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David W. E. Hone & Eric Buffetaut (Guest Editors)

Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer; design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

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The palaeohistology of pterosaur bone: an overview

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Abstract

The study of pterosaur bone histology dates back to the middle of the 19th century, with the pioneering microscopical studies of Bowerbank (1848) and Quekett (1849a, b, 1855) on UK material. In recent years, well-preserved bone material from the Romualdo Member of the Santana Formation, Brazil, has become available for histological study, but specimens from other localities have also proved informative. Most pterodactyloid bones are predominantly composed of highly vascular reticular fibrolamellar bone, similar to that of most extant birds. Lines of arrested growth are uncommon. This suggests that pterosaur bones grew rapidly, usually without interruption, until skeletal maturity was attained. Like birds, pterosaurs had very thin-walled bones, which possessed various histological and micro-architectural features to resist structural failure. These features should be taken into account in biomechanical studies of the pterosaurian skeleton.

Key words: pterosaurs, fibrolamellar, bone, histology, thin sections, ontogeny, biomechanics.

Zusammenfassung

Die histologische Untersuchung von Flugsaurierknochen reicht mit den Arbeiten von Bowerbank (1848) und Quekett (1849a, 1849b, 1855) über britisches Material bis ins 19. Jahrhundert zurück. Sowohl gut erhaltenes Knochenmaterial aus dem Romualdo Member der Santana Formation als auch weiteres Material aus anderen Lokalitäten hat sich in den vergangenen Jahren für histologische Untersuchungen als sehr informativ erwiesen. Ähnlich den Knochen heutiger Vögel bestehen die Knochen der meisten Pterodactyloidea aus stark vaskulären, netzartigen und fibrolamellaren Knochen. Unterbrochene Wachstumslinien sind selten. Dies weist darauf hin, dass die Knochen von Flugsauriern schnell und normalerweise ohne Unterbrechung wuchsen, bis die Geschlechtsreife der Tiere erreicht war. Flugsaurier besitzen wie Vögel dünnwandige Knochen mit unterschiedlichen histologischen und mikroarchitektonischen Charakteristika, die die Gefahr von Brüchen minimieren. Diese Charakteristika sollten in biomechanischen Studien an Flugsaurier-Skeletten berücksichtigt werden.

Schlüsselwörter: Pterosaurier, fibrolamellar, Knochen, Histologie, Dünnschliff, Ontogenese, Biomechanik.

1. Introduction

Palaeohistology, the study of fossil tissues, can provide valuable information about the biology of fossils. Although the organic components of mineralised tissues generally decay after death, the inorganic components of bone preserve the spatial orientation of organic components such as osteocyte lacunae, vascular canals, collagen fibres and hence the histology of the bone. Bone histology can provide important insights into the physiology of the organism concerned. For example, the organisation of the collagen fibril matrix and the degree of vascularisation of bone indicate the relative rates of bone deposition (e.g., Amprino 1947; Currey 1984), while the presence of growth marks such as lines of arrested growth (LAGs) or resorption lines in primary compact bone shows whether bone deposition was continuous, interrupted or cyclical (Peabody 1961; de Ricqlès 1969, 1975; Klevezal 1996; Castanet 1985, 1987; Meunier et al. 1988; Chinsamy 1997). The amount of secondary bone present shows the extent of primary bone resorption and redeposition, and therefore the amount of remodelling during ontogeny (Enlow 1963; Frost 1964). Functional aspects of bone morphology may be inferred from the macroscopic appearance of the bone as well as from its micro-architecture, and the distribution of different tissue types throughout the skeleton or within a single bone may reflect biomechanical functions (Currey 1959, 1968, 1970, 1979, 1981, 1984, 1987, 1990a, 1990b; Keaveny & Hayes 1993; Bonser 1995; Cubo & Casinos 1998a, 1998b, 2000). Thus, bone histology reflects ontogeny, growth dynamics and biomechanics,

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as well as recording various events (such as trauma or disease) that punctuate the life history of an individual. Increasingly, authors are attempting to interpret palaeohistology in terms of physiology, ontogeny, growth dynamics, biomechanics and ecology of the living animal, and to some extent, to relate palaeohistology to the systematics of living and fossil groups (e.g., Padian et al. 2004; Scheyer & Sander 2004).

Bone palaeohistology is an active area of study, and has been for many years, with most, if not all, major fossil vertebrate groups now represented in the literature. The purpose of this paper is to present an overview of our current understanding of pterosaur bone histology, including a review of the published literature, complemented by the results of some hitherto unpublished work (Steel 2004, unpublished PhD thesis).

2. History of pterosaur bone palaeohistological studies

The earliest published observations of pterosaur bone histology are those by Bowerbank (1848). Fragments of bones from the Cretaceous of southern England were placed in water, and examined microscopically. Bowerbank described the morphology of the osteocyte lacunae and compared them with those of birds, recent reptiles and mammals.

The first comprehensive survey of fossil vertebrate hard tissues was by Quekett (1849a, 1849b, 1855). In addition to slides prepared from recent animal tissues, his study included thin sections of bones from a range of fossil vertebrates including fishes, amphibians, ichthyosaurs, dinosaurs, and other groups. Among them were fifteen thin sections of pterosaur bones, most of which were made from bones originally belonging to John Hunter, the founder of the Hunterian Museum in London (Bramwell 1972). The pterosaur material is mostly described as "*wing bones*", but there were two sections from a scapulo-coracoid. Much of Quekett's thin section collection survives to this day in the Hunterian Museum of the Royal College of Surgeons of London (Steel 2003).

Quekett described vascular canals, lacunae and canaliculi, and trabecular endosteal bone. Quekett also saw "Haversian canals" in many of the sections. True Haversian canals containing concentric rings of secondary lamellar bone are not evident in any of his figures, so he possibly meant simple or primary canals. Features that he described as "*cell nuclei*" were probably grains of carborundum powder from the grinding process, or diagenetic minerals (see Martill & Unwin 1997, but also Moodie 1923 and Schweitzer & Horner 1999). Neither Quekett nor Bowerbank had the opportunity to use crossed polarised light, as this technique was not developed until 1874 (see Enlow & Brown 1956), thus their observations are limited to those features discernible in plane polarised light. Polarised light reveals the orientation of the hydroxylapatite crystallites, and therefore the orientation of the collagen fibres which were originally associated with them.

The structure of pterosaur bones from the Stonesfield 'Slate' (Bathonian, Middle Jurassic, England) was observed by Phillips (1871). He noted that pterosaur bones contained longitudinal "*Haversian canals*" and figured "*lacunae… with many short excurrent somewhat branched tubules*" (p. 225) – a reference to the canaliculi. He recognised similarities between the histology of these bones and those of other reptiles, but especially with birds. He also observed pneumatic foramina and interpreted thin plates of bone spanning the lumen of a scapula as conferring strength where it was needed (p. 226).

A comprehensive analysis of fossil and recent reptile bone histology was undertaken by Seitz (1907). Pterosaurs were represented by wing bones of *Pteranodon* and *Rhamphocephalus*. Seitz described the tissue of the *Rhamphocephalus* wing phalanx as fairly homogeneous, with concentric layering and densely packed bone cells. Like Quekett, Seitz noted small "Haversian canals" within the lamellae, but these were probably simple vascular canals or primary osteons rather than true Haversian canals. Secondary resorption had taken place on the endosteal surface to enlarge the pneumatic space in the centre of the bone, which was lined by avascular tissue. The trabeculae in the *Pteranodon* bone were composed of parallel axial lamellae and many showed signs of resorption and redeposition. The cortical bone was composed of concentric lamellae, containing primary vessels (referred to as Haversian canals). The osteocyte lacunae generally appeared elongate. Like many other authors, Seitz considered that pterosaur bone tissue was very similar to that of birds rather than typically reptilian.

The bone histology of fossil amphibians and reptiles, including the pterosaur *Dorygnathus* was described by Gross (1934). A *Dorygnathus* bone was described as hollow, lined with 'marrow bone' (endosteal bone) and lacking spongiosa. The endosteal tissue contained circumferentially oriented cells and was separated from the periosteal bone by a resorption line. A reticular network of canals filled the periosteal bone, except for the outermost layers, which were almost avascular. The spindle-shaped bone cells were circumferentially oriented and generally aligned with the canals, as noted by Quekett (1855). The histology of this element was noted to be similar to that of the *Rhamphocephalus* wing phalanx described by Seitz (1907). Gross (1934) added that the overall similarity to bird bone, especially to that of the Limicolae (waders) was striking.

A histological survey of fossil and recent bone tissues was undertaken by Enlow & Brown (1956, 1957, 1958). The second part contained a brief study of pterosaur bone (Enlow & Brown 1957: pp.199–200). The authors stated that many regions in the compacta of pterosaurs were similar to those of other archosaurs, with concentric undulating lamellae containing longitudinal primary canals. However, other areas of bone tissue were very different, containing a reticular pattern of primary canals, similar to that of modern birds. A transverse section through a rib of *Pteranodon*, illustrating reticular tissue (pl. 21, fig. 9,) was compared with a transverse section of a bird femur (pl. 26, fig. 7). Haversian canals in pterosaur bone were not recorded in this study. More importantly, Enlow & Brown (1956) introduced a classification of bone tissues based upon the presence or absence of vascular canals, their orientation and other histological features.

A brief histological description appeared in a report of a giant pterosaur wing metacarpal from the Upper Cretaceous (Maastrichtian) of Jordan by Arambourg (1959). The histology of this specimen was compared with that of the tibiae of *Pteranodon* and *Phoenicopterus ruber* (pink flamingo). Differences in the size, shape and density of the osteocytes were noted between the two pterosaurs and the flamingo. In the pterosaurs, the osteocytes were less numerous and also longer and narrower than in the flamingo. The canaliculi of the osteocytes of *Pteranodon* were fewer and shorter than in the other two specimens. ARAMBOURG suggested that this might be due to generic differences or to differing modes of fossilisation. He also stated that his findings confirmed those of BOWERBANK (1848). The specimen later became the holotype of *Arambourgiania* and was reinterpreted as a cervical vertebra (FREY & MARTILL 1996; MARTILL et al., 1998).

