Plate 45: C). Two 'morphotypes' of scales were observed: 'rhombohedral and trapezoid' shaped scales (Plate 45) and 'long and thin' scales (Plate 46). These differences are not taxonomically distinctive and a single specimen can exhibit both 'morphotypes' (e.g. NBRL040).

Given the thinness of cuticular scales, their preservation within the Nova Olinda Member is truly remarkable. Scales are frequently preserved complete and apparently undamaged (Figure 47; Plates 45 and 46). In rare cases, they also retain partially damaged micro-spines (microtrichium, Plate 47). The lower relief of scales (compared to setae) presumably protects them from some erosion, allowing them to be extremely well preserved immediately adjacent to areas of poor preservation or non-mineralisation (Plate 14: E; Plate 16: G-H) or in otherwise exposed areas (Plate 48: A-C).

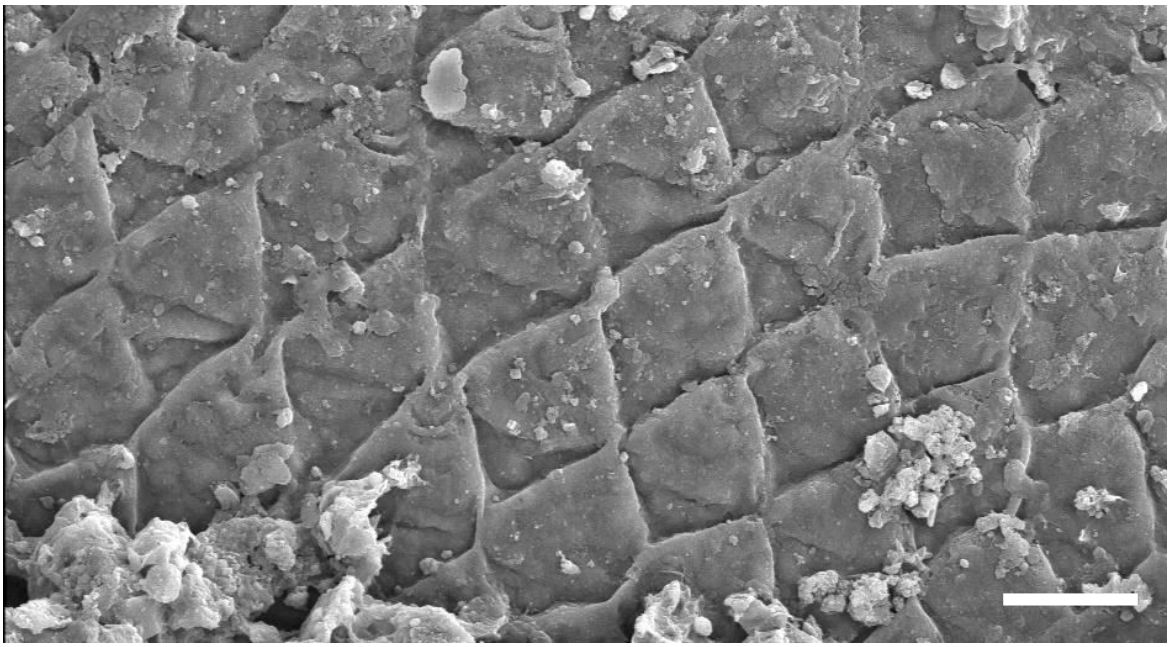


Figure 47. Remarkable preservation of rhombohedral-shaped cuticular scales. Specimen FLO38 (Hemiptera). Scale bar = 10 µm.

Due to their extremely fine structure and low relief, their preservation is also a strong indication that mineralisation initiated in the epicuticle (from the exterior surface of the carcass), rather than from deeper within the cuticle itself, as preservational fidelity generally decreases with 'depth' into the cuticle (discussed in section 3. 5. 1. 1.; Plate 31: A). Cuticular scales are extensions of the epicuticle and, although they have a slightly increased surface area, they should not be

prone to mineralisation any more so than other areas of cuticle. This further supports the hypothesis that their exceptional preservation is a result of their position on the carcass, rather than due to some inherent structural difference.

3. 5. 1. 4. Cuticular ridges, spines, etc.

Insects possess a bewildering array of morphologies and the ornamentation of their cuticle is no exception. In addition to scales and setae, cuticle can exhibit ridges, bumps, domes, spines, pits, and many other topographical variations with a variety of sizes (Grimaldi and Engel, 2005).

Two elcanid (Orthoptera: Elcanidae) specimens (NBRL044 and NBRL051) retained a remarkably preserved mesh-work of cuticular ridges on their vertex and gena (Figure 48: A; Plate 49). While the identity of these structures has yet to be confirmed, their position above other cuticular elements strongly suggest that they are epicuticular in nature and may correspond to similar mesh-like structures found in the cement and wax layers of modern orthopteran epicuticle. Wing cuticle can also possess low-relief ridged surface structures. One orthopteran specimen (NBRL070) retained parallel ridges along its wing cuticle, each covered in perpendicular micro-ridges (Plate 48: D-F). In some taxa, portions of cuticle are covered in irregular topographic variations, probably modified cuticular scales, forming domes (Plate 50: A-D). A more angular version of these structures is also present in odonate pterostigma (Plate 50: E-F).

Many beetles, including fossil forms, possess a variety of cuticle features across their elytra, including deep pits (Ponomarenko, 2003). In the Nova Olinda Member, even where elytra cuticle is relatively poorly preserved, these pits were easily discernible along with spiracles (Plates 51, 52: A-B, and 53: C-F).

Some insects possess large (> 100 µm) robust spines, usually along their limbs, which are often preserved in fossil forms (Plate 54: A). However, in the Nova Olinda Member, many of these spines are preserved with a lower fidelity than their smaller counterparts. They are frequently broken and pressed flat against the body, preserving cuticular ridges along their length (Plate 55). Where they are perpendicular to bedding, they can lose all surface morphology (Figure 48: B-C). Nevertheless, limbs and their spines are often preserved perpendicular to bedding, even penetrating multiple laminae where relief is highest (Figure 48: B).

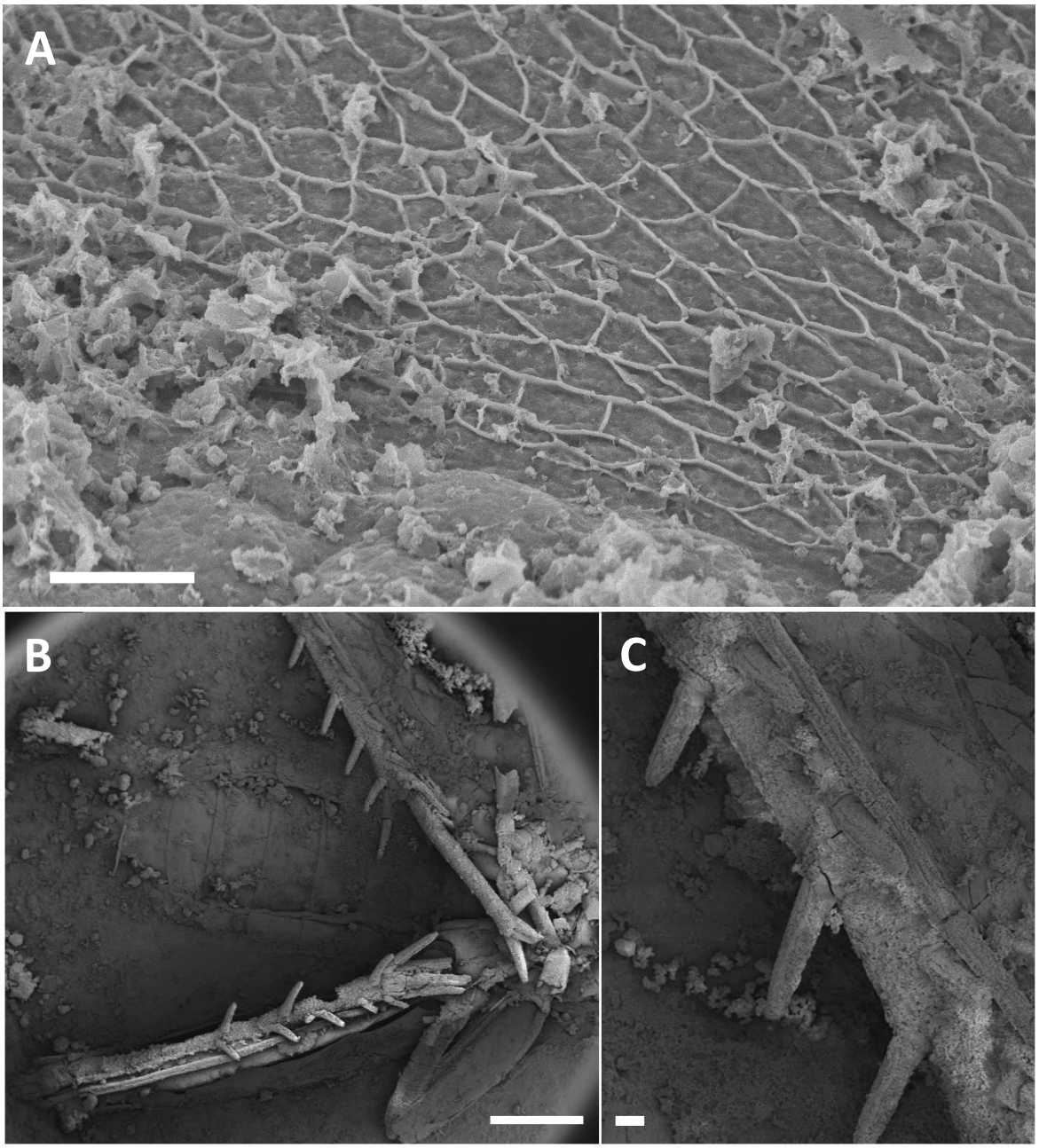


Figure 48. A, Meshwork of cuticular ridges of an elcanid orthopteran (Orthoptera: Elcanidae). B, Orthopteran limb spines perpendicular to bedding. C, Higher magnification image of limb spines. A, Specimen NBRL044-55. B-C, Specimen NBRL059-03. A, Scale bar = 20 µm. B, Scale bar = 1 mm. C, Scale bar = 100 µm.

3. 5. 1. 5. Eyes and ommatidia

Insects possess complex compound eyes, constituted of a honeycomb-lattice of ommatidia. Each ommatidium is capped with a lens covering a crystalline protein cone, which overlies pigment and receptor cells, and finally a rhabdom, all connected to the optic nerve by an axon (Grimaldi and Engel, 2005; Briscoe, 2008).

Almost every insect fossil studied in this project that retained a head, also retained its eyes. This is mostly due to them being a large organ, typically comprising about ~30% of the head, but also because they are relatively durable structures (Grimaldi and Engel, 2005; Briscoe, 2008).

Nevertheless, preservation of insect eyes varies within the Nova Olinda Member and most specimens only retain loosely articulated and poorly mineralised ommatidia (Plates 56-58). However, they can be exceptionally well-preserved (Figure 49; Plate 59). In one specimen (specimen NBRL057), physical damage to the eye removed the ommatidia, revealing what appears to be a mineralised optic nerve beneath (Plate 12: A-D).

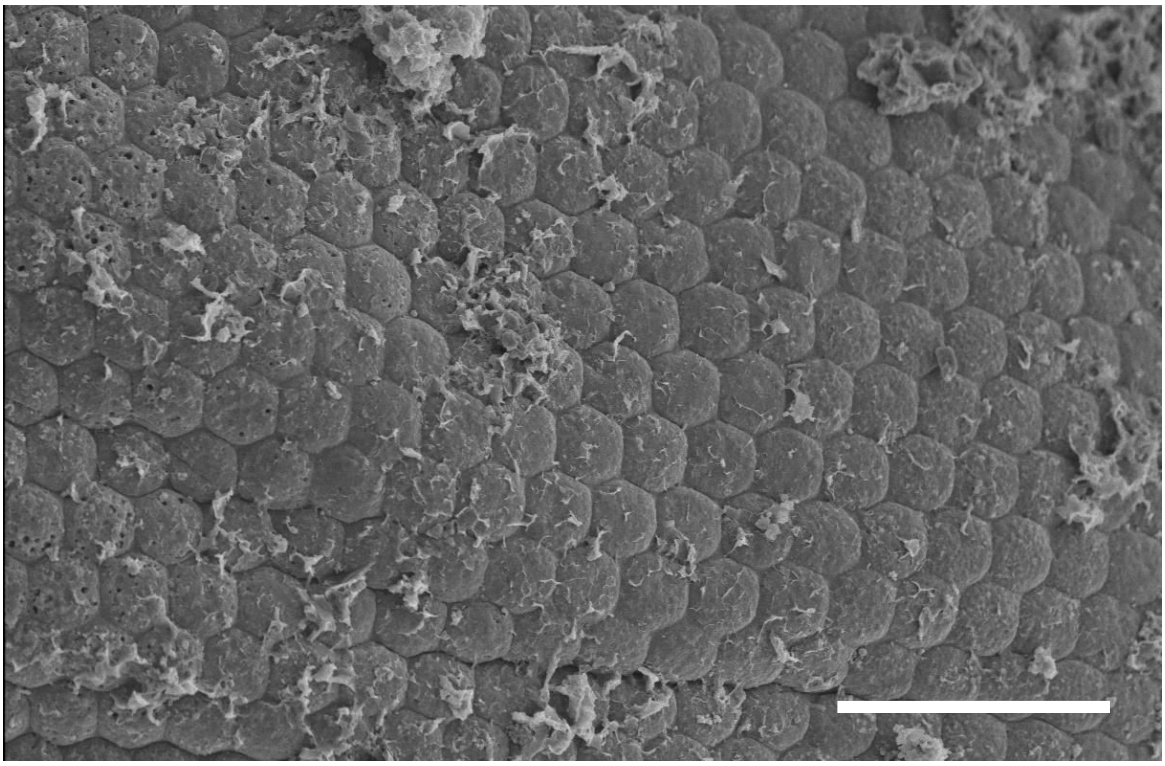


Figure 49. Exceptionally well-preserved orthopteran eye, revealing intact and articulated ommatidia. Specimen NBRL044-18. Scale bar = 100 μm.

3. 5. 1. 6. Other external features

Several other structures and organs preserved in the Nova Olinda Member insects cannot be classified with those above. These are typically non-ubiquitous or gender-specific structures such as feeding apparatus and external genitals. A single specimen (FLO15) retained specialised feeding apparatus in the form of a large proboscis (Plate 60: A-B). In addition to the proboscis, this specimen also preserved the external features of its genitals with high fidelity (Plate 61: A-C). Another specimen (JW614 (SMNS 700902– *Parviformosus* holotype)) also preserved a large external genital feature; its ovipositал sheath (Plate 15) which disarticulated during acid preparation. This sheath is now mounted on a separate stub, housed with the rest of the type specimen.

Several areas of cuticle possessed ambiguous structures or fabrics. Two areas retained folded and deformed cuticle (Plate 62: A-D). These may represent portions of wing venation (Plate 62: A-B) or soft, pliable cuticle around the anus (Plate 62: C-D). Finally, cryptic meshes of tissue were exposed

beneath sediment (or resin where transferred) infrequently, which may represent fragments of wing venation (Plate 62: E-F).

3. 5. 2. Internal labile soft tissues

Where cuticle is lost in Nova Olinda Member insects, either by abrasion, decay, or mechanical preparation, internal tissues can be exposed. The majority of internal tissues are simply obliterated by pseudoframboid-like aggregate growth, but infrequently they can be preserved with a high fidelity by calcium phosphate impregnations and encrustations. Below, examples of the highest fidelity preservation of internal tissues is presented.

3. 5. 2. 1. Muscle

Of these rarer discernible internal tissues, muscle fibres are the most abundant. These are preserved by calcium phosphate impregnation and encrustation in a manner similar to 'Orsten'-type preservation, sometimes with very high fidelity (Maas *et al*., 2006; Eriksson *et al*., 2012). One specimen (FLO19) retains entire muscles within its limbs (Plate 63: A-B). However, in most cases muscle fibres are only preserved as 'scrappy traces' of fibrous material amongst the mass of globular and spherical replacement fabrics (Figure 50; Plate 63: C-H and Plate 64).

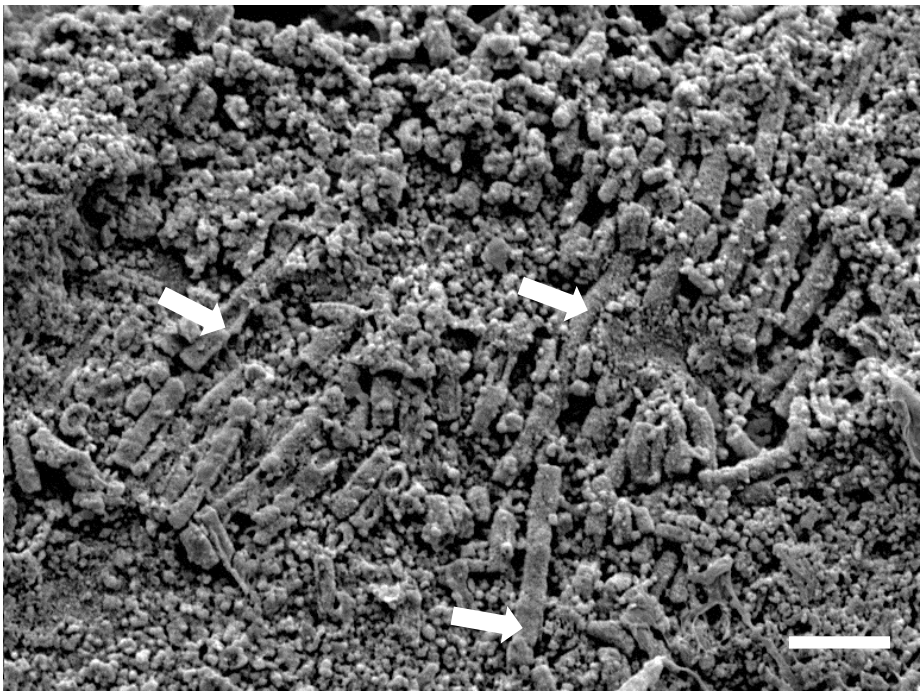


Figure 50. Example of typical preservation of muscle fibres. Arrows highlight fibres. Specimen JW291-083. Scale bar = 10 µm.

3. 5. 2. 2. Internal and external gills

External gills are an outgrowth of the tracheal system that rely on diffusion to supply aquatic insects with oxygen (Grimaldi and Engel, 2005). In the Nova Olinda Member, several aquatic larvae retained their gills with remarkable fidelity (Plate 65). These are extremely fragile

structures and are frequently abraded, revealing details of their internal structure (Grimaldi and Engel, 2005; Plates 66, 67, and 68). They consist of simple hollow tubes (Plate 68: A-E), but can extend into the caudal filaments, forming tightly bound spiral structures (Figure 51; Plates 66: C-D and 67: E-H).

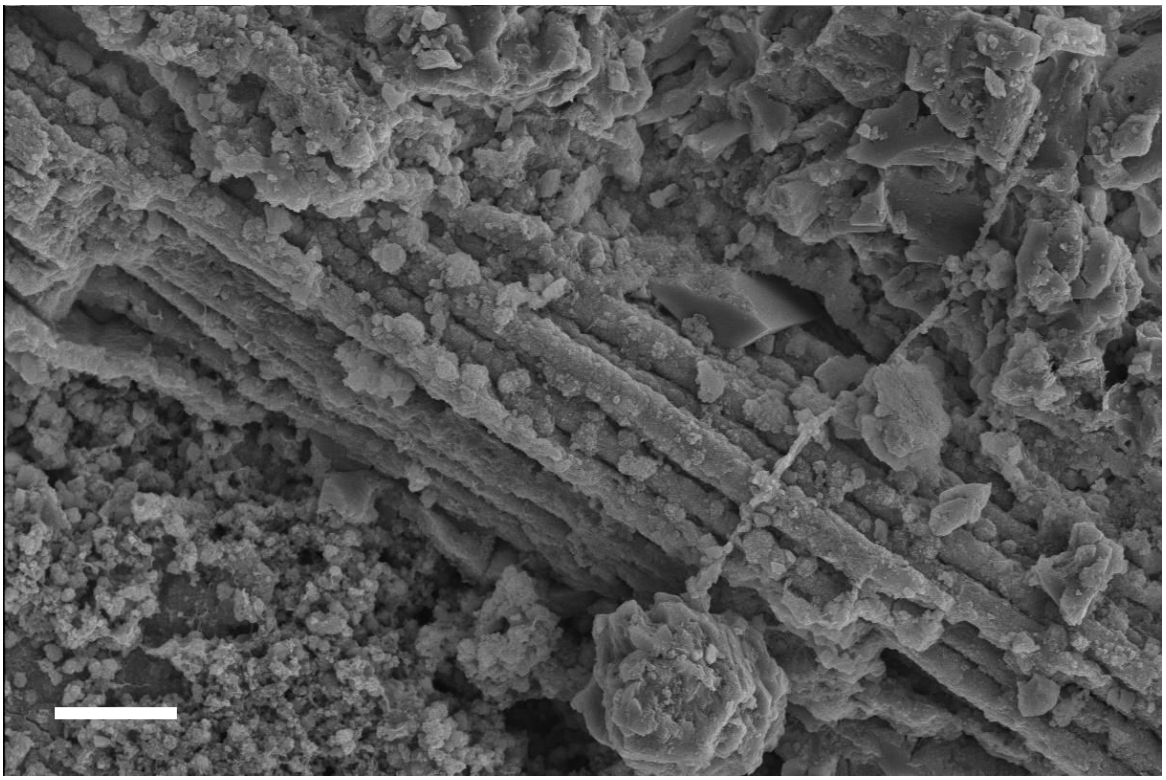


Figure 51. Broken caudal filament of Ephemeroptera larva revealing an internal spiral structure composed of gill tubes. Specimen FLO37-53. Scale = 10 μm.

3. 5. 2. 3. Genitals

One specimen (FLO19) was mechanically prepared by Florence Gallien prior to donation for this project. It exposes exquisitely preserved internal genitals replicated in calcium phosphate. Internal insect genitals are extremely labile and can decay within hours of death (Allison and Briggs, 1993; Briggs, 1995a,b). The specimen is a female dipteran, possibly a brachyceran (Diptera: Brachycera) (Plate 69: D). The size, position, and morphology of the genitals indicates that they are ovaries (Figure 52; Plate 61: D). The ovary is bound to the posterior portion of the abdomen by fibrous structures that likely represent muscles used in oviposition or connective tissue (Plate 61: E-H).

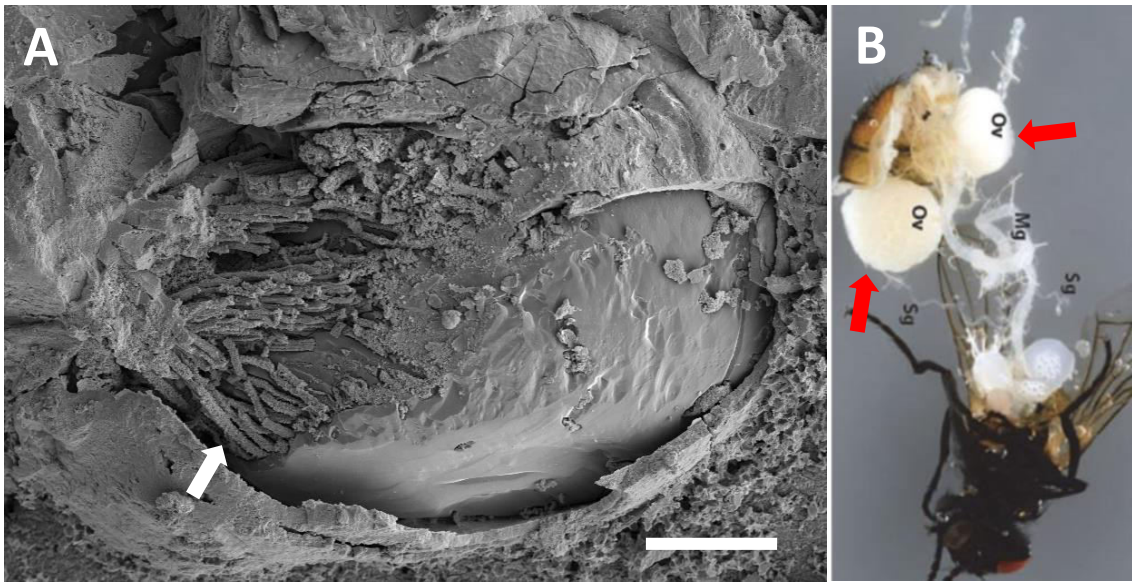


Figure 52. Genitals preserved in Nova Olinda dipteran compared to modern fly genitals. A, Nova Olinda specimen FLO19. Arrow highlights fibrous structures. B, Modern healthy female *Musca domestica*, ovaries marked by 'Ov' and arrows. Image adapted from Kariithi *et al*. (2013). Scale = 100 µm.

3. 5. 2. 4. Fat body and tracheal system

As well as the tissues discussed above, insects possess numerous internal tissues and structures that may be preserved in fossils (Figure 15: C). Several tissue types are presented below that are well-preserved, but still difficult to identify.

There are two examples of 'wavy' internal tissue exposed beneath the cuticle that could represent fat body (Plate 70). Insect fat body is a mesodermal tissue composed of lobes of protein, lipid, and glycogen storing tissues (Grimaldi and Engel, 2005). It functions in a similar manner to that of a vertebrate liver, but is distributed throughout much of the insect body.

A single specimen (FLO19) preserved a tubular structure within the thorax (Figure 53; Plate 71: E-F). The size and positioning of the tube suggests that it may be part of the tracheal system. However, it could alternatively be part of the digestive tract. The digestive tract contains arguably the most labile tissues (Allison and Briggs, 1993; Briggs, 1995a,b). This is because it also contains digestive enzymes, strong acids, and bacterial colonies, all of which readily degrade the surrounding tissues upon death (a process termed autolysis). If this structure is part of the digestive tract, it represents the most labile tissue observed within the Nova Olinda Member fossil insects.

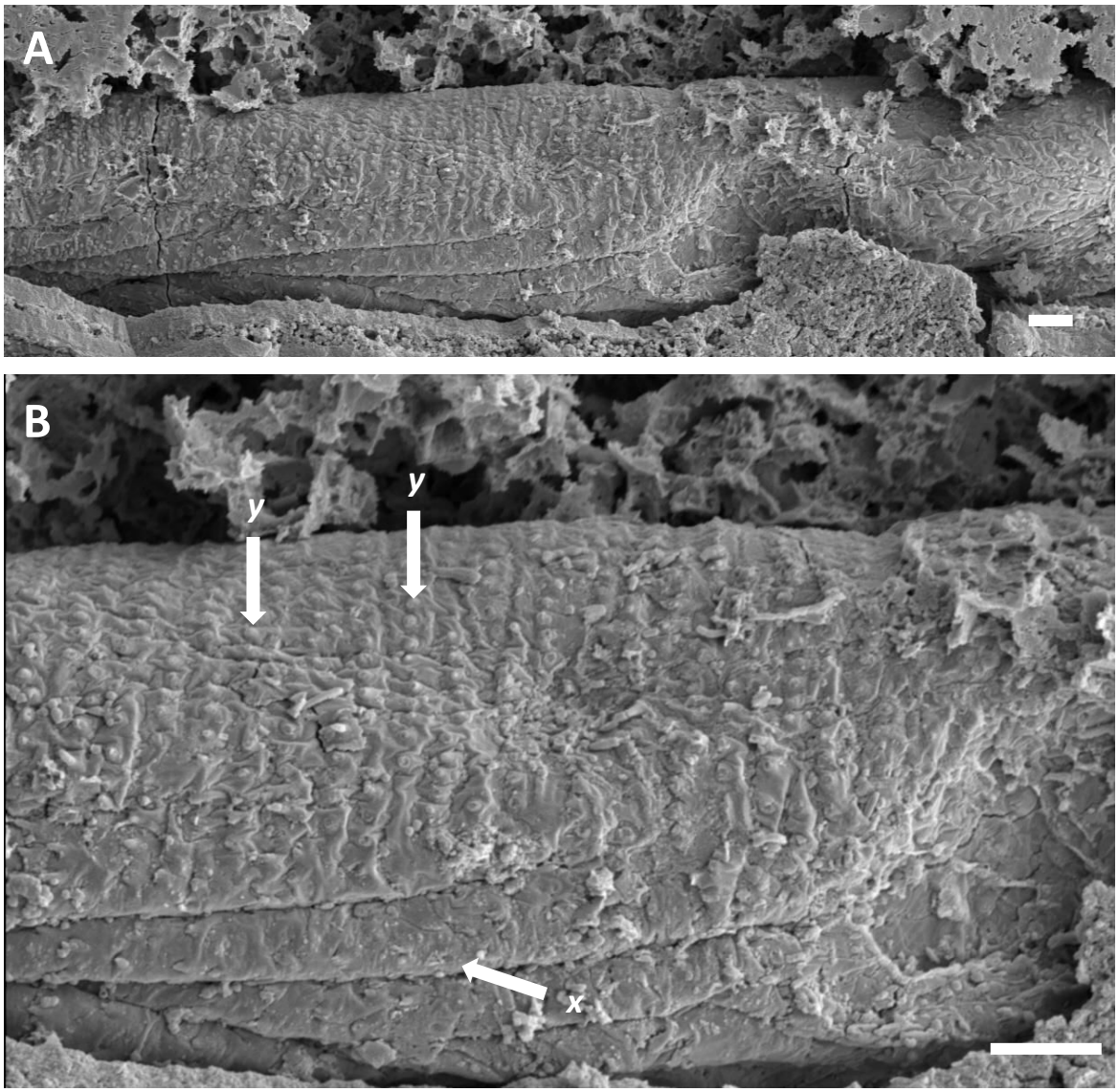


Figure 53. Tubular structure in thorax of specimen FLO19 that could represent part of the tracheal system or digestive tract. A, Overview. B, Higher magnification image highlighting surface structures of the tube. *x*, Folding of soft tissue. *y*, Rows of annulae, or possibly bases of broken micro-spines that can coat arthropod guts (see Soonthornchai *et al*., 2014), amongst 'rippled' tissue fabric. Scale bars = 10 µm.

Finally, a row of large (100 µm) parallel cylindrical structures with rounded edges were imaged in the limb of a hemipteran (Plate 71: A-D). The origin of these structures is unknown, but they are certainly an aspect of the original insect morphology, as they bear no resemblance to other replacement minerals or fabrics suggestive of decay observed in this project. Given their bundled and tubular nature, they probably represent a tight bundle of large muscle fibres used in limb locomotion.

3. 6. Fabrics representing decay

Determining which fabrics of a fossil are a result of decay, rather than original insect morphology or replacement mineral morphologies can be problematic. Decay itself can alter original tissues to

an unrecognisable globular ‘mess’ and these decayed tissues may not be a suitable substrate for mineral precipitation (Briggs and Kear, 1993a; Martínez-Delclòs and Martinell, 1993; Briggs, 1995a,b). Instead, crystals may grow in cavities around the decayed tissue, moulding them. This results in the decay fabric being replaced by an unrelated mineral fabric. This process has already been suggested for some of the fabrics observed in the Nova Olinda Member insects (Osés *et al*., 2016). Alternatively, decay simply may be represented by areas of non-mineralisation. However, areas that represent decay can be inferred from the current understanding of insect taphonomy. Areas of cuticle that are particularly thin or contain perforations are known to degrade before others as internal tissues decay (Smith *et al*., 2006). This results in a loss of fidelity at these locations and there are numerous examples within the Nova Olinda Member insects. Setal bases (Plate 36: A-B; Plate 41: E-F; Plate 72: C-H; Plate 73), spiracles (Plate 74: E-F), and segment boundaries (Plate 75 and 76: A-E) all are frequently surrounded by areas of poorly preserved cuticle. The fabrics observed in these areas can then be used as an analogue for identifying patches of decay elsewhere in the specimens. Areas where fidelity is lost without these corresponding ‘decay fabrics’ are interpreted here as areas of non-mineralisation.

The majority of these poorly preserved areas differ from the typical pseudoframboid-like aggregate replacement fabric. Instead, they exhibit a varying globular fabric composed of disordered micro-grains (Figure 54). In some areas, this transitions into the typical pseudoframboid-like aggregate replacement fabric (Plate 75: C-F; Plate 76: A-E), but in others there is a sharp contact to well-preserved insect tissues (Plate 72: D-G; Plate 73: A). In other specimens, decay may be represented by globular fabrics (Plates 21, 77, and 78). Additionally, where phosphatisation has encrusted internal tissues in ‘bubble-like’ fabrics, it is likely that this is a result of the decay of adjacent tissues (Maas *et al*., 2006; Eriksson *et al*., 2012).

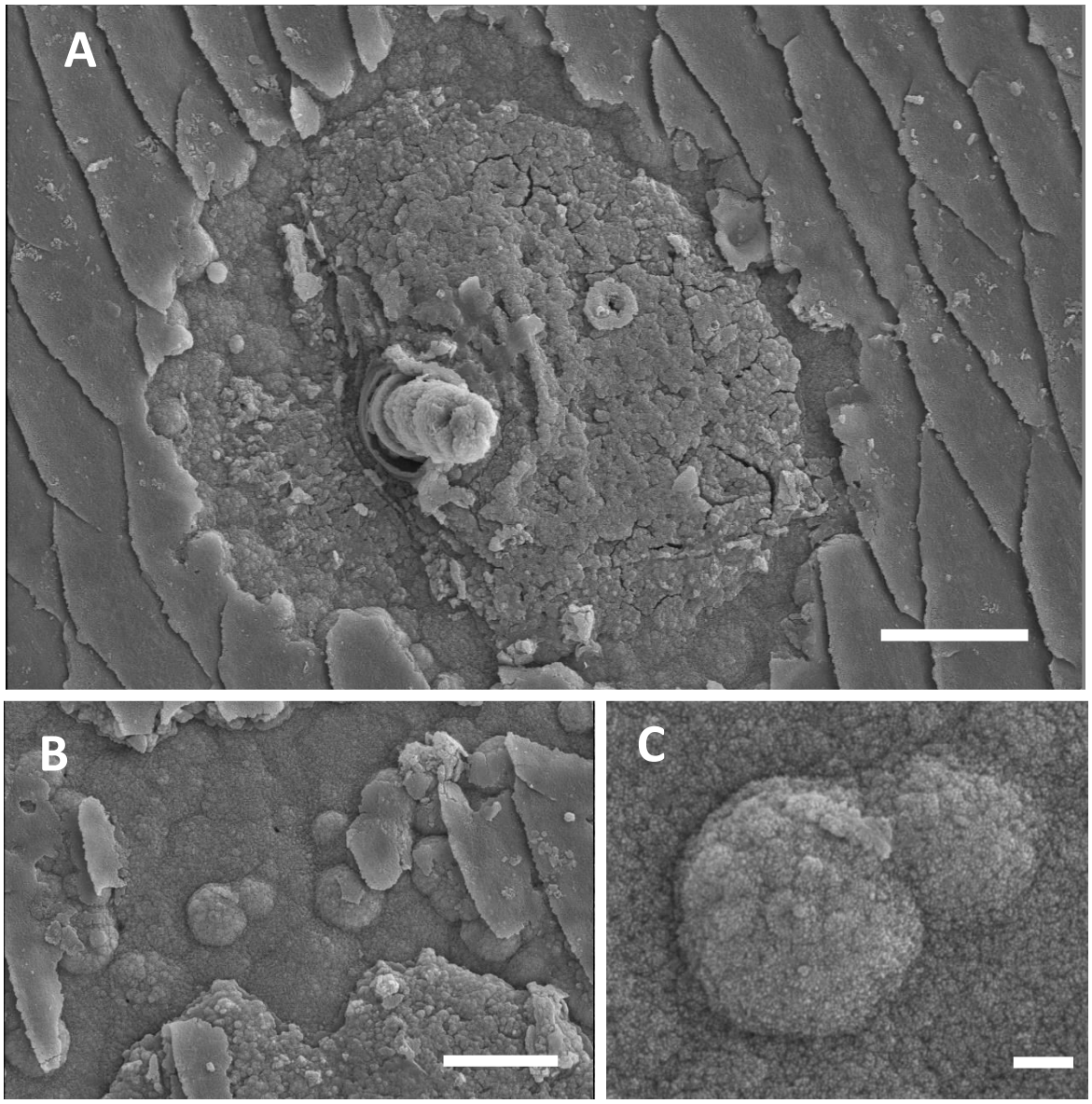


Figure 54. Fabrics associated with areas of decay within Nova Olinda Member insects. A, Globular fabric associated with perforation in cuticle (setae). B, Globular fabric adjacent to well-preserved cuticle (near setae). C, Subspherical structures in otherwise globular fabric. Specimen NBRL054. A, Scale bar = 100 µm. B, Scale bar = 10 µm. C, Scale bar = 1 µm.

Alternatively, insect tissues that have been warped or otherwise altered in a plastic manner could represent areas of decay. Warping is most prominently seen in setae (Plate 43). Nevertheless, these setae still retain many surface features and remain articulated with the cuticle, suggesting that their alteration may not be a result of decay. In some areas, cuticle simply loses all fabric, resulting in a near-smooth surface (Plate 37 and 79). Determining the cause of such an alteration may not be possible.

3. 7. Artefacts of preparation

The majority of insect tissues preserved in the Nova Olinda Member are replaced by brittle iron minerals (Menon and Martill, 2007; Barling *et al*., 2015; Minerals.net, 2015). This renders them particularly prone to damage during extraction, transport, and preparation. Identifying areas damaged in this manner is important for determining artefacts that may affect taphonomic analyses. Artefacts of transport/preparation/curation are distinguished based on their occurrence without associated mineralogical fabrics (i.e. a crack without infilling fabrics of mineral growth/precipitation).

By far the most common artefact of handling and preparation is the cracking of large cuticular sclerites (Plate 16: A-F; Plate 80). Long thin sections of cuticle (e.g. wing veins) can also break easily (Plate 81: A-D; Plate 82: B-D). These brittle breakages can even be in immediate contact with areas of exceptional preservation (Plate 83). Insect cuticle is a relatively flexible material and could not have broken in this manner prior to mineralisation (Hopkins and Kramer, 1992).

In some areas, this brittle nature causes the connection between the epicuticle and exocuticle to weaken, resulting in a vulnerability to erosion. The epicuticle becomes easy to dislodge and abrasion can cause the outermost features to delaminate (Plate 16: G-H; Plate 84: A-B). During chemical preparation, acetic and hydrochloric acid were used to remove the calcium carbonate sediment. While the preserving iron minerals are insoluble in these acids, the reactions produce effervescence, which could cause damage to the specimens. This damage resulted in the creation of artefacts that could be falsely interpreted as decay. Cuticle in high relief areas (e.g. limb spines) were exposed to more effervescence and ultimately the cuticle would appear ‘degraded’ as if it were decaying (Plates 85 and 86). In the most extreme cases, the weak connection between all cuticular layers (presumably in cuticle that did not have a massive internal fabric) would fail, causing the epicuticle to ‘flake’ away (delaminate, see Chapter 2. 2. 1. 3.; Figure 21). In one specimen (JW614, SMNS 700902– *Parviformosus* holotype), the effervescence caused damage to its fragile ovipositал sheath, ultimately resulting in it disarticulating from the rest of the specimen (Plate 15). The association of effervescence during acid digestion with this fabric is yet to be experimentally verified, and so is currently unsubstantiated.

Some areas may indicate clumsy mechanical preparation prior to acquisition for this project, where the cuticle was punctured (Figure 55; Plate 84: H). These punctures may have been caused by a needle, but are of particular importance as they could be confused with *in vivo* interactions, such as the predatory traces of Reduviidae (Sahayaraj *et al*., 2010). However, their diffuse boundary revealing the replacement fabric and extremely small size suggests against them being artefacts of preparation. Currently, their cause is unknown.

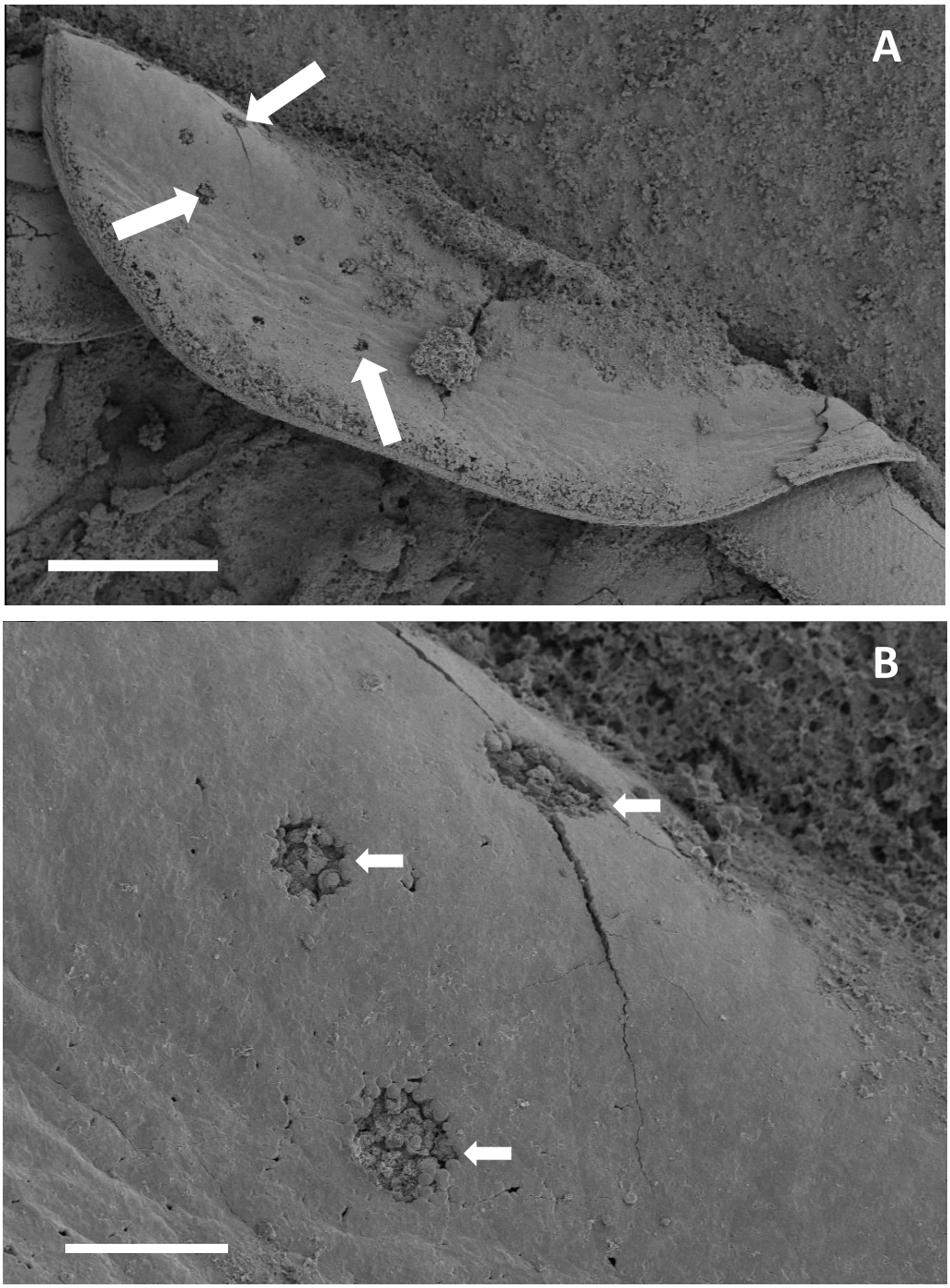


Figure 55. A, Puncture marks on orthopteran prothoracic plate possibly caused by clumsy mechanical preparation, creating an artefact of *in vivo* interactions (predation). Arrows highlight several of the puncture marks. B, Higher magnification image of puncture marks, revealing that the damage traces pseudoframboid-like replacement fabric beneath. However, the occurrence of the exposed replacement fabric and their diffuse boundaries suggest that they may instead simply be areas of incomplete mineralisation. Specimen NBRL054. A, Scale bar = 500 µm. B, Scale bar = 100 µm.

3. 8. Results of statistical analyses

3. 8. 1. Taphonomic index

The taphonomic indices described in Chapter 2. 3. 8. 1. were designed to provide simplistic summaries of the preservational quality of insect specimens. This was achieved by normalising character data into values between 0 and 1, and averaging them. Three indices were generated, based on the type of data included (all taphonomic characters, completeness characters, and non-completeness characters). This resulted in a taphonomic index value for each specimen, which are presented below binned into ranges of 0.1 (Figures 56-58). These figures illustrate the distribution of taphonomic indices within the collection, revealing a near-normal bell-curve distribution for all three measurements.

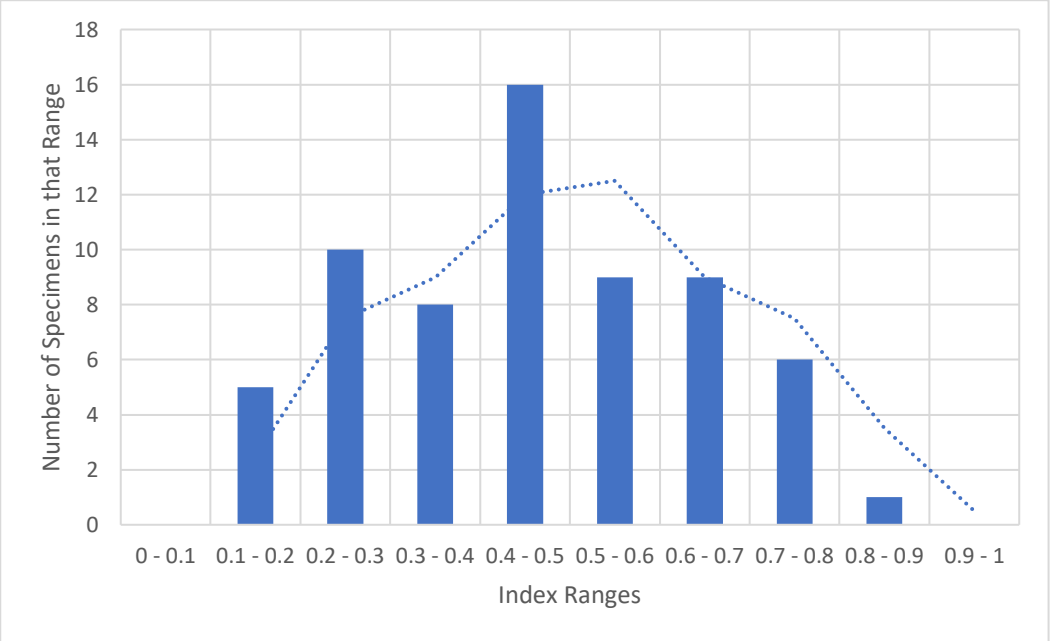


Figure 56. Taphonomic indices (average score from normalised taphonomic character data) from all taphonomic characters measured. Bar graphs showing the distribution of taphonomic indices calculated from all characters, binned into ranges of 0.1 between zero and one. Line of best fit shows that there is a near-normal bell-curve distribution.

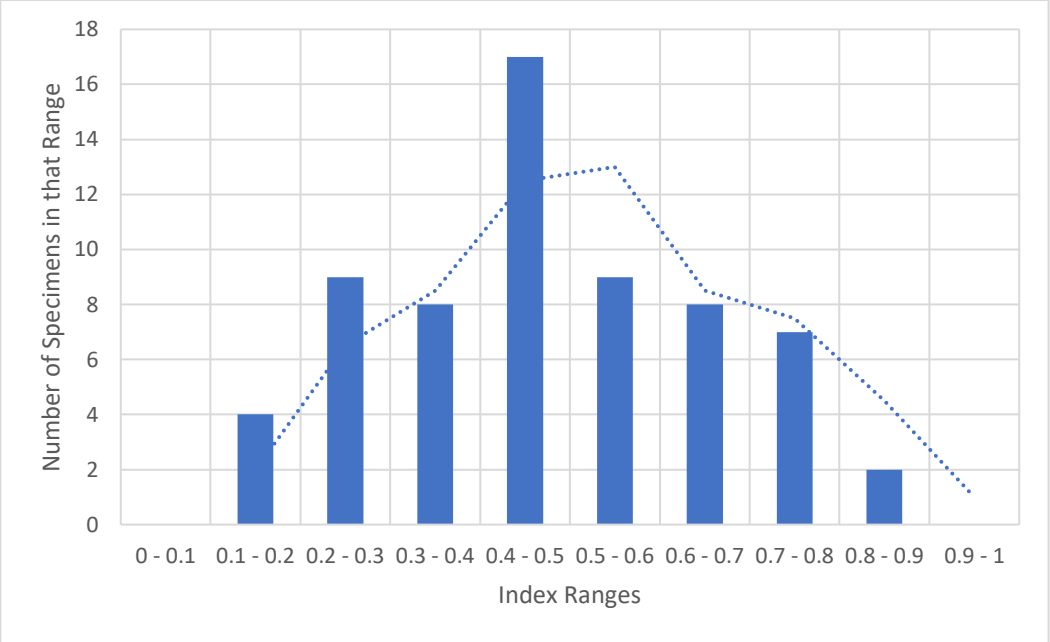


Figure 57. Taphonomic indices (average score from normalised taphonomic character data) from completeness taphonomic characters only. Bar graphs showing the distribution of indices calculated from completeness characters only, binned into ranges of 0.1 between zero and one. Line of best fit shows that there is a near-normal bell-curve distribution.

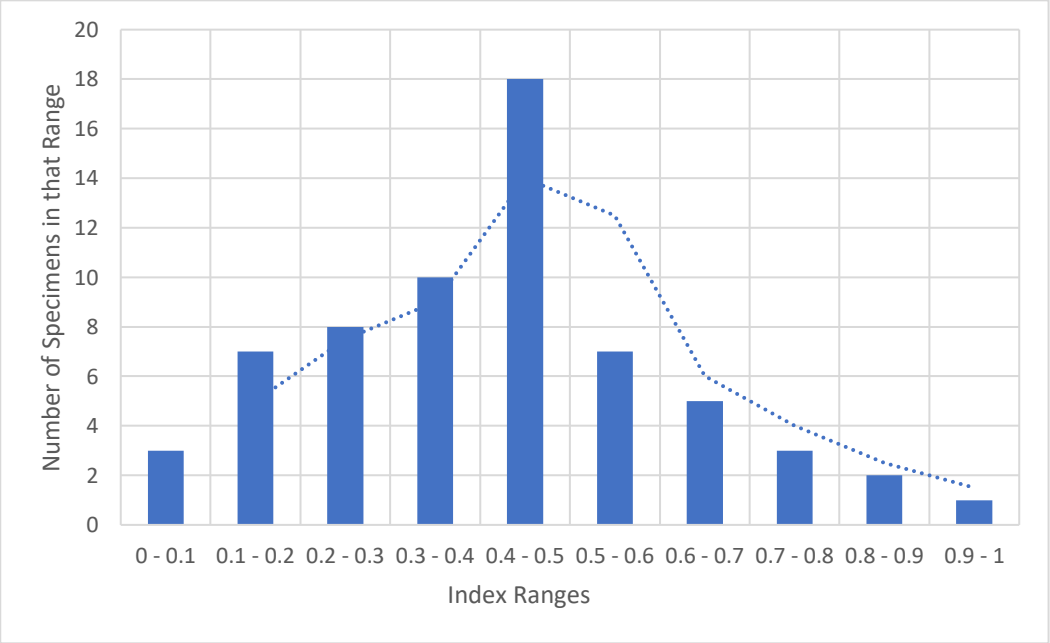


Figure 58. Taphonomic indices (average score from normalised taphonomic character data) from non-completeness taphonomic characters only. Bar graph showing the distribution of indices calculated from non-completeness characters only, binned into ranges of 0.1 between zero and one. Line of best fit shows that there is a near-normal bell-curve distribution, with a slight skew towards poorer preservation.

3. 8. 2. Cluster analyses

The results of the PAST cluster analyses are presented below in the form of dendrograms (Figures 59-64). For the R-mode analyses, taxonomic identifications were added to family level where

possible. Two datasets were used: all taphonomic characters (Figures 59 and 60) and completeness characters only (Figures 61 and 62). A dendrogram was not created for non-completeness characters, as there were comparatively few characters. As described in Chapter 2. 3. 8. 2., two similarity indices were used (Euclidean and Gower), resulting in a total of four R-mode analyses dendrograms.

For the Q-mode cluster analyses, all taphonomic characters were used, excluding the "Other:_____" abdominal character. As with the R-mode analyses, both Euclidean and Gower similarity indices were used, resulting in a further two dendrograms (Figures 63 and 64). All cluster analyses applied the Paired Grouping (UPGMA) algorithm.

Author note: As will be discussed in Section 3. 9. 4. below, the term '*definitive*' is italicised here as it has a specific meaning in cluster analyses generated in the software PAST, relating to the strength of the cluster (Hammer, 2017).

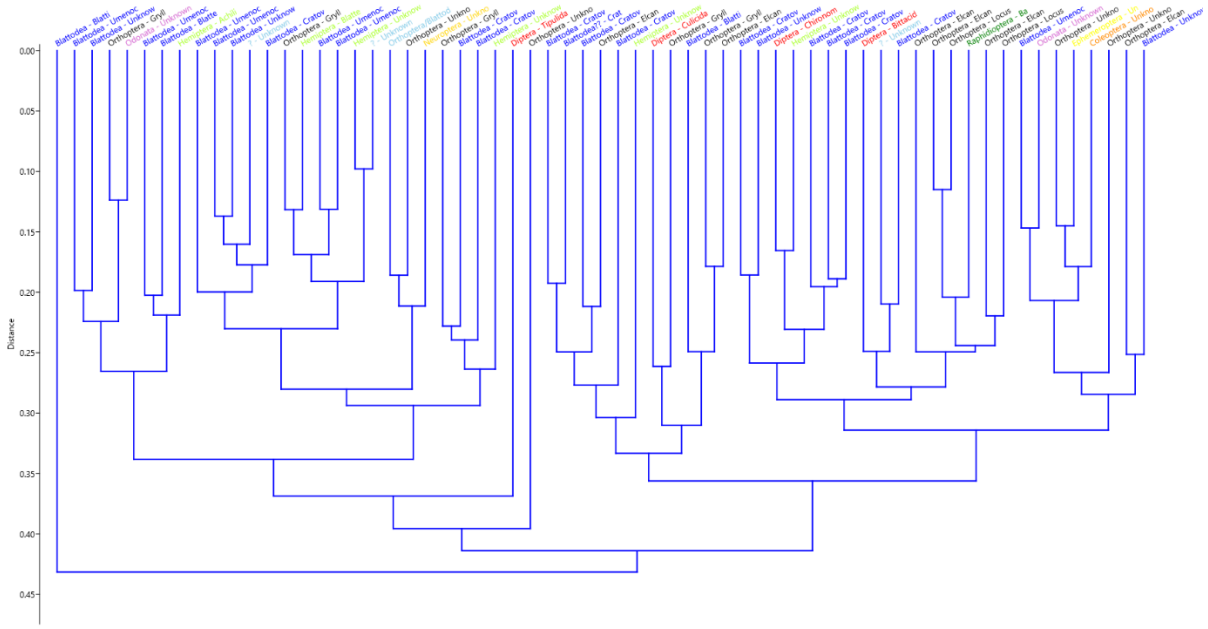


Figure 59. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. All taphonomic characters are included. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Gower similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here). Text colour corresponds to insect order identification (see Figure 65 below).

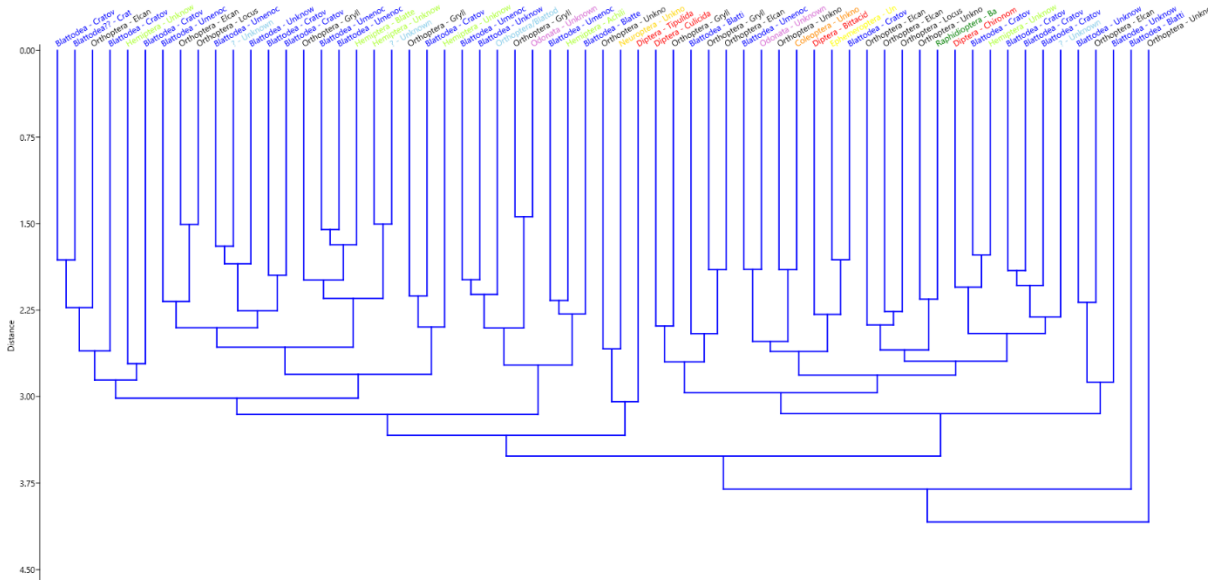


Figure 60. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. All taphonomic characters are included. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Euclidean similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here). Text colour corresponds to insect order identification (see Figure 65 below).

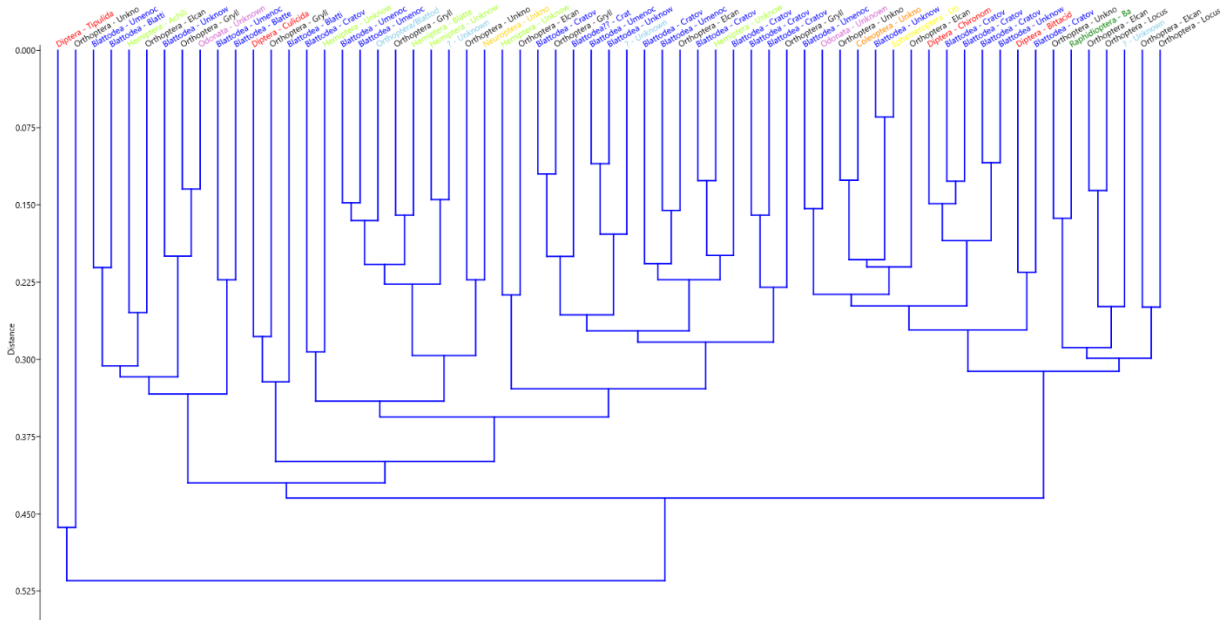


Figure 61. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. Only completeness characters are included. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Gower similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here). Text colour corresponds to insect order identification (see Figures 65 and 71 below).

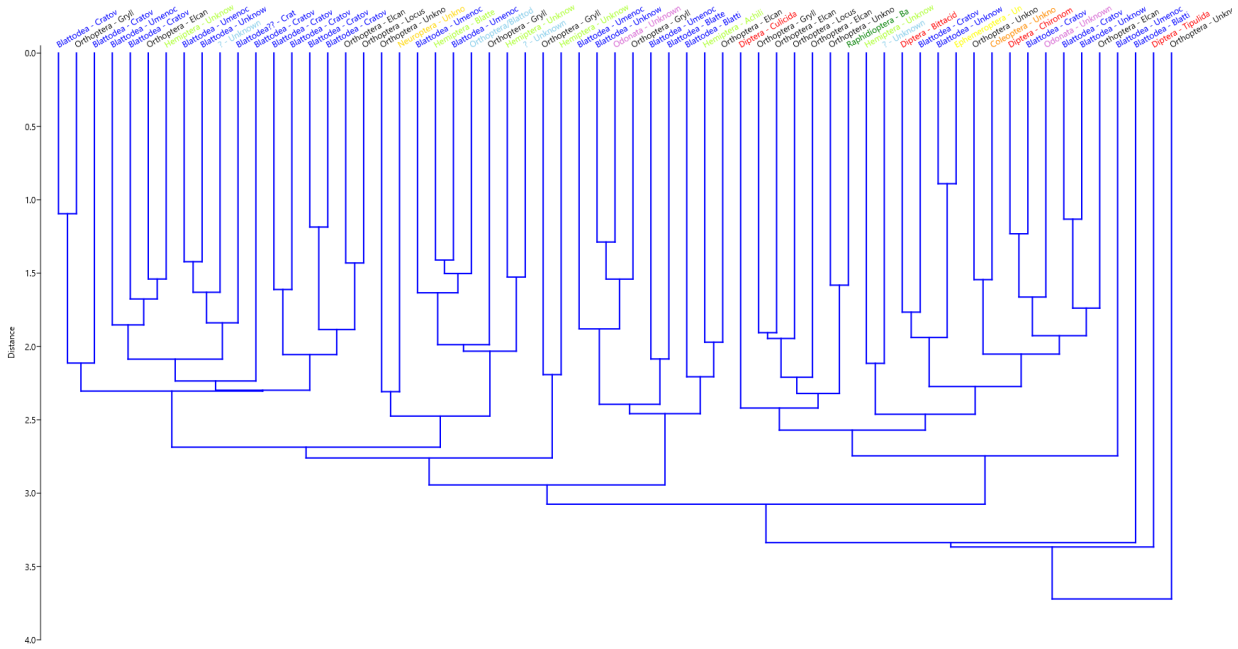


Figure 62. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. Only completeness characters are included. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Euclidean similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here). Text colour corresponds to insect order identification (see Figures 65 and 71 below).

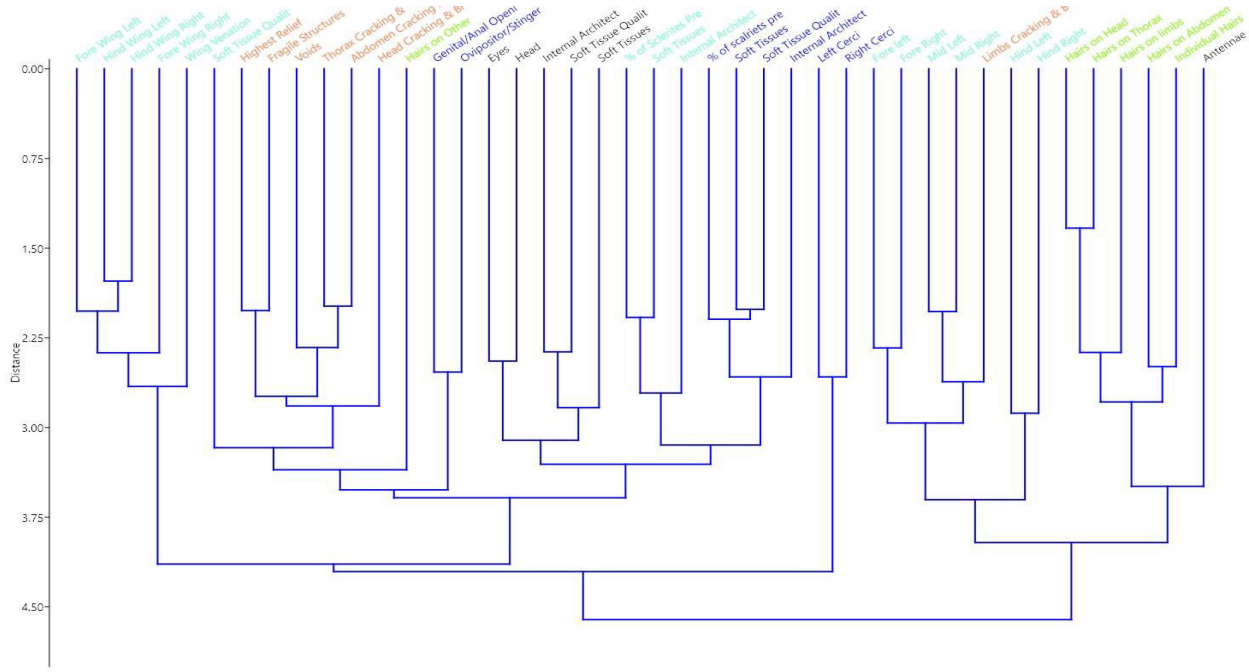


Figure 63. Q-mode cluster analysis dendrogram showing the relationship between characters. Characters are colour coded: black for completeness of the head, light blue for completeness of the thorax, dark blue for completeness of the abdomen, green for characters relating to setal preservation, and orange for non-completeness characters. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Euclidean similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here).

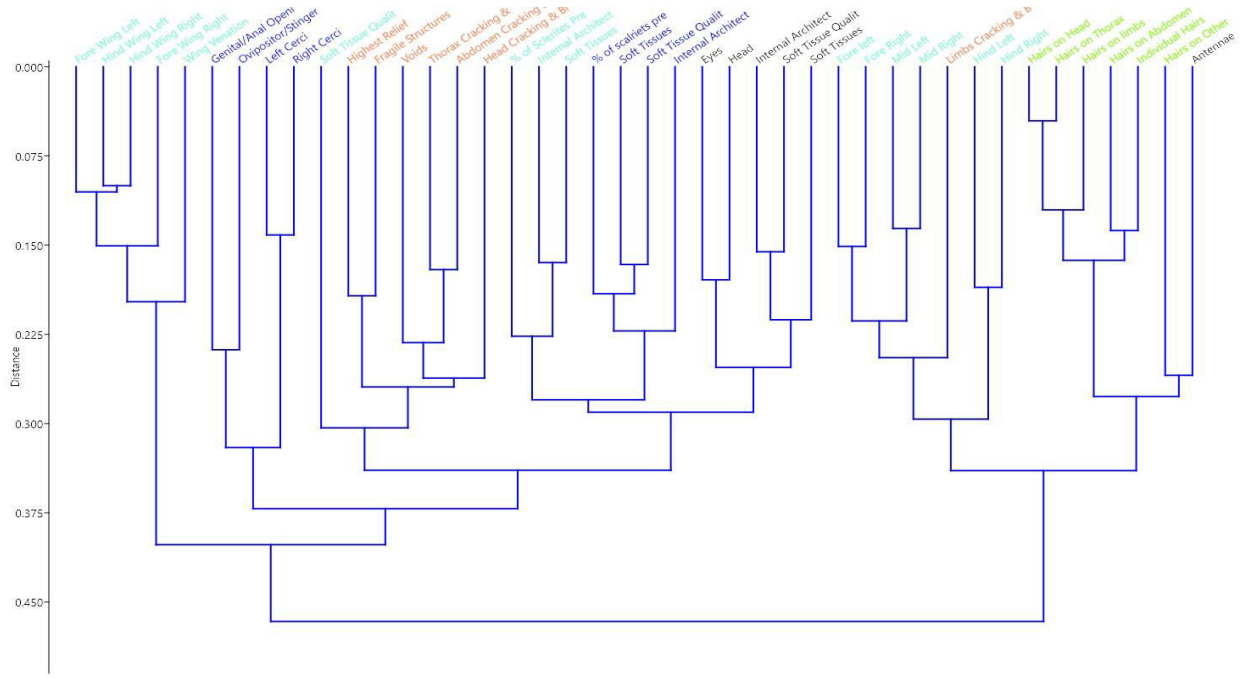


Figure 64. Q-mode cluster analysis dendrogram showing the relationship between characters. Characters are colour coded: black for completeness of the head, light blue for completeness of the thorax, dark blue for completeness of the abdomen, green for characters relating to setal preservation, and orange for non-completeness characters. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Gower similarity index. A higher distance between branches denotes a stronger relationship. *Definitive* clusters are denoted by a change in branch colour (none present here).

3. 8. 3. Principle Coordinate Analysis

To corroborate clusters observed in the cluster analysis (discussed further below), principle coordinate analyses were also undertaken. Both data for 'all taphonomic characters' and 'completeness only characters' are presented as principle coordinate scatter plots (Figures 66 and 67), along with a key (Figure 65).

Order - Family	Symbol
Unknown - Unknown	●
Orthoptera/Blattodea - Unknown	●
Blattodea - Blattellidae	●
Blattodea - Cratovitismidae	+
Blattodea - Umenocoleidae	■
Blattodea - Unknown	◊
Coleoptera - Unknown	●
Diptera - Bittacidae	●
Diptera - Chironomidae?	+
Diptera - Culicidae??	■
Diptera - Tipulidae	◊
Ephemeroptera - Unknown	●
Hemiptera - Achilidae??	●
Hemiptera - Blattellidae	+
Hemiptera - Tettigarctidae??	■
Hemiptera - Unknown	◊
Neuroptera - Unknown	●
Odonata - Unknown	●
Orthoptera - Elcanidae	●
Orthoptera - Gryllidae	+
Orthoptera - Locustopsidae	■
Orthoptera - Unknown	◊
Raphidioptera - Baissopteridae??	●

Figure 65. Taxon symbol key for principle coordinate analyses. Colours of symbols correspond to insect order identifications, as with the cluster analyses presented above. Light blue = Unknown; dark blue = Blattodea; orange = Coleoptera; red = Diptera; yellow = Ephemeroptera; light green = Hemiptera; gold = Neuroptera; purple = Odonata; black = Orthoptera; dark green = Raphidioptera.

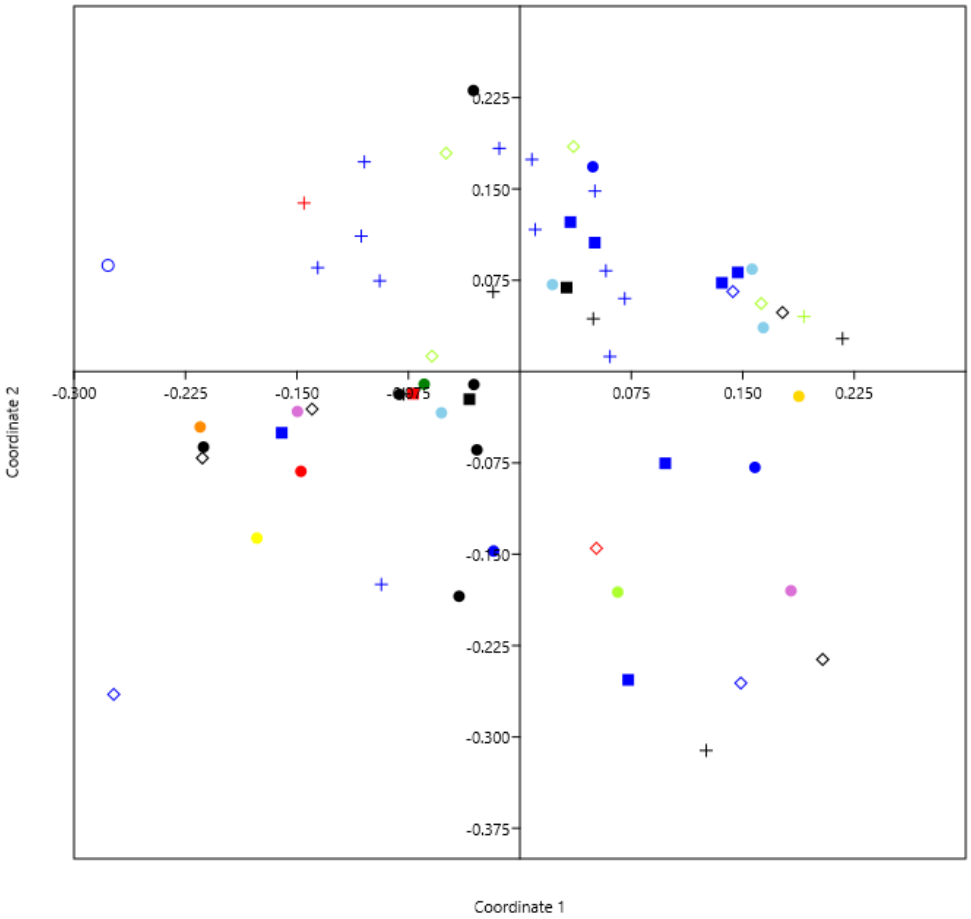


Figure 66. Principle coordinate analysis scatter plot showing the relationships between specimens, based on their taphonomic measurements. All taphonomic characters are included. This analysis used a Gower similarity index. A shorter distance between points denotes a stronger relationship.

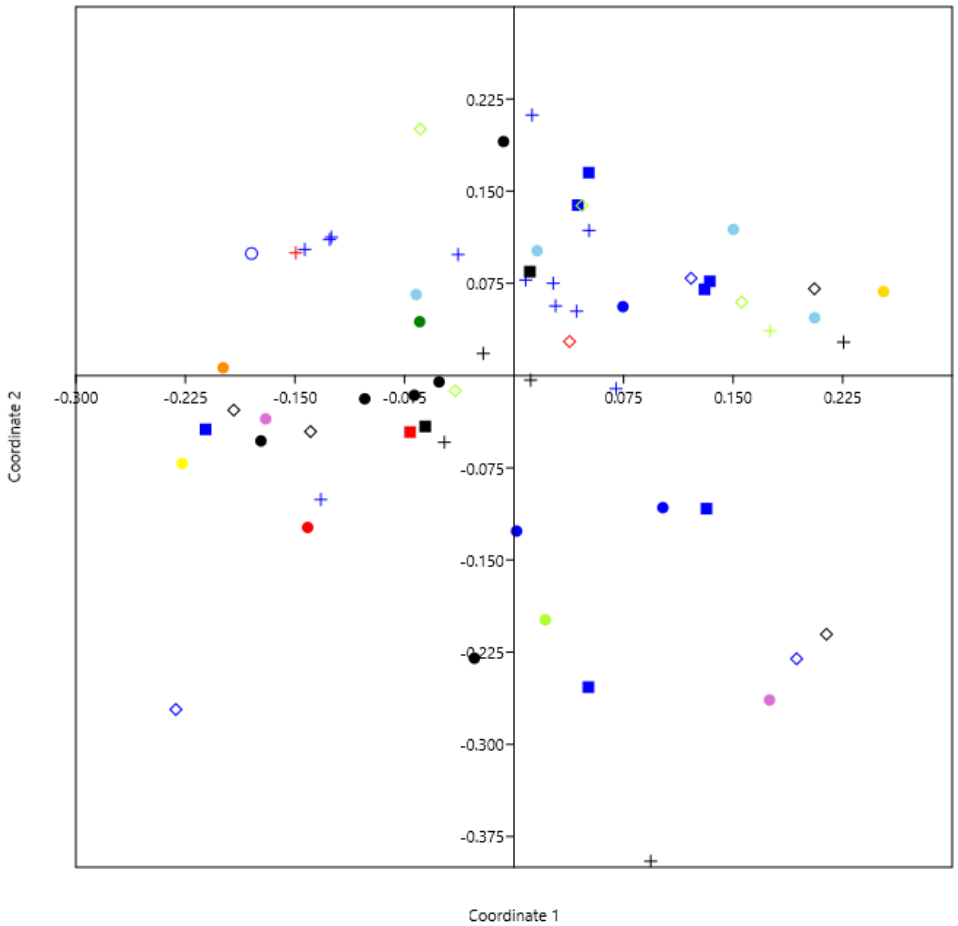


Figure 67. Principle coordinate analysis scatter plot showing the relationships between specimens, based on their taphonomic measurements. Only completeness taphonomic characters are included. This analysis used a Gower similarity index. A shorter distance between points denotes a stronger relationship.

3. 9. Discussion of statistical analyses

The graphs presented above allow for the statistical analyses undertaken here to be visualised and scrutinised. Their primary purpose is to identify trends in taphonomy that could be linked to taxonomy or ecology. Below, the results of these analyses are discussed and important features highlighted.

3. 9. 1. Taphonomic index

A simplistic scheme for determining a taphonomic index for each specimen was included in this thesis (as outlined in Chapters 2. 3. 8. 1. and 3. 8. 1.). This index represents an average of the preservational fidelity of any given specimen, including measurements of its completeness, internal tissue preservation, relief, void infills, etc. (Tables 8a-8c in Appendices 8. 7.). The dataset created are of value for larger scale taphonomic analyses, potentially allowing for taphonomic comparisons across time, geography, climate, and paleoecology.

The indices were binned into ranges of 0.1 and plotted on histograms to visualise their distribution. The graphs display a normal or near-normal bell-curve distribution, as shown by the lines of best fit (Figures 56-58 From this, it could be interpreted that the Nova Olinda Member has 'moderately' or 'averagely' preserved insects compared to other Lagerstätten (discussed later in Chapter 4. 1.). However, the index value that constitutes a 'well-preserved' specimen must first be established. A majority of non-amber fossil insect localities yield only fragmentary remains (Rasnitsyn and Quicke, 2002; Schlüter, 2003; Grimaldi and Engel, 2005; Penny and Jepson, 2014). Fragmentary remains studied in this analysis typically have an index value of 0.01 – 0.2 (Tables 8a-8c in Appendices 8. 7.), and so the majority of insect localities would be shifted negatively significantly. Consequently, a normal distribution likely represents an abnormally high fidelity of preservation. Additionally, considering that the specimens studied here were donated on the basis of their poor preservation, a distribution based on an unbiased collection from the Nova Olinda Member may be significantly higher (shifted positively).

3. 9. 2. Index box and whisker plots

The taphonomic indices that were generated from the three datasets (all characters, completeness only characters, and non-completeness only characters) were separated into taxonomic groups (insect orders) and plotted as box and whisker plots (Figures 68-70). These allowed for taphonomic index scores to be compared against their taxonomic identification (only to order-level in this case), aiding in the identification of taphonomic trends. The 'box' in box and whisker plots denotes where the majority of scores fall, with its lower limit marking the 25th quartile and upper limit marking the 75th quartile. The 50th quartile is represented by a horizontal line within the box and the average index score is highlighted by a cross. Outliers fall between the

'whiskers', with extreme outliers plotted as unattached points. Typically, a box that is positioned higher or lower than others suggests a significant difference in results (in this case how well-preserved insects are from that order).

Figure 68 summarised the taphonomic indices generated from all taphonomic characters in the form of a box and whisker plot. Hemiptera appears to have a higher and tighter box than others. However, as they are represented by relatively few specimens (six), their box is more vulnerable to skewing from outliers. Consequently, Blattodea and Orthoptera are likely the only orders that can be investigated, due to their relative abundance of specimens (25 and 16 respectively). Of the two, Blattodea has a tighter box range, between 0.52 and 0.33, with a median of 0.42 and an average score of 0.45. This indicates that most of their index scores fall between 0.52 – 0.33, a range that could be considered moderate-to-low. The orthopteran taphonomic index box has a larger range, but also extends notably higher (between 0.63 and 0.35, with a median of 0.49 and an average index score of 0.51). This indicates that, within this collection, members of Orthoptera generally have a higher fidelity of preservation than members of Blattodea.

The box and whisker plot summarising taphonomic indices from the completeness only characters (Figure 69) is similar to the one described above (Figure 68, summarising all taphonomic characters). The box range for Blattodea is almost identical at 0.52 – 0.34, as is the median (0.43) and the average index score (0.45). The box range for Orthoptera is, again, almost identical at 0.63 – 0.37, the median and average very similar (0.49 and 0.51 respectively). This extreme similarity is simply a result of the two analyses sharing a majority of characters. In fact, non-completeness characters only account for seven out of the forty-three characters measured.

The indices calculated from this small number of non-completeness characters were also plotted in a box and whisker plot (Figure 65). Despite their relatively few characters, these indices can provide useful insights into how different orders can be affected by non-completeness taphonomic characters (e.g. resistance to compaction). For both Blattodea and Orthoptera, the upper limit of the box (75th quartile) remained relatively similar, whereas the lower limit of the box (25th quartile) dropped. Notably, Blattodea also developed two extreme outliers at 1 and 0.89. These indicate that at least two of the Blattodea specimens resisted compaction exceptionally well. Conversely, one of the Hemiptera specimens also plotted as an outlier, but at an extremely low index of 0.14. This specimen resisted compaction poorly and was heavily crushed.

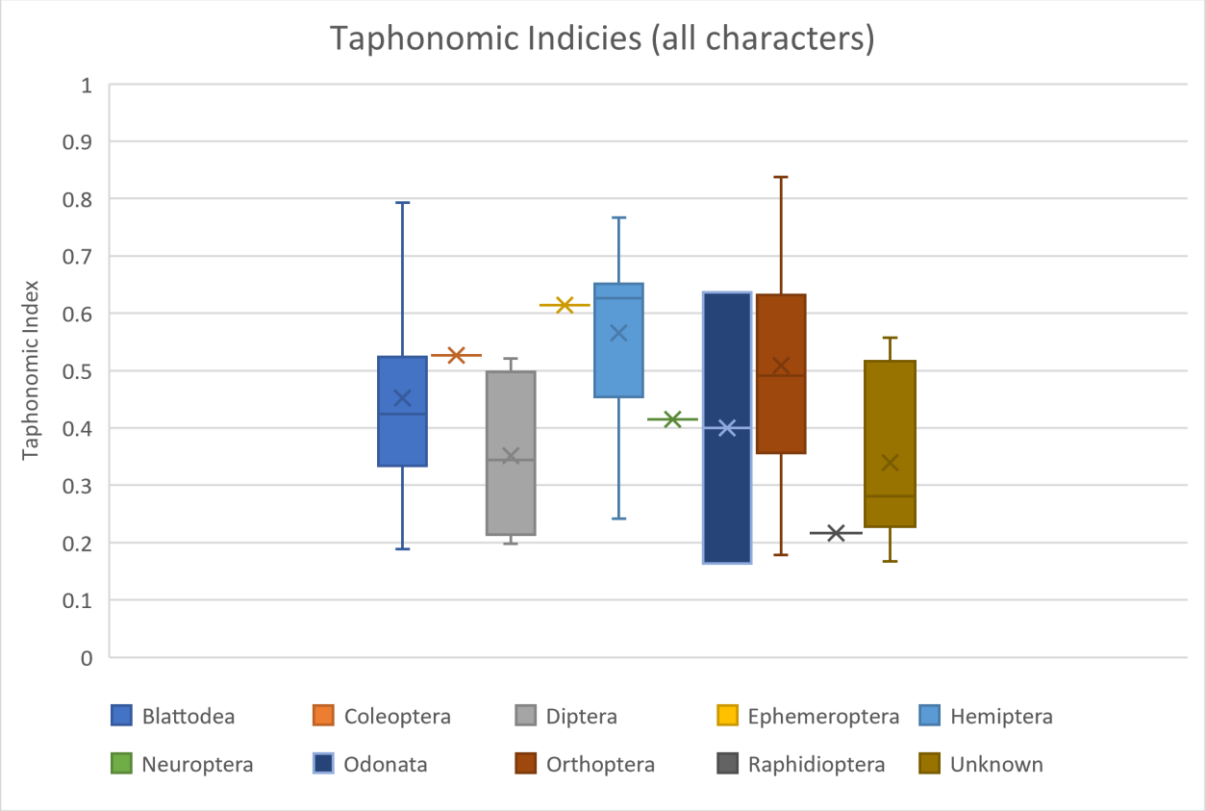


Figure 68. Box and whisker plots of the taphonomic index scores, including all taphonomic characters. Insects are separated into taxonomic groups (orders). Number of specimens for each order is as follows: Blattodea, 25; Coleoptera, 1; Diptera, 4; Ephemeroptera, 1; Hemiptera, 6; Neuroptera, 1; Odonata, 2; Orthoptera, 16; Raphidioptera, 1; and Unknown, 6. The median quartile for the taphonomic index values of each insect order are represented by a horizontal line, bound by the interquartile range (25^{th} and 75^{th} quartiles), creating a coloured 'box'. Outliers are represented by 'whiskers'. Extreme outliers are represented by unconnected points. The average taphonomic score is marked with an X.

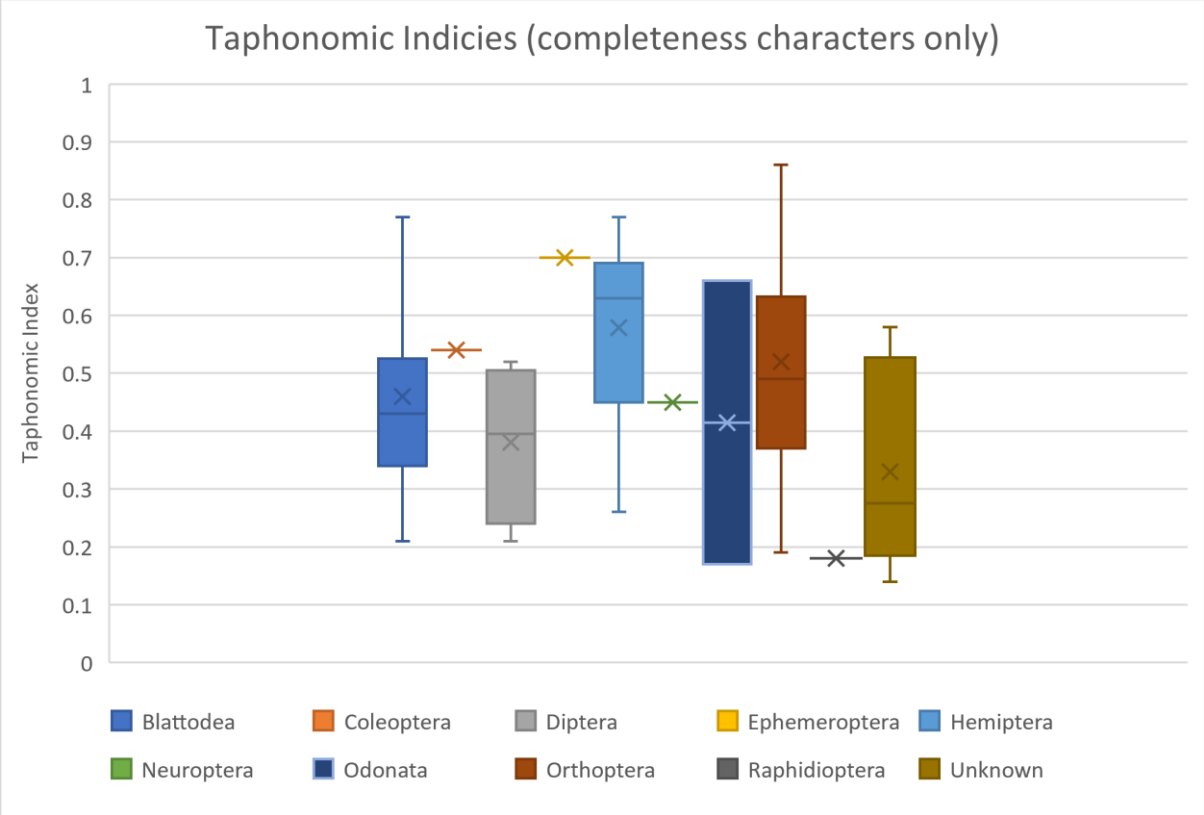


Figure 69. Box and whisker plots of the taphonomic index scores, including completeness characters only. Insects are separated into taxonomic groups (orders). Number of specimens for each order is as follows: Blattodea, 25; Coleoptera, 1; Diptera, 4; Ephemeroptera, 1; Hemiptera, 6; Neuroptera, 1; Odonata, 2; Orthoptera, 16; Raphidioptera, 1; and Unknown, 6. The median quartile for the taphonomic index values of each insect order are represented by a horizontal line, bound by the interquartile range (25th and 75th quartiles), creating a coloured 'box'. Outliers are represented by 'whiskers'. Extreme outliers are represented by unconnected points. The average taphonomic score is marked with an X.

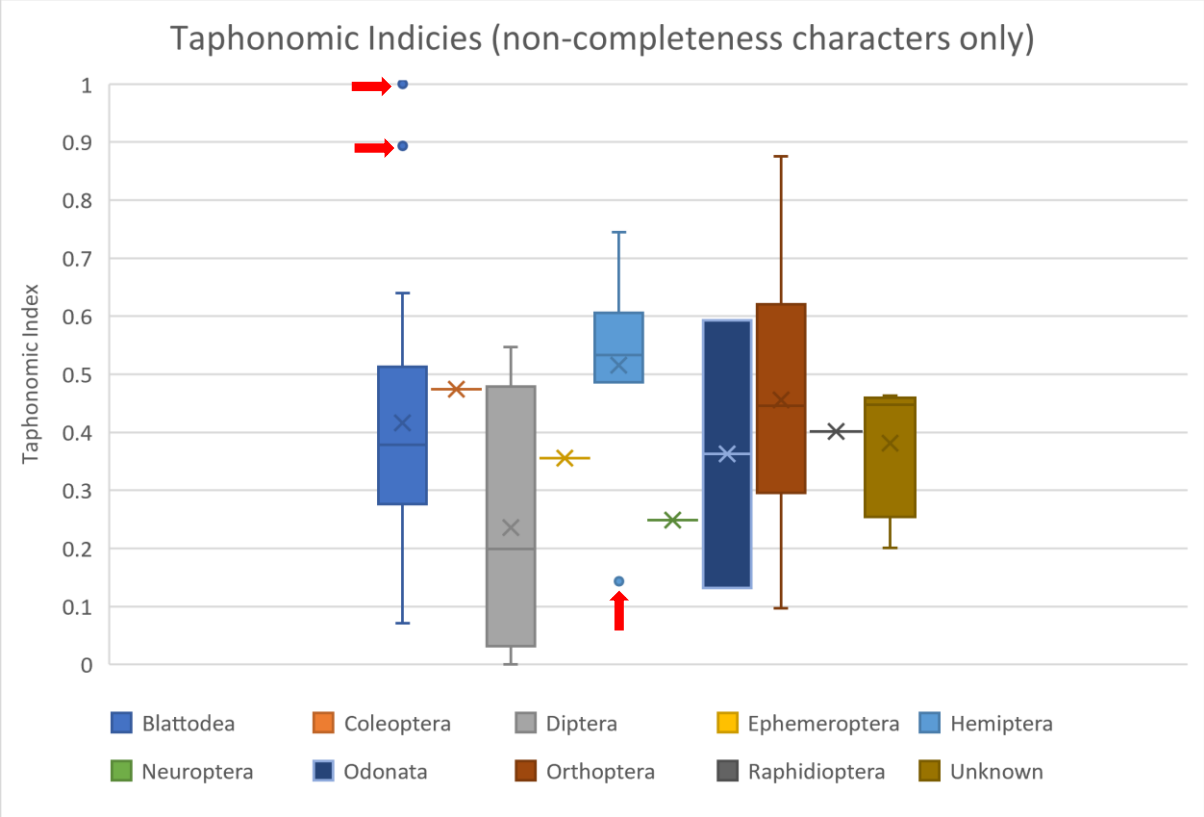


Figure 70. Box and whisker plots of the taphonomic index scores, including non-completeness characters only. Insects are separated into taxonomic groups (orders). Number of specimens for each order is as follows: Blattodea, 25; Coleoptera, 1; Diptera, 4; Ephemeroptera, 1; Hemiptera, 6; Neuroptera, 1; Odonata, 2; Orthoptera, 16; Raphidioptera, 1; and Unknown, 6. The median quartile for the taphonomic index values of each insect order are represented by a horizontal line, bound by the interquartile range (25th and 75th quartiles), creating a coloured 'box'. Outliers are represented by 'whiskers'. Extreme outliers are highlighted by arrows. The average taphonomic score is marked with an X.

3. 9. 3. Challenges

While fossil insect preservational qualities have been categorised previously (Henning, 2011), no other study has attempted to quantify preservation in this manner. As such, no data are available for other Lagerstätten and therefore a quantified comparison is not possible. Instead, a qualitative comparison of preservational fidelity between different Lagerstätten is included in Chapter 4. 1.

No weighting is applied to the characters measured in this analysis and each character is treated equally. This is because, due to the diversity of insect forms, any universal completeness weighting would inaccurately represent many taxa. Additionally, some components that make up a small proportion of total body mass are disproportionally important for measuring taphonomy (e.g. setae). Consequently, determining an appropriate weighting scheme was not deemed possible within the timeframe available. However, as setae are ubiquitous among insects, they could be used as a simple proxy for overall taphonomy (discussed further in Chapter 6. 4. 4.).

Regardless of weighting and appropriate datasets for comparison, the taphonomic indices presented here are of limited use. This is not due to the methodology, but rather the restricted diversity of the collection. A taxonomic distribution for Nova Olinda insect fossils was presented by Menon and Martill (2007) (see Figure 13), and differs significantly from that of the collection examined here (Figure 71). Here, both Blattodea and Orthoptera are over-represented (at 41% and 26% respectively), restricting the interpretation of results to these two groups.

Nevertheless, the index developed here could be a powerful tool for studying chronological, geographical, sedimentological, and taxonomic taphonomic trends. If a universal index were developed, with appropriate guides for weighting and applied to multiple Lagerstätten, taphonomic trends could be quantified, greatly enhancing our understanding of the fossil record.

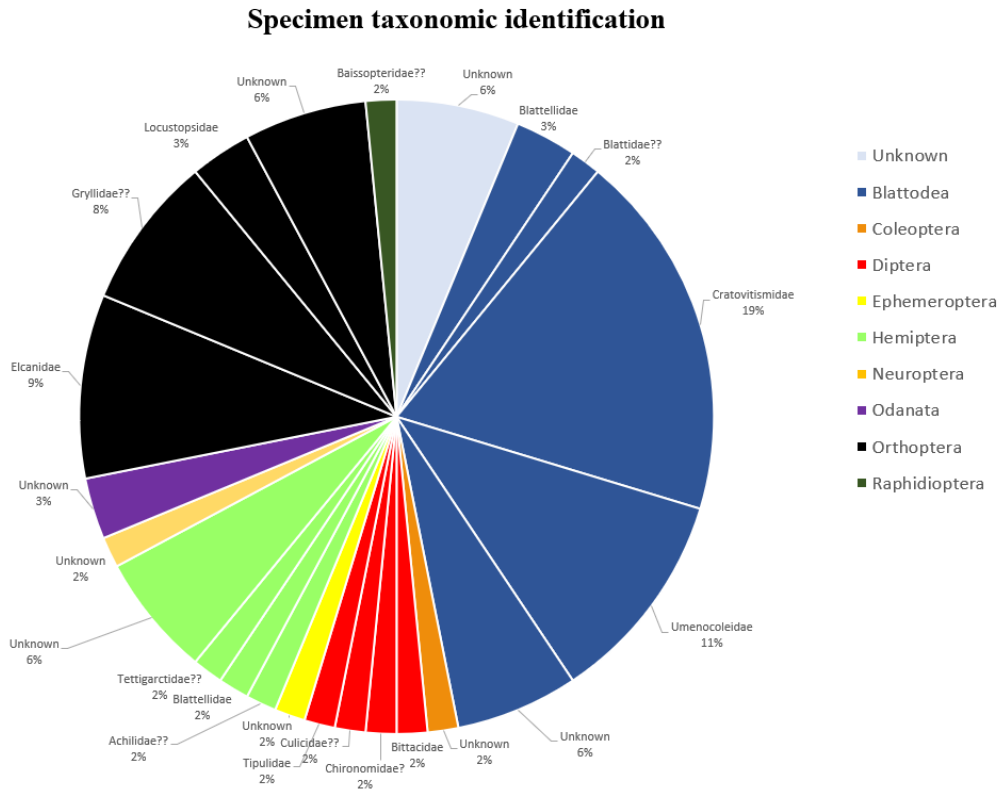


Figure 71. Taxonomic distribution of the collection studied in this project. Each order is labelled with its percentage representation within the collection. Blattodea (41%) and Orthoptera (26%) are over-represented.

3. 9. 4. Cluster analyses

In calculating the taphonomic indices, the data are greatly simplified as an average is taken from all characters. This allows for easy comparisons, but results in the loss of information about the relationships between each character. To combat this, the data were subject to explorative R-mode cluster analyses in the software PAST (see Chapter 2. 3. 8. 2.; Hammer and Harper, 2006). Despite the relatively low diversity of the collection, some taxa tended to cluster, although no *definitive* clusters were identified. Whether a cluster is *definitive* or not can only be informally

decided and should be based on how well separated it is from the other clusters (Hammer and Harper, 2006). However, PAST automatically assists in the identification of *definitive* clusters by colour coding (from blue to red, 'cold-to-hot') (Hammer, 2017).

In a cluster analysis, the distance (Y axis) between bifurcations relates to the strength of that cluster (Hammer and Harper, 2006). High distances indicate a reliable cluster, that likely represents an actual relationship. Low distances indicate an unreliable cluster.

In the 'completeness only' Gower similarity analysis (Figure 72), insect families (and orders) are well dispersed across the dendrogram. The cluster with the highest distance (highlighted in red) also contains a diverse array of insect families.

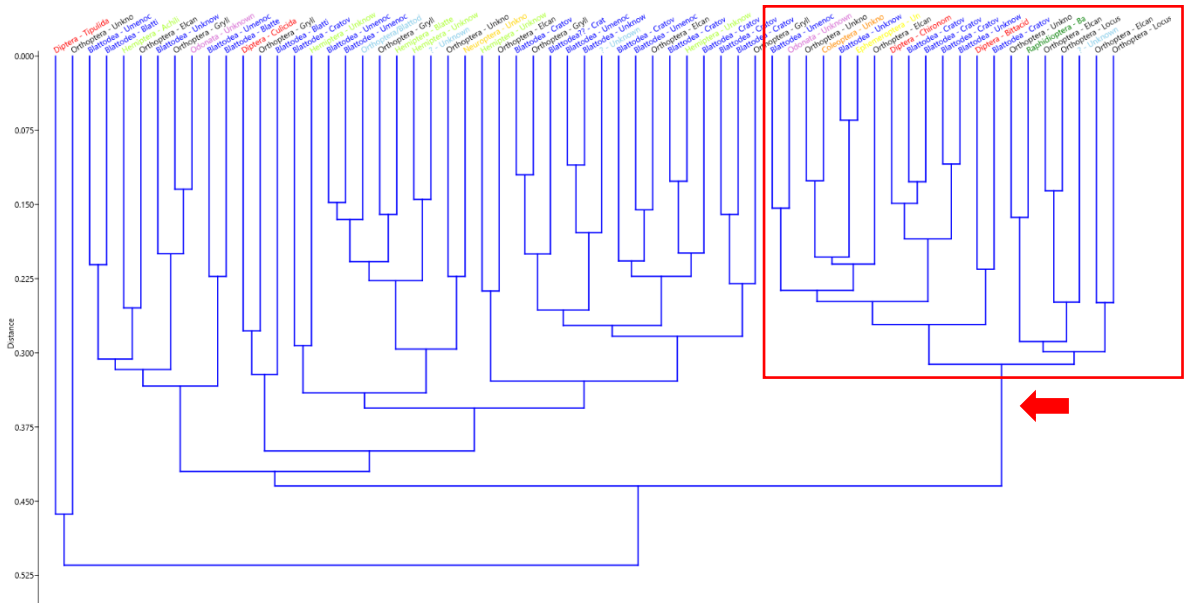


Figure 72. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. Only completeness characters are included. This analysis used an unweighted Paired Group method with arithmetic mean (UPGMA), with a Gower similarity index. A higher distance between branches denotes a stronger relationship. Red box highlights the cluster with the highest distance (highlighted by the red arrow), indicating that this is a relatively reliable cluster.

When a Euclidean similarity index is applied, this cluster breaks down (Figure 73). This indicates that the cluster is unreliable and probably does not represent an actual taphonomic relationship between these specimens, despite its apparent strength. Within the Euclidean similarity index analysis, two small weakly supported clusters formed that were largely composed of a single family (Figure 73: A) and multiple families from a single order (Figure 73: B). Although these are the only evidence of taxonomic-specific clustering in these analyses, their low distances and absence in the Gower analysis suggests that they do not represent an actual taphonomic relationship. Dendrograms produced including all taphonomic characters also provided poorly-supported and taxonomically diverse clusters.

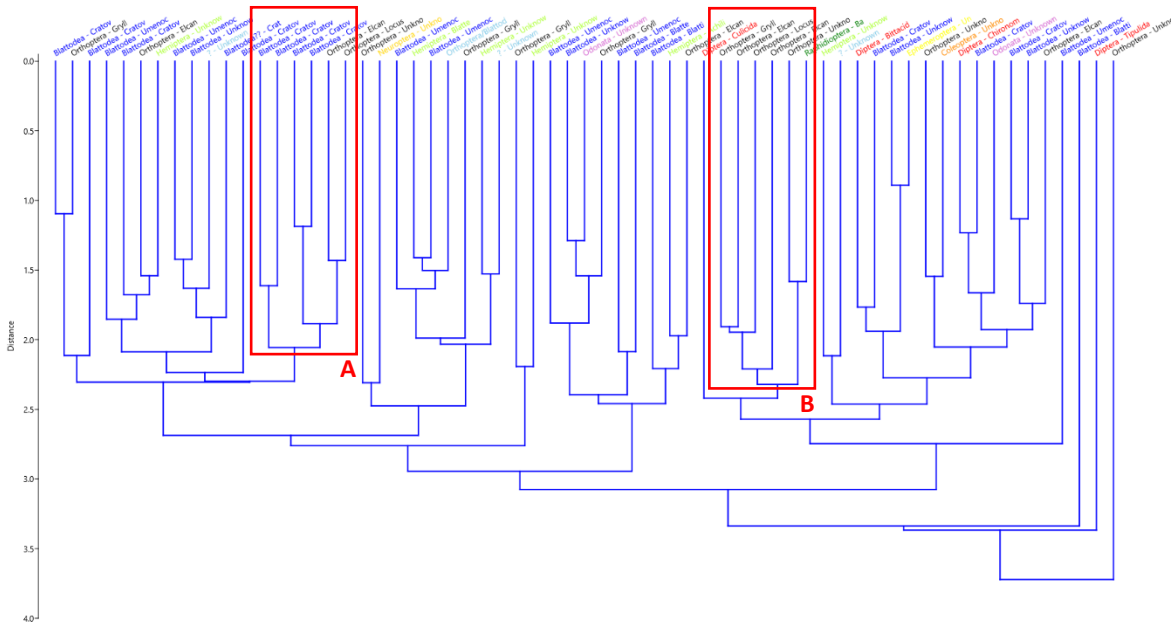


Figure 73. R-mode cluster analysis dendrogram showing the relationships between specimens, based on their taphonomic measurements. Only completeness characters are included. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Euclidean similarity index. A higher distance between branches denotes a stronger relationship. A, Weakly supported cluster for Blattodea – Cratovitismidae. B, Weakly supported cluster for Orthoptera (multiple families). Both clusters are highlighted in red.

Overall, the dendrograms generated by these analyses are unreliable and show no *definitive* clusters. This is demonstrated by the short distances between most bifurcations and the fact that the results differ greatly when an alternative similarity is used (Gower vs Euclidean) (Hammer and Harper, 2006; Hammer, 2017). This may be due to a relatively small sample size, incomplete data, or the poor diversity of the collection. Alternatively, these results could indicate that taxonomy has no control over preservational fidelity and instead the controls are largely post-depositional.

Q-mode cluster analyses explored the relationships between characters, producing clusters based on the co-occurrence of those characters. As with the standard R-mode cluster analyses above, both Euclidean and Gower similarity indices were used. These produced similar dendrograms, both of which contain some moderately well-clustered groups (Figures 74 and 75). As might be expected, characters for body parts located close together on an insect generally clustered, and this is denoted by the coloured text in Figures 74 and 75 (black for head, light blue for thorax, and dark blue for abdomen). This is most prominently seen in Clusters A (Figure 74: A and Figure 75: A), where both dendrograms produced a relatively high-distance cluster consisting of wing characters. This suggests that specimens tend to preserve multiple wings rather than a single wing. Alternatively, this clustering could be an artefact of several wingless specimens (larval forms) being included in the analyses.

One exception to characters for closely positioned body parts clustering was that the posterior structures of the abdomen (cerci, anus, genitals, etc.) did not cluster in the Euclidean similarity analysis. Instead, they formed two small clusters with relatively high distances (Figure 74: B and C). In the Gower similarity analysis, they were clustered together (Figure 75: B). Non-segment specific characters generally also clustered (green for setae preservation, and orange for non-completeness characters), suggesting that they tend to co-occur.

In both analyses a large cluster was produced containing limb characters, characters measuring the preservation of setae, and the character for antennae preservation (Figure 74: D, Figure 75 C). Although this cluster had a moderate distance in the Euclidean similarity analysis, it was well supported with a high distance in the Gower similarity analysis, suggesting a real relationship between these characters. It is probable that these characters share a controlling factor. Given the fragility of setae and antennae (Carlton, 2007) and the protruding nature of the limbs, it is possible that this controlling factor is abrasion during transport.

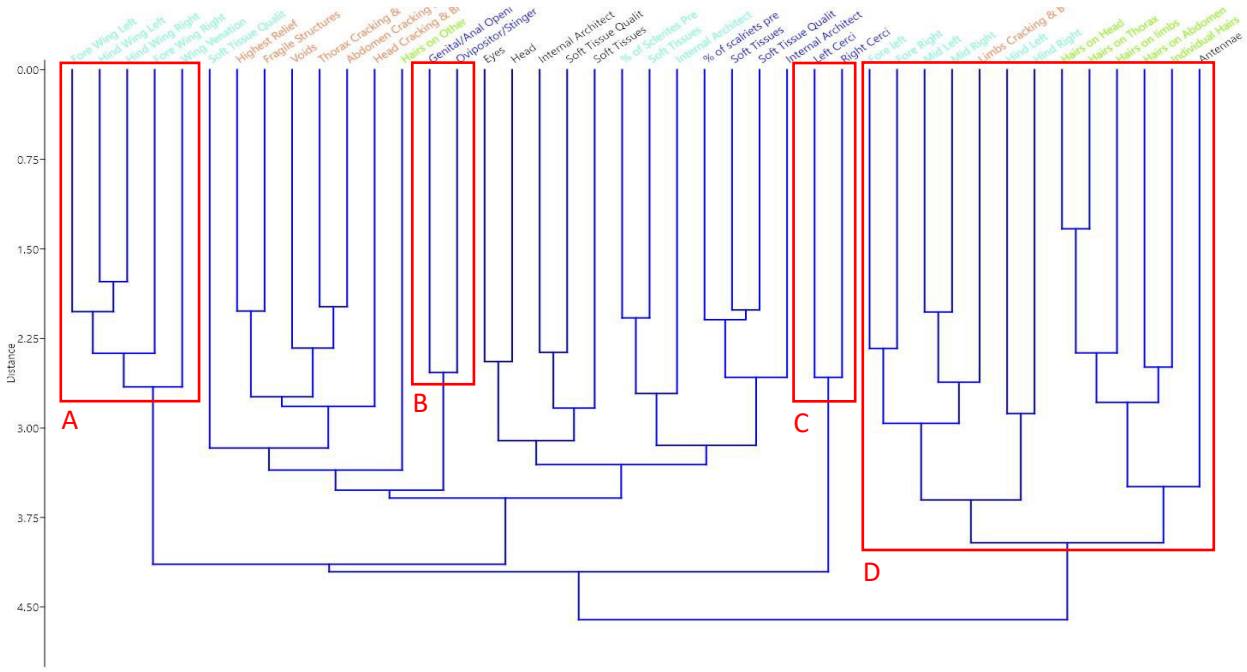


Figure 74. Q-mode cluster analysis dendrogram showing the relationship between characters. See Figures 63 and 64 for characters colour coding. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Euclidean similarity index. Four clusters highlighted. A, Wing characters. B and C, Characters relating to structures at the posterior abdomen. D, Characters relating to limbs, setae, and antennae. *Definitive* clusters are denoted by a change in branch colour (none present here).

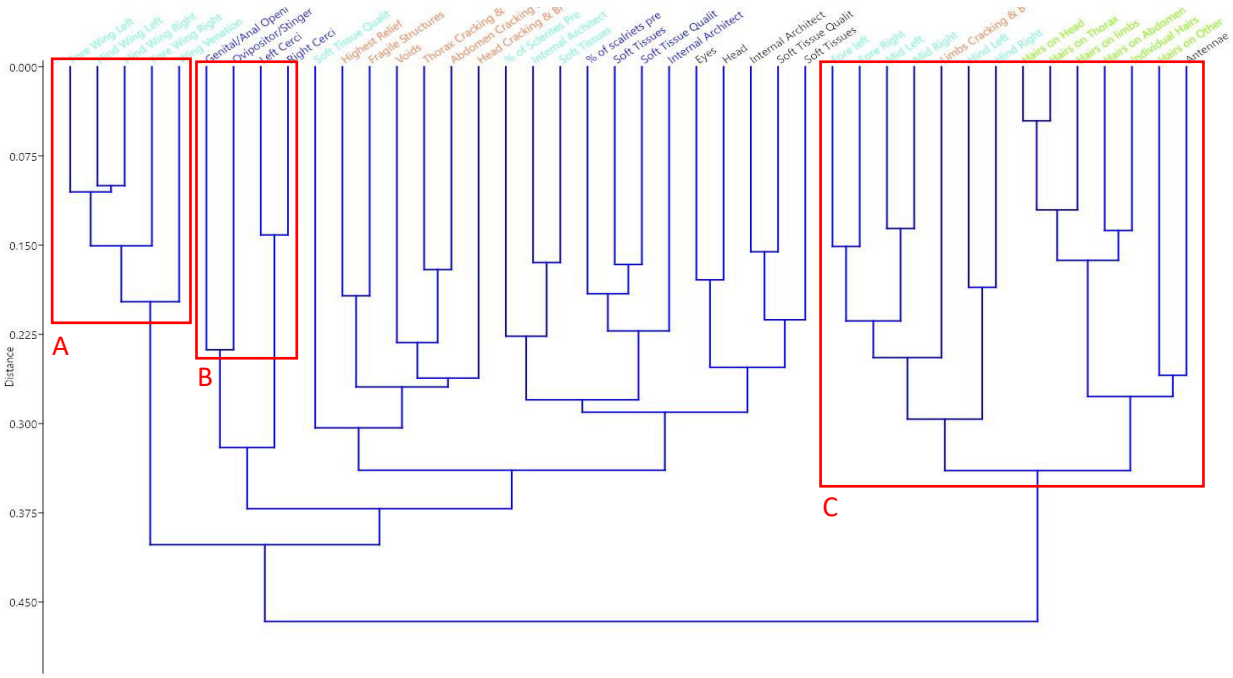


Figure 75. Q-mode cluster analysis dendrogram showing the relationship between characters. See Figures 63 and 64 for characters colour coding. This analysis used an unweighted paired group method with arithmetic mean (UPGMA), with a Gower similarity index. Four clusters highlighted. A, Wing characters. B, Characters relating to structures at the posterior abdomen. C, Characters relating to limbs, setae, and antennae. *Definitive* clusters are denoted by a change in branch colour (none present here).

3. 9. 5. Principle Coordinate Analysis

The scatter plots generated by the principle coordinate analyses (Chapters 2. 3. 8. 3. and 3. 8. 3.) allowed for an alternative visualisation of the taphonomic data (Gower, 2005; Hammer and Harper, 2006). In these scatter plots, closely placed points can be informally clustered. If closely positioned points are the same colour (and symbol), then they may represent a taphonomic trend for a particular taxonomic group.

For all taphonomic characters, four informal clusters were highlighted that included multiple insect orders (Figure 76, clusters one, two, three, and four in red). Due to the low diversity of the collection, these clusters were dominated by specimens of Blattodea and Orthoptera. Nevertheless, cluster one was particularly tightly packed. This multi-order cluster (including members of Blattodea, Hemiptera, Orthoptera, and indeterminate) could simply represent the most fragmentary specimens. This could explain why two specimens within the cluster could not be identified even to order-level. Cluster two is relatively diffuse, but contains a large number of Blattodea (especially Cratovitismidae) specimens. Cluster three is relatively densely packed with half of its members belonging to Orthoptera, possibly indicating a real taphonomic relationship. This cluster was not present within the cluster analyses. Although relatively disperse, cluster four is dominated by Cratovitismidae (Blattodea), and along with clusters two, provides a further example where this family tends to cluster.

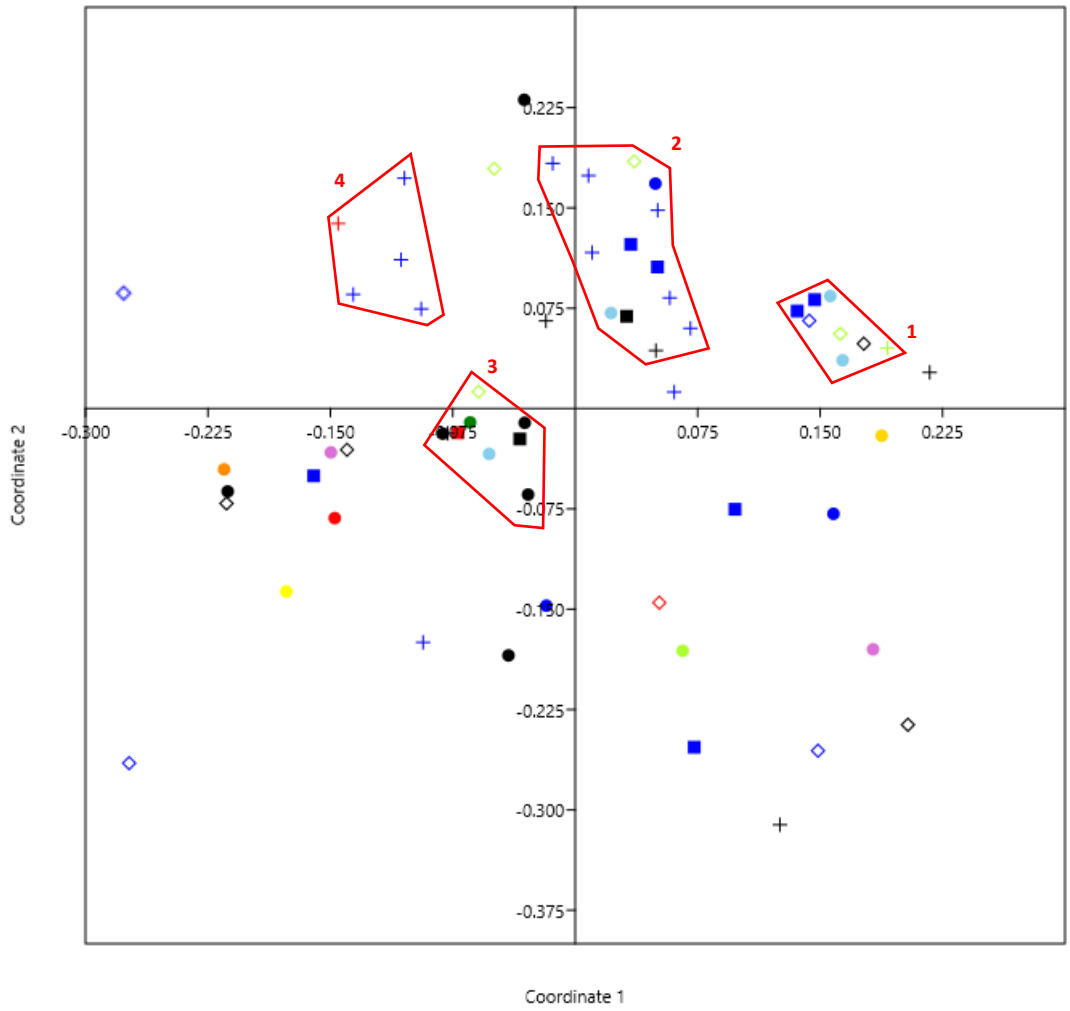


Figure 76. Principle coordinate analysis scatter plot showing the relationships between specimens, based on their taphonomic measurements. All taphonomic characters are included. This analysis used a Gower similarity index. Four clusters are marked with red outlines. 1, A tightly packed cluster of multiple insect orders. 2, A more diffuse cluster, consisting largely of Cratovitismidae (Blattodea) and other Blattodea. 3, A moderately tightly packed cluster, consisting of Orthoptera and several other orders. 4, A relatively disperse cluster of Cratovitismidae (Blattodea).

When only completeness characters were included (Figure 77), all clusters altered to some degree. In cluster one, the taxonomically unidentified specimens dispersed, along with the Orthoptera specimen, leaving only members of Blattodea and Hemiptera. Cluster two partially dispersed, but still retained most of its Blattodea specimens. Of these, the majority of them belong to Cratovitismidae (Blattodea). In cluster three, one additional Orthoptera specimen clustered and two specimens from other insect orders dispersed, resulting in this cluster now being dominated by members of Orthoptera. Although one Cratovitismidae (Blattodea) specimen left cluster four, it was replaced by an unidentified Blattodea specimen and the cluster became significantly more constrained. These analyses suggest that there is a tendency for members of Cratovitismidae (Blattodea) to cluster, however this may be an artefact of their relatively high abundance in the collection examined (see Figure 71).

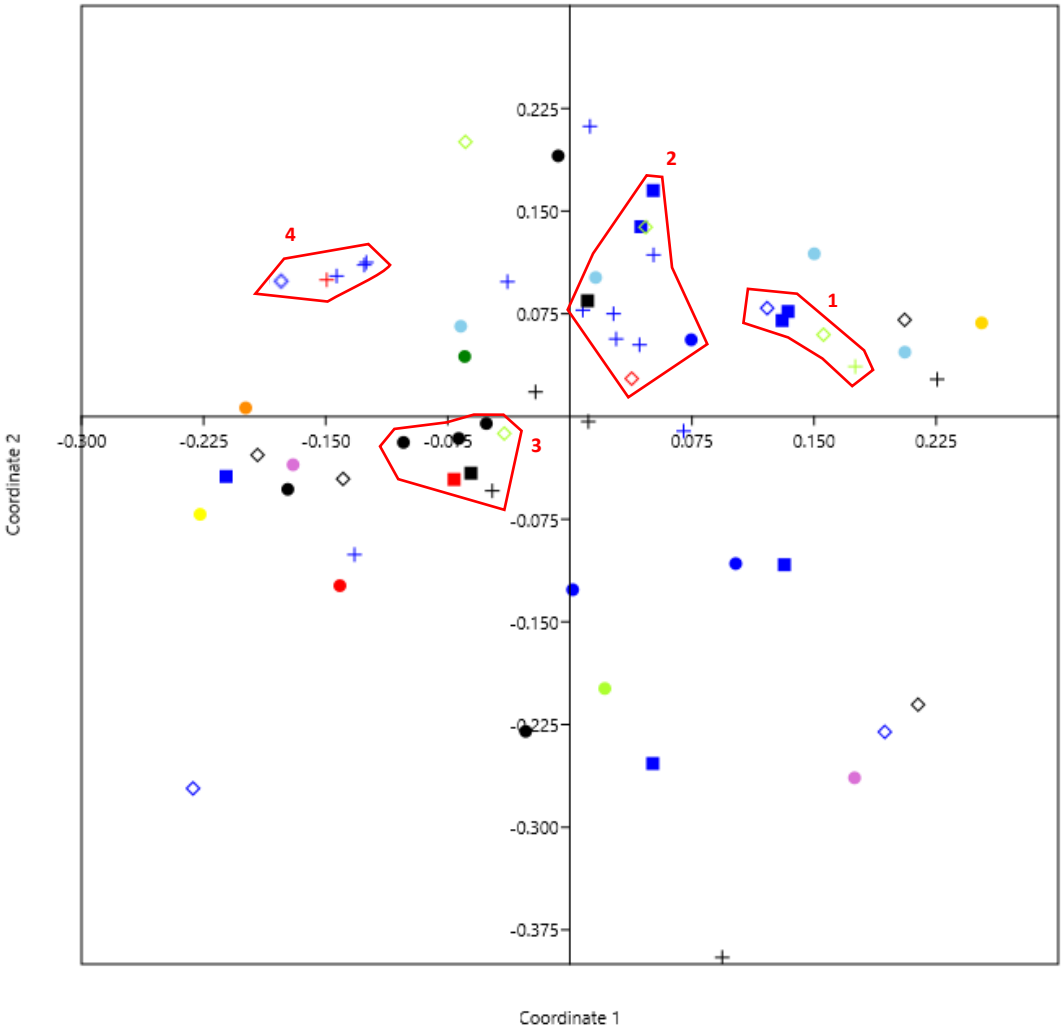


Figure 77. Principle coordinate analysis scatter plot showing the relationships between specimens, based on their taphonomic measurements. Only completeness taphonomic characters are included. This analysis used a Gower similarity index. Four clusters are marked with red outlines. 1, Cluster that was previously tightly packed has lost its taxonomically unidentified members, indicating that it was poorly supported. However, Blattodea and Hemiptera specimens remain relatively close. 2, Has become slightly more constrained but lost some members, leaving mostly Cratovitismidae (Blattodea) specimens. 3, Several specimens have left and joined this cluster, resulting in a more constrained cluster consisting largely of Orthoptera. 4, Has become much more tightly confined and is still dominated by members of Cratovitismidae (Blattodea).

3. 10. Fidelity of preservation conclusions

The replacement fabrics identified in the Nova Olinda Member fossil insects vary considerably, but are typically globular or subspherical. This, combined with XRD results, indicates an original mineralogy dominated by pyrite pseudoframboids, with another iron sulphide mineral (possibly greigite ($Fe^{2+}Fe^{3+}{}_2S_4$)) also replacing some tissues. Weathered Nova Olinda Member fossil insects are pseudomorphed in goethite. Globular fabrics representing areas of decay are identified based on their association to cuticular perforations (e.g. setal bases and spiracles), and these fabrics

often appear as an intermediate between well-preserved cuticle and the pseudoframboid-like aggregate replacement fabric (i.e. pseudoframboids are only partially discernible (intergrown) with finer grains, or cuticle is more coarsely impregnated with a 'granular' fabric). Labile internal tissues are preserved in calcium phosphate and are typically 'scrappy', but can be remarkably well-preserved on rare occasions. Where they are well-preserved, they are nearly indistinguishable from modern insects. The rarity of this exceptional preservation may partially be a result of an unwillingness by preparators to remove exceptionally preserved cuticle. If so, then exceptionally preserved internal tissues may be more common than observed here. The process that gave rise to this outstanding preservation and these mineralogical fabrics is discussed further in Chapter 4. 2.

Taphonomic characters were recorded, normalised, and averaged to generate an index value for each specimen, allowing for a quick and simple comparison of taphonomy. These indices were then plotted in box and whisker plots to allow for further comparisons against taxonomic identifications. Although the limited taxonomic diversity of the collection examined (dominated by Blattodea and Orthoptera) restricts most groups from being investigated, those that are abundant reveal several interesting points. Overall, the majority of indices for both Blattodea and Orthoptera fell between the ranges of approximately 0.6 and 0.3 for all three datasets. This is lower than might be expected for a Lagerstätte with 'exceptional preservation'. Between the two groups, Orthoptera generally had higher box heights, indicating that within this collection they have a higher preservational fidelity than members of Blattodea. When non-completeness characters were examined separately, three extreme outliers were identified. Two of these were for Blattodea, with remarkably high indices of 1 and 0.89, indicating that these two specimens resisted compaction and breakage extremely well. Conversely, the outlier identified for Hemiptera had a remarkably low index of 0.14, indicating that this fossil was heavily crushed and compacted.

The calculation of these indices also resulted in a loss of character relationship data, and so R-mode cluster analyses were undertaken to detect relationships between specimens, based on their taphonomic character measurements. These identified several weak clusters and one stronger cluster, which all dispersed upon the use of a different similarity index. Principal coordinate analyses were undertaken to corroborate the R-mode cluster analyses. These also identified several weak clusters, some of which appear to favour members of Cratovitismidae (Blattodea). However, this is likely a result of the relative abundance of Cratovitismidae specimens in the collection. As a result, no *definitive* taphonomic clusters could be identified. These analyses suggest that taxonomy has no control over preservational fidelity. Q-mode cluster analyses examined the relationships between the taphonomic characters used. These identified strong clusters for characters coding for body parts located close together.

Ultimately, the quantification of the fidelity of preservation of these insects encountered several key issues. Firstly, the collection examined here was donated on the basis of its relatively poor preservation, inherently biasing the results to poorer preservation. Secondly, the collection was taxonomically biased to Orthoptera and Blattodea, preventing accurate taxonomic comparisons. Thirdly, no other Lagerstätten have been quantified in this manner, and so comparisons to other sites can only be qualitative. Until an unbiased (or less-biased) collection can be analysed and other sites investigated in a similar manner, quantifiable comparisons cannot be made. However, from the observations in this project, the Nova Olinda Member insects undoubtedly possess an extremely high-fidelity of preservation, preserving tissues that should decay within hours of death. They also do not appear to be subject to normal taxonomic controls, with no apparent bias towards specific insect groups.

Chapter 4. Comparisons and taphonomic models

4. 0. Preface

Examining the preservation of the Nova Olinda Member insects is useful for determining preservational fabrics, original morphology, and artefacts of decay. However, without comparisons to other appropriate Lagerstätten, labelling the Nova Olinda Member fossil insects as 'exceptional' would be unsubstantiated. Below, several key arthropod-bearing Lagerstätten are examined. Their preservational fidelity and the types of preservation are compared with the Nova Olinda Member. Following this, models are presented for the geochemical pathways of preservation, as well as the general taphonomy of Nova Olinda Member insects.

4. 1. Comparisons with other Lagerstätten

4. 1. 1. Introduction

Lagerstätten that yield fossil insects often share similarities (e.g. their age, palaeogeographic location, lithology, preserving minerals, taphonomic pathways, etc.) and there are many sites are similar to the Nova Olinda Member. Several well-known fossil-yielding localities were selected for comparison on the basis of reports of exceptionally preserved arthropods (excluding amber inclusions), a similar depositional setting (i.e. lagoonal, lacustrine, or fluvial), or preservational style (i.e. iron sulphide preservation). For a comprehensive list of major fossil insect-bearing localities, see Penney and Jepson (2014). The selected localities are summarised in Table 4 and discussed below in alphabetical order. As stated in the scope of this project (page iii), energy dispersive X-ray and X-ray diffraction analyses of replacing minerals were not undertaken for these comparable Lagerstätten. This was due to project time constraints and, instead, mineralogical interpretations are based on previously published data.

Table 4. Comparable fossil arthropod Lagerstätten. Table summarising fossil arthropod Lagerstätten that were compared to the Nova Olinda Member. Formation, location, and age are listed.

Name	Formation	Location	Age
Beecher's Trilobite Bed	Frankfort Fm.	New York, USA	Late Ordovician
Daohugou	Tiaojishan Fm.	Hebei, Inner Mongolia, and Liaoning, China	Middle to Upper Jurassic (Bathonian-Oxfordian)
Florissant	Florissant Fm.	Central Colorado, USA	Upper Eocene to Lower Oligocene
Green River	Green River Fm.	North-western Colorado, USA	Lower to Middle Eocene
Koonwarra	Wonthaggi Fm.	Gippsland Basin, Victoria, Australia	Lower Cretaceous (Aptian or Albian)
Las Hoyas	Calizas de la Huérguina Fm.	Near Cuénca, Central Spain	Lower Cretaceous (Barremian)
London Clay	London Clay Fm.	London and Hampshire Basins, UK notably Isle of Sheppey, UK	Lower Eocene (Ypresian)
Montsec	'La Cabrua' quarry (no consensus)	Lleida, Spain	Lower Cretaceous (Lower Barremian)
Rubielos de Mora Basin	'Rubielos de Mora' (no consensus)	Eastern Spain	Lower Miocene
Solnhofen	Solnhofen Fm.	Central Bavaria, Germany	Upper Jurassic (Kimmeridgian-Tithonian)
Yixian	Yixian Fm.	Liaoning, China	Lower Cretaceous (Barremian-Aptian)

4. 1. 2. Frankfort Formation (Beecher's Trilobite Beds)

The Frankfort Formation, part of the Lorraine Group, is a sequence of Late Ordovician sediments located in Cleveland's Glen, Oneida, New York, USA (Briggs *et al.*, 1991; Farrell *et al*., 2009). The formation is famous for its pyritised trilobite fauna and is regarded as a classic example of soft tissue pyritization (Farrell and Briggs, 2008). It contains a series of dark grey mudstones, commonly known as 'The Beecher's Trilobite Beds', interbedded with coarser sediments. Each of these mudstones is between 4 - 9 cm thick and represents a turbidity flow deposited along the margins of the Ordovician Laurentian continent (Briggs *et al.*, 1991; Raiswell *et al.,* 2008; Farrell *et al*., 2009). These turbidity flows carried trilobites from the oxygenated continental shelf and rapidly buried them at the site of deposition. In addition, the turbidity flows transformed the site of deposition from a dysoxic bottom water with some burrowers (minor bioturbation), to an organic-rich inhospitable anoxic sediment. This, combined with reactive iron enrichment prior to deposition, allowed for the formation of pyrite throughout the sediment, including as disseminated grains, burrow linings, and replacing some arthropod soft tissues (Farrell *et al*., 2009). In cases where soft tissues were not replaced by pyrite, some fossils may be calcified (Farrell *et al*., 2009). The majority of the fossils preserved are trilobites, but ostracods, brachiopods, gastropods, eurypterid fragments, and conulariids are also present, along with burrows.

Both mechanical preparation and X-ray analysis have revealed that the soft tissues of many of these fossils are preserved articulated in pyrite. The fossils are typically mostly complete and preserved as golden replacements in pyrite (Figure 78; Farrell *et al*., 2009).

Figure 78. Images from Farrell *et al*. (2009). Pyrite replacement in the Beecher's Trilobite Bed. A, *Triarthus eatoni* (YPM 509231). Arrow highlights ostracod. B, *Triarthus eatoni* (YPM 223935). C, Ostracod (YPM 223936). D, Possible crustacean (YPM 223937). E, *Cryptolithus bellulus* (YPM 509987). F, Ophiuroid (YPM 509229). G, Possible algae fossil (YPM 223942). A-B and D-G, Scale bars = 1 cm. C, Scale bar = 1 mm.

To compare the fidelity of preservation between the Beecher's Trilobite Beds and the Nova Olinda Member, specimen YPM IP 73015 (*Triarthus eatoni*) was loaned by Yale Peabody Museum for uncoated SEM analysis. The surface fabrics of the fossil were examined to identify discernible soft-tissue preservation, the preservation of cuticular ornamentation, and to determine the replacement fabric (Figure 79). Despite the presence of pyritised soft tissues reported in many specimens, YPM IP 73015 retains no original cuticle surface structure. Instead, the cuticle is coarsely replaced by 5 - 20 µm anhedral grains (Figure 79: A-B). In some areas, variations in this preservational style occurs, with finer- or coarser-grained fabrics (Figure 79: C). Regardless, no fine-scale cuticular structures or fabrics are observed. Disseminated pyrite framboids (or pseudoframboids?) are also present, scattered infrequently across the cuticle, usually in pits or grooves (Figure 79: D). The high contrast between bright patches of euhedral crystals (pyrite) in Figure 79: B, C, and D, and the other darker anhedral minerals suggests that the majority of cuticle

is not preserved in pyrite. This contradicts previously published data, and instead it is possible that these darker areas are where cuticle has been lost during extraction/curation, revealing a mould of the cuticle by the surrounding matrix.

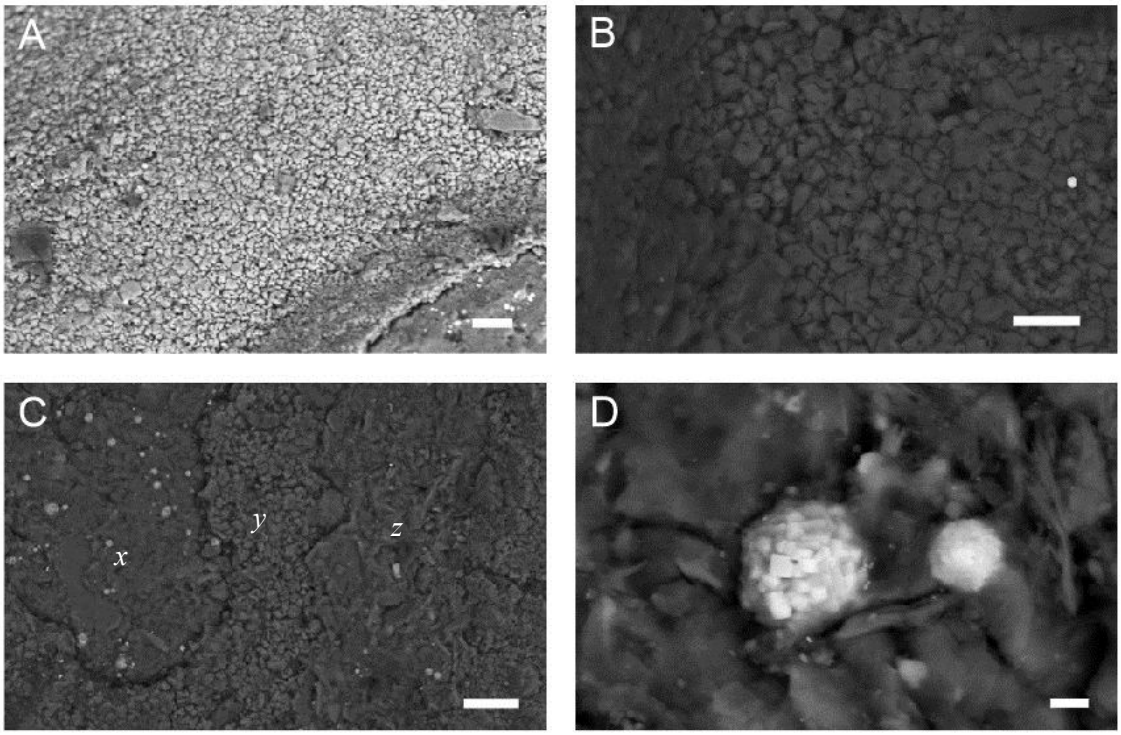


Figure 79. Uncoated backscatter scanning electron micrographs of cuticle from specimen YPM 73015 (*Triarthrus eatoni*). A and B, Preservation of cuticle in anhedral grains. C, Three variations in the apparent fabric of replacement of cuticle, with differing grain sizes (x, y, and z). Scattered pyrite grains also visible in x and z (highlighted by bright colour). D, Framboidal (or pseudoframboidal) pyrite with euhedral cubic crystals, highlighted by bright colour. Working distance = 11.5 mm. 20 kV. I probe varied between 20 and 100 pA. A and C, Scale bars = 20 µm. B, Scale bar = 10 µm. D, Scale bar = 2 µm.

While the replacement mineral of the Beecher's Trilobite beds (pyrite) is similar to that of the Nova Olinda Member, its fossils lack pseudoframboids infilling the body cavities (where present instead 'erupting' through the cuticle: Figure 79: D), no micron-scale cuticle morphology is preserved, and internal labile soft-tissues are preserved as relatively 'scrappy traces' in pyrite (rather than calcium phosphate). Despite the superficially similar mineralogy of these two Lagerstätten, the lack of calcium phosphate preserving tissues in Beecher's Trilobite Beds and its differing preservational fabric(s) indicate a different mode of preservation. This different mode did not preserve labile internal soft tissues, nor micron-scale cuticular features, ultimately resulting in a lower fidelity of preservation.

4. 1. 3. Tiaojishan Formation (Daohugou)

The Daohugou beds of the Tiaojishan Formation have received much attention over the last decade (Wang *et al*., 2005; Gao and Re, 2006; Zhang *et al*., 2008; Zhang, 2010, 2013; Jarzembowski *et al*., 2012). They crop out across several provinces in north-eastern China (Hebei,

Inner Mongolia, and Liaoning) and are most famous for their abundant, diverse, and well-preserved vertebrate fauna, including amphibians, pterosaurs, and dinosaurs (Wang *et al*., 2006; Li *et al*., 2010; Lü *et al*., 2010). The beds are also an important insect Lagerstätte, possessing a highly diverse insect fauna (e.g. Zhang *et al*., 2008; Zhang, 2010, 2013; Jarzembowski *et al*., 2012).

The age of the Tiaojishan Formation has been a matter of considerable and heated debate (Wang *et al*., 2005; Gao and Re, 2006; Zhang and Li, 2012), with a Middle to Upper Jurassic (Bathonian-Oxfordian) age being the current consensus (Zhang and Li, 2012). The sediments of the Tiaojishan Formation are largely pyroclastic, with interspersed tuffaceous and siliciclastic layers (Ren *et al*., 2010; Zhang and Li, 2012). The palaeoenvironment represented is a lacustrine setting in a subtropical-to-temperate warm and humid zone, with a consistent and distinctly seasonal climate (Wang *et al*., 2006). This reconstruction is based largely on the dominant flora of Bennettitales, ferns, Nilssoniales, and fossil tree stumps (Wang *et al*., 2006).

The Tiaojishan Formation insects have been subject to scanning electron microscopy and energy dispersive X-ray analysis to determine their taphonomy (Wang *et al*., 2009). The fossils are mostly compressions preserved in brownish organic remains, but four distinct modes of preservation are known (Wang *et al*., 2009). These are: (1) Brown compressions with distinct body segments. (2) Grayish-brown compressions with strongly deformed body segments. (3) Partially brown and partially translucent (usually abdomen) compressions with typically no wings preserved. (4) Yellowish-brown pyritised replacements with low relief and appendages absent. Pyrite granules are distinct and this preservation is intimately associated with grey/greyish-yellow thinly bedded tuffaceous siltstones (Wang *et al*., 2009). Of these four preservational modes, **99%** of insect fossils are preserved as ‘mode 2’ (grayish-brown compressions with strongly deformed body segments, Figure 80) (Wang *et al*., 2009).

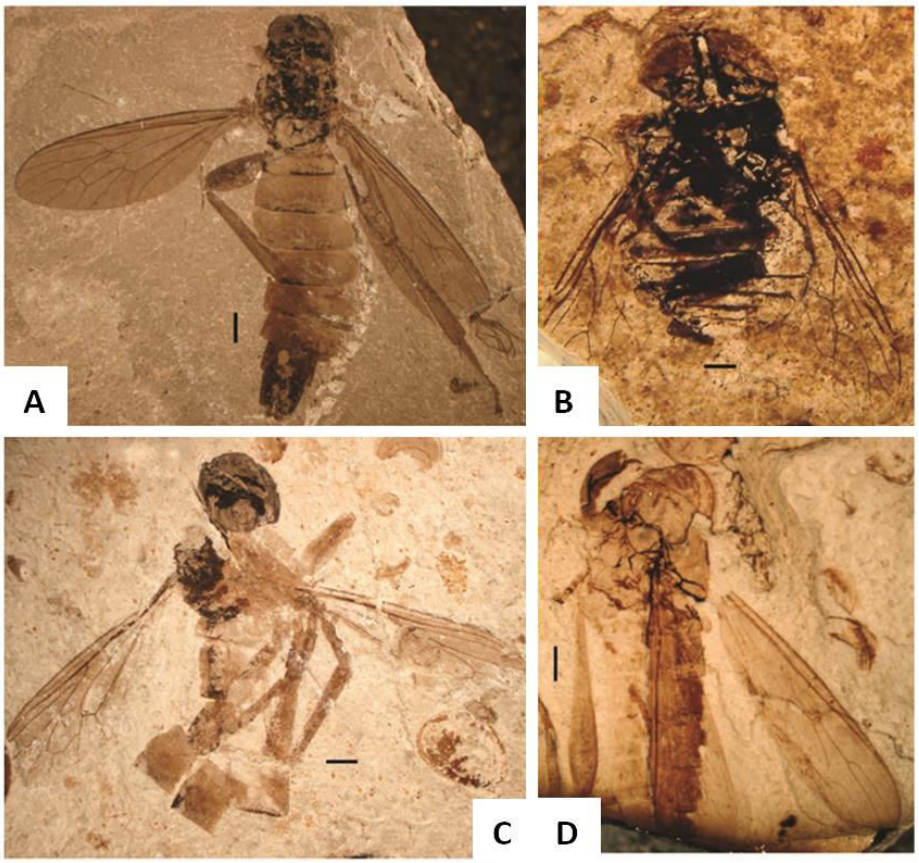


Figure 80. Daohugou preservation. Images from Zhang (2010). A, *Mostovskiargus portentosus*. Specimen DHG 200751. B, *Jurassinemestrinus orientalis*. Specimen DHG 200754. C, *Calosargus sinicus*. Specimen DHG 200753. D, *Mostovskiargus signatus*. Specimen DHG 200752. Scale bars = 1 mm.

The variation in preservational modes strongly indicates that at least four separate microenvironments were present, allowing for the unique preservational styles (Wang *et al*., 2009; Wang *et al*., 2013). Where 'mode 4' preservation is present, the replacement chemistry appears to be similar to that of the Jehol Biota preservation, and so the microenvironment likely recreated similar conditions of the Jehol 'fossil envelope' model (Wang *et al*., 2009). The fossil envelope model can be summarised as: the rapid burial of a carcass in extremely fine grained lacustrine sediments with fine laminae (< 1 mm) and associated volcanic sediments (ashes, lavas), resulting in the carcass being 'sealed' from the surrounding sediment, protecting it from bioturbation and stimulating microcrystalline pyrite impregnation/moulding (Benton *et al*., 2008).

Figures provided by Wang *et al.* (2009) reveal coarse (between 0.5 and 2 µm) well defined euhedral pyrite crystals arranged loosely in striae across the cuticle (Figure 81). No direct replications of cuticle surface fabrics are visible, and the crystals simply occur where cuticle formerly was present. The pyrite crystals are coarse (~2 – 3 µm in diameter) and do not replicate the fine details of the cuticle (Zhu *et al*., 2005; Cai and Hua, 2007). For 'mode 2' preservation, energy dispersive X-ray analysis revealed that some areas of the fossils have a high iron content,

likely the result of Fe^{2+} absorption by structural biopolymers during, and subsequently inhibiting, decay (Petrovich, 2001; Wang *et al*., 2009).

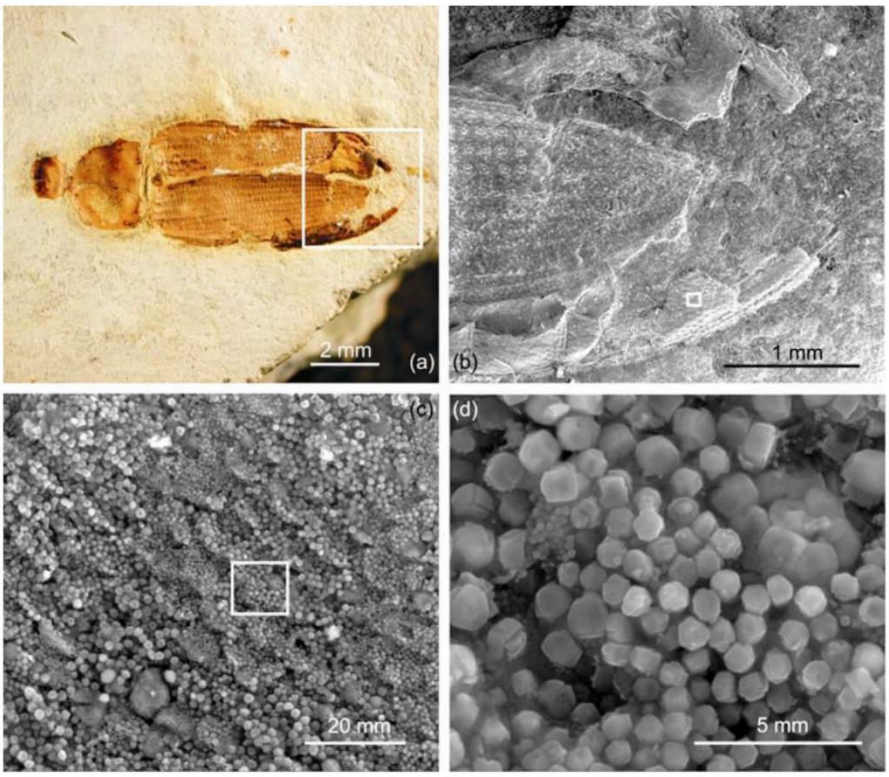


Figure 81. Daohugou micro-preservation. Images from Wang *et al*. (2009). Squares highlight area examined in following image. A-B, Increasing magnification images of posterior beetle elytra. C, Striations in beetle elytra resemble those seen in Plate 53. D, Euhedral pyrite grains have obliterated most cuticular fabrics, (excluding coarse striations?). Specimen NIGP 149371. Scales provided in images, although C and D are mislabelled as mm instead of µm.

Despite some superficial similarities, preservation in the Daohugou beds differs significantly from the Nova Olinda Member. Most notably, the majority of fossils are simple compression 'stains' between laminae, albeit with patches of high iron content. When pyrite replication is present, fossils preserve with moderate relief (Figure 81: A). However, the pyrite crystals are coarse (~2 – 3 µm in diameter), loosely organised, euhedral, and do not replicate cuticle surface fabrics or internal tissues with high fidelity (Figure 81: D). Only large, sturdy, low relief cuticular structures (such as pits and grooves, Figure 81: C) are replicated with low fidelity. In addition, the Daohugou palaeoenvironment and palaeoclimate are significantly different to that of the Nova Olinda Member.

4. 1. 4. Florissant Formation

The Late Eocene to Early Oligocene Florissant Formation in central Colorado, USA, is a Lagerstätte that yields exceptionally labile plant fossils (e.g. fruit and flowers), gigantic silicified redwood trees, and a diverse aquatic and terrestrial fauna (Meyer, 2003). It represents a calm lacustrine

environment surrounded by a lush redwood forest, with a nearby volcano (Henning *et al*., 2012). The formation consists of millimetre scale alternating layers of smectitic clay, shale, mudstone, conglomerate, and volcanic ashes (O'Brien *et al*., 2008).

The lake was formed initially by pyroclastic flows blocking a fluvial system. This flooded the surrounding forest in a five-metre-thick liquid cement, resulting in the initial silicaeous replication event that preserved the giant red wood trees (Henning, 2011). During periods of volcanic activity, metastable silica minerals were deposited in the surrounding catchment area, and later transported into the water column by seasonal rainfall or meltwater (Meyer and Weber, 1995; Foos and Hannibal, 1999; Harding and Chant, 2000; O'Brien *et al*., 2008; Veach and Meyer, 2008; Henning *et al*., 2012). The fossils are intimately associated with biofilms of extracellular polymeric diatomatic secretions (EPDS) and are also coated in diatom body fossils (O'Brien *et al*., 2008). Decay was retarded by rapid sedimentation and anoxia from diatom blooms stimulated by an influx of volcanic silica (O'Brien *et al*., 2008; Henning, 2011). The fossils are often associated with layers of kerogen (Stankiweicz *et al*., 1998) and are preserved by early mineralisation in pyrite, calcite, or calcium phosphate (McCobb, *et al*., 1998; Duncan *et al*., 1998).

The formation yields a diverse insect fauna, with numerous Hymenoptera, Coleoptera, Diptera, and Hemiptera, and rarer Trichoptera, Lepidoptera, Dermaptera, Ephemeroptera, and Isoptera (Henning, 2011). These insects have been studied extensively, especially as examples of near-palaeoshore and far-palaeoshore assemblages (Wilson, 1988; Smith and Moe-Hoffman, 2007). Other studies used them for determining insects as a controlling factor for mineral growth (Martínez-Délclòs *et al*., 2004), or understanding the preservational styles of insects in differing lithologies and water current energies (Henning *et al*., 2012). A taphonomic study by Henning (2011) revealed that only 55% of these fossil insects are complete. Many are preserved 'fairly' with some damage and at least one morphological character present, while relatively few are considered 'exceptional' with no damage at all (Henning, 2011). The Florissant fossil insects, like many other localities, can be preserved in iron sulphides (McCobb, *et al*., 1998; Duncan *et al*., 1998) and published figures suggest they are largely black with extremely low-relief (Figure 82; Henning *et al*., 2012).

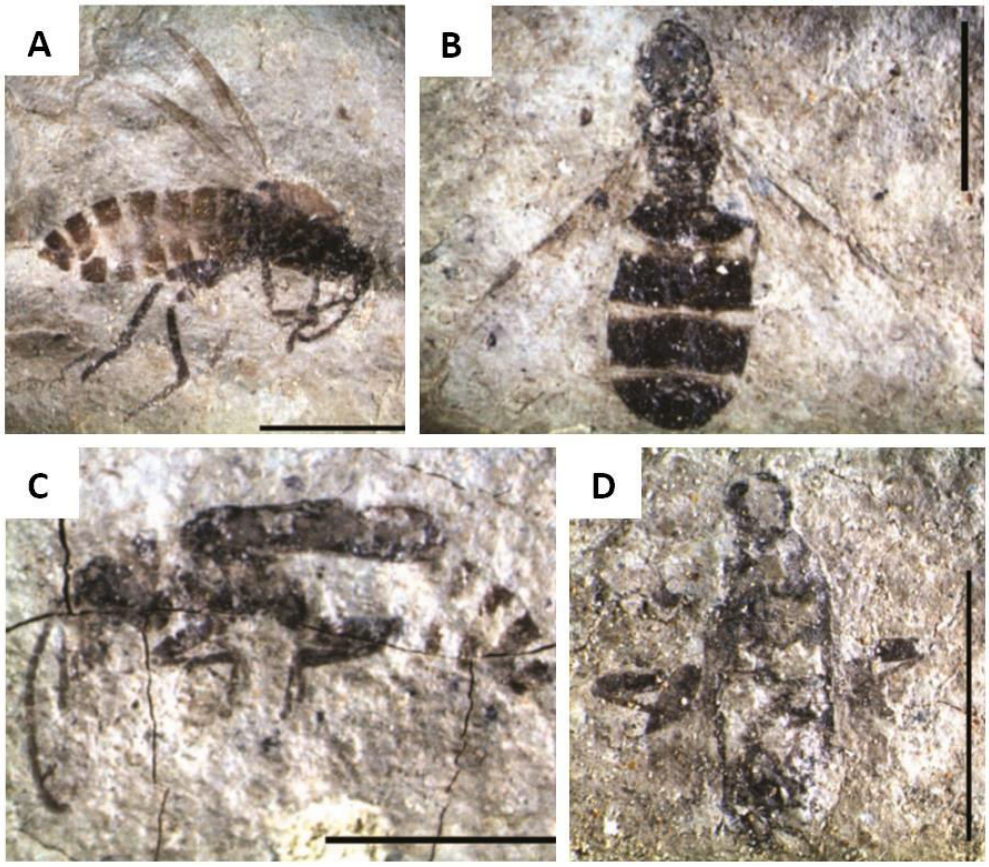


Figure 82. The range of preservational qualities of Florissant Formation insect fossils. Images from Henning *et al*. (2012). A, Diptera, 'excellent' preservation. FLFO 7092. B, Hymenoptera, 'good' preservation. FLFO 7320. C, Coleoptera, 'fair' preservation. FLFO 7743. D, Indeterminate, 'poor' preservation. FLFO 7165. Scale bars = 5 mm.

The insects of the Florissant Formation have also been examined under SEM, revealing micrometre scale details of their preservation and extremely low-relief three-dimensionality (restricted to a single lamina) that is not visible in hand specimen (O'Brien *et al*., 2008). This analysis revealed well-preserved diatoms, but relatively poorly preserved insect cuticular surface ornamentation (O'Brien *et al*., 2008; Figure 83). Despite their infrequent 'exceptional' preservation in hand specimen, preservation is more accurately described as 'fair' with 66% of specimens showing a 'low preservational quality' (Henning, 2011; Henning *et al*., 2012). Although the preservation of micron-scale cuticular structures and three-dimensionality renders the Florissant Formation one of the few localities comparable in preservational quality to the Nova Olinda Member, the overall micron-scale preservational fidelity of its fossils are poor. This is because the majority of them are obscured by an insoluble sheet of diatoms and, where micron-scale preservation is visible, it is coarse and does not replicate original morphology with high fidelity (Figure 83: B).

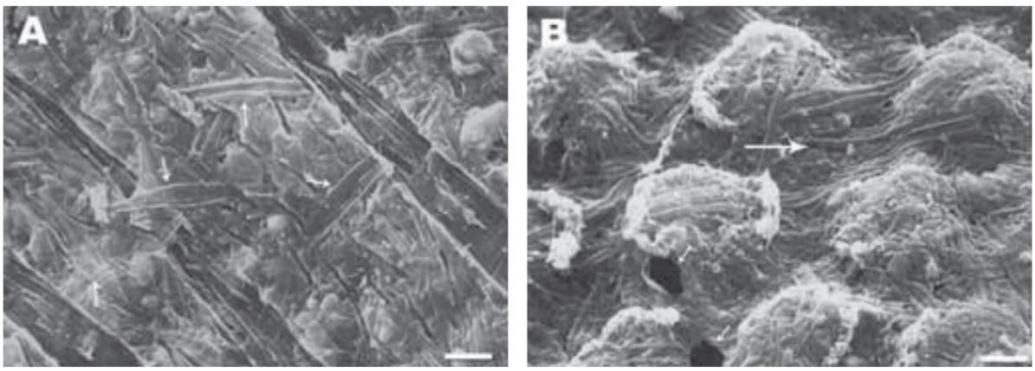


Figure 83. Florissant micro-preservation. Images from O'Brien *et al*. (2008). SEM images of Florissant Formation insect preservation. A, Setae and setal bases coated in EPDS. B, Coarsely preserved ommatidia also coated in EPDS. Scale bars = ~7 µm. No specimen numbers recorded.

4. 1. 5. Green River Formation

The Green River Formation is a world-renown and extensively studied Early to Middle Eocene Lagerstätte in north-western Colorado and south-western Wyoming, USA (Bradley, 1929; McGrew, 1975; Grande, 1984; Fischer and Roberts, 1991; Buchheim, 1994; Dayvult *et al*., 1995; Ferber and Wells, 1995; Buchheim and Surdam, 1997; Buchheim and Eugster, 1998; Froehlich and Breithaupt, 1998; Schieber, 2007; Smith *et al*., 2008; Buchheim *et al*., 2011; Hellawell and Orr, 2012). It represents a temperate to sub-tropical lacustrine setting that persisted for several million years (Grande and Buchheim, 1994; Shcherbakov, 2006; Hellawell and Orr, 2012). The lithology consists of buff-coloured micrites and fine-scale organic-rich lacustrine mudstones, with some particularly kerogen-rich laminae (Pietars and Carroll, 2006; Hellawell and Orr, 2012). In addition, there are also interspersed thin layers of limonite clays that represent an influx of volcanic ashes (Buchheim *et al*., 2011).

The formation is divided into three members; the Road Hollow, Fossil Butte, and Angelo members that represent over-filled, balance-filled, and under-filled periods of lake evolution respectively (Buchheim *et al*., 2011). The lack of bioturbation and soft sediment 'disturbance' suggests the absence of benthic organisms (Grande, 1984) and there is abundant evidence for microbial mats at the sediment-water interface (Bradley, 1929; Bradley, 1948; Crowley *et al*., 1986; McGrew, 1975; Hellawell and Orr, 2012). This, combined with a highly restricted nekton, suggests that the water was hostile, stratified, and had a deoxygenated bottom (Bradley, 1948; Hellawell and Orr, 2012).

Within this formation, only fish fossils have been analysed taphonomically (Hellawell and Orr, 2012). They revealed little evidence for soft tissue preservation, either as organic remains or authigenic mineral replication, however many skeletons are completely or nearly completely articulated (Hellawell and Orr, 2012). There is a common occurrence of 'half and half' preservation whereby the posterior portion of the fish is well-preserved (articulated with

'exquisite detail') and the anterior portion is very poorly-preserved (disarticulated) (Hellawell and Orr, 2012). Rapid burial was previously suggested as the key factor for the exceptional preservation of Green River fossils (McGrew, 1975), however more recent studies suggest that they were buried progressively, which may account for the 'half and half' preservation (Hellawell and Orr, 2012). Mass mortality events are also recorded, but are restricted to a few laminae (Grande, 1984).

While fish are undoubtedly the dominant fossil group, there is also an abundant and diverse insect assemblage (Dayvult *et al*., 1995; Shcherbakov, 2006; Anon., 2015). Insects are described as 'beautifully preserved', with ommatidia discernible, but there is no discussion of cuticle fabric or internal preservation (Dayvult *et al*., 1995). There are reports of colour associations between the extent of weathering, similar to the Nova Olinda Member, whereby 'black' specimens are associated with blueish sediments and 'orange-brown' specimens associated with paler buff-coloured sediments (Anon., 2015). Despite vertebrate fossils being preserved with high relief (Hellawell and Orr, 2012), insects appear to only retain moderate-to-low relief in areas of high sclerotisation (Anon., 2015; Figure 84).

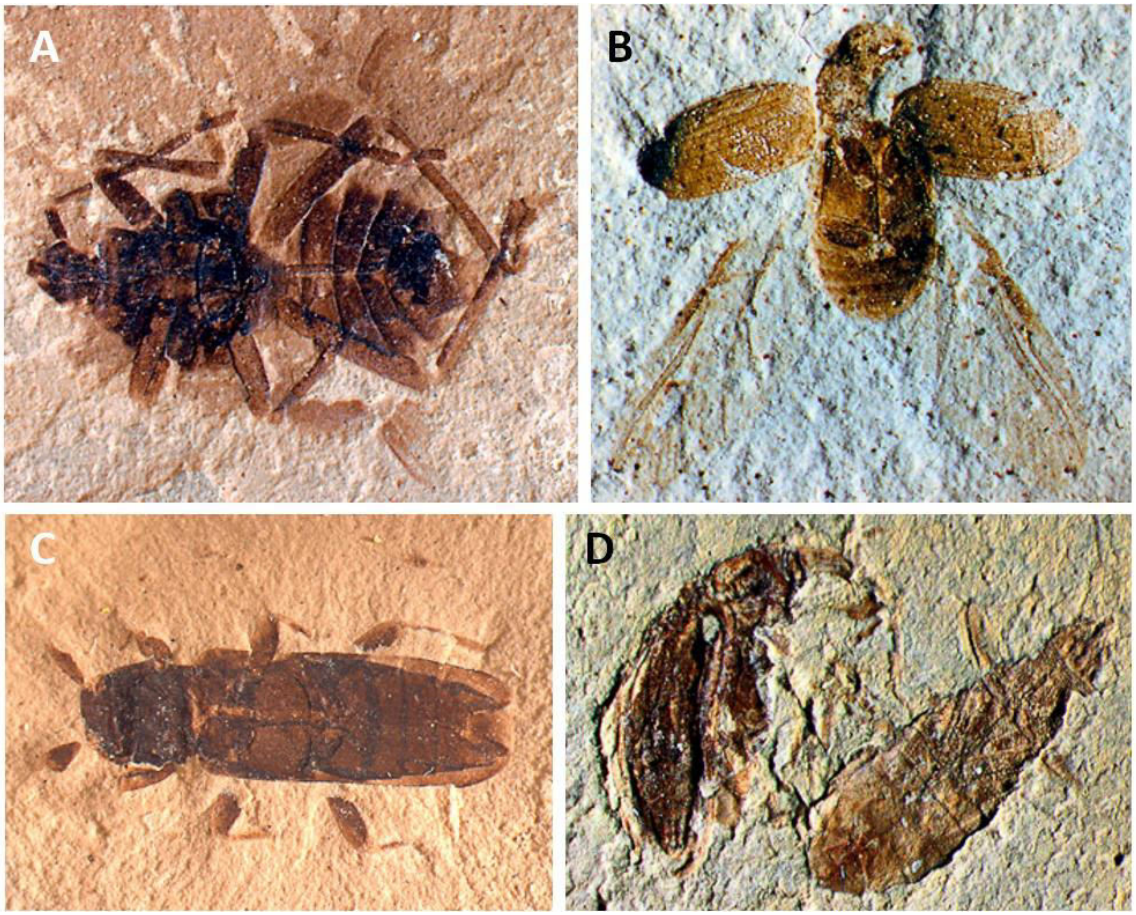


Figure 84. Green River insect preservation. All images are copyright of the Smithsonian Museum of Natural History (Anon., 2015). A, Hemiptera(?) with well-preserved limbs. Fossil number 148. B, Coleoptera showing low relief. Fossil number 53209. C, Orthoptera(?) with appendages through bedding plane. Fossil number 25810. D, Coleoptera: Curculionoidea with moderate relief. Fossil number 75802. No scales recorded. For a slideshow of these fossils, see: http://paleobiology.si.edu/greenRiver/insectPhotos.html

A fossil rich sample (GR001) was obtained for analysis and examined by SEM here. The specimen has numerous examples of *Plecia pealei* (Diptera: Bibionidae) on a single lamina. An isolated abdomen that appeared to retain the thickest cuticle was selected for analysis (Figure 85). The abdomen possessed thin, flat, featureless cuticle under SEM (Figure 85: B-C), with rare cubic pyrite crystals embedded within it (Figure 85: D). The similarities in colour association and the presence of pyrite replacing specimens from the Green River Formation suggest that the chemistry of preservation may be comparable to the Nova Olinda Member. However, the Green River fossil insects have low-to-no relief, do not preserve any delicate cuticular structures (setae, spines, etc.), or any labile internal tissues. Their preservation is considerably poorer than that of the Nova Olinda Member in all regards.

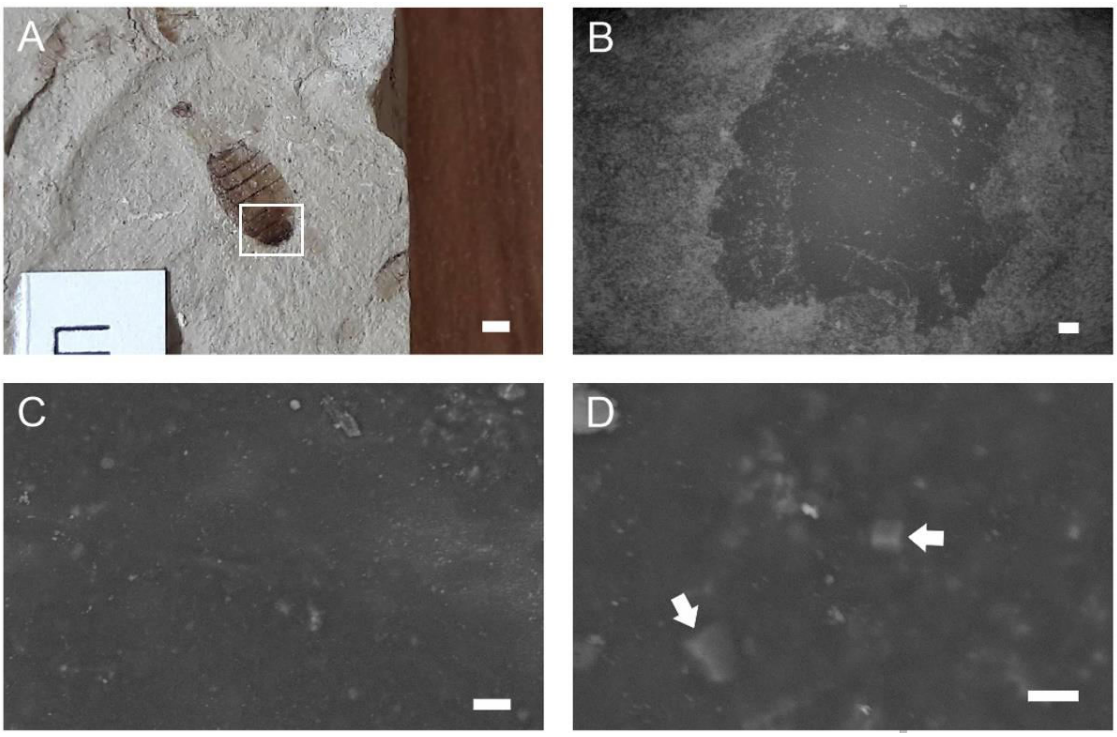


Figure 85. Specimen GR001 (Diptera: Bibionidae: *Plecia pealei*). A, Light microphotograph of disarticulated *Plecia pealei* abdomen on specimen GR001. Square highlights area examined in B. B, Scanning electron micrograph revealing area of exposed cuticle. C, Higher magnification image of cuticular surface, revealing smooth, featureless surface. D, Cubic pyrite crystals embedded into cuticular surface, highlighted by arrows. Working distance = 15.5 – 16 mm. 20 kV. I Probe = 30 – 100 pA. A, Scale bar = 1 mm. B, Scale bar = 200 µm. C, Scale bar = 20 µm. D, Scale bar = 10 µm.

4. 1. 6. Wonthaggi Formation (Koonwarra)

The Koonwarra fossil beds of the Wonthaggi Formation are located in the Gippsland Basin of Victoria, Australia, and yield an abundant and diverse insect fauna (Jell and Duncan, 1986; Krzemiński *et al*., 2015). They are estimated to be Lower Cretaceous (Aptian or Albian) in age and represent a freshwater lacustrine or fluvial(?) environment (Huang, 2015). They are composed of finely laminated and varved brown to yellowish-green mudstones (Huang, 2015; Krzemiński *et al*.,

2015). During the Early Cretaceous, Australia was connected to Antarctica and located within the southern polar region, resulting in a much colder climate (Jell and Duncan, 1986). Consequently, the insect fauna is reminiscent of modern alpine stream and lake faunas (Jell and Duncan, 1986; Riek, 1970). While Hemiptera and Coleoptera are the most diverse orders present, the formation is undoubtedly dominated by aquatic larval Ephemeroptera and Diptera (Jell and Duncan, 1986). In addition, Odonata, Blattodea, Plecoptera, Orthoptera, Psocoptera, Mecoptera, Trichoptera, and Hymenoptera are also present, along with a diverse plant, arachnid, crustacean, brachiopod, and vertebrate assemblage (Huang, 2015).

The mechanism of preservation of these insects has been debated over the last half-century (Riek, 1970; Jell and Duncan, 1986; Elder and Smith, 1988; Huang, 2015). Originally, they were believed to be preserved in a shallow lake bed during cold periods, whereby the shallow portion of the lake was isolated by ice and became anoxic (Elder and Smith, 1988). While supported by palaeoclimate reconstructions, this mode of preservation is inconsistent with sedimentological data (Elder and Smith, 1988). Additionally, the presence of intact fish carcasses and undisturbed varves demonstrates that preservation could not be a seasonal phenomenon in a shallow lake. This is because dissolved decompositional gasses would disturb the carcasses in warmer months (Elder and Smith, 1988). Instead, a deep lake with a stratified water column is suggested (Elder and Smith, 1988; Krzemiński *et al*., 2015).

No fossil insects from the Wonthaggi Formation could be obtained for analysis in this project and no other SEM analyses have been published. Nevertheless, the fossil insect preservation is described as ‘dark brownish and yellow-brownish films caused by weathered pyrite’, but no other taphonomic or geochemical information is presented and the exact mechanism of preservation remains enigmatic (Figure 86; Huang, 2015). Photographs of specimens indicate that very low relief may be present in otherwise flat specimens, but is restricted to areas of heavy sclerotisation, (Huang, 2015). The black to orangey-brown colours of preservation are similar to that of Nova Olinda insects (Figure 86), and so the preserving minerals may also be similar. While both formations represent a deep stratified setting, there is no indication of a marine influence, restricted fish fauna, or microbial mat in the Koonwarra fossil beds (the latter of which may well have been present). In addition, the preservational fidelity, while not yet examined at the micron-scale, appears poor in comparison to the Nova Olinda Member (Huang, 2015). Specimens do not appear to retain any three-dimensionality or cuticular surface details, with only the gross morphology retained (albeit complete and articulated).

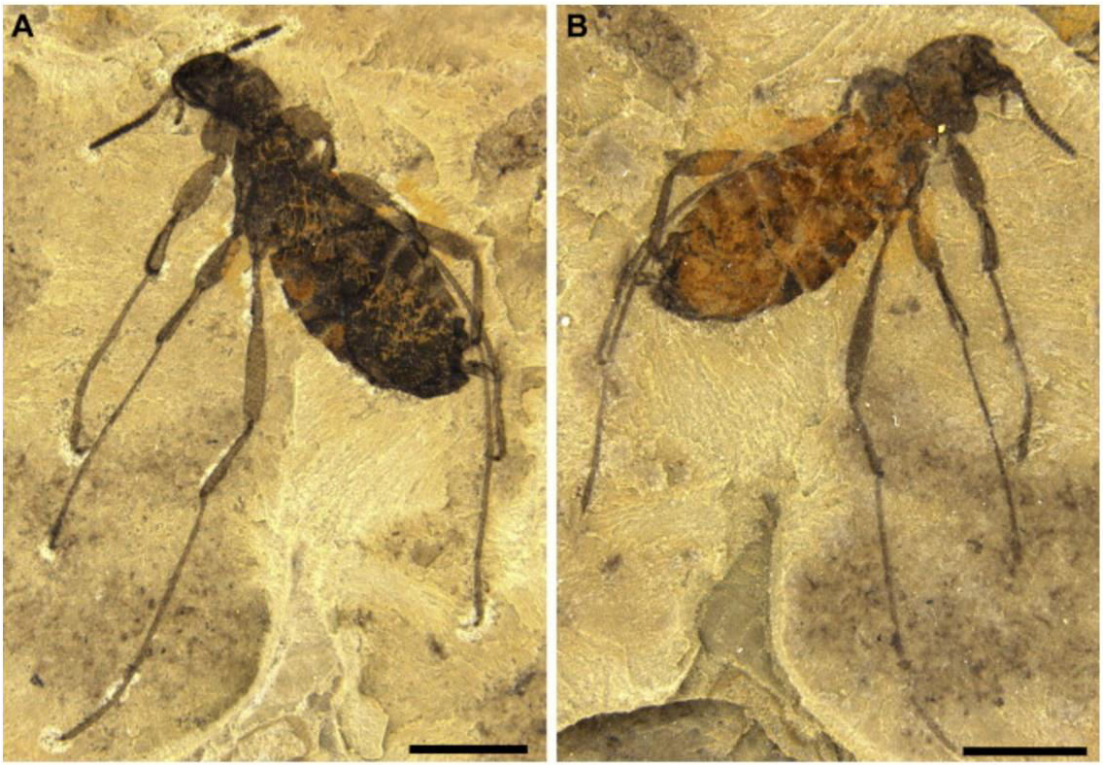


Figure 86. Koonwarra preservation. Images from Huang (2015). Part (A) and counter-part (B) specimens of *Tarwinia australis* holotype. Specimen NMVP 26202. Scale bars = 2 mm.

4. 1. 7. Calizas de la Huérgina Formation (Las Hoyas)

The Calizas de la Huérgina Formation ('Las Hoyas' or the Una Formation) comprises the Las Hoyas Konservat-Lagerstätte (Weishampel, 2004). This Early Cretaceous (Late Barremian) formation is located near Cuenca, Central Spain (Iberian Ranges) (Buscalioni and Fregenal-Martínez, 2010). It comprises finely-grained alternating dark and pale (varved) carbonate sediments, with the darker layers referred to as 'muddy' (Diéguez *et al.,* 1995; Buatois *et al*., 2000). The palaeoenvironment was a relatively low-energy lake fed by fluvial sediments located in a subtropical, seasonal wetland (Diéguez and Meléndez, 2000; Buscalioni and Fregenal-Martínez, 2010). Despite this, it yields xeromorphic plant fossils (Diéguez and Meléndez, 2000). The lake is reported to have had continuous fine-grained carbonate production, along with periodic mild turbidite flows, a largely anoxic bottom-water, and climatically driven cyclic water-level oscillations (Buatois *et al*., 2000; Diéguez and Meléndez, 2000; Buscalioni and Fregenal-Martínez, 2010). It yields a diverse insect fauna, and the presence of insect-feeding mammals suggests that insects were also abundant (Diéguez and Meléndez, 2000; Grimaldi and Engel, 2005; Buscalioni and Fregenal-Martínez, 2010; Martin *et al*., 2015). For an overview of the palaeoentomology from this formation, see Peñalver *et al.* (1999).

Fossil preservation in this formation varies 'extraordinarily' (Diéguez and Meléndez, 2000). Many fossils are preserved merely as discoloured siliceous compressions, but others are preserved with relatively high fidelity and high relief (Briggs *et al.,* 1997; Diéguez and Meléndez, 2000). In many

cases, calcite and/or pyrolousite has precipitated in cavities left after the decay of internal soft tissues (Martínez-Delclòs *et al*., 2004). Vertebrate soft tissues are replicated by iron carbonates (siderite), are often restricted to a single lamina, and accompanied by coccoid microbial mats that are preserved in apatite (Briggs *et al.,* 1997; Báez, 2013).

Specimens were not available for analysis in this project and little information on their taphonomy is published. Figures of fossils show them to be dark compared to the surrounding limestone matrix with varying, but typically low, relief (Figure 87; Peñalver *et al.,* 1999; Grimaldi and Engel, 2005). As vertebrate fossils are preserved as siderite, and it is likely that arthropods are preserved in the same manner (or alternatively in iron sulphides). Further research into the taphonomy of this formation is needed to identify the preserving minerals and corroborate the reports of high-fidelity preservation before an adequate comparison to the Nova Olinda Member can be made (Diéguez and Meléndez, 2000).

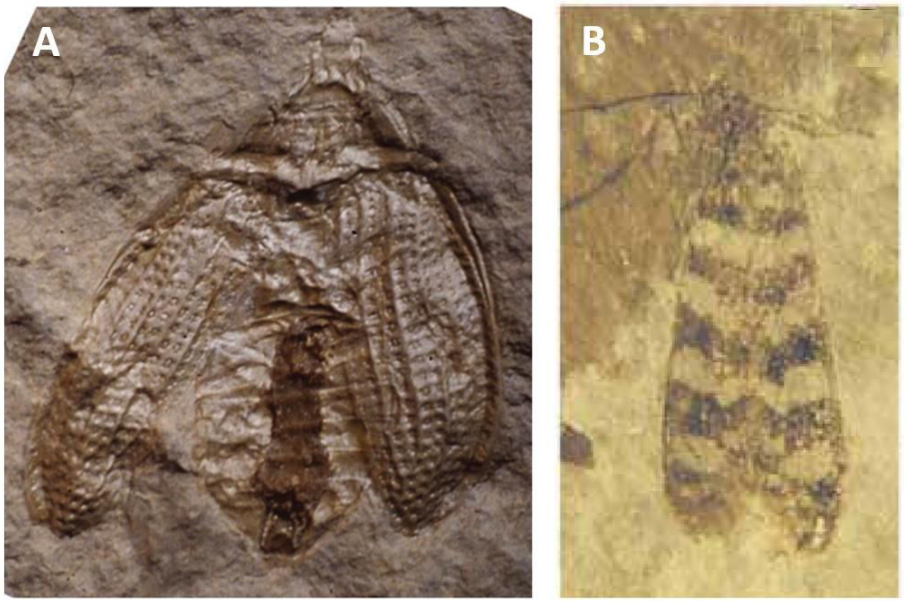


Figure 87. Las Hoyas preservation. Composite image from previous publications showing variation in Las Hoyas insect preservation. A, Cupedid beetle with moderate-to-low relief. Image from Grimaldi and Engel (2005). B, Mecoptera compression fossil with wing colour banding. Image from Buscalioni and Fregenal-Martínez (2010). No scales or specimen numbers were recorded.

4. 1. 8. The London Clay Formation

The Lower Eocene (Ypresian) London Clay Formation is a wide-spread sequence of strata in the southeast of the United Kingdom. It lies predominately within the London Basin, but is also present in the Hampshire Basin (Allison, 1988c; Sumbler, 1996). The most studied outcrop is on the Isle of Sheppey, where approximately 50 m of strata is exposed, although the formation varies greatly in thickness between 4.6 m and 165 m elsewhere (Allison, 1988c; Sumbler, 1996). The formation represents deposition in a shallow (up to 200 m at its deepest point), warm tropical/subtropical sea approximately 160 km east of a lush forested landmass.

The clay is described as ‘stiff bluish’, but is brown when weathered (Sumbler, 1996). It contains abundant nodules of pyrite, calcium phosphate, and calcitic septarian concretions (Allison, 1988c; Sumbler, 1996). The formation yields an abundant arthropod assemblage including rare insects (mostly Coleoptera), but is dominated by crabs and lobsters (Venables and Taylor, 1963; Rundle and Cooper, 1971; Allison, 1988c). Both adult and larval insects can be found, but are all wood-boring taxa associated with driftwood (Venables and Taylor, 1963).

Most fossils are preserved in concretions of pyrite or calcium phosphate and all fossils are three-dimensional (Allison, 1988c). Preservation of arthropod tissues in pyrite is typically non-framboidal. Instead, bipyramidal crystallites of pyrite between < 1 - 4 µm or an indiscernible sheet of nanocrystalline pyrite replaces cuticle (Allison, 1988c). Descriptions of preservational quality vary, with reports of only pore canals and cuticular laminations preserved, and the presence of fragile spines and setae (revealed by X-ray analysis) elsewhere (Allison, 1988c). Pyrite is also reported to infill cavities (Allison, 1988c).

Uncoated backscatter scanning electron analyses were undertaken on a specimen (LC001) loaned by the University of Portsmouth (from the teaching collection) for this project. It revealed well-preserved cuticle retaining easily discernible sutures, pits, and even the dimpled fabric of the original cuticular surface (Figure 88: A-B). However, no protruding structures were preserved and higher magnification images revealed 1 µm globular grains replacing the cuticle (Figure 88: C). Rarely, well-preserved microfossils (possibly coccoliths) were observed in pits on the fossil (Figure 88: D).

The replication of cuticular surface structures and reports of preserved spines and setae clearly demonstrate that the London Clay preserves arthropods exceptionally. Internal tissues are reported for other animal and plant groups, but it appears that most arthropods are infilled with pyrite (Allison, 1988c). Regardless, no labile internal tissues (e.g. muscle, genitals, or guts) are preserved in a manner similar to the Nova Olinda Member. While the London Clay is undoubtedly a site of exceptional preservation of arthropods, the coarser size of its impregnating crystals renders its fidelity of preservation significantly poorer than that of the Nova Olinda Member.

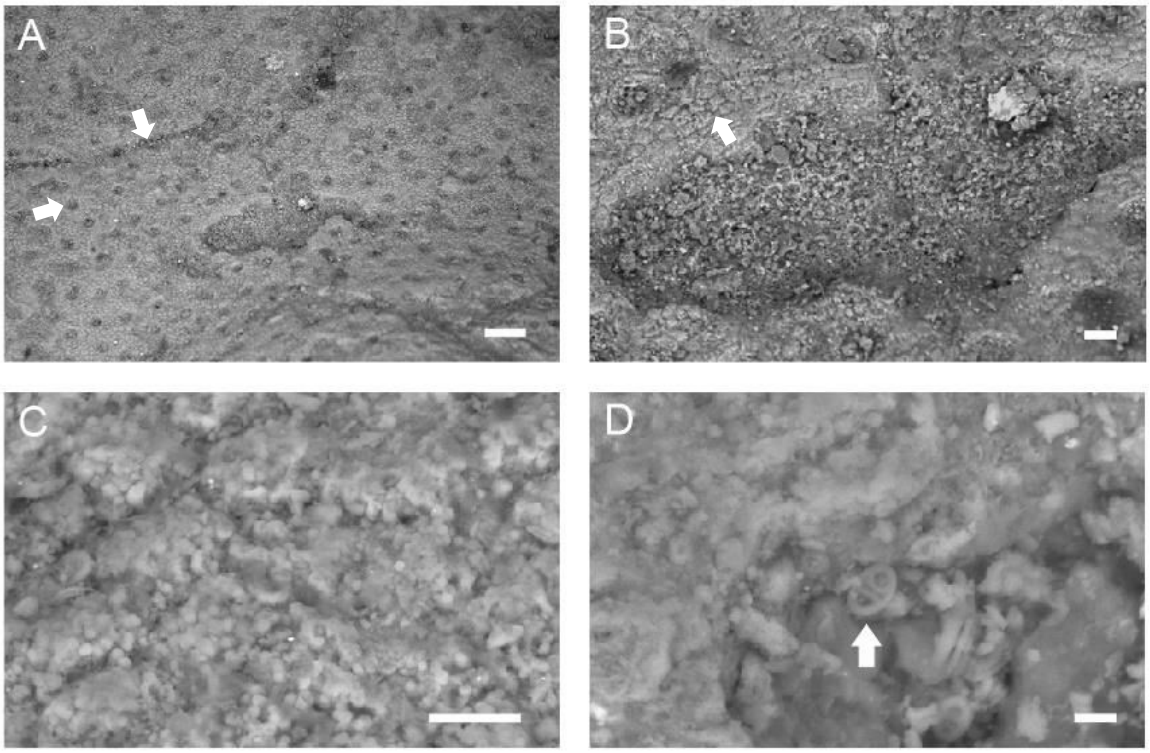


Figure 88. Scanning electron micrographs of London Clay decapod (Brachyura). A, Overview of cuticular preservation, revealing preserved sutures and pits highlighted by arrows. B, Higher magnification image of cuticular preservation showing grooved mesh-like cuticular surface fabric, highlighted by arrow. C, Higher magnification of cuticular surface, revealing a globular replacement fabric. D, Globular fabric of preservation and microfossil structure (coccolith?, highlighted by arrow). Specimen LC001. Working distance = 10.5 mm. 20 kV. I probe varied between 25 and 50 pA. A, Scale bar = 100 µm. B, Scale bar = 20 µm. C, Scale bar = 10 µm. D, Scale bar = 3 µm.

