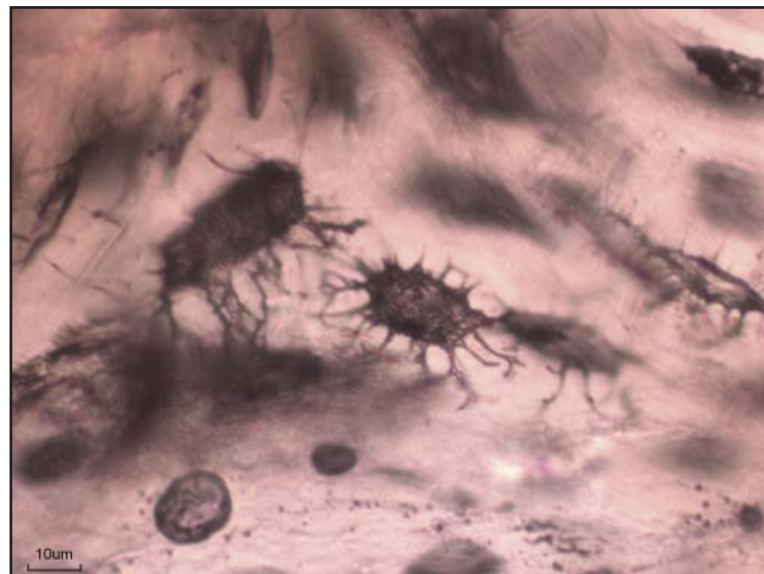# Osteo-histology of Mesozoic marine tetrapods – implications for longevity, growth strategies and growth rates

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Bachelor thesis in Geology at Lund University - Lithosphere and Biogeosphere Sciences, no. 257 (15 hskp/ECTS)

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Osteo-histology of Mesozoic marine tetrapods – implications for longevity, growth strategies and growth rates

Bachelor Thesis
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Contents

Cover Picture: Cross section of femur in Chelonia, showing lacunae representative of the sample. Note the pronounced canaliculi.

Osteo-histology of Mesozoic marine tetrapods – implications for longevity, growth strategies and growth rates

JOHAN GREN

Abstract: Osteo-histology provides information on age, growth strategies, and lifestyles of both recent and ancient animals. This study deals with the histology of fossilized bone from three groups of tetrapods – sea turtles, ichthyosaurs and plesiosaurs – all secondarily adapted to marine life, but with rather different bone microstructures. As a result of extensive vascularization (i.e. osteoporosis), ichthyosaur bone is light, which may have contributed to increased manoeuvrability in open waters. This structure is comparable to that of most extant whales and dolphins. Plesiosaur bone, on the other hand, is very dense (i.e. pachyosteosclerotic) and therefore heavy. This extra weight may have been used for ballasting in a near-shore, shallow marine environment, indicative of habits similar to those of modern sirenians. Sea turtles display a lamellar, moderately vascularized bone pattern comparable to that of most recent turtles and crocodiles. This structure also indicates relatively slower growth rates compared to those of ichthyosaurs. The maturity of the animals at hand has also been investigated, and the sea turtle is adult, displaying at least 17 annual growth rings, whereas the ichthyosaur is a young adult or late juvenile and the plesiosaur is immature.

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Osteohistologi hos mesozoiska marina tetrapoder – implikationer för livscykler, tillväxtstrategier och tillväxthastigheter

