

Morphological and histological data on the structure of the lingual toothplate of *Arapaima gigas* (Osteoglossidae; Teleostei)

by

François J. MEUNIER* (1), Paolo M. BRITO (2) & Maria-Eduarda C. LEAL (2)



© SFI
Received: 6 May 2013
Accepted: 21 Nov. 2013
Editor: J.Y. Sire

Key words

Osteoglossidae
Arapaima gigas
Tooth
Basibranchial toothplate
Plicidentine
Histology

Abstract. – The pirarucu, *Arapaima gigas* (Osteoglossidae) has a basibranchial toothplate that supports a great density of teeth and helps the food transfer from the oral cavity towards the oesophagus. The lingual teeth appear early during ontogeny of the hyoid and branchial skeleton. On the basibranchial toothplate the teeth are closely set but without any connection, contrary to the “coalesced teeth”. The lingual teeth are 4 mm long and 1.0 to 1.5 mm wide; they are constituted of a cone of orthodontine with a distal cap of enameloid. Dentine is divided into two layers: an inner layer of circumpulpal dentine and an external one of pallial dentine. A peculiar specificity of the lingual teeth is the presence of plicidentine in their basal part. So in Actinopterygii, plicidentine is not limited to lepisosteids only. Owing to (i) the different aspect of plicidentine in the two taxa and (ii) their relative phylogenetic distance, we can interpret plicidentine in Actinopterygii as a morphofunctional adaptation to a predation diet.

Résumé. – Quelques données morphologiques et histologiques sur la structure de la plaque dentaire linguale d'*Arapaima gigas* (Osteoglossidae; Teleostei).

Le pirarucu, *Arapaima gigas* (Osteoglossidae) possède une plaque dentaire linguale très développée avec une grande densité de dents. Cette plaque facilite le transit des proies de la cavité buccale vers l'œsophage. Les dents linguales apparaissent très tôt lors de l'ontogenèse du squelette de la corbeille branchiale. Les dents font 4 mm de longueur et 1,0 à 1,5 mm de diamètre. Elles sont couvertes, à leur apex, par de l'émailloïde, un tissu hyperminéralisé, et sont constituées d'une dentine stratifiée : une couche externe de dentine paléale et une couche interne de dentine circum-pulpaire. À la base de la dent, la dentine est plissée, ce qui caractérise la présence de plicidentine. Parmi les Actinoptérygiens la plicidentine n'est donc pas limitée aux seuls Lepisosteidae. Nous considérons que la présence de plicidentine chez des taxons aussi éloignés (Lepisosteidae et Osteoglossidae) est probablement la marque d'une adaptation fonctionnelle à la prédation chez les Actinoptérygiens.

Among the bones forming the architecture of the buccopharyngeal cavity of teleosts, particularly the branchial arches, many bear odontodes (Nelson, 1969; Lauder and Liem, 1983), which are generally less developed than jaw teeth. The entire oral and pharyngeal epithelium is of ectodermal-endodermal origin (Soukup *et al.*, 2008), and the oral-pharyngeal odontodes are epithelio-mesenchymal formations (Fraser *et al.*, 2010) like skin odontodes (Ørvig 1977; Sire and Huysseune, 2003). In teleosts, the gill arch skeleton and the musculature became closely involved in food intake and its transit to the oesophagus (Vandewalle *et al.*, 2000). In some teleost families these pharyngeal odontodes and their bony support are well-developed, forming a jaw system located at the posterior region of the oropharyngeal cavity, just anterior to the opening of the oesophagus. These pharyngeal jaws characterize the “pharyngognathes” fishes (Daget, 1964; Nelson, 1967; Peyer, 1968; Liem and Greenwood, 1981; Vandewalle *et al.*, 1994). Such jaws were described in Cyprinidae (Edwards, 1929; Vasnecov, 1939; Eastman and Underhill, 1973; Nakajima, 1979, 1990; Sib-

bing, 1982), Cichlidae (Ismail *et al.*, 1982; Casciotta and Arratia, 1993; Huysseune *et al.*, 1994), Scaridae (Boas, 1879; Monod, 1951a; Gobalet, 1989), Labridae (Liem and Sanderson, 1986) and Carangidae (*Trachinotus*: Monod, 1951b; Meunier and Trébaol, 1987; Trébaol *et al.*, 1991; Francillon-Vieillot *et al.*, 1994). In fact, these pharyngeal jaws are the sole “chewing” elements present in Cyprinidae, in which the anterior jaws (premaxillary and dental) lack teeth.

Osteoglossomorpha and Elopomorpha are the more primitive teleostean lineages with modern representatives, and each lineage has been alternatively considered as the most basal (see, e.g. Lauder and Liem, 1983; Arratia, 1997). Extant Osteoglossomorpha assemble Osteoglossoidei, Notopteridei and Hiodontidae (Arratia, 1997). In the past, extant osteoglossids were grouped in one family, Osteoglossidae (Nelson, 1994), but they are now considered as two families: the Osteoglossidae (*Osteoglossum* and *Sleropages*) and the Arapaimatidae (*Arapaima* and *Heterotis*) (Ferraris, 2003a, b). The genus *Arapaima* is currently represented in South America, in the Amazon Basin (Ferraris Jr., 2003a,

(1) UMR 7208 (CNRS-MNHN-IRD-UPMC), BOREA, Département des milieux et peuplements aquatiques, Muséum national d'Histoire naturelle, CP 26, 43 rue Cuvier, 75231 Paris CEDEX 05, France.

(2) Departamento de Zoologia, Universidade do Estado do Rio de Janeiro. Rua São Francisco Xavier 524, Maracanã, 20559-900, Rio de Janeiro, Brazil. [pbrito@paleo@yahoo.com.br] [mecl@centroin.com.br]

* Corresponding author [meunier@mnhn.fr]

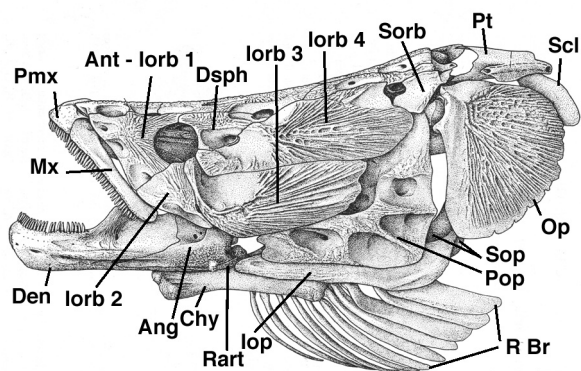


Figure 1. - *Arapaima gigas*. Lateral view of the skull (After Taverne, 1977). (Ang = Angular ; Ant = Antorbital ; Chy = Ceratohyal ; Den = Dental ; Dsph = Dermosphenotic ; Iop = Infraopercular ; Iorb 1-4 = Infraorbital ; Iop = Infraopercular ; Mx = Maxilla ; Op = Opercular ; Pmx = Premaxilla ; Pop = Preopercular ; Pt = Posttemporal ; Sop = Subopercular). Scale bar = 2 cm.

b; Brito *et al.*, 2007). Although traditionally regarded as a monotypic genus, *Arapaima* was recently considered as having more than one species (Stewart, 2013). Fossil arapaimids are known from the Cretaceous and Tertiary (Gayet and Meunier, 1998; Gayet *et al.*, 2001).

