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Non-marine selachians from the basal Cretaceous of Charente, SW France

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ABSTRACT

A gypsum quarry at Cherves-de-Cognac in south-western France exposes a large section of Berriasian (basal Cretaceous) sediments deposited in a lagoonal environment. The sediments have yielded rich vertebrate faunas, but only two species of selachians are present; the lonchidiid hybodont *Parvodus celsucuspus* sp. nov. and the batoid *Belemnobatis variabilis*. The composition of the fauna, including only a single, seemingly endemic, hybodont species from a time when hybodont faunas are relatively well investigated in Europe, indicate that small hybodonts were not able to migrate longer distances. The recorded batoid species also occurs in southern England, demonstrating that these batoids were primarily marine fishes that regularly explored areas with reduced salinity.

1. Introduction

Hybodont sharks have a long history, originating in the Devonian (Ginter et al., 2010), and representing one of the most long-lived selachian clades of all time. They inhabited a wide variety of ecological niches and different environments during the Mesozoic, including both marine and freshwater settings. In Early Cretaceous times, they were apparently very numerous and diverse in non-marine environments throughout the world (e.g., Patterson, 1966; Rees, 2002; Underwood and Rees, 2002; Cappetta et al., 2006; Cuny et al., 2004, 2006, 2008; Klug et al., 2010). Judging by the wide range of dental morphologies found among hybodont sharks and their substantial variation in body size, they were apparently adapted for many different life strategies, from durophagous sharks with crushing dentitions to species with piercing teeth, presumably adapted to a life in open water (e.g., Rees and Underwood, 2008). A few genera (e.g. *Priohybodus* d'Erasmo, 1960, and *Thaiodus* Cappetta et al., 1990) even developed a cutting dentition, allowing them to consume larger prey items (Cappetta et al., 1990, 2006; Duffin, 2001; Duffin and Cuny, 2008; Cuny et al., 2009a; Cappetta, 2012). There are a few external features that appear to be typically hybodont, including large and ornamented dorsal fin spines and, in males, paired cephalic spines above and posterior to the orbits.

The major modern neoselachian groups, including batoids, first began to diversify in the later part of the Early Jurassic (e.g., Underwood, 2006; Kriwet et al., 2009). During the Middle and Late Jurassic, further neoselachian radiation occurred, resulting also in a higher diversity of batoids. Isolated teeth that can be referred to *Spathobatis* Thiollière, 1854 or *Belemnobatis* Thiollière, 1854 are commonly found in marine and non-marine strata from the Middle Jurassic to the Lower Cretaceous of Europe (e.g., Thies, 1983; Underwood and Rees, 2002; Underwood and Ward, 2004; Rees, 2005), and these batoids are also known from complete skeletons (e.g., Cavin et al., 1995). Recently, isolated teeth of *Belemnobatis* have also been found in Thailand (Cuny et al., 2009b). These early batoids had a pointed snout, strongly enlarged pectoral fins and two dorsal fins on the tail, both equipped with a short fin spine. They are the most common neoselachians found in association with hybodonts, forming the typical elements of a selachian fauna from areas where the salinity was considerably lower than in the open ocean (e.g., Underwood and Rees, 2002).