JOHAN GREN

Sammanfattning: Genom osteohistologiska analyser kan stora mängder information erhållas. Förutom möjligheten att uppskatta åldern och mognadsgraden hos ett djur kan tillväxtsmärken i skelettet, så kallade 'growth marks' eller GM, också innehålla information om benens tillväxthastighet, djurets tillväxtstrategi och till och med levnadssätt. Denna studie avhandlar histologin hos fossiliserade ben tillhörande en havssköldpadda, en fisködla och en svanödla, vilka alla var sekundärt anpassade till ett marint liv men hade skild skelettuppbyggnad. Fisködlebenet uppvisar en mycket stor kärlfrekvens (osteoporos) vilket kan ha minskat skelettets totala vikt och därmed förbättrat djurets rörelse- och manövreringsmöjligheter i öppna vatten. Denna benstruktur är jämförbar med den vi ser i de flesta av dagens valar och delfiner. Svanödlebenet är mycket kompakt (pachyosteosklerotiskt) vilket troligtvis bidragit till att skelettet var tungt. Denna extra vikt kan ha använts som ballast i en kustnära grundhavsmiljö, analogt med den livsstil dagens sirendjur har. Havssköldpaddan har en laminär, måttligt vaskulariserad benstruktur, jämförbar med nutida havssköldpaddor och krokodiler. Denna struktur påvisar också en långsam tillväxthastighet i förhållande till den hos fisködlan. Djurens ontogeni har också studerats och havssköldpaddebenet bedöms vara från ett vuxet djur, med en ålder av minst 17 år baserat på antalet tillväxtringar, fisködlan var en äldre juvenil eller ett ungt vuxet djur, medan svanödlan var ett ungdjur.

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1 Introduction

To understand growth patterns and aging mechanisms in animals, many different fields of research are applied, and to understand how different growth patterns have evolved, the study of fossil material is essential. Whereas determination of life spans and growth strategies in extant animals is possible through direct observation, this approach is inapplicable for fossil material (Castanet et al. 1993). In fossils, longevity and growth patterns may instead be studied in the field of osteohistology, where the inner microstructures of bones are investigated (e.g. Peabody 1961; Castanet et al. 1993).

The successive growth of bone can be interpreted by examining the presence of so-called growth marks (GM hereafter). GM may be observed in two different ways: either on the surface of bones, or as local histological variations in polished bone sections (Castanet et al. 1993). In long bones, bone growth primarily occurs centripetally around the core, making the outermost bone the youngest. New bone is also created at the centre of the bone, but this is mainly through remodelling of existing bony tissues. Such remodelling destroys the primary bone, including its GM and other histological features, rendering it impossible to use in studies of longevity and growth rates. The inner parts of the bone are also densely vascularized, resulting in that cyclical GM become less evident. Since the more peripheral parts of the bone are less exposed to this kind of remodelling, the cortices are where GM are most readily observed.

GM are similar to the growth rings of trees; a growth cycle is divided into a period of fast bone growth, followed by a decrease in growth rate occasionally leading to a temporary full stop. Growth periods are depicted in the bone as relatively wide circumferentially aligned growth zones, interlayered by thin stripes of so-called annuli and LAGs (Lines of Arrested Growth) representing periods of decreased bone accretion (Castanet et al. 1993). A great deal of research has been conducted in order to reveal the periodicity behind these growth cycles (e.g. Peabody 1961) and most studies suggest that the cycles indicate annual seasonal variations (e.g. Peabody 1961; Hua & de Buffrenil 1996; Adams & Organ 2005; Horner et al 2005). Peabody (1961), in his rather thorough investigation of GM in both extant and extinct vertebrates, also concludes that the distance between GM can be used to quantify the amount of annual growth in an animal.

Within the field of vertebrate palaeontology, the method of growth mark aging has gained broad acceptance due to its proven efficiency in studies of living animals (Peabody 1961; Erickson 2005), and the presence of GM in vertebrates is now considered a general phenomenon (Castanet et al. 1993).

In addition to the presence of GM, other osteohistological features may also be observed. Some species have very cancellous bone (a condition referred to as osteoporosis), frequently observed in e.g. recent cetaceans, while others, such as sirenians, have far more compact bone (pachyosteosclerosis) (Wiffen et al. 1995). The cancellousness of the bone is believed to be morphological adaptations connected to the lifestyle of the organism. Because vascular canals contain lipids and fluid-filled blood vessels transporting nutrients (Cooper et al. 1966), an increase of these structures make the bone lighter. Conversely, animals with dense, pachyosteosclerotic bony tissues may use the increased weight as ballast, whereas species with lighter, osteoporotic-like bone may have advantages in swimming speed and manoeuvrability (Wiffen et al. 1995).

