PECULIAR TOOTH RENEWAL IN A JURASSIC RAY-FINNED FISH (LEPISOSTEIFORMES, †SCEENSTIA SP.)

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Abstract: Tooth replacement in vertebrates is extremely diverse, and its study in extinct taxa gives insights into the evolution of the different dental renewal modes. Based on μ-CT scans of a left lower jaw of the extinct fish †Sceenstia (Actinopterygii, Lepisosteiformes), we describe in detail a peculiar tooth replacement mode that is, as far as we could ascertain from the literature, unique among vertebrates. The formation of the replacement teeth comprises a 180° rotation of their acrodin cap that occurs intraosseously within bony crypts, and their setting up appears to be synchronous. We propose a model for the dental renewal process and identify complementary anatomical features visible in the tomography such as the junction between the different tooth-bearing bones (prearticular–coronoid and dentary), as well as cavities corresponding to intraosseous crypts, nervous and/or vascular canals. The location of the cavities and their subsequent identification (e.g. Meckel’s cavity, mandibular sensory canal) help us to identify the function of pores visible on the bone surface and understand their relation to internal anatomical features. Finally, recognition of this tooth replacement mode raises the question of whether it is specific to †Sceenstia or related to a particular dentition type and thus potentially occurs in other lineages.

Key words: synchronous tooth replacement, dental renewal, intraosseous tooth formation, Lepisosteiformes, μ-CT scan.

Dental renewal in vertebrates is an evolutionarily ancient process necessary to cope with dental wear, diet changes and tooth growth (Berkovitz & Shellis 2017). While the fundamental pattern of tooth development is genetically very stable among vertebrates (Tucker & Fraser 2014; Smith et al. 2015), mechanisms of dental renewal are highly diverse. Unique, continuous, one-to-one, many-for-one, synchronous, independent, alternate, straight up and rotating are some of the dental replacement mechanisms found in extant gnathostomes (Trapani 2001; Tucker & Fraser 2014; Berkovitz & Shellis 2017), and most of them are found in actinopterygians. The development of replacement teeth also varies from extraosseous, in which teeth are formed in the soft tissue close to their predecessor, to intraosseous, in which they are formed in crypts located within the bone. This latter formation mode appears to be the derived state among gnathostomes (Trapani 2001; Chen et al. 2016). Tooth formation and replacement modes are closely linked to the dentition type and dental pattern, and consequently to diet (Tucker & Fraser 2014).

Durophagy is a common diet in fishes and related adaptations have evolved several times in all major clades (placoderms, chondrichthians, lungfishes, actinopterygians). In ray-finned fishes (Actinopterygii), adaptations to durophagy occur in the oral or pharyngeal cavities (e.g. Cypriniformes, Cichlidae) with specialized teeth that are often enlarged and hemispherical. In the oral cavity, the upper teeth are borne by the paired jaw bones (e.g. premaxillae in sparids; Linde et al. 2004), paired bones of the suspensorium (e.g. dermopalatines in Anarhichas (Bemis & Bemis 2015), dermopalatines and ectopterygoids in †Ticinolepis (López-Arbarello et al. 2016)) and paired (vomers) or unpaired bone (paraphenoid) from the base of the braincase (e.g. in osteoglossiforms; Taverner 1977). The lower teeth are borne by the paired mandibular bones (dentary in

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teleosts plus coronoids and prearticular in non-teleostean actinopterygians) and in some groups by an unpaired tooth plate resting on the basihyal–basibranchial complex (e.g. in mormyriiforms; Tavenor 1972). A peculiar tooth arrangement adapted for a crushing diet (phyllodonty) is present in some extinct ray-finned fishes. It consists of several layers of superimposed, rounded teeth forming a median plate-like structure that occurred independently in several fish clades, such as in the Permian †Platysomidae (Fracasso & Hovorka 1987), the Triassic †Bobasatraniformes (Böttcher 2014) or the Cretaceous †Phyllodontidae (Estes 1969). In the derived mid-Cretaceous notopterid †Palaeonotopterus, the unpaired dental plates are formed by several superimposed layers of closely packed teeth, with the external crushing face forming a smooth surface (Meunier et al. 2013). †Pycnodontiformes are extinct neopterygians ranging from the Triassic to the Eocene with a specialized crushing dentition in the vast majority of taxa. Crushing teeth of the upper jaw are borne on the vomer, and on the prearticulirs in the lower jaw. The mode of tooth replacement in pycnodonts is still controversial, but it seems that replacement is occasional and occurs in the posterior part of the tooth rows (Kriwet 2005). In the pycnodont Cenozoic genus †Pygnodus, new small teeth grow in the anterior part of the dentition but the replacement appears to be interstitial with resorption of part of the pre-existing worn tooth (Longbottom 1984).

