Long bone and vertebral microanatomy and osteo-histology of ’*Platecarpus*’ *ptychodon* (Reptilia, Mosasauridae) – implications for marine adaptations

Miriam Heingård

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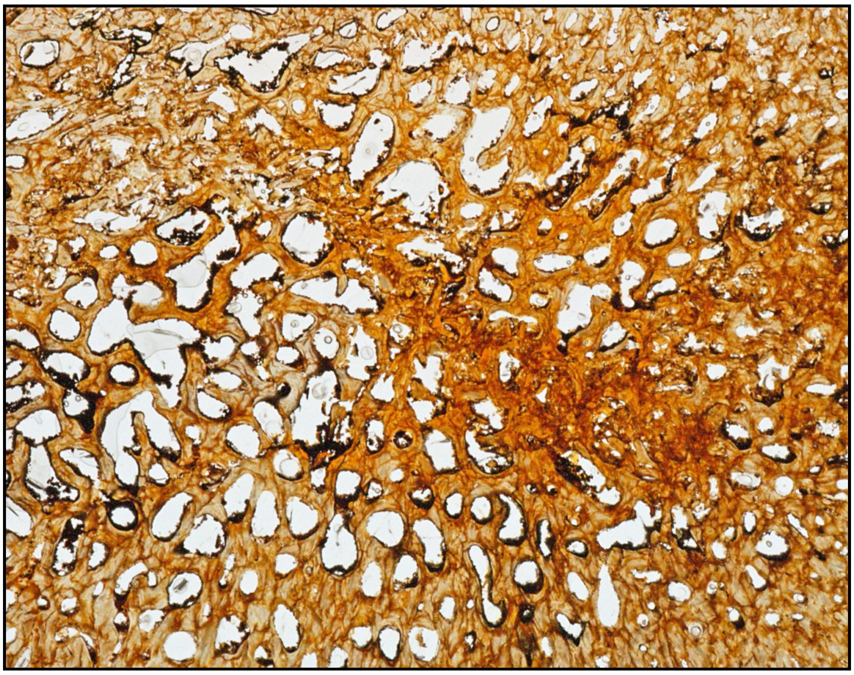

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Cover Picture: Humeral microanatomy of '*Platecarpus*' *ptychodon*.

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Abstract: The inner bone architecture and histology provide information about life history traits of extant as well as extinct animals. Mosasaurs (family Mosasauridae) are a group of secondarily adapted marine squamates that radiated in the Late Cretaceous, resulting in the evolution of a body plan adapted for pelagic habitats. Specialisations in this group can be observed at different levels of skeletal anatomy, including bone microstructures and osteo-histology. This study describes the histological features and microanatomy observed in bone sections of a vertebra and a long bone (humerus) from derived mosasaur ’*Platecarpus*’ *ptychodon*. Bone sections consist mainly of cancellous bone with a gradual transition to a rather thin outer layer of cortical bone. The bone histology in both sections is characterised by poorly organised tissue; fibro-lamellar bone is abundant throughout the sections, displaying randomly organised lacunae and lamellar bone in osteons, whereas parallel-fibered bone (lamellar-zonal bone) is observed only in one area of the vertebra. This implies a rapid growth rate possibly similar to some ichthyosaurs and plesiosaurs. The present contribution demonstrates that ’*P*’. *ptychodon* exhibit microstructures consistent with life in pelagic environments and show evidence for rapid growth rate and an active marine lifestyle. Furthermore, a structure found in the vertebra is probably related to avascular necrosis, a disease caused by decompression sickness, which adds information about the ecology of this species.

Keywords: bone histology, bone microanatomy, mosasaurs, aquatic adaptations, growth rate

Supervisor(s): Johan Lindgren

Subject: Bedrock Geology

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Osteohistologi och mikrostrukturer i ett överarmsben och en ryggkota från *’Platecarpus’ ptychodon* - implikationer för marina anpassningar

MIRIAM HEINGÅRD

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Sammanfattning: Den inre strukturen och vävnaden hos ben ger information om livsstil hos nutida och utdöda djur. Mosasaurier (familj Mosasauridae) är en grupp sekundärt anpassade marina reptiler som utvecklades och spred sig under sen krita, vilket resulterade i en kropp väl anpassad för marina miljöer. Marina anpassningar hos den här gruppen kan observeras på olika nivåer i skelettanatomin, exempelvis mikrostrukturer och benvävnad. Den här studien beskriver histologiska och mikroanatomiska kännetecken i ett överarmsben och en ryggkota hos den väl anpassade mosasaurien ’*Platecarpus*’ *ptychodon*. Tunnslip visar att benen till stor del består av trabekulärt ben med en gradvis övergång till det mer kompakta yttre benlagret. Detta är jämförbart med många moderna valar. Benhistologin karaktäriseras av en avsaknad av organiserad vävnad. Fibro-laminärt ben med slumpmässigt orienterade lakuner finns rikligt i båda benen och laminärt ben finns i osteoner. Parallellfibröst ben observeras endast i en del av ryggkotan. Detta antyder en snabb tillväxthastighet, eventuellt liknande den hos vissa ichthyosaurier och plesiosaurier. Den här studien visar att ’*P*’ *ptychodon* har mikrostrukturer som stämmer överens med en aktiv pelagisk livsstil. Den uppvisar även tecken på en snabb tillväxthastighet. En struktur i ryggkotan är troligtvis relaterad till osteonekros, en sjukdom som orsakas av tryckfallssjuka, vilket bidrar till förståelsen av den här artens ekologi.

