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To cite this version:

Louise Zylberberg, François J Meunier, Michel Laurin. A microanatomical and histological study of the postcranial dermal skeleton of the Devonian actinopterygian Cheirolepis canadensis. Acta Palaeontologica Polonica, 2016, 61 (2), pp.363-376. 10.4202/app.00161.2015 . hal-01344107

HAL Id: hal-01344107
https://hal.sorbonne-universite.fr/hal-01344107v1

Submitted on 11 Jul 2016

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A microanatomical and histological study of the postcranial dermal skeleton of the Devonian actinopterygian *Cheirolepis canadensis*

LOUISE ZYLBERBERG, FRANÇOIS J. MEUNIER, and MICHEL LAURIN

Zylberberg, L., Meunier, F.J., and Laurin, M. 2016. A microanatomical and histological study of the postcranial dermal skeleton of the Devonian actinopterygian *Cheirolepis canadensis*. *Acta Palaeontologica Polonica* 61 (2): 363–376.

The Devonian stem-actinoterygian *Cheirolepis canadensis* is potentially important to understand the evolution of the dermal skeleton of osteichthyans, but the last detailed histological study on this taxon was published more than forty years ago. Here, we present new data about the morphology and the histological structure of scales, fulcra, and fin-rays in the Devonian actinopterygian *Cheirolepis canadensis* through SEM and photomicroscopy. The scales have a typical palaeoniscoid organisation, with ganoine layers overlaying dentine and a bony basal plate, but the ganoine surface lacks the characteristic microtubercles that have been described on the ganoine surface of the scales of polypterids and many other actinopterygians. Fin-rays are composed of segmented and ramified lepidotrichia that show a structure reminiscent of scales, with ganoine and dentine components lying on a thick bony base. We describe articular processes between lepidotrichia that are reminiscent of, and plausibly homologous with, the peg-and-socket articulations between the scales. The analysis of the postcranial dermal skeleton of *Cheirolepis canadensis* shows that structural similarities between scales and lepidotrichia of this basal actinopterygian are greater than in more recent actinopterygians. The new data on histological and microanatomical structure of the dermal skeleton lend additional support to the hypothesis that lepidotichia are derivatives of scales, though they are also compatible with the more general hypothesis that scales, lepidotrichia and fulcra belong to the same morphogenetic system.

Key words: Actinoterygia, *Cheirolepis*, scales, ganoine, dentine, paleohistology, Devonian, Canada.

Louise Zylberberg [louise.zylberberg@upmc.fr], Sorbonne Universités, ISTEP, UMR 7193 (CNRS/UPMC), Université Paris VI, 4 place Jussieu, B.C.19, F-75252 Paris cedex 05, France.
François J. Meunier [meunier@mnhn.fr], BOREA, UMR 7208 (CNRS/IRD/MNHN/UPMC), Département des Milieux et Peuplements Aquatiques, Muséum national d'Histoire naturelle, C.P. 26, 43 rue Cuvier, F-75231 Paris cedex 05, France.
Michel Laurin [laurin@mnhn.fr] (corresponding author), CR2P, UMR 7207 (CNRS/MNHN/UPMC/Sorbonne Universités), Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, Muséum National d'Histoire Naturelle, Bâtiment de Géologie, C.P. 48, 43 rue Buffon, F-75231, Paris cedex 05, France.

Received 16 March 2015, accepted 7 August 2015, available online 7 September 2015.

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Introduction

The post-cranial dermal skeleton of actinopterygians is composed of mineralised elements including scales, fin rays, scutes, fulcra and spines (Schultze and Arratia 1989; Arratia 2008, 2009) that are frequently interpreted as homologous structures despite their differences in morphology, histological structure, and functions (e.g., Arratia 2008). Based on morphological observations, evolutionary relationships have been established between the two main components of the dermal skeleton in Actinopterygii: on the one hand, the scales, mineralised plates covering the body, and on the other hand, the lepidotrichia, segmented bony rays that sustain paired and median fins. Lepidotrichia have been considered as transformed scales by Goodrich (1904) and by Jarvik (1959) because of the morphological continuity and because of histological similarities between the scales and the lepidotrichia. Goodrich (1904) and Jarvik (1959) supported their hypothesis for the relationships between scales and lepidotrichia by observations of these two dermal components in extinct Actinopterygii and in basal extant ones, especially the Polypteridae. However, other papers have endorsed only more general suggestions about the link between scales and lepidotrichia (Géraudie and Landis

http://dx.doi.org/10.4202/app.00161.2015

1982; Géraudie 1988; Johanson et al. 2005; Arratia 2008) and agree with the suggestion by Schaeffer (1977) that: "scales and lepidotrichia composed of enameloid, dentine and bone are somewhat differently shaped manifestations of the same morphogenetic system". Thus, Schaeffer's (1977) hypothesis is compatible with, but does not necessarily imply, the hypotheses of Goodrich (1904) and Jarvik (1959) that can be considered to be nested within Schaeffer's (1977) hypothesis. Schaeffer's (1977) hypothesis explains the presence of the same tissues and of odontodes both on scales and on lepidotrichia (as well as in oral teeth, which are also formed by the same morphogenetic system), but it does not necessarily predict that as we go back in time, scales and lepidotrichia (or teeth, for that matter) will resemble each other more closely, at the histological or anatomical levels, because this morphogenetic system also produces oral teeth that comprise the same tissues, but their anatomical organization differs rather drastically. Indeed, Schaeffer (1977: 44) implicitly acknowledged that his hypothesis did not require greater similarities in early osteichthyans than in extant ones between scales and lepidotrichia in the following quote: "lepidotrichia and scales in early actinoptergians and sarcoptergians frequently look alike and they may be covered with enameloid (enamel) and dentine. But this does not necessarily indicate that lepidotrichia literally evolved from scales—there is little evidence for that. It is perhaps more meaningful to propose that scales and lepidotrichia composed of enameloid, dentine and bone are somewhat differently shaped manifestations of the same morphogenetic system". The "But" and "necessarily" in this quote imply partial opposition between similarity (between scales and lepidotrichia of early osteichthyans) and Schaeffer's hypothesis, or at least, this suggests that Schaeffer was aware that his hypothesis was not the best explanation for this fact. On the contrary, the hypothesis supported by Goodrich (1904) and Jarvik (1959) does make the prediction that this similarity should decrease over time (that it should be greatest in the oldest taxa); observation of a contrary pattern would falsify it, whereas it would not falsify Schaeffer's (1977) hypothesis. Note that both (histological and anatomical) levels are to some extent independent; thus, the odontodes of teeth, fulcra, scales and lepidotrichia are composed of the same tissues, but their anatomical organization differs, with teeth being generally composed of a single odontode, while scales and lepidotrichia can bear several odontodes or odontocomplexes. Thus, both hypotheses can be tested at both levels.