A very brief description of a pterosaur 'limb bone' in thin section was included in a study of a pathological dinosaur bone by CAMPBELL (1966). The pterosaur bone was described as comprising dense 'non-annulated' cortical tissue with inner and outer circumferential lamellae and no resorption cavities. This is entirely consistent with other descriptions, but the tissue was also described as having well-formed Haversian systems. This may be a misuse of the term, but it is correctly used elsewhere in the paper, where the pathological dinosaur bone is described. Unfortunately the pterosaur bone was not figured, and no museum catalogue number was provided.

In a monograph on the pterosaurs of the Upper Jurassic of southern Germany, WELLNHOFER (1970) described the histology of a wing phalanx of *Pterodactylus antiquus*. The bird-like compacta was less than 0.5 mm thick, and contained reticular vascular canals, which is typical of pterosaur bone and in agreement with other studies (e.g., SEITZ 1907; ENLOW & BROWN 1956, 1957; DE RICQLÈS et al. 2000). WELLNHOFER's study is notable for the first description of pterosaur dental histology in thin section.

DE RICQLÈS (1976) included pterosaurs in a discussion on reptile bone histology. Although very brief, his account emphasised the structural similarities with bird bones such as the large diaphyseal medullary cavities enclosed by a dense cortex, with spongiosa in the epiphyseal regions. The reticular pattern of primary osteons in fibrolamellar cortical bone was figured for *Rhamphocephalus*, but the cortices of smaller pterosaur bones were described as zoned and less vascular.

BENNETT (1993) examined bone histology as part of a study of *Pteranodon* ontogeny, examining thin sections of wing metacarpals from an adult and a juvenile. Both bones were composed of fibrolamellar bone, characteristic of rapidly growing animals. The immature bone contained a reticular pattern of numerous vascular canals, some of which opened onto the periosteal surface . In contrast, the mature bone was poorly vascularised near the periosteal surface. BENNETT (1993) concluded that juvenile *Pteranodon* bone underwent rapid periosteal deposition, whereas the minimal vascularisation of the periosteal bone in the mature animal indicated that the rate of bone growth had slowed before death.

The wing bone histology of an azhdarchid pterosaur was examined by PADIAN et al. (1995), to determine whether the specimen represented an adult of a small species or a juvenile of a larger species. The periosteal bone was described as lamellar, with few primary osteons and 'plywood-like' layering. The endosteal lamella and the trabeculae showed traces of remodelling. Secondary osteons were present in the deepest regions of the cortex, although it is not clear from the description whether these occurred in the endosteal or the periosteal tissue. The histology of this specimen was contrasted with that of an unspecified bone of *Quetzalcoatlus* sp. and a wing bone of a turkey vulture (*Cathartes aura*), the tissues of which were highly vascular and, in the case of *Cathartes*, are correlated with rapid growth. The azhdarchid specimen was identified as an adult due to the extent of endosteal remodelling and the presence of secondary osteons.

DE RICQLÈS et al. (1997) re-examined the similarities between pterosaur bone tissue and that of extant birds, especially with regard to the thinness of the compacta and the presence of richly vascular fibrolamellar tissue, indicative of rapid continuous growth. Circumferential growth marks, present in pterosaur bones but not in bird bones, were interpreted as temporary slowing of growth associated with changes in the bone fibrillar organisation. This produces a 'plywood-like' tissue, which the authors proposed is related to biomechanical factors. Erosion and remodelling of the endosteal surface was noted, as was the occasional formation of secondary osteons. Articular calcified cartilage and subchondral bone plates were briefly mentioned.

CHIAPPE & CHINSAMY (1996) used dental histology to determine that the teeth of *Pterodaustro* were true teeth, and not baleen-like structures. In the same year, UNWIN et al. (1996) confirmed that the pteroid was an endochondral bone, rather than a sesamoid or a calcified tendon. The histology of a pteroid from a Santana Formation ornithocheirid was consistent with that of other endochondral bones from the same individual. Calcified tendons and sesamoids are composed of metaplastic bone, a mineralised tissue that differs from endochondral bone in its microstructure (HAINES & MOHUIDDIN 1968).

An extensive study of pterosaur bone histology was produced by DE RICQLÈS et al. (2000). These workers described Jurassic and Cretaceous pterosaur bone tissues from individuals of most ontogenetic stages, but the majority of their samples were Late Cretaceous pteranodontids and azhdarchids from North America. DE RICQLÈS et al. (2000) concurred with previous studies that fibrolamellar tissues formed the bulk of the periosteal cortex in most pterosaur bones. Secondary osteons (Haversian systems) were observed in the deep cortex of azhdarchid long bones. Furthermore, a 'plywood-like' tissue was described, in which the orientation of the bone fibres changes by 90° from one lamella to the next, strikingly illustrated in colour in figure 5G (p. 367). This study also contained the first description of the structure of a pterosaur epiphysis. It was suggested that pterosaurs grew rapidly until a determinate adult size was reached, whereupon growth ceased suddenly. The authors also discussed the biomechanical properties of some aspects of pterosaur bone histology and microstructure, namely the 'plywood-like' organisation, Haversian substitution and endosteal struts and 'pipes'.

In the first histological analysis of a Triassic pterosaur, JENKINS et al. (2001) examined the histology of a femur of a small species of *Eudimorphodon* from Greenland, to determine its ontogenetic stage. It was determined to be a juvenile, because it lacked features expected of either a neonate or adult. The diaphyseal cortex was approximately 15–20% of the shaft diameter. The tissue matrix was parallel-fibred, with longitudinally oriented primary vascular canals. The epiphysis contained endochondral trabeculae and calcified cartilage. Unfortunately, this very valuable contribution to pterosaur bone histology lacked any figures to accompany the description, although it was stated that diagenetic alteration had rendered the histology difficult to interpret.

Recently, SAYÃO et al. (2000) and SAYÃO (2003) reported on the use of thin section techniques to compare an ornithocheirid from the Santana Formation with an azhdarchoid from the Crato Formation. In the ornithocheirid skeleton, the position of histological features such as LAGs varied among different bones, thus supporting previous suggestions (DE RICQLÈS et al. 1997, 2000) that limited information can be obtained by studies on isolated elements. In contrast, the azhdarchoid skeleton had no LAGs and lacked histovariability. Pneumatic canals were reported in the femoral cortex of the former specimen, represented by a pair of erosion cavities between 200–300 µm wide, located within the compacta. Similar structures were previously figured by DE RICQLÈS et al. (2000: fig. 4D).

The most recent examination of pterosaur bone histology was PADIAN et al.'s (2004) comparison of small pterosaurs with small dinosaurs, in which the bone histology of *Eudimorphodon cromptonellus* (previously described by JENKINS et al. 2001), *Dimorphodon macronyx* and *Rhamphorhynchus* was examined. Although the histology of *E. cromptonellus* was not well preserved, the other species had well vascularised fibrolamellar tissues with longitudinal primary osteons, LAGs and endosteal lamellae. The tissues of these three pterosaurs suggest fairly rapid growth during early ontogeny, slowing as adulthood was reached. In the larger and older individuals, endosteal resorption had removed much of the tissues deposited early in their ontogeny, making it impossible to reconstruct the complete growth history of an individual. Despite these difficulties, PADIAN et al. (2004) compared the fibrolamellar tissues in small pterosaurs, dinosaurs, fossil crocodilians and fossil birds with those of extant birds and crocodilians for which absolute growth rates are known, and superimposed these figures on a cladogram of archosaurian taxa. The phylogenetic distribution of higher bone growth rates suggested that smaller taxa grew at slower rates than larger ones, and that faster growth rates had appeared several times in different lineages.

Throughout the development of histological studies, there has been a gradual shift from simply presenting descriptions of bone histology to making palaeobiological interpretations based upon it. In some cases, palaeohistology has helped to answer questions which could not be resolved by any other means (e.g., UNWIN et al. 1996; CHIAPPE & CHINSAMY 1996). There is now considerable interest in the biomechanical properties of pterosaur bones, particularly those involved in flight. It is well known that histology and microstructure are relevant to the properties of biomaterials (e.g., CURREY 1990). Discussion of pterosaur growth rates and physiology has been rekindled by recent descriptions of eggs and embryos, so a review of pterosaur bone histology is timely.

3. Materials and methods

The samples in this study were acquired as bone fragments or whole bones from museum and university collections (see Table 1). Pterosaur bones are difficult to cut and polish without losing material from the section. These difficulties can be overcome by coating or embedding the specimen in a proprietary epoxy resin before cutting. CHINSAMY & RAATH (1992) and WILSON (1994) give accounts of the standard process for producing histological thin sections from fossil bones.

For this study, most specimens were embedded, coated or infilled with Buehler 'Epo-Thin' or Devcon 'Two-Ton Epoxy' resins. Some specimens were cut longitudinally, some transversely, and some were cut in both directions. The sawn surface of each specimen was lapped down manually in three stages. Firstly, coarse saw marks were removed with 150-grade carborundum powder and water with the specimen on a steel grinding wheel. Lapping continued using 300-grade carborundum powder and water. After thoroughly rinsing the samples in water, they were polished using 600 grade carborundum powder and water on a sheet of plate glass. The lapped surface of each specimen was bonded to a glass slide using Devcon 'Two-ton Epoxy'. The slide and sample were placed on a hot plate at 80–90°C, and lightly pressed together by a spring-loaded piston, making the layer of resin as thin as possible. A thick layer can cause the mounted section to lie unevenly on the slide and result in uneven lapping, but can also contract with age, causing cracking. It can also alter the light transmitting properties of the slide, resulting in poor photomicroscopy (WILSON, 1994: p. 218). After setting (30 minutes), the sample was sawn off on a Buehler 'Petro-Thin' thin sectioning machine.

Each section was lapped down on a Buehler 'Petro-Thin' to 35–38 µm thick. They were then hand finished on plate glass with 600-grade carborundum, to approximately 30µm thick, the standard thickness of petrological thin sections. The sections were rinsed in water and allowed to dry. A glass coverslip was fixed to the exposed surface using 'DPX', a microscopy mountant manufactured by BDH.