Based on µ-CT scans, we present a reconstruction of the internal anatomy of a left lower jaw of †Scheenstia (Osteichthyes, Actinopterygii, Ginglymodi, Lepisosteiformes sensu López-Arbarello 2012) from the Late Jurassic (Kimmeridgian) of north-western Switzerland. We describe in detail a dental replacement mode of a durophagous dentition, which is, as far as we could ascertain from the literature, unique among vertebrates: replacement teeth achieve a 180° rotation, which occurs during their intraosseous formation. In the early and middle twentieth century, several authors (Woodward 1916; Weitzel 1930; Peyer 1954) had already observed the peculiar upside-down position of replacement acrodine (enameloid) caps in this genus, but made no further inferences about the mechanism of replacement. We also describe and identify elements of the nervous and vascular systems. Finally, we discuss phylogenetical implications of these observations.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The studied material is part of a rich palaeontological collection uncovered by the Paléontologie A16 team during the building of the A16 motorway in the canton of Jura, north-western Switzerland. It comes from the locality of Courtedoux–Tchâfouë (Fig. 1), and from bed 4500 of the Lower Virgula Marls, from the Eudoxus ammonite zone (upper Kimmeridgian, Upper Jurassic). This very fossiliferous horizon is part of the Chevenez Member, Reuchenette Formation (Comment et al. 2015), characterized by an alternation of marly and limestone deposits. The depositional environment is interpreted as a shallow-marine carbonate platform. The vertebrate fossil record of the Lower Virgula Marls is diverse and composed of turtles (Anquetin et al. 2015; Püntener et al. 2015, 2017), crocodylians (Schaefer et al. 2018), pterosaurs (Marty & Billon-Bruyat 2009), chondrichthyans (Leuzinger et al. 2017a), as well as actinopterygians, mainly pycnodonts, lepisosteiforms and caturids (Leuzinger et al. 2017b). Additionally, the former presence of dinosaurs is attested by numerous trackways (Marty 2008). Invertebrates and wood remains complete the fossil record of the Lower Virgula Marls (Philippe et al. 2010; Koppka 2015).

MATERIAL AND METHOD

The scanned material is part of a fossil specimen of †Scheenstia sp. (Osteichthyes, Actinopterygii, Ginglymodi, Lepisosteiformes sensu López-Arbarello 2012) that is, curiously, the only bony fish found in an association of several bones (see Leuzinger et al. 2017b, pp. 217–230), despite a long period of intense and large-scale excavations. It is housed under the collection number MJN TCH005-353 (Musée Jurassien des Sciences Naturelles, locality of Tchâfouë-Courtedoux) at the Jurassica Museum in Porrentruy, canton Jura, Switzerland.

The left lower jaw was scanned. An external scan was first performed at the Jurassica Museum using a photometric scanner (Artec Space Spider) to get an external 3D model of the specimen with a rendering of the texture. A micro-computed tomography (µ-CT scan) was performed on the same fossil piece at the University of Fribourg, Switzerland. We used the software MeshLab to process the data of the surface scan, and Avizo for the segmentation and 3D modelling. The volume of the preserved acrodin (enameloid) tooth caps (functional, replacement and pre-functional teeth) was calculated with the segmentation software Avizo. The animation of the 3D model (see video in Leuzinger et al. 2019) was realized using Adobe Premiere.

RESULTS

General morpholgy of a left lower jaw of †Scheenstia

The preserved fragment of a left lower jaw (Fig. 2) includes the dentary and a medial ossification interpreted as the fusion of at least one coronoid and the
prearticular. Resembling the other species of the genus †Scheenstia, this anterior lower jaw is very robust with a broad symphysis, and bears powerful teeth corresponding to the strongly tritoral dentition of Jain (1983).

