A Berriasian actinopterygian fauna from Cherves-de-Cognac, France: Biodiversity and palaeoenvironmental implications

Joane Pouech [a, b, *], Jean-Michel Mazin [a], Lionel Cavin [c], Francisco J. Poyato-Ariza [d]

[a] Laboratoire de Géologie de Lyon, UMR 5276 CNRS, ENS, Université Lyon 1, Campus de la Doua, Bt. Géode, 69622 Villeurbanne Cedex, France
[b] Centre de recherche sur la Paléobiodiversité et les Paléoenvironnements, UMR 7207 CNRS, MNHN, Université Pierre et Marie Curie Paris 6, Tour 46/56, 4 Place Jussieu, 75252 Paris Cedex 05, France
[c] Muséum d'histoire naturelle, CP 6434, 1211 Genève 6, Switzerland
[d] Unidad de Paleontología, Departamento de Biología, Universidad Autónoma de Madrid, c/ Darwin 2, Cantoblanco, 28049 Madrid, Spain

ABSTRACT

The paleontological site of Cherves-de-Cognac (Charente, southwestern France) is an 81-levels sedimentary series, which records deposits from a coastal lagoon to a continental lake, reflecting the general regressive context of the Upper Jurassic-Lower Cretaceous. This site has yielded a rich and diversified vertebrate fauna from the Lower Cretaceous, including numerous actinopterygian remains described here. Cranial bones and scales have been found as macro-remains during excavations, and are all referable to the ginglymodian *Scheenstia mantelli*. In parallel, an important program for extracting and sorting vertebrate dental micro-remains from the 63 fossiliferous levels of the series, has led to a collection of more than 26,000 actinopterygian isolated teeth. Among these specimens, eleven tooth morphotypes can be distinguished. Tooth morphotypes 1 and 2 are the more commonly found and are identified as respectively "oral" and "pharyngeal" teeth of *S. mantelli*. Tooth morphotypes 3 to 5 are less frequent and referred to *Caturus* sp., *Belonostomus* sp. and *Thrissops* sp. respectively. Tooth morphotypes 6 to 11 correspond to Pycnodontiformes morphologies, morphotype 6 being the most represented in the sedimentary series after morphotype 1. Review of known ecologies of these taxa, together with palaeoenvironmental data available for the site of Cherves-de-Cognac, indicate a fresh to brackish life environment for *S. mantelli* and Pycnodontiformes.

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1. Introduction

Fish remains, mainly isolated teeth and isolated bones, are very common in various Mesozoic outcrops, but paradoxically they are not systematically collected and studied. This is probably due to the particular field processing required to get micro-vertebrate assemblages, which necessitates washing and screening of large amounts of sedimentary rocks. However, beside the difficulties in the field collecting, the laboratory handling and the imaging process, the main reason for neglecting isolated fish teeth is probably due to the difficulty in determination. While, for example, Mesozoic mammal isolated teeth are characterized by a complex crown morphology supporting taxonomic identification, fish teeth often show a simple crown morphology which bears few diagnostic features. Moreover, fish tooth morphology usually displays variation in a single specimen depending on the location of the teeth in the buccal and pharyngeal apparatus. Nevertheless, it has been shown for a long time that isolated fish teeth provide important information in paleontological studies, as exemplified by several fundamental works dealing with micro-vertebrate remains (i.e. Estes and Sanchíz, 1982; Cuny et al., 1991; Mudroch and Thies, 1996; Kriwet et al., 1997).

The aim of the present work is to describe and to characterize the significant actinopterygian assemblage collected from the site of Cherves-de-Cognac (Berriasian, France) and to assess its palaeoenvironmental signal.

2. Geological setting

The quarry of Champblanc is located near the village of Cherves-de-Cognac, in the vicinity of the town of Cognac (south-western

* Corresponding author. Laboratoire de Géologie de Lyon, UMR 5276 CNRS, ENS, Université Lyon 1, Campus de la Doua, Bt. Géode, 69622 Villeurbanne Cedex, France.
E-mail addresses: joane.pouech@univ-lyon1.fr (J. Pouech), jean-michel.mazin@univ-lyon1.fr (J.-M. Mazin), lionel.cavin@ville-ge.ch (L. Cavin), francisco.poyato@uam.es (F.J. Poyato-Ariza).

France) (Fig. 1). It is a huge open quarry of gypsum which exposes a 40 m section made up of an alternation of 81 levels of claystones, marlstones and limestones, intercalated with several banks of gypsum (Fig. 2). Historically considered as Late Jurassic in age (Purbeckian facies from the Tithonian) (Coquand, 1858, 1860; Bourgueil et al., 1986; Hervat and Hervat, 1993; Le Loeuff et al., 1996), new biostratigraphic dating based on ostracods, charophytes and dinoflagellates indicate a early to middle Berriasian age, making the section of Champblanc an equivalent of the middle of the English Purbeck Limestone Group (Colin et al., 2004; El Albani et al., 2004).

The first sedimentary studies recognized a progression from a hypersaline lagoon at the bottom of the series to continental freshwater lacustrine environments in the uppermost levels (El Albani et al., 2004; Mazin et al., 2008), which is in accordance with the paroxysm of the general regressive context in Western Europe during the uppermost Jurassic and the basal Cretaceous. The faunal distribution of micro-vertebrate in the series reflects this pattern (Pouech, 2008; Pouech and Mazin, 2008).

All the non-gypseous levels (63 of the 81 layers) of the Champblanc section are fossiliferous. 1763 vertebrate macro-remains have been extracted from a complex of four marly levels (C34 to C37), an assemblage dominated by crocodilians (Mazin et al., 2006, 2008). Simultaneously, vertebrate micro-remains, including 35,638 isolated teeth, have been collected by screen-washing from the 63 non-gypseous levels. The whole vertebrate assemblage (macro- and micro-remains) contains all the main vertebrate clades: Chondrichthyes, Actinopterygii, Amphibia, Testudines, Lepidosauromorpha, Crocodylia, Dinosauria including Aves, Pterosauria, and Mammalia, representing at least 33 families. Most of these vertebrate are thought to be allochtonous or para-utochtonous to the depositional environment and the quantitative analysis of micro-remain biodiversity reveals a taphocenosis mainly from continental origin, transported by watercourses from the proximal emerged lands and concentrated in a littoral lagoon (Pouech, 2008; Pouech and Mazin, 2008).

3. Material and methods

Isolated bones and scales described here have been found as macro-remains during excavations, in the levels C34 to C37 (Fig. 2). For micro-remains research, about 200 kg of dry sedimentary deposits from each level have been sampled and treated by screen-washing. The dissociation of sedimentary rocks was performed with water and peroxide, and, if necessary, with formic (methanoic) acid for carbonate dissolution. Screen-washing was made on three successive sieves of 3 mm, 1 mm and 0.5 mm of mesh. After drying of the residue, teeth were manually sorted from the 1 mm and 0.5 mm mesh and counted under a Leica MZ 7.5 stereomicroscope.

The teeth abundances mentioned in the text correspond to the amount of specimens actually extracted. However, in order to compare proportions of taxa between levels, these values were extrapolated to the mass of sedimentary rocks corresponding to the largest collected sample, namely 306 kg (Appendix A). Statistical test have been performed with the free software PAST (PAleontological STatistics, Hammer et al., 2001).

Most imaging of the actinopterygian tiny isolated teeth used X-Ray microtomography at the European Synchrotron Radiation Facility (ESRF, Grenoble, France), on beamlines BM05 and ID19. Tomography specifications (pixel size, propagation distance and energy) are notified in the legend of each figure. Data processing and 3D reconstructions have been made with the softwares Octave, Matlab and VGStudioMax 1 and 2, under ESRF's licences. Some specimens have been imaged with SEM Hitachi S-570 of UMR 5125 of University of Lyon 1. Isolated ossifications were photographed with a digital camera.

Specimens are kept at the Museum of Angoulême (Département de la Charente, France), under collection number with the following syntax: CHVmyy.nnn, where "CHV" is an abbreviation of Cherves-de-Cognac, "m" means micro-remain (missing for macro-remains such as isolated bones and scales), "yy" the year of discovery and "nnn" the specimen number.

4. Bones and scales

Subclass Actinopterygii Cope, 1887
Series Neopterygii Regan, 1923
Super Division Holostei sensu Grande, 2010
Division Ginglymodi sensu Grande, 2010
Order Lepisosteiformes sensu López-Arbarello, 2012
Genus *Scheenstia* López-Arbarello and Sferco, 2011
Scheenstia mantelli (Agassiz, 1833)

Material. Isolated cranial bones referable to *Scheenstia mantelli*, as well as numerous isolated ganoid scales have been found during excavation (Fig. 3).