4. 1. 9. 'La Cabrúa' (Montsec)

The Montsec mountains of Lleida, Spain, yield a highly diverse insect fauna from a select few quarries near the abandoned village of Rúbies (Selden, 1990). There is currently no consensus on formation names, and the Montsec outcrops are often discussed with the Las Hoyas outcrops for simplicity (Selden and Nudds, 2012). One quarry, referred to as 'La Cabrúa', is particularly fossiliferous and is Early Cretaceous (Lower Barremian) in age (Selden, 1990; Rasnitsyn and Ansorge, 2000). The sediments of 'La Cabrúa' are pale, fine-grained (~3 µm diameter grains), thinly-bedded, laminated limestones (Selden, 1990). They represent a shallow (as shown by terrestrial vertebrate trackways) coastal lagoon, with large algal flats, and a seasonally dry climate (Selden, 1990; Rasnitsyn and Ansorge, 2000; Vršanský and Ansorge, 2001). The lagoon was partially restricted, leading to fresh-to-brackish conditions (Rasnitsyn and Ansorge, 2000). At some stages during basin evolution, tranquil lacustrine depositional episodes may have occurred (Lacasa and Martinez, 1986).

The Montsec quarries yield a rich and well-preserved assemblage of autochthonous or parautochthonous aquatic insect larvae and allochthonous terrestrial insects (Rasnitsyn and Ansorge, 2000). Most studies of these insects have focused on their systematics and much of their preservation is simply described as 'exceptional' (Selden and Nudds, 2012). Figures of specimens suggest that preservation is 'scrappy', with body segments articulated but much of the cuticle lost (Figure 89; Rasnitsyn and Martínez-Delclòs, 2000).

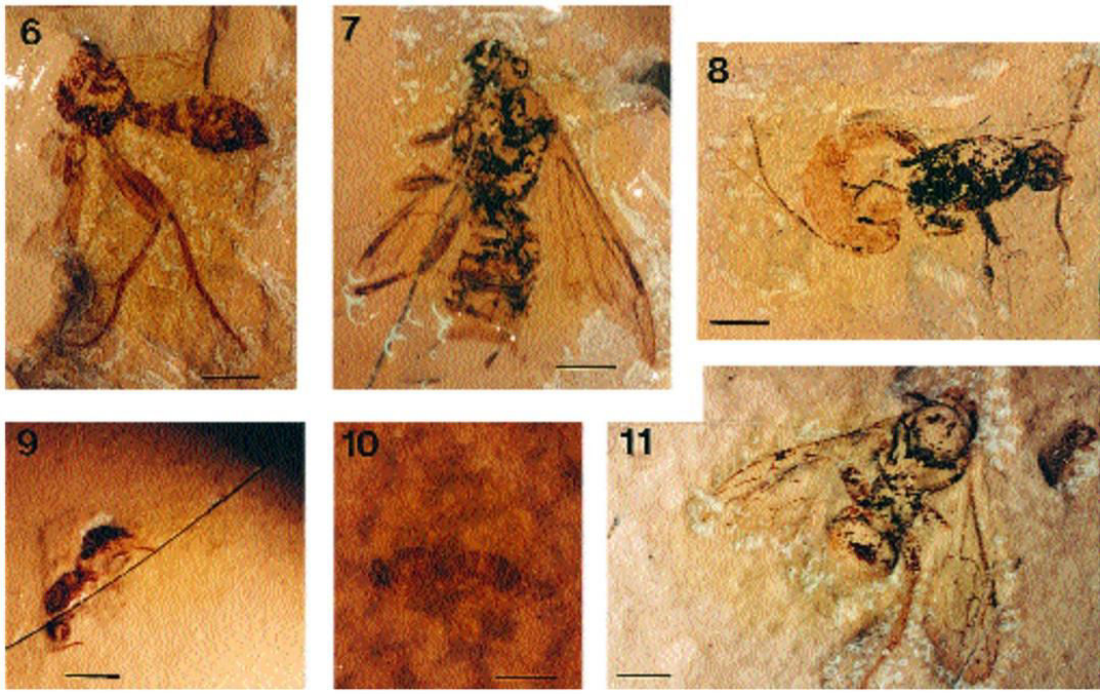


Figure 89. Images of Montsec Hymenoptera from Rasnitsyn and Martínez-Delclòs (2000), demonstrating their preservational fidelity. 6, *Karataus hispanicus* IEI LC-1427. 7, *Pompilopterus noguerensis* IEI LC-2673. 8, *Andrenelia pennata* EP LC-036. 9, *Cretoserphus gomezi* IEI LP-0652. 10, *Praeaulacidae* IEI LC-3313. 11, *Angarosphex penyalveri* IEI LP-0163. Scale bars = 2 mm.

Several specimens from Montsec were donated to this project for analysis (courtesy of Antonio Lacasa), two of which were subject to SEM analysis (Figure 90). These revealed poorly preserved cuticle, retained only as two-dimensional 'scrappy' traces (Figure 90: A-D). When viewed at higher magnification, cuticle is either represented as a discolouration (also visible in backscatter) on the sediment surface (Figure 90: B), or as a 'scrappy' cracked layer (Figure 90: D). In one specimen, crystals of *circa* 100 µm long (possibly calcium phosphate or calcite) were embedded within the cuticle (Figure 90: E). Many of the fossils are preserved as deep black to pale orangey-brown discolourations compressed to a single lamina (Figure 89), suggesting an iron sulphide weathering to iron oxyhydroxides similar to the Nova Olinda Member (Selden and Nudds, 2012). This, combined with the presence of rare calcium phosphate crystals, suggests a similar geochemical environment to the Nova Olinda Member. Nevertheless, the preservational quality of Montsec insect fossils is extremely poor compared to the Nova Olinda Member, largely due to excessive compaction.

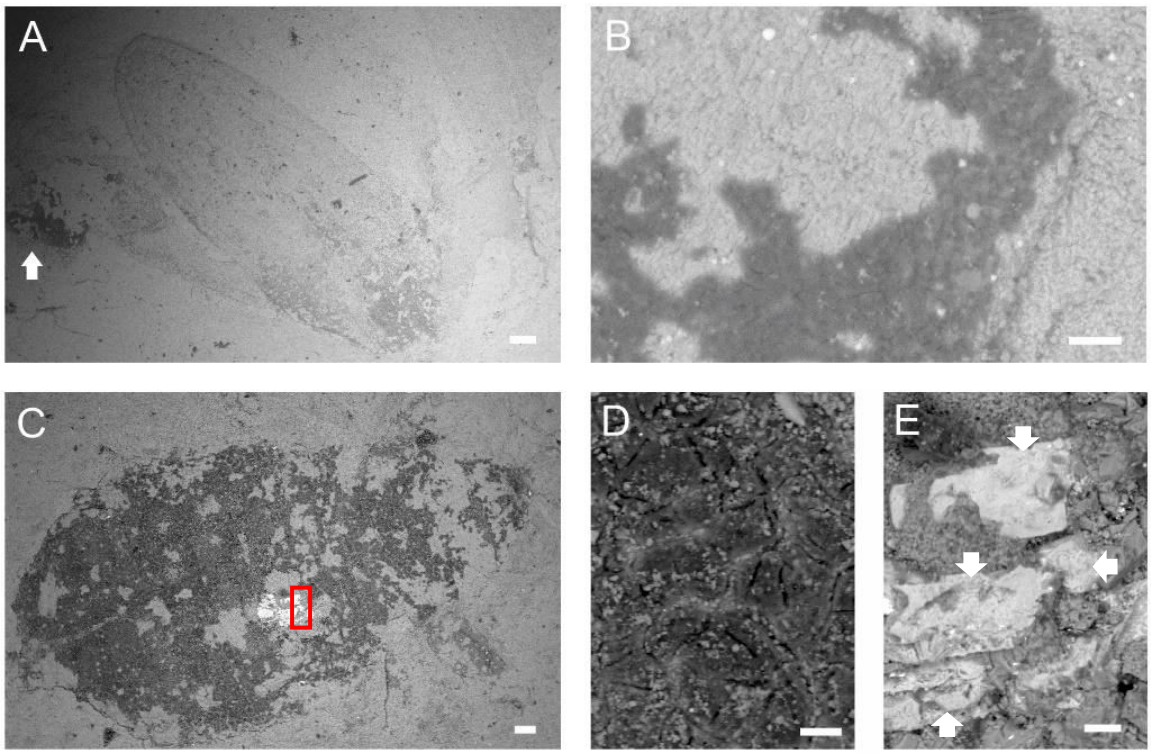


Figure 90. Specimens from the 'La Cabrúa' Montsec. A, Overview of Diptera specimen (MontA) wing and portion of abdomen, highlighted by arrow. B, Higher magnification image of abdominal cuticle, showing little-to-no discernible features of the fossil material aside from colour. C, Overview of 'scrappy' Coleoptera specimen ($MontD_1$). Red box highlights area shown in E. D, Higher magnification image of cuticle. E, Higher magnification image of large calcium phosphate crystals (or calcite), highlighted by arrows. A-B, 15 kV, working distance = 14.5 mm and I Probe = 75 pA. C-E, 20 kV, working distance = 16.5 mm and I Probe 100 pA. A, Scale bar = 200 µm. B, D and E, Scale bar = 20 µm. C, Scale bar = 100 µm.

4. 1. 10. Rubielos de Mora Basin Lagerstätte

The Rubielos de Mora Basin is located in eastern Spain, east of the city of Teruel. It is a half-graben filled with a 600 m thick Early Miocene sequence, divided into three major components (Anadón *et al*., 1988; Engel and Peñalver, 2006; Jiménez-Moreno *et al*., 2007). Currently, there is no consensus on formation boundaries or names, and as such the sequence is divided into *Upper*, *Middle*, and *Lower* units. The lower unit consists of sandstones interbedded with mudstones and conglomerates; the middle unit consists of lacustrine limestones interbedded with mudstones and sandstones; and the upper unit consists of alluvial deltaic, marginal lacustrine, and open lacustrine facies (Engel and Peñalver, 2006; Jiménez-Moreno *et al*., 2007). Much of the sequence is organic-poor and non-laminated, but where organic rich laminated layers are present (laminated oily grey mudstone), fossil plants and insects are abundant (Anadón *et al*., 1988; Jiménez-Moreno *et al*., 2007). These organic rich laminated mudstones contain a diverse assemblage of insects, including members of Diptera, Hymenoptera, Thysanoptera, Hemiptera, Coleoptera, Orthoptera, and Trichoptera, and likely represent lacustrine deposition (Peñalver and Seilacher, 1995; Engel and Peñalver, 2006). Of these, Hymenoptera has the highest diversity, with

11 families represented. Plants are also diverse and alternate between thermophilous (arid-loving) and mesothermic-riparian (sub-arid- and water-loving) taxa, associated with matching sedimentological fluctuations (Jiménez-Moreno *et al*., 2007). The presence of thermophilous plants indicates a dry subtropical climate with seasonality, however the alternations with riparian taxa suggests a fluctuating overall climate and corresponding lake level fluctuations (Jiménez-Moreno *et al*., 2007).

The Rubielos de Mora insect fossils are described as preserved with 'outstanding fidelity', and accompanying images reveal articulated and complete fossils, albeit with low relief (Figure 91; Peñalver, 1998a,b; Peñalver and Seilacher, 1995; Peñalver and Martinez-Delclòs, 2003; Engel and Peñalver, 2006). Specimen MPV-2419-RM was made available for this project for comparative analysis (courtesy of Dr Enrique Peñalver and the Natural Sciences Museum of Valencia) and, despite it appearing exceptionally preserved in hand specimen (Figure 92: A), revealed remarkably poor preservation at the microscopic scale (Figure 92: B-D). Cuticle appears to be preserved as an extremely thin (1 – 2 μm) brittle compression that is readily cracked (Figure 92: B-C). No three-dimensional preservation was observed, nor were any internal soft tissues or cuticular surface structures. Only the gross morphology of the cuticle, including fragile appendages (antennae, limbs, wings, etc.), are preserved. Alternatively, the thin cracked surface observed could be a thin translucent lamina coating the fossil material. Regardless, specimens from the Rubielos de Mora Basin appear extremely well-preserved in hand specimen and many of their taxonomically important features (i.e. wing venation, antenna segments) are easily discernible. Nevertheless, they lack three-dimensional preservation and no micron-scale cuticular features have been observed.

Figure 91. Rubielos de Mora preservation. Image from Engel and Peñalver (2006). Type specimen of *Halictus petrefactus* (Hymenoptera: Halictidae). Exceptionally preserved as black discrete cuticular plates, but with no apparent relief. Specimen MPZ 98/423. Scale bar = ~1 mm.

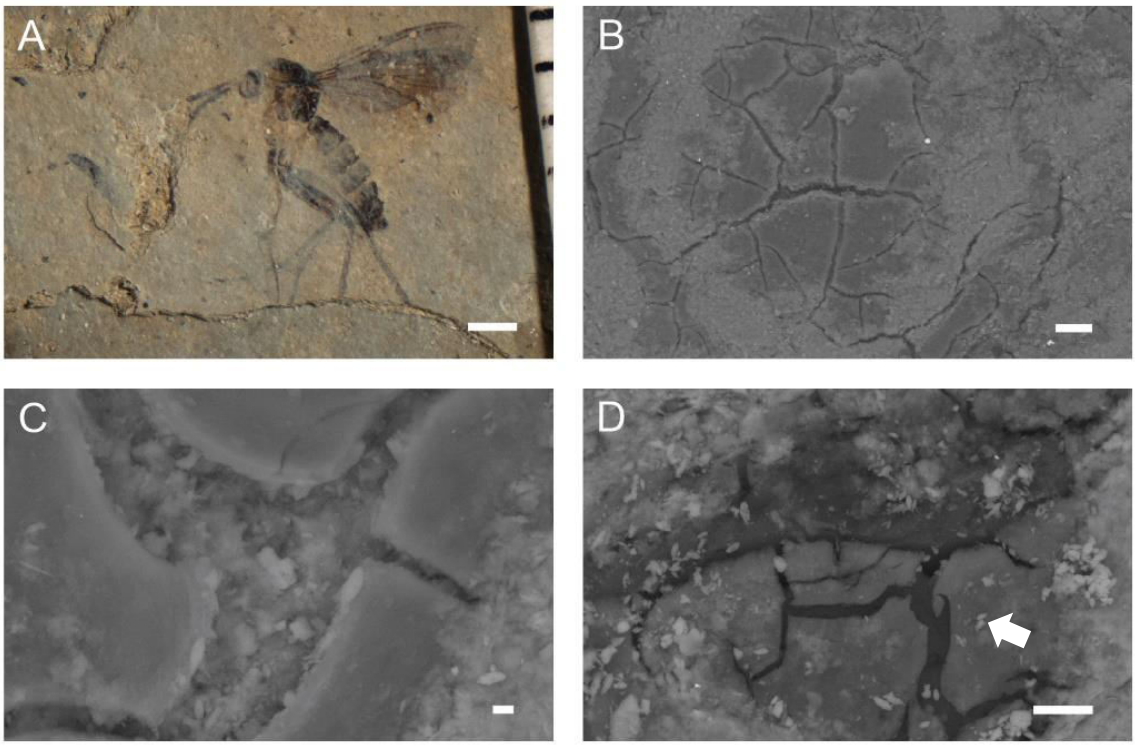


Figure 92. Specimen MPV-2419-RM (Diptera: Mycetophilidae). A, Light photograph overviewing the specimen. B, Scanning electron micrograph of the thorax, revealing remarkably poor preservation. C, Higher magnification image showing cracked cuticle and internal contents. D, Posterior abdomen with cracked cuticle and pellet-shaped contaminant grains (highlighted by arrow). Working distance = 12.5 mm. 20 kV. I Probe = 25 pA. A, Scale bar = 1 mm. B, Scale bar = 20 µm. C, Scale bar = 2 µm. D, Scale bar = 10 µm.

4. 1. 11. Solnhofen Formation knowledgeable personable.

The Late Jurassic (Kimmeridgian-Tithonian) Solnhofen Formation is arguably the most famous fossil Lagerstätte and the word ‘plattenkalk’ originates from its description (Ponomarenko, 1985; Martínez-Delclòs *et al*. 2004; Grimaldi and Engel, 2005). This fame is largely due to the iconic Solnhofen theropod fossil *Archaeopteryx* (Kemp, 2002; Grimaldi and Engel, 2005). The formation crops out in central Bavaria, Germany, and has been extensively studied over the past 200 years (Ponomarenko, 1985; Barthel, *et al*., 1990; Viohl, 1990; Werner *et al*., 1994; Tischlinger, 2001; Kemp, 2002; Arratia *et al*., 2015; etc.). It is comprised of very fine-grained and thinly bedded micrites, representing a lagoon (Martínez-Delclòs *et al*., 2004; Grimaldi and Engel, 2005). This lagoon was isolated, anoxic, and hypersaline, as shown by the highly restricted benthos and *Mesolimulus* death trails (Arratia *et al*., 2015).

The insects of the Solnhofen Formation have been extensively studied, mostly for the taxonomic composition of the assemblage. It is biased towards strong-flying adult insects, with imago Odonata representing approximately 25% of all insect specimens (Ponomarenko, 1985). No larvae of these strong flyers are present, as the formation represents a marine environment (Ponomarenko, 1985). Over fifty genera of insects have been described, however some of the classical descriptions were based on poorly preserved specimens and may be dubious (Carpenter 1932; Kuhn, 1961; Ponomarenko, 1985). The preservational quality of these insects has conflicting reports. Martínez-Delclòs *et al*. (2004) cite them as examples of exceptional preservation in plattenkalks, however they are frequently described as being particularly poorly-preserved (Ponomarenko, 1985; Tischlinger, 2001; Grimaldi and Engel, 2005). The latter of these is the more accurate description (Grimaldi and Engel, 2005; Figure 93). Additionally, information regarding their replacement mineralogy appears contradictory. Dedicated studies describe them as being mostly poor-quality (sometimes called ‘rough’) calcite and pyrolousite casts that retain some three-dimensionality (Ponomarenko, 1985; Viohl, 1990; Martínez-Delclòs *et al*., 2004; Grimaldi and Engel, 2005). Despite this, Martínez-Delclòs *et al*. (2004) describe Solnhofen as a typical site of phosphatisation for insects. Phosphatisation is otherwise uncommon in the formation, with less than 8% of fish specimens phosphatised (Wilby *et al*., 1995).

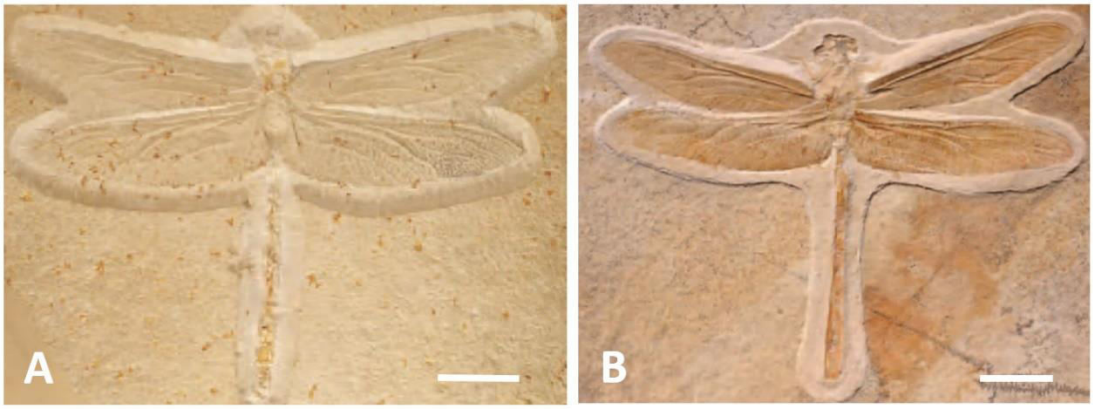


Figure 93. Solnhofen preservation. Images from Grimaldi and Engel (2005). A, *Libelluium longialata.* Specimen NHM 28201. B, Private collection specimen, unusually well-preserved for this formation. A, Scale bar = ~3 cm. B, Scale bar = ~2 cm.

Specimen SH001 was subject to SEM analysis to determine its micron-scale preservational fabrics (Figure 94). This revealed exceptionally poor preservation, with the majority of tissues obliterated by calcium phosphate crystals (Figure 94: A and C) or a combination of calcium phosphate and globular material (Figure 94: B). Cuticle is preserved very rarely and where preserved is fragile and featureless (Figure 94: D). Despite the similarities in sedimentology, bottom water conditions, the presence of calcium phosphate, and palaeoenvironment, the Solnhofen Formation insect preservation is very different from, and considerably poorer than, the Nova Olinda Member.

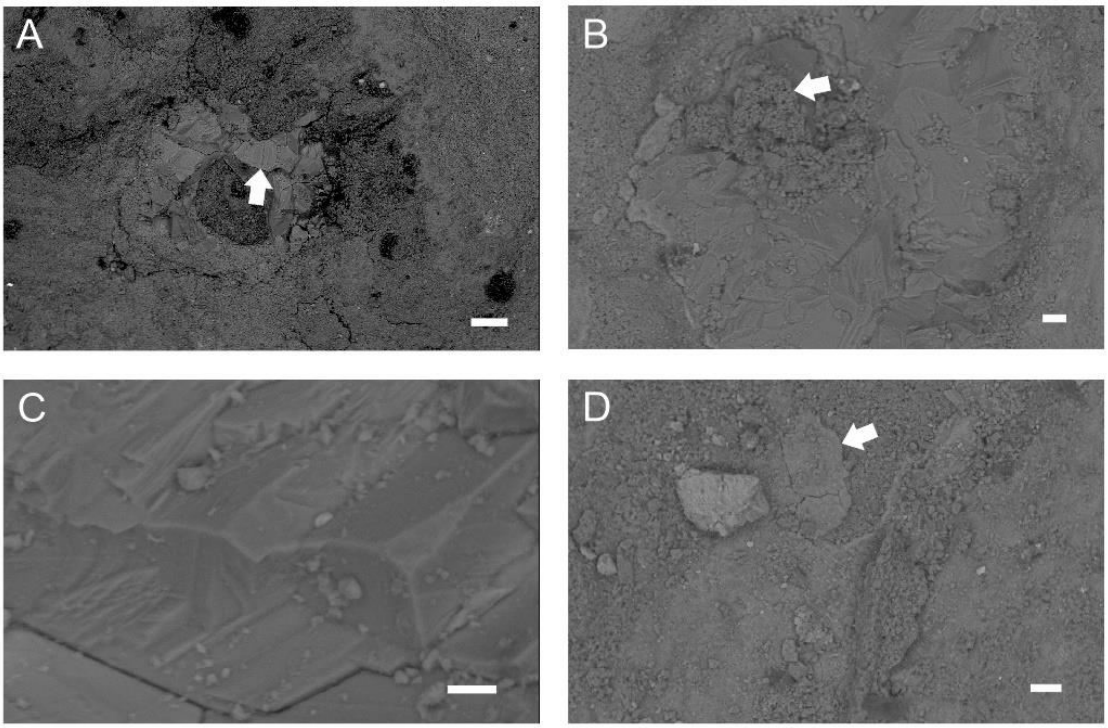


Figure 94. Specimen SH001 (Odonata). A, Insect body tissue replaced by coarse calcium phosphate or calcite crystals, highlighted by arrow. B, Insect body tissue with calcium phosphate crystals and globular replacement , highlighted by arrow. C, Higher magnification image of calcium phosphate crystal. D, Thin fragments of cuticle, highlighted by arrow. Working distance = 18 – 19 mm. 20 kV. A, I Probe = 150 pA. C-D, I Probe = 10 pA. A, Scale bar = 100 µm. B and D, Scale bars = 20 µm. C, Scale bar = 10 µm.

4. 1. 12. Yixian Formation

The Early Cretaceous (Barremian-Aptian) Yixian Formation, of the lowermost Jehol Group, is one of the most famous and species rich Mesozoic insect Lagerstätte (Chang *et al*., 2007), and is located in the Liaoning province, north-east China. Its sedimentology can be summarised as a finely laminated siliciclastic sediment (no common classification), interbedded with organic-rich siliclastic mudstones, shales, and volcanic ash (Wang *et al.,* 1998; Ding *et al*., 2003; Chen *et al*., 2004; Zhang and Sha, 2012). The formation is well known for the exceptional preservation of both vertebrate and invertebrate fossils, attributed to a combination of periodic anoxia, volcanic input, and rapid burial (Fürsich *et al*., 2007; Zhang and Sha, 2012). Periodic anoxia caused seasonal mass mortality events, whereby the water stagnated in the coldest season and was re-oxygenated via thermal convection in warmer seasons (Fürsich *et al*., 2007). Additionally, episodic volcanic eruptions and flash floods may account for many of the most exceptionally preserved fossils, especially the vertebrates (Fürsich *et al*., 2007). Original chitin components of the insect exoskeleton may be retained, however the majority of fossils are compressed and faintly coated in a black mineral described as 'an amorphous dark mineralised substance' (Wang *et al*., 2007; Fürsich *et al*., 2007). Despite their compression, the fossils show little fragmentation or breakage (Zhang and Sha, 2012). Many fossils are also impregnated with iron oxides, which are intimately associated with the siliclastic mudstone, with reddish/purple/greenish-grey colours indicating the presence of Fe^{3+}, and greenish-grey/grey/black indicating abundant Fe^{2+} (Zhang and Sha, 2012).

Preliminary studies of the fossilisation process in the Yixian Formation provide descriptions of 'amorphous black minerals' and evidence of abundant sedimentary iron (Wang *et al*., 2007; Zhang and Sha, 2012), however pyrite framboids were originally considered rare (Leng and Yang, 2003). A more comprehensive study of iron mineral phase replication within the Jehol Biota (Yixian and Dabeigou formations) revealed that pyrite framboids pseudomorphed by iron oxide are widespread (Zhang F. *et al*., 2010; Wang *et al*., 2012). Additionally, there are also halos of pyrite around many fossils (Briggs, 2003; Wang *et al*., 2012).

Initial palaeoenvironmental reconstructions of the Yixian Formation suggested a freshwater habitat, however this would not normally allow for pyrite framboid formation (Allison, 1988b). Fossils preserved in pyrite were only recovered from those lacustrine sediments with nearby volcanic tuffs, which supplied the lake waters with abundant reactive iron and sulphur mineral phases, and ultimately allowed for framboid formation (Wang *et al*., 2012). Although the pyritization is reported as widespread, it is still restricted to a select few horizons that exhibit this combination of characteristics, and the majority of fossils are 'carbonaceous compressions' (Wang *et al*., 2012).

Pyrite replacement occurs in two distinct forms within the Yixian Formation: a three-dimensional replacement, whereby the exoskeleton acted as a template for pyrite framboid precipitation (Figure 95) and a two-dimensional 'carpet' of pyrite microcrystals replacing the fossil (Wang *et al*., 2012). Three-dimensional framboid replacement is coarse-grained and does not replicate cuticle microstructure (Wang *et al*., 2012). The framboids are disordered, composed of poorly aligned microcrystals between 0.1 and 0.5 µm in diameter (Figure 95: E and F; Wang *et al*., 2012). Extremities of some fossils do not retain three-dimensionality, and may only be replicated as 'carbonaceous compressions'. Alternatively, pyrite replacement may only preserve the fossils as a two-dimensional carpet of microcrystals. This flattened preservation indicates conditions with a lower Eh and a different microenvironment from that of the three-dimensional specimens according to Wang *et al*. (2012).

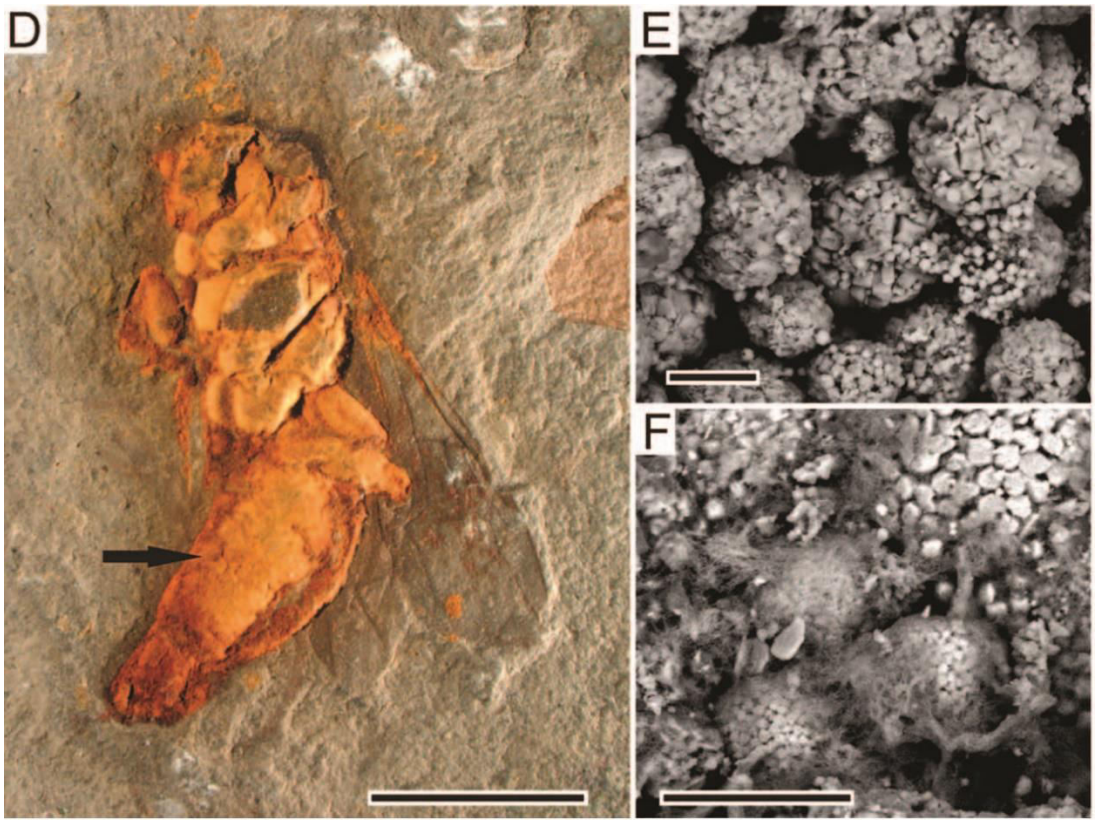


Figure 95. Yixian preservation. Images from Wang *et al*. (2012). Specimen NIGP 154959 (Hymenoptera: Sphecidae). D, Photomicrograph with arrow highlighting area imaged in E and F. E and F, SEM images of pyrite framboid replacement fabric. D, Scale bar = 5 mm. E and F, Scale bars = 10 µm.

Fossil insects from the Yixian Formation share many similarities in preservation with the Nova Olinda Member insects. Although pyrite and its subsequent weathering products replace insect tissues in both Lagerstätten, the Yixian Formation pyrite crystals are much coarser and restricted to framboids. Consequently, the Yixian Formation preserves no cuticle microstructure, nor faithfully replicates the external surface of the insect cuticle. Nevertheless, despite the significantly differing sedimentology (abundant siliciclastics, some volcanic sediments, and little or

no carbonate), pyrite framboids formed and so the geochemical conditions must have been grossly similar to the Nova Olinda Member. However, the rare pyritization of Yixian insects is attributed to variations in the microgeochemical environments surrounding them, which may be considerably different from the gross sedimentological geochemical environment (Wang *et al*., 2012). Consequently, further research is required to reconstruct the microgeochemical environments of the Yixian Formation and determine how they compare to those of the Nova Olinda Member.

4. 1. 13. Comparison Summary

Of the eleven comparable fossil Lagerstätten examined here, none appeared to yield fossil insects with as high a preservational fidelity as the Nova Olinda Member. Although many of the insect fossils from these sites were complete and articulated, none retained high-fidelity micron-scale preservation of cuticular structures or internal labile soft tissues. Although each Lagerstätten is subtly different in terms of sedimentology, palaeoenvironment, and fossil assemblage (and many other aspects), there are several key factors that prevented their fossils from being preserved with as high a fidelity as the Nova Olinda Member. In most of the examined Lagerstätten, preservational fidelity was lost via excessive compaction or cuticle obliteration by mineral growth. Below, suggestions for why each Lagerstätte possesses relatively poor preservation are presented.

The Beecher's Trilobite Beds preserve fossil arthropods as internal and external pyrite moulds, but not impregnations (Farrell *et al*., 2009). Despite previous descriptions of soft-tissue preservation, no labile internal soft-tissues were observed in these fossils. Only cuticle was preserved in coarse (5 – 20 μm) grains of pyrite (or the cuticle was lost leaving only an impression in the matrix). Regardless, the presence of coarsely grained framboids (Figure 79) and other larger anhedral grains moulding the cuticle, obliterated any micron-scale cuticular morphology. The grains were simply too large to retain the morphology of setae and cuticular scales etc.

The Daohugou Lagerstätte suffers a similar problem, with cuticular micro-structures obliterated by coarse (2 – 3 μm) anhedral pyrite crystals (Wang *et al*., 2009). In specimens where these coarse pyrite crystals are absent, compaction has crushed the insects to a single lamina, also obliterating any cuticular micro-structure.

The Florissant Formation is unique among the compared Lagerstätten in that it preserves micron-scale cuticular morphology (O'Brien *et al*., 2008). However, these cuticular structures are masked by a sheet of diatom body fossils (Figure 83). This sheet of microfossils is the primary mechanism of preservation and is inseparable from the fossil insect tissues. As such, they have essentially obliterated any micron-scale cuticular surface morphology via immovable encrustation.

The Green River Formation fossil insects do not preserve micron-scale cuticular features (Dayvult *et al*., 1995; Shcherbakov, 2006). The primary reason for this is excessive compaction, with most fossils being restricted to a single lamina. It appears that either mineralisation was insufficient to prevent compaction, or that it occurred post-compaction. The presence of kerogen-rich laminae also suggests that the formation may have undergone thermal maturation, which could have caused further degradation of the fossils. Finally, the rare occurrence of relatively large (10 µm, Figure 85) cubic pyrite crystals embedded within the cuticle indicates that some cuticular features were obliterated by mineral growth.

Both the Koonwarra and Las Hoyas Lagerstätten appear to preserve fossil insects relatively poorly, compacted to a single lamina (Diéguez and Meléndez, 2000; Martínez-Delclòs *et al*., 2004; Huang, 2015). However, both of these Lagerstätten remain largely un-investigated and little information is available regarding their fidelity of preservation. Further research is required before conclusive comments can be made about their modes and fidelities of preservation, as well as restricting factors.

The London Clay Formation preserves fossil arthropods via impregnation by anhedral pyrite crystals approximately 1 - 4 µm in size (Allison, 1988c). These preserve the gross morphology of the arthropod, but do not allow for the retention of micron-scale cuticular features. Although reports suggest that nanocrystalline impregnation of the cuticle does occur (Allison, 1988c), it was not observed in this project. Unlike many of the other Lagerstätten preserving in pyrite, no framboids were observed associated with these fossils in this project.

For both the Montsec and Rubielos de Mora Basin Lagerstätten, fossils are preserved as compressions (Rasnitsyn and Martínez-Delclòs, 2000; Jiménez-Moreno *et al*., 2007), with very low relief restricting them to a single lamina. Compaction has obliterated all fine-scale morphology of the cuticle, leaving only ‘scrappy traces’.

The Solnhofen Formation preserves insects relatively poorly. Despite the three-dimensionality of these fossils, the ‘rough calcite and pyrolusite’ mineral growths have obliterated all internal structure, as well as most of the cuticle, leaving only the gross morphology of the insect and ‘scraps’ of featureless cuticle (Ponomarenko, 1985).

Finally, the Yixian Formation preserves fossils in framboidal pyrite, without nano-crystalline impregnation of the cuticle, or preservation of labile internal soft tissues (Wang *et al*., 2012). This has resulted in all cuticular morphology being obliterated by coarse framboid growth, leaving only the gross morphology of the insect.

Of the Lagerstätten examined here, arguably the most comparable to the Nova Olinda Member (in terms of preservational fabric) is the Yixian Formation. It possesses a framboidal infilling fabric

reminiscent of the pseudoframboid-like aggregates found in the Nova Olinda Member insects. Nevertheless, it lacks the other two key fabrics: nanocrystalline impregnation of cuticle and globular impregnation/incrustation of labile internal soft tissues. Even when specimens are entirely uncompacted, without these other fabrics, no cuticular micron-scale morphology is preserved, nor are internal labile tissues. These comparisons suggest that the Nova Olinda Member insects underwent a unique diagenetic sequence, combining several distinct mineral fabrics preserving different tissue types, which protected their tissues from compaction and obliteration and ultimately allowed for the highest-fidelity preservation of fossil insects outside of amber.

4. 2. Taphonomic models

The comparisons above have established that the preservation of Nova Olinda Member insects is different from other arthropod Lagerstätten, even those that preserve fossils in similar minerals. Therefore, to determine the mode of preservation, a mineral replacement pathway model must be created.

4. 2. 1. Previous models

Several analyses have included models for the process of fossilisation in the Nova Olinda Member (Menon and Martill, 2007; Delgado *et al*., 2014; Osés *et al*., 2016). Of these, Delgado *et al*. (2014) and Osés *et al*. (2016) provide comprehensive chemical analyses of the fossils and present detailed descriptions of the modes of preservation.

Delgado *et al*. (2014) used a series of analytical techniques to examine pseudomorphed pseudoframboids in the Nova Olinda Member fossil insects. They outlined two distinct fabrics of iron mineral preservation, one replacing the exterior most cuticle, and the other replacing internal tissues. This was supported by non-quantitative measurements of elemental composition between the two fabrics, highlighting differing amounts of the same elements in each sample (Delgado *et al*., 2014). They described the external cuticle replacement as ‘pseudomorphs of framboidal pyrite > 5 µm in diameter’, and the internal replacement as ‘framboidal pyrite pseudomorphs ca. 1 µm of diameter’. This description is in stark contrast to the observations presented here, where the external most cuticle is preserved in nanocrystalline goethite (pseudomorphing pyrite) impregnations and the internal body cavity is infilled by coarser pseudomorphed pseudoframboids (or pseudoframboid-like aggregates). The importance of sulphate reducing bacteria and the environments that allowed them to thrive are noted by Delgado *et al.* (2014). Finally, these authors determined that the high degree of fidelity is a consequence of the small crystal size of the replacing minerals.

Osés *et al*. (2016) provided a much more detailed explanation of the high-fidelity preservation of Nova Olinda Member fossil insects, including descriptions of the geochemistry and a summary taphonomic model (see figure 10 in Osés *et al*., 2016). They consider that the primary mode of preservation is via pyrite replacement in two-stages, stimulated by the concentration of ions in microbial mats surrounding the carcass. Firstly, the internal tissues were replaced (obliterated) by framboidal pyrite of differing sizes in different tissues. Secondly, nanocrystalline pyrite over-grew these framboids, replicating the cuticle with high-fidelity. The ions supplying the first stage of replacement were proposed to have entered the carcasses through microcracks in the cuticle. However, cuticle is a flexible material that does not crack in this manner unless mineralised (Grimaldi and Engel, 2005; Smith *et al*., 2006), which in their model is proposed to have occurred *after* the mineralisation of internal tissues. They also propose that the sulphates required for pyritization originated from 'evaporites' (Osés *et al*., 2016), presumably referring to the only evaporites in the basin, the *overlying* Ipubi Formation. However, the Ipubi Formation was not deposited until long after the mineralisation of these fossils, possibly millions of years later. Nevertheless, pyritization occurred and Osés *et al*. (2016) explained that this was due to a low content of scattered organic matter within the sediment, a lack of bioturbation, and persistent anoxic bottom water conditions. The fabrics of replacement are described as anhedral and euhedral nanocrystals replacing the exoskeleton and figures of 500 – 600 nm crystal moulds are provided. The descriptions of the replacement fabric and figured moulds do not correspond to the replacement fabrics figured elsewhere by Osés *et al*. (2016), nor with the observations presented here. The replication of sub-micron cuticular features with a high fidelity (such as 500 nm thick cuticular scales: Plates 45 and 46) indicates that external cuticle replication is significantly finer grained (likely in the tens-of-nanometres) than suggested by Osés *et al*. (2016). Additional descriptions of the fabrics of preservation suggest that micron-sized spherical structures within the cuticle are micro-framboidal pyrite. This is a reasonable interpretation, but cannot be confirmed until higher magnification images reveal their structure. The influx of aquatic insects is attributed to mass mortality events from 'excessive hydrogen sulphide production' (suggested to be from 'hypersalinity episodes') and the prevention of carcass collapse is a result of early mineralisation (Osés *et al*., 2016). For further critique of Osés *et al*. 2016, see Chapter 1. 10. 3.

The preservation of insect tissues in other minerals is discussed briefly. Apatite is noted to be associated with pyrite replication in the Nova Olinda Member and suggested to originate from carcass decay, rather than from the surrounding pore water (Osés *et al*., 2016). This hypothesis is supported by previous studies on the mineralisation of arthropod 'soft-tissues' in calcium phosphate (Wilby and Briggs, 1997; Martinez-Delclòs *et al*., 2004; Maas *et al*., 2006; Eriksson *et al*., 2012). Additionally, most continental waters, excluding highly alkaline Ca-poor waters, do not typically contain enough phosphate to allow for apatite formation (Wilby and Briggs, 1997;

Martinez-Delclòs *et al*., 2004). However, where the most labile tissues are preserved (i.e. muscles, genitals, and guts), decay must have been minimal, and so may not have provided sufficient phosphate for mineralisation. Alternatively, soil contains abundant phosphate, and rapid soil erosion can contribute significantly to freshwater phosphate content (Pearlman, 2016). Consequently, a combination of periodic flash floods and concentration by evaporation could account for apatite formation without the requirement for extensive decay.

The rare presence of siliceous halos is also noted (see Plate 3: A, in Menon and Martill, 2007; Barling *et al*., 2015). The inclusion of heavy metals into arthropod cuticle is noted (Gonzalez-Davila and Millero, 1990) and correlated with heavy metals detected via EDX in the Nova Olinda Member fossil insect bodies (Osés *et al*., 2016). Finally, as with Delgado *et al*. (2014), carbon-rich pliable material (that is interpreted here as fungal contamination) is interpreted as fossilised EPS.

4. 2. 2. Pyrite geochemistry recap

As the models described above do not account for many of the observations in this study, a refined preservational model is presented below. It is undoubtable that pyrite framboids and pseudoframboids are the primary preserving fabric in the Nova Olinda insects. Instead of repeating their geochemistry here, the reader is advised to review Section 1. 9. 4. 1. in Chapter 1, where low-temperature framboid formation is outlined, before continuing. As per the descriptions presented in that section, metastable non-pyritic iron sulphides must precipitate before pyrite can form (Berner, 1964, 1967, 1970; Rickard, 1969; Vaughn and Craig, 1978; Newman, 1998; Joeckel *et al*., 2005; Ohfuji and Rickard, 2005; Rickard, 2012), which then transforms into pyrite via sulphur gain (as appose to iron loss). This can be inferred in the Nova Olinda Member insect fossils because, although brittle cracking is present (Plate 80), there is no clear evidence of concentric or radiating shrinkage.

To accurately interpret the mineralogical fabrics replacing Nova Olinda Member fossil insects, pyrite weathering (its pseudomorphing in goethite) must first be outlined as it can alter pyrite fabrics. Below, the (relatively) modern weathering of Nova Olinda Member insect fossils is discussed.

4. 2. 3. Modern weathering

Weathered fossil insects of the Nova Olinda Member have been described as mostly preserved in goethite (Menon and Martill, 2007), and that interpretation is agreed with here. Goethite (FeO(OH)) is the dominant iron oxyhydroxide mineral in marine and lacustrine sediments (Zee *et al*., 2003; Schulz and Zabel, 2006), and even relatively stable iron sulphides will eventually oxidise to it (Newman, 1998). Previous work has suggested that it must precipitate directly from solution, which is typically stimulated by Fe cycling near an oxic-anoxic boundary (Zee *et al*., 2003).

However, this is clearly not the case for the Nova Olinda Member, where it replaced iron sulphides instead of precipitating in pore spaces. Goethite crystal grains can be up to 100 nm in diameter, but are typically ~10 nm, both in natural and synthetic forms (Zee *et al*., 2003). It is orthorhombic with perfect cleavage, and can form large (hand specimen) reniform and stellate crystals (Barthelmy, 2015a). Crystals of this size and morphology are not present in the Nova Olinda Member, however micro/nanometre scale versions may be. More importantly, goethite can have a lower crystallinity in the presence of other trace metals and instead form spikey, globular, and acicular particles (Kairies *et al*., 2005), all of which closely resemble some of the fabrics observed in Nova Olinda Member insect fossils. Goethite is also reported to replace arthropod cuticle in ostracods from the Middle Miocene of Antarctica as tabular, crudely prismatic, or, more importantly, globular aggregates (Williams *et al*., 2008). 'Globular aggregates' of goethite directly match the majority of fabrics observed in the Nova Olinda Member, and so possibly represent a similar process, but no figures of the aggregates are presented for comparison (Williams *et al*., 2008).

Due to these variations in crystal morphology, and the lack of morphological change between weathered and unweathered phases, other weathering products were investigated. Ferrihydrite ($(Fe^{3+})_2O_3 \bullet 0.5H_2O$) is a mineral similar to goethite that forms at pH 5 – 6 (whereas goethite forms at pH > 6.0) (Kairies *et al*., 2005). Ferrihydrite has a dark brown powdery fabric and forms crystal aggregates only visible with microscopy, which are similar to the weathered fabrics found in the Nova Olinda Member (Barthelmy, 2015b). Additionally, diagenetic oxidation is well-known to mostly yield ferrihydrite (Thamdrup, 2000). However, ferrihydrite is the least stable ferric oxyhydroxide and readily transforms into goethite or hematite (Cudennec and Lecerf, 2006).

As goethite is not the only weathering product of pyrite, X-ray diffraction was undertaken to identify the weathered insect material (Figure 32 and Table 3 in Chapter 3. 3. 5.). This confirmed goethite as the weathered product. Additionally, reactive iron oxides and oxyhydroxides are dissolved in anaerobic sediments (Froelicher *et al*., 1979; Fowler and Yang, 2003; Zee *et al*., 2003), resulting in the release of $Fe^{2+}_{(aq)}$ and the precipitation of further authigenic iron oxides/oxyhydroxides as the aqueous Fe^{2+} diffuses and re-oxidises (Froelicher *et al*., 1979; Fowler and Yang, 2003; Zee *et al*., 2003). Consequently, no further sedimentary anoxia could have occurred after weathering without dissolving the fossils, suggesting that the oxidation event is recent.

4. 2. 4. A new preservational model for Nova Olinda Member fossil insects

The observations and analyses presented here have established that the models described above for the replacement of Nova Olinda Member fossil insect tissues are either (1) too simplistic to appropriately describe the preservational fabrics, or (2) inaccurately describe the fabrics of replacement or, more likely, (3) describe the fabrics based on few specimens. Below, a refined model is presented that attempts to remedy this. The model is presented primarily as a figure (Figure 96) separated into six simplified sections (A-F), but a written narrative is also provided. In addition to the model below, a further model for the origins and transportation of insect carcasses to the site of deposition is presented later in this Chapter (section 4. 3.).

A. The lake/lagoon waters were supplied with abundant dissolved ions by a restricted connection to the south Atlantic (Ponte, 1992; Martill *et al*., 2007a; Neto *et al.,* 2013). Tributaries and small-scale flash floods also provided soil-derived ions (Martínez-Delclòs *et al*., 2004; Pearlman, 2016). The restricted oceanic connection limited water exchange and the hot arid climate concentrated ions via evaporation, resulting in hypersaline bottom waters. The insect carcasses arrived at the site of deposition and were rapidly entombed by partially soupy sediments (Martill, 1993b) and an extensive microbial mat (as shown by ripple and tearing structures: Figure 7; Martill *et al.,* 2007b; Heimhofer *et al.,* 2010). Due to the hostile sedimentary environment, most notably the high salinity and anoxia, no scavenging or burrowing metazoans were present, and the mat was dominated by sulphate reducing bacteria (Siegrist *et al*., 1999; Schieber, 2002). Minor decay that had already begun in many carcasses was greatly slowed or halted by the hostile lake/lagoon floor environment (Allison and Briggs, 1993; Holliger *et al*., 1998; Siegrist *et al*., 1999).
B. The entombing microbial mat and sediment physically ‘isolated’ each carcass (Briggs and Kear, 1993b). Microgeochemical environments that favour mineralisation were generated by the minor decay of the most labile ‘soft’ tissues, which created ‘active sites’ for precipitation and liberated ions. This ultimately allowed for calcium phosphate (apatite) to precipitate (Kapolos and Koutsoukos, 1999), encrusting and impregnating some of the remaining internal soft-tissues, resulting in high fidelity replications similar to ‘Orsten’-type preservation (Martill *et al*., 1992; Allison and Briggs, 1993; Martínez-Delclòs and Martinell, 1993; Briggs, 1995b; Wilby and Briggs, 1997; Maas *et al*., 2006; Eriksson *et al*., 2012; Barling *et al*., 2015; Figure 41; Plates 53, 61, 64, 66, 67, and 71). Dissolution and reprecipitation of the calcium carbonate sediment allowed for some voids to be infilled by calcite (also see Figure 43).
C. The metabolic activities of the microbial mat concentrated ions, forming a geochemical gradient within the epicuticle of each carcass which, in turn, stimulated mineral precipitation (Berner, 1981; Sorensen and Jorgensen, 1987; Allison, 1988a; Henrichs,

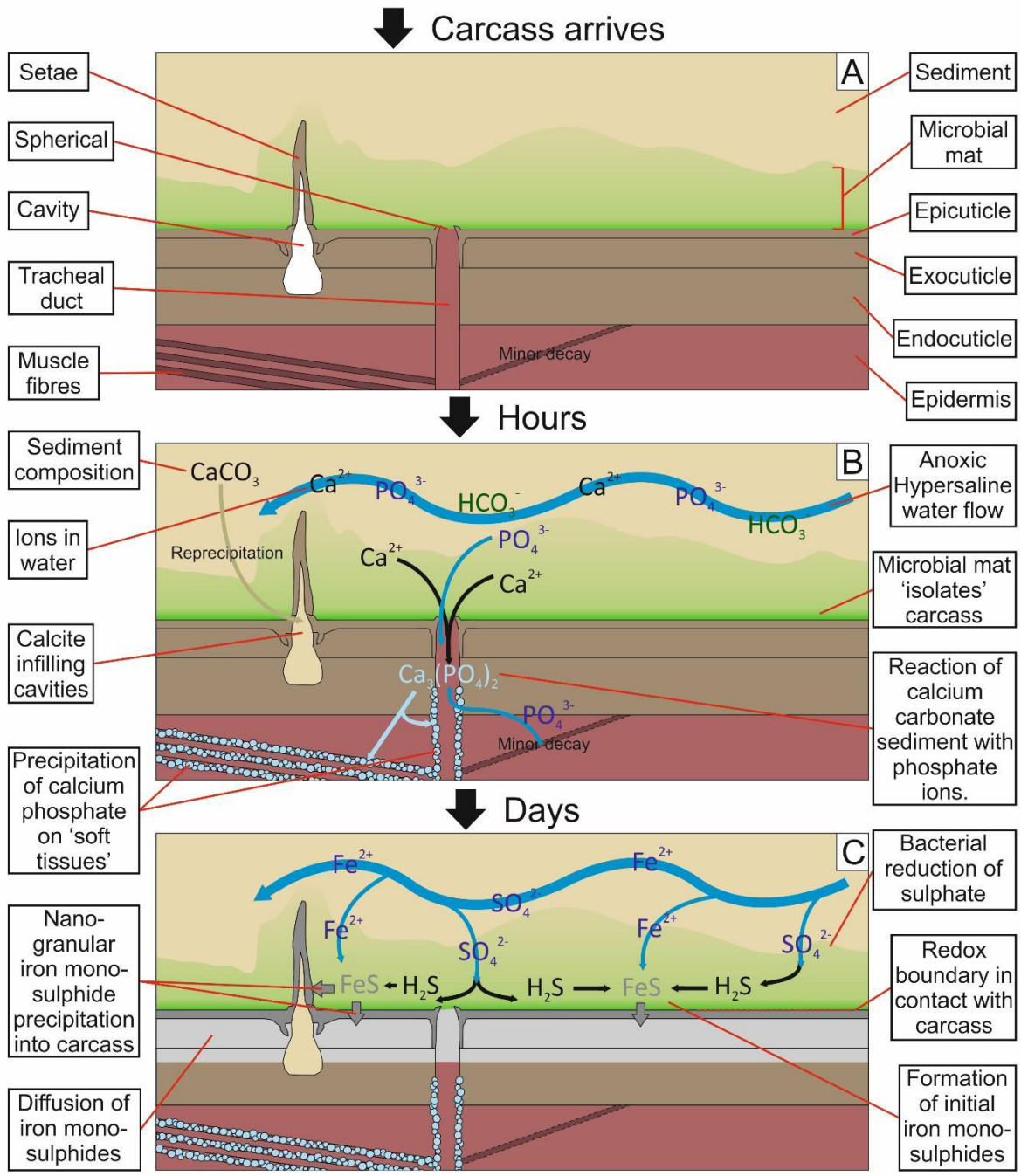
1992; Aller, 1982; Simon et al., 1994). Specifically, sulphate ions present in the hypersaline bottom waters were reduced by the microbial mat, generating hydrogen sulphide (Briggs and Kear, 1994b; Chester and Jickells, 2012). This combined with aqueous iron(II) present in the anoxic bottom waters, forming iron monosulphide (Chester and Jickells, 2012). As per the current understanding of pyrite formation (see Chapter 1. 9. 4. 1.), initial precipitation was amorphous iron monosulphide (disordered mackinawite), which then stabilised to nanocrystalline non-framboidal iron monosulphide/greigite, resulting in impregnation of the epicuticle by nanocrystals (Sagemann *et al*., 1999; Canfield and Raiswell, 1991). Iron monosulphides also continued to diffuse into the carcass.

D. In some cases, impregnation of the cuticle continued deeper into the carcass, resulting in slower growing, larger (but still submicron-size), crystals (Aust, 1972) and ultimately resulting in the replication of the exocuticle without preserving its internal structure (Figure 44; Plate 31). Continued bacterial sulphate reduction (possibly aided by further influx of ions from continuing small-scale terrestrial flash-floods) formed more hydrogen sulphide, which continued to react with iron(II), forming more iron monosulphide. By the time the remaining interior of the carcass began to mineralise, iron monosulphides had reached supersaturation, resulting in the formation of precursor structures to pyrite framboids and a different replacement fabric (Berner, 1964, 1967, 1970; Rickard, 1969; Vaughn and Craig, 1978; Vietti *et al*., 2015). As with the nanocrystalline impregnation described above, these would have initially precipitated as an amorphous iron monosulphide (disordered mackinawite), which then stabilised (into either ordered mackinawite or greigite, or both) (Berner, 1970; Lennie and Vaughan, 1996; Wolthers *et al*., 2003; Schoonen, 2004; Ohfuji and Rickard, 2005; Hunger and Benning, 2007; Wu *et al*., 2012). These precursor ‘protoframboids’ (Vietti *et al*., 2015) varied in size depending on the unique microgeochemical environments within each insect carcass/tissue (Plates 19 and 28). In some cases, they grew against the internal surface of the already mineralised epicuticle, forming hemispherical-protoframboids (Plates 24, 25, and 30). The formation of these protoframboids obliterated any remaining internal morphology that had not already been replicated in calcium phosphate or nanocrystalline iron sulphides.

E. As bacterial sulphate reduction continued, the pH within the carcass decreased (Briggs and Kear, 1994b) and the aqueous iron(II) was eventually depleted. This resulted in a transition from reactions that form amorphous iron monosulphide to those that form metastable crystalline iron sulphides (ordered mackinawite and pyrite) (Vaughn and Craig, 1978; Wolthers *et al*., 2003; Ohfuji and Rickard, 2005). The epicuticle (and in some places exocuticle) that had already been mineralised in nanocrystalline iron monosulphides was

replaced by nanocrystalline pyrite (or possibly metastable mackinawite in some areas), with a minimal loss of fidelity. Within the carcass, pyrite overprinted its precursor phases in coarser crystals. Conditions were not appropriate for the formation of true framboids, resulting in pseudoframboids instead, identified by their hollow interiors (Plate 22).

F. Many millions of years later, overburden was removed from the sediment, exposing it to oxygenated groundwater flow. This allowed for slow *in situ* weathering, replacing the pyrite and any other iron sulphide phases with goethite (Menon and Martill, 2007). The epicuticle (and in some places exocuticle) were pseudomorphed by nano-crystalline goethite, preventing a loss of fidelity. The internal pseudoframboids were also pseudomorphed in goethite. However, their coarser cubic crystal structure was replaced by aggregates of micro- and nano-crystals, giving rise to the preservational fabric observed today.


Carcass arrives
Setae
Spherical
Cavity
Tracheal duct
Muscle fibres
A
Sediment
Microbial mat
Epicuticle
Exocuticle
Endocuticle
Epidermis
Minor decay
Hours
Sediment composition
Ions in water
Calcite infilling cavities
Precipitation of calcium phosphate on 'soft tissues'
B
Anoxic Hypersaline water flow
Microbial mat 'isolates' carcass
Reaction of calcium carbonate sediment with phosphate ions.
Reprecipitation
Minor decay
Days
Nano-granular iron mono-sulphide precipitation into carcass
Diffusion of iron mono-sulphides
C
Bacterial reduction of sulphate
Redox boundary in contact with carcass
Formation of initial iron mono-sulphides

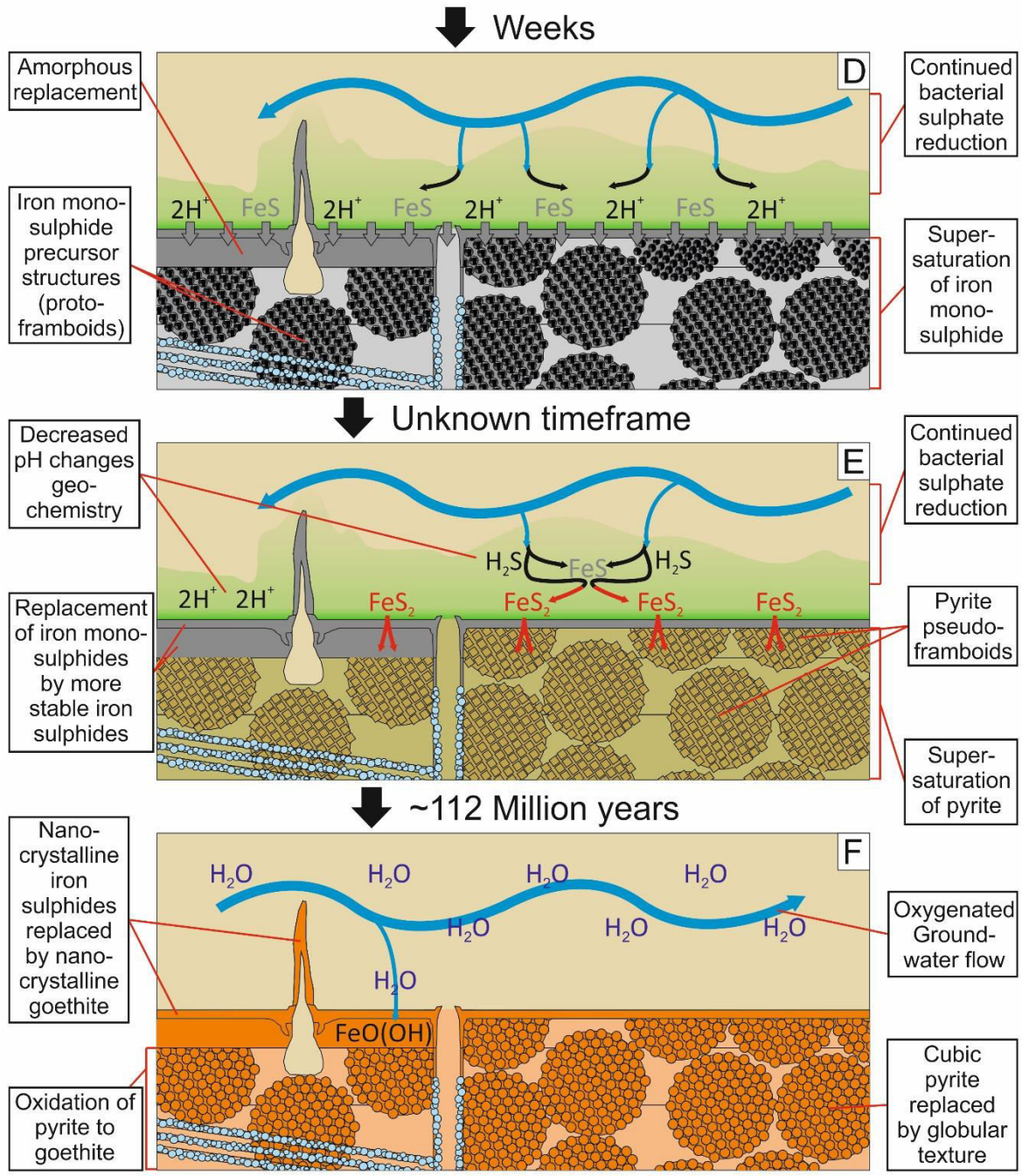


Figure 96. Proposed taphonomic pathway for the replacement of Nova Olinda Member insects. A, Insect upon arrival at site of burial. B, Rapid replication of labile tissues in calcium phosphate. C, Nano-replication of exterior most features in iron sulphides. D, Coarser replication of remaining internal tissues in iron sulphides. E, Stabilisation of iron sulphides by replacement in metastable phases. F, Oxidation of all iron sulphides to goethite. For more detailed descriptions of these stages, see text in section 4. 2. 4. This figure solely addresses the replication of insect tissues. It does not include the mineralisation of EPS around the carcass in calcite or rare siliceous 'halos' around some fossils.

4. 2. 5. Model limitations

The diagenetic sequence presented above outlines the typical replacement pathways within the Nova Olinda Member insects. In reality, every carcass was filled with an array of microgeochemical environments depending on the extent of decay, heavy metal absorption by

the cuticle, metabolic activities of the microbial mat, etc. This resulted in a wide range of preservational fabrics. Pseudoframboid size varied greatly (Plates, 18, 19, 22, 26, 27, and 28), depending on growth times (Vietti *et al*., 2015). In some areas, decay was more substantial, resulting in more globular morphologies (Plates 30, 73, 75, 76, and 84: A-F). In other areas, the internal mesh-work structure of cuticle was replicated (in calcite), resulting in mesh-like structures (Figures 38 and 48: A; Plates 20 and 49). Rarely, the pseudomorphing goethite adopted a needle-like nanocrystalline habit, resulting in 'fuzzy' crystal boundaries (Plates 29, 38, and 79).

In addition to these variations, the model is limited by the current understanding of low-temperature pyrite framboid formation (Lennie and Vaughan, 1996; Butler and Rickard, 2000; Schoonen, 2004; Ohfuji and Rickard, 2005; Hunger and Benning, 2007; Vietti *et al*., 2015). The precursor protoframboids presented in Figure 96: D are hypothetically labelled as iron monosulphides, based on the known requirement of an iron monosulphide precursor phase prior to pyrite replacement (Berner, 1964, 1967, 1970; Rickard, 1969; Vaughn and Craig, 1978; Ohfuji and Rickard, 2005). It is unclear if these structures would have been overprinted by pyrite almost instantly as they were forming, persisted for hours, days, or weeks etc. The stability ranges (Eh-pH, temperature, etc.) of these initial iron monosulphide phases may have been very small, and they will have only persisted so long as the microgeochemical environment remained within their ranges. Their persistence is important as their size ultimately controls the size of the subsequent pyrite crystals, which in turn controls the fidelity of preservation. The microgeochemical environments undoubtedly changed as continued bacterial sulphate reduction reduced pH, and so the fidelity of preservation was controlled by the rates of bacterial sulphide reduction. Images of protoframboids recorded by Vietti *et al*. (2015) suggest that pyrite may first overprint in nano-grains prior to the formation of larger euhedral crystals.

Additionally, which iron sulphide phases these precursor minerals transform into is not entirely clear. The presence of pseudomorphed pseudoframboids, along with XRD data, indisputably identifies pyrite. However, the XRD data is unresolved with unmatched iron sulphide peaks and the currently identified pyrite is supposedly synthetic (see Chapter 3. 3. 5.), indicating that the XRD results are not entirely accurate. This may be a result of a currently undocumented pyrite signature, or more than one iron sulphide mineral phase being present with overlapping signatures. The presence of both magnetic and non-magnetic 'black' material strongly suggests the latter (see Chapter 3. 3. 3.). If this is the case, then the original unweathered preservation may have been in pyrite, as well as more stable forms of ordered mackinawite, marcasite, or greigite. However, the stability of these other iron sulphide phases varies greatly, but from what is known of low-temperature pyrite framboid formation, the precursor monosulphide phases could not have survived 112 million years (Berner, 1964, 1967, 1970; Rickard, 1969; Vaughn and Craig, 1978; Ohfuji and Rickard, 2005). Regardless, pyrite is present and whichever mineral may have caused

the unmatched peak appears to be present in such small quantities that it is unlikely to be identified with currently available techniques.

Finally, no pyrite pseudoframboids have been observed in the unweathered specimens, even those with high relief. This could indicate that these fossils in fact represent two distinct modes of preservation, as suggested by Osés *et al*. (2017) for the Nova Olinda Member fossil fish. This is discussed further in Chapter 6. 4. 2.

4. 3. Transport model

The model presented above in Figure 96 provides an explanation for the preservation of insects in the Nova Olinda Member. However, the fossils are preserved with a variety of fidelities (see Chapter 3. 10.). This varied preservational fidelity is interpreted here to be a result of the original state of the carcasses upon reaching the site of burial, rather than variations in the preservational mechanism (although some subtle variations undoubtedly occurred).

To understand how the pre-mineralisation conditions altered the carcasses, the transport processes must be modelled. Below, a taphonomic pathway figure (Figure 97, presented on a separate fold-out) outlines the effects of transport on insect carcasses from different habitats, and in different 'states', to the site of deposition. As will be examined in Chapter 5. 1., the insects are hypothesised to originate from three distinct environments. These are 1) an arid area around the palaeolake, 2) a humid delta, and 3) an upstream forested area. The model then outlines key events that occurred in the process of transporting a carcass to the palaeolake. Several example starting stages are presented for each palaeoenvironment, typically outlining the differences between a live insect, a 'fresh' carcass, and a carcass that has undergone prolonged decay. Each environment has a different impact on the insect carcass, but those that have undergone decay typically disintegrate at some stage and arrive at the palaeolake as fragments.

Carcasses entering the palaeolake are divided into three categories, depending on their condition upon arrival. These are 1) complete, 2) fragmentary, and very rarely 3) encased in resin. Resin is only included to highlight that it undergoes a distinct preservational process. The processes that affect complete and fragmentary remains are described, and eventually the pathway concludes by referring back to Figure 96 for the process of mineralisation.

[Physical copies will have the foldout glued to this page.]

[In digital copies, the foldout can be found on an A2-sized page at the end of the PDF document.]

Chapter 5. Palaeoecology of the insect fauna

5. 0. Preface

To determine taphonomic trends between different fossil organisms from a large area, their ecology and the environments in which they inhabited must be modelled. This allows for differences in their preservational fidelity to be compared against not only their morphology, but also their ecology, their probable duration of transport, and the conditions in which they began to decay. Without this comprehensive approach, taphonomic models are inherently flawed.

In general, fossil insects from non-amber localities are preserved as a taphocoenosis (Penney and Jepson, 2014). In other words, they do not form *part* of a single ecological community (a palaeobiocoenosis). Instead, they died at different times, in different locations, were part of different ecological communities, and, by chance, were transported to the same location (Penney and Jepson, 2014). Consequently, insect fossils from the Nova Olinda Member are considered to come from 'hinterland' environments and can provide a wealth of information about them.

5. 1. Environmental preferences

As noted in Chapter 1. 5. 1. and 1. 6., the Nova Olinda Member catchment area has historically been hypothesised as an arid scrubby environment (Grimaldi, 1990; Dunlop, 1998; Dunlop and Martill, 2002; Martill *et al*., 2007a; Heimhofer *et al.,* 2010; Osés *et al*., 2016). This conclusion was based on broad sweeping generalisations of abundant insect taxa that might be associated with scrubby arid environments (cockroaches, crickets, grasshoppers, and wasps), more indicative groups such as whipspiders and whipscorpions, and several plant species (*Cariria orbiculiconiformis*, *Friedsellowia gracilifolia*, and *Schenkeriphyllum glanduliferum*) (Grimaldi, 1990; Dunlop, 1998; Dunlop and Martill, 2002; Dunlop *et al*., 2007; Martill *et al*., 2007a; Mohr *et al.*, 2007; Heimhofer *et al.,* 2010; Kunzmann *et al*., 2011; Loewe *et al*., 2012; Mohr *et al*., 2013; etc.). The generalisation of Nova Olinda Member insects prompted further investigations to assess the accuracy of this environmental association. Here, these insects are compared to their modern relatives and summarised to give estimated simplified environmental preferences, with some modes-of-life also explored.

Earlier in this thesis (Chapter 1. 5. 1.), six example families (Sapygidae (Hymenoptera), Gryllotalpidae (Orthoptera), Trogossitidae (Coleoptera), Dytiscidae (Coleoptera), Rhinotermitidae (Blattodea), and Zhangsolvidae (Diptera)) were presented to provide evidence for a broad range of palaeoenvironments, from hot dry scrubland to freshwater aquatic settings (see Figure 12 in

Chapter 1). Below, a list of the estimated general environmental and mode-of-life preferences of insect families identified in the Nova Olinda Member is presented, providing a more comprehensive interpretation of the palaeoenvironment (Table 5).

Although the preferences presented in Table 5 are also generalisations, they are clarified to family-level and are based on previous studies of each group (or closely related groups, described in detail in Appendix 8. 3.). For some groups, the listed preference simply reflects the habitat in which their diversity is highest. Each preference is a simplified summary of several different potential environments and lifestyles:

1) **Aquatic**: Including families that are entirely adapted to an aquatic life-style, as well as those that require persistent bodies of water for reproduction.
2) **Riparian**: Including semi-aquatic groups, those that require moist soils around water, and coastal-dwelling groups.
3) **Highland**: Groups that are indicative of high-altitudes or cold environments.
4) **Burrowing / Cryptic**: Larvae or adults that are believed to be burrowing or otherwise cryptic soil-dwellers, also includes groups that are associated with soft substrates. Although burrowing and cryptic insects describes their 'mode-of-life', rather than their environmental preference, it is distinguished here due to its importance in insect taphonomy.
5) **Scrubby / Shrubby**: Including insects that thrive in open-habitats and also rely on small plants for reproduction/food. Insects that pollinate small plants are also included.
6) **Woody**: Insect that are specifically associated with woody trees (or bark) or decaying matter from them.
7) **Humid**: Including groups that have their highest diversity in warm, moist environments, or are associated with moist rotting material.
8) **Arid**: Includes groups that inhabit open sunny areas, semi-arid areas, hot arid regions, or dry plant matter. Also includes groups that parasitize other arthropods indicative of arid regions.
9) **N/A or Cosmopolitan**: Includes groups that are specifically listed as differing from their modern relatives, that there are no modern analogues for, are cosmopolitan in most environments, or are only described as 'highly generalised'.

In some cases, the families of an order are not treated separately, as most members of that order were associated with a single preference (e.g. Odonates requiring water for reproduction).

Table 5. Colour-coded environmental preferences (or mode-of-life) for insect families and number of recorded species of that family in the Nova Olinda Member. Preference numbers are described above in section 5. 1. Key references are also provided. See Appendicies 8. 3. for detailed descriptions of the environmental preferences and additional references for each group.

Order	Family	# sp.	Key References	Pref.
Diplura	Untreated	1	Staniczek and Bechly, 2007	4
Zygentoma	Untreated	1	Strum, 1998	4
Coxoplectoptera	Untreated	1	Staniczek *et al*., 2011	9
Ephemeroptera	Untreated	22	McCafferty, 1990; Martins-Neto, 1996a; Staniczek, 2007	1
Odonata	Untreated	52	Ponomarenko, 1985; Bechly, 1997a-c, 1998a-d, 2007b, 2010, etc.	1
Dermaptera	Anisolabididae	1	Haas, 2007	2
	Labiduridae	2	Martins-Neto, 1990a; Haas, 2007	9
	Spongiphoridae	3	Popham, 1990; Engel and Chatzimanolis, 2005; Haas, 2007	9
Orthoptera	Hagloidea (superfamily)	2	Martins-Neto, 1991	9
	Schizodactylidae	1	Heads and Leuzinger, 2011	8
	Gryllotalpidae	3	Heads and Martins-Neto, 2007; Capinera, 2008	4
	Gryllidae	11	Martins-Neto, 1987-2002	9
	Baissogryllidae	19	Martins-Neto, 1991	9
	Tridactylidae	2	Heads and Martins-Neto, 2007	4
	Proscopiidae	1	Heads and Martins-Neto, 2007	5
	Locustopsidae	18	Heads and Martins-Neto, 2007	9
	Elcanidae	2	Heads and Martins-Neto, 2007; Fang *et al*., 2015	4
	Bouretidae	1	Heads and Martins-Neto, 2007	9
Chresmododea	Untreated	1	Martínez-Delclós, 1989; Bechly, 2007d	2
Phasmatodea	Untreated	1	Grimaldi, 2007	9
Mantodea	Untreated	3	Grimaldi, 2007	9
Blattodea (Inc. Isoptera)	Mesoblattinidae	1	Bechly, 2007b	7
	Blattellidae	2	Bechly, 2007b; Wei and Ren, 2013	7
	Blattidae	1	Pinto, 1989	9
	Blattulidae	2	Bechly, 2007b; Wang *et al.*, 2007	9
	Raphidiomimidae	1	Bechly, 2007b	6
	Ponopterixidae	4	Vršanský, 1999; Bechly, 2007b; Nel *et al*., 2014	9
	incertae sedis	1	Bechly, 2007b	9
	Cratomastotermitidae	1	Bechly, 2007c	8
	Kalotermitidae	1	Bechly, 2007c	8
	Termopsidae	1	Bechly, 2007c	7
	Hodotermitidae	3	Bechly, 2007c	5
Hemiptera	Cicadellidae	3	Menon *et al*., 2007	9
	Myerslopiidae	2	Menon *et al*., 2007; Rakitov, 2015	6
	Tettigarctidae	2	Menon, 2005; Menon *et al*., 2007	3
	Cercopionidae	6	Menon *et al*., 2007	9
	Palaeontinidae	8	Menon *et al*., 2007; Wang *et al*., 2008	9
	Cixiidae	1	Szwedo, 2007	4
	Lalacidae	15	Szwedo, 2007	4
	Achilidae	3	Szwedo, 2007, 2008	6
	Peloridiidae	1	Pinto and Ornellas, 1974; Martins-Neto, *et al.*, 1999; Martins-Neto, 2002b	6
	Belostomatidae	4	Nel and Paicheler, 1992; Zamboni, 2001; Nel and Waller, 2006	1

	Nepidae	2	Jattiot *et al*., 2012	1
	Naucoridae	2	Ruf *et al.,* 2005	1
	Notonectidae	1	Bechly and Szwedo, 2007	1
	Corixidae	1	Bechly and Szwedo, 2007	1
	Gelastocoridae and Pseudonerthridae	3	Ruf *et al*., 2005	2
	Archegocimicidae	1	Bechly and Szwedo, 2007	2
	Hydrometridae	2	Nel and Popov, 2000; Goodwyn, 2002	2
	Veliidae and Mesoveliidae	2	Bechly and Szwedo, 2007	2
	Cimicomorpha	1	Bechly and Szwedo, 2007	9
	Pachymeridiidae	2	Martins-Neto, *et al.*, 1999; Yunzhi *et al*., 2008	7
	Alydidae	1	Bechly and Szwedo, 2007	8
	Coreidae	1	Bechly and Szwedo, 2007	6
	Aradidae	1	Bechly and Szwedo, 2007	6
	Cydnidae	1	Pinto and Ornellas, 1974; Bechly and Szwedo, 2007	4
Hymenoptera	Unicalcarida (unranked)	1	Krogmann and Nel, 2012	9
	Sepulicidae	1	Darling and Sharkey, 1990; Rasnitsyn *et al*., 1998; Роман, 2004	9
	Siricidae	1	Osten, 2007; Archibald and Rasnitsyn, 2016	6
	Tenthredinoidea	1	Osten, 2007	5
	Vespidae	1	Brown, 1941; Wenzel, 1990; Carpenter and Rasnitsyn, 1990; Osten, 2007	9
	Pompilidae	1	Osten, 2007	8
	Sapygidae	1	Osten, 2007	8
	Tiphiidae	1	Darling and Sharkey, 1990; Osten, 2007	5
	Formicidae	1?	-	9
	Scoliidae	3	Rasnitsyn and Martinéz-Delclòs, 1999; Osten, 2007; Nel *et al*., 2013	8
	Angarosphecidae	4	Osten, 2007	5
	Ampulicidae	1	Darling and Sharkey, 1990; Osten, 2007	9
	Apidae?	1	Darling and Sharkey, 1990; Osten, 2007	9
	Ichneumonidae	1	Osten, 2007	9
	Ephialtitdae and Proctotrupidae	2	Sharkey, 1990; Darling and Sharkey, 1990; Osten, 2007	9
	Mesoserphidae	1	Osten, 2007	9
	Chalcidoidea (superfamily)	1	Barling *et al*., 2013	9
Raphidioptera	Baissopteridae	4	Martins-Neto *et al*., 2007	6
	incertae sedis	1	-	9
Megaloptera	Corydalidae	2	Martins-Neto *et al*., 2007; Jepson and Heads, 2016	1
Neuroptera	Osmylidae	4	Menon and Makarkin, 2008; Martins-Neto and Rodrigues, 2009, 2010; Myskowiak *et al.,* 2015	2
	Ithonidae	1	Martins-Neto *et al*., 2007	4
	Chrysopidae *et al*	13	Nel *et al*., 2005; Martins-Neto and Rodrigues, 2009	5
	Berothidae	2	works by Martins-Neto; Winterton, 2010	9
	Sisyridae	1	Martins-Neto, 1997	1
	Psychopsidae	2	Martins-Neto *et al*., 2007; Martins-Neto and Rodrigues, 2010	9
	Nemopteridae	5	Martins-Neto, 2000	8
	Nymphidae	1	Myskowiak *et al*., 2016	4
	Myrmeleontidae	4	Martins-Neto, 2000; Heads *et al*., 2005	8
	Ascalaphidae	1	Martins-Neto and Vulcano, 1997	8

	Kalligrammatidae	2	Martins-Neto, 1995; Bechly and Makarkin, 2016	9
	Araripeneuridae *et al*	34	Martins-Neto, 1990-2002; Martins-Neto and Vulcano, 1989, 1997; Menon and Makarkin, 2008; Martins-Neto and Rodrigues, 2010; Myskowiak and Nel, 2016	9
Coleoptera	Archostemata: (2 cf taxa)	2	Wolf-Schwenninger and Schawaller, 2007	6
	Dytiscidae	1	Grimaldi and Maisey, 1990; Heads pers. comm., 2016	1
	Carabidae	2	Martins-Neto, 2005	9
	Staphylinidae	5	Schomann and Solodovnikov, 2012	7
	Hydrophilidae	1	Wolf-Schwenninger and Schawaller, 2007	1
	Scarabaeidae	2	Grimaldi and Maisey, 1990; Grimaldi and Engel, 2005	8
	Buprestidae	1	Wolf-Schwenninger and Schawaller, 2007	6
	Dryopidae	1	Grimaldi and Engel 2005	1
	Elateridae	1	Grimaldi and Engel 2005	9
	Nitidulidae	1	Grimaldi and Maisey, 1990; Wolf-Schwenninger and Schawaller, 2007	6
	Cucujidae	1	Wolf-Schwenninger and Schawaller, 2007	6
	Trogossitidae	1	Wolf-Schwenninger and Schawaller, 2007	6
	Lymexylidae	1	Wolf-Schwenniger, 2011	6
	Tenebrionidae	1	Wolf-Schwenninger and Schawaller, 2007	6
	Pyrochroidae	1	Wolf-Schwenninger and Schawaller, 2007	9
	Chrysomelidae	2	Wolf-Schwenninger and Schawaller, 2007	5
	Curculionoidea (superfamily)	7	Zherikhin and Gratshev, 2004; Santos *et al*., 2011	6
Trichoptera	Leptoceridae	1	Bechly, 2007f	1
	Hydroptilidae	4	Bechly, 2007f	1
	incertae sedis	2	Martins-Neto, 2001	9
Lepidoptera	Untreated	5	Bechly, 2007f	9
Mecoptera	Bittacidae	1	Petrulevičius and Martins-Neto, 2007, Bechly, 2007f, Petrulevičius *et al.,* 2012	7
	incertae sedis	1	-	9
Diptera	?Chironomidae	1	Willkommen and Grimaldi, 2007	1
	Simuliidae	1?	Willkommen and Grimaldi, 2007	2
	Mycetophilidae	1	Willkommen and Grimaldi, 2007	2
	Sciaridae	1	Willkommen and Grimaldi, 2007	6
	Bibionidae	1	Willkommen and Grimaldi, 2007	5
	Psychodidae? or Tanyderidae?	1	Grimaldi and Engel, 2005; Willkommen and Grimaldi, 2007	7
	Tipulidae	4	Ribeiro and Lukashevich, 2014; Ribeiro *et al.*, 2015	9
	Limoniidae	2	Ribeiro and Martins-Neto, 1999; Ribeiro and Krzemiski, 2000	9
	Zhangsolvidae	3	Mazzarolo and Amorim, 2000; Arillo *et al.*, 2015	7
	Tabanidae	1	Willkommen and Grimaldi, 2007	9
	Rhagionidae?	1	Watson and Dallwitz, 2007	9
	Mydidae	1	Evenhuis, 1994; Willkommen and Grimaldi, 2007	8
	Therevidae	1	Willkommen and Grimaldi, 2007	8
	Asilidae	2	Grimaldi, 1990	8

As shown by the presence of various families of Blattodea (Cratomastotermitidae, Kalotermitidae), Hemiptera (Aradidae), Hymenoptera (Pompilidae, Sapygidae, Scoliidae), Neuroptera (Nemopteridae, Myrmeleontidae, Ascalaphidae), Coleoptera (Scarabaeidae), and

Diptera (Mydidae, Therevidae, Asilidae) in Table 5 above, there is most certainly a large arid component to the Nova Olinda Member hinterland. This arid area was probably populated by small scrubby plants, as suggested by the presence of certain families of Orthoptera (Proscopiidae), Blattodea (Hodotermitidae), Hymenoptera (Tenthredinoidea, Tiphiidae, Angarosphecidae), Neuroptera (Chrysopidae), Coleoptera (Chrysomelidae), and Diptera (Bibionidae).

However, there are also a wealth of other groups that are suggestive of different environments. A wide array of insect families may be suggestive of more water-associated (riparian, coastal, etc.) environments, including Dermaptera (Anisolabididae), Chresmododea, Hemiptera (Gelastocoridae/Pseudonerthridae, Archegocimicidae, Hydrometridae, Veliidae/Mesoveliidae), Neuroptera (Osmylidae), and Diptera (Simuliidae, Mycetophilidae). Linked with these are insects generally indicative of adjacent moister environments, including families of Blattodea (Mesoblattinidae, Blattellidae, Termopsidae), Hemiptera (Pachymeridiidae), Coleoptera (Staphylinidae), Mecoptera (Bittacidae), and Diptera (Psychodidae/Tanyderidae, Zhangsolvidae). Aquatic (either as larvae or imago) families are also abundant, with many examples from Ephemeroptera and Odonata, as well as Hemiptera (Belostomatidae, Nepidae, Naucoridae, Notonectidae, Corixidae), Megaloptera (Corydalidae), Neuroptera (Sisyridae), Coleoptera (Dytiscidae, Hydrophilidae, Dryopidae), Trichoptera (Leptoceridae, Hydroptilidae), and Diptera (?Chironomidae).

Additionally, there are a wealth of insect families that suggest the presence of woody trees including, Blattodea (Raphidiomimidae), Hemiptera (Myerslopiidae, Achilidae, Peloridiidae, Coreidae, Aradidae), Hymenoptera (Siricidae), Raphidioptera (Baissopteridae), Coleoptera (Archostemata, Burprestidae, Nitidulidae, Cucuiidae, Trogossitidae, Lymexylidae, Tenebrionidae, Curculionoidea), and Diptera (Sciaridae). These groups, combined with the exceedingly rare presence of amber, suggests a woody forested area may have been present.

Aside from those listed above, there are many insect families that are cosmopolitan or inhabited unknown environments. Finally, a single taxon suggests a high altitude cold environment (Tettigarctidae), which is likely the result of differing environmental preferences between modern and fossil forms. These familial preferences are summarised in Figure 98 below.

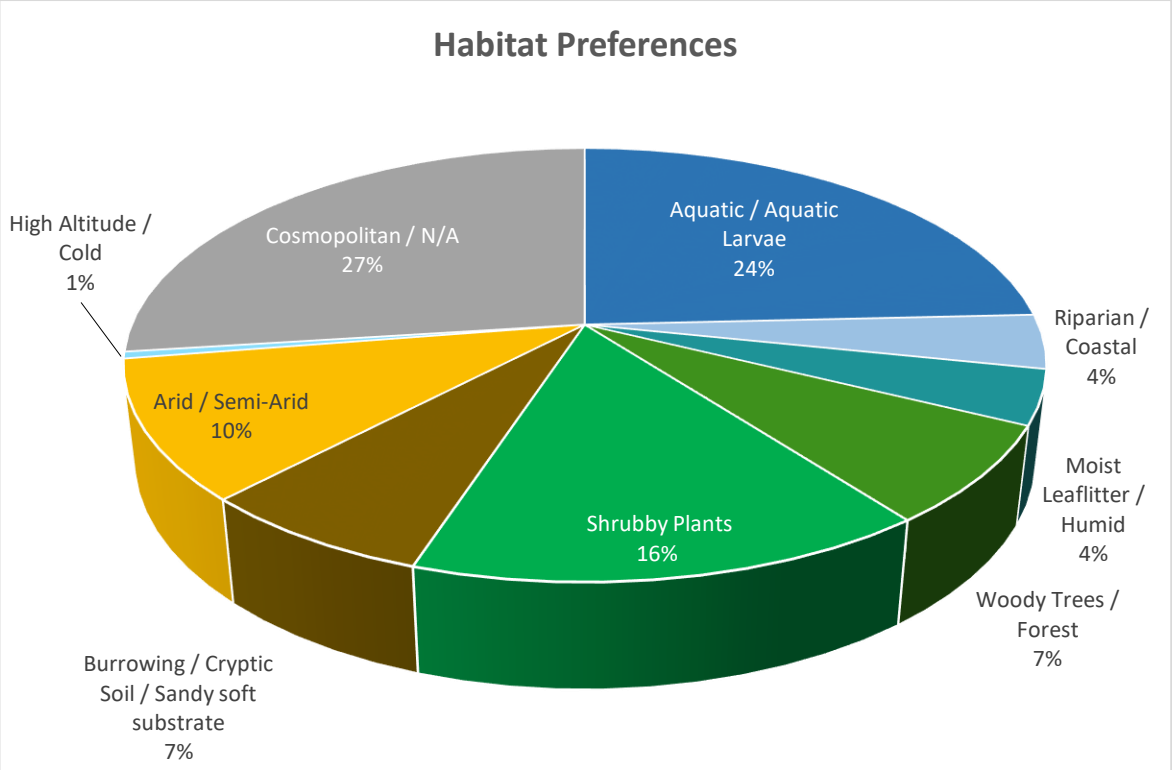


Figure 98. Environmental preferences (or modes-of-life) of species known from the Nova Olinda Member. Preference for each species is based on familal- or ordinal-level typical preference of modern relatives, or the habitat that yields the highest diversity of their group. See Appendix 8. 3. for descriptions and references. n = 396.

Based on these groups, and several other fossil taxa, a palaeoenvironmental reconstruction is presented, identifying three key regions (Figure 99):

• An arid scrubland zone surrounds the majority of the palaeolake. In this area, arid-loving arthropods are abundant. Scrubby, small plants dominate the flora, with few-to-no large trees. Small arid-loving angiosperms are present with associated pollinating insects (especially Hymenoptera). Many burrowing arthropods inhabited the dry sandy soils. This region accounts for approximately 33-60% of the insect diversity from the Nova Olinda Member.

• A relatively humid zone is located around a scrubby delta (or multiple tributaries) feeding into the palaeolake, with abundant riparian plants and animals. The delta supported freshwater aquatic insects, including benthic larvae. Understory plants, such as *Hexagyne pjilippiana* (Coiffard *et al.*, 2014), are also common in this area, along with insects that thrive in moister habitats and wet rotting plant matter. Additionally, haloclines may have extended this zone around the edges of the Nova Olinda palaeolake, providing a marginal habitable zone for freshwater insects. This region accounts for approximately 32-59% of the insect diversity from the Nova Olinda Member.

• Finally, a (tentatively assumed) distant conifer forest is present much further upstream from the palaeolake and delta. This accounts for the extremely rare occurrences of amber and resin-filled

cones that could have floated many miles before coming to rest in the palaeolake. However, it is possible that these could represent reworked resins instead (Mohr *et al*., 2007). Nevertheless, wood-boring beetles that require larger trees have been reported (Ponomarenko, 2003). This region may account for approximately 1-8% of the insect diversity from the Nova Olinda Member, however some of these species may have alternatively inhabited a forested area around the fluvial/deltaic region.

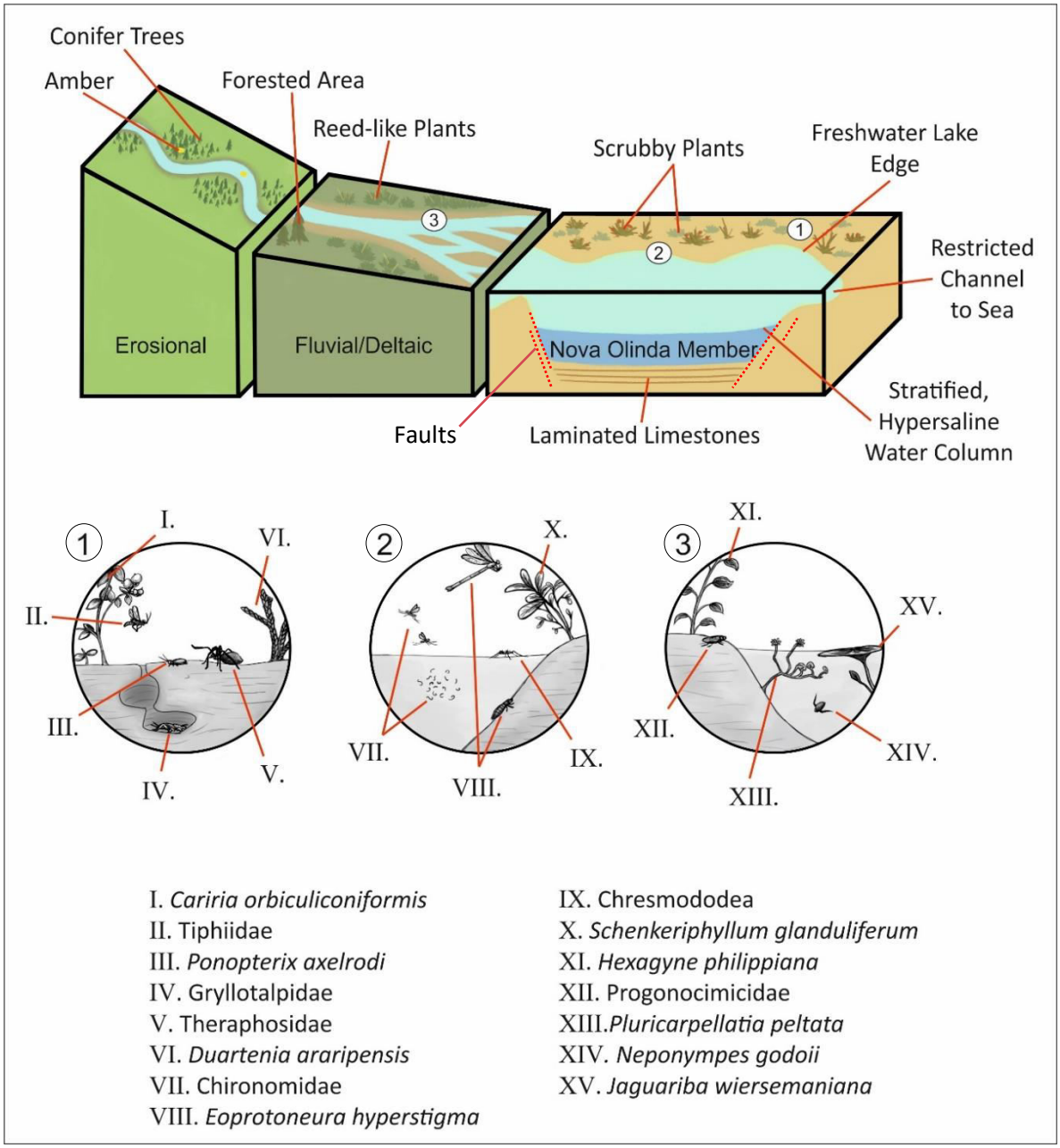


Figure 99. Simplified palaeoenvironmental reconstruction of the Nova Olinda Member catchment areas. Major components are labelled. Numbers highlight example niches that Nova Olinda Member fossil insects likely inhabited. Each niche is reconstructed with example organisms labelled. 1), Arid scrubland niche with xerophytic plants and arthropods, as well as burrowing taxa. 2), Freshwater niche at the edge of the palaeolake, separated from saline waters by a halocline and populated by insects with aquatic larvae. 3), Freshwater niche in fluvial/deltaic tributary, dominated by freshwater aquatic, riparian, and understory plants, as well as aquatic and humid-loving insects.

5. 2. Transport

In addition to the palaeoenvironments outlined above, the mechanisms that transported these insects from their habitats to the site of deposition can also be hypothesised. The abundance of burrowing and cryptic soil-dwelling insects such as Diplura, Zygentoma, some Orthoptera (Gryllotalpidae, Tridactylidae, Elcanidae), some Hemiptera (Cixiidae, Lalacidae, Cydnidae), and the larvae of some Neuroptera (Ithonidae, Nymphidae), suggests a mechanism for removing them from their burrows/cryptic habitats.

For arthropod carcasses to remain articulated, they must reach the site of deposition before structurally critical tissues are lost to decay (their taphonomic threshold) and before desiccation occurs (Briggs and Kear, 1993a; Briggs, 1995a,b). It has also been established that, regardless of the starting environment, rapid transport is required to preserve the labile internal tissues observed in Nova Olinda Member fossil insects (Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Martínez-Délclòs and Martinell, 1993; Briggs, 1995a,b). These two additional factors indicate that the cryptic insects must have been transported from their burrows rapidly. Combined with varved sediments, this strongly supports a wet/dry seasonality with annual small-scale 'flash floods' (at least on a scale that might be considered a 'flash flood' by an insect).

This hypothesis is further supported by the presence of two plant species: *Duartenia araripensis,* which has characteristic growth patterns and leaves of a seasonally dry climate, and *Cariria orbiculiconiformis,* which is proposed to fill a niche of rapid reproduction in disturbed habitats, possibly after floods (Mohr *et al*., 2012). The presence of two other arthropod groups also supports this hypothesis. Whipscorpions and whipspiders, despite generally living in arid environments, desiccate easily and spend most of their lives underground, emerging only after periods of rain (Dunlop *et al*., 2007). A single taxon is known from each of these groups from the Nova Olinda Member (*Mesoproctus rowlandi* and *Britopygus weygoldti*), further suggesting a seasonally wet/dry climate. Finally, the abundance of freshwater benthic insects suggests a mechanism for 'sweeping' them away from their freshwater habitat into the hypersaline waters. Again, small scale 'flash-floods' account for this.

Considering this additional evidence, the model of small-scale 'flash floods' as the primary mechanism of transport for Nova Olinda Member fossil insects, as proposed by Dunlop *et al*. (2007) and Menon and Martill (2007), is agreed with here. For a reconstruction of the taphonomic processes affecting Nova Olinda Member insects during transport, see Figure 97 in Chapter 4.

5. 3. Taphonomy inferred from ecology: flotsam and hydrodynamic sorting

Some insect carcasses can float on the water surface for a prolonged period (Lutz, 1984, 1990; Martínez-Delclòs and Martinell, 1993; Smith *et al*., 2006; Corbet and Brooks, 2008). Without a mechanism to break surface tension, low-density taxa will decay long before sinking to the sediment surface (Martínez-Delclòs and Martinell, 1993). The presence of extremely small low-density insect fossils (e.g. *Parviformosus wohlrabeae*), indicates that a mechanism to force them through the water meniscus is present. Heavy rain from annual storms provides such a mechanism. Additionally, this also provides an explanation for the variations in preservational fidelity among Nova Olinda Member insects. Prior to any rain, insect carcasses present on the water surface would have been there for a varied amount of time, and therefore be at various stages of decay. The influx of fresh carcasses from 'flash floods', combined with the indiscriminate sinking of all carcasses on the water surface would have allowed for both the preservation of exceptionally labile internal tissues, and a variety of poorly-preserved specimens, as observed in the Nova Olinda Member.

Evidence of prolonged floatation is present in several insect fossils. If an insect carcass remains floating on the water surface for a prolonged period, its internal tissues will decay, it will swell, and it may eventually burst across sutures, typically between the thorax and abdomen (Martínez-Delclòs and Martinell, 1993; Smith *et al*., 2006). Rare examples of this swell-bursting are present in the Nova Olinda Member (Figure 100), indicating that some carcasses floated for a prolonged period.

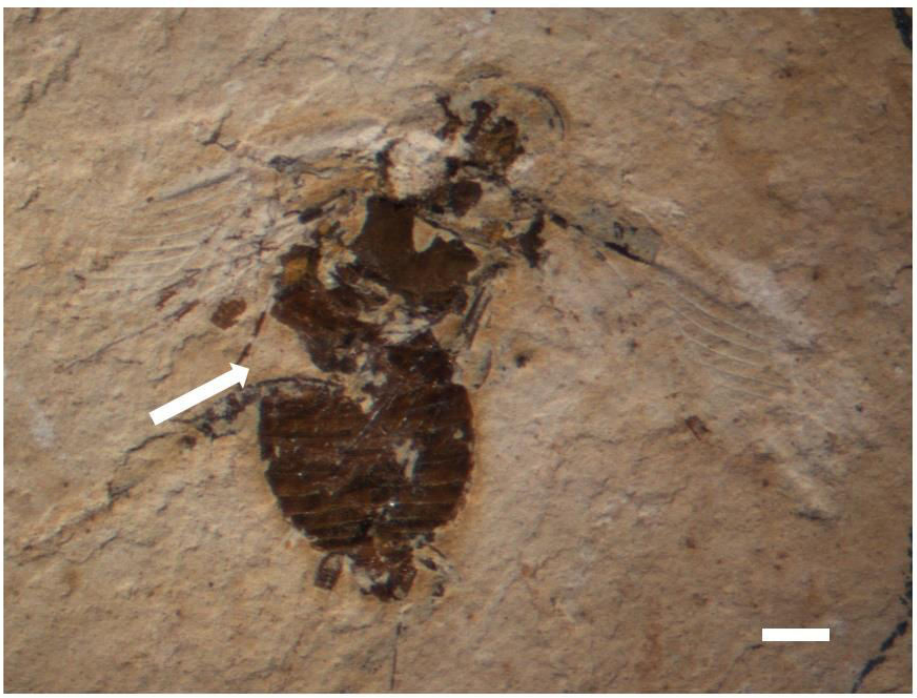


Figure 100. Crato Formation cockroach with typical 'swell-bursting' of abdomen, indicative of water saturation and a prolonged period of floatation on the water surface. Arrow highlights abdominal rupture. NBRL040. Scale bar = 2 mm.

During floatation, the insect carcass 'seeps' nutrients through cuticular perforations (e.g. setal bases, spiracles) and between sutures as their internal tissues decay (Smith *et al*., 2006). This can stimulate the growth of a microbial community that not only protects the carcass from abrasion and disarticulation, but will also cause it to adhere to other flotsam it contacts. Fossilised examples of this are known from the Nova Olinda Member (Figure 101).

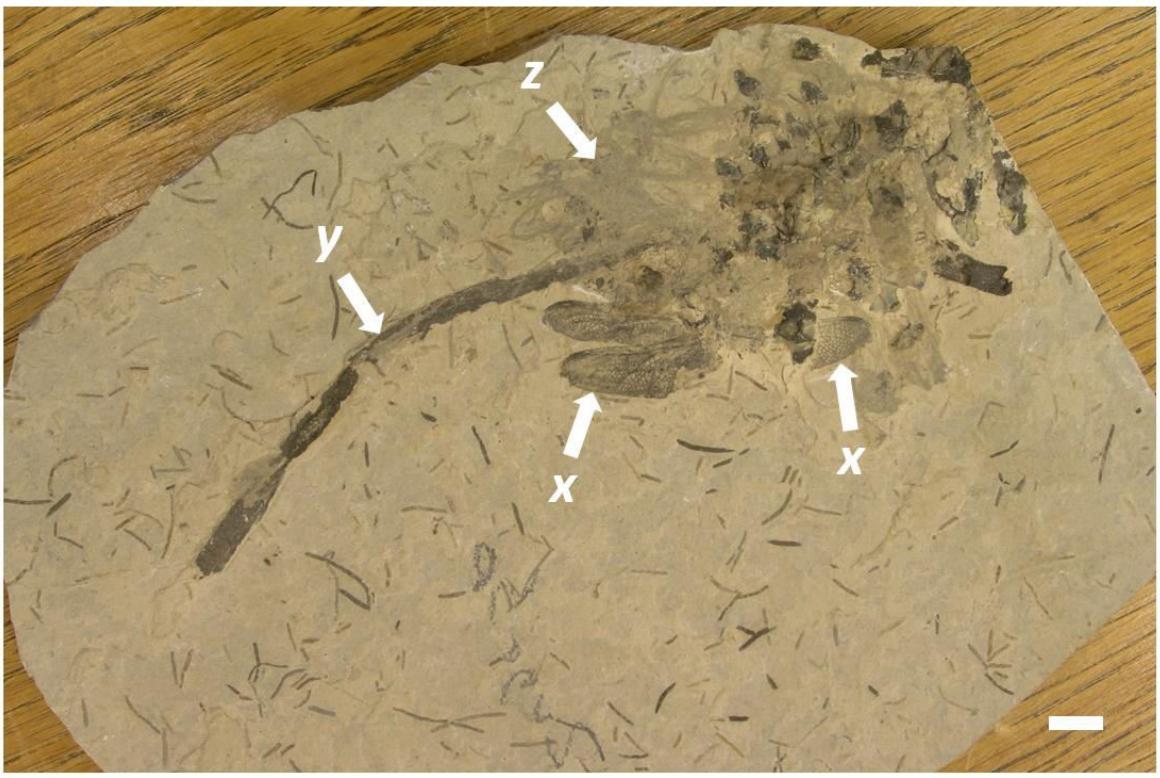


Figure 101. Example of Nova Olinda Member flotsam, including odonate and plant material. *x*, Odonata wings. *y*, Plant stem. *z*, Discolouration likely representing area of microbial community binding material together. Unnumbered Karlsruhe specimen (SMNK #). Photo courtesy of Robert Loveridge. Scale bar = 1 cm.

There is also a distinct lack of large fossil trees and large terrestrial animals in the Nova Olinda Member, although a log may have been found (Heads pers. comm., 2016). The rare large animals that are present, are volant or possibly semi-aquatic (e.g. pterosaurs, crocodilians, and birds). An unknown filter is preventing larger terrestrial fossils from being incorporated or preserved. The most likely explanation is that hydrodynamic sorting causes the largest material to be deposited at the margins of the water body, rather than in the deeper water, and lighter material is being concentrated by gyres. This would explain the rare occurrence of bound flotsam and account for the lack of larger fossils. Regardless, it is not impossible to hypothesise the presence of another Lagerstätte somewhere near the Nova Olinda Member, composed almost entirely of larger fossil material.

Even though the Nova Olinda Member fossils are believed to have been deposited a considerable distance from the palaeoshore (Heimhofer and Martill, 2007; Heimhofer *et al*., 2010; Martill pers. comm., 2015) and perhaps concentrated by gyres, this does not prevent insect carcasses from

being rapidly transported there. It is commonly known among entomologists that storms and strong winds can transport insects for hundreds of miles, often alive, very quickly (Grimaldi and Engel, 2005). Consequently, this model accounts for all current observations regarding the transport and taphonomy of Nova Olinda Member fossil insects.

5. 4. *Parviformosus wohlrabeae*

Within the collection of Nova Olinda Member insects donated to this project, one specimen represented a new taxon. This fossil was identified as probably a chalcid wasp (Hymenoptera: Chalcidoidea). Although the fossil was systematically described and published in 2013 (Barling *et al*., 2013; included in Appendices 8. 2. 1.), its description is included here. As Barling *et al.* (2013) is a multi-author paper, the contributions are as follows: N. Barling (80%), S. W. Heads (10%), and D. M. Martill (10%).

Hymenoptera is one of the most diverse orders of insects. It is characterised by impoverished wing venation (most veins simple, excluding rare SC branching and RS forking (forewing), pterostigmal cell lost or thick, M fused with Cu sub-basally), the presence of hamuli on the hind wings, haplodiploid sex determination, and the presence of a protibial spur with velum (Rasnitsyn, 2002; Grimaldi and Engel, 2005). The hymenopteran fossil record is well-documented and data suggests that hymenopterans are a sister taxon to Panorpida and likely diverged during the Carboniferous (Beutel *et al*., 2011). Hymenoptera underwent a series of explosive adaptive radiations in the Jurassic, Cretaceous, and Paleogene through which they attained their astonishing modern diversity (Riek, 1955; Rasnitsyn, 1969, 2002; Grimaldi and Engel, 2005; Michez *et al*., 2009). Their hyperdiversity is at least in part due to the evolution of microscopic parasitoid wasps, which constitute the vast majority of species in the order (Kristensen, 1981; Rasnitsyn, 2002; Grimaldi and Engel, 2005). Below, a microscopic wasp is described from the Nova Olinda Member (Barling *et al*., 2013).

5. 4. 1. Systematic paleontology

- Order Hymenoptera Linnaeus, 1758
- Suborder Apocrita Gerstaecker, 1867
- Superfamily Chalcidoidea Latreille, 1817
- Family Pteromalidae Dalman, 1820
- Subfamily *incertae sedis*
- Genus *Parviformosus* Barling *et al*., 2013

Derivation of name: *Parvi*, Latin, small; *formos*, Latin, beauty.

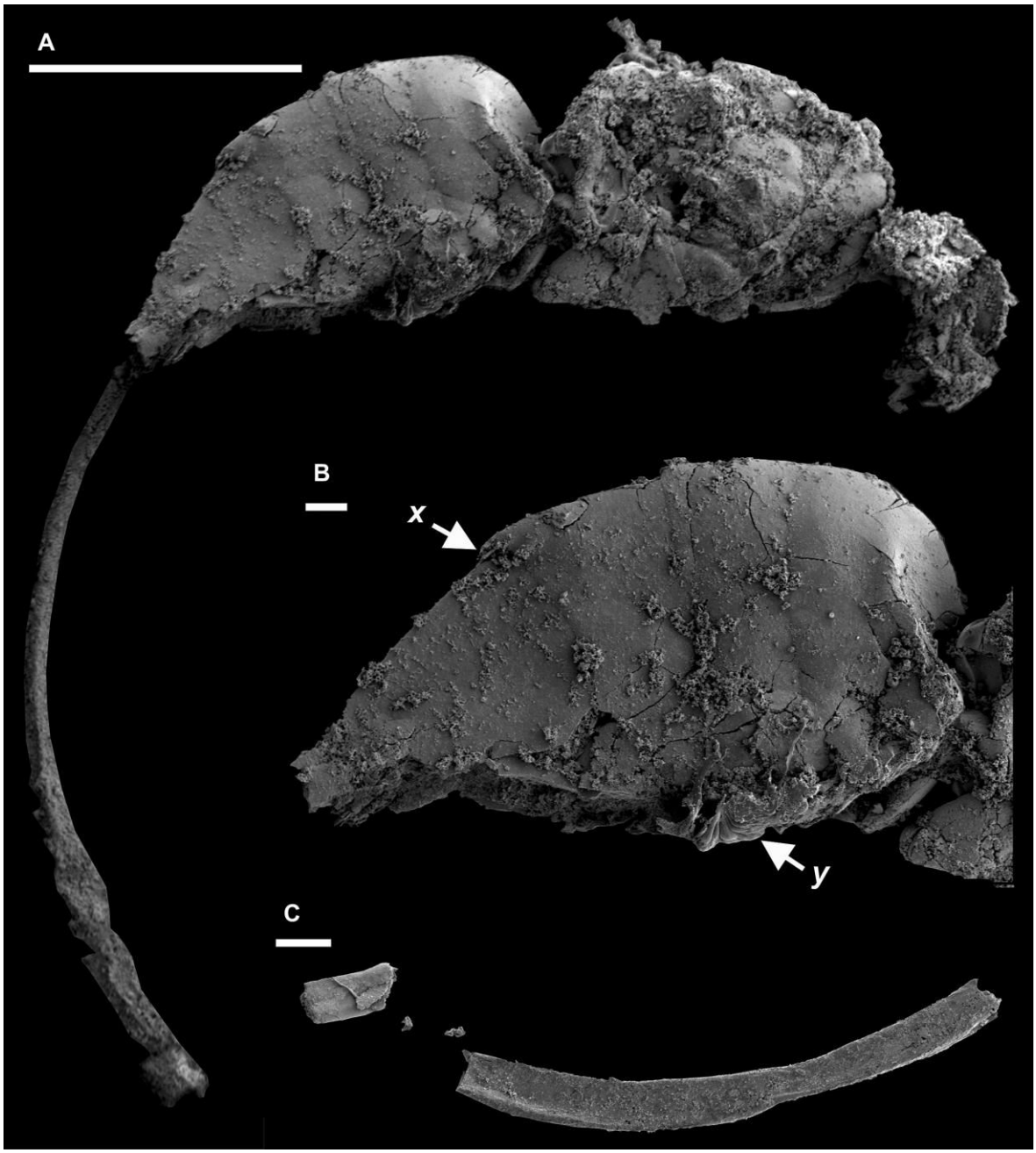


Figure 102. A, Scanning electron micrograph of holotype of *Parviformosus wohlrabeae* sp. nov. (SMNS 700902) in right lateral view. B, Scanning electron micrograph of metasoma. *x*, Highlights the dorsal 'lip' on metasomal segment four. *y*, Highlights contamination. C, Scanning electron micrograph of the detached ovipositor found in residue. A, Scale bar = 1 mm. B, Scale bar = 100 µm. C, Scale bar = 200 µm.

Diagnosis: Small (5.1 mm (3.5 mm excluding ovipositor)) female ♀ pteromalid wasp (Figure 102). Ovipositor elongate and ventrally curved. Mesosoma robust with particularly robust scutellum and mesopleuron. Mesopleuron large, elongate and ventrally positioned, overlapping ventral portions of petiole. Complex propodeumepetiole junction with petiole extending into mesosoma and hooking under propodeum. Metasoma with well-defined segmentation. Metasomal segment four with posteriorly curved dorsal 'lip' approximately 100 µm in length anteroposteriorly and 75 µm in depth extending dorsoventrally over metasomal segment five.

Remarks: Familial placement for *P. wohlrabeae* is extremely difficult and should be considered tentative due to the lack of three key taxonomic structures; the legs, the wings, and the antennae.

- *Parviformosus wohlrabeae* Barling *et al*., 2013

Holotype: SMNS 700902.

Derivation of name: After Judith Wohlrabe who discovered the holotype while studying Nova Olinda Member fossils at the University of Portsmouth.

Type locality: Most likely from an area of active quarrying between Santana do Cariri, Nova Olinda and Tatajuba, flanks of the Chapada do Araripe, Ceará, Brazil (precise quarry unknown).

Horizon: Nova Olinda Member, Crato Formation, Santana Group.

Age: Early Cretaceous, Aptian.

Diagnosis: As for the genus, by monotypy.

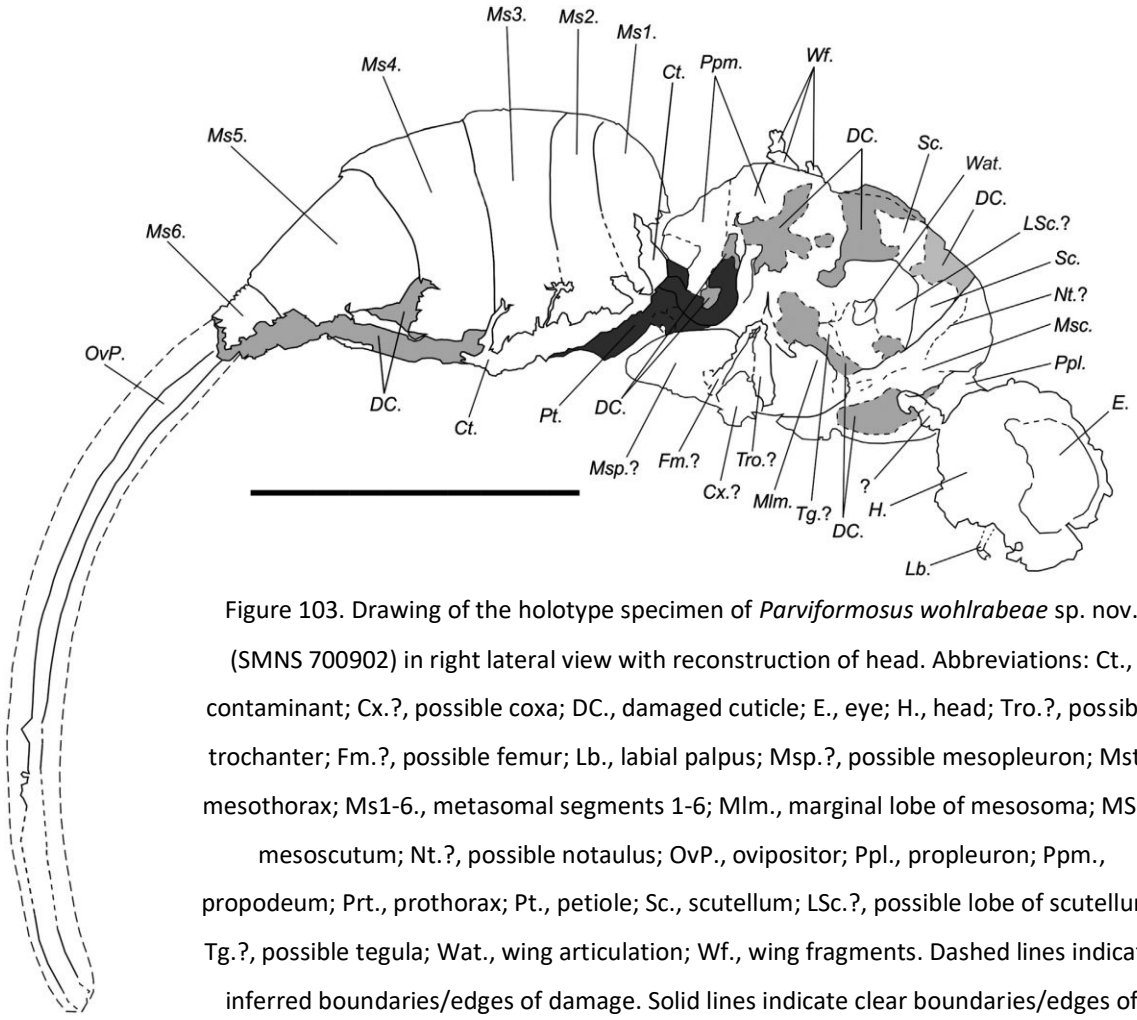


Figure 103. Drawing of the holotype specimen of *Parviformosus wohlrabeae* sp. nov. (SMNS 700902) in right lateral view with reconstruction of head. Abbreviations: Ct., contaminant; Cx.?, possible coxa; DC., damaged cuticle; E., eye; H., head; Tro.?, possible trochanter; Fm.?, possible femur; Lb., labial palpus; Msp.?, possible mesopleuron; Mst., mesothorax; Ms1-6., metasomal segments 1-6; Mlm., marginal lobe of mesosoma; MSc., mesoscutum; Nt.?, possible notaulus; OvP., ovipositor; Ppl., propleuron; Ppm., propodeum; Prt., prothorax; Pt., petiole; Sc., scutellum; LSc.?, possible lobe of scutellum; Tg.?, possible tegula; Wat., wing articulation; Wf., wing fragments. Dashed lines indicate inferred boundaries/edges of damage. Solid lines indicate clear boundaries/edges of damage. Dark grey area highlights petiole. Light grey area highlights damaged cuticle. Scale bar = 1 mm.

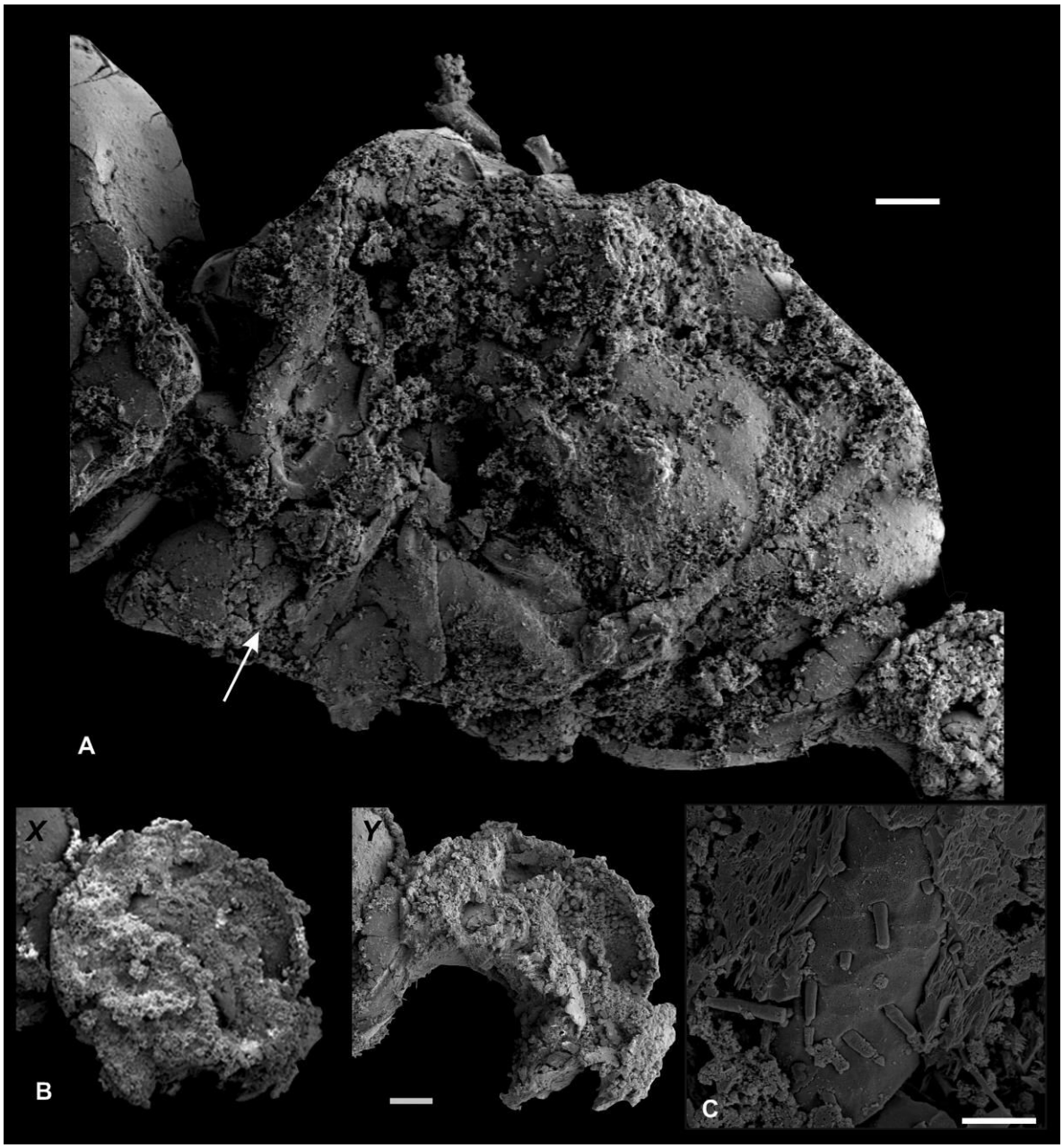


Figure 104. A, Scanning electron micrograph of the mesosoma. Arrow indicates the structure identified as a mesopleuron, but may alternatively represent an enlarged coxa. B, Comparison between specimen head before and after damage. *X*, before damage (Image by Judith Wohlrabe). The semicircular cavity visible in the ventral area may represent aperture for mouth. *Y*, after damage, loss of majority of ventro-anterior sclerites. C, Left labial palpus cropping out from matrix and surrounding calcium carbonate crystals. Setae ranging in size from 4 to 9 µm are present sparsely along the entire length. A – B, Scale bars = 100 µm. C, Scale bar = 10 µm.

5. 4. 2. Description

Incomplete adult female imago preserved in right lateral aspect, comprising head, mesosoma, metasoma and ovipositor (Figures 102 and 103); body length 3.5 mm, total length including ovipositor 5.1 mm.

Head. The head of the specimen was severely damaged during transport. Most of the postero-ventral half of the head was lost, leaving only an area representing the vertex, part of the eye and the clypeus/frons(?) (Figure 104: B). Much of the cuticle on the right lateral surface of the head is absent. It is approximately circular in outline, but slightly dorsoventrally compressed in lateral view. The entire head measures 900 µm antero-posteriorly and ~700 µm dorso-ventrally. The eye is preserved in outline as a deep cavity within the head. The eye is large (approximately 40 – 45% of the head), anteriorly positioned and kidney-shaped. It measures 440 µm dorso-ventrally and approximately 375 µm antero-posteriorly, however it may have been larger in life. Antennae are not preserved, however, a notch is present on the anterior surface where the antennae originally articulated. This notch is located ~200 µm down the anterior surface of the head, but lies above the base of the eye. Ocelli are not preserved. Only fragments of the mouthparts are preserved and accurate identification of individual elements is not possible. A semicircular cavity with a diameter of ~250 µm is present on the ventral surface of the head and probably represents the former position of the mouthparts (Figure 104: B). In the central portion of this cavity a bulbous appendage with fine setae represents the left labial palpus. It has a maximum visible diameter of ~20 µm and length of ~70 µm and the setae are sparse with a length of 4 – 9 µm (Figure 104: C). Some are pointed, but others appear rod-like and are truncated with sub-parallel margins.

Mesosoma. The total anteroposterior length of the mesosoma is 1.14 mm and the greatest dorsoventral depth is 0.92 mm (Figure 102: A). The boundary between the prothorax and the mesothorax is clearly discernible. The prothorax appears simple and takes up approximately one fifth of the whole mesosoma, measuring 875 µm dorso-ventrally and 275 µm antero-posteriorly. Only patches of the mesothorax are preserved uncrushed. The boundary between the mesothorax and propodeum is partially crushed, but visible in the dorsal and ventral areas. Crushed areas have been filled with matrix, making some segment boundaries in these areas difficult to define. A group of sclerites are visible slightly anterior to the centre of the mesosoma. The dorsal portion may represent a lobe of the scutellum, but the sutures of the ventral areas are ill defined. It is robust and is emphasised by high relief. The prepectus is not visible, and is probably internalised, as in many pteromalid subfamilies. There are fragments of sclerites that probably represent the tegula, and a marginal lobe of the mesopleuron. Three wing fragments are visible. A wing fragment on the right lateral surface of the mesosoma appears to represent a forewing articulation, while the more dorsally located fragments may represent a segment of hind wing. A large (~680 µm antero-posterior, ~225 µm dorso-ventral) structure preserved on the ventral edge of the mesosoma may represent one of two structures. It could be an enlarged coxa that has been taphonomically displaced along the side of the mesosoma or, alternatively, a mesopleuron that has shifted ventrally in its anterior portion, giving a ‘semi-detached’ appearance. Due to the positioning, size and apparent fusion to the mesothorax, we consider it

more likely that this structure is a mesopleuron. If this structure should prove to represent an enlarged coxa then the other leg element identifications are incorrect. Only a single fragmentary leg remains. The trochanter and possible femur are preserved semi-articulated in a folded position and crushed over the lateral surface of the mesopleuron. There is a patch of crushed cuticle below the femur that may represent the remnants of a coxa. The articulation of this limb is not discernible, however its positioning suggests it is 'right limb two'. The ventral portions of the limb and the mesopleuron are heavily compacted and are partially crushed together. The leg is short and narrow with a femur 300 µm long and 58 µm wide and a tibia ~325 µm long and ~30 µm wide. The distal end of the tibia is also heavily crushed, and may have extended further. The width of the mesothorax is estimated due to compaction, but the dorsal-most suture (to the propodeum) is still clearly visible. The mesothorax is ~840 µm in length in the dorsal portion and ~400 µm in length in the central region. The propodeum appears reduced, however this may be an artefact of preservation. It is 360 µm in width and 565 µm in height. The petiole is short and the boundary between the petiole and the propodeum is ill defined.

Metasoma. The metasoma consists of seven clearly defined segments (petiole + six segments with ovipositor). The cuticle is somewhat fractured throughout the metasoma, with the least amount of damage occurring in metasomal terga four and five. Metasomal sterna one, two, and three are overlain with a layer of carbon putty that conceals the cuticle (Figure 102: B). Metasomal sterna four, five, and six have been severely crushed and are only visible as flaked cuticle and impressions in the matrix. Separate sterna and terga are not distinguishable. Excluding the ovipositor and petiole, the metasoma is 1.6 mm in length with metasomal segments that increase in length posteriorly (excluding segment six) from a 165 µm length of segment one, to a 580 µm length of segment five. Metasomal segment six is 150 µm in length. The entire metasoma is slightly recurved underneath the body in a typical 'wasp death position'. In terms of segment morphology, segments one and two are curved slightly anteriorly. Segment three is curved anteriorly on the anterior edge and curved posteriorly on the posterior edge. Segment four has a 100 µm long posteriorly curved dorsal 'lip' that retracts after 75 µm to a gentle dorsal curve (Figure 102: B). Segment five greatly decreases (from 580 µm to 250 µm) in dorsoventral height posteriorly. Segment six is 260 µm in length and 215 µm in height, but is heavily damaged and the hypopgyium is not preserved. A trace of the ovipositor is preserved on the slab as a raised ridge on the matrix. The ovipositor has fallen away and been transferred to another SEM stub (Figure 102: C). Along the crest of the raised line, the matrix infrequently breaks to reveal needle-like crystals. These range in size from 3 to 8 µm in length and have a width of 0.5 – 1 µm. The total length of the ovipositor is ~2.2 mm. Identification of separate valves is not possible, but the preserved size of the ovipositor has been reconstructed using the SEM stub specimen (Figure 103).

5. 4. 3. Discussion

The holotype and only known specimen of *Parviformosus wohlrabeae* (at 5.1 mm total length) currently represents the smallest described hymenopteran from the Nova Olinda Member. There are two suborders within Hymenoptera, Symphyta and Apocrita. Interestingly, a specimen has been described from the Nova Olinda Member that forms a sister clade to Xiphydriidae (within Symphyta) + Euhymenoptera, and so represents an extremely basal form, probably outside of the two suborders. It was named *Cratoenigma articulate* by Krogmann and Nel (2012) and sits within a new group called Unicalcarida. Although many key characters are absent, the presence of a petiole confirms the position of *P. wohlrabeae* within Apocrita.

Within Barling *et al*. (2013), *P. wohlrabeae* was tentatively described as nesting within Pteromalidae, possibly Sycophaginae based on remarks by J.-Y. Rasplus, R. Burks, and M. Yoder (pers. comm., 2012, 2013), which would also place it within Chalcidoidea. These assignments were respectively based on: 1) the shape of the posterior end of the gaster and the morphology of the ovipositor (J.-Y. Rasplus, pers. comm., 2012), and 2) the length and shape of the ovipositor, height relative to width of the gaster, short pronotum, shortened head, and an apically expanding ovipositor sheath (R. Burks and M. Yoder, pers. comm., 2013). Since this description, J.-Y. Rasplus has expressed regret and disassociation with his comments. He was not aware that we were taking his expert opinion as anything more than a suggestion. The *very* tentative placement within the subfamily Sycophaginae would adjust its familial placement to Agaonidae. Chalcid wasp systematics are still in a state of flux and the explanation provided by Jean-Yves Rasplus was mistaken as implying that the current consensus was that Sycophaginae had been transferred to Pteromalidae.

As such, the current tentative placement within Pteromalidae, subfamily *incertae sedis* (Barling *et al*., 2013) is probably incorrect. Recent reviews of fossil Sycophaginae have concluded that *P. wohlrabeae* does not preserve enough characters to warrant its placement within Chalcidoidea (Farache *et al*., 2016), although its morphology is certainly suggestive of this group (Noyes, 2012).

In addition to the confusion regarding familial placement, there is one oversight within Barling *et al*. (2013). It was stated that, if the placement of this taxa is correct, then this hints at the presence of figs (*Ficus*) 50-60 million years earlier than current estimates. In fact, the molecular data *supports* the possible presence of figs in the Early Cretaceous (Rønsted *et al*., 2005).

The fossil record of chalcid wasps is extensive, with examples from the Middle Jurassic of China (Rasnitsyn and Zhang, 2010), Lower Cretaceous of Lebanon (Basibuyuk *et al*., 2002), the Late Jurassic/Early Cretaceous of Mongolia (Rasnitsyn *et al*., 2004) and the Cenozoic of Europe (Grissell, 1980; Skalski, 1988; Simutnik, 2002; Gibson, 2008; Heraty and Darling, 2009). As such,

the presence of Chalcidoidea within the Lower Cretaceous Nova Olinda Member would be unsurprising if confirmed.

The Nova Olinda Member boasts a broad diversity of hymenopterans, including three members of the phytophagous, petiole-lacking Symphyta (Sawflies) (Darling and Sharkey, 1990; Rasnitsyn *et al*., 1998; Роман, 2004; Grimaldi and Engel, 2005; Osten, 2007; Archibald and Rasnitsyn, 2016), and, including *P. wohlrabeae*, a total of nineteen distinct (but not yet all described) aprocritan species within fourteen families are reported (Brandao *et al*., 1989; Darling and Sharkey, 1990; Rasnitsyn, 1993; Rasnitsyn and Martinéz-Delclòs, 1999; Pulawski and Rasnitsyn, 2000; Osten, 2007; Nel *et al*., 2013; Barling *et al*., 2013). This diversity encompasses a broad spectrum of life-styles, from stinging predatory vespid wasps (Vespidae: Carpenter and Rasnitsyn, 1990; Osten, 2007), to parasitic spider wasps (Pompilidae: Osten, 2007), and even solitary pollinating 'flower ants' (Tiphiidae: Rasnitsyn, 1986).

Regardless of the issues faced with the placement of *P. wohlrabeae*, it is still a remarkable fossil. It is highly atypical for an insect of this size to be preserved outside of amber (Penney and Jepson, 2014), and its presence is a testament to the unique combination of preservational mechanisms of the Nova Olinda Member Lagerstätte.

Chapter 6. Conclusions

6. 0. Preface

Three primary goals were outlined in this thesis: 1) to determine the fidelity of preservation of the Nova Olinda Member fossil insects, 2) to determine the preservational mechanisms that allowed for their high fidelity of preservation, and 3) to investigate how the insect fauna can be used to determine the palaeoenvironment and how this affected their taphonomy.

Each of these questions was examined, culminating in quantitative and qualitative quantifications of preservational fidelity, a new preservational model, and a new palaeoenvironmental reconstruction. Here, those findings are summarised and future work is proposed.

6. 1. Fidelity of preservation

To assess the Nova Olinda Member fossil insect preservational fidelity, a two-fold approach was taken. Firstly, each fossil had a series of taphonomic characters recorded, creating a data matrix for the assembled collection. This was then normalised and an index value generated. The data were also subject to explorative statistical analyses. Secondly, a qualitative comparison of the macro and micron-scale preservation was undertaken, comparing the Nova Olinda Member to several other key arthropod Lagerstätten, including the Yixian Formation, Calizas de la Huérguina Formation (Las Hoyas), 'La Cabrua' quarry (Montsec), Green River Formation, Solnhofen Formation, Florissant Formation, Rubielos de Mora Basin, Tiaojishan Formation (Daohugou), Wonthaggi Formation (Koonwarra), Frankfort Formation (Beecher's Trilobite Bed), and the London Clay Formation. However, before these can be addressed, the range and fabrics of preservation must first be outlined, along with what tissues they preserve.

6. 1. 1. Range of preservation

In Chapters 3. 10. and 4. 1. 13., the fidelity of preservation of Nova Olinda Member fossil insects and their relative fidelity to other Lagerstätten were investigated. They have an extremely broad range of preservational fidelities, ranging from 'scrappy' low-relief barely discernible traces of low fidelity to complete fully-articulated high-relief specimens with sub-micron-scale replication of both external and internal morphology. Despite this variability, both examples preserve 'soft tissue' (i.e. non-mineralised cuticle) and so would both traditionally be considered 'exceptionally preserved'. The disparity between these two extremes demonstrates the necessity for a clearer, perhaps quantifiable, definition of 'exceptional preservation' in fossil insects.

While emphasising the extremes of preservation, it is important also to highlight the modal preservational fidelity. In the Nova Olinda Member, insect fossils are most commonly preserved with moderate-to-high relief, but can vary greatly in preservational fidelity within a single fossil. Frequently, they retain outstandingly well-preserved cuticle with sub-micron replication of morphological detail, revealing cuticular scales, setae, and spiracles (highlighted in Chapter 3. 5. 1.). These exceptionally preserved regions are, however, surrounded by areas of considerably poorer-preservation, where surface details are abraded/non-mineralised and cuticular structures are lost (highlighted in Chapter 3. 6.). Transitions from exceptional preservation to poor preservation can be relatively diffuse, occurring over > 100 µm, or be abrupt (e.g. Plate 72: D-G; Plate 73: A).

6. 1. 2. Fabrics of preservation

Three distinct fabrics of preservation are identified: 1) high-fidelity sub-micron impregnations in nano-crystalline pyrite (unweathered) and goethite (weathered), 2) a pseudoframboid-like – to – globular infill fabric (depending on whether pseudoframboids are individually discernible) preserved in goethite (weathered from pyrite), and 3) globular high-fidelity impregnations/encrustations of internal tissues by calcium phosphate, similar to 'Orsten'-type preservation (Maas *et al*., 2006; Eriksson *et al*., 2012). How these fabrics are formed is discussed below in Section 6. 2. Here, the tissues preserved by each fabric are outlined, along with their fidelity of preservation.

'Fabric 1' (nano-crystalline pyrite impregnation) is a common fabric replicating the majority of the epicuticle in most specimens. Most commonly, it preserves the gross morphology of the epicuticle, with cuticular features (such as setae) retained albeit relatively poorly (e.g. Plates 38 and 41). However, in some specimens the epicuticle is remarkably well-preserved, retaining micron-scale cuticular features with life-like fidelity (i.e. setae: Plates 32-36 and scales: Plates 45-46).

'Fabric 2' (pseudoframboid-like – to – globular aggregates) infills the vast majority of the body cavities in most fossils. This fabric does not preserve insect morphology. Instead, it simply occupies the space where insect tissues once were. Original insect morphology was obliterated by coarse euhedral pyrite crystals during pseudoframboid growth. However, these framboids allowed the insect fossils to retain much of their three-dimensionality by infilling the vast majority of the body cavity. In some areas, individual pseudoframboid/aggregates are not discernible, and instead an array of globular grains simply infill the fossil.

'Fabric 3' (globular high-fidelity impregnations/encrustations of internal tissues) infrequently replicates the most labile parts of the insect carcass. When it does so, it can either encrust the

tissues, resulting in a micron-scale ‘bubble-like’ globular fabric partially obscuring original morphology (Plate 61: G-H), or impregnate the tissues with submicron-scale globular grains. When the latter occurs, the highest fidelity of preservation of internal soft tissues is achieved (Plates 63, 64, and 71). These extremely labile tissues can be replicated to the submicron-scale.

On occasion, the combination of these fabrics allowed for a truly remarkable fidelity of preservation, with original morphology retained in three dimensions to the submicron scale. To draw further conclusions regarding the fidelity of preservation both statistical analyses and qualitative comparisons were undertaken. These are summarised below.

6. 1. 3. Statistical analyses

The Nova Olinda Member fossil insects examined in this project had a series of interval and ordinal taphonomic characters measured, creating a matrix of taphonomic data. These data were normalised (into values between 0 and 1) and subject to several explorative statistical analyses using the software ‘PAST’ to detect taphonomic trends. These included both R- and Q-mode cluster analyses, as well as principal coordinate analyses. As discussed in Chapter 3. 9. 4., all analyses revealed no *definitive* clusters, which would have been denoted by a colour change in the dendrograms. Nevertheless, some weak clusters were present in several of them. The Q-mode cluster analyses revealed that characters coding for features positioned closely together on the insect tended to cluster. One of the R-mode cluster analyses showed two weak clusters of insect families and principal coordinate analyses were undertaken to corroborate them. These also revealed weak clustering corresponding to taxonomy. Additionally, some clusters were present in the principal coordinate analyses that did not correspond to taxonomy and may instead represent a collection bias. In all cases, clusters (at least partially) dispersed when an alternative similarity index was used, indicating that they are unreliable. Ultimately, the lack of robust clusters indicates that either the collection was too taxonomically restricted to draw definitive correlations between taxonomy, ecology, and preservational fidelity, or that taxonomy has little control over preservational fidelity in the Nova Olinda Member insect assemblage. The latter of these is the proposed conclusion here and, instead, it is likely that post-mortem and taxon-agnostic processes have the greatest control of preservational fidelity.

A taphonomic index was also generated for each fossil in the collection. The aim of this was to create an easy-to-read value summarising each specimens preservational fidelity. This was achieved by normalising the character data into values between zero and one, and averaging them, resulting in a value between zero and one that represented the average preservational fidelity of each specimen. However, no weighting could be applied for each character, resulting in an inaccurate representation of preservational fidelity. The application of weighting was investigated, but deemed too time-consuming to include in this project. This is due to the

morphological diversity of insects, which would cause many fossils to be represented inaccurately by a generalised weighting system. If this system could be developed further, with appropriate weighting, it could prove to be a powerful tool for studying taphonomic trends across time, geography, climate, habitat, etc.

Although no other Lagerstätten have been investigated with similar quantifiable indexing systems, comparisons based on fossil descriptions and SEM analyses were undertaken. These allowed for a qualitative comparison of preservational fidelity between the Nova Olinda Member and other Lagerstätten.

6. 1. 4. Comparisons to other Lagerstätten

Macro and micro-scale comparisons were made with eleven fossil arthropod Lagerstätten, gauging the fidelity of the Nova Olinda Lagerstätte against other sites of 'exceptional preservation'. It appears that few other Lagerstätten preserve micron-scale cuticular surface structures or high-fidelity internal tissues. In most cases, insects are preserved either as compressions or coarser grained three-dimensional impregnations. This has resulted in sites that either preserve cuticle with high-fidelity but compressed flat (e.g. the Green River, Montsec, and Rubielos de Mora Lagerstätten), or with high-relief but obliterated cuticular micro-structure (e.g. the Beecher's Trilobite Beds, Daohugou, London Clay, and Solnhofen Lagerstätten). One Lagerstätte (the Florissant Formation) is unique in that it preserves cuticular micro-structure with moderate relief via diatom encrustation. This, however, has resulted in poor-preservation of the micro-structures, with the majority of them obscured by an irremovable encrusting layer of diatom microfossils. However, it should be noted that some sites that yield relatively poorly-preserved insect fossils as compressions may actually be more useful for palaeoentomology. These sites allow for taxonomically important structures (e.g. wing venation) to be viewed more easily than in the Nova Olinda Member.

In terms of replacement minerals and fabrics, the Yixian Formation most closely resembles the majority replacement fabric of the Nova Olinda Member insects, but also differs in several key ways. First and foremost, the fidelity of preservation of Yixian Formation insects is an order of magnitude poorer, with replacing framboids ten times coarser than the Nova Olinda Member. Secondly, no cuticular surface details or labile internal tissues are replicated, as the only preserving fabric is that of framboids. Without nano-crystalline impregnation of the cuticle or impregnations/encrustations of internal labile tissues, the framboids simply occupy the area where the insect tissues used to be and do not preserve micron-scale morphology (Figure 95 *vs* Figures 39, 40, and 47; Wang *et al*., 2012). This is likely a result of differing geochemical conditions between the two Lagerstätten, with the Yixian Formation reaching pyrite supersaturation (stimulating framboid formation) before the non-framboidal fabrics could precipitate. The cause

of this rapid supersaturation may be a result of differing sedimentology, with the Yixian Formation largely consisting of organic-rich siliclastic mudstones, shales, and occasional volcanic ashes. Alternatively, abundant sulphur may have been supplied from decaying organic matter in the lush forested area surrounding the Yixian palaeolake, along with soil-derived iron, resulting in supersaturation of iron sulphides within the sediment (Wang *et al.,* 1998; Ding *et al*., 2003; Chen *et al*., 2004; Zhang and Sha, 2012). Conversely, in Lagerstätten preserving insects as iron sulphide compressions, it is probable that supersaturation was not achieved, and only a thin sheet of nano-crystalline iron sulphides impregnated their epicuticle. This lone thinly impregnated layer was insufficient to protect the fossil from compaction.

Most non-amber insect Lagerstätten compared in this project appear to preserve insects in iron sulphides. Although many insect Lagerstätten are awaiting spectroscopic analyses, the majority seem to preserve insects with similar fabrics and colours to that of the Nova Olinda Member. Weathering products confirm the presence of iron, and it is likely that similar geochemical processes preserved insects in many of these localities.

Ultimately, all investigations here indicate that the fidelity of preservation of Nova Olinda Member fossil insects far exceeds that of other Lagerstätten, and it is quite possible that they have the highest preservational fidelity of any non-amber insect Konservat-Lagerstätten.

6. 2. Replacement pathway

There have been several investigations into the replacement processes that allowed for the exceptional preservation of Nova Olinda Member insects (Grimaldi and Maisey, 1990; Bechly, 1998c; Menon and Martill, 2007; Delgado *et al.*, 2014; Osés *et al*., 2016). These investigations have all contributed significantly to our understanding of the geochemistry of these fossils, but are either based on superficial low-magnification observations, few specimens, or do not match new observations. The models presented herein are supported by hundreds of electron micrograph images, energy-dispersive X-ray analyses, X-ray diffraction analyses, insect comparative anatomy, and the current understanding of pyrite framboid formation. Before the model can be summarised, how each fabric formed must first be discussed.

The high-fidelity sub-micron impregnation fabric in nano-crystalline goethite (‘fabric 1’) is the result of non-framboidal nano-crystalline pyrite impregnation of the cuticle. This is a consequence of moderate sedimentary pyrite saturation levels during precipitation, as well as the positioning of the tissues. In the initial stages of pyrite precipitation, pyrite was present in high enough concentrations to stimulate precipitation, but not high enough for framboid formation (Berner, 1970; Newman, 1998; Joeckel *et al*., 2005; Ohfuji and Rickard, 2005; Rickard, 2012). This allowed

for nano-crystalline pyrite to impregnate the cuticle (after several other phases of iron sulphides precipitated). Only the exterior-most epicuticle is preserved in this fabric as the conditions for this preservation were generated within the epicuticle by the sulphate-reducing microbial mat immediately adjacent to the carcass. The metabolic activities of these microbes created a geochemical gradient within the epicuticle, which later transitioned into the interior of the carcass (discussed below).

'Fabric 2' (pseudoframboid-like aggregates and related globular textures) is a result of the same process for 'fabric 1', albeit with supersaturation of pyrite. Although the controls of pyrite framboid formation are complex, polyphase, and inherently difficult to study, where pseudoframboids are present, it can be assumed that the continued metabolic activities of a microbial mat resulted in pyrite supersaturation within the carcass (Berner 1969; Farrand, 1970; Sweeney and Kaplan, 1973; Kribek, 1975; Stanton and Goldhaber, 1991; Wang and Morse, 1996; Morse and Wang, 1997; Butler and Rickard, 2000; Wolthers *et al*., 2003; Ohfuji and Rickard, 2005; Rickard, 2012). Although all instances of 'fabric 2' are mineralogically identical, the pseudoframboids vary in size as well as their discernibility as discrete structures. In some areas, the variations of this fabric can be inferred to be a result of tissue decay by their consistent association with particularly decay-prone tissues (e.g. cuticle adjacent to perforations: Figure 54) (Martill, 1990; Allison and Briggs, 1993; Briggs and Kear, 1993a,b; Briggs, 1995a,b). Where this occurs, 'fabric 1' can also be obliterated. In other areas, the variations (particularly size of pseudoframboid) are a result of the local microgeochemical environment, which changed as bacterial sulphate reduction progressed.

'Fabric 3' is the globular encrustation and impregnation of internal labile soft-tissues (i.e. genitals, muscle, guts, etc.) in apatite. This replacement fabric is similar to 'Orsten'-type preservation of arthropods (Maas *et al*., 2006; Eriksson *et al*., 2012). This fabric is a result of 'minor' decay of internal labile soft-tissues, which liberated ions and created chemically 'active sites' for precipitation (Maas *et al*., 2006). Combined with the ion-rich hypersaline waters, many internal tissues (but certainly not all) were fossilised either as globular encrustations (i.e. Figure 41: A in Chapter 3) or high-fidelity (submicron globular grained) impregnations (Figure 53 in Chapter 3). However, internal soft tissues are still relatively rare and in many instances are only preserved as 'scrappy traces' (i.e. Figures 41: C and 50). Further exceptionally preserved internal tissues could be masked by exceptionally preserved cuticle, resulting in the exceptionally preserved internal tissues being obscured. If this is the case, then exceptionally preserved internal tissues may be much more common than currently observed.

The model proposed here (Figure 96) states that the first mineralisation event was the replication of some internal labile soft-tissues in calcium phosphate (Fabric 3), in a process similar to 'Orsten'-

type preservation (Maas *et al*., 2006; Eriksson *et al*., 2012). Ions necessary for this mineralisation were liberated by decay, which also created 'active sites' for mineral precipitation. Some of this may have even occurred prior to the carcass reaching the site of burial, although mineralisation of internal labile tissues probably occurred only once the carcass settled in the anoxic sediment. This was followed by amorphous iron monosulphide mineral precipitation as nano-grains (Fabric 1) in the epicuticle of the insect carcass, brought about by sulphate reducing bacteria. Further diffusion and eventual supersaturation of ions within the carcass allowed for pseudoframboid precursor structures to precipitate within the carcass (Fabric 2). As sulphate reduction continued, the pH decreased, resulting in a transition from the production of unstable amorphous iron monosulphides to relatively stable iron sulphides. These may have included ordered iron monosulphides (mackinawite) or the sulphur analogue of magnetite (greigite), but were dominated by pyrite. These directly overprinted the amorphous iron monosulphide as nano-crystals in 'fabric 1' and pyrite pseudoframboids in 'fabric 2'. A relatively recent weathering event finally caused these to be pseudomorphed by goethite.

The discussion of iron sulphide geochemical pathways is invariably hypothetical, due to the oxygen-sensitive nature of the precursor phases. Nevertheless, the model described here accounts for the myriad fabrics of preservation in the weathered Nova Olinda Member insects and matches all current observations. However, one of these fabrics (notably Fabric 2, the pseudoframboid-like aggregates) was not observed in the unweathered fossils. This may be a result of the extremely limited number and relatively poor condition of unweathered specimens analysed. Alternatively, this could indicate that the 'unweathered' specimens underwent a different preservational process entirely (discussed further below in Section 6. 4. 2.).

6. 3. Palaeoenvironmental reconstructions

The palaeoenvironmental reconstructions presented here include three distinct environments, with several example niches (Figure 99 in Chapter 5). These reconstructions are based on fossil evidence from many taxonomic groups, but predominately Insecta. The environmental associations of these insects are based on their modern relatives, with approximately 112 million years of evolution between them. Despite this, the taxonomic diversity of the Early Cretaceous is similar to modern faunas and the morphology of many fossils are similar to their modern relatives, particularly those that are indicative of specific environments (Martill *et al*., 2007a; Mohr *et al.*, 2007; Penney and Jepson, 2014). While the specific preference of any one fossil insect family presented here could differ from their modern relatives, it is unlikely that all of the families representing any one environment are incorrectly associated. The only exception to this is the association of Tettigarctidae to high altitude/cold environments, as it is the only family

representing this environment. Regardless, the identification of an arid scrubby, riparian/deltaic and associated freshwater, and woody forested environments can now be confirmed for the Nova Olinda Member hinterlands.

It was determined that the insects must have been transported to the site of deposition alive, or shortly after death. Desiccation or decay in any of the palaeoenvironments prior to transportation would have resulted in carcass disintegration. The primary mode of transport for Nova Olinda Member fossil insects were seasonal 'flash floods'. This conclusion is supported by a wealth of fossil taxa that thrive in a wet/dry seasonal climate or inhabit burrows, but also by varved sediment, taphonomic swell-bursting of insects, bound flotsam, and the presence of small low-density insects. Once within the palaeolake, the hostile hypersaline and anoxic conditions prevented scavenging and extensive decay. Finally, the description, diagnosis, and further discussions of the fossil wasp *Parviformosus wohlrabeae* are presented (also see Barling *et al*., 2013; Appendix 8. 2. 1.).

6. 4. Future analyses

The goals of this project were achieved, but there are still many questions regarding the exceptional preservation of Nova Olinda Member fossil insects that require further investigation. Below, future studies are proposed.

6. 4. 1. Iron sulphide fossilisation

Although the mineralisation of animal tissues in iron sulphides is well-documented and experiments have been undertaken to replicate it in the laboratory, these have been of limited success, and often do not accurately recreate the fabrics observed in some fossils (Schoonen, 2004; Brock *et al.,* 2006; Darroch *et al*., 2012; Wu *et al*., 2012; Vietti *et al*., 2015). In addition, due to the oxygen-sensitive nature of its mineral phases, low-temperature pyrite framboid formation is still relatively poorly understood (Berner 1969; Farrand, 1970; Sweeney and Kaplan, 1973; Kribek, 1975; Stanton and Goldhaber, 1991; Lennie and Vaughan, 1996; Wang and Morse, 1996; Morse and Wang, 1997; Butler and Rickard, 2000; Wolthers *et al*., 2003; Schoonen, 2004; Ohfuji and Rickard, 2005; Hunger and Benning, 2007; Rickard, 2012; Wu *et al*., 2012). To tackle this, novel techniques for actuo-palaeontological iron sulphide fossilisation experimentation must be developed (Briggs and McMahon, 2016). Techniques must be non-invasive to prevent the introduction of oxygen into the experiment. Hyperspectral phasor analysis or autopilot light-sheet microscopy of mineralisation against a translucent surface could be used as an alternative to invasive spectroscopic microprobes (Royer *et al*., 2016; Cutrale *et al*., 2017). If these are not appropriate, then long-term immersion of microprobes prior to the experimentation could allow

for stabilisation of the anoxic environment, preventing the microprobe from introducing contaminating elements (specifically oxygen).

It is now believed that sulphate reducing bacteria play a much larger role in the replication of tissues in iron sulphides than just providing reaction components (Schoonen, 2004; Wu *et al*., 2012). Previous studies have encountered problems when implementing microbial communities into their experimentation, possibly cultivating the wrong taxa and hindering mineralisation (Brock *et al.,* 2006; Darroch *et al*., 2012). Tighter controls are required for the cultivation of appropriate microbes to result in successful experimentation.

Additionally, the conditions required to stimulate precipitation of each fabric observed here require investigation. Specifically, the extent of decay and pyrite saturation levels required to stimulate precipitation of the two iron sulphide fabrics (nano-crystalline impregnation and pseudoframboid coatings) is currently unknown. Actuo-palaeontological decay experiments undertaken with varying sedimentary pyrite saturation levels and varying levels of carcass decay could reveal the conditions required for each of these fabrics. Experiments are yet to be undertaken examining the nano-crystalline impregnation of cuticle by pyrite, as previous experiments have focused solely on pyrite framboid formation (Darroch *et al*., 2012; Wu *et al*., 2012; Vietti *et al*., 2015). Consequently, following the geochemical models presented here, the next step for this line of research is to undertake actuo-palaeontological experimentation with these key factors in mind, allowing for a better understanding of the time-frame and requirements for this style of preservation.

6. 4. 2. Nova Olinda Member ‘unweathered’ preservation

While the models presented here are supported by all available evidence, one key piece of evidence is absent. Here, it is assumed that the ‘black’ iron sulphide insects are an unweathered version of the typical ‘brown’ goethite specimens. However, every ‘black’ specimen examined has lacked the pseudoframboid-like aggregate replacement fabric. Even specimen HT001, which retained high relief, showed no sign of this or other spherical/subspherical fabrics. This suggests that the ‘black’ specimens may not represent unweathered versions of the same process, but instead be a distinct mode of preservation. Current research on Nova Olinda Member fossil fish suggests that two distinct modes of preservation may be present; pyritization (as described in this thesis) and ‘kerogenization’, whereby the carcass was fossilised in a ‘methanogenesis zone’ (Osés *et al*., 2017). Regardless, further investigations of the ‘black’ ‘unweathered’ fossils are required, with a much larger sample size, as only a limited number of these ‘black’ specimens were available for this study.

If this alternative hypothesis is correct, then the 'unweathered' X-ray diffraction data presented in this project corresponds to a different preservational process. Despite this, the preservational model presented here for the weathered specimens remains robust. This is because the proposed initial replacement mineral phases are based on textural observations combined with the known parameters of pyrite framboid formation. If the hypothesis proposed by Osés *et al*. (2017) is applicable to the insect fossils, then the taphonomic model proposed here cannot be applied to the 'unweathered' (i.e. black) specimens, but is still applicable to the weathered (goethite) specimens.

Regardless, a comprehensive fossil collecting project from 'unweathered' Nova Olinda Member sediments is required. Excavations should be undertaken to yield abundant 'unweathered' insects, which should be analysed or stabilised as quickly as possible. Ideally, horizon levels should be recorded for both preservational types, allowing for a quantitative comparison between overburden thickness and weathering locations.

6. 4. 3. Systematics of the Nova Olinda Member insect fauna

Many insect groups from the Nova Olinda Member require significant review and re-description. A thorough re-description of Ephemeroptera, Orthoptera, and Neuroptera are required (Heads and Martins-Neto, 2007; Heads *et al*., 2007; Staniczek, 2007; Heads and Leuzinger, 2011).

The placement of *Parviformosus* was clarified in this thesis, but most of the fossil wasps from the Nova Olinda Member have not been systematically reviewed in over a decade. In addition, *Parviformosus* represents the only microscopic wasp described from the Nova Olinda Member. A thorough investigation of ambiguous microscopic insect fossils may reveal many more micro-hymenopterans, providing a wealth of important information regarding their diversity during the radiation of angiosperms (Mohr *et al.*, 2007).

As noted above, the exceptional preservation of internal soft tissues may be more common than currently observed. If this is the case, it could allow for the application of modern systematic techniques to Nova Olinda Member insect fossils. Currently, fossil insect systematics is predominately based on wing venation, limbs, antennae, or other easily discernible appendages, whereas many modern insects are identified by differences in their genital structure (Grimaldi and Engel, 2005). This results in a 'mismatch' between modern and fossil insect systemics that likely lowers our estimations of insect diversity in the fossil record. The fact that internal and external features of insect genitals *can* be preserved in the Nova Olinda Member offers the unique opportunity to apply modern systematics to Mesozoic fossil insects (Plate 61). This would currently be difficult to achieve, but as new innovative imaging techniques develop, the Nova Olinda Member fossil insects offer an ideal opportunity to study insect diversity more accurately.

Additionally, at least 55 specimens representing new taxa across almost every order in the Nova Olinda Member are awaiting description (see Appendices 8. 4.).

6. 4. 4. Taphonomic indexing proxy

A taphonomic indexing system was presented as a by-product of recording taphonomic data. The aim was to create a value that represented the 'average' preservation of each specimen, and would allow for specimens to be sorted and compared by preservational fidelity. However, the index lacked weighting, resulting in potentially unreliable measurements of 'average' preservation. Due to the morphological diversity of insects and the ambiguity of fossil forms, weighting was deemed not possible within the timeframe of this project.

If ultimately it is not possible to appropriately weight a taphonomic index for fossil insects, a proxy could be developed. Setae are fragile surface structures ubiquitous in arthropods that can be preserved in both compressions and three-dimensional fossils (Grimaldi and Engel, 2005; Carlton, 2007; Penney and Jepson, 2014). They could be used as a proxy for measuring overall taphonomy, allowing for a quick comparison between insect fossils from different sites. However, this will preclude the identification of internal labile soft-tissues, which may be particularly important for future fossil insect systematics (see section 6. 4. 3. above).

Consequently, a distinct project centred on calculating appropriate weighting for insect groups and developing a universal taphonomic indexing system, similar to the one presented here, could allow for accurate measurements of morphological and taphonomic characteristics across many Lagerstätten. If achieved, this would undoubtedly be a powerful tool for examining taphonomic trends across time, geography, taxonomy, ecology, sedimentology, etc.

6. 5. Final comments

The Nova Olinda Member fossil insects are indisputably remarkably well-preserved and provide a detailed insight into an array of ancient habitats. Their preservational fidelity is unmatched among non-amber Lagerstätten and their preservational process appears to be a unique combination of otherwise common fabrics. These insects, and the rocks in which they are entombed, are truly worthy of study.

7. References

Abbott, M., 1950. A paleobotanical transfer method. *Journal of Paleontology*, **24**, 619-621.

Abbott, R. E., and Abbott, M. 1952. A simple paleobotanical transfer technique. *Ohio Journal of Science*, **52**, 258-260.

Alexandre, J. T., Gilst, R. I. van, Rodríguez-López, J. P., and Boer, P. L. 2010. The sedimentary expression of oxeanic anoxic event 1b in the North Atlantic. *Sedimentology*, **58**, 1217-1246.

Aller, R. C. 1982. Carbonate dissolution in nearshore terrigenous muds: the role of physical and biological reworking. *The Journal of Geology*, **90**, 79-95.

Allison, P. A. 1986. Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport. *Geology*, **14**, 979-981.

Allison, P. A. 1988a. Konservat-Lagerstätten: Cause and classification. *Paleobiology*, **14**, 331-344.

Allison, P. A. 1988b. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology*, **14**, 139-154.

Allison, P. A. 1988c. Taphonomy of the Eocene London Clay biota. *Palaeontology*, **31**, 1079-1100.

Allison, P. A. 1990. Variation in rate of decay and disarticulation of echinodermata: implications for application of taphonomic data. *Palaios*, **5**, 432-440.

Allison, P. A., and Briggs, D. E. G. 1991a. The taphonomy of soft-bodied animals. *In*. Donovan, S. K. (Ed.). *The Processes of Fossilization*. Columbia University Press, New York, Pp. 303.

Allison, P. A., and Briggs, D. E. G. 1991b. Taphonomy of non-mineralized tissues. *In*. Allison, P. A., Briggs, D. E. G. (Eds.). *Taphonomy: Releasing the data locked in the fossil record*. Plenum Press, New York, 25-70.

Allison, P. A., and Briggs, D. E. G. 1993. Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic. *Geology*, **21**, 527-530.

Anadón, P., Cabrera, L., and Julià, R. 1988. Anoxic-oxic cyclical lacustrine sedimentation in the Miocene Rubielos de Mora Basin, Spain. *Geological Society Special Publications*, **40**, 353-367.

Andrade, J. A. F. G. de. 2007. Commercial exploitation of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Andres, D. 1989. Phosphatisierte Fossilien aus dem unteren Ordoviz von Siidschweden. *Berliner geowissenschaftliche Abhandlungen (A)*, **106**, 9-19.

Andrews, S., Norton, I., Salunkhe, A. S., Goodluck, H., Aly, W. S. M., Mourad-Agha, H. and Cornelis, P. 2013. Chapter 7, Control of Iron Metabolism in Bacteria. *In*. Banci, L. (Ed.). *Metallomics and the Cell*. *Metal Ions in Life Sciences*, *12*, Springer, Pp. 609.

Anonymous. Palaeobiology.si.edu. 2015. [Online] Green River Fossils. [Accessed 22 Dec. 2015]. Smithsonian Museum of Natural History. http://paleobiology.si.edu/greenRiver/

Arai, M. 2000. Chapadas: relicts of mid-Cretaceous interior seas in Brazils. *Revista Brasileira de Geociências*, **30**, 436-438.

Arai, M., Coimbra, J. C. and Silva-Telles, A. C. 2001. Síntese bioestratigráfica da bacia do Araripe (nordeste do Brasil), Pp. 109–117, 122–124. *In.* Barros, L. M., Nuvens, P. C. and Filgueira, J. B. M. (Eds.). *Atas do II Simpósio sobre a bacia do Araripe e bacias interiores do Nordeste*. Comunicações (Coleção Chapada do Araripe number 1). Crato, Ceará State, Brazil: Universidade Regional do Cariri (URCA).

Archibald, S. B., and Rasnitsyn, A. P. 2016. New early Eocene Siricomorpha (Hymenoptera: Symphyta: Pamphiliidae, Siricidae, Cephidae) from the Okanagan Highlands, western North America. *Canadian Entomologist*, **148**, 209-228.

Arillo, A., Peñalver, E., Perez-De, La F., R., Delclòs, X., Criscione, J., Barden, P. M., Riccio, M. L., and Grimaldi, D. A. 2015. Long-proboscid brachyceran flies in Cretaceous amber (Diptera: Stratiomyomorpha: Zhangsolvidae). *Systematic Entomology*, **40**, 242-267.

Arratia, G., Schultze, H.-P., Tischlinger, H., and Viohl, G. 2015. *Solnhofen. A Window into the Jurassic*. [In German] Verlag Dr. F. Pfeil. Pp. 620.

Arrese, E. L., and Soulages, J. L. 2011. Insect Fat Body: energy, metabolism, and regulation. *Annual Review of Entomology*, **55**, 207-225.

Assine, M. L. 1992. Analise estratigrafica da Bacia do Araripe, nordeste do Brasil. *Revista Brasileira de Geociências,* **22**, 289-300.

Assine, M. L. 2007. Araripe basin. *Boletim de Geociencias da Petrobras*, **15**, 371-389.

Aust, K. T. 1972. Principles of crystal growth from the solid state in relation to the preparation of large crystals. *Journal of Crystal Growth*, **13-14**, 57-61.

Báez, A. M., Moura, G. J. B., and Gómez, R. O. 2009. Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians. *Cretaceous Research*, **30**, 829-846.

Báez, A. M. 2013. Anurans from the Early Cretaceous Lagerstätte of Las Hoyas, Spain: New evidence on the Mesozoic diversification of crown-clade Anura. *Cretaceous Research*, **41**, 90-106.

Bagarinao, T. 1994. Systematics, genetics and life history of milkfish, *Chanos chanos*. *Environmental Biology of Fishes*, **39**, 23-41.

Bao, H., Koch, P. L., and Hepple, R. P. 1998. Haematite and calcite coatings on fossil vertebrates. *Journal of Sedimentary Research*, **68**, 727-738.

Barling, N., Heads, S. W., and Martill, D. M. 2013. A new parasitoid wasp (Hymenoptera: Chalcidoidea) from the Lower Cretaceous Crato Formation of Brazil: The first Mesozoic Pteromalidae. *Cretaceous Research*, **45**, 258-264.

Barling, N., Martill, D. M., Heads, S. W., and Gallien, F. 2015. High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research*, **52**, 605-622.

Barreto, A. M. F., Bernardes-de-Oliveira, M. E. C., Dilcher, D. L., Mandarim-de-Lacerda, A. F., and Viana, M. S. S. 2000. Early Cretaceous monocarpelar fruit of the Crato Member, Santana Formation, Araripe Basin, Northeastern Brazil. *Geosciencias,* **5**, 121-124.

Barthel, K. W., Swinburne, N. H. M., and Conway-Morris, S. 1990. *Solnhofen. A Study in Mesozoic Palaeontology*. Cambridge University Press, Cambridge, Pp. 236.

Barthelmy, D. 2015a. [Online] Goethite Mineral Data. *Webmineral.com*. [Accessed 15 Dec. 2015]. http://webmineral.com/data/Goethite.shtml#.VnPO7_mLTIU.

Barthelmy, D. 2015b. [Online] Ferrihydrite Mineral Data. Webmineral.com. [Accessed 15 Dec. 2015]. http://webmineral.com/data/Ferrihydrite.shtml#.VnPV0fmLTIU.

Basibuyuk, H. H., Rasnitsyn, A. P., Fitton, M. G., and Quicke, D. L. J. 2002. The limits of the family Evaniidae (Insects: Hymenoptera) and a new genus from Lebanese Amber. *Insect Systematics and Evolution*, **33**, 23-34.

Bate, R. H. 1972. Phosphatised ostracods with appendages from the Lower Cretaceous of Brazil. *Palaeontology,* **15**, 379-393.

Batten, D. J. 2007. Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 1997a. Die Libellen (und einige andere fossile Insekten) aus der Unterkreide von Brasilien (Santana). *4. Fachgespräch "Fossile Insekten", Clausthal-Zellerfeld*, 28-29 June 1997, Abstracts.

Bechly, G. 1997b. Dragonflies from the Lower Cretaceous of Brazil. *Meganeura,* **1**, 27-28.

Bechly, G. 1997c. Dragonflies from the Lower Cretaceous of Brazil. *Inclusion Wrostek,* **27**, 9.

Bechly, G. 1998a. New fossil dragonflies from the Lower Cretaceous Santana Formation of north-east Brazil (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde, Serie* B, **264**, 1-66.

Bechly, G. 1998b. Santana – Schatzkammer fossiler Insekten. *Fossilien,* **2/98**, 95-99.

Bechly, G. 1998c. Santana – Forschungsgeschichte und Fauna. *Fossilien,* **3/98,** 148-156.

Bechly, G. 1998d. New fossil dragonflies from the Lower Cretaceous Crato Formation of north-east Brazil (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde, Serie B,* **264**, 1-66.

Bechly, G. 2007a. Odonata: damselflies and dragonflies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2007b. 'Blattaria': cockroaches and roachoids. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2007c. Isoptera: Termites. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2007d. Chresmododea: fossil 'water striders'. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2007e. Mecoptera: scorpionflies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2007f. Trichoptera and Lepidoptera: caddisflies and butterflies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G., and Szwedo, J. 2007. Coleorrhyncha: moss bugs. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Bechly, G. 2010. Additions to the fossil dragonfly fauna from the Lower Cretaceous Crato Formation of Brazil (Insecta: Odonata). *Palaeodiversity*, **3**, 11-77.

Bechly, G., and Makarkin, V. N. 2016. A new gigantic lacewing species (Insecta: Neuroptera) from the Lower Cretaceous of Brazil confirms the occurrence of Kalligrammatidae in the Americas. *Cretaceous Research*, **58**, 135-140.

Behrensmeyer, A. K., Kidwell, S. M., and Gastaldo, R. A. 2000. Taphonomy and paleobiology. *Paleobiology*, **26**, 103-147.

Bender, J., and Phillips, P. 2004. Microbial mats for multiple applications in aquaculture and bioremediation. *Bioresource Technology*, **94**, 229-238.

Benton, M. J., Zhou, Z., Orr, P. J., Zhang, F., and Kearns, S. L. 2008. The remarkable fossils frm the Early Cretaceous Jehol Biota of China and how they have changed our knowledge of Mesozoic life. *Proceedings of the Geologists' Association*, **119**, 209-228.

Bernardes-de-Oliveira, M. E. C., Lima, M. R., and Pons, D. 1993. Folhas de Araucariaceae da Formaçao Santana, Cretáceo do Nordeste do Brasil. *Anais Academia Brasileira de Ciencias,* **65**, 329-330.

Berner, R. A. 1964. Iron sulfides formed from aqueous solution at low temperatures and atmospheric pressure. *Journal of Geology*, **72**, 293-306.

Berner, R. A. 1967. Diagenesis of iron sulfide in recent marine sediments. *In*. Lauff, G. (Ed.). Estuaries. *American Association for the Advancement of Science*, **83**, 268-272.

Berner, R. A. 1968. Calcium Carbonate Concretions Formed by the Decomposition of Organic Matter. *Science*, **159**, 195-197.

Berner, R. A. 1969. The synthesis of framboidal pyrite. *Economic Geology*, **64**, 383-384.

Berner, R. A. 1970. Sedimentary Pyrite Formation. *American Journal of Science*, **268**, 1-23.

Berner, R. A. 1981. Authigenic mineral formation resulting from organic matter decomposition in modern sediments. *Fortschritte der Mineralogie*, **59**, 117-135.

Berthou, P.-Y. 1994. Critical analysis of the main publications about the stratigraphical framework of the Paleozoic and Mesozoic sedimentary deposits in the Araripe Basin (northeastern Brazil). *Boletim do 3^0 Simpósio sobre o Cretácico do Brasil (1994). UNESP – Campus de Rio Claro/SP*, Pp. 123-126.

Beurlen, G. 1994. Critical analysis of the main publications about the stratigraphical framework of the Paleozoic and Mesozoic sedimentary deposits in the Araripe Basin (northeastern Brazil). *Boletim do 3o Simpósio sobre o Cretácico do Brasil. UNESP – Campus de Rio Claro/SP*, 123-126.

Beurlen, K. 1963. Geologia e estratigrafia da Chapada do Araripe. *17◦ Congresso Brasiliera de Geologia, Recife*, 1-47.

Beurlen, K. 1971. As condiçoes ecologicas e faciologicas da Formaçao Santana na Chapada do Araripe (nordeste Brasil). *Anais da Academia Brasileira de Ciências,* **43**, 411-415.

Beutel, R. G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof, B., Whiting, M. F., and Vilhelmsen, L. 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Clasdistics*, **27**, 341-355.

Boggs, S. 2006. *Principles of Sedimentology and Stratigraphy* (4^{th} Ed). Pearson Education, Pp. 662.

Bonfim, F. C. 2002. Phylogenetic position of *Tijubina pontei* Bonfim and Marques, 1997 (Lepidosauria, Squamata) a basal lizard from the Santana Formation, Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology,* **22(3)**, 37A.

Boyero, L., Cardinale, B. J., Bastian, M., and Pearson, R. G. 2014. Biotic vs. Abiotic Control of Decomposition: A Comparison of the Effects of Simulated Extinctions and Changes in Temperature. *PLoS One*, **9(1)**, e87426.

Bradley, W. H. 1929. Varves and climate of the Green River Epoch. *U.S. Geological Survey Professional Paper*, **158**, 87-110.

Bradley, W. H. 1948. Liminology and the Eocene lakes of the Rocky Mountain Region. *Geological Society of America Bulletin*, **59**, 635-648.

Brandao, C. R. F., Martins-Neto, R. G., and Vulcano, M. A. 1989. The earliest known fossil ant (First southern hemisphere Mesozoic record) (Hymenoptera: Formicidae: Myrmeciinae). *Psyche,* **96**, 195-208.

Brett, C. E., and Thomka, J. R. 2013. *Fossils and Fossilisation*. eLS: Citable Reviews in the life Sciences, Pp. 12.

Briggs, D. E. G., Bottrell, S. H., and Raiswell, R. 1991. Pyritization of soft-bodied fossils: Beechers Trilobite Bed, Upper Ordovician, New York State. *Geology*, **19**, 1221-1224.

Briggs, D. E. G., and Kear, A. J. 1993a. Decay and preservation of polychaetes: taphonomic thresholds in soft-bodied organisms. *Paleobiology*, **19**, 107-135.

Briggs, D. E. G., and Kear, A. J. 1993b. Fossilization of soft-tissue in the laboratory. *Science*, **259**, 1439-1442.

Briggs, D. E. G., Kear, A. J., Martill, D. M., and Wilby, P. R. 1993. Phosphatization of soft-tissue in experiments and fossils. *Journal of the Geological Society of London*, **150**, 1035-1038.

Briggs, D. E. G., and Kear, A. J., 1994a. Decay of the lancelet *Branchiostoma lanceolatum* (Cephalochordata): implications for the interpretation of soft-tissue preservation in conodonts and other primitive chordates. Lethaia, **26**, 275-287.

Briggs, D. E. G., and Kear, A. J., 1994b. Decay and mineralization of shrimps. *PALAIOS*, **9**, 431-456.

Briggs, D. E. G. 1995a. Preservation of soft-tissues in the fossil record. *Eclogae Geology Helvetiae*, **88**, 623-625.

Briggs, D. E. G. 1995b. Experimental taphonomy. *Palaios*, **10,** 539-550.

Briggs, D. E. G., Wilby, P. R., Bernardino, P., Perez-Moreno, B. P., Sanz, J. L., and Fregenal-Martinez, M. A. 1997. The mineralisation of dinosaur soft tissue in the Lower Cretaceous of Las Hoyas, Spain. *Journal of the Geological Society*, **154**, 587-588.

Briggs, D. E. G. 1999. Molecular taphonomy of animal and plant cuticles: Selective preservation and diagenesis. *Philosophical Transactions B of the Royal Society Publishing*, **354**, 7-16.

Briggs, D. E. G., and Crowther, P. R. 2001. *Palaeobiology II*. Blackwell, Oxford, Pp. 583.

Briggs, D. E. G. 2003a. The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Science*, **31**, 275-301.

Briggs, D. E. G. 2003b. The role of biofilms in the fossilization of non-biomineralized tissues. *In*. Krumbein, W. E., Paterson, D. M., and Zarvarzin, G. A. (Eds.). *Fossil and Recent Biofilms*. Kluwer Academic Publishers, 281-290.

Briggs, D. E. G., and McMahon, S. 2016. The role of experiments in investigating the taphonomy of exceptional preservation. *Palaeontology*, **59(1)**, 1-11.

Briscoe, A. D. 2008. Reconstructing the ancestral butterfly eye: focus on the opsins. *Journal of Experimental Biology*, **211**, 1805-1813.

Brito I. M. 1984. Nota preliminar sobre os insetos de Formaçao Santana, Cretaceo interior da Chapada do Araripe. *Annual XXXIII Congresso Brasileiro de Geologia, Rio de Janeiro*, (***33***), 530-535.

Brito, P. M. 2007. The Crato Formation fish fauna. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Brito, P. M., Yabumoto, Y., and Grande, L. 2008. New Amiid fish (Halecomorphi: Amiiformes) from the Lower Cretaceous Crato Formation, Atatipe Basin, Northeast Brazil. Journal of Vertebrate *Paleontology*, **28**, 1007-1014.

Brock, F. R., Parkes, J., and Briggs, D. E. G. 2006. Experimental Pyrite formation associated with decay of plant material. *PALAIOS*, **21**, 499-506.

Brown, R. W. 1941. The comb of a wasp nest from the upper Cretaceous of Utah. *American Journal of Science,* **239**, 54-56.

Buatois, L. A., Mangano, M. G., Fregenal-Martinez, M. A., de and Gibert, J. M. 2000. Short-term colonization trace-fossil assemblages in a carbonate lacustrine Konservat-Lagerstätte (Las Hoyas fossil site, Lower Cretaceous, Cuenca, central Spain). *Facies*, **43**, 145-156.

Buchheim, H. P. 1994. Paleoenvironments, lithofacies and varves of the Fossil Butte Member of the Eocene Green River Formation, southwestern Wyoming. *Contributions to Geology*, **30**, 3-14.

Buchheim, H. P., and Surdam, R. C. 1997. Fossil catfish and the depositional environment of the Green River Formation, Wyoming. *Geology*, **5**, 196-198.

Buchheim, H. P., and Eugster, H. P. 1998. Eocene Fossil Lake: The Green River Formation of Fossil Basin, southwestern Wyoming. *In*. Pitman, J. K., and Carroll A. R. (Eds.). *Modern and ancient lake systems; new problems and perspectives*. Utah Geological Association (26), Utah, Pp. 328.

Buchheim, H. P., Cushman, R. A., and Biaggi, R. E. 2011. Stratigraphic revision of the Green River Formation in Fossil Basin, Wyoming. *Rocky Mountain Geology*, **46**, 165-181.

Bunch, A. 2009. The impact of cold climate on the decomposition process. *Journal of Forensic Identification*, **59**, 26-44.

Buscalioni, A. D., and Fregenal-Martínez, M. A. 2010. A holistic approach to the palaeoecology of Las Hoyas Konservat-Lagerstatte (La Huéhuina Formation, Lower Cretaceous, Iberian Ranges, Spain). *Journal of Iberian Geology*, **36**, 297-326.

Butler, I. B., and Rickard, D. 2000. Framboidal pyrite formation via the oxidation of iron (II) monosulphide by hydrogen sulphide. *Geochimica et Cosmochimica Acta*, **64**, 2665-2672.

Butts, S. H. 2014. Silicification. *In*. Laflamme, M., Scgiffbauer, J. D., and Darroch, S. A. F. (Eds). *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization*. The Paleontological Society Papers, Volume 20.

Cai, Y. P., and Hua, H. 2007. Pyritization in the Gaojiashan Biota. *Chinese Science Bulletin*, **52**, 645-650.

Campos, D. R. B. 1986. Primeiro registro fossil de Scorpionidae na Chapada do Araripe (Cretáceo Inferior), Brasil. *Anais Academia brasileira, Ciencias* **58**, 135-137.

Campos, D. A. and Kellner, A. W. A. 1996. An unusual crested pterosaur from the Early Cretaceous of Brazil. *Journal of Vertebrate Paleontology,* **16**, 25A.

Campos, D. A. and Kellner, A. W. A. 1997. Short note on the first occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. *Anais da Academia Brasileira de Ciências,* **69**, 83-87.

Canfield, D. E., and Raiswell, R. 1991. Pyrite formation and fossil preservation. *In*. Allison, P. A., and Briggs, D. E. G. (Eds.). *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, 337-387.

Capinera, J. L. 2008. *Encyclopaedia of Entomology*. Springer Science & Business Media. Pp. 4346.

Cardarelli, F. 2008. *Materials Handbook: A Concise Desktop Reference*. Springer Science & Business Media, Pp. 640.

Carlton, J. T. 2007. *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon, Completely Revised and Expanded*. University of California Press, California, Pp. 1019.

Carmo, D. A., Rafael, R. M. L., Vilhena, R. M., and Tomassic, H. Z. 2004. Redescription of *Theriosynoecum silvai* and *Darwinula martinsi*, Crato Member (Santana Formation), Lower Cretaceous, Araripe Basin, NE Brazil. *Revista Brasileira de Paleontologia,* **7**, 151-158.

Carpenter, E. M. 1932. Jurassic insects from Solnhofen in the Carnegie Museum and the Museum of Comparative Zoology. *Annals of the Carnegie Museum*, **21**, 97-129.

Carpenter, J. M., and Rasnitsyn, A. P. 1990. Mesozoic Vespidae. *Psyche,* **97**, 1-20.

Carvalho, I. de S. and Viana, M. S. S. 1993. Os conchostráceos da Bacia do Araripe. *Anais da Academia Brasileira de Ciências,* **65**, 181-888.

Carvalho, M. G. P. de, and Lourenço, W. R. 2001. A new family of fossil scorpions from the Early Cretaceous of Brazil. *Comptes rendu de l'Acadèmie des Sciences Paris, Sciences de la Terre et des planets,* **332,** 711-716.

Carvalho, I. de S., Novas, F. E., Agnolín, F. L., Isasi, M. P., Freitas, F. I., and Andrade, J. A. 2015. A Mesozoic bird from Gondwana preserving feathers. *Nature Communications*, **6**, 7141.

Catto, B., Jahnert, R. J., Warren, L. V., Varejao, F. G., and Assine, M. L. 2016. The microbial nature of laminated limestones: Lessons from the Upper Aptian, Araripe Basin, Brazil. *Sedimentary Geology*, **341**, 304-315.

CFAMM. 2018. [Online] Central Facility for Advanced Microscopy and Microanalysis. *Concise introductory texts to the principles of electron microscopy and e-beam microanalysis: 3, Introduction to Energy Dispersive X-ray Spectroscopy (EDX) of bulk specimens*. University of California, Riverside. [Accessed 30th May 2018] https://cfamm.ucr.edu/documents/eds-intro.pdf

Chang, H. K., Kowsmann, R. O. and Figueiredo, A. M. F. 1988. New concepts on the development of East Brazilian Marginal Basins. *Episodes*, **11**, 194-202.

Chang, M.-M., Chen, P.-J., Wang, Y.-Q., Wang, Y., and Miao, D.-S. 2007. *The Jehol Fossils: The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*. Academic Press, London, Pp. 208.

Chen, P., Wang, Q., Zhang, H., Cao, M., Li, W., Wu, S., and Shen, Y. 2004. Jianshangou Bed of the Yixian Formation in West Liaoning, China. *Science in China Series D: Earth Sciences*, **48**, 298-312.

Chen, X., Wang, W., Shang, Q., Lou, Y., Liu, X., Cao, C., and Wang, Y. 2009. Experimental evidence for eukaryotic fossil preservation: Onion skin cells in silica solution. *Precambrian Research*, **170**, 223-230.

Chester, R., and Jickells, T. D. 2012. *Marine Geochemistry (Third Edition)*. Wiley-Blackwell, Pp. 420.

Chumakov, N. M., Zharkov, M. A. Herman A. B., Doludenko, M. P., Kalandadze, N. M., Lebedev, E. L., Ponomarenko, A. G., and Rautian, A. S. 1995. Climatic belts of the mid-Cretaceous time. *Stratigraphy and Geological Correlation*, **3**, 241-260.

Clarkson, E. N. K. 1998. *Invertebrate Palaeontology and Evolution (Fourth Edition)*. Blackwell Publishing, Oxford, Pp. 452.

Coiffard, C., Mohr, B. A. R., and Bernardes-de-Oliveire, M. E. C. 2013. The Early Cretaceous Aroid, *Spixiarum kipea* gen. et sp. nov., and implications on early dispersal and ecology of basal monocots. *Taxon*, **62**, 997-1008.

Coiffard, C., Mohr, B. A. R., and Bernardes-de-Oliveira, M. E. C. 2014. *Hexagyne philippiana* gen. et sp. nov., a piperalean angiosperm from the Early Cretaceous of northern Gondwana (Crato Formation, Brazil). *Taxon*, **63**, 1275-1286.

Coimbra, J. C., Arai, M., and Careño, A. L. 2002. Biostratigraphy of Lower Cretaceous microfossils from the Araripe Basin, north-eastern Brazil. *Geobios*, **35**, 687-698.