The gape is broad, the anterior portion of the dentary bone bends medially and its ventral border is concave. The bone has a maximal length of 82 mm at the level of the tooth row, and a length of 67 mm at its ventral border. The dorsal border of the dentary is approximately straight along the toothed portion, which is 36.5 mm in length, and then bends dorso-laterally at an angle of approximately 70°. The large coronoid process (Fig. 2D) has a maximal length of 33 mm. The minimal depth of the bone is 26 mm right behind the toothed portion, and its maximal depth is 62 mm at the apex of the coronoid process. The symphysial surface is very large with a maximal depth of 34.7 mm representing more than half of the maximal depth of the lower jaw at the coronoid process (see Leuzinger et al. 2019, fig. 1), and a maximal length of 21 mm representing almost 60% of the length of the toothed area of the jaw. The pos-teroventral process of the dentary (Fig. 2D) is short, representing only about 18% of the length of the jaw ventral border, and does not extend beyond the posterior border of the dentary coronoid process.

On the labial surface of the dentary, parallel series of pores running rostro-caudally reveal the passage of nervous and sensory canals (e.g. mandibular sensory canal, ‘oral canal’) described further below. Ventral to these pores, the dentary makes a marked longitudinal step giving the ventral margin the form of a longitudinal shelf (see Leuzinger et al. 2019, fig. 1B).

The tomography of the specimen allowed us to clearly detect the junction between two tooth-bearing bones (Fig. 3A–D): the dentary, with a single row of five teeth, and the ‘prearticular-coronoid’ bone bearing all other 36 functional teeth. We thus identified a single lingual toothed bone in the lower jaw of †Scheenstia that extends posteriorly from the symphysis along the medial side of the coronoid process and completely covers the Meckel's cavity. In gars and most fossil ginglymodians, the same area is occupied by the tooth-bearing coronoids (normally two) and prearticular bones (Grande 2010). Therefore, we consider that the single lingual toothed ossification in †Scheenstia corresponds to the fusion between the prearticular and one or several coronoids, although we cannot spot any suture that could help distinguish the prearticular from the coronoids.

The five dentary teeth are cylindrical, their height is about twice their diameter and they have clearly conical, highly mineralized tooth caps with a distinct papilla (Morphotype 1 of Bermúdez-Rochas & Poyato-Ariza 2015). In fish, the highly mineralized portion of the tooth consists of enameloid, a tissue that differs from enamel in its origin, which is not only ectodermic, but also mesenchymal (Richter & Smith 1995; Huysseune & Thesleff 2004). Later, we will refer to the tooth enameloid as acrodin caps, a term describing the enameloid that concentrates in a thick cap on the crown in actinopterygians, rather than covering the dentinuous shaft as, for instance, in chondrichthyans (Richter & Smith 1995). The teeth of the prearticular–coronoid are more densely packed than those of the dentary and have variable shapes (Fig. 3A). Most of these teeth are cylindrical, with a height to diameter ratio of 1–1.3, circular to oval transverse section, and ovate crowns with an apical papilla (Morphotype 2 of Bermúdez-Rochas & Poyato-Ariza 2015). Only the medialmost teeth are button-like, with a height to diameter ratio less than 1, convex crown and without distinct

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**FIG. 1.** Geographical map of the Ajoie region, Canton Jura, Switzerland (modified from Püntener et al. 2015). The excavation site Courtedoux–Tchafou (TCH) yielding the study material is marked along the A16 motorway.
papilla. The size and shape of the teeth change gradually from relatively small and slender Morphotype 2 teeth in the lateral and anterior rows, to larger and button-like in the internal rows. Some teeth are broken off and only represented by their annular pedicel (Figs 2C–D, 3A–B).

**Detailed internal anatomy**

*Functional vs replacement teeth.* Looking at the internal structure, numerous partially formed replacement teeth are visible in both the dentary and the prearticular-coronoid (Fig. 3E–H). These replacement teeth consist of acrodin caps still completely devoid of dentine. There are 37 of these intraosseous replacement acrodin caps, i.e. four less than the functional loci (n = 41). The replacement acrodin caps are organized in a single plane but differ in their individual orientation (Fig. 3H), the majority being oriented upside down compared to the functional position. An additional tooth stands out from this general pattern: it occupies an intermediate position between the functional and replacement tooth planes (see Fig. 3), it is inclined (c. 50°) compared to the functional position and has its dentine formed. We refer to this replacement tooth as ‘pre-functional’ in the figures and further in the text.