Nyckelord: benhistologi, mikroanatomi, mosasaurier, akvatisk anpassning, tillväxthastighet

Handledare: Johan Lindgren

Ämnesinriktning: Berggrundsgeologi

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1 Introduction

Marine vertebrates that originated on land show a range of aquatic adaptations, and to understand the evolution of these groups the study of their fossilised remains is essential. In extant species the determination of lifestyle and life history traits is possible through direct observation, whereas in extinct vertebrates skeletal remains provide some of that information. The lifestyle of an animal is often reflected at different levels of their skeletal anatomy, ranging from gross anatomy to bone microstructures. Studies have shown a relationship between microanatomy and lifestyle, e.g. in amniotes (Germain & Laurin 2005; Kriloff et al. 2008; Canoville & Laurin 2010). The inner bone organisation of tissue is studied in the field of osteo-histology. Analysis of the bone tissue is a useful tool for providing additional ecological data and work as a complement to anatomical data from extant as well as extinct taxa. The study of histological and microanatomical features in fossil taxa can thus be used as a source of information on life history traits. Additionally, the lifestyle(s) of taxa whose habitats are uncertain can be inferred to some extent.

1.1 Bone development and aquatic adaptations in tetrapods

Bone is organised into two types of osseous tissue; cancellous and cortical bone (Fig. 1). Cortical bone is dense and forms the exterior surrounding the medullary cavity in long bones. In contrast, cancellous bone (synonymous with trabecular or spongious bone) consists of interconnecting structures called trabeculae, making it porous. The primary functional unit of cortical bone is the osteon. It contains osteocytes (bone cells) in small spaces called lacunae, organised in lamellae around the central Haversian canal. Depending on the growth rate different tissues develop with varying levels of organisation of the lacunae.

The endochondral ossification occurring during the neonatal stage of all tetrapods is controlled by the genetics of the organism (Carter et al. 1991). Further development of the bone is affected by the physical environment and the mechanical stresses acting during bone maturation (Beaupre et al. 1990; Carter et al. 1991). Terrestrial and aquatic environments require special adaptations due to different mechanical stresses, resulting in differences in bone histology and microstructures between terrestrial animals and those adapted to aquatic environments. This difference has long been known (Nopcsa 1923), and can be seen in, for instance, marine reptiles and mammals whose bone microstructures differ from their terrestrial relatives (Wall 1983; de Buffrénil & Schoevaert 1988; de Ricqlès & de Buffrénil 2001; Houssaye 2012). Bone microanatomy of terrestrial tetrapods is the direct result of living under the influence of loading due to gravity. In water, this loading is negligible, or at least greatly reduced, and the absence of stress causes infilling of the medullary cavity by endosteal deposition of trabeculae (Pitts et al. 1983; Patterson-Buckendahl et al. 1987). This ultimately results in heavy reduction or complete loss of the medullary cavity, a feature that can be seen in many aquatic tetrapods (Fig. 2A). Terrestrial tetrapods, however, have a large medullary cavity surrounded by a peripheral region of cortical bone (Fig. 2B).

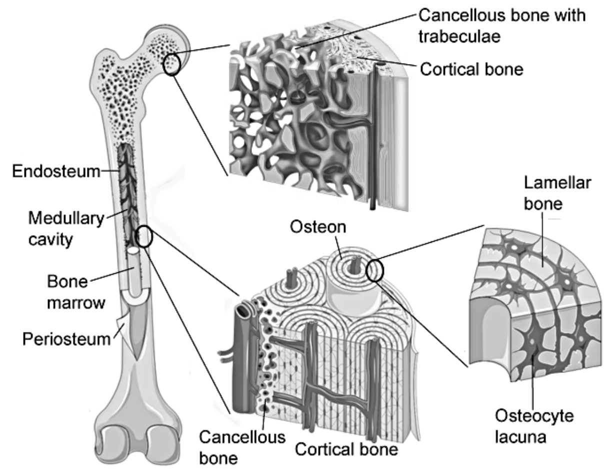

Fig. 1. Illustration of the bone anatomy and composition of a long bone, displaying different types of osseous tissue. Illustration modified from Bao et al. (2013).

Aquatic tetrapods exhibit two main osseous microanatomical specialisations: bone mass increase and osteoporosis. Bone mass increase can be described as pachyosteosclerosis which is the frequent combination of pachyostosis and osteosclerosis. Pachyostosis refers to a thickening of the bone wall, and, as a consequence, altered external bone morphology, whereas osteosclerosis is an increase in inner bone compactness which has no effect on the external morphology. Pachyosteosclerosis has been recorded in semiaquatic taxa that are secondarily adapted to aquatic environments and live in shallow marine habitats. Furthermore, it has been linked to rather slow and passive swimmers (de Ricqlès & de Buffrénil 2001; Houssaye 2009). Conversely, an osteoporotic state has been encountered in fast and active swimmers capable of high speeds and/or manoeuvrability (de Ricqlès & de Buffrénil 2001; Houssaye 2009), such as the extinct ichthyosaurs (de Buffrénil & Mazin 1990) and extant cetaceans (de Buffrénil & Schoevaert 1988). This shift in microanatomy reflects an evolution from poor swimmers living in shallow marine habitats to agile pelagic swimmers, as well as a change in the mode of buoyancy control. Buoyancy and body trim are important adaptations in aquatic animals as they allow them to stay submerged and remain at desired level in the water column. The buoyancy of an animal is dependent on the density of the body, thus, by altering the density and volume of different components in the body, the buoyancy can change (Taylor 1994). Vascular canals contain fluids and lipids.

