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Écailles, émail, cosmine, ganoïne et premiers ostéichthyens

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ABSTRACT

Ganoine is a different enamel from “true” enamel. The crystallites end in the middle of the projection of epidermal cell onto the ganoine surface. In contrast, “true” enamel shows the borders of the hexagonal epidermal cells. Cosmine is a combination of tissues (“true” enamel and dentine) and a structure (the pore–canal system). The pore–canal system opens in regular arranged pores on the scale surface and has a network of horizontal canals (mesh canals). Cosmine is limited to sarcopterygians possibly above actinistians and onychodonts, ganoine to actinopterygians. – Actinopterygian scales possess a narrow peg, an anterodorsal extended corner and ganoine either as overlapping or as multilayered enamel, whereas sarcopterygian scales have a broad based peg, no extended anterodorsal corner with two exceptions, but sometimes an anteroventral extension and cosmine. – The genera *Andreolepis*, *Dialipina*, *Naxilepis*, *Terenolepis*, *Ligulalepis* and *Orvikuina* are actinopterygians based on their scale characters. Additionally, *Guiyu*, *Meemannia*, *Achoania* and *Psarolepis* possess actinopterygian features. According to its scale characters *Lophosteus* is a stem osteichthyan.

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R É S U M É

La ganoïne est un émail différent de l'émail « vrai ». Les cristallites s'y terminent au centre de la projection des cellules épidermiques sur la surface de la ganoïne. Au contraire, l'émail « vrai » conserve la trace des bords des cellules épidermiques hexagonales. La cosmine est une combinaison d'un tissu (émail « vrai » et dentine) et d'une structure (le système pores–canaux). Le système pores–canaux s'ouvre en un arrangement régulier à la surface de l'écaille et possède un réseau de canaux horizontaux (canaux en réseau). La cosmine est limitée aux sarcoptérygiens, éventuellement plus dérivés que les actinistiens et onychodontes, la ganoïne aux actinoptérygiens. Les écailles des actinoptérygiens possèdent un tenon articulaire étroit, un angle antéro-dorsal prononcé et de la ganoïne à émail soit recouvrant, soit pluristratifié, tandis que les écailles de sarcoptérygiens ont un tenon articulaire à large embase, pas d'angle antéro-dorsal prononcé, sauf deux exceptions, mais parfois une extension antéro-ventrale et de la cosmine. Les genres *Andreolepis*, *Dialipina*, *Naxilepis*, *Terenolepis*, *Ligulalepis* et *Orvikuina* sont des actinoptérygiens d'après les caractères de leurs écailles. En outre, *Guiyu*, *Meemannia*, *Achoania* et *Psarolepis* présentent des traits d'actinoptérygiens. D'après les caractères de ses écailles, *Lophosteus* est un ostéichthyen souche.

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1. Introduction

At the beginning of palaeoichthyology, Agassiz's classification of fossil and recent fishes was based on scale morphology. Agassiz (1833–1843) grouped the fishes into four orders based on scale morphology: Ordres des Cycloïdes, des Cténoïdes, des Ganoïdes et des Placoïdes. His orders Cycloïdes and Cténoïdes represent the teleosts in today's classification and the order Placoïdes the chondrichthyans. The order Ganoïdes represents a mixed bag including lower actinopterygians (Holostei and Palaeonisciformes), armored teleosts, dipnoans, coelacanth and acanthodians. The scale terms are still in use even though Peters (1841) and many other subsequently have shown that there is no distinction between cycloid and ctenoid scales, except for serration or ctenae on the free field of ctenoid scales; both scale types may occur on the same fish (e.g., *Percichthys*; Arratia, 1982). Roberts (1993) has shown that the ornamentation and the serrations are different in different ctenoid scales, and that ctenoid scales developed independently in different teleostean lineages from cycloid scales. Cycloid (and ctenoid) scales are round scales with circuli. This type of scales occurring in teleosts crownward to *Leptolepis coryphaenoides* (= *Leptolepis coryphaenoides* and more advanced teleosts; Arratia, 1999) alone can be distinguished from all other round scales with radial structures in the covered field.

French colleagues since Bertin (1944) use the term elasmoid scale for both kinds of round scales. The basal layer of elasmoid scales (see Meunier and Géraudie, 1980 for a survey of the term) is composed of fibrous layers in plywood fashion (Meunier, 1984); these layers of crossed fibers were previously described by Agassiz (1833–1843) and other researchers in the 1800s. Elasmoid scales developed from ganoid scales in many lineages by losing the superficial layer (ganoine or cosmine), transforming the basal layer into a thin superficial layer with or without bone cells, and forming a new flexible basal layer in plywood fashion (Schultze, 1966, 1977, 1996). Sire (1990) observed the new formation of a flexible layer in early stages of *Polypterus* scales, which is a parallel appearance in lower actinopterygians judging from the phylogenetic position of *Polypterus*. Nevertheless, it may indicate an early ontogenetic formation of the flexible layer. Meunier and Brito (2004) argued that the outer layer is a new formation, a layer without bone cells, as occurring in an undetermined 'pholidophorid' (*Pholidophorus* sp.) above the ganoine, and that the bony base transforms into the flexible basal layer losing the bone cells. Consequently, the ganoine layer disappears. That scenario seems unlikely, because the structure in the undetermined pholidophorid is unique within basal teleosts (Meunier and Brito, 2004), in addition it does not explain the occurrence of bone cells in the superficial layer of elasmoid scales, although the transformation of bone (isopedine) into a layer of superimposed fiber layers in elasmoid scales is difficult to comprehend.

I will deal here with Agassiz's third order, the Ganoïdes. Agassiz included in this order fishes with more or less rhomboid scales with an enamel layer over a bony base that displays bone cell spaces. He described many histological features we are now familiar with, like wide vascular

canals and fine tubular canals (later called Williamson's canals). Subsequently Williamson (1849) dealt in detail with the histology of ganoid scales; he introduced the term "ganoine" (Williamson, 1849, foot note, p. 438) for the surface layer of rhomboid scales in actinopterygians, because of the difference from the prismatic structure of enamel. In addition, he introduced the term "kosmine" (Williamson, 1849, p. 442) for the dentine of *Lepidotes*, palaeoniscoid, and sarcopterygian scales to distinguish it from dentine in teeth. The interchange between dentine and cosmine existed for a long time, e.g., Aldinger (1937) used the term cosmine for the dentine in actinopterygian scales.

Williamson (1849) described and figured the scales of *Megalichthys* as very different from those of basal actinopterygians. The pores on the surface of the scales of *Megalichthys* are openings of trumpet-shaped cavities, which are connected by horizontal canals, the system we call today the pore–canal system. The canal system changes into a spongy bony layer, which is underlain by a lower laminated layer. Nevertheless, Williamson (1849) did not introduce a separate term for the scales.

Goodrich (1907, 1909) published the classic three-dimensional figures of ganoid (Goodrich, 1909, fig. 198: *Eurynotus crenatus*; fig. 199: *Lepisosteus osseus*; fig. 203: *Polypterus bichir*) and cosmoid (Goodrich, 1909, fig. 197: *Megalichthys hibberti*) scales (Fig. 1). Goodrich distinguished two kind of ganoid scales after their histology: (1) palaeoniscoid (with dentine) and (2) lepidosteid (without dentine). He used the term cosmoid scale for sarcopterygian scales with the pore–canal system and one thin enamel layer even though he used cosmine as interchangeable with dentine. Gross (1956) described the pore–canal system in detail in different sarcopterygian scales; later, Ørvig (1969) underlined that cosmine is not a tissue but a combination between different tissues (enamel and dentine) and the pore–canal system.

The basal osteichthyan taxa discussed here are mainly or exclusively known by scales. Friedman and Brazeau (2010) gave a correct description of the shape of rhomboid scales in actinopterygians and sarcopterygians. I also agree that "articular pegs are primitively present in crown-group osteichthyans. . ." (Friedman and Brazeau, 2010, p. 39), nevertheless the peg (as well as the keel on the inside of the scale) is also present in basal (stem) osteichthyans like *Lophosteus* (Gross, 1969, fig. 1), a taxon, which Friedman and Brazeau (2010) were unable to place within osteichthyans because of the supposed lack of a peg. Friedman and Brazeau (2010) offer no phylogenetic analysis, and overlooked such an analysis published by Schultze and Märss (2004). Qu et al. (2013) introduced new terms for the morphology of rhomboid scales without consideration of the relations of the scales to the neighboring ones, as it occurs in rhomboid scales of other osteichthyans. The scales of *Psarolepis* overlap like other osteichthyan scales; their margins are steeper and shorter, but not as narrow as those of *Cheirolepis*. Figure 3F (Qu et al., 2013) shows overlap and overlapping areas like in osteichthyan scales, therefore the normal terminology is applicable.

The main problem, to which Friedman and Brazeau (2010) referred, is the distinction between ganoine and

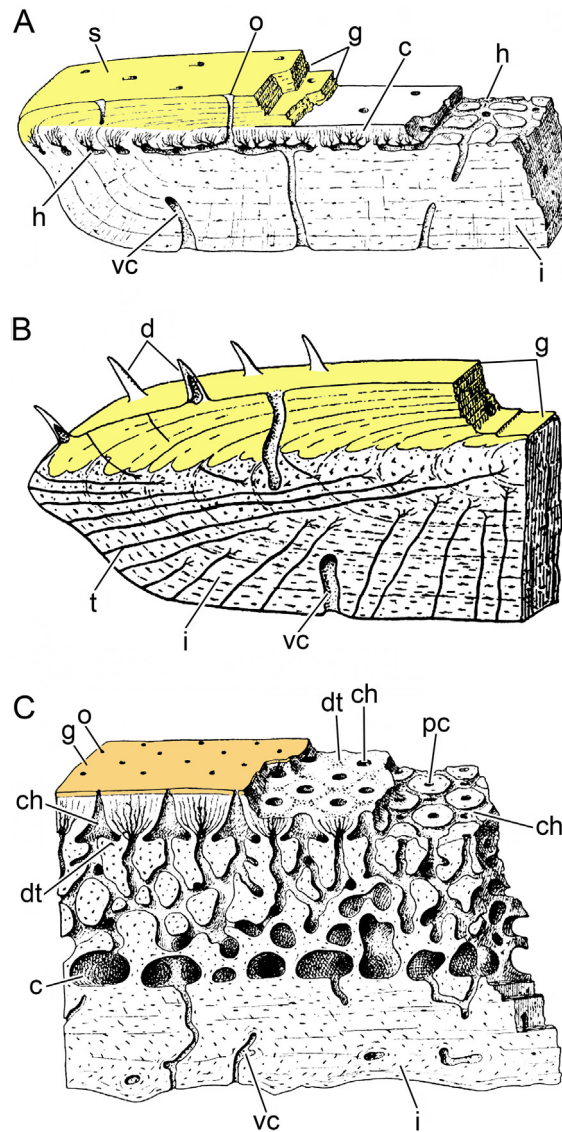


Fig. 1. (Color online.) Three-dimensional scale reconstructions: (A) palaeoisoid scale of the actinopterygian *Eurynotus crenatus*, Lower Carboniferous (modified after Goodrich, 1907, fig. 198B and Goodrich, 1909, fig. 191B); (B) lepidosteoid scale of the actinopterygian *Lepidosteus osseus*, Recent (modified after Goodrich, 1907, fig. 199 and Goodrich, 1909, fig. 192); (C) cosmoid scale of the sarcopterygian *Megalichthys hibberti*, Carboniferous (modified after Goodrich, 1907, fig. 197A and Goodrich, 1909, fig. 190A). Abbreviations: ap = articulating process (= peg), c = large vascular cavity, ch = chamber of cosmine layer, d = superficial denticles, dt = canaliculi of cosmine (= dentine), g [in a and b] = ganoine, g [in c] = thin outermost shiny layer ["true" enamel], i = inner bony layer or isopedine, o = opening of chamber on outside, pc = pulp cavity from which canaliculi radiate, t = tubules with branching inner ends (= Williamson's canals), vc = vertical canal (= vascular canal). Not to scale.

