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Source: Acta Palaeontologica Polonica, 55(3) : 459-470

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.1109

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A microanatomical and histological study of the postcranial dermal skeleton in the Devonian sarcopterygian *Eusthenopteron foordi*

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Zylberberg, L., Meunier, F.J., and Laurin M. 2010. A microanatomical and histological study of the postcranial dermal skeleton in the Devonian sarcopterygian *Eusthenopteron foordi*. *Acta Palaeontologica Polonica* 55 (3): 459–470.

The fin rays and two types of scales (enlarged and regular) of the Devonian sarcopterygian *Eusthenopteron foordi* are redescribed using light, scanning and transmission electron microscopy. The fin rays consist of lepidotrichia composed of ossified, jointed and branched segment pairs. The basal segments are cylindrical, but more distal elements are crescentic in section. The distribution of Sharpey's fibres varies along the lepidotrichia. In the proximal segments, lateral bundles form a belt connecting adjacent hemisegments. In the distal segments, thin bundles are restricted to the area facing the fin surface. Both enlarged and regular scales have a similar spatial organisation. They are composed of a superficial highly mineralised layer covering a thick basal plate where the fibrils are distributed in superimposed strata forming a plywood-like structure. Nevertheless, the enlarged and regular scales differ in their shape, in the mineralised tissues of the superficial layer, and in the organisation of the plywood-like structure. The superficial layer of the enlarged scales is composed of parallel-fibered bone covering a deeper layer of woven-fibered bone. The basal plate is made of an orthogonal plywood-like structure. The thin, lamellar, imbricated regular scales display the characteristics of elasmoid scales. The mineralised tissue forming the superficial layer resembles that of extant teleost scales. In the basal plate, the twisted plywood-like structure is composed of closely packed fibrils that are preserved down to the ultrastructural level owing to the persistence of bridges connecting the fibrils. The enlarged and the regular scales of *Eusthenopteron foordi* do not present superficial odontodes, in contrast to ancestral thick rhomboid scales. The disappearance of enamel/enameloid and dentine may be related to the evolutionary trend towards a lightening of the dermal skeleton that would improve the swimming abilities of the animal. The characteristics of the dermal skeleton of *Eusthenopteron foordi* support the hypothesis that this process began early in osteichthyans.

Key words: Sarcopterygii, Tetrapodomorpha, Tristichopteridae, *Eusthenopteron*, fin ray, elasmoid scales, paleohistology, transmission electron microscopy, Devonian.

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Received 11 September 2009, accepted 25 February 2010, available online 8 March 2010.

Introduction

The Late Devonian (Frasnian) sarcopterygian *Eusthenopteron foordi* Whiteaves, 1881, a tristichopterid tetrapodomorph (Janvier 1996), is one of the most abundant tetrapodomorphs in the fossil record and has been described in detail (Jarvik 1944, 1965; Ørvig 1957; Andrews and Westoll 1970; Schultze 1984; Cloutier 1996; Cote et al. 2002). It documents one of the latest stages in the evolution of this group before much of the dermal scale cover was lost. Detailed anatomical data on *Eusthenopteron* can be obtained because the abundance of the material is sufficient to allow sectioning (Andrews and Westoll 1970; Schultze 1984; Cote et al. 2002), and the good preservation enables histological descriptions. Despite this, histological studies on the dermal skeleton of *Eusthenopteron* are few (Laurin et al. 2007). To our knowledge, histological data on the scale structure of *Eusthenopteron* have been published by Goodrich (1907) and by Ørvig (1957), but no paleohistological study concerns the fin rays and the dermal plates, also called hemicylindrical scales, or enlarged scales (Andrews and Westoll 1970). Yet, the dermal skeleton can reveal interesting clues about the affinities of various vertebrates (e.g., Khemiri et al. 2001; Scheyer and Sander 2009).

doi:10.4202/app.2009.1109

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The good preservation of *Eusthenopteron* and its phylogenetic position prompted us to study the structure of the various elements of the dermal skeleton using histological techniques including scanning and transmission electron microscopy. Organic molecules are known to fossilise in exceptional cases, and mineralised tissues can be preserved down to the ultrastructural level (Pawlicki et al. 1966; Zocco and Schwartz 1994; Rimblot et al. 1995; Kemp 2002; Schweitzer et al. 2008). Collagen may be preserved well enough to be sequenced (Service 2009). The new data presented below should facilitate comparison with more primitive rhomboid scales described in other early Sarcopterygii (Goodrich 1907; Ørvig 1957; Schultze 1977) on the one hand, and with the derived elasmoid scales of extant Sarcopterygii like *Neoceratodus* (Meunier and François 1980), *Protopterus* (Zylberberg 1988) or *Latimeria* (Smith et al. 1972; Castanet et al. 1975; Miller 1979; Meunier and Zylberberg 1999; Hadiaty and Rachmatika 2003; Meunier et al. 2008) on the other hand. These data should also help comparisons with other elements forming the dermotrichia, such as the camptotrichia of the fins of extant Dipnoi (Géraudie and Meunier 1984), and may help assess hypotheses about homologies and evolution of various dermal skeletal elements of sarcopterygians.

Institutional abbreviations.—CNRS, Centre national de la Recherche scientifique, Paris, France; MHNM, Musée d'Histoire Naturelle de Miguasha, Québec, Canada; MNHN, Museum National d'Histoire Naturelle, Paris, France; UPMC, Université Pierre et Marie Curie, Paris, France.

Materials

The study of the dermal skeleton of *Eusthernopteron foordi* was carried out on several reasonably complete skeletons, specimens MHNM 06-241A and B, 06-615A, 06-342, and 06-1169A of the collections of Parc de Miguasha. These specimens were collected from Miguasha (Gaspésie, Québec, Canada), and come from the Escuminac Formation (Frasnian, Late Devonian; 48°06'36"N; 66°21'56"W). It preserves an estuarine environment. Pectoral and pelvic fins, as well as enlarged and regular scales, were removed from slabs containing the skeletal remains.

Methods

Light microscopy.—Parts and counterparts were glued back together and prepared from one side using a pneumatic hammer, a dental drill, and a mounted needle under a binocular microscope. The lepidotrichia, dermal bones and scales were then embedded in stratyl resin and sectioned for histological examination. The sections were polished down to a thickness of about 80 μm and observed under transmitted natural and polarised light with a Nikon Eclipse E66 POL and with a Zeiss Axiovert 35 equipped with Nomarski Differential Interference Contrast (DIC).

Scanning Electron Microscopy (SEM).—After soft cleaning with a 1% sodium hypochlorite solution, the surfaces of the fragments were dried and coated with gold and observed in a Jeol-SEM-35 scanning electron microscope at 20kV.