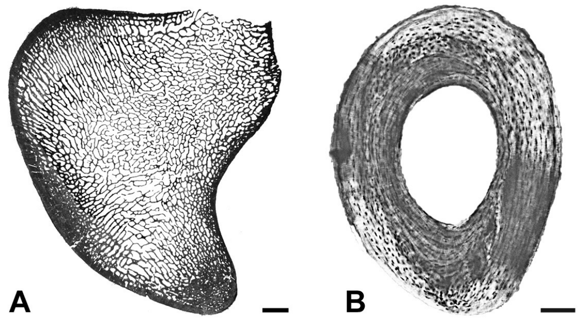

Fig. 2. Bone sections of an aquatic tetrapod (A) and a terrestrial tetrapod (B). **A.** Humeral bone section belonging to derived mosasaur *Prognathodon* sp. Scale bar equals 5.6 mm. Illustration modified from Houssaye et al. (2013). **B.** Humeral bone section belonging to *Varanus caudolineatus*. Scale bar equals 100 µm.

Consequently, an increase in these structures indicates large quantities of stored lipids and fluids, making the bone lighter, as seen in extant cetaceans and turtles (Wall 1983; Taylor 1994). This condition is indicative of a hydrodynamic control of buoyancy and body trim (Taylor 1994). Conversely, animals displaying bone mass increase may use this as ballast in regulation of a hydrostatic control of buoyancy and body trim (Taylor 2000; de Ricqlès & de Buffrénil 2001). As suggested by Taylor (1994), an increase in bone density would require greater lung capacity to make up for the loss in buoyancy. However, larger lung volume could increase drag when swimming, resulting in slower swimming speeds (Taylor 2000), as seen in sirenians (de Buffrénil et al. 2008). Faster swimming animals often dive deep as part of their lifestyle, and hydrodynamic buoyancy control cannot involve a large lung volume, since oxygen storage in the lungs would make them highly susceptible to decompression sickness (Taylor 2000). An osteoporotic condition together with reduced lung volume would result in an animal achieving neutral buoyancy over a broad range of water depths, whereas bone mass increase gives a shallow and narrow range of neutral buoyancy (Taylor 1994).

1.2 Mosasaur evolution and adaptation

Mosasaurs are secondarily adapted marine squamates that first appeared in the Cenomanian about 98 Ma and went extinct at the Cretaceous-Paleogene boundary about 66 Ma. During their existence they attained a global distribution as apex predators of the Late Cretaceous seas and oceans. After the evolutionary divergence from their closest terrestrial relatives it is believed that mosasaurs achieved advanced marine adaptations in less than 10 million years (Lindgren et al. 2010). A high metabolic rate has been proposed for various marine reptiles, including mosasaurs (Bernard et al. 2010), and it is likely that they were capable of maintaining a high body temperature. This might have been a crucial adaptation in attaining a worldwide distribution as it might have enabled them to extend to cooler waters, as has been suggested for other Mesozoic marine reptiles (Klein 2010).

It is possible to distinguish different stages and morphologies in the evolution from land dwellers to highly aquatically-adapted squamates. These morphologies reflect different ecological niches and an evolution towards open-ocean habitats and more efficient swimming (Lindgren et al. 2011). This ecological transition is apparent in the skeletal anatomy at the gross level as well as in the microstructures and histology of the bones. Adaptations at the gross anatomical level include the acquisition of a streamlined body combined with a reorganisation of internal organs (Lindgren et al. 2010; Konishi et al. 2012), a hypocercal tail fin where the axial support is bent downwards (Lindgren et al. 2010), and modifications of the pelvic girdle and limbs (Caldwell 2002; Caldwell & Palci 2007).

Three principal morphotypes have been recognised that mirror the transition from terrestrial to pelagic lifestyle in mosasaurs (Caldwell & Palci 2007; Houssaye et al. 2013): (1) forms typically smaller than 2 metres in length having an overall terrestrial-like anatomy; i.e., plesiopedal limbs suitable for terrestrial locomotion and a pelvic girdle with a plesiomorphic squamate anatomy; (2) larger forms (3-6 metres long) displaying plesiopedal limbs but possessing a modified pelvic girdle; i.e., some degree of hydropelvic anatomy; and (3) mosasauroids completely adapted to marine environments, displaying not only an increase in size (4 to 15 metres long) but also hydropedal limbs and a hydropelvic anatomy; i.e., paddle-like limbs and a modified pelvis. Houssaye & Tafforeau (2012) demonstrated that hydropelvic mosasaurs were efficient swimmers from a very young age and likely better swimmers than adult plesiopelvic forms. Juvenile hydropelvic mosasauroids have a bone architecture and microstructures similar to those of adults, implying that the ecology and functional requirements of hydropelvic mosasauroids remained much the same throughout ontogeny (Houssaye & Tafforeau 2012). This is notably different from plesiosaurs, another lineage of Mesozoic marine reptiles, in which a change in microanatomy from pachyosteosclerosis (in juveniles) to osteoporosis (in adults) has been observed, indicating a shift in ecology during ontogeny (Wiffen et al. 1995).