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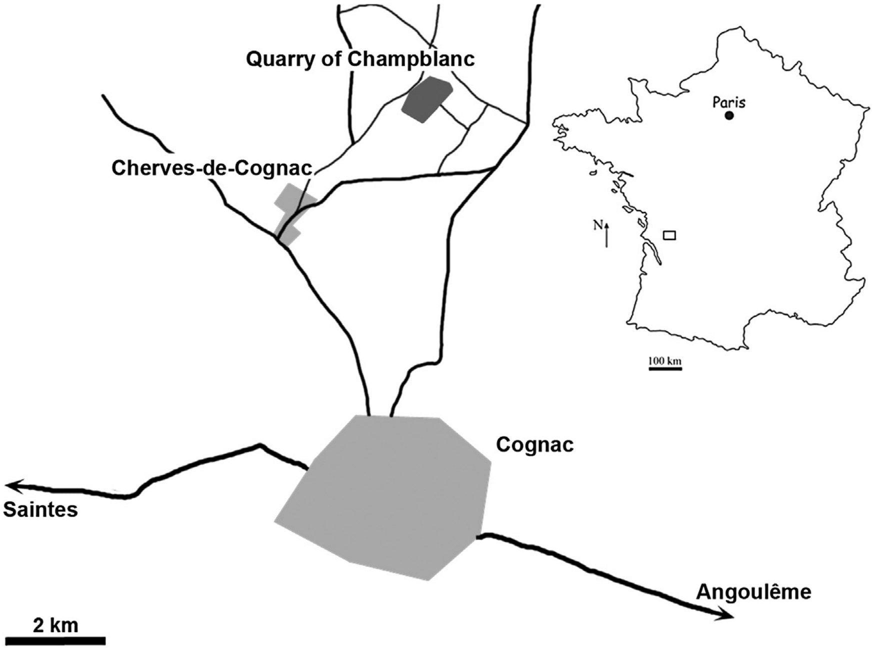

Fig. 1. The village of Cherves-de-Cognac is located 7 km north of the town of Cognac (Charente, south-western France).

2. Geological setting

The village of Cherves-de-Cognac is located in south-western France, on the northern margin of the Aquitaine Basin (Fig. 1). Material was collected from the so-called *Carrière de Champblanc*, a huge gypsum quarry in which a sedimentary series of 81 horizons, comprising carbonates, marls and evaporites, is exposed (Fig. 2). The section at Cherves-de-Cognac represents deposition of non-marine sediments in a lagoonal environment in which two successive lithological units have been identified (El Albani et al., 2004; Fig. 2). The basal unit (U1) is dominated by gypsum, with alternating thin beds of marl and clay, reflecting hypersaline conditions in a lagoon where occasional marine influx and low, but regular freshwater influx lead to the deposition of thick layers of evaporites. The second unit (U2) mainly includes more or less carbonate-rich marl beds with alternating clay horizons, overlain by lacustrine limestone deposits. This unit reflects deposition of continental material within the lagoon and there is a progressive increase of freshwater influence towards the top of the unit. The section has been dated by means of ostracods, charophytes and dinoflagellates, which all indicate a lower to middle Berriasian age of the Lower Cretaceous and suggest correlation with the lower part of the Middle Purbeck of southern England (Colin et al., 2004; El Albani et al., 2004).

The first occurrence of vertebrate fossils from these so-called “black marls” in the vicinity of Cognac was indicated by Coquand (1860), who reported isolated fish teeth and scales. After the opening of a large gypsum quarry, occasional vertebrate fossils were recorded from the succession in the 1980’s and 1990’s (Buffetaut et al., 1989; Hervat and Hervat, 1993; Le Loeuff et al., 1996; Vignaud et al., 1994). From 2001 to 2007, systematic excavations of these fossiliferous levels resulted in extensive collections of more than 1800 specimens of fossil vertebrates (Mazin et al., 2006, 2008), representing bony fishes, sharks and a wide variety of reptiles. Each of the 63 non-gypseous, marly horizons within the section was sampled and screen-washed in order to collect vertebrate microremains (Pouech et al., 2006; Pouech, 2008). All levels yielded microremain assemblages, revealing the presence of at least 28 vertebrate families, including amphibians and mammals. Selachian remains occur in 38 of the fossiliferous levels (Fig. 2), and the richest beds have yielded more than 1000 teeth per 100 kg of sediment.

3. Material and methods

Larger hybodont remains (cephalic spines and fin spines) were extracted during the excavations, whereas all selachian teeth were collected by means of screen-washing. For this purpose, 200 kg of sediment were sampled from each of the non-gypseous levels, with the exception of some very thin horizons. The samples were dissociated in water, combined with hydrogen peroxide and, for the more calcareous levels, diluted methanoic acid was used. The material was washed through sieves with mesh sizes of 1 mm, 0.500 mm and 0.315 mm. This process was repeated three times for each sample, in order to concentrate microvertebrates. Washing performance reached between 95% and 99.9% depending on the nature of the sediment. In two samples (beds 32 and 35), the fraction between 0.315 and 0.500 mm was treated with buffered acetic acid (see Jeppsson et al., 1999). Microvertebrate fossils were sorted under a stereomicroscope Leica MZ 7.5 and digital images of teeth and denticles were obtained through a Hitachi Scanning Electron Microscope.

