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Licenciatura em Biologia celular

Mestrado em Sistemática, Evolução, e Paleobiodiversidade

Microvertebrates of the Lourinhã Formation (Late Jurassic, Portugal)

Dissertação para obtenção do Grau de Mestre em

Paleontologia

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FACULDADE DE CIÊNCIAS E TECNOLOGIA UNIVERSIDADE NOVA DE LISBOA

Dezembro 2018

MICROVERTEBRATES OF THE LOURINHÃ FORMATION (LATE JURASSIC, PORTUGAL)

ACKNOWLEDGMENTS

First of all, I would like to dedicate this thesis to my late grandfather "Papi Joël", who wanted to tie me to a tree when I first start my journey to paleontology six years ago, in Paris. And yet, he never failed to support me at any cost, even if he did not always understand what I was doing and why I was doing it. He is always in my mind. Merci papi !

This master thesis has been one-year long project during which one there were highs and lows. It also comes to conclude three years of working in Portugal and starts new beginnings in paleontology fields. Because I could not achieve this journey alone, I have some people to thank for helping me through this adventure.

I would like to thank my family, who supports me since the very beginning, and especially both my parents, without whose nothing could have been enable, who let their son go to a foreign country without assurance of what he will find. More than anything else, they both have been, beyond all expectations, understanding and supportive since the time this little boy was saying "I want to study dinosaurs!", even if it was sometimes scary and uncharted. My family was present for me, even if it was only to make jokes about the size of my croc teeth, and for that I am grateful.

I would like to thank my supervisor Dr. Miguel Moreno-Azanza, who introduce me to the world of microvertebrates, help me in each stage of this thesis, support and motivate me during the low times, and share all the advises and knowledge I needed to complete this work. I would like to thank also my co-supervisor Prof. Octávio Mateus, who welcomed me in his team three years ago and provide the tools and environment to broaden my background and prepare my future career in paleontology.

I would like to thank the Museu da Lourinhã for letting me work and use its facilities, and more particularly: Carla Alexandra Tomás in her help to store and prepare the new sediment samples, Alexandre Audigane, Bruno Pereira, and Carla Abreu in their help to organize and facilitate my work at the museum. I would like to thank the Departamento de Ciências da Terra of the Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa for allowing to use its equipment and facilities, and more particularly: Maria Eduarda Ferreira in her help to process the bulk samples collected on the field, and Prof. Paulo Legoinha for giving me the opportunity

to follow this master program and this master thesis. I would like to thank Prof. José Mirão and Luis Dias to enable the access to the scanning electron microscope in HERCULES facilities.

I would like to express all my love and gratitude to Céline Viquesnel, who jumped on the bandwagon few months ago and decided to stay longer for bearing me, giving me the strength and motivation to complete this thesis; and to Alexandra Fernandes, who always believed in me and was inspiring and understanding when I needed courage and could not find the light in the darkest times, and for her amazing help in picking. For them, I will be always grateful.

I would like to thank Eduardo Puértolas-Pascual, in his help of the description and analysis of the croc teeth, giving me thus the training to describe the other material studied during this thesis; Filippo Rotatori, my partner for so many things, for his friendship and all the motivation we mutually give to each other; André Saleiro, for having screen washed alone all the bulk sample from Valmitão used for this thesis, but also for his unique friendship and all the fun we have together; and to Francisco Costa, for his friendship and understanding as roommate during this year. I would like to thank my other classmate of the master, namely Darío Estraviz López, Tiago Pereira, and João Velez, for the special friendship we will always share. I would like to thank the students of the year 6 of the Master of Paleontology of FCT: André Bonito, Vincent Cheng, Miguel Marx, Helena Oliveira, Roberto Silva, Cátia Ribeiro, and Victor Takev, for their help in picking Valmitão sediments and their respective friendships. I would like to thank Carl Melhing, from the American Museum of Natural History, for the amazing revision on the English he has done in an impossible deadline and all his support.

I would like to thank all my friends of the Lourinhã Paleo team that have not been named yet: Hugo Campos, João Marinheiro, Marco Marzola, Simão Mateus, João Muchagata, João Pratas, João Russo, and Sara Sneltorp. I would like to thank my friends back to France, particularly Adrien Aimard, Aurore Fino, Laurent Henry, Maxime LeCesne, Charlène Selva, Benoît Thevenot, and Thibaut Totis, for whom going back is always a pleasure. I would like to thank the “Héros de Papier Froissé” internet community, and particularly “Norya”, “Crystallina”, “Bibi”, and “princesse”, to have been this safety valve that allowed to clear my mind when I needed it. My final thank is for Steven Spielberg, who first gave me the dream to become a paleontologist and keeps making me dream 23 years later.

Thank you all!

ABSTRACT

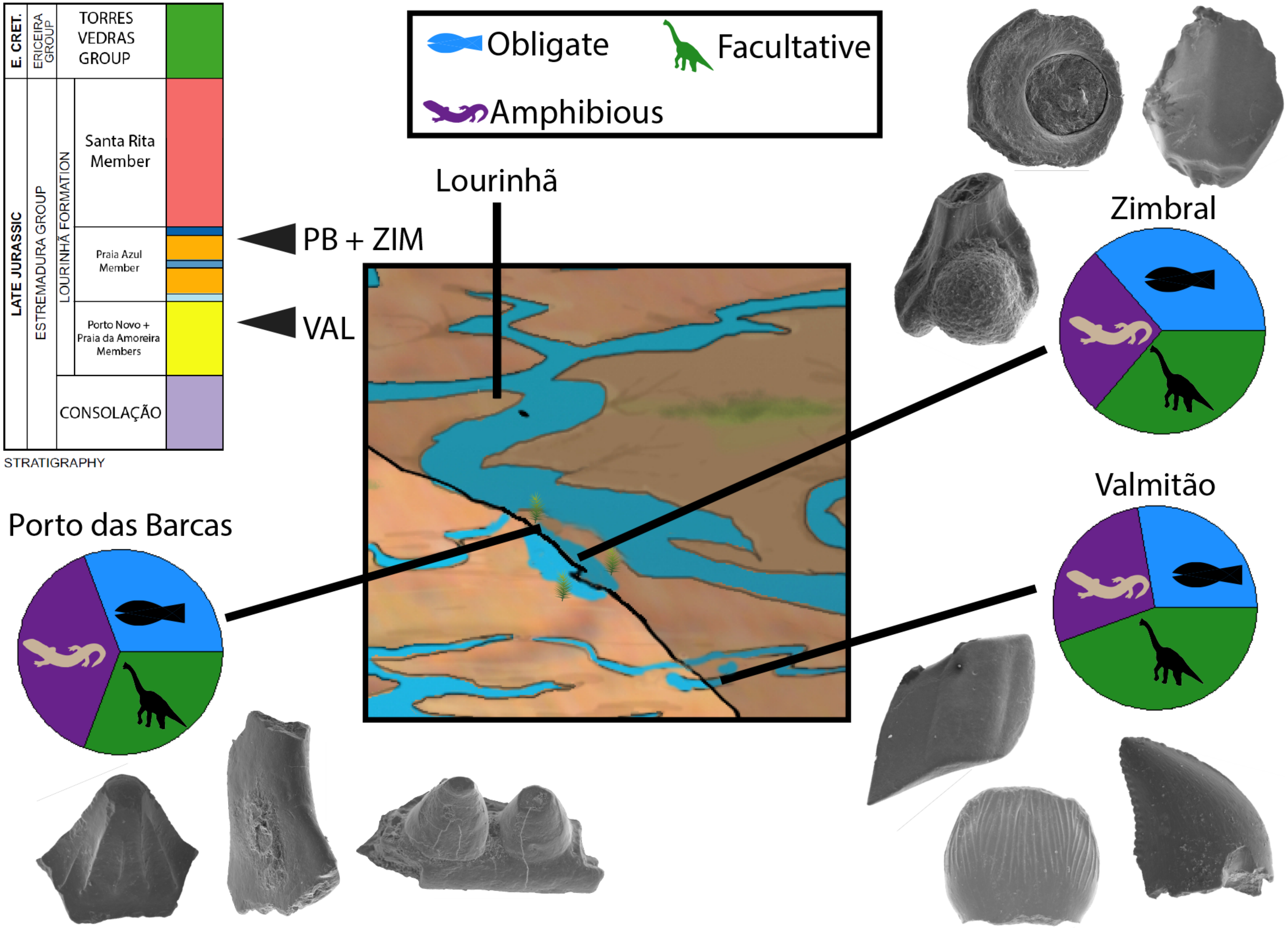
The Upper Jurassic of Portugal has been globally known for its microfossil vertebrate fauna thanks to the Konzentrat-Lagerstätte of the Guimarota mine, which provided thousands of bone fragments, isolated teeth, and even complete specimens. Other vertebrate microfossil assemblages have been studied around the world. Besides Guimarota, no other Portuguese Jurassic assemblage has been extensively studied. Hereby is presented a revision of the state of the art on Portuguese microvertebrate record, and the first microvertebrate studies on three localities from the Lourinhã Formation (Late Jurassic) hosted by a Portuguese institution; Porto das Barcas, Zimbral, and Valmitão has provided 2,497 microvertebrates skeletal remains and teeth, from which 824 specimens have been identified, described and assessed to the conservative-most taxa. The stratigraphy and sedimentology of the localities suggest that Porto das Barcas and Zimbral were floodplain mud deposits, and Valmitão was an oxbow lake mud deposit, with a slow rate of sedimentation. The remains have been attributed to fishes, amphibians, squamates, crocodylomorphs, and dinosaurs; but unfortunately, no mammaliaform material has been collected. Paleoecological analyses suggest Zimbral and Valmitão were dominated by a terrestrial fauna and more diverse than Porto das Barcas, dominated by an amphibious fauna. The Lourinhã Formation appears to have been closer to the shoreline than American localities in the Morrison and Cloverly Formations were, but more continental than Buenache and Las Hoyas localities (Spain) with swamp to lacustrine paleoenvironments. A detailed study on 125 crocodylomorph teeth from Valmitão support the presence of Goniopholididae, at least two Atoposauridae taxa, and Bernissartiidae in the Late Jurassic of Portugal, with a fauna either dominated by relative small individuals, either juveniles or adults or small taxa.

Keywords: Crocodylomorpha, Albanerpetontidae, Dinosauria, Lusitanian Basin, Kimmeridgian-Tithonian, Paleoecology

RESUMO

O Jurássico Superior de Portugal tem sido mundialmente conhecido pela sua fauna de vertebrados microfósseis graças à Konzentrat-Lagerstätte da mina de Guimarota, que forneceu milhares de fragmentos ósseos, dentes isolados e até espécimes completos. Outros cortejos de microfósseis de vertebrados foram estudadas noutras partes do globo. Além da Guimarota, nenhuma localidade de microvertebrados jurássicos tem sido extensivamente estudada. É apresentada uma revisão do registo dos microvertebrados portugueses, e os primeiros estudos de microvertebrados de três localidades da Formação da Lourinhã (Jurássico Superior). Porto das Barcas, Zimbral e Valmitão forneceram 2.797 restos esqueléticos e dentes de microvertebrados, dos quais 824 espécimes foram identificados os táxons de forma conservadora. A estratigrafia e sedimentologia das localidades sugerem que Porto das Barcas e Zimbral eram depósitos de planície de inundação, e Valmitão era um depósito de planície de inundação, com baixa taxa de sedimentação. Os restos mortais foram atribuídos a peixes, anfíbios, escamas, crocodilomorfos e dinossauros; mas, infelizmente, nenhum mamífero foi identificado. Análises paleoecológicas sugerem que Zimbral e Valmitão eram dominados por uma fauna terrestre e mais diversa do que Porto das Barcas, dominada por uma fauna anfíbia. A Formação da Lourinhã parece ter estado mais perto da costa do que as localidades americanas nas Formações Morrison e Cloverly, mas mais continentais do que as localidades Buenache e Las Hoyas (Espahna), com paleoambientes pantanosos a lacustres. Um estudo detalhado em 125 dentes de crocodilomorfos de Valmitão suportam a presença de Goniopholidae, pelo menos dois táxones de Atoposauridae, e Bernissartiidae no Jurássico Superior de Portugal, com uma fauna dominada por animais de pequeno porte, possivelmente juvenis a jovens adultos ou formas pequenas.

Termos chave: Crocodylomorpha, Albanerpetontidae, Dinosauria, Bacia Lusitania, Kimmeridgiano-Tithoniano, Paleoecologia


E. CRET.
ERICEIRA GROUP
TORRES VEDRAS GROUP
LATE JURASSIC
ESTREMADURA GROUP
LOURINHÃ FORMATION
Santa Rita Member
Praia Azul Member
Porto Novo + Praia da Amoreira Members
CONSOLAÇÃO
STRATIGRAPHY
PB + ZIM
VAL
Obligate
Facultative
Amphibious
Lourinhã
Zimbral
Valmitão
Porto das Barcas

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ABBREVIATIONS

INSTITUTIONS:

ML: Museu da Lourinhã

DCT: Departamento de Ciências da Terra, FCT-UNL

FCT-UNL: Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa

LOCALITIES:

PB: Porto das Barcas

ZIM: Zimbral

VAL: Valmitão

1. INTRODUCTION

1.1 Importance and significance of vertebrate microfossil record

Vertebrate microfossil –or microvertebrate– assemblages (VMA) are multi-individual accumulations of disarticulated and dissociated vertebrate hard parts dominated by elements in the millimeter to the centimeter size range, where the maximum size of at least 75% of the element does not exceed 5 cm (Eberth *et al*., 2007a; Rogers & Brady, 2010). They play (Figure 1) a significant role in community-level reconstruction of paleofaunas, being important indicators of temperature, salinity (in case of aquatic environments) and other environmental factors (Brinkman *et al*., 2005a; Carrano & Velez-Juarbe, 2006; Baszio, 2008; Rogers & Brady, 2010; Oreska *et al*., 2013). They also document relative taxonomic abundance in ancient vertebrate communities (Brinkman *et al*., 2005a; Baszio, 2008; Oreska *et al*., 2013; Carrano *et al*., 2016; Rogers *et al*., 2017), and provide data on the taphonomy of the locality, reconstruction of paleoenvironments, paleobiogeography, paleobiology, and evolution of taxa represented (Brinkman *et al*., 2005a; Baszio, 2008).

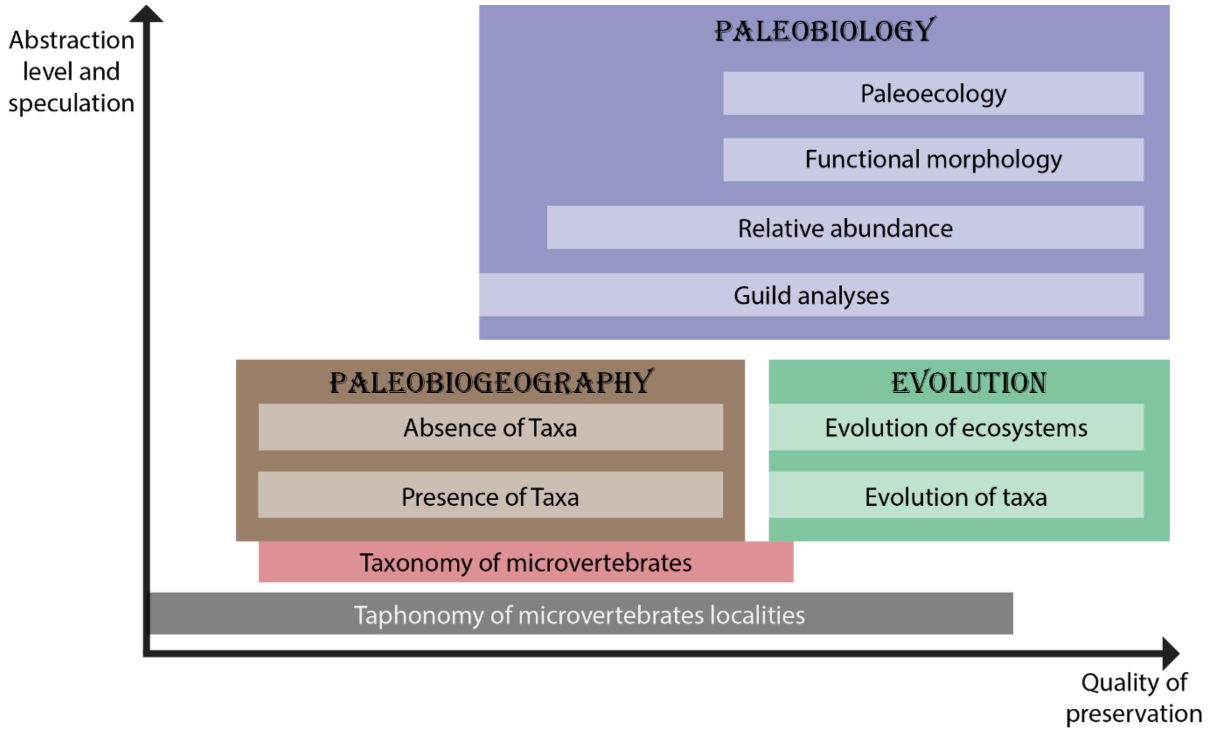

Figure 1: Questions that can be addressed by analyzing vertebrate microfossil assemblages (modified from Bazio, 2008).

These assemblages usually occur in one stratigraphically limited sedimentary unit, characterized by a greater abundance and diversity of preserved vertebrates than the surrounding strata (Rogers & Brady, 2010), thus providing more suitable samples for statistical analysis than macrofossil quarries or surface collecting (Oreska *et al*., 2013; Carrano *et al*., 2016). Indeed, vertebrate microfossil assemblages preserved taxa that are not usally found with decades of prospecting, even by dedicating unlimited time and efforts into surface collecting (Oreska *et al*., 2013). This is because these assemblages provide more complete records of the paleocommunities of the locality, and that the large amount of specimens recovered tends towards the limit of the aggregation rarefaction curve, or only an even larger amount of specimens would highlight new taxa in the diversity (Oreska *et al*., 2013).

Vertebrate microfossils can be preserved in diverse types of depositional environments. In pond/lake bonebeds, the disarticulated and dissociated hard parts of a variety of aquatic, semiaquatic and fully terrestrial animal can be found (Rogers & Brady, 2010). Localities having experienced more intense or longer-acting weathering processes are expected to include fewer identifiable skeletal elements on average (Rogers *et al*., 2017), most of the remains exhibiting evidence of breakage and surface degradation, probably caused prior to fossilization (Rogers & Brady, 2010). Therefore, this type of depositional environment is a mechanically stressful environment for microvertebrate remains before and during burial and can be associated with in situ accumulation via attritional mortality in aquatic ecosystems with low rate of sedimentation (Rogers & Brady, 2010).

All the remains come from the same origin as the sediments, making these assemblages parauchthonous *sensu* Kidwell *et al.*, 1986 (Rogers & Brady, 2010). However, the taphonomic quality and comparability of studied samples will affect the quality of the ecological inferences, paleoecological analyses being more robust if localities shared similar taphonomic histories and have been sampled and studied in an analogous way (Rogers *et al*., 2017). Additionally, facies context cannot be used as a predictor of the faunal composition in a vertebrate microfossil assemblage (Rogers *et al*., 2017). As statistical analyses are used to study these assemblages, the surface collected and screenwashed samples need to be large enough and the methods to be adapted for the respective taphonomic setting of the locality (Brinkman *et al*., 2005a; Baszio, 2008; Rogers *et al*., 2017). However, it has to be kept in mind than even if a preleminary test is negative, it is not a reason to avoid investigating for meaningful comparisons (Rogers *et al*., 2017). On other hand, channel-hosted bonebeds exhibit the same type of vertebrate microfossil assemblages, but they are usually more concentrated and better sorted than pond/lake assemblages (Rogers & Brady, 2010). These depositional environments are reworked from the living habitat and the resulting preserved facies are from a different locality than the site of accumulation, making them allochthonous (Kidwell *et al.*, 1986). In both cases, these microvertebrate assemblages are mostly found in direct association with concentrated invertebrates remains, plants debris (Rogers & Brady, 2010), and vertebrate macrofossils occurring in the same bed (Brinkman *et al.*, 2005a). This can aid in the study and comprehension of the paleoenvironment of the locality. Indeed, during diagenesis, bones and teeth can be exposed to fluids able to dissolve shell debris and even impact the smallest vertebrate bioclasts (Rogers *et* al., 2017). Furthermore, allochthonous and autochthonous assemblages preserve similar overall proportion of taxa and size distribution of animals, suggesting than channel-hosted bonebeds could be a subsample of pond/lake bonebeds (Rogers & Brady, 2010). Vertebrate microfossil assemblages formed under similar taphonomic conditions, and temporal and geographic regimes (Brinkman, 1990; Brinkman *et al.*, 2005a; Carrano *et al.*, 2016; Rogers *et al.*, 2017), and lacustrine assemblages capture a time-averaged picture of their surrounding paleoenvironment, the size of the composite paleocommunity depending on the size of the watershed supplying the deposit through time (Carrano *et al.*, 2016).

Because of the size range considered for microfossil vertebrates, their study involves small animals like fishes, amphibians, small reptiles and mammals, but they also included small remains, notably teeth, from bigger animals, like dinosaurs. There is a strong bias in vertebrate microfossils assemblages toward larger animals, mostly because small vertebrates received less attention from paleontologists and most findings are based on single bones or teeth, which are harder to identify to species level. This, in turn, leads to an underestimation of their diversity, making them appear relatively infrequent (Carrano & Velez-Juarbe, 2006). Added to this is the difficulty in estimating the relative fossil abundance from a microvertebrates assemblages using only surface collections (Rogers *et al.*, 2017). With that perspective, variation in taxa between different localities with different sedimentological and taphonomic histories, but also within the confines of individual localities, can reflect the restricted areas of origin of the source community and the partitioning inside these paleocommunities (Brinkman *et al.*, 2005a; Oreska *et al.*, 2013; Carrano *et al.*, 2016; Rogers *et al.*, 2017).

Because of the high tooth diversity and high potential for diagnoses allowing to describe them, mammalians tend to be more studied than other groups (Carrano & Velez-Juarbe, 2006). Microfossil assemblables have been sampled since the mid-1960s, but at that time the focus was only on mammals, especially the Late Cretaceous ones, in order to study their evolution, taxonomy, biostratigraphy and biogeography (Brinkman *et al.*, 2005a; Baszio, 2008). Later, nonmammalian (Estes, 1964; Baszio, 2008) microvertebrates were used to interpret paleoecology of their assemblages (Dodson, 1983, 1987), and it was quickly noticed that a taphonomic setting allowing preservation of dinosaurs was not necessarily the most suitable for microvertebrates (Baszio, 2008).

1.2 Studies on microvertebrates from the Jurassic

The Jurassic is a key time in the evolution and radiation of terrestrial vertebrates where most current clades started to diversify (Metcalf *et al.*, 1992). Occurrences of albanerpetontids in the Middle Jurassic of England and the basal Cretaceous of Africa can be explained by immigration from Europe (Gardner *et al.*, 2003). Squamates have an extensive record from the Middle and Late Jurassic of Laurasia (Evans, 1998b) but not from Gondwana (Evans *et al.*, 2002). There is a temporal and geographical gap in fossil record, but indirect evidences suggest that squamates had diversified during the Jurassic into all major modern lineages (Metcalf *et al.*, 1992; Evans, 2003). Finally, mammals usually constitute one of the most diverse taxa in Jurassic VMAs (Carrano & Velez-Juarbe, 2006; Sweetman, 2007; Vasile & Csiki, 2010), which can be related to their major adaptive radiation during the Middle to Late Jurassic (Close *et al.*, 2015).

1.2.1. CHONDRICHTHYES

The cartilaginous fishes appeared back to the Late Ordovician and have kept a similar body plan for of the species known (Benton, 2014). Hybodonts marine to fresh waters sharks are known since the Devonian, but they diversified during the Triassic to become the dominant fish predator in the Jurassic of Europe and North America (Benton, 2014), before becoming extinct during the Late Cretaceous (Case & Cappetta, 1997). They have a fully heterocercal tail and exhibit a large diversity of tooth shapes, from pointed high-crowned to low-crowned, implying a large variety of feeding behaviors (Benton, 2014). Modern forms chimeras appeared during the Jurassic, but they are known since the carboniferous and Permian (Benton, 2014).

Neoselachians may first occur in the late Paleozoic (Kriwet, 2004; Benton, 2014), they radiated through the Late Jurassic and Early Cretaceous to reach the diversity observed today (Compagno *et al.*, 2005). They are characterized by: (1) calcified vertebra centrum enclosing the notochord; (2) a great mobility between palaquadrate and hyomandibular; (3) a snout longer than the lower jaw, allowing the jaw to open beneath the head instead of at the front; (4) serrated teeth; and (5) the fusion or a firm connection in the midline of the hind girdles (Benton, 2014). Batoid appeared in the early Jurassic (Kriwet, 2004) and are characterized by: (1) flattened body with broad, flip-like pectoral fins; (2) mouth and gills are located under the head; and (3) eyes shifted to the top of the head (Benton, 2014)

1.2.2. ACTINOPTERYGII

The ray-finned bony fishes appeared during the Silurian, and have since radiated through at least three major outbreaks: (1) the "basal" actinopterygian radiation, between the Devonian and the Triassic; (2) the basal neopterygian during the Triassic and the Jurassic; and (3) the teleosts from the Jurassic to nowadays (Benton, 2014). They have been the most successful vertebrate clade, representing nowadays almost half of the entire Vertebrata phylum. Because of their striking diversity, only few groups will be here discussed. Pycnodontiformes are known from the Late Triassic to the Eocene all over the word, except Australia and Antartica, and can be characterized by: (1) an high body shape; (2) a preopercular hypertrophied; (3) a reduced opercular process of the hyomandibular; (3) the absence of the suboperculum and the interoperculum; (4) a reduced opercular; (5) crushing vomering teeth, primitively circular in outline; (6) a small dentary, primitively posteriorly bifid; (7) crushing prearticular teeth, primitively circular in outline; (9) the presence of prearticular teeth forming rows; and (10) dorsal and ventral contours scales differentiated (Poyato-Ariza & Wenz, 2002). The pavement formed by their teeth suggested they were used to crush mollusk and echinoderms (Benton, 2014).

Semionotiformes are freshwater fishes known from the late Permian to the Late Cretaceous from all over the world and are characterized by: (1) the absence of a premaxilla; (2) no contact between the maxilla and the opercular bones; (3) one extra suborbital; (4) presence of an interopercular; and (5) ganoid scales (Carroll, 1988; Grande & Bemis, 1998). Different species seems to have lived together, as it is suggested by their great diversity in some localities, like the Newark Gourp in North America (Benton, 2004). Another holostean group are the Amiiforms thar are known since the Early Jurassic of England, with the caturid *Caturus heterurus* Agassiz, 1833 to nowadays and are characterized by: (1) two or less ossified ural neural arches; and (2) loss of the opisthotic and pterotic bones (Grande & Bemis, 1998). Caturidae are a family that expends until the Late Cretaceous of US and are characterized by the presence of paired, block-like, ural neural arch ossifications.

Pachycormidae are a teleost group of suspension feeders known from the Middle Jurassic of England to the Upper Jurassic of England, Japan, and US (Friedman *et al.*, 2010), to which belongs the giant *Leedsichthys problematicus* Woodward, 1889, the largest bony fish of all time from the Middle and Late Jurassic of Europe (Liston & Noè, 2004; Liston, 2010). They are characterized by: (1) and elongated bony rostrum; (2) presence of small, lateral, mobile premaxilla; (3) presence of one supramaxilla; (4) no contact between the symplectic and articular bones; (5) vomers paired; (6) elongated, serrated, scythe-like pectoral fins; (7) pelvic fins reduces or absent; and (8) a separated first hypural, with the second one fused to several others and forming a broad, triangular plate (Carroll, 1988). Because of their large size and their feeding behaviour, it has been proposed they were the ecological analogous of modern whales (Friedman *et al.*, 2010; Benton, 2014)

1.2.3. AMPHIBIANS

Albanerpetontids are an extinct group of terrestrial salamander-like animals (Figure 2). They occur from the Middle Jurassic of England and France (Gardner *et al.*, 2003; Gardner & Böhme, 2008) until the Late Pliocene of Italy (Delfino & Sala, 2007) and Hungary (Szentesi *et al.*, 2015). This highly distinctive and derived group is characterized by: (1) fused frontals with polygonal ornementation; (2) a two-part craniovertebral joint; (3) a interdigitating intermandibular joint; (4) distinctive non-pedicellate teeth with chisel-shaped, tricuspid crowns; (5) and two modified cervical vertebrae lacking a neural arch, forming a tripartite facet similar to the atlas-axis complex in mammals (Gardner, 2001: Rees *et al.*, 2002; Evans *et al.*, 2004; Gardner & Böhme, 2008; Carroll, 2009; Schoch, 2014).

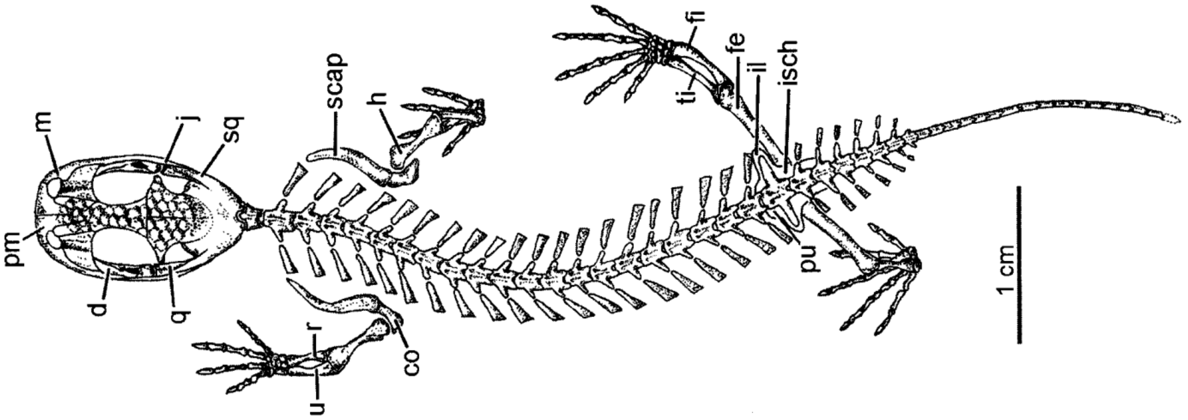

Figure 2: Skeleton of *Celtedens megacephalus* (from Carroll, 2009). **co**, coracoid; **d**, dentary; **fe**, femora; **fi**, fibula; **h**, humerus; **il**, ilium; **isch**, ischium; **j**, jugal; **m**, maxillary; **pm**, premaxilla; **pu**, pubis; **q**, quadrate; **r**, radius; **scap**, scapula; **sq**, squamosal; **ti**, tibia; **u**, ulna.

Based on their cranial, vertebral and tooth structure, they have been interpretated as fossorial animals, living in humid soil and freshwater ponds, and having a shearing bite fo feeding on arthropods (Wiechmann, 2000; Gardner, 2001; Schoch, 2014). Phylogenetic analysis consider them as a sister-group of Lissamphibia, clade of crown "modern" amphibians composed by Gymnophiona, Salienta (modern and fossil frogs) and Caudata (McGowan & Evans, 1995; Gardner, 2001; McGowan, 2002; Ruta *et al.*, 2003a,b; Anderson, 2007), but the relation between them is unclear (Gardner & Böhme, 2008). Their temporal and geographic range make them one of the most successful clades of microvertebrates (Gardner & Böhme, 2008): they are known from Laurasian localities (Figure 3) in North America, Central Asia and Europe (Rees *et al.*, 2002; Gardner & Böhme, 2008), plus one Gondwana locality in Early Cretaceous of Morocco, which could be explained by immigration from Europe (Gardner *et al.*, 2003) and could suggest that they had a much broader geographic distribution than the one implied by the Laurasian fossil record (Gardner & Böhme, 2008).

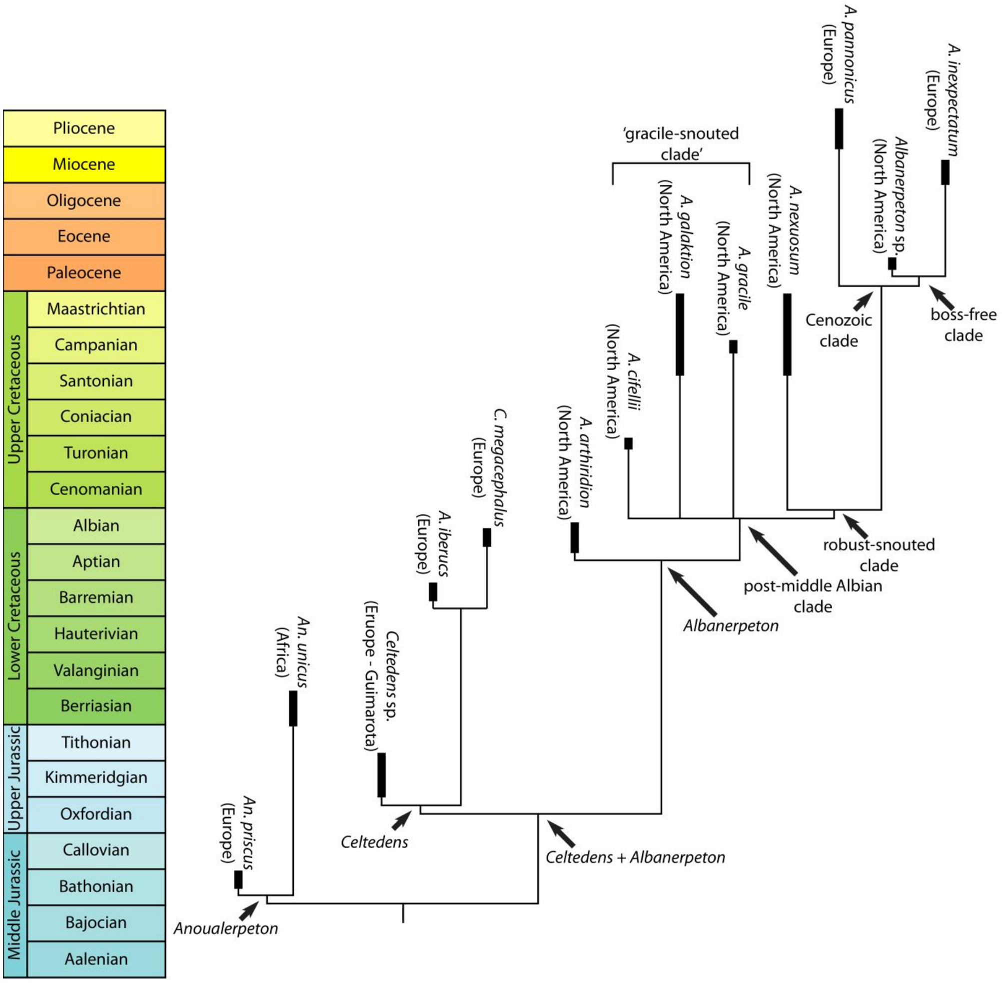

Figure 3: Time-calibrated cladogram illustrating pattern of relationships within the Albanerpetontidae, constrained against the geological timescale to show ranges of terminal taxa and estimated divergence times (modified from Gardner & Böhme, 2008).

Anurans display a unique body plan, highly constrained by their jumping mode of locomotion: (1) very long hindlimbs, with a flexible pelvis and elongated ankle bones, (2) the ilia run far forwards, with posterior vertebrae fused into an urostyle; (3) the forelimbs and the pectoral girdle are modified to absorb landing impacts; (4) the vertebral column is very short (4 to 9 trunk vertebrae) with the ribs fused to the vertebrae; (5) frontal and parietal bones are fused or co-ossified; (6) the parasphenoid is T-shaped; (7) the presence of an annulus typanicus in adult frogs; (8) a lower jaw without teeth; and (9) zeugopod bones are fused (Benton, 2014; Schoch, 2014). The anurans have a worldwide distribution, being the most successful amphibian clade, and are known since the Early Triassic, with *Triadobatrachus* from Madagascar and *Czatkobatrachus* from Poland (Rage & Roček, 1989; Evans & Borsuk-Białynicka, 2009; Benton, 2014). The jumping ability has been acquired in the stem-group of anurans during the Early Jurassic, as suggested by *Prosalirus* from Arizona (Jenkins & Shubin, 1998), but it could have been lost in some lineages (Schoch, 2014). The specialized characters can be already observed in *Viraella*, one of the earliest forms from the Middle Jurassic of Patagonia, and in *Notobratachus*, from the Middle to Late Jurassic of Patagonia (Báez & Basso, 1996). Crown-group anurans occur during the Jurassic of the US and UK, then spread into Gondwana and Laurasia during the Cretaceous, finally attaining their worldwide distribution by the Late Cretaceous (Sanchíz, 1998; Roček, 2000). However, fossil frogs are mostly represented by isolated bones, which can make their specific identification difficult.

Urodeles show fewer specializations than do anurans, with an elongated body and four short walking limbs (Benton, 2014). This monophyletic group includes caudates and all their stem taxa (Frost *et al.*, 2006), and they are known from the Middle Jurassic, with *Marmorerpeton* from England (Evans & Milner, 1994; Milner, 1994), and *Kokartus* from Kyrgyzstan (Skutschas & Martin, 2011). Caudates do not share many autapomorphies, and most of their typical features are actually plesiomorphic: (1) remodeling of the palatine and palatoquadrate, which becomes resorbed during metamorphosis; (2) a wide, flat parasphenoid; and (3) the presence of an odontoid peg (Schoch, 2014). They are known since the Middle Jurassic of Mongolia, with *Chunerpeton* (Gao & Shubin, Earliest known crown-group salamanders, 2003), and the Late Jurassic of China, with *Beiyanerpeton* (Gao & Shubin, 2012).

1.2.4 MAMMALIAFORMS AND MAMMALS

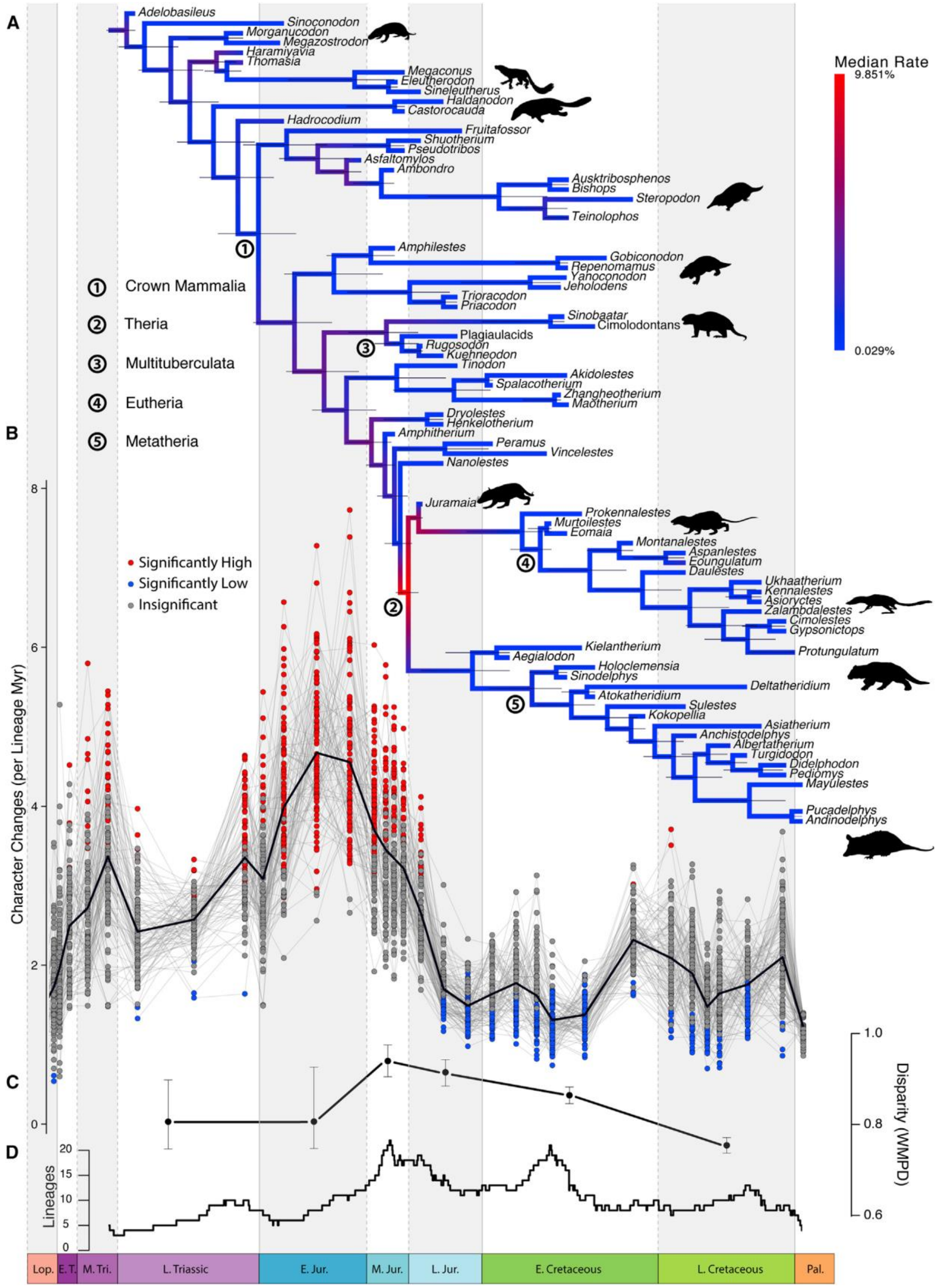

Figure 4: Morphological rates, disparity, and phylogenetic lineage diversity in Mesozoic mammals (from Close *et al.*, 2015).

Mammals usually constitute one of the most abundant taxa in post-Jurassic terrestrial localities (Carrano & Velez-Juarbe, 2006; Sweetman, 2007; Vasile & Csiki, 2010), which is at least partly due to a sampling bias for the Mesozoic. This is consistent with the major adaptive radiation of mammals observed during the Middle to Late Jurassic (Luo & Wible, 2005; Meng, 2014; Newham *et al.*, 2014; Close *et al.*, 2015), even though the rate was lower in Late Jurassic (Figure 4). However, mammals had already spread worldwilde at this time, and were particularly diverse in North America (Kielan-Jaworowska *et al.*, 2004).

Even if the Middle Jurassic is the most poorly known period in mammalian history (Kielan-Jaworowska *et al.*, 2004), it saw the diversification of docodonts, theriiform mammals, and australosphenidian mammaliaforms (Luo, 2007). On other hand, the Late Jurassic witnessed the rise of the Multituberculata, which were the most diverse group (Kielan-Jaworowska *et al.*, 2004), the Eutriconodonta, and the Cladotheria diversification (Newham *et al.*, 2014). It also appeared that Jurassic mammals were cosmopolitan, while they became regional throughout the Cretaceous Period, which can be explained by the expansion of the Atlantic ocean (Rich & Vickers-Rich, 2012).

The study of the post-cranial skeleton suggests that mammals already displayed diverse feeding behaviour and locomotor strategies in the Late Jurassic (Chen & Wilson, 2015), contrary to what has been hypothezied previously (Luo, 2007). Statistical analyses (Figure 5) shows a noticable increase in the mammalian diversity during this period (Newham *et al.*, 2014), which coincindes with this radiation and burst of morphological innovation (Gavrilets & Losos, 2009) notably with the appearance of the characteristic triboshenic molar, the single jaw joint between the dentary and the squamosal, and the middle ear ossciles (Luo *et al.*, 2001, 2011a; Rose, 2006; Kielan-Jaworowska, 2013; Zhou *et al.*, 2013).

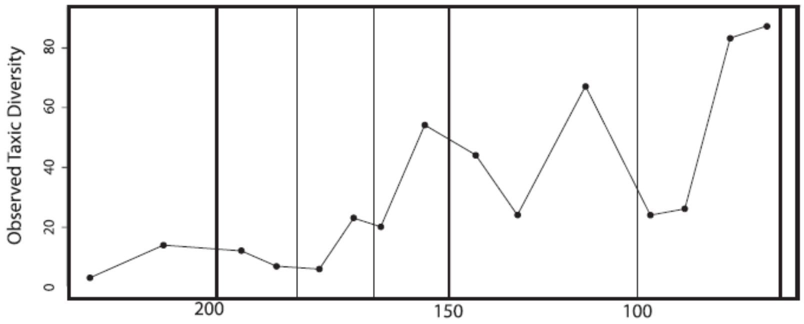

Figure 5: Observed mammaliaform generic taxonomic diversity estimate. Vertical lines represent the Triassic/Jurassic boundary, Early/Mid Jurassic boundary, Mid/Late Jurassic boundary, Jurassic/Cretaceous boundary, and Early/Mid Cretaceous boundary respectively (from Newham *et al.*, 2014).

For a long time, the Mesozoic mammals record was sparse, known mainly from teeth and jaw fragments (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005; Rose, 2006; Kielan-

Jaworowska, 2013). However, during the last two decades, more data from around the world have been shared (Kielan-Jaworowska *et al.*, 2004; Luo, 2007; Meng, 2014), including fossils from groups, previously limited to Laurasia, found in localities from Gondwana (Rich & Vickers-Rich, 2012; Krause, 2013; Bi *et al.*, 2014), suggesting that major groups of mammals already had a global distribution during their evolution in the Jurassic (Bi *et al.*, 2014; Meng, 2014). However, there is still a geographical and temporal gap in the Mesozoic mammal record (Kielan-Jaworowska *et al.*, 2004; Rich & Vickers-Rich, 2012).

There are around 30 mammalian families (Figure 6) recorded from the Jurassic and the Cretaceous Periods (Kielan-Jaworowska *et al.*, 2004), but these are mainly based on teeth and incomplete material, making their relationships hard to assess (Benton, 2014). The main difficulty is to determine which features are synapomorphic, and which ones are homoplasic (Kemp, 2005), while it seems that convergence was very common in the early evolution of mammals (Lillegraven & Krusat, 1991). Some authors questioned why Mesozoic mammals stayed relatively small, considering the Mesozoic represents two-third of the all mammal evolution with dinosaurs occupying the niches of large-bodied animals, but then witnessed a massive radiation and indeed evolved in much larger sizes during the Cenozoic (Kemp, 2005).

