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Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica

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Abstract. Ankylosaurian remains from the Late Cretaceous (Campanian) Santa Marta Formation of the James Ross Island in the Antarctic Peninsula include several types of armour, the most abundant being tiny, button-like ossicles (less than 5 mm in diameter). An histological study of these small ossicles evidences an original tissue structure. We notice the very small amount of vascularisation and of bone remodeling. Some structural aspects strongly suggest a direct (metaplastic) mineralization of the preexisting *stratum compactum* of the dermis. However, some contradictory evidences support instead the hypothesis of the structures originating *de novo* at the limit of the *stratum compactum* and *stratum spongiosum* of the dermis and experiencing further growth via neoplasy.

Keywords. Ankylosauria. Late Cretaceous. Antarctica. Dermal armour. Histology.

Introduction

In 1986, ankylosaurian remains were discovered in the vicinity of the Santa Marta Cove on James Ross Island, at the northern tip of the Antarctic Peninsula. This was the first dinosaur to be found in Antarctica (Gasparini *et al.*, 1987). The material, a partial skeleton of a small single individual, was recovered from shallow marine Late Cretaceous (Campanian) deposits of the lower Gamma Member of the Santa Marta Formation, in the lowermost part of the Marambio Group (Olivero *et al.*, 1991). It consists of a lower jaw, teeth, cervical, dorsal, sacral? and caudal vertebrae, ribs, parts of the scapula and ilium, autapodial bones, and dermal elements (Museo de La Plata 86-X-28-1). Preliminary descriptions of the ankylosaurian material were given by Gasparini *et al.* (1987) and Olivero *et al.* (1991). Gasparini *et al.* (1996) discussed the affinities of the Antarctic ankylosaur and referred to it as Nodosauridae gen. et sp. indet. The aim of this paper is to describe the most abundant type of dermal armour found in association with the Antarctic ankylosaur and to examine the bone histology of these ossifications.

Material and methods

The dermal armour is represented by five different kinds of elements: keeled, hollow-based scutes, massive bulging plates; co-ossified flat scutes, overlapping each other and enclosed by small polygonal ossicles; oval, low-keeled scutes; and tiny, button-like ossicles (Gasparini *et al.*, 1987, 1996). The latter are the most abundant dermal elements and were found scattered around the skeletal remains. As preserved in the rock matrix, the dermal ossicles look at first sight as mineralized scutes (figure 1.A). These ossifications are oval to subrectangular in outline; some ossicles are nearly semicircular, others are flat. The internal side is convex and show faint concentric ridges and crossing fibres (figures 1.B-D), while the external side is flat or concave and very irregular. This small armour (diameter less than 5 mm) probably floated in the skin and formed a continuous pavement between the large dermal elements permitting supple movements of the body and limbs (see Carpenter, 1997).

The preparation of the fossil remains was carried out in the laboratory of the Museo de La Plata using mechanical techniques. Some osteoderms were freed from the matrix for photography and further studies. Photographs of figure 1 were made by D. Serrette (UMR 8569 CNRS). The histological work has been completed in the Laboratoire d'Anatomie Comparéee of the Université Paris VII (UMR 8570 CNRS). Osteoderms were studied mainly on petrographic thin sections. Vertical sections were selected from the samples in order to examine the histological features of the ossicles. Sections were studied by optical mi-

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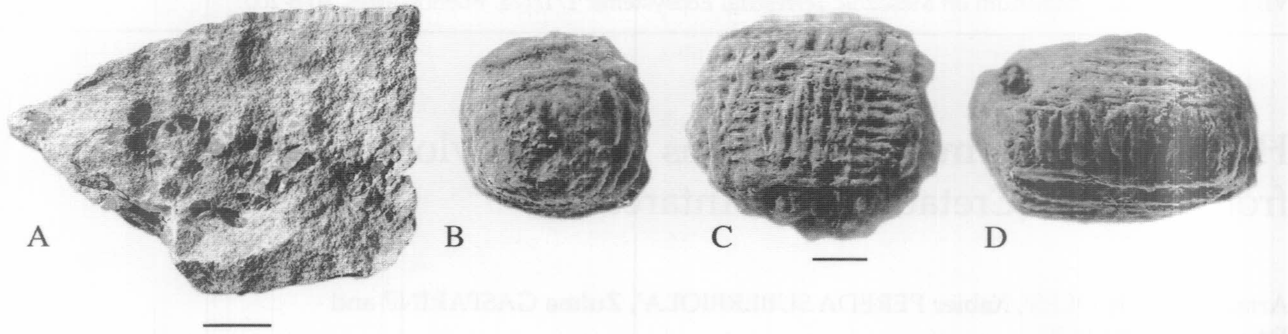