The level of marine adaptation in mosasaurs is also apparent on a microanatomical level. Plesiopelvic mosasauroids generally display pachyosteosclerosis (Houssaye 2009; Houssaye 2013). Osteoporosis has been described in the hydropelvic mosasauroids *Clidastes* and *Tylosaurus* and pachyostosis in *Platecarpus* (Sheldon 1997). However, more recent analyses of ribs and vertebrae of these mosasaurs reveal the absence of both an osteoporotic-like condition and bone mass increase in hydropelvic mosasauroids (Houssaye & Bardet 2012). The inner bone organisation of hydropelvic mosasauroids is known to be spongious and displays development of a true trabecular organisation, while the peripheral layer of the cortical bone is generally rather thin (Sheldon 1997; Houssaye 2012; Houssaye & Bardet 2012; Houssaye et al. 2013).

1.3 Aim of the study

The present study describes histological features and microanatomical structures observed in a humerus and a vertebra of '*Platecarpus*' *ptychodon*, a hydropelvic and hydropedal mosasaur hitherto described exclusively from isolated teeth (Arambourg 1952). Sections of the bones were examined in order to describe and analyse the bone histology and microanatomy, and to relate these structures to marine adaptations in this derived mosasaur.

2 Material and methods

Mosasaur bone samples (a humerus and a vertebra) belonging to different individuals of '*Platecarpus*' *ptychodon* were collected from marine sediments of Maastrichtian age near Bentiaba, Angola (Mateus et al. 2012). The vertebra belongs to a semi-complete skeleton. The humerus was identified from a characteristic crest in the distal lateral part of the bone. Prior to histological sectioning the bones were photographed and casted. Casts were made using clay moulds and silicone mixed with a hardening agent. The bones were cut longitudinally into three pieces, of which the middle piece of each bone was selected for analysis. This was encased in a two component epoxy (Araldite) to create support and to prevent the bones from shattering during cutting and polishing. A Buehler Isomet low speed diamond saw was used to cut two sections of approximately 1 mm thickness from each of the encased bones. The sections were attached to glass slides using epoxy and polished to desired thickness. Bone sections were examined under an optical microscope, using magnifications ranging from 4x to 50x.

The histological terminology is based on Houssaye et al. (2013).