In the present study, sections of bones from three animals are examined in order to determine their growth rates, growth strategies and longevity. The bones are all propodials and belong to a sea turtle, an ichthyosaur, and a plesiosaur, respectively. These animals are all marine tetrapods that are secondarily adapted to aquatic life, but their inferred lifestyles differ considerably which may be of importance for how their respective growth strategies have evolved.

Marine turtles (superorder Chelonia) are represented in the fossil record from the late Early Cretaceous, around 110 Ma, and they still exist today (Legler & Georges 1993; Hirayama 1998; Benson et al. 2010). Recent species of Chelonia have their lives divided into different stages, where juveniles hatch on land and then migrate out to the oceanic zone with water depths exceeding 200 m. They live in this environment until they reach an age of about 3-5 years when they return to the neritic zone, where they spend the remainder of their lives (Carr 1987; Reich et al. 2007). Most sea turtles feed on zooids in suspension (Hawkes et al. 2009), and have thus no need of active swimming abilities when foraging.

The piscine ichthyosaurs evolved around 250 Ma, and went extinct at the Cenomanian-Turonian boundary, around 90 Ma. The reptile group probably belongs in the Diapsida, although their origin and affinities are debated (Motani et al. 1996; Motani et al. 1998). They were active predators in the Mesozoic seas, capable of rapid sustained swimming (Massare 1988).

The order Plesiosauria, with its suborders Plesiosauroidea and Pliosauroidea, arose around 220 Ma during the Late Triassic. Plesiosaurs evolved from basal sauropterygians, and went extinct at the Cretaceous/Tertiary boundary approximately 65 Ma (O'Keefe 2002). They were outstanding predators in the Mesozoic oceans (Wiffen et al. 1995), but whether they caught their prey through pursuit or by ambush is unsure (Massare 1988). Wiffen et al. (1995) suggested that the juveniles had different lifestyles than did the adults, due to an apparent ontogenetic change in bone structure from pachyosteosclerosis to osteoporosis. This would imply a limitation in swimming capability in juveniles, to suggest that young plesiosaurs may have remained in calm, shallow waters until they had undergone a certain amount of bone transformation.

2 Materials and methods

The specimens examined are all collected from separate localities. The sea turtle, belonging in the superorder Chelonia, was found in a marine sand deposit of latest early Campanian age at the Åsen locality, southernmost Sweden (see e.g. Lindgren et al. 2007 for locality description).

The genus *Ichthyosaurus* is known from the latest Triassic through Early Jurassic (Motani 2005). The specimen examined was found in marine strata of Early Jurassic age near the hamlet of Lyme Regis, southernmost England (for stratigraphy and locality description, see e.g. Hallam 1989).

The plesiosaur limb bone examined herein was collected from a loosely consolidated calcarenite of latest early Campanian age in the Ignaberga quarry, southernmost Sweden. As the bone is not very well preserved, it is kept in open nomenclature.

Thin sections were constructed according to the following protocol: initially, a cast was made of the entire bone to be used as a reference. Thereafter, an approximately 10 mm thick mid-diaphyseal section was cut by using a diamond saw. This section was then cast into epoxy and mm-thick sections were produced using a slow speed diamond saw. These sections were then glued onto glass slides and manually polished until they reached the desired thickness.

The investigated samples are all from long bones, as these are considered to be best suited for osteo-histological studies in amphibians and reptiles (Castanet et al. 1993). The long bones may be divided into three general parts; the epiphyses, metaphyses, and diaphysis. Castanet et al. (1993) declares that for measurements of individual age or longevity mid-diaphyseal sections provide the best results. The sea turtle and ichthyosaur are represented by femora, whereas the precise location of the plesiosaur prepodial is unknown. Nonetheless, it is clear that it is a proximal limb bone (femur or humerus).