Description. Skull remains: The bones of the skull show no traces of enamel. A fine granulation is present on the opercle and, even more
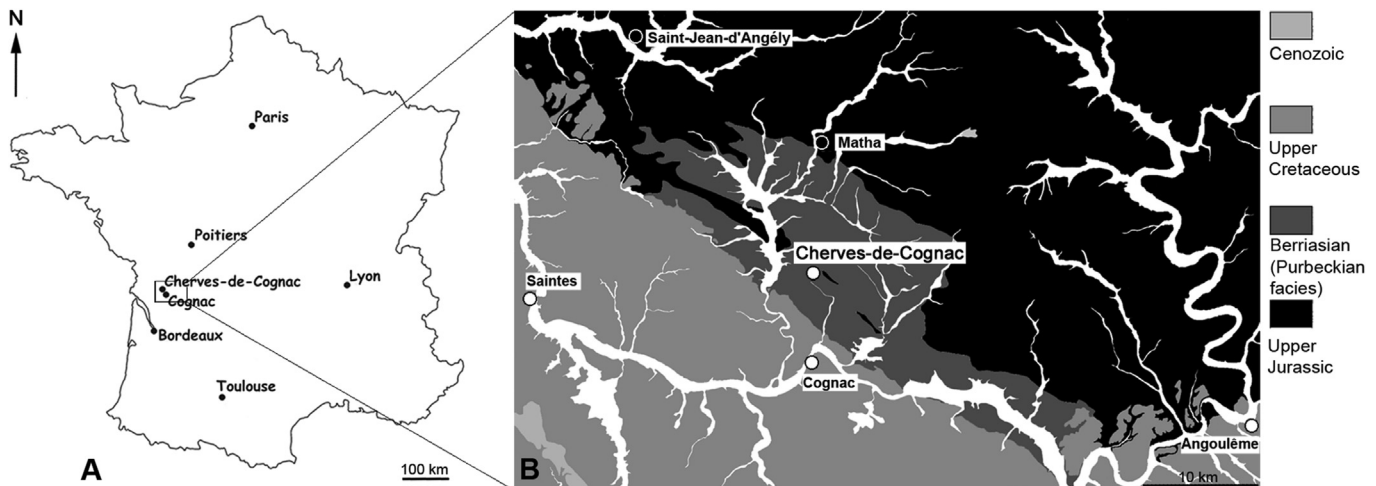

Fig. 1. The gypsum quarry of Champblanc is located near the village of Cherves-de-Cognac, in the vicinity of the town of Cognac (Département de la Charente, South Western France). A, Location of Cherves-de-Cognac on a map of France. B, geological map of Cherves-de-Cognac surroundings.
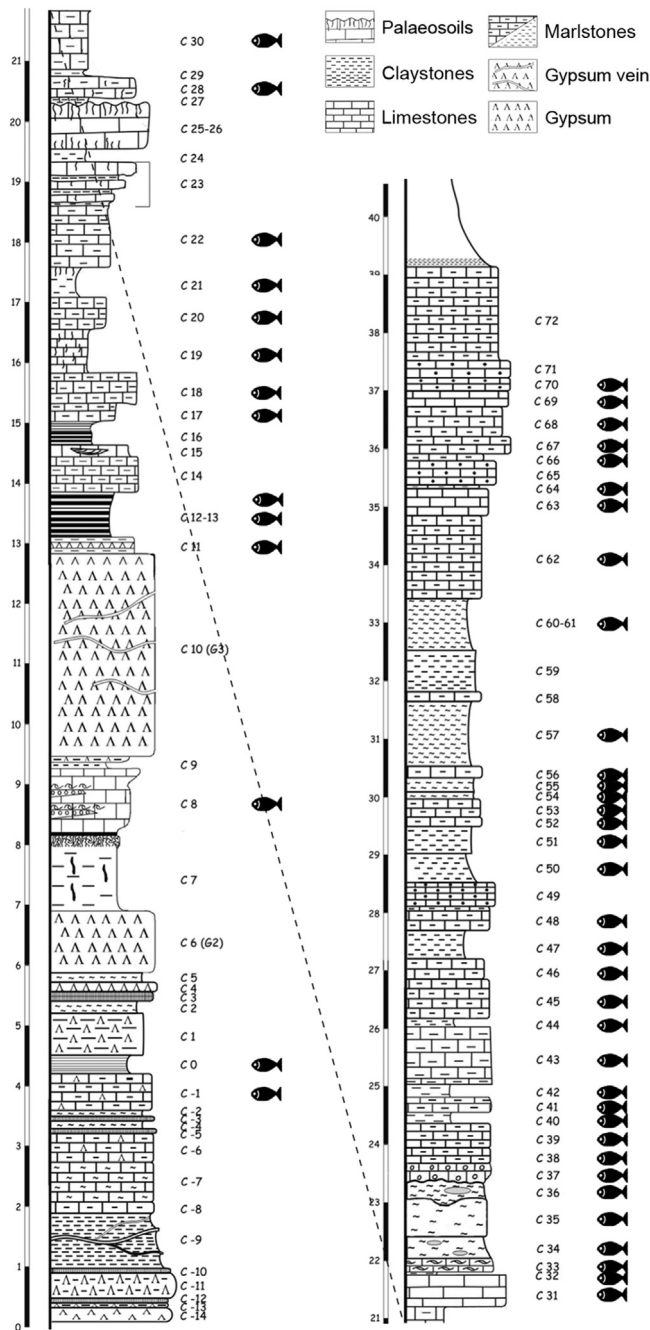
Fig. 2. The exposed section of Champblanc comprises 81 levels from which 63 are fossiliferous and yield vertebrate micro-remains. 49 of these fossiliferous levels yield osteichthyan isolated teeth.

faintly, on the posterior part of the skull roof (part of the frontals, parietals, dermopterotics) and cheek bones.

Three right frontals (Fig. 3A) have been recovered (CHV02.231, CHV02.161 and CHV05.81). The bone is between 2.5 and 3 times longer than wide. The anterior extremity is significantly narrower than the posterior one. The lateral margin of the bone is straight, with no marked concavity or narrowing at the level of the orbit. The medial margin draws a sigmoidal line in one specimen (CHV02.161), and slightly extends on the opposite moiety of the skull roof in another specimen (CHV02.231). A series of pores parallel to the lateral margin of the bone marks the path of the supraorbital sensory canal. A single, probably left, parietal

(CHV05.191) has been recognized (Fig. 3B). Its anterior margin forms a triangular process that delimitated the limit between both frontals anteriorly, indicating that the suture-line between paired ossifications of the skull roof was not in the mid-line. The medial margin of the parietal is marked with a notch in its posterior part indicative of an asymmetry between both parietals. The lateral margin of the parietal marks a concavity, in which fitted a corresponding convexity of the dermopterotic. Two right dermopterotics (Fig. 3C) have been found (CHV04.43 and CHV07.144). They are roughly triangular in outline, the length being 1.8 longer than the width, with their anterior extremity narrower than the posterior one. The medioposterior corner of the ossification develops a blunt process that extended under the extrascapular series. The ventral side of the dermopterotic bears a curved crest.

Several isolated tooth-bearing bony plates are present. Two (CHV03.130 and CHV06.112) are thin and plate-like ossifications, which correspond likely to the dermopalatine dentitions (Fig. 3D). Another one (CHV07.330), symmetrical and bearing on its aboral face a ridge along its lateral margins, is probably a vomerine dentition. Other fragments are too incomplete and can be regarded either as palatal dentitions (dermopalatine or vomerine) or internal dentitions of the mandible (prearticular or coronoid). All the teeth borne by these elements have a similar general shape, i.e. a pedicel supporting a bulbous to conical crown. The small teeth are proportionally thinner.

Except for the dermopalatines, no other elements of the suspensorium are known, but a fragment of a hyomandibula (CHV05.233). It has a regularly curved articular head and show the base of a broken opercular process.

Several isolated ossifications are referred to cheek bones. Three plate-like anamestic ossifications (CHV01.217, CHV05.33 and CHV07.413) probably belong to the suborbital series (Fig. 3E), and one (CHV04.045), crossed by a small sensory canal probably belong to the infraorbital series (Fig. 3F). The latter has a complex shape with a plate-like half, which is ornamented, and a narrower half, which bears a process. It is reminiscent of the last infraorbital of S. mantelli (BMNH P.6933). If this interpretation is right, we may suspect that a dermal component of the autosphenotic was visible on the cheek as in many other Lepisosteiformes (Deesri et al., 2014).

