ONTOGENETIC EVOLUTION OF BONE STRUCTURE IN LATE CRETACEOUS PLESIOSAURIA FROM NEW ZEALAND

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ABSTRACT

Histological observations of homologous bones (vertebrae, ribs, humerus, phalanges) among conspecific juvenile and adult Upper Cretaceous plesiosaurs from New Zealand (elasmosaurs and pliosaurs) demonstrates a unique "ontogenetic trajectory" of skeletal histogenesis in these animals. While juveniles demonstrate a "pachyosteosclerotic" condition of the skeleton, adults have a very light "osteoporotic-like" bone structure. Until now, one *or* the other of these histological specializations was known among aquatic tetrapods, adapted along contrasting pathways to this environment, either by ballasting (pachyosteosclerosis : e.g. sirenians) or by lightening (osteoporotic-like adaptation : e.g. modern cetaceans) of the skeleton. The successive occurrence of these constrasting conditions during ontogenesis of a single organism had never been reported, as far as we know, but could well be an ontogenetic characteristic of Plesiosaurs *sensu lato*. The significance of these findings are discussed in various phylogenetical, functional and paleoecological contexts. The ontogenetic trajectory of the plesiosaur skeleton is interpreted within the general framework of developmental heterochrony. Specifically, it suggests that juvenile plesiosaurs kept a conservative (plesiomorphic) ecology for sauropterygians, as poorly mobile, lagoon or shore dwellers while, in contrast, the adults would shift towards much more active locomotory behaviours in the open sea.

KEY-WORDS : PLESIOSAURS, BONE, HISTOLOGY, ONTOGENESIS, EVOLUTION, NEW ZEALAND.

RÉSUMÉ

L'observation histologique d'os homologues (vertèbres, côtes, humérus, phalanges) chez des juvéniles et des adultes conspécifiques de plésiosaures du Crétacé supérieur de Nouvelle-Zélande (élasmosaures et pliosaures) révèle l'existence d'une "trajectoire ontogénique" très particulière, intéressant l'histogénèse du squelette, chez ces organismes. Tandis que les juvéniles présentent une nette "pachyostéosclérose", les adultes ont, au contraire, une structure osseuse très allégée, "ostéoporotique", sans que ces termes aient ici de connotation pathologique. Jusqu'à présent, l'une *ou* l'autre de ces spécialisations histologiques n'était connue que chez des tétrapodes aquatiques adaptés à ce milieu selon des modalités très distinctes, voire opposées, correspondant soit à l'alourdissement (pachyostéosclérose : ex. les siréniens), soit à l'allègement ("ostéoporose" : ex. cétacés modernes) du squelette. Leur présence successive au cours de l'ontogénèse d'un même organisme n'avait jamais, à notre connaissance, été signalée mais pourrait être une caractéristique du développement propre aux plésiosaures *sensu lato*. Les implications de ces observations sont discutées selon divers contextes : phylogénétique, fonctionnel et paléoécologique. On interprète la "trajectoire ontogénique" particulière du squelette des plésiosaures en termes d'hétérochronie. Celle-ci révèlerait le maintien, chez les juvéniles, d'une écologie d'animaux côtiers et relativement peu mobiles, condition sans doute plésiomorphe chez les sauroptérygiens, qui serait suivie, chez les plésiosaures adultes, par une adaptation différente, liée à une active locomotion en haute mer.

MOTS-CLÉS : PLÉSIOSAURES, OS, HISTOLOGIE, ONTOGENÈSE, ÉVOLUTION, NOUVELLE-ZÉLANDE.

INTRODUCTION

In the tetrapods secondarily adapted to aquatic life, the microstructure of the skeleton displays more or less spectacular specializations, as compared to the forms which retain the original terrestrial habitat (*int. al.* Nopcsa 1923a ; Nopcsa & Heidsieck 1934 ; de Ricqlès 1989). This general statement applies to a wide range of taxa within mammals, birds, reptiles or amphibians. In these animals, the structural specialization of bone presents two general aspects : ballasting or lightening of the skeleton.

In certain groups, the inner organisation of bone looks very compact, with a characteristic lack of a free medullary cavity or extensive cancellous formations, which is often associated with an hyperplasy of periosteal cortices. In such cases, it is frequent that the calcified cartilage formed at a subepiphyseal level is not resorbed during growth, while it is sequentially relocated towards the diaphyseal region of the bones. This particular type of structural specialization of bone, termed pachyostosis (when there is only an hyperplasy of periosteal cortices) or pachyosteosclerosis (cortical hyperplasy associated with compactness of the inner structure of the bones), is well exemplified by the Sirenia (*int. al.* Fawcett 1942 ; de Buffrénil & Schoevaert 1989), the archaeocetes (de Buffrénil *et al.* 1990a), certain species of penguins (Meister 1962), the nothosaurs (Zangerl 1935), Cenomanian snake-like squamates (Nopcsa 1923b, 1925 ; de Buffrénil & Rage 1993), mesosaurs (de Ricqlès 1974, 1975a,b), champsosaurs (de Buffrénil *et al.* 1990b), and several other taxa (see also the review in Nopcsa & Heidsieck 1934). Of course, though reminicent of some diseases of bone in terrestrial tetrapods (Fawcett 1942), this skeletal specialization is by no means pathological in aquatic forms.

Conversely, in osteoporotic-like states (again, non-pathological states), which are mainly exemplified by modern cetaceans (Felts & Spurrell 1965, 1966 ; de Buffrénil & Schoevaert 1988), ichthyosaurs (Kiprijanoff 1881-1883 ; de Buffrénil & Mazin 1990), thalattosuchians (Seitz 1907 ; Gross 1934 ; Buffetaut 1979), and certain marine turtles (Rhodin *et al.* 1981 ; Rhodin 1985), the bones display an extremely cancellous structure, with a nearly complete lack of compact bone tissue.

As interpreted in reference to the actual physiological mechanisms from which they arise (cf. de Ricqlès 1975a, 1989), or to their functional or ecologic correlates, these two types of structural specialization of bone differ sharply from one-another. The main functional consequence of pachyosteosclerosis would be to create a natural ballast with bone tissue, thus allowing a hydrostatic (passive) control of body trim in water (Hoffstetter 1955 ; Domning & de Buffrénil 1990). This condition seems to be rather typical of slow moving animals, feeding in shallow waters upon fixed food or non-elusive prey. Conversely, osteoporotic-like states would reduce the inertia of the body, by reducing selectively the mass of the skeleton, and improve its capabilities for acceleration and manoeuvres, (cf. Webb & de Buffrénil 1990). Hence, this peculiarity would mainly characterize predatory forms, highly adapted to rapid swimming and long cruises in the open sea.

In respect to these considerations, it seems clear that the study of bone structure may be a significant clue for the paleoecological interpretation of various taxa of fossil marine tetrapods.

Though the plesiosaurians (plesiosaurs *sensu stricto*, and pliosaurs) are amongst the outstanding groups of Mesozoïc marine tetrapods, few studies were hitherto specifically conducted on the structure of their bones. The various descriptions of bone histology in this group mainly deal with the genus *Plesiosaurus* (Kiprijanoff 1881 ; Seitz 1907 ; Enlow & Brown 1957), and, to a lesser extent, the genera *Peloneustes*, *Cryptoclidus* (Gross 1934) and *Pliosaurus* (Nopcsa & Heidsieck 1934). These genera are from Lower (*Plesiosaurus*) to Middle-Upper Jurassic formations (*Cryptoclidus*, *Peloneustes*, *Pliosaurus*). The majority of these studies are relatively short descriptions of the structure of periosteal deposits : i.e. lamellar-zonal bone tissue with a moderate vascularization, and very obvious evidence of a cyclic growth. This type of cortical bone, very common indeed in poikilothermic tetrapods (see de Ricqlès 1975a) is considered by the authors quoted above as quite similar to that of the nothosaurs.

