



Evolution

Histology of *Polypterus senegalus* fin rays revisitedRévision de l'histologie des rayons de nageoires de *Polypterus senegalus*Louise Zylberberg^{a,*}, François J. Meunier^b^a CNRS UMR 71 93, ISTEP, université Pierre-et-Marie-Curie, 4, place Jussieu, BC 19, 75252 Paris cedex 05, France^b CNRS UMR 72 08 (IRD-UPMC-MNH), BOREA-DMPA, Muséum national d'histoire naturelle, CP 026, 43, rue Cuvier, 75231 Paris cedex 05, France

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ABSTRACT

The present comparative histological study of the pectoral, caudal and anal fins of the polypterid *Polypterus senegalus* reveals the presence of a layer of dentine identified between the superficial ganoine patches and the bony part of the lepidotrichia in the three fins. Its extent varies depending on the fins. Similarly, the ganoine layer present at the surface of the proximal lepidotrichia shows fin-dependent differences in extent and distribution. The dentine layer is crossed by a system of thin worm-like vascular canaliculi that reach the ganoine layer and even penetrate within it as in the scales. In the lepidotrichia, the dentine lays directly on bone, which differs from the scales where dentine lies on isopedine, a plywood-like structure. Another difference between scales and lepidotrichia is the presence of actinotrichia that are unmineralised, fusiform rods of elastoidine located at the tip of the fins. Ontogenesis with differentiation of actinotrichia has no equivalent in scale formation. Although structural features are shared by lepidotrichia and scales in *P. senegalus*, observations on the scales and lepidotrichia support the hypothesis of Schaeffer (1977) that "scales and lepidotrichia are somewhat differently shaped manifestations of the same morphogenetic system".

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R É S U M É

La présente étude histologique comparée des nageoires pectorales, caudales et anales d'un polyptéridé, *Polypterus senegalus*, révèle la présence d'une couche de dentine située entre les plaques de ganoïne et le tissu osseux des lépidotriches des trois catégories de nageoires observées. L'importance de cette couche de dentine varie selon les nageoires, comme c'est le cas des plaques de ganoïne. La couche de dentine est parcourue par un réseau de fins canaliculi vermiformes et ramifiés, qui atteignent la couche de ganoïne et peuvent s'y insinuer, comme c'est le cas dans les écailles. Dans les lépidotriches, la couche de dentine repose directement sur le tissu osseux, alors que dans les écailles, la dentine est déposée sur l'isopéidine, une structure en contreplaqué. Une autre différence entre les écailles et les lépidotriches réside en la présence d'actinotriches, bâtonnets collagéniques, fusiformes, non minéralisés, situés à la pointe des nageoires. Une ontogenèse avec différenciation d'actinotriches n'a pas d'équivalent au cours de la formation des écailles. En dépit de certains caractères structuraux communs aux lépidotriches et aux écailles, nos observations étayent l'hypothèse de Schaeffer (1977), selon qui « les écailles et les lépidotriches sont des manifestations d'un même système morphogénétique à l'origine de formes variées ».

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1. Introduction

The post-cranial skeleton of Actinopterygii is composed of several kinds of mineralised elements: scales, fin rays, scutes, fulcra and spines (Arratia, 2008, 2009; Schultze and Arratia, 1989). These skeletal elements show various differences in morphology, histological structure, and function; nevertheless they are frequently interpreted as homologous structures (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, bony rays that sustain pair and impair fins. In a pioneering work, Baudelot (1873) already noted structural similarities between scales and fin rays in Teleostei and he suggested a relationship between scales and fin rays. Lepidotrichia have been considered as transformed scales by Goodrich (1904) and Jarvik (1959) because of the morphological continuity between the scales and the lepidotrichia and because of histological similarities. Goodrich (1904) and Jarvik (1959) established their hypothesis on observations of these two dermal components in extinct Actinopterygii and in the extant ones that have preserved plesiomorphic features. The rhombic scales of *Acipenser ruthenus* were described as a primary form submitted to size and shape transformations. The diagram of transformations (Vorob'eva, 2012) shows that lepidotrichia are derivatives of the rhombic scales. But similar morphological studies carried out in extant Teleostei have shown differences in organisation and ontogeny between scales (i.e. Fouda, 1979; Goodrich, 1907; Meunier, 1984; Neave, 1936; Schönborner et al., 1979; Sire, 1986; Sire and Géraudie, 1983; Sire and Meunier, 1981; Zylberberg and Nicolas, 1982) and lepidotrichia (i.e. Becerra et al., 1983; Géraudie, 1983; Goodrich, 1904; Lanzing, 1976; Montes et al., 1982). Because of these differences and the lost of ganoine and dentine in the scales and in the lepidotrichia of Teleostei, the hypothesis that lepidotrichia derive from scales appears inappropriate when applied to Teleostei (Géraudie and Landis, 1982). More recently, this hypothesis was discussed by Johanson et al. (2005) and Arratia (2008). According to Arratia (2008), previous observations on basal Actinopterygii revealed similarities between scales, fins and fulcra including ganoine ornaments but the “scale–fin ray connection is not observed in advanced Actinopterygii”.

