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**A tomographic study of the histological structure of teeth in the gilthead sea bream,
Sparus aurata (Teleostei, Perciformes, Sparidae)**

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Abstract. – X-ray tomography shows that caniniform and molariform teeth of the gilthead sea bream, *Sparus aurata*, have a simplexodont plicidentine organization. Together with an insertion of the teeth in alveolae, and the presence of bony shafts sustaining the dental plate, the simplexodont plicidentine is linked to the durophagous diet of the fish.

Key-Words : teeth, dentine, plicidentine, bone, *Sparus*.

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INTRODUCTION

Plicidentine is a specific organization of the dentine walls of teeth, forming complex infoldings, and capable to fill the whole pulp cavity of the teeth (Tomes, 1878; Bystrow, 1939, 1942; Schultze, 1969, 1970; and others). Three types of plicidentine were described in the Sarcopterygii: dendrodont, eusthenodont and polyplocodont (Schultze, 1969, 1970; Vorobyeva, 1977), and according to Schultze (1970, p. 8), they are considered as highly advanced, moderately advanced and primitive types of folded teeth, respectively. During several decades the presence of plicidentine was considered as a characteristic of many Sarcopterygii and basal tetrapods (Schultze, 1969; Vorobyeva, 1977; Scanlon and Lee, 2002; Kearney and Rieppel, 2006; Maxwell *et al.*, 2011, 2012; MacDougall *et al.*, 2014; among

others). Among the Actinopterygii, the Lepisosteidae have also teeth with eusthenodont plicidentine (Tomes, 1878; Peyer, 1968; Schultze, 1969; Meunier and Brito, 2017). Plicidentine is thought to reinforce the fixation of teeth to the jaw in predatory species (Peyer, 1968; Maxwell *et al.*, 2011). The presence of plicidentine in teeth is frequently revealed by external ridges at the base of these teeth (Scanlon and Lee, 2002; Meunier, 2015; Meunier *et al.*, 2015a; Meunier and Germain, 2018; Texereau *et al.*, 2018).

It is the presence of such external ridges at the base of stout teeth that has allowed the description of a fourth type of plicidentine (simplexodont plicidentine) in some predatory teleostean fishes: Erythrinidae (Meunier *et al.*, 2015a) and Lophiidae (Meunier, 2015) for example. The simplexodont plicidentine is constituted of simple non-ramified folds of the dentine walls, and that are localized in the basal region of the pulp cavity (Meunier *et al.*, 2013a; Germain *et al.*, 2016). In fact simplexodont plicidentine is relatively spread in a number of predatory teleosts like the Osteoglossidae (Meunier *et al.*, 2013a), Mormyridae and Notopteridae (Germain *et al.*, 2016), but also in the primitive actinopterygian *Polypterus* and *Amia* (Germain and Meunier, 2017) as well as in *Latimeria*'s fangs (Meunier *et al.*, 2015b). For most of the teleostean species with simplexodont plicidentine, there are no external ridges on teeth, contrary to the ridges of Erythrinidae teeth cited above. So to reveal its presence in teeth it is necessary to use specific techniques such as histology or, better, non-destructive X-ray tomography (Germain *et al.*, 2016).

In a comparative histological study of teeth of three sparid species (*Acanthopagrus australis*, *Pagrus auratus* and *Rhabdosargus sarba*), Hughes *et al.* (1994) illustrated their study with three figures that show an irregular dentine surface of the pulp cavity (Hughes *et al.*, 1994; Fig. 2B,E and 6A), and that may represent simplexodont plicidentine. To verify this hypothesis we have done a study of tooth organization in the gilthead sea bream, using X-ray tomography, a non-destructive technique. The gilthead sea bream *Sparus aurata* Linné, 1768 (Sparidae) is a common North-Atlantic marine species (Tortonese, 1973; Quero, 1984; Béarez *et al.*, 2017), that has a durophagous diet composed essentially of molluscs, decapod crustaceans, sea urchins... (Rossecchi, 1985; Chaoui *et al.*, 2005; Figueiredo *et al.*, 2005; El Bakary, 2012; and others). This specialized durophagous diet has an anatomical impact on the

morphology of their teeth, most of which are molariform (Fig. 1). We confirm the presence of simplexodont plicidentine in teeth of *Sparus aurata*.