The segmentation of the specimen reveals that except for the pre-functional tooth, the teeth are organized in individual pairs of functional and corresponding replacement tooth (Fig. 3). Tooth pairs could be spotted based on the following observations: the arrangement of the replacement teeth is a faithful reproduction of the pattern seen in the functional population (compare Figs 3A and E, also see Leuzinger et al. 2019, fig. 2A–B), and each replacement acrodin cap has a similar size and shape as its functional counterpart located just above. The volume of the acrodin caps preserved as pairs (see Leuzinger et al. 2019, fig. 2C) shows indeed no significant difference between the mean volume of functional and replacement tooth population (n = 33, t = −0.30441, p = 0.7618).
Dentary bone + tooth dentine  
Prearticular–coronoid bone + tooth dentine  
Canal for the trigeminal (V) and facial (VII) nerves  
Mandibular sensory canal and lateral line nerve

FIG. 3. µ–CT based 3D model showing replacement teeth, and nervous and sensory canals. Acrodin caps of a single pair are painted with the same colour. A–D, entire specimen (without pore sediment infill) showing the separation of the dentary and prearticular-coronoid bones in: A, occlusal; B, lingual; C, mesial; D, labial view. Note the replacement acrodin caps poking out from the peripheral replacement pores of the prearticular-coronoid. E–H, corresponding views showing internal structures: replacement acrodin caps, pre-functional tooth and the main canals of the dentary. Note that the pre-functional tooth has its dentine formed. Abbreviations: art.t., artificially tilted tooth (preparation mishandling); PF, pre-functional tooth; r.b., ridge of bone.
Replacement pores and crypts. In †Scheenstia, every acrodin cap is individually enclosed in a rounded crypt that extends into a replacement pore (Figs 4, 5). Every replacement pore opens separately at the oral surface of the bone, at the base of the corresponding functional tooth.

Crypts of the prearticular-coronoid are interconnected at their bases from which several canals branch radially towards lingual exits of this bone (Figs 4, 5B–C, also see video in Leuzinger et al. 2019). All crypts of the prearticular-coronoid connect to a large cavity located just at the junction between the prearticular-coronoid and the dentary. Because of its location, part of this large cavity is also identified as the accommodation space for the Meckel’s cartilage (Figs 4, 5) (Grande 2010).

In the dentary, the crypts also interconnect but are more distant to one another (Fig. 5A, D). They do not connect to the Meckel’s cavity, but a few connections exist between some of the crypts and a massive canal that runs ventrally (Figs 4, 5; see also video in Leuzinger et al. 2019), identified as the canal accommodating the trigeminal and facial nerves (see below).

Nervous and vascular canals. In the dentary, a thin canal that gives off at least nine regularly spaced exits to the labial side is interpreted as the mandibular sensory canal (López-Arbarello & Sferco 2011) (Figs 3E–H, 4, 5). From the sensory canal, at least six posteriorly curved branches extend ventro-lingually (Fig. 3; see also video in Leuzinger et al. 2019). They were probably connected to a continuous canal that accommodated the lateral line nerve innervating the mandibular sensory canal and running parallel to it. The lateral line nerve most likely split from the facial nerve posteriorly in the mandible (Song & Northcutt 1991), at the posterior margin of the dentary based on the position of the posteriormost branch. However, its path remains unclear and difficult to follow. It is obscured by the presence of an unidentified, large cavity in the mesial portion of the dentary bone (Fig. 5D; see also video in Leuzinger et al. 2019).

Still in the dentary, dorsally to the mandibular sensory canal, a thicker and significantly shorter canal branches labially from the caudal part of the Meckel’s cavity (Fig. 5D; see also video in Leuzinger et al. 2019) and extends into the dentary following its labial curvature. Its position is consistent with the mandibular branch of the
trigeminal nerve (V; ramus mandibularis trigemini) and of the facial nerve (VII; ramus mandibularis facialis) that run alongside each other. Several thin canals branch from this main one and open through pores along a line on the labial surface of the dentary (Fig. 3D). Dechaseaux (1943) and Wenz (1968) were the first to describe a second series of pores parallel to that of the mandibular sensory canal in †Lepidotes elvensis. They regarded these pores as corresponding to a supplementary sensory canal called the 'oral canal'. As for the interconnection among the different canals, several vertical connections between the trigeminal nerve, the mandibular sensory canal and the unidentified cavity in the dentary are visible (Fig. 5D; see also video in Leuzinger et al. 2019).