Thin sections were examined using a binocular petrological microscope. Observations were made in plain polarised light (PPL) and crossed polarised light (XPL). Crossed polarised light reveals the orientation of the hydroxylapatite crystallites within the tissue, thus facilitating its description and classification. Hydroxylapatite appears black in full extinction, which obscures histological detail, so a 1-lambda tint plate was used to alter the cross polarisation colours from black and white to bright colours (XPL+T in Figure captions). Photography was carried out using a digital SLR camera mounted on the petrological microscope.

Bone histology is described in terms of fibrillar matrix type and orientation, osteocyte density, vascular density, type and organisation of the tissue, whether it is periosteal or endosteal and primary or secondary in origin. There is a long history of classifying mineralised tissues by these variables (e.g., FOOTE 1916; WEIDENREICH 1930; GROSS 1934; ENLOW & BROWN 1956, 1957, 1958; DE RICQLÈS 1975; FRANCILLON-VIEILLOT et al. 1990; DE RICQLÈS et al. 1991). In the past, there has been some confusion of terms by successive authors (see explanation in REID 1983, 1984a). The latter two classifications of bone histology (FRANCILLON-VIEILLOT et al. 1990; DE RICQLÈS et al. 1991) are followed here.

Stratigraphic abbreviations:

SS: Stonesfield Slate, UK; WF: Wessex Formation, UK; RM: Romualdo Member, Brazil; CG: Cambridge Greensand Member, UK; GC: Grey Chalk Subgroup, UK; BG: Balqa

Table 1: Sources of skeletal elements

Element	SS	WF	RM	CG	GC	BG	Md'A	DC
Premaxilla / maxilla			UP 2000.3 UP 2000.1	CAMSM B54485 CAMSM B54425 CAMSM B54486				
Jugal			UP 2000.3 UP 2000.1	CAMSM B54485 CAMSM B54425				
Dentary			UP 2000.3 UP 2000.1	CAMSM B54427				
Ceratohyal			UP 2000.3					
Tooth			UP 2000.3	CAMSM B54458				
Vertebra				CAMSM B54319		UJ VF1	MDE ME104	
Scapulo-coracoid			SMNK 1135 UP 2000.5					
Humerus			UP2000.6a	CAMSM B54065 CAMSM B54086				
Ulna			UP 2000.8 UP 2000.2 UP 2000.6b SMNK 1252 SMNK 1134 SMNK 1254	CAMSM B54119 CAMSM B54116				
Radius			SMNK 1254	CAMSM B54131				
Carpal				CAMSM B54169a				
Wing metacarpal			SMNK 1134	CAMSM B54186 CAMSM B54206				
Wing Phalanges		IWCMS 2001.234	UP 2000.9 UP 2000.6c UP 2000.6d	CAMSM B54225 CAMSM B54222 CAMSM B54231				
Manual ungual				CAMSM B54251				
Femur				CAMSM B54265 CAMSM B54272				
Tibiofibula			SMNK 1133	CAMSM B54292 CAMSM B54298				
Metatarsal			UP 2000.10	CAMSM B54245				
Sesamoids			UP 2000.7a SMNK 1133					
Indet. cranial								UB R1083
Indet. postcranial	HM Bb-69		UP 2000.7b UP 2000.7c UP 2000.7d		HM Bb-63 HM Bb-65 HM Bb-66 HM Bb-67			

Group, Jordan; Md'A: Marnes d'Auzas Formation, France; DC: Densus-Ciula Formation, Romania.

Institutional / collection abbreviations: **HM**: Hunterian Museum of the Royal College of Surgeons of London, UK; **MDE**: Musée des Dinosaures, Espéraza, France; **CAMSM**: Sedgwick Museum, Cambridge, UK; **SMNK**: Staatliches Museum für Naturkunde, Karlsruhe, Germany; **UB**: University of Bucharest Faculty of Geology and Geophysics, Romania. **UJ**: University of Jordan, Amman, Jordan; **UP**: University of Portsmouth School of Earth and Environmental Sciences, UK

To obtain the least reworked bone, and avoid an inaccurate impression of the histology of an element, it is important to sample the mid-diaphysis. This avoids the zone of metaphyseal relocation, where cancellous tissue is compacted and resorbed, before periosteal deposition re-commences, leaving a reversal line. Chinsamy (1990, 1994, 1997) suggests that the mid-diaphysis of the femur should be the standard site for taking thin sections. Other long bones are more deeply modified by locomotor adaptations (Cubo et al. 2005). However, the femur is not always available for analysis, as is the case in many pterosaur bone histology studies, including this one.

4. Pterosaur bone histology

4.1 Pterosaurian primary bone

Juvenile periosteal primary bone in the process of deposition appears in several examples, but is best demonstrated in a pterodactyloid humerus, UP 2000.6b, from the Romualdo Member (Fig. 1). The thin cortex is entirely composed of fibrolamellar primary bone, with numerous vascular canals arranged in a reticular to laminar pattern. The canals underlying the periosteal surface are broad, opening to the periosteal surface, and had not become primary osteons by the time the animal died. There are no growth marks such as annuli or LAGs. In addition, this bone lacks any endosteal secondary tissue (compare with Fig. 2, a mature bone, but note different scale). Other wing bones preserved in articulation with this humerus (ulna and wing phalanges) exhibit similar histology, and the juvenile ontogenetic stage of this individual is confirmed by an unfused humeral epiphysis. A juvenile ?azhdarchid wing bone was described by de Ricqlès et al. (2000), but differed in having more radially-trending vascular canals. In the present study, radial vascular orientation was only observed within processes, keels or ridges (cf. Erickson & Tumanova 2000).

Mature fibrolamellar bone is easily recognisable in thin section by the reduction in vascularity as the periosteal surface is approached. Finally, a series of avascular periosteal lamellae described by some authors (after Cormack 1987) as the EFS (external fundamental system) is deposited when bone growth ceases. These features are illustrated in an ornithocheirid ulna (UP 2000.2) from the Romualdo Member (Figs 2, 3).

Some pterosaur bones from the Romualdo Member contain LAGs (lines of arrested growth). These features, which record pauses in bone deposition, are seen in cranial bones of an ornithocheirid, UP 2000.3 (Fig. 4), and a pterodactyloid metatarsal, UP 2000.10 (Fig. 5). In the premaxilla of UP 2000.3, the compacta contains mostly small-diameter longitudinal canals, although a few short oblique canals appear dorsally. The compacta is divided into four concentric layers, separated by four concentric undulating LAGs. These layers reach their greatest thickness at the dorsal apex of the premaxilla, where the outermost layer is the thickest (0.9 mm as preserved) and they become thinner endosteally (0.4 mm, 0.35 mm and 0.25 mm respectively).

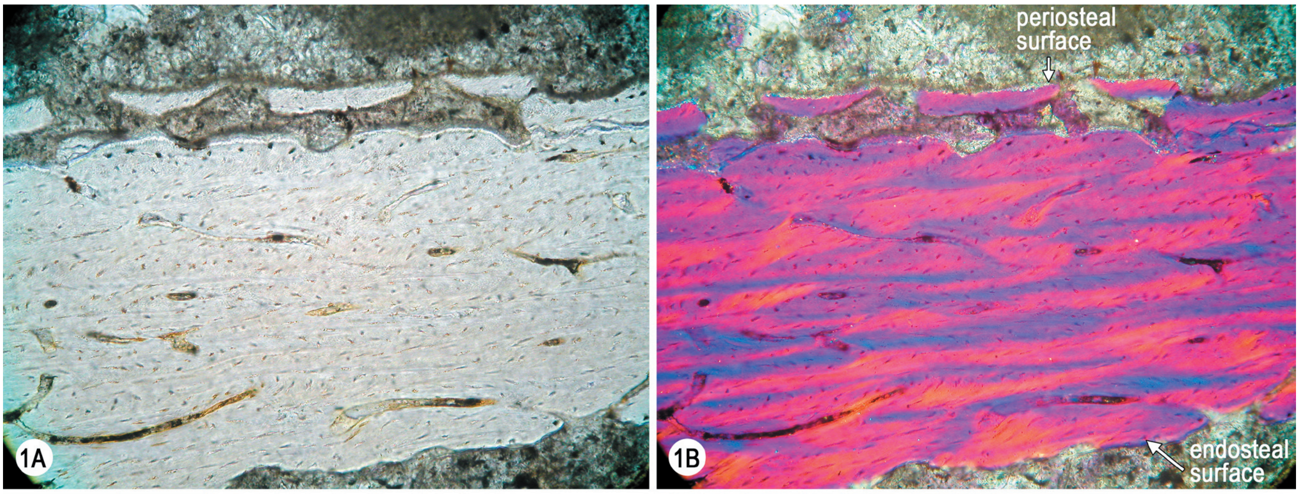
One possible LAG is present in the ceratobranchial of the same specimen, and at least one is present in the dentaries. LAGs are absent from all other cranial material examined, namely UP 2000.4 (Romualdo Member ornithocheirid premaxilla), CAMSM B54485 (*Ornithostoma*), UP 2000.1 (*Tupuxuara*), CAMSM B54425 (*Ornithocheirus cuvieri* premaxilla), CAMSM B54427 (*Ornithocheirus cuvieri* dentary), CAMSM B54486 (*Lonchodectes microdon* premaxilla) and FGGUB R1083 (*Hatzegopteryx thambema* skull). LAGs were not seen in any postcranial material apart from the aforementioned metatarsal, UP 2000.10 (Fig. 5). This bone is circular in transverse section although one side has been abraded. The periosteal compacta is approximately 0.3 mm thick, poorly vascularised by longitudinal vascular canals, and contains concentric LAGs. There are three main concentric layers of tissue, but the outermost of these appears to be subdivided by LAG into five thinner and less obvious lamellae. The boundaries between these five lamellae are discontinuous. The layers of tissue have been selectively endosteally resorbed to shift the size, shape and position of the bone. Some endosteal deposition has also taken place.