Figure 1. Ankylosaur dermal ossicles from the Late Cretaceous (Campanian) of Antarctica, all specimens MLP 86-X-28-1. A, pavement of ossicles as preserved in matrix; **B-D,** three ossicles in bottom view, after preparation using mechanical techniques. Scale bars, 1 cm (A) and 1 mm (B-D).

croscopy under ordinary and polarized light. Infography of the figures 1 and 2 by H. Lavina (UMR 8569 CNRS).

Histological observations

Thanks to the availability of a few isolated scutes freed from the matrix, it has been possible to assess the shape of the scutes and their general orientation relative to the skin surface. Accordingly, it proved possible to decipher the orientations of numerous scutes on thin sections directly obtained from grinding of the matrix still containing the scutes. In this process, while most scutes are cut at random according to various oblique orientations, a few of them are cut in almost perfect vertical orientations and allow precise histological observations (figure 2.A). What we interpret as the external (superficial) surface of a scute is rather flat or irregular and shows a characteristic ornamentation by a system of polygonal or irregular pits lined by acute ridges. The internal (deep or basal) surface of the scutes is generally convex, even hemispherical and is not ornamented. It clearly shows evidences of a system of strong straight horizontal fibers which cross orthogonally. On a vertical section, the material forming the external surface and about the external quarter to the external fifth of a scute appears distinctly different from the rest of the scute (figure 2.A). It is much more translucent and less colored. For practical purposes one may distinguish this "ornamented region" from a "central region" and a "non ornamented (basal) region". Both the "central" and "basal" regions have generally similar structures and optical reactions. Together, they form about the 3/4 to the 4/5 of the total thickness of a scute.

The ornamented (superficial) region

On a vertical section, its free (external) surface is marked by projections and inward angles which match the morphological ornamentations. Projections may be acute at their tips while the intervening "valleys" are gently sloped and rounded (figure 2.B). The matrix is entirely formed by a dense packing of mineralized (collagenous) fibers. Most fibers appear to run parallell to the free surface but there is another, less developed fibrous system which runs perpendicular to the surface of the scute (figure 2.C). There are no evidence that the superficial ornamentation is the result of either differential rates of deposition (with more active fibrillar deposition on the projections and less active deposition in the valleys) or of differential resorption (in the valleys). Vascularisation of the matrix, if any, appears extremely scarce.

The non ornamented (basal) region (figure 2.D)

Its free surface is regular and convex. This region contains a series of superimposed "growth lines" parallel to each other and to the free surface. It is entirely formed by closely packed, highly ordered systems of mineralized collagenous fiber bundles. Small cell spaces within or between fiber bundles are probably numerous but difficult to observe. Vascularity is very low, accounting to a few simple primary vascular canals. The spatial organisation of the vessels is ill defined but they would roughly diverge from the center of the scute, some of them opening on the convex (deep) surface.

The central region (figure 2.D)

It is formed by the same systems of collagenous bundles than the basal region but differs by its vascularisation. Some vascular canals have a large diameter and a few erosion bays occur. A secondary (Haversian) reconstruction has taken place around most erosion bays.

