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Morphogenesis of Bone Ornamentation in Extant and Extinct Crocodilians

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Summary. Histological study of bone in the skull and osteoscutes of extant and extinct Crocodylia reveals that the skeletal ornamentation of crocodiles is caused by a process of differential, superficial resorption of bone. A partial reconstruction follows the resorption, and several resorption-reconstruction cycles are necessary to suit pit dimensions to overall bone growth. Bone ornamentation is a dynamic structure during ontogeny: the shape and the location of a given pit or groove vary in accordance with the instantaneous regional trends of skeletal growth. This supports the contention that bone ornamentation can be used as a reliable indicator of regional bone growth trends.

Introduction

A pattern of bone ornamentation consisting of grooves and circular or polygonal pits is found mainly in poikilothermic amphibious tetrapods. The skull roof and osteoscutes of the labyrinthodonts (sensu Lehman 1955; i.e. Temnospondyli and Anthracosauria), crocodilians, and numerous cotylosaurs (Captorhinidae, Pareiasauridae) frequently bear such pits and grooves. These are also found (but less frequently) amongst chelonians, pelycosaurs (especially in the genus *Cotylorhynchus*), thecodonts, and squamates.

Existing data on the morphogenesis of this kind of bone ornamentation are scare and imprecise. The classic works of Bystrow (1935, 1947) on the skull bones of labyrinthodonts revealed the possible relationship between the local rate of bone growth and the morphological characters of the ornamentation. In particular, the presence of grooves in the periphery of the dermal bones was considered by Bystrow (1935, 1947) to be a result of a high, local growth rate of these bones. Although this interpretation is accepted by some authors (e.g. Lehman 1955; Piveteau 1955), it remains largely intuitive, insofar as it does not rely on a precise study of the osteogenic causes of bone ornamentation.

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On the other hand, various authors have tried to explain the presence of bone ornamentation by functional considerations referring either to cutaneous respiration (Bystrow 1947) or to mechanical properties of the skull (e.g. Fox 1964; Coldiron 1974). In both cases, the morphogenesis of the ornamentation is not taken into account, although it constitutes a prerequisite to any functional interpretation.

The present work deals with an anatomical and histological study of bone ornamentation in various extant and extinct crocodilians. Its aim is to investigate the nature of the osteogenic mechanisms which may be directly responsible for the formation of pits and grooves, as well as the possible relationship between the local trends of bone growth and the morphological features of the ornamentation.

B. Materials and Methods

Observations of the anatomical characters of bone ornamentation were made on specimens in the osteological collections of the Muséum National d'Histoire Naturelle, Paris (Laboratoire d'Anatomie Comparée). Several different sized specimens of all recent crocodilian species (except *Crocodylus johnstoni* and *Crocodylus novaeguinae*) were studied in these collections.

The investigation on the histological structure of bone ornamentation was based on ground sections of dry bone (80–150 µm thick), viewed in ordinary and polarized light. These sections were taken from the frontal bone, parietal bone, and osteoscutes of several extant and extinct taxa. The recent forms studied were *Crocodylus niloticus* (five skulls with snout-supraoccipital lengths ranging from 75 to 495 mm), *Crocodylus moreletii* (one skull, snout-supraoccipital length 280 mm), *Crocodylus siamensis* (one skull, snout-supraoccipital length 268 mm). The fossil material consisted of the frontal bone and cranial table (i.e. parietal, postorbitals, squamosals, and supraoccipital) of one *Crocodylus affinis* (Yale Peabody Museum no. 511) from the Middle Eocene Bridger beds of Wyoming (see de Buffrénil and Buffetaut, 1981), the rear parts of the skull and several osteoscutes of two individuals of *Diplocynodon* from the Lower Miocene of Saint-Gérand-le-Puy, France (Muséum National d'Histoire Naturelle, Paléontologie no. 1960-8), and two osteoscutes of undetermined eusuchians from the Eocene beds of Wyoming (Yale Peabody Museum no. 1353–879).