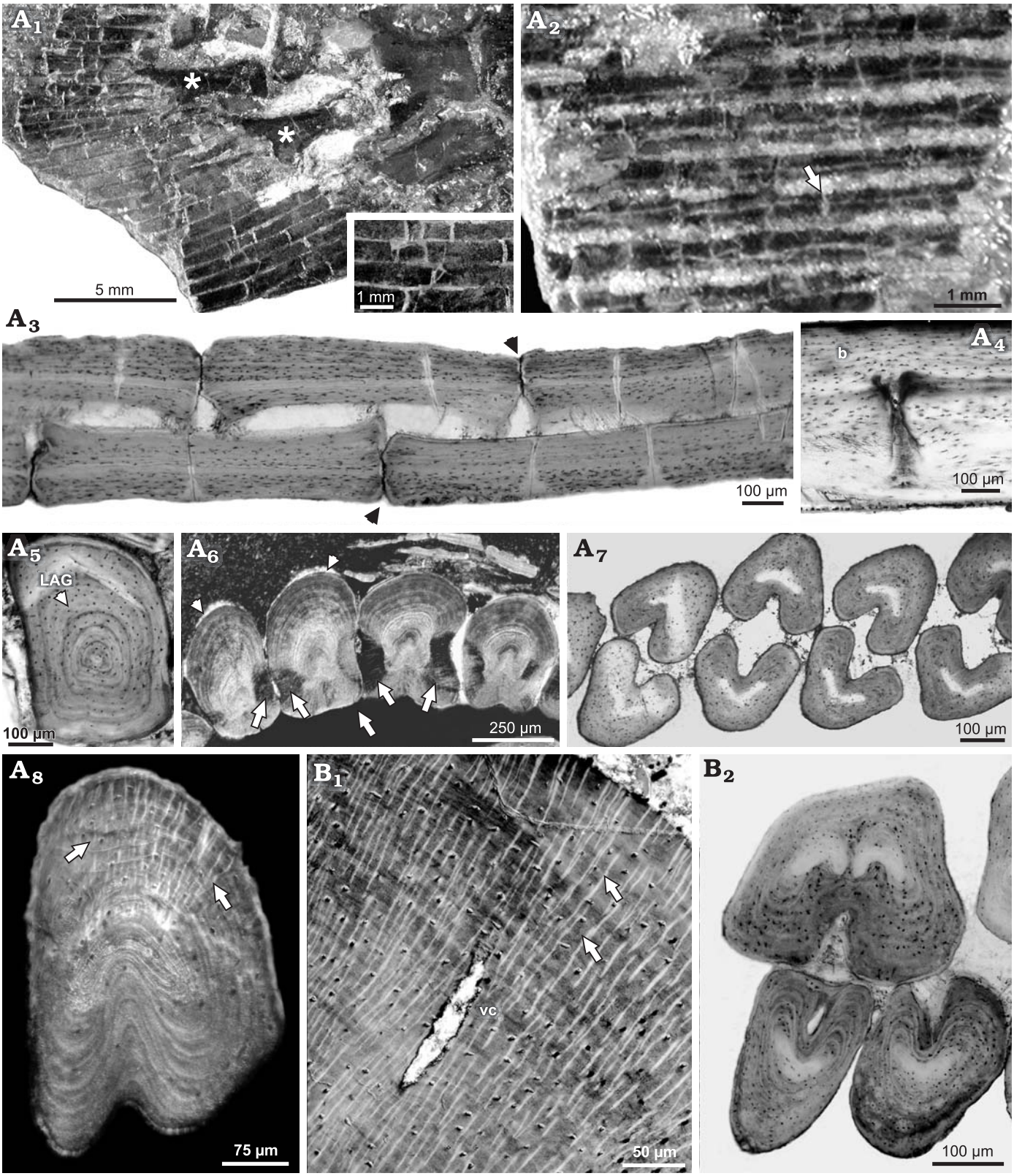
Transmission Electron Microscopy (TEM).—Small, thin pieces (3–5 mm thick) containing scales in their original, partly overlapping positions were isolated and cleaned with a solution of 2.5% formic acid. The pieces were rinsed in ethanol, air-dried, and embedded in epon. Polymerisation was performed at 60°C. The blocks were sectioned to obtain sections about 10 μm thick and containing the whole scale thickness. These thick sections were submitted to demineralisation procedures for TEM examination. Both surfaces of these sections were covered with a thin layer of epon that was polymerised before demineralisation to prevent the breaking up of the tissues that were weakened during demineralisation. Various demineralisation procedures were carried out using either 0.1 N hydrochloric acid, 0.1 M citric acid, 5% formic acid, or 5% EDTA (ethylene diamino tetracetic acid). The demineralisation agent was added to the fixative solution composed of 1.5% paraformaldehyde and 1.5% glutaraldehyde in a 0.1 M cacodylate buffer. The demineralisation solution was changed every two days during one month. Demineralisation was stopped when the thick sections became less opaque and more flexible. The sections were then post-fixed in a solution of 2% osmium tetroxide in the same buffer, then dehydrated in a graded series of ethanol solutions, left for 12 hours in a 1/1 ethanol-epon mixture and embedded in epon. Semi-thin sections (1 μm thick) were stained with a buffered toluidine blue solution (pH 4) and examined by light microscopy using natural transmitted light and DIC to select appropriate areas for TEM examination. Toluidine blue was used only to stain the preserved organic matrix in order to select areas for TEM observation. This staining does not allow discrimination between collagen and other proteins. Ultrathin sections (100 nm thick) were stained with uranyl acetate and lead citrate and observed in a Philips EM 201 transmission electron microscope with an operating voltage of 80 kV.

Results

Observations carried out on three components of the dermal skeleton (the fin rays and both enlarged and regular scales)

Fig. 1. Lepidotrichia of the sarcopterygian *Eusthenopteron foordi* Whiteaves, 1881 from the Late Devonian, Escumenac Bay, Quebec, Canada. **A**. MNHM 06-1169A. A_1. SEM. Pelvic fin showing the axial appendicular endoskeleton (asterisks) and the lepidotrichia (parallel structures to the left of the figure). Insert: detail of lepidotrichia. A_2. SEM. Detail of six rays composed of paired series of segments and their joints (arrow). A_3. Transmitted natural light. Longitudinal section of lepidotrichia showing the joints (arrowheads). A_4. Transmitted natural light. Longitudinal section of a joint →

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surrounded by bone (b). A_5. Transmitted natural light. Cross-section of a lepidotrichium showing the concentric cementing lines of arrested growth (LAG). A_6. Transmitted natural light. Cross-section of lepidotrichia showing thin (arrowheads) and thick (arrows) bundles of Sharpey's fibres. A_7. Transmitted natural light. Cross-section of lepidotrichia in the distal part of the fins where they show a crescentric shape with a central clear area. A_8. Nomarski interference optical micrograph. Cross-section showing the thin Sharpey's fibres in the outer part of a lepidotrichium (arrows). **B**. MHNM 06-241. B_1. Polarised light. Cross-section of a lepidotrichium. Detail of the outer part with Sharpey's fibres (arrows), vc, vascular canal. B_2. Transmitted natural light. Cross-section of a lepidotrichium showing (above) the division of the hemisegments and (bottom) the two rami of the forked lepidotrichium.