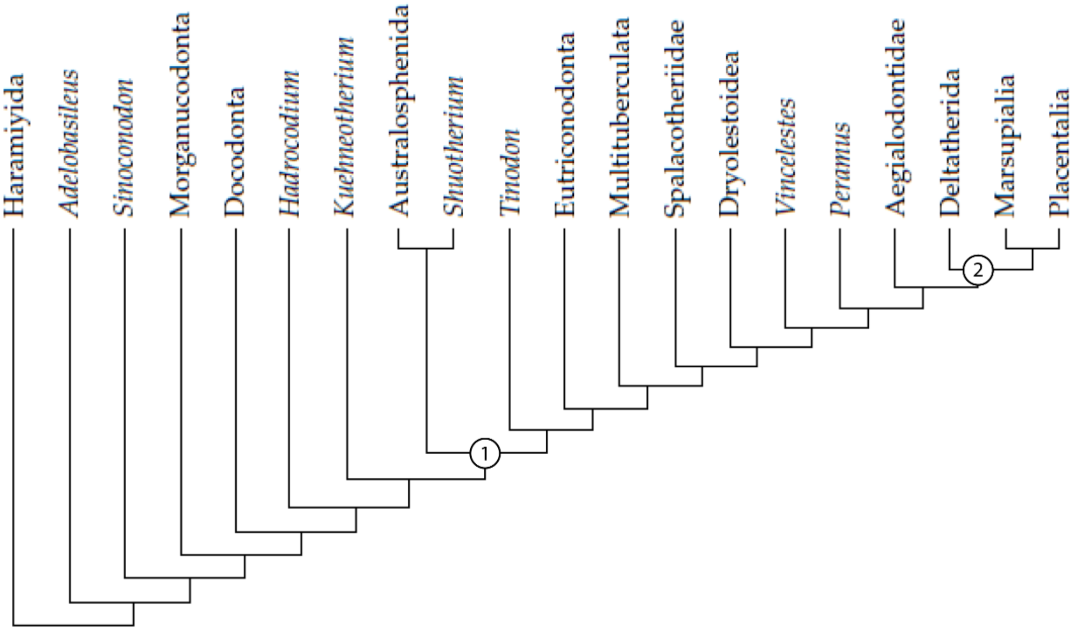

Figure 6: Simplified Mesozoic mammaliaform phylogeny from Luo et al., 2002 (modified from Kemp, 2005). (1) denotes the node of the crown-group Mammalia; (2) denotes the node of the crown-group Theria.

Docodonta are known from the Middle Jurassic of Scotland, England, and China, to the Early Cretaceous of England, Mongolia, and Russia; with occurences in the Late Jurassic of Portugal, United States and Mongolia (Martin & Nowotny, 2000; Kielan-Jaworowska *et al.*, 2004; Martin, 2005, Ji *et al.*, 2006). Some authors also attributed remains from the Late Triassic of France (Sigogneau-Russell & Godefroit, 1997), and the Late Cretaceous of Argentina (Pascual *et al.*, 2000), but these identifications have been challenged (Butler, 1997; Kielan-Jaworowska *et al.*, 2004). They exhibit a mosaic of characters, with plesiomorphic postcranial and cranial features but their molars seems to be more synapomorphic. They could shear and may have been capable of grinding, the lowers being elongated longitudinally with two row of cusps similar to those of therians. Docodonts molars also developped a strong, transverse crest connecting the cusps (Kielan-Jaworowska *et al.*, 2004), which shows the convergence of the teeth in a functionally tribosphenic-like structure (Luo & Martin, 2007), and form complex occluding surfaces, suggesting a diet composed of plants and insects (Kemp, 2005). The group's post-cranial morphology is mainly known from *Haldanodon* Kühne and Krusat 1972 from the Guimarota Mine (Martin & Nowotny, 2000) and *Castorocauda* Ji *et al.*, 2006 from the Jiulongshan Formation, which both suggest adaptation for a semiaquatic lifestyle (Kielan-Jaworowska *et al.*, 2004; Ji *et al.*, 2006; Benton, 2014).

Eutriconodonta is one of the most diverse groups of Mesozoic mammals, although its monophyly, while accepted (Luo *et al.*, 2002), is not well supported (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005). They are mainly known from isolated teeth and jaw bones from the Middle Jurassic of England, China and Mexico to the Late Cretacous of Argentina, but they had a worldwilde and diverse distribution during the Late Jurassic and the Early Cretaceous (Kielan-Jaworowska *et al.*, 2004). Their body size was significantly larger than most of the others mammalian groups, with some of the largest mammals from the entire Mesozoic (Kielan-Jaworowska *et al.*, 2004). One of their main features is the specialization for a carnivorous diet incorporating vertebrate preys, with notably: (1) the presence of long sharp canines; (2) premolars with tall, trenchant main cusps of equal size; (3) limitation of molar function to shearing; (4) strong development of the mandibular adductor musculature; (5) relatively shorter, more robust jaws than other mammals; and (6) a greater development of the coronoid process (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005).

Teeth and jaw fragments from the Middle Jurassic of Madagascar (Flynn *et al.*, 1999) and South America (Rauhut *et al.*, 2002) have been attributed to the endemic Gondwanian clade Australosphenida, which includes monotremes (Luo *et al.*, 2002, 2003; Kielan-Jaworowska *et al.*, 2004; Davis, 2011; Benton, 2014).

Multituberculata are the largest group of Mesozoic mammals, having a worldwide distribution for their paleontological record (Kielan-Jaworowska *et al.*, 2004, Kemp, 2005). They are uncontestably known from the Late Jurassic of Portugal to the Eocene of North America, but isolated teeth from the Late Triassic of Belgium and the Middle Jurassic of England have tentatively attributed to this clade (Kielan-Jaworowska *et al.*, 2004). For a long time, they have been restricted to Laurasian localities (Rose, 2006; Rich & Vickers-Rich, 2012), from the Morrison Formation; the Early Cretaceous of England, North America, Mongolia, and China; the Late Cretaceous of Mongolia, North America, and Europe; and the Paleocene and Eocene of North America, Europe, and China (Kielan-Jaworowska *et al.*, 2004). However, they are now also known from the Early Cretaceous of Morocco and Australia, and the Late Cretaceous of Madagascar and Argentina (Kielan-Jaworowska *et al.*, 2004; Rose, 2006; Rich *et al.*, 2009; Rich & Vickers-Rich, 2012). Multituberculates are characterized by: (1) multicusped (up to eight cusps) premolars and molars, covered by two longitudinal rows of low cusps of the same height; (2) presence of two upper incisors for a single lower one; (3) presence of two upper molars; (3) none to four lower premolars and two lower molars; (4) lingual shifting of M2 with respect to M1, both of them having broad occlsal surfaces; (5) bladelike-shaped lower premolar; (6) wide and dorsoventrally compressed skull; (7) postorbital process situated on the parietal in some groups; (8) very large orbit; (9) strong and laterally expanded zygomatic arch; (10) large and flat glenoid fossa; (11) and jugal on the medial side of the zygomatic arch not visible in lateral view (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005; Rose, 2006 Benton, 2014).

Symmetrodontans are a poorly-known paraphyletic group, mainly characterized by a simple reversed-triangle molar pattern, which represents an “intermediate” structure between the tricodont molar and the mammalians tribosphenic arrangement (Kielan-Jaworowska *et al.*, 2004). However, the monophyly of this clade has long been debated, and it has been proved that this feature was actually convergent in several mammal linages (Rougier *et al.*, 1996; Pascual *et al.*, 2002). They are known from the Late Triassic of France, Britain, Greenland, and India, to the Late Cretaceous of Argentina, North America, and Uzbekistan, with occurences in the Early Jurassic of India; the Middle-Late Jurassic of China; the Late Jurassic of North America; and the Early Cretaceous of Britain, Spain, China, and Morocco (Kielan-Jaworowska *et al.*, 2004).

Eupantotheres are a paraphyletic grade which refers to an important Mesozoic mammal group including paremurids, amphitheriids and dryolestoids, and group inside Cladotheria (Kielan-Jaworowska *et al.*, 2004, Kemp, 2005). They are known from the Middle Jurassic of Europe to the Paleocene of Argentina, but they are also known in the Late Jurassic of Portugal, North America and Africa, the Early Cretaceous of Britain, Morocco, Mongolia, South America and Australia, and the Late Cretaceous of America (Kielan-Jaworowska *et al.*, 2004). They can be characterized by: (1) presence of an angular process of the dentary; (2) upper and lower molars forming a series of reversed and interlocking triangles; (3) upper molars wider than lowers; (4) molars with a lingual root and more strongly developed labial stylar cusps; (5) the talonid of the lower molars is clearly differentiated from the trigonid; and (6) the absence of entoconid, talonid basin, and protocone (Kielan-Jaworowska *et al.*, 2004).

Dryolestoidea are small mammals mostly known from isolated teeth and the incredibly preserved *Henkelotherium* Krebs, 1991 from the Guimarota Mine (Krebs, 2000). They can be characterized by: (1) typical dentary-squamosal mammalian jaw joint; (2) mandibular angle extends horizontally from the ventral border of the mandibular horizontal ramus; (3) well developed stylar cusps; (4) presence of the metacone; (5) median ridge joining the paracone either to the median stylar cusps or the stylocone; and (6) transversely wide and mesiodistally short upper molars, sharing a superficial similarity with docodonts (Kielan-Jaworowska *et al.*, 2004). Dryolestidae are the most abundant and diverse family of dryolestoids (Rose, 2006), and are known from the Middle Jurassic of Britain to the Late Cretaceous of Argentina, and possibly US, with occurrence in the Late Jurassic of Portugal and US, and the Early Cretaceous of Britain and Spain (Kielan-Jaworowska *et al.*, 2004). They can be characterized by: (1) upper and lower molars strongly shortened mesiodistally and widened labiolingually; (2) a more robust and larger anterior root than posterior in lower molars (Kielan-Jaworowska *et al.*, 2004). Paurodontidae are known from the Late Jurassic of US, Portugal, and Tanzania to the Early Cretaceous of Britain; and can be characterized by: (1) robust and anteriorly high dentary, with a vertical symphysis; (2) slighly labiolingually narrow upper molars; (3) absence of the median stylar cusps and median ridge; (4) shelf-like paraconid; and (5) metaconid shorter than the paraconid (Kielan-Jaworowska *et al.*, 2004). Amphiteriidae are known from the Middle Jurassic of England, and can be characterized by: (1) a labial talonid cusp; (2) posterior root smaller than the anterior one in posterior molars; (3) a continuous lingual cingulids in premolars; and (4) a downturned mandibular angle (Kielan-Jaworowska *et al.*, 2004). Zatheria are known from the Late Jurassic of Portugal to the Early Cretaceous of Argentina and

Mongolia, and can be characterized by: (1) presence of three molars; (2) a basined talonid; (3) the presence of hypoconulid and hypoconid; and (4) a reduced stylocone (Prothero, 1981).

Juramaia sinensis Luo *et al.*, 2011 from the Middle-Late Jurassic of China is considered as the earliest eutherian currently known (Luo *et al.*, 2011b; Kielan-Jaworowska, 2013), placing the origin of the Eutheria at 160 Myr, and suggesting that the Boreosphenida, for which the oldest occurrence is from the Early Cretacous of China (Ji *et al.*, 2002; Luo *et al.*, 2003), originated during the Middle Jurassic (Benton, 2014). Additionally, highly derived eutherian teeth have been found in the Berriasian of Britain (Sweetman *et al.*, 2017).

1.2.5. TURTLES

Testudinata is the clade from which arose a complete turtle shell homologous to the shell present in *Chelonia mydas* (Linnaeus, 1758). Sensu Gaffney & Meylan, a shell is composed of: (1) one carapace formed from costal bones with fused thoracic vertebrae, and marginal bones; (2) one plastron formed from interclavicle, clavicle, and three to five paired bones sutured together; (3) carapace and plastron articulated at lateral margin and enclosing the shoulder and pelvic girdles (Gaffney & Meylan, 1988; Joyce *et al.*, 2004). The definition can be interpreted in various ways, making the origin of turtles highly debatable (Joyce, 2015). Turtles could have originated late in the Paleozoic, or early in the Mesozoic with *Eunotosaurus africanus* Seeley, 1892 from the Middle Permian of South Africa, *Pappochelys rosinae* Schoch & Sues, 2015 from the Middle Triassic of Germany, and *Odontochelys semitestacea* Li *et al.*, 2008 from the Late Triassic of China (Benton, 2014; Joyce, 2017).

The Late Jurassic turtle record is mainly dominated by the two major Testudines groups Pleurodira and Cryptodira, which originated during the Middle Jurassic and gather all the living turtles, and will diversify during this period in Europe, North America, and South America (Joyce, 2007, 2017; Benton, 2014). In extant species, both groups can be differentiated with the articulation of the neck: pleurodires pull the head in by bending in the neck sideways, while cryptodires pull the head in by bending in the neck vertically (Benton, 2014). However, that can be challenged in the fossil record (Joyce *et al.*, 2004), pleurodires share 16 synapomorphies, while cryptodires are characterized by: (1) the secondary loss of paired pits on the ventral surface of the basisphenoid; (2) the loss of the spenials; (3) the acquisition of an eighth cervical centrum significantly shorter than the centrum of the seventh cervical; (4) and the loss of the cleithra (Joyce, 2007).

1.2.6. LEPIDOSAURS

Lepidosauria, commonly called “lizards”, is a clade composed by the last common ancestor of Rhynchocephalia and Squamata and all its descendants, sharing 55 derived characters (Evans, 1998b, 2003; Reynoso, 1998; Jones *et al.*, 2013; Pyron *et al.*, 2013; Benton, 2014). Their preservation generally requires a low energetic depositional environment with fine sediment, and are more numerous in assemblages depositing in lacustrine-lagoonal conditions, in association with freshwater animals and small vertebrates (Evans, 1998b, 2003). The first radiation of this group was during the Middle Triassic, with the rise of the rhynchocephalians, then a second one occured during the Jurassic and Cretaceous, with the rise of the “lizards” and the snakes and which could be correlated to the diversification of angiosperms during the Cretaceous (Benton, 2014). Lepidosaurian can be characterized by: (1) the presence of a thyroid fenestra; (2) a broad opening in the pelvis between the pubis and the ischium; (3) the fusion of the astragalus with the calcaneum; (4) and a metatarsal 5 hooked in two planes (Benton, 2014).

Rhynchocephalia had a worldwide distribution during the Mesozoic (Figure 7**)**, with around 30 genera described (Evans, 2003), but are currently represented only by two species. They are characterized by: (1) an acrodont dentition; (2) an elongated lateral palatine tooth row running parallel or sub-parallel to the maxillary row, permitting either preopalinal or orthal shear; (3) a posterior extension of the dentary, which braces the accessory jaw bones; (4) and the loss or the fusion of supratemporal bones (Evans, 2003). They are defined with the Early Jurassic genus *Gephyrosaurus* Evans, 1980 as sister taxa of all others species (Evans, 2003), but they have both Triassc and Jurassic records. They occurr in Middle and Upper Triassic deposits in North America, Europe, Asia, Madagascar and Brazil (Evans *et al.*, 2001; Jones *et al.*, 2013) but most of specimen are poorly preserved.

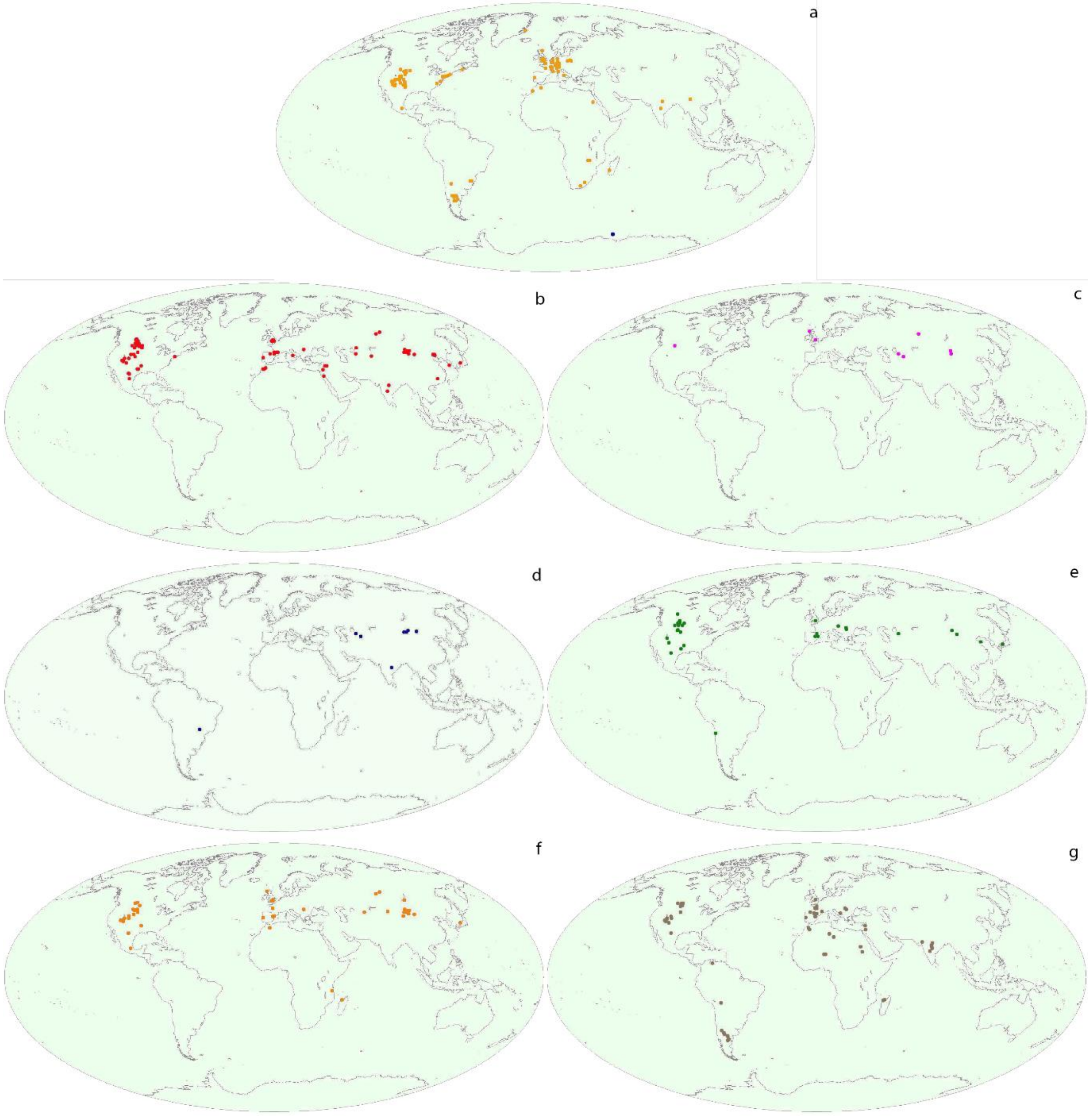

Figure 7: Known localities yielding Mesozoic fossil lepidosaurs plotted onto modern world maps, using data from PaleoBiologyDatabase Fossilwork. **a**, Rhynchocephalia; **b**, Anguimorpha; **c**, Gekkota; **d**, Iguania; **e**, Lacertoidea; **f**, Scincoidea; **g**, Serpentes.

There is no true squamate record prior to the Jurassic Period, but indirect evidence suggest they evolved by at least the Middle Triassic, deriving from rhynchocephalians in Late Triassic or Early Jurassic (Evans, 2003; Benton, 2014). Then diversified into existing major lineages before the end of the Jurassic (Evans, 2003). The earliest records of true squamates are from the Early-Middle Jurassic of the Kota Formation in India (Evans *et al*., 2002), and then from Middle Jurassic of Britain (Evans, 1994; 1998a; Reynoso, 1998) and Central Asia (Fedorov & Nessov, 1992). Even though their classification is highly debated, squamates are composed of the six clades : (1) Gekkota; (2) Scincoidea; (3) Lacertoidea, which includes Amphisbaenia; (4) Iguania; (5) Anguimorpha; (6) and Serpentes (Pyron *et al*., 2013). However, there is a major temporal and biogeographic gap in the Mesozoic squamate record (Figure 8), with Gondwana appearing to have only a fraction of the diversity in Laurasia (Evans, 1998b, 2003; Evans *et al*., 2002; Chatterjee & Scotese, 2007; Simões *et al*., 2015, 2017), but evidences suggest all these major clades were already diverging by the Late Jurassic (Evans, 2003; Gauthier *et al*., 2012; Simões *et al*., 2017).

The first well documented occurrences of Gekkota are from the Aptian-Albian and Santonian-Campanian of Mongolia and West Siberia and refer to intact and articulated cranial material from an adult specimen (Alifanov, 1989; Daza *et al*., 2014). However, some authors refer *Eichstaettisaurus* from the Late Jurassic of Germany and Early Cretaceous of Spain and Germany as the most 'basal' stem gekkotan (Evans, 1993, 1994; Gauthier *et al*., 2012), although some of the features supporting it are neither characteristic or unique to this clade (Daza *et al*., 2014). Additionally, some vertebrae from the Middle Jurassic of England have been tentatively attributed to gekkotans (Evans, 1998a; Daza *et al*., 2014).

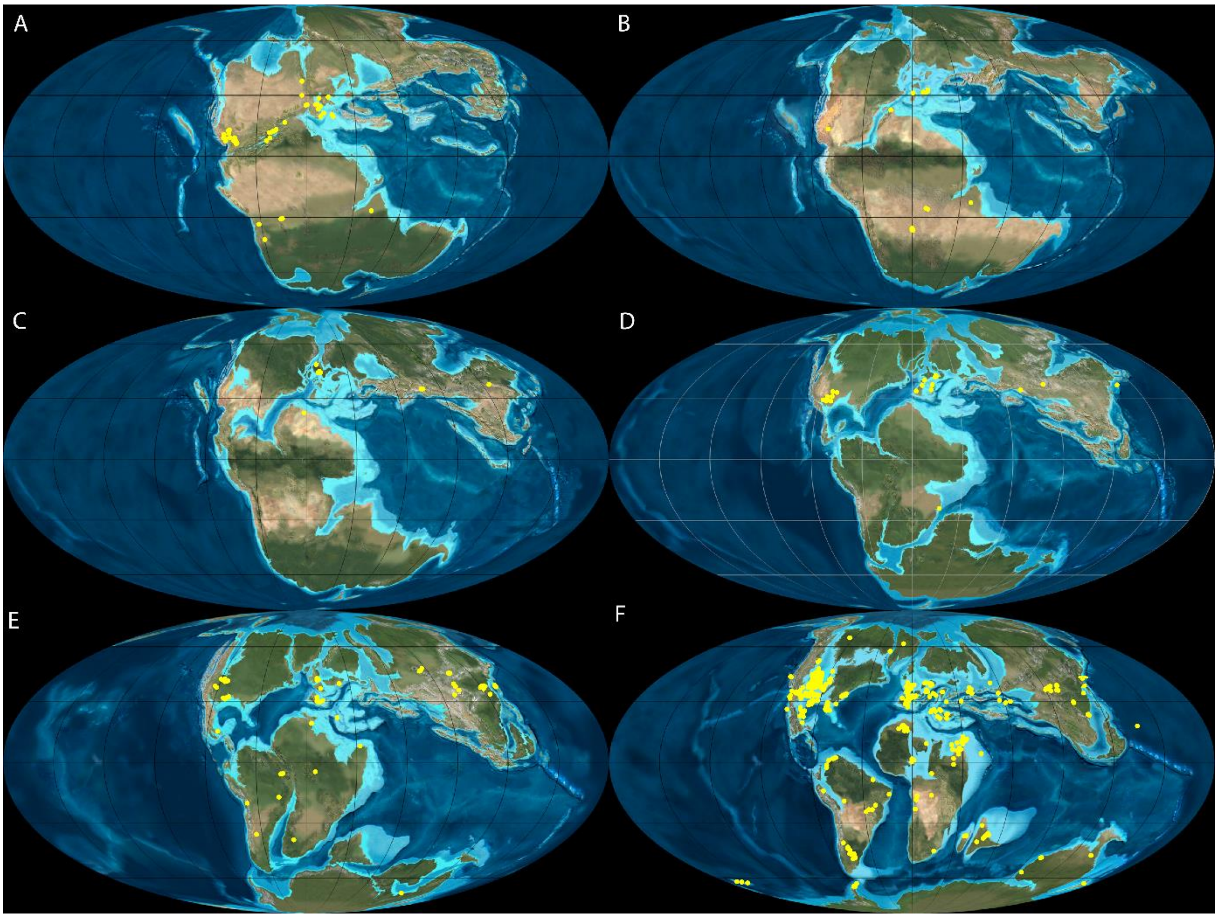

Figure 8: Paleobiogeographic distributions of lepidosaurians through the Mesozoic, using the data from PaleoBiology Database. Paleomaps from Global Paleogeographic Views of Earth History, NAU. **A**, Late Triassic (220 Ma); **B**, Early Jurassic (200 Ma); **C**, Middle Jurassic (170 Ma); **D**, Late Jurassic (150 Ma); **E**, Early Cretaceous (120 Ma); **F**, Late Cretaceous (90 Ma).

If poorly preserved remains suggest Iguania were already present in the Kota Formation, Early-Middle Jurassic of India (Evans *et al.*, 2002; Evans, 2003), the earliest uncontested records are from the Aptian-Albian of Mongolia (Alifanov, 1993) and the Albian of Mexico (Reynoso, 1998). First occurences of Anguimorpha are also known at least from the Late Jurassic of England (Hoffstetter, 1967; Conrad, 2008; Conrad, Ast, Montanari, & Norell, 2011; Benton, 2014) and Portugal (Broschinski, 2000).

Lacertoidea and Scincoidea were usually grouped together in the clade Scincomorpha (Estes *et al.*, 1988; Evans, 2003; Conrad, 2008; Gauthier *et al.*, 2012; Benton, 2014), however recent phylogenies based on molecular data split them, making scincomorphs paraphyletic (Pyron *et al.*, 2013). These clades are commonly found in Laurasian lizard assemblages from Mesozoic localities, first occurences being in the Middle Jurassic of England (Evans, 1998a) and Late Jurassic of Portugal (Broschinski, 2000), US (Evans & Chure, 1998), Kazakhstan (Hecht & Hecht, 1984), China (Li, 1985) and Tanzania (Broschinski, 1999), suggesting an origin before the breakup of Pangea (Evans, 2003).

For a long time, Serpentes was thought to have originated during the Late Cretaceous, and already had a relatively worldwide and diverse distribution by then, mainly in Gondwana, which went against the pattern observed in others squamates (Evans, 2003). However, descriptions and revisions of specimens from the Bathonian of England, the Kimmeridgian of Portugal and Colorado, and the Tithonian-Berriasian of England pushed back this origin to the Middle-Late Jurassic, coincident with the radiation of the other squamate clades during the final stages of Atlantic opening (Caldwell *et al.*, 2015). There are occurrences from the Albian-Cenomanian of Utah (Gardner & Cifelli, 1999) and the Cenomanian of Algeria (Cuny *et al.*, 1990), France, Portugal, Egypt, Sudan (Rage & Werner, 1999), where the material is the most diverse (Evans, 2003), Argentina, Middle-East (Caldwell & Lee, 1997), the Cenomanian-Turonian of Bosnia-Herzegovina (Lee *et al.*, 1999) and Argentina (Apesteguía & Zaher, 2006), and the Coniacian of Argentina (Caldwell & Albino, 2002).

1.2.7. CHORISTODERES

Choristodera are freshwater aquatic diapsids reptiles with uncertain phylogenetic position: analyses support their appurtenance to Archosauromorpha (Evans, 1988; Gauthier *et al.*, 1988), but other studies considered them as a sister-group of Archosauromorpha, Archosauromorpha+Lepidosauromorpha, or of Euryapsida (Matsumoto & Evans, 2010 and references therein). They are known from the Middle Jurassic of England (Evans, 1990) and Scotland (Evans & Waldman, 1996), with the genus *Cteniogenys* Gilmore, 1928, and unamed material from Kyrgyzstan (Averianov *et al*. 2006), to the early Miocene of Czech Republic (Matsumoto & Evans, 2010). Material tentatively attributed to *Pachystropheus* von Huene, 1935 from the Late Triassic of Germany (Storrs & Gower, 1993; Storrs *et al*., 1996), but the lack of skull material, where are most of the choristodere diagnostic features, provides to support this assessment (Matsumoto & Evans, 2010).

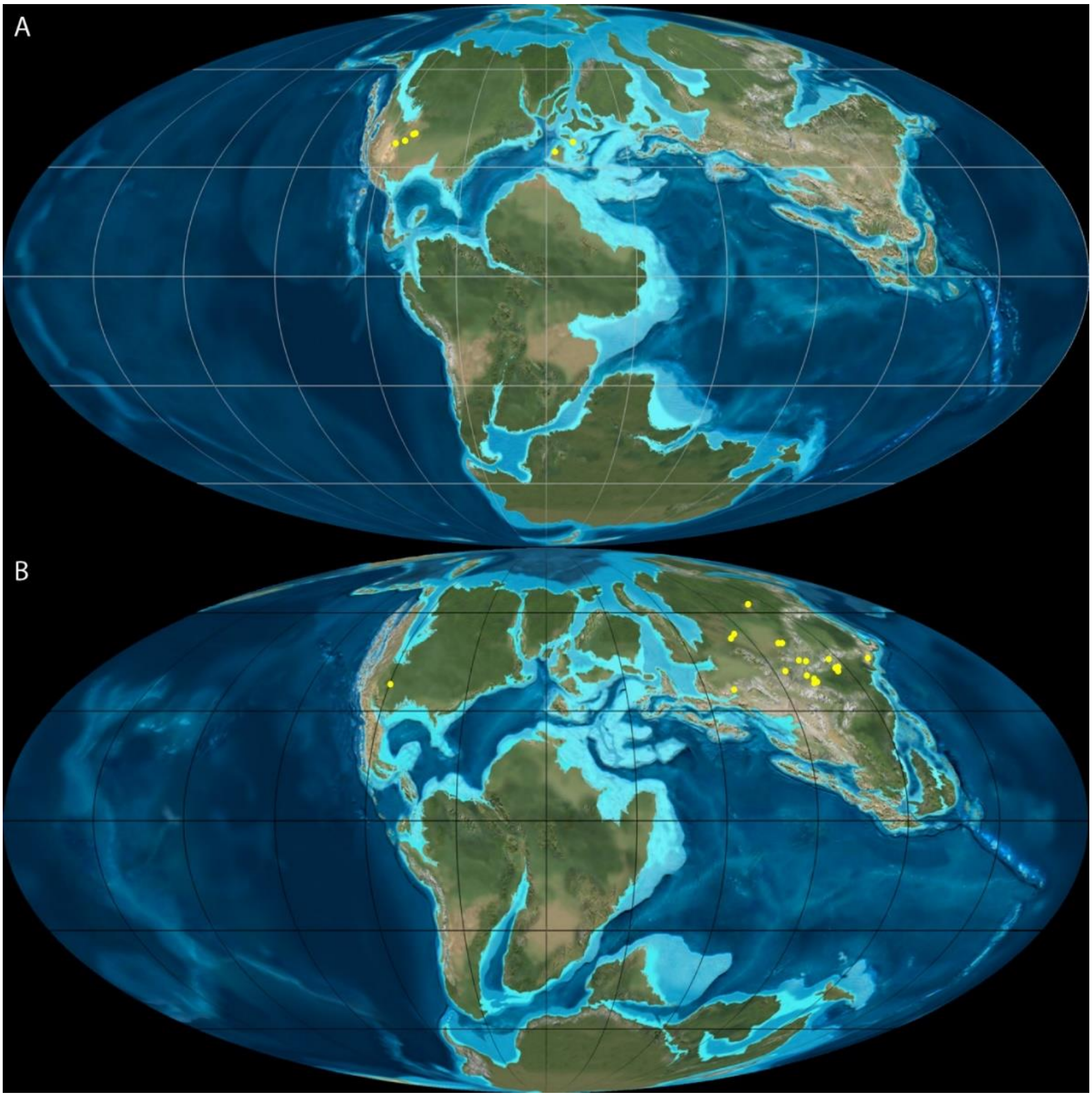

Figure 9: Paleobiogeography distributions of choristoderes in the Late Jurassic (**A**, 150 Ma) and the Early Cretaceous (**B**, 120 Ma) using the data from PaleoBiology Database. Paleomaps from Global Paleogeographic Views of Earth History, NAU.

Cteniogenys is also known from the Kimmeridgian of Portugal and North America, event though it was not evenly distributed through the Morrison VMAs (Matsumoto & Evans, 2010 and references therein), and from the Tithonian of France, even though only by scarce material (Vullo *et al.*, 2014). Choristoderes diversified during the Early Cretaceous in Asia, where they have the biggest diversity (**Figure 9**), and North America, passing from lizard-like morphologies to forms exhibiting also gavial-like and long-necked morphologies, and with a gradual increase in maximum size during the Jurassic-Cretaceous transition (Matsumoto & Evans, 2010 and references therein). Choristoderes remains are commonly found in shallow freshwater environments close to coastal margins rich in other small vertebrates, with which they were in competition for ressources (Matsumoto & Evans, 2010).

1.2.8. ARCHOSAURS

Among the pseudosuchians, only Crocodylomorpha crossed the Triassic-Jurassic boundary (Nesbitt, 2011; Toljagić & Butler, 2013) and became morphologically and ecologically diverse during the Jurassic and the Cretaceous (Young & de Andrade, 2009; Parrilla-Bel *et al.*, 2013; Pol *et al.*, 2013; Toljagić & Butler, 2013) with around 200 species described in the Mesozoic (Benton, 2014). They were also found in marine deposits from Europe, Asia, and South and Central America (Pol & Gasparini, 2009). Crocodylomorphs are composed of Sphenosuchia and Crocodyliformes (Walker, 1968). Sphenosuchians are considered as basal members, and are known worldwide, except Antarctica and Australasia, from the Late Triassic to the Late Jurassic (Clark *et al.*, 2004). Their phylogenetical status has long been debated (Clark, 1994; Clark *et al.*, 2004; Göhlich *et al.*, 2005), and it was first thought they were paraphyletic (Benton & Clark, 1988; Parrish, 1991; Clark & Sues, 2002). However, later phylogenetic analyses agreed on the monophyly of the clade, as sister taxa of Crocodyliformes (Sereno & Wild, 1992; Wu & Chatterjee, 1993; Clark *et al.*, 2000; Sues *et al.*, 2003). Sphenosuchia represents a highly terrestrialized step in crocodylomorph evolution (Clark *et al.*, 2004), crocodylomorphs being more marine during the Jurassic and terrestrial during the Cretaceous (Stubbs *et al.*, 2013; Benton, 2014). The majority of crocodyliform taxa from the Late Jurassic are part of the clade Neosuchia (de Andrade *et al.*, 2011; Bronzati, 2012), in which Eusuchia leads towards Cenozoic and modern crocodilians (Benton, 2014).

Atoposauridae are small-bodied terrestrial to semi-aquatic crocodyliforms (Lauprasert *et al.*, 2011; Tennant & Mannion, 2014) characterized by: (1) a short rostral length; (2) paired external nares; (3) a relatively small supratemporal fenestrae; (4) slender limbs; (5) a dermal armor absent or reduced; (6) a squamosal not bent ventrally; (7) and dental hypertrophy absent (Lauprasert *et al.*, 2011). The atoposaurid fossil record ranges from the Late Bajocian-

Bathonian of France and the UK (Evans & Milner, 1994; Kriwet *et al*., 1997; Knoll *et al*., 2013; Young *et al*., 2016) to the Maastrichtian of Romania (Martin *et al*., 2010, 2014). Most atoposaurid remains have been discovered in Europe (Lauprasert *et al*., 2011), but found also in Asia, North America and in Africa (Tennant & Mannion, 2014; Young *et al*., 2016). The most emblematic atoposaurid is the genus *Theriosuchus* Owen, 1878, which has been described mainly from Europe, particularly in the Iberian Peninsula and in southern England, but isolated teeth have been described in North America and Asia (Lauprasert *et al*., 2011). However, the monophyly of this genus has been debated, some species not sharing the diagnostic autapomorphies of the genus (Young *et al*., 2016), and recent studies have even reattributed some specimens to the genera *Sabresuchus* Tennant *et al*., 2016 and *Knoetschkesuchus* Schwarz *et al*., 2017, considering that these are different enough to form a new clades: the sister-group to *Theriosuchus* (Tennant *et al*., 2016; Schwarz *et al*., 2017). It has been suggested that the high atoposaurid diversity in Europe could be related to the island archipelago system during the Late Jurassic (Tennant & Mannion, 2014, Schwarz *et al*., 2017), which would also explain also the small body size, as an ecological partitioning with thalattosuchian and goniopholidids, or insular dwarfism (Tennant & Mannion, 2014).

Bernissartiidae are characterized by their dentition adapted to a durophagous diet. Skeletal remains are known in the Lower Cretaceous of Europe (Sweetman *et al*., 2015), and teeth have been found in the Late Jurassic (Schwarz-Wings *et al*., 2009; Puértolas-Pascual *et al*., 2015b).

Goniopholididae have been found in freshwater and marine sediments (Benton, 2014), suggesting a semi-aquatic ecology. Their morphology is similar to modern crocodylians, even if they retain some plesiomorphies, like ‘mesosuchian’ choanae (de Andrade *et al*., 2011). Their radiation through the Early Jurassic to Late Cretaceous left an abundant fossil record, notably during the Late Jurassic and Early Cretaceous of Western Europe, and particularly the Iberian Peninsula (Puértolas-Pascual *et al*., 2015a). However, there are also records in Asia, North America (Puértolas-Pascual *et al*., 2015a), and maybe Africa (Sereno, 2009; de Andrade *et al*., 2011). The genus-type *Goniopholis* Owen, 1841 is typical from Europe, with range from the Kimmeridgian to the Berriasian (de Andrade *et al*., 2011), and shares strong similarities with the asian *Sunosuchus* Young, 1948 in terms of distribution, ecology success and spatial history (Wings *et al*., 2010).

Thalattosuchia are derived neosuchians mostly from the Jurassic of Europe, with long narrow snouts for hunting fish in shallow waters (Benton, 2014), making them highly adapted to marine environments (Wilberg, 2015). Teleosauridae morphology is characterized by: (1) an elongated and tubular rostrum; (2) high upper and lower jaw tooth counts; (3) a large supratemporal fenestrae; (4) polydont snout; and (5) dorsally directed orbit (Young & Steel, 2014; Young *et al.*, 2014). This suggests they were adapted to a marine lifestyle in estuarine and coastal environments, acting as nearshore marine ambush predators like the extant Indian gavial (Young & Steel, 2014; Wilberg, 2015). *Machimosaurus* von Meyer, 1837 is the most characteristic representative of this clade, even if its craniodental and post-cranial morphologies have created taxonomic confusion (Young & Steel, 2014; Young *et al.*, 2014). This genus is mostly known from the Late Oxfordian to the Early Tithonian of Europe and Ethiopia (Young *et al.*, 2014).

The Metriorhynchidae's 'aberrant' morphology is characterized by: (1) a skull and a highly streamlined body; (2) paddle-like hind limbs; (3) and extremely reduced hydrofoil-like forelimbs; (4) hypocercal tail; (5) large salt glands; (6) loss of the osteoderm armor; (7) sclerotic ossicles (Young *et al.*, 2012; Parrilla-Bel *et al.*, 2013; Wilberg, 2015), making them among the most extensively marine-adapted archosaurs (Langston, 1973; Wilberg, 2015). They are considered as passive or active pelagic predators (de Andrade *et al.*, 2010; Young *et al.*, 2012; Wilberg, 2015), and they spread from the Middle Jurassic to the Early Cretaceous from America, Europe and Russia (Young & de Andrade, 2009; Young *et al.*, 2014).

Because shed teeth of the crocodylomorphs are commonly found in vertebrate microfossils assemblages (Thies & Broschinski, 2001; Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Gasca *et al.*, 2012; Ullmann *et al.*, 2012; Kuzmin *et al.*, 2013; Puértolas-Pascual *et al.*, 2015b), they can have a high potential for taxonomic determination based on their shape (Wings *et al.*, 2010). However, because of their great intraspecific variation, the high dependency of the tooth morphology with ecological factors, and shortage of phylogenetic information, it is difficult to assign taxonomic identification at a generic level to isolated crocodylomorph teeth (Prasad & de Lapparent de Broin, 2002; Buscalioni *et al.*, 2008; Wings *et al.*, 2010; Puértolas-Pascual *et al.*, 2015b; Young *et al.*, 2016). Studies have shown similar crocodylomorph faunal associations across contemporaneous European communities (Figure 10), composed mainly by taxa *Bernissartia* Dollo, 1883, *Theriosuchus*, *Goniopholis*, in association with different other taxa according each localities (Schwarz-Wings *et al.*, 2009).

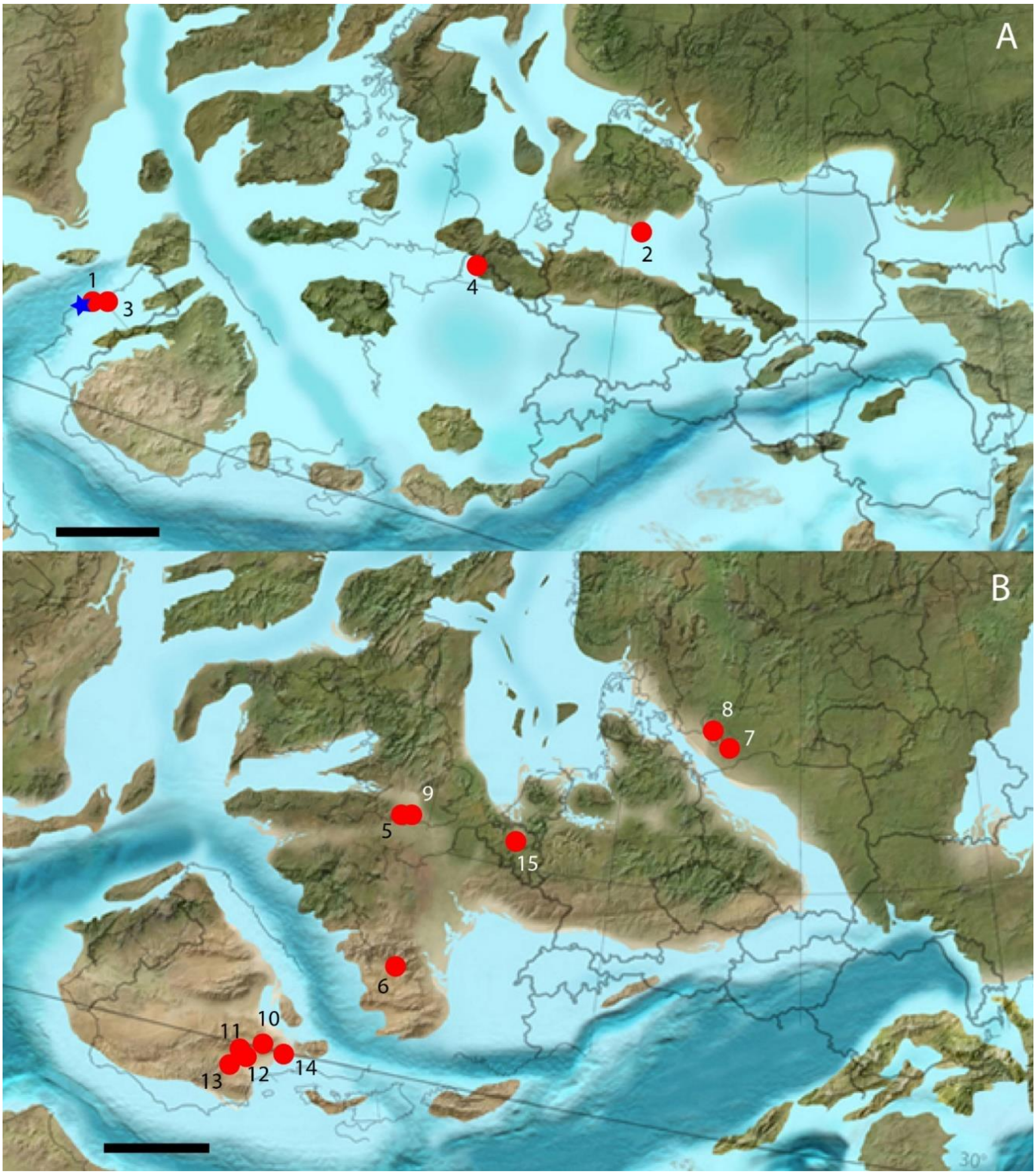

Figure 10: Paleogeographic maps of Europe with Upper Jurassic (A) and Lower Cretaceous (B) localities yielding mesoeucrocodylian communities with Goniopholis, Theriosuchus, and Bernissartia. Blue star indicates the locality of Valmitão, Lourinhã Formation (Ribamar, Portugal). **1**. Guimarota, Guimarota mine, Alcobaça Formation (Leira, Portugal); **2**. Langenberg/Oker, Langenberg Formation (Germany); **3**. Andrès, Alcobaça Formation (Pombal, Portugal); **4**. Montrouge and La Rochette II, the Formations généreuses (Boulogne-sur-Mer & Wimille, France); **5**. Swanage, Purbeck Limestone Group (Dorset, England); **6**. Cherves-de-Cognac, gypsum and marlstone units equivalent to Purbeck Limestone Group (France); **7**. Arnager, Rabekke Formation (Bornholm, Denmark); **8**. Eriksdal, Annero Formation (Skåne, Sweden); **9**. Isle of Wight, Wessex Formation (England); **10**. Galve, El Castellar Formation and Camarillas Formation (Teruel, Spain); **11**. Uña, Uña Formation (Cuenca, Spain); **12.** Pio Pajarón, Uña Formation (Cuenca, Spain); **13**. Buenache de la Sierra, La Huérguina Limestone Formation (Cuenca, Spain); **14**. Vallipón and La Cantalera, Artoles Formation and Blesa Formation (Teruel, Spain); **15**. Bernissart, Sainte-Barbe clays (Belgium). Modified from Schwarz-Wings *et al.*, 2009, paleomaps from Colorado Plateau Geosystem. Scale bar is 400km.

First vertebrates to have been adapted to fly, Pterosauria are known from the Late Triassic of Europe and North America (Barrett *et al.*, 2008), then diversify and reached a worldwilde distribution through the Jurassic and the Cretaceous (Wellnhofer, 1978; Buffetaut & Mazin, 2003; Witton, 2013; Martill *et al.*, 2014), to become extinct at the K-Pg boundary. The earliest forms displayed already the characteristic features of this group: (1) a short body; (2) reduce and fused hip bones; (3) five elongate toes; (4) a long neck; (5) large head with pointed jaws; (6) three short digits and an elongate fourth finger supporting the wing membrane; (7) the presence of the pteroid bone, attached to the wrist and suporting the anterior flight membrane; (8) the presence of a prepubic bone, attached to the pelvis; and (9) an stiffed tail with elongate zygapophyses and chevrons (Benton, 2014). Most basal taxa are grouped into the paraphyletic 'Rhamphorhynchoidea', while the most diverse ones within the clade Pterodactyloidea, which first occurred in the Middle Jurassic of China with *Kryptodrakon progenitor* Andres *et al.*, 2014 and Russia (Barrett *et al.*, 2008; Andres *et al.*, 2014). By the Late Jurassic, pterosaurs were already well diversify, with at least 40 species, with a worldwilde distribution except in Australia (Barrett *et al.*, 2008).