Actually, the richest source of information on plesiosaurian bone structure is the basic work of Kiprijanoff (1881). According to the illustrations of this author (the terminology used by Kiprijanoff to describe bone histology is somewhat uneasy to interpret, conversely, his illustrations are extremely clear and detailed : see plates 15 to 19), bone histology in "*Plesiosaurus bernardi*", "*P. neocomiensis*" and "*P. helmersenii*" (these taxa are no longer valid today, and should be considered as *Plesiosauria indet.*, which does not alter the value of Kiprijanoff's histological study), is characterized by three elements : 1) The calcified cartilages formed at a sub-epiphyseal level were not submitted to a complete resorption and persisted,

as more or less important remnants, in the medullary regions of the bones. 2) The periosteal cortices are generally compact, with a moderate vascularisation. Moreover, they display very obvious evidence of a cyclic growth. 3) Endosteal remodeling involves mainly deep (perimedullar) regions of the cortices. However, some Haversian substitution is also noticeable within the cortices.

This general picture of plesiosaurian bone structure deals only with genera representing a rather early radiation of the Plesiosauria, whereas the evolution of this order continued up to the end of the Cretaceous. In the various lineages of marine tetrapods, the histologic features of the skeleton show distinctive evolutionary modifications, while adaptation to an aquatic habitat becomes more and more specialized (see e.g. the case of the ichthyosaurs : de Buffrénil & Mazin 1990, or that of the cetaceans : de Buffrénil et al. 1990a ; see also Nopcsa 1923a ; Nopcsa & Heidsieck 1934; de Ricqlès 1989). Hence, the descriptions dealing with Jurassic forms provide only a partial information.

The present study provides complementary data about adult and juvenile plesiosaurian specimens from the Upper Cretaceous, thus allowing a more detailed interpretation of the evolutionary trends in plesiosaurian skeletal specializations.

MATERIAL AND METHODS

The paleontological sample for this study consists of 10 bones (Fig. 1, 2) from the Campanian-Maastrichtian marine sediments of Mangahouanga Stream (Hawkes Bay ; New-Zealand). During the last ten years, a rich paleofauna was discovered at this site, including terrestrial (cf. Wiffen & Molnar 1988, 1989) and aquatic reptiles (cf. Wiffen 1980, 1990 ; Wiffen & Moisley 1986).

Our bone samples (as indicated on Fig. 1), vertebrae, ribs, limb bones and phalanges, have been selected from approximately the same

regions in both adult and juvenile specimens. They represent the two taxa of Plesiosauria found in the Late Cretaceous sediments of New Zealand, and commonly discovered at this site, the Plesiosauroidea (the long necked type) and Pliosauroidea (the short necked, long headed type). In each taxon, adult and juvenile specimens share the same basic morphological features, and can be considered as conspecific with high plausibility (see on this topic Wiffen & Moisley 1986).

1 - Elasmosauridae (Plesiosauria, Plesiosauroidea). This is a large long necked form, up to 7-9 m in length, found only from the Upper Cretaceous in New Zealand, and relatively common in the marine sediments of Mangahouanga Stream. Though not identifiable with certainty at a generic level on the basis of our material (isolated bones ; cf Wiffen & Moisley 1986), this form might eventually be *Mauisaurus*. Eight skeletal elements (Fig. 2), belonging either to juvenile or to adult specimens were used for this study.
The distinction between juvenile and adult bones refers to several criteria : small size ; absence or poor development of insertional surfaces for muscles ; poor development of articular heads of limb bones (especially absence of separation between capitulum and trochanter or tuberosity) ; poor development of perforated surfaces at the extremities of limb bones ; unfused vertebral processes.
The paleontological material of the family Elasmosauridae includes : 2 vertebrae (one from a juvenile), 2 ribs (one from a juvenile), 2 phalanges (one from a juvenile), and 2 humeri (one from a juvenile).

2 - Pliosauridae (Plesiosauria, Pliosauroidea). This large headed, short necked form is widely distributed in the Upper Cretaceous of Europe, North America and the Pacific region, though less commonly found at the Mangahouanga site. Two pliosaur vertebrae (Fig. 2) were examined, one of which being from a juvenile. Again, this material belongs to a series of isolated bones (cf
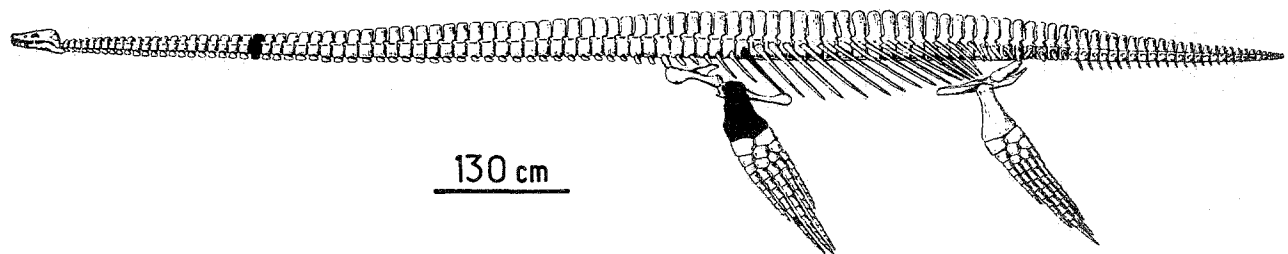

130 cm

Figure 1 - Paleontological sample : general view of a plesiosaur skeleton, indicating the bones (in black) included in our sample.
Echantillon paléontologique : vue générale du squelette d'un plésiosaure, indiquant les os (en noir) qui figurent dans l'échantillon.
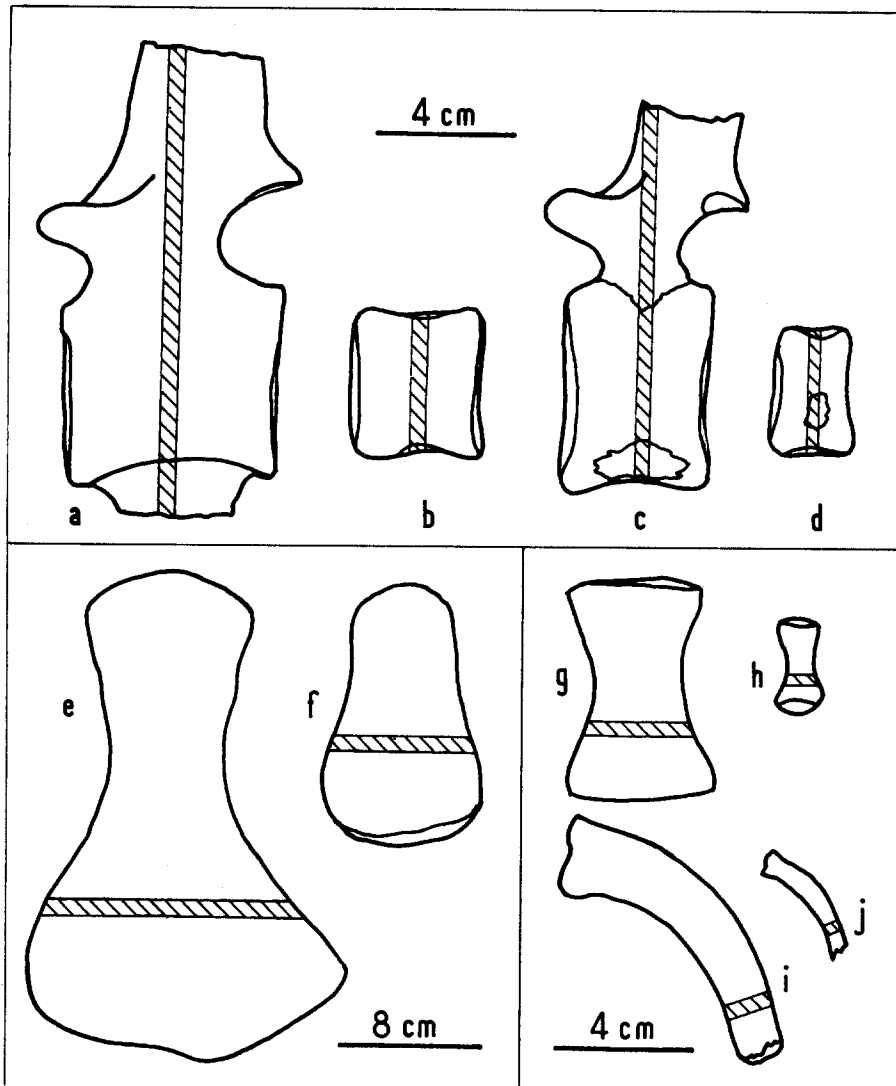
Figure 2 - Paleontological sample : adult and juvenile bones used in this study. a - Adult elasmosaur vertebra in lateral view. The hatched area localises the position and orientation of the cross sections (the same symbol is used for the other bones). b - Juvenile elasmosaur vertebra (lateral view). c - Adult pliosaur vertebra (lateral view). d - Juvenile pliosaur vertebra (lateral view). e - Adult elasmosaur humerus (lateral view). f - Juvenile elasmosaur humerus (lateral view). g - Adult elasmosaur phalanx (lateral view). h - Juvenile elasmosaur phalanx (lateral view). i - Adult elasmosaur rib (fragment in lateral view). j - Juvenile elasmosaur rib (fragment in lateral view). *Echantillon paléontologique : os adultes et juvéniles utilisés dans cette étude. a, vertèbre d'élasmosaure adulte en vue latérale. La bande hachurée montre la localisation et l'orientation des coupes (même figuré pour tous les os). b, vertèbre d'élasmosaure juvénile (vue latérale). c, vertèbre de pliosaure adulte (vue latérale). d, vertèbre de pliosaure juvénile (vue latérale). e, humérus d'élasmosaure adulte (vue latérale). f, humérus d'élasmosaure juvénile (vue latérale). g, phalange d'élasmosaure adulte (vue latérale). h, phalange d'élasmosaure juvénile (vue latérale). i, côte d'élasmosaure adulte (vue latérale). j, côte d'élasmosaure juvénile (vue latérale).*