The selachian material from Cherves-de-Cognac is housed in the public collections of Musée d’Angoulême (France), prefixed CHV, and a smaller part of the material is deposited in the collections of the Natural History Museum of Copenhagen (Denmark), GM-V-2008 and MGUH 30420.

4. Systematic palaeontology

Cohort Euselachii Hay, 1902
Superfamily Hybodontoidea Owen, 1846 *sensu* Zangerl, 1981
Family Lonchidiidae Herman, 1977 *sensu* Rees, 2008
Genus *Parvodus* Rees and Underwood, 2002

Type species. Lissodus rugianus Ansorge, 1990 from the Lower Cretaceous of Rügen, northern Germany.

Remarks. When this genus was first recognized and erected (Rees and Underwood, 2002), only three species were included; *Parvodus*

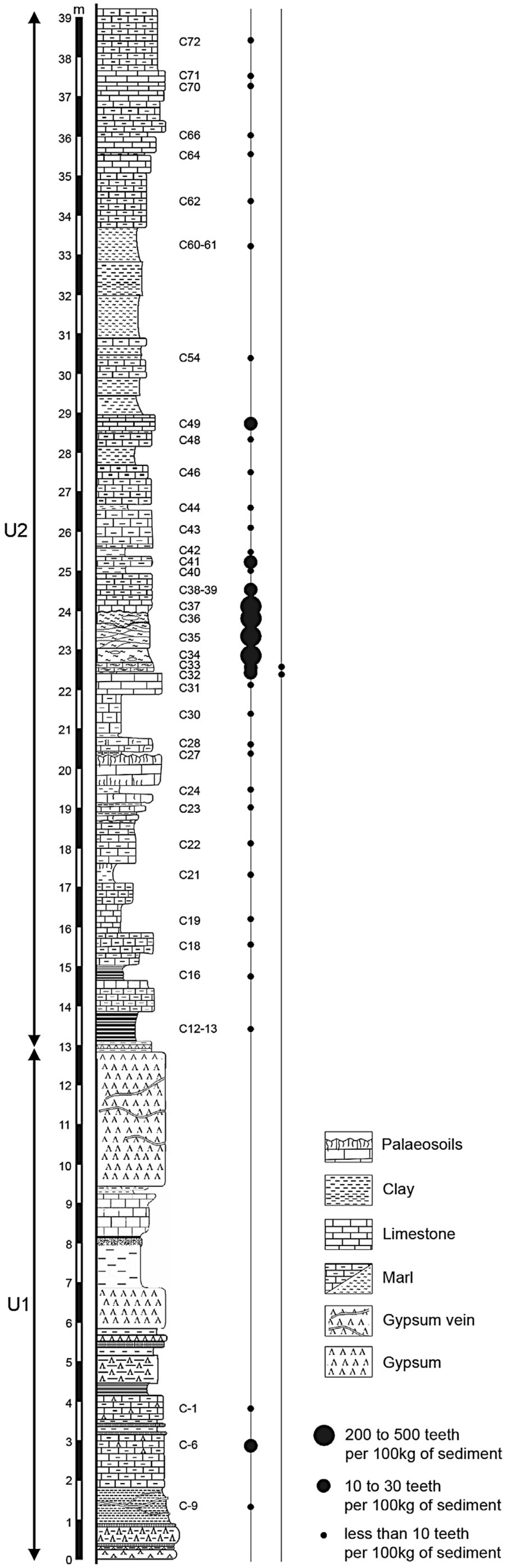

Fig. 2. The section of the *Carrière de Champblanc*, lower to middle Berriasian, Cherves-de-Cognac, France. The 38 selachian bearing beds are noted and the black circles indicate the abundance of selachians (*Parvodus celsucuspus* on the left and *Belemnobatis variabilis* on the right).