Fig. 1. (Couleur en ligne.) Reconstitutions tridimensionnelles d'écailles. (A) écaille paléoiscoïde de l'actinoptérygien *Eurynotus crenatus*, Carbonifère inférieur (modifié d'après Goodrich, 1907, fig. 198B et Goodrich, 1909, fig. 191B); (B) écaille lépidostéoïde de l'actinoptérygien *Lepidosteus osseus*, Actuel (modifié d'après Goodrich, 1907, fig. 199 et Goodrich, 1909, fig. 192); (C) écaille cosmoïde du sarcoptérygien *Megalichthys hibberti*, Carbonifère (modifié d'après Goodrich, 1907, fig. 197A et Goodrich, 1909, fig. 190A). Abréviations: ap = tenon articulaire (= peg), c = vaste cavité vasculaire, ch = chambre de la couche de cosmine, d = denticules superficiels; dt = canalicules de la cosmine (= dentine), g [en a et b] = ganoïne, g [en c] = mince couche externe luisante [« vrai » émail], i = couche interne osseuse ou isopédine, o = ouverture de la chambre sur l'extérieur, pc = cavité pulpaire à partir de laquelle rayonnent les canalicules, t = tubules avec terminaisons internes ramifiées (=canaux de Williamson), vc = canal vertical (= canal vasculaire). La figure n'est pas à l'échelle.

enamel. They (Friedman and Brazeau, 2010, p.45) deny the distinction between the two kinds of enamel, and accept the occurrence of enamel in acanthodians (Richter and Smith, 1995; Richter et al., 1999) and in conodonts (Donoghue et al., 2006; Janvier, 1996). Still they accept enamel as a synapomorphy for osteichthyans, even though enamel unites Ischnacanthiformes, Acanthodiformes and

Osteichthyes (Brazeau and Friedman, 2014, character 48^A in fig. 13A; a data matrix for analysis is not provided). Cosmine is a synapomorphy of sarcopterygians (Brazeau and Friedman, 2014, p. 47–48). In contrast, Qu et al. (2013) doubted the distinction between pore–canal system in sarcopterygians, the characteristic feature of cosmine, and dentinal canal systems in actinopterygians.

Herein I have compiled and revised mainly published data on scales of osteichthyans. I would like to show that ganoine and cosmine are useful terms, and that the canal system in sarcopterygian scales is different from that in actinopterygian scales. In contrast, [Friedman and Brazeau \(2010\)](#) argued that the term ganoine is obsolete because one cannot distinguish enamel and ganoine in early osteichthyans, and [Qu et al. \(2013\)](#) argued that the pore–canal system, the identifier of cosmine, is not a useful term. I will first present the different scale types in osteichthyans and definitions of histological terms, followed by the systematic distribution of the two kinds of enamel and the canal system to explain the problem in basal osteichthyans, and finally place basal osteichthyans after their scale characters.

2. Material and methods

Most of the discussions in this paper are based on published data as cited. In addition, thin sections prepared by W. Gross (Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Germany) were chosen for the investigation, because he prepared and published first on the histology of early osteichthyans ([Gross, 1968, 1969](#)) and dealt extensively with the canal system in bones and scales of these fishes ([Gross, 1956](#)). He prepared ‘thicker’ thin sections (40 μ) so that he could follow the canal systems, whereas his contemporary paleohistologist T. Örvig, Naturhistoriska Riksmuseet, Stockholm, Sweden, preferred ‘thinner’ (petrographic) sections (below 20 μ) to distinguish tissues.

I will deal here with scale characters. Even though there are only few scale characters, a phylogenetic analysis is possible ([Schultze and Märss, 2004](#), fig. 7). [Friedman and Brazeau \(2010, fig. 10B\)](#) mapped the taxa on a given tree despite their explicit statement that they attempted to use a sophisticated phylogenetic analysis. Mapping characters on a given tree is an old method. The procedure was done in pre-computer phylogenetic analyses (e.g., [Patterson and Rosen, 1977](#); [Schultze, 1977](#)). [Schultze \(1977\)](#) presented the distribution of scale characters on a tree to justify the placement of taxa. A computed analysis of scale characters in early osteichthyans was published by [Schultze and Märss \(2004](#); not cited by [Friedman and Brazeau, 2010](#)). [Brazeau and Friedman \(2014, p. 35\)](#) referred to the “importance of phylogenetic background assumptions in argumentation about the systematic significance of characters...”, which implies selections of character interpretation and explains some of the disagreements at least.

Abbreviations of Institutions:

BMNH = Natural History Museum, London, Great Britain
 MB.Hi = histology collection of Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung at the Humboldt-University Berlin, Germany
 MMMC = microfossil collection of the Geological Survey of New South Wales, housed at the WB Clarke Geoscience Centre at Londonderry in outer western Sydney, Australia
 NHMW = Natural History Museum, Vienna, Austria

3. Definitions

3.1. Scales

Rhomboid scale: [Francillon-Vieillot et al. \(1990\)](#) compiled the characteristics of scales. They distinguished between rhomboid (rhombic) and elasmoid scales within osteichthyans. Rhomboid scales ([Fig. 2](#)) are thick, possess peg-and-socket articulation and the longest (diagonal) axis of the scales is oblique to the long axis of the fish ([Gross, 1966](#); [Schultze, 1966](#)), whereas elasmoid scales are thin, overlap each other widely, and their long axis is parallel to the long axis of the fish. The rhomboid scale possesses a free exposed field, which is covered by ganoine, enamel or exposes bone, whereas the anterior and dorsal areas surrounding the free area, are covered by surrounding scales and formed by bone; they slope towards the margin. The ‘anterior ledge’ ([Qu et al., 2013](#)) is the anterior overlapped area of a rhomboid scale. The overlapped area extends from the anterior margin of the scale ([Qu et al., 2013](#), fig. 4a, b; [Schultze, 1966](#), fig. 1a) over to the dorsal margin ([Schultze, 1966](#), fig. 1a), where it is not marked in [Qu et al. \(2013, fig. 4a, b\)](#). The anterior margin is covered by scales of the preceding vertical scale row and the dorsal margin by the dorsal following scale in the same vertical row. The rhomboid scale is the basic structure of osteichthyans; it is divided based on histology into cosmoid and ganoid scales, and within the ganoid scale into palaeoniscoid and lepidosteoid scales.

Elasmoid scale: Elasmoid scales appear in different lineages of ganoid and cosmoid scales. The elasmoid scale can be divided in two types, the amioid scale with radial ridges in the covered part of the scale ([Fig. 3A](#)), and the cycloid scale with concentric rings parallel to the margin ([Fig. 3B](#)) in the covered part of the scale ([Schultze, 1966, 1996](#)). Amioid scales occur in different lineages of sarcopterygians and actinopterygians ([Fig. 4](#); [Schultze, 1977, 1996](#), fig. 3), whereas cycloid scales are restricted to teleosts (= *Leptolepis* and all more advanced teleosts). Ctenoid scales are derivations from cycloid scales in different lineages of euteleosts ([Roberts, 1993](#)).

Distribution of scale morphology and histology:

Rhomboid (rhombic) scales	Osteichthyes
Cosmoid scales	Sarcopterygii
Bony scales	Elpistostegalia
Ganoid scales	Actinopterygii
Palaeoniscoid scales	Palaeoniscimorpha
Lepidosteoid sales	Holostei, most
	Teleosteomorpha
Bony	Chondrostei, <i>Aspidorhynchus</i> ,
scales/scutes/shields	Pycnodonti, diverse Teleostei
Elasmoid scales	
Amioid scales	Actinistia, advanced Dipnoi,
	Onychodontida
	Holoptychiida, Tristichopterida
	some Palaeoniscimorpha,
	Amiidae, Caturidae, one teleost
	(<i>Eurycormus</i>)
	Teleostei (<i>Leptolepis</i>
	<i>coryphaenoides</i> + more
	advanced teleosts)
Cycloid scales (including ctenoid scales)	

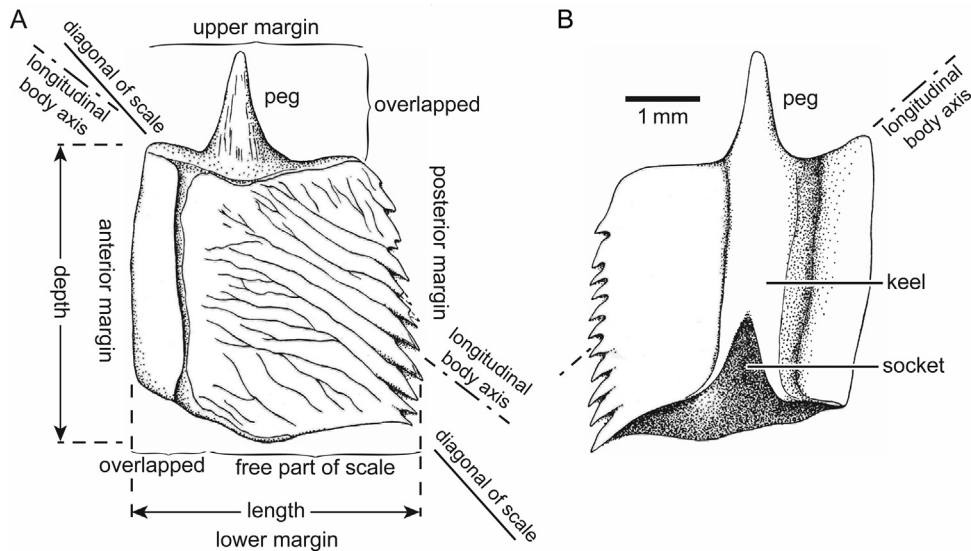


Fig. 2. Rhomboid ganoid scale of the actinopterygian *Siemensichthys macrocephalus* (NHMW B.X.1282.1876, Lower Tithonian, Upper Jurassic, Solnhofen, Bavaria). (A) external side with ganoine on the free, uncovered field and bone on the anterior and dorsal margin; (B) internal side with keel and socket for the peg. Arrows point rostral. Modified after Schultze (1966, fig. 1).

Fig. 2. Écaille ganoïde rhomboïde de l'actinoptérygien *Siemensichthys macrocephalus* (NHMW B.X.1282. 1876, Tithonien inférieur, Jurassique supérieur, Solnhofen, Bavière). (A) côté externe avec ganoïne sur le champ libre découvert et os sur la marge antérieure et dorsale; (B) côté interne avec carène et mortaise pour l'insertion du tenon. La flèche indique l'avant. Modifié d'après Schultze (1966, fig. 1).

3.2. Histology

Enamel: Enamel is a highly mineralized tissue deposited by basal epidermal cells, called ameloblasts. Hexagonal imprints of epidermal cells (e.g., *Dipterus*: Bemis and Northcutt, 1992, fig. 35; Schultze, 1977) indicate a similar prismatic structure and formation as in enamel of tetrapods. The hexagonal imprints alone do not prove the existence of enamel (Märss, 2006). Enamel is deposited centrifugally to underlying dentine, so that there is a sharp boundary between these two tissues. There is a vast amount of literature to describe the formation and structures of enamel, so that there is no need to discuss it here.

Smith and Hall (1990) interpreted the tissue of the outer layer of tubercles in an Ordovician agnathan as enamel. This is the clear transparent tissue, which Denison (1967, fig. 26) described as durodentine (= enameloid) in scales of a “Vertebrate indet. A”. The dentine tubules reach into the transparent tissue, which does not show the properties of enamel under crossed Nichols.

Friedman and Brazeau (2010) repeated the proposition that conodonts have enamel, whereas it has not only been shown that the tissue in question (lamellar tissue) has not the properties of enamel under crossed Nichols, and also chemical analyses indicate no similarities with enamel (Kemp, 2002; Kemp and Nicoll, 1995, 1996; Trotter et al., 2007; see further discussion in Turner et al., 2010).

Ganoine: Ganoine is a multi-layered enamel (Fig. 1A, B; see Richter and Smith, 1995 for an extensive review). There appears always a sharp boundary to the underlying dentine. Ganoine was described by Williamson (1849) in the extant *Lepisosteus* and the fossil *Lepidotes*, where it overlays bone (isopedin) in many layers. This kind of rhomboid scale within actinopterygians was named lepidosteoid

scale (Goodrich, 1907, 1909; Gross, 1966; Schultze, 1966: “*Lepisosteus*-Typus” after the old term for *Lepisosteus*; Francillon-Vieillot et al., 1990: lepisosteid scales). In contrast, dentine and a vascular layer are intercalated between ganoine and lamellated bone (= isopedine) in the palaeoniscoid scale (Fig. 1A; Aldinger, 1937; Francillon-Vieillot, 1990; Goodrich, 1907, 1909; Gross, 1966: “*Palaeoniscus*-Typus”). The canals of the vascular layer house blood vessels (Sewertzoff, 1932), which serve the odontoblasts of the dentine. One can compare these canals with the pulp cavity of a tooth. Sometimes the ganoine of overlying ridges does not superimpose the earlier ganoine layer; it is single layered in such actinopterygian scales. Ørving (1978b) wrote about “odontodes” in *Boreosomus* (Ørving, 1978b, figs. 10–17), *Gyrolepis* (Ørving, 1978b, figs. 27, 28), and *Plegmolepis* (Ørving, 1978b, figs. 23–26), where single layered ganoine is covered by dentine of the next younger ridge. Multi-layered ganoine occurs in these scales too (Ørving, 1978b, figs. 25–29). Multilayered ganoine is the common situation in palaeoniscimorph and holostean scales as seen also in Devonian actinopterygians like *Moythomasia* (Fig. 5; Jessen, 1968, fig. 6) and *Orvikuina* (Fig. 6; Gross, 1953, figs. 9, 12, 13; Schultze, 1968, fig. 18).