MATERIAL AND METHODS

Material

The studied dead fish, an adult specimen (385 mm TL), has been purchased in a fishmonger's shop. The upper and lower jaws of the fish (Fig. 1) were sampled and soaked in boiling water for removing the soft flesh, and air dried. The right upper jaw was used for the CT scan study and the left one for ground sections.

Methods

Non destructive X-ray tomography. The teeth and their supporting bone were X-rayed utilizing a Computed Tomography (CT) imaging system (AST-RX platform and Ge Sensing and inspection Technologies phoenix-ray v|tome|x L240-180 CT scanner) at the Muséum National d'Histoire Naturelle, with nanofocus RX source 180kV/15W and detector 400 × 400 mm with a matrix of 2024 pixels (pixel size: 200 × 200 μm). 1800 images were acquired with the following scan parameters: voltage 80KV, current 180 μA, exposure 333 ms, voxel size 14.34 μm. The micro-CT data were processed utilizing *datos/x* reconstruction software (Phoenix|x-ray, release 2.0) and then exported as a 16 bits TIFF image stack. VG studio max software (Volume Graphics, release 2.2) was used for the virtual slice visualization and 3D rendering.

Ground sections. The left jaw was immersed in Araldite 20/20B. After 48h of drying in an incubator, the bones embedded in the resin were sawed into thin horizontal slices. The slices were then polished to obtain a thickness of 50-60 μm. The sections were observed under transmitted natural light with an Olympus BX51 microscope. Pictures were taken with a digital camera Olympus Camedia C-5060.

The sections are registered in the histological collection of the Muséum National d'Histoire Naturelle: MNHN-F-Histos 2333 and 2334.

RESULTS

The gilthead sea bream is a heterodont fish (Fig. 1). On each jaw there are two (or three) caniniform teeth in front of two or three rows of round molariform teeth, the two or three more posterior ones of which are very stout with an ovoid shape of their crown (Fig. 1, 2). Some small round teeth with a minute pointed apex are dispersed between the caniniform teeth and the lateral row of molariform teeth in the anterior part of the jaw (Fig. 1, 2). The sagittal (Fig. 3A,B) or transversal (Fig. 3C,D) virtual sections show that the teeth are inserted on a bony plate that is separated from the bottom of the jaw by a more or less large medullary cavity. Several bony shafts inserted between the bony plate and the bony wall of the jaw are seen (Fig. 3A,C). These vertical shafts strengthen the jaw especially when the fish crushes its preys (Fig. 3A,C, 4A,B). The dentigerous bone is constituted of spongy bone (Fig. 2B, 3). The bony tissue shows many vascular cavities, either primary or secondary (Fig. 5B). These secondary vascular cavities are limited by a reversal cementing line (Fig. 5B) and they result from the bone remodelling following tooth replacement. The virtual sections also reveal the presence of tooth buds that are localized just underneath a functional tooth (Fig. 3A,B, 4C). These tooth buds represent very young replacement teeth.

Caniniform teeth as well as molariform teeth are constituted of a crown separated from a pedicel by an unmineralized thin ligament (Fig. 3B,C, 4B,C). They are inserted in bony alveolae (Fig. 3) (see also Hughes *et al.*, 1994). As mentioned by Peyer (1968) for the Sparidae, the teeth of *S. aurata* are constituted of three different hard substances: a thick bulk of orthodentine (= circumpulpal dentine) around the pulp cavity, a thick layer of “modified dentine” (= pallial dentine) above the former and a thin hypermineralized enamel layer that overlays the crown of the teeth (Fig. 3B-D, 4B,C). This histological organization, observed on the virtual tooth sections is confirmed by the ground sections (Fig. 5A).

The virtual sagittal and transversal sections of the teeth reveal small dentine foldings in the pulp cavity essentially under the ligament region in molariform teeth (Fig. 3B, 4B) as well as in caniniform teeth (Fig. 4C). These folded dentine walls are also seen on a horizontal section of the jaw (Fig. 4D, E). The teeth are surrounded by spongy bone of attachment (Fig. 4D, E). This spongy bone constitutes a part of the dentigerous plate. In the more basal part of the teeth, the pulp cavity can be partially invaded by minute bony arches: see teeth 15-17, 21 (Fig. 2B, 4D); they replace the upper dentine foldings (Fig. 4C).