The lower jaw is represented by a subcomplete left hemimandible (Fig. 3G) (CHV04.59), a partial left dentary (CHV02.297) and a poorly preserved left coronoid (CHV04.64). The most complete specimen (CHV04.59) shows a deep and rounded anterior moiety of the coronoid process, which is formed by the surangular. The angular and other posterior ossifications of the mandible are not preserved. The dentary has a long posterior process (we cannot ascertain if it reached the posterior margin of the mandible because that part is not preserved). Anteriorly to the coronoid process, the dentary has almost parallel dorsal and ventral margins. The bone curves inwards and slightly downwards. The symphysis bears strong indentation, indicating a tight suture between both hemimandibles. The oral margin of the dentary bears ca five teeth. Each tooth has an elongated pedicel and a conical, semi-crushing crown. Several openings of the mandibular sensory canal open along the dentary. A second series of pores, situated on a line dorsal to the mandibular canal on its anterior part, form the oral sensory canal. The coronoid is incomplete and we cannot determine the number of teeth. Those are bigger than the dentary teeth and have a shorter pedicel; they are regarded as crushing teeth. Some replacement teeth with their apex pointing ventrally are visible on the internal face.

Six fragmentary (CHV02.282, CHV03.30, CHV02.206, CHV05.203, CHV03.153, CHV05.130) and two complete (CHV07.414, CHV07.397) preopercles have been found (Fig. 3H). Both limbs of

the preopercle are individualized and form between them an angle of *ca* 115°. The vertical limb is narrow with a slight broadening at its dorsal extremity. The horizontal limb is wider than the vertical one and tapers anteriorly. A ridge runs along the mid-width of the vertical limb and along the ventral third of the horizontal one. Anterior to this ridge the surface of the bone is smooth, whilst posteriorly to the ridge the surface is finely ornamented on the vertical limb and bears some coarser ornamentation ventral to the ridge on the horizontal limb. Two to four pores open on the dorsal part of the vertical limb, and no pore open along most of the ventral part of the vertical limb, except one or two in some specimens. *Circa* ten pores open regularly along the horizontal limb. One complete left (CHV07.382) and one fragmentary right (CHV07.328) opercles are present (Fig. 3I). The opercle is roughly rectangular, with the dorsal and ventral margins straight and parallel, and with the anterior and posterior margins parallel but slightly curved. An oval articular facet lies on the internal side of the bone at the dorsal third of its height. On the external side of the opercle, a groove runs along the dorsal part of the anterior margin. It accommodated the posterior margin of the vertical limb of the preopercle.

Three complete (CHV05.147, CHV04.61 and CHV04.137) and two fragmentary (CHV02.59 and CHV06.58) supracleithra have been found (Fig. 3J). The articular facet is well-developed and surrounded by broad processes. The main body of the bone has almost parallel margins. The ventral extremity forms a narrower arm, which is proportionally thinner and longer in the small (young) individual (CHV04.137) than in the larger ones. The posterior area of the ossification is ornamented with coarse ridges in its dorsal part and fine punctuation is the ventral part. A stout ridge runs medially on the internal side of the bone. One subcomplete (CHV06.144) and one incomplete (CHV03.10) cleithra are present (Fig. 3K). The vertical limb is proportionally narrow and curved slightly backward at its dorsal extremity. On the internal side of the ossification are deep ridges, which delimitate grooves anteriorly oriented. Several series of tiny denticulations run on the external side of the bone, along the anterior margin of the curvature. Most of the horizontal limb is not preserved and there is no trace of an internal wing. Two complete (CHV02.05 and CHV07.396) and one fragmentary (CHV05.128) dermal ossifications are interpreted as postcleithra (Fig. 3L). The subtriangular surface is covered with a thin layer of enamel, and the dorsal extremity ends with two or three pointed processes.

Numerous isolated scales have been found (Fig. 3M–R). The surface of the enameloid is smooth when observed with naked-eye. The morphology of the scales varies according to their location on the body: scales from the anterior part of the body bear a pair of anteriorly-oriented pegs. Some well-preserved scales show a fine denticulation of the posterior margin of the enamel layer.

Identification. A number of species have been referred to the genus "*Lepidotes*" and numerous are not valid or in need of revision. Recently, efforts have been made to better define the relationships between species of the genus "*Lepidotes*" and several new genera have been erected. Our material is not complete enough for being included into a phylogenetic analysis, and consequently we compare it directly with various former "*Lepidotes*" species.

Our comparison indicates that the material from Cherves-de-Cognac fits better with *Scheenstia mantelli* from the Wealden and upper Purbeck of UK. Formerly regarded as a *Lepidotes*, this species was included in the genus *Scheenstia* by López-Arbarello (2012). Our material shows no autapomorphies of this genus as defined by López-Arbarello (2012), and the species was not re-diagnosed since its detailed description by Woodward (1919). Based on the initial Woodward's diagnosis and by direct observation of the material housed in the NHM in London (LC), the taxon from Cherves-de-Cognac shares with the British material: frontal with similar

proportions (*ca* 3× longer than wide); dermal bones more or less rugose or tuberculated; a mandibular symphysis very robust, the dentary horizontally extended to support the large tooth-bearing coronoid (='splenial' of Woodward); inner teeth very short, smooth, usually with slightly acuminate crown when unworn; marginal teeth also stout, smooth and acuminate; maximum length of the opercle equals nearly two-thirds of its depth (in the Cherves-de-Cognac material, the length/depth ratio is about 3/5, but the direct observation of this feature on a specimen of *S. mantelli* – BMNH P.6933 – indicates that the ratio equals 0.625, and consequently is closer to 3/5 than to 2/3, as mentioned by Woodward for this species). Differences between the Cherves material and *S. mantelli* are also observed, such as the suture between both frontals, which is straight in *S. mantelli* and apparently sinusoidal in the Cherves-de-Cognac taxon. But examination of this feature in a large population of the ginglymodian, *Thaiichthys buddhabutrensis* from the Lower Cretaceous of Thailand, indicates that the pattern of the suture between paired bones on the skull roof may vary within a species (Cavin et al., 2012).

The shape of the preopercle, with a marked angle, and the rectangular-shaped opercule of the taxon found in the Cherves-de-Cognac locality allow to exclude it from the genera *Lepidotes*, *Callipurbeckia*, *Macrosemimimus* and the species '*Lepidotes*' *microrhis*, and *Scheenstia maximus* (Jain, 1985; Wenz, 2003; López-Arbarello, 2012; Schröder et al., 2012). *Scheenstia laevis* is a species from the Upper Jurassic of Cerin, whose taxonomic status is in need of revision. The shape of its frontal, however, which is almost as broad anteriorly as posteriorly (Saint-Seine de, 1949) differs from the frontals found in Cherves-de-Cognac.

The comparison of cranial characters from the Cherves-de-Cognac locality with cranial characters of ginglymodian species from the Upper Jurassic to Lower Cretaceous of Europe, together with the characters of the isolated teeth found in the same locality (see below), allow referring this material with caution to *S. mantelli*. More complete and articulated material, however, is necessary to confirm this identification.

5. Isolated teeth

Actinopterygian teeth are particularly abundant in the Champblanc section of Cherves-de-Cognac. Indeed, 26,346 micro-teeth have been collected, coming from 50 of the 63 fossiliferous levels. This fish fauna represents more than 70% of the about 36,000 vertebrate micro-teeth found in the whole section.

This large amount of micro-teeth includes an important morphological diversity, reflecting a higher taxonomic diversity than the diversity recognized on the basis of the macro-remains (bones and scales). However, the taxonomic attribution of these isolated teeth remains problematic, as actinopterygians teeth often bear few (or no) diagnostic characters and show a high morphological variability, making their identification difficult at low taxonomic rank. For these reasons, we chose to treat these specimens not by taxonomic group, as conventionally done, but by morphotypes, with a discussion of their possible taxonomic assessment.

Eleven morphotypes have been recognized, six of which (tooth morphotype 6–11) could be referred to Pycnodontiformes.