The clade Dinosauria is undoubtably one of the most successful vertebrate clades that have ever existed: their time range spans over 230 Myr, they have a worldwide distribution, reached all the ecosystems, and they dominated terrestrial environments for most of the Mesozoic Era. They are among the best-known and most intensively studied fossil groups, thanks to the famous fossils they provided around the world (*Tyrannosaurus rex* Osborn, 1905 is most likely the only non-human species known by its specific name and not only the generic one), and are so among the best-known and most intensively studied groups. The name was coined by Owen (1842), and their monophyly is well supported (Nesbitt, 2011 and references therein), even though relationships inside the group has been recently debated (Baron *et al.*, 2017; Langer *et al.*, 2017) by peculiar synapomorphies: (1) the supratemporal fossa anteriorly located to the supratemporal fenestra, suggesting enlarged attachment sites for a strong temporal musculature acting on the jaw; (2) postaxial anterior cervical vertebrae with epipophyses; (3) the apex of the deltopectoral crest situated at a point corresponding to more than 30% down the length of the humerus; (4) the radius is shorter than 80% of humerus length; (5) proximal articular surfaces of the ischium with the ilium and the pubis separated by a large concave surface; (6) an asymetric crest-like fourth trochanter, the distal margin forming a steeper angle to the shaft; (7) cnemial crast arcs anterolaterally; (8) distinct proximodistally oriented ridge present on the posterior face of the distal end of the tibia; (9) distinct proximodistally oriented ridge present on the posterior face of the distal end of the tibia; (10) proximal articular facet for fibula of the astragalus occupies less than 30% of the transverse width of the element; and (11) concave articular surface for the fibula of the calcaneum (Nesbitt, 2011 and references therein; Brusatte, 2012; Fastovsky & Weishampel, 2016; Naish & Barrett, 2016). An extenvely perforated acetabulum has usually been considered as a synapomorphy of dinossaurs (Bakker & Galton, 1974; Juul, 1994; Fraser, 2002; Benton, 2004; Brusatte, 2010, 2012; Fastovsky & Weishampel, 2016; Naish & Barrett, 2016; Norman *et al.*, 2017), however the states of character for this feature are conflicted across archosaurian taxa and the ventral margin of the illium is prefered, even though this character becomes ambigous (Nesbitt, The early evolution of archosaurs: relationships and the origin of major clades, 2011).

If the origin of dinosaurs remains unclear (Brusatte *et al.*, 2010; Langer *et al.*, 2010), footprints attributed to *Prorotodactylus* Ptaszyński 2000 from the early Olenekian of Poland exhibit morphologies closely matching the feet synapomorphies of the earliest dinosaurs and their close relative (Brusatte *et al.*, 2010; Brusatte, 2012, 2018; Fastovsky & Weishampel, 2016). Those footprints suggest that the dinosauromorph lineage dawn was few millions years after the Permo-Triassic mass extinction, and could have been part of its recovery (Brusatte *et al.*, 2010) contrary to what had been previously suggested (Benton, 2004). The earliest unquestionnable dinosaur occurrences are the theropod *Eodramus murphi* Martinez *et al.*, 2011 and the sauropodomorph *Eoraptor lunensis* Sereno *et al.*, 1993, from the upper Carnian Ischigualasto Formation, in Argentina (Martinez *et al.*, 2011). By the end of Carnian, dinosaurs already starts to diversify in Argentina with the three major clade present: the ornistichian *Pisanosaurus mertii* Casamiquela, 1967, the sauropodomorphs *Panphagia protos* Martinez & Alcober, 2009 and *Chromogisaurus novasi* Ezcurra, 2010, and the theropods *Herrerasaurus ischigualastensis* Reig, 1963 and *Sanjuansaurus gordilloi* Alcober & Martinez, 2010 (Sereno, 1999; Martinez *et al.*, 2011; Fastovsky & Weishampel, 2016; Naish & Barrett, 2016; Brusatte, 2018). However, scattered material from the upper Anisian Manda beds, in Tanzania, has been attributed to *Nyasasaurus parringtoni* Nesbitt *et al.*, 2013 and described as either the earliest dinosaur or the sister-group of Dinosauria (Nesbitt *et al.*, 2013), and has even been recovered as a derived sauropodomorph by some authors (Baron *et al.*, 2017).

The occurences suggest that dinosaurs were scarce in the Early-Late Triassic (Benton, 2004), but had gradual ascent in diversity and size during the Carnian-Norian transition, which witnessed small extinction event (Irmis, 2010; Martinez *et al.*, 2011), before ultimately dominating terrestrial ecosystems in the Early Jurassic (Brusatte *et al.*, 2010; Langer *et al.*, 2010), setting the real start of the "Age of Dinosaurs" (Brussate, 2012, 2018; Fastovsky & Weishampel, 2016). Even though less diverse than the Early and Late Cretaceous, the Late Jurassic has been called the "Golden Age of Dinosaurs" and most of emblematic dinosaurs (the gigantic sauropods, the stegosaurs, the allosaurs, and the first birds) have been described in this age (Weishampel *et al.*, 2004). The apparent low diversity in the Middle Jurassic compared to the incredible one observed in the Late Jurassic and the fact that the Cretaceous was not yet fully studied by the end of the 19th, when people started thinking about a "golden age", could explain this enthousiam (Weishampel *et al.*, 2004; Fastovsky & Weishampel, 2016). Late Jurassic faunas are well known thanks to dinosaurs from the Morrison Formation in North America, which has been extenvely studied thanks to the rivalty between Edward Drinker Cope and Othniel Charles Marsh during their "Bone War", the Tendaguru beds in Tanzania, which produced notably a specimen of *Giraffatitan brancai* (Janensch, 1914) recognized by one of the largest and the tallest mounted skeleton in the world nowadays, localities China and England, and the Lourinhã Formation, in Portugal.

Despite the gigantic size they could reach, dinosaurs are still concerned by microvertebrates studies, VMAs are commonly composed by bone fragments, eggshells, and especially teeth that provide a good sample for identification helpful for diversities analyses of the paleoenvironments (Carrano & Velez-Juarbe, 2006; Buscalioni *et al.*, 2008, 2018; Oreska, *et al.*, 2013; Hendrickx & Mateus, 2014; Moreno-Azanza *et al.*, 2014, 2015; Hendrickx *et al.*, 2015; Carrano *et al.*, 2016; Gerke & Wings, 2016; Gasca *et al.*, 2017; Malafaia *et al.*, 2017).

1.3. Microvertebrates from the Late Jurassic of Portugal

The Late Jurassic of Portugal has proven to be very productive for vertebrates (*Table 1*; Figure 11), notably in microvertebrates as illustrated by the Guimarota Mine (Martin & Krebs, 2000). As shown before, the Late Jurassic seems to be a critical period for evolution of many vertebrate clades and at this time, Portugal was in the center of North Atlantic rifting (Mateus *et al.*, 2017), meaning that it was a region where variances occurred. This phenomenon is known to be decisive for the emergence of new lineages by the creation of a barrier between two populations and gene flow (Albert & Carvalho, 2011; Gutiérrez *et al.*, 2014). However, VMAs from the Late Jurassic as scarce and are mostly located in the Morrison Fm., in US (Carrano & Velez-Juarbe, 2006 and reference therein), meaning that any data provided by any sites could bring to the light new insights on systematics and paleobiogeography of Europe.

In other words, Portugal, because of its paleogeographical location and the quality of its outcrop, is key place for the study of microvertebrates in the Late Jurassic. Unfortunately, as in the rest of the world, these have been neglected in profit of bigger vertebrates, as dinosaurs. On top of that, studying the diversity outside the range of the Guimarota Mine may allow to give a better understanding on the paleoenvironments and paleoecosystems of Portugal during the Late Jurassic.

Table 1: List of vertebrate species found in the Late Jurassic of Portugal according their taxonomic groups (data compiled from Zinke, 1998; Martin & Krebs, 2000; Rauhut, 2001, 2003; Martin, 2002, 2013, 2015; Antunes & Mateus, 2003; Balbino, 2003; Kielan-Jaworowska *et al.*, 2004; Kriwet, 2004; Weichmann, 2004; Gao & Brinkman, 2005; Escaso *et al.*, 2007, 2014; Mateus, 2006, 2007; Ortega *et al.*, 2006; Mateus *et al.* 2009, 2014; Schwarz-Wing *et al.*, 2009, 2017; Mannion *et al.*, 2013; Escaso, 2014; Hendrickx & Mateus, 2014; Mocho *et al.*, 2014; Caldwell *et al.*, 2015; Boas, 2016; Malafaia *et al.*, 2017, 2018; and references therein).

- **Chondrichthyes Huxley, 1880**
  - Euselachii Hay,1902
    - Hybodontidae Owen, 1864
      - *Hybodus* sp. Agassiz, 1837
      - *Hybodus lusitanicus* (Kriwet, 2004)
      - *Hybodus* cf. *reticulatus* Agassiz, 1837
    - Acrodontidae Casire, 1959
      - *Asteracanthus biformatus* Kriwet, 1995
  - Neoselachii Compagno, 1977
    - Family incertae sedis
      - Neoselachii indet.
    - Scyliorhinidae Gill, 1852
      - Scyliorhinidae indet
    - Batoidae Compagno, 1973
      - *Leiribatos alienus*
      - Batoidae indet.
- **Actinopterygii Klein, 1885**
  - Pycnodontiformes Berg, 1937
    - Pycnodontidae Agassiz, 1833
      - *Macromesodon* sp. Blake 1905
      - *Coelodus* sp.Heckel, 1854
  - Holostei Müller, 1846
    - Semionotidae Woodward, 1890
      - *Lepidotes* sp. 1 Agassiz, 1833
      - *Lepidotes* sp. 2
    - Ionoscopidae Lehman 1966
      - Ionoscopidae indet.
    - Macrosemiidae Thiollière, 1858
      - Macrosemiidae indet.
    - Caturidae Owen, 1860
      - cf. *Caturus* Agassiz, 1834
      - Caturidae indet.
  - Teleostei Müeller, 1846
    - Pachycormidae Woodward, 1895
      - Pachycormidae indet.
- **Amphibia Linné, 1758**
  - Allocaudata Fox & Nayler, 1982
    - Albanerpetontidae Fox & Nayler, 1982
      - *Celtedens guimarotae* Weichmann, 2004
      - Albanerpetontidae indet.
  - Caudata Oppel 1811

Family incertae sedis
cf. *Marmorerpeton* Evans *et al.*, 1988
Anura Rafinesque, 1815
Discoglossidae Günther *et al*., 1858
Discoglossidae indet.
Mammaliaformes Rowe, 1988
Docodonta Kretzoi, 1946
Docodontidae Simpson, 1929
Haldanodon exspectatus Kühne & Krusat, 1972
Mammalia Linnée, 1758
Multituberculata Cope, 1884
Paulchoffatiidae Hahn, 1969
Bathmochoffatia hapax Hahn & Hahn, 1998
Guimarotodon leiriensisi Hahn, 1969
Henkelodon naias Hahn, 1977
Kielanodon hopsoni Hahn, 1987
Kuehneodon barcasensis Hahn & Hahn, 2001
Kuehneodon dietrichi Hahn, 1969
Kuehneodon dryas Hahn, 1977
Kuehneodon guimarotensis Hahn, 1969
Kuehneodon hahni Antunes, 1998
Kuehneodon simpsoni Hahn, 1969
Kuehneodon uniradiculatus Hahn, 1978
Kuehneodon sp. Hahn, 1969
Meketibolodon robustus (Hahn, 1978)
Meketichoffatia krausei Hahn, 1993
Meketichoffatia sp. Hahn, 1993
Paulchoffatia delgadoi Kühne, 1961
Paulchoffatia sp. Kühne, 1961
Plesiochoffatia peparethos (Hahn & Hahn, 1998)
Plesiochoffatia staphylosi (Hahn & Hahn, 1998)
Plesiochoffatia thoas (Hahn & Hahn, 1998)
Pseudobolodon krebsi Hahn & Hahn, 1994
Pseudobolodon oreas Hahn, 1977
Pseudobolodon sp. Hahn, 1977
?*Pseudobolodon* sp.
Renatodon amalthea Hahn, 2001
Xenachoffatia oinopion Hahn & Hahn, 1998
Paulchoffatiidae indet. 1
Paulchoffatiidae indet. 2
Paulchoffatiidae indet. 3
Paulchoffatiidae indet. 4
Paulchoffatiidae indet. 5
Paulchoffatiidae indet. 6
Paulchoffatiidae indet. 7
Albionbaataridae Kielan-Jaworowska & Ensom, 1994
Proalbionbaatar plagiocyrtus Hahn & Hahn, 1998
Dryolestida Prothero, 1981
Dryolestidae Marsh, 1879
Dryolestes leiriensis Martin, 1999
Guimarotodus inflatus Martin, 1999
Krebsotherium lusitanicum Martin, 1999
Dryolestida incertae sedis
Paurodontidae Marsh, 1887
Henkelotherium guimarotae Krebs, 1991
Drescheratherium acutum Krebs, 1998
Amphitheriida Prothero, 1981
Zatheria McKenna, 1975
Nanolestes drescherae Martin, 2002
Nanolestes krusati Martin, 2002

- **Testudines Batsch, 1788**
    - Paracryptodira Gaffney, 1875
        - Pleurosternidae Cope, 1868
            - Pleurosternidae indet. 1
            - Pleurosternidae indet. 2
            - *Selemys lusitanica* Pérez-Garcia & Ortega, 2011
    - Eucryptodira Gaffney, 1975
            - *Hylaeochelys kappa* Pérez-Garcia & Ortega, 2014
        - Plesiochelydae Bau, 1888
            - *Plesiochelys* sp. Rütimeyer, 1873
            - *Tropidemys* sp. Rütimeyer, 1873
            - *Craspedochelys choffati* (Sauvage 1897-1898)
            - *Craspedochelys* sp. Rütimeyer, 1873
    - Pleurodia Cope, 1870
        - Platychelyidae Bräm, 1965
            - *Platychelys* sp. Wagner, 1853
- **Rhynchocephalia**
    - Sphenodontia
        - Opisthodontia Apesteguia & Novas, 2003
            - *Opisthias* sp. Gilmore, 1905
- **Squamata Oppel, 1811**
    - Scincomorpha Camp, 1923
        - Paramacellodidae Estes 1983
            - *Becklesius hoffstetteri* (Seiffert, 1973)
            - *Paramacellous* sp.
        - Scincoidea Oppel, 1811
            - *Saurillodon proraformis* (Seiffert, 1973)
            - *Saurillodon ?henkeli* (Seiffert, 1973)
            - *Saurillodon* cf. *obtusus* (Owen, 1850)
        - Scincomorpha indet.
    - Anguimorpha Fürbringer 1900
        - Family incertae sedis
            - *Dorsetisaurus pollicidens* (Seiffert, 1973)
    - Serpentes Linnaeus, 1758
            - *Portugalophis lignites* Caldwell *et al.*, 2015
- **Choristodera Cope, 1884**
        - Cteniogenidae Seiffert, 1973
            - *Cteniogenys.* sp Gilmore, 1928
- **Crocodyliformes Benton & Clark, 1988**
    - Mesoeucrocodylia Whetstone & Whybrow, 1983
        - Family incertae sedis
            - *Lisboasaurus estesi* Seiffert, 1973
            - *Lusitanisuchus mitracostatus* (Seiffert, 1970)
    - Neosuchia, Benton & Clark, 1988
        - Goniopholididae Cope, 1875
            - *Goniopholis baryglyphaeus* (Schwarz, 2002)
        - Atoposauridae Gervais 1871
            - *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005)
        - Bernissartidae Dollo, 1883
            - *Bernissartia* sp. Dollo, 1883
        - Teleosauridae Cope, 1871
            - *Machimosaurus hugii* von Meyer, 1837
- **Pterosauria Kaup, 1834**
    - Rhamphorhynchoidea Plieninger, 1901
        - Rhamphorhynchidae Seeley, 1870
            - aff. *Ramphorhynchus* v. Meyer 1847
            - Ramphorynchinae indet.
    - Pterodactyloidea Plieninger, 1901
        - Family incertae sedis
- **Dinosauria Owen ,1842**

- Sauropoda Marsh, 1878
  - Eusauropoda incertae sedis Upchurch, 1995
    - *Zby atlanticus* Mateus *et al.*, 2014
  - Camarasauridae Cope, 1877
    - *Lourinhasaurus alenquerensis* (de Lapparent & Zbyszewski, 1957)
  - Brachiosauridae Riggs, 1904
    - *Lusotitan atalaiensis* (de Lapparent & Zbyszewski, 1957)
    - Brachiosauridae indet.
  - Diplodocidae Marsh, 1884
    - *Supersaurus lourinhanensis* (Bonaparte & Mateus, 1999)
- Theropoda Marsh, 1881
  - Family incertae sedis
    - *Lourinhanosaurus antunesi* Mateus, 1998
    - Tetanurae indet.
  - Ceratosauridae Marsh, 1884
    - *Ceratosaurus dentisulcatus* Madsen & Welles, 2000
  - Abelisauridae Bonaparte & Novas, 1985
    - Abelisauridae indet.
  - Megalosauroidea Fitzinger, 1843
    - *Torvosaurus gurneyi* Hendrickx & Mateus, 2014
    - Megalosauroidae indet.
  - Allosauroidae Marsh, 1878
    - *Allosaurus fragilis* Marsh, 1877
    - *Allosaurus europaeus* Mateus *et al.*, 2006
    - *Allosaurus* sp.
    - Allosauroidea indet.
    - Carcharodontosauria indet.
  - Tyrannosauroidea
    - *Aviatyrannis jurassica* Rauhut, 2003
    - Tyrannosauroidea indet. 1
    - Tyrannosauroidea indet. 2
  - Compsognathidae Cope, 1871
    - cf. *Compsognatus* sp. Wagner, 1861
  - Aviale Gauthier, 1986
    - cf. *Archaeopteryx* sp. Von Meyer, 1861
  - Dromeosauridae
    - cf. *Dromeosaurus* sp. Matthew & Brown, 1922
    - cf. *Richardoestesia* sp. Currie *et al.*, 1990
    - *Richardoestesia* aff. *R. gilmorei* Currie *et al.*, 1990
    - Dromeosauridae indet. 1
    - Dromeosauridae indet. 2
  - Troodontidae Gilmore, 1924
    - *Paronychodon* sp. Cope, 1876
    - Troodontidae indet.
- Ornitischia Seeley, 1887
  - Stegosauridae Marsh, 1880
    - *Dacentrurus armatus* Owen, 1875
    - *Miragaia longicollum* Mateus *et al.*, 2009
    - *Stegosaurus* cf. *ungulatus* Marsh, 1877
  - Nodosauridae Marsh, 1890
    - *Dracopelta zbyszewskii* Galton, 1980
  - Neornithischia incertae sedis.
    - *Alocodon kuehnei* Thulborn, 1975
    - *Trimucrodon cuneatus* Thulborn, 1975
  - Hypsilophodontidae Dollo, 1882
    - *Phyllodon henkeli* Thulborn, 1973
    - *Hypsilophodon* sp. Huxley, 1869
  - Dryosauridae Milner & Norman, 1984
    - aff. *Dryosaurus* Marsh, 1894
    - *Eousdryosaurus nanohallucis* Escaso *et al.*, 2014

Dryosauridae indet. 1
Dryosauridae indet. 2
Ankylopollexia Sereno, 1986
Draconyx loureiroi Mateus &Antunes, 2001
Ankypollexia indet. 1
Ankypollexia indet. 2
Ankypollexia indet. 3

1.3.1. THE GUIMAROTA MINE

Portugal provided one of the richest vertebrate microfossil assemblages in the world for the Late Jurassic: the Guimarota mine, which could be considered as a "Konzentrat-Lagerstätte" because of the high concentration of microfossil remains found (Seilacher, 1970; Martin, 2000). Although the exact age of Guimarota mine is a matter of debate, it is considered as part of Alcobaça Formation, which is Kimmeridgian in age (Schudack, 2000).

The Guimarota mine is an old Jurassic brown coal mine which was still being mined in late 1950s, near the town of Leiria in Portugal. The first paleontological prospecting started in the spring of 1960, during which several remains of early mammals have been found by Kühne and his team (Krebs, 2000) until the closure of the mine because of economic reasons. This led to the discovery of huge sample of mammal jaws and teeth fragments, allowing the mine to be the richest Late Jurassic mammal locality (Kielan-Jaworowska *et al.*, 2004), but the mine is also rich in fishes, amphibians, and reptiles. Another mining campaign took place for ten years during the 70s, under Krebs' supervision. It brought even more isolated teeth and jaws, with sometimes complete skeleton from such diverse taxa as amphibians, mammals, turtles, lizards, crocodyliforms, pterosaurs, fishes, and dinosaurs (Martin & Krebs, 2000).

The Guimarota mine is one of the richest fossil Lagerstätten in the world for microvertebrates from the Late Jurassic (Martin, 2000), and it is the one of the few documented localities for this kind of fossils in Portugal. It provided a substantial number of specimens from different taxa, mainly mammalian material, which were the main interest of Krebs' team. Guimarota mine seems to present a terrestrial to lagoonal environment ecosystem with occasional freshwater influx and salt water flooding (Martin, 2000; Schwarz *et al.*, 2017), underlining its importance for paleobiogeography and evolution of terrestrial microvertebrates. Indeed, other microvertebrate localities of this age from Morrison Formation seem to have been swamps, small lakes, and shallow ponds (Carrano & Velez-Juarbe, 2006), as well as a permanent water source (Foster & Heckert, 2011).

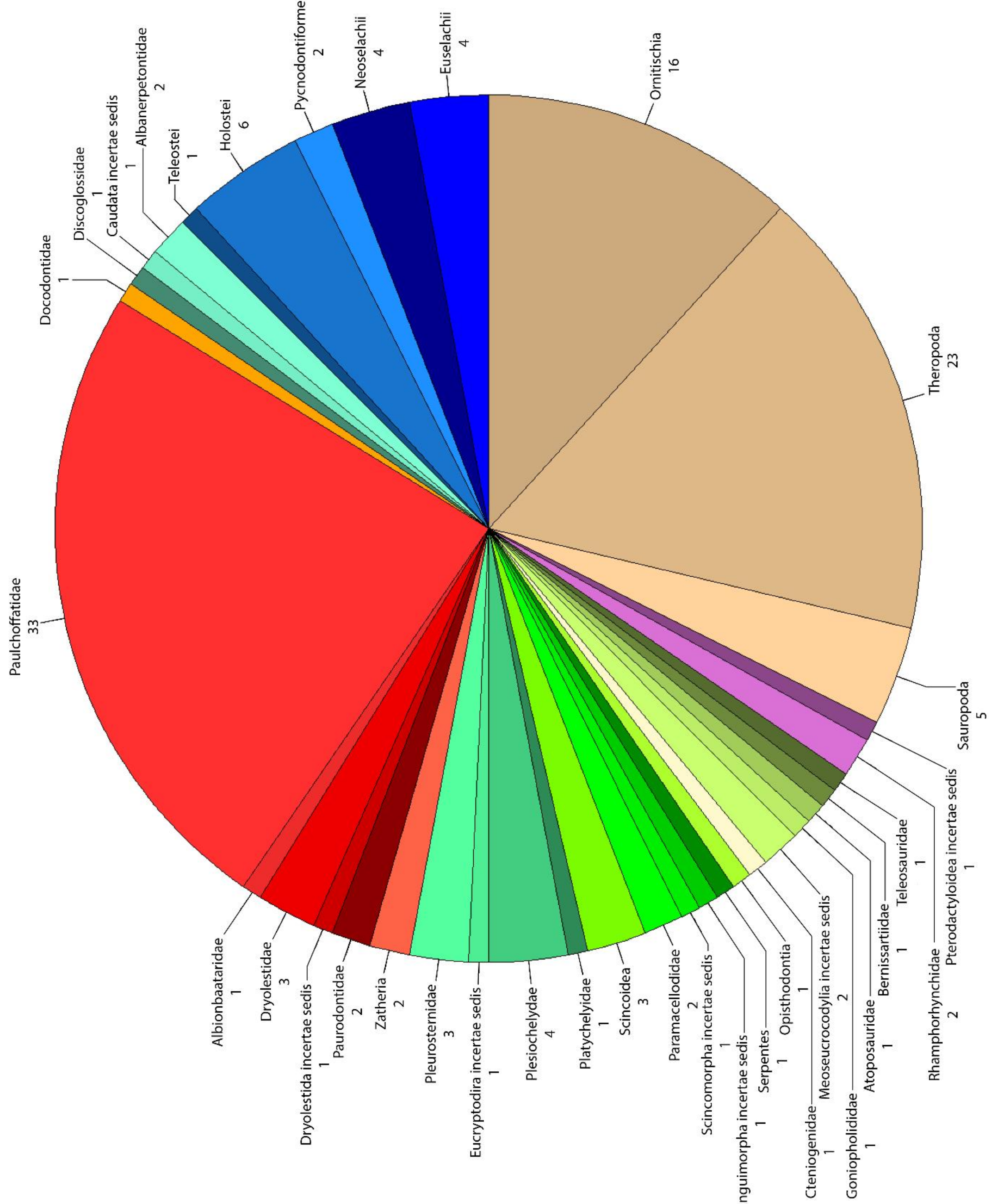

Figure 11: Number of species in the main vertebrate taxonomic clades found in the Upper Jurassic of Portugal, sorted according their respective phylogenetic positions. Blue colors refer to “fishes”, blue-greenish to amphibians, orange to mammaliaforms non-mammals, red to mammals, turquoise to turtles, light green colors to squamates, light kaki to choristoderes, dark green colors to crocodylomorphs, purple to pterosaurs, and beige to dinosaurs (according data from Table 1 and references used). Dinosaurs have been sorted according the three main clades because of their high diversity, which has already been well studied in Portugal. “Fishes” have been sorted according their main groups (separating chondrichthyans and actinopterygians) because their phylogenetic and taxonomic assessment can be highly debatable.

1.3.2. FISHES

Even though it is considered as a grade (a non-monophyletic clade) and has no systematic value, the word “fish” will be use in this section to refer to any non-tetrapod marine vertebrate. The fish fauna from Guimarota mine is similar to other faunas observed from the Late Jurassic of Europe, representing a relative broad spectrum despite the poor preservation of most of the specimens preventing a generic level assessment (Kriwet, 2000). Chondrichthyans, rarer than in contemporaneous localities, are known by isolated teeth, scales, and head- and fine-spines, mainly hybodont, including the large-size species *Asteracanthus biformatus* or the endemic *Hybodus lusitanicus*, but also few neoselachians, notably early-form rays (Kriwet, 2000, 2004). Hybodont teeth and spines have been also recovered from the Lourinhã Fm., but remains scarce (Balbino, 2003). On top of teeth and scales, some undetermined bones attributed to osteichthyians, mainly holosteans, have also been recovered from the Guimarota mine, including isolated skull bones attributed to *Lepidotes*, one fragmentary articulated skull attributed to Caturidae, and small teleosts vertebral centra (Krebs, 2000).

1.3.3. AMPHIBIANS

The Guimarota mine provided the highest number of isolated amphibians fragments from a single locality, with more than 9,000, making them one of the best represented taxonomic groups. Most of these fragments are from albanerpetonids, whose frontals share similarities with the genus *Celtedens* (Wiechmann, 2000), and have been later described as a new species *Celtedens guimarotae* Wiechmann, 2004, for which remains have been also recorded from Porto Dinheiro (Wiechmann, 2004). Remains have also been recovered from Porto das Barcas, but the absence of diagnostic features only allowed identification as an unidentified albanerpetontid, even though the proximity of Guimarota and Porto Dinheiro would suggest they also are from *C. guimarotae* (Wiechmann, 2004).

Stem salamander remains attributed to cf. *Marmorerpeton* Evans *et al.*, 1998 from Guimarota have been recovered (Kühne, 1968; Milner, 1994; Evans & Milner, 1996; Wiechmann, 2000), as well as discoglossid material (Wiechmann, 2000), but no extensive studies on this material seems to have been carried.

1.3.4. MAMMALIAFORMS AND MAMMALS

Works on the material from the Guimarota mine focused mainly on mammals (Lillegraven & Krusat, 1991; Martin & Krebs, 2000; Martin, 1997,2002, 2005, 2013, 2015; Schwarz, 2002; Ruf *et al.*, 2009; Luo *et al.*, 2012), mostly because they constitute by far the most diverse taxonomic group observed in this vertebrate microfossil assemblage (Figure 11). Four orders of Mesozoic mammals have been described from the Guimarota mine: the Docodonta, the Multituberculata (both extinct), the Dryolestida and the Zatheria (both closely-related to the Theria). Specimens are mainly known from teeth and jaws. The mammalian fauna seems to be endemic, with lack of triconodontids, spalacotherrids, and tinodontids, usually common in the Early Cretaceous of Europe, but also in the Morrison Formation (Kielan-Jaworowska *et al.*, 2004).

The docodonts are represented only by *Haldanodon exspectatus* Kühne & Krusat, 1972, which provided around ten skulls and even one partially preserved skeleton. The characters observed suggest that *H. expectatus* would have been a ground dweller (Martin & Nowotny, 2000). The teeth exhibit a complex structure but lack the basal tricuspid of the Theria, confirming that this taxon represents a lineage which developed a complex pattern in its molars independently from the lineage leading to current mammals (Martin & Nowotny, 2000).

The multituberculates are an extinct group of mammals, known from the Jurassic to the Oligocene, and considered as one of the most successful and diverse mammals group known (Agustí & Antón, 2002). In the Guimarota Mine, they are represented mainly by members of Paulchoffatiidae, which is the oldest known family of this order (Hahn & Hahn, 2000). The large eye socket found in all preserved specimen suggest a nocturnal lifestyle, and their olfactory lobes in the brain (the relatively largest known within mammals) suggest their olfaction was well developed. No post-cranial remains have been found nor identified from the Guimarota mine, and no skull have been found in association with lower jaw (Hahn & Hahn, 2000; Martin, 2015).

With around 500 jaws and skull remains and one almost complete skeleton, eupantotheres are the most common mammalian group found in the Guimarota mine (Martin, 2000). While they can be described as one of the ancestral groups of modern mammals, eupantotheres teeth structures lack the protocone in the molar of the upper jaw, making this group pre-tribosphenic mammals (Martin, 2000). In the Guimarota mine, they are represented by the Dryolestidae and the Paurodontidae. Dryolestids can be identified by a mesio-distally shortened and labio-lingually broadened molar. The specimen in the Guimarota mine are the second youngest after two isolated molars of the lower jaw from the Late Bathonian of England (Martin, 2000). In Guimarota, dryolestids are only known from teeth, jaws and a fragmented skull.

The Paurodontidae are mainly represented by two henkelotheriids species. They are less abundant than dryolestids and exhibit molars as long as wide (Krebs, 2000). *Henkelotherium guimarotae* Krebs, 1991 is based on an almost complete skeleton, which make it not only one of the most remarkable specimens found in the Guimarota mine but also the first articulated mammal skeleton from the Late Jurassic ever discovered (Krebs, 2000). This precious specimen gives a glimpse into what the level of organization of mammals was 150Myr ago, corresponding to the base of the radiation of the Theria. The study of its skeleton suggests *H. guimarotae* was a small insectivorous animal, with an arboreal lifestyle (Krebs, 2000). On the opposite extreme, *Drescheratherium acutum* Krebs, 1998 is only known from isolated upper and lower jaws with their dentition. Its main characteristic is the large, pointed, needle-like canine in the upper jaw (Krebs, 2000).

1.3.5. TURTLES

Late Jurassic turtles are known in Portugal since the middle of the 19th century (Ribeiro & Sharpe, 1853). All species and specimens reported since then have been attributed to Testudines. From the Guimarota mine, isolated and fragmentary bony elements of the shell and postcranial remains have been discovered (Gassner, 2000). They have been attributed to an undertermined pleurosternid (de Lapparent de Broin, 2001; Pérez-García *et al*., 2008), and to *Platychelys* sp. (de Lapparent de Broin, The European turtle fauna from the Triassic to the Present, 2001), which is the only occurrence of Platychelyidae, a pleurodire family, in the Upper Jurassic of Portugal. An undetermined pleurosternid has also been reported in Porto das Barcas, in the Praia Azul member of the Lourinhã Formation (de Lapparent de Broin, 2001; Ortega, 2009), and *Selemys lusitanica* in both Santa Rita and Praia de Caniçal, respectively from the Porto Novo-Praia de Amoreira and Praia Azul members of the Lourinhã Formation (Pérez-García & Ortega, 2011; Boas, 2016).

Hylaeochelys kappa, a basal eucryptodire, has also been reported in Porto Barril, in the Freixal mb. (Pérez-García & Ortega, 2014), and in Praia de Caniçal (Boas, 2016). The eucryptodire family Plesiochelyidae is the most diverse one with: *Plesiochelys* sp. from Porto das Barcas (Boas, 2016) and Ulsa, in the Freixial mb. of the Lourinhã Formation (Pérez-García *et al.*, 2008); *Craspedochelys* sp. from São Romão, in the Alcobaça Formation (de Lapparent de Broin *et al.*, 1996; de Lapparent de Broin, 2001), and Praia Azul (Boas, 2016); *Craspedochelys choffati* from Vila Franca do Rosário, in the Freixal mb. (Sauvage, 1897-1898; Pérez-García, 2012); and *Tropidemys* sp. from Praia Azul (Pérez-García, 2015).

1.3.6. LEPIDOSAURS

Sphenodontian cranial material, attributed to *Opisthias*, has been reported from Andrés, establishing the first evidence of this group in the Late Jurassic of the Iberian Peninsula, contemporaneously with material found in North America and England (Ortega, 2009; Malafaia, *et al.*, 2010).

Guimarota provided derived lacertilians with some Scincomorpha and early Anguimorpha, but not the more basal Iguania nor Gekkota (Broschinski, 2000). This distribution is consistent with other Mid-Jurassic localities in England, but not with the assumptions made according to the phylogenetic reconstruction which suggests that iguanians and gekkotans should already have been diversifed at this point (Evans, 1998a). The high number of fragments found allows evaluation of the intraspecific variability, in particularly in growth sequence (Broschinski, 2000). Several genera have been identified among the Guimarota remains.

Saurillodon Estes, 1983 is the most abundant taxon and it is represented by many jaws, more or less complete, rarely in association with vertebrae or limb bone remains. The level of preservation in certain specimens allowed the description of several main characters and confirms the burrowing style of life of the taxon, marking the evolution of a worm-like body (Broschinski, 2000).

The Paramacellodidae *Becklesius* Estes, 1983 is the second most abundant taxa found in the Guimarota remains (almost as abundant as *Saurillodon*), represented notably by two very well preserved associated specimens. No osteoderms related to preserved associated specimen have been found, bringing into question the completely body armor as a synapomorphy of the Paramacellodidae (Broschinski, 2000), as it has been proposed.

The Paramacellodidae *Paramacellodus* Hoffstetter, 1967 had been described from the Guimarota Mine later after the last excavation, after a revision of fragments referred to *Saurillus obtusus* Owen, 1855 (Broschinski, 2000). Its characteristics could suggest that it is a new species of this genus, but that needs more investigation and comparison with material from the Morrison Formation (Evans & Chure, 1998; Broschinski, 2000). Because of the differences between its teeth and the one observed in *Becklesius* specimens, *Paramacellodus* could be from another habitat not too far from the Guimarota ecosystem (Broschinski, 2000). Other material referred to *S. obtusus* represents indeterminate scincomorphs, mostly toothless jaws for which some of them show a tooth replacement pattern (Broschinski, 2000).

Dorsetisaurus Hoffstetter, 1967 is represented by several fragmented maxilla, teeth and parietals (Broschinski, 2000). Teeth are flattened transversally and have an anterior and posterior cutting edge. The most informative squamate found in the Guimarota mine (Broschinski, 2000) is the snake *Portugalophis* Caldwell *et al*., 2015, previously described as *Parviraptor* Evans, 1984 (Caldwell *et al*., 2015). Their occurrence during the Mid-Late Jurassic is coincident with the diversification of other squamate clade and confirm *Portugalophis* as one of the oldest snakes in the world, predated by *Eophis* from Middle Jurassic of Kirlington Cement Work Quarry, and contemporaneous with *Diabolophis* Caldwell *et al*.,1915 from the Morrison Formation (Caldwell *et al*., 2015), which contradict the hypothesis that snakes would have diversified in Gondwana (Evans, 2003).

1.3.7. CHORISTODERES

Fragmentary material from the dentary of *Cteniogenys*, a basal ‘non-neochoristoderes’, has been reported from Guimarota (Seiffert, 1973; Evans, 1990; Gao & Brinkman, 2005; Ortega, 2009; Matsumoto & Evans, 2010), but the material seems to not have been studied or fully described since its first report by Seiffert.

1.3.8. ARCHOSAURS

For now, six crocodylomorphs species have been described in the Late Jurassic of Portugal, mainly from the Guimarota mine (Krebs & Schwarz, 2000), from isloated teeth and skeletal fragments: *Machimosaurus hugii* (Krebs, 1967, 1968; Young *et al*., 2014), *Bernissartia* sp. (Brinkmann, 1989), *Lisboasaurus estesi* (Buscalioni *et al*., 1996), *Goniopholis baryglyphaeus* (Schwarz, 2002), *Lusitanisuchus mitracostatus* (Schwarz & Fechner, 2004) and *Knoetschkesuchus guimarotae* (Schwarz & Salisbury, 2005; Schwarz *et al*., 2017). All these crocodylomorphs occupied specific ecological niches, with different diets that can be assessed by their tooth morphologies (Schwarz *et al.*, 2017).

On top of that, isolated teeth attributed to *L. mitracostatus* have been recovered in the Lourinhã Formation (Schwarz & Fechner, 2004), and one isolated tooth attributed to *M. hugii* has been reported in the Alcobaça Formation (Young *et al.*, 2014). More isolated teeth, cranial, and post-cranial remains from the Alcobaça Formation (Kimmeridgian-Tithonian) have been attributed to *Theriosuchus* sp. and *Goniopholis* sp., but a detailed comparison allowing a more specific assignment of these remains could not be done (Malafaia *et al.*, 2010). However, specimens described as *Theriosuchus guimarotae* Schwarz & Salisbury, 2005 has been since redescribed as *Knoetschkesuchus guimarotae* (Schwarz *et al.*, 2017), and the status of *Theriosuchus* material from Alcobaça Formation has not been reviewed since. The heterodonty is characteristic of *Theriosuchus*, but taxonomic identification based on crocodylomorph teeth is difficult (Young *et al.*, 2016). Crocodylomorph eggs and eggshells from the Lourinhã Formation have been attributed to *Suchoolithus portucalensis* Russo *et al.*, 2017 and *Krokolithes dinophilus* Russo *et al.* 2017, which are the oldest crocodylomorph eggs currently known (Russo *et al.*, 2017). Tracks attributed to a metriorhynchid trackmaker, based on the size and the shape, has been also reported from the Lourinhéa Formation (Mateus & Milàn, 2010).

The Guimarota mine also provided more than 300 isolated pterosaur teeth and some skeletal remains, but no skull elements have been preserved (Wiechman & Gloy, 2000). Teeth have attributed to both *Rhamphorynchus* and Pterodactyloidea, but postcranial remains exhibit features sharing similarities only with Rhamphorhynchinae. The poor preservation of the material precludes a more precise determination (Wiechman & Gloy, 2000). Pterosaur teeth have been also reported in Andrés, with a needle-like morphology and smooth enamel, similar to the ones found in Guimarota and attributed to *Rhamphorynchus* (Malafaia *et al.*, 2010). The Lourinhã and Azóia Formations provided tracks that have been attributed to a pterosaur trackmaker (Mateus & Milàn, 2010), and suggest bigger size pterosaurs would have been present in the area.

The Late Jurassic of Portugal has been productive in dinosaur remains (Antunes & Mateus, 2003) with more than 30 species described, making it one of the richest countries in the world for that period. Most of the fossils are bone remains, including large-size sauropods (Mannion *et al.*, 2013; Mateus *et al.*, 2014; Mocho *et al.*, 2014) and theropods (Hendrickx & Mateus, 2014), exhibiting a shared fauna with the Morrison Formation (Mateus, 2006 ; Mateus *et al*., 2006). On microfossil studies, most of the specimen are from the Guimarota Mine, which provided more than 600 isolated teeth and some rare bone remains representing small animals (Rauhut, 2000). Saurpod are represented by only five teeth and tooth fragments, and teeth have been attributed to the basal ornitischians *Alocodon kuehnei* and *Trimucrodon cuneatus*, the hypsilophodont *Phyllodon henkeli* (Thulborn, 1973). The theropod teeth are the most abundant from Guimarota and have been referred to *Compsognathus*, *Ceratosaurus*, *Richardoestesia* and other unidentified dromeosaurids, *Paronychodon* and another unidentified troodontid, and *Archaeopteryx* (Zinke, 1998; Rauhut, 2000; Wiechman & Gloy, 2000). An almost complete right ilium constitute the only bone remains which could have been attributed at specific level, the tyrannosaurid *Aviatyrannis jurassica*, one of the earliest confirmed occurrence of this family (Rauhut, 2003). Theropod isolated teeth have been commonly found in the Lourinhã Formation (Hendrickx & Mateus, 2014; Hendrickx *et al*., 2015; Malafaia *et al*., 2017). Nevertheless, the Lourinhã Formation is famous across the world for its remarkable theropod nests, some of which preserving embryos (Mateus *et al*., 1997; Castanhinha *et al*., 2009; Araújo *et al*., 2013). The Lourinhã Formation also provided diverse dinosaurs footprints, including therodpod, saurpod, ornithopod, and stegosaur (Mateus & Milàn, 2008, 2010; Mateus *et al*., 2011; Guillaume *et al*., 2017).

1.4. Geological settings

1.4.1. GENERAL CONTEXT OF THE MESOZOIC OF PORTUGAL

The opening of the North Atlantic Ocean, leading to the breakup of the Laurasia while the Gondwana remained a unique landmass, started in the Late Triassic and gradually occurred all over the Jurassic (Kullberg *et al*., 2006; Tucholke *et al*., 2007). During a second episode, in the Late Jurassic-Early Cretaceous, the break-up accelerated (Figure 12), with succesive rifting events allowing ocean floor formation and spreading (Russo, 2016). Because of its position between the proto-Atlantic and the Tethys Sea, the Iberian Plate (Figure 13) was greatly affected by major tectonic events, mainly northward and counterclockwise rotations, that determined its current position (Wilson, 1988; Kullberg *et al*., 2006).

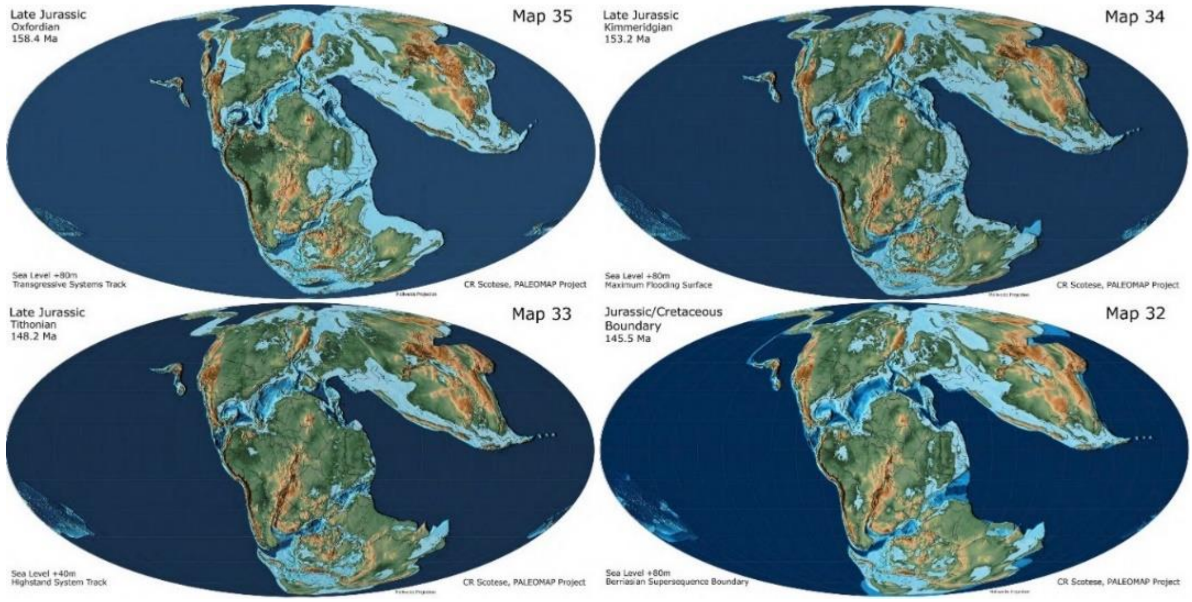

Figure 12: Paleogeographical reconstructions of the Late Jurassic illustrating the opening of the North Atlantic Ocean during this period (from Scotese, 2014).

Dramatic changes in global climates occurred because of the breakup of Pangea and the resultant disruption of ocean currents, volcanic activity, and eustatic sea level fluctuations (Moore *et al*., 1992). The maximum eustatic level was actually reached during the Kimmeridgian, while Iberia was one of the largest islands of the European archipelago system, surrounded by warm, shallow epicontinental sea, with several transgressive/regressive transitions (Moore *et al.*, 1992; Martinius & Gowland, 2011; Myers *et al.*, 2012).

Figure 13: Paleogeography of Europe during the Late Jurassic. Paleomaps from Colorado Plateau Geosystem. Scale bar is 400km.

1.4.2. THE LUSITANIAN BASIN

The Lusitanian Basin (Figure 14) is the largest of Portugal's six sedimentary basins, developing over the western part of the country and extending offshore over 22,000 km² with a maximum sedimentary pile up to 6 km thick (Wilson *et al.*, 1989; Alves *et al.*, 2003). It was formed during the opening of the North Atlantic Ocean, and was filled during four rifting episodes and one major sea floor spreading, spanning from the Late Triassic to Early Cretaceous (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.*, 2017). The third rifting episode, during the late Oxfordian to earliest Kimmeridgian (Mateus *et al.*, 2017), was the most important and culminated in the creation of several complex fault-bounded and diapir-bounded sub-basins (Taylor *et al.*, 2014; Gowland *et al.*, 2017), where most of the bounding faults are following a north-east to south-west Hercynian trend (Martinius & Gowland, 2011).