C. Results

Anatomical Characteristics of Bone Ornamentation in Eusuchian Crocodilians

Anatomical characteristics of bone ornamentation are rather similar in all extant and fossil taxa of the suborder Eusuchia. Ornamentation is mainly located on the external surfaces of: (a) the osteoscutes, (b) the dermal bones of the skull roof, (c) the lower jaw. It is never present on the internal surfaces of these elements.

Ornamented bones and osteoscutes are present along the dorsal surface of the crocodilian body, from the snout to the base of the tail, and on the lateral side of the lower jaw. However, in animals where a ventral shield exists (more frequent in fossil than in recent eusuchians), its osteoscutes are also ornamented.

Bone ornamentation does not appear immediately after birth. Anatomical observation of 26 *C. niloticus* skulls in the collections of the Muséum National

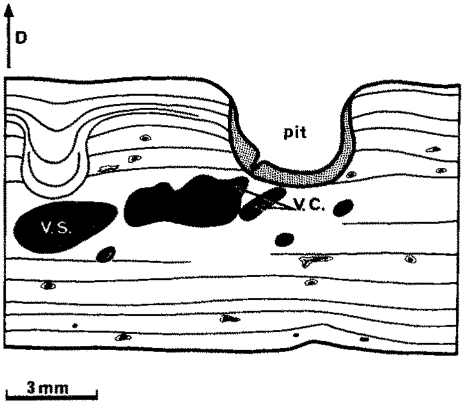

Fig. 1. Schema of the vascularization of a pit in an osteoscute (undetermined crocodilian from the Eocene of Wyoming). *Dark dotted areas:* secondary haversian bone; *light dotted area:* bone deposited at the bottom of the pit; *D:* dorsal direction; *v.c.:* vascular canal; *v.s.:* vascular sinus. The vascular canals and vascular sinus indicated in this example have the structure of secondary osteons (i.e. 'haversian canals'). The *thick black lines* surrounding them thus represent cementing lines

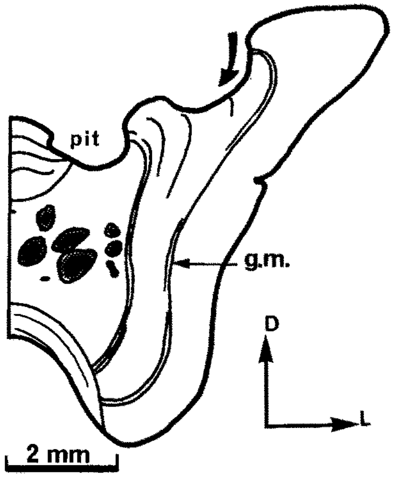

Fig. 2. Schema of the cross section of the frontal bone of a young *C. niloticus* (snout-supraoccipital length = 120 mm). The pits appear as simple notches in the bone cortex. *Dotted areas:* secondary haversian bone; the *bent arrow* symbolises the resorptive process; *D:* dorsal direction; *g. m.:* growth mark; *L:* lateral direction

d'Histoire Naturelle, Paris, shows the absence of clearly characterized ornamentation on skulls less than 100–120 mm long. When ornamentation appears, it is first located on the bones of the cranial table (i.e. parietal, squamosals, and postorbitals), on the jugals and on the anterior third of the snout (premaxillaries and rostral ends of the maxillaries). When size increases, ornamentation spreads to include the frontal bone and the entire surface of the snout (see also Mook 1921).

Morphologically, crocodilian bone ornamentation consists of polygonal or subcircular pits separated by a continuous network of ridges (Fig. 3c), the degree of development of which varies regionally. On the snout (premaxillaries, maxillaries) the degree of development of the ridges is reduced compared with other skull territories. The dimensions of the pits increase during ontogeny and seem proportional to the size of the animal. In skulls of *C. niloticus*, the average diameters of the frontal pits are: 1.5 mm on a skull 145 mm long, 3.5 mm on a skull 270 mm long, and 6 mm on a skull 495 mm long.