**DISCUSSION**

**Intraosseous tooth formation and rotation of replacement teeth**

The presence of replacement acrodin caps within the bone indicates a fully intraosseous odontogenesis for most of the teeth. However, the situation is slightly different for peripheral teeth of the prearticular-coronoid. As exposed above, replacement acrodin caps and functional teeth are organized in pairs, which suggests a one-to-one replacement. Considering all functional loci (i.e. including broken-off teeth, n = 41) the replacement acrodin cap of four of them could not be spotted at the expected location. Instead, individual cavities are clearly visible. This is the case for three broken-off teeth located at the lingual margin of the prearticular-coronoid (Fig. 2C–D), and one at the labial margin of the same bone. These cavities suggest that the replacement acrodin caps were present but have been lost post mortem as a consequence of soft tissue decay. The semi-open configuration of these three lingual crypts could indicate a younger stage of their development, which suggests that the addition of new teeth occurs on the lingual margin. Along the lingual and distal bone margins, several replacement acrodin caps poke out of the bone (Figs 2, 3), showing that the bony crypts at the periphery of the prearticular-coronoid are slightly open. This does not occur on the labial margin of the specimen, since the replacement teeth of the dentary are located lingually to their functional counterpart, meaning that their bony crypts are further away from the labial bone margin.
Intraosseous tooth formation implies that the replacement teeth entirely form within individual or collective bony crypts in contact with epithelium, supplied by vascular and nervous canals necessary for tooth development (Trapani 2001). In the case of †Scheenstia, individual crypts are clearly visible (Figs 4, 5), each one of them being connected to the oral surface through an individual replacement pore, through which the replacement tooth eventually erupts (Figs 4, 5). Within these crypts, replacement acrodin caps must fulfil a 180° rotation coupled with an ascension to reach their functional position. In our specimen, the replacement acrodin caps are located on a single plane, nonetheless differing in both their inclination and orientation (Fig. 3E–H). Some of them are inclined less than 90° compared to their functional position, while others are completely overturned. This suggests that most of the rotation of the acrodin caps occurs in the basal plane, before the ascension and dentine formation, which is probably necessary for all replacement teeth to form more or less simultaneously. Indeed, the very densely packed dental pattern would not allow all replacement teeth to be rotating at the same time if the dentine had already started to mineralize in their initial position. Interestingly, even the acrodin caps that are closest to achieving their 180° rotation have not started to mineralize dentine yet. It appears that dentine only forms once the tooth has started its vertical ascension, but nevertheless before both the rotation and eruption are complete, as seen in the prefunctional tooth (Fig. 3E–H).

Within a single tooth pair, functional and replacement acrodin caps have similar volumes (see Leuzinger et al. 2019, fig. 2C), irrespective of the rotation stage of the replacement cap. This indicates that the acrodin formation of the replacement tooth is complete for every pair spotted in our specimen. It also suggests that the acrodin formation entirely occurs before the rotation has started in †Scheenstia. In fish, rotation of the replacement teeth during their setting up may occur extraosseously, as for instance in the muraenid Enchelycore (Trapani 2001, fig. 4), ‘semi-intraosseously’ in the characiform Hepsetus in which replacement teeth form in a bony trench (Trapani 2001, fig. 5) or intraosseously in Hydrocynus, in which the replacement teeth develop in a recumbent position (Berkovitz & Shellis 2017, fig. 10.4). But in all these instances, the rotation angle is only about 90° or slightly greater. In †Scheenstia, we have shown that the setting up is intraosseous.

Dental lamina, innervation and vascularization of the forming teeth

Odontogenesis requires the presence of epithelium, as well as canals for innervation and vascularization at the site of tooth formation (Trapani 2001). In actinopterygians with an intraosseous tooth development, the connection with the epithelium occurs via a replacement pore, which is located close to, or at the base of, the functional tooth. In Pomatomus for instance, the pores are located labially in the premaxilla and lingually on the dentary (Bemis et al. 2005). In Anarhichas, very large and often persistent replacement pores are located in the mandible, both labially and lingually, allowing the development of two rows of molariform teeth. In †Scheenstia, replacement pores are located lingually to the functional tooth in the lingualmost rows of the prearticular-coronoid, and labially in its labialmost rows. In the dentary, they are located lingually to the functional tooth (Fig. 4).