Both Osteoglossiformes (Osteoglossidae, Arapaimatidae, Mormyridae, and Notopteridae) and Albulidae have toothed oral jaws (Fig. 1) and rather reduced pharyngeal jaws, except for the fossil Notopteridae from the continental northwest Cretaceous of Morocco, †*Palaeonotopterus greenwoodi*. This species has stout pharyngeal jaws, the histological organization of which was described as “coalesced-like teeth” (Meunier *et al.*, 2013). In extant Osteoglossiformes, a third jaw system is located between the oral and pharyngeal jaws. It consists of a “lingual” jaw (= hyoid jaw), which opposes to a fixed set of teeth on the ventral surface of the neurocranium (Nelson, 1968; Greenwood, 1973; Taverne, 1972, 1977, 1978). This lingual jaw is formed by a single toothed plate (Fig. 2), which lies dorsally to basibranchials 1-3 (Shaklee and Tamaru, 1981; Sanford and Lauder, 1990); it is referred to as either the “tongue”, or lingual toothplate or basibranchial toothplate. This medial hyoid toothplate is one of the essential characteristics of the group (Lauder and Liem, 1983) and explains the origin of the English name of this taxon: the “bony-tongue” fish.

Within Osteoglossiformes and Albulidae taxa, the teeth supported by the hyoid jaws are quite well developed. The toothplates, on which teeth are inserted, play a role in the mechanical transfer of food into the oesophagus (Lauder and Liem, 1983; Sanford and Lauder, 1989 1990; Lauder and Wainwright, 1992; Sanford, 2001). This function has been clearly experimentally demonstrated in *Arapaima gigas* (Kershaw, 1976). However, to our best knowledge, no study was conducted on the histological structure of the basi-

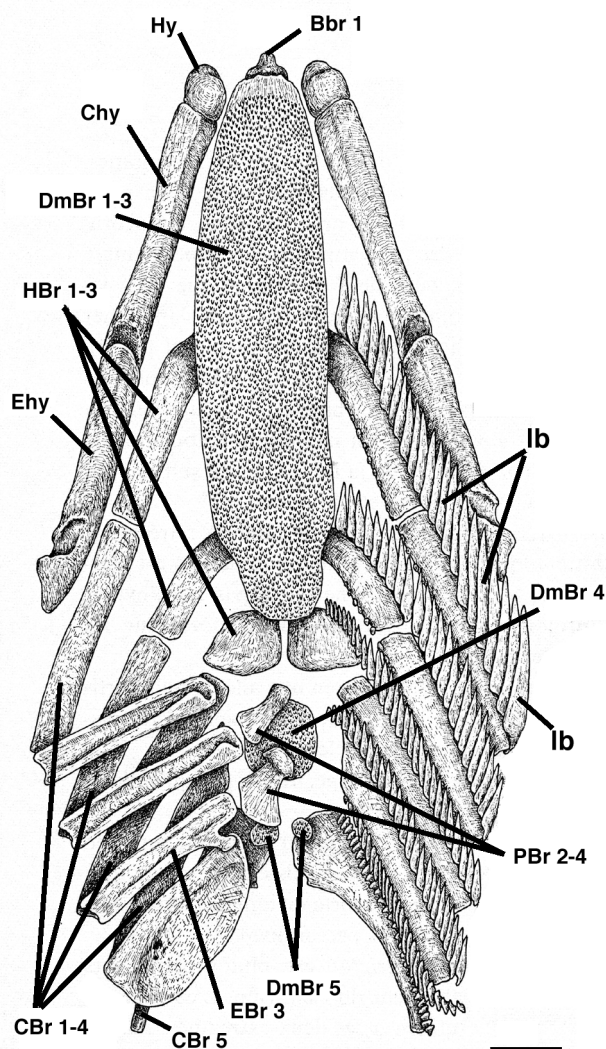


Figure 2. - *Arapaima gigas*. Dorsal view of the hyoid and branchial skeleton (After Taverne, 1977). (Bbr 1 = Basibranchial ; Cbr 1-5 = Ceratobranchial ; Chy = Ceratohyal ; DmBr 1-5 = Dermobasibranchial ; Ebr = Epibranchial ; Ehy = Epihyal ; HBr 1-3 = Hypobranchial ; lb = gill rakers ; PBr = Pharyngobranchial 2-4). Scale bar = 2 cm.

branchial bone plate or its teeth. Here, we partially fill this gap by studying the histological organization of the basibranchial toothplate in *Arapaima gigas*.

MATERIAL AND METHODS

Material

We studied ontogenetic development of the basibranchial toothplate in several developmental stages of *Arapaima gigas* (pirarucu): postembryos, whose standard length (SL) ranged from 16 to 24 mm, as well as juveniles. Ethanol-