3 Results

3.1 Humerus

The section is characterised by cancellous medullary

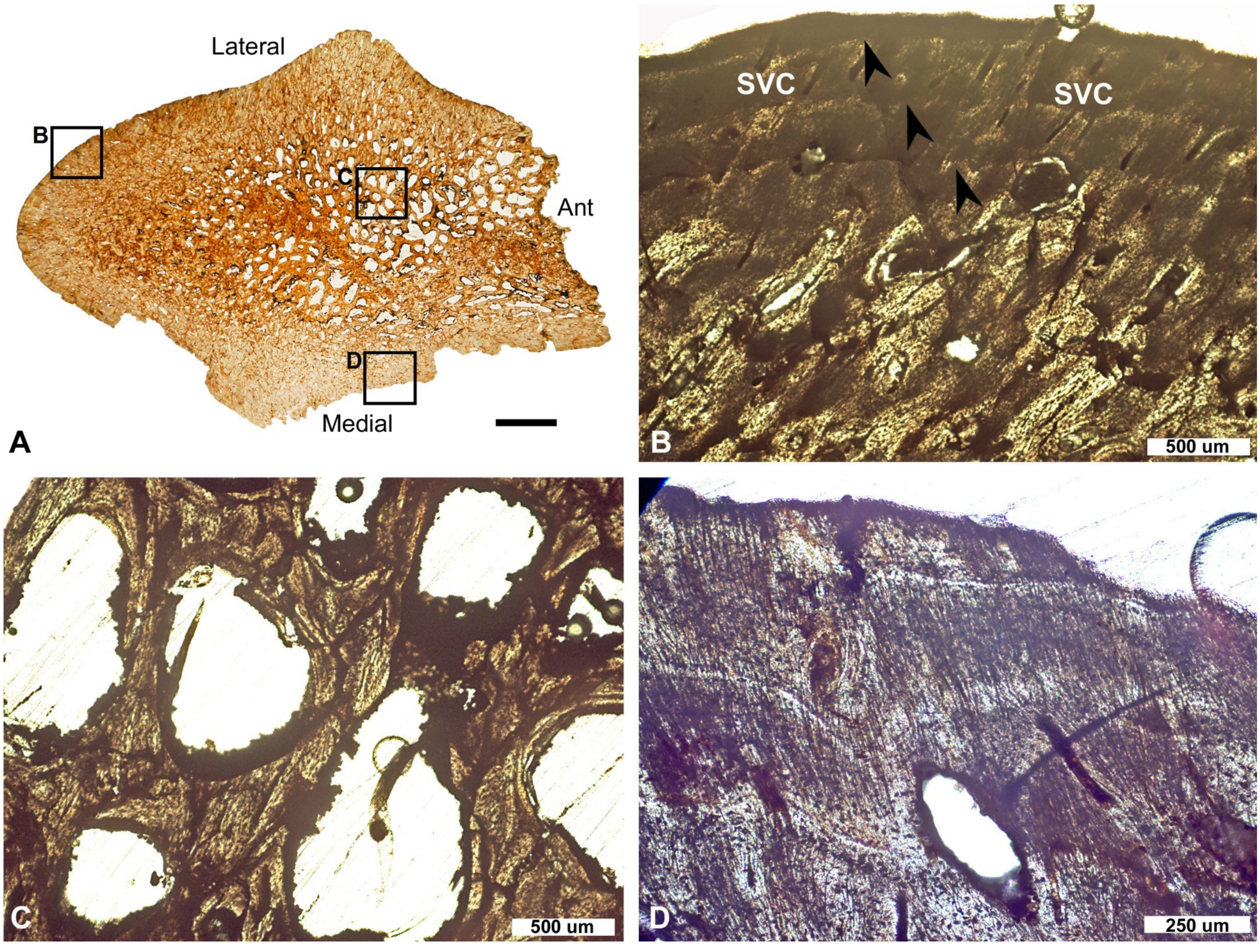

Fig. 3. The humeral section. **A.** Overview of the humeral mid-diaphyseal section. Scale bar equals 5 mm. **B.** Posterior cortex, displaying radially oriented simple vascular canals (SVC) and lines of arrested growth (arrows). **C.** Cancellous bone in the centre of the section. Intertrabecular spaces are rather homogenous. **D.** Cortical medial region displaying abundance of collagen fibres (Sharpey's fibres).

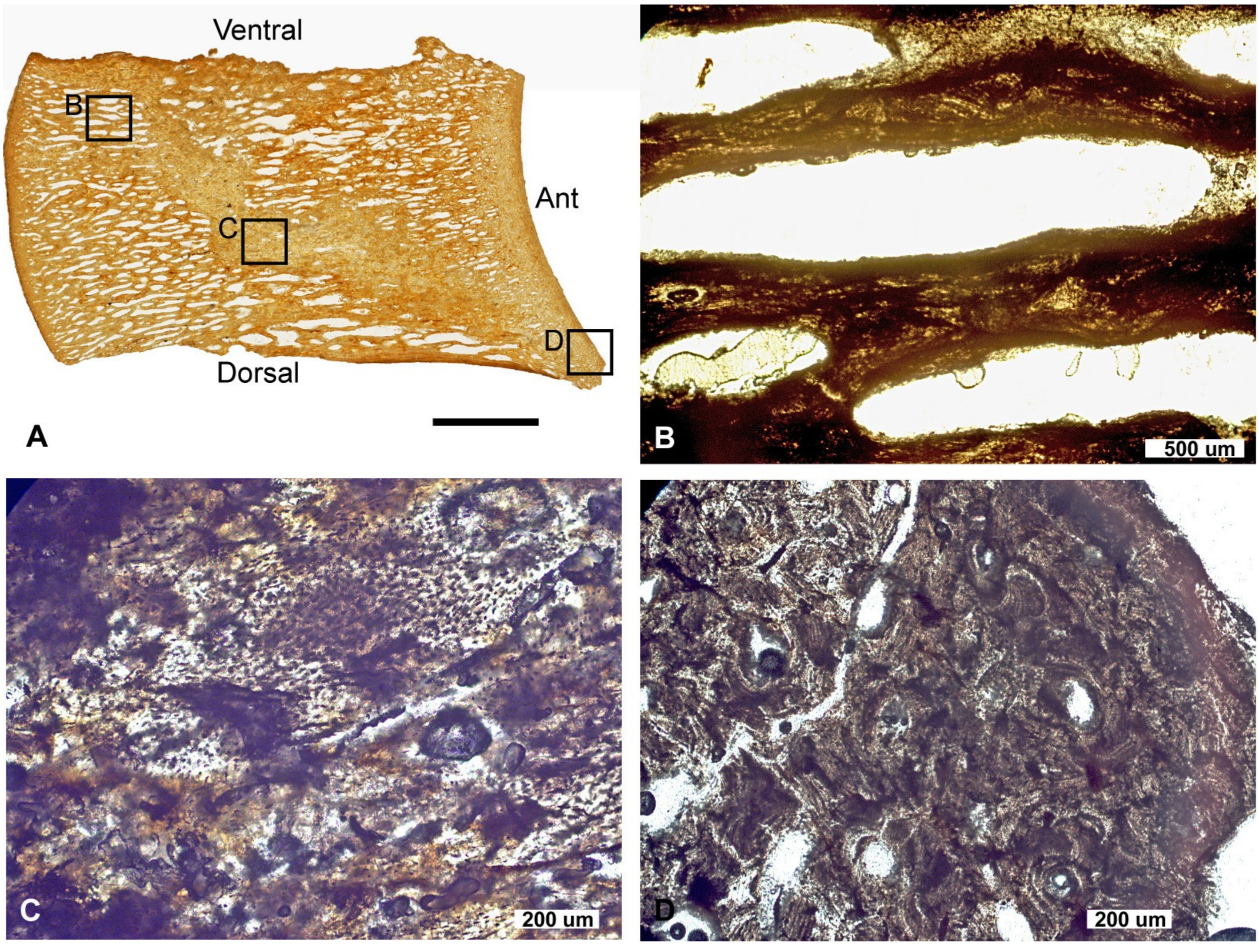

Fig. 4. The vertebral section. **A.** Overview of the vertebral section. Scale bar equals 10 mm. **B.** Organization of the trabecular network. Note; rather large and elongated intertrabecular spaces. **C.** Poorly vascularised zone of dense bone interrupting the trabecular network. **D.** Anterior cortex penetrated by some secondary osteons, indicating bone remodelling.

bone surrounded by a peripheral layer of cortical bone; however, there is no clear transition from the cancellous bone to the peripheral layer but rather a gradual change in density (Fig. 3A). The central spongiosa consists of a rather homogenous trabecular network (Fig. 3C), although the size of the intertrabecular spaces varies over the section. The shape of the intertrabecular spaces is consistent throughout most of the section but variations do occur, specifically towards the anterior end where they are elongated (Fig. 3A). Some central trabeculae are crushed (Fig. 5A).