Two taxa of extant Actinopterygii, the Lepisosteidae and the Polypteridae, which retain plesiomorphic features in their dermal skeleton, yield recent data in the context of possible relationships between scales and lepidotrichia. The dermal skeleton of the Lepisosteidae shows some specialisations such as Williamson's cells and canaliculi in bony tissues (Schultze, 1977; Sire and Meunier, 1994), and the lack of dentine, at least in the extant taxa (see for extinct Lepisosteidae: Brito et al., 2000), between the ganoine layer and the bony basal plate of the scales (Goodrich, 1907; Kerr, 1952; Sewertzoff, 1932; Sire et al., 2009) and lepidotrichia (Goodrich, 1904). This lack of dentine may be related to an evolutionary trend towards the

reduction of the dermal skeleton (Francillon-Vieillot et al., 1990; Zylberberg et al., 1992a; Zylberberg et al., 2010). Polypteridae which occupy a more basal position than the Lepisosteidae in the phylogeny of Actinopterygii (Daget, 1950; Gardiner and Schaeffer, 1989; Lauder and Liem, 1983; Patterson, 1982; Zhu and Schultze, 2001) retain dentine in their scales between the superficial ganoine layer and the basal plate (i.e. Daget et al., 2001; Kerr, 1952; Meunier, 1980). The data concerning the presence of dentine in polypterid lepidotrichia are uncertain. Indeed, in his review of the structure of the dermal fin rays, Goodrich (1904) mentioned that when lepidotrichia “grow older the segments gradually acquire a structure exactly similar to that of the body-scales with a covering coat of ganoine” (page 479) but he did not indicate whether dentine is present or not. Dentine was not found in the polypterid lepidotrichia neither by Meunier (1980) nor by Meinke (1982); Géraudie (1988) also failed to find dentine in the pectoral fins in *Polypterus senegalus* and *Erpetoichthys calabaricus* using TEM techniques. Only Schaeffer (1977) showed in some lepidotrichia of the caudal fin of *Polypterus*, a layer located beneath the enamel that was presumed to be dentine.

In this study, we reinvestigate the histological organisation of lepidotrichia in pectoral, caudal and anal fins of *P. senegalus* to obtain more precise comparative data, especially about the dentine layer. These data are needed to establish an eventual link between lepidotrichia and scales. For the histological structure of scales, we refer to the basic morphological studies of Goodrich (1907), Sewertzoff (1932), Kerr (1952), Meunier (1980) and Sire (1989, 1990).

2. Material and methods

2.1. Material

The present study was carried out on the fins of an adult male *P. senegalus* (Cuvier, 1829) (254 mm length) from Ivory Coast. The left pectoral, anal and caudal fins were fixed in 70% ethanol.

2.2. Ground sections

The fin samples were dehydrated in absolute ethanol, transferred into acetone, and embedded in straryl polymer. Transversal and longitudinal sections (150–200 µm thick) were cut with an Isomet sawing machine and ground to 50–75 µm in thickness. The sections were observed under transmitted natural and polarised light with a Zeiss Axiovert 35 microscope equipped with Nomarski Differential Interference Contrast (DIC).