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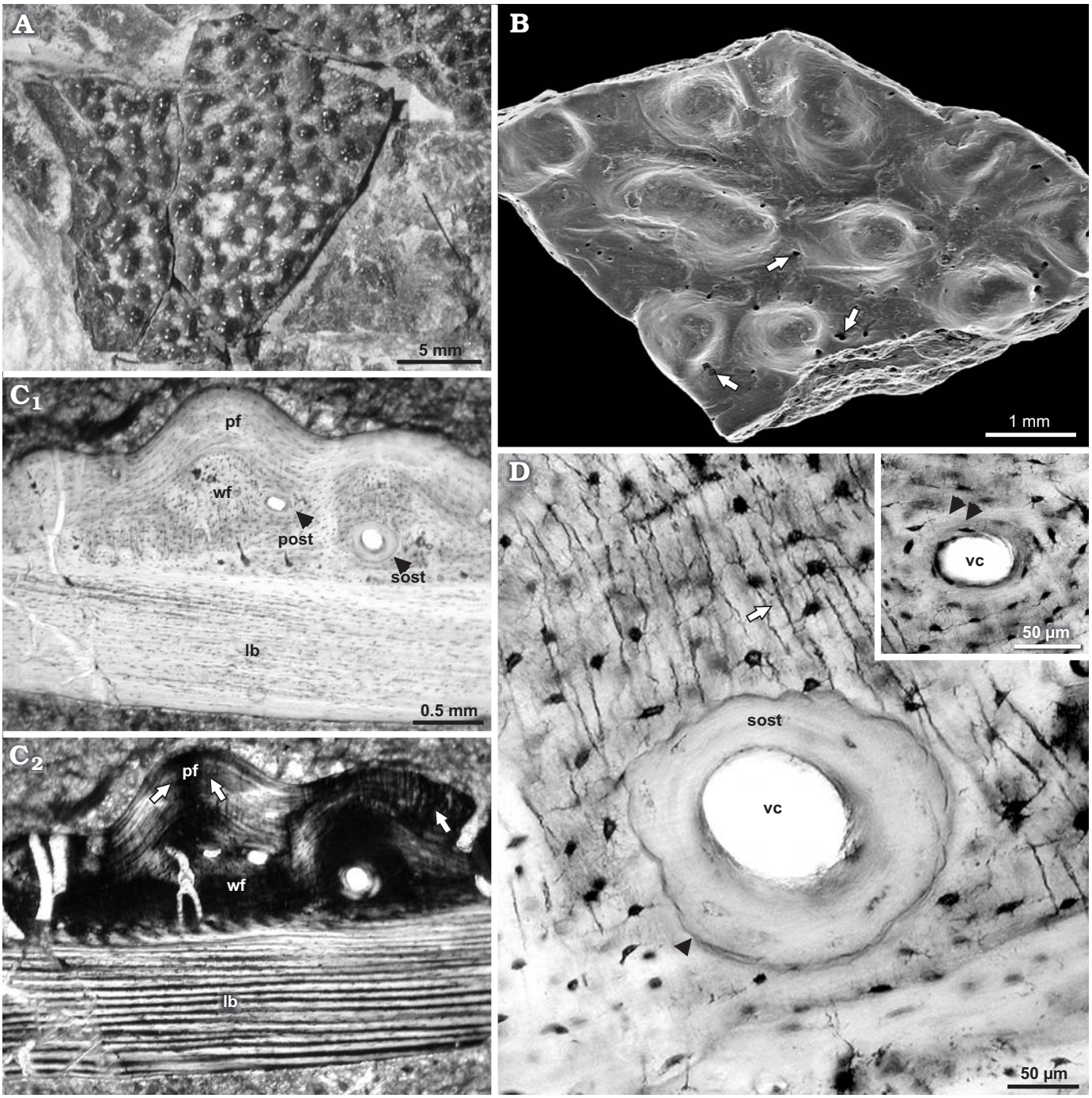


Fig. 2. Enlarged scales of the sarcopterygian *Eusthenopteron foordi* Whiteaves, 1881 (MNHM 06-342) from the Late Devonian, Escumenac Bay, Quebec, Canada. **A**. SEM. Ornamentation of the outer surface of an enlarged dermal scale. **B**. SEM. Detail of the ornamentation of the outer surface of an enlarged dermal scale. The holes (arrows) correspond with the aperture of vascular canals. **C**. Vertical section of an enlarged dermal scale in transmitted natural light (C_1) and in polarised light (C_2). The outer layer composed of superficial parallel-fibered bone covers a discontinuous layer of woven-fibered bone containing primary and secondary osteons. Sharpey's fibres (white arrows) cross the superficial parallel-fibered bone. The basal plate is characterised by the presence of lamellar bone. **D**. Transmitted natural light (detail of C). The outer layer of an enlarged dermal scale. The secondary osteon is separated by a resorption line (black arrowhead) from the surrounding primary bone where Sharpey's fibres (white arrow) are abundant. Insert: the primary osteon, showing the absence of a resorption line (black arrowheads). Abbreviations: lb, lamellar bone; pf, parallel-fibered bone; post, primary osteon; sost, secondary osteon; vc, vascular canal; wf, woven-fibered bone.

show the very good preservation of the *Eusthenopteron* remains at the histological level. Moreover, despite the rough treatment required for demineralisation, the organic residues of the fossilised scales were retained with their original spatial arrangement and ultrastructural characteristics after demineralisation by formic acid or EDTA.

In this study, vertical sections of scales refer to sections perpendicular to the body surface.

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Fin rays.—The basal part of the fin rays in *Eusthenopteron foordi* lie in the vicitnity of the radials, the distal elements of the endoskeleton (Fig. $1A_1$). The fin rays are composed of slender, elongated elements that lie parallel to each other. Each ray or lepidotrichium is composed of repetitive segments, 1 to 3 mm long, in the proximal part of the fin ray (Fig. $1A_1$). More distally, the segments are composed of two parallel series of mineralised elements close to each other, one near each surface of the fin (Fig. $1A_2$). These are called the hemisegments (Lanzing 1976; Géraudie 1988). Adjacent segments are separated by thin joints (Fig. $1A_1$–A_4). Longitudinal sections of fin rays show that the joints are very narrow unmineralised spaces between adjacent segments (Fig. $1A_3$). Mineralised, longitudinal fibres form an osseous mantle at the periphery of some joints (Fig. $1A_4$). In the fin rays, the axes of the osteocyte lacunae are parallel to the fibres that are oriented along the longitudinal axis of the segments (Fig. $1A_3$, A_4).