In an attempt to test the hypotheses of Goodrich (1904) and Jarvik (1959), we present a comparative histological and anatomical study of scales, fulcra and lepidotrichia of *Cheirolepis canadensis*. As one of the oldest known stem-actinopterygians (Swartz 2009), *Cheirolepis* is a key taxon for comparative studies of the evolution of dermal skeleton in early actinopterygians. The genus comprises two well-known species, *C. canadensis* (Whiteaves 1881, 1889; Lehman 1947) and *C. trailli* (Agassiz 1833–44; Traquair 1875), and three other more poorly known species (see Gross 1973; Arratia and Cloutier 2004). The anatomy of the former is relatively well known owing to an abundant material (Lehman 1947; Reed 1992; Arratia and Cloutier 1996). In addition to its systematic position and geological age, a criterion for the choice of *Cheirolepis canadensis* for this study is the quality of fossil material from Miguasha, which was recently illustrated by studies on *Eusthenopteron foordi* (Zylberberg et al. 2010; Meunier and Laurin 2012 Sanchez et al. 2012). Even though *Cheirolepis canadensis* is represented by well-preserved material, the last detailed histological descriptions of its scales were published by Aldinger (1937) and later by Gross (1973), which followed those of Traquair (1875) and Goodrich (1907). Then, in a comparative study of fossil vertebrate scale morphology and microanatomy, Gross (1953, 1966) reported some data on *Cheirolepis canadensis* and *Cheirolepis trailli*. More recently, in a comparative microscopical study of the ganoine tissue, Richter and Smith (1995) gave more detailed data on ganoine organisation in *Cheirolepis*' scales and they pointed out that the term ganoine was used to describe well-mineralised tissues but that the phylogenetic significance of the pattern of ganoine variation remained to be resolved. The histology of fulcra and lepidotrichia was studied even less; the most recent report (Goodrich 1904) harks back to the early 20th century and followed those of Agassiz (1843–44) and Traquair (1875).

Below, we compare the cheirolepid dermal skeleton with that of Recent polypterids (Sewertzoff 1924, 1932; Meunier 1980; Zylberberg and Meunier 2013), since the extant Cladistia are considered to occupy a basal position in the phylogeny of Actinopterygii (Ørvig 1957, 1968; Patterson 1982; Lauder and Liem 1983; Gardiner and Schaeffer 1989; Min and Schultze 2001; Betancur-R. et al. 2015). Lepisosteidae, which are slightly less basal than polypterids, also constitute a good basis for comparison, given that their dermal skeleton displays some intermediate features between that of polypterids and teleosts.

Institutional abbreviations.—MHNM, Musée d'Histoire Naturelle de Miguasha, Québec, Canada.

Other abbreviations.—AER, apical ectodermal ridge; ECM, extracellular matrix; SCPPS, secretory calcium-binding phosphoproteins; SPARC; secreted protein, acidic, cysteine-rich like.

Material and methods

The present study is based on histological examination of two incomplete specimens of *Cheirolepis canadensis* (Whiteaves, 1881). The scales, paired fulcra and lepidotrichia of a caudal appendage were observed on the specimen MHNM 05-132 (Fig. 1A) and the scales on a lateral fragment of skin of MHNM 05-142 (Fig. 1B). It is difficult to estimate precisely the body size from such incomplete

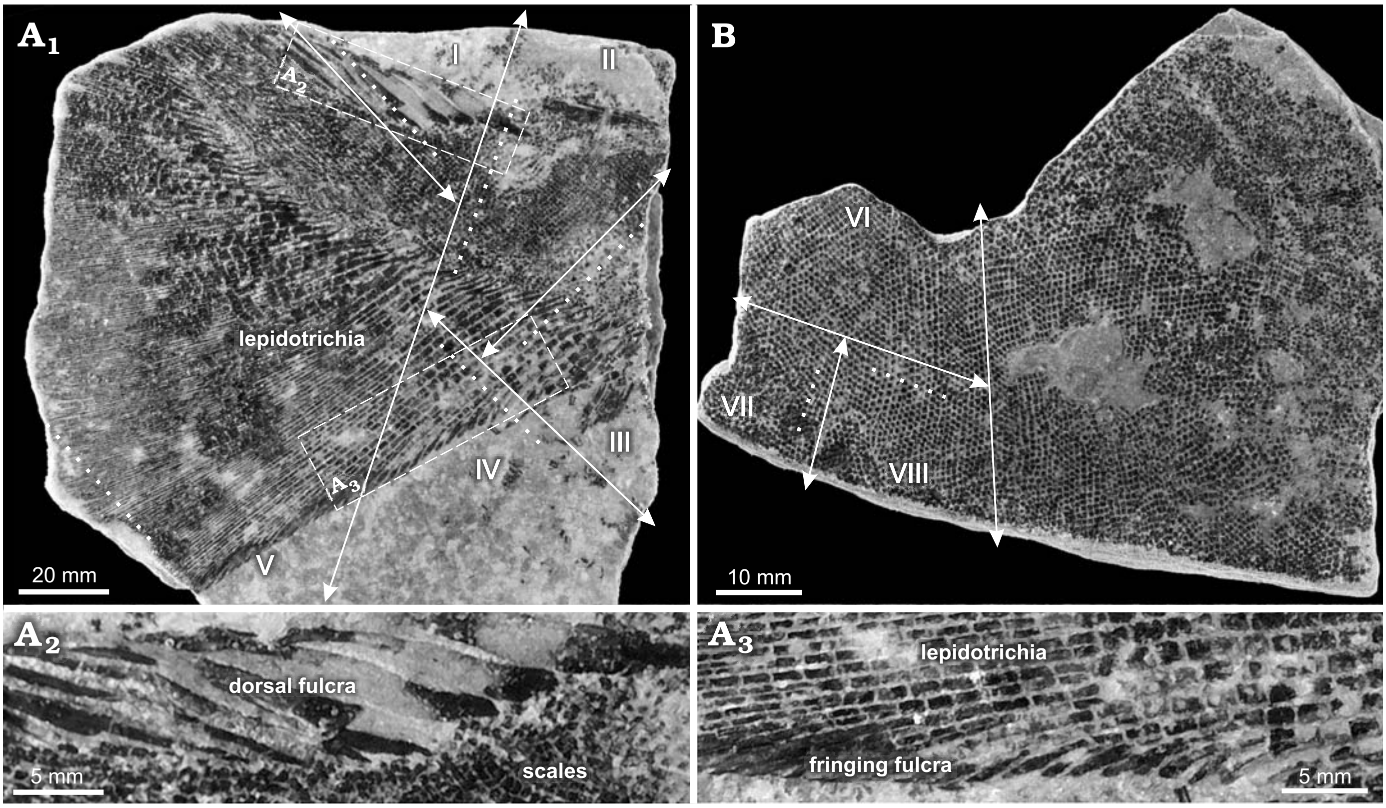


Fig. 1. The Devonian actinopterygian *Cheirolepis canadensis* Whiteaves, 1881 from Miguasha, Canada. **A**. MHNM 05-132, general view of the right side of the caudal fin (A$_1$), showing the dorsal fulcra (detail in A$_2$) and the numerous ventral segmented and ramified lepidotrichia and the basal fringing fulcra (detail in A$_3$). The double-arrows indicate the caudal fin fragments (I–V), sectioned in the planes indicated by the doted lines to obtain ground sections of fulcra and lepidotrichia (I), transversal sections of fulcra and scales and longitudinal sections of the basal segment of lepidotrichia (II), longitudinal sections of the lepidotrichia (III), transversal sections of lepidotrichia and fulcra (IV), and the very distal part of lepidotrichia (V). Dorsal fulcra of the dorsal margin of the caudal fin (A$_2$). Basal fringing fulcra and segments of lepidotrichia (A$_3$). **B**. MHNM 05-142, fossilised skin showing the scales organised in parallel rows. The double-arrows indicate fragments (VI–VIII), sectioned in the planes indicated by the doted lines to obtain ground sections of scales: tangential (VI), longitudinal (VII), transversal (VIII).

material, but both specimens must have been at least 30 cm long, judging by the size of the preserved fragments and by comparisons with more complete material, such as the specimen figured by Agassiz (1833–44: pl. 1d); the size of this species could reach 50 cm in total body length. The caudal fin was removed from the blocks that contained the rest of the fossilised skeleton for sectioning.