The ganoine surface (Fig. 7; Reissner, 1859: *Polypterus*, *Lepisosteus*; Kerr, 1952: *Polypterus*: very small grooves; Schultze, 1966: *Eugnathus*; Schultze, 1977: *Dapedium*; Ørving, 1967: *Colobodus*, *Nephrotus*; Ermin et al., 1971: *Polypterus*; Gayet and Meunier, 1986: *Lepidotes*, *Polypterus*, *Lepisosteus*, *Atractosteus*; Meunier et al., 1988: *Lepisosteus*, *Erpetoichthys*, *Polypterus*; Gayet et al., 1988: *Lepisosteus*, polypterid; Gayet and Meunier, 1992: *Polypterus*, *Dajetella*, *Lepisosteus*, *Atractosteus*; Daget et al., 2001: *Polypterus*; Märss, 2006: *Dapedium*) can be marked by small tubercles, representing the center of the epidermal cells. Reissner

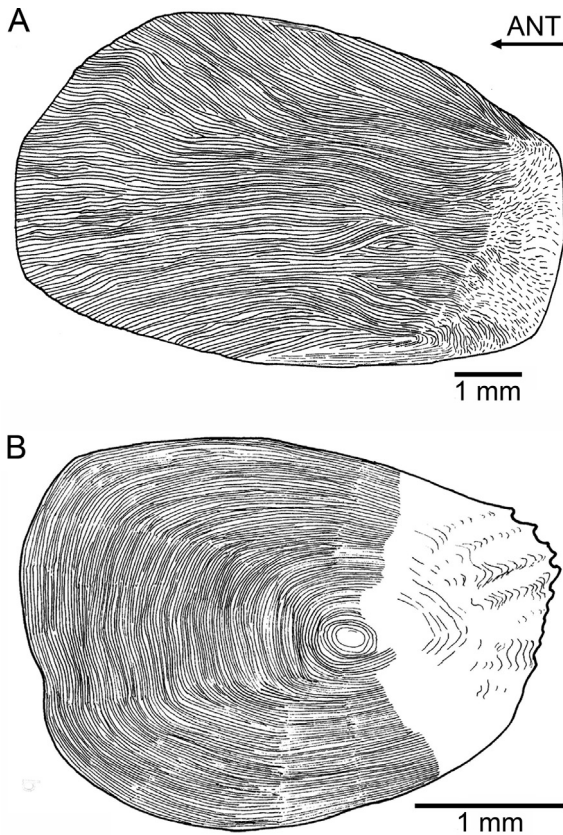


Fig. 3. Elasmoid scales, external side. (A) amioïd scale of the actinopterygian *Ionoscopus desori*, BMNH P. 4702; Lower Tithonian, Upper Jurassic, Cerin, France; (B) cycloïd scale of the actinopterygian *Anaethalion knorri*, BMNH P. 1095L Lower Tithonian, Upper Jurassic, Kelheim, Bavaria. Arrow points rostrad. Modified after Schultze (1996, fig. 3).

Fig. 3. Écailles élasmoïdes, côté externe. (A) écaille amioïde de l'actinoptérygien *Ionoscopus desori* BMNH P. 4702, Tithonien inférieur, Jurassique supérieur, Cerin, France; (B) écaille cycloïde de l'actinoptérygien *Anaethalion knorri*, BMNH P. 1095, Tithonien inférieur, Jurassique supérieur, Kelheim, Bavière. La flèche indique l'avant. Modifié d'après Schultze (1996, fig. 3).

(1859) was the first to describe small “hills” on the surface of the ganoine of scales of *Lepisosteus* and *Polypterus*, which are separable only microscopically. These small tubercles rediscovered by Schultze (1966), Ørvig (1967) and Ermin et al. (1971) were used by Gayet and Meunier (1986), Meunier et al. (1988), and Meunier and Gayet (1992, 1996) to distinguish species. They are typical for the ganoine surface and indicate a different secretion process of the basal layer of the epidermis in actinopterygians (Sire et al., 1986, 1987). The tubercles on the surface of ganoine (Fig. 7) have been observed on Mesozoic and Recent holostean and polypterid scales.

A similar surface ornamentation like the small tubercles of actinopterygian ganoine occurs in few acanthodians (Derycke and Chancogne-Weber, 1995; Märss, 2006: *Acanthodes*-type). The surfaces of acanthodian scales show either different ornamentation or no structure (smooth), reaching from hexagonal arrangements in *Cheiracanthus*, more irregular structures to small tubercles (Märss, 2006:

fig. 11). It means that one has to be careful when using the surface structure to characterize a special tissue. In contrast to enamel (ganoine or true enamel), the clear outer zone that sometimes occurs around each box in acanthodian scales is not separated from the underlying dentine below, as can be seen in figure 3A, B of Richter and Smith (1995); the dentine tubuli reach to the upper limit of the higher mineralized layer. It may represent enameloid (“durodentine” of different authors; see Ørvig, 1951, 1967). Märss (2006) showed too that a hexagonal surface structure similar to that of enamel appears on the surface of scales of chondrichthyans, thelodonts and acanthodians, even though these scales possess no enamel but only enamloid.

Sire et al. (1986, 1987) and Sire (1994, 1995) have shown that ganoine is enamel with successive deposition of layers by the epidermis. In earlier time, two opinions contradicted each other: ganoine was considered either enamel (e.g., Ermin et al., 1971; Hertwig, 1879; Reissner, 1859; Schultze, 1966; Scupin, 1896; Sewertzoff, 1932) or durodentine, an enamloid (e.g., Gross, 1966, Ørvig, 1967), a highly mineralized dentine. Ørvig (1978a, fig. 5) labels as ‘collariform ganoine’ enamel on the lateral side of teeth of palaeonisciform actinopterygians (e.g., *Birgeria*). That tissue occurs widely in actinopterygians (Thomasset, 1930, “émail du collet,” Schmidt and Keil, 1958, Kragendurodentin; Peyer, 1968, enamel) and shows an outside deposition of enamel (Peyer, 1968, pl. 27, fig. c; Schmidt and Keil, 1958, fig. 137). Birefringence and deposition on the outside is taken as indication of “true” enamel (Peyer, 1968; Schmidt and Keil, 1958), whereas Ørvig (1978a) identified it as ganoine based on the layered deposition. A study of its growth in extant actinopterygians would be desirable.

In conclusion, ganoine is a special kind of enamel of actinopterygians secreted in a different way than “true” enamel in sarcopterygians. In contrast to “true” enamel, ganoine grows by superposition, so that partial overlap of the enamel surface layer indicates ganoine as seen in Mesozoic forms (Ørvig, 1978b) and in Devonian (Figs. 5, 6) and Silurian forms. To my best knowledge the typical surface structure of ganoid scales of Mesozoic and Recent actinopterygians ganoid scales has not been observed in Paleozoic actinopterygians; there is thus a difficulty to identify ganoine in early actinopterygians on the basis of the surface structure, as Friedman and Brazeau (2010) pointed out. Multilayered enamel occurs only in ganoine, even partial overlap of enamel (Figs. 5, 6) is found only in ganoine. Thus, ganoine can be defined as multilayered or partially overlapping enamel with a tuberculated surface in Mesozoic and Recent ganoid scales.

Cosmine: Cosmine (Figs. 1C, 8) is a combination of tissues and one structure: a single thin layer of “true” enamel covers dentine interrupted by pores of the pore–canal system (*Megalichthys*: Goodrich, 1907, 1909; Ørvig, 1969, p. 241; Williamson, 1849). One has to use cosmine in this sense and not confuse it with dentine as has been done often in the literature. It does not occur in any recent fish, only in fossil sarcopterygians. The pores open to flask-like cavities, which are connected by a mesh of canals. The mesh canals (“Maschenkanal” of Gross, 1956) form a second canal system besides the dentinal canal system (Fig. 9) as has been

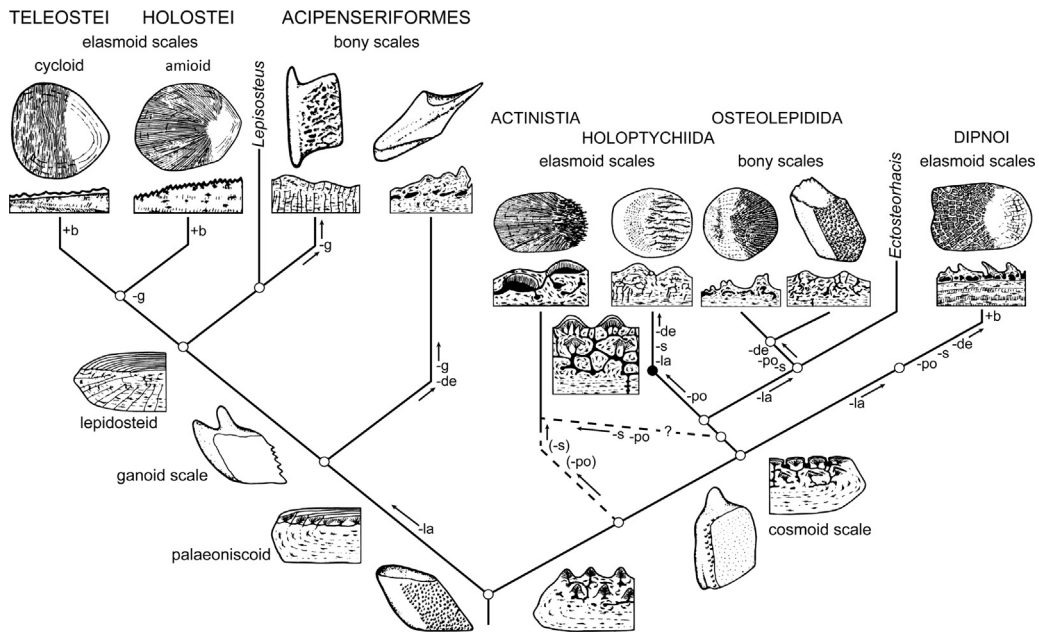


Fig. 4. Multiple parallel occurrences of elasmoid and bony scales from ganoid (Actinopterygii) and cosmoid (Sarcopterygii) scales in osteichthyans. Abbreviations: + b = addition of basal fiber layer, -de = loss of dentine, -g = loss of ganoine, -la = reduction of sequential layers, -s = loss of enamel; -po = pore-canal system not included; (-) supposed loss. Modified after Schultze (1977, fig. 2).

Fig. 4. Apparitions parallèles multiples d'écaillles élasmoïdes et osseuses à partir d'écaillles ganoïdes (Actinoptérygiens) et cosmoïdes (Sarcoptérygiens) chez les ostéichthyens. Abréviations : +b = adjonction d'un feuillet basal de fibres, de = perte de la dentine, g = perte de la ganoïne, -la = réduction de la série de couches, -s = perte de l'émail, -po = système pores-canaux non inclus; (-) perte supposée. Modifié d'après Schultze (1977, fig. 2).

shown by Williamson (1849, fig. 17) and Goodrich (1907, fig. 197A; here Fig. 1C). Both systems are connected in some places, generally in the deeper spongious part of the scale.

Williamson (1849) used interchangeable dentine and cosmine. Goodrich (1907, 1909) defined the cosmoid scale as built by three layers: a layer of dentine (for him cosmine)+pore-canal system underlain by a vascular layer and isopedin, and covered by a thin layer of enamel. Rauther (1929) and many others followed Goodrich (1907, 1909). Gross (1956) dealt extensively with cosmine in different sarcopterygians (*Dipterus*, *Rhino-dipterus*, *Porolepis*, *osteolepids*), and showed differences between taxa and differences to cosmine-like structures in agnathans (*Tremataspis*). Enamel extends into the pores in dipnoans and porolepiforms (Figs. 9, 10B₁, C₁), whereas it ends at the border of the pores in osteolepiforms

(Figs. 8, 10A₁). The pore of the pore-canal system widens to a single flask-like space in dipnoans and porolepiforms (Fig. 10B, C) in contrast to osteolepiforms, where a bony plate divides the flask-like space into an upper and lower division (Fig. 10A).

Because there is no extant fish with cosmine, growth and function of cosmine is difficult to access. Gross (1956, p. 96, fig. 83A) compared cosmine with the "flaschenförmigen Sinnesorganen" (flask-like sensory organs) of the South American lungfish *Lepidosiren* (Fahrenholz, 1929, fig. 2). Bemis and Northcutt (1992) compared it with blood vessel structures in the snout of the Australian lungfish *Neoceratodus forsteri*.

In contrast to ganoid scales of actinopterygians, one does not observe any resorption in cosmoid scales of sarcopterygians except in dipnoan scales with Westoll-lines.



Fig. 5. (Color online.) Scale of the actinopterygian *Moythomasia perforata*, vertical section MB Hi. 1553; lower Upper Devonian, Frasnian (Cellulosa marls); Koknese (Kokenhusen), Latvia. Abbreviations: ga.m = multilayered ganoine, ga.ps = partial overlapping ganoine, ga.s = single layered ganoine.
Fig. 5. (Couleur en ligne.) Écaïlle de l'actinoptérygien *Moythomasia perforata*, coupe verticale MB Hi. 1553, base du Dévonien supérieur, Frasnien (marnes à Cellulosa); Koknese (Kokenhusen), Lettonie. Abréviations : ga.m = ganoïne pluristratifiée, ga.ps = ganoïne en partie recouvrante, ga.s = ganoïne monostratifiée.