Wiffen & Moisley 1986), which are identifiable with certainty only at the level of the family.

All these fossils are fairly well preserved, and perfectly suited to histological studies since they are free of crushing or severe epigenization. They were imbedded in an epoxy resin, and several sections 3 to 4 mm thick were sampled from them. The position and orientation of these sections are indicated on Figure 2. These various samples were finally used to make thin sections 50 to 80 µm thick, which were observed at low (x 25) to medium (x 100) power magnification, under ordinary or polarized transmitted light.

OBSERVATIONS

VERTEBRAL STRUCTURE

Juveniles

At low magnification, the cross sections of the vertebral centra of juvenile specimens display an extremely compact structure (Fig. 3a). However, a cavity is visible in the middle of each centrum. This represents a large vascular sinus, from which some vascular canals with a small diameter radiate. Medullary and cortical regions form a homogeneous, solid mass, quite deprived of spongy component. At higher magnification, the vascularization of bone appears rather abundant, with narrow vascular canals showing irregular orientations. No qualitative difference is noticeable between the elasmosaurid and pliosaurid vertebrae. The bulk of each centrum is mainly composed of calcified cartilage. Under transmitted ordinary light, this tissue typically appears to be formed of a vitrous intercellular matrix, perforated by numerous chondrocyte lacunae, more or less connected to each other, and disposed wi-
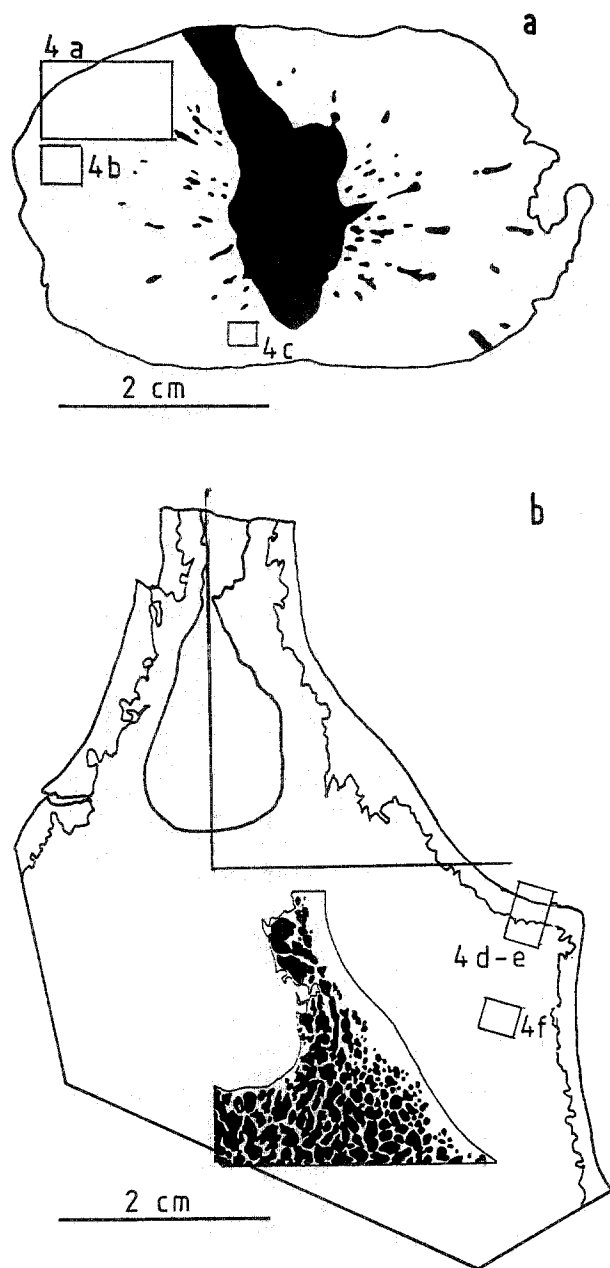
Figure 3 - General aspect of the cross sections in the vertebrae. The squares and rectangles localize the photographs displayed on Figure 4. **a**, juvenile ; **b**, adult. *Aspect général des coupes transversales de vertèbres. Les carrés et rectangles indiquent les champs photographiques représentés à la figure 4.* **a**, *juvénile.* **b**, *adulte.*

Ricqlès 1975b). Most often, the vascular canals within the cartilage are surrounded by a rather thick, centripetally deposited layer of bone tissue. The spindle-like morphology of the cell lacunae, as well as the mass birefringence of the bone matrix, which does not display a subdivision into lamellae, both indicate the presence of pseudolamellar bone tissue. On each juvenile centrum examined here, the calcified cartilage extends up to the peripheral margin of the bone. However, the continuity of this tissue is interrupted, at the level of the extremities of the big vascular sinus, by two small triangular formations of periosteal bone tissue (Fig. 4c).

This tissue displays a strong opacity in ordinary transmitted light, and a monorefringent reaction in polarized light. The numerous osteocytic lacunae which are embedded in it have a stellate shape, and are disposed without definite order within the bone matrix. No indication of a cyclic growth is noticeable. Such histologic features are characteristic of the "woven-fibered" bone tissue, which is typically indicative of a high, sustained rate of periosteal accretion (see on this topic : Amprino 1947 ; de Ricqlès 1976b ; Francillon-Vieillot *et al.* 1990). The numerous vascular canals in this tissue are surrounded by a sheath of fine fibered bone and form primary osteons. Their orientation is mainly radial, with also an oblique and, to a lesser extent, a longitudinal component. Hence, bone vascularisation roughly displays the aspect of a radiating network.

Adults

The inner structure of the vertebral centra of adult individuals (Fig. 3b) shares nearly no common feature with that of juveniles. In the elasmosaurid and pliosaurid adults, the vertebral centra have only a thin cortex (1 to 2 mm thick) of compact periosteal bone ; the greater part of the sectional area being occupied by a loose spongiosa, the trabeculae of which are thin and form a honeycomb-like network (absence of a predominant spatial orientation).