Corbet, P. S., and Brooks, S. 2008. *Dragonflies: New Naturalist Series*. Harper-Collins, London. Pp. 312.

Crane, P. R. 1991. Fossil plants. *In* Maisey, J. G. (Ed.). S*antana Fossils: an Illustrated Atlas*. Neptune City, T.F.H. Publications Inc., Pp 459.

Cridland, A. A., and Williams, J. L. 1966. Plastic and epoxy transfers of fossil plant compressions. *Bulletin of the Torrey Botanical Club*, **5**, 311-322.

Crowley, K. D., Duchon, C. E., and Rhi, J. 1986. Climate record in varved sediments of the Eocene Green River Formation. *Journal of Geophysical Research*, **91**, 8637-8647.

Cudennec, Y., and Lecerf, A. 2006. The transformation of ferrihydrite into goethite or hematite, revisited. *Journal of Solid State Chemistry*, **179**, 716-722.

Cullen, T. M., and Evans, D. C. 2016. Palaeoenvironmental drivers of vertebrate community composition in the Belly River Group (Campanian) of Alberta, Canada, with implications for dinosaur biogeography. *Biomedical Central Ecology*, **16:52**, 1-16.

Cutrale, F., Trivedi, V., Trinh, L. A., Chiu, C.-L., Choi, J. M., Artiga, M. S., and Fraser, S. E. 2017. Hyperspectral phasor analysis enables multiplexed 5D in vivo imaging. *Nature Methods*, **14**, 149-152. Doi:10.1038/nmeth.4134

Darling, D. C., and Sharkey, M. J. 1990. Order Hymenoptera. *In* Grimaldi, D. A. (Ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History, Pp. 195.

Darroch, S. A. F., LaFlamme, M., Schiffbauer, J. D., and Briggs, D. E. G. 2012. Experimental formation of a microbial death mask. *PALAIOS*, **27**, 293-303.

Davis, S. P., and Martill, D. M. 2003. The Gonorynchiform fish Dastilbe from the Lower Cretaceous of Brazil. *Palaeontology*, **42(4)**, 715-740.

Dayvault, R. D., Codington, L., Kohls, D., Hawes, W., and Ott, P. 1995. Fossil insects and spiders from three locations in the Green River Formation of the Piceance Creek Basin, Colorado. *In*. Averett, W. R. (Ed.). *The Green River Formation in Piceance Creek and Eastern Uinta Basins*. Grand Junction, Grand Junction Geological Society, Pp. 97-115.

de Lima, F. J., Saraiva, A. A. F., da Silva, M. A. P., Bantim, R. A., and Sayão, J. M. 2014. A new angiosperm from the Crato Formation (Araripe Basin, Brazil) and comments on the Early Cretaceous Monocotyledons. *Anais da Academia Brasileira de Ciencia*s, **86**, 1657-1672.

Delgado, A. de O., Buck, P. V., Osés, G. L., Ghilardi, R. P., Rangel, E. C., Pacheco, M. L. A. F. 2014. Paleometry: a brand new area in Brazilian science. *Materials Research*, **17**, 1434-1441.

Depeche, F., Berthou, P.-Y., and Campos, D. de A. 1990. Quelques observations sur les Faunes d'ostracodes du Crétacé du Bassin d'Araripe (NE du Br´esil). *Atlas do I Simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste Crato,* **14 + 16**, 293-308.

Diéguez, M. C., Trincao, P., and Loâ Pez-Moroâ N, N. 1995. Palaeontology. Flora. *In* Meleândez, N. (Ed.). *Las Hoyas. A lacustrine Konservat-Lagerstätte, Cuenca, Spain*. Universidad Complutense de Madrid, Madrid, Pp. 89.

Diéguez, M. C., and Meléndez, N. 2000. Early Cretaceous ferns from lacustrine limestones at Las Hoyas, Cuenca Province, Spain. *Palaeontology*, **43**, 1113-1141.

Dietz, K. 2007. Redescription of Dastilbe Crandalle (Chanidae, Eutelostei) from the early Cretaceous Crato Formation of north-eastern Brazil. *Journal of Vertebrate Paleoutology,* **27**, 8-16.

Ding, O. H., Zhang, L. D., Guo, S. Z., Zhang, C. J., Peng, Y. D., Jia, B., Chen, S. W., and Xian, D. H. 2003. Paleoclimatic and palaeoenvironmental proxies of the Yixian Formation in the Beipiao area, western Liaoning. *Geological Bulletin of China*, **22**, 186-191.

Downen, M. R., and Selden, P. A. 2016. Spider diversity of the Crato Formation, an Early Creatceous Fossil-Lagerstätte of northeastern Brazil. *Geological Society of America Abstracts with Programs*, **48**, 7.

Downen, M. R., Selden, P. a., and Hasiotis, S. T. 2016. Spider leg flexure as an indicator of salinity in lacustrine palaeoenvironment. *Palaeogrography, Palaeoclimatology, Palaeoecology*, **445**, 115-123.

Duarte, L. 1985. Vegetais fósseis da Chapada do Araripe, Brasil. *Coletânea de Trabalhos Paleontológicos do VIII Congresso Brasileiro de Paleontologia 1983, Sárie Geologia 27, Seçäo Paleontologia e Estatigrafia 2, Brasilia*, **2**, 557–563.

Duarte, L. 1993. Restos de Araucariaceas da Formação Santana – Membro Crato (Aptiano), NE do Brasil. *Anais Academia Brasileira, Ciencias,* **65**, 357-362.

Duncan, I. J., Briggs, D. E. G., and Archer, M. 1998. Three-dimensionally mineralized insects and millipedes from the Tertiary of Riversleigh, Queensland, Australia. *Palaeontology*, **41**, 835-851.

Duncan, I. J., Titchener, F., and Briggs, D. E. G. 2003. Decay and disarticulation of the cockroach: Implications for the preservation of the blattoids of Writhlington (Upper Carboniferous), UK. *Palaios*, **18**, 256-265.

Dunlop, J. A. 1996. Arácnidos fósiles (con exclusíon de arãnas y escorpiones). *Boletin de la Sociedad Entomologica Aragonesa, PaleoEntomologica,* **16**, 77-92.

Dunlop, J. A. 1998. A fossil whipscorpion from the Lower Cretaceous of Brazil. *Journal of Arachnology,* **26**, 291-295.

Dunlop, J. A., and Martill, D. M. 2002. The first whipspider (Arachnida: Amblypygi) and three new whipscorpions (Arachnida: Thelyphonida) from the Lower Cretaceous Crato Formation of Brazil. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **92**, 325-334.

Dunlop, J. A., and Martill, D. M. 2004. Four additional specimens of the fossil camel spider *Cratosolpuga wunderlichi* Selden 1996 from the Lower Cretaceous Crato Formation of Brazil. *Revista Ibérica de Arachnología,* **9**, 143-156.

Dunlop, J. A. 2007. A large parasitengonid mite (Acari, Erythraeoidea) from the Early Cretaceous Crato Formation of Brazil. *Fossil Record,* **10**, 91-98.

Dunlop, J. A., Menon, F., and Selden, P. A. 2007. Arachnida: spiders, scorpions and allies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Efremov, J. A. 1940. Taphonomy: new branch of paleontology. *Pan American Geologist*, **74**, 81-93.

Efremov, J. A. 1950. Taphonomy and the geological record. *Trudy Paleontologicheskogo Instituta* Akademii Nauk *SSSR*, **24**, 1-177.

Elder, R. L., and Smith, G. R. 1988. Fish taphonomy and environmental inference in Paleolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **62**, 577-592.

Elgin, R. A., and Frey, E. 2012. A nearly complete ornithocheirid pterosaur from the Aptian (Early Cretaceous) Crato Formation of NE Brazil. *Acta Palaeontologica Polonica*, **57**, 101-110.

Engel, M. S., and Chatzimanolis, S. 2005. Early Cretaceous earwigs (Dermaptera) from the Sanatana Formation, Brazil. *Polskie Pismo Entomologiczne,* **74**, 219-226.

Engel, M. S., and Peñalver, E. 2006. A Miocene Halictine Bee from Rubielos de Mora Basin, Spain (Hymenoptera: Halictidae). *American Museum Novitates*, **3503**, 1-10.

Eriksson, M., Terfelt, F., Elofsson, R., and Marone, F. 2012. Internal Soft-Tissue Anatomy of Cambrian 'Orsten' Arthropods as revealed by Synchrotron X-Ray Tomographic Microscopy. *PLoS ONE*, **7(8)**, e42582.

Escapa, I. H., Axsmith, B. J., Taylor, T. N., and Taylor, E. L. 2010. Modifications of the transfer technique for studying complex plant structures. *Review of Paleobotany and Palynology*, **159**, 62-68.

Etter, W., and Kuhn, O. 2000. An articulated dragonfly (Insecta, Odonata) from the Upper Liassic Posidonia Shale of northern Switzerland. *Palaeontology*, **43**, 967-977.

Evamy, B. D. 1963. The application of a chemical staining technique to a study of dedolomitisation. *Sedimentology*, **2**, 164-170.

Evans, S. E., and Yabumoto, Y. 1998. A lizard from the Early Cretaceous Crato Formation, Araripe Basin, Brazil. *Neues Jahrbuch für Geologie und Pal¨aontologie, Monatsefte*, **6**, 349-364.

Evenhuis, N. L. 1994. *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*. Leiden, Backhuys, Pp. 600.

Fang, Y., Wang, B., Zhang, H., Wang, H., Jarzembowski, E. A., Zheng, D., Zhang, Q., Li, S., and Liu, Q. 2015. New Cretaceous Elcanidae from China and Myanmar (Insecta, Orthoptera). *Cretaceous Research*, **52**, 323-328.

Farache, F. H. A., Rasplus, J.-Y., Azar, D., Pereira, R. A. S., and Compton, S. G. 2016. First record of a non-pollinating fig wasp (Hymenoptera: Sycophaginae) from Dominican amber, with estimation of the size of its host figs. *Journal of Natural History*, **50**, 35-36.

Farrand, M. 1970 Framboidal sulphides precipitated synthetically. *Mineralium Deposita*, **5**, 237-247.

Farrell, Ú. C., and Briggs, D. E. 2008. Pyritized olenid trilobite faunas of upstate NY: Palaeoecology and taphonomy. *In.* Cusack, M., Owen, A., and Clark, N. (Eds). *Programme with Abstracts*, *Palaeontological Association Annual Meeting, 2008,* **52**, Glasgow, UK.

Farrell, Ú. C., Martin, M. J., Hagadorn, J. W., Whiteley, T., and Briggs, D. E. G. 2009. Beyond Beecher's Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician Taconic foreland basin. *Geology*, **37**, 907-910.

Ferber, C. T., and Wells, N. A. 1995. Paleolimnology and taphonomy of some fish deposits in "Fossil" and "Uinta" Lakes of the Eocene Green River Formation, Utah and Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **117**, 185-210.

Fielding, S., Martill, D. M., and Naish, D. 2005. Solnhofen-style soft-tissue preservation in a new species of turtle from the Crato Formation (Early Cretaceous, Aptian) of north-east Brazil. *Palaeontology*, **48**, 1301-1310.

Figueiredo, R. G., and Kellner, A. W. A. 2009. A new crocodylomorph specimen from the Araripe Basin (Crato Member, Santana Formation), northeastern Brazil. *Palaeontologische Zeitschrift*, **83**, 323-331.

Figueiredo, R. G., Saraiva, A. A. F., Moreira, J. K., and Kellner, A. W. A. 2009. New susisuchid remains from the Crato Formation (Santana Group, Araripe Basin) northeastern Brazil. *Journal of Vertebrate Paleontology*, **29**, 95A-95A.

Figueiredo, R. G., Moreira, J. K. R., Saraiva, A. A. F., and Kellner, A. W. A. 2011. Description of a new specimen of Susisuchus anatoceps (Crocodylomorpha: Mesoeucrocodylia) from the Crato Formation (Santana Group) with comments on Neosuchia. *Zoological Journal of the Linnean*, **163**, S273-S288.

Filshie B. K. 1980. Insect cuticle though the electron microscope - distinguishing fact from artifact. *Insect Biology in the Future*, 59-77.

Fischer, A. G., and Roberts, L. T. 1991. Cyclicity in the Green River Formation (lacustrine Eocene) of Wyoming. *Journal of Sedimentary Research*, **61**, 1146-115.

Foos, A., and Hannibal, J. 1999. *Geology of the Florissant Fossil Beds National Monument*. Field Guide, Pp. 9.

Forbes, S. L. 2008. Decomposition Chemistry in a Burial Environment. *In*. Tibbett, M., and Carter, D. O. (Eds.). Soil Analysis in Forensic Taphonomy. CRC Press, Pp. 364.

Fowler, A. C., and Yang, X. S. 2003. Dissolution/precipitation mechanisms for diagenesis in sedimentary basins. *Journal of Geophysical Research*, **108**, B10.

Frey, E., and Martill, D. M. 1994. A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. *Neues Jahrbuch für Geologie und Paläontologie Abhandlung,* **194**, 379-412.

Frey, E., and Tischlinger, H. 2000. Weichteilanatomie der Flugsaurierfuße und Bau der Scheitelkämme: Neue Pterosaurierfunde aus den Solnhofener Schichten (Bayern) und der Crato-Formation (Brasilien). *Archaeopteryx*, **18**, 1-16.

Frey, E., Martill, D. M., and Buchy, M.-C. 2003a. A new species of tapejarid pterosaur with soft-tissue head crest. *In.* Buffetaut, E., and Mazin, J.-M. (Eds.). *Evolution and Palaeobiology of Pterosaurs*. Geological Society of London, Special Publication, **217**.

Frey, E., Martill, D. M., and Buchy, M.-C. 2003b. A new crested ornithocheirid from the Lower Cretaceous of northeast Brazil and the unusual death of an unusual pterosaur. *In.* Buffetaut, E., and Mazin, J.-M. (Eds.). *Evolution and Palaeobiology of Pterosaurs*. Geological Society of London, Special Publication, **217**.

Frey, E., Tischlinger, H., Buchy, M.-C., and Martill, D. M. 2003c. New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. *In.* Buffetaut, E., and Mazin, J.-M. (Eds.). *Evolution and Palaeobiology of Pterosaurs*. Geological Society of London, Special Publication, **217**.

Frey, E., and Salisbury, S. W. 2007. Crocodilians of the Crato Formation: evidence for enigmatic species. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Froehlich, D. J., and Breithaupt, B. H. 1998. Mammals from the Eocene epoch Fossil Butte Member of the Green River Formation, Fossil Basin, Wyoming. *Journal of Vertebrate Paleontology*, **18**, 43A.

Froelicher, P. N., Klinkhammer, G. P., Bender, M. L., Luedtke, N. A., Heath, G. R., Cullen, D., Dauphin, P., Hammond, D., Hartman, B., and Maynard, V. 1979. Early oxidation of organic

matter in pelagic sediments of the eastern equatorial Atlantic: Suboxic diagenesis. *Geochimica et Cosmochimica Acta*, **43**, 1075-1090.

Fürsich, F. T., Sha, J., Jiang, B., and Pan, Y. 2007. High resolution palaeoecological and taphonomic analysis of Early Cretaceous lake biota, western Liaoning (NE-China). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **253**, 434-457.

Gall, J.-C. 1990. Les voiles microbiens, Leur contribution á la fossilisation des organismes de corp mou. *Lethaia*, **23**, 21-28.

Gall, J.-C., Duringer, P. H., Krumbein, W., and Paicheler, J.C. 1994. Impact des écosystèmes microbiens sur la sédimentation. *Palaeogeography, Palaeoclimatology, and Palaeoecology*, **111**, 17-28.

Gall, J.-C. 1995. Biofilms et mattes microbiennes; leur contribution á la sédimentogenése. *Comptes Rendus Academic Sciences, Paris, séries IIa,* **321**, 823-835.

Gao, K., and Ren, D. 2006. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Beds. *Acta Geologica Sinica English Edition*, **80**, 42-45.

Garm, A. 2004. Revising the definition of the crustacean seta and setal classification systems based on examinations of the mouthpart setae of seven species of decapod. *Zoological Journal of the Linnean Society*, **142**, 233-252.

Gaston, K. J. 1991. The magnitude of global insect species richness. *Conservation Biology*, **5**, 283-296.

Gibson, G. A. P. 2008. Description of Leptoomus janzeni gen. n. and sp. n. (Hymenoptera: Chalcidoidea) from Baltic amber, and discussion of its relationships and classification relative to Eupelmidae, Tanaostigmatidae and Encyrtidae. *Zootaxa*, **1730**, 1-26.

Gobbo-Rodrigues, S. R., do Carmo, D. A., Vilhena, R. M., and Rafael, R. M. L. 2005. *Candona* sp., a limnic ostracod from the Santana Formation (Lower Cretaceous), Araripe basin, NE-Brazil: palaeoecology and biostratigrahic implications. *In 15th International Symposium on Ostracoda*, 2005, Berlin. *Berliner Paläobiologische Abhandlungen,* **6**, 8.

Goldstein, J. I., Newbury, D. E., Joy, D. C., Lyman, C. E., Echlin, P., Lifshin, E., Sawyer, L., Michael, J. R. 2007. *Scanning Electron Microscopy and X-ray Microanalysis, 3rd Edition*. Springer, Pp. 689.

Gonzalez-Davila, M., and Millero, F. J. 1990. The absorption of copper to chitin in seawater. *Geochim Cosmochim Acta*, **54**, 761-768.

Goodwyn, P. J. P. 2002. A new genus of water measurer from the Lower Cretaceous Crato Formation in Brazil (Insecta: Heteroptera: Gerromorpha: Hydrometridae). *Stuttgarter Beiträge Naturkunde, Serie B,* **316**, 1-9.

Gower, J. C. 2005. Principal Coordinates analysis. *In*. Armitage, P., and Colton, T. (Eds.). *Encyclopaedia of Biostatistics*. Wiley Publishing, Milton Keynes, Pp. 6100.

Graham, M., and Allington-Jones, L. 2015. Challenges encountered during acid resin transfer preparation of fossil fish from Monte Bolca, Italy. *Palaeontologia Electronica*, **18.2.4T**, 1–9.

Grande, L. 1984. Palaeontology of the Green River Formation, with a review of the fish fauna. 2nd Edition. *Geological Survey of Wyoming Bulletin*, **63**, 1-333.

Grande, L., and Buchheim, H. P. 1994. Paleontological and sedimentological variation in Early Eocene Fossil Lake. *Contributions to Geology*, **30(2)**, 33-56.

Green, O. R. 2001. *A Manual of Practical Laboratory and Field Techniques in Palaeobiology*. Springer, Pp. 556.

Grimaldi, D. A. 1990. *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History 195*,* New York, Pp*.* 191**.**

Grimaldi, D. A., and Maisey, J. G. 1990. Introduction. *In*. Grimaldi, D. A. (Ed.) *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History, Pp. 195.

Grimaldi, D. A., and Engel, M. S. 2005. *Evolution of the Insects*. Cambridge, Cambridge University Press, Pp. 755.

Grimaldi, D. A. 2007. Mantodea: praying mantises. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Grissell, E. E. 1980. New Torymidae from Tertiary amber of the Dominicane Republic and a world list of fossil Torymids (Hymenoptera, Chalcidoidea). *Proceedings of the Entomological Society of Washington*, **82**, 252-259.

Haas, F. 2007. Dermaptera: earwigs. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Hammer, Ø., and Harper, D. A. T. 2006. *Paleontological Data Analysis*. Blackwell Publishing, Oxford, Pp. 351.

Hammer, Ø. 2017. PAleontological STatistics version 3.16 Reference Manual. [Online] https://folk.uio.no/ohammer/past/past3manual.pdf [Accessed 18 Sept 2017].

Harding, I. C., and Chant, I. C. 2000. Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant lake beds, Colorado, United States. *Geology*, **28**, 195-198.

Hart, L. A., Bowker, M. B., Tarboton, W., and Downs, C. T. 2014. Species composition, distribution and habitat types of Odonata in the iSimangaliso Wetland Park, KwaZulu-Natal, South Africa and the associated conservation implications. *PLoS One*, **9**, e92588.

Harvey, M. S. 2002. The neglected cousins: what do we know about the smaller arachnid orders. *Journal of Arachnology,* **30**, 357-372.

Harvey, M. S. 2003. *Catalogue of the smaller arachnid orders of the world*. Collingwood, CSIRO Publishing, Pp. 385.

Hass, F., Gorb, S., and Wootton, R. J. 2000. Elastic joints in dermapteran hind wings: Materials and wing folding. *Arthropod Structure and Development*, **29**, 137-146.

Heads, S. W., Martill D. M., and Loveridge, R. F. 2005. An exceptionally preserved antlion (Insecta, Neuroptera) with colour pattern preservation from the Cretaceous of Brazil. *Palaeontology*, **48**, 1409-1417.

Heads, W. S., and Martins-Neto, R. G. 2007. Orthopteridae: grasshoppers, crickets, locusts and stick insects. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Heads, S. W., and Leuzinger, L. 2011. On the placement of the Cretaceous orthopteran Brauckmannia groeningae from Brazil, with notes on the relationships of Schizodactylidae (Orthoptera, Ensifera). *Zookeys*, **77**, 17-30.

Heimhofer, U., and Martill, D. M. 2007. The sedimentology and depositional environment of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S. P., Martill, D. M., and Riso-Netto, A. M. 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-eastern Brazil). *Sedimentology*, **57**, 677-694.

Hellawell, J., and Orr, P. J. 2012. Deciphering taphonomic processes in the Eocene Green River Formation of Wyoming. *Palaeobiodiversity and Palaeoenvironments*, **93**, 353-365.

Henning, J. T. 2011. *Taphonomy of Insects from the Florissant Formation, Colorado*. University of Colorado, Masters Thesis. Pp. 43.

Henning, J. T., Smith, D. M., Nufio, C. R., and Meyer, H. W. 2012. Depositional setting and fossil insect preservation; a study of the Late Eocene Florissant Formation, Colorado. *PALAIOS*, **27**, 481-488.

Henrichs, S. M. 1992. Early Diagenesis of organic matter in marine sediments: progress and perplexity. *Marine Chemistry*, **39**, 119-149.

Heraty, J. M., and Darling, D.C. 2009. Fossil Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea) from Baltic Amber. *Zootaxa*, **2306**, 1-16.

Hermann, W. 1966. *Ground plan of insects* [German]. Gustav Fischer Publishing House, Stuttgart, Pp. 322.

Hobbs, C. R. B. 1954. Staining methods for differentiating limestones and dolomites. *Virginia Journal of Science*, **5**, 4.

Holliger, C., Wohlfarth, G., and Diekert, G. 1998. Reductive dichlorination in the energy metabolism of anaerobic bacteria. *FEMS Microbiology Reviews*, **22**, 383-398.

Hopkins, T. L., and Kramer, K. J. 1992. Insect Cuticle Sclerotization. *Annual Review of Entomology*, **37**, 273-302.

Huang, D. 2015. *Tarwinia australis* (Siponaptera: Tarwiniidae) from the Lower Cretaceous Koonwarra fossil bed: Morphological revision and analysis of its evolutionary relationship. *Cretaceous Research*, **52**, 507-515.

Hunger, S., and Benning, L. G. 2007. Greigite: a true intermediate on the polysulfide pathway to pyrite. *Geochemical Transactions*, **8**, 1-20.

Jarzembowski, E. A., Yan, E. V., Wang, B., and Zhang, H. C. 2012. A new flying water beetle (Coleoptera: Schizophoridae) from the Jurassic Daohugou lagerstätte. *Palaeoworld,* **21,** 160-166.

Jattiot, R., Bechly, G., Garrouste, R., and Nel, A. 2012. An enigmatic Nepoidea from the Lower Cretaceous of Brazil (Hemiptera: Heteroptera). *Cretaceous Research*, **34**, 344-347.

Jell, P. A., and Duncan, P. M. 1986. Invertebrates, mainly insects, from the freshwater Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *In.* Jell, P. A., and Roberts, J. (Eds.). *Plants and Invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria.* Memoirs of the Association of Australasian Palaeontologists *3*, 205.

Jeong, H. Y., Lee, J. H., and Hayes, K. F. 2008. Characterization of synthetic nanocrystalline mackinwite: crystal structure, particle size, and specific surface area. *Geochim Cosmochim Acta*, **72(2)**, 493-505.

Jepson, J. E., and Heads, S. W. 2016. Fossil Megaloptera (Insecta: Neuropterida) from the Lower Cretaceous Crato Formation of Brazil. *Zootaxa*, **4098**, 134-144.

Jiménez-Moreno, G., Aziz, H. A., Rodrígues-Tovar, F. J., Pardo-Igúzquiza, E., and Suc, J.-P. 2007. Palynological evidence for astronomical forcing in Early Miocene lacustrine deposits from Rubielos de Mora Basic (NE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **252**, 601-616.

Joeckel, R. M., Clement, B. J. A., and Bates, L. R. VF. 2005. Sulfate-mineral crusts from pyrite weathering and acid rock drainage in the Dakota Formation and Graneros Shale, Jefferson County, Nebraska. *Chemical Geology*, **215**, 433-452.

Kairies, C. L., Capo, R. C., and Watzlaf, G. R. 2005. Chemical and physical properties of iron hydroxide precipitates associated with passively treated coal mine drainage in the Bituminous Region of Pennsylvania and Maryland. *Applied Geochemistry*, **20**, 1445-1460.

Kalkman, V. J., Clausnitzer, V., Dijkstra, K.-D. B., Orr, A. G., Paulson, D. R., and van Tol, J. 2008. Global diversity of dragonflies (Odonata) in freshwater. *In*. Balian, E., Martens, K., Lévêque, C., and Segers, H. (Eds.). A global assessment of animal diversity in freshwater. *Hydrobiologia*, **595**, 351-363.

Kapolos, J., and Koutsoukos, P. G. 1999. Formation of Calcium Phosphates in Aqueous Solutions in the Presence of Carbonate Ions. *Langmuir*, **15(19)**, 6557-6562.

Kariithi, H. M., Oers, M. M. van, Valk, J. M., Verysen, M. J. B., Parker, A. G., and Abd-Alla, A. M. M. 2013. Virology, Epidemiology and Pathology of Glossina Hytrosavirus, and Its Control Prospects in Laboratory Colonies of the Tsetse Fly, Glossina pallidipes (Diptera; Glossinidae). *Insects*, **4(3)**, 287-319.

Kellner, A. W. A., and Campos, D. A. 1986. Primeiro registro de amphibia (Anura) do Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. *Anais Academia Brasileira Ciencias,* **58**, 610.

Kellner, A. W. A. 1991. The Santana Formation pterosaurs. Supplementary notes and comments. *In* Maisey, J. G. (Ed.). *Santana Fossils: an Illustrated Atlas*. Neptune City, T.F.H. Publications Inc., Pp 459.

Kellner, A. W. A., Maisey, J. G., and Campos, D. A. 1994. Fossil down feather from the Lower Cretaceous of Brazil. *Palaeontology*, **37**, 489-492.

Kellner, A. W. A. 2002. A review of avian Mesozoic fossil feathers. *In.* Chiappe, L. M., and Witmer, L. M. (Eds.). *Mesozoic Birds: Above the Heads of Dinosaurs*. Berkeley, University of California Press, Pp. 532.

Kemp, R. 2002. Generation of the Solnhofen tetrapod accumulation. *Archaeopteryx*, **19**, 11-28.

Klug, H. P., and Alexander, L. E. 1974. *X-ray diffraction procedures for polycrystalline and amorphous materials* (2nd Edition). Wiley Publishing, New York, Pp 992.

Kosman, D. J. 2003. Molecular mechanisms of iron uptake in fungi. *Molecular Microbiology*, **47**, 1185-1197.

Kribek, B. 1975. The origin of framboidal pyrite as a surface effect of sulphur grains. *Mineralium Deposita*, **10**, 389-396.

Kristensen, N. P. 1981. Phylogeny of insect orders. *Annual Review of Entomology*, **26**, 135-157.

Krogmann, L., and Nel, A. 2012. On the edge of parasitoidism: a new Lower Cretaceous woodwasp forming the putative sister group of Xiphydriidae plus Euhymenoptera. *Systematic Entomology*, **37**, 215-222.

Krömmelbein, K., and Weber, R. 1971. Ostracoden des “Nordost-Brasilianischen Wealden”. *Geologisches Jahrbuch,* **115**, 1-69.

Krzemiński, W., Soszyńska-Maj, A., Bashkuev, A. S., and Kopeć, K. 2015. Revision of the unique Early Cretaceous Mecoptera from Koonwarra (Australia) with description of a new genus and family. *Cretaceous Research*, **52**, 501-506.

Kuhn, O. 1961. Die Tier- und Pflanzenwelt der Solnhofener Schiefers, mit vollständigem Arten- und Schriftenwerzeichnis. *Geologica Bavarica*, **48**, 5-68.

Kühne, W. 1961. Präparation von flachen Wirbeltieren auf künstlicher Matrix. *Paläontologische Zeitschrift*, **35**, 251–252.

Kunzmann, L., Mohr, B. A. R. and Bernardes-de-Oliveira, M. E. C. 2004. Gymnosperms from the Lower Cretaceous Crato Formation (Brazil). I. Araucariaceae and *Lindleycladus* (incertae sedis). *Mitteilungen Museum für Naturkunde Berlin, Geowissenschaften,* **7**, 155-174.

Kunzmann, L., Mohr, B. A. R., and Bernardes-de-Oliveira, M. E. C. 2007. *Novaolindia dubia* gen. et sp. nov., an enigmatic seed plant from the Early Cretaceous of northern Gondwana. *Review of Palaeobotany and Palynology*, **147**, 94-105.

Kunzmann, L., Mohr, B. A. R., and Bernardes-de-Oliveira, M. E. C. 2009. *Cearania heterophylla* gen. et p no., a fossil gymnosperm with affinities to the Gnetales from the Early Cretaceous of northern Gondwana. *Review of Palaeobotany and Palynology*, **158**, 193-212.

Kunzmann, L., Mohr, B. A. R., Wilde, V., and Bernardes-de-Oliveira, M. E. C. 2011 A putative gnetalean gymnosperm *Carira orbiculiconiformis* gen. nov et spec. nov from the Early Cretaceous of northern Gondwana. *Review of Palaeobotany and Palynology*, **165**, 75-95.

Kwon, K. D., Refson, K., Bone, S., Qiao, R., Yang, W.-L., Liu, Z., and Sposito, G. 2011. Magnetic ordering in mackinawite (tetragonal FeS): evidence for strong itinerant spin fluctuations. *Physical Review B*, **83**, 064402.

Labandeira, C. 1997. Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics*, **28**, 153-193.

Lacasa, A., and Martinez, X. 1986. Fauna y flora de los yacimentos Neocomienses del Montsec (Prov. Lérida). *Paleontología i Evolución*, **20**, 215-223.

Larson, P. L., and Russell, D. 2014. The benefits of commercial fossil sales to 21st-century paleontology. *Palaeontologia Electronica*, **17**, 1-7.

Leal, M. E. C., and Brito, P. M. 2006. Anura do Cretáceo Inferior da Bacia do Araripe, Nordeste do Brasil. *In.* Gallo, V., Brito, P. M., Silva, H. M. A., and Figueiredo, F. J. (Eds.). *Paleontologia de Vertebrados – grandes temas e contribuições científicas*. Rio de Janeiro, Interciência, Pp 330.

Leal, M. E. C., Martill, D. M., and Brito, P. M. 2007. Anurans of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Lee, H.-G., An, D.-S., Im, W.-T., Liu, Q.-M., Na, J.-R., Cho, D. A., Jin, C. W., Lee, S.-T., and Yang, D.-C. 2007. Chitinophaga ginsengisegetis so. Nov. and *Chitinophaga ginsengisoli* sp. Nov., isolated from soil of a ginseng field in South Korea. *International Journal of Systematic and Evolutionary Microbiology*, **57**, 1396-1401.

Leng, Q., and Yang, H. 2003. Pyrite framboids associated with the Mesozoic Jehol Biota in northeastern China: Implications for microenvironment during early fossilization. *Progress in Natural Science*, **13**, 206-212.

Lennie, A. R., and Vaughan, D. J. 1996. Spectroscopic studies of iron sulfide formation and phase relations at low temperatures. *Mineral Spectroscopy: A Tribute to Roger G. Burns*. Special Publication **5**, 1-16.

Li, Q., Gao, K.-Q., Vinther, J., Shawkey, M. D., Clarke, J. A., Meng, Q., Briggs, D. E. G., and Prum, R. O. 2010. Plumage color patterns of an extinct dinosaur. *Science*, **327**, 1369-1372.

Lima, M. R. de. 1978. Palinologia da Formação Santana (Cretaceo do Nordeste do Brasil). I. Introduçao geologica e descriçao sistematicados esporos da Subturma Azonotriletes. *Ameghiniana*, **15**, 333-365.

Lima, M. R. de. 1979. Palinologia da Formação Santana (Cretaceo do Nordeste do Brasil). II. Descrição sistematica dos espores da Subturma Zonotriletes e Turma Monoletes, e dos polens das Turmas Saccites a Aletes. *Ameghiniana,* **16,** 27-63.

Lima, M. R. de. 1980. Palinologia da Formação Santana (Cretáceo do Nordeste do Brasil). III. Descrição systematica dos polens da Turma Plicates (Subturma Costates). *Ameghiniana,* **17**, 15-47.

Lima, M. R. de. 1989. Palinologia da Formaçao Santana (Cretaceo do Nordeste do Brasil). IV. Descriçao systematica dos polens da Turma Plicates e Poroses, incertae sedis e Microplancton Marinho. *Ameghiniana,* **26**, 63-81.

Lockley, M. G., and Rice, A. 1990. Volcanism and Fossil Biotas. *Geological Society of America Special Paper*, **244**, 1-125.

Loewe, S. A., Mohr, B. A. R., Coiffard, C., Bernardes-de-Oliveira, M. E. C., and Mary, E. C. 2012. *Friedsellowia gracilifolia* gen. nov. et sp. nov., a new gnetophyte from the Lower Cretaceous Crato Formation (Brazil). *Palaeontographica Abteilung B-Palaophytologie*, **289**, 139-177.

Lü, J., Unwin, D. M., Jin, X., Liu, Y., and Ji, Q. 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society B,* **277**, 383-389.

Lutz, H. 1984. Parallelophoridae - isolierte Analfelder eozäner Schaben (Insecta: Blattodea). *Paläontologische Zeitschrift*, **58**, 145-147.

Lutz, H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg*, **124**, Pp. 165.

Ma, X., Hou, X., Edgecombe, G. D., and Strausfeld, N. J. 2012. Complex brain and optic lobes in an early Cambrian arthropod. *Nature*, **490**, 258-261.

Maas, A., Braun, A., Dong, X.-P., Donoghue, P. C. J., Müller, K. J., Olempska, E., Repetski, J. E., Siveter, D. J., Stein, M., and Waloszek, D. 2006. The 'Orsten'–More than a Cambrian Konservat-Lagerstätte yielding exceptional preservation. *Palaeoworld*, **15**, 266-282.

Mabesoone, J. M., and Tinoco, I. M. 1973. Palaeoecology of the aptian santana formation (Northeastern Brazil). *Palaeogeography Palaeoclimatology Palaeoecology*, **14**, 97-118.

MaCobb, L. M. E., Duncan I. J., Jarzembowski, E. A., Stankiewicz, B. A., Wills, M. A., and Briggs, D. E. G. 1998. Taphonomy of insects from the insect bed (Bembridge Marls), late Eocene, Isles of Wight, England. *Geology Magazine*, **135**, 553-563.

Maisey, J. G. 1990. Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous) of northeast Brazil. *In.* Grimaldi, D. A. (Ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History, Pp. 195.

Maisey, J. G. 1991. *Santana Fossils: an Illustrated Atlas*. Neptune City, T.F.H. Publications Inc., Pp 459.

Maisey, J. G., and da Carvalho, M. G. P. 1995. First records of fossil sergestid decapods and fossil brachyuran crab larvae (Arthropoda, Crustacea), with remarks on some supposed palaemonid fossils, from the Santana Formation (Aptian-Albian, NE Brazil). *American Museum Novitates,* **3132**, 1-17.

Margalef, R. 1983. *Limnologia*. Ed, Omega, Barcelona, Pp. 1010.

Martill, D. M. 1990. Macromolecular resolution of fossilized muscle tissue from an elopomorph fish. *Nature*, **346**, 171-172.

Martill, D. M., and Harper, E. 1990. Critical point drying, a technique for palaeontologists. *Palaeontology*, **33**, 423-428.

Martill, D. M., Wilby, P. R., and Williams, N. 1992. Elemental mapping: a technique for investigating delicate phosphatized fossil soft tissues. *Palaeontology*, **35**, 869-874.

Martill, D. M. 1993a. Fossils of the Santana and Crato Formations, Brazil. Field Guide to Fossils, no. 5. London, The Palaeontological Association, Pp. 159.

Martill, D. M. 1993b. Soupy Substrates: A Medium for the Exceptional Preservation of Ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia – Darmstädter Beiträge zur Naturgeschichte*, **2**, 77-97.

Martill, D. M., and Wilby, P. R. 1993. Stratigraphy. *In*. Martill, D. M. (Ed.). *Fossils of the Santana and Crato Formations, Brazil*. Field Guides to Fossils, **5**. London, The Palaeontological Association, Pp. 159.

Martill, D. M., and Filgueira, J. B. M. 1994. A new feather from the Lower Cretaceous of Brazil. *Palaeontology,* **37**, 483-487.

Martill, D., M. 1998. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology*, **31(1)**, 1-18.

Martill, D. M., and Barker, M. J. 1998. A new centipede (Arthropoda, Chilopoda) from the Crato Formation (Lower Cretaceous, Aptian) of N. E. Brazil. *Neues Jahrbuch für Geologie and Paläontologie, Abhandlungen,* **207**, 395-404.

Martill, D. M., and Davis, P. G. 1998. Did dinosaurs come up to scratch? *Nature,* **396**, 528-529.

Martill, D. M., and Frey, E. 1998. A new pterosaur Lagerstätte in N. E. Brazil (Crato Formation; Aptian, Lower Cretaceous): preliminary observations. *Oryctos,* **1**, 79-85.

Martill, D. M., and Frey, E. 1999. A possible azhdarchid pterosaur from the Crato Formation (Early Cretaceous, Aptian) of northeast Brazil. *Geologie en Mijnbouw,* **78**, 315-318.

Martill, D. M., and Davis, P. G. 2001. A feather with possible ectoparasite eggs from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **219**, 241-259.

Martill, D. M., Bernardes-de-Oliveira, M. E. C., and Castro-Fernandes, C. M. 2005. Diversity of putative nymphaealean waterplants in the Lower Cretaceous of the Araripe Basin, Brazil. *17th International Botany Congress, Vienna*, 425.

Martill, D. M., Loveridge, R. F., Ferreira Gomes de Andrade, J. A., and Herzog Cardoso, A. 2005. An unusual occurrence of amber in laminated limestones: the Crato Formation Lagerstätte (Early Cretaceous) of Brazil. *Palaeontology,* **48**, 1399-1408.

Martill, D. M. 2007a. The geology of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martill, D. M. 2007c. Lizards of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martill, D. M. 2007d. Miscellaneous biota. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martill, D. M., and Heimhofer, U. 2007. Stratigraphy of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martill, D. M., Bechly, G., and Loveridge, R. F. 2007a. *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martill, D. M., Loveridge, R., and Heimhofer, U. 2007b. Halite pseudomorphs in the Crato Formation (Early Cretaceous, Late Aptian-Early Alvian), Araripe Basin, northeast Brazil: further evidence for hypersalinity. *Cretaceous Research*, **28**, 613-620.

Martill, D. M., Loveridge, R. F., and Heimhofer, U. 2008a. Dolomite pipes in the Crato Formation fossil lagerstätte (Lower Cretaceous, Aptian), of northeastern Brazil. *Cretaceous Research*, **29**, 78-86.

Martill, D. M., Brito, P. M., and Washington-Evans, J. 2008b. Mass mortality of fishes in the Santana Formation (Lower Cretaceous, ?Albian) of northeast Brazil. *Cretaceous Research*, **29**, 649-658.

Martill, D. M., Tischlinger, H., and Longrich, N. R. 2015. A four-legged snake from the Early Cretaceous of Gondwana. *Science*, **349**, 416-419.

Martin, R. E. 1999. *Taphonomy: A process Approach (Cambridge Paleobiology Series)*. Cambridge University Press, Pp. 526.

Martin, T., Marugán-Lobón, J., Vullo, R., Martin-Abad, H., Luo, Z.-X., and Buscalioni, A. D. 2015. A Cretaceous eutriconodont and integument evolution in early mammals. *Nature*, **526**, 380-384.

Martínez-Delclós, X. 1989. *Chresmoda aquatica* n. sp. insecto Chresmodidae del Cretácico inferior de la Sierra del Montsech (Lleida, España). *Revista Española de Paleontología***, 4**, 67-74.

Martínez-Delclós, X., and Martinell, J. 1993. Insect taphonomy experiments. Their application to the Cretaceous outcrops of lithographic limestones from Spain. *Darmstádter Beitrage zur Naturgeschichte*, **2**, 133-144.

Martínez-Delclòs, X., Nel, A., and Popov, Y. A., 1995. Systematic and functional morphology of *Iberonepa romerali* n.gen. and sp., Belostomatidae from the Spanish Lower Cretaceous (Insecta, Heteroptera). *Journal of Paleontology*, **69**, 496-508.

Martínez-Delclòs, X., Briggs, D. E. G., and Peñalver, E. 2004, Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **203**, 19-64.

Martins-Neto, R. G. 1987a. Um novo gênero de Orthoptera (Insecta, Grylloidea) da Formação Santana, Bacia do Araripe (Cretáceo Inferior) nodeste do Brasil. *Congresso Brasiliera de Paleontologia*, *Rio de Janeiro*, **10**, 599-609.

Martins-Neto, R. G. 1988a. A new fossil insect (Homoptera, Cixiidae) from the Santana Formation (Lower Cretaceous), Araripe Basin, Northeast Brasil. *Interciencia*, **13**, 313-316.

Martins-Neto, R. G., and Kellner, A. W. A. 1988. Primeiro registro de pena na Formação Santana (Cretaceo Inferior), Bacia do Araripe, nordeste do Brasil. *Anais Academia brasileiro, Ciencias,* **60**, 61-68.

Martins-Neto, R. G. 1989a. A new fossil insect (Homoptera, Cixiidae) from the Santana Formation (Lower Cretaceous), Araripe Basin, Northeast Brasil. *Acta Geologica Leopoldensia*, **26**, 7-14.

Martins-Neto, R. G. 1989b. Primeiro registro de Phasmatodea (Insecta: Orthopteromorpha) na Formação Santana, Bacia do Araripe (Cretáceo Inferior), nordeste do Brasil. *Acta Geologica Leopoldensia (Estudos Tecnológicos),* **12**, 91-104.

Martins-Neto, R. G., and Vulcano, M. A. 1989a. Primeiro registro de Raphidioptera (Neuropteroidea) na Formação Santana (Cret´aceo Inferior), Bacia do Araripe, nordeste do Brasil. *Revista Brasileira de Entomologia,* **34**, 241-249.

Martins-Neto, R. G., and Vulcano, M. A. 1989b. Amphiesmenoptera, (Trichoptera + Lepidoptera) na Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. I – Lepidoptera (Insecta). *Anais da Academia Brasileira de Ciências*, **61**, 459-465.

Martins-Neto, R. G. 1990a. Primeiro registro de Dermpatera (Insecta, Orthopteromorpha) na Formação Santana (Cretáceo inferior), Bacia do Araripe, nordeste do Brasil. *Revista Brasileira de Entomologia,* **34,** 775-784.

Martins-Neto, R. G. 1990b. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. VI. Ensaio filogenético das espécie do genera *Blittersdorffia* Martins Neto and Vulcano, com descrição de nova espécie. *Acta Geologica Leopoldensia,* **13**, 3-12.

Martins-Neto, R. G. 1991a. Sistemática dos Ensifera (Insecta, Orthopteroida) da Formação Santana, Cretáceo Inferior do nordeste do Brasil. *Estudio Technológicos, Acta Geologica Leopoldensia,* **32**, 3-162.

Martins-Neto, R. G. 1991b. *Cratogryllus cigueli*, nova espécie de Ensifera (Insecta, Grylloidea) da Formação Santana (Cretáceo Inferior) Bacia do Araripe, nordeste do Brasil. *Acta Geologica Leopoldensia,* **33**, 153-156.

Martins-Neto, R. G. 1991c. Evidências de especiação alocrônica na fauna de Ensifera (Insecta, Orthopteroida) da Formação Santana, Cretáceo do nordeste do Brasil. *Revista de Geologia,* **4**, 61-80.

Martins-Neto, R. G. 1991d. A Paleoentomofauna do Nordeste Brasileiro: Estado da Arte. *Atas XIV Simposio de Geologia do Nordeste, Recife,* **12**, 59-62.

Martins-Neto, R. G., and Mezzalira, S. 1991. Descrição de crustáceos (Caridea) da Formação Santana, Cretáceo Inferior do Nordeste do Brasil. *Anais da Academia Brasileira de Ciências,* **63**, 155-160.

Martins-Neto, R. G. 1992b. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. VII. Palaeoleontinae, nova subfamilia de Myrmeleontidae e descrição de novos táxons. *Revista Brasileira de Entomologia,* **36**, 803-815.

Martins-Neto, R. G. 1994. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. IX. Primeiros resultados da composição da fauna e descrição de novos táxons. *Acta Geologica Leopoldensia,* **17,** 269-288.

Martins-Neto, R. G. 1995a. Araripelocustidae, fam. n. uma nova famìlia de gafanhotos (Insecta, Caelifera) da Formação Santana, Cretáceo Inferior do nordeste do Brasil. *Revista Brasil Entomologia,* **39**, 311-319.

Martins-Neto, R. G. 1995b. Complementos ao estudo sobre os Ensifera (Insecta, Orthopteroida) da Formação Santana, Cret´aceo Inferior do nordeste do Brasil. *Revista Brasil Entomologia,* **39**, 321-345.

Martins-Neto, R. G. 1996a. New mayflies (Insecta, Ephemeroptera) from the Santana Formation (Lower Cretaceous), Araripe Basin, Northeastern Brazil. *Revista Española de Paleontologia,* **11**, 177-192.

Martins-Neto, R. G. 1997a. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. X. Descrição de novos táxons (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae e Psychopsidae). *Revista Universidade de Guarulhos, Sárie Ciências Exatas e Technológicas,* **2**, 68-83.

Martins-Neto, R. G., and Vulcano, M. A. 1997. Neuropteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. VIII – Descrição de novos taxa de Myrmeleontidae, Ascalaphidae e Nemopteridae. *Revista Universidade Guarulhos, Série Ciêencias Biológicas,* **2**, 64-81.

Martins-Neto, R. G. 1998a. A new genus of the family Locustopsidae (Insecta, Caelifera) in the Santana Formation (Lower Cretaceous, northeast Brazil). *Revista Española de Paleontología,* **13**, 133-138.

Martins-Neto, R. G. 1998b. A new subfamily of Ensifera (Insecta, Grylloidea) from the Santana Formation (Lower Cretaceous), Araripe Basin, NE Brazil. *Proceedings of the First International Palaeoentomological Conference*, *Moscow, 1998*, 91-97.

Martins-Neto, R. G. 1998c. *Conan barbarica* n. gen. et n. sp. (Insecta, Coleoptera, Coptoclavidae) – uma gigantesca larva da Forma¸c*ão* Santana, Cret´aceo Inferior, Bacia do Araripe, Brasil. *Geociências São Paulo,* **17**, 109-114.

Martins-Neto, R. G. 1998d. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. XI. Descrição de novos táxons de

Myrmeleontidae (Palaeoleontinae e Pseudonymphinae). *Revista Universidade de Guarhulhos, Série Ciências Biológicas e da Saúde,* **3**, 38-42.

Martins-Neto, R. G. 1998f. Novos registro de Palaeontinideos (Insecta: Hemiptera) na formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. *Acta Geologica Leopoldensia*, **21**, 69-74.

Martins-Neto, R. G. 1999a. Estado actual del conocimiento de la paleoentomofauna brasileña. *Revista de la Sociedad Entomologica Argentina,* **58**, 71-85.

Martins-Neto, R. G., Popov, Yu. A., and Zamboni, J. A. 1999. First South Hemisphere Cretaceous record of Coreoidea (Insecta, Heteroptera) from Santana Formation (Lower Cretaceous, Northeast Brazil), representing a new genus et species. *Bolletim do 5o Simposio Sobre o Cret´aceo do Brasil,* 525-530.

Martins-Neto, R. G. 2000. Remarks on the neuropterofauna (Insecta, Neuroptera) from the Brazilian Cretaceous, with keys for the identification of the known taxa. *Acta Geologica Hispanica,* **35**, 97-118.

Martins-Neto, R. G. 2001a. Review of some Insecta from Mesozoic and Cenozoic Brazilian deposits with descriptions of new taxa. *Acta Geologica Leopoldensia,* **24**, 115-124.

Martins-Neto, R. G. 2001b. Primeiro registro de Trichoptera (Insecta) na Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil, com descrição de sete novos táxons. *Simpósio sobre a Bacia do Araripe e bacias interiores do Nordeste*, **1** e **2**, Crato, 1990/1997. *Boletim*, 212-226.

Martins-Neto, R. G. 2002a. The Santana Formation Paleoentomofauna reviewed. Part I. Neuropteroida (Neuroptera and Raphidioptera): systematic and phylogeny, with descriptions of new taxa. *Acta Geologica Leopoldensia,* **25**, 35-66.

Martins-Neto, R. G. 2002b. *Insetos fósseis como bioindicadores em depósitos sedimentares: um estudo de caso para o mesozóico sul-americano*. São Leopoldo: CPGEO, UNISINOS, Pp. 214.

Martins-Neto, R. G. 2005a. The Santana Formation palaeoentomofauna reviewed: Polyneoptera (Isoptera, Blattoptera, Dermaptera, Orthoptera) with description of six new species, one new genus and one new combination. *3rd International Congress of Palaeoentomology, Abstracts*, 7–11 February 2005, Pretoria, South Africa, **1**, 24.

Martins-Neto, R. G. 2005b. Estágio atual da paleoartropologia brasileira: Hexápodes, miriápodes, crustáceos (Isopoda, Decapoda, Eucrustacea e Copepoda) e quelicerados. *Arquivos do Museu Nacional, Rio de Janeiro,* **63**, 471-494.

Martins-Neto, R. G., Heads, S. W., and Bechly, G. 2007. Neuroptera: snakeflies, dobsonflies and lacewings. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Martins-Neto, R. G., and Rodrigues, V. Z. 2009. Novos neurópteros (Insecta: Osmylidae e Mesochrysopidae) da Formação Santana (Cretáceo Inferior, nordeste do Brasil) com descrição de novos taxons/New Neuroptera (Insecta, Osmlidae and Mesochrysopidae) from the Santana Formation (Lower Cretaceous, Northeast Brazil) with descriptions of new taxa. *Gaea Journal of Geoscience*, **5**, 15-20.

Martins-Neto, R. G., and Rodrigues, V. Z. 2010. New neuropteran insects (Osmylidae, Palaeoleontidae, Araripeneuridae and Psychopsidae) from the Santana Formation, Early Cretaceous NE Brazil. *Gaea Journal of Geoscience*, **6**, 1-8.

Mattos, R. M. D. 1992. The northeast Brazilian rift system. *Tectonics*, 11, 766-791.

Mattos, R. M. D. 1999. History of the northeast Brazilian rift system: kinematic implications for the break-up between Brazil and West Africa. *In*. Cameron, N. R., Bate, R. H., and Clure, V. S. (Eds.). *The Oil and Gas Habitats of the South Atlantic*. Geological Society of London, Pp. 400.

May, R. M. 1986. How many species are there?. *Nature*, **324**, 514-515.

Mayr, G., Poschmann, M., and Wuttke, M. 2006. A nearly complete skeleton of the fossil galliform bird Palaeortyx from the late Oligocene of Germany. *ACTA ORNITHOLOGICA*, **41**, 129-136.

Mazzarolo, L. A., and Amorim, D. S. 2000. *Cratomyia macrorrhyncha*, a Lower Cretaceous brachyceran fossil from the Santana Formation, Brazil, representing a new species, genus and family of the Stratiomyomorpha (Diptera). *Insect Systematics & Evolution,* **31,** 91-102.

McCafferty, W. P. 1990. Ephemeroptera. *In* Grimaldi, D. A. (Ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History*,* Pp. 195.

McCobb, L., Duncan, I. J., Jarzembowski, E. A., and Wills, M. A. 1998. Taphonomy of the insects from the Insect Bed (Bembridge Marls), late Eocene, Isle of Wight, England. *Geological Magazine*, **135(4)**, 553-563.

McCoy, V. 2013. Patterns in Palaeontology: Exceptional Preservation of Fossils in Concretions. Palaeontology Online, **3(7)**, 1-14.

McGrew, P. O. 1975. Taphonomy of Eocene fish from Fossil Basin, Wyoming. *Fieldiana Geology*, **33**, 257-270.

McNamara, M. E. 2013. The Taphonomy of colour in fossil insects and feathers. *Palaeontology*, **56**, 557-575.

Menon, F., Penney, D., Selden, P. A., and Martill, D. M. 2003. A new fossil Scolopendromorph centipede from the Crato Formation of Brazil. *Bulletin of the British Myriapod and Isopod Group*, **19**, 62-66.

Menon, F. 2005. New record of Tettigarctidae (Insecta, Hemiptera, Cicadoidea) from the Lower Cretaceous of Brazil. *Zootaxa,* **1087**, 53-58.

Menon, F. 2007. Higher systematics of scorpions from the Crato Formation, Lower Cretaceous of Brazil. *Palaeontology,* **50**, 185-195.

Menon, F., and Martill, D. M., 2007 Taphonomy and preservation of Crato Formation arthropods. 2007. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Menon, F., Heads, S. W., and Bechly, G. 2007. Cicadomorpha: cicadas and relatives. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Menon, F., and Makarkin, V. N. 2008. New fossil lacewings and antlions (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation of Brazil. *Palaeontology*, **51**, 149-162.

Mesquita, M. V. 1996. *Cretaraneus martinsnetoi* n. sp. (Araneoidea) da Fromação Santana, Cretáceo Inferior da Bacia do Araripe. *Revista Univesidade Guarulhos, Série Geociências,* **1**, 24-31.

Meurgues, G. 1982. Synthetic resins can be dangerous. *Museum,* **34**, 60-61.

Meyer, H. W., and Weber, L. 1995. Florissant Fossil Beds National Monument: Preservation of an Ancient Ecosystem. *Rocks and Minerals*, **70**, 232-239.

Meyer, H. W. 2003. *Fossils of Florissant*. Smithsonian Books, Washington D. C., Pp. 258.

Michez, D., Meulemeester, T. D., Rasmont, P., Nel, A., and Patiny, S. 2009. New fossil evidence of the early diversification of bees: Paleohabropoda oudardi from the French Paleocene (Hymenoptera, Apidae, Anthophorini). *Zoological Scripta*, **38**, 171-181.

Minerals.net. 2015. [Online] Goethite: The mineral goethite information and pictures. [Accessed 8 Dec. 2015]. http://www.minerals.net/mineral/goethite.aspx

Minerals.net. 2018. [Online] Calcite: The mineral goethite information and pictures. [Accessed 7 May 2018]. http://www.minerals.net/mineral/calcite.aspx

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, A. J., Aspöck, U., Aspöck, H., Bartel, D., Blanke, A., Berger, S., Böhm, A., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, A. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., Reumot, B. M. von., Schütte, K., Sekiya, K., Shimizu, S., Slipinski, A., Stamatakis, A., Song, W., Su, X., Szucsich, N. U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K. F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K.,

Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Li Y., Xu, X., Zhang, Y., Yang., H., Wang, J., Wang, Ju., Kjer, K. M., and Zhou, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763-767.

Mohr, B. A. R., and Friis, E. M. 2000. Early angiosperms from the Lower Cretaceous Crato Formation (Brazil), a preliminary report. *International Journal of Plant Science,* **161**, 155-167.

Mohr, B. A. R., and Eklund, H. 2003. *Araripia florifera*, a magnoliid angiosperm from the Lower Cretaceous Crato Formation (Brazil). *Review of Palaeobotany and Palynology,* **126**, 279-292.

Mohr, B. A. R and Bernardes-de-Oliveira, M. E. C. 2004. *Endressinia brasiliana*, a magnolialean angiosperm from the Lower Cretaceous Crato Formation (Brazil). *International Journal of Plant Science,* **165**, 1121-1133.

Mohr, B. A. R., Dernardes-de-Oliveira, M. E. C., and Loveridge, R. F. 2007. The macrophyte flora of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Mohr, B. A. R., Schultka, S., Suess, H., Bernardes-de-Oliveira, M. E. C. 2012. A new drought resistant gymnosperm taxon *Duartenia araripensis* gen. nov et sp nov (Cheirolepidiaceae?) from the Early Cretaceous of Northern Gondwana. *Palaeontographica Abteilung B-Palaophytologie*, **289**, 1-25.

Mohr, B. A. R., Coiffard, C., and Bernardes-de-Oliveira, M. E. C. 2013. *Schenkeriphyllum glanduliferum*, a new magnolialean angiosperm from the Early Cretaceous of Northern Gondwana and its relationships to fossil and modern Magnoliales. *Review of Palaeobotany and Palynology*, **189**, 57-72.

Monod, L., and Lourenço, W. R. 2005. Hemiscorpiidae (Scorpiones) from Iran, with descriptions of two new species and notes on biogeography and phylogenetic relationships. *Revue Suisse de Zoologie*, **112**, 869-941.

Morse, J. W., and Wang, Q. 1997. Pyrite formation under conditions approximating those in anoxic sediments: II. Influence of precursor iron minerals and organic matter. *Marine Chemistry*, **57**, 187-193.

Myskowiak, J., Escuillie, F., and Nel, A. 2015. A new Osmylidae (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation in Brazil. *Cretaceous Research*, **54**, 27-33.

Myskowiak, J., and Nel, A. 2016. New antlion species (Insecta, Neuroptera, Palaeoleontidae) from the Lower Cretaceous Crato Formation in northeastern Brazil. *Cretaceous Research*, **59**, 278-284.

Myskowiak, J., Huang, D., Azar, D., Cai, C., Garrouste, R., and Nel, A. 2016. New lacewings (Insecta, Neuroptera, Osmylidae, Nymphidae) from the Lower Cretaceous Burmese amber and Crato Formation in Brazil. *Cretaceous Resea*rch, **59**, 214-227.

Naish, D. 2007. Turtles of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Naish, D., Martill, D. M., and Merrick, I. 2007. Birds of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Nel, A., and Paicheler, J.-C. 1992. Les Heteroptera aquatiques fossils, état actuel des connaissances (Heteroptera: Nepomorpha et Gerromorpha). *Entomologica Gallica,* **3**, 159-182.

Nel, A., and Popov, Yu. A. 2000. The oldest known fossil Hydrometridae from the Lower Cretaceous of Brazil (Heteroptera: Gerromorpha). *Journal of Natutal History,* **34**, 2315-2322.

Nel, A., Bechly, G., Garouste, R., Pohl, B., and Escuillié, F. 2005. A new extraordinary neuropterid family from the Lower Cretaceous Crato Formation of Brazil: a new insect order? (Insecta, Neuropterida). *Cretaceous Research,* **26**, 845-852.

Nel, A., and Waller, A. 2006. A giant water bug from the Lower Cretaceous Crato Formation of Brazil (Heteroptera: Belostomatidae: Lethocerinae). *Zootaxa,* **1220**, 63-68.

Nel, A., Escuillie, F., and Garrouste, R. 2013. A new scoliid wasp in the Early Cretaceous Crato Formation in Brazil (Hymenoptera: Scoliidae). *Zootaxa*, **3717**, 395-400.

Nel, A., Nel, P., Krief-Jacquier, R., Pouillon, J.-M., and Garrouste, R. 2014. Exceptionally preserved insect fossils in the Late Jurassic lagoon of Orbagnous (Rhone Valley, France). *PeerJ*, **2**, e510.

Neto, J. A., Mort, H., Pereira, R., Barbosa, J., Neumann, V., Vortisch, W., Filho, O. J. C., Brandão, P. de A. L. S., and Pacheco, J. G. A. 2013. *Carbonaceous Shales in the Araripe Basin, NE Brazil: A Potential Shale Gas Reservoir*. Search and Discovery Article, 80309.

Neumann, V. H., Borrego, A. G., Cabrera, L., and Dino, R. 2003. Organic matter composition and distribution through the Aptian-Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *International Journal of Coal Geology,* **54**, 21-40.

Newbury, D. E. 2009. Mistakes encountered during automatic peak identification of minor and trace constituents in electron-excited energy dispersive X-ray microanalysis. *Scanning*, **31**, 1-11.

Newman, A. 1998. Pyrite oxidation and museum collections: A review of theory and conservation treatments. *The Geological Curator*, **6 (10)**, 363-371.

Nichols, G. 2009. *Sedimentology and Stratigraphy*. Wiley-Blackwell, Pp. 432.

Noyes, J. S., 2012. *Universal Chalcidoidea Database*. World Wide Web electronic publication. http://www.nhm.ac.uk/chalcidoids.

Nuvens, P. C., Sayão, J. M., Silva, H. P., Saraiva, A. A., and Kellner, A. W. A. 2002. A coleção de pterossauros do Museu de Paleontologia de Santana do Cariri, Nordeste do Brasil. *Arquivos do Museu Nacional, Rio de Janeiro,* **60**, 235-240.

O'Brien, N. R., Meyer, H. W., and Harding, I. C. 2008. The role of biofilms in fossil preservation, Florissant Formation, Colorado. *Geological Society of America Special Papers*, **435**, 19-31.

Ohfuji, H., and Rickard, D. 2005. Experimental syntheses of framboids – a review. *Earth-Science Reviews*, **71**, 147-170.

Oliveira, G. R., and Kellner, A. W. A. 2005. First occurrence of *Araripemys barretoi* Price, 1973. *In*. The Crato Member, Santana Formation (Early Cretaceous) northeastern Brazil. *Boletim de Resumos/ II Congresso Latino-Americano de Paleontologia de Vertebrados,* Museo Nacional, Rio de Janeiro, Pp. 193.

Oliveira, G. R., Saraiva, A. A. F., Silva, H. D., de Andrade, J. A. F. G., and Kellner, A. W. A. 2011. First turtle from the Ipubi Formation (Early Cretaceous), Santana Group, Araripe Basin, Brazil. *Revista Brasileira de Paleontologia*, **14**, 61-66.

Oliveira-Babinski, M. E. C. and de Lima, M. R. 1991. *Pteridophyte remains from the Lower Cretaceous, Santana Formation, Araripe Basin, Northeastern Brazil*. 12◦ Congresso Brasileiro de Paleontologia (Sao Paulo), Boletim de Resumos, Pp. 491.

Ollivier, B., Caumette, P., Garcia, J. L., and Mah, R. A. 1994. Anaerobic bacteria from hypersaline environments. *Microbiological Reviews*, **58**, 27-38.

Omarov, Kh. B., Absat, Z. B., Aldabergenova, S. K., Siyazova, A. B., Rakhimzhanova, N. J., and Sagindykova, Z. B. 2016. Studying the process of deposition of antimony with calcium carbonate. *Asian Research Publishing Network Journal of Engineering and Applied Sciences*, **11**, 9941-9945.

Osés, G. L., Petri, S., Becker-Kerber, B., Romero, G. R., Rizzutto, M. de A., Rodrigues, F., Galante, D., Silva, T. F. da, Curado, J. F., Rangel, E. C., Ribeiro, R. P., and Pacheco, M. L. A. F. 2016. Deciphering the preservation of fossil insects: a case study from the Crato Member, Early Cretaceous of Brazil. *PeerJ*, **4**, e2756.

Osés, G. L., Petri, S. Voltani, C. G., Prado, G. M. E. M., Galante, D., Rizzutto, M. A., Rudnitzki, I. D., da Silva, E. P., Rodrigues, F., Rangel, E. C., Sucerquia, P. A., and Pacheco, M. L. A. F. 2017. Deciphering pyritization-kerogenization gradient for fish soft-tissue preservation. Scientific Reports, **7**, 1468. DOI:10.1038/s41598-017-01563-0.

Ősi, A. 2011. Feeding-related characters in basal pterosaurs: implications for jaw mechanism, dental function and diet. *Lethaia*, **44**, 136-152.

Osten, T. 2007. Hymenopter: bees, wasps and ants. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Paz, J. D. S., and Rossetti, D. F. 2006. Paleohydrology of an Upper Aptian lacustrine system from northeastern Brazil: integration of facies and isotopic geochemistry. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**, 247-266.

Pearlman, H. 2016. [Online] Phosphorus and Water. *U.S. Geological Survey*. [Accessed 03 Oct. 2017]. https://water.usgs.gov/edu/phosphorus.html.

Peñalver, E., and Seilacher, A. 1995. Rubielos de Mora – Eine untermiozäne Fossil-Lagerstätte. *Fossilien*, **12**, 211-216.

Peñalver, E. 1998a. *Estudio tafonómico y paleoecológico de los insectos del Mioceno de Rubielos de Mora (Teruel)*. Instituto de Estudios Turolenses, Teruel, Pp. 177.

Peñalver, E. 1998b. Rubielos de Mora y Ribesalbes: Dos yacimientos españoles del Neógeno con insectos fósiles. *Cidaris: Revista Ilicitana de Paleontología y Mineralogía*, **13-14**, 17-29.

Peñalver, E., Martínez-Delclós, X., and Arillo, A. 1999. Yacimientos con insectos fósiles en España. *Revista Española de Paleontología*, **14**, 231-245.

Peñalver, E., and Martínez-Delclòs, X. 2003. Insects in the gut content of immature amphibians (family Salamandridae): an exceptional preservation in the Lower Miocene of Rubielos de Mora Basin (Teruel, Spain). *In.* Exceptional Preservation EPA Workshop 2003. Teruel, Spain: Fundación Conjunto Paleontológico de Teruel – Museo Nacional de Ciencias Naturales, Pp. 182.

Penney, D., and Jepson, J. E. 2014. *Fossil Insects: An introduction to palaeoentomology*. Siri Scientific Press, Manchester, Pp. 222.

Perán, A., Velasco, J., and Millan, A. 1999. Life cycle and secondary production of *Caenis luctuosa* (Ephemeroptera) in semiarid streams (Southeast Spain). *Hydrobiologia*, **400**, 187-194.

Pereira, R., Carvalho, I. de S., Simoneit, B. R. T., Azevedo, D. de A. 2009. Molecular composition and chemosystematic aspects of Cretaceous amber from the Amazonas, Araripe and Reconcavo basins, Brazil. *Organic Geochemistry*, **40**, 863-875.

Petrovich, R. 2001. Mechanisms of fossilization of the soft-bodied and lightly armored faunas of the Burgess Shale and some other classical localities. *American Journal of Science*, **301**, 683-726.

Petrulevičius, J. F., and Martins-Neto, R. G. 2007. A new proterogomphid dragonfly from the Lower Cretaceous of Brazil. *Palaeontology,* **37**, 923-930.

Petrulevičius, J. F., Martins-Neto, R. G., Azar, D., Makhoul, E., and Nel, A. 2012. Full description of *Cordulagomphus primaerensis* from Santana Formation (Lower Cretaceous of Brazil) (Odonata: Aeshnoptera: Proterogomphidae). *Zootaxa,* **3503**, 55-60.

Pietars, J. T., and Carroll, A. R. 2006. High-resolution stratigraphy of an underfilled lake basin: Wilkins Peak Member, Eocene Green River Formation, Wyoming, U.S.A. *Journal of Sedimentology Research*, **76**, 1197-1214.

Pinto, J. D., and Ornellas, L. P. 1974. New Cretaceous Hemiptera (Insects) from the Codo Formation – Northern Brazil. *Anais 28th Congresso Brasileiro do Geologia*, **28**, 289-304.

Pinto, J. D. 1989. A second new blattoid from the Cretaceous of Brazil. *Resumo das Comunicações do Congresso Brasileiro de Paleontologia,* **11**, 295-300.

Plotnick, E. 1986. Taphonomy of a modern shrimp: Implications for the arthropod fossil record. *Palaios*, **1**, 286-293.

Plotnick, E. 1990. Paleobiology of arthropod cuticle. *In*. Mikulic, D.G. (Ed.). *Arthropod Paleobiology*. Short Courses in Paleontology 3, Paleontological Society, Dallas, TX, Pp. 256.

Ponomarenko, A. G. 1985. Fossil insects from the Tithonian 'Solnhofener Plattenkalke' in the Museum of Natural History, Vienna. *Annalen des Naturhistorischen Museums in Wien A*, **87**, 135-144.

Ponomarenko, A. G. 2003. Ecological evolution of beetles (Insecta: Coleoptera). *Acta Zoologica Cracoviensia,* **46**, 319-328.

Pons, D., Berthou, P. Y., Melo-Filgueiras, J. B., and Alcantara-Sampaio, J. J. 1996. Palynologie des unités, Fundão Crato et Ipubi (Aptien supérieur à Albien inférieur –moyen, bassin d'Araripe, nord-est du Brésil): enseignements paléoécologiques, stratigraphiques et climatologiques. *Géologie de l'Afrique et de l'Atlantique Sud: Actea Colloques Angers, **1994***, 383-401.

Ponte, F. C., and Appi, C. J. 1990. Proposta de revisão da coluna litoestratigrfiáca da Bacia do Araripe. *Congresso Brasileiro de Geologia,* **36**, 211-236.

Ponte, F. C. 1992. Origin and evolution of small Cretaceous basins in the Northeast of Brazil, in UNESP / IGCE, Brazilian Symposium on Cretaceous Basins, Abstracts, 2., Rio Claro, Pp. 55-58.

Ponte, F. C., and Ponte Filho, F. 1996. Evoluçao tectonica e classificação da Bacia do Araripe. *In*. *Boletim do 4 Simpósio sobre o Cretáceo do Brasil* UNESP. Campus de Rio Claro, São Paulo, Pp. 123–133.

Роман, К. 2004. Где живут сепульки: [О двух видах палеонтологических перепончатокрылых — Sepulka mirabilis и Sepulenia syricta]. *Новая интересная газета (Киев)*, **1**, С-5.

Popham, E. J. 1990. Dermaptera. *In.* Grimaldi, D. A. (Ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bulletin of the American Museum of Natural History, Pp. 195.

Popov, Y. A., and Bechly, G. 2007. Heteroptera: bugs. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Potts, M. 1994. Desiccation tolerance of prokaryotes. *Microbiology and Molecular Biology Reviews*, **58**, 755-805.

Prado, G. M. E. M., Anelli, L. E., Petri, S., and Romero, G. R. 2016. New occurrences of fossilized feathers: systematics and taphonomy of the Santana Formation of the Araripe Basin (Cretaceous), NE, Brazil. *PEERJ*, **4**, e1916.

Proctor, H. C. 2003. Feather mites (Acari: Astigmata): ecology, behavior, and evolution. *Annual Review of Entomology,* **48**, 185-209.

Pulawski, W. J., and Rasnitsyn, A. P. 2000. *Cretobestiola*, a replacement name for *Bestiola* Pulawski and Rasnitsyn, 1999 (Hymenoptera: Sphecidae). *Acta Geologica Hispanica,* **35**, 53.

Punzo, F. 1998. *The Biology of Camel Spiders (Arachnida, Solifugae)*. Boston, MA, Kluwer Academic Publishers, Pp. 301.

Raiswell, R., Newton, R. J., Bottrell, S. H., Coburn, P. M., Briggs, D. E. G., Bond, D. P. G., and Poulton, S. W. 2008. Turbidite depositional influences on the diagenesis of Beechers Trilobite Bed and the Hunsruck Slate; sites of soft tissue pyritization. *American Journal of Science*, **308**, 105-112.

Rakitov, R. 2015. Observations on the Biology and Anatomy of Myerslopiidae (Hemiptera, Membracoidea). *Psyche*, **ID 898063**, 1-10.

Rasnitsyn, A. P. 1969. Origin and evolution of lower Hymenoptera. *Trudy Paleontologicheskogo Instituta, Akademii Nauk S*SSR, **123**, 1-196. (In Russian).

Rasnitsyn, A. P. 1986. Review of the fossil Tiphiidae, with description of a new species (Hymenoptera). *Psyche,* **93**, 91-101.

Rasnitsyn, A. P. 1993. Archaeoscoliinae, an extinct subfamily of scoliid wasps (Insecta: Vespida = Hymenoptera: Scoliidae). *Journal of Hymenoptera Research,* **2**, 85-96.

Rasnitsyn, A. P., Jarzembowski, E. A. and Ross, A. J. 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of Southern England and their biostratigraphical and paleoenvironmental significance. *Cretaceous Research*, **19**, 329-391.

Rasnitsyn, A. P., and Martínez-Delclòs, X. 1999. New Cretaceous Scoliidae (Vespida Hymenoptera) from the Lower Cretaceous of Spain and Brazil. *Cretaceous Research,* **20**, 767-772.

Rasnitsyn, A. P., and Ansorge, J. 2000. New Early Cretaceous hymenopterous insects (Insecta: Hymenoptera) from Sierra del Montsec (Spain). *Paläontologiesche Zeitschrift*, **74**, 335-341.

Rasnitsyn, A. P., and Martínez-Delclòs, X. 2000. Wasps (Insecta: Vespida = Hymenoptera) from the Early Creactous of Spain. *Acta Geologica Hispanica*, **35**, 65-95.

Rasnitsyn, A. P. 2002. Infraclass Gryllones. *In.* Rasnitsyn, A. P. and Quicke, D. L. J. (Eds.). *History of Insects*. Dordrech Kluwer, Pp. 517.

Rasnitsyn, A. P., and Quicke, D. L. J. 2002. *History of Insects*. Kluwer Academic Publishers, New York, Pp. 517.

Rasnitsyn, A. P., Basibuyuk, H. H., and Quicke, D. L. J. 2004. A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. *Insect Systematics and Evolution*, **35**, 123-135.

Rasnitsyn, A. P., and Zhang, H. C., 2010. Early evolution of Apocrita (Insecta, Hymenoptera) as indicated by new findings in the Middle Jurassic of Daohugou, Northeast China. *Acta Geologica Sinica*, **84**, 834-873.

Ren, D., Shih, C., Gao, T., Yao, Y., and Zhao, Y. 2010. *Silent Stories – Insect Fossil Treasures from Dinosaur Ear of the Northeastern China*. Science Press Beijing, Pp. 322.

Ribeiro, G. C., and Martins-Neto, R. G. 1999. A new Tipulidae (Insecta, Diptera) from the Santana Formation (Araripe Basin, Lower Cretaceous, Northeastern Brazil). *Boletim do 5th Simpósio sobre o Cretáco do Brasil (UNESP, Sao Paulo, 1999)*, **98**, 207-212.

Ribeiro, G. C., and Krzemiski, W. 2000. New information on Limoniidae (Diptera: Tipulomorpha) from the Lower Cretaceous Santana Formation (northeastern Brazil). *Polskie Pismo Entomologiczne,* **69**, 451-457.

Ribeiro, G. C., and Lukashevich, E. D. 2014. New Leptotarsus from the Early Cretaceous of Brazil and Spain: the oldest members of the family Tipulidae (Diptera). *Zootaxa*, **3753**, 347-363.

Ribeiro, G. C., Santos, D., and Nicolau, R. C. R. 2015. A new species of Leptotarsus (Diptera: Tipulidae) from the Lower Cretaceous Crato Formation of Brazil. *Cretaceous Research*, **56**, 244-249.

Rickard, D. 1969. The chemistry of iron sulphide formation at low temperatures. *Stockholm Contributions in Geology*, **20**, 67-95.

Rickard, D. 1974. Kinetics and mechanism of the sulfidation of goethite. *American Journal of Science*, **274**, 941-952.

Rickard, D. 1997. Kinetics of pyrite formation by H_2S oxidation of iron (II) monosulphide in aqueous solutions between 25 and 125°C: The rate equation. *Geochimica et Cosmochimica Acta*, **61**, 115-134.

Rickard, D. 2012. *Sulfidic Sediments and Sedimentary Rocks*. Elsevier, Pp. 816.

Riek, E. E. 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Australian Journal of Zoology*, **3**, 654-691.

Riek, E. F. 1970. Lower Cretaceous fleas. *Nature*, **227**, 746-747.

Rønsted, N., Weiblen, G. D., Cook, J. M., Salamin, N., Machado, C. A., and Savolainen, V. 2005. 60 million years of co-divergence in the fig-wasp symbiosis. *Proceedings of the Royal Society B, Biological Sciences*, **272**, 2593-2599.

Royer, L. A., Lemon, W. C., Chhetri, R. K., Wan, Y., Coleman, M., Myers, E. W., and Keller, P. J. 2016. Adaptive light-sheer microscopy for long-term, high-resolution imaging in living organisms. *Nature Biotechnology*, **34**, 1267-1278. Doi:10.1038/nbt.3708

Ruf, M. L., Goodwyn, P. P., and Martins-Neto, R. G. 2005. New Heteroptera (Insecta) from the Santana Formation, Lower Cretaceous (Northeastern Brazil), with description of a new family and new taxa of Naucoridae and Gelastocoridae. *Gaea,* **1,** 68-74.

Rundle A. J., and Cooper, J. 1971. Occurrence of a fossil insect larvae from the London Clay of Herne Bay, Kent. *Proceedings of the Geologists' Association*, **82**, 239-296.

Sagemann, J., Bale, S. J., Briggs, D. E. G., and Parkes, R. J. 1999. Controls on the formation of authigenic minerals in association with decaying organic matter: An experimental approach. *Geochimica et Cosmochimica Acta*, **63**, 1083-1095.

Sahayaraj, K., Ayyachamy, V. K., and Subramanian, M. K. 2010. Gross Morphology of Feeding Canal, Salivary Apparatus and Digestive Enzymes of Salivary Gland of Catamirus brevipennis (Servile) (Hemiptera: Reduviidae). *Journal of the Entomological Research Society*, **12**, 37-50.

Salisbury, S. W., Frey, E. Martill, D. M. and Buchy, M.-C. 2003a. A new mesosuchian crocodilian from the Lower Cretaceous Crato Formation of north-eastern Brazil. *Palaeontographica, Abteilung A (Paläozoologie – Stratigraphie),* **270**, 3-47.

Santos, M. F. de A., Mermudes, J. R. M., and Fonseca, V. M. M. da. 2011. A specimen of Curculioninae (Curculionidae, Coleoptera) from the Lower Cretaceous, Araripe Basin, north-eastern Brazil. *Palaeontology*, **54**, 807-814.

Sayão, J. M., and Kellner, A. W. A. 1998. Pterosaur wing with soft tissue from the Crato Member (Aptian-Albian), Santana Formation, Brazil. *Journal of Vertebrate Paleontology*, **18(3)**, 75A.

Sayão, J. M., and Kellner, A. W. A. 2000. Description of a pterosaur rostrum from the Crato Member, Santana Formation (Aptian-Albian) northeastern Brazil. *Boletin do Museu Nacional Nova Serie Rio de Janeiro – Brasil, Geologia*, **54**, 1-8.

Sayão, J. M. 2003. Histovarability in bones of two pterodactyloid pterosaurs from the Santana Formation, Araripe Basin, Brazil: preliminary results. *In.* Buffetaut, E., and Mazin, J.-M. (Eds.). *Evolution and Palaeobiology of Pterosaurs*. Geological Society of London, Special Publication, Pp. 354.

Sayão, J. M., and Kellner, A. W. A. 2006. Pterossauro do Membro Crato (Aptiano) Formação Santana, Bacia do Araripe, e o pós-crânio dos Tapejaridae. *Boletim de Resumos da Reuniao Annual da Sociedade Brasileira de Paleontologia*, **57**, 41.

Sayão, J. M., Saraiva, A. A. F., and Uejima, A. M. K. 2011. New evidence of feathers in the Crato Formation supporting a reappraisal on the presence of Aves. *Anais da Academia Brasileira de Ciencias*, **83**, 197-210.

Scherer, C. M. S., Goldberg, K., and Bardola, T. 2015. Facies architecture and sequence stratigraphy of an early post-rift fluvial succession, Aptian Barbalha Formation, Araripe Basin, northeastern Brazil. *Sedimentary Geology*, **322**, 43-62.

Schieber, J. 2002. Sedimentary pyrite: A window into the microbial past. *Geology*, **30**, 531-534.

Schieber, J. 2007. Benthic microbial mats as an oil shale component: Green River Formation (Eocene) of Wyoming and Utah. *In*. Schieber, J., Bose, P. K., Eriksson, P. G., Banerjee, S., Sarkar, A., Altermann, W., and Catuneau, O. (Eds.). *Atlas of microbial mat features preserved within the Siliciclastic rock record*. Elsevier, Amsterdam, Pp. 324.

Schlüter, T. 2003. Fossil insects in Gondwana–localities and diversity trends. *Acta Zoological Cracoviensia*, **46**, 345-371.

Schomann, A., and Solodovnikov, A. 2012. A new genus of Staphylinidae (Coleoptera) from the Lower Cretaceous: the first fossil rove beetles from the Southern Hemisphere. *Systematic Entomology*, **37**, 379-386.

Schoonen, M. A. A. 2004. Mechanisms of sedimentary pyrite formation. Geological Society of America Special Papers, **379**, 117–133.

Schopf, J. M. 1975. Modes of Fossil Preservation. *Review of Palaeobotany and Palynology*, **20**, 27-53.

Schulz, H. D., and Zabel, M. 2006. *Marine Geochemistry*. Springer-Verlag, Pp. 455.

Schweigert, V. G., and Dietl, G. 1997. Ein fossilier Hundertfüssler (Chilopoda, Geophilida) aus dem Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B,* **254**, 1-11.

Schweigert, V. G., Martill, D. M., and Williams, M. 2007. Crustacea of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Selden, P. A. 1990. Lower Cretaceous Spiders from the Sierra de Montsech, North-East Spain. *Palaeontology*, **33**, 257-285.

Selden, P. A., and Shear, W. A. 1996. The first Mesozoic solifuge (Arachnida), from the Cretaceous of Brazil, and a redescription of the Palaeozoic solifuge. *Palaeontology,* **39**, 583-604.

Selden, P. A., da Costa Casado, F. and Mesquita, M. V. 2006. Mygalomorph spiders (Araneae: Dipluridae) from the Lower Cretaceous Crato Lagerstätte, Araripe Basin, north-east Brazil. *Palaeontology,* **49**, 817-826.

Selden, P. A., and Nudds J. 2012. *Evolution of Fossil Ecosystems: Second Edition*. Academic Press, Pp. 288.

Sharkey, M. J. 1990. Taxonomic names, in Insects from the Santana Formation, Lower Cretaceous, of Brazil. Chapter 7: Order Hymenoptera. *Bulletin of the American Museum of Natural History,* **195**, 123-153

Shcherbakov, D. E. 2006. The earliest find of Tropiducidae (Homoptera: Auchenorrhyncha) representing a new tripe, from the Eocene of Green River, USA, with notes on the fossil record of higher Fulgoroidea. *Russian Entomological Journal*, **15**, 315-322.

Shear, W. A., and Edgecombe, G. D. 2010. The geological record and phylogeny of the Myriapoda. *Arthropod Structure & Development*, **39**, 174-190.

Shelley, D. 1985. *Optical mineralogy*. *Second Edition*. Elsevier, New York, Pp. 545.

Siegrist, H., Brunner, I., Koch, G., Phan, L. C., and Le, V. C. 1999. Reduction of biomass decay rate under anoxic and anaerobic conditions. *Water Science and Technology*, **39**, 129-137.

Silva J. H. da., Ferire, P. T. C., Abagaro, B. T. O., Silva, J. A., Saraiva, G. D., de Lima, F. J., Barros, O. A., Bantim, R. A., Saraiva, A. A., Viana, B. X. 2013. Spectroscopic studies of wood fossils from the Crato Formation, Cretaceous Period. *Spectrochimica Acta Part A-Molecular and Biomolecular Spectroscopy*, **115**, 324-329.

Silva, M. A. M. de. 1978a. Ostracodes da Formação Santana (Cretáceo Inferior) – Grupo Araripe Nordeste do Brasil. I. Novas especies do genero *Bisulcocypris*. *Anais 30◦ Congresso Brasileiro de Geologia,* **2**, 1014-1021.

Silva, M. A. M. de. 1978b. Ostracodes da Formação Santana (Cretaceo Inferior) – Grupo Araripe Nordeste do Brasil. III. Nova especie do genero *Darwinula* Brady and Robertson, 1885. *Anais 30◦ Congresso Brasileiro de Geologia,* **2**, 1028-1030.

Silva, M. A. M. de. 1979. Contibução do ostracodes para a paleoecologia e paleogeofrafia da Formação Santana (Grupo Araripe, Cretáceo Inferior, Nordeste do Brasil). *Universidade Federal de Pernambuco,* Departamento *Geologia Estudos Pesquisas,* **3**, 97-106.

Silva, M. A. M. da. 1986. Lower Cretaceous sedimentary sequences in the Araripe Basin, *Revista Brasileira de Geosciênces,* **16**, 311-319.

Silva, M. A. M. da. 1988. Evaporitos do Cretáceo da Bacia do Araripe: ambientes de deposição e historia diagenetica. *Boletim de Geosciências da Petrobrás,* **2,** 53-63.

Silva-Telles, A. C. da, and Viana, M. S. S. 1990. Ostracoda paleoecology of the Santana Formation (Aptian-Albian), Araripe Basin: an ontogenetic study of populations. *Atlas do I Simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste,* **14 + 16**, 309-327.

Simoes, T. R. 2012. Redescription of *Tijubina pontei*, an Early Cretaceous lizard (Reptilia; Squamata) from the Crato Formation of Brazil. *Anais da Academia Brasileira de Ciencias*, **84**, 79-93.

Simon, A., Poulicek, M., Velimirov, B., and Mackenzie, F. T. 1994. Comparison of anaerobic and aerobic biodegradation of skeletal structures in marine and estuarine conditions. *Biogeochemistry*, **25**, 167-195.

Simutnik, S. A. 2002. A new genus of encyrtid wasp (Hymenoptera, Chalcidoidea, Encyrtidae) from Late Eocene Rovno amber(Ukraine). *Vestnik Zoologii*, **36**, 99-102.

Skalski, A. W. 1988. A new fossil trichogrammatid from the Sicilian amber Hymenoptera Chalcidoidea Trichogrammatidae. *Fragmenta Entomologica*, **21**, 111-116.

Skinner, B. J., Erd, R. C., and Grimaldi, F. S. 1964. Greigite, the thiospinel of iron, a new mineral. *American Mineralogist*, **49**, 543-555.

Small, H. 1913. Geologia e suprimento de agua subterranea no Ceará e parte do Piaui. *Inspetoria Federal de Obras Contra as Seccas, Serie Geologia*, **25**, 1-180.

Smith, D. M. 2000. Beetle taphonomy in a Recent ephemeral lake, Southeastern Arizona. *Palaios*, **15**, 152-160.

Smith, D. M., Cook, A., and Nufio, C. R. 2006. How physical characteristics of beetles affect their fossil preservation. *PALAIOS*, **21**, 305-310.

Smith, D. M., and Moe-Hoffman, A. 2007. Taphonomy of diptera in lacustrine environments: A case study from Florissant Fossil Beds, Colorado. *PALAIOS*, **22**, 623-629.

Smith, M. E., Carroll, A. R., and Singer, B. S. 2008. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin*, **120**, 54-84.

Soonthornchai, W., Chaiyapechara, S., Jarayabhand, P., Söderhäll, K., and Jiravanichpaisal, P. 2014. Interaction of Vibrio spp. With the inner surface of the digestive tract of Penaeus monodon. *PLOS one*. **10(8)**: doi:10.1371/journal.pone.0135783.

Sørensen, J., and Jørgensen, B., B. 1987. Early diagenesis in sediments from Danish coastal waters: Microbial activity and Mn- Fe-S geochemistry. *Geochimica et Cosmochimica Acta*, **51**, 1583-1590.

Staniczek, A. H. 2007. Ephemeroptera: mayflies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Staniczek, A. H., and Bechly, G. 2007. Apterygota: primarily wingless insects. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Staniczek, A. H., Bechly, G., and Godunko, R. J. 2011. Coxoplectoptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera). *Insect Systematics & Evolution*, **42**, 101-138.

Stankiewicz, B. A., Scott, A. C., Collinson, M. E., Finch, P., Mosle, B., Briggs, D. E. G., and Evershed, R. P. 1998. Molecular taphonomy of arthropod and plant cuticles from the Carboniferous of North America: implication for the origin of kerogen. *Journal of the Geological Society, London*, **155**, 453-462.

Stanton, M. R., and Goldhaber, M. B. 1991. An experimental study of goethite sulfidization—relationships to the diagenesis of iron and sulphur. *In*. Tuttle, M. L. (Ed.). *Geochemical, Biogeochemical and Sedimentological Studies of the Green River Formation, Wyoming, Utah and Colorado*. U.S. Geological Survey Bulletin, **1973E**, 1-20.

Strangway, D. W., Honea, R. M., McMahon, B.E., and Larson, E. E. 1968. The Magnetic Properties of Naturally Occurring Goethite. *Geophysical Journal International*, **15**, 345-359.

Strum, H. 1998. Erstnachweis fischchenartiger Insekten (Zygentoma, Insecta) für das Mesozoikum (Untere Kreide, Brazilien). *Senckenbergiana Lethaea*, **78**, 135-140.

Sumbler, M. G. 1996. *London and the Thames Valley (British Regional Geology)* (4th Ed). British Geological Survey, Pp. 183.

Suzuki, Y., Tsujimoto, Y., Matsui, H., Watanabe, K. 2006. Decomposition of extremely hard-to-degrade animal proteins by thermophilic bacteria. *Journal of Bioscience and Bioengineering*, **102**, 73-81.

Sweeney, R. E., and Kaplan, I. R. 1973. Pyrite framboid formation: laboratory synthesis and marine sediments. *Economic Geology*, **68**, 618-634.

Syrio, V. N., and Rios-Netto, A. M. 2002. Ostracodes from the Rio da Batateiras Formation (Lower Cretaceous, Araripe Basin): preliminary results on systematics, biostratigraphy and paleoecology. *Anais da Academia Brasileira de Ciencias*, **74**, 369.

Szwedo, J. 2007. Fulgoromorpha: planthoppers. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Szwedo, J. 2008. Achilidae from the Eocene Baltic amber. *Bulletin of Insectology*, **61**, 109-110.

Thamdrup, B. 2000. Bacterial manganese and iron reduction in aquatic sediments. *Advances in Microbial Ecology*, **16**, 41-84.

Tischlinger, H. 2001. Bemerkungen zur Insekten-Taphonomie der Solnhofener Plattenkalke. *Archaeopteryx*, **19**, 29-44.

Unwin, D., and Martill, D. M. 2007. Pterosaurs of the Crato Formation. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Vaughn, D. J., and Craig, J. R. 1978. Mineral chemistry of metal sulphides. Cambridge University Press. Cambridge, UK, Pp. 512.

Veach, S. W., and Meyer, H. W. 2008. History of Paleontology at the Florissant Fossil Beds, Colorado. *Geological Society of America, Special Paper*, **435**, 1-18.

Venables E. M., and Taylor, H. E. 1963. An insect fauna of the London Clay. *Proceedings of the Geologists' Association*, **73**, 273-279.

Viana, M. S. S., and Neumann, V. H. L. 1999. The Crato Member of the Santana Formation, Ceará State. *In.* Schobennhaus, C., Campos, D. de A., Queiroz, E. T., Winge, M. and Berbert B. (Eds.). *Sitios Geologicos e Paleontologicos do Brasil*.

Vietti, L. A., Bailey, J. V., Fox, D. L., and Rogers, R. R. 2015. Rapid formation of framboidal sulphides on bone surfaces from a simulated marine carcass fall. *PALAIOS*, **30(4)**, 327-334.

Viohl, G. 1990. Taphonomy of fossil-Lagerstätten. Solnhofen lithographic limestones. *In*. Briggs, D. E. G., and Crowther, P. R. (Eds.) *Palaeobiology: a synthesis*. Blackwell, Oxford, Pp. 583.

Vršanský, P. 1999. Lower Cretaceous Blattaria. *In*. Vršanský, P. (Ed.). *Proceedings of the First Palaeoentomological Conference Moscow 1998*. Bratislava, AMBA Projects International, Pp. 199.

Vršanský, P., and Ansorge, J. 2001. New Lower Cretaceous polyphagid cockroaches from Spain (Blattaria, Polyphagidae, Vitisminae subfam. N.). *Cretaceous Research*, **22**, 157-163.

Walton, J. 1923. On a new method for investigating fossil plant impressions or incrustations. *Annals of Botany*, **37**, 379-391.

Wang, B., Zhang, H., Fang, Y., Wang, D., and Ji, S. 2008. New data on Cretaceous Palaeontinidae (Insecta: Hemiptera) from China. *Cretaceous Research*, **29**, 551-560.

Wang, B., Li, J-F., Fang, Y., and Zhang, H.-C. 2009. Preliminary elemental analysis of fossil insects from the Middle Jurassic of Daohugou, Inner Mongolia and its taphonomic implications. *Chinese Science Bulletin*, **54**, 783-787.

Wang, B., Zhao, F., Zhang, H., Fang, Y., and Zheng, D. 2012. Widespread pyritization of insects in the Early Cretaceous Jehol Biota. *PALAIOS*, **27**, 708-712.

Wang, B., Zhang, H., Jarzembowski, E. A., Fang, Y., and Zheng, D. 2013. Taphonomic variability of fossil insects: a biostratinomic study of Palaeontinidae and Tettigarctidae (Insecta: Hemiptera) from the Jurassic Daohugou Lagerstätte. *PALAIOS*, **28**, 233-242.

Wang, Q., and Morse, J. W. 1996. Pyrite formation under conditions approximating those in anoxic sediments: I. Pathway and morphology. *Marine Chemistry*, **52**, 99-121.

Wang, T., Ren, D., Liang, J.-H., and Shih, C. 2007. New Mesozoic Cockroaches (Blattiria: Blattulidae) from Jehol Biota of Western Liaoning in China. *Annales Zoologici*, **57**, 483-495.

Wang, X., Wang, Y., Wang, Y., Xu, X., Tang, Z., Zhang, F., and Hu, Y. 1998. Stratigraphic sequence and vertebrate-bearing beds of the lower part of the Yixian Formation in Sihetun and neighboring area, western Liaoning, China. *Vertebrata PalAsiatica,* **36**, 81-101.

Wang, X., Zhou, Z., He, H., Jin, F., Wang, Y., Zhang, J., Wang, Y., Xu, X., and Zhang, F. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chinese Science Bulletin*, **50**, 2369-2376.

Wang, X., Kellner, A. W., Zhou, Z., and Campos, D. de A. 2007. A new pterosaur (Ctenochasmatidae, Archaeopterodactyloidea) from the Lower Cretaceous Yixian Formation of China. *Cretaceous Research*, **28**, 245-260.

Wang, Y., Ken, S., Zhang, W., and Zheng, S. 2006. Biodiversity and palaeoclimate of the Middle Jurassic floras from the Tiaojishan Formation in western Liaoning, China. *Progress in Natural Science*, **16**, 222-230.

Watling, L., and Thiel, M. 2013. Na*tural History of the Crustacea Volume 1: Functional Morphology and Diversity*. Oxford University Press, New York, Pp. 516.

Watson, L., and Dallwitz, M. J. 2007. [Online] "Rhagionidae". *British Insects: the Families of Diptera*. [Accessed 17 July 2015] http://delta-intkey.com/britin/dip/www/rhagioni.htm.

Weeks, L. G. 1956. Origin of the carbonate concretions in shales, Magdalena Valley, Colombia. *Bulletin of the Geological Society of America*, **66**, 95-102.

Wei, D., and Ren, D. 2013. Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic-Lower Cretaceous Yixian Formation (Liaoning Province, NE China). *Geologica Carpathica*, **64**, 291-304.

Weishampel, D. B. 2004. Provincia de Quenca, Spain; 4. Calizas de la Huérgina Formation. *In*. Weishampel, D. B., Dodson, P., and Osmólska, H. (Eds.). *The Dinosauria, 2nd Edition*. Berkeley, University of California Press, Pp. 880.

Wenzel, J. W. 1990. A social wasp nest from the Cretaceous period, Utah, USA, and its biogeographical significance. *Psyche,* **97**, 21-29.

Werner, K., Swinburne, N. H., Conway-Morris, S., and Barthel, K. W. 1994. *Solnhofen: a study in Mesozoic palaeontology (2nd Edition?*). Cambridge University Press, Cambridge, Pp. 246.

Wilby, P. R., Briggs, D. E. G., and Viohl, G. 1995. Controls of the phosphatization of soft tissues in Plattenkalks. *International Symposium on Lithographic Limestones, 1995, Lleida-Cuenca, Spain. Extended abstracts, II*. Ediciones Universidad Autonóma de Madrid, 165-166.

Wilby, P. R., Briggs, D. E. G., Bernier, P., and Gaillard, C. H. 1996. Role of microbial mats in the fossilization of soft-tissues. *Geology*, **24**, 787-790.

Wilby, P. R., and Briggs, D. E. G. 1997. Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft-tissues. *Geobios*, **20**, 493-502.

Wilkommen J., and Grimaldi, D. A. 2007. Diptera: true flies, gnats and crane flies. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Williams, M., Siveter, D. J., Ashworth, A. C., Wilby, P. R., Horne, D. J., Lewis, A. R., and Marchant, D. R. 2008. Exceptionally preserved lacustrine ostracods from the Middle Miocene of Antarctica: implications for high-latitude palaeoenvironment at 77° south. *Proceedings of the Royal Society*, **275**, 2449-2454.

Wilson, H. M. 1988. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. *Palaeogeography, Palaeoclimatology, and Palaeoecology*, **62**, 609-623.

Wilson, H. M. 2001. First Mesozoic scutigeromorph centipede, from the Lower Cretaceous of Brazil. *Palaeontology,* **44,** 489-495.

Wilson, H. M. 2003. A new scolopendromorph centipede (Myriapoda: Chilopoda) from the Lower Cretaceous (Aptian) of Brazil. *Journal of Paleontology,* **22**, 73-77.

Winterton, S. L. 2010. A new species of Stenobiella Tillyard (Neuroptera, Berothidae) from Australia. *Zookeys*, **64**, 1-8.

Wolf-Schwenninger, K., and Schawaller, W. 2007. Coleoptera: beetles. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Wolf-Schwenniger, K. 2011. The oldest fossil record of Lymexylidae (Insecta: Coleoptera) from the Lower Cretaceous Crato Formation of Brazil. *Insect Systematics and Evolution*, **42**, 205-212.

Wolthers, M., van der Gaast, S. J., and Rickard, D. 2003. The structure of disordered mackinawite. *American Mineralogist*, **88**, 2007-2015.

Wu, Ll., Druschel, G., Findlay, A., Beard, B. L., and Johnson, C. M. 2012. Experimental determination of iron isotope fractionations among Fe-aq(2+)-FeSaq-Mackinawite at low temperatures: Implications for the rock record. *Geochimica et cosmochimica Acta*, **89**, 46-61.

Yuan, H.-W., Wang, M.-K., Chang, W.-L., Wang, L.-P., Chen, Y.-M., and Chious, C.-R. 2006. Soil composition affects the nesting behaviour of blue-tailed bee-eaters (Merops philippius) on Kinmen Island. *Ecological Research*, **21**, 510-512.

Yunzhi, Y., Wanzhi, C., and Dong, R. 2008. New Jurassic Fossil True Bugs of the Pachymeridiidae (Hemiptera: Pentatomorpha) from Northeast China. *Acta Geologica Sinica*, **82**, 35-47.

Zamboni, J. C. 2001. Contribution to the knowledge of the aquatic paleoentomofauna from Santana Formation (Araripe Basin, Lower Cretaceous, Northeast Brazil) with description of new taxa. *Acta Geologica Leopoldensia,* **24,** 129-135.

Zee, C. V. D., Roberts, D. R., Rancourt, D. G., and Slomp, C. P. 2003. Nanogoethite is the dominant reactive oxyhydroxide phase in lake and marine sediments. *Geology*, **31**, 993-996.

Zhang, F., Kearns, S. L., Orr, P. J., Benton, M. J., Zhou, Z., Johnson, D., Xu, X., and Wang, X. 2010. Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature*, **463**, 1075-1078.

Zhang, J. F. 2010. Records of bizarre Jurassic brachycerans in the Daohugou biota, China (Diptera, Brachycera, Archisargidae and Rhagionemestriidae). *Palaeontology*, **53**, 307-317.

Zhang, J. and Li, H. J. 2012. New taxa of snipe flies (Diptera: Brachycera: Rhagionidae) in the Daohugou biota, China. *Paleontological Journal*, **46**, 157-163.

Zhang, J. 2013. Snipe flies (Diptera: Rhagionidae) from the Daohugou Formation (Jurassic), Inner Mongolia, and the systematic position of related records in China. *Palaeontology*, **56**, 217-228.

Zhang, K., Yang, D., Ren, D., and Ge, F. 2008. New Middle Jurassic tangle−veined flies from Inner Mongolia, China. *Acta Palaeontologica Polonica*, **53**, 161-164.

Zhang, X., and Sha, J. 2012. Sedimentary laminations in the lacustrine Jianshangou Bed of the Tixian Formation at Sihetun, western Liaoning, China. *Cretaceous Research*, **36**, 96-105.

Zherikhin, V. V., and Gratshev, V. G. 2004. Fossil Curculionoid Beetles (Coleoptera, Curculionoidea) from the Lower Cretaceous of Northeastern Brazil. *Paleontological Journal,* **38**, 528-537.

Zhou, Y., Zhang, S., Liu, Y., and Yang, H. 2014. Biologically induced deposition of fine suspended particles by filter-feeding bivalves in lane-based industrial marine aquaculture wastewater. *PLOS one*, **9(9),** e107798.

Zhu, M. Y., Babcock, L. E., and Steiner, M. 2005. Fossilization modes in the Chengjiang Lagerstätte (Cambrian of China): Testing the roles of organic preservation and diagenetic alteration in exceptional preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**, 31-46.

8. Appendices

8. 1. Plates

8. 1. 1. SEM Plates

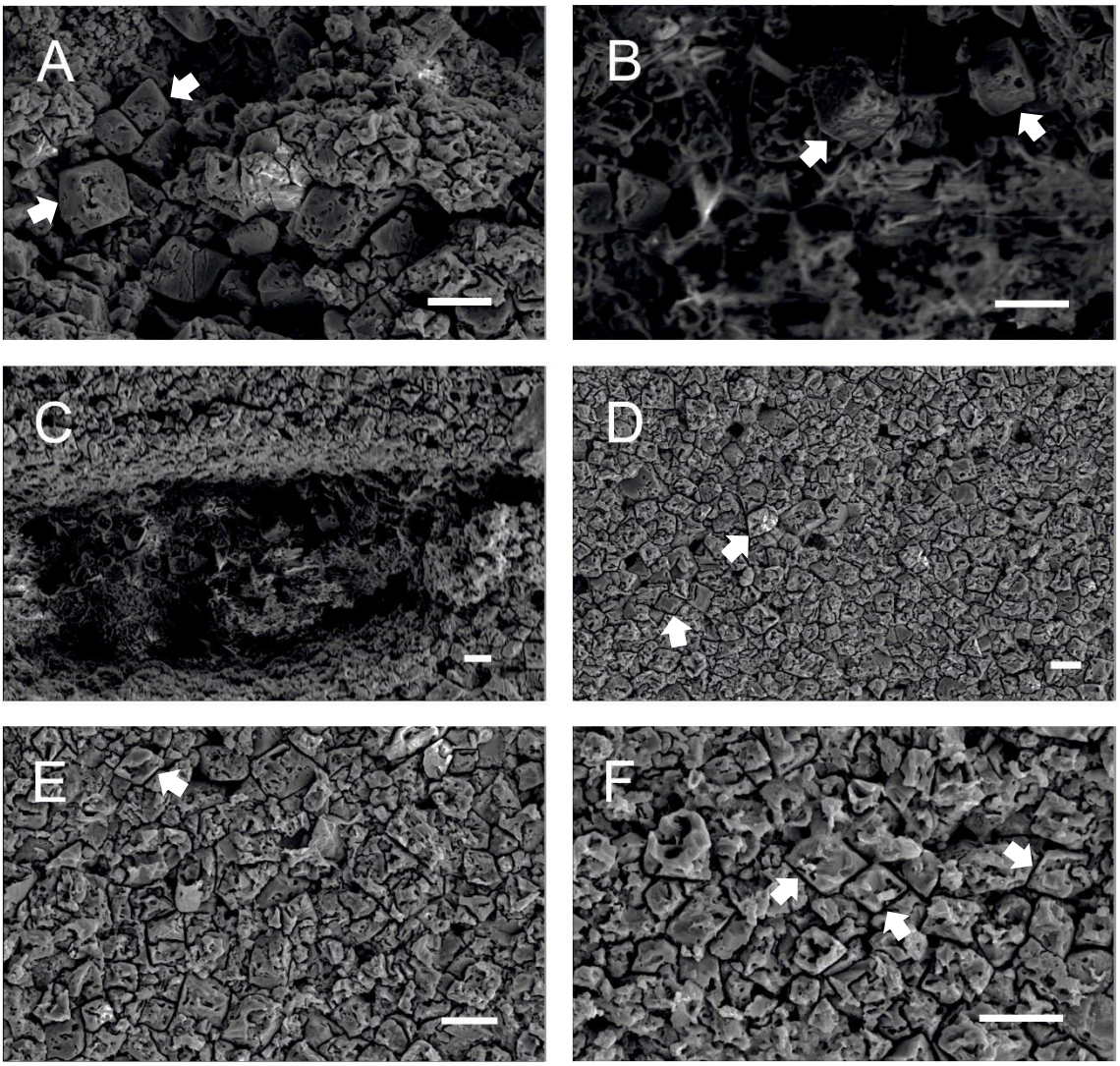


Plate 1: Rhombohedral crystal morphology of the Nova Olinda Member matrix. A-B, Matrix crystal morphology revealed in 'crevasses' (created by dislodged *Dastilbe* coprolite), highlighted by arrows. C, Lower magnification of 'crevasse' where crystal morphology is revealed. D-F, Etched surface of matrix parallel to bedding, revealing interlocking rhombohedral crystals, highlighted by arrows. Magnification increasing with each image. Specimen and image numbers: A, NBSED11(stub)-015; B, NBSED11(stub)-006; C, NBSED11(stub)-003; D, NBSED11(stub)-011; E, NBSED11(stub)-010; F, NBSED11(stub)-009. Scale bars = 10 µm.

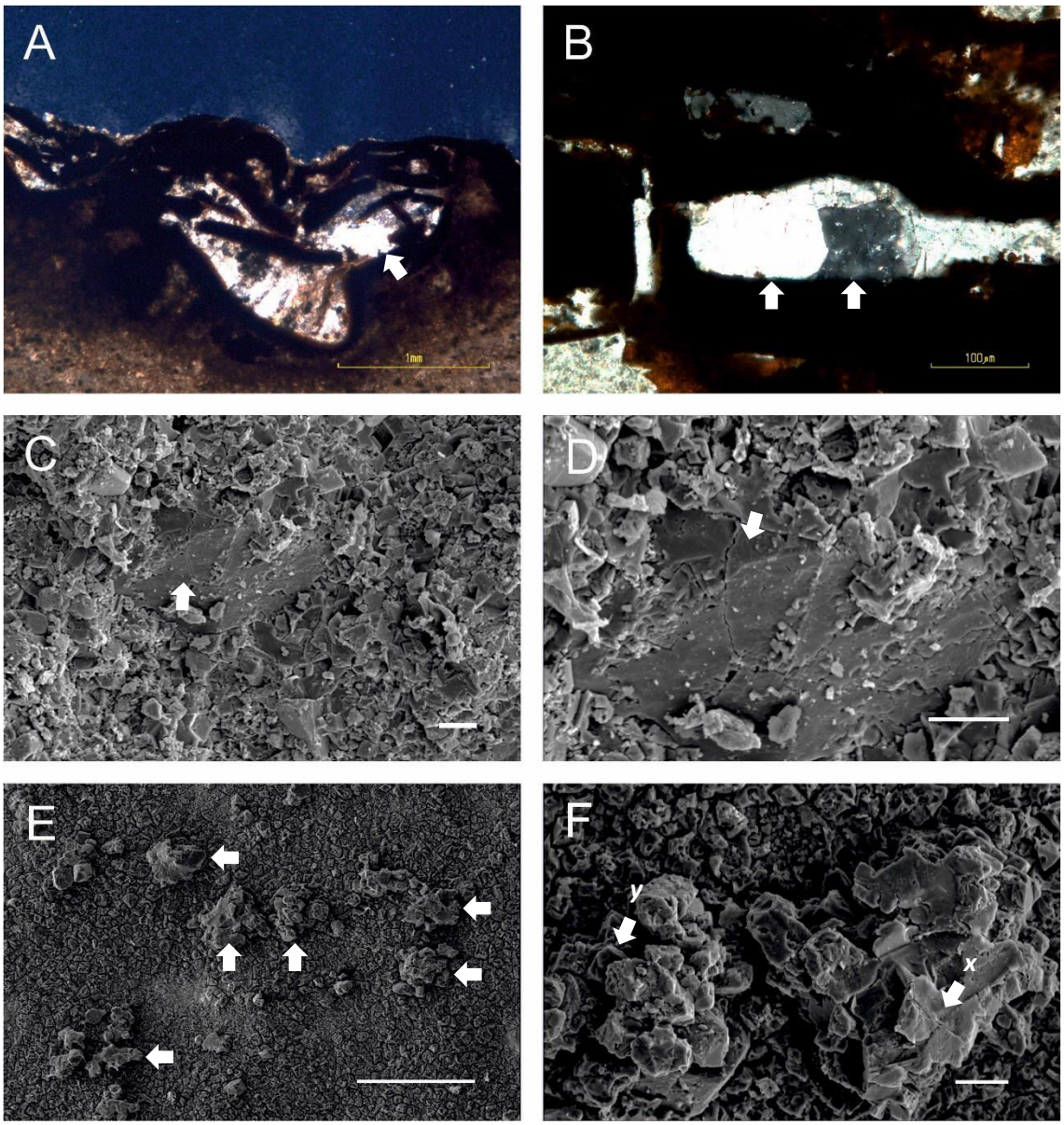


Plate 2: Calcite infilling Nova Olinda Member insect body cavities and cementing sediment grains. A and B, Thin section images showing sparry calcite infills within insect body cavities under cross polarised light. Arrows highlight individual crystals revealed in cross polarised light. C and D, Scanning electron micrograph of a large isolated calcite crystal within the sediment, highlighted by arrow. E, Acetic acid etched (10%) sediment revealing calcite matrix crystals bound by a relatively large, partly-digested, calcite cement forming 'lumps' of crystals. F, Higher magnification images of 'lumps' of crystals, revealing angular moulds from disarticulated rhombohedral grains (*x*) and rhombohedral grains embedded in them (*y*), highlighted by arrows. Specimen and image numbers: A, NBRL011-TS04; B, NBRL011-TS01; C, NBSED01-05; D, NBSED01-06; E, NBSED02b-17; F, NBSED02b-16. A, Scale bar = 1 mm. B and E, Scale bars = 100 µm. C-D and F, Scale bars = 10 µm.

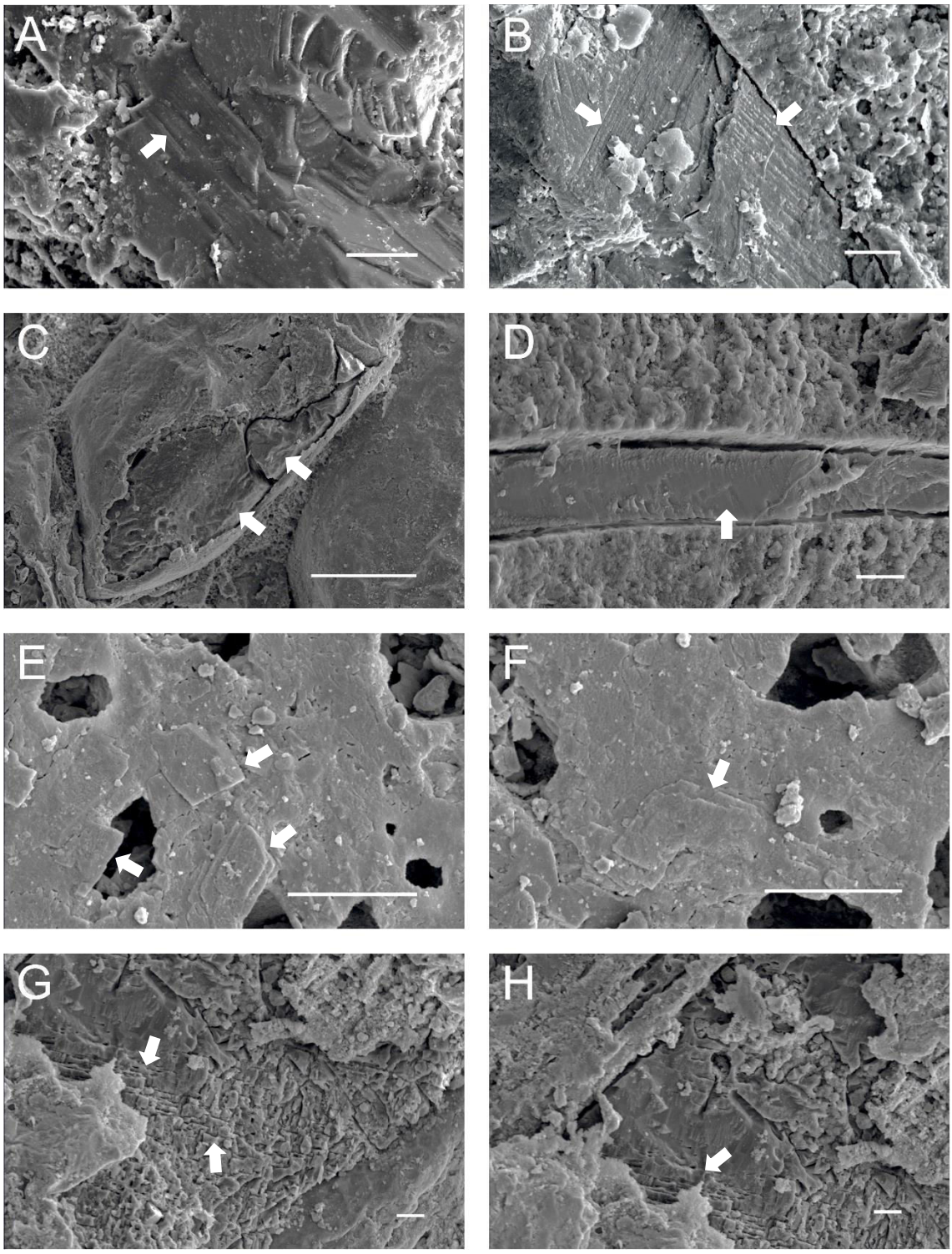


Plate 3: Calcite mineral infills in Nova Olinda Member insect internal cavities. A and B, Calcite infills within thorax (A) and abdomen (B) of fly. Arrows highlight cleavage. C and D, Calcite infills within insect cuticle. C, Two calcite crystals infilling limb, highlighted by arrows. D, Calcite infilling dorsal cuticle in head, highlighted by arrow. E-F, Thin sheet of inter-grown calcite crystals beneath cuticle of posterior abdomen. Rhombohedral cleavage is highlighted by arrows G-H, Acetic acid etched (10%) calcite infill within thorax cavity, revealing many planes of cleavage, highlighted by arrows. Specimen and image numbers: A, NBRL057-47; B, NBRL057-63; C, FLO13-55; D, FLO36-23; E, NBRL078-38; F, NBRL078-37; G, FLO13-31; H, FLO13-32. Scale bars = 10 µm.

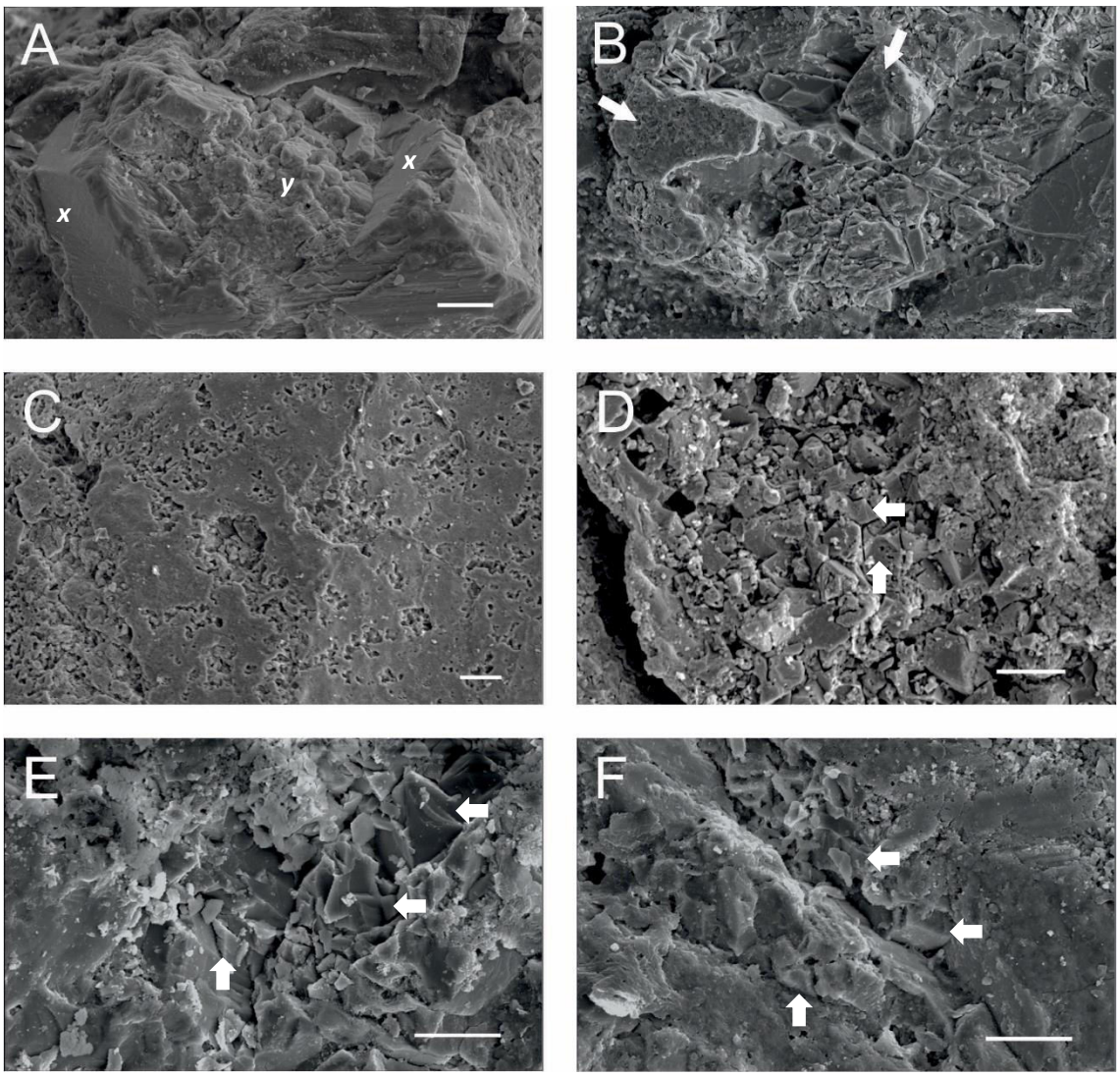


Plate 4: Abraded calcite mineral infills within the Nova Olinda Member insect fossils. A, Abraded calcite mineral infill, resulting in smooth cleaved surfaces (*x*) and a globular surface (*y*). B, Anhedral mineral infills, as a result of 10% acetic acid etched calcite. Arrows highlight larger calcite infills. C, Abraded surface of calcite mineral infill of insect body. D-F, Disorganised anhedral calcite crystals infilling insect body cavities, highlighted by arrows. Specimen and image numbers: A, NBRL071-08; B, NBRL057-28; C, NBRLxxx-37; D, JW02#-020; E, NBRL057-42; F, NBRL057-40. Scale bars = 10 µm.

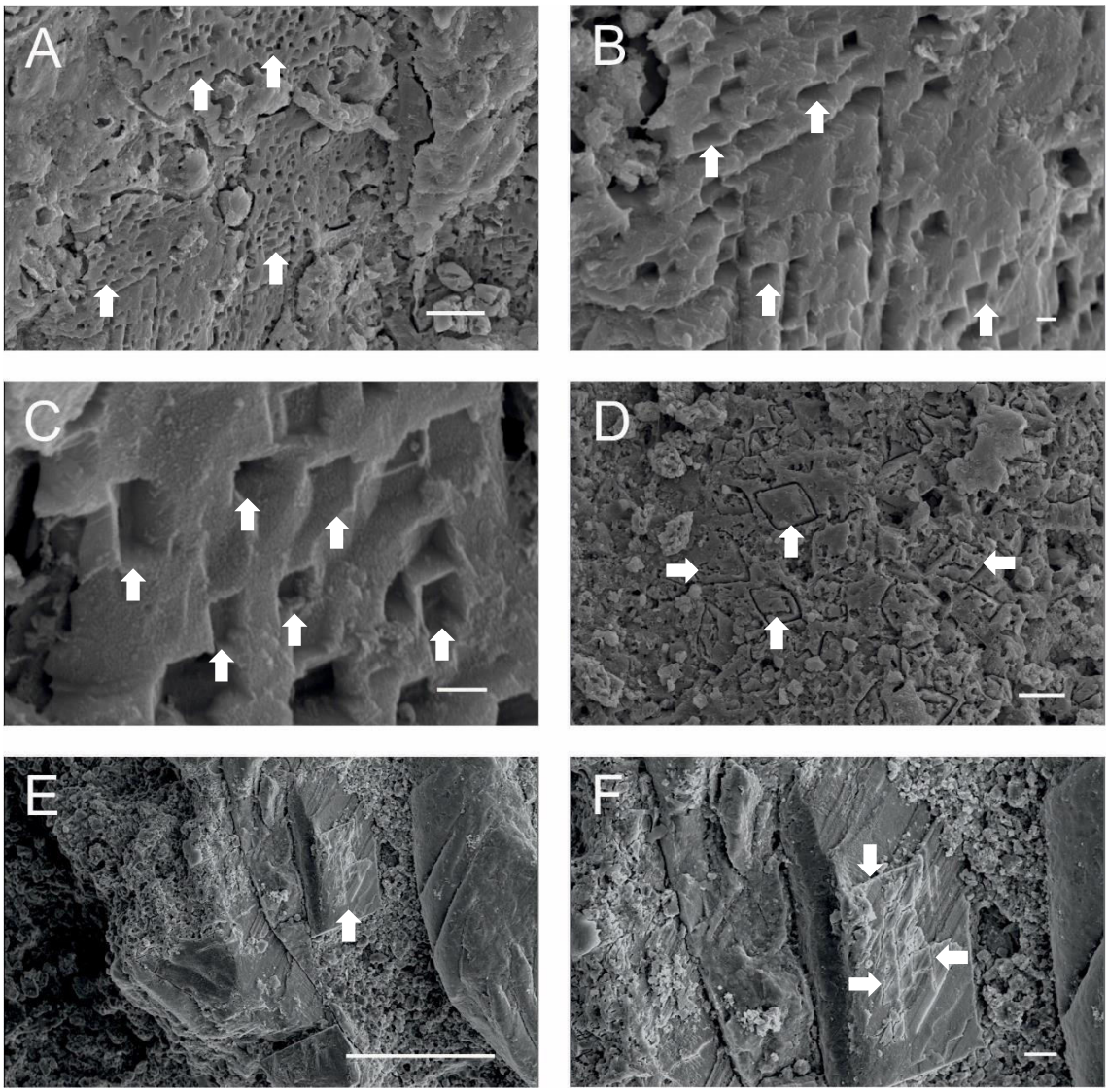


Plate 5: Rhombohedral calcite infilling Nova Olinda Member fossil insect body cavities. A-C, Discrete calcite rhombohedral termini, highlighted by arrows, within calcite infill. D, Acid etched calcite revealing discrete recrystallized rhombohedra within the calcite mineral infill, highlighted by arrows. E-F, 'Large' calcite infills within insect body with cleavage, highlighted by arrows. Specimen and image numbers: A, FLO36-65; B, FLO36-66; C, FLO36-73; D, FLO43-55; E, NBRL057-60; F, NBRL057-61. A, D and F, Scale bars = 10 µm. B-C, Scale bars = 1 µm. E, Scale bar = 100 µm.

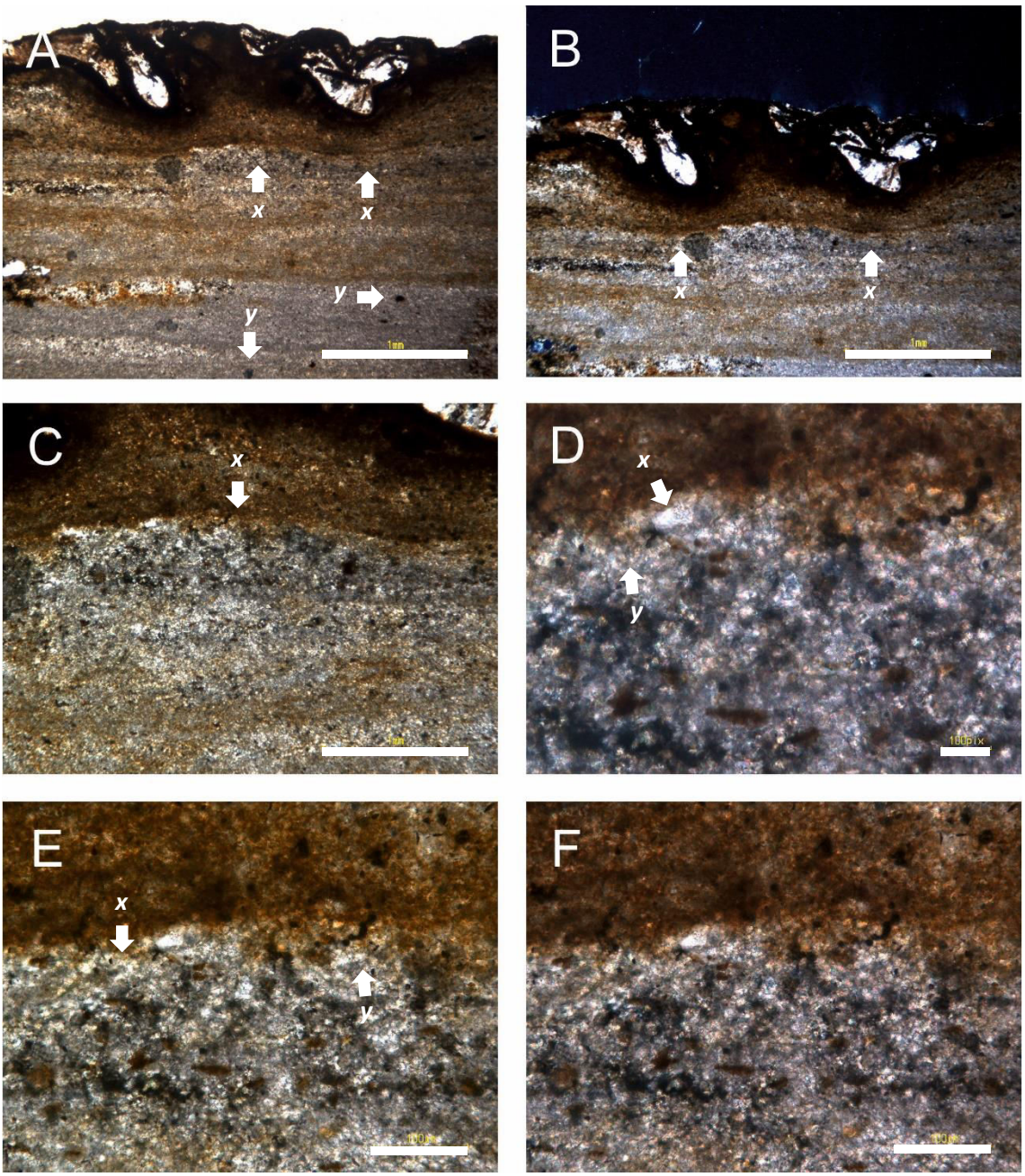


Plate 6: Thin sections of the Nova Olinda Member sediment and fossils perpendicular to bedding, revealing laminae structure and sediment deformation. A-C, Thin section images of laminae deformed around fossils (*x*) and dispersed microfossils/fossilised detritus (*y*), highlighted by arrows. D-F, Higher magnification images of laminae boundaries showing both sharp (*x*) and relatively gradual (*y*) contacts. E, Plane polarised light; F, Cross polarised light of same field of view. Specimen and image numbers: A, NBRL017-TS01; B, NBRL017-TS08; C, NBRL017-TS09; D, NBRL017-TS10; E, NBRL017-TS12; F, NBRL017-TS13. A-C, Scale bars = 1 mm; D, Scale bar = 100 pix; E and F, Scale bars = 100 µm.

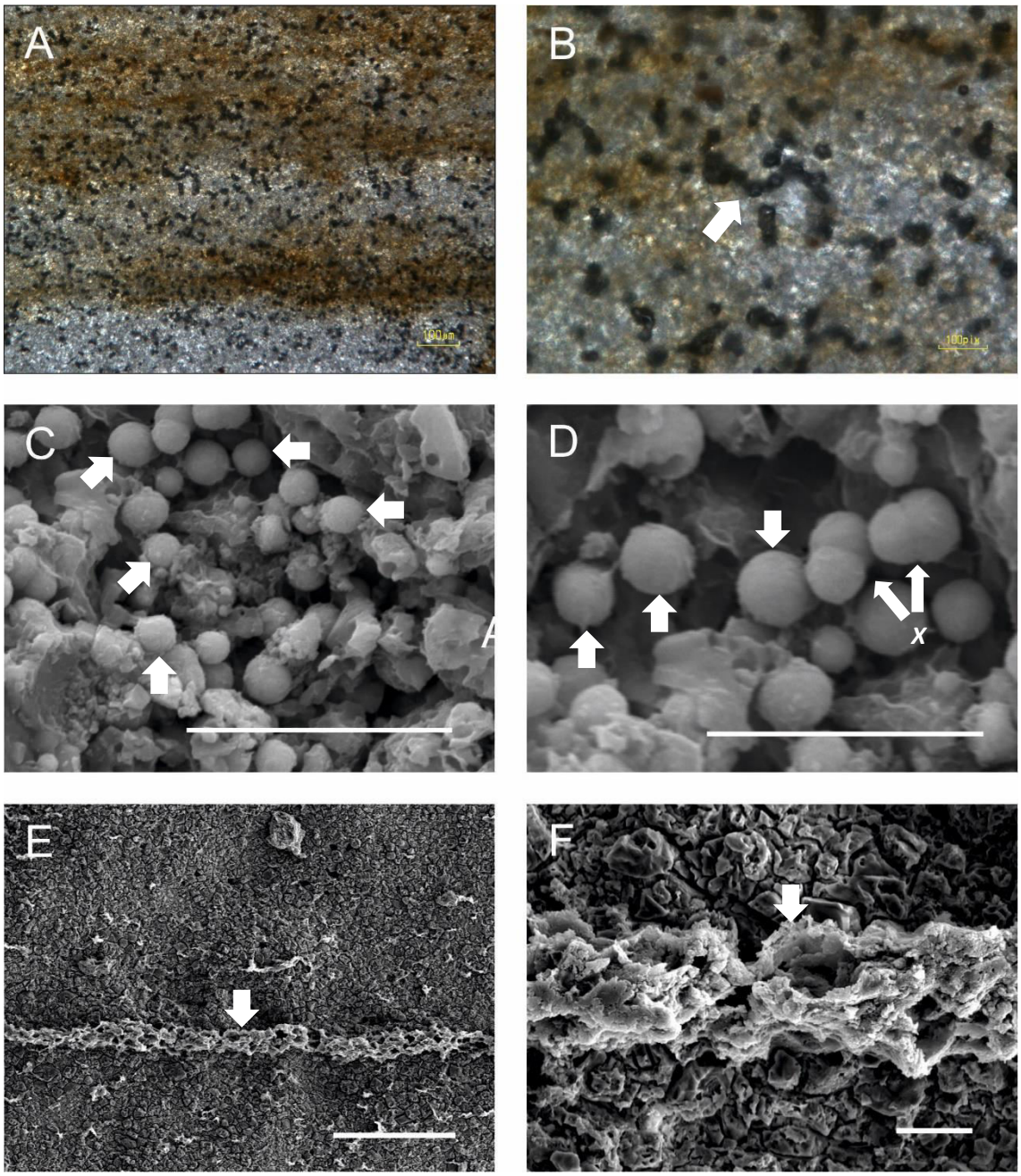


Plate 7: Microfossils and elongate lens of globular iron sulphide and clay material within the Nova Olinda Member sediment. A-D, Hollow black microspheres (microfossils) distributed throughout the sediment. A and B, Thin section images perpendicular to bedding. B, Arrow highlights chains of microfossils. C and D, Scanning electron micrographs of the same microfossils. Arrows highlight microspheres, (*x*) highlights preservation of cells undergoing mitosis. E and F, Elongate lens of globular iron sulphide and clay material, highlighted by arrow. Specimen and image numbers: A, NBRL017-TS15; B, NBRL017-TS22; C, NBSED02a EDX Site of Interest 1; D, NBSED02a EDX Site of Interest 2; E, NBSED02b-22; F, NBSED02b-23. A and E, Scale bars = 100 µm. B, Scale bar = 100 pix. C, Scale bar = 9 µm. D, Scale bar = 6 µm. F, Scale bar = 10 µm.

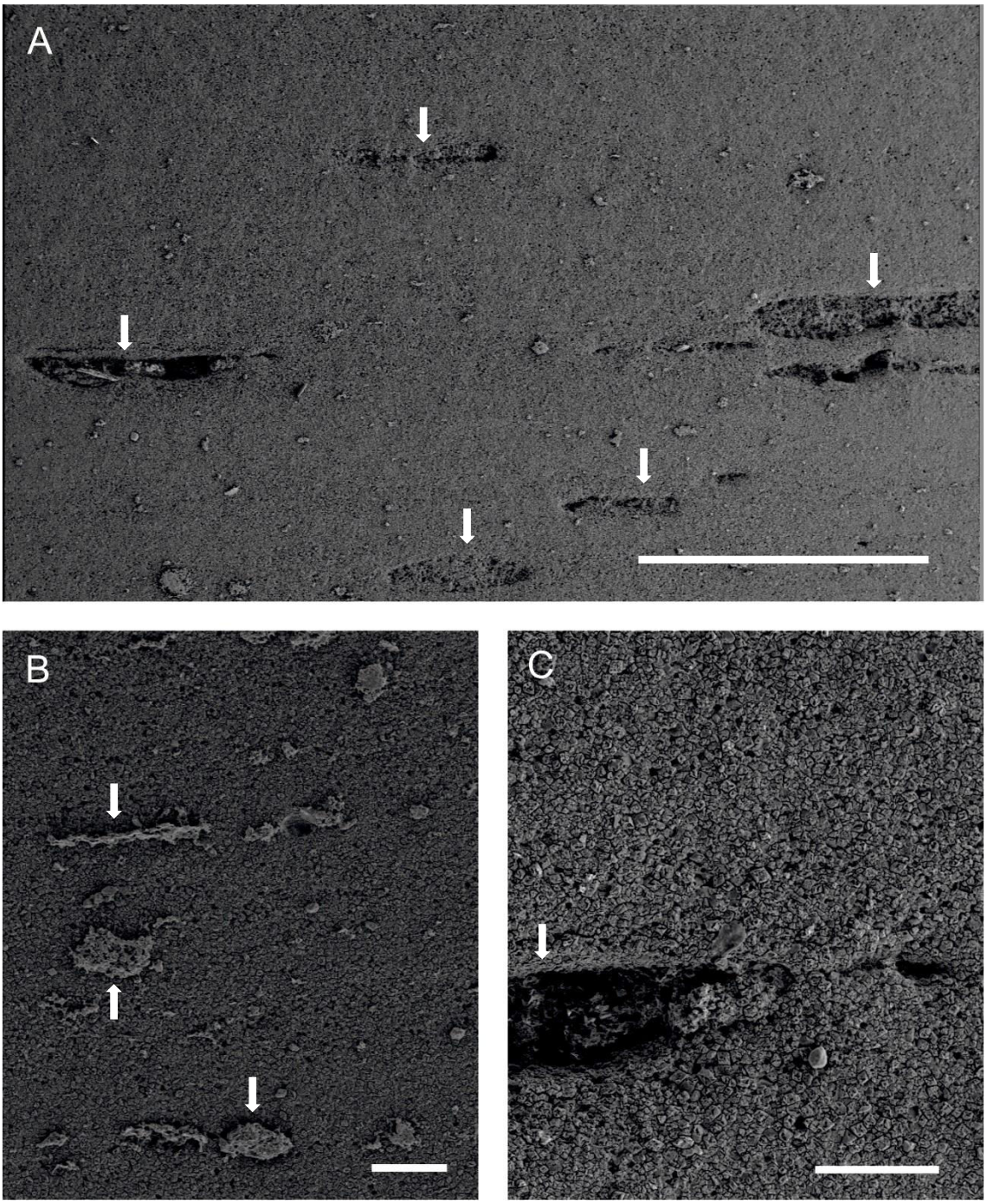


Plate 8: Overviews of the Nova Olinda Member matrix and its contents. A and C, Un-etched overviews of sediment perpendicular to bedding at varying magnifications. B, Acetic acid (10%) etched overview of sediment perpendicular to bedding, highlighting undigested organic matter. Arrows highlight *Dastilbe* coprolites, preserved as indents in A and C, and as high relief in B. Specimen and image numbers: A, NBSED11(stub)-001; B, NBSED11(stub)-002; C, NBSED11(stub)-016. A, Scale bar = 1 mm, B and C, Scale bars = 100 µm.

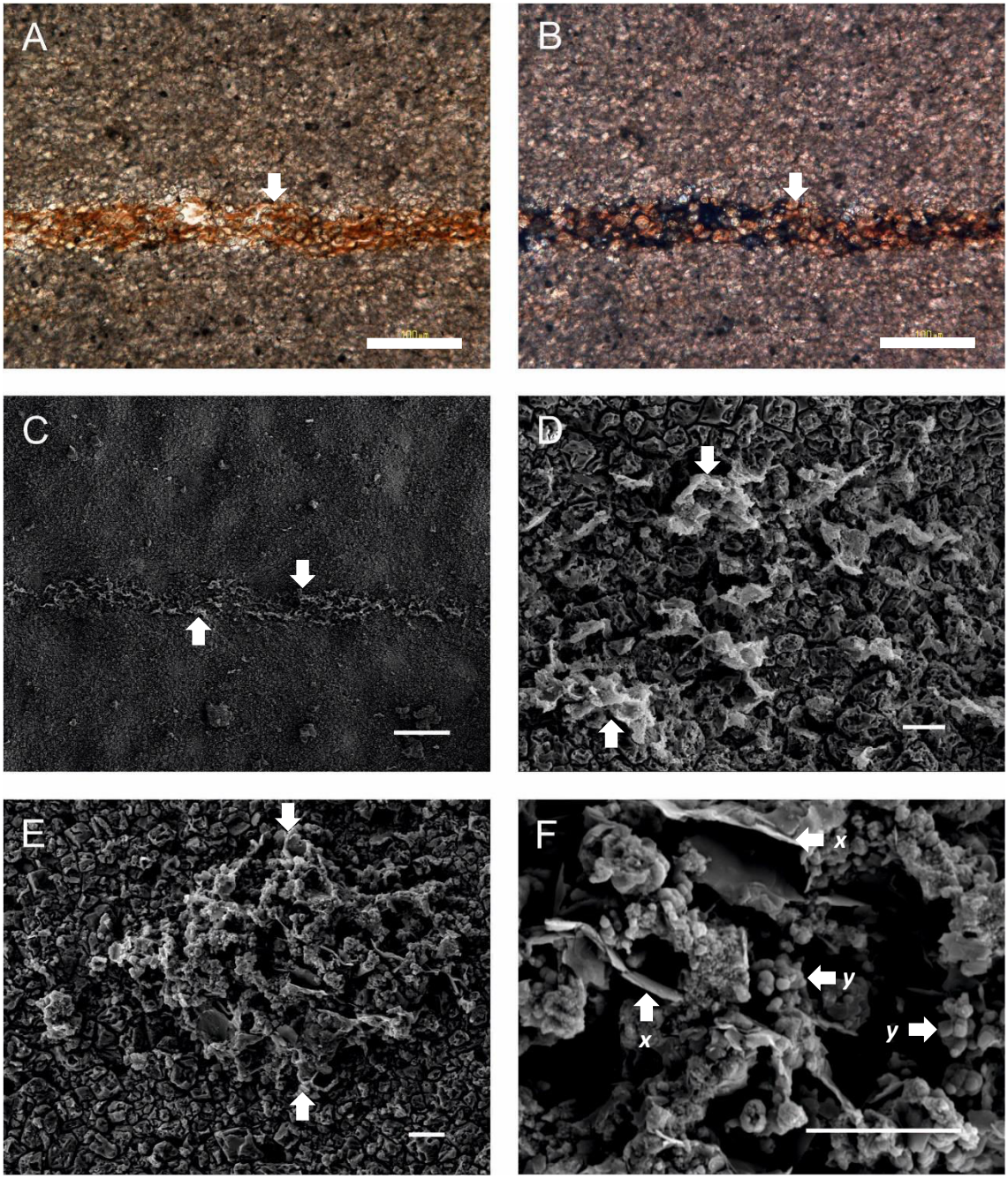


Plate 9: Images of Nova Olinda Member sediment with structures interpreted as *Dastilbe* coprolites, revealing their globular goethite and clay content. A and B, Coprolites in thin section, highlighted by arrows. A, Plane polarised light; B, Cross polarised light. C and D, Scanning electron micrographs of 'scrappy' coprolite in cross section along its length, highlighted by arrow. E and F, Scanning electron micrograph of coprolite in cross section along its width. E, Arrows mark top and bottom of coprolite. F, Arrows highlight (*x*) clay minerals and (*y*) globular material. Specimen and image numbers: A, NBSED02-TS07; B, NBSED02-TS-08; C, NBSED02b-12; D, NBSED02b-14; E, NBSED11(stub)-007; F, NBSED11(stub)-008. A-C, Scale bars = 100 µm. D-F, Scale bars = 10 µm.

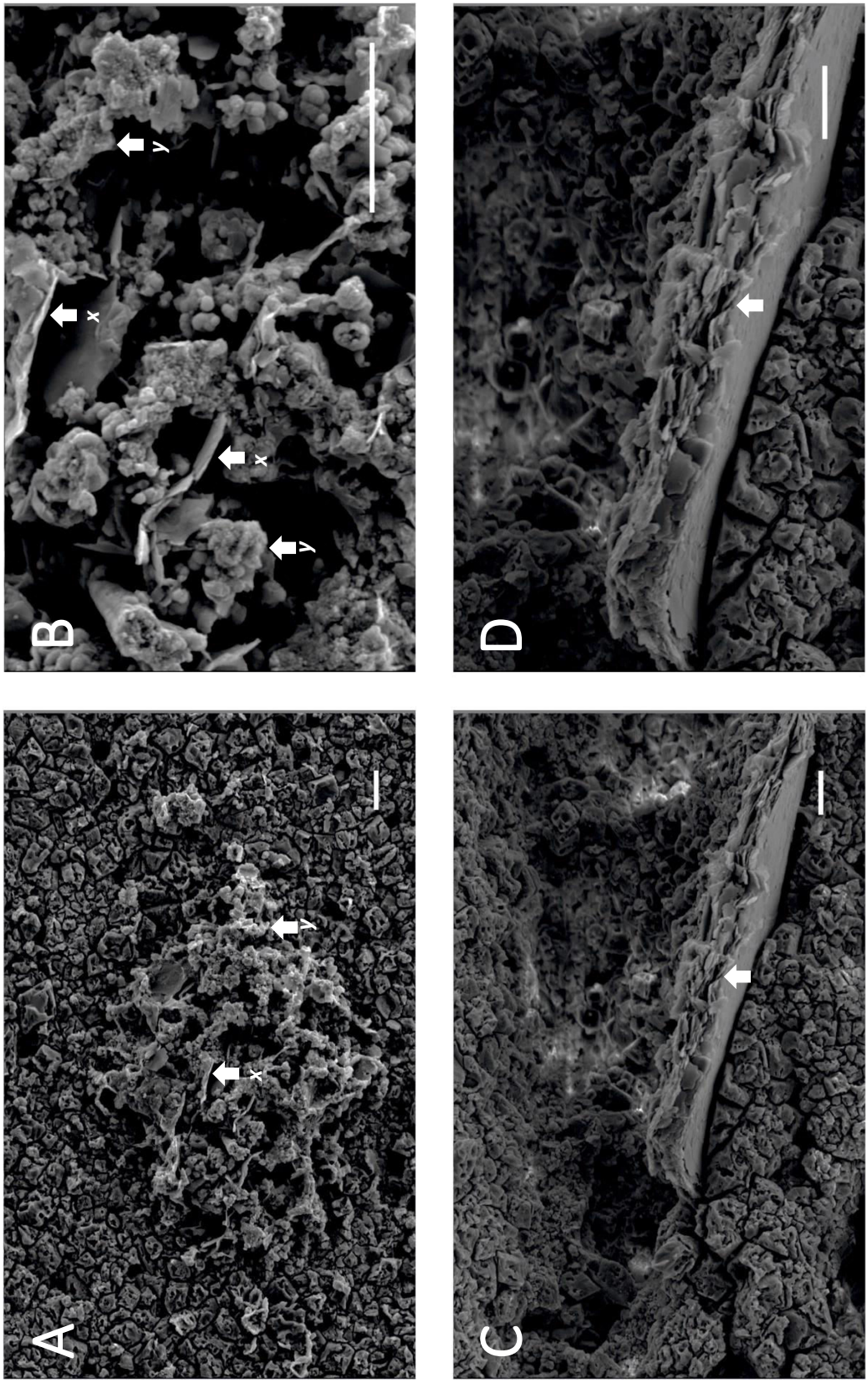


Plate 10: Clay minerals associated with globular material in *Dastilbe* coprolites. A and B, Blade-like clay minerals (*x*) with globular material (*y*). C and D, Large bundle of delaminating platy clay minerals associated with globular matter (not present in these images), highlighted by arrows. Clays likely represent detrital illite. Specimen and image numbers: A, NBSED11(stub)-007; B, NBSED11(stub)-008; C, NBSED11(stub)-013; D, NBSED11(stub)-014. Scale bars = 10 µm.

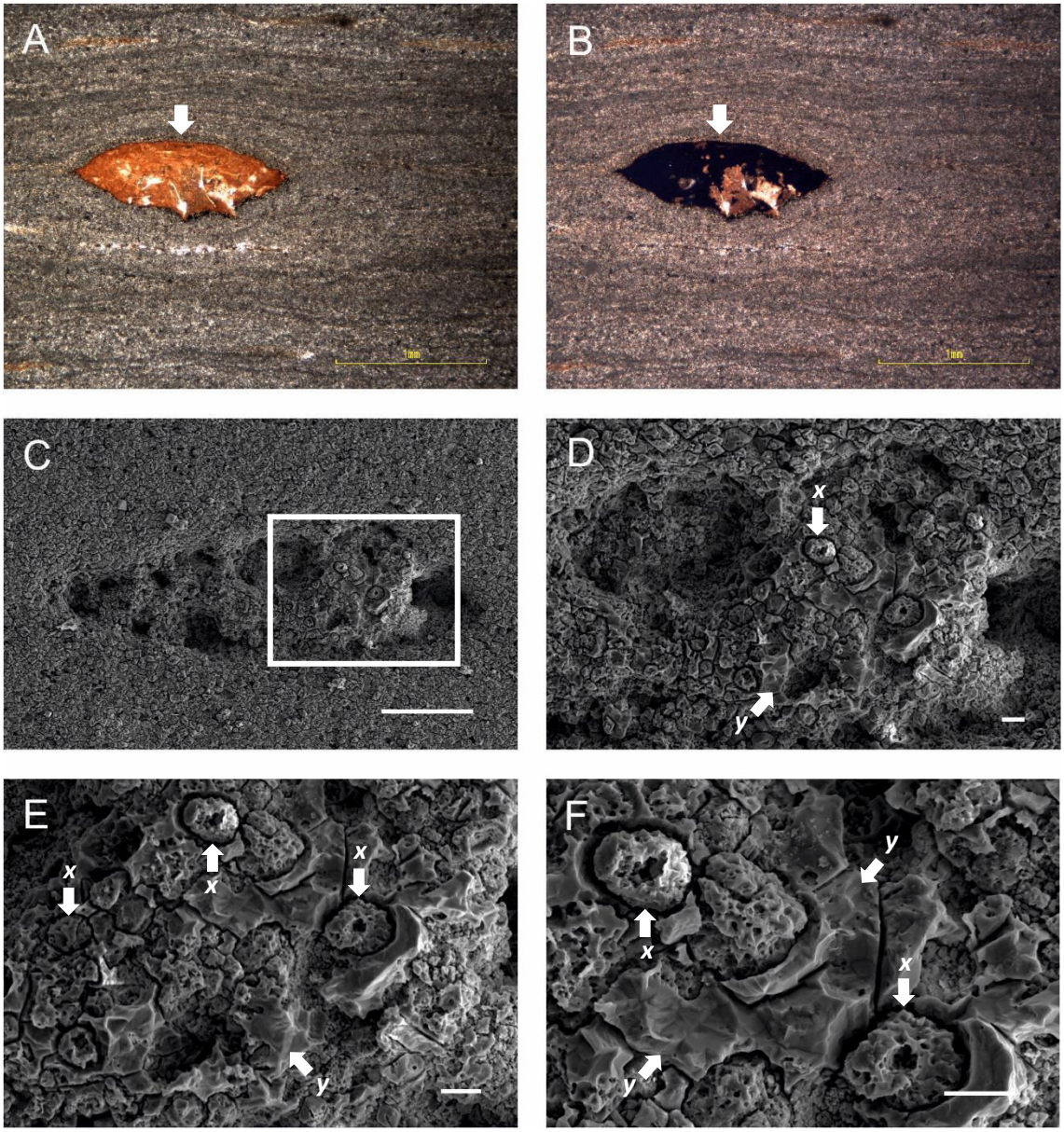


Plate 11: Calcitic structures within the Nova Olinda Member sediment. A and B, Fossil material resembling an ostracod viewed in thin section, highlighted by arrow, including laminae deforming around the fossil. A, Plane polarised light; B, Cross polarised light. C-F, Calcitic structure etched by 10% acetic acid. C, Square highlights area magnified in images D-F. E and F, Subspherical bodies (*x*) likely represent calcified bacteria (Catto *et al*., 2016). Etched calcite surrounding them (*y*) likely represents calcified extracellular polymeric substances (Catto *et al*., 2016). Alternatively, C-F could represent a mould of a gastropod, although this is unlikely given the depositional settings. Specimen and image numbers: A, NBSED02-TS01; B, NBSED02-TS02; C, NBSED11(stub)-020; D, NBSED11(stub)-021; E, NBSED11(stub)-022; F, NBSED11(stub)-023. A and B, Scale bars = 1 mm. C, Scale bar = 100 µm. D-F, Scale bars = 10 µm.

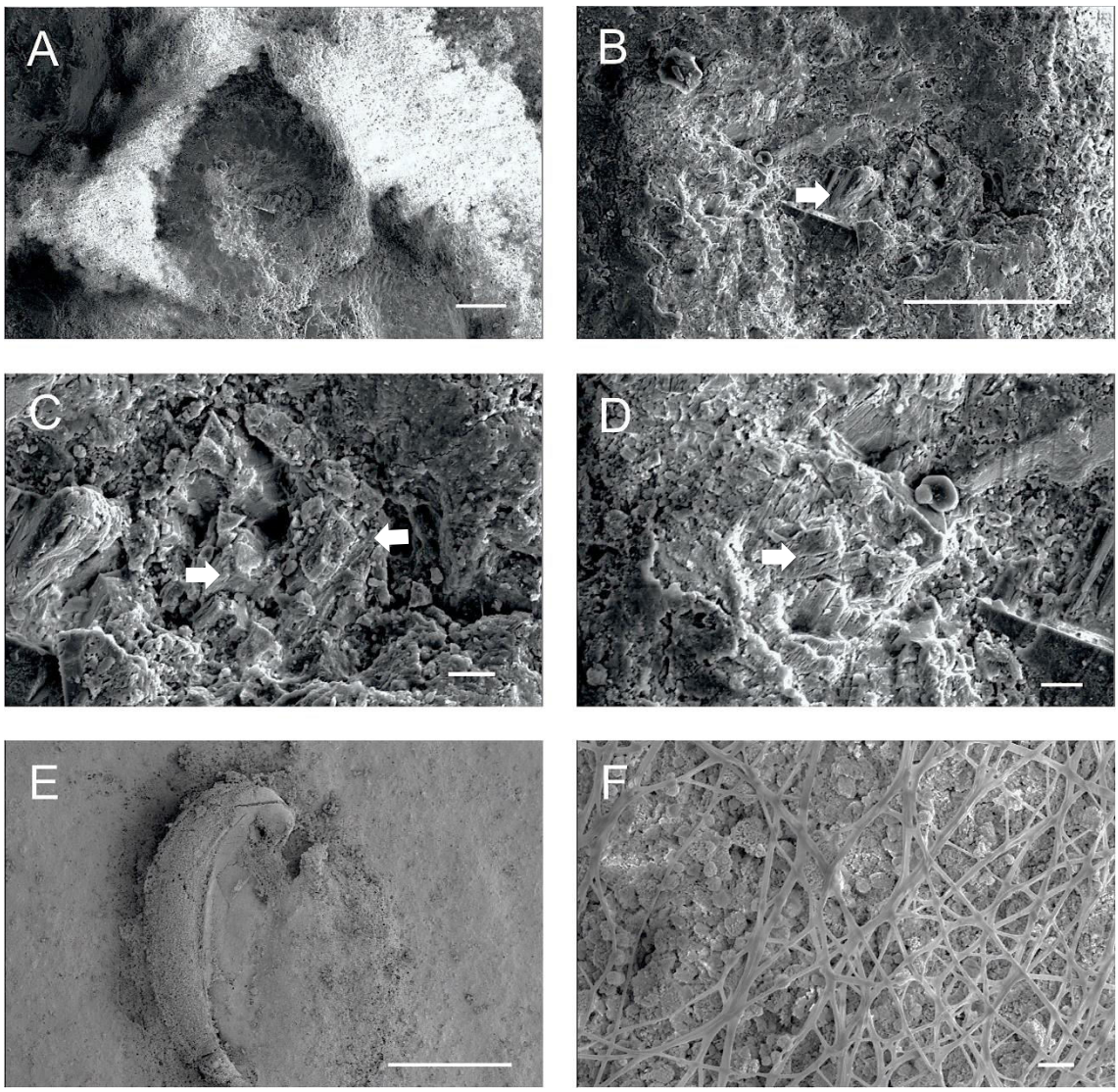


Plate 12: Curation damage to Nova Olinda Member fossil insect eyes. A, Abrasion damage to eye, resulting in the loss of ommatidia and charging when viewed under SEM. B-D, Abrasion removing ommatidia has revealed calcite mineral infill, possibly replicating the optic nerve, highlighted by arrow. E, Overview of very poorly preserved Raphidioptera head, including a single eye. F, Higher magnification image of eye revealing disarticulated ommatidia and extreme contamination by actinomycete bacteria filaments. Specimen and image numbers: A, NBRL057-19; B, NBRL057-20; C, NBRL057-22; D, NBRL057-24; E, NBRL073-02; F, NBRL073-09. A-B, Scale bars = 100 µm. C-D and F, Scale bars = 10 µm. E, Scale bar = 1 mm.

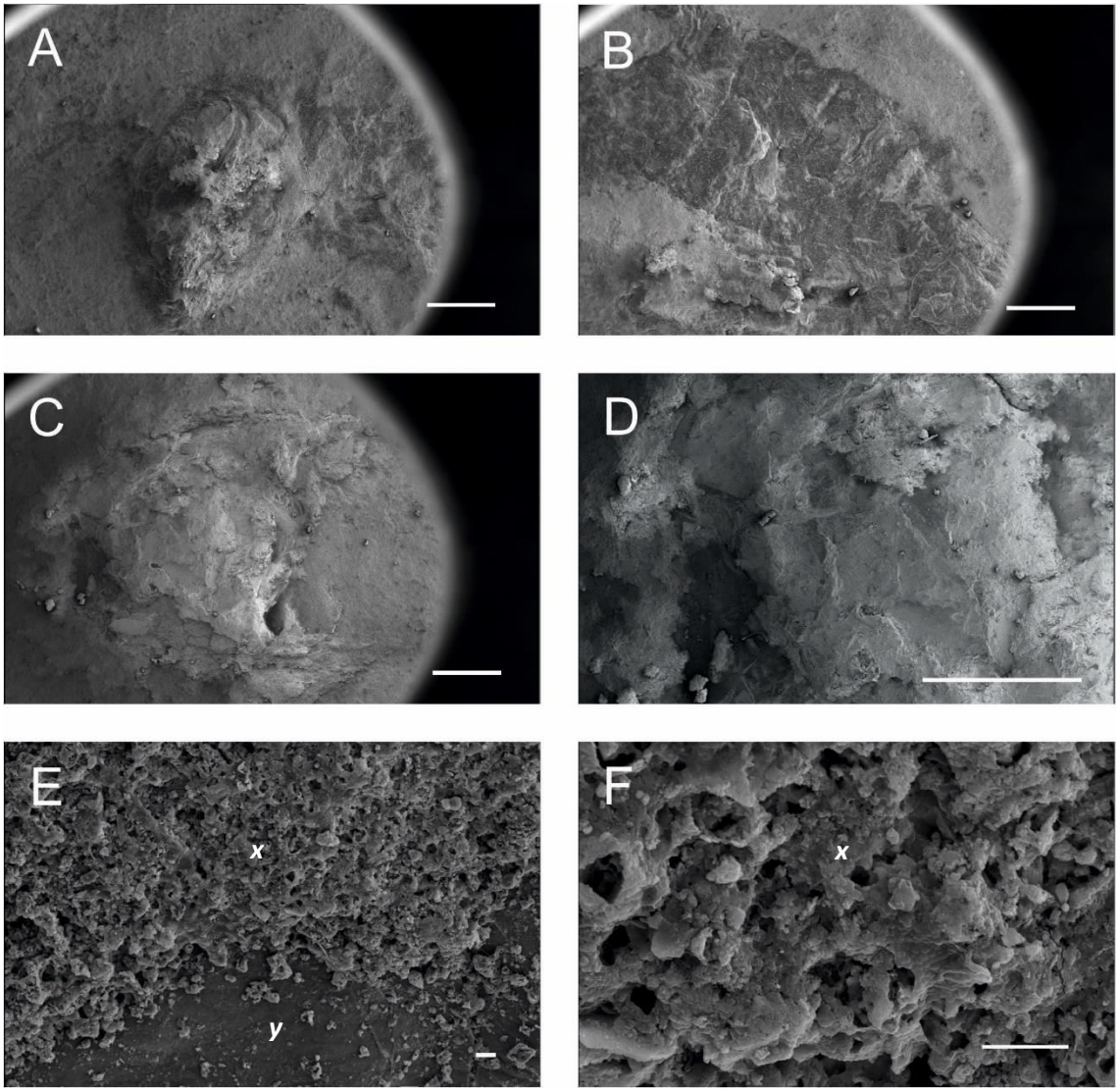


Plate 13: Examples of poor preservation of Nova Olinda Member insects. A, Overview of poorly preserved orthopteran head, with high relief, but no preservation of cuticular features. B, Overview of poorly preserved Orthoptera abdomen, with low relief and minimal preservation of cuticular features. C-D, Indeterminate insect thorax, with very poorly preserved (abraded?) cuticle. E-F, Mineralised fossil contamination that may have originally been organic detritus preserved as globular material (*x*) covering smooth, featureless cuticle (*y*). Specimen and image numbers: A, NBRL061-01; B, NBRL061-03; C, NBRL075-01; D, NBRL075-03; E, FLO38-77; F, FLO38-80. A-D, Scale bars = 1 mm. E-F, Scale bars = 10 µm.

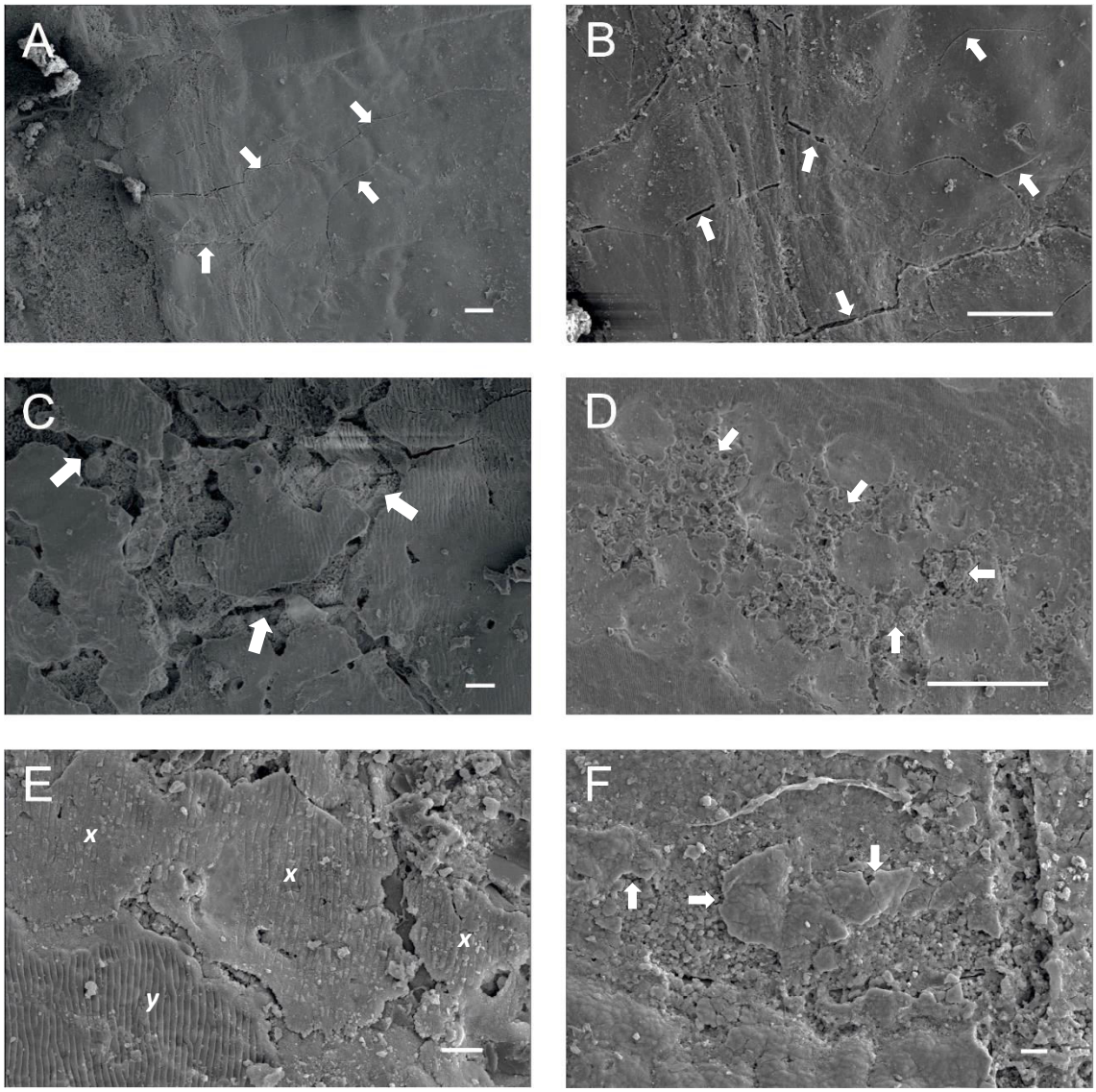


Plate 14: Examples of ‘peeling’ (delaminating) and breaking cuticle in Nova Olinda Member insect fossils. A-B, Cracked cuticle breaking into thin layers, highlighted by arrows. C, ‘Deep crevices’, highlighted by arrows, in damaged cuticle with granular fabric underneath. D, Damage to cuticle revealing globular breaks, highlighted by arrows. E, Poorly-preserved epicuticle with remnants of scales beginning to delaminate (*x*), adjacent to well-preserved cuticle with scales (*y*). F, Epicuticle delaminating, highlighted by arrows. Specimen and image numbers: A, FLO38-97; B, FLO38-88; C, NBRL018-20; D, NBRL036-51; E, NBRL036-53; F, FLO38-47. A-B and D, Scale bars = 100 µm. C and E-F, Scale bars = 10 µm.

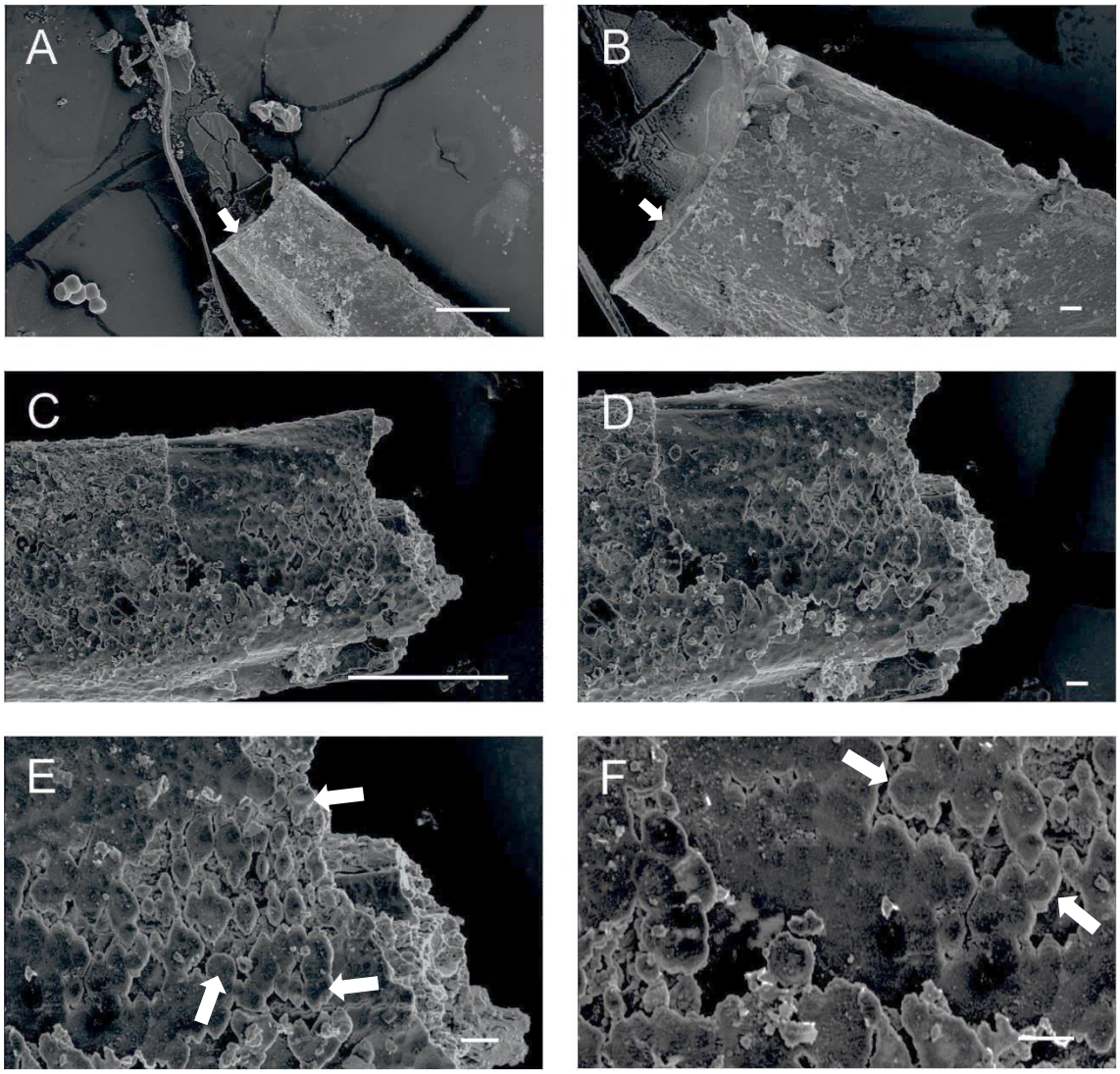


Plate 15: Disarticulated ovipositoral sheath of specimen SMNS 700902 [*Parviformosus wohlrabeae* holotype]. A-B, Overviews of leftmost (proximal?) end, however much of this end has been lost. Arrow highlights sharp break. C-D, Overviews of rightmost (distal?) end, however extremities of this end have also been lost. E-F, Higher magnification images showing the surface fabric of the ovipositor. Arrows highlight sub-circular shapes which may represent hemispherical pseudomorphed pseudoframboids replacing the sheath, exposed via effervescence during 10% acetic acid digestion. Specimen SMNS 700902, image numbers: A, JW614(resi)-005; B, JW614(resi)-001; C, JW614(resi)-016; D, JW614(resi)-010; E, JW614(resi)-011; F, JW614(resi)-014. A and C, Scale bars = 100 µm. B and D-F, Scale bars = 10 µm.

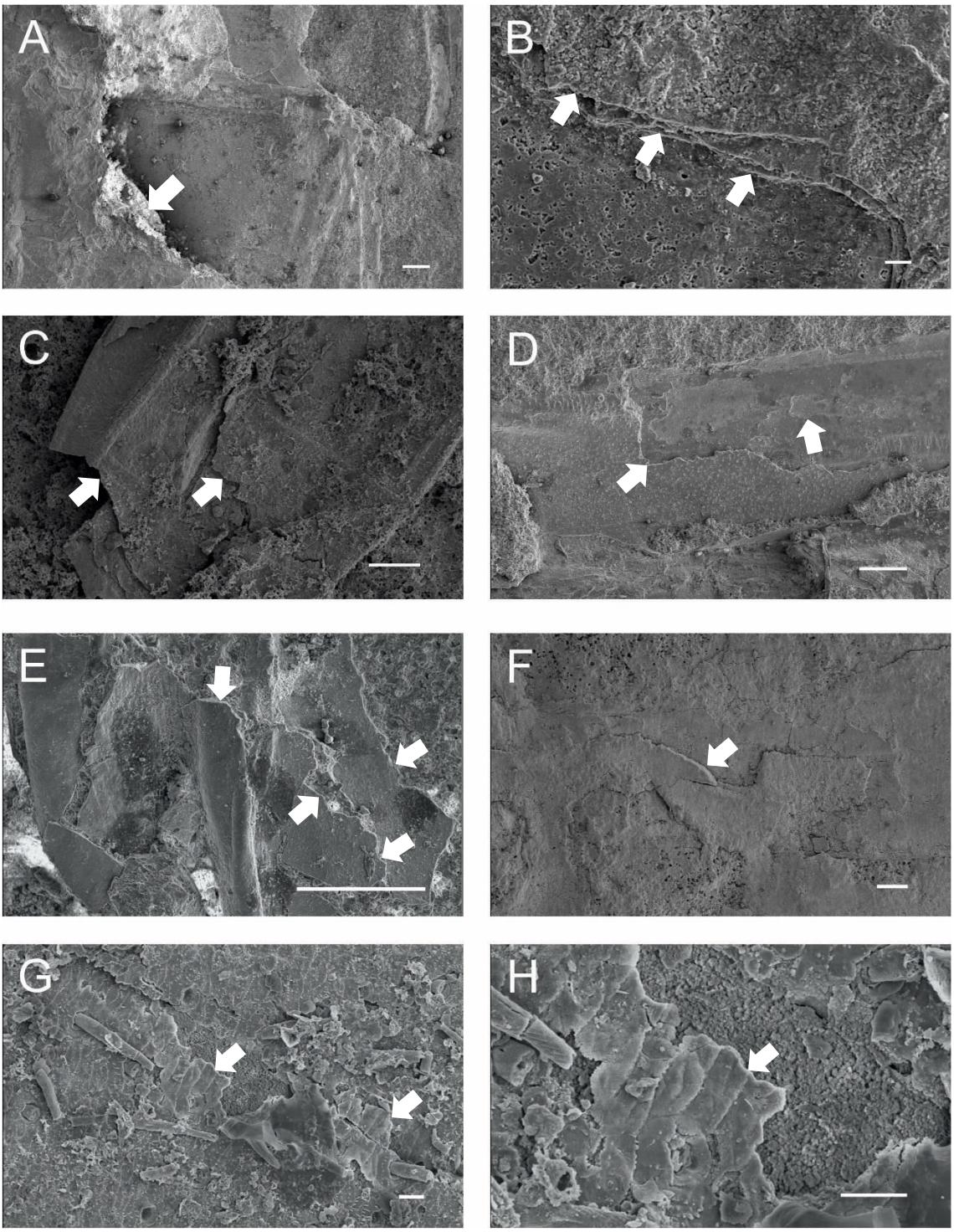


Plate 16: Examples of damaged cuticle in Nova Olinda Member insect fossils. A, Specimen with large portions of cuticle disarticulated, leaving loosely articulated cuticle that charges under scanning electron microscopy, highlighted by arrow. B- E, Broken cuticle delaminating in multiple thin layers, likely the result of structural differences between epi- exo- and endocuticle, highlighted by arrows. F, Cuticle delaminating in a single large thick layer, highlighted by arrow. G-H, Extremely thin, well-preserved epicuticle delaminating, highlighted by arrows. This damage may be the result of effervescence during acid digestion or mild abrasion. Specimen and image numbers: A, NBRLXXX-20; B, NBRLXXX-39; C, NBRL079-35; D, NBRL071-17; E, NBRL071-15; F, NBRL078-28; G, NBRL059-45; H, NBRL059-46. A and C-F, Scale bars = 100 µm. B and G-H, Scale bars = 10 µm.

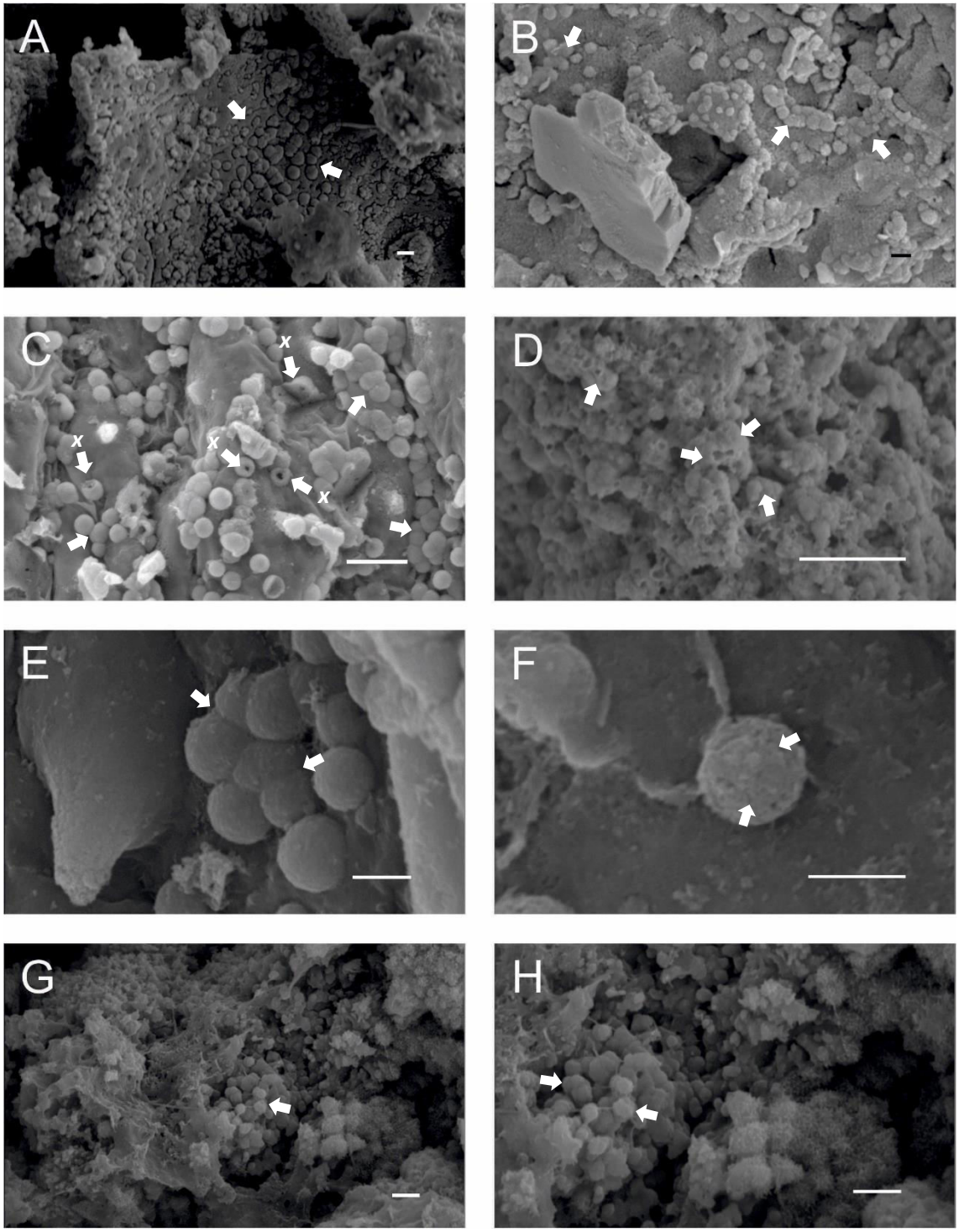


Plate 17: Examples of clustered 'microspheres' on the surface of poorly-preserved cuticle from Nova Olinda Member fossil insects, possibly representing bacterial contamination. A, Cluster of 'microspheres' intergrown in a crevasse of broken cuticle, highlighted by arrow. B-C, Clusters of inter-grown 'microspheres' across smoothed cuticle, highlighted by arrows. Some are broken, revealing their hollow interiors (*x*). D, Clusters of hollow 'microspheres' replacing area of cuticle (possibly decayed), highlighted by arrows. E-F, Higher magnification images of 'microspheres', revealing many intergrown (E), and a granular surface (F). G-H, Clusters of large 'microspheres' loosely aggregated in poorly preserved insect tissues, highlighted by arrows. Specimen and image numbers: A, JW614-088; B, NBRL054-39; C, NBRL045-33; D, JW291-022; E, NBRL045-##58; F, NBRL045-##63; G, NBRL054-80; H, NBRL054-82. A-B and E-H, Scale bars = 1 µm. C, Scale bar = 5 µm. D, Scale bar = 10 µm.

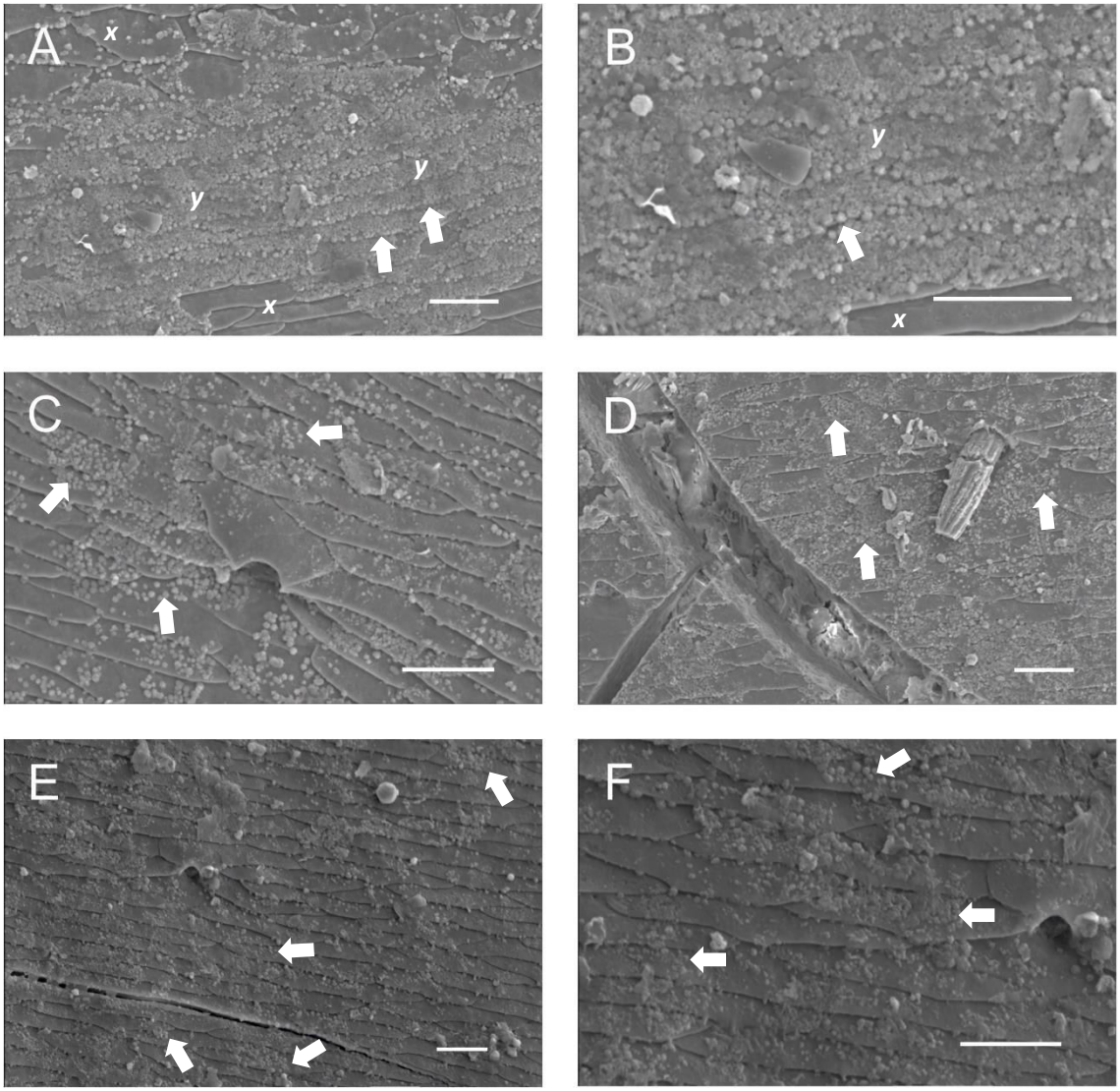


Plate 18: Examples of granular ‘microspheres’ coating and replacing insect cuticle in Nova Olinda Member fossil insects. A-B, Well-preserved cuticle with scales (*x*) surrounding area of cuticle replicated in ‘microspheres’ (*y*), while retaining traces of scales, highlighted by arrows. C-F, Patches of ‘microspheres’ coating the surface of cuticular scales, rather than directly replacing them, highlighted by arrows. Specimen and image numbers: A, NBRL040-53; B, NBRL040-54; C, NBRL040-55; D, NBRL040-65; E, NBRL040-120; F, NBRL040-126. Scale bars = 10 µm.