Ground sections.—All samples used for histological study were embedded in polyester resin (GBS 1; Brot) and sectioned for the study of scales, fulcra and lepidotrichia. We prepared transversal and longitudinal sections of fin rays, fulcra and scales and specific tangential sections for scales (Fig. 1). The sections were polished to a thickness of about 60−80 μm. The sections were observed under transmitted natural light and polarized light with a Zeiss Axiovert 35 equipped with Nomarski Differential Interference Contrast (DIC). Pictures were taken with a digital camera Olympus Camedia C-5060.

SEM.—A scale sample (Fig. 1B) was prepared for SEM examination. It was cleaned with caution with a 1% sodium hypochlorite in water and air-dried. Some scales of this sample were fractured to expose cross-sectioned surfaces. The surface of all samples was coated with a carbon layer and observed in a SEM microscope Zeiss Supra SS VP operating at 10kV and 6mA.

Results

Morphology of the caudal appendage.—The tail of *Cheirolepis* is heterocercal, a primitive feature for actinopterygians; the caudal fin is stiffened by lepidotrichia bordered by the fulcra (Arrratia 2008: fig. 16). Because of its heterocercal fin together with its highly streamlined body that minimise energy expenditure during swimming (Webb 1978, 1980; Wainwright 1983; Fletcher et al. 2014), *Cheirolepis* could be considered to have had efficient swimming performance (Cloutier et al. 1996).

According Arratia's terminology (Arratia 2009: figs. 1, 10), the sample examined shows paired basal fulcra on the dorsal side (Fig. 1A$_1$, A$_2$) and basal fringing fulcra on the ventral side or leading margin of the ventral lobe (Fig. 1A$_1$, A$_3$). Unpaired basal fulcra were not preserved in the sample of the caudal fin examined (MNHM 05-132). Lepidotrichia are segmented and bifurcated (Fig. 1A$_1$, A$_3$). Between the dorsal fulcra and the ventral fin rays (MNHM 05-142), the caudal body of *Cheirolepis* was covered with rhombic scales (Fig. 1B).

Scale organization.—*SEM observations*: The scales are distributed in regular rows (Fig. 1B). Their oblique anterodorsal to posteroventral arrangement on the body (Fig. 1B) differs from the caudal region that shows an oblique anteroventral to posterodorsal arrangement. They are approximately rhombic and they show four to seven low longitudinal superficial crests (Fig. 2A$_1$, A$_2$). They have an uninterrupted ganoine layer deposited on the exposed surface (Fig. 2A$_1$, A$_2$, B$_1$, B$_2$). The thin longitudinal ridges may have had a hydrodynamic function that regularised the water flow at the skin surface as suggested by Burdak (1979). The wavy external surface of the ganoine is smooth (Fig. 2A$_1$–A$_4$); it is entirely deprived of the characteristic microtubercles that have been described on the ganoine surface of the scales of polypterids and many other Actinopterygii (Ørvig 1967; Schultze 1966; Gayet and Meunier 1986, 1992; Meunier and Gayet 1996). The surface of the ridges in the posterior part of the scales appears to be longitudinally finely rippled (Fig. 2A$_3$, A$_4$). This superficial layer is gradually replaced at the anterior basis of the superficial ridges by aggregates of mineralised globules whose surface is flattened, as it is on the ridges (Fig. 2A$_5$). In the anterior part of the scales, spheritic globules whose diameter reaches 3 μm are aggregated into large elongated clusters (Fig. 2A$_3$, A$_5$).

In fractured scales, the outer layer of ganoine appears composed of superimposed strata quite homogeneous and does not show distinct crystallites (Fig. 2A$_6$). No distinct bundles were observed, as noted by Richter and Smith (1995). However, in the outermost layer, the crystallites appear to be approximately perpendicular to the outer surface of the scale (Fig. 2A$_6$).

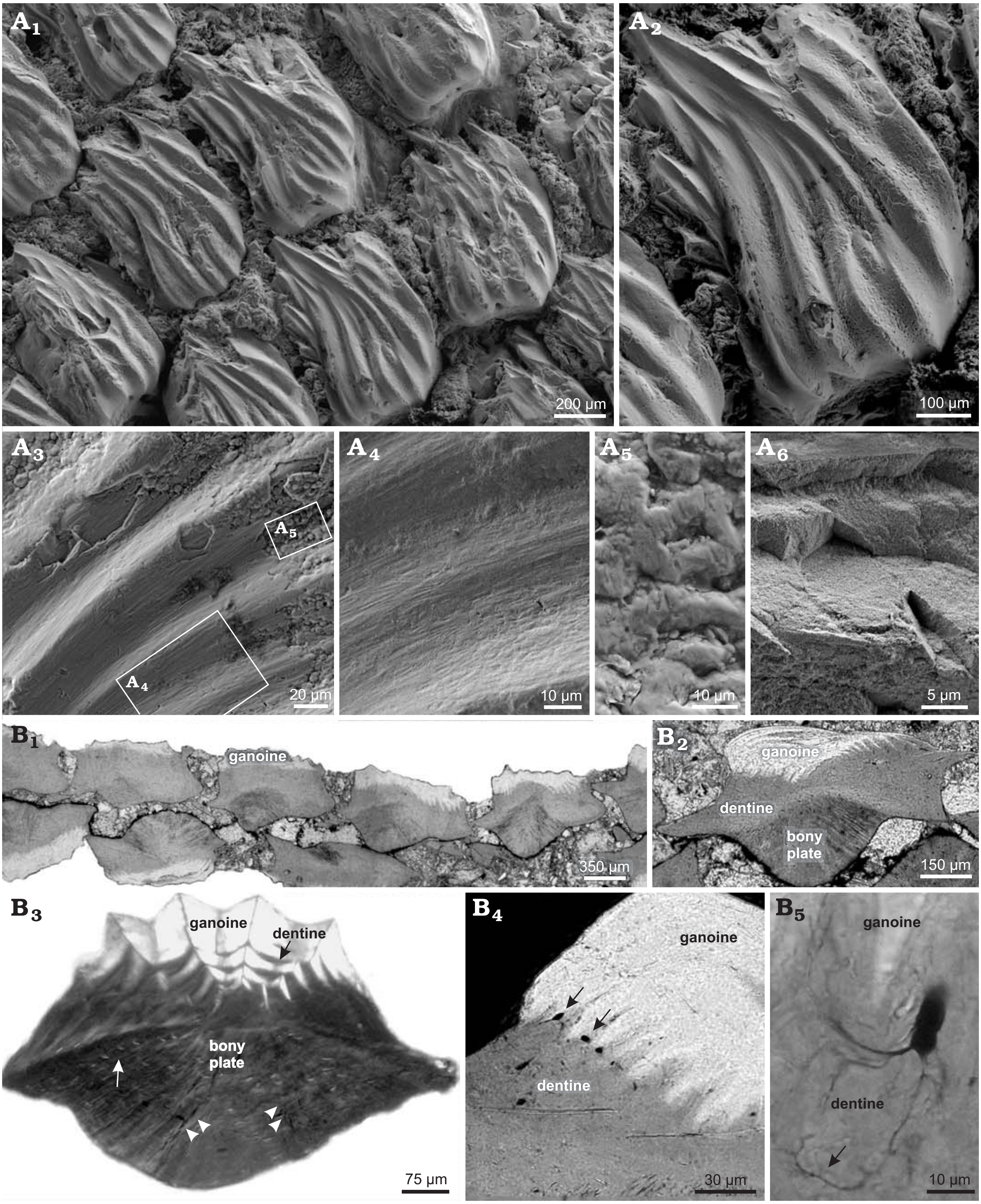
Histological observations: Transversal and longitudinal sections show the three components from the top to the bottom: ganoine, dentine and bony basal plate (Fig. 2B$_1$–B$_3$). The scales are strictly juxtaposed with rudimentary peg-and-socket articulations (Fig. 2B$_1$); each scale shows a lateral apophysis on the basal plate that corresponds to a concavity on the adjacent scale (Fig. 2B$_1$, B$_2$). The deep face of the scale is obviously convex and forms a keel (Fig. 2B$_1$–B$_3$) composed of cellular bone (Fig. 2B$_2$, B$_3$). The numerous Sharpey's fibres (Fig. 2B$_2$, B$_3$) crossing the keel and the lateral sides of the scales are thought to have firmly anchored the scale into the stratum compactum of the dermis. Vascular canals are absent or very scarce in the bony basal plate (Fig. 2B$_2$, B$_3$). The ganoine layer is composed of several strictly superposed strata (at most a dozen in the material examined) that are clearly separated from each other laterally by dentine (Fig. 2B$_3$, B$_4$). Between two successive layers of ganoine, when dentine is present, it is organised around small vascular spaces or canals (Fig. 2B$_4$, B$_5$) and it is crossed by thin ramified odontoblastic canalicles (Fig. 2B$_4$, B$_5$). Thus, the multilayered ganoine is separated from the layer of dentine by an obvious boundary with a peculiar jagged aspect (Fig. 2B$_3$, B$_4$).