The cortex is penetrated by numerous radially oriented, simple vascular canals (Fig. 3B, 5B). Primary and secondary osteons are present, the latter indicating some degree of bone remodelling. At least three, possibly up to five, lines of arrested growth (LAGs) are visible in the cortex (Fig. 3B, 5B). Bundles of collagenous fibres occur frequently in the peripheral region (Fig. 3D).

Different types of bone tissue are present: fibrous bone with randomly oriented lacunae is abundant throughout most of the section (Fig. 3D, 5B-C) whereas lamellar bone with aligned lacunae is present in osteons (Fig. 5C). Notably, the bone lacks true parallel-fibered bone.

3.2 Vertebra

The section consists mainly of cancellous bone, with a thin peripheral layer of cortical bone at the anterior (cotyle) and posterior (condyle) ends (Fig. 4A). The overall organisation of the spongiosa is fairly homogenous. The trabecular network is largely intact and almost uncrushed. The trabeculae are oriented sub-parallel to one another throughout much of the section and intertrabecular spaces are consistently elongated (Fig. 4B), although somewhat varying in size, with relatively large spaces in some parts. The bone displays signs of remodelling and numerous secondary osteons are present (Fig. 4D, 5D). Some radially oriented, simple vascular canals exist, but the thin cortex is generally rather poorly vascularised.

Lamellar bone is present in osteons whereas fibrous bone is abundant throughout the section (Fig. 5D). A tendency towards lamellar-zonal bone is found in one area which is characterised by aligned lacunae, perhaps corresponding to parallel-fibered bone (Fig. 5E). The same area also displays putative LAGs (these are not seen in other areas of the section).