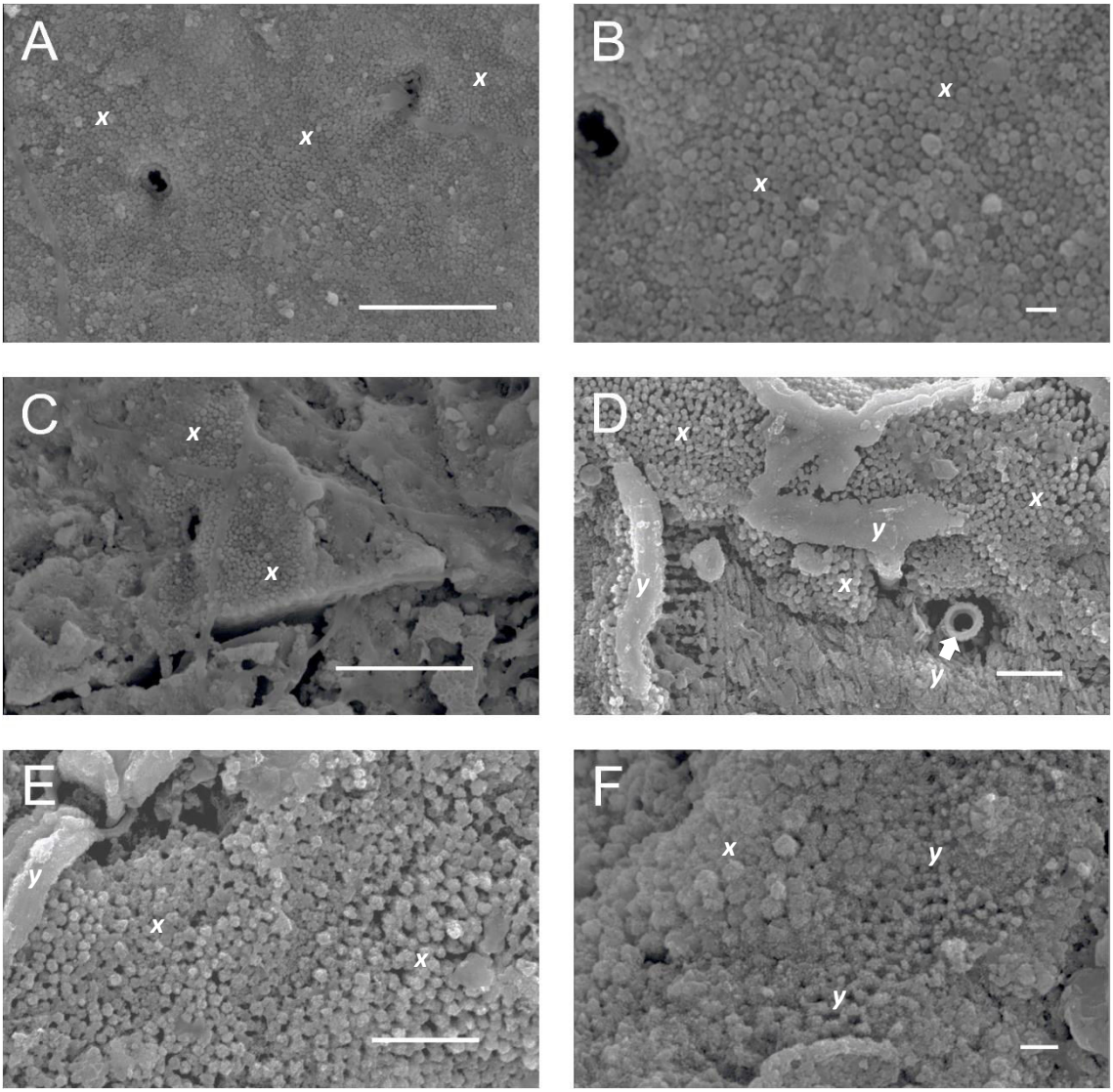


Plate 19: Examples of poor-replication of cuticle by aggregates of ‘microspheres’ (possibly very small pseudoframboids). A-C, ‘Microspheres’ coarsely replacing flat cuticle (*x*), preserving no original cuticular surface structures. D-E, ‘Microspheres’ coarsely replacing beetle elytra (*x*), while some cuticular structures are retained (*y*). F, ‘Microspheres’ of varying sizes, including relatively coarse (*x*) and fine (*y*) replacing beetle cuticle. Specimen and image numbers: A, FLO36-44; B, FLO36-46; C, FLO36-38; D, NBRL045-75; E, NBRL045-59; F, NBRL045-##28. A and C, Scale bars = 10 µm. B and F, Scale bars = 1 µm. D-E, Scale bars = 5 µm.

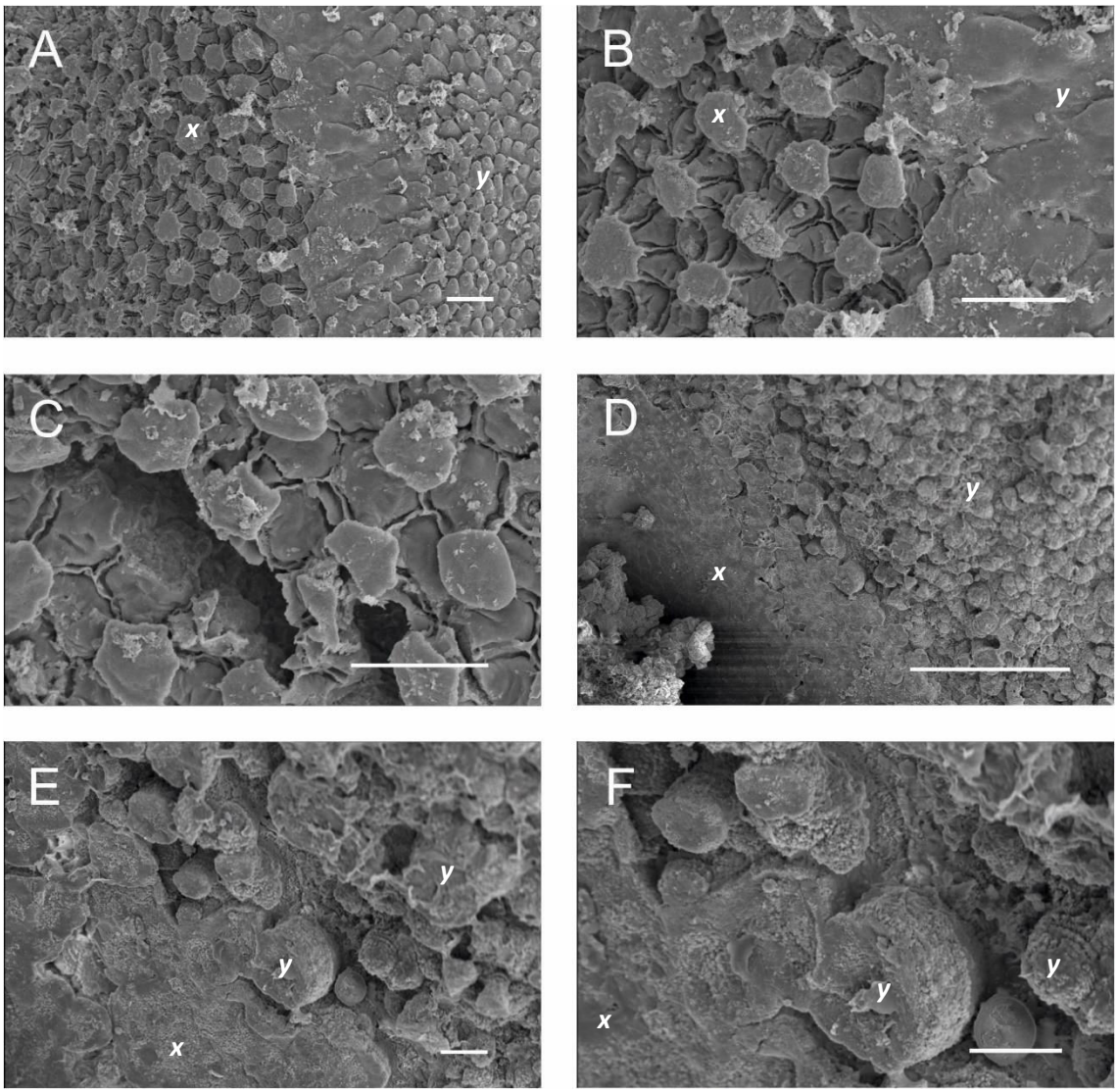


Plate 20: Examples of poorly-preserved cuticle in sharp contact with well-preserved cuticle in Nova Olinda Member fossil insects. A-C, Raised isolated fragments of smooth cuticle, held aloft by a lattice of cement over mineral infills (*x*), near well-preserved cuticle with cuticular scales (*y*). Mineral infills are calcite and lattice is likely fossilisation of sub-surface re-inforcing mesh found in some insect cuticle. D-F, Moderatly-preserved smooth cuticle (*x*) immediately adjacent to very poorly-preserved cuticle as disarticulated hemispherical pseudomorphed pseudoframboids (*y*). Specimen and image numbers: A, NBRL014-25; B, NBRL014-26; C, NBRL014-54; D, NBRL040-12; E, NBRL040-13; F, NBRL040-14. A-C and E-F, Scale bars = 10 µm. D, Scale bar = 100 µm.

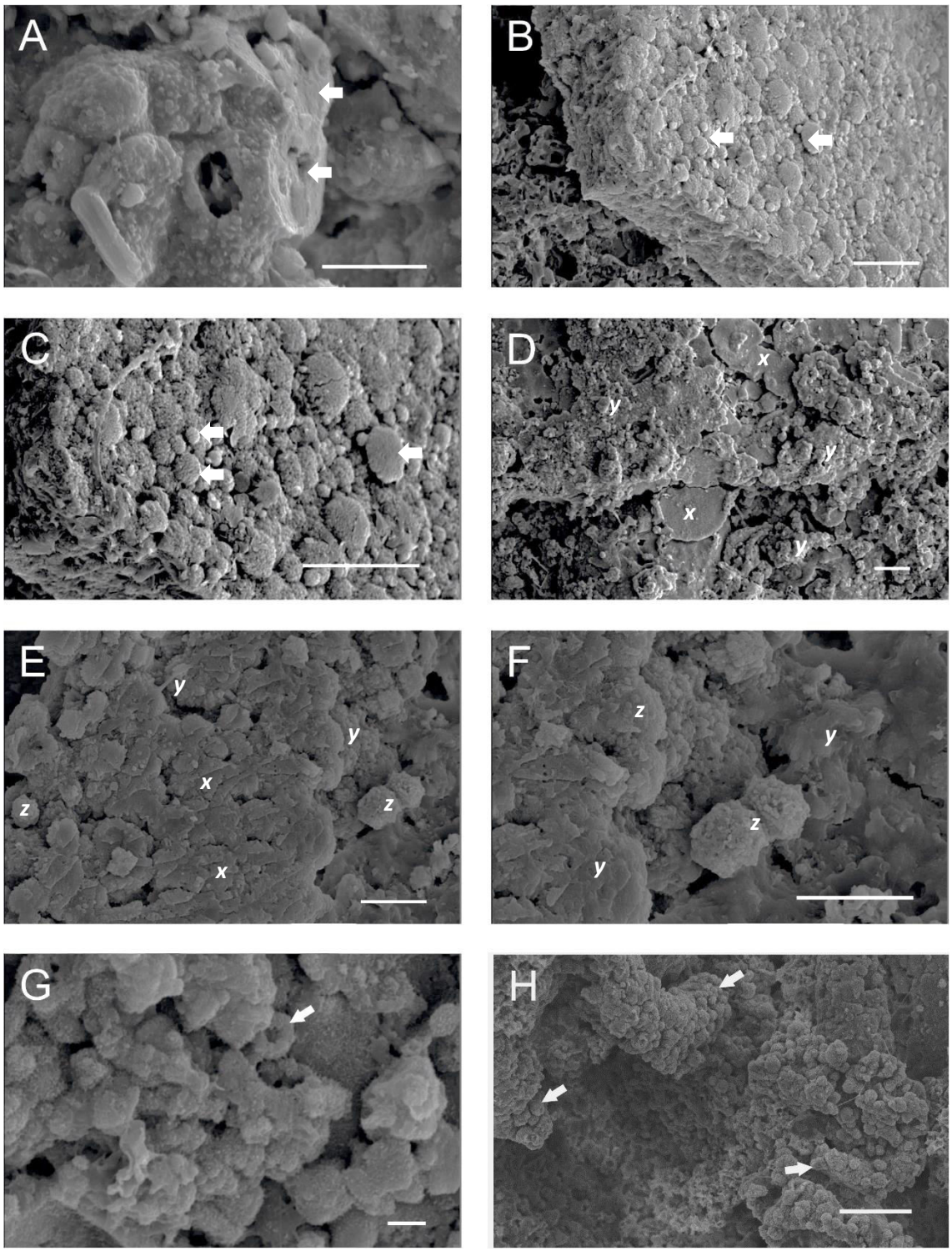


Plate 21: Examples of globular preservational fabrics from Nova Olinda Member fossil insects. A, Bulbous, globular fabric (possibly representing decay), fractured to reveal massive interior, highlighted by arrows. B-C, Sheet of cuticle that has bulbous hemispherical growths of variable size, highlighted by arrows. D, Smooth cuticle fabric (*x*) overgrown with 'globular mass' (*y*), possibly representing decay. E-F, Poorly-preserved cuticle with remnants of scales (*x*) overgrown by aggregated granular material (*y*), sometimes forming spherical aggregates (*z*). G, Globular spherical and sub-spherical structures. Arrow highlights fractured sphere, revealing hollow interior. H, Similar fabric to G, but also forms larger structures made of many smaller aggregates, possibly representing cuticular structures that have decayed or been poorly replicated, highlighted by arrows. Specimen and image numbers: A, FLO13-86; B, JW735-011; C, JW735-014; D, JW291-089; E, NBRL022(review)-39; F, NBRL022(review)-40; H, NBRL022(review)-67; G, NBRL022-17. A-F, Scale bars = 10 µm. G, Scale bar = 1 µm. H, Scale bar = 50 µm.

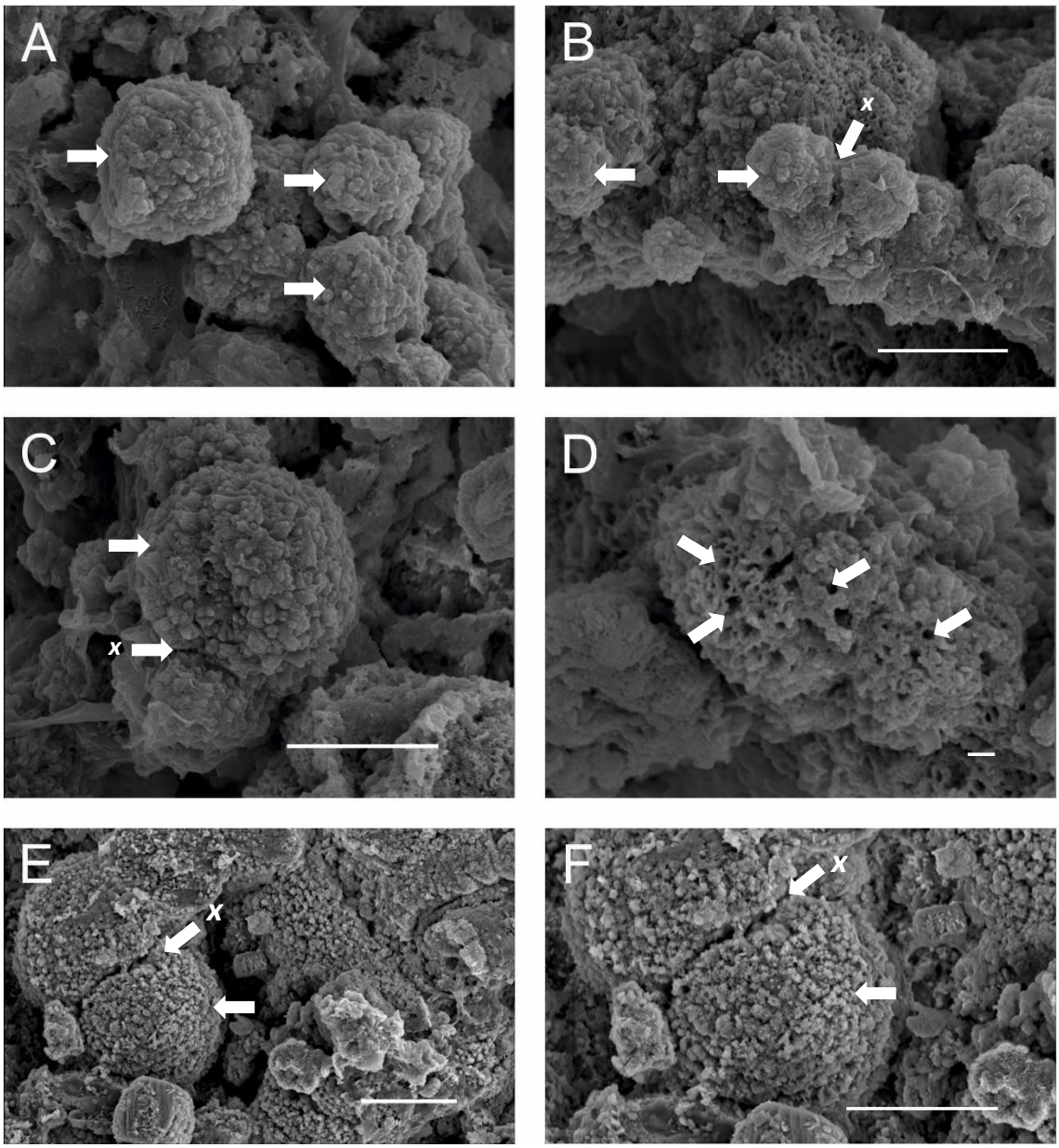


Plate 22: Examples of subspherical pseudomorphed pseudoframboids replacing Nova Olinda Member insect tissues. A-C, Distinct pseudomorphed pseudoframboids of varying sizes, highlighted by arrows, and partially intergrown (*x*). D, Partially damaged pseudomorphed pseudoframboids, revealing mesh-like framework and hollow cavities in some grains, highlighted by arrows. E-F, Larger aggregates of finer crystals, highlighted by arrows, partially merged or intergrown (*x*). Specimen and image numbers: A, NBRL022(review)-30; B, NBRL022(review)-16; C, NBRL022(review)-14; D, NBRL022(review)-19; E, NBRL051-90; F, NBRL051-87. A, Scale unknown, however largest sphere is likely approximately 10 µm in diameter. B-C and E-F, Scale bars = 10 µm. D, Scale bar = 1 µm.

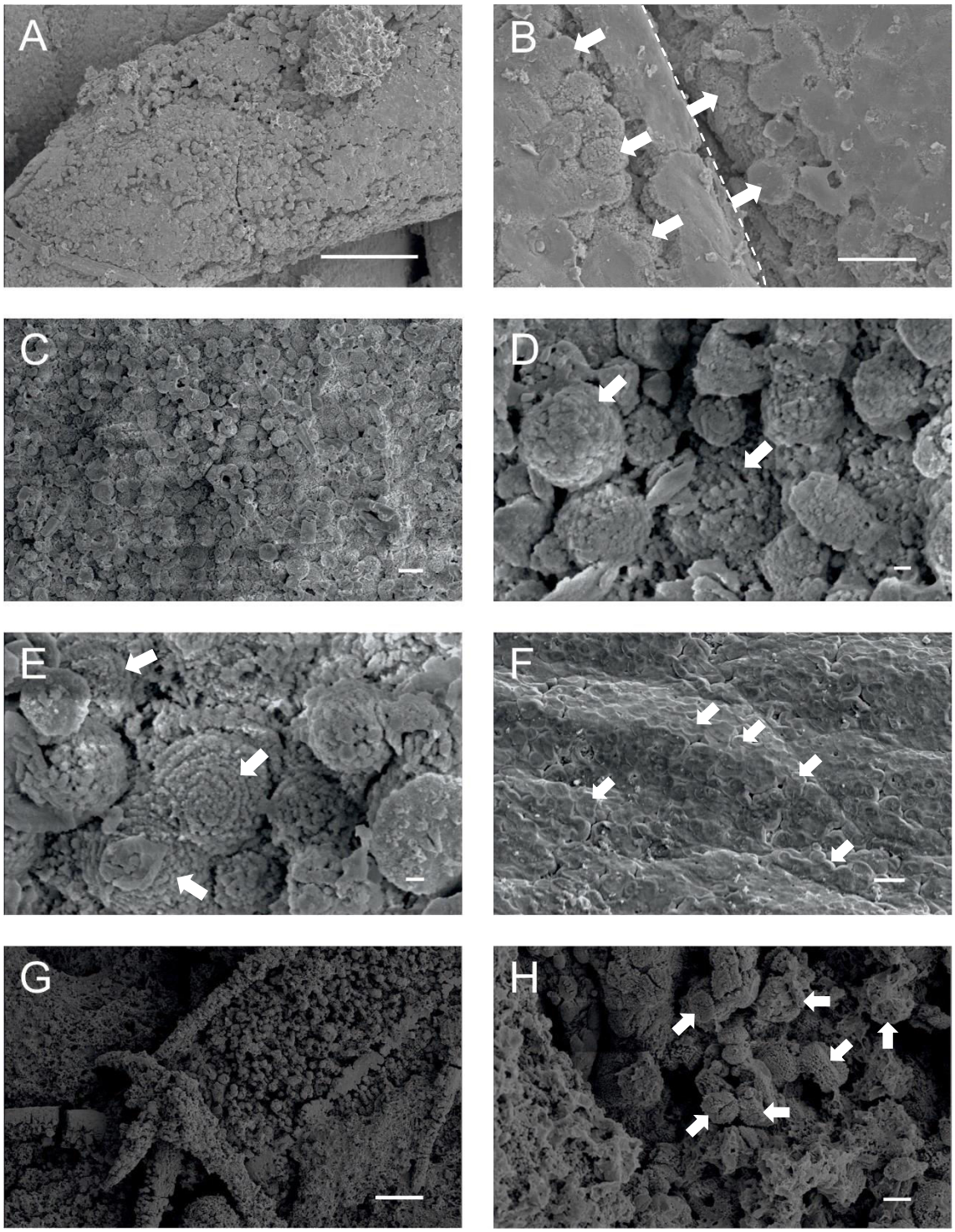


Plate 23: Examples of poorly-preserved cuticle in Nova Olinda Member fossil insects, revealing the mineralogical fabric of their preservation as goethite pseudomorphs of pseudoframboids (pseudoframboid-like aggregates). A, C, and G, Overviews of very poorly preserved cuticle, disintegrating into individual sub-spherical aggregates. B, Poorly-preserved cuticle along suture (highlighted by dashed line), revealing individual sub-spherical aggregates, highlighted by arrows. D-E, Higher magnification images of sub-spherical aggregates, revealing spiral patterning across their surface, highlighted by arrows. F, Poorly-preserved smoothed cuticle, revealing that it is constituted of many intergrown hemispherical aggregates, highlighted by arrows. H, Extremely poorly-preserved cuticle, preserved only as loose and fragmentary hemispherical aggregates, highlighted by arrows. Specimen and image numbers: A, NBRL014-34; B, NBRL014-49; C, NBRL066(resi)-16; D, NBRL066(resi)-10; E, NBRL066(resi)-13; F, NBRL054-16; G, NBRL054-67; H, NBRL054-68. A and G, Scale bars = 100 µm. B-C, F and H, Scale bars = 10 µm. D-E, Scale bars = 1 µm.

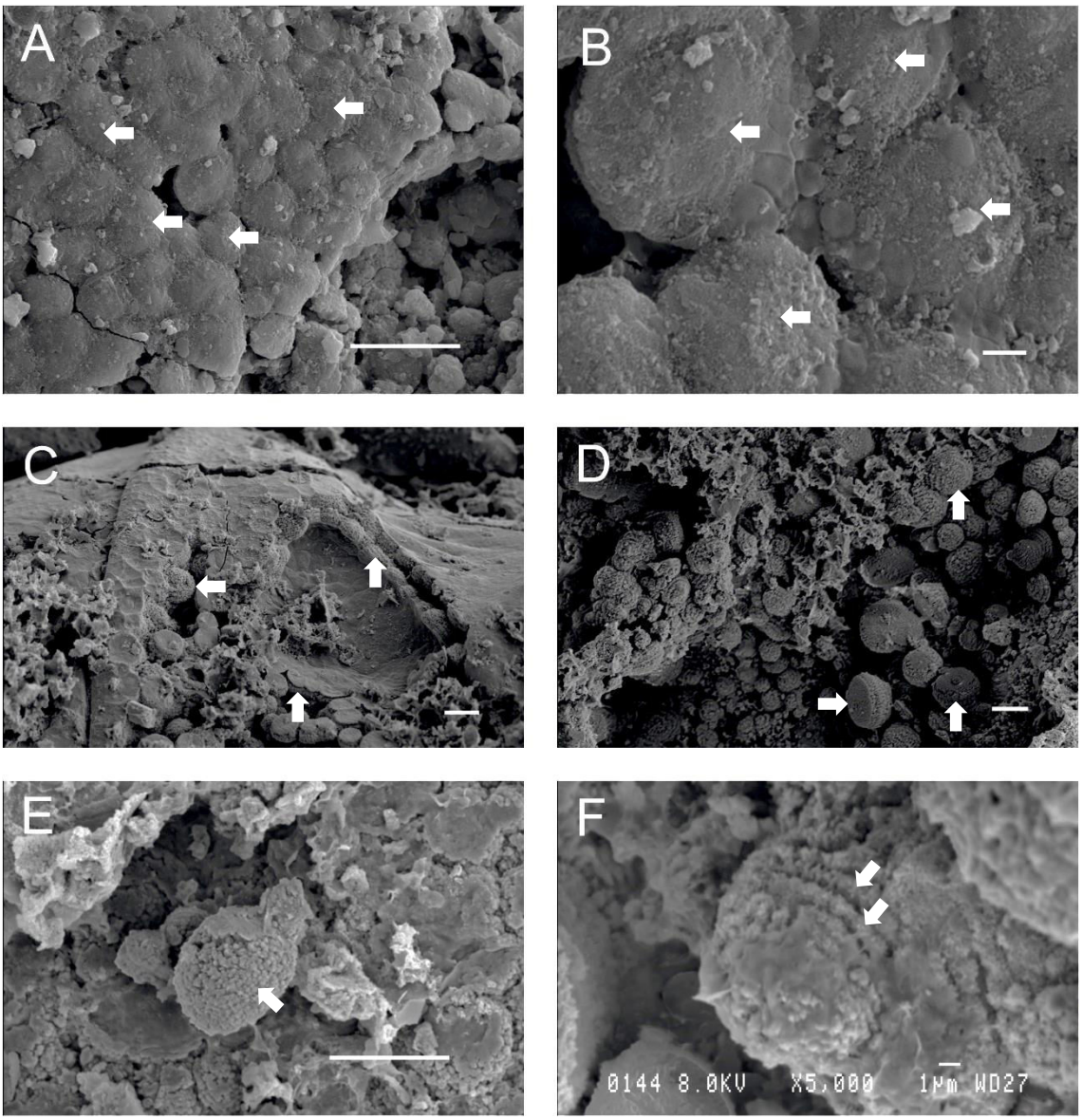


Plate 24: Examples of hemispherical pseudomorphed pseudoframboids replacing Nova Olinda Member insect tissues. A and B, Loosely connected spherical or hemispherical bodies replacing insect cuticle that are likely pseudomorphed pseudoframboids partially revealed by poor replication of the epicuticle, highlighted by arrows. C, Discernible hemispherical pseudomorphed pseudoframboids directly replacing cuticle revealed by damage during extraction, highlighted by arrows. D, Similar hemispherical pseudomorphed pseudoframboids loose within head cavity, highlighted by arrows. E and F, Hemispherical pseudoframboid-like aggregates with a roughly spiral (E) or distinct spiral (F) arrangement of grains, highlighted by arrows. Specimen and image numbers: A, FLO38-124; B, FLO38-128; C, JW614-082; D, JW614-004; E, NBRL079-51; F, NBRL040-15. A and C-E, Scale bars = 10 µm. B and F, Scale bars = 1 µm.

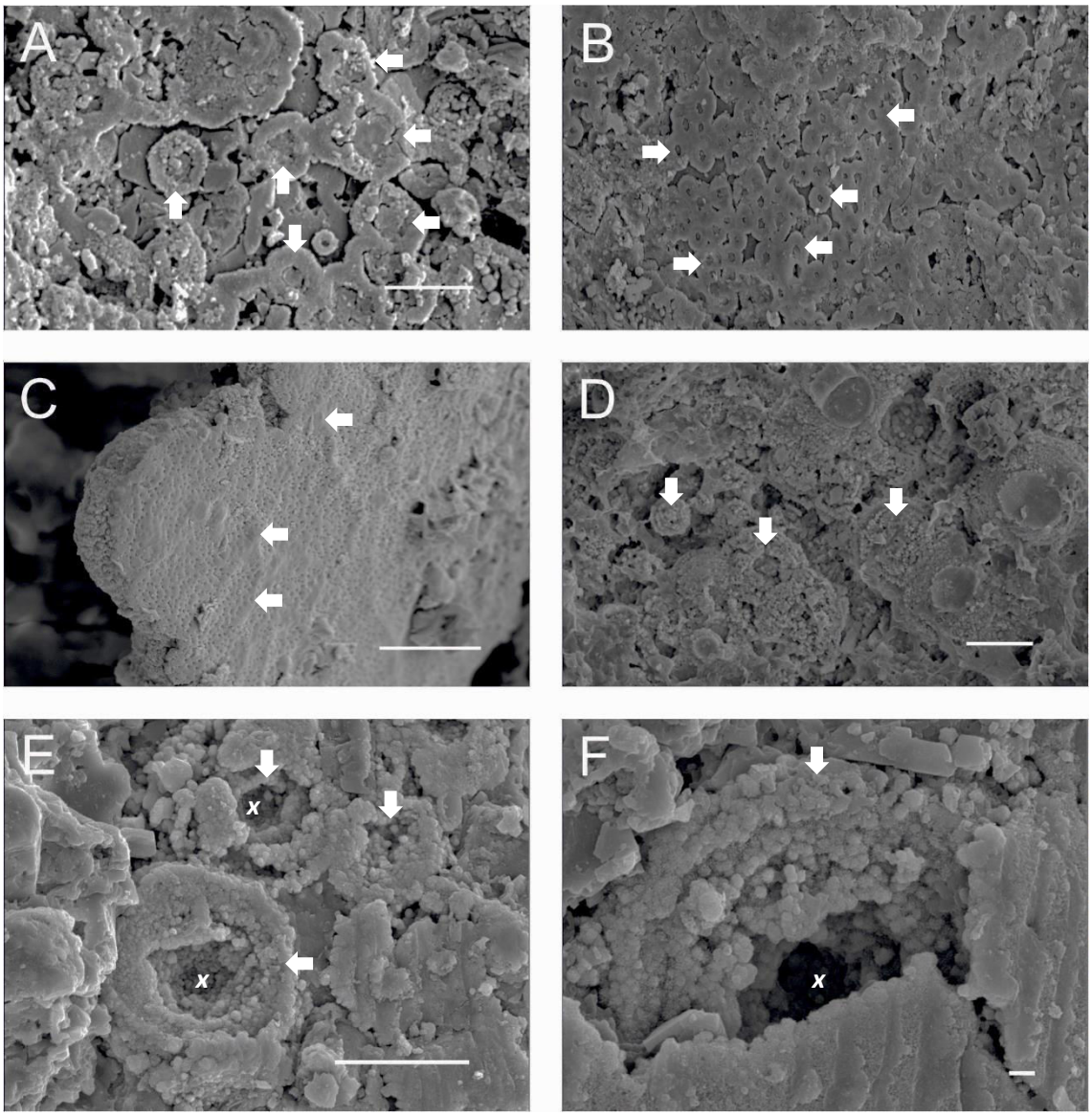


Plate 25: Examples of rings and flattened discs as a result of variations of the pseudomorphed pseudoframboid fabric replacing Nova Olinda Member fossil insects. A and B, Extremely thin (< 0.5 µm) ringed structures that appear to have grown between two closely positioned parallel layers, highlighted by arrows. C, Replaced cuticle, preserved as several thin (~4 µm) discs 'merged' together discernible only by raised traces, highlighted by arrows. D-F, Ringed pseudomorphed pseudoframboid structures grown presumably against a flat surface, giving a series of ringed patterns when exposed. E-F, Also highlight hollow interiors (x). Specimen and image numbers: A, JW02#-019; B, Unnumbered image called "wing 1.6" (likely belongs to JW660, JW646, JW024, or JW568). No scale provided; C, JW614-076; D, NBRL040-88; E, NBRL036-60; F, NBRL036-66. A and C-E, Scale bars = 10 µm. B, No scale recorded. F, Scale bar = 1 µm.

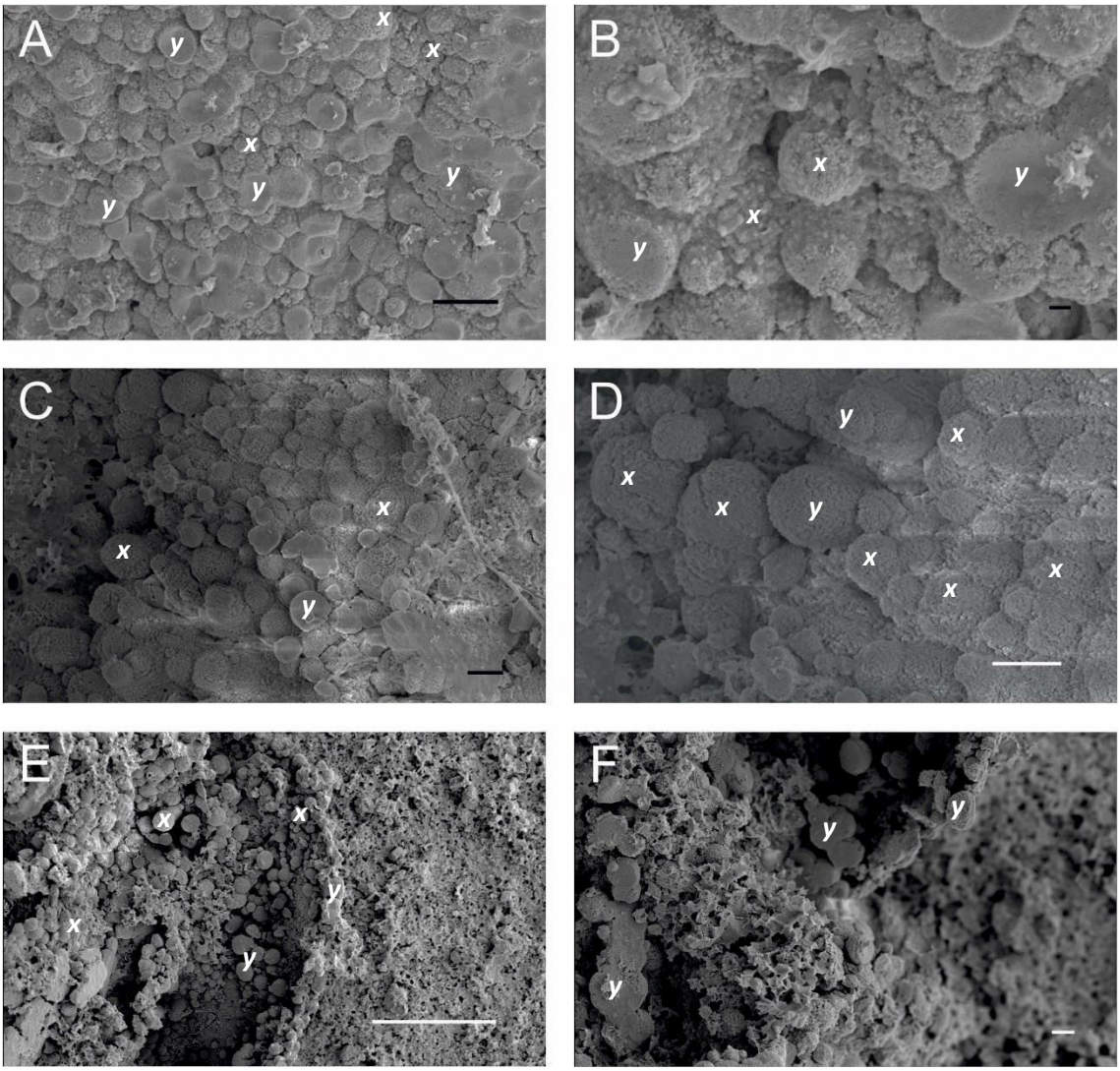


Plate 26: Examples of pseudomorphed pseudoframboids replacing Nova Olinda Member insect tissues. A-F, Varying images of pseudomorphed pseudoframboids replacing insect cuticle, including spherical (*x*) and hemispherical (*y*) aggregates. Images are presented in pairs: an overview and then higher magnification image. Specimen and image numbers: A, NBRL014-18; B, NBRL014-19; C, NBRL073-20; D, NBRL073-21; E, JW614-060; F, JW614-074. A, C-D, F, Scale bars = 10 µm. B, Scale bar = 1 µm. E, Scale bar = 100 µm.

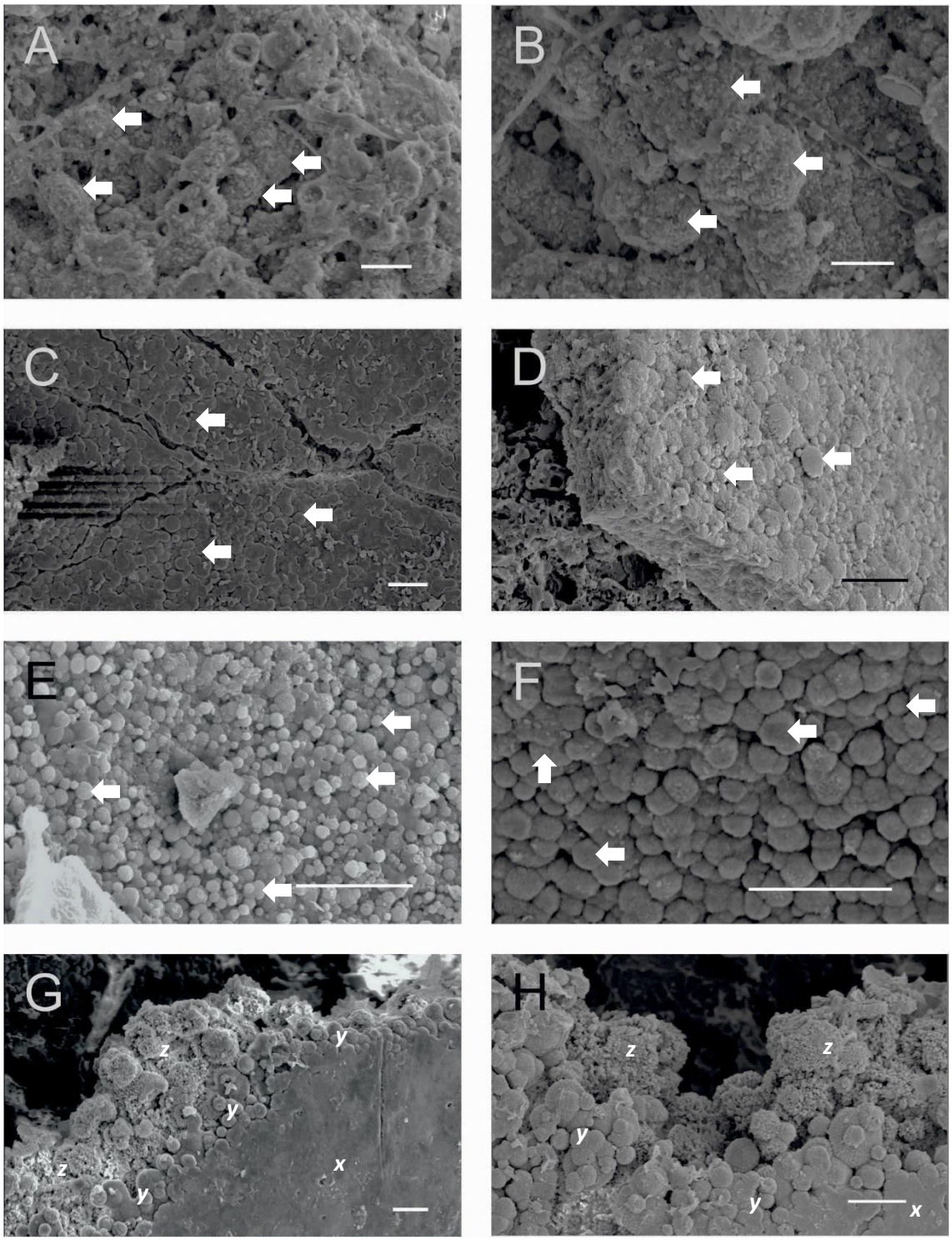


Plate 27: Examples of pseudomorphed pseudoframboids and other spherical/globular replacement textures of varying sizes in the Nova Olinda Member fossil insects. A-B, Subspherical structures of various sizes cropping out from otherwise globular replacement, highlighted by arrows. C, Cuticle with incomplete mineralisation, revealing partially inter-grown or completely fused pseudomorphed pseudoframboids of varying sizes, highlighted by arrows. D, Cuticle fragment with hemispheres of varying sizes along its surface, highlighted by arrows. E-F, Sheets of loosely bound (E) or partially inter-grown (F) spherical aggregates, highlighted by arrows. G-H, Moderately-preserved smooth cuticle (*x*) transitioning into tightly packed small spheres (*y*), then larger coarser grained pseudomorphed pseudoframboids (*z*). Specimen and image numbers: A, FLO13-22; B, FLO13-27; C, NBRL037-44; D, JW735-011; E, NBRL026-27; F, NBRL037-42; G, NBRL054-18; H, NBRL054-45. Scale bars = 10 µm.

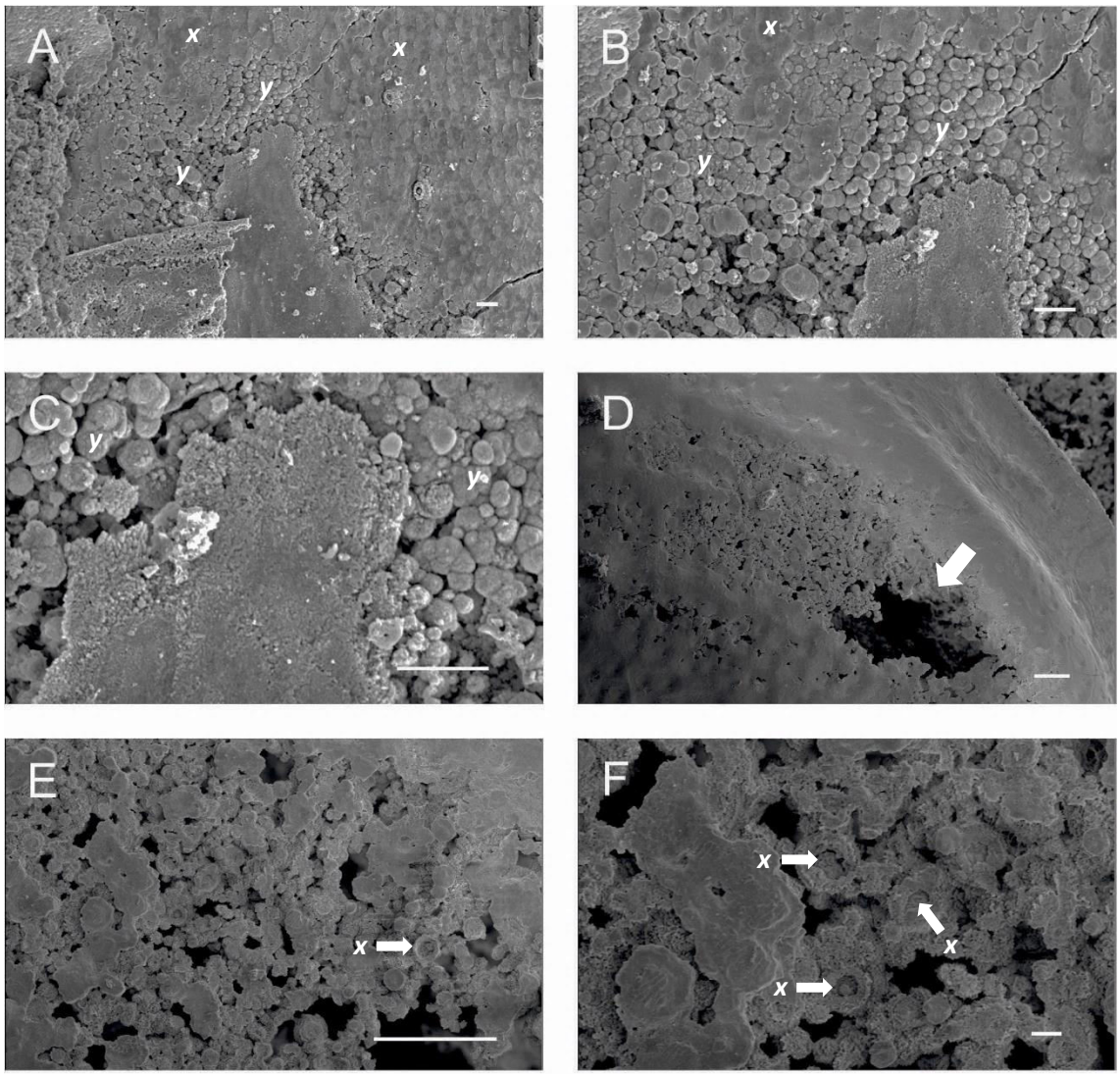


Plate 28: Examples of poorly preserved cuticle in Nova Olinda Member fossil insects, revealing details of their mineral replacement fabric. A-C, Moderately preserved cuticle (*x*) transitioning to poorly preserved cuticle (*y*), revealing globular and subspherical aggregates (pseudomorphed pseudoframboids or pseudoframboid-like aggregates) replacing cuticle. D-F, Beetle elytra with patch of heavily 'degraded' cuticle highlighted by arrow, possibly the result of abrasion from effervescence during acid digestion, revealing hollow (*x*) subspherical structures. Specimen and image numbers: A, NBRL037-27; B, NBRL037-28; C, NBRL037-29; D, NBRL018-34; E, NBRL018-35; F, NBRL018-36. A-C and F, Scale bars = 10 µm. D-E, Scale bars = 100 µm.

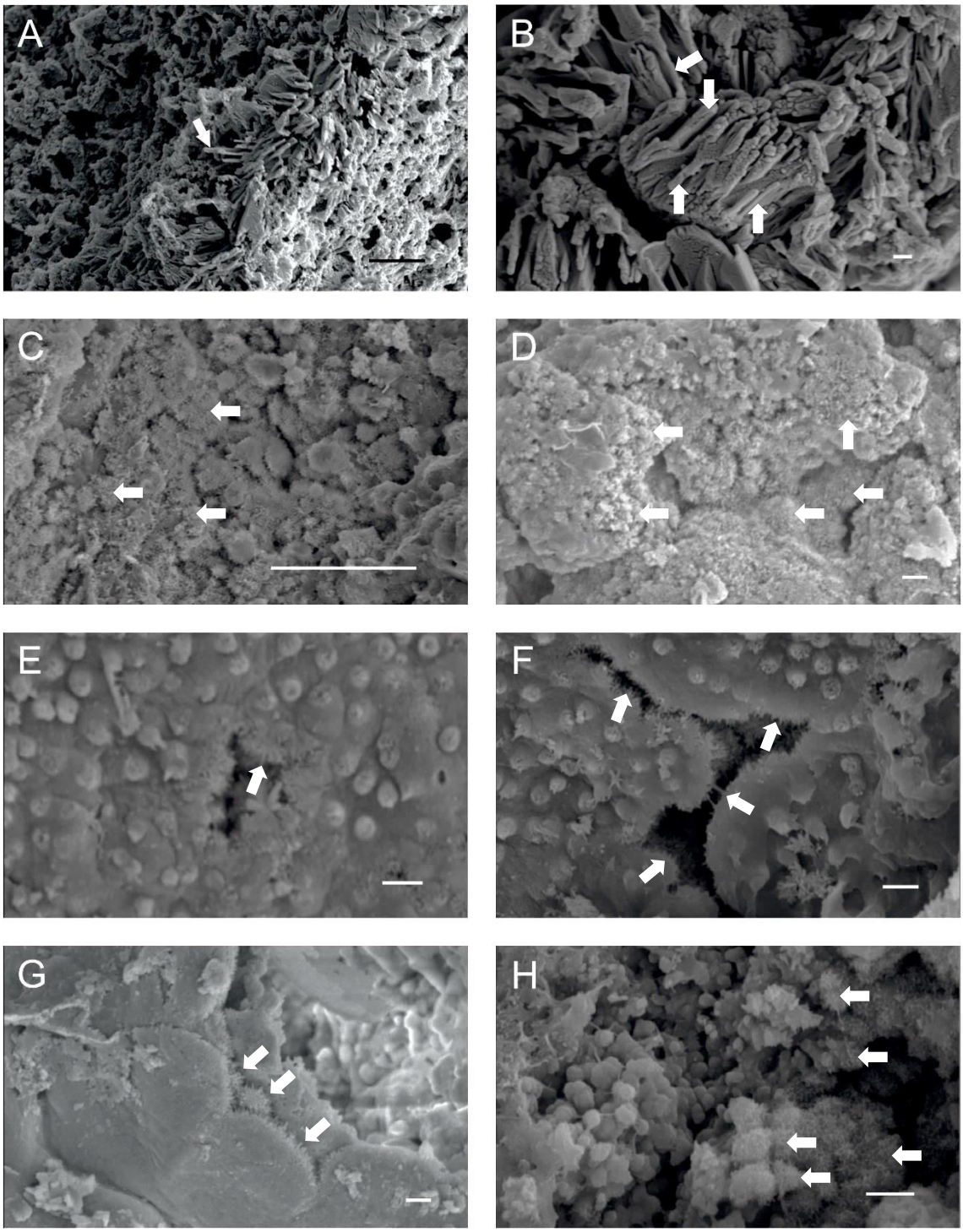


Plate 29: Examples of micro/nano-sized needle-like crystals replacing cuticle of fossil insects from the Nova Olinda Member. A-B, Trace left by disarticulated hymenopteran ovipositor, revealing a trail of needle-like crystals in transfer resin, highlighted by arrows. C-D and H, Small spherical aggregates of needle-like crystals, highlighted by arrows. E-G, Circular structures, likely the flat surfaces of hemispherical pseudomorphed pseudoframboids replacing cuticle, with needle-like crystal margins, highlighted by arrows. Specimen and image numbers: A, JW614-031; B, JW614-091; C, NBRL030-35; D, NBRL014-11; E, NBRL055-66; F, NBRL055-92; G, NBRL014-66; H, NBRL054-82. A and C, Scale bars = 1 µm. B and D-H, Scale bars = 1 µm.

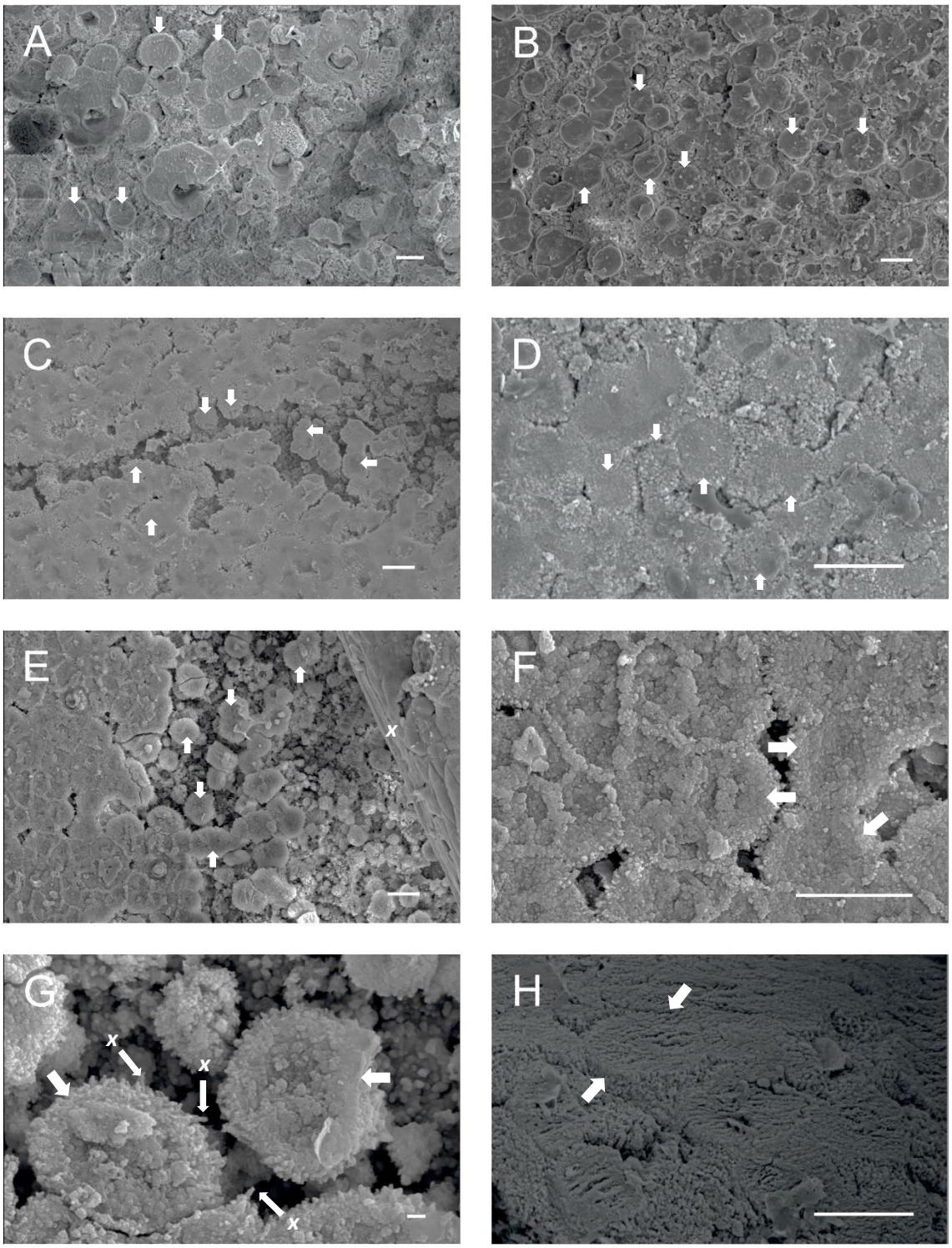


Plate 30: Examples of hemispherical aggregates (pseudomorphed pseudoframboids) replacing insect cuticle in the Nova Olinda Member. A-B, Poorly-preserved cuticle that is mostly preserved as scattered hemispheres, highlighted by arrows. C-D, Cuticle with 'crack' of poor preservation, revealing hemispherical aggregates, highlighted by arrows. E, Transition of moderately-preserved cuticle to poorly preserved cuticle near suture (*x*), preserved only as hemispherical aggregates, highlighted by arrows. F-H, Higher magnification images of hemispherical aggregates as (F) partially intergrown, (G) separate, and (H) entirely intergrown. Arrows highlight hemispherical aggregates, (*x*) highlights needle-like/acicular crystals. Specimen and image numbers: A, NBRL055-71; B, NBRL040-73; C, NBRL037-17; D, NBRL059-34; E, NBRL054-118; F, NBRL054-122; G, NBRL054-120; H, NBRL054-71. A-F and H, Scale bars = 10 µm. G, Scale bar = 1 µm.

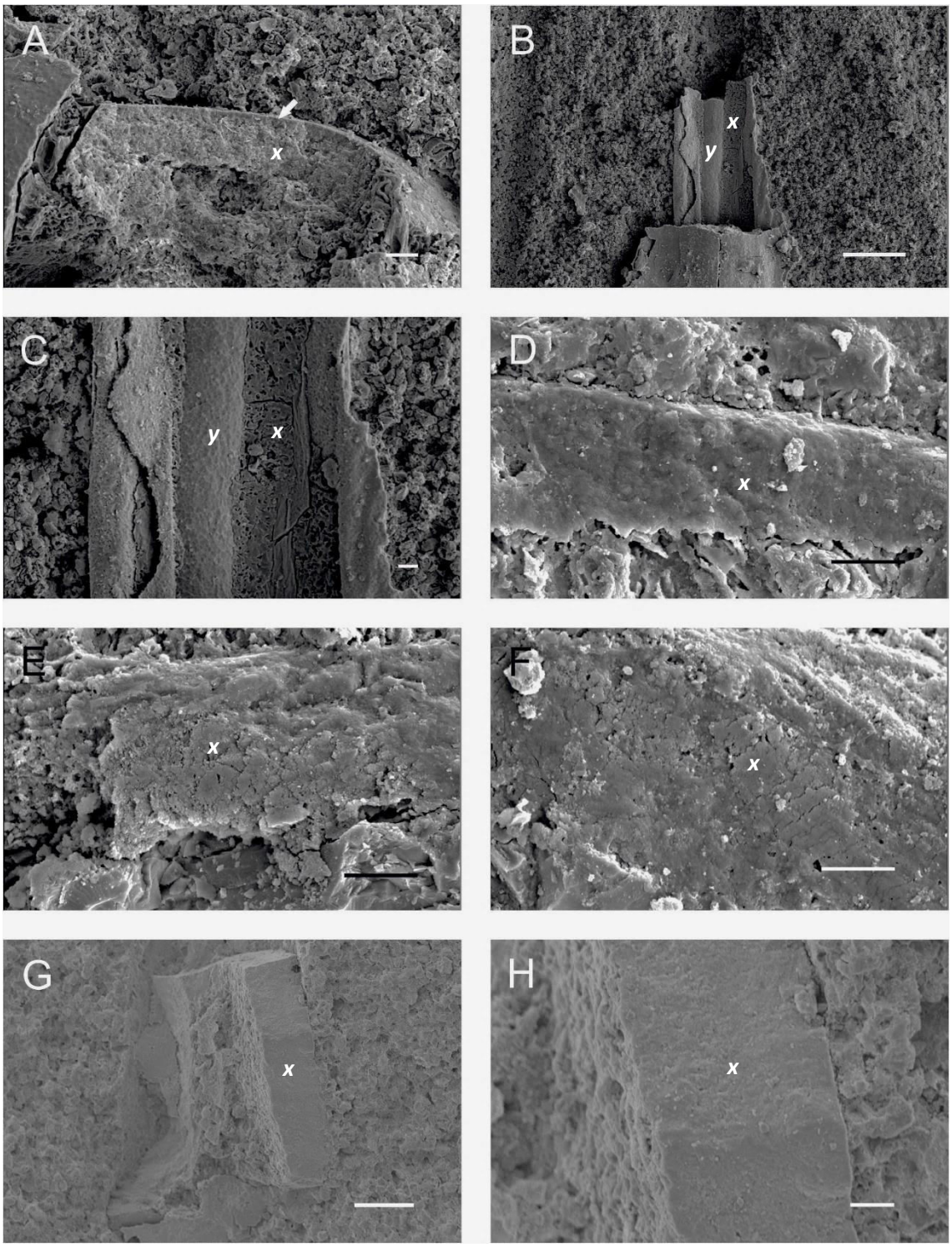


Plate 31: Cross sections through cuticle in Nova Olinda Member insects. A, Section through cuticle with differing preservational fabrics between epicuticle and exo/endocuticle. Densely mineralised and well-preserved epicuticle highlighted by arrow. Exo/Endocuticle below is featureless with no discernible internal structure (*x*). B-C, Cracked wing vein, revealing 'spongey' layer (*x*) between exterior cuticle and central core tubercle (*y*). D-F, Abraded sections through cuticle, revealing poorly-preserved massive internal fabric (*x*). G-H, Sharp breaks through brittle cuticle showing massive internal fabric (*x*). Specimen and image numbers: A, JW735-007; B, JW735-021; C, JW735-22; D, NBRL057-34; E, NBRL057-32; F, NBRL057-38; G, NBRL048-33; H, NBRL048-35. A, C-F, and H, Scale bars = 10 µm. B, Scale bar = 100 µm. G, Scale bar = 50 µm.

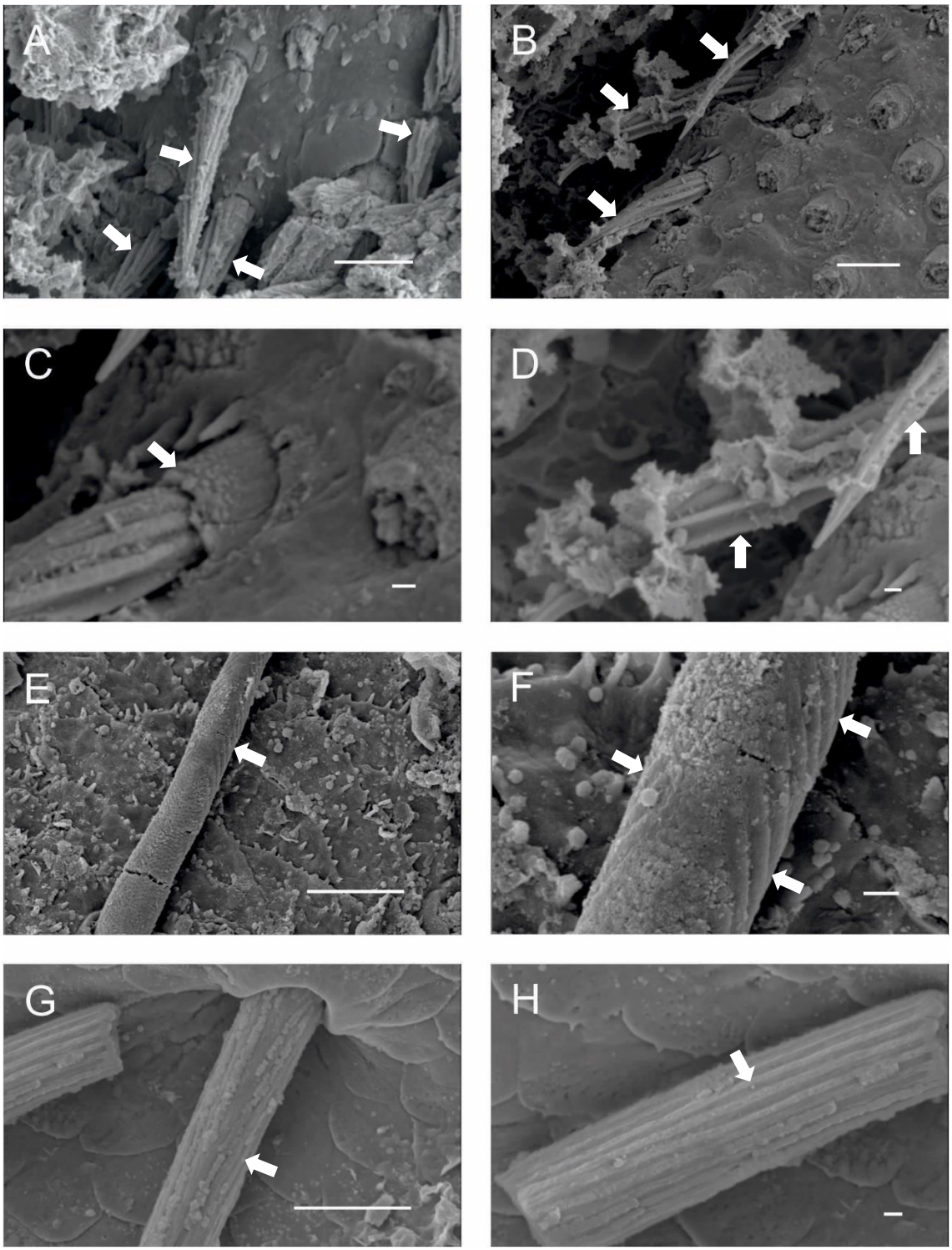


Plate 32: Exceptionally preserved setae with ridges from Nova Olinda Member fossil insects. A-D, Fine setae with extremely prominent ridges almost parallel, but spiralling around, setal length, highlighted by arrows. C, Arrow highlights setal base. E-F, Abraded setae with tightly packed ridges running down lateral edges, highlighted by arrows, at roughly 45° angles to setal length. G-H, Multiple shallow, but distinct, ridges running parallel to setal length, highlighted by arrows. Specimen and image numbers: A, FLO19-39; B, FLO19-28; C, FLO19-27; D, FLO19-26; E, NBRL059-24; F, NBRL059-25; G, NBRL040-96; H, NBRL040-98. A-B, E and G, Scale bars = 10 µm. C-D, F and H, Scale bars = 1 µm.

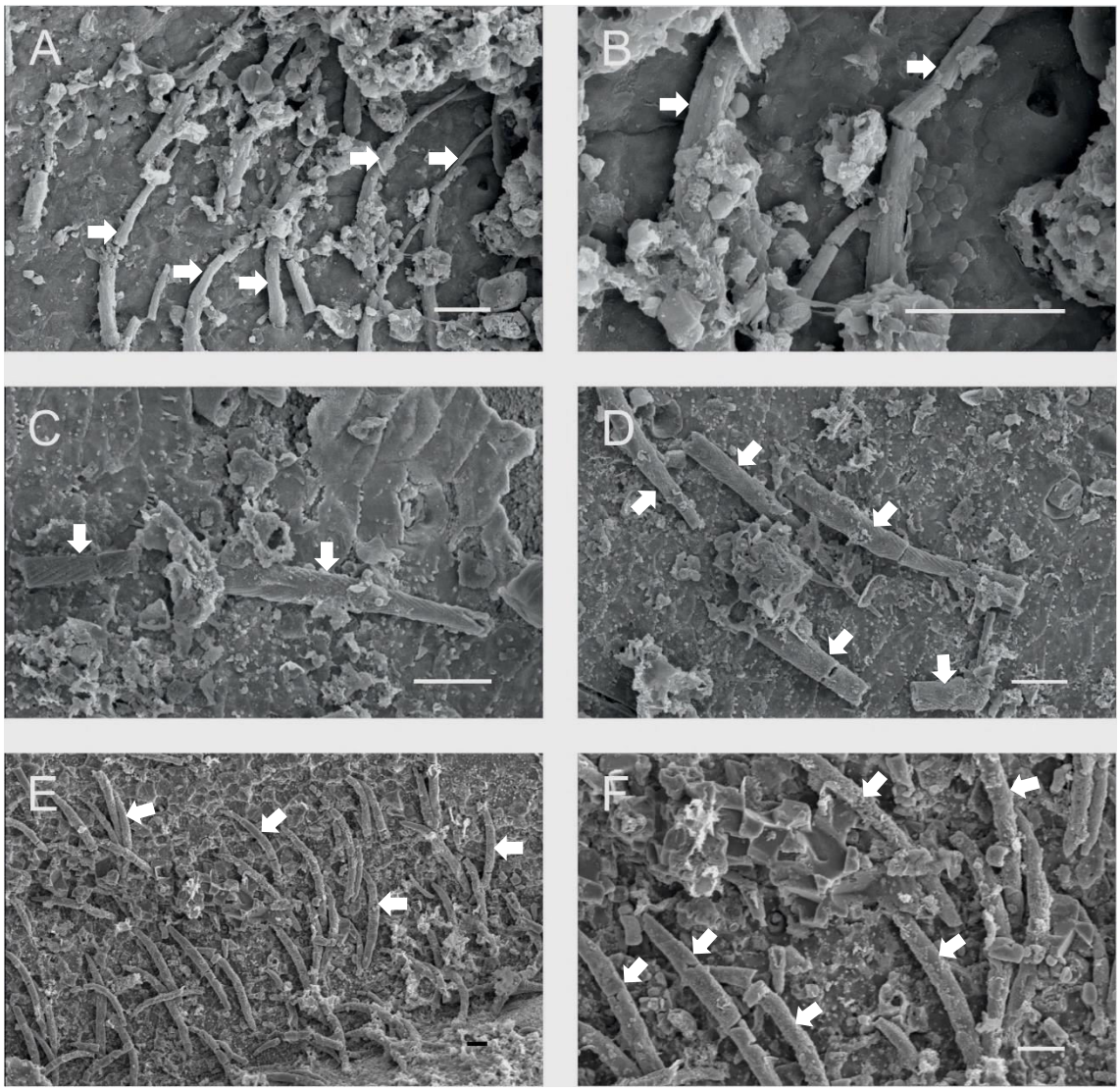


Plate 33: Long, curved setae preserved pressed flat against cuticle in Nova Olinda Member fossil insects. A-B, Setae curved in the same direction, pressed flat against cuticle, highlighted by arrows. C-D, Abraded cuticle with broken and disarticulated long setae pressed flat against it, highlighted by arrows. E-F, Long, curved setae covered in matrix and flattened against cuticle, highlighted by arrows. Specimen and image numbers: A, FLO38-08; B, FLO38-11; C, NBRL059-51; D, NBRL059-52; E, NBRL051-24; F, NBRL051-25. Scale bars = 10 µm.

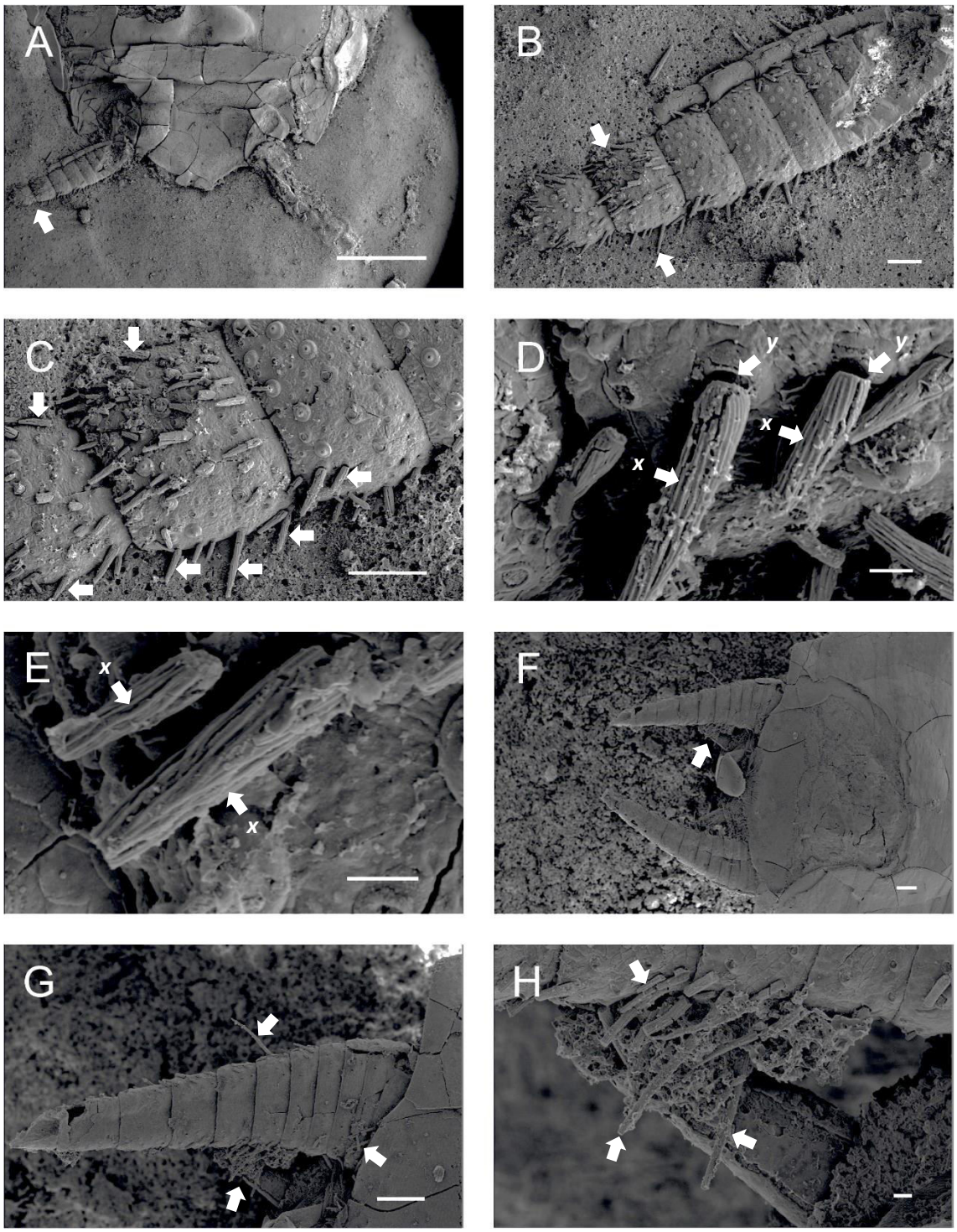


Plate 34: Exceptionally preserved cerci and their setae in Nova Olinda Member fossil insects. A-C, Overview of cerci on Blattodea specimen, showing setae preserved at the distal end of left cercus, highlighted by arrows. D-E, Higher magnification images of these setae, displaying ridges (*x*) and minor disarticulation from their bases (*y*). F-G, Overviews of another Blattodea specimen with setae preserved at the anterior portion of the cerci, highlighted by arrows. H, Higher magnification of setae, highlighted by arrows, revealing their long thin fragile morphology. Specimen and image numbers: A, JW291-005; B, JW291-006; C, JW291-007; D, JW291-012; E, JW291-014; F, NBRL018-03. G, NBRL018-05; H, NBRL018-13. A, Scale bar = 1 µm. B-C and F-G, Scale bars = 100 µm. D-E and H, Scale bars = 10 µm.

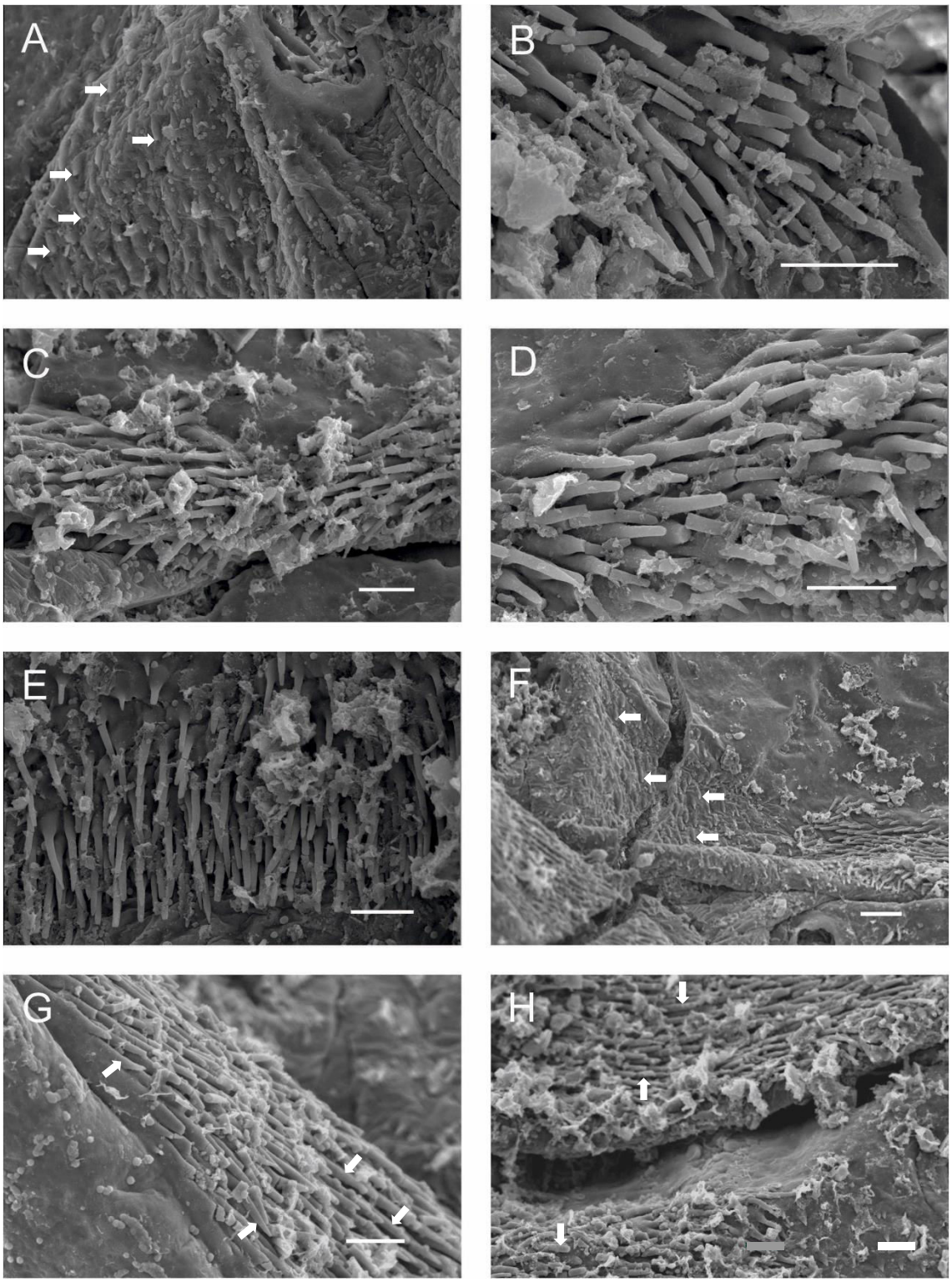


Plate 35: Exceptionally preserved densely packed fine sheets of micro-setae (microtrichium) preserved in Nova Olinda Member fossil insects. A and F, Overview of a sheet of fine setal bases, highlighted by arrows. Setae themselves have been lost. B-D, 'Rim' of fine, long thin, setae around the abdomen of Coleoptera specimen. E, Broad sheet of finely packed setae, along abdominal segment margin of Coleoptera specimen. G-H, Abraded 'rim' of setae, resulting in short broken setae pressed flat against the cuticle, highlighted by arrows. Specimen and image numbers: A, NBRL045-##51; B, NBRL045-##73; C, NBRL045-##79; D, NBRL045-##70; E, NBRL045-##75; F, NBRL045-21; G, NBRL045-24; H, NBRL045-25. A, No scale bar given. B-E and G-H, Scale bars = 10 µm. F, Scale bar = 20 µm.

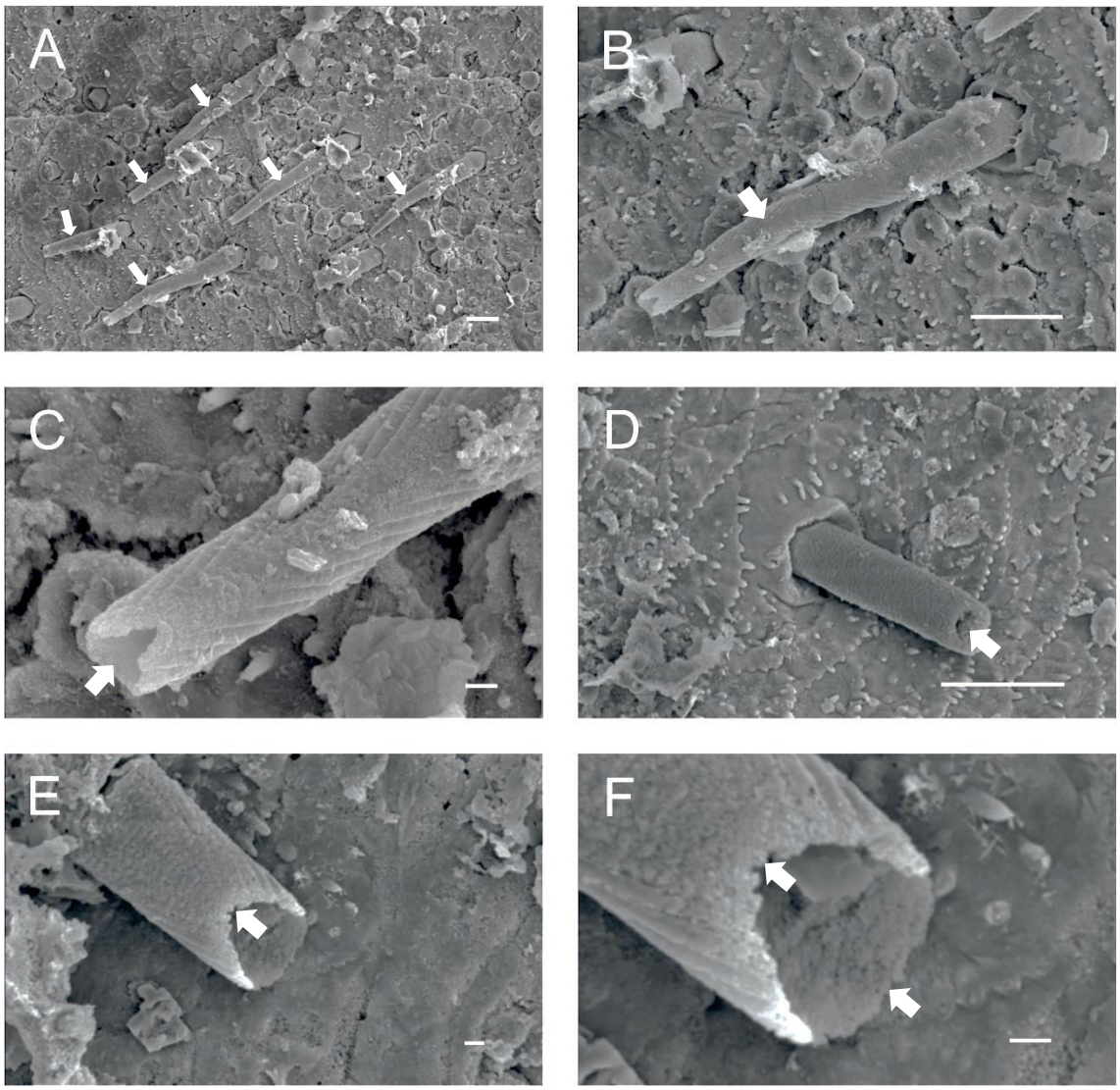


Plate 36: Examples of abraded setae from Nova Olinda Member fossil insects, revealing their hollow interiors. A-B, Overview of elongate setae, pressed against moderately-preserved cuticular surface, highlighted by arrows. C-D, Setae tips broken to reveal hollow interior, highlighted by arrow. E-F, Higher magnification images of hollow setae, revealing abrasion damage likely caused by effervescence during digestion in 10% acetic acid, highlighted by arrows. Specimen and image numbers: A, NBRL059-75; B, NBRL059-77; C, NBRL059-84; D, NBRL059-54; E, NBRL059-58; F, NBRL059-60. A-B and D, Scale bars = 10 µm. C and E-F, Scale bars = 1 µm.

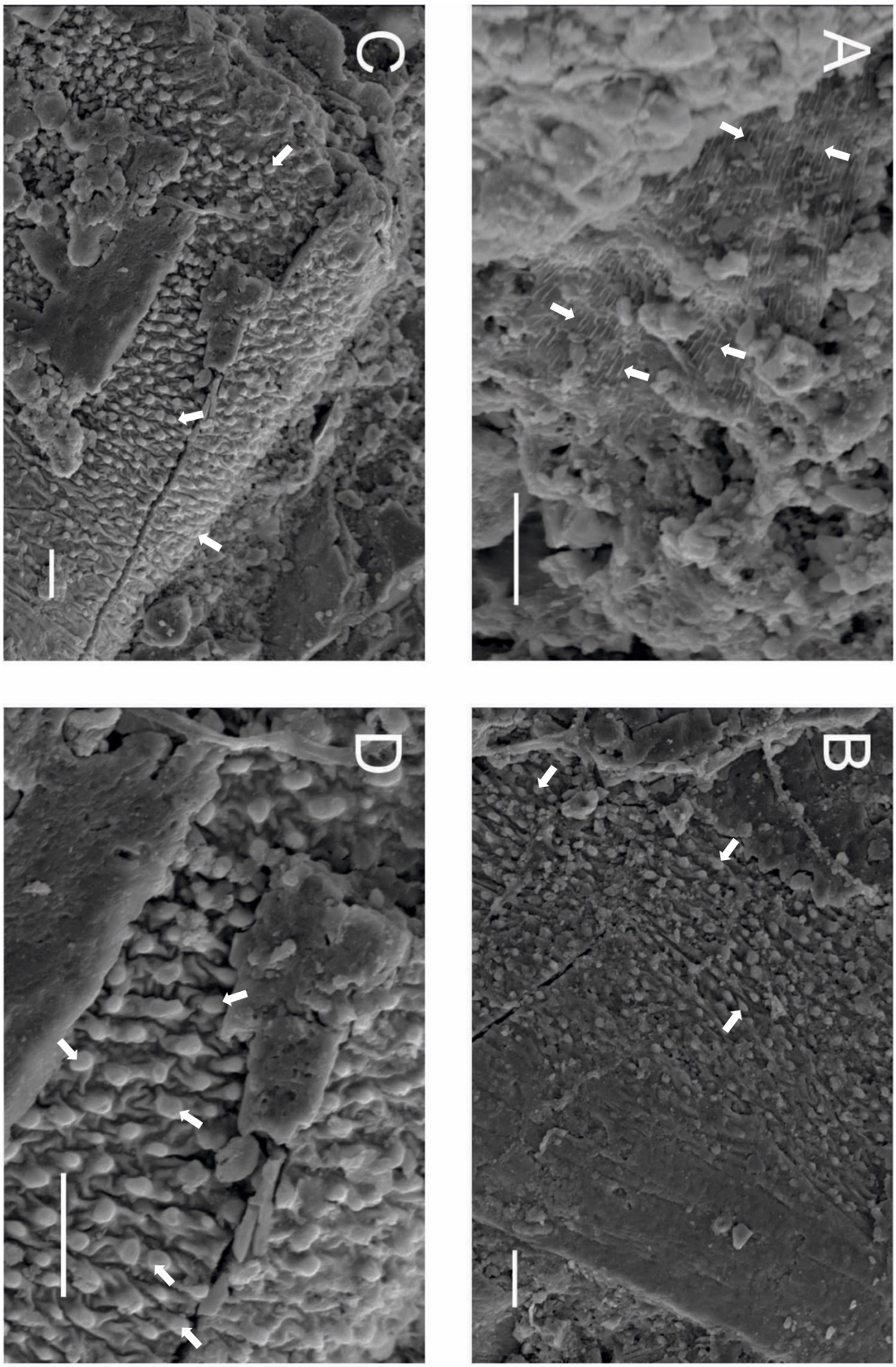


Plate 37: Examples of micro-setae (microtrichium) and their bases in Nova Olinda Member fossil insects. A, Very thin and fine micro-setae partially obscured by matrix, highlighted by arrows. B-D, Bases of damaged micro-setae covering cuticle with a 'wavy' fabric, highlighted by arrows. Alternatively, this fabric could be the result of abraded epicuticle revealing subsurface cuticular structures. Specimen and image numbers: A, FLO13-39; B, FLO27-61; C, FLO27-65; D, FLO27-67. Scale bars = 10 µm.

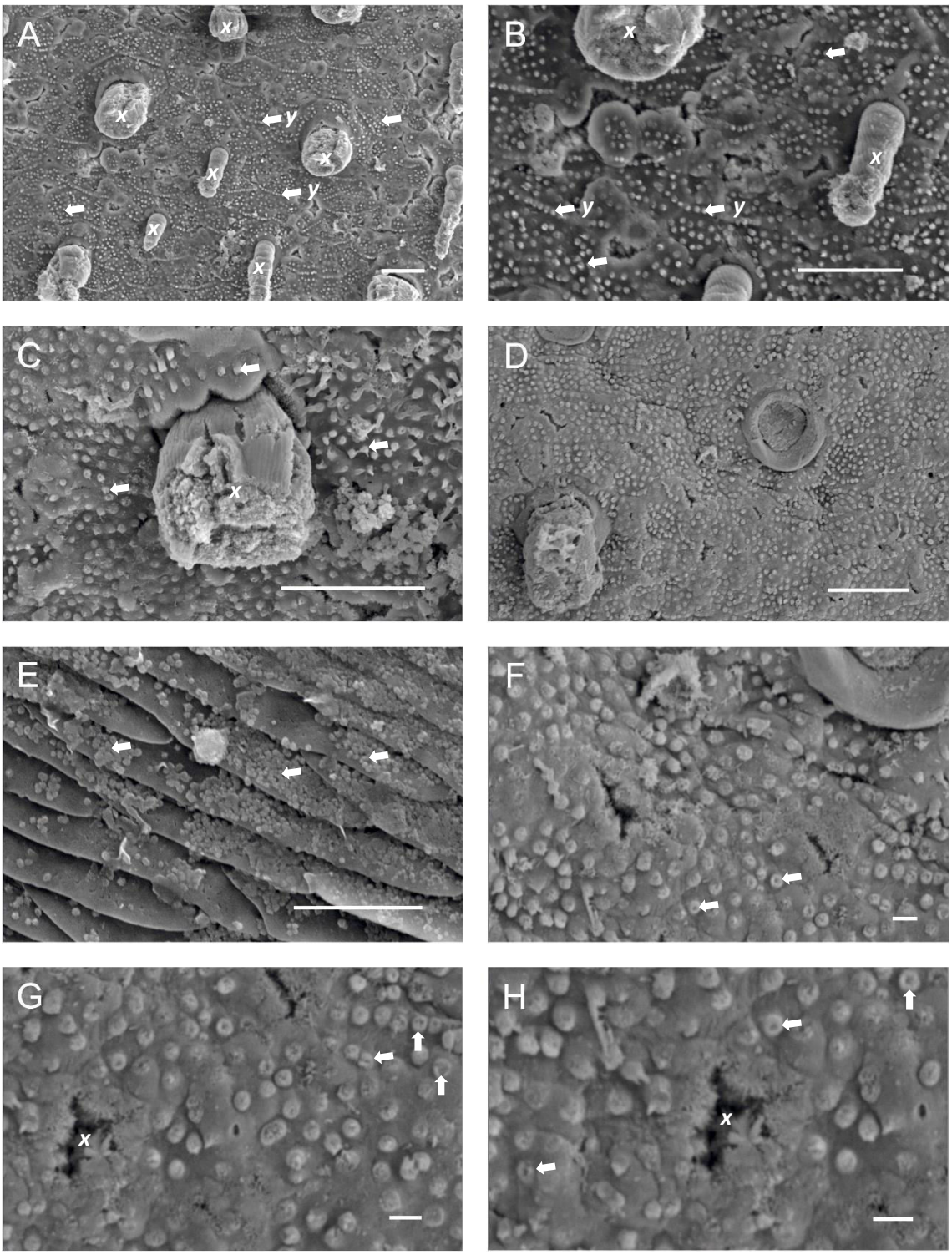


Plate 38: Examples of disarticulated micro-setae (microtrichinum), leaving only micro-setal bases in Nova Olinda Member fossil insects. A-B, Examples of micro-setal bases across insect cuticle, highlighted by arrows, near larger poorly-preserved setae (*x*), and infrequently arranged in lines (*y*). C, Micro-setal bases, highlighted by arrows, surrounding larger fragmentary setae (*x*). D, Densely packed micro-setal bases covering all insect cuticle. E, Arrows highlight granular micro-sphere coating/replacing cuticular scales that are chemical in origin, and should not be confused with micro-setal bases. F-H, Higher magnification images of micro-setal bases, revealing their hollow interiors, highlighted by arrows, and rare needle-like crystals replacing cuticle (*x*). Specimen and image numbers: A, NBRL055-10; B, NBRL055-11; C, NBRL055-90; D, NBRL055-63; E, NBRL040-168; F, NBRL055-64; G, NBRL055-65; H, NBRL056-65. A-E, Scale bars = 10 µm. F-H, Scale bars = 1 µm.

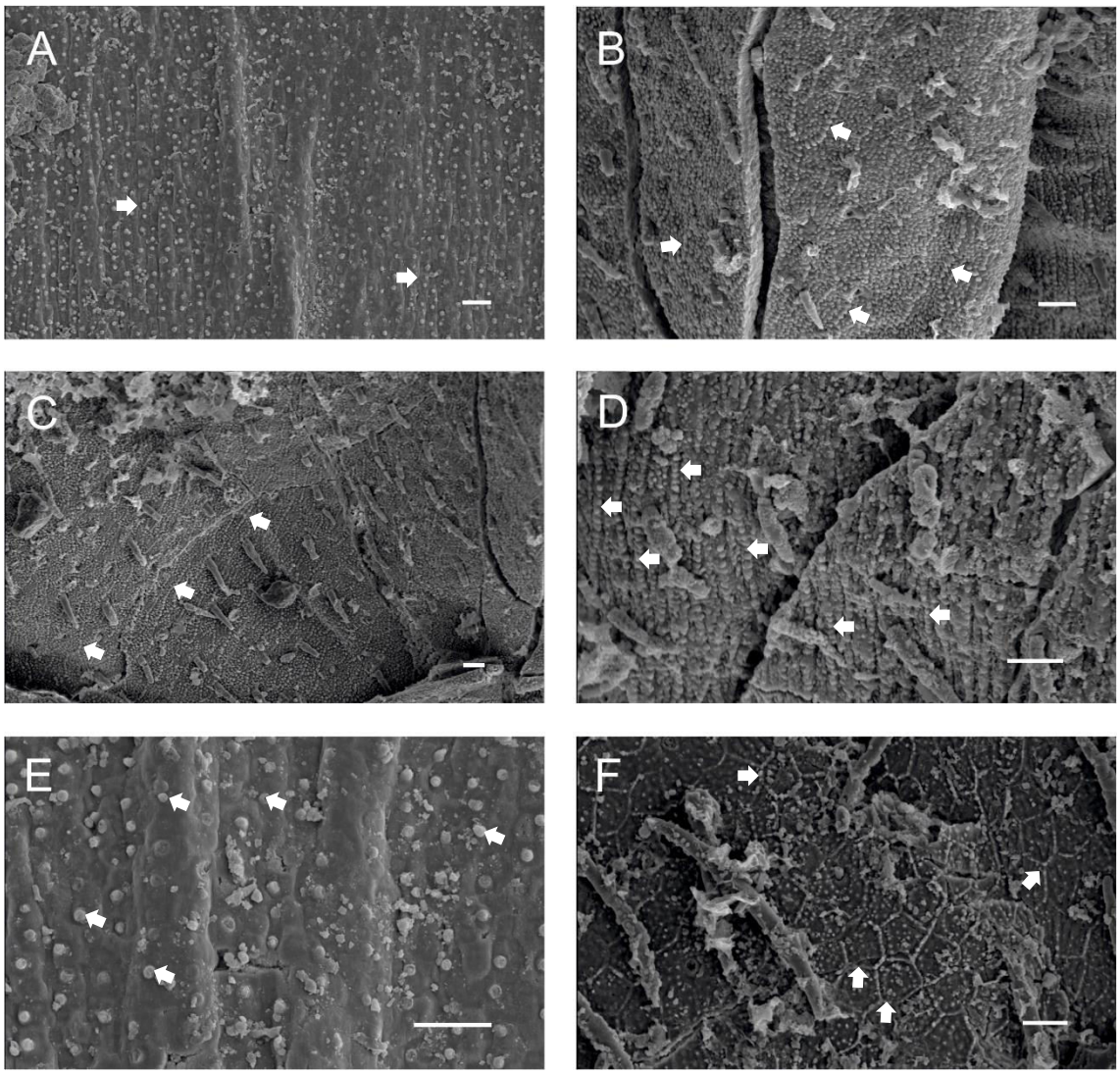


Plate 39: Examples of spherical microstructures (informally called ‘microspheres’) coating fossil insect cuticle in the Nova Olinda Member. Although these structures are morphologically similar, they appear to have different origins. A, ‘Microspheres’ arranged as faintly discernible vertical lines across insect cuticle, highlighted by arrows. These may represent the ‘bases’ of broken microtrichium. B-C, Cuticle coated in sheet of ‘microspheres’, some arranged into undulating lines, highlighted by arrows. These spheres appear to trace the edges of cuticular scales and may be mineralogical in origin. D, Cuticle coated in sheet of ‘microspheres’, frequently arranged into densely packed vertical lines, highlighted by arrows. These may represent structure of the exocuticle exposed by incomplete mineralisation. E, Higher magnification image of ‘microspheres’ spread evenly across cuticle, highlighted by arrows. These spheres could represent fossilised bacteria adhering to the epicuticle. F, ‘Microspheres’ arranged in loosely hexagonal pattern, possibly outlining scale boundaries, highlighted by arrows. Again, these trace the edges of cuticular scales and may be mineralogical in origin. Specimen and image numbers: A, FLOXX-31; B, NBRL051-33; C, NBRL051-34; D, NBRL051-32; E, FLOXX-32; F, NBRL051-28. Scale bars = 10 μm.

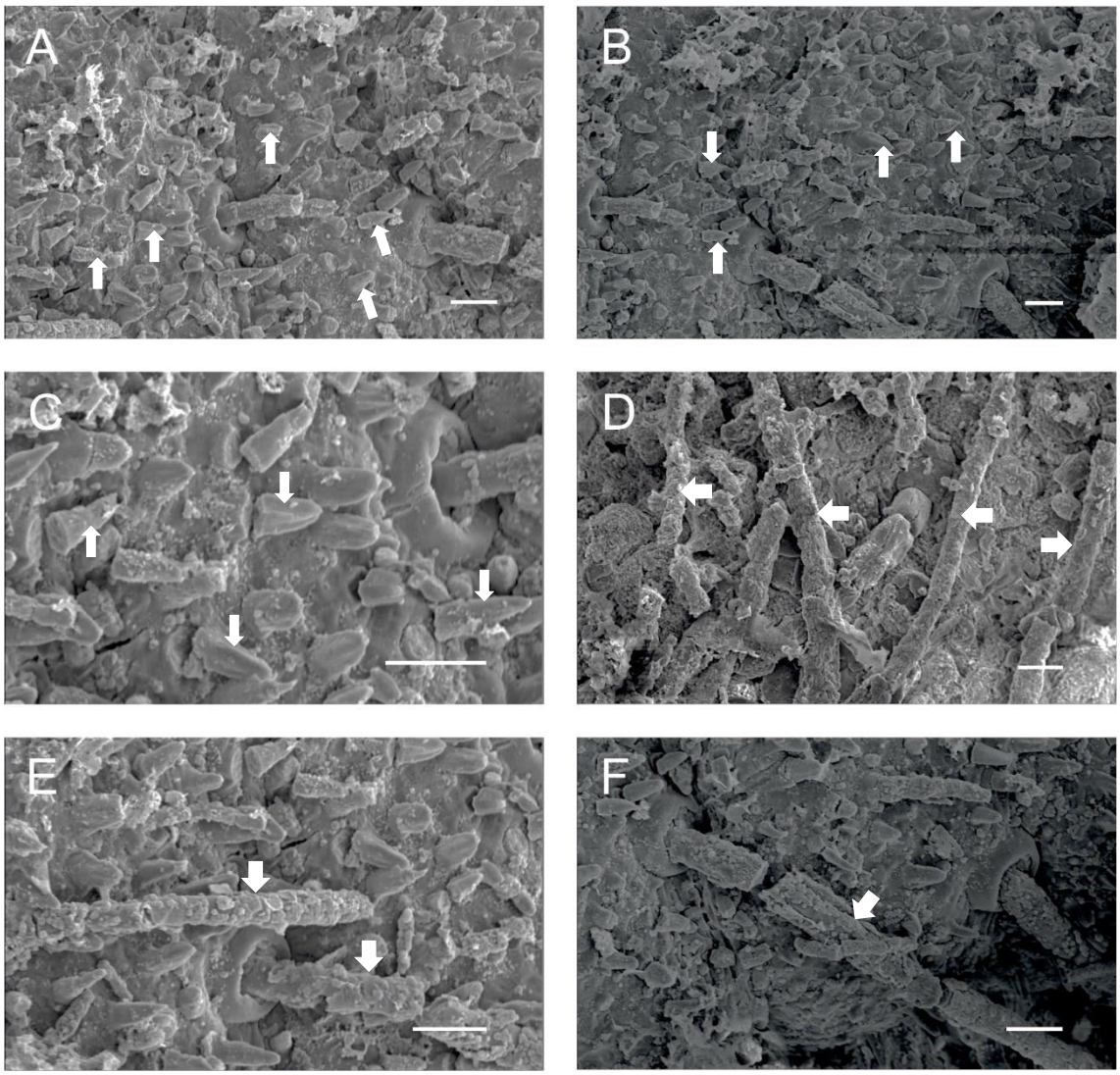


Plate 40: Examples of fractured and broken setae from Nova Olinda Member fossil insects. A-C, Heavily damaged setae, typically preserved as only short ‘spikes’, highlighted by arrows (either attached to their bases or disarticulated). D-F, Fractured elongate setae, highlighted by arrows. Specimen and image numbers: A, NBRL051-62; B, NBRL051-91; C, NBRL051-63; D, NBRL051-90; E, NBRL051-61; F, NBRL051-92. Scale bars = 10 µm.

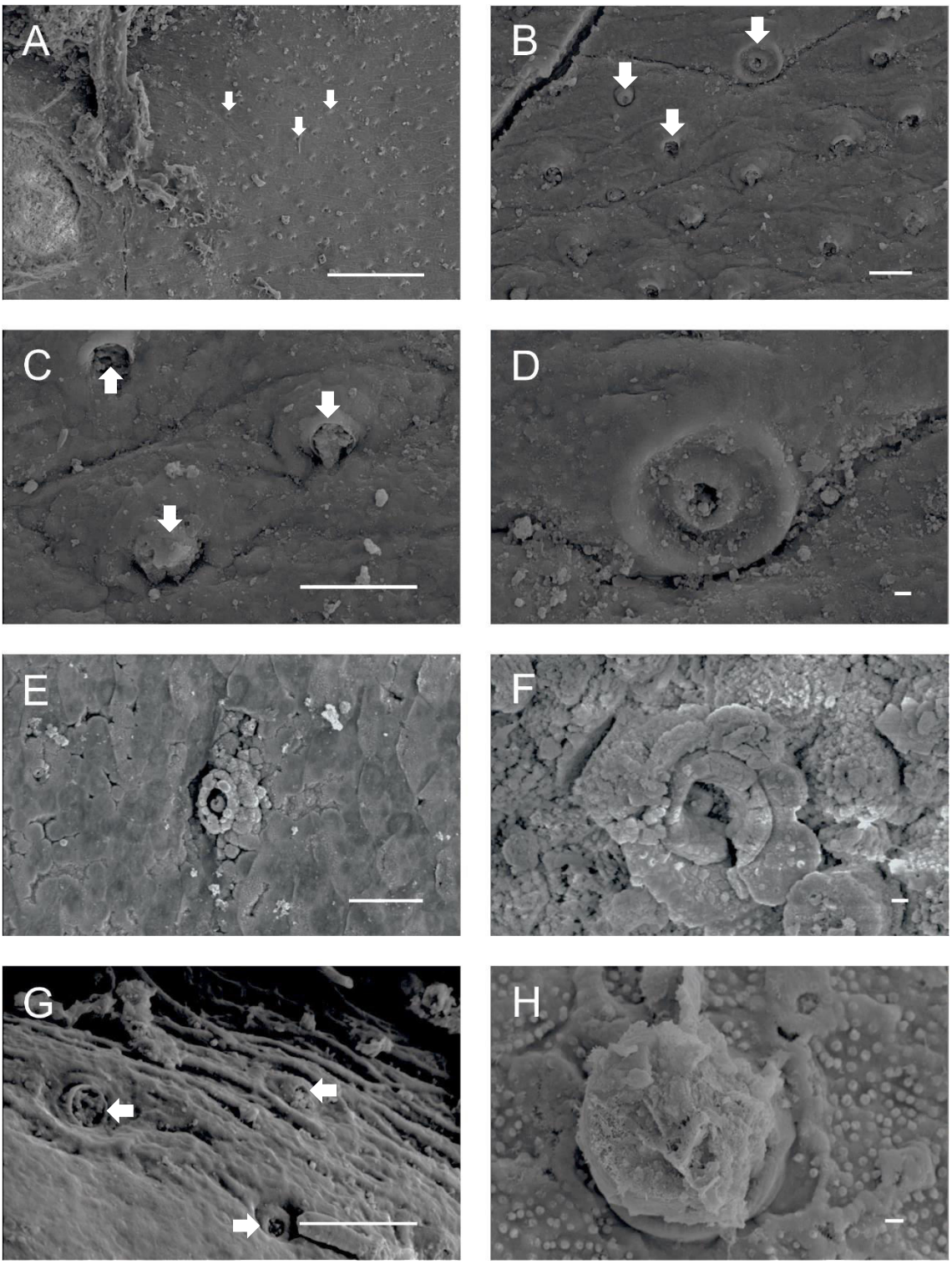


Plate 41: Examples of disarticulated setae, leaving only setal bases, in Nova Olinda Member fossil insects. A-B, Overview of cuticle with only setal bases remaining, highlighted by arrows. C-D and G, Higher magnification images of setal bases, highlighted by arrows. E-F, Poorly-preserved bulbous setal bases, setal morphology deformed by the growth of the preserving minerals or by decay processes prior to replacement. H, Poorly preserved setae, with only the proximal part of the setae remaining. Specimen and image numbers: A, FLO69-28; B, FLO69-31; C, FLO69-33; D, FLO69-35; E, NBRL037-33; F, NBRL066(resi)-15; G, FLO15-02; H, NBRL055-120. A, Scale bar = 100 µm. B-C, E and G, Scale bars = 10 µm. D and H, Scale bars = 1 µm.

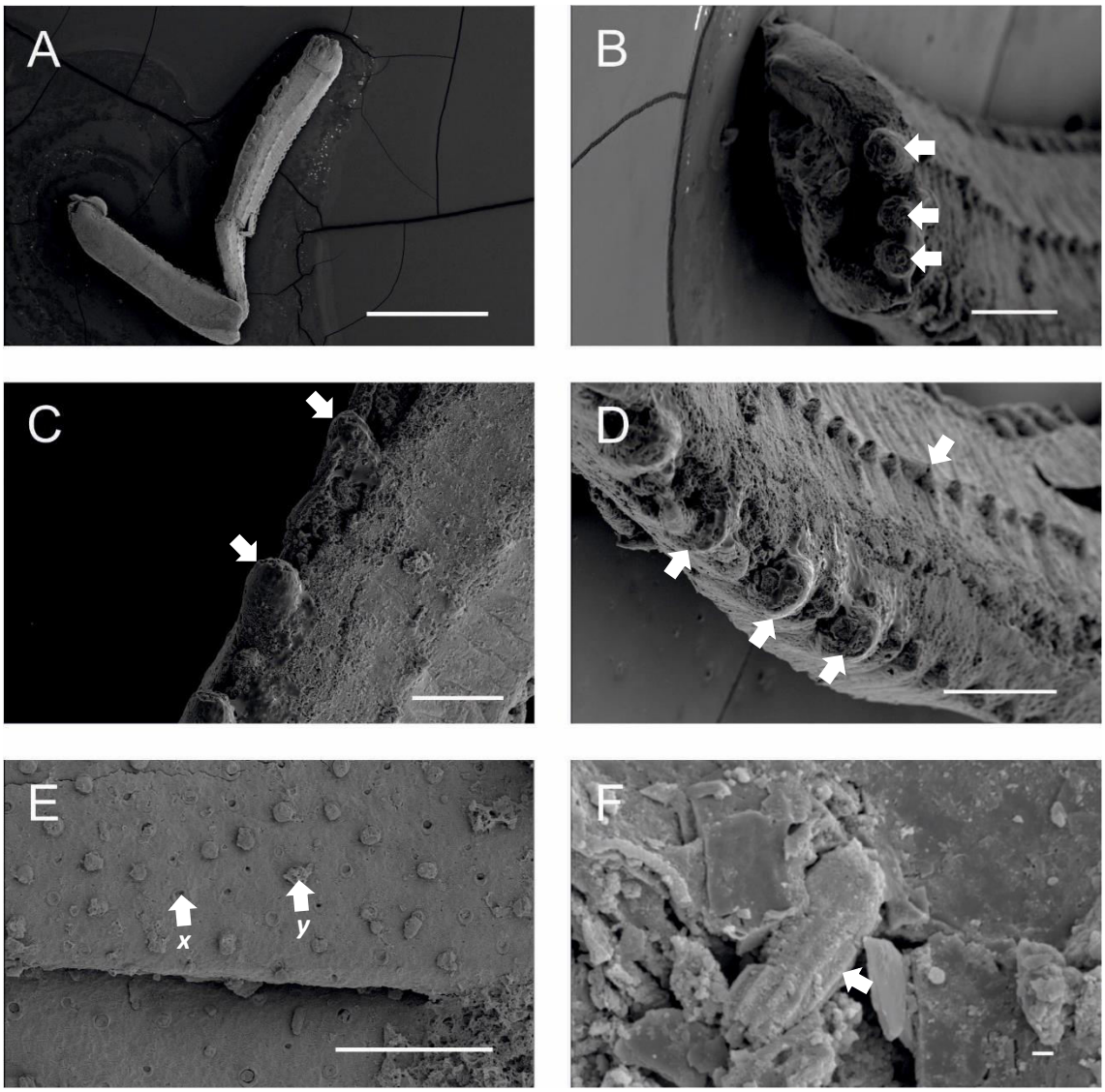


Plate 42: Examples of high-relief structures preserved as disarticulated fragments in the Nova Olinda Member fossil insects. A, Overview of disarticulated limb after complete acid digestion. B-D, Higher magnification images showing cuticular spines, highlighted by arrows. Spines are 'degraded', likely a result of abrasion from effervescence during 10% hydrochloric acid digestion. E, Cuticle with setae mostly disarticulated, leaving setal bases (*x*) or extremely poorly-preserved setae fragments (*y*). F, Single setae fragment with ridges preserved embedded in a crack in the cuticle, highlighted by arrow. Specimen and image numbers: A, FLO17-32; B, FLO17-02; C, FLO17-22; D, FLO17-41; E, NBRL055-61; F, NBRL078-21. A, Scale bar = 1 mm. B-E, Scale bars = 100 µm. F, Scale bar = 1 µm.

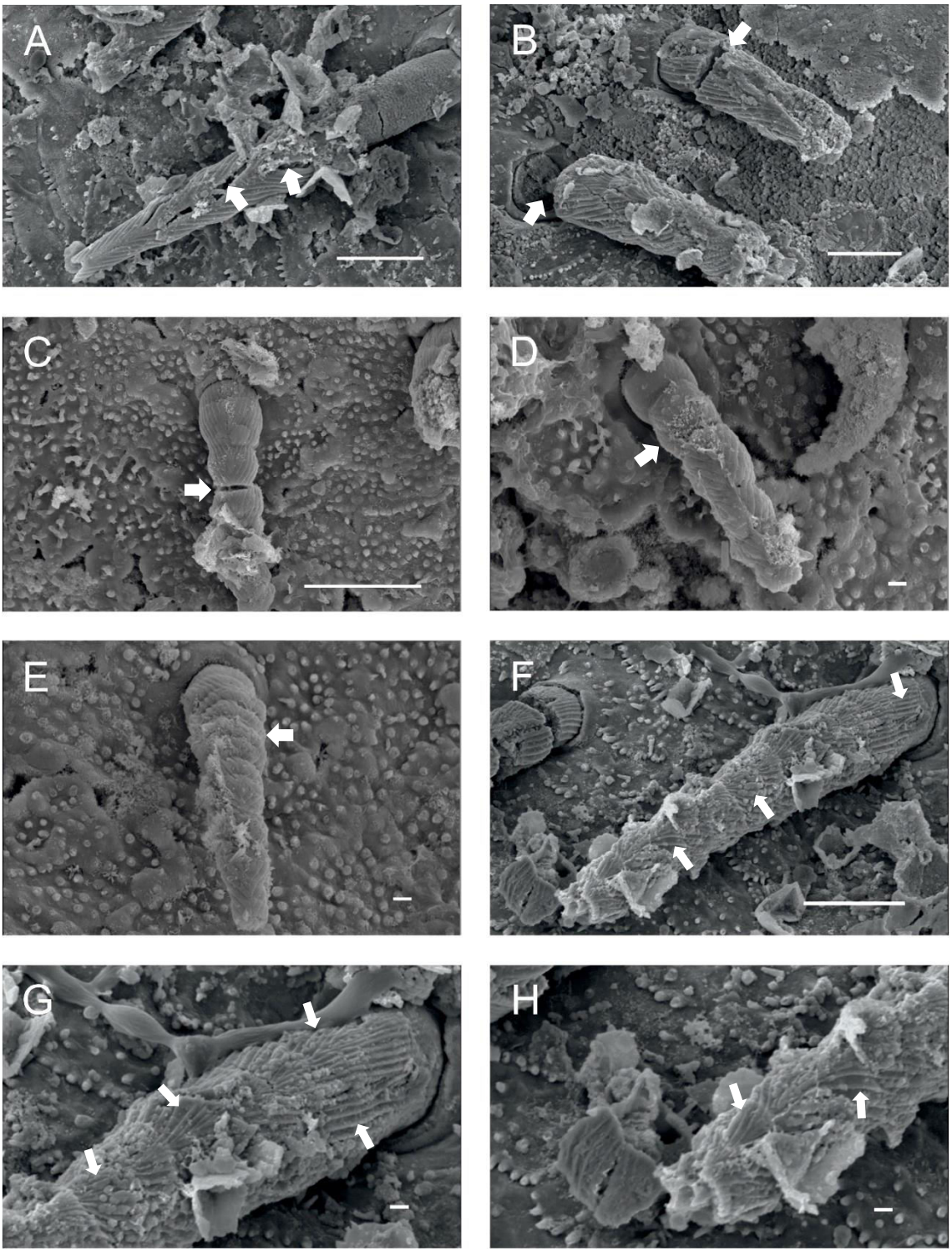


Plate 43: Examples of setae from Nova Olinda Member fossil insects that are bulbous or otherwise warped. A-C, Warped setae that have split along their length or broken perpendicular to their length. Cracks and breaks highlighted by arrow. D-E, Setae with bulbous swellings, giving them a 'bead-like' appearance, highlighted by arrows. F-H, Setae with ridges, highlighted by arrows, that form distinct segments, similar to the bulbous swelling. Specimen and image numbers: A, NBRL059-63; B, NBRL059-72; C, NBRL055-99; D, NBRL055-108; E, NBRL055-118; F, NBRL059-68; G, NBRL059-69; H, NBRL059-71. A-C and F, Scale bars = 10 µm. D-E and G-H, Scale bars = 1 µm.

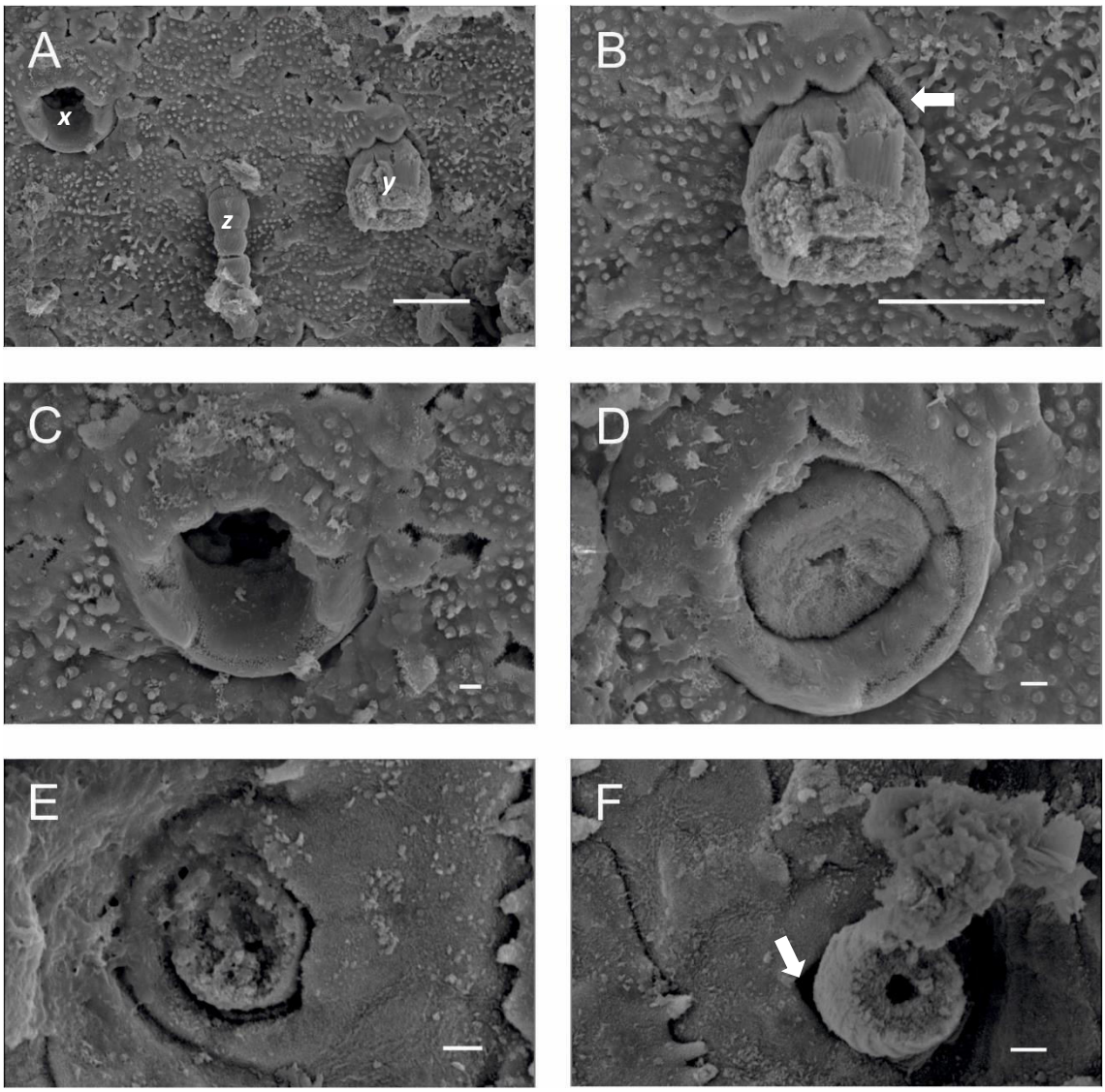


Plate 44: Disarticulated setae, revealing exceptionally preserved setal bases in Nova Olinda Member fossil insects. A, Various types of setal bases within a single specimen, including completely disarticulated setae (x), partially disarticulated setae (y), and articulated, but fractured setae, with no discernible base (z). B and F, Higher magnification image of partially disarticulated setae that appears to erupt from cuticle, rather than from a distinct base, highlighted by arrow. C, Higher magnification image of completely disarticulated setae, leading empty setal base. D-E, Higher magnification images of disarticulated setae, leaving broken fragment of setae terminus embedded into setal base. Specimen and image numbers: A, NBRL055-87; B, NBRL055-89; C, NBRL055-93; D, NBRL055-103; E, NBRL059-19; F, NBRL059-16. A-B, Scale bars = 10 µm. C-F, Scale bars = 1 µm.

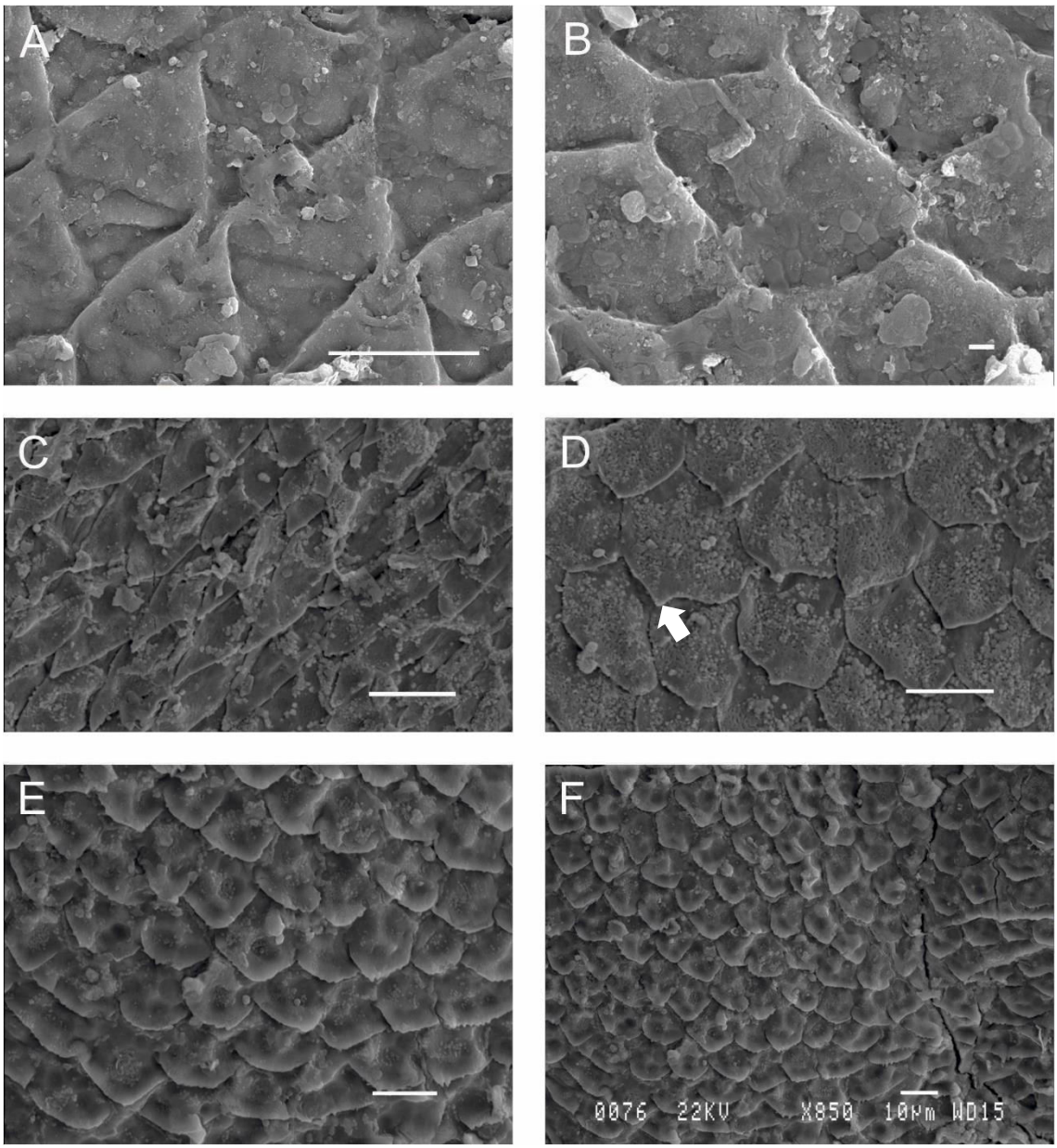


Plate 45: Exceptionally preserved rhombohedral and trapezium-shaped scales from Nova Olinda Member fossil insects. A and C, Relatively thin rhombohedral scales. B and E-F, Broader trapezoid scales, with rounded tips. D, Broad curved scales with an angular tip, highlighted by arrow. Specimen and image numbers: A, FLO38-20; B, FLO38-28; C, NBEL040-79; D, NBRL040-81; E, NBRL040-144; F, NBRL040-145. B, Scale bar = 1 µm. A and C-F, Scale bars = 10 µm.

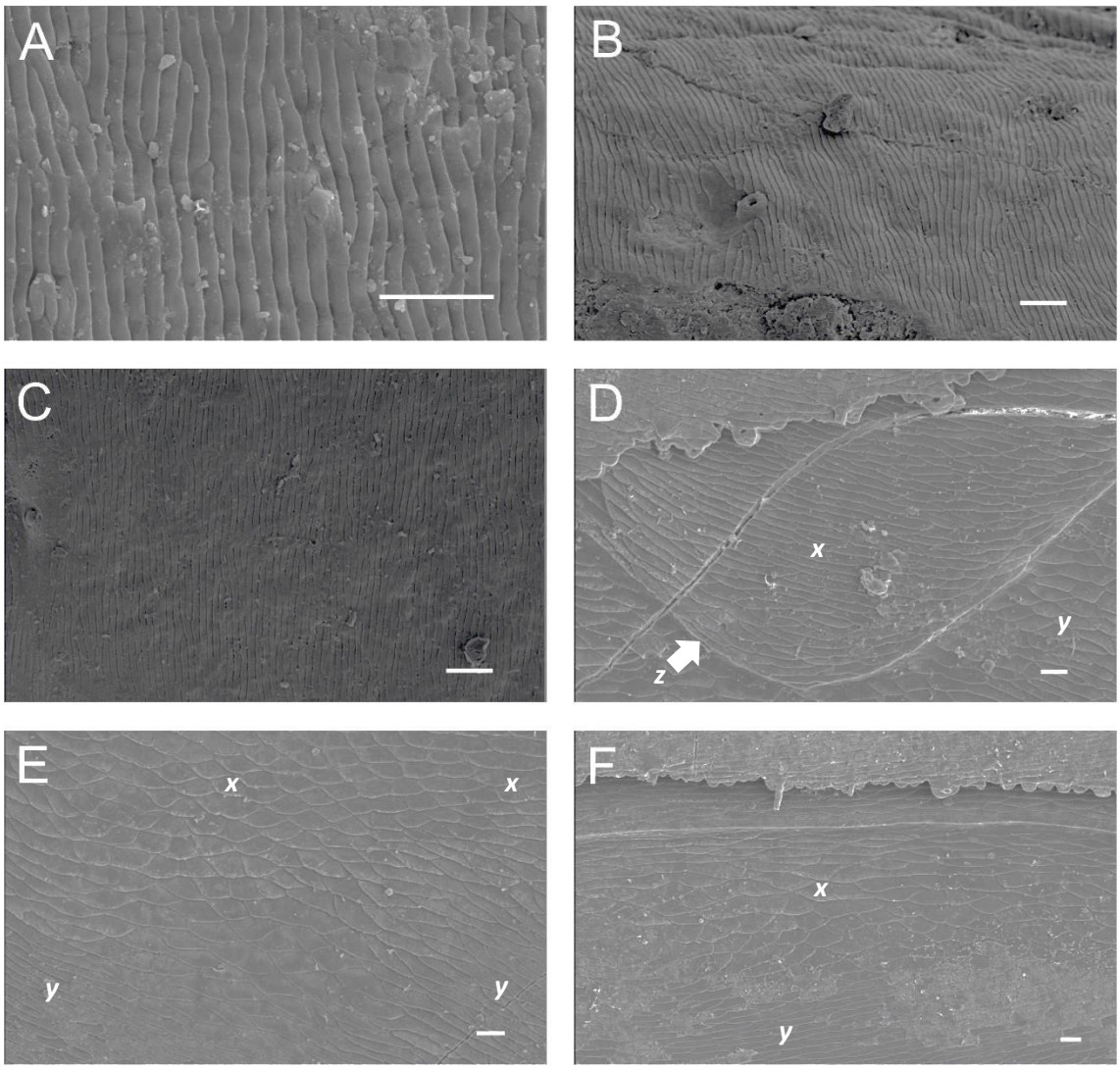


Plate 46: Exceptionally preserved “long and thin” scales from Nova Olinda Member fossil insects. A-C, Extremely thin and broad scales. D, Patch of thin, broad scales (*x*), surrounded by stouter scales (*y*), separated by a suture (*z*). E-F, Diffuse transition from curved scales (*x*) into thin, broad scales (*y*). Specimen and image numbers: A, NBRL036-54; B, NBRL036-36; C, NBRL018-19; D, NBRL040-58; E, NBRL040-56; F, NBRL040-52. Scale bars = 10 µm.

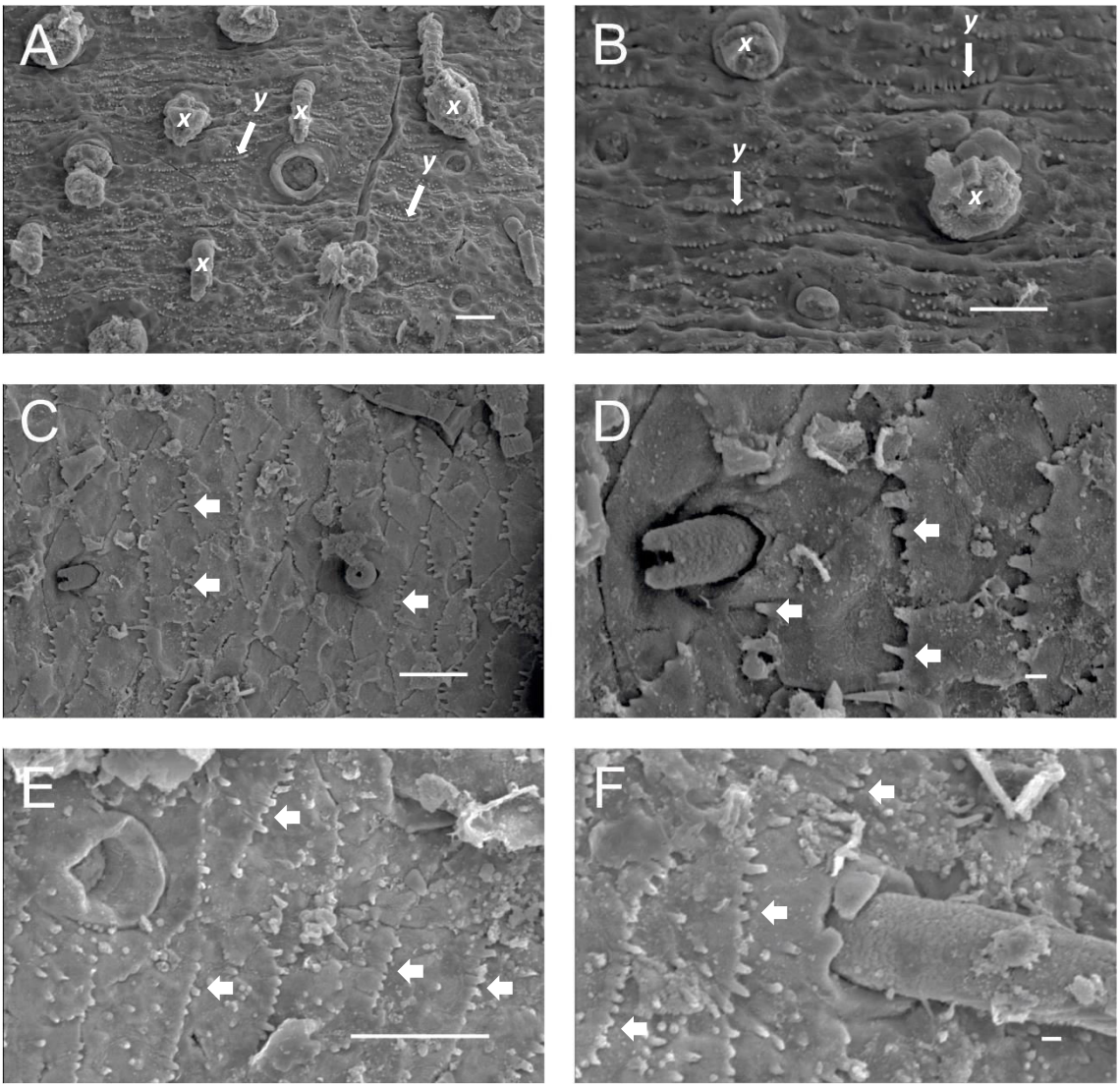


Plate 47: Examples of micro-spines (microtrichium) preserved from Nova Olinda Member fossil insects. A and B, Portion of moderately preserved cuticle, with poorly preserved setae (*x*) and scales edged by micro-spines (*y*), viewed at a 45° angle. C-F, Scales with micro-spines on distal margin, giving them a jagged appearance, highlighted by arrows. Specimen and image numbers: A, NBRL055-08; B, NBRL055-07; C, NBRL059-14; D, NBRL059-18; E, NBRL059-56; F, NBRL059-57. D and F Scale bars = 1 µm. A-C and E, Scale bars = 10 µm.

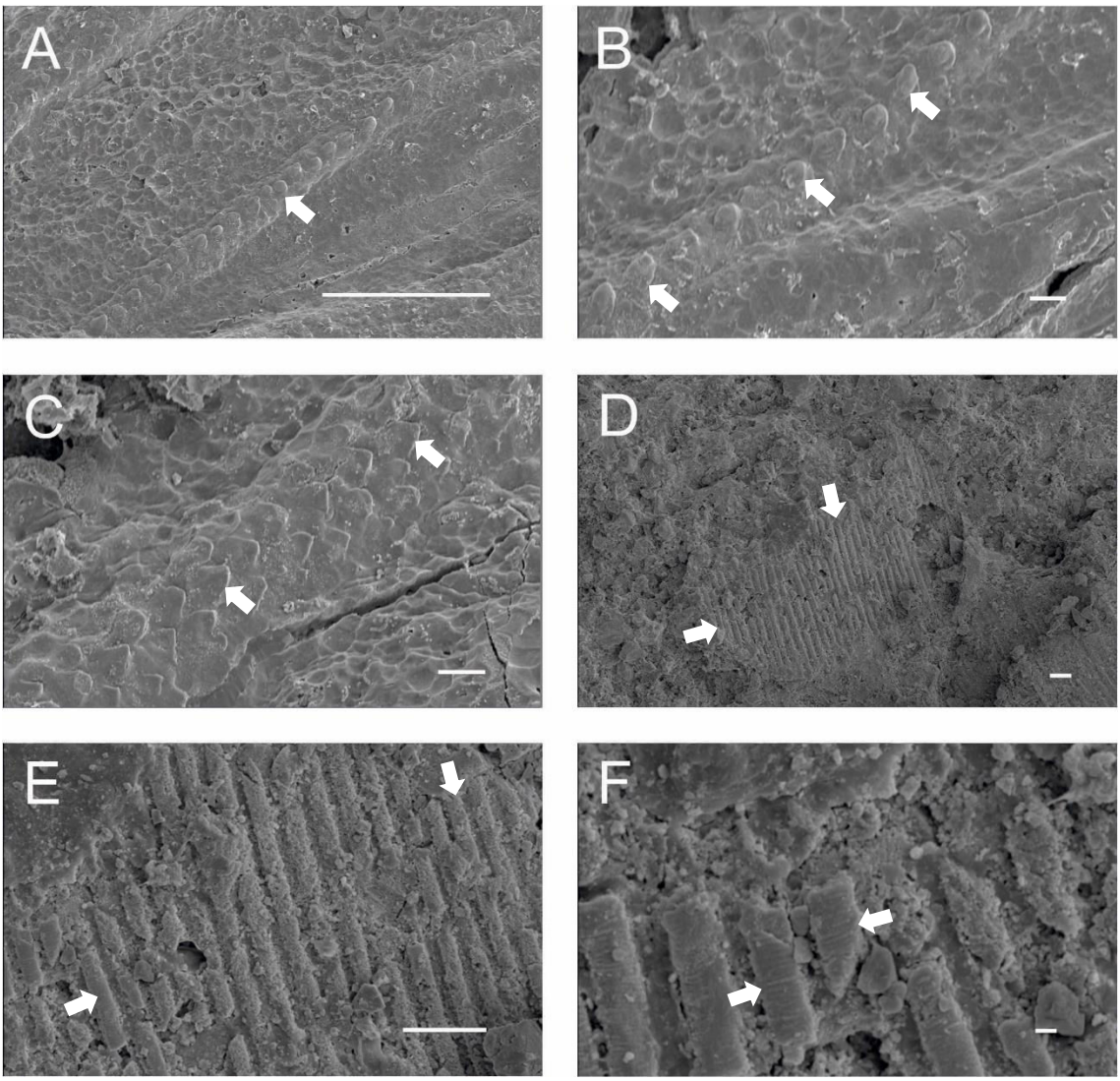


Plate 48: Examples of micro-spines and ridging in Nova Olinda Member fossil insects. A-C, Lines of micro-spines that appear to be adapted cuticular scales, highlighted by arrows. D-E, Wing cuticle with striations, highlighted by arrows. F, Higher magnification image revealing that each striation is covered in smaller perpendicular striations, highlighted by arrows. Specimen and image numbers: A, NBRL051-53; B, NBRL051-50; C, NBRL051-55; D, NBRL070-20; E, NBRL070-21; F, NBRL070-22. A, Scale bar = 100 µm. B-E, Scale bars = 10 µm. F, Scale bar = 1 µm.

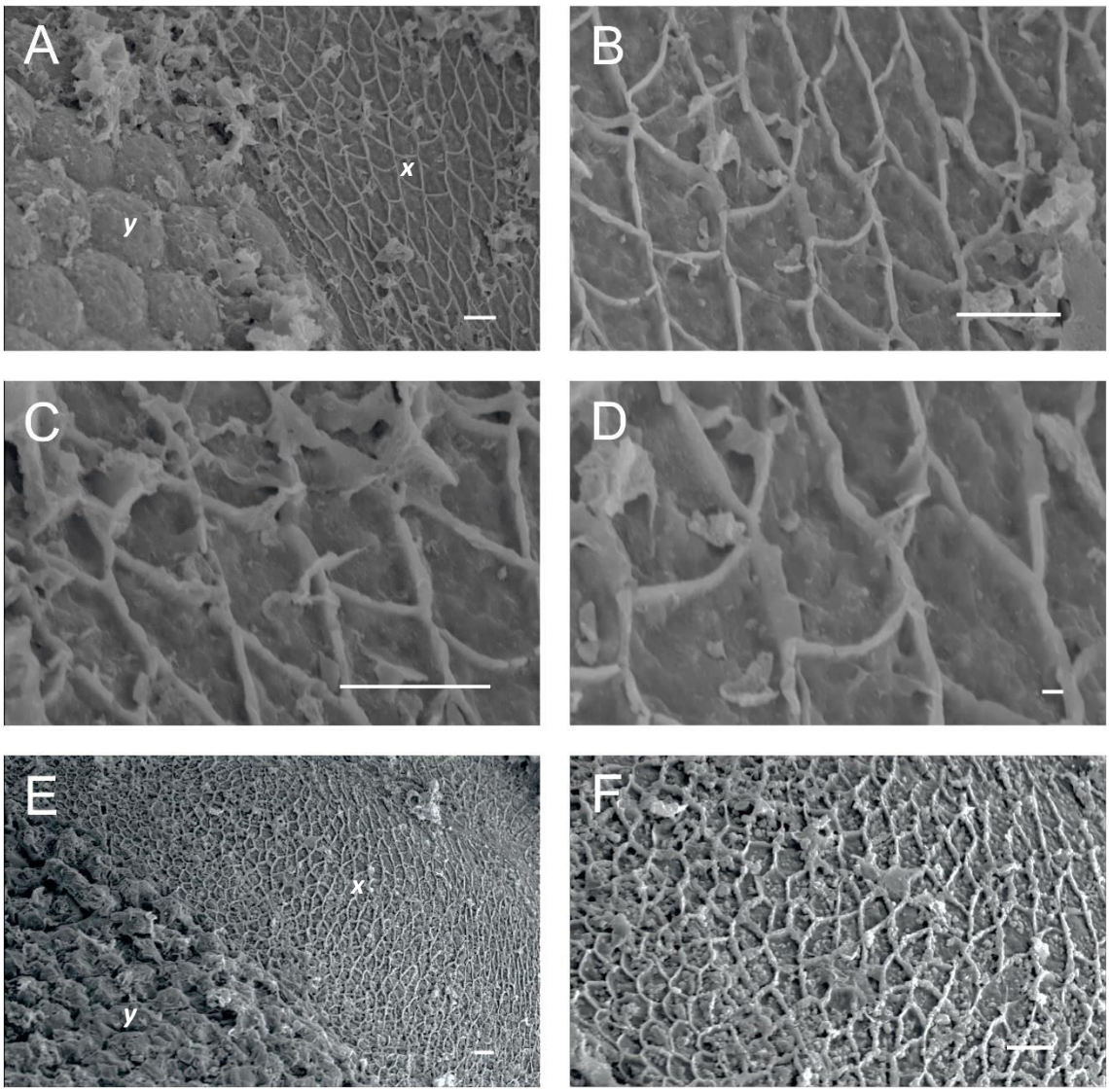


Plate 49: Exceptionally preserved Orthoptera: Elcanidae head cuticle from the Nova Olinda Member, preserving a meshwork of cuticular ridges, similar to structures found in the cement and wax layers of modern orthopteran epicuticle. A, Mesh-like ridged cuticle (*x*) immediately adjacent to ommatidia (*y*). Likely vertex or gena, showing sharp contact between eye and cuticle with these ridges. B-D, Higher magnification images of mesh-like ridged cuticle. E-F, Another Orthoptera: Elcanidae specimen with the same structures covering the head, albeit with poorer preservation. Specimen and image numbers: A, NBRL044-##20; B, NBRL044-##23; C, NBRL044-##22; D, NBRL044-##25; E, NBRL051-13; F, NBRL051-14. A-C and E-F, Scale bars = 10 µm. D, Scale bar = 1 µm.

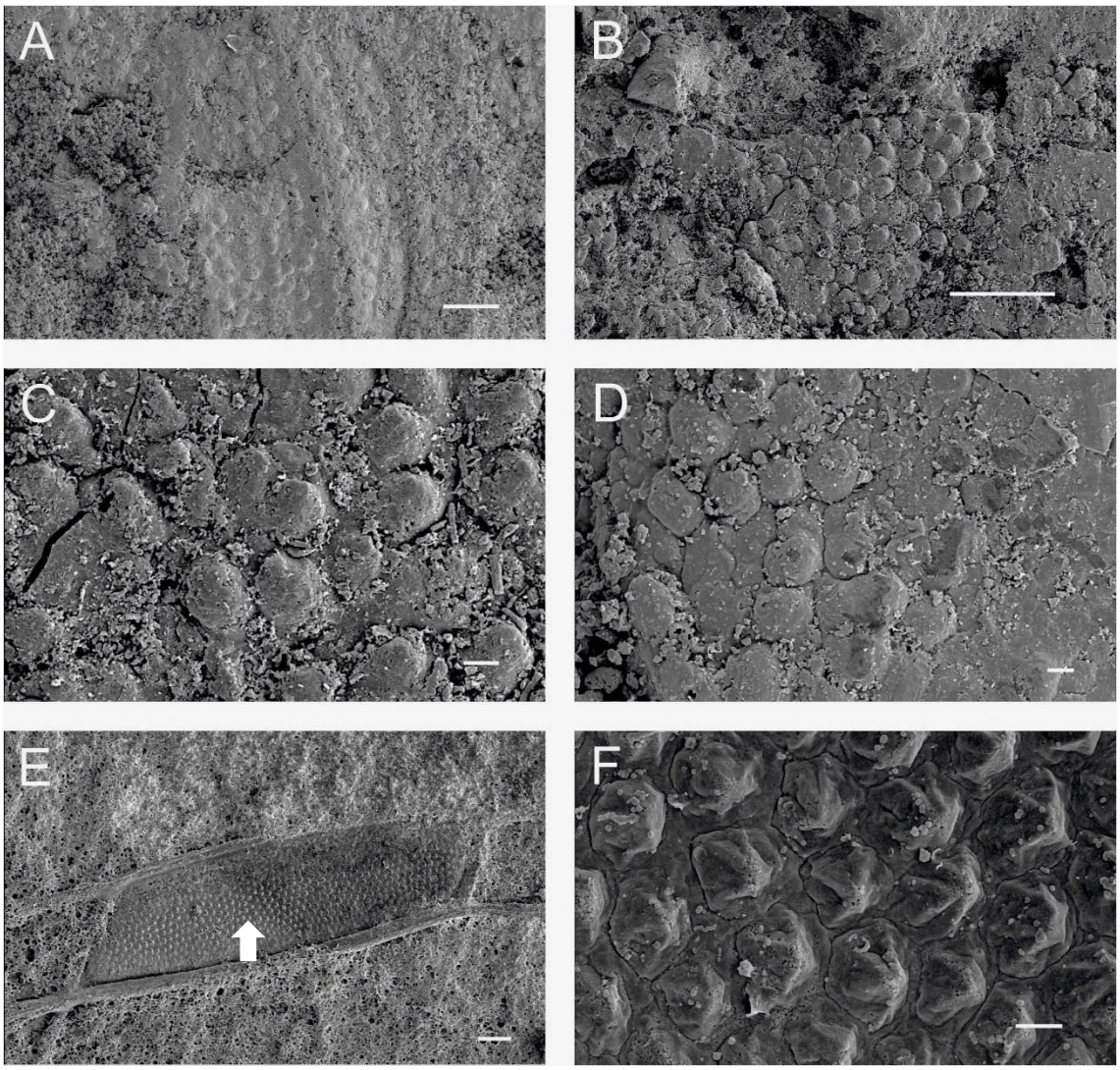


Plate 50: Examples of domed and bumped cuticle from Nova Olinda Member insects. A-D, Unidentified insect with domes across head and thorax cuticle. E and F, Odonate pterostigma (darkened cuticle in distal anterior of forewings) cuticle with typical pyramid pterostigma cuticular morphology. F is higher magnification image of area highlighted by arrow in E. Specimen and image numbers: A, JW522-011; B, JW522-004; C, JW522-005; D, JW522-009; E, UnNum.FLO-31; F, UnNum.FLO-19. A and B, Scale bars = 100 µm; C-F, Scale bars = 10 µm.

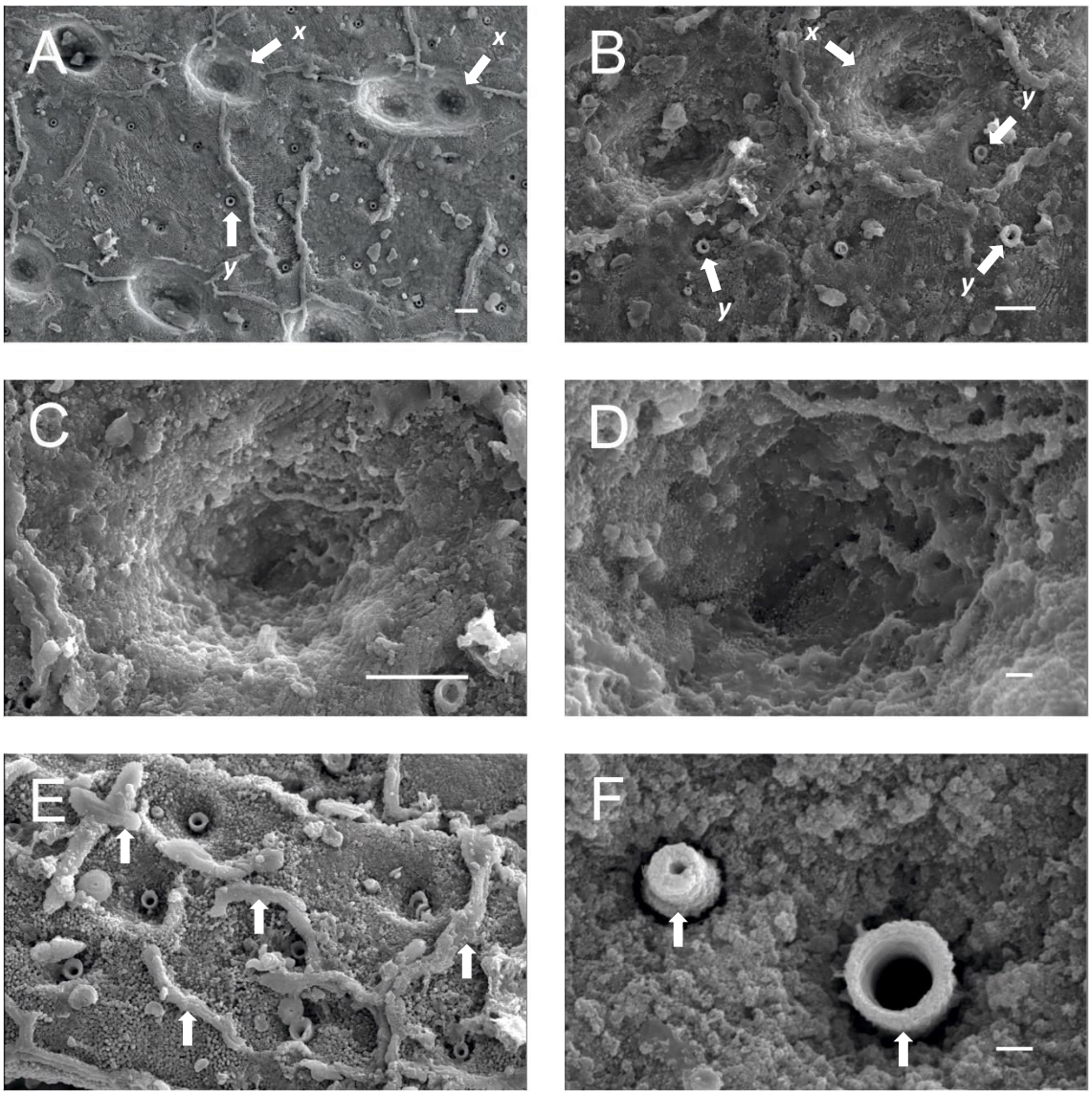


Plate 51: Well-preserved elytra from Nova Olinda Member fossil beetles. A-B, Overviews of beetle elytra, showing their overall morphology including: deep pits *(x*) and spiracles(?) (*y*). C-D, Deep pit in elytra, replicated in discernible micro-granules. E, Reinforcing mesh-like raised cuticle covering elytra highlighted by arrows, implying that the epicuticle has been stripped away. F, Spiracles or other opening preserved in shallow pits, highlighted by arrows. Specimen and image numbers: A, NBRL045-##01; B, NBRL045-##40; C, NBRL045-##46; D, NBRL045-##48; E, NBRL045-##39; F, NBRL045-##36. A-C, Scale bars = 10 µm. D and F, Scale bars = 1 µm. E, No scale recorded.

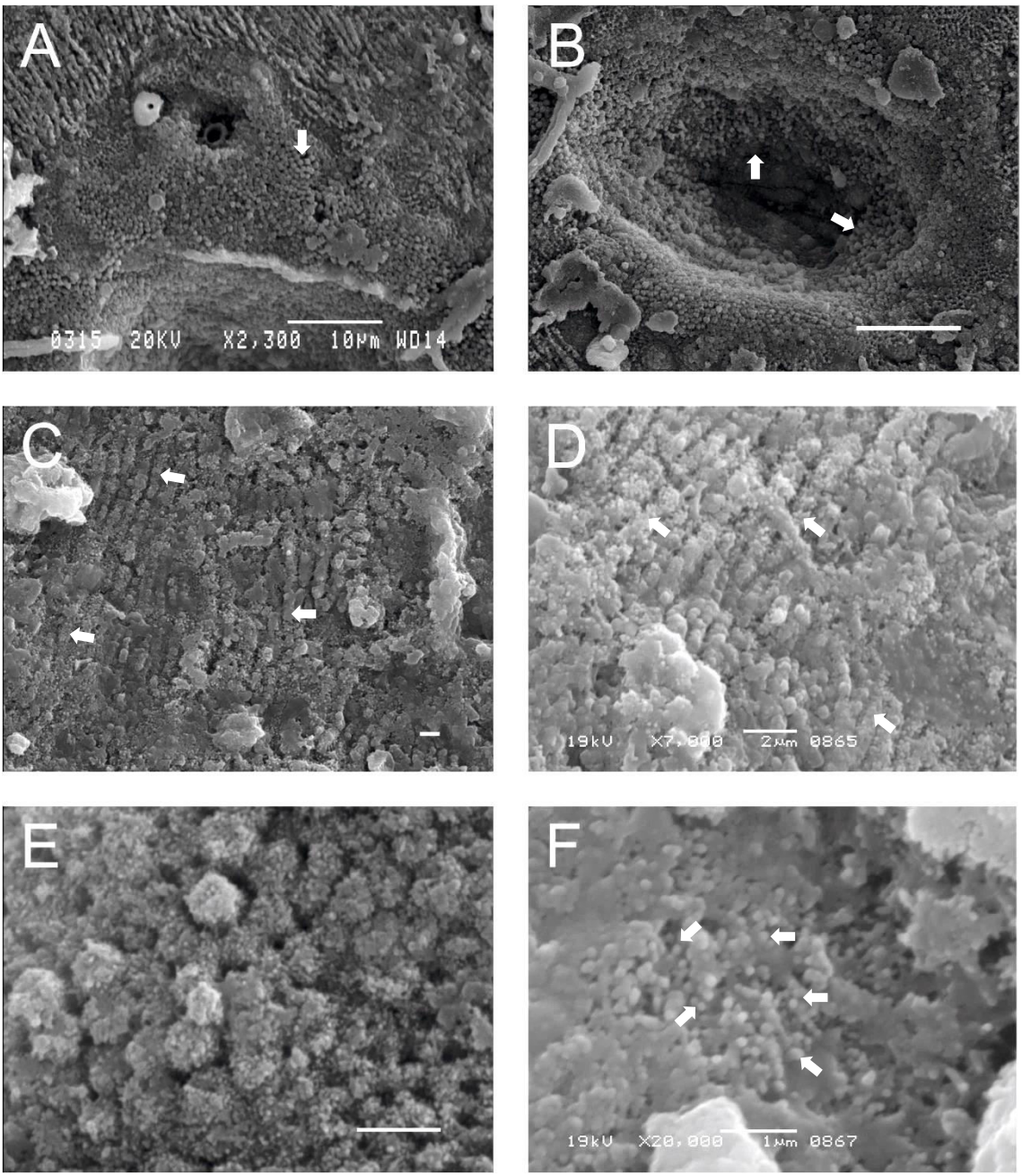


Plate 52: Micro-spherical and micro-subspherical-aggregate replacement fabric of fossil beetle elytra in the Nova Olinda Member. A-D, Sub-micron subspherical aggregates replacing the fossil elytra of beetles. These can be arranged loosely (A), on both the cuticular surface and within cuticular pits (B), or in striations (C-D), all highlighted by arrows. E, Higher magnification of 'microspheres', revealing their granular fabric. F, Submicron subspherical aggregates of crystallites that have disarticulated, that the microspheres are presumably constituted of, highlighted by arrows. Alternatively, these submicron aggregates of crystallites are a result of excessive Au-Pd sputter coating. Specimen and image numbers: A, NBRL045-##05; B, NBRL045-##26; C, NBRL045-##42; D, NBRL045-81; E, NBRL045-##30; F, NBRL045-83. A-B, Scale bars = 10 µm. C and E-F, Scale bars = 1 µm. D, Scale bar = 2 µm.

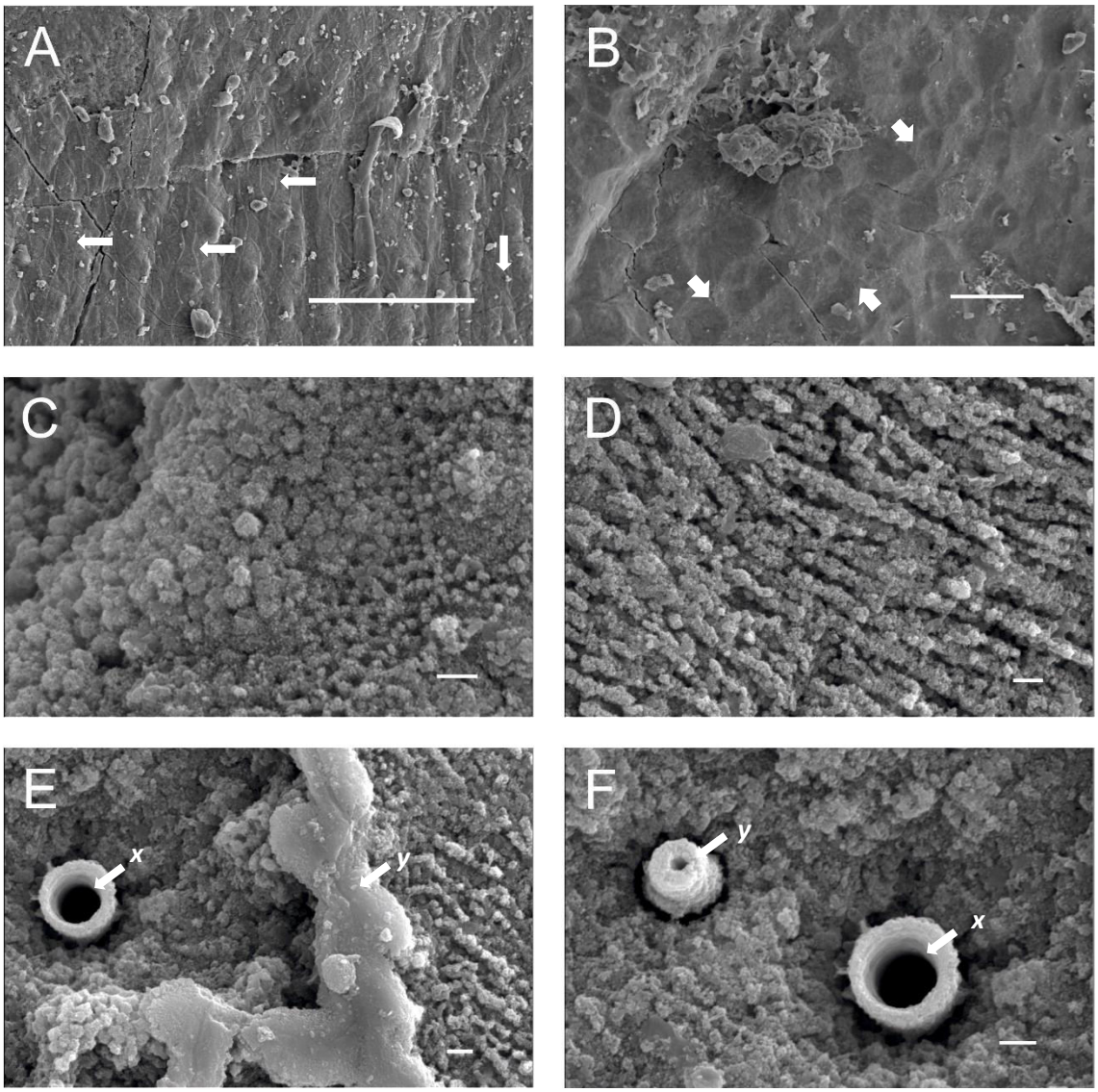


Plate 53: Examples of differing cuticular morphology in the Nova Olinda Member fossil insects. A, Remnants of scales outlined by raised cuticle, highlighted by arrows. B, Wing cuticle with a 'crumpled' morphology, highlighted by arrows. C and D, Two types of preservation of beetle elytra; subspherical (C) and striated (D). E, Beetle elytra with spiracles (*x*) and raised lines of durable cuticle (*y*) (forming a mesh over elytra). F, Broad (*x*) and narrow (*y*) spiracles(?) in beetle elytra. Specimen and image numbers: A, FLO69-08; B, NBRL079-37; C, NBRL045-##31; D, NBRL045-##32; E, NBRL045-##34; F, NBRL045-##36. A, Scale bar = 100 µm; B, Scale bar = 10 µm. C-F, Scale bars = 1 µm.

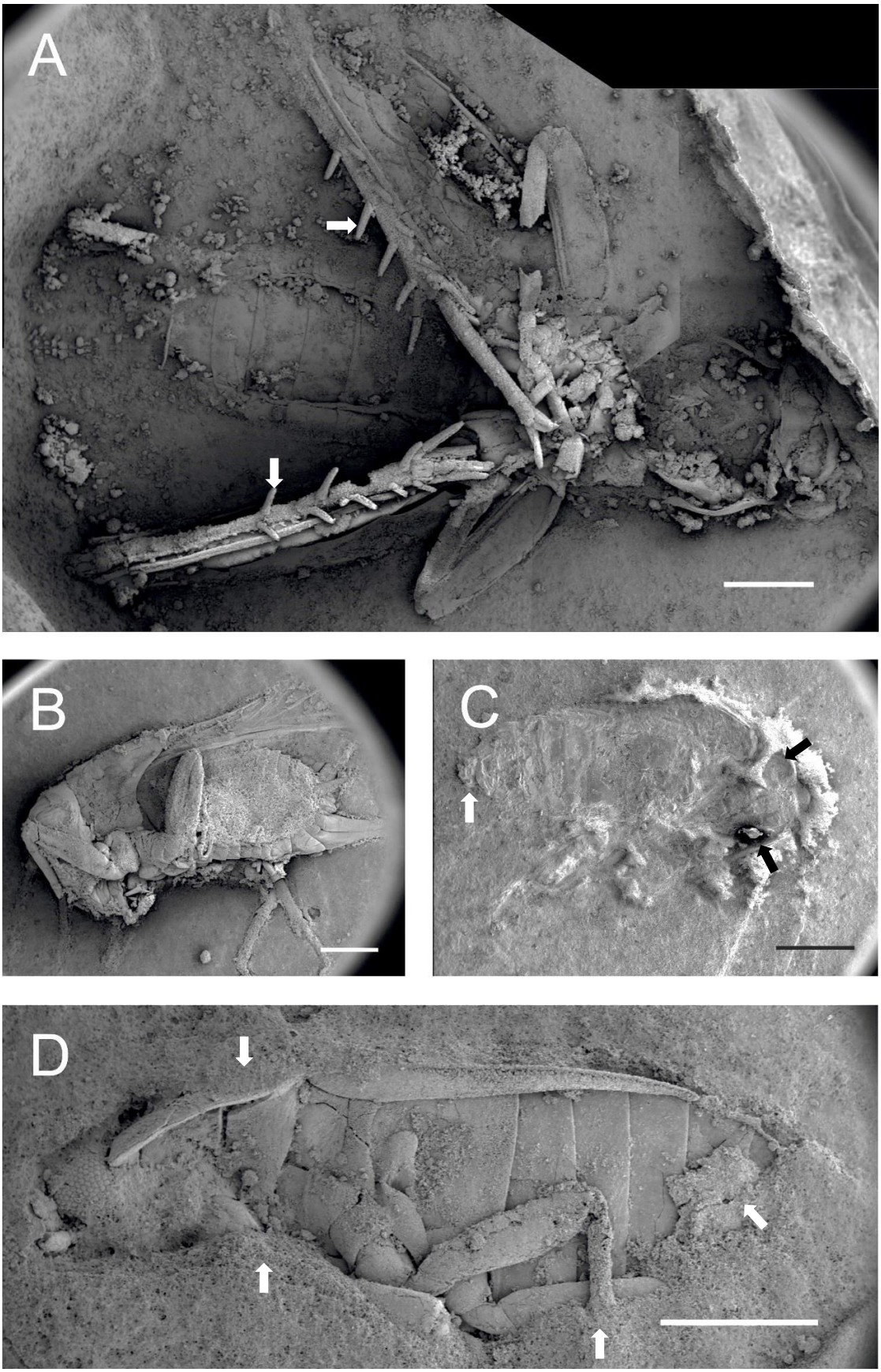


Plate 54: Examples of Nova Olinda Member fossil insect specimens with high relief. A-B, Successfully resin transferred Orthoptera (B, Elcanidae) specimens with high relief. A, Limbs remain intact and articulated with large spines, highlighted by arrows. C, Un-transferred orthopteran with charging and abraded surface. White arrow highlights cuticle with relief, despite the damage. Black arrows highlight charging. D, Resin-transferred specimen, with resin penetrating around the specimen, highlighted by arrows. Specimen and image numbers: A, Composite image NBRL059-01-03; B, NBRL051-42; C, NBRL057- 25; D, NBRL014-01. Scale bars = 1 mm.

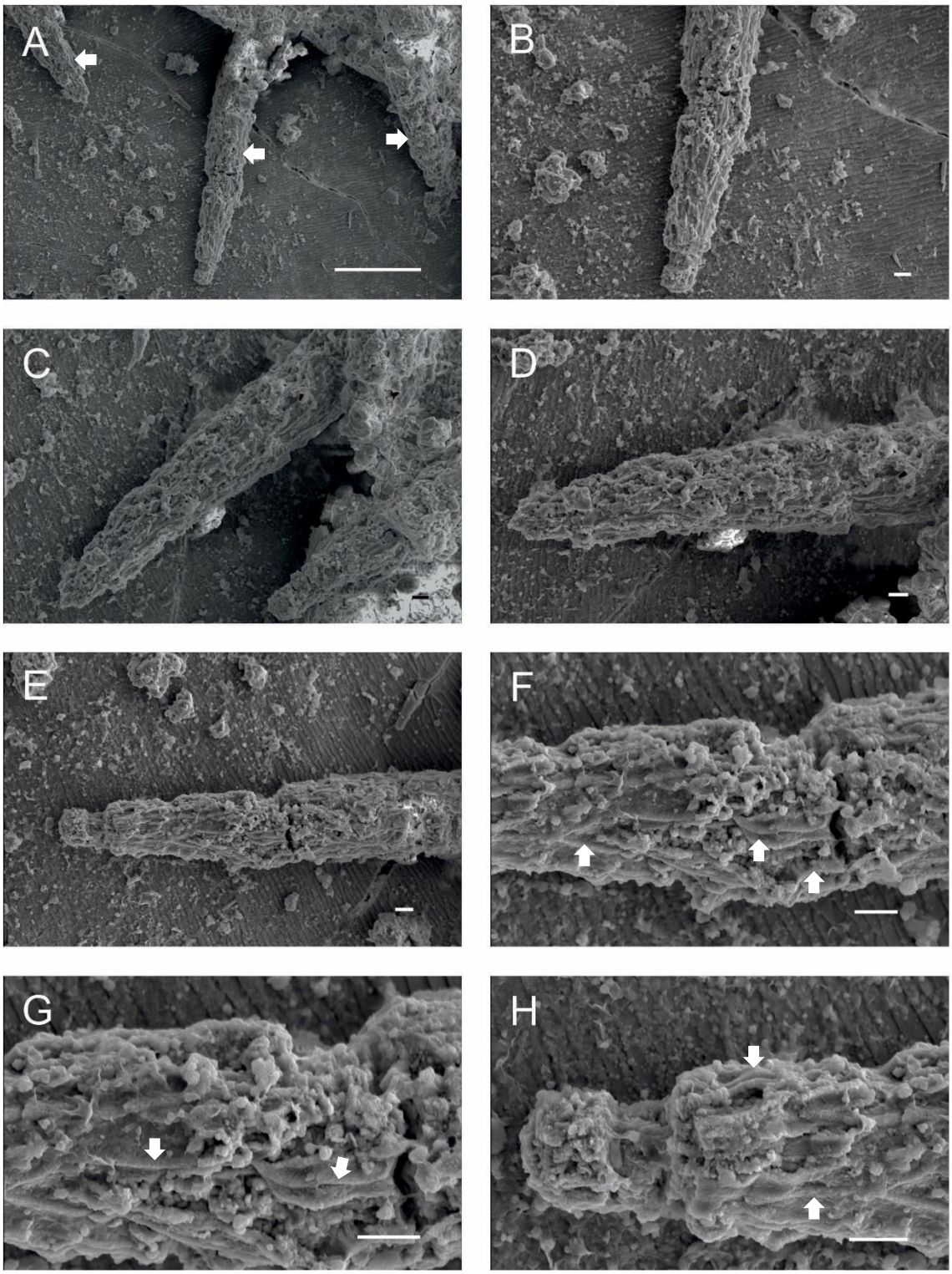


Plate 55: Examples of large cuticular limb spines/spurs preserved in Nova Olinda Member fossil insects. A-E, Spines preserved partially disarticulated and pressed against cuticle along orthopteran limb, highlighted by arrows in A. F-H, Higher magnification images of spines, showing undulating ridges extending along them, highlighted by arrows. Specimen and image numbers: A, NBRL040-101; B, NBRL040-102; C, NBRL040-111; D, NBRL040-112; E, NBRL040-103; F, NBRL040-105; G, NBRL040-107; H, NBRL040-109. A, Scale bar = 100 µm. B-H, Scale bars = 10 µm.

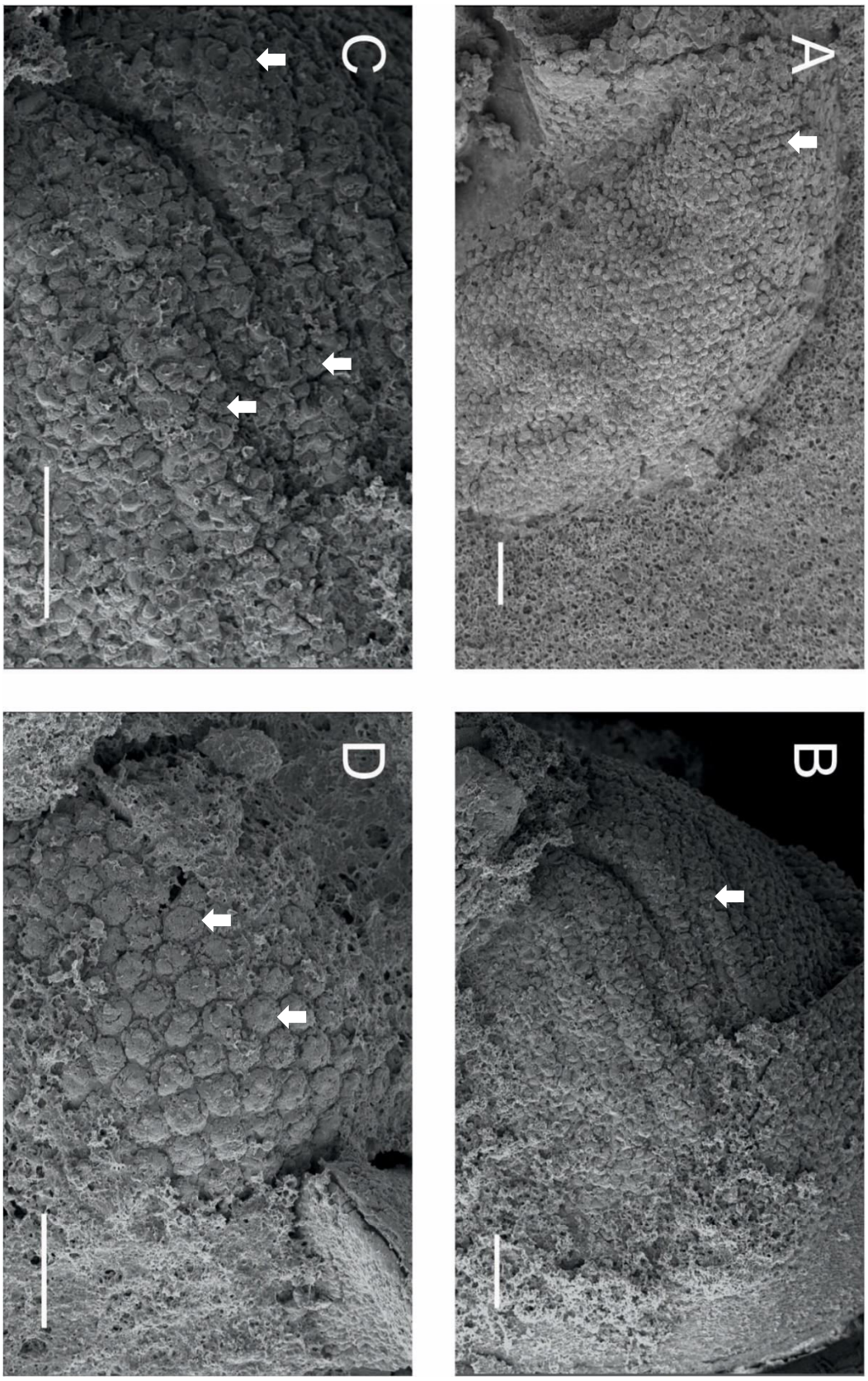


Plate 56: Examples of typical preservation of ommatidia in the Nova Olinda Member fossil insects. A, Overview of eye with partially disarticulated ommatidia, highlighted by arrow. B-C, Higher magnification of poorly-preserved and partially disarticulated ommatidia, highlighted by arrows. D, Partial eye with large, articulated, but poorly preserved, and abraded ommatidia, highlighted by arrows. Specimen and image numbers: A, NBRL040-07; B, NBRL051-76; C, NBRL051-77; D, NBRL014-06. Scale bars = 100 µm.

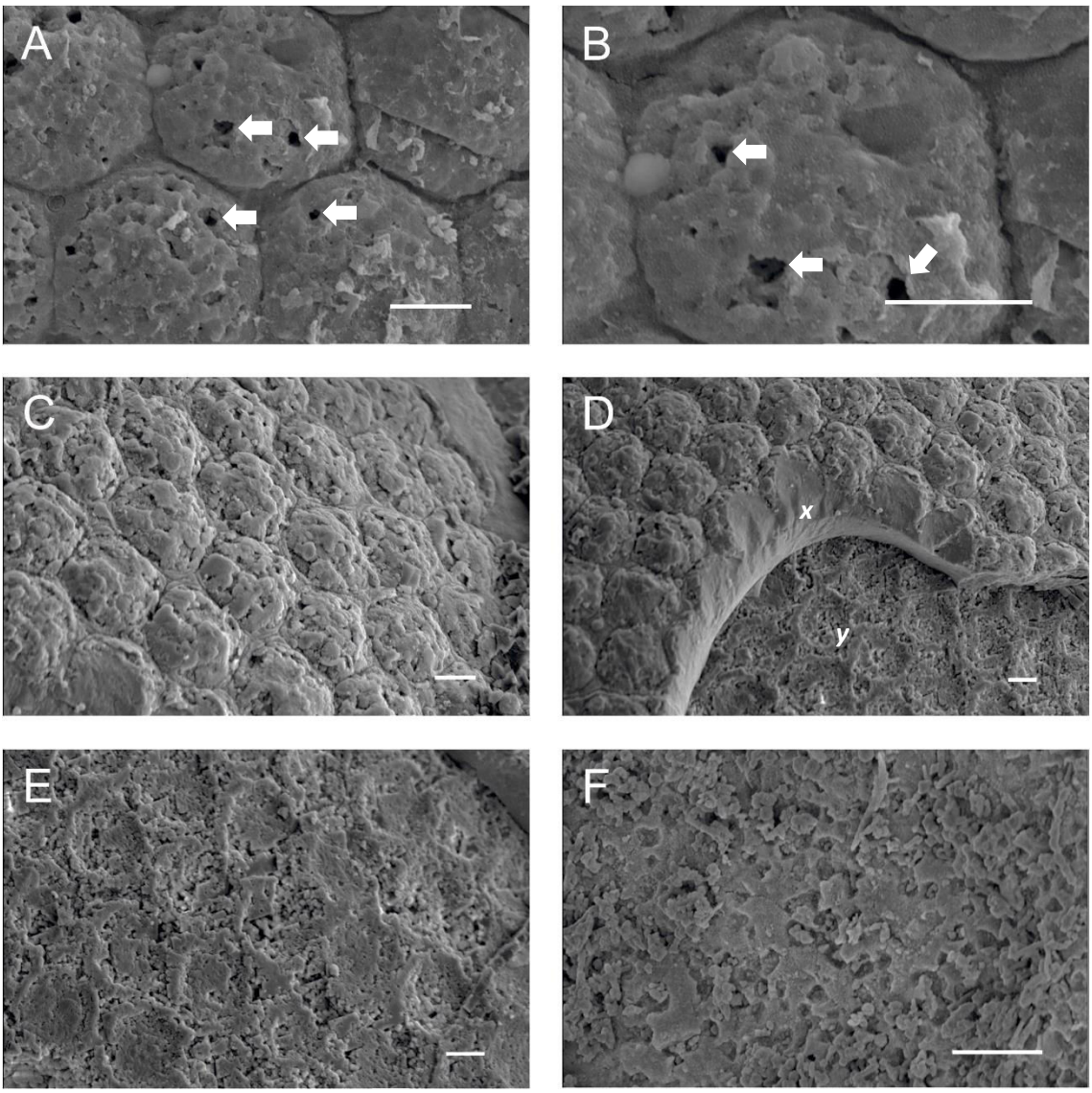


Plate 57: Examples of the variation in preservation of ommatidia in Nova Olinda Member fossil insects. A-B, Moderate-to-well preserved ommatidia with small gaps in mineralisation, highlighted by arrows. C, Poorly-preserved ommatidia with only the 'rough' honeycomb structure discernible and no visible surface details. D, Edge of cracked eye, revealing the massive internal replacement of ommatidia (*x*) and the impressions they leave on the tissues below (*y*). E-F, Ommatidia lost, leaving only their impression in the tissues preserved beneath their original position. Internal replacement is otherwise a combination of smooth material with angular impressions and globular material (F). Specimen and image numbers: A, NBRL044-##08; B, NBRL044-##09; C, FLO27-10; D, FLO27-09; E, FLO27-12; F, NBRL018-75. Scale bars = 10 µm.

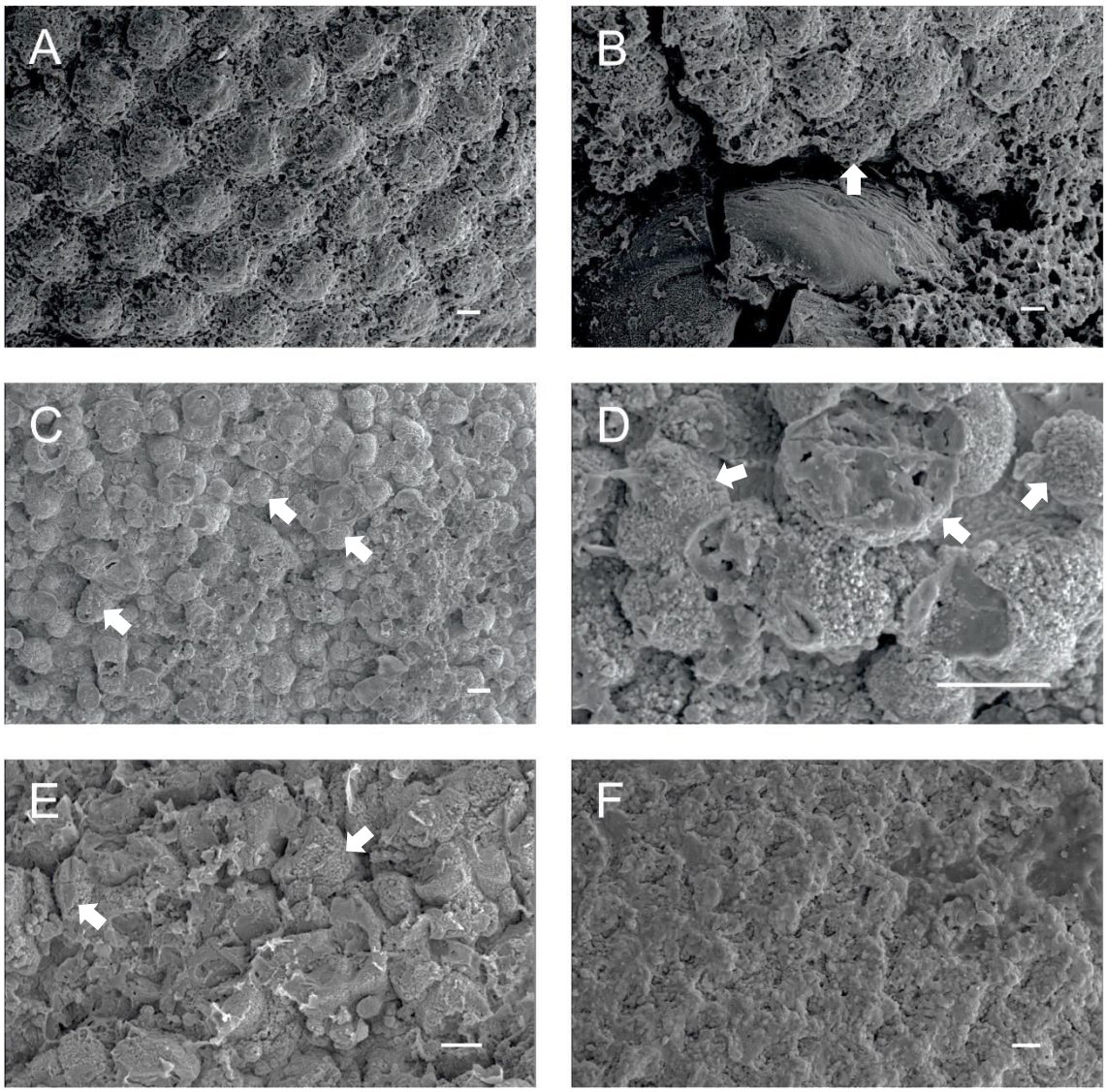


Plate 58: Further examples of variation in preservational quality of Nova Olinda Member fossil insect ommatidia. A-B, Poorly-preserved articulated ommatidia with no original cuticular surface morphology preserved, highlighted by arrow in (B). C-E, Disarticulated and poorly preserved ommatidia, highlighted by arrows. F, Ommatidia entirely lost and no discernible original morphology remains. Specimen and image numbers: A, FLO15-01; B, FLO15-03; C, NBRL040-08; D, NBRL040-09; E, NBRL051-80; F, FLO36-09. Scale bars = 10 µm.