5.1. Tooth morphotype 1 (Fig. 4A–C)

Material. This morphotype is the most common in the Champblanc section, as it represents more than 60% of the actinopterygians micro-teeth and is known in 39 of the 63 fossiliferous levels.
Description. These teeth have a low rounded shape, with a circular cross-section, almost always covered with a translucent cap of acrodine. There is neither superficial ornamentation nor carina, but
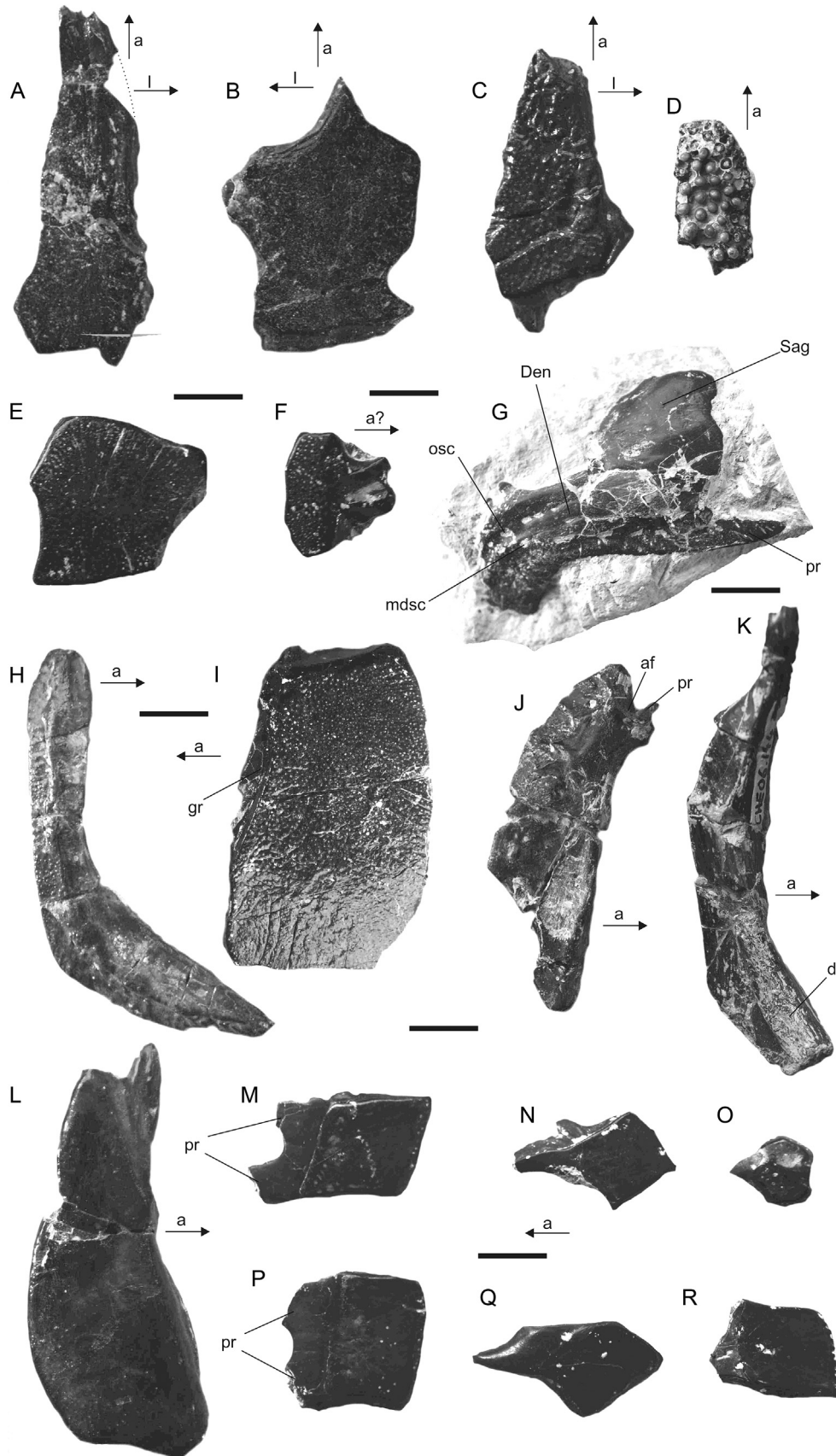
Fig. 3. Champblanc Quarry, Cherves-de-Cognac, France, Berriasian. Lepisosteiformes, *Scheenstia mantelli*, isolated bones. A, CHV02.231, right frontal, dorsal view; B, CHV05.191, left parietal, dorsal view; C, CHV07.177, right dermopterotic, dorsal view; D, CHV06.112, dermopalatine?, occlusal view; E, CHV01.217, suborbital, lateral view; F, CHV04.45, infraorbital bone (last one?), lateral view; G, CHV 04.59, left mandible (without the posterior part), lateral view; H, CHV07.414, right preopercle, lateral view; I, CHV07.382, left opercle, lateral

sometimes a small apical tubercle. Some teeth show a sub-horizontal wear facet in the apical region.

Identification. Isolated teeth with this morphology are commonly found in actinopterygian assemblages in the Jurassic and Cretaceous of Western Europe, and has been described and figured by Estes and Sanchíz (1982), Cuny et al. (1991), Mudroch and Thies (1996), Thies and Mudroch (1996), Kriwet et al. (1997), Buscalioni et al. (2008) and always referred to "oral" teeth of the genus *Lepidotes*. This genus gathers numerous species and was recently split into several genera (*Isaniichthys* Cavin and Suteethorn, 2006; *Scheenstia* López-Arbarello and Sferco, 2011; *Macrosemimimus* Schröder et al., 2012; *Callipurbeckia* López-Arbarello, 2012; *Thaiichthys* Cavin et al., 2012). Dentition varies considerably between these taxa, and three main kinds of dentition are distinguished (Jain, 1983; Cavin, 2010): species with no crushing teeth, species with a moderate crushing dentition and species with a strong crushing dentition. Isolated oral teeth from Cherves-de-Cognac are referable to the strongly crushing type, which occurs in the species on the genus *Scheenstia* (López-Arbarello, 2012). Consequently, we refer isolated teeth of the morphotype 1 to *S. mantelli*, which is known in this site by skull remains (see above).

5.2. Tooth morphotype 2 (Fig. 4D–J)

Material. This morphotype is the second most common among actinopterygian micro-teeth in Cherves-de-Cognac. It is known by 5922 teeth in 23 levels and represents more than 20% of all actinopterygian specimens.

Description. These teeth are rounded in section with a more or less bulged base and a curved conical apex mainly composed of a translucent cap of acrodine. The base is more or less bulged, giving these teeth various morphologies ranging from short and massive to thin needle-shaped teeth. All intermediaries between the illustrated morphologies are known.

Identification. The taxonomic assessment of this second morphotype is more questionable. Cuny et al. (1991), Mudroch and Thies (1996), Thies and Mudroch (1996), Kriwet et al. (1997) refer them to "pharyngeal" teeth of *Lepidotes*, but Estes and Sanchíz (1982) consider that the styliform teeth can be referred to *Lepidotes*, while those with a bulged base are characteristic of the Pycnodontidae, a view followed in part by Kriwet (1999). The examination of the large sample from Cherves-de-Cognac reveals that intermediate morphologies between the styliform and bulge-based teeth are present and included in morphotype 2. Thus, it is not possible to discriminate two independent morphological populations within the available sample of teeth of morphotype 2, indicating that this morphotype is likely referable to a single taxon. A chi square analysis was performed on the percentage distribution of morphotypes along the sedimentary series (for each morphotype, percentage of sampled specimens in each level relative to the total number of specimens known in the series; Fig. 5). The distribution of morphotype 2 was compared to the distribution of morphotype 1 (d.f. = 42; p = 0.999), to morphotype 6 (the most common pycnodontiform morphotype; d.f. = 48; p < 0.001) and to combined morphotypes 6 to 11 (all pycnodontiforms, d.f. = 49; p < 0.001). These results suggest that morphotype 1 and 2 are strongly associated in the sedimentary series and support a common taxonomic attribution of morphotypes 1 and 2 to *Scheenstia mantelli*. However, indistinguishable styliform to bulged-shaped pharyngeal teeth are broadly present in pycnodonts (e.g., Poyato-Ariza and Wenz, 2002: pp.210–211, figs. 21, 46; 2005: p.32, fig.4),

so part of this sample, in small quantities, may belong to the Pycnodontiformes, but this seems impossible to discriminate morphologically and quantitatively.

5.3. Tooth morphotype 3 (Fig. 6)

Material. Although not very abundant, these arrow-shaped teeth are commonly found among the micro-remains of Cherves-de-Cognac, with 259 specimens from 15 levels. They are more frequent in the middle part of the section.

Description. The base is columnar and robust, and sometimes bulged in the upper half. A light ornamentation of thin parallel grooves covers the lingual face of the base. The crown is arrow-shaped, a characteristic outline due to two strong sharp carinae, mesial and distal. According to morphological variability, the crown can be vertical with straight carinae (Fig. 6A) or lingually curved with slightly sigmoid carinae (Fig. 6B).

Identification. These features are diagnostic for the genus *Caturus*, as pointed out by Cuny et al. (1991), Mudroch and Thies (1996), Thies and Mudroch (1996), Kriwet et al. (1997) and Buscalioni et al. (2008).

5.4. Tooth morphotype 4 (Fig. 7A)

Material. Only eight specimens of this tooth morphotype have been found in the section of Cherves-de-Cognac. They are restricted to two levels, C32 and C33, which record a marine influx (El Albani et al., 2004).

Description. Teeth are conical and robust, with a translucid lingually curved crown and a light lingual bulge on the upper part of the root. The base is entirely covered with a characteristic ornamentation made of numerous thin vertical and parallel grooves. The apex has no carinae.