At medium magnification, the outermost region of the periosteal cortex appears to be made of a thin layer of primary lamellar-zonal bone tissue, with evidence of a cyclic growth in form of transluscent annuli and more opaque zones (for the terminology of these structures, see Castanet *et al.* 1993). The underlying part of the cortex is extensively occupied by secondary osteons, and turns to a dense Haversian bone tissue (Fig. 4d). Some rare erosion lacunae are also visible at this level. It is noteworthy that the secondary osteons are not composed of true lamellar bone, as such

thout obvious spatial structuration (Fig. 4a,b). Polarized light reveals that the intercellular matrix is composed of numerous birefringent spherules forming polarization crosses. This peculiar histological organisation is characteristic of globular calcified cartilage (cf. Ørvig 1951 ; de
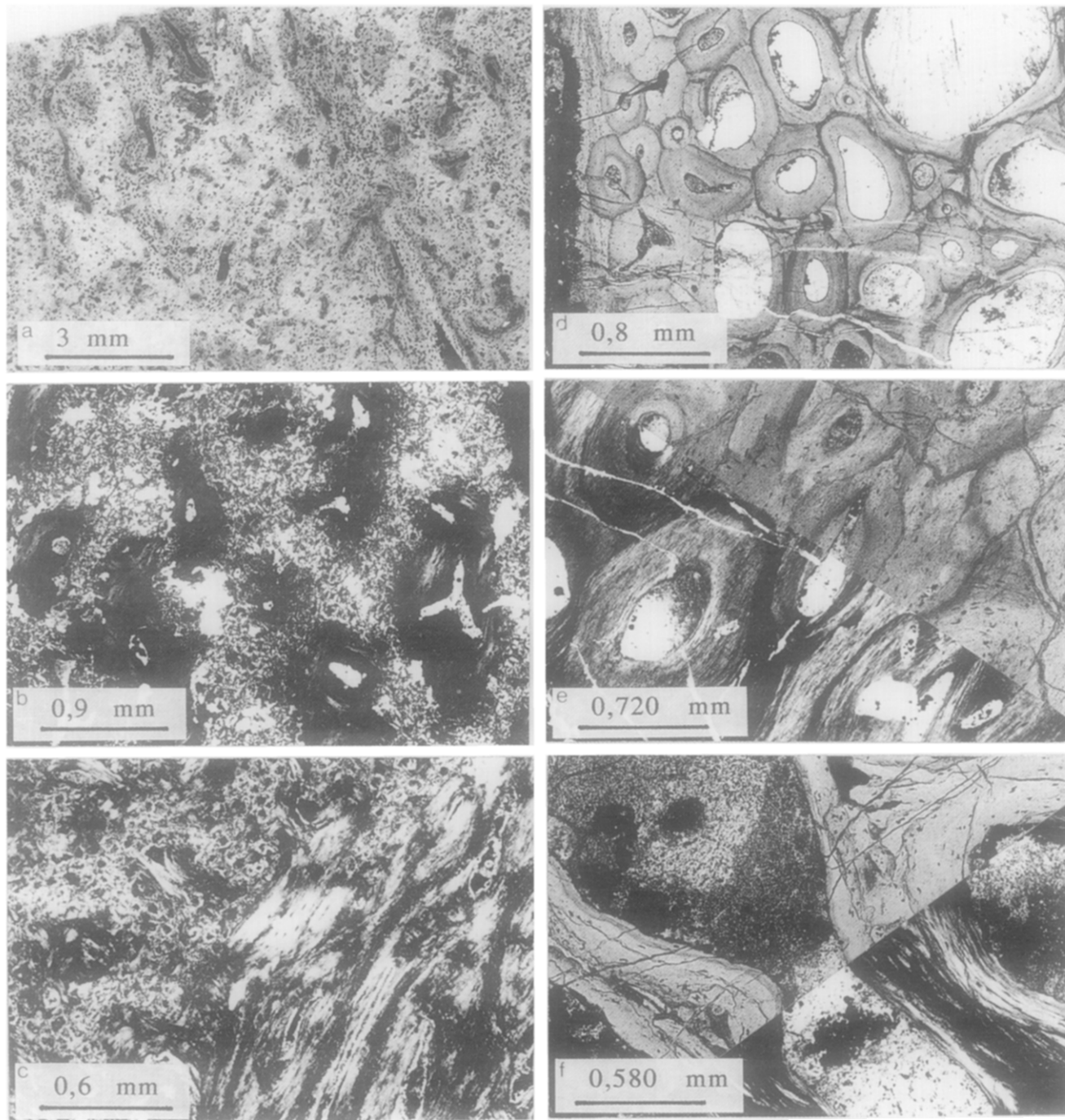
Figure 4 - Histological characteristics of elasmosaur vertebrae. **a** - compact mass of calcified cartilage forming the vertebral centra in juvenile individuals. Natural transmitted light. **b** - calcified cartilage in the same individual, viewed in polarized light. Remark the presence of birefringent cartilage globules, and that of intracartilagineous "pipes" of endosteal bone (arrow). **c** - Woven-fibered periosteal bone (right side), flanking the calcified cartilage in the ventral region of a juvenile centrum. Polarized light. **d** - Dense Haversian bone forming the cortex of the vertebral centrum in an adult individual. Natural transmitted light. **e** - Secondary osteons made of pseudolamellar bone tissue in the cortex of an adult vertebra. The left half is viewed in polarized light. **f** - Trabeculae of remodeled endosteal lamellar bone tissue in an adult individual. Remnants of calcified cartilage (arrow) are still visible in the core of the trabeculae. The right half is viewed in polarized light. *Caractères histologiques des vertèbres d'élasmosaures.* **a** - *Masse compacte de cartilage calcifié formant les centrums vertébraux des juvéniles. Lumière ordinaire transmise.* **b** - *Cartilage calcifié chez le même individu. Lumière polarisée. A noter la présence de globules cartilagineux biréfringents et celle de gros canaux intracartilagineux bordés d'os endostéal.* **c** - *Os périostique "à fibres enchevêtrées" (côté droit) bordant le cartilage calcifié dans la région ventrale d'un centrum juvénile. Lumière polarisée.* **d** - *Os haversien dense formant le cortex du centrum vertébral chez l'adulte. Lumière naturelle transmise.* **e** - *Ostéones secondaires composés de tissu pseudolamellaire dans le cortex d'un centrum adulte. La moitié gauche est vue en lumière polarisée.* **f** - *Travées d'os endostéal lamellaire remanié chez l'adulte. Des restes de cartilage calcifié (flèche) demeurent au coeur des travées. Moitié droite : lumière polarisée.*

The trabeculae of the spongy formations are typically composed of true lamellar bone tissue, with evidence of an intense remodeling (Fig. 4f). Nearly all trabeculae are thus built of a more or less complex set of bone platings, separated from each other by reversion lines. Moreover, the presence of numerous Howship's lacunae on the surface of the trabeculae is quite general. In the central (innermost) region of the vertebral centra, some trabeculae retain scarce remnants of calcified cartilage, under the superficial platings of lamellar bone tissue (Fig. 4f).

PHALANGES

The metaphyseo-diaphyseal region of the juvenile elasmosaurid phalanx is formed of a periosteal cortex with a medium thickness (1 to 1.4 mm, which represents 20 to 25% of the bone radius on the cross sections) and a rich vascular supply (Fig. 5a). The medullary territory is occupied by a very dense spongiosa, made of short and massive trabeculae, separated by narrow intertrabecular spaces (Fig. 6a,b).

The bone tissue forming the periosteal cortex is quite identical to that observed in some limited territories of the juvenile vertebral centra : woven-fibered tissue including a very rich vascular supply in form of a plexiform network of primary osteons (Fig. 6a).

The trabeculae of the medullary spongiosa display the typical structure of primary endosteo-endochondral trabeculae (cf. Haines 1938) : a thick core of calcified cartilage, covered by platings of pseudolamellar endosteal bone (Fig. 6b). Such trabeculae are formed during the early stages of endochondral osteogenesis, but they are "normally" (i.e. in the plesiomorphic condition in tetrapods) located in the epiphyso-metaphyseal region of the bones, not at a level close to the diaphysis, as it occurs here.