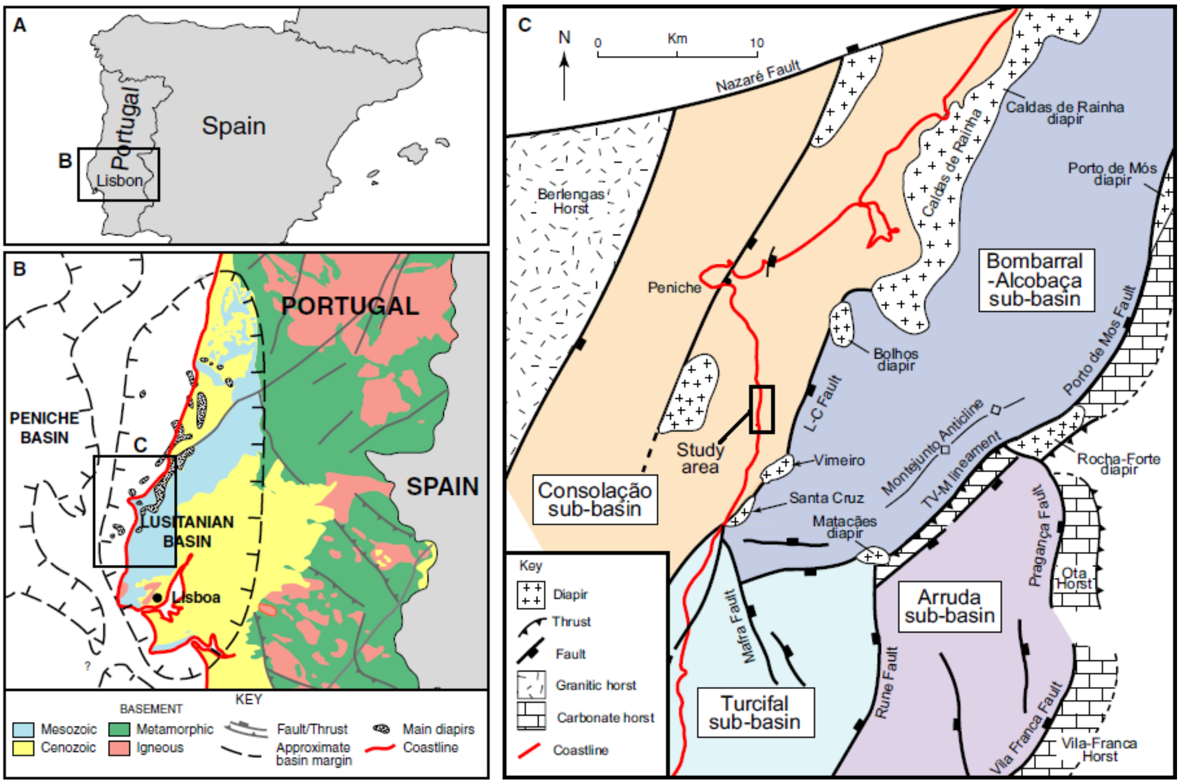

Figure 14: A, overview map of Portugal with the location of the Lusitanian Basin indicated; B, simplified geological map of Portugal showing major basin features; C, map showing the distribution of sub-basins in the Western and Central Lusitanian Basin (modified from Martinus & Gowland, 2011; Taylor *et al.*, 2014, Gowland *et al.*, 2017).

The western part of the Lusitanian Basin is therefore composed by 4 sub-basins: (1) Arruda; (2) Turcifal; (3) Bombarall-Alcobaça; and (4) Consolação (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.*, 2017; Mateus *et al.*, 2017). Their filling started with middle-Oxfordian-aged platform carbonates, forming the Montejunto Formation, followed by a mixed clastic and carbonate basin/shelf, forming the Abadia Fm., that shallows into the terrigenous, largely continental deposit of the Lourinhã Fm. (Leinfelder & Wilson, 1989; Leinfelder, 1993). The Consolação sub-basin, in which the study area is located, is flanked by the Berlengas Horst to the west, the Nazaré Fault to the north, and the north-east trending fault connecting Vimeiro, Bolhos, and Caldas de Rainha diapirs to the east (Martinius & Gowland, 2011; Taylor *et al*., 2014). During the deposition of the Lourinhã Fm., the Lusitanian Basin was situated around 30-35° northern latitudes (Stampfli & Borel, 2002), and its considered paleoclimate was warm, with winter-wet and summer-dry seasonallity (Martinius & Gowland, 2011).

1.4.3. GEOLOGY OF THE LOURINHÃ FORMATION

Figure 15: Geographical locations of the vertebrate microfossil assemblages studied. Scales: Zimbral, 10m; Porto de Barcas, 20m; Valmitão, 50m; Global, 1km. Images from Google Earth (19/06/2016).

This work focused on three localities of the Lourinhã Formation, from North to South: Porto das Barcas, Zimbral, and Valmitão (Figure 15). A specific number has been attributed to each bulk of sediment, specifying the name of the locality, the date it has been collected, and the order it has been processed.

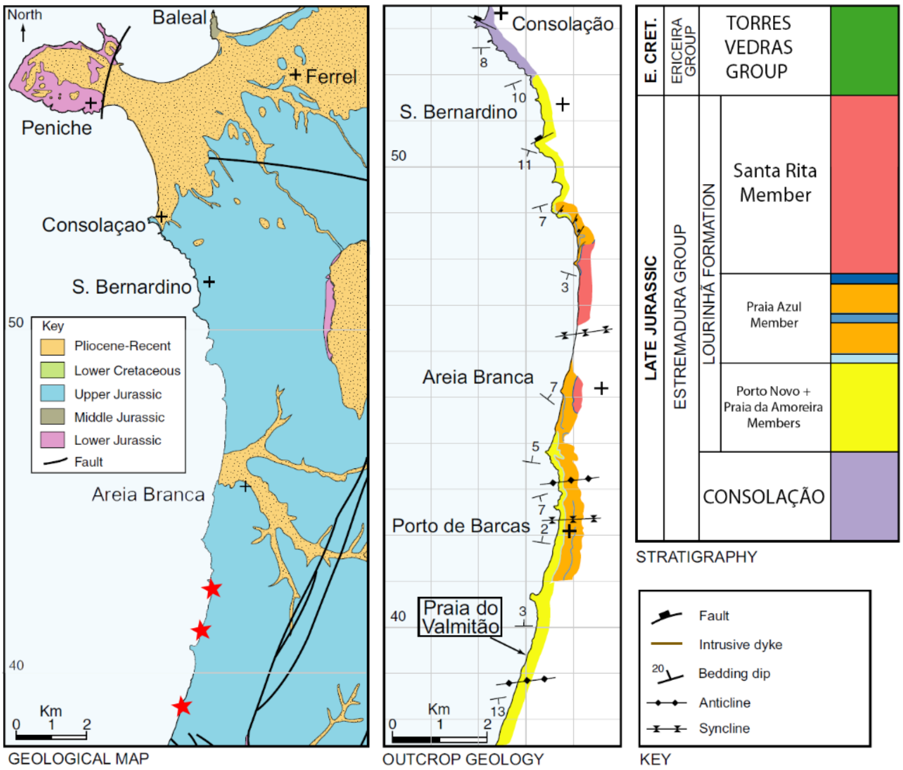

Figure 16: Geological map of the onshore part of the Consolação sub-basin south of Peniche, with the north-south section (modified from Gowland *et al*., 2017) and the corresponding lithostratigraphic framework (based on Mateus *et al*., 2017). The red stars indicate the three localities studied, from North to South: Porto das Barcas, Zimbral, Valmitão.

The Lourinhã Fm. (Figure 16) is named after the local town of Lourinhã, 70 km to North of Lisbon. It is a widely adopted term for the clastic continental succession sediments throughout the Lusitanian Basin, ranging in thickness from 200m to 1,100m (Leinfelder & Wilson, 1989; Wilson *et al*., 1989, Taylor *et al*., 2014). This variation according the paleogeographic position can be explained by the transitionnal/regressive boundaries between the members of the Lourinhã Fm. (Mateus *et al*., 2017). Always considered as Late Jurassic in age, recent studies confirm its age range from Late Kimmeridgian to Late Tithonian, between the Consolação Unit and the Porto da Calada Formation (Taylor *et al*., 2014; Mateus *et al*., 2017). The base of the laterally extensive Lourinhã Fm. is traditionnaly taken as the first significant and sustained development of continental deposits, above either the shallow marine to estuarine sandstones of the Sobral Fm., the oolitic limestone of the Amaral Fm., the shelfal corbonates of the Consulação Unit/Alcobaça Fm., or the shelf to deepwater clastics of the

Abadia Fm. (Taylor *et al.*, 2014). Its dominant continental deposits are sandy channel-fills and contemporaneous muddy floodplain deposits (Martinius & Gowland, 2011; Taylor *et al.*, 2014; Gowland *et al.*, 2017).

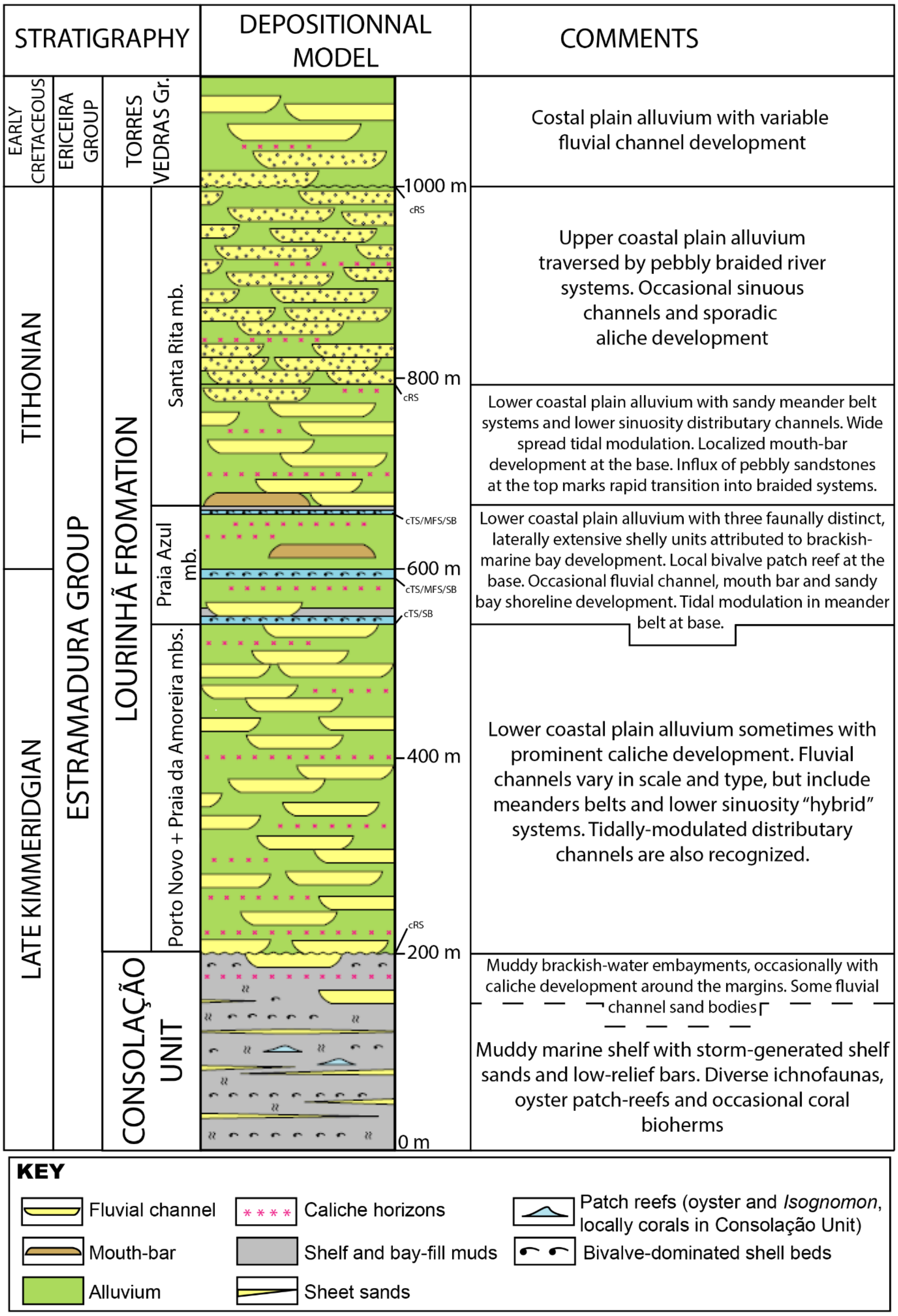

Figure 17: Lithostratigraphic framework of the Lourinhã Formation in the Consolacão sub-basin, showing simplified depositional elements (modified from Martinus & Gowland, 2011, based on Mateus *et al.*, 2017).

Some channels exhibit sedimentary structures suggesting tidal modulation, and lacustrines intervals, mouth-bar developments, crevasse channel/splay deposits, and various floodplain paleosols can also be observed (Hill, 1989; Martinius & Gowland, 2011; Myers *et al*., 2012). Those facies representing braided to sinuous paralic fluvial systems, with distal alluvial fans and upper delta, punctuated by episodes of estuarines and lagoon sediments, with shallow-marine to brackish macrofauna (Mateus *et al*., 2017). Paleocurrent data and regional-scale modelling suggest the main fluvial plain were flowing from the igneous Berlengas Horst toward south to southwest deltaic system (Wilson *et al*., 1989; Mateus *et al*., 2017).

Based on shell beds distributions, change in grain-size, composition, and sedimentary structures, the Lourinhã Fm. can be subdivided into three to four distinct members (Figure 17): (1) the regressive nature of the base, with the Praia da Amoreira and Porto Novo mbs.; (2) three episodes of marine transgressions, with the Praia Azul mb.; and (3) a regressive surface above which interpreted fluvial channel morphologies switch from single-channel to braided systems within the Assenta mb., which has been subdivided by some authors into Areia Branca and Ferrel mbs., the regressive surface being at the base of the Ferrel mb. (Martinius & Gowland, 2011; Taylor *et al*., 2014; Gowland *et al*., 2017, Mateus *et al*., 2017). With the Alcobaça Fm., it is the unit most diverse in vertebrate remains in Portugal, and even in Europe, and studies highlight shared fauna with the Morrison Fm. (Mateus, 2006; Escaso *et al*.; 2007; Lockley *et al*., 2008). The sedimentology of the Lourinhã Fm. suggests a semi-arid climate, in mean temperature range from 16°C to 19°C, with seasonal rainfall lower than 500 mm –wetter conditions than in the Morrison Fm. (Mateus *et al*., 2017).

1.5. Objectives

Vertebrate microfossil assemblages (VMAs) provide a diverse and rich database for paleoecological and systematics studies. The Late Jurassic is a key time in the evolution of modern lineages of small vertebrates, with the first occurrence and the radiation of most of the clades, and Portugal seems to be one of the best spots to focus on the study of VMAs. The objectives of this master thesis are:

- A bibliographic revision of the state of the art of the main microvertebrate clades of the Portuguese Late Jurassic fossil record.
- Sample three VMAs in the Lourinhã Formation. (Porto das Barcas, Zimbral, and Valmitão),establishing a sampling and processing protocol for future studies.

- Asses the stratigraphy and sedimentology of each locality, correlate them within the Lourinhã Formation, and interpret their respective depositional environments, to prepare further paleoecological reconstructions.
- Describe, identify and asses the taxonomy of the new specimens collected.
- Evaluate the taxonomic abundances and diversities of each VMA, and compare them with other Mesozoic VMAs.

2. MATERIAL AND METHODS

2.1. Sampling and preparation of the sediments

Bulk sampling paired with sieving and picking under light microscope has been recognized as the best methods for managing and reducing bias in fossil collections to study fossils from small animals (Mckenna, 1962; Wolff, 1973, 1975; Smith *et al.*, 1988; Peterson *et al.*, 2011; Rogers *et al.*, 2017). Small and isolated skeletal elements are not always easy to identify because: (1) vertebrate microfossil assemblages rarely provide articulated skeleton, and a taxonomic attribution often requires taxonomic keys for a given skeletal element; (2) the quality of preservation is usually low after transport and weathering; (3) intraspecific variation, ontogeny, sexual dimorphism can make the identification harder (Baszio, 2008).

2.1.1. PORTO DOS BARCAS

Figure 18: Porto dos Barcas microfossil vertebrate assemblage locality.

Porto dos Barcas microfossil vertebrate assemblage (**Figure 18**) is located in the small locality of Porto de Barcas, in Atalaia. For the purpose of this work, 7 bulk samples have been collected, for a total weight of 182 kg (*Table 2*). The site is known to have previously produced mammal and dinosaur teeth (Hahn & Hahn, 2001; Hendrickx & Mateus, 2014; Malafaia *et al.*, 2017), turtle remains (de Lapparent de Broin, 2001; Ortega, 2009), and crocodile eggshells (Russo *et al.*, 2017).

Table 2: Bulk samples from Porto dos Barcas locality.

Bulk name	Date	Weight (in kg)	Preparation (nb of cycles)	Collectors
PB-06-17-01	30/06/2017	29	ML (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-06-17-02	30/06/2017	24	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-06-17-03	30/06/2017	24	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-06-17-04	30/06/2017	31	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-06-17-05	30/06/2017	24	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-06-17-06	30/06/2017	34	ML (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
PB-10-17-01	29/10/2017	23	ML (2)	A. Bonito, V. Cheng, A. Fernandes, A. Guillaume, M. Marx
PB-10-17-02	29/10/2017	23	ML (2)	A. Bonito, V. Cheng, A. Fernandes, A. Guillaume, M. Marx

2.1.2. ZIMBRAL

Figure 19: Zimbral microfossil vertebrate assemblage locality.

Zimbral (Figure 19) is a locality near Porto Dinheiro. For the purpose of this work, six bulk samples of sediments from three separate places have been collected during two seasons, for a total weight of 137 kg (*Table 3*). The site is already known to have produced dinosaur bones (Mateus, 2006, 2007) and teeth (Malafaia *et al.*, 2017), mammal teeth (Krusat, 1969; Martin, 2002, 2010), albanerpetontid (Wiechmann, 2004), and crocodile eggshells (Russo *et al.*, 2017).

Table 3: Bulk samples from Zimbral locality.

Bulk name	Date	Weight (in kg)	Preparation (nb of cycles)	Collectors
ZIM-11-16-01	28/11/2016	8	ML + FCT-UNL (2+1)	A. Guillaume
ZIM-11-16-02	28/11/2016	8	FCT-UNL (1)	A. Guillaume
ZIM-06-16-01	29/06/2017	38	ML + FCT-UNL (1+1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
ZIM-06-16-02	29/06/2017	19	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
ZIM-06-16-03	29/06/2017	35	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
ZIM-06-16-04	29/06/2017	29	FCT-UNL (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
ZIM-06-16-05	29/06/2017	31	ML (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo
ZIM-06-16-06	29/06/2017	32	ML (1)	T. Dale Albrecht; M. Moreno-Azanza; F. Rotatori; J. Russo

2.1.3. VALMITÃO

Figure 20: Valmitão microfossil vertebrate assemblage locality.

Valmitão microfossil vertebrate assemblage (Figure 20) is located near the Praia do Valmitão, in Ribamar. For the purpose of this work, one bulk sample has been collected, for a total weight of 58 kg (*Table 4*). The site is previoulsy known to have produced dinosaur teeth and remains (Antunes & Mateus, 200; Mateus *et al.*, 2006; Ortega, 2009; Hendrickx & Mateus, 2014; Mocho Lopes, 2016; Malafaia *et al.*, 2017).

Table 4: Bulk samples from Valmitão locality.

Bulk name	**Date**	**Weight (in kg)**	**Preparation (nb of cycles)**	**Collectors**
VAL-06-16-01	06/2016	??	ML	J. Marinhero; O. Mateus; F. Rotatori
VAL-10-17-01	10/2017	58	FCT-UNL (1)	M. Moreno-Azanza

2.1.4. PREPARATION OF THE SEDIMENTS

The study of vertebrate microfossil assemblages requires several steps (Eberth *et al.*, 2007b; Buscalioni *et al.*, 2008, 2018; Gasca *et al.*, 2017; Rogers *et al.*, 2017): (1) collecting bulk sediment; (2) letting it dry; (3) soaking them in oxidant solution, chosen according to the aim of the study; (4) screen washing them through sieves of different size according to what is sought; (5) picking the concentrates using a binocular lens (Figure 21). It may sometimes be necessary to conduct at several drying/soaking/screen washing cycles, according to the quality of the process.

For this thesis, two slightly different methodologies have been used according if the sediments have been prepared in the Museu da Lourinhã, or in the Departmento de Ciências da Terra of FCT-UNL facilities. After being collected, bulk sediments have been stored in Museu da Lourinhã for periods from one week to one year. It seems that the period of storage does not affect the quality of the material found, but sediments stored for shorter time will require a couple more soaking/screen washing cycles. This could be due to the high humidity in Lourinhã and the museum storage conditions, slowing the drying. Sediments have been soaked in a bucket full of a solution of 50L of water and 0.5L to 1L of hydrogen peroxide (H_2O_2, original solution at 50%), for periods from one day to one week. The bulk sample VAL-06-16-01 had been soaked for one year, but that does not seem to have affected the sample result. Then, sediments have been screen washed using a sieving table composed of three levels of mesh: 2mm, 1mm and 0.5 mm. Some bulk samples required a second soaking/screen washing cycle. This step usually required 3 to 8 hours. During a second soaking, PB-10-17-01 reacted strongly with the H_2O_2, probably because of the sulfur present in the wood remains.

Figure 21: The different setups for preparation of the sediments. **A**, collecting in the field (Porto Barcas locality, 14/06/2018); **B**, bulk sample collected; **C**, bulk samples soaking in hydrogen peroxide; **D** and **E**, sieve table with 2mm, 1mm and 0.5mm meshes; **F**, plastic bags used to store sediments once they have been screen washed; **G** and **H**, binocular lenses in the Museu da Lourinhã (G) and FCT facilities equipped with a camera (H); **I**, sample boxes used for organizing specimens according their locality, their description and their taxonomic identification; **K** and **L**, labels used to identify specimen boxes (K) and sediments screen washed (L); **M**, boxes used for the storage and the transport of the specimens.

In DCT facilities, sediments have been soaked in small buckets, with a solution of 3 to 4L of water, and H_2O_2 (original solution at 30%), according to how much sediment was soaked. Three buckets were used simultaneously, for a total of 1L of H_2O_2. The soaking was processed during 24 to 48h. Then, sediments have been screen washed using only one 0.5 mm sieve for 6 hours. Because of that, only material bigger than 0.5 mm had been concentrated. In order to be able to sieve the concentrates, they have been dried in a dryer, at 50°C, for 24h. Then, they have been sieved (dry sieving) using a screening machine (10 min at amplitude 60), using three levels of mesh: 2mm, 1mm and 0.5mm.

Once prepared, all sediments have been picked by using binocular lens, a Leica MZ6 in ML and an Olympus SZ51 in FCT-UNL. Each fraction was picked separately using a paintbrush, and each new specimen has been stored in plastic box specifying the locality, from which bulk sample and its date of sampling, and in which the fraction it has been picked. Picking has been carried on in both FCT-UNL and the ML (*Table 5*) during at least 750 hours of personal work, and with the appreciative help of the 1st year (2017-2018) Master students in the scope of their Methods in paleontology class, the 2nd year (2016-2017) Master student Tiago Pereira, in the scope of his master thesis on amphibians from the Upper Jurassic of Portugal; and the Museu da Lourinhã's volunteers. However, because of the massive amount of time required for this step, not all bulk samples processed could be picked. Pictures have been taken using Leica M165C binocular lens equipped with a Leica DFC295 camera and using the software Leica Application Suite, Version 4.10.0, developed by Leica Microsystems CMS GmbH. Measurements of the teeth were done by using ImageJ (Rasband, 2003).

Table 5: Bulks used for picking and data collecting.

Bulk name	Picked at	Pickers	Used for
PB-06-17-01	ML	A. Guillaume	-
PB-10-17-02	ML + FCT-UNL	A. Guillaume; V. Cheng; A. Fernandes; M. Marx	Biodiversity + taxonomy
VAL-06-16-01	ML + FCT-UNL (unfinished)	A. Guillaume; A. Bonito; V. Cheng; A. Fernandes; M. Marx; H. Oliveira; R. Pereira; C. Ribeiro; V. Takev	Biodiversity + Taxonomy
VAL-10-17-01	FCT-UNL (unfinished)	T. Pereira	-
ZIM-11-16-01	ML	A. Guillaume; A. Fernandes; F. Rotatori; J. Russo ; J. Pratas ; H. Oliveira; M. Moreno-Azanza; D. Estraviz-López	-
ZIM-11-16-02	ML	A. Guillaume	Biodiversity + taxonomy
ZIM-06-17-01	ML	A. Guillaume; A. Fernandes	Biodiversity + taxonomy

2.2. Stratigraphy

For the purpose of this thesis, stratigraphy field work has been carried out establishing the lithostratigraphic sequence of the three localities, and to correlate them into the Lourinhã Fm. and its members. Measurements were taken using a measuring tape and a Jacob's bar (Figure 22). The Jacob's bar is a stratigraphic tool allowing the measurement of the thickness of the different layers, considering their inclination and their direction. It is made of a wood stick and a wood board onto which a protractor and a bubble level have been mounted. The top of the wood board is usually set up at 1.5m and it is used as a standard measurement for each step. For Porto das Barcas and Zimbral sections, the aims were to locate the different shells layers, and draw the sequence between them. It must be noted than the upper shell layer in Porto das Barcas was not seen during this field work, but isolated bivalve shells were observed. That would suggest that the layer was covered somewhere in the plant field above the locality. For the Valmitão locality, the aims were to determine the sequence by following it laterally as far the cliff allowed safe prospecting.

Figure 22: Jacob's bar (**A**) and its use in the field (**B**).

2.3. Electron microscope

For pictures with higher magnification, focal depth, and details than regular binocular lenses used for picking, a scanning electron microscope (SEM) has been used for 55 specimens, from all localities (Figure 23). The pictures have been taken in HERCULES facilities, of the University of Évora, with the authorization of Prof. José Mirão. Contrary to optical binocular lenses, the signal used to produce an image is not from optical light but from the interaction of an electron beam with the atoms at the surface of the sample, which allows high magnification and high resolution. Because bones do not conduct electrons, the sample needs to be previously prepared: (1) mounting on an aluminium holder with a conductive adhesive; and (2) coating with conductive material (Au).

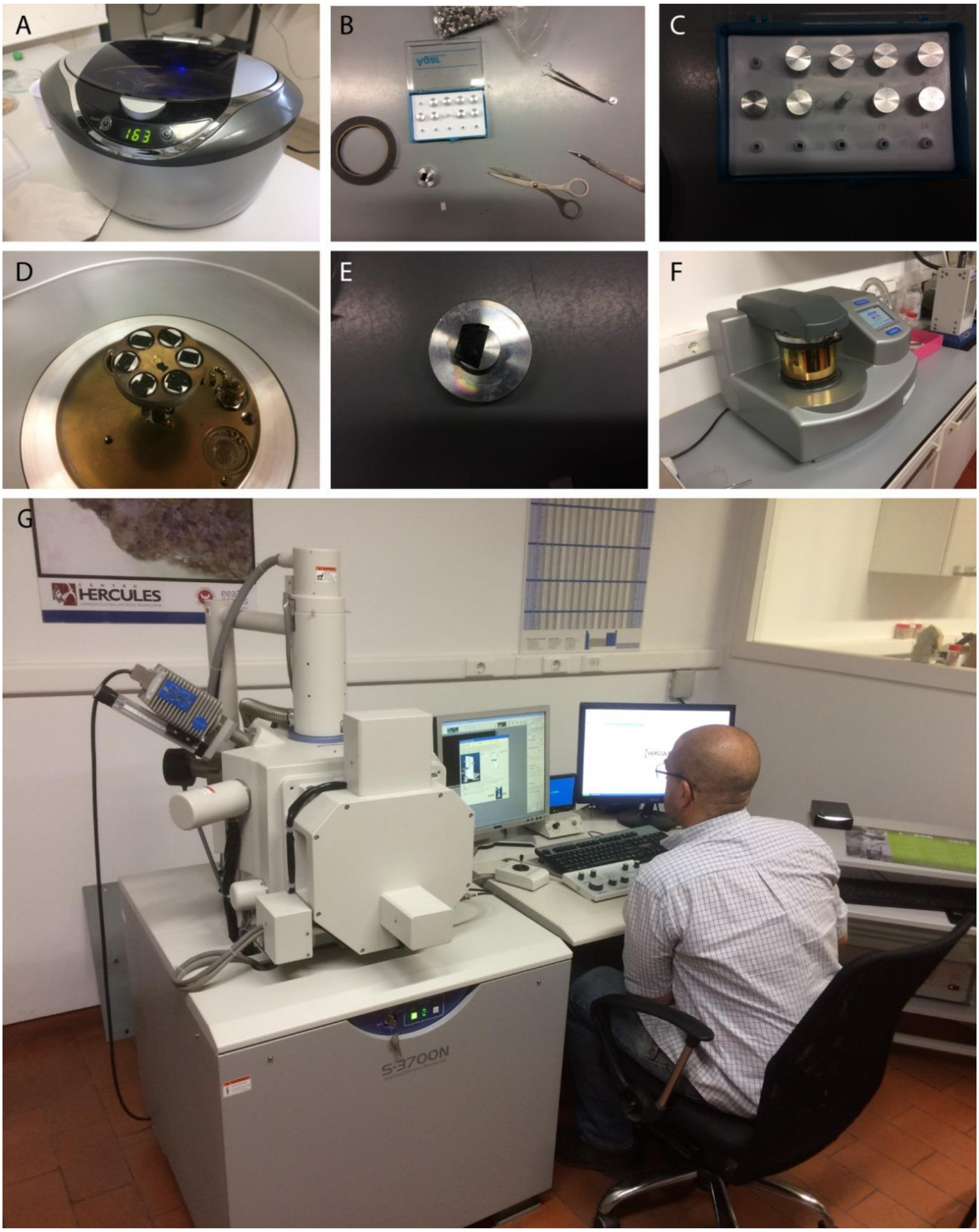

Figure 23: Equipment used to prepare, mount, and coat the specimens for the scanning electron microscope. **A**, ultrasonic bath used to clean the specimens; **B**, equipment to mount the specimens; **C**, box of support for the mounting; **D**, holder used for the coating; **E**, one support with the specimen mounted; **F**, Quorum Q150R ES to coat the specimens; **G**, SEM S-3700N used for the thesis in HERCULES facilities.

Before being prepared, several specimens have been washed using an ultrasonic bath in DCT facilities. Because of the size and the fragility of some specimens, not washing them was preferred to a long bath that could have broken them. Both mounting and coating was carried out in HERCULES facilities, under supervision of the local team. Each specimen was mounted on holder with carbon double side tape, then coated with a gold/palladium alloy coating with a Quorum Q150R ES. Pictures were taken with a SEM S-3700N, with the help of Luis Dias. For each specimen, the most informative view was preferred to be in orthogonal position, and in the case where to opposite view could be required, they were taken using tilt and rotating the holder. However, since the tilt could not be too inclined (23° max) as per procedures of the HERCULES facilities, some of these specimens need to be mounted again in the future to take the missing views. Unfortunately, because of the time required to process all the specimens, not all those prepared (over a hundred) were photographed in the SEM.

The process of mounting can be very stressful for the specimen: several broke during the procedure, and most exhibit small recent open fractures on the SEM pictures. That might be due to the origin of the sample or their storage in the Museu da Lourinhã, where the humidity is not controlled. Breakage might also be due to the ultrasonic washing, that could weaken the specimen or because they did not dry properly (the water could have softened the bone tissue), or because of the vacuum conditions, which can also open cracks. However, the ultrasonic washing is not the only cause, since unwashed specimen broke during the mounting. To prevent this from happening during future sessions, more controlled storage and increased care during the mounting (by spending more time), both to be provided soon by the Museu da Lourinhã and FCT, will be set. Also, access to the SEM in DCT facilities will soon allow a greater control of the specimens and the pictures needed for future studies.

2.4. Statistical analyses

Statistical analyses have been used to characterize the taxonomic abundance and diversity of each VMA locality. Abundance and diversity have been calculated using respectively the number of specimens and the number of different taxa used in these analyses. The number of specimen corresponds to the number of individual remains that were identified to a taxon. All microvertebrate remains that could have been attributed to a taxon have been sorted in ecological categories, following the scheme proposed by van der Valk: (1) obligate wetland taxa are found either in the water column or in flood soils, and cannot survive without standing water; (2) amphibious taxa spend at least part of their life cycle in wetlands and the remainder in a terrestrial environments; (3) and facultative taxa can be found both in wetlands and terrestrial environments, and do not have to have part of their life cycle occurring in water (van der Valk, 2012). Data from Carrano & Velez-Juarbe, 2006, Carrano *et al.*, 2016, and

Buscalioni *et al.*, 2018 included also non-vertebrates taxa, which has been removed for the purpose to compare only the difference in the vertebrate diversities.

A set of diversity indexes was selected, based on previous works on other VMA (Carrano *et al*., 2016; Buscalioni *et al*., 2018), to explore components of diversity, richness and evenness in each locality: (1) the Shannon's index is a direct measurement of the number of equiprobable taxa contained in the sample (Shannon & Weaver, 1949; Whittaker, 1972); (2) the Simpson's diversity index gives the probability that two randomly chosen individuals from a given community are different taxa (Simpson, 1949; Pielou, 1969); (3) the Simpson's measure of evenness, which is not sensitive to richness (Smith & Wilson, 1996); and (4) the Pielou's evenness index provides the evenness for the taxa of a given sample (Pielou, 1969, 1975). Those indexes have been calcultated with the number of specimens used in the paleoecological analyses.

3. RESULTS

Hereby are presented the main results of this thesis. The stratigraphy logs of the three localities (Porto das Barcas, Zimbral, Valmitão) have been assessed, located within the Lourinhã Fm., and preliminary paleoenvironments have been proposed for each of them. Because of the large number of specimens found, a closer look on the crocodylomorph teeth association from the Valmitão locality was carried out, with the description and the identification of 125 teeth. 3.348 specimens were picked from the three localities, among which 824 microvertebrates specimens have been identified, described, and attributed to a taxon.

3.1 Geology and correlation of the vertebrate microfossil assemblage sites

3.1.1. DESCRIPTION

The locality of Porto das Barcas (Figure 24) is part of the Praia Azul mb. of the Lourinhã Formation, from a latest Kimmeridgian to earliest Tithonian age (Mateus *et al.*, 2017). The microfossil vertebrate assemblage is located at the top of the sequence, in a greyish mudstone layer. The complete 15 layer-section is composed by 33.8m of mudstones, with intercalations of sandstones and limestones.

Layer 0 => Over 2m of sandstone brown and white, with flat top and bottom surfaces, and cross bedding.

Layer 1=> 3,5m of massive mudstone, greyish for the first 50cm, then turn dark red.

Layer 2 => 1,6m of massive mudstone, grey.

Layer 3 => 3m of intercalated limestone and mudstone. There are 4 levels of limestones. The bottom layer is a packstone, very rich in bivalves. The other layers are wackestones, with fewer bivalves. The mudstones are grey and have sparse fossils.

Layer 4 => 35cm of mudstone, grey, partially covered.

Layer 5 => 3,20m of mudstone, red, highly bioturbated, with caliche.

Layer 6 => 55cm of medium grained sandstone with channel bases, planar crossbedding, and bioturbation.

Layer 7 => 1m of interacted decimetric levels of sandstone and mudstone. Sandstone irregular bases and tops, and crossbeddings. Mudstone laminated, red.

Layer 8 => 5m of mudstone, laminated, greyish at the first 50cm then brown, with bioturbations (large sandstone burrows) and caliche at the top (abundant). Presence of plant remains.

Layer 9 => 2m of sandstone, fine to medium at the base, white, with crossbeddings and layers of coal marking laminations. In the middle, coarse grained to microconglomerate, with plant remains (abundant). At the top, fine grained, with fewer plant remains and more mica.

Layer 10 => 1,10 m of mudstone, brownish-red to grey, highly bioturbated.

Layer 11 => Porto das Barcas vertebrate microfossil assemblage site; 3m of mudstone, grey, with microvertebrates, bivalves and plant remains. The top has yellowish cracks that came from the overlaying level.

Layer 12 => 3m of mudstone, yellowish greenish.

Layer 13 => 1,5m of fine sandstone, yellowish/whitish.

Layer 14 => 5m of mudstone, brownish, with lost clams (the second clam layer has not been found).

The locality of Zimbral (Figure 25) is located on top of Porto Dinheiro sequence, and is part of the Praia Azul mb. of the Lourinhã Formation, from a latest Kimmeridgian to earliest Tithonian age (Mateus *et al.*, 2017). The microfossil vertebrate assemblage is in the middle of the sequence, in a greyish mudstone layer. The complete 26 layers-section is composed by 40.25m of mudstones with intercalations of sandstones and limestones.

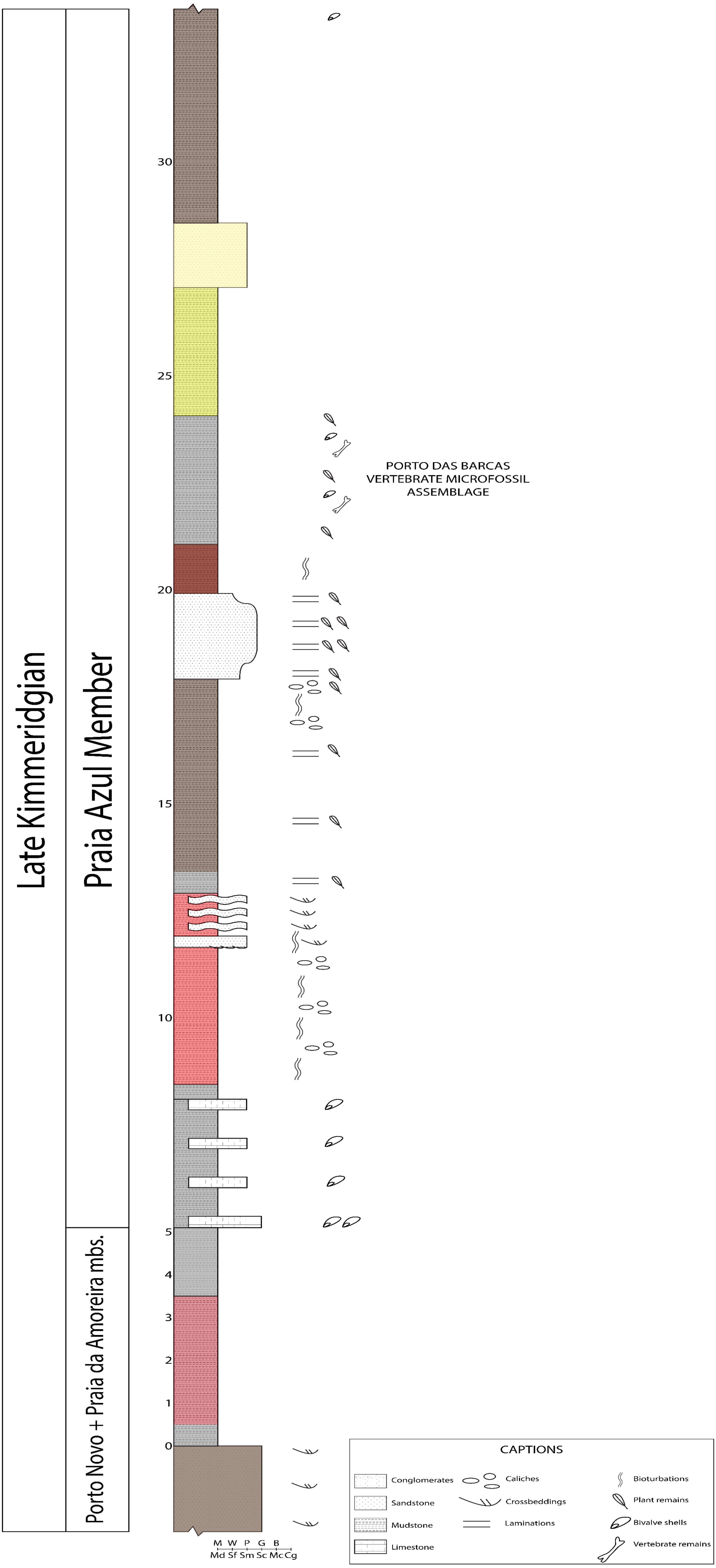

Figure 24: Stratigraphic log of the locality of Porto das Barcas

Layer 0 => Over 15cm of mudstone, grey

Layer 1 => 40cm of polymectite matrix supported microconglomerate, grey, with shell fragments

Layer 2 => 20 to 30cm of coarse sandstone, with irregular top and base, channeliform, crossbedding, grey, and layers of coal

Layer 3 => 6.75m of mudstone, more brownish toward the top, with caliche

Layer 4 => 60cm of laminated sandy mudstones, with bioturbation (burrows), greyish to reddish

Layer 5 => 1m of sandstone, with irregular top, maybe chanelliform, bioturbation (burrows more abundant toward the top), and crossbedding, grey-reddish; composed by different decimetric levels, thicker in the middle, with a vertical gradual increase of the grain size, from fine to coarse

Layer 6 => 4.25m of mudstone, brownish, with caliche

Layer 7 => 25cm of massive coarse sandstone, with bioturbation, brown, and presence of lots of mica

Layer 8 => 2.65m of laminated mudstone with bioturbation (burrow), brown-redish, and presence of calcihe

Layer 9 => Centimetric level of developed caliche

Layer 10 => 3m of massive mudstone, brownish, with caliche

Layer 11 => 3m of mudstone, with bioturbation, grey

Layer 12 => 1.2m of mudstone, with greyish veine, beige

Layer 13 => 20cm of sandstone, with chanelliform base, grey, and presence of mica

Layer 14 => Zimbral vertebrate microfossil assemblage site; 2m of mustone, grey, with microvertebrate, plant remains, and ostreid fragments.

Layer 15 => 7.5m mudstone, yellowish, with caliche in the last 6m (centimetric size, but decreasing size to the top)

Layer 16 => 80cm of laminated mudstone, less laminated on the top, with yellow and grey patches, with bioturbation, red

Layer 17 => 1m of mudstone, brownish, with caliche

Layer 18 => 50cm of mudstone, grey

Layer 19 => 40 cm of packstone/greystone limestone with shells; shells are bigger and more abundant on the top

Layer 20 => 1m of mudstone with orange veins on the top, grey

Layer 21 => 50cm of laminated mudstone, orange

Layer 22 => 20cm of laminated mudstone with bioturbation, grey

Layer 23 => 30cm of mudstone with bioturbation, orange

Layer 24 => 35cm of medium grain size sandstone with planar crossbedding indicating 2 opposite paleocurrent directions, and bioturbation (burrows), white

Layer 25 => More than 2m of mudstone covered on the top, brown, with caliche

The locality of Valmitão (Figure 26) is part of the Praia da Amoreira and Porto Novo mbs. of the Lourinhã Formation, dated from Late Kimmeridgian (Gowland *et al.*, 2017; Mateus *et al.*, 2017). The vertebrate microfossil assemblage is located at the top of the sequence, in a greyish mudstone layer. The complete 38 layer-section is composed by 22m of mudstones with intercalations of sandstones.

Layer 1 => More than 2m of mudstone, red

Layer 2 => Decimetric level of sandstone with irregular base

Layer 3 => Around 1m of mudstone, light greyish

Layer 4 => Around 1 m of fine sandstone, with crossbedding, greyish, with intercalation of medium to coarse sandstone

Layer 5 => 75cm of laminated mudstone, red

Layer 6 => 80cm of medium grain sandstone, with channeliform basis and crossbedding, red, laterally pass to a decimetric level of fine grain sandstone, with galleries and crossbeding, and to level 5.

Layer 7 => 1m of mudstone massively bioturbated, grey, laterally pass to laminated mudstone, red.

Layer 8 => 52cm of coarse sandstone with polymectic microconglometrate lenses poorly sorted with quartz and feldspar, and soft clasts of mudstone, grey, vertically pass to fine sandstone with crossbedding and channeliform base

Layer 9 => 20 cm of coarse sandstone, with irregular base and bioturbations, reddish-brown

Layer 10 => 60cm of laminated mudstone, red

Layer 11 => 55cm of sandstone with gradual increase in grain size, from fine to coarse, poorly sorted and polymectic, with crossbeddings and channeliform base, red, laterally pass to mudstone

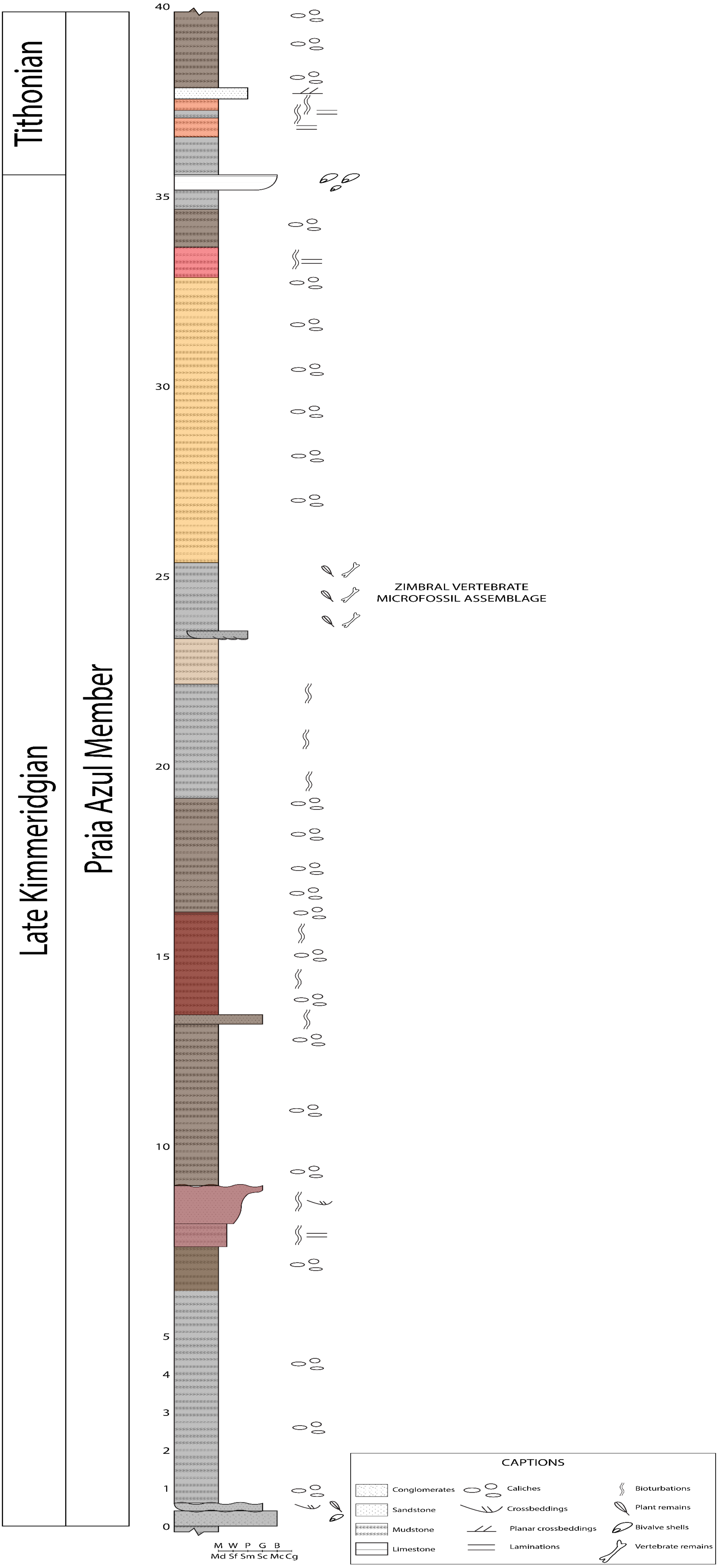

Figure 25: Stratigraphic log of the locality of Zimbral.