Identification. This general tooth morphology, associated with this particular basal ornamentation, strongly evokes the features of the teeth of the genus *Belonostomus* according to Mudroch and Thies (1996) and Thies and Mudroch (1996).

5.5. Tooth morphotype 5 (Fig. 7B)

Material. Only four teeth of this morphotype were found in the whole section. They are coming exclusively from the level C36.

Description. These teeth are elevated, needle-like and lingually curved. They are bucco-lingually compressed and the apex is covered by a very small translucent cap of acrodine. There is no enamel ornamentation, but two sharp carinae, distally and mesially located, running on the whole height of the crown.

Identification. This teeth morphology was described by Mudroch and Thies (1996) and Thies and Mudroch (1996) and referred to the genus *Thrissops*.

5.6. Pycnodontiformes (Fig. 8)

Isolated teeth referable to Pycnodontiformes are regularly represented along the section with 2976 teeth (11.3% of all actinopterygian isolated teeth), known from 41 of the 63 fossiliferous levels. However, it may be noted that the pattern of distribution is different from those of previous morphotypes, the ginglymodian remains being relatively more abundant in the lower and middle part of the section while the pycnodontiforms dominate in the upper part of the section.
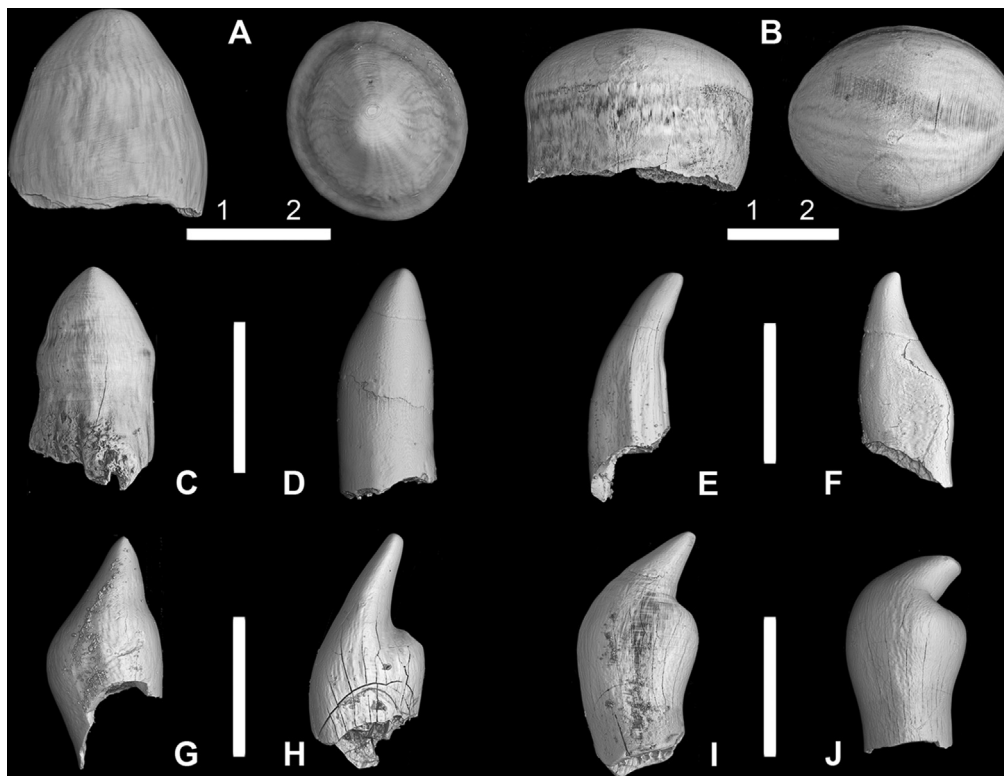
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view; J, CHV04.137, left supracleithrum, internal view; K, CHV06.144, right cleithrum, lateral view; L, CHV07.396, right postcleithrum, lateral view; M–R, scales, lateral views. Abbreviations: a, anterior; af, articular facet; d, denticles; Den, dentary; gr, groove; l, lateral; msc, mandibular sensory canal; osc, oral sensory canal; pr, process; Sag, surangular; soc, supraorbital sensory canal. Scales bars: 10 mm.

Fig. 4. Champblanc Quarry, Cherves-de-Cognac, France, Berriasian. Isolated teeth attributed to the lepisosteiforms *Scheenstia mantelli*. A—C: Tooth morphotype 1, oral teeth; A, CHVm03.288, lateral (1) and occlusal (2) views; B, CHVm03.285, lateral (1) and occlusal (2) views; C, CHVm03.280, lateral view. D—J: Tooth morphotype 2, pharyngeal teeth, lateral view; D, CHVm03.291; E, CHVm03.297; F, CHVm03.298; G, CHVm03.299; H, CHVm03.300; I, CHVm03.301; J, CHVm03.302. 3D micro-tomography reconstructions, ESRF (beamline ID19; pixel size: 1.4 μm for B-D and 2.8 μm for A, E-J; propagation distance: 50 mm; energy: 20 KeV). Scale bars: 1 mm.
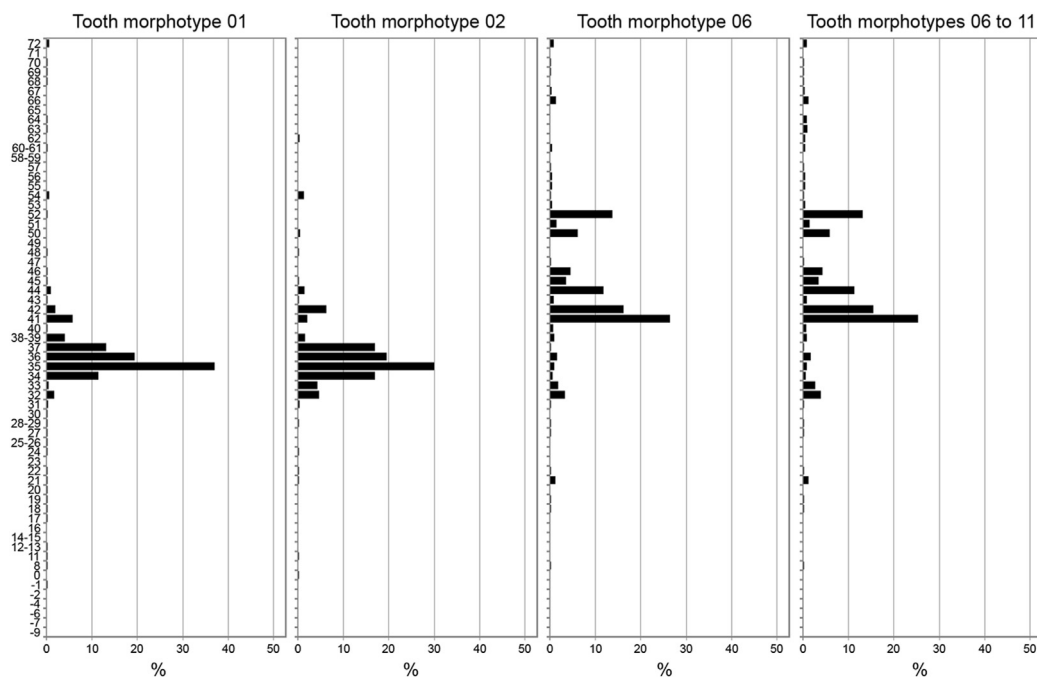