In the adult specimens (Fig. 5b), the structural organisation of the phalanx is very similar to that of adult vertebral centra. The bone is entirely occupied by a spongiosa with thin trabeculae formed by extensively remodelled lamellar endosteal tissue (Fig. 6c). On the sections examined here, there is no compact cortex at all : the spongiosa extending continuously up to the periphery of the bone. Nevertheless, it seems possible that the complete absence of a typical periosteal cortex could be an artifact related to taphonomical conditions.
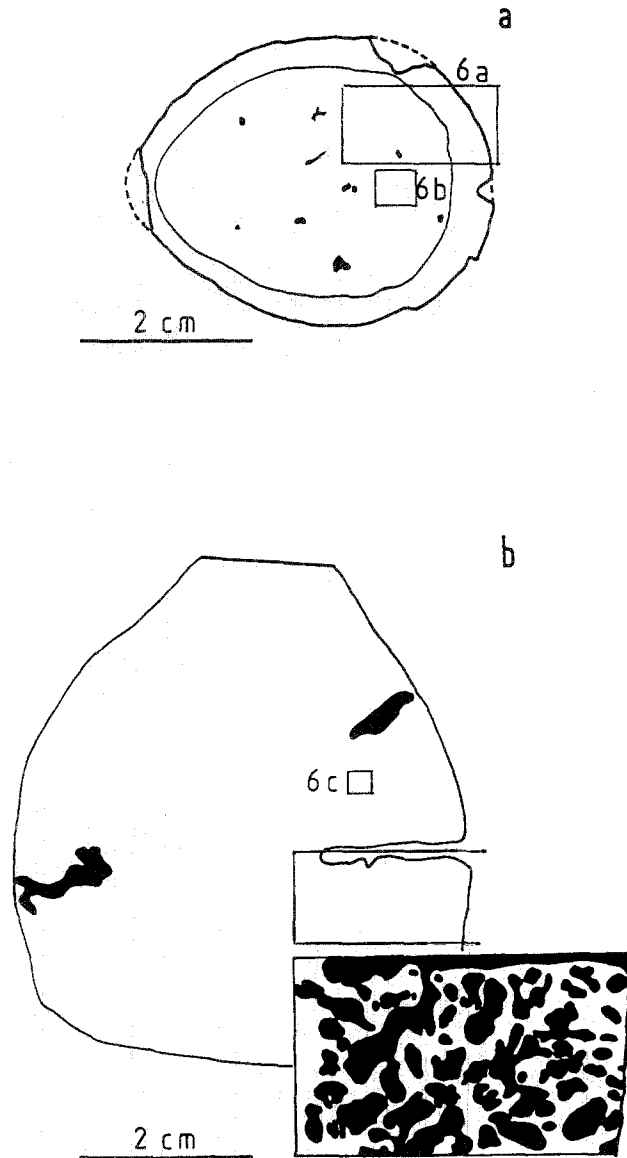
Figure 5 - General aspect of the cross sections in the phalanges. **a**, juvenile ; **b**, adult. *Aspect général des coupes transversales de phalanges. a, juvénile. b, adulte.*

structures usually are. Under polarized light, they show a global (mass) birefringence, without a subdivision into lamellae (Fig. 4e), and thus appear to be formed of pseudolamellar bone tissue. The deepest regions of the cortex display large erosion lacunae, the walls of which are indented by numerous Howship's lacunae. This shows that, at the death of the specimens to which the bones belonged, the deep territories of the periosteal cortex were submitted to an active resorptive process.
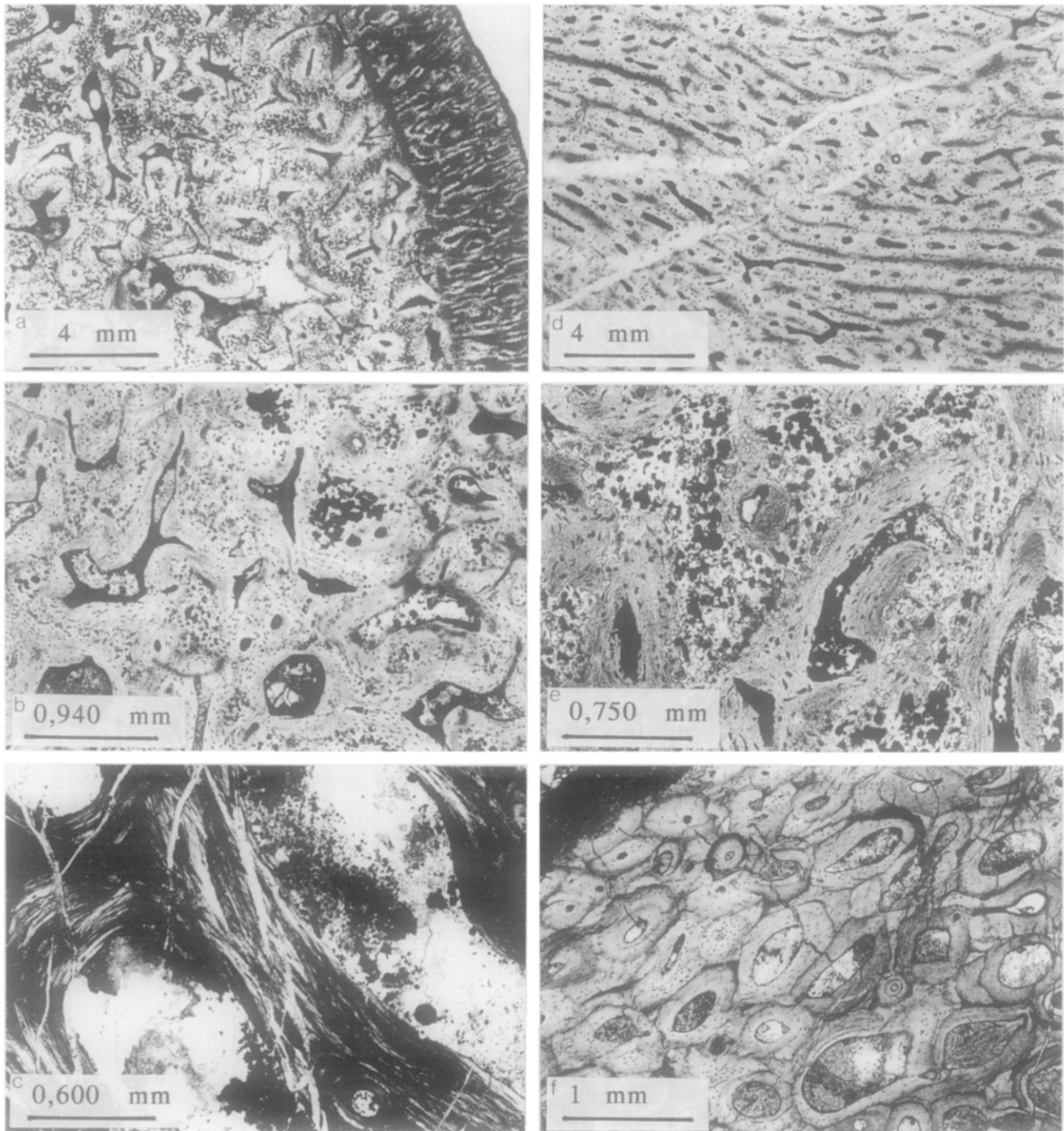
Figure 6 - Histological characteristics of the phalanges and humerus in the elasmosaur specimens. **a** - Periosteal cortex and subjacent cartilaginous medulla in a juvenile phalanx. Natural transmitted light. **b** - Detailed view of the primary trabeculae in the medullary region. The trabeculae are made of a thick core of calcified cartilage, covered by platings of pseudolamellar endosteal bone. Natural transmitted light. **c** - Remodeled endosteal trabeculae in the medullay region of an adult phalanx. At least two successive cycles of resorption and reconstruction are visible. Polarized light. **d** - Humeral cortex of the juvenile individual. The cortex is composed of woven-fibered bone tissue, with an abundant plexiform-like vascular supply. Natural transmitted light. **e** - Calcified cartilage in the medullary region of the juvenile humerus. Natural transmitted light. **f** - Cortex made of dense Haversian bone in the adult humerus. Natural transmitted light.

HUMERUS

In the juvenile specimen, a naked-eye observation of the sections reveals the existence of a very thick cortex (15 mm in the average, i.e. 65% of the bone radius), actually separated from the medullary region by a gap (Fig. 7a). The bone displays a high compactness, though the medullary region is pierced by numerous large erosion lacunae (diameter up to 1.5 or 2 mm), scattered randomly within the medulla.

Histologically, the periosteal cortex of the humerus is identical to that of the phalanx : it is a typical formation of woven-fibered bone, with a particularly rich plexiform or radiating-like vascular network (Fig. 6d). The medullary region is essentially composed of globular calcified cartilage, including thin longitudinal vascular canals (Fig. 6e). Centripetal deposits of pseudolamellar tissue around the lumen of the canals form secondary osteon-like structures embedded in the cartilage (cf. de Ricqlès 1975b). The walls of the erosion lacunae generally display Howship's lacunae.

In the adult, the humerus is quite cancellous, but nevertheless displays a compact cortex, the thickness of which varies locally (Fig. 7b). The latter is composed of woven-fibered tissue, submitted to an intense Haversian remodeling (Fig. 6f). Its deep region is dissected by abundant erosion lacunae. The trabeculae of the medullary spongiosa contain some scarce remnants of calcified cartilage, but they are mainly formed of a lamellar tissue, intensely remodelled by repeated cycles of resorption and reconstruction.

