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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.

RÉSUMÉ

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, *Guiya*, *Meemania*, *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 Ctenoïdes 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, coelacanths 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 spongious 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