The prepared sections were studied both under stereo microscope and optical transmission microscope to provide a good overview of the samples and to see details of the inner microstructure of the bones. The magnification used varied between 5x and 40x, and photographs of the sections were gradually taken at 20x and 40x magnification, respectively.
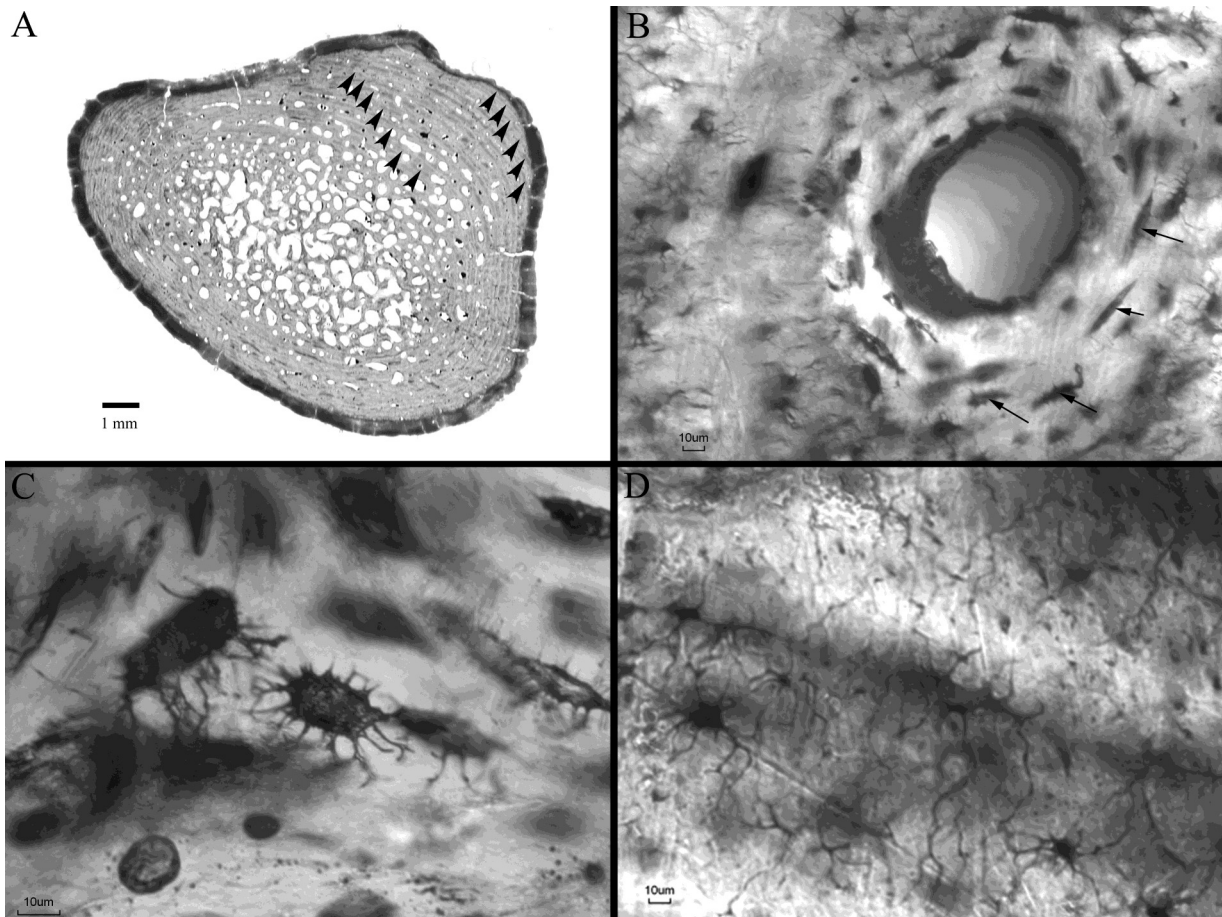

Fig. 1. **A**. Overview over the studied Chelonia cross section with LAGs marked (arrows). **B**. Cross section of femur in Chelonia, displaying a Haversian canal surrounded by secondary bone. Note the centripetal alignment of the lacunae in the new bone (arrows) as opposed to the more irregular pattern in the surrounding bone. **C**. Cross section of femur in Chelonia, showing lacunae representative of the sample. Note the pronounced canaliculi. **D**. Cross section of femur in Chelonia, displaying an intricate network of canaliculi connecting the osteocyte lacunae.