Longitudinal sections show that the scales grew in thickness by deposition of new ganoine units in the anterior area of the scale (Fig. 2B$_2$) and that they also grew in length caudally. Reversion lines indicating odontode resorption-redeposition processes were not observed on our material, contrary to the scales of the Upper Permian actinopterygian *Yaomoshania minutosquama* (Poplin et al. 1991). For this study, according to the definition of Ørvig (1967, 1968, 1977), the term odontode defines a unit produced by "an epithelial dental organ not belonging to dentition *sensu stricto*" and composed of dentine or dentinous tissue topped by an enameloid or enamel cap and the term odontocomplexe refers to "clusters of odontodes that have developed directly upon or beside each other" (Ørvig 1977:54).

Fin ray organization.—Cheirolepid fin rays display all diagnostic features of true lepidotrichia. They form bony rods composed of adjacent segments (Fig. 1A). Each ray is formed of a long basal segment prolonged by a series of variably regular segments (Fig. 1A$_1$, A$_3$). Each lepidotrichium is composed of two symmetrical elements named "demirays" (Kemp and Park 1970) or "hemisegments" (Lanzing 1976), as described in teleostean fins (Fig. 3A, B). The ligament between two successive hemisegments is partly mineralised (Fig. 3C, F). The surface of the hemisegments, especially the basal ones, shows shiny ridges (Fig. 3C–H) that represent ganoine, as mentioned by Lehman (1947).

On longitudinal sections, two adjacent hemisegments are in relatively close contact (Fig. 3C). Cross-sections also occasionally show some apophyses on the lateral surface of the lepidotrichia that touch the adjacent fin rays (Fig. 3D). On all lepidotrichia, the apophysis is on the same side (Fig. 3D). Thus, adjacent elements of lepidotrichia are juxtaposed with peg-and-socket articulations that are more rudimentary that those identified in the scales (Fig. 2B$_2$). However, this articulation between the lepidotrichia of the caudal fin, to our knowledge, was not discussed in the literature; it may

Fig. 2. Scales of the Devonian actinopterygian *Cheirolepis canadensis* Whiteaves, 1881 from Miguasha, Canada. **A**. MHNM 05-142, fragment V (see Fig. 1B). General view of scales showing their spatial relationships (A$_1$). Detail of a scale surface showing the antero-posterior ridges (A$_2$), anterior is at bottom right. Detail of the ridge surface (A$_3$), smooth in the posterior part of the ridges and granular in the anterior part. Detail of the surface of the posterior part of the ridges (A$_4$); the smooth surface of the ridges is longitudinally rippled. Detail of the anterior part of the ridges (A$_5$) ornamented with clusters composed of vaguely globular elevations. Fracture through three strata of the ganoine layer (A$_6$). **B**. Longitudinal ground sections of MHNM 05-132, fragment II (see Fig. 1A), cranial to the left. Series of scales showing the articulation between adjacent scales (B$_1$). Ground section of a scale (B$_2$), showing the various components of the scales (cranial to the left); thick bundles, probably Sharpey fibers cross the basal bony part composed of cellular bone. The scale (in cross section) composed of superimposed layers of ganoine covering the ridges (B$_3$); dentine (arrow) is wedged between two layers of →



ganoine; the basal bony part made of cellular bone is crossed by thick Sharpey's fibres (arrowheads); osteocyte lacunae are visible (arrow); superimposed strata of ganoine are laterally separated from each other by dentine. Vascular canals (arrows) located between two adjacent strata of ganoine (B_4). Detail of a vascular canal (B_5). SEM photographs (A_1–A_6), transmitted natural light photographs (B_1, B_2, B_4, B_5), Nomarski interference (B_3).