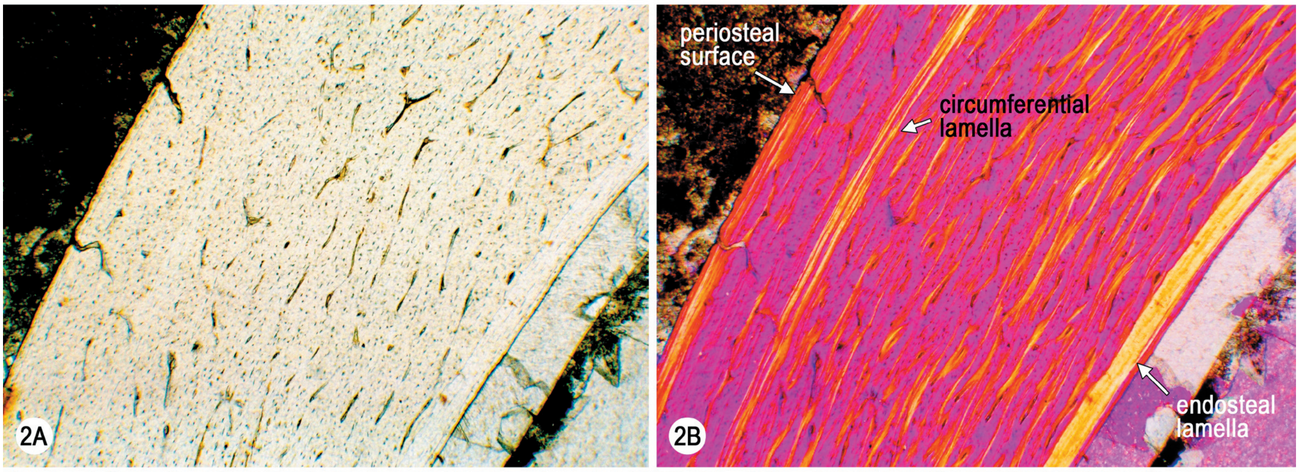
A clear example of 'plywood-like" tissue is present in the pterygoid of the same ornithocheirid (UP 2000.3) described above. The orientation of the fibres alternates between longitudinal and circumferential in relation to the long axis of the bone. The contrasting layers are seen clearly as different colours in crossed polarised light (Fig. 6). The osteocyte lacunae appear elongate in the circumferential lamellae because they have been cut along their long axes, and globular in the longitudinal lamellae because they have been cut across their width.

4.2 Pterosaurian secondary bone

Secondary bone is defined as any bone which is deposited on a previously resorbed surface. In pterosaurs, secondary bone is seen in most specimens, particularly in bones belonging to adults and subadults. At maturity, an endosteal lamella is deposited on the endosteal surface after endosteal resorption has ceased, as observed in an ornithocheirid ulna (UP 2000.2) from the Romualdo Member (Fig. 3). The endosteal lamella is always avascular, circumferentially oriented, and contains elongate osteocyte lacunae. The presence of an endosteal lamella is accompanied by the formation of an EFS, indicating that periosteal growth has also ceased or slowed to a negligible rate.

Coarse cancellous bone sometimes becomes transformed into compacted coarse cancellous bone. This type of tissue is illustrated by an ornithocheirid wing phalanx 1 (IWCMS 2002.234) from the Wessex Formation of the Isle of Wight, UK (Steel et al. 2005) (Fig. 7). The cancellous spaces have become filled with bone in order to transform a cancellous spongiosa into compacted cancellous bone. Subsequent periosteal resorption of this compacted tissue, followed by periosteal deposition





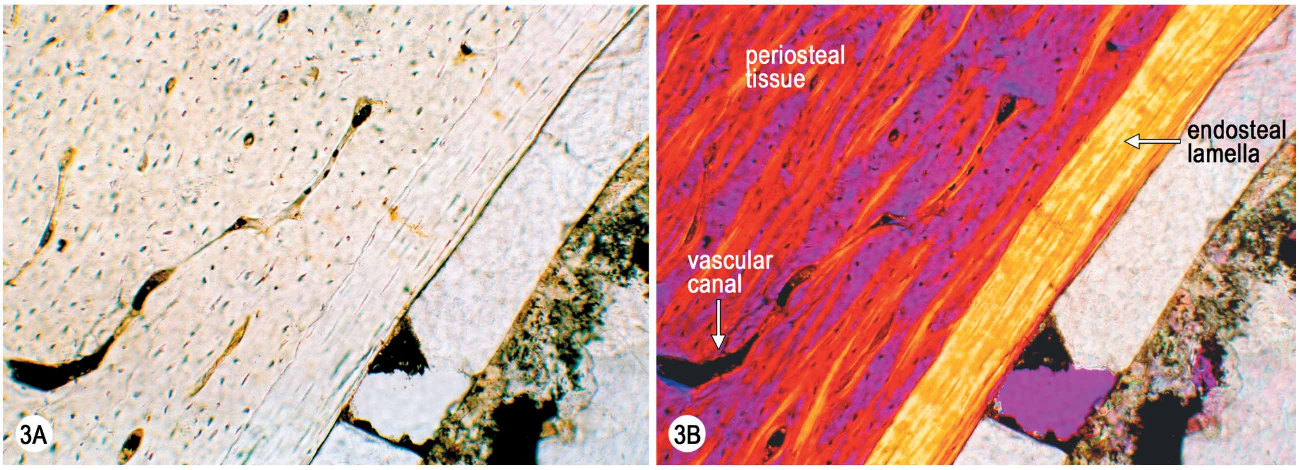


Figure 1: Transverse section (Section 2) through UP 2000.6b (distal end of a humerus) showing periosteal apposition of fibrolamellar bone. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 0.7 mm.

Figure 2: Transverse section through UP 2000.2 (?ulnar diaphysis) showing laminar-reticular fibrolamellar compacta interrupted by a circumferential lamella (arrowed) and lined by an avascular endosteal lamella (bottom right). A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 1.3 mm.

Figure 3: Enlargement of Figure 2. Transverse section through UP 2000.2 (?ulnar diaphysis). The endosteal layer (internal fundamental system) is clearly visible, suggesting that endosteal resorption had ceased in this specimen. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 0.54 mm.

of secondary bone has truncated the compacted spongiosa and left a reversal line between the compacted spongiosa and the periosteal secondary compact bone. This sequence of events happens in the zone of metaphyseal relocation, where cancellous bone becomes incorporated into the diaphysis during growth (Fig. 10).

Although secondary bone of some form or another is found throughout the skeleton, secondary osteons (Haversian systems) are rare and generally restricted to the bases of trabeculae. In this study, they were observed only in the vicinity of a trabeculum in the dentary of a Romualdo Member ornithocheirid, UP 2000.3 (Fig. 11), in which they are arranged as two pairs of longitudinally oriented canals. They are simple structures, lacking the multiple concentric lamellae that are usually found in secondary osteons.

4.3 Trabeculae

In thin section, the histological composition of pterosaur bone trabeculae can be examined. They often contain primary periosteal tissue at their core, which is continuous with the primary periosteal tissue forming the cortex of the bone. It is left behind during the process of medullary expansion that normally removes the older (deeper) periosteal tissue. A second phase of construction follows, whereby endosteal tissue is deposited on the surface of the trabeculum, and this can be seen in a pterodactyloid ulna from the Romualdo Member, UP 2000.8 (Fig. 8). Further phases of resorption and redeposition alter the shape of the trabeculum, and may remove most of the original periosteal tissue. Surprisingly, secondary bone is present in a remodelled trabeculum in a juvenile pterodactyloid wing phalanx from the Romualdo Member, UP 2000.6d (Fig. 9).

4.4 'Epiphyses'

The term 'epiphysis', in its strict anatomical sense, refers to a secondary ossification separated from the diaphysis by a cartilaginous region, at which point growth can occur until the diaphysis and epiphysis fuse (Haines 1942, 1969).

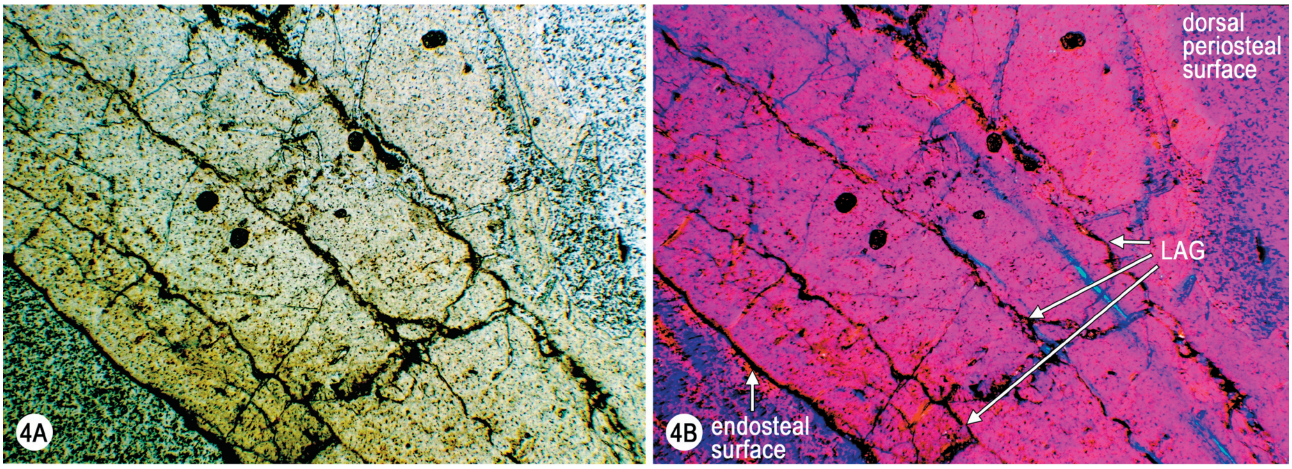
Several wing phalanges from the Romualdo Member (UP 2000.7b, UP 2000.7c, UP 2000.9) were longitudinally thin sectioned in order to examine their epiphyseal structure (Figs 12, 13). A pterosaur growth plate consists of a thin layer of subchondral bone, supported by longitudinally oriented trabeculae (Fig. 12). This is covered by calcified cartilage, which contains globular chondrocyte lacunae and lacks transphyseal canals (Fig. 13). These appear to be immature growth plates; the endosteal trabeculae are incompletely ossified, as is the layer of subchondral bone. Two other specimens, wing phalanges from the Cambridge Greensand of the UK, CAMSM B54225 and B54231 have a similar structure but are not as well preserved.