Sections have been carefully examined with particular focus on GM, such as LAGs, annuli and growth zones. Notes were made concerning the amount of vascularization, shape and size of the lacunae, presence or absence of collagen fibres and canaliculi.

3 Results

3.1 Chelonia

The centre of the section consists of intensely vascularized, spongy bone (Fig. 1). This part of the bone has suffered severe remodelling and a lot of the bone is secondary with the consequence that no primary GM are preserved. Around the vascular canals the lacunae are elongated and centripetally aligned in relation to the canals (Fig. 1b). From the lacunae, distinct canaliculi reach out in all directions (Fig. 1c), but with a preferred orientation parallel to the orientation of the lacuna on which they are situated. The surrounding cortices, on the other hand, consist of very characteristic lamellar bone, rich in LAGs. At least 17 growth cycles were identified, and the structures of these GM are constant through the cortex, although the cycles are gradually narrower the further they are from the centre. The vascular canals primarily occur parallel to the annuli/LAGs; the same is true also for the lacunae, and even more so the closer to the bone periphery they are. Additionally, the lacunae are more circumferentially elongated distally. The farther from the centre of the bone they are, the lacunae also seem to be connected through more and longer canaliculi, and in the outermost parts of the lamellar bone the canalicular network is very complex (Fig. 1d). Close to the periosteum, mineralized collagen fibres, known as Sharpey's fibres, were observed. These appear in bundles, connecting the outermost few lamellae to the periosteum. The outermost portion of the cortex (~50-100μm) is opaque (probably a taphonomic effect), with narrow canals (probably traces of bone boring bacteria) radially penetrating the interior.

3.2 *Ichthyosaurus* sp.