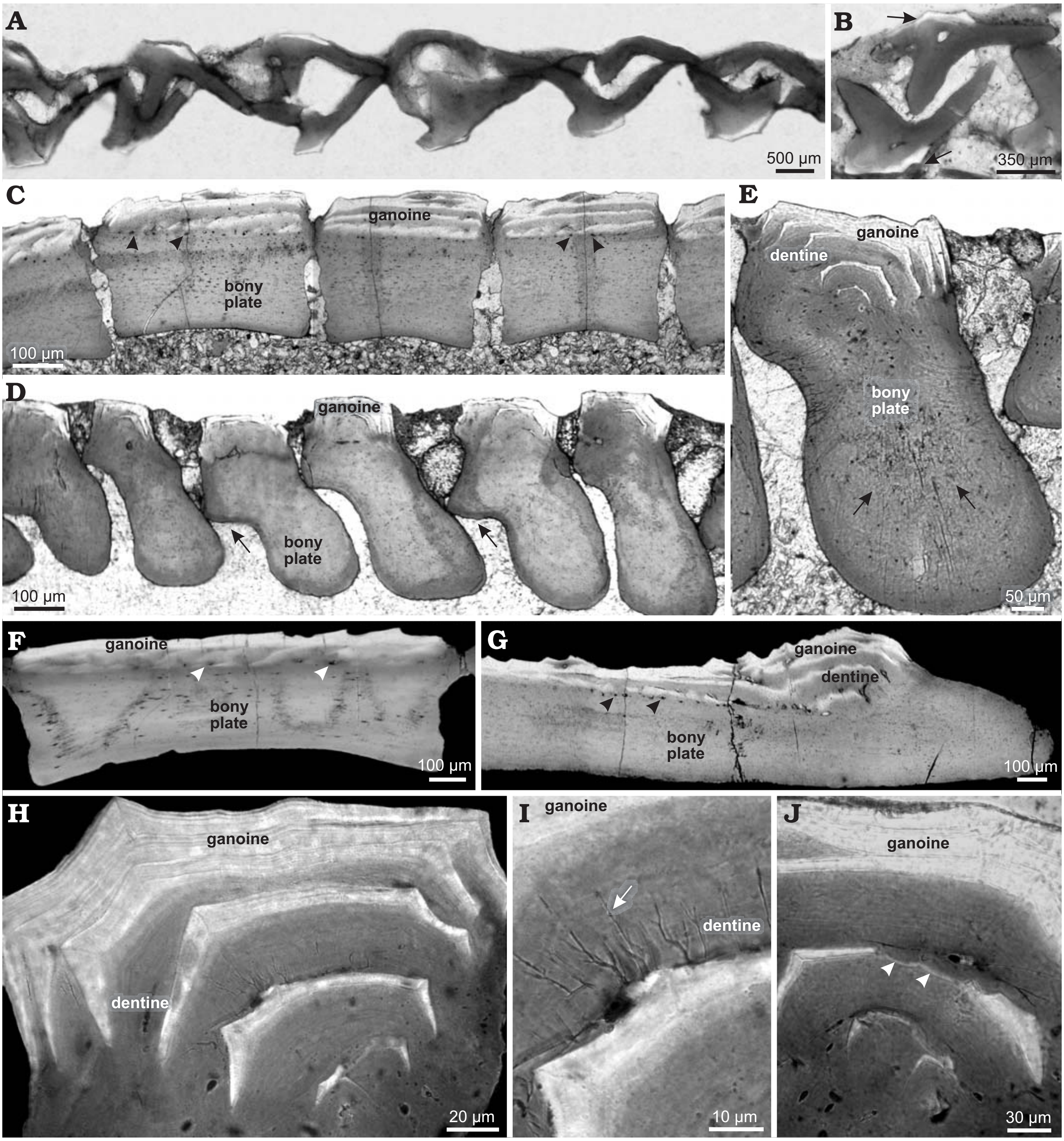


Fig. 3. Lepidotrichia of the Devonian actinopterygian *Cheirolepis canadensis* Whiteaves, 1881 from Miguasha, Canada; sample MHNM 05-132, photographed in transmitted natural light. **A**. Fragment IV (see Fig. 1A). Transversal section of the very distal part of lepidotrichia showing two opposite hemisegments. **B**. Enlargement of the same area as in A, showing ganoine (arrow) covering odontodes. **C**. Fragment I (see Fig. 1A). Longitudinal ground section showing hemisegments covered by several layers of ganoine, the dentine layers, and the bony basal plate; arrowheads point to vascular canal of the dentine. **D**. Fragment IV (see Fig. 1A). Transversal ground section showing several hemisegments; arrows point to the apophyses between two adjacent hemisegments. **E**. Fragment IV. Transversal ground section showing a hemisegment with several layers of ganoine separated by the dentine layers and the bony basal plate; arrows point to the zone where Sharpey's fibers cross the bony plate. **F**. Fragment III (see Fig. 1A). Longitudinal ground section illustrating a basal segment with ganoine covering the dentine layer and vascular canals (arrowheads). **G**. Fragment I (see Fig. 1A). Longitudinal ground section of a terminal segment showing the ganoine with the underlying dentine layer and vascular canals (arrowheads); distal is to the right. **H**. Fragment IV (see Fig. 1A). Transversal ground section, detail of the superimposed ganoine layers separated by dentine. **I**. Enlargement of H showing odontoblastic canalicles in the dentine layer (arrow). **J**. Detail of the same area as H, ganoine layers showing erosion bays (arrowheads).

be an adaptation to stiffen the caudal fin, thus enhancing swimming performance, or it may simply represent a structure that was ancestrally present in scales (see the last section of the discussion).

The deep bony part of the hemisegment is composed of cellular bone (Fig. 3C, E, F) and it is crossed by numerous Sharpey's fibers (Fig. 3E), which indicates a tight link with the dermis of the fin. Cross-sections in the proximal part of the lepidotrichia show the three characteristic components of the dermal skeleton of early actinopterygians: ganoine, dentine and a thick bony basal part (Fig. 3D, E). Ganoine strata lay on vascularised dentine, itself lying on a thick bony base (Fig. 3E, H). In the median axis of each hemisegment, ganoine strata are strictly superposed on each other, except for the deepest layers, but laterally, they are obviously separated by dentine layers (Fig. 3E, H). Thus, the top of each hemisegment grows owing to the deposition of new odontodes that are progressively wider (Fig. 3E, H). At the same time, the bony basal part thickens laterally and basally. Lepidotrichia become thinner distally (Fig. 3G). Lepidotrichia are typically crescentic in cross-sections, as is well known in teleosteans. The surface of the distal hemisegment shows patches of ganoine (Fig. 3G). The very terminal part of the segment is made up only of an osseous tissue (Fig. 3G). The patches of dentine trapped between two adjacent layers of ganoine are organized around vascular canals (Fig. 3H, I) from which ramified odontoblastic canalicles extend toward the overlying ganoine (Fig. 3I).

Between two successive deposits of odontodes on a hemisegment, a process of resorption of dentine and ganoine can be seen (Fig. 3J). This phenomenon is rare and it may result from local injury. Osteoclastic activity led to cicatrisation of the wound surfaces before the deposition of a new odontode.

Structure of paired basal fulcra.—The histological organisation of fulcra is close to that of a typical palaeoniscoid scale (e.g., Goodrich 1907: fig. 198). A ganoine layer overlays the whole surface of the fulcra above a vascularised layer of dentine (Fig. 4A, B). Cross sections show the superposed strata of ganoine (Fig. 4C, D). The first deposited odontodes are deeply inserted within the fulcra and are covered by the more recent ones (Fig. 4C–E). Each odontode is organised around vascular canals (Fig. 4D, E) and is covered by a layer of ganoine (Fig. 4D, E). As in the scales and lepidotrichia, the ganoine layer is composed of superposed strata that are laterally separated from each other by dentine surrounding a vascular canal (Fig. 4E, F). Numerous ramified odontoblastic canalicles extend from the vascular canals deep into the dentine layer (Fig. 4F). The main part of the fulcra is made of avascular cellular bone (Fig. 4B, C) that is crossed by Sharpey's fibers (Fig. 4C). Erosion bays, some of which reach the dentine, are observed at the surface of ganoine layers and even in deep layers of buried odontodes (Fig. 4G).

Discussion

In this study, the morphology and structure of the postcranial dermal skeleton of *Cheirolepis canadensis* have been analysed using both original investigations and earlier published data. Three kinds of dermal skeletal elements (scales, lepidotrichia, and fulcra) are composed of the three characteristics components of the dermal post-cranial skeleton of early actinopterygians: the superficial hypermineralised ganoine overlays the vascular dentine layer located above a thick cellular bony plate. The ganoine covering these three skeletal elements of *Cheirolepis canadensis* appears as a stratified layer like the ganoine found in other early actinopterygians (many of which were formerly called Palaeonisciformes) and in the extant Cladistia and Lepisosteidae (Ørvig 1978; Schultze 1977; Sire et al. 1987; Francillon-Vieillot et al. 1990). This tissue thus appears to have been present in the last common ancestor of the crown group of actinopterygians. The nature of ganoine has long been debated; whether ganoine was homotypic (produced by ectodermal cells) and represents a type of enamel or bitypic (produced by both mesenchymal and ectodermal cells) and is a kind of enameloid has long remained controversial. Thus, it will be helpful to briefly review the relationships between ganoine and enamel.

Characteristics of actinopterigian ganoine.—Two important features were thought to characterise ganoine of actinopterygians: the presence of microtubercles on the surface of scales (Schultze 1966; Ørvig 1967; Ermin et al. 1971; Gayet et al. 1988; Meunier et al. 1988; Sire et al. 1987; Märss 2006) and its epidermal origin (Schultze 1966; Sire et al. 1986, 1987; Richter and Smith 1995; Zylberberg et al. 1997; Sasagawa et al. 2007, 2013).