DISCUSSION-CONCLUSION

The replacement teeth of the gilthead seabream are encased in bone just under the functional teeth. They move beneath the functional teeth to take their place when the latter are shed. This intraosseous development of replacement teeth is a derived state according to Trapani (2001, Fig. 1), occurring relatively frequently in the Actinopterygii, the plesiomorphic state being extraosseous odontogenesis, which is widespread in basal teleosts (Trapani, 2001, Fig. 1).

Sparus aurata is an acellular-boned fish (Sire and Meunier, 2017). Its teeth consist of three hard substances: enamel, orthodentine and “modified dentine” (Peyer, 1968). In the present study we have shown that the molariform teeth as well as the caniniform teeth have a plicidentine organization of the dentine walls albeit limited to the base of the teeth. The folding of the dentine is simple without any ramification, so this is a simplexodont plicidentine (Meunier *et al.*, 2013a, 2015a), first described in fangs of predatory teleostean fishes (*Arapaima gigas*, *Chitala chitala*, *Hoplias aimara*, *Lophius piscatorius*, *Dissostichus eleginoides*) that eat living preys (Meunier *et al.*, 2013a, 2015a; Meunier, 2015; Germain *et al.*, 2016).

The discovery of simplexodont plicidentine in the hyoidian molariform teeth of the mormyrid *Hyperopisus bebe* (Germain *et al.*, 2016; Meunier *et al.*, 2018), with a durophagous diet, has come as a surprise. Yet, the presence of plicidentine in *H. bebe* increases the attachment surface of the tooth to the basal bone and so reinforces the toughness of teeth and jaw during crushing. Subsequently, another example of molariform teeth that have developed simplexodont plicidentine was described in the northern wolffish *Anarhichas denticulatus* (Meunier and Germain, 2018), which feeds notably on molluscs, echinoids, asterids and crustaceans. Simplexodont plicidentine in the teeth of *Sparus aurata* is a new example of this specialization in molariform teeth. The gilthead seabream feeds on molluscs, decapod crustaceans, sea urchins..., i.e., whole prey with a hard exoskeleton. The molariform teeth of *S. aurata* and their attachment to the jaw require strengthening in the form of simplexodont plicidentine to resist the strong mechanical constraints during crushing these hard prey. Simplexodont plicidentine is also present in the caniniform teeth of *Sparus*, as well as in the

molariform ones. The anterior caniniform teeth are inclined and they facilitate the capture of prey (Castaldi *et al.*, 1987). The seizure of hard prey probably involves significant mechanical constraints that can explain the differentiation of dentine plies in the pulp cavity and so strengthen its jaw.

To sum up, the durophagous gilthead seabream has developed specializations (at least simplexodont plicidentine, tooth insertion in alveolae, and bony shafts) to strengthen its jaws. These tooth specializations of *S. aurata* appear to be more evolved than those of the Anarhichadidae, whose molariform teeth also have simplexodont plicidentine (Meunier and Germain, 2018), but are devoid of bony alveolae (Bemis and Bemis, 2015; Meunier and Germain, 2018) and of bony shafts to reinforce the jaw (Meunier and Germain, 2018). Yet, the specialization of sparid teeth is totally different from the very derived specialization of the so-called “coalesced teeth” (Britski *et al.*, 1985) of, for example, the Carangidae *Trachinotus teraia* (Meunier and Trebaol, 1987; Trebaol *et al.*, 1991; Francillon-Vieillot *et al.*, 1994), the tetraodontids (Andreucci *et al.*, 1982) and the fossil Osteoglossomorpha *Paleonotopterus* (Meunier *et al.*, 2013b). These fishes, also specialized in crushing hard prey, have developed stout pharyngeal jaws with an abrasive surface. Here, odontogenesis takes place deep within the jaw cavity and young teeth progressively migrate toward the abrasive surface (Trebaol *et al.*, 1991; Francillon *et al.*, 1994; Meunier *et al.*, 2013b).