2.3. Scanning electron microscopy (SEM)

After a soft cleaning with a 1% sodium hypochlorite solution, the samples were dehydrated in a graded series of ethanol and air-dried. The air-dried samples were glued on copper stubs, coated with gold and observed in a JEOL-SEM 35 scanning microscope at 25 kV.

3. Results

3.1. Morphology

The fin rays of polypterids are formed by the lepidotrichia bony rods composed of short adjacent segments (Fig. 1(a), (b)) connected by joints. Each lepidotrichium consists of two parallel and symmetrical concave bony elements named “demirays” (Kemp and Park, 1970) or “hemisegments” (Lanzing, 1976), as described in teleostean fins. The most proximal segments of *Polypterus* fins show patches of ganoine on their upper surface (Fig. 1(a), (b)). The patches are irregular and more or less developed depending on the fins. All fins were observed at the proximal level to avoid structural variations that could be related to their location. The patches of ganoine are liable to erosion (Fig. 1(a), (b), (d)). The ganoine surface appears smoother than the bony one (Fig. 1(a), (b)). However, SEM examination at high magnification reveals the presence of small rounded elevations scattered on the ganoine surface (Fig. 1(c)). The diameter of the elevations (2.19–3.20 μm) and the distance (5.57–8.54 μm) between them have been shown to be characteristic of the extant Polypteridae (Gayet and Meunier, 1986; Meunier et al., 1987). Similar structures in scales of extinct actinopterygians were coined tubercles by Schultze (1966). Because of the small size of these elevations in *P. senegalus*, we call them microtubercles. Holes at the bony surface (Fig. 1(a), (b)) correspond to the openings of vascular canals that cross the hemisegments.

3.2. Histology

The histological characteristics of the pectoral, caudal and anal fins were observed on ground sections. In order to prevent repetition of similar descriptions throughout this article, the histological characteristics shared by the hemisegments of the fins are first described and their specific aspects regarding the different fins will be reported afterwards. They mainly concern the ganoine cover and the underlying dentine layer.

The opposing concave segment pairs form a partially enclosed space for connective tissue (Fig. 1(e)), the intrasegmental region (Becerra et al., 1983).

Cross sections of lepidotrichia (Fig. 1(f)–(l)) show that collagen bundles called intralepidotrichial ligaments by Becerra et al. (1983) cross this space, connecting the segments of the same pair (Fig. 1(k)). Cross sections of the distal part of the lepidotrichia show that they are branched. Each hemisegment of the same pair divides dichotomously into two more distal hemisegments (Fig. 1(g)). The lateral sides of the hemisegments are crossed by strong bundles of collagen, the interlepidotrichial ligaments (Becerra et al., 1983), which connect adjacent lepidotrichia (Fig. 1(i)).

The lepidotrichia are made up of cellular bone (Fig. 1(l)).

The organisation of the collagen fibrils defines different areas in a hemisegment. The classification of bone tissues by Francillon-Vieillot et al. (1990) referring to collagen fibril organisation is used throughout the text. The outer part of a lepidotrichial hemisegment is composed of a parallel

fibred bone tissue (Fig. 1(h), (l)). The orientation of the collagen fibrils is roughly parallel to the outer surface of the hemisegment (Fig. 1(h), (k), (l)). Osteocytes randomly distributed in the outer matrix are spindle-like with short cellular processes (Fig. 1(l)). The central core of a hemisegment is made of a more compact woven fibred bone where osteocytes are rare.

In ground sections, the ganoine appears as individual units that can be considered as odontodes. These units show a clear-cut limit with the underlying layer, the location and aspect of which correspond to the “presumed dentine layer” described by Schaeffer (1977). This layer, more or less developed depending on the fins, does not show a sharp limit with the bony tissue that constitutes the main part of hemisegments. Dentine is crossed by thin odontoblastic canaliculi that appear as irregular, worm-like ramifications (Fig. 2(a)–(d)).

An organisation of the collagen fibrils resembling a plywood-like structure was not observed between dentine and bone (Fig. 1(l), Fig. 2(a)).