As noted by Richter and Smith (1995), the absence of ornamental microtubercles does not preclude the superficial multilayered tissue of the scales of *Cheirolepis* from being ganoine, even if microtubercles have been considered as a characteristic of actinopterygian ganoine and were of a taxonomic value in distinguishing among species, at least among actinopterygian genera (Schultze 1966; Gayet et al. 1988). Moreover, the surface of the multilayered hypermineralised tissues covering the scales of acanthodians and considered as enamel is ornamented with microtubercles but they are randomly distributed (Derycke and Chancogne-Weber 1995; Richter and Smith 1995; Märss 2006).

Since Williamson (1849), who argued that the shiny hypermineralised outer layer of osteichthyan scales was of mesodermal origin, ganoine had long been considered to be an enameloid, a mesodermal product (Nickerson 1893; Goodrich 1907; Kerr 1952; Ørvig 1967; Poole 1967), whereas enamel was considered to be an ectodermal structure (Hertwig 1879; Moss 1968; Ermin et al. 1971; Schaeffer 1977; Reif 1982; Janvier 1996). Enamel, which has long been considered to be restricted to sarcopterygians (Donoghue 2001), thus differs genetically and developmentally from enameloid (Kawasaki 2009). Recent experimental fine structural and immunohistochemical studies suggest that ganoine is homologous to enamel. Indeed, like mature enamel, mature ganoine is composed of densely packed crystallites and a reduced organic matrix (Zylberberg et al. 1985, 1997; Sire et al. 1986, 1987; Sire 1994; Richter and Smith 1995; Janvier 1996). The ganoine of extant Polypteridae and Lepisosteidae is synthesised by epidermal cells (Zylberberg et al. 1985; Sire 1994; Sasagawa et al. 2013, 2014) and shows intense immuno-reactivity to anti-mammalian amelogenin antibodies (Kogaya 1997; Zylberberg et al. 1997; Sasagawa et al. 2007, 2013, 2014). *Polypterus* enamel and ganoine contain a domain that closely resembles the C-terminal region of porcine amelogenin (Sasagawa et al. 2007). Amelogenin is a component of the extracellular matrix (ECM) of developing enamel and belongs to the family of calcium-binding proteins (SCPPS) involved in the regulation of extracellular calcium phosphate concentration in bone, dentine, enameloid and enamel. Enamel mineralisation involves the subfamily proline/glutamine-rich SCPPs containing more than 20% of proline and glutamine. This differs from the other subfamily of acidic-residue-rich SCPPs found in dentine and bone, which have more than 25% acidic amino acids (glutamic acid and aspartic acid) (Kawasaki and Weiss 2006, 2008). Despite their differences, SCPPs all originate by tandem duplication from a common ancestral gene SPARCL 1 (secreted protein, acidic, cysteine-rich like) arising from SPARC (Kawasaki et al. 2004, 2005). SCPP gene duplications in vertebrate phylogeny may have played an important role in the diversification of the major vertebrate mineralised tissues (bone, dentine, enamel, and even cartilage), as suggested by Donoghue et al. (2006) who also hypothesised that the SCPP gene duplications were concomitant with the origin of the gnathostomes. Recent investigations on the SCPP genes of the coelananth support the hypothesis that "true enamel evolved much earlier than the origin of tetrapods" (Kawasaki and Amemiya 2014). As proposed by Kawasaki (2011) "the phenotypic complexity of vertebrate hard tissues correlates with gain and loss in members of the SCPP gene family". These authors support the hypothesis that the "topology, association, and histology of the mineralised tissue types are fundamentally distinct from their origin", formulated by Moss (1964) and Maisey (1988).

The multilayered ganoine layer in *Cheirolepis canadensis* shares characteristics with ganoine of the extant Polypteridae and can be considered homologous with enamel. Given that ganoine of actinopterygians is now considered as enamel, parsimony suggests that it is homologous with enamel of sarcopterygians. Ganoine may also be homologous with similar tissues in more distant taxa, such as acanthodians (Derycke and Chancogne-Weber 1995; Janvier 1996; Märss 2006; Friedman 2007). Chondrichthyans, some osteostracans (Janvier 1985: fig. 65a) and perhaps galeaspids (Janvier 1996) also have a hypermineralized superficial tissue, possibly an enameloid that may have given rise to true enamel (summarized in Gillis and Donoghue 2007). Alternatively, enamel may have appeared before enameloid (Smith 1992, 1995). Either way, an enamel-like tissue is probably diagnostic of the dermal skeleton of a fairly large clade of early vertebrates (at least osteichthyans, potentially a larger clade including even some agnathan taxa).

These data prompt us to compare the scales of *Cheirolepis canadensis* on the one hand with those of other gnathostosomes and on the other hand with the other elements of the dermal post-cranial skeleton (lepidotrichia and fulcra) that show similarly organised odontode structures.

The scales of *Cheirolepis canadensis* compared to those of other gnathostomes.—The multilayered ganoine that overlays dentine layers located above a bony basal plate in *Cheirolepis canadensis* represents a structure typical of ganoid scales (Goodrich 1907; Aldinger 1937). The superposed layers represent several odontode generations attached to a basal bony plate, thus constituting odontocomplexes sensu Ørvig (1977), characteristic of polyodonte scales that are thought to be primitive for jawed vertebrates (Qu et al. 2013). Our pictures reveal new data and subtle differences compared to previously published accounts. For instance, our SEM pictures (Fig. $2A_1$–A_6) show fine details of the ornamentation of the scales that Goodrich (1907: fig. 202) did not illustrate, such as microtubules. Goodrich (1907) reconstructed the layer of odontocomplexes as having a smooth, continuous border with the underlying dentine. This border is far more irregular, apparently because bone was deposited on top of previously formed odontocomplexes (Fig. $2B_2$, B_4), and there is less dentine in our material than illustrated by Goodrich (1907: text-fig. 202). Thus, *Cheirolepis canadensis* appears to be more advanced than previously believed in the dentine reduction—already hypothesized by Ørvig (1977: 67)—that gave rise to the lepisosteoid scale displayed by gars (among others), in which ganoin is superposed directly onto bone, and in which dentine is absent. The superposition of a layer of ganoine over dentine is a structural organisation unique to some actinopterygians (inter alia Gardiner and Schaeffer 1989; Janvier 1996).

Like *Cheirolepis*, most late Silurian (*Lophosteus*, *Andreolepis*) and Devonian (*Lingulalepis*, *Moythomasia*) osteichthyans have small scales (Jessen 1968, 1972; Gross 1969; Janvier 1971, 1978, 1996; Pearson and Westoll 1979; Schulze 1992; Schultze and Märss 2004), but they differ in their structural organisation. The scales of *Andreolepis* are covered by a monolayer of ganoine (Schlutze 1977; Märss 2001; Chen et al. 2012). A recent 3D analysis shows that in the stem-osteichthyan *Andreolepis* (Botella et al. 2007; Friedman and Brazeau 2010; Chen et al. 2012; Brazeau and Friedman 2014), the odontodes located side by side are sequentially added onto the bony basal plate (Qu et al. 2013). *Dialipina* (Schultze 1968, 1992; Schultze and Cumbaa 2001) and *Ligulalepis* (Schultze 1968), whose affinities are controversial, but are certainly fairly basal osteichthyans (Swartz 2009), have scales with thin single-layered ganoine representing an odontocomplex in which each odontode is often fairly clearly visible, even

