Chelonia of the Bouldnor Formation (Eocene/Oligocene), Isle of Wight: Taphonomy and pathologies

A thesis submitted to The University of Manchester for the degree of Master of Philosophy (MPhil) in the Faculty of Science and Engineering

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ABSTRACT

This study aims to establish that chelonian carapace and plastron from the Bouldnor Formation display the presence of pathologies, whilst considering the impacts of taphonomic grade and depositional environment. Describing healed injuries and evidence of disease features in detail when assessing the cause of such pathologies, causes can include disease, parasitic behaviour, predation, or post-mortem scavenging. Evaluating the impact and effects of taphonomic processes on specimens can help when diagnosing the cause of any described abnormalities. Anatomical abnormalities in Chelonians from the Bouldnor Formation are rarely documented and are also poorly preserved thus making it difficult to determine the cause for observed pathologies. Using samples collected during this study, along with museum specimens and the application of micro-CT, it is possible to identify and diagnose endogenous from exogenous impacts that have given rise to chelonian pathologies.

The evidence collated in this study suggests that specimens from the Bouldnor Formation display multiple pathologic features from several different causes. Specimens show evidence of both pre-and post-mortem processes that have left distinctive marks that can be identified. This study illustrates that there is value in analysing partial specimens that other studies might have overlooked, this permits the identification of key structures that can be compared between both extinct and extant chelonians to better constrain their genesis. The evidence presented in this study indicates a wealth of information is present in fossils of extinct chelonian that give insight into the scars of injury and disease (pathologies) and suggest this would make a productive area for future research.

The University of Manchester

The Degree of Master of Philosophy (MPhil) Chelonia of the Bouldnor Formation (Eocene/Oligocene), Isle of Wight: Taphonomy and Pathologies.

2023

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DEDICATIONS

This study is dedicated to everyone who has stood by me during some difficult times, including my mother (Joanna Davies), Father (John Davies), brother (Deryn Davies), sister (Ava Davies), Girlfriend (Eleanor Wild), Grandma (Jackie Davies) and late Grandfather (Brendan Davies) for never failing to support me in my quest to become a Palaeontologist.

In each of their own ways they have helped me and wanted me to succeed, and I will never be able to thank them enough for their efforts.

ABBREVIATIONS

- **NHMUK** (The Natural History Museum, London)
- **MIWG** (Dinosaur Isle Museum, Sandown)
- **UOM** (University of Manchester)

Other abbreviations

- **IOW** (Isle of Wight)
- **XRT** (X-ray tomography)
- **CT** (Computerised tomography

ACKNOWLEDGEMENTS

- Before I begin with my research project, I would like to thank many individuals for making this project possible. Firstly, I would like to thank my Supervisors Prof. Phil Manning and Dr Victoria Egerton for their unwavering support and encouragement of me and my project. No matter the personal hardships they have endured over the 2 years they always believed in me, and I hope this work can reflect their trust in me to complete this project. I can’t thank them both enough for the work they do supporting all the students under their supervision and long may this continue.
- I would also like to thank Dr Martin Munt, the curator and manager of Dinosaur Isle Museum (DIM), for allowing access to the museum’s collections and allowing me to photograph said specimens for use in my project.
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1. INTRODUCTION

The lithostratigraphy and biostratigraphy of the Isle of Wight have been extensively studied for centuries, along with its rich fossilised record of both flora and fauna from the Lower Cretaceous to Pleistocene (Hooker and Sweetman 2009, Hopson 2011, Jenkins et al. 2011, Downes 2021). The Solent Group is one such facet of the island's geological history and has been analysed in detail, giving insight into the palaeoenvironments of the late Eocene and early Oligocene epochs (Daley 1999). Within the Solent Group, the Bouldnor Formation consists of a series of interbedded clays, silts, and sands that frequently preserve the remains of turtles (Chelonia) (Insole and Daley 1985). Chelonian fossils have been much neglected from the Isle of Wight for many decades, with only a handful of publications, stating chelonian fossils in the Bouldnor Formation in the past 50 years (Moody 1980; Hooker et al. 1995, Benton and Spencer. 1995, Hooke 1998, Donovan and Simpson. 2021). The fossil Chelonia from the Bouldnor Formation, specifically the Hamstead Beds that sit within this formation, is known to exhibit possible pathologies which might reflect the organism's response to trauma and disease, but also the taphonomic history of the organism (Brandt 1989; Behrensmeyer et al. 2000). However, a detailed study of potential pathologies has not been undertaken, especially when also accounting for possible taphonomic overprint. This study aims to examine pathologies in the fossil remains of turtles from the Bouldnor Formation (Isle of Wight) to better understand their occurrence and origin within a taphonomic framework. I hypothesize:

- The temporal and spatial occurrence of chelonian fossils and their taphonomic grade link impact the interpretation of specimens and are a function of the depositional environment of the Lower and Upper Hamstead Members.
- Chelonian pathologies from the Bouldnor Formation exhibit comparable pathologies with other extinct chelonians from Eocene-aged locations.

- Pathologies in extant chelonians are directly comparable to those observed in the extinct chelonians from the Bouldnor Formation and can identify and diagnose injury, ancient disease, and parasitism.

Scant research has been conducted on the chelonians of the Bouldnor Formation (Moody 1980; Hooker et al. 1995, Benton and Spencer. 1995, Hooke 1998, Donovan and Simpson. 2021), so this study aims to explore the following research questions:

- Most chelonian specimens found from the Bouldnor Formation are fragmentary and disarticulated, but is this related to the taphonomic grade or depositional environment?
- If chelonian specimens from the Bouldnor Formation display observable pathologies, is the cause related to predation, disease, or parasitic behaviour?
- To what extent are pathologies from extant chelonians comparable to those found in the extinct species from the Bouldnor Formation?
-

1.1. THE GEOLOGICAL HISTORY OF THE ISLE OF WIGHT

The Isle of Wight is a diamond shape with four distinct points occurring at Cowes (north), Bembridge (east), St. Catherine’s Point (south), and The Needles (west) (Figure 1). The sides are slightly concave and generally trend downwards towards the sea from the centre of the island (White 1921; West 2015). A chalk monocline runs east to west across the centre of the island for 23.5 miles, extending from the Needles in the west and to Bembridge and Culver down in the east (Mortimore 2011, West 2015, Gale 2021). This chalk ridge separates the southern successions, which are predominantly Cretaceous in age, from the northern successions, which are Palaeogene in age (Insole and Daley 1985, Daley 1999, Mortimore 2011).

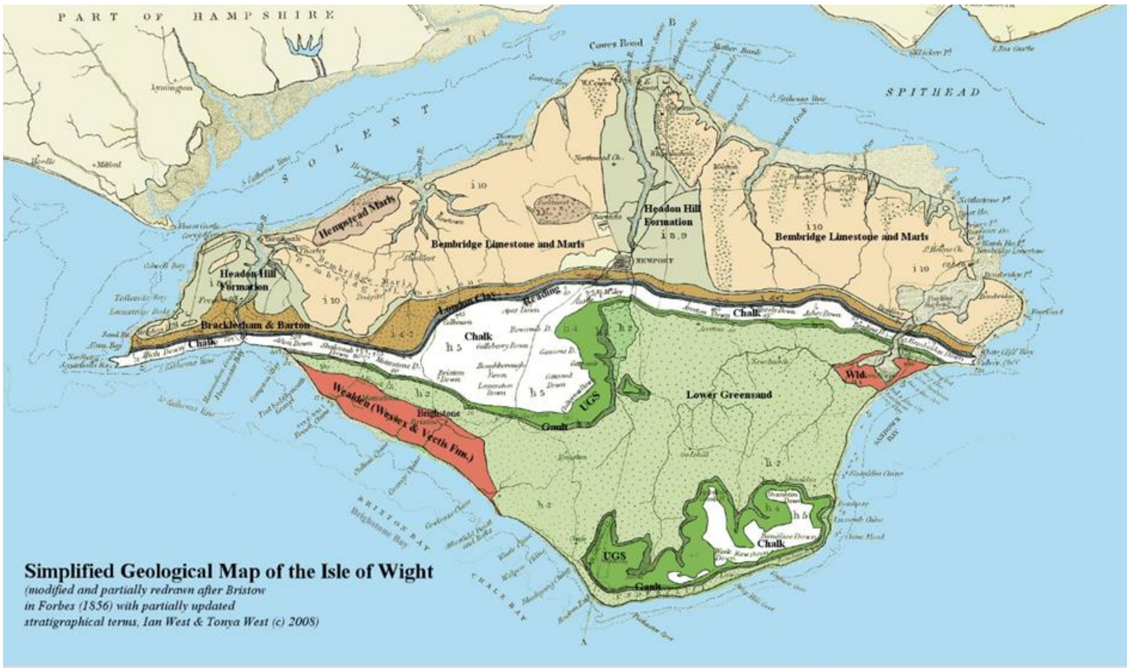


Figure 1 - Simplified Geological Map of the Isle of Wight. Adapted by Ian West and Tonya West in 2008. This geological map clearly illustrates the 4 points of the island and the distinct stratigraphical units deposited north of the chalk and south of the chalk, with the Cretaceous deposits lying south and the Tertiary deposits lying to the north (West 2015)

The Cretaceous succession of the Isle of Wight includes the Wealden Group, the Lower Greensand Group, the Selborne Group, and the Chalk Group (Mortimore 2011, Gale 2021). The Wealden beds, which include the Wessex and Vectis Formations, are the oldest exposed strata on the Isle of Wight (Stewart and Daley 1979, Stewart et al. 1991) The Cretaceous succession comprises fluvial deposits from fast-flowing rivers and streams on a coastal floodplain (West 2015). The Isle of Wight is notable for its dinosaur remains, including bones and ichnofossils all found within the Wealden Group (Radley et al. 1998). The Lower Greensand Group (Aptian-Albian) overlays the Wealden Group and preserves an abundance of marine fossils and structures and is interpreted as having been deposited in a shallow marine environment (West 2015). These beds coarsen upwards and with periods of erosion, followed by cycles of deposition and then colonisation, with fauna and substrate conditions altering in response to repetitive marine flooding (Ruffell et al. 1998). The overlying Selborne Group consists of the Gault Clay and Upper Greensand Formations (Albian) and are well exposed on the island (West 2015).

These two formations were deposited in a marine environment with the Gault Formation having been interpreted as deep marine, while the Upper Greensand Formation has been interpreted as a shallow marine shelf (Ruffell and Wach 1998, Woods et al. 2008, West 2015). The Chalk Group (Cenomanan to Campanian) consists of two subgroups, the White Chalk Subgroup and the Grey Chalk Subgroup (Insole et al. 1998, Gale 2021). The chalk succession at Culver Down has been correlated with similar exposures located in south-eastern England, such as the cliffs between Beachy Head and Brighton (Hopson et al. 2007). The chalk is composed of coccolithophores in a biomicrite. Amongst the coccolithophores, other fossil fragments can be found, although rare, including ostracods, foraminifera, and molluscs (Hopson 2011; West 2015, Gale 2021).

North of the chalk monocline, the Cenozoic succession is exposed and consists of the Paleocene Lambeth Group; the Eocene Thames Group, Bracklesham Group, and Barton Group; and the Eocene to Oligocene Solent Group (Hopson 2011, West 2015). The Lambeth Group strata are approximately 55 million years old and are overlain by the Thames Group, the deposits consist of shallow marine clays and coarse sands (Skipper 2000, Hopson 2011). Overlying the Lambeth Group is the Thames Group, which ranges in age from 56 to 49 million years old and is a series of blue and brown clays famed for its fossiliferous content (Sumbler 1996). The Bracklesham Group is a series of clays and marls with interbedded sands that age from the middle Eocene, named for its exposure in Bracklesham, Sussex, and famed for its preservation of fossiliferous remains (Reid 1902, Hopson 2011). Overlaying this is the Barton Group, a series of clays and sands ranging in age from the Lutetian to Priabonian, 41 to 37 million years old (Hopson 2011). The Eocene successions can be found in the east and west of the island, with exposures occurring north of Whitecliff Bay in the east and Alum Bay in the west. Whitecliff Bay itself preserves the exposures of the Middle Eocene Bracklesham Group, as this is also where the group is most fossil-rich (West 2015).

The Solent Group, comprising the Headon Hill, Bembridge Limestone, and the focus of this study, the Bouldnor Formation. These are all well-exposed northward of the Eocene deposits, with Headon Hill being an area of exceptional exposure along with northern parts of Whitecliff Bay (West 2015). These sediments consist of clays, marls, sands, and limestones deposited in brackish, lagoonal, and lacustrine environments (West 2015). The Bouldnor Formation comprises alternating brackish and marine silts, marls, and sands, which preserve exceptional fossils (Insole and Daley 1985; West 2015). These fossils include mammals, turtles, crocodilians, insects, molluscs, and reptiles from the late Eocene/ early Oligocene, with the Oligocene strata being exposed at Hamstead and Bouldnor Cliff coastal sections (Insole and Daley 1985; West 2015; Momber et al. 2020).

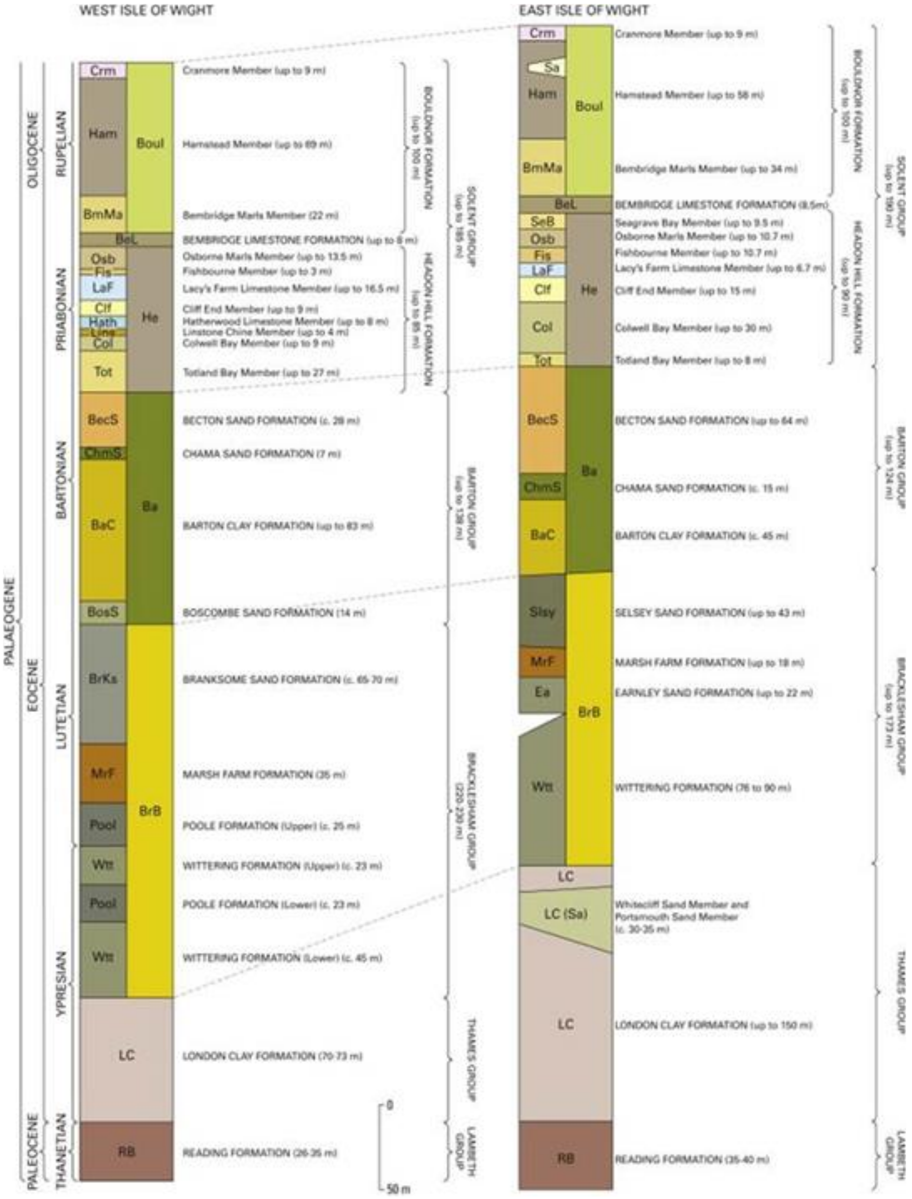


Figure 2 - The Palaeogene strata of the east and west of the Isle of Wight. Adapted from Hopson 2011.

1.2. THE BOULDNOR FORMATION

The Bouldnor Formation occurs within the Hampshire Basin of southern England but is also well exposed on the Isle of Wight. On the Isle of Wight, it is exposed along the shore between Yarmouth and Hamstead in the Bouldnor cliff and varies in thickness from 45 to 115 metres (Insole and Daley 1985; Momber et al. 2020). This formation is the youngest of the Solent Group (Daley 1999), having a stratigraphic range of 38 to 28 million years ago (Priabonian–Rupelian) (Insole and Daley 1985; Gale et al. 2006). The Bouldnor Formation is bounded by the underlying freshwater Bembridge Limestone Formation and the overlying Pleistocene and Holocene deposits. The significantly younger overlying deposits demonstrate the presence of a hiatus in deposition from the early Oligocene to the Pleistocene (Insole et al. 1985; Armenteros and Daley 1998, Daley 1999, Gale et al. 2006, Momber et al. 2020). This formation was first established in 1985 with 3 distinct members by Bembridge Marls Member, Hamstead Member, and Cranmore Member (Insole and Daley 1985; Daley 1999).

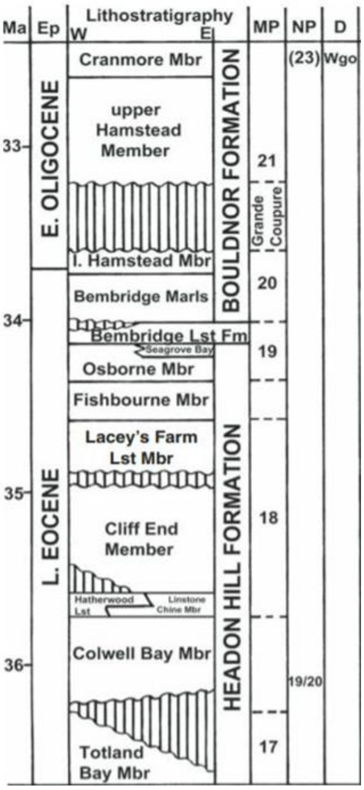


Figure 3 - Stratigraphic column of the Solent Group and its formations and members. Adapted from Daley 1999.

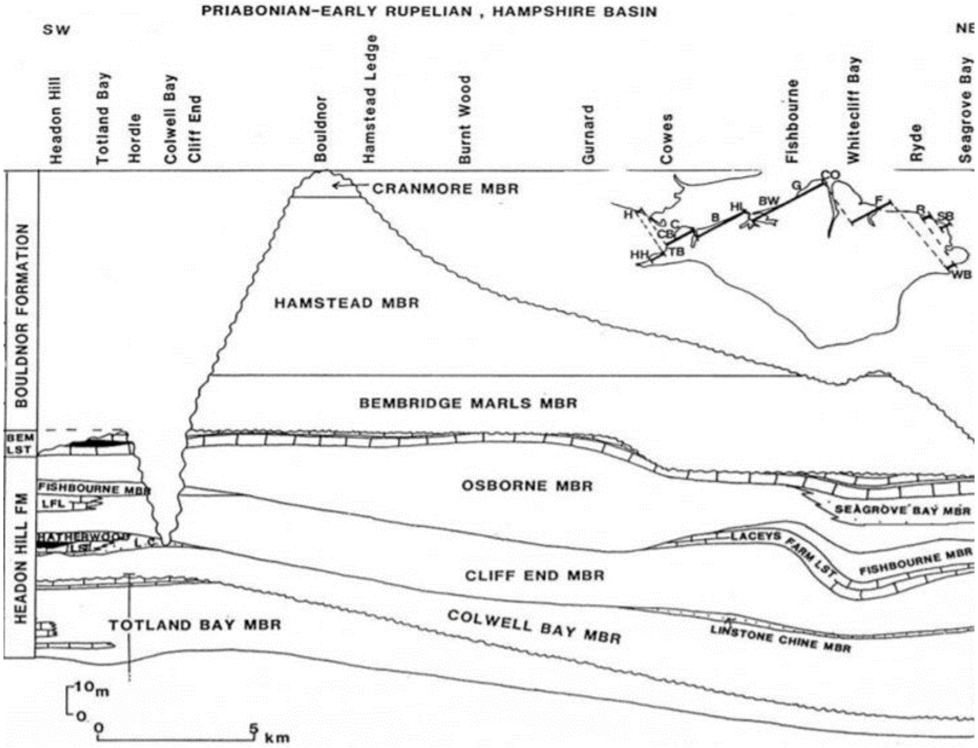


Figure 4 - Cross section through late Eocene (Priabonian) to early Oligocene (Rupelian) strata within the Hampshire Basin, Isle of Wight. Adapted from Hooker et al. 2009.

THE BEMBRIDGE MARLS MEMBER

The oldest member of the Bouldnor Formation, the Bembridge Marls Member (previously known as the Gurnard Member), ranges in age from 34.0 to 33.75 million years (upper Priabonian) (Munier-Chalmas and de Lapparent, 1893; Insole et al. 1985). The Bembridge Marls Member is typically 20 to 23 metres thick; however, it can be up to 35 metres thick (Insole et al. 1985) (Figure 4). Much of the member is comprised of layered blue-grey and green-grey clays/marls with some darker fossiliferous horizons. These sediments are interpreted to have been deposited in a fresh or brackish estuarine environment based on the presence of Cirripedia (Barnacles) and Gastropods, such as *Terebia* (Insole et al. 1985). Horizons within the Bembridge Marls Member, such as the Bembridge Oyster Bed, show that the mainly freshwater palaeoenvironments were occasionally subjected to marine incursions based on the presence of the saltwater bivalve genera *Corbicula* and *Nucula* (Daley 1972). The upper portion of the member has abundant freshwater snails (prosobranchs), such as *Viviparus,* indicating a change to more terrestrial, slow-moving river systems (Daley 1972).

HAMSTEAD MEMBER

Directly topping the Bembridge Marls Member is the 20 to 70-metre-thick Hamstead Member, which is subdivided into upper and lower sections by the '*Nematura* bed' (Insole et al. 1985). The lower Hamstead Member is a 10-metre-thick package of sediment with a 40 cm layer of dark green to black sediments at the base. This 'Black Band' contains a large amount of organic material consisting of rootlets, calcrete nodules, and various fragments of flora, and is inferred to have been deposited in brackish water conditions (Collinson 1983; Insole et al. 1985, Hayes et al. 2013). Deposited above the 'Black Band' is 4 m of inter-layering green-grey and blue-grey clay and siltstones, followed by another 3-4 metres of blueish to brownish laminated clays which include some fossiliferous horizons mainly containing molluscs and bivalves (Insole et al. 1985; Munt 2013). The clays are overlain by a metre-thick layer known as the 'Log Bed' which is a layer of blueish-greyish clays and sands with pronounced structures such as ball-and-pillow, convolute and contorted laminations or bedding planes (Insole et al. 1985).

This indicates dewatering processes taking place within the layer during diagenesis; furthermore, the layer is interpreted as gravitationally unstable, evident by these structures (Insole et al. 1985). The 'Log Bed' gets its name from the 5-metre-long tree trunks which are preserved within the bed. Other plant fossils are preserved, including *Potamogeton* seeds and Monocotyledon and Dicotyledon leaves (Collinson 1983; Insole et al. 1985, Hayes et al. 2013). The layer is inferred to be the last sediment layer before a 350,000-year hiatus which follows the 'Log Bed' unconformity (Stehlen 1910; Insole et al. 1985, Zachos et al. 2001, Hooker 2004, Gale et al. 2006; Hooker 2009). Following the hiatus is the '*Nematura* bed' which is the final layer in the lower Hamstead Member. It is a 1-metre-thick bed consisting of brown ripple marks with alternating clays and sands (Insole et al. 1985). The '*Nematura* bed' gets its name from the large mollusc, *Nematura,* however, other fossils in this bed include marine dinoflagellates and ostracods. This bed is interpreted as having been deposited in brackish water conditions due to the presence of organic material and reworked wood fragments and rootlets (Collinson 1983; Insole et al. 1985, Munt 2013).

The upper Hamstead Member is estimated to reach 60 metres thick and consists of several layers of silts and sands. The basal 3 metres consists of alternating greenish to greyish clays and silts with the remains of decalcified Polymesoda shells (Insole et al. 1985). Roughly 10 metres from the base of the member is the '*Eomys* bed' which gets its name from the fossilised remains of the Eomyid rodent, *Eomys*, the earliest flying rodent in the fossil record (Storch et al. 1996). Directly following the '*Eomys* bed' is the 'White Band' which, as the name suggests, is a band of lighter white sediment containing the decalcified remains of Polymesoda (Insole et al. 1985). Overlying the 'White Band' is the 'Crocodile Bed' containing a large selection of crocodilian remains, including, most notably, the crocodylomorph *Diplocynodon hantoniensis.* which has been diagnosed with the first occurrence of necrotizing dermatitis within its osteoderms (Insole et al. 1985; Wolff et al. 2007, Rio et al. 2020). Overlying the 'Crocodile Bed' is approximately 8 metres of blue to turquoise clays with orange to reddish spots with occasional layers of brown or red laminated clays and fossiliferous shelly horizons (Insole et al. 1985).

CRANMORE MEMBER

The Cranmore Member is the uppermost member of the Bouldnor Formation and marks the end of deposition within the Hampshire Basin (Insole et al. 1985). The member is 5-9 metres thick and begins with non-marine facies at the base, preserving the remains of the mollusc *Cerithium*. The palaeoenvironment shifts to deeper marine facies upwards and contains bivalves, such as *Corbicula,* and other marine gastropods as seen in the Bembridge Marls Member (Insole et al. 1985). However, freshwater gastropods (*Viviparus*) are also preserved (Insole et al. 1985).

1.3. EOCENE/OLIGOCENE BOUNDARY

The strata from the Solent Group, and more specifically the Bouldnor Formation, contain the sequence boundary between the Eocene and the Oligocene; however, placing this boundary has been difficult to identify (Munier-Chalmas et al. 1893, Insole et al. 1985). The

Eocene/Oligocene boundary has been proposed to have been related to global cooling during the late Eocene (transitioning from a ‘Greenhouse’ to an ‘Icehouse’ climate) (Hooker et al. 2004; Katz et al. 2008). Global cooling began around 49 million years ago, coinciding with the earliest evidence of westbound Antarctic counter currents. Changes to ocean currents would have led to cool Antarctic waters being transported towards the equator by deep-sea seawater currents, cooling global seawater (Bijl et al. 2013). Temperatures at the poles before the Eocene/Oligocene boundary were around 20 degrees, contrasting to temperatures of only 5 degrees at the boundary itself (Liu et al. 2009). Global cooling during this time has also been attributed to the Himalayan orogenesis (Hou et al. 2012), North Atlantic rift-related, eruptions (Jolley and Widdowson 2005) and the opening of the Tasmanian gateway and the Drake Passage (Bijl et al. 2013).

During this global cooling phase, a break in deposition spanning 350,000 years is observable in strata in different countries (Hooker et al. 2004). Early studies had suggested that the hiatus coincides with the Eocene/Oligocene boundary; however, more recent work has proposed that the hiatus is linked with the first Oligocene Oi-1 glaciation in the transition to an ‘Icehouse’ climate (Hooker 1992; De Coninck 2001; Hooker et al. 2004; Katz et al. 2008). Within the lower Hamstead Member of the Bouldnor Formation, the unconformity separating the ‘Log Bed’ and the overlying ‘*Nematura* Bed’ has been interpreted to be this same hiatus (Munier-Chalmas et al. 1893; Stehlen 1910; Insole et al. 1985; Hayes et al. 2013; Collinson 1983). Regression due to a glaciation event may explain why deposition within the Hampshire Basin appears to have stopped entirely (Hooker et al. 2004; Katz et al. 2008).

Also associated with the Eocene/Oligocene boundary in Europe is the ‘Grande Coupure’, or ‘Great Break.’ This is a major European mammalian turnover event associated with the widespread extinction of endemic European mammals and the arrival of Asian mammals (Wing et al. 2003; Hooker et al. 2004). It has been proposed that this event happened in stages with taxa going extinct due to changes in the ecosystem. The ‘Grande Coupure’ can be linked to vegetation changes affecting European mammalian taxa (Hooker et al. 2004) and competition with radiating immigrants from Asia. Within the Bouldnor Formation, a major mammalian turnover proposed to be the ‘Grand Coupure’ occurs in the Hamstead Member with 11 mammalian taxa disappearing and 16 new mammalian taxa appearing (Insole et al. 1985; Wing et al. 2003, Hooker 2010). New taxa present after the ‘Grande Coupure’ includes enteledonts, amphicyodon, castorid, eomyid rodents, and lipotyphlans (Hooker et al. 2009).

Paleosols and fossil flora have also been used to help identify climatic changes across the Eocene/Oligocene boundary within the Solent Group. However, the palaeoclimatic results from these palaeosols do not indicate late Eocene cooling, instead, they show steady mean annual temperatures and an increase in precipitation (Katz et al. 2008; Sheldon et al. 2009). The fossil floras indicate a consistently humid environment across the Eocene/Oligocene boundary. This is in contrast with both paleosols and floral changes elsewhere globally (e.g., North America, and South America) which show general long-term cooling linked to the Oi-1 glaciation event (Sheldon et al. 2009).

The boundary between the Eocene and Oligocene is generally linked to the cooling of the late Eocene (which ties into the Oi-1 glaciation event), this has drastic changes to the flora and fauna of the ecosystems and thus a change in the stratigraphic and biostratigraphic record (Hooker et al. 2004; Katz et al. 2008). However, within the Bouldnor Formation, placing the boundary is less absolute, with no obvious cooling at a particular point within the formation based on the paleosols and the fossil flora. However, the placement of the Eocene/Oligocene boundary can be refined to at least the Hamstead Member based upon the hiatus and the timing of the ‘Grande Coupure’ (Wing et al. 2003; Hooker et al. 2004, Katz et al. 2008, Sheldon et al. 2009).

1.4. TURTLE EVOLUTION AND ANATOMY

Three hundred sixty-five species of terrestrial turtle can be found today, living on all continents except Antarctica, in both salt and fresh water, with the greatest number of species occurring in North America and South Asia (Zug 2023). However, the evolutionary history of turtles has been shrouded in debate for hundreds of years; the origin of the unique anatomy of turtles has been a contentious subject. However, despite this, discoveries over the past two decades have aided in determining the origin and understanding of the evolution of anatomical features associated with turtles. The oldest fossil turtles appear within the fossil record 210 million years ago, during the Late Triassic, with a species called *Proganochelys quenstedtii* (Gaffney and Meeker 1983, Lyson et al. 2013). First described in 1887 by Georg Baur, Fossils of *P. quenstedtii* have been discovered from Germany to Thailand and preserve upper and lower shell coverings, known as a carapace (dorsal body covering) and plastron (ventral shell covering) (Gaffney and Meeker 1983, Lyson et al. 2013, Cordero 2017). The shell is constructed using both skeletal and dermal bone; the vertebra and ribs fuse with the dermal scutes to create a complete enclosure (Cordero 2017).

Late Triassic turtles displayed anatomical features like extant turtles, although the origin of the shell was argued for the next century until a discovery in China in 2008 provided some answers (Li et al. 2008). The described species, *Odontochelys semitestacea*, dates to 220 million years ago which predates *P. quenstedtii* by 10 million years (Figure 5 and 6) (Gaffney and Meeker 1983; Li et al. 2008, Lyson et al. 2013, Schoch and Sues 2015, Cordero 2017). The preserved specimen lacks the carapace seen in later turtles such as *P. quenstedtii*; however, the plastron is present (Gaffney and Meeker 1983; Li et al. 2008, Lyson et al. 2013, Schoch and Sues 2015, Cordero 2017). Additionally, *O. semitestacea* has flattened ribs which provides a clue as to the evolution of the carapace which appears later in the Triassic (Li et al. 2008, Schoch and Sues 2015, Cordero 2017). The hypothesis for the evolution of the plastron includes defence from predators from beneath within the marine environment (Li et al. 2008, Schoch and Sues 2015).

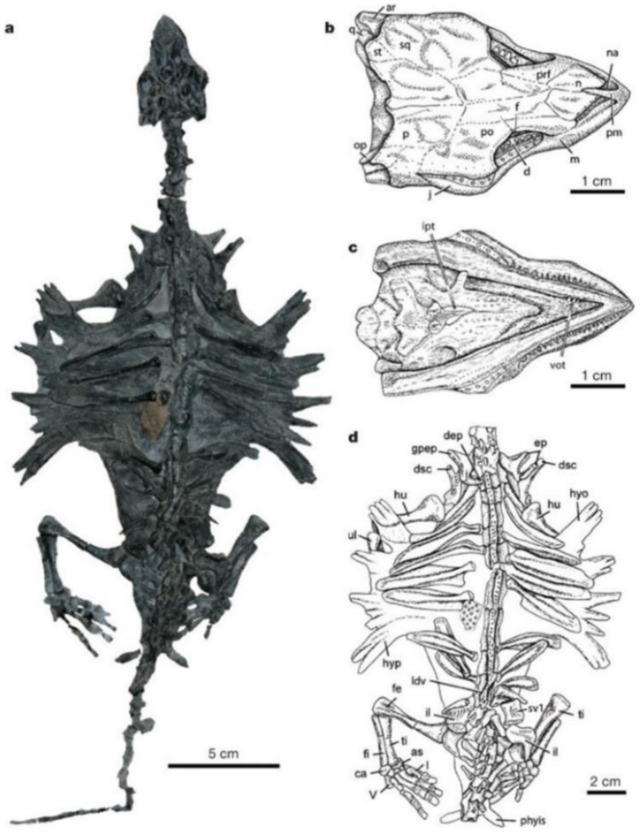


Figure 5 - *Odontochelys semitestacea* A - Skeleton of in dorsal view. B – Skull of in dorsal view. C - Skull of in ventral view. D – line drawing of the skeleton in dorsal view. Adapted from Li et al. 2008.

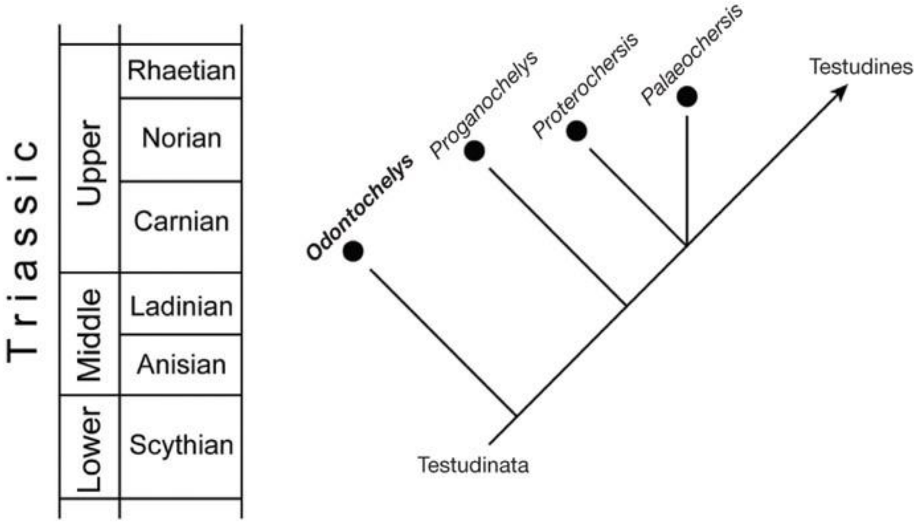


Figure 6 - **Left**: Geological timetable of the Triassic period including Lower, Middle, and Upper sections, with relevant stages. **Right**: Stratigraphic positioning of basal members of Testundinata represented in a cladogram illustrating the phylogenetic relationships between *Odontochelys* and other described Triassic examples such as *Proganochelys* (Schoch and Sues 2015). Image adapted from Li et al. 2008.

These discoveries consolidated the evolutionary history of turtles, thus aiding in understanding how the shell evolved. Despite this, questions remained about the evolutionary relationship between turtles and diapsid reptiles. In 2015, a new species, *Pappochelys rosinae,* was described. *P. rosinae* is a small reptile approximately 20cm long with large, flat ribs contributing which gives it a rounder body shape than other diapsids. This 240-million-year-old diapsid lacked a shell but has anatomical features linking it to later Chelonia and is now considered to be a transitional form (Schoch and Sues 2015, Cordero 2017, Schoch et al. 2019).

Another transitional form between diapsids and turtles is *Eunotosaurus africanus*. This species was originally described in 1892 by H.G. Seeley and is approximately 260 million years old. This species has large, flattened T-shaped ribs and elongated vertebrae contributing to a rounder body shape than seen in *P. rosinae*. These features are attributed to a fossorial lifestyle, with the adaptations to both species increasing stability during digging and burrowing (Gow 1997, Schoch and Sues 2015). Most of the early transitional species and early turtles are thought to have been terrestrial with some evidence of a semi-aquatic lifestyle, which would gradually lead to the evolution of sea turtles, that transitioned from terrestrial or semi-aquatic to a predominantly aquatic lifestyle (Gow 1997; Schoch and Sues 2015, Schoch et al. 2019).

The oldest known sea turtle, *Santanachelys gaffneyi*, is from the Early Cretaceous (112 million years ago). It is a small 20 cm turtle with adaptations for an aquatic lifestyle, including partially formed flippers and larger spaces within the skull for salt glands (Hirayama 1988, Bever et al. 2015). The gaps in the skull allow modern marine turtles to survive in the high salinity of saltwater using salt glands (Hirayama 1988, Bever et al. 2015). The shell of this species also has incomplete ossification between the ribs and vertebra, which also occurs in extant species of marine turtles. This gives them a flatter appearance compared with the domed shells of terrestrial extant tortoises (Hirayama 1988, Cordero 2017).

1.5. TAPHONOMY

Taphonomy is the study of the transition of biological matter from the biosphere into the lithosphere and was first described by palaeontologist I.A. Efremov in 1940 (Lyman et al. 2010). Taphonomy has important uses in palaeobiology including the assessment of sample/ specimen quality by observing taphonomic agents, processes, and circumstances, and the effects on fossilized material (Behrensmeyer et al. 2000). These agents directly influence the potential for an individual to fossilise and become part of the fossil and sedimentological records, meaning that areas of low or high preservation result from variations in taphonomic agents (Behrensmeyer et al. 2000). Early studies of taphonomy laid the structure, stages, and grades on which modern studies have been able to give a greater understanding, for example in the controls of preservation, more specifically in soft tissue preservation (Behrensmeyer 1978; Brandt 1989, Behrensmeyer et al. 2000). Taphonomy also aims to understand the effects of physical, chemical, and biological processes that can cause alterations in preserved organic material through analysing evidence of these processes on preserved samples/specimens (Behrensmeyer et al. 2000).