The spongious bone exhibit a zone of dense bone

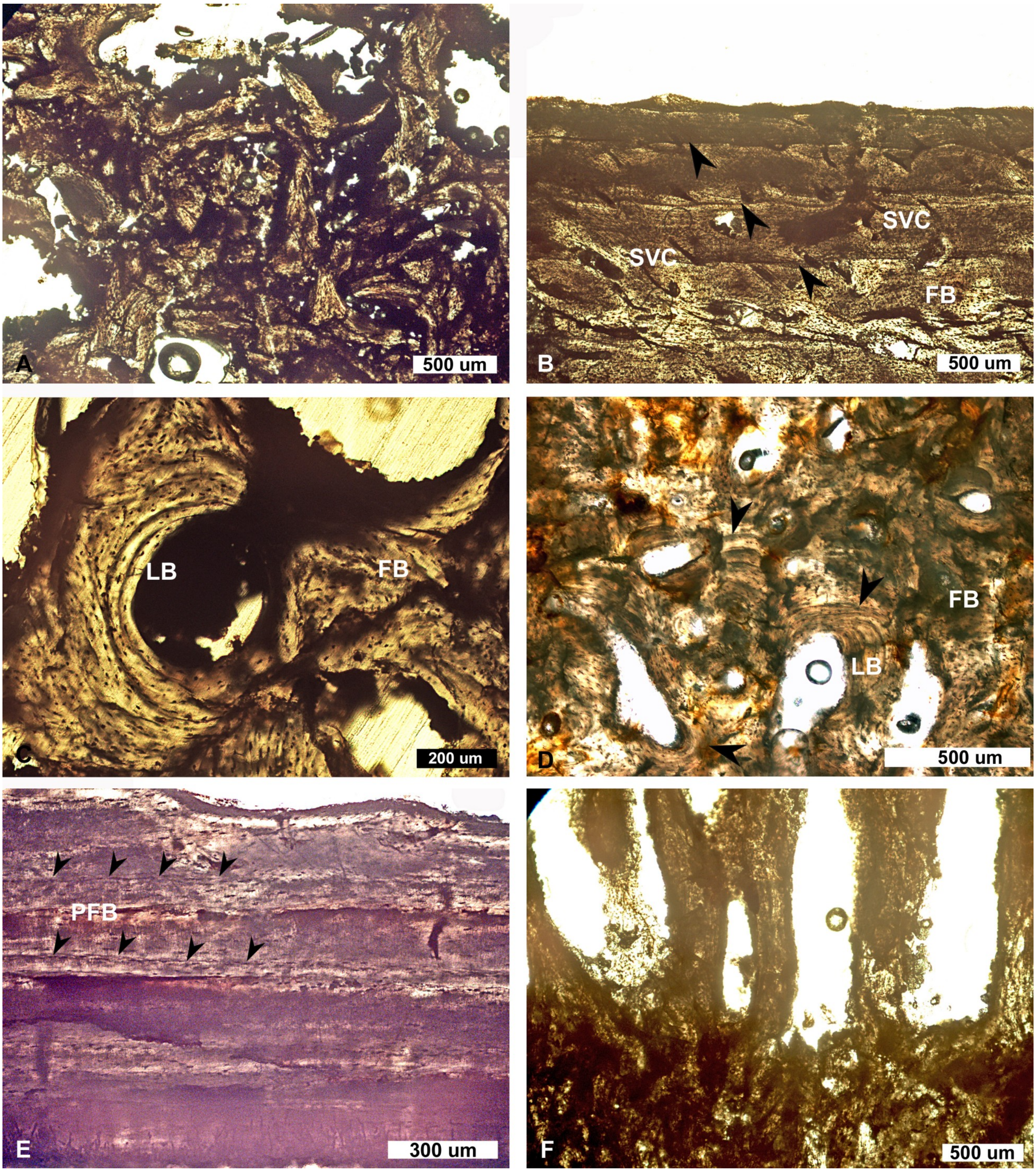

Fig. 5. Histological features of the humeral (A-C) and vertebral (D-F) sections. **A.** Crushed trabeculae in the centre of the section . **B.** Anterior cortex illustrating LAGs (arrows) and radially oriented simple vascular canals. **C.** Lamellar bone (LB) in osteon surrounded by fibrous bone (FB). **D.** Signs of bone remodelling (arrows) in the cortex. Lamellar bone (LB) is present in osteons and fibrous bone (FB) can be seen around it. **E.** Cortex with possible LAGs and a tendency to aligned lacunae (arrows), i.e. more organized tissue, perhaps corresponding to parallel-fibered bone (PFB). **F.** Intact trabeculae at the border beween area of increased density interrupting the cancellous bone and the trabecular network.

(Fig. 4C) extending uninterrupted through the section. This area is characterised by a mass of bony tissue with few (if any) vascular canals. Osteocyte lacunae are present throughout the zone but vary in density. Trabeculae adjacent to this zone are intact and seemingly unaffected by the density change. The transition from the dense bone to the spongiosa is sharp, with large intertrabecular spaces and intact trabeculae bordering the zone (Fig. 5F).

4 Discussion

4.1 Humerus

The humeral section displays cancellous bone occupying the medullary cavity, and this tissue is surrounded by dense but vascularised bone. The medullary cavity is completely filled with trabeculae. This is consistent with the condition in other derived mosasauroids, as well as derived aquatic tetrapods in general. The spongiosa is rather homogenous compared to some hydropelvic mosasauroids (Houssaye et al. 2013) and lacks distinct zones. It could be argued that the few elongated intertrabecular spaces present make up a zone, and since the anterior end is broken other microanatomical structures might be missing.

The remodelling of the bone reveals that this individual is not a juvenile, which is corroborated by the presence of 3–5 LAGs. Lines of arrested growth, also known as Harris lines, are lines marking periods of temporary slower bone growth rate generally linked to a seasonal change in resources.

4.2 Vertebra

The majority of the vertebral section consists of cancellous bone with occasionally very large intertrabecular spaces. The cortex at the condyle is very thin and somewhat thicker at the cotyle. Parallel-fibered bone has a slower growth rate than fibrous bone and indicates varying growth rates within the bone. Although the section displays putative LAGs, it is primarily the relatively extensive remodelling of the bone tissue that implies that this individual is not a juvenile animal.

The peculiar band of dense bone diagonally across the section (Fig. 4A, 4C) is probably related to avascular necrosis, a disease caused by interrupted blood supply to certain skeletal components (Resnick et al. 1981). When the blood supply ceases the bone tissue dies, resulting in the loss of structure and a possible collapse, leaving a permanent zone of dead bone. In this case, a change has occurred in a distinct zone without affecting any of the surrounding trabeculae. The density change is localised to a distinct band and the overall intactness of the trabecular network indicates little, if any, crushing during burial. This implies that this structure is not taphonomic in origin. A collapse of the trabecular network due to taphonomic processes would probably yield a different pattern than that observed. The structure seen in the material at hand is superficially very similar to what Rothschild & Martin (1987) documented in *Platecarpus* vertebrae, with the difference that the structure related to avascular necrosis therein was described as a band of decreased density. The increase in density seen herein could perhaps be explained by secondary infilling of some cavities. However, acellular areas would be expected if post-collapse infilling of the cavities had occurred, but such areas are not observed.

4.3 Adaptive and ecological implications

Convergent evolution has created analogous characters in mosasaurs, cetaceans, ichthyosaurs, and other marine vertebrates, including similar skeletal microanatomy, acquisition of a streamlined body shape and a hypocercal tail fin in some marine reptiles (Lindgren et al. 2010; Konishi et al. 2012). The evolution seen in mosasaurs shows a clear transition from life on land to active pelagic swimming, and suggests similar ecological adaptations to those seen in other groups secondarily adapted to an aquatic existence. The change in microanatomy and thus change from hydrostatic to hydrodynamic buoyancy control and body trim is comparable to what has been observed in early Cetacea (Gray et al. 2007; Uhen 2010).