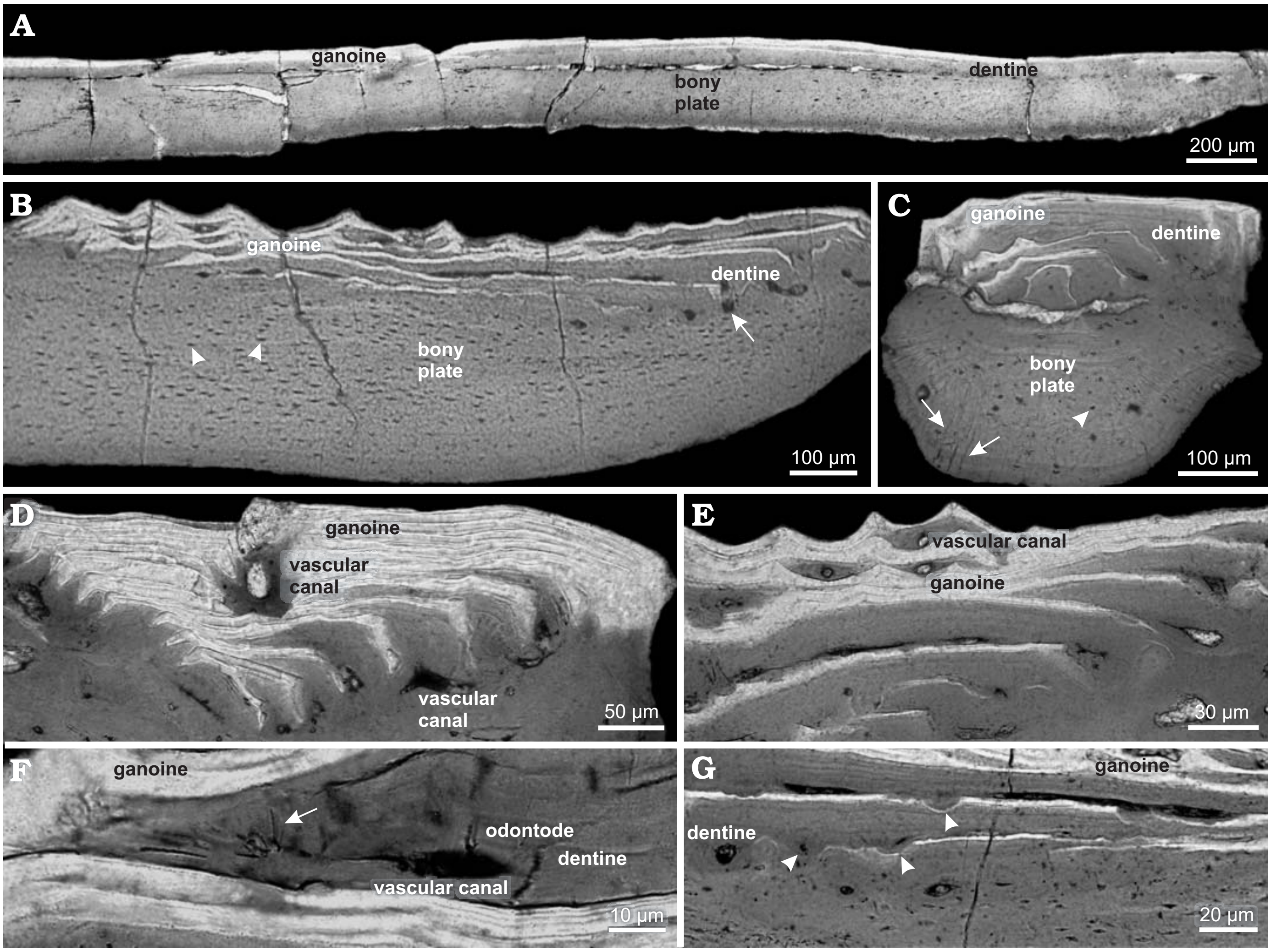


Fig. 4. Dorsal fulcra of the Devonian actinopterygian *Cheirolepis canadensis* Whiteaves, 1881 from Miguasha, Canada; sample MHNM 05-132, photographed in transmitted natural light. **A**. Fragment I (see Fig. 1A). Longitudinal section showing the organisation of a basal paired fulcrum, a layer of ganoine overlays the vascularised dentine and the bony base. **B**. Fragment I (see Fig. 1A). Longitudinal section of a dorsal fulcrum showing several superimposed layers of ganoine covering the vascularised dentine (arrow indicates a vascular canal) and the bony basal part; osteocyte lacunae are indicated by arrowheads. **C**. Fragment IV (see Fig. 1A). Cross-section of a fulcrum. Superimposed ganoine layers cover the dentine and the bony basal part is crossed by bundles of Sharpey's fibers (arrows). Arrowhead shows an osteocyte lacuna. **D**. Fragment II (see Fig. 1A). Cross-section showing the superimposed layers of ganoine organised around a central vascular canal. **E**. Fragment II (see Fig. 1A), showing superimposed layers of ganoine; each odontode is organised around a vascular canal. **F**. Fragment II. Cross section showing detail of the dentine layer and odontoblastic canalicles (arrow) that originate from a vascular canal. **G**. Fragment II. Cross section showing detail of the ganoine layers with erosion bays (arrowheads).

though it may be partly fused with adjacent odontodes. Recent works suggest that the presence of superimposed odontodes in the dermal skeleton is shared by basal osteichthyans (Zhu et al. 1999, 2006).

After a comparison of cheirolepid scale histology with that of *Dialipina*, Schultze and Cumbaa (2001) considered the micromeric scales of *Cheirolepis* as derived, contrary to Pearson (1982), who estimated that micromery was primitive; if Pearson (1982) is correct, the scales of *Cheirolepis* are more primitive than those of *Ligulalepis* and *Dialipina*, in some respects. Moreover, the scales of *Ligulalepis* and *Dialipina* are connected by a well-developed peg-and-socket apparatus (Pearson 1982), whereas we have observed only a rudimentary peg and socket between the adjacent scales of *Cheirolepis* (Fig. $2B_1$). This rudimentary articulation is probably primitive compared with the more elaborate peg-and-socket articulations found in earlier (*Ligulalepis* and *Dialipina*) and more recent actinopterygians (Pearson 1982; Gardiner 1984; Gemballa and Bartsch 2002).

Comparaisons between fringing fulcra and lepidotrichia.—Fulcra are commonly present in basal actinopterygians. Because considerable differences in pattern and distribution have occurred between lepidotrichia and fringing fulcra within actinopterytgians during their history, the potential homology between these elements remains to be demonstrated (Arratia 2008). In *Cheirolepis canadensis*, as in the earliest actinopterygians, the fringing fulcra consist of expanded terminal segments of the marginal rays. Our micrographs show that the histological organisation of the fringing fulcra of *Cheirolepis canadensis* resembles that of lepidotrichia and scales: a layer of ganoine overlapping dentine, both being deposited on a basal bone. This suggests some form of homology, or at least common developmental origin between these three skeletal dermal elements.