There are four main stages into which taphonomy can be broken down: necrology, biostratinomy, burial, and diagenesis (Figure 7) (Gastaldo et al. 1996, Grupe 2018). Additionally, post-burial exposure and weathering should be considered as impacting the taphonomic grade of specimens and is further discussed here. The first stage of taphonomy involves the death of an organism (necrology) which can be influenced by a range of factors such as disease, infection, old age, predation, or sudden changes in the palaeoenvironment or paleoclimate (Gastaldo et al. 1996, Grupe 2018, Behrensmeyer and Kidwell 1985).

Biostratinomy is the study of environmental factors that alter organic material between necrology and the burial of remains (Lawrence 1979; Behrensmeyer and Kidwell 1985, Grupe 2018). This encompasses the entire post-mortem history of organic remains, and this can be affected by the decomposition and decay of soft tissue, the abrasion and solution of hard parts, the reworking of hard parts, and re-orientation (Lawrence 1968;

Lawrence 1979). Post-mortem decomposition is instigated by the microbial processes during the decay of the organism’s cells after death. Studies into the preservation potential of marine invertebrates concluded that due to the absence of resistant hard parts around 70% would not be preserved and therefore lost to the fossil record (Lawrence 1979, Grupe 2018). In addition to microbial activity, larger organisms may also scavenge and alter the body after death, leading to disarticulation. Modern-day examples of post-mortem scavenging have been observed to accelerate the decomposition of a corpse and leave distinguishable marks on the bones (Reeves 2009).

Abrasion and solution of a specimen take place as soon as the organism has died and are more prevalent in marine settings where the effects of water and marine movement of sediment are constant, leading to additional disarticulation and altering the orientation of the corpse before burial (Lawrence 1968; Lawrence 1979). Modern-day studies of abrasion of shells have resulted in increased shell reductions correlating with more coarse abrading sediment (Driscoll and Weltin 1973). Transport of material away from the site of death is a key contributor to the loss of information from fossil assemblages (Lawrence 1968).

The conditions of a specimen’s burial are key factors in determining its preservation potential. After the specimen has become entombed in sediment, over time it will gradually be subject to increased pressures such as compaction because of additional sedimentation above (Gastaldo et al. 1996). Specific conditions are required to preserve a specimen in a recognizable form. Within the burial environment processes upon the corpse such as enzymatic, bacterial, and dissolution must be decreased to increase preservation potential (Gastaldo et al. 1996).

Diagenesis is the cumulation of all the processes associated with the lithification of sediment, coupled with the chemical reactions with water trapped between clasts during burial (Behrensmeyer and Kidwell 1985; Gastaldo et al. 1996). The fossilization of specimens is site-specific, influenced by the depositional setting, resulting in patterns between terrestrial and marine depositional environments. Very few fossil-bearing strata are identical, but similarities exist (Behrensmeyer and Kidwell 1985; Gastaldo et al. 1996). Biomineralized tissues are the most preserved body fossils and are the leading source of bulk fossil tissue available for geochemical study. Biomineralized tissues are chemically altered post-mortem and affected over time by the chemical composition of the sediment it was deposited in. This alteration can obscure the original biological features (Trueman 2013). However, it is also possible to analyse new chemical information from altered specimens to infer more about possible depositional environments (Trueman 2013).

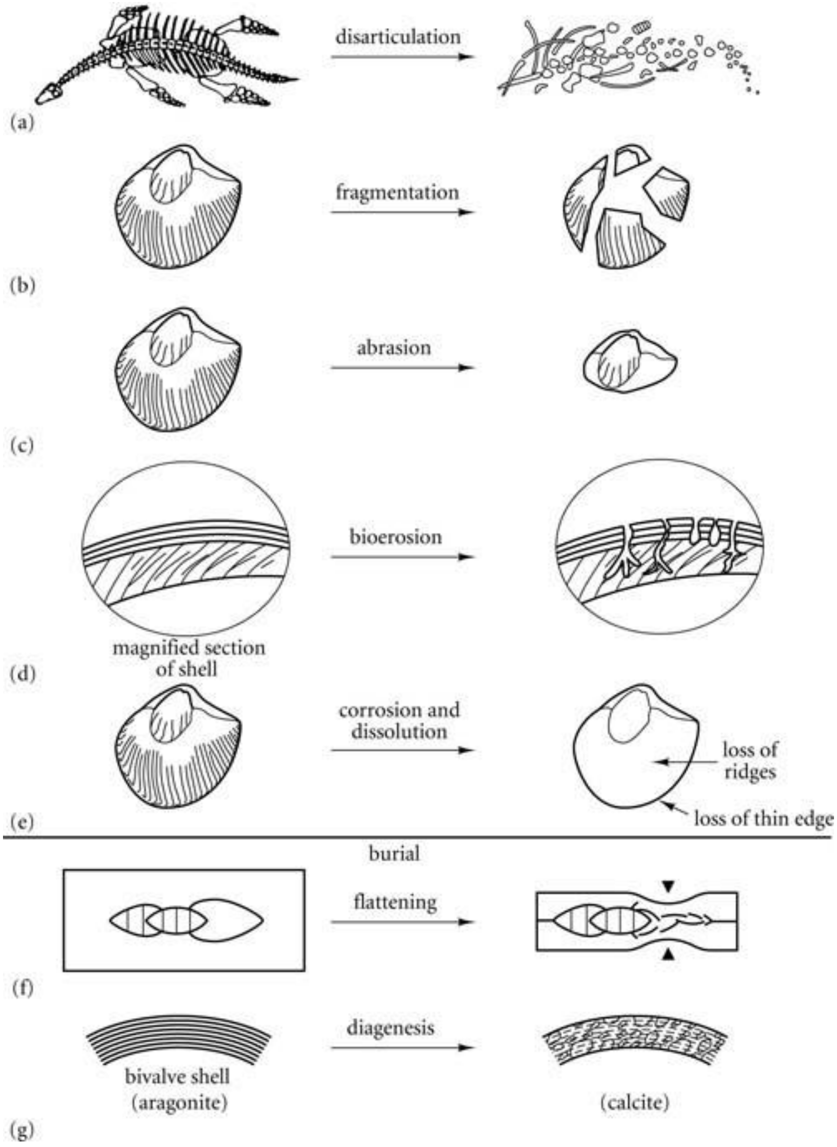


Figure 7 - **Taphonomic** processes from stages 2: Biostratinomy (**A-F**) and stage 3: Diagenesis (G), with illustrated examples of each process. **A –** dissarticualtion **B –** Fragmentation **C –** Abrasion **D –** Bioerosion **E –** Corrosion and dissolution **F –** Flattening **G –** Diagenesis. Image adapted from Benton and Harper 2020.

Not established as a stage of taphonomy by Gastaldo et al 1996 but associated with an organism’s preservation potential post-mortem, post-burial exposure is a critical stage in evaluating the effects of taphonomic processes on specimens. Exposure can be caused by shifting of strata post-burial, thus exposing the material to different chemical and physical settings, for example, exposure due to cliff erosion and sudden movement of sediment (Mottershead 2013). Exposed material in coastal settings especially has similar processes identified in biostratinomy such as abrasion and solution and multiple re-workings of preserved hard parts and possible re-orientation (Lawrence 1968; Lawrence 1979). The difference between post-burial exposure and biostratinomy is that the latter occurs within a short time frame of death, whereas post-burial exposure can occur millions of years after burial, thus causing further alteration of preserved material (Mottershead 2013). This process can lose previously preserved material, as exposure often results in transportation and additional weathering (Lawrence 1968; Mottershead 2013).

2. VERTEBRATE FOSSILS OF THE BOUDNOR FORMATION

The focus of this study, the Bouldnor Formation, contains a diverse vertebrate fossil assemblage of mammals, lizards, snakes, birds, crocodilians, amphibians and fish with mammalian taxa being the most well-studied (e.g., Insole et al. 1985; Wolff et al. 2007, Hooker et al. 2009, Hooker 2010). The vertebrate remains are often found as disarticulated, isolated specimens of bones, teeth or scales but can also include shed skin from squamates and avian feathers (Hooker 2009; Hooker 2019).

The mammalian fauna from the Bouldnor Formation has been extensively collected and analysed to reconstruct the biodiversity across the Eocene/Oligocene boundary (Hooker et al. 2004; Hooker 2010). Hooker (2010) reviewed all the mammalian taxa found within the formation to identify the impact of the ‘Grande Coupure’ on the changing biodiversity. They were able to identify two separate mammalian groups belonging to either the Headonian (Eocene) or the Suevian (Oligocene) European Land Mammal Ages (ELMA) (Hooker et al.

2009). Those belonging to the Headonian Land Mammal Age had been typically endemic to Europe and are inferred to have evolved in isolation due to early Eocene Europe being an archipelago separated from the other continents (Hooker et al. 2009). Key mammals include glirid and theridomyid rodents, large ungulates, palaeotheres, anoplotheres, omomyid and adapid primates, as well as rare carnivorans and creodonts (Hooker et al. 2009). However, those from the Suevian Land Mammal Age included new fauna, such as enteledonts, amphicyodon, castorid, eomyid rodents and lipotyphlans and the extirpation of all palaeotheres, anoplotheres and the majority of endemic nyctitheres, artiodatyls and omomynids (Hooker et al. 2009). However, it is the chelonian (turtle) fossils from the Bouldnor Formation that remain an understudied facet of this established ecosystem and is now the focus of this work.

2.1. CHELONIA OF THE BOULDNOR FORMATION

Chelonia fossils identified and described from the Bouldnor Formation include *Trionyx incarassatus* and *Emys* sp and are present in the collections of both the Natural History Museum, London (NHMUK) and Dinosaur Isle (Moody 1997; Daley 1999, Hooker et al. 2004, Hooker et al. 2009, Hooker 2010, Donovan and Simpson 2020). Remains are often found as disarticulated carapace and plastron fragments or sections, but rarely articulated or semi-articulated (but commonly as carapace fragments).

Unlike the other vertebrates from the Bouldnor Formation, (more specifically the upper and lower Hamstead members within), chelonian fossils have not been well-studied (Insole and Daley 1985; Hooker 2010). Either mentioned as a footnote within other literature exploring the vertebrates of the Bouldnor Formation or explained in little detail within papers over 3 decades old, the literature on the chelonian fossils of the Hamstead beds is limited (Moody 1997; Daley 1999, Hooker et al. 2004, Hooker et al. 2009, Hooker 2010). Due to the often-poor condition (fragmented) of chelonian fossils (e.g., disarticulated and/or severely damaged) in the Bouldnor Formation due to is often difficult to identify the genus or species

(Hooker et al. 2009). Because of these challenges, only one recent study has been published on chelonians from the Bouldnor Formation (Donovan and Simpson 2020).

Donovan and Simpson (2020) and Daley (1999) have both identified *Emys sp.* within the Bouldnor Formation. This species belongs to a small group of pond turtles from the family *Emydidae* (Ernst et al. 1994). Characteristics of the family include: low, arch-shaped carapaces, but can be bowl or dome-shaped; possibly a pair of ridges (keels) which run craniocaudally along the carapace; a prominent bridge connecting the carapace to the plastron; a larger plastron compared to body size than in other families of Chelonia; smaller skulls compared to body size; and some species have a moveable hinge that separates petoral and abdominal sections (Ernst et al. 1994).

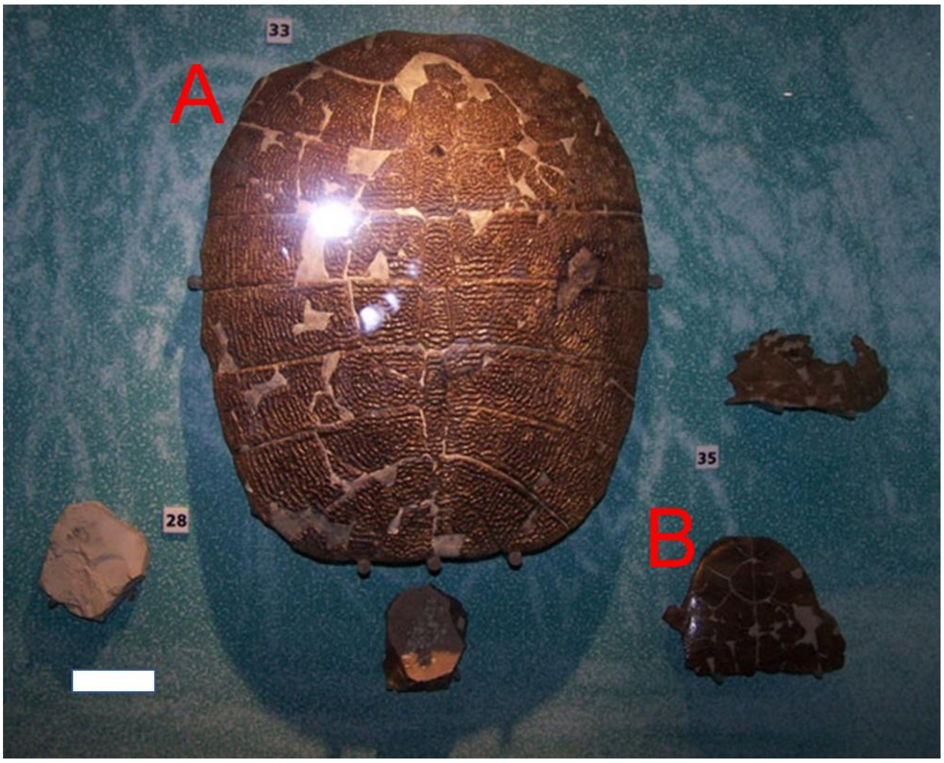


Figure 8 - Isle of Wight fossil turtles. A. A preserved *Trionyx incrassatus* carapace (Centre) B. *Emys sp.* plastron found at Fishbourne (Right). Due to the lack of a scale bar in the photos, the white scale bar is estimated to be 15mm in length. Images credited to MIWG were adapted from (Chatfield 2009).

Other turtle fossils reported from the Bouldnor Formation include *Trionyx incrassatus* (Owen 1849) (Figure 8); a species of turtle belonging to the Trionychinae family. This family are commonly known as softshell turtles and extant examples are some of the world's largest freshwater turtles (Meylan 1987; Engstrom et al. 2004, Webb 2022, Zug 2023). The name "softshell" is used because of the lack horny scutes on the turtle's carapace. The central part of the carapace still consists of a solid layer of bone underneath the leathery external covering of the carapace (Rhodin et al. 2010). Some species of the family also retain ossified bone in the plastron; however, unlike *Emydidae*, these are not moveable and do not join the top and bottom shells. The flexibility of the modified shell makes moving through the water easier and in, turn makes these animals faster in water and on land than the other chelonian families (Ernst et al. 1997; Rhodin et al. 2010).

The primary distinguishing difference between *Trionyx* carapace fragments and *Emys* carapace fragments is that the *Trionyx* samples have distinctive ornamentation upon the surface of the carapace while *Emys* does not (Webb 1990, Pamfilie et al. 2022) (Figure 9).

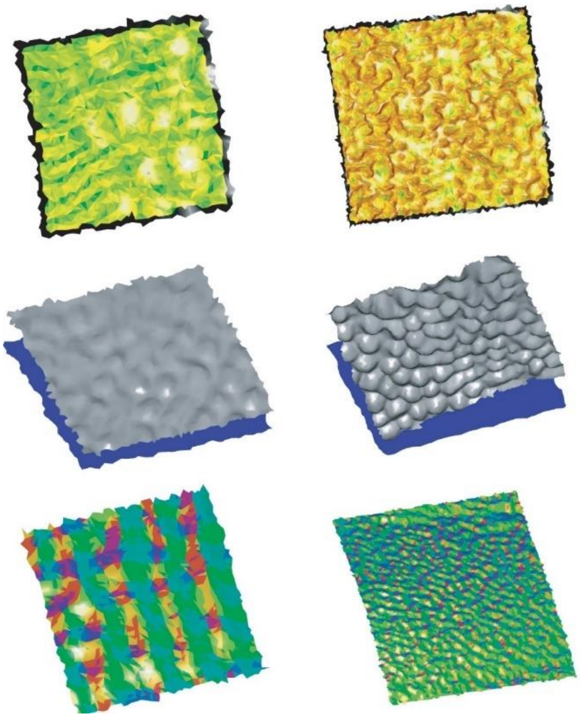


Figure 9 - Scans of six different cuttings of soft-shelled turtle carapace, displaying distinct textures which can be used to identify *Trionyx* fragments in this study.

Image adapted from Pamfilie et al. 2022.

Additionally, *Trionyx* carapaces have bony protrusions on the edges of the carapace where the rib meets the shell wall (Pamfilie et al. 2022). These are rare to find however are a key distinguishing factor (Webb 1990). Plastrons of both genera are smooth, making these specimens harder to identify (Webb 1990). However, another way to distinguish the two genera is size; *Trionyx* specimens are on average much larger than that of *Emys*, however, this depends on the age of an individual and the taphonomic grade of the specimen (Webb 1990; Brandt 1989). Considering these distinguishable features between the two genera it is possible to identify fragments obtained in the field or those observed in collections.

3. CHELONIAN PATHOLOGIES

Pathology is the study of the effects of disease or injury on an individual's anatomy, modern day practises of this study combine scientific understanding and diagnostic methods to further improve prevention and treatment (Underwood 2016). Pathology analyses functional and structural alterations in disease in patients, aiding in the medical understanding of specific diseases, and identifying causes and mechanisms of disease (Underwood 2016). Approximately 70% of clinical diagnoses in the USA involve the study of pathology and clinical examples of pathology include Histopathology, Cytopathology, Haematology, Microbiology, Immunology, Chemical pathology and Forensic pathology (Underwood 2016).

Palaeopathology is the study of ancient disease and injury, through the analysis and descriptions of fossils, skeletal remains, mummified tissue and coprolites, and the causation of any observable damage that happened whilst the organism was still alive (Buikstra and Cook 1980; Waldron 2020). Palaeopathology differs from pathology in that the causes of identified pathological features can be observed in real-time, whereas in Palaeopathology causes of pathological features are often inferred or even unknown (Buikstra and Cook 1980; Zonneveld et al. 2015, Waldron 2020). Pathologies identified within extant turtle species are described below including Palaeopathologies evident in extinct chelonian remains.

Pathological descriptions of extant chelonians are well documented, whilst studies into pathologies of extinct chelonians are rare (Rothschild et al. 2013; Botfalvai et al. 2014, Norton and Wyneken 2014). Extant chelonian pathologies that may affect the shell may be the result of disease (e.g., ulcerative dermatitis), parasitism (e.g., barnacles), injury (e.g., fractures, predation) (Rothschild et al. 2013; Norton and Wyneken 2014). Extinct turtle pathologies are poorly documented; many displays similar features to those in extant species, however studies correlating the two are scarce and are speculative (Rothschild et al. 2013; Botfalvai et al. 2014, Zonneveld et al. 2015, Zonneveld et al. 2021). Studies have illustrated the presence of disease, predation, parasitic behaviour and post-mortem scavenging but the pathological contributor is often unknown (Zonneveld et al. 2015; Zonneveld et al. 2021).

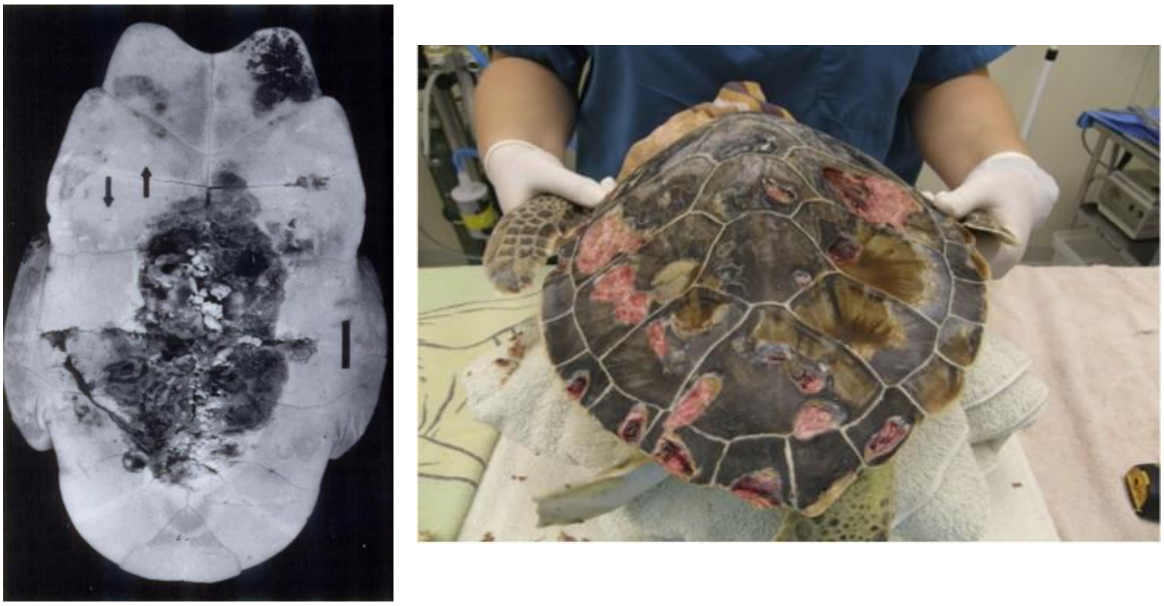


Figure 10 - Examples of ulcerative dermatitis on the plastron of *Trachemys scripta* (Left: Garner et al.1997) and on the carapace of a Green Sea Turtle (*Chelonia mydas*) (Right: Norton and Wyneken 2014).

Ulcerative dermatitis is a bacterial disease which causes deep lesions in the shell (Maas 2013; Rothschild et al. 2013, Norton and Wyneken 2014). It is observed in multiple families of chelonians, affecting individuals of all ages and sizes (Garner et al. 1997; Maas 2013, Norton and Wyneken 2014). Followed by the formation of cysts and ulcers lesions that form on the surface of the carapace and plastron causing large sections of the shell to become exposed, inducing further infection (Garner et al. 1997). Lesions are spaced erratically and follow no pattern of formation. Infection lesions can spread and create large areas of carapace and plastron bone tissue to become destroyed (Garner et al.1997) (Figure 10).

Parasitism has been observed extensively within modern-day chelonians. Turtle epibionts predominantly settle on the carapace and plastron and cause damage to the bone depending on the length of attachment (Frick et al. 1998, Pfaller et al. 2006, Janssen et al. 2013). Parasitic taxa that have been identified on turtles include barnacles and Lampreys, observed in both fresh and saltwater environments and upon the shells of Cheloniidae, *Trionychidae* and *Emydidae* (Hayashi and Tsuji 2008). Damage caused by parasitic activity is concentrated on the carapace or plastron (The largest accessible section of a turtle's anatomy (Zonneveld et al. 2015, Cordero 2017), it is thought to be due to the large surface area of turtle shells, which allows for a higher chance of successful attachments (Hayashi and Tsuji 2008, Janssen et al. 2013). Multiple forms of parasitism can be observed upon an individual, evident in both extant and extinct species, meaning multiple parasitic organisms can occupy a host whilst it is still alive (Hayashi and Tsuji 2008, Janssen et al. 2013).

Examples of parasitic behaviour in extinct species have been generally well documented, but uncertainties remain surrounding the causes of some parasitic examples, however, actively contributing to the alteration and damaging of shells is evident (Janssen et al. 2013; Zonneveld et al. 2015, Zonneveld et al. 2021). Evidence of parasitic borings have been observed in turtle specimens from both the Eocene and Miocene, with examples of both penetrative and non-penetrative borings (Zonneveld et al. 2015; Zonneveld et al. 2021). Four new ichnospecies of boring parasites were identified upon the carapace and plastron of the Eocene turtle from the Wasatch Formation, Wyoming, three types of non-penetrative boring ichnospecies were identified as *Karethraichnus lakkos, Karethraichnus kulindros and Thatchtelithichnus holmani* (Zonneveld et al. 2015*). Karethraichnus fiale* penetrated fully through the shell of the host, creating deep cylindrical pits in the carapace (Zonneveld et al.

2015). Zonneveld et al. 2015 concludes the findings by correlating the positioning of the borings upon the shell of the specimens, with evidence of healing within most of the borings indicating that the borings were emplacements by ectoparasites (Zonneveld et al. 2015).

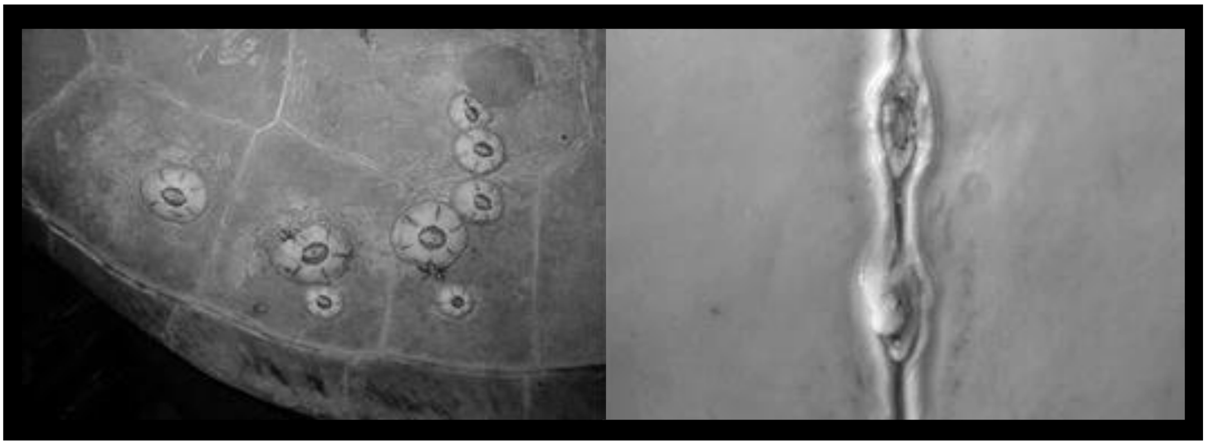


Figure 11 - images adapted from Hayashi and Tsuji. 2008, showing *C. testudinaria* and *S. transversa* and their differing positions on the carapace on the same individual. Left: *C. testinudaria* imbedded into the carapace of *Chelonia mydas*. Right: *S. transversa* positioned within the plastron sulcus.

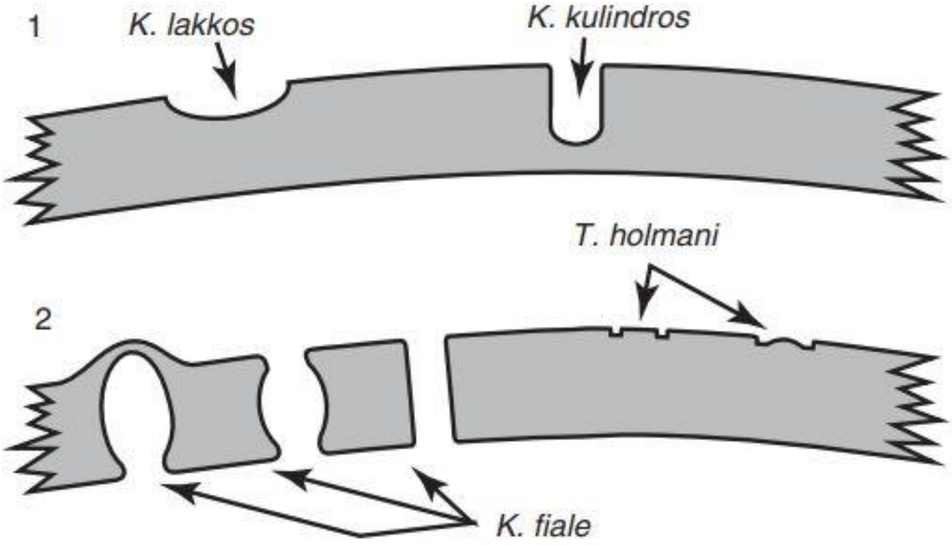


Figure 12 - Differences between the 4 ichnospecies, *Karethraichnus lakkos, Karethraichnus kulindros, Karethraichnus fiale* and *Thatchtelithichnus holmani* and their boring types into turtle shells found within the Wasatch Formation, Wyoming adapted from Zonneveld et al. 2015.

The latter study, Zonneveld et al. (2021) discusses the occurrences of borings upon the carapaces of the terrestrial tortoise and aquatic turtle specimens, as included in Zonneveld et al. 2015, the *Karethraichnus lakkos* holotype is identified within numerous specimens of aquatic turtle carapaces (Zonneveld et al. 2021). With these findings, it can be assumed the parasitic relationship between tortoises/ turtles and ectoparasites extends as far back as the early Miocene, or if correlated with older specimens, even older (Zonneveld et al. 2021).

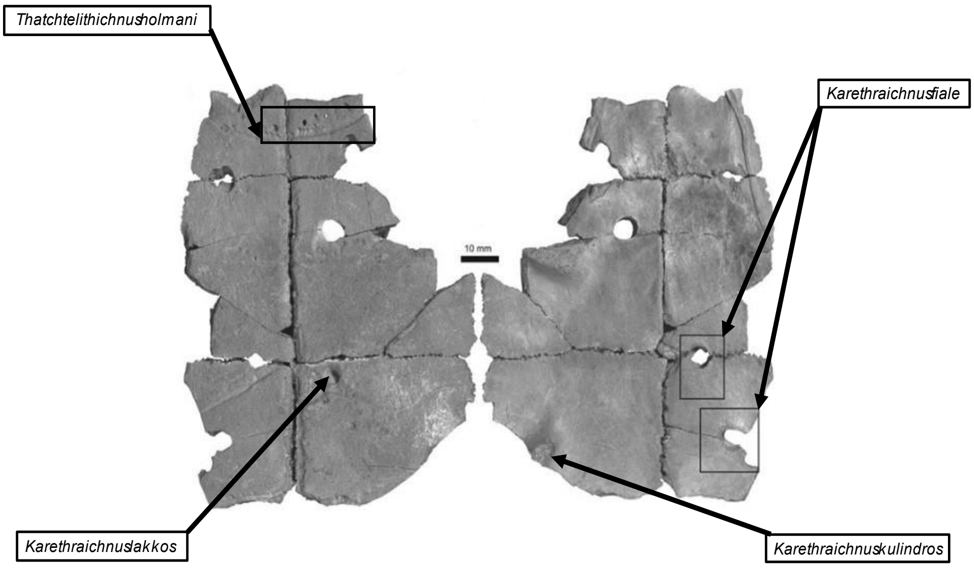


Figure 13 - A specimen of *Echmatemys* sp. exhibiting both non-penetrative borings of *K.kulindros, K.lakkos and T.holmani* and more significantly, penetrative boring traces, *K.fiale*. (Zonneveld et al. 2015).

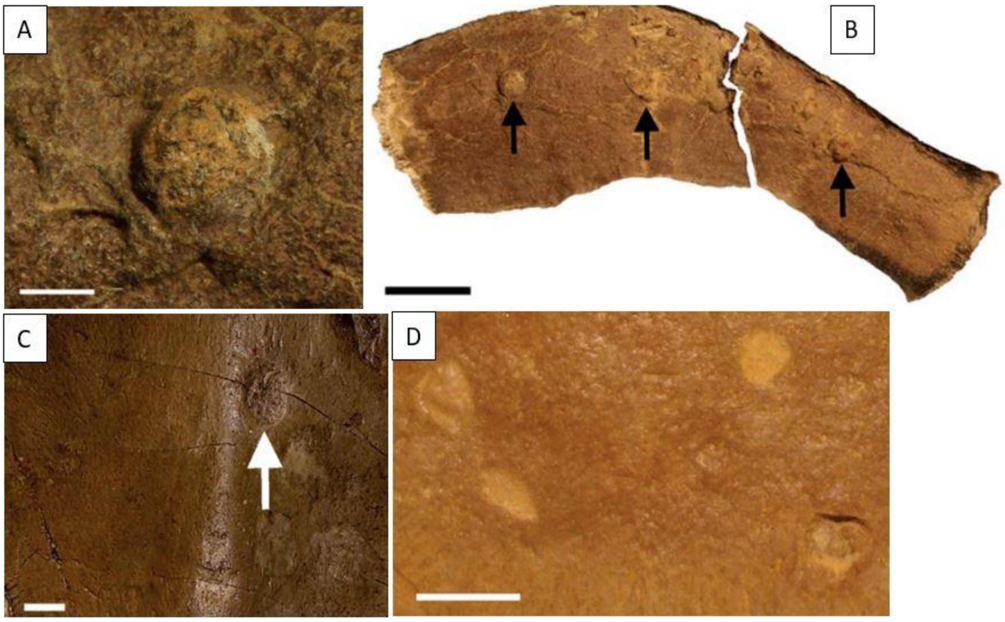


Figure 14 - Images showing lesions present upon various segments of bone tissue of *Allopleuron hofmanni*. A. Magnified image of a pit-like lesion (Scale bar = 10mm), showing the circular structure, depressed outer perimeter and raised inner structure. interpreted to be barnacle attachment with possibility of bone regrowth after trauma. B. A collection of pit-like lesions located on the anterior peripheral rim (Scale bar = 50mm). C. A deeper circular lesion interpreted to be a barnacle embedment (Scale bar = 10mm) D. A cluster of shallower circular lesions located on the carapace, intrepreted to be caused by parasitic behaviour or disease caused by trauma (Scale bar = 10mm) (Adapted from Janssen et al. 2013).

Another example of parasitism on extinct specimens is discussed by Janssen et al. (2013) who observed and described the damage caused by borings of bivalves and radula traces of Molluscs, it is suggested that the borings are similar in dimensions to that of the modern-day boring bivalves domichnia (Janssen et al. 2013). Several radula traces are observed but it is uncertain as to whether the trauma occurred as the specimen was still alive or post-mortem, however, similarly to the traces left by the bivalves, extant species of mollusc exhibit the same characteristics as modern-day sea turtles (Janssen et al. 2013).

Chelonian fossils occasionally have bite marks or impact damage, determining if the damage is from predation whilst the animal is still alive or scavenging post-mortem is challenging (Rothschild et al 2013, Janssen et al 2013). Marks appear on the carapace and plastron as these are the largest areas and are most likely to be attacked or scavenged. In the fossil record, these appear as scrapes or gouging (Figures 15 and 16) of the bone, indentations (Figures 12 and 14) or holes in the bone (Figure 13) (Janssen et al 2013, Botfalvai et al. 2014, Zonneveld et al. 2021). Interpretation of predation versus scavenging has been based on the amount of scrapping (Janssen et al 2013), and the number of potential tooth indentations (Botfalvai et al. 2014, Zonneveld et al. 2021). With no clear evidence of bone healing, any marks should be perimortem (at best) or post-mortem scavenging (Rothschild et al 2013).

Figure 15 - Image showing the repeated linear gouges on the carapace of *Alloplueron hofmanni* interpreted to be post-mortem scavenging (adapted from Janssen et al. 2013)

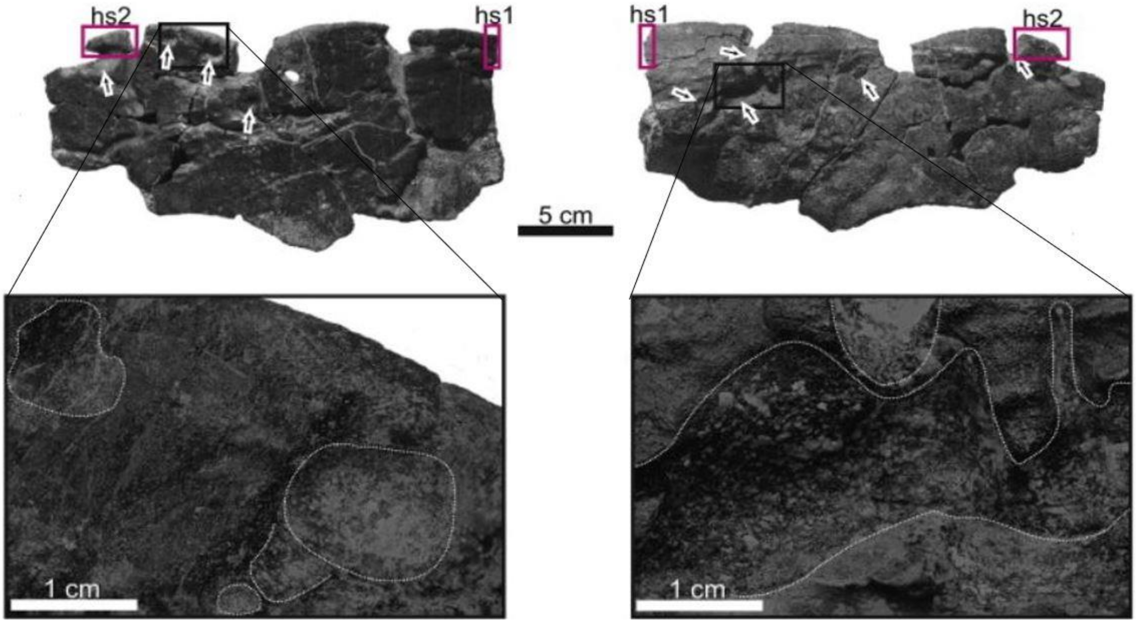


Figure 16 - *Foxemys* carapace from the Iharkút locality. White arrows are pointing to pathologies (upper images), with magnified views below. These are interpreted to have been caused a large predator within the same ecosystem (adapted from Botfalvai et al. 2014).

4. X-RAY MICROTOMOGRAPHY AS A TECHNIQUE TO STUDY FOSSILS AND EXTANT BONE

Micro-computer tomography (micro-CT) has been used in medical imaging for over four decades, the roots of this have come in the form of Computerised Axial Tomography (CAT/CT) (Stock 2009, Orhan 2020). Micro-CT is an imaging technique that utilizes X-rays to image the internal and external structure of an object. Specimens can be imaged with high resolution and with small pixel sizes, as small as 100 nanometres (Orhan 2020). Scanners capture a set of 2D X-ray images that can be reconstructed and processed in 3-D models or 3-D printed as physical objects (Orhan 2020). The X-rays are created by a source that transmits the energy through the desired object with each scan recorded by an X-ray detector as a 2-D image (Orhan 2020). To create the 3-D image, the object has rotated a fraction of a degree and the process is repeated through a 180 degree although this can sometimes be a 360-degree arc (Orhan 2020). The set of collected 2-D X-rays is then analysed by a computer and reconstructed to be altered to suit the needs of any study (Orhan 2020).