The portion of oral epithelium involved in tooth formation (the dental lamina) is thought to have entered the individual crypts through these replacement pores. Recently, Bemis et al. (2019) proposed a new term, the ‘direct dental lamina’, to refer to such cases where the epithelium directly enters the replacement pores, by contrast with the ‘successional dental lamina’ (Huysseune 2006) that partly connects to the lamina of the tooth predecessor. In †Scheenstia, a direct dental lamina is probably present, as observed in other fishes with intraosseous tooth development (Bemis et al. 2019). The enamel organ (Bemis et al. 2005), responsible for amelogenesis and crown shaping, as well as for the initiation of dentinogenesis, must have been present in the crypts where it enclosed the replacement acrodin caps. Its irrigation most probably occurred through the replacement pores as well, as for instance in Pomatomus (Bemis et al. 2005, fig. 10) (Fig. 4), through which it could connect with the gum epithelium (Bemis & Bemis 2015).

Dental innervation in teleosts mainly occurs through the trigeminal nerve (Holje et al. 1986). The μ–CT segmentation shows that on its rostral portion, several branches of the trigeminal nerve communicate with the crypts of the dentary (Figs 4, 5D; see also video in Leuzinger et al. 2019). However, no clear connections are visible between the trigeminal nerve and the crypts of the prearticular-coronoid (Figs 4, 5). This suggests that in †Scheenstia, an individual branch of the trigeminal nerve was responsible for the innervation of all prearticular-coronoid teeth, which most probably ran within the Meckel’s cavity. In the bichir, a basal ray-finned fish with prearticular and coronoid bones, a split of the mandibular branch of the trigeminal nerve is located just after its entry into the mandible (Piotrowski & Northcutt 1996). We can think of a similar situation in †Scheenstia. In addition to a nervous canal, the Meckel’s cavity probably also contained elements for the irrigation of the forming teeth of the prearticular-coronoid.
Tooth attachment

In bony fish, teeth can be attached to the jaw bone in a more or less rigid way to cope with feeding behaviour and diet (predation, grinding, durophagous diet, etc.) or as a result of the development mechanism of tooth replacement (intradosseous vs extradosseous) (Berkovitz & Shellis 2017). In †Scheenstia, all teeth show the Type 2 tooth attachment (sensu Fink 1981) also called pedicellate attachment, meaning that the tooth is not directly ankylosed to the jaw bone (Fig. 4). Instead, it is connected by fibrous tissues to a mineralized structure (the pedicel) that is in turn rigidly attached to the bone. The pedicel forms at the very final stage of the tooth development, after dentine formation and before eruption (Chen 2017).

It is indeed already formed in the pre-functional tooth of our specimen (Fig. 3E–H). However, its pedicel is not anchored to the bone, meaning that the pre-functional tooth was most probably still entirely covered with epithelium, since the final position had not yet been reached (see Leuzinger et al. 2019, fig. 3) (Holje et al. 1986; Wacker et al. 2001). The pedicellate attachment is the most common attachment type in teleosts, however the pedicel is described as being shorter than the crown in this group (Berkovitz & Shellis 2017). In †Scheenstia, the pedicel is generally at least as long as the crown (Fig. 4). Since the fibrous attachment between the crown and the pedicel confers a certain mobility to the tooth, this attachment type is commonly associated with grazing behaviour, in which the fish scrapes hard surfaces. The pedicellate attachment helps the dentition to conform to the shape of the hard substrate. However, since the fibrous joint can also have a shock-absorbing function (Berkovitz & Shellis 2017), this kind of attachment also makes sense in durophagous fish. The resistance of the joint depends on the shape of crown and pedicel extremities at their junction. The fibrous tissue of the joint can get thicker or thinner towards the pulp cavity to fill in the gap between crown and pedicel (Berkovitz & Shellis 2017). In our CT scans, it is difficult to clearly define the shape of the junction, but the base of the crown and the pedicel generally seem to interlock so that the joint thickness does not vary (Fig. 4). This probably considerably limits the mobility of the teeth. During tooth replacement, partial or total resorption of the pedicel occurs, causing the rest of the tooth to be shed (Hughes et al. 1994). A total resorption of the functional teeth has been reported in Perciformes (Berkovitz & Shellis 2017), which might allow a remobilization of the minerals. In †Scheenstia, due to a matter of space, replacement teeth must have pushed out the functional teeth from below, implying a basal resorption of the attachment tissues. Shortly before eruption, we cannot exclude a lateral contact within a tooth pair causing lateral resorption of the functional tooth, as in other ray-finned fishes (e.g. Pomatomus; Bemis et al. 2005, fig. 10).