Cross-sections in the proximal region where the fins are covered with scales (Fig. $1A_5$, A_6) show that the rays are approximately cylindrical at that level. They exhibit concentric layers of cellular bone separated by cementing lines of arrested growth (LAGs). The cross-sections of the fin rays in more distal portions of the fins show that the shape of the segments is modified progressively. First, a furrow appears on the inner surface (Fig. $1A_6$). More distally, the two hemisegments whose inner face gradually becomes concave assume a crescentic shape in section (Fig. $1A_7$). They form a series of opposing concave segment pairs; within each segment, a clear central area appears (Fig. $1A_7$). These segments are composed of thin concentric layers with cellular lacunae inserted between the layers, as shown by Nomarski transmitted light (Fig. $1A_8$). The osteocyte lacunae whose axes are oriented along the longitudinal axis of the segments appear isodiametric in cross section (Fig. $1B_1$). The distribution of the Sharpey's fibres varies concomitantly with the shape modification of the segments. In the proximal cylindrical segments, abundant Sharpey's fibres oriented orthogonally to the lateral surface of the fin ray connect the adjacent hemisegments like a belt, and thin bundles are present in the outer part of the hemisegments (Fig. $1A_6$). Distally, the bundles are also present but they are restricted to the outer part of the hemisegments (Fig. $1A_8$), and they become less abundant and thinner (Fig. $1B_1$). A few longitudinal and radial vascular canals are also present (Fig. $1B_1$). The lepidotrichia of *Eusthenopteron* are forked; each hemisegment gives rise to two more distal hemisegments (Fig. $1B_2$).

Enlarged scales.—Enlarged scales, the hemicylindrical scales of Andrews and Westoll (1970: text-fig. 17), are located at the proximal part of the preaxial edge of the fins. They are characterised by the presence of tubercles that form rounded elevations of about 0.5–1 mm on the outer surface (Fig. 2A, B). The holes observed at the surface of the enlarged scales represent the apertures of vascular canals (Fig. 2B). Vertical ground sections show that the enlarged scales are composed of two layers: a thin superficial bony layer whose elevations form the tubercles, and a thick basal plate composed of dense lamellar bone (Fig. 2C). The outer part of the superficial layer (the only one that forms a continuous sheet) is composed of poorly vascularised parallel-fibered bone (Fig. 2C), also called pseudo-lamellar bone (Francillon-Vieillot et al. 1990). Osteocyte lacunae inserted among the fibres are spindle-shaped (Fig. $2C_1$). Bundles of woven-fibered bone located under the layer of parallel-fibered bone form the tubercles (Fig. $2C_1$). The woven-fibered bone contains isodiametric osteocyte lacunae measuring 5–7 μm in diameter. Most of the scale vascularisation occurs in this woven-fibered, discontinuous layer (Fig. 2C), although the vascular canals obviously had to cross the superficialmost layer to reach the scale surface (Fig. 2B). Both primary and secondary vascular canals occur (Fig. 2D). The former lack delimiting cement lines (Fig. 2D insert) whereas the latter, whose walls are made of a secondary lamellar bone, are separated from the surrounding primary bone by cementing lines and lack Sharpey's fibres (Fig. 2D). Sharpey's fibres are observed in the entire superficial layer, where their direction is approximately perpendicular to the scale surface. They form loose bundles in the woven-fibered bone (Fig. 2D), and thicker bundles that perpendicularly cross the fibres of the parallel-fibered bone (Fig. $2C_2$).

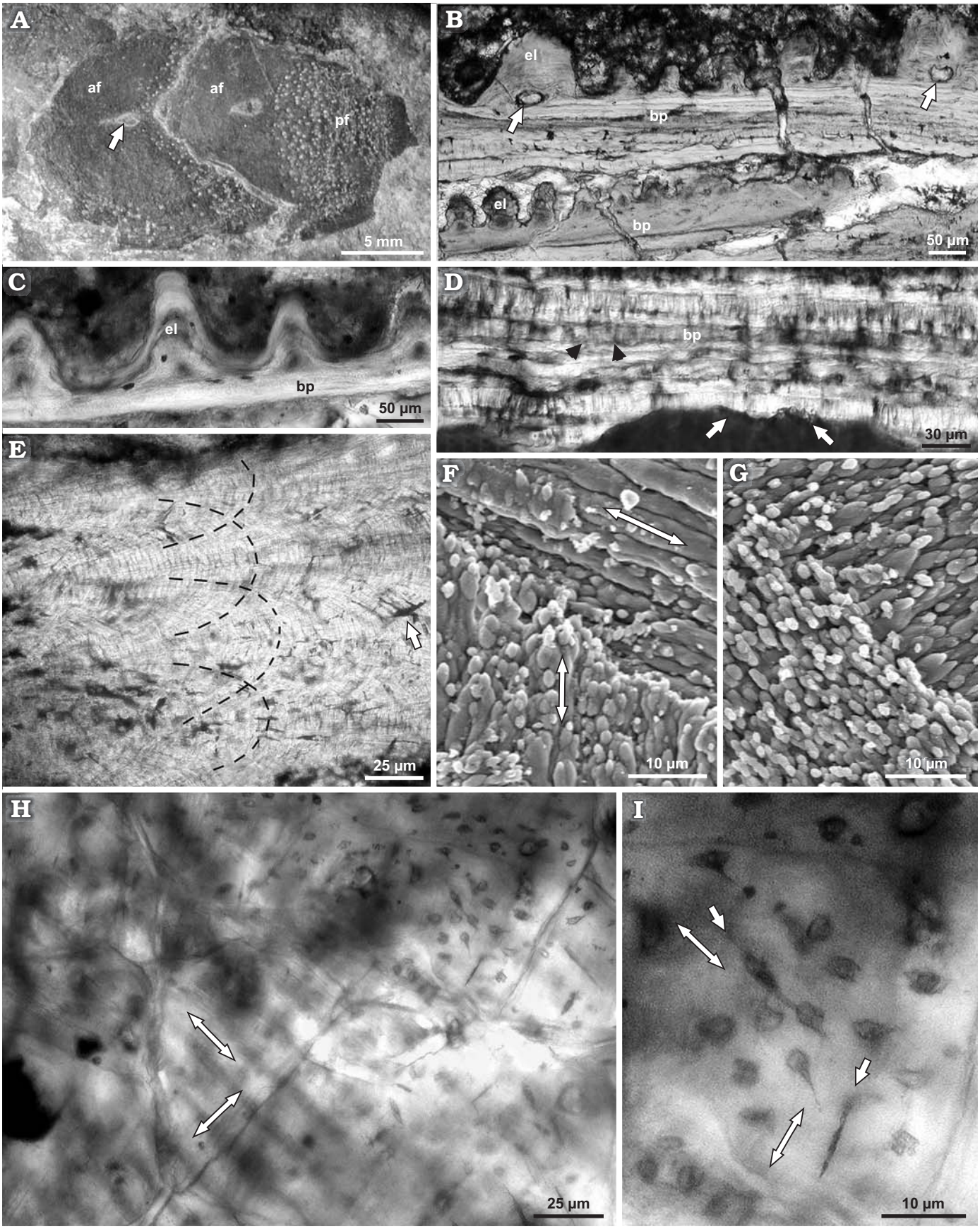
The lamellar bone of the basal part of the enlarged scales is made of superimposed strata of aligned fibres parallel to each other in each stratum, but whose direction varies by about 90° from stratum to stratum, thus forming an orthogonal plywood-like architecture (Fig. $2C_2$). The thickness of each stratum is about 6–8 μm. The osteocytes of the basal plate are located in lenticular lacunae about 2.5 μm thick and 12–14 μm in diameter (not illustrated).