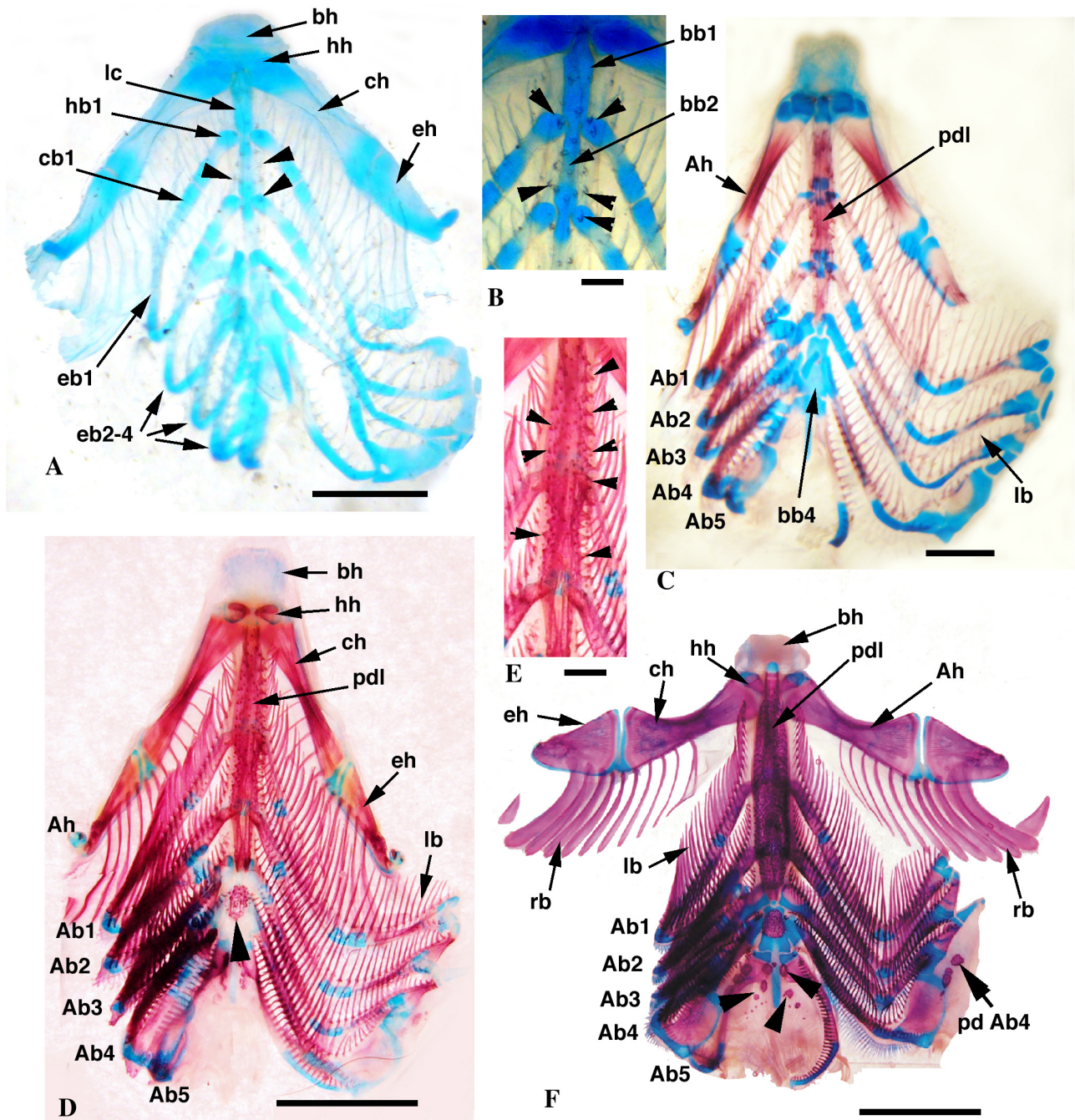


Figure 3. - *Arapaima gigas*. Dorsal view of cleared and stained gill arches from specimens of various ontogenetic stages. The visceral arches on the left are in anatomical position, whilst those on the right are unfolded. **A:** Specimen UERJ PMB-127 (16.7 mm SL). The endoskeleton is fully cartilaginous, lacking any ossification centre, but showing a few teeth (arrowheads) developing in front of the line of copulas between the hyoid arch and second branchial arch (see detail Fig. 3B). **B:** Same specimen. Detail of the anterior half of the line of copulas showing lingual teeth (arrowheads). **C:** Specimen UERJ PMB-135 (27.6 mm SL). Basibranchial elements 1-3 and “hypo”, “cerato” and “epi” elements show clear areas of diaphyseal ossification. Gill rakers and branchiostegal rays are ossified. **D:** Specimen UERJ PMB-159 (62.2 mm SL). The tongue plate (basibranchial toothplate) is clearly differentiated. There is at least one posterior toothplate on the surface of basibranchial 4 (arrowhead). **E:** Same specimen. Detail of the first two basibranchials showing many lingual teeth (arrowheads). **F:** Specimen UERJ PMB-106 (110 mm SL). The entire hyoid (except basihyal) and branchial skeleton are ossified, with the only joint areas remaining cartilaginous (coloured blue). Some small bony toothplates are located posterior to the line of copulas (arrowheads) at the base of the fifth gill arch. (Ab1-Ab5 = gill arches 1-5; Ah = hyoid arch; bb1-bb4 = basibranchial 1-4; bh = basihyal; cb1 = ceratobranchial 1; ch = ceratohyal; eb1-4 = epibranchial 1-4; eh = epihyal; hb1 = hypobranchial 1; hh = hypohyal; lb = gill rakers; lc = line copulas; pd Ab4 = branchial arch 4 toothplate; pdl = lingual (basibranchial) toothplate ; rb = branchiostegal rays). Scale bars: A, C, E = 1 mm; B = 250 μ m; D = 5 mm; F = 10 mm.

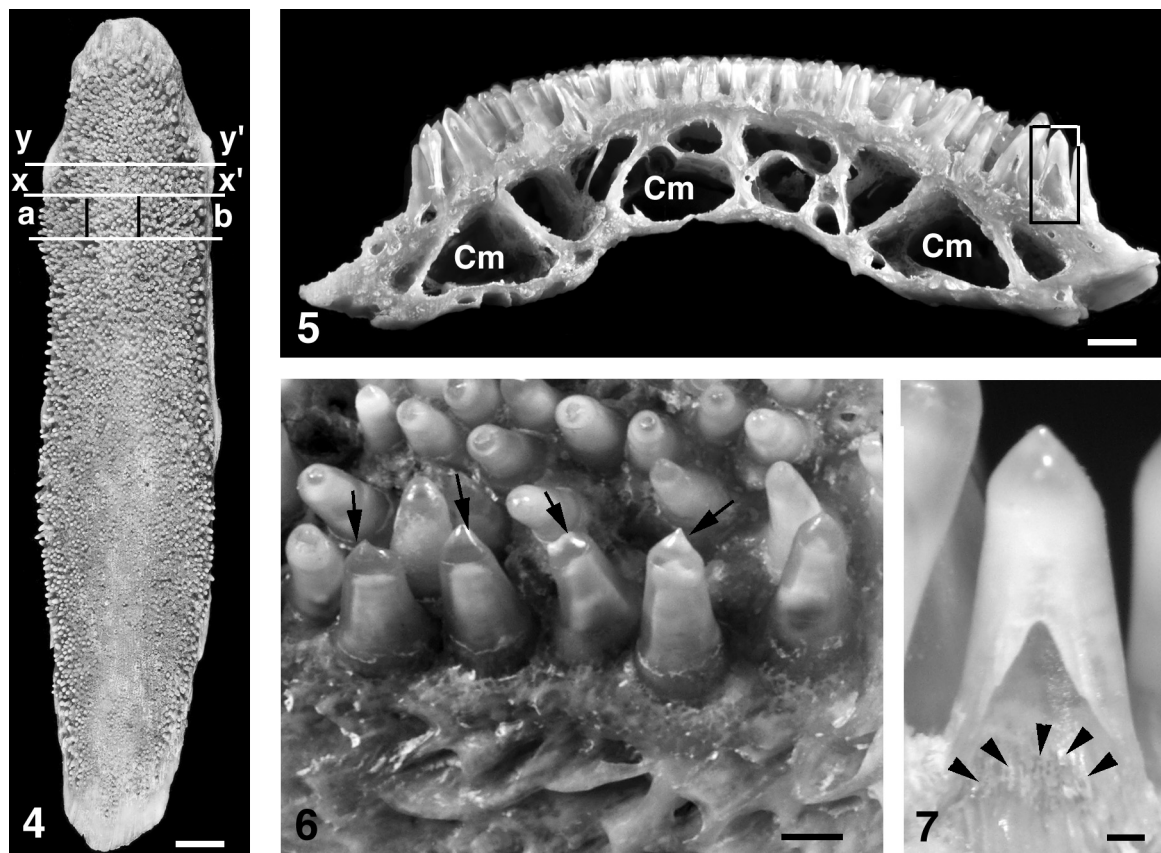


Figure 4. - *Arapaima gigas*. Dorsal view of the surface of the lingual dentary plate showing numerous teeth. Axis xx' and yy' demarcate the localisation of the transverse sections and the rectangles a and b point to the frontal sections. Scale bar = 1 cm.