3.3. Pectoral fin

Cross sections of the pectoral fin show that the ganoine cover forms a small surface at the top of each hemisegment (Fig. 1(i)). Few superimposed units were observed at the surface of the pectoral fins (Fig. 1(j)). The ganoine unit shows a clear-cut separation from the thin layer of dentine inserted between the ganoine unit and the underlying bone (Fig. 1(j)). Very few and thin odontoblastic canaliculi form a loose web that reaches the ganoine.

3.4. Caudal fin

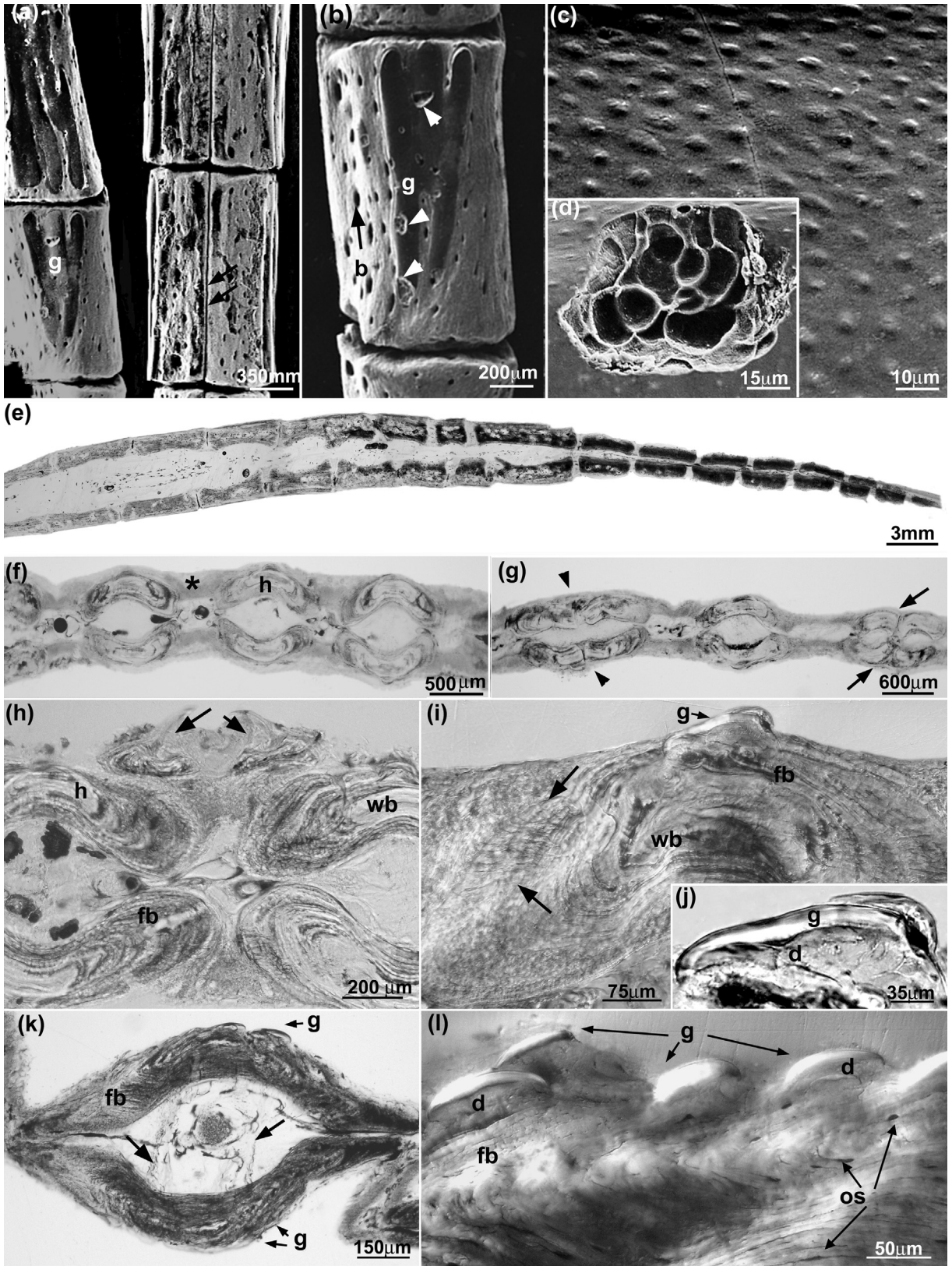
The hemisegment of the caudal fin is covered by series of odontodes (Fig. 1(k), (l)). The ganoine units are distributed side-by-side rather than overlapping (Fig. 1k, l). A thin layer of dentine underlies the ganoine units. This layer is crossed by very thin odontoblastic canaliculi irregularly distributed in the different odontodes (Fig. 2(a)).