The ichthyosaur bone (Fig. 2) is very cancellous. It is thoroughly vascularized by numerous, though rather narrow, canals. The vascularization is not limited to the central parts of the bone; randomly
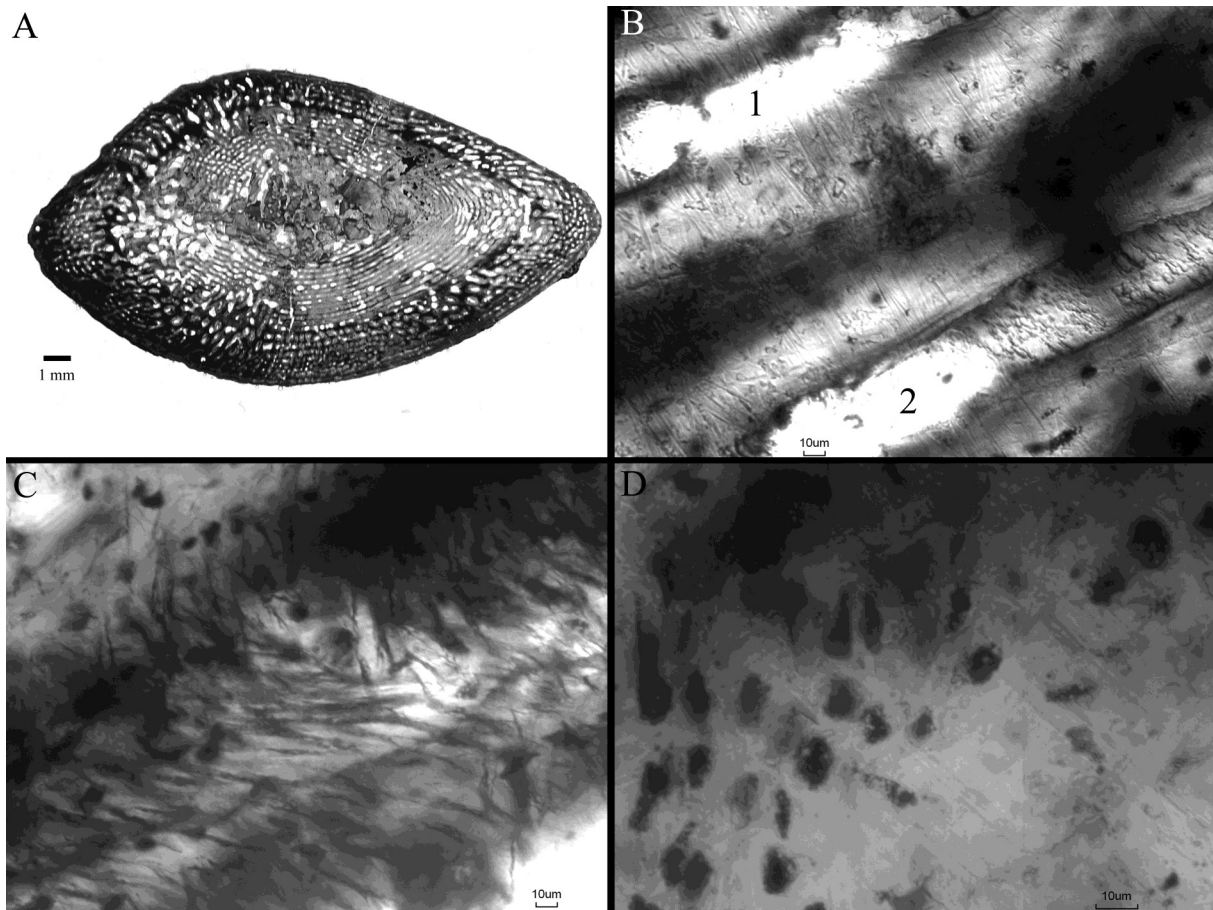
Fig. 2. **A**. Overview over the studied *Ichthyosaurus* cross section. **B**. Cross section of femur in Ichthyosaurus, displaying elongation of vascular canals (1 and 2). **C**. Cross section of femur in *Ichthyosaurus* showing bundles of collagen fibres which are very frequent in the peripheral regions of the bone. **D**. Cross section of femur in *Ichthyosaurus* showing lacunae representative of the sample. Note the lack of canaliculi.
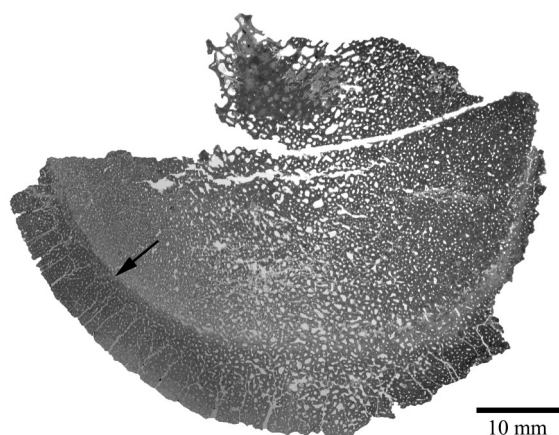
Fig. 3. Overview over the studied Plesiosauria cross section with LAG marked (arrow).

distributed canals are common throughout the entire section and the bone is thus by definition osteoporotic. In the inner parts of the cortex, the canals have their longitudinal axis parallel to the bone periphery, creating a network of cancellous trabeculae (Fig. 2b). Further from the centre, frequent Volkmann's canals are connecting the bone to its periphery. Between the many canals, the outermost part of the section appears darker. This is partly due to a large abundance of collagen fibres, stretching toward the periphery (Fig. 2c). The fibres appear in dense bundles between the vascularities and are more abundant and longer than in the marine turtle sample. The bone is also slightly denser in the outermost 1-2 mm, thus enhancing the colour difference. The lacunae in the ichthyosaur femur are very similar to those of the turtle, with the exception that there are very few preserved canaliculi (probably a taphonomic effect) (Fig. 2d).