Figure 5. - *Arapaima gigas*. Frontal view of the cross section (yy') of the lingual dentary plate. Detail of the spatial arrangement of the bony trabeculae between the two bony laminae. A sagittally-sectioned tooth is squared (see Fig. 7). Cm = medullary cavity. Scale bar = 2 mm.

Figure 6. - *Arapaima gigas*. External view of the lingual dentary plate showing the translucent tooth tips (arrows). Scale bar = 1 mm.

Figure 7. - *Arapaima gigas*. Detail of the pulp cavity of the lingual tooth squared in Fig. 5. We observe thin infolds of the dentine wall in the pulp cavity (arrowheads). Scale bar = 250 μm .

preserved specimens were kindly provided by Lucia R. Py-Daniel (INPA-Manaus, Brazil). Following Kunz (2004) we used the term “postembryos” when referring to specimens between post-hatching and the end of yolk absorption, and

“juveniles” when referring to specimens after the end of yolk absorption but still sexually immature. The onset of sexual maturity in *A. gigas* is observed in specimens larger than 150 cm SL (Imbiriba, 2001).

Figure 8. - *Arapaima gigas*. Cross section of the lingual dentary plate (natural transmitted light) showing numerous teeth (arrows) attached to the upper bony lamina (Lsp), the lower bony lamina (Lif), and the bony trabeculae between the two laminae (arrow heads). Cm = medullary cavity; Cp = pulp cavity. Scale bar = 3 mm.

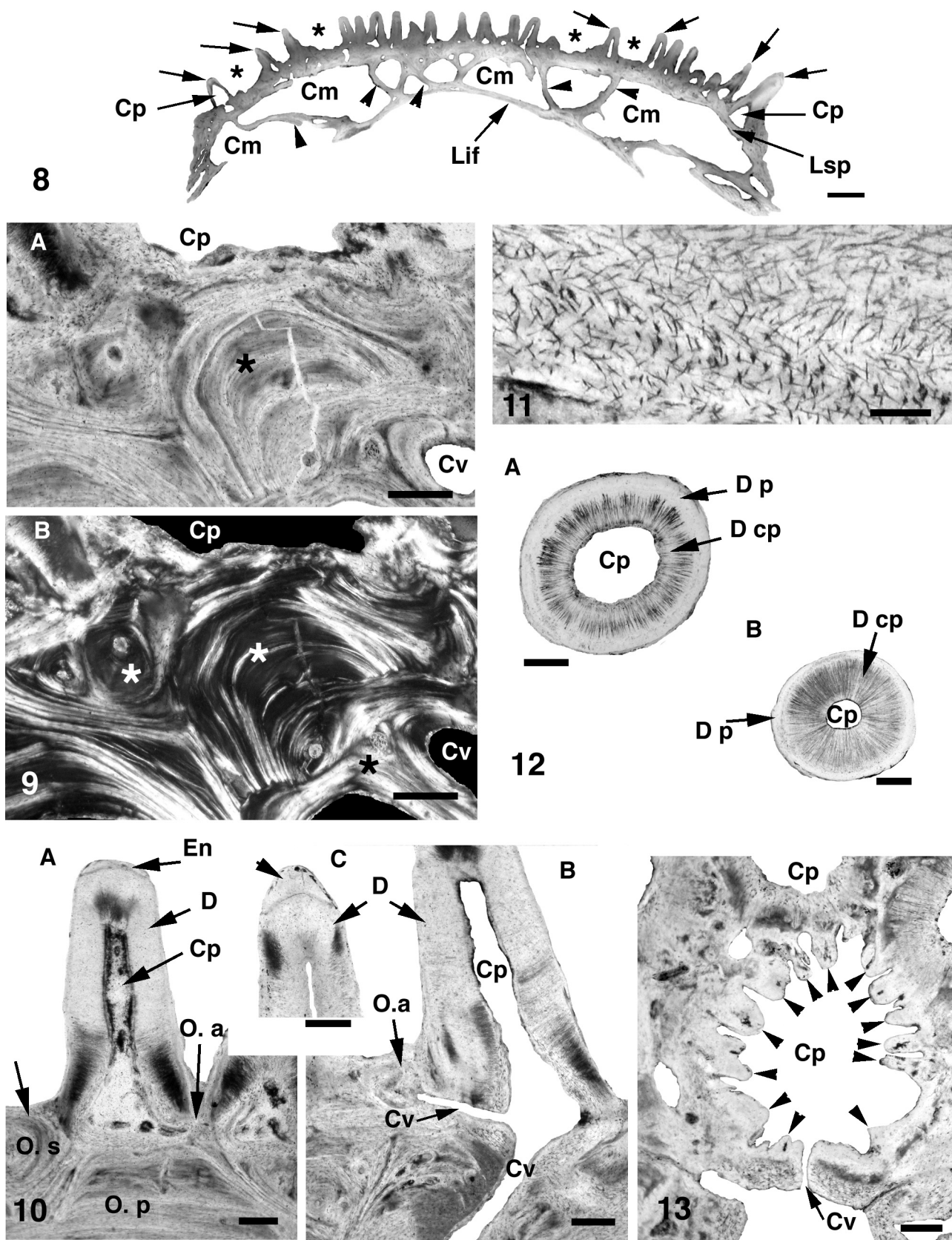
Figure 9. - *Arapaima gigas*. Transverse section of the lingual dentary plate. **A**: Natural transmitted light; **B**: Polarized light. Presence of a large quantity of secondary bone (*) showing that the bone localised under a tooth is frequently resorbed. Cp = pulp cavity; Cv = vascular cavity. Scale bar = 250 μm .

Figure 10. - *Arapaima gigas*. Transverse section of the lingual dentary plate (natural transmitted light) showing three longitudinal tooth sections. **A**: The tooth is attached to the upper lamina that is made of primary bone (O.p) and secondary bone (O.s). **B**: The pulp cavity of the tooth communicates other bone support via two vascular canals (Cv), the first one being lateral and the second plunging deeply in the bony lamina. **C**: Detail of a tooth with its distal cap of enameloid (arrow). Cp = pulp cavity; D = dentine; En = enameloid; O.a = bone of attachment. Scale bar = 250 μm .

Figure 11. - *Arapaima gigas*. Transverse section of the lingual dentary plate (natural transmitted light). Detail showing the osteocytes in the primary bone of the upper lamina. Scale bar = 100 μm .