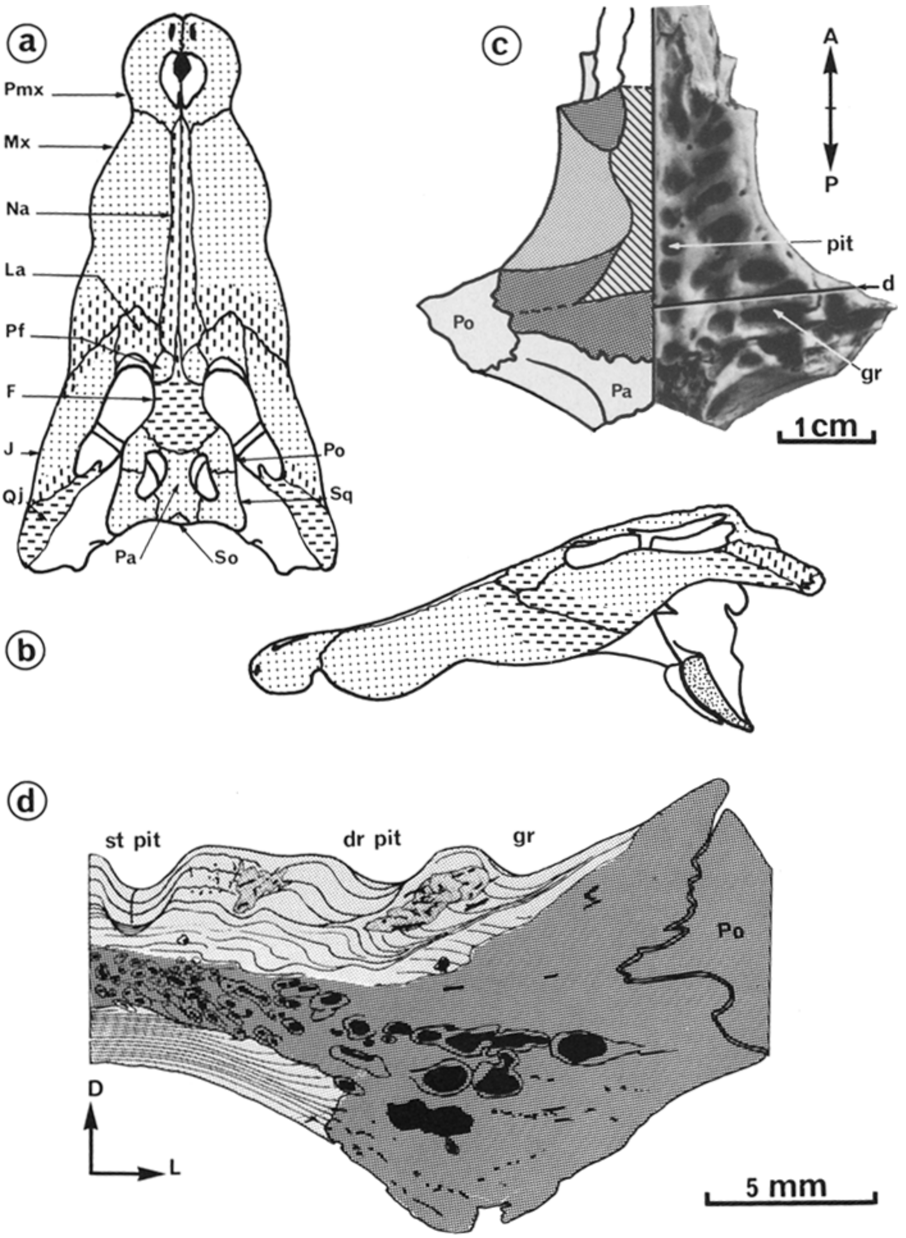

Fig. 3a, b. Localisation of pits and grooves on the dermal skull of crocodilians. *Points* indicate the pits; *broken lines* indicate the grooves and their orientation; **a** dorsal view; **b** lateral view (left side). **c** Frontal bone of *C. moreletii. Right half:* dorsal view of the bone showing pits and grooves (the segment '*d*' indicates the localisation and direction of the cross section represented in Fig. 3d). *Left half:* bone tissues composing the frontal. *Hatched area:* remodelled bone; *dark dotted area:* bone deposited by sutures; *light dotted area:* subperiosteal lamellar-zonal bone. **d** Schema of a cross section in the frontal of *C. moreletii.* Same symbols as in '*c*'. *A:* anterior direction; *D:* dorsal direction; *dr. pit:* drifting pit; *F.:* frontal bone; *gr.:* groove; *J.:* jugal bone; *L:* lateral direction; *La.:* lacrimal bone; *Mx.:* maxillary bone; *Na.:* nasal bone; *Pa.:* parietal bone; *Pf.:* prefrontal bone; *Pmx.:* premaxillary bone; *Po.:* postorbital bone; *Qj.:* quadratojugal bone *So.:* supraoccipital bone; *Sq.:* squamosal bone; *st. pit.:* pit with stable position