Fig. 5. Quantitative distribution of tooth morphotypes 1 (referred to *Scheenstia mantelli*), 2 (referred to *Scheenstia mantelli*), 6 (the most frequent Pycnodontiformes morphotype) and 6 to 11 total (all Pycnodontiformes morphotypes added) along the sedimentary series of Cherves-de-Cognac. The abscissa axis represents, for each morphotype, the percentage of teeth found in each level, compared to the total number of teeth known in the whole series.
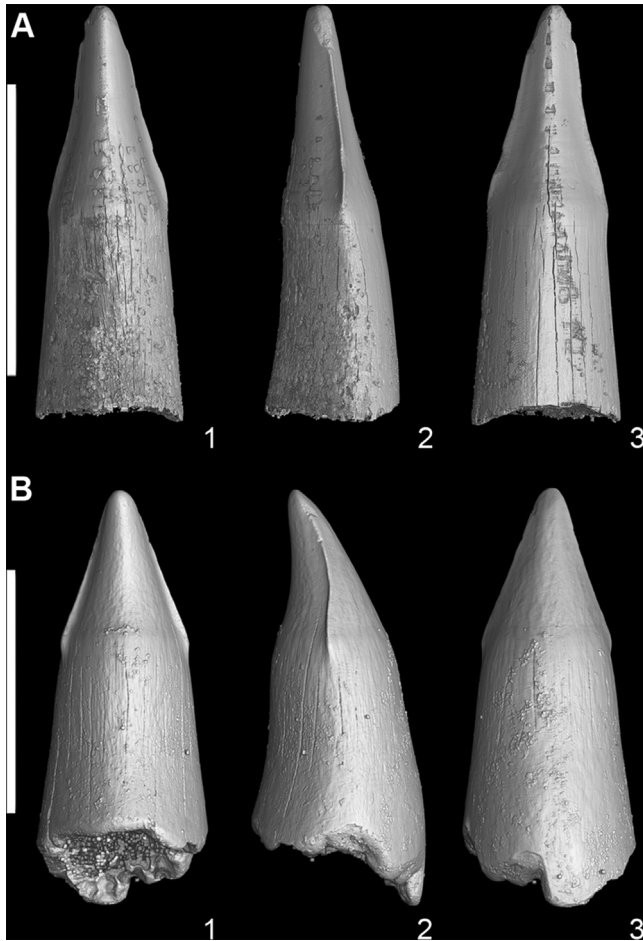
Fig. 6. Champblanc Quarry, Cherves-de-Cognac, France, Berriasian. Tooth morphotype 3, isolated teeth attributed to Caturidae, *Caturus* sp. A: CHVm03.303; lingual (1), mesial or distal (2) and buccal (3) views; B: CHVm03.306; lingual (1), mesial or distal (2) and buccal (3) views. 3D micro-tomography reconstructions, ESRF (beamline ID19 for A and BM05 for B; pixel size: 1.4 μm; propagation distance: 50 mm for A and 30 mm for B; energy: 20 KeV). Scale bars: 1 mm.

Fig. 7. Champblanc Quarry, Cherves-de-Cognac, France, Berriasian. A: Tooth morphotype 4, isolated tooth attributed to Aspidorhynchidae, *Belonostomus* sp. CHVm03.296; lingual (1), mesial or distal (2) and buccal (3) views. B: Tooth morphotype 5, isolated tooth attributed to Ichthyodectiformes, *Thrissops* sp. CHVm03.508; lingual (1), mesial and distal (2–3) and buccal (4) views. 3D micro-tomography reconstructions, ESRF (beamline ID19; pixel size: 1.4 μm; propagation distance: 50 mm; energy: 20 KeV). Scale bars: 1 mm.

The great morphological variability of Pycnodontiformes teeth has been pointed out by several authors (i.e. Cuny et al., 1991; Buscalioni et al., 2008). Furthermore, Poyato-Ariza and Wenz (2002) note that these teeth show very few diagnostic features. These reasons explain the great confusion in the scientific literature for identification of these teeth, and the difficulty to propose a robust taxonomic assessment.

Six morphotypes can be distinguished within the sample of pycnodontiform teeth (morphotypes 6–11) from Cherves-de-Cognac. Among them, one clearly dominates the assemblage (tooth morphotype 6), whereas the other five remain anecdotic in terms of quantities and frequency along the sedimentary series (tooth morphotypes 7–11).

5.6.1. Tooth morphotype 6 (Fig. 8A)

Material. This morphotype is represented by 2872 teeth found in 37 levels of the series. This is the second most common one along the series and the third most abundant actinopterygian morphotype. It represents more than 96% of all pycnodontiform teeth.
Description. Teeth morphology of this group varies from pear-shaped to kidney-shaped in occlusal view. The horizontal occlusal surface is translucid and bears a depression in which a more or less elevated cusp is located. The narrow extremity of the crown often bears a small tubercle. There is no constriction at the crown-root junction.
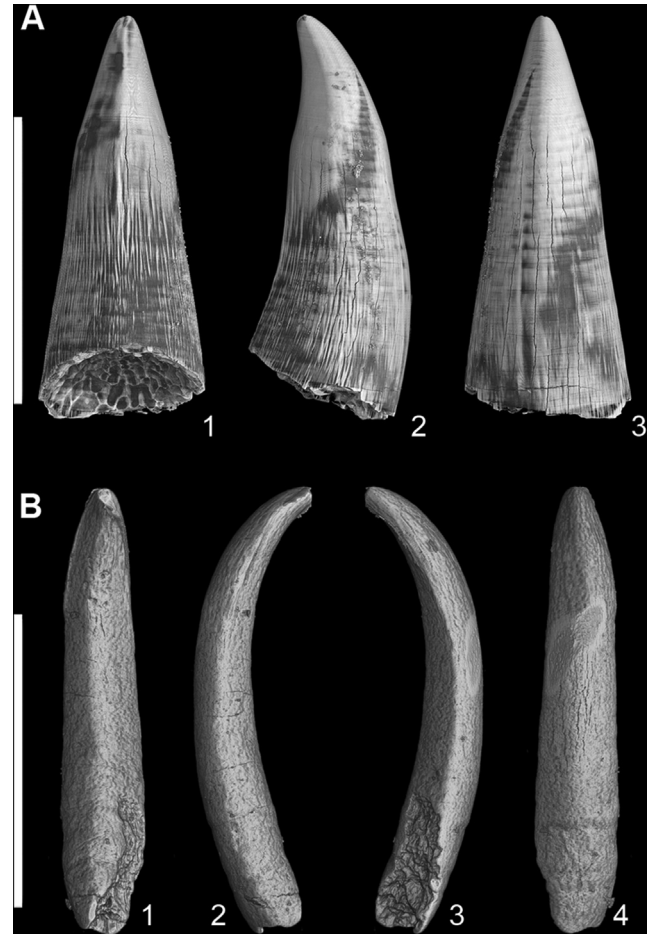
Identification. The presence of a central conical papilla is a diagnostic character of the genus *Gyrodus* (Poyato-Ariza and Wenz, 2002, p.218). As discussed by these authors, this is the only pycnodont genus in which a central papilla occurs, no other pycnodont presents such a feature (op. cit., p.177 and Appendix 3).

5.6.2. Tooth morphotype 7 (Fig. 8B)

Material. 17 teeth have been found in eight levels of the series.
Description. Elongated kidney-shaped teeth in occlusal view, bearing two elevated rounded tubercles, one on each extremity of the occlusal surface. Two parallel crests run along the crown, between the two tubercles, delimiting a longitudinal groove in between. There is no wear surface.
Identification. This kind of low molariform crushing teeth is characteristic of pycnodontiform fishes. However, it is difficult to propose a more precise taxonomic assessment. It could be regarded as a variation of a rather similar morphology observed in *Arcodonichthys* (Poyato-Ariza and Bermúdez-Rochas, 2009).

5.6.3. Tooth morphotype 8 (Fig. 8C)

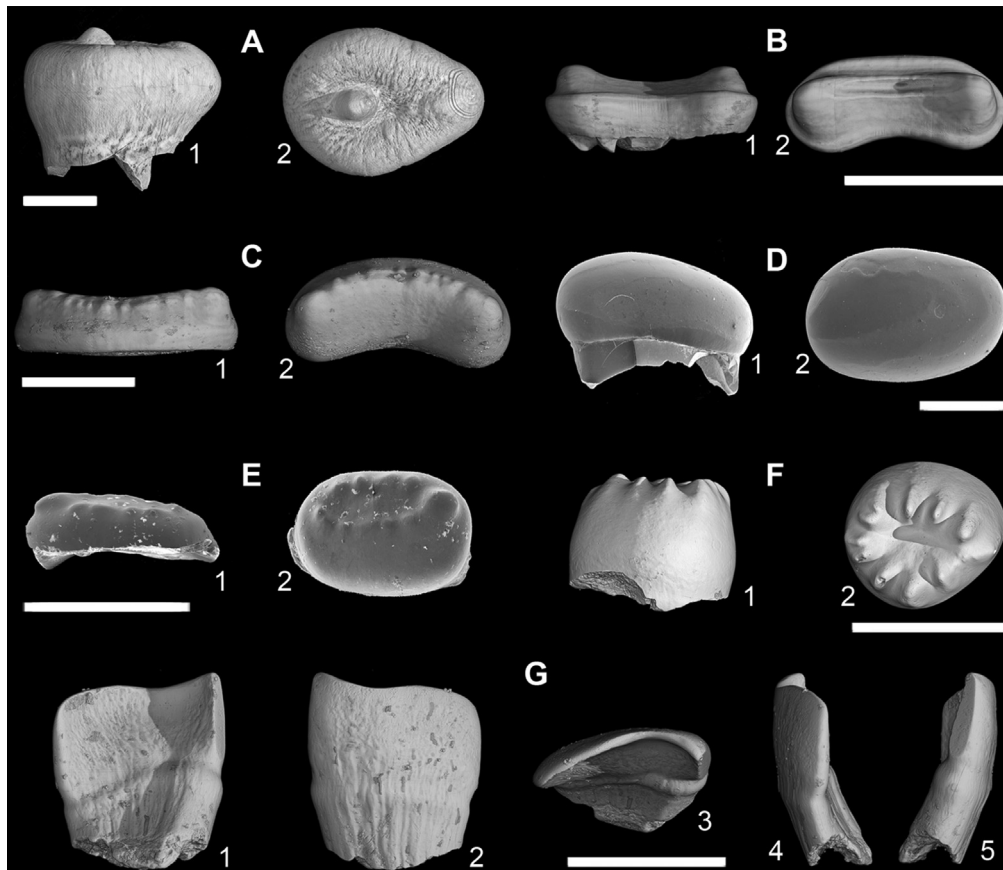*Material.* Six teeth are known from two levels, C32 and C33, recording a marine influx.