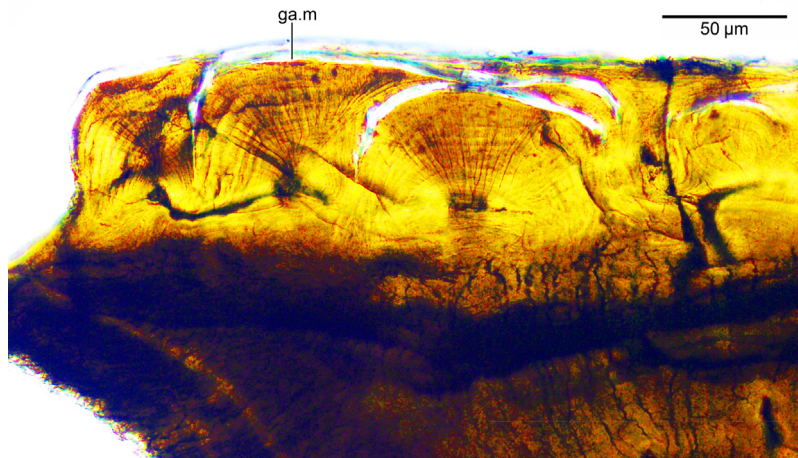


Fig. 6. (Color online.) Scale of the actinopterygian *Orvikuina vardiaensis*, vertical section MB Hi. 1441; Middle Devonian, Eifelian; Vardia, Estonia. Abbreviations: ga.m = multilayered ganoine.

Fig. 6. (Couleur en ligne.) Écaille de l'actinoptérygien *Orvikuina vardiaensis*, coupe verticale MB Hi 1441, Dévonien moyen, Eifélien, Vardia, Estonie. Abréviations : ga.m = ganoïne pluristratifiée.

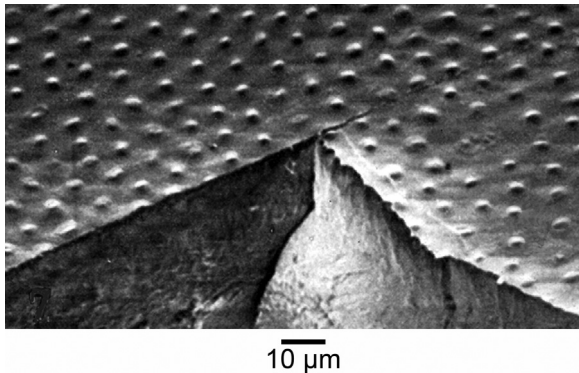


Fig. 7. Ganoine surface of a scale of the actinopterygian *Polypterus*, SEM-picture; Recent. From Ermin et al. (1971, pl. 1, fig. 7).

Fig. 7. Surface de ganoïne d'une écaille de l'actinoptérygien *Polypterus*. Image MEB, Actuel. D'après Ermin et al., 1971, pl. 1, fig. 7.

Therefore, it is difficult to understand the marginal enlargement of the scales. Thomson (1977) argued that the whole surface is resorbed and formed new. However, I checked and re-studied the material described by Thomson (1977) and found but no sign of resorption in the scales of *Ectosteorhachis* (Thomson, 1977, fig. 2; Thomson, 1975, figs. 2, 15, 23) and *Megalichthys* (Thomson, 1977, fig. 3). Borgen (1989) showed reabsorbed grooves on osteolepidid jaws, which look like postmortem or even post-fossilization etchings and have nothing to do with the growth process of these fishes.

Zhu et al. (2010) placed *Meemannia* together with *Andreolepis* and actinopterygians as a group without resorption at the base of their cladogram. Resorption is common in actinopterygian scales (e.g., Aldinger, 1937; Ørvig, 1977, 1978a,b) even in basal forms like *Ligulalepis* und *Orvikuina* (Schultze, 1968, figs. 5, 19). *Meemannia* shows resorption (see below) like *Psarolepis* (Zhu et al.,

2010, fig. 8: “partial resorption”). Zhu et al. (2010, fig. 8) accepted Thomson's (1977) concept of complete resorption in rhipidistians, for which I cannot find any evidence. Resorption is often difficult to detect, nevertheless it occurs undoubtedly in scales of actinopterygians and may be in scales and bones of *Meemannia* and *Psarolepis*.

In the past, cosmine was considered an electrosensory system (Thomson, 1977, fig. 9), but there is no fish with such an extensive distribution of electric organs, therefore Bemis and Northcutt (1992) compared it with the vascular system (vertical capillary loops) in *Neoceratodus* and found good concordance with the pore–canal system. Campbell et al. (2010) doubted the comparison; they argued that the canals in the snout of Devonian dipnoans are occupied by nerves, whereas the blood vessels are positioned outside the bony canals. They argued that there is no space for a returning vessel in the canals, which cannot be the case in the expanded spaces of the pores and the mesh canals of the pore–canal system. The mesh canals are even wider than the dentinal canals (Fig. 9). Campbell et al. (2010) were mostly concerned with the vascularisation of the snout, whereas Bemis and Northcutt (1992) dealt with the smaller units of dermal–epidermal interface (dermal papillae, ampullary organs, etc.). Gross (1965) described the distribution of pores in Devonian dipnoans and distinguished between pores of the pore–canal system and larger pores, which reach to a deeper system; the pores get larger towards the front and have a larger distance between each other. The same situation can be seen in figures of Campbell et al. (2010, figs. 2, 11A–D, 29), where the fine pores of the pore–canal system are gone. Thus the interpretation by Bemis and Northcutt (1992) refers to the pore–canal system not to the vascular system of the snout in general and appears to be the most likely explanation for the pore–canal system.

Canal system: The canal system in ganoid scales, which serves the dentine, has been intensively studied and figured since Williamson (1849, pl. 40 fig. 7, pl. 41, fig. 8:

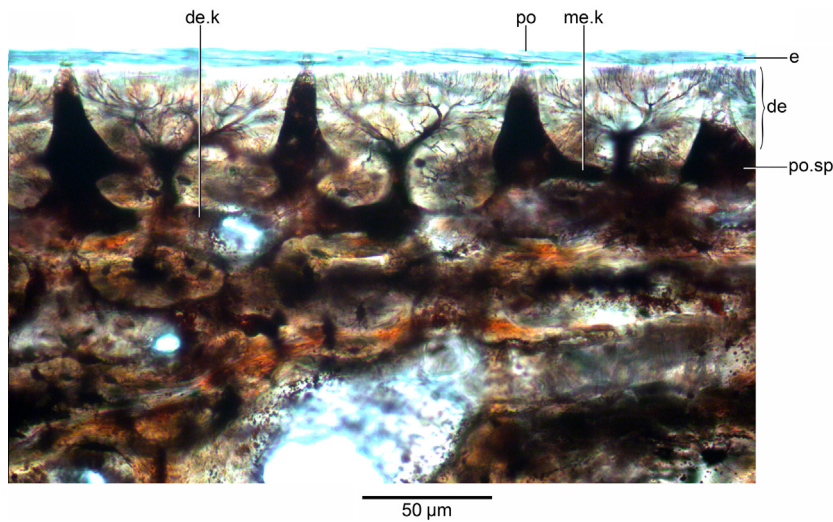


Fig. 8. (Color online.) Scale of the sarcopterygian *Osteolepis* sp., vertical section MB Hi.1230; Middle Devonian; NW-Russia. Abbreviations: e = “true” enamel, de = dentine, de.k = dentinal canal, me.k = mesh canal, po.sp = pore–canal space.

Fig. 8. (Couleur en ligne.) Écaille du sarcoptérygien *Osteolepis* sp., coupe verticale MB Hi1230, Dévonien moyen, Nord-Ouest de la Russie. Abréviations : e = émail « vrai », de = dentine, de.k = canal de la dentine, me.k = canal en réseau, po.sp = espace du système pores–canaux.

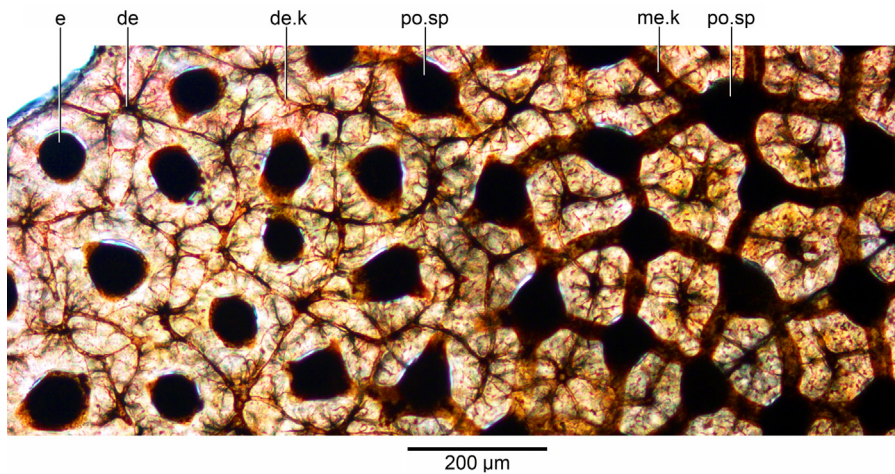


Fig. 9. (Color online.) Scale of the sarcopterygian *Parolepis posnaniensis*, horizontal section MB Hi.1221 near scale surface; Middle Devonian; erratic from Międzyrzec Podlaski (former Meseritz), Poland. Abbreviations: e = “true” enamel, de = dentine, de.k = dentinal canal (mainly on the left side), me.k = mesh canal (mainly on the right side), po = pore, po.sp = pore–canal space.

Fig. 9. (Couleur en ligne.) Écaille du sarcoptérygien *Parolepis posnaniensis*, coupe horizontale MB Hi. 1221, près de la surface de l’écaille, Dévonien moyen, bloc erratique de Międzyrzec Podlaski (anciennement Meseritz), Pologne. Abréviations : e = émail « vrai » ; de = dentine, de.k = canal de la dentine (surtout sur le côté gauche), me.k = canal en réseau (surtout sur le côté droit), po = pore, po.sp = espace du système pores–canaux.

Palaeoniscum). It has been described and figured for the extant *Polypterus* by Reissner (1859), Hertwig (1879, pl. 3, fig. 5, bone or dentine around canals to ganoine surface), Goodrich (1907), Sewertzoff (1932), Kerr (1952, and fig. 11), and for the extant *Erpetoichthys* [*Calamoichthys*] by Rauther (1929, fig. 136). Goodrich (1907: *Eurynotus*, *Gonatodus*, *Cheirolepis*), Aldinger (1937: *Cheirolepis*, *Boreolepis*, *Palaeoniscum*, *Plegmolepis*, *Acropholis*, *Glaucolepis*, *Ganolepis*, *Gonatodus*, *Elonichthys*, *Platysomus*, *Scanilepis*), Wilson (1953: *Lawnia*), Cavender (1963: *Elonichthys*, *Gonatodus*, *Pteronisculus*, *Holurus*, *Rhadinichthys*, *Eurynothus*, *Eurylepidoides*, *Haplolepis*, *Cryphirolepis*, *Watsonichthys*, *Acrolepis*, “*Aetheretmon*-type,” *Amblypterus*,

Lawnia, *Brachydegma*, *Aeduella*, *Cheirolepis*) and Ørvig (1978a: *Gyrolepis*, *Reticolepis*, *Ganolepis*, *Ptycholepis*, *Eurynotus*, *Aetheretmon*, *Canobius*) showed it in scales of many lower actinopterygians. Aldinger (1937) dealt extensively with the horizontal canal system, he distinguished longitudinal, cross, and radial canals. The canal system has connections to the surface, the margin and to the inner side of the scale; on the surface the canals open with pores between ganoine ridges (e.g., Gayet and Meunier, 1992; *Dajetella*) but also on the ganoine surface (Fig. 11; see also Goodrich, 1907, fig. 198B; here Fig. 1A). The canals can be wide or narrow, and this changes from genus to genus. Considering the early actinopterygians, one finds wide