RIBS

The juvenile rib appears entirely compact (Fig. 8a), with exception for some large cavities (up to 1.2 mm in diameter) localised in the medullary region. The periosteal cortex is remarkably thick, especially on the lateral side of the bone (off-centering of growth). Hence, the medullary region, clearly separated from the cortex by a very opaque layer of bone, does represent but a small fraction (20 to 23%) of the sectional area.
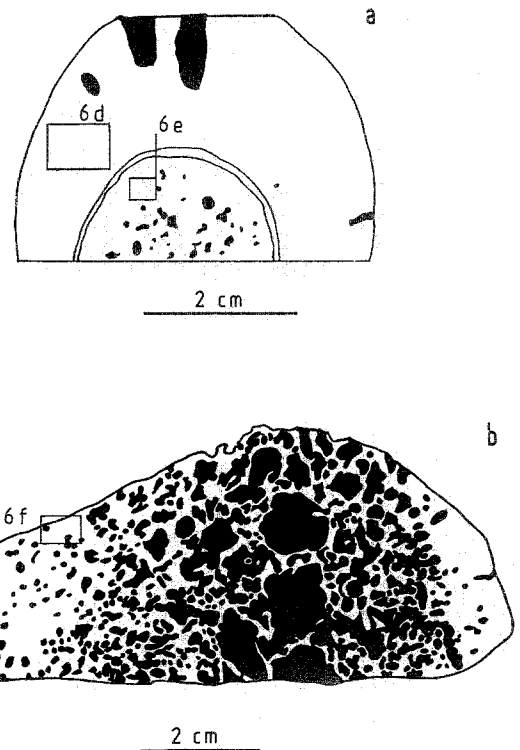
Figure 7 - General aspect of the cross sections in the humerus. a, juvenile ; b, adult. *Aspect général des coupes transversales d'humérus. a, juvénile. b, adulte.*

The histological nature of the cortex closely corresponds to the descriptions already given about the phalangeal and humeral cortices : the bone tissue is of the woven-fibered type, with an abundant plexiform vascularization including thin vascular canals bordered by centripetal deposits of lamellar or pseudolamellar tissues (primary osteons). The opaque line separating cortical and medullary territories corresponds to a thin layer of woven-fibered bone with a particularly high concentration of cell lacunae. This may correspond to the first periosteal deposition of bone around the original cartilaginous anlage of the rib (cf. Ørvig 1951). The histological characteristics of the medulla are also similar to those described in the vertebrae and the various appen-

Caractères histologiques des phalanges et de l'humérus chez les élasmosaures. a - Cortex périostique et médulla cartilagineuse dans la phalange juvénile. Lumière ordinaire transmise. b - Détail des travées primaires de la région médullaire. Les travées sont formées de cartilage calcifié recouvert de placages d'os endostéal pseudolamellaire. lumière ordinaire transmise. c - Travées endostéales remaniées dans la région médullaire d'une phalange adulte. Au moins deux cycles résorption et de reconstruction successifs sont visibles. Lumière polarisée. d - Cortex de l'humérus d'un spécimen juvénile. Le cortex est formé d'os "à fibres enchevêtrées", pourvu d'un abondant réseau vasculaire de type plexiforme. Lumière ordinaire transmise. e - Cartilage calcifié dans la médulla de l'humérus juvénile. Lumière ordinaire transmise. f - Cortex composé de tissu haversien dense chez l'adulte. lumière ordinaire transmise.
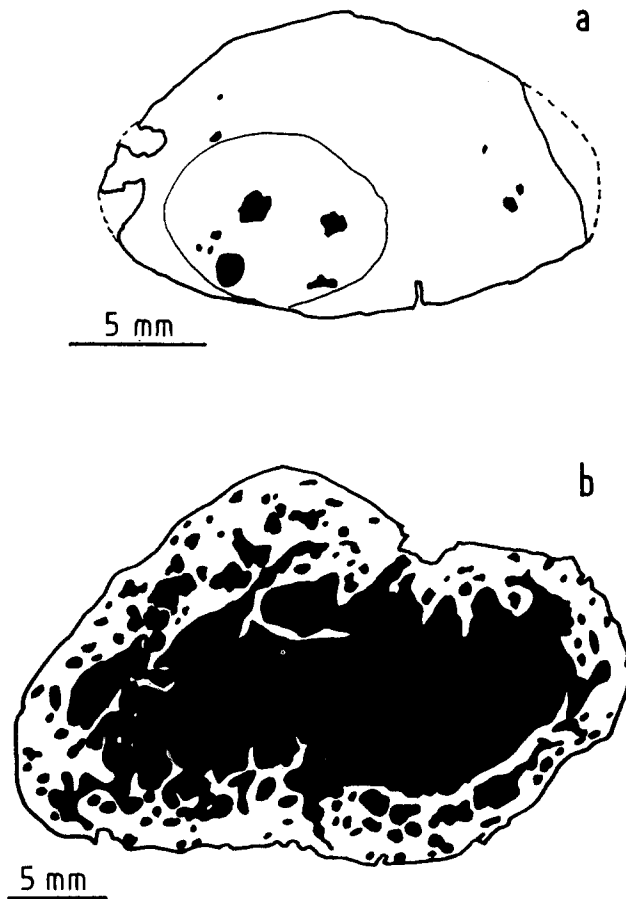
Figure 8 - General aspect of the cross sections in the ribs. **a**, juvenile ; **b**, adult. *Aspect général des coupes transversales de côtes.* **a**, *juvénile.* **b**, *adulte.*

dicular elements (calcified cartilage associated with "pipes" of endosteal pseudolamellar bone). Evidence of a resorptive activity, in the form of large erosion lacunae, is present, but less pronounced than in the diaphyseal medulla of the humerus.

In the adult (Fig. 8b), the general texture of bone is extremely cancellous, as in the other skeletal elements. In the central region of the diaphysis, the fusion of several large erosion lacunae creates a wide axial cavity with an irregular outline. Morphologically, this can be considered as a medullary cavity.

The cortical region is more or less spongy in texture (numerous resorption cavities scattered randomly), and made of a dense Haversian tissue displaying several subsequent generations of secondary osteons. In deeper territories, the trabeculae forming the spongiosa are composed of a complex set of endosteal platings, produced by an

intense, repeated activity of resorption and reconstruction.

DISCUSSION

PECULIARITIES OF BONE GROWTH : THE SHIFT FROM A PACHYOSTEOSCLEROTIC TO AN OSTEOPOROTIC-LIKE STATE.

The sections examined here suggest that the modalities of osteogenesis, as it occurred in the vertebrae, ribs and appendicular skeleton of the plesiosaurians, had certain original features that were not hitherto encountered among other groups of aquatic tetrapods.

The characteristics of bone structure in the juveniles fit exactly the definition of pachyosteosclerosis (cf. Domning & de Buffrénil 1991) : periosteal cortices are most often hyperplasic, whilst the medullary region is solid and compact. However, it is not quite obvious that all the bones of the skeleton shared the same peculiarities. The girdles seem to have had a rather unspecialized diploë structure (Wiffen pers. obs.). It is also to be kept in mind that, in the long limb bones and phalanges, the sections are at a metaphyso-diaphyseal level, not in the middle of the diaphyses. Hence, the presence of calcified cartilage at this level in our bone samples, though much more extensive than in "normal" bones, could be partly related to topographical reasons (relative proximity of the epiphyses).

The osteosclerotic features in the skeleton of the young plesiosaurians are exactly similar to the structural peculiarities described in the ribs, limbs and some skull bones of the sirenians (Fawcett 1942 ; de Buffrénil & Schoevaert 1988). As first demonstrated by Nopcsa & Heidsiek (1934), several other groups share the same specialization of bone structure, sometimes extended to the whole skeleton : various rachitomous and stereospondylous stegocephalians (de Ricqlès 1975a), mesosaurs (de Ricqlès 1974, 1975a,b.), champsosaurs (de Buffrénil *et al.* 1990), pachypleurosaurids (Zangerl 1935 ; Sander 1990), Cenomanian snake-like squamates (Nopcsa 1923b, 1925 ; de Buffrénil & Rage 1993), and even the primitive cetaceans (Basilosauridae), the ribs of which are highly pachyosteosclerotic (de Buffrénil *et al.* 1990a). In all cases, the peculiarities of bone structure arise apparently from the same cause : a steep inhibition of chondroclastic and, to a lesser extent, osteoclastic activities, which finally results in a delay or a deficit in endochondral bone differentiation. In the young plesiosaurs, the destruction of calcified cartilage by the

chondroclastic cells of the conjonctivo-vascular invasion front visibly ceased at an early stage. Nevertheless, some erosion lacunae were formed within the calcified cartilage, around the blood vessels. They were then filled up by endosteal deposits of pseudolamellar bone, which led to their nearly complete occlusion.