Apertures of large vertical vascular canals, the centrocupular canals, emerge at the centre of the pits. There is generally a single large vascular canal in the pits of the skull, and two in those of the osteoscutes.

Pits may become elongated to form short grooves in certain clearly defined regions: (1) peripheral areas of the osteoscutes: radial groove elongation; (2) base of the snout (region of maxillary-jugal and maxillary-lacrimal sutures): antero-posterior elongation; (3) nasal bones: antero-posterior elongation; (4) frontal and quadratojugal bones: Lateral elongation; (5) extremities of the jugal bones: antero-posterior elongation; see Fig. 3a, b, c). On a single skull, grooves are rarely visible in the five regions altogether; moreover, amongst individuals of a specific population, groove ornamentation is not consistently present in a given cranial region. However, in *Gavialis gangeticus*, the frontal and the snout bones in all the specimens studied bore a groove ornamentation.

2. Histological Appearance of Bone Ornamentation in Crocodilians

a) Histological Structure of the Osteoscutes and Dermal Bones. Osteoscutes and dermal bones in the Crocodylia consist of lamellar-zonal bone tissues (Fig. 4: a3, b3, c3, d). These tissues, widely distributed amongst poikilothermic tetrapods (e.g. Enlow 1969; Enlow and Brown 1957; de Ricqlès 1975, 1976, 1979), can be recognised by the regular spatial organization of their collagenous meshwork (when observed in polarized light) and by the presence in them of cyclical growth marks, 'zones' and 'annuli' (see also Castanet et al. 1977; de Buffrénil 1980a, b). Vascularization of crocodilian lamellar-zonal bone tissues is dense and arranged as simple vascular canals and primary osteons forming vascular sheets superimposed upon each other.

b) Structural Characteristics of Bone Ornamentation. The centrocupular canals correspond to primary or secondary osteons[1], the diameters of which range from 200 to 600 µm. These vascular canals are diverticles of large horizontal or oblique vascular sinuses located in the depth of the bones and showing the remodelled structure of secondary osteons (Fig. 1). Bone ornamentation of *Platyops watsoni*, a labyrinthodont from the Permian of Eastern Europe (Bystrow 1947), shows a vasular supply very similar to that of the crocodilians.

In their simplest state, the pits and grooves appear as notches (that is localized absences of bone) affecting the outer layers of the compact cortical bone (Fig. 2). Every pit or groove causes an abrupt cut in the local bone structure, suggesting that the ornamentation results from a process of localized resorption of the bone surface. The ridges separating the pits thus represent remnants of the original bone understroyed by the pit resorption (see Fig. 4d).

In young individuals, all pits and grooves have the above structure, suggesting that their morphogenesis relies entirely on a resorptive process. In older individ-

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[1] Primary and secondary osteons are sheaths of bone tissue surrounding the intrinsic blood vessels of bone. The former are centripetally deposited around the blood vessels at the periphery of the bones during skeletal growth. The latter (also called 'haversian canals') arise from the inner remodelling of the bones. Their deposition follows a process of local perivascular bone resorption, and they are also deposited centripetally as very regular bone lamellae; see e.g. de Ricqlès 1976