Are lepidotrichia transformed scales?—The old hypothesis of homology between scales and lepidotrichia, initially formulated by anatomists, harks back more than a century (Baudelot 1873; Gegenbaur 1878; Hertwig 1879) and it was clearly formalized by Goodrich (1904), but it still remains controversial. Based on the comparative study of an abundant fossil (*Cheirolepis* included) and extant material, Goodrich (1904) observed that the histology of the lepidotrichia resembles that of the scales of the species to which they belong and that there is a gradation in form and arrangement between the scales and the fin ray elements; thus, he concluded (1904: 499): that "… it may be said that the evidence derived from the study of the fossil actinopterygians points undoubtedly to the view that the lepidotrichia are homologous with the body scales, from which they have been partially, if not entirely derived." Half a century later, the same hypothesis was formulated by Jarvik (1959: 7) "… the lepidotrichia … of the fins of the teleostomes are modified scale rows and the segments are scales." Goodrich's (1904) and Jarvik's (1959) hypotheses predict that as we go back in time, lepidotrichia and fulcra should resemble scales more closely. As noted by Johanson et al. (2005) and Arratia (2008), observations of similarities between scales, lepidotrichia, and fulcra were reported in most representatives of basal actinopterygians. A diagram of transformations shows transitory stages between rhombic scales to lepidotrichia (Vorob'eva 2012).

However, observations of fin formation (Lanzing 1976; Géraudie and Landis 1982; Géraudie 1988; Durán et al. 2011; Zhang et al. 2010) and scale formation in extant actinopterygians (Neave 1936; Schönbörner et al. 1979; Sire and Akimenko 2004) pointed out differences in structural and embryologic features between these two dermal skeletal elements (Zylberberg et al. 1992). Indeed, a recent study showed that even if a dentine layer is present in scales and lepidotrichia of *Polypterus senegalus* (Zylberberg and Meunier 2013), the fine structure of these two skeletal elements differs since the dentine lies on bone in the lepidotrichia, whereas in the scales, it lies on isopedine, a peculiar osseous tissue with a plywood-like structure (Sire 1990; Daget al. 2001). As far as we know such a plywood-like structure was not described in any osteichthyan lepidotrichium. The absence of the plywood-like structure in *Cheirolepis* documents greater similarity between scales and lepidotrichia in this taxon than in geologically more recent actinopterygians.

Contrary to the scales that are formed by dermal cells, the scleroblasts (Klaatsch 1890), located within the mesoderm and that appear independently from each another, the lepidotrichia originate in an epidermal-dermal space delimited by an epithelial fold of the apical ectodermal ridge (AER), the fin fold. The successive lepidotrichial hemisegments appear and mineralise in a proximo-distal direction. The distal margin of the fins contains slender, unjoined, unmineralised rods (the actinotrichia) whose formation precedes that of lepidotrichia (Bouvet 1974; Géraudie 1977, 1988).

Since actinotrichia are unmineralised structures, they were not preserved in fossils, with very few exceptions, such as the thin fibrous actinotrichia recently described in an Amiidae of the Early Cretaceous, *Sinamia liaoningensis* (Zhang 2012). The use of ultraviolet light provides new information on such structures as shown by Tischlinger and Arratia (2013) on Late Jurassic fishes. Actinotrichia are also known from the tips of the fins of several extant actinopterygians (Bouvet 1974; Géraudie and Meunier 1980, 1982; Wood 1982; Géraudie 1977; Géraudie and Landis 1982; Schultze and Arratia 2013) and sarcopterygians (Géraudie and Meunier 1980, 1982; Géraudie 1984; Arratia et al. 2001). Thus, the presence of actinotrichia at the tip of fins and enclosed within the fin fold can be considered as a synapomorphy of Osteichthyes, or possibly of a slightly more inclusive taxon, given that their distribution in extinct taxa is very difficult to assess. As *Cheirolepis canadensis* appears to be an actinopterygian according to all phylogenetic analyses (Swartz 2009), we can infer that actinotrichia were developed at the extremity of the lepidotrichia, presumably in its paired and median fins.

The structural features reported on scales and lepidotrichia of *Cheirolepis canadensis,* especially the presence of similar articular processes in both structures (which were previously unknown in lepidotrichia) and the absence of a plywood-like structure in its scales support the hypothesis that lepidotrichia and scales are homologous (Goodrich 1904; Jarvik 1959), in addition to being produced by the same morphogenetic system (Schaeffer 1977), because as predicted by this hypothesis, as we go back in time, lepidotrichia and scales appear to resemble each other more closely. The alternative, more general hypothesis does not make this prediction, and it does not explain why lepidotrichia resemble scales more than fulcra (in having articulations, for instance) or (for their superficial portion) even oral teeth, which are also odontodes (but lack articular processes such as described here in scales and lepidotrichia). Obviously, the morphogenetic processes that generated the dermal skeletal elements in the Devonian taxon *Cheirolepis* were already able, by then, of generating highly differentiated structures (as demonstrated by the great anatomical differences between teeth and scales or lepidotrichia), but nevertheless, scales and lepidotrichia resembled each other closely, more so than in geologically more recent actinopterygians. Recent gene expression studies support a deep homology between odontodes of the scales and those of the oral teeth (Debiais-Thibaud et al. 2011). However, this does not imply that odontodes from various parts of the body (from tail to buccal cavity) necessarily look increasingly similar to each other as we go back in time because they may have appeared over a body that was already regionalised (with at least median fins), a hypothesis compatible with our knowledge of the complex evolution of the dermal skeleton in Paleozoic vertebrates (Janvier 1996). A similar reasoning has recently been applied to arthropod appendages, and as Minelli (2003: 579) concluded: "A strictly homonomous body on whose segments identical serially homologous appendages were borne has probably never existed except in the mind of typologically thinking biologists". Yet, these appendages (antennae, mandibulae, chelicerae, walking legs and book gills, among others) are produced by the same morphogenetic system (Minelli 2003), like the scales and lepidotrichia of osteichthyans. Thus, while the hypotheses of Goodrich (1904) and Jarvik (1959) predict that an early vertebrate had fins covered by structures very similar to scales, Schaeffer's (1977) more general hypothesis does not make this prediction (though it is compatible with it). Our data lend additional support to the hypothesis that lepidotricha are transformed scales, even though differences between both structures already existed in the Devonian stem-actinopterygian *Cheirolepis*.

Concluding remarks

Our histological study illustrates the excellent preservation of the *Cheirolepis* fossil material that has allowed microscopic observations down to the ultrastructural level. A similar histological organisation is shared by the three dermal skeletal elements: scales, fulcra and lepidotrichia. They contain, from the surface to the deep dermis, pluristratified ganoine, a vascularised dentine layer and a bony basal plate. Each of the elements of the dermal postcranial skeleton performs a different function: scales have a protective function, in addition to strengthening the axial skeleton (at least in early osteichthyans) and reducing hydrodynamic drag (Reif 1978; Burdak 1979), whereas lepidotrichia sustain the fins, and fulcra strengthen the leading edge of fins. The three elements belong to the same morphogenetic system, as already mentioned by Schaeffer (1977), but their morphology was probably modulated to better perform their respective functions. New similarities between scales and lepidotrichia documented here support the idea that lepidotrichia may be derived from scales.

Acknowledgements

We thank Johanne Kerr and Sylvain Desbiens (both Parc de Miguasha, Quebec, Canada) for loaning the specimens of *Cheirolepis canadensis* and for giving permission to section them. We are grateful to Vincent Rommevaux (MNHN, Paris) for his technical assistance with ground sections and to Omar Boudouma (Institut des Sciences de la Terre de Paris, Université Pierre et Marie Curie, Paris, France) for his assistance using the SEM facility at the Service commun de Microscopie à Balayage of the ISTEP. We also thank Alessandro Minelli (University of Padova, Italy) and Patrick Laurenti (Université Paris 7-Denis Diderot, France) for constructive discussions and papers that they sent us, Gloria Arratia (University of Kansas, Lawrence, USA) for useful comments on the draft, and the Editor, Stephen Brusatte (University of Edinburgh, UK), for his efficient handling of the draft.

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