Layer 12 => 84cm of mudstone, bioturbated, purple

Layer 13 => 50cm of laminated fine grain sandstone

Layer 14 => 20cm of coarse to medium grain size sandstone laminated at the bottom, grey, highly concentrated in mica

Layer 15 => 90cm of mudstone, greysih to dark grey, with charcoal

Layer 16 => 5cm of heteromictite conglomerate with irregular surface. VAL-SEC 1 was collected.

Layer 17 => 4.5m of mudstone, greyish to dark grey (black when fresh), with few charcoal remains, with centimetric intercalation of fine sandstone, white. VAL-SEC 2 was collected

Layer 18 => 40cm of laminated mudstone, red, with flashes of mudstone, white, and fluctuation structures.

Layer 19 => 70cm of sandstone poorly sorted, highly bioturbated (galleries on the top), reddish-brown, with one mudstone layer, and intercalation with crossbedding.

Layer 20 => 25cm of finely laminated mudstone, greyish-purple

Layer 21 => 10cm of laminated sandstone, with bioturbation, greyish, and rich in organic matter

Layer 22 => 30cm of conglomerates, with irregular surfaces, crossbedding and bioturbation

Layer 23 => 20cm of very fine massive sandstone, grey

Layer 24 => 1.6m of mudstone, red, with one flash of conglomerate, finely laminated (weavy)

Layer 25 => 22cm of conglomerates heteromictites, poorly sorted, and laminated, with charcoal remains

Layer 26 => 10 cm of very fine sandstone, grey

Layer 27 => 70cm of mudstone with vertical progression to medium sandstone at 45cm from the base, with laminated transition bioturbation in sandstone, red

Layer 28 => 42cm of mudstone, red

Layer 29 => 30cm of fine sandstone, grey

Layer 30 => 70cm of poorly-laminated mudstone, reddish-purple, with one layer of fine sandstone.

Layer 31 => 50cm to 1m of coarse sandstone and conglomerates, with convergent surfaces forming a lenticular channel, orange

Layer 32 => 0 to 60cm of clays laminated toward the top, red , with intercalation of white clay and fluctuation structures.

Layer 33 => 70cm to 1m sandstone and microconglomerate, with channeliform base, and sygmoidal crossbedding

Layer 34 => 50cm of mudstone, red

Layer 35 => 30cm of mudstone with planar crossbedding, purple

Layer 36 => Valmitão vertebrate microfossil assemblage site. 2.5m of mudstone, grey, with microfossil vertebrates and plant remains, decimetric layer of fine sandstone at 1.5m from the base

Layer 37 => More than 70cm of mudstone, partially covered, brown

3.1.2. LOCATION WITHIN THE LOURINHÃ FORMATION

The stratigraphic analysis of the three localities allowed their location within the synthetic stratigraphic log of the Lourinhã Formation (**Figure 27**). Valmitão site is located in the upper half of Porto Novo and Praia da Amoreira mbs., while Zimbral and Porto das Barcas are both located between the first and the second bivalve shell layers in Praia Azul mb.. Consequently, Valmitão is the oldest locality, while Zimbral and Porto das Barcas are similar age, since correlation can be difficult in continental context with quick lateral changes, and the layers could not be followed during the field trip because of human construction. The uppermost layers of Zimbral section are Tithonian in age (Mateus *et al*., 2017).

3.1.3. INTERPRETATION OF THE PALEOENVIRONMENTS

The Porto das Barcas section is a succession of thick mudstone layers, with intercalations of small sandstone layers, some of them rich in carbonaceous material. Most of the mudstone layers are richly bioturbated, and the section is delimitated at its base by a shell-rich layer. No such layer has been observed on the top, but loose material was collected in the area, suggesting that another shell-rich layer should be close and covered by the plant field. The Zimbral section exhibits a similar succession of thick mudstone layers and small sandstone layers, delimitated by shell-rich layers.

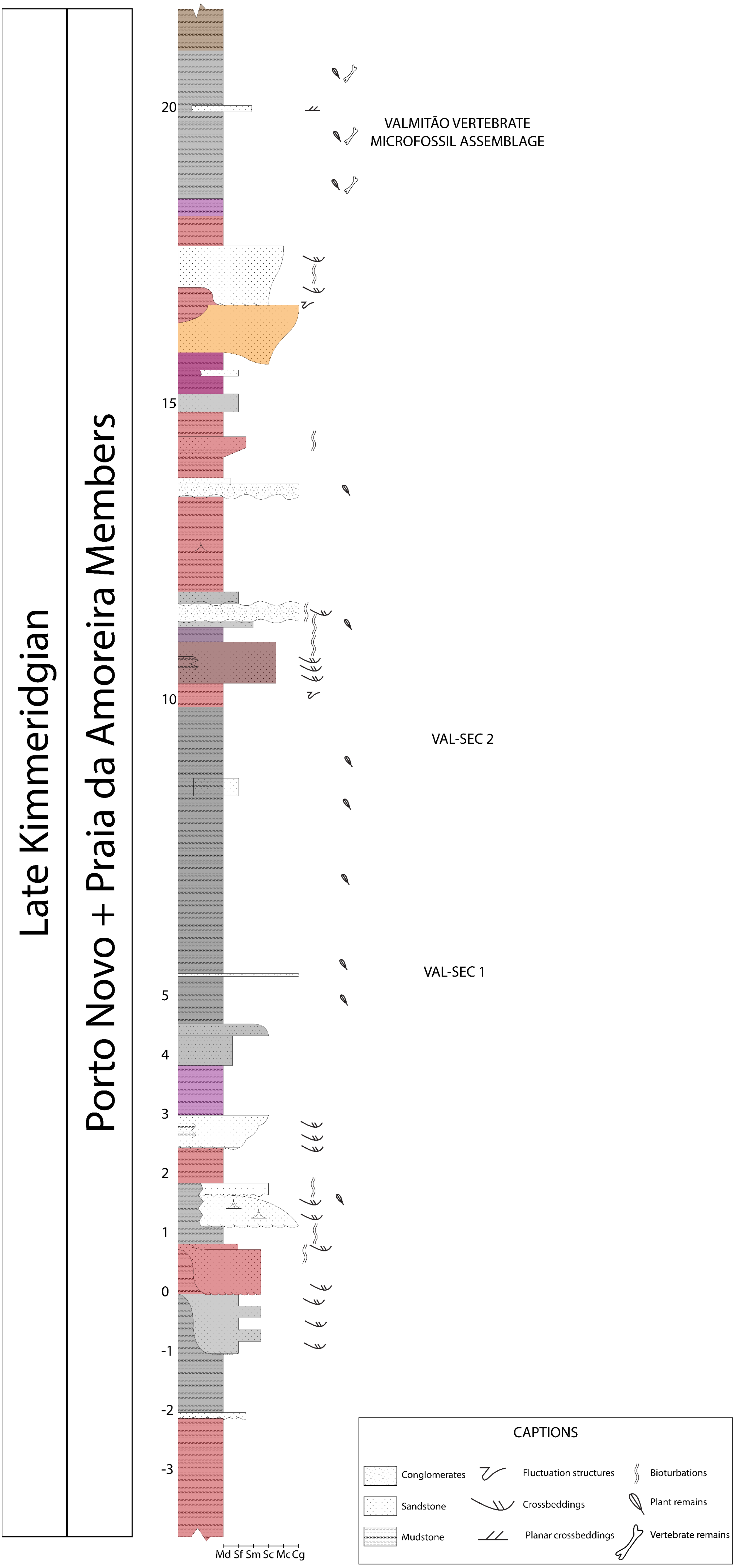

Figure 26: Stratigraphic log of the locality of Valmitão.

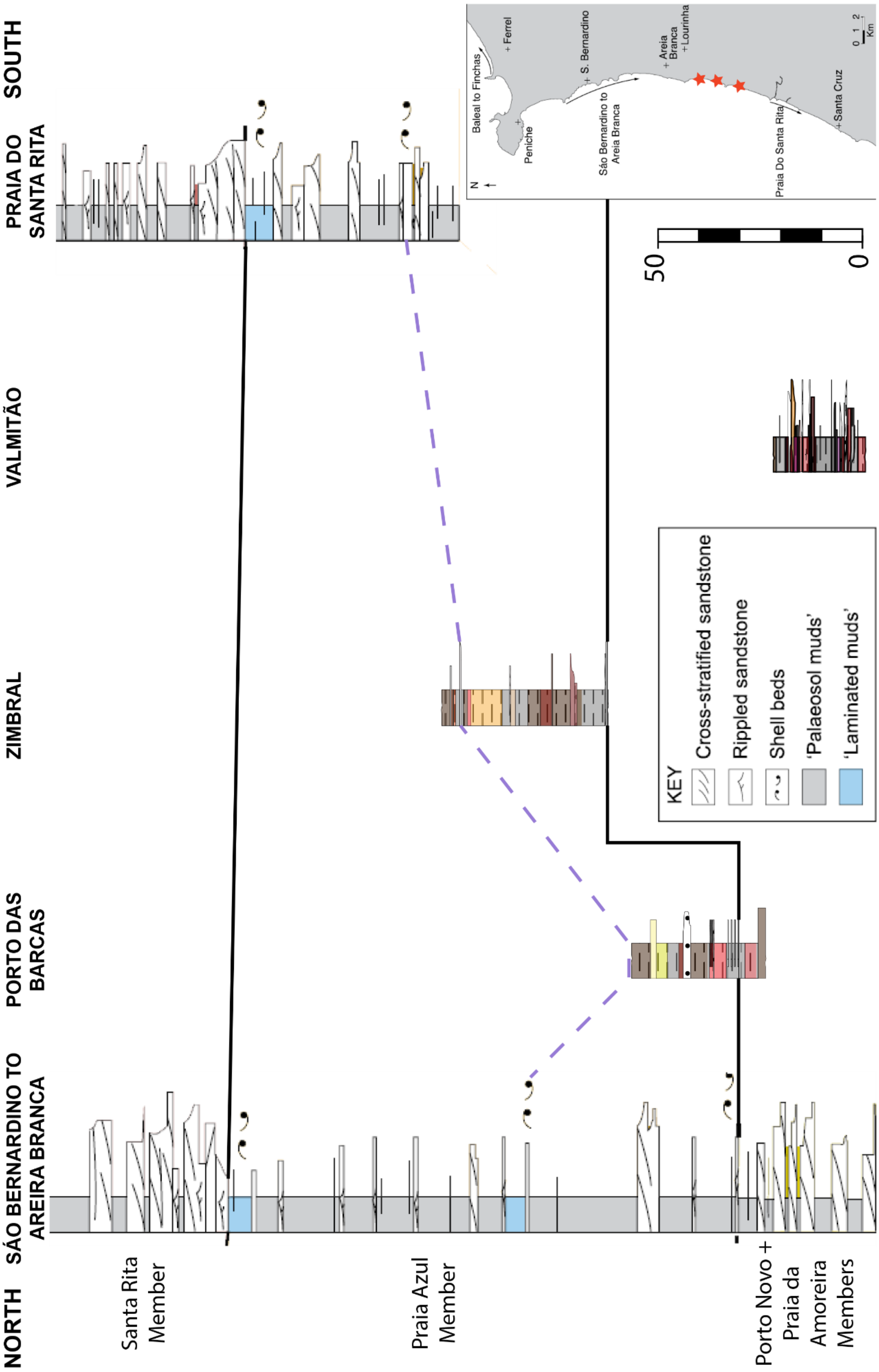

Figure 27: Stratigraphic summary of the Lourinhã Formation and correlation of the three VMA sections, represented by the red stars on the map (modified from Taylor *et al*., 2014). Colons are not at horizontal scale. The purple dotted line represents correlation with the second bivalve shell layer. Scale is in meters.

Both sections can be interpreted similarly as successions of different floodplain mud deposits, with occasional fluvial meandering channels, and occasional mouth-bars and sandy bay shorelines (Taylor *et al.*, 2014). The shell-rich layer at the base is actually a succesion of sandy bioclastcic limestone and laminated mudstones rich in bivalve remains, and represent periodic incursions onto a low-lying coastal plain in the form of brackish-marine bays (Taylor *et al.*, 2014). Both MVA sites are located in floodplain mud deposits, younger than the transgressional event characterizing the beginning of the Praia Azul mb..

The Valmitão section is a succession of sandstone and mudstone layers, which has been interpreted as fluvial channel sands and calcrete-bearing floodplain muds, forming mainly a meandering system where crevasse splays are rare (Taylor *et al.*, 2014). Darker greyish mudstones rich in organic matter, as the one observed at the MVA Valmitão site have been interpretaed as lacustrine mud, probably deposited in an oxbow lake, with a slow rate of sedimentation. The immediately underlaying sandstones under the Valmitão VMA may represent an eolian deposit, which would rise the question on the origin of the Valmitão assemblage, which may have deposited in a lagoonal pond. However, further studies on detailed sedimentlogy are needed to confirm it.

3.2. Vertebrate microfossil assemblages from the Lourinhã Formation

3.2.1. SYSTEMATIC PALEONTOLOGY

A total number of 2,467 microvertebrates remains (bone fragments + teeth) have been picked and observed from the three localities (*Table 6*). Because most of the specimens are fragmentary and poorly preserved, and because they do not necessarily exhibit diagnostic features, a higher taxonomic identification with good support has been chosen, and specimen description and assessment have been based on visual comparison with the literature.For the purpose of simplifying the descriptions in this section, the word fish will refer to any non-tetrapod marine vertebrate.

Table 6: Raw counting of microfossil remains from the three microfossil vertebrate assemblage localities.

Bulks	Invertebrates	Vertebrates remains (total)	Vertebrates remains identified	Teeth	Eggshells	Plant remains	Total
ZIM-06-17-01	299	819	222	76	67	109	1370
PB-10-17-02	14	642	74	27	18	53	754
ZIM-11-16-02	38	361	116	107	1	34	541
VAL-06-16-01	123	277	219	158	75	50	683

CHONDRICHTHYES Huxley, 1880

ELASMOBRANCHII Bonaparte, 1838

HYBODONTIFORMES Patterson, 1966

HYBODONTIDAE Owen, 1846

Hybodus Agassiz, 1837

Hybodus (?) *lusitanicus* Kriwet, 2004

Localities – PB-10-17-02

Material – 3 isolated teeth (**Figure 28**, A)

Description – Teeth did not preserve the lateral cusplets, but their breakage marks can be observed on the mesial and distal sides. The central cusps are symmetrical, relatively small, higher than wide, and not compressed, neither labiolingually or mesiodistally. They bear folds (4 to 5) on the labial surface, and on the lingual surface (3 to 4), converging toward the apex of the teeth and forming ridges. The teeth are faintly lingually curved, the base of the labial surface being convex at the base of the cusp in lateral view. The root is not preserved.

Remarks – Symmetric central cusps are characteristic of the teeth of *Hybodus* Agassiz, 1837, in contrast to *Egertonodus* Maisey, 1987 and *Polyacrodus* Jaekel, 1889. The small and massive morphology of the teeth in general outline is similar to the one observed in *H. lusitanicus* Kriwet, 2004, and differs from teeth of *H. reticulatus* Agassiz, 1837, which are high-crowned (Kriwet, 2004. figs 2, 3). However, the absence of the lateral cusplets precludes a tighter identification.

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Cope, 1887

PYCNODONTIFORMES Berg, 1937

Pycnodontiformes indet.

Localities – ZIM-06-17-01; ZIM-11-16-02

Material – 4 isolated teeth (**Figure 28**, B1-B2)

Description – The teeth are molariform with a blunt apex, labiolingually compressed, elliptical in apical view. The enamel cap is transparent, envelops only the upper part of the teeth, and it is constricted at the base. The enamel exhibits some faint ornamentation at the base of the enamel cap, leaving the apical platform smooth and unornamented.

Remarks – Molariform teeth with blunt apex are usually attributed to pycnodontiforms (Kriwet *et al.*, 1997; Sweetman, 2007; Buscalioni *et al.*, 2008; Cuny *et al.*, 2010; Müller, 2011; Oreska *et al.*, 2013). However, identification based on isolated pycnodontiform teeth is hazardous (Cuny *et al.*, 2010): when found as palate jaw association, they can be more confidently identified. Since non of those palate jaws has been found so far in the three localities, this identification to pycnodontiforms is tentative, the teeth being different from the others found in the sample.

NEOPTERYGII Regan, 1923
HOLOSTEI Müller, 1846 *sensu* Grande, 2010
SEMIONOTIFORMES Arambourg & Bertin, 1958
SEMIONOTIDAE Woodward, 1890
Lepidotes Agassiz, 1833
Lepidotes sp.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Material – 10 isolated teeth (**Figure 28**, C1-C4)

Description – Teeth are hemispherical, with a subcircular to elliptical outline in apical view. The enamel cap is transparent, envelops most of the teeth, expanding sometimes at the root, and it is constricted at its base. The hemispherical shape and the expansion of the enamel cap differ from one tooth to another, but they are still observable and distinct features. A faint protuberance, strongly exuberant in some teeth, can be observed at the apex. The enamel is smooth, without any ornamentation.

Remarks – The hemispherical teeth, with the enamel cap expanding toward the base and the faint apical protuberance are diagnostic features of *Lepidotes* Agassiz, 1833 (Kriwet *et al.*, 1997; Sweetman, 2007; Buscalioni *et al.*, 2008. fig 5; Cuny *et al.*, 2010. fig 2; Müller, 2011. fig 4; Oreska *et al.*, 2013. fig 3), which has been previously recorded in the Guimarota mine (Kriwet, 2000). However, since there is high variability in this taxon (Cuny *et al.*, 2010), only a conservative genus level identification was chosen.

AMIIFORMES Hay, 1929
CATURIDAE Owen, 1860
Caturus Agassiz, 1834
Caturus sp.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Material – 6 isolated teeth (**Figure 28**, D1-D2)

Description – The teeth are conical, lingually curved with an acute apex, and a constricted base of the crown. The tip is transparent. They are weakly labio-lingually compressed, making the base of the crown subcircular to elliptical in cross-section. However, the lingual surface is subplanar, while the labial surface is more convex. Both distal and mesial surfaces exhibit a basiapical carina, expanding downward from the apex to the end of the enamel cap. The enamel is covered by parallel basiapical striations.

Remarks – Conical teeth with mesial and distal carina are commonly found in Amiiformes (Sweetman, 2007; Ullmann *et al.*, 2012; Oreska *et al.*, 2013). With an ornamented enamel lingually flattened and labially convex, a well-developed carina expanding along the crown, the teeth are similar to those observed in *Caturus* Agassiz, 1834 (Kriwet *et al.*, 1997; Buscalioni *et al.*, 2008. fig 4; Cuny *et al.*, 2010. fig 4; Müller, 2011. fig 8), and therefore this conservative assessment was chosen.

Neopterygii indet.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02

Material – 7 vertebra centra (**Figure 28**, E1-E2)

Description – None of the centra are complete, and only one preserved the notochordal canal. They are subcircular in anteroposterior view. The centra are deeply amphicoelous, with the notochordal canal widely opened. Their diameter is longer than the anteroposterior axis. The anterior and posterior surfaces are smooth. The lateral surfaces are convex, mainly smooth, except for two elliptic pits which extend along the anteroposterior axis.

Remarks – Circular, deep amphicoelous vertebra, with a notochordal canal opened and a large height-to-anteroposterior width ratio, are typical of “fishes” (Brinkman *et al.*, 2005b; Cuny *et al.*, 2010. fig 4; Oreska *et al.*, 2013). The two pits may be described as articulation pit for the haemal arch (Buscalioni *et al.*, 2008). Nevertheless, because of the lack of well-preserved specimens, the vertebrae have been conservatively attributed only to Neopterygii.

Actinopterygii indet.

Localities – ZIM-06-17-01

Material – 1 pharyngeal element (**Figure 28**, F)

Description – The specimen is broken, and no tooth crown has been preserved. It is subovoid shape. One surface is smooth, while the other one is covered by subcircular to ovoid structures composed of enamel, suggesting they are base of tooth crowns. They a compressed along the longer axis of the fragment, and three are aligned along this axis. At least three to four other unpreserved teeth are aligned on the right part of the longer axis, but none on the left part.

Remarks – The structure of the specimen is similar to vomer and other pharyngeal elements in Actinopterygii by the structure and the disposition of the teeth (Sweetman, 2007. fig 3.2; Cuny *et al.*, 2010. fig 2; Müller, 2011; Oreska *et al.*, 2013), however the poor preservation and the lack of any preserved teeth prevent a more specific identification.

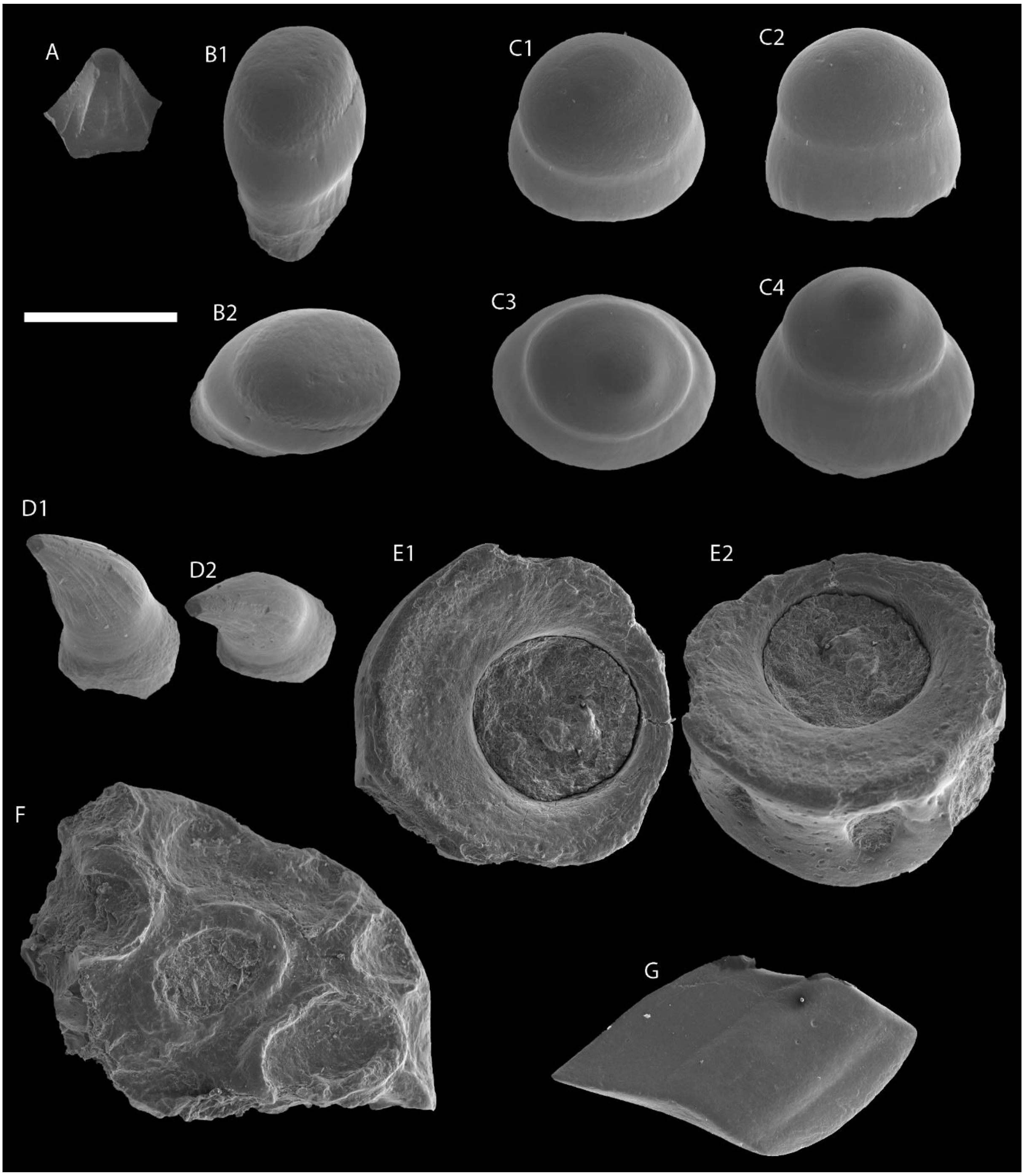

Figure 28: Fish material recovered from the three VMAs. **A**, *Hybodus* tooth; **B1-B2**, Pycnodontiformes tooth in lateroapical and apical views; **C1-C4**, *Lepidotes* teeth in apical, lateral, apical, and lateroapical views; **D1-D2**, *Caturus* tooth in apicolateral and apical views; **E1-E2**, fish vertebra in antero/posterior and antero/postero-ventral views; **F**, Actinopterygii pharyngeal element in ventral view; **G**, Actinopterygii ganoid scale in ventral view. Scale bar is 1mm.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-0; VAL-06-16-01

Material – 329 isolated scales (**Figure 28**, G)

Description – Scales are subcircular to angular rhombic, with unserrated edges. The inner surface exhibits a ridge, expanding on one end into a small peg fitting in a small articular notch in the other end of the next scale. The outer surface is smooth. The scales are covered with unornamented enamel-like layer of ganoine. This layer is not preserved in all the scales, and in those cases, they show evidences of growth rings.

Remarks – Fish scales are ubiquitous in most of the vertebrate microfossil assemblages (Brinkman *et al*., 2005b; Ullmann *et al*., 2012; Oreska *et al*., 2013; Gilbert *et al*., 2018), and they are the most common item from the three localities. They have characteristic of ganoid scales (Brinkman, 1990; Buscalioni *et al*., 2008; Cuny *et al*., 2010; Müller, 2011; Moran, 2011), which are rigid and jointed articulating scales, covered by a thin hydroxyapatite layer, called ganoine, on top of a bony foundation (Helfman *et al*., 2009; Sherman *et al*., 2016). These scales are usually attributed to *Lepidotes* or other Semionotiformes fishes (Poyato-Ariza *et al*., 1999; Kriwet, 2000; Cuny *et al*., 2010; Müller, 2011; Oreska *et al*., 2013), but they are actually also present in other non-teleostean taxa (Buscalioni *et al*., 2008; Gilbert *et al*., 2018) and thus will be consequently conservatively attributed only to a non-teleostean Actonopterygii.

SARCOPTERYGII Romer, 1955
TETRAPODA Goodrich, 1930
LISSAMPHIBIA Haeckel, 1866
ALLOCAUDATA Fox an& Naylor, 1982
ALBANERPETONTIDAE Fox & Naylor, 1982
Celtedens McGowan & Evans, 1995
Celtedens guimarotae (Wiechmann, 2004).

Localities – VAL-06-16-01

Material – 3 proximal parts of femora, 3 distal parts femora (**Figure 29**, A1-A2; B1-B2)

Description – The femoral head is not preserved, but the contact with the epiphysis is convex in antero-posterior view. In the distal part, the femur shaft expands laterero-medially to form the triangular-shaped head. The center of the head exhibits a subtriangular to subcircular fossa delimited by two crests in anterior view. In the proximal part of the femur, the condyles are not preserved either, but the shaft seems to enlarge latero-medially with two crests delimited a small fossa on the posterior surface. The fossa expands into a thin proximo-distal groove, in the middle of the axis of the shaft.

Remarks – Femora of albanerpetontids are not commonly found and are poorly diagnostic. However, the features observed in the distal part (triangular-shaped head, subtriangular to subcircular fossa delimited by two crests) and the proximal part (small posterior fossa delimited by two crests expanding into a thin proximo-distal groove) have been reported in material from Guimarota which has been attributed to *C. guimarotae*; and differ from *Albanerpeton* femora, which have an undulated shaft and a shorter femoral head (Wiechmann, 2004. plate XII). Consequently, the material was attributed to *C. guimarotae*, confirming the presence of the taxa in the Lourinhã Fm.

Albanerpetontidae indet.

Localities – PB-10-17-02

Material – 1 frontal (**Figure 29**, C1-C4)

Description – The frontal is fused, but the intranasal process, the anterolateral process and the prefrontal contact have not been preserved. In dorso-ventral view, the shape is subtriangular with the ventrolateral margin and the orbital margins diverging laterally on both sides. In lateral view, the orbital margin is expanding dorsally in the posterior part, while it is expanding ventraly in the anterior part, giving it an undulated axis. In ventral view, the suture can be seen in the middle of the frontal. Two faint anteroposterior crests can be seen between the suture and the ventrolateral margins. In dorsal view, the surface is smooth, and no ornamentation is observed.

Remarks – The fused frontal is a characteristic of albanerpetontids (Estes & Hoffstetter, 1976; Wiechmann, 2000, 2004; Oreska *et al.*, 2013; Sweetman & Gardner, 2013), and its elongated narrow shape is characteristic to the material attributed to *Anoualerpeton* Gardner *et al.*, 2003 from the Lower Cretaceous of Morocco (Gardner *et al.*, 2003. figs 1, 2, 4). However, the missing anterior part, one of the diagnostic features to distinguish the genera within albanerpetontids, and the absence of any kind of ornamentation, another key diagnostic feature of the family, leads to identify this frontal only to Albanerpetontidae.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Material – 14 dentaries (**Figure 29**, D1-D3; D4-D6)

Description – Dentaries are commonly recovered from the three studied localities, but none of them is complete and only few exhibit complete teeth. The dentaries are thin, and the longest ones are lingually curved, with pleurodont teeth. The subdental shelf is thin toward the anterior part and enlarge until the subtriangular opening for the Meckelian canal. Its ventral part is round. The teeth are tubular and long, terminating in a labiolingual tricuspid crown. They are mesiodistally compressed, making their cross-sections ovoid at the base, but they become labiolingually compressed toward the top. On the longest dentary preserved, sixteen tooth sockets have been counted. None of the dentaries seems to preserve the symphyseal end. The labial surface is smooth and exhibits foramen which seem to be on the posterior-most part of the bone according the longest specimen.

Remarks – While none of them is complete, the dentaries recovered from all localities exhibit features that are commonly observed in albanerpetontids (Estes & Hoffstetter, 1976; Gardner, 1999; Wiechmann, 2000, 2004; Rees *et al.*, 2002; Company & Szentesi, 2012; Oreska *et al.*, 2013; Sweetman & Gardner, 2013), notably the tricuspid pleurodont tooth which is one of the diagnostic features of the family (Gardner, 2001), the lingual curvation, the subtriangular opening for the Meckelian canal of the subdental shelf, or the presence of foramen on the labial surface. However, because of their incompletness, they have been identified only to the family level.

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Material – 31 vertebrae (**Figure 29**, E1-E4)

Description – Vertebrae are the most common albanerpetontid remains recovered from the three localities, however most of them only preserved the centrum and only few preserved the neural arch and/or the transverse processes. The vertebrae are amphicoelous, with an anteroposterior hourglass shape, and the concave interlocking surfaces. A longitudinal crest extends laterally on the anteroposterior axis, in the middle of the body, and are connected to the neural arch and the transverse processes. The neural arch has a small fossa at the base, on its anterior surface.

Remarks – The vertebral bodies observed share the hourglass shape with lateral crests characteristic to albanerpetontid, (Estes & Hoffstetter, 1976; Gardner, 1999; Wiechmann, 2000, Wiechmann, 2004. plate XI; Oreska *et al.*, 2013. fig 8; Sweetman & Gardner, 2013. fig 11). However, because of their poor preservation, they have been identified only to the family level.

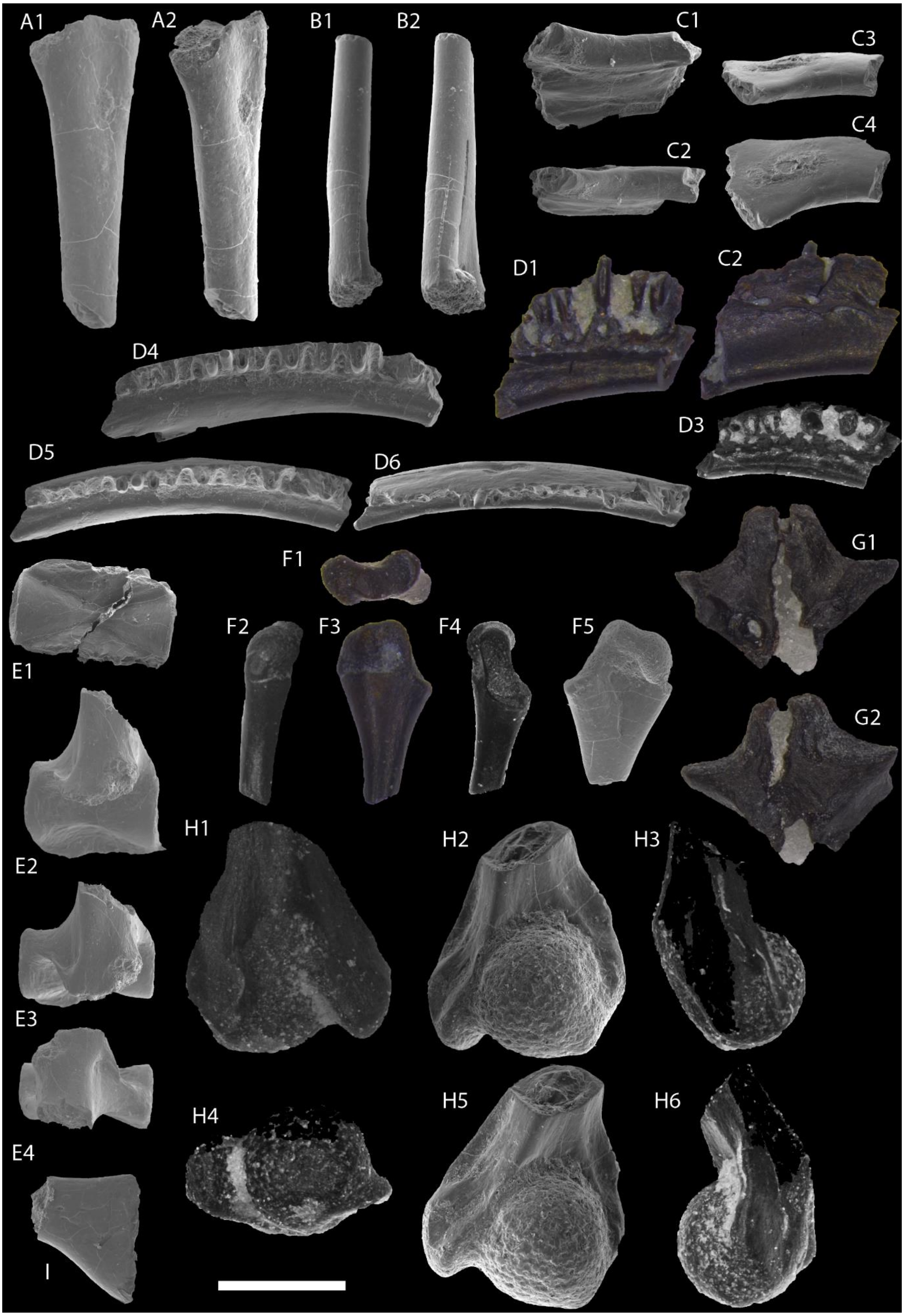

Figure 29: Amphibian material recovered from the three VMAs. **A1-A2**, *Celtedens guimarotae* proximal femur in lateroanterior and lateral views; **B1-B2**, *Celtedens guimarotae* distal femur in lateral and lateroposterior views;

C1-C4, albanerpetontid frontal in ventral, lateroventral, laterodorsal, and dorsal views; **D1-D3**, albanerpetontid dentary in medial, ventrolateral, and dorsal views; **D4-D6**, albanerpetontid dentary in mediodorsal, dorsal, laterodorsal views; **E1-E4**, albanerpetontid vertebrae in ventral, dorsal, laterodorsal, and lateral views; **F1-F5**, albanerpetontid proximal humerus in proximal, medial, posterior, lateral, and anterior views; **G1-G2**, Scapherpetontidae atlas in ventral and dorsal views; **H1-H6**, discoglossid distal humerus in posterior, anterior, medial, distal, apicoanterior, and lateral views; **I**, lissamphibian ilium in medial/lateral view. Scale bar is 1mm.

Localities – ZIM-06-17-01

Material – 2 proximal parts of a right humeri (**Figure 29**, F1-F5)

Description – The proximal part of the humerus is broken below the upper depression. The overall shape is pentagonal. The humeral head is in two parts: one sub-hemispherical, pointing anteromesially, and one more cylindric toward the ventral crest. In proximal view, the humeral head curves posteriorly. Both ventral and dorsal crests delimite the upper depression, which is subtriangular. The surface laterally connecting the ventral crest and humeral head is oblong, with an irregular texture. Following this surface, the ventral crest extends laterally.

Remarks – The proximal part of the humerus is rarely used to identify albanerpetontids, but the humeral head is usually less developed than the radial condyle (Sweetman & Gardner, 2013). It differs from *Celtedens guimarotae* (McGowan & Evans, 1995), where the proximal part of the humerus is more square, with a ventral crest less laterally extended (Wiechmann, 2000, Wiechmann, 2004. plate XII). However, this lateral expansion of the ventral crest has been observed in *A. inexpectatum* or in *Wesserpeton evansae* Sweetman & Gardner, 2013, with which this humerus is similar (Estes & Hoffstetter, 1976; Wiechmann, 2004. plate XII; Sweetman & Gardner, 2013. fig 11). However, since *A. inexpectatum* is from the Miocene of France and. *W. evansae* is from the Barremian of England, and because of its poor preservation, the specimen has been only attributed to Albanerpetontidae.

CAUDATA Scopoli, 1777

URODELA, Duméril, 1806

SCAPHERPETONTIDAE Auffenberg & Goin, 1959

Scapherpetontidae indet.

Localities – VAL-06-16-01

Material – 1 atlas (**Figure 29**, G1-G2)

Description – The odontoid process is not preserved. The overall shape is trullate, shaped like a bricklayer's trowel, in dorsal and ventral views. The anterior cotyles expend laterally, with deltoid to flabellate articular facets, perpendicular to the anteroposterior axis.

Remarks – Atlantes of scapherpetontids are one of the characteristics features of this group, with a base of the odontoid process straight to constricted and subcircular cotyles (Gardner, 2005. fig 10.1; Oreska *et al*., 2013. fig 7), features observed in the specimen from Valmitão. It differs from those in albanerpetontids by exhibiting a slender base to the odontoid process (Gardner, 1999. fig 2, Wiechmann, 2004. plate XI), its overal shape supports a salamander origin (Evans & Milner, 1996. fig.9). However, because of the poor preservation of the specimen and the lack of the odontoid process, one diagnostic feature, no closer identification could have been reached. Also, if this is confirmed later, this specimen will be the first record in Europe so far, and the oldest in the world, the family having been restricted to the mid-Cretaceous to Eocene of North America (Gardner, 2005).

ANURA Fischer von Waldheim, 1813

DISCOGLOSSIDAE Günther, 1858

Discoglossidae indet.

Localities – ZIM-06-17-01

Material – 1 distal part of a left humerus (**Figure 29**, H1-H6)

Description – The distal part of the humerus is broken before the foramen, but the part preserved is in fair condition. The humeral ball is hemispherical, protuberant, and fully ossified, with a width two-third of the width between the ulnar epicondyle and the radial epicondyle. The ulnar epicondyle is round in lateral view and is connected to the shaft by the ulnar crest. It exhibits a small groove on this anterior part, extending from the middle to the top. The anterior-most ridge of this groove extends to a crest connected to the shaft, following the contact with the radial condyle, while the other one ends with the condyle. The radial epicondyle is weaker than both the humeral ball and the ulnar epicondyle and it is connected to the shaft by the radial crest. The fossa cubitus ventralis is not entirely preserved, but it seems to be triangular, touching the radial condyle on its top. On posterior and medial views, an olecranon scar can be observed, extending from the base of the humeral ball to approximately its top.

Remarks – While only the distal part has been preserved, the humerus can be easily assigned to amphibians thanks to the shape of its protuberant, ossified humeral ball, as it has been observed in Guimarota material (Estes & Hoffstetter, 1976; Gardner, 1999; Rage & Hossini, 2000; Wiechmann, 2000, 2004; Sweetman, 2007; Sweetman & Gardner, 2012; Oreska *et al.*, 2013). A complex ulnar condyle and an extended olecranon scar have been observed in discoglossid from Quarry 9 in Como Bluff (Evans & Milner, 1993. fig 3), and that is why this specimen is identified as an undertemined discoglossid (Blain, pers. comm.). However, a putative albanerpetontid origin cannot be ruled out, as they exhibit a fully ossified humeral ball, a similar distal part of the humerus, and have been recovered from the Guimarota mine and the Lourinhã Fm. (Weichmann, 2000; 2004). The distal part of the humerus differs from those observed in *Celtedens guimarotae* Wiechmann, 2004 and other Portuguese specimens by having a more developed and complex ulnar condyle, while those features have been observed in *Albanerpeton* Estes & Hoffstetter, 1976 (Wiechmann, 2004. plate XII). However, it differs from *Albanerpeton inexpectatum* Estes & Hoffstetter, 1976 by being less massive (Estes & Hoffstetter, 1976; Wiechmann, 2004. plate XII), and so similar to what have been observed in material refered to *A. nexuosum* (Estes, 1981) from the Upper Cretaceous of Spain (Blain *et al.*, 2010. fig 2) and undetermined albanerpetontid from Uña, Barremian in age from Spain (Wiechmann, 2004. plate XII). Consequently, since first occurrence of Albanerpetontidae is from the Early Cretaceous, the humerus has been attributed to an undetermined discoglossid (Blain, pers. comm.), even though an albanerpetontid origin cannot be entirely rejected and would suggest a higher albanerpetontid diversity than previously reported for the Late Jurassic of Portugal.

Lissamphibia indet.

Localities – ZIM-06-17-01

Material – 1 proximal part of a scapula (**Figure 29**, I)

Description – Only the proximal-most part of the scapula has been preserved. Its overall shape is subtriangular to boot-shaped. Both surfaces are smooth, except for four small foramina. Three of them are located near the broken part, and organized in a triangle, while the fourth one is below the middle one.

Remarks – The subtriangular to boot-shaped morphology is similar to other ilia observed in amphibians (Evans & Milner, 1993; Gardner, 2005; Blain *et al.*, 2010; Gardner & DeMar, 2013; Oreska *et al.*, 2013; Sweetman & Gardner, 2013). However, the absence of the acetabular fossa,a dorsal tubercule, nor an acetabulum refute this hypothesis; while, the morphology is closed to wht is observed for the scapula in discoglossids (Blain, pers. comm.). This specimen remains problematic, as so its identification and assesment, that could be later refuted.

AMNIOTA Haeckel, 1866
SAUROPSIDA Huxley, 1864
DIAPSIDA Osborn, 1903
LEPIDOSAURIA Haeckel, 1866
SQUAMATA Oppel, 1811
SCINCOMORPHA Camp, 1923
PARAMACELLODIDAE Estes, 1983
Paramacellodidae indet.

Localities – ZIM-06-17-01; VAL-06-16-01

Material – 6 frontals (**Figure 30**; A)

Description – Flat bones, heavily built. One surface is smooth or occasionally faintly striated, while the other one is sculptured with an irregular pattern of pits and grooves.

Remarks – While extremely fragmentary, the sculptured pattern exhibited by the specimens is similar to the one observed in frontals of *Paramacellodus* Hoffstetter, 1967 in both Guimarota (Broschinski, 2000. fig 9.7) and United States (Evans & Chure, 1998; Nydam & Cifelli, 2002. fig 5). However, because it is highly fragmented and mostly incomplete, it has been identified only to Paramacellodidae.

Localities – PB-10-17-02

Material – 1 dentary (**Figure 30**; B1-B3)

Description – The fragment is long but broken on both extremities. The supradental shelf is smooth and concave, while the labial surface is not preserved, but a small crest labially extends on the ventral surface. Th ventral surface is preserved. Two pleurodont teeth are preserved. They are higher than wide, with an overall conical shape. However, the base of the crown is square and slightly mesiodistally compressed, while the crown becomes more labiolingually compressed toward the top. The enamel preserved on the top of one tooth exhibits six basiapical parallel striae. The apex is not preserved, but its axis seems to be slightly rotated.

Remarks – While the bone is poorly preserved, its ventral surface supports the identification as a dentary, and both preserved pleurodont teeth share similarities with teeth observed in Paramacellodidae: tall proportions, a swollen base, a crown concavity, and rotated cusps on the apex (Waldman & Evans, 1994. fig 4; Nydam & Cifelli, 2002. fig 8; Oreska *et al.*, 2013. fig 10). In that, the teeth are similar to what has been observed in *Paramacellodus* from the Guimarota mine (Broschinski, 2000. fig 9.12), but because of the missing apex, preventing observation of the cusps and the carina, a more conservative identification to Paramacellodidae has been chosen.

Scincomorpha indet.

Localities – PB-10-17-02

Material – 1 frontal part of a premaxilla? (**Figure 30**; C1-C2)

Description – Fragmentary bone surmounted by six teeth, one broken, three on each sides of the premaxilla. At the base of the teeth, the bone exhibits small foramina. Both rows are connected by a convex bony edge. Teeth seem to be acrodont, but it is hard to assess exactly because they are partially covered by matrix on their lingual surface. The pars furcata is broad an apically angular, terminating into a lingual cuspid. The labial cuspid is broader. Both cuspids are separated by a mesial and distal groove.