3.5. Anal fin

The anal fin shows more numerous ganoine units (Fig. 2(b)). They form superimposed generations (Fig. 2(c)). Each ganoine unit lies on a layer of dentine (Fig. 2(c), (d)). The limit between ganoine and dentine is sharp, whereas that between dentine and the underlying lamellar bone is not clear-cut. In the anal fins, the network formed by odontoblastic canaliculi is more developed than in the other two fins examined; nevertheless, the odontoblastic canaliculi that cross the dentine are very thin. They extend toward the ganoine, contact it (Fig. 2(d)), and even penetrate it.

4. Discussion

This histological examination of the pectoral, caudal and anal fins of the polypterid *P. senegalus* confirms the presence of ganoine at the surface of the proximal lepidotrichia but with differences in the extent and distribution of odontodes depending on the fins. The results reported



in the present study concern observations of the proximal level of all fins. Odontode frequency is lesser on the pectoral fins and greater on the anal fins, where they form superimposed layers (this study Fig. 2(c), (d)). The formation of odontodes at the surface of the lepidotrichia has already been described either as isolated, superimposed (Hertwig, 1879), or organised in odontocomplexes (Ørving, 1978).

Our micrographs reveal the presence of a thin layer wedged between the superficial ganoine and the bony part of the lepidotrichia in the three fins. This layer displays structural characteristics of dentine. Indeed, it could be compared to the dentine described in the scales of the polypterids where it is characterised by a system of thin and worm-like odontoblastic canaliculi without an obvious central canal (Daget et al., 2001; Ørving, 1978). In the lepidotrichia of the anal and caudal fins of *P. senegalus*, where ganoine units are more numerous than in the pectoral fins, our micrographs show that the thin odontoblastic canaliculi reach the ganoine layer and even penetrate within it as in the scales of *Polypterus bichir* represented by Ørving (1978). The occurrence of dentine in the lepidotrichia of *P. senegalus* supports Goodrich's report (1904) concluding that the "segments of lepidotrichia (of polypterids) acquire a structure exactly similar to that of body-scales".

However, there is a structural difference between lepidotrichia and scales in Polypteridae. In lepidotrichia, dentine lies directly on bone (this study Fig. 1(i), (l), Fig. 2(a)), whereas in the scales, dentine lies on isopedine (=elasmodine, Schultze, 1996), a plywood-like structure described in scales of extant (Sire, 1989, 1990) and extinct (Gayet and Meunier, 1992; Meunier and Gayet, 1996; Smith et al., 2006) Polypteridae, among other taxa.

Another difference between scales and lepidotrichia is the presence of actinotrichia at the tip of polypterid fins, as in other actinopterygian fins (i.e., Blanc, 1951; Géraudie, 1988; Goodrich, 1904; Prenant, 1937; Ryder, 1884). In Actinopterygians, actinotrichia are unmineralised,

alised, fusiform rods of elastoidine found at the tip of each lepidotrichium where they provide a flexible support to the fin end. To our knowledge, ontogenesis of lepidotrichia with formation of actinotrichia has no equivalent in scales. The only structures that show actinotrichia at their tip are the ventral caudal fulcra (the "fulcral scales" of Goodrich, 1904, p.500) that border the ventral most principal caudal ray of the caudal fin in *Lepisosteus osseus* (Schultze and Arratia, 1989, Fig. 18), but these fulcra are more similar to lepidotrichia than to scales.