Fig. 8. Champblanc Quarry, Cherves-de-Cognac, France, Berriasian. Isolated teeth attributed to Pycnodontiformes indet. A: Tooth morphotype 6, CHVm03.163; lateral (1) and occlusal (2) views. B: Tooth morphotype 7, CHVm03.322; distal (1) and occlusal (2) views. C: Tooth morphotype 8, CHVm03.325; mesial (1) and occlusal (2) views. D: Tooth morphotype 9, CHVm04.505; lateral (1) and occlusal (2) views. E—F: Tooth morphotype 10 in lateral (1) and occlusal (2) views; E, CHVm03.318; F, CHVm05.151. G: Tooth morphotype 11, incisor-like anterior tooth, CHVm03.242; lingual (1), labial (2), occlusal (3), distal (4) and mesial (5) views. A, B, C, F, G: 3D micro-tomography reconstructions, ESRF (beamline ID19 for A, B, F, G and BM05 for C, pixel sizes: 1.4 μm for A, C, G and 2.8 μm for B, F; propagation distance: 50 mm for A, B, F, G and 30 mm for C; energy: 20 KeV). D, E: SEM photographs. Scale bars: 1 mm.

Description. This morphology is characterized by low and arched kidney-shaped crown in occlusal view. A single crest, made of aligned small tubercles, runs along the mesial side of the crown.
Identification. Like for the previous morphotype, these low molariform crushing teeth can be referred to pycnodontiforms.

5.6.4. Tooth morphotype 9 (Fig. 8D)

Material. Nine teeth are known from four levels of the series.
Description. Teeth with low smooth, oval to quadrangular crown, without tubercles or ornamentation. The surface does not show any apparent abrasion or wear mark.
Identification. This kind of morphology could be seen in taxa bearing originally smooth teeth, as described in specimens attributed to Pycnodontidae indet. (Cuny et al., 1991).

5.6.5. Tooth morphotype 10 (Fig. 8E—F)

Material. This morphotype is known by 62 teeth, from ten levels.
Description. Teeth with low oval to quadrangular, to elevated sub-cylindrical crown. They bear small tubercles arranged along a sub-circular to oval crest on shallow crown or along a circular crest on high teeth, delimiting a slight or deep central depression, respectively.
Identification. Teeth from Cherves-de-Cognac could easily enter in the variability of several resembling morphologies attributed to Pycnodontidae (Cuny et al., 1991, no figuration), *Coelodus* (Mudroch and Thies, 1996, plate 2 fig. 6; Kriwet et al., 1997, fig. 5d), *Macromesodon* (Mudroch and Thies, 1996, plate 1 fig. 18; Thies and Mudroch, 1996,

plate 1 fig. 6), *Ocloedus* (Buscalioni et al., 2008, fig. 6) or *Proscinetes* (Thies and Mudroch, 1996, plate 1 fig. 7).

5.6.6. Tooth morphotype 11 (Fig. 8G)

Material. Ten teeth from three levels have been found.
Description. Incisor-like teeth, linguo-labially compressed, lingually concave and buccally convex, with an arched shape in occlusal view. The crown-root junction is marked by a slight mesial and distal constriction, and a "cingulum" on the lingual face. The root shows some vertical grooves.
Identification. This morphology is typical for incisiform teeth borne on the premaxilla and dentary of the suborder Pycnodontoidea (Poyato-Ariza and Wenz, 2002; Buscalioni et al., 2008, morphotype 4, fig. 7).

6. Palaeoenvironmental implications

6.1. Life environments of fish taxa

Scheenstia mantelli (bones, scales and isolated teeth morphotypes 1 and 2). The ginglymodians are present in the Jurassic and Cretaceous deposits worldwide, whatever the depositional environments. For this reason, their occurrence is not representative of a specific environment. Recent descriptions of new ginlymodian taxa, together with taxonomic revisions and phylogenetic analyses, have shed a new light on the evolutionary history of that clade. In particular, a clade called Lepisosteiformes, including gars and several stem groups, has been recognized (Cavin, 2010; López-

Arbarello, 2012; Cavin et al., 2013; Gibson, 2013; Bermúdez-Rochas and Poyato-Ariza, in press; Deesri et al., 2014). The basal-most genus of this clade, *Lepidotes*, is restricted to the Lower Jurassic and represented mostly by marine species. The other genera of lepisosteiforms, however, are represented mostly by brackish or freshwater species (*Scheenstia, Isanichthys, Thaiichthys, Pliodetes*, ? *Araripelepidotes* and lepisosteoid genera). *Scheenstia*, a genus present in the Upper Jurassic and Lower Cretaceous, also includes species discovered in marine deposits, with *S. laevis* from Cerin, *S. maximus* and *S. decoratus* from Solnhofen, but also from brackish deposits, such as *S. degenharditi* and *S. hauchecornei* from the 'Wealden' of Germany and *S. mantelli* (López-Arbarello, 2012).

Scheenstia mantelli was firstly described from the Weald of southern England. In particular, remains of this species were identified as gut content of the supposedly piscivorous theropod dinosaur *Baryonyx walkeri* (Charig and Milner, 1997). The palaeoenvironment of the Weald correspond to a large lake of fresh to brackish water. More precisely, the bed in which *Baryonyx* was found was interpreted as a fluvial and/or mudplain environment, with areas of shallow water, lagoons and marsh (Ross and Cook, 1995).

In the case of Cherves-de-Cognac section, *Scheenstia mantelli* teeth and bones constitute the largest component of fish remains. The determination of the palaeoenvironment, by the way of sedimentological and micro-fossils indicators, suggest an important continental influx in the depositional environment (Mazin et al., 2008). Furthermore, the concordance of the distribution of *S. mantelli* isolated teeth along the sedimentary series with those of freshwater fauna (in particular crocodilians and sharks) leads to suggest a freshwater life environment for this taxa, at least in the section of Cherves-de-Cognac (Pouech, 2008; Pouech and Mazin, 2008; Rees et al., 2013).

Caturus sp. (Tooth morphotype 3). Caturidae fishes were active predators (Wenz et al., 1994; Senn, 1996; Kriwet et al., 1997), living in marine (Senn, 1996) or coastal environments (Wenz et al., 1994), but also able of occasional freshwater incursions (Wenz et al., 1994). Kriwet et al. (1997) report caturid teeth from brackish to freshwater environments of the English Wealden. In the case of Cherves-de-Cognac, occurrence of caturids is too regular throughout the section to regard them as indicator of marine inputs, as it is probably the case for *Belonostomus* and possibly *Thrissops*. According to the continental influence recorded in the deposits (Schnyder, 2003; Colin et al., 2004; El Albani et al., 2004; Mazin et al., 2008), we consider a brackish to freshwater life environment for caturids found in the Cherves-de-Cognac section, as suggested by Kriwet et al. (1997).

Belonostomus sp. (Tooth morphotype 4). The aspidorhynchids, notably *Belonostomus*, are commonly encountered in the Upper Jurassic-Lower Cretaceous interval of Western Europe. They are considered as marine predators (Senn, 1996; Thies and Mudroch, 1996; Kriwet et al., 1997), maybe coastal dwellers (Wenz et al., 1994), with freshwater representative occurring in the Upper Cretaceous only (Brito, 1997). In sedimentary deposits of Cherves-de-Cognac site, their presence remains anecdotic, as they are known only from two levels (C32 and C33), with very low abundances (eight teeth on a total of 1255 specimens, that is 0.6% of the bony fishes micro-teeth). Furthermore, these two levels record a marine influx indicated by ostracods and by the presence of marine ray remains (Colin et al., 2004; Rees et al., 2013). Thus, the rare aspidorhynchids remains found in the continental Cherves-de-Cognac section are likely indications of restricted, marine incursions.