Numerous studies have taken place into the use of microtomography to study modern and fossilised bones and teeth (e.g., Stock 2009, Zonneveld et al. 2022, Wilson 2023, Ferriera et al. 2023). Additionally, micro-CT has been used to diagnose pathological conditions in modern turtles including soft tissue (e.g., Stock 2009; Weisbrod et al. 2020, Krahl et al. 2020) and bone (e.g., Lintner et al. 2012, Chen et al. 2015, Ganjbakhsh et al. 2020). Micro-CT is used extensively in recent literature, more specifically in modern species of turtle. For example, Chen et al. (2015) used micro-CT to evaluate the differences between Leatherback Sea turtles and other members of the family Cheloniidae by analysing the bone structure to study suture lines of the carapace (Figure 17) (Chen et al. 2015). Micro-CT also allows for 3-D reconstructions of scanned material that is otherwise flattened or disarticulated.

For example, Lintner et al. 2012 reconstruct a 3-D skull and hyolingual skeleton, displayed in ventral, dorsal and lateral views based on micro-CT data (Lintner et al. 2012) (Figure 18). This technique can be further utilised to diagnose chelonian pathologies in the fossil record, although this is very limited (Schoch et al. 2019, Haridy et al. 2019, Carabajal et al. 2013). By using micro-CT, the internal microstructure of bone can be examined to identify if there has been an osteological response to bone damage (Welsh et al. 2020, Wang et al. 2022, Zonneveld et al. 2022). If there is evidence of healing, that indicates a physiological response has occurred while the animal was alive. If there is no evidence of healing or resorption, then the pathology must have happened perimortem or post-mortem (Janssen et al. 2013, Bothalvai et al. 2014).

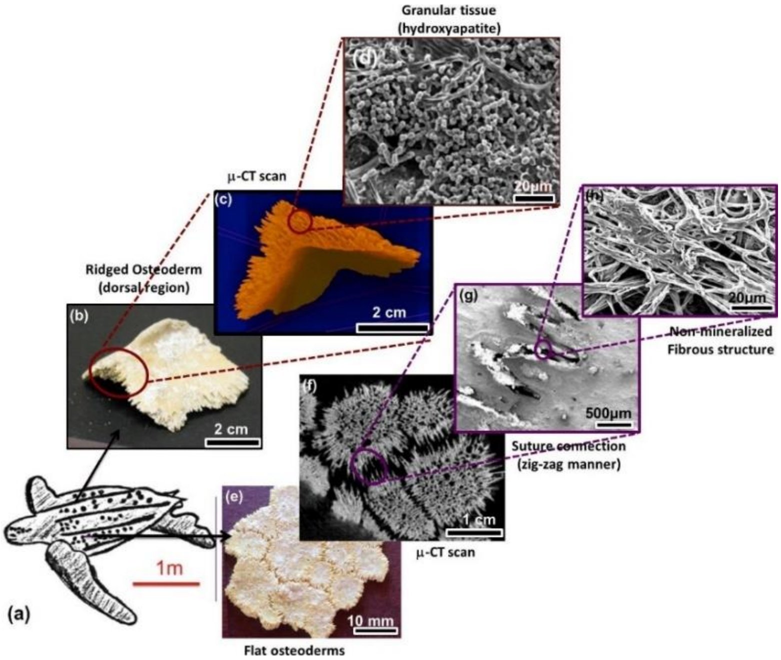


Figure 17 - **A-** Leatherback turtle shell, **B-** Ridged osteoderm for scanning, **C-** micro-CT scan of the ridged osteoderm, **D-** Showing high magnification of granular morphology. **E-** Flat osteoderm for scanning, **F-** micro-CT scan indicating porous morphological features, **G-** suture design with connectors. Image credited to Chen et al. 2015.

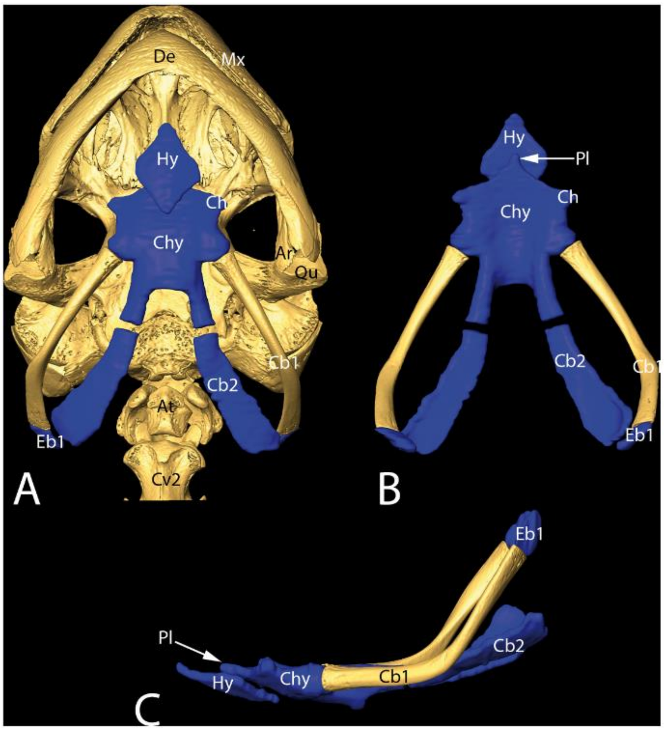


Figure 18 - (A-C) 3-D reconstructions created based on micro-CT scans. **A-** Ventral view of skull showing the position of the hyolingual skeleton, **B + C-** Dorsal and Lateral views (Removing skull). Image credited to Lintner et al. 2012.

Micro-CT of fossils can reveal pathological conditions within ancient biota (Surmik et al. 2018, Chen et al. 2015, Ganjbakhsh et al. 2020, Carabajal et al. 2013). For example, a respiratory infection (pneumonia) within a 245-million-year-old Triassic reptile, *Proneusticosaurus silesiacu* has been diagnosed and studied using micro-CT of lesions on its left dorsal ribs (Figure 19) (Rothschild and Martin 2006; Surmik et al. 2018). Similar bone lesions can be found in extant species, including humans, exhibiting symptoms of *Mycobacterium tuberculosis* (Naples and Rothschild 2011; Anson et al. 2012, Surmik et al. 2018).

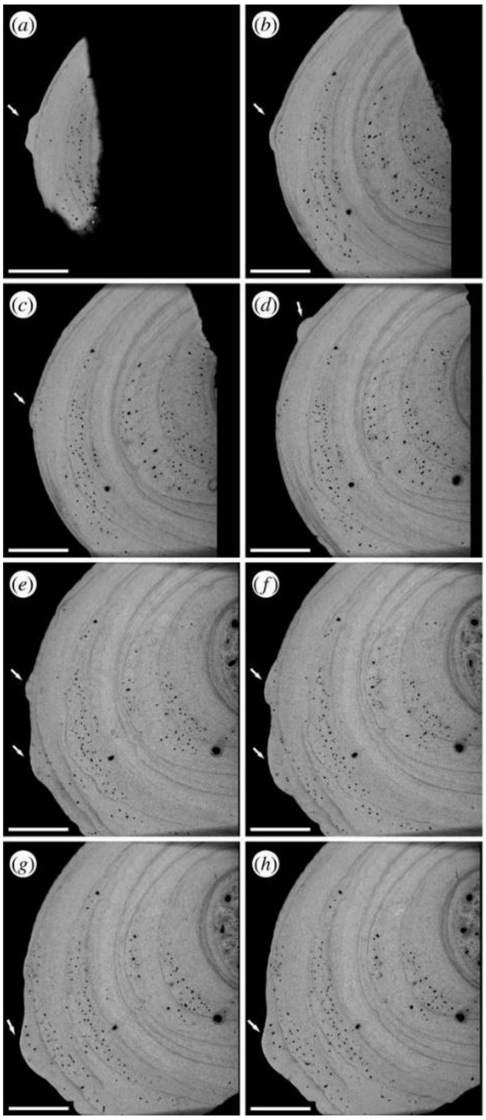


Figure 19 - X-ray microtomographic images of the dorsal rib sections of *Proneusticosaurus silesiacus* showing lesions (arrows) observed on the left side of the animal. 2018. Scale bar equals 1 mm. Adapted from Surmik et al. 2018.

Other examples of micro-CT being utilised to highlight palaeopathologies include identifying a highly malignant bone tumour (Osteosarcoma) in the femur of the Triassic stem turtle *Pappochelys rosinae* (Schoch et al. 2019, Haridy et al. 2019). The micro-CT scans allowed researchers to observe the delineation between the compact cortex and the dense cortical bone to easily distinguish them from the cancellous overlying mass (Figure 20) (Haridy et al. 2019).

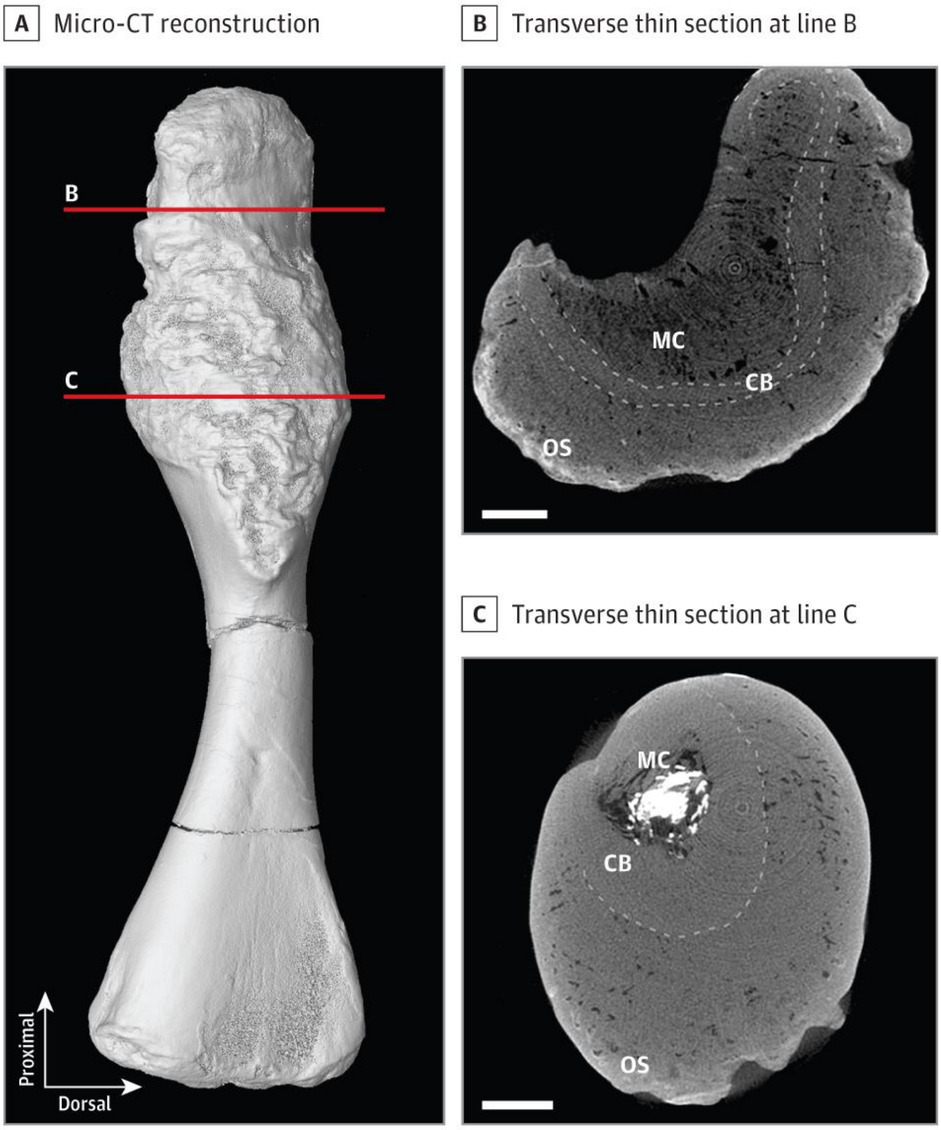
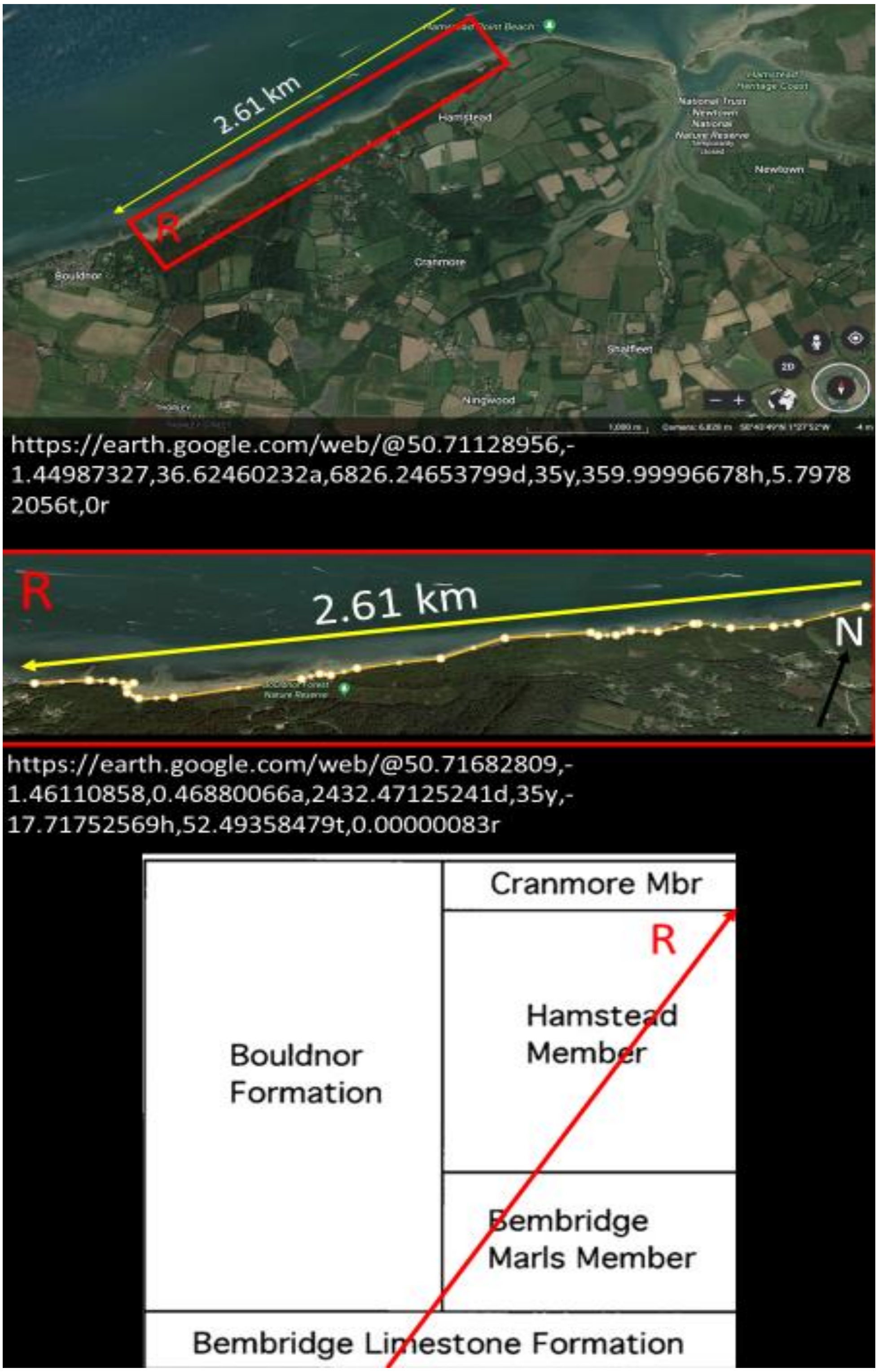


Figure 20 - Micro-CT scans of the specimen identified in Haridy et al. 2019. A – Scan showing the full femur, with red lines representing the thin section scans shown in B and C. All scale bars represent 1mm. CB= cortical bone, MC= medullary cavity, OS= identified Osteosarcoma.

5. MATERIALS AND METHODS

5.1 SAMPLE COLLECTION



https://earth.google.com/web/@50.71128956,-1.44987327,36.62460232a,6826.24653799d,35y,359.99996678h,5.79782056t,0r

https://earth.google.com/web/@50.71682809,-1.46110858,0.46880066a,2432.47125241d,35y,-17.71752569h,52.49358479t,0.00000083r

Figure 21 - Satalite images of the route taken from Hamstead to Bouldnor (R) for sample collection, outlined in red on both map sections. The lower image shows the stratigraphic column and the overall route across the the formations and members exposed along the 2.61 kilometre route ending at Bouldnor (R). Two map sections adapted from Google Earth; Stratigraphic column adapted from Gale et al. 2006.

Chelonian fossils were collected during fieldwork on the Isle of Wight in August 2022; the collection of samples was dictated by the double tide regime on the Island. Samples were collected walking east along the coastline from Hamstead (coordinates: 50.724117, -1.433861) to Bouldnor (coordinates: 50.708212, -1.480290). Along the 3000-metre stretch of coastline that was sampled, the Headon Hill Formation, Bembridge Limestone Formation, and both Upper and Lower Hamstead Members of the Bouldnor Formation were exposed (Figure 21). Fossil collection was prioritised for the Upper and Lower Hamstead Members. The boundaries between formations were identified using BGS Geo-viewer, location coordinates and visual interpretation of rock strata. Fossils identified from the Headon Hill Formation and Bembridge Limestone Formation were collected but not included in the study.

Samples were collected whilst walking along the coastline, every fossil identified was collected and specimens were placed into separate sample bags and labelled (Figure 21). Ninety specimens were collected during the fieldwork undertaken. Most fossils were found in loose unconsolidated sediment *ex-situ*; however, some samples were found within sections of debris that had fallen from or been washed along the shoreline (a function of longshore drift). All samples were photographed with a scale bar, using a Canon G12 camera once collected and returned from the field. Fragments collected were compared to specimens previously observed within the Dinosaur Isle Bouldnor collection and the Natural History Museum Bouldnor collection to help with identification and separation.

5.2. MUSEUM COLLECTIONS

Eocene and Oligocene Isle of Wight Chelonia specimens from the London Clay, Headon Hill, and Wittering Formations were examined at Dinosaur Isle (The Isle of Wight Museum) and The Natural History Museum London. Both museums have a mixture of complete and fragmentary carapace and partial skeletal remains. Dinosaur Isle has 52 fragmentary samples of *Emys* sp. and *Trionyx* sp. (Appendix A) and the Natural History Museum London has 49 (Appendix B) in their collections. These were all photographed (Appendix A) and examined for potential pathologies and to identify the taphonomic grade.

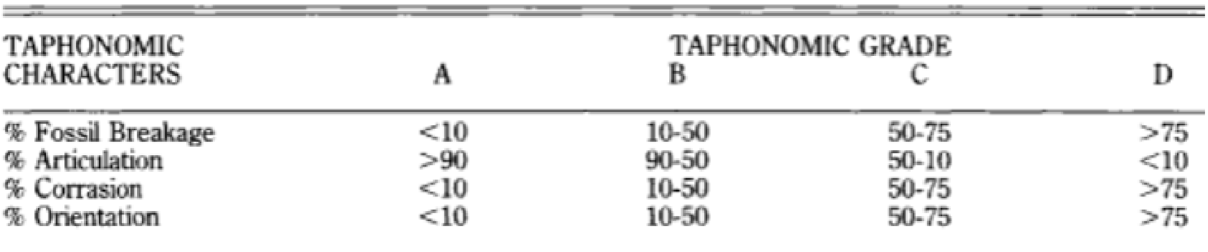
All samples were photographed on a Canon G12 camera and processed in Photoshop as necessary.

5.3. MICRO-CT

Micro-CT analysis was conducted at the National X-ray Computed Tomography facility at the University of Manchester on a piece of pathological carapace from *Emys* sp. collected by project supervisor Prof. Phillip Manning and donated to this study. The micro-CT unit used was the Zeiss Xradia Versa XRM-500T (Unit number:345360-0000-032) located within the Henry Mossley Centre at the University of Manchester. The magnification was 0.5X with projections over 360º and includes a total of 1938 projections. The exposure time was 0.07 seconds with a voxel size of 1x1x1 pixel^3 and the voltage at 90Kv. The three-dimensional images and slices of the carapace were processed using FIJI (https://fiji.sc) (Schindelin et al. 2019).

5.4. TAPHONOMIC GRADE

The taphonomic grade refers to how well a specimen is preserved which is then graded depending on certain factors (e.g., breakage, articulation, corrasion and orientation) that are influential to fossiliferous remains (Brandt 1989) (Figure 22). This thesis follows the basic principles established in Brandt (1989), and that is expanded further by Behrensmeyer et al. (2000).



TAPHONOMIC CHARACTERS	TAPHONOMIC GRADE A	B	C	D
% Fossil Breakage	<10	10-50	50-75	>75
% Articulation	>90	90-50	50-10	<10
% Corrasion	<10	10-50	50-75	>75
% Orientation	<10	10-50	50-75	>75

Figure 22 - Taphonomic characters: Fossil Breakage, Articulation, Corrasion and Orientation expressed as percentages. Adapted from Brandt 1989.

Based on the taphonomic characters established by Brandt (1989), any specimens ranked in grade A are exceptionally preserved specimen showing very little fossil breakage, corrasion and orientation, but also have high percentages of articulation (being complete or near complete samples). Grade B specimens are well-preserved examples that are near or partially complete; however, they are less intact than grade A or show further signs of corrasion. Grade C specimens are large fragmentary remains, sections of skeleton or carapace that are weathered and corroded, these specimens are subject to more weathering than that of Grade A and B. Grade D specimens are small fragmentary remains that are badly preserved, either highly weathered or too small to identify any pathologies.

6. RESULTS

Independent fieldwork and sample collection at the Bouldnor Cliffs were carried out in August 2022 to acquire and collect additional specimens. From the 3 days of fieldwork, 67 specimens of *Emys* sp. were collected, along with 12 *Trionyx* sp., 10 crocodilian specimens (possibly *Diplocynodon*), including 2 crocodilian vertebrate specimens and 1 mammalian specimen, giving a total of 90 specimens overall (Figure 19). No articulated remains were found. Additionally, chelonian remains from the Bouldnor Formation were observed and analysed from the collections at the Natural History Museum (NHMUK PAL R8136) and Dinosaur Isle Museum (MIWG Sample 3, MIWG 4112, MIWG 4114, MIWG 4115, MIWG 4429, MIWG 4430 and MIWG 4882).

Most specimens observed are fragmentary, partial, or complete carapaces and plastrons of species of *Emydidae* and *Trionychidae*. The samples that displayed damage or irregularities were grouped separately from specimens that did not, then organised into sections based on the type or damage the specimen displayed. These sections are pitting/ borings which have non-penetrating and penetrating variants, scoring/ gouging, and taphonomic damage. The groupings have been categorised in Tables 1 and 2. Table 1 provides all the observed specimens from the two museum collections at the NHMUK and MIWG and Table 2 lists all observed specimens that displayed damage.

NHMUK 30408	30408	1	*Trionyx incrassatus*	B	Hordwell	Upper Eocene	Partial carapace.
NHMUK 12737	12737	1	*Trimyclid ?*	B	Bracklesham bay, Sussex	Eocene	Partial carapace. Pathologies identified.
NHMUK?	?	1	*Trionyx*. sp	B	Hamstead Beds	Eocene	Partial carapace and partial skeleton.
NHMUK Moody	Moody	28	*Trionyx*. sp	B	Bembridge Marls member	Oligocene	Fragments of carapace, vertebra and partial skeleton. Pathologies identified.
NHMUK?	?	1	*Trionyx*. sp	B	Hordle, I.O.W.	Eocene/ Oligocene	Partial carapace. Pathologies identified.
NHMUK 12788	12788	1	*Eurycephalochelys fowleri*	A	West Wittering, Sussex	Eocene	Complete carapace.
NHMUK 8694	R 8694	1	*Eurycephalochelys fowleri*	A	West Wittering, Sussex	Eocene	Complete skull.
NHMUK 844	R 844	1	*Eurycephalochelys fowleri*	B	West Wittering, Sussex	Eocene	Partial skull.
NHMUK 8695	R 8695	1	*Eurycephalochelys fowleri*	B	East Wittering, Sussex	Eocene	Partial skull.
NHMUK 221	R 221	1	*Emyda vittata*	C	Gulf of Cambay, India	Pliocene	Partial skull.
NHMUK 39833	R 39833	1	*Emyda vittata*	B	Siwalik Hills, India	Pliocene	Partial carapace.
NHMUK 39618	R 39618	1	*Emyda vittata*	B	Siwalik Hills, India	Pliocene	Partial carapace.
NHMUK 30409	R 30409	1	*Trionyx Barbarre*	A	Hordwell, Hampshire	Upper Eocene	Complete carapace.
NHMUK 1592	R 1592	1	*Trionyx Barbarre*	B	Hordwell, Hampshire	Upper Eocene	Partial carapace.
NHMUK 30406	R 30406	1	*Trionyx henrici*	A	Hordwell, Hampshire	Upper Eocene	Complete carapace.
NHMUK 30413	R 30413	1	*Trionyx henrici*	A	Hordwell, Hampshire	Upper Eocene	Complete carapace.
NHMUK 39843	R 39843	1	*Trionyx gangenticus*	B	Narbada valley, India	Pleistocene	Partial skull.
NHMUK 4127	R 4127	1	*Lytoloma planimentum*	A	Harwich, London clay	Eocene	Complete skull.
NHMUK 37205	R 37205	1	*Lytoloma crassicostatum*	A	Harwich, London clay	Eocene	Complete skull.
NHMUK 38950	R 38950	1	*Puppigerus camperi*	A	London Clay, Sheppey	Eocene	Complete carapace and plaston.
NHMUK 3964	R 3964	1	*Eochelys classicostata*	B	London Clay, Sheppey	Eocene	Complete plastron. Partial skull and skeletal fragments.
NHMUK 1481	R 1481	1	*Lytoloma crassicostatum*	A	Sheppey, Kent	Eocene	Complete carapace and plastron.

Table 1 - List of observed samples from the MIWG collection and NHMUK collection, labelling museum ID number, collection, number of specimens, species, taphonomic grade, location, epoch and description.

Museum ID number	Collection	specimens	Species	Taphonomic grade	Location	Epoch	Description
MIWG 4112	4112	1	*Emys*. sp	C	Lower Hamstead beds	Eocene	Single fragment of carapace. Pathology identified.
MIWG 4114	4114	4	*Emys*. sp	C	Lower Hamstead beds	Eocene	Four fragments of scute/ carapace. Pathologies identified.
MIWG 4113	G.T.Woods	9	*Emys*. sp	D	Lower Hamstead beds	Eocene	Nine fragments of scute/ carapace.
MIWG 4430	H.F.Poole	3	*Emys*. sp	D	Lower Hamstead beds	Eocene	Three fragments of carapace.
MIWG 1629	J.F.Jackson	2	*Emys*. sp	D	Lower Hamstead 'Black Band'	Eocene	Two Fragments of carapace.
MIWG 3849	J.F.Jackson	1	*Emys*. sp	D	Hamstead Member	Eocene	Single fragment of carapace.
MIWG 913	Newport Museum	5	*Emys*. sp	D	Lower Hamstead	Eocene	Five fragments of scute.
MIWG 4882	W.H.Daniels	1	*Emys*. sp	D	Lower Hamstead	Eocene	Single fragment of carapace.
MIWG 4115	G.T.Woods	12	*Trionyx*. sp	C	Lower Hamstead beds	Eocene	Twelve fragments of scute/ carapace. Pathologies identified.
MIWG 4429	H.F.Poole	3	*Trionyx*. sp	D	Lower Hamstead	Eocene	Three fragments of carapace.
IWCMS-1998.26	IWCMS-1998.26	1	*Trionyx*. sp	D	?	?	One fragment of carapace and partial skeleton.
MIWG 2131	J.F.Jackson	2	*Trionyx*. sp	D	Lower Hamstead beds	Eocene	Two Fragments of scute.
MIWG 914	Newport Museum	8	*Trionyx*. sp	C	Lower Hamstead beds	Eocene	Eight fragments of carapace with partial skeleton.
MIWG ? Sample 3	Sample 3	1	*Trionyx*. sp	D	Lower Hamstead beds	Eocene	One fragment of carapace.
MIWG 3731	MIWG	1	*Trionyx*. sp	D	Lower Hamstead 'White band'	Eocene	One fragment of Carapace.
IWCMS-2007.486	IWCMS-2007.486	1	*Trionyx*. sp	-	?	?	Cast of partial skull and Jaw.
MIWG 4883	W.H.Daniels	4	*Trionyx*. sp	C	Lower Hamstead beds	Eocene	Four fragments of scute/ carapace.
NHMUK R981	R981	1	*Emys.sp?*	D	Hamstead Beds	Eocene	Single fragment of carapace.
NHMUK 26691	26691	1	*Emys.sp?*	D	?	?	Single fragment of carapace.
NHMUK 34950	34950	1	*Clemmys Bicarinata*	A	London Clay, Sheppey	Early Eocene	Complete carapace, pathologies identified.
NHMUK 37210	37210	1	*Emys comptoni*	A	London Clay, Sheppey	Early Eocene	Complete carapace.
NHMUK 8136	R 8136	1	*Trionyx incrassatus*	B	Lower Bembridge marls	Oligocene	Partial carapace with vertebra. Pathologies identified.
NHMUK 1433	R 1433	1	*Trionyx incrassatus*	B	Hordwell	Lower Oligocene	Partial carapace. Pathologies identified.

Table 1 CONT – List of observed samples from the MIWG collection and NHMUK collection, labelling museum ID number, collection, number of specimens, species, taphonomic grade, location, epoch and description.

Museum ID number	Species	Taphonomic Grade	Location	Epoch	Brief damage descriptions	Damage type
MIWG 4112	Emys sp.	C	Lower Hamstead beds	Eocene	Specimen 1 - 22mm long and 3mm wide (at its widest) smooth groove along the surface of the carapace (Figure	Scoring/ Gouging
MIWG Sample 3	Trionyx sp.	D	Lower Hamstead beds	Eocene	Specimen 1 - semi-circular indentations of varying sizes upon the surface of the carapace	Pitting/ Boring
MIWG 4882	Emys sp.	D	Lower Hamstead	Eocene	Specimen 1 - Circular damage to the edges.	Taphonomic
MIWG 4429	Trionyx sp.	D	Lower Hamstead	Eocene	Specimen 1 - shallow 1-2mm grooves that lightly penetrate the ventral side of the carapace fragment (Figure.	Scoring/Gouging
MIWG 4430	Emys sp.	D	Lower Hamstead beds	Eocene	Specimen 1 - multiple linear grooves running in various directions, edges of the grooves are irregular and not smooth (Figure	Scoring/Gouging
MIWG 4114	Emys sp.	C	Lower Hamstead beds	Eocene	Specimen 1 - two distinct circular indentations 12mm apart.	Scoring/ Gouging
MIWG 4115	Trionyx sp.	C	Lower Hamstead beds	Eocene	Specimen 1 - distinct cracked texture, this observed on both dorsal and ventral angles.	taphonomic
NHMUK 8136	*Trionyx Icrassatus*	B	Lower Bembridge marls	Oligocene	Specimen 1 - A near complete *Trionyx icrassatus* carapace, displaying multiple clustered areas of pitting, clusters appear around suture lines.	Pitting/ Boring
NHMUK 12737	*Trimyclid?*	B	Bracklesham bay, Sussex	Eocene	Specimen 1 - A partial Trimyclid turtle plastron, displaying over 30 irregularities, indentations varying in depth and shape.	Pitting/ Boring
NHMUK 1433	*Trionyx Incrassatus*	B	Hordwell	Oligocene	Specimen 1 - A partial *Trionyx icrassatus* carapace, displaying 4 indentations upon the carapace.	Pitting/ Boring

Table 2 - List of observed samples from the NHMUK collection, labelling museum ID number, collection, number of specimens, species, taphonomic grade, location, epoch and description.

6.1. FIELDWORK COLLECTED SPECIMENS

Figure 23 – **A**- Collected *Emys sp*. carapace and plastron from the Bouldnor Formation.

B – Collected *Trionyx sp*. carapace and plastron from the Bouldnor Formation.

Overall, 88% of the fossils collected were from chelonians; however, they comprised only small fragments (Figure 23). Of the 67 *Emys* sp. fragments found, the largest fragment collected was 39mm in height and 37mm in width and the smallest was 12mm in height and 8mm in width (Figure 23). *Emys* sp. shells are often thick and dark-coloured fragments with a smooth carapace texture and can be fairly large but are often small fragments found on the foreshore. The samples show different stages of weathering, some samples are weathered smooth, and the material lacks any sharp edges around fractures and surfaces are smooth to the touch, other samples display rough and jagged edges that are sharp to the touch and resist when rubbed with the hand. Two specimens are crocodilian vertebrae where the neural spine has broken off. Identifying pathologies upon the samples was difficult due to the small size of the specimens collected and the different stages of weathering of each sample. Only 12 *Trionyx* sp. specimens (fragments) were collected from the study area (Figure 23). The largest fragment was 59mm x 42mm. Each specimen has a differing stage of weathering; however, most can be identified by the mottled texture of the carapace (Pamfilie et al. 2022).

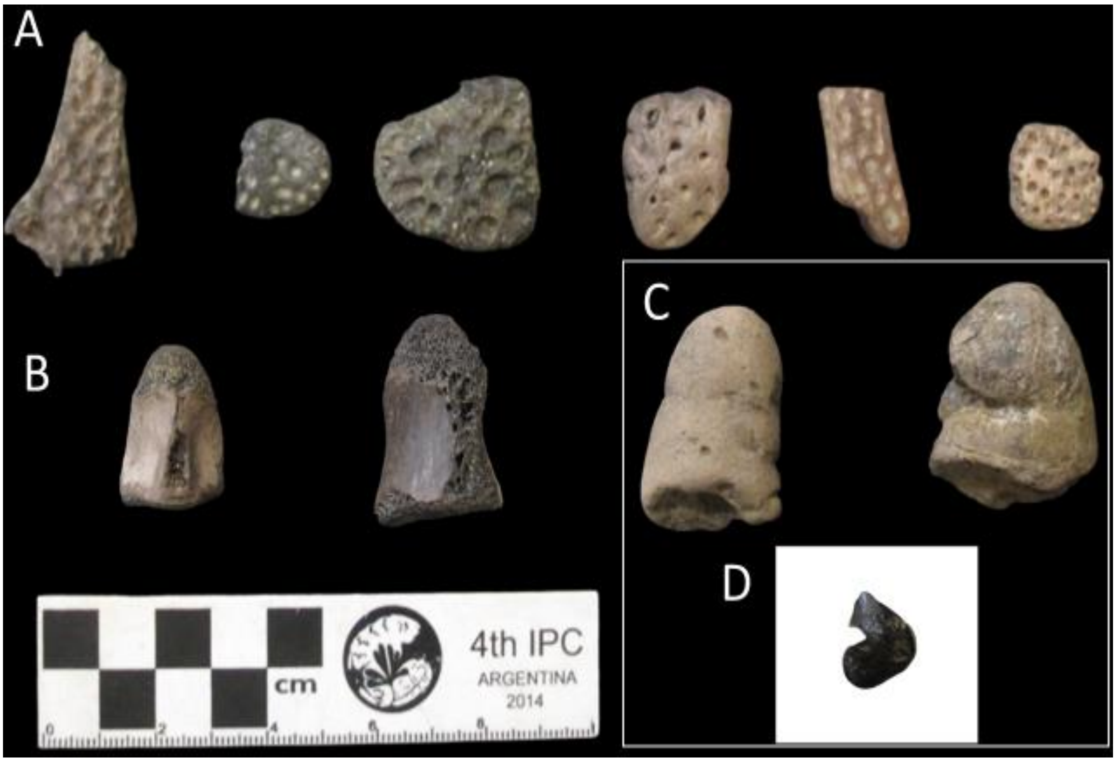


Figure 24 - Collected fossil vertebrate material from the Bouldnor Formation. A. Crocodilian fragments. B. Two crocodilian vertebra, C. Two fossil coprolites and D. One unidentified mammalian tooth fragment (below).

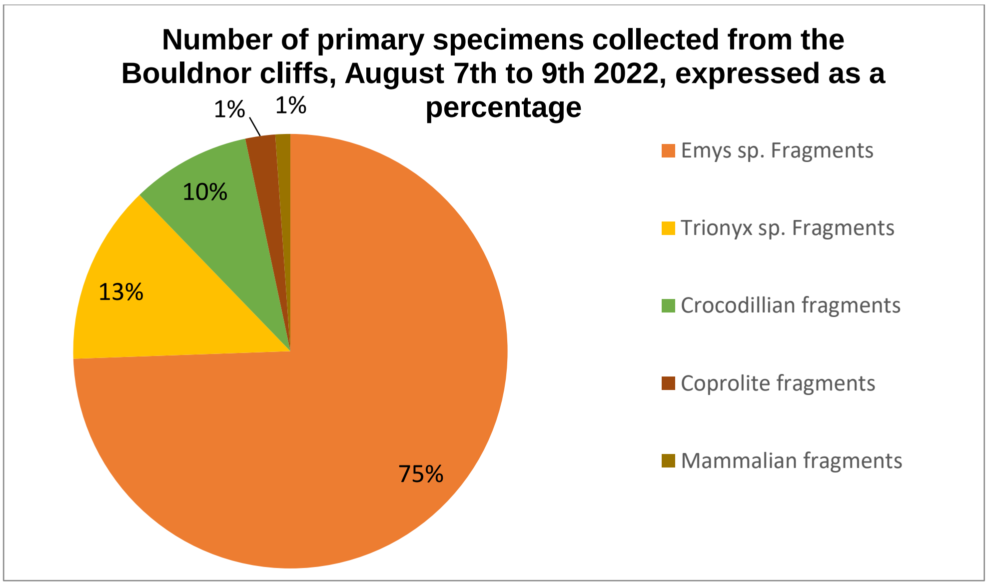


Figure 25 - Number of primary specimens collected during fieldwork, expressed as percentages and displayed in a pie chart.