3.3   Plesiosauria indet.

The plesiosaur bone is substantially larger than the other skeletal elements studied. The shear size of the bone made it impractical to study under a polarization microscope, and thus most of the observations were made by the naked eye and through a stereo microscope with only limited magnification abilities. This thin section (Fig. 3) shows a histological structure rather different from those hitherto described. Instead of a rich vascularization through large canals, the bone is rather compact. There are vascular canals randomly distributed throughout the entire section, but relative to the preceding bones these are very narrow and do not cover nearly as much of the sectioned area. At the centre of the section the canals are generally larger than in the periphery. The cortex may be divided into two parts, where the inner part is slightly darker and contains fewer Volkmann's canals than the outer part. The outer part appears paler with frequent canals running perpendicular to the circumference and branching off inside the bone. The border between these two parts is sharp and identified as a LAG about 8-10 mm from the

bone rim. As the sample was only studied at very low power magnification, little can be said about the structure of the lacunae, canaliculi or collagen fibres.

4 Discussion
4.1   Chelonia

The sea turtle section shows a medullary cavity containing cancellous trabeculae, surrounded by lamellar cortical bone. These features fit the pattern of lamellar bone as described by Enlow (1969), which is typical of both turtles and crocodilians (Hua & de Buffrenil 1996). The specimen appears to be an adult, based on the multiple (at least 17) LAGs or annuli, rather tightly and regularly spaced, and a medullary cavity surrounded by areas of extensive bone remodelling. The 17 annuli would correspond to 17 growth cycles (probably 17 years), but the animal was probably older, since the first annuli probably were destroyed in the process of remodelling (Castanet 2006). The fact that the growth rings are slightly tighter spaced distally in the section suggests that the animal did not grow as much when these LAGs were formed. This leads to the conclusion that the animal was an adult. The vascular canals and lacunae show circumferential alignment together with the LAGs/annuli. This observation is consistent with the general bone structure of turtles and crocodilians, and suggests that the bone had plenty of time to become vascularized in its outer parts as it grew. Consequently, this implies rather slow, typical reptilian growth rates (Enlow 1969).

4.2   *Ichthyosaurus* sp.

The ichthyosaur bone displays a rich cancellousness (osteoporosis); both the medullary cavity and the cortical bone are thoroughly vascularized. This is a very different condition from that of the sea turtle. In the ichthyosaur, the cortical bone is woven-fibred in structure, and lacks the distinct cyclical pattern indicative of slow growth rates. Instead, this type of bone is normally deposited during growth stages connected with extensive bone formation in a relatively short time span (Enlow 1969). The bone contains frequent Volkmann's canals in the outer cortex. These canals run perpendicular to the Haversian canals. Based on the open – though now intensely mineralized – medullary cavity and the extent of bone remodelling, the animal appears to be a late juvenile or subadult. The dense vascularization has probably destroyed most of the primary GM, precluding any aging attempt of this animal.

4.3   Plesiosauria indet.

In the plesiosaurian bone, the cortices are much more compact than in the above mentioned samples. The tissues are vascularized, but the canals are fewer and much narrower than in both the turtle and ichthyosaur. This pachyosteosclerotic condition is described only to occur in juvenile plesiosaurs, as they sometime during their ontogeny are believed to undergo a reorganiza-

tion of their bone structure to a more osteoporotic-like state (Wiffen et al. 1995). Together with the observation of only a single LAG, this suggests that the animal was still juvenile when it died. The presence of frequent Volkmann's canals in the outermost parts of the cortex suggests that the animal was still growing at the time of death, and the amount of bone deposited reflects a rapid growth rate, corroborating the conclusion that the animal was young.

4.4 Comparisons with recent analogues and possible lifestyle implications

The bone of vertebrates is always more or less vascularized (Castanet et al. 1993). The vascular canals commonly contain lipids, and an increased presence of such biomolecules makes the skeleton lighter (Cooper et al. 1966). In marine animals this bone modification has effects on swimming speeds, manoeuvrability, and ultimately, the lifestyle of the animal (Wiffen et al. 1995). Because the three animal groups studied have all rather different levels of vascularization and histological organizations, this may be linked to differences in lifestyles.