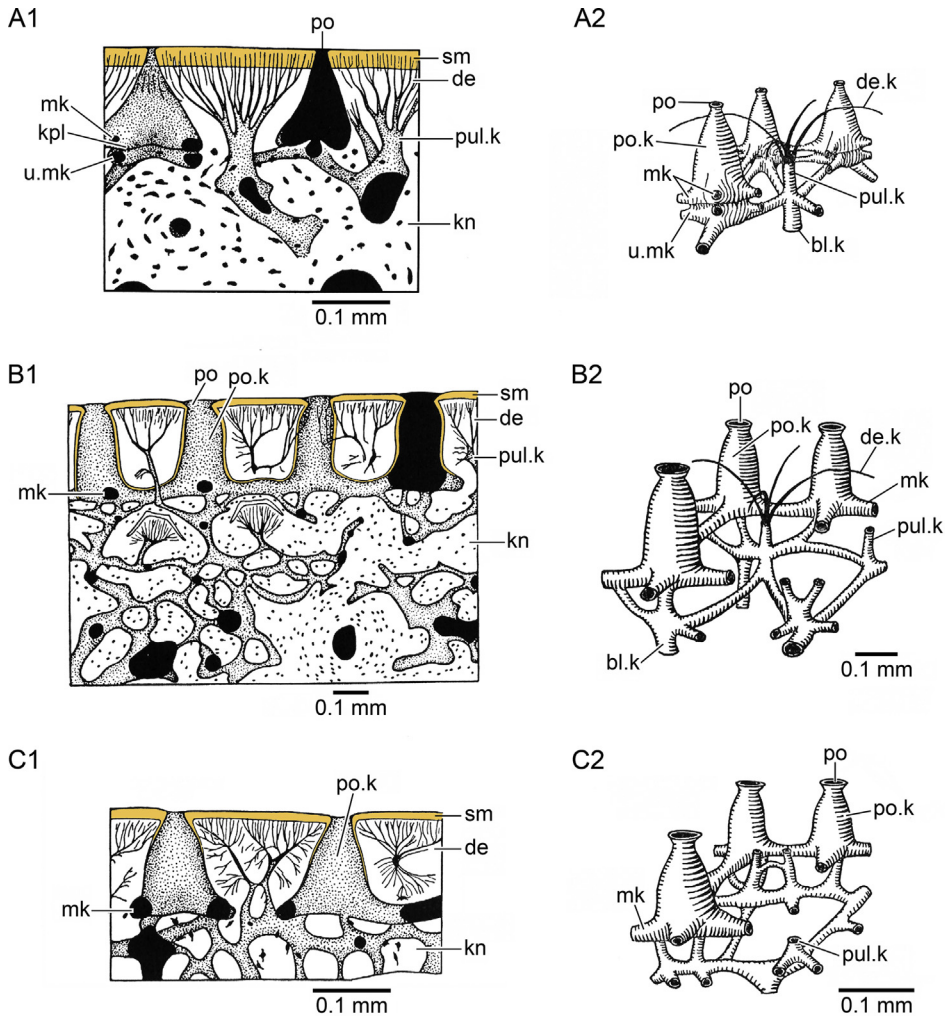


Fig. 10. (Color online.) Pore–canal system in scales of sarcopterygians, left side (A1–C1) = vertical section, right side (A2–C2) = reconstruction of pore–canal and dentinal system. (A) *Osteolepididae* gen. et sp. indet.; (B) *Porolepis posnaniensis*; (C) *Dipterus* sp. Modified after Schultze (1969, fig. 42, compilation from Gross, 1956). Abbreviations: bl.k = canal of blood vessel, de = dentine, de.k = dentine caniculli, kn = bone, kpl = imperforated bony plate, mk = mesh canal (“Maschenkanal” = horizontal canal connecting pore–canal system), po = pore (= external opening of pore–canal system), po.k = flask-like expanded tube, pul.k = pulpa canal, sm = enamel, u.mk = lower mesh canal.

Fig. 10. (Couleur en ligne.) Système pores–canaux dans des écailles de sarcoptérygiens, côté gauche (A1–C1) = coupe verticale, côté droit (A2–C2) = reconstitution du système pores–canaux et de la dentine. (A) *Osteolepididae* gen. et sp. indet.; (B) *Porolepis posnaniensis*; (C) *Dipterus* sp. Modifié d’après Schultze (1969, fig. 42, compilation d’après Gross, 1956). Abréviations : bl.k = canal vasculaire, de = dentine, de.k = canalicules de la dentine, kn = os, kpl = plaque osseuse non perforée, mk = canal en réseau (« Maschenkanal » = canal horizontal se connectant au système pores–canaux), po = pore (= ouverture extérieure du système pores–canaux), po.k = tube renflé en forme de gourde, pu.k = canal pulpaire, sm = émail, u.mk = canal en réseau inférieur.

canals in *Cheirolepis* (Aldinger, 1937, fig. 51A–D) and in *Ligulalepis* (Schultze, 1968, fig. 4), but also in the stem osteichthyan *Lophosteus* (Gross, 1969, fig. 11). Narrow dentinal canals are more common in palaeoniscimorphs (Aldinger, 1937, many figs.) and are present in scales of *Dialipina*, *Orvikuina* (Schultze, 1968, figs. 11, 17) and *Andreolepis* (Gross, 1968, fig. 12A). They are commonly placed below sculptures as pulpa canals of the dentine (Fig. 12: l.ca). The canals to the surface branch off dorsolaterally (always very clear in cross sections). The dentinal canal system is variable (Fig. 12), and it nourishes the dentine. It seems to be the primitive state in osteichthyans.

Gross (1956) dealt specifically with the canal systems in cosmoid scales and put special emphasis on the canal

systems. There is the dentinal system, which forms the pulpa canals below the dentine (Fig. 10: pul.k changing into bl.k), and in addition the pore–canal system with its mesh canals (Fig. 10: mk; Gross, 1956, “Maschenkanal”). Both systems form horizontal canals.

Acrodin: Actinopterygian teeth have a tip of highly mineralized dentine named acroclin by Ørvig (1973). Acroclin is a unique feature of actinopterygians accepted by all, including Friedman and Brazeau (2010). Not all actinopterygian possess teeth with acroclin. It is missing, e.g., in teeth of *Cheirolepis*, a taxon, which possesses multi-layered ganoine in its scales. On the other side, *Ligulalepis*, placed by Friedman and Brazeau (2010) outside the actinopterygians, possesses acroclin (Fig. 13).

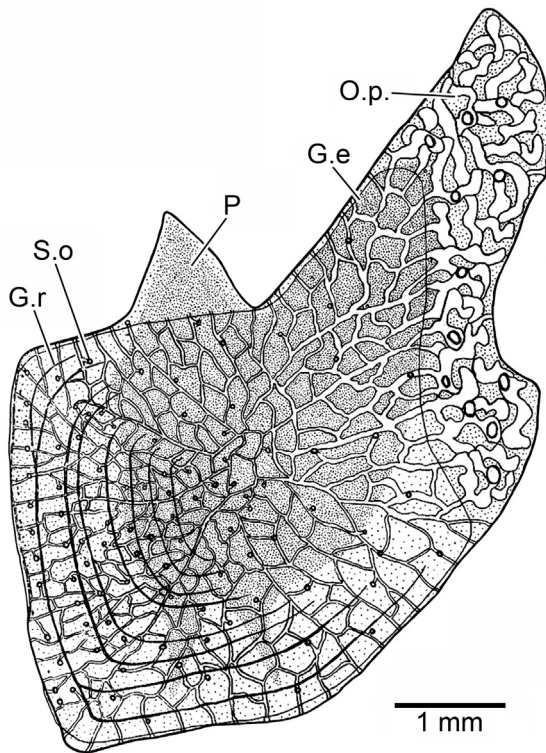


Fig. 11. Canal system in a scale of the actinopterygian *Polypterus bichir*, scale of the right side in transmission light; Recent. Abbreviations: G.e=edge of ganoine layer; G.r=growth ring; O.p=portion of scale not covered by ganoine and overlapped by scales of row in front; P=conical projection fitting into socket of scale above in the same row; S.o=surface opening of vertical branch from horizontal canal system. From Kerr (1952, fig. 1).

Fig. 11. Système de canaux dans une écaille de l'actinoptérygien *Polypterus bichir*, écaille du côté droit en lumière transmise, Actuel. Abréviations: G.e=bord de la couche de ganoïne; G.r=anneau de croissance; O.p=portion d'écaille non recouverte par la ganoïne, chevauchée par les écailles de la rangée précédente; P=tenon conique s'insérant dans la mortaise de l'écaille suivante, au-dessus dans la même rangée; S.o=ouverture externe d'une branche verticale issue du système horizontal de canaux. D'après Kerr (1852, fig. 1).

Dentine: The tissue termed dentine in this paper is orthodentine in the sense of Ørvig (1951, 1967). The hard tissue encompasses the parallel running dentinal tubules, which branch distally, whereas the cell body, the odontoblast, remains in the pulp cavity or canal.

4. Distribution of characters

4.1. Enamel

Enamel is a synapomorphy of osteichthyans. It does not occur in acanthodians (contrary to published accounts: Richter and Smith, 1995; Richter et al., 1999). It occurs in two forms, the multilayered ganoine on scales and bones of actinopterygians (even in those with a tuberculated surface) and the single layered “true” enamel (Francillon-Vieillot et al., 1990; Peyer, 1968) on bones and scales of sarcopterygians. Lateral superposition (partial overlap) of enamel is considered here as indication of ganoine, because

it occurs frequently in actinopterygians, and not in sarcopterygians.

4.2. Ganoine

Ganoine is limited to actinopterygians (Goodrich, 1909, p.217: “the true ganoid scale”). Usually multilayered enamel is accepted as ganoine. The lateral overlapping enamel in tubercles and ridges occurs in rhomboid scales of Paleozoic (e.g., Aldinger, 1937, figs. 7, 90, pl. 18, fig. 1) and Mesozoic (e.g., Ørvig, 1978b, figs. 10–12, 18, 19, 23, 24) actinopterygians. It represents the first step towards multilayered ganoine. This feature can be seen, sometimes, even in scales of the extant *Polypterus* (Poole, 1967, figs. 15, 16). Friedman and Brazeau (2010) accept the presence of ganoine in acanthodians, as published by Richter and Smith (1995), Richter et al. (1999), and Derycke and Chancogne-Weber (1995). A thin surface layer covers the subsequent growth addition in some acanthodians (“*Acanthodes*-Typ” of Gross, 1973, with enameloid, ‘Durodentin’). However the layer is not separated from the underlying dentine. This is an enameloid. The surface micro-ornament of acanthodian scales is variable, from hexagonal to tuberculated or smooth (Märss, 2006), and gives no indication of enamel or ganoine.

The canal system in ganoid scales serves the dentine (emphasized by Ørvig, 1978b). That can be compared with the pulp cavity of teeth. The canal system in ganoid scales and its variations were intensively described by Aldinger (1937). Cavender (1963) did a doctoral dissertation on the histology of palaeoniscoid scales and showed variation in the distribution of the canal system similar to the results of Aldinger (1937). Cavender (1963, pl. 5, fig. A = *Haplolepis*, B = *Cryphiolepis*, and F = “*Aetheretmon*-type”) showed that lateral pores extend from the main canals and open in the bony furrows between the ganoine ridges [also described and figured by Aldinger, 1937: fig. 13 ‘breiter Kanal in einer Kosmin (=dentine) lamelle erster Art’]. Gross has shown that the pores open lateral to the sculpture ridges in *Lophosteus* (Gross, 1969, figs. 1A, 11; Schultze and Märss, 2004, figs. 4, 5) and *Andreolepis* (Gross, 1968, figs. 1–6, 12A; Janvier, 1978, pl. 2, figs. 1, 6, 7, 10, 12; also Märss, 2001, pl. 1, figs. 4, 10, 11, 13, pl. 2, 5). That is the common situation in actinopterygians, as shown for *Cheirolepis* (Aldinger, 1937, fig. 50A, 51; p. 201: no canals to scale surface). Long and Trinajstić (2000) showed the canal openings in grooves between ridges (pl. 3, figs. 1, 3) and pores in a closed ganoine surface (pl. 3 figs. 2, 4) of scales of *Moythomasia*.

4.3. Cosmine

Cosmine is limited to sarcopterygians (*Megalichthys*: Goodrich, 1909, p. 217: “the cosmoid scale”). In the cephalaspid *Tremataspis* a distantly comparable pore–canal system lies in the bony layer (Gross, 1956, figs. 84, 88, 89, 93; Schultze, 1969, fig. 42a), a sieve plate extends along the whole canal system and a superficial enamel layer is missing; mesodentine forms the superficial layer. Gross (1956) described a pore–canal system in *Poracanthus* and *Radiopporacanthodes* (Gross, 1956, fig. 99, 104, and arrangement of canals in figs. 105–114, pl. 14, fig. 6, pl. 15, pl. 16, figs. 1, 2). It

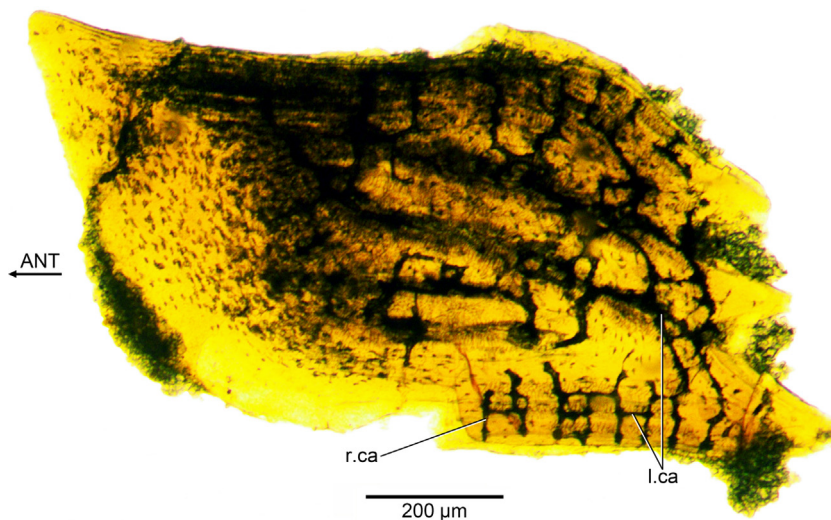


Fig. 12. (Color online.) Scale of the actinopterygian *Moythomasia perforata*; horizontal section MB Hi. 1558; lower Upper Devonian, Frasnian (Cellulosa marls); Koknese (Kokenhusen), Latvia. Arrow points rostrad. Abbreviations: ANT= arrow points rostrad (anteriorly); l.ca = longitudinal canal; r.ca = radial canal.