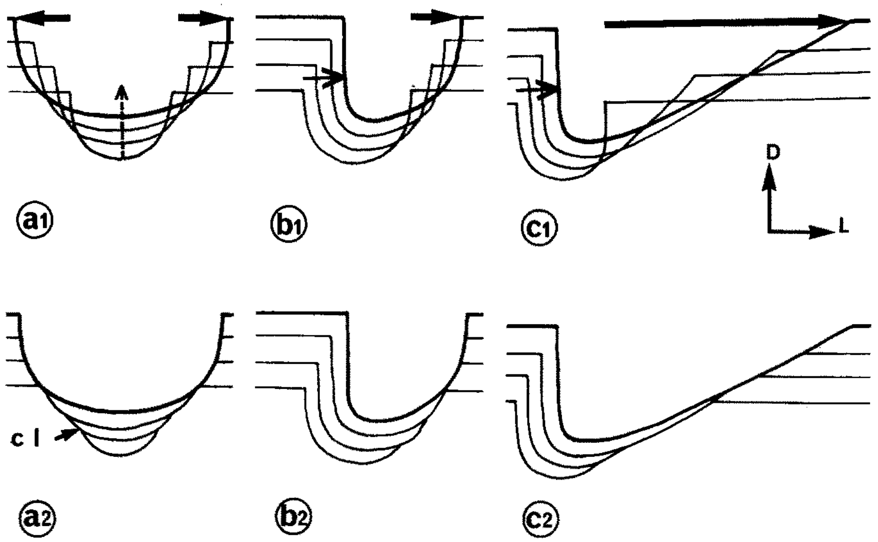

Fig. 4. Dynamic characters of bone ornamentation. *a1, a2, a3*: Morphogenesis of a pit, the position of which is stable and the diameter of which increases during ontogeny; *a1*: growth pattern of the pit; *a2*: schema of the histological aspect of this pit; same pit in the frontal of *C. affinis* (YPM. 511), thin section in transmitted light. *b1, b2, b3*: Same demonstration as for 'a', but applied to a drifting pit; *b3*: drifting pit in the parietal of *C. affinis*, thin section in transmitted light. *c1, c2, c3*: Same demonstration applied to a groove; *c3*: groove formation in the frontal of *C. affinis*, thin section in transmitted light. *d*: Ornamentation in the frontal bone of *C. affinis*, thin section in transmitted light. In all figures, *thick arrows* indicate resorption; *thin arrows* indicate reconstruction. Same abbreviation as in Fig. 3; c.l.: cementing line; *fi. pit*: pit filled by subperiosteal deposition; *ri.*: ridge

uals however, the simple, localized resorption of the bone surface is principally seen at the distal end of the grooves, particularly in the peripheral areas of the bones (Fig. 4d). In these cases, the site of active bone resorption is far from the centrocupular canal which is located at the proximal end of the groove.

In the central areas of the frontal and parietal bones of medium and large specimens, the histological structure of the ornamentation is more complex. On transverse sections, layers of bone tissue, distinctly demarcated from the rest of the bone by cementing lines[2], can be seen at the bottom of numerous pits (Fig. 4: a3, b3). The presence of such cementing lines indicates that these bone layers are secondarily deposited at the bottom of the pits after the resorptive process has ceased. They partially reconstruct the bone cortex after local resorption and they grow upwards, in a dorsal direction, as indicated by the orientation of their lamellae. In the frontal and parietal bones of adult specimens of *C. niloticus* and *C. moreletii*, the strata of bone deposited at the bottom of the pits are frequenly covered by a sheet of primary subperiosteal bone spreading at the surface over pits and ridges.