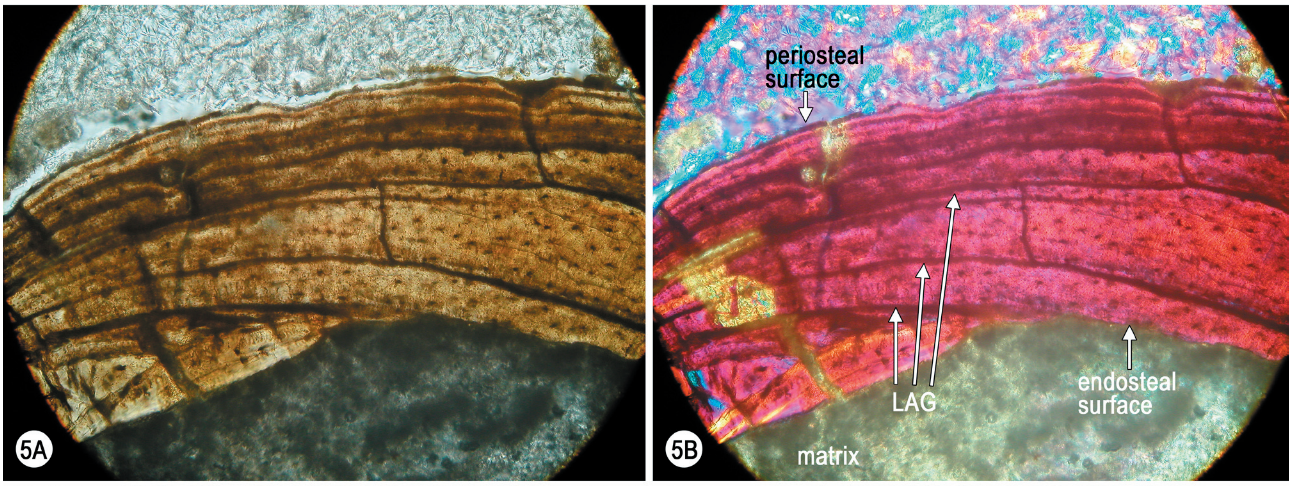
5. Discussion

Among extant taxa, highly vascular fibrolamellar bone is common in mammals and birds, particularly those that grow rapidly to reach a large adult size (e.g., Amprino & Godina 1947; Enlow & Brown 1957; Castanet et al. 1996, 2000; de Margerie 2002; de Margerie et al. 2002). It is also found in dinosaurs (e.g., Gross 1934; de Ricqlès 1980; Reid 1984b, 1996, but see also Reid, 1981, 1995), and other large extinct taxa (e.g., Ray et al. 2004). Fibrolamellar bone is not typically found in most extant reptiles (Enlow 1969). This has tempted speculation that the growth rates and physiology of pterosaurs were more similar to those of extant birds rather than to 'typical' reptiles (Bennett 1993; de Ricqlès et al. 2000) and that pterosaurs reached adult size within a few years (Bennett 1993) or less (de Ricqlès et al. 2000). Although the degree of vascularity in fibrolamellar bone is strongly correlated with the rate of growth, the vascular pattern itself is not linked (de Margerie et al. 2002). Rapid growth of fibrolamellar tissue can be seen in numerous bones within the present study (for example, Fig. 1). Often, the most superficial periosteal deposits are less vascular than older tissues underlying them, showing that growth slowed as the individual matured. This type of histology is present in *Montanazhdarcho*, a small azhdarchid (Padian et al. 1995), in large pterodactyloids (de Ricqlès et al. 2000) and in some pterodactyloid bones in this study (Fig. 2). Some specimens have an EFS (Cormack 1987), a series of thin avascular lamellae which is deposited periosteally when adult size is reached (Fig. 2), showing that at least some pterosaurs had determinate growth, as was suggested by Bennett (1993) based on bone histology and epiphyseal ossification.

Recently, Unwin (2004) and Unwin & Deeming (2004) proposed that pterosaurs grew relatively slowly. This argument is based on the recognition of juveniles preserved in circumstances consistent with the ability to fly and with wing proportions similar to those of adults. It was argued that the energetic demands of flight diverted resources that might otherwise have been used to sustain rapid skeletal growth. This hypothesis is not supported by pterosaur bone histology, although it must be admitted that very little data on bone histology of juvenile pterosaurs is available, and no hatchling pterosaur bones have been sectioned.

Lines of arrested growth (LAGs) form when periosteal bone growth temporarily ceases, and are commonly, but not exclusively, found in lamellar-zonal tissues of ectothermic reptiles with cyclical growth (Enlow 1969). Recently, LAGs have been employed in ontogenetic studies of fossil tetrapods, particularly in dinosaurs, but LAGs have only recently been reported for pterosaur bones (de Ricqlès et al. 2000). A study of a partial pterosaur skeleton showed that some bones contain LAGs within fibrolamellar tissues, indicating that high growth rates were not constantly maintained (Sayão 2003). The present study has confirmed the occurrence of LAGs in the pterosaurian skeleton, but in different bones from those noted by Sayão (2003). The premaxilla of a Romualdo Member ornithocheirid contains up to three LAGs (Fig. 4), numerous LAGs are present in a metatarsal from the same strata (Fig. 5), but no LAGs were found in any other bones. However, LAGs were reported to occur widely in a broad range of pterosaurs (de Ricqlès et al. 2000), in a Cretaceous ornithocheirid by Sayão (2003) and in small Jurassic pterosaur bones by Padian et al. (2004). LAGs are rare in large pterosaurs (according to the present study) and the reasons why they are detected so infrequently (contra de Ricqlès et al. 2000) warrant further investigation. Perhaps the taxonomic differences in sampling is the source of





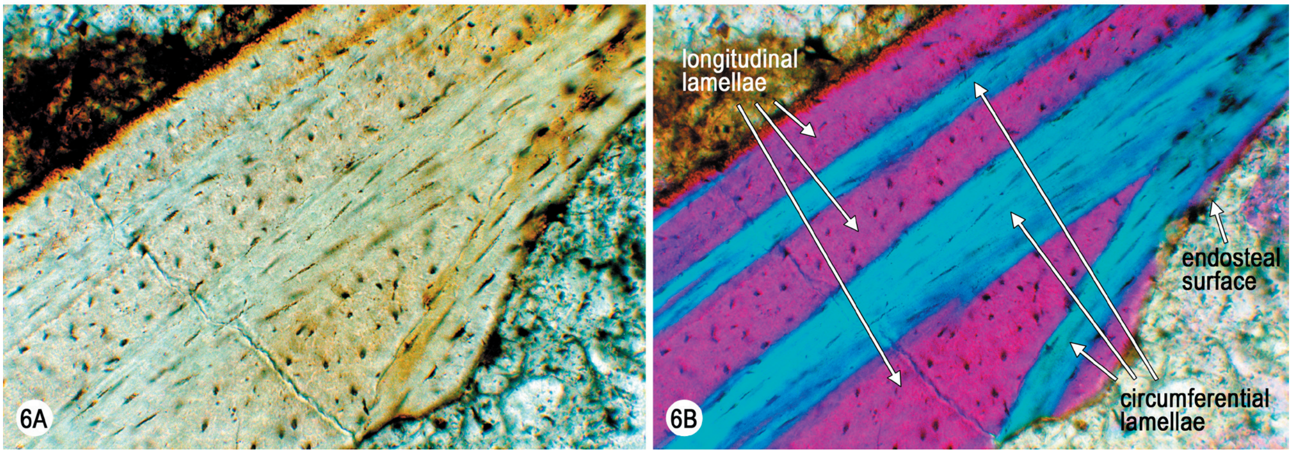


Figure 4: Transverse section through the dorso-lateral portion of the premaxilla of UP 2000.3 showing three LAGs (arrowed). The periosteal surface is damaged. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 1.3 mm.

Figure 5: Transverse section through UP 2000.10 (metatarsal diaphysis), showing LAGs which are closer together towards the periosteal surface. The lamellae are endosteally truncated by resorption and redeposition. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 0.7 mm.

Figure 6: Transverse section through the dorsal compacta of the right pterygoid of UP 2000.3, showing orthogonal 'plywood' with alternating lamellae. Periosteal surface to top left. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 0.2 mm.

the difference; de Ricqlès et al. (2000) examined mostly Late Cretaceous North American pterdactyloids, whereas most of my samples were from the Early Cretaceous of South America and the UK. Histological differences between two Romualdo Member taxa were detected by Sayão (2003), so there may be potential to use bone histology for taxonomic purposes, but this would require further investigation. A similar occurrence in dinosaurs may reflect different growth strategies (CHINSAMY et al. 1998) and this could explain the differences between the Romualdo Member pterosaurs.

Annually formed LAGs are widely used to calculate the age of extant vertebrates (e.g., PEABODY 1961; CASTANET 1985, 1987; MEUNIER et al. 1988; CASTANET & SMIRINA 1990; CASTANET et al. 1993; KLEVEZAL 1996) but it is problematic to use them for the same purpose in fossils, where the frequency of occurrence of LAGs cannot be experimentally confirmed and individual longevity is unknown. The earliest LAGs formed in most tetrapod bones are removed by endosteal resorption during skeletal growth, except in some sauropod dinosaurs (see SANDER, 1999, 2000). However, endosteal resorption in pterosaurs is always extensive due to the need to maintain a thin cortex in order to minimise bone mass. Therefore, it is unlikely that skeletochronology will ever be successfully applied to pterosaurs.