Additional fossils discovered include crocodilian scutes, crocodilian vertebrae, coprolites, and a partial mammal tooth (Figure 24). The distinct indented texture identifies crocodilian scutes, although similar in appearance to that of *Trionyx* sp. carapace the circular patterns are deeper and more pronounced, making the fragments distinguishable (Pamfilie et al. 2022). The largest scute collected was 40mm in length and 22mm at its widest point. Two possible crocodilian vertebrae were also collected (Figure 24). They are heavily weathered and only preserve the centrum. The largest of these 2 specimens was 40mm in height and 22mm in width. Two fossil coprolites from unidentified species were discovered, identified by their uneven shape and distinct texture. Lastly, a mammalian tooth fragment was discovered and identified because of its distinctive smooth texture and black shine from the enamel and the two partial roots. However, due to it being incomplete, it is not possible to identify a species.

The temporal and spatial occurrence and taphonomic grade will be directly linked to the preservation of specimens, and the depositional environment of the Lower and Upper Hamstead Members will directly influence this. The chelonian specimens collected from the Hamstead beds, of the Bouldnor Formation, are all fragmentary pieces of either carapace or plastron, that range in size from 12 mm to 59 mm. All specimens are weathered by various processes and are assigned to the taphonomic grade of D based on the disarticulation of specimens, coupled with the abundant evidence of corroded and abraded specimens (Brandt 1989).

These findings consolidate the proposed research questions and confirm that from primary specimens, it can be assumed that most samples collected from the Bouldnor Formation on average are fragmentary remains. Data from the primary collections reinforces original thinking further by indicating the presence of crocodilian species within the rock strata, creating possible predator/ prey relationships that can be observed through observable anomalies.

DAMAGE TO CARAPACE AND PLASTRON

6.2. PENETRATIVE AND NON-PENETRATIVE BORINGS

MICRO-CT SPECIMEN

A sample *Emys* sp. fragment from the University of Manchester displayed an observable boring. This fragment was collected from the shores of the Bouldnor Formation by a supervisor of this study, Prof. Phillip Manning, and was later donated for Micro-CT scanning, to further understand the effect of the observable damage on the underlying bone tissue of the carapace (Figure 25 CONT). This specimen had a non-penetrative pit/dimple-like structure preserved on the upper surface of the outer edge of the carapace, overlapping 2 bony suture lines (Figure 25). The damage has a central raised crest with a depressed ring around the circumference. The bone structure underneath the depressed ring is smoothed and shifted outward from the central crest, and the edges of the depressed ring are elevated and are more pronounced on the left side. The carapace within the area of the raised crest is compacted inwards and pinched to form the crest (Figure 25). the structure is 11mm in width and 9mm in height, resulting in an oblong-shaped appearance (Figure 25).

Slices 900 to 1400 display the damage as seen in Figure 26 CONT. Slide 900 is the first slide that has observable damage, with a gently curved indentation evident on the base of the fragment. A smaller indentation is present at the centre of the suture line with minor cracks observable, the underlying bone tissue remains unaffected.

Slide 1000 extrapolates the structures seen in slide 900 as the curved sides of the damage become more pronounced, and the sides of the central indentation expand out further from the carapace surface, creating a central crest. The underlying bone tissue surrounding the central crest is altered slightly, curving inwards into the deeper bone tissue by the pressure of the damage above (Figure 26 CONT).

Slide 1100 displays an increase in the elevation of the central crest, the curved sides of the damage become steeper and more pronounced. Deep penetrating cracks around the circumference of the damage are still present (Figure 26 CONT).

Slide 1200 continues to show the steep sides of the central crest; however, the sides of the damage are gentler than slide 1100. A small deep penetrating crack can be observed from the central indentation expanding into the deeper bone tissue beneath. Underlying bone tissue on either side of the central crest is now pushed deeper into the carapace than that seen in slices 1000 and 1100 (Figure 26 CONT).

Slide 1300 sees the damage subsiding; the central crest is less pronounced and the height of the damage decreases. The curved sides of the damage become shallow, and the central crack is no longer visible. Underlying bone tissue continues to gently bend into the carapace however the indented bone is gentler than slices 1000 to 1300 (Figure 26 CONT).

Slide 1400 is like slide 900 in that the observed damage is less evident than in slices 1000 to 1300. The central indentation remains to display the suture line; however, the central crest is flattened as the damage subsides (Figure 26 CONT).

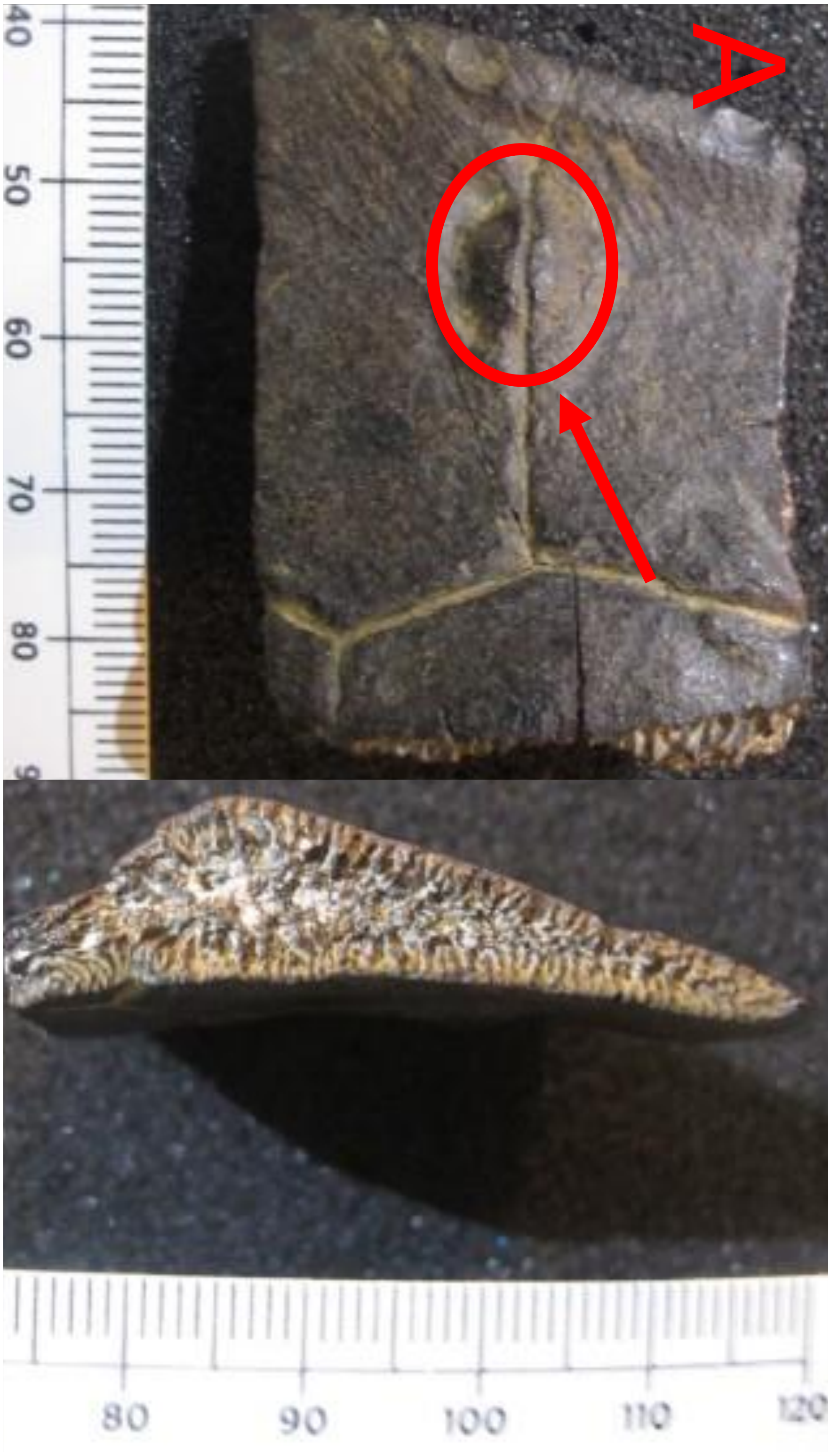


Figure 26 - A - Specimen of *Emys sp*. Carapace selected for XRT scanning. Picture above shows the damage.

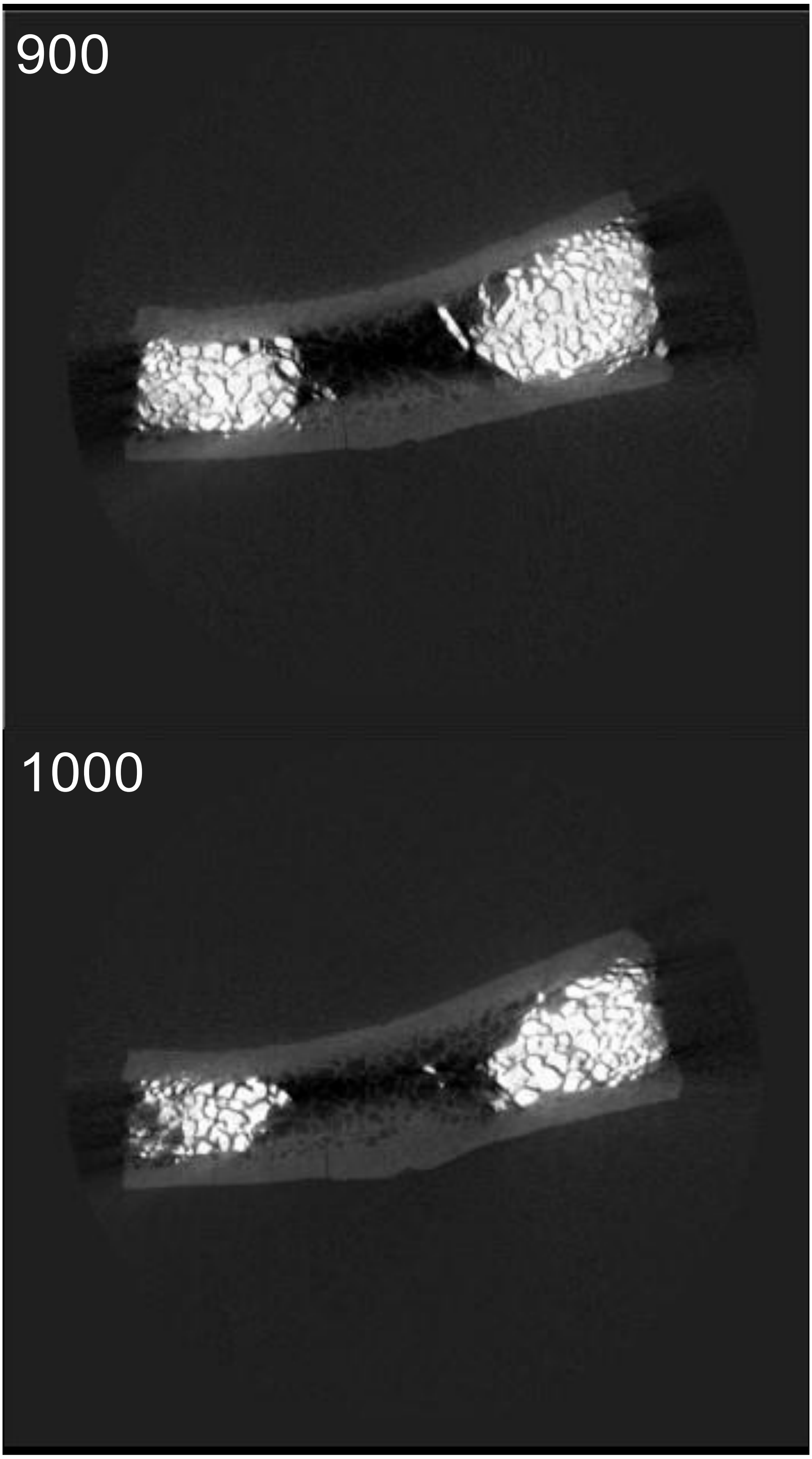
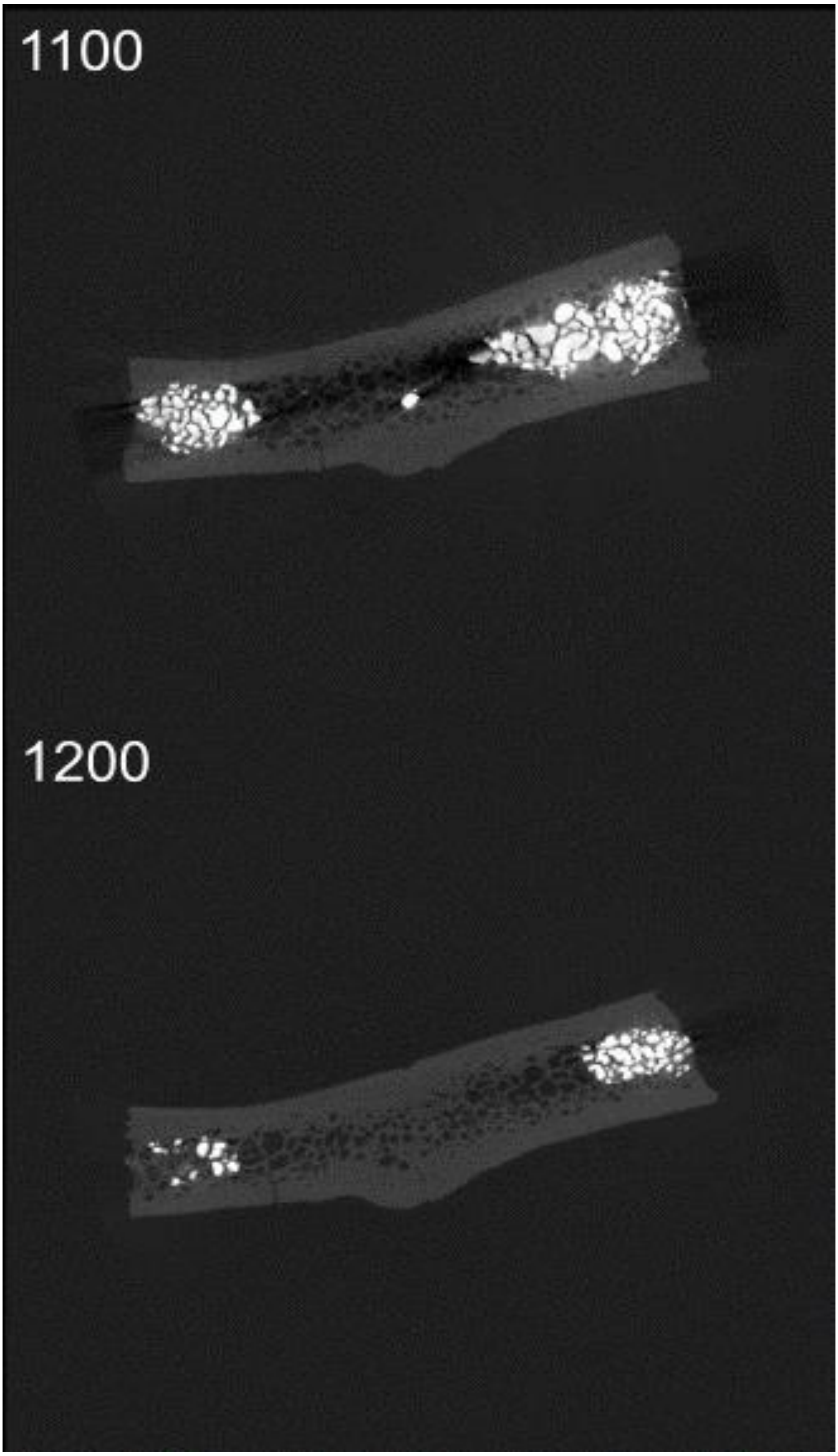
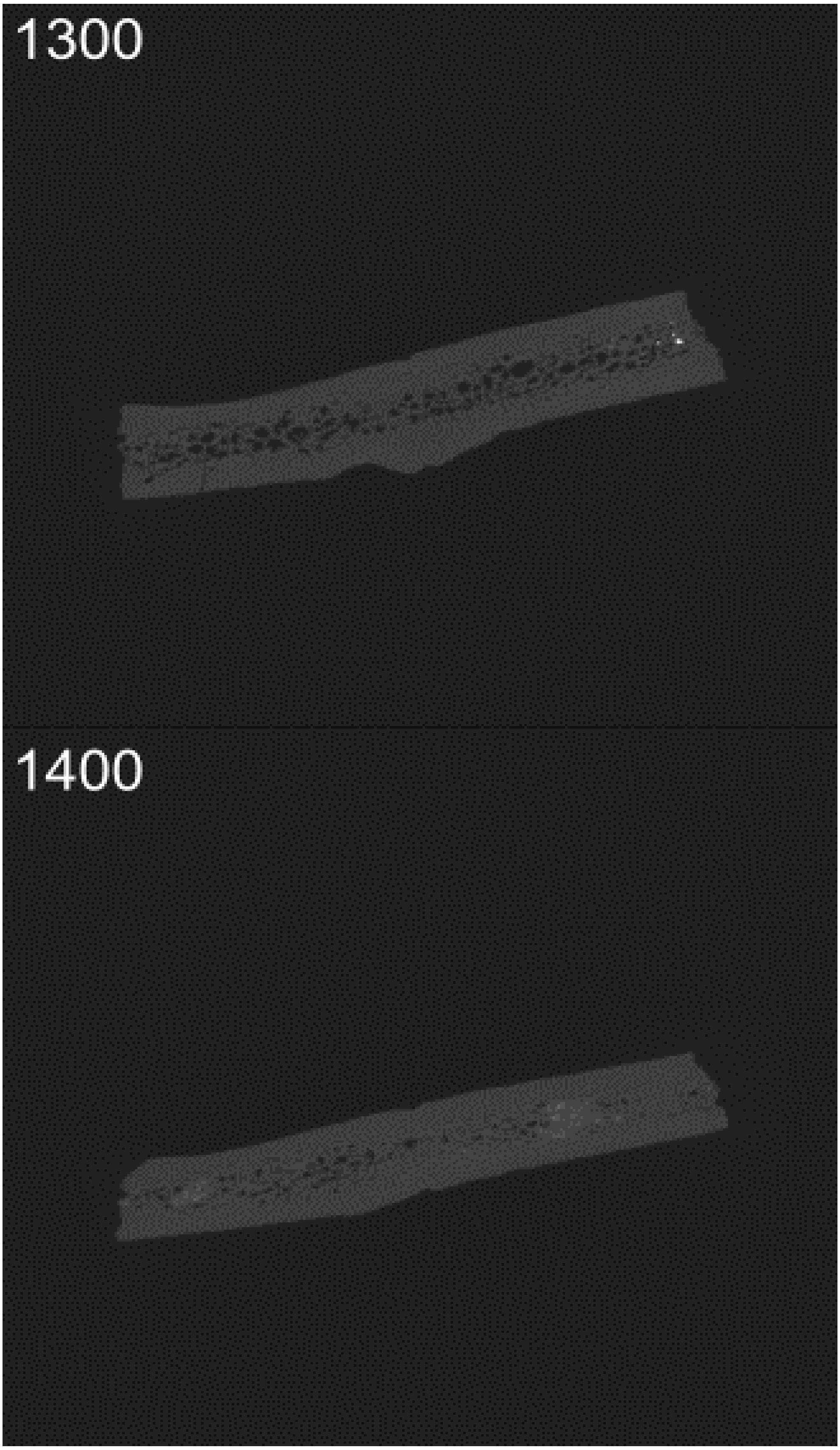


Figure 26 CONT - Specimen of *Emys sp*. Carapace selected for XRT scanning. Slices 900 to 1400, shown at intervals of 100 slices, 0.5X magnification. The pathology is present from slices 900 to 1400.


1100
1200


1300
1400

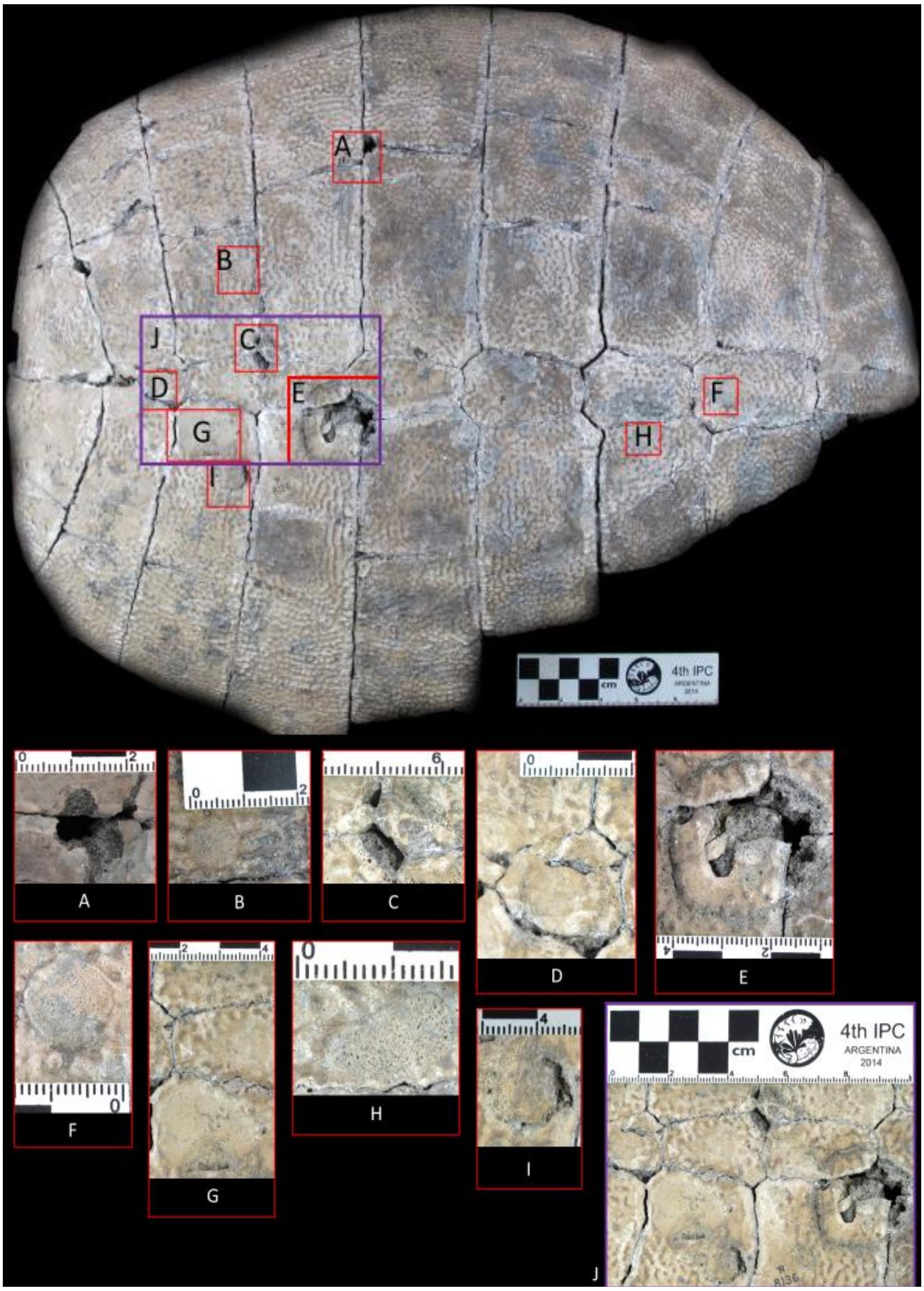


Figure 27 - NHMUK PAL R8136. A near complete *Trionyx incrassatus* carapace from the Bembridge Marls Member of the Bouldnor Formation. Boxes highlighting the damage to the specimen. **A** – Penetrative Boring overlying a carapace suture line, displays areas of rough surface around the central damage. **B** - Small circular non- penetrative boring around 10mm in diameter. **C** – Larger circular penetrative boring with a depressed ring surrounding the circumference, 13mm in diameter. **D** – Larger non-penetrative boring, 15mm in diameter, located between 3 carapace suture lines. E – Extremely large penetrative boring, 32mm in diameter, displaying a large, depressed ring round the circumference of the damage, breakdown of material within the circumference varies with full penetration of the carapace occurring on the left of the boring. F- small circular non- penetrative boring, 11mm in diameter with a crested ring around the circumference. **G** – Large oblong shaped non-penetrative boring, 16mm long and 12mm wide at its widest. **H** – Small oblong shaped non-penetrative boring 12mm long and 6mm wide. **I** – small circular non penetrative boring, 9mm in diameter, with a deeper penetrating left circumference edge. **J** – A broader image of observed damage encompassing borings C, D, G and E

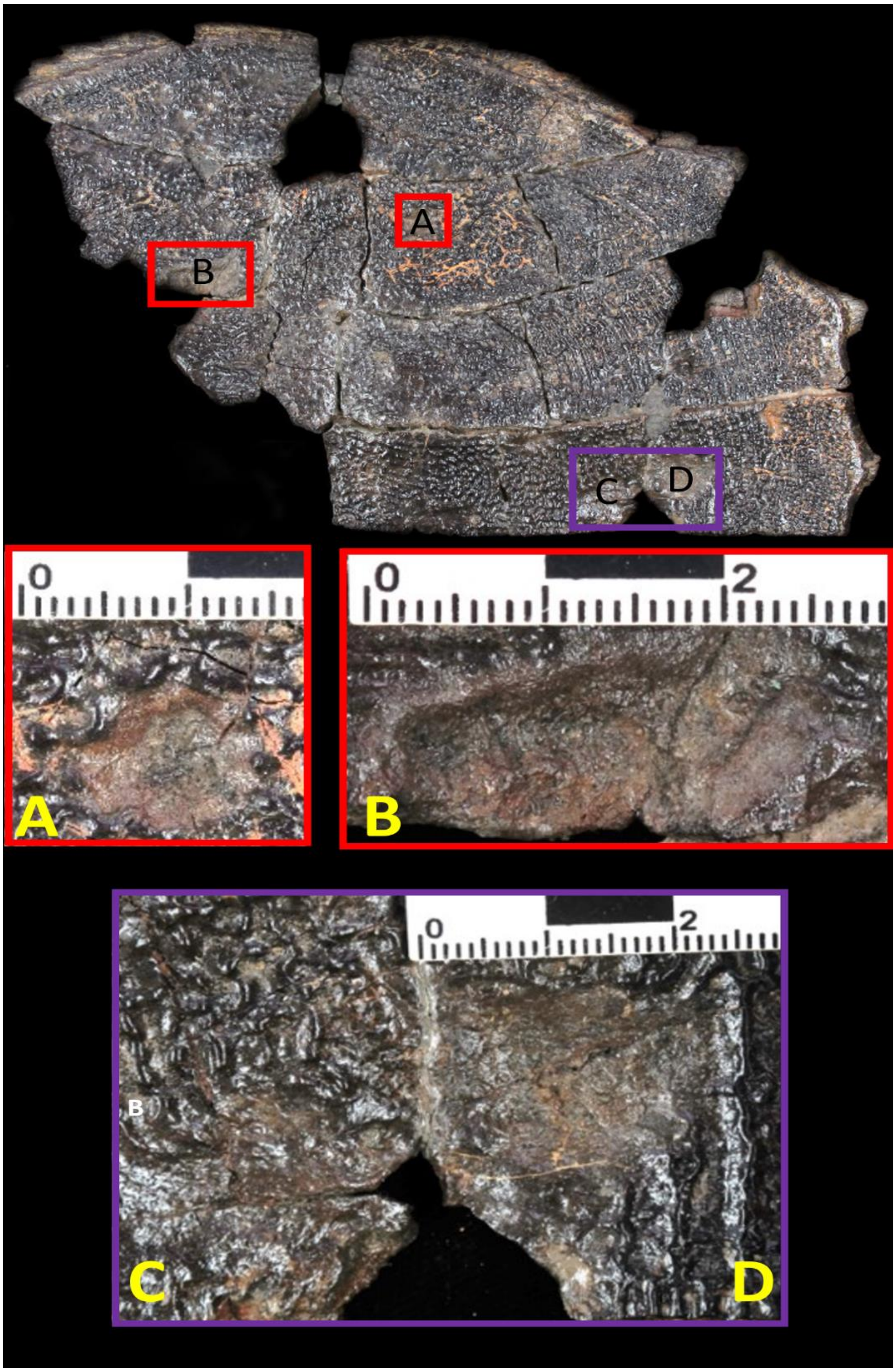


Figure 28 - A partial *Trionyx incrassatus* carapace, NMHUK PAL R1433, from Hordwell, Hampshire, Lower Oligocene. Damaged areas are highlighted in red boxes. Purple box encompasses two irregular features. **A** – Small circular non-penetrative boring 10mm in diameter with a crested circumference crest. **B** – Partially incomplete long oblong shaped non-penetrative boring, 23mm long and 8mm wide. **C/D** – **C** is a small rounded non-penetrating boring, 10mm in diameter, located along a suture line, along the same suture line is **D**, an oblong shaped non-penetrative boring 25mm long and 12mm wide.

NHMUK PAL R8136 is a near complete *T. incrassatus* carapace from the Bembridge Marls Member of the Bouldnor Formation. This specimen has multiple circular ringed lesions, each lesion/pit is of varying size, shape, and diameter (Figure 27 A to J). Figures 27 B, F, and H show smaller, shallower pits that are circular or oval shaped usually no larger than 20mm in size. These do not penetrate the carapace but have eroded top layers of bone tissue to leave exposed bone structure underneath. They are located mostly on random plates of the carapace and do not seem to congregate around bone plate margins. Figures 27 A, C, D, E and I show larger, deeper penetrating circular ringed pits, which have a darkened area where the presence of the organism has eroded or stained the bone tissue. Not all, but most, pits result in penetration through the carapace, causing visible holes and damage to the remaining bone tissue (Figure 27 A, C and E). The lesions vary in size, but they can reach bigger sizes than the non-penetrating lesions. Figure 27 E is 32mm in diameter and shows the biggest hole punctured through the carapace in the centre of its darkened ring. Figure 27 J displays borings C, D, G, and E, Penetrative borings C and E are found where multiple suture lines of the carapace meet, whereas the non-penetrating borings of D and G are situated more sporadically on the carapace surface.

A partial *T. incrassatus* carapace, NMHUK PAL R1433, from Hordwell, Hampshire, Lower Oligocene has multiple oval and circular pits and lesions on the carapace surface; however, being a partially complete carapace, it is uncertain how large some of these pathologies might be. Figure 28 A shows a tiny (10mm in diameter) rounded indentation which resembles the smaller pit-like lesions that are present in Figure 27. Figure 28 B shows a large, rounded-edged indentation that resides at a plate margin. It penetrates deeper into the bone tissue than in Figure 28 A and is considerably larger at 28mm in length. Figures 28 C and D show two individual circular pits that meet along a plate margin. Both C and D could be the same instance of damage just separated because of the incomplete status of the specimen. All borings have crested circumferences and the carapace within these circumferences is smoothed and lacks the distinctive uneven and mottled texture of *Trionyx Incrassatus* specimens.

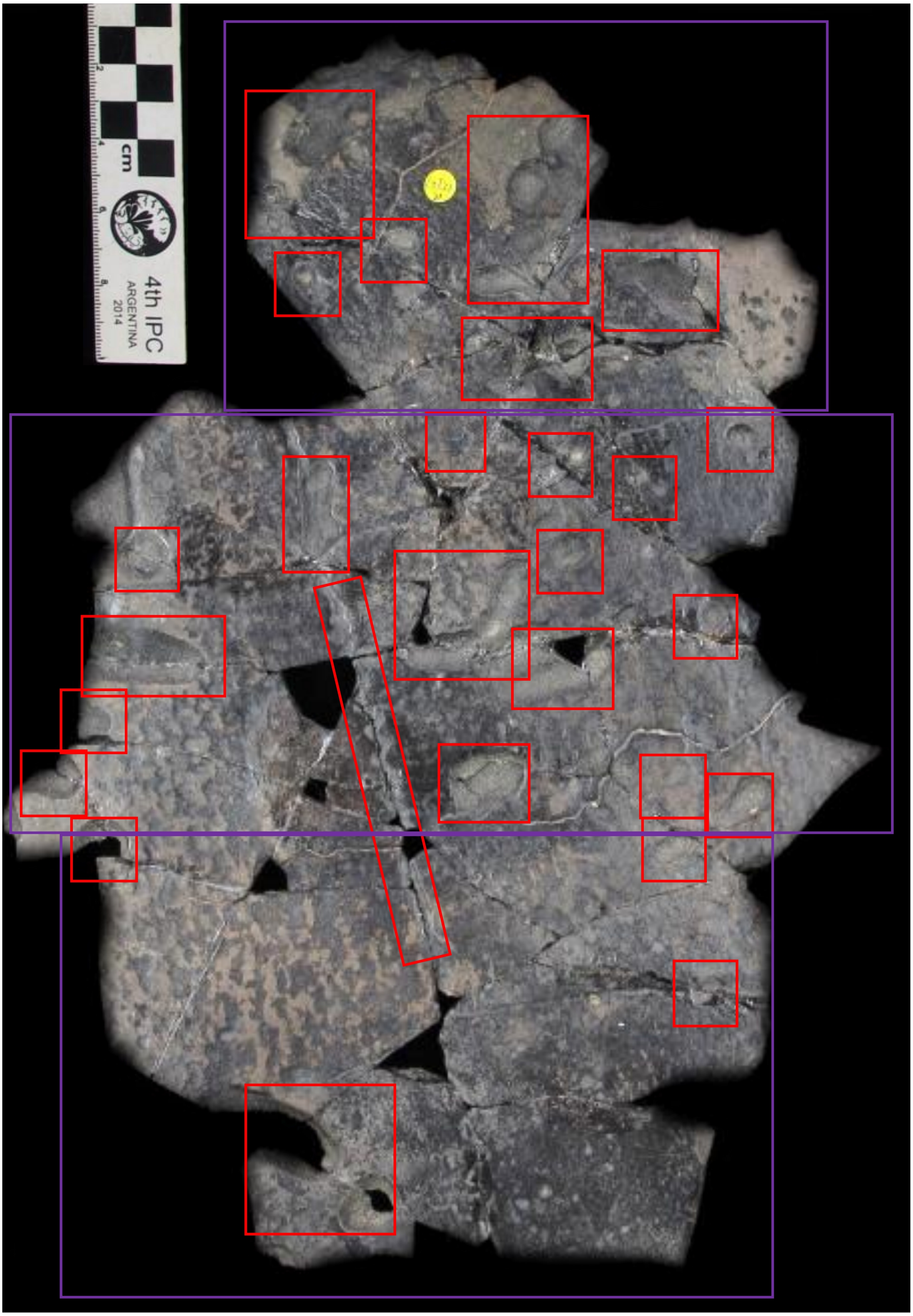


Figure 29 - A partial *Trimyclid* turtle plastron, NMHUK PAL RF 539/ R12737 from Bracklesham Bay. Red boxes highlighting damage to the plastron. The purple boxes dividing the specimen into sections for closer analysis of the features. Upper box, Figure 28, middle box figure 29 and lower box figure 30

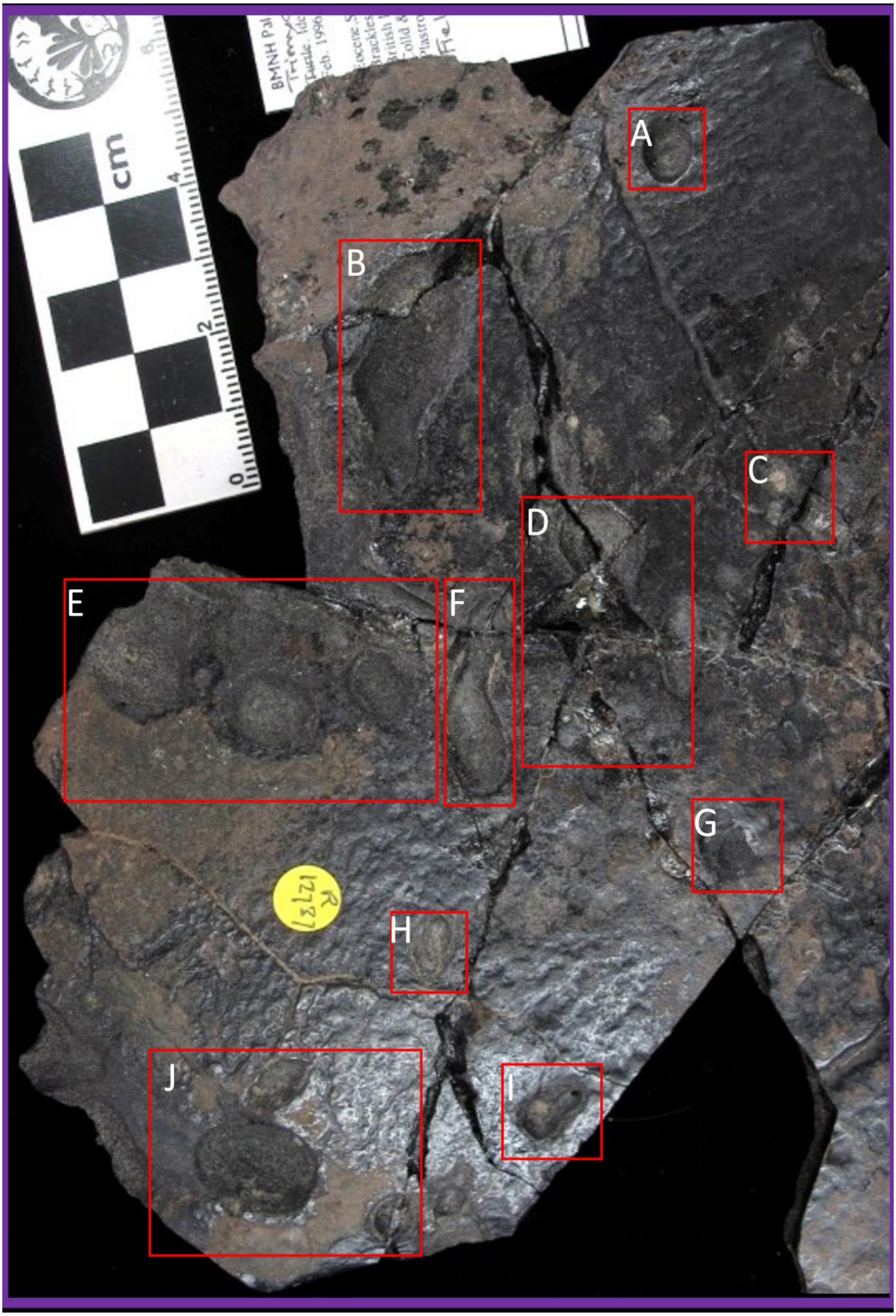


Figure 30 - Close up of Figure 29, upper box of a partial *Trimyclid* turtle plastron, NMHUK PAL RF 539/ R12737, highlighting damage A-J.