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Figure legends

Figure 1. *Sparus aurata*. Lingual view of the two lower jaws and the two upper jaws showing the anterior sharp teeth (caniniform teeth) (arrowheads), a number of molariform teeth and the posterior stout molariform teeth (arrows). (Scale bar = 5 mm)

Figure 2. *Sparus aurata*. Tomographic imaging of the right upper jaw. **A.** Three-dimensional reconstruction of the palatal face of the jaw showing the various teeth: the two main anterior caniniform teeth (1,2) and the numerous molariform teeth, the most posterior ones being particularly stout, and a number of smaller teeth, distributed in the anterior half of the jaw. The asterisk points to a shed tooth. (Scale bar = 2.5 mm). **B.** Virtual longitudinal section crossing the pulp cavities of the teeth except for the molariform teeth N° 23, 24 and 26. Teeth are surrounded by the spongy bone of the dentigerous plate. (Scale bar = 2.5 mm)

Figure 3. *Sparus aurata*. Tomographic imaging of the right upper jaw. **A.** Virtual longitudinal section (along the axis “tooth N°13 to tooth N°18”) showing the micro-anatomy of the jaw: a large cavity under the dentigerous plate sustained by several bony shafts (arrowheads). Teeth are inserted on spongy bone (asterisks), and a tooth bud (**tb**) (caniniform tooth replacement) is seen under tooth N°1. (Scale bar = 2.5 mm). **B.** Virtual longitudinal section along the lateral molariform teeth (from “tooth N°2 to tooth N°10”) showing the dentine folds in the pulp cavities (white arrow-heads), one molariform tooth bud (**tb**), and on the right between molariform teeth small teeth with their lightly pointed crown. Asterisks point to the spongy bone around the teeth. (Scale bar = 2.5 mm). **C.** Virtual cross section (along the axis tooth “N°8 to tooth N°16”) showing the dentine folding at the bottom of the pulp cavity of tooth N°8, the spongy bone of the dentigerous plate and a bony shaft (**sh**) under tooth N°16. (**li** = tooth ligament). (Scale bar = 1 mm). **D.** Virtual cross section (along the axis “tooth N°11 to tooth N°26”) showing the spongy bone constituting the dentigerous plate under the molariform teeth. (Scale bar = 1 mm).

Figure 4. *Sparus aurata*. Tomographic imaging of the right upper jaw. **A.** Detail of a bony shaft (arrow) and of the spongy bone (asterisks) in the upper jaw median cavity just under the dentigerous plate. (Scale bar = 1 mm). **B.** Virtual transversal section of the jaw showing the insertion of a molariform tooth (tooth N° 18) on the dentigerous plate made of spongy bone (arrow-heads). The dentigerous plate is sustained by a bony shaft (**bs**) that crosses the jaw cavity (asterisks) (**en** = enamel; **fd** = folded dentine; **md** = modified dentine; **od** = orthodentine). (Scale bar = 200 μ m). **C.** Virtual transversal section of the jaw (along the axis tooth "N°1 to tooth N°2") showing the histological organization of two caniniform teeth. Folding of the dental wall in the pulp cavity is clearly seen (**fd**), as is a tooth bud (**tb**) under the caniniform tooth N°1. Arrowheads point to the tooth ligament. (**ba** = bony arches; **en** = enamel; **md** = modified dentine; **od** = orthodentine). (Scale bar = 1 mm). **D.** Detail of a virtual horizontal section of the jaw showing the histological organization of the molariform teeth. The section of teeth 3 to 7 shows the minute foldings of the dentine walls. On tooth 8 the unmineralized ligament is seen (white arrowhead). On teeth 15, 16 and 21 the pulp cavity is invaded by some minute ramified bony arches. On tooth 20, the dentine layer is surrounded by bone of attachment. The minute teeth (see the row below the upper molariform teeth 3 to 8) show a similar structure than the larger teeth. (Scale bar = 1 mm). **E.** Detail of a virtual horizontal section of tooth N°2 showing the folding of the dentine wall. The caniniform tooth is surrounded by spongy bone of attachment (Scale bar = 500 μ m)

Figure 5. *Sparus aurata*. Ground sections (transmitted light). **A.** Detail of a cross section of a molariform tooth showing the histological structure of the crown. (**cpd** = circumpulpal dentine; **en** = thin enamel layer; **pc** = pulp cavity; **pd** = pallial dentine). (Scale bar = 50 μ m). **B.** Ground section in the alveolar bony tissue. One can distinguish primary (**I vc**) and secondary (**II vc**) vascular cavities. The secondary vascular cavities are surrounded by secondary bone that is separated from primary bone by reversal cementing lines (arrows). (Scale bar = 50 μ m)