rugianus, *P. pattersoni* (Duffin, 1985), and *P. curvidens* (Duffin and Thies, 1997), with a collective stratigraphic range from the Bathonian (Middle Jurassic) to the Valanginian (Early Cretaceous). Geographically, the genus was limited to northwest Europe, but teeth of *Parvodus* have subsequently been recognized in the Upper Triassic of India (Prasad et al., 2008), the Late Jurassic to Early Cretaceous of Brazil (Cupello et al., 2012), and in Lower Cretaceous strata of Thailand (Cuny et al., 2006). Teeth approaching those of *Parvodus* in morphology have also been recorded from Lower Jurassic strata in northern Europe (Delsate and Duffin, 1993; Rees, 2001), as well as from the Middle Jurassic and Middle Triassic of China (Chen et al., 2007; Shang et al., 2008). The Kimmeridgian (Late Jurassic) species “*Hybodus*” *lusitanicus* Kriwet, 2004 from Portugal appear to have a dentition typical of *Parvodus*, including all characters originally constituting the generic diagnosis (Rees and Underwood, 2002), although displaying a higher central cusp in anterior teeth and a slightly smaller labial protuberance. Anterior teeth of *P. lusitanicus* are rather robust (Kriwet, 2004, fig. 2e–q), more so than in any other known species of the genus, but laterals and posteriors are very similar to teeth of the type species. We consider *P. lusitanicus* to belong in the genus *Parvodus*, and possessing the most pronounced piercing dentition of all known species so far described. The Portuguese species also shows the highest degree of intraspecific variation so far encountered within the genus, primarily due to the high-cusped nature of the anterior teeth. Despite the similarities between different species within *Parvodus*, there are also distinct characters that separate them, particularly in reconstructed dentitional patterns. It is thus crucial that new species are erected only on sufficient material, where the entire range of variation can be observed.

Parvodus celsucuspus sp. nov.
Figs. 3–5

1993 *Polyacrodus parvidens* (Woodward); Hervat and Hervat, p.43, figs. 1–8.

Derivation of name. The specific epithet is formed by *celsus*, Latin for high, and *cuspus*, in reference to the remarkably high central cusp in anterior teeth.

Type material. Holotype: CHVm03.634, anterior tooth (Fig. 3A–C); paratypes: CHVm03.636, juvenile tooth (Fig. 3G, H); CHVm03.637, lateral tooth (Fig. 3I–K); CHVm03.638, lateral tooth (Fig. 3L–N); CHVm03.641, posterior tooth (Fig. 3S, T); CHV03.006, cephalic spine (Fig. 4).

Type stratum. Horizon C35 of the section of the *Carrière de Champblanc* (Cherves-de-Cognac, France), lower to middle Berriasian, Lower Cretaceous.

Additional material. Several hundred complete teeth and tooth-crowns, numerous fragmentary teeth, around 20 cephalic spines, and several dozens of dorsal fin spines (more or less complete).

Diagnosis. The dentition of this species is characterized by the following combination of characters: (1) anterior teeth with high and slender central cusp ornamented with weak vertical folds; (2) convex crown–root junction on the lingual side in lateral teeth; (3)