Regular scales.—The flat scales are regularly imbricated and cover the body, including the lateral line organ, with canals that open to the surface through large pores (Fig. 3A). Because of their overlap, only the posterior field of the scale is normally exposed; it is ornamented with thick tubercles while the lateral and anterior fields have thin radial ridges (not illustrated). In vertical sections, the scales appear to be composed of two superimposed layers: a superficial layer, and a thick basal plate (Fig. 3B), both of which are composed entirely of bone. Very thin superimposed growth lines were observed in the external layer. They are more obvious within the tubercles, suggesting that throughout ontogeny, a cyclic thickening occurred in the whole superficial layer, but it was more dominant in the tubercles (Fig. 3C, D). As in the enlarged scales, the vascularisation is largely confined to the deep part of the tubercles.

The basal plate is composed of series of superimposed plies about 10–12 μm thick (Fig. 3D). Each ply is formed by a layer of thick bundles of closely packed parallel collagen fibres oriented in the same direction. The fibre direction varies from one ply to the next by a specific angle of rotation. On a micrograph showing an oblique section of the basal plate, the direction of the fibres in each ply is represented by lines parallel to the fibres (Fig. 3E). The lines of successive odd and even plies form a double system of nested arches (Fig. 3E). This double system of arches corresponds to a twisted

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plywood structure (Giraud et al. 1978). Numerous densely packed ovoid corpuscles, Mandl's corpuscles, are observed in SEM micrographs of the mineralisation front of the basal plate (Fig. 3F, G). Their long axes are oriented in the same direction as the mineralised fibrils that form sheets with which they are co-aligned.

Osteocyte lacunae are present in both the superficial layer and the basal plate (Fig. 3B, E, H, I). Flat, elongated, spindle-shaped cell lacunae are located between adjacent plies across the whole thickness of the basal plate (Fig. 3E). Their abundance is best observed in vertical ground sections of scales embedded in toto in epon for TEM observations after a demineralisation carried out with formic acid or EDTA (Fig. 3H, I). These sections became transparent enough to be observed with a transmitted light microscope even if the presence of opaque dots indicates that the demineralisation was not completely achieved. The osteocyte lacunae are 25 to 35 μm long and about 2.5 μm thick, and their long axis is parallel with the surrounding collagen fibrils. They are equipped with numerous long canaliculi that were occupied by cellular processes and extended between the plies (Fig. 3H, I).

These sections show that the direction of the fibrils varies, suggesting that the organisation of the fibrils in the plywood-like structure was preserved during the demineralisation procedures for TEM observations. Indeed, the semi-thin sections perpendicular to the scale surface show that the general organisation of the scale is preserved (Fig. 4A–D), even though abundant fractures (Fig. 4B) and bacteria are visible on the surface (Fig. 4D). Staining with toluidine blue indicates that organic material was preserved in both layers, even though the scales are not completely demineralised; tissues that remain mineralised are not stained with toluidine blue (Fig. 4A). In section of the external layer, well-stained, thin lines parallel to the surface (Fig. 4C) may represent remains of growth lines, also observed in ground sections in light microscopy (Fig. 3B, C). The basal plate observed with Nomarski optics shows a surface (Fig. 4D) covered with ripples parallel to each other. At the ultrastructural level, long, compact fibrillary structures are composed of closely packed fibrils (Fig. 4E). Adjacent fibrils are linked to each other by regularly spaced bridges (Fig. 4E, F). The 100 nm thick fibrils do not show the specific striation that characterises the fibrils of type I collagen present in osseous tissues of extant vertebrates; however, the regular banding that can occasionally be observed in the *Eusthenopteron* scales may represent a remnant of the original structure (Fig. 4G). Mineral still present in thin sections after demineralisation procedures forms patches associated with the fibrils and is regularly distributed along these fibrils (Fig. 4G).

Discussion

Fin rays.—Our data on the morphology and structure of the fin rays of *Eusthenopteron foordi* support previous interpretations (Goodrich 1904) that this taxon possesses true lepidotrichia composed of ossified, jointed and branched segment pairs (Fig. 1A_5, A_8), whereas extant dipnoans have unsegmented, cylindrical camptotrichia (Géraudie and Meunier 1982, 1984) that do not form paired structures, unlike the lepidotrichia of *Eusthenopteron*. In *Neoceratodus,* mineralisation is present along the whole length of the camptotrichia, but it is interrupted in some places, which increases flexibility. The superficial, subepidermal area is mineralised while the deep "dermal one" is not. *Dipterus* had true lepidotrichia (Goodrich 1904) but reduction of mineralisation was observed in more Recent dipnoids, such as *Scaumenacia* (Géraudie and Meunier 1984). These camptotrichia must represent an apomorphic condition (Géraudie and Meunier 1984), as lepidotrichia were presumably present in most, if not all, Palaeozoic sarcopterygians (Janvier 1996). Lepidotrichia and camptotrichia may only share a deep homology, to the extent that they are both derived from a same morphogenetic system.