Simultaneous (synchronous) tooth replacement

A few ray-finned fish species are known to replace their dentition in a synchronous fashion, leaving them edentate for a short time (Bemis & Bemis 2015; Berkovitz & Shellis 2017). Simultaneous replacement occurs with conical teeth, such as the tigerfish (Hydrocynus) over a period of about 5 days, in characiforms with multicuspid teeth, such as the tetra (Astyanax), and in characiforms with slicing interlocked teeth, such as the piranhas (e.g. Serrasalmus) (Berkovitz & Shellis 2017). Simultaneous replacement is also seen in some pleuronectids, such as Pleuronectes (Berkovitz & Shellis 2017), and in the molariform teeth of the wolfish, Anarhichas (Bemis & Bemis 2015). The timing of tooth replacement can vary within a single species from one bone to the other, and also depending on the environment or the ontogeny of the fish. Synchronous tooth replacement may be related to a growth season for example (Berkovitz & Shellis 2017), and thus to a marked seasonality. There is no absolute character that allows us to recognize simultaneous replacement in a fish skeleton. However, if all functional and replacement teeth are at the same stage of development, this is a strong indication that such a mode of replacement is present (Bemis & Bemis 2015, p. 892) as it is the case in the lower jaw of †Scheenstia, at least in our specimen. The presence of individual replacement pores connecting each crypt with the oral surface (Figs 4, 5) is a further argument supporting a synchronous replacement (Bemis & Bemis 2015). Additionally, we can observe that only one generation of replacement teeth forms at a time in †Scheenstia.

On the pre-functional tooth

The pre-functional tooth deviates from the dental pattern described above in several aspects: it is located in an intermediate plane between replacement and functional teeth, it does not have a counterpart (neither as functional tooth nor as replacement cap), the volume of its acrodin cap is considerably smaller than the acrodin caps of adjacent tooth pairs (see Leuzinger et al. 2019, fig. 2C), the dentine is already formed, and the tooth is almost in a functional position (Fig. 3E–H). Its nature is puzzling and it is not clear whether it represents a replacement tooth, a first-generation tooth or a teratologic tooth. We could argue that the bulge visible close to it at the labiomesial margin of the bone surface (Fig. 3A–C) is a remnant of the tooth pedicel of the former functional tooth that had already been pushed out and shed. This bulge...
could correspond to the ‘ridge of bone’ mentioned by Bemis et al. (2005, p. 320), to which the tooth is ankylosed. On the other hand, some ray-finned fishes are known to generate new teeth close to the symphysis (e.g. pycnodontiforms, Longbottom 1984; wolffish, Bemis & Bemis 2015), which could be the case of the pre-functional tooth in our specimen.

**Tooth replacement mechanism in †Scheenstia**

In light of the above, the dental renewal mechanism in †Scheenstia implies:

1. An intraosseous development of the replacement teeth.
2. A one-to-one replacement.
3. A 180° rotation of the replacement acrodin caps coupled with a vertical ascension to reach their functional position.
4. A synchronous replacement.

We interpret the replacement as occurring as follows: (1) amelogenesis in individual crypts (acrodin caps entirely form in an upside-down position); (2) initiation of the intraosseous rotation of the acrodin caps in a single plane; (3) ascension of the not fully rotated acrodin caps through individual replacement pores; (4) dentinogenesis at an advanced stage of the ascension and rotation of the acrodin cap; (5) completion of ascension and rotation; and (6) ankylosis of the tooth to the bone through a pedicel once it has reached its final position.