'*Platecarpus*' *ptychodon* is considered a highly derived mosasaur. The features observed in the present study corroborate this notion. Both the humeral and the vertebral section display features typical of pelagic animals. The reduced medullary cavity is consistent with life in water where the force of gravity is less apparent. Both sections are largely dominated by cancellous bone, the vertebral section in particular, indicating that considerable quantities of lipids and other fluids were located in the voids, hence making the skeleton lighter. This suggests that the animal relied on a hydrodynamic buoyancy control, which would imply that it inhabited open-ocean environments. The lightened skeleton probably also has implications for speed and manoeuvrability, as these aspects are known to correlate with a light skeleton in marine tetrapods (de Ricqlès & de Buffrénil 2001; Houssaye 2009). '*P*'. *ptychodon* was thus likely a fast and active animal capable of high speed swimming.

In a comparative study, Houssaye (2012) concluded that collagenous weave and vascular network in different groups of aquatic reptiles seem to inform mainly of growth rate and basal metabolic rates. Generally, poorly organised bone tissue is indicative of elevated growth rates (de Margerie et al. 2002). Growth rate increases with the density of the vascularisation; conversely, it decreases with increased organisation of the collagenous fibres. Bone growth rate has indirectly been linked to basal metabolic rate (Montes et al. 2007). It is thus possible to use bone tissue to make inferences about basal metabolic rate and the thermal physiology of an animal (Montes et al. 2007).

Primary periosteal bone can be divided into two main types: lamellar-zonal bone (lamellar or parallel-fibered bone) and fibro-lamellar bone. Fibro-lamellar bone is typically highly vascularised with frequent osteons, whereas lamellar-zonal bone is generally poorly vascularised with few primary osteons. Fibro-lamellar bone has a faster rate of bone deposition and is present in all extant endotherms and has been linked to a high body temperature (de Ricqlès et al. 2003; Chinsamy et al. 2009). However fibro-lamellar bone is also present in animals considered ectothermic, which implies that the formation of fibro-lamellar bone does not necessarily require a high metabolic rate (Chinsamy-Turan 2005). Parallel-fibered bone has been recorded in vertebrae (Houssaye & Bardet 2012; Houssaye & Tafforeau 2012) and long bones (Houssaye et al. 2013) of hydropelvic mosasauroids. However, the sections examined herein largely lack apparent parallel-fibered bone and instead they display a bony tissue more similar to fibro-lamellar bone. This reflects a faster growth rate than typical parallel-fibered bone. The dominance of fibro-lamellar bone in ichthyosaurs and plesiosaurs (Houssaye 2012; Houssaye et al. 2014) indicates rather high growth and basal metabolic rates in these groups compared to hydropelvic mosasaurs (Motani 2002). However, the sections studied in the present study indicate that the growth and basal metabolic rate of '*Platecarpus*' *ptychodon* might have been comparable to that of some ichthyosaurs and plesiosaurs.

Avascular necrosis has been described in different genera of mosasaurs, and is interpreted as an effect of decompression sickness (Rothschild & Martin 1987). The phenomenon has also been identified in extant as well as extinct marine turtles and in Jurassic ichthyosaurs (Rothschild et al. 2012), of which at least the latter are believed to have engaged in deep diving (Motani et al. 1999). Some whales are known to frequently dive deep to feed. Consequently, decompression sickness would be expected in these animals but is nonetheless strikingly absent in all modern taxa (Beatty & Rothschild 2008). Since avascular necrosis could inflict damage to bone it would be expected that animals frequently engaging in deep diving would evolve protective mechanisms to counteract decompression sickness. Indeed, the absence of avascular necrosis in modern cetaceans has long been attributed to anatomical modifications, such as improved circulatory physiology (Beatty & Rothschild 2008). The frequent occurrence of avascular necrosis in mosasaurs suggests they lacked physiological adaptations similar to those seen in cetaceans. Mosasaurs existed for a geologically brief period of time (~32 million years) compared to whales, ichthyosaurs and plesiosaurs. It is possible that it was not enough time to develop protective measures against decompression syndrome (Rothschild & Martin 1987). Although ichthyosaurs existed for a significantly longer time than did mosasaurs, the presence of avascular necrosis has been attributed to a possible change in lifestyle and prey (Rothschild et al. 2012). Avascular necrosis would imply that '*Platecarpus*' *ptychodon* had a pelagic lifestyle that included occasional deep diving habits as a means of feeding and/or escaping from predators.

5 Conclusions

Mosasaurs radiated in the Late Cretaceous, resulting in different adaptations and the evolution of a body plan adapted for pelagic environments. The present study shows that the humeral and vertebral microanatomy of *'Platecarpus' ptychodon* is consistent with highly derived mosasauroids. The vertebral section consists mainly of cancellous bone and a very thin cortex, whereas the humeral section displays medullary cancellous bone and a gradual transition to a thin peripheral layer of cortical bone. This is largely consistent with an active aquatic lifestyle and more specifically tetrapods in open-ocean habitats relying on a hydrodynamic buoyancy and body trim control.

Histological features show a general tendency for rapid growth rates. The dominant type of bone in both sections is fibro-lamellar; i.e., fibrous bone with lamellar bone in osteons, which is indicative of elevated growth rates and a high metabolic rate compared to that of extant reptiles. A high growth rate is also indicated by the prevalence of radially oriented, simple vascular canals that occur in both sections, but are more frequent in the long bone.

The possible presence of avascular necrosis adds information on the ecology of '*P*'. *ptychodon*.

6 Acknowledgements

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