In the proximal parts of the fins that are covered with enlarged or regular scales, the basalmost segments of the lepidotrichia are circular in cross-section and are made of concentric layers of cellular bone. These basal segments do not appear much more elongated than the distal ones (Goodrich 1904; Andrews and Westoll 1970; Jeffery 2001). In that respect, *Eusthenopteron foordi* differs from rhizontids, whose elon-

← Fig. 3. Scale structure of the sarcopterygian *Eusthenopteron foordi* Whiteaves, 1881 (MNHM 06-615A) from the Late Devonian, Escumenac Bay, Quebec, Canada. **A**. SEM. Two scales of the lateral line are pierced by a pore (arrow) through which the lateral line organ reached the surface. The scales have been displaced during fossilisation, the anterior scale covering the posterior. Note that their anterior field is less ornamented than the posterior field. **B**. Transmitted natural light. Cross-section of two superimposed scales showing the two main layers: the ridged external layer and the stratified basal plate. A vascular canal (arrows) is present in the two prominent ridges. **C**. Transmitted natural light. Vertical section at the margin of the scale. Details of the external layer whose elevations form the superficial ornamentation with cyclic deposition and of the underlying basal plate. **D**. Transmitted natural light. Cross-section showing details of the basal plate composed of superimposed strata. The thin striations (black arrowheads) show that one stratum is made of thick fibres oriented in the same direction. The mineralising front (white arrows) is irregular. **E**. Transmitted natural light. Tangential section of the basal plate. The direction of the fibres in each ply is represented by lines parallel to the fibres. The lines of successive odd and even plies form a double system of arches. The osteocyte lacuna shape reflects the orientation of the collagen fibres; their cellular processes are mostly parallel to the fibres (arrow). **F**. SEM. Deep surface of the basal plate showing the thick bundles of mineralised fibres of homogeneous orientation in each stratum (double headed arrows). Ovoid Mandl's corpuscles are present on the deep surface; their axes have the same direction as the bundles on which they lie. **G**. SEM. The axes of the ovoid Mandl's corpuscles are parallel to each other within any given stratum but their orientation varies from one stratum to another, like the bundles of mineralised fibres (see F). **H**. Transmitted natural light. Epon frontal thick section of a scale after demineralisation for observation in TEM. Note the preservation of the scale organisation: osteocyte lacunae and collagen fiber distribution (double-headed arrows). **I**. Transmitted natural light (detail of H). The shape of the osteocyte lacunae and their canaliculi (arrows) are obviously related to the orientation of the surrounding fibres (double-headed arrows). Abbreviations: af, anterior field; bp, basal plate; el, external layer; pf, posterior field.

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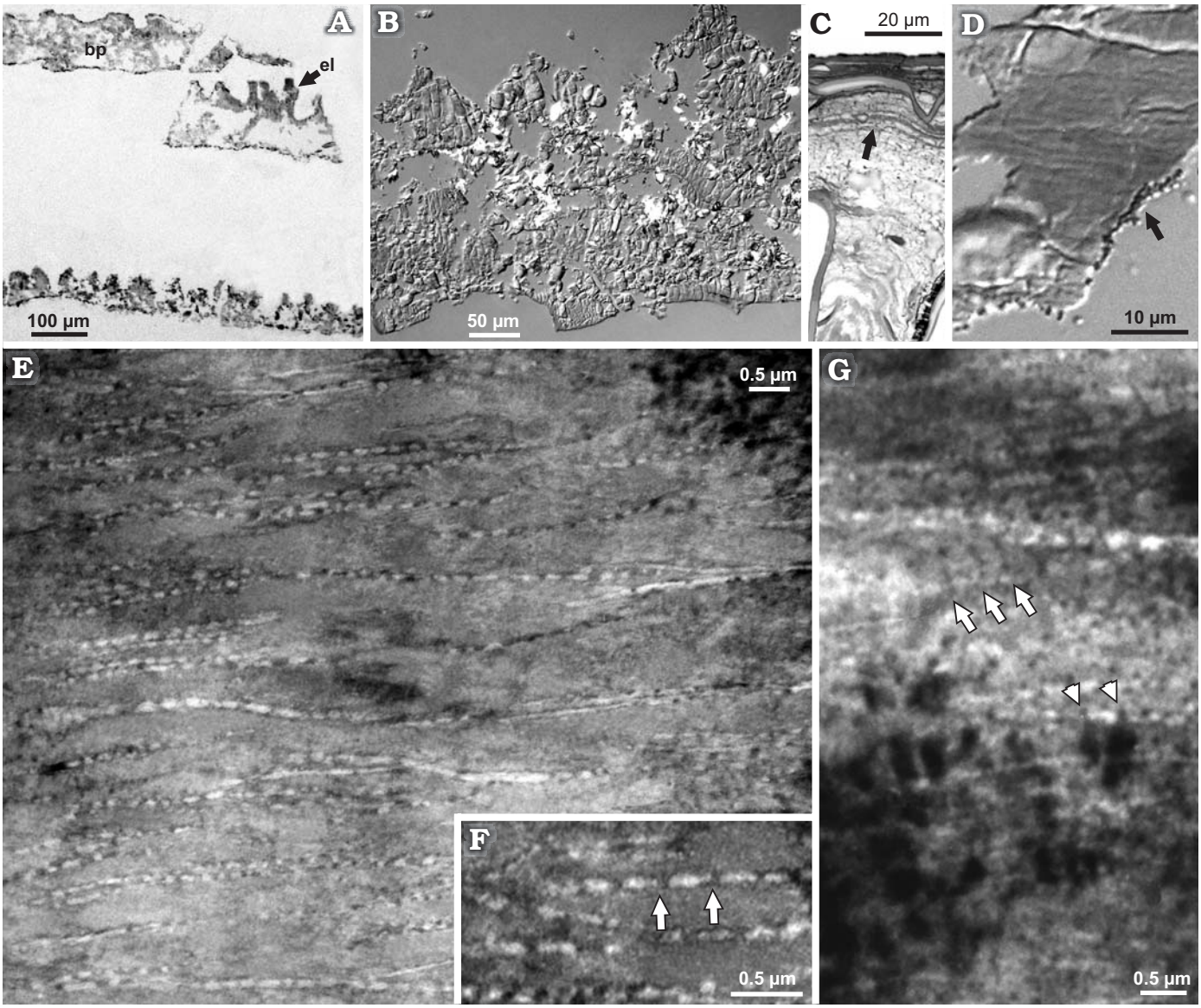


Fig. 4. Scale ultrastructure of the sarcopterygian *Eusthenopteron foordi* Whiteaves, 1881 (MNHM 06-615A) from the Late Devonian, Escumenac Bay, Quebec, Canada. **A**. Transmitted natural light, semi-thin section. Toluidine blue staining showing three vertically-sectioned scales. The organic matrix is stained in the external layer; in the basal plate, the mineral remnants are black (arrow). **B**. Nomarski interference optical micrograph. Semi-thin vertical section of a demineralised scale. Fractures are abundant, but the general organisation of the scale is still preserved. **C**. Transmitted natural light, semi-thin section, toluidine blue staining. Detail of the outer layer where a fuzzy material forms intensively stained stratified lines (arrow). **D**. Nomarski interference optical micrograph. Semi-thin vertical section. The surface of the basal plate shows parallel ripples. Micro-organisms, probably bacteria, are attached to the side of the basal plate (arrow). **E**. TEM. Demineralised basal plate of scale. The closely packed fibrils, roughly oriented in the same direction, are connected by bridges. **F**. TEM. Basal plate. Detail showing the regularly spaced bridges connecting two adjacent fibrils (arrows). **G**. TEM. Partially demineralised scale. Regularly distributed mineral crystals remain attached to the fibrils (arrowheads). Some fibrils show a discernible periodic structure (arrows). Abbreviations: bp, basal plate; el, external section.

gated basal segments extend to the endoskeleton of the pectoral fin (Andrews 1985; Davis et al. 2001, 2004; Jeffery 2001; Johanson et al. 2005). Distally, the hemisegments gradually acquire a crescentic cross-section. The paired hemisegments align to enclose a central area. The presence of articulations between successive segments of the fin rays in *Eusthenopteron* suggests that they could bend when the fins moved.