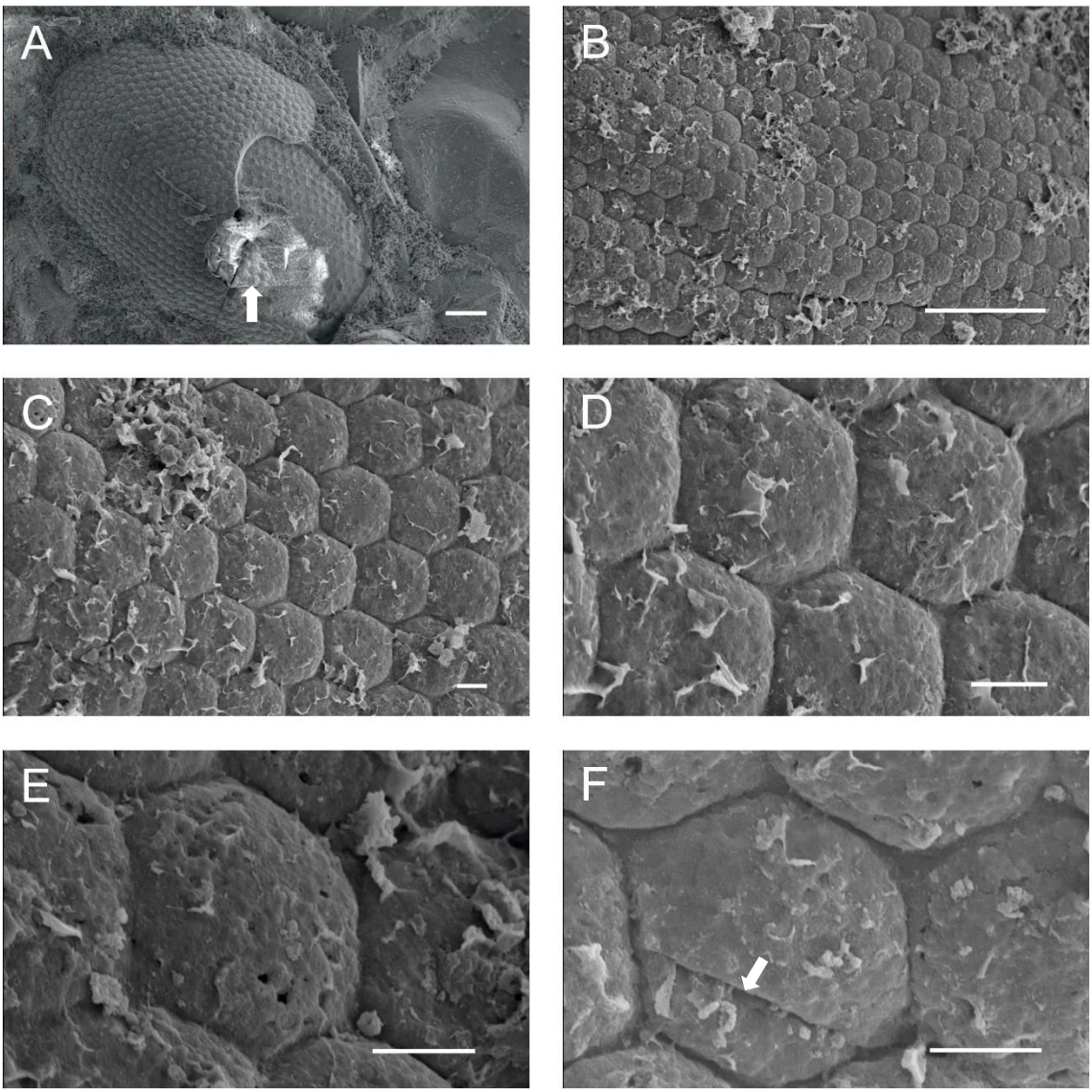


Plate 59: Exquisitely preserved ommatidia in Nova Olinda Member insect fossils. A, Overview of Hemiptera eye. Arrow highlights penetration damage, possibly caused by preparation prior to acquisition. B-E, Exquisitely preserved Orthoptera: Elcanidae ommatidia at varying magnifications. F, Arrow highlights a straight fracture through ommatidia, revealing solid and featureless infill interior in the same preserving mineral as the external surface. Specimen and image numbers: A, FLO27-06; B, NBRL044-##18; C, NBRL044-##16; D, NBRL044-##12; E, NBRL044-##03; F, NBRL044-##05. A-B, Scale bars = 100 µm. C-F, Scale bars = 10 µm.

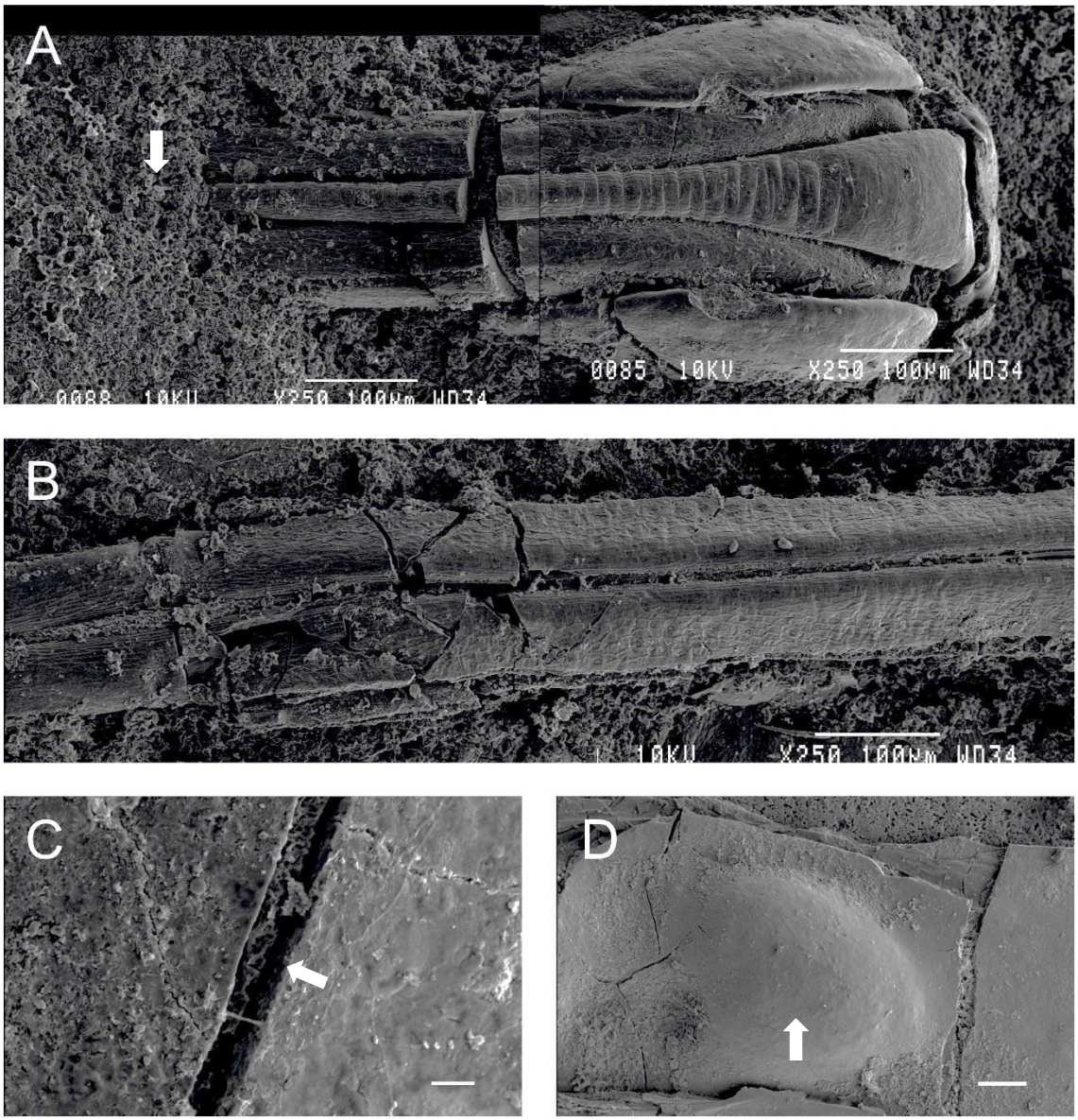


Plate 60: Uncategorised large external cuticular features of the Nova Olinda Member insects. A-B, Composite images showing well preserved hemipteran proboscis. A, Base of proboscis with the distal area partially covered by resin, highlighted by arrow. B, Right-to-left proximal-to-distal. Increasing damage to proboscis distally. C, Arrow highlights large crack in cuticle along raised ridge (may be taphonomic artefact). D, Arrow highlights large dome in cuticle, possibly representing cavity or mineral infilled void beneath. Specimen and image numbers: A, Composite image of FLO15-11 and FLO15-15; B, Composite image of FLO15-14 and FLO15-13; C, JW735-027; D, JW291-056. A-B and D, Scale bars = 100 µm. C, Scale bar = 10 µm.

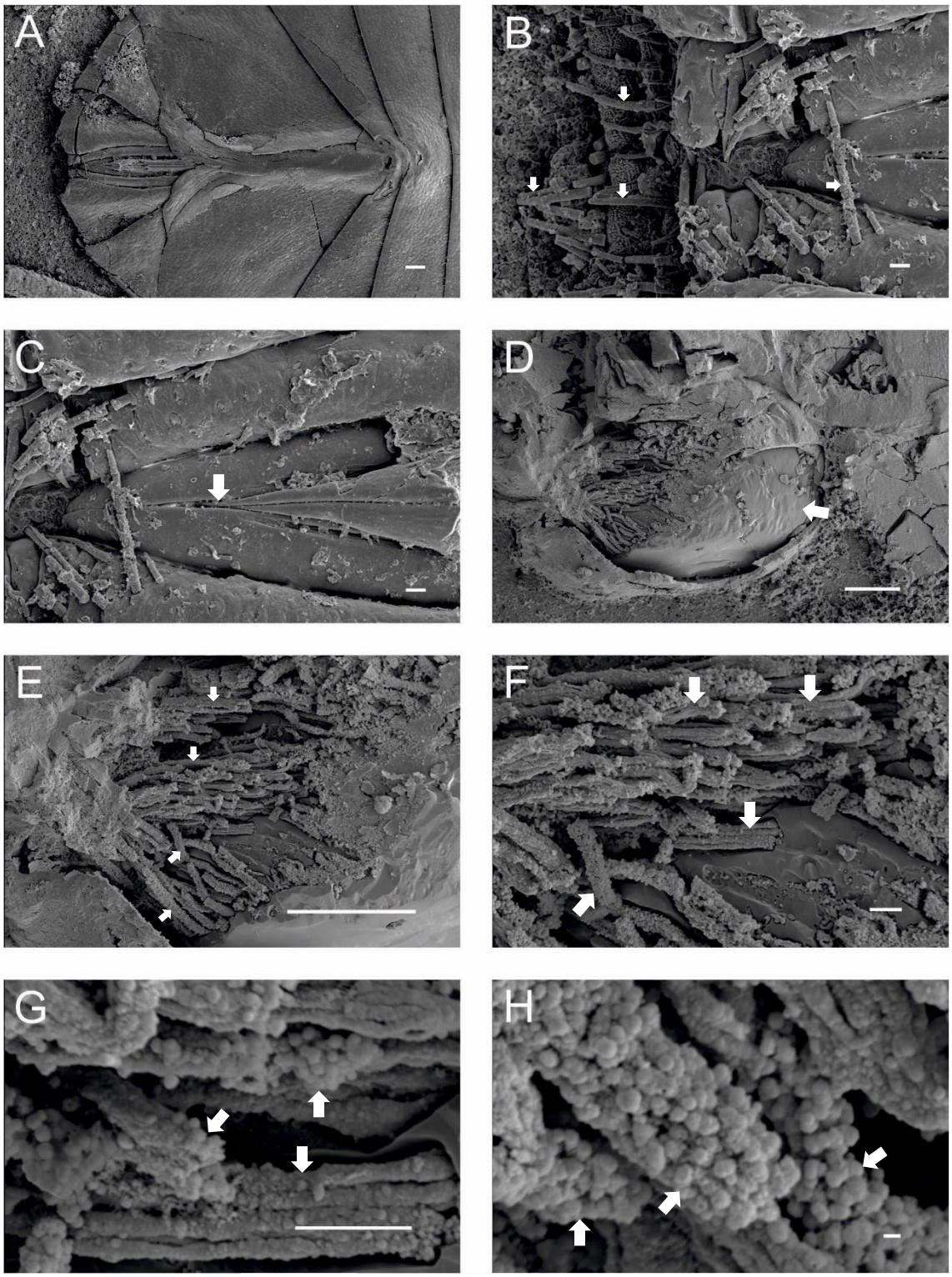


Plate 61: Scanning electron micrographs of genitals from the Nova Olinda Member fossil insects. A-C, Exterior view of Hemiptera genitals. B, Arrows highlight setae posterior of genital opening. C, Genital opening, highlighted by arrow. D, Preservation of Diptera ovary, highlighted by arrow. E-F, Muscle fibres or connective tissue used for oviposition, highlighted by arrows. G-H, Globular fabric of replacement of the muscle fibres/connective tissue, highlighted by arrows. Specimen and image numbers: A, FLO15-18; B, FLO15-17; C, FLO15-08; D, FLO19-16; E, FLO19-14; F, FLO19-13; G, FLO19-15; H, FLO19-18. A and D-E, Scale bars = 100 µm. B-C and F-G, Scale bars = 10 µm. H, Scale bar = 1 µm.

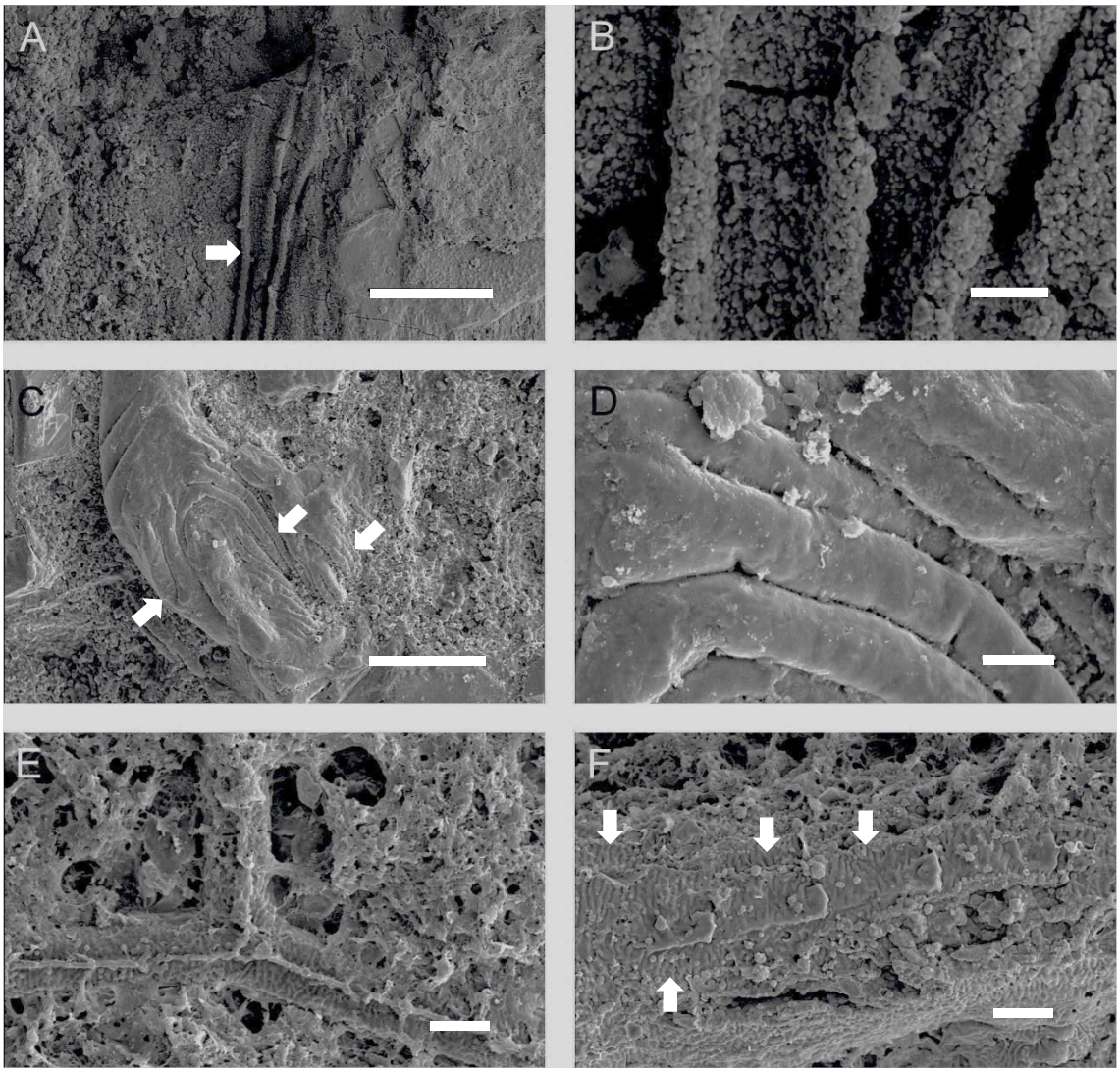


Plate 62: Cryptic cuticular structures, resulting from folding(?), in Nova Olinda Member fossil insects. A-B, Three anteroposterior folds in cuticle running roughly parallel, highlighted by arrow. C-D, Curved and folded cuticle near anal region, highlighted by arrows. E-F, Interlinked tubes of cuticle cropping out amongst resin, possibly representing wing venation. The tubes are covered in a micron-scale folded or 'wavy' surface morphology, highlighted by arrows. Specimen and image numbers: A, JW291-087; B, JW291-088; C, NBRL057-12; D, NBRL057-67; E, UnNum.FLO-6; F, UnNum.FLO-30. A and C, Scale bars = 100 µm. B and D-F, Scale bars = 10 µm.

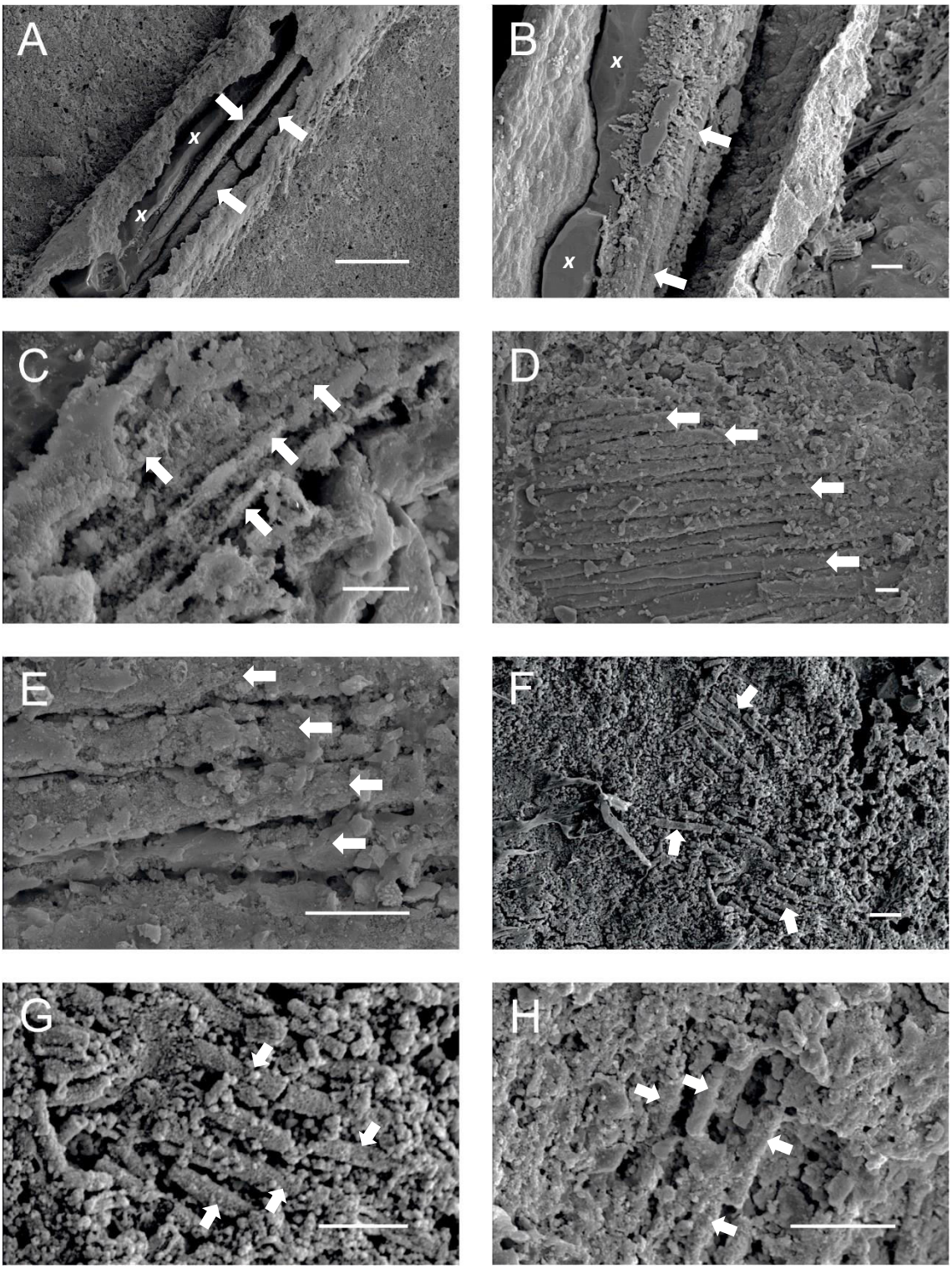


Plate 63: Exceptionally preserved muscle fibres in Nova Olinda Member fossil insects, preserved in calcium phosphate. A-C, Dipteran leg with cracked cuticle, exposing large muscles, highlighted by arrows. Calcite infills are also present (*x*). D-E, Tightly packed bands of muscle fibres, highlighted by arrows, forming a sheet of tissue above anus. F-H, Examples of the typical preservation of muscle fibres in Nova Olinda Member insects, as 'scrappy traces' of loosely aggregated fibres, highlighted by arrows, cropping out amongst globular and spherical replacement fabrics. Specimen and image numbers: A, FLO19-44; B, FLO19-42; C, FLO13-66; D, FLO43-61; E, FLO43-64; F, JW291-083; G, JW291-084; H, NBRL070-44. A, Scale bar = 100 µm. B-H, Scale bars = 10 µm.

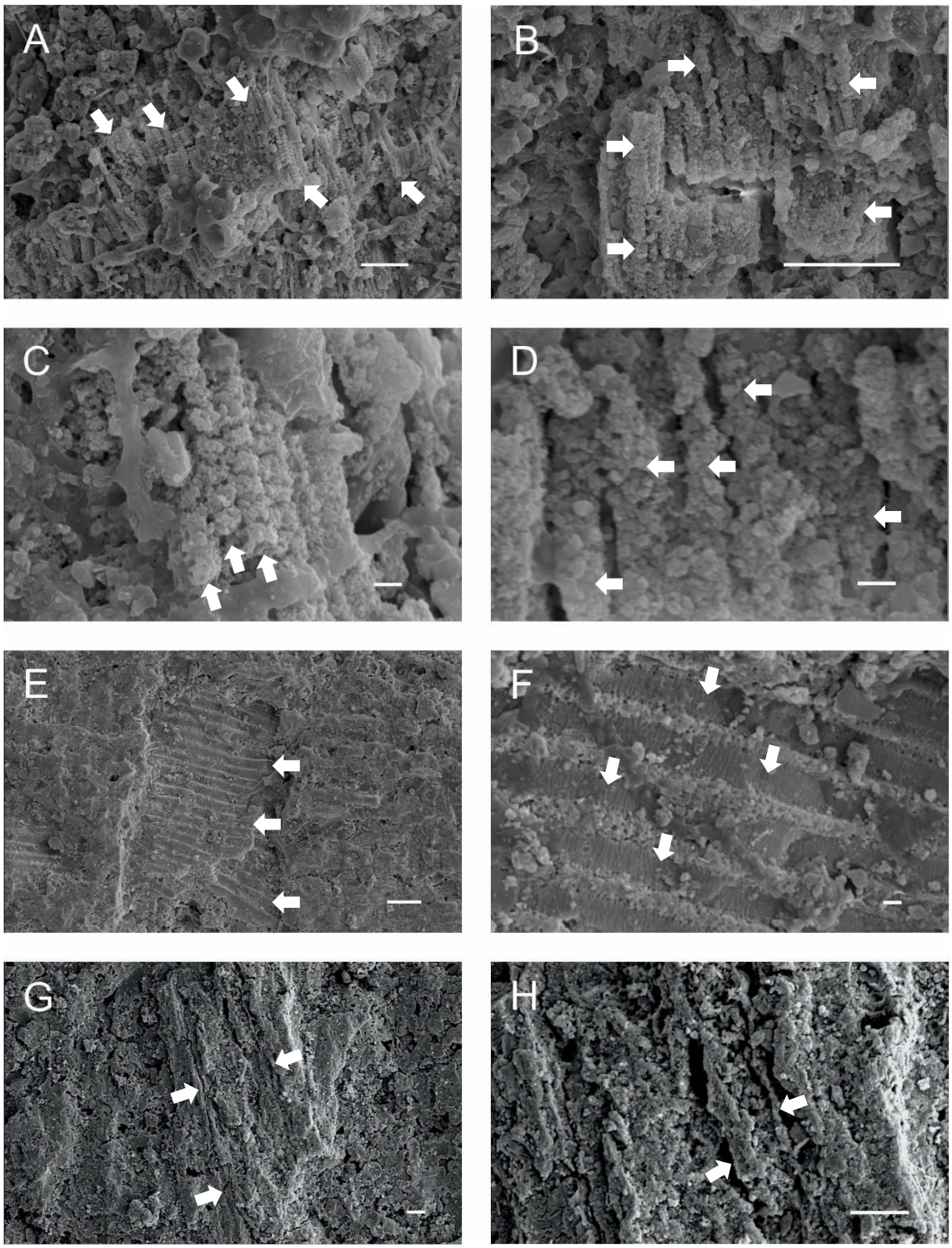


Plate 64: Fragmentary traces of high-relief fibres in Nova Olinda Member fossil insects, preserved in calcium phosphate. A-D, Fibrous chains of interlocked granular structures highlighted by arrows, likely representing thoracic muscle fibres. E-F, Fibres in cross-section, highlighted by arrows, with perpendicular striations to their filament direction, which may represent muscle fibres. G-H, Wing venation in cross-section, showing striations of soft tissue within, highlighted by arrows, possibly representing tracheal tubes. Specimen and image numbers: A, FLO43-10; B, FLO43-16; C, FLO43-14; D, FLO43-18; E, NBRL070-30; F, NBRL070-32; G, JW02#-017; H, JW02#-018. A-B, E and G-H, Scale bars = 10 µm. C-D and F, Scale bars = 1 µm.

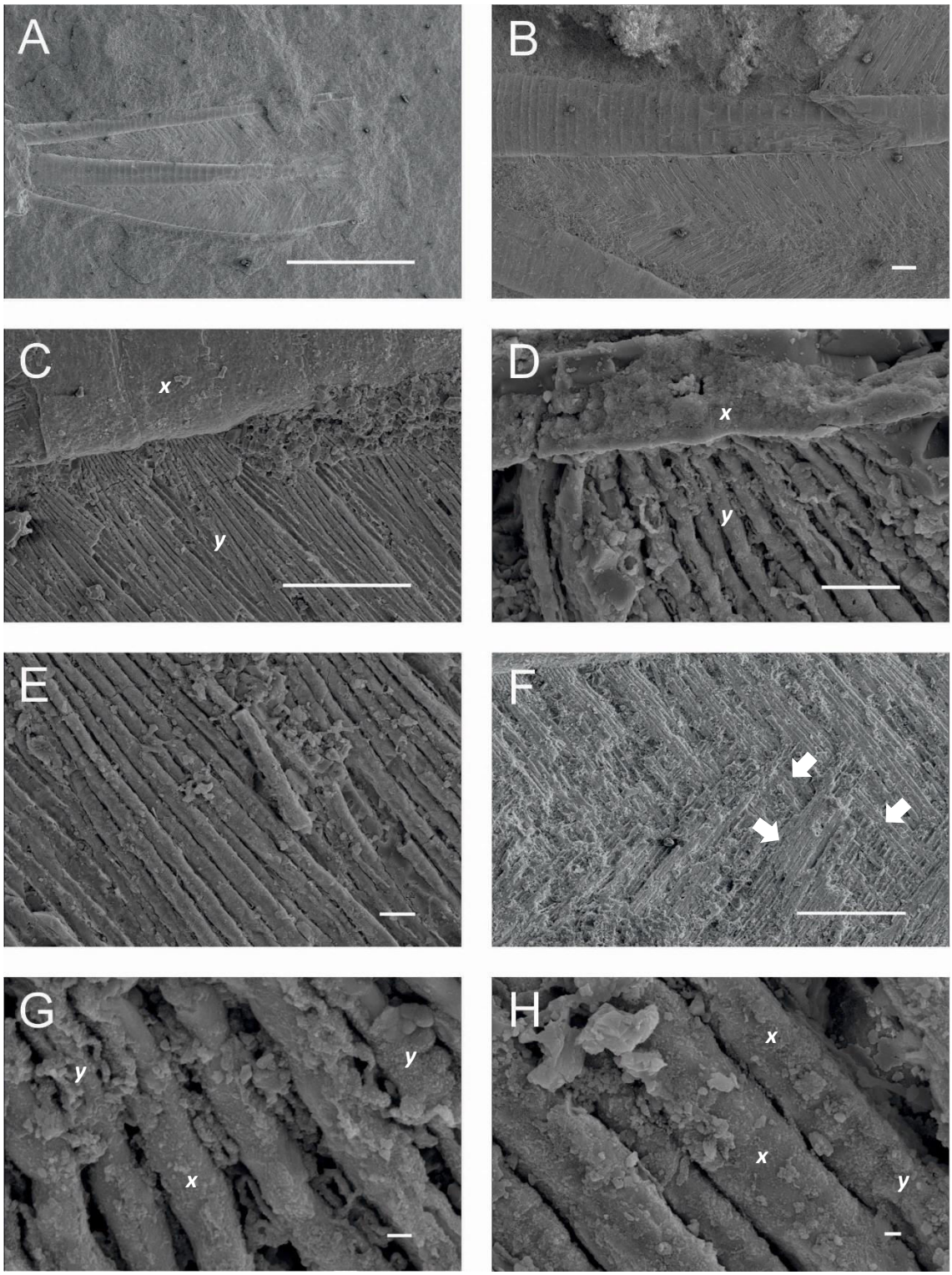


Plate 65: Exceptionally preserved external gills of a fossil Ephemeroptera larva from the Nova Olinda Member. A-B, Overviews of three posterior caudal filaments, to which the gill structures are attached. C-D, Higher magnification images showing the connection between caudal filament (*x*) and external gill fibres (*y*). F, Example of gill fibres, originating from different caudal filaments interlocking, highlighted by arrows. E and G-H, Higher magnification images of gill filaments, revealing their smooth(*x*)-to-globular(*y*) replacement fabric. Specimen and image numbers: A, NBRL060-04; B, FLO37-02; C, FLO37-39; D, FLO37-12; E, FLO37-23; F, NBRL060-10; G, FLO37-15; H, FLO37-24. A, Scale bar = 1 mm. B-C and F, Scale bars = 100 µm. D-E, Scale bars = 10 µm. G-H, Scale bars = 1 µm.

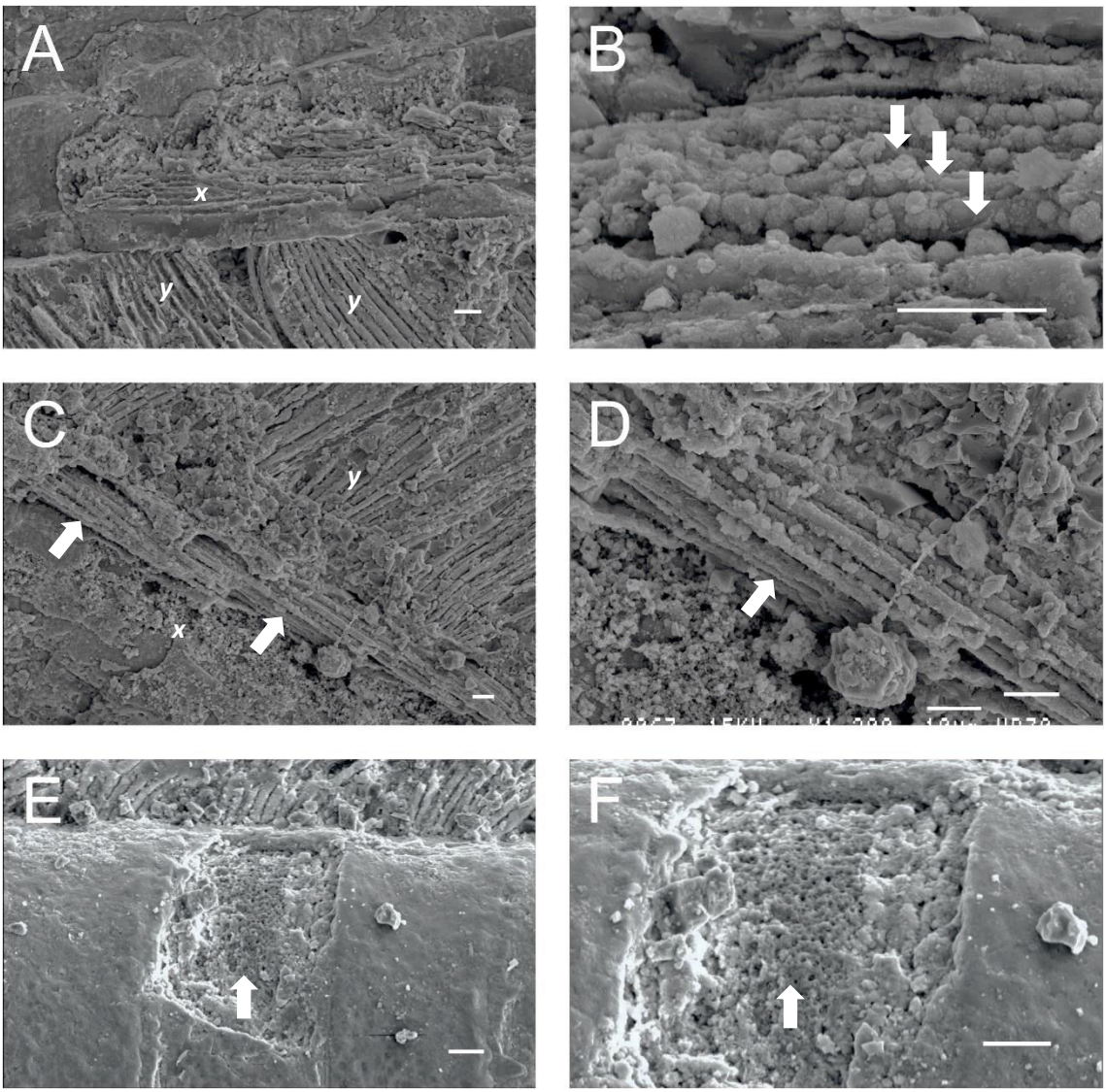


Plate 66: Abraded caudal filaments (and associated gills) in Nova Olinda Member fossil Ephemeroptera larva, revealing their internal structure. A, Internal fabric of caudal filament (*x*) and abraded external gills (*y*). B, Higher magnification image of internal fabric of caudal filament, revealing globular replacement in rows, highlighted by arrows. C-D, Arrows highlight spiral gill filaments within caudal filament (*x*), presumably connecting to exterior gills (*y*). E-F, Cracked caudal filament, revealing spongey internal soft tissues below, highlighted by arrow. Specimen and image numbers: A, FLO37-05; B, FLO37-11; C, FLO37-49; D, FLO37-53; E, NBRL060-07; F, NBRL060-08. Scale bars = 10 µm.

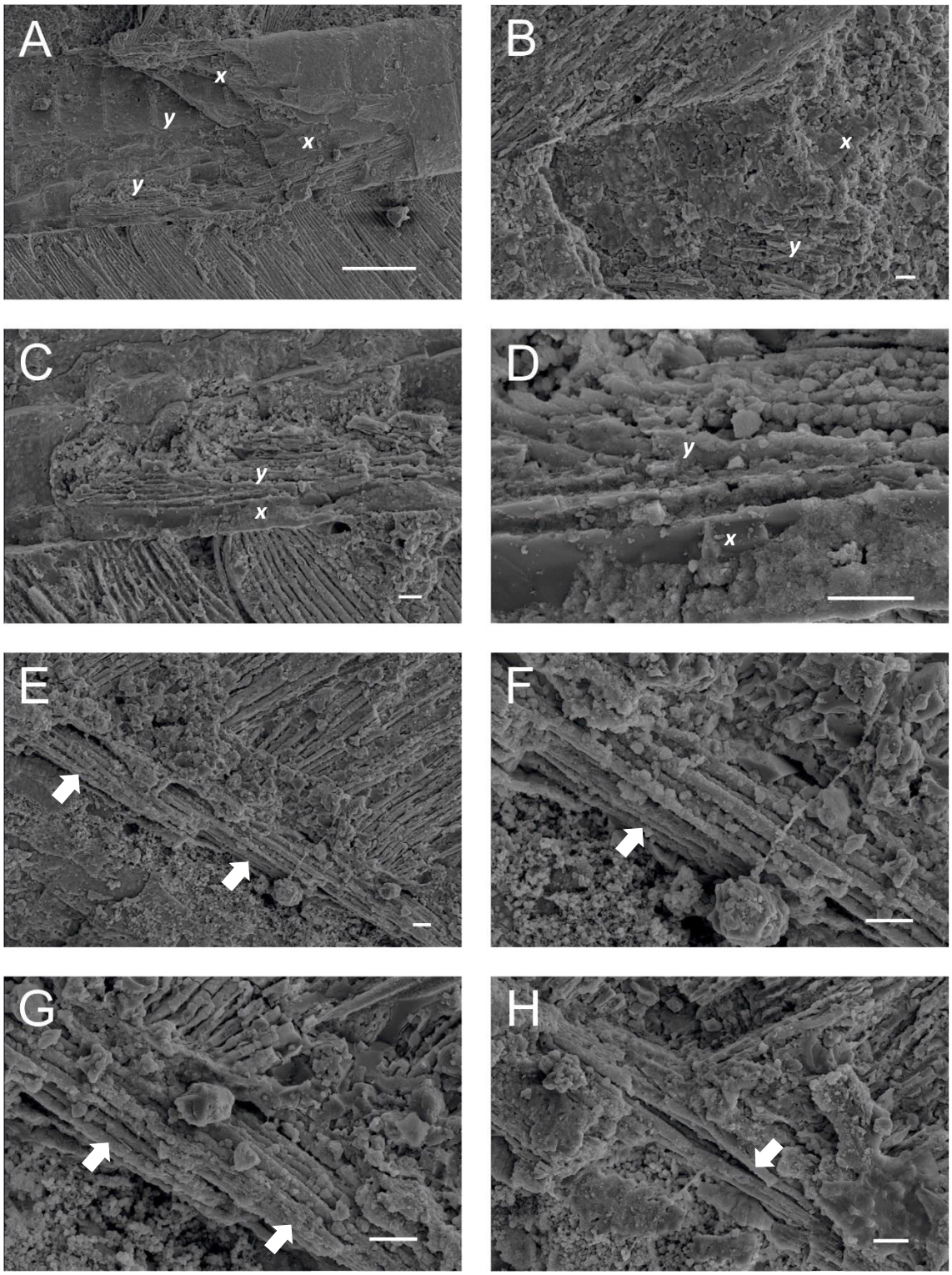


Plate 67: Abraded caudal filaments of a fossil Ephemeroptera larva from the Nova Olinda Member, revealing its exceptionally preserved internal structure. A-B, Abraded caudal filament with broken surface (*x*), revealing soft tissue gill structures (*y*). C-D, Broken caudal filament (*x*) with moulds of internal gill filaments (*y*). E-H, Broken caudal filament, revealing internal spiral stranded wire-like gill structure, running along internal margin of caudal filament, highlighted by arrows. Specimen and image numbers: A, FLO37-03; B, FLO37-47; C, FLO37-05; D, FLO37-07; E, FLO37-49; F, FLO37-53; G, FLO37-55; H, FLO37-57. A, Scale bar = 100 µm. B-H, Scale bars = 10 µm.

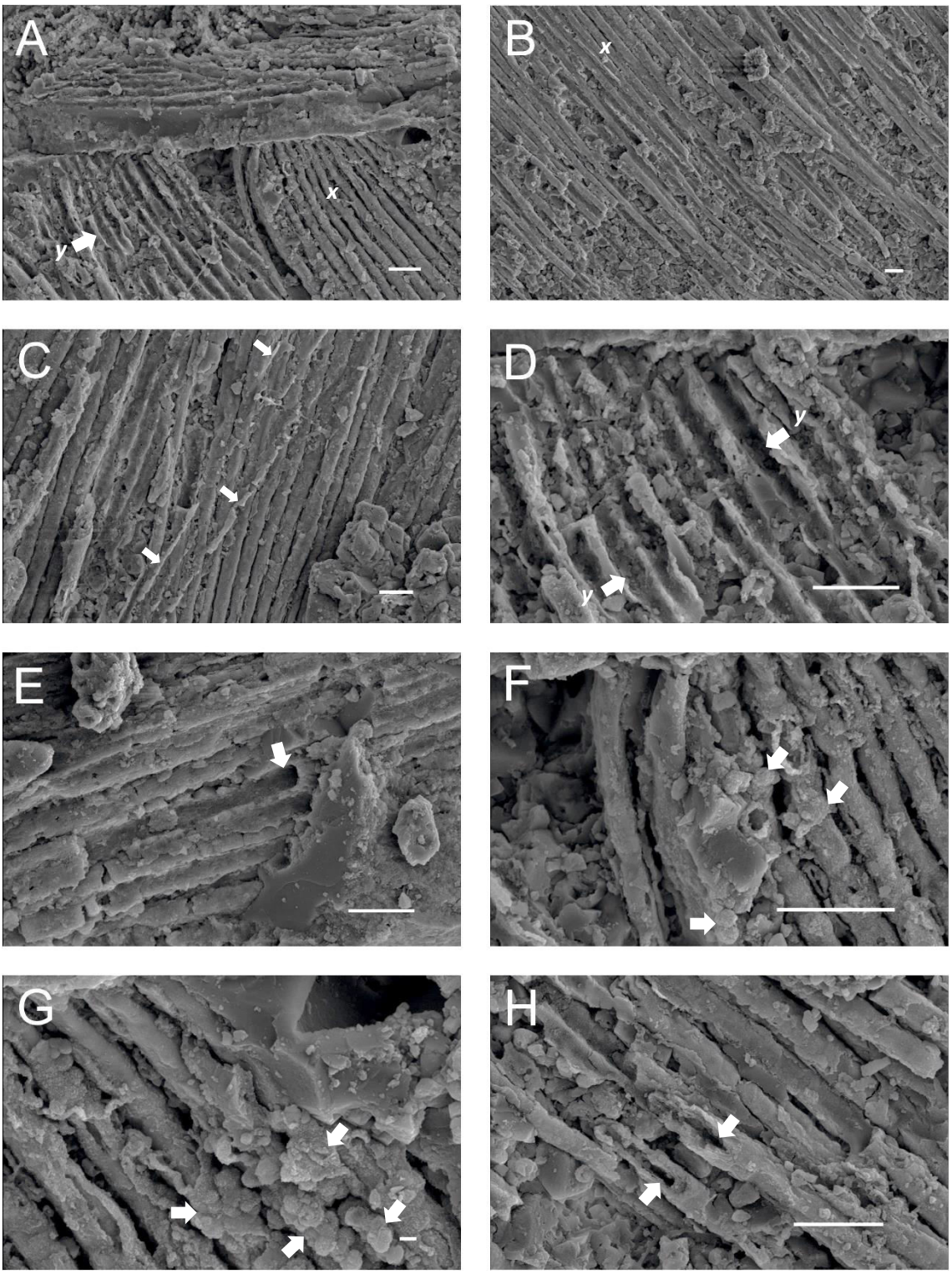


Plate 68: Abraded gill fibres of a fossil Ephemeroptera larvae from the Nova Olinda Member, revealing their exceptionally preserved internal structure. A-B and D, Exceptionally preserved gill fibres (*x*) with some areas abraded, leaving moulds of fibres (*y*). C, External moulds of gill fibres, highlighted by arrows. E and H, Broken gill fibres, revealing their hollow interiors, highlighted by arrows, overlying well-preserved gill fibres. F-G, Examples of globular material covering portions of gill fibres, highlighted by arrows. Specimen and image numbers: A, FLO37-21; B, FLO37-26; C, FLO37-43; D, FLO37-22; E, FLO37-33; F, FLO37-19; H, FLO37-17; G, FLO37-29. A-F and G, Scale bars = 10 µm. H, Scale bar = 1 µm.

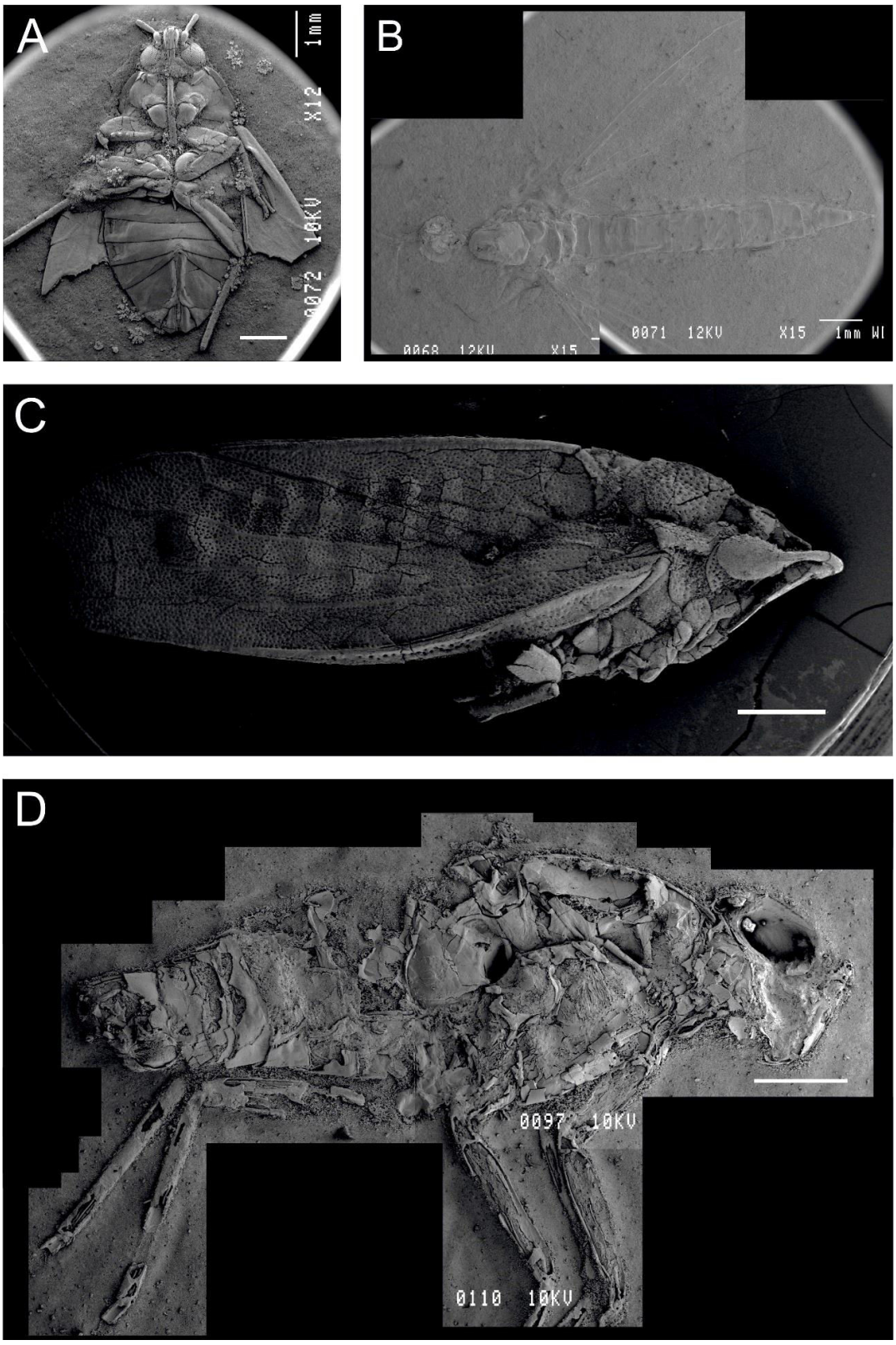


Plate 69: Composite overviews of whole Nova Olinda Member fossil insect specimens, prepared with various techniques. A, Overview of a heavily acid (10% acetic) digested Hemiptera specimen revealing a well-preserved and intact specimen. B, Unprepared Diptera: Nematocera revealing the typical preservation of Crato insects when viewed unprepared under SEM. C, Fulgoromorpha specimen prepared with complete sediment acid (10% acetic) digestion. D, Diptera: Brachycera specimen prepared with resin transfer technique, revealing exquisitely preserved fossil and internal organs as well as cuticular details. Specimen and image numbers: A, FLO15-19; B, Composite image FLOXX-01, 04, 06; C, Composite image FLO17-33, 36, 38, 39; D, Composite image FLO19-02-08, 17. Scale bars = 1 mm.

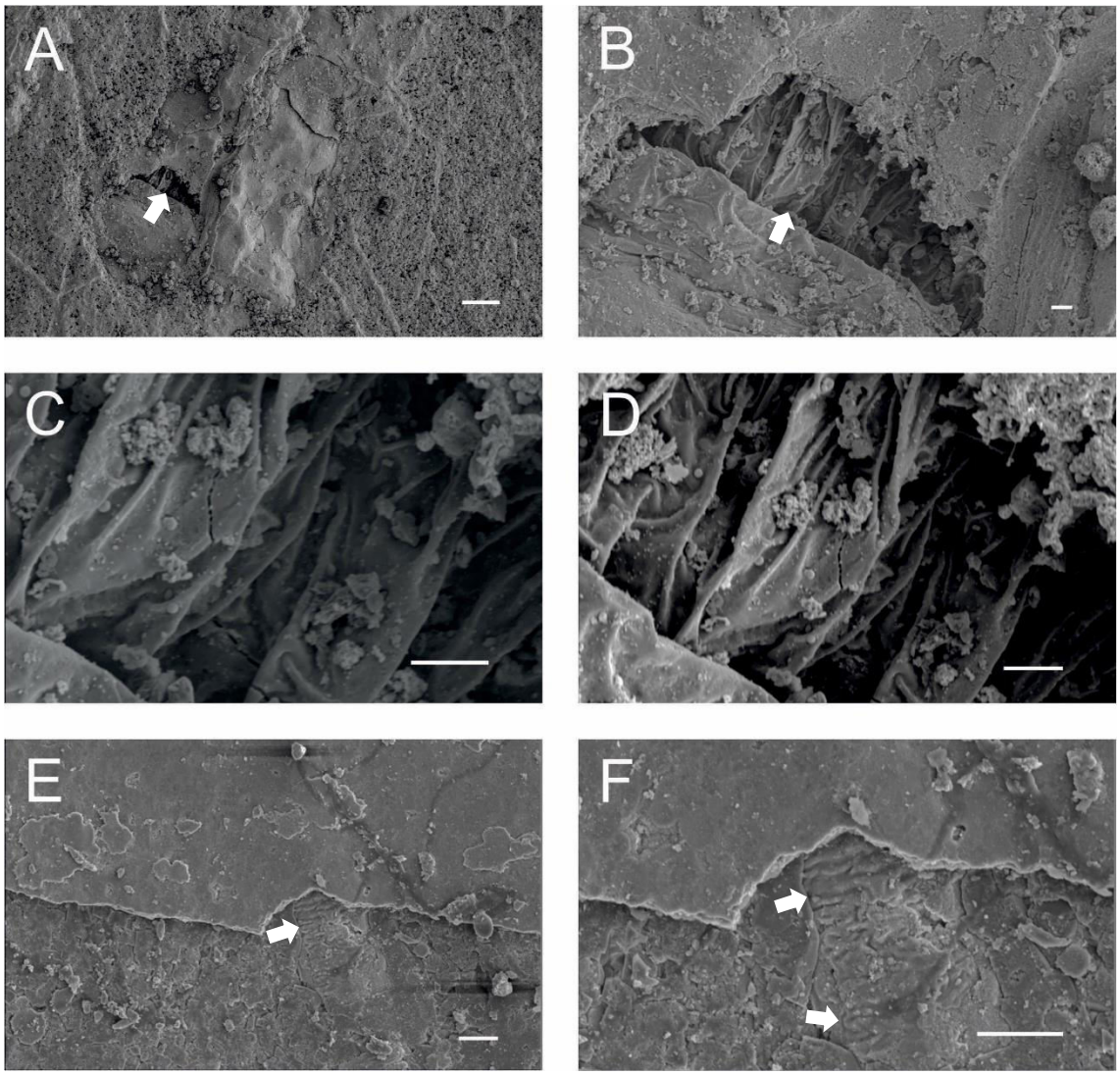


Plate 70: Examples of ‘wavy’ internal soft tissues within Nova Olinda Member fossil insects that likely represents insect fat body. A-B, Broken abdomen revealing an internal void space above ‘wavy’ internal soft tissues, highlighted by arrow. C-D, Higher magnification images of the ‘wavy’ internal tissue. E-F, Cracked cuticle revealing a layer of ‘wavy’ internal soft tissue beneath, highlighted by arrows. Specimen and image numbers: A, JW02#-007; B, JW02#-010; C, JW02#-012; D, JW02#-013; E, NBRL062-33; F, NBRL062-34. A, Scale bar = 100 µm. B-F, Scale bars = 10 µm.

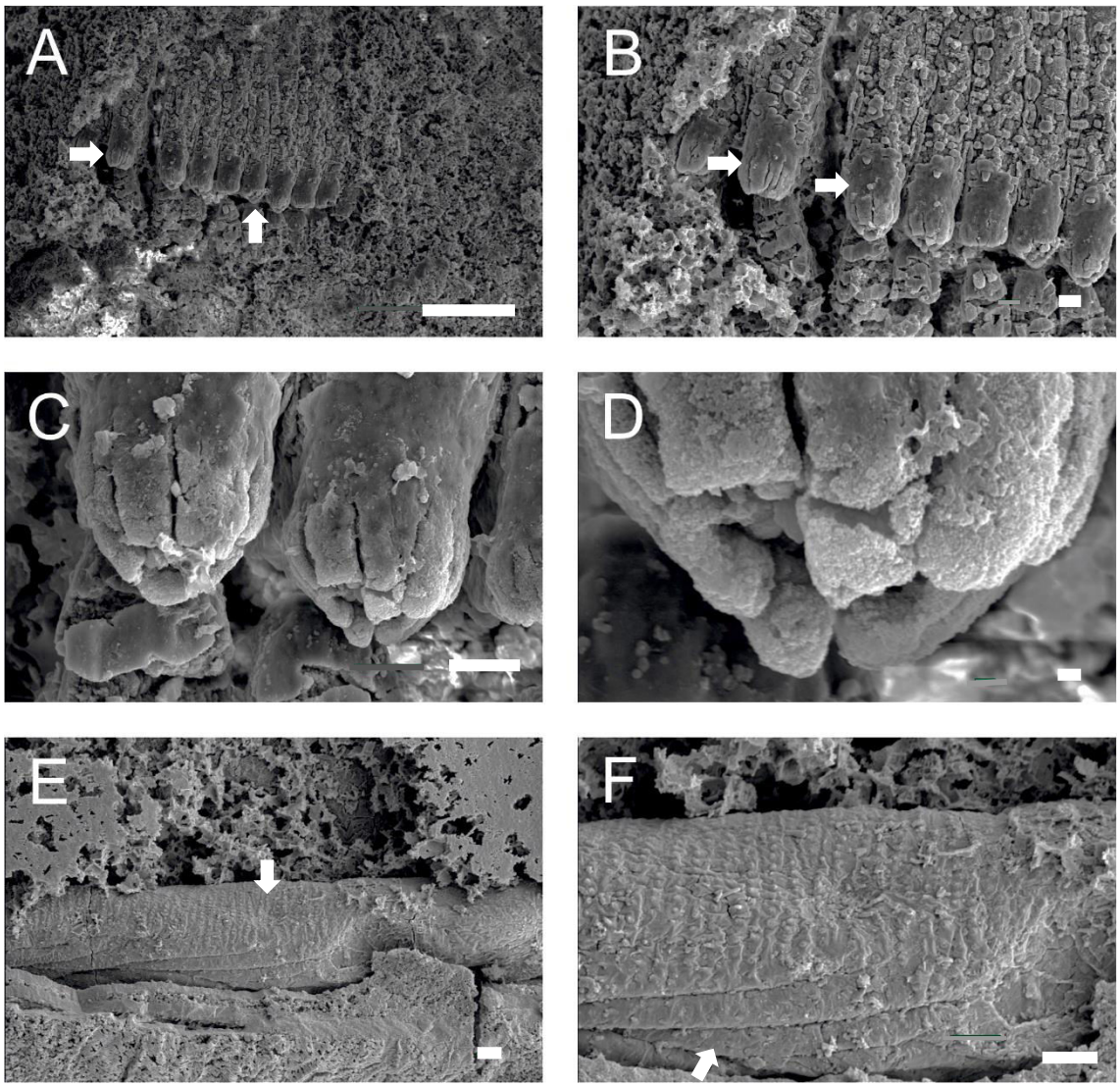


Plate 71: Examples of unidentified tubular internal soft tissues in Nova Olinda Member insect fossils. A-D, Unidentified tubular internal soft tissue structure along limb that may represent a muscle bundle or sensory structure, highlighted by arrows. E-F, Unidentified tubular internal soft tissue structure within Diptera thorax, highlighted by arrow. Structure likely represents tracheal tube, but could alternatively be a portion of the gut. F, Arrow highlights 'soft' folded portion of the tube. Specimen and image numbers: A, UnNumFLO-09; B, UnNumFLO-10; C, UnNumFLO-11; D, UnNumFLO-12; E, FLO19-20; F, FLO19-24. A, Scale bar = 100 µm. B-C and E-F, Scale bars = 10 µm. D, Scale bar = 1 µm.

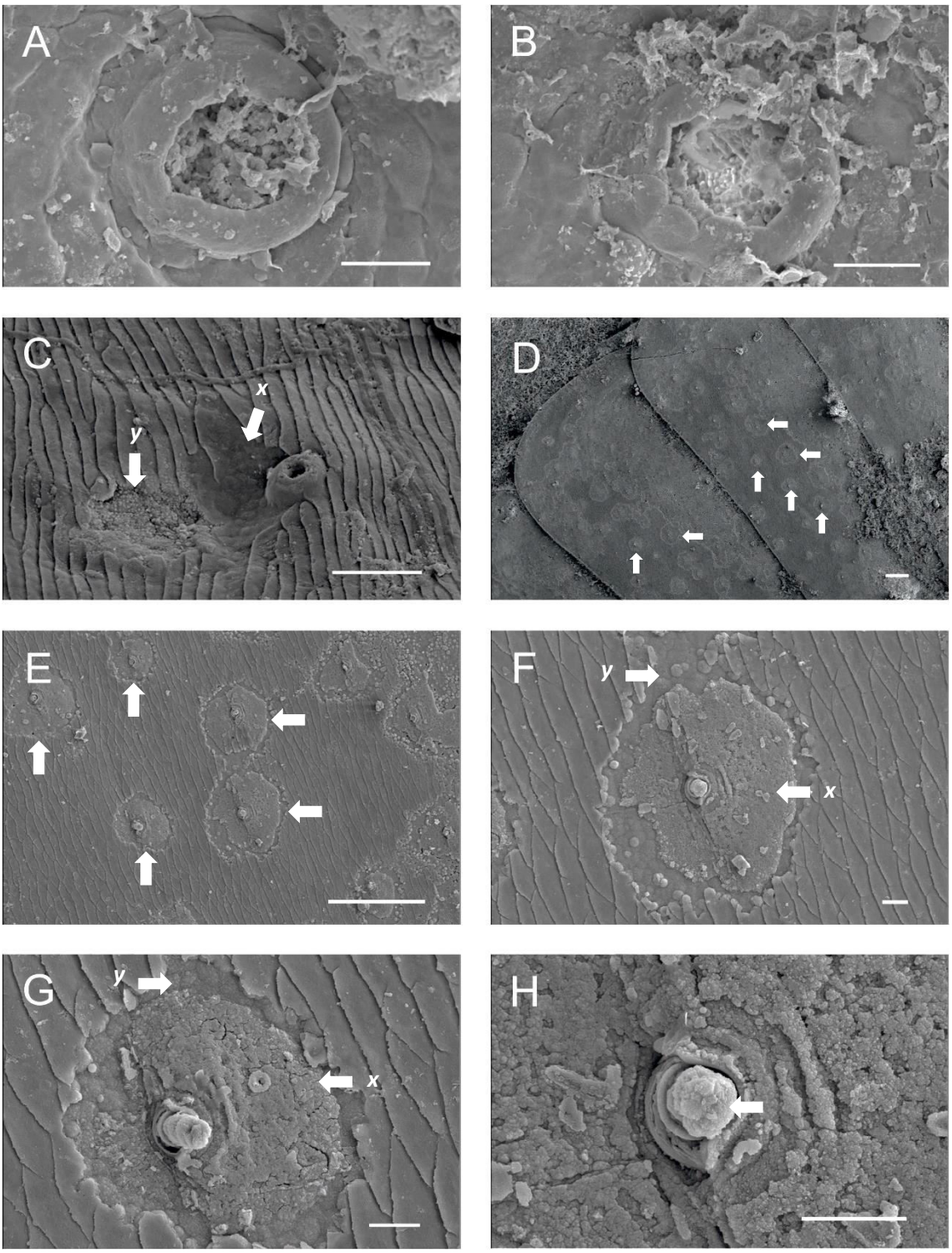


Plate 72: Fabrics that may represent areas of decay associated with setae in Nova Olinda Member insects (1). A-B, Dislodged setae, leaving 'empty' setal bases. These are either filled with a mess of decayed material (A), or are mostly hollow (B). Alternatively, they represent spiracles. C, Two patches of decay associated with a setal base: loss of scale texture and the formation of a globular-to-smooth surface (*x*); and a sharply contacted circular area of degradation with a granular texture (*y*). D-E, Overviews of orthopteran abdomen with circular patches of decay forming around setae, highlighted by arrows. F-G, Individual very poorly preserved setae with associated patches of decay. Texture of decay transitions from coarsely globular (*x*) to smoothly globular (*y*). H, Higher magnification image of poorly-preserved setae, highlighted by arrow. Specimen and image numbers: A, NBRL014-62; B, NBRL014-65; C, NBRL036-37; D, NBRL054-11; E, NBRL054-83; F, NBRL054-85; G, NBRL054-100; H, NBRL054-95. A-C and F-H, Scale bars = 10 µm. D-E, Scale bars = 100 µm.

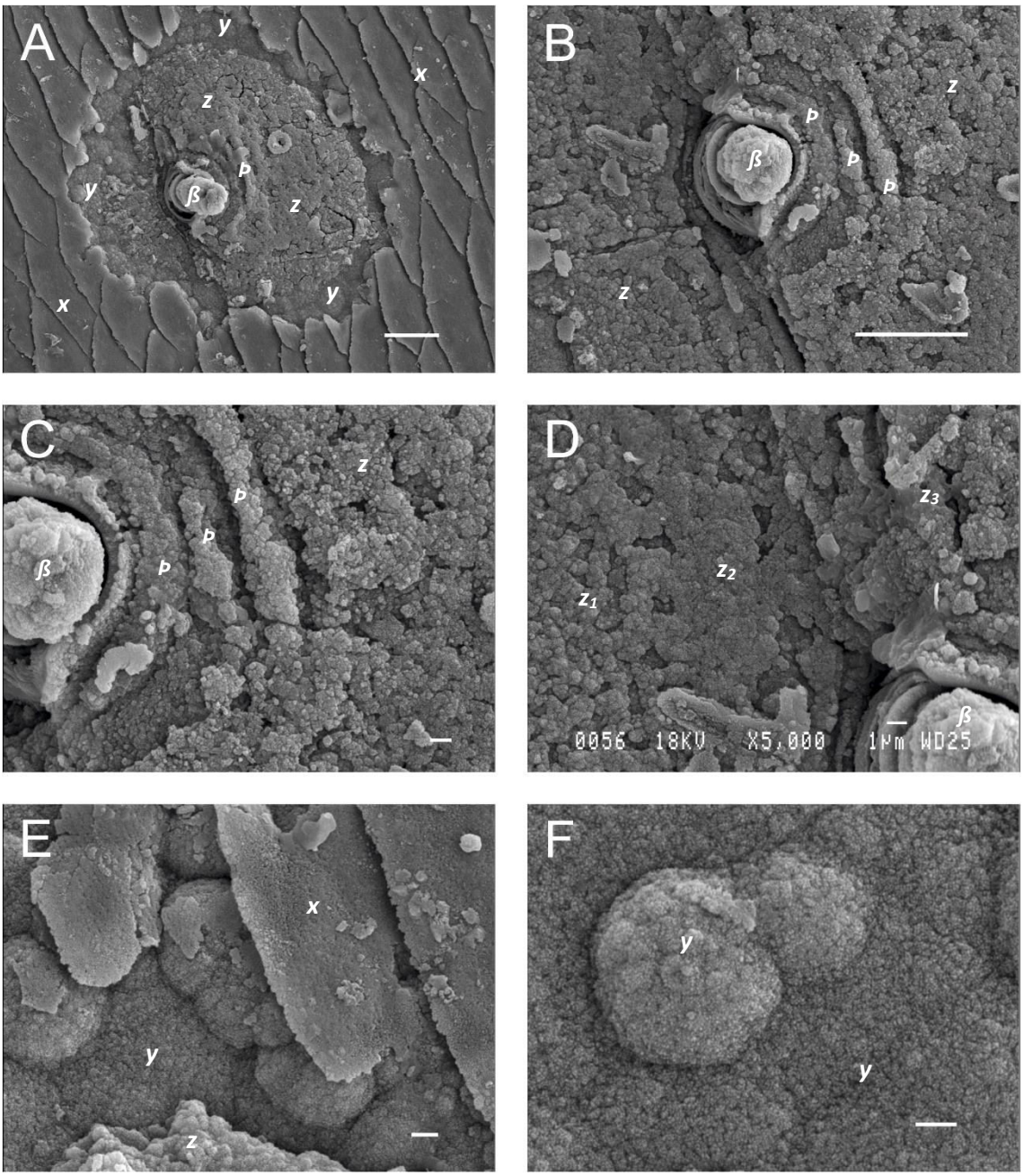


Plate 73: Granular and globular fabrics and a loss of fidelity of preservation associated with setae in Nova Olinda Member fossil insects. A-F, Exceptionally preserved cuticle with scales (*x*) rapidly transitioning into a globular fabric consisting of microgranules of goethite (*y*), then a more granular fabric (*z*), including ringed ridges as a result of original cuticular structure (*p*), around setae (*ß*). E and F particularly highlight the globular fabric consisting of microgranules of goethite. D also shows three variations in the 'more granular' fabric (z_1-z_3). Specimen and image numbers: A, NBRL054-101; B, NBRL054-96; C, NBRL054-98; D, NBRL054-99; E, NBRL054-94; F, NBRL054-92. A-B, Scale bars = 10 µm. C-F, Scale bars = 1 µm.

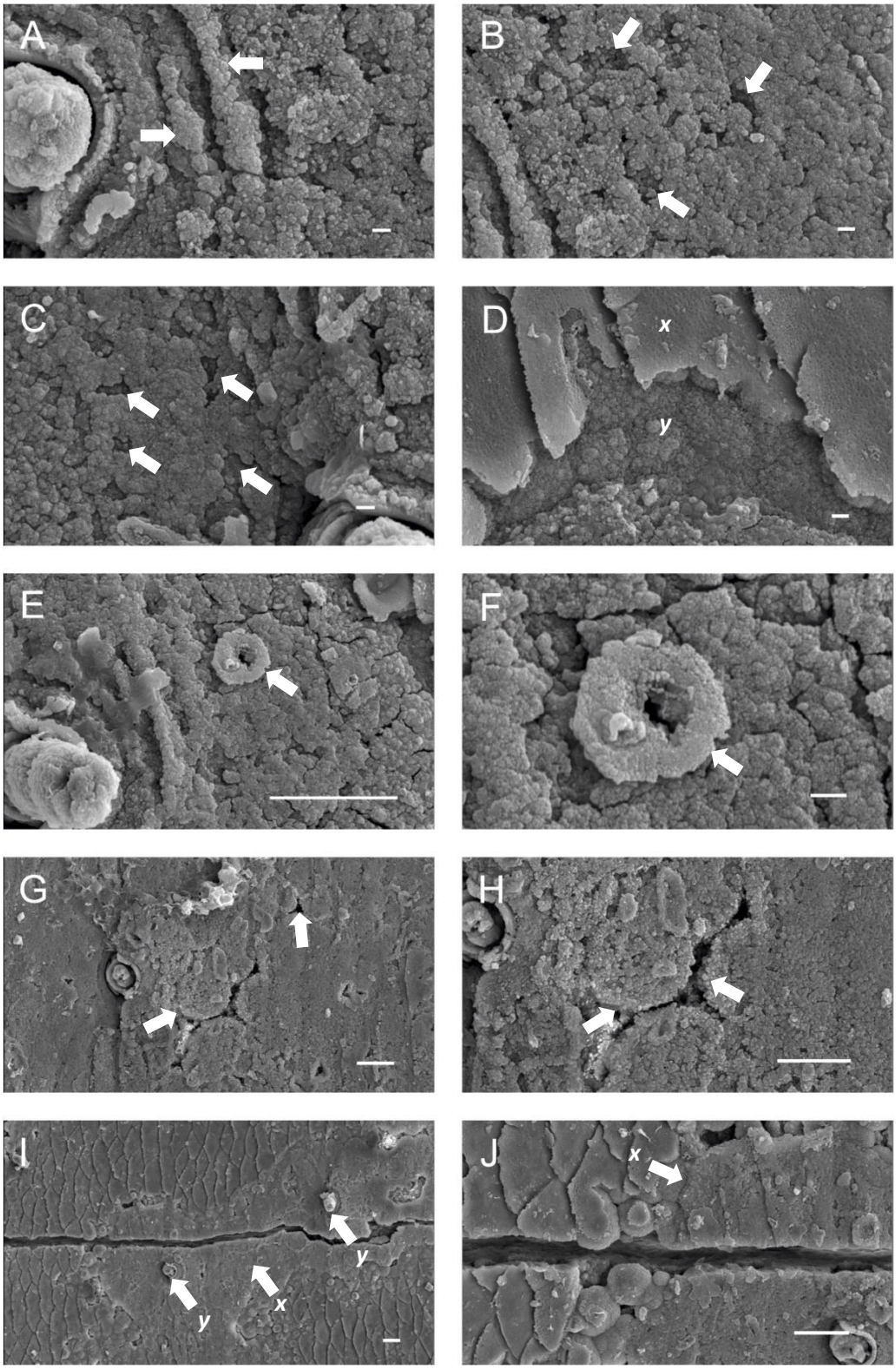


Plate 74: Fabrics that may represent areas of decay, associated with setae in Nova Olinda Member insects (2). A, Rings of this fabric centred around the setae, highlighted by arrows, that likely represent cuticular structure. B-C, Patchy granular fabric, with gaps revealing another layer of granular fabric beneath, highlighted by arrows. D, Sharp contact between well-preserved cuticle with scales (*x*) and areas of 'smoother' globular decay (*y*). This outermost decay region is unbroken, has larger 'globular' structures, but is still constituted from inter-grown sub-spherical aggregates. E-F, Raised ring of granular cuticle near setae highlighted by arrow, likely represents decay of spiracles. G-H, Arrows highlight mineral fabric exposed as areas constituted of inter-grown circles of granular aggregate (probably the flat surface of hemispherical pseudoframboid pseudomorphs), likely the result of loss of exocuticle by decay. I-J, Smooth-to-globular fabric that may be associated with decay (*x*) around setae (*y*). Crack likely recent. Specimen and image numbers: A, NBRL054-97; B, NBRL054-87; C, NBRL054-99; D, NBRL054-106; E, NBRL054-102; F, NBRL054-104; G, NBRL054-112; H, NBRL054-114; I, NBRL054-108; J, NBRL054-110. A-D and F, Scale bars = 1 µm. E and G-J, Scale bars = 10 µm.

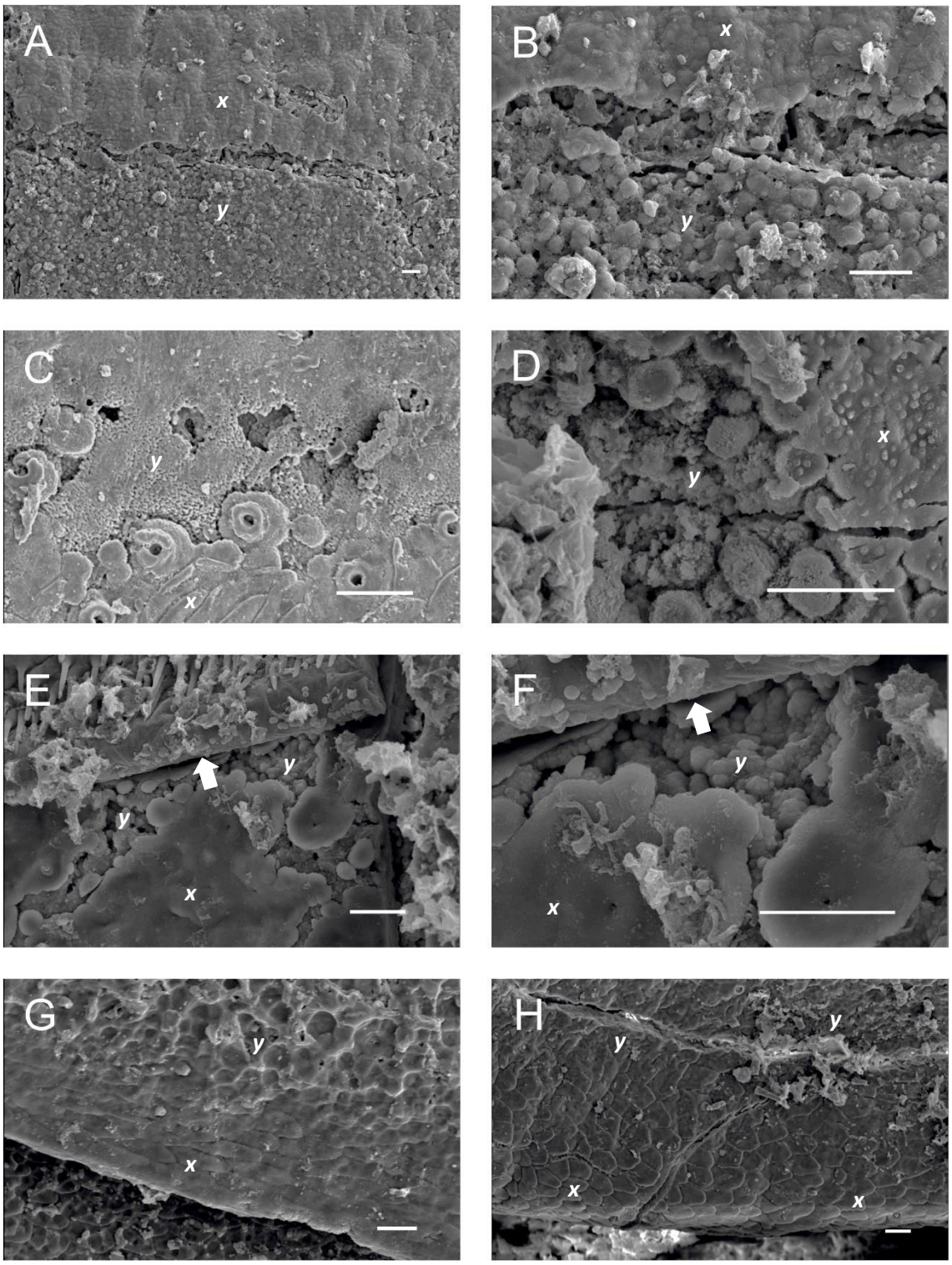


Plate 75: Sharp losses of fidelity of preservation, often near sutures and segment boundaries, in Nova Olinda Member fossil insects. A-B, Sharp contact associated with a crack between poorly-preserved partially-globular cuticle (*x*) and extremely poorly preserved highly-globular cuticle (*y*). C, Sharp contact between well-preserved cuticle with scales and setal bases (*x*) and exposed granular sub-cuticular surface (*y*). D-F, Moderately-preserved cuticle (*x*) transitioning to globular or subspherical fabrics (*y*) adjacent to suture, highlighted by arrow. G-H, Well-preserved cuticle with scales (*x*) revealed beneath overgrowth with polygonal impressions (*y*). Overgrowth is mineralised EPS with polygonal impressions from surrounding rhombohedral sedimentary matrix grains (see Plate 1). Specimen and image numbers: A, FLO38-40; B, FLO38-41; C, NBRL018-53; D, NBRL055-110; E, NBRL045-##86; F, NBRL045-##88; G, NBRL051-37; H, NBRL051-39. Scale bars = 10 µm.

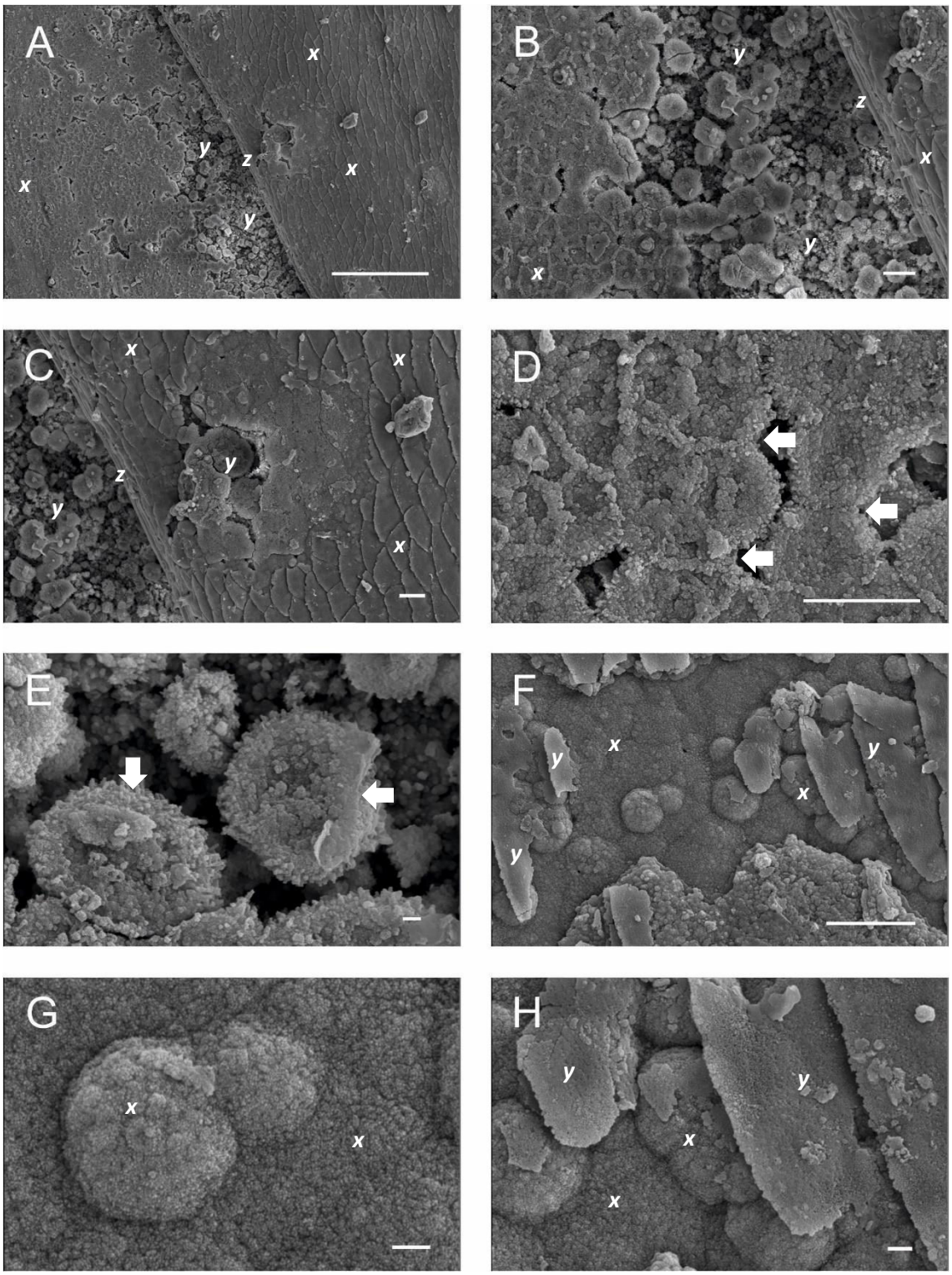


Plate 76: Examples of poorly-preserved cuticle adjacent to exceptionally well-preserved cuticle in Nova Olinda Member fossil insects. A-C, Exceptionally preserved cuticle with cuticular scales (*x*) rapidly transitioning to poorly-preserved cuticle replicated as sparse hemispherical aggregates (*y*) adjacent to a suture (*z*). In these areas, the high-fidelity replacement of the epicuticle is lost, revealing the internal pseudoframboid fabric that coated the internal surface of the epicuticle and replaced the exo- and endocuticle. In some areas, without the impregnated epicuticle, there was no flat surface for pseudoframboids to precipitate on. D-E, Higher magnification images of hemispherical aggregates, revealing their interlocking (D) or isolated (E) nature, highlighted by arrows. F-H, Globular fabric constituted of micro-grains of goethite (*x*) beneath exceptionally well-preserved cuticle with scales (*y*). Specimen and image numbers: A, NBRL054-116; B, NBRL054-118; C, NBRL054-124; D, NBRL054-122; E, NBRL054-120; F, NBRL054-89; G, NBRL054-91; H, NBRL054-93. A, Scale bar = 100 µm. B-D and F, Scale bars = 10 µm. E and G-H, Scale bars = 1 µm.

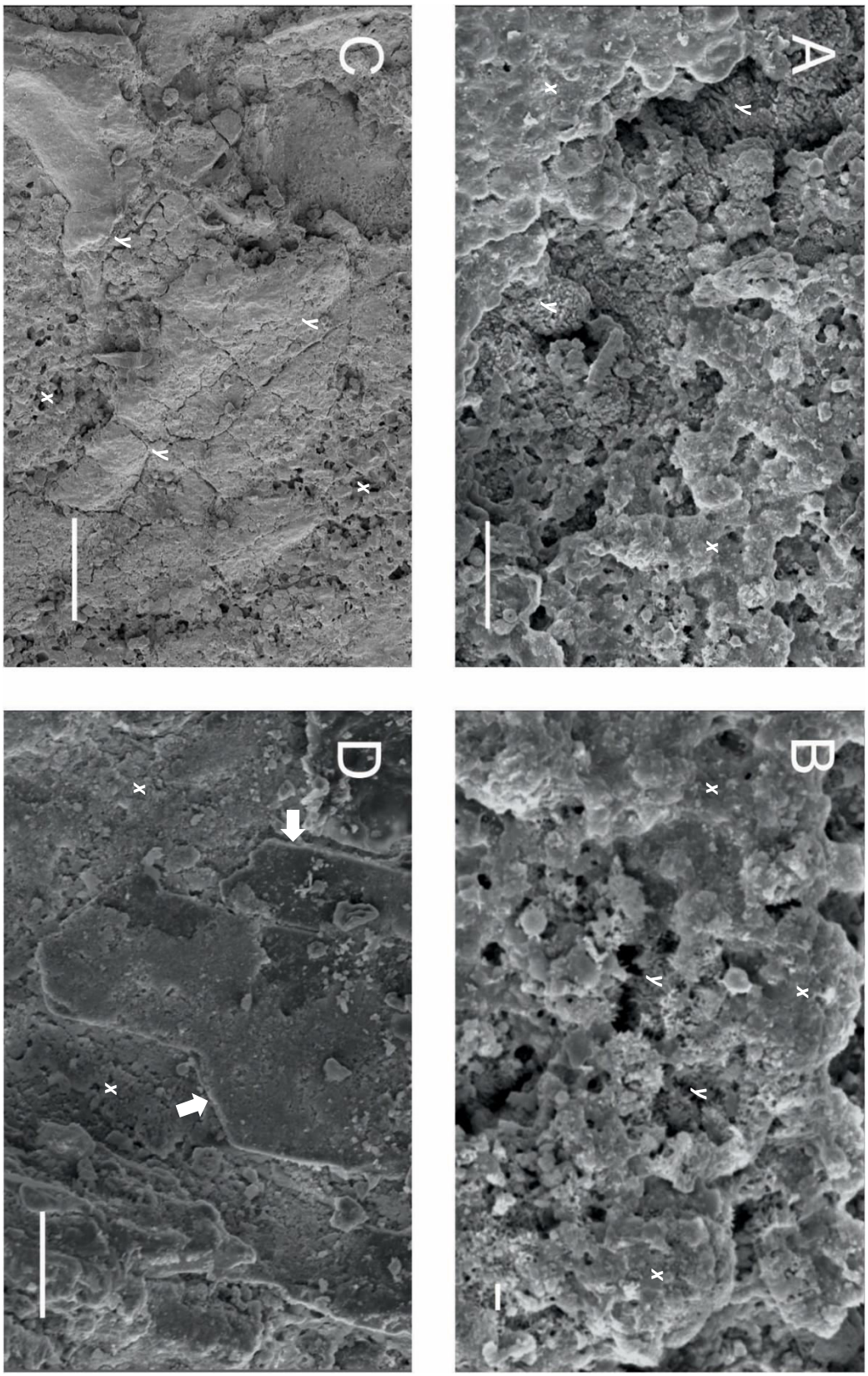


Plate 77: Examples of fabrics possibly representing areas of decay in the Nova Olinda Member fossil insects. A, 'Fused' globular and subspherical fabrics (*x*) overlying coarser globular fabrics (*y*) that are exposed by the loss of the nano-crystalline impregnated epicuticle. B, Cuticle surface with fused globular fabrics (*x*) and nano-sized needle-like crystals (*y*). C, Fragmentary globular cuticle (*x*) around cracked and deformed cuticle (*y*). D, Poorly preserved (almost massive) cuticle (*x*) near broken cuticle with sharp edges, highlighted by arrows. Specimen and image numbers: A, NBRL065(resi)-17; B, NBRL065(resi)-18; C, NBRL078-13; D, NBRL062-30. A and D, Scale bars = 10 µm. B, Scale bar = 1 µm. C, Scale bar = 100 µm.

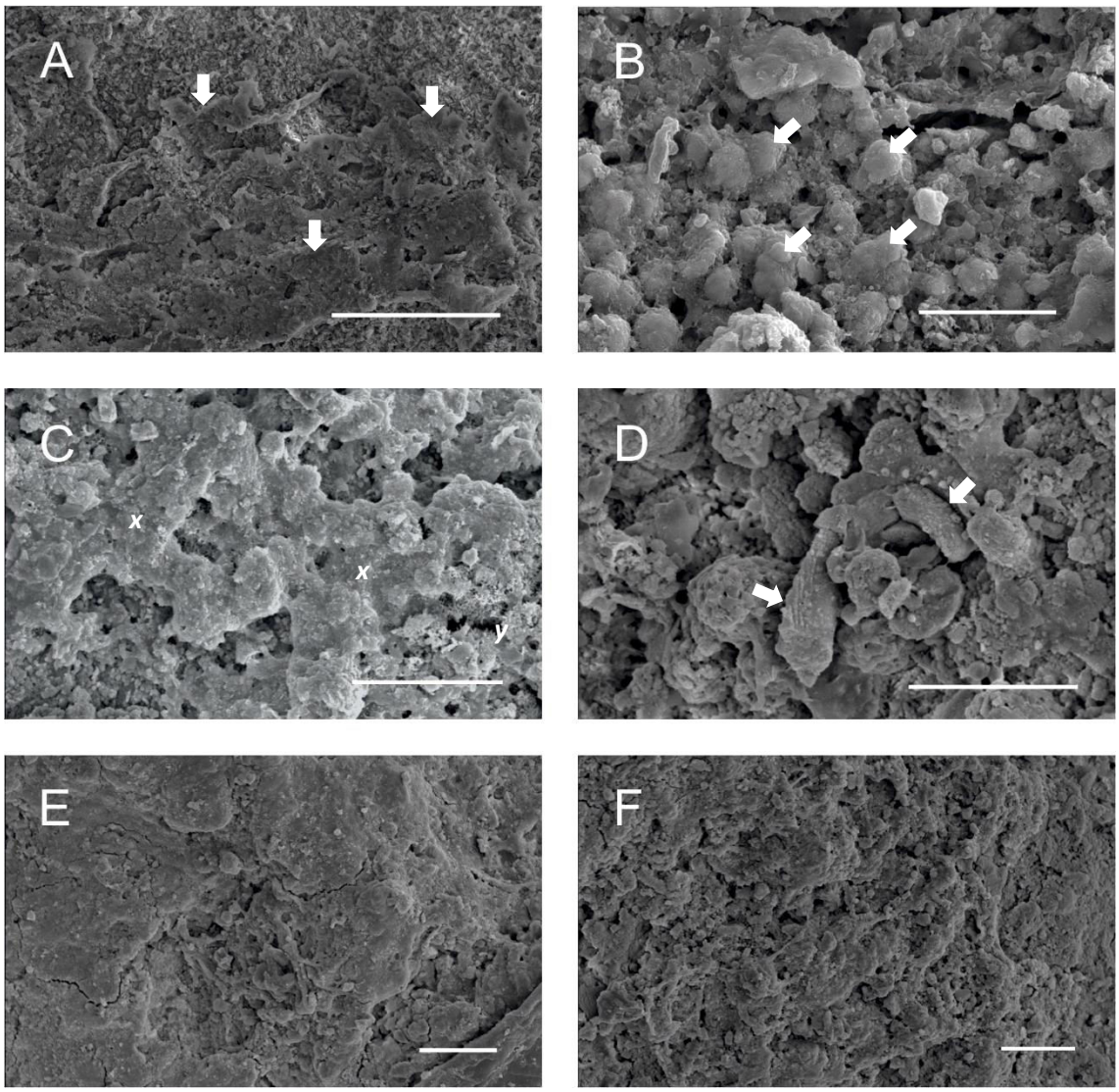


Plate 78: Examples of the poorest preservation of insect cuticle from the Nova Olinda Member, that may represent decay. A, Example of 'ripped' or 'flaky' (delaminating) fabric of extremely poorly-preserved cuticle, highlighted by arrows. B, Example of globular fabric replacing extremely poorly-preserved cuticle, highlighted by arrows. C, Fused/intergrown globular cuticle (*x*) with rare needle-like nanocrystals (*y*). D, Arrow highlights possible cuticular elements (setae?). Despite the poor preservation of the surrounding cuticle, this appears to retain some micro-structure (micron-scale striations). E-F, Cuticle(?) with no discernible original features, preserved as globular-to-smooth(ish) fabrics. Specimen and image numbers: A, FLO13-123; B, FLO38-43; C, NBRL065(resi)-21; D, NBRL066(resi)-05; E, NBRL070-49; F, NBRL070-50. A, Scale bar = 100 µm. B-F, Scale bars = 10 µm.

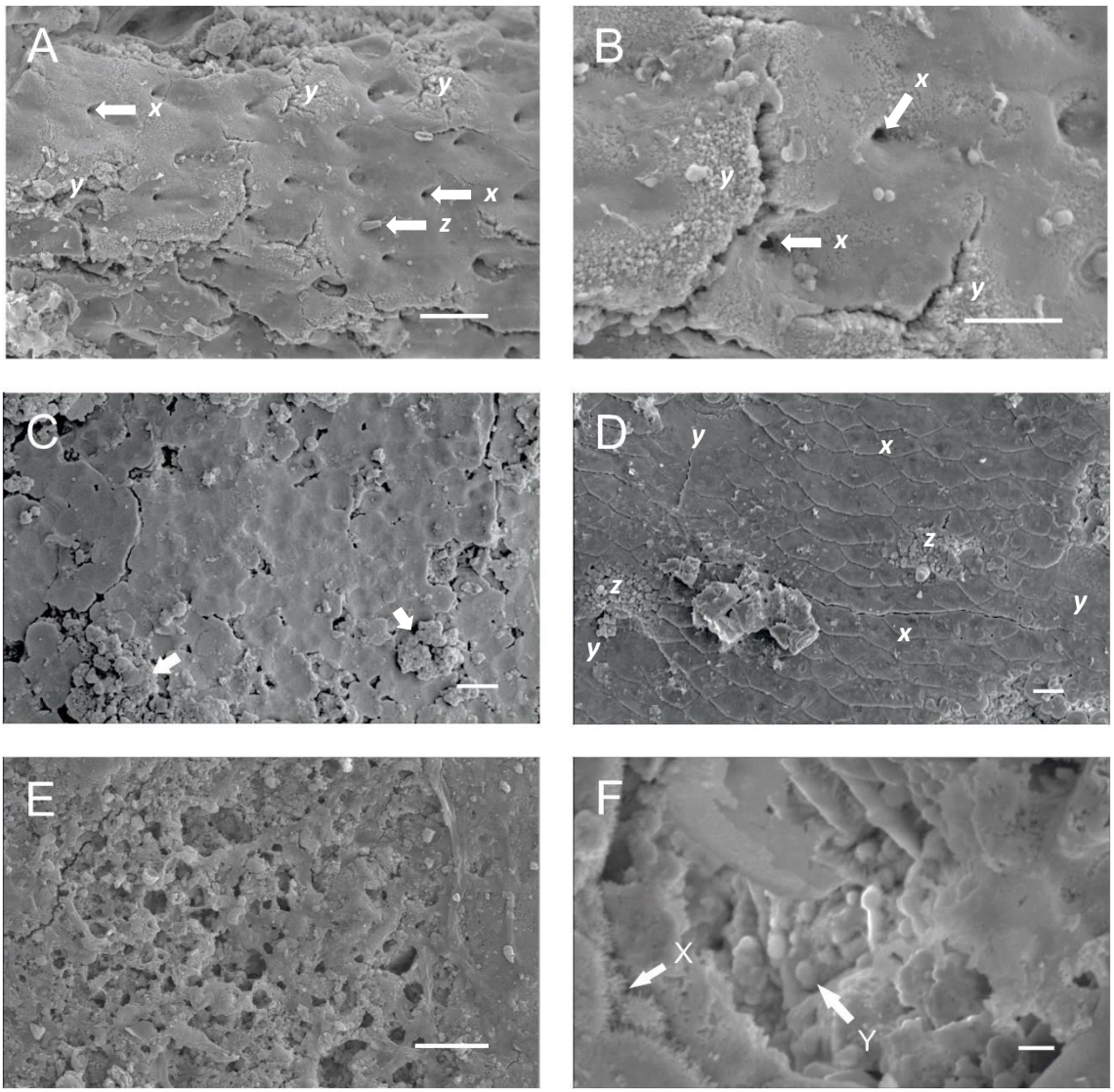


Plate 79: Examples of poorly-preserved cuticle that loses its surface morphology in Nova Olinda Member insects. A-B, 'Smoothed' limb cuticle, with setae lost but setal bases still visible (*x*). Granular fabrics associated with cracking (*y*). *z* highlights setae, demonstrating that this is epicuticle. C, Mostly smooth cuticle with faint circles visible representing sub-surface pseudoframboid-like aggregates. Arrows highlight globular fabric covering a portion of the cuticle. As with A, structures observed elsewhere demonstrate that this smooth surface is epicuticle. D, Well-preserved cuticle with scales (*x*) with areas of poor-preservation that result in a smooth surface (*y*), or granular fabrics (*z*). E, Total loss of cuticular surface morphology, revealing globular fabric with cavities. F, High magnification image of crevice in cuticle (possibly tracheal opening), with needle-like nanocrystals (X) and sub-spherical structures lining the inside of the crevice (Y). Specimen and image numbers: A, NBRL045-47; B, NBRL045-48; C, JW291-090; D, NBRL054-19; E, FLO42-28; F, NBRL014-68. A, Scale bar = 20 µm. B-E, Scale bars = 10 µm. F, Scale bar = 1 µm.

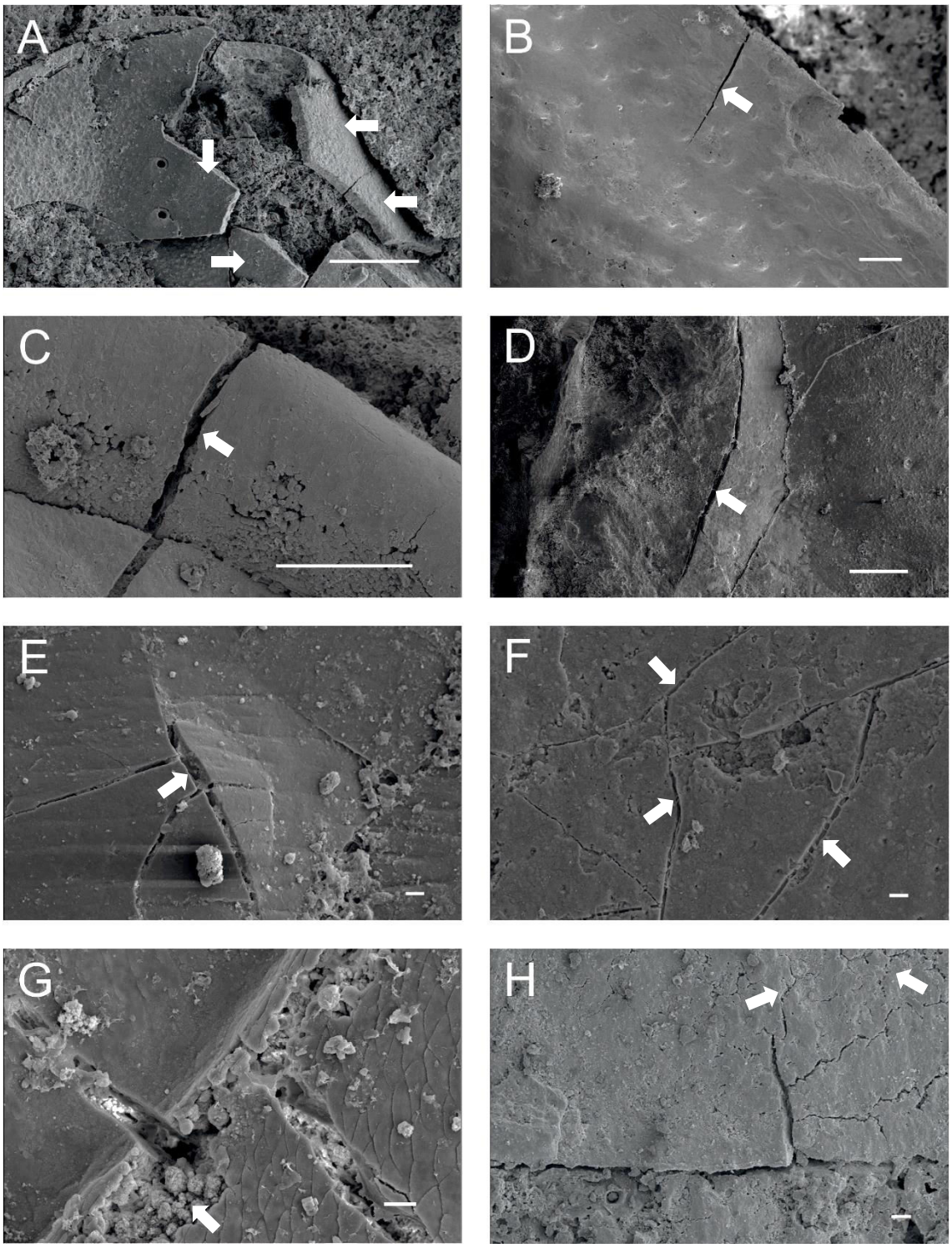


Plate 80: Brittle nature of insect cuticle in the Nova Olinda Member. A, Shattered cuticle breaking away, highlighted by arrows. B, Early stages of brittle damage along beetle elytra, highlighted by arrow. C, Deep crack through entire specimen, highlighted by arrow. D-E, 'Erupted' cracked cuticle caused by mineral growth or damage during extraction/transport/handling, highlighted by arrow. F, Moulds of shallow cracking across cuticle that may cause it to delaminate if left to weather, highlighted by arrows. G, Wide cracks infilled with globular aggregates, highlighted by arrow. In both F and G, cracking must be ancient as F represents moulds of cracks and G contains mineral growth between the cracks. However, this cracking occurred post-mineralisation. H, Cracking around the edges of pseudoframboid-like hemispherical aggregates, highlighted by arrows. Specimen and image numbers: A, JW735-006; B, NBRL018-37; C, NBRL054-53; D, JW735-026; E, FLO38-113; F, FLO36-34; G, BRL054-76; H, NBRL078-19. A-D, Scale bars = 100 µm. E-H, Scale bars = 10 µm.

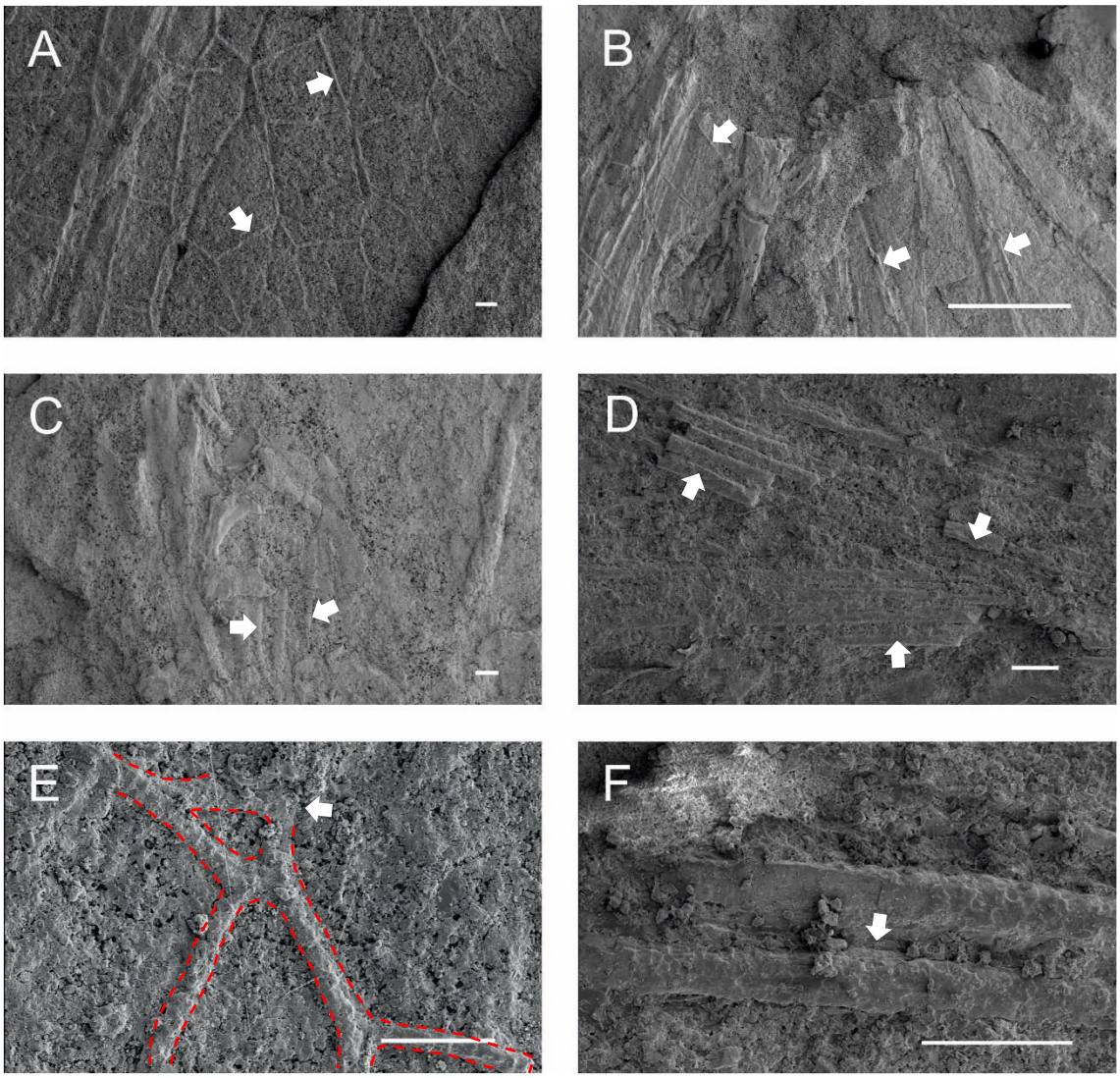


Plate 81: Examples of wing venation from Nova Olinda Member fossil insects. A, Overview of mesh-like wing venation, highlighted by arrows. B-D, Examples of cracked and fractured wing venation at various magnifications. Arrows highlight wing venation. E, Faint traces of wing venation, highlighted by dashed lines, remain in an otherwise poorly-preserved specimen. F, Fractured wing vein, revealing its internal tubular structure, highlighted by arrow. Specimen and image numbers: A, JW02#-006; B, JW02#-001; C, NBRL078-11; D, NBRL070-70; E, JW02#-004; F, NBRL070-78. A and C-F, Scale bars = 100 µm. B, Scale bar = 1 mm.

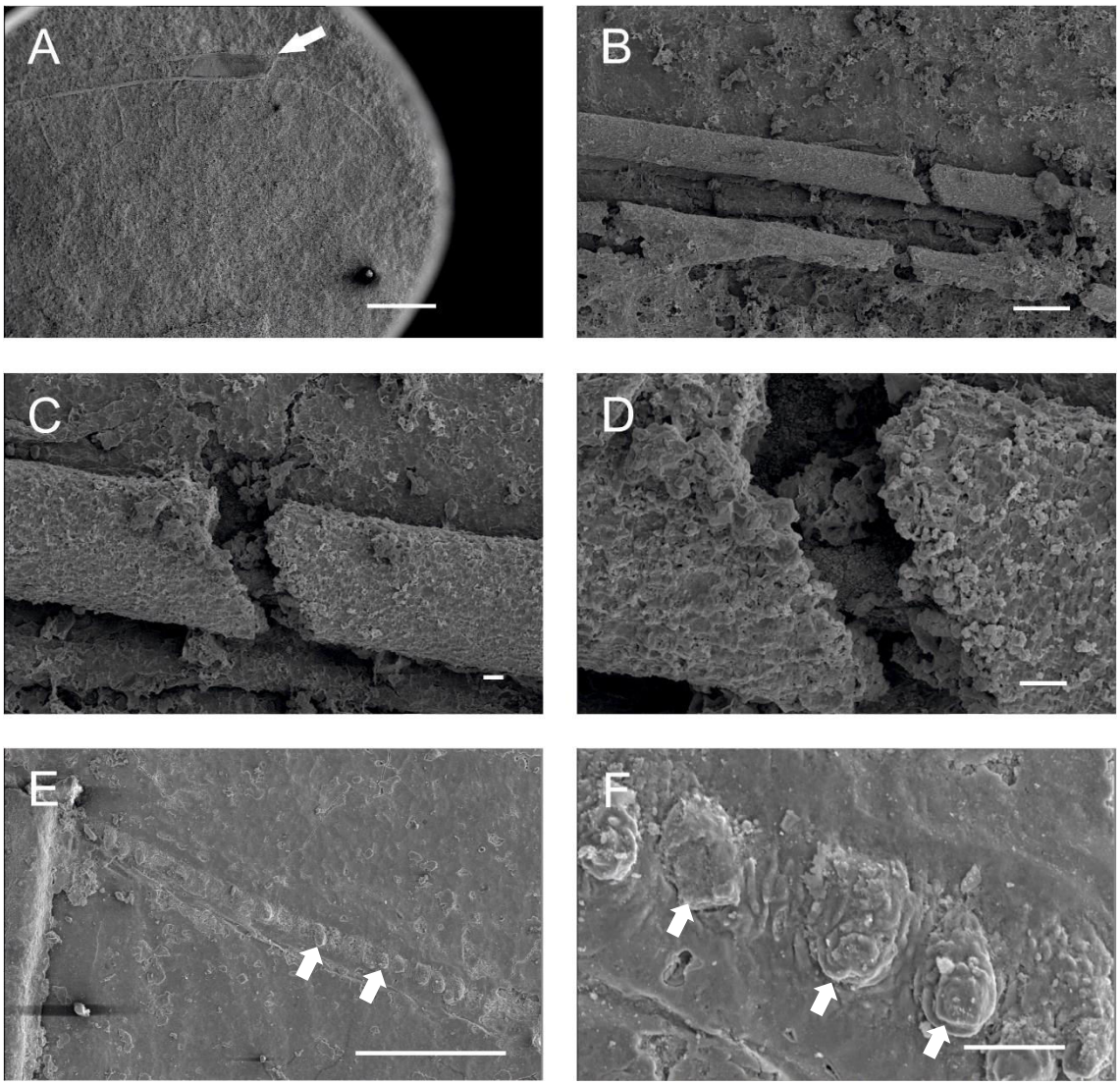


Plate 82: Examples of brittle damaged wing venation in Nova Olinda Member fossil insect wings. A, Overview of relatively poorly preserved Odonata wing with only faintly visible venation. Arrow highlights pterostigma. B-D, Brittle and fractured three-dimensional neuropteran wing venation. E-F, Heavily abraded wing cuticle, with remnants of spines visible only as truncated bases, highlighted by arrows. Specimen and image numbers: A, UnNumFLO-01; B, NBRL079-30; C, NBRL079-31; D, NBRL079-32; E, NBRL062-38; NBRL062-37. A, Scale bar = 1 mm. B and E, Scale bars = 100 µm. C-D and F, Scale bars = 10 µm.

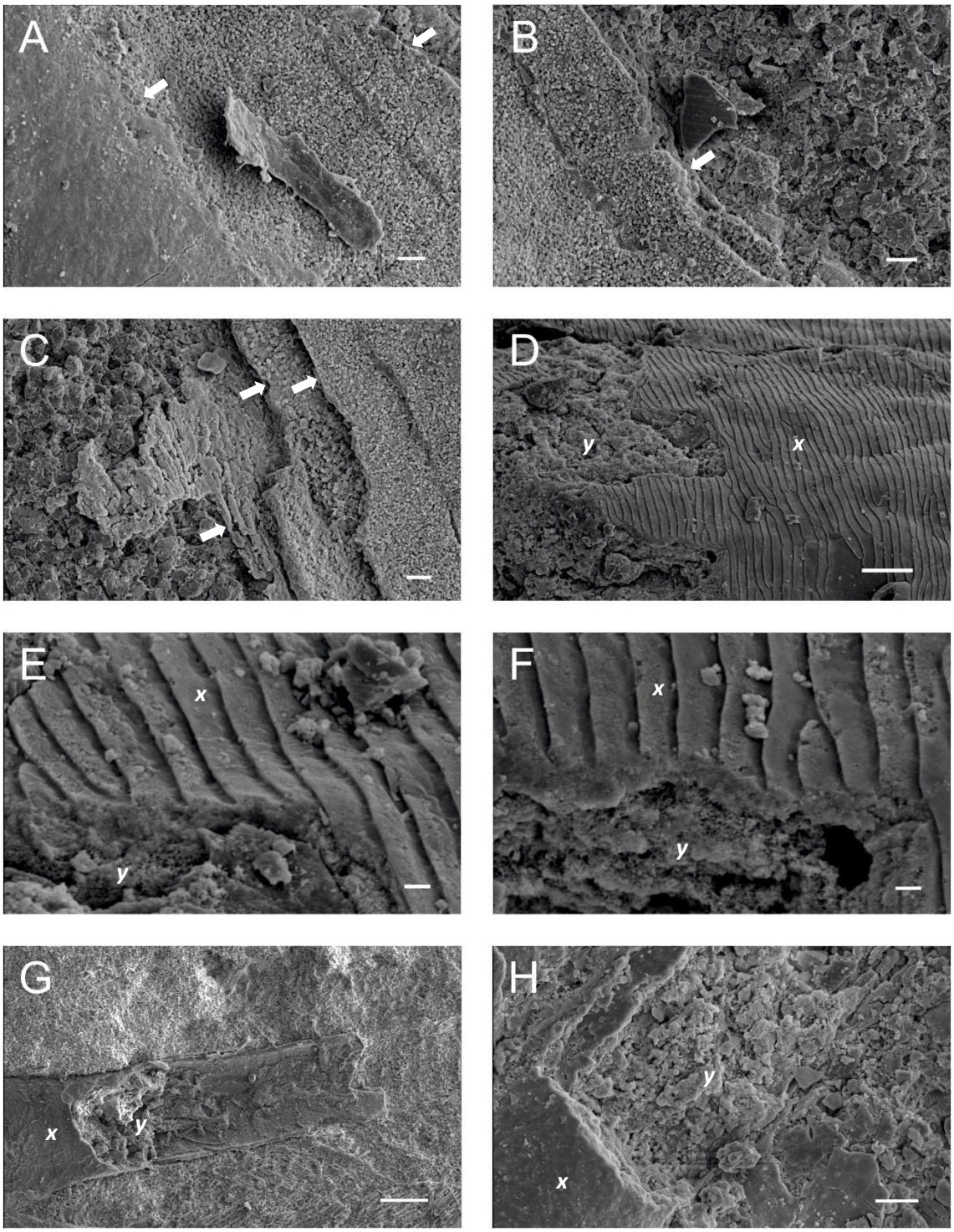


Plate 83: Examples of brittle breakages of cuticle in immediate contact with areas of exceptional preservation in Nova Olinda Member fossil insects. A-C, Smooth cuticle broken in several layers, highlighted by arrows, to reveal a micro-spherical fabric beneath. D-F, Extremely well-preserved cuticle with cuticular scales (*x*), with a sharp break revealing granular preservation beneath (*y*). G-H, Well-preserved cuticle (*x*) of broken caudal filament revealing globular tissue beneath (*y*). Specimen and image numbers: A, NBRL026-16; B, NBRL026-17; C, NBRL026-18; D, NBRL036-40; E, NBRL036-41; F, NBRL036-42; G, FLO13-80; H, FLOXX-47. A-D and H, Scale bars = 10 µm. E-F, Scale bars = 1 µm. G, Scale bar = 100 µm.

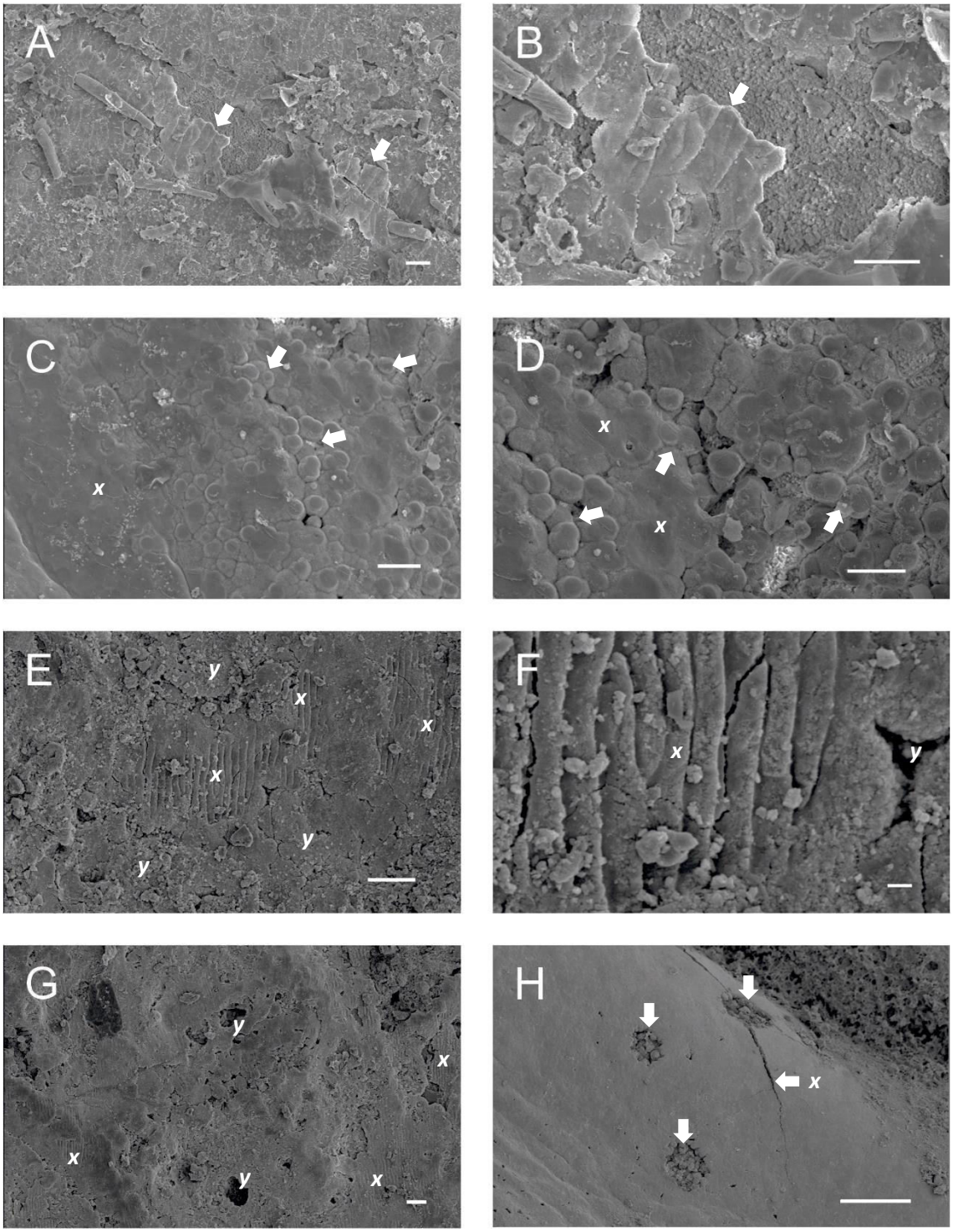


Plate 84: Examples of variations in the quality of preservation of Nova Olinda Member fossil insects as a result of different processes. A-B, Abrasion resulting in well-preserved epicuticle with scales 'peeling' (delaminating) away, highlighted by arrows. C-D, Examples of poorly-preserved smooth cuticle (*x*) 'degrading' into hemispherical fragments (likely formed around pseudomorphed pseudoframboids), highlighted by arrows, as a result of incomplete mineralisation. E-G, Patches of well-preserved cuticle with scales (*x*), surrounded by very poorly-preserved cuticle (*y*) as a result of both abrasion and incomplete mineralisation. H, Exceptionally preserved prothoracic plate with puncture holes, highlighted by arrows, possibly due to clumsy mechanical preparation as suggested by post-mineralisation cracking (*x*). Specimen and image numbers: A, NBRL059-45; B, NBRL059-46; C, NBRL030-14; D, NBRL030-18; E, NBRL036-31; F, NBRL036-32; G, NBRL036-34; H, NBRL054-48. A-E and G, Scale bars = 10 µm. F, Scale bar = 1 µm. H, Scale bar = 100 µm.

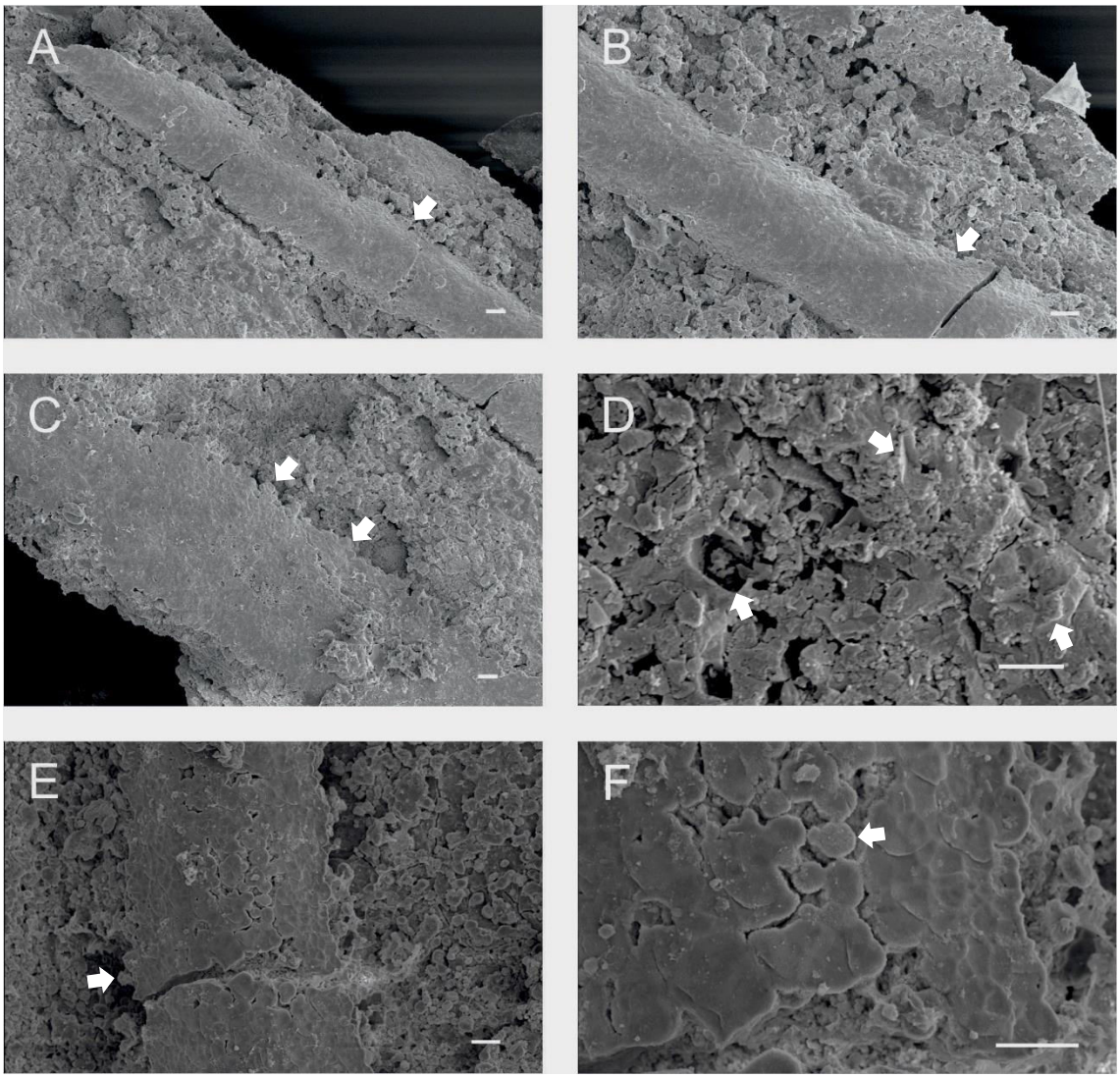


Plate 85: Examples of damage possibly caused by effervescence during acid digestion of Nova Olinda Member insect fossils. A-C, Poorly preserved wing vein with frayed edge. Preservational fabric revealed as an amalgamation of sub-spherical pseudoframboid-like aggregates, highlighted by arrows. D, Vein composed of irregular crystals, highlighted by arrows, exposed during 10% acetic acid digestion. E-F, Undigested broad, flat and poorly-preserved wing vein that possesses the same mineralogical fabric exposed in A-C, also highlighted by arrows. Specimen and image numbers: A, NBRL065(resi)-15; B, NBRL065(resi)-27; C, NBRL065(resi)-26; D, JW02#-005; E, NBRL030-26; F, NBRL030-27. Scale bars = 10 µm.

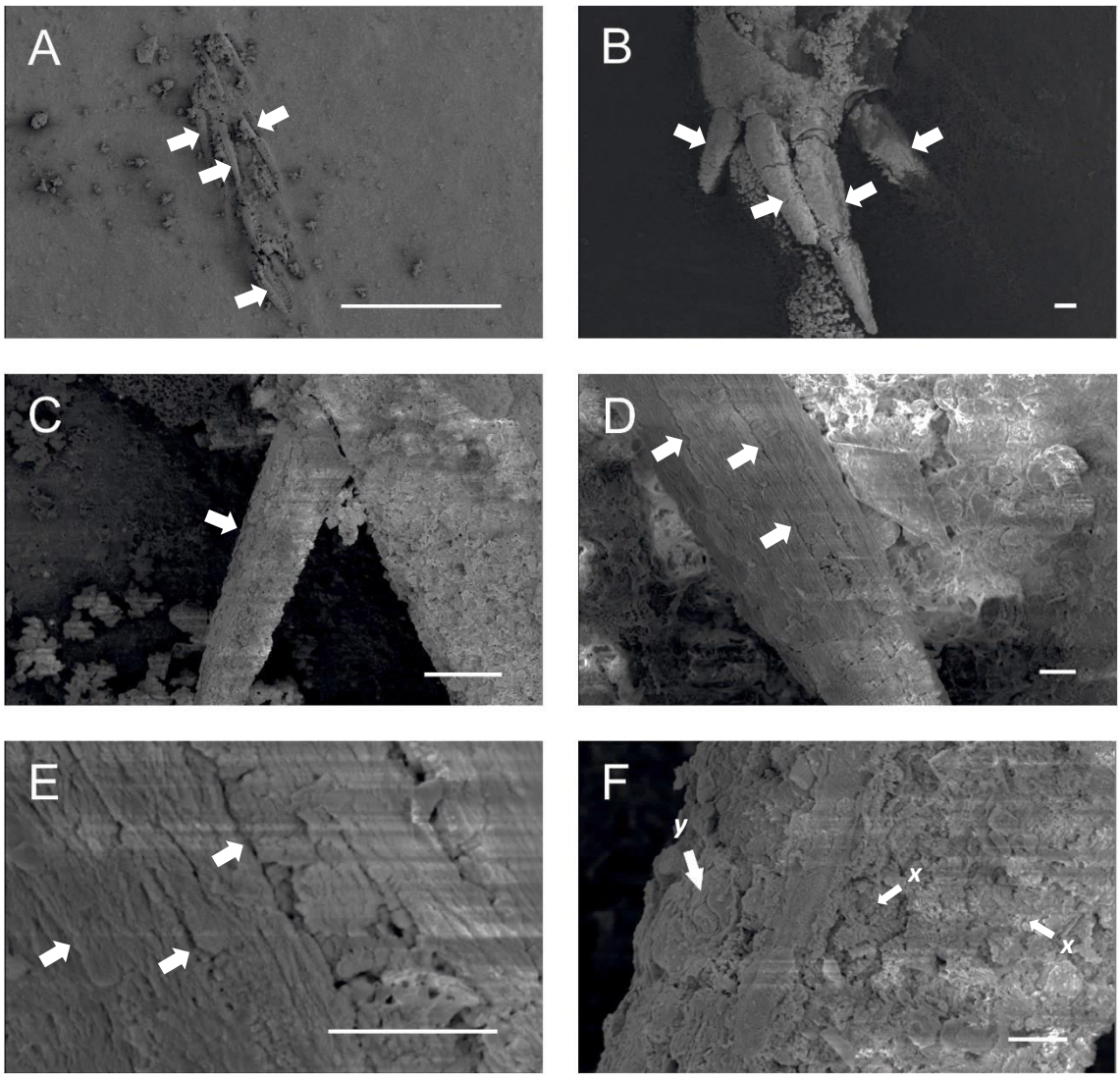
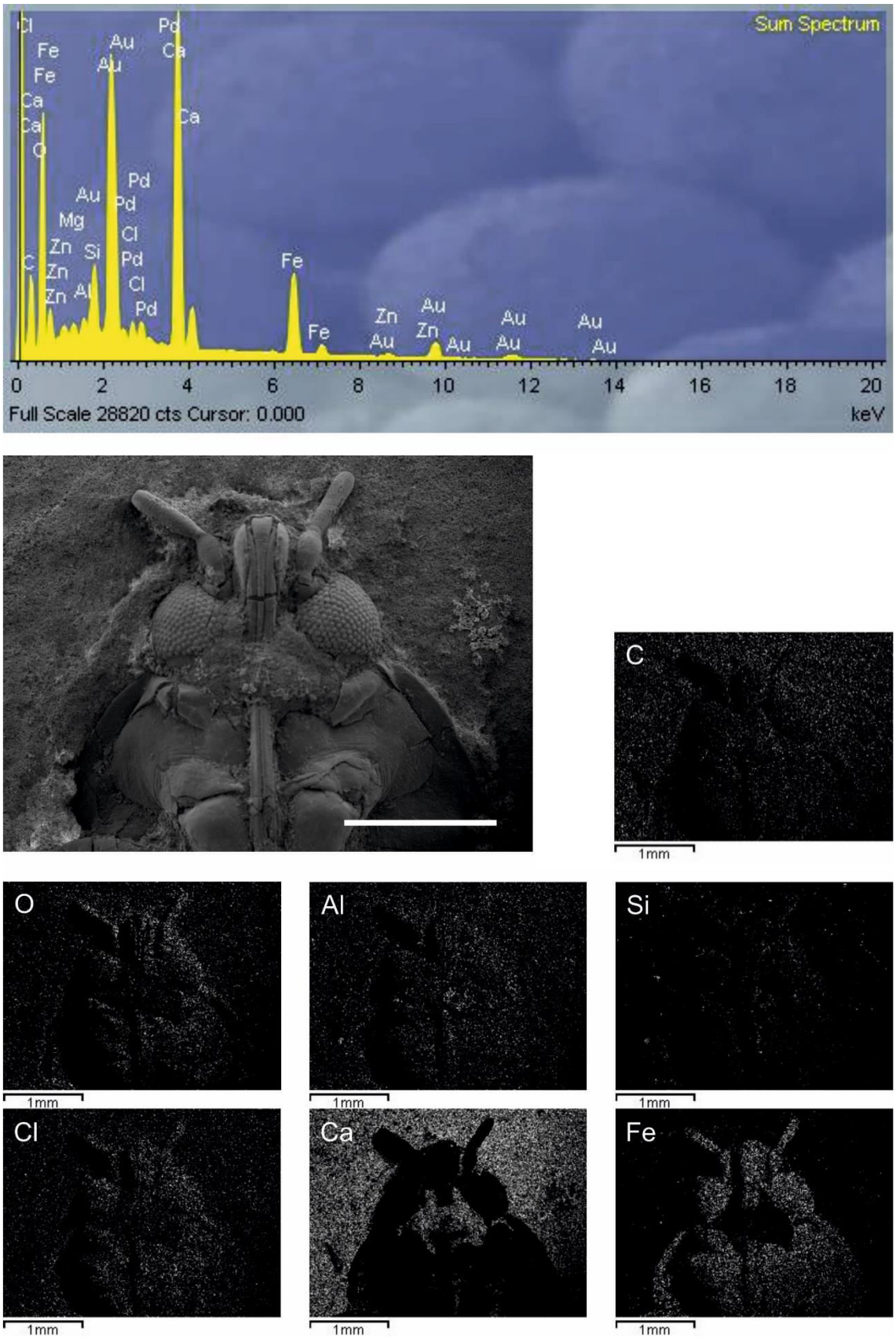
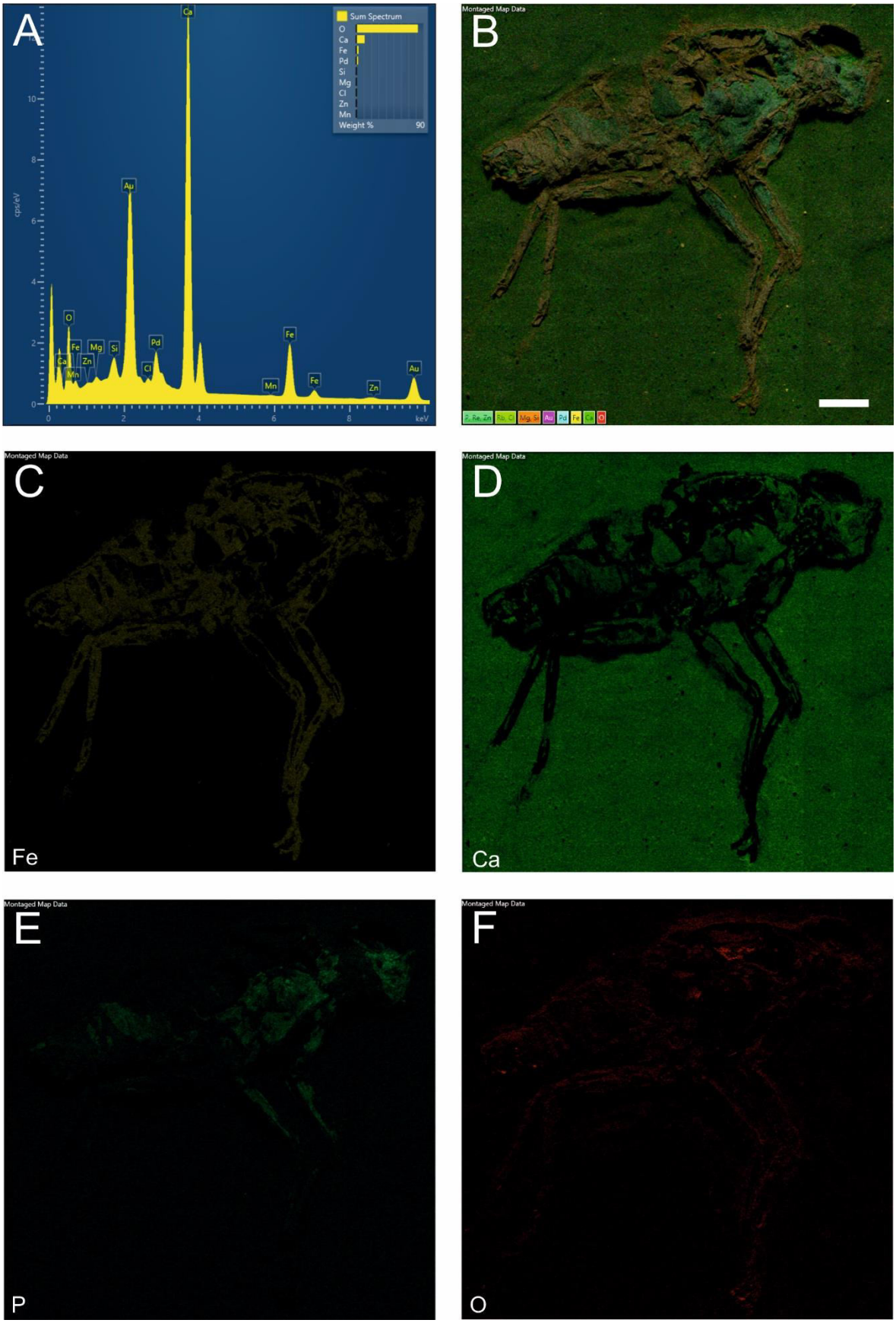


Plate 86: Examples of spines of Nova Olinda Member insect fossils possibly abraded by effervescence during 10% hydrochloric acid digestion. A, Overview of limb spines from very poorly-preserved limb. Spines are essentially the only remaining aspect of the limb, highlighted by arrows. B, Heavily charging shattered femur spines (at distal end), highlighted by arrows. C, Intact, but partially disarticulated, spine with heavily abraded cuticle, highlighted by arrow. D-E, Spine with striation-like cracks running parallel to its length, highlighted by arrows, likely the result of effervescence abrasion. F, Heavily abraded spine cuticle, with a granular surface fabric (*x*) and rare setal bases (*y*). Specimen and image numbers: A, NBRL072-13; B, NBRL055-15; C, NBRL059-12; D, NBRL072-06; E, NBRL072-08; F, NBRL059-13. A, Scale bar = 1 mm. B-C, Scale bars = 100 µm. D-F, Scale bars = 10 µm.

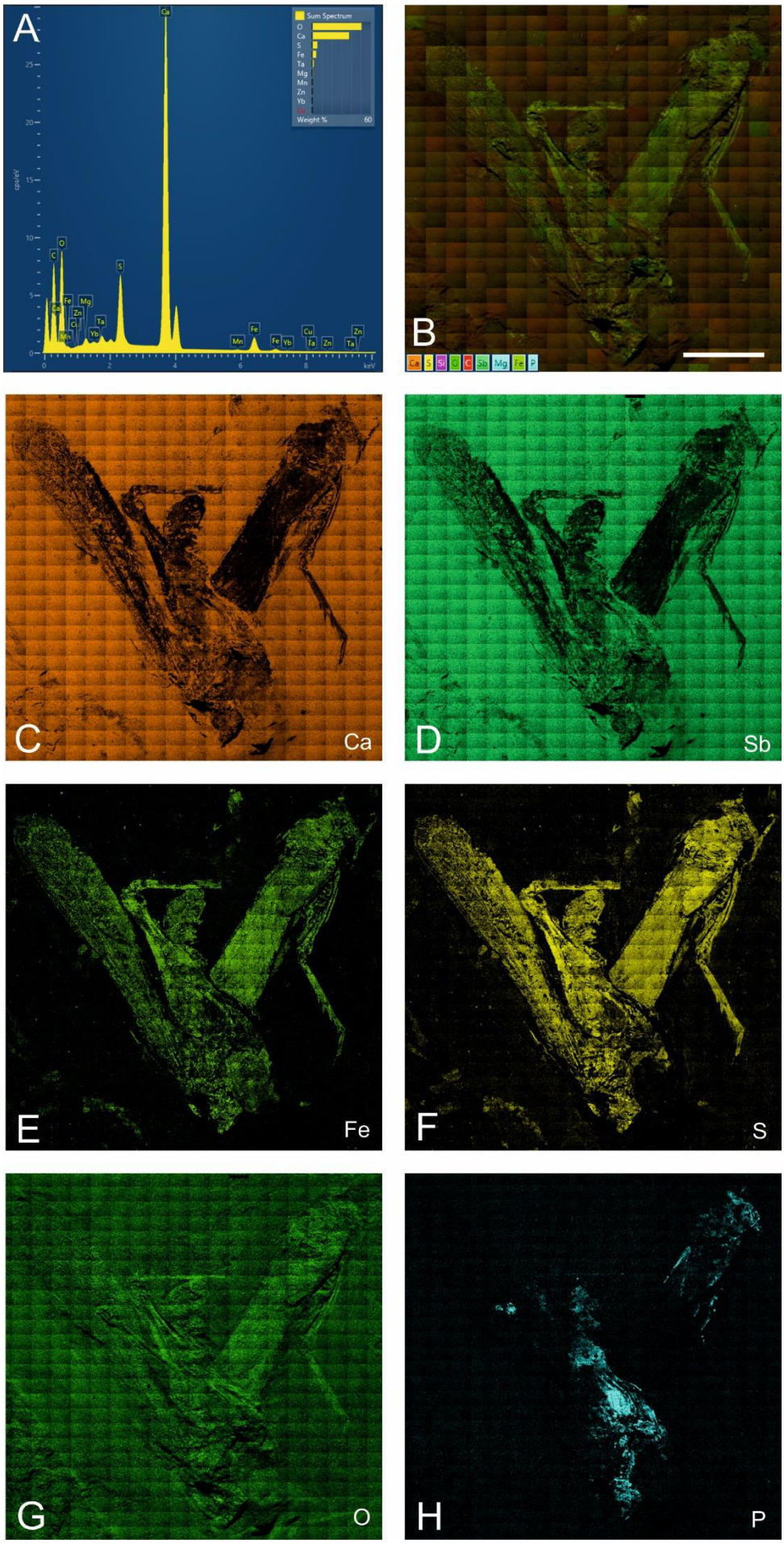
8. 1. 1. EDX Plates



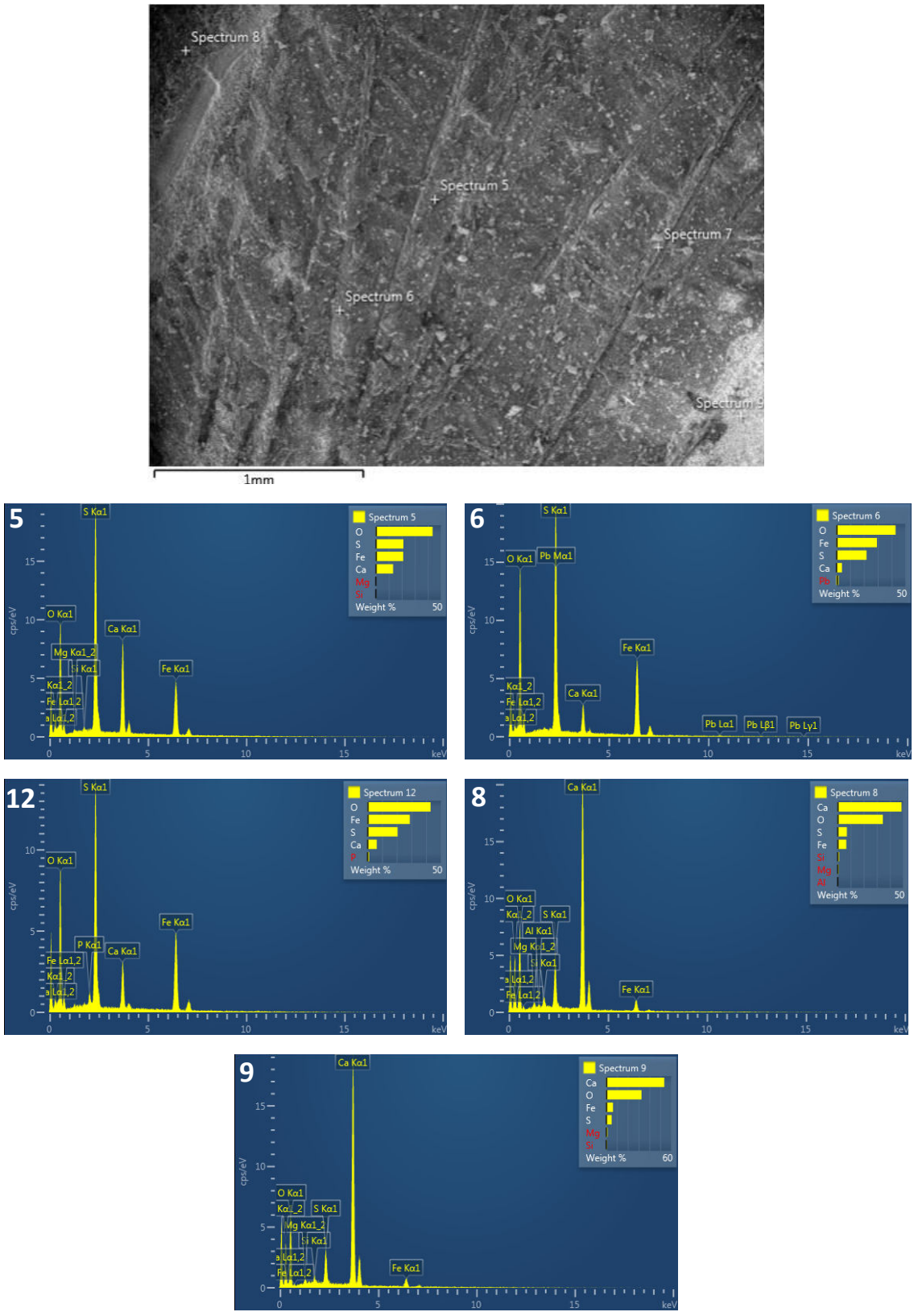
EDX Plate 1: Elemental composition of Nova Olinda hemipteran fossil *versus* matrix. Maps of individual elements presented. Brightness corresponds to relative elemental abundance. Replacement of insect tissue is dominated by Fe and O, further suggesting preservation in goethite (H not detectable). Abundance of O on insect fossil may be partly topographic effect. Surrounding matrix maps as Ca, O, and rarer C. Rare patches of Al and Si suggest small aggregates of clay minerals that may have adhered to the fossil. Clays are otherwise only observed within *Dastilbe* coprolites. Abundance of Cl may be a background peak. Spectrum summarises entire specimen, however several elements may be concealed by Au-Pd sputter coating. Specimen number FLO15. EDX file: Project 1; Sample 1; Site of Interest 3. SEM image scale bar = 1 mm. 28820 counts.



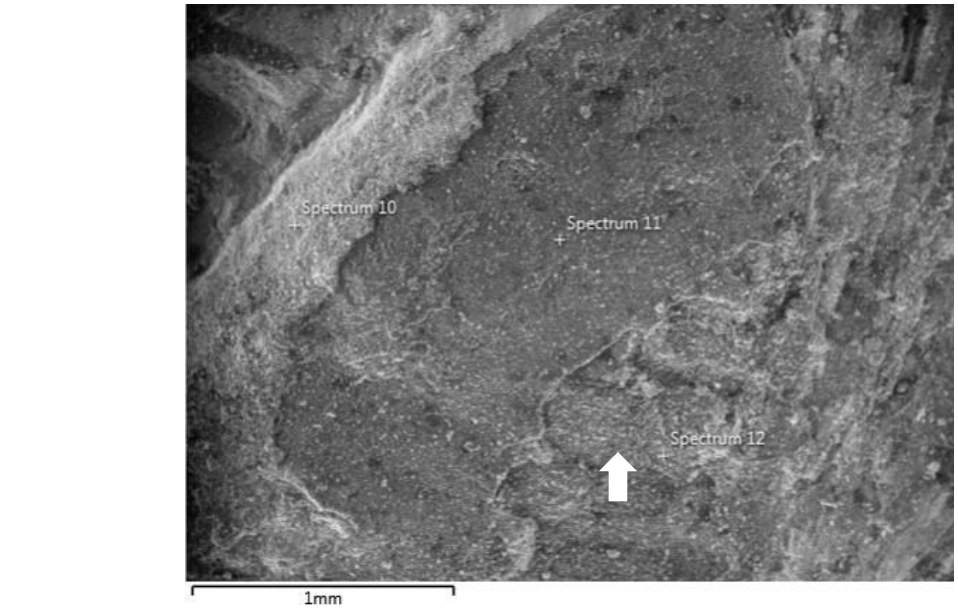
EDX Plate 2. Energy dispersive X-ray spectroscopic map of specimen FLO19. A, Sum spectrum. Abundance of gold is due to gold sputter coating. B, Montaged layered energy dispersive X-ray spectroscopic map of specimen FLO19. Element colour asignments are denoted in the bottom left. Matrix consists of calcitic mineral, fossil cuticle is preserved as an iron oxide mineral, and internal soft-tissues are phosphatic. C, Montaged energy dispersive X-ray spectroscopic map of Fe. D, Montaged energy dispersive X-ray spectroscopic map of Ca. E, Montaged energy dispersive X-ray spectroscopic map of P. F, Montaged energy dispersive X-ray spectroscopic map of O. Four hour spectrum run-time. Kv = 20, WD = 14.5 mm, I Probe = 200 pA. Scale bar = 1 mm.

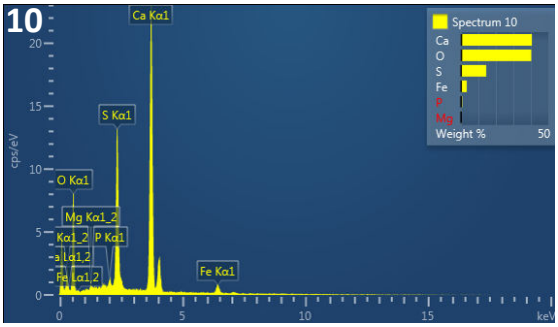


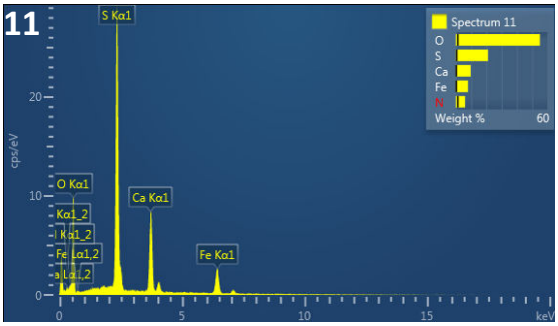
EDX Plate 3. Energy dispersive X-ray spectroscopic map of specimen HT001. A, Sum spectrum. Abundance of gold is due to gold sputter coating. B, Montaged layered energy dispersive X-ray spectroscopic map of specimen HT001. Element colour asignments are denoted in the bottom left. Matrix consists of calcitic mineral, fossil cuticle is preserved as an iron sulphide, and internal soft-tissues are phosphatic. Subsequent images provide energy dispersive X-ray spectroscopic maps of several key elements, denoted in the bottom right. C, Montaged map of Ca. D, Montaged map of Sb, resulting from misidentified Ca peaks (Newbury, 2009). E, Montaged map of Fe. F, Montaged map of S. G, Montaged map of O. H, Montaged map of P. Nine hour spectrum run-time. Kv = 20, WD = 14.5 mm, I Probe = 200 pA. Scale bar = 5 mm.

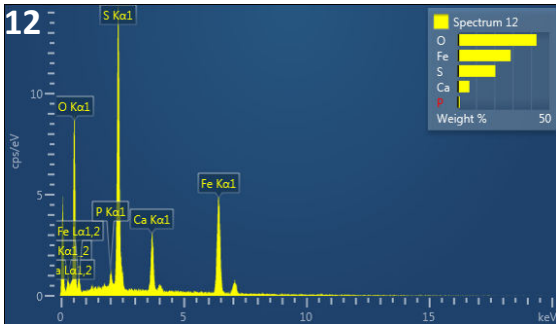


EDX Plate 4: Insect wing cuticle with five EDX point analyses from supposedly 'unweathered' specimen. Spectra 5, 6, and 12 are dominated by O, Fe, and S, suggesting an iron sulphide replacement mineralogy and its oxidised derivative, perhaps goethite(?), also present. This suggests that the wings of this specimen have weathered. Spectra 8 and 9 are dominated by Ca and O, suggesting calcium carbonate matrix. Possible trace elements are also present as Mg and Si in spectrum 5; Pd in spectrum 6; P in spectrum 12; Si, Mg, and Al in spectrum 8; and Mg and Si in spectrum 9. Due to C sputter coating, spectra do not record the presence of C. Elements marked in red had a 1σ error of > 10%. Specimen HT001. Kv = 20, WD = 11 mm, I Probe = 200 pA. Scale bar = 1 mm.

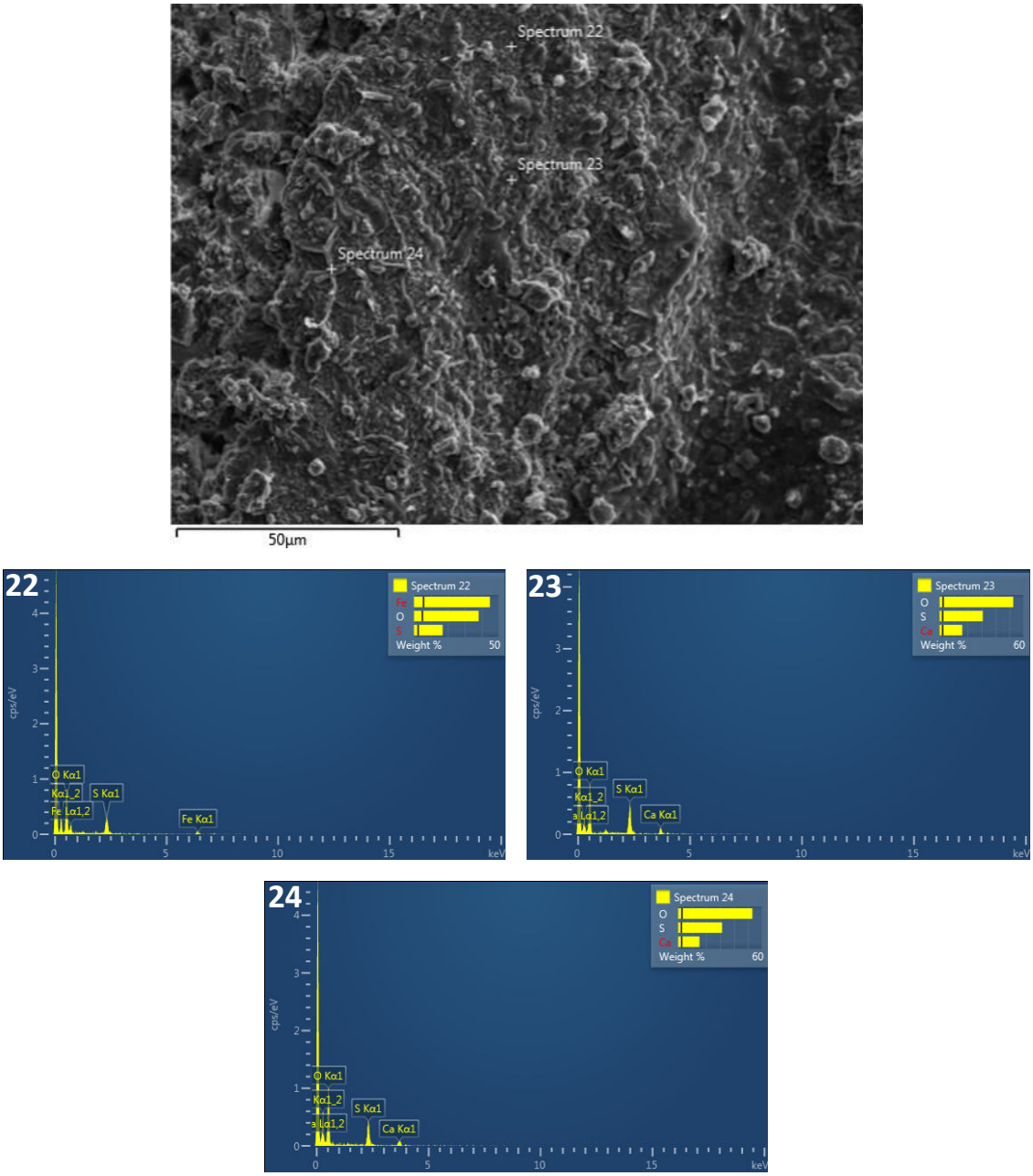




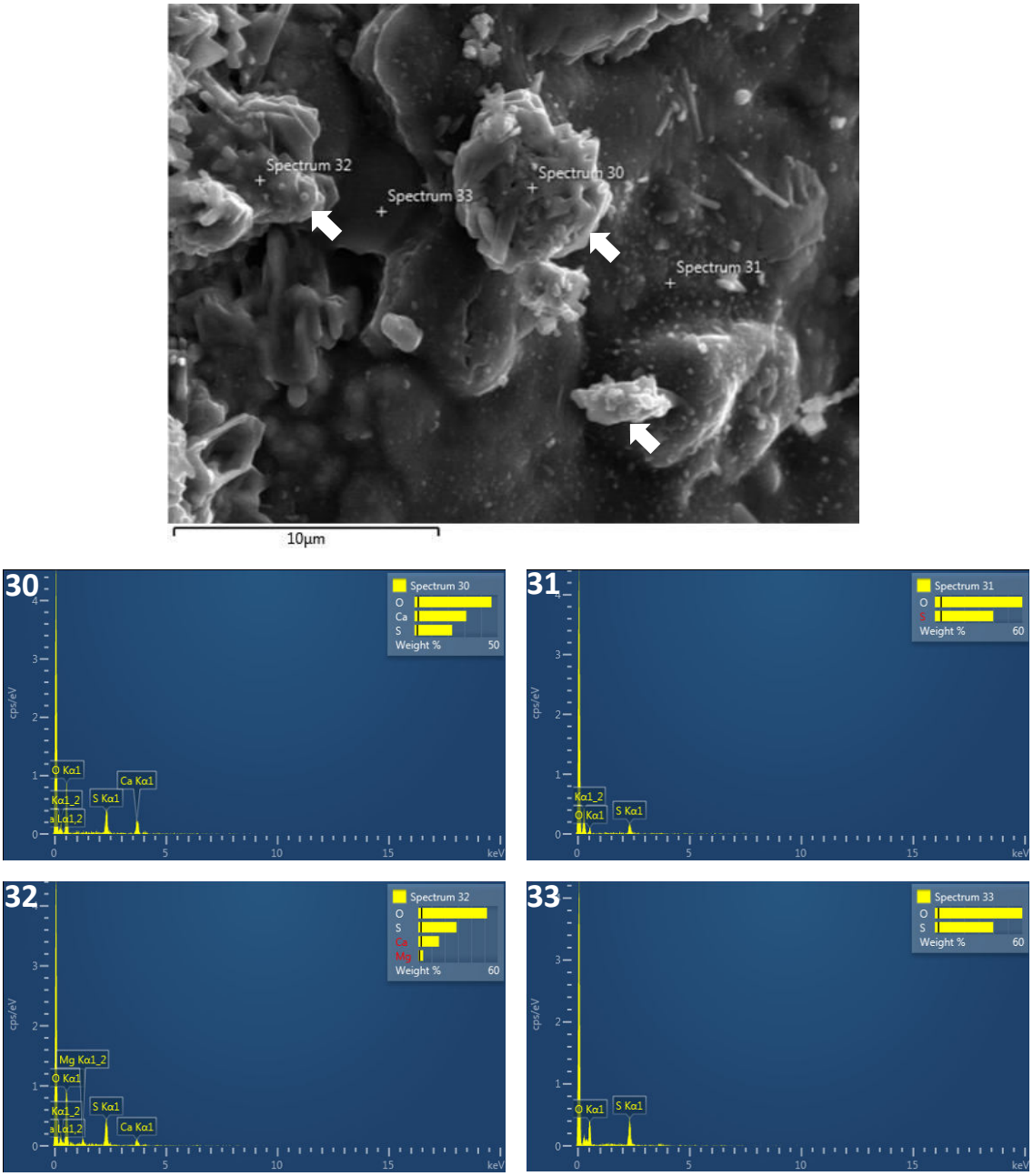




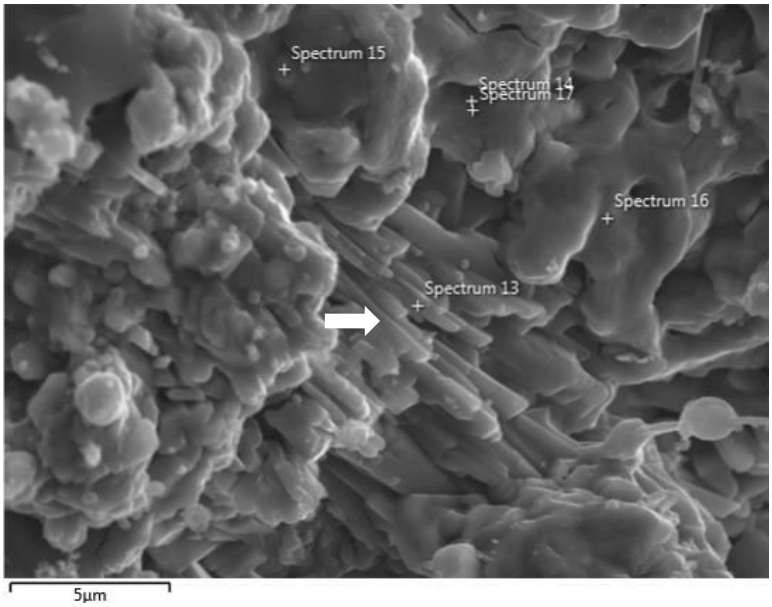
EDX Plate 5: Relatively unweathered (contains pyrite) insect cuticle (thorax/anterior abdomen), with three EDX point analyses. Cuticle is broken, exposing internal preservation, highlighted by arrow. Spectrum 10 is located on sediment immediately adjacent to insect cuticle, dominated by Ca, O, and S, suggesting calcium sulphate. Extremely rare P and Mg also present. Spectrum 11 is located on insect cuticle, dominated by O, and to a lesser extent S. Rarer Ca, Fe, and possible N. Mineralogy likely represents iron sulphide and subsurface calcium carbonate. Spectrum 12 is located on internal preservation, revealing O, Fe, S, and rarer Ca. P is also present, but extremely rare. Elements marked in red had a 1σ error of > 10%. Specimen HT001. Kv = 20, WD = 10.5 mm, I Probe = 200 pA. Scale bar = 1 mm.

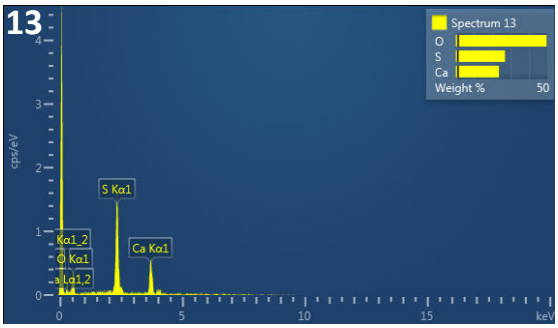


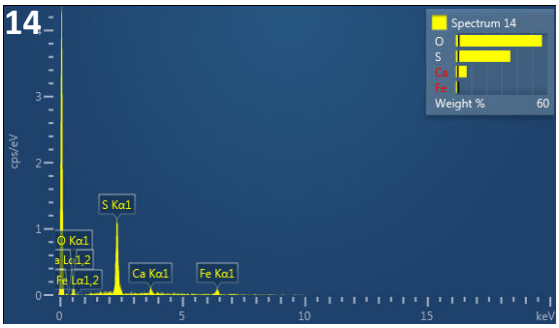
EDX Plate 6: Unweathered insect cuticle retaining three-dimensionality, with three EDX point analyses. Spectrum 22 is located on a section of smooth cuticle, revealing Fe, O, and S. Spectra 23 and 24 are located on anhedral grains coating the surface of the cuticle, revealing O, S, and Ca. Elements marked in red had a 1σ error of > 10%, and are less reliable identifications. Usually, elements marked in red are only present as traces. However, in this analysis, several abundant elements have a high 1σ error. Specimen HT001. Kv = 10, WD = 13 mm, I Probe = 5 pA. Scale bar = 50 µm.

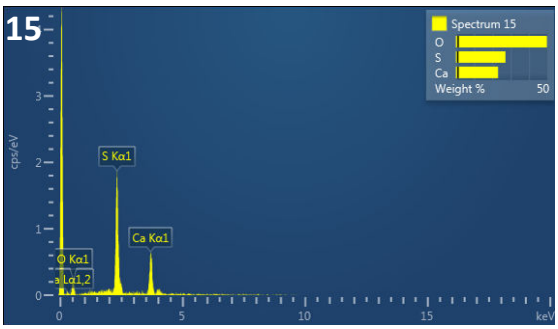


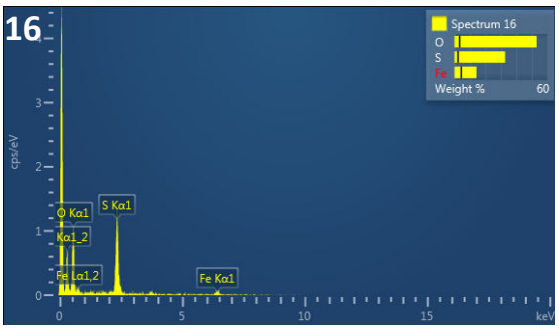
EDX Plate 7: Higher magnification image of unweathered insect cuticle, with four EDX point analyses. Fragments of internal material have disarticulated and are on the surface, highlighted by arrows. Spectra 31 and 33 are located on smooth insect cuticle. Only O and S are detected, however S oxides do not form solids in this manner at surface temperatures and pressures, suggesting that the spectrum are incomplete, perhaps due to the exclusion of C. Spectra 30 and 32 are located on disarticulated fragments of internal tissue preservation, revealing O, Ca, and S (with rare Mg in spectrum 32), further suggesting calcium sulphate (gypsum). Elements marked in red had a 1σ error of > 10%. Specimen HT001. Kv = 10, WD = 13 mm, I Probe = 5 pA. Scale bar = 10 um.

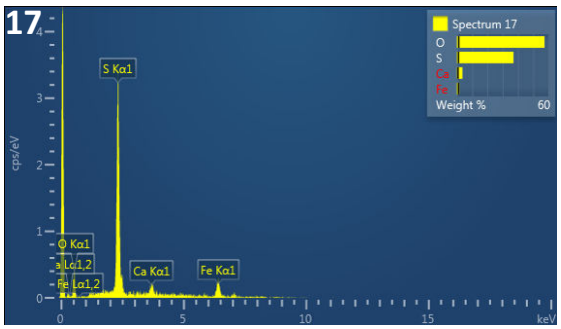




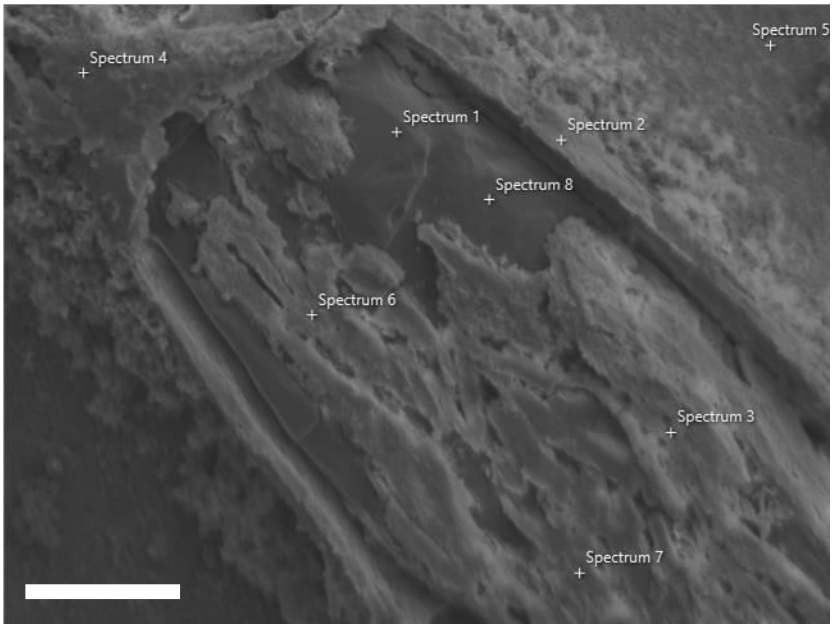




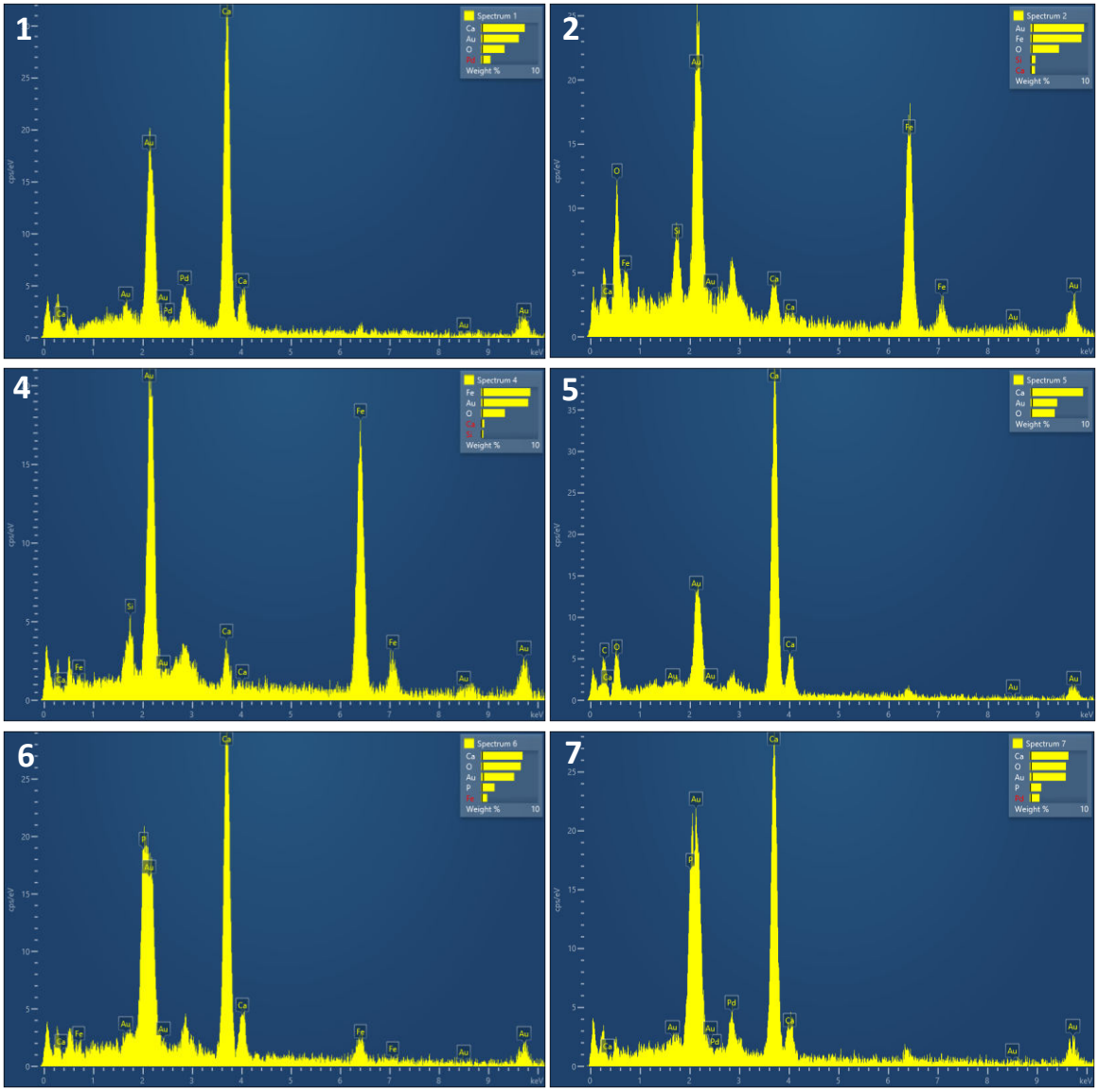


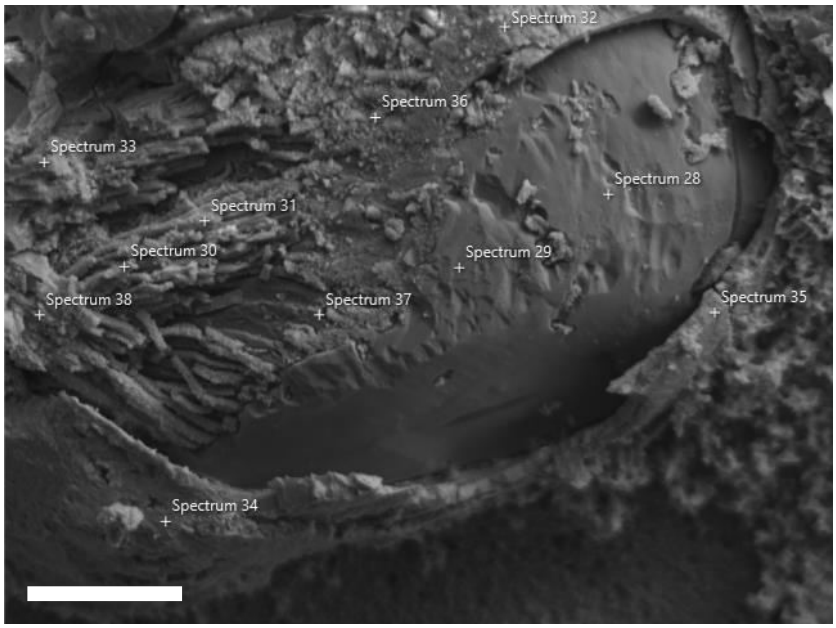


EDX Plate 8: Needle-like crystals, highlighted by arrow, embedded in unweathered, but globular, insect cuticle with five EDX point analyses. Spectra 13 located on needle-like crystals, revealing O, S, and Ca. This composition, combined with the crystal morphology strongly suggest that these are gypsum crystals, formed as a result of minor weathering of pyrite. Spectrum 15 also reveals O, S, and Ca although present on globular material (cuticle?), rather than the needle-like crystals. Spectra 14, 16, and 17 are located on surrounding globular material, revealing a majority S, O and Fe. Elements marked in red had a 1σ error of > 10%. Specimen HT001. Kv = 10?, WD = 13 mm?, I Probe = 5 pA?. Scale bar = 5 um.

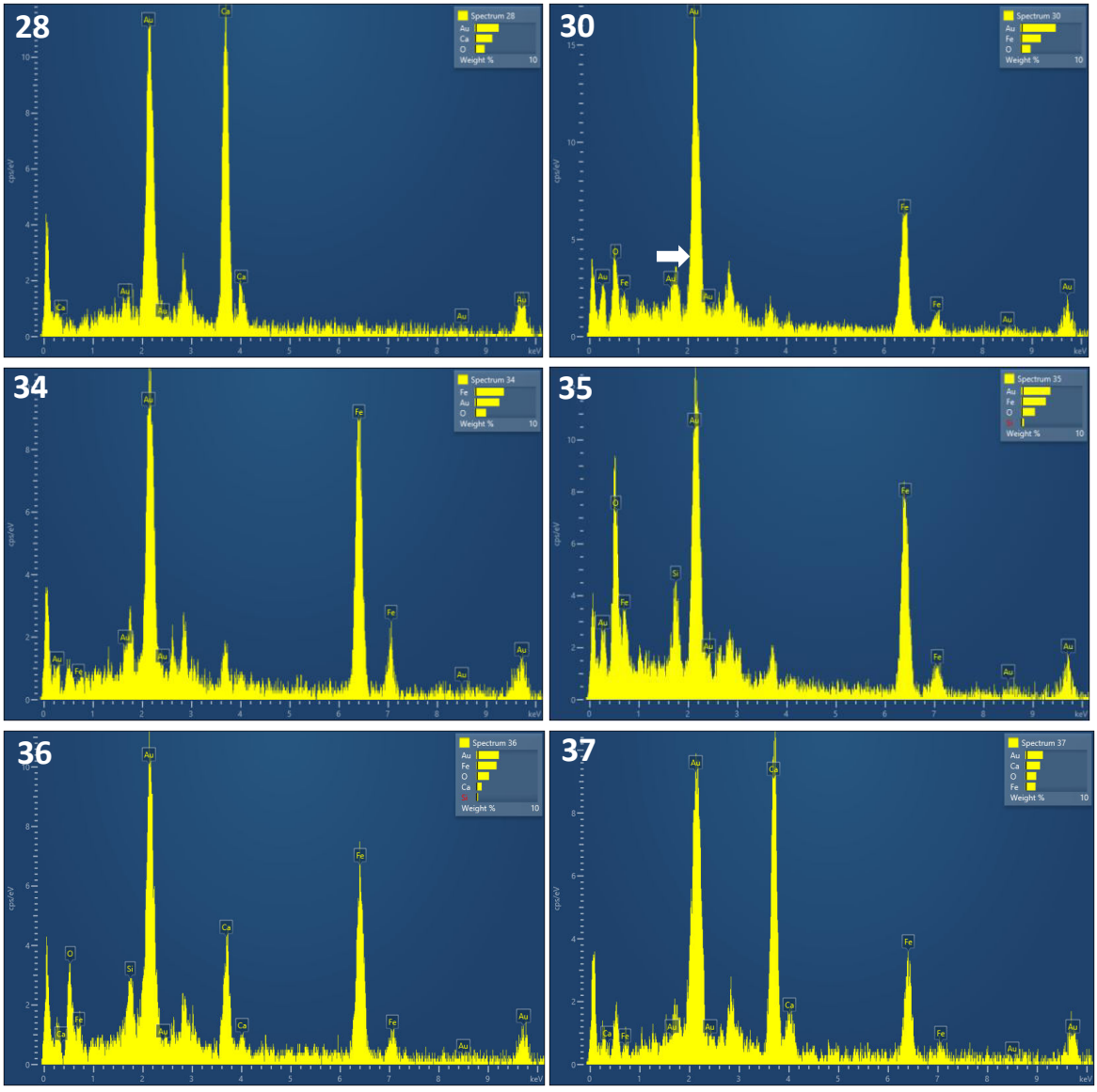


EDX Plate 9: FLO19 forelimb preservation. Spectra 3 and 8 are excluded due to near-identical results to others here. C also excluded. Abundance of Au a result of Au-Pd sputter coating. Spectra 1 and 8 reveal infilling mineral as calcite. Spectra 2 and 4 reveal Fe and O preservation of cuticle. Spectrum 5 reveals calcium carbonate matrix. Spectra 6 and 7 reveal calcium phosphate preservation of muscle fibers. Elements marked in red had a 1σ error of > 10%, and are less reliable identifications. Kv = 20, WD = 14.5 mm, I Probe = 200 pA. Scale bar = 100 µm.

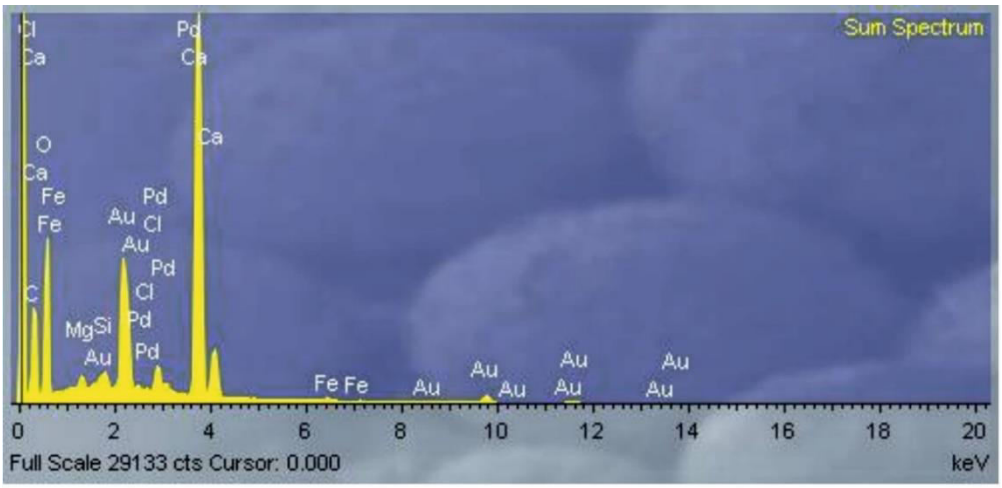


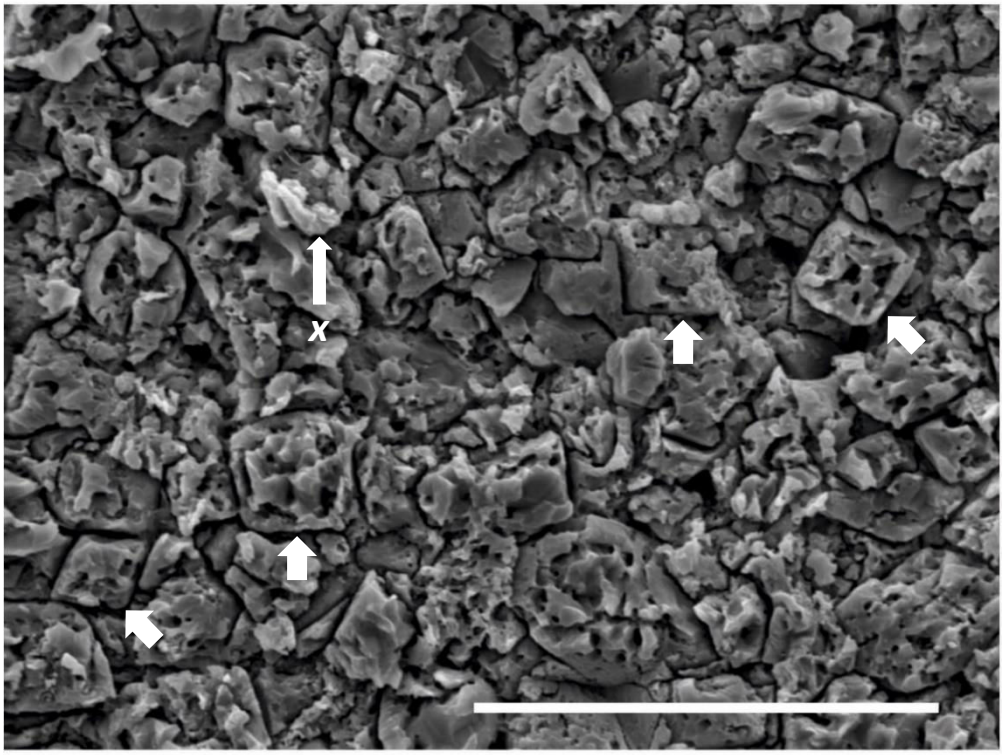


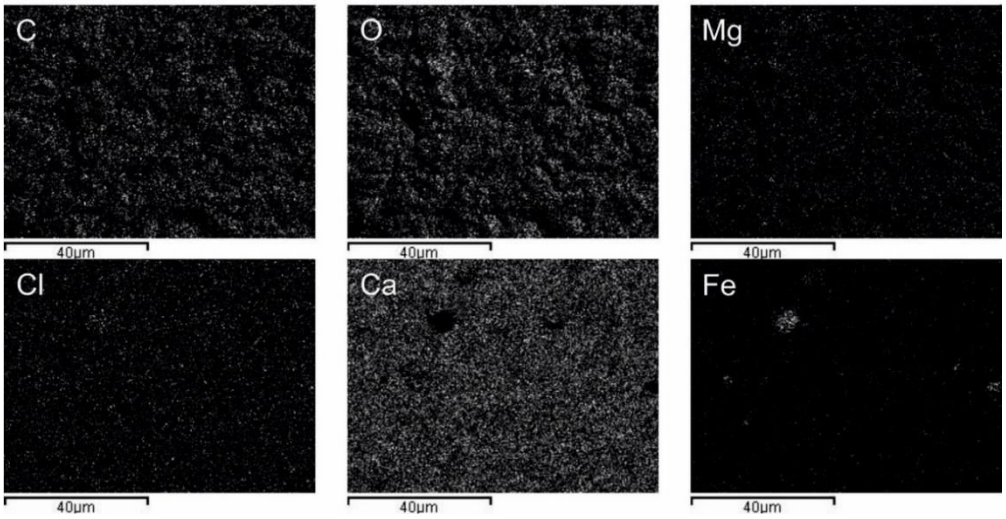
EDX Plate 10: FLO19 internal genital preservation. Spectra 29, 31-33, and 38 are excluded due to near-identical results to others here. C also excluded. Abundance of Au a result of Au-Pd sputter coating. Spectrum 28 reveals infilling mineral as calcite. Spectra 30 suggests that the soft tissue fibers are preserved in Fe and O, however P may be masked by large Au peak (highlighted by arrow). Spectra 34 and 35 reveal Fe and O preservation of cuticle, with some evidence



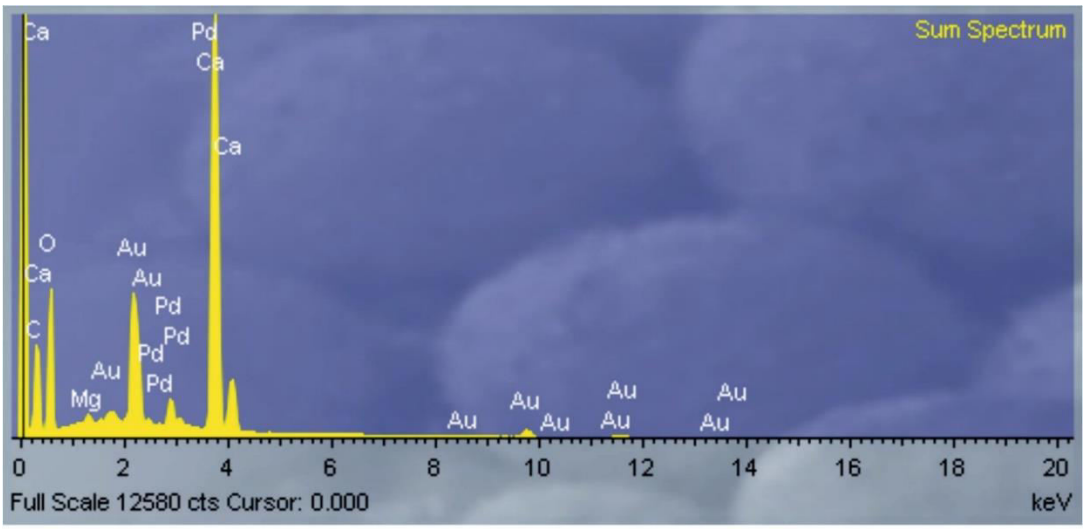
of trace Si. Spectra 36 and 37 yield an amalgamation of elements from both mineral infills and internal soft-tissue preservation. Elements marked in red had a 1σ error of > 10%, and are less reliable identifications. Kv = 20, WD = 14.5 mm, I Probe = 200 pA. Scale bar = 100 µm.