Figure 12. - *Arapaima gigas*. Frontal sections of the lingual dentary plate (natural transmitted light) showing transverse tooth sections. The sections cross the mid-region of the tooth (**A**) and the distal third of the tooth (**B**), respectively. Two zones are visible in the dentine: the outer pallial dentine (D p) and the inner circumpulpal dentine (D cp), which shows many odontoblastic tubules. Pallial dentine is reduced compared to the circumpulpal dentine in Fig. 12B. Cp = pulp cavity. Scale bar = 250 μm .

Figure 13. - *Arapaima gigas*. Frontal section of the lingual dentary plate (natural transmitted light). The section crosses the tooth base and shows folding of the inner dentine (arrows heads) = plicidentine. Cp = pulp cavity; Cv = vascular cavity. Scale bar = 250 μm .



We have also examined a basibranchial toothplate measuring 170 mm in length and 35 mm in maximum width, from a specimen, in which the neurocranium was 21 cm in length. Unfortunately we did not know the total length of the animal.

Methods

Juvenile specimens were cleared and double stained following a technique modified from Taylor and Van Dyke (1985). Anatomical preparations were observed under a binocular microscope.

The basibranchial toothplate was cleared of soft tissue, dried and dehydrated (Fig. 4). A first sample was taken at the anterior third of the plate and embedded in resin in order to make ground cross-sections through the entire width of the toothplate (Fig. 4). The teeth were cut along their proximal-distal axis. A second sample, also embedded in resin, was cut into two fragments (Fig. 4) for tangential sections, thus yielding transverse tooth sections. These preparations were observed under a binocular microscope using natural and polarized light.

RESULTS

Development of the basibranchial toothplate

The branchial elements of 16–17 mm SL specimens are entirely cartilaginous, without any visible point of ossification (Fig. 3A). However several teeth are already present on the line of copulas (Fig. 3B). The toothplate appears as a translucent fibrous tissue, bearing its first teeth. The ossification centres of the bony elements appear at stages 25–30 mm SL, involving the “hypo” and “epi” elements of the gill arches, the basibranchials 1–3 and the basibranchial toothplate. By this time, all of them show areas of red (alizarin) staining characterizing mineralization and, in the present case, an ossification process (Fig. 3C). In the 60 mm SL specimen alizarin stains all bony elements of the branchial skeleton, including gill rakers and branchiostegal rays (Fig. 3D, E). Only the articular areas remain cartilaginous (Fig. 3D). The basibranchial toothplate appears clearly above the basibranchials 1–3 (Fig. 3D). There is no ossified basihyal but an unossified basihyal element is present in postembryos and juveniles (bh: Fig. 3A, C, D, F), above the dorsal hypohyal and the basibranchial 1. This fibrocartilaginous element carries numerous teeth, but has not been observed in the adult (Fig. 3D, E). Small, posterior toothplates appear in the 60 mm SL specimen, anterior to the basibranchial 4 (Fig. 3D), then behind (Fig. 3E). These small toothplates remain independent from the basibranchial toothplate.

Morphology of the basibranchial toothplate

The basibranchial toothplate has a large number of teeth (50 per mm²) positioned one against the other (Figs 4, 5).

They are firmly attached by their base to the bony plate by bone of attachment (see below). Occasionally, spaces are devoid of teeth; they represent functional areas from where the tooth naturally fell or was lost during the preparation of the material.

The basibranchial toothplate consists of two bony laminae: a dorsal lamina and a ventral one, the lower face of which is slightly concave (Fig. 5). These two laminae are connected by ossified trabeculae, which delimit large medullary cavities (Fig. 5). These trabeculae act as true struts, which consolidate the whole basibranchial plate architecture.

The teeth have roughly uniform shape and size; the largest ones being 4 mm high and 1.0–1.5 mm in diameter at their base. Tooth size and density decrease slightly from the anterior to the posterior region of the basibranchial toothplate. They are slightly curved towards the posterior region. The diameter of each tooth gradually decreases from its base towards its tip, with a tapered end (Fig. 6). The outer contour of the largest teeth is smooth, but by transparency a fine striation is seen on their base. This striation corresponds to the folds of the inner wall of the pulp cavity (Fig. 7 and see below “Histology”).

Histology of the basibranchial toothplate

The two bony laminae constituting the basibranchial toothplate and the trabeculae supporting them are made of bone tissue of various thickness (Fig. 8). The ventral lamina is thinner than the dorsal tooth-bearing lamina (Fig. 8). Each lamina consists essentially of primary cellular bone. However, the dorsal lamina shows numerous remodelled areas near the sites of tooth attachment (Figs 9A, B, 10A, B). Polarized light clearly shows processes of resorption and reconstruction of bone tissue resulting from periodical tooth renewal (Fig. 9B). The bone tissue contains star-shaped osteocytes possessing numerous cytoplasmic extensions (Fig. 11).

Vascular canals issued from the bone plate (Fig. 10B) penetrate the pulp cavity of the teeth (Figs 9A, 12A, B). Teeth consist of an elongated cone of dentine (Fig. 10A, B) covered by a layer of a slightly birefringent substance representing enamel or enameloid (Fig. 10C), perhaps acrodine (see Ørvig, 1978: 308–309). Numerous tubules, issued from the odontoblasts located in the pulp cavity and lining the dentine, perpendicularly penetrate the matrix (Fig. 12A, B). These tubules, house cytoplasmic extensions of the odontoblasts and characterize orthodentine. Odontoblast tubules turn less broad when approaching the outer surface of the tooth (Fig. 12A, B). The dentine is divided into two concentric layers: 1) an inner, thick layer, the circumpulpal dentine, rich in odontoblastic tubules; and 2) a peripheral, more homogeneous layer, the pallial dentine, with few tubules or devoid of them (Fig. 12A, B). Finally, the walls of the basal region of the tooth show noticeable folds in a radial arrangement (Fig. 13). From this level arise vascular canals that connect the vascular network

of the dorsal bone plate to the pulp cavity (Fig. 13). The folds of the pleated dentine in the tooth base are welded to the bony tissue constituting bone of attachment (Fig. 13).

DISCUSSION-CONCLUSION

The presence of a well-developed dentigerous basi-branchial toothplate in early stages of development (16–17 mm SL postembryos) suggests that its function in assisting prey transit has an early onset. Indeed, postembryos we studied were fed on live prey, particularly ostracod crustaceans, as indicated by the stomach contents visible after clearing and staining procedures.

The lingual teeth of *Arapaima gigas* are present at a high density, being almost contiguous near their place of attachment to the basibranchial bony plate. Their attachment is built through bone tissue; these well-anchored teeth belong to “Type 1” anchoring category of teeth as defined by Fink (1981). Type 1 corresponds to complete ankylosis and is considered by this author as more primitive than “mobile” teeth (Types 2, 3 and 4; Fink, 1981). The lingual teeth of *A. gigas* are subject to continual renewal as evidenced by the significant bone remodelling of the upper part of the toothplate. Teeth form a single bed and are extremely close each other. They are neither surrounded nor covered by a mineralized tissue as on the “coalesced teeth” (following Britski *et al.*, 1985) of the mandibular jaws of various teleosts: Scaridae, Tetraodontidae (Andreucci, 1968; Peyer, 1968; Britski *et al.*, 1985; Fraser *et al.*, 2012; Meunier, 2012), or of the pharyngeal jaws of *Trachinotus* (Monod, 1951b; Meunier and Trébaol, 1997) or on the basibranchial toothplate of the fossil Notopteridae †*Palaenotopterus greenwoodi* (Meunier *et al.*, 2013). This high tooth density on the basibranchial toothplate of *A. gigas* clearly allows functioning as “conveyor belt” for the prey passing through the mouth towards the posterior pharyngeal region (Kershaw, 1976) before entering oesophagus.