We have identified Sharpey's fibres, whose distribution changes along the segments. In the proximal cylindrical segments, Sharpey's fibres form strong bundles connecting the proximal elements to each other like a reinforcing belt. These Sharpey's fibres most probably correspond to the interlepidotrichial ligaments described in the fin rays of extant teleosts (Beccera et al. 1983). Distally, thin bundles of Sharpey's fibres are restricted to the external part of each hemisegment. Such thin bundles perpendicular to the surface of the lepidotrichia cross the dermis to reach the dermo-epithelial membrane in extant teleosts. The distribution of Sharpey's fibres could be related to the organisation of the lepidotrichia in a fan configuration in the paired fins.

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Surprisingly, in the lepidotrichia of extant teleosts, fibrils of type I collagen have a narrower diameter (about 30 nm) than those of the surrounding dermis of the lepidotrichia (Landis and Géraudie 1990). Similarly in the external layer of the elasmoid scales of teleosts, thin type I collagen fibrils (about 30 nm) differ from the thick type I collagen fibrils (about 100 nm) of the basal plate (Zylberberg and Nicolas 1982). Moreover, in the lepidotrichia and in the scale external layer, the crystals are not oriented by the thin collagen fibrils as in a regular osseous tissue. These ultrastructural data support the hypothesis formulated by Jarvik (1959) and Andrews and Westoll (1970) that lepidotrichia and scales (where enamel/enameloid, dentine and bone are identified) are somewhat differently-shaped manifestations of the same morphogenetic system (Schaeffer 1977; Zylberberg et al. 1992).

Enlarged and regular scales.—In this part, we will first consider data concerning the structure of the enlarged and regular scales and then the evolutionary trend to reduction of the scales.

Our histological and ultrastructural investigations carried out on these two dermal elements provide new data on the structure of the basal plate. In these scales, Mandl's corpuscles were identified only in the regular scales (Fig. 3F); we did not observe them in enlarged scales. Indeed, these mineralised globules located ahead of the mineralisation front were first considered as a characteristic of the basal plate of elasmoid scales of teleosts (Schönbörner et al. 1981). However, in subsequent studies, Mandl's corpuscles were described in elasmoid scales of other taxa, such as the holostean *Amia* (Meunier 1980; Meunier and Poplin 1995) and the dipnoan *Protopterus* (Meunier and François 1980; Zylberberg 1988; Meunier and Poplin 1995). They were also observed in the early stage of formation of ganoid scales in polypterids (Daget et al. 2001). Moreover, similar corpuscles have been described in the basal plate of the osteoderms of a reptile, the squamate *Chalcides viridanus* (Zylberberg et al. 1992). The basal plates of the elasmoid scales in the Gymnophiona (caecilians) do not have such mineralised globules ahead of the mineralisation front (Zylberberg et al. 1980; Zylberberg and Wake 1990). Functional and/or evolutionary significance of such mineralised corpuscles that precede the mineralisation front in the basal plate of the integumental skeletal elements sheathing the body of various osteichthyans remains unsolved.

The ultrastructural preservation of the twisted plywood-like structure of the basal plate (Fig. 4E), despite the cracks and the presence of bacteria, may have been facilitated by the high density of the fibrils within the plies. The twisted plywood-like structure of the regular scales is more compact than the orthogonal plywood-like structure of the enlarged scales. In the plies where the fibrils are closely packed, abundant bridges connecting the fibrils are preserved, even if these bridges may have formed during fossilisation and may not correspond to the bridges composed of glycosaminoglycans and glycoproteins found in fresh osseous tissues (Fawcett 1994; Vogel 1994). The fibrils show an occasional striation evoking that of the type I collagen of osseous tissues. Their thickness (100 nm in diameter) is frequently observed in the fibrils of the basal plate in elasmoid scales of extant teleosts (Zylberberg et al. 1992). Studies dealing with the ultrastructural preservation of collagen in fossil bone showed a loss of striation characteristic of bone type I collagen fibrils, and of the ability of these fibrils to be stained (Pawlicki et al. 1966; Doberenz and Wikoff 1967). The processes that affect bone preservation in fossils are complex because bone consists of interrelated mineral and organic components whose degradation depends on intrinsic factors, such as composition and structure, and extrinsic factors, such as the conditions of burial and post-depositional history (Schweitzer et al. 2008).

The enlarged and regular scales differ owing to their shape, the type of mineralised tissues forming the superficial layer, the organisation of the plywood-like structure of the basal plate (either orthogonal for enlarged scales or twisted in regular scales; see below), and its mineralisation.

In enlarged scales, the superficial layer is proportionately thicker than that of regular scales and its outer surface does not show exposed or overlapped fields with different ornamentations like the regular scales. This layer is composed of outer parallel-fibered bone covering woven-fibered bone, both being vascular bone. The basal plate is composed of a largely avascular orthogonal plywood-like structure forming lamellar bone apparently devoid of Mandl's corpuscles; the mineralisation front is regular.

Comparisons

The present study supports the hypothesis that only the regular scales of *Eusthenopteron* are elasmoid scales since they show characteristics of such scales as defined by Bertin (1944): they are thin lamellar and imbricated plates composed of a thin mineralised and ornamented outer layer overlying a thick basal layer with a plywood-like structure; nevertheless, we consider enlarged scales and regular scales to be homologous.

The superficial layer of the scales of *Eusthenopteron* resembles that in the scales of extant dipnoan taxa that also lack odontodes (Meunier and François 1980; Zylberberg 1988), especially *Neoceratodus* (Meunier and François 1980). The mineralised tissue of the superficial layer also has similarities to that of elasmoid scales of extant teleosts (Schönbörner et al. 1979; Zylberberg and Nicolas 1982). The basal plate is composed of thick collagen fibrils organised in regular superimposed plies forming a twisted plywood-like structure, the isopedine (Francillon et al. 1990).