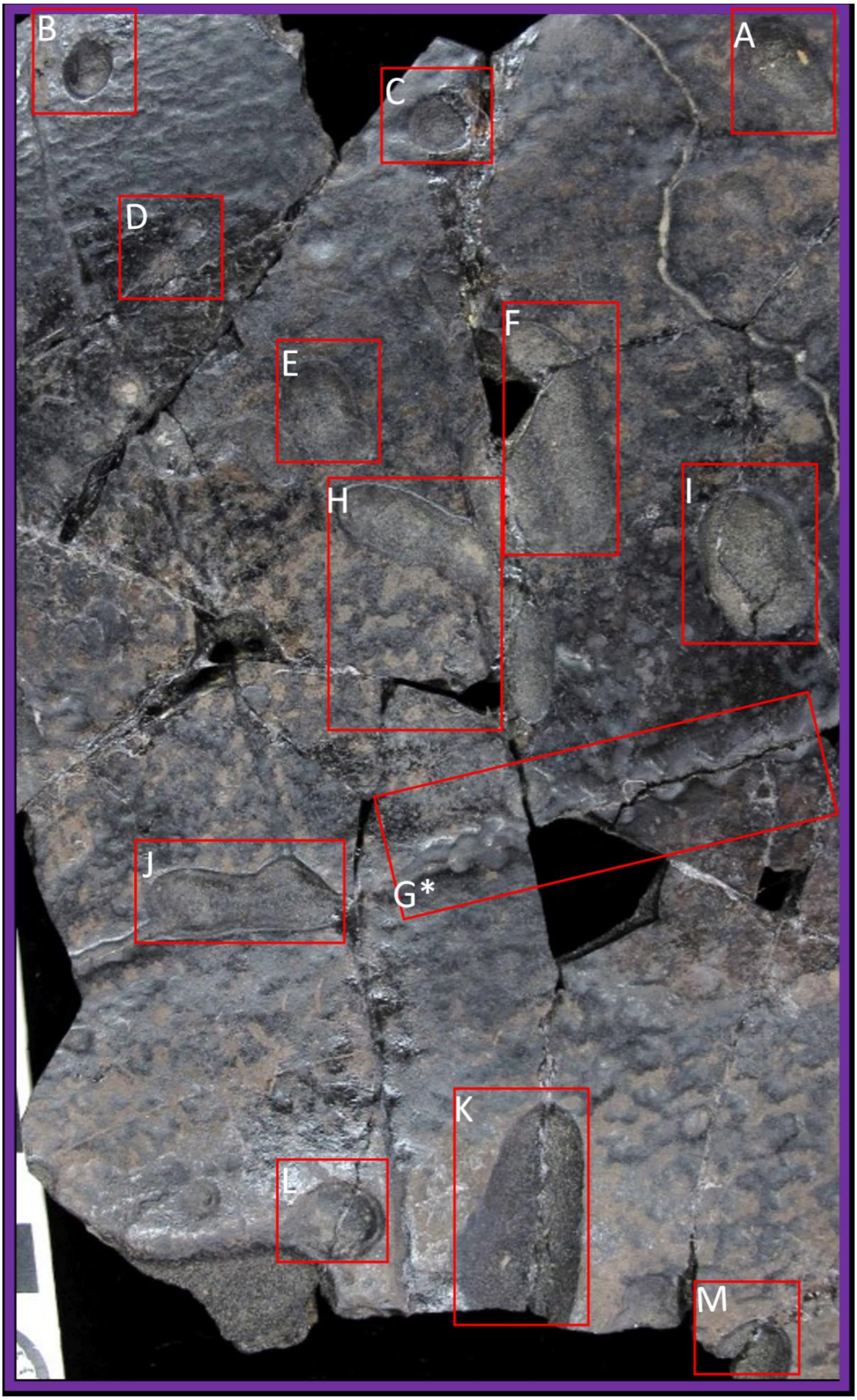


Figure 31 - Close up of Figure 29, middle box of partial a *Trimyclid* turtle plastron, NMHUK PAL RF 539/ R12737, highlighting damages A-M. Damage G* continues into figure 32.

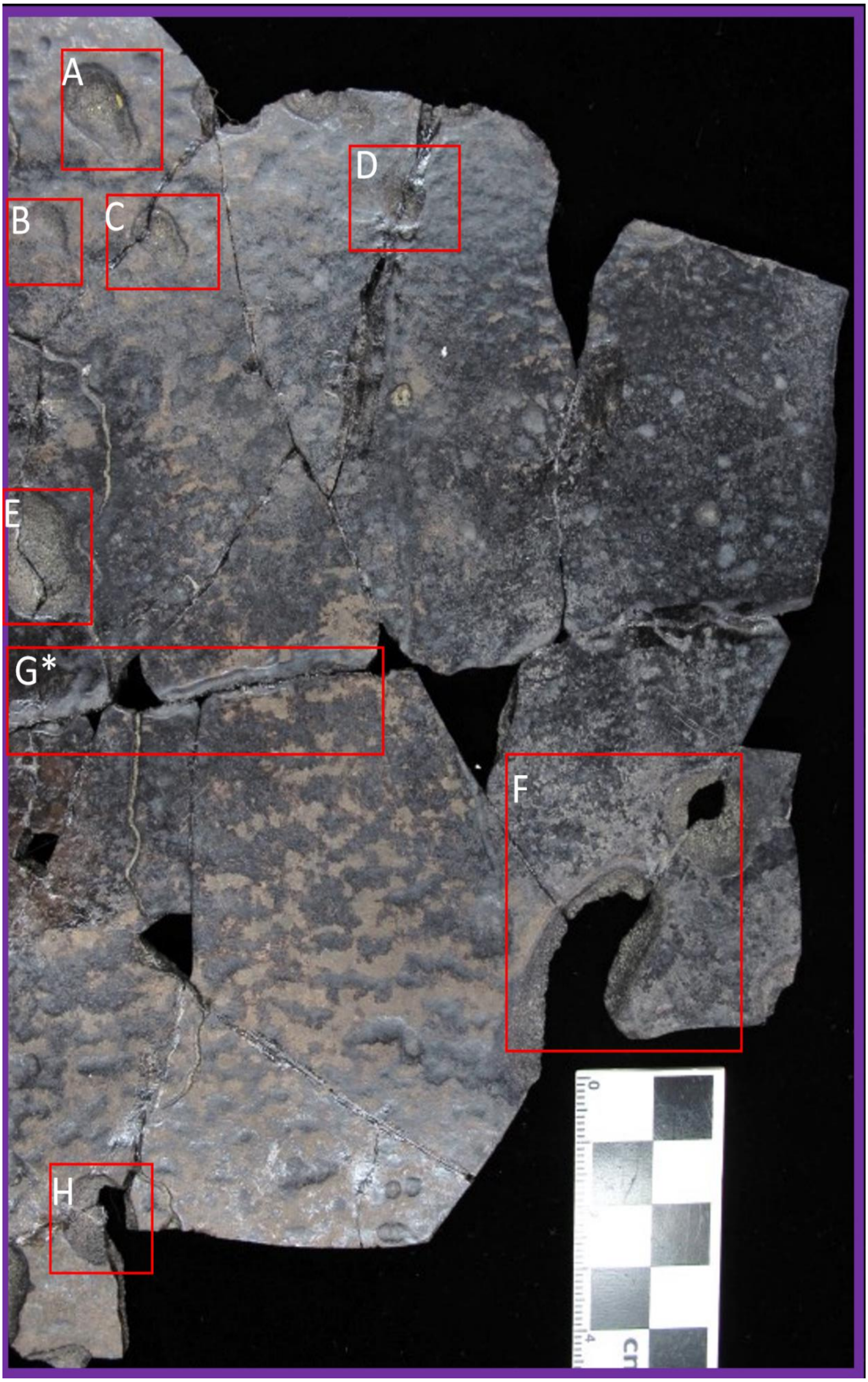


Figure 32 - Close up Figure 29, lower box, of a partial *Trimyclid* turtle plastron, NMHUK PAL RF 539/ R12737, highlighting damage A-H.

A partial *Trimyclid* turtle plastron, NMHUK PAL RF 539/ R12737 from Bracklesham Bay has 29 areas of varied damage. Seventeen small circular/ oval non-penetrative borings have eroded and smoothed the carapace surface beneath, ranging in size from 4mm in diameter and height to 18mm and 10mm (seen in Figure 30 A, C, G, H, and I, figure 31 A, B, C, D, E, L and M and Figure 32 A, B, C, D, and H), Most of these borings have similar dimensions and observable structures observed in figures 27 A, B, C, D, F, H and I, and 28 A and B, the edges of these indentations have a shallower angle of penetration into the carapace. Most of the smaller, less penetrative borings seem to be sporadically situated on the carapace, placed within the centre of a carapace plate evenly spaced between other damage, as seen in Figures 27 A, B, H and F and Figures 28 A and B.

There are 10 larger, circular to oblong shaped borings that penetrate deeper into the surface of the carapace, they vary in size from 12mm in diameter and height of 10mm to 34mm and 17mm (seen in Figure 30 B, D, and E and J, figure 31 I, J and K and Figure 32 F and E). These larger pits have defined edges and display raised crested circumferences as seen in the larger borings of figures 27 E and G and 28 C/D, the edges of these borings seem to have a steeper angle of penetration into the surface of the carapace.

Two long deep penetrating pits can range in size from 25mm long to 32mm long (seen in Figure 30 F, figure 31 F, and H). Again, these borings display similar steep penetration angles as the circular and oblong deeper borings described above and are similar in dimensions to the oblong irregularity seen in Figure 28 C and D. Most of the deeper penetrating borings congregate around suture lines on the carapace, some even encompass suture lines within MIWG 4429 their circumference, deformation of the bone tissue beneath can span over multiple carapace segments as seen in figure 27 E and 28 C/D.

In relation to the research questions, specimens displaying non-penetrative and penetrative borings are found on near- complete/ partially complete disarticulated samples, however half the samples do not originate from the Bouldnor Formation. Specimens display large quantities of observable pathologies which are inferred to be a result of parastitic behaviour and/ or disease. Although links can be made to disease structures observed in extant species, most knowledge of is from extinct species from differing strata.

6.3. SCORING/ GOUGING

Most samples with identified scoring of gouges are within the MIWG collections (MIWG Sample 3, MIWG 4429, MIWG 4114, MIWG 4430, MIWG 4112), although similar observable damage can be found within the NHMUK specimens (NMHUK PAL RF 539/ R12737). Most samples from the MIWG are partial or fragmentary segments of carapace belonging to species of the *Trionychidae* family, with most specimens belonging to *Trionyx incrassatus* or *Trionyx* sp. The ages of the material with described groves range from early Eocene to late Eocene. Specimens from the MIWG museum are exclusively found from the Hamstead beds of the Bouldnor Formation, the one specimen from the NHMUK collection is found within the Bracklesham Group. The samples described below have a lower taphonomic grade, due to the disarticulation, increased corrasion, and abrasion of the specimens, the MIWG collection is graded from C to D (Brandt 1989) (Figure 22).

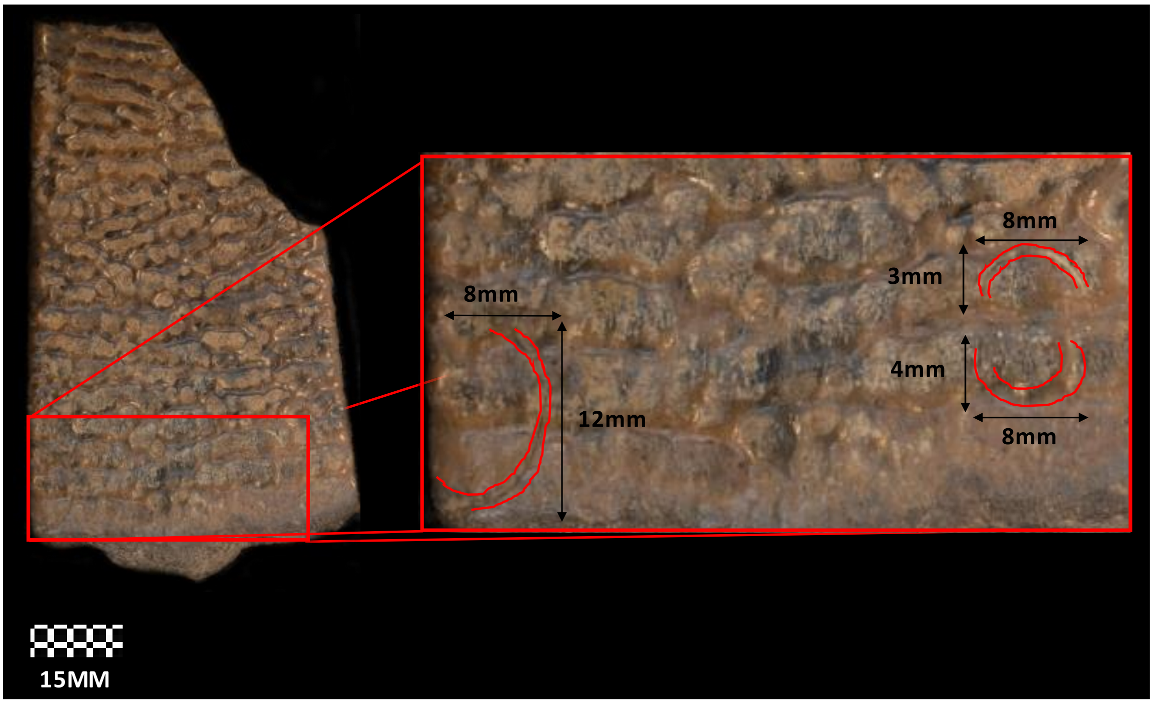


Figure 33 - A *Trionyx incrassatus* specimen, MIWG Sample 3. This specimen has semi-circular indentations of varying sizes upon the surface of the carapace, the largest being 12mm in height and 8mm wide at its widest point along the circumference. Two smaller indentations can be observed closer together, however, they are not connected to the larger one

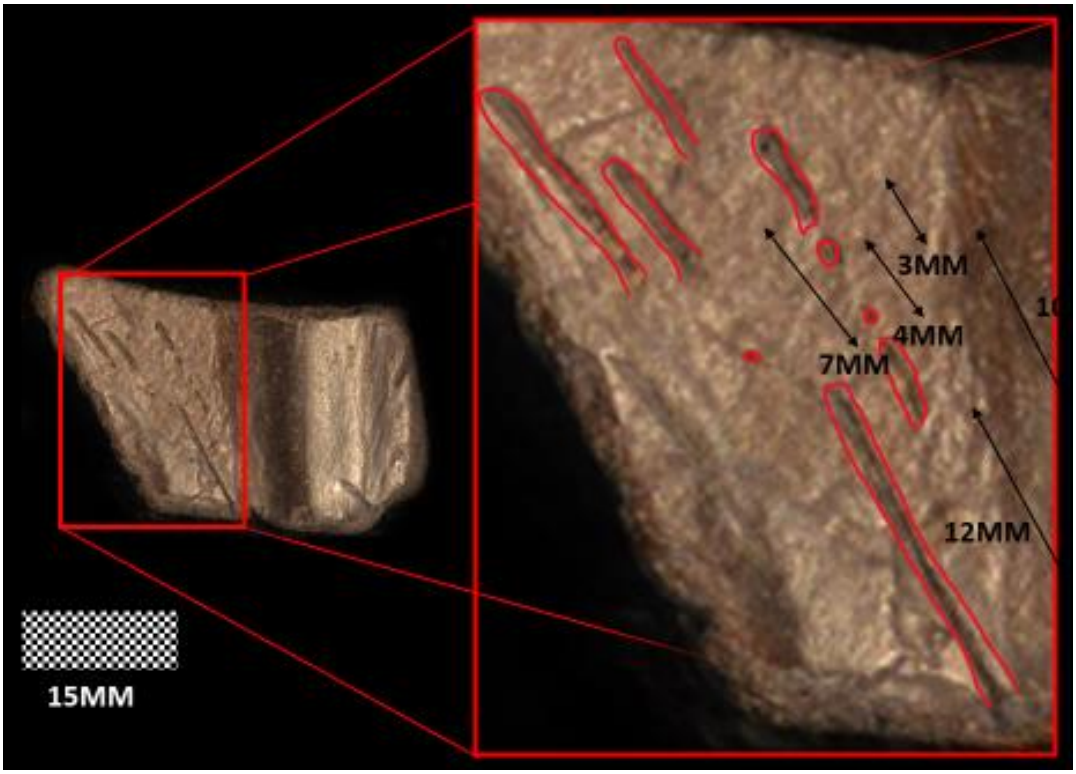


Figure 34 - A *Trionyx incrassatus* specimen, MIWG 4429, has shallow 1-2mm grooves that lightly penetrate the ventral side of the carapace fragment.

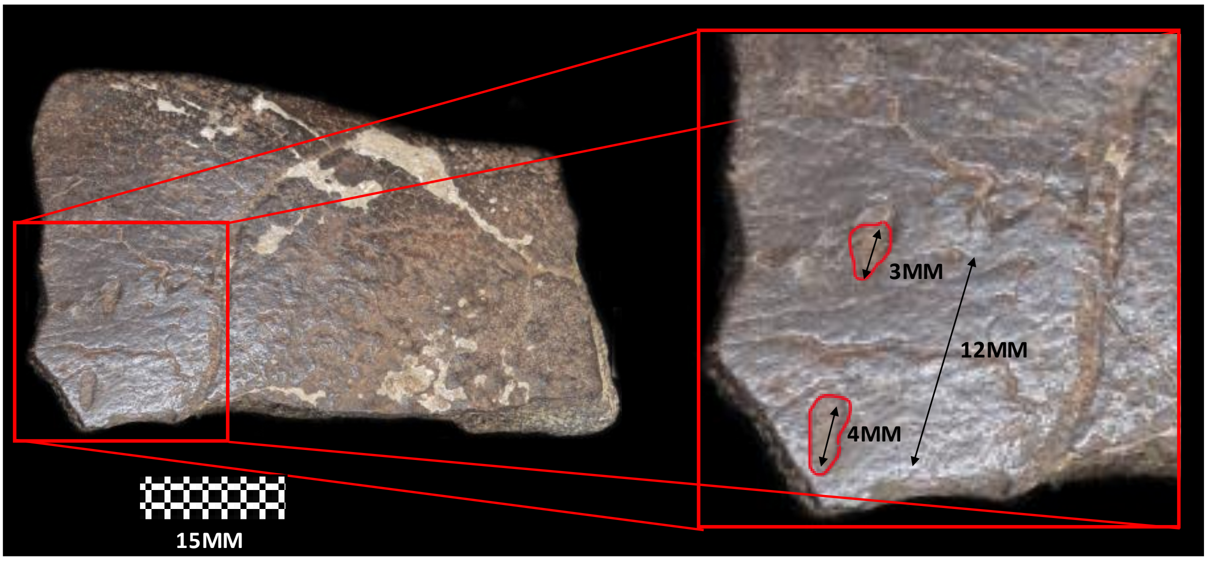


Figure 35 - *Emys* sp. carapace fragment, MIWG 4114, with two distinct circular indentations 12mm apart.

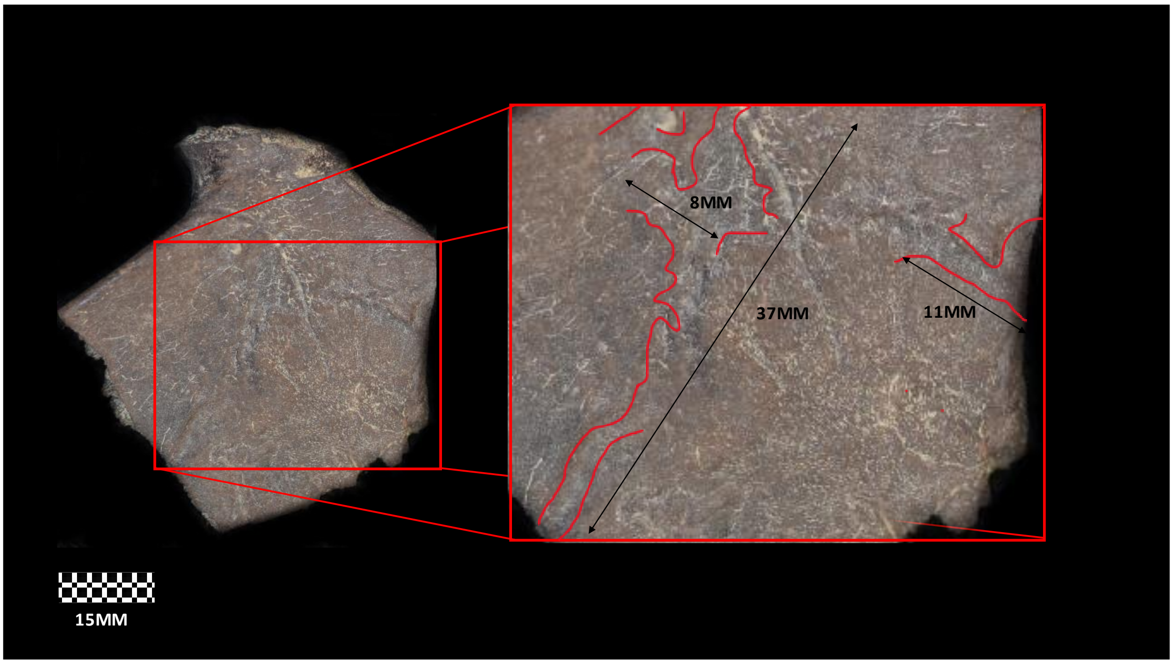


Figure 36 - *An Emys* sp. fragment, MIWG 4430, with shallow penetrating meandering grooves, the damage seems to lack any orientation resulting in a sporadic pattern upon the surface of the carapace

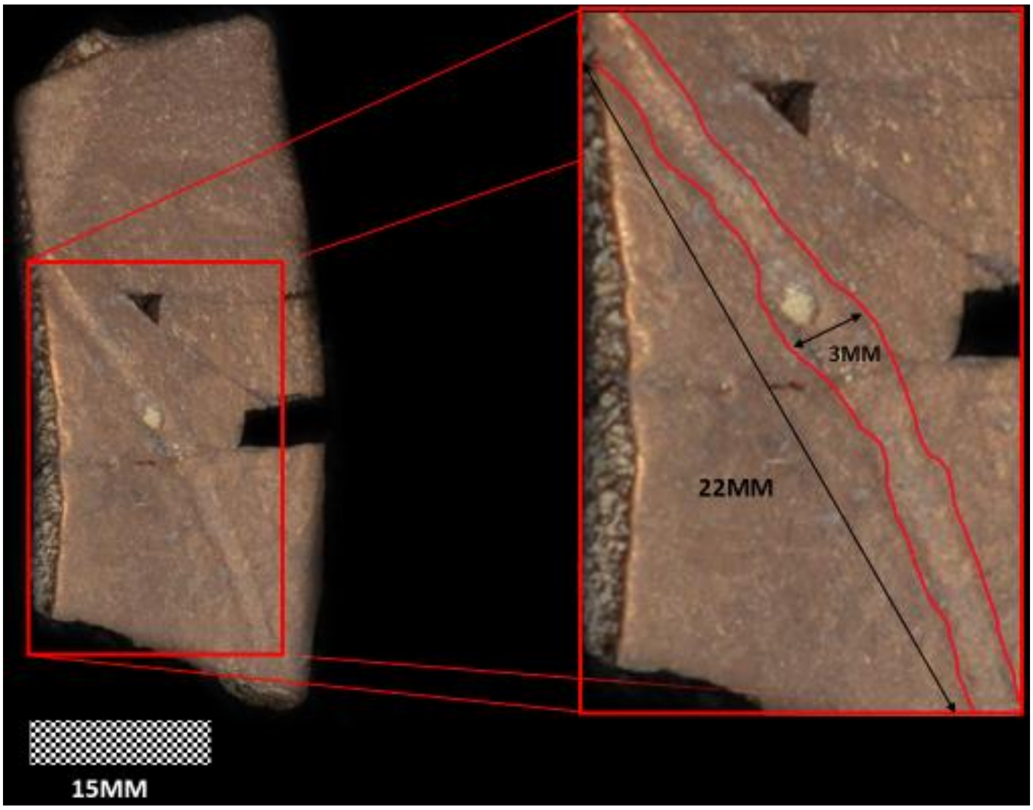


Figure 37 - Emys sp. fragment, MIWG 4112, with a groove

MIWG Sample 3 (Figure 33) is a fragmentary sample of *T. incrassatus* carapace with an uneven and mottled surface texture and multiple semi-circular indentations of varying sizes and orientations. The two smaller indentations can be observed closer together; however, they are not connected, as the projected path of the circular indentations does not match up. The smaller circular indentations lightly penetrate the carapace following the semi-circular structure, whereas the larger indentation penetrates the surface of the carapace deeper in comparison.

MIWG 4429 (*T. incrassatus)* has multiple linear grooves running in the same direction, although there are a few isolated examples that run in another direction. The grooves are shallow and lightly penetrate the ventral side of the carapace fragment. The grooves are 1-2 mm wide and can be up to 12mm in length (Figure 34).

Another type of damage seen in the Dinosaur Isle collections are circular indentations. MIWG 4114 is an *Emys* sp. carapace fragment with 2 distinct circular indentations 12mm apart. These indentations penetrate the carapace surface, exposing the internal bone structure (Figure 35). The specimen also has ta suture line to the right of the damage which could be mistaken for additional gouging damage.

MIWG 4430, another *Emys* sp. specimen, also has grooves (Figure 36) lacking the smooth and linear patterns seen in Figures 34 and 35, the damage is more irregular and wider but not as long as the comparative material as shown in MIWG 4112 (Figure 37). The latter fragment has a 22mm long and 3mm wide (at its widest) smooth groove along the surface of the carapace (Figure 37).

Specimens displaying scoring/ gouging consolidate the research questions, they are found on fragmentary pieces of plastron and carapace of the species *Emys* and *Trionyx*, the disarticulation is inferred to be the result of depositional environment. The observable anomalies are hypothesized to be the result of post-mortem scavenging by multiple organisms. Similar anomalies are observed in extant species of chelonians however the specimens are of a grander scale, the knowledge of these anomalies is sourced from other extinct species.

6.4. TAPHONOMIC DAMAGE

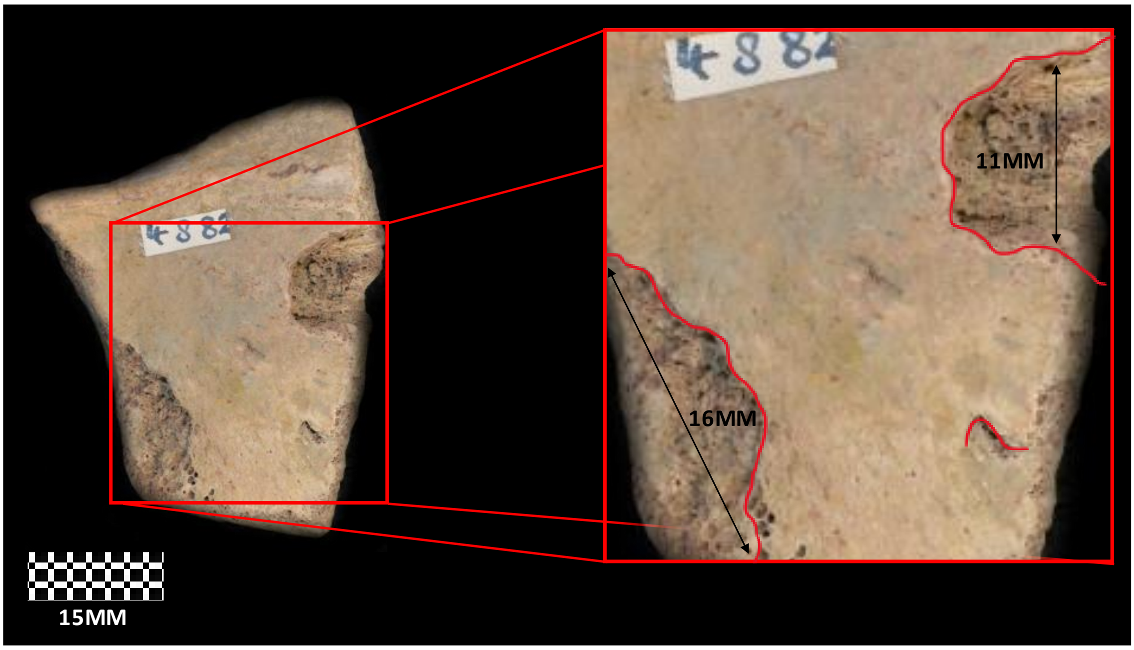


Figure 38 - An Emys sp. carapace fragment, MIWG 4882**,** with damage to the edges.

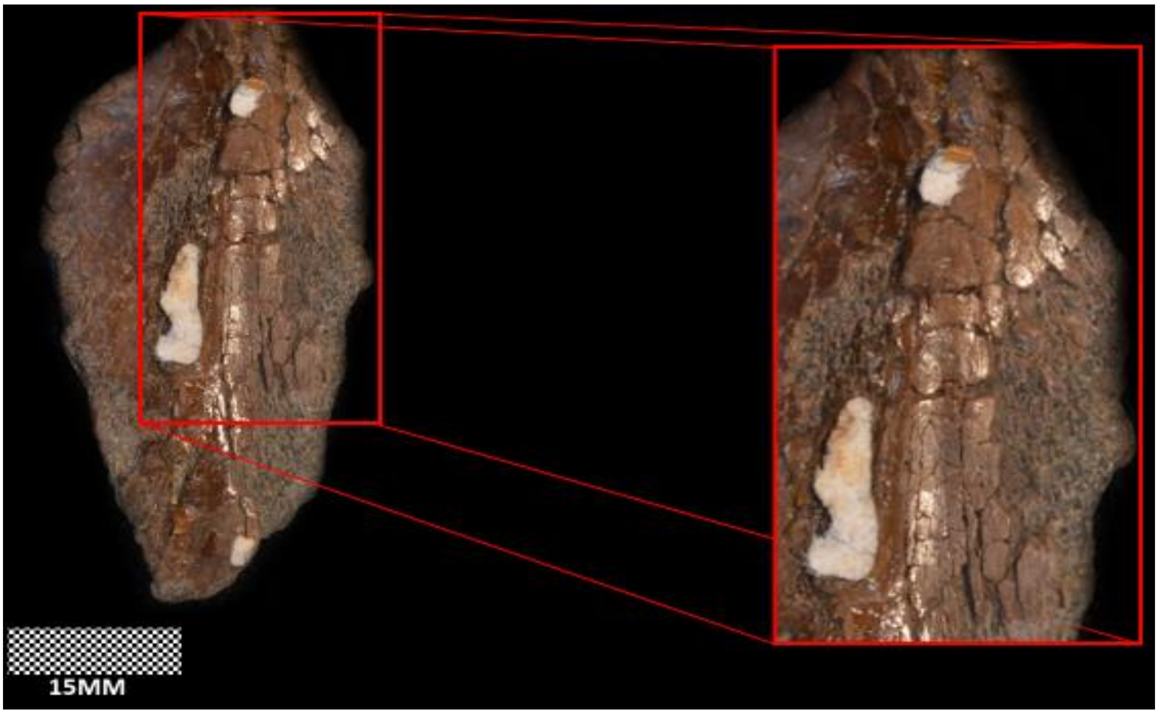


Figure 39 - **A** *Trionyx incrassatus* specimen, MIWG 4115, with a distinct cracked texture, this observed on both dorsal and ventral angles.

MIWG 4112 is a fragment of *Emys* sp. and shows the ventral side of the carapace, two distinct abnormalities can be observed, one on the right side of the specimen and one on the left side (Figure 38). These abnormalities are circular indentations into the bone of the specimen, however, the penetration into the carapace is not complete. The edge of the damage is rough and jagged in appearance with exposed bone structure underneath. The left side damage is larger with a shallower angle of penetration, although it displays the same rough and jagged texture as the deeper penetrating damage to the left of the specimen. MIWG 4115 is a fragment of *T. incrassatus* which displays a distinct cracked texture that can be observed on both the dorsal and ventral sides of the specimen (Figure 39). The edges of the cracked bone tissue are angled and sharp with some outer carapace being completely missing, exposing deeper material below. The top of the specimen exhibits the largest cracks and the further down the fragment that is observed, the smaller and more compact the cracks become until smaller fragments are completely missing. The texture would continue over the entire specimen as fragments of material otherwise absent in places is present in others.

Taphonomic damage is present in all specimens observed for this study, and correlations can be made to the research questions. Although it is inferred that depositional environment is responsible for the disarticulation of specimens, it seems taphonomic grade of specimens could be influenced by secondary exposure. While these samples share little insight into the causes of pathological phenomena or any links to extant species they provide evidence of secondary exposure and weathering on fragmentary remains.

7. DISCUSSION

Two different Chelonia genera have been identified within the Bouldnor Formation, *Trionyx* and *Emys*. Based on extant relatives and studies into the palaeoenvironment of the Bouldnor Formation, it is possible to identify the effects the palaeoenvironment can have upon preservation potential (Insole and Daley 1985; Hooker et al. 2004, Chatfield 2009). For example, an individual dies in a small pond, estuary, or lagoon, and the resulting corpse during necrology will either sink or be transported by fluvial processes to settle elsewhere (Brandt 1989, Hooker et al. 2004, Chatfield 2009). Brackish and fluctuating freshwater fluvial systems constantly change, depositing and abrading material as the flow of the fluvial system fluctuates (Hooker et al. 2004, Chatfield 2009). Especially with the Bouldnor Formation, it is hypothesized that the palaeoenvironment, which is often flooded, would dramatically increase the physical effects upon any articulated remains by water (Hooker et al. 2004, Chatfield 2009). Alternatively, it can be buried rapidly, increasing the chances of an articulated specimen. This is a rarity, but articulated carapaces are collected from Bouldnor Formation, as seen in NHMUK PAL R8136 (Figure 27).

During biostratinomy, the corpse is altered by fluvial processes or interacted with by other organisms within the same palaeoenvironment. This can cause traces of scavenging by various inferred organisms. Specimens MIWG 4429 and MIWG 4114 (Figures 34 and 35) exhibit scavenging structures by larger predators within the ecosystem, and MIWG Sample 3, MIWG 4430, MIWG 4112 (Figures 33, 36 and 37) display scavenging structures by smaller scavengers. Interaction with other organism's post-mortem would cause increased disarticulation before burial (Brandt 1989, Hooker et al. 2004, Chatfield 2009). After the burial, the corpse will then be subjected to additional pressures of compaction and crushed into smaller fragments or flattened because of the weight of the material and water above (Benton and Harper 2020).

Fully articulated specimens are likely to be disarticulated by processes such as cliff slumping, and cliff fall which is common along the shoreline beneath the Bouldnor Formation (Mottershead 2013, Downes 2021). Bouldnor's cliffs are comprised of thick mud and clays and are constantly under pressure from physical processes that result in slumping (Figure 35) (Insole and Daley 1985; Downes 2021). The movement of the mud and clays breaks fully articulated specimens up during slumping events, being churned into fragments as the cliff material falls or slumps (Mottershead 2013, Downes 2021). Any fragments on the beach then are dragged out during low tide dissolving the surrounding clays and mud, separated by seawater. Additionally, during high tide, fragments could be re-deposited on the beach (Mottershead 2013). These physical processes will affect a specimen's taphonomic grade; fragments from coastal exposures are highly likely to be disarticulated, corroded, and weathered, meaning a lower taphonomic grade (Brandt 1989).

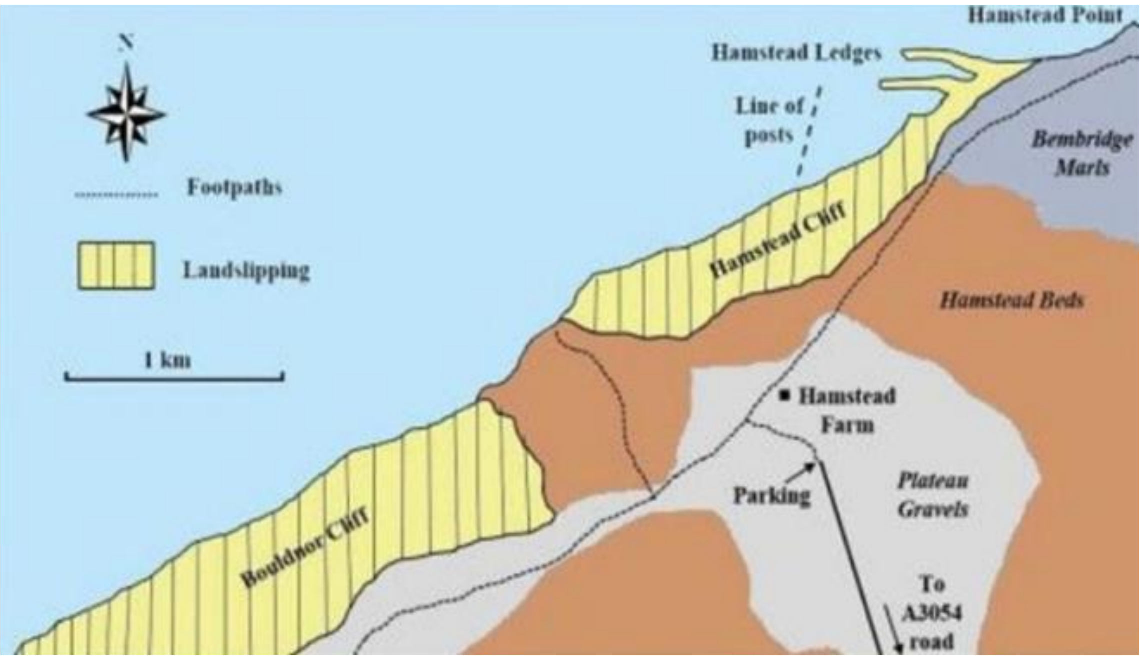


Figure 40 - Bird-eye drawn map of the coastal exposures of the Bouldnor Cliffs and Hamstead Cliffs with highlighted areas of land slipping (Downes 2021).

The specimens collected during fieldwork may not be a representable sample for species abundance and distribution of the Bouldnor Formation because of the fragmentary nature of the fossils, which is directly influenced by the taphonomy of the Bouldnor Formation. Physical processes (e.g., tides, and storms) could have redistributed fragments from another location. Specimens collected were found along the beachfront and foreshore of the Bouldnor cliffs and not *in situ,* meaning fragments may have travelled into the study area from another location and may not be from the Hamstead beds or even the Bouldnor Formation. However, *Emys* sp. is the dominant species collected with 75% of specimens collected, thus *Emys* sp. may have been more abundant within the palaeoenvironment based on the abundance of *Emys* sp. fragments collected. It could be assumed that more observable pathologies should be found on *Emys* sp. fragments than *T. incrassatus*. *T. incrassatus* is a member of the soft-shelled turtle family and has a cartilaginous shell covered by a mottled structure that can obscure smaller pathologies from view (Pamfilie et al. 2022).