An interesting structural feature of lingual teeth of *A. gigas* lies in the presence of a folded orthodentine wall at the base of the dentine cone. This organization in more or less regular folds is characteristic of plicidentine. This term was coined by Owen (1841 in Tomes, 1878), then clarified by Tomes (1878) as designating “the folded internal wall of the basal area of the tooth surrounding the pulp cavity, as in lepisosteids” (Peyer, 1968). The plicidentine is best known as a feature of many sarcopterygian taxa (Bystrow, 1939, 1942, 1950; Lison, 1954; Bradford, 1967; Ørving 1967; Schultze, 1969, 1970; Vorobyeva, 1977), and shows various structural arrangements (Kearney and Rieppel, 2006; Maxwell *et al.*, 2011). So far, in the actinopterygian lineage the plicidentine has been reported only for the oral teeth of Lepisosteidae (Peyer, 1968; Grande, 2010). Peyer has mentioned plicidentine in some teleosts, but with a limited development to the

base of the teeth, without mentioning the names of the taxa investigated (Peyer, 1968: 98–100). Among the other authors who have studied the tooth structure in many actinopterygian taxa, only Thomasset (1930) reported the presence of plicidentine in a teleost: “The genus *Hydrocyon* [= *Oligosarcus*] has teeth folded at the base, without reflecting on the intimate structure of dentine”. However, Thomasset does not provide details or illustration supporting his assertion on the tooth structure of this characid predator from South America.

The teeth of Lepisosteidae (genus *Atractosteus* and *Lepisosteus*) have folds of orthodentine characterizing plicidentine (Schultze, 1969; Wiley, 1976; Grande, 2010: Fig. 45). In *A. gigas*, unlike Lepisosteidae, in which dentine folds are clearly visible externally in the form of parallel grooves (Peyer, 1968: Fig. 48; Grande, 2010: Figs 45, 240), the basal external area of lingual teeth is smooth, while the folds are visible on the inner surface of the tooth facing the pulp cavity. Even if the occurrence of plicidentine remains extremely limited in teleosts, the differences in its development in Lepisosteidae and Osteoglossidae, and the phylogenetic distance of these two lineages (Lauder and Liem, 1983), lead us to believe that this folded organization of dentine is a morpho-functional adaptation, i.e. a convergent character with no relationship.

The basibranchial toothplate of *A. gigas* assists in the backward movement of prey into the oesophagus (Kershaw, 1976), particularly helped by the teeth with their backward-directed tip. These teeth are subject to mechanical stress requiring a strong anchoring onto the basibranchial bone plate. The plicidentine folds greatly increase the attachment surface for teeth compared to single orthodentine ring, which is the most frequent condition (Fink, 1981). A similar functional adaptation was proposed to explain the structural diversity of plicidentine in Sarcopterygii (Scanlon and Lee, 2002; Modesto and Reisz, 2008; Maxwell *et al.*, 2011). Ongoing research allowed us to observe traces of folding in the external surface on the tooth base of another teleost, *Hoplias aimara* (Erythrinidae), a fish-eating Characiforme from the Amazon basin bearing large canine-like teeth on its jaws. The presence of plicidentine on this species, if confirmed, would reinforce our adaptive hypothesis related to fish predation, since Characiformes and Osteoglossiformes are separate teleost lineages.

Acknowledgements. – We would like to thank Vincent Rommevaux (Laboratoire de Géologie, Département des Sciences de la Terre, Muséum national d’Histoire naturelle) for his technical assistance in the preparation of ground sections and Claude Ferreira (UMR 7208, BOREA, Muséum national d’Histoire naturelle) for photographs of lingual toothplate. We also thank Lucia Rapp Py-Daniel (INPA-Manaus) who provided specimens for the ontogenetic study. MECL expresses her appreciation to the Visiting Professor Program (Sr2-UERJ). We are grateful to Dr Clara Lord (UMR 7208, BOREA, Muséum national d’Histoire naturelle) for her corrections of the English language.