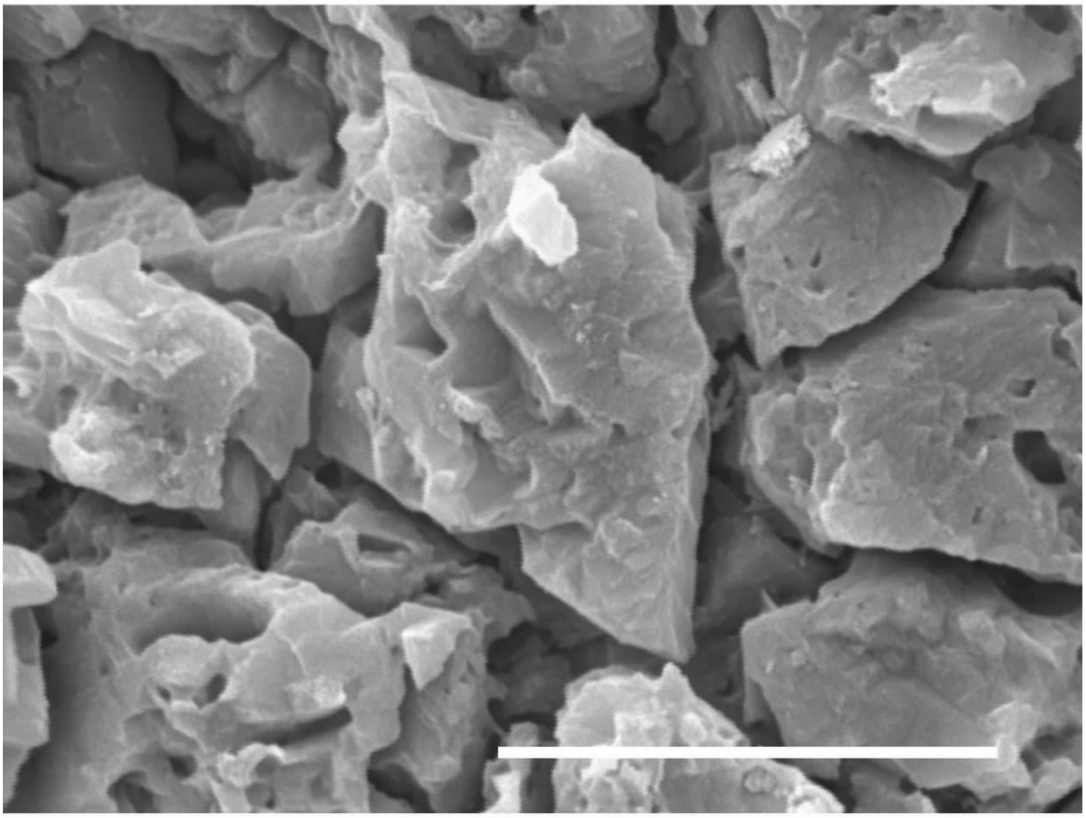


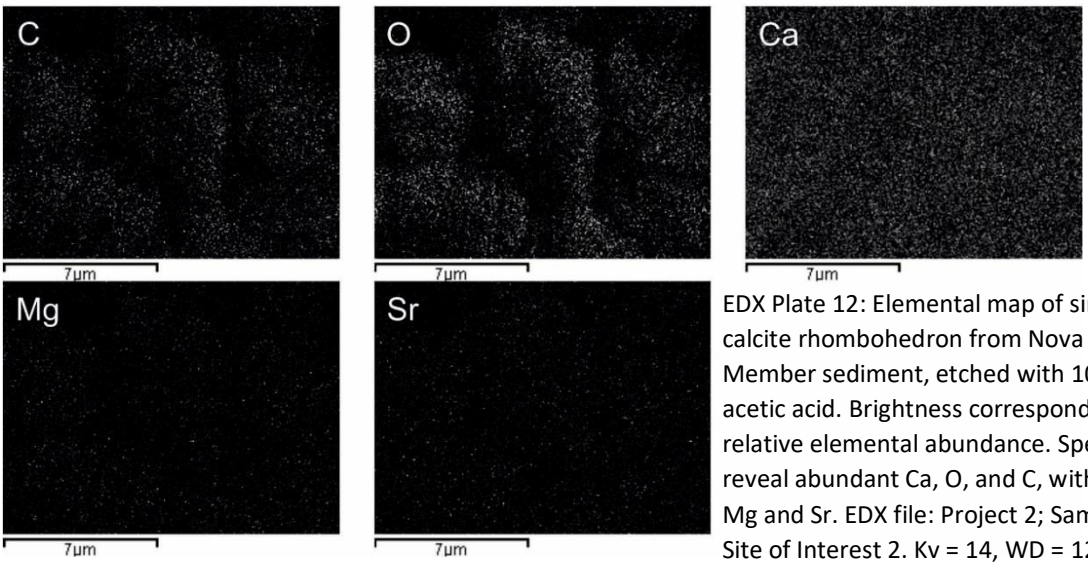




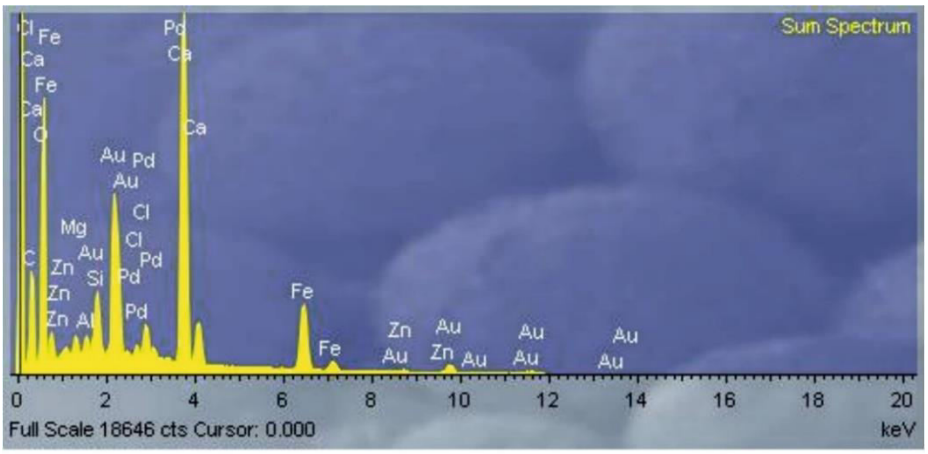
EDX Plate 11: Elemental map of a sample of Nova Olinda Member sediment etched with 10% acetic acid. Brightness corresponds to relative elemental abundance. Distinct calcium carbonate rhombohedron are highlighted by arrows. Elemental map reveals abundant Ca, O, and C. Rarer Cl (and possibly Mg?) may be a result of the etching process. *x*, Highlights isolated Fe-rich grain. EDX file: Project 1; Sample 1; Site of Interest 5. 29133 counts. Kv = 14, WD = 12 mm, I Probe = 90 pA. Scale bar = 40 µm.

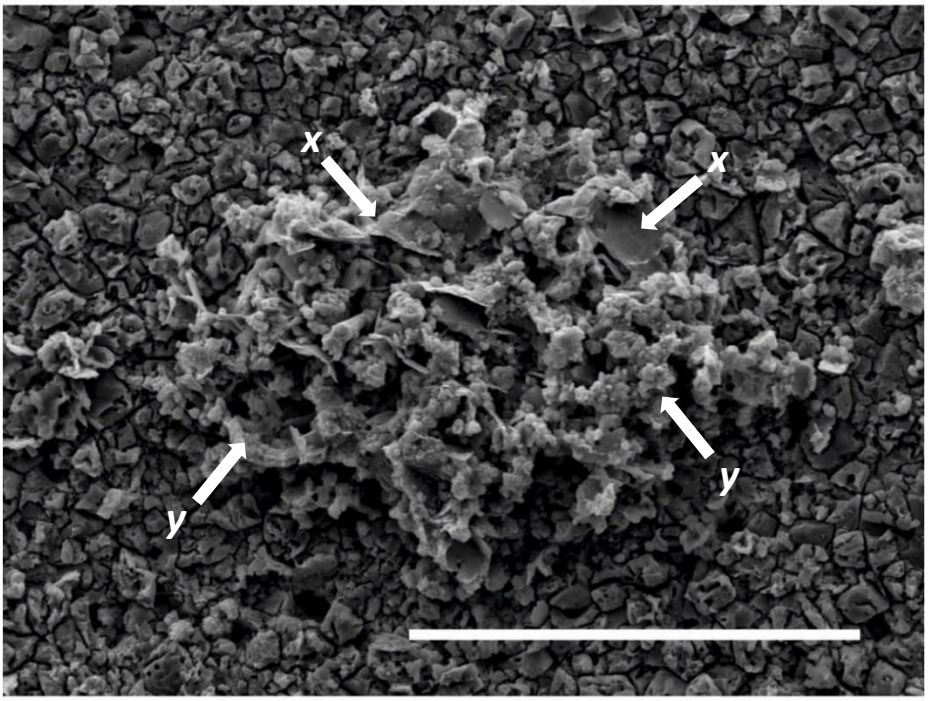


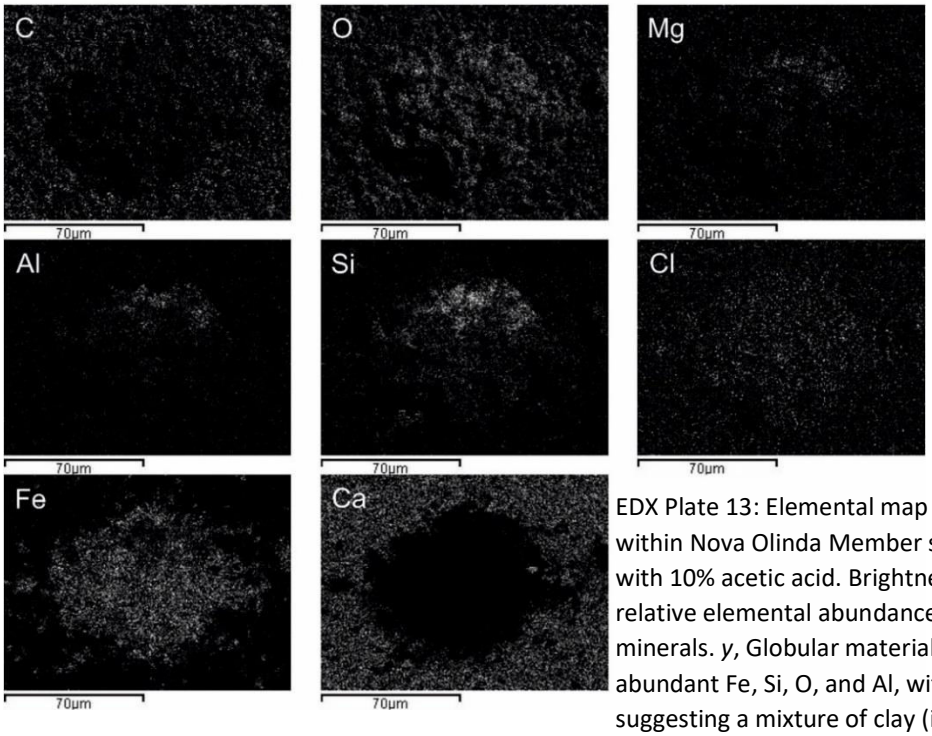




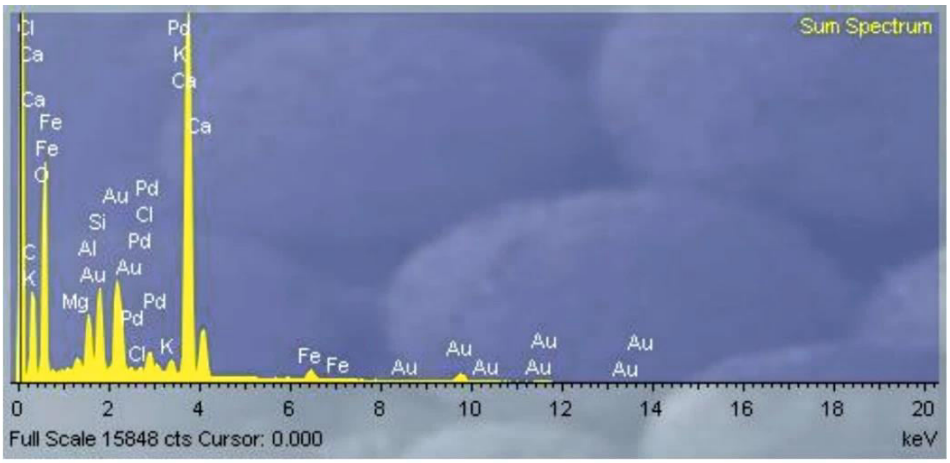
EDX Plate 12: Elemental map of single calcite rhombohedron from Nova Olinda Member sediment, etched with 10% acetic acid. Brightness corresponds to relative elemental abundance. Spectra reveal abundant Ca, O, and C, with trace Mg and Sr. EDX file: Project 2; Sample 2; Site of Interest 2. Kv = 14, WD = 12, I Probe = 90 pA. Scale bar = 7 µm. 12580 counts.

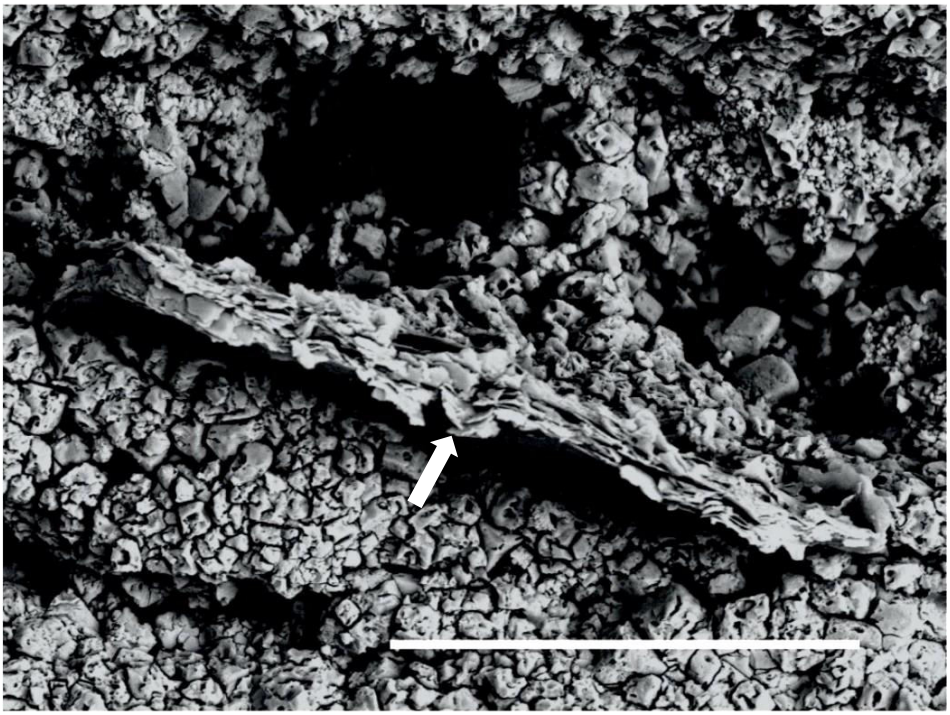


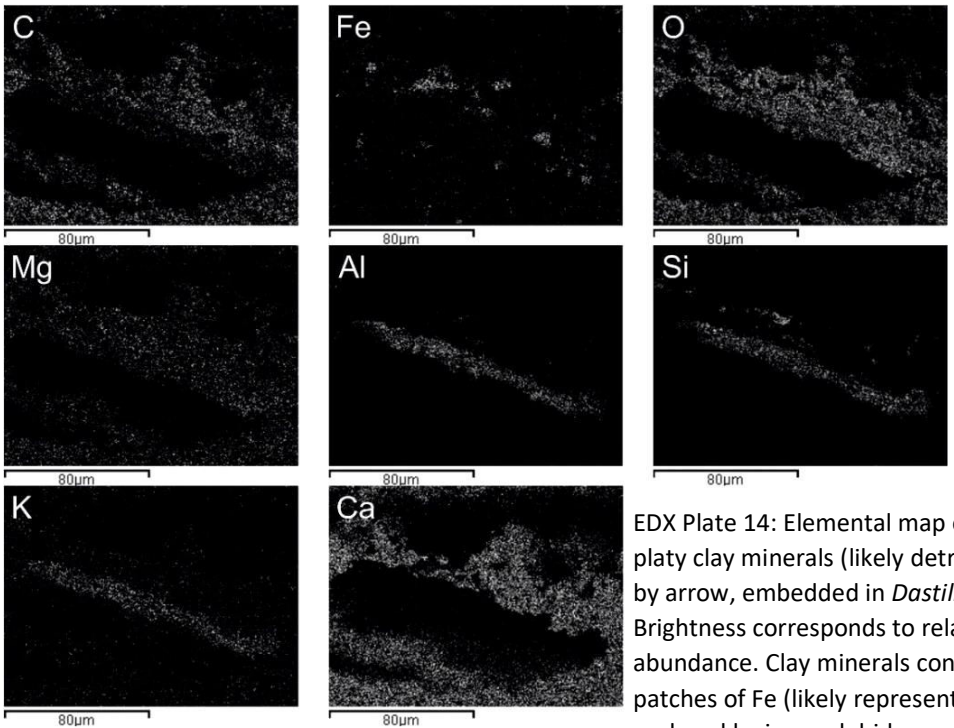




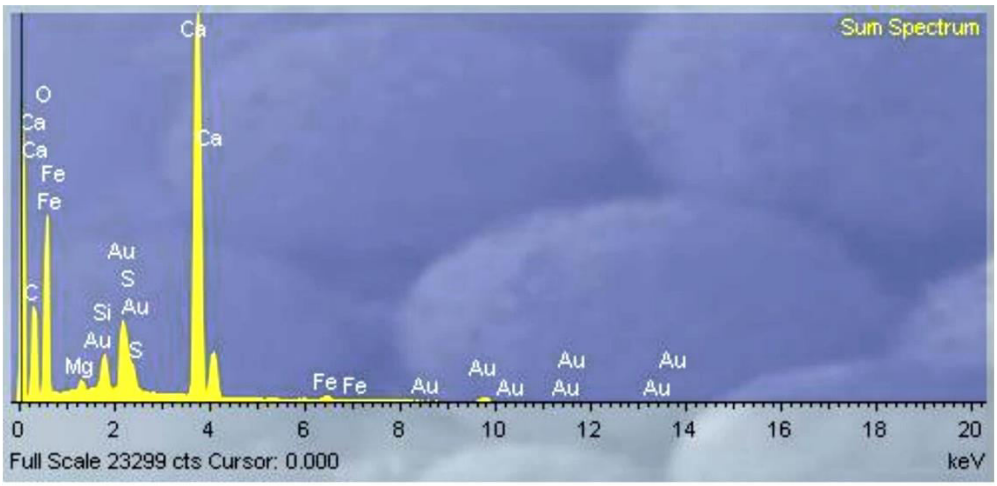
EDX Plate 13: Elemental map of *Dastilbe* coprolite within Nova Olinda Member sediment, etched with 10% acetic acid. Brightness corresponds to relative elemental abundance. *x*, Blade-like clay minerals. *y*, Globular material. Coprolites contain abundant Fe, Si, O, and Al, with rarer Mg suggesting a mixture of clay (illite) and weathered iron minerals (goethite). Ca, O, and C represent calcium carbonate matrix. Cl is likely a contaminant from etching. EDX file: Project 1; Sample 1; Site of Interest 6. Kv = 14, WD = 12, I Probe = 90 pA. 18646 counts. Scale bar = 70 µm.

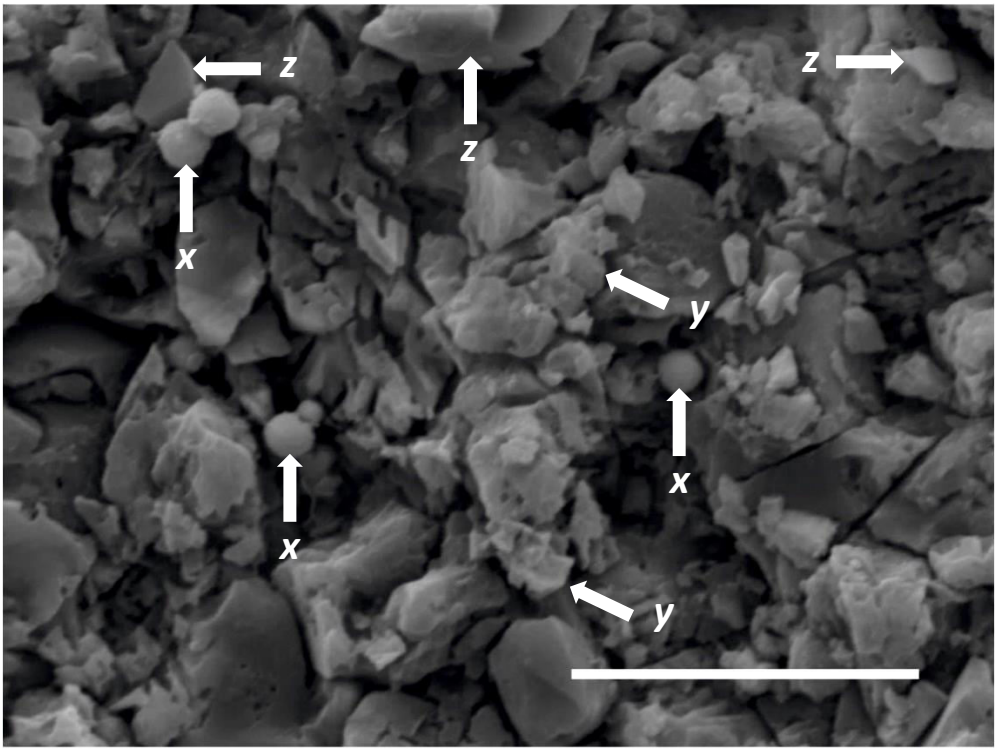


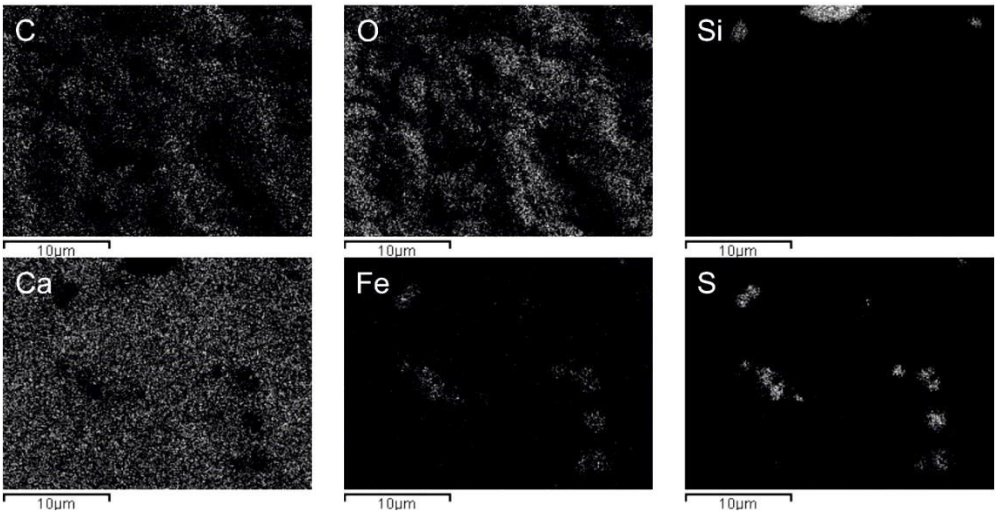




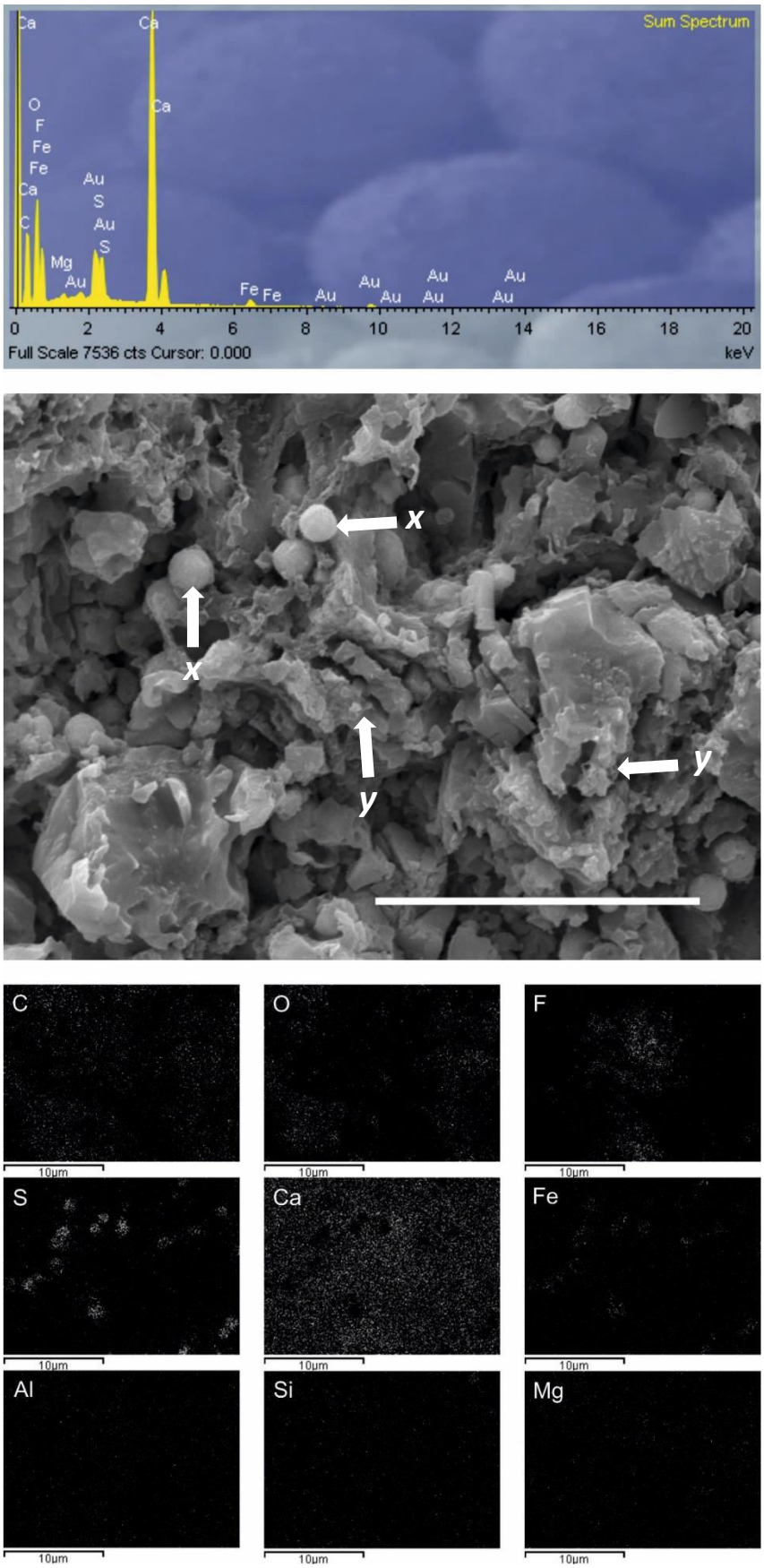
EDX Plate 14: Elemental map of large aggregate of platy clay minerals (likely detrital illite), highlighted by arrow, embedded in *Dastilbe* coprolite. Brightness corresponds to relative elemental abundance. Clay minerals consist of Al, Si, K, and patches of Fe (likely representing organic matter replaced by iron sulphides and later oxidised to goethite). Surrounding matrix consists of Ca, C, and O (calcium carbonate). EDX file: Project 1; Sample 1; Site of Interest 7. Kv = 14, WD = 12, I Probe = 90 pA. Scale bar = 80 µm. 15848 counts.



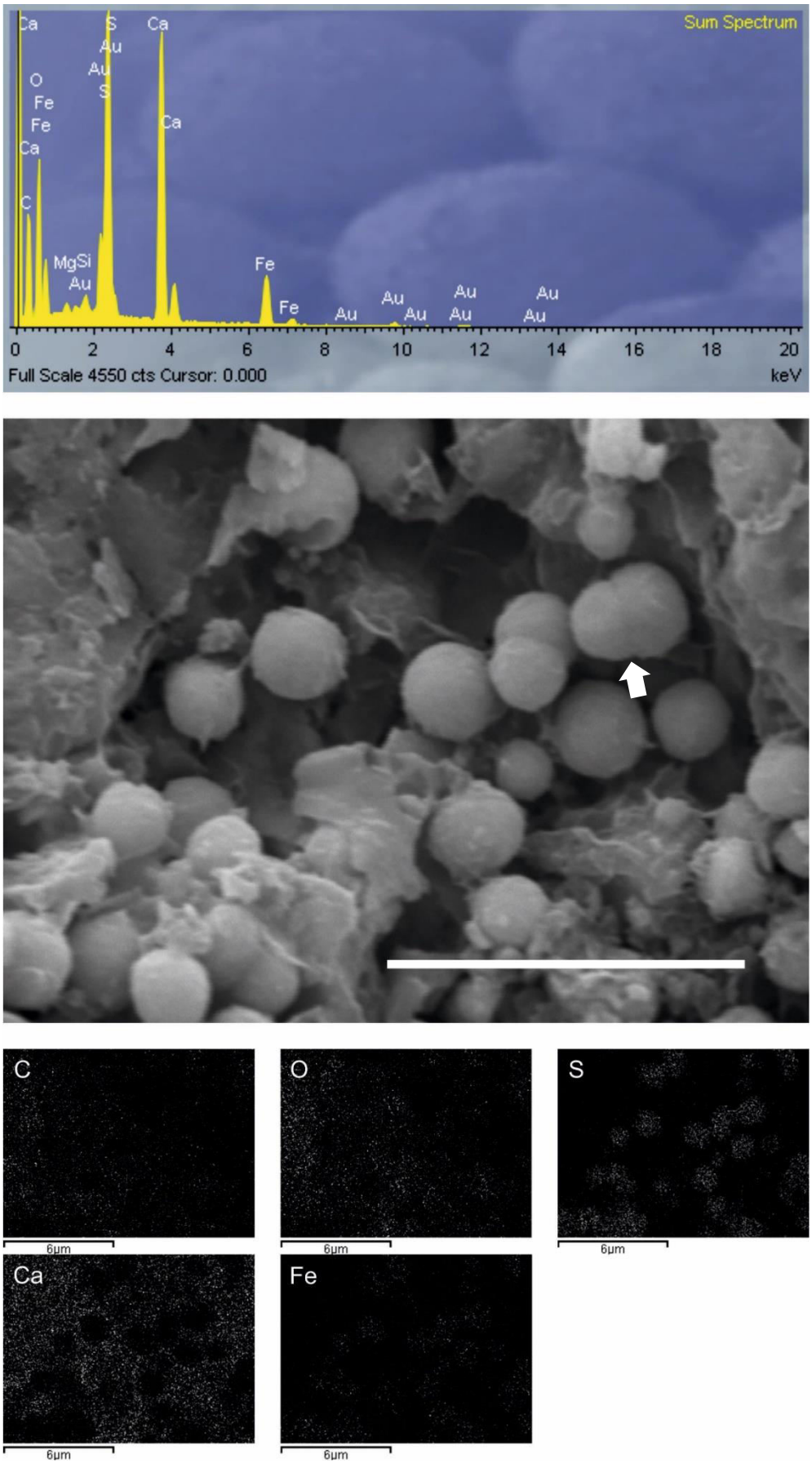




EDX Plate 15: Elemental map of 'unweathered' Nova Olinda Member sediment, containing spherical microfossils (*x*) and anhedral matrix grains (*y*). Brightness corresponds to relative elemental abundance. Microfossils consist of Fe and S (pyrite), whereas matrix is Ca, O, and C (calcium carbonate). Rare Si grains are also present (*z*). EDX file: Project 1; Sample 1; Site of Interest 14. Kv = 14, WD = 12, I Probe = 90 pA. Scale bar = 10 µm. 23299 counts.



EDX Plate 16. Elemental map of 'unweathered' matrix, containing spherical microfossils (*x*) and non-rhombohedral calcium carbonate (*y*). Brightness corresponds to relative elemental abundance. Aside from the Ca, O, and C in the matrix, F is also present. However, it could be a result of Fe peak overlap or contamination. Microfossils are replaced in Fe and S (pyrite). Trace Al, Si, and Mg are also present. EDX file: Project 2; Sample 1; Site of Interest 6. Kv = 14, WD = 12, I Probe = 90 pA. Scale bar = 10 µm. 7536 counts.



EDX Plate 17: Higher magnification elemental map of spherical microfossils in unweathered limestone matrix. Brightness corresponds to relative elemental abundance. Arrow highlights microfossils preserved during mitosis. Microfossils are composed of Fe and S (pyrite). Surrounding matrix is composed of Ca, O, and C (calcium carbonate). EDX file: Project 2; Sample 1; Site of Interest 2. Kv = 14, WD = 12, I Probe = 90 pA. Scale bar = 6 µm. 4550 counts.

8. 2. Published Papers

8. 2. 1. Barling *et al*., 2013

Cretaceous Research 45 (2013) 258–264

Contents lists available at SciVerse ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

A new parasitoid wasp (Hymenoptera: Chalcidoidea) from the Lower Cretaceous Crato Formation of Brazil: The first Mesozoic Pteromalidae

Nathan Barling [a], Sam W. Heads [b], David M. Martill [a,*]

[a] School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Road, Portsmouth PO1 3QL, UK
[b] Illinois Natural History Survey, University of Illinois at Urbana–Champaign, 1816 South Oak Street, Champaign, IL 61820, USA

ARTICLE INFO

Article history:
Received 12 February 2013
Accepted in revised form 14 May 2013
Available online 14 June 2013

Keywords:
Brazil
Crato Formation
Aptian
Hymenoptera
Chalcidoidea
Pteromalidae

ABSTRACT

A new genus and species of small (3.5 mm excluding ovipositor) parisitoid wasp is described from the Lower Cretaceous (Aptian) Crato Formation Lagerstätte of Brazil. *Parviformosus wohlrabeae* gen. et sp. nov. is known from a single female imago and is assigned to Pteromalidae. It is diagnosed by the robustness of the scutellum, the structure, size and positioning of the mesopleuron, the complexity of the propodeum–petiole junction and a posteriorly curved dorsal 'lip' on metasomal segment 4. At only 3.5 mm in length, *P. wohlrabeae* is the smallest fossil wasp from the Cretaceous of South America and the first Mesozoic representative of Pteromalidae.

1. Introduction

The Hymenoptera is one of the most diverse orders of insects. It is characterised by impoverished wing venation (most veins simple, excluding rare SC branching and RS forking (forewing), pterostigmal cell lost or thick, M fused with Cu sub-basally), the presence of hamuli on the hind wings, haplodiploid sex determination, and the presence of a protibial spur with velum (Rasnitsyn, 2002; Grimaldi and Engel, 2005). The hymenopteran fossil record is well-documented and data suggests that hymenopterans are a sister taxon to Panorpida and likely diverged during the Carboniferous (Beutel et al., 2011). Hymenoptera underwent a series of explosive adaptive radiations in the Jurassic, Cretaceous and Paleogene through which they attained their astonishing modern diversity (Riek, 1955; Rasnitsyn, 1969, 2002; Grimaldi and Engel, 2005; Michez et al., 2009). Their hyperdiversity is at least in part due to the evolution of microscopic parasitoid wasps, which constitute the vast majority of species in the order (Kristensen, 1981; Rasnitsyn, 2002; Grimaldi and Engel, 2005).

Here, we describe a new genus and species of tiny parasitoid wasp from the Lower Cretaceous (Aptian) Crato Formation, a heterolithic sequence of interbedded laminated limestones, sandstones, marls and clays within the Araripe Basin of north-east Brazil (Heimhofer and Martill, 2007; Heimhofer et al., 2010). At its base is the Nova Olinda Member, a fossil Konservat–Lagerstätte of Aptian age that is well known for the abundance and exceptional preservation of arthropods, vertebrates and flora (Grimaldi, 1990; Martill, 1993; Martill et al., 2007). This member crops out around the north-eastern to south-eastern edges of the Chapada do Araripe, a typical Brazilian tableland in the north-eastern state of Ceará. The outcrop between Nova Olinda, Santana do Cariri and Tatajuba is especially fossiliferous, yielding large numbers of insects (Martill, 1993; Heads et al., 2008).

2. Material and methods

Material. The specimen described here comprises a single adult female wasp preserved in right lateral aspect on a circular slab (diameter 32 mm, depth 10 mm) of fine-grained laminated limestone. It has been replaced by goethite, which may be a consequence of the weathering of an original iron sulphide replacing mineral (Menon and Martill, 2007). It is largely preserved in three-dimensions with only slight compactional damage, largely concentrated over the metathorax and propodeum. The specimen is deposited in the Staatliches Museum für Naturkunde, Stuttgart with accession number SMNS 70092.

Methods. The partially exposed insect was etched in 10% hydrochloric acid to reveal more anatomical detail but was not removed from the

* Corresponding author.
E-mail addresses: nathan.barling@port.ac.uk (N. Barling), swheads@illinois.edu (S.W. Heads), david.martill@port.ac.uk (D.M. Martill).

0195-6671/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.cretres.2013.05.001

slab. It was then mounted on an aluminium stub and sputter coated first with carbon and later with gold. The acid etching exposed considerable detail but left the specimen in an extremely fragile condition. Scanning electron microscopy was performed using a JEOL JSM–6100 SEM and images captured and analysed using PC digitiser and 'SemAfore' software. Image manipulation and construction of illustrations was performed using CorelDRAW X5 and Corel PaintShop Photo Pro X3. The fossil sustained some damage after initial examination on the SEM, losing aspects of the head, wings and some metasomal sterna. The fossil has also acquired some contamination on the remaining metasomal sterna (excluding propodeum) by carbon putty. Some images reproduced here were taken prior to damage and have been rescaled (using the same image ratio) and digitally rotated to allow a complete image to be formed of the original specimen. Images of the wing articulations before damage are not included due to severe charging. Note that due to the lack of diagnostic characters in the fossil comparable with modern chalcidoids, the diagnosis is, of necessity, descriptive rather than comparative. For chalcidoid morphology the reader is referred to Gibson (1997).

3. Systematic palaeontology

Hymenoptera Linnaeus, 1758
Apocrita Gerstaecker, 1867
Chalcidoidea Latreille, 1817
Pteromalidae Dalman, 1820
Genus *Parviformosus* gen. nov.

Derivation of name. Parvi, L. small; formos, L. beauty.

Diagnosis. Small (5.1 mm (3.5 mm excluding ovipositor)) pteromalid wasp. Ovipositor elongate and ventrally curved. Mesosoma robust with particularly robust scutellum and mesopleuron. Mesopleuron large, elongate and ventrally positioned, overlapping ventral portions of petiole. Complex propodeum–petiole junction with petiole extending into mesosoma and hooking under propodeum. Metasoma with well-defined segmentation. Metasomal segment 4 with posteriorly curved dorsal 'lip' approximately 100 μm in length anteroposteriorly and 75 μm in depth extending dorsoventrally over metasomal segment 5.

Remarks. Familial placement for *P. wohlrabeae* is extremely difficult due to the lack of three key taxonomic structures; the legs, wings and antennae. However, the shape of the posterior end of the gaster and the morphology of the ovipositor suggest that *P. wohlrabeae* belongs within Pteromalidae (J.-Y. Rasplus, pers. comm. 2012). The length and shape of the ovipositor, height relative to width of the gaster, short pronotum, shortened head and an apically expanding ovipositor sheath suggest that *P. wohlrabeae* may even be resolved to the Sycophaginae (R. Burks and M. Yoder, pers. comm. 2013). However, the character set for Sycophaginae is relatively poor and these morphological similarities are not sufficient to confirm placement. *P. wohlrabeae* is therefore, tentatively placed within Pteromalidae subfamily incertae sedis.

Parviformosus wohlrabeae sp. nov.
Figs. 1–3

Derivation of name. After Judith Wohlrabe who discovered the holotype while studying Crato Formation fossils at the University of Portsmouth.
Holotype. SMNS 700902.
Type locality. Most likely from an area of active quarrying between Santana do Cariri, Nova Olinda and Tatajuba, flanks of the Chapada do Araripe, Ceará, Brazil (precise quarry unknown).
Horizon. Nova Olinda Member, Crato Formation, Araripe Group. Early Cretaceous, Aptian.
Diagnosis. As for the genus, by monotypy.

3.1. Description

Incomplete adult female imago preserved in right lateral aspect, comprising head, mesosoma, metasoma and ovipositor (Figs. 1 and 2); body length 3.5 mm, total length including ovipositor 5.1 mm.

Head. The head of the specimen was severely damaged during transport. Most of the posteroventral half of the head was lost, leaving only an area representing the vertex, part of the eye and the clypeus/frons(?) (Fig. 3B). Much of the cuticle on the right lateral surface of the head is absent. It is approximately circular in outline, but slightly dorsoventrally compressed in lateral view. The entire head measures 900 μm anteroposteriorly and ~700 μm dorsoventrally. The eye is preserved in outline as a deep cavity within the head. The eye is large (approximately 40–45% of the head), anteriorly positioned and kidney–shaped. It measures 440 μm dorsoventrally and approximately 375 μm anteroposteriorly, however it may have been larger in life. Antennae are not preserved, however, a notch is present on the anterior surface where the antennae originally articulated. This notch is located ~200 μm down the anterior surface of the head, but lies above the base of the eye. Ocelli are not preserved. Only fragments of the mouthparts are preserved and accurate identification of individual elements is not possible. A semicircular cavity with a diameter of ~250 μm is present on the ventral surface of the head and probably represents the former position of the mouthparts (Fig. 3B). In the central portion of this cavity a bulbous appendage with fine setae represents the left labial palpus. It has a maximum visible diameter of ~20 μm and length of ~70 μm and the setae are sparse with a length of 4–9 μm (Fig. 3C). Some are pointed, but others appear rod–like and are truncated with sub–parallel margins.

Mesosoma. The total anteroposterior length of the mesosoma is 1.14 mm and the greatest dorsoventral depth is 0.92 mm (Fig. 3A). The boundary between the prothorax and the mesothorax is clearly discernible. The prothorax appears simple and takes up approximately one fifth of the whole mesosoma, measuring 875 μm dorsoventrally and 275 μm anteroposteriorly. Only patches of the mesothorax are preserved uncrushed. The boundary between the mesothorax and propodeum is partially crushed, but visible in the dorsal and ventral areas. Crushed areas have been filled with matrix, making some segment boundaries in these areas difficult to define. A group of sclerites are visible slightly anterior to the centre of the mesosoma. The dorsal portion may represent a lobe of the scutellum, but the sutures of the ventral areas are ill defined. It is robust and is emphasised by high relief. The prepectus is not visible, and is probably internalised, as in many pteromalid subfamilies. There are fragments of sclerites that probably represent the tegula, and a marginal lobe of the mesopleuron. Three wing fragments are visible. A wing fragment on the right lateral surface of the mesosoma appears to represent a forewing articulation while the more dorsally located fragments may represent a segment of hind wing. A large (~680 μm anteroposterior, ~225 μm dorsoventral) structure preserved on the ventral edge of the mesosoma may represent one of two structures. It could be an enlarged coxa that has been taphonomically displaced along the side of the mesosoma or, alternatively, a mesopleuron that has shifted ventrally in its anterior portion, giving a 'semi–detached' appearance. Due to the positioning, size and apparent fusion to the mesothorax, we consider it more likely that this structure is a mesopleuron. If this structure should prove to represent an enlarged coxa then the other leg element identifications are incorrect. Only a single fragmentary leg remains. The trochanter and possible femur are preserved semi-articulated in a folded position and crushed over the lateral surface

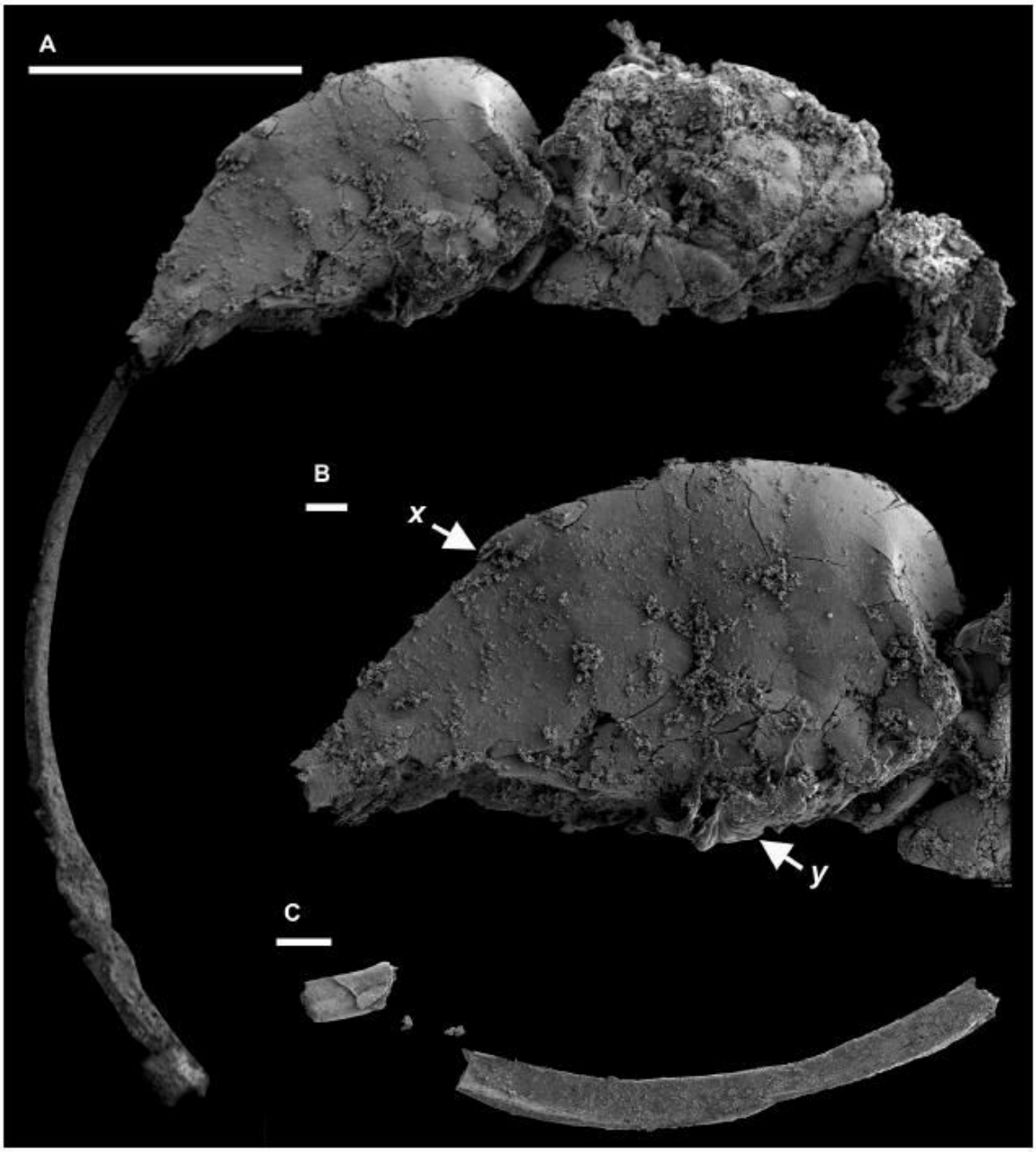


Fig. 1. A. Scanning electron micrograph of holotype of *Parviformosus wohlrabeae* sp. nov. (SMNS 70090/2) in right lateral view. Scale bar = 1 mm; B. Scanning electron micrograph of metasoma. *x*, highlights the dorsal 'lip' on metasomal segment 4. *y*, highlights contamination. Scale bar = 100 μm; C. scanning electron micrograph of the detached ovipositor found in residue. Scale bar = 200 μm.

of the mesopleuron. There is a patch of crushed cuticle below the femur that may represent the remnants of a coxa. The articulation of this limb is not discernible, however its positioning suggests it is right limb 2. The ventral portions of the limb and the mesopleuron are heavily compacted and are partially crushed together. The leg is short and narrow with a femur 300 μm long and 58 μm wide and a tibia ~325 μm long and ~30 μm wide. The distal end of the tibia is also heavily crushed, and may have extended further. The width of the mesothorax is estimated due to compaction, but the dorsal-most suture (to the propodeum) is still clearly visible. The

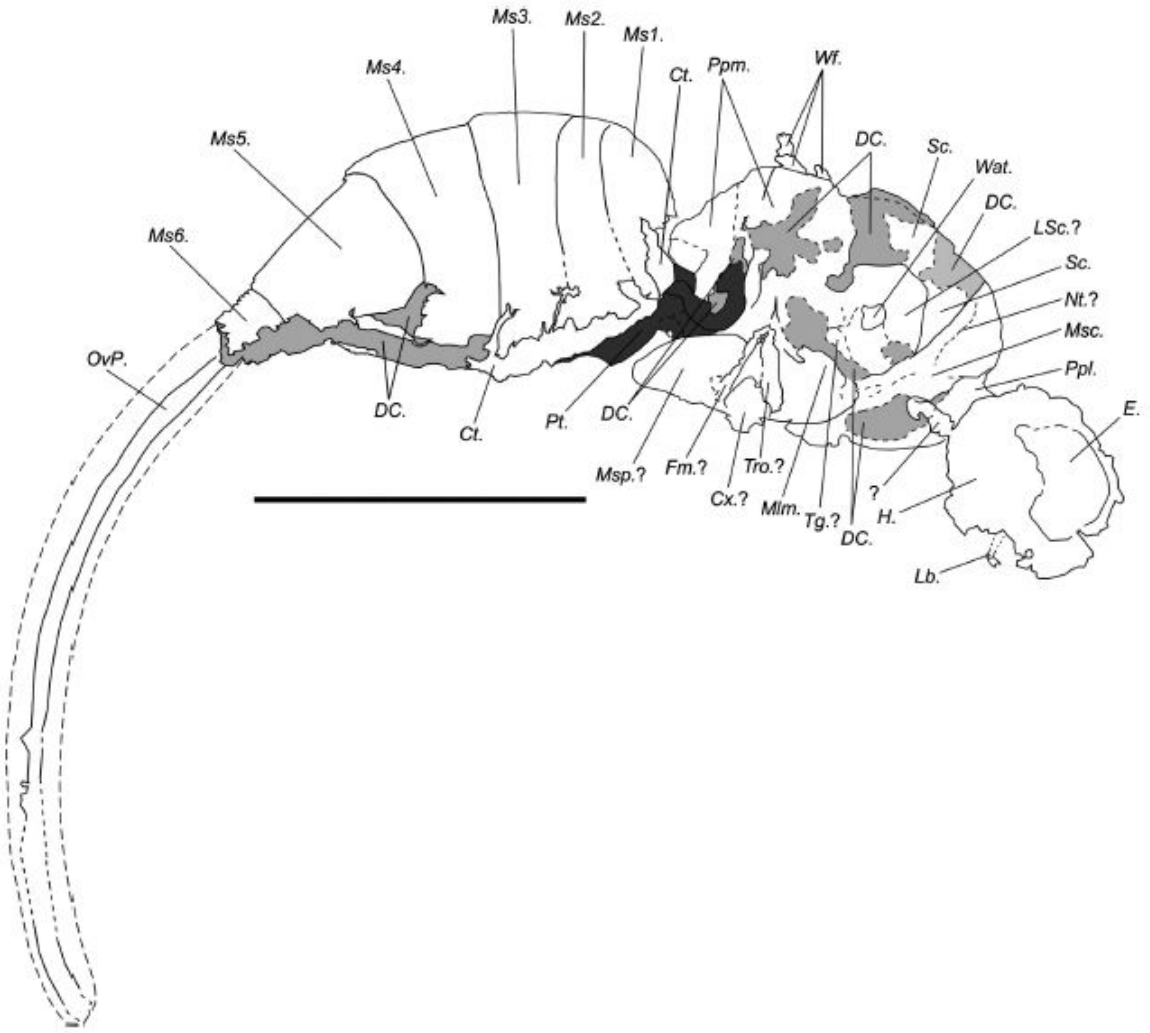


Fig. 2. Drawing of the holotype specimen of *Parviformosus wohlrabeae* sp. nov. (SMNS 700902) in right lateral view with reconstruction of head. Abbreviations: *Ct.*, contaminant; *Cx.?*, possible coxa; *DC.*, damaged cuticle; *E.*, eye; *H.*, head; *Tro.?*, possible trochanter; *Fm.?*, possible femur; *Lb.*, labial palpus; *Msp.?*, possible mesopleuron; *Mst.*, mesothorax; Ms_{1-6}, metasomal segments 1–6; *Mlm.*, marginal lobe of mesosoma; *MSc.*, mesoscutum; *Nt.?*, possible notaulus; *OvP.*, ovipositor; *Ppl.*, propleuron; *Ppm.*, propodeum; *Prt.*, prothorax; *Pt.*, petiole; *Sc.*, scutellum; *LSc.?*, possible lobe of scutellum; *Tg.?*, possible tegula; *Wat.*, wing articulation; *Wf.*, wing fragments. Dashed lines indicate inferred boundaries/edges of damage. Solid lines indicate clear boundaries/edges of damage. Dark grey area highlights petiole. Light grey area highlights damaged cuticle. Scale bar = 1 mm.

mesothorax is ~840 μm in length in the dorsal portion and ~400 μm in length in the central region. The propodeum appears reduced, however this may be an artefact of preservation. It is 360 μm in width and 565 μm in height. The petiole is short and the boundary between the petiole and the propodeum is ill defined.

Metasoma. The metasoma consists of seven clearly defined segments (petiole + 6 segments with ovipositor). The cuticle is somewhat fractured throughout the metasoma, with the least amount of damage occurring in metasomal terga 4 and 5. Metasomal sterna 1, 2 and 3 are overlain with a layer of carbon putty that conceals the cuticle (Fig. 1B). Metasomal sterna 4, 5 and 6 have been severely crushed and are only visible as flaked cuticle and impressions in the matrix. Separate sterna and terga are not distinguishable. Excluding the ovipositor and petiole, the metasoma is 1.6 mm in length with metasomal segments that increase in length posteriorly (excluding segment 6) from a 165 μm length of segment 1, to a 580 μm length of segment 5. Metasomal segment 6 is 150 μm in length. The entire metasoma is slightly recurved underneath the body in a typical 'wasp death position'. In terms of segment morphology, segments 1 and 2 are curved slightly anteriorly. Segment 3 is curved anteriorly on the anterior edge and curved posteriorly on the posterior edge. Segment 4 has a 100 μm long posteriorly curved dorsal 'lip' that retracts after 75 μm to a gentle dorsal curve (Fig. 1B). Segment 5 greatly decreases (from 580 μm to 250 μm) in dorsoventral height posteriorly. Segment 6 is 260 μm in length and 215 μm in height, but is heavily damaged and the hypopgyium is not preserved. A trace of the ovipositor is preserved on the slab as a raised ridge on the matrix. The ovipositor has fallen away and been transferred to another SEM

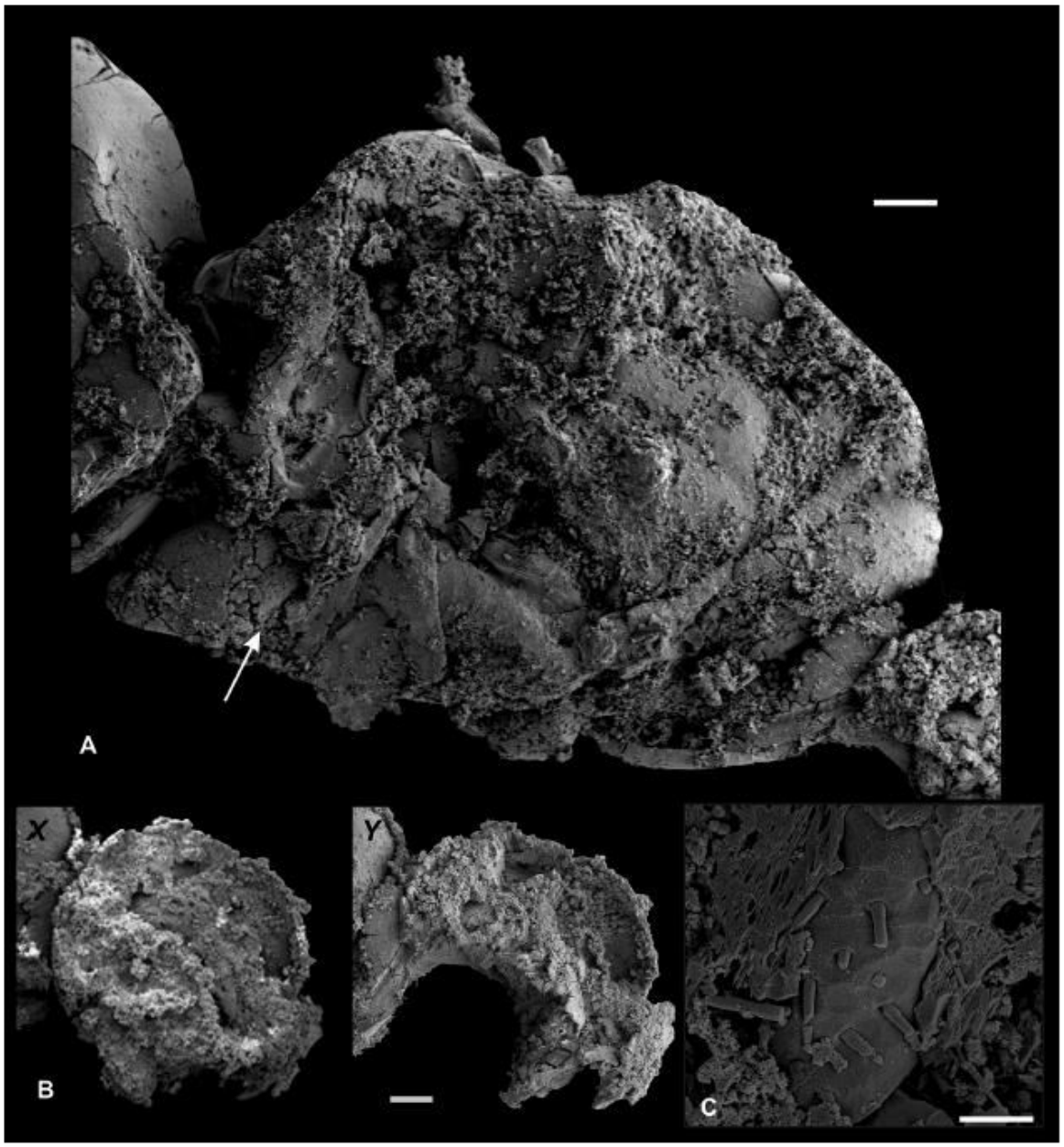


Fig. 3. A. Scanning electron micrograph of the mesosoma. Arrow indicates the structure identified as a mesopleuron, but may represent an enlarged coxa. Scale bar = 100 μm; B. Comparison between specimen head before and after damage. X, before damage (Image by Judith Wohlrabe). The semicircular cavity visible in the ventral area may represent aperture for mouth; Y, after damage, loss of majority of ventro-anterior sclerites. Scale bar = 100 μm; C. Left labial palpus cropping out from matrix and surrounding calcite crystals. Setae ranging in size from 4 to 9 μm are present sparsely along the entire length. Scale bar = 10 μm.

stub (Fig. 1C). Along the crest of the raised line, the matrix infrequently breaks to reveal needle–like crystals. These range in size from 3 to 8 μm in length and have a width of 0.5–1 μm. The total length of the ovipositor is ~2.2 mm. Identification of separate valves is not possible, but the preserved size of the ovipositor has been reconstructed using the SEM stub specimen.

4. Discussion

The holotype and only known specimen of *Parviformosus wohlrabeae*, at only 5.1 mm total length represents the smallest hymenopteran reported thus far from the Crato Formation. Although the incompleteness of the specimen renders its precise

taxonomic affinities obscure, the presence of the petiole indicates a position within Apocrita, while its diminutive size, elongate ovipositor and the configuration of the mesosoma all suggest placement in Chalcidoidea (Noyes, 2012). See *remarks* above for details on familial placement.

The fossil record of the chalcidoid wasps is extensive, with examples from the Middle Jurassic of China (Rasnitsyn and Zhang, 2010), Lower Cretaceous of Lebanon (Basibuyuk et al., 2002), the Late Jurassic/Early Cretaceous of Mongolia (Rasnitsyn et al., 2004) and the Caenozoic of Europe (Grissell, 1980; Skalski, 1988; Simutnik, 2002; Gibson, 2008; Heraty and Darling, 2009).

The fossil record of Pteromalidae is poor with examples recorded only from two amber sites: the Oligo–Miocene Dominican amber (Darling, 1996; Engel, 2009; Krogmann, 2013) and the Late Eocene Rovno amber locality of the Ukraine (Perkovsky et al., 2003). *Parviformosus wohlrabeae* represents the oldest member of this family, extending the lineage by 72 Ma from the Late Eocene back to the Latest Aptian (~110 Ma) (Batten, 2007). Moreover, the general habitus of *P. wohlrabeae* and the presence of apically expanded ovipositor sheaths suggests a possible affinity with Sycophaginae (R. Burks pers. comm.), a group of non-pollinating fig-associated pteromalids. If confirmed, such a placement would hint at the presence of figs (*Ficus*) in the Early Cretaceous, some 50–60 million years earlier than current estimates of their origin (Rønsted et al., 2005).

The Late Jurassic/Early Cretaceous chalcidoid *Khutelchalcis gobiensis* of Mongolia is putatively considered to be basal within the clade. It is a plesion with synapomorphies for Chalcidoidea + Serphitoidea (including Mymarommatidae) + Jurapriidae (Rasnitsyn et al., 2004). The occurrence of a pteromalid in the Cretaceous of Brazil could suggest that Pteromalidae may be a basal family within Chalcidoidea. However, a molecular study by Munro et al. (2011), considers Pteromalidae to be polyphyletic, and recognises a 'pteromaloid complex' (Cratominae + Miscogastrinae + Otitesellinae + Panstenoninae + Pteromalinae + Sycoecinae + Sycoryctinae) as relatively derived within Chalcidoidea.

Although *P. wohlrabeae* represents the smallest wasp described from the Crato Formation (the previous smallest being a mesoserphid at ~4 mm excluding ovipositor (Osten, 2007)), its size is by no means exceptional within the Pteromalidae. A smaller fossil specimen (*Spalangiopelta*) has been described from the Dominican amber with a total length of only 1.3 mm excluding ovipositor (Darling, 1996).

Previous accounts of hymenopterans from the Crato Formation have identified both Apocrita and Symphyta (Osten, 2007). The Symphyta (woodwasps and sawflies), an undoubtedly paraphyletic group (Grimaldi and Engel, 2005), are rare with only members of the Anaxylidae (2 species in the genus *Prosyntexis*) and Siricidae represented (Martins–Neto et al., 2007; Osten, 2007). In contrast, the Apocrita are significantly more diverse, with the spheciform genera *Cretosphex* and *Cretobestiola* (Angarosphecidae) being most common (Darling and Sharkey, 1990). There are two extinct families represented: Ephialtitidae (*Cratephialtites kourious*) and undescribed Mesoserphidae (Darling and Sharkey, 1990; Osten, 2007). Other families recorded include Ampulicidae; Sapygidae (Fedtschenkiinae); possible Formicidae (*Cariridris bipetiolata*), but quite possibly a spheciform apoid; Pompilidae; Proctotrupidae (*Protoprocto* sp.); Scoliidae (Archaeoscoliinae: *Cretoscolia brasiliensis*); Tiphiidae (Anthoboscinae: *Architiphia rasnitsyni*) and Vespidae (Eumenidae). There are also possible representatives of the Apidae and Mutillidae, though these are questionable (Darling and Sharkey, 1990; Osten et al., 2007).

Acknowledgements

We are very grateful to Jean-Yves Rasplus, Matt Yoder, John Heraty, Gary Gibson and Roger Burks for useful discussion concerning the familial and subfamilial placement of the specimen. Many thanks also are due to Annabelle Hayes and Mark Witton for assistance with illustrations and Christine Hughes, Tony Butcher and David Loydell for assistance with scanning electron microscopy. Thanks to Lars Krogmann (Stuttgart) for discussion on fossil chalcidoids. Financial support was provided by the School of Earth and Environmental Sciences, University of Portsmouth. Thanks to two anonymous referees for helpful comments on this paper and Dr André Nel for editorial assistance.

References

Basibuyuk, H.H., Rasnitsyn, A.P., Fitton, M.G., Quicke, D.L.J., 2002. The limits of the family Evaniidae (Insects: Hymenoptera) and a new genus from Lebanese Amber. Insect Systematics and Evolution 33, 23–34.

Batten, D.J., 2007. Spores and pollen from the Crato Formation: biostratigraphic and palaeoenvironmental implications. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato fossil beds of Brazil: window into an ancient world. Cambridge University Press, Cambridge, pp. 566–573.

Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof, B., Whiting, M.F., Vilhelmsen, L., 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. Cladistics 27, 341–355.

Dalman, J.W., 1820. Försök till Uppställning af Insekfamiljen Pteromalini, i synnerhet med åseende på de i Sverige funne arter. Kungliga Svenska Vetenskapsakademiens Handlingar 41, 340–385.

Darling, D.C., 1996. A new species of Spalangiopelta (Hymenoptera; Pteromalidae; Ceinae) from Dominican amber: phylogenetic and biogeographic implications. Journal of the Kansas Entomological Society 69 (suppl.), 248–259.

Darling, D.C., Sharkey, M.J., 1990. Order Hymenoptera. 123–153. In: Grimaldi, D.A. (Ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History, 195 pp.

Engel, M.S., 2009. The first fossil leptofoenine wasp (Hymenoptera: Pteromalidae): a new species of *Leptofoenus* in Miocene amber from the Dominican Republic. Zookeys 13, 57–66.

Gerstaecker, C.E.A., 1867. Beitrag zur Insekten–fauna von Zanzibar, nach dem wahrend der Expedition des Baron v.d. Decken gesammelten Material zusammengestellt. Archhiv für Naturgeschichte 33, 1–49.

Gibson, G.A.P., 1997. Chapter 2, Morphology and terminology. In: Gibson, G.A.P., Huber, J.T., Woolley, J.B. (Eds.), Annotated keys to the genera of nearctic Chalcidoidea (Hymenoptera). NRC Research Press, Ottawa, pp. 16–44.

Gibson, G.A.P., 2008. Description of *Leptoomus janzeni* gen. n. and sp. n. (Hymenoptera: Chalcidoidea) from Baltic amber, and discussion of its relationships and classification relative to Eupelmidae, Tanaostigmatidae and Encyrtidae. Zootaxa 1730, 1–26.

Grimaldi, D., 1990. Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History 195, 1–191.

Grimaldi, D., Engel, M.S., 2005. Evolution of the Insects. Cambridge University Press, Cambridge, 755 pp.

Grissell, E.E., 1980. New Torymidae from Tertiary amber of the Dominican–Republic and a world list of fossil Torymids (Hymenoptera, Chalcidoidea). Proceedings of the Entomological Society of Washington 82, 252–259.

Heads, S.W., Martill, D.M., Loveridge, R.F., 2008. Palaeoentomological paradise: the Cretaceous Crato Formation of Brazil. Antenna 32, 91–98.

Heimhofer, U., Martill, D.M., 2007. The sedimentology and depositional environment of the Crato Formation. 44–62. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. Cambridge University Press, United Kingdom, 625 pp.

Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios–Netto, A.M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North–eastern Brazil). Sedimentology 57, 677–694.

Heraty, J.M., Darling, D.C., 2009. Fossil Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea) from Baltic Amber. Zootaxa 2306, 1–16.

Kristensen, N.P., 1981. Phylogeny of insect orders. Annual Review of Entomology 26, 135–157.

Krogmann, L., 2013. First fossil record of cerocephaline wasps with a description of a new genus and species from Dominican amber (Hymenoptera: Chalcidoidea: Pteromalidae: Cerocephalinae). Historical Biology 25, 43–49.

Latreille, P.A., 1817. Les crustacés, les arachnides et les insectes. In: Cuvier, G. (Ed.), Le règne animal distribué d'après son organization: pour servir de base à l'histoire naturelle des animaux et d'introduction à anatomie comparée, first ed., vol. 3. Paris, 653 pp.

Linnaeus, C., 1758. Systema Naturae per Regna Tria Naturae: secundum classes, ordines, genera, species cum characteristibus, differentiis synonymis, locis. Tenth ed., revised. Laurentius Salvius, Holmiae, 824 pp.

Martill, D.M., 1993. Fossils of the Santana and Crato formations, Brazil. Field Guides to Fossils, 5. Palaeontological Association, London, 159 pp.

Martill, D.M., Bechly, G., Loveridge, R.F., 2007. The Crato Fossil Beds of Brazil: Window into an Ancient World. Cambridge University Press, New York, 625 pp.

Martins-Neto, R.G., Melo, A.C., Prezoto, F., 2007. A new species of wasp (symphyta, Sepulcidae) from the Santana Formation (Lower Cretaceous, Northeast Brazil). Journal of the Entomological Research Society 9, 1–6.
Menon, F., Martill, D.M., 2007. Taphonomy and preservation of Crato Formation arthropods, 79–96. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. Cambridge University Press, United Kingdom, 625 pp.
Michez, D., Meulemeester, T.D., Rasmont, P., Nel, A., Patiny, S., 2009. New fossil evidence of the early diversification of bees: *Paleohabropoda oudardi* from the French Paleocene (Hymenoptera, Apidae, Anthophorini). Zoological Scripta 38, 171–181.
Munro, J.B., Heraty, M., Burks, R.A., Hawks, D., Mottern, J., Cruaud, A., Rasplus, J.-Y., Jansta, P., 2011. A Molecular Phylogeny of the Chalcidoidea (Hymenoptera). PLoS One 6, 1–27.
Noyes, J.S., 2012. Universal Chalcidoidea Database. World Wide Web electronic publication. http://www.nhm.ac.uk/chalcidoids.
Osten, T., 2007. Hymenoptera: bees, wasps and ants. 350–365. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. Cambridge University Press, New York, 625 pp.
Perkovsky, E.E., Zosimovich, V.Y., Vlaskin, A.Y., 2003. Rovno amber fauna: a preliminary report. Acta Zoologica Cracoviensia 46, 423–430.
Rasnitsyn, A.P., 1969. Origin and evolution of lower Hymenoptera. Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR 123, 1–196. (In Russian).
Rasnitsyn, A.P., 2002. Order Hymenoptera Linné. 242–254. In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), History of Insects. Kluwer Academic Publishers, Dordrecht, 517 pp.
Rasnitsyn, A.P., Basibuyuk, H.H., Quicke, D.L.J., 2004. A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. Insect Systematics and Evolution 35, 123–135.
Rasnitsyn, A.P., Zhang, Z., 2010. Early Evolution of Apocrita (Insecta, Hymenoptera) as Indicated by New Findings in the Middle Jurassic of Daohugou, Northeast China. Acta Geologica Sinca – English Edition 84, 834–873.
Riek, E.E., 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. Australian Journal of Zoology 3, 654–691.
Ranstedt, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, V., 2005. 60 million years of co-divergence in the fig-wasp symbiosis. Proceedings of the Royal Society B, Biological Sciences 272, 2593–2599.
Simutnik, S.A., 2002. A new genus of encyrtid wasp (Hymenoptera, Chalcidoidea, Encyrtidae) from Late Eocene Rovno amber (Ukraine). Vestnik Zoologii 36, 99–102.
Skalski, A.W., 1988. A new fossil trichogrammatid from the Sicilian amber Hymenoptera Chalcidoidea Trichogrammatidae. Fragmenta Entomologica 21, 111–116.

8. 2. 2. Barling *et al*., 2015

Cretaceous Research 52 (2015) 605–622

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil

Nathan Barling [a, *], David M. Martill [a], Sam W. Heads [b], Florence Gallien [a]

[a] School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK
[b] Illinois Natural History Survey, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, IL 61820, USA

ARTICLE INFO

Article history:
Received 27 January 2014
Accepted in revised form 7 May 2014
Available online 7 June 2014

Keywords:
Insect
Taphonomy
Early Cretaceous
Aptian
Crato Formation
Brazil

ABSTRACT

Fossil insects from the Lower Cretaceous (Aptian) Crato Formation of north-east Brazil are preserved as goethite replacements in laminated limestones of lacustro-lagoonal origin. They display remarkable degrees of morphological detail down to the macromolecular level in some examples. We document the fidelity of preservation and reveal an astonishing variety of morphological detail comparable in some instances with that found in amber inclusions.

1. Introduction

The Crato Formation represents one of the richest Cretaceous fossil Konservat-*Lagerstätten* in the world, yielding an exceptionally well preserved and diverse palaeobiota (Martill et al., 2007a). Although the formation yields abundant vertebrates, including rare dinosaurs, crocodiles and abundant pterosaurs and fishes, it also preserves diverse crustaceans, arachnids, and plants. However, it is perhaps most famous for the astonishing diversity and remarkable preservation of its fossil insects (Grimaldi, 1990; Martill et al., 2007a; Heads et al., 2008).

The insects of the Crato Formation are extremely important for our understanding of insect evolution for a number of reasons. In particular, their Late Aptian (Early Cretaceous) age coincides with a time at which angiosperms were diversifying (Hochuli et al., 2006) and developing the complex relationships with insects that so strongly influenced their subsequent evolution and characterizes their biology to this day (Ehrlich and Raven, 1964; Labandeira et al., 1994; Hu et al., 2008). In addition, with other fossils, the overall assemblage provides a unique glimpse of an ancient biota that existed at this time. Understanding the development of these relationships is vital to understanding not only the Mesozoic record of plant-insect interactions, but ultimately the structure and stability of modern terrestrial ecosystems. Furthermore, the Crato Formation is the only well-documented insect Lagerstätte of its age from Gondwana, representing an extremely valuable source of data concerning diversification and austral biogeography during one of the most complex continent scale vicariance events in insect history (Amedegnato, 1993; Heads, 2008).

The Crato Formation boasts an extremely high diversity and abundance of fossil insects, with at least 18 different orders represented and over 350 named species described to date. In addition, many families are represented by as yet unnamed taxa (Bechly, 2007, 2010; Staniczek et al., 2011). These fossils are preserved exceptionally well, with details visible at the micrometer and sometimes nanometre scale. Despite this, little is known about the processes of preservation, and the high quality of preservation of Crato insects is often under-reported in species descriptions.

Here we illustrate the exceptional quality of preservation displayed by the Crato Formation insects, describe the preservational fabrics, and suggest possible mechanisms that resulted in such preservation.

2. Locality and geological background

The Crato Formation crops out on the northern flanks of the Chapada do Araripe, a ~150 km east-west plateau, located on the borders of the north-east Brazilian states of Ceará, Pernambuco and

* Corresponding author.
E-mail addresses: nathan.barling@port.ac.uk (N. Barling), david.martill@port.ac.uk (D.M. Martill), swheads@illinois.edu (S.W. Heads), fgallien@hotmail.com (F. Gallien).

http://dx.doi.org/10.1016/j.cretres.2014.05.007
0195-6671/

Piauí (Fig. 1). The formation is mined extensively for commercial purposes in the vicinity of Santana do Cariri and Nova Olinda in Ceará, and it is from these areas that most fossils are obtained.

The formation itself is a ~60 m thick heterolithic sequence dominated in its middle part by laminated limestones, interbedded at their base with claystones, siltstones, and sandstones (Martill and Heimhofer, 2007). The formation consists of four distinct members, though only the lowest Nova Olinda Member yields exceptionally preserved fossils (Martill et al., 2007a). The Nova Olinda Member is a finely laminated limestone, formed authigenically by algae (Heimhofer et al., 2010). The laminae average 1 mm in thickness, alternating between light and dark-blue grey colours when freshly exposed and likely represent wet and dry seasonal cycles (Heimhofer et al., 2010). The depositional environment represented is that of a restricted lacustrine or lagoonal setting with a stratified water column. The upper water column was likely brackish and well oxygenated, whereas the lower column and lake/lagoon bottom was hypersaline and anoxic (Heimhofer et al., 2010). More detailed geological and sedimentological information can be found in Martill et al. (2007a) and Heimhofer et al. (2010).

3. Materials and methods

3.1. Collection

Specimens used in this research were donated to the University of Portsmouth by Judith Wohlrabe in 2011. They were obtained via a German fossil dealer and, somewhat ironically, given to Ms. Wohlrabe on account of their perceived poor quality and lack of aesthetic appeal. They were made available to the senior author and assigned new research numbers. Some of the specimens were subjected to destructive analysis and no longer survive (NBRL034 and FLO27), but photographs of them are included within the text nonetheless.

The collection is dominated by specimens of Blattodea (cockroaches), but also includes examples of Orthoptera (grasshoppers and crickets), Odonata (dragon- and damselflies), Hymenoptera (wasps), Hemiptera (true bugs), Diptera (flies), Neuroptera (lacewings and antlions) and Coleoptera (beetles).

Ninety two specimens were studied for this analysis. The majority of unprepared specimens were stored in sealed plastic containers and specimens prepared for SEM viewing were either stored in desiccators or secured by foam in sealed plastic containers with cobalt chloride granules.

3.2. Preparation techniques

Many Crato Formation insects are damaged by the quarrymen collectors who routinely rub the specimens to 'clean' them, often severely damaging the exposed surface. Consequently, all specimens were initially examined under a light microscope for subjective evaluations of their quality of preservation. The unexposed surface of the insect adjacent to the limestone usually remains pristine. To examine the unadulterated surface we transferred the specimens to resin blocks (Walton, 1923; Cridland and Williams, 1966; Escapa et al., 2010).

Several techniques were used to prepare the insect specimens. In some cases, a simple wash with water was sufficient to reveal details of the specimen for light microscopy. In other examples excess matrix was removed using fine needles under the microscope. For examination by electron microscopy we employed three techniques: hydrochloric or acetic acid wash to expose the specimen on the limestone slab; acid transfer onto resin blocks, or in some cases the complete removal of the fossil from the matrix using acids. Acid etching and complete digestion of matrix were done with 10% acetic acid or 5–10% hydrochloric acid, depending on the degree of weathering.

Photomicrographs were taken using an Olympus SZ-STS light microscope with a mounted Nikon DS-Fi1 camera and a Nikon Digital Sight attachment. Images were saved as JPEG or Tiff files.

Two scanning electron microscopes were used for this project: a JEOL JSM-6100 Scanning Microscope and a JEOL JSM-6060LV Scanning Electron Microscope. Specimens were prepared by mounting on aluminium stubs with a black carbon pad or carbon cement (Conductive Carbon Cement Leit-C). They were then cleaned with a soft squeeze blower and/or acetone to remove any grease and dust. Any remaining gaps between the specimen and the stub were sealed with additional carbon cement and finally they were sputter coated with a gold-palladium alloy using a Quorum Q150RES Sputter Coater. Images were captured and analysed using PC digitiser and 'SemAfore' software. Image manipulation and construction of illustrations was performed using CorelDRAW X5 and Corel Paint-Shop Photo Pro X3.

Fig. 1. Locality map showing the outcrop of the Crato Formation on the flanks of the Chapada do Araripe, north-east Brazil. The two most important localities for fossil insects are indicated: Santana do Cariri and Nova Olinda. The town of Crato is also indicated.

3.3. Exceptional preservation

Fossils are widely considered to be exceptionally preserved if they preserve volatile nonmineralizing tissues (soft tissues) that are readily degraded by bacteria (Allison and Briggs, 1991a, 1991b, 1993). As insect fossils are entirely 'soft tissue', their preservation in any manner is often regarded as exceptional. However, this definition allows for no clarification between insect fossils of varied preservation. We consider a specimen to be exceptionally well preserved if it displays fragile morphological structures (e.g. scales, setae, sulci, pits, tubercles, carinae), detail at the cellular level or smaller and perhaps the preservation of colour or colour patterning. This can include preservation of fabrics brought about by decomposition and other taphonomic processes. Many of the Crato Formation insects display all or most of these features. The preservation of colour may reflect only the colour pattern, but structural colour does occur (Bechly, 2007).

Many Crato Formation insect fossils appear extremely well preserved in hand specimen and are often complete with appendages intact (Fig. 2, A and B). As might be expected from a Konservat Lagerstätte, these specimens often show a remarkable amount of detail preserved at the micro- and nanometer scale (See

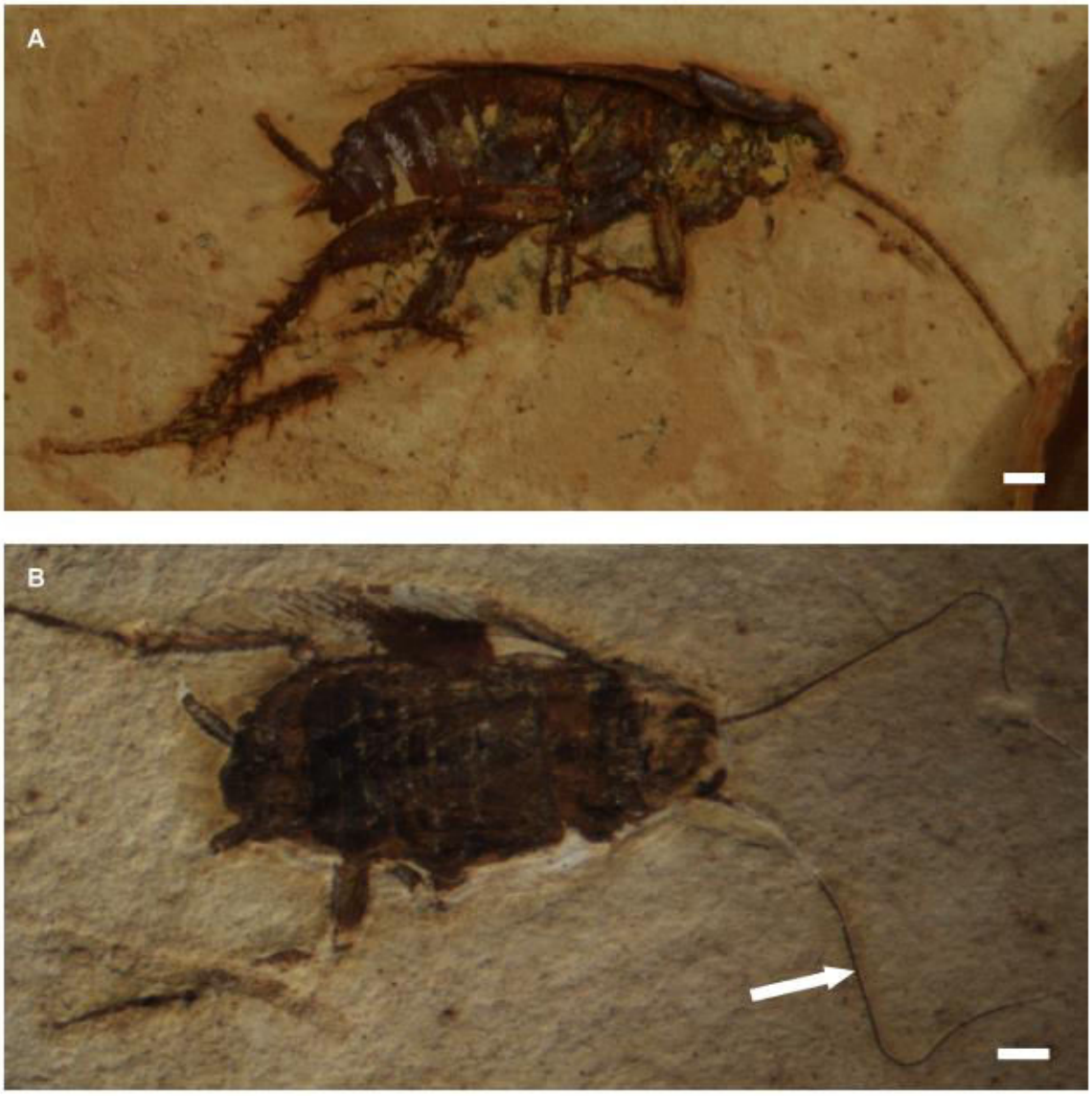


Fig. 2. Photomicrographs of Crato Formation cockroaches A. Specimen showing remarkable completeness (NBRL054). Scale bar = 1 mm; B. Specimen (NBRL034) with arrow highlighting extremely fragile yet completely preserved antenna. Scale bar = 1 mm.

Sections 4.3 and 4.4). Unusually, many specimens preserved as fragmentary remains or isolated segments still retain this remarkable micro- and nanometer scale preservation. Although many of these fossils may appear poorly preserved in hand specimen (as they are fragmentary), closer examination shows identical fidelity to intact specimens. This suggests that damage to the Crato Formation insect fossils is probably not caused by incomplete fossilisation or diagenetic alteration, but rather is the result of *in-vivo* damage (perhaps attributable to predation, intra species competition, or sexual activity) or post-mortem damage, caused by prolonged decay or scavenging prior to burial. As such, we do not consider these fragmentary specimens to be poorly preserved, but rather that they reflect the taphonomic state of the specimen upon arrival to the site of burial.

There are, of course, exceptions to this and some specimens that appear complete and well preserved in hand specimen reveal little to no morphological detail at the micro- and nanometer scale (Fig. 3, A and B). This 'poor' preservation appears to be less common and may be restricted to specific laminae.

In a similar vein, many Crato Formation insects appear to be flattened on the bedding plane surface. However, in reality they are mostly restricted to a single lamina and may exhibit varying degrees of three-dimensionality within the lamina. Thus, the insects mainly lie within a thin lamina, and not at the interface between laminae, i.e. not on a bedding plane. Indeed, some appendages, especially limbs, may lie at a high angle to the plane of bedding (Fig. 4, A), suggesting submersion in somewhat soupy substrates (*sensu* Martill, 1997).

In addition to the preservation of the exoskeleton, we have discovered several specimens that have internal, non-sclerotized anatomy preserved. In particular we have noted the preservation of muscles and genitalia (see below) beneath preserved cutide where the specimens have been damaged to expose internal surfaces.

4. Results

The preservation of Crato Formation insects is truly exceptional for non-amber-hosted fossil insects. Below we present descriptions and images of the preservation at various levels of magnification documenting macro-, micro- and ultrastructural detail. Our studies show that the quality of preservation can be variable between specimens or even within a single specimen and is in part controlled by the taphonomic state of the specimen at its time of burial/diagenesis.

4.1. Fossilization

The Crato Formation fossils are most commonly encountered as goethite (limonite) replacements of original cuticle. This appears as an orange to brown seemingly amorphous material that is friable and can be easily damaged by touching the specimen. This style of preservation is mostly encountered in the weathered, buff coloured limestones (Menon and Martill, 2007). In unweathered (blue/grey) Crato Formation limestone the fossils are usually black, and more delicate. The goethite specimens are weathered versions of the blue/grey fossils, in which the original replacement mineral, probably an iron sulphide phase (Fig. 5, A) with carbonaceous material, has been oxidised *in situ* over a prolonged period, perhaps in the last few thousand years. There are examples of specimens that appear to be a halfway stage between these two preservation states.

Non-cuticular soft tissues, such as muscles, are preserved as replacements by apatite minerals (Menon and Martill, 2007). Possible biofilms surrounding some Crato Formation insects are preserved as silica halos (Fig. 6).

4.2. Macro-structure preservation

In both hand specimen and when viewed under a light microscope, it becomes immediately apparent that the Crato Formation insects display a level of preservation worthy of detailed study, and provide a degree of morphological detail rarely seen in fossil insects preserved in limestones or clastic lithologies. Crato insects are commonly complete (abdomen, thorax, head, appendages and wings articulated), often uncompacted, with significant 3-dimensionality (Fig. 4, A and B) and commonly reveal colour patterns and iridescence (Fig. 7, A–D; also see Heads et al., 2005). Internal soft

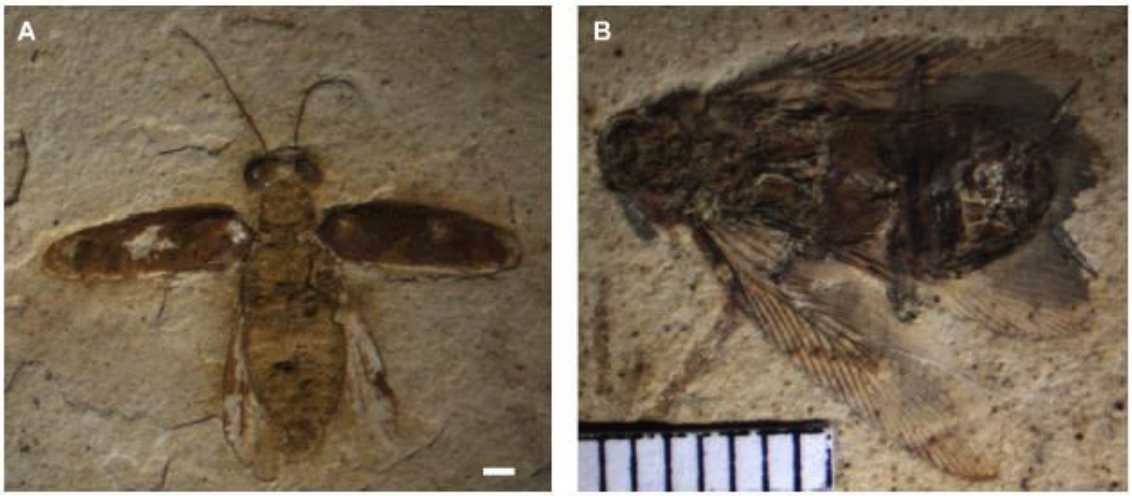


Fig. 3. Photomicrographs of Crato Formation cockroaches. A. Complete specimen of *Ponopterix axelrodi* (NBRI.025) with indistinct internal contents (likely the result of collector damage). Scale bar = 1 mm; B. Complete specimen of *Mesoblattina limai* (NBRI.027) appearing to be well preserved, but showed no detail under SEM. Scale bar = 1 mm.

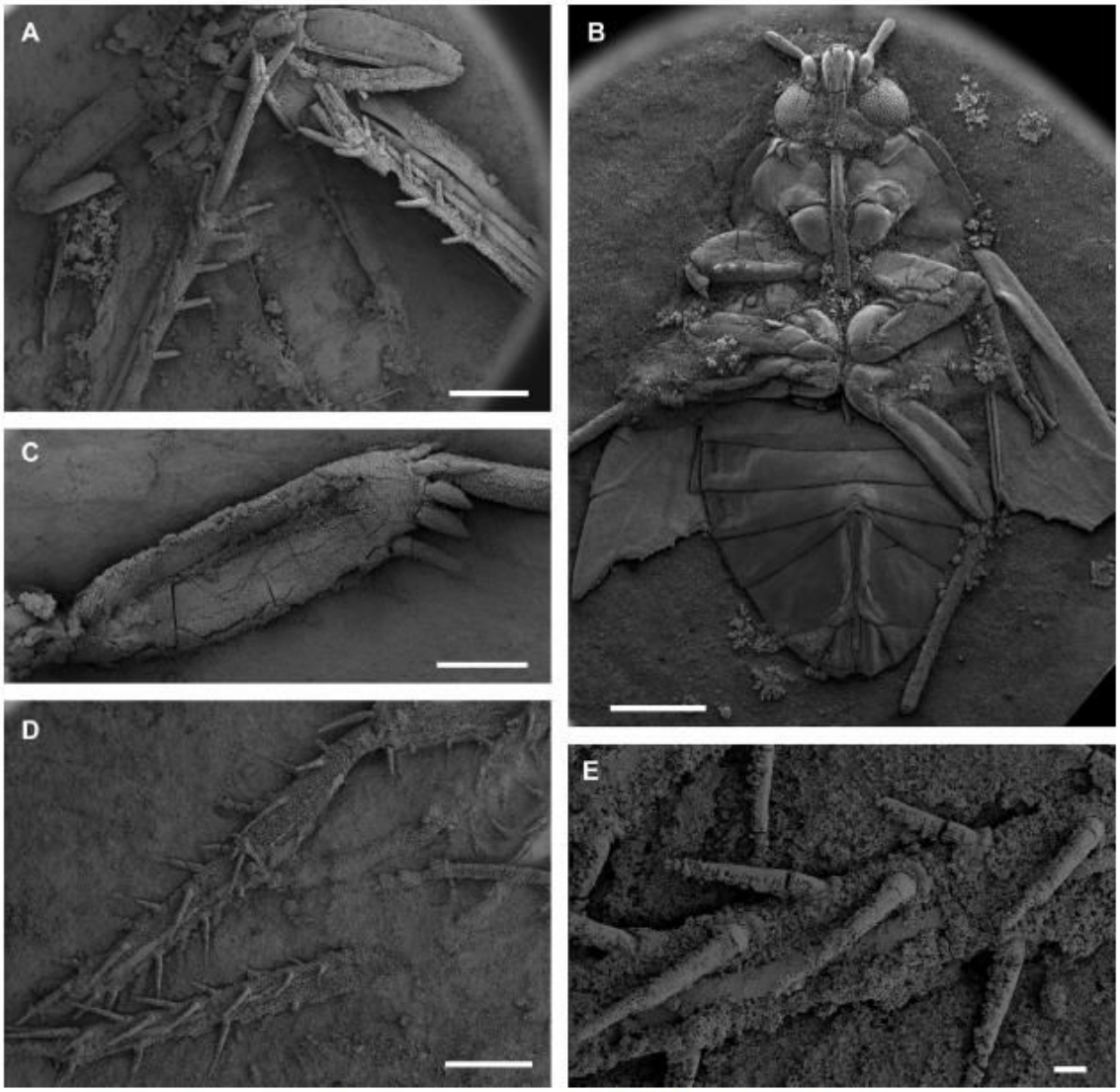


Fig. 4. Scanning electron micrographs of Crato Formation insects revealing 3D preservation with high relief. A. Indeterminate grasshopper (NBRL059) showing intact legs at a high angle to sedimentary laminae. Scale bar = 1 mm; B. Indeterminate true bug (FL015) showing 'flattened' three-dimensionality and high fidelity of preservation. Scale bar = 1 mm; C. Gryllotalpid grasshopper *Cratotettrapinus fossorius* (NBRL055) with intact cuticular structures (spurs) on mesotibia. Scale bar = 1 mm; D. Indeterminate cockroach (NBRL054) with numerous leg spurs at a varying angles to sedimentary laminae. Scale bar = 1 mm; E. Higher magnification image of D, highlighting spurs. Scale bar = 100 μm.

tissues are not necessarily obvious in hand specimens unless the splitting plane has passed through, rather than around the margins of the specimen. Most Crato Formation insects reveal details of the head and head appendages (preservation of the antennae, eyes and mouth parts is common), the thorax with wings or elytra (usually displaying well defined venation or ornamentation), thoracic appendages with spurs, spines and larger setae, and abdominal segmentation and structures associated with the terminalia such as cerci, ovipositor, caudal gills and other filaments. These can be preserved intact and perpendicular to bedding (Fig. 4, C–E), while other structures are so well preserved they are nearly indistinguishable from modern counterparts (Fig. 7, E and F).

4.3. Micro-structure preservation

Hear we illustrate structures that are only clearly visible under light and electron scanning microscopy (<~250 μm). The finer details visible at higher magnification demonstrate that the fidelity of preservation of the Crato Formation insects is far better than might be expected from fossils preserved as oxidised replacements. Fine details of exoskeletal structures include individual cuticular scales (Fig. 8, A–H), setae and other sensilla (Fig. 9, A–H), ommatidia (Fig. 10, A–H) and cuticular surface structures (Fig. 4, D and E) are preserved intact and are often numerous. Softer tissues like muscle fibres, genitalia and gill structures can be preserved in

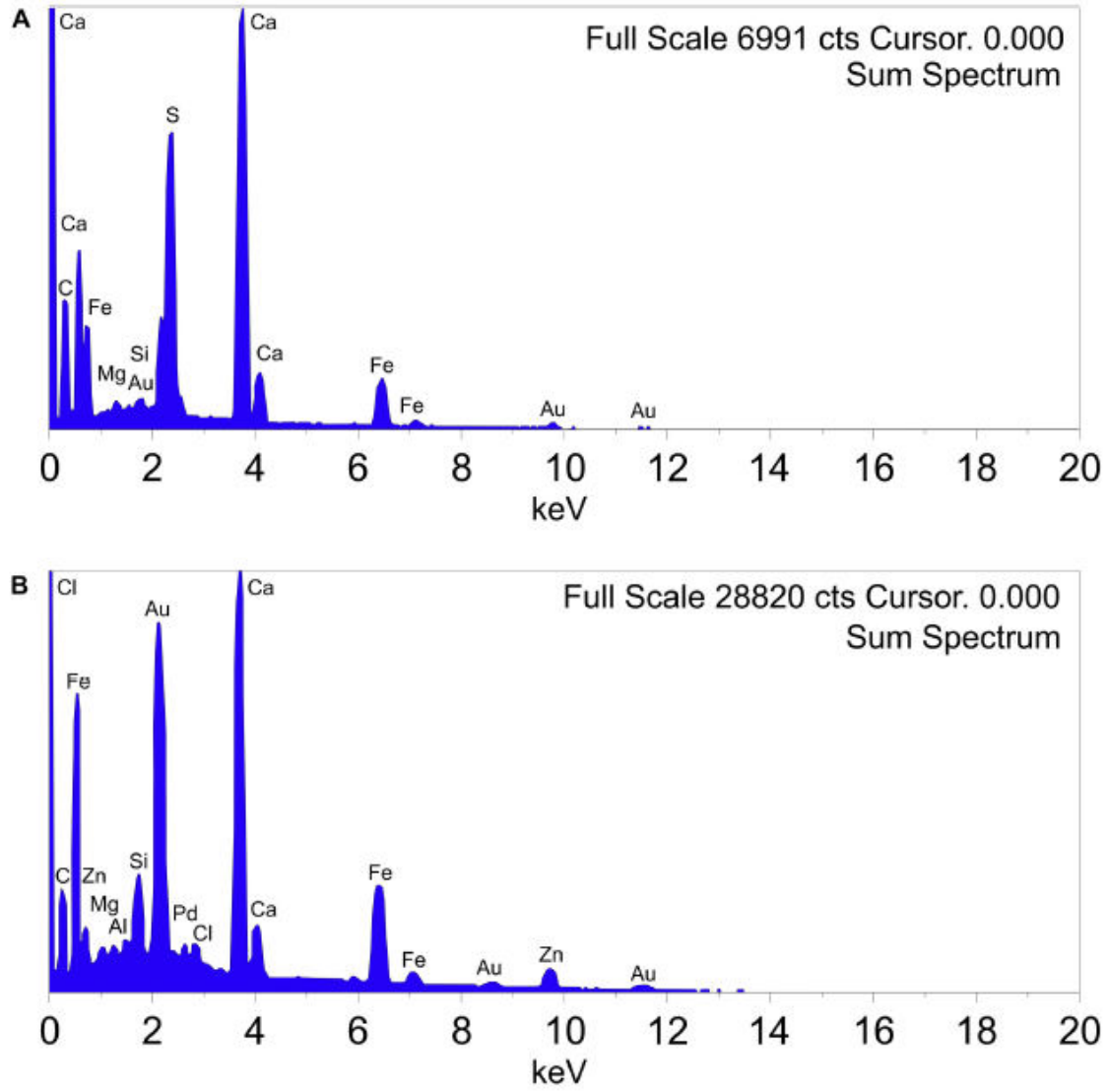


Fig. 5. A. Results of an EDX analysis of unweathered 'blue' Crato limestone (offcuts). The presence of a sulphur peak along with an iron peak indicates that the iron in present in a sulphide phase. Peaks of gold, palladium and carbon are the result of coating for SEM analysis; B. Results of an EDX analysis of indeterminate true bug (FLO15) (See Fig 4. B.). The presence of Cl likely represents contamination from washing (from previous handling, as all specimens in this project were cleaned with deionised water). The lack of a sulphur peak rules out the presence of pyrite as the preserving mineral for these specimens. There is a direct correlation between visible cuticle and iron peaks, indicating that the insects are preserved in an iron oxide or hydroxide (supported by the 'rusty' colour of the fossils). Calcium is restricted to the surrounding matrix. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

phosphate and may also display high fidelity (Fig. 11, A–F; Fig. 12, A–C) despite their expected lower preservation potential (Briggs et al., 1993).

4.4. Cellular and ultrastructure

Here we consider structure at the cellular and sub cellular (ultrastructural) level. It refers to the finest details seen within the cuticle or other soft tissues, including muscle fibres, cuticular laminae and micro-papillae. At high magnifications a number of distinctive features are apparent on cuticular surfaces, some of which have a regular appearance and resemble biogenic features that are part of the original cuticle (Fig. 13, A). In general the cuticle appears massive in cross section with internal laminae only rarely visible (Fig. 13, F), however cutting and polishing a section of cuticle may reveal more detail. In some cases fabrics found within the cuticle at high magnification may represent the morphology of the preserving minerals, rather than the ultrastructure of the insect (Fig. 14, A and E). Frequently seen ultrastructures within the cuticle include hollow spherical or semi-spherical bodies somewhat

Fig. 6. Microphotograph of a Gryllotalpid grasshopper (NBRL055) showing a thin coating of siliceous matrix partially covering the fossil that was revealed during acid digestion. Specimen also shows the deep brown-orange colour of the weathered goethite Crato insects. Scale bar = 2 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

resembling pyrite framboids and pyrite pseudoframboids (Fig. 14, B, C and F), both of which we regard as preservational fabrics and described below. We do not consider these objects to be pyrite framboids as our EDX analysis did not produce a peak for sulphur associated with these structures (Fig. 5, B). However, there remains the possibility that some of these structures are decomposed framboids now preserved as goethite pseudomorphs. More problematic are spherical aggregates of crystallites arranged in a spiral fashion (Fig 14, D), which have never been described previously as a mineralising fabric, nor have they ever been reported for Recent insect cuticle.

Ultrastructural detail on the surface of the cuticle is apparent on some ommatidia, including densely distributed micro-papillae with diameters of ~100 nm (Fig. 13, B). Some cuticle displays micro-setae, some of which appear to be hollow at their bases and have diameters of 0.5 μm (Fig. 13, A). Some setae display patterned fine ridges with widths of ~300 nm on their external surface (Fig. 13, C and D). On rare occasions, ultrastructural detail of internal anatomy may be preserved with exceptional fidelity (Fig. 13, E). In addition to the above, we have also observed an open meshwork comprising elevated ridges delimiting numerous subquadrate "cells" on the head capsules of elcanid orthopterans (grasshoppers) (Fig. 15 A–F). This meshwork pattern is present on the posterior region of the vertex and on the genae. While the identity of these structures has yet to be confirmed, their position above other cuticular elements strongly suggest that they are epicuticular in nature and may correspond to similar mesh-like structures found in the cement and wax layers of modern orthopteran epicuticle. This feature has not been observed on any other insect cuticle in this study.

4.5. Ultrastructure vs preservational fabric

Crato Formation fossil preservation is dominated by one fabric consisting of small (~100 nm diameter) crypto-crystallites of iron hydroxide. In the best preserved specimens, these directly replace the tissues of the insect and are only revealed by high magnification electron microscopy (Fig. 9, D). However, they are also commonly arranged into hollow spherical or cylindrical aggregates that vary in size between 1 μm and 20 μm diameter (Fig. 14, A–F). These can show a weakly laminar arrangement or, rarely, have needle-like clusters of radial arranged crystallites around the hollow sphere (Fig. 14, B; Fig. 12, E). In rare cases, it appears that the hollow spheres have formed between two parallel surfaces resulting in an unusual toroid pattern (Fig. 12, F), however it is possible that this pattern may be the result of an unrecognised precursor mineral. In some instances, the hollow spheres appear to be merged into larger globular aggregates (Fig. 12, D).

Although these structures may appear to be of biological origin (superficially resembling coccoid microbial bodies or autolithified bacteria (Wuttke, 1983; Frey and Martill, 1995; Briggs, 2003) Bacteria by Frey and Martill, 1995 re-interpreted as melanin bodies by Vinther et al. (2008)), they may better be interpreted as preservational fabrics produced during the fossilization process, on account of their external similarity to oxidised pyrite framboids and pseudoframboids (Berner, 1970, 1984; Ohfuji and Rickard, 2005). However, these structures differ in two key aspects that separate them from framboids and pseudoframboids: the lack of discrete euhedral crystals, and the lack of an ordered (in the case of true framboids), disordered or massive (in the case of pseudoframboids) internal texture (Berner, 1970, 1984; Ohfuji and Rickard, 2005). In addition, no such structures have been observed within extant insect cuticle and the preservational fabric is consistent across different orders of Insecta. As such, we do not attribute these spherical aggregates to the original micro-structure of insect cuticle.

4.6. Preservational minerals

The Crato Formation insects are preserved in a variety of mineral phases. The majority of specimens in museum collections are brown or orange-brown coloured goethite replacements of the original cuticle. Soft tissues such as muscle are preserved as replacements in apatite minerals, and while the precise mineral species has not been determined, it is most likely francolite on the basis of its buff colour and cryptocrystalline habit (e.g. Martill, 1988). Unweathered specimens appear black and are probably preserved as amorphous iron monosulphide or perhaps the crystalline pyrite precursor forms mackinawite and greigite (Berner, 1984). A combination of these three iron sulphide phases are likely present, as only some material responded to magnetic separation. This strongly suggests the presence of greigite (Skinner et al., 1964), but as the sediment only partially responded there are likely other phases present as well. Pyrite and/or marcasite may also be present as these phases occur within the sediment at some horizons. Overgrowths of pyrolusite dendrites occur rarely around some insects while silica, calcite and barite may fill voids within uncrushed specimens (Menon and Martill, 2007). Halite pseudomorphs of silica and other phases also occur in the Crato Formation (Martill et al., 2007b).

5. Discussion

Preservation of Crato Formation insects can be extremely variable and the causes of this variation are an important aspect

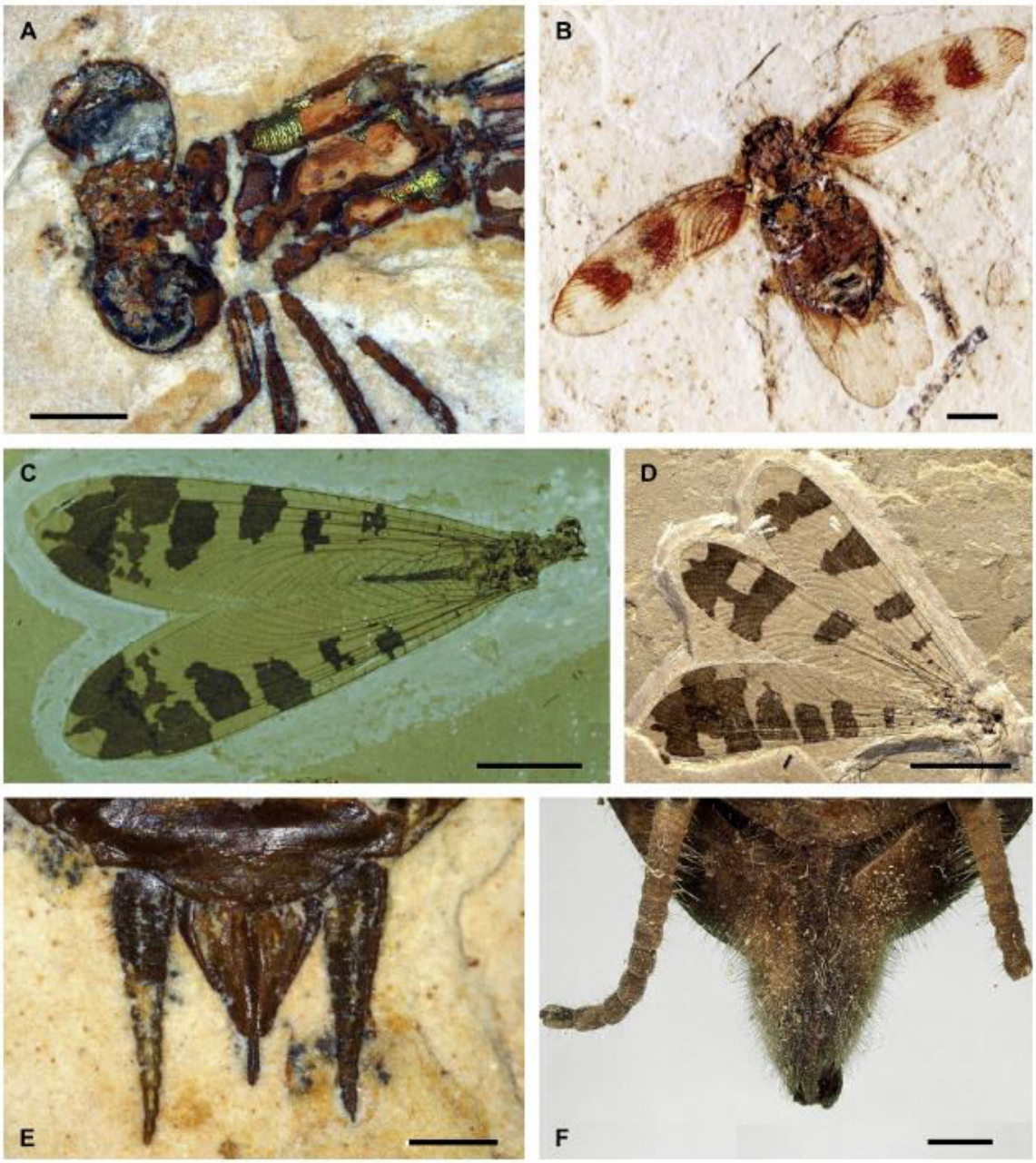


Fig. 7. Photomicrographs of Crato Formation insects with colour patterns and structural iridescence preserved (A–D). A. Damselfly *Parahemiphlebia mickoleiti* (SMNS66558) showing structural iridescence. Scale bar = 1 mm; B. Cockroach *Elisama americana* (SMNS66558) showing colour banding on forewings. Scale bar = 1 mm; C. Antlion cf. *Baissopardus* sp. (Unknown number) with intricate colour banding. Scale bar = 10 mm; D. *Baisopardus cryptohymen* holotype (SMNS66328) with similar colour banding, but subtly distinct from that in C. Scale bar = 15 mm; Photomicrographs comparing Recent and fossil cockroaches (E–F). E. *Ponopterix maxima* cerci (SMNS66328) from the Crato Formation. Scale bar = 500 μm; F. Recent cockroach cerci (*Sphodromantis viridis*). Scale bar = 1 mm. Photomicrographs kindly supplied by Günter Bechly.

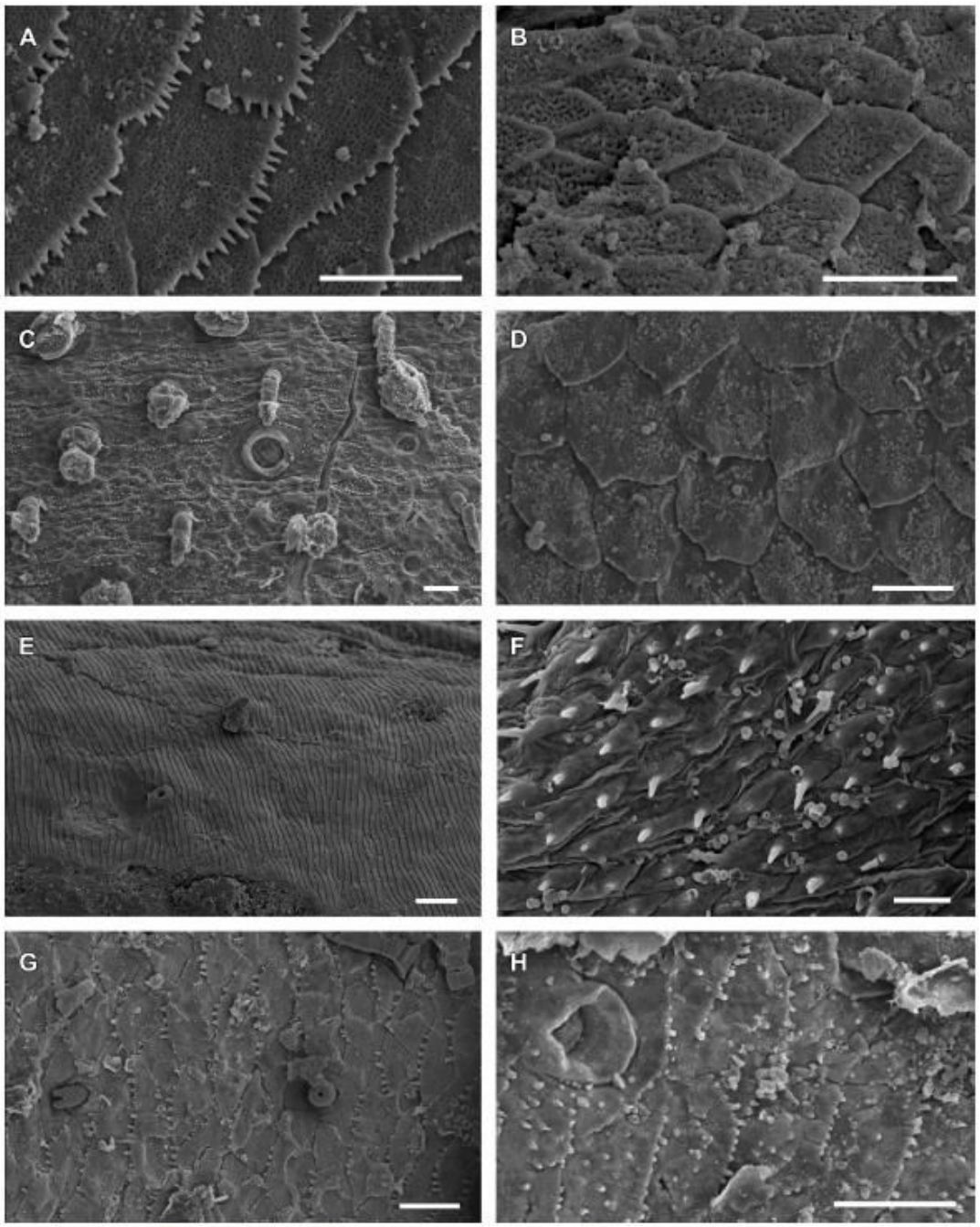


Fig. 8. Scanning electron micrographs of cuticular scales in Crato Formation insects. A. Cockroach (JW339) showing spined cuticular scales with a dimpled texture. Scale bar = 10 μm; B. Cockroach(?) hind limb femur (JW475) with coarse, dimpled cuticular scales. Scale bar = 10 μm; C. Gryllotalpid grasshopper *Cratotettrispinus fossorius* (NBRL055) with 'rough' cuticular scales highlighted by nano-papillae and micro-setae. Scale bar = 10 μm; D. Cockroach *Cratovitisma oldreadi*(?) (NBRL040) with broad diamond-shaped cuticular scales. Scale bar = 10 μm; E. Cockroach *Ponopteria axelrodi* (NBRL036) with extremely broad and short cuticular scales appearing like ridges. Scale bar = 10 μm; F. Indeterminate beetle (NBRL045) wing(?) cuticle with a heavily folded texture and nano-setae. Scale bar = 10 μm; G. Indeterminate grasshopper (NBRL059) with broad-spined cuticular scales and broken micro-setae. Scale bar = 10 μm; H. Higher magnification scanning electron micrograph of G, highlighting spiny texture. Scale bar = 10 μm.

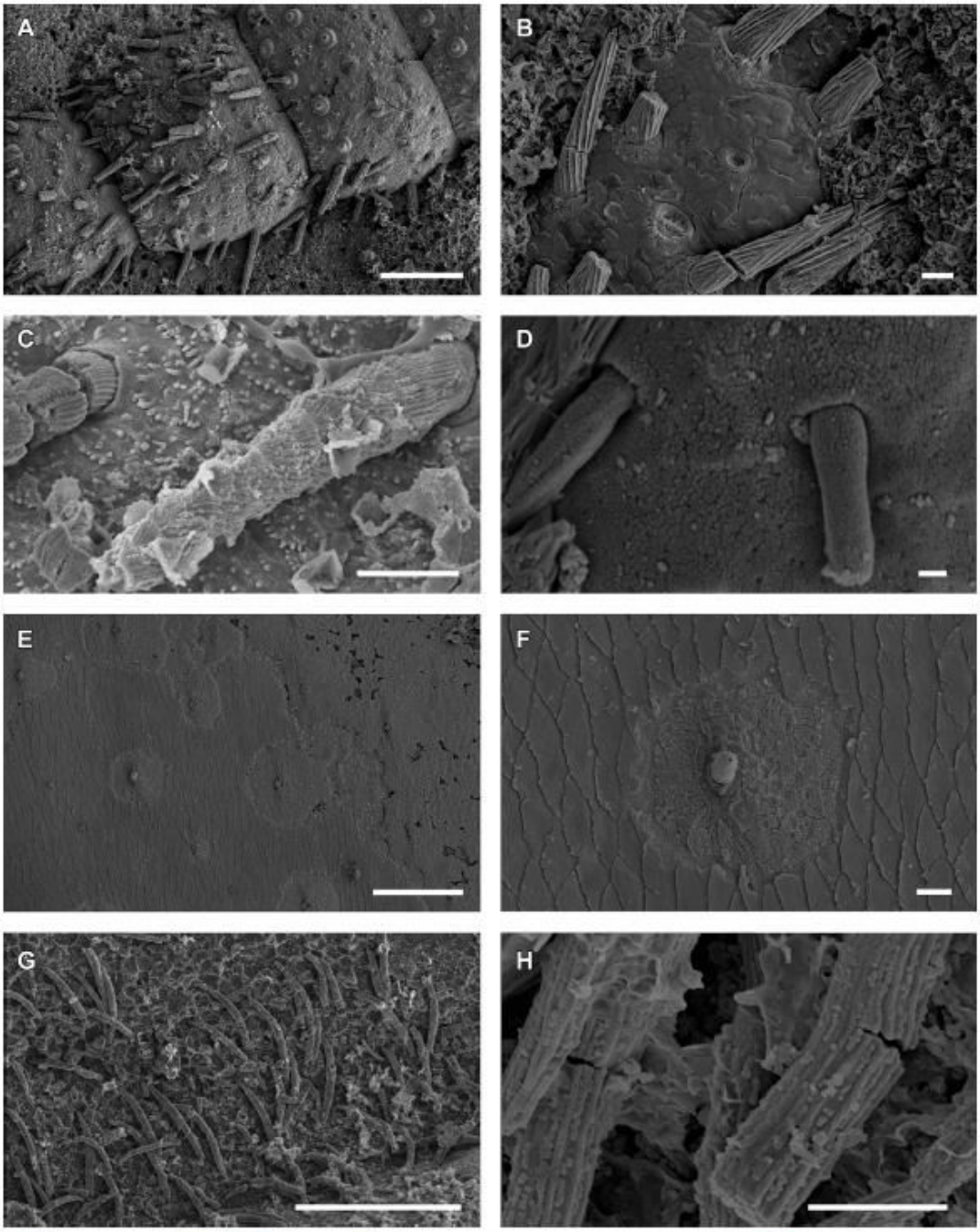


Fig. 9. Scanning electron micrographs of Crato Formation insects with preserved setae, micro-setae and nano-setae. A. Indeterminate cockroach (JW291) circus showing numerous setae. Scale bar = 100 μm; B. Indeterminate cockroach (JW339) cercus showing coarse setae with ridges. Scale bar = 10 μm; C. Indeterminate grasshopper (NBRL059) with ridges spiralling around setae. Scale bar = 10 μm; D. Pteromalid wasp *Parviformosus wohlrabeae* holotype (SMNS70092) labial palpus with nano-setae. Feint ridges are visible on the leftmost setae. Scale bar = 1 μm; E. Indeterminate cockroach (NBRL054) showing areas of decay around setae. Scale bar = 100 μm; F. Higher magnification scanning electron micrograph of E, highlighting decay texture around setae obliterating cuticular scales. Scale bar = 10 μm; Grasshopper *Cratoelcana zessini* (NBRL051) showing numerous and intact setae. Scale bar = 100 μm; H. Cockroach *Panopterix axelrodi* (NBRL018) coarse setae. Setae show distinct ridges with mineral growth them. Scale bar = 10 μm.

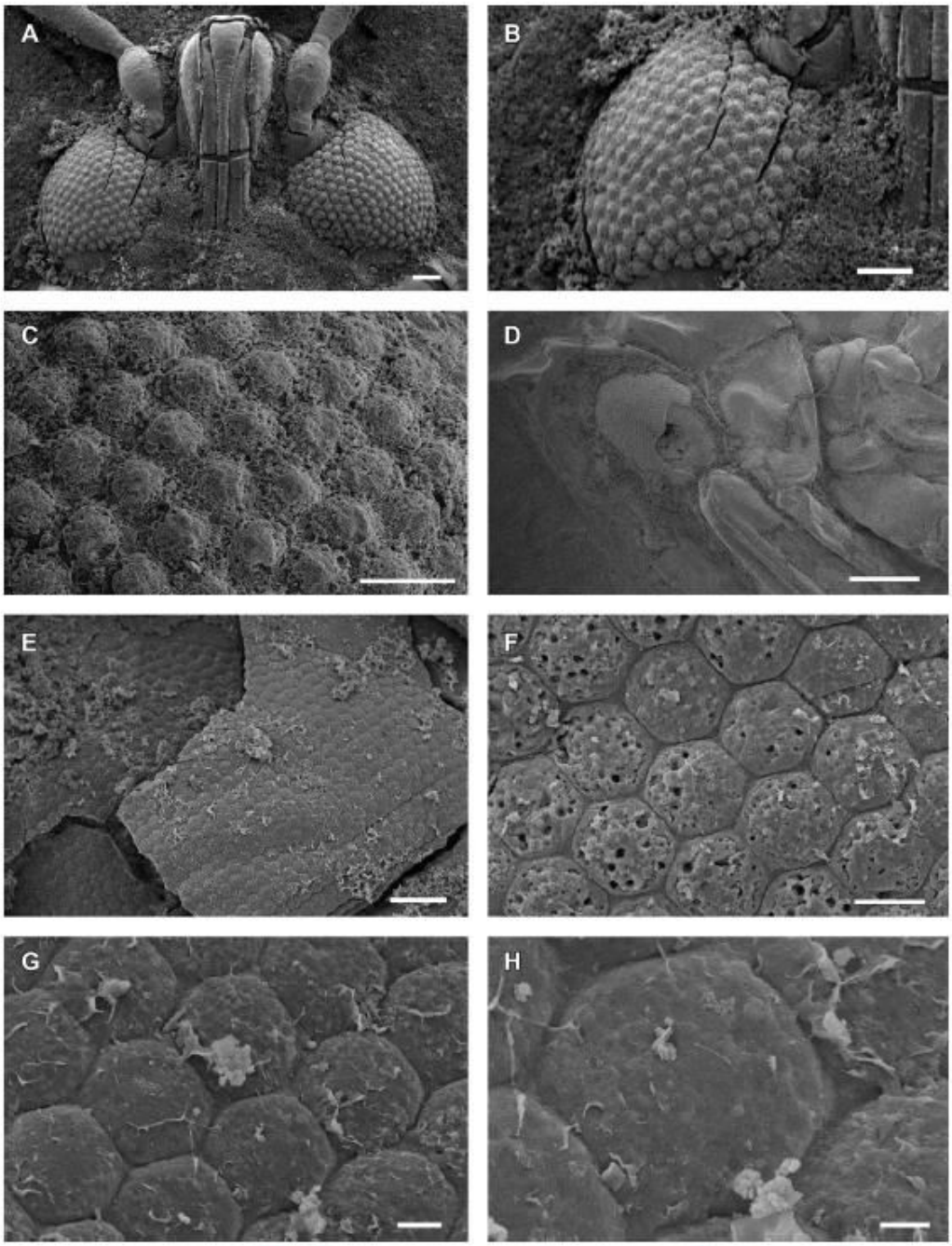


Fig. 10. Scanning electron micrographs of Crato Formation insects with preserved eyes and ommatidia. A. Overview of head of indeterminate true bug (FLO15). Scale bar = 100 μm; B. Higher magnification image of A, highlighting right eye in ventral aspect. Scale bar = 100 μm; C. Higher magnification image of B, showing individual ommatidia. Scale bar = 50 μm; D. Indeterminate cicada (FLO27) showing uncompacted, but damaged, left eye. Scale bar = 100 μm; E. Fractured eye of indeterminate elcanid grasshopper (NBRL044). Scale bar = 100 μm; F. Higher magnification image of E, showing ommatidia with post-mortem perforations, cause unknown. Scale bar = 20 μm; G. Higher magnification image of E, showing pristine ommatidia. Scale bar = 10 μm; H. Higher magnification image of G, showing individual ommatidia. Scale bar = 5 μm.

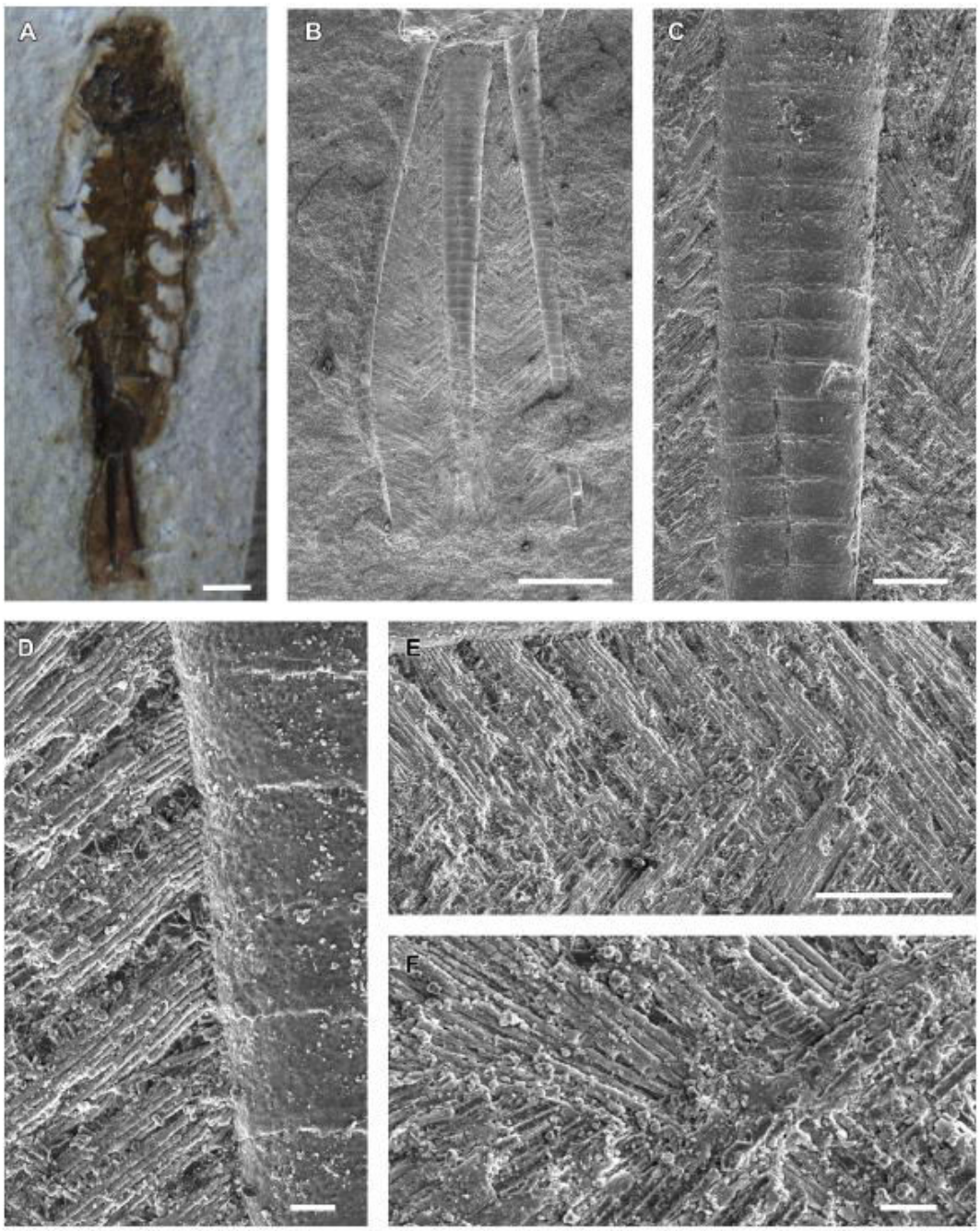


Fig. 11. Photomicrograph and scanning electron micrographs of mayfly nymph (NBRI1060), highlighting soft tissue preservation in caudal filaments. A. Photomicrograph of entire specimen. Scale bar = 1 mm; B. Overview of caudal filaments. Scale bar = 500 μm; C. Largest central caudal filament with horizontal ridges. Scale bar = 100 μm; D. Micro-filament clusters attaching to central caudal filament. Scale bar = 20 μm; E. Interdigitation of micro-filaments from separate caudal filaments. Scale bar = 100 μm; F. Higher magnification image of E, showing interdigitation. Individual micro-filament ~2 μm in diameter. Scale bar = 20 μm.

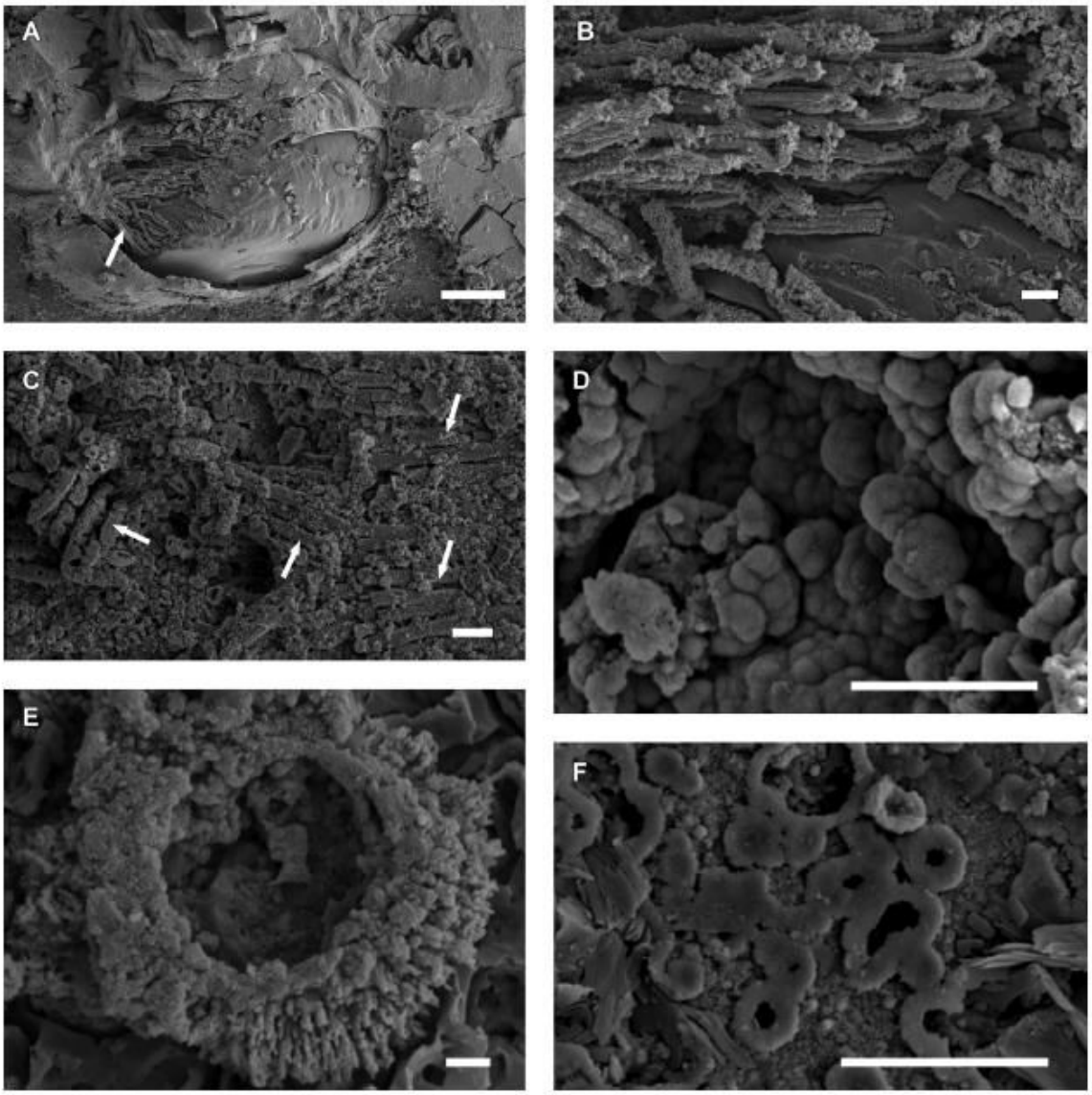


Fig. 12. Scanning electron micrographs of Crato Formation insects highlighting soft tissue preservation (A–C), and unusual replacement fabrics (D–F). A. Indeterminate fly (FLO19) with preserved genitalia. Arrow highlights tubular structures connecting to mineralised genital chamber. Scale bar = 100 μm; B. Higher magnification image of A, tubular structures within ?testes. Scale bar = 10 μm; C. Soft tissue preservation in an indeterminate cockroach (JW339). Arrows highlight individual muscle fibres. Scale bar = 10 μm; D. Unusual 'globular aggregate' texture in indeterminate wasp(?) (JW078). Scale bar = 10 μm; E. Hollow spherical structure composed of needle-like crystals in an indeterminate cockroach(?) (JW475). Scale bar = 2 μm; F. Unusual circular patterning in an indeterminate cockroach (JW339). Scale bar = 10 μm.

of the formation's taphonomy. The insects display a spectrum of preservation qualities ranging from near perfect examples that appear to have 'died yesterday' to specimens that may have undergone considerable biodegradation before being preserved. The preservation allows fine detail to be observed, sometimes at the nanometre scale, but some very fine features within the cuticle may be artefacts of mineralisation. Nonetheless, the fine detail can enable the identification of features of value for taxonomic and phylogenetic studies. Until now, such fine detail has largely been ignored by systematists working on the Crato palaeoentomofauna. While we accept that there may be a reluctance to prepare specimens for routine SEM analysis involving coating with conductive materials, or a fear of risking the integrity of a specimen undergoing acid digestion, we strongly urge workers to consider using these techniques, especially if multiple specimens are available.

Despite this variation, there does not appear to be any taxonomic bias influencing preservation. It is well known that large insects with heavily sclerotized cuticle (e.g. many Coleoptera and some Blattodea) have increased preservation potential resulting in

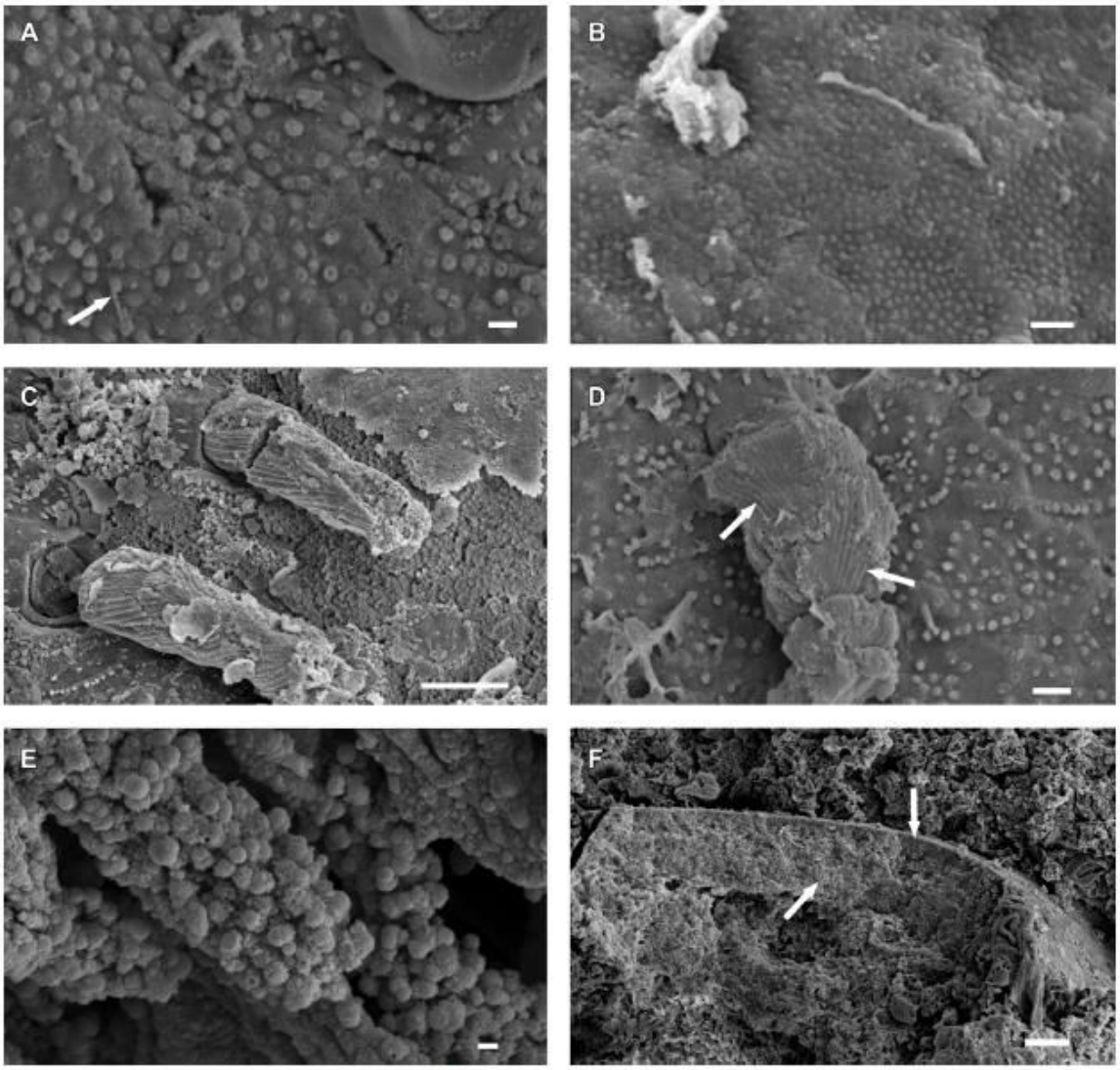


Fig. 13. Scanning electron micrographs of Crato Formation insects highlighting ultrastructure preservation (A–E) and a cross section through cuticle (F). A. Bases of broken nano-setae covering external surface of cuticle in gryllotalpid grasshopper *Cratotetraspinus fossorius* (NBRL055). Arrow highlights semi-intact nano-setae. Scale bar = 1 μm; B. Nano-papillate texture on ommatidia in indeterminate elcanidae grasshopper (NBRL044). Scale bar = 1 μm; C. Multiple setae with nano-scale ridges in gryllotalpid grasshopper *Cratotetraspinus fossorius* (NBRL055). Scale bar = 10 μm; D. Higher magnification image of similar setae with ridges in same in C. Arrows highlight curvature in ridges. Scale bar = 2 μm; E. Nanometre scale soft tissue preservation of genitalia in indeterminate fly (FLO19) (Fig. 10 A and B). Scale bar = 1 μm; F. Cross section through indeterminate cockroach (JW735) cuticle. Uppermost arrow highlights well preserved exocuticle, lowermost arrow highlights amorphous endocuticle. Scale bar = 10 μm.

a bias towards larger, more durable insects in fossil assemblages (Martínez-Delclòs et al., 2004; Smith et al., 2006). Both small insects (Barling et al., 2013) and fragile insect structures (see Fig. 2, B) are preserved with astounding fidelity. This indicates that size and robustness are not controlling factors of preservation in the Crato Formation. We examined 10 of the 18 insect orders recorded by Bechly (2007) for the Crato Formation insect assemblage, including Blattoidea, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Neuroptera, Odonata, Orthoptera and Rhaphidioptera. We also examined an arachnid, *Cretaraneus* cf. *martinsnetoi* and found high fidelity preservation in all specimens. We also studied other insect orders and non-insect arthropods using binocular microscopy and these too appear to be preserved with the same fidelity. The relative abundance of Crato Formation insect orders is provided by Menon and Martill (2007).

Although the precise geochemical conditions giving rise to this formation's preservation are still poorly understood, the formation of pyrite and other iron sulphides is usually attributed to the presence of sulphate reducing bacteria (Berner, 1985) and high fidelity preservation in other localities is frequently attributed to

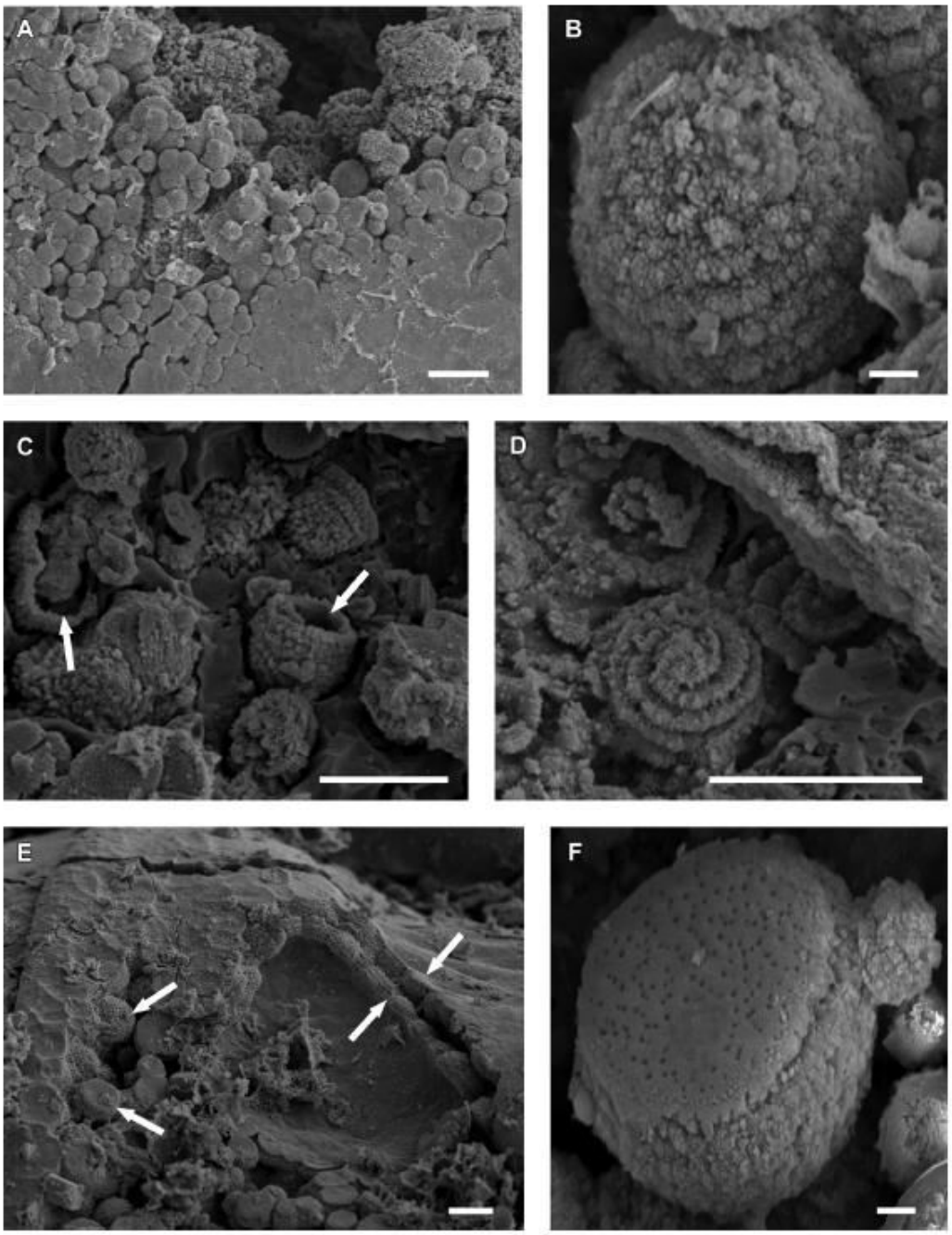


Fig. 14. Scanning electron micrographs of common preservational fabrics seen in the Crato Formation insects. A. Incomplete cuticle (possibly decay fabric) revealing textures within cuticle in an indeterminate cockroach (NBRL054). Scale bar = 10 μm; B. Spherical ringed aggregate of cryptocrystalline grains (most common preservational texture) in the pteromalid wasp *Parvifarmosus wohlrabeae* holotype (SMNS70092). Scale bar = 2 μm; C. Incomplete spherical aggregates revealing a hollow interior in indeterminate cockroach (JW339). Scale bar = 10 μm; D. Rare spiral structures, possibly representing compacted spherical ringed aggregates in indeterminate cockroach(?) (JW475). Scale bar = 10 μm; E. Mesosomal cuticle of pteromalid wasp *Parvifarmosus wohlrabeae* holotype (SMNS70092) demonstrating that even well preserved cutide consists of many spherical aggregates merged together. Arrows highlight individual spherical aggregates. Scale bar = 10 μm; F. Individual semi-spherical aggregate replacing cutide in pteromalid wasp *Parvifarmosus wohlrabeae* holotype (SMNS70092). Flat surface represents exterior surface of cuticle. Scale bar = 2 μm.

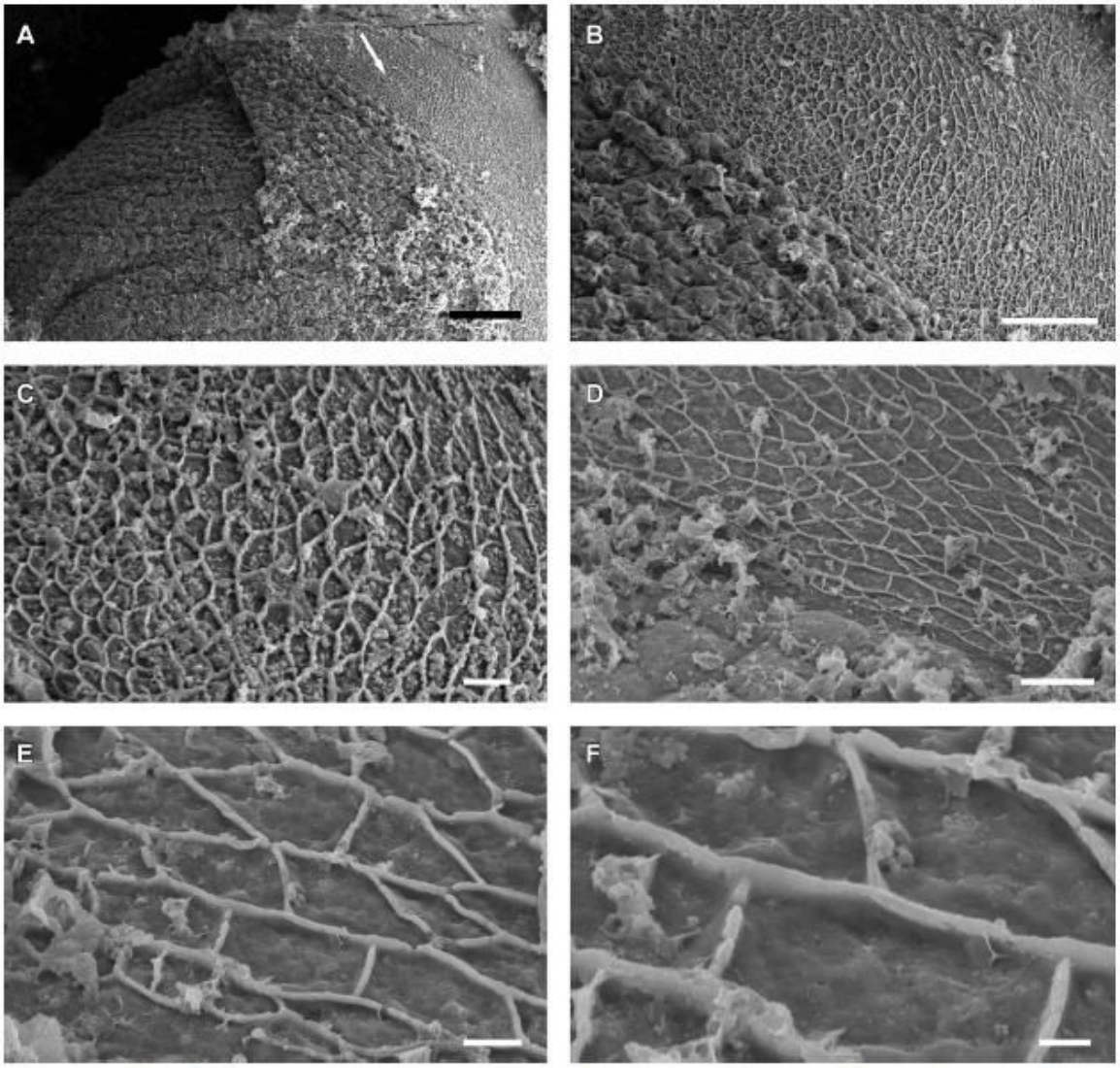


Fig. 15. Scanning electron micrographs highlighting elevated ridges delimiting numerous subquadrate "cells" on the head capsules of two elcanid grasshoppers from the Crato Formation. A. Overview of eye and posterior vertex in *Cratoelcana zessini* (NBRL051). Arrow highlights position of ridges. Scale bar = 100 μm; B. Magnified image of region highlighted by arrow in A. Scale bar = 50 μm; C. Image of ridges in *Cratoelcana zessini* (NBRL051) showing subquadrate "cells". Scale bar = 10 μm; D. Overview of similar ridges seen in another indeterminate elcanid grasshopper (NBRL044). Scale bar = 20 μm; E. Higher magnification image of D, showing elevated ridges. Scale bar = 5 μm; Higher magnification image of E, showing individual "cells". Scale bar = 2 μm.

benthic microbial communities (Wilby et al., 1996) and anoxia (Farrell et al., 2013). Although there is a general lack of physical evidence for a benthic microbial community in the Crato Formation (Heimhofer et al., 2010), Martill and Heimhofer (2007, fig. 4.4 a, b) and Martill et al. (2007b) figure ripple-like microbial mats, some with tears for some bedding planes. These suggest that, at times, extensive benthic microbial communities were present in significant numbers to bind the sediment, and may have influenced fossil preservation, but we note that insect fossils have not yet been recovered from a rippled lamina. However, this may be due to the infrequent occurrence of the limestone being split at these rippled horizons.

The preservational textures seen in the cuticle of insects from the Crato Formation presents a unique challenge in determining the process of fossilisation. The cylindrical to spherical aggregates may be the result of failed pyrite framboid formation within the cuticle or could perhaps be artefacts generated by the macromolecular fabric of cuticular laminae as iron sulphide diffused through the cuticle, or a combination of both.

Somewhat similar preservational textures in fossil insects are reported by Wang et al. (2012) from the Early Cretaceous Jehol Biota of China. These textures differ in three key aspects, but may represent a similar geochemical origin. They differ in that they are on a much coarser scale, are made of discrete, but poorly ordered

crystals (more accurately representing pseudoframboids), and do not directly replace the cuticle surface.

There remains considerable work to be undertaken to understand fully the diagenetic environment under which the Crato Formation insects were preserved, but the exquisite preservation is clearly a combination of early diagenetic, microbially induced mineralisation, and later *in situ* weathering.

6. Conclusions

The Crato Formation palaeoentomofauna is extremely well preserved. Details of the gross morphology, cellular and cuticular structure and ultrastructural detail are frequently visible.

Some seemingly 'poorly' preserved specimens are in fact excellently preserved examples of partially decayed individuals. Such specimens may have floated for prolonged periods prior to fossilisation.

The exceptional quality of preservation of insect cuticle does not appear to be size or taxon limited and is found in a wide range of insect orders and also in some non-hexapod Arthropoda such as scorpions and spiders. The preserving medium in weathered limestones is the iron hydroxide goethite, and in unweathered limestones appears to be a mix of greigite, possibly an amorphous iron monosulphide, and perhaps mackinawite. In addition, pyrite and marcasite may also be present. Other diagenetic minerals occurring as cavity infills enabling 3D insect preservation include; calcite, silica and rare barite.

Microfabrics, including micro-spheres, hollow micro-spheres and aggregates of these may represent bacterially mediated Fe mineral growths, with some perhaps representing autholithified bacteria. This study did not aim to address the genesis of the microfabrics, but we suggest this would be an important avenue for further research.

Labile soft tissues such as muscle fibre, is sometimes preserved in the calcium phosphate mineral francolite, as well as goethite. Some insects also appear to have manganese dioxide (pyrolusite) as a preserving medium, but this is considerably rarer than goethite.

Preservation of the insects by goethite may be a consequence of stalled pyrite formation during early diagenesis under anoxic and probably hypersaline bottom conditions. This was later followed by oxidation of Fe sulphide phases during surface weathering of the outcrop, at a currently unknown time.

Acknowledgements

Our work on the Crato Formation has benefited from considerable input from other scientists. Judith Wohlrabe is warmly thanked for allowing us to use her SEM data and for donating her specimens. Particular thanks are due to Betimar Filgueiras and Artur Andrade of the DNPM in Crato for their assistance with fieldwork. Dr Paulo Brito of UERJ is thanked for his considerable help. Uli Heimhofer, Robert Loveridge, Federica Menon, Paul Selden, and Dino Frey were all members of various field expeditions to Brazil. Günter Bechly (Stuttgart) has always encouraged our work on the Crato Formation palaeoenvironments and has made specimens available for us to study. Michael Schwikert of MS Fossils and Annesuse Raquet of Fossils World Wide are thanked for supplying some specimens and photographs. Geoff Long helped prepare samples and Elaine Dyer and Christine Hughes assisted with SEM analysis. We thank two anonymous referees for their constructive critique of the manuscript and the editors of Cretaceous Research for their additional help. Finally, we would like to note that none of this research would be possible if it wasn't for the keen eyes of the Crato limestone quarry men and we thank them greatly for their contribution to our work.

References

Allison, P.A., Briggs, D.E.G., 1991a. The taphonomy of soft-bodied animals. 120–140. In: Donovan, S.K. (Ed.), The process of fossilization. Columbia University Press, New York, 303 pp.

Allison, P.A., Briggs, D.E.G., 1991b. Taphonomy of non-mineralized tissues 25–69. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy: Releasing the data locked in the fossil record. Plenum Press, London, 560 pp.

Allison, P.A., Briggs, D.E.G., 1993. Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic. Geology 21, 527–530.

Amedegnato, C., 1993. African-American relationships in the acridians (Insecta, Orthoptera). 59–75. In: George, W., Lavocat, R. (Eds.), The African-South American connection. Clarendon Press, Oxford, 184 pp.

Barling, N., Heads, S.W., Martill, D.M., 2013. A new parasitoid wasp (Hymenoptera: Chalcidoidea) from the Lower Cretaceous Crato Formation of Brazil: The first Mesozoic Pteromalidae. Cretaceous Research 45, 258–264.

Bechly, G., 2007. Insects of the Crato Formation: Introduction. 142–149. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an ancient world. Cambridge University Press, Cambridge, 625 pp.

Bechly, G., 2010. Additions to the fossil dragonfly fauna from the Lower Cretaceous Crato Formation of Brazil (Insecta: Odonata). Palaeodiversity Supplement 3, 11–17.

Berner, R.A., 1970. Sedimentary Pyrite Formation. American Journal of Science 268, 1–23.

Berner, R.A., 1984. Sedimentary pyrite formation: an update. Geochimica et Cosmochimica Acta 48, 605–615.

Berner, R.A., 1985. Sulfate reduction, organic-matter decomposition and pyrite formation. Philosophical Transactions of the Royal Society 315, 25–38.

Briggs, D.E.G., Kear, A.J., Martill, D.M., Wilby, P.R., 1993. Phosphatization of soft-tissue in experiments and fossils. Journal of the Geological Society 150, 1035–1038.

Briggs, D.E.G., 2003. The role of biofilms in the fossilization of non-biomineralized tissues. 281–290. In: Krumbein, W.E., Paterson, D.M., Zavarzin, G.A. (Eds.), Fossil and Recent Biofilms: A Natural History of Life on Earth. Kluwer Academic Publishers, Dordrecht, 482 pp.

Cridland, A.A., Williams, J.L., 1966. Plastic and epoxy transfers of fossil plant compressions. Bulletin of the Torrey Botanical Club 5, 311–322.

Ehrlich, P.R., Raven, P.H., 1964. Butterflies and plants: a study of coevolution. Evolution 8, 586–608.

Escapa, I.H., Asmith, B.J., Taylor, T.N., Taylot, E.L., 2010. Modifications of the transfer technique for studying complex plant structures. Review of Palaeobotany and Palynology 159, 62–68.

Farrell, U.C., Briggs, D.E.G., Hammarlund, E.U., Sperling, E.A., Gaines, R.R., 2013. Paleoredox and pyritization of soft-bodied fossils in the Ordovician Frankfort Shale of New York. American Journal of Science 313, 452–489.

Frey, E., Martill, D.M., 1995. A possible oviraptosaurid theropod from the Santana Formation (Lower Cretaceous, ?Albian) of Brazil. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 1995, 397–412.

Grimaldi, D., 1990. Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History 195, 1–191.

Heads, S.W., 2008. The first fossil Prosopiidae (Insecta, Orthoptera, Eumastacoidea) with comments on the historical biogeography and evolution of the family. Palaeontology 51, 499–507.

Heads, S.W., Martill, D.M., Loveridge, R.F., 2005. An exceptionally preserved antlion (Insecta, Neuroptera) with colour pattern preservation from the Cretaceous of Brazil. Palaeontology 48, 1409–1417.

Heads, S.W., Martill, D.M., Loveridge, R.F., 2008. Palaeoentomological paradise: the Cretaceous Crato Formation of Brazil. Antenna 32, 91–98.

Heimhofer, U., Arizteguí, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios-Netto, A.M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-eastern Brazil). Sedimentology 57, 677–694.

Hochuli, P.A., Heimhofer, U., Weissert, H., 2006. Timing of early angiosperm radiation: recalibrating the classical succession. Journal of the Geological Society 163, 587–594.

Hu, A., Dilcher, D.L., Jarzen, D.M., Taylor, D.W., 2008. Early steps of angiosperm–pollinator coevolution. Proceedings of the National Academy of Sciences of the United States of America 105, 240–245.

Labandeira, C.C., Dilcher, D.L., Davis, D.R., Wagner, D.L., 1994. Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. Proceedings of the National Academy of Sciences of the United States of America 91, 12278–12282.

Martill, D.M., 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Palaeontology 31, 1–18.

Martill, D.M., 1997. Fish oblique to bedding in early diagenetic concretions from the Cretaceous Santana formation of Brazil – Implications for substrate consistency. Palaeontology 40, 1011–1026.

Martill, D.M., Bechly, G., Loveridge, R.F., 2007a. The Crato Fossil Beds of Brazil: Window into an ancient world. Cambridge University Press, Cambridge, 625 pp.

Martill, D.M., Heimhofer, U., 2007. Stratigraphy of the Crato Formation. 25–43. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an ancient world. Cambridge University Press, Cambridge, 625 pp.

Martill, D.M., Loveridge, R.F., Heimhofer, U., 2007b. Halite pseudomorphs in the Crato Formation (Early Cretaceous, late Aptian-early Albian), Araripe Basin,

Northeast Brazil: Further evidence for hypersalinity. Cretaceous Research 28, 613–620.

Martínez-Delclòs, X., Briggs, D.E.G., Peñalver, E., 2004. Taphonomy of insects in carbonates and amber. Palaeogeography, Palaeoclimatology. Palaeoecology 203, 19–64.

Menon, F., Martill, D.M., 2007. Taphonomy and preservation of Crato Formation arthropods. 79–96. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an ancient world. Cambridge University Press, Cambridge, 625 pp.

Ohfuji, H., Rickard, D., 2005. Experimental syntheses of framboids – a review. Earth-Science Reviews 71, 147–170.

Skinner, B.J., Erd, R.C., Grimaldi, F.S., 1964. Greigite, the thiospinel of iron, a new mineral. American Mineralogist 49, 543–555.

Smith, D.M., Cook, A., Nufio, C.R., 2006. How physical characteristics of beetles affect their fossil preservation. PALAIOS 21, 305–310.

Staniczek, A.H., Bechly, G., Godunko, R.J., 2011. Coxoplectoptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group mayflies (Ephemeroptera). Insect Systematics and Evolution 42, 101–138.

Vinther, J., Briggs, D.E.G., Prum, R.O., Saranathan, V., 2008. The colour of fossil feathers. Biology Letters 4, 522–525.

Walton, J., 1923. On a new method for investigating fossil plant impressions or incrustations. Annals of Botany 37, 379–391.

Wang, B.O., Zhao, F., Zhang, H., Fang, Y., Zheng, D., 2012. Widespread pyritization of insects in the Early Cretaceous Jehol Biota. Palaios 27, 707–711.

Wilby, P.R., Briggs, D.E.G., Bernier, P., Gillard, C., 1996. Role of microbial mats in the fossilization of soft tissues. Geology 24, 787–790.

Wuttke, M., 1983. 'Weichteil-Erhaltung' durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefen der 'Grube Messel' bei Darmstadt. Senckenberg. Senckenbergiana Lethaia 64, 509–527.

Appendix 8. 3. Details of insect environmental preferences

8. 3. 0. Preamble

The Nova Olinda Member boasts a bewildering array of, often exquisitely preserved, fossil insects (Martill *et al*., 2007a). In this supplementary material, each order (and family where applicable) identified from the Nova Olinda Member is introduced, along with brief descriptions of their ecology and environmental preferences. Systematics is presented in accordance with works by Misof *et al*. (2014). The aim of this is to construct a comprehensive understanding of not only the catchment areas around the Nova Olinda Member, but also the insect faunas that filled them. The taphonomy of these organisms cannot be fully understood without first understanding where and how they lived.

Insect groups will only be discussed to family-level if there is considerable variation among the order. For example, odonates are relatively morphologically conservative and share the same niche. As such, they are not discussed at family-level. Superfamilies and suborders will only be listed if they are particularly prevalent in the literature or otherwise of particular importance. The environmental preference for each group is based on its extant members and, as such, may differ from the true preference of the fossil forms. Despite this, it still allows for an approximate ecological context to be established for each group. In many cases, the morphology of fossil forms is very similar to modern forms and they presumably inhabited similar niches and environments. Ultimately, the ecological framework established in this chapter will aid in understanding the Nova Olinda Member catchment areas and subsequently the taphonomy of its insect assemblage.

In addition to this, an updated (2016) version of the Martill *et al*. (2007a) valid species list is also presented below (Appendix 8. 4.), followed by additional references cited herein (Appendix 8. 5.). All *nomina nuda* have been removed, renamed taxa are updated, and new taxa have been added. Table 6 summarising the text below and provides a summary of the specific niche associated with each insect group.

Table 6. Table of Nova Olinda Member insect familial environmental preferences, with additional details.

Order	Family	Environmental Preference & Key	# sp.
		Aquatic / Riparian / Humid / Woody Scrubby / Burrowing / Highland / Arid / N/A	
Diplura	Untreated	Cryptic soil-dwelling	1
Zygentoma	Untreated	Cryptic soil-dwelling	1
Coxoplectoptera	Untreated	N/A	1
Ephemeroptera	Untreated	Freshwater littorial-to-benthic larvae	22
Odonata	Untreated	Clean freshwater, likely around palaeolake	52
Dermaptera	Anisolabididae	Diversity highest in costal / riparian regions	1
	Labiduridae	N/A	2

	Spongiphoridae	N/A	3
Orthoptera	Hagloidea	N/A	2
	Schizodactylidae	Desert (majority) / sand / costal / lagoonal	1
	Gryllotalpidae	Burrowing	3
	Gryllidae	Grassland/scrubland/forests/marshes/beaches/caves (generally shrubby)	11
	Baissogryllidae	Grassland/scrubland/forests/marshes/beaches/caves (generally shrubby)	19
	Tridactylidae	Shallow burrowers, tropical-subtropical regions	2
	Proscopiidae	Intimate association with plants (mimic)	1
	Locustopsidae	Similar to Locusts, general	16
	Araripelocustidae	N/A	2
	Elcanidae	Soft substrate / sand etc.	2
	Bouretidae	N/A	1
Chresmododea	Untreated	Semi-aquatic	1
Phasmatodea	Untreated	Variety of habitats	1
Mantodea	Untreated	Variety of habitats	3
Blattodea	Mesoblattinidae	Generally prefer warm, humid environments	1
(Inc. Isoptera)	Blattellidae	Generally prefer warm, humid environments	2
	Blattidae	Highly generalised (Cosmopolitan)	1
	Blattulidae	Cosmopolitan	2
	Raphidiomimidae	Convergent with mantises (see above)	1
	Ponopterixidae	Beetle-like, N/A	4
	incertae sedis	N/A	1
	Cratomastotermitidae	Roachlike	1
	Kalotermitidae	Dry wood, xerophytic	1
	Termopsidae	Moist or rotting plant material	1
	Hodotermitidae	Intimate association with plants (nest in)	3
Hemiptera	Cicadellidae	Cosmopolitan	3
	Myerslopiidae	Damp, rotting wood: bog/forest/open habitats	2
	Tettigarctidae	Modern are high-altitude cold environments	2
	Cercopionidae	N/A	6
	Palaeontinidae	N/A	8
	Cixiidae	Dark, humid, often subterranean environments	1
	Lalacidae	Likely dark, humid, or subterranean environments	15
	Achilidae	Often found in amber, tree association	3
	Peloridiidae	Moss / *Nothofagus* forests	1
	Belostomatidae	Aquatic adults & larvae	4
	Nepidae	Aquatic adults & larvae (some brackish tolerance)	2
	Naucoridae	Aquatic adults & larvae	2
	Notonectidae	Primarily aquatic	1
	Corixidae	Aquatic adults & larvae, including sea water	1
	Gelastocoridae and Pseudonerthridae	Higher diversity in the tropics; Riparian	3
	Archegocimicidae	Coastal / riparian	1
	Hydrometridae	Semi-aquatic, on plants at edges of ponds/marshes	2
	Veliidae and Mesoveliidae	Semi-aquatic, on plants at edges of ponds/lakes	2
	Cimicomorpha	N/A	1
	Pachymeridiidae	Humid and warm-temperate climates	2
	Alydidae	Most abundant in tropical arid and sandy habitats	1
	Coreidae	Plant/tree association - sap feeding	1
	Aradidae	Cryptic, in decaying twigs and wood debris, or in moist forest litter	1
	Cydnidae	Deep soil burrowers	1
Hymenoptera	Unicalcaridae	N/A	1

	Sepulicidae	N/A	1
	Siricidae	Dying / felled trees	1
	Tenthredinoidea	Associated with plants	1
	Vespidae	Cosmopolitan	1
	Pompilidae	Intimately associated with spiders associated with tropical areas or xeric regions	1
	Sapygidae	Indicative of hot, dry climates along with 'desert' flora	1
	Tiphiidae	Intimately associated with angiosperms	1
	Formicidae	Presence refuted	1?
	Scoliidae	Hot, dry, savannah or desert environments	3
	Angarosphecidae	Dependant on host species preference	4
	Ampulicidae	Parasitizes cockroaches (generalised)	1
	Apidae?	Cosmopolitan, intimately associated with angiosperms	1
	Ichneumonoidae	Higher diversity in temperate regions	1
	Ephialtitdae and Proctotrupidae	N/A	2
	Mesoserphidae	N/A	1
	Chalcidoidea (superfamily)	Cosmopolitan	1
Raphidioptera	Baissopteridae	Feed exclusively on trees and their larvae live under bark or in soil	4
	incertae sedis	N/A	1
Megaloptera	Corydalidae	Freshwater aquatic larvae	2
Neuroptera	Osmylidae	Larvae are possibly aquatic, as adults prefer moist habitats near water	4
	Ithonidae	Larvae are believed to be subterranean	1
	Chrysopidae *et al*	Associated with shrubby plants	13
	Berothidae	N/A	2
	Sisyridae	Aquatic larvae	1
	Psychopsidae	N/A	2
	Nemopteridae	Arid	5
	Nymphidae	Cryptic group, debris and detritus	1
	Myrmeleontidae	Generally arid	4
	Ascalaphidae	Diverse in xeric and mountainous regions	1
	Kalligrammatidae	N/A	2
	Araripeneuridae *et al*	N/A	34
Coleoptera	Archostemata: (2 cf taxa)	Feed on dead, fungus-infected wood and wood-borers.	2
	Dytiscidae	Aquatic	1
	Carabidae	N/A	2
	Staphylinidae	Generally moist temperate and some coastal	5
	Hydrophilidae	Predominantly aquatic	1
	Scarabaeidae	Most abundant in arid regions	2
	Buprestidae	Associated with woody plants	1
	Dryopidae	Aquatic	1
	Elateridae	Cosmopolitan	1
	Nitidulidae	Live in bark / flowers	1
	Cucujidae	Generally live under bark	1
	Trogossitidae	Live in and feed on tree bark	1
	Lymexylidae	Bore into living and decaying wood	1
	Tenebrionidae	Compact, short-legged forest-dwelling forms	1
	Pyrochroidae	N/A *nomen nudum*	1
	Chrysomelidae	Coevolution with primitive angiosperms	2
	(Superfamily) Curculionoidea	Feed on tree bark	7
Trichoptera	Leptoceridae	Aquatic larvae	1

	Hydroptilidae	Aquatic larvae can live in fresh or brackish, flowing or still water, but benthic	4
	incertae sedis	N/A	2
Lepidoptera	Untreated	N/A morphologically different from modern forms	5
Mecoptera	Bittacidae	Associated with humid or seasonally dry areas	1
	incertae sedis	N/A	1
Diptera	?Chironomidae	Associated with almost every aquatic environment	1
	Simuliidae	Most common in tropical river basins	1?
	Mycetophilidae	Moist or wet environments, (forests, swamps, and moist heaths or grasslands)	1
	Sciaridae	Rotten wood, under bark of fallen trees, or other decaying plant matter	1
	Bibionidae	Many larvae scavenge decaying plant material	1
	Psychodidae? or Tanyderidae?	Inhabit moist environments	1
	Tipulidae	Broad variety of habitats	4
	Limoniidae	N/A	2
	Zhangsolvidae	Rotten plant matter, under bark, or in other decaying wet substances	3
	Tabanidae	N/A blood/nectar feeders, reliant on vertebrate / plant preferences	1
	Rhagionidae?	N/A blood feeders, reliant on vertebrate preference	1
	Mydidae	Arid to semi-arid environments with open vegetation	1
	Therevidae	Most diverse in arid and semi-arid regions	1
	Asilidae	Prefer open, sunny, and dry (even arid) habitats with scattered vegetation	2

8. 3. 1. Orders Diplura, Archaeognatha, and Zygentoma (basal non-insect hexapods and basal wingless insects)

Diplura (two-pronged bristletails) is an order of basal wingless hexapods. It is within the class Entognatha, along with Protura (coneheads) and Collembola (springtails), and they are distinguished from true insects by their entognathous mouthparts (held within the gnathal pouch, within the head capsule) and their fully musculated antennal flagellum (Grimaldi and Engel, 2005). As would be expected from a basal group, members of Diplura possess a collection of plesiomorphic traits that make them fairly 'generic' in appearance, and also greatly impact their preservation potential. In general, these hexapods are lightly sclerotized and have a cryptic soil-dwelling lifestyle (Staniczek and Bechly, 2007). This results in a greatly lowered preservation potential and, consequently, their fossil record is extremely sparse. A single species of dipluran is described from the Nova Olinda Member, *Ferrojapyx vivax* (Wilson and Martill, 2001), with a handful of other undescribed (possibly indescribable) specimens (Staniczek and Bechly, 2007).

The orders Archaeognatha (jumping bristletails) and Zygentoma (silverfish) are basal wingless insects, and (aside from distinguishing mouth and flagellum characters) share some plesiomorphic traits with Entognatha. They are also typically lightly sclerotized cryptic soil-dwellers, and so share the same preservation potential and poor fossil record issues as

members of Entognatha. They are fundamentally different in genital structure from other insect groups. Unlike the primitive condition of indirect fertilization for Hexapoda, Archaeognatha and Zygentoma have external genitals used in direct fertilization (Grimaldi and Engel, 2005). Two specimens of Zygentoma are reported from the Nova Olinda Member, both belonging to Lepismatidae (Strum, 1998). Unfortunately, due to their poor preservation, no genus or species descriptions or assignments could be made (Staniczek and Bechly, 2007).

In addition to these, one beautifully preserved basal wingless insect is on display in the digital museum fossilmuseum.net. This appears to be an undescribed specimen, and most likely represents a new taxon. As of 2016, the fossil can be viewed via the following url: http://www.fossilmuseum.net/Fossil_Sites/Santana-Formation/thysanura/thysanura.htm.

8. 3. 2. Coxoplectoptera

Coxoplectoptera (chimera wings) is an extinct order of basal insect with close affinities to stem-group Ephemeroptera. As their common name suggests, they possess a suite of characters superficially similar to many groups (including mantises, odonates, and even gammarid shrimp). Most notably of these is the raptorial forelimbs that both larvae and adults possess, indicating a predatory lifestyle and, combined with their large wings, a possible odonate-like niche (Staniczek *et al*., 2011).

These fossils were originally presented in a 1998 meeting by Martill, described as persisting-type stem-group Ephemeroptera, assigned to the genus *Cretereisma* (two species: *C. antiqua* (type species) and *C. schwickertorum*), and confirmed by the figuring of further specimens (Bechly *et al.,* 2001a; Willmann, 2007). However, Staniczek *et al*. (2011) erected the order Coxoplectoptera and reassigned these specimens into a single genus and species within the new order. The taxon *Mickoleitia longimanus* was erected and placed within a new family (Mickoleitiidae). The justification for the erection of this new order is a suite of derived and plesiomorphic characters. The two most important being: derived specialised forelimbs (with strongly elongate coxae, single-clawed pretarsus, and a distinctly skewed pterothorax) and plesiomorphic enlarged hind wings with a widened anal area (Staniczek *et al*., 2011). Due to the varying assignments of these fossils, total specimen count is difficult, however it appears that there are at least four alate specimens. Nymphs of this group are known and are easily identified by the presence of four wing pads of almost equal size and well-developed meso- and meta- thoraxes (Willmann, 2007). The overall large size of adult taxa suggests that the nymphs should also be large and nymphs matching these characteristics are uncommon (but not rare) in the Nova Olinda Member.

8. 3. 3. Ephemeroptera

The fossil Ephemeroptera (mayflies) are extremely abundant in the Nova Olinda Member, accounting for 14% of all fossil insects (Staniczek, 2007), were first reported by Costa-Lima (1950), and later described by Demoulin (1955). They are among the most basal winged insects and their fossils provide an important insight into the evolution of insect flight. They are reliable indicators for water quality (specifically dissolved oxygen levels), are critical for filtering particulate matter (Grimaldi and Engel, 2005), and are an important proteinaceous base component of the freshwater food chain (Allan, 1995). As both of their names suggest, Ephemeroptera are generally ephemeral as adults. Extant taxa cannot feed once emerged and may only live for a few hours or days. During this period, they emerge *en-masse*, reproduce, disperse, and then die *en-masse*. There are, of course, exceptions to this rule, and the European taxa *Caenis luctuosa* is known to have relatively asynchronous development, resulting in continuously emerging adults between March and July each year (Perán *et al*., 1999). Undoubtedly, when the adults emerge *en-masse*, a mass mortality event will follow in the perusing days. There are no known Ephemeroptera mass mortality events in the Nova Olinda Member, but fossils of both alate and larval stages are common. This, combined with the differing morphology from modern forms (discussed below), suggests that the Nova Olinda Ephemeroptera filled a very different niche to that of their modern relatives. Additionally, as discussed below, the group is in need of heavy revision. As such, this group is not examined at family-level here.

Ephemeroptera are the only order of pterygote insect that have a winged subimago stage and this can make distinguishing subimagos and imagos difficult. The winged subimago and imago stages are collectively referred to as the alate stage to distinguish them from their non-winged larvae (Grimaldi and Engel, 2005) and many of the characters that define Ephemeroptera allow for their alate stages to be easily identified. These include a greatly reduced or absent brace at the base of the forewing, lack of any anal region of the hind wings, elongate forelimbs, lack of mouthparts, and bared penes in males (Grimaldi and Engel, 2005). Unfortunately, many of these characteristics are less prominent or entirely different in Mesozoic Ephemeroptera. Unlike their modern relatives, fossils forms had homonomous wings and well-developed mouthparts as adults (Grimaldi and Engel, 2005; Staniczek, 2007). This has prompted their placement within the distinct suborder Permoplectoptera, which is now believed to be polyphyletic (Grimaldi and Engel, 2005; Staniczek, 2007). Nevertheless, alate specimens can usually be identified by the presence of extremely long cordial filaments (up to four times the body length) and equally long cerci. Fossil larval Ephemeroptera are generally easy to identify,

although can bare a closer resemblance to fossil Odonata larvae than extant ones do, and care should be taken when distinguishing the two (Grimaldi and Engel, 2005). They also possess long cordal filaments, as well as distinctive lateral gills running down the sides of their abdomens. Specimens usually preserve in dorso-ventral aspect (Martínez-Delclòs and Martinell, 1993), and this often displays their gills and other appendages distinctly. Mesozoic forms are generally considered to have a low diversity, but can be much larger than extant Ephemeroptera, reaching sizes of 40 mm in length and a 90 mm wingspan. Some taxa develop unusual appendages, including elaborate 'tusks' (in larval stages) from modified forelimbs or mandibular processes, which are used for digging burrows or feeding, and genital forceps modified from genostyles for mid-flight copulation (Keltner and McCafferty, 1986; McCafferty and Bae, 1992; Bae and McCafferty, 1995). Generally, the larval stages occupy freshwater littoral-to-benthic zones, however they are capable of limited 'swimming'.

There have been three major studies on Ephemeroptera of the Nova Olinda Member: McCafferty (1990), Martins-Neto (1996a), and Staniczek (2007), and other minor contributions include Brito (1987), Martins-Neto and Caldas (1990), Polegatto and Zamboni (2001), and Bechly *et al.* (2001a). There are currently approximately eight families recorded, with at least nine definitive species, although there have been many other taxa described with controversy. Staniczek (2007) overviewed previous studies, suggesting that there are at least four dubious identifications, ten synonyms, and 17 or more undescribed/unidentifiable taxa. Unfortunately, it appears that the majority of these synonyms and dubious identifications were the result of work by Martins-Neto, and caution should be used when referencing his work. The Nova Olinda Member Ephemeroptera is undoubtedly in need of heavy revision.

Grimaldi and Engel, 2005 provide a list of major references on the Ephemeroptera, including works by Needham *et al*. (1935), Burks (1953), Peters and Peters (1970), Edmunds (1972), Edmunds *et al*. (1976), Hubbard and Peters (1978), Flanagan and Marshall (1980), Campbell (1987), Hubbard (1990), Alba-Tercedor and Sanchez-Ortega (1991), Corkum and Ciborowski (1995), and Domínguez (2001). For more up-to-date research, see Jandry *et al*. (2014), Hamid and Rawi (2014), Qin and Zhou (2014), and Sartori and Brittain (2015). For studies of Mayfly cladistics, see Bae and McCafferty (1995), Wang and McCafferty (1995), Wang *et al*. (1997), and McCafferty and Wang (2000). Also see Li *et al*. (2014).

8. 3. 4. Odonata

Odonates are an ecologically important group of insects and the Nova Olinda Member is arguably the second most important fossil Odonata Lagerstätte. Only the Solfhofen Formation

yields as diverse or abundant an odonate fauna as the Nova Olinda Member (Ponomarenko, 1985). They compromise approximately 2% of the total insect fauna within the formation and there are 51 described species with well over 1,000 specimens (Bechly, 1998a, 2007b, 2010).

Odonates can occupy a variety of habitats including but not limited to, highland bogs, lush tropical forests, semi-arid scrublands, waterfalls, and even in the centre of arid regions (Waterston and Pittaway, 1991; Kalkman *et al*., 2008). However, the vast majority of them require a clean freshwater source for reproduction, with only a handful of species adapted to brackish or saline waters, and so the majority of species live around streams, rivers, ponds, pools, and lakes. This makes their presence an important indicator for a healthy freshwater ecosystem (Kalkman *et al*., 2008; Hart *et al*., 2014). Despite these freshwater ties, some taxa are known to migrate thousands of miles in large swarms and can be found over oceans (Russell *et al*., 1998; Anderson, 2009). Larval odonates are an extremely important component of the freshwater food chain. They are primarily benthic and are ferocious and indiscriminate predators (Grimaldi and Engel, 2005).

Despite their presence in various habitats, adult odonates essentially fill only a single niche: that of acrobatic grasping aerial predators. Their morphology is conservative relative to other insect groups and their behaviour mostly only differs in subtle styles of hunting, breeding, courtship, and territorial disputes. Given the abundance and diversity of odonates in the Nova Olinda Member, specifically their freshwater benthic larvae, it is extremely likely that they inhabited the edge of the palaeolake (possibly supported by seasonal films of freshwater at the palaeoshore) and the freshwater tributaries feeding into the palaeolake. As such, even though odonates are diverse in the Nova Olinda Member, the biology of each family will not be covered herein.