The histological features of the primary periosteal cortices reflect a high, sustained rate of periosteal bone accretion. Woven-fibered bone with a more or less typical plexiform-like or even radiating (*sensu* de Ricqlès 1975b) vascular network is indeed encountered in rapidly growing mammals with a large specific size (bovids, equids, etc.), and some fossil reptiles among the largest ones (especially dinosaurs ; cf. de Ricqlès 1976 a,b).

The most remarkable characteristic of plesiosaurian bone is the reversion from the pachyosteosclerotic condition of the juveniles to the osteoporotic-like condition that occurred in the adults. At a growth stage which cannot be specified, due to the small number of specimens available here, a considerable increase in resorptive activity took place, destroying not only the calcified cartilage still in place (as evidenced by the residues of this tissue present in the core of some medullary trabeculae), but also the newly-formed endosteal and periosteal bone deposits, as evidenced by the number of resorption lacunae dissecting the deep layers of compact cortices. This led to an osteoporotic-like state quite similar to that described in the dolphins or the ichthyosaurs (*int. al.* de Buffrénil 1990).

The abundance of resorption lacunae in the deep cortical regions, as well as the intense remodelling to which the trabeculae of the spongy formations were submitted, both suggest that the osteoporotic-like state of adult plesiosaurs probably resulted from a quantitative imbalance between the destructive (osteoclastic) and reconstructive (osteobastic) stages involved in bone remodelling. A similar mechanism has been described in cetaceans (de Buffrénil & Schoevaert 1988) and could have occurred as well in the ichthyosaurs (cf. de Buffrénil & Mazin 1990).

The possibility of a reversion in the pattern of osteogeny, which would turn a pachyosteosclerotic state into an osteoporotic-like one during ontogeny, has specific bearings on the interpretation of the determinisms of these states. Rather different hypotheses have indeed been proposed to explain the presence of osteosclerosis in aquatic tetrapods.

POSSIBLE CAUSES OF JUVENILE OSTEOSCLEROSIS.

According to the first hypothesis, mainly proposed in reference to the sirenians (de Buffrénil 1990 ; see also Fawcett 1942), osteosclerosis could reflect an osteopetrotic mutation, involving the skeleton in part or as a whole. Several types of such metabolic anomalies of bone are known among laboratory animals (see Johnson's synthesis 1986). They are due to the recessive mutation of diverse genes, the chromosomal localisation of which varies according to the type of osteopetrosis and the zoological group considered. However, in each case, the mutation seems to involve a single locus. The symptoms of mutational osteopetrosis are quite diverse, but all create a very compact structure of bone, related to the inhibition of chondroclastic and osteoclastic activities. The cytogenetical or histophysiological mechanisms of this deficiency remain poorly understood. It could possibly be due to a perturbation of clastic cells differentiation, or to an incompetence of these cells to answer to their local or systemic regulators (*int. al.* Marks & Seifert 1985 ; Marks & Popoff 1989). In response to adaptive requirements (especially foraging strategy and locomotory pattern) of the various taxa of aquatic tetrapods, a positive selection of these mutations could have occurred.

This hypothesis could eventually account for the presence of osteosclerosis in the young plesiosaurian specimens, but it does not seem relevant to explain the complex evolution of this character in the course of ontogeny.

The second hypothesis, already suggested by Nopcsa (e.g. 1923a) and developed by de Ricqlès (1975a, 1989) relies on a general interpretive frame which refers to the knowledge hitherto available about the heterochronic development (paedomorphism by neoteny) of the skeleton in some urodeles (for a definition of the terms used in the studies of developmental heterochrony, see Gould 1977 ; Alberch *et al.* 1979). This interpretation involves a rather complex cascade of physiologic and genetic determinisms.

It may be appropriate here to review first the data relevant to the immediate, physiologic, determinisms that may be involved, at the individual level, in the heterochronic development of the skeleton, and then to discuss how such a process could have a bearing on adaptive and phylogenetic issues.

In the tetrapods re-adapting to an aquatic habitat, the light, pressure and temperature constraints which characterise this medium have an influence on hypophyseal activity (via a direct action on the epiphyso-diencephalic complex), and tend to inhibit the production of thyreostimuline hormone (TSH), while the production of prolactine is conversely increased. The secretion of growth hormone (GH), which is involved in the control of dermo-periosteal ossifications, is but slightly modified, or can be increased, in this context.

Hence, the general endocrinian equilibrium of the organism is finally modified, with a level of circulating thyroxine (and perhaps also parathormone) more or less steeply reduced, and a level of calcitonine (produced by the activation of ultimobranchial body by prolactine), and perhaps also growth hormone, increased. Thyroïdian hormones have an activating effect on the basal metabolic level of the organism, and also on the clastic cells involved in the resorption of cartilage and bone. Conversely, calcitonin inhibits the activity of these cells. In reference to these elements, it can be admitted that the general endocrine terrain induced by the abiotic parameters of an aquatic habitat could explain the persistance of calcified cartilages (inhibition of chondroclasts activity), the consecutive regression of endochondral ossification, and, to a lesser extent, the hyperplasy of periosteal cortices (action of growth hormone). Such determinisms would exist in amphibians, where they were principally studied, but also in various groups of aquatic tetrapods with an osteosclerotic skeleton (see references in e.g. de Ricqlès 1975a, 1989).

In the amphibian taxa for which a developmental heterochrony is facultative, the constraints of an aquatic habitat have a direct, epigenetic action. Hence, their ultimate effect on e.g. skeletal structure may admit some lability (see discussion *in* Breuil 1992). Conversely, in the taxa for which a developmental heterochrony is not facultative (e.g. proteids and sirenids), it seems likely that one or several mutations of regulatory genes, with inhibiting or activating effects at any level of the cascade of factors controlling osteogenesis, have been positively selected during evolution, as a relevant answer to the adaptive requirements of life in water.

It is noteworthy that this genetic control of a paedomorphic skeletal development could well be, within a given taxonomic lineage, evolutionary subsequent to an initial stage at which the deter-

minism of this developmental pattern was essentially epigenetic (Baldwin effect). This would by no means involve a Lamarckian interpretation, but a shift (towards paedomorphy) in the genetic program of skeletal development, by means of a genetic selection under definite selective pressures from the aquatic habitat.

In its main aspects, this hypothesis could account rather well for the observations made herein, whether bone osteosclerosis of the juveniles is considered as an epigenetically-derived (purely somatic) heterochrony of skeletal development, or as the result of a (more probable) genetic evolution. The action of epigenetic factors only (especially the thermic constraints of sea water), acting specifically on juveniles in relation, for example, to their small body mass and limited thermal inertia, seems to be possible, but would have to face some contradictory elements. Indeed, the rapid periosteal accretion visible on most bones suggests that the growth rate of the juveniles, and perhaps also their metabolic activity, were high and sustained (*int. al.* de Ricqlès 1972, 1976a). In this respect, the hypothesis of e.g. a systemic thyroïdian deficiency would seem unlikely.

Conversely, the hypothesis of an evolutionary modification of the program controling the timing of skeletal development might seem more easily acceptable. Within this frame, one could suppose that the new programm would integrate a complex information involving an early inhibition, followed by a later increase, of clastic cells activities, the whole pattern taking place on the background of a high growth rate of the body.

It is noteworthy that the hypothesis of heterochronic mechanisms for explaining the peculiarities of bone in the juvenile plesiosaurs would also integrate a complementary aspect, dealing with phylogenetic trends within the Plesiosauria, which will be discussed in the following section.