Remarks – Tooth support is one important key feature in identification within squamates, but it could not be confidently determined in this case. However, the fragment could be a premaxilla, the bony edges being part of the ascending process, which would explain the position of the teeth. The teeth, however, are similar to the type 9 observed in the Early Cretaceous of the Wessex Formation, notably by its columnar shape and the structure of the lingual cuspid and how it is separated from the labial one with mesial and distal grooves (Sweetman, 2007. fig 4.10), which has been attributed to Scincomorpha. Therefore, this identification has been followed, even if the crown has some similarties with *Becklesius* Estes, 1983 teeth observed in Guimarota mine in the cuspid shape (Broschinski, 2000. fig 9.9), but being slender. The poor preservation prevents a more precise identification confirming this hypothesis.

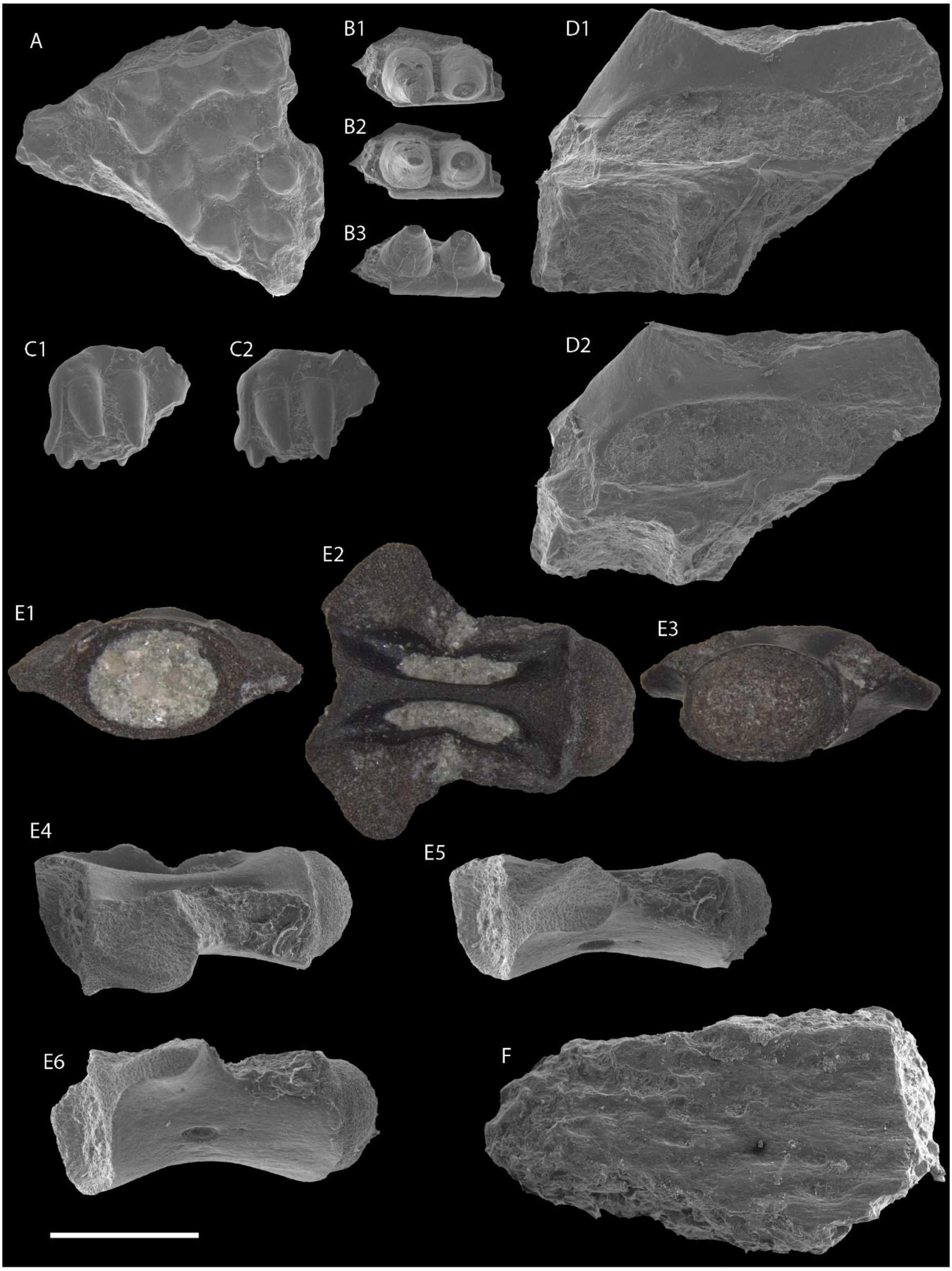

Figure 30: Squamate material recovered from the three VMAs. **A**, Paramacellodidae frontal in dorsal view; **B1-B3**, Paramacellodidae in dorso-labial, dorsal, and dorso-lingual views; **C1-C2**, Scincomorpha premaxilla in latero-ventral and lateral views; **D1-D2**, squamate maxilla in mesial and dorsomesial views; **E1-E6**, squamate vertebra in dorso-lateral, ventro-lateral, lateral, anterior, dorsal, and posterior views; **F**, squamate osteoderm in dorsal views. Scale bar is 1mm.

Squamata indet.

Localities – ZIM-06-17-01

Material – 1 maxillary? (**Figure 30**; D1-D2)

Description – Fragmentary piece of bone, composed of one shelf surmounted by one crest: the shelf is thick and exhibits one, maybe two, vertical perforations that could be tooth sockets. The anterior part of the crest is inclined and exhibits a smooth edge, which could be the narial margin. The top of the crest seems to be broken, but the edge seems to expand into an articular surface, partially preserved. Just below, a faint puncture is visible. At its base, the crest exhibits a fossa extending along most of the length of the fragment, and more than half of the height of the crest preserved and could be the fossa for the nasal capsule.

Remarks – The specimen is extremely fragmentary, but has been identified as a potential maxillary, without teeth preserved. However, because of its incompleteness, it has been identified only as Squamata.

Localities – VAL-06-16-01

Material – 1 vertebra (**Figure 30**; E1-E6)

Description – Only the body of the vertebra and two prezygapophyses have been preserved. The vertebra is procoelous, with a cylindric body. The interlocking surfaces are ovoid and are the same size. In lateral view, the body is convex dorsally and ventrally, with a more pronounced curved on the ventral face. The prezygapophyses are subtriangular to deltoid, and their surfaces are slightly inclined toward the anterior part. They connect to the body in the upper part of the anterior interlocking surface. The neural canal is crossed by two lateral grooves, constricting the body. Two subcentral foramina are present on the ventral surface, close to the anterior part of the vertebra. In ventral view, the margins of the body are parallel.

Remarks – Procoelous vertebrae are commonly observed in several squamate clades (Rage & Werner, 1999; Nydam, 2000. fig 5; Blain *et al.*, 2010. fig 6), and the vertebra shares affinities with anguimorphan ones with its cylindrical body and the subtriangular to deltoid prezygapophyses (Blain *et al.*, 2010). However, the convex ventral surface distinguishes the vertebra from others of this clade, where the ventral surface is flat (Blain *et al.*, 2010), and for that reason, it has been identified only as Squamata.

Localities – ZIM-06-17-01; VAL-06-16-01

Material – 7 osteoderms (**Figure 30**; F)

Description – Fragmentary flat bones with one smooth surface, while the other is ornamented by longitudinal ridges, either longitudinal or irregular.

Remarks – The specimens seem to be osteoderms, but they are different from those observed in crocodylomorphs by the absence of circular pits (Schwarz-Wings *et al.*, 2009. fig 4), and some of them exhibit a striated ornementation similar to those observed in paramacellodidae (Nydam & Cifelli, 2002. fig 6). However, because they are highly fragmented and incomplete, they have been identified only as Squamata.

ARCHOSAURIA Cope, 1870
AVEMETATARSALIA Benton, 1999
CROCODYLOMORPHA Walker, 1970 *sensu* Clark, 1986
MESOEUCROCODYLIA Whetstone & Whybrow, 1983 *sensu* Benton & Clark, 1988
NEOSUCHIA Benton & Clark, 1988
GONIOPHOLIDIDAE Cope, 1875

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Referred material – 33 isolated slender conical teeth from VAL-06-16-01 (**Figure 31**, A1-A4); 18 isolated blunt conical teeth from VAL-06-16-01 (**Figure 31**; B1-B4)

Size range – 0.964 to 1.793 mm wide / 1.931 to 3.337 mm high (ratio 1.790 to 2.943) for the slender conical teeth; 1.882 to 2.474 mm wide / 2.089 to 4.539 mm high (ratio 1.110 to 2.097) for the blunt conical teeth

Description – *Slender conical*- The teeth have a long slender conical shape, which can be triangular, acuminate or more belonid (needle-shaped), with a lingually curved apex (13° to 41°), and a weak mesiodistal constriction at the base of the crown. Their cross-section is labio-lingually compressed with ration from 0.719 to 0.985, resulting in a subcircular to ovoid base of the crown. In lateral view, the labial surface is convex toward the base of the crown, while the lingual surface is faintly flattened. The lingual and labial surfaces are separated by a carina in both mesial and distal margins. These carinae are adjacent to a concave basiapical groove on the lingual surface. On both surfaces, the enamel is composed of parallel basiapical ridges; six to ten on the lingual surface, seven to nine on labial surface. These ridges are more marked on the lingual surface than on the labial surface, which consequently appears smoother. On the lingual surface, the ridges extend from the base to the apex of the crown, while they only extend from the upper two-third of the crown on the labial surface. On both lingual and labial surfaces, the ridges join each other toward the apex, with the lateral-most ones parallel to the mesial and distal margins. However, some teeth exhibit a smooth enamel on both surfaces.

Broad conical- The teeth have a broad conical shape, which is lingually curved in the biggest ones (23° to 38°) and blunter in the smallest. Their cross-sections are labio-lingually compressed with ratio from 0.754 to 0.961, resulting in subcircular to ovoid base of the crown. In lateral view, the labial surface is convex toward the base, while the lingual surface is curved to straight according the size of the teeth. Lingual and labial surface are separate by a carina in both mesial and distal margins. These carinae are adjacent to a concave basiapical groove on the lingual surface, more prominent in the bigger teeth. On the lingual surface, the enamel is covered by nine to ten ridges from the base to the top, forming parallel striations which seem to join each other toward the apex. On the labial surface, the enamel is covered by eleven to twelve ridges from the base to the top, forming parallel striations too, but these ridges are smoother on the first third lower part of the tooth in the biggest teeth. In one tooth, almost none of the enamel has been preserved except a thin portion at the base of the crown. The enamel seems to be smooth on both surfaces.

Remarks – The tooth morphologies described here are characteristic of Goniopholididae (Averianov, 2000; Krebs & Schwarz, 2000; Salisbury, 2002; Schwarz, 2002; Schwarz-Wings *et al*., 2009; Kuzmin *et al*., 2013; Puértolas-Pascual *et al*., 2015). Nevertheless, these morphologies can be observed in other crocodylomorphs, in the anteriorly located teeth in taxa with heterodont dentition (Puértolas-Pascual *et al*., 2015). Despite this, all the teeth belonging to Goniopholididae exhibit conical teeth with weak labio-lingual compression and acute, curved apex, and with a carina more or less developed according the size of the crown. The enamel ridges also vary according to the size of the crown (Schwarz-Wings *et al*., 2009). It has been suggested there could be ontogenetic difference within *Goniopholis* (Schwarz-Wings *et al*., 2009), and small difference in the global morphologies of the teeth could be referred to different species within goniopholidids. Broad conical teeth have two overall shapes, that could be the result of their position in the tooth row. The taller and curved teeth would correspond with more mesial positions, probably in the mid-part of the jaw, while the blunter ones would be distally located, in the posterior part of the jaw. However the conservative approach prohibits tighter identification of these teeth, even if only specimens belonging to *Goniopholis* have been reported from Portugal up to now (Krebs & Schwarz, 2000; Schwarz-Wings, Rees, & Lindgren, 2009; Malafaia *et al*., 2010).

BERNISSARTIIDAE Dollo, 1883

Localities – PB-10-17-02; ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Referred material – 1 isolated conical tooth from VAL-06-16-01 (**Figure 31**, C1-C6); 18 isolated molariform teeth from VAL-06-16-01

Size range – 1.279 mm wide / height undetermined for the conical tooth; 0.976 mm to 2.553 mm wide / 0.711 to 1.484 mm high (ratio 0.581 to 0.795) for the molariform teeth.

Description – *Conical tooth*- The tooth is conical. The apex is not preserved, but it seems to be broad, and the base of the crown is constricted. Its cross-section is labio-lingually compressed with a ratio of 0.890, resulting in subcircular base of the crown. In lateral view, the lingual surface is convex, while the labial surface is flat. Both mesial and distal margins are broadened. The enamel is covered by fourteen ridges on the labial surface, and nineteen ridges on the lingual surfaces. On both surfaces, it forms on both surfaces parallel basiapical striations, extending on the upper two-thirds of the labial surface, but until the upper three-quarter of the lingual surface. However, since the apex is not preserved, the total length of the ridges cannot be determined.

Molariform teeth- The teeth are molariform, with bulky, low, round crown, blunt apex, and a mesiodistal constriction at the base of the crown. Their cross-sections are labio-lingually compressed, with ratio of 0.393 to 0.553, resulting in elliptical, reniform base of the crown. Some teeth exhibit a weak groove on the lingual surface. In apical view, the lingual surface is concave while the labial surface is convex. No carinae have been observed on both mesial and distal margins, which are consequently broadened. The enamel is covered by 19 to 30 ridges on the labial surfaces, and 17 to 32 ridges on the lingual surfaces. It forms parallel basiapical striations on both surfaces extending on the two-third upper part of the teeth, but some teeth exhibit ridges from the base of the crown to the apex.

Remarks – The molariform crown with a reniform, or kidney-shaped, cross-section is a characteristic of Bernissartiidae (Buffetaut & Ford, 1979; Sanz *et al*., 1984; Schwarz-Wings *et al*., 2009; Ullmann *et al*., 2012; Puértolas-Pascual *et al*., 2015), and has been associated to a durophagous feeding diet. *Bernissartia* is usually associated with Cretaceous localities (Schwarz-Wings *et al*., 2009), but it has been reported from the

Guimarota mine microfossil vertebrate assemblage (Brinkmann, 1989; Krebs & Schwarz, 2000), which is approximately from the same age than Valmitão, and no other bernissartiid has been reported yet from the Lourinhã Formation. Conical teeth with lower, blunter crowns, with subcircular cross-section have been considered to come from most anterior part of the jaw in Bernissartiidae, while the molariform ones would come from posterior parts (Buffetaut & Ford, 1979; Schwarz-Wings *et al.*, 2009; Sweetman *et al.*, 2014 ; Puértolas-Pascual *et al.*, 2015). Bernissartiid teeth can be distinguish from atoposaurid teeth, such as *Theriosuchus*, by the lack of mesial and distal carniae, by the presence of basiapical, parallel ridges, by being multicuspid, and by their strong labiolingually compression (Salisbury & Naish, 2011; Tennant *et al.*, 2016).

ATOPOSAURIDAE Gervais, 1871

Theriosuchus Owen, 1879

Theriosuchus sp.

Localities – ZIM-06-17-01; VAL-06-16-01

Referred material – 14 isolated teeth from VAL-06-16-01 (**Figure 31**, D1-D3)

Size range – 1.490 to 1.949 mm high / 0.763 to 0.952 mm wide (ratio 1.940 to 2.457)

Description – The teeth are conical to sublanceolate, with a sharp lingually curved apex (29° to 43°), making it hamiform, or hook-shaped, in the smallest teeth. Their cross-sections are labiolingually compressed with a ratio of 0.409 to 0.815, resulting in a subcircular to elliptical base of the crown. Both distal and mesial margins exhibit a carina lacking denticles. Enamel is smooth on the labial surface, while it exhibits twelve to thirteen ridges forming striations on the lingual surface. These striations have a flabelliform, or fan-shaped distribution: the center-most ones are basiapically directed, while the lateral most ones are from the base of the crown and diverge to the carinae.

Remarks – Conical teeth with flabelliform basoapical striations on the enamel of labial surface, and a smooth enamel on the lingual surface, have been described as *Theriosuchus* teeth from the anterior part of the jaw (Brinkmann, 1992; Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Tennant *et al.*, 2016; Young *et al.*, 2016), supporting the identification to this genus for our sample. However, the hamiform, or hooked-shape, apex has never been reported before.

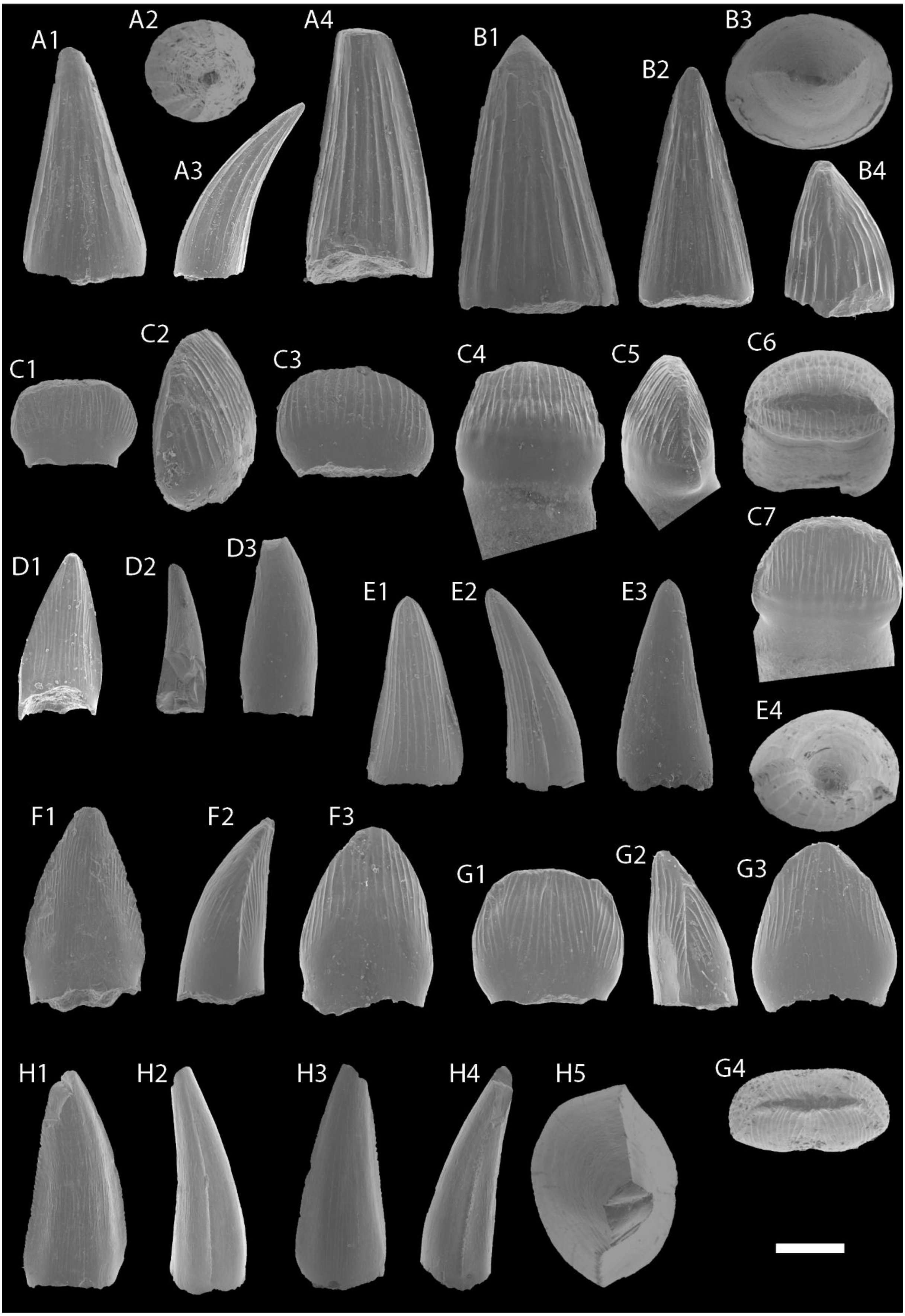

Figure 31: Crocodylomorph teeth assemblage from Valmitão. **A1-A4**, slender conical goniopholidid teeth, in labial, apical, lateral, and lingual views; **B1-B4**, broad conical goniopholidid teeth, in labial, lingual, apical, and

lateral views; **C1-C3**, molariform bernissartiid teeth in lingual, lateral, and labial views; **C4-C6**, molariform bernissartiid tooth with root preserved, in labial, lateral, lingual, and apical views; **D1-D3**, conical *Theriosuchus* teeth in lingual, lateral, and labial views; **E1-E4**, conical *Knoetschkesuchus* teeth in lingual, lateral, labial, and apical views; **F1-F3**, lanceolate to leaf-shaped atoposaurid teeth in lingual, lateral, and labial views; **G1-G4**, molariform atoposaurid teeth in lingual, lateral, labial, and apical views; **H1-H5**, ziphodont mesoeucrocodylian teeth, in labial, lateral, lingual, lateral, and apical views. Scale bar is 1mm (0.66mm for E1-E3, D1-D3, G1-G3, F2; 0.33mm for H3).

Knoetschkesuchus Schwarz *et al.*, 2017

Knoetschkesuchus sp.

Localities – PB-10-17-01; ZIM-06-17-01

Referred material – 11 isolated teeth from VAL-06-16-01 (**Figure 31**, E1-E4)

Size range – 0.667 to 0.773 mm wide / 1.223 to 1.345 mm high (ratio 1.582 to 2.016)

Description – The teeth are conical to sublanceolate, with lingually curved acute apex (16.403° to 20.397°). Their cross sections are labiolingually compressed with a ratio of 0.797 to 0.805, resulting in a subcircular base of the crown. Both distal and mesial margins exhibit a carina without denticles. In lateral view, the labial surface is convex at the base of the crown, as the lingual surface though it is less marked. The enamel on the labial surface can be smooth or covered by ten ridges, forming parallel basiapical striae. On the lingual surface, the enamel is covered by eleven to fourteen ridges forming basiapical stria, parallel to the distal and mesial margins.

Remarks – Conical teeth with parallel basoapical striations on the enamel of labial surface, and a smooth enamel on the lingual surface, have been as tooth morphology from the anterior part of the jaw of both Knoetschkesuchus species (Schwarz & Salisbury, 2005; Schwarz *et al.*, 2017), supporting the identification to this genus for our sample.

Atoposauridae indet. Gervais, 1871

Localities – PB-10-17-02; ZIM-06-17-01; VAL-06-16-01

Referred material – 10 isolated lanceolate teeth (**Figure 31**, F1-F3); 15 leaf-shaped teeth from VAL-06-16-01 (**Figure 31**, G1-G4)

Size range – 1.035 to 2.577 mm high / 0.760 to 1.680 mm wide (ratio 1.362 to 1.534) for the lanceolate teeth; 1.162 to 1.489 mm high / 1.043 to 1.474 mm wide (ratio 0.887 to 1.114) for the leaf-shaped teeth.

Description – *Lanceolate teeth*- Teeth are lanceolate, with a pointed apex and a weak mesiodistal constriction at the base of the crown. Their cross-sections are labiolingually compressed, with a ratio of 0.653 to 0.737, resulting in an elliptical base of the crown. Mesial and distal carinae are present. The labial surface is slightly convex, while the lingual surface is slightly concave. The enamel on the labial surface is smooth at the base and in the center of the crown, but exhibits parallel, longitudinal ridges, forming basiapical striations extending towards the distal and mesial margin carinae. On the lingual surface, the ridges cover almost all the upper part, leaving only the base and a small portion of the center smooth, forming striations with a flabelliform, or fan-shaped, distribution. The center-most ridges form striations extending up to the apex, while the lateral-most one extending up to the mesial and distal carinae. In some cases, these ridges may form false denticles in the carinae (false ziphodont).

Leaf-shaped teeth- Teeth are broad leaf-shaped, with a horizontal, blunt apex and a weak mesiodistal constriction at the base of the crown. Their cross-sections are labio-lingually compressed with a ratio of 0.531 to 0.629, resulting in an elliptical crown base. A faint carina is present in both mesial and distal margins, adjacent to a faint basiapical groove. The labial surface is strongly convex on the lower part, while less on the lingual surface. The enamel is covered by more than fifteen ridges on both labial and lingual surfaces forming vertical striations extending on the upper two-thirds of the crown. On the labial surface, striae are basiapical, while their distribution on the lingual surface gives the enamel a flabelliform ornamentation. In some cases, the contact of the ridges or striae with the carinae may form false ziphodont serrations.

Remarks – Teeth attributed to atoposaurids reflect the largest morphological variability observed in the sample, with three clear different morphologies usually attributed to *Theriosuchus*: conical, lanceolate, and broad leaf-shaped (Schwarz & Salisbury, 2005; Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Puértolas-Pascual *et al.*, 2015; (Schwarz *et al.*, 2017), which would be connected to the position of the tooth in the dental arcade, respectively from the rostrum to the distal part of the jaw (Schwarz-Wings *et al.*, 2009). If the conical teeth can be missinterpretated as goniopholidids, and the broad leaf-shaped as bernissaartids and have only been observed in *Sabresuchus ibericus* (Brinkmann, 1989) and *Theriosuchus pusillus* Owen, 1978 (Schwarz-Wings *et al.*, 2009; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011; Young *et al.*, 2016), the lanceolate form is characetristic of *Theriosuchus* (Brinkmann, 1989, 1992; Salisbury, 2002; Schwarz & Salisbury, 2005; Schwarz-Wings *et al.*, 2009). However, the pattern adopted by the ridges is specific to this genus and allow one to distinguish teeth regardless of their shapes. Indeed, *Theriosuchus* teeth exhibit ridges forming striations with a flabelliform distribution, with the central ridges leading towards the apex, and the mesial and distal ridges leading to the margins where they can form small false denticles (Schwarz-Wings *et al.* 2009; Puértolas-Pascual *et al.*, 2015). *Theriosuchus* is known from the Late Jurassic of Portugal (Krebs & Schwarz, 2000; Schwarz & Salisbury, 2005), but this attribution has lately been challenged (Schwarz *et al.*, 2017). Lanceolate and leaf-shaed teeth have been previously attributed to *Theriosuchus* teeth in other crocodylomorph faunal assemblages and *T. pusillus* (Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Gasca *et al.*, 2012; Puértolas-Pascual *et al.*, 2015; Tennant *et al.*, 2016; Young *et al.*, 2016); they have also been described as one morphology in *K. langenbergensis* and *K. guimarotae* (Schwarz & Salisbury, 2005; Schwarz *et al.*, 2017). The diversity observed in our sample could be the result of ontogenic variation (Schwarz-Wings *et al.*, 2009), but also reflects a higher atoposaurid diversity than previously thought, as it has already been proposed (Tennant & Mannion, 2014; Puértolas-Pascual *et al.*, 2015; Tennant *et al.*, 2016; Schwarz *et al.*, 2017), suggesting that both *Theriosuchus* and *Knoetschkesuchus* may have been present in Portugal during the Late Jurassic.

Figure 32: Archosaur material recovered from the three VMAs. ; **A1-A2**, crocodylomorph osteoderm in dorsal and ventral views; **B1-B4**, Rhamphorhynchidae tooth in lateral, lingual, basal, and apical views; **C**, unidentified pterosaur bone; **D**, archosaur tooth in lingual view; **E1-E7**, archosaur vertebra in anterior, ventral, ventrolateral, dorsal, dorsolateral, lateral, and posterior views; **F1-F5**, archosaur claw in proximal, distal, dorsal, lateral, and ventral views. Scale is 2mm (5mm for E).

Mesoeucrocodylia indet.

Localities – ZIM-11-16-02; VAL-06-16-01

Referred material – 5 isolated teeth from VAL-06-16-01 (**Figure 31**, H1-H5)

Size range – 3.595 to 3.653 mm high / 1,279 to 1.830 mm wide (ratio 1.996 to 2.354)

Description – The teeth are coronoid, or beak-shaped, to conical with a lingually curved (14.299° to 15.152°), sharp apex and a lateral curvature (7.600° to 12.531° to the right in lingual view). Their cross-sections are labiolingually compressed, with an occasional labially shifted center, with a ratio of 0.685 to 0.781, resulting in a lenticular base of the crown. The lingual surface is flat to weakly curved, while the labial one is convex toward the base. Both surfaces are separated by acute and crenate carinae where small true denticles can be observed, especially in the lower half of the carinae. The denticles have irregular size and shape. The enamel on both sides is smooth, but some teeth exhibit shallow ridges on the upper part, forming faint, diffuse striations.

Remarks – Teeth with true denticles on the carinae are called ziphodont (Prasad & de Lapparent de Broin, 2002; Puértolas-Pascual *et al.*, 2015), and have since long be applied to Mesoeucrocodylia genera without monophyletic relationships. The irregular shape and size of the denticles confirmed their crocodylomorph origins, and differs from others ziphodont teeth observed in theropods. Because of its ecological instead of phylogenetic value, it can not be used as a feature for taxonomic classification (Turner, 2006; Andrade & Bertini, 2008; Puértolas-Pascual *et al.*, 2015). However, the presence of these denticles, which are not observed in any other morphotypes, nor in all the usual families referred above, allows separation of this morphology from the rest.

Localities – ZIM-06-17-01; ZIM-11-16-02; VAL-06-16-01

Material – 39 osteoderms (**Figure 32**, A1-A2)

Description – The bones are flat and uncomplete. While the ventral surface is smooth, the dorsal surface is covered by subcircular pits. They are not equal in size, and they seem to be randomly distributed over the surface.

Remarks – While incomplete, the osteoderms' ornamentation with unequal-sized subcircular pits randomly distributed on the dorsal surface is similar to what can be observed in others mesoeucrocodylian taxa (Schwarz-Wings *et al.*, 2009. fig 4), but no closer attribution could be reached.

ORNITHODIRA Gauthier, 1986

PTEROSAURIA Kaup, 1834

RHAMPHORHYNCHIDAE Seeley, 1870

Rhamphorhynchidae indet

Localities – VAL-06-16-01

Material – 1 tooth (**Figure 32**, B1-B4)

Description – The tooth is ensiform to spikelike, being thin, long, conical tooth, and lingually curved. The base of the crown is labiolingually compressed, making the cross-section elliptical to ovoid. The apex is acute and compressed labiolingually, making it flattened in distal/mesial views, and it shows a weak lateral curvature. The upper half of the crown is covered by a thin layer of enamel (**Figure 33**). The enamel is smooth with faint parallel basiapical striations. The base of the enamel cap is irregular, expending more basally in distal and mesial surfaces than in labial and lingual ones.

Remarks – The spikelike shape of the teeth and the ornamentation of the enamel cap, with faint parallel basiapical striations and irregular base, are the same that the ones observed in Rhamphorhynchidae (Evans & Milner, 1994. fig 18.6; Wiechman & Gloy, 2000. fig 12.1; Sweetman, 2007. fig 5.5; Buscalioni *et al.*, 2008), supporting this conservative identification for the tooth, even though *Rhamphorhynchus* Meyer, 1846 is known from the Guimarota mine (Wiechman & Gloy, 2000).

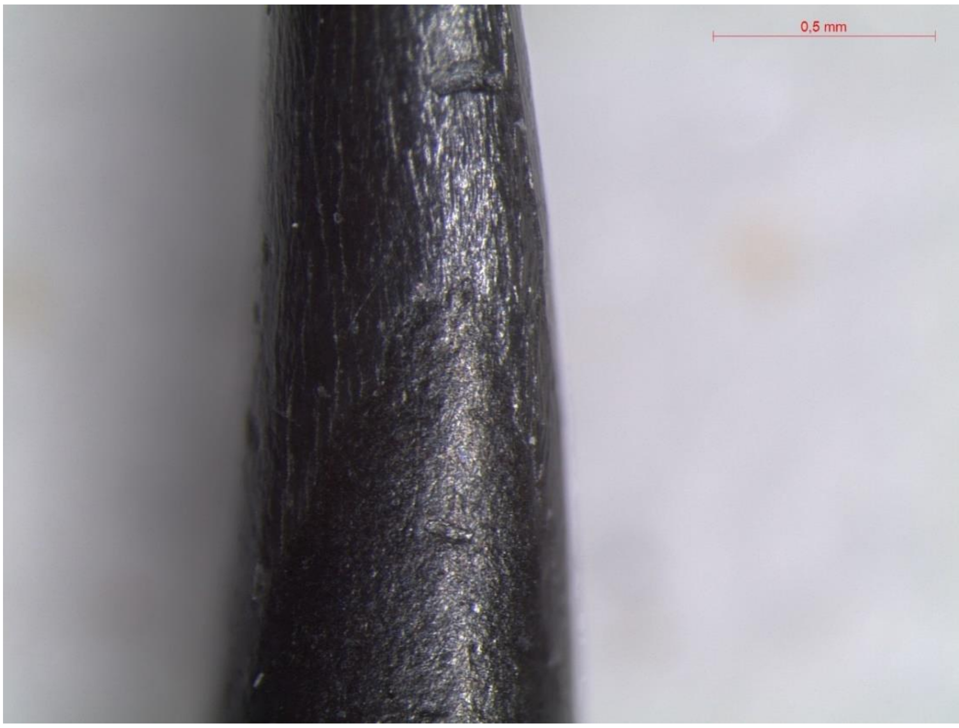

Figure 33: Detail on the enamel from Rhamphorhynchidae tooth. Scale is 0.5mm.

Pterosauria indet.

Localities – ZIM-11-16-02

Material – 1 unidentified bone (**Figure 32**, C)

Description – Fragmentary bone, slightly curved. The concave surface is smooth, while the convex one is covered by small pits. This surface exhibits small bony structures that erupt from the surface to possibly form some arches.

Remarks – The bone is unidentified, but it seems to be part of the shaft of a long bone, the smooth surface being the cortical surface, while the other one would be the medullar surface. If that is confirmed, the curvature of the bone would suggest a very large medullar cavity for a very thin cortical bone. The bony structures observed on the medullar surface could be part of the struts, inner structures developed in response to stress during flight (Rosenbach *et al.*, 2018). These observations would attribute this bone to Pterosauria, the size suggested by the curvature being far bigger than any pterosaur known from the Late Jurassic of Portugal, and it is probably from a different taxon than the tooth described above.

DINOSAURIA Owen, 1842
ORNITISCHIA Seeley, 1887
NEORNITHISCHIA Cooper, 1985
HYPSILOPHODONTIDAE Dollo, 1882
Phyllodon henkeli Thulborn, 1973

Localities – VAL-06-16-01

Material – half of an isolated maxillary tooth (**Figure 28**, F1-F2)

Description – The root and the apex are not preserved. The tooth is broken in half and seems to be subtriangular in overall shape, higher than wide, labiolingually compressed toward the top, and slightly labially/lingually curved. The base of the crown is swollen and seems to be strongly constricted. The lateral edge exhibits a carina with 5 strong triangular denticles, the uppermost one being broken, bending toward the apex, and similar in size. On the lateral part of the base, the crown is cordate, or heart-shaped, with two round ridges joining into a small triangular denticles just below the lowermost carina denticle and separate from it by a cingulum. The enamel appears to be smooth on both lingual and labial surface, and no ridges supporting the denticles are visible.

Remarks – The subtriangular crown higher than wide and the presence of strong denticles on its distal and mesial margins are diagnostic features of teeth attributed to

Phyllodon henkeli described from the Guimarota material (Rauhut, 2000. fig 11.1; Rauhut, 2001. fig 3), and the presence of a cingulum on the distal margin, also diagnostic, supports its assessment as a maxillary tooth, since dentary teeth do lack it (Rauhut, 2001). However, hypsilophodontid teeth enamel usually exhibits priary and secondary ridges supporting the denticles (Rauhut, 2001; Galton, 2006), which have not been observed in the specimen. However, secondary ridges can be weakly developped (Rauhut, 2001), and that may be the case is, and the primary ridge could have not been preserved as the tooth, is partially broken and the apex is not preserved.

Neornithischia indet.

Localities – ZIM-11-16-02

Material – 1 isolated maxillary tooth (**Figure 34**, D)

Description – The tooth is subrhomboid, with a convex apex in lingual/labial view, but acute in distal/mesial view, and a mesiodistally constricted base of the crown. The tooth is compressed labiolingually. The distal and mesial margins become more labiolingually compressed toward the apex. They both exhibit subtriangular denticles, pointed toward the apex. The labial surface exhibits a pronounced central ridge, while the denticles are in the extension of shallower lateral ridges. The enamel is smooth.

Remarks – The subrhomboid shape, the subtriangular denticles on mesial and distal margins, and the strong central ridge on the labial surface are similar to those observed in teeth usually attributed to Neornithischia (Galton, 2006; Ullmann *et al.*, 2012. fig 7; Oreska *et al.*, 2013. fig 13), and possibly to iguanodontian maxillary teeth fromGuimarota material (Rauhut, 2000. fig 11.3; Rauhut, 2001. fig 5). However, because of the lack of more diagnostic features and other specimens to compare, no closer identification has been given.

THYREOPHORA Nopsca, 1915

Thyreophora indet.

Localities – VAL-06-16-01

Material – 1 isolated tooth (**Figure 34**, B1-B2)

Description – The tooth is leaf-shaped, with a mesiodistally constricted base and labiolingual compression of the crown. The acute apex is subtriangular in labial/lingual view, with one side longer than the other one. The lingual surface of the lower part is slightly basiapically concave, while the labial surface is almost planar. The upper and lower part are separated by a horizontal groove, and the apex exhibits a mesiodistal groove on its margin. The enamel is smooth, and the tooth does not exhibit denticles.

Remarks – The tooth features (leaf-shaped, mesiodistally constricted base of the crown, subtriangular acute apex, smooth enamel) are similar to those observed in teeth usually attributed to Thyreophora (Norman *et al*., 2004; Galton, 2006; Canudo *et al*., 2010. fig 3; Ullmann *et al*. 2012. fig 7; Blows & Honeysett, 2013; Oreska *et al*., 2013. fig 13), and it differs from isolated teeth attributed to dinosaurs from the Guimarota mine (Rauhut, 2000; Rauhut, 2001). However the lack of diagnostic features prevent a tighter identification.

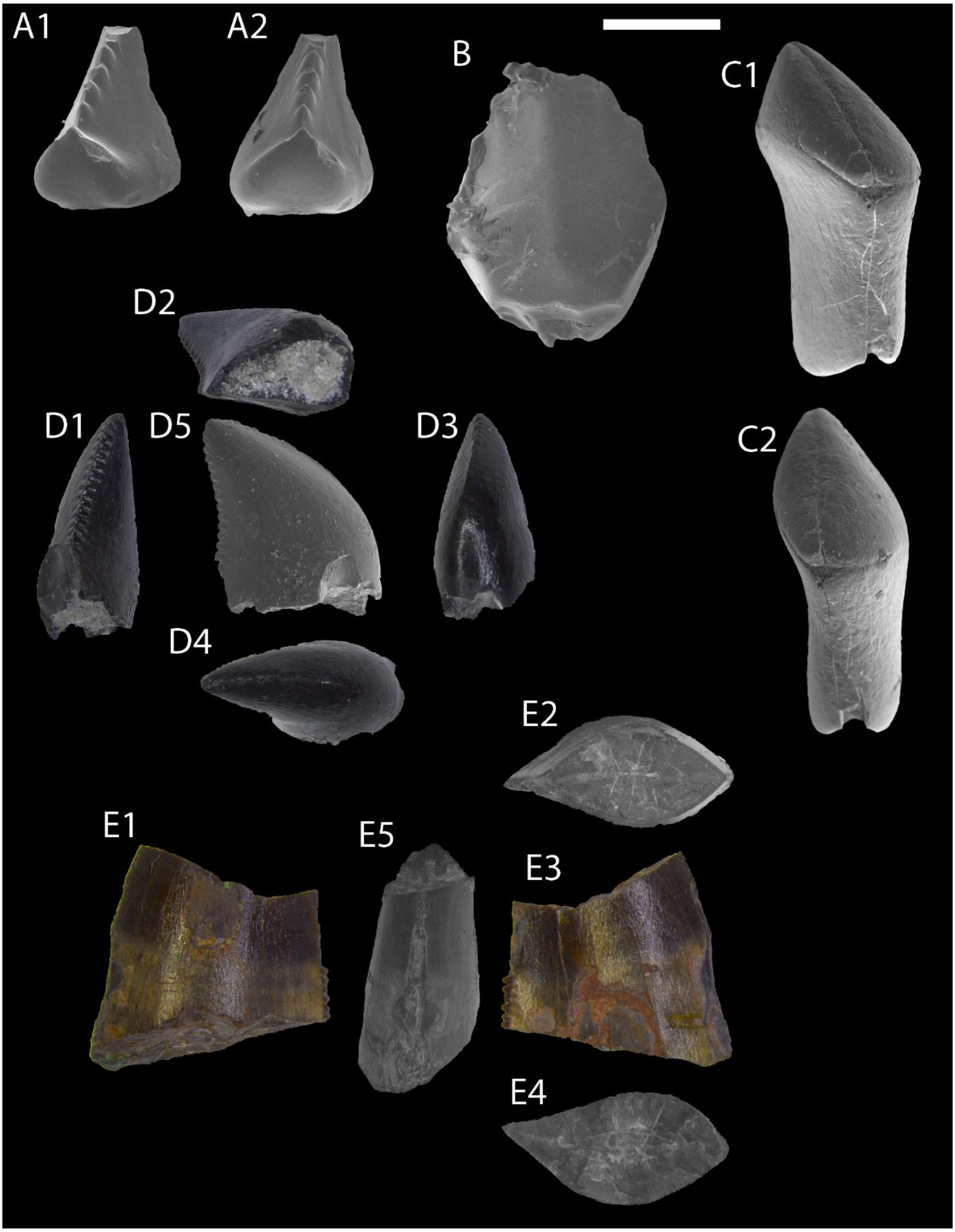

Figure 34: Dinosaur teeth material recovered from the three VMAs. **A1-A2**, *Phyllodon henkeli* maxillary tooth in labiodistal and distal views; **B**, neornistichian tooth in lingual view; **C1-C2**, tyreophoran tooth in latero-lingual and lateral view; **D1-D5**, *Richardoestesia* tooth in mesial, basal, distal, apical, and labial views; **E1-E5**, megalosaurid tooth in labial, apical, lingual, basal and, mesial views. Scale bar is 1mm (2mm for **E**).

SAURISCHIA Seeley, 1887

THEROPODA Marsh, 1881

COELUROSAURIA Huene, 1914

DROMAEOSAURIDAE Matthew & Brown, 1922

aff. *Richardoestesia* Currie *et al.*, 1990

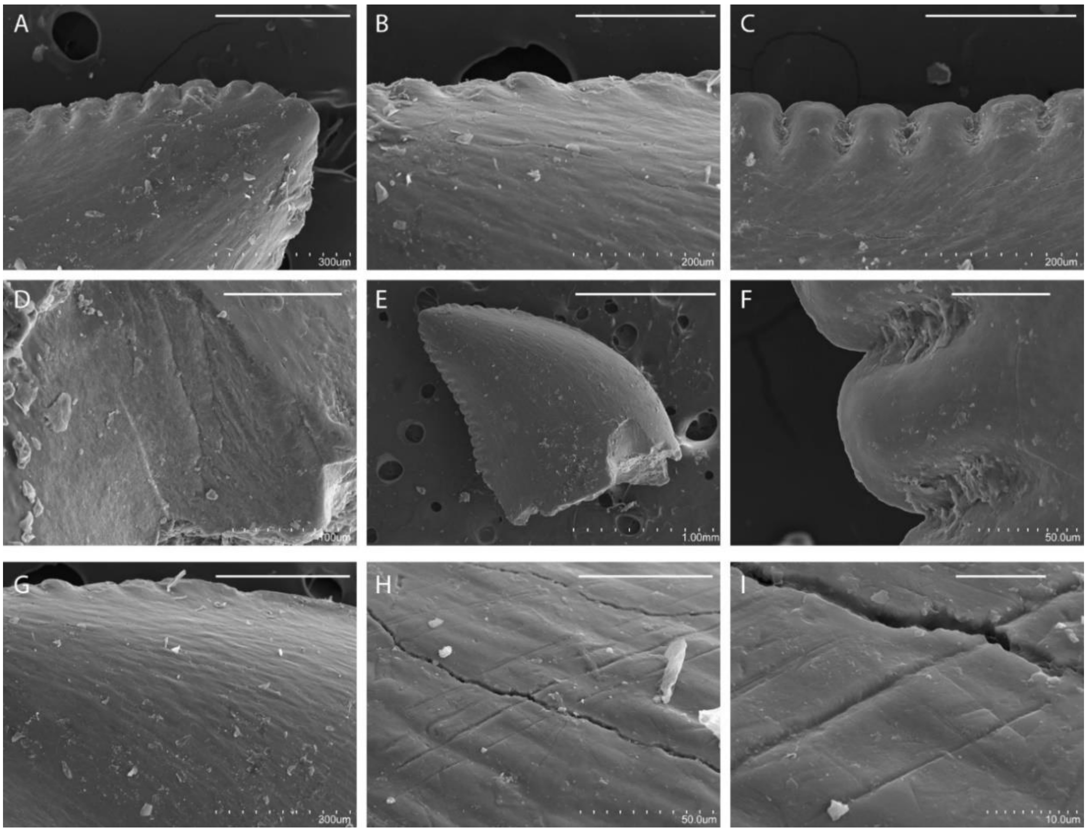

Figure 35: *Richardoestesia* tooth (**E**), with details of the denticles (**A-C**, **F**), the dentine (**D**), and the enamel (**G-I**). Scales are 1mm for E, 300µm for A, 200µm for B, C, G, 100µm for D, 50µm for F and H, 10µm for I.

Localities – VAL-06-16-01

Material – 2 isolated teeth (**Figure 34**, A1-A5; **Figure 35**, E)

Description – The teeth are broken at the base, preserving only the crown, and are mesiodistally constricted at the base. Because of the breakage, the cross-section at the base cannot be determined. They are foliodont, labiolingually compressed, distally curved, with a bulbous base of the crown and an acute apex. The distal surface is weakly concave, while the mesial surface is strongly convex. The mesial carina is serrated by denticles from the base to the apex (11 denticles/mm), while the distal carina is serrated only on the first third upper part. On the distal carina, the denticles are mesiodistally subquadrangular, perpendicular to the carina to slightly curved toward the apex for the apical-most one, with a symmetrically convex external margin, a shallow, narrow interdenticular space, and shallow, acuminate interdenticular slit (**Figure 35**, A, C, F). The denticles are of similar size, even though a slight decreasing basiapical gradient can be observed. On the mesial carina, the denticules are less well preserved, but they seem to be smaller in size, hook-shaped, apically inclined, with almost no interdenticular space (**Figure 35**, B). The enamel is preserved, and it is covered by small parallel basiapical striations (**Figure 35**, G). The enamel exhibits faint horizontal to oblique parallel grooves, interpreted as dental microwear texture patterns (**Figure 35**, H, I). Dentine is exposed in the broken part of the crown and exhibits narrow labiolingual holes (**Figure 35**, D).