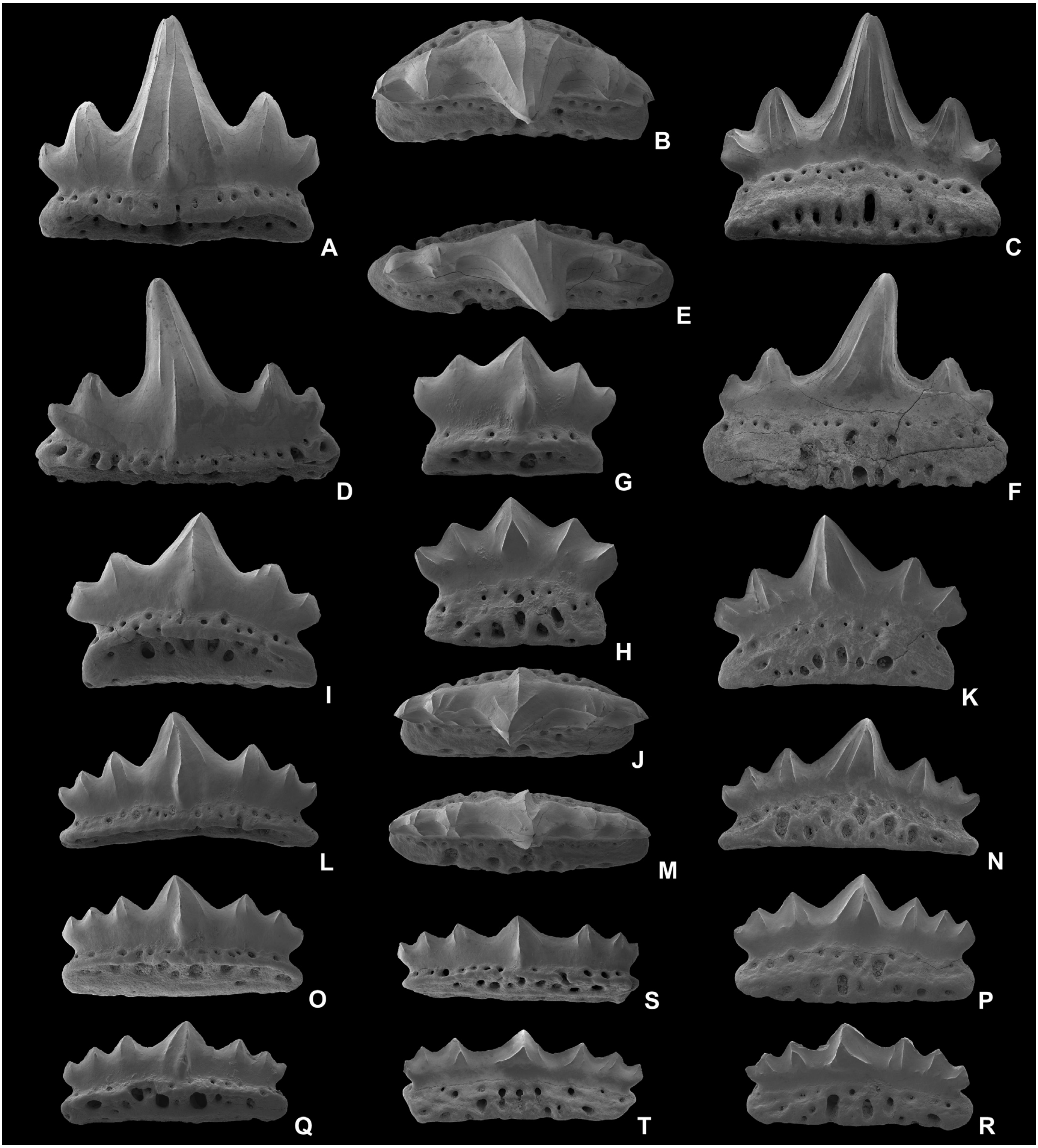

Fig. 3. Teeth of *Parvodus celsucuspus* sp. nov. **A**–**C**. CHVm03.634, holotype, anterior tooth in labial (A), occlusal (B) and lingual (C) views, ×20. **D**–**F**. CHVm03.635, anterior tooth in labial (D), occlusal (E) and lingual (F) views, ×20. **G**, **H**. CHVm03.636, paratype, juvenile tooth in labial (G) and lingual (H) views, ×30. **I**–**K**. CHVm03.637, paratype, lateral tooth in labial (I), occlusal (J) and lingual (K) views, ×25. **L**–**N**. CHVm03.638, paratype, lateral tooth in labial (L), occlusal (M) and lingual (N) views, ×20. **O**, **P**. CHVm03.639, lateral tooth in labial (O) and lingual (P) views, ×25. **Q**, **R**. CHVm03.640, posterior tooth in labial (Q) and lingual (R) views, ×25. **S**, **T