Elasmoid scales probably appeared convergently at least five times in various osteichtyians: actinistians (Smith et al. 1972; Miller 1979; Meunier et al. 2008), all extant (Meunier and François 1980) and some early dipnoans (such as the Late Devonian phaneropleurids *Phaneropleuron* and *Scaumenacia* (Ørvig 1957), the Middle Devonian (Givetian) porolepiform *Holoptychius* (Ørvig 1957), amiids (Meunier

doi:10.4202/app.2009.1109

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1980; Meunier and Poplin 1995), and teleosts (Meunier 1984, 1987; Meunier and Brito 2004). The last common ancestor of extant sarcopterygians almost certainly retained the plesiomorphic cosmoid scales composed of a thick ossified layer covered with cosmine, as defined by Ørvig (1969), Thomson (1975), and Meinke (1984). This is suggested by the retention of cosmoid scales in the slightly less crownward ostelepidids, in megalichthyids (Goodrich 1907; Ørvig 1957, 1969; Thomson 1975), in *Ectosteorhachis* (Thomson 1975), in *Porolepis*, and in *Dipterus* (Ørvig 1957). Among extant osteichthyans, the superficial odontodes have persisted only on the elasmoid scales of the extant coelacanthid *Latimeria* (Castanet et al. 1975; Miller 1979; Hadiaty and Rachmatika 2003; Meunier et al. 2008).

The enlarged and regular scales of *Eusthenopteron foordi* lack several tissues and structures that were primitively present in the earliest sarcopterygians, such as the early Middle to Late Devonian dipnomorph *Glyptolepis* and the Middle Devonian tetrapodomoprh *Osteolepis*, and that persisted in some more recent tetrapodomorphs, such as the Early Permian *Ectosteorhachis* (Thomson 1975). The latter had cosmoid scales comprised of three layers (Ørvig 1951, 1968; Sire et al. 2009). The most superficial layer was formed of cosmine, a special arrangement of odontodes and a pore canal system (presumably representing mostly vascular spaces); the odontodes are formed of orthodentine, with a superficial layer of enamel or enameloid. These sometimes formed odontocomplexes, rather than completely distinct odontodes. Beneath the cosmine, a thick layer of spongy bone was typically present (Thomson 1975), and was underlain by a much less densely vascularised layer of lamellar bone similar to the basal layer of the enlarged and regular scales in *Eusthenopteron*. The scales (both enlarged and regular) of *Eusthenopteron* lack the cosmine, the enamel (or enameloid) and the dentine, although bony tubercles occur. These tubercles may have a hydrodynamic function (Burdak 1986). *Eusthenopteron* also lacks the layer of spongy, densely vascularised bone found in older, more basal sarcopterygians (e.g., *Glyptolepis, Osteolepis*), or even the more recent (Early Permian) tetrapodomorph *Ectosteorhachis* (Thomson 1975).

Eusthenopteron shares the loss of the cosmine (enamel/enameloid and dentine) with stegocephalians. However, the loss of the spongy bone layer is probably convergent with several extant tetrapods, such as gymnophionans (Zylberberg et al. 1980; Zylberberg and Wake 1990), that typically lack spongy bone in their scales, or lepidosaurs, that lack spongy bone in their osteoderms (Vickaryous and Sire 2009: fig. 10). Spongy bone is found in some extant tetrapod osteoderms, such as in crocodilians and mammals (Vickaryous and Sire 2009: fig. 10). More importantly, the Late Permian temnospondyl *Australerpeton cosgriffi* retained a spongy bone layer in its ventral scales (Dias and Richter 2002). There is currently a debate about the affinities of temnospondyls. The traditional viewpoint, still upheld by some authors (e.g., Ruta and Coates 2007), is that temnospondyls are stem-amphibians, but some recent studies suggest that they represent stem-tetrapods (Laurin 1998; Marjanović and Laurin 2009). Under both hypotheses, the condition found in Permian temnospondyls is more likely to be primitive than that found in extant gymnophionans. The lack of a vascular layer in the scales of our specimens contrasts with the current schematic depiction of its scales as having a densely vascularised middle layer (Vickaryous and Sire 2009: fig. 10). The extent to which our findings apply to other tristichopterids will need to be determined by further histological investigations.

This argument of a convergent loss of the vascular layer between *Eusthenopteron* and gymnophionans rests on the acceptance of the homology between genuine scales and gastralia of early stegocephalians. The only histological study of sections of the ventral dermal ossifications of early stegocephalians suggests that these are indeed genuine scales, rather than osteoderms, based especially on their taxonomic distribution (Dias and Richter 2002: 477; Witzmann 2007). Another supporting argument is their overlapping pattern and their lack of dermal sculpturing. Thus, these gastralia may represent transformed scales, rather than new structures.

Conclusions

Our new data on the dermal skeleton of *Eusthenopteron* are further evidence of a pervasive evolutionary trend towards a lightening of the dermal skeleton in osteichthyans and other vertebrates (Zylberberg et al. 1992; Sire et al. 2009; Vickaryous and Sire 2009). A similar trend is also obvious in the geologically most recent osteostracans (jawless vertebrates), which were slightly older (Middle Devonian) than *Eusthenopteron.* In osteostracans, the reduction in thickness or complexity of the dermal skeleton probably appeared convergently at least three times in the most recent lineages: once in *Afanassiaspis porata* (Otto and Laurin 1999, 2001a), once in *Yvonaspis*, and once in *Balticaspis latvica* (Otto and Laurin 2001b).

This trend is more advanced in the regular than in the enlarged scales of *Eusthenopteron*. The lightening probably improves swimming abilities (Burdak 1986) without impairing various other functions of the integument, especially protection and hydrodynamics. The ornamentation of the scale surface probably improved hydrodynamics of the animal by regularising water flow in the limiting layer at the surface of the skin, experimentally demonstrated on two extant species (one chondrichthyan and one teleostean) by Burdak (1986). *Eusthenopteron* is considered to be an ambush predator (Clack 2002), so it needed relatively high acceleration abilities to seize its preys. Both the ornamentation (reducing hydrodynamic drag) and lightening of the scales (reducing inertia) may have contributed to improving swimming performance. The lesser degree of lightening of the enlarged scales may be explained by biomechanical constraints: they may have been subject to substantial mechanical stress, because of their position near the base of the paired fins.

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Acknowledgments

We thank Sylvain Desbiens and Johanne Kerr (Parc de Miguasha, Québec, Canada) for loaning us the specimens of *Eusthenopteron* and for permission to section them, and Philippe Janvier (MNHN, Paris, France) for providing us with some specimens and for his help to contact the Parc de Miguasha. We are grateful to Françoise Allizard (CNRS, UPMC, Paris, France), Christiane Chancogne (MNHN, Paris, France) for their technical assistance respectively for TEM and SEM, to Michel Lemoine (MNHN, Paris, France) and Marie-Madeleine Loth (CNRS, UPMC, Paris, France) for ground sections, and to Florian Witzmann for bibliographic data on gastralia. TEM observations were carried out in the Department of Electron Microscopy, IFR Biologie Intégrative, CNRS and Université Pierre et Marie Curie.

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