The structural differences between scales and lepidotrichia prompted us to compare their ontogenetic stages. The polypterid scales appear as cycloid scales (Guittel, 1914) that acquire very early an isopedine layer wedged between an overlying dentine layer and a subjacent bony basal plate (Sire, 1989, 1990). The scales arise independently from each other like the cycloid scales of other actinopterygians (Neave, 1936). Scales of *P. senegalus* develop later than lepidotrichia of the fins in ontogeny (Bartsch et al., 1997), like the scales of teleosts (Sire and Akimenko, 2004).

The formation of lepidotrichia is directed by actinotrichia in *Polypterus* and *Erpetoichthys* (Géraudie, 1988). The first lepidotrichium segment appears within an epidermal-dermal space; then, the successive hemisegments are formed in a proximo-distal direction, and they are calcified in the same direction by neoplastic ossification (Géraudie, 1988). This is similar to what is known in other osteichthyans (Blanc, 1951; Géraudie, 1978, 1983; Ryder, 1884). The relationships between actinotrichia and lepidotrichia were particularly well illustrated in teleosts by Kemp and Park (1970), Géraudie (1978, 1983), Montes et al. (1982), Géraudie and Landis (1982), Becerra et al. (1996) and, Durán et al. (2011). Actinotrichia are thought to maintain the structural integrity of the early fin fold from which the lepidotrichia originate (Dane and Tucker, 1985).

This hypothesis could be supported by recent data on specific proteins identified in teleostean actinotrichia.

Fig. 1. a–d: SEM. Segments of lepidotrichia of the caudal fin. a: two hemisegments separated by a narrow space (arrows). Ganoine patch (g) on the surface of a segment. b: detail of part a showing the ganoine patch (g). Holes (arrow) correspond to openings of blood vessels arising from the bony tissue (b). Erosion areas are visible on the ganoine (g) surface (arrow heads). c: microtubercles scattered on the ganoine surface. d: detail of an erosion lacuna at the surface of the ganoine patch. e: caudal fin. Natural light. Longitudinal ground section showing the two opposed hemisegments of a lepidotrichium. f: pectoral fin. Natural light. Ground cross section. Interlepidotrichial ligaments (asterisk) connecting two adjacent hemisegments (h). g: pectoral fin. Natural light. Ground cross section. A hemisegment is dividing into two hemisegments (arrowheads). Dichotomised hemisegments (arrows). h: pectoral fin. Natural light. Ground cross section. Denticles (arrows) between two hemisegments (h). fb: parallel fibered bone; wb: woven bone. i: pectoral fin. Natural light. Ground cross section. A ganoine unit composed of two odontodes (g). Sharpey fibres (arrows) connecting the hemisegment to the surrounding connective tissue. fb: parallel fibered bone; wb: woven bone. j: pectoral fin. Detail of i showing the ganoine layer (g) covering a thin layer of dentine (d). k: caudal fin. Natural light. Ground cross section. Intralepidotrichial ligaments (arrows). fb: pseudo-parallel fibered bone. g: ganoine. l: caudal fin. Nomarski interference. Ground cross section. Superficial ganoine (g) covering patches of dentine (d). Dentine lies on a parallel fibered bone (fb). os: osteocytes.