The ichthyosaur bone structure is very similar to that of the leatherback turtle, *Dermochelys coriacea* (Rhodin 1985), and is comparable to what is commonly seen in many extant marine mammals, such as whales and dolphins, which are adapted for sustained swimming, often over large distances (Felts & Spurrel 1965; Massare 1988). As the ichthyosaurs were active predators, the increase in speed and manoeuvrability that a lighter skeleton provides would have aided in the pursuit of prey.

As for the plesiosaur, sustained pursuit of prey would be harder. Massare (1988) refers to plesiosaurs as 'ambush predators', capable of quick bursts of speed to capture a passing prey, but not capable of high sustained cruising speeds. Wiffen et al. (1995) suggested changes from a pachyosteosclerotic condition to an osteoporotic-like state during ontogeny, which led to a drastic change in lifestyle. An animal with a pachyosteosclerotic skeleton would, due to its extra weight, probably have encountered problems when swimming in open oceans. Juvenile plesiosaurs may therefore have preferred more shallow water environments as sirenians do today, and may have fed upon fixed organisms or non-elusive prey. Adults, on the other hand, may have lived in more open marine environments. The plesiosaurian osteo-histological pattern, if an ontogenetic change in bone reorganization indeed did occur, differs from that of any known extant animal group.

The observed histological features of the sea turtle are consistent with Peabody's (1961) and Rhodin's (1985) descriptions of the general bone microstructures in modern chelonians (excluding *D. coriacea*; see Rhodin 1985). As their main prey items are plankton, sea grass and algae (Reich et al. 2007),

swimming speed is of less importance for modern sea turtles when foraging. The chelonian bone is more cancellous than that of the plesiosaur, making it easier for it to move across larger distances as less amounts of energy are needed with a lighter skeleton.

Comparisons can also be made between these three marine tetrapod groups and other Mesozoic reptiles, such as the terrestrial dinosaurs. A lot of research has been conducted on the osteo-histology of dinosaurs and not only have histological patterns been used as a platform to assess dinosaur growth rates (Chinsamy & Hillenius 2004; Erickson et al. 2001; Padian 2001; Erickson 2005; Horner et al. 2005), but they have also served to help formulating theories on thermoregulation (Paladino et al. 1990), ontogenetic patterns (Adams & Organ 2005), and insular dwarfism (Sander et al. 2006). Studies on dinosaurian growth show that this group did not grow as other reptiles. Most other reptiles deposit woven-fibred bone only during their first few growth cycles, and then start producing lamellar bone. Dinosaurs never underwent this change in bone structure, but continued to produce woven-fibred bone all the way though adulthood. Parallels can thus be drawn to ichthyosaur bone, which also lacks lamellar bone typical of many reptiles, including chelonians. The deposition of woven-fibred bone throughout ontogeny is somewhat similar to what is found in most extant birds and mammals, to suggest a steep sigmoidal growth curve, reaching a plateau rather early in adulthood, as opposed to most reptiles where the growth curve is more linear (Horner et al. 2005).

4.5 Concluding remarks

Sea turtles, ichthyosaurs and plesiosaurs show very different osteo-histological patterns. Although they are all tetrapods secondarily adapted to a marine life, they have skeletal microstructures indicating very different growth strategies and/or lifestyles.

Sea turtles display lamellar, slow-growing bone, present in many recent reptiles. This bone organization indicates a continuous bone growth throughout adulthood (Enlow 1969), and the LAGs present in the sample at hand indicate the femur originates from an adult animal. The vascularized limb bones presumably provided manoeuvrability in open waters, although sea turtles lack the osteoporotic adaptations found in e.g. ichthyosaurs.

The ichthyosaur skeleton is made up by osteoporotic bone presumably as an adaptation for increased speed and manoeuvrability. The bone is primarily of woven-fibred type, indicating a fast growth to adult size (Horner et al. 2005).

In the plesiosaur bone, a pachyosteosclerotic pattern is observed. This pattern increased the skeletal weight due to increased density, and was probably used as ballast in a shallow water environment (Wiffen et al. 1995).

5 Acknowledgements

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