Spatial organization of the fibrillar systems

Polarization microscopy allows to decipher the complex and highly ordered spatial organization of the fiber bundles systems in the central and basal regions of the scute. There are at least three orthogonal systems of fiber bundles which criss cross each others from the center of the scute to its surface. One system of fibrillar bundles is "vertical" (figure 2.E). Its fibers, roughly parallel to each others (in fact fan shaped), reach perpendicularly the surface of the non ornamented region. Thus, they cross at right angle the successive "growth lines" parallel to the scute surface. This fibrillar material, which actually forms a cone in space (the summit of which beeing at the center of the scute) reminds of the system of attachment fibers (or Sharpeys fibers) observed in the basal plate of rhombic scales in early Osteichthyans (Meunier, 1984; Sire, 1990). Two other systems of fiber bundles, orthogonal to the vertical one and alternating with it are set horizontally within the scute (figure 2.E). They match the systems observed on the convex free surface of the scute. In space, the two horizontal systems are also alternating orthogonally to each others. They form piled up plates which together also shape a cone pointing to the center of the scute. This is close to the "orthogonal plywoods" described in the basal plate of elasmoid scales in many advanced Osteichthyans (Meunier, 1984; Sire, 1990).

Discussion and conclusions

Nature of the ornamented region

The stricking optical difference between the superficial (ornamented) region and the central and basal ones would not be caused by occurence of distinct tissues but mostly by differences in the spatial organization of the mineralized bundles systems. In the ornamented region, the system of "vertical" fibers is far less developed and the orthogonal orientation between two horizontal systems is apparently lacking (figure 2.C). Also, the vascularization of the superficial region is even poorer than in the basal region. Since non collagenous mineralized matrices