Fig. 12. (Couleur en ligne.) Écaille de l'actinoptérygien *Moythomasia perforata*, coupe horizontale MB Hi. 1558, base du Dévonien supérieur, Frasnien (marnes à Cellulosa), Koknese (Kokenhusen), Lettonie. La flèche indique l'avant (ANT). Abréviations : l.ca = canal longitudinal, r.ca = canal radial.

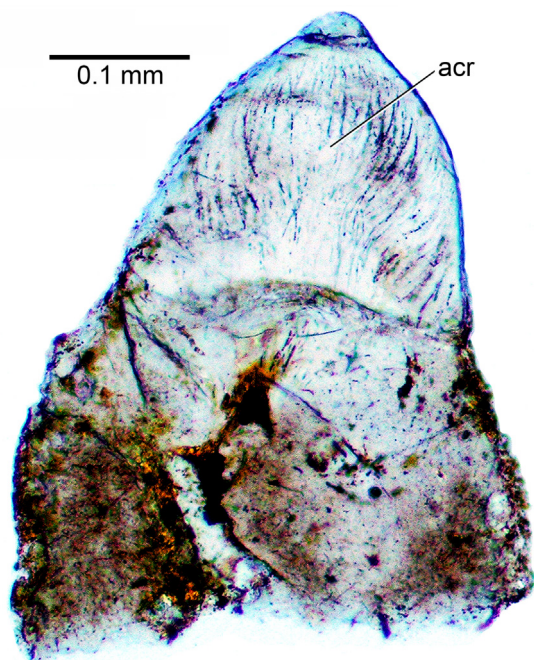


Fig. 13. (Color online.) Acrodin in the actinopterygian *Ligulalepis toombsi*, MMMC 4755, vertical section through a tooth of jaw MMMC 4754; Troffs Formation or equivalent, Trundle Group, Middle Pragian – Lower Emsian, Lower Devonian; Locality C657 (see Burrow, 2002, p. 78, fig. 2 and p. 136), NE of Kadungle, central New South Wales, Australia. Abbreviation: acr = acrodin. Courtesy C. Burrow.

Fig. 13. (Couleur en ligne.) L'acrodine chez l'actinoptérygien *Ligulalepis toombsi* MMMC 4755, coupe verticale au travers d'une dent de la mâchoire MMMC 4754, Formation de Troffs ou équivalente, Groupe de Trundle, Praguien moyen – Emsien inférieur, Localité C657 (voir Burrow, 2002, p. 78, fig. 2 et p. 136), Nord-Est de Kadungle, Nouvelle Galles du Sud centrale, Australie. Abréviations : acr = acrodine (avec la permission de C. Burrow).

is a canal system with longitudinal or circular (corresponding to growth additions) canals, which open vertically on the surface by many pores. The canal system is independent from the dentine like pore–canal system in cosmine, only its complexity of narrow and wide longitudinal canals (Gross, 1956, figs. 99, 104) and in some cases antler-like branching of the pores into many small pores (Gross, 1956, figs. 114A, B, 118) is very unlike cosmine.

Scales of the extant polypterids show pores on the ganoine and bone surface, which are connected to a dentinal vascular system (e.g., Kerr, 1952; Rauter, 1929) and do not represent an independent pore–canal system like in cosmine (Fig. 11). The vascular canals as pulp canals are shown in vertical sections (e.g., Goodrich, 1909, fig. 265; Rauter, 1929, fig. 137).

Cosmine has been described and figured for the osteolepidids *Megalichthys* (Goodrich, 1907, 1909; Gross, 1956; Williamson, 1849), *Osteolepis* (Gross, 1966) and *Ectosteorhachis* (Thomson, 1975), the porolepidid *Porolepis* (Gross, 1956, 1966), the dipnoan *Rhinodipterus*, *Dipterus* (Gross, 1956; Bemis and Northcutt, 1992), *Ganorhynchus* (Gross, 1956, 1965) and *Chirodipterus* (Bemis and Northcutt, 1992) and the basal sarcopterygian *Styloichthys* (Zhu et al., 2006). Cosmine has not been recorded in the sarcopterygian onychodonts and actinistians, where only elasmoid scales are known. This may be an indication that cosmine occurs only above onychodonts and actinistians in sarcopterygians: *Styloichthys*, *Dipnomorpha* and *Tetrapodomorpha* (Long et al., 2014; Lu and Zhu, 2008).

4.4. Acrodin

Teeth of actinopterygians possess a tip of highly mineralized dentine named acrodin by Ørving (1973). Friedman and Brazeau (2010) accepted acrodin as a feature of

actinopterygians, even though some actinopterygians do not possess it. Nevertheless *Ligulalepis*, which possesses acroдин (Fig. 13), is placed by the two authors outside the actinopterygians.

Acroдин has not been described from teeth of *Dialipina* and *Andreolepis*. *Lophosteus* does not possess acroдин. It is lacking in *Cheirolepis* as far as known, but known in other Palaeozoic actinopterygians.

Occurrence of tissues:

Enamel	Osteichthyes
Ganoine	Actinopterygii
“true” enamel	Sarcopterygii
Acroдин	Actinopterygii
Dentine (Orthodentine)	Gnathostomata above
	Placodermi and some ‘Agnatha’
Cosmine	Sarcopterygii (except Actinistia and Onychodontida)

5. Placement of basal osteichthyan taxa

Ligulalepis, *Dialipina*, *Terenolepis*, *Orvikuina*, *Naxilepis* and *Andreolepis* were placed on the line between acanthodians and osteichthyans by Friedman and Brazeau (2010). They considered the genera as stem osteichthyans, not closer related to either actinopterygians or sarcopterygians. They did not place *Lophosteus* on their tree because of insufficient data (Friedman and Brazeau, 2010, p. 50: “incertae sedis”). Zhu et al. (2009) placed *Lophosteus* and *Andreolepis* as stem osteichthyans, whereas *Dialipina* and *Orvikuina* were considered actinopterygians and *Ligulalepis* a stem sarcopterygian together with *Meemannia*, *Guiyu*, *Psarolepis* and *Achoania*. Dupret et al. (2014) placed *Lophosteus*, *Dialipina*, *Meemannia* and *Ligulalepis* as stem osteichthyans; the clade (*Guiyu* (*Psarolepis* + *Achoania*)) appears as sister group of the sarcopterygians. In the phylogenetic hypothesis of Long et al. (2014, fig. 6), *Lophosteus* appears as stem osteichthyan, whereas *Dialipina*, *Meemannia* and *Ligulalepis* appear within actinopterygians with the clade (*Guiyu* (*Psarolepis* + *Achoania*)) as sister group. Thus the basal taxa have quite different positions in recent phylogenetic schemes (see below).

5.1. Stem Osteichthyes

Lophosteus: Gross (1969, 1971) described in detail the morphology and histology of the scales of the genus, which was first published by Pander (1856). In contrast to Friedman and Brazeau’s (2010, p. 50) statement, scales of *Lophosteus* have a peg-and-socket articulation combined with a keel on the inner side of the scales; a socket for the peg is present ventral to the keel (Fig. 14; Gross, 1971, fig. 1A, B and Gross, 1969, fig. 1). The peg is broad-based as on scales of sarcopterygians, therefore Schultze (1977, fig. 1) indicated the possibility of placing the genus with the sarcopterygians. The peg-and-socket articulation places *Lophosteus* within osteichthyans. The posterior margin of the scales is straight even though the free surface is covered with ridges, which can reach posteriad above the posterior margin. In cross sections, scales of *Lophosteus* show a sequence of each other overlying units of dentine without enamel (Gross, 1969, figs. 12A, B, 13C, 14A, 15E). In osteichthyans, the overlying units possess enamel, therefore

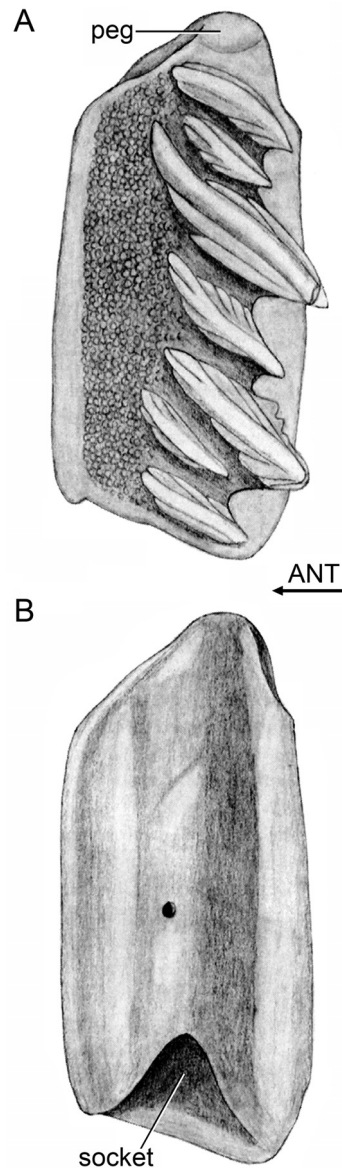


Fig. 14. Peg and socket of stem osteichthyan *Lophosteus superbus*. (A) external surface with broad based peg, (B) internal side with broad-based peg, keel and socket; Beyrichienkalk, Pridoli, Upper Silurian; erratics, northern Germany. Arrow points rostrad. Modified after Gross (1971, fig. 1).

Fig. 14. Tenon articulaire et mortaise correspondante de l’ostéichthyen souche *Lophosteus superbus*. (A) surface externe avec tenon à large embase, (B) surface interne avec tenon à large embase, carène et mortaise, Calcaire à Beyrichia, Pridoli, Silurien supérieur, blocs erratiques, Nord de l’Allemagne. La flèche indique l’avant. Modifié d’après Gross (1971, fig. 1).

Lophosteus has to be placed below the branching point of actinopterygians and sarcopterygians.

Lophosteus possesses broad sensory grooves (Gross, 1969, figs. 5H, 6D, 7 A, B; Märss, 1986, pl. 35, figs. 6, 7), whereas the lateral line system is enclosed in canals in osteichthyans. The lateral line system lies in open grooves in acanthodians, chondrichthyans and most placoderms.

Thus this primitive feature places *Lophosteus* below the branching point of actinopterygians and sarcopterygians. The preserved piece of a maxilla described by Botella et al. (2007) shows similarities to that of onychodonts, an indication that the genus is close to osteichthyans, whereas the fin spines look like those of acanthodians (Otto, 1991) and thus are a primitive feature compared to osteichthyans. Burrow (1995b) compared the scale ornamentation with that of placoderms, a feature, which was considered superficial by Märss (2001). A detailed discussion of the systematic position of *Lophosteus* can be found in Schultze and Märss (2004).

In conclusion, morphology and histology of the scales of *Lophosteus* look like scales that one would expect from a stem osteichthyan. In agreement, *Lophosteus* appears in most recent phylogenetic analyses (e.g., Dupret et al., 2014; Long et al., 2014; Zhu et al., 2009, 2013; Fig. 15) as stem osteichthyan.

5.2. Actinopterygii

Andreolepis: *Andreolepis* was first described by Gross (1968) and placed within actinopterygians. That placement was accepted by Schultze (1977, 1992) and Janvier (1978). Janvier (1996) and Schultze and Märss (2004) placed *Andreolepis* as sister group of all other actinopterygians, whereas Botella et al. (2007), Zhu et al. (2009, 2010), and Chen et al. (2012) placed the genus as basal osteichthyan (Fig. 15A). An extended anterodorsal process and ganoine (= overlapping enamel) places the genus at the base of the actinopterygians (Schultze and Märss, 2004). The broad based peg of *Lophosteus* may represent the primitive osteichthyan condition. The posterior margin of the scales is straight, except in the anterior deeper flank scales ('Type 1' in Chen et al., 2012). The histology of the scales is similar to that of scales of the actinopterygian *Moythomasia*; the histology together with the extended anterodorsal process points towards a placement of the genus within the actinopterygians.

Dialipina: Scales of *Dialipina salgueiroensis* were first described by Schultze (1968), and additional material by Schultze (1992) and Schultze and Cumbaa (2001). Schultze (1968, 1992), Schultze and Cumbaa (2001), Zhu et al. (2009), Janvier (2007) and Long et al. (2014) placed *Dialipina* as basal actinopterygian (Fig. 15A, C). Friedman and Brazeau (2010) and Dupret et al. (2014) considered *Dialipina* as stem osteichthyan (Fig. 15B). The shape of the scales (narrow dorsal peg, anterodorsal extended corner, serrated posterior margin), histology (ridges with overlapping enamel = ganoine) and the bone arrangement on the skull roof indicate a placement within actinopterygians. The presence of two dorsal fins is a primitive feature; the triphycercal tail is an autapomorphy occurring independently in similar fashion within different groups of sarcopterygians. A short-based peg, an extended anterodorsal process and ganoine (= overlapping enamel) place the genus within actinopterygians above *Andreolepis* (Schultze and Märss, 2004). The lateral line runs inside the dermal bones, as in all osteichthyans, and in contrast to *Lophosteus*.