REFERENCES

- ANDREUCCI R.D., 1968. - Macroscopic and microscopic morphology of *Spheroides testudineus* teeth (checkered puffer). *Acta Anat.*, 71: 448-471.
- ARRATIA G., 1997. - Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica*, 7: 5-168.
- BOAS J.E.V., 1879. - Die Zähne der Scaroiden. *Zeit. Wissensch. Zool.*, 32: 189-215.
- BRADFORD E.W., 1967. - Microanatomy and histochemistry of dentine. In: Structural and Chemical Organization of Teeth, Vol. II (Miles A.E.W., ed.), pp. 3-34. City: Printer?
- BRITO P., MEUNIER F.J. & DE LEAL M.E., 2007. - Origine et diversification de l'ichtyofaune néotropicale. In: 3^e Rencontres d'ichtyologie en France (SFI, ed.). *Cybium*, 31(2): 139-153.
- BRITSKI H.A., ANDREUCCI R.D., MENEZES N.A. & CARNEIRO J., 1985. - Coalescence of teeth in fishes. *Rev. Brasil. Zool.*, 2: 459-484.
- BYSTROW A.P., 1939. - Zahnstruktur der Crossopterygier. *Acta Zool.*, 20: 283-338.
- BYSTROW A.P., 1942. - Deckknochen und Zahn der *Osteolepis* und *Dipterus*. *Acta Zool.*, 23: 263-289.
- BYSTROW A.P., 1950. - Microscopic structure of bone and teeth in the carboniferous Crossopterygian *Megalichthys* (Osteolepidae). *Doklady Akad. Nauk SSSR*, 74(1): 119-121. [in Russian]
- CASCIOTTA J.R. & ARRATIA G., 1993. - Jaws and teeth of American cichlids (Pisces: Labroidei). *J. Morphol.*, 217: 1-36.
- DAGET J., 1964. - Le crâne des téléostéens. *Mém. Mus. Nat. Hist. Nat.*, Sér. A, Zool., 36(2): 163-341.
- EASTMAN J.T. & UNDERHILL J.C., 1973. - Intraspecific variation in the pharyngeal tooth formulae of some Cyprinid fishes. *Copeia*, 1973(1): 45-53.
- EDWARDS L.F., 1929. - The origin of the pharyngeal teeth of the carp (*Cyprinus carpio* Linnaeus). *Ohio J. Sci.*, 29(3): 93-130.
- FERRARIS C.J. Jr., 2003a. - Family Osteoglossidae (Arowanas). In: Check List of the Freshwater Fishes of South and Central America (Reis R.E., Kullander S.O. & Ferraris C.J. Jr., eds.), p. 30. Porto Alegre: Epiducrs.
- FERRARIS Jr., 2003b. - Family Arapaimatidae (Bonytongues). In: Check List of the Freshwater Fishes of South and Central America (Reis R.E., Kullander S.O. & Ferraris C.J. Jr., eds.), p. 31. Porto Alegre: Epiducrs.
- FINK W.L., 1981. - Ontogeny and phylogeny of tooth attachment modes in Actinopterygian fishes. *J. Morphol.*, 167(2): 167-184.
- FRANCILLON-VIEILLOT H., MEUNIER F.J., TRÉBAOL L. & SLEMBROUCK J., 1994. - Histological study of odontogenesis in the pharyngeal jaws of *Trachinotus teraia* (Cuvier & Valenciennes, 1832) (Osteichthyes, Teleostei, Carangidae). *J. Morphol.*, 220(1): 11-24.
- FRASER G.J., CERNY R., SOUKUP V., BRONNER-FRASER M. & STREELMAN J.J., 2010. - The odontode explosion: the origin of tooth-like structures in vertebrates. *Bioessays*, 32(9): 808-817.
- FRASER G.J., BRITZ R., HALL A., JOHANSON Z. & SMITH M.M., 2012. - Replacing the first-generation dentition in pufferfish with a unique beak. *Proc. Nat. Acad. Sci.*, 109(21): 8179-8184.
- GAYET M. & MEUNIER F.J., 1998. - Maastrichtian to Early Late Paleocene freshwater Osteichthyes of Bolivia: additions and comments. In: Phylogeny and Classification of Neotropical Fishes (Malabarba L.R., Reis R.E., Vari R.P., Lucena Z.M. & Lucena C.S., eds), pp. 85-110. Porto Alegre: Epiducrs.
- GAYET M., MARSHALL L.G., SEMPÉRÉ T., MEUNIER F.J., CAPPETTA H. & RAGE J.C., 2001. - Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. *Paleogeogr. Palaeoclimatol. Palaeoecol.*, 169(1-2): 39-68.
- GOBALET K.W., 1989. - Morphology of the parrotfish pharyngeal jaw apparatus. *Am. Zool.*, 29(1): 319-331.
- GRANDE L., 2010. - An empirical pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Am. Soc. Ichthyol. Herpet.*, Special Publ. 6. Suppl. Issue *Copeia*, 10(2A): 1-871.
- GREENWOOD P.H., 1973. - Interrelationships of Osteoglossomorphs. In: Interrelationships of Fishes (Greenwood P.H., Miles R.S. & Patterson C., eds). *Zool. J. Linn. Soc.*, 53(suppl., 1): 307-332.
- HUYSSSEUNE A., SIRE J.Y. & MEUNIER F.J., 1994. - Comparative study of lower pharyngeal jaw structure in two phenotypes of *Astatoreochromis alluaudi* (Teleostei: Cichlidae). *J. Morphol.*, 221(1): 25-43.
- IMBIRIBA E.P., 2001. - Potencial de Criação de pirarucu em cativado. *Acta Amazonica*, 31(2): 299-316.
- ISMAIL M.H., VERRAES W. & HUYSSSEUNE A., 1982. - Developmental aspects of the pharyngeal jaws in *Astatotilapia elegans* (Trewavas, 1933) (Teleostei: Cichlidae). *Neth. J. Zool.*, 32(4): 513-543.
- KEARNEY M. & RIEPPEL O., 2006. - An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. *Copeia*, 2006(3): 337-350.
- KERSHAW D.R., 1976. - A structural and functional interpretation of the cranial anatomy in relation to the feeding of osteoglossoid fishes and a consideration of their phylogeny. *Trans. R. Soc. Lond.*, 33(3): 173-252.
- KUNZ Y.W., 2004. - Developmental Biology of Teleost Fishes. 636 p. Fish & Fisheries Series, 28. Springer, The Netherlands.
- LAUDER G.V. & LIEM K.F., 1983. - The evolution and interrelationships of the Actinopterygian fishes. *Bull. Mus. Comp. Zool.*, 150(3): 95-197.
- LAUDER G.V. & WAINWRIGHT P.C., 1992. - Function and history: the pharyngeal jaw apparatus in primitive ray-finned fish. In: Systematics, Historical Ecology, and North American Freshwater Fishes (Mayden R. ed.), pp. 472-491. Stanford: Stanford Univ. Press.
- LIEM K.F. & GREENWOOD P.H., 1981. - A functional approach to the phylogeny of the pharyngognath teleosts. *Am. Zool.*, 21(1): 83-101.
- LIEM K.F. & SANDERSON S.L., 1986. - The pharyngeal jaw apparatus of labrid fishes: a functional morphological perspective. *J. Morphol.*, 187(2): 143-158.
- LISON L., 1954. - Les dents. In: Traité de zoologie, Vol. 12 (Grassé P.P., éd.), pp. 791-853. Paris: Masson.
- MAXWELL E.E., CALDWELL M. & LAMOUREUX D.O., 2011. - The structure and phylogenetic distribution of amniote plicidentine. *J. Vert. Paleont.*, 31(3): 553-561.
- MEUNIER F.J., 2012. - Morphologie et structure histologique comparées des "dents coalescentes" chez les téléostéens actuels et fossiles : une adaptation à la durophagie. Actes des XIII^e Journées tunisiennes des sciences de la mer et 2^e Rencontre tuniso-française d'ichtyologie (Madhia, Tunisie, 26-29 nov. 2011). *Bull. Inst. Nat. Sci. Techn. Mer*, Salammbô, N° Sp. 15: 28-34.
- MEUNIER F.J. & TRÉBAOL L., 1987. - Données histologiques sur les mâchoires pharyngiennes de *Trachinotus teraia* (Cuvier 1832), Carangidae (Osteichthyen, Perciforme) d'Afrique tropicale. *J. Biol. Buc.*, 15: 239-248.