Remarks – A basal constriction of the crown has been observed in many coelurosaurs, and low crown with small denticles are unlikely belonging to non-maniraptoriform theropods (Hendrickx & Mateus, 2014). The high number of denticles per millimeter has only been observed in *Richardoestesia* Currie *et al.*, 1990, and the morphological conditions observed in distal denticles are shared by *Richardoestesia gilmorei* Currie *et al.*, 1990 (Hendrickx & Mateus, 2014), while the shape of the crown is closer to what have been observed in *Richardoestesia* sp. (Baszio, 1997) and *Richardoestesia isosceles* (Sankey, 2001), all of them from the Late Cretaceous of North America. The dental microwear pattern is similar to what have been observed in other dromaeosaurids (Torices *et al.*, 2018). A tooth attributed to *Richardoestesia* aff. *Richardoestesia gilmorei* has been previously recovered from Valmitão (Hendrickx & Mateus, 2014); and similar teeth have been recovered from the Guimarota mine, but attributed to other dromaeosaurids, and different teeth have been attributed to *Richardoestesia* (Zinke, 1998; Rauhut, 2000). Consequently, only a conservative genus level identification as *Richardoestesia* has been applied for these specimens.

MEGALOSAUROIDEA Huxley, 1889
MEGALOSAURIDAE Huxley, 1869
Megalosauridae indet.

Localities – ZIM-11-16-02; VAL-06-16-01

Material – 1 isolated tooth (**Figure 34**, C1-C5), 1 carina with denticles

Description – The tooth is poorly preserved; the apex and the base of the crown being broken. However, the tooth seems to be ziphodont, labiolingually compressed, and weakly lingually curved toward the base. The cross-section is lenticular to lanceolate and becomes more lenticular toward the top. Both distal and mesial edge are straight, but the poor preservation prevents to be affirmative. The mesial carina is not preserved, while the distal carina is only preserved toward the base, exhibiting 6 denticles. The denticles are mesiodistally subquadrangular, nearly perpendicular to the carina, with a symmetrically convex external margin, a deep, wide interdenticular space, and deep, acuminate interdenticular slit. The enamel is partially preserved, and its texture seems to be irregular in both lingual and labial surfaces.

Remarks – The ziphodont shape and the lenticular to lanceolate cross-section suggest that the tooth is from Megalosauridae (Hendrickx & Mateus, 2014; Hendrickx *et al.*, 2015). However, because of its poor preservation, with the lack of the apex and most of the carinae, no tighter identification was possible.

Archosauria indet.

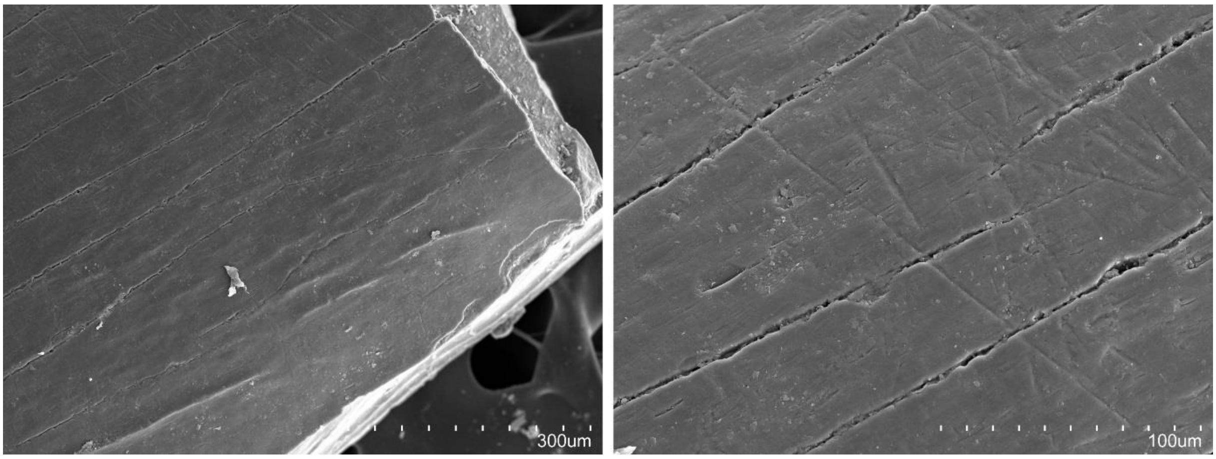

Figure 36: Details on the enamel of archosaurian tooth. Scale are 300 and 100µm.

Localities – PB-10-17-02

Material – 2 teeth (**Figure 32**, D)

Description – The teeth are slender conical. Neither the apex or the root is preserved. The enamel is covered by faint basiapical ridges near the margin (**Figure 36**, A). A carina is present on the margin preserved, with no denticles. On most of its surface, the enamel exhibits also faint horizontal to oblique non-parallel grooves, that cross each other, interpreted as dental microwear texture patterns (**Figure 36**, B).

Remarks – The teeth differ from what has been observed in amphibians and squamates by its size and overall robustness, the enamel and the absence of denticles distinguish them from theropods and pterosaurs, and the shape does not fit with ornithischian dinosaurs (Sweetman , 2007; Buscalioni *et al.*, 2008; Malafaia *et al.*, 2010; Ullmann *et al.*, 2012; Oreska *et al.*, 2013). The teeth are not preserved well enough to confirm a crocodylomorph identification and have consequently been attributed only to

Archosauria. The dental microwear texture patterns differ from those observed in carnivorous dinosaur (Torices *et al.*, 2018), suggesting another feeding behavior. While these scratches can cross, they seem to have two preferred direction, and those with the same direction are parallel, meaning the pattern has a high anisotropy (Scott *et al.*, 2005); which can be linked to grazers or flesh consumers (DeSantis, 2016).

Localities – ZIM-06-17-01; ZIM-11-16-02

Material – 2 vertebrae (**Figure 32**, E1-E7)

Description – Only the centrum has been preserved. The vertebrae are faintly amphicoelous, with an hourglass-shaped constricted centrum. The neural canal is marked by two fossae on both side of the body, making the centrum more constricted in dorsal view than in ventral view. Small foramina can be observed in the ventral surface. The interlocking surfaces are elliptic to lenticular in anteroposterior axis view, and the anterior one is smaller than the posterior one. The transverse processes are ventrally convex and are extending from one interlocking surface to the other.

Remarks – The amphicoelous and constricted body of the vertebrae shares affinities with archosaurian vertebrae, but no closer identification could be made because of the lack of more diagnostic characters.

Localities – ZIM-11-16-02; VAL-06-16-01

Material – 2 unguals. (**Figure 32**, F1-F5)

Description – The distal ungual phalanges are ventrally curved with an acute apex; the dorsal surface is convex while the ventral surface is flat. They bear a deep lateral groove along the entire longitudinal axis of the claw. In proximal view, the groove separates the distal ungual phalanges in two distinct parts, with the dorsal part bigger than the ventral one, giving an hourglass shape. Also, the unguals are mediolaterally compressed, the dorsoventral axis being longer than the mediolateral axis. The proximal part did not preserve the flexor and abductor tubercles.

Remarks – The claws are similar to archosaurian claws by being ventrally curved, with an acute apex and a deep lateral groove (Nesbitt, 2011. fig 49). The deep groove could be used for the attachment of keratinous claw. Their size would suggest they are from a juvenile or even an embryo. Nevertheless, no tighter identification than Archosauria could be made because of the lack of more diagnostic characters.

Sauropsida indet.

Localities – ZIM-06-17-01

Material – Dentary? (**Figure 37**, A1-A3)

Description – The heavily built bone is fragmented, but it preserved one convex surface covered by foramina. The broken bone exposed is covered by small holes. The inner surface seems to be rugose and exhibits tooth sockets. The subdental shelf is straight and its surface is smooth.

Remarks – The specimen has been identified as a probable piece of dentary. The tooth sockets would suggest they could be pleurodont, and the small holes observed on the broken surfaces suggest the bone was highly vascularized. Its heavy construction would exclude it from amphibians. However, because of its poor preservation and the absence of teeth, it has only been identified as Sauropsida.

Localities – VAL-06-16-01

Material – 1 Humerus? (**Figure 37**, B)

Description – Fragmentary piece of long bone, missing both distal and proximal end. The shaft is expanding mediolaterally at one of the extremities. On one side, the shaft is prolongated by a crest along its entire axis. The edge of the crest exhibits a small notch at the extremity where the shaft expands.

Remarks – This specimen has been identified as a humerus, the crest being interpreted as a deltopectoral crest. However, its taxonomic identification remains unknown: it differs from humeri usually observed in amphibian by being much more developed, as seen previously in the sample specimens. Combined with the developed deltopectoral crest, this suggests that this humerus can be identified as Sauropsida.

Localities – VAL-06-16-01

Material – Femur 1 (**Figure 37**, C1-C2)

Description – The femur shaft is slender and anteroposteriorly compressed. Only the lower part, with the condyles, is preserved. The condyles are hemispherical and have the same size and are connected to the shaft by the two supracondylar lines. A fossa surmounted the lateral condyle.

Remarks – The remains could have been identified as a femur, likely a left one. However, its taxonomic identity remains unknown, even if it differs from amphibian femora observed in the sample specimens, which would suggest it could belong to Sauropsida.

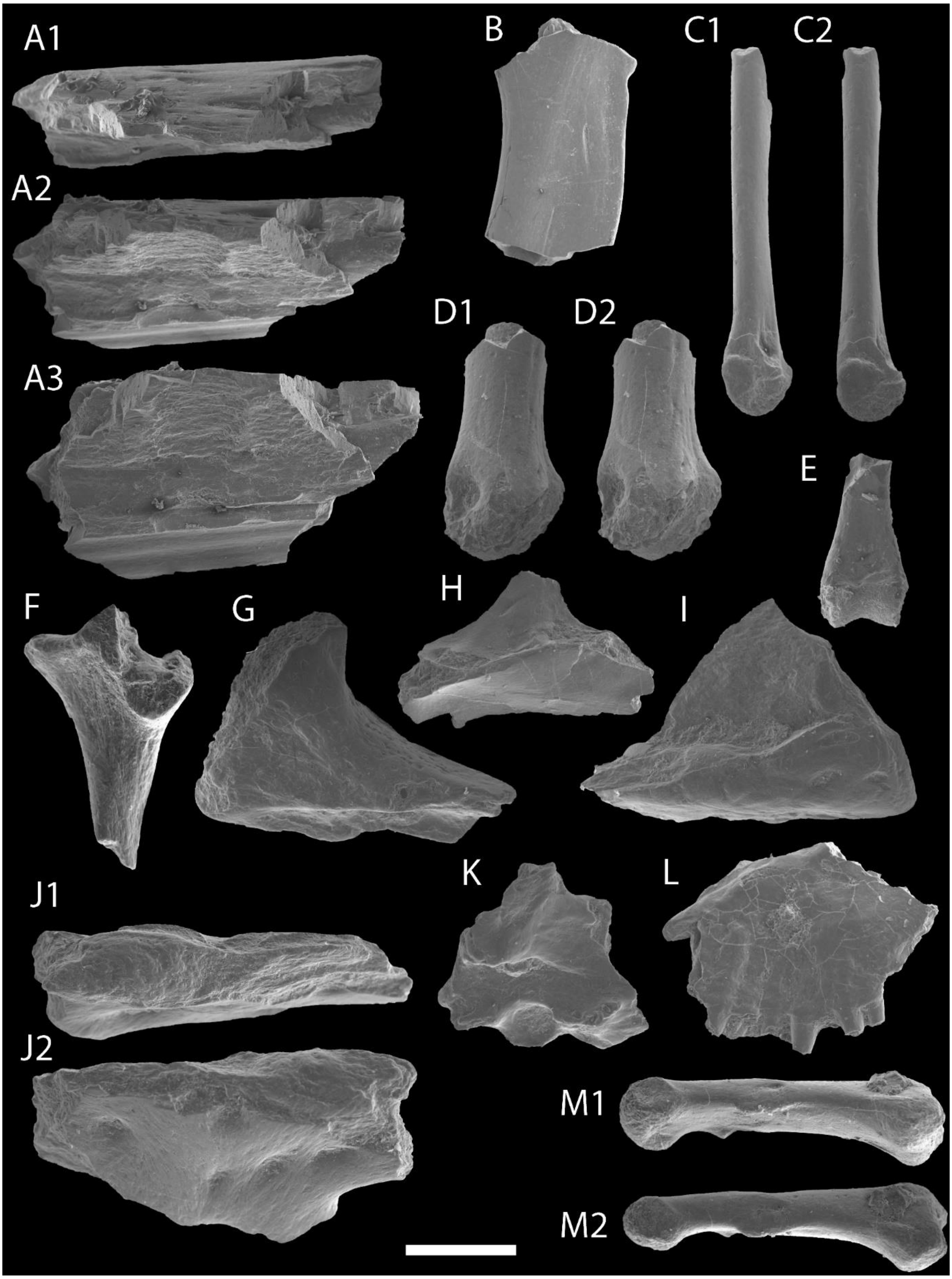

Figure 37: Fragmented bone sample with no precise taxonomic attribution material from the three VMAs. **A1-A3**, sauropsid dentary (?) in dorsolabial, dorsal, and dorsolingual views; **B**, sauropsid humerus (?) in anterior/posterior view; **C-D**, distal part of sauropsid femora in lateroposterior and lateral views; **E**, distal part of a saurpsid femora in posterior view; **F**, proximal part of a sauropsid tibia in posterior view; **G-K**, tetrapod cranial elements; **L**, tetrapod premaxilla; **M1-M2**, tetrapod phalanx in lateroventral and lateral views. Scale bar is 1mm (0.5mm for E, I, F1 and F; 2mm for M).

Localities – VAL-06-16-01

Material – Femur 2 (**Figure 37**, D1-D2)

Description – Only the distal part is preserved. The condyles, badly preserved, are rounded. One foramen is present anteriorly on the lateral side. On the posterior surface, from the intercondylar fossa, faint grooves extend vertically toward the shaft.

Remarks – While badly preserved, the fragment is identified as a femur. However, its taxonomic identity remains unknown, even if it differs from amphibian femora observed in the sample specimens, which would suggest it could belong to Sauropsida.

Localities – VAL-06-16-01

Material – Femur 3 (**Figure 37**, E)

Description – Only the distal part is preserved. The condyles are not preserved, but the section on both sides of the intercondylar fossa suggests they are round. The lateral line of the shaft is straight, in line with the condyle, while the medial line is oblique to the condyle and non-parallel to the lateral line. The intercondylar fossa is constricted in the center, making it hourglass-shaped.

Remarks – The remains could be identified as a femur, likely a right one. However, its taxonomic identity remains unknown, even if it differs from amphibian femora observed in the sample specimens, which would suggest it could belong to Sauropsida.

Localities – VAL-06-16-01

Material – 1 proximal part of a left tibia (**Figure 37**, F)

Description – Only the proximal part has been preserved. The shaft seems to be slightly lateromedially compressed. The lateral condyle and the lateral tibial plateau are perpendicular to the shaft. The medial tibial plateau deeps posterodistally on the medial condyle. The intercondylar eminence is not complete but seems to be acute. The posterior intercondylar area is triangular.

Remarks – The specimen has been identified as a proximal part of a left tibia. The shaft has only one medullary cavity, which excludes this bone from amphibians. However, because of its poor preservation and lack of distinct features, it has been assessed only to Sauropsida.

Tetrapoda indet.

Localities – PB-10-17-02

Material – Cranial element 1 (**Figure 37**, G)

Description – The bone is boot-shaped, with the anterior part expanding dorsally and being posterior curved. The ventral surface exhibit a groove, while the dorsal part is covered by small pits. The anterior part of the bone seems to be an articular surface.

Remarks – Cranial element 1 remains unidentified, while its shape is similar to a lachrymal bone, delimiting the ventral part of the orbit. However, because of its poor preservation and lack of distinct features, it has been identified only as Tetrapoda.

Localities – ZIM-11-16-02

Material – Cranial element 2 (**Figure 37**, H)

Description – The bone fragment is subpyramidal shaped, with one face longer than the two others. The three faces are smooth and convex toward the center of the fragment and are separated by sharp crests. The base of the two small faces are concave, and the crest separating them extends posteriorly.

Remarks – Cranial element 2 is unidentified, but the shape of the different crests may suggest they are ridges of two different fenestrae in the skull. However, because of its poor preservation and lack of distinct features, it has been identified only as Tetrapoda.

Localities – ZIM-11-16-02

Material – Cranial element 3 (**Figure 37**, I)

Description – The is composed of one tubular part at its base, surmounted by a bone plate. The tubular part of the bone has small foramina.

Remarks – Cranial element 3 is an unidentified bone, but its structure suggest is part of a skull. However, because of its poor preservation and lack of distinct features, it has been identified only as Tetrapoda.

Localities – ZIM-06-17-01

Material – Cranial element 4 (**Figure 37**, J1-J2)

Description – Fragmented flat bone, which seems to expand laterally toward its upper part. One smooth surface exhibits at least five foramina, three of them being aligned along the lateral expansion.

Remarks – Cranial element 4 remains unidentified, but its structure suggest is part of a skull. However, because of its poor preservation and lack of distinct features, it has been identified only as Tetrapoda.

Localities – PB-10-17-02

Material – Cranial element 5 (**Figure 37**, K)

Description – The fragment is a complex bone; its surface is composed by lots of reliefs.

Remarks – Cranial element 5 is an unidentified bone, but its structure suggests it is part of a skull. However, because of its poor preservation and lack of distinct features, it has been identified only as Tetrapoda.

Localities – PB-10-17-02

Material – 1 premaxilla (**Figure 37**, L)

Description – Bone fragmented, with some uncomplete teeth on one side. The surface is smooth, but the socket of the teeth can be observed. The bone seems to extend dorso-posteriorly toward the teeth, the edges seems to have articular surfaces. The teeth seem to be pleurodont and conical, with smooth enamel.

Remarks – The specimen is highly fragmented, but it could have been identified as a premaxilla. However, because of its poor preservation and the lack of complete teeth, it could only have been identified as Tetrapoda.

Localities – VAL-06-16-01

Material – 5 phalanges (**Figure 37**, M1-M2)

Description – The bones are long and cylindric, with a rounded distal part and a wide proximal part. The dorsal surface is convex, while the ventral surface is flat. In lateral view, the dorsal line is straight while the ventral line is weakly concave. The edges between the ventral and dorsal surface extend in a small crest at mid-length, on both sides. The crests are more distally pronounced. Above the crests, a small foramen can be observed. The distal head is composed of two round condyles. The proximal part is composed of two square condyles with a concave articular facet.

Remarks – The specimens could be identified as phalanges, without specifying if they are from the hand or the foot. Since all of them exhibit distal ends with two condyles, it can be assumed none of them are the distal-most ones. However, because they were isolated and lack diagnostic features, they only could have been identified as Tetrapoda. Also, even though some are broken, these elements include the only complete specimen recovered from the picking, beside teeth and fish scales.

3.2.2. TAXONOMIC ABUNDANCE AND DIVERSITY INDEXES

For the paleoecological analyses, the number of different taxa and the number of individual remains (bones, teeth, scales) that were identified to a taxon, or number of specimens, have been used. The taxonomic abundance of each locality has been assessed based on the counts from the different bulk samples used (Figure 38, *Table 7*, Annex 1). In term of abundance, Porto das Barcas and Zimbral are both dominated by obligate taxa (found either in the water column or in flood soils, and cannot survive without standing water), which represent respectively 50% and 48.93% of the total abundance, while Valmitão is dominated by amphibious taxa (spend at least part of their life cycle in wetlands and the remainder in a terrestrial environments), which represent 55.48% of the total abundance. In Zimbral, amphibious taxa are almost as common as obligate ones (47.64%), while the difference is more marked in Porto das Barcas (40.79%). In Valmitão, obligate taxa represent 36.75% of the total abundance, and are 33.76% less common than the amphibious ones. In the three localities, facultative taxa (can be found both in wetlands and terrestrial environments, and do not have to have part of their life cycle occurring in water) are the less abundant ones, with 9.21% for Porto das Barcas, 3.22% for Zimbral and 10.6% for Valmitão. In global abundance, it appears so that the three localities combined are dominated by amphibious taxa (49.76%), with obligate taxa slightly less abundant (44.9%), and facultative taxa are the least abundant (6.31%). This analysis represents only the abundance of specimen, which can be biased by the high number of fish scales and teeth that have been found.

In term of diversity, at the family level, it appears that Zimbral and Valmitão are both dominated by facultative taxa, with respectively 8 different taxa each (respectively 36.36% and 44.44%), while Porto das Barcas is dominated by amphibious taxa, with 5 different taxa (38.46%). In Zimbral, obligate taxa are as common as facultative ones, while amphibious taxa are the less common (6 different taxa, 27.27%). The same thing is observed in Porto das Barcas, where obligate and facultative taxa are both as common, with 4 different taxa each (30.77%); while in Valmitão, amphibious and obligate species are both as common, with 5 different taxa each (27.78%). In global diversity, it appears so that the three localities combined are dominated by facultative taxa, with 11 different taxa (44%), following by amphibious (8 taxa, 32%), and finally obligate (6 different taxa, 24%).

Table 7: Microfossil vertebrates remains identified by VMAs bulks.

	PB-10-17-02	*ZIM-06-17-01*	*ZIM-11-16-02*	*VAL-06-16-01*
Actinopterygii	30	149	60	101
Neopterygii	2	4	1	0
Semionotidae	1	4	4	1
Pycnodontiformes	0	2	2	0
Caturidae	2	1	1	2
Hybodontidae	3	0	0	0
Amphibian	0	4	1	0
Scapherpetontidae	0	0	0	1
Albanerpetontid	7	15	6	27
Crocodylomorph	24	72	124	129
Sauropsida	0	1	0	5
Lepidosaur	3	8	0	12
Scincomorpha	1	0	0	0
Paramacellodidae	1	1	0	5
Archosaur	2	1	2	1
Pterosaur	0	0	1	1
Dromaeosauridae	0	0	0	2
Megalosauridae	0	0	1	1
Thyreophora	0	0	0	1
Neornitischia	0	0	1	0

In addition to the specimen counts, diversity indices for each bulk sample from which specimen were identified has been estimated (*Table 8*). PB-10-17-02 was rich in wood remains and bivalves shells, yet presents the lowest number of microvertebrate specimen counted (76), while VAL-06-16-01 is the higher (289). However, PB-10-17-02 present the highest diversity indices, while ZIM-11-1602 has the lowest ones.

Table 8: Diversity indices of the four VMAs bulk samples studied. S, number of different taxa; $2^{H'}$, Shannon's index; 1-D, Simpson's index; $E_{1/D}$, Simpson's measure of evenness; J, Pielou's evenness index; N, number of specimens.

	S	$2^{H'}$	*1-D*	$E_{1/D}$	*J*	*N*
PB-10-17-02	11	1,664	0,7303	0,48	0,6939	76
ZIM-11-16-02	12	1,09	0,5424	0,248	0,4388	204
ZIM-06-17-01	12	1,26	0,596	0,2938	0,5071	262
VAL-06-16-01	14	1,408	0,6674	0,292	0,5335	289

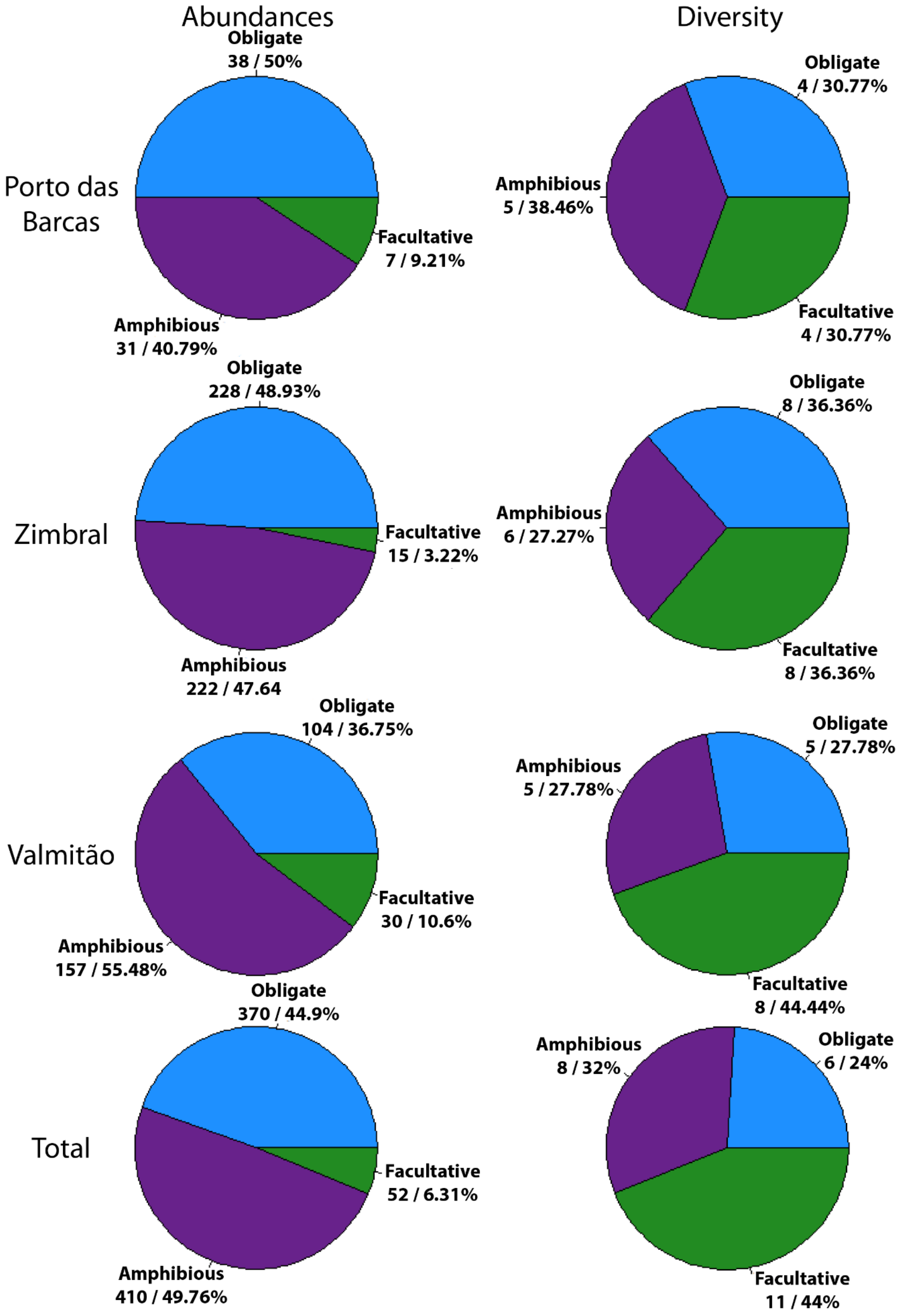

Figure 38: Faunal assemblages in the three vertebrate microfossil assemblages according their respective abundance and diversity. The first number is the number of specimens/taxa, the second number is the percentage (N Porto das Barcas (PB-10-17-02) = 76; N Zimbral (ZIM-06-17-01 + ZIM-11-16-02) = 465; N Valmitão (VAL-06-16-01) = 283; N Total = 832).

4. DISCUSSION

4.1. Vertebrate microfossil assemblages from the Lourinhã Formation

4.1.1. TAPHONOMY

The sedimentology of the three VMA localities indicate they all were formed under a low-energy depositional environment. The near-total disarticulation and fragmentation of specimens is one of the most noticeable taphonomic features, and it is actually similar to what have been observed in other VMAs (Carrano & Velez-Juarbe, 2006; Buscalioni *et al.*, 2008, 2018; Canudo *et al.*, 2010; Rogers *et al.*, 2010, 2017; Vasile & Csiki, 2010; Ullmann *et al.*, 2012; Oreska *et al.*, 2013; Carrano *et al.*, 2016). The lack of invertebrate borings and other types of weathering suggests bones were not exposed long enough to be affected by subaerial exposure (Hasiotis *et al.*, 1999; Carrano & Velez-Juarbe, 2006). Disarticulation may have occurred in an aquatic to semi-aquatic environment, while fragmentation could be the result of bioturbation in the pond/lake bottoms (Carrano & Velez-Juarbe, 2006); however the state of preservation of the microvertebrate remains can also be partly due to the methods used to screen-wash the sediments. Indeed, both medtohs used present limits in their process: in dry screening, the force in shaking from the screening machine could have broken the bones, while the water spurt in wet screening may have done the same by pushing the remains through the different mesh layers.

Most of the crocodylomorph teeth collected from Valmitão assemblage sediments are well preserved, showing little or no sign of transportation. On top of that, almost none of the teeth found preserved the root, and most of them have wear facets, and sometimes broken apices. That would indicate they were shed teeth, lost during the normal process of tooth replacement that occurs in crocodylomorphs (Kieser *et al.*, 1993); and their presence would imply that Valmitão assemblage is located close to their habitat (Schwarz-Wings *et al.*, 2009). Some teeth, however, show some trace of abrasion, having partially or completely lost the enamel (**Figure 31**, B3), or are even broken. This would suggest that some teeth could have been transported over short distance, but the methods of collecting, preparing, and sieving the sediments could have also contributed to the abrasion and breakage observed (Schwarz-Wings *et al*., 2009). Finally, few teeth seem to have been digested, and could have originated either from predation, or have been swallowed by their owner when they were shed.

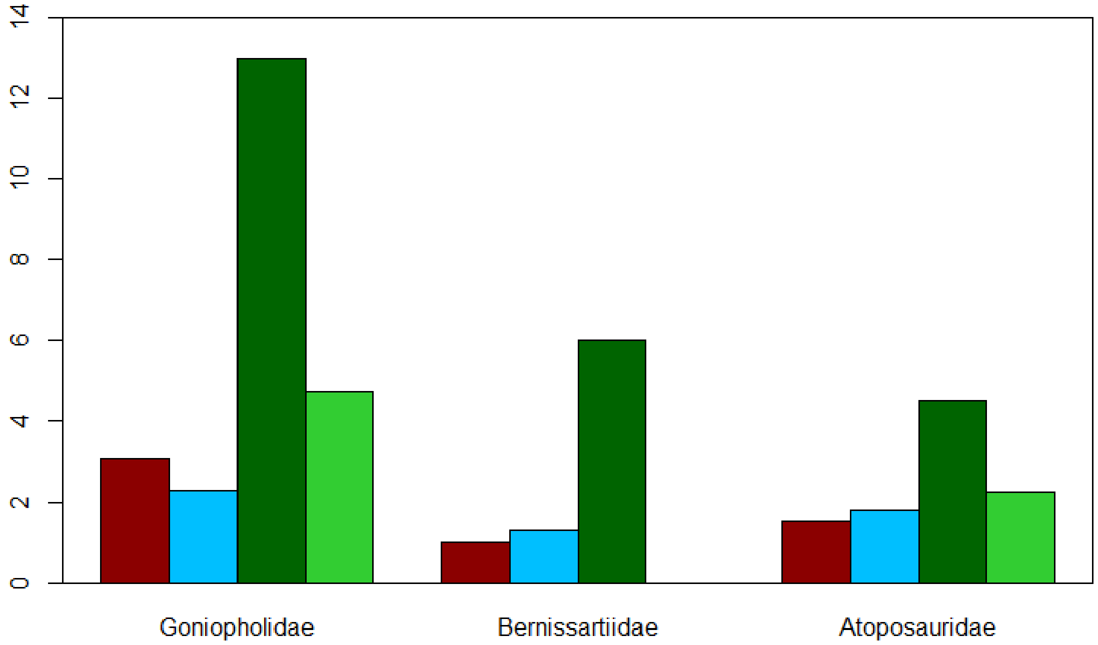

Figure 39: Comparison of the maximum height (in mm) in crocodylomorph teeth observed from Valmitão (dark red), La Cantalera in Spain (blue), and in adult (dark green) and juvenile (light green) specimens (data from Puértolas-Pascual *et al*., 2015 and references therein).

Crocodylomorph teeth from the Valmitão assemblage seem to have belonged to small animals (Figure 39). Indeed, the average size is 2.113mm in the sample studies, with 3.083mm for the teeth attributed to goniopholidids, 3.624mm for the ziphodont teeth, 0.985mm for the teeth attributed to bernissartiids, and 1.515mm for the teeth attributed to atoposaurids. Atoposaurids and bernissartids are crocodylomorphs reaching small size, around 50-60cm long (Schwarz-Wings *et al*., 2009; Salisbury & Naish, 2011; Puértolas-Pascual *et al*., 2015; Schwarz *et al*., 2017). However adult-size teeth range between 2 to 10mm for atoposaurids, and 3 to 6mm for bernissartiids (Puértolas-Pascual *et al*., 2015), which would suggest that the Valmitão assemblage is composed of only juvenile bernissartids, and both juvenile and young adult atoposaurids. In the same way, goniopholidids are large crocodylomorphs, reaching size of 4m long with teeth with an average height of 13mm (Buscalioni *et al*., 2008; Puértolas-Pascual *et al*., 2015), which would suggest that the Valmitão assemblage is mainly composed of juvenile goniopholidids. This could be explained either by taphonomic factors, or by environmental shifting, linked to dietary changes, from juveniles to adults (Schwarz-Wings *et al*., 2009). However, the small size of the teeth could be also an indication that the Valmitão assemblage was composed by smaller species than others known from other localities, as Guimarota.

Mainly crocodylomorph, but also theropod, eggshell fragments have been collected, during the preparation of the sediments. In extant crocodylomorphs, freshwater wetlands are the most common places for nesting, the hatchlings and younglings remaining around the nest and nearby areas with their mother for weeks, or even couple of years, before dispersing (Brazaitis & Watanabe, 2011), however more complete eggs need to be found to support those localities was a nesting area or nearby, as eggshell fragments could be transported.

It appears that teeth and scales are the most common remains recovered, following by dentary, cranial remains, osteoderms, and vertebrae. That can be explained by their durability and/or the high number of these elements in each individual. However, given the high number of bone fragments that remain unidentified in the samples, this representation is unlikely to be a collecting bias (Carrano & Velez-Juarbe, 2006), but it can infer taphonomic biases (Carrano *et al.*, 2016). The presence of carophytes thalli and well-sorted, deeply ornamented eggshells with angular borders would suggest a minimal transport, which is consistent with a low-gradient, non-stepped fluvio-lacustrine model in which elements would have been gradually accumulated, forming autochtonous to parautochtonous assemblages (Arenas-Abad *et al.*, 2010; Buscalioni *et al.*, 2018).

Therefore, it is unsurprising to have a relative high abundance of crocodylomorph and fish remains, considering their aquatic to amphibious lifestyle and fairly durable elements, while more terrestrial vertebrates, such as lizards, mammals, and pterosaurs, or taxa with more delicate elements, such as amphibians, will suffer taphonomic and proximity biases (Oreska *et al.*, 2013; Carrano *et al.*, 2016). For now, no mammal cranial/skeletal remains have been positively identified, and no mammal teeth have been recovered; but that could be a sampling bias due to the sample size. The abundance observed is also consitent with the idea that element diversity in deposits increases with proximity of life habit to the site of deposition (Shotwell, 1955).

4.1.2. PALEOENVIRONMENT AND PALEOECOLOGY

Lourinhã Fm. paleoclimatic data from previous studies all point toward warm and wet conditions, with strong seasonal precipitation patterns in winter months (Martinius & Gowland, 2011; Myers *et al.*, 2012; Gowland *et al.*, 2017; Mateus *et al.*, 2017). Stratigraphy suggest the Valmitâo VMA was an oxbow lake deposit, while Porto das Barcas and Zimbral VMAs were both floodplain mud deposits (**Figure 40**).

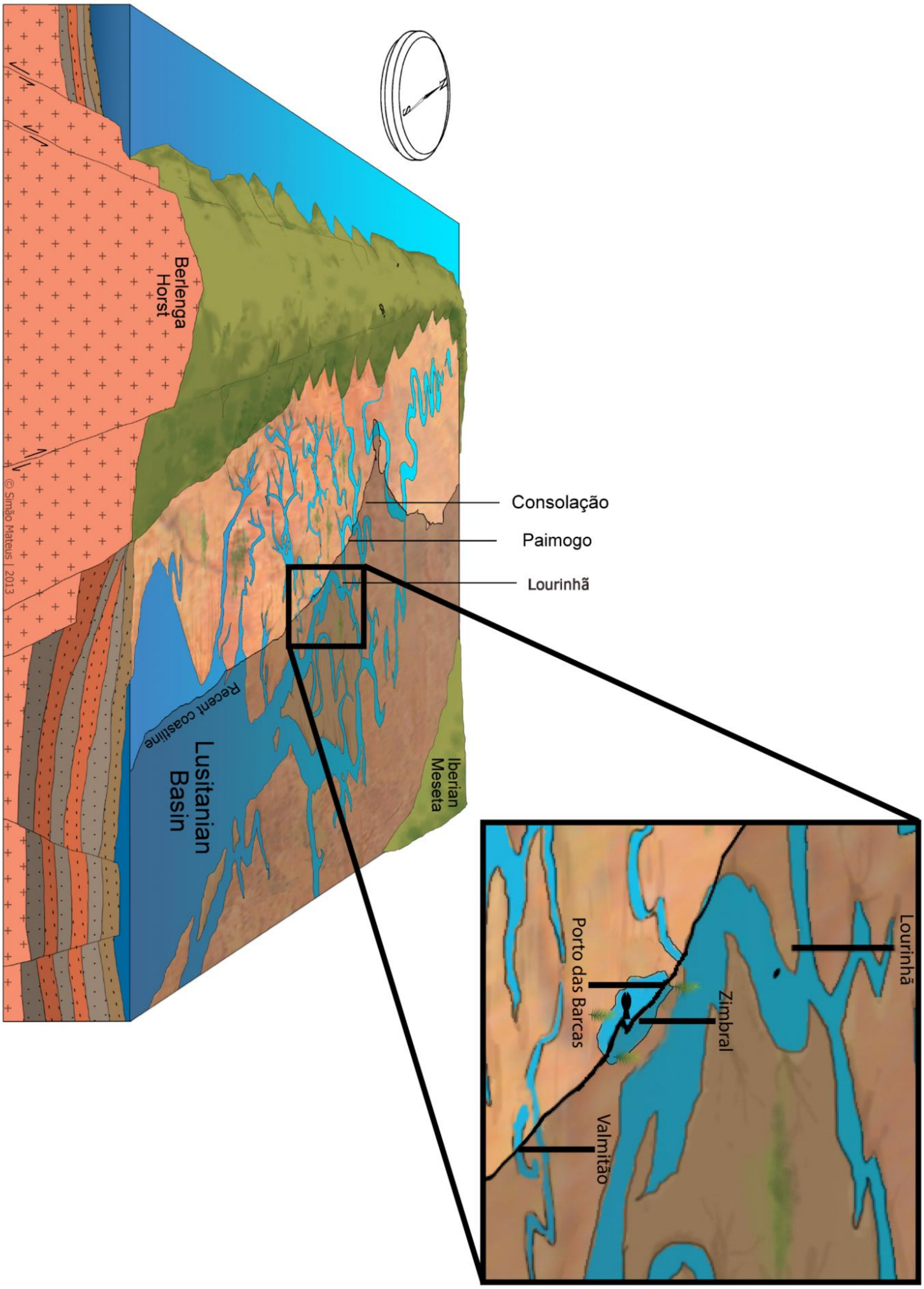

Figure 40: Paleogeographic reconstruction of the Lusitanian Basin at the Late Jurassic, with details on the VMAs studied and the interpretation of their paleoenvironments (modified from Mateus *et al.*, 2017, reconstruction by Simão Mateus, 2017). All three VMAs are assumed to be contemporary for clarity purpose, although the Valmitão VMA has been proved to be significantly older than both Zimbral and Porto das Barcas VMAs.

Increasing the sample size seems to increase the diversity richness in the different bulk samples studied, which suggest that lacustrine VMAs capture a time-average picture of their surrounding paleocommunities (Rogers & Brady, 2010; Carrano *et al.*, 2016). However, these VMAs localities do not record a single, uniform paleo-metacommunity, since they do not have the same evenness values. That could mean either they recorded different paleocommunities with different relative abundance distributions, or they recorded the same paleo-metacommunity but with different biases for different taxa, or a combination of both signals (Carrano *et al.*, 2016). PB-10-17-02 shows higher evenness values than other bulk samples, linked with high Shanon's and Simpson indices, while it is the one with less diversity and abundance. That may suggest a co-dominance of a few abundant taxa (Buscalioni *et al.*, 2018). ZIM-11-16-02 and ZIM-06-17-01 show similar diversity indices, with low evenness, suggesting they were composed of several equally-represented taxa. VAL-06-16-01 shows diversity indices slightly higher but in the same range, which would suggest it was composed of a more diverse fauna. Obligate and amphibious taxa were the most abundant, but with less taxonomic diversity than facultative taxa. That indicates all localities were brackish water paleoenvironments for aquatic and amphibious taxa (Carrano & Velez-Juarbe, 2006). This kind of environment provided a necessary water source for terrestrial organisms, and an abundant supply of potential prey items, which would have been attractive for the semi-arid paleoclimate of the Lourinhã Fm., as it has been previously proposed for its American equivalent, the Morrison Fm. (Engelmann *et al.*, 2004; Parrish *et al.*, 2004; Carrano & Velez-Juarbe, 2006). The co-occurrence of diverse small carnivores, presumbly sympatric, in the VMAs suggests a complicated niche partitionning and community assembly processes (Oreska *et al.*, 2013).

Porto das Barcas and Zimbral, which seem to be close in age and space range, share similar abundances but widely different diversity indices. That would mean they had similar paleonenvironments, but Zimbral was more diversified. The relative higher abundance of obligatetaxa identified in Zimbral can imply that the water table was more stable in this area, allowing a more developed aquatic community. This is also supported by the abundance of carophytes and ostracods (Annex 2), suggesting some lacustrine influence. The presence of oister fragments in Porto das Barcas suggest some degree of marine influence. On the other side, Valmitão was dominated by amphibious taxa and facultative taxa were more diverse, which would suggest a more continental environment. That is actually consistent with the fact that Porto das Barcas and Zimbral localities are in the Praia Azul mb., characterized by transitional environments with several transgressional events; while Valmitão is in the Porto

Novo and Praia da Amoreira mbs., which has been interpretated as more continental. Those interpretations are consistent with previous works on the Lourinhã Fm. (Mateus, 2006; Mateus *et al.*, 2017), and support that the vertebrate microfossil assemblages used for this study are good proxies for a better understanding of the paleoecosystems and paleoenvironments of the Late Jurassic of Portugal, outside the Guimarota Mine. Bigger sampling in the future will allow to narrow the interpretations and obtain a better data base.

It can be stated than wetland ecosystems are transversal in time and space, which means even if the fauna can taxonomically change between two wetlands, they stay the same type of ecosystem, and the actualism principle can be applied. That is why VMAs considered as wetland ecosystems from the Late Jurassic and Early Createcous of US and from the Early Cretaceous of Spain has been used to compare with VMAs from the Lourinhã Formation (*Table 9*).

Table 9: List of Mesozoic vertebrate microfossil assemblages use to compare with Lourinhã Fm.

Locality	**Age**	**Country**	**References**
Las Hoyas	Barremian	Spain	Buscalioni *et al.*, 2008 Buscalioni *et al.*, 2018
Buenache	Barremian	Spain	Buscalioni *et al.*, 2008 Buscalioni *et al.*, 2018
Uña	Barremian	Spain	Buscalioni *et al.*, 2008 Buscalioni *et al.*, 2018
Quarry 9	Kimmeridgian/Tithonian	Wyoming (USA)	Carrano *et al.*, 2006
Cloverly Fm. localities	Aptian/Albian	Montana (USA) Wyoming (USA)	Oreska *et al.*, 2013 Carrano *et al.*, 2016

Taxonomic diversity analyses (**Figure 41**) suggest that Quarry 9 in Commo Bluff from the Morrison Fm. represents a more terrestrial environment than the VMAs in the Lourinhã Fm., with a higher representation of facultative taxa, with respectiveley 81.54% of the taxa against 44% (see Fig. 4 in Carrano & Velez-Juarbe, 2006). Lourinhã Fm. and Morrison Fm. have been stated to share a common macrofauna (Mateus, 2006; Escaso *et al.*; 2007; Lockley *et al.*, 2008), but the diversity of microvertebrate seems to change dramatically between both.

However, Quarry 9 is well known to be extremely rich in mammal remains (Marsh, 1980; 1987; Carrano & Velez-Juarbe, 2006 and reference therein), while no mammaliaforms remains have been picked during this master's thesis, which may result in a sample bias explaining this difference observed. Quarry 9 also provided a notable diversity of dinosaurs, which are the second most diverse after mammals (Carrano & Velez-Juarbe, 2006), while again only four teeth have been found in Lourinhã Fm. VMAs. The Lourinhã Fm. is known to have provided a high diversity of dinosaurs (Mateus, 2006), and so this underepresentation is probably another sample bias. However, as for the Lourinhã Fm. VMAs, Quarry 9 presents a higher diversity in amphibious taxa than in obligate (Carrano & Velez-Juarbe, 2006). This overall view would suggest that Quarry 9 was probably more continental than the Lourinhã Fm., still with some brackish water.

VMA localities in the Cloverly Fm. are also dominated by facultative taxa (**Figure 41**), with 54% of the total diversity, and it appears to be rich in amphibious taxa remains (see Fig. 6 in Carrano *et al.*, 2016), as for the global abundance observed in Lourinhã Fm VMAs, and notably Valmitão. Howerver, with respect to the taxonomic diversity, obligate taxa surpass the amphibious ones in the Cloverly Fm. (Carrano *et al.*, 2016), while the amphibious taxa are more diverse than obligate in the Lourinhã Fm. VMAs from the Cloverly Fm. present a high variability in their indices, but the aggregate has a higher Simpson's indices than those observed for the VMAs in the Lourinhã Formation (0.86 against 0.54 to 0.73), while it has a similar Pielou's index (0.65) to the one observed for PB-10-17-02, and so is higher than those observed in Valmitão and Zimbral. If Cloverly Fm. VMAs represent a terrestrial environment, the difference observed with those from the Lourinhã Fm. would suggest that Cloverly was either more coastal and close to the shoreline, while Lourinhã was in the upstream part of the deltaic system., or with an more important water source, in a paleonenvirnment co-dominated by few abundant taxa more strongly marked than it has been suggested for Porto das Barcas.