Some pterosaur bones contain an unusual type of primary periosteal tissue, which has been termed 'plywood-like' (DE RICQLÈS et al. 2000), in which the bone fibres, lacunae and vascular canals in each lamella have a preferred orientation, and this varies from one lamella to the next. Such structural organisation has been noted in coelacanth scale isopedin (GIRAUD et al. 1978), human femoral secondary osteons (GIRAUD-GUILLE 1988) and rat tibial primary cortex (WEINER et al. 1991). However, there are differences between these examples. The pterosaur bone is orthogonal 'plywood'; in which successive lamellae are oriented within the same plane but at 90° to one another. The coelacanth scale and human secondary osteon are examples of 'twisted plywood', where the orientation of the alternating lamellae differs from one another by less than 90°. The rat bone is 'rotated plywood' in which the bone fibres alternate between lying parallel to the lamellar boundaries, and lying oblique to them (WEINER et al. 1991).

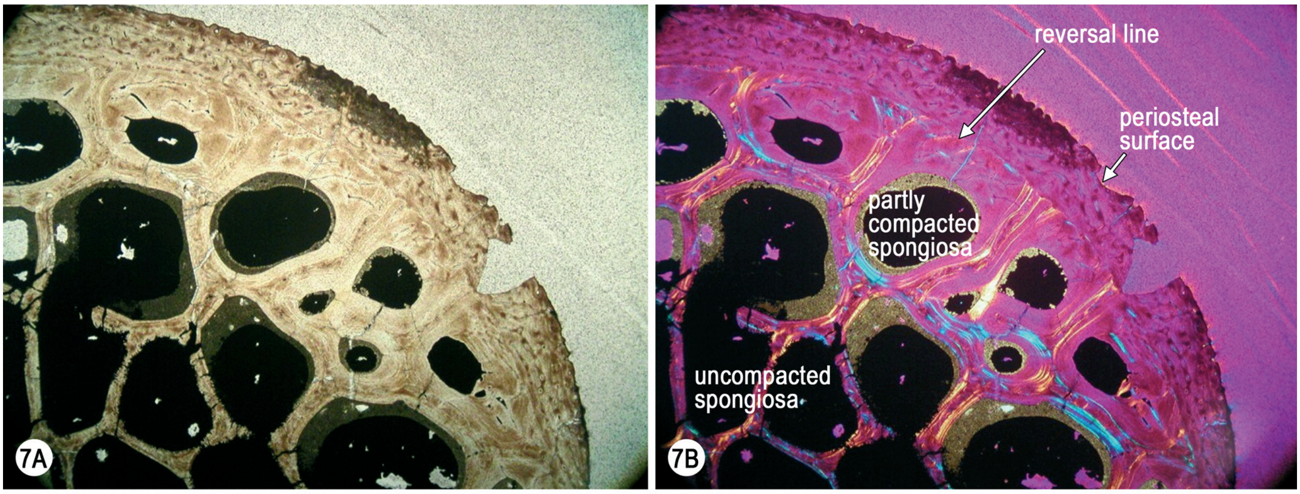
Pterosaurian orthogonal 'plywood-like' bone is commonly avascular or poorly vascular. According to DE RICQLÈS (pers. comm. 2004) it is found "*mainly in the smaller bones of fairly large pterosaurs rather than in the main bones of very small pterosaurs*". The pterygoid of UP 2000.3 (Fig. 6), contains alternating lamellae of approximately equal thickness, although the circumferential lamellae tend to be slightly thinner than their longitudinal counterparts. However, some specimens contain very narrow circumferential lamellae, e.g., a humerus, UP 2000.6b, and wing metacarpals CAMSM B54186 and CAMSM B54206. Whether to classify these tissues as 'plywood-like' or not is problematic, especially as the circumferential lamellae often thin out and disappear in parts of the section. In a mature bone, the whole cortex could be considered 'plywood-like' because it is composed of fibrolamellar tissue with longitudinal and obliquely oriented fibres 'sandwiched' between circumferential periosteal and endosteal lamellae (DE RICQLÈS et al. 2000).

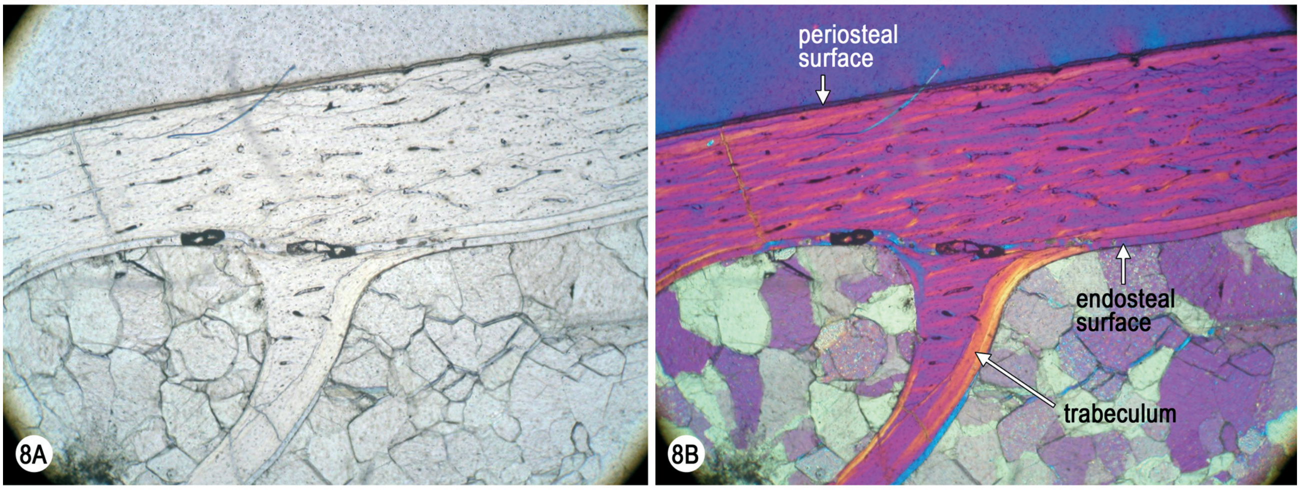
Plywood-like tissues may hinder microcrack propagation in bones (CURREY 1990; BOND et al. 1995), and could resist tensile and compressive forces from different directions, offering a biomechanical compromise to a bone in which the directions of stress vary. High bending and torsional stresses would be predicted to act upon pterosaur wing bones in flight, as these forces have been measured in flying pigeons (BIEWENER & DIAL 1995). In the present study, well-developed 'plywood-like" tissue was found in the pterygoids of an ornithocheirid, small elements that may have been subjected to sudden impacts or bending during feeding.

According to BOWERBANK (1848), QUEKETT (1855), SEITZ (1907), GROSS (1934), ENLOW & BROWN (1957), WELLNHOFER (1970), DE RICQLÈS (1976), BENNETT (1993) and this study, pterosaur bones lack dense Haversian tissue, and very rarely exhibit secondary osteons. The only secondary osteons seen in this study were found in the dentary of an ornithocheirid from the Romualdo Member. However, SAYÃO (2003) reports secondary osteons in the wing metacarpal, wing phalanx 1 and femur of an adult ornithocheirid from the Romualdo Member, while DE RICQLÈS et al. (2000) found them in wing phalanges of *Montanazhdarcho*, and *Quetzalcoatlus sp*, Late Cretaceous azhdarchids. In all occurrences described by SAYÃO (2003) and DE RICQLÈS et al. (2000), the secondary osteons are oriented longitudinally within the bone. The tissue within the osteon is also oriented longitudinally, rather than being organised into concentric alternating lamellae, which is usually seen in secondary osteons. In both studies, the secondary osteons were found to occur mainly in the deeper (older) periosteal tissues of the cortex, and DE RICQLÈS et al. (2000) noted that they were associated with the bases of trabeculae, which is confirmed by the present study. One possible explanation for this is that secondary osteons were present in all regions of the deep periosteal cortex, but were mostly removed by endosteal resorption. The periosteal cortex is thicker at the base of trabeculae and the secondary osteons are visible there because the deeper periosteal cortex was not endosteally resorbed (see DE RICQLÈS et al. 2000: p. 367, fig. 5F). If this was the case, earlier ontogenetic stages would have Haversian tissue in the deep cortex. However, this has not been observed in any study, and Haversian tissue in tetrapods usually develops in adulthood (AMPRINO 1967). Perhaps significantly, DE RICQLÈS et al. (2000) reported Haversian tissue only in the trabecular bases of *Quetzalcoatlus* sp. and *Montanazhdarcho*. The presence of Haversian tissue in these taxa and absence or poor development in the Late Cretaceous *Pteranodon* and in Early Cretaceous ornithocheirids (shown by the present study) may reflect an unknown aspect of azhdarchid biology.

The commonality of rich vascularisation and dense Haversian tissue to dinosaurs and mammals supports arguments for a common endothermic physiology, and the same could be argued for pterosaurs. It has been claimed that dinosaurs were rapidly growing endotherms (DE RICQLÈS 1969, 1974, 1980), an idea that has gained wide acceptance from some (e.g., BAKKER 1972, 1975, 1980, 1986; DESMOND 1975) but not from others (REID 1984a, 1984b, 1987, 1995, 1996; CHINSAMY 1994). However, this argument is not without flaws. The bones of small mammals are not always richly vascularised, or contain secondary osteons, whereas many fossil and extant reptiles can develop secondary osteons (ENLOW 1969; BOUVIER 1977), and dense Haversian tissue comparable with that of mature human bone occurs in chelonian bones (AMPRINO & GODINA 1947; REID 1984b).