Fig. 1. a–d : MEB. Articles de lépidotriche de la nageoire caudale. a : les deux moitiés d'un article sont séparées par un espace étroit (flèches). Plaque de ganoïne (g) à la surface d'un article. b : détail de la figure a montrant la plaque de ganoïne (g). Les orifices (flèche) correspondent aux débouchés des vaisseaux sanguins du tissu osseux (b). Des zones d'érosion (têtes de flèche) sont visibles à la surface de la ganoïne (g). c : microtubercules dispersés à la surface de la ganoïne. d : détail d'une zone d'érosion à la surface de la ganoïne. e : nageoire caudale. Lumière naturelle. Coupe longitudinale d'un lépidotriche montrant les deux moitiés d'articles disposées en vis-à-vis. f : nageoire pectorale. Lumière naturelle. Coupe transversale. Ligaments interlépidotrichiens (astérisque) réunissant les deux moitiés d'articles adjacents (h) d'un lépidotriche. g : nageoire pectorale. Lumière naturelle. Coupe transversale. Chaque article se divise en deux (têtes de flèche) donnant naissance à deux articles par dichotomie (flèches). h : nageoire pectorale. Coupe transversale. Denticules (flèches) entre deux articles (h). fb : os à fibres parallèles ; wb : os à fibres enchevêtrées. i : nageoire pectorale. Lumière naturelle. Coupe transversale. La plaque de ganoïne comprend deux odontodes (g). Des fibres de Sharpey (flèches) unissent l'article du lépidotriche au tissu conjonctif environnant. fb : os à fibres parallèles ; wb : os à fibres enchevêtrées. j : nageoire pectorale. Détail de la figure i montrant la couche de ganoïne (g) couvrant une fine couche de dentine (d). k : nageoire caudale. Lumière naturelle. Coupe transversale. Ligaments intralépidotrichiens (flèches). fb : os à fibres parallèles. g : ganoïne. l : nageoire caudale. Contraste interférentiel différentiel (Nomarski). Coupe transversale. La ganoïne superficielle couvre des îlots de dentine (d) qui reposent sur de l'os à fibres parallèles (fb). os : ostéocytes.

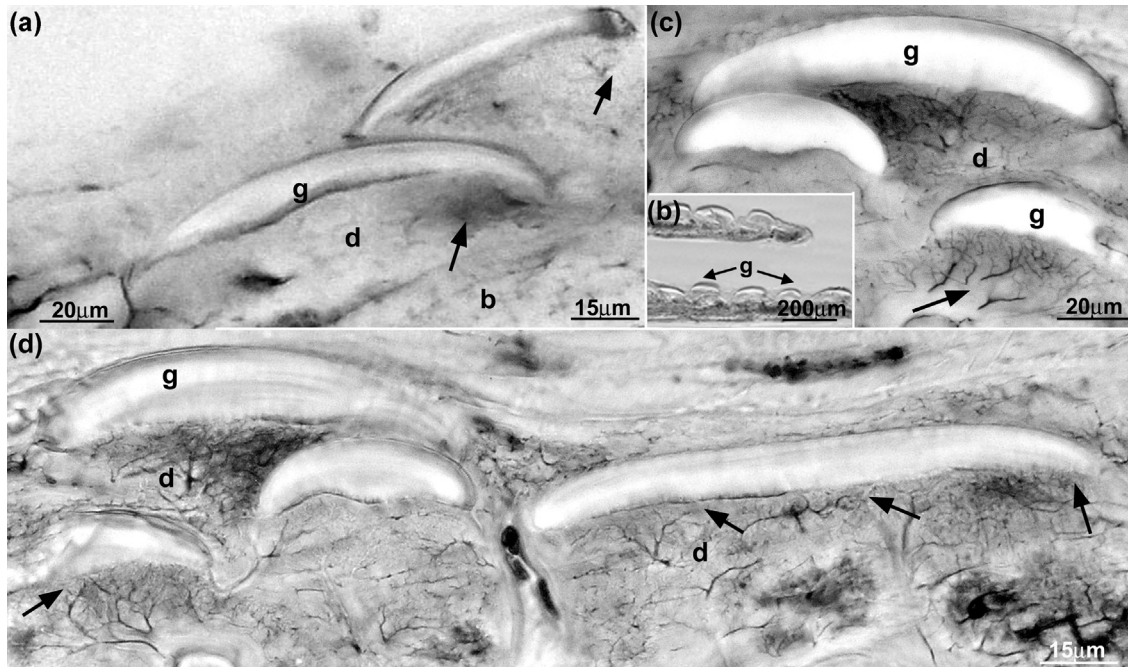


Fig. 2. a: caudal fin. Natural light. Ground cross section. Ganoine (g) and dentine (d) layers. The dentine lies on the osseous tissue (b). Few very thin odontoblastic canaliculi in the dentine (arrows). b: anal fin. Natural light. Longitudinal ground section. General view. g: ganoine. c: anal fin. Natural light. Ground longitudinal section. Ganoine (g) and dentine (d) layers. Beneath the ganoine units, the dentine layer show a network formed by thin odontoblastic canaliculi (arrow). d: anal fin. Natural light. Ground longitudinal section showing details of ganoine units (g). The thin odontoblastic canaliculi of the dentine (d) are in contact with the ganoine (arrows).