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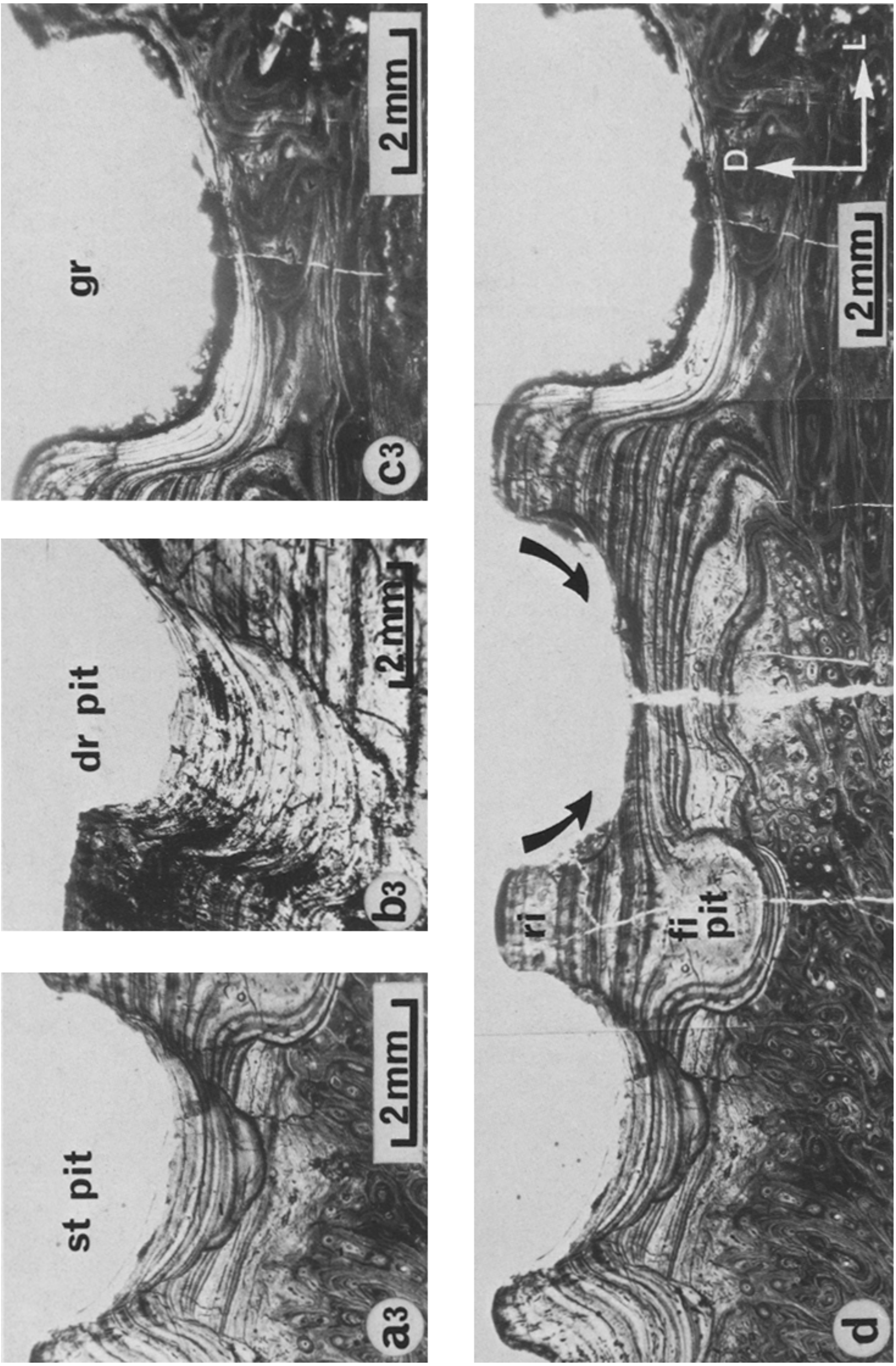
[2] In ground sections of bone, the cementing lines (or 'resorption lines') referred to here appear as obvious lines separating two masses of bone tissues, which are generally different from one another in their gross spatial orientations. Cementing lines indicate the limits of an ancient resorptive process, which has been followed locally by the deposition of new (or 'secondary') bone; see e.g. de Ricqlès 1975 for discussion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As a general rule, in peripheral areas of the frontal and parietal bones the secondary reconstruction of pits and grooves is asymmetrical, occurring only at the medial side of the pits and the medial (proximal) end of the grooves. In these cases, secondary reconstruction progresses in lateral or dorso-lateral directions (Fig. 4: b3, c3).

c) Dynamic Characters of Bone Ornamentation. Since the bones of crocodilians are poorly remodelled (e.g. Enlow 1969; Enlow and Brown 1957; de Ricqlès 1976), ontogenic modifications of the ornamentation are recorded in the inner structure of bone as patterns of resorption, reconstruction, and primary rapid or slow depositions. The inner structure of the frontal and parietal bones enables the recognition of the main spatio-temporal variations in bone ornamentation.