PHYLOGENETICAL CONSIDERATIONS

The most generalized, or plesiomorphic, Plesiosauria are supposed to be the pistosaurs, from the Upper Muschelkalk (Middle Triassic). They represent a transition with the paraphyletic grade of primitive Triassic sauropterygians, collectively designated under the term nothosaurs. The latter are supposed to have had an amphibious, but mainly aquatic, habitat in neritic zones (*int. al.* Saint-Seine 1955 ; Mazin 1988). Among these forms, pachyosteosclerosis has been re-

cognized and described histologically in several genera : e.g. *Pachypleurosaurus, Seresiosaurus, Neusticosaurus, Proneusticosaurus*, all being relatively small forms (see. *int. al.* Nopcsa & Heidsieck 1934 ; Zangerl 1935 ; Sander 1990 ; de Ricqlès 1992). This structural specialization of the skeleton can be understood as a skeletal paedomorphosis, at the histological level. Indeed, the "ontogenetic trajectory" of the endoskeleton is not completed, due to the relative retardation of endochondral ossification. Hence, according to the terminology of Alberch *et al.* (1979), the morphological condition (paedomorphosis) would be the result of a neotenic process.

There is a very close histological similarity between the Triassic nothosaurs and the Upper Cretaceous juvenile plesiosaurs and pliosaurs described above. This similarity obviously involves the osteosclerotic state of endochondral ossification, and the pachyosteotic hyperplasy of periosteal cortices. In this respect, the ontogenic trajectory of skeletal histogenesis in our Cretaceous sauropterygians could readily be interpreted as an excellent example of "recapitulation", as defined by Alberch *et al.* (1979). Indeed, the juvenile individuals of the advanced forms would reproduce, during their ontogenetic development, structural stages which were those of adults in the primitive forms of the lineage. Later on, the end of their ontogenic development would be characterized by the final addition of a new, original stage in their developmental program, not present in ancestral forms.

An alternative to this scenario would be to consider a phenomenon of evolutionary parallelism : i.e. the original ontogenic trajectory of the Upper Cretaceous forms, especially the strong pachyosteosclerosis of the juveniles, would itself be an evolutionary novelty, derived from immediate ancestors with a "normal" (non-pachyosteosclerotic) development. Hence, this specialization would have been acquired recently, without close relationship to the one (though identical) already present in Triassic nothosaurs. This hypothesis is plausible, if one takes into account the important geological durations involved, and the frequent recurrency of pachyosteosclerosis among tetrapods secondarily adapted to life in water (at least, in the early stages of this adaptation). Moreover, it could be possible to test this hypothesis, since paleontological material from the Upper Jurassic or Lower Cretaceous would allow a reconstruction of the ontogenic trajectory of the closer ancestors of our Upper Cretaceous fossils.

Nevertheless, in the absence of such material, the structural descriptions given by previous authors (see Introduction) give a reasonable term of comparison between early (Early or Middle Jurassic) and late (Late Cretaceous) plesiosaurians. Two main differences distinguish the structural characteristics of bone between these two groups: 1) The rate of periosteal accretion seems much higher in the Late Cretaceous forms. Moreover, the evidence of a cyclicity in growth rate is very faint in these animals, whereas it is quite obvious in the Jurassic specimens. A rapid periosteal accretion would thus be a derived condition. 2) Remodelling activity (occuring either as Haversian substitution or as a superficial remodelling of the medullary trabeculae) is more pronounced in the Late Cretaceous forms, with a typical imbalance between resorption and reconstruction leading to a cancellous structure of periosteal cortices. This would also be a derived condition. Conversely, the persistance of calcified cartilages in the juvenile skeletons would have been already present (though less spectacular) in *Plesiosaurus*, as shown by Kiprijanoff's ilustrations. Hence, this would indeed represent a primitive (plesiomorphic) condition.

These elements would suggest that the more parsimonious hypothesis remains, for the present, that of a historical continuity of a specialized ontogenic trajectory, which would be maintained, for some of its aspects (histological paedomorphosis with extensive and protracted persistance of calcified cartilages), within the Sauropterygia, from the Triassic up to the Late Cretaceous. In spite of the geological durations involved, the persistance of such a specialization is likely : among sirenians, the specialized histogenesis of the skeleton appears to be one of the most constant characteristics of the clade (*int. al.* Savage 1976).

In this measure, the Late Cretaceous plesiosaurs would have retained, and even increased, during their juvenile stages of growth, a specialized pattern of skeletal development already present in the early plesiosaurids and their nothosaurian ancestors (histological paedomorphosis in endoskeletal development). But they would have added to this pattern two derived conditions : a rapid postnatal growth, which would be consistant with their large size ; and a considerable increase in bone resorption during the late stages of somatic growth.

However, if one takes into account the probable functional consequences of a pachyosteosclerotic state of the skeleton on the various ecological characteristics of the taxa, especially their locomotion and equilibration in water (see below), it seems hardly relevant to exclusively interpret the ontogenic trajectory of skeletal development in

the Upper Cretaceous forms as a consequence of "phylogenetic constructional constraints", which would be imposed to their developmental pattern, with no reference to adaptive considerations (e.g. de Ricqlès 1992, 1993). The geological durations involved are indeed so important, that natural selection must have had a bearing on all developmental aspects. Hence, the peculiar ontogenic trajectory of the Upper Cretaceous forms must have also met definite selective constraints ; in other words, it is consistent with a peculiar, ecological adaptation. At first glance, the histological characteristics of the skeleton in the juveniles would suggest a poor mobility in animals living in a neritic habitat ; conversely those of the adults would be consistant with good swimming abilities in open seas.

Hence, the "recapitulation" observed at a histological level could actually be an indirect expression (and the evidence) of a biologically much more significant recapitulation, with an eco-ethologic significance, which would bear on the developmental cycle of the animals. The young plesiosaurs would have retained a "plesiomorphic" way of life, as compared to the adults of their own species, which would be reminiscent of their very ancient ancestors : the neritic nothosaurs. This hypothesis will be developed with a different approach in the following section of the discussion.

FUNCTIONAL CONSIDERATIONS

The pachyosteosclerotic condition of the juveniles, undoubtedly increased the mass of the skeleton and, as a consequence, the inertia of the body moving in water. This most probably led to a drastic limitation of the swimming speed, and capabilities of the animals to perform rapid manoeuvres (acceleration, slackening, short-radius turning, etc.), since these characteristics of aquatic locomotion are directly influenced by body inertia (cf. Webb & Skadsen 1979 ; Webb & de Buffrénil 1990). Conversely, pachyosteosclerosis may have facilitated a hydrostatic (passive) regulation of body trim. As already mentioned (cf. Introduction), this morpho-functional adaptation of the skeleton is mainly present in shallow water animals (or animals supposed to have been so in the case of fossils), more or less strictly confined to regions of estuaries, zones of undertow, or intertidal limits. In reference to these comparative elements, it seems rather plausible to conclude that, during a juvenile stage (the duration of which cannot be assessed precisely here), plesiosaurians lived in shallow coastal waters, and did not enter the high sea. Moreover, they might have fed upon fixed organisms or non-elusive prey.

This conclusion, based on histological evidence, would be in close agreement with some aspects of the taphonomical interpretation of the Mangahouanga Stream site proposed by Wiffen & Moisley (1986). These authors indeed hypothesize that the shallow water, coastal and/or estuarine environment once present locally (for description of Mangahouanga Stream paleoenvironment, see Crampton & Moore 1990) would have been a convenient breeding ground for plesiosaurians ; a hypothesis which would explain the rather high proportion of juvenile specimens in the fossil record from this site.

Conversely, adult bone structure typically corresponds to that of large, pelagic predators, well "designed" for long cruises in open waters (cf. Introduction). Hence, a drastic change in habitat preferences and eco-ethologic adaptations most probably occurred during ontogeny in the plesiosaurs. It is also possible that this change was correlative of physiological modifications of the animals, bearing especially on their thermal regime. In *Dermochelys coriacea*, the progressive increase of body volume during growth leads to some type of endotherm-homeotherm-like physiology in the adult (mass endothermy or gigantothermy ; cf. Frair 1972 ; Rhoding *et al.* 1981 ; Paladino *et al.* 1990). One can hypothesize that the huge specific size of the adults in the two taxa studied here, led also to this type of thermal regime, and contributed to an improvement of the capabilities of the animals to resist heat loss by conduction in an open sea habitat.

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