When comparing the abundance and distribution of pathologies of turtles from the Bouldnor Formation with other Paleocene turtles from the UK, this is not the case. *Emys* sp. fragments are common in museum collections and some specimens do display palaeopathologies, such as the specimens MIWG 4114, MIWG 4430, and MIWG 4112 (Figures 35, 36 and 37) as examples. However, when looking at Tables 1 and 2 and studying all the museum-observed-specimens (NHMUK and MIWG), the biggest and most noticeable pathologies are found on the carapace of the larger *T. incrassatus,* see NMHUK PAL RF 539/ R12737, NMHUK PAL R1433 and NMHUK PAL RF 539/ R12737(Figures 27, 28, 29, 20, 31 and 32). The complete carapaces of *Emys* sp. and its family found in the NHMUK collections, show very few identifiable pathologies. This contrasts with collected specimens and the Dinosaur Isle collections, as these are predominantly fragmentary remains of carapace and plastron, which make identifying pathologies harder compared to those seen on complete carapaces.

7.1. BORINGS/ PITTINGS DAMAGE

The *Emys* sp. fragment selected for micro-CT displayed an 11mm by 9mm non-penetrative boring, with a central elevated crest situated on a suture line of the carapace. The circumference of the elevated crest is surrounded by a depressed penetrating ring which is pushed outward from the central elevation causing the outer circumference to be slightly elevated (Figure 41). This palaeopathology is located on a suture line, a similar pattern is observed in NHMUK PAL R8136, NMHUK PAL R1433 and NMHUK PAL RF 539/ R12737 (Figures 27, 28, 30, 31 and 32). The presence of the raised central elevation is a characteristic observed for the ichnospecies *T. holmani* as seen in Figures 12 and 13. (Zonneveld et al. 2015, Zonneveld et al. 2021). Additionally, the micro-CT data shows the effects of the pathology and the response from the bone tissue (Figures 25 and 41). The depressed ring observable on the surface of the carapace slice creates a U-shaped indentation in the cross-section (Figure 41). Directly below this, the underlying bone tissue is altered by the overlying pathology (Figure 41). The bone tissue underneath is pushed deeper into the central matrix of the shell, creating a gentle but observable curved depression, directly below the circumference of the pathology as seen in Figure 25.

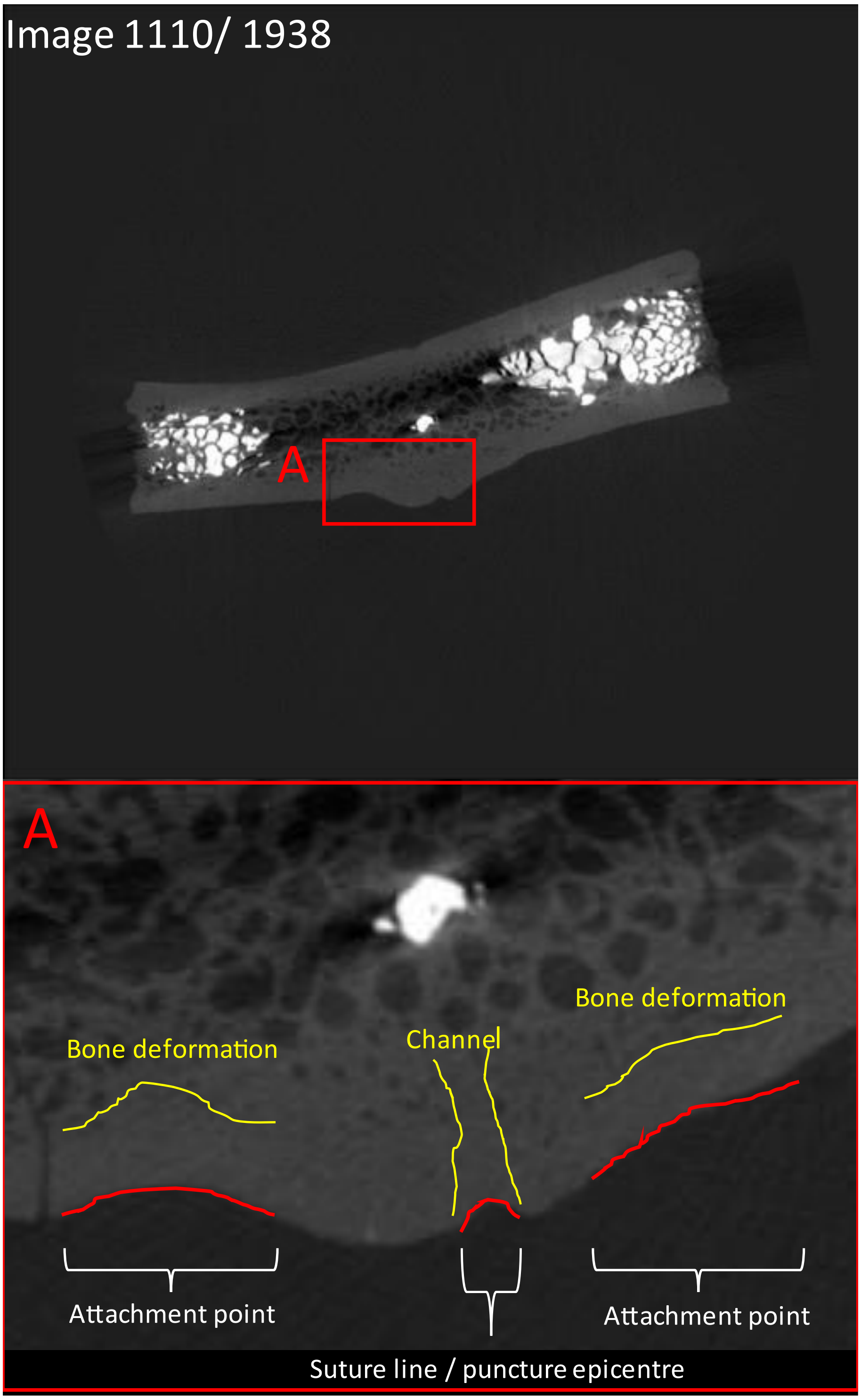


Figure 41 - XRT scan of *Emys sp*. The carapace fragment is shown in Figure 25. A = observed pathology cross-section, with attachment points and resulting bone deformation.

The central crest pinches the bone tissue from both sides of the carapace, pushing adjacent material outward, and causing the underlying bone tissue to warp. Within the centre of the pathology, a channel-like structure can be observed deep into the carapace beneath representing a possible feeding trace. Similar structures have been observed in *Echmatemys* sp*.* (Figure 13) and were assigned to the ichnotaxa, *T. holmani* (Zonneveld et al. 2021). Its location on a suture line and not penetrating the carapace are indicative of barnacle attachments as seen in Figures 10 and 11 (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2022).

One specimen observed and described from the Bouldnor Formation exhibited both penetrative and non–penetrative borings, NHMUK PAL R8136 (Figure 24). This specimen is a nearly complete carapace of *T. incrassatus* which has nine circular indentations on the surface of its carapace, these borings are comparative to those identified in Zonneveld et al. (2015), Zonneveld et al. (2021) and Zonneveld et al. (2022). Zonneveld et al. (2015) and (2021) interpret the lesions to result from several ichnotaxa which cause both penetrative (*Karethraichnus fiale*) and non-penetrative (*Karethraichnus lakkos, Karethraichnus kulindros,* and *Thatchtelithichnus holmani*) forms of borings (Zonneveld et al. 2015, Zonneveld et al. 2021).

Borings seen in NHMUK PAL R8136 (Figure 27) are similar in size and structure to those of Zonneveld et al. 2015, exhibiting the shallow penetration of smaller borings and the steeper penetration angles of penetrating borings as seen in Figures 12 and 13 above. There is little evidence of bone regrowth within the circumference of the borings as the bone tissue structure underneath is often left exposed or destroyed. It is uncertain whether these types of borings would cause an individual to die. The larger lesions congregate where plate margins meet where the bone tissue is thinner (Figure 27 A and E), and the larger lesions resemble the ichnospecies, *K. fiale* which is inferred to be responsible for penetrative types of borings (Zonneveld et al. 2015, Zonneveld et al. 2021). The larger lesions penetrate through the carapace (Figure 27 E), showing the erosion and destruction of bone tissue like what is seen in Figures 12, 13, and 14 (Zonneveld et al. 2015) Based on this, these lesions are most likely caused by parasitic activity; although it is unknown what organism may cause the occurrence of these borings or the process involved with creating them.

Other Paleocene turtles also have penetrative and non-penetrative borings that can be compared to those from the Bouldnor Formation. A carapace and plastron of species from the *Trionychidae* family (NMHUK PAL R1433) were observed to display similar borings (Figure 28) to that of specimen NHMUK PAL R8136 from the Bouldnor Formation. NMHUK PAL R1433 (Figure 28) is a partial *T. incrassatus* carapace from Hordwell in Hampshire with 2 small circular non-penetrating borings and 2 larger deeper non-penetrating borings comparative to those described on NHMUK PAL R8136. The other specimen, NMHUK PAL RF 539/ R12737 (Figures 29, 30, 31, and 32), is a partial Trimyclid turtle plastron from Bracklesham Bay in Sussex with 30 observable areas of damage, most are small non-penetrative borings, but larger penetrative forms of borings are observable.

All the damage identified on NMHUK PAL R1433 (Figure 28) is non-penetrative with no borings breaking the surface of the carapace. The bone tissue in the area of the borings is extensively smoothed similar to the ichnospecies descriptions for both *Karethraichnus lakkos, Karethraichnus kulindros* (Zonneveld et al. 2015, Zonneveld et al. 2021). Both are attributed to smaller non-penetrative forms of borings (Figures 12, 13 and 14). The two larger borings on the carapace (Figure 28 C and D) on R1433 converge at a margin between plates of the plastron, a pattern observed in NHMUK PAL R8136 (Figure 27) and various literature (Zonneveld et al. 2015, Zonneveld et al. 2021 and Zonneveld et al. 2022). However, the true extent of the parasitic activity upon this specimen is unknown because of the interference of taphonomic processes on specimens during the stages of taphonomy illustrated from the Bouldnor Formation. The absence of the complete carapace leaves questions of the presence of penetrative forms of borings unanswered. The damage seen in 26 A and B is likely isolated instances of non-penetrative parasitic activity on the surface of the carapace, showing similar forms of boring to K. *lakkos* and *K. kulindros* (Zonneveld et al. 2015, Zonneveld et al. 2021).

Specimen NMHUK PAL RF 539/ R12737 (Figures 29, 30, 31, and 32) is an excellent example of the effects of both types of borings upon bone tissue, as this specimen displays over 30 different examples. Seventeen are small non-penetrative borings as seen on other specimens NHMUK PAL R8136 and NMHUK PAL R1433 (Figures 27 and 28), these smaller indentations are the most common of the identified boring palaeopathologies and can converge at plate margins or suture lines (Figures 27 J, 28 C and D, 30 A, C, G, H and I, 31 C, A and L, 32 B, C, and H). However, they can also be sporadically placed on the surface of the carapace (Figures 27 A, B, H, and F, 28 A and B, 30 B, D and M, 32 A). These small borings could be caused by isolated or small clusters of non-penetrating parasitic ichnotaxa as inferred within the NMHUK PAL R1433 (Figure 28) and NHMUK PAL R8136 (Figure 27). Larger borings are plentiful but only a few penetrate the plastron bone tissue fully as seen in NMHUK PAL RF 539/ R12737 (Figure 32 F and H), this could be caused by the same organism responsible for penetrative forms of borings assigned to the ichnotaxa *K. fiale* (Zonneveld et al. 2015, Zonneveld et al. 2021).

However, the main difference between NMHUK PAL RF 539/ R12737 and other specimens exhibiting borings is the number of observable borings, with over 30 identified areas of damage on a partially complete plastron (Cordero 2017). This could be because of the anatomy of the turtle’s shell, because of the thicker structure and domed nature of the carapace it may be easier for a parasitic organism to attach to the flatter plastron and penetrate the bone tissue, meaning more organisms can successfully attach resulting in the clustering of borings seen in Figures 30, 31 and 32 (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2015, Cordero 2017, Zonneveld et al. 2021). Congregations of borings around suture lines is a common pattern and means any parasitic organism may attach more successfully by wedging part of itself into the margin between the plates of the carapace or plastron increasing surface area for attachment (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2015, Cordero 2017, Zonneveld et al. 2021).

Extant examples of shell borings are varied and the causes of shell borings in extant species differ from the identified damage to fossil material (Zonneveld et al. 2015, Zonneveld et al. 2021). The most common example of shell boring within modern-day turtles is due to individual barnacles or clusters of barnacles which attach to the carapace or plastron and erode the keratin lining and bone tissue beneath as seen in Figure 11 and described in the literature (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2022). Once a barnacle detaches, it leaves a shallow non-penetrating boring on the surface of the carapace or plastron and the depth of penetration depends on the length of attachment, the larger a barnacle grows the more material underneath it erodes (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2022).

Based on these principles the smaller shallow and circular non-penetrative borings seen on extinct specimens in NHMUK PAL R8136, NMHUK PAL R1433 and NMHUK PAL RF 539/ R12737 (Figures 27, 28, 29, 30, 31, and 32), could be ancient barnacle attachments (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2022). Oblong-shaped borings (for example 31 J and K) could be multiple smaller barnacles occupying the same area on the surface of the shell and over time the separate individual barnacle exoskeletons merge (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2022).

However, the observed damage of barnacles on modern-day species does not explain the larger penetrative borings seen on extinct specimens, these are likely the result of another example of extant shell turtle borings. The detailed descriptions of a disease called ulcerative dermatitis within extant species of turtles may hold the answer. Ulcerative dermatitis has been observed in many species of terrestrial and sea turtles, spanning many families of Testudines (Maas 2013; Rothschild et al. 2013, Norton and Wyneken 2014). The disease causes both shallow and deep penetrating circular borings into the carapace and plastron, as seen in Figure 10. Often the borings destroy the bone of the shell within the affected area and leave internal tissues exposed (Maas 2013; Rothschild et al. 2013, Norton and Wyneken 2014).

The borings can form in the centre or around the edges of the carapace and have no distinct orientation (Maas 2013; Rothschild et al. 2013, Norton and Wyneken 2014). Figure

10 displays these characteristics, characteristics like some borings identified within the extinct species. Ulcerative dermatitis is another probable cause of high quantities of both penetrative and non-penetrative borings (Maas 2013; Rothschild et al. 2013, Norton and Wyneken 2014). Ulcerative dermatitis may be the most likely cause for the number of borings seen on extinct examples, especially Specimen NMHUK PAL RF 539/ R12737, which displays both penetrative and non-penetrative examples of borings, with seemingly no orientation. Lampreys are often discussed for the possibility of causing circular borings to the shells of both freshwater and sea turtles, but very little evidence exists from credible sources and is a subject of future research.

Pathologies seen in MIWG Sample 3 (Figure 33) could be the evidence of borings, displaying similar circular structures but lacking the central eroded material within the circumference as seen in NHMUK PAL R8136, NMHUK PAL R1433 and NMHUK PAL RF 539/ R12737 (Figures 27, 28, 29, 30, 31, and 32) Based on the structures observed, the palaeopathologies present in MIWG Sample 3 (Figure 33) could be failed attachment attempts by parasites or barnacles as seen in extant species (Hayashi and Tsuji 2008, Hayashi et al. 2011, Zonneveld et al. 2015, Zonneveld et al. 2021).

7.2. SCORING/ GOUGING

Most specimens are small to medium fragmentary remains that have a taphonomic grade of D based on taphonomic characters, with high percentages of disarticulation, corrasion, and abrasion (Brandt 1989; Downes 2021). All specimens from the Bouldnor Formation displaying scoring/gouging are fragmented pieces of carapace and plastron. Chelonia specimens exhibiting damage preserved a variety of identifiable scoring and gouges in specimens MIWG Sample 3, MIWG 4429, 4430, MIWG 4114 and MIWG 4112 (Figures 33, 34, 35, 36, and 37). Despite the samples being small shell fragments of *Emys sp* and *T. incrassatus*. the damage identified has been interpreted to have been caused by interaction with the corpse post-mortem, inferring likely scavenging by various organisms within the same ecosystem (Reeves 2009, Janssen et al. 2013, Botfalvai et al. 2014).

MIWG Sample 3 (Figure 33) has semi-circular indentations (one large and two smaller) on the surface of the carapace. The two smaller indentations pathologies are closer together; however, they are not connected as the projected path of the circular indentations does not match up. The surface around indentations seems marginally smoother than the rest of the carapace; however, this could just be the disparity of weathering in certain areas of the specimen. It is interpreted that these indentations are the result of post-mortem scavenging by small organisms such as molluscs or bivalves that feed on corpses once it has settled (Janssen et al. 2013).

Janssen et al. (2013) identified traces of Mollusca radula and bivalve activity on the carapace of other extinct terrestrial species of turtle, noting that mollusc radula can make small trench-like indentations into the bone tissue (Janssen et al. 2013). These trenches can change direction often and represent where the organism has changed direction to feed (Janssen et al. 2013). Similar trench-like gouges are seen in MIWG Sample 3, MIWG 4429, MIWG 4114 and MIWG 4112 (Figures 33, 34, 36, and 37), although all are different and could even represent multiple examples of the same organism feeding at the same time. The semi-circular trench-like indentations in MIWG Sample 3 could be the result of multiple post-mortem feedings from molluscs or bivalves (Figure 14) (Janssen et al. 2013, Botfalvai et al. 2014).

MIWG 4114 (Figure 35) has circular indentations that could be inferred as simply scavenging like Figure 16 (Botfalvai et al. 2014); however, the pathology also shows the linear structures present in Figure 15 (Reeves 2009, Janssen et al. 2013).
Drawing two parallel lines between the two pits show they are aligned, and this would suggest they may have been caused by a bite onto the surface of the carapace similar to those seen in Figure 15 (Janssen et al. 2013; Zonneveld et al. 2015). Similar structures are observed upon the ventral surface of specimen MIWG 4429 (Figure 34), a *T.*

incrassatus carapace fragment, with shallow 1-2 mm wide linear gouges on the ventral side. The linear pattern is very similar to the post-mortem scavenging damage observed in Janssen et al. 2013 and in Figures 15 (Janssen et al. 2013) in specimen MIWG Sample 3 (Figure 33). The indentations in both MIWG 4429 and 4114 (Figures 34 and 35) show no sign of tissue regrowth or healing, so it is interpreted the marks are from post-mortem scavenging (Reeves 2009, Jansen et al. 2013). The presence of *Diplocynodon* fossils within museum collections, and crocodilian vertebra from fieldwork collections of the Bouldnor Formation show its presence within the palaeoenvironment (Wolff et al. 2007; Rio et al. 2020). Because of the relatively small pits, it is likely a small predator inflicted the marks in Figure 15 (Janssen et al. 2013) a scavenger such as a juvenile *Diplocynodon* (Wolff et al. 2007, Reeves 2009, Janssen et al. 2013, Rio et al. 2020).

MIWG 4430 (Figure 36) exhibits shallow, smooth, and mottled gouges into the surface of the *Emys* sp. carapace. The structures meander and lack any linear structures seen in other forms of scoring/ gouging (Figures 33 and 34). The lack of structure to the damage is characteristic of palaeopathologies attributed to post-mortem scavenging by smaller organisms, such as various species of molluscs (Janssen et al. 2013, Munt 2013).

The presence of gastropods, *Lymnaea longiscata,* and *Viviparus angulosus* to name a few species, are present within the strata of the Bouldnor Formation, meaning interaction between the body of an individual and species of smaller scavengers is highly likely (Munt 2013). Molluscs would not be the only scavengers present within the Bouldnor Formation; however, they are amongst some of the most abundant marine invertebrates from the formation and, based on findings of freshwater and brackish species, it seems they have a wide distribution within the palaeoenvironenvironment (Munt 2013).

Similar interpretations could be associated with MIWG 4112 (Figure 37), a fragment of *Emys sp*. which preserves a long smooth deeper penetrating gouge. This gouge is wider and longer than the gouges seen in MIWG 4429 (Figure 34). However, MIWG 4112 also exhibits a linear meandering palaeopathology which displays a similar smoothed meandering texture as Figure 34 but also exhibits a basic linear structure. It could be interpreted that the palaeopathology results from scavenging by a larger predator, as the tip of a large tooth is dragged across the surface of the carapace creating a linear meandering pattern (Wolff et al. 2007; Reeves 2009, Janssen et al. 2013, Rio et al. 2020). Although because of the lack of other similar scavenging marks and the incomplete status of specimen MIWG 4112, it is more likely that the gouge is the pathway of a smaller scavenger feeding post-mortem (Reeves 2009; Janssen et al. 2013, Munt 2013).

Other Paleocene specimens from the UK also have similar scoring and gouging features as seen in Chelonia from the Bouldnor Formation. NHMUK PAL RF 539/ R12737 (Figures 30, 31, and 32), a partial Trimyclid plastron from Bracklesham Bay, Sussex, exhibits a long, snaking, deeply penetrating gouge into the surface of the plastron. This damage is labelled G*, as the damage can be seen across multiple sections of the full plastron (NHMUK PAL RF 539/ R12737, Figures 31 and 32). This pathology snakes through the surface of the plastron following a suture line underneath, the bone tissue underneath is smoothed as seen in MIWG 4430 (Figure 36) and MIWG 4112 (Figure 37) and in literature (Reeves 2009; Janssen et al. 2013, Botfalvai et al. 2014, Zonneveld et al. 2022). The damage observed is interpreted to have been post-mortem scavenging by a small organism and is comparable to other scorings and gouges present on other specimens (Figures 34 and 35). However, it preserves unique structures not seen in comparable material or literature, meaning the species responsible for the scavenging pathology may never be discovered (Zonneveld et al. 2015).

Extant examples of scoring/ gouges are clear within the literature (Chamberlain and Corsini 2007, Zonneveld et al. 2022). Zonneveld et al. 2022 give background knowledge of the preserved evidence of scavenging, breaking it down into clawing, gnawing, biting, and scratching, giving examples of each (Zonneveld et al. 2022). Chamberlain and Corsini interpret similar structures (seen in Figures 33, 34, 35, 36, and 37) to result from post-mortem scavenging/ gnawing of a turtle carcass by small mammals within the ecosystem (Chamberlain and Corsini 2007). Using modern examples, it is likely that specimens MIWG

Sample 3 (Figure 33), MIWG 4429 (Figure 34), and MIWG 4114 (Figure 35) are attributed to post-mortem scavenging/ gnawing by a semi-aquatic or terrestrial organism, as palaeopathologies identified from the Bouldnor Formation show comparable pathologies to extant turtle scavenging.

8. CONCLUSIONS

The rarity of discovering complete turtle remains is a by-product of a high-energy fluvial palaeoenvironment and the later re-exposure and weathering of fossils in a tide-dominated modern environment. The high-energy brackish floodplain where the animals died caused the initial disarticulation and transport of remains by fluvial processes. Interaction with other organisms within the ecosystem during biostratinomy contributes to increased separation of corpses, caused by the detachment of fragments during scavenging. Any articulated material unaffected by fluvial processes or interaction with predators would have been buried relatively quickly and re-exposed during the shift or fall of rock strata, during storms, and during periods of heavy rainfall.

Any articulated remains are disarticulated during cliff fall events and eroded from their surrounding matrix to be deposited as smoothed fragmentary pieces of carapace and plastron. Storms and heavy periods of precipitation over the Bouldnor Formation, cause the exposed strata to become waterlogged, increasing the weight of the clays, mud and siltstones. This sudden increase in weight increases pressure on faults and weaknesses in the rock strata due to the impact of gravity. The increased pressure on areas of weakness causes sudden separation of material, which results in the falling or slumping of the affected area. Any material deposited at the base of the cliffs below is subjected to fluvial processes such as abrasion, attrition and corrasion, fossilised remains within the fallen debris become separated from their surrounding matrix as a result of these processes. Articulated skeletal remains not affected by the cliff fall events are separated during the breaking and dissolving of the surrounding matrix by the ocean. Fragmentary skeletal remains are then redistributed along the coastline and deposited by tidal systems. The Carapace and Plastron are the largest exposed areas of a turtles anatomy and are most likely to preserve, as such Carapace and Plastron fragments are the most abundant chelonian remains found within the Bouldnor Formation, with fully articulated specimens being scarce.

Both penetrative and non-penetrative borings are clear on samples found from the Bouldnor Formation, displaying multiple pathological causes in one individual. Overall, the non-penetrative forms of damage are a result of parasitic behaviour caused by large and small barnacles. Barnacles cannot survive in true freshwater but can survive in brackish conditions, indicating attachments are more common during flood events when there would have been higher water salinity. Larger penetrative forms of borings from the Bouldnor Formation have been attributed to ulcerative dermatitis a disease seen in extant turtle species. Alternatively, the larger borings could be larger examples of barnacle attachments or an unidentified burrowing parasite.

Borings described from other Eocene rock strata, including the Thames Group and the Bracklesham Group, display comparative pathologies associated with barnacle attachments, and shallow circular non-penetrating borings. Oblong-shaped borings are likely the clustering of multiple barnacles within a small surface area of the carapace, a behaviour observed in extant species of sea turtles. The true cause of penetrative borings remains uncertain, because of multiple causes of pathologies exhibiting similar but subtly different structures. Scoring/ Gouging pathologies described from the Bouldnor Formation are the result of post-mortem scavenging by opportunistic organisms within the palaeoenvironment. Larger linear grooves observed upon fragments of carapace and plastron are caused by larger scavengers, whilst feeding the teeth or claws causes trench-like gouges into the surface of the material. Shallow penetrating gouges often display meandering structures and have little orientation. These structures represent scavenging by smaller organisms like molluscs upon or under the surface of the carapace after death. The path of the pathology is the path of the organism feeding on the corpse, similar structures can be observed in specimens from the Bracklesham Group.

Micro-Ct data is an intuitive way to analyse pathological damage both above and below surface level. It allows for the study of penetrative and non-penetrative borings in greater detail, using Micro-Ct to analyse the response of bone tissue to pathological contributors. Observing and analysing the surface curvature of identified pathologies using Micro-Ct is imperative in distinguishing the differences between penetrative and non-penetrative borings. Penetrative borings on average display steeper angles of incision into the carapace or plastron compared to the (on average) shallower circular incisions of non-penetrative borings. Measuring the thickness of affected bone tissue using Micro-Ct is vital in understanding the differing effects each type of boring displays. Penetrative borings destroy the underlying bone tissue within the circular pits and areas around the absent material is thinned by the presence of the pathological contributor. Non-penetrative borings also thin the underlying bone tissue however, the extent of the damage caused is not as great. Using Micro-Ct to observe and analyse the differing phenomena associated with pathologies is important in separating and quantifying characteristics displayed by the two types of borings. The aid of Micro-Ct analysis allows for easier identification between the two types of shell borings present within the Bouldnor Formation.

The Bouldnor Formation specimens display multiple phases of alteration, combining parasitism whilst the individual was still alive and scavenging post-mortem. Observed pathologies provide a story of a specimen’s life within the palaeoenvironment. Contrasting and comparing the palaeopathologies with alternate Eocene localities allows for an interpretation of the spread and distribution of pathological causes. The taphonomic grade of specimens provides an insight into the processes of disarticulation and explains the taphonomy of fragments collected from the Bouldnor Formation.

9. FUTURE RESEARCH

This study aimed to assess if chelonian fossils found within the Bouldnor Formation displayed any observable pathologies and deduce if these pathologies could be attributed to any pathological contributors, such as disease, parasitic behaviour or scavenging. After observing the fossil collections at the Isle of Wight Museum, Natural History Museum and personal collections, chelonian fossils from the Bouldnor Formation display multiple pathological structures. Another aim of this study was to attempt to infer potential causes for pathological structures, using extant examples as a reference to compare pathological characteristics. Using these comparisons, it is possible to link structures seen in extant species to those seen in the extinct species of the Bouldnor Formation. However, due to a lack of primary research on extinct chelonian pathologies, the difficulty in grouping pathologies by inferred causes dramatically increased.

Further investigation into the varying types of pathologies observed on the shells of extant and extinct turtles is required to develop more conclusive causes. Additional examples of articulated and disarticulated remains of chelonians from the Bouldnor Formation and other fossiliferous Eocene rock strata are needed for further analysis of pathological phenomena. Access to more archived specimens in other museums or private collections could be granted and allow for the analysis of anomalies.

In addition, more extensive fieldwork is required to obtain a greater quantity of primary specimens, to acquire fragments displaying observable pathologies. Observing and quantifying the taphonomic grade of these specimens would show its effects on the preservation potential of pathologies and aid in the understanding of pathological characteristics. Any specimens displaying exceptional preservation of pathologies could be presented for Micro-Ct scanning. With additional scans of pathological phenomena, quantifying unique characteristics would be faster. With this research, identifying and labelling pathologies and inferring their cause would be simpler, resulting in more definitive examples of different pathological structures. The ability to definitively say whether specific pathological structures are the cause of one contributor would benefit this study and any future studies on turtle palaeopathologies.

10. REFERENCE LIST

Anson, C., Rothschild, B. and Naples, V. 2012. Soft Tissue Contributions to Pseudopathology of Ribs. 02.

Armenteros, I. and Daley, B. 1998. Pedogenic modification and structure evolution in palustrine facies as exemplified by the Bembridge limestone (late Eocene) of the Isle of Wight, southern England. 119, 275–295.

Armenteros, I., Daley, B. and García, E. 1997. Lacustrine and palustrine facies in the Bembridge Limestone (late Eocene, Hampshire Basin) of the Isle of Wight, southern England. 128, 111–132.

Augé, M. and Smith, R. 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene-Oligocene transition. 155, https://doi.org/10.1111/j.1096-3642.2008.00435.x.

Augé, M.L. 2003. La faune de Lacertilia (Reptreal-timeamata) de l'Éocène inférieur de Prémontré (Bassin de Paris, France). Geodiversitas 25 (3):. 539–574.

Augé, M.L. 2005. Évolution des lézards du Paléogène en Europe. Muséum national d'Histoire naturelle, Paris,.(Mémoires du Muséum national d'Histoire naturelle ; 192). 1–369.

Barrett, P.M. 2008. M. J. Benton, E. Cook & J. J. Hooker 2005. Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain. Geological Conservation Review Series no. 32. xvi + 215 pp. Peterborough: Joint Nature Conservation Committee. Price £55.00 (hard covers). ISBN 1 86107 480 8. 145, https://doi.org/10.1017/S0016756807004037.

Beamish, D. and White, J.C. 2011. A radiometric airborne geophysical survey of the Isle of Wight. 122, 787–799.

Behrensmeyer, A.K. 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4, 150–162.

Behrensmeyer, A.K. and Kidwell, S.M. 1985. Taphonomy's contributions to paleobiology. Paleobiology, 11, 105–119.

Behrensmeyer, A.K., Kidwell, S.M. and Gastaldo, R.A. 2000a. Taphonomy and paleobiology. Paleobiology, 26, 103–147.

Behrensmeyer, A.K., Kidwell, S.M. and Gastaldo, R.A. 2000b. Taphonomy and paleobiology. Paleobiology, 26, 103–147.

Benton, M.J. and Harper, D.A.T. 2020. Introduction to Paleobiology and the Fossil Record. inton, M.J. and Spencer, P.S. 1995. British Caenozoic fossil reptile sites. In: Fossil Reptiles of Great Britain. 271–299.

Bever, G.S., Lyson, T.R., Field, D.J. and Bhullar, B.-A.S. 2015. Evolutionary origin of the turtle skull. Nature, 525, 239–242.

Bijl, P.K., Bendle, J.A.P., et al. 2013. Eocene cooling is linked to early flow across the Tasmanian Gateway. 110, https://doi.org/10.1073/pnas.1220872110.

Bolet, A. and Evans, S.E. 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain), https://doi.org/10.26879/354.

Bosma, A.A., de Bruijn, H. and Wessels, W. 2022. A large Eomys antiquus (Aymard, 1853)(Mammalia, Rodentia) from the early Oligocene sedimentary deposits at Bouldnor Cliff (Isle of Wight, England, UK). Palaeobiodiversity and Palaeoenvironments, 1–18.

Botfalvai, G., Prondvai, E. and Ősi, A. 2014. Inferred bite marks on a Late Cretaceous (Santonian) bothremydid turtle and a hylaeochampsid crocodilian from Hungary. 50, 304–317.

Brandt, D.S. 1989. Taphonomic Grades as a Classification for Fossiliferous Assemblages and Implications for Paleoecology. Palaios, 4, 7 pages.

Brodie, P.B. 1878. On the discovery of a large and varied series of fossil insects and other associated fossils, in the Eocene (Tertiary) strata of the Isle of Wight. 1–12.

Buikstra, J.E. and Cook, D.C. 1980. Palaeopathology: An American Account. Annual review of anthropology, 9, 433–470.

Cadena, E.A. and Parham, J.F. 2015. Oldest known marine turtle? A new protostegid from the Lower Cretaceous of Colombia. PaleoBios, 32, https://doi.org/10.5070/p9321028615.

Carabajal, A.P., Sterli, J., Müller, J. and Hilger, A. 2013. Neuroanatomy of the marine Jurassic turtle Plesiochelys etalloni (Testudinata, Plesiochelyidae). PloS one, 8, e69264.

Chamberlain, H. and Corsini, J. n.d. Characterization of a Modern Turtle Deathsite and Comparison with a Paleo-Deathsite. Eastern Oregon Science Journal.

Chen, I.H., Yang, W. and Meyers, M.A. 2015. Leatherback sea turtle shell: A tough and flexible biological design. Acta biomaterialia, 28, 2–12.

Collinson, M.E. 1983. Palaeofloristic assemblages and palaeoecology of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. 86, 177–225.

Collinson, M.E., Fowler, K. and Boulter, M.C. 1981. Floristic changes indicate a cooling climate in the Eocene of southern England. 291, 315–317.

Cordero, G.A. 2017. The turtle’s shell. Current biology: CB, 27, R168–R169.

Corsini, J.A. and Chamberlain, H. 2009. Characterization of modern turtle death sites for comparison with late Eocene and early Oligocene turtle sites. 161, 96–109.

Daley, B. 1968a. Sedimentary Structures from a Non-Marine Horizon in the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, England. 38, https://doi.org/10.1306/74D718ED-2B21-11D7-8648000102C1865D.

Daley, B. 1968b. Sedimentary Structures from a Non-Marine Horizon in the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, England. 38, https://doi.org/10.1306/74D718ED-2B21-11D7-8648000102C1865D.

Daley, B. 1972a. Macroinvertebrate assemblages from the Bembridge Marls (Oligocene) of the Isle of Wight, England, and their environmental significance. 11, 11–32.

Daley, B. 1972b. Some problems concerning the Early Tertiary climate of southern Britain. 11, 177–190.

Daley, B. 1972c. Some problems concerning the Early Tertiary climate of southern Britain. 11, 177–190.

Daley, B. 1973. The palaeoenvironment of the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire. 84, 83–93.

Daley, B. 1999. Palaeogene sections in the Isle of Wight. A revision of their description and significance in the light of research undertaken over recent decades.

Daley, B. and Stewart, D.J. 1979. Weekend field meeting: The Wealden Group in the Isle of Wight 17–19 June 1977. Proceedings of the Geologists' Association. Geologists' Association, 90, 51–54.

De Coninck, J., de Ruijter, M.J. and Voué, M. 2001. Dynamics of wetting. 6, 49–53.

Donovan, S.K. and Simpson, M.I. 2021. An etched turtle bone from the Paleogene of the Isle of Wight, UK. 28, 56–59.

Downes, J. 2021. Isle of Wight: Landscape and Geology.

Driscoll, E.G. and Weltin, T.P. 1973. Sedimentary parameters as factors in abrasive shell reduction. Palaeogeography, palaeoclimatology, palaeoecology, 13, 275–288.

Edwards, N., Jarzembowski, E.A., Pain, T. and Daley, B. 1998. Cocoon-like trace fossils from the lacustrine-palustrine Bembridge Limestone Formation (Late Eocene), Southern England. 109, 25–32.

Engstrom, T.N., Shaffer, H.B. and McCord, W.P. 2004. Multiple data sets, high homoplasy, and the phylogeny of softshell turtles (Testudines: Trionychidae). Systematic biology, 53, 693–710.

Ernst, C., Barbour, R. and Lovich, J. 1994. Turtles of the United States and Canada.,(Smithsonian Institution Press: Washington.).

Ferreira, G.S., Werneburg, I., Lautenschlager, S. and Evers, S.W. 2023. Contrasting Brains and Bones: Neuroanatomical Evolution of Turtles (Testudinata). In: Dozo, M. T., Paulina-Carabajal, A., Macrini, T. E. and Walsh, S. (eds) Paleoneurology of Amniotes : New Directions in the Study of Fossil Endocasts. 79–121.

Flint, M., Patterson-Kane, J.C., Limpus, C.J., Work, T.M., Blair, D. and Mills, P.C. 2009. Postmortem diagnostic investigation of disease in free-ranging marine turtle populations: a review of common pathologic findings and protocols. 21, 733–759.

Gaffney, E.S. and Meeker, L.J. 1983. Skull morphology of the oldest turtles: a preliminary description of Proganochelys quenstedti. Journal of Vertebrate Paleontology, 3, 25–28.

Gaffney, E.S. and Meylan, P.A. 1988. A phylogeny of turtles.

Gaffney, E.S., Meylan, P.A. and Wyss, A.R. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. 7, 313–335.

Gale, A.S. 2021. The stratigraphy of the upper Campanian Chalk of the southern English coast (Isle of Wight, Dorset), United Kingdom. 124, 104775.

Gale, A.S., Huggett, J.M., PÄlike, H., Laurie, E., Hailwood, E.A. and Hardenbol, J. 2006a. Correlation of Eocene–Oligocene marine and continental records: orbital cyclicity, magnetostratigraphy and sequence stratigraphy of the Solent Group, Isle of Wight, UK. 163, 401–415.

Gale, A.S., Huggett, J.M., PÄlike, H., Laurie, E., Hailwood, E.A. and Hardenbol, J. 2006b. Correlation of Eocene–Oligocene marine and continental records: orbital cyclicity, magnetostratigraphy and sequence stratigraphy of the Solent Group, Isle of Wight, UK. 163, 401–415.