Thrissops sp. (Tooth morphotype 5). *Thrissops* fishes were mostly marine predators during the Late Jurassic (Thies and Mudroch,

1996). However, *Thrissops curtus* was described by Woodward (1919) from the hypersaline lagoonal deposits of the lower Purbeck (Batten, 2002) of the Isle of Portland (England). Although the generic status of this species is dubious (Cavin et al., 2013), this occurrence is an evidence that ichthyodectiforms close to *Thrissops* were present in non-fully marine environments. However, these two teeth have been only found in the C36 level, which is one of the richest layers of the section, and represent about 0.06% of the micro-fauna (4 teeth of 6221 specimens). We suggest that their occurrence in Cherves-de-Cognac section is accidental.

Pycnodontiformes (Tooth morphotypes 6 to 11). The Pycnodontiformes are known with many taxa from the Norian (Late Triassic) to the Eocene (Nursall, 1996). For a long time, they were considered as durophagous fishes feeding not necessarily on corals, but also on shelled invertebrates (Nursall, 1996) or crustaceans (Poyato-Ariza et al., 1998). However, ecomorphological evidence (Poyato-Ariza, 2005) suggested that their diet and their potential adaptation to a variety of niches may have been more diversified than previously thought. Moreover, pycnodonts had been considered as strictly marine fishes according to their general morphological similarity with extant reef-dweller fishes (i.e. Wenz et al., 1994; Nursall, 1996; Thies and Mudroch, 1996). However, several pycnodont occurrences in brackish to freshwater environments have been recorded in the Lower Cretaceous of Belgium (Traquair, 1911), England (Schaeffer and Patterson, 1984), Spain (Wenz, 1989a), Texas (Thurmond, 1974) and Brazil (Wenz, 1989b). Furthermore, a multidisciplinary study of pycnodonts from the upper Barremian of Las Hoyas, Spain, clearly reveals their presence in a continental environment, without marine influx (Poyato-Ariza et al., 1998). Estes and Sanchíz (1982) and Kriwet (1999) suggest a displacement of their environment from marine to freshwater in association with the Upper Jurassic regression.

In the series of Cherves-de-Cognac, pycnodontiforms are mainly represented in the uppermost part of the section, which is characterized by a sedimentological shift with the first occurrence and development of lacustrine limestones (Mazin et al., 2008; Pouech, 2008). These observations suggest a freshwater environment for the Berriasian Pycnodontiformes from Charente.

6.2. Contribution to Cherves-de-Cognac palaeoenvironment

In Western Europe and North America (Brinkman et al., 2013), the kind of association of actinopterygians found in Cherves-de-Cognac, dominated by ginglymodians and pyncodontiforms, seems common in Upper Jurassic-Lower Cretaceous vertebrate assemblages, whatever are the depositional environment and the origin (marine or continental) of the associated vertebrate fauna.

In the section of Cherves-de-Cognac, the sedimentary and palaeoenvironmental studies have shown that the depositional environment was evolving from brackish (lagoon type) to lacustrine, and filled with continental sediments (El Albani et al., 2004; Mazin et al., 2006, 2008). The vertebrate fauna associated with bony fishes is mainly continental in origin, collected and transported from freshwater (sharks, amphibians, crocodilians, turtles) or terrestrial (dinosaurs, birds, mammals) life environments (Mazin et al., 2006, 2008; Pouech and Mazin, 2008). Apart from actinopterygian data, the only clear marine influence indicated by vertebrates are few rays teeth found in levels C32 and C33 in very small quantities (8 teeth for 1255 extracted specimens from quantified samples) (Pouech and Mazin, 2008; Rees et al., 2013).

Although conventionally regarded as marine forms, ginglymodians and pyncodontiforms, the most frequently found taxa, clearly appear as freshwater to brackish dwellers in the Cherves-de-Cognac site, as it has also been demonstrated in other deposits

(Poyato-Ariza et al., 1998). However, the distribution of these two most frequent and abundant taxa along the sedimentary series suggests that they were living in two different environments (Fig. 9). Isolated teeth of *S. mantelli* are regularly found but this species dominates the actinopterygian assemblage in the lower part of the series. In these levels, variations of teeth abundances of *S. mantelli* are following those of freshwater (sharks and crocodilians) and terrestrial (mainly dinosaurs and mammals) fauna, exhibiting identical increases and maximum of abundance (Pouech, 2008; Pouech and Mazin, 2008). This depositional pattern, as well as the prevalence of this taxon in the actinopterygian assemblage, suggest a life environment in upstream waters close to the depositional lagoon, as confirmed by geochemical analysis (Pouech et al., 2014).

On the contrary, pycnodont seem to be more represented in the upper levels, where calcareous deposits are becoming predominant, with the deposition of lacustrine limestones in the uppermost
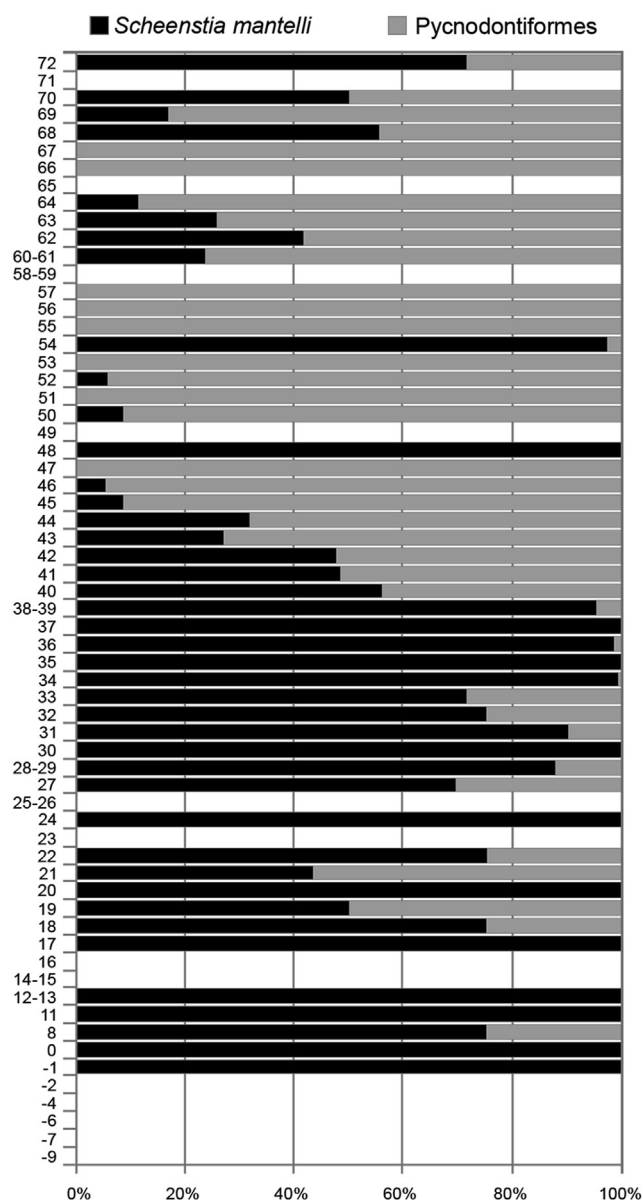

Fig. 9. Relative proportion of isolated teeth of *Scheenstia mantelli* (morphotypes 1 and 2; in black) and Pycnodontiformes (morphotypes 6 to 11; in gray) found in the sedimentary series of Cherves-de-Cognac, France, Berriasian.

layers. Furthermore, their teeth distribution along the sedimentary series does not match with any other vertebrate micro-teeth distribution. Therefore, these observations lead to propose a lacustrine life environment for Cherves-de-Cognac pycnodontiforms.

7. Conclusion

The rich collection of Cherves -de- Cognac site (Berriasian, Charente, France) allows a diversified actinopterygian fauna to be described. While bony macro-remains are better material for precise taxonomic identification, dental micro-remains are particularly informative to assess whole diversity and variation of the recorded fauna, thanks to a large collection of over 26,000 specimens. These quantified data also permit to solve a taxonomic identification issue and to refer isolated teeth of morphotype 2, frequently reported from coeval deposits, to the species *Scheenstia mantelli*.

Although this fish fauna is common in European deposits of the Upper Jurassic and Lower Cretaceous (*i.e.* Estes and Sanchíz, 1982; Cuny et al., 1991; Thies and Mudroch, 1996; Buscalioni et al., 2008), sedimentological and palaeoenvironmental data available for Cherves-de-Cognac (Colin et al., 2004; El Albani et al., 2004; Mazin et al., 2006, 2008), as well as quantitative distribution of vertebrates along the sedimentary series (Pouech, 2008; Pouech and Mazin, 2008; this study), lead us to propose a continental life environment at least for the two most represented taxa: *S. mantelli* and Pycnodontiformes. The site of Cherves-de-Cognac is a new example of clear fresh-to brackish water life environment for these two taxa, whose habitat is still debate.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.01.001.