During ontogeny, the anatomical position of a pit may remain fixed or it may drift. In the first case, the pit lies vertically on top of the sheets of bone deposited at its base. This stable position of pits is found most frequently in the central territories of the frontal and parietal bones (Fig. 4: a3, d). In the latter case, the sheets of bone deposited at the bottom of a given pit are gradually displaced throughout the thickness of the bone (that is at the various stages of bone growth); so that the most superficial sheets, immediately underlying the pit, are the most lateral (Fig. 4: b3).

In most cases, several cementing lines of increasing length are seen in the bone layers deposited at the bottom or on the medial side of the pits and grooves. These lines correspond to successive increases in the diameter of the pit, from the depth of the bone to its periphery (Fig. 4: a3).

Some pits progressively disappear, being filled by a local intense accretion of subperiosteal bone tissue.

d) Interpretation of Histological Results. The structural details of bone ornamentation in the Crocodylia suggest a general interpretation, integrating these details with a plausible causal relationship.

Pits are first initiated by the localized, superficial resorption of the bones, as can be seen in young individuals and in the peripheral (most recently formed) areas of the bones of older specimens. A partial reconstruction follows the resorption, the bone thus deposited being separated from the primary bone tissues by cementing lines. In the central areas of the frontal and parietal bones, the reconstruction progresses outwards and seems to have the practical result of maintaining a constant depth to the pits by compensating for the increase in height of the ridges (Fig. 4: a1, a3). In peripheral areas of the same bones, the reconstruction progresses in lateral or dorso-lateral directions.

The presence of several cementing lines of increasing dimensions in the bone sheets deposited at the bottom of the pits indicates that, during skeletal growth, pit dimensions are constantly adapted to skull size by several resorption-reconstruction cycles. The osteoclasts responsible for bone resorption thus appear to act in a discontinuous manner; their activity pattern being governed by a complex programme which integrates the general increase of skeletal dimensions. During ontogeny, some pits are rapidly filled and disappear.

In the lateral regions of the frontal and parietal bones, the position of the pits is subject to progressive spatial drift, directed to the lateral margins of these bones. In this case, the reconstruction also progresses in a lateral direction and is located on the medial side of the pit, opposite to the side affected by resorption (Fig. 4: b1, b3). It seems plausible to hypothesize that the spatial drift of the ornamentation is linked to a shifting of the osteoclasts and osteoblasts responsible for the superficial resorption and reconstruction of the bone surface. Depending upon the intensity of the resorptive drift and the rate of reconstruction, two main consequences may occur: (a) if the resorptive shifting is slow and entirely compensated for by reconstruction on the opposite side of the pit, then the pit does not change its shape and is simply displaced laterally during growth (Fig. 4: b1, b2, b3); (b) if the resorptive shift is rapid and reconstruction is slower, then the pit gradually turns into a groove with a distal (lateral) end undergoing resorption, and a proximal (medial) end undergoing reconstruction (Fig. 4: c1, c2, c3). The two ends move in the same lateral direction, but at different speeds, which leads to their relative relocation and a lengthening of the groove in a lateral direction.

Another consequence of this process is an increase in the distance between the centrocupular canal and the site of active resorption. It can be argued that the osteoclasts responsible for the resorption probably result from a temporary, local differentiation of periosteal cells and would not arise from the intrinsic, inner blood supply of the bone.

D. Discussion

The results of the present investigation suggest that the ornamentation of crocodilians is primarily formed by the differential resorption of the bony surface. It is also possible that, at the same time, a preferential subperiosteal deposition occurs on top of the ridges, thus enhancing the convex reliefs of the ornamentation. The latter mechanism was recognized in labyrinthodonts by Bystrow (1935) and de Ricqlès (pers. comm.), and may exist as well in certain squamates (Castanet, pers. comm.). However, such a preferential growth of the ridges would play a minor role, if any, in the morphogenesis of crocodilian ornamentation. The difference in ornamentation morphogenesis between crocodilians and labyrinthodonts could be related to the fact that bone ornamentation has been acquired independently by the former and is not inherited from the ancestors of the lineage (Kälin 1955): bone ornamentation of the Crocodylia is thus analogous, but not homologous, to that of the other poikilotherms, especially the labyrinthodonts.