Ganjbakhsh, S.E., Park, S.-M., Sung, H.-C. and Kim, E.-S. 2020. Non-destructive Imaging of Skeletal Structures of Freshwater Turtles Using Computed Tomography.

Garner, M.M., Herrington, R., et al. 1997. Shell disease in river cooters (Pseudemys concinna) and yellow–bellied turtles (Trachemys scripta) in a Georgia (USA) lake. Journal of wildlife diseases, 33, 78–86.

Gastaldo, R.A., Savrda, C. and Lewis, R.D. 1996. Deciphering Earth History: A Laboratory Manual with Internet Exercises.

Geological Survey of Great Britain and Reid, C. 1902. The Geology of the Country around Southampton.

Gow, C.E. 1997. A reassessment of Eunotosaurus africanus Seeley (Amniota: Parareptilia). Palaeontologia africana, 34, 33–42.

Green, B.P. 1998. Fossil lizard assemblages from the Hampshire Basin (Palaeogene) of southern England.

Grimes, S.T., Collinson, M.E., Hooker, J.J., Mattey, D.P., Grassineau, N.V. and Lowry, D. 2004. Distinguishing the diets of coexisting fossil theridomyid and glirid rodents using carbon isotopes. 208, 103–119.

Grupe, G. 2018. Taphonomy and fossilization. The International Encyclopedia of Biological Anthropology, 1–8, https://doi.org/10.1002/9781118584538.ieba0482.

Haridy, Y., Witzmann, F., Asbach, P., Schoch, R.R., Fröbisch, N. and Rothschild, B.M. 2019. Triassic Cancer—Osteosarcoma in a 240-Million-Year-Old Stem-Turtle. JAMA Oncology, 5, 425–426.

Hayashi, R. and Tsuji, K. 2008. Spatial distribution of turtle barnacles on the green sea turtle, Chelonia mydas. 23, 121–125.

Hayashi, R., Takuma, S., Narazaki, T. and Sato, K. 2011. Chelonia mydas agassizii (Black [Pacific] sea turtle). Epibiont barnacles. Herpetological review, 42, 264–265.

Hayes, P.A. and Collinson, M.E. 2013. The Flora of the Insect Limestone (latest Eocene) from the Isle of Wight, southern England. 104, 245–261.

Hirayama, R. 1998. Oldest known sea turtle. Nature, 392, 705–708.

Hoffmann, M., Hilton-Taylor, C., et al. 2010. The impact of conservation on the status of the world’s vertebrates. 330, 1503–1509.

Hooke, J.M. 1998. Coastal Defence and Earth Science Conservation.

Hooker, J. and Sweetman, S. n.d. EARLY CRETACEOUS AND PALEOGENE VERTEBRATE LOCALITIES OF THE ISLE OF WIGHT, SOUTHERN ENGLAND.

Hooker, J.J. 1987. Mammalian faunal events in the English Hampshire Basin (late Eocene–early Oligocene) and their application to European biostratigraphy. 10, 109–116.

Hooker, J.J. 1989. British mammals in the Tertiary period. 38, 9–21.

Hooker, J.J. 2010. The ‘Grande Coupure’in the Hampshire Basin, UK: taxonomy and stratigraphy of the mammals on either side of this major Palaeogene faunal turnover. 147–215.

Hooker, J.J., Jj, H., An, I., Rtj, M. and Ca, W. 1980. The distribution of cartilaginous fish, turtles, birds and mammals in the British Palaeogene.

Hooker, J.J., Van Bergen, P.F., Singer, R.L., Collinson, M.E., De Leeuw, J.W. and Jones, T.P. 1992. Reconstruction of Tertiary palaeoenvironments using a combination of molecular and conventional palaeobiology. 6, 134–134.

Hooker, J.J., Collinson, M.E., Van Bergen, P.F., Singer, R.L., de Leeuw, J.W. and Jones, T.P. 1995. Reconstruction of land and freshwater palaeoenvironments near the Eocene-Oligocene boundary, southern England. Journal of the Geological Society, 152, 449–468.

Hooker, J.J., Collinson, M.E. and Sille, N.P. 2004a. Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. 161, https://doi.org/10.1144/0016-764903-091.

Hooker, J.J., Collinson, M.E. and Sille, N.P. 2004b. Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. 161, https://doi.org/10.1144/0016-764903-091.

Hooker, J.J., Evans, S.E. and Davis, P.G. 2019. Vertebrate remains from the Insect Limestone (latest Eocene), Isle of Wight, UK. 110, 281–287.

Hopson, P. 2011. The geological history of the Isle of Wight: An overview of the ‘diamond in Britain’s geological crown’. 122, 745–763.

Hou, Z.-Q., Zheng, Y.-C., et al. 2012. Eocene–Oligocene granitoids in southern Tibet: Constraints on crustal anatexis and tectonic evolution of the Himalayan orogen. 349-350, https://doi.org/10.1016/j.epsl.2012.06.030.

Hutchinson, J.H. and Frye, F.L. 1989. Pathologies of the shell in Eocene turtles. 9, 26A.

Insole, A. and Daley, B. 1985. A revision of the lithostratigraphical nomenclature of the Late Eocene and Early Oligocene strata of the Hampshire Basin, southern England.

Jacobson, E.R., Mansell, J.L., et al. 1989. Cutaneous fibropapillomas of green turtles (Chelonia mydas). Journal of comparative pathology, 101, 39–52.

Janssen, R., Van Baal, R.R. and Schulp, A.S. 2013. Bone damage in Allopleuron hofmanni (Cheloniidae, Late Cretaceous)·. 92, 153–157.

Jenkins, G.O., Foster, C. and Hopson, P.M. 2011. Geology as a control on landslides on the Isle of Wight: An overview. 122, 906–922.

Jolley, D.W. and Widdowson, M. 2005. Did Paleogene North Atlantic rift-related eruptions drive early Eocene climate cooling? 79, 355–366.

Kak, A.C., Slaney, M. and Wang, G. 2002. Principles of computerized tomographic imaging.

Katz, M.E., Miller, K.G., Wright, J.D., Wade, B.S., Browning, J.V., Cramer, B.S. and Rosenthal, Y. 2008. Stepwise transition from the Eocene greenhouse to the Oligocene icehouse. 1, https://doi.org/10.1038/ngeo179.

Kemp, D., Kemp, L. and Ward, D. n.d. AN ILLUSTRATED GUIDE TO THE BRITISH MIDDLE EOCENE VERTEBRATES.

King, C. n.d. The Hampshire Basin and adjacent areas, https://doi.org/10.1144/SR27.15.

Klembara, J. and Green, B. 2010. Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Late Eocene of the Hampshire Basin of southern England. 8, 97–129.

Krahl, A., Lipphaus, A., Sander, M.P., Maffucci, F., Hochscheid, S. and Witzel, U. 2020. Humerus osteology, myology, and finite element structure analysis of Cheloniidae. Anatomical record , 303, 2177–2191.

Lada, G.A. and Boldyreva, M.P. 2018. Pholidosis abnormalities and injuries in the European pond turtle (Emys orbicularis) in the conditions of the Khopersky Nature Reserve. 87–91.

Landis, E.N. and Keane, D.T. 2010. X-ray microtomography. 61, 1305–1316.

Lawrence, D.R. 1968. Taphonomy and Information Losses in Fossil Communities. GSA Bulletin, 79, 1315–1330.

Lawrence, D.R. 1979. BiostratinomyBiostratinomy. In: Paleontology. 99–102.

Lew, D.P. and Waldvogel, F.A. 1997. Osteomyelitis. The New England journal of medicine, 336, 999–1007.

Li, C., Wu, X.-C., Rieppel, O., Wang, L.-T. and Zhao, L.-J. 2008. An ancestral turtle from the Late Triassic of southwestern China. Nature, 456, 497–501.

Lindars, E.S., Grimes, S.T., Mattey, D.P., Collinson, M.E., Hooker, J.J. and Jones, T.P. 2001. Phosphate δ18O determination of modern rodent teeth by direct laser fluorination: An appraisal of methodology and potential application of palaeoclimate reconstruction. 65, 2535–2548.

Lintner, M., Weissenbacher, A. and Heiss, E. 2012. The oropharyngeal morphology in the semiaquatic giant Asian pond turtle, Heosemys grandis, and its evolutionary implications. PloS one, 7, e46344.

Liu, Z., Pagani, M., et al. 2009. Global Cooling During the Eocene-Oligocene Climate Transition. 323, https://doi.org/10.1126/science.1166368.

Lucas, A.M. 1972. Avian anatomy integument.

Lyman, R.L. and Others. 2010. What taphonomy is, what it isn't, and why taphonomists should care about the difference. Journal of Taphonomy, 8, 1–16.

Lyson, T.R., Bever, G.S., Scheyer, T.M., Hsiang, A.Y. and Gauthier, J.A. 2013. Evolutionary origin of the turtle shell. Current biology: CB, 23, 1113–1119.

Maas, A.K., III. n.d. Vesicular, Ulcerative, and Necrotic Dermatitis of Reptiles.

Mantell, G.A. 1854. Geological Excursions Round the Isle of Wight, and Along the Adjacent Coast of Dorsetshire: Illustrative of the Most Interesting Geological Phenomena and Organic Remains.

McCOBB, L.M.E., Duncan, I.J., Jarzembowski, E.A., Stankiewicz, B.A., Wills, M.A. and Briggs, D.E.G. 1998. Taphonomy of the insects from the Insect Bed (Bembridge Marls), late Eocene, Isle of Wight, England. 135, 553–563.

Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). Bulletin of the AMNH; v. 186, article 1https://digitallibrary.amnh.org/handle/2246/972.

Milner, A.C., Ac, M. and Ar, M. 1982. Amphibians and squamates from the upper Eocene of Hordle Cliff, Hampshire, a preliminary report.

Momber, G., Mason, B., Gillespie, J., Heamagi, C., Satchell, J., Ferreira, R. and Noble-Shelly, J. 2020. New evidence from Bouldnor Cliff for technological innovation in the mesolithic, population dispersal and use of drowned landscapes, https://doi.org/10.1016/j.quaint.2020.11.048.

Moody, R.T.J. 1968. A turtle, Eochelys crassicostata (Owen) from the London Clay of the Isle of Sheppey. 79, 129–IN3.

Moody, R.T.J. 1980a. Notes on some European Palaeogene turtles. 2, 161–168.

Moody, R.T.J. 1980b. The distribution of turtles in the British Palaeogene. Tertiary Research, 3, 21–24.

Moody, R.T.J. 1997. The paleogeography of marine and coastal turtles of the North Atlantic and Trans-Saharan regions. 259–278.

Moody, R.T.J. and Rtj, M. 1974. The taxonomy and morphology of Puppigerus camperi (Gray), an Eocene sea-turtle from northern Europe.

Mortimore, R. 2011. Structural geology of the Upper Cretaceous Chalk Central Mass, Isle of Wight, U.K. Proceedings of the Geologists' Association. Geologists' Association, 122, 298–331.

Mottershead, D. 2013. Coastal weathering. In: Treatise on Geomorphology. Volume 4, Weathering and Soils Geomorphology. 228–244.

Munt, M.C. 2013. Mollusca from the Insect Limestone (Bembridge Marls Member: Bouldnor Formation: Solent Group), Palaeogene, Isle of Wight, southern England. 104, 263–274.

Murray, J.W. and Jw, M. 1974. PALAEOGENE FORAMINIFERIDA AND PALAEOECOLOGY, HAMPSHIRE AND PARIS BASINS AND THE ENGLISH CHANNEL.

Naples, V.L. and Rothschild, B.M. 2011a. Do ribs actually have a bare area? A new analysis. 62, 368–373.

Naples, V.L. and Rothschild, B.M. 2011b. Do ribs actually have a bare area? A new analysis. 62, https://doi.org/10.1016/j.jchb.2011.08.001.

Newell, A.J. and Evans, D.J. 2011. Timing of basin inversion on the Isle of Wight: New evidence from geophysical log correlation, seismic sections and lateral facies change in the Palaeogene Headon Hill Formation. 122, 868–882.

Norton, T. 2014. Sea Turtle Physical Examination: Part 2 Wyneken, J. (ed.).

Orhan, K. 2020. Introduction to Micro-CT Imaging. In: Orhan, K. (ed.) Micro-Computed Tomography (micro-CT) in Medicine and Engineering. 1–5.

Pamfilie, A.M., Espinal, M.D. and Vitek, N.S. 2022. Quantifying shell patterning helps identify species of Trionychidae. Anatomical record, https://doi.org/10.1002/ar.25064.

Radley, J.D. and Barker, M.J. 1998. Palaeoenvironmental analysis of shell beds in the Wealden Group (Lower Cretaceous) of the Isle of Wight, southern England: an initial account. 19, 489–504.

Radley, J.D., Barker, M.J. and Harding, I.C. 1998. Palaeoenvironment and taphonomy of dinosaur tracks in the Vectis Formation (Lower Cretaceous) of the Wessex Sub-basin, southern England. 19, 471–487.

Rage, J.-C. and Augé, M. 1993. Squamates from the Cainozoic of the western part of Europe. A review. 7, 199–216.

Ratcliffe, K.T. and Moody, R.T.J. 1993. The stratigraphy of the Taoudeni basin, west Africa. 77.

Reeves, N.M. 2009. Taphonomic effects of vulture scavenging. Journal of forensic sciences, 54, 523–528.

Rhodin, A.G.J., van Dijk, P.P., Iverson, J.B. and Shaffer, H.B. 2010. Turtles of the world, 2010 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. 5, 0–85.

Rio, J.P., Mannion, P.D., Tschopp, E., Martin, J.E. and Delfino, M. 2020. Reappraisal of the morphology and phylogenetic relationships of the alligatoroid crocodylian Diplocynodon hantoniensis from the late Eocene of the United Kingdom. 188, 579–629.

Ross, A.J. and Self, A. 2013. The fauna and flora of the Insect Limestone (late Eocene), Isle of Wight, UK: introduction, history and geology. 104, 233–244.

Rothschild, B.M., Schultze, H.-P. and Pellegrini, R. 2013a. Osseous and Other Hard Tissue Pathologies in Turtles and Abnormalities of Mineral Deposition. In: Brinkman, D. B., Holroyd, P. A. and Gardner, J. D. (eds) Morphology and Evolution of Turtles. 501–534.

Rothschild, B.M., Schultze, H.-P. and Pellegrini, R. 2013b. Osseous and other hard tissue pathologies in turtles and abnormalities of mineral deposition. 501–534.

Ruffell, A. and Wach, G. 1998. Firmgrounds - key surfaces in the recognition of parasequences in the Aptian Lower Greensand Group, Isle of Wight (southern England). 45, https://doi.org/10.1046/j.1365-3091.1998.00147.x.

Scheyer, T.M. and Sánchez-Villagra, M.R. 2007. Carapace bone histology in the giant pleurodiran turtle Stupendemys geographicus: phylogeny and function. 52.

Scheyer, T.M., Martin Sander, P., Joyce, W.G., Böhme, W. and Witzel, U. 2007. A plywood structure in the shell of fossil and living soft-shelled turtles (Trionychidae) and its evolutionary implications. 7, 136–144.

Scheyer, T.M., Danilov, I.G., Sukhanov, V.B. and Syromyatnikova, E.V. 2014. The shell bone histology of fossil and extant marine turtles revisited. 112, 701–718.

Schoch, R.R. and Sues, H.-D. 2015. A Middle Triassic stem-turtle and the evolution of the turtle body plan. Nature, 523, 584–587.

Schoch, R.R., Klein, N., Scheyer, T.M. and Sues, H.-D. 2019. Microanatomy of the stem-turtle Pappochelys rosinae indicates a predominantly fossorial mode of life and clarifies early steps in the evolution of the shell. Scientific reports, 9, 10430.

Seeley, H.G. 1892. On a New Reptile from Welte Vreden (Beaufort West), Eunotosaurus africanus (Seeley). Quarterly Journal of the Geological Societyhttps://www.lyellcollection.org/doi/abs/10.1144/GSL.JGS.1892.048.01-04.43.

Selden, P.A. 2013. Spiders (Arachnida: Araneae) from the Insect Limestone (Bembridge Marls, Late Eocene) of the Isle of Wight, southern England. 104, 275–282.

Sheldon, N.D., Mitchell, R.L., Collinson, M.E. and Hooker, J.J. 2009. Eocene-Oligocene transition paleoclimatic and paleoenvironmental record from the Isle of Wight (UK). 452, 249–259.

Skipper, J.A. 2000. The Stratigraphy of the Lambeth Group (Palaeocene) of South East England. Imperial College London (University of London).

Stewart, D.J., Ruffell, A., Wach, G. and Goldring, R. 1991. Lagoonal sedimentation and fluctuating salinities in the Vectis Formation (Wealden Group, Lower Cretaceous) of the Isle of Wight, southern England. Sedimentary geology, 72, 117–134.

Storch, G., Engesser, B. and Wuttke, M. 1996. Oldest fossil record of gliding in rodents. 379, https://doi.org/10.1038/379439a0.

Sumbler, M.G. 1996. British Regional Geology: London and the Thames Valley.

Surmik, D., Szczygielski, T., Janiszewska, K. and Rothschild, B.M. 2018. Tuberculosis-like respiratory infection in 245-million-year-old marine reptile suggested by bone pathologies. 5, https://doi.org/10.1098/rsos.180225.

Underwood, J.C.E. 2018. What is pathology? Underwood’s Pathology: A Clinical Approach, 2.

Waldron, T. 2020. Palaeopathology.

Wang, D., Xing, L., Rothschild, B.M., Persons, W.S. and Liu, J. 2022. A palaeopathological specimen of the Late Miocene Parataxidea sp. (Mammalia: Carnivora) from the Linxia Basin, China. Historical biology, 1–6.

Webb, R.G. 1990. Trionyx. Catalogue of American Amphibians and Reptiles (CAAR).

Webb, R.G. 2022. North American Recent Soft-Shelled Turtles (Family Trionychidae).

Weisbrod, T.C., Stacy, N.I., Stedman, N.L. and Norton, T.M. 2020a. Diagnosis and surgical management of a paratesticular cyst in a rehabilitating juvenile male green turtle (Chelonia mydas). 7, 69.

Weisbrod, T.C., Stacy, N.I., Stedman, N.L. and Norton, T.M. 2020b. Diagnosis and Surgical Management of a Paratesticular Cyst in a Rehabilitating Juvenile Male Green Turtle (Chelonia mydas). 7, 69.

Welsh, H., Nelson, A.J., van der Merwe, A.E., de Boer, H.H. and Brickley, M.B. 2020. An Investigation of Micro-CT Analysis of Bone as a New Diagnostic Method for Paleopathological Cases of Osteomalacia. International journal of paleopathology, 31, 23–33.

West, I. 2015. Introduction to the Geology of the Isle of Wight.

Williams, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. Bulletin of the AMNH; v. 94, article 9.

Wilson, L.E. 2023. Rapid growth in Late Cretaceous sea turtles reveals life history strategies similar to extant leatherbacks. PeerJ, 11, e14864.

Wing, S., Gingerich, P., Schmitz, B., and Thomas, E.,. 2003. Causes and consequences of globally warm climates in the early Paleogene: 455–457.

Wolff, E.D.S., Fowler, D.W. and Bonde, J.W. 2007. A possible case of necrotizing dermatitis in the crocodylian Diplocynodon, from the Oligocene of the Isle of Wight, United Kingdom. 19, 203–207.

Woods, M.A., Wilkinson, I.P., Lott, G.K., Booth, K.A., Farrant, A.R., Hopson, P.M. and Newell, A.J. 2008. A reappraisal of the stratigraphy and depositional development of the Upper Greensand (Late Albian) of the Devizes district, southern England. 119, 229–244.

Zardus, J. and Balazs, G. 2007. Two Previously Unreported Barnacles Commensal with the Green Sea Turtle, Chelonia Mydas (Linnaeus, 1758), in Hawaii and a Comparison of their Attachment Modes. Crustaceana, 80, 1303–1315.

Zonneveld, J.-P., Bartels, W.S., Gunnell, G.F. and McHugh, L.P. 2015. Borings in early Eocene turtle shell from the Wasatch Formation, South Pass, Wyoming. 89, 802–820.

Zonneveld, J.-P., Zonneveld, Z.E.E., Bartels, W.S., Gingras, M.K. and Head, J.J. 2022a. BONE MODIFICATION FEATURES RESULTING FROM BARNACLE ATTACHMENT ON THE BONES OF LOGGERHEAD SEA TURTLES (Caretta caretta), CUMBERLAND ISLAND, GEORGIA, USA: IMPLICATIONS FOR THE PALEOECOLOGICAL, AND TAPHONOMIC ANALYSES OF FOSSIL SEA TURTLES. Palaios, 37, 650–670.

Zonneveld, J.-P., Fiorillo, A.R., Hasiotis, S. and Gingras, M.K. 2022b. Tooth marks, gnaw marks, claw-marks, bite marks, scratch marks, etc: terminology in ichnology. Ichnos, 29, 93–101.

Zug, G.R. 2023. Turtle. Encyclopedia Britannicahttps://www.britannica.com/animal/turtle-reptile.

11. APPENDICES - **COLLECTION NUMBER: 4114**

Isle of Wight museum collections

Collection number: 4114

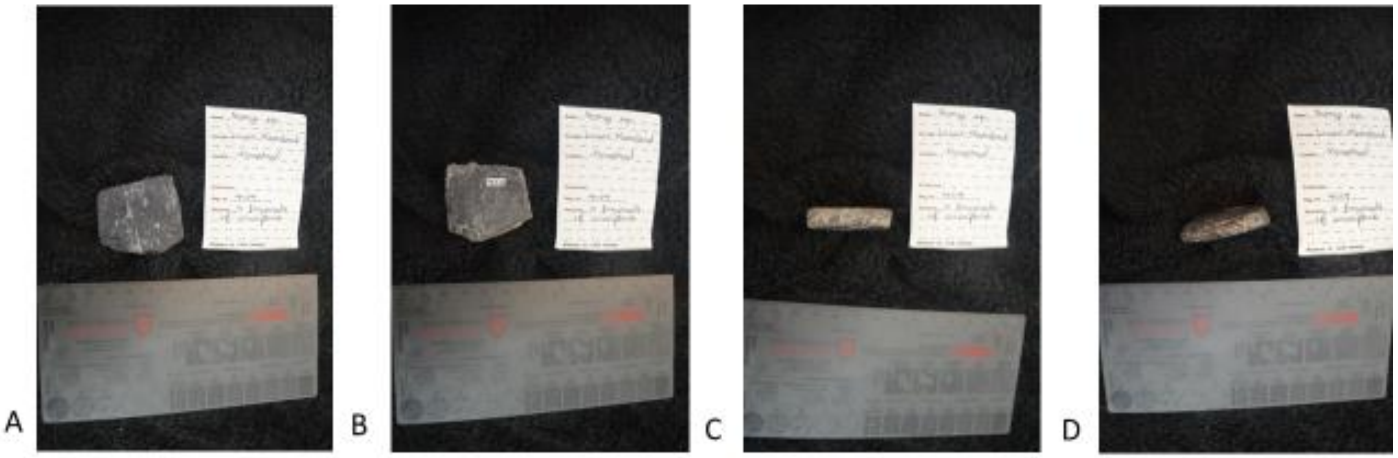
Species: *Emys. Sp*

Locality:

Remarks: 3 Fragments of carapace

Sample number: 3

Pictures: 4



Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: 4114

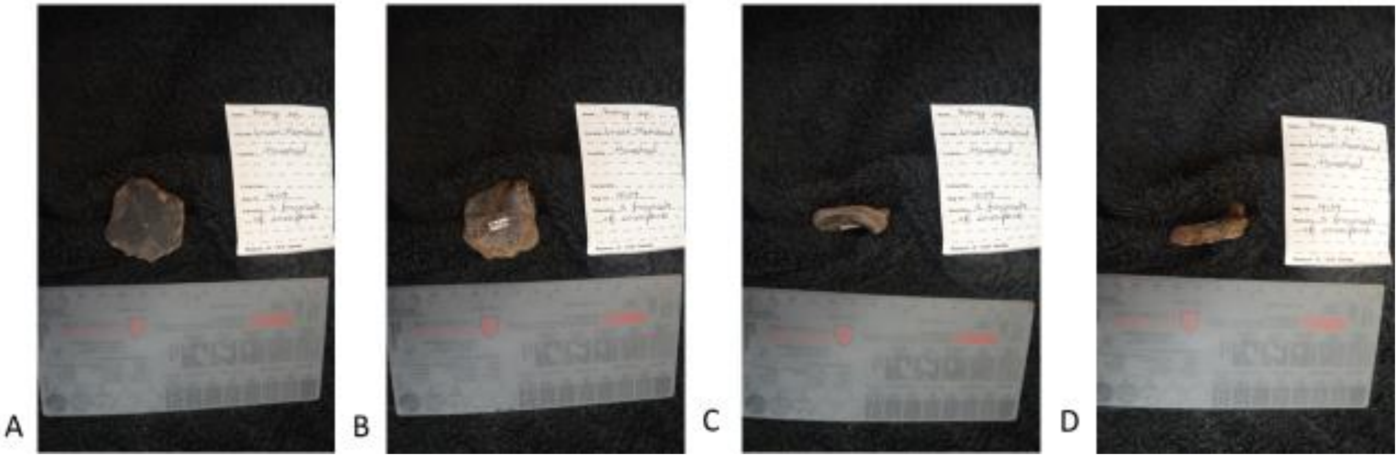
Species: *Emys. Sp*

Locality:

Remarks: 3 Fragments of carapace

Sample number: 4

Pictures: 4



Isle of Wight museum collections

Collection number: 4114

Species: *Emys . Sp*

Locality:

Remarks: 3 Fragments of carapace

Sample number: 1

Pictures: 4

A

B

C

D

Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: 4114

Species: *Emys . Sp*

Locality:

Remarks: 3 Fragments of carapace

Sample number: 2

Pictures: 4

A

B

C

D

COLLECTION NUMBER: G.T.Woods 4113

Isle of Wight museum collections

Collection number: G.T.Woods 4113

Species: *Emys . Sp*

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 5

Pictures: 4

Isle of Wight museum collections

Collection number: G.T.Woods 4113

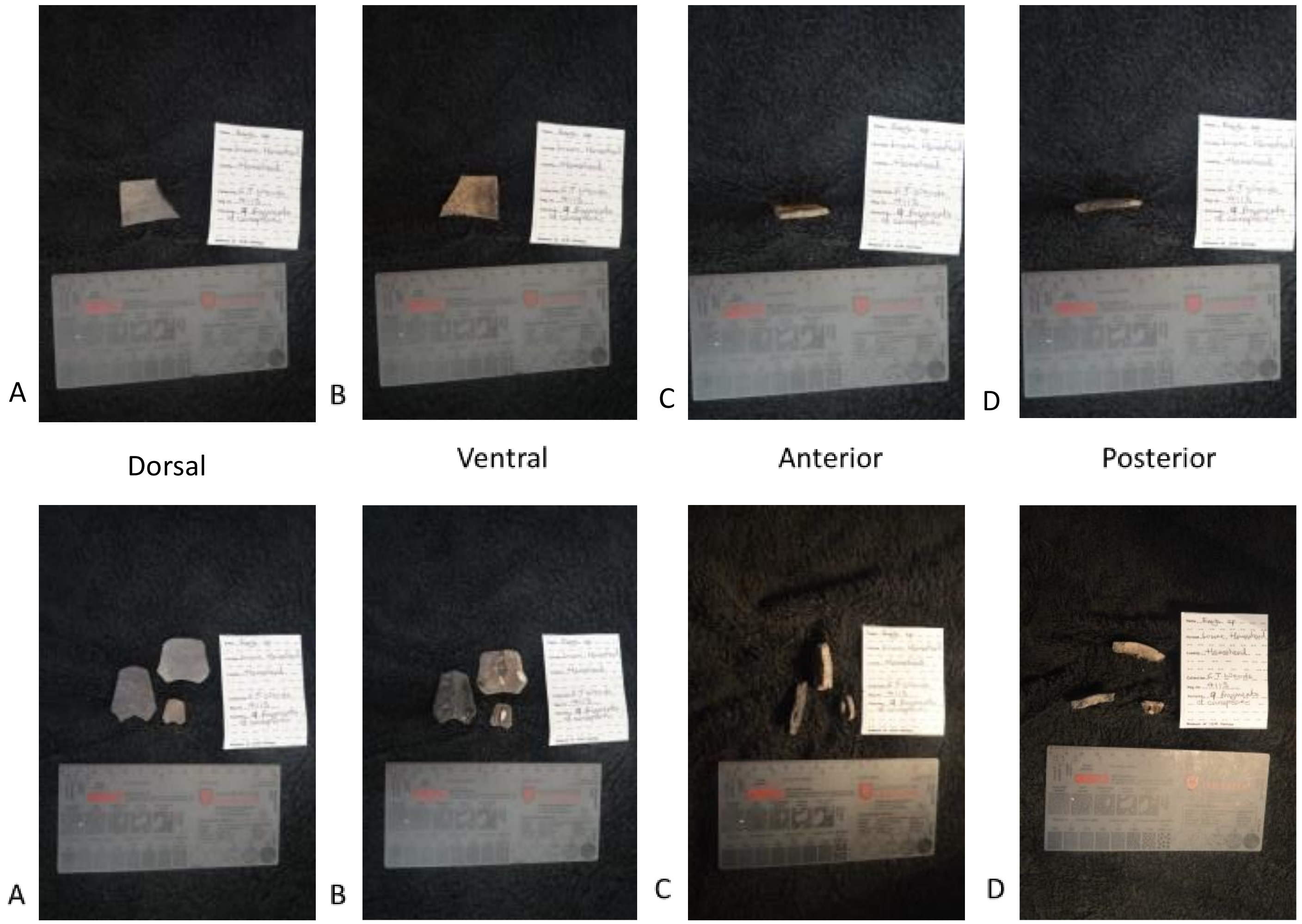
Species: *Emys . Sp*

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 6 - 7 - 8

Pictures: 4



Isle of Wight museum collections

Collection number: G.T.Woods 4113

Species: *Emys . Sp*

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 3

Pictures: 4

A

B

C

D

Dorsal

Ventral

Anterior

Posterior

Isle of Wight museum collections

Collection number: G.T.Woods 4113

Species: *Emys . Sp*

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 4

Pictures: 4

A

B

C

D

Isle of Wight museum collections

Collection number: G.T.Woods 4113

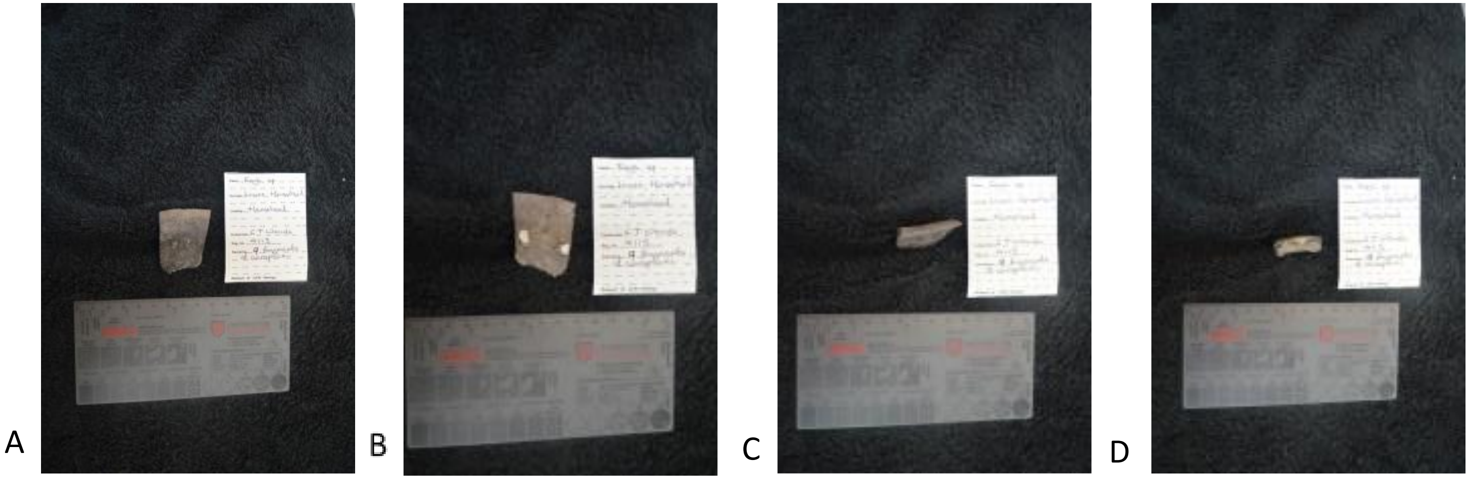
Species: ***Emys . Sp***

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 1

Pictures: 4



Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: G.T.Woods 4113

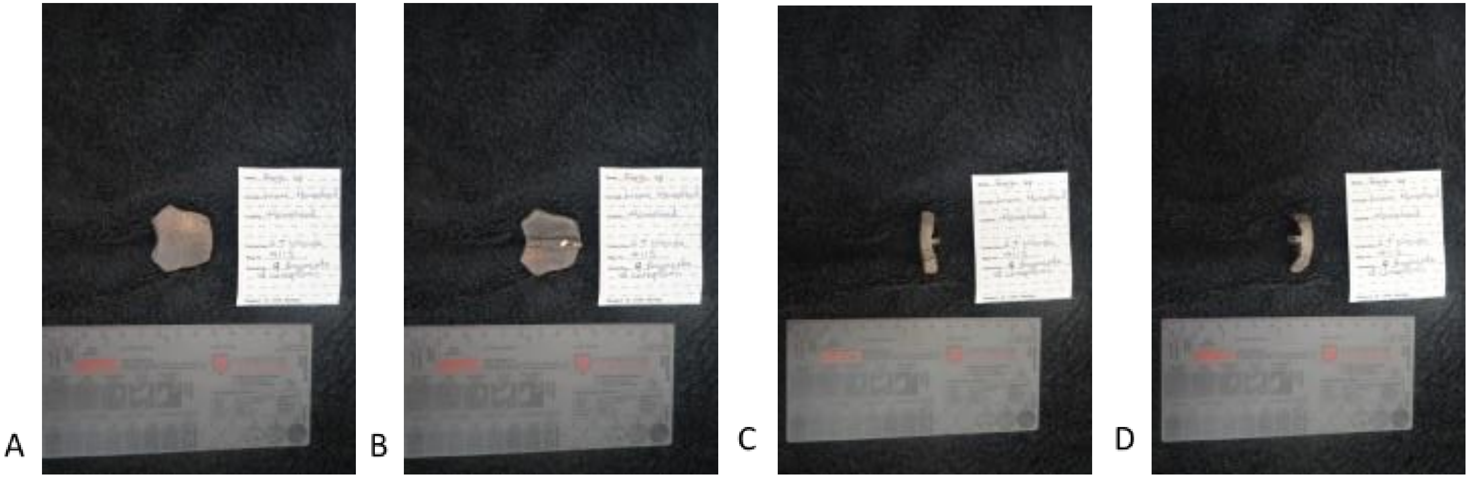
Species: ***Emys . Sp***

Locality: -Hamstead

Remarks: 9 Fragments of carapace

Sample number: 2

Pictures: 4



<u>Isle of Wight museum collections</u>

Collection number: G.T.Woods 4113

Species: *Emys . Sp*

Locality: Hamstead

Remarks: 9 Fragments of carapace

Sample number: 9

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: J.F.Jackson 1629

Isle of Wight museum collections

Collection number: J.F.Jackson 1629

Species: *Emys . Sp*

Locality: Bouldnor Cliff, Hamstead

Remarks : Scute and fragments

Sample number: 1

Pictures: 1

A

B

C

D

Isle of Wight museum collections

Collection number: J.F.Jackson 1629

Species: *Emys . Sp*

Locality: Bouldnor Cliff, Hamstead

Remarks : Scute and fragments

Sample number: 2

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: J.F.Jackson 3849

Isle of Wight museum collections

Collection number: J.F.Jackson 3849

Species: *Emys . Sp*

Locality: Bouldnor Cliff, Hamstead

Remarks: Scute fragment

Sample number: 1

Pictures: 3

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: J.F.Jackson 3854

Isle of Wight museum collections

Collection number: J.F.Jackson 3854

Species: *Emys . Sp*

Locality: Bouldnor Cliff, Hamstead

Remarks : 4 fragments of carapace

Sample number: 1

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: Newport Museum 913

Isle of Wight museum collections

Collection number: Newport Museum 913

Species: *Emys . Sp*

Locality: Lower Hamstead

Remarks: 5 fragments

Sample number: 1

Pictures: 1

A

B

C

D

Isle of Wight museum collections

Collection number: Newport Museum 913

Species: *Emys . Sp*

Locality: Lower Hamstead

Remarks: 5 fragments

Sample number: 2

Pictures: 4

Dorsal

A

Ventral

B

Anterior

C

Posterior

D

COLLECTION NUMBER: W.H.Daniels 4882

Isle of Wight museum collections

Collection number: W.H.Daniels 4882

Species: ***Emys . Sp***

Locality: Hamstead

Remarks: fragments of carapace

Sample number: 1

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: H.F.Poole 4430

Isle of Wight museum collections

Collection number: H.F.Poole 4430

Species: ***Emys . Sp***

Locality: Lower Hamstead

Remarks: 3 specimens

Sample number: 1

Pictures: 4

Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: H.F.Poole 4430

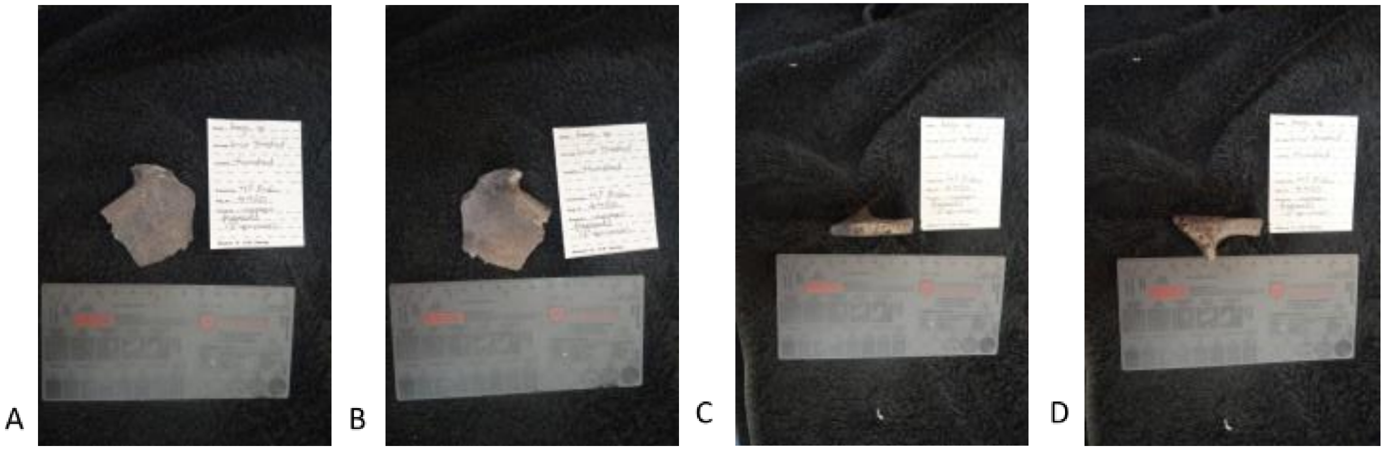
Species: ***Emys . Sp***

Locality: Lower Hamstead

Remarks: 3 specimens

Sample number: 2

Pictures: 4



<u>Isle of Wight museum collections</u>

Collection number: H.F.Poole 4430

Species: *Emys . Sp*

Locality: Lower Hamstead

Remarks: 3 specimens

Sample number: 3

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: *Emys* sp. 4112

Isle of Wight museum collections

Collection number: Emys.sp 4112

Species: *Emys . Sp*

Locality: Lower Hamstead

Remarks : -

Sample number: 1

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: G.T.Woods 4115

Isle of Wight museum collections

Collection number: G.T.Woods 4115

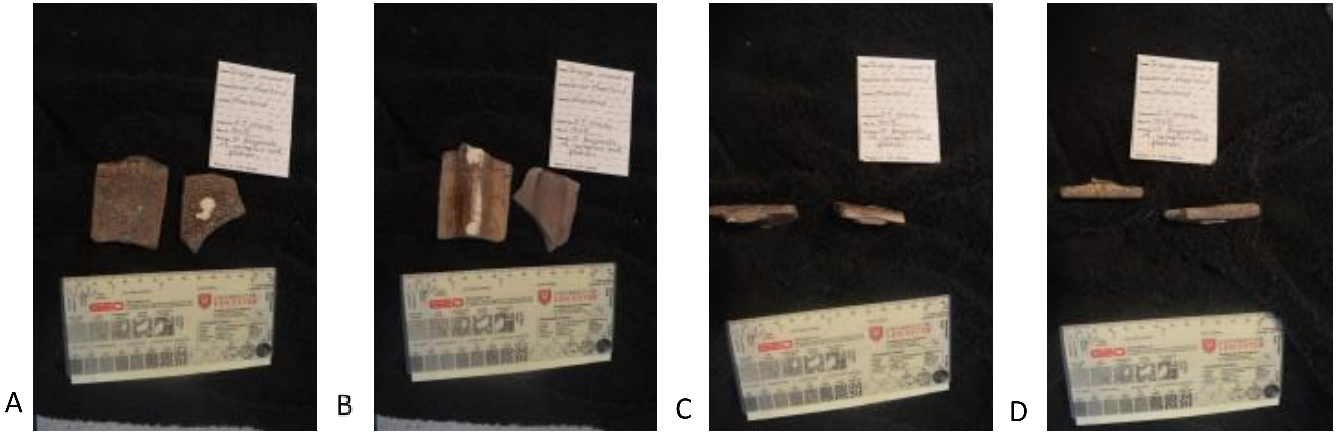
Species: ***Trionyx***

Locality: Lower Hamstead

Remarks : Scute fragments

Sample number: 1 - 2

Pictures: 4



Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: G.T.Woods 4115

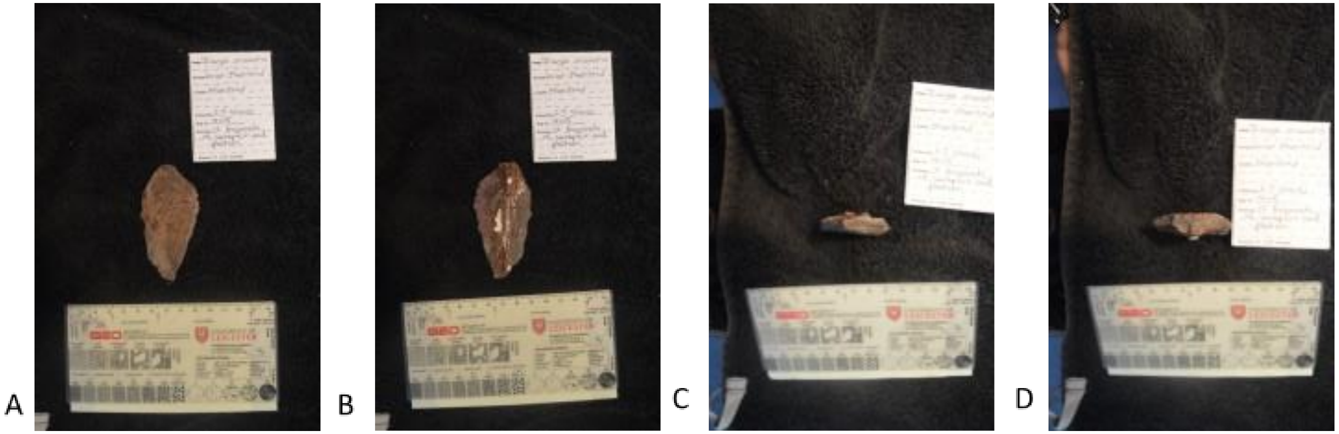
Species: ***Trionyx***

Locality: Lower Hamstead

Remarks : Scute fragments

Sample number: 3

Pictures: 4



Isle of Wight museum collections

Collection number: G.T.Woods 4115

Species: *Trionyx*

Locality: Lower Hamstead

Remarks: Scute fragments

Sample number: 4 - 5 - 6 - 7

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: H.F.Poole 4429

Isle of Wight museum collections

Collection number: H.F.Poole 4429

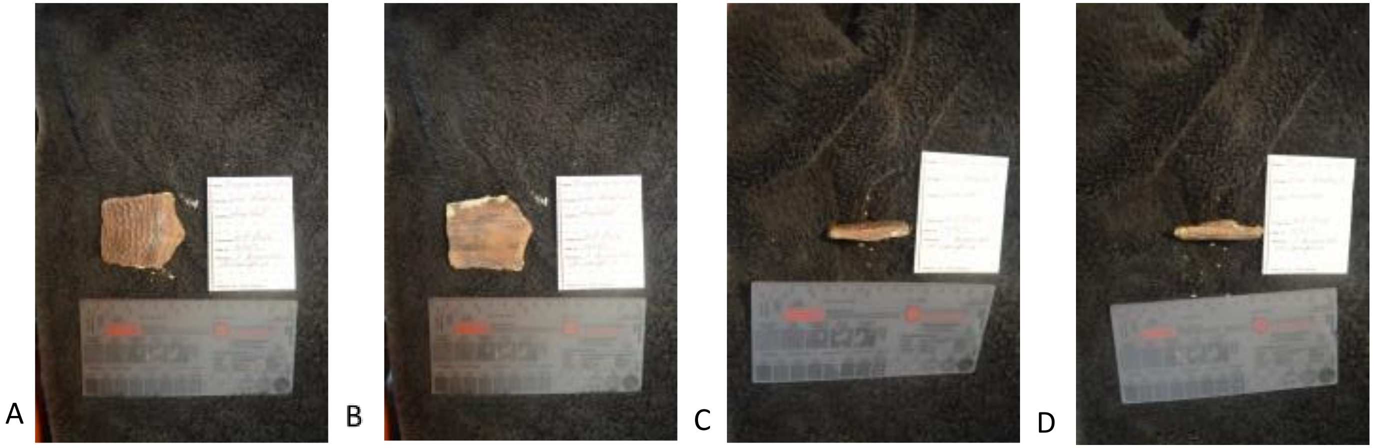
Species: *Trionyx incrassatus*

Locality: Lower Hamstead

Remarks: 3 fragments of carapace

Sample number: 1

Pictures: 4



Dorsal Ventral Anterior Posterior

Isle of Wight museum collections

Collection number: H.F.Poole 4429

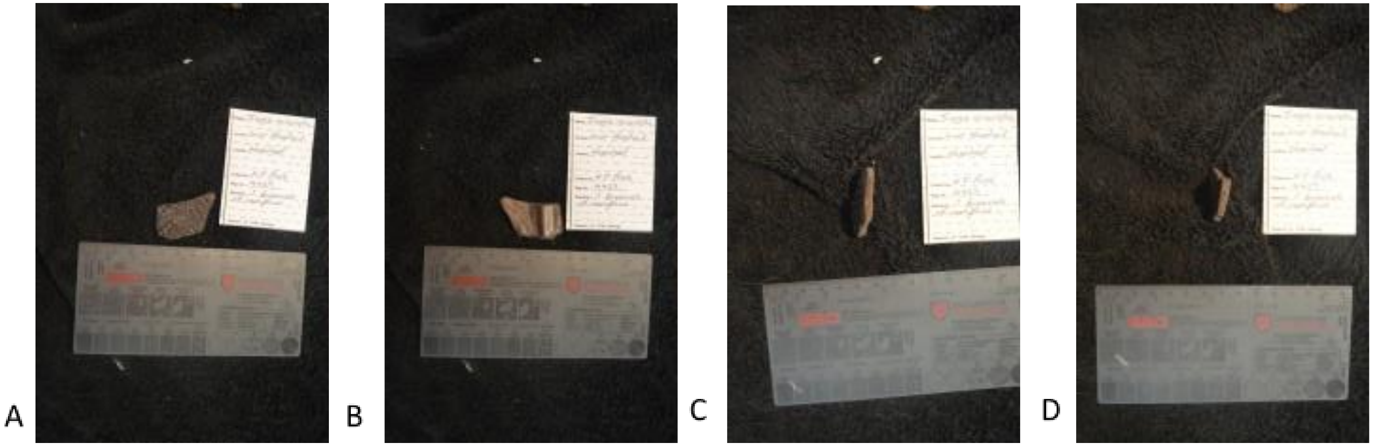
Species: *Trionyx incrassatus*

Locality: Lower Hamstead

Remarks : 3 fragments of carapace

Sample number: 2

Pictures: 4



Isle of Wight museum collections

Collection number: H.F.Poole 4429

Species: ***Trionyx incrassatus***

Locality: Lower Hamstead

Remarks: 3 fragments of carapace

Sample number: 3

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: IWCMS-1998.26

Isle of Wight museum collections

Collection number: IWCMS-1998.26

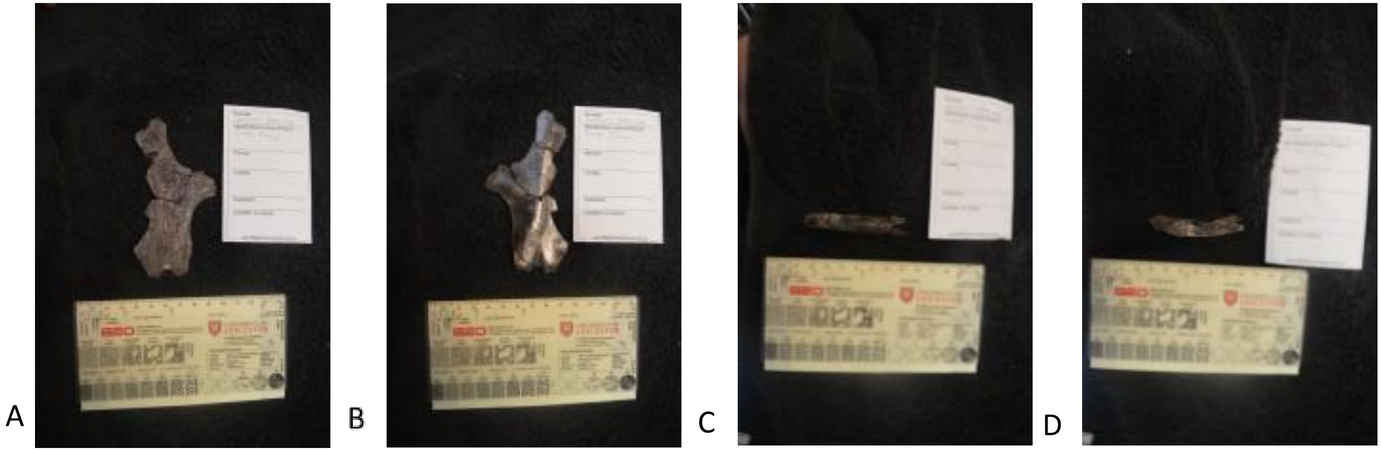
Species: *Trionyx incrassatus*

Locality: -

Remarks: -

Sample number: 1

Pictures: 4



Isle of Wight museum collections

Collection number: IWCMS-1998.26

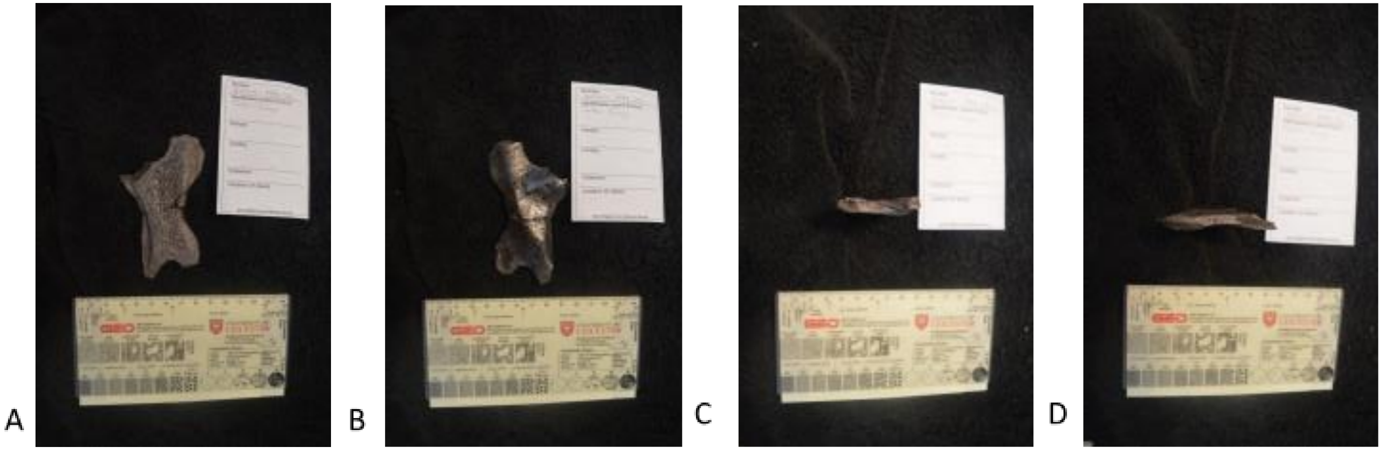
Species: *Trionyx incrassatus*

Locality: -

Remarks: -

Sample number: 2

Pictures: 4



COLLECTION NUMBER: J.F.Jackson 2131

Isle of Wight museum collections

Collection number: J.F.Jackson 2131

Species: ***Trionyx incrassatus***

Locality: "white Band" Bouldnor cliff

Remarks : fragment of scute

Sample number: 1

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: Newport Museum 914

__Isle of Wight museum collections__

Collection number: Newport Museum 914

Species: *Trionyx incrassatus*

Locality: Hamstead

Remarks : Portions of scute and plastron

Sample number: 1

Pictures: 4

A

B

C

D

Dorsal Ventral Anterior Posterior

__Isle of Wight museum collections__

Collection number: Newport Museum 914

Species: *Trionyx incrassatus*

Locality: Hamstead

Remarks : Portions of scute and plastron

Sample number: 2

Pictures: 4

A

B

C

D

<u>Isle of Wight museum collections</u>

Collection number: Newport Museum 914

Species: *Trionyx incrassatus*

Locality: Hamstead

Remarks: Portions of scute and plastron

Sample number: 3

Pictures: 4

A

B

C

D

Dorsal

Ventral

Anterior

Posterior

<u>Isle of Wight museum collections</u>

Collection number: Newport Museum 914

Species: *Trionyx incrassatus*

Locality: Hamstead

Remarks: Portions of scute and plastron

Sample number: 4

Pictures: 4

A

B

C

D

COLLECTION NUMBER: Sample 3

Isle of Wight museum collections

Collection number: Sample 3

Species: ***Trionyx incrassatus***

Locality: -

Remarks: fragment of plastron

Sample number: 1

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

COLLECTION NUMBER: W.H.Daniels 4883

Isle of Wight museum collections

Collection number: W.H.Daniels 4883

Species: ***Trionyx incrassatus***

Locality: Lower Hamstead

Remarks: Portions of scute and plastron

Sample number: 1

Pictures: 4

A


B


C


D


Dorsal

Ventral

Anterior

Posterior

Isle of Wight museum collections

Collection number: W.H.Daniels 4883

Species: ***Trionyx incrassatus***

Locality: Lower Hamstead

Remarks: Portions of scute and plastron

Sample number: 2

Pictures: 4

A


B


C


D


Isle of Wight museum collections

Collection number: W.H.Daniels 4883

Species: *Trionyx incrassatus*

Locality: Lower Hamstead

Remarks: Portions of scute and plastron

Sample number: 3 - 4

Pictures: 4

A

Dorsal

B

Ventral

C

Anterior

D

Posterior

Natural History Museum collections

Collection number: R981 (1887)

Species: *Emys . Sp?*

Locality: Hempstead beds, Hempstead

Remarks: Part of costal plate of *Emys . sp*?

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

<u>Natural History Museum collections</u>

Collection number: R981 (1887)

Species: *Emys. Sp?*

Locality: Hempstead beds, Hempstead

Remarks: Part of costal plate of *Emys. sp?*

Sample number: 1

Pictures: 9

ADDITIONAL IMAGES

COLLECTION NUMBER: 26651

Natural History Museum collections

Collection number: 26651

Species: *Emys . Sp?*

Locality: Unknown

Remarks: carapace fragment of *Emys . sp*?

Sample number: 1

Pictures: 3

A

Dorsal

B

Ventral

C

Posterior

Natural History Museum collections

Collection number: 26651

Species: *Emys . Sp?*

Locality: Unknown

Remarks: Carapace fragment of *Emys . sp*?

Sample number: 1

Pictures: 6

ADDITIONAL IMAGES

COLLECTION NUMBER: 34950

Natural History Museum collections

Collection number: 34950

Species: *Emys . Sp?*

Locality: Sheppey

Remarks: carapace of *Emys . sp*

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

Natural History Museum collections

Collection number: 34950

Species: ***Emys . Sp?***

Locality: Sheppey

Remarks: carapace of ***Emys . sp***

Sample number: 1

Pictures: 4

ADDITIONAL IMAGES

<u>Natural History Museum collections</u>

Collection number: 37210

Species: *Emys . comptini*

Locality: Sheppey

Remarks: carapace of *Emys . comptoni*

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

<u>Natural History Museum collections</u>

Collection number: 37210

Species: *Emys. comptini*

Locality: Sheppey

Remarks: carapace of *Emys. comptoni*

Sample number: 1

Pictures: 3

ADDITIONAL IMAGES

COLLECTION NUMBER: R8136 (1887)

<u>Natural History Museum collections</u>

Collection number: R8136 (1887)

Species: *Trionyx incrassatus*

Locality: Bembridge Marls, Isle of Wight

Remarks : Near complete carapace with vertebrate associated

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

Natural History Museum collections

Collection number: R8136 (1887)

Species: ***Trionyx incrassatus***

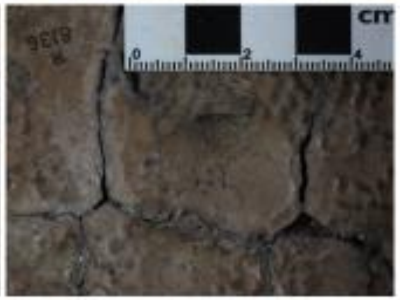
Locality: Bembridge Marls, Isle of Wight

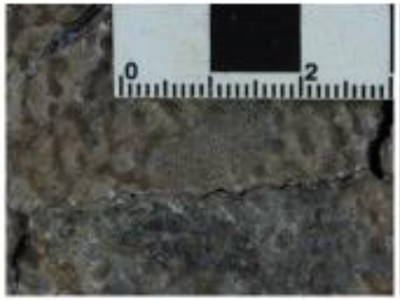
Remarks: Near complete carapace with vertebrate associated

Sample number: 1

Pictures: 9

ADDITIONAL IMAGES





COLLECTION NUMBER: R1433

Natural History Museum collections

Collection number: R1433

Species: ***Trionyx incrassatus***

Locality: Hordwell

Remarks : Type Specimen

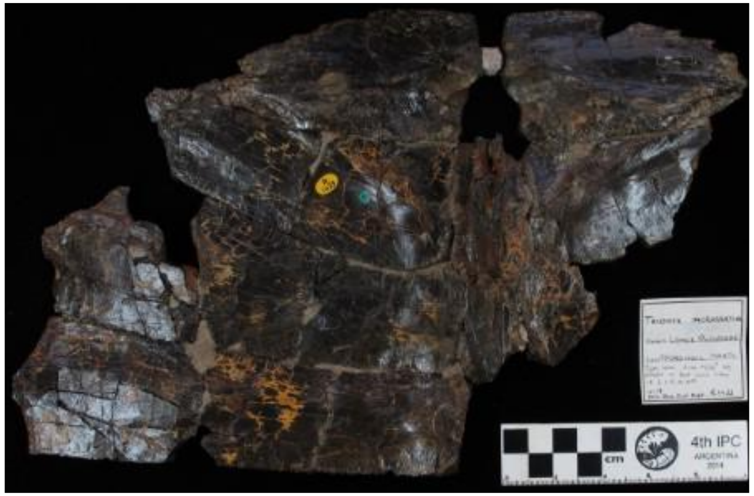
Sample number: 1

Pictures: 2

A

Dorsal

B



Ventral

Natural History Museum collections

Collection number: R1433

Species: ***Trionyx incrassatus***

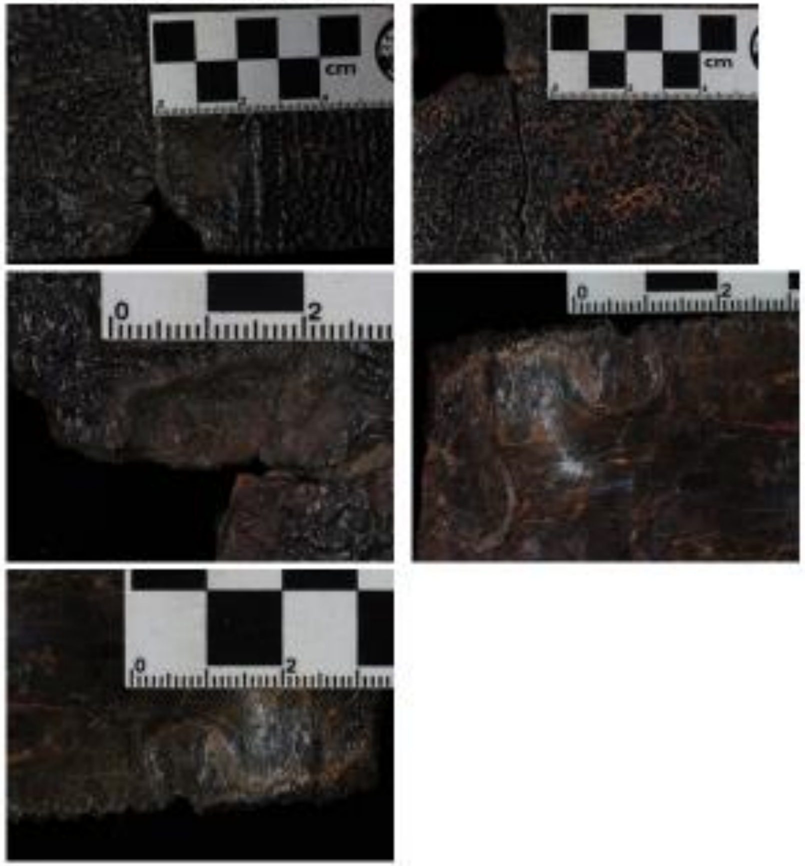
Locality: Hordwell

Remarks: Type Specimen

Sample number: 1

Pictures: 6

ADDITIONAL IMAGES



COLLECTION NUMBER: 30408

Natural History Museum collections

Collection number: 30408

Species: ***Trionyx incrassatus***

Locality: Hordwell

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Dorsal 2

Natural History Museum collections

Collection number: 30408

Species: ***Trionyx incrassatus***

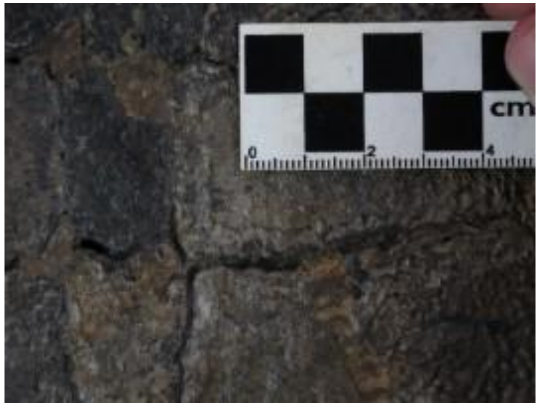
Locality: Hordwell

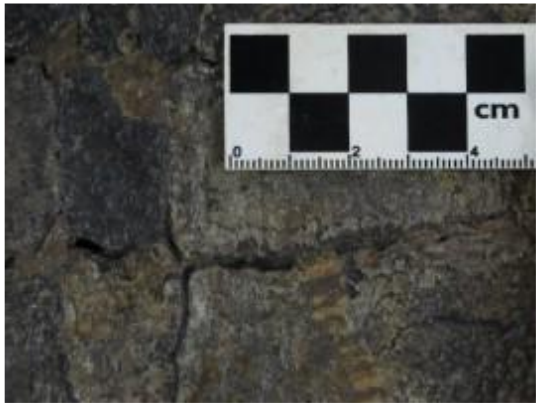
Remarks: complete carapace

Sample number: 1

Pictures: 2

ADDITIONAL IMAGES





COLLECTION NUMBER: 30409

Natural History Museum collections

Collection number: 30409

Species: *Trionyx barbarre*

Locality: Hordwell

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Dorsal 2

COLLECTION NUMBER: RF 539

<u>Natural History Museum collections</u>

Collection number: RF 539

Species: ***Trionyx incrassatus***

Locality: Hordwell

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

Natural History Museum collections

Collection number: R1433

Species: ***Trionyx incrassatus***

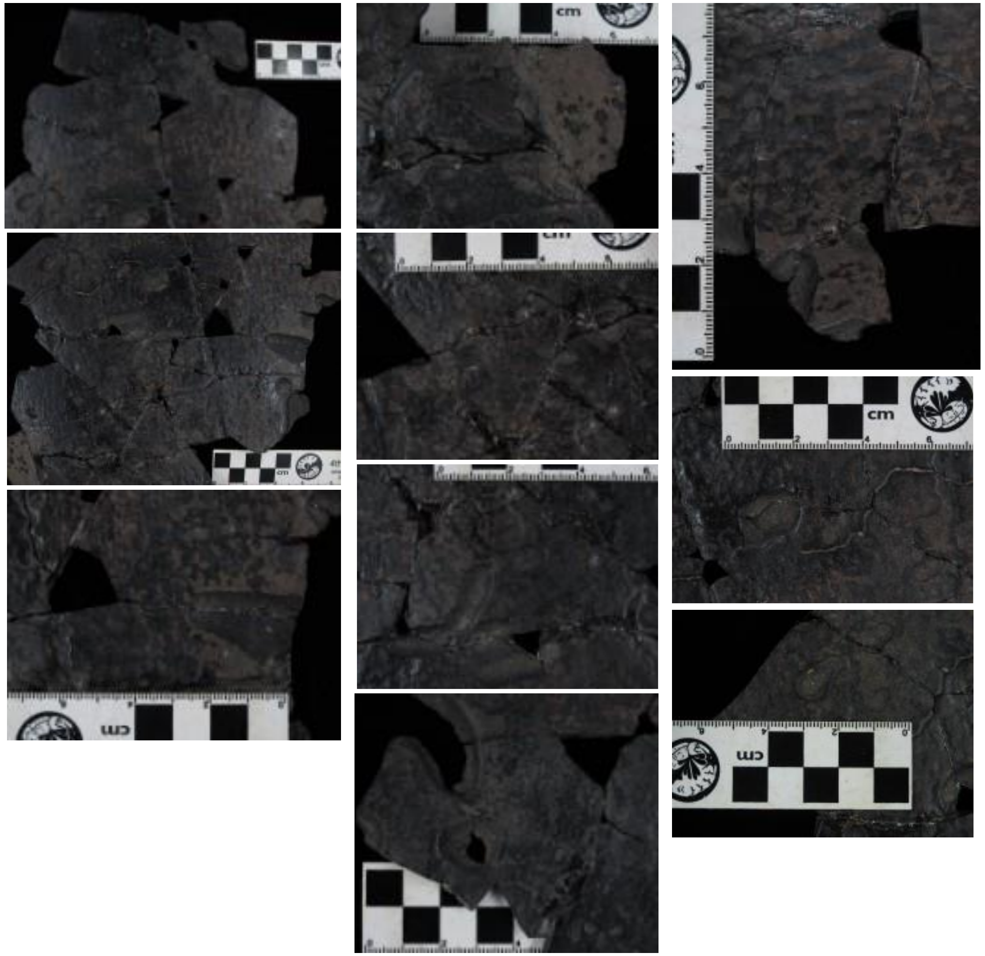
Locality: Hordwell

Remarks: Type Specimen

Sample number: 1

Pictures: 6

ADDITIONAL IMAGES



COLLECTION NUMBER: (1943)

Natural History Museum collections

Collection number: ? (1943)

Species: ***Trionyx. Sp ?***

Locality: Hamstead beds, Isle of Wight

Remarks : partial carapace and skeleton

Sample number: 1

Pictures: 1

A

Dorsal

COLLECTION NUMBER: R.Moody collection

Natural History Museum collections

Collection number: R.Moody collection

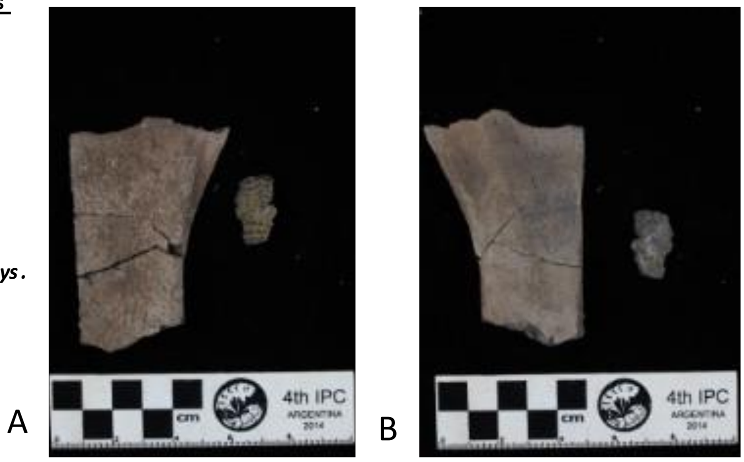
Species: ***Trionyx. Sp ?***

Locality: Bembridge Marls, Isle of Wight

Remarks: Part of costal plate of ***Emys. sp*?**

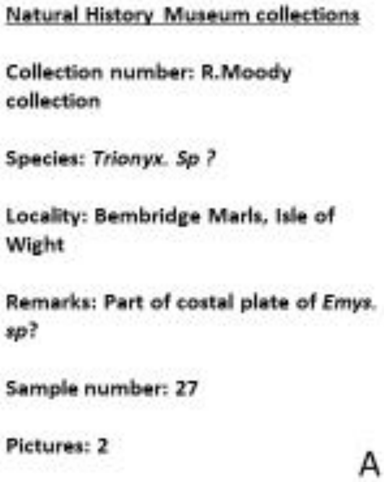
Sample number: 1 - 3

Pictures: 4



Dorsal Ventral

Dorsal Ventral



Natural History Museum collections

Collection number: R.Moody collection

Species: ***Trionyx. Sp ?***

Locality: Bembridge Marls, Isle of Wight

Remarks: Part of costal plate of ***Emys. sp?***

Sample number: 27

Pictures: 2

Dorsal Ventral

Natural History Museum collections

Collection number: R.Moody collection

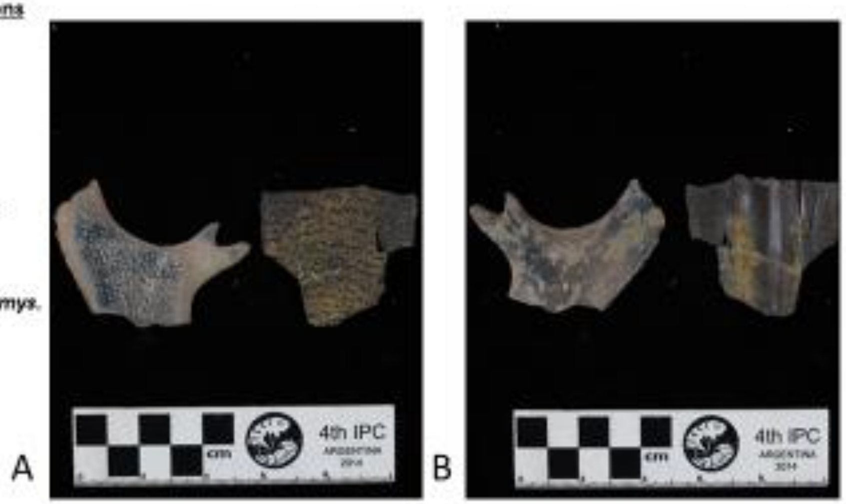
Species: *Trionyx. Sp ?*

Locality: Bembridge Marls, Isle of Wight

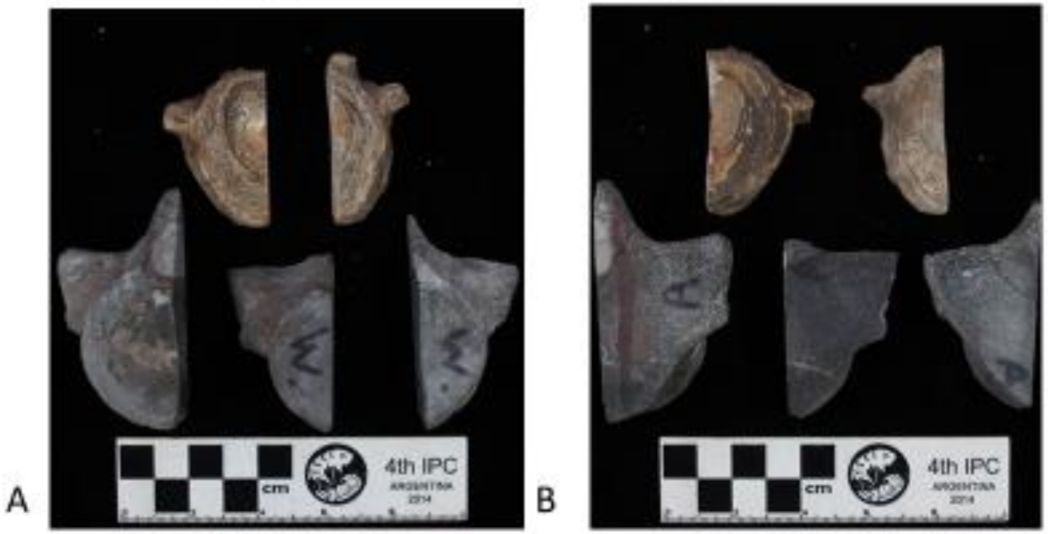
Remarks: Part of costal plate of *Emys. sp?*

Sample number: 4 - 10

Pictures: 4



Dorsal Ventral



Dorsal Ventral

<u>Natural History Museum collections</u>

Collection number: R.Moody collection

Species: *Trionyx. Sp ?*

Locality: Bembridge Marls, Isle of Wight

Remarks: Part of costal plate of *Emys. sp*?

Sample number: 10 - 22

Pictures: 4

A


Dorsal

B


Ventral

A


Dorsal

B


Ventral

Natural History Museum collections

Collection number: R.Moody collection

Species: ***Trionyx. Sp ?***

Locality: Bembridge Marls, Isle of Wight

Remarks: Part of costal plate of ***Emys . sp*****?**

Sample number: 23 - 26

Pictures: 4

A

Dorsal

B

Ventral

A

Dorsal

B

Ventral

COLLECTION NUMBER: ?

Natural History Museum collections

Collection number: ?

Species: ***Trionyx. Sp?***

Locality: Hordle, Isle of Wight

Remarks: Fragmentar y carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

Natural History Museum collections

Collection number: ?

Species: ***Trionyx. Sp?***

Locality: Hordle, Isle of Wight

Remarks: Fragmentar y carapace

Sample number: 1

Pictures:

ADDITIONAL IMAGES

COLLECTION NUMBER: R1592

Natural History Museum collections

Collection number: R1592

Species: *Trionyx. barbarre*

Locality: Hordle, Isle of Wight

Remarks: Near complete carapace

Sample number: 1

Pictures: 1

A

Dorsal

COLLECTION NUMBER: 30306

Natural History Museum collections

Collection number: 30306

Species: ***Trionyx henrici***

Locality: Hordwell, Hampshire

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Dorsal 2

COLLECTION NUMBER: 30413

Natural History Museum collections

Collection number: 30413

Species: ***Trionyx henrici***

Locality: Hordwell, Hampshire

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Dorsal 2

COLLECTION NUMBER: R12788

Natural History Museum collections

Collection number: R12788

Species: *Eurocephalochelys fowleri*

Locality: East Wittering, Oyster bed

Remarks: complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

COLLECTION NUMBER: 39618

Natural History Museum collections

Collection number: 39618

Species: Emyda vittata

Locality: Sinalik Hills, India

Remarks : Near complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

COLLECTION NUMBER: 39833

Natural History Museum collections

Collection number: 39833

Species: ***Emyda vittata***

Locality: Sinalik Hills, India

Remarks: Near complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

COLLECTION NUMBER: 58150

<u>Natural History Museum collections</u>

Collection number: 58150

Species: ***Puppigerus camperi***

Locality: Sheppey

Remarks : Complete carapace

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral

COLLECTION NUMBER: R3964

Natural History Museum collections

Collection number: R3964

Species: *Eochelys classicostata*

Locality: Sheppey

Remarks: Complete carapace and skeletal remains

Sample number: 1

Pictures: 2

A

Dorsal

B

Ventral