Spain provided several VMAs (**Figure 41**), even though they are Barremian in age (Buscalioni *et al.*, 2008, 2018). Buenache appears to be dominated by obligate taxa (38%), even though amphibious taxa seems to have a similar composition (33%), which would suggest it is more aquatic to any of the VMAs studied from the Lourinhã Fm., probably close to an important and permanent water source. Its interpretation as a swamp environment (Buscalioni *et al.*, 2018) is consistent with this observation. However, the scarcity observed in mammaliaforms and dinosaur records, which usually contribute incidentally to taxonomic diversity analyses

(Carrano & Velez-Juarbe, 2006; Buscalioni *et al*., 2008), could constitue a sampling bias. El Inglés locality present higher diversity indexes (see Table 5 in Buscalioni *et al*., 2018) than Portugues ones, suggesting it was dominated by few abundant taxa; while the other localities present indexes similar or lower to what have been observed in Zimbral, suggesting they were more diversify. However, those indexes took into account the non-vertebrate remains too, which could have affected the final results, as the high Shannon's indexes observed in all localities may support.

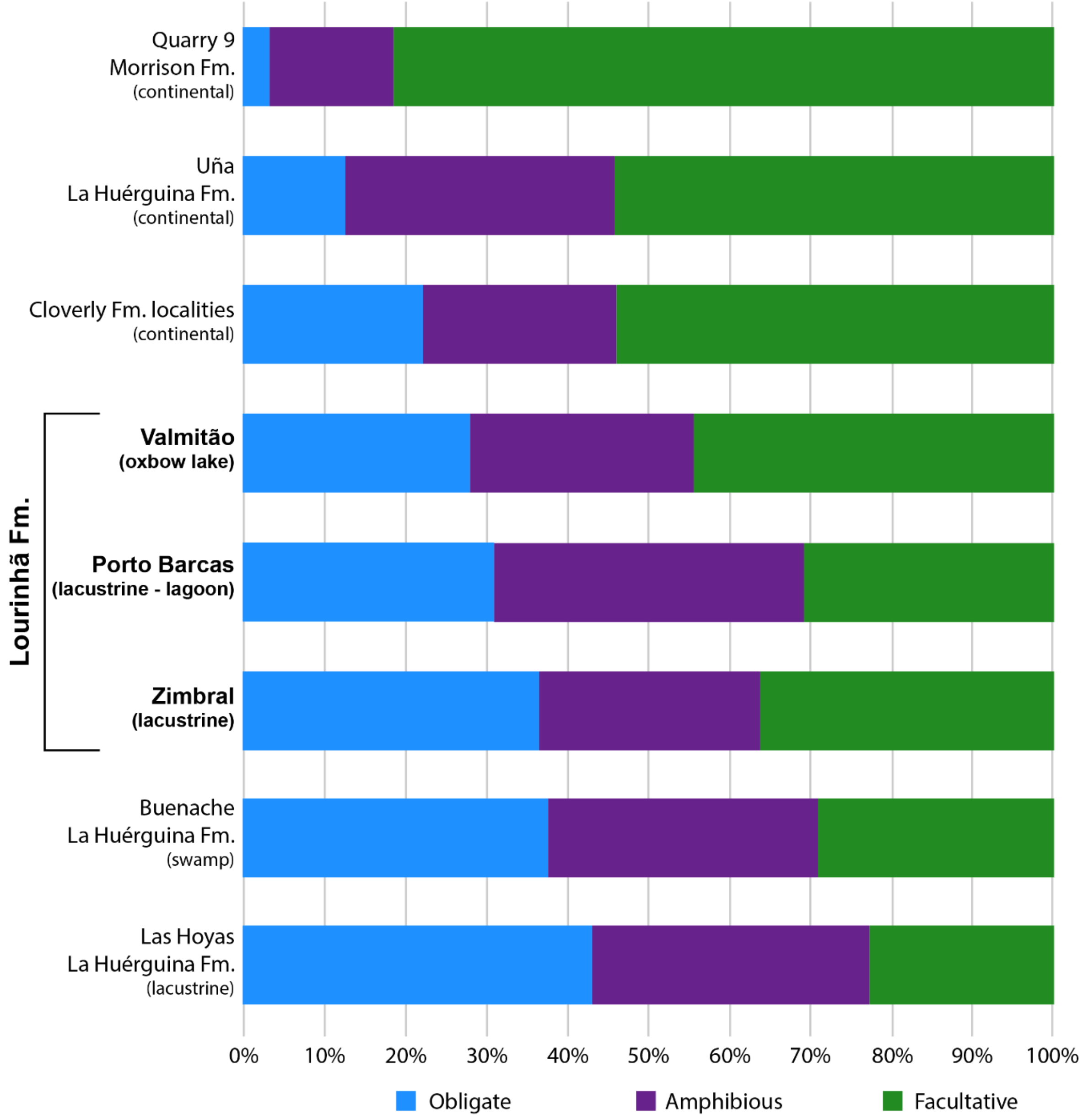

Figure 41: Comparison between different faunal assemblages from Spain (Las Hoyas, Buenache, and Uña), US (Cloverly Formation and Quarry 9), and the three VMA localities studied, taking in count only microfossil vertebrates remains (data from Carrano & Velez-Juarbe, 2006, Buscalioni *et al*., 2008, 2018, Carrano *et al*., 2016). The VMAs have been sorted from the less to the richest in obligate taxa, and their respective geological formation and paleoenvironment proposed has been indicated.

Uña, however, is dominated by facultative taxa (54%), more than any other VMAs used in this analysis beside Quarry 9 (**Figure 41**), while obligate taxa are really rare (13%). It would suggest Uña was most likely in terrestrial environment, being more continental than VMAs from the Lourinhã Fm., with periodical small brakrish waters for amphibious taxa to sustain, but not obligate ones, which is consistent with its interpretation as fluvio-lacustrine environment. However, Buscalioni *et al.* report that fished were not yet studied (2008), which would definitely affect this analysis. It has also been highlighted the high abundance of allochtonous terrestrial taxa could be explained by the presence of an upstream monospecific woody area, as the great concentration cheriolepidaceous cuticles suggests (Buscalioni *et al.*, 2008).

Las Hoyas is one Konservat-Lagerstätte from the Barremian of Cuenca, and it consists in one of the most paradigmatic example from the Late Jurassic-Early Cretaceous deposits, by the quality of its preservation with numerous articulated specimens among 70% preserving exquesite morphological details (including soft tissues), and the compositionnal fidelity of its faunal and flaural paleocommunities (Buscalioni & Poyato-Ariza, 2016). Focussing on its vertebrate remains (**Figure 41**), it is dominated by obligate taxa (43%), which are better represented than in the previous two localities (Buscalioni *et al.*, 2008). It would suggest that the environment was more aquatic than Lourinhã Fm., and so closer to what has been proposed for Buenache. Las Hoyas has been interpretated as a lacustrine environment, as Valmitão, dominated by meadows of carophytes (Buscalioni *et al.*, 2008, 2018). However, Valmitão is dominated by facultative taxa. Because of its quality of preservation, it can be assumed that there is no sample bias in the vertebrate remaines from Las Hoyas ; and so two hypotheses could explain this contradiction: (1) there is a sample bias toward obligate taxa in Valmitão that need to be address by a bigger sampling ; (2) a more detailed stratigraphy and sedimentology need to be address to validate its interpretation as a lacustrine environment. The localities from Las Hoyas present similar Shannon's index and Simpson's measure of eveness to those from the Lourinhã Fm., while they have lower Simpson's and Pielou's indexes (see Table 5 in Buscalioni *et al.*, 2018). That would suggest that Las Hoyas are much more diverse than Lourinhã Fm., but Konservat-Lagerstätten better and more accurate paleocommunities record could explain it.

It appears the Lourinhã Fm. represent an intermediate paleoenvironment between Uña and Americans localities, and Buenache and Las Hoyas, – the former being upstream to the later. Valmitão has been interpreted as an oxbow lake environment (**Figure 40**), yet appears to be less diverse in obligate taxa than Buenache and Las Hoyas. That could suggest Buenache and Las Hoyas were respectively closer to the shoreline than Valmitão, however possible eolian deposits predating Valmitão deposits may infer it was not far from shallow sea. Nevertheless, Valmitão faunal assemblage seems to be more closely related to Uña and Cloverly facultative-dominated paleoenvironments. The low aquatic diversity may infer Valmitão was dryer than Cloverly, or at least reliant on a water source, which is consistent with the regression event observed throughout Porto Novo and Praia da Amoreira mbs. Both Zimbral and Porto das Barcas faunal assemblages are analogous to what have been observed Buenache and Las Hoyas, even though Porto das Barcas is the only one dominated by amphibious taxa. Porto das Barcas is rich in plant remains and bivalve shells, and Zimbral abundant in ostracods and charophytes material (Annex 2), which would relate them to Las Hoyas paleoenvironment. The higher amphibious diversity in Porto Barcas would infer it may have been less influenced by shallow seas than Zimbral, but this is contradicted with the relative abundance of ostreid fragments found. This analysis supports the Lourinhã Fm. as a good model to study vertebrate microfossil assemblages in wetland ecosystems and, by being ones the few of its kind, it highlight its importance for taxonomic, faunal, and paleobiogeography studies for assemblages from the Late Jurassic in Europe.

4.2. Further discussion on the Valmitão crocodylomorph assemblage

The Valmitão VMA 1mm and 0.5mm fractions provided a remarkable amount of 125 crocodylomorph teeth (*Table 10*). Their morphologies represent a good sample of the intraspecific variations within crocodylomorphs (Figure 42), and thus they have been used for a more detailed paleoecological and palaeobiogeographical analyses. A set of 31 teeth has been used for the measurements of the different morphologies to proceed PCA analysis (*Table 11*).

4.2.1. PALEOECOLOGY

The conical teeth represent 77 of the crocodylomorph teeth observed (61.6%), but could have been attributed to the three different families: 51 to goniopholidids (40.8%), one to bernissartiids (0.80%), 25 to atoposaurids (20%). The abundance observed confirms they are common in the anterior dental region of crocodylomorphs with heterodont dentition (Buffetaut & Ford, 1979; Schwarz & Salisbury, 2005; Lauprasert *et al.*, 2011; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015). However, differences in the shape of the cross-section and the pattern of the enamel was observed, allowing separation into different morphologies. Associated with the high abundance of this shape, those differences show that it is unlikely they only came from the anterior jaws of heterodont crocodylomorphs (Puértolas-Pascual *et al.*, 2015), but there is at least one morphology belonging to Goniopholididae. Conical teeth have been associated with generalist diets, based on shelly and soft preys items (Puértolas-Pascual *et al.*, 2015; Schwarz *et al.*, 2017), which is the ecological feeding behaviour proposed for goniopholidids (Schwarz, 2002).

Table 10: Teeth counting of the crocodylomorphs assemblage from Valmitão.

Morphologies	*Number of teeth*	*Percentage*	*Number of teeth*	*Percentage*
Goniopholidid slender conical	33	26.40	51	40,80
Goniopholidid broad conical	18	14.40		
Ziphodont	5	4.00	5	4.00
Bernissartiid conical	1	0.80	19	15.20
Bernissartiid molariform	18	14.40		
Atoposaurid conical – flabelliform striations	14	11.20	50	40.00
Atoposaurid conical – parallel striation	11	8.80		
Atoposaurid lanceolate	10	8.00		
Atoposaurid leaf-shaped	15	12.00		
Total	125	100	125	100

The ziphodont teeth are the scarcest morphotype, representing only five of the crocodylomoprh teeth observed (4%). This morphology is found in such broad range of mesoeucrocodylian taxa that its use for taxonomic and phylogenetic purposes is discouraged, and instead has ecological implications, being associated with highly predatory terrestrial crocodylomoprhs (Turner, 2006; Andrade & Bertini, 2008; Puértolas-Pascual *et al.*, 2015).

The blunt molariform teeth represent 18 of the crocodylomorph teeth observed (14.4%), is usually associated with bernissartiids, since this morphology is common in taxa such as *Bernissartia* and *Koumpiodontosuchus* (Buffetaut & Ford, 1979; Sweetman *et al.*, 2014). However, this assignments must be used with care, since it can also been observed in taxa not closely related to Bernissartiidae (Buffetaut & Ford, 1979; Brinkmann, 1992; Puértolas-Pascual *et al.*, 2015), even if the kidney-shaped base seems to be characteristic of this family (Schwarz-Wings *et al.*, 2009). Therefore, this morphology may be more closely linked to a specific ecological diet than phylogenetic relationships (Buffetaut & Ford, 1979). In that case, it has been associated with a durophagous diet, subsisting mainly on animals with shells and crushing hardfood feeding behaviours (Buffetaut & Ford, 1979; Puértolas-Pascual *et al.*, 2015).

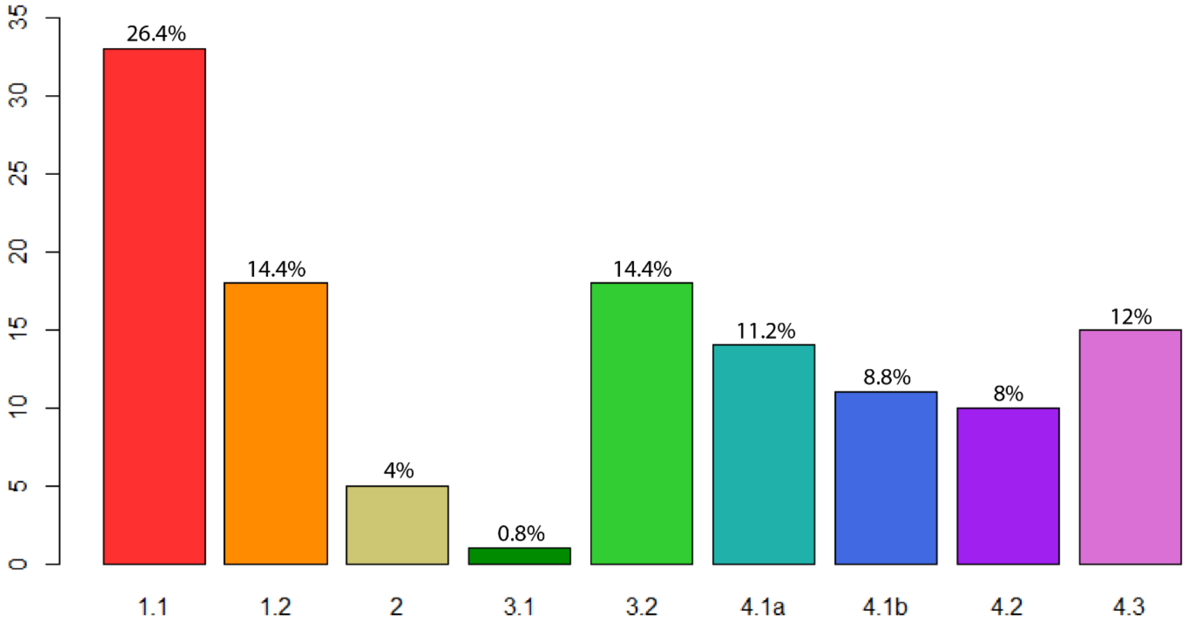

Figure 42: Distribution of the teeth according the morphologies and the taxonomy to which they have been attributed. **1.1**, slender conical goniopholidid teeth; **1.2**, broad conical goniopholidid teeth; **2**, ziphodont teeth; **3.1**, conical bernissartiid teeth; **3.2**, molariform bernissartiid teeth; **4.1a**, conical striations atoposaurid teeth with flabelliform; **4.1b**, conical atoposaurid teeth with parallel striations; **4.2**, lanceolate atoposaurid teeth; **4.3**, leaf-shaped atoposaurid teeth.

The lanceolate and leaf-shaped teeth represent 25 of the crocodylomorph teeth observed (20%), and those morphologies are usually associated with atoposaurids (Schwarz & Salisbury, 2005; Schwarz-Wings *et al.*, 2009; Salisbury & Naish, 2011; Puértolas-Pascual *et al.*, 2015; Schwarz *et al.*, 2017). Correlated to the size atoposaurids could reach, they have been associated with an insectivorous diet (Buscalioni & Sanz, 1988; Puértolas-Pascual *et al.*, 2015), also including small vertebrates such as amphibians and mammals (Brinkmann, 1989; Schwarz & Salisbury, 2005; Schwarz *et al.*, 2017). The small size of atoposaurids and their specific diet could be explained by ecological partitionning with other contemporary crocodylomorphs, such as goniopholidids, and may have allowed these crocodylomorphs to live sympatrically within the same habitat (Schwarz & Salisbury, 2005; Tennant & Mannion, 2014).

Also, the conical teeth attributed to atoposaurids suggest there are at least two different taxa of this family, confirming the diversity in the Late Jurassic of this clade (Tennant & Mannion, 2014; Tennant *et al.*, 2016; Young *et al.*, 2016). The differences observed in the morphologies could indicate dietary specializations between *Theriosuchus* and *Knoetschkesuchus*, in response to paleoenvironmental changes, which would have allowed to access to specific ecological niches for both species (Schwarz *et al*., 2017). The morphological diversity of dentition has been proposed to be one of the potential drivers of the evolution of atoposaurids in the Middle to Late Jurassic (Young *et al*., 2016), and the observations made from the Valmitão assemblage are consistent and support the biogeogeographical and taxonomical variation observed in previous studies (Tennant & Mannion, 2014; Tennant *et al*., 2016; Schwarz *et al*., 2017).

When compared to other assemblages in Europe, the Valmitão crocodylomoprh assemblage is similar in the presence of atoposaurids, bernissartiids, and goniopholidids. However, the propotion of each taxon differs from one site to another (Figure 43). Conical teeth are often the most represented morphotypes, which can be explained by its presence in most heterodont crocodylomorphs (Buscalioni *et al*., 2008; Schwarz-Wings *et al*., 2009; Puértolas-Pascual *et al*., 2015). That also implies they can be attributed to different taxa, even though goniopholidid conical teeth are the most abundant ones (Puértolas-Pascual *et al*., 2015). Scandinavian assemblages are dominated by lanceolate to leaf-shape teeth (58.56%), characteristic of atoposaurids, and are also both the northernmost and westermost localities in Europe (Schwarz-Wings *et al*., 2009). That would suggest atoposaurids were highly specialized for the environments of this region during the Late Jurassic.

On the contrary, the Valmitão and La Cantalera (Spain, Barremian in age) assemblages are both dominated by goniopholidid teeth, where they represent around 40-45% of the teeth observed. And ziphodont teeth, while absent from Scandinavia, are the rarest morphotype found in the two localities of the Iberian Peninsula. However, Valmitão and La Cantalera differ significantly in the representation of bernissartiids and atoposaurids. Indeed, bernissartiids are more common in Spain (45.6%) than the atoposaurids (7.14%), while it is the other way around in Portugal, where atoposaurids are more common (40%) than the bernissartiids (15.2%). Two reasons could explained this switch in the representation of these taxa. The first one would be a bias in the observation and the attribution of the morphotype. Indeed, no conical tooth attributed to atoposaurid has been found in Spain; while, in Portugal, only one conical tooth has been attributed to bernissartiids. Because this morphology is widespread in heterodont crocodylomorphs, conical teeth can be difficult to assign to a specific taxon (Schwarz-Wings *et al*., 2009; Puértolas-Pascual *et al*., 2015). The same can be applied to molariform teeth, which can be found either in bernissartiids or atoposaurids, even though some differences allow them to be distinguished (Tennant *et al*., 2016). However, when the proportions for each morphotype are compared between both localities, it seems that the main bias is from the counting and the attribution of conical teeth.

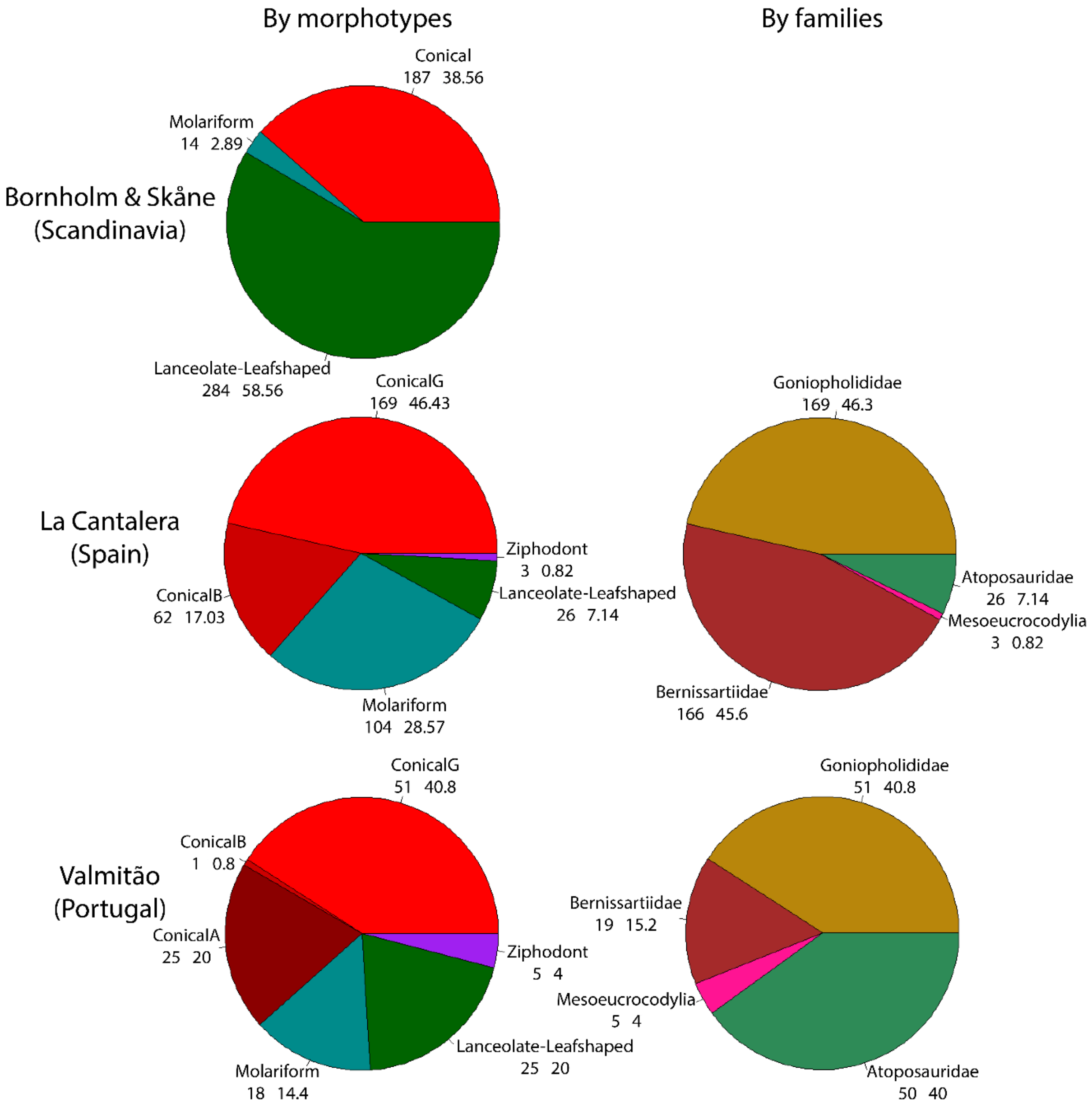

Figure 43: Crocodylomorph tooth assemblages from Scandinavia, La Cantalera (Spain), and Valmitão (Portugal), according the tooth morphologies, and their taxonomic attribution (data from Schwarz-Wings *et al.*, 2009 and Puértolas-Pascual *et al.*, 2015).

If methodological bias can not be completely excluded, another reason for this difference would be that the Scandinavian, Valmitão and La Cantalera assemblages represent different paleoenvironments. The Borhnholm & Skåne assemblages, dominated by atoposaurids, suggest terrestrial environments, fitting an ecosystem where atoposaurids could diversify (Schwarz & Salisbury, 2005). The inverted proportion of bernissartiids and atoposaurids between Valmitão and La Cantalera could reflect a major shift in the environment between both localities. The La Cantalera assemblage has already been described as a floodplain deposit with temporary lacustrine episodes in an area of marshy vegetation (Aurell *et al.*, 2004), dominated by terrestrial taxa (Puértolas-Pascual *et al.*, 2015). The higher abundance of atoposaurids in the Valmitão assemblage would suggest it was more terrestrial (Schwarz & Salisbury, 2005). However this statement is challenged by the overall analysis on both localities, terrestrial fauna being more represented in La Cantalera than in Valmitão, respectiveley with 64.86% against 44.44% (Gasca *et al.*, 2012), which would support the methodological bias hypothesis.

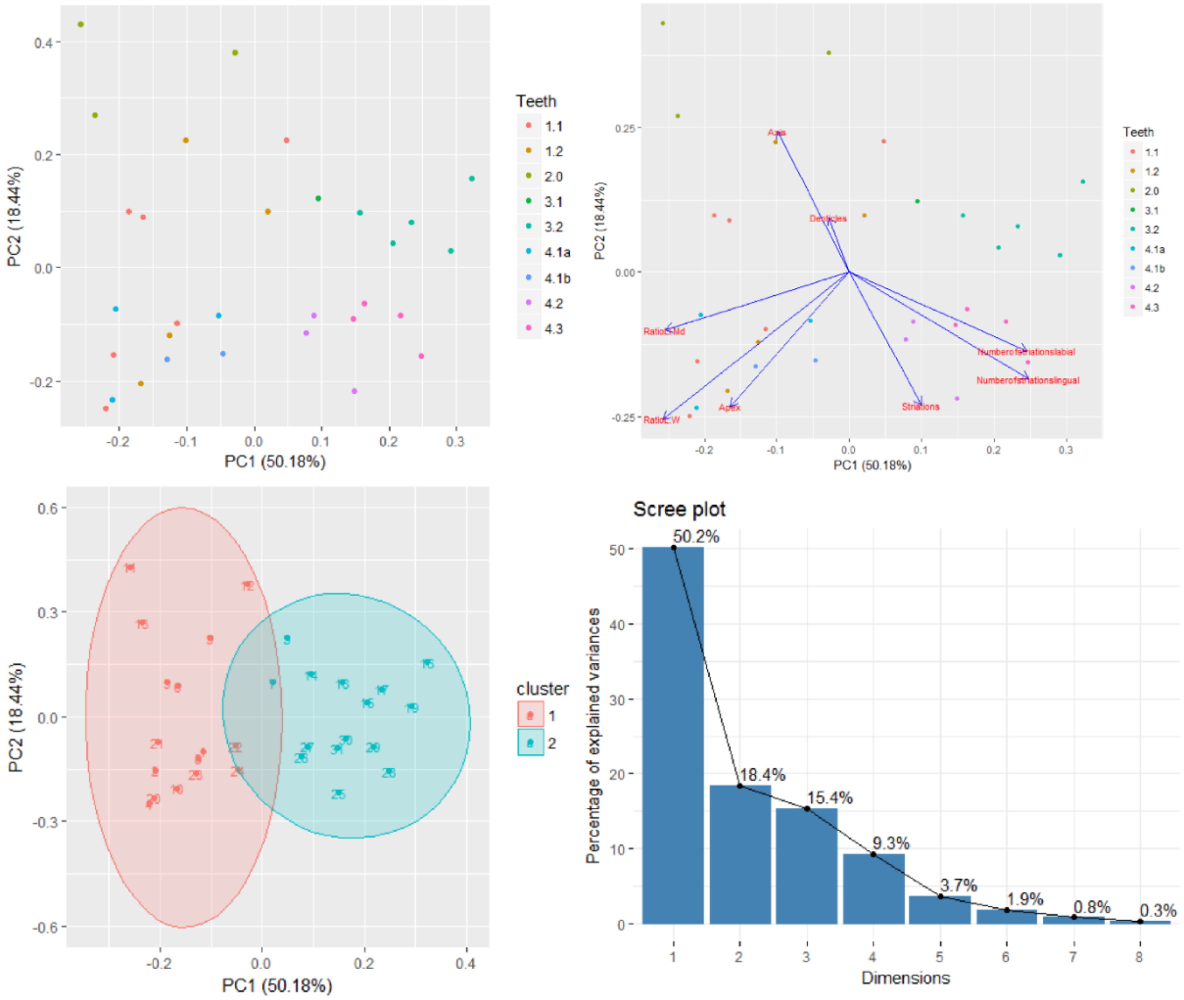

Figure 44: Measurement morphometrics analysis using PCA to cluster teeth according their morphologies and taxa. From right to left, top-down: PCA analysis, PCA analysis with the vectors of each measures, PCA analysis with the cluster grouping conical teeth (cluster 1) and non-conical teeth (cluster 2); the variance explained by each component.

Table 11: Measurements (in mm) of the crocodylomorphs teeth morphologies.

Teeth	Length	Width	Ratio L/W	Labiolingual	Mesiodistal	Ratio Ll/Md	Apex	Axis	Number of striations lingual	Number of striations labial	Denticles	Striations
1.1 - 1	3,337	1,689	1,976	1,208	1,591	0,759	32,125	0,000	9	7	Absent	Parellel
1.1 - 2	2,861	0,972	2,943	0,867	0,880	0,985	13,206	0,000	6	9	Absent	Parellel
1.1 - 3	-	1,793	-	1,471	1,676	0,878	-	0,000	10	7	Absent	Parellel
1.1 - 4	2,889	1,034	2,794	0,905	1,028	0,880	41,148	0,000	8	8	Absent	Parellel
1.1 - 5	2,787	1,557	1,790	1,291	1,474	0,876	15,556	0,000	0	0	Absent	Absent
1.1 - 6	1,931	0,964	2,003	0,686	0,954	0,719	18,054	0,000	0	0	Absent	Absent
1.2 - 1	2,089	1,882	1,110	1,445	1,916	0,754	-	0,000	10	12	Absent	Parellel
1.2 - 2	4,079	2,237	1,823	2,165	2,252	0,961	23,486	0,000	11	11	Absent	Parellel
1.2 - 3	3,237	2,474	1,308	1,873	2,447	0,765	-	0,000	0	0	Absent	Absent
1.2 - 4	4,539	2,165	2,097	1,918	2,080	0,922	37,925	0,000	9	12	Absent	Parellel
2.0 - 1	3,653	1,830	1,996	1,215	1,616	0,752	14,299	12,531	0	0	Present	Absent
2.0 - 2	-	1,759	-	1,253	1,605	0,781	-	-	0	0	Present	Absent
2.0 - 3	3,595	1,527	2,354	1,010	1,474	0,685	15,152	7,600	0	0	Present	Absent
3.1 - 1	-	1,279	-	0,992	1,115	0,890	-	-	19	14	Absent	Parellel
3.2 - 1	1,195	1,780	0,671	0,676	1,223	0,553	0,000	0,000	21	30	Absent	Parellel
3.2 - 2	0,758	1,071	0,708	-	-	-	0,000	0,000	21	23	Absent	Parellel
3.2 - 3	0,711	1,090	0,652	0,325	0,827	0,393	0,000	0,000	27	19	Absent	Parellel
3.2 - 4	0,776	0,976	0,795	0,338	0,689	0,491	0,000	0,000	17	19	Absent	Parellel
3.2 - 5	1,484	2,553	0,581	0,373	0,941	0,396	0,000	0,000	32	28	Absent	Parellel
4.1a - 1	1,875	0,763	2,457	0,533	0,654	0,815	42,610	0,000	12	0	Absent	Parellel
4.1a - 2	1,949	0,952	2,047	0,580	0,728	0,797	29,200	0,000	0	0	Absent	Parellel
4.1a - 3	1,490	0,768	1,940	0,287	0,701	0,409	33,270	0,000	13	0	Absent	Parellel
4.1b - 1	1,345	0,667	2,016	0,521	0,654	0,797	20,397	0,000	11	0	Absent	Flabelliform
4.1b - 2	1,223	0,773	1,582	1,159	1,440	0,805	16,403	0,000	14	10	Absent	Flabelliform
4.2 - 1	2,577	1,680	1,534	1,128	1,530	0,737	0,000	0,000	30	31	Absent	Flabelliform
4.2 - 2	1,432	0,966	1,482	0,622	0,896	0,694	0,000	0,000	21	18	Absent	Flabelliform
4.2 - 3	1,035	0,760	1,362	0,438	0,671	0,653	0,000	0,000	19	18	Absent	Flabelliform
4.3 - 1	1,381	1,474	0,937	0,637	1,055	0,604	0,000	0,000	33	34	Absent	Flabelliform
4.3 - 2	1,225	1,381	0,887	0,571	1,041	0,549	0,000	0,000	24	31	Absent	Flabelliform
4.3 - 3	1,489	1,357	1,097	0,595	1,121	0,531	0,000	0,000	24	19	Absent	Flabelliform
4.3 - 4	1,162	1,043	1,114	0,579	0,921	0,629	0,000	0,000	23	23	Absent	Flabelliform

In order to help in the assignmment of the teeth to a morphotype, measurement morphometrics analysis has been conducted, with a PCA (Figure 44). Unfortunately, no conclusive results have been found, the PCA being able only to distinguish conical from non-conical teeth, which can already be done by direct observations. However a trend can be observed: bernissartid teeth are grouped together and so are lanceolate and leaf-shaped atoposaurid teeth. Within the conical teeth, the PCA could not distinguish goniopholidid from atoposaurid teeth, but the ziphodont teeth are grouped together. To confirm if morphometrics can help to resolve the high interspecific variability, more specimens need to be added, one of the limits being that PCA requires at least 3 to 4 specimens to create a cluster. 84.02% of the variance is explained by the first 3 principal compoments, and 96.99% by the first 5 principal components, and focus on those could also improve the results in future analyses.

4.2.2. PALEOBIOGEOGRAPHY

The crocodylomorph assemblage from Valmitão is similar in its composition to several contemporaneous assemblages of Europe by the presence of atoposaurids, bernissartiids, and goniopholidids (Schwarz-Wings *et al.*, 2009). However, it differs from Guimarota by the absence of *Machimosaurus hugii*. None of the teeth studied could have been attributed to either *Lusitanisuchus mitracostatus* nor *Lisboasaurus estesi*, also found in Guimarota. Even if the ziphodont morphology could not be attributed to a more precise taxa than Mesoeucrocodylia, it differs from what have been observed in these both species (Buscalioni *et al.*, 1996; Schwarz & Fechner, 2004, 2008).

Geographically, the Portuguese localities (Guimarota, Andrés, and Valmitão) represent the westernmost distribution of this typical continental Late Jurassic-Early Cretaceous crocodylomorph assemblages in Europe, and also the southernmost for the Late Jurassic (Figure 10), around 30° latitude North. However, if skeletal remains of atoposaurids, goniopholidids, and bernissartiids have been reported in Late Cretaceous localities; bernissartiids are only known by isolated teeth in the Late Jurassic localities (Schwarz-Wings *et al.*, 2009). The presence of all these taxa in different Portuguese localities suggests that by the Late Jurassic, crocodylomorphs were already common and diversified.

During the Late Jurassic, Asia and North America were the main land masses of Laurasia in northern hemisphere, while Europe and the eastern region of North America were mostly covered by shallow epicontinental seas forming an island archipelago system (Ziegler, 1988). With the opening of the North Atlantic ocean, the extensional tectonics resulted in lagoonal environments with continental islands, as the Iberian Meseta/plate (Figure 13), forming the continental margins (Ziegler, 1988). On top of that, periodic eustatic sea-level changes occuring in the Late Jurassic may have provoked extensive regression (Allen, 1975). This would have turned the freshwater environments, as observed in Guimarota, into more brackish water environments, as observed in Purbeck facies (Miller *et al.*, 2005). However progressive uplift of the basin margin at the end of the Late Jurassic would have changed the environments in more fluvial clastics ones, as observed in Wealden facies (Wilson *et al.*, 1989).

The tectonic story of Europe could explain the distribution observed in crocodylomorph faunas through the Late Jurassic and the Early Cretaceous. Indeed, goniopholidid remains have been found on the margin of epicontinental seas, which would suggest they prefer more semi-aquatic environments (Buffetaut, 1982; Schwarz, 2002), while atoposaurids prefered more terrestrial environments (Schwarz & Salisbury, 2005). Also, the archipelago in Europe during the Late Jurassic could have helped allopatric speciation among atoposaurids (Tennant & Mannion, 2014; Schwarz *et al.*, 2017). Indeed, the presence of at least two atoposaurid taxa only in Valmitão assemblage supports the diversity of this clade, even already during the Late Jurassic, with twelve genera described by now around the world (Tennant *et al.*, 2016; Young *et al.*, 2016, Schwarz *et al.*, 2017). The uplift of the basin margin started in the Oxfordian (Wilson *et al.*, 1989) could have been the trigger to the speciation between *Knoetschkesuchus* and *Theriosuchus* (Schwarz *et al.*, 2017). On top of that, the small body size observed in atoposaurids and bernissartiids could reflect insular dwarfism, driven by sea-levels changes (Tennant & Mannion, 2014), as it has been proposed for the sauropod dinosaur *Europasaurus* (Sander *et al.*, 2006). However, the Iberian plate was a continental-sized land mass, and it is known for large body-sized dinosaurs, which challenges the suggested effect of insular dwarfism on crocodylmorphs.

4.3. Suggestions about the methodology and thesis' outputs

The 2mm fraction allow to provide few big bone fragments that can be easily identified, the 1mm fraction provides fragments that can be recognized and assess easily with binocular lens, and the 0.5mm is the one providing most of the specimens. However, the 2mm fraction does not have a lot of diversity; and the 0.5mm fraction is highly time-consuming, requires trained/sharp eyes, ant most of the specimens picked are not identify. Consequently, in the aim to optimize the picking and the identification, the 2mm fraction can be processed by untrained volunteers and students, while the 1mm fraction must be processed by supervised volunteer and students, and the 0.5mm fraction should be processed only by trained researchers. The paleoecological analyses in this thesis suggest that Valmitão and Zimbral are the most promising localities to look for vertebrate microfossils, even though Porto das Barcas provided some unique elements, as the Paramacellodidae dentary, and seems to present a higher amphibious diversity. The absence of mammaliaforms remains is most likely linked to the small sampling of each locality, which can be corrected with more sampled sediments.

This master thesis is the first study on the microvertebrates from the Late Jurassic of Portugal hosted by Portuguese Institutions and supervised by a Portuguese team. Although it has been only preliminary, the research produced during this year allowed: (1) sediment sampling, screen-washing, and picking from three Portuguese VMA localities, preparing so the protocol for further, more exhaustive studies; (2) lithostratigraphic analysis and localization of these localities in the context of the Lourinhã Fm.; (3) creation of a new microvertebrate collection composed by newly described specimens; (4) a preliminary paleoenvironmental analysis on the diversity of these localities; (5) the production of two oral communications in international congresses, and the publication of at least one paper in a peer review journal planned for the end of 2018; and (6) training of the student in the field of microvertebrate paleontology, making him suitable to pursue the research and leading investigations on this topic for the future.

5. CONCLUSION

The bibliographic revision of the state of the art of the main microvertebrate clades highlighted the richness and the diversity of the Portuguese Late Jurassic record, supporting its suitable conditions for microvertebrates studies, while the main focus for paleontology had been for decades on dinosaurs and mammals. Thereby, Portugal can be a good model to study the vertebrate diversity and paleobiogeography of Europe in the Late Jurassic.

Three Mesozoic VMAs of the Lourinhã Fm. have been sampled: Porto das Barcas, Zimbral, and Valmitão. Over 572 kilograms of sediments have been screen-washed, and over 69 kg have been used for picking. From those, 3,348 remains have been picked, including 2,497 microvertebrates skeletal remains and teeth, 999 of which have been identified. From those identified remains, 824 items have been described and identified to the most conservative taxon.

Those provide a good data base for preliminary studies on vertebrate microfossil from Portugal outside the Guimarota Mine.

The stratigraphic analysis shows that the Valmitão VMA site is part of Porto Novo and Praia da Amareira mbs., and it has been interpreted as an oxbow lake. The Porto das Barcas VMA and Zimbral VMA are part of Praia Azul mb., and they have been interpreted as floodplain mud deposits.

Following the most conservative identifications of the elements described the microfossil vertebrate assemblage localities are composed by at least: (1) one family of Chondrichthyes; (2) three families of Osteichthyes; (3) three families of amphibians, including albanerpetontid, frog, and salamander taxa with the possibility of the first record of Scapherpetontidae in Europe and in the Late Jurassic; (4) one family of Squamata, and probably more taxa; (5) four families of Mesoeucrocodylia; (6) two taxa of Pterosauria; (7) five families of Dinosauria. However, it has to be noticed the absence of remains attributed to Choristodira, even though they have been reported from the Late Jurassic of Portugal, or Anura, but most of all the absence of any mammaliaforms remain, which have yet been previously reported from the Lourinhã Fm., notably in Porto das Barcas and Zimbral.

Abundance and diversity analyses on all the microvertebrate remains identified show that globally, the three localities are dominated by obligate and amphibious taxa, but facultative taxa were more diverse, suggesting all three VMAs were accumulated in brackish water paleoenvironments. It also appears that Porto das Barcas and Zimbral share similar abundances, being respectively a fluvial meandering channel-lagoon and a sandy bay shoreline, but Zimbral was more diverse; while Valmitão seems to have been more continental than the other two. These preliminary results support that the Lourinhã Formation, even though if it provided less material than the Guimarota Mine, can be used for a proxy on the paleoenvironments of the Late Jurassic of Portugal and paleobiogeography of vertebrates in the Late Jurassic of Europe.

The most representative result of these descriptions are the 125 crocodylomorph teeth from the Valmitão locality, which have been described as four main morphologies: (1) conical teeth with few parallel basiapical striations, attributed to Goniopholididae; (2) conical to molariform teeth with abundant parallel basiapical striations, attributed to Bernissartiidae; (3) conical, lanceolate, leaf-shaped teeth with a smooth labial surface and a lingual enamel ornamented by abundant parallel to flabelliform basiapical striations, attributed to

Atoposauridae; (4) true ziphodont teeth with smooth to faintly striated enamel, attributed to Mesoeucrocodylia. The crocodylomorph teeth assemblage shows that crocodylomorphs were already well diversified by the Late Jurassic and is similar to other contemporaneous west-European assemblages with, however, different proportions. The preservation of the teeth suggests they were lost during tooth replacement, close to the habitat; and their size suggest that the Valmitão assemblage is mainly composed of juvenile to young adult individuals.

For further studies, a better sampling of Porto Barcas could be carried on, for a better characterization of the locality and its paleoenvironment; however, the efforts should be put on sampling both Zimbral and Valmitão, the most promising localities. Finally, and due to their taxonomic interest, each locality needs to be more sampled with the aim to find, describe, and identify mammaliaforms material.

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ANNEXES

Annex 1: Locality–taxon raw data of bulk-sampled VMAs from the Lourinhã Formation.

		ZIM-06-17-01				ZIM-11-16-02				PB-10-17-02				VAL-06-16-01
		2mm	1mm	0,5mm	Total	2mm	1mm	0,5mm	Total	2mm	1mm	0,5mm	Total	Total
Bivalves			58	229	287	21	10	2	33			11	11	56
Gastropods			4	4	8	1	3	1	5			2	2	65
Ostracods					0				0		1		1	2
Unidentified invertebrate			3	3	6				0				0	0
Neopterygii	Vertebra		3	1	4		1		1		1	1	2	0
Actinopterygii	Teeth			3	3		1	2	3		0	0	0	3
Caturidae	Teeth			1	1			1	1			2	2	2
Actinopterygii	Teeth				0				0				0	1
Semionotidae	Teeth			3	3			1	1				0	0
Semionotidae	Teeth	1			1			3	3		1		1	1
Pycnodontiformes	Teeth		1	1	2			2	2				0	0
Actinopterygii	Scales		15	130	145			57	57	1	3	26	30	97
Actinopterygii	Tooth battery			1	1				0				0	0
Hybodontidae	Teeth				0				0			3	3	0
Tetrapod	Vertebra				0				0		1		1	0
Tetrapod	Premax				0				0			1	1	0
Amphibian	Femur		1		1			1	1				0	0
Amphibian	Fibiotibula		1		1				0				0	0
Amphibian	Illium			1	1				0				0	0
Scapherpetontidae	Vertebra				0				0				0	1
Amphibian	Unidentified			1	1				0				0	0
Albanerpetontid	Dentary			3	3			1	1			1	1	9
Albanerpetontid	Humerus dist			2	2				0				0	0
Albanerpetontid	Humerus prox		1		1				0				0	0
Albanerpetontid	Frontal				0				0			1	1	0
Albanerpetontid	Vertebra			9	9			5	5		2	3	5	12
Albanerpetontid	Femur				0				0				0	6
Sauropsida	Humerus				0				0				0	1
Sauropsida	Femur				0				0				0	3
Sauropsida	Tibia				0				0				0	1
Sauropsida	Dentary		1		1				0				0	0
Lepidosaur	Maxillary		1		1				0				0	0
Lepidosaur	Dentary		1		1				0				0	0
Lepidosaur	Jaw			1	1				0				0	0
Lepidosaur	Cranial element				0				0		2		2	0
Lepidosaur	Vertebra			4	4				0			1	1	6
Lepidosaur	Osteoderms		1		1				0				0	6
Scincomorpha	Premax				0				0			1	1	0
Paramacellodidae	Dentary				0				0			1	1	0
Paramacellodidae	Frontal		1		1				0				0	5
Archosaur	Vertebra			1	1	1			1				0	0
Archosaur	Claw				0			1	1				0	1
Archosaur	Teeth				0				0			2	2	0
Pterosaur	Unidentified bone				0	1			1				0	0
Pterosaur	Teeth				0				0				0	1
Thyreophora	Teeth				0				0				0	1
Neornitischia	Teeth				0		1		1				0	0
Dromaeosauridae	Teeth				0				0				0	2
Megalosauridae	Teeth				0	1			1				0	1
Crocodylomorph	Teeth		12	54	66	1	12	82	95		5	19	24	125
Crocodylomorph	Osteoderms	3		3	6	1	17	11	29				0	4
UTO	Dentary			2	2				0				0	0
UTO	Claw			1	1				0				0	0
UTO	Unidentified			1	1	1		6	7		1	17	18	0
UTO	Skull tetrapod			9	9				0				0	0
UTO	Jaw				0			1	1				0	0

UTO	Vertebral arch tetrapod			2	2				0			1	1	41
UTO	Vertebra				0				0				0	9
UTO	Teeth				0				0				0	22
UTO	"Sandwich bone"			3	3	1	2	1	4				0	0
UTO	Osteoderms				0				0			1	1	9
UTO	Cranial element				0		5	2	7			3	3	1
UTO	Phallanx				0				0				0	5
UTO	Identifiable			22	22				0				0	1
Splint bones		2	55	540	597	4	35	211	250		26	542	568	58
Plant remains	Miscelenous	3	3		6	8	26		34	7	3	43	53	1
Plant remains	Charcoal	2	77	24	103				0				0	49
Amber				3	3			1	1			2	2	0
Eggshells				67	67			1	1		8	10	18	75

Annex 2: Sample of the ostracods (**A1-A5**) and charophytes (**B1-B5**) assemblages from Zimbral. Scale is 1mm.