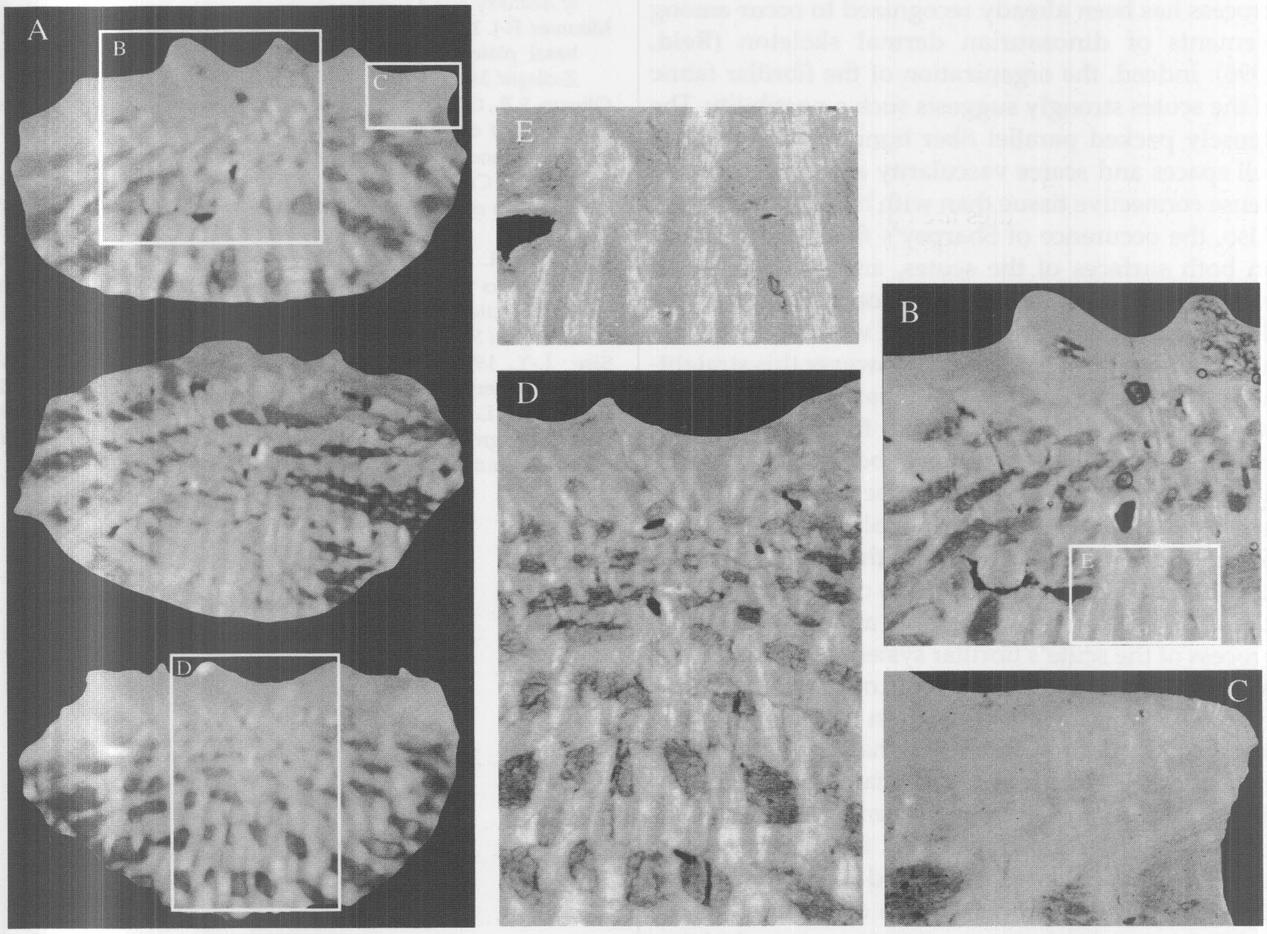

Figure 2. A, vertical thin sections of three dermal ossicles; the putative external surface is at the top and the internal surface at the bottom; actual osteoderm width: circa 5 mm, magnification x 12; **B**, detail of the superficial and central regions of an ossicle, x 20 - note the external surface with a system of fibers crossing it; a few vascular cavities evolved as secondary osteons in the central region; **C**, enlargement of the superficial region of one ossicle, x 50 - two perpendicular systems of (collagenous) fibers may be observed; **D**, vertical section and general view of the basal region of an ossicle, x 26 - note the three orthogonal systems of densely packed collagenous fiber bundles; E, detail of the basal region of an ossicle, x 50 - note the growing size (and hence distance between each others) of the systems of fiber bundles as they expand away from the central region.

have been discovered in the superficial regions of some reptilian osteoderms (Zylberberg and Castanet, 1985; Levrat-Calviac and Zylberberg, 1986; Levrat-Calviac, 1986-87) occurrence of such matrices may not be ruled out in this case and could perhaps account for the distinctness of the ornamented region. However, close examination of the superficial region demonstrate extensive occurrence of densely packed collagenous fibers quite similar to the ones forming the other regions of the scute. Non collagenous mineralized matrices in lizard osteoderms mostly develop in regions devoid of collagenous fibers (Zylberberg and Castanet, 1985). This hardly supports extensive occurrence of non collagenous matrices in this case.

On scutes formation: neo- versus metaplasia?

At first sight, the simplest interpretation of scute formation would appear to be a direct metaplastic ossification of the *stratum compactum* of the dermis. This process has been already recognized to occur among elements of dinosaurian dermal skeleton (Reid, 1996). Indeed, the organization of the fibrillar fabric of the scutes strongly suggests such a possibility. The densely packed parallel fiber bundles with discrete cell spaces and scarce vascularity agree more with a dense connective tissue than with bone tissue proper. Also, the occurence of Sharpey's fibers like systems on both surfaces of the scutes, and of openings of vascular canals on the basal surface demonstrate that the scute were entirely embedded within the skin, actually within the dermis itself. However this straightforward interpretation would have to meet some contradictory evidences. Indeed, from the radiating center located at the boundary between the "ornamented" and "central" regions the fibrillary systems are organized according to radial growth patterns. The mesh size and diameters of the bundles also increase radially for all the systems of bundles (figures 2.A, D), which strongly suggests an intrinsic growth process of the scute's fibrillar system as a whole. This would not be the case if the scute originated from the simple metaplastic mineralization of the preexisting matrix of the dermis. Indeed, in that case, one would expect that the mesh size and diameter of the bundles would be the same in the center and periphery of the scute, since the mesh size, the one of the dermis itself, would have preexisted to its mineralization. One would be thus lead to consider a *de novo* differenciation of the scutes structures (neoplasia) as original elements, perhaps originating from radiation centers initially located at the limit of *stratum spongiosum* and *stratum compactun* of the dermis, rather than a simple mineralization in situ of the preexisting dermal fibers (metaplasia). If so, the small scutes of ankylosaurs would be an original dermal construction, built by neoplasia, and not merely a simple local ossification of a preexisting dense connective tissue.

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