The frontal bone of crocodilians, bearing both pits and grooves, makes it possible to study the relationship between the local, morphological characteristics of the ornamentation (pits or grooves) and the regional trends of skull growth.

Morphometric studies of the growth of the frontal bone in various crocodilians (Dodson 1975, for *Alligator mississipiensis*; Webb and Messel, 1978, for *Crocodylus porosus*; see also Mook 1921; Kälin 1955; Kramer and Medem 1955) have revealed a strong positive allometry in the lateral expansion of this bone relative to other cranial dimensions.

Moreover, the shape of the frontal bone changes during ontogeny. In very young specimens, the frontal bone is long and narrow; it becomes relatively shorter and wider as the skull grows. This preferential widening of the frontal seems to correspond to an intensive subperiosteal accretion on its lateral margins; the lengthening of the bone being caused by a slower osseous deposition at the frontal-prefrontal and frontal-parietal sutures (Fig. 3c; see also Buffrénil 1980c). The rapid lateral drift of the resorption of bone surface, interpreted as the morphogenetic cause of the grooves, thus appears to follow the direction of the preferential growth of the frontal, and is located in the places where bone deposition is most active.

In a given species, the main morphogenetic trends of the frontal bone are identical for all individuals and seem to be fairly constant during ontogeny (see in particular Webb and Messel 1978). However, as already stated, the presence of grooves on this bone is not general in all specimens (except in *Gavialis gangeticus*). This apparent contradiction can be explained by the characteristics of ornamentation morphogenesis. These involve various factors: i.e. local growth rate, duration of osteoclastic activity, and extent and speed of the reconstruction. Consequently, in a given skeletal territory, a high rate of growth, a prolonged osteoclastic activity and a slow reconstruction will produce very clear and extensive grooves (probably the case in *C. moreletii* frontal bone). Conversely, a decrease of the first two factors or an increase in the third will reduce the clarity and length of the grooves. Groove formation can thus be seen as a gradual phenomenon insofar as it depends on a multifactorial causality, the different elements of which are antagonistic and protagonistic; and all of which can act with different degrees of intensity. Groove formation equally appears as a facultative morphological result because, even irrespective of their intensity, the three main factors which cause it may not always be synchronous in the various regions of a single skull, and among individuals at the same level of ontogenic development. However, despite these elements of variability, the morphogenesis of the ornamentation seems to be basically related to the instantaneous, local intensity of bone growth. It can be thus stated that grooves, when present, indicate a relatively high, local growth rate, and their orientation, the direction of this growth. These considerations agree well with Bystrow's main conclusions (1935) and justify the use of bone ornamentation to study skeletal growth.

Morphological characteristics of bone ornamentation in the skull of crocodilians suggest that three territories undergo preferential growth during ontogenv (Fig. 3a, b): the frontal bone (lateral growth), the snout (antero-posterior growth), and the quadratojugal bones (lateral growth). Data on the skull growth in crocodilians (Mook 1921; Kälin 1955; Kramer and Medem 1955; Dodson 1975; Webb and Messel 1978) indicate that these regions during ontogeny show a positive allometry relative to skull length. Moreover, Webb and Messel (1978) stressed that these different allometries are not synchronous during life, a fact which supports our interpretation of the presence or absence of grooves.

Lastly, ornamentation characteristics suggest that the preferential growth of the snout is mainly located in the proximal region, that is, on both sides of the maxillary-jugal and maxillary-lacrimal sutures.

E. Conclusion

Numerous aspects of bone ornamentation morphogenesis remain to be studied; in particular the origin, location, and precise action of the osteoclasts responsible for the localized resorption of bone surface.

Although bone ornamentation in extant and extinct tetrapods superficially shows very consistent anatomical features, detailed studies remain to be performed for each discrete group. However, it seems very likely that the local growth of a bone and the nature of its ornamentation have a general relationship to each other in all taxa where bone ornamentation is well characterized. Also, if the morphogenesis and the anatomical characteristics of bone ornamentation do not reveal the precise function of the latter, they must nevertheless be integrated into any functional interpretation.

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