Ligulalepis: *Ligulalepis* was first described by Schultze (1968) and placed within actinopterygians. This was

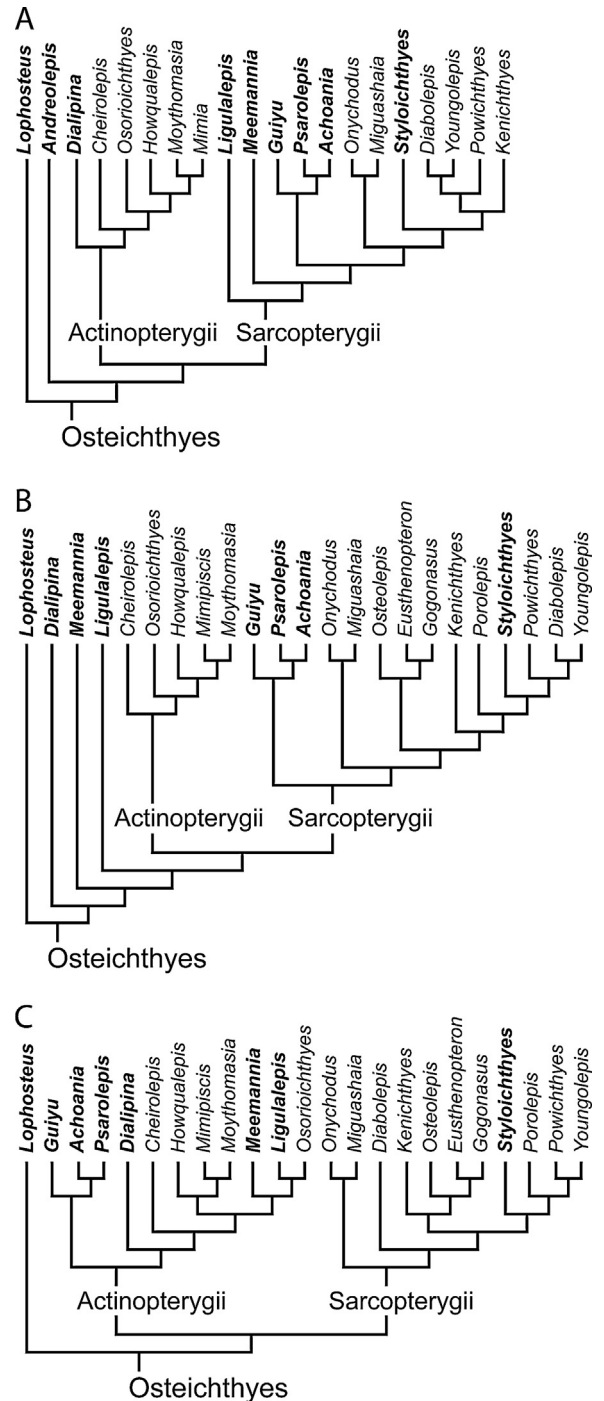


Fig. 15. Osteichthyan section of phylogenetic hypotheses by (A) Zhu et al. (2009, Supplementary information fig. 1), (B) Dupret et al. (2014, Extended data fig. 1) and (C) Long et al. (2014, Extended data fig. 6). Bold = taxa dealt with in the article.

Fig. 15. Branche concernant les ostéichthyens extraite des hypothèses phlogénétiques de (A) Zhu et al. (2009, informations supplémentaires, fig. 1), (B) Dupret et al. (2014, données complémentaires, fig. 1) et (C) Long et al. (2014, données augmentées, fig. 6). En gras = taxons relatifs à cet article.

followed by Wang and Dong (1989: Silurian *Ligulalepis* from China), Burrow (1994), Janvier (1996), Märss (2001) and others. Zhu et al. (2006) placed *Ligulalepis* with *Dialipina* as stem actinopterygian or as “higher” actinopterygian with *Osorioichthys*, whereas Zhu et al. (2009) considered *Ligulalepis* as a stem sarcopterygian together with the clade (*Meemannia* (*Guiyu* (*Psarolepis* + *Achoania*))) (Fig. 15A). Friedman and Brazeau (2010) and Dupret et al. (2014) considered the genus to be a stem osteichthyan (Fig. 15B). In contrast, *Ligulalepis* appears with *Osorioichthys* within the actinopterygians in Long et al. (2014), one option) already proposed in Zhu et al. (2006).

The scales of *Ligulalepis* possess a narrow based peg, a well developed anterodorsal process, ganoine (=overlapping enamel) forming ridges, deep scales otherwise known only in actinopterygians and a serrated posterior border. Sarcopterygian scales possess a straight posterior margin with one exception (osteolepidid indet., Young and Schultze, 2005). The best indication for a placement of *Ligulalepis* within actinopterygians is the presence of acrodin in the teeth (Fig. 13).

Naxilepis: Wang and Dong (1989) described actinopterygian scales from the Silurian of China. The low and elongated scales occur usually in the ventral region of the body. The anterodorsal process is strongly extended, and the posterior margin serrated. Wang and Dong (1989) compared the scales with those of *Orvikuina*. *Naxilepis* appears in the phylogenetic analysis of Schultze and Märss (2004) within the actinopterygians crownward to *Andreolepis*. Lu and Zhu (2008) considered the genus as a basal osteichthyan. Strongly extended anterodorsal process and ganoine (=overlapping to multilayered enamel) point to a placement within actinopterygians.

Terenolepis: Scales of this genus were described by Burrow (1995a) as actinopterygian scales from the Lower Devonian of Australia. *Terenolepis* appears in the phylogenetic analysis of Schultze and Märss (2004) within the actinopterygians above *Andreolepis*, only the inclusion of the genus results in an unresolved interrelationship within actinopterygians. None of the scales figured by Burrow (1995a) seems to be complete so that it is not clear how strongly the anterodorsal process is developed. There is an internal keel (Burrow, 1995a, pl. 1, fig. 3 and fig. 3d, f), but peg and socket are not preserved. The posterior margin may be serrated (Burrow, 1995a, pl. 1, figs. 3, 5, and fig. 2b). Ganoine is sporadically developed; it is described as single layered Burrow (1995a, fig. 2b, explanation as fig. 3b), and it shows overlaying enamel layers. Despite insufficient information, the interpretation of the genus as an actinopterygian seems the only acceptable one.

Orvikuina: Gross (1953) described ventral scales of an actinopterygian from the Middle Devonian of Estonia. The scales possess an anterodorsal extended corner, but a dorsal peg is not formed as is typical for elongated ventral scales. A keel is present on the inner side. Schultze (1968) described shorter and deeper scales of *Orvikuina* from the Middle Devonian of Spitsbergen. They show a small peg and a shallow socket ventral of the keel (Schultze, 1968, fig. 13, pl. 3, fig. 7a, b). The dorsal surface is covered with long ridges formed by dentine and covered by enamel. The enamel of the ridges overlaps laterally (Gross,

1953, figs. 9A, B, 13; Schultze, 1968, fig. 16) and sometimes for a longer distance (Gross, 1953, fig. 12; Schultze, 1968, fig. 17), that is a feature of ganoine and not found in “true” enamel of sarcopterygians. The scales have all characters of an actinopterygian, so that it is difficult to understand why Friedman and Brazeau (2010) placed the genus as stem osteichthyan. *Orvikuina* appears in the phylogenetic analysis of Schultze and Märss (2004) within the actinopterygians above *Andreolepis* based on the presence of an anterodorsal process and ganoine (=overlapping and multilayered enamel; Gross, 1953, figs. 9, 12, 13, pl. 7 figs. 3, 4, Ørving, 1957, fig. 3A, B; Schultze, 1968, figs. 16, 18).

5.3. Actinopterygii or Sarcopterygii

In recent years a number of basal osteichthyans have been described from the Upper Silurian and Lower Devonian of China. Their position within osteichthyans has varied much; they have been placed with the Sarcopterygii initially. I will discuss here the position mainly based on scale characters.

Guiyu: Zhu et al. (2009) described the Silurian osteichthyan, *Guiyu*, which they placed with *Ligulalepis* and *Meemannia* as stem sarcopterygian [*Ligulalepis* (*Meemannia* (*Guiyu* (*Psarolepis* + *Achoania*) (Sarcopterygii)))] (Fig. 15A), while they stated it displays a mixture of actinopterygian and sarcopterygian features. Qiao and Zhu (2010) and Dupret et al. (2014) placed the clade (*Guiyu* (*Psarolepis* + *Achoania*)) as basal sarcopterygians (Fig. 15B), whereas Long et al. (2014) moved the three genera to a basal actinopterygian position (Fig. 15C).

Guiyu has the snout of an actinopterygian with ganoine ridges (Qiao and Zhu, 2010, fig. 4a, b), which expose the bone sutures. The premaxillaries meet in the middle in front of the rostral as in *Mimipiscis* and *Moythomasia*. The position of both nares between the bones of the snout compares with *Cheirolepis* and *Paratarrasius*. *Guiyu* possesses many branchiostegals and a large preoperculum, as in actinopterygians and in contrast to sarcopterygians. The similarities in the cheek region between *Guiyu* and actinopterygians are interpreted as primitive osteichthyan characters by Zhu et al. (2009, p. 473). In contrast, the skull roof shows an intracranial joint between parietal and post-parietal (Qiao and Zhu, 2010, fig. 1). Taking the scales (Zhu et al., 2009: fig. 4i and suppl. info. figs. 1, 9b) into consideration, these show only actinopterygian features with ridges of ganoine (Qiao and Zhu, 2010, p. 1837; Zhu et al., 2009, p. 473), an anterodorsal process, a narrow based peg, and a serrated posterior margin. The double ridged keel is reminiscent of that in scales of *Ligulalepis*. The ridges are covered by “a glossy outer dermal coating of single or multilayer enamel” (Qiao and Zhu, 2010, p. 1837), typical for ganoine of actinopterygians.

Achoania: Zhu et al. (2001) and Zhu and Yu (2002) placed *Achoania* close to *Psarolepis* as stem sarcopterygian (Fig. 15A). Long et al. (2014) moved it to a basal actinopterygian position together with *Psarolepis* and *Guiyu* (Fig. 15C). Only the anterior cranial portion is known from the Lochkovian of China, but no scales. The snout is very similar to that of *Psarolepis* (Qiao and Zhu, 2010, figs. 4c, d, 9).

Psarolepis: Yu (1998) described the new genus *Psarolepis* from the Silurian and Lower Devonian of China as porolepiform sarcopterygian. In Zhu et al. (1999), and Zhu and Schultze (2001), the taxon appears as a stem osteichthyan, but in Zhu et al. (2006, 2010) as a stem sarcopterygian, Zhu et al. (2012) and Qu et al. (2013) offer both variants, either as stem osteichthyan or stem sarcopterygian. In Long et al. (2014), *Psarolepis* appears with *Achoania* at the base of the Actinopterygii (Fig. 15C): clade (*Guiyu* (*Achoania* + *Psarolepis*)) (all other actinopterygians).

Qu et al. (2013) described the histology of the scales of *Psarolepis romeri*; they argued that *Psarolepis* possesses cosmine with a developing pore–canal system. The surface of the scales shows large pores arranged in longitudinal rows (Qu et al., 2013, figs. 2A–G, 3A, 4A, B) as it can be found in actinopterygians, a very similar case are the scales of the Carboniferous *Acrolepis wilsoni* (Fig. 16; Traquair, 1909, pl. 25, figs. 12, 13). The surface of the scales of *Psarolepis romeri* does not show the fine pore system of cosmoid scales. The sections (Qu et al., 2013, figs. 5A–D, 7A, B, 8A, D, E, 10A) show a canal system with few large openings to the surface. There is only one canal system, which serves the dentine. The presence of one canal system only is especially clear in the two horizontal sections (Qu et al., 2013, fig. 9A, B). Only longitudinal canals are visible with a vertical connection near the posterior border and radial canals near the lower (ventral) margin. That is the typical situation in actinopterygian scales as shown many times by Aldinger (1937, see above) and is figured here (Fig. 5) for *Moythomasia*, where the dentine tubuli are visible to demonstrate the connection of dentine with the longitudinal canals. A second canal system, a mesh canal system as it appears in cosmine (see Fig. 9), is missing completely in the scales of *Psarolepis*. The arrangement of enamel corresponds to that of actinopterygians also, overlapping and even multilayered ganoine is present (Qu et al., 2013, fig. 7E). The sequence of additional growth (Qu et al., 2013, figs. 5B, D, 6A, 7B, F) looks like that in actinopterygian scales (Figs. 5, 6). Zhu et al. (2006, fig. 3a) considered such growth correctly as typical for actinopterygians. Thus, Qu et al. (2013, fig. 12) compare the scales in morphology and histology – in my opinion correctly – with those of *Ligulalepis* and *Andreolepis*, two basal actinopterygians. All scale characters point towards a position as sister group to *Achoania* and *Guiyu* and all other actinopterygians (Long et al., 2014).