Fig. 2. a : nageoire caudale. Lumière naturelle. Coupe transversale. Couches de ganoïne (g) et de dentine (d). La dentine est au contact du tissu osseux (b). De fins canalicules odontoblastiques (flèches) sont peu nombreux dans la dentine. b : nageoire anale. Lumière naturelle. Coupe longitudinale. Vue générale. g : ganoïne. c : nageoire anale. Lumière naturelle. Coupe longitudinale. La dentine située sous la ganoïne est parcourue par un réseau de fins canalicules odontoblastiques (flèche) dentine : d ; ganoïne g. d : nageoire anale. Lumière naturelle. Coupe longitudinale. Les fins canalicules odontoblastiques de la dentine (d) sont au contact de la ganoïne (flèches). Plaques de ganoïne : g.

Besides two regular fibrillar collagens, type I collagen, a heterotrimer constituted of three α chains ($\alpha 1(1)$)₂ ($\alpha 2(1)$) chains encoded by *col1a1* gene and by *col1a2* gene respectively and type II collagen a homotrimer constituted of three identical α chains ($\alpha(II)$)₃ encoded by the *col2a1* gene, the actinotrichia of the teleosts *Carassius auratus* and *Danio rerio* contain a different form of type II collagen encoded by the *col2a1b* gene arising as a duplication of the *col2a1* gene (Durán et al., 2011). Specific proteins actinodin 1 and 2 (Zhang et al., 2010) have been identified in the actinotrichia of the zebrafish *Danio rerio* and in the ceratotrichia of the chondrichthyan *Callorhynchus milii* (homologous of teleostean actinotrichia (Kemp, 1977)). The specific type II collagen and actinodins 1 and 2 are essential for actinotrichia morphogenesis and thus, for fin formation. The absence of these specific components in tetrapods is thought to be a prerequisite for the evolution from fins to limbs concomitant to the origin of tetrapods (Durán et al., 2011; Zhang et al., 2010).

In contrast, another duplicated gene expressed in the scales of actinopterygians gives a peculiar type I collagen that does not appear to play a role in scale formation. Indeed, the actinopterygians scales contain a peculiar type I collagen encoded by three genes *col1a1*, *col1a2* and *col1a3* (Kimura et al., 1987, 1991; Piez, 1965; Saito et al., 2001) that differs from the regular type I collagen encoded by only two

genes *col1a1* and one *col1a2*. The gene *col1a3* is thought to have arisen by duplication of *col1a1* gene (Zylberberg et al., 1992b) that may have occurred during the duplication of the actinopterygian genome, soon after the divergence between actinopterygians and sarcopterygians (Movan-Dubois et al., 2003). The $\alpha 3$ chain of type I collagen is not restricted to the scales; rather, it is synthesised in various dermal connective tissues and in osseous tissues of actinopterygians (Kimura et al., 1987, 1991; Piez, 1965; Saito et al., 2001). The widespread distribution of scales in extinct and extant osteichthyans and their transient persistence in the basal tetrapods might be related to the function of these reinforcing mineralised structures that sheath the body surface and act as a barrier protecting the underlying soft tissues (i.e.; Vorob'eva, 2012; Witzmann, 2007, 2011; Zylberberg et al., 1992a).

This study evidences some structural features shared by lepidotrichia and scales in *Polypterus senegalus*. However, the recent observations of fin formation in teleosts (Durán et al., 2011; Zhang et al., 2010) and sarcopterygians (Zylberberg et al., 2010), together with previous reports (Arratia, 2008; Géraudie and Landis, 1982; Johanson et al., 2005) on embryologic and structural features, support the hypothesis of Schaeffer (1977) that "lepidotrichia and scales share the same components: enameloid, dentine, bone, which reflects the existence of the same

morphogenetic system responsible for both the maintenance of basic morphological arrangements and the generation of diversity”.

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