The function of secondary osteons remains controversial. The generally accepted view is that they are a source of phosphate and calcium ions for metabolic activity (e.g., AMPRINO 1948, 1967; MEISTER 1951). However, ENLOW (1963, 1969) and





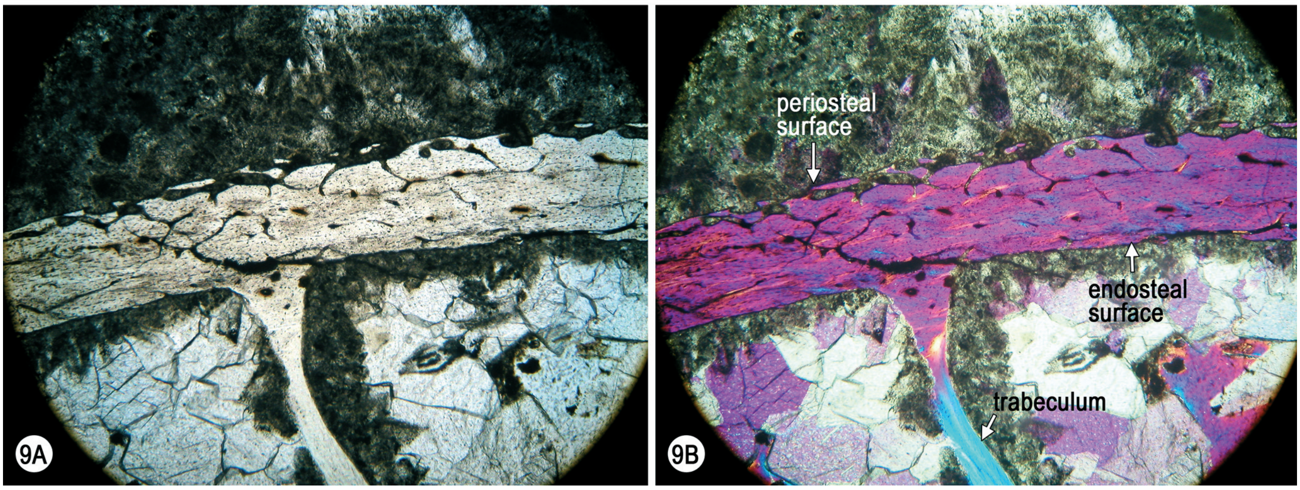


Figure 7: Transverse section through IWCMS 2002.234 (wing phalanx), showing several distinct phases of periosteal and endosteal deposition and resorption (see text). A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 4.2 mm.

Figure 8: Transverse section (Section A3a) through UP 2000.8 (ulna) showing a trabeculum composed of a core of selectively non-resorbed periosteal tissue and a layer of endosteal tissue deposited on its surface. A: plane polarised light; B: crossed polarised light. Height of images = 1.63 mm.

Figure 9: Transverse section through UP 2000.6d (wing phalanx 2) showing fibrolamellar bone in the process of periosteal growth. A trabeculum contains periosteal and endosteal tissues. A: plane polarised light; B: crossed polarised light. Height of images = 1.63 mm.

Currey (1960, 1968, 1970) argued that secondary osteons are primarily a mechanism to remove and replace necrotic tissue. A biomechanical function was suggested by Carter et al. (1976), who proposed that the presence of secondary osteons in compact bone inhibits the spread of microfractures, and this idea was cautiously accepted by Currey (1984, 1990a). Endothermy

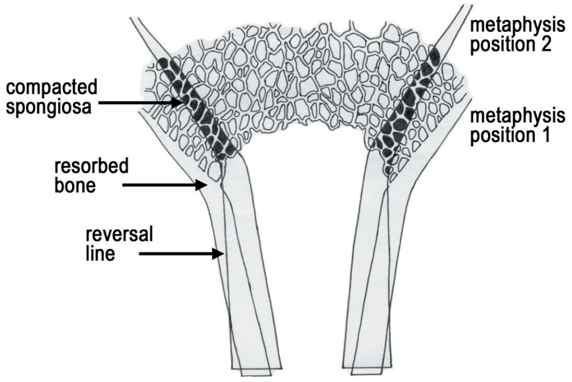


Figure 10: During the growth of long bones, the spongiosa at the metaphyses has to become part of the diaphysis (Enlow 1963; Currey 1984). This is achieved by a process of metaphyseal reduction, which has two phases. The periosteal surface of the metaphysis is resorbed to reduce its diameter, which exposes the trabeculae. Spaces within the remaining spongiosa are filled (compacted) with endosteal bone to form a new cortex. Partially compacted spongiosa in a pterosaur wing phalanx is shown in Figure 7.

in pterosaurs should not be discounted simply because they generally lack dense Haversian tissue.

There appears to be a correlation between compacta thickness and the occurrence of Haversian tissue. In extant mammals, small species with thin compacta lack Haversian tissue, whereas larger species with thicker compacta often have dense Haversian tissue (see Foote 1916 and Amprino & Godina 1947, for numerous examples). The compacta of pterosaur bones varies in thickness, but is frequently less than 1 mm thick in even the longest bones, so perhaps it is of insufficient thickness to support dense Haversian tissue, which is mechanically weaker than primary lamellar bone (Currey 1959, 1981, 1987). This weakening may be of little consequence in the thick compacta of large terrestrial and aquatic mammals that typically possess it, but perhaps in the thin compacta of pterosaurs it would be more deleterious. This could also explain the absence of dense Haversian tissue in extant volant birds, although secondary osteons do occur (see Foote 1916: pls 5–7 for examples of bird femoral histology).

Trabeculae are particularly important in bird bones, where they enhance the stiffness, strength and toughness of the bone (Rogers & LaBarbera 1993). Pterosaur bones have similar trabecular structures spanning the lumen and it is reasonable to assume that pterosaur bones benefited from the same strengthening properties. Trabecular remodelling (alterations to the shape and orientation of trabeculae) are consistent with optimising skeletal strength whilst minimising body mass, as early authors recognised (Phillips 1871).

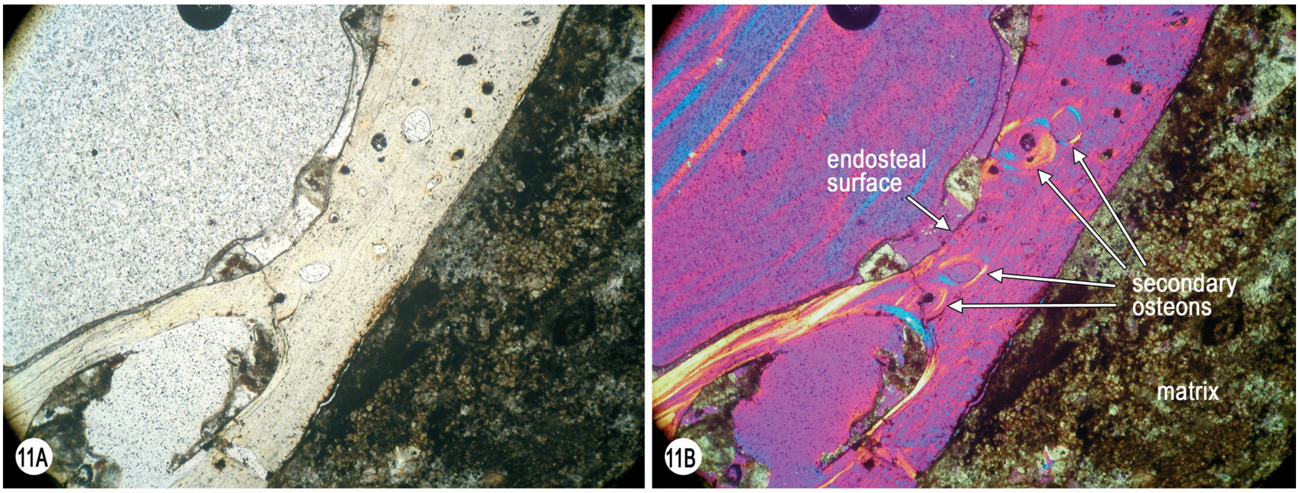
In the diaphyses of many of the bones examined in this study, ridges were found on the endosteal surfaces. Similar structures occur in large mammalian femora (Foote 1916; pers. obs.) and were noted in a pterosaur bone by Currie & Russell (1982). It is likely that these ridges have a biomechanical function, as suggested by de Ricqlès et al. (2000). However, it is difficult to explain why Warren struts (transverse trabeculae) should be found in some pterosaur bones and endosteal ridges should be found in others. One possible explanation is that endosteal ridges are found when the lumen of the bone was occupied by a soft tissue structure such as an air sac, whose function may have been impaired by intervening trabeculae. However, although Warren struts are well documented in modern bird bones (e.g., Foote 1916; Bellairs & Jenkin 1960; Currey 1984), endosteal ridges have not been reported. Alternatively, it is possible that endosteal ridges and Warren struts provide bones with different biomechanical properties, a hypothesis that requires testing.

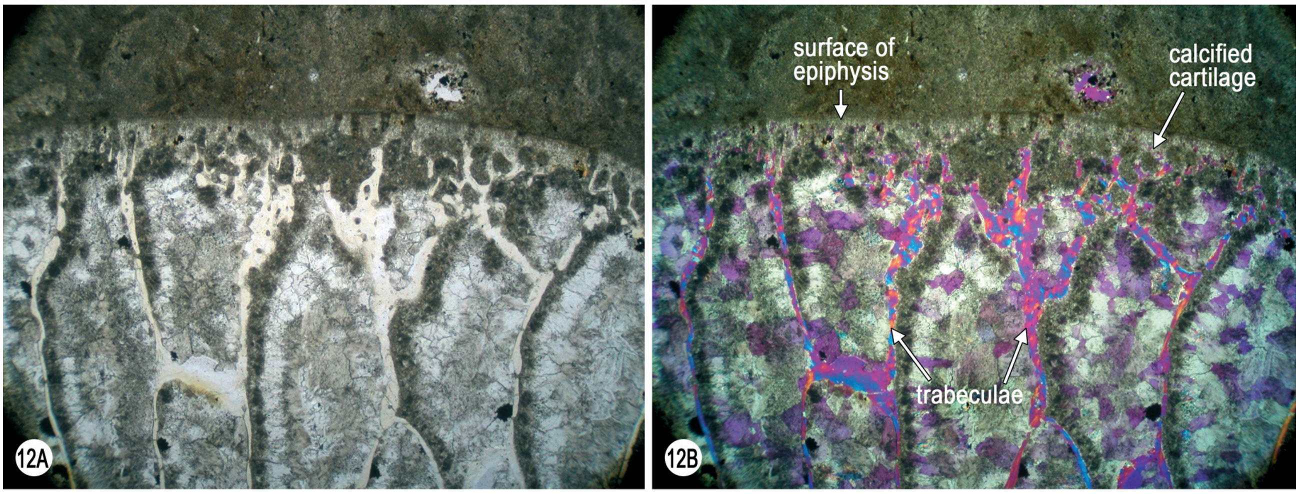
Occasionally, endosteal ridges are hollow, and form a system of longitudinal tubes between the compacta and the lumen (the three-dimensional structure is confirmed by longitudinal and transverse sections). They were first noted in pterosaur bones by de Ricqlès et al. (2000), who described them as 'pipes' and suggested that they were pneumatic channels, an idea accepted by Sayão (2003). They mainly occur in the epiphyseal and metaphyseal regions of smaller long bones with an ovoid cross section. Similar tubular structures in plant stems, porcupine (*Hystrix*) quills and hedgehog (*Erinaceus*) spines were described by Karam & Gibson (1994). In these examples, tubular structures increase resistance to local buckling under bending loads, which was the main hazard faced by the thin-walled long bones of pterosaurs (Currey 1984; Currey & Alexander 1985). The absence of endosteal tubes in the diaphyses may be due to the thicker compacta there rendering them unnecessary, or to other unknown biomechanical reasons.