Meemannia: Zhu et al. (2006) placed the new taxon, *Meemannia*, at the base of the Sarcopterygii despite similarities in the arrangement of skull roofing bones with the pattern in actinopterygians (Zhu et al., 2006, compare fig. 1c with fig. 1d [*Dialipina*], g [*Cheirolepis*]) and only a cosmine-like dermal surface. Zhu et al. (2010) and Janvier (2007) placed the genus as stem sarcopterygian below *Psarolepis* (Fig. 15A). In contrast, *Meemannia* is placed with *Ligulalepis* and *Osorioichthys* in higher actinopterygians in Long et al. (2014; Fig. 15C).

Zhu et al. (2006, fig. 2c) give a free reconstruction of a pore–canal system in *Meemannia*. The sections (Zhu et al., 2006, fig. 2a, b) show sequential overgrowth (“odontodes”) of dentine + single enamel layers, with partially overlapping enamel like ganoine in actinopterygian scales, and no pore–canal system. Scales are unknown for the genus,

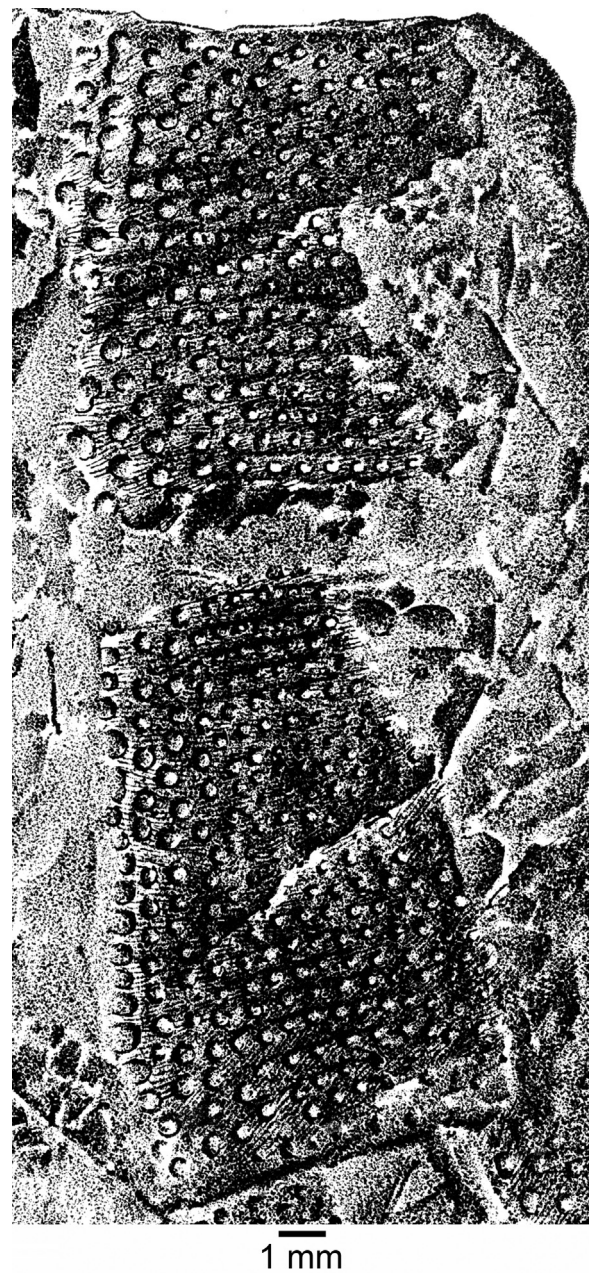


Fig. 16. Scales of the actinopterygian *Acrolepis wilsoni* (section out of Traquair, 1909, pl. 25, figs. 12), holotype BMNH P.5329; Yoredale Series, Lower Carboniferous; Turnditch near Belper, Derbyshire, England.

Fig. 16. Écailles de l'actinoptérygien *Acrolepis wilsoni* (coupe issue de Traquair, 1909, pl. 25, figs. 12), holotype BMNH P.5329, Séries de Yoredal, Carbonifère inférieur, Turnditch près Belper, Derbyshire, Angleterre.

nevertheless skull roof pattern and histology point to a placement close to actinopterygians.

Of the four genera, *Guiyu*, *Psarolepis* and *Achoania* are placed in close relationship to each other in recent phylogenies, whereas the position of *Meemannia* is uncertain. *Meemannia* may be an actinopterygian, but the position of *Guiyu*, *Psarolepis* and *Achoania* is more uncertain. The characters discussed here, seem to support the placement of

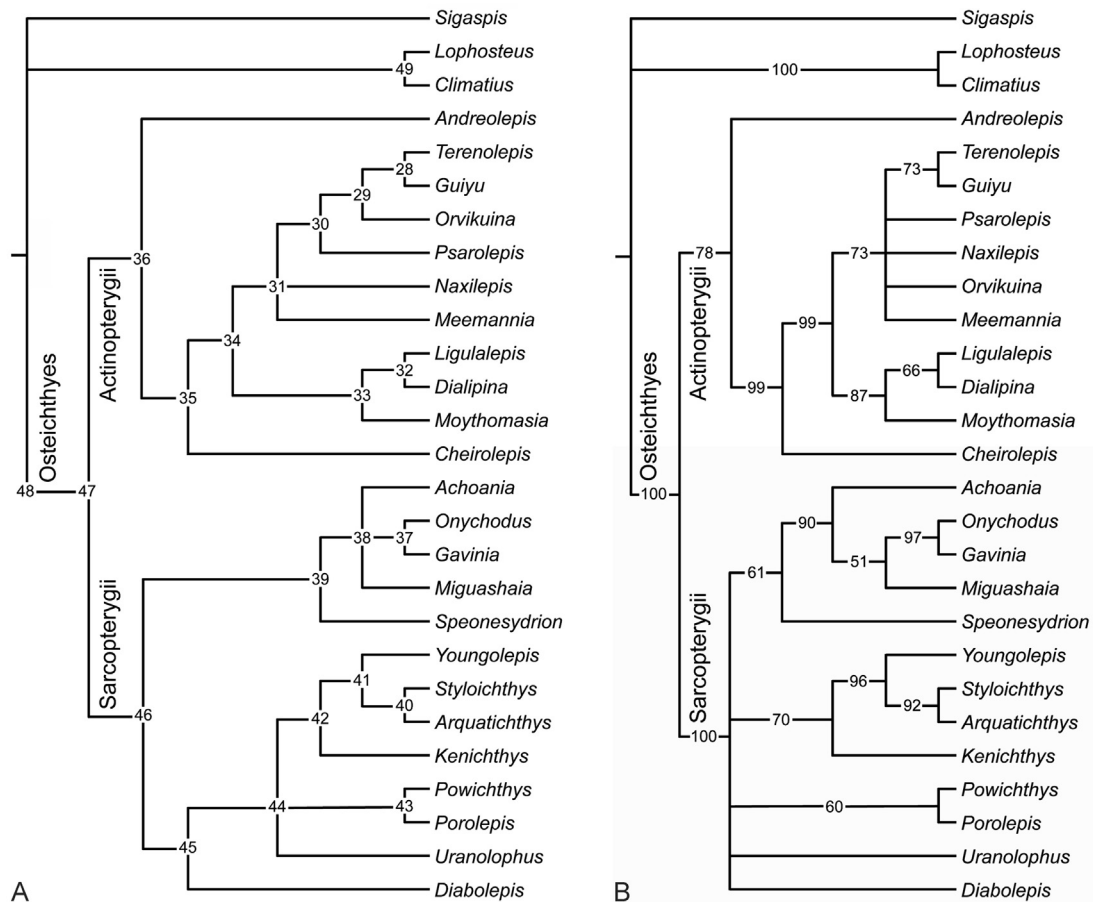


Fig. 17. Phylogenetic relationships of early osteichthyans based on scale characters alone. (A) Best resolved tree; (B) 50% Majority-rule consensus tree (for data see [supplementary information](#)).

Fig. 17. Relations phylogénétiques d'ostéichthyens souche, basées uniquement sur les caractères des écailles. (A) Arbre le mieux résolu; (B) Arbre de consensus à règle majoritaire de 50% (pour les données, voir les [informations supplémentaires](#)).

Long et al. (2014). Nevertheless *Guiyu*, *Psarolepis* and *Achoania* possess an intracranial joint considered a feature of sarcopterygians (lost in dipnoans and tetrapods), but also discussed as a primitive structure; an old controversy.

5.4. Sarcopterygii

Arquaticthys: Lu and Zhu (2008) described a new Early Devonian taxon, *Arquaticthys*, based on a lower jaw and detached scales. The scales possess an anteroventral process, which occurs also in *Powichthys* and *Youngolepis* after Lu and Zhu (2008). The authors placed the genus between Dipnoi and Porolepiformes. The presence of cosmine, a broad based peg and a straight posterior margin support a placement within sarcopterygians.

Styloichthys: *Styloichthys* was first described by Zhu and Yu (2002); they placed the genus within the sarcopterygians as sister taxon to Porolepiformes, Dipnoi and Tetrapodomorpha. The scales of the genus show typical cosmine with a single enamel layer and pore–canal system (Zhu and Yu, 2002, supplementary information); the enamel layer reaches into the pores (Zhu et al., 2006). These characters place the genus clearly within sarcopterygians

supporting studies by Zhu and Yu (2002), Zhu et al. (2006), Lu and Zhu (2008), Long et al. (2014) and Giles et al. (2015). The scales of *Styloichthys* and *Youngolepis* possess an anterodorsal process (Lu and Zhu, 2008), an appearance of the character in parallel to that in actinopterygians.

Placement in cladogram (Fig. 17A, B; for character list, data matrix and apomorphy list see supplementary data): Schultze and Märss (2004) presented an analysis based mainly on scale characters. Using that analysis with addition of the four new taxa *Styloichthys*, *Arquaticthys*, *Meemannia*, and *Guiyu* and two additional characters, there appears a clear division between actinopterygians and sarcopterygians. Osteichthyes possess two common characters, the lateral line canal within dermal bone and no paired fin spines (with a reversal in *Guiyu*). The actinopterygians are characterized by overlapping enamel, here accepted as indication of ganoine. Multilayered ganoine occurs only in two taxa included in this analysis, *Cheirolepis* and *Moythomasia*. “True” enamel (=single layered enamel) occurs only together with cosmine in sarcopterygians. *Guiyu*, *Psarolepis* and *Meemannia* appear within the actinopterygians together with basal actinopterygians, *Terenolepis*, *Orvikuína* and

Naxilepis similar to Long et al. (2014). The sister group of these basal actinopterygians is the clade (*Moythomasia* (*Ligulalepis* + *Dialipina*)) and all higher actinopterygians. The synapomorphy for sarcopterygians is the broad-based peg and cosmine with the occurrence of single layered enamel, “true” enamel. The sarcopterygians are artificially separated into forms with rounded scales (including *Achoania*) and those with rhombic scales. *Lophosteus* appears outside the osteichthyans together with *Climatius*. The division into the two taxa Actinopterygii and Sarcopterygii is well supported and is in congruence with Long et al. (2014), nevertheless the distribution of taxa within each group should not be taken too seriously because the number of characters is too small for the number of taxa.

The phylogenetic analysis of Long et al. (2014) is based on the data set of Dupret et al. (2014), which is based on earlier data sets like that of Zhu et al. (2013) and others. Nevertheless the tree topologies of Long et al. (2014) are quite different from earlier published ones based on the same data sets (and different from Giles et al., 2015). Long et al. (2014) reanalyzed the data set of Dupret et al. (2014) and retrieved the same tree topologies as for their data set enlarged by seven taxa (total of 85 taxa). It is interesting that the analysis of the much smaller data set of scale characters with few taxa (27) results in a similar tree topology like that of Long et al. (2014).

6. Concluding remarks

1. Ganoine is the specific enamel (often multilayered) of actinopterygians, which is difficult to identify in the most primitive actinopterygians. Partial overlap may be the feature to distinguish ganoine from single layered “true” enamel.

2. Cosmine is a specific combination of tissues and one structure, the pore–canal system, within sarcopterygians. The pore–canal system is characterized by horizontal mesh canals as addition to the horizontal dentinal canals. The pore–canal system may not be present in the most primitive sarcopterygians.

3. Enamel may or may not be present in basal osteichthyans. The features of ganoine (fine tubercles on the surface and multilayered enamel) have not been found in basal actinopterygians and those of “true” enamel not in basal sarcopterygians.

4. The histological features and the anterodorsal process place *Andreolepis*, *Dialipina*, *Naxilepis*, *Terrenolepis*, *Ligulalepis*, and *Orvikuina* within actinopterygians. *Guiyu*, *Psarolepis* and *Meemannia* may be basal actinopterygians. *Arquatchichthys* and *Styloichthys* are sarcopterygians, and *Lophosteus* is a stem osteichthyan.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2015.04.001>.

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