**Physiological and ecological considerations**

Intraosseous development presents several advantages: it allows the complete replacement of densely packed dentitions where there would be no room for extraosseous tooth formation; it maintains a precise dental pattern that may be functionally needed; and it protects the forming teeth from occlusal stress (Shellis & Berkovitz 1976; Trapani 2001). All arguments are meaningful in the case of †Scheenstia considering its tight dentition pattern where all functional teeth work in a single plane, and its very probable durophagous diet. However, a dental renewal including a 180° intraosseous rotation of the replacement acrodin caps is surprising as it implies a considerable energetic cost. We have shown that replacement acrodin caps start rotating intraosseously only once entirely formed in †Scheenstia. This might have had a protective effect against occlusal stress for not fully grown, thin acrodin caps, enhancing thereby the protective effect of the intraosseous development itself. Also, a synchronous replacement is probably linked to the necessity of having the whole set of teeth at the same developmental stage and working at a time, which is the case for durophagous taxa. Although the mode of tooth replacement is very different in chondrichthians, we note that in durophagous species of rays with teeth packed in an alternating pattern forming a pavement, the replacement is achieved by a simultaneous loss of a complete tooth row (Berkovitz & Shellis 2017). This replacement mode is functionally comparable to the mode of tooth replacement interpreted for †Scheenstia.

An important blood supply was certainly necessary for the simultaneous formation of so many replacement teeth. The lower jaw of †Scheenstia appears to have been highly innervated and vascularized. As in other actinopterygians, the mandibular sensory canal must have hosted neuromasts (generally one between each labial exit; Fig. 3H) sensitive to water movement. The presence of several pores on the labial surface of the jaw in †Scheenstia (Fig. 3D) and other ginglymodians (the ‘oral canal’) may indicate that the anterior part of the mandible was highly sensitive in these fishes. The presence of the ‘oral canal’ among ginglymodians is an important feature regularly used in phylogenetic analyses of this clade. It was considered either as a split of the anterior section of the mandibular sensory canal (Wenz 1968) (its potential connection with the mandibular sensory canal were then discussed by Cavin & Suteethorn (2006, p. 345)) or as an independent canal derived from the dentary pit line present in some fossil actinopterygians (Thies 1989a, b). Our 3D reconstruction of the mandible of †Scheenstia allows us to reinterpret the ‘oral canal’ present in some ginglymodians, showing that its pores lead in fact to the trigeminal-facial canal (Fig. 3D, H). It may thus have accommodated rami of one of these nerves, probably of the trigeminal one by comparison with the situation in the cichlid *Tilapia mariae*, in which the ramus labialis exits through a single pore and innervates the skin (Holje et al. 1986). The large size of the trigeminal–facial canal (Figs 3E–H, 5) also suggests a high sensitivity of this part of the mandible, with the possible development of dermal sensory structures such as barbels or hypertrophied lips.

**CONCLUSION**

To our knowledge, an intraosseous, upside-down replacement mode as described here has so far only been observed in species of †Scheenstia, formerly ascribed to the genus †Lepidotes (Woodward 1916; Weitzel 1930; Peyer 1954; Jain 1983; see López-Arbarello 2012). As far as we could trace back in the literature, it has never been reported in other actinopterygians, and not even in any other vertebrate. A considerable rotation of the replacement teeth is known to occur in other fishes (e.g.
paddlefish, Smith et al. 2015; saw-teeth of sawfish and sawshark, Welten et al. 2015) but it is achieved extraos- ously. In contrast, the peculiarity of the replacement mode described for †Scheenstia lies in the fact that the 180° rotation of the replacement teeth takes place during their intraosseous formation. One selective pressure for the evolution of intraosseous tooth formation is that the removal of replacement teeth from the oral epithelium provides more space for functional teeth, in particular for fishes with molariform, densely packed dentition (paraphenoid teeth of Albula, some pharyngeal and dentary teeth of Anarhichus lupus) (Trapani 2001; Bemis & Bemis 2015). It also requires a certain thickness of the bone. Intraosseous development of replacement teeth is considered apomorphic in actinopterygians and developed independently in several lineages of teleosts, and in †Scheenstia (Lepisosteiformes). It has so far only been observed in the palate and branchial dentition of Albula (elopomorphs), in the oral teeth of characiforms, beryciforms, scorpaei- forms, tetraodontiforms, in the pharyngeal teeth or some of the oral teeth of cyprinodontids and it is predominant in Percomorphaceae (Trapani 2001; Berkovitz & Shellis 2017). This study shows that intraosseous development has also evolved in Holostei (Ginglymodi, Lepisosteiformes) (sensu López-Arbarello 2012), which broadens the conclusions drawn by Trapani (2001). Further investigation into other ginglymodians will help our understanding of how this replacement mode, implying a 180° rotation of replacement acrodin caps, is distributed within the clade.

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