Moodie (1908) stated that epiphyses are absent in pterosaurs. However, they were observed in pterosaurs many years ago (e.g., Seeley 1870), and are well known in the humerus and ulna (e.g., Kellner & Tomida 2000), but were not examined in thin section until recently (de Ricqlès et al. 2000). Strictly speaking, the pterosaurian growth structures described in this study (termed 'epiphyses' by de Ricqlès et al. 2000) are growth plates (*sensu* Barreto et al. 1993, Barreto 1994). This term refers to the terminal cartilaginous region of a bone that permits growth. The descriptions of these structures in Late Cretaceous *Pteranodon* and *Montanazhdarcho* (de Ricqlès et al. 2000) are entirely consistent with the epiphyseal tissues of the Romualdo Member pterodactyloid phalanges, which unfortunately cannot be confidently assigned to any particular taxon. The preservation of calcified cartilage is said to be rare (de Ricqlès 1972) but it can be extremely well preserved in some cases (Barreto et al. 1993; Barreto 1994) as it is in these pterosaur bones from the Romualdo Member. Uncalcified tissues overlying the calcified cartilage are not preserved, which is consistent with material described by Horner et al. (2001).

Until recently, no undisputed pterosaur nest sites or eggs were known, and there was no convincing evidence of viviparity. However, recent reports of pterosaur eggs and embryos from the Lower Cretaceous of China and Argentina (Wang & Zhou 2004; Ji et al. 2004; Chiappe et al. 2004) confirmed that pterosaurs were oviparous, as are other members of their extant phylogenetic bracket (crocodiles and birds).

In oviparous tetrapods, the calcium required to form the shell of a cleidoic egg is sequestered from the skeleton of the female. In birds, it is obtained from the medullary bone, a highly calcified woven tissue deposited in the long bones of females prior to egg laying, that may fill the medulla completely. Medullary bone is metabolised much faster than cortical bone,





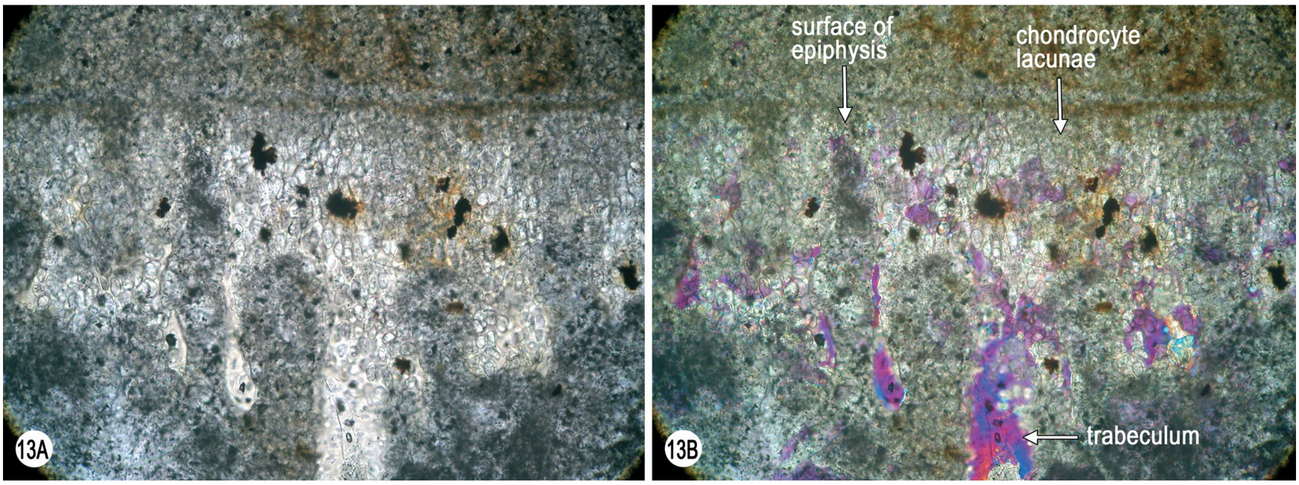


Figure 11: Transverse section (Section 1) through the medial surface of the left dentary of UP 2000.3. The tissue contains two pairs of secondary osteons. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 1.8 mm.

Figure 12: Longitudinal section (Section 3) through the proximal end of UP 2000.9 (wing phalanx 4), showing calcified cartilage supported by columns of bone. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 4.2 mm.

Figure 13: Longitudinal section (Section 1) through the proximal end of UP 2000.9 (wing phalanx 4) showing the cartilaginous proximal surface with ovoid chondrocyte lacunae. A: plane polarised light; B: crossed polarised light with tint plate. Height of images = 0.7 mm.

to provide the calcium and phosphate ions for the egg shell as it passes through the oviduct (Bloom et al. 1941; Meister 1951; Dacke et al. 1993; Dacke 1998). Most amniotes lack this specialised mineral source, but nevertheless remove minerals from their skeleton for oögenesis. Examples of this occurrence in fossils include intensive Haversian replacement in thalattosuchian bone (Hua & de Buffrénil 1996) and the long bones of the 'female morph' of the Upper Jurassic sauropod *Barosaurus* (Sander 1999, 2000). Similarly, the occurrence of large perimedullary resorption cavities in the femoral compacta of the robust forms of the theropod dinosaur *Syntarsus* support sexual dimorphism in this genus (Chinsamy 1990). Similar perimedullary cavities have been described in pterosaurs, but were interpreted as pneumatic spaces (Sayão 2003).

As noted above, pterosaur bones generally lack dense Haversian tissue and usually lack secondary osteons, so a possible source of mineral ions for oögenesis is not immediately obvious. If pterosaurs removed calcium from the endosteal lamella lining their bones, it would show signs of reworking in females that have undergone at least one reproductive cycle. No such reworking has been detected. The most highly reworked parts of a pterosaur bone are the trabeculae, but it is unlikely that they were a source of calcium for eggshell, given their biomechanical importance. The solution to this apparent problem of why pterosaur bones lack any obvious signs of reproductive bone resorption such as medullary bone may lie in the nature of the recently described eggs (Wang & Zhou 2004; Ji et al. 2004; Chiappe et al. 2004); the calcified shell is very thin. Although bone histology may be sexually dimorphic in some saurischian dinosaurs (Chinsamy 1990; Sander 1999, 2000), it is unlikely that such dimorphism will ever be found in pterosaurs.

Historically, the investigation of palaeohistology has been fraught with problems, particularly the lack of material available for destructive analysis. A single section through an opportunistically-obtained fragment of bone does not necessarily give an accurate view of the general histology of that element, or indeed of the individual. As Castanet et al. (1996) and Sayão (2003) have shown, bone histology does not only vary along the length of a single element but can also be different in other parts of the same skeleton. It is preferable to sample more than one element of the same individual. However, this is not always possible, therefore we must consider the limitations of the material under study before making generalisations.

6. Conclusions

Pterosaur bones are structurally and histologically similar to bird bones, in being thin-walled and predominantly composed of fibrolamellar bone, but pterosaur bones exhibit specialised features not yet described in birds, such as "plywood-like" tissue. Periosteal deposition was balanced by endosteal resorption to maintain a thin-walled tubular structure, but endosteal structures such as trabeculae and ridges remained for biomechanical reasons. These were frequently remodelled by further endosteal resorption and deposition. Elongation of skeletal elements took place at terminal epiphyses, whose structure is similar to those of birds. Metaphyseal relocation is recorded by the compaction of spongiosa and the formation of reversal lines.

Pterosaur bones grew rapidly, but occasionally with cyclical interruption, which may have occurred annually in response to seasonal changes in food availability or other variables. Cranial and pedal bones from two Romualdo Member specimens show LAGs that record these events, but other specimens from the same site do not. A similar occurrence in dinosaurs may reflect different growth strategies (Chinsamy et al. 1998) and this could explain the differences between the Romualdo Member pterosaurs.

Young pterosaurs grew rapidly, but growth rates slowed when sub-adult size was reached, whereupon an endosteal lamella formed on the endosteal surface and an EFS formed on the periosteal surface. Dense Haversian tissue is absent, but occasional secondary osteons formed in the deep compacta of some bones, particularly in the vicinity of trabecular bases.

Pterosaur bones appear to lack any type of specialised reproductive mineral deposits, which correlates well with the recent description of a pterosaur embryo in a thin-shelled egg (Wang & Zhou 2004). Therefore, bone histology cannot be used for gender determination in pterosaurs.

Well-preserved pterosaur bones reveal fine structural and histological details. Unfortunately, abrasion and bioerosion obscure these features in many pterosaur-bearing strata.

A better understanding of pterosaur bone histology has the potential to contribute to biomechanical studies, especially computer modelling of pterosaur wing biomechanics where the bone is usually assumed to be a simple tube of homogeneous composition and structure. This is clearly not the case, so perhaps future work will take bone histology and microstructure into account when modelling the behaviour of pterosaur bones in flight.

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