The biology of odonates has been well studied over the last half-century (Corbet, 1962, 1999; Corbet and Brooks, 2008) and this is in part due to their ecological importance, but also due to their interesting morphology and behaviour. There are approximately 6000 modern species and well over 700 fossil species described (including the 51 Nova Olinda Member taxa) (Grimaldi and Engel, 2005).

The first Nova Olinda Member odonates were mentioned by Westfall (1980), and later described by Wighton (1987). It is a fair statement to say that the majority of work on the Nova Olinda Member Odonata has been undertaken by Günter Bechly (Bechly, 1997a, 1997b, 1997c, 1998a, 1998b, 1998c, 1998d, 1999, 2000, 2005, 2007b, 2010; Bechly *et al*., 1998, 2001b,c; Bechly and Ueda, 2002), however other important contributions include: Wighton (1988), Carle and Wighton (1990), Grimaldi (1991), Nel and Escuillié (1994), Nel and Paicheler

(1994a, 1994b), Martill and Nel (1996), Nel *et al*. (1998), Jarzembowski *et al*. (1998), Fleck *et al*. (2002), Martins-Neto (2005a, 2005b), Grimaldi and Engel (2005), and Nel and Bechly (2009).

8. 3. 5. Dermaptera

Dermaptera (earwigs) are reclusive nocturnal insects that tend to live in narrow spaces, under stones or bark, in decaying wood, leaf litter, flowers, and leaf axles but may also inhabit a variety of riparian habitats (Chopard, 1938; Grimaldi and Engel, 2005; Haas, 2007). They can be found the world over (excluding Antarctica and colder regions of the arctic), however are generally less diverse in colder environments. The majority of their diversity occurs in tropical to warm-temperate zones, where their reproduction is seasonally controlled (Grimaldi and Engel, 2005). They reproduce during wetter seasons as this provides increased plant material, higher rates of decay, and coincides with the reproduction of other insect groups (Boukary *et al*., 1996).

Although feeding strategies are highly varied, highly specialised feeding adaptations are extremely rare. The majority of Dermaptera are omnivorous, but exclusively carnivorous, herbivorous, and sporophagous forms are not uncommon, as these adaptions require only minor mouthpart alterations (Haas, 2007). Unfortunately, these adaptations are almost always unclear in fossil species.

Dermaptera possess a complex mechanism for folding their hindwings down to one tenth the surface area, which likely evolved in the Cretaceous and remains unchanged in modern taxa (Hass *et al.,* 2000; Hass 2007). This unfolding process is complex and requires the use of the cerci. Additionally, all extant Dermaptera display maternal care. Despite a large variation in egg-laying behaviour, mothers will guard eggs and first instars until their second molt, where they will then cannibalise the offspring if they do not leave (Marzke and Klass, 2005; Grimaldi and Engel, 2005).

There are currently approximately 2,200 species (including fossil taxa) known, and the vast majority of these belong to Forficulina (common earwigs) (Haas, 2007). Dermaptera are not particularly common in the Nova Olinda Member and identification of fossils is generally considered difficult due to their morphological similarities with Japygidae, larval Anisoptera, and Staphylinidae (Carle, 1995). Six species of Dermaptera in three families are described from the Nova Olinda Member. Unusually, no larval Dermaptera have been identified. Due to their maternal reproductive strategy, there is a chronological and special overlap in generations and, as such, larval forms should be present along with the adults. Previous authors have

attributed this to the lower preservation potential of nymphs, or that the fossils found represent males venturing from their secluded homes to seek females (Haas, 2007).

8. 3. 5. 1. Anisolabididae

Anisolabididae is a paraphyletic family of earwigs with a cosmopolitan modern distribution (Petr *et al*., 2013). Males of this group are easily identified by an inward-bent right cercus and the most common extant members are wingless (Langston and Powell, 1975; Petr *et al*., 2013). Oddly, despite having a cosmopolitan distribution, modern diversity of this group is highest in coastal regions (Langston and Powell, 1975). A single member of this group is described from the Nova Olinda Member as *Cratoborellia gorbi* (Haas, 2007).

8. 3. 5. 1. Labiduridae

Labiduridae (striped earwigs) as their name suggests, possess striped patterning. This patterning is located down the length of the forewings and, when the wings are folded, results in a light stripe down the middle of the dorsal thorax. The group is characterised by particularly long antennae and large cerci that, in some cases, can have more than 25 segments and help distinguish this family (Rentz and Kevan, 1991). The family is reported as cosmopolitan, but unfortunately is 'taxonomically unstable' and so no definitive environmental preferences can be drawn (Engel and Haas, 2007). A single genus (*Caririlabia*) of Labiduridae is described by Martins-Neto (1990a) from the Nova Olinda Member with two species: *C. brandaoi* (Martins-Neto, 1990a) and *C. berghoffi* (Haas, 2007).

8. 3. 5. 1. Spongiphoridae

Spongiphoridae (little earwigs) is a family synonymous with 'Labiidae' and is paraphyletic (Engel and Haas, 2007; Petr *et al*., 2013). As their common name suggests, these earwigs are particularly small and are typically < 1.5 cm in length. Presumably they are also fungiphagous as the familial name implies (feeding on *Spongiforma* fungi?), however little information is available regarding their ecology. Aside from their putative size, these earwigs are otherwise simply described as 'unremarkable' (Allaby, 1999). Three species in two genera of Spongiphoridae are described from the Nova Olinda Member. The first earwig was described in 1990 as *Cretolabia cearae* (Popham, 1990), followed by *Kotejalabis goethitica* (Engel and Chatzimanolis, 2005) and later *K. haeuseri* (Haas, 2007) species was attributed to *Kotejalabis.*

Finally, a single staphylinid beetle from the Nova Olinda Member (*Carirriderma pilosa,* Martins-Neto 1990a) has been erroneously identified as an earwig.

8. 3. 6. Orthoptera

Orthoptera (grasshoppers, crickets, and locusts) are the most diverse group among Polyneoptera with 22,500 extant species (Grimaldi and Engel, 2005), and this diversity is well represented in the Nova Olinda Member. They are the most numerous and diverse group from the formation (Grylloidea are most diverse, Elcanidae are most abundant), making up approximately 27% of the fossil specimens and over 75% of the species described (Martins-Neto, 1987-2003), although these numbers are likely in need of revision, and at least one taxon has been reassigned to the extant genus *Schizodactylus* (Heads and Leuzinger, 2011). This makes the Nova Olinda Member hugely important for orthopteran palaeontology, and it is their most diverse and well-preserved Mesozoic assemblage (Martins-Neto, 1991a-d, 2003; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). As a result, they are hugely ecologically important for the formation as they represent the bulk of its diversity. Orthoptera is divided into two primary groups, the Ensifera (crickets, katydids and their allies) and Caelifea (grasshoppers and locusts).

Most orthopterans are phytophagous, and feed on roots or leaves, however some species are known to specialise on other foods. Some taxa feed on fungi, pollen, nectar, flowers, specific plant species, are omnivorous, or predacious. Some species of Caelifea are particularly known for their formation of gigantic swarms that consume all plant matter in their path, devastating agriculture across North America and Africa. These swarms are formed when a population size exceeds the ability of the environment to provide salts and protein. Cannibalism becomes rife within the swarm, and they migrate by essentially chasing each other (Simpson *et al*., 2006).

Orthoptera are probably most well-known for their vocalisations, which can even play a role in their systematics (Marshall and Haes, 1988; Rentz, 1996; Grimaldi and Engel, 2005), and their astonishing jumping ability (Heads and Martins-Neto, 2007). However, many lineages of Orthoptera have also developed complex mimicry, imitating leaves, twigs, or flowers, similar to their close relatives the Phasmatodea. Others have aposematic colouration and behaviour to confuse predators (Heads and Martins-Neto, 2007). The Nova Olinda Member yields one specimen (*Eoproscopia martilli*) that has a remarkable stick-like morphology, and is considered the oldest definitive fossil twig mimic (Heads, 2008; Wedmann, 2010). For major references on Orthoptera biology, see Uvarov (1928, 1966), Chopard (1938), Otte (1981, 1984, 1994), Gwynne and Morris (1983), Gangwere *et al*. (1997), Field (2001), Gwynne (2001), and Béthoux and Nel (2002), and for their systematics, see Jost and Shaw (2006), Fenn *et al*. (2008), and Hiatt and Whiting (2013).

8. 3. 6. 1. Suborder Ensifera

8. 3. 6. 1. 1. Hagloidea

Hagloidea today is low-diversity relic superfamily, although its diversity was significantly higher in the Mesozoic (Grimaldi and Engel, 2005). Members of this family have traits that intermingle with other gryllids, but it is generally considered the most basal family within Ensifera (Grimaldi and Engel, 2005; Jost and Shaw, 2006). However, recent genomic studies suggest that it is in fact a sister group to the superfamily Rhaphidophoroidea and more closely related to Tettigonioidea than gryllids (Zhou *et al*., 2014). It is currently believed that the diversity of this family diminished in the Cretaceous, and this is supported by its low diversity in the Nova Olinda Member. Only two species in two genera have been described from the Nova Olinda Member, both by Martins-Neto (1991).

8. 3. 6. 1. 2. Schizodactyloidae

Schizodactylidae (dune crickets), as their common name suggests, are associated with desert or sandy areas, but also moist areas with sand (i.e. lagoons and coasts) (Aydin and Khomutov, 2008). They are typically nocturnal, burrowing, flightless insects that are largely insectivorous and even cannibalistic (Grimaldi and Engel, 2005; Aydin and Khomutov, 2008). They have particularly unusual legs, with splayed, almost leaf-like, tarsal protrusions and this strange character has led to their other name, the ‘splay-footed crickets’. These protrusions are an adaptation to moving on loose sand but are also extremely important for burrowing (Aydin and Khomutov, 2008). Only a single taxon of Schizodactylidae is known from the Nova Olinda Member and it was originally described as *Brauckmannia groeningae* by Martins-Neto. However, it has now been reassigned to the extant genus *Schizodactylus* (Heads and Leuzinger, 2011).

8. 3. 6. 1. 3. Gryllotalpidae

Gryllotalpidae (mole crickets) are a family of morphologically distinct and ecologically interesting orthopterans. As their common name suggests, they occupy an unusual burrowing niche and have several distinctive adaptations to a subterranean lifestyle. Most notable are their robust and ‘clawed’ fossorial forelimbs, but they can also be recognised by their heavily sclerotized head and prothorax, which forms a large protective plate (Grimaldi and Engel, 2005; Capinera, 2008). They typically feed on various plant roots and have a relatively low modern diversity (Grimaldi and Engel, 2005). Only three species in three genera are described from the Nova Olinda Member, but their presence is particularly important. Although females will fly at night in search of singing males (Capinera, 2008), mole crickets spend the vast majority of their time underground. As such, their presence within the Nova Olinda Member further provides evidence for seasonal flash floods bringing insects into the palaeolake.

8. 3. 6. 1. 4. Gryllidae

Gryllidae (true crickets) are, as the common name suggests, what most non-entomologists envision when ‘crickets’ are mentioned. They have a high modern diversity, with 900 described species, but are typically characterised by large, round heads, cylindrical bodies, long antennae, and forewings adapted into sound-producing (but also protective) elytra (Resh and Cardé, 2009). They have a cosmopolitan distribution (excluding colder regions) although their diversity is highest in tropical regions (Huber, 1989; Resh and Cardé, 2009). They are typically nocturnal and can be found in a variety of habitats, including grasslands, scrubland, forests, marshes, beaches, and caves and many taxa have become secondarily flightless (Huber, 1989). While some taxa can be exclusively herbivorous or even predatory, the majority of species are omnivorous and eat a wide variety of organic matter (Huber, 1989; Resh and Cardé, 2009). Gryllidae have a moderate diversity within the Nova Olinda Member, with 11 species in four genera all described by Martins-Neto (1987-2002).

8. 3. 6. 1. 5. Baissogryllidae

Baissogryllidae is an extinct family of crickets closely related to Gryllidae that is currently restricted to the Cretaceous and was erected be Gorochov (1985). Despite their abundance and diversity within the Nova Olinda Member (19 species in six genera), there is little information on their ecology or morphology, which may be a result of the lack of English translations of original descriptive material. Presumably, based on their systematics, they had a similar ecology to the extant Gryllidae.

8. 3. 6. 1. 6. *Incertae sedis*

A single tentatively assigned genus and species (*Phasmomimella*? *araripensis*) is reported as family *incertae sedis* (Martins-Neto, 1991). The genus name suggests placement in the family Phasmomimidae.

8. 3. 6. 2. Suborder Caelifera

For early discussions regarding Nova Olinda Member Caelifera, see Martins-Neto (2003a).

8. 3. 6. 2. 1. Tridactylidae

Tridactylidae (pigmy mole crickets) are a family of tiny (< 20 mm, but often < 10 mm) cricket-like grasshoppers that are somewhat convergent with members of Gryllotalpidae (Grimaldi and Engel, 2005). They are gregarious shallow burrowers that mostly occur in tropical and subtropical regions (Grimaldi and Engel, 2005). Some taxa could possibly be considered semi-aquatic as they are able to run along the water surface, swim, dive, and even jump off the

water surface (Picker *et al*., 2002). There are two species described from a single genus of Tridactylidae in the Nova Olinda Member.

8. 3. 6. 2. 2. Proscopiidae

Proscopiidae (false stick insects) are, as their common name clearly indicates, highly convergent with members of Phasmatodea. They have a stick-like habitus with a long, slender body, a long angular head, and tend to be wingless (Grimaldi and Engel, 2005). Only a single genus, with a single species, is described from the Nova Olinda Member.

8. 3. 6. 2. 3. Locustopsidae (or Locustopseidae) and Araripelocustidae

Locustopsidae (and its subfamily(?) Araripenlocustidae) is an extinct family of Caelifera that represents one of the earliest definitive records of caeliferans. Little information is available about this group, other than that it may in fact be a stem-group of modern superfamilies (Grimaldi and Engel, 2005). They were clearly very successful in the Nova Olinda Member as they are abundant and diverse. They are, in fact, the most diverse family of orthopterans, with 16 species described across four genera (and two species of Araripenlocustidae in a single genus) (Heads and Martins-Neto, 2007). However, it is likely that many descriptions are in need of heavy revision. They are morphologically similar to modern locusts (Heads and Martins-Neto, 2007) and, if their ecology is similar, swarming behaviour could account for their abundance in the Nova Olinda fossil record. However, no obvious mass mortalities of Locustopsidae are reported. It is possible that the names Locustopsidae and Araripelocustidae are no longer used, and the Nova Olinda Member members have yet to be updated to modern nomenclature.

8. 3. 6. 2. 4. Elcanidae

Elcanidae (elcanid grasshoppers) is a particularly phylogenetically confusing group of extinct orthopterans. While one of their most distinctive characters is the presence of flattened spurs on the dorsal surface of the hind tibia (Fang *et al*., 2015), which is likely an adaptation for jumping on soft substrates, they also possess a suite of ensiferan-like characters (Grimaldi and Engel, 2005). In addition to this, members from the Nova Olinda Member also possess an unusual micron-scale mesh of cuticular ridges over their heads (Barling *et al*., 2015). Because of this confusing, yet distinctive array of characters, they have previously been considered members of Ensifera, are currently considered Caelifera, but could also be a sister group to all of Orthoptera (Fang *et al*., 2015). This family has a low diversity within the Nova Olinda Member, with only two species within a single genus described. Despite this, they completely dominate the orthopteran fauna and are extremely common (Heads and Martins-Neto, 2007).

8. 3. 6. 2. 5. Bouretidae?

A single, poorly preserved, specimen from the Nova Olinda Member led to this family being (tentatively?) erected. It appears to have close affinities to either Locustopsidae or Tetrigidae, however due to the poor preservation of the holotype, no information on ecology is available (Heads and Martins-Neto, 2007).

8. 3. 7. Chresmododea

Chresmododea (fossil 'waterstriders') is an extinct order(?) of insects that is exclusively found in the Mesozoic and share a surprisingly similar morphology and habitus to the extant Hemiptera family Gerridae (water striders). They likely fed on other insects (although with chewing mouthparts, rather than piercing ones) while 'striding' on the water surface. Despite their similarities, the two groups are not closely related. Chresmododea possessed long multi-segmented flagellate tarsi, with more than 40 tarsomeres, a trait unique within Insecta (Nel *et al*., 2004; Delclòs *et al.,* 2008).

The phylogenetic relationships of this family has a history of controversy, including heated disputes and forged data. Previous work has suggested that Chresmododea contained four families (Aerophasmatidae, Necrophasmatidae, Aeroplanidae, and Chresmodidae) (Martynova, 1962, 1991), however recent work has demonstrated otherwise. Of these families, it is now believed that Chresmodidae is the sole family within Chresmododea, which has been re-established as a distinct orthopteroid group (possibly a distinct order?), rather than a suborder/family of Phasmatodea. For a full history of the phylogenetics of this group, see Bechly (2007e) and Delclòs *et al.* (2008).

Only a single genus and species (*Chresmoda neotropica*) of Chresmodidae is known from the Nova Olinda Member from six specimens (Grimaldi and Engel, 2005; Delclòs *et al.*, 2008). It was first reported by Bechly (1998b), figured by Bechly *et al*. (2001a), and later described by Engel and Heads (2008). Unusually, all of these specimens are alate adults with long wings.

It has been previously discussed that *Chresmoda* represents the only autochthonous aquatic insect within the Nova Olinda Member, inhabiting the palaeolake/lagoon edges (Bechly, 2007e). However, it is possible that other groups also inhabited the lake edges and, as only alate forms are known, it is also possible that these represent individuals dispersing away from other aquatic localities.

For overviews of this exclusively fossil taxon, see Handlirsch (1906–1908), Esaki (1949), Ponomarenko (1986), Martínez-Delclòs (1989), Carpenter (1992), Rasnitsyn (2002), Nel *et al*. (2004), Grimaldi and Engel (2005), and Delclòs *et al.*, (2008).

8. 3. 8. Phasmatodea

Phasmatodea (stick insects) are famously cryptic insects that mimic twigs, branches, and leaves. Their mimicry is not only morphological, but can also be behavioural, with many species swaying in the wind or remaining perfectly still during the day and feeding only at night (Grimaldi and Engel, 2005). It can even extend to their eggs, which often mimic seeds (Sellick, 1997, 1998). For overviews of their mimicry, see Bedford (1978), Key (1991), and Grimaldi and Engel (2005). They are a relatively diverse group, with approximately 3,000 modern species and are restricted to temperate and tropical habitats (Grimaldi and Engel, 2005). They can reach extremely large sizes, up to 555 mm in length. As one might expect, phasmatodeans live in intimate association with plants and are exclusively phytophagous. For overviews of their biology, see Bedford (1978), Mazzini and Scali (1987), Brock (1999), and Bradler (2003).

Only a single species within the extinct family Aerophasmatidae is described from the Nova Olinda Member and it is known only from an isolated wing, suggesting that the specimen likely represents input from a distant temperate-to-tropical wooded or scrubland area (Martins-Neto 1989b; Heads and Martins-Neto, 2007). This preservation is typical of Mesozoic phasmatodeans (Gorochov and Rasnitsyn, 2002) and they do not preserve enough detail to confirm a Mesozoic mimic morphology. These early fossils are believed to represent stem-group Phasmatodea, and so the extent of the mimicry is unknown (Willmann, 2003; Grimaldi and Engel, 2005).

8. 3. 9. Mantodea

Mantodea (mantises) are beautiful, but vicious, voracious, and indiscriminate predators. They are easily recognised by their distinctive spiny raptoral forelimbs (held in the ‘praying pose’ at rest) and are most well known for their ferocity, cannibalism, and the speed at which they ambush prey (Grimaldi, 2003; 2007; Grimaldi and Engel, 2005). It is now believed that this cannibalism is largely an artefact of human interference, as they are thinly dispersed solitary animals in their natural habitat, with nymphs scattering immediately after hatching (Grimaldi and Engel, 2005). The vicious and indiscriminate nature of mantises, the prolonged contact they experience during copulation, and the stress induced by a human presence all likely

contribute to cannibalism during copulation (Grimaldi and Engel, 2005). These aspects of their biology dominate the public mindset of mantises, but undoubtedly the most fascinating and often overlooked aspect of their biology is their astounding array of mimicry. They are ambush predators living in intimate association with, and mimicking, various leaves (both living and dead), flowers, and twigs. Basal Mantodea are believed to have chased down their prey along branches and tree trunks before they evolved complex mimicry (Vršanský, 2002b; Grimaldi, 2007).

Despite their interesting biology, their phylogeny has been largely ignored until relatively recently (Grimaldi and Engel, 2005; Svenson and Whiting, 2009). The only major non-regional studies of their phylogeny were undertaken by Beier (1968), Roy (1999), and Svenson and Whiting (2009), and approximately 2,300 modern species are described. Much of the classification work carried out on mantises does not accurately represent their true phylogeny and approximately only half of the families, subfamilies, and tribes erected are monophyletic (Svenson and Whiting, 2009). This is likely a result of their complex mimicry making characters difficult to discern, as well as major morphological convergences (Grimaldi and Engel, 2005; Svenson and Whiting, 2009).

Mantodea are extremely rare in the fossil record and this is likely a result of their thinly dispersed nature and association with plants (Grimaldi, 2007). They do not live in environments that promote fossilisation and do so in small numbers. Only 28 fossil Mantodea species have been described and the Nova Olinda Member is no exception to this rarity, with only two species described from 26 specimens (Grimaldi, 2007; Hoernig *et al*., 2013; Lee, 2014). In addition to these described species, another is noted, but lacks sufficient diagnostic material to warrant a full description (Grimaldi, 2007). Their presence further suggests input from a forested or scrubland hinterland. Crown group Mantodea are suggested to have a Cretaceous gondwanan origin, and so the Nova Olinda Member could be of particular importance for understanding their confusing phylogenetics (Svenson and Whiting, 2009). However, more recent molecular studies suggest a Late Carboniferous origin (Legendre *et al.,* 2015).

8. 3. 10. Blattodea

Blattodea (cockroaches) are an extremely successful group of insects. They are cosmopolitan in arid and humid environments (Bechly, 2007c), although have a higher diversity in wet, tropical forests (Grimaldi and Engel, 2005). They are generally cryptic and prefer to dwell under stones, bark, leaf litter, or in logs and emerge during darkness. Many taxa can be diurnal or nocturnal,

however others are troglodytes and are adapted to living in complete darkness (often associated with bat colonies) (Grimaldi and Engel, 2005). All Blattodea are extremely polyphagous and are known to feed on decaying/fresh leaves, fruits, fungi, rotten wood, bird droppings, guano, dung, meat, hair, books, and most other organic substances (Grimaldi and Engel, 2005; Orkin, 2015). Despite these broad feeding strategies, many species of cockroaches are highly habitat-specific (Bechly, 2007c) and it is believed that many of the taxa yielded by the Nova Olinda Member are characteristic of shrub vegetation (Vršanský pers. comm. *in* Bechly, 2007c). Cockroaches have a relatively high preservation potential, as their forewings are heavily sclerotized (Martínez-Delclós *et al*., 2004; Smith *et al*., 2006). The majority of cockroach taxa are able to fly, however some lineages are secondarily flightless (Grimaldi and Engel, 2005).

There are approximately 4,000 modern and 1,000 fossil species of Blattodea (Vršanský, 2002a, 2005), however the higher systematics of this group is uncertain. Recent studies have found several families, including the largest Blattidae, to be non-monophyletic (Legendre *et al*., 2015). Blattodea are generally common in the fossil record, and are especially abundant in Carboniferous coal swamps. The Nova Olinda Member also has an especially abundant cockroach fauna with them comprising approximately 26% of all insect fossils (Bechly, 2007c). This fauna is dominated by Blattellidae, with approximately 60% of all cockroach specimens belonging to this group. The first Nova Olinda cockroaches were described in the mid and late 80s (Pinto and Purper, 1986; Pinto, 1989). There are currently six formally described species, two species that have morphological descriptions, but are not named, and a further two that are distinct but as yet undescribed (Bechly, 2007c). In addition to these, there are many specimens that are yet to be studied and likely represent new species (Bechly, 2007c). For major studies of cockroach biology, see Guthrie and Tindal (1968), Cornwell (1968), Roth (1991), and Vršanský *et al*. (2002). For an overview of their phylogeny, see Djernaes *et al*. (2012).

8. 3. 10. 1. Mesoblattinidae

Mesoblattinidae is an extinct family of roaches that, until relatively recently, was only known from fragmentary remains (Wei and Ren, 2013). They are now known to be morphologically very similar to Blattellidae, which may be descendants of Mesoblattinidae. They differ in that they have several key plesiomorphic wing venation characters and a primitive oothecal reproductive method (Wei and Ren, 2013). Only a single distinct taxon has been reported from the Nova Olinda Member, but is yet to be described (Bechly 2007c).

8. 3. 10. 2. Blattellidae

The family Blattellidae (= Ectobiidae; Wei and Ren, 2013) (wood cockroaches) are the most commonly recognised roaches, as the majority of household pest species reside within this family. These insects generally prefer warm, humid environments and are (as with most cockroaches) highly polyphagous. Only a single species of this family is described from the Nova Olinda Member (Pinto and Purper, 1986), although another distinct undescribed species (listed as 'undescribed species A' in Bechly, 2007c) is also reported (Bechly 2007c). Despite the shared niche of this family, it is probably paraphyletic (Grimaldi and Engel, 2005).

8. 3. 10. 3. Blattidae

Blattidae (American, Asian, German, and brown-banded cockroaches) is the largest cockroach family, with 525 described modern species. This also includes the common pest genus *Periplaneta* (Grimaldi and Engel, 2005). They possess the morphology of the 'classically recognised' cockroach and generally share the same niche as Blattellidae. The family is non-monophyletic (Legendre *et al*., 2015) and Blattidae *sensu stricto* is characterised by the production of an ootheca after sclerotisation of an internal ovipositor. Only a single species has been described in the Nova Olinda Member (Pinto, 1989).

8. 3. 10. 4. Blattulidae

Blattulidae is an extinct group of roaches currently only known from the Mesozoic. They possess strongly 'toothed' mandibles, likely used in a broad omnivorous habit, and had cursorial limbs (Wang *et al.*, 2007). This provided them with a high adaptability, however they were outcompeted towards the end of the Mesozoic by the superior oothecal reproductive system of other roaches (Wang *et al*., 2007). The phylogenetics of this group are uncertain, however they may be closely related to Polyphagidae (Bechly, 2007c).

While they are the dominant roaches in other Cretaceous localities (Yixian Formation), they have a very low diversity in the Nova Olinda Member (Bechly, 2007c; Wang *et al.*, 2007). Only a single genus and species is described, however another distinct genus is still undescribed (Bechly, 2007c).

8. 3. 10. 5. Raphidiomimidae

Raphidiomimidae is an unusual family of cockroaches that have convergent characters with mantises (Grimaldi and Ross, 2004). They are exclusively Mesozoic and are highly specialised, which is unusual for primitive cockroach groups (Grimaldi and Engel, 2005). They have moderately long antennae, a large and wide pronotum, tergal glands on males (important for species determination within this family), and a head with synapomorphic characteristics with living cockroaches (Wei and Ren, 2013). However, their most prominent characteristic is

unusual raptoral forelimbs implying a predatory lifestyle, which is rare among cockroaches (Grimaldi and Ross, 2004). In other formations they are preserved with vivid colour patterning, which is typically indicative of a humid environment (Ding *et al*., 2003; Wei and Ren, 2013). They are, unfortunately, rare in the Nova Olinda Member and only a single undescribed specimen is reported (Bechly, 2007c).

8. 3. 10. 6. Ponopterixidae

Ponopterixidae (formally within Umenocoleoidea) is an extremely unusual beetle-like family of roachoid (Nel *et al*., 2014). They possess thick saddle/shield-like elytra, well-developed cerci, and wing venation similar to Blattulidae (Bechly, 2007c). However, they also have an external ovipositor, which excludes them from modern cockroaches (Nel *et al*., 2014). The specimens described from the Nova Olinda Member were originally placed within Umenocoleoidea, however the type genus *Umenocoleus* has been re-evaluated and transferred to Coleopterida. As these specimens are clearly cockroaches, they were transferred to Blattodea: Cratovitismioidea: Ponopterixidae (Nel *et al*., 2014). Only three species are described, but despite this low diversity, they are particularly common in the Nova Olinda Member (Vršanský, 1999; Bechly, 2007c; Nel *et al*., 2014).

8. 3. 10. 7. Family *incertae sedis*

One additional unnamed, but distinct, roach specimen is reported as family *incertae sedis* (Bechly, 2007c).

8. 3. 11. Isoptera (infraorder within Blattidae)

Isoptera (termites) are probably the second most *ecologically* important group of insects, surpassed only by hymenopterians. Despite Isoptera being an infraorder of Blattidae, here they are examined separately due to their ecological importance, distinct behaviour, and differing morphology. They have a diversity of approximately 2,960 modern species and 280 fossil species, although 80% of this diversity is within the derived extant family Termitidae (Grimaldi and Engel, 2005; Martins-Neto and Pesenti, 2006; Bechly, 2007d; Vršanský and Aristov, 2014). They first become prevalent in the fossil record during the Early Cretaceous, although arose in the Late Jurassic (Grimaldi and Engel, 2005). They are generally soft-bodied, and so their preservation potential outside of amber is relatively low, however their intimate association with some woody trees greatly increases their likelihood of inclusion in amber.

Termites are abundant in all tropical, sub-tropical, and most arid environments, although are virtually absent above or below 45°N and 45°S. They are abundant in such numbers that they can account for up to 10% of the total animal biomass in tropical areas. Their success in largely due to both their complex eusocial colonies and their ability to exploit a vast array of plant matter for food. Their colonies can either be constructed within their food substrate (i.e. household pest termites 'one-piece nesting'), or as complex mound structures from which they forage. Their colonies differ from that of hymenopterans in that termite soldiers and workers belong to both sexes and that members are able to transform into other castes depending on pheromone distribution.

They are able to feed on both living and dead plant matter via a symbiotic hindgut microbiota and/or via symbiotic fungi within some colonies, as well as fungi, soil, and organic detritus (Bechly, 2007d). These provide termites with the means to digest all forms of cellulose, or feed on fungi that are able to (Honigberg, 1970; Breznak and Brune, 1994; Breznak, 2000; Inoue *et al*., 2000).

Most insects have important ecological roles, and termites are no exception to this. In fact, they have a profound impact on every environment they inhabit. They are key for the recycling of plant matter that many organisms find difficult to digest and can consume up to 20% of an environments total annual plant material (Bechly, 2007d). This means that they are second only to forest fires for their ability to clear dead plant material (Grimaldi and Engel, 2005). They are absolutely vital in the formation, mineralization, and humification of soil in the areas they inhabit, as they are able to redistribute digested plant matter into it. Mound building termites can process, alter, and move an astonishing amount of sediment. A single colony can construct towers up to 8 m tall and subterranean tunnels can exceed 12 meters in diameter, amounting to over 15 tons of earth, and there may be many thousands of colonies per square mile. The highest estimated population sizes can be up to 6.99 million individuals, however most colonies likely harbour under one million members (Evans *et al*., 1998). The sheer number of individuals moving sediment (at only a mandible-full of grains at a time) over the course of the last 50 million years or so (the radiation of mound building termites) has undoubtedly had a profound and immeasurable impact on global geological history (Bechly, 2007d). It is possibly that entire formations may have been homogenised, destroyed, or created by termites alone.

For overviews of termite biology, see Wood (1978), Wood and Sands (1978), and Bignell and Eggleton (2000). For major reviews of the termite fossil record, see Nel and Paicheler (1993) and Thorne *et al*., (2000). For an overview of their phylogeny, see Legendre *et al*. (2008).

The Nova Olinda Member is extremely important for Isoptera palaeontology. It yields a relatively large number of specimens (several hundred) and, until recently, was the oldest fossil records of definitive termites (Bechly, 2007d; Vršanský and Aristov, 2014). The oldest termites are now known from the Jurassic/Cretaceous transitional beds of Chernovskie Kopi (Vršanský and Aristov, 2014). Termites were clearly abundant in the hinterlands of the Nova Olinda Member and are generally indicative of woody plants, despite an unusual lack of woody material in the formation. In fact, the number of termite specimens is greater than the number of twigs over 10 cm in length (Bechly, 2007d). Shrubs and herbs are common in the Nova Olinda Member and it is possibly that these termites fed primarily on small twigs provided by abundant gnetaleans (Bechly, 2007d), however it is also possible that there is a taphonomic factor controlling the input of large terrestrial material into the formation (Martill pers. comm., 2014).

Interestingly, all fossil termites recovered from the Nova Olinda Member are alate stages, either with or without wings, and no workers or soldiers have been recovered. The absence of workers and soldiers is clearly not a biostratinomic issue, as other terrestrial flightless insects are present in abundance (Bechly, 2007d). Their absence is likely largely a result of 'one-piece nesting' style, as the workers and soldiers would rarely leave the confines of the colony. This hypothesis is supported by the fact that many Nova Olinda Member termites are considered basal taxa, or 'lower termites' (Grimaldi and Engel, 2005). This is further supported by phylogenetic studies that show the families present within the Nova Olinda Member are basal (Legendre *et al*., 2008). These families are believed to have constructed small 'one-piece' colonies within their food substrate, excluding the family Hodotermitidae (*Meiatermes* and *Cretarhinotermes*) (Grimaldi *et al*., 2008). These genera may represent a more derived taxa and could have produced small burrows and mounds, however periodic flooding of the Nova Olinda hinterland (as suggested by the cyclic input of organic matter) also suggests against this, as the burrows would probably have flooded annually (Bechly, 2007d). Regardless, it is highly unlikely that large and complex mounds were created by Nova Olinda Member termites.

8. 3. 11. 1. Cratomastotermitidae

Cratomastotermitidae, as the name suggests, is closely related to the termite family Mastotermitidae (Vršanský and Aristov, 2014). It is widely accepted as the most basal family and Cratomastotermitidae + Mastotermitidae form a group that is sister to all other termites (Legendre *et al*., 2008). Extant members of Mastotermitidae are restricted to Australia (Grimaldi and Engel, 2005). As might be expected, this family has many basal characteristics and is much more cockroach-like than other termites (Vršanský and Aristov, 2014). Only a single species in a single genus is known from the Nova Olinda Member (Bechly, 2007d).

8. 3. 11. 2. Kalotermitidae

Kalotermitidae (drywood termites) is an extant basal family of primarily xerophytic termites, as suggested by their common name. This trait, however, is believed to be a relatively recent adaption and their ancestors may not have been as well adapted to dry climates (Tompson *et al*., 2000). As with many basal termite families, they are one-piece nesters that construct very simple burrows within their food substrate. Only a single species within a single genus is described from the Nova Olinda Member (Bechly, 2007d).

8. 3. 11. 3. Termopsidae

Termopsidae (rottenwood or dampwood termites), in stark contrast to Kalotermitidae, thrive in moist or rotting wood. They are, again, a basal one-piece nesting family but also have a disjointed modern distribution (Grimaldi and Engel, 2005). Again, only a single species within a single genus is described from the Nova Olinda Member (Bechly, 2007d).

8. 3. 11. 4. Hodotermitidae

Hodotermitidae (harvester termites) are the most derived family of termites known from the Nova Olinda Member (Bechly, 2007d; Legendre *et al*., 2008). As their common name indicates, they construct a nest, then forage plant material from the surrounding area. Modern members of this family mostly consume grasses (ripe, or damaged by frost or drought) and some tree and shrub material, which obviously was not the case in the Cretaceous (Symes and Woodborne, 2010). While this group does construct mounds, they are relatively small. Interestingly, this derived family is the most diverse termite family within the Nova Olinda Member, but still restricted to three species within two genera (Bechly, 2007d).

8. 3. 11. 5. Familial placement corrections

Two other genera and species (*Caatingatermes megacephalus* and *Araraiptermes native*) have been described by Martins-Neto *et al*., (2006) that were later demonstrated to be *nomen incorrectum* (Engel *et al*., 2009). These were placed within a newly erected single subfamily (Caatingatermitinae) that was also demonstrated to be synonymous with Hodotermitinae (Engel *et al*., 2009). Another species (*N. obesa*) erected in the same volume was attributed to the genus *Nordestinatermes* in the family Cretatermitinae and is also a *nomen incorrectum* (Engel *et al*., 2009). *Cretatermes pereirai* (Fontes and Vulcano, 1998) was also proposed to be a junior synonym of *M. ararpena*. Additionally, the species *M. araripena* (Krishna, 1990) was incorrectly placed by Bechly (2007d), and Grimaldi *et al*., (2008) restored the position of *M. araripena* within Hodotermitidae. Finally, *Cretarhinotermes* was repositioned to within

Hodotermitidae, rather than Rhinotermitidae as its namesake (Grimaldi *et al*., 2008; Engel *et al*., 2009).

8. 3. 12. Hemiptera

Hemiptera (true bugs) is an extremely diverse group with an estimated diversity of up to 80,000 modern species. Despite this diversity, they are clearly monophyletic, distinguished by a distinct and complex mouth structure (Grimaldi and Engel, 2005). They have lost their maxillary and labial palps, developed a unique rostrum structure, and evolved a 'pumping' system of muscles that together form a unique 'sucking beak' (Grimaldi and Engel, 2005). This combination of features allows them to feed on fluids, and some groups have further adapted their digestive system to compensate. Many members possess a specialised gut system called an 'alimentary filter system' which absorbs and excretes excess water and sugar rapidly, producing 'honeydew' excrement (Grimaldi and Engel, 2005).

Hemiptera has a particularly confusing history of phylogenetic, with ordinal-level name variations. Hemiptera, Homoptera, and Heteroptera have all been suggested as ordinal-level names, however Hemiptera is now the accepted name (Poisson, 1951; Miller, 1956; Carver *et al*., 1991; Schuh and Slater, 1995; Grimaldi and Engel, 2005; Song *et al*., 2012). There has been similar confusion among subordinal names, and it is now accepted that there are four distinct suborders: Auchenorrhyncha, Coleorrhyncha, Sternorrhyncha, and Heteroptera (Li *et al*., 2012; Song *et al*., 2012).

8. 3. 12. 1. Suborder Auchenorrhyncha

8. 3. 12. 1. 1. Infraorder Cicadomorpha

Cicadomorpha is among the most diverse group of phytophagous insects with approximately 35,000 modern species described (Cryan, 2005; Grimaldi and Engel, 2005). Virtually all of these feed solely on plant vascular fluid, however a few taxa have adapted to feeding on fungal fluids. They are generally cryptic insects and some lineages have developed complex leaf and seed mimicry (Grimaldi and Engel, 2005). Despite this, cicadomorphs are probably most well-known for their periodic emergence *en masse*, with a handful of taxa that emerge after an extremely long hiatus (specifically North American *Magicicada*). Nymphs can live for up to 17

years underground, feeding on xylem fluid from tree roots before emerging simultaneously in a gigantic swarm (Grimaldi and Engel, 2005). This unusual lifecycle is restricted to members of Cicadidae and, although some relatives of this group are present, no actual members have been found from the Nova Olinda Member. Another interesting aspect of cicadomorph biology is the ability of some nymphs to secrete a calcareous material, which hardens to form a protective mineral tube. This ability resides solely in the African and Australasian family Macherotidae (Grimaldi and Engel, 2005). Some cicadomorphs nymphs are gregarious, and are often tended to symbiotically by hymenopterans in exchange for honeydew (Grimaldi and Engel, 2005). For an overview of their biology, see Grimaldi and Engel (2005) and Dietrich (2009).

Studies on the Nova Olinda Member cicadomorphs first began in the 1990s (Hamilton, 1990, 1996) and has continued into the 2000s (Menon and Heads, 2005; Menon *et al*., 2005; 2007). Despite all of this attention, cicadomorphs are relatively rare in the Nova Olinda Member and only 21 species have been described (Menon *et al*., 2007), with the most abundant and diverse fossils belong to the genus *Hallex* (Myerslopiidae) (Menon *et al*., 2007). The Nova Olinda Member is of importance for Auchenorrhyncha phylogeny as it contains examples of some early and stem group cercopoid (Ueda, 1997; Grimaldi and Engel, 2005; Menon *et al*., 2007).

8. 3. 12. 1. 1. 1. Superfamily Membracoidea

8. 3. 12. 1. 1. 1. 1. Cicadellidae

Cicadellidae (leafhoppers) are the largest family of Cicadomorpha and the second largest family of Hemiptera, with almost 20,000 modern species described (Grimaldi and Engel, 2005). Even though this family is highly diverse, all member share modified hind limbs for jumping and are phytophagous, hence their common name (Stiller, 2009). They are typically small and often vividly coloured, with elaborate stripes and spots (Grimaldi and Engel, 2005; Stiller, 2009). They have a cosmopolitan modern distribution, and are abundant throughout temperate and tropical regions (Stiller, 2009). Some taxa are highly specialised parasites of a single plant species and can be particularly problematic agricultural pests, causing significant economic damage (Bentz and Townsend, 2005; Stiller, 2009). Leafhopper diversity is low in the Nova Olinda Member, with only three species described across two subfamilies (Menon *et al*., 2007).

8. 3. 12. 1. 1. 1. 2. Myerslopiidae

Myerslopiidae are a small and highly-cryptic extant family that, until recently, little was known about. This is a result of their small size, cryptic life-style, camouflage/translucency, and their

tendency to jump a considerable distance when disturbed (Rakitov, 2015). Studying these insects alive in the wild is nearly impossible, as even a subtle disturbance will immediately cause them to disappear into the undergrowth. They are strong jumpers with stout, heavily sclerotized bodies, elytra-like medially sealed tegmina, and lack hind wings (Rakitov, 2015). They have not been *observed* feeding on living plant matter, but are presumed to feed on roots or stems within leaf litter. They have, however, been observed feeding on damp, rotting wood and are known from bog, forested, and open habitats (Rakitov, 2015). While phylogenetic analyses place them within Membracoidea (Cryan, 2005), more recent studies of their morphology suggest they may in fact be a distinct sister group to Membracoidea (Rakitov, 2015). If they are *within* Membracoidea, they are one of the few lineages that do not secrete brochosomes (small spherical micro-structures used as a water-repellent) and have a unique Malpighian tubule organisation (Rakitov, 2015). Seven species in two genera are described from the Nova Olinda Member and interesting, only 19 morphologically similar modern species are described (Menon *et al*., 2007; Rakitov, 2015). These modern taxa have a disjunct distribution, suggesting a gondwanan origin. As such, the Nova Olinda Member fossils are likely of significant importance for understanding the evolution and phylogeny of this cryptic family.

8. 3. 12. 1. 1. 2. Superfamily Cicadoidea

8. 3. 12. 1. 1. 2. 1. Tettigarctidae

Tettigarctidae (hairy cicadas) are a small relic family and their highest diversity appears to have been during the Mesozoic (Kaulfuss and Moulds, 2015). They are morphologically primitive and form a sister group to Cicadidae (singing cicadas) (Grimaldi and Engel, 2005; Kaulfuss and Moulds, 2015). They can be distinguished from singing cicadas by an expanded pronotum, completely developed forewing venation, and lacking tympanal auditory organs. As such, they are unable to produce sound in the same manner as typical singing cicadas and instead transmit sound via substrate vibration (Kaulfuss and Moulds, 2015). Modern hairy cicadas inhabit high-altitude cold environments, but the ancestral Mesozoic Tettigarctidae likely had a very different environmental preference. Despite a high Mesozoic diversity, only two species in two genera are described from the Nova Olinda Member (Menon, 2005; Menon *et al*., 2007).

8. 3. 12. 1. 1. 3. Superfamily Palaeontinoidea

8. 3. 12. 1. 1. 3. 1. Palaeontinidae

Palaeontinidae (giant cicadas) are a family of cicadomorphs that became extinct during the mid-Cretaceous. They are easily characterised by their large bodies, small heads, broad wings,

and stout setae forming bristles covering their entire body, and have even been reported as moth-like (Ying and Dong, 2007). They are believed to be phytophagous and their extinction may be linked to the decline of ginkophytes (Shcherbakov, 2000). There are eight species described from four genera in the Nova Olinda Member, and the formation is of particular importance in understanding the evolution and decline of this group (Udea, 1997; Menon *et al*., 2007; Wang *et al*., 2008).

8. 3. 12. 1. 1. 4. Superfamily Cercopoidea

8. 3. 12. 1. 1. 4. 1. Cercopionidae

Cercopionidae (froghoppers) are an extinct family restricted entirely to two formations in the Mesozoic: The Nova Olinda Member and the Mount Crosby Formation (Evans, 1956; Menon *et al*., 2007). They were first described from the Nova Olinda Member by Hamilton (1990, 1992) and are distinguished from other cercopoids in their 'busy' and distinct wing venation, scarcely produced head, ocelli between eyes, and pronotum longer than crown (Menon *et al*., 2007). Only a single species is described from the Nova Olinda Member.

8. 3. 12. 1. 2. Infraorder Fulgoromorpha

Fulgoromorpha (planthoppers) have a modern diversity of 12,500 species and are morphologically very similar to many Cicadamorpha. However, they can be distinguished by an enlarged or bulbous antennal pedicel, tegulae on the mesothorax, and the base of the middle coxae widely separated (Scherbakov and Popov, 2002). They also feed almost exclusively on plant fluids, much like cicadomorphs, with a few troglobitic taxa that likely feed on fungi (Romero, 2009). Some taxa are able to jump very high in a similar fashion to grasshoppers, and this is where their common name comes from (Grimaldi and Engel, 2005).

Many fulgoromorphs are remarkable seed and leaf mimics, while others have complex and colourful patterning to confuse predators (Grimaldi and Engel, 2005). These include extravagant wing patterns that mimic eyes, dazzling predators (Grimaldi and Engel, 2005). Planthopper nymphs are morphologically diverse, with some taxa developing elongate snout-like heads, while other nymphs secrete long fluffy strands of wax from their abdomens as a waste product. Some planthoppers coat their bodies in microscopic intricately structured granules (brochosomes) to protect themselves from their own sticky waste product (Rakitov and Gorb, 2013).

For overviews of Fulgoromorpha biology, see Szwedo, (2007), Grimaldi and Engel (2005), Szwedo *et al*. (2004, 2006), and Song and Liang (2013), the latter of which also covers their accepted phylogeny.

8. 3. 12. 1. 2. 1. Cixiidae

Cixiidae is a family of typically small fulgoromorphs with a moderate modern diversity of 2,000 described species (Ceotto and Bourgoin, 2008). They can be recognised by their narrow pronotum, particularly long and narrow head, as well as translucent wings. While adults of this family feed on various shrubs, the nymphs typically prefer dark, humid, often subterranean environments (Ceotto and Bourgoin, 2008). Their phylogeny is complex and still debated, but they are widely accepted as basal within Fulgoromorpha (Ceotto and Bourgoin, 2008).

Only a single species is described from the Nova Olinda Member (Szwedo, 2007). The Nova Olinda Member has been depicted as one of the oldest records of this family, however there are other examples that date back to the Jurassic (Grimaldi and Engel, 2005).

8. 3. 12. 1. 2. 2. Lalacidae

Lalacidae is a family that was specifically erected for fulgoromorph fossils unique to the Nova Olinda Member (Hamilton 1990; Lin *et al*., 2010). It is relatively diverse (at least compared too other Nova Olinda Fulgoromorpha) with 20 species across nine genera in three subfamilies (Szwedo, 2007). This family is closely related to Cixiidae, and so likely shared much of the same environmental preferences (Grimaldi and Engel, 2005).

8. 3. 12. 1. 2. 3. Achilidae

Achilidae is a small family of Fulgoromorpha, with approximately 460 described modern taxa (Szwedo, 2008). They are often cryptically coloured, but can be distinguished from other fulgoromorphs by their overall flattened habit and their posteriorly overlapping wings (Wilson, 2005). They are most notably found in the fossil record inside amber inclusions, and only two species within a single genus are described from the Nova Olinda Member (Szwedo, 2007, 2008).

8. 3. 12. 2. Suborder Coleorrhyncha

Coleorrhyncha (moss bugs) (specifically Peloridiidae) are a group of small and cryptic insects that lie within their own separate suborder (Schlee, 1969; Ouvrard *et al*., 2000). As the name suggests, these insects are intimately associated with mosses and generally live and feed on them. Modern Coleorrhyncha are only found in southern hemisphere *Nothofagus* forests, throughout South America, Australia, Tasmania, New Caledonia, Lord Howe Island, and New Zealand. Despite this, they had a broader distribution across Europe and Asia in the Jurassic (Schlee, 1969; Ouvrard *et al*., 2000; Grimaldi and Engel, 2005). Their fossil record dates back to the Upper Permian and their distribution strongly supports an early Gondwanan origin of their crown group. Some modern taxa are known to feed on moss rhizoids, fungi, or lichens (Popov

and Shcherbakov, 1996). Unlike most other hemipteran groups, coleorrhynchan diversity is surprisingly restricted. Only 25 modern species are described, however their diversity was much higher during the Jurassic. Recently a number of new species have been described from the Jurassic of China and Europe (Popov and Shcherbakov, 1991, 1996; Carpenter, 1992; Szwedo, 2011; Szwedo *et al*., 2011; Dong *et al*., 2012a,,b).

Only a single undescribed species of Coleorrhyncha is recorded from the Nova Olinda Member (Bechly and Szwedo, 2007) and, due to their low modern diversity, is likely of phylogenetic significance (Evans, 1981; Burckhardt and Agosti, 1991; Burckhardt and Cekalovic, 2002). There are several specimens of Progoncimicidae yet to be described from the Nova Olinda Member and three taxa have been previously assigned to it, but were later removed (*Latiscutella santosi* Pinto and Ornellas, 1994; *Cratocoris schechenkoae* Martins-Neto, *et al.*, 1999; *Cratogocimex popovi* Martins-Neto, 2002b).

For overviews of Coleorrhyncha biology and palaeontology, see Grimaldi and Engel (2005), Burckhardt (2009), and Dong *et al*. (2012b).

8. 3. 12. 3. Suborder Heteroptera

8. 3. 12. 3. 1. Infraorder Nepomorpha

8. 3. 12. 3. 1. 1. Belostomatidae

Belostomatidae (giant waterbugs, toe-biters, electric-light bugs, or alligator ticks) are a family of predatory aquatic bugs that contain the largest hemipterans (Cullen, 1969; Popov, 1971). As many of their common names suggest, they are aggressive predators that will attack larger vertebrates. They are typically found in freshwater streams and ponds, are present throughout many tropical and temperate regions, but are notably absent from Palaearctic regions (Cullen, 1969). The largest members of this family are within the subfamily Lethocerinae, and this group is present in the Nova Olinda Member (Waller, 2006). A total of four species across four genera in two subfamilies are described from the Nova Olinda Member (Nel and Paicheler, 1992; Zamboni, 2001; Waller, 2006).

8. 3. 12. 3. 1. 2. Nepidae

Nepidae (water scorpions) are an exclusively aquatic family of bugs that often superficially resemble scorpions (as their common name suggests), but can also resemble members of Phasmatodea (Tawfik *et al*., 2009). They can be characterised by a long posterior process on the abdomen (which can resemble a scorpion ‘tail’), but have a variety of overall morphologies, including broad, flat bodies, or long, narrow bodies (Grimaldi and Engel, 2005). They are predaceous and typically feed on invertebrates, but are also known to hunt small

vertebrates (Tawfik *et al*., 2009). Some taxa have an unusual reproductive strategy, whereby males carry a sheet of eggs on their backs until they hatch (Tawfik *et al*., 2009). As mentioned above, they are exclusively aquatic and can be found predominately in fresh or slightly brackish water (Tawfik *et al*., 2009). Only a single species of Nepidae is described from the Nova Olinda Member, but several other distinct species are awaiting description (Jattiot *et al*., 2012).

8. 3. 12. 3. 1. 3. Naucoridae

Naucoridae (creeping water bugs) are a family of predatory aquatic bugs that are very similar to Belostomatidae (giant water bugs) in many ways. They are exclusively aquatic, encapsulating their bodies in a bubble of air and some taxa possess raptoral forelimbs (Mepherson *et al*., 1987). Unusually, the common name of this family is misleading and Naucoridae can in fact swim very rapidly (Mepherson *et al*., 1987). One of their most prominent characteristics is antennae appearing absent, which are in fact hidden in grooves under their eyes. Most species inhabit lotic ecosystems including fast-moving streams, rivers, and even waterfalls. However, some taxa also inhabit slower, marginal areas or even stagnant water (Zettel and Lane, 2011). They have a largely global distribution (excluding the Antarctic), are most abundant in tropical regions, and have a surprisingly low abundance in temperate regions (Zettel and Lane, 2011). Two species within two genera of Naucoridae are described from the Nova Olinda Member (Ruf *et al.,* 2005).

8. 3. 12. 3. 1. 4. Notonectidae

Notonectidae (backswimmers or greater water boatman) are a cosmopolitan family of primarily aquatic bugs that are easily recognised by their unusual mode of swimming. They lay in the water with their ventral side towards the surface, hence the common name backswimmers. In this position, they propel themselves with their hind limbs in an oar-like motion, hence their other common name (greater water boatman) (Grimaldi and Engel, 2005). They are similar in appearance to members of the family Corixidae, but are typically much larger (Grimaldi and Engel, 2005). Notonectidae feed on insects that fall onto the water surface, but are also aggressive predators and actively hunt for aquatic prey, including small vertebrates (Hungerford, 1933). Their oar-like hind limbs possess a row of coarse setae that give a ‘fringed’ appearance, and allow them to swim rapidly. They inhabit clam fresh water, typically lakes, ponds, and marshes, but are not *entirely* aquatic, as they can disperse by flying to new water sources (Hungerford, 1933). One genus and species is described from the Nova Olinda Member, with another possible (undescribed?) species in the same genus (Bechly and Szwedo, 2007).

8. 3. 12. 3. 1. 5. Corixidae

Corixidae (water boatmen, or lesser water boatmen) are an oddity among Nepomorpha. Although similar in appearance and some biology (notably their oar-like limbs and ability to fly) to Notonectidae, they can be readily distinguished by behaviour. Firstly, they swim 'normally' with their dorsal side up, and secondly, while not truly benthic, they tend to stay near the water bottom. Unlike other Nepomorpha, Corixidae are primarily herbivorous, feeding on algae or injecting enzymes into plant stems and then sucking out the digested tissues (Hogue, 1992). While typically inhabiting clam fresh water, such as ponds or slow-moving streams, many taxa are able to tolerate a wide-range of salinities, including sea water, mildly brackish, and fresh waters (Hogue, 1992). As such, these insects can be found along sheltered coasts, estuaries, and salt marshes (Hogue, 1992). An undescribed species with affinities to *Rhomboidella* is reported from the Nova Olinda Member (Bechly and Szwedo, 2007).

8. 3. 12. 3. 1. 6. Gelastocoridae and Pseudonerthridae

Gelastocoridae (toad bugs) and Pseudonerthridae (sister to Gelstocoridae) are two closely related families (Bechly and Szwedo, 2007) and are presented here together. Gelastocoridae are largely convergent with some toads, as their common name suggests. They have a warty and bulbous appearance with protruding eyes and an overall broad oval body shape (Merritt and Cummins, 1996). They also possess toad-like cryptic colouration and even a leaping movement, which they use to pounce onto prey (Merritt and Cummins, 1996). Their distribution is cosmopolitan, with a higher diversity in the tropics. Both adults and larvae are riparian, inhabiting the edges of streams and ponds, however larvae bury themselves in sand and silt (Merritt and Cummins, 1996). Two species within a single genus of Gelastocoridae, and a single species of Pseudonerthridae, are described from the Nova Olinda Member (Ruf *et al*., 2005).

8. 3. 12. 3. 2. Infraorder Leptopodomorpha

8. 3. 13. 3. 2. 1. Archegocimicidae

Archegocimicidae are an extinct family of Leptopodomorpha (shore bugs or spiny shore bugs) that appear to be restricted to the Mesozoic (Ryzhkova and Coram, 2016). While their systematics has historically been uncertain, they are now considered to be within Leptopodomorpha due to morphological similarities with Saldidae (extant shore bugs) (Ryzhkova and Coram, 2016). They can, however, be distinguished by some wing characters.

Extant Leptopodomorpha are most common around shorelines, but may also inhabit other riparian niches around streams or lakes. A single undescribed specimen from the Nova Olinda Member is tentatively assigned to Archegocimicidae (Bechly and Szwedo, 2007).

8. 3. 12. 3. 3. Infraorder Gerromorpha

For overviews of Gerromorpha morphology, biogeography, and phylogeny, see Andersen (1982, 1998).

8. 3. 12. 3. 3. 1. Hydrometridae

Hydrometridae (marsh treaders or water measurers) are semi-aquatic bugs that superficially resemble members of Phasmatodea. They are relatively large with long, slender bodies, a head longer than their thorax, and long thread-like legs (Merritt *et al*., 2008). Most members of this family are wingless, however some taxa retain their wings. These adaptations allow members of Hydrometridae to stride across the water surface, where they predate upon weak (newly emerged, slow moving, dying, or dead) invertebrates (Merritt *et al*., 2008). Their distribution is cosmopolitan, however they are most diverse in the tropics where they live on floating vegetation around the edges of ponds, marshes, and slow-moving streams (Merritt *et al*., 2008). There are currently two species within two genera of Hydrometridae described from the Nova Olinda Member (Nel and Popov, 2000; Goodwyn, 2002).

8. 3. 12. 3. 3. 2. Veliidae and Mesoveliidae

Veliidae (rifle bugs, smaller water striders, or broad-shouldered water striders) and Mesoveliidae (water treaders) are families of bugs that are very closely related to Gerridae (water striders). Veliidae can be distinguished from Gerridae by their overall smaller sizer and a broader pronotum (hence their latter common name), whereas Mesoveliidae do not have a broad pronotum and are instead identified by a thickened, vein-less wing membrane (Merritt *et al*., 2008). They both have a mostly global distribution and are typically found amongst vegetation of temporary or permanent ponds, lake margins, or other placid waters. Some taxa of Veliidae are adapted to faster moving streams or rapids, and others are found on mudflats or around saltwater habitats (Merritt *et al*., 2008). Veliidae are predaceous and hunt surface-dwelling arthropods via vibration, whereas Mesoveliidae are primarily feed on aquatic vegetation (Merritt *et al*., 2008). A single undescribed species of each family is reported from the Nova Olinda Member (Bechly and Szwedo, 2007).

8. 3. 12. 3. 4. Infraorder Cimicomorpha

Cimicomorpha is the largest infraorder of Heteroptera and accounts for approximately 90% of all described Heteroptera species, encompassing a huge variety of morphologies and lifestyles

(Grimaldi and Engel, 2005). Their high diversity is presumed to be a result of some lineages adapting to plant feeding, however other taxa have evolved predatory or parasitic lifestyles. Most notable of the parasitic groups are the family Cimicidae (bed bugs) who parasitize humans (Grimaldi and Engel, 2005). Despite this high diversity, only a single undescribed species of Cimicomorpha is reported from the Nova Olinda Member and is family *incerte sedis* (Bechly and Szwedo, 2007).

8. 3. 12. 3. 5. Infraorder Pentatomomorpha

8. 3. 12. 3. 5. 1. Pachymeridiidae

Pachymeridiidae is an exclusively Mesozoic family of Pentatomomorpha that is primarily diagnosed on forewing venation characteristics. They appear to be closely related to Mesopentacoridae and are known from other Mesozoic localities that indicate humid and warm-temperate climates (Yunzhi *et al*., 2008). Many fossil taxa are presumed to be herbivorous, feeding on gymnosperms and early angiosperms (Yunzhi *et al*., 2008). A summary of fossil localities that include members of Pachymeridiidae was presented in 2008 showing a solely Eurasian distribution and excluded the Nova Olinda Member (Yunzhi *et al*., 2008). Currently a single species is described from the Nova Olinda Member, with another awaiting description (Martins-Neto, *et al.*, 1999), however it is possible that they are no longer considered members of Pachymeridiidae. If the Nova Olinda Member species is valid, it represents the first member of this family outside of Eurasia.

8. 3. 12. 3. 5. 2. Alydidae

Alydidae (broad-headed bugs) are a family of true bugs that are characterised as strong fliers with slender bodies, long thin legs, and, of course, a broad head (Schaefer, 1999). In addition, some members of the family are adapted as remarkable ant-mimics. They are closely related to Coreidae and are phytophagous, primarily eating seeds (Schaefer, 1999). Alydidae are distributed throughout most temperate and warm regions, but they are most abundant in tropical arid and sandy habitats (Schaefer, 1999). A single undescribed species of Alydidae is reported from the Nova Olinda Member (Bechly and Szwedo, 2007).

8. 3. 12. 3. 5. 3. Coreidae

Coreidae (leaf-footed bugs, squash bugs, twig-wilters, or tip-wilters) are a morphologically diverse family of Heteroptera. They are typically oval-shaped with leaf-shaped tibiae, but can vary greatly and even contain the largest species of Heteroptera (Baranowski and Slater, 1986). Some taxa can be particularly spiny or bristly, or are able to produce foul-smelling odours when attacked. Most species are phytophagous and generally feed on sap (Baranowski and

Slater, 1986). Only a single undescribed Coreidae is reported from the Nova Olinda Member (Bechly and Szwedo, 2007).

8. 3. 12. 3. 5. 4. Aradidae

Aradidae (flat bugs and bark bugs) are a diverse family of Heteroptera with over 1,800 described modern species (Larivière and Larochelle, 2006). As their common names suggest, most taxa are dorsoventrally compressed and associated with woody plants. They are highly cryptic, living under the bark of decaying trees, in twigs and wood debris, or in moist forest litter, where they feed on the internal fluids of fungal hyphae (Larivière and Larochelle, 2006). Some taxa are secondarily wingless, and this appears to be correlated with inhabiting rainforest environments (Larivière and Larochelle, 2006). Only a single undescribed Aradidae is reported from the Nova Olinda Member (Bechly and Szwedo, 2007).

8. 3. 12. 3. 5. 5. Cydnidae

Cydnidae (shield bugs, burrowing bugs, or burrower bugs) are a family of small (typically 2 – 20 mm) cryptic insects, with approximately 750 modern described species. They are often regarded as primitive among true bugs, but in fact have a suite of derived characters (Lis *et al*., 2000). These include a broad and flattened head, rows of strong setae or spines, and heavily spinose anterior tibiae. All of these characters are adaptions for digging and make them powerful burrowers (Lis *et al*., 2000). They are typically brown or black and are largely fossorial, living deep within soil where they feed on xylem fluids from roots (Lis *et al*., 2000). Non-fossorial members are rare, but may forage for seeds on the soil surface or be troglodytic (Klys and Lis, 2013). A single species of Cydnidae has been described from the Nova Olinda Member and its presence may provide further evidence for periodic/seasonal flooding flushing burrowing insects into the palaeolake/lagoon (Ornellas, 1974; Bechly and Szwedo, 2007).

8. 3. 12. 4. Heteroptera *incertae sedis*

A single species from the Nova Olinda Member has been described as Heteroptera *incertae sedis* (*Cratogocimex popovi*) (Martins-Neto, 2002a) and there are several other undescribed species with an indeterminate position within Heteroptera (Bechly and Szwedo, 2007).

8. 3. 13. Hymenoptera

Hymenoptera are the third largest order of insects with over 150,000 described species and an estimated total diversity ranging from 600,000 to 1,200,000 species. Nevertheless, their described taxa already account for approximately 8% of all recorded species (Grimaldi and Engel, 2005; Davis *et al*., 2010). Hymenoptera includes sawflies, wasps, bees, and ants, however the majority of their diversity lies in the largely unexplored microhymenoptera (Davis

et al., 2010). The species richness of Hymenoptera is a result of numerous, distinct, phylogenetic radiations within already large clades, rather than any single key factor. Such radiations are likely a result of specific anatomical innovations, exploitation of rich host groups, and an intimate association with angiosperms (Davis *et al*., 2010). It has been estimated that, over the next few million years, their astonishing ability to diversify will cause them to overtake Coleoptera as the most diverse group of animals on the planet (Davis *et al*., 2010).

Hymenoptera are arguably the most important group of animals on the planet. They are the primary pollinators of angiosperms and, when creating burrowing nests, are a geological force unto themselves. They are easily recognisable by the presence of a petiole (the 'wasp waist') in all but the most basal taxa, and reduced hindwings that are connected to the forewings by a series of hooks called hamuli (Grimaldi and Engel, 2005). Interestingly, the majority of wasps are solitary, with only a few lineages developing the recognisable subsociality too advanced eusociality. Eusocial groups are complex societies that can range from casts fulfilling specific roles and working as a 'well-oiled' entity, too hierarchical, bickering sisters fighting over egg laying rights (Grimaldi and Engel, 2005).

They inhabit almost every suitable (non-aquatic, non-polar) habitat and are abundant, resulting in a large and diverse fossil record, with the Cretaceous being no exception to this (Rasnitsyn 1988, Grimaldi, 1990, and Grimaldi and Engel, 2005; Krogmann *et al.,* 2013). Surprisingly, the Nova Olinda Member has comparatively few hymenopterans, with only 23 distinct (although not all described) species. Species description can be difficult at the best of times, as the high diversity of the order produces subtle differences between taxa that can be impossible to determine in fossils. Despite this, the Nova Olinda Member is still of importance for hymenopteran evolution as it contains the oldest record of Sapygidae: Fedtschenkiinae, a rare relic group that can reveal extremely important details of the coevolution of hymenopterans with angiosperms (Grimaldi and Engel, 2005; Osten, 2007). Overall, Nova Olinda Member Hymenoptera fossils suggest a heterogeneous habitat with relatively humid biotpes of dense vegetation (forested area, supported by the abundant beetle fauna), hot dry scrubland areas, and finally sparsely vegetated rocky deserts (there is no evidence for dunes).

Unfortunately, Hymenoptera phylogeny has a history of confusion and debate. Many of the established clades frequently shift position, change names, or are found to be completely obsolete. For example, Vespomorpha is synonomous with Aculeata, Symphyta and Evaniomorpha are paraphyletic, and Proctotrupoidea and Mymarommatoidea are likely invalid (Davis *et al*., 2010; Mao *et al*., 2015). Groups are examined below in accordance with Mao *et al*. (2015).

For an overview of hymenopteran biology, see Austin and Dowton (2001), Grimaldi and Engel (2005), and Davis *et al*. (2010). For an overview of their phylogenetics, see Mao *et al.* (2015).

There are two suborders within Hymenoptera, Symphyta and Apocrita. Interestingly, a specimen has been described from the Nova Olinda Member that forms a sister clade to Xiphydriidae (within Symphyta) + Euhymenoptera, and so represents an extremely basal form, probably outside of the two suborders. It was named *Cratoenigma articulate* by Krogmann and Nel (2012) and sits within a new group called Unicalcarida.

8. 3. 13. 1. 'Suborder' Symphyta

Symphyta (sawflies) has long been known to be a demonstrably paraphyletic clade, and is essentially an informal description of any hymenopteran outside of Apocrita (Grimaldi and Engel, 2005; Martins-Neto, 2007; Mao *et al.,* 2015). Hymenopterans placed within this group are generally basal and their biology can vary greatly. They typically have caterpillar-like larvae and are intimately associated with plants, with the majority of species being phytophagous (Grimaldi and Engel, 2005). Symphyta are often misidentified as non-hymenopterans as many of them lack a petiole.

8. 3. 13. 1. 1. Sepulicidae

Sepulicidae is an extinct family of, presumably basal, sawflies largely from the Mesozoic. The family name was originally described in Russian, and there has been much confusion over its English translation (Роман, 2004). Only a single species is described from the Nova Olinda Member by Darling and Sharkey (1990), but was been moved to Sepulcidae: Thrematothoracinae (Rasnitysn *et al*., 1998; Jattiot *et al*., 2011). Little is known about the habitat preference of this family.

8. 3. 13. 1. 2. Pseudosiricidae/Siricidae

Siricidae (horntails or wood wasps) are a relatively basal family of hymenopterans. Both of their common names reflect their anatomy and biology, as they possess a spike-like extended terminal tergite (hence horntails), as well an intimate association with dying (or felled) trees (hence wood wasps). They are largely xylophagous, with wood-boring larvae. Mature females also possess a remarkably drill-like ovipositor (Step, 1932). Only a single, as yet undescribed, species is reported from the Nova Olinda Member (Osten, 2007), which was later reappraised and attributed to the extinct family Pseudosiricidae (Archibald and Rasnitsyn, 2016). This extinct family, as the name suggests, is remarkably similar to Siricidae, but lacks key identifying characters.

8. 3. 13. 1. 3. Superfamily Tenthredinoidea (family *incertae sedis*)

Tenthredinoidea is the largest and most derived sawfly superfamily, with over 7,000 described modern species (Davis *et al*., 2010; Mao *et al*., 2015). The majority of members of Tenthredinoidea belong to the family Tenthredinidae, and they are characteristically flattened compared to other sawflies. This family has an abundant fossil record and its caterpillar-like larvae are phytophagous, suggesting an association with shrubby plants (Grimaldi and Engel, 2005). However, only a single species is described from the Nova Olinda Member and has no familial placement within Tenthredinoidea (Osten, 2007).

8. 3. 13. 2. Suborder Apocrita

8. 3. 13. 2. 1. Infraorder(?) Aculeata

8. 3. 13. 2. 1. 1. Superfamily Vespoidea

Vespoidea is a particularly successful superfamily with a broad diversity. However, its families are often described as 'in a state flux' (Brothers, 1999; Pilgrim *et al*., 2008), and so determining their relationships is extremely difficult. Below, they are arranged in accordance with the phylogeny presented by Debevec *et al*. (2012). Despite their differences, these families (excluding possible Formicidae) are indicative of a dry, warm subtropical climate, with possible areas of savannah/desert vegetation. Additionally, the parasitic requirement of some of these families also suggest a relatively humid wooded or forested area (as well as confirming the dry scrubland) to supply ample host species (Osten, 2007).

8. 3. 13. 2. 1. 1. 1. Vespidae

Vespidae (potter, pollen, paper, and hover wasps, as well as yellowjackets and hornets) are the most recognisable (excluding fossils) wasps. When an entomologist says 'wasp', it is this group that comes to the public mind, and it generally does not do so fondly. These insects are characterised as aggressive pests that invade human activities (mostly during picnics apparently). This is, of course, a result of their monumental success (Rasnitsyn, 1988). They are cosmopolitan with approximately 4,500 described species and can be solitary, subsocial, or eusocial. They are ecologically important as pollinators, but also control other insect populations (Osten, 2007). Vespids are very rare in the Cretaceous (although nest fossils are known) and only a single undescribed taxon is recorded from the Nova Olinda Member (Brown, 1941; Wenzel, 1990; Carpenter and Rasnitsyn, 1990; Osten, 2007). The undescribed specimen (SMNS 66295) possibly belongs to the subfamily Priorvespinae, however defining forewing characters are unfortunately absent.

8. 3. 13. 2. 1. 1. 2. Pompilidae

Pompilidae (spider wasps and tarantula hawks) are a family of vespoid wasp that, as their name suggests, exclusively parasitize spiders. They will attack a wide range of spiders, including giant tarantulas, wolf spiders, small ground spiders, and even orb-web spinners. They are rather diverse with approximately 5,000 described recent species, are cosmopolitan, and can be quite large (reaching up to 50 mm). Pompilidae are generally associated with tropical areas or xeric regions (Grimaldi and Engel, 2005; Osten, 2007), and of course, require a suitable spider population for reproduction. Only a single undescribed specimen is recorded from the Nova Olinda Member.

8. 3. 13. 2. 1. 1. 3. Sapygidae

Sapygidae (club-horned wasps) is a very small family of solitary, robust, parasitic wasps with only 80 described modern species. They are cleptoparasites or ectoparasites of Megachilidae, Apidae, or Eumeninae, and have powerful stings used for defence or oviposition (Grimaldi and Engel, 2005; Osten, 2007). Overall, their biology is very poorly understood, although some attempts to study it have been undertaken (Torchio, 1972). They are extremely rare in the fossil record, and so the single taxa described from the Nova Olinda Member is of great importance (Osten, 2007). Its wing venation is nearly identical to that of modern members of the subfamily Fedtschenkiinae. This subfamily has an extremely disjointed distribution, however is indicative of hot, dry climates along with 'desert' flora (Osten, 2007).

8. 3. 13. 2. 1. 1. 4. Tiphiidae

Tiphiidae (flower ants) are a moderately diverse group with approximately 2,000 described species and a cosmopolitan distribution. All members of this group are ectoparasites, however some males are also inadvertent orchid pollinators. Some plant taxa have evolved flowers mimicking the shape and pheromones of female Tiphiidae, and so are able to pollinate by attracting aroused males (Grimaldi and Engel, 2005). The group can possess sexual dimorphism, causing difficulty in matching holotypes to allotypes, which can usually only be achieved if specimens are found *en copula* (Osten, 2007). They are uncommon as fossils, and are only known from the Nova Olinda Member, Myanmar amber, and several Oligocene-Miocene Asian sites (Rasnitsyn, 1986; Zhang *et al*., 1994; Grimaldi and Engel, 2005; Engel *et al*., 2009). A single species is described from the Nova Olinda Member (*Architiphia rasnitsyni*, Darling and Sharkey, 1990), based on two specimens, one of which is particularly beautiful. Two additional undescribed specimens may also be members of Tiphiidae.

8. 3. 13. 2. 1. 1. 5. Formicidae

Formicidae (ants) are an incredibly important group of insects, both ecologically and geologically. They have a modern diversity of approximately 9,500 described species, are highly social, and mostly flightless (only reproductive members have wings, with a few groups being completely flightless). In some lineages, nests can contain overlapping generations, where they cooperatively care for the brood. They are most diverse in forested tropical river basins, where they can exceed the vertebrate biomass by four times and a single colony can house millions of individuals (Grimaldi and Engel, 2005). Much like termites, large colonies can shift an extraordinary amount of earth. Their importance to modern ecosystems is reflected in the number of taxa that mimic them (approximately 2000), and the fact that many taxa parasitize them. Ants have an extensive fossil record, and this is probably due to the sheer number of individuals that actively explore their surroundings (Grimaldi and Engel, 2005). However, older deposits yield progressively fewer ant fossils, and by the Early Cretaceous eusocial colonies would only have a few members. Only a single species is known from the Nova Olinda Member (*Carirdris bipetiolata*) (Brandao *et al*., 1989). The original attribution of this family was not confident and has been heavily disputed. Two further specimens were described by Osten (2007) that further suggest the presence of Formicidae and clarified the placement to Myrmeciinae (bulldog ants), although discussions at the 2016 International Palaeoentomological Society conference (Fossil X3) suggest that these have been refuted. Extant Myrmeciinae are entirely restricted to Australia and its surrounding islands.

8. 3. 13. 2. 1. 1. 6. Scoliidae

Scoliidae (scoliid wasps) is a relatively small family with approximately 570 described modern species. Surprisingly, little is known about the biology of this group, however they are ectoparasites of scarab beetles (Scarabaeidae) (Rasnitsyn, 1977; Day *et* al., 1981; Osten, 2007). As such, the environmental preference of this group is identical to that of scarabs (hot, dry, savannah or desert environments). Females are equipped with spined forelimbs for digging and have a powerful paralyzing sting. Three subfamilies are present in the Nova Olinda Member (Archaeoscoliinae, Proscoliinae, and *cf.* Campsomerinae). Differentiation between these subfamilies can be extremely difficult as many taxa are remarkably morphologically similar but also possess sexual dimorphism (Osten, 2007). There are currently only three taxa described from the Nova Olinda Member (Rasnitsyn and Martinéz-Delclòs, 1999; Osten, 2007; Nel *et al*., 2013).

8. 3. 13. 2. 1. 2. Superfamily Apoidea

Apoidea (digger wasps, bees, and bumble bees) are a very large family (20,000 extant species) of easily recognisable insects that are absolutely vital for modern angiosperm pollination.

Without this group, humanity would starve and most terrestrial ecosystems would collapse (Grimaldi and Engel, 2005). The most familiar Apoidea, bees and bumble bees (*Apis* and *Bombus*) only account for a small portion of their diversity, with the vast majority being solitary bees (Grimaldi and Engel, 2005). These solitary bees do not rely solely on nectar and pollen for their life cycle and generally parasitize various arthropods during their larval stage.

8. 3. 13. 2. 1. 2. 1. Angarosphecidae

Angarosphecidae are a primitive group of bees that were abundant during the Cretaceous (Rasnitsyn *et al.,* 1999). As with all Apoidea, they are intimately associated with angiosperms, but also rely on other arthropods for their parasitic larval stage (Bohart and Menke, 1976). There are only four species described across three genera, yet they account for about 50% of hymenopteran fossils from the Nova Olinda Member, and so are relatively abundant and often beautifully preserved. Their abundance implies the presence of a large (and possibly diverse) flower assemblage, along with large numbers of host insect species, such as Diptera, Hymenoptera, Orthoptera, Lepidoptera, or Coleoptera (Osten, 2007).

8. 3. 13. 2. 1. 2. 2. Ampulicidae

One of the most primitive bee groups, Ampulicidae (cockroach wasps), was first tentatively recorded from the Nova Olinda Member by Darling and Sharkey (1990), and later confirmed by Osten (2007), but is yet to be described. As their common name suggests, this family parasitizes cockroaches and therefore share their environmental preferences (Grimaldi and Engel, 2005).

8. 3. 13. 2. 1. 2. 3. Apidae?

In addition to the families described above, there are also a number of specimens that have been informally identified as ‘primitive bees’ (Apidea; bees, bumblebees, and honey bees). Unfortunately, properly distinguishing them from ‘primitive ‘sphecids’’ is extremely difficult, if not impossible (Darling and Sharkey, 1990; Osten, 2007). If these specimens can be identified as bees, they will represent the oldest record of the group (Engel, 2000).

8. 3. 13. 2. 2. Infraorder Ichneumonomorpha

8. 3. 13. 2. 2. 1. Ichneumonoidae?

Ichneumonoidae (ichneumon wasps) are major parasites of other terrestrial arthropods. They are exceedingly diverse, with over 24,000 described species and an estimated total diversity of up to 100,000 species (Grimaldi and Engel, 2005). Unusually, they have a higher diversity in temperate regions, as oppose to tropical regions which is typical to most other insects (Sime

and Brower, 1998). A single specimen may represent an ichneumon wasp from the Nova Olinda Member, but is yet to be described (Osten, 2007).

8. 3. 13. 2. 3. Infraorder Proctotrupomorpha

8. 3. 13. 2. 3. 1. Ephialtitidae

Ephidltitidae is an extinct family of wasps, known only from the Mesozoic, and was most successful during the Jurassic (Zhang et al., 2014). The phylogenetic position of this family is disputed, and it has even been suggested to be outside of Proctotrupomorpha (Rasnitsyn and Zhang, 2010; Zhang *et al*., 2014; Mao *et al*., 2015). Despite only a single species described from the Nova Olinda Member, it is the most common 'parasitic wasp' (Apocrita, excluding Aculeata). The original genus (*Karatous*) (Darling and Sharkey, 1990) erected for this species is now known to be a synonym of *Cratephialtites* (Grimaldi and Engel, 2005; Osten, 2007).

8. 3. 13. 2. 3. 2. Superfamily Proctotrupoidea

8. 3. 13. 2. 3. 2. 1. Proctotrupidae

Proctotrupidae is the largest family of Proctotrupomorpha and has over 1,000 (possibly closer to 2,000) described species. They are all endoparasitoids of larval Coleoptera, Hymenoptera, Neuroptera, or Diptera, and are abnormally large for parasites (Whitfield, 1998). While Proctotrupidae is (currently) recognised as monophyletic, Proctotrupoidea is, unfortunately, a 'dumping ground' for many taxa and is undoubtedly polyphyletic (Grimaldi and Engel, 2005; Osten, 2007). A single species of Proctotrupidae was described from the Nova Olinda Member by Sharkey (1990).

8. 3. 13. 2. 3. 3. Mesoserphidae

Mesoserphidae is an extinct family of small (1.7 – 8 mm) wasps, characterised by 11-18 antennal segments and a specific wing venation (Shih *et al*., 2011). Twenty-nine fossil species have been described, and a possible, but as yet undescribed, specimen may be present within the Nova Olinda Member (Osten, 2007).

8. 3. 13. 2. 3. 4. Chalcidoidea

Despite Chalcidoidea being a widely accepted monophyletic group (Grimaldi and Engel, 2005), its internal relationships have been heavily disputed (Whitfield, 1998). Chalcids are extremely diverse, minute wasps, with more than 23,000 species described and a bewildering array of morphologies (Munro *et al*., 2011). They are certainly vastly more diverse than this, with an estimated total diversity of 500,000 morphological distinct species **among the non-cryptic taxa alone!** Most chalcids are parasitic, but some are phytophagous and symbiotic (Munro *et al*.,

2011). The first comprehensive phylogenetic analysis of Chalcidoidea was undertaken by Munro *et al*. (2011).

8. 3. 13. 2. 3. 4. 1. *Parviformosus wohlrabeae*

In addition to cataloguing the currently known Nova Olinda Member insects, the description of a new(ish) genus and species is included as part of this Ph.D. submission. The anatomy and biology of this group (Chalcidoidea: Agaonidae: Sycophaginae) is summarised within the paper.

This was published in Cretaceous Research in 2013 (Barling *et al*., 2013) and a copy is included in the appendices. The aim of this paper was to demonstrate skills in systematics, species description, SEM imaging, and paper-writing. There are, however, points that require amendment. Importantly, the tentative placement of this fossil within Pteromalidae was based on an email communication with Jean-Yves Rasplus, who has since expressed regret and disassociation with this. He was not aware that we were taking his expert opinion as anything more than a suggestion. Additionally, the *very* tentative placement within the subfamily Sycophaginae would adjust its familial placement to Agaonidae. Chalcid wasp systematics are still in a state of flux and I mistook the explanation by Jean-Yves Rasplus as implying that the current consensus was that Sycophaginae had been transferred to Pteromalidae.

Aside from this confusion, there is one oversight within the paper: we stated that, if the placement of this taxa is correct, then this hints at the presence of figs (*Ficus*) 50-60 million years earlier than current estimates. In fact, the molecular data *supports* the possible presence of figs in the Early Cretaceous (Rønsted *et al*., 2005).

8. 3. 14. Raphidioptera

Raphidioptera (snakeflies) are most easily recognised by their elongated prothorax. Aside from this, their diagnostic characters are not immediately evident, and so species identification can be difficult. Their modern diversity is low and they are typically considered a relic lineage, with only 220 extant species (Grimaldi and Engel, 2005). Unusually, their low modern diversity is reflected in the Nova Olinda Member, with only six species in four genera identified, all within the extinct family Baissopteridae. They were first reported by Martins-Neto and Vulcano (1989a) and species positions within Raphidioptera have been adjusted numerous times over the last 20 years (Engel, 2002; Jepson *et al*., 2011).

For summaries of Raphidioptera biology, see Martynova (1961), Aspöck *et al*. (1991), H. Aspöck (1998, 2002), U. Aspöck and H. Aspöck (2003a), and Aspöck *et al*. (2012).

8. 3. 14. 1. Baissopteridae

Fossil Baissopteridae from the Nova Olinda Member are, importantly, the only southern hemisphere occurrence of the family, despite a 'global' distribution for most of their fossil history (Grimaldi and Engel, 2005; Martins-Neto *et al*., 2007). They have suffered an extensive extinction, and this is likely due to changes in climate. Extant snakeflies live exclusively on trees and their larvae live under bark or in soil and detritus at the bases of shrubs (H. Aspöck, 2002). Many taxa have long ovipositors for injecting eggs under bark or into detritus. Unusually, they require a period of cold (near freezing) temperatures to complete development. This requirement has completely dominated their modern distribution, but it is clear from their fossil record that this was not the case for the majority of their history. They were diverse and widely distributed during the Late Jurassic and Early Cretaceous, where they inhabited many ecosystems and persisted in humid and tropical environments until the Early Cenozoic (Grimaldi and Engel, 2005; Jepson *et al*., 2011).

8. 3. 15. Megaloptera

Megaloptera (alderflies and dobsonflies) are a group of typically large insects that are possibly paraphyletic. The order contains only two families: Corydalidae (dobsonflies) and Sialidae (alderflies), of which only Corydalidae is present within the Nova Olinda Member. They contain approximately 300 modern species and are generally regarded as primitive among Megaloptera (Grimaldi and Engel, 2005). Their larvae are aquatic and this appears to be an independently derived trait. Specimens that had previously been identified as adult Megaloptera held in the SMNS collection have now been described as two new species, each within their own genus (Jepson and Heads, 2016).

8. 3. 15. 1. Corydalidae

Corydalidae (dobsonflies) are a family of Megaloptera that are easily distinguished by enormous sickle-shaped mandibles, three retained ocelli, and a simple fourth tarsomere (Grimaldi and Engel, 2005). There are approximately 200 modern described species and they are generalist predators or scavengers. Their larvae are aquatic, typically found in freshwater streams. Despite the wide variety of other insects with freshwater aquatic larvae, Corydalidae are extremely rare in the Nova Olinda Member (Martins-Neto *et al*., 2007; Jepson and Heads, 2016). This rarity could, however, be the result of short-lived adult forms that typically only survive for 1-2 weeks (Grimaldi and Engel, 2006).

8. 3. 16. Neuroptera

Neuroptera (lacewings, antlions, and their relatives) is a diverse order of insects (approximately 6,000 modern species) that likely had a higher diversity throughout their fossil history (Grimaldi and Engel, 2005). They are readily identifiable by their complex 'mesh' venation, but are defined by the association of the ninth gonocoxites with the gonarcus and unique larval mouthparts that form a distinctive sucking tube (Grimaldi and Engel, 2005). Neuroptera contains three suborders; Hemerobiiformia, Myrmeleontiformia, and Nevrothiformia, the latter of which is the smallest and little is known about (Zwick, 1967; New 1978; Malicky, 1984).

Importantly, the internal phylogeny of Neuroptera has been debated considerably, and only recently has been resolved (Yan *et al*., 2014). The Nova Olinda fossils have been documented extensively by Martins-Neto and Vulcano (1989b,c, 1990a,b, 1997) and Martins-Neto (1998b, 1990b, 1991d, 1992b, 1994, 1997a, 1998d, 2000, 2002a, 2005a; Martins-Neto and Rodrigues, 2009, 2010), with a full key provided by Martins-Neto (2000). Of the suborders, only Myrmeleontiformia and Hemerobliformia are known from the Nova Olinda Member with 67 described species in 41 genera within 16 families. The vast majority of these species require re-description and a comprehensive revision of all Nova Olinda Member Neuroptera is desperately needed.

8. 3. 16. 1. Hemerobiiformia

Hemerobiiformia is the most controversial of the three suborders of Neuropterida. Its members are heterogeneous, with a variety of morphologies, and its phylogeny has been in disputed (New, 1975; Oswald, 1993; Martins-Neto *et al*., 2007). It is now considered paraphyletic (Yan *et al*. 2014). Many of the families within this group have primitive wing venation, making species assignment difficult. The suborder arose in the Mesozoic and is abundant and diverse in the Nova Olinda Member (Martins-Neto *et al*., 2007).

8. 3. 16. 1. 1. Osmylidae

The family Osmylidae (osmylid lacewings) are primitive and diverse, especially in the Old World. Their larvae are possibly aquatic, as adults prefer moist habitats near water. They are abundant in the fossil record (Lambkin, 1988), however are described as relatively rare from the Nova Olinda Member (Myskowiak *et al.,* 2015). Four species across three genera (two within distinct subfamilies) are described from the Nova Olinda Member (Makarkin, 2008; Martins-Neto and Rodrigues, 2009, 2010; Myskowiak *et al.,* 2015).

8. 3. 16. 1. 2. Ithonidae

The family Ithonidae (moth lacewings) are large, with wingspans up to 60 mm, and are surprisingly robust. Their biology is still relatively poorly understood, as they possess several basal characteristics (Grimaldi and Engel, 2005). Their larvae are believed to be subterranean, living for up to 2-3 years, and may be detritivores, rather than predators (New, 1986). Unusually for lacewings, this family undergoes *en masse* emergences. Only a single species of Ithonidae is described from the Nova Olinda Member (Martins-Neto *et al*., 2007).

8. 3. 16. 1. 3. Chrysopidae, Mesochrysopidae, Allopteridae and Limaiidae

Chrysopidae (green lacewings) are a diverse family with approximately 1500 modern species and a worldwide distribution. They are one of the most intensely studied Neuroptera families (almost as much as antlions) and this is largely due to their use in agriculture (New, 1975, 1999, 2002). They are indeed generally green as their common name suggests, although some taxa are brown, yellow, or red (Grimaldi and Engel, 2005). Interestingly, their larvae are mostly arboreal predators and others are ambush predators, concealing themselves in debris. These larvae feed on many aphids, and so are used for agricultural pest-control (New 1975, 1999, 2002). Many adults are predators, but others are specialists, feeding on honeydew via symbiotic yeast. They are also able to detect bat echolocation and communicate via substrate-bourne vibrations using ‘ears’ at the base of their forewing radial vein. Confusingly, Nel *et al.* (2005) reported that the Nova Olinda Member is dominated by Chrysopoidea (the superfamily in which Chrysopidae resides) and this is due to other families classically residing within it (such as Osmylidae, which now resides in Osmmyloidea). While no true members of Chrysopidae are present in the Nova Olinda Member, many taxa have been described of very closely related families. Two species within a single genus of Mesochrysopidae, three species in three genera of Allopteridae, and eight species within four genera of Limaiidae are describe, all of which share characteristics with Chrysopidae (Nel *et al*., 2005; Martins-Neto and Rodrigues, 2009).

8. 3. 16. 1. 4. Superfamily Coniopterygidea

A comprehensive study of Coniopterygidea was undertaken by U. Aspöck *et al*. (2001), and further work was carried out later by U. Aspöck *et al*. (2012), however, more work is needed to completely clarify its internal relationships.

8. 3. 16. 1. 4. 1. Berothidae

Berothidae (beaded lacewings) have a small diversity of 100 modern taxa and are recognised by an elongate pronotum (Winterton, 2010). Only a single subfamily has a global distribution,

and the rest are restricted. Their biology is generally primitive, with predaceous larvae living in detritus. Two species have been described from the Nova Olinda Member, and represent the oldest fossils of this family (works by Martins-Neto; Winterton, 2010).

8. 3. 16. 1. 4. 2. Sisyridae

Sisyridae (spongillaflies) are an interesting family of lacewings with a low diversity of ~60 modern species. Their distribution is cosmopolitan and their larvae are freshwater predators or omnivores, and hunt aquatic insects (Grimaldi and Engel, 2005). These larvae have specially adapted elongate sucking and piercing mouthparts, feeding on pollen, fungi, plant matter, and small arthropods, whereas the adults are omnivorous. Unusually, this group spins silken cocoons for pupation. A single species described from the Nova Olinda Member was tentatively placed in Sisyridae (Martins-Neto, 1997), however none of the diagnostic features of the family are preserved and so must be considered *incertae sedis*.

8. 3. 16. 2. Myrmeleontiformia

Suborder Myrmeleontiformia contains some of the largest, most impressive, and most well-known neuropterans. Of its five families, four are present within the Nova Olinda Member (Millet and Nel, 2010). These are Psychopsidae (silky lacewings or 'true' lacewings), Nemopteridae (spoon-winged & thread-winged), Ascalaphidae (owlflies), Nymphidae (split-footed lacewings), and Myrmeleontidae (antlions). Of these, only Psychopsidae is not found within the Nova Olinda Member (although reported by Martins-Neto, 1997, familial placement is doubtful), however other 'stem 'myrmeleontoids'' are also present (Martins-Neto *et al*., 2007). There are 48 species of Myrmeleontiformia described from the Nova Olinda Member, making it one of the most diverse groups found there, however much of this likely requires revision (Makarkin and Menon, 2007; Makarkin *et al*., 2017). Their fossil record is generally diverse, and so their high diversity in Nova Olinda is not particularly unusual.

8. 3. 16. 2. 1. Psychopsidae

Psychopsidae (silky lacewings) are a spectacular family of lacewings that have a very low diversity, with only 26 described extant taxa (Yan *et al*., 2014). They have large butterfly-like wings and have a narrow distribution across Australia, Asia, and Africa. While the familial relationships of Psychopsidae are not fully resolved, it is believed to be sister to all other Myrmeleontiformia (Yan *et al*., 2014). Only two species within two genera are described from the Nova Olinda Member, one of which has a doubtful familial placement (Martins-Neto *et al*., 2007; Martins-Neto and Rodrigues, 2010).

8. 3. 16. 2. 2. Nemopteridae

The Nemopteridae are among the most visually striking lacewings, with odd spoon or leaf-shaped hind wings. They have approximately 150 modern species, and inhabit arid environments. The larvae of this family are generalist predators and the adults feed on pollen. Their larvae can burrow, and do so head-first after capturing prey to consume it underground (Grimaldi and Engel, 2005). Five species of Nemopteridae are present in the Nova Olinda Member and this is unsurprising given the largely arid Nova Olinda hinterland environment (Martins-Neto, 2000). However, it is unclear if adult Nova Olinda Nemopteridae were pollen feeders and so no conclusions on potential flora can be drawn. They had a much broader distribution for most of their fossil record, but were greatly reduced during the Eocene-Oligocene climatic shift (Grimaldi and Engel, 2005).

8. 3. 16. 2. 3. Nymphidae

Larval members of the extremely low diversity (27 species) family Nymphidae (split-footed lacewings) are known to cover themselves in debris and detritus, likely as a form of camouflage. Little is known about this cryptic group, and they have a mix of pleisomorphic characters (Archibald *et al*., 2009). The adults of this family can be extremely large, and reach up to 80 mm in wingspan (Grimaldi and Engel, 2005). A single species of Nymphidae is was recently described from the Nova Olinda Member (Myskowiak *et al*., 2016).

8. 3. 16. 2. 4. Myrmeleontidae

Arguably the most well-known neuropteran family is Myrmeleontidae (antlions). They are the most diverse family among Neuroptera, with over 2,000 described modern taxa. They are well researched and this is largely due to the fascinating pit traps that some larvae create (although these trap-creators make up only a small portion of their diversity) (Grimaldi and Engel, 2005). Like most neuropterans, their larvae are predaceous and the majority of antlion larvae are ambush predators hiding underneath soil and rocks, or covered in lichens. Many adults of this family can have decorative or cryptic patterning on their wings, and specimens from the Nova Olinda Member are no exception (Heads *et al*., 2005; Barling *et al*., 2015). This group was first reported by Martins-Neto (2000) and for an overview of their biology, see Stange and Miler (1990) and Makarkin *et al*. (2017).

8. 3. 16. 2. 5. Ascalaphidae

Ascalaphidae (owlflies) are a readily distinguishable and relatively diverse (for Neuroptera) family, with more than 430 described species. The adults are aerial predators with long clubbed antennae and have characters that are superficially similar to other insect groups (specifically odonates), resulting in them sometimes being described as ‘hybrids’ (Grimaldi and

Engel, 2005). They are most diverse in xeric and mountainous regions, and are exceedingly rare in the fossil record. Only a single species is described from the Nova Olinda Member (Martins-Neto and Vulcano, 1997).

8. 3. 16. 2. 6. Kalligrammatidae

Kalligrammatidae are an extinct group of large, spectacular lacewings that are restricted to the Mesozoic (Yang, *et al*. 2014). They are morphologically similar to butterflies, possessing large, coloured, wings with a variety of dramatic patterns. Many possess eye spots, indicating that they were diurnal and their patterns were used to confuse predators, most likely pterosaurs and early birds (Yang, *et al*. 2014). Only two species within a single genus of Kalligrammatidae are described from the Nova Olinda Member (Martins-Neto, 1995; Bechly and Makarkin, 2016).

8. 3. 16. 2. 7. Araripeneuridae, Babinskaiidae, and Palaeoleontidae

While examples of Palaeoleontidae are known from other localities (Lu *et al*., 2017), Araripeneuridae is known only from the Nova Olinda Member (Ponomarenko, 1997; Lu *et al*., 2017). They are highly diverse, but there has been much confusion and debate as to the validity of many of their taxa, as well as the positions of each family (Martins-Neto, 1990, 1992, 1995, 1997, 2002; Martins-Neto and Vulcano, 1989, 1997; Menon and Makarkin, 2008; Martins-Neto and Rodrigues, 2010; Myskowiak and Nel, 2016). Twenty species in ten genera of Araripeneuridae, four species in two genera of Babinskaiidae, and eight species in five genera of Palaeoleontidae are described from the Nova Olinda Member. These families all likely need of heavy revision (Heads pers. comm., 2016).

8. 3. 17. Coleoptera

Coleoptera (beetles) are, without question, the most diverse group of animals. They are probably the third (or second) most ecologically important group of insects and are easily recognised by thick hardened forewings into their characteristic elytra. Most authors have previously attributed the diversity of beetles to their close co-evolution with angiosperms, however this does not account for the high diversity of much of Polyphaga (Grimaldi and Engel, 2005). Their co-evolution with angiosperms is, of course, a major contributing factor to their diversity, but they are also one of only two winged insect groups that have invaded cryptic ground niches (the other being Hymenoptera, which are also extremely diverse) (Grimaldi and Engel, 2005). Beetles occupy an extremely wide variety of habitats from seashores, up to 5 km altitudes, all types of forests, savannahs, deserts, freshwaters, and have

essentially colonised every suitable environment on earth, excluding deep marine regions. However, the bulk of their diversity lies in tropical regions and this is probably because they are ancestrally arboreal (Crowson, 1981; Wolf-Schwenninger and Schawaller, 2007). Recent Coleoptera are divided into four suborders with 166 families (Lawrence and Newton, 1995).

The Nova Olinda Member yields a very diverse assemblage of beetles. Unfortunately, many beetle taxa are distinguished by subtle variations in their genitalia, which fossils rarely preserve to a useable degree. Despite the rare occurrence of genital preservation (Plate 12; Barling *et al*., 2015), many taxa from the Nova Olinda Member are still undescribed and tentatively placed in families (Wolf-Schwenninger and Schawaller, 2007).

For overviews of the Coleoptera fossil record, see Arnold'di *et al.* (1992), Ponomarkenko (2003), Lubkin and Engel (2005). For overviews of their phylogeny, see Hunt *et al*. (2007) and Lawrence *et al*. (2011).

8. 3. 17. 1. Suborder Archostemata

The suborder Archostemata (reticulated beetles) is a very small group with under 50 modern species. Despite its low modern diversity, the group was diverse and common in the Mesozoic. Two specimens are known from the Nova Olinda Member and are placed as *cf.* Cupedidae and *cf.* Ommatidae, although it is probable that they reside in Cupedidae and Ommatidae proper (Wolf-Schwenninger and Schawaller, 2007). Larvae of the family Ommatidae are assumed to feed on dead, fungus-infected wood, whereas Cupedidae larvae are wood-borers.

8. 3. 17. 2. Suborder Adephaga

The suborder Adephaga (ground, tiger, predacious diving, and whirligig beetles) is extremely diverse, with approximately 40,000 modern recorded species, accounting for ~10% of total beetle diversity (Grimaldi and Engel, 2005). They are highly specialised with the majority of families, including their earliest fossil records, being aquatic. Two families of Adephaga are recorded from the Nova Olinda Member.

8. 3. 17. 2. 1. Dytiscidae

Dytiscidae (diving beetles) are predaceous aquatic beetles that are rare in the Mesozoic. There have been suggestions that multiple members of Dytiscidae may be present in the Nova Olinda Member (Grimaldi and Maisey, 1990), and at least one example is awaiting description (Heads pers. comm., 2016).

8. 3. 17. 2. 2. Carabidae

The family Carabidae (ground and tiger beetles) were first reported in the Nova Olinda Member by Grimaldi and Maisey (1990), although no taxa were formally described until 2004 (Cassola and Werner, 2004). The Nova Olinda Carabidae represents the oldest known tiger beetle and another specimen has been mentioned by Martins-Neto (2005), although no follow-up research has been undertaken. Carabidae larvae are, as their reference to tigers suggests, aggressive predators and have raptorial forelimbs for snatching prey (Ponomarenko, 1992).

8. 3. 17. 2. 3. Erroneous Coptoclavidae

A single giant larva was described as a member of Coptoclavidae (*Conan barbarica*) by Martins-Neto (1998c), however it is in fact a giant dragonfly larva. Later Zamboni (2001) confirmed that Coptoclavidae is not present in the Nova Olinda Member.

8. 3. 17. 3. Suborder Polyphaga

The suborder Polyphaga is the largest and most diverse modern group of Coleoptera. It is comprised of 16 superfamilies with 144 families and an astonishing 300,000 described species. This group accounts for about ~90% of currently described beetle diversity (Grimaldi and Engel, 2005). There are many examples of this suborder in the Nova Olinda Member.

8. 3. 17. 3. 1. Staphylinidae

The family Staphylinidae (rove beetles) includes 31 subfamilies, seven of which are present in the Nova Olinda Member (Olisthaerinae, Omaliinae, Oxytelinae, Piestinae, Staphylininae, Tachyporinae, and Trigonurinae). Most genera of this family generally live in moist niches of temperate or coastal regions, and possess a diverse array of feeding strategies, including palynivory, carnivory, saprophagy, phytophagy, and mycophagy (Frank and Ahn, 2011). Of these strategies, saprophagy is their archetypal feeding mode, but carnivory and palynivory are the dominant modern strategies (Grimaldi and Engel, 2005). There are at least eight reported specimens of Staphylinidae in the Nova Olinda Member. However, only two are described ‘properly’ (several have very poor descriptions). Unfortunately, this is a result of modern taxa being identified by genital dissection. Some of these specimens are figured by Martins-Neto (2002b) and Grimaldi and Engel (2005), and further specimens are mentioned by Martins-Neto (2005b). Two species were fully described and placed within a single genus in the subfamily Staphylininae (Schomann and Solodovnikov, 2012).

8. 3. 17. 3. 2. Hydrophilidae

Hydrophilidae (water scavenger beetles) are a family of predominantly aquatic beetles that are most easily recognised by elongate maxillary palpi, which are longer than their antennae.

Modern members dwell in standing or slow-running freshwater or their adjacent moist habitats, where they feed primarily on aquatic plants and aquatic plant debris. Only a single larval specimen is known from the Nova Olinda Member and is, unfortunately, only resolvable to family-level (Wolf-Schwenninger and Schawaller, 2007).

8. 3. 17. 3. 3. Scarabaeidae

Scarabaeidae (dung beetles) are an important group of insects for not only their obvious role in waste recycling, but also as an icon in historic human culture (Grimaldi and Engel, 2005). They had a broad distribution throughout the Mesozoic (Arnold'di *et al*., 1992; Scholtz and Chown, 1995). However, evidence for dung beetle coprophagy does not appear until the Upper Cretaceous (Chin and Gill, 1996), and so they were presumably ancestrally xylomycetophagous. Typically, Scarabaeidae are most abundant in arid regions, but are also present in tropical and temperate regions. There are 14 specimens of Scarabaeidae recorded from the Nova Olinda Member, 11 of which are presumed to belong to Aphodiinae (small dung beetles) (Grimaldi and Maisey, 1990; Grimaldi and Engel, 2005).

8. 3. 17. 3. 4. Buprestidae

Buprestidae (jewel beetles or metallic wood-boring beetles), as their name suggests, are glossy iridescent beetles that were abundant at the end of the Lower Cretaceous (Ponomarenko, 2003). Many fossil taxa are known from Russia, Kazakhstan, and Mongolia (Alexeev, 1993, 1996, 2000) and the subfamily Parathyreinae was erected to accommodate them. There are reportedly many well-preserved and intact specimens of this group in the Nova Olinda Member, with at least one undescribed species, however very little information has been published about them (Wolf-Schwenninger and Schawaller, 2007).

8. 3. 17. 3. 5. Dryopidae

The family Dryopidae (long-toed water beetles) are aquatic beetles with larvae that occur in leaf litter and soil. A single tentative specimen is reported in the Nova Olinda Member, but is not described (Grimaldi and Engel 2005).

8. 3. 17. 3. 6. Elateridae

Elateridae (click beetles) are a cosmopolitan family, characterised by a prosternal process that slots into a mesoternal groove, producing a 'click' when suddenly flexed. Some taxa have reportedly developed bioluminescence (Grimaldi and Engel, 2005). Despite these interesting features, their biology is still relatively poorly understood and their larvae inhabit a variety of habitats. They appear diverse in the fossil record, especially from the Late Jurassic and

Cretaceous, but unfortunately are still largely understudied within the Nova Olinda Member, and only a single undescribed taxon is reported (Grimaldi and Engel, 2005).

8. 3. 17. 3. 7. Nitidulidae

Nitidulidae (sap beetles) are generally small (2 – 6 mm) beetles with bulbous-tipped antennae that feed on decaying fruit and vegetables, and, of course, sap. They occupy a variety of habitats, but can typically be found in their food substrate, living in bark, or in flowers. They first appeared in the Lower Cretaceous (Kirejtshuk and Ponomarenko, 1990), and so the Nova Olinda Member represents an early glimpse into their evolution. A single specimen (SMNS 66470) has been described from the Nova Olinda Member and attributed to this family (Grimaldi and Maisey, 1990), and an additional specimen is assigned, but not described (Wolf-Schwenninger and Schawaller, 2007).

8. 3. 17. 3. 8. Cucujidae

The family Cucujidae (flat bark beetles) are a group of medium-sized, dorsoventrally compressed beetles. The phlogeny of this group and its host superfamily (Cucujoidea) seems to be unclear, with the superfamily possibly being polyphyletic (Hunt *et al*., 2007). These insects generally live under bark and have received considerable taxonomic attention in recent years (Grimaldi and Engel, 2005). Three specimens from the Nova Olinda Member (SMNS 66469, SMNS 66468, and 'unusual carabid beetle', Grimaldi and Engel, 2005: 370 figure 10.17) may represent members of Cucujoidea, possibly Cucujidae and, if so, are the oldest fossils of this group (Wolf-Schwenninger and Schawaller, 2007).

8. 3. 17. 3. 9. Trogossitidae

Trogossitidae (bark-gnawing beetles) are a relatively small family with approximately only 600 modern species. As their common name suggests, they live in and feed on tree bark. A single undescribed specimen is reported from the Nova Olinda Member and likely resides within the subfamily Peltinae (Wolf-Schwenninger and Schawaller, 2007). Its flat body morphology is consistent with that of a bark-living lifestyle.

8. 3. 17. 3. 10. Lymexylidae

The family Lymexylidae (ship-timber beetles) are long, slender, soft beetles that bore into living and decaying wood. Interestingly, this is possibly the first beetle group to evolve agriculture and some taxa are 'farmers' of the fungi *Endomyces hylecoeti* and *Ascoides* spp. (Grimaldi and Engel, 2005). A single species within the subfamily Atractocerinae has been described from the Nova Olinda Member (Wolf-Schwenniger, 2011). Previous workers have

placed Lymexylidae outside of Polyphaga (Wheeler, 1986), however it is now known be nested within Polyphaga, at the base of Tenebrionoidea (Hunt *et al*., 2007).

8. 3. 17. 3. 11. Tenebrionidae

Tenebrionidae (darkling beetles) is one of the most species-rich beetle families and contains approximately 20,000 described species. The family is cosmopolitan, but can be divided into two morphotypes; slender, long-legged arid-dwelling forms and compact, short-legged forest-dwelling forms (Wolf-Schwenninger and Schawaller, 2007). There are currently no Mesozoic records of this family, however a single specimen (SMNS 66472) from the Nova Olinda Member could represent a compact, short-legged form. If accurately identified, this would be a significant discovery for understanding the evolution of this large family.

8. 3. 17. 3. 12. Pyrochroidae

Pyrochroidae (fire-coloured beetles) is a small family with only approximately 150 modern species. A single species described and placed in 'Pirochoidae' (Martins-Neto, 2005b: clearly a *lapsus calami* Heads pers. comm., 2016) is now believed to belong to Pyrochroidae (Wolf-Schwenninger and Schawaller, 2007). Another specimen was described by Vulcano and Pereira (1987), however this was only published in a congress abstract and so must be considered a *nomen nudum*.

8. 3. 17. 3. 13. Chrysomelidae

Chrysomelidae (leaf beetles) are an exceedingly diverse group with approximately 38,000 described modern species worldwide (with an estimated 50,000 total diversity), and a fossil record dating back to the Jurassic (Jolivet and Verma, 2002; Grimaldi and Engel, 2005). It contains 12 subfamilies, eight of which are known from the Mesozoic (Sagrinae, Clytrinae, Cryptocephalinae, Chrysomelinae, Eumolpinae, Galerucinae, Alticinae, and Cassidinae). As with many large beetle groups, diagnostic features can be extremely difficult to see in fossils, and so it is likely that some specimens have been incorrectly identified (Santiago-Blay, 1994). The high diversity of this group is largely attributed to their coevolution with primitive angiosperms, which is suggested by the abundance of pollen feeding in both basal and derived members. Pollen feeding may also have been possible before the rise of angiosperms, as conifers, cycads, and angiosperm precursors would have also produced pollen (Samuelson, 1994). In addition to this, classic Chrysomelidae feeding damage has been recorded on Cretaceous Zingiberales (Wilf *et al*., 2000). Two fossils from the Nova Olinda Member are believed to belong to Chrysomelidae, however one of them (SMNS 66471) has no clearly preserved diagnostic

features, and so could belong to Eumolpinae instead (Wolf-Schwenninger and Schawaller, 2007).

8. 3. 17. 3. 14. Superfamily Curculionoidea

The superfamily Curculionoidea (weevils) contains 11 families and is the largest beetle superfamily with 44,000 recent taxa. Adults have an unusually elongate rostrum with mandibles and modified mouthparts forming a distinctive 'snout', as well as clubbed antennae (Grimaldi and Engel, 2005). Despite their snout, weevils are not 'sucking' insects as commonly believed, and in fact possess chewing mouthparts. Their larvae are apodous, and basal forms possess small limbs. In the Late Jurassic, Curculionoidea diversified and became one of the most diverse and abundant groups (Arnol'di *et al*., 1992). Weevils are arguably one of the most economically important groups of beetles and this is due to their voracious appetite for tree bark. They have a history of devastating acres of forest and were responsible for the California 2003 wildfires, as well as numerous other ecological disasters (Grimaldi and Engel, 2005). Some taxa have evolved a fungal feeding strategy whereby they transmit an aggressive ambrosia fungus in specialised pockets (mycangia) and then feed on the fungi as it destroys the tree. There are, however, small numbers of Curculionoidea that have adapted down different paths, with some aquatic members and others that are convergent with dung beetles. Their fossil record is reasonably well studied (Gratshev and Zherikhin, 2003) and this is almost certainly because of easy identification due to their characteristic 'snout'.

There are six species of Curculionoidea described from Nova Olinda Member (Zherikhin and Gratshev, 2004; Santos *et al*., 2011). Two members of Nemonychidae (Rhinorhynchinae: Rhunorhynchini) (pine flower snout beetles) that are primitive and feed on pollen from araucartan conifers. One Belidae (?Pachyurinae: ?Pachyruini) (oxycorunid weevils) that are wood-boring as larvae and adults (Grimaldi and Engel, 2005). One possible Eccoptarthridae, a relic beetle family whose relatives are present in Australia and South America. One Curculionidae (true weevils) has relatively recently been described (Santos *et al*., 2011). Finally, one Brentidae (?Eurhynchinae) (straight-snouted weevils) whose recent relatives feed on the Broom and Pea families of plants, or bore through wood.

Additionally, there are two undescribed specimens (SMNS 66553 and SMNS 66449) that resemble Oxycoryninae and Attelabidae: Rhynchitinae respectively.

8. 3. 18. Trichoptera

The order Trichoptera (caddisflies) comprises a group of insects that have only a few distinguishing features. These include long filiform antennae, thoracic segments with very little variation (a slightly smaller prothorax), hairs on their wings (rather than scales in Lepidoptera), and mouthparts adapted into a haustellum (Ivanov and Sukatsheva, 2002; Grimaldi and Engel, 2005; Bechly, 2007g). They are generally medium-sized and moth-like, with aquatic larvae and an extant diversity of approximately 11,500 species (Bechly, 2007g). Interestingly, the larvae construct living 'cases' from stones, shells or plant debris (Wiggins, 1977, 1996). Adults of this order feed on liquids in a similar way to flies, but this has been poorly observed. Some taxa are convergent with butterflies, and are brightly coloured and feed from flowers.

Fossils of this group from the Nova Olinda Member are rare as adults and completely unknown as larvae. A total of seven species have been described, all of which were by Martins-Neto (2001b) and are likely in need of review (Bechly, 2007g). Many of the descriptions contradict their diagnoses or the figures. In addition, there is alleged sexual dimorphism that is unsupported and indistinguishable from taxonomic variation. There are also three specimens in the SMNS collection that are 'clearly' new species and are awaiting description (SMNS 66282, 66287, and 66568) (Bechly, 2007g).

8. 3. 18. 1. Leptoceridae

Leptoceridae (Long-horned caddisflies) are among the largest families of caddisflies, with over 1,560 described species, that likely represents only a fraction of their true diversity (Holzenthal and Pes, 2004). They are characterised by extremely long, slender antennae that can be twice as long as the rest of their body. Their diversity is highest in the neotropics, where many taxa still likely remain undescribed (Holzenthal and Pes, 2004). They are extremely rare in the Nova Olinda Member, with only a single species described (Bechly, 2007g).

8. 3. 18. 2. Hydroptilidae

Hydroptilidae (microcaddisflies or purse-case caddisflies) are, as their first common name indicates, extremely small caddisflies that rarely reach sizes larger than 5 mm (Harris *et al*., 2012). Aside from their diminutive size, they can be characterised by three well developed and relatively heavily sclerotized plates over their thorax in larval forms (Harris *et al*., 2012). Their aquatic larvae can live in fresh or brackish, flowing or still water, but require crevices, cracks, or rocks to hide under. They typically feed on filamentous green or red algae, but are also known to parasitize the pupae of other caddisflies (Wells, 2005). A single genus with four species is described from the Nova Olinda Member, all by Martins-Neto (2001). The genus is diagnosed on the basis of a composite of characters from its four species and so this group is in need of revision (Bechly, 2007g).

8. 3. 18. 3. Family *incertae sedis*

Two species of Trichoptera in two genera were described as family *incertae sedis* by Martins-Neto (2001).

8. 3. 19. Lepidoptera

The order Lepidoptera (butterflies and moths) are described as 'the most enjoyed insects' and possess a dazzling array of patterning, wing shapes, and colour (Grimaldi and Engel, 2005). They can be small to large insects, with overlapping scales that generate vibrant structural colour (particularly on their wings). Moths are typically smaller and nocturnal, whereas butterflies are larger and diurnal. Most taxa, except some of the basal micro-lepidopterans (Clarke, 1941-1969), have a long proboscis for feeding on nectar and other fluids, such as water, vertebrate blood and eye fluids, carrion, and excrement (Pivnik and McNeil, 1987; Bänziger, 1992; Erhardt and Rusterholz, 1998; Bechly, 2007g; Krenn, 2014). They are the largest lineage of primarily plant-feeding insects, reaching a modern diversity of approximately 130,000 species and radiated surprisingly recently (Grimaldi and Engel, 2005; Bechly, 2007g). Importantly, all larval forms (caterpillars) are soft-bodied and terrestrial and, as such, have a very low preservation potential. The large wings of most adult Lepidoptera can also greatly lower their preservation potential (discussed later in Chapter 3. 2. 1. 1.). Consequently, they are exceedingly rare in the fossil record.

For overviews of their biology see Grimaldi and Engel (2005), Kozlov *et al*. (2002), and Krenn (2014), and for an important monograph of extant species, see Seitz (1906-1933). For an overview of their phylogeny, see Regier *et al*. (2014).

Lepidopterans are extremely rare in the Nova Olinda Member and only five species have been described. All of them are attributed too small, basal families (Micropterygidae, Undopterygidae, and Eolepidopterigidae) (Bechly, 2007g). These families lack many of the typical Lepidoptera characteristics and are typically small in size with no proboscis, instead retaining functional mandibles (Kristensen, 1998). Due to the similarities in morphology between these families, and their contrast to extant taxa, they are not examined here individually. Another specimen has been figured by Grimaldi and Engel (2005) that is morphologically similar to Eriocraniidae or Acanthopteroctetidae (both within Glossata) that, if correct, could represent the most derived Lower Cretaceous lepidopteran.

8. 3. 20. Mecoptera

The Mecoptera (Scorpionflies) are a group of small-to-medium (1.7 to 35 mm) insects with an unusual morphology (Bechly, 2007f). They appear to be an amalgamation of several groups of arthropods, with scorpion-like ‘tails’ (male genitals) and a weevil-like elongate ‘snout’ (formed by elongation of the clypeus + labrum, mandibles, hypopharynx, and other mouthparts). These characters are a direct result of a long, diverse, and complex evolutionary history (Grimaldi and Engel, 2005). Their extant lineages are vestiges of a much broader diversity that has been fragmented by extinctions, and resulted in an extremely disjunct distribution (Grimaldi and Engel, 2005). Their biology is interesting, with eruciform larvae that possess three pairs of well-developed limbs, as well as an adult-like pupal stage. They are either carnivorous, phytophagous, or saprophagous and generally prefer moist habitats, with only a few species adapted to dryer habitats (Osten, 2007). This habitat preference is reflected by their rarity in the Nova Olinda Member, with only two distinct taxa, one undescribed and the other unnamed. It is likely that their low diversity within the Nova Olinda Member is a direct result of a majority dry and hot climate. The undescribed specimen has been suggested to belong to Panorpoidea which appears to be an outdated term (*circa* 1950s) used to described a polyphyletic ‘pool’ of insects distributed throughout the orders Mecoptera, Trichoptera, Lepidoptera, Diptera and Aphaniptera (last available reference Hinton, 1955).

For overviews of the Mecoptera fossil record, see Handlirsch (1906-1908), Willmann (1978), Carpenter (1992), Novokschonov (1997, 2002), and Grimaldi and Engel (2005).

8. 3. 20. 1. Bittacidae

The only described, but unnamed, taxon of Mecoptera from the Nova Olinda Member is attributed to Bittacidae (hanging flies). Care should be taken when identifying this group as they are morphologically similar to Tipulidae (crane flies), but can be distinguished by the presence of four wings rather than two (Petrulevičius and Martins-Neto, 2001). In accordance with their common name, members of Bittacidae ‘hang’ from perches during copulation. Their larvae are caterpillar-like, but are distinguished by the presence of ocelli. Adults may be associated with seasonally dry marsh areas (Preston-Mafham and Preston Mafham, 1993).

8. 3. 21. Diptera

Diptera (true flies) are an extremely successful and diverse order of insects. They have an extant diversity of approximately 134,000 species with a variety of body forms, sizes, and feeding strategies (Gullan and Cranston, 2005). Their larvae inhabit almost all aquatic environments and are essential components of aquatic food chains. Their adults have

colonised almost all non-Antarctic habitats and are especially abundant in boreal regions. Feeding strategies can range from predators, extoparasites, saprophages, bloodsuckers, to feeding on nectar and pollen, or even adults not feeding at all (Willkommen and Grimaldi, 2007). The order is characterised by a single pair of forewings, with the hind wings adapted into small knobbed gyroscopic organs called halteres, giving them outstanding flight control and manoeuvrability (McAlpine, 1981; Willkommen and Grimaldi, 2007). Their wing venation is considered their most important taxonomic character, followed by leg and antennae structure. For an overview of the Diptera ground-plan, see Henning (1954) and for their phylogeny, see Huchard *et al*. (2006).

Dipteran fossils from the Nova Olinda Member are surprisingly diverse when compared to other Cretaceous Lagerstätte, but are also relatively very rare. In other localities dipteran fossils can account for 30-50% of all specimens, whereas the Nova Olinda Member dipterans account for only 2% of all fossil insects. Although it is accepted that there is likely a collection bias away from small flies, this is still an astonishing comparison (Willkommen and Grimaldi, 2007). In addition to this, the Nova Olinda Member dipteran fauna more closely resembles that of Tertiary faunas, rather than that of other Cretaceous deposits, and includes families that are reportedly abundant in arid environments (Willkommen and Grimaldi, 2007).

8. 3. 21. 1. Infraorder Culicomorpha

Culicomorpha (mosquitoes and black flies, bloodworms, and midges etc.) is a particularly important infraorder of Diptera as they can be vectors of serious epidemic diseases. Only a single species of Culicomorpha is described from the Nova Olinda Member, with another specimen awaiting description. The undescribed specimen is only partially preserved, but clearly possesses no proboscis, and so is tentatively assigned to Chironomidae (Willkommen and Grimaldi, 2007).

8. 3. 21. 1. 1. ?Chironomidae

The family Chironomidae (non-biting midges) superficially resemble mosquitoes, bar their lack of a proboscis. They are estimated to have 10,000 modern species, although far fewer have been described. The group has a plethora of common names (lake flies, bay flies, sand flies (incorrect though), muckleheads, muffleheads, Canadian soldiers, American soldiers, blind mosquitoes, Bloodworms (larvae), and chizzywinks) and are associated with almost every aquatic environment. Their larvae are aquatic or semi-aquatic and adapted to virtually all water conditions, including heavily polluted anoxic waters (Armitage *et al*., 1995). As stated above, a single specimen from the Nova Olinda Member is tentatively placed in this family.

8. 3. 21. 1. 2. Simuliidae

The Simuliidae (blackflies) can form ‘scourges’ (swarms) of female blood-sucking parasites in many tropical river basins, while the males feed mostly on nectar. Approximately 1,800 taxa have been described and they typically possess short legs and antennae. Their fossil record is overviewed by Currie and Grimaldi (2000), and they are extremely rare in the Cretaceous except for Australian larvae (Jell and Duncan, 1986). A single species was recorded and described from the Nova Olinda Member by Vulcano (1985), however no type specimen was designated and no diagnosis provided. As such, the taxa must be considered a *nomen nudum* (Willkommen and Grimaldi, 2007).

8. 3. 21. 2. Infraorder Bibionomorpha

Only three specimens with uncertain familial placements in the infraorder Bibionomorpha are known from the Nova Olinda Member (Grimaldi, 1990). Bibionomorpha is a large and diverse group, with varying morphologies (both for larvae and adults), however their larvae are all terrestrial saprophages or fungivores. Modern bibonids are known for swarming in tropical and semi-tropical regions, which is believed to help them minimize dehydration (Willkommen and Grimaldi, 2007).

8. 3. 21. 2. 1. Mycetophilidae

Mycetophilidae (fungus gnats) are a diverse family of small flies with approximately 3,000 described species, and this likely represents only a fraction of their true diversity. They are most diverse and abundant in moist or wet environments, typically wet forests, swamps, and moist heaths or grasslands (Arnett, 2000). Their larvae are sporophagous and often bind themselves to fleshy sporophores, or spin glutinous webs around sites of fungal activity (Evenhuis, 1989). A single undescribed species is reported from the Nova Olinda Member (Willkommen and Grimaldi, 2007).

8. 3. 21. 2. 2. Sciaridae

Sciaridae (dark-winged fungus gnats) are a family of small flies with a homogenous morphology that has deterred extensive taxonomic work (Evenhuis, 1989). As such, the 1,700 described species represent only a portion of their diversity, which is estimated to exceeding 20,000 species. Their larvae typically feed on and live in rotten wood, under bark of fallen trees, or other decaying plant matter and, in rare cases, can be associated with termites (Evenhuis, 1989). A single undescribed species of Sciaridae is reported from the Nova Olinda Member (Willkommen and Grimaldi, 2007).

8. 3. 21. 2. 3. Bibionidae

Bibionidae (march flies or lovebugs) are a relatively small family with only approximately 700 described modern species. They are most abundant in temperate regions and are phytophagous (Evenhuis, 1989). Many larvae scavenge decaying plant material or feed on roots and can be major agricultural pests. Some of the adults are nectar feeders and pollinators, further increasing their agricultural importance. A single undescribed species from the Nova Olinda Member is tentatively placed in Bibionidae (Willkommen and Grimaldi, 2007).

8. 3. 21. 3. Infraorder Psychodomorpha

8. 3. 21. 3. 1. Psychodidae? or Tanyderidae?

Psychodidae (drain flies, sink flies, moth flies, or sewer gnats) are characterised as short-legged, weak-flying flies that, as their common names indicate, inhabit moist environments (Duckhouse and Lewis, 1989). While they are commonly associated with human water sources, they are most abundant in damp forests, where their larvae feed on fallen leaves and other decaying plant material. Some members of this group possess coarse setae covering their wings, giving them a 'hairy' appearance (Willkommen and Grimaldi, 2007).

The family Tanyderidae (primitive crane flies) is an extremely small family (with less than 50 described species) and has been considered a sister to Psychodidae (Willkommen and Grimaldi, 2007). However, more recent studies have suggested that this placement is uncertain (Wipfler *et al*., 2012). The position of this group has been disputed heavily and is still under discussion (Wipfler *et al*., 2012). As their common name suggests, they are long, thin, delicate insects that superficially resemble members of Tipulidae.

A single genus and species (*Megapsychoda araripina*) from the Nova Olinda Member has been described and its familial placement is debated. While it was tentatively assigned to Psychodidae (Azar and Nel, 2002), later authors discussed its possible placement within Tanyderidae (Willkommen and Grimaldi, 2007).

8. 3. 21. 4. Infraorder Tipulomorpha

The infraorder Tipulomorpha (crane flies and their kin) is large and contains the largest dipteran family (based on descriptions, rather than estimated diversity), Tipulidae, with approximately 15,000 described modern species. They are gracile insects with long delicate legs. Their larvae are distinctive, with a partly sclerotized and retractable head, and live in semi-aquatic habitats or moist soils (Grimaldi and Engel, 2005). They were traditionally considered the most basal Diptera and their distribution is bipolar, with taxa occurring in colder temperate areas of the Holarctic, and South America, Australia, and sub-Antarctic islands (Grimaldi and Engel, 2005).

8. 3. 21. 4. 1. Tipulidae

Tipulidae (crane flies or daddy longlegs) are one of the largest fly families, with over 15,000 described species and a cosmopolitan distribution. They are easily recognisable by their overall slender habit, narrow wings, and long, slender legs and can range in size from 5 to 50 mm (Jong *et al*., 2008). They are typically most diverse in the tropics, but their larvae can be found in a variety of habitats, varying from strictly aquatic to terrestrial and even high-altitude environments (Jong *et al*., 2008). Recently four species of Tipulidae were described within a single genus from the Nova Olinda Member (Ribeiro and Lukashevich, 2014; Ribeiro *et al*., 2015).

8. 3. 21. 4. 2. Limoniidae

Limoniidae (meadow crane flies?) are a paraphyletic assemblage of flies that are similar to Tipulidae. The clade was previously treated as a subfamily of Tipulidae (Evenhuis, 1989). They can be distinguished from Tipulidae by the position of their wings at rest, which are held back parallel over the body. There are currently two species within two genera assigned to Limoniidae from the Nova Olinda Member (Ribeiro and Martins-Neto, 1999; Ribeiro and Krzemiski, 2000).

8. 3. 21. 5. Infraorder Stratiomyomorpha

8. 3. 21. 5. 1. Zhangsolvidae

Zhangsolvidae is an extinct family of flies suggested to belong in Stratiomyomorpha, however the Mesozoic relationships of this group is still poorly understood (Arillo *et al*., 2015). The biology of Zhangsolvidae is believed to be similar to its close relatives Xylomyidae and Stratiomyidae. Larvae of these groups live in rotten plant matter, under bark, or in other decaying wet substances, and adults of Zhangsolvidae likely fed on nectar (Rozkosny, 2000). Nova Olinda stratiomyomorphs were previously placed in their own family, Cratomyiidae, which is now recognised as a junior synonym of Zhangsolvidae (Arillo *et al*., 2015). Additionally, the genus *Cratomyoides* was also shown to be a synonym of *Cratomyia*, and so the genera have been merged, culminating in three species within a single genus (Mazzarolo and Amorim, 2000; Arillo *et al*., 2015).

8. 3. 21. 6. Infraorder Tabanomorpha

8. 3. 21. 6. 1. Tabanidae

Recent members of the family Tabanidae (horse and deer flies) are mostly blood-feeders and vectors for diseases in humans and livestock. They can also be pollen or nectar feeders and are important pollinators for some angiosperm species, with mouthparts adapted for specific flowers (Willkommen and Grimaldi, 2007). They are typically strong fliers and are considered 'study' (= heavily sclerotized?) insects (Daniels, 1989). The fossil record of this family dates back to the Cretaceous, and they are known from many Cretaceous localities. However, the Nova Olinda Member represents their only gondwanan record, with a single species described by Martins-Neto and Santos (1994). Unfortunately, the wing venation of this specimen differs from other members of the family, and so this placement may need revision (Willkommen and Grimaldi, 2007).

8. 3. 21. 6. 2. Rhagionidae?

A single described, but unnamed specimen is placed putatively in the family Rhagionidae (snipe flies) (Willkommen and Grimaldi, 2007). In addition to this, the family is currently considered polyphyletic, and as such this placement is liable to change or the family may be rearranged. Nevertheless, these insects are generally medium-to-large and can be blood-suckers or predators of other insects. They are typically brown or yellow and their larvae are mostly predatory and terrestrial, although some are aquatic (Watson and Dallwitz, 2007).

8. 3. 21. 7. 'Infraorder' Asilomorpha

The infraorder Asilomorpha is no longer an officially recognised phylogenetic clade, as it is undoubtedly paraphyletic and the its members have an exceedingly diverse morphology and biology (Willkommen and Grimaldi, 2007). Nevertheless, it is included here for the distinction of the following families.

8. 3. 21. 7. 1. Mydidae

The Mydidae (mydas flies) are a highly diverse and cosmopolitan family. They tend to prefer arid to semi-arid environments with open vegetation, and so their presence in the Nova Olinda Member is not surprising. Their larvae are generally predators, while adults primarily visit blossoms (Willkommen and Grimaldi, 2007). Some members of this family mimic stinging hymenopterans and their adult lifespans can be surprisingly short. As such, little is known about the biology of the adults of this family (Lyons and Dikow, 2010). A single taxon is described from the Nova Olinda Member, and this represents the oldest known, and second fossil described from this group (Evenhuis, 1994; Willkommen and Grimaldi, 2007). Other fossils of close relatives are known from China, but are not 'true' Mydidae (Zhang *et al*., 2007).

8. 3. 21. 7. 2. Therevidae?

Therevidae (stiletto flies) biology is still relatively poorly understood, but they inhabit a wide variety of environments. This family has approximately 1,600 modern taxa and a nearly global distribution, excluding only Antarctica (Irwin and Lyneborg, 1989). However, they are most diverse in arid and semi-arid regions, where their terrestrial larvae prey upon soil-dwelling larvae of other arthropods or feed off of insect excretions (Irwin and Lyneborg, 1989). A single very poorly preserved specimen, that was previously attributed to *Cratotabanus* (Martins-Neto, 2003b), is now considered undescribed and tentatively placed in Therevidae (Willkommen and Grimaldi, 2007). Another unnamed species from the Nova Olinda Member may also be a member of this family.

8. 3. 21. 7. 3. Asilidae

The family Asilidae (robber flies or assassin flies) is a group of highly aggressive aerial predators. They are characterised by a short sturdy proboscis with a sharp sucking hypopharynx, stout spiny legs, and large eyes. They are depicted as 'powerful hunters' and will attack and kill insects that are generally seen as 'dangerous' (such as stinging hymenopterans, odonates, and powerful orthopterans) (Wood, 1981). They are cosmopolitan, with approximately 7,000 described species, but generally prefer open, sunny, and dry (even arid) habitats with scattered vegetation. There are currently two species described from the Nova Olinda Member, however one is unnamed and its familial placement is uncertain (Grimaldi, 1990). This family is exceedingly rare in the fossil record, and only four definitive Cretaceous records are known (Grimaldi and Cumming, 1999; Grimaldi, 1990, 2007, Willkommen and Grimaldi, 2007; Dikow and Grimaldi, 2014).

8. 4. Valid insect taxa list

As a by-product of identifying every insect family currently described from the Nova Olinda Member, a list of valid species was created and is presented here. Many of the Nova Olinda fossil taxa require heavy revision. Nevertheless, all (possibly excluding Formicidae) of the species listed here are currently considered valid.

Diplura

- Japygoidea
    - Family *incertae sedis*
        - *Ferrojapyx vivax* Wilson and Martill, 2001

Zygentoma

- Lepismatidea
    - Lepismatidae
        - Gen. spec. 'Araripe' Strum, 1998

Coxoplectoptera

- Mickoleitiidae
    - *Mickoleitia* Staniczek *et al*., 2011
        - *M. longimanus* Staniczek *et al*., 2011

Ephemeroptera

- Hexagenitidae
    - *Protoligoneuria* Demoulin, 1955
        - *P. limai* Demoulin, 1955
    - *Cratohexagenites* Staniczek, 2007
        - *C. longicercus* Staniczek, 2007
        - *C. minor* Staniczek, 2007
- Oligoneuriidae
    - *Colocrus* McCafferty, 1990
        - *C. indivicum* McCafferty, 1990
        - *C.? magnum* Staniczek, 2007
- Ephemeroidea (*sensu* McCafferty 1990)
    - Potamanthidae?
        - *Olindinella* Martins-Neto and Caldas, 1990 – validity doubtful
            - *O.gracilis* Martins-Neto and Caldas, 1990 – validity doubtful.
    - Euthyplociidae
        - *Pristiplocia* McCafferty, 1990
            - *P. rupestris* McCafferty, 1990
    - Ephemeridae
        - *Australiephemera* McCafferty, 1990
            - *A. revelata* McCafferty, 1990
        - *Microephemera* McCafferty, 1990
            - *M. neotroica* McCafferty, 1990
        - *Cratonympha* Martins-Neto and Caldas, 1990 – validity doubtful.
            - *C. microcelata* Martins-Neto and Caldas, 1990 – validity doubtful.
    - Polymitarcyidae?
        - *Caririnympha* Martins-Neto, 1990 – validity doubtful.
            - *C. mandibulata* Martins-Neto, 1990 – validity doubtful.
    - Baetiscidae
        - *Protobaetisca* Staniczek, 2007
            - *P. bechlyi* Staniczek, 2007
    - Siphlonuridae?
        - Three Undescribed/unnamed sp. McCafferty, 1990
    - Ephemeroidea
        - Two *incertae sedis* Staniczek, 2007
    - Leptophlebiidae?
        - Unnamed/unnamed McCafferty, 1990
    - Family *incertae sedis*
        - Two Unnamed/unnamed McCafferty, 1990
        - Unnamed/unnamed Grimaldi and Engel, 2005
        - Unnamed/unnamed Bechly *et al*., 2001a
        - Unnamed/unnamed Staniczek, 2007
        - *Costalimella* Martins-Neto, 1996a
            - *C. nordestina* Martins-Neto, 1996a
        - *Caririephemera* Zamboni, 2001
            - *C. marquesi* Zamboni, 2001

Odonata

- Zygoptera
    - Family *incertae sedis* (probably Hemiphlebiidae)
        - *Cretarchistigma* Jarzembowski *et al*., 1998
            - *C*(?) *essweini* Bechly 1998c
    - Hemiphlebiidae
        - *Parahemiphlebia* Jarzembowski *et al.,* 1998
            - *P. cretacica* Jarzembowski *et al.,* 1998
            - *P. mickoleiti* Bechly, 1998c
            - Spec nov. Bechly 1998c (possibly described in Bechly, 2010)
    - Protoneuridae
        - Isostictinae
            - Eoprotoneurini

- *Eoprotoneura* Carle and Wighton, 1990
  - *E. hyperstigma* Carle and Wighton, 1990
- Thaumatoneuridae
  - Thaumatoneuridae
    - Euarchistigmatini
      - *Euarchistigma* Carle and Wighton, 1990
        - *E. atrophium* Carle and Wighton, 1990
        - *E. marialuiseae* Bechly, 2007b
        - *E. peterknobli* Bechly, 2010
    - Family *incertae sedis*
      - *Santanagrion* Bechly, 2010
        - *S. longipes* Bechly, 2010

- 'Anisozygoptera'
  - Stenophlebioptera
    - Stenophlebiiae
      - *Cratostenophlebia* Bechly, 2007b
        - *C. schwickerti* Bechly, 2007b

- Anisoptera
  - Nothomacromiidae (substitute name for Pseudomacromiidae Carle and Wighton, 1990)
    - *Nothomacromia* Carle, 1995 (substitute name for Pseudomacromia Carle and Wighton, 1990)
      - *N. sensibilis* Carle and Wighton, 1990
  - Aeschnidiidae
    - *Wightonia* Carle in Carle and Wighton, 1990
      - *W. araripina* Carle in Carle and Wighton, 1990
    - *Santanoptera* Martill and Nel, 1996
      - *S. gabotti* Martill and Nel, 1996
  - Cretapetaluridae
    - *Cratopetalura* Nel *et al*., 1998
      - *C. petruleviciusi* Nel and Bechly, 2009
      - *C. brasiliensis* Nel *et al.,* 1998
    - *Eotanypteryx* Bechly, 2007b
      - *E. paradoxa* Bechly, 2007b
  - Liupanshaniidae
    - *Paramesuropetala* Bechly *et al*., 2001b
      - *P. gigantean* Bechly *et al*., 2001b
    - *Araripeliupanshania* Bechly *et al*., 2001b
      - *A. annesuseae* Bechly *et al*., 2001b
  - Gomphaeschnidae
    - Gomphaeschnaoidinae
      - *Gomphaeschnaoides* Carle and Wighton, 1990
        - *G. obliquus* Wighton, 1987
        - *G. petersi* Bechly *et al*., 2001b
        - *G. betoreti* Bechly *et al*., 2001b
        - *G. magnus* Bechly *et al*., 2001b
      - *Progomphaeschnaoides* Bechly *et al*., 2001b
        - *P. ursulae* Bechly *et al*., 2001b
        - *P. staniczeki* Bechly *et al*., 2001b
      - *Paramorbaeschna* Bechly *et al*., 2001b
        - *P. araripensis* Bechly *et al*., 2001b
      - *Anomalaeschna* Bechly *et al*., 2001b
        - *A. berndschusteri* Bechly *et al*., 2001b
  - Araripegomphidae
    - *Araripegomphus* Nel and Paicheler, 1994b
      - *A. cretacicus* Nel and Paicheler, 1994b
      - *A. andreneli* Bechly, 1998c
      - *A. hanseggeri* Bechly, 2000
      - New taxa Bechly, 2007b
  - Proterogomphidae
    - Cordulagomphinae
      - *Cordulagomphus* Carle and Wighton, 1990
        - *C. tuberculatus* Carle and Wighton, 1990
        - *C. fenestratus* Carle and Wighton, 1990
        - *C. winkelhoferi* Bechly, 2007b

- *C. hanneloreae* Bechly, 2007b
- Subgenus: *Procordulagomphus* Nel and Escuillié, 1994, also see Petrulevičius *et al*., 2012
  - *C. (P.) xavieri* Nel and Escuillié, 1994
  - *C. (P.) senckenbergi* Bechly, 1998
  - *C. (P.) primaerensis* Petrulevičius and Martins-Neto, 2007b
  - *C. (P.) michaeli* Bechly, 2007b
- *Paracordulagomphus* Bechly, 2010
  - *P. aberrans* Bechly, 2010
  - *P. divergens* Bechly, 2010
- *Pauciphlebia* Bechly, 2010
  - *P. novaolindense* Bechly, 2010
- *Cratogomphus* Bechly, 2010
  - *C. erraticus* Bechly, 2010

- Lindeniidae
  - Lindeniinae
    - *Cratolindenia* Bechly, 2000
      - *C. knuepfae* Bechly, 2000
- Araripephlebiidae
  - *Araripephlebia* Bechl, 1998c
    - *A. mirabilis* Bechly, 1998c
- Araripechlorogomphidae
  - *Araripechlorogomphus* Bechly and Ueda, 2002
    - *A. muratai* Bechly and Ueda, 2002
- Araripelibellulidae
  - Araripelibellulinae
    - *Araripelibellula* Nel and Paicheler, 1994
      - *A. martinsnetoi* Nel and Paicheler, 1994
    - *Cratocordulia* Bechly, 1998c
      - *C. borschukewitzi* Bechly, 1998c
- Mesuropetaloidea
  - Mesuropetalidae
    - *Paraeschnopsis* Bechly, 2010
      - P. *brasiliensis* Bechly, 2010
- Hageniidae
  - *Cratohagenius* Bechly, 2010
    - *C. erichweberi* Bechly, 2010
- Megaphlebiidae
  - *Megaphlebia* Bechly, 2010
    - *M. rayandressi* Bechly, 2010
- Magnathemidae
  - *Magnathemis* Bechly, 2010
    - *M. marcusthorhalli* Bechly, 2010
- Cratopetaliidae
  - *Cratopetalia* Bechly, 2010
    - *C. whiteheadi* Bechly, 2010

Dermaptera

- Anisolabididae
  - *Cratoborellia* Haas, 2007
    - *C. gorbi* Haas, 2007
- Labiduridae
  - *Caririlabia* Marins-Neto, 1990a
    - *C. berghoffi* Haas, 2007
    - *C. brandaoi* Martins-Neto, 1990a
- Eudermaptera
  - Spongiphoridae
    - *Cretolabia* Popham, 1990
      - *C. cearae* Popham, 1990
    - *Kotejalabis* Engel and Chatzimanolis, 2005
      - *K. haeuseri* Haas, 2007
      - *K. goethitica* Engel and Chatzimanolis, 2005

Fossil erroneously identified as a Dermaptera:

Carirriderma pilosa Martins-Neto 1990a – this is a staphylinid beetle.

Orthoptera

- Ensifera
  - Hagloidea *incertae sedis*
    - *Cratohaglopsis* Martins-Neto, 1991
      - *C. santanaensis* Martins-Neto, 1991
    - *Kevania* Martins-Neto, 1991
      - *K. araripensis* Martins-Neto, 1991
  - Schizodactyloidea
    - Schizodactylidae Karny, 1927
      - *Schizodactylus*
        - *S. groeningae* (Martins-Neto) in Heads and Leuzinger, 2011
  - Gryllotalpidae
    - *Archaeogryllotalpoides* Martins-Neto, 1991
      - *A. ornatus* Martins-Neto, 1991
    - *Palaeoscapteriscops* Martins-Neto, 1991
      - *P. cretacea* Martins-Neto, 1991
    - *Cratotetraspinus* Martins-Neto, 1995
      - *C. fossorius* Martins-Neto, 1995
  - Gryllidae
    - *Araripegryllus* Martins-Neto, 1987
      - *A. caposae* Martins-Neto, 1987
      - *A. femininus* Martins-Neto, 1991
      - *A. marianoi* Martins-Neto, 1991
      - *A. nanus* Martins-Neto, 1991
      - *A. serrilhatus* Martins-Neto, 1991
      - *A. spinosus* Martins-Neto, 1991
    - *Brontogryllus* Martins-Neto, 1991
      - *B. excelsus* Martins-Neto, 1991
    - *Cratogryllus* Martins-Neto, 1991
      - *C. pentagonalis* Martins-Neto, 1991
      - *C. guimaraesae* Martins-Neto, 1991
      - *C. ciguelli* Martins-Neto, 1991
    - *Nanoararipegryllus* Martins-Neto, 2002
      - *N pigamaeus* Martins-Neto, 2002
  - Baissogryllidae
    - *Caririgryllus* Martins-Neto, 1991
      - *C. elongates* Martins-Neto, 1991
      - *C. pilosus* Martins-Neto, 1991
      - *C. arthaudi* Martins-Neto, 1991
      - *C. mesai* Martins-Neto, 1991
      - *C. brevipterus* Martins-Neto, 2002
    - *Cearagryllus* Martins-Neto, 1991
      - *C. monstrusosus* Martins-Neto, 1991
      - *C. robustus* Martins-Neto, 1991
      - *C. gorochovi* Martins-Neto, 1991
      - *C. perforatorius* Martins-Neto, 1991
      - *C. poliacanthus* Martins-Neto, 1991
      - *C. microephalus* Martins-Neto, 1991
      - *C. revelatus* Martins-Neto, 1998
      - *C. previstus* Martins-Neto, 1998
    - *Santanagryllus* Martins-Neto, 1991
      - *S. hesselae* Martins-Neto, 1991
    - *Castillogryllus* Martins-Neto, 1995
      - *C. complicates* Martins-Neto, 1995
    - *Notocearagryllus* Martins-Neto, 1998
      - *N. dutrae* Martins-Neto, 1998
      - *N. leipnitzi* Martins-Neto, 2002
    - *Olindagryllus* Martins-Neto, 1998
      - *O. obliterates* Martins-Neto, 1998
      - *O. rotundus* Martins-Neto, 1998
  - Ensifera incertae sedis
    - *Phasmomimella*? Kevan and Wighton, 1981

- *P. araripensis* Martins-Neto, 1991

- Caelifera
  - Tridactylidae
    - *Cratodactylus* Martins-Neto, 1990
      - *C. ferreirai* Martins-Neto, 1990
      - *C. kellneri* Martins-Neto, 1990
  - Proscopiidae
    - *Eoproscopia* Heads, 2008
      - *E. martilli* Heads, 2008
  - Locustopseidae
    - *Cratozeunerella* Martins-Neto, 1998
      - *C. neotropica* Martins-Neto, 1998
      - *C. amedegnatoi* Martins-Neto, 1998
      - *C. godoii* Martins-Neto, 2003
      - *C. nervosa* Martins-Neto, 2003
      - *C. soaresi* Martins-Neto, 2003
      - *C. titanella* Martins-Neto, 2003
    - *Cratolocustopsis* Martins-Neto, 2003
      - *C. cretacea* Martins-Neto, 2003
      - *C. araripensis* Martins-Neto, 2003
      - *C. contumax* Martins-Neto, 2003
    - *Zessinia* Martins-Neto, 1990
      - *Z. pulcherrima* Martins-Neto, 1990
      - *Z. caririensis* Martins-Neto, 1990
      - *Z. reticulate* Martins-Neto, 1990
      - *Z. petruleviciusi* Martins-Neto, 2003
      - *Z. vikingi* Martins-Neto, 2003
    - *Locustrix* Martins-Neto, 2003
      - *L. gallegoi* Martins-Neto, 2003
      - *L. audax* Martins-Neto, 2003
  - Araripelocustidae
    - *Araripelocusta* Martins-Neto, 1995
      - *A. longinota* Martins-Neto, 1995
      - *A. brevis* Martins-Neto, 1995
  - Elcanidae
    - *Cratoelcana* Martins-Neto, 1991
      - *C. damianii* Martins-Neto, 1991
      - *C. zessini* Martins-Neto, 1991
  - Bouretidae (possible junior synonym of Tetrigidae)
    - *Bouretia* Martins-Neto, 2001
      - *B. elegans* Martins-Neto, 2001

Chresmododea (fossil 'water striders')

- Archaeorthoptera
  - Chresmodidae
    - *Chresmoda* Germar, 1839
      - *C. neotropica* Engel and Heads, 2008 *In* Delclòs, *et al*., 2008

Phasmatodea

- Aerophasmatidae
  - Cretophasmatinae
    - *Cretophasma* Martins-Neto, 1989b
      - *C. araripensis* Martins-Neto, 1989b

Mantodea

- Chaeteessidae
  - *Cretophotina* Lee, 2014
    - *C. santanensis* Lee, 2014
- Family *incertae sedis*
  - *Santanmantis* Grimaldi, 2003
    - *S. axelrodi* Grimaldi, 2003 and revisions by Hoernig *et al*., 2013.
  - Undescribed, but distinct species Grimaldi, 2007.

Blattodea

- Blattellidae
  - '*Mesoblattina'* Pinto and Purper, 1986 [incorrect genus according to Bechly 2007c]
    - *'M'. limai* Pinto and Purper, 1986
  - Unnamed new genus (A) Bechly, 2007c
    - Unnamed new species (A) Bechly, 2007c
- Mesoblattinidae
  - Undescribed genus Vršanský, 2004
    - Undescribed species Vršanský, 2004
- Blattidae
  - *Mesoblattinopsis* Pinto, 1989
    - *M. schneideri* Pinto, 1989
- Blattulidae
  - *Elisama* Vršanský, 2002
    - *E. americana* Vršanský, 2002
  - Undescribed genus and species (Bechly, 2007c)
- Raphidiomimidae
  - Undescribed taxon Grimaldi and Engel, 2005; Bechly, 2007c
- Ponopterixidae
  - Cratovitismidae Bechly, 2007c
    - *Cratovitisma* Bechly, 2007c
      - *C. oldreadi* Bechly, 2007c
  - Umenocoleidae
    - *Ponopterix* Vršanský, 1999
      - *P. axelrodi* Vršanský, 1999
      - *P. maxima* Bechly, 2007c
      - *P. buckhardi* Nel *et al*. 2014
- Family *incertae sedis*
  - Unnamed new genus (B) Bechly, 2007c
    - Unnamed new species (B) Bechly, 2007c

Isoptera (technically infraorder within Blattidae)

- Cratomastotermitidae Engel *et al*., 2009
  - *Cratomastotermes* Bechly, 2007d
    - *C. wolfschwenningeri* Bechly, 2007d
- Kalotermitidae
  - *Cratokalotermes* Bechly, 2007d
    - *C. santanensis* Bechly, 2007d
- Termopsidae
  - Subfamilia *incertae sedis*
    - *Mariconitermes* Fontes and Vulcano, 1989
      - *M. talicei* Fontes and Vulcano, 1989
- Hodotermitidae
  - *Meiatermes* Engel *et al*., 2009
    - *M. hariolus* Grimaldi *et al*., 2008
    - *M. araripena* Krishna, 1990
  - *Cretarhinotermes* Bechly, 2007d
    - C*. novaolindense* Bechly, 2007d

Hemiptera

- Auchenorrhyncha
  - Cicadomorpha
    - Membracoidea
      - Cicadellidae
        - Cicadellinae
          - Proerrhomini
            - *Proerrhomus* Hamilton, 1990
              - *P. rugosus* Hamilton, 1990
        - Ledrinae
          - Paracarsonini
            - *Paracarsonus* Hamilton, 1990
              - *P. aphrodoides* Hamilton, 1990
            - *Platyjassites* Hamilton, 1990
              - *P. inflatifrons* Hamilton, 1990
      - Myerslopiidae

- Ovojassini
  - *Ovojassus* Hamilton, 1990
    - *O. concavifer* Hamilton, 1990
    - *O. minor* Hamilton, 1990
- Cicadoidea
  - Tettigarctidae
    - Cicadoprosbolinae
      - *Architettix* Hamilton, 1990
        - *A. compacta* Hamilton, 1990
      - *Tettagalma* Menon, 2005
        - *T. striata* Menon, 2005
- Palaeontinoidea
  - Palaeontinidae
    - *Parawonnacottella* Udea, 1997
      - *P. araripensis* Udea, 1997
      - *P. penneyi* Menon *et al*., 2005
    - *Cratocossus* Martins-Neto, 1998
      - *C. magnus* Martins-Neto, 1998
    - *Baeocossus* Menon and Heads, 2005
      - *B. fortunatus* Menon and Heads, 2005
    - *Colossocossus* Menon *et al*., 2005
      - *C. loveridgei* Menon *et al*., 2005
      - *C. rugose* Menon *et al*., 2005
      - *C. bechlyi* Menon and Heads, 2005
      - *C. giganticus* Menon *et al*., 2007
- Cercopoidea
  - Cercopionidae
    - *Cercopion* Hamilton, 1990
      - *C. reticulate* Hamilton, 1990
    - Hallicini
      - *Hallex* Hamilton, 1990
        - *H. xestocephalus* Hamilton, 1990
        - *H. gongrogony* Hamilton, 1990
        - *H. brevipes* Hamilton, 1990
        - *H. laticeps* Hamilton, 1990
        - *H. gracilior* Hamilton, 1990

- Fulgoromorpha
  - Cixiidae
    - *Cretofennahia* Martins-Neto 1998
      - *C. cretacea* Martins-Neto, 1988
  - Lalacidae
    - Protodelphacinae
      - Protodelphacini
        - *Protodelphax* Hamilton, 1990
          - *P. chamus* Hamilton, 1990
          - *P. macroceps* Hamilton, 1990
          - *P. miles* Hamilton, 1990
          - *P. rhinion* Hamilton, 1990
    - Ancoralinae
      - Ancoralini
        - *Ancorale* Hamilton, 1990
          - *A. flaccidum* Hamilton, 1990
          - *A. aschemon* Hamilton, 1990
      - Kinnarocixiini
        - *Kinnarocixius* Hamilton, 1990
          - *K. quassus* Hamilton, 1990
          - *K. sp*. (possibly distinct genus) Hamilton 1990
    - Lalacinae
      - Lalacini
        - *Lalax* Hamilton, 1990
          - *L. mutabilis* Hamilton, 1990
        - *Patulopes* Hamilton, 1990
          - *P. setosa* Hamilton, 1990
          - *P. myndoides* Hamilto, 1990

- Carpopodini
  - *Carpopodus* Hamilton, 1990
    - *C. difficilis* Hamilton, 1990
    - *C. sp. A* Hamilton, 1990
    - *C. sp. B* Hamilton, 1990
  - *Psestocixius* Hamilton, 1990
    - *P. fuscus* Hamilton, 1990
    - *P. delphax* Hamilton, 1990
  - *Vulcanoia* Hamilton, 1990
    - *V. membranosa* Martins-Neto, 1988
    - *V. apicalis* Hamilton, 1990
    - *V. acuceps* Hamilton, 1990
- Achilidae
  - *Acixiites* Hamilton, 1990
    - *A. immodesta* Hamilton, 1990
    - *A. costalis* Hamilton, 1990
  - Familia *incertae sedis* (Boreoscytidae?)
    - *Megaleurodes* Hamilton, 1990
      - *M. megocellata* Hamilton, 1990

- Coleorrhyncha
  - Peloridioidea
    - Progonocimicidae
      - Undescribed sp.
- Heteroptera
  - Nepomorpha
    - Belostomatidae
      - Belostomatinae
        - *Araripebelostomum* Nel and Paicheler, 1992
          - *A. martinsnetoi* Nel and Paicheler, 1992
        - *Neponymphes* Zamboni, 2001
          - *N. godoii* Zamboni, 2001 (likely nymph of *Araripebelostomum*)
        - *Paranoika* Zamboni, 2001
          - *P. placida* Zamboni, 2001
      - Lethocerinae
        - *Lethocerus* Nel and Waller, 2006
          - *L. vetus* Nel and Waller, 2006
    - Nepidae
      - Undescribed spp.
      - *Cmtonepa* Jattiot *et al*., 2012
        - *C. enigmatica* Jattiot *et al*., 2012
    - Naucoridae
      - *Cratocora* Ruf *et al.,* 2005
        - *C. crassa* Ruf *et al*., 2005
      - *Cratopelocoris* Ruf *et al*., 2005
        - *C. carpinteroi* Ruf *et al.*, 2005
    - Notonectidae
      - Notonectinae
        - ?*Canteronecta*
          - ?*C. sp.*
          - *Note: Type specimen for this taxon is a composite fossil from another Formation.*
    - Corixidae
      - Velocorixinae
        - *sp.* with aff. *Rhomboidella*
    - Gelastocoridae
      - Nerthrinae
        - *Cratonerthra* Ruf *et al*., 2005
          - *C. corinthiana* Ruf *et al*., 2005
          - *C. estevezae* Ruf *et al*., 2005
    - Pseudonerthridae
      - *Pseudonerthra* Ruf *et al*., 2005
        - *P. gigantea* Ruf *et al*., 2005
  - Leptopodomorpha

- Archegocimicidae?
  - Undescribed *sp*.
- Gerromorpha (Amphibicorisae)
  - Hydrometridae
    - *Cretaceometra* Nel and Popov, 2000
      - *C. brasiliensis* Nel and Popov, 2000
    - *Incertametra* Goodwyn, 2002
      - *I. santanensis* Goodwyn, 2002
  - Veliidae
    - Undescribed sp.
  - Mesoveliidae
    - Undescribed sp.
- Cimicomorpha
  - Familia *incertae sedis*
    - Undescribed sp.
- Pentatomomorpha
  - Pachymeridiidae
    - *Cratocoris* Martins-Neto, *et al.*, 1999
      - *C. shevchenkoae* Martins-Neto, *et al.*, 1999
    - Undescribed sp.
  - Alydidae
    - Undescribed sp.
  - Coreidae
    - Undescribed sp.
  - Aradidae
    - Mezirinae
      - Undescribed sp.
  - Cydnidae
    - Amnestinae?
      - *Latiscutella* Pinto and Ornellas, 1974
        - *L. santosi* Pinto and Ornellas, 1974
- Heteroptera *incertae sedis*
  - *Cratogocimex* Martins-Neto, 2002a
    - *C. popovi* Martins-Neto, 2002a
  - Several other undescribed genera

Hymenoptera

- Unicalcarida
  - *Cratoenigma* Krogmann and Nel, 2012
    - *C. articulatagen* Krogmann and Nel, 2012
- Symphyta
  - Sepulcidae
    - Trematothoracinae
      - *Prosyntexis* Darling and Sharkey, 1990 (?)
        - *P. gouleti* Darling and Sharkey, 1990 (also see Jattiot *et al*., 2011)
  - Pseudosiricidae
    - Undescribed sp.
  - Tenthredinoidea
    - Unplaced
      - *Atefia* Krogmann *et al*., 2013
        - *A. rasnitsyni* Krogmann *et al*., 2013
- Aprocrita
  - Aculeata
    - Vespoidea
      - Vespidae
        - Undescribed sp.
      - Pompilidae
        - ?Pompilinae
          - Undescribed sp.
      - Sapygidae
        - Fedtschenkiinae
          - *Cretofedtschenkia* Osten, 2007
            - *C. santanensis* Osten, 2007
      - Tiphiidae

- *Architiphia*
  - *A. rasnitsyni* Darling and Sharkey, 1990
- Formicidae
  - Myrmeciinae
    - *Cariridris*
      - *C. bipetiolata* Brandao *et al*., 1989
- Scoliidae
  - ?Proscoliinae
    - *Cretaproscolia* Rasnitsyn and Martinéz-Delclòs, 1999
      - *C. josai* Rasnitsyn and Martinéz-Delclòs, 1999
  - Archaeoscoliinae Rasnitsyn, 1993
    - *Cretoscolia* Rasnitsyn, 1993
      - *C. brasiliensis* Osten, 2007
  - *Cf*. Campsomerinae
    - *Araripescolia* Nel *et al*., 2013
      - *A. magnifica* Nel *et al*., 2013

- Apoidea
  - Angarosphecidae
    - *Cretosphex* Ansorge, 1993
      - *C. parvus* Darling and Sharkey, 1990
      - *C. magnus* Darling and Sharkey, 1990
    - *Mesorhopalosoma* Darling and Sharkey, 1990
      - *M. ceareae* Darling and Sharkey, 1990
    - *Cretobestiola* Pulawski and Rasnitsyn, 2000
      - *C*. sp. nov. (SMNS 66297) Osten, 2007
  - Ampulicidae
    - Undescribed sp.
  - Apidae?
    - Undescribed sp.

- Ichneumonomorhpa
  - ? Ichneumonoidea
    - Undescribed sp.
- Proctotrupomorpha
  - Ephialtitidae
    - *Cratephialtites*
      - *C. kourios* (Originally described in the genus *Karatous*)
  - Proctotrupidae
    - *Protoprocto* Sharkey, 1990
      - *P. asode* Sharkey, 1990
  - Mesoserphidae
    - Undescribed sp.
  - Chalcidoidea
    - ?Agaonidae
      - ?Sycophaginae
        - *Parviformosus* Barling *et al*., 2013
          - *P. wohlrabeae* Baring *et al*., 2013

Raphidioptera

- Raphidiomorpha
  - Baissopteridae
    - *Austroraphidia*
      - *A. brasiliensis* Net *et al*, 1990
    - *Baissoptera* Martynova, 1961
      - *B. pulchra* Martins-Neto and Nel, 1992
      - *B. brasiliensis* Oswald, 1990
      - *B. lisae* Jepson *et al*., 2011
  - Family *incertae sedis*
    - *Arariperaphidia* Martins-Neto and Vulcano, 1989a
      - *A. rochai* Martins-Neto and Vulcano, 1989a

Megaloptera

- Corydalidae
  - *Cratocorydalopsis* Jepson and Heads, 2016
    - *C. brasiliensis* Jepson and Heads, 2016

- *Lithocorydalus* Jepson and Heads, 2016
  - *L. fuscata* Jepson and Heads, 2016

Neuroptera

- Hemerobiiformia
  - Osmylidae
    - Gulliminae
      - *Nuddsia* Menon and Makarkin, 2008
        - *N. longiantennata* Menon and Makarkin, 2008
        - *N. repatriate* Matins-Neto and Rodrigues, 2010
    - *Cratovoluptia* Martins-Neto and Rodrigues, 2009
      - *C. criptoneura* Martins-Neto and Rodrigues, 2009
    - Cratosmylinae
      - *Cratosmylus* Myskowiak *et al*., 2015
        - *C. magnificus* Myskowiak *et al*., 2015
  - Ithonidae
    - *Principiala* Makarkin and Menon, 2007
      - *P. incerta* Makarkin and Menon, 2007
  - Mesochrysopidae
    - *Dryellina* Martins-Neto and Rodrigues, 2009
      - *D. especiosa* Martins-Neto and Rodrigues, 2009
      - *D. placida* Martins-Neto and Rodrigues, 2009
  - Allopteridae
    - *Kareninia* Martins-Neto, 1997
      - *K. breviptera* Martins-Neto, 1997
    - *Armandochrysopa* Nel *et al*., 2005
      - *A. borschukewitzi* Nel *et al*., 2005
    - *Triangulochrysopa* Menon and Makarkin, 2008
      - *T. Formosa* Menon and Makarkin, 2008
  - Limaiidae
    - *Limaia* Martins-Neto and Vulcano, 1989
      - *L. conspicua* Martins-Neto and Vulcano, 1989
      - *L. adicotomica* Martins-Neto, 1997
    - *Mesypochrysa* Martins-Neto and Vulcano, 1989
      - *M. criptovenata* Martins-Neto and Vulcano, 1989
      - *M. confuse* Martins-Neto and Vulcano, 1989
    - *Araripechrysa* Martins-Neto and Vulcano, 1989
      - *A. magnifica* Martins-Neto and Vulcano, 1989
    - *Cratochrysa* Martins-Neto, 1994
      - *C. willmanni* Martins-Neto, 1994
      - *C. sublapsa* Martins-Neto, 1997
      - *C. martinsnetoi* Nel *et al*., 2005
  - Berothidae
    - *Araripeberotha* Martins-Neto and Vulcano, 1990
      - *A. martinsi* Martins-Neto and Vulcano, 1990
    - *Carirriberotha* Martins-Neto and Vulcano, 1990
      - *C. fairchildi* Martins-Neto and Vulcano, 1990
  - Sisyridae
    - *Cratosysirops* Martins-Neto, 1997
      - *C. gonzagai* Martins-Neto, 1997
- Myrmeleontiformia
  - Psychopsidae
    - *Pulchroptilonia* Martins-Neto 1997 (familial placement doubtful)
      - *P. espatifata* Martins-Neto 1997 (familial placement doubtful)
    - *Putzneura* Martins-Neto and Rodrigues, 2010
      - *P. parcimoniosa* Martins-Neto and Rodrigues, 2010
  - Nemopteridae
    - *Roesleriana* Martins-Neto and Vulcano, 1989
      - *R. exotica* Martins-Neto and Vulcano, 1989
    - *Cratonemopteryx* Martins-Neto and Vulcano, 1989
      - *C. robusta* Martins-Neto and Vulcano, 1989
      - *C. audax* Martins-Neto, 1995
      - *C. speciose* Martins-Neto and Vulcano, 1997
    - *Krila* (?)

- *K. pilosa* Martins-Neto, 1992

- Nymphidae
  - *Rafaelnymphes* Myskowiak *et al*., 2016
    - *R. cratoensi* Myskowiak *et al*., 2016
- Myrmeleontidae
  - *Pseudonymphes* Martins-Neto and Vulcano, 1989
    - *P. araripensis* Martins-Neto and Vulcano, 1989
    - *P. ponomarenkoi* Martins-Neto, 1995
    - *P. brunherottae* Martins-Neto, 1994
    - *P. zambonii* Martins-Neto, 1998
- Ascalaphidae
  - *Cratoscalapha* Martins-Neto and Vulcano, 1997
    - *C. electroneura* Martins-Neto and Vulcano, 1997
- Kalligrammatidae
  - *Makarkinia* Martins-Neto, 1995
    - *M. adamsi* Martins-Neto, 1995
    - *M. kerneri* Bechly and Makarkin, 2016
- Araripeneuridae
  - *Araripeneura* Martins-Neto and Vulcano, 1989
    - *A. regia* Martins-Neto and Vulcano, 1989
    - *A. gracilis* Martins-Neto and Vulcano, 1989
  - *Blittersdorfia* Martins-Neto and Vulcano, 1989
    - *B. pleoneura* Martins-Neto and Vulcano, 1989
    - *B. volkheimeri* Martins-Neto and Vulcano, 1989
    - *B. dicotomica* Martins-Neto, 1990
    - *B. polyplusia* Martins-Neto, 1997
    - *B. pulcherrima* Martins-Neto and Vulcano, 1997
  - *Caldasia* Martins-Neto and Vulcano, 1989
    - *C. cretacea* Martins-Neto and Vulcano, 1989
  - *Cariririneura* Martins-Neto and Vulcano, 1989
    - *C. microcephala* Martins-Neto and Vulcano, 1989
    - *C. damianii* Matins-Neto, 1992
    - *C. crassaella* Martins-Neto, 1992
    - *C. nemopteroides* Martins-Neto, 2002
  - *Cratoalloneura* Martins-Neto, 1992
    - *C. acuminate* Martins-Neto, 1992
  - *Cratoneura* Martins-Neto, 1992
    - *C. longissimi* Martins-Neto, 1992
    - *C. pulchella* Martins-Neto, 1992
    - *C. dividens* Martins-Neto, 1994
  - *Paracaririneura* Martins-Neto and Vulcano, 1997
    - *P. priscila* Martins-Neto and Vulcano, 1997
  - *Cratopteryx* Martins-Neto and Vulcano, 1989
    - *C. robertosantosi* Martins-Neto and Vulcano, 1989
  - *Bleyeria* Martins-Neto, 1995
    - *B. nordestina* Martins-Neto, 1995
  - *Diegopteryx* Martins-Neto and Rodrigues, 2010
    - *D. raptorius* Martins-Neto and Rodrigues, 2010
- Babinskaiidae
  - *Babinskia* Martins-Neto and Vulcano, 1989
    - *B. pulchra* Martins-Neto and Vulcano, 1989
    - *B. Formosa* Martins-Neto and Vulcano, 1989
  - *Neliana* Martins-Neto, 1992
    - *N. maculate* Martins-Neto, 1992
    - *N. impolluta* Martins-Neto, 1997
- Palaeoleontidae
  - *Baisopardus* Martins-Neto, 1992
    - *B. araripensis* Martins-Neto, 1992
    - *B. polyhymnia* Martins-Neto, 1997
    - *B. gigas* Martins-Neto and Vulcano, 1997
    - *B. cryptohymen* Heads *et al*., 2005
    - *B. escuilliei* Myskowiak and Nel, 2016
    - *B. pumilio* Myskowiak and Nel, 2016
  - *Paraneurastenyx* Martins-Neto, 1995

- *P. ascalaphix* Martins-Neto, 1995
- *Parapalaeoleon* Menon and Makarkin, 2008
  - *P. magnus* Menon and Makarkin, 2008
- *Araripeleon* Millet and Nel, 2010
  - *A. alphonsei* Millet and Nel, 2010
- *Neurastenyx* Martins-Neto and Vulcano, 1997
  - *N. conani* Martins-Neto and Rodrigues, 2010

Coleoptera

- Archostemata
  - *Cf.* Ommatidae
    - Undescribed sp.
  - *Cf.* Cupedidae
    - Undescribed sp.
- Adephaga
  - Dytiscidae
    - Undescribed sp.
  - Carabidae
    - Cicindelinae
      - *Oxycheliopsis* Cassola and Werner, 2004
        - *O. cretacicus* Cassola and Werner, 2004
    - Subfamilia incertae sedis
      - *Alexcarabus* Martins-Neto, 2002
        - *A. megagnathus* Martins-Neto, 2002
- Polyphaga
  - Staphylinidae
    - *Carinderma* Martins-Neto, 1990
      - *C. pilosa* Martins-Neto, 1990
    - *Cratophyllia* Martins-Neto, 2002
      - *C. minuscula* Martins-Neto, 2002
      - Undescribed spp.
    - *Apticaxgen* Schomann and Solodovnikov, 2012
      - *A. volanssp* Schomann and Solodovnikov, 2012
      - *A. solidussp* Schomann and Solodovnikov, 2012
  - Hydrophilidae
    - Undescribed larva
  - Scarabaeidae
    - Aphodiiae
      - Undescribed sp.
    - Subfamilia *incertae sedis*
      - Undescribed spp.
  - Buprestidae
    - Undescribed spp.
  - Dryopidae
    - Undescribed sp.
  - Elateridae
    - Undescribed spp.
  - Nitidulidae
    - Undescribed spp.
  - Cucujidae
    - Undescribed sp.
  - Trogossitidae
    - ?Peltinae
      - Undescribed sp.
  - Lymexylidae
    - Atractocerinae
      - *Cratoatractocerus* Wolf-Schwenniger, 2011
        - *C. grimaldii* Wolf-Schwenniger, 2011
  - Tenebrionidae
    - Possible undescribed sp.
  - ?Pyrochroidae
    - *Cretaceimelittomoides* Vulcano and Pereira, 1987
      - *C. cearensis* Vulcano and Pereira, 1987 (probably *nomen nudum*)
  - Chrysomelidae

        - ?Eumolpinae
            - Undescribed sp.
        - Subfamilia *incertae sedis*
            - Undescribed sp.
    - Curculionoidea
        - Curculionidae
            - *Arariperhinus* Santos *et al*., 2011
                - *A. monnei* Santos *et al*., 2011
        - Nemonychidae
            - Rhinorhynchinae
                - Rhinorhynchini
                    - *Cratomacer* Zherikhin and Gratschev, 2004
                        - *C. immerses* Zherikhin and Gratschev, 2004
                        - *C. ephippiger* Zherikhin and Gratschev, 2004
        - Belidae
            - ?Pachyurinae
                - ?Pachyurini
                    - *Davidibelus* Zherikhin and Gratschev, 2004
                        - *D. cearensis* Zherikhin and Gratschev, 2004
            - ?Oxycoryninae
                - Undescribed sp.
        - ?Eccoparthridae (not recognised online)
            - *Martinsnetoa* Zherikhin and Gratschev, 2004
                - *M. dubia* Zherikhin and Gratschev, 2004
        - Brentidae?
            - Eurhynchinae
                - *Axelrodiellus* Zherikhin and Gratschev, 2004
                    - *A. ruptus* Zherikhin and Gratschev, 2004

Trichoptera

- Leptoceridae
    - *Araripeleptocerus* Martins-Neto, 2001
        - *A. primaevus* Martins-Neto, 2001
- Hydroptilidae
    - *Cratorella* Martins-Neto, 2001
        - *C. magna* Martins-Neto, 2001
        - *C. media* Martins-Neto, 2001
        - *C. minuta* Martins-Neto, 2001
        - *C. feminina* Martins-Neto, 2001
- Familia *incertae sedis*
    - *Raptortrichops* Martins-Neto, 2001
        - *R. sukatsheva* Martins-Neto, 2001
    - *Senka* Martins-Neto, 2001
        - *S. crassatella* Martins-Neto, 2001

Lepidoptera

- Micropterygidae
    - *Parasabatinca* Martins-Neto and Vulcano, 1989
        - *P. caldasae* Martins-Neto and Vulcano, 1989
- Undopterygidae
    - *Undopterix* Martins-Neto and Vulcano, 1989
        - *U. carirriensis* Martins-Neto and Vulcano, 1989
- Eolepidopterigidae
    - *Xena* Martins-Neto, 1999
        - *X. nana* Martins-Neto, 1999
    - *Psamateia* Martins-Neto, 2002
        - *P. calipsa* Martins-Neto, 2002
- Familia *incertae sedis*
    - *Gracilepterix* Martins-Neto and Vulcano, 1989
        - *G. pulchra* Martins-Neto and Vulcano, 1989

Mecoptera

- Bittacidae
    - Unnamed sp. Petrulevičius and Martins-Neto, 2001

- Familia *incertae sedis*
    - Undescribed sp.

Diptera

- Culicomorpha
    - Chironomoidea
        - ?Chironomidae
            - Undescribed sp.
- Bibionomorpha
    - Mycetophilidae
        - Macrocerinae?
            - Undescribed sp.
    - Sciaridae
        - Undescribed sp.
    - Bibionidae?
            - Undescribed sp.
- Psychodomorpha
    - Psychodidae?
        - *Megapsychoda* Azar and Nel, 2002
            - *M. araripina* Azar and Nel, 2002
    - Tanyderidae? (position uncertain)
- Tipulomorpha
    - Tipulidae
        - *Leptotarsus* Guérin-Méneville, 1831
            - *L. grimaldii* Ribeiro and Lukashevich, 2014
            - *L. cretaceus* Ribeiro and Lukashevich, 2014
            - *L. martinsnetoi* Ribeiro and Lukashevich, 2014
            - *L. lukashevichae* Ribeiro *et al*., 2015
    - Limoniidae
        - *Cratotipula* Ribeiro and Martins-Neto, 1999
            - *C. latialata* Ribeiro and Martins-Neto, 1999
        - *Okrenomyia* Ribeiro and Krzemiski, 2000
            - *O. araripensis* Ribeiro and Krzemiski, 2000
- Stratiomyomorpha
    - Zhangsolvidae
        - *Cratomyia* Mazzarolo and Amorim, 2000
            - *C. macrorrhyncha* Mazzarolo and Amorim, 2000
            - *C. cretacicus* Willkommen *in* Willkommen and Grimaldi, 2007 (Validity may need confirmation, previous genera synonyms)
            - *C. santanensis* Willkommen *in* Willkommen and Grimaldi, 2007 and Arillo *et al*., 2015
- Tabanomorpha
    - Tabanoidea
        - Tabanidae (familial placement under question)
            - *Cratotabanus* Martins-Neto and Santos, 1994
                - *C. stenomyomorphus* Martins-Neto and Santos, 1994
        - Rhagionidae?
            - Unnamed sp.
- Asilomorpha
    - Mydidae
        - *Cretomydas* Wilkommen and Grimaldi, 2007
            - *C. santanensis* Wilkommen and Grimaldi, 2007
    - Therevidae (?)
        - *Cratotabanus* Martins-Neto and Santos, 1994 (considered undescribed Willkommen and Grimaldi, 2007)
            - *C. stenomyomorphus* Martins-Neto and Santos, 1994 (considered undescribed Willkommen and Grimaldi, 2007)
    - Asilidae
        - *Araripogon* Grimaldi, 1990
            - *A. axelrodi* Grimaldi, 1990
        - Unnamed new species (possibly Therevidae instead)

Additional taxa described during the publication of this thesis:

- Myrmeleontoidae
  - Babinskaiidae
    - *Parababinskaia* Makarkin *et al*., 2017
      - *P. elegans* Makarkin *et al*., 2017
    - *Pseudobabinskaia* Makarkin *et al*., 2017
      - *P. martinsnetoi* Lu *et al*., 2017

8. 5. Additional references

Alba-Tercedor, J., and Sanchez-Ortega, A. 1991. *Overview and Strategies of Ephemeroptera and Plecoptera*. Sandhill Crane Press, Gainesville, Florida, Pp. 588.

Alexeev, A. V. 1993. Jurassic and Lower Cretaceous Buprestidae (Coleoptera) from Eurasia. *Paleontological Journal*, **27**, 9-34.

Alexeev, A. V. 1996. New taxa of metallic wood-boring beetles (Coleoptera, Buprestidae) from the Mesozoic of Russia, Kazakhstan, and Mongolia. *Paleontological Journal,* **30**, 310-117.

Alexeev, A. V. 2000. On Mesozoic Buprestids (Coleoptera: Buprestidae) from Russia, Kazakhstan, and Mongolia. *Paleontological Journal,* **34 (3)**, 323-326.

Allaby, M. 1999. [Online] 'Labiidae.' A Dictionary of Zoology. *Encylopedia.com*. [Accessed 17 May 2016]. http://www.encyclopedia.com/doc/1O8-Labiidae.html

Allan, J. D. 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London, UK, Pp. 388.

Andersen, N. M. 1982. The semiaquatic bugs (Hemiptera: Gerromorpha): Phylogeny, adaptations, biogeography, and classification. *Entomonograph,* **13**, 1-455.

Andersen, N. M. 1998. Water striders from the Paleogene of Denmark with a review of the fossil record and evolution of semiaquatic bugs (Hemiptera, Gerromorpha). *Biologiske Skrifter,* **50**, 1-157.

Anderson, R. C. 2009. Do dragonflies migrate across the western Indian Ocean?. *Journal of Tropical Ecology*, **25**, 347-348.

Archibald, S. B., Makarkin, V. N., and Ansorge, J. 2009. New fossil species of Nymphidae (Neuroptera) from the Eocene of North America and Europe. *Zootaxa*, **2157**, 59-68.

Armitage, P. D., Cranston, P. S., and Pinder, L. C. V. 1995. *The Chironomidae: biology and ecology of non-biting midges*. London, Chapman and Hall, Pp. 572.

Arnett, R. H. 2000. *American Insects: A Handbook of the Insects of America north of Mexico*. CRC Press, Pp. 1024.

Arnold'di, L. V., Zherikhin, V. V., Nikritin, L. M. and Ponomarenko, A. G. 1992. *Mesozoic Coleoptera*. Washington D C, Smithsonian Institution Libraries and The National Science Foundation, Pp. 285.

Aspöck, H., Aspöck, U., and Rausch, H. 1991. *Die Raphidiopteren der Erde: Eine monographische Darstellung der Systematik, Taxonomie, Biologie, Ökologie und Chorologie der rezenten Raphidiopteren der Erde, mit einer zusammenfassenden Übersicht der fossilen Raphidiopteren (Insecta: Neuropteroidea)*. Goecke and Evers, Krefeld, Germany, vol. 1, Pp. 730; vol. 2, Pp. 550.

Aspöck, H. 1998. Distribution and biogeography of the order Raphidioptera: Updated facts and a new hypothesis. *Acta Zoologica Fennica,* **209**, 33-44.

Aspöck, U., Plant, J. D., and Nemeschkal, H. L. 2001. Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). *Systematic Entomology,* **26**, 73-86.

Aspöck, H. 2002. The biology of Raphidioptera: A review of present knowledge. *Acta Zoologica Academiae Scientiarum Hungaricae,* **48**, 35-50.

Aspöck, U., and Aspöck. H. 2003a. Ordnung Raphidioptera, Kamelhalsfliegen. Pp. 542–552. *In.* Dathe, H. H. (Ed.). *Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere. 5. Teil: Insecta*. Spektrum Akademischer Verlag, Heidelberg, Germany, Pp. 961.

Aspöck, U., Haring, E., and Aspöck, H. 2012. The phylogeny of the Neuropterida: long lasting and current controversies and challenges (Insecta: Endopterygota). *Arthropod Systematics & Phylogeny*, **70**, 119-129.

Austin, A., and Dowton, M. 2001. *Hymenoptera: Evolution, Biodiversity and Biological Control*. CSIRO Publishing, Pp. 480.

Aydin, G., and Khomutov, A. 2008. The Biology, Nymphal Stages, and Life Habits of the Endemic Sand Dune Cricket *Schizodactylus inexpectatus* (Werner, 1901) (Orthoptera: Schizodactylidae). *Turkish Journal of Zoology*, **32**, 427-432.

Azar, D., and Nel, A. 2002. New Cretaceous psychodid flies from Lebanese amber and Santana Formation (Chapada do Araripe, Brazil) (Diptera). *Annales de la Societe Entomologique de France,* **38**, 253-262.

Bae, Y. J., and McCafferty, W. P. 1995. Ephemeroptera tusks and their evolution. Pp. 377–405. *In.* Corkum, L. D., and Ciborowski, J. (Eds.). *Current Directions in Research on Ephemeroptera*. Canadian Scholars Press, Inc., Toronto, Canada, Pp. 478.

Bänziger, H. 1992. Remarkable new cases of moths drinking human tears in Thailand (Lepidoptera: Thyatiridae, Sphingidae, Notodontidae). *Natural History Bulletin of the Siam Society,* **40**, 101-102.

Baranowski, R. M., and Slater, J. A. 1986. Coreidae of Florida (Hemiptera: Heteroptera). *Florida Department of Agriculture and Consumer Services, Division of Plant Industry*, **12**, 1-82.

Bechly, G., Nel, A., Martínez-Delclòs, X., and Fleck, G. 1998. Four new dragonfly species from the Upper Jurassic of Germany and the Lower Cretaceous of Mongolia (Anisoptera: Hemeroscopidae, Sonidae, and Proterogomphidae fam. nov.). *Odonatologica,* **27**, 149-187.

Bechly, G. 1999. *Phylogeny and Systematics of Fossil Dragonflies (Insecta: Odonatoptera) with Special Reference to some Mesozoic Outcrops*. Published PhD thesis, Eberhard-Karls-Universität Tübingen.

Bechly, G. 2000. Two new fossil dragonfly species (Insecta: Odonata: Anisoptera: Araripegomphidae and Lindeniidae) from the Crato Limestone (Lower Cretaceous, Brazil). *Stuttgarter Beiträge zur Naturkunde, Serie B,* **296**, 1-16.

Bechly, G., Haas, F., Schawaller, W., Schmalfuss, H., and Schmid, U. 2001a. Ur-Geziefer – Die faszinierende Evolution der Insekten. *Stuttgarter Beiträge zur Naturkunde, Serie C,* **49,** 1-96.

Bechly, G., Brauckmann, C., Zessin, W., and Gröning, E. 2001b. New results concerning the morphology of the most ancient dragonflies (Insecta: Odonatoptera) from the Namurian of Hagen Vorhalle (Germany). *Journal of Zoological Systematics and Evolutionary Research,* **39**, 209-226.

Bechly, G., Nel, A. Martínez-Delclòs, X., Jarzembowski, E. A., Coram, R., Martill, D. M., Fleck, G., Escuillieâ, F., Wisshak, M. M., and Maisch, M. 2001c. A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). *Neue paläontologische Abhandlungen,* **4**, 1-219.

Bechly, G., and Ueda, K. 2002. The first fossil record and first New World record for the dragonfly clade Chlorogomphida (Insecta: Odonata: Anisoptera: Araripechlorogomphidae n. fam.) from the Crato Limestone (Lower Cretaceous, Brazil). *Stuttgarter Beiträge zur Naturkunde, Serie B,* **328**, 1-11.