- MEUNIER F.J., DUTHEIL D. & BRITO P.M., 2013. - Histological study of the median lingual dentary plate of the Cretaceous fish †*Palaeonotopterus greenwoodi* (Teleostei: Osteoglossomorpha) from the Kem-Kem beds, Morocco. *Cybium*, 37(1-2): 121-125.
- MODESTO S.P. & REISZ R.R., 2008. - New material of *Colobomycter pholeter*, a small parareptile from the Lower Permian of Oklahoma. *J. Vert. Paleont.*, 28(3): 677-684.
- MONOD T., 1951a. - Note sur le squelette viscéral des Scaridae. *Bull. Soc. Hist. Nat., Toulouse*, 86: 191-194.
- MONOD T., 1951b. - Dents à fonction non alimentaire chez un téléostéen. *Bull. Mus.*, 1^e sér., 23(4): 357-359.
- NAKAJIMA T., 1979. - The development and replacement pattern of the pharyngeal dentition in the Japanese Cyprinid fish, *Gnathopogon coeruleus*. *Copeia*, 1979(1): 22-28.
- NAKAJIMA T., 1990. - Morphogenesis of the pharyngeal teeth in the Japanese Dace, *Tribolodon hakonensis* (Pisces: Cyprinidae). *J. Morphol.*, 205(2): 155-163.
- NELSON G.J., 1967. - Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotidae, Labridae, and Scaridae. *J. Nat. Hist.*, 47: 289-293.
- NELSON G.J., 1968. - Gill arches of teleostean fishes of the division Osteoglossomorpha. *Zool. J. Linn. Soc.*, 47: 261-277.
- NELSON G.J., 1969. - Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. Nat. Hist.*, 141(4): 477-552.
- NELSON J.S., 1994. - *Fishes of the World*. 600 p. New York: John Wiley & Sons.
- ØRVIG T., 1967. - Phylogeny of tooth tissues: evolution of some calcified tissues in early Vertebrates. In: *Structural and Chemical Organization of Teeth*, Vol. I (Miles A.E.W., ed.), pp. 45-110. London: Academic Press.
- ØRVIG T., 1977. - A survey of odontodes ('dermal teeth') from development, structural, functional, and phyletic point of view. In: *Problems in Vertebrate Evolution* (Andrews E.D., Miles R.S. & Walker A.D., eds). *Linn. Soc. Symp. Ser.*, London, 4: 53-75.
- ØRVIG T., 1978. - Microstructure and growth of the dermal skeleton in fossil Actinopterygian fishes: *Nephrotus* and *Colobodus*, with remark on the dentition in other forms. *Zool. Scripta*, 7: 297-326.
- PEYER B., 1968. - Osteichthyes. In: *Comparative Odontology* (Zangerl R., ed.), pp. 80-110. Univ. Chicago Press.
- SANFORD C.P.J., 2001. - The novel "tongue-bite apparatus" in the knifefish family Notopteridae (Teleostei: osteoglossomorpha): are kinematic patterns conserved within a clade? *Zool. J. Linn. Soc.*, 132(2): 259-275.
- SANFORD C.P.J. & LAUDER G.V., 1989. - The functional morphology of the "tongue-bite" in the osteoglossomorph fish *Notopterus*. *J. Morphol.*, 202(3): 379-408.
- SANFORD C.P.J. & LAUDER G.V., 1990. - Kinematics of the tongue-bite apparatus in osteoglossomorph fishes. *J. Exp. Biol.*, 154: 137-162.
- SCANLON J.D. & LEE M.S.Y., 2002. - Varanoid-like dentition in primitive snakes (Madtsoiidae). *J. Herpetol.*, 36(1): 100-106.
- SCHULTZE H.-P., 1969. - Die Faltenzähne der Rhipidisiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus* nebst einer Beschreibung der Zahnstruktur von *Onichodus* (Struniiformer Crossopterygier). *Palaeont. Italica*, New Ser. 35, 65: 63-137.
- SCHULTZE H.P., 1970. - Folded teeth and the monophyletic origin of Tetraodes. *Am. Mus. Novitates*, 2408: 1-10.
- SHAKLEE J.B. & TAMARU C.S., 1981. - Biochemical and morphological evolution of Hawaiian bonefishes (*Albula*). *Syst. Zool.*, 30(2): 125-146.
- SIBBING F.A., 1982. - Pharyngeal mastication and food transport in the carp (*Cyprinus carpio* L.): a cineradiographic and electromyographic study. *J. Morphol.*, 172(2): 223-258.
- SIRE J.Y. & HUYSSSEUNE A., 2003. - Formation of dermal skeletal and dental tissues in fish: a comparative and evolutionary approach. *Biol. Rev.*, 78(2): 219-249.
- SOUKUP V., EPPERLEIN H.H., HORÁČEK I. & CERNÝ R., 2008. - Dual epithelial origin of vertebrate oral teeth. *Nature*, 455: 795-798.
- STEWART D.J., 2013. - Re-description of *Arapaima agassizii* (Valenciennes), a rare fish from Brazil (Osteoglossomorpha: Osteoglossidae). *Copeia*, 2013(1): 38-51.
- TAVERNE L., 1972. - Ostéologie des genres *Mormyrus* Linné, *Mormyrops* Müller, *Hyperopisus* Gill, *Isiethys* Gill, *Myomyrus* Boulenger, *Stomatorhinus* Boulenger et *Gymnarchus* Cuvier. Considérations générales sur la systématique des poissons de l'ordre des Mormyriiformes. *Ann. Mus. R. Afr. Cent. Sci. Zool.*, 200: 1-194.
- TAVERNE L., 1977. - Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du super-ordre des ostéoglossomorphes. Première partie. Ostéologie des genres *Hiodon*, *Eohiodon*, *Lycopera*, *Osteoglossum*, *Scleropages*, *Heterotis* et *Arapaima*. *Acad. R. Belg., Mém. Cl. Sci.*, 32(3): 1-235.
- TAVERNE L., 1978. - Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du super-ordre des ostéoglossomorphes. Deuxième partie. Ostéologie des genres *Phareodus*, *Phareoides*, *Brychaetus*, *Musperia*, *Pantodon*, *Singida*, *Notopterus*, *Xenomystus* et *Papyrocranus*. *Acad. R. Belg., Mém. Cl. Sci.*, 32(6): 1-213.
- TAYLOR W.R. & VAN DYKE G.C., 1985. - Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2): 107-119.
- THOMASSET J.J., 1930. - Recherches sur les tissus dentaires des poissons fossiles. *Arch. Anat. Micr.*, 11: 6-153.
- TOMES C.S., 1878. - On the structure and development of vascular dentine. *Phil. Trans. R. Soc., Lond.*, 169: 25-47.
- TRÉBAOL L., FRANCILLON-VIEILLOT H. & MEUNIER F.J., 1991. - Étude de la croissance des mâchoires pharyngiennes chez *Trachinotus teraia* (Carangidae, Perciforme) à l'aide de la technique du marquage vital. *Cybium*, 15(4): 263-270.
- VANDEWALLE P., HUYSSSEUNE A., AERTS P. & VERRAES W., 1994. - The pharyngeal apparatus in teleost feeding. In: *Biomechanics of Feeding in Vertebrates: Advances in Comparative and Environmental Physiology*, Vol. 18 (Bels V.L., Chardon M. & Vandewalle P., eds), pp. 59-92. Berlin: Springer Verlag.
- VANDEWALLE P., PARMENTIER E. & CHARDON M., 2000. - The branchial basket in teleost feeding. *Cybium*, 24(4): 319-342.
- VASNECOV V.V., 1939. - Evolution of the pharyngeal teeth in Cyprinidae. À la mémoire de A.N. Severtzoff, 1: 439-491. [In Russian]
- VOROBYEVA E.I., 1977. - Evolutionary modifications of the teeth structure in the Palaeozoic Crossopterygii. *J. Palaeontol. Soc. India*, 20: 16-20.
- WILEY E.O., 1976. - The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Univ. Kansas, Mus. Nat. Hist., Misc. Publ.*, 64: 1-111.