Bechly, G. 2005. A re-description of '*Stenophlebia*' *casta* (Insecta: Odonata: Parastenophlebiidae n. fam.) from the Upper Jurassic Solnhofen Limestone in Germany. *Stuttgarter Beiträge zur Naturkunde, Serie B,* **359**, 1-12.

Bedford, G. O. 1978. The biology and ecology of the Phasmatodea. *Annual Review of Entomology,* **23**, 125-149.

Beier, M. 1968. Mantodea (Fangheuschrecken). *Handbuch der Zoologie*, vol. IV, *Band Arthropoda, 2 Hälfte: Insecta. Zweite Auflage*, 1-47.

Bentz, J.-A., and Townsend, A. M. 2005. Diversity and abundance of leafhopper species (Homoptera: Cicadellidae) among red maple clones. *Journal of Insect Conservation*, **9**, 29-39.

Béthoux, O., and Nel, A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa,* **96**, 1-88.

Bignell, D. E., and Eggleton, P. 2000. Termites in ecosystems. *In*. Abe, T., Bignell D. E., and Higashi M. (Eds.). *Termites: evolution, sociality, symbioses, ecology*. Dordrecht, Kluwer Academic Publishers, Pp. 466.

Bohart, R. M., and Menke, M. S. 1976. *Sphecid wasps of the world. A generic revision*. Los Angeles, University of California Press, Berkeley.

Boukary, I. B., Tourneur, J. C., and Gingras, J. 1996. Life cycle of *Forficula senegalensis* Serv. (Dermaptera: Forficulidae) and its relationship to the development of bulrush millet in Sundanese-Sahelian zone of Niger. *Canadian Entomologist,* **128**, 831-838.

Bradler, S. 2003. Phasmatodea, Gespenstschrecken. Pp. 251–61. *In.* Dathe, H. H. (Ed.). *Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere. 5. Teil: Insecta*. Spektrum Akademische.

Breznak, J. A., and Brune, A. 1994. Role of microorganisms in the digestion of lignocellulose by termites. *Annual Review of Entomology,* **39**, 453-487.

Breznak, J. A. 2000. Ecology of prokaryotic microbes in the guts of wood- and litter-feeding termites. *In.* Abe, T., Bignell, D. E., and Higashi, M. (Eds.). *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, the Netherlands, Pp. 466.

Brito, I. M. 1987. Nota preliminar sobre uma nova efêmera do Cretáceo do Ceará (Insecta Ephemeroptera). *Anais do X Congresso Brasileiro de Paleontologia,* **2**, 593-597.

Brock, P. D. 1999. The amazing world of stick and leaf-insects. *The Amateur Entomologist,* **26**, 1-165.

Brothers, D. J. 1999. Phylogeny and evolution of wasps, ants and bees (Hymenoptera, Chrysisoidea, Vespoidea, and Apoidea). *Zoologica Scripta,* **28**, 233-249.

Burckhardt, D., and Agosti, D. 1991. New records of South American Peloridiidae (Homoptera: Coleorrhyncha). *Revista Chilena Entomologia,* **19**, 71-75.

Burckhardt, D., and Cekalovic, T. K. 2002. An anomalous moss-bug from southern Chile and notes on *Pantinia darwini* (Hemiptera, Coleorryncha, Peloridiidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft / Bulletin de la Société entomologique Suisse,* **75**, 57-59.

Burckhardt, D. 2009. Taxonomy and phylogeny of the Gondwanan moss bugs or Peloridiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift*, **56**, 173-235.

Burks, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. *Bulletin of the Illinois Natural History Survey, **26***, 1-216.

Campbell, I. C. 1987. *Mayflies and Stoneflies: Life Histories and Biology*. Kluwer Academic Publishers, Dordrecht, the Netherlands, Pp. 366.

Carle, F. L., and Wighton, D. C. 1990. Odonata. *In.* Grimaldi, D. A. (Ed.). Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History*, vol. 195.

Carle, F. L. 1995. Evolution, taxonomy, and biogeography of ancient Gondwanian Libelluloids, with comments on anisopterid evolution and phylogenetic systematics (Anisoptera: Libelluloidea). *Odonatologica,* **24**, 383-424.

Carpenter, F. M 1992. Superclass Hexapoda. *In.* Kaesler, R. L. (Ed.). *Treatise on Invertebrate Paleontology, R, Arthropoda 4, 3/4*. Boulder and Lawrence: Geological Society of America and University of Kansas, Pp. 560.

Carver, M., Gross, G. F. and Woodward, T. E. 1991. Hemiptera (bugs, leafhoppers, cicadas, aphids, scale insects etc.). Pp. 429–509. *In.* Naumann, I. D. (Ed.). *The Insects of Australia: A Textbook for Students and Research Workers, Volume 1* [2nd Edition]. Cornell University Press, Ithaca, New York, Pp. 542.

Cassola, F. and Werner, K. 2004. A fossil tiger beetle specimen from the Brazilian Mesozoic: *Oxycheilopsis cretacicus* n. gen., n. sp. *Mitteilungen der Münchener entomologischen Gesellschaft,* **94**, 75-81.

Ceotto, P., and Bourgoin, T. 2008. Insights into the phylogenetic relationships within Cixiidae (Hemiptera: Fulgoromorpha): cladistics analysis of a morphological dataset. *Systematic Entomology*, **33**, 484-500.

Chin, K., and Gill, B. D. 1996. Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaios,* **11**, 280-285.

Chopard, L. 1938. *La Biologie des Orthoptères*. Lechevalier, Paris, France, Pp. 541.

Clarke, J. F. G. 1941–1969. *Catalogue of the Type Specimens of Microlepidoptera in the British Museum (Natural History) Described by Edward Meyrick* [7 volumes]. Trustees of the British Museum (Natural History). London, UK, Pp. 3133.

Corbet, P. S. 1962. *A Biology of Dragonflies*. Witherby Ltd, London, Pp. 247.

Corbet, P. S. 1999. *Dragonflies: Behavior and ecology of Odonata*. Cornell University Press. Ithaca, New York, Pp. 864.

Corkum, L. D., and Ciborowski, J. 1995. *Current Directions in Research on Ephemeroptera*. Canadian Scholars Press, Toronto, Canada, Pp. 478.

Cornwell, P. B. 1968. *The Cockroach, vol. 1. A Laboratory Insect and an Industrial Pest*. Hutchinson; London, UK, Pp. 391.

Costa-Lima, A. da. 1950. Ninfa de Efemerídeo fossil do Ceará. *Anais Academia, Brasileira*, *Ciências,* **22**, 419-420.

Crowson, R. A. 1981. *The Biology of Coleoptera*. New York, Academic Press, Pp. 802.

Cryan, J. R. 2005. Molecular phylogeny of Cicadomorpha (Insecta:Hemiptera: Cicadoidea, Cercopoidea and Membracoidea): adding evidence to the controversy. *Systematic Entomology*, **30**, 563-574.

Cullen, M. J. 1969. The biology of giant water bugs (Hemiptera : Belostomatidae) in Trinidad. *Proceedings of the Royal Entomological Society of London, Series A, General Entomology*, **44**, 123-136.

Currie, D. C., and Grimaldi, D. 2000. A new blackfly (Diptera: Simuliidae) genus from mid-Cretaceous (Turonian) amber of New Jersey. *In.* Grimaldi, D. (Ed.). *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Leiden, Backhuys, Pp. 498.

Daniels, G. 1989. Family TABANIDAE. *In*. Evenhuis, N. L. (Ed.). *Catalog of the Diptera of Australasian and Oceanian Regions*. Bishop Museum Press, Pp. 1155.

Davis, R. B., Baldauf, S. L., and Mayhew, P. J. 2010. The origins of species richness in the Hymenoptera: insights from a family-level supertree. *BMC Evolutionary Biology*, **10**, 1-109.

Day, M. C., Else, G. R., and Morgan, D. 1981. The most primitive Scoliidae (Hymenoptera). *Journal of Natural History,* **15,** 671-684.

Debevec, A. H., Cardinal, S., and Danforth, B. N. 2012. Identifying the sister group to the bees: a molecular phylogeny of Aculeata with an emphasis on the superfamily Apoidea. *Zoologica Scripta*, **41**, 527-535.

Delclòs, X., Nel, A., Azar, D., Bechly, G., Dunlop, J. A., Engel, M. S., and Heads, S. W. 2008. The enigmatic Mesozoic insect taxon Chresmodidae (Polyneoptera): New palaeobiological and phylogenetic data, with the description of a new species from the Lower Cretaceous of Brazil. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, **247**, 353-381.

Demoulin, G. 1955. Sur une larve siphlonuridienne d'Ephémère fossile du Brésil. *Bulletin et Annales de la Société Royale d' Entomologie de Belgique,* **91**, 270-271.

Dietrich, C. H. 2009. Auchenorrhyncha. *In.* Resh, V. H., and Cardé, R. T. (Eds.). *Encyclopaedia of Insects*. Academic Press, Pp. 1024.

Dikow, T., and Grimaldi, D. A. 2014. Robber flies in Cretaceous ambers (Insecta: Diptera: Asilidae). *American Museum Novites*, **3799**, 1-19.

Djernaes, M., Klass, K.-D., Picker, M. D., and Damgaard, J. 2012. Phylogeny of cockroaches (Insecta, Dictyoptera, Blattidea), with placement of aberrant taxa and exploration of out-group sampling. *Systematic Entomology*, **37**, 65-83.

Domínguez, E. 2001. *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic Publishers, Dordrecht, the Netherlands, Pp. 478.

Dong, Q-P., Tao, Y-Z., and Ren, D. 2012a. A new species of Progonocimicidae (Hemiptera: Coleorrhyncha) from northeastern China. *Zootaxa*, **3495**, 73-78.

Dong, Q-P., Yao, Y-Z., and Ren, D. 2012b. Progress in the study of Coleorrhyncha fossils. *Acta Zootaxonomica Sinica*, **36**, 498-505.

Duckhouse, D. A., and Lewis, D. J. 1989. Family PSYCHODIDAE. *In*. Evenhuis, N. L. (Ed.). *Catalog of the Diptera of Australasian and Oceanian Regions*. Bishop Museum Press, Pp. 1155.

Edmunds, G. F. 1972. Phylogenetic biogeography of mayflies. *Annals of the Missouri Botanical Garden,* **62**, 251-263.

Edmunds, G. F., Jensen, S. L., and Berner, L. 1976. *The Mayflies of north and central America*. University of Minnesota Press, Minneapolis, Minnesota, Pp. 330.

Engel, M. S. 2000. A New Interpretation of the Oldest Fossil Bee (Hymenoptera: Apidae). *American Museum Novitates*, **3296**, 1-11.

Engel, M. S. 2002. The smallest snakefly (Raphidioptera: Mesoraphidiidae): A new species in Cretaceous amber from Myanmar, with a catalog of fossil snakeflies. *American Museum Novitates,* **3363,** 1-22.

Engel, M. S., and Haas, F. 2007. Family-group names for earwigs (Dermaptera). *American Museum Novitates*, **3567**, 1-20.

Engel, M. S., and Heads, S. W. 2008. Cresmoda neotropica name, *In*. The enigmatic Mesozoic insect taxon Chresmodidae (Polyneoptera): new palaeobiological and phylogenetic data, with the description of a new species from the Lower Cretaceous of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **247,** 353-381.

Engel, M. S., Grimaldi, D. A., and Krishna, K. 2009. Termites (Isoptera): Their Phylogeny, Classification, and Rise to Ecological Dominance. *American Museum Novitates*, **3650**, 1-27.

Engel, M. S., Ortega-Blanco, J., and Bennett, D. J. 2009. A Remarkable Tiphiiform Wasp in Mid-Cretaceous Amber from Myanmar (Hymenoptera: Tiphiidae). *Transactions of the Kansas Academy of Science*, **112**, 1-6.

Erhardt, A., and Rusterholtz, H. P. 1998. Do Peacock butterflies (*Inachis io*) detect and prefer nectar amino acids and other nitrogenous compounds?. *Oecologia,* **117**, 536-542.

Esaki, T. 1949. The occurrence of the Mesozoic insect *Chresmoda* in the far east. *Insecta Matsumarana,* **17**, 4-5.

Evans, J. W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Australian Journal of Zoology*, **4**, 165-258.

Evans, J. W. 1981. A review of the present knowledge of the family Peloridiidae and new genera and new species from New Zealand and New Caledonia (Hemiptera: Insecta). *Records of the Australian Museum,* **34**, 381-406.

Evans, T. A., Lenz, M., and Gleeson, P. V. 1998. Testing assumptions of mark-recapture protocols for estimating population size using Australian mound-building, subterranean termites. *Ecological Entomology*, **23**, 139-159.

Evenhuis, N. L. 1989. *Catalog of the Diptera of Australasian and Oceanian Regions*. Bishop Museum Press, Pp. 1155.

Fenn, J. D., Song, H., Cameron, S. L., and Whiting, M. F. 2008. A preliminary mitochondrial genome phylogeny of Orthoptera (Insecta) and approaches to maximizing phylogenetic signal found within mitochondrial genome data. *Molecular Phylogenetics and Evolution*, **49**, 59-68.

Field, L. H. 2001. *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Oxon, UK, Pp. 540.

Flanagan, J. F., and Marshall, K. E. 1980. *Advances in Ephemeroptera Biology*. Plenum Press, New York, New York, Pp. 552.

Fleck, G., Bechly, G., Nel, A., and Escuillié, F. 2002. The larvae of the Mesozoic family Aeschnidiidae and their phylogenetic implications (Insecta: Odonata: Anisoptera). *Palaeontology*, **45**, 165-184.

Fontes, L. R., and Vulcano, M. A. 1998. Cupins fósseis do Novo Mundo. *In.* Fontes, L. R., and Filho, E. B. (Eds.). *Cupins – O desafio do conhecimento*. Piracicaba, Fundação de Estudios Agrários Luiz de Queiroz FEALQ.

Frank, J. H., and Ahn, K.-J. 2011. Coastal Staphylinidae (Coleoptera): A worldwide checklist, biogeography and natural history. *Zookeys*, **107**, 1-98.

Gangwere, S. K., Muralirangan, M. C., and Muralirangan, M. 1997. *The Bionomics of Grasshoppers, Katydids and their Kin*. CABI Publishing, Oxon, UK, Pp. 529.

Gorochov, A. V. 1985. Mesozoic Crickets (Orthoptera, Grylloidea) of Asia. *Paleontological Journal*, **19**, 56-66.

Gorochov, A. V., and Rasnitsyn, A. P. 2002. Superorder Gryllidea Laicharting, 1781 (= Orthopteroidea Handlirsch, 1903). *In.* Rasnitsyn, A. P., and Quicke, D. L. J. (Eds.). *History of Insects*. Dordrecht, Kluwer, Pp. 517.

Gratshev, V. G., and Zherikhin, V. V. 2003. The fossil record of weevils and related beetle families (Coleoptera, Curculionoidea). *Acta Zoologica Cracoviensia,* **46**, 129-138.

Grimaldi, D. A., and Cumming, J. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History,* **239**, 1-124.

Grimaldi, D. A. 2003. A revision of Cretaceous mantises and their relationships, including new taxa (Insecta: Dictyoptera: Mantodea). *American Museum Novitates,* **3412**, 1-47.

Grimaldi, D. A., and Ross, A. J. 2004. Raphidiomimula, an enigmatic new cockroach in cretaceous amber from Myanmar (Burma) (Insecta: Blattodea: Raphidiomimidae). *Journal of Systematic Palaeontology*, **2**, 101-104.

Grimaldi, D. A., Engel, M. S., and Krishna, K. 2008. The Species of Isoptera (Insecta) from The Early Cretaceous Crato Formation: A Revision. *American Museum Novitates*, **3626**, 1-30.

Gullan, P. J., and Cranston, P. S. 2005. *The Insects – an Outline of Entomology*. Oxford, Blackwell Publishing, Pp. 584.

Guthrie, D. M., and Tindall, A. R. 1968. *The Biology of the Cockroach*. St. Martin Press, New York, New York, Pp. 408.

Gwynne, D. T., and Morris. G. K. 1983. *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*. Westview Press, Boulder, Colorado, Pp. 376.

Gwynne, D. T. 2001. *Katydids and Bush-Crickets: Reproductive Behavior and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca, New York, Pp. 317.

Hamid, S. A., and Rawi, C. S. M. 2014. Ecology of Ephemeroptera, plecoptera and trichoptera (insect) in rivers of the gunung jerai forest reserve: diversity and distribution of functional feeding groups. *Tropical life sciences research*, **25**, 61-73.

Hamilton, K. G. A. 1990. Homoptera. *In.* Grimaldi, D. (Ed.). Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History,* **195**, 82-122.

Hamilton, K. G. A. 1992. Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a New Superfamily and Synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America*, **85**, 423-430.

Hamilton, K. G. A. 1996. Cretaceous Homoptera from Brazil: Implications for Classification. *In.* Schaefer, C. W. (Ed.). *Studies on Hemipteran Phylogeny*. Langham, MD, Thomas Say Publications in Entomology, Entomological Society of America, Pp. 244.

Handlirsch, A. 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. *Ein Handbuch für Paläontologen und Zoologen*. Leipzig, Engelmann.

Harris, S. C., Rasmussen, A. K., and Denson, D. R. 2012. An annotated list of the caddisflies (Trichoptera) of Florida: Part I. The family Hydroptilidae, with descriptions of five new species. *Insecta Mundi*, **273**, 1-32.

Heads, S. W. 2008. The first fossil Proscopiidae (Insecta, Orthoptera, Eumastacoidea) with comments on the historical biogeography and evolution of the family. *Palaeontology*, **51**, 499-507.

Henning, W. 1954. Flügelgeäder und System der Dipteren. *Beiträge zur Entomologie*, **4**, 245-388.

Hiatt, K., and Whiting, M. F. 2013. Family-level phylogeny of Orthoptera (Arthropoda: Insecta) Based in complete Mitochondrial Genome Data. *Journal of Undergraduate Research*, Brigham Young University.

Hinton, H. E. 1955. On the structure, function, and distribution of the prolegs of the Panorpoidea, with a criticism of the Berlese-imms Theory. *Transactions of the Royal Entomological Society of London*, **106**, 455-540.

Hoernig, M. K., Haug, J. T., and Haug, C. 2013. New details of *Santanmantis axelrodi* and the evolution of the mantodean morphotype. *Palaeodiversity*, **6**, 157-168.

Hogue, C. L. 1992. *Insects of the Los Angeles Basin (2nd edition)*. Natural History Museum of Los Angeles, Los Angeles, Pp. 173.

Holzenthal, R., and Pes, A. M. O. 2004. A new genus of long-horned caddisfly from the Amazon basic (Trichoptera: Leptoceridae: Grumichellini). *Zootaxa*, **621**, 1-16.

Honigberg, B. M. 1970. Protozoa associated with termites and their role in digestion. *In.* Krishna, K., and Weesner, F. M. (Eds.). *Biology of Termites, Volume II*. Academic Pres, New York, New York, Pp. 643.

Hubbard, M. D., and Peters, W. L. 1978. *Environmental Requirements and Pollution Tolerance of Ephemeroptera*. Environmental Protection Agency, Springfield, Virginia, Pp. 461.

Hubbard, M. D. 1990. Mayflies of the world: A catalog of the family and genus group taxa (Insecta: Ephemeroptera). *Flora and Fauna Handbook,* **8**, 1-119.

Huber, F. 1989. *Cricket Behavior and Neurobiology*. Cornell University Press, Pp. 565.

Huchard, E., Martinez, M., Alout, H., Douzery, E. J. P., Lutfalla, G., Berthomieu, A., Berticat, C., Raymond, M., and Weill, M. 2006. Acetylcholinesterase genes within the Diptera: takeover and loss in true flies. *Proceedings of the Royal Society B*, **273**, 2595-2604.

Hungerford, H. B. 1933. The genus *Notonecta* of the world (Notonectidae-Hemiptera). *Kansas University Science Bulletin*, **21**, 5-195.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., St. John, O., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Boack, L., and Vogler, A. P. 2007. A comprehensive Phylogeny of Beetles Reveals the Evolutionary Origins of a Superradiation. *Science*, **318**, 1913-1916.

Inoue, T., Kitade, O., Yoshimura, T., and Yamaoka, I. 2000. Symbiotic associations with protists. *In.* Abe, T., Bignell, D. E., and Higashi M. (Eds.). *Termites: Evolution, Sociality, Symbioses, Ecology*. Kluwer Academic Publishers, Dordrecht, the Netherland, Pp. 466.

Irwin, M. E., and Lyneborg, L. 1989. Family THEREVIDAE. *In*. Evenhuis, N. L. (Ed.). *Catalog of the Diptera of Australasian and Oceanian Regions*. Bishop Museum Press, Pp. 1155.

Ivanov, V. D., and Sukatsheva, I. D. 2002. Order Trichoptera Kirby, 1813. The caddisflies. *In.* Rasnitsyn, A. P., and Quicke, D. L. J. (Eds.). *History of Insects*. Kluwer Academic Publishers, Dordrecht, the Netherlands, Pp. 517.

Jandry, J., Brulin, M., Parinet, B., and Grandjean, F. 2014. Ephemeroptera communities as bioindicators of the suitability of headwater streams for restocking with white-clawed crayfish, *Austropotamobius pallipes*. *Ecological Indicators*, **46**, 560-565.

Jarzembowski, E. A., Martínez-Delclòs, X., Bechly, G., Nel, A., Coram, R., and Escuillié, F. 1998. The Mesozoic non-calopterygoid Zygoptera: description of new genera and species from the Lower Cretaceous of England and Brazil and their phylogenetic significance (Odonata, Zygoptera, Coenagrionoidea, Hemiphlebioidea, Lestoidea). *Cretaceous Research,* **19**, 403-444.

Jattiot, R., Krogmann, L., and Nel, A. 2011. Revision: of Prosyntexis from the Lower Cretaceous Crato Formation of Barzil (Hymenoptera: Sepulcidae: Trematothoracinae). *Zootaxa*, **3058**, 55-62.

Jell, P. A., and Duncan, P. M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), south Gippsland, Victoria. *Memoirs of the Association of Australasian Palaeontologists*, **3**, 111-205.

Jepson, J. E., Ansorge, J., and Jarzembowski, E. A. 2011. New snakeflies (Insecta: Raphidioptera) from the Lower Cretaceous of the UK, Spain and Brazil. *Palaeontology*, **54**, 385-395.

Jolivet, P., and Verma, K. K. 2002. *Biology of Leaf Beetles*. Intercept Ltd., Andover, Pp. 322.

Jong, H. de, Oosterbroek, P., Gelhaus, J., Resch, H., and Young, C. W. 2008. Global diversity of crane flies (Insecta: Diptera: Tipulidae or Tipulidae sensu lato) in fresh water. *Hydrobiologia*, **595**, 457-467.

Jost, M. C., and Shaw, K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**, 510-530.

Kaulfuss, U., and Moulds, M. 2015. A new genus and species of tettigarctid cicada from the early Miocene of New Zealand: Paratettigarcta zealandica (Hemiptera, Auchenorrhyncha, Tettigarctidae). *ZooKeys*, **484**, 83-94.

Keltner, J., and McCafferty, W. P. 1986. Functional morphology of burrowing in the mayflies *Hexagenia limbata* and *Pentagenia vittigera*. *Zoological Journal of the Linnean Society,* **87**, 139-162.

Kirejtshuk, A. G., and Ponomarenko, A. G. 1990. Fossil beetles of the Peltidae and Nitidulidae families (Coleoptera). *Paleontological Journal*, **24**, 79-90.

Klys, G., and Lis, J. A. 2013. First cave records for Palearctic burrower bugs (Hemiptera: Heteroptera: Cydnidae) from Tajikistan, with a checklist of the World Cydnidae associated with caves. *Zootaxa*, **3686**, 493-496.

Kozlov, M. V., Ivanov, V. D., and Rasnitsyn, A. P. 2002. Order Lepidoptera Linné, 1758. The butterflies and moths. *In.* Rasnitsyn, A. P., and Quicke, D. L. J. (Eds.). *History of Insects*. Dordrecht, Kluwer, Pp. 517.

Krenn, H. W. 2014. Feeding Mechanisms of Adult Lepidoptera: Structure, Function, and Evolution of the Mouthparts. *Annual Review of Entomology*, **55**, 307-327.

Krishna, K. 1990. Isoptera. *In* Grimaldi, D. A. (Ed.). *Insects from the Santana Formation, Lower Cretaceous, of Brazil.* Bulletin of the American Museum of Natural History, Pp. 195.

Kristensen, N. P. 1998. *Lepidoptera, Moths and Butterlies. Volume 1: Evolution, Systematics, and Biogeography*. Handbook of Zoology, Part 35, New York, Pp. 491.

Krogmann, L., Engel, M. S., Bechly, G., and Nel, A. 2013. Lower Cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta). *Journal of Systematic Palaeontology*, **11**, 83-89.

Lambkin, K. 1988. A re-examination of *Lithosmylidia* Riek from the Triassic of Queensland with notes on Mesozoic 'osmylid-like' fossil Neuroptera (Insecta: Neuroptera). *Memoirs of the Queensland Museum,* **25**, 445-458.

Langston, R. L., and Powell, J. A. 1975. The Earwigs of California (Order Dermaptera*). Bulletin of the Californian Insect Survey*, **20**, 1-25.

Larivière, M.-C., and Larochelle, A. 2006. An overview of flat bug genera (Hemiptera, Aradidae) from New Zealand, with considerations on faunal diversification and affinities. *Kataloge de OÖ, Landesmuseen Neue Serie 50*, **19**, 181-214.

Lawrence, J. F., and Newton, A. F. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). *In.* Pakaluk, J., and Slipinski, S. A. (Eds.). *Biology, Phylogeny, and Classification of Coleoptera*, vol. 2. Warsaw, Muzeum I Instytut Zoologii PAN, Pp. 1006.

Lawrence, J. F., Ślipiński, A., Seago, A. E., Thayer, M. K., Newton, A. F., and Marvaldi, A. E. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologic,* **61**, 1-217.

Lee, S.-W. 2014. New Lower Cretaceous basal mantodean (Insecta) from the Crato Formation (NE Brazil). *Geologica Carpathica*, **65**, 285-292.

Legendre, F., Whiting, M. F., Bordereau, C., Cancello, E. M., Evans, T. A., and Grandcolas, P. 2008. The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: Implications for the evolution of the worker and pseudergate castes, and foraging behaviors. *Molecular Phylogenetics and Evolution*, **48**, 615-627.

Legendre, F., Nel, A., Svenson, G. J., Robillard, T., Pellens, R., and Grandcolas, P. 2015. Phylogeny of Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular Data and Controlled Fossil Evidence. *PLOS one*, **10(7)**, e0130127.

Li, M., Tian, Y., Zhao, Y., and Bu, W. 2012. Higher Level Phylogeny and the First Divergence Time Estimation of Heteroptera (Insecta: Hemiptera) Based on Multiple Genes. *PLOS one*, **2**, e32152.

Li, D., Qin, J-C., and Zhou, C-F. 2014. The phylogeny of Ephemeroptera in Pterygota revealed by the mitochondrial genome of *Siphluriscus chinensis* (Hexapoda: Insecta). *Gene*, **545**, 132-140.

Lin, Q., Szwedo, J., Diying, H., and Stroiński, A. 2010. Weiwoboidae fam. Nov. of 'Higher' Fulgoroidea (Hemiptera: Fulgoromorpha) from the Eocene Deposits of Yunnan, China. *ACTA Geologica Sinica*, **84**, 751-755.

Lis, J. A., Becker, M., and Schaefer, C. W. 2000. *Chapter 12. Burrower Bugs (Cydnidae)*. *In*. Schaefer, C. W., and Panizzi, A. R. (Eds.). *Heteroptera of Economic Importance*. CRC Press, London, Pp. 856.

Lu, X. M., Zhang, W. W., Liu, X. Y. 2017. Discovery of the family Babinskaiidae (Insecta: Neuroptera) from the mid Cretaceous amber of Myanmar. *Cretaceous Research*, **71**, 14-23.

Lubkin, S. H., and Engel, M. S. 2005. *Permocoleus*, New Genus, the First Permian Beetle (Coleoptera) from North America. *Annals of the Entomological Society of America*, **98**, 73-76.

Lyons, K. M., and Dikow, T. 2010. Taxonomic revision of *Ectyphus* Gerstaecker, 1868 and *Parectyphus* Hesse, 1972 with a key to world Ectyphinae (Insecta, Diptera, Mydidae). *ZooKeys,* **73**, 25-59.

Makarkin, V. N., and Menon, F. 2007. First record of fossil 'rapismatid-like' Ithonidae (Insecta, Neuroptera) from the Lower Cretaceous Crato Formation of Brazil. *Cretaceous Research*, **28**, 743-753.

Makarkin, V. N., Heads, S. W., and Wedmann, S. 2017. Taxonomic study of the Cretaceous lacewing family Babinskaiidae (Neuroptera: Myrmeleontoidea: Nymphidoidae), with description of new taxa. *Cretaceous Research*, **78**, 149-160.

Malicky, H. 1984. Ein Beitrag zur Autökologie und Bionomie der aquatischen Netzflüglergattung *Neurorthus* [sic] (Insecta, Neuroptera, Neurorthidae). *Archiv für Hydrobiologie,* **101**, 231–46.

Mao, M., Gibson, T., and Dowton, M. 2015. Higher-level phylogeny of the Hymenoptera inferred from mitochondrial genomes. *Molecular Phylogenetics and Evolution*, **84**, 34-43.

Marshall, J. A., and Haes, E. C. M. 1988. *Grasshoppers and allied insects of Great Britain and Ireland*. Colchester, Harley Books, Pp. 252.

Martill, D. M., and Nel, A. 1996. A new dragonfly from the Crato Formation (Lower Cretaceous, Aptian) of N. E. Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte,* **5**, 279-292.

Martins-Neto, R. G., and Vulcano, M. A. 1989a. Primeiro registro de Raphidioptera (Neuropteroidea) na Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. *Revista Brasileira de Entomologia*, **34**, 241-249.

Martins-Neto, R. G., and Vulcano, M. A. 1989b. Amphiesmenoptera, (Trichoptera + Lepidoptera) na Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. I – Lepidoptera (Insecta). *Anais da Academia Brasileira de Ciências*, **61**, 459-465

Martins-Neto, R. G., and Vulcano, M. A. 1989c Neuropteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. 1. Familia Chrysopidae. *Anais Academia Brasileira de Ciências,* **60**, 189-201.

Martins-Neto, R. G., and Vulcano, M. A. 1990a. Neuropteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. III – Superfamilia Mantispoidea. *Revista Brasileira de Entomologia,* **34**, 619-625.

Martins-Neto, R. G., and Vulcano, M. A. 1990b. Neuropteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. VI – Ensaio filogenético das espécies do gênero *Blittersdorfia*, com descrição de nova espécie. *Acta Geologica Leopoldensia,* **31,** 3-12.

Martins-Neto, R. G., and Caldas, E. B. 1990. Efêmeras escavadoras (Insecta, Ephemeroptera, Ephemeroidea) na Formação Santana (Cretáceo Inferior), Bacia do Araripe Nordeste do Brasil: Descrição de três novos gêneros e três novas espécies (ninfas). *Atas do I Simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste Crato*, 265-275.

Martins-Neto, R. G., and Santos, J. C. K. 1994. Um novo gênero e una nova espécie de Mutuca (Insecta, Diptera, Tabanidae) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. *Acta Geologica Leopoldensia,* **39**, 289-297.

Martins-Neto, R. G. 2003a. Systematics of the Caelifera (Insecta, Orthopteroidea) from the Santana Formation, Araripe Basin (Lower Cretaceous, northeast Brazil), with a description of new genera and species. *Acta Zoologica Cracoviensia,* **46,** 205-228.

Martins-Neto, R. G. 2003b. The fossil Tabanids (Diptera Tabanidae): When they began to appreciate warm blood and when they began transmit diseases? *Memorias do Instituto Oswaldo Cruz,* **98 (1)**, 29-34.

Martins-Neto, R.G., and Pesenti, M. 2006. The first fossil Termitidae (Isoptera) from the Oligocene of South America: the Entre-Córregos Formation of the Aiuruoca Basin, Minas Gerais, Brazil. *Journal of the Entomological Research Society*, **8**, 63-68.

Martins-Neto, R. G. 2007. Systematic paleontology. *In* A new species of wasp (Symphyta, Sepulcidae) from the Santana Formation (Lower Cretaceous, northeast Brazil). *Journal of the Entomological Research Society,* **9**, 1-6.

Martynova, O. M. 1961. Sovremennye i vymershie verblyudki (Insecta, Raphidioptera). *Paleontologicheskii Zhurnal*, **1961(3)**,73-83.

Martynova, O. M. 1962 (reprinted 1991). Order Phasmatodea. *In.* Rohdendorf, B. B. (Ed.). *Fundamentals of Paleontology*, vol. 9, *Arthropoda, Tracheata, Chelicerata*. Washington D. C., Smithsonian Institution Libraries and The National Science Foundation, Pp. 894.

Marzke, D., and Klass, K.-D. 2005. Reproductive biology and nymphal development in the basal earwig *Tagalina papua* (Insecta: Dermaptera: Pygidicranidae), with a comparison of brood care in Dermaptera and Embioptera. *Entomologische Abhandlungen*, **62**, 99-102.

Mazzini, M., and Scali, V. 1987. *Stick Insects: Phylogeny and Reproduction*. University of Siena, Siena, Italy, Pp. 224.

McAlpine, J. F. 1981. Morphology and terminology – adults. *In.* McAlpine, J. F., and Woods, D. M. (Eds.). *Manual of Nearctic Diptera*, *vol. 1*. Ottawa, Biosystematics Research Institute, Pp. 674.

McCafferty, W. P., and Bae, Y. J. 1992. Filter-feeding habits of the larvae of *Anthopotamus* (Ephemeroptera: Potamanthidae). *Annales de Limnologie,* **28**, 27-34.

McCafferty, W. P., and Wang, T.-Q. 2000. Phylogenetic systematics of the major lineages of pannote mayflies (Ephemeroptera: Pannota). *Transactions of the American Entomological Society,* **126**, 9-101.

Menon, F., and Heads, S. W. 2005. New species of Palaeontinidae (Insecta: Cicadomorpha) from the Lower Cretaceous Crato Formation of Brazil. *Stuttgarter Beiträge zur Naturkunde, Serie B,* **357,** 1-11.

Menon, F., Heads, S. W., and Martill, D. M. 2005. New Palaeontinidae (Insecta: Cicadomorpha) from the Lower Cretaceous Crato Formation of Brazil. *Cretaceous Research*, **26**, 837-844.

Mepherson, J. E., Packauskas, R. J., and Korch, P. P. 1987. Life history and laboratory rearing of *Pelocoris femoratus* (Hemiptera: Naucoridae), with descriptions of immature stages. *Proceedings of the Entomological Society of Washington*, **89**, 288-295.

Merritt, R. W., and Cummins, K. W. 1996. *An Introduction to Aquatic Insects of North America (1st Edition)*. Kendall/Hunt Publishing, Pp. 861.

Merritt, R. W., Cummins, K. W., and Berg, M. B. 2008. *An Introduction to the Aquatic Insects of North America (4th Edition).* Kendall Hunt Publishing, Pp. 1158.

Miller, N. C. E. 1956. *The Biology of the Heteroptera*. Leonard Hill Books, London, UK, Pp. 162.

Millet, J., and Nel, A. 2010. A new myrmeleontoid genus from the Crato Formation of northeast Brazil (Lower Cretaceous) (Insecta: Neuroptera: Palaeoleontidae). *Zootaxa*, **2353**, 49-54.

Needham, J. G., Traver, J. R., and Hsu, Y.-C. 1935. *The Biology of Mayflies, with a Systematic Account of North American Species*. Comstock Publishing, Ithaca, New York, Pp. 759.

Nel, A., and Paicheler, J.-C. 1993. Les Isoptera fossiles. État actuel des connaissances, implications paléoécologiques et paléoclimatogiques [Insecta, Dictyoptera]. *In.* Nel, A., X. Martínez-Delclòs, and Paicheler, J.-C. *Essai de Révision des Aeschinioidea [Insecta, Odonata, Anisoptera] / Les Isoptera Fossiles [Insecta, Dictyoptera]*. CNRS Editions [Cahiers de Paléontologie], Paris, France, Pp. 179.

Nel, A., and Escuillé, F. 1994. A new dragonfly from the Lower Cretaceous of Brazil. *Palaeontology,* **37,** 923-930.

Nel, A., and Paicheler, J.-C. 1994a. Les Gomphidae fossiles. Un inventaire critique (Odonata: Gomphidae). *Annales de la Société Entomologie de France (n.s.),* **30**, 55-77.

Nel, A., and Paicheler, J.-C. 1994b. Les Libelluloidea fossiles autres que Libellulidae. Un inventaire critique (Odonata, Corduliidae, Macromiidae, Synthemistidae, Chlorogomphidae et Mesophlebiidae). *Nouvelle Revue d'Entomologie (N.S.),* **11**, 321-334.

Nel, A., Bechly, G., Jarzembowski, E. A., and Martínez-Delclòs, X. 1998. A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida). *Paleontologia Lombarda,* **10**, 1-68.

Nel, A., Azar, D., Martínez-Delclós, X., and Makhoul, E. 2004. A new Upper Cretaceous species of *Chresmoda* from Lebanon – a latest representative of Chresmodidae (Insecta: Polyneoptera inc. sed.): first record of homeotic mutations in the fossil record of insects. *European Journal of Entomology,* **101**, 145-151.

Nel, A., Delclos, X., and Hutin, A. 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société entomologique de France (N.S.)*, **41**, 29-69.

Nel, A., and Bechly, G. 2009. The Third Petalurid Dragonfly from the Lower Cretaceous of Brazil (Odonata: Cretapetaluridae). *Annales Zoologici*, **59**, 281-285.

Nel, A., Prokop, J., Grandcolas, P., Garrouste, R., Lapeyrie, J., Legendre, F., Anisyutkin, A., and Kirejtshuk, A. G. 2014. The beetle-like Palaeozoic and Mesozoic roachoids of the so -called 'umenocoleoid' lineage (Dictyoptera: Ponopterixidae fam. Nov.). *Comptes Rendus Palevol*, **13**, 545-554.

New, T. R. 1975. The biology of Chrysopidae and Hemerobiidae (Neuroptera) with reference to their usage as biocontrol agents: A review. *Transactions of the Royal Entomological Society, London,* **127**, 115-40.

New, T. R. 1986. A review of the biology of Neuroptera Planipennia. *Neuroptera International, Supplemental Series,* **1**, 1-57.

New, T. R. 1999. Neuroptera and biological control. *Stapfia,* **60**, 147-166.

New, T. R. 2002. Prospects for extending the use of Australian lacewings in biological control. *Acta Zoologica Academiae Scientiarum Hungaricae,* **48 (2)**, 209-216.

Orkin (Company) 2015. [Online] ORKIN Pest Control guide to pest Cockroach species. [Accessed 17 July 2015]. http://www.orkin.com/cockroaches/

Oswald, J. D. 1993. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society,* **101**, 143-299.

Otte, D. 1981. *The North American Grasshoppers, Volume I: Acrididae: Gomphocerinae and Acridinae*. Harvard University Press, Cambridge, Massachusetts, Pp. 275.

Otte, D. 1984. *The North American Grasshoppers, Volume II: Acrididae: Oedipodinae*. Harvard University Press, Cambridge, Massachusetts, Pp. 275.

Otte, D. 1994. *The Crickets of Hawaii: Origin, Systematics, and Evolution*. The Orthopterist Society and Academy of Natural Sciences, Philadelphia, Pennsylvania, Pp. 396.

Ouvrard, D., Campbell, B. C., Bourgoin, Th., and Chan, K. L. 2000. 18S rRNA secondary structure and phylogenetic position of Peloridiidae (Insecta, Hemiptera). *Molecular Phylogenetics and Evolution,* **16**, 403-417.

Peters, W. L., and Peters, J. G. 1970. *Proceedings of the First International Conference on Ephemeroptera*. Brill, Leiden, the Netherlands, Pp. 344.

Petr, K., Vaclav, J., and Pavel, H. 2013. When the Body Hides the Ancestry: Phylogeny of Morphologically Modified Epizoic Earwigs Base on Molecular Evidence. *PLOS ONE*, **8(6)**, e66900.

Petrulevičius, J. F., and Martins-Neto, R. G. 2001. A bittacid from the Santana Formation, Lower Cretaceous of Brazil. Legal, ethical and systematic aspects. *Acta Geologcal Leopoldensia*, **24**, 125-127.

Picker, M., Griffiths, C., and Weaving, A. 2002. *Field Guide to Insects of South Africa*. Struik, Cape Town, Pp. 436.

Pilgrim, E., von Dohlen, C., and Pitts, J. 2008. Molecular phylogenetics of Vespoidea indicate paraphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta,* **37,** 539-560.

Pinto, I. R., and Purper, I. 1986. A new blattoid from the Cretaceous of Brazil. *Pesquisas Instituto de Geociências Universidad Federal do Rio Grande do Sul,* **18**, 5-10.

Pivnik, K., and McNeil, J. N. 1987. Puddling in butterflies: sodium affects reproductive success in *Thymelicus lineola*. *Physiological Entomology,* **12**, 461-472.

Poisson, R. 1951. Ordre de Hétéroptères. *In.* Grassé, P. P. (Ed.). *Traité de Zoologie, Tome 10*. Masson et Cie, Paris, France, Pp. 1948.

Polegatto, C. M., and Zamboni, J. C. 2001. Inferences regarding the feeding behavior and morphoecological patterns of fossil mayfly nymphs (Insecta Ephemeroptera) from the

Lower Cretaceous Santana Formation of northeastern Brazil. *Acta Geologica Leopoldensia,* **24,** 145-160.

Ponomarenko, A. G. 1986. *Scarabaeiformes incertae sedis*. *In* Rasnitsyn, A. P. (Ed.). *Nasekomye v rannemelovykh ekosistemakh Zapadonoy Mongolii*. *Trudy Sovmestnaya Sovetsko – Mongol'skaya Paleontologicheskaya Ehkspeditsiya,* **28**, 1-213.

Ponomarenko, A. G. 1992. Suborder Adephaga. *In*. Arnold'di, L. V., Zherikhin, V. V., Nikritin, L. M., and Ponomarenko, A. G. (Eds.). *Mesozoic Coleoptera*. Smithsonian Institution Libraries, Washington D.C., Pp. 285. (English translation of Ponomarenko, 1977)

Ponomarenko, A. G. 1997. Taxonomy, Fossil Insects from Israel. *Paleontological Journal*, **31**, 528-533.

Popov, Y. A. 1971. The historical development of bugs of the infraorder Nepomorpha (Heteroptera). *Proceedings of the Paleontological Institute of the Academy of Sciences of the USSR,* **129**, 1-230. [In Russian]

Popov, Y. A., and Shcherbakov, D. E. 1991. Mesozoic Peloridioidea and their ancestors (Insecta: Hemiptera, Coleorrhyncha). *Geologica et Palaeontologica,* **25**, 215-235.

Popov, Y. A., and Shcherbakov, D. E. 1996. Origin and evolution of the Coleorrhyncha as shown by the fossil record. *In.* Schaefer, C. W. (Ed.). *Studies on Hemipteran Phylogeny*. Proceedings. Entomological Society of America. Lanham, MD, Thomas Say Publications in Entomology, Pp. 244.

Preston-Mafham, R., and Preston-Mafham, K. 1993. *The Encylopedia of Land Invertebrate Behaviour*. MIT Press, Pp. 320.

Rakitov, R., and Gorb, S. N. 2013. Brochosomes protect leafhoppers (Insecta, Hemiptera, Cicadellidae) from sticky exudates. *Journal of the Royal Society Interface*, **10 (87)**, 1-5.

Rasnitsyn, A. P. 1977. A new subfamily of scoliid wasps (Hymenoptera, Scoliidae, Proscoliinae). *Zoologicheskii Zhurnal,* **56**, 522-529.

Rasnitsyn, A. P. 1988. An outline of evolution of the hymenopterous insects (Order Vespida). *Oriental Insects,* **22,** 115-145.

Rasnitsyn, A. P., Pulawski, W. J., and Martinéz-Delclòs, X. 1999. Cretaceous digger wasps of the new genus *Bestiola* Pulawski and Rasnitsyn (Hymenoptera: Sphecidae: Angarosphecinae). *Journal of Hymenoptera Research,* **8,** 23-34.

Regier, J. C., Mitter, C., Zwick, A., Bazinet, A. L., Cummings, M. P., Kawahara, A. Y., Sohn, J.-C., Zwickl, D. J., Cho, S., Davis, D. R., Baixeras, J., Brown, J., Parr, C., Weller, S., Lees, D. C., and Mitter, K. T. 2014. A Large-Scale, Higher-Level, Molecular Phylogenetic Study of the Insect Order Lepidoptera (Moths and Butterflies). *Plos ONE*, **8**, e58568.

Rentz, D. C. F., and Kevan, D. K. McE. 1991. Dermaptera (Earwigs). *In.* Naumann, I. D. (Ed.). *The Insects of Australia. A textbook for students and research workers*. Melbourne, Melbourne University Press, Volume one, Pp. 542.

Rentz, D. C. F. 1996. *Grasshopper country: the abundant orthopteroid insects of Australia*. Sydney: New South Wales University Press, Pp. 284.

Resh, V. H., and Cardé, R. T. 2009. *Encyclopaedia of Insects*. Academic Press, Pp. 1024.

Romero, A. 2009. *Cave Biology: Life in Darkness*. Cambridge, Cambridge University Press, Pp. 306.

Roth, L. M. 1991. Blattodea, Blattaria (cockroaches). *In.* Naumann, I. D. (Ed.). *The Insects of Australia: A Textbook for Students and Research Workers, Volume 1* [2nd Edition]. Cornell University Press, Ithaca, New York, Pp. 542.

Roy, R. 1999. Morphology and taxonomy. *In.* Prete, F. R., Wells, H., Wells, P. H., and Hurd, L. E. (Eds.). *The Praying Mantids*. Johns Hopkins University Press, Baltimore, Maryland, Pp. 362.

Rozkosny, R. 2000. Stratiomyidae. *In.* Papp, L., and Darvas, B. (Eds.). *Manual of Palaearctic Diptera, vol. 2*. Budapest, Science Herald, Pp. 880.

Russell, R. W., May, M. L., Soltesz, K. L., and Fitzpatrick, J. W. 1998. Massive swarm migrations of dragonflies (Odonata) in eastern North America. *The American Midland Naturalist*, **140**, 325-342.

Ryzhkova, O. V., and Coram, R. A. 2016. Archegocimicidae (Insecta: Heteroptera) from the Purbeck Limestone Group (Lower Cretaceous: Berriasian) of southern England. *Cretaceous Research*, **61**, 199-208.

Samuelson, G. A. 1994. Pollen consumption and digestion by leaf beetles. *In.* Jolivet, P. H., Cox, M. L., and Petitpierre, E. (Eds.). *Novel Aspects of the Biology of Chrysomelidae*. Dordrecht, Kluwer Academic Publishers, Pp. 582.

Santiago-Blay, J. A. 1994. Paleontology of leaf beetles. *In.* Jolivet, H., Cox, M. L., and Petitpierre, E. (Eds.). *Novel Aspects of the Biology of Chrysomelidae*. Dordrecht: Kluwer Academic Publishers, Pp. 582.

Sartori, M., and Brittain, J. E. 2015. Order Ephemeroptera. *In*. Thorp, J. H., and Rogers, D. C. (Eds.). *Ecology and General Biology, Vol I: Thorp and Covich Freshwater Invertebrates, 4th Edition*. Academic Press, Pp. 1148.

Schaefer, C. W. 1999. The higher classification of the Alydidae (Hemiptera : Heteroptera). *Proceedings of the Entomological Society of Washington*, **101**, 94-98.

Scherbakov, D. E., and Popov, Y. A. **2002**. Order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc.. *In.* Rasnitsyn, A. P., and Quicke, D. L. J. (Eds.). *History of Insects*. Kluwer Academic Publishers, New York, Pp. 517.

Schlee, D. 1969. Morphologie und Symbiose; ihre Beweiskraft für die Verwandtschaftsbeziehungen der Coleorrhyncha (Insecta, Hemiptera). *Stuttgarter Beiträge zur Naturkunde, Serie C,* **210**, 1-27.

Scholtz, C. H., and Chown, S. L. 1995. The evolution of habitat use and diet in the Scarabaeoidea: a phylogenetic approach. *In.* Pakaluk, J., and ´Slipínski, S. A. (Eds.), *Biology, Phylogeny, and Classification of Coleoptera*, vol. 1. Warsaw, Muzeum I Instytut Zoologii PAN, Pp. 1006.

Schuh, R. T., and Slater, J. A. 1995. *True Bugs of the World (Hemiptera:Heteroptera): Classification and Natural History*. Cornell University Press, Ithaca, New York, Pp. 337.

Seitz, A. 1906-1933. *Macrolepidoptera of the World*. Other important series are the 'MONA' series (*Moths of North America*), *Die Schmetterlinge Mitteleuropas*, the *Fauna of British India*, *Lepidoptera Indica*, *Monographs on Australian Lepidoptera*, and *The Moths and Butterflies of Great Britain and Ireland*.

Sellick, J. T. C. 1997. Descriptive terminology of the phasmid egg capsule, with an extended key to the phasmid genera based on egg structure. *Systematic Entomology,* **22**, 97-122.

Sellick, J. T. C. 1998. The micropylar plate of the eggs of Phasmida, with a survey of the range of plate form within the order. *Systematic Entomology,* **23**, 203-228.

Shcherbakov, D. E. 2000. Permian Faunas of Homoptera (Hemiptera) in Relation of Phytogeography and the Permo-Triassic Crisis. *Paleontological Journal*, **34**, 251-267.

Shih, C., Feng, H., and Dong, R. 2011. New Fossil Heloridae and Mesoserphidae Wasps (Insecta, Hymenoptera, Proctotrupoidea) From the Middle Jurassic of China. *Entomological Society of America*, **104**, 1334-1348.

Sime, K. R., and Brower, A. V. Z. 1998. Explaining the latitudinal gradient anomaly in ichneumonid species richness: evidence from butterflies. *Journal of Animal Ecology*, **67**, 387-399.

Simpson, S. J., Sword, G. A., Lorch, P. D., and Couzin, I. D. 2006. Cannibal crickets on a forced march for protein and salt. *Proceedings National Academy of Sciences USA*, **103**, 4152-4156.

Song, N., Liang, A.-P., and Bu, C.-P. 2012. A Molecular Phylogeny of Hemiptera Inferred from Mitochondrial Genome Sequences. *PLOS one*, **7(11)**, e48778.

Song, N., and Liang, A.-P. 2013. A Preliminary Molecular Phylogeny of Planthoppers (Hemiptera: Fulgoroidea) Based on Nuclear and Mitochondrial DNA Sequences. *PLOS one*, **8(3)**, e58400.

Stange, L. A., and Miller, R. B. 1990. Classification of the Myrmeleontidae based on larvae (Insecta: Neuroptera). *In.* Mansell, M. W., and H. Aspöck (Eds.). *Advances in Neuropterology: Proceedings of the Third International Symposium on Neuropterology*. Department of Agriculture Development, Pretoria, South Africa, Pp. 298.

Step, E. 1932. *Bees, Wasps, Ants and Allied Insects of the British Isles*. Frederick Warne & Co., London, Pp. 238.

Stiller, M. 2009. Leafhoppers associated with grasslands of South Africa. Part I. Grassland Biome endemics. *The Grassland Society of southern Africa*, **9(4)**, 1-3.

Svenson, G. J., and Whiting, M. F. 2009. Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics*, **25**, 468-514.

Symes, C. T., and Woodborne, S. 2010. Estimation of food composition of *Hodotermes mossambicus* (Isoptera: Hodotermitidae) based on observations and stable carbon isotope ratio. *Insect Science*, **18**, 175-180.

Szwedo, J., Lefebvre, T. H., and Bourgoin, F. 2004. *Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An annotated catalogue with notes on Hemiptera classification***.** Studio 1, Pp. 199.

Szwedo, J., Bourgoin, T., and Lefebvre, F. 2006. New Mnemosynini taxa (Hemiptera, Fulgoromorpha: Cixiidae) from the Palaeogene of France with notes on their early association with host plants. *Zootaxa*, **1122**, 25-45.

Szwedo, J. 2011. The Coleorrhyncha (Insecta: Hemiptera) of the European Jurassic, with a description of a new genus from the Toarcian of Luxembourg. *Volumina Jurassica*, **9**, 3-19.

Szwedo, J., Azar, D., and Ziade, K. 2011. The first Progonocimicidae (Insecta: Hemiptera: Coleorrhyncha) from Lower Cretaceous Lebanese amber. *Insect Systematics & Evolution*, **42**, 161-177.

Tawfik, M. F. S., El-Sherif, S., and Lutfallah, A. F. 2009. On the life-history of the giant water-bug Limnogeton fieberi Mayr (Hemiptera: Belostomatidae), predatory on some harmful snails. *Journal of Applied Entomology*, **86**, 138-145.

Thorne, B. L., Grimaldi, D., and Krishna, K. 2000. Early fossil history of the termites. *In*. Abe, T., Bignell, D. E., and Higashi, M. (Eds.). *Termites: evolution, sociality, symbioses, ecology*. Dordrecht, Kluwer Academic Publishers, Pp. 466.

Tompson, G. J., Miller, L. R., Lenz, M., and Crozier, R. H. 2000. Phylogenetic analysis and trait evolution in Australian lineages of drywood termites (Isoptera, Kalotermitidae). *Molecular Phylogenetics and Evolution*, **17**, 419-429.

Torchio, P. F. 1972. *Sapyga pumila* Cresson, a parasite of *Megachile rotundata* (F.) (Hymenoptera: Sapygidae; Megachilidae). I: Biology and description of immature stages. *Melanderia,* **10**, 1-22.

Udea, K. 1997. A new palaeontinid species from the Lower Cretaceous of Brazil (Homoptera: Palaeontinidae). *Bulletin of the Kitakyushu Museum of Natural History*, **16**, 99-104.

Uvarov, B. P. 1928. *Locusts and Grasshoppers: A Handbook for Their Study and Control*. Imperial Bureau of Entomology, London, UK, Pp. 352.

Uvarov, B. P. 1966. *Grasshoppers and Locusts: A Handbook of General Acridology*. *Volume 2*. Cambridge University Press, Cambridge, UK, Pp. 588.

Vršanský, P. 2002a. Cretaceous Gondwanian Cockroaches (Insecta: Blattaria). *Entomological Problems*, **34**, 49-54.

Vršanský, P. 2002b. Origin and evolution of mantises. *AMBA Projekt*y, **6**, 1-16.

Vršanský, P., Vishniakova, V. N., and Rasnitsyn, A. P. 2002. Order Blattida Latreille, 1810. The cockroaches. *In.* Rasnitsyn, A. P., and Quicke, D. L. J. (Eds.). *History of Insects*. Kluwer Academic Publishers, Dordrecht, the Netherlands, Pp. 517.

Vršanský, P., and Aristov, D. 2014. Termites (Isoptera) from the Jurassic/Cretaceous boundary: Evidence for the longevity of their earliest genera. *European Journal of Entomology*, **111**, 137-141.

Vulcano, M. A. 1985. *Cretaceosimulium araripensis* gen. et sp. nov. da Chapada do Araripe, Ceará Brasil (Diptera: Simuliidae). *Resumos do Congresso Brasileiro de Zoologia,* **12**, 107.

Vulcano, M. A., and Pereira, F. S. 1987. Entomofauna fossil da Chapada do Araripe, Ceará, Brasil – *Cretaceimelittomoides cearensis* gen. nov., sp. nov. (Coleoptera: Pyrochroidae). *X Congreso Brasileiro de Paleontologia, 1987, Rio de Janeiro. Resumo das Comunicações*, **27**.

Wang, T.-Q., and McCafferty, W. P. 1995. Relationships of the Arthropleidae, Heptageniidae, and Pseudironidae (Ephemeroptera: Heptagenioidea). *Entomological News,* **106**, 251-256.

Wang, T.-Q., McCafferty, W. P., and Bae, Y. J. 1997. Sister relationships of the Neoephemeridae and Caenidae (Ephemeroptera: Pannota). *Entomological News,* **108**, 52-56.

Waterston, A. R., and Pittaway, A. R. 1991. The Odonata or Dragonflies of Oman and neighbouring territories. *Journal of Oman Studies,* **10**, 131-168.

Wedmann, S. 2010. A brief review of the fossil history of plant masquerade by insects. *Palaeontogrphica Abteilung B-Palaophytologie*, **283**, 175-182.

Wells, A. 2005. Parasitism by bydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. *Australian Journal of Entomology*, **44**, 385-391.

Westfall, M. J. 1980. Cretaceous dragonfly discovery in Brazil. *Selysia,* **9**, 22.

Wheeler, Q. D. 1986. Revision of the genera of Lymexylidae (Coleoptera: Cucujiformia). *Bulletin of the American Museum of Natural History,* **183**, 115-210.

Whitfield, J. B. 1998. Phylogeny and evolution of host-parasitoid interactions in Hymenoptera. *Annual Review of Entomology*, **43**, 129-151.

Wiggins, G. B. 1977. *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press, Toronto, Canada, Pp. 401.

Wiggins, G. B. 1996. *Larvae of the North American Caddisfly Genera (Trichoptera)* [2nd Edition]. University of Toronto Press, Toronto, Canada, Pp. 457.

Wighton, D. C. 1987. *Gomphaeschna obliqua* spec. nov., a new species of Gomphaeschninae from the Lower Cretaceous of northeastern Brazil (Anisoptera, Aeshnidae). *Odonatologica,* **16**, 311–314.

Wighton, D. C. 1988. Odonate fossils from the Lower Cretaceous of northeastern Brazil. *Proceeding of the 18th International Congress on Entomology*, Vancouver, Abstract 64.

Wilf, P., Labandeira, C. C., Kress, W. J., Staines, C. L., Windsor, D. M., Allen, A. L., and Johnson, K. R. 2000. Timing the radiations of leaf beetles: hispines on gingers from Latest Cretaceous to Recent. *Science,* **289**, 291-294.

Willmann, R. 2003. Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. *Verhandlungen Westdeutscher Entomologentag,* **2001**, 1-64.

Willmann, R. 2007. Persisting-type stem-group Ephemeroptera. *In*. Martill, D. M., Bechly, G., and Loveridge, R. F. (Eds.). *The Crato Fossil Beds of Brazil: Window into an ancient world*. Cambridge University Press, Cambridge, Pp. 625.

Wilson, E. O., and Martill, D. M. 2001. A new Japygid Dipluran from the Lower Cretaceous of Brazil. *Palaeontology*, **44**, 1025-1031.

Wilson, S. W. 2005. Keys to the families of Fulgoromorpha with emphasis on planthoppers of potential economic importance in the southeastern United States (Hemiptera: Auchenorrhyncha). *Florida Entomologist*, **88**, 464-481.

Wipfler, B., Courtney, G. W., Craig, D. A., and Beutel, R. G. 2012. First µ-CT-based 3D reconstruction of a dipteran larva-the head morphology of Protanyderus (Tanyderidae) and its phylogenetic implications. *Journal of Morphology*, **273**, 968-980.

Wood, G. C. 1981. Asilidae. *In*. McAlpine, J F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R., and Wood, D. M., (Eds.). Manual of Nearctic Diptera. Volume 1. *Research Brant, Agriculture Canada, Monographs*, **27**, 549-573 (Ottawa).

Wood, T. G. 1978. The food and feeding habits of termites. *In*. Brian M. V. (Ed.). *Production ecology of ants and termites.* Cambridge University Press, Cambridge, Pp. 428.

Wood, T. G., and Sands, W. A. 1978. The role of termites in ecosystems. *In*. Brian, M. V. (Ed.). *Production ecology of ants and termite*. Cambridge, Cambridge University Press, Pp. 428.

Yan, Y., Wang, Y., Liu, X., Winterton, S. L., and Yang, D. 2014. The First Mitochondrial Genomes of Antlion (Neuroptera: Myrmeleontidae) and Split-footed Lacewing (Neuroptera: Nymphidae), with Phylogenetic Implications of Myrmeleontiformia. *International Journal of Biological Sciences*, **10**, 895-908.

Yang, Q., Wang, Y., Labandeira, C. C., Shihi, C., and Ren, D. 2014. Mesozoic lacewings from China provide phylogenetic insight into evolution of the Kalligrammatidae (Neuroptera). *BMC Evolutionary Biology*, **14**, 126.

Ying, W., and Dong, R. 2007. Two new genera of fossil palaeontinids from the Middle Jurassic in Daohugou, Inner Mongolia, China (Hemiptera, Palaeontinidae). *Zootaxa*, **1390**, 41-49.

Zettel, H., and Lane, D. J. W. 2011. The creeping water bugs (Insecta: Heteroptera: Naucoridae) of Brunei. *Annalen des Haturhistorischen Museums in Wien, B*, **112**, 163-171.

Zhang, J.–E., Sun, B., and Zhang, X.-Y. 1994. *Miocene Insects and Spiders from Shanwang, Shandong*. Science Press, Beijing, China, Pp. 298. [In Chinese, with English summary]

Zhang, K., Yang, D., and Ren, D. 2007. Notes on the extinct family Protapioceridae, with description of a new species from China (Insecta: Diptera: asiloidae). *Zootaxa*, **1530**, 27-32.

Zhang, Q., Zhang, H.-C., Rasnitsyn, A. P., Wang, H., and Ding, M. 2014. New Ephialititidae (Insecta: Hymenoptera) from the Jurassic Daohugou Beds of Inner Mongolia, China. *Palaeoworld*, **23**, 276-284.

Zhou, Z., Shi, F., and Zhao, L. 2014. The First Mitochondrial Genome for the Superfamily Hagloidea and Implications for Its Systematic Status in Ensifera. *PLOS one*, **9(5)**, e97542.

Zwick, P. 1967. Beschreibung der aquatischen Larve von *Neurorthus* [sic] *fallax* (Rambur) und Errichtung der neuen Planipennierfamilie Neurorthidae [sic] fam. nov. *Gewässer und Abwässer,* **44/45**, 65-86.

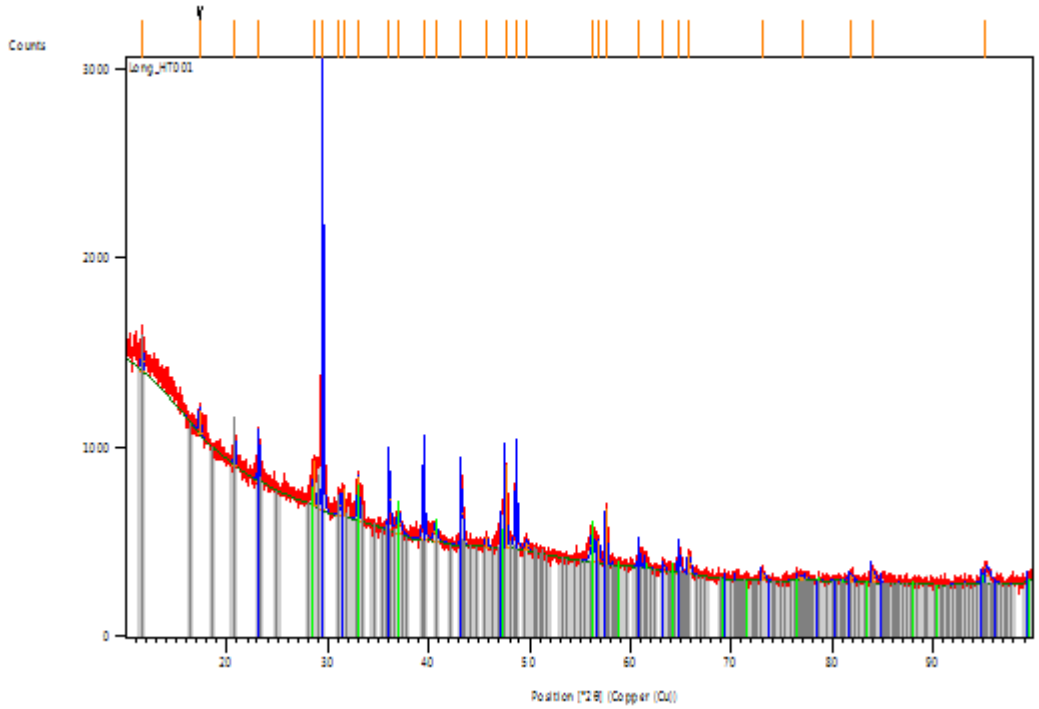
8. 6. XRD settings and additional information

8. 6. 1. Specimen HT001 (unweathered)

Anchor Scan Parameters

Dataset Name:	Long_HT001
File name:	C:\XRD Data\Nathan Barling\Long_HT001.xrdml
Sample Identification:	HT001
Comment:	Configuration=Stage Spinner, Owner=Joe, Creation date=7/7/2014 11:31:04 AM Goniometer=PW3050/60 (Theta/Theta); Minimum step size 2Theta:0.001; Minimum step size Omega:0.001 Sample stage=Reflection-Transmission Spinner PW3064/60; Minimum step size Phi:0.1 Diffractometer system=XPERT-3 Measurement program=C:\PANalytical\Data Collector\Programs\Emily Scan.xrdmp, Identifier={548B10C9-4D87-48D7-9A40-EE05665A54D7} Batch program=C:\PANalytical\Data Collector\Programs\2 Sample Batch.xrdmp, Identifier={B9015489-E80A-42A4-96EA-37EA233FFD2E} Emily's Scan
Measurement Start Date/Time:	7/6/2017 1:20:58 PM
Operator:	Univ of Portsmouth
Raw Data Origin:	XRD measurement (*.XRDML)
Scan Axis:	Gonio
Start Position [°2θ]:	10.0116
End Position [°2θ]:	99.9846
Step Size [°2θ]:	0.0130
Scan Step Time [s]:	198.6450
Scan Type:	Continuous
PSD Mode:	Scanning
PSD Length [°2θ]:	3.35
Offset [°2θ]:	0.0000
Divergence Slit Type:	Fixed
Divergence Slit Size [°]:	0.2177
Specimen Length [mm]:	10.00
Measurement Temperature [°C]:	25.00
Anode Material:	Cu
K-Alpha1 [Å]:	1.54060
K-Alpha2 [Å]:	1.54443
K-Beta [Å]:	1.39225
K-A2 / K-A1 Ratio:	0.50000
Generator Settings:	35 mA, 40 kV
Diffractometer Type:	0000000011158042
Diffractometer Number:	0
Goniometer Radius [mm]:	240.00
Dist. Focus-Diverg. Slit [mm]:	100.00
Incident Beam Monochromator:	No
Spinning:	Yes

Graphics



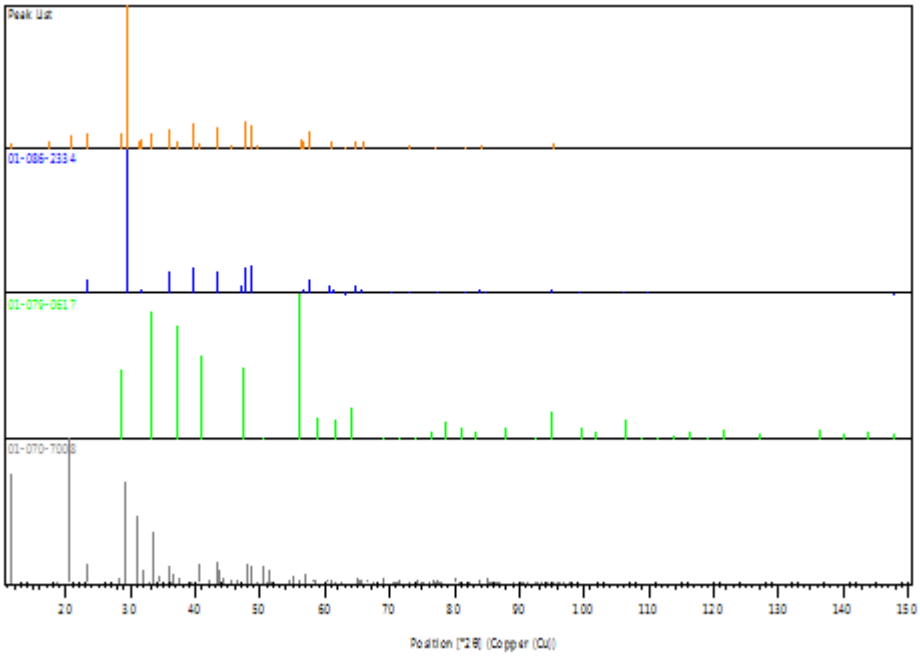
Peak List

Pos.[°2θ]	Height [cts]	FWHMLeft[°2θ]	d-spacing [Å]	Rel. Int. [%]	TipWidth	Matched by
11.6022	100.00	0.2237	7.62105	4.26	0.2684	01-070-7008
17.3070	135.38	0.2047	5.12392	5.77	0.2456	
20.7264	233.40	0.1023	4.28566	9.94	0.1228	01-070-7008
23.1206	242.94	0.1279	3.84701	10.35	0.1535	01-086-2334
28.6042	242.90	0.1535	3.12076	10.35	0.1842	01-079-0617
29.5029	2347.06	0.1023	3.02771	100.00	0.1228	01-086-2334
31.1193	114.64	0.2047	2.87404	4.88	0.2456	01-070-7008
31.5283	147.00	0.1023	2.83768	6.26	0.1228	01-086-2334
33.0018	238.10	0.2047	2.71428	10.14	0.2456	01-079-0617,01..
36.0845	328.69	0.2047	2.48915	14.00	0.2456	01-086-2334,01..
37.0176	104.64	0.5117	2.42853	4.46	0.6140	01-079-0617
39.4801	424.40	0.2303	2.28255	18.08	0.2763	01-086-2334,01..
40.6700	92.03	0.4093	2.21847	3.92	0.4912	01-079-0617,01..
43.2652	338.92	0.1791	2.09122	14.44	0.2149	01-086-2334,01..
45.6977	57.02	0.3070	1.98541	2.43	0.3684	01-070-7008
47.6252	442.72	0.1279	1.90946	18.86	0.1535	01-086-2334,01..
48.6245	384.00	0.2558	1.87253	16.36	0.3070	01-086-2334,01..
49.6631	50.27	0.3070	1.83578	2.14	0.3684	01-070-7008
56.1634	158.64	0.3070	1.63775	6.76	0.3684	01-079-0617,01..
56.7646	120.83	0.3070	1.62182	5.15	0.3684	01-086-2334,01..
57.5554	298.48	0.1023	1.60141	12.72	0.1228	01-086-2334,01..
60.8154	108.40	0.2047	1.52314	4.62	0.2456	01-086-2334,01..
63.2243	38.41	0.3070	1.47079	1.64	0.3684	01-086-2334
64.7736	127.97	0.2558	1.43930	5.45	0.3070	01-086-2334,01..
65.8416	103.19	0.2558	1.41852	4.40	0.3070	01-086-2334,01..
73.1238	47.74	0.3070	1.29419	2.03	0.3684	01-086-2334,01..
76.9587	19.92	1.2280	1.23899	0.85	1.4736	01-086-2334,01..
81.7522	37.56	0.6140	1.17804	1.60	0.7368	01-086-2334,01..
84.0756	62.21	0.4093	1.15130	2.65	0.4912	01-086-2334,01..
95.2313	87.74	0.7164	1.04373	3.74	0.8596	01-086-2334,01..

Pattern List

Ref.Code	Compound Name	Scale Fac.	Chem. Formula	Mineral Name	SemiQuant[%]
01-086-2334	Calcium Carbonate	0.970	Ca (C O3)	Calcite	80
01-079-0617	Iron Sulfide	0.072	Fe S2	Pyrite, syn	7
01-070-7008	Calcium Sulfate Hy..13	0.084	Ca (S O4) (H2 O..		

Graphics



Document History

Insert Measurement:
- File name = 'Long_HT001.xrdml'
- Modification time = '7/7/2017 8:10:27 AM'
- Modification editor = 'Univ of Portsmouth'

Default properties:
- Measurement step axis = 'None'
- Internal wavelengths used from anode material: Copper (Cu)
- Original K-Alpha1 wavelength = '1.54060'
- Used K-Alpha1 wavelength = '1.54060'
- Original K-Alpha2 wavelength = '1.54443'
- Used K-Alpha2 wavelength = '1.54443'
- Original K-Beta wavelength = '1.39225'
- Used K-Beta wavelength = '1.39225'
- Irradiated length = '10.00000'
- KBeta filter material = 'Ni'
- KBeta filter thickness = '0.02000'
- Receiving slit size = '0.10000'
- Step axis value = '0.00000'
- Offset = '0.00000'
- Sample length = '10.00000'
- Modification time = '7/7/2017 8:10:27 AM'
- Modification editor = 'Univ of Portsmouth'

Interpolate Step Size:
- Initial Scan Range = 10.01160 - 99.99340
- Initial Step Size = 0.01313
- Derived Step Size = 0.01300
- Use Derived Step Size = 'Yes'
- Modification time = '7/7/2017 8:10:27 AM'
- Modification editor = 'PANalytical'

Determine Background:
- Add to net scan = 'Nothing'
- User defined intensity = '0'
- Correction method = 'Automatic'
- Bending factor = '2'

Delete Peak(s):
- Start position = '10.3970'
- End position = '10.3970'
- Modification time = '7/7/2017 8:14:49 AM'
- Modification editor = 'Univ of Portsmouth'

Search & Match:
- Allow pattern shift = 'Yes'
- Auto residue = 'Yes'
- Data source = 'Profile and peak list'
- Demote unmatched strong = 'Yes'
- Multi phase = 'Yes'
- Restriction set = 'Default'
- Restriction = 'None'
- Subset name = ''
- Match intensity = 'Yes'
- Two theta shift = '0'
- Identify = 'No'
- Max. no. of accepted patterns = '5'
- Minimum score = '50'
- Min. new lines / total lines = '60'
- Search depth = '10'
- Minimum new lines = '5'
- Minimum scale factor = '0.1'
- Intensity threshold = '0'
- Use line clustering = 'Yes'
- Line cluster range = '1.5'
- Search sensitivity = '1.8'
- Use adaptive smoothing = 'Yes'
- Smoothing range = '1.5'
- Threshold factor = '3'
- Modification time = '7/4/2017 9:05:29 AM'
- Modification editor = 'Univ of Portsmouth'

Search & Match:
- Allow pattern shift = 'Yes'
- Auto residue = 'Yes'
- Data source = 'Profile and peak list'

- Minimum significance = ‘0.66’
- Minimum tip width = ‘0’
- Maximum tip width = ‘1’
- Peak base width = ‘2’
- Use smoothed input data = ‘Yes’
- Granularity = ‘16’
- Modification time = ‘7/7/2017 8:14:04 AM’
- Modification editor = ‘Univ of Portsmouth’

Search Peaks:
- Minimum significance = ‘2’
- Minimum tip width = ‘0.00999999977648258’
- Maximum tip width = ‘2.24999999999999’
- Peak base width = ‘3’
- Method = ‘Minimum 2nd derivative’
- Modification time = ‘3/15/2017 11:11:34 AM’
- Modification editor = ‘Univ of Portsmouth’

Delete Peak(s):
- Start position = ‘11.5844’
- End position = ‘11.5844’
- Modification time = ‘7/7/2017 8:14:33 AM’
- Modification editor = ‘Univ of Portsmouth’

Delete Peak(s):
- Start position = ‘14.9433’
- End position = ‘14.9433’
- Modification time = ‘7/7/2017 8:14:37 AM’
- Modification editor = ‘Univ of Portsmouth’

- Demote unmatched strong = ‘Yes’
- Multi phase = ‘Yes’
- Restriction set = ‘Minerals’
- Restriction = ‘Restriction set’
- Subset name = ‘’
- Match intensity = ‘Yes’
- Two theta shift = ‘0’
- Identify = ‘No’
- Max. no. of accepted patterns = ‘5’
- Minimum score = ‘50’
- Min. new lines / total lines = ‘60’
- Search depth = ‘10’
- Minimum new lines = ‘5’
- Minimum scale factor = ‘0.1’
- Intensity threshold = ‘0’
- Use line clustering = ‘Yes’
- Line cluster range = ‘1.5’
- Search sensitivity = ‘1.8’
- Use adaptive smoothing = ‘Yes’
- Smoothing range = ‘1.5’
- Threshold factor = ‘3’
- Modification time = ‘8/4/2017 11:02:37 AM’
- Modification editor = ‘Univ of Portsmouth’

Insert Peak:
- Peak position [°2θ] = ‘11.6022’
- Modification time = ‘8/4/2017 11:03:45 AM’
- Modification editor = ‘Univ of Portsmouth’

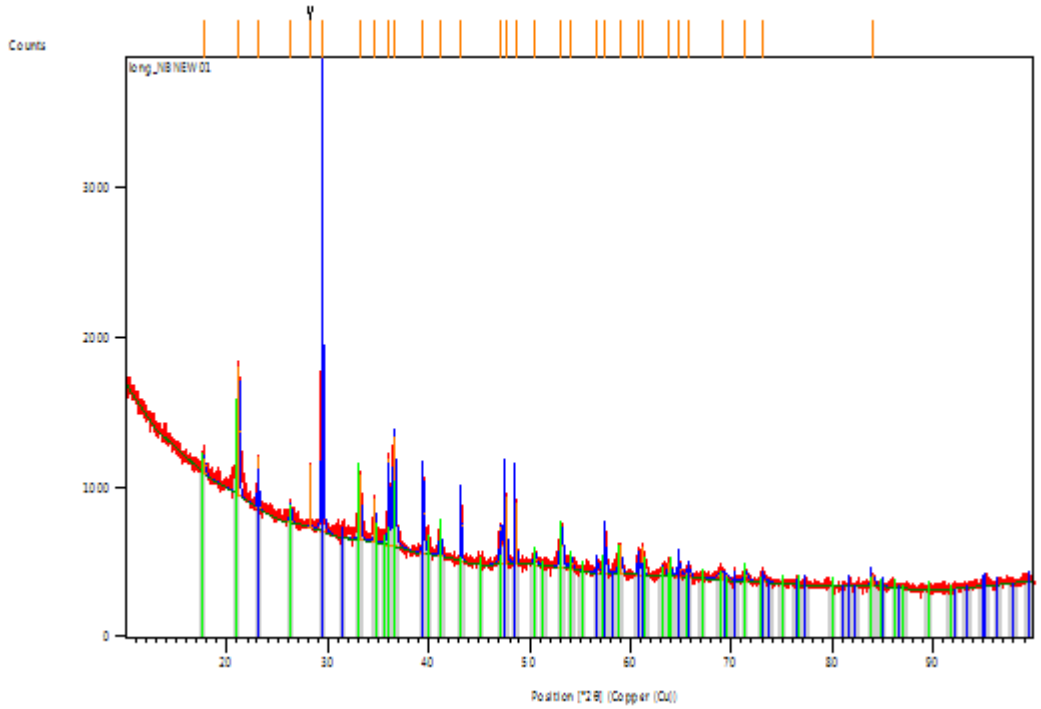
8. 6. 1. Specimen NBNEW01 (weathered)

Specimen NBNEW01
Anchor Scan Parameters

Dataset Name:	long_NBNEW01
File name:	C:\XRD Data\Nathan Barling\long_NBNEW01.xrdml
Sample Identification:	NBNEW01
Comment:	Configuration=Stage Spinner, Owner=Joe, Creation date=7/7/2014 11:31:04 AM Goniometer=PW3050/60 (Theta/Theta); Minimum step size 2Theta:0.001; Minimum step size Omega:0.001 Sample stage=Reflection-Transmission Spinner PW3064/60; Minimum step size Phi:0.1 Diffractometer system=XPERT-3 Measurement program=C:\PANalytical\Data Collector\Programs\Emily Scan.xrdmp, Identifier={548B10C9-4D87-48D7-9A40-EE05665A54D7} Batch program=C:\PANalytical\Data Collector\Programs\2 Sample Batch.xrdmp, Identifier={B9015489-E80A-42A4-96EA-37EA233FFD2E} Emily's Scan
Measurement Start Date/Time:	7/6/2017 2:54:55 PM
Operator:	Univ of Portsmouth
Raw Data Origin:	XRD measurement (*.XRDML)
Scan Axis:	Gonio
Start Position [°2θ]:	10.0116
End Position [°2θ]:	99.9846
Step Size [°2θ]:	0.0130
Scan Step Time [s]:	198.6450
Scan Type:	Continuous
PSD Mode:	Scanning
PSD Length [°2θ]:	3.35
Offset [°2θ]:	0.0000
Divergence Slit Type:	Fixed

Divergence Slit Size [°]:	0.2177
Specimen Length [mm]:	10.00
Measurement Temperature [°C]:	25.00
Anode Material:	Cu
K-Alpha1 [Å]:	1.54060
K-Alpha2 [Å]:	1.54443
K-Beta [Å]:	1.39225
K-A2 / K-A1 Ratio:	0.50000
Generator Settings:	35 mA, 40 kV
Diffractometer Type:	0000000011158042
Diffractometer Number:	0
Goniometer Radius [mm]:	240.00
Dist. Focus-Diverg. Slit [mm]:	100.00
Incident Beam Monochromator:	No
Spinning:	Yes

Graphics



Peak List

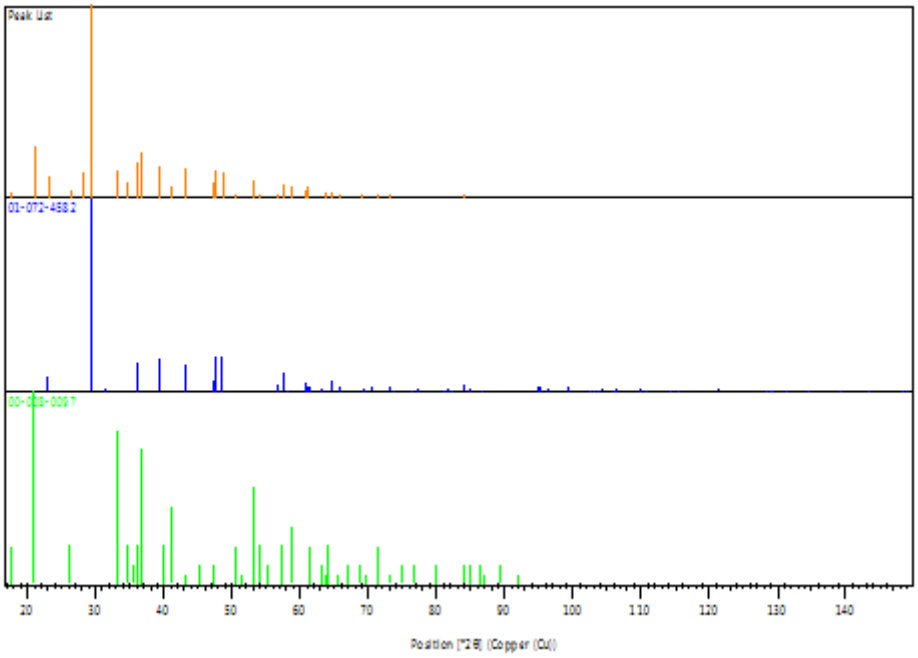
Pos.[°2θ]	Height [cts]	FWHMLeft[°2θ]	d-spacing [Å]	Rel. Int. [%]	TipWidth	Matched by
17.7376	109.07	0.3070	5.00048	3.42	0.3684	00-008-0097
21.1788	859.10	0.1279	4.19512	26.96	0.1535	00-008-0097
23.0816	350.53	0.1023	3.85342	11.00	0.1228	01-072-4582
26.2791	123.64	0.2047	3.39136	3.88	0.2456	00-008-0097
28.2509	431.05	0.0384	3.15898	13.53	0.0461	
29.4536	3186.49	0.1151	3.03267	100.00	0.1382	01-072-4582
33.1898	446.22	0.1535	2.69933	14.00	0.1842	00-008-0097
34.6293	290.31	0.1279	2.59035	9.11	0.1535	00-008-0097
36.0291	586.34	0.1279	2.49286	18.40	0.1535	01-072-4582,00..
36.5781	747.59	0.2814	2.45669	23.46	0.3377	00-008-0097
39.4620	532.65	0.1791	2.28355	16.72	0.2149	01-072-4582
41.1306	191.08	0.2047	2.19468	6.00	0.2456	00-008-0097
43.2121	483.25	0.0624	2.09194	15.17	0.0749	01-072-4582,00..
47.1757	253.94	0.3070	1.92660	7.97	0.3684	01-072-4582,00..
47.6223	449.95	0.1791	1.90957	14.12	0.2149	01-072-4582
48.5896	415.20	0.1279	1.87379	13.03	0.1535	01-072-4582
50.5280	78.03	0.3070	1.80636	2.45	0.3684	00-008-0097
53.1186	289.73	0.3070	1.72421	9.09	0.3684	00-008-0097

54.0828	82.20	0.3070	1.69573	2.58	0.3684	00-008-0097
56.6674	86.44	0.2558	1.62437	2.71	0.3070	01-072-4582
57.4900	238.27	0.1535	1.60307	7.48	0.1842	01-072-4582,00..
58.9202	191.50	0.3070	1.56753	6.01	0.3684	00-008-0097
60.7630	146.32	0.1535	1.52433	4.59	0.1842	01-072-4582
61.1851	190.01	0.1535	1.51482	5.96	0.1842	01-072-4582,00..
63.8220	100.99	0.3070	1.45845	3.17	0.3684	00-008-0097
64.7630	107.82	0.3070	1.43951	3.38	0.3684	01-072-4582
65.6903	58.86	0.5117	1.42142	1.85	0.6140	01-072-4582,00..
69.1197	57.09	1.0234	1.35904	1.79	1.2280	01-072-4582
71.3917	66.40	0.4093	1.32127	2.08	0.4912	00-008-0097
73.0767	76.76	0.2047	1.29491	2.41	0.2456	01-072-4582,00..
83.9492	74.33	0.4093	1.15271	2.33	0.4912	01-072-4582,00..

Pattern List

Ref.Code	Compound Name	Scale Fac.	Chem. Formula	Mineral Name	SemiQuant[%]
01-072-4582	Calcium Carbonate	0.963	Ca (C O3)	Calcite	-
00-008-0097	Iron Oxide Hydrate	0.165	Fe2 O3 · H2 O	Goethite	-

Graphics



Document History

- File name = 'long_NBNEW01.xrdml'
- Modification time = '7/7/2017 8:10:28 AM'
- Modification editor = 'Univ of Portsmouth'

Default properties:
- Measurement step axis = 'None'
- Internal wavelengths used from anode material: Copper (Cu)
- Original K-Alpha1 wavelength = '1.54060'
- Used K-Alpha1 wavelength = '1.54060'
- Original K-Alpha2 wavelength = '1.54443'
- Used K-Alpha2 wavelength = '1.54443'
- Original K-Beta wavelength = '1.39225'
- Used K-Beta wavelength = '1.39225'
- Irradiated length = '10.00000'
- KBeta filter material = 'Ni'
- KBeta filter thickness = '0.02000'

Insert Measurement:
Search & Match:
- Allow pattern shift = 'Yes'
- Auto residue = 'Yes'
- Data source = 'Profile and peak list'
- Demote unmatched strong = 'Yes'
- Multi phase = 'Yes'
- Restriction set = 'Default'
- Restriction = 'None'
- Subset name = ''
- Match intensity = 'Yes'
- Two theta shift = '0'
- Identify = 'No'
- Max. no. of accepted patterns = '5'
- Minimum score = '50'
- Min. new lines / total lines = '60'
- Search depth = '10'

- Receiving slit size = ‘0.10000’
- Step axis value = ‘0.00000’
- Offset = ‘0.00000’
- Sample length = ‘10.00000’
- Modification time = ‘7/7/2017 8:10:28 AM’
- Modification editor = ‘Univ of Portsmouth’

Interpolate Step Size:
- Initial Scan Range = 10.01160 - 99.99340
- Initial Step Size = 0.01313
- Derived Step Size = 0.01300
- Use Derived Step Size = ‘Yes’
- Modification time = ‘7/7/2017 8:10:28 AM’
- Modification editor = ‘PANalytical’

Determine Background:
- Add to net scan = ‘Nothing’
- User defined intensity = ‘0’
- Correction method = ‘Automatic’
- Bending factor = ‘1’
- Minimum significance = ‘0.66’
- Minimum tip width = ‘0’
- Maximum tip width = ‘1’
- Peak base width = ‘2’
- Use smoothed input data = ‘Yes’
- Granularity = ‘16’
- Modification time = ‘7/6/2017 10:07:53 AM’
- Modification editor = ‘Univ of Portsmouth’

Search Peaks:
- Minimum significance = ‘2’
- Minimum tip width = ‘0.00999999977648258’
- Maximum tip width = ‘2.24999999999999’
- Peak base width = ‘3’
- Method = ‘Minimum 2nd derivative’
- Modification time = ‘3/15/2017 11:11:34 AM’
- Modification editor = ‘Univ of Portsmouth’
- Minimum new lines = ‘5’
- Minimum scale factor = ‘0.1’
- Intensity threshold = ‘0’
- Use line clustering = ‘Yes’
- Line cluster range = ‘1.5’
- Search sensitivity = ‘1.8’
- Use adaptive smoothing = ‘Yes’
- Smoothing range = ‘1.5’
- Threshold factor = ‘3’
- Modification time = ‘7/4/2017 9:05:29 AM’
- Modification editor = ‘Univ of Portsmouth’

Delete Peak(s):
- Start position = ‘81.7052’
- End position = ‘81.7052’
- Modification time = ‘7/7/2017 8:12:36 AM’
- Modification editor = ‘Univ of Portsmouth’

Delete Peak(s):
- Start position = ‘95.2649’
- End position = ‘95.2649’
- Modification time = ‘7/7/2017 8:12:57 AM’
- Modification editor = ‘Univ of Portsmouth’

8. 7. Supplementary data tables

Table 7. Supplementary specimen information. This table presents additional supplementary information for many of the specimens listed in Table 1. Specimen numbers are provided in in the first column. The extent of preparation, including if specimens have been resin transferred, mounted and coated, and SEM viewed are provided in the second and third columns. The forth column presents data on the quality of preservation, the condition of the fossil, and/or the techniques used in preparation. The fifth and sixth columns present taxonomic information, typically class and order if discernible, followed by photograph numbers in the seventh column. Finally, additional notes are presented in the eighth column. A total of 109 specimens are notes in this table.

Specimen Number	Mounted and Coated?	SEM Viewed?	Condition/Techniques	Class	Order	Photo Numbers	Additional Notes
NBRL001	N/A	N/A	Severe pyrite decay	(plant)		NBRL 001 photo 01 - 05	Bob L. decaying plant, kept in own box.
NBRL002	n	n	astounding wing venation, but body is preserved as thin slivers of black cuticle, limbs are stains on rock, leave alone	Insecta	Odonata	NBRL 002 photo 01 - 04	Part and counter-part: a & b.
NBRL003	n	n	Partly oxidised body, outer rim appears black, may not have any three-dimensionality	Insecta	Diptera??	NBRL 003 photo 01 - 02	
NBRL004	needs clean, then coat	n (not great specimen)	mostly mould, jet black remnants remain	Insecta	Orthoptera	NBRL 004 photo 01 - 03	
NBRL005	n	n	Oxidised, but some black remains (<15%) LARGE and Heavily damaged	Insecta	Orthoptera	NBRL 005 photo 01 - 03	Largest sample in the unweathered box
NBRL006	n	n	Low relief, restricted to main body. Will unlikely yield results, but could be coated and viewed after cleaning	Insecta	Diptera	NBRL 006 photo 01 - 03	
NBRL007	n	n	Completely compacted, transfer might reveal detail, but unlikely. Extremely dirty.	Insecta	Blattodea	NBRL 007 photo 01 - 03	
NBRL008	N/A		Almost totally preserved unoxidized	Insecta	Orth/Blatt	NBRL 008 photo 01 - 04	Best specimen, laminae appear denser
NBRL009	transferred	n	Fully 3d, but still appears scrappy. Transfer should be undertaken - WET TRANSFER UNDERTAKEN	Insecta		NBRL 009 photo 01 - 03	Although superficially similar to a hoverfly the wing venation is too complex to be a member of Diptera

NBRL010	n	n	Isolated pair of elytra, fully 3d but lacking any texture - will likely be destroyed by transfer and SEM viewing	Insecta	? Poss Blatt	NBRL 010 photo 01 - 04	Just preserved wings
NBRL011	n	n	Fossil is essentially just colouration on the rock, doubtful that any information will be gathered.	Insecta	Cicadomorpha??	NBRL 011 photo 01 - 04	Possibly 2 insects on this slab
NBRL012	N/A		Scatterings of unoxidized material, rest is oxidised	Insecta	Hymenoptera	NBRL 012 photo 01 - 05	
NBRL013	N		Patches of possibly unoxidized material, however may be later mineral growth	Insecta?		NBRL 013 photo 01 - 06	Insect appears broken up
NBRL014	transferred		Moderate level of oxidation, again a black 'rim' is visible around the fossil - WET TRANSFER UNDERTAKEN	Insecta	?	NBRL 014 photo 02 - 03	
NBRL015	N		Very poorly preserved fossil: insect almost just a mould, however black preservation of surrounding biomatter	Insecta	Coleopter/Hemi	NBRL 015 photo 01 - 05	V. small head with elongate antenna
NBRL016			Partial pyrite decay and minimal gypsum formation. Black colouration of all of the fossil	(plant)		NBRL 016 photo 01 - 06	Donated plant for bob, well preserved.
NBRL017			Oxidised and poorly preserved - deeply contained within sample rock	Insecta	Orthoptera	NBRL 017 photo 01 - 04	
NBRL018	Y	Y	V. well preserved, dark deep brown oxidised colour - Heavy acid etching used to reveal astonishing detail.	Insecta	Blattodea	NBRL 018 photo 01 - 23	Umenocoleidae - *Ponopterix axelrodi*
NBRL019			Heavily oxidised, wings extended and only partially preserved. Large chunks of abdomen lost.	Insecta	Cicadomorpha??	NBRL 019 photo 01 - 03	
NBRL020	transfer, N coat/mont	Too large	V. large and relatively well preserved, oxidised, large ovipositor preserved	Insecta	Orthoptera	NBRL 020 photo 01 - 04	unusually large
NBRL021			Limbs and wings preserved v. well, body and head heavily damaged	Insecta	Blattodea	NBRL 021 photo 01	"Blattulidae, gen?"
NBRL022	Y	Y	Extremely well preserved, high 3D preservation - one wing case lost, other damaged, no wings.	Insecta	Blattodea	NBRL 022 photo 01	"Cockroach, Umenoloceidae, *Ponopterix axelrodi*
NBRL023	destroyed by transfer		Large, but 'scraped', heavily damaged, but some patches reveal high detail in the centre of body	Insecta	Blattodea	NBRL 023 photo 01 - 05	"Female, Blattellidae, Gen et sp. Nov."

NBRL024	transfer, N coat/mont	Needs clean	Small and intact wing cases, abdomen scraped	Insecta	Blattodea	NBRL 024 photo 01	Stouter body than *P. axelrodi*, but same head
NBRL025			Very well preserved, wing covers fully extended, but wings not covered.	Insecta	Blattodea	NBRL 025 photo 01	Umenocoleidae - *Ponopterix axelrodi*
NBRL026	N (needs cutting)		ventral view, very good preservation, but wing tips and limbs	Insecta	Blattodea	NBRL 026 photo 01 - 04	
NBRL027	Y	Y	v. well preserved, slight loss of internal contents in abdomen	Insecta	Blattodea	NBRL 027 photo 01	"Blattellidae, *Mesoblattina limai*"
NBRL028			Scrappily preserved, ,but almost complete, both wing covers extended	Insecta	Blattodea	NBRL 028 photo 01	Umenocoleidae - *Ponopterix axelrodi*
NBRL029	transfer, N coat/mont	Mostly destroyed	Well preserved, oxidised and slightly stained at the posterior end of the abdomen.	Insecta	Orthoptera?	NBRL 029 photo 01	i.d. unsure, could be Blattodea too
NBRL030	y	?	Fragments of head, abdomen and wing cases preserved, centre of fossil lost	Insecta	Blattodea	NBRL 030 photo 01	Martill 2007, p.g. 243 G (new taxa was described)
NBRL031	transfer, N coat/mont		Deeply inset into sediment, scruffy and covered in debris - appears intact.	Insecta	Blattodea	NBRL 031 photo 01 - 02	Extremely fragile structures poking through sediment.. However became damaged
NBRL032	Where is this specimen?		One wing and half an antenna lost, otherwise well preserved - long antennae	Insecta	Blattodea	NBRL 032 photo 01 - 02	"Blattellidae, unsure of genus (A. Ross may want to have a look at this) DISPLAYED IN CASE" - *Mespblattina limai*???
NBRL033	destroyed by transfer		Extremely small specimen, possibly limb fragment	Insecta	Culicidae??	NBRL 033 photo 01	
NBRL034	Transferred, needs clean	Destroyed	High level of preservation of the body, some limbs and head. Long antenna are preserved, but no wings	Insecta	Blattodea	NBRL 034 photo 01	"Blattulidae, unsure of genus"
NBRL035	specimen cannot be found		High relief, darker black in colour (not totally oxidised), almost complete, but small	Insecta	Blattodea	NBRL 035 photo 01	Umenocoleidae - *Ponopterix axelrodi*
NBRL036	N (needs cutting)		abdomen and wings heavily damaged, but eyes well intact, moderate relief	Insecta	Blattodea	NBRL 036 photo 01	Umenocoleidae - *Ponopterix axelrodi*
NBRL037	transfer, N coat/mont		Extremely well preserved, high 3D preservation - sadly lost detail after transfer, but still should be SEM mounted	Insecta	Blattodea	NBRL 037 photo 01 - 02	Extremely dense and complex wing venation, flat head and spiked limbs
NBRL038	transfer, N coat/mont		Isolated, but well-preserved abdomen and cerci.	Insecta	Blattodea	NBRL 038 photo 01	"Blattellidae, Gen et sp. Nov."

NBRL039	specimen cannot be found		Partially covered, but intact - moderate relief, good preservation	Insecta	?	NBRL 039 photo 01	Could possibly do with acid preparation
NBRL040	y	I thought I had	Specimen shows waterlogging and explosion of the abdomen/thorax on the left ventral surface	Insecta	Blattodea	NBRL 040 photo 01	*Cratovitisma oldreadi*? Or other taxa ejecting guts/eggs on upon bursting? Shows textbook 'water bursting' along abdomen
NBRL041	N	N	Low relief, interesting well-formed quartz crystals - view under SEM	Insecta	Diptera	NBRL 041 photo 01 - 02	Martill 2007 pg 368 - Mecoptera: Bittacidae
NBRL042	transferred		Well preserved and set in the sediment, but heavily damaged, transfer technique needed - GOLD SHINE on limb	Insecta	Achilidae??	NBRL 042 photo 01	Eyes and limbs imply planthopper.
NBRL043	transferred	likely useless	Poorly preserved fossil insect, but extensive *Dastilbe* coprolites. - fish weren't eating the insects. WET TRANSFER UNDERTAKEN.	Insecta	Orthoptera?	NBRL 043 photo 01 - 02	Do not prep - explanatory fossil.
NBRL044	Y	Y	Moderately preserved, might transfer well	Insecta	Orthoptera	NBRL 044 photo 01	Elcanidae
NBRL045	Y	Y	Very small insect, possible internal contents visible - SEM	Insecta	Coleoptera?	NBRL 045 photo 01	
			- FOURTH LEVEL OF BLUE BOX (lowest draw, filing cabent) REACHED -				
TEST SPECIMEN	y	y	Extremely poorly preserved insect that as transferred with Wilkinson Resin and revealed amazing preservation	Insecta	Blattodea	Rsn Tst 01 -29	Folder: "Test specimen with Wilkinson Resin"
Additional specimens:			Transferred using the new 'Wilkinson Resin Transfer Technique'				
NBRL046	y		Preserved in lateral view, looks asif well preserved, but has been worn away.	Insecta	Blattodea?		
NBRL047	transfer, N coat/mont		Very scrappy and preserved in a lighter colour than usual, ovipositor present at about 0.9cm in length	Insecta	Orthoptera??		
NBRL048	y		Well preserved beetle on a 1.5x1.5x1.5cm square	Insecta	Coleoptera		more precise taxon can probably be established

NBRL049 - duplicate?	transfer, N coat/mont	Needs clean	Possible preservation of organs!! Large hindlimbs preserved outstretched, I.D. unclear. - sem mount!	Insecta	Orthoptera		
NBRL050	transfer, N coat/mont	Needs clean	isolated abdomen with long ovipositor	Insecta	Orthoptera??		
NBRL051	Y	Y		Insecta	Orthoptera	NBRL 051 photo 01-05	*Cratoelcana zessini* Martins-Neto 1991 - Elcanidae
NBRL052	transfer, N coat/mont		Clear pyrite framboids - or pseudoframboids	Insecta	Hemiptera??		
NBRL053	transfer, N coat/mont	maybe-clean		Insecta	Neuroptera		
NBRL054	Y	Y		Insecta	Blattodea	NBRL 054 photo 01-05	Exceptional fossil, but lateral view makes I.d. difficult from Martill *et al* 2007.
NBRL055	Y	Y		Insecta	Orthoptera	NBRL 055 photo 01-02	Gryllotalpidae - Sam ID (*Tetraspinus fossirus* Martins-Neto 1995??)
NBRL056	transfer, N coat/mont	No data	Isolated possible abdomen. Staggered layering of sclerites	Insecta	Orthoptera??		
NBRL057	REPAIR NEEDED	Y	V. well preserved, being lightly acid etched and then mounted	Insecta	Tabanidae (Diptera?)		
NBRL058	Needs cutting	n	V. well preserved, being lightly acid etched and then mounted	Insecta	Odonata		Dragonfly nymph
NBRL059	Y	Y	On edge of slab, well preserved limbs with sections through cuticle, ovipositor and cerci	Insecta	Orthoptera	NBRL059 photo 01 - 06	
NBRL060	Y	Y	Well preserved, worth imaging before transferring	Insecta	Ephemeroptera	NBRL060 photo 01 - 05	Mayfly nymph
NBRL061	Y	Y	High relief, but scrappy. Suitable for resin transfer. Requires cutting	Insecta	Orthoptera	NBRL061 photo 01 - 08	
NBRL062	Y	Y	NOT TO BE TRANSFERRED - very well preserved with full wing venation intact - requires light cleaning	Insecta	Orthoptera	NBRL062 photo 01 - 05	
NBRL063	y		Possible organs preserved!!	Insecta	Orthoptera??	NBRL063 photo 01 - 12	

NBRL064			Relatively poorly preserved and crappy, but structures are still visible - UNDERGOING COMPLETE ACID DIGESTION	Insecta	Orthoptera??	?	currently on phone (_161237, _161242, _161244)
NBRL065	Y	Y	Cracked & missing most of thorax, some segments of cuticle appear very well preserved HCL COMPLETE ACID DIGEST	Insecta	Orthopt/Blatt??	NBRL065 photo 01 - 27	Includes post partial acid digestion (14-27)
NBRL066	Y	Y	Fractured, limbs preserved only as stains, mild relief, body is mostly scrappy and dirty HCL COMPLETE ACID DIGEST	Insecta	Orthoptera	NBRL066 photo 01 - 09	
NBRL067	y	charging	Sadly, broken detailed, well preserved specimen. Reconstruction attempted on an SEM stub.	Insecta	Orthoptera	stub mounted after breaking	
NBRL068	mounted, not coated		Some relief and limb 2 was present, but has been buffed off (apart from coxa & distal elements)	Insecta	Orthoptera	NBRL068 photo 01 - 17	
NBRL069	mounted, not coated		Sediment appears too compacted to be suitable for acid digestion, otherwise moderately preserved	Insecta	Orthoptera	NBRL069 photo 01 - 12	
NBRL070	y	y	FAKE ANTANAE Dirty, but with amazing NANOMETRE PRESERVATION - gross morphology is rough, but high mag is great	Insecta	Orthoptera	NBRL070 photo 01 - 23	Antenna are grooves carved in by seller - FAKE - possibly *Cratolocustopsis cretacea* (beware, Martins-Neto taxon)
NBRL071	Y	Y	Extremely well preserved with outstanding relief. Very detailed body with empty voids crushed in.	Insecta	Blattodea?	NBRL071 photo 01 - 11	
NBRL072	y	y	Scrappy preserved thorax (only preserved as outline). Fragments of abdomen and limbs. Limb spines visible, but charging	Insecta	Orthopt/Blatt??	NBRL072 photo 01 - 10	Can not find images - likely lost
NBRL073			Very poorly preserved snakefly.	Insecta	Raphidioptera	NBRL073 photo 01 - 05	resin transfer has seeped; through to fresh surface around head
NBRL074	y		high relief and phosphate? Infilling in thorax & head. Overall good preservation, but appendages poor.	Insecta	Orthoptera	NBRL074 photo 01 - 14	
NBRL075	Y	Y	Isolated thorax and single poorly preserved wing, possible large pyrite crystals in anterior thorax, high relief	Insecta	?	NBRL075 photo 01 - 09	

NBRL076				Insecta	?	NBRL076 photo 01 - 05	4 wings - short, fat body and 'neck'
NBRL077	y	y	Extreme charging, little to no information visible.	Insecta	Blattodea?	NBRL077 photo 01 - 05	
NBRL078	Needs cutting + coating	n		Insecta	Blattodea	NBRL078 photo 01 - 02	
NBRL079	transferring: Needs coating	n		Insecta	Neuroptera	NBRL079 photo 01 - 03	
NBRL080	cut			Insecta	?	NBRL080 photo 01 - 05	Wings do not have enough cells to be neuropteran. Venation long and simple like Trichoptera, but with 4 wings.
NBRL081	cut		CLEAN WITH ACETONE BEFORE COATING - extensive mineral infill	Insecta	Hemiptera	NBRL081 photo 01 - 06	Cicadellidae (leafhopper)
NBRL082	cut		Amazing preserved cerci, most of abdomen has chipped off, large portions of head and thorax covered in matrix	Insecta	Blattodea	NBRL082 photo 01 - 06	
Judith W. Specimens							
jw339	y	y	cockroach	Insecta	Blattodea		
jw735	y	y					
jw522	y	y					
jw291	y	y		Insecta	Blattodea		
jw677	y						
jw528	y	n	likely need recoating				
jw465	y	n	likely need recoating				
jw456	y	n	likely need recoating				
JW02#	y	y	No clear overview and ID is unclear, but lots of beautiful preservation and mineral textures.	Insecta	Possibly Blattodea?		
Additional Specimens:							
FLO13	cut		Mayfly Larvae - nice 3D preservation	Insecta	Ephemeroptera	FLO13 photo 01 - 06	

FLO27	cut		Extremely well prepared - exceptional preservation	Insecta	Hemiptera	FLO27 photo 01 - 05	Cicadellidae (leafhopper)
FLO28	cut			Insecta	Diptera	FLO28 photo 01 - 05	
FLO35	cut			Insecta	Blattodea	FLO35 photo 01 - 08	
FLO64	cut		Very high relief	Insecta	Hemiptera	FLO64 photo 01 - 06	Cicada
FLO33	Y	Y	EXTREMELY IMPORTANT - preserved in blue limestone, no relief and patchy cuticle, but colour banding preserved	Insecta	Blattodea	FLO33 photo 01 - 11	Has a band of oxidation running through the abdomen, may reveal if detail is lost through oxidation. NEEDS TO BE MARKED OUT BEFORE STUB MOUNTING
FLO15	y	y		Insecta	Hemiptera		
FLO31 (a,b)	needs cutting smaller	n	Part and counterpart, 7mm length, looks scrappy, possibly Diptera	Insecta	Diptera?		
FLO29	needs cutting smaller	n	very small (3mm) but well preserved dipteran, missing head and part of thorax, possibly belongs in Nematocera	Insecta	Diptera		
FLO36	Needs trimming	n	partially prepared, missing most limbs. Belongs in Auchenorrhyncha	Insecta	Hemiptera		
FLO38	-	n	very well preserved. Would benefit from light acid etching or preparation	Insecta	Hemiptera		
FLO37	-	n	extremely well preserved, large nymph	Insecta	Ephemeroptera		
FLO19	y	y	Amazing genitals preserved	Insecta	Diptera: Brachycera		
FLO17	y	By FLO	Completely digested planthopper	Insecta	Fulgoromorpha	N/A	
FLO43	y	y	Head is disarticulated, possible petiole suggests Hymenoptera	Insecta	Hymenoptera?		
NBSED01	y	y					
NBSED02, 02a	y	y					
nbstub003	y	y					
nbstub004	y	y					

Table 8a. Quantification of all taphonomic characters. Taxon, orientation, and photograph information is also included. Gaps represent characters that were not taxonomically present (i.e. wings on a larval form), were obscured from view (not clearly absent), or required SEM viewing (and the specimen had not been mounted for SEM viewing). These characters are excluded from determining the final taxonomic index, rather than counting negatively towards total preservation as they could not be measured. Specimens that are entirely blank could not be studied at all, usually as a result from specimen destruction through preparation problems/errors. A total of 64 specimens were taphonomically quantifiable.

Keys:

Head:

Head (A)	Antennae (B)	Eyes (C)	Internal Architecture (D)	Soft Tissues (E)	Soft Tissue Quality (F)
2 = Present (I=1)	5 = Complete (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)
1 = Partial (I=0.5)	4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.5)
0 = Absent (I=0)	3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0)
N/A = Can't see	2 = 50-25% (I=0.4)	N/A = Can't see	N/A = Can't see	N/A = Can't see	N/A = None Present
	1 = <25% (I=0.2)				
	0 = Absent/Can't see (I=0)				

Thorax:

% of Sclerites Present (G)	Internal Architecture (H)	Soft Tissues (I)	Soft Tissue Quality (J)
5 = Complete (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)
4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.5)
3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0)
2 = 50-25% (I=0.4)	N/A = Can't see	N/A = Can't see	N/A = None Present
1 = <25% (I=0.2)			
0 = Absent/Can't see (I=0)			

Orientation	Wing Positions	Leg Position
DV = Dorso-ventral	R = Rest	U = Under Body
L = Lateral	M = Mixed	M = Mixed
PA = Postero-anteri	E = Extended	E = Extended
N/A	N/A	N/A

Limbs:	Matching part, or equivalent number				
Fore left (K)	Fore Right (L)	Mid Left (M)	Mid Right (N)	Hind Left (O)	Hind Right (P)
5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)
4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)
3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)
2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)
1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)
0 = Lost/Can't See (I=0)	0 = Lost/Can't See (I=0)	0 = Lost/Can't See (I=0)	0 = Lost/Can't See (I=0)	0 = Lost/Can't See (I=0)	0 = Lost/Can't See (I=0)

Wings:				
Fore Wing Left (Q)	Fore Wing Right (R)	Hind Wing Left (S)	Hind Wing Right (T)	Wing Venation (U)
2 = Present (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Clear (I=1)
1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (I=0.5)
0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)
N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present

Abdomen:				
% of Sclerites Present (V)	Internal Architecture (W)	Soft Tissues (X)	Soft Tissue Quality (Y)	Genital/Anal Opening (Z)
5 = Complete (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)	2 = Present (I=1)
4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.66)	1 = Partial (I=0.5)
3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0.33)	0 = Absent (I=0)
2 = 50-25% (I=0.4)	N/A = Can't see	N/A = Can't see	0 = None Present (I=0)	N/A = Can't see
1 = <25% (I=0.2)				
0 = Absent/Can't see (I=0)				

Abdominal Appendages:

Ovipositor/Stinger (AA)	Left Cerci (AB)	Right Cerci (AC)	Other: _____ (AD)
5 = Complete (I=1)	5 = Complete (I=1)	5 = Complete (I=1)	5 = Complete (I=1)
4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)
3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)
2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)
1 = <25% (I=0.2)	1 = <25% (I=0.2)	1 = <25% (I=0.2)	1 = <25% (I=0.2)
0 = Absent/Can't see (I=0)	0 = Absent/Can't see (I=0)	0 = Absent/Can't see (I=0)	0 = Absent/Can't see (I=0)

Bristles/Hairs: SEM Images required

Hairs on Head (AE)	Hairs on Thorax (AF)	Hairs on Abdomen (AG)	Hairs on limbs (AH)	Hairs on Other (AI)	Individual Hairs (AJ)
3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Mostly Intact (I=1)
2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Mostly Broken (I=0.66)
1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Mostly Destroyed (I=0.33)
0 = None/Can't see (I=0)	0 = None/Can't see (I=0)	0 = None/Can't see (I=0)	0 = None/Can't see (I=0)	0 = None/Can't see (I=0)	0 = None preserved at all (I=0)
				N/A = No 'other'	

Compaction:

Highest Relief (AK)	Fragile Structures (AL)	Voids (AM)
3 = High (Un/almost uncompacted) (I=1)	3 = Uncompacted and Perpendicular to bedding (I=1)	3 = Preserved hollow (Even if Broken) (I=1)
2 = Moderate (Compacted) (I=0.66)	2 = Uncompacted and Parallel to bedding (I=0.66)	2 = In filled with mineral growth (I=0.66)
1 = Low (Crushed) (I=0.33)	1 = Compacted (I=0.33)	1 = In filled with matrix (I=0.33)
0 = None (restricted to one laminae) (I=0)	0 = Completely Crushed (I=0)	0 = Crushed (I=0)
	N/A = Not present/visible	N/A = Not visible

Fracturing and Breaking:

Head Cracking & Breaking (AN)	Thorax Cracking & Breaking (AO)	Abdomen Cracking & Breaking (AP)	Limbs Cracking & Breaking (AQ)
4 = None (I=1)	4 = None (I=1)	4 = None (I=1)	4 = None (I=1)
3 = Rare (I=0.75)	3 = Rare (I=0.75)	3 = Rare (I=0.75)	3 = Rare (I=0.75)
2 = Partial (I=0.5)	2 = Partial (I=0.5)	2 = Partial (I=0.5)	2 = Partial (I=0.5)
1 = Extensive (I=0.25)	1 = Extensive (I=0.25)	1 = Extensive (I=0.25)	1 = Extensive (I=0.25)
0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)

Table:

Specimen No.	Order	Photos	Orent.	Wing Pos.	Leg Pos.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V
NBRL002	Odonata	NBRL 002 photo 01 - 04	DV	E	N/A	1	0	0	0.5	0		0.2	0	0		0	0	0	0	0	0	0.5	0.5	0.5	0.5	1	0.2
NBRL003	Diptera?	NBRL 003 photo 01 - 02																									
NBRL004	Orthoptera	NBRL 004 photo 01 - 03	DV	N/A	E	0.5	0.4	0.5	0	0		0.2	0	0		0.4	0	0.6	0.4	0.6	0.6	0	0	0	0	0	0.4
NBRL005	Orthoptera	NBRL 005 photo 01 - 03	DV	N/A	E	1	0.2	0.5	0	0		0.2	0	0		0.6	0.6	0.6	0.8	1	1	0	0	0	0	0	0.4
NBRL006	Diptera	NBRL 006 photo 01 - 03	DV	R	M	0.5	0		0	0		0.6	0	0		1	0	0	0	0	0	1	1			0.5	0.6
NBRL007	Blattodea	NBRL 007 photo 01 - 03	DV																								
NBRL008	Orth/Blatt	NBRL 008 photo 01 - 04	DV																								
NBRL009	Indet.	NBRL 009 photo 01 - 03	DV																								
NBRL010	Possible Blatt.	NBRL 010 photo 01 - 04	N/A																								
NBRL011	Cicadomorpha?	NBRL 011 photo 01 - 04	L?																								
NBRL012	Hymenoptera	NBRL 012 photo 01 - 05	L																								
NBRL013	Indet.	NBRL 013 photo 01 - 06	N/A																								
NBRL014	Indet.	NBRL 014 photo 02 - 03	L																								
NBRL015	Coleoptera/Hemi	NBRL 015 photo 01 - 05	DV																								
	Orthoptera	NBRL 017 photo 01 - 04	DV																								
NBRL017	Blattodea	NBRL 018 photo 01 - 23	DV	M	U																						
NBRL018	Cicadomorpha?	NBRL 019 photo 01 - 03	DV	M	N/A	1	0	1	1	1	0.5	1	1	1	1	0.2	0.4	0.2	0.4	0.4	0.2	0.5	1				1
NBRL019	Orthoptera	NBRL 020 photo 01 - 04	L	R	E	0.5	0.2	0.5	0.5	0		0.8	0.5	0		0	0	0	0	0	0	0.5	0.5	0.5	0.5	0.5	0.8
NBRL020	Blattodea	NBRL 021 photo 01	PA	M	M	1	0	1	0.5	1	0.5	0.6	1	0.5	0	0.6	1	0.6	0	0	1	1	1			0	0.8

NBRL021	Blattodea	NBRL 022 photo 01	DV	E	E	0	0.6	0	0	0		0.4	0.5	0		1	1	1	1	0	0	0.5	1			1	0
NBRL022	Blattodea	NBRL 023 photo 01 - 05	DV	E	M	1	0	0.5				1				0.4	0	0.4	0	0	0	0	0.5	0.5	0.5	0	1
NBRL023	Blattodea	NBRL 024 photo 01	DV	M	N/A	0.5	0	0.5	0.5	0		0.8	0	0		0.2	0.2	0.2	0.4	0.2	1	0.5	0.5			0.5	0.6
NBRL024	Blattodea	NBRL 025 photo 01	DV	M	N/A	1	0	1	1			0.8	0.5	0.5	0.5	0	0	0	0	0	0	0.5	1	0.5	0.5	0	1
NBRL025	Blattodea	NBRL 026 photo 01 - 04	DV	E	E	1	1	1		1	1	1	0.5	0.5	0	0	0	0	0	0	0	1	1	1	1	0.5	1
NBRL026	Cicadomorpha?	NBRL 027 photo 01	DV	R	U	1	0	0.5	0	0.5	0	1	0	0.5	0	0.4	1	1	1	1	1	0.5	0.5			0.5	0.6
NBRL027	Blattodea	NBRL 028 photo 01	DV	M	N/A	1	0	1	1	1	1	1	1	1	1	0.2	0.2	0.2	0.2	0.6	0.6	1	1	1	1	1	0.8
NBRL028	Cicadomorpha?	NBRL 029 photo 01	DV	R	N/A	0.5	0	0.5	0	0		0.6	0.5	0.5	0	0	0	0	0	0	0	1	1	0	0.5	0	0.6
NBRL029	Blattodea	NBRL 030 photo 01	DV	M	N/A	1	0	0.5	1	1	0.5	0.6	0	0.5	0	0	0	0	0	0	0	1	1	1	1	1	0.8
NBRL030	Blattodea	NBRL 031 photo 01 - 02	DV	R	N/A	1	0.8	0.5	0.5	0.5	0	0.2	0	0	0	0	0	0	0	0	0	1	0.5			0.5	0.6
NBRL031	Blattodea	NBRL 032 photo 01 - 02	DV	E	E	1	0	1	0.5	1	0.5	0.6	0.5	0.5	0	0	0	0	0	0	1	0	1			0.5	1
NBRL032	Culicidae?	NBRL 033 photo 01	PA?	E	E	1	0.8	1	1	1	1	0.8	1	1	1	0	0	0	0	1	1	0.5	1			0.5	0.8
NBRL033	Blattodea	NBRL 034 photo 01	DV	R	E		0		0	0.5	0	0.8	0	0.5	0	0.8	0.8	0	0	1	0.6	0.5	1			0	0.8
NBRL034	Blattodea	NBRL 035 photo 01	DV	R	U	0.5	0.8	0.5	0	0.5	0	1	0.5	1	0.5	0	0	0	0.6	1	1	0.5	0			0.5	1
NBRL035	Blattodea	NBRL 036 photo 01	DV	E	U?	1	0.6	1				0.8				0.4	0.4	0	0	0	0.4	0.5	1			0	1
NBRL036	Blattodea	NBRL 037 photo 01 - 02	L	R	U	1	0	1				0.8	0.5	0.5		0	0	0	0	0	0	0.5	0.5	0.5	0.5	0	0.6
NBRL037	Blattodea	NBRL 038 photo 01	DV	N/A	N/A	1	0.2	1	1	2	1	0.8	1	1	1	1	0	1	1	1	0	0.5	0			0.5	1
NBRL038	Indet.	NBRL 039 photo 01	DV	M	U	0	0	0	0	1		0	0	0		0	0	0	0	0	0	0	0			0	1
NBRL039	Blattodea	NBRL 040 photo 01	DV	E	E	0.5	0	0.5	0.5	0.5	0.5	0.8	1	0.5	1	0.2	0.4	1	0.4	0.8	1	0.5	0.5			0.5	0.6
NBRL040	Diptera	NBRL 041 photo 01 - 02	DV	E	N/A	0.5	0	0.5	0	0.5	0.5	0.6	0	0.5	0	0.4	0	0.6	0	0	0	0.5	0.5			0.5	0.8
NBRL041	Achilidae?	NBRL 042 photo 01	L	N/A	U	1	0.6	0.5	0	0.5	0	0.8	1	1	0.5	0	0	0	0	0	0	1	1	1	1	1	1
NBRL042	Orthoptera?	NBRL 043 photo 01 - 02	DV	R	E	1	0	1	1	0.5	0	1	1	1	1	0.6	0.8	0.6	0.6	0.6	0.8					0	0.8
NBRL043	Orthoptera	NBRL 044 photo 01	L	R	M	1	0	0.5	0.5	1	0.5	1	0	1	0	0.4	0.6	0.4	0.6	0.6	0.6	0	0	0	0	0	0.8
NBRL044	Coleoptera?	NBRL 045 photo 01	DV	E	N/A	1	0.8	1	1	1	1	1	1	1	1	0.2	0	1	0.8	1	1	1	0.5			1	1
NBRL045	Blattodea	Rsn Tst 01 -29	L	R?	U	1	0.8	1	1	0.5	0.5	0.8	0.5	0.5	0	0	0	0	0	0	0			1	1	0.75	0.8
TEST SPECIMEN	Blattodea?					0.5	1	0.5	1	1	1	1	1	1	1	0	0	1	0.8	1	1	1	1				1
NBRL046	Orthoptera?																										
NBRL047	Coleoptera																										
NBRL048	Blattodea	FLO33 01- 11	DV	E	N/A																						
FLO33	Orthoptera					1	0	0.5	0	0.5	0.5	0.6	0	0.5	0	0	0.4	0	0	0	0	1	1	1	1	1	0.6

NBRL049	Orthoptera?																									
NBRL050	Orthoptera	NBRL 051 photo 01-05	L	R	U																					
NBRL051	Hemiptera?					1	1	1	1	1	1	1	1	1		0.4	0.4	0	0	1	1	1	1			0.5	1
NBRL052	Neuroptera																									
NBRL053	Blattodea	NBRL 054 photo 01-05	L	R	U																					
NBRL054	Orthoptera	NBRL 055 photo 01-02	DV	N/A	E	0.5	0.8	1	0.5	0.5	1	1	1	1	1	0.8	0.8	0.4	0.4	1	1	1	1				1
NBRL055	Orthoptera?					1	0	0.5	1	1	1					1	1	1	1	1	1						1
NBRL056	Diptera: Tabanid																									
NBRL057	Odonata																									
NBRL058	Orthoptera	NBRL059 photo 01 - 06	DV	N/A	E?																					
NBRL059	Odonata	NBRL060 photo 01 - 05	DV	N/A	N/A	0.5	0	0.75	0.5	1	0.5	0.8	0.5	1	0.5	0	0	0	0	0.6	0.8	0	0			0	0.8
NBRL060	Orthoptera	NBRL061 photo 01 - 08	L	E?	U	1		0.5	0.5	1	0	0.6	0	0.5	1												0.8
NBRL061	Orthoptera	NBRL062 photo 01 - 05	L	R	U	1	0	1	1	1	1	0.8	1	1	0.75	0.2	0	0.8	0.8	1	0.6	0.5	0.5			0	1
NBRL062	Orthoptera?	NBRL063 photo 01 - 12	DV	N/A	E	1	0.2	1	1	1	0.5	0.4	1	0.5	0	0.4	0.4	0	0	1	0.8	1	0			1	0.6
NBRL063	Orthoptera?					0.5	0.2	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0.5	1	0.6	0.8	0.7	0.8	0.8	0.5	0			0	0.8
NBRL064	Orthopt/Blatt?	NBRL065 photo 01 - 27	L	N/A	U																					
NBRL065	Orthoptera	NBRL066 photo 01 - 09	DV	R	M?	1	0.6	0.75	1	1	1	0.6	1	0.75	1	0	0	0.4	0.6	1	0.6	0	0			0.5	0.8
NBRL066	Orthoptera					0.5	0	1	1	1	1	1	1	1	0.5	0.4	0.2	0.2	0	0.6	0.8	0.5	0.5			0.5	0.8
NBRL067	Orthoptera	NBRL068 photo 01 - 17	L	R	E																					
NBRL068	Orthoptera	NBRL069 photo 01 - 12	DV	N/A	E	0.5	0.7	1	1	0.5	1	0.8	1	1	0.5	0.6	0.2	0.2	0	1	1	0.5	0			0.5	0.6
NBRL069	Orthoptera	NBRL070 photo 01 - 23	L	N/A	E	1	0	0.5	1	1	1	0.8	1	0.5	0.5	0.4	0.4	0.4	0.2	0.6	0.2	0	0			0	0.8
NBRL070	Blattodea?	NBRL071 photo 01 - 11	DV	M	E?	0.5	0.6	0	0	0		1	1	0.5	0.5	0	0	0.6	0.6	0	0	0	0			0	1
NBRL071	Orthopt/Blatt?	USING SEM TRANSFER	DV	N/A	E	0.5	0	0.5	1	1	1	0.8	1	1	0.5	0.4	0	0	0	0	0	0.5	0.5			0.5	0.6
NBRL072	Raphidioptera	NBRL073 photo 01 - 05	DV	M	N/A	0.5	0	1	0	0.25	0.5	0.2	0	0	0	0.4	0.2	0.4	0.6	0.8	0.8						0
NBRL073	Orthoptera	NBRL074 photo 01 - 14	L	R	U	0.5	0	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0	0	0	0	0	0	0	0.5	0.5			0.5	0.2
NBRL074	Indet.	NBRL075 photo 01 - 09	DV	R	N/A	1	0.6	0	1	1	1	1	1	1	1	0	0	0	0	1	0.6	0	0.5			0.5	0.8
NBRL075	Indet.	NBRL076 photo 01 - 05	L	E	N/A	0	0	0	0	0		0.8	1	1	1	0	0	0	0	0	0	0	0.5			0	0
NBRL076	Blattodea?	NBRL077 photo 01 - 05	DV	R	E	1	0	1	0.5	0.5	0.5	0	0	0		0	0	0	0	0	0	1	1	1	0.5	1	0.6

NBRL077	Blattodea	NBRL078 photo 01 - 02	DV	E	E?	0.5	0	0.5	0.5	0.5	1	0.8	0	1	0	0	0.4	0	0	0	0.6	1	1	0.5	1	1	0.8
NBRL078	Neuroptera	NBRL079 photo 01 - 03	L	E	N/A	0.5	0	0.5	0.5	0.25	0.5	0.8	0.5	0.5	0.5	0	0	0	0	0	0.6	0	0.5			0.5	0.8
NBRL079	Indet.	NBRL080 photo 01 - 05	DV	R	E	0.5	0	0	0.5	0.5	0.5	1	1	1	0.5	0.4	0	0.6	0	0.4	0	1	1	1	0.5	1	0.8
NBRL080	Hemiptera	NBRL081 photo 01 - 06	L	R	U	0	0	0	0	0		0.4	0.5	0.5	0	0	0	0	0	0	1	1	1	1	1		0
NBRL081	Blattodea	NBRL082 photo 01 - 06	DV	M	N/A	1	0	1	1	1	1	0.6	1	1	0.5	0	1	0	0.6	0	1	1	1			1	0.8
NBRL082	Ephemeroptera	FLO13 photo 01 - 06	DV	N/A	U	0	0	0	0	0		0.8	1	1	0.5	0	0	0	0.2	0	0.2	0.5	1	0.5	0.5	0.5	0.4
FLO13	Hemiptera	FLO27 photo 01 - 05	L	R	U	1		0.5	1	1	1	1	1	1	1	0.2	0.4	0	0.4	0	0.6						0.8
FLO27	Diptera	FLO28 photo 01 - 05	DV	E	N/A	1	0	1	1	1	1	1	1	1	1	1	1	0.8	0.6	1	1	1	1			1	1
FLO28	Blattodea	FLO35 photo 01 - 08	DV	M	M	1	0.6	0.75	0.5	1	0.5	0.8	1	1	0.5	0	0	0	0	0	0	0.5	1			0.5	1
FLO35	Hemiptera	FLO64 photo 01 - 06	L	R	U	1	1					0.8	1	1	0.5	0	0	1	0	1	1	1	1	1	1	1	0
FLO64						1		1	1	1	0.5	1	1	1	0.5	0.8	1	0.8	0.8	1	0.8	1	1			0.75	0.6

Table continued:

Specimen No.	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	No. Char.	Calc.	Index
NBRL002	0	0		0	0				0	0	0	0		0	0.66			0	0	0	0	34	0.163529	0.1635
NBRL003																								
NBRL004	0	0	0	0.5	0.2	0.2	0.2		0	0	0	0.33		0	0.33	0		0	0	0.25	0	38	0.178649	0.1787
NBRL005	0	0		0.5	0.2	0.6	0.6		0	0	0	0		0	0.33	0		0.25	0	0	0.25	37	0.26027	0.2603
NBRL006	0	0			0				0	0	0	0			0	0		0.25	0.25	0	0.25	30	0.198333	0.1983
NBRL007 to NBRL017 are blank (removed)																								
NBRL018	1	1	1	1	1	1	1		0	0	0.33	0	1	1	1	0.66	1	0.25	0.75	0.75	0	39	0.680513	0.6805
NBRL019	0.5	0.5	0.33	0	0	0	0.8		0	0	0	0		0	0	0	0	0.25	0.5	0.25	0	39	0.241795	0.2418
NBRL020	1	0.5	0.66	1	0.8				0.66	0.33	0	1		1	0.66	0.33	0.66		0.25	0.5	0.25	36	0.602778	0.6028
NBRL021	0	0			0	0	0		0	0	0	1			0.15	0.33	0	0	0	0	0.5	34	0.293529	0.2935
NBRL022				1	1	0	1		0	0.33	1	0.33		1	0.66	0.33		0.5	0.75	0.75	0	31	0.466129	0.4661
NBRL023	0	0		0.5		0	0		0	0	0	0		0	0.66	0.66	0.66	0.25	0.5	0.25	0	35	0.288	0.288
NBRL024	0.5	0		1	0.6	0	0		0	0	0.33	1	0	1	1		0.66	1	0.75	0.25	0	38	0.444474	0.4445

NBRL025	0.5	0.5	0.33	0.5	0	0	0		0	0	0	0		0	0.66	0.33	0.66	0.5	0.25	0.25	0	40	0.4245	0.4245
NBRL026	0	0.5	0.33	0.5		0.6	0.6		0	0	0	0		0	0.33	0		0.5		0.25	0.5	36	0.419722	0.4197
NBRL027	1	1	0.66	0.5		0.8	0.8		0	0	0	0	0	0	0.8	0.66	0.66	0.75	0.75	0.5	0	41	0.626341	0.6263
NBRL028	0	0.5	0.33	0.5	0.2	0	0		0	0	0	0	0	0	0	0	0	0	0.25	0.25	0	41	0.188537	0.1885
NBRL029	0.5	0.5	0.66	1		0.6	0.6		0	0	0	0		0	0.66	0.66	0.33	0.75	0.5	0.5	0	40	0.454	0.454
NBRL030	0	0.5	0.66	0	0	0.8	0.8		0	0	0	0	0	0	0.33	0.33	0	0.5	0	0.25	0	40	0.25675	0.2568
NBRL031	1	1	0.66	0.5	0				0	0	0		1	1	0.33	0.33	0	0.75	0.25	0.75	0	37	0.450541	0.4505
NBRL032	1	1	1	0.5		0.8	0.8								0.66	0.33	0	0.5	0.5	0.25	0.75	33	0.681515	0.6815
NBRL033	0	0.5	0.33	1					0	0	0	0	0	0	0	0	0	0	0	0	0	35	0.260857	0.2609
NBRL034	1	1	1	1		0.8	0.6		0.33	0.33	0.33	0.33	0.33	0.33	0.66	0.33		0.25	0.5	0.75	0.5	38	0.533421	0.5334
NBRL035	1	1	0.8			0.6	0								1	0.66	0.8	1		0.5	?	25	0.5144	0.5144
NBRL036	0	0.5	0.33	0	0	0.2	0.2		0	0	0	0		0	0.33	0	0.33	0.5	0.25	0.25	0	37	0.251081	0.2511
NBRL037	1	1	1	1	0.8	1	1		0		0	0		0	0.66	0.66	0.66	1	0.25	0.25	1	38	0.717895	0.7178
NBRL038	1	1	1	1		1	1		0	0	1	0			1	1	0.66	0	0	0.25	0	35	0.340286	0.3403
NBRL039	0.5	0.5	0.66	0		0	0								0.33	0.66	0	0.5	0.5	0.5	0.75	33	0.50303	0.503
NBRL040	0.5	1	1	1		0.6	0.6	0.8	0	0.33	0.66	0		0.66	0.33	0.33	0.33	0.25	0.5	0.5	0	39	0.404872	0.4049
NBRL041	0.5	1	0.33	1					0	0	0	0	0	0	0.33	0.33	0	0.5	0.5	0.25	0	39	0.426667	0.4267
NBRL042	1	1	1	0.5	0										0.66	0.66	0.66	0.5	0.25	0.75	0.25	30	0.651	0.651
NBRL043	0	1	0.33		0	0	0		0	0	0	0		0	0.33	0	0	0.5	0	0	0.5	40	0.304	0.304
NBRL044	1	1	1		0.8	0	0		0					0	1	0.66	0.66	1	0.75	0.75	0.75	35	0.762	0.762

NBRL045	0.5	1	0.66	1	0.8				0	0	1	0.33	1	1	0.66	0.33	0.33	1	0.5	0.5	0	38	0.526579	0.5266
TEST SPECIMEN	1	1	1			1			0	0	0	0	1	0.66	1	1	1	1	1	1	1	36	0.790556	0.7906
NBRL046																								
NBRL047																								
NBRL048																								
FLO33	0	0.5	0.33	1	0.6	0.4	0.8		0	0	0	0	0	0	0	0	0	0.5	0.25	0.25	0	42	0.33881	0.3388
NBRL049																								
NBRL050																								
NBRL051	1	1		1	1				1	1	1	1	1	0.66	1	0.66	1	0.88	0.88	0.88	0.75	36	0.788056	0.7881
NBRL052																								
NBRL053																								
NBRL054	1	1	1	1	1	0	1		0	0	1	0.66	1	0.33	1	1	1	0.75	1	1	0.5	39	0.793333	0.7933
NBRL055	1	1	1	1	0.2				1	0	1	1		0.33	1	1	1	0.25		1	1	29	0.837241	0.8372
NBRL056																								
NBRL057																								
NBRL058																								
NBRL059	1	0.5	0.33	1	0.8	0.8	0.8		0	0	1	1	0	0.66	0.66	0.33	0.33	0.25	0.25	0.25	0.25	40	0.44275	0.4428
NBRL060	0.5	1	0.66	1				0.8							0.66	0.66	0.33	0.5	0.25	0.75	1	22	0.636818	0.6368
NBRL061	1	1	1	1	0.8	0.8	0.8		0	0	0	0		0	1	1	0.66	1	0.5	0.5	0.75	39	0.641282	0.6413
NBRL062	1	0.5	0.66	1					0	0	0	0		0	0.66	0.33	0.66	0.25	0.25	0.25	0.5	36	0.496111	0.4961
NBRL063	0.5	1	1	1	0.4	0	0								0.66	0.45	0.33	0.5	0.25	0.5	0.5	34	0.486471	0.4865
NBRL064																								
NBRL065	1	1	1	1	1	0	0		0.33	0.33	0.33	0.33	1	0.66	0.8	1	0.45	0.75	0.25	0.25	0.5	40	0.557	0.557
NBRL066	0.5	1	0.66	0.5	0	0	0		0	0	0	0		0	0.66	0.66	0.33	0.5	0.5	0.5	0	39	0.469487	0.4694
NBRL067																								

NBRL068	0.5	1	0.33	1	0.8	1	0.8		0	0	0.33	0		1	0.66	0.66	0.33	0.25	0.25	0.5	0.5	39	0.559231	0.5592
NBRL069	0.25	1	0.66	0.5	0.8	1	0.8		0	0	0	0	0	0	0.66	0.66	0.33	0.5	0.5	0.5	0.5	40	0.474	0.474
NBRL070	1	1	0.66	0.5					0	0	0	0		0	0.66	0.33	0	0.25	0.5	0.25	0	35	0.327143	0.3271
NBRL071	0.5	0.5	1	0.5		0	0		0	0	0	0		0	0.66	0.33	0.33	0.25	0.5	0.25	0	38	0.384737	0.3847
NBRL072	0	0	0	0		0	0		0	0	0	0		0	1	1		0.25	0	0	0.5	34	0.247059	0.2471
NBRL073	0	0	0	0		0	0		0	0	0	0		0	1	0.66		0.75	0	0	0	37	0.216486	0.2165
NBRL074	0.5	0.5	0.66	1		0	0		0	0	0	0		0	0.66	0.66	1	0.25	0.5	0.75	0.75	38	0.506053	0.5061
NBRL075	0	0	0	0		0	0		0	0	0	0		0	0.66	0.66	0.33	0	0.25	0	0	37	0.167568	0.1676
NBRL076	0	0.5	0.33	0					0		0	0		0	0.33	0.33	0	0.5	0	0.25	0	36	0.301111	0.3011
NBRL077	0.5	1	0.66	1					0	0	0	0		0	0.66	0.33	0.33	0.75	0.5	0.25	0.25	38	0.456053	0.4561
NBRL078	0.5	1	0.825	0.5		0.8	0.6		0	0	0	0	0	0	0.33	0		0	0.25	0.5	0.25	38	0.329079	0.3291
NBRL079	0	1	0.33	0.5					0	0	0	0		0	0.66	0.33	0	0	0.5	0	0.25	38	0.415	0.415
NBRL080	0	0	0	0	0				0	0	0	0.15		0	0.66	0.33	0.33	0	0.75	0	1	37	0.26	0.26
NBRL081	0.5	0.5	0.66	0.5					0.33	0	0	0.33		0	1	0.66	0.66	0.25	0.25	0.25	0.5	36	0.580278	0.5803
NBRL082	1	1	1	0		1	0								1	0.66	0	0	0.5	0.25	0	34	0.397353	0.3974
FLO13	1	1	1	0				0.8							0.66	0.33	0	0.25	0.25	0.75	0.25	28	0.613929	0.6139
FLO27	1	1	1	1					0	0	0	0		0	1	0.66	0.8	0.75	0.75	0.25	1	36	0.766944	0.7669
FLO28	1	1	1	1	0.8				0	0	0	0		0	1	0.33	1	0.25	0.5	0.75	0	37	0.521081	0.5211
FLO35	0	0	0	0		0	0			0	0	0		0	0.66	0.33	0		0.25	0	0.87	34	0.453235	0.4532
FLO64	0.5	1	0.66	0	0				0	0	0	0		0	1	0.66	0.33	0.5	0.5	0.5	0.75	36	0.6375	0.6375

Table 8b. Quantification of completeness characters only. Gaps represent characters that were not taxonomically present (i.e. wings on a larval form), were obscured from view (not clearly absent), or required SEM viewing (and the specimen had not been mounted for SEM viewing). These characters are excluded from determining the final taxonomic index, rather than counting negatively towards total preservation as they could not be measured. Specimens that are entirely blank could not be studied at all, usually as a result from specimen destruction through preparation problems/errors. A total of 64 specimens were taphonomically quantifiable.

Keys:

Head:

Head (A)	Antennae (B)	Eyes (C)	Internal Architecture (D)	Soft Tissues (E)	Soft Tissue Quality (F)
2 = Present (I=1)	5 = Complete (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)
1 = Partial (I=0.5)	4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.5)
0 = Absent (I=0)	3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0)
N/A = Cannot see	2 = 50-25% (I=0.4)	N/A = Cannot see	N/A = Cannot see	N/A = Cannot see	N/A = None Present
	1 = <25% (I=0.2)				
	0 = Absent/Cannot see (I=0)				

Thorax:

% of Sclerites Present (G)	Internal Architecture (H)	Soft Tissues (I)	Soft Tissue Quality (J)
5 = Complete (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)
4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.5)
3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0)
2 = 50-25% (I=0.4)	N/A = Cannot see	N/A = Cannot see	N/A = None Present
1 = <25% (I=0.2)			
0 = Absent/Cannot see (I=0)			

Orientation	Wing Positions	Leg Position
DV = Dorso-ventral	R = Rest	U = Under Body
L = Lateral	M = Mixed	M = Mixed
PA = Postero-anteri	E = Extended	E = Extended
N/A	N/A	N/A

Limbs:	Matching part, or equivalent number				
Fore left (K)	Fore Right (L)	Mid Left (M)	Mid Right (N)	Hind Left (O)	Hind Right (P)

5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)	5 = Full limb (I=1)
4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)	4 = Up to Tibia (I=0.8)
3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)	3 = Up to Femur (I=0.6)
2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)	2 = Up to Trochanter (I=0.4)
1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)	1 = Coxa only (I=0.2)
0 = Lost/Cannot See (I=0)	0 = Lost/Cannot See (I=0)	0 = Lost/Cannot See (I=0)	0 = Lost/Cannot See (I=0)	0 = Lost/Cannot See (I=0)	0 = Lost/Cannot See (I=0)

Wings:

Fore Wing Left (Q)	Fore Wing Right (R)	Hind Wing Left (S)	Hind Wing Right (T)	Wing Venation (U)
2 = Present (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Present (I=1)	2 = Clear (I=1)
1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (<75%) (I=0.5)	1 = Partial (I=0.5)
0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)	0 = Absent (I=0)
N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present	N/A = Taxonomically not present

Abdomen:

% of Sclerites Present (V)	Internal Architecture (W)	Soft Tissues (X)	Soft Tissue Quality (Y)	Genital/Anal Opening (Z)
5 = Complete (I=1)	2 = Present (I=1)	2 = Extensive (I=1)	3 = Well (I=1)	2 = Present (I=1)
4 = 99-75% (I=0.8)	1 = Partial (I=0.5)	1 = Patchy (I=0.5)	2 = Moderate (I=0.66)	1 = Partial (I=0.5)
3 = 75-50% (I=0.6)	0 = Absent (I=0)	0 = Absent (I=0)	1 = Poor (I=0.33)	0 = Absent (I=0)
2 = 50-25% (I=0.4)	N/A = Cannot see	N/A = Cannot see	0 = None Present (I=0)	N/A = Cannot see
1 = <25% (I=0.2)				
0 = Absent/Cannot see (I=0)				

Abdominal Appendages:

Ovipositor/Stinger (AA)	Left Cerci (AB)	Right Cerci (AC)	Other: _____ (AD)
5 = Complete (I=1)	5 = Complete (I=1)	5 = Complete (I=1)	5 = Complete (I=1)
4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)	4 = 99-75% (I=0.8)
3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)	3 = 75-50% (I=0.6)
2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)	2 = 50-25% (I=0.4)
1 = <25% (I=0.2)	1 = <25% (I=0.2)	1 = <25% (I=0.2)	1 = <25% (I=0.2)
0 = Absent/Cannot see (I=0)	0 = Absent/Cannot see (I=0)	0 = Absent/Cannot see (I=0)	0 = Absent/Cannot see (I=0)

Bristles/Hairs: SEM Images required

Hairs on Head (AE)	Hairs on Thorax (AF)	Hairs on Abdomen (AG)	Hairs on limbs (AH)	Hairs on Other (AI)	Individual Hairs (AJ)
3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Extensive (I=1)	3 = Mostly Intact (I=1)
2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Patchy (I=0.66)	2 = Mostly Broken (I=0.66)
1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Few (I=0.33)	1 = Mostly Destroyed (I=0.33)
0 = None/Cannot see (I=0)	0 = None/Cannot see (I=0)	0 = None/Cannot see (I=0)	0 = None/Cannot see (I=0)	0 = None/Cannot see (I=0)	0 = None preserved at all (I=0)
				N/A = No 'other'	

Table:

Specimen No.	Order	Photos	Orientation	Wing Positions	Leg Position	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
NBRL002	Odonata	NBRL 002 photo 01 - 04	DV	E	N/A	1	0	0	0.5	0		0.2	0	0		0	0	0	0	0	0	0.5
NBRL003	Diptera?	NBRL 003 photo 01 - 02																				
NBRL004	Orthoptera	NBRL 004 photo 01 - 03	DV	N/A	E	0.5	0.4	0.5	0	0		0.2	0	0		0.4	0	0.6	0.4	0.6	0.6	0
NBRL005	Orthoptera	NBRL 005 photo 01 - 03	DV	N/A	E	1	0.2	0.5	0	0		0.2	0	0		0.6	0.6	0.6	0.8	1	1	0
NBRL006	Diptera	NBRL 006 photo 01 - 03	DV	R	M	0.5	0		0	0		0.6	0	0		1	0	0	0	0	0	1
NBRL007	Blattodea	NBRL 007 photo 01 - 03	DV																			

NBRL008	Orth/Blatt	NBRL 008 photo 01 - 04	DV																			
NBRL009	Indet.	NBRL 009 photo 01 - 03	DV																			
NBRL010	Possible Blatt.	NBRL 010 photo 01 - 04	N/A																			
NBRL011	Cicadomorpha?	NBRL 011 photo 01 - 04	L?																			
NBRL012	Hymenoptera	NBRL 012 photo 01 - 05	L																			
NBRL013	Indet.	NBRL 013 photo 01 - 06	N/A																			
NBRL014	Indet.	NBRL 014 photo 02 - 03	L																			
NBRL015	Coleoptera/Hemi	NBRL 015 photo 01 - 05	DV																			
NBRL017	Orthoptera	NBRL 017 photo 01 - 04	DV																			
NBRL018	Blattodea	NBRL 018 photo 01 - 23	DV	M	U	1	0	1	1	1	0.5	1	1	1	1	0.2	0.4	0.2	0.4	0.4	0.2	0.5
NBRL019	Cicadomorpha?	NBRL 019 photo 01 - 03	DV	M	N/A	0.5	0.2	0.5	0.5	0		0.8	0.5	0		0	0	0	0	0	0	0.5
NBRL020	Orthoptera	NBRL 020 photo 01 - 04	L	R	E	1	0	1	0.5	1	0.5	0.6	1	0.5	0	0.6	1	0.6	0	0	1	1
NBRL021	Blattodea	NBRL 021 photo 01	PA	M	M	0	0.6	0	0	0		0.4	0.5	0		1	1	1	1	0	0	0.5
NBRL022	Blattodea	NBRL 022 photo 01	DV	E	E	1	0	0.5				1				0.4	0	0.4	0	0	0	0
NBRL023	Blattodea	NBRL 023 photo 01 - 05	DV	E	M	0.5	0	0.5	0.5	0		0.8	0	0		0.2	0.2	0.2	0.4	0.2	1	0.5
NBRL024	Blattodea	NBRL 024 photo 01	DV	M	N/A	1	0	1	1			0.8	0.5	0.5	0.5	0	0	0	0	0	0	0.5
NBRL025	Blattodea	NBRL 025 photo 01	DV	M	N/A	1	1	1		1	1	1	0.5	0.5	0	0	0	0	0	0	0	1
NBRL026	Blattodea	NBRL 026 photo 01 - 04	DV	E	E	1	0	0.5	0	0.5	0	1	0	0.5	0	0.4	1	1	1	1	1	0.5
NBRL027	Cicadomorpha?	NBRL 027 photo 01	DV	R	U	1	0	1	1	1	1	1	1	1	1	0.2	0.2	0.2	0.2	0.6	0.6	1
NBRL028	Blattodea	NBRL 028 photo 01	DV	M	N/A	0.5	0	0.5	0	0		0.6	0.5	0.5	0	0	0	0	0	0	0	1
NBRL029	Cicadomorpha?	NBRL 029 photo 01	DV	R	N/A	1	0	0.5	1	1	0.5	0.6	0	0.5	0	0	0	0	0	0	0	1
NBRL030	Blattodea	NBRL 030 photo 01	DV	M	N/A	1	0.8	0.5	0.5	0.5	0	0.2	0	0	0	0	0	0	0	0	0	1
NBRL031	Blattodea	NBRL 031 photo 01 - 02	DV	R	N/A	1	0	1	0.5	1	0.5	0.6	0.5	0.5	0	0	0	0	0	0	1	0
NBRL032	Blattodea	NBRL 032 photo 01 - 02	DV	E	E	1	0.8	1	1	1	1	0.8	1	1	1	0	0	0	0	1	1	0.5
NBRL033	Culicidae?	NBRL 033 photo 01	PA?	E	E		0		0	0.5	0	0.8	0	0.5	0	0.8	0.8	0	0	1	0.6	0.5
NBRL034	Blattodea	NBRL 034 photo 01	DV	R	E	0.5	0.8	0.5	0	0.5	0	1	0.5	1	0.5	0	0	0	0.6	1	1	0.5
NBRL035	Blattodea	NBRL 035 photo 01	DV	R	U	1	0.6	1				0.8				0.4	0.4	0	0	0	0.4	0.5
NBRL036	Blattodea	NBRL 036 photo 01	DV	E	U?	1	0	1				0.8	0.5	0.5		0	0	0	0	0	0	0.5
NBRL037	Blattodea	NBRL 037 photo 01 - 02	L	R	U	1	0.2	1	1	2	1	0.8	1	1	1	1	0	1	1	1	0	0.5

NBRL038	Blattodea	NBRL 038 photo 01	DV	N/A	N/A	0	0	0	0	1		0	0	0		0	0	0	0	0	0	0
NBRL039	Indet.	NBRL 039 photo 01	DV	M	U	0.5	0	0.5	0.5	0.5	0.5	0.8	1	0.5	1	0.2	0.4	1	0.4	0.8	1	0.5
NBRL040	Blattodea	NBRL 040 photo 01	DV	E	E	0.5	0	0.5	0	0.5	0.5	0.6	0	0.5	0	0.4	0	0.6	0	0	0	0.5
NBRL041	Diptera	NBRL 041 photo 01 - 02	DV	E	N/A	1	0.6	0.5	0	0.5	0	0.8	1	1	0.5	0	0	0	0	0	0	1
NBRL042	Achilidae?	NBRL 042 photo 01	L	N/A	U	1	0	1	1	0.5	0	1	1	1	1	0.6	0.8	0.6	0.6	0.6	0.8	
NBRL043	Orthoptera?	NBRL 043 photo 01 - 02	DV	R	E	1	0	0.5	0.5	1	0.5	1	0	1	0	0.4	0.6	0.4	0.6	0.6	0.6	0
NBRL044	Orthoptera	NBRL 044 photo 01	L	R	M	1	0.8	1	1	1	1	1	1	1	1	0.2	0	1	0.8	1	1	1
NBRL045	Coleoptera?	NBRL 045 photo 01	DV	E	N/A	1	0.8	1	1	0.5	0.5	0.8	0.5	0.5	0	0	0	0	0	0	0	
TEST SPECIMEN	Blattodea	Rsn Tst 01 -29	L	R?	U	0.5	1	0.5	1	1	1	1	1	1	1	0	0	1	0.8	1	1	1
NBRL046	Blattodea?																					
NBRL047	Orthoptera?																					
NBRL048	Coleoptera																					
FLO33	Blattodea	FLO33 01- 11	DV	E	N/A	1	0	0.5	0	0.5	0.5	0.6	0	0.5	0	0	0.4	0	0	0	0	1
NBRL049	Orthoptera																					
NBRL050	Orthoptera?																					
NBRL051	Orthoptera	NBRL 051 photo 01-05	L	R	U	1	1	1	1	1	1	1	1	1		0.4	0.4	0	0	1	1	1
NBRL052	Hemiptera?																					
NBRL053	Neuroptera																					
NBRL054	Blattodea	NBRL 054 photo 01-05	L	R	U	0.5	0.8	1	0.5	0.5	1	1	1	1	1	0.8	0.8	0.4	0.4	1	1	1
NBRL055	Orthoptera	NBRL 055 photo 01-02	DV	N/A	E	1	0	0.5	1	1	1					1	1	1	1	1	1	
NBRL056	Orthoptera?																					
NBRL057	Diptera: Tabanid																					
NBRL058	Odonata																					
NBRL059	Orthoptera	NBRL059 photo 01 - 06	DV	N/A	E?	0.5	0	0.75	0.5	1	0.5	0.8	0.5	1	0.5	0	0	0	0	0.6	0.8	0
NBRL060	Odonata	NBRL060 photo 01 - 05	DV	N/A	N/A	1		0.5	0.5	1	0	0.6	0	0.5	1							
NBRL061	Orthoptera	NBRL061 photo 01 - 08	L	E?	U	1	0	1	1	1	1	0.8	1	1	0.75	0.2	0	0.8	0.8	1	0.6	0.5
NBRL062	Orthoptera	NBRL062 photo 01 - 05	L	R	U	1	0.2	1	1	1	0.5	0.4	1	0.5	0	0.4	0.4	0	0	1	0.8	1
NBRL063	Orthoptera?	NBRL063 photo 01 - 12	DV	N/A	E	0.5	0.2	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0.5	1	0.6	0.8	0.7	0.8	0.8	0.5
NBRL064	Orthoptera?																					
NBRL065	Orthopt/Blatt?	NBRL065 photo 01 - 27	L	N/A	U	1	0.6	0.75	1	1	1	0.6	1	0.75	1	0	0	0.4	0.6	1	0.6	0

NBRL066	Orthoptera	NBRL066 photo 01 - 09	DV	R	M?	0.5	0	1	1	1	1	1	1	1	0.5	0.4	0.2	0.2	0	0.6	0.8	0.5
NBRL067	Orthoptera																					
NBRL068	Orthoptera	NBRL068 photo 01 - 17	L	R	E	0.5	0.7	1	1	0.5	1	0.8	1	1	0.5	0.6	0.2	0.2	0	1	1	0.5
NBRL069	Orthoptera	NBRL069 photo 01 - 12	DV	N/A	E	1	0	0.5	1	1	1	0.8	1	0.5	0.5	0.4	0.4	0.4	0.2	0.6	0.2	0
NBRL070	Orthoptera	NBRL070 photo 01 - 23	L	N/A	E	0.5	0.6	0	0	0		1	1	0.5	0.5	0	0	0.6	0.6	0	0	0
NBRL071	Blattodea?	NBRL071 photo 01 - 11	DV	M	E?	0.5	0	0.5	1	1	1	0.8	1	1	0.5	0.4	0	0	0	0	0	0.5
NBRL072	Orthopt/Blatt?	USING SEM TRANSFER	DV	N/A	E	0.5	0	1	0	0.25	0.5	0.2	0	0	0	0.4	0.2	0.4	0.6	0.8	0.8	
NBRL073	Raphidioptera	NBRL073 photo 01 - 05	DV	M	N/A	0.5	0	0.5	0.5	0.5	0.5	0.4	0.5	0.5	0	0	0	0	0	0	0	0.5
NBRL074	Orthoptera	NBRL074 photo 01 - 14	L	R	U	1	0.6	0	1	1	1	1	1	1	1	0	0	0	0	1	0.6	0
NBRL075	Indet.	NBRL075 photo 01 - 09	DV	R	N/A	0	0	0	0	0		0.8	1	1	1	0	0	0	0	0	0	0
NBRL076	Indet.	NBRL076 photo 01 - 05	L	E	N/A	1	0	1	0.5	0.5	0.5	0	0	0		0	0	0	0	0	0	1
NBRL077	Blattodea?	NBRL077 photo 01 - 05	DV	R	E	0.5	0	0.5	0.5	0.5	1	0.8	0	1	0	0	0.4	0	0	0	0.6	1
NBRL078	Blattodea	NBRL078 photo 01 - 02	DV	E	E?	0.5	0	0.5	0.5	0.25	0.5	0.8	0.5	0.5	0.5	0	0	0	0	0	0.6	0
NBRL079	Neuroptera	NBRL079 photo 01 - 03	L	E	N/A	0.5	0	0	0.5	0.5	0.5	1	1	1	0.5	0.4	0	0.6	0	0.4	0	1
NBRL080	Indet.	NBRL080 photo 01 - 05	DV	R	E	0	0	0	0	0		0.4	0.5	0.5	0	0	0	0	0	0	1	1
NBRL081	Hemiptera	NBRL081 photo 01 - 06	L	R	U	1	0	1	1	1	1	0.6	1	1	0.5	0	1	0	0.6	0	1	1
NBRL082	Blattodea	NBRL082 photo 01 - 06	DV	M	N/A	0	0	0	0	0		0.8	1	1	0.5	0	0	0	0.2	0	0.2	0.5
FLO13	Ephemeroptera	FLO13 photo 01 - 06	DV	N/A	U	1		0.5	1	1	1	1	1	1	1	0.2	0.4	0	0.4	0	0.6	
FLO27	Hemiptera	FLO27 photo 01 - 05	L	R	U	1	0	1	1	1	1	1	1	1	1	1	1	0.8	0.6	1	1	1
FLO28	Diptera	FLO28 photo 01 - 05	DV	E	N/A	1	0.6	0.75	0.5	1	0.5	0.8	1	1	0.5	0	0	0	0	0	0	0.5
FLO35	Blattodea	FLO35 photo 01 - 08	DV	M	M	1	1					0.8	1	1	0.5	0	0	1	0	1	1	1
FLO64	Hemiptera	FLO64 photo 01 - 06	L	R	U	1		1	1	1	0.5	1	1	1	0.5	0.8	1	0.8	0.8	1	0.8	1

Table continued:

Specimen No.	R	S	T	U	V	W	X	Y	Z	AA	Ab	AC	AD	AE	AF	AG	AH	AI	AJ	No. Char.	Calc.	Index
NBRL002	0.5	0.5	0.5	1	0.2	0	0		0	0				0	0	0	0		0	7	0.168966	0.17
NBRL003																						

NBRL004	0	0	0	0	0.4	0	0	0	0.5	0.2	0.2	0.2		0	0	0	0.33		0	4	0.188438	0.19
NBRL005	0	0	0	0	0.4	0	0		0.5	0.2	0.6	0.6		0	0	0	0		0	5	0.283871	0.28
NBRL006	1			0.5	0.6	0	0			0				0	0	0	0			12	0.216667	0.21
NBRL007 to NBRL017 are blank (removed)																						
NBRL018	1				1	1	1	1	1	1	1	1		0	0	0.33	0	1	1	4	0.691563	0.69
NBRL019	0.5	0.5	0.5	0.5	0.8	0.5	0.5	0.33	0	0	0	0.8		0	0	0	0		0	4	0.263438	0.26
NBRL020	1			0	0.8	1	0.5	0.66	1	0.8				0.66	0.33	0	1		1	6	0.635	0.64
NBRL021	1			1	0	0	0			0	0	0		0	0	0	1			9	0.333333	0.33
NBRL022	0.5	0.5	0.5	0	1				1	1	0	1		0	0.33	1	0.33		1	11	0.4584	0.46
NBRL023	0.5			0.5	0.6	0	0		0.5		0	0		0	0	0	0		0	8	0.253571	0.25
NBRL024	1	0.5	0.5	0	1	0.5	0		1	0.6	0	0		0	0	0.33	1	0	1	4	0.413438	0.41
NBRL025	1	1	1	0.5	1	0.5	0.5	0.33	0.5	0	0	0		0	0	0	0		0	3	0.434242	0.43
NBRL026	0.5			0.5	0.6	0	0.5	0.33	0.5		0.6	0.6		0	0	0	0		0	5	0.436452	0.44
NBRL027	1	1	1	1	0.8	1	1	0.66	0.5		0.8	0.8		0	0	0	0	0	0	2	0.634118	0.63
NBRL028	1	0	0.5	0	0.6	0	0.5	0.33	0.5	0.2	0	0		0	0	0	0	0	0	2	0.212647	0.21
NBRL029	1	1	1	1	0.8	0.5	0.5	0.66	1		0.6	0.6		0	0	0	0		0	3	0.447273	0.45
NBRL030	0.5			0.5	0.6	0	0.5	0.66	0	0	0.8	0.8		0	0	0	0	0	0	3	0.268485	0.27
NBRL031	1			0.5	1	1	1	0.66	0.5	0				0	0	0		1	1	6	0.475333	0.48
NBRL032	1			0.5	0.8	1	1	1	0.5		0.8	0.8								10	0.75	0.75
NBRL033	1			0	0.8	0	0.5	0.33	1					0	0	0	0	0	0	8	0.326071	0.33
NBRL034	0			0.5	1	1	1	1	1		0.8	0.6		0.33	0.33	0.33	0.33	0.33	0.33	4	0.54	0.54
NBRL035	1			0	1	1	1	0.8			0.6	0								17	0.510526	0.51
NBRL036	0.5	0.5	0.5	0	0.6	0	0.5	0.33	0	0	0.2	0.2		0	0	0	0		0	6	0.254333	0.25
NBRL037	0			0.5	1	1	1	1	1	0.8	1	1		0		0	0		0	5	0.735484	0.74
NBRL038	0			0	1	1	1	1	1		1	1		0	0	1	0			8	0.321429	0.32
NBRL039	0.5			0.5	0.6	0.5	0.5	0.66	0		0	0								10	0.513846	0.51
NBRL040	0.5			0.5	0.8	0.5	1	1	1		0.6	0.6	0.8	0	0.33	0.66	0		0.66	4	0.423438	0.42
NBRL041	1	1	1	1	1	0.5	1	0.33	1					0	0	0	0	0	0	4	0.460313	0.46
NBRL042				0	0.8	1	1	1	0.5	0										13	0.686957	0.69

NBRL043	0	0	0	0	0.8	0	1	0.33		0	0	0		0	0	0	0		0	3	0.328182	0.33
NBRL044	0.5			1	1	1	1	1		0.8	0	0		0					0	8	0.753571	0.75
NBRL045		1	1	0.75	0.8	0.5	1	0.66	1	0.8				0	0	1	0.33	1	1	5	0.538387	0.54
TEST SPECIMEN	1				1	1	1	1			1			0	0	0	0	1	0.66	7	0.74	0.74
NBRL046																						
NBRL047																						
NBRL048																						
FLO33	1	1	1	1	0.6	0	0.5	0.33	1	0.6	0.4	0.8		0	0	0	0	0	0	1	0.378	0.38
NBRL049																						
NBRL050																						
NBRL051	1			0.5	1	1	1		1	1				1	1	1	1	1	0.66	7	0.86069	0.86
NBRL052																						
NBRL053																						
NBRL054	1				1	1	1	1	1	1	0	1		0	0	1	0.66	1	0.33	4	0.771563	0.77
NBRL055					1	1	1	1	1	0.2				1	0	1	1		0.33	13	0.827391	0.83
NBRL056																						
NBRL057																						
NBRL058																						
NBRL059	0			0	0.8	1	0.5	0.33	1	0.8	0.8	0.8		0	0	1	1	0	0.66	3	0.466364	0.47
NBRL060					0.8	0.5	1	0.66	1				0.8							21	0.657333	0.66
NBRL061	0.5			0	1	1	1	1	1	0.8	0.8	0.8		0	0	0	0		0	4	0.6125	0.61
NBRL062	0			1	0.6	1	0.5	0.66	1					0	0	0	0		0	7	0.515862	0.52
NBRL063	0			0	0.8	0.5	1	1	1	0.4	0	0								9	0.511111	0.51
NBRL064																						
NBRL065	0			0.5	0.8	1	1	1	1	1	0	0		0.33	0.33	0.33	0.33	1	0.66	3	0.578182	0.58
NBRL066	0.5			0.5	0.8	0.5	1	0.66	0.5	0	0	0		0	0	0	0		0	4	0.47375	0.47
NBRL067																						
NBRL068	0			0.5	0.6	0.5	1	0.33	1	0.8	1	0.8		0	0	0.33	0		1	4	0.583125	0.58
NBRL069	0			0	0.8	0.25	1	0.66	0.5	0.8	1	0.8		0	0	0	0	0	0	3	0.463939	0.46
NBRL070	0			0	1	1	1	0.66	0.5					0	0	0	0		0	8	0.337857	0.34

NBRL071	0.5			0.5	0.6	0.5	0.5	1	0.5		0	0		0	0	0	0		0	5	0.396774	0.4
NBRL072					0	0	0	0	0		0	0		0	0	0	0		0	8	0.201786	0.2
NBRL073	0.5			0.5	0.2	0	0	0	0		0	0		0	0	0	0		0	5	0.180645	0.18
NBRL074	0.5			0.5	0.8	0.5	0.5	0.66	1		0	0		0	0	0	0		0	5	0.472903	0.47
NBRL075	0.5			0	0	0	0	0	0		0	0		0	0	0	0		0	6	0.143333	0.14
NBRL076	1	1	0.5	1	0.6	0	0.5	0.33	0					0		0	0		0	7	0.325172	0.33
NBRL077	1	0.5	1	1	0.8	0.5	1	0.66	1					0	0	0	0		0	5	0.46	0.46
NBRL078	0.5			0.5	0.8	0.5	1	0.825	0.5		0.8	0.6		0	0	0	0	0	0	4	0.349219	0.35
NBRL079	1	1	0.5	1	0.8	0	1	0.33	0.5					0	0	0	0		0	5	0.452581	0.45
NBRL080	1	1	1		0	0	0	0	0	0				0	0	0	0.15		0	6	0.218333	0.22
NBRL081	1			1	0.8	0.5	0.5	0.66	0.5					0.33	0	0	0.33		0	7	0.597241	0.6
NBRL082	1	0.5	0.5	0.5	0.4	1	1	1	0		1	0		SEM	SEM	SEM	SEM	SEM	SEM	9	0.411111	0.41
FLO13					0.8	1	1	1	0				0.8	SEM	SEM	SEM	SEM	SEM	SEM	15	0.7	0.7
FLO27	1			1	1	1	1	1	1					0	0	0	0		0	7	0.772414	0.77
FLO28	1			0.5	1	1	1	1	1	0.8				0	0	0	0		0	6	0.515	0.52
FLO35	1	1	1	1	0	0	0	0	0		0	0			0	0	0		0	8	0.475	0.48
FLO64	1			0.75	0.6	0.5	1	0.66	0	0				0	0	0	0		0	7	0.645172	0.65

Table 8c. Quantification of non-completeness taphonomic characters only, including relief, 'fragile structures', voids, and cracking/breaking across different segments. Gaps represent characters that were not taxonomically present (i.e. wings on a larval form), were obscured from view (not clearly absent), or required SEM viewing (and the specimen had not been mounted for SEM viewing). These characters are excluded from determining the final taxonomic index, rather than counting negatively towards total preservation as they could not be measured. Specimens that are entirely blank could not be studied at all, usually as a result from specimen destruction through preparation problems/errors. A total of 64 specimens were taphonomically quantifiable.

Keys:

Compaction:

Highest Relief (A)	Fragile Structures (B)	Voids (C)
3 = High (Un/almost uncompacted) (I=1)	3 = Uncompacted and Perpendicular to bedding (I=1)	3 = Preserved hollow (Even if Broken) (I=1)
2 = Moderate (Compacted) (I=0.66)	2 = Uncompacted and Parallel to bedding (I=0.66)	2 = In filled with mineral growth (I=0.66)
1 = Low (Crushed) (I=0.33)	1 = Compacted (I=0.33)	1 = In filled with matrix (I=0.33)
0 = None (restricted to one laminae) (I=0)	0 = Completely Crushed (I=0)	0 = Crushed (I=0)
	N/A = Not present/visible	N/A = Not visible

Fracturing and Breaking:

Head Cracking & Breaking (D)	Thorax Cracking & Breaking (E)	Abdomen Cracking & Breaking (F)	Limbs Cracking & Breaking (G)
4 = None (I=1)	4 = None (I=1)	4 = None (I=1)	4 = None (I=1)
3 = Rare (I=0.75)	3 = Rare (I=0.75)	3 = Rare (I=0.75)	3 = Rare (I=0.75)
2 = Partial (I=0.5)	2 = Partial (I=0.5)	2 = Partial (I=0.5)	2 = Partial (I=0.5)
1 = Extensive (I=0.25)	1 = Extensive (I=0.25)	1 = Extensive (I=0.25)	1 = Extensive (I=0.25)
0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)	0 = Not preserved to see (I=0)

Table:

Specimen No.	A	B	C	D	E	F	G	No. Characters	Calculation	Index
NBRL002	0.66			0	0	0	0	2	0.132	0.132
NBRL003									0	
NBRL004	0.33	0		0	0	0.25	0	1	0.096667	0.0967
NBRL005	0.33	0		0.25	0	0	0.25	1	0.138333	0.1383
NBRL006	0	0		0.25	0.25	0	0.25	1	0.125	0.125
NBRL007									0	
NBRL008									0	
NBRL009									0	
NBRL010									0	
NBRL011									0	
NBRL012									0	
NBRL013									0	
NBRL014									0	
NBRL015									0	

NBRL016									0	
NBRL017									0	
NBRL018	1	0.66	1	0.25	0.75	0.75	0	0	0.63	0.63
NBRL019	0	0	0	0.25	0.5	0.25	0	0	0.142857	0.1429
NBRL020	0.66	0.33	0.66		0.25	0.5	0.25	1	0.441667	0.4417
NBRL021	0.15	0.33	0	0	0	0	0.5	0	0.14	0.14
NBRL022	0.66	0.33		0.5	0.75	0.75	0	1	0.498333	0.4983
NBRL023	0.66	0.66	0.66	0.25	0.5	0.25	0	0	0.425714	0.4257
NBRL024	1		0.66	1	0.75	0.25	0	1	0.61	0.61
NBRL025	0.66	0.33	0.66	0.5	0.25	0.25	0	0	0.378571	0.3786
NBRL026	0.33	0		0.5		0.25	0.5	2	0.316	0.316
NBRL027	0.8	0.66	0.66	0.75	0.75	0.5	0	0	0.588571	0.5886
NBRL028	0	0	0	0	0.25	0.25	0	0	0.071429	0.0714
NBRL029	0.66	0.66	0.33	0.75	0.5	0.5	0	0	0.485714	0.4857
NBRL030	0.33	0.33	0	0.5	0	0.25	0	0	0.201429	0.2014
NBRL031	0.33	0.33	0	0.75	0.25	0.75	0	0	0.344286	0.3443
NBRL032	0.66	0.33	0	0.5	0.5	0.25	0.75	0	0.427143	0.4271
NBRL033	0	0	0	0	0	0	0	0	0	0
NBRL034	0.66	0.33		0.25	0.5	0.75	0.5	1	0.498333	0.4983
NBRL035	1	0.66	0.8	1		0.5	?	1	0.526667	0.5267
NBRL036	0.33	0	0.33	0.5	0.25	0.25	0	0	0.237143	0.2371
NBRL037	0.66	0.66	0.66	1	0.25	0.25	1	0	0.64	0.64
NBRL038	1	1	0.66	0	0	0.25	0	0	0.415714	0.4157
NBRL039	0.33	0.66	0	0.5	0.5	0.5	0.75	0	0.462857	0.4629
NBRL040	0.33	0.33	0.33	0.25	0.5	0.5	0	0	0.32	0.32
NBRL041	0.33	0.33	0	0.5	0.5	0.25	0	0	0.272857	0.2729
NBRL042	0.66	0.66	0.66	0.5	0.25	0.75	0.25	0	0.532857	0.5329
NBRL043	0.33	0	0	0.5	0	0	0.5	0	0.19	0.19
NBRL044	1	0.66	0.66	1	0.75	0.75	0.75	0	0.795714	0.7957
NBRL045	0.66	0.33	0.33	1	0.5	0.5	0	0	0.474286	0.4743
TEST SPECIMEN	1	1	1	1	1	1	1	0	1	1
NBRL046										
NBRL047										
NBRL048										
FLO33	0	0	0	0.5	0.25	0.25	0	0	0.142857	0.1429
NBRL049										
NBRL050										
NBRL051	1	0.66	1	0.88	0.88	0.88	0.75	0	0.487143	0.4871
NBRL052										
NBRL053										
NBRL054	1	1	1	0.75	1	1	0.5	0	0.892857	0.8929
NBRL055	1	1	1	0.25		1	1	1	0.875	0.875
NBRL056										
NBRL057										
NBRL058										
NBRL059	0.66	0.33	0.33	0.25	0.25	0.25	0.25	0	0.331429	0.3314
NBRL060	0.66	0.66	0.33	0.5	0.25	0.75	1	0	0.592857	0.5929
NBRL061	1	1	0.66	1	0.5	0.5	0.75	0	0.772857	0.7729
NBRL062	0.66	0.33	0.66	0.25	0.25	0.25	0.5	0	0.414286	0.4143
NBRL063	0.66	0.45	0.33	0.5	0.25	0.5	0.5	0	0.391429	0.3914
NBRL064										
NBRL065	0.8	1	0.45	0.75	0.25	0.25	0.5	0	0.457143	0.4571

NBRL066	0.66	0.66	0.33	0.5	0.5	0.5	0	0	0.45	0.45
NBRL067										
NBRL068	0.66	0.66	0.33	0.25	0.25	0.5	0.5	0	0.45	0.45
NBRL069	0.66	0.66	0.33	0.5	0.5	0.5	0.5	0	0.521429	0.5214
NBRL070	0.66	0.33	0	0.25	0.5	0.25	0	0	0.284286	0.2843
NBRL071	0.66	0.33	0.33	0.25	0.5	0.25	0	0	0.331429	0.3314
NBRL072	1	1		0.25	0	0	0.5	1	0.458333	0.4583
NBRL073	1	0.66		0.75	0	0	0	1	0.401667	0.4017
NBRL074	0.66	0.66	1	0.25	0.5	0.75	0.75	0	0.652857	0.6529
NBRL075	0.66	0.66	0.33	0	0.25	0	0	0	0.271429	0.2714
NBRL076	0.33	0.33	0	0.5	0	0.25	0	0	0.201429	0.2013
NBRL077	0.66	0.33	0.33	0.75	0.5	0.25	0.25	0	0.438571	0.4386
NBRL078	0.33	0		0	0.25	0.5	0.25	1	0.221667	0.2217
NBRL079	0.66	0.33	0	0	0.5	0	0.25	0	0.248571	0.2486
NBRL080	0.66	0.33	0.33	0	0.75	0	1	0	0.438571	0.4386
NBRL081	1	0.66	0.66	0.25	0.25	0.25	0.5	0	0.51	0.51
NBRL082	1	0.66	0	0	0.5	0.25	0	0	0.344286	0.3443
FLO13	0.66	0.33	0	0.25	0.25	0.75	0.25	0	0.355714	0.3557
FLO27	1	0.66	0.8	0.75	0.75	0.25	1	0	0.744286	0.7443
FLO28	1	0.33	1	0.25	0.5	0.75	0	0	0.547143	0.5471
FLO35	0.66	0.33	0		0.25	0	0.87	1	0.351667	0.3517
FLO64	1	0.66	0.33	0.5	0.5	0.5	0.75	0	0.605714	0.6057

Matt Guille <matthew.guille@port.ac.uk> 14/11/2013

Dear Nathan,

I am happy to confirm that the AWERB has granted ethical approval for your project: "A*n examination of the fidelity of preservation of the insects from the Crato Formation".* Please keep this email as confirmation that your application has been approved. The Board wishes you the very best with your research programme.

best wishes,

Matt

--
Matt Guille
Professor of Developmental Genetics
School of Biological Sciences
University of Portsmouth
King Henry Building
King Henry I Street
Portsmouth PO1 2DT

Tel: 02392 842047

FORM UPR16

Research Ethics Review Checklist

Please include this completed form as an appendix to your thesis (see the Postgraduate Research Student Handbook for more information

Postgraduate Research Student (PGRS) Information			**Student ID:**	419523
PGRS Name:	Nathan Barling			
Department:	SEES	**First Supervisor:**	David M. Martill	
Start Date: (or progression date for Prof Doc students)		**Oct 1st 2011**		
Study Mode and Route:	Part-time ☒ Full-time ☐	MPhil ☐ PhD ☒	MD ☐ Professional Doctorate ☐	

Title of Thesis:	Fidelity of Preservation of Insects from the Crato Foramtion (Lower Cretaceous) of Brazil
Thesis Word Count: (excluding ancillary data)	65,545

If you are unsure about any of the following, please contact the local representative on your Faculty Ethics Committee for advice. Please note that it is your responsibility to follow the University's Ethics Policy and any relevant University, academic or professional guidelines in the conduct of your study

Although the Ethics Committee may have given your study a favourable opinion, the final responsibility for the ethical conduct of this work lies with the researcher(s).

UKRIO Finished Research Checklist:
(If you would like to know more about the checklist, please see your Faculty or Departmental Ethics Committee rep or see the online version of the full checklist at: http://www.ukrio.org/what-we-do/code-of-practice-for-research/)

a) Have all of your research and findings been reported accurately, honestly and within a reasonable time frame?	YES ☒ NO ☐
b) Have all contributions to knowledge been acknowledged?	YES ☒ NO ☐
c) Have you complied with all agreements relating to intellectual property, publication and authorship?	YES ☒ NO ☐
d) Has your research data been retained in a secure and accessible form and will it remain so for the required duration?	YES ☒ NO ☐
e) Does your research comply with all legal, ethical, and contractual requirements?	YES ☒ NO ☐

Candidate Statement:

I have considered the ethical dimensions of the above named research project, and have successfully obtained the necessary ethical approval(s)

Ethical review number(s) from Faculty Ethics Committee (or from NRES/SCREC):	N/A

If you have *not* submitted your work for ethical review, and/or you have answered 'No' to one or more of questions a) to e), please explain below why this is so:

Work was granted ethical approval as research did not involve the use of live animals, humans, or data protected under the data protection act. An experiment involved live insects was planned (and ethically approved), but was not carried out due to time constraints.

Signed *(PGRS)*:		**Date:** 15/08/2018

Terrestrial Insect
Dead Terrestrial Insect
Aquatic Insect
Dead Aquatic Insect
Fragmentary Insect Remains
Rigidity and Resistance to Penetration
Aerobic Microbial Community
Filter-feeding *Dastilbe*
Larger or Vertebrate Remains
Fluvial System
Resin or Amber
Seasonal Wind and Rain
Transport and Rapid Transport
Long Distance Transport
Movement of water into/out of carcass
H_2O
Coniferous Forest Habitat
Humid Riverside or Delta
Hydro-dynamic sorting
Fresh Water
Brackish or Saline Water

Key

Forested Zone

Insect lives in coniferous forested habitat far upstream from the palaeolake.

Insect dies or enters water and is transported a significant distance over a long period of time.

Decay, transport, and scavenging cause the carcass to disarticulate.

Only rare durable fragmentary remains reach the Crato palaeolake.

Insect lives in coniferous forested habitat upstream from the palaeolake.

Insect becomes entombed in resin secreted by conifer trees. Resin, on occasion, drops into river system.

Carcass is protected from scavenging, disarticulation, and most decompositional processes by resin.

Humid Zone

Insect lives in moist habitat around deltaic or fluvial system that drains into the Crato palaeolake.

Insect enters the water alive and, as it drowns, it actively draws water in though its tracheal system.

Density, rigidity, and resistance to penetration are all increased. The carcass floats for a shorter duration and resists fragmentation.

Rapid transport down the deltaic or fluvial system prevents scavenging by fish or other non-aquatic scavengers.

Hydrodynamic sorting removes large material, preventing most large organisms from reaching the site of deposition.

Insect lives in moist habitats around a deltaic or fluvial system that drains into the Crato palaeolake.

The insect dies on land and decays rapidly in the moist environment surrounding the delta/river.

Heavily damaged fragmentary remains may be washed into the river by rain and are transported to the palaeolake.

The insect lives within the freshwater tributaries and streams. Either dead or alive, the insect is flushed downstream.

Live insects resist decay and carcasses are more likely to fragment, depending on the duration of transport.

Rapid transport prevents the insect or carcass from being predated or scavenged.

Hydrodynamic sorting removes large material, preventing most large organisms from reaching the site of deposition.

Arid Zone

The insect dies on land and its carcass remains undisturbed. The carcass is desiccated by the arid Crato environment.

The carcass is transported into the Crato palaeolake via wind or seasonal rainfall.

The carcass rapidly disintegrates upon entering the water. Only fragmentary remains continue to the next step.

Disintergration

The insect dies before entering the Crato palaeolake, but is rapidly transported there.

As the insect is already dead, it saturates more slowly, increasing its floatation time.

This increases the duration that decay may act. However, high salinity and microbial action still hinder decay.

Slow Saturation

Potentially increased decay

The insect is forced into the water alive by strong winds, heavy rainfall, or other means.

The insect is unable to escape and, as it drowns, it actively draws water in though its tracheal system.

Density, rigidity, and resistance to penetration are all increased. The carcass floats for a shorter duration and resists fragmentation.

Insect lives in small freshwater niche around the edge of the Crato palaeolake, along arid zone.

Insect dies and drifts out into the wider lake, or is forced into the hostile waters by strong currents or heavy rainfall.

Freshwater benthic insect carcasses float in the higher-density saline waters.

Palaeolake

Further decay of the fragments is inhibited by the increased salinity of the Crato palaeolake.

The hostility of the palaeolake waters prevents a diverse fish assemblage. Only filter-feeding *Dastilbe* thrive.

Most fragments are typically not consumed by the filter-feeding fish *Dastilbe*.

Heavy rain causes fragments to break water surface tension, allowing them to sink.

Resin is transported a great distance to palaeolake. Specific circumstances, possibly heavy rain, are required for the resin to sink.

Resin undergoes unique preservation process not comparable with the insect carcasses. Requires pre-compaction cementation.

Further decay of the carcass is inhibited by the increased salinity of the Crato palaeolake.

While floating, the carcass may become encased by an aerobic microbial community, increasing its density.

As the microbial community grows, it 'binds' the carcass, preventing disarticulation and scavenging.

The hostility of the palaeolake waters prevents a diverse fish assemblage. Only filter-feeding *Dastilbe* thrive.

The carcasses float on the saline/brackish waters and may be concentrated into one area by gyres.

On rare occasions, microbially bound carcasses that come into contact with each other adhere.

Carcass sinks, either after a prolonged period on the surface, or rapidly when heavy rains destabilise water surface.

Continue to Figure 96.

Figure 97. Transport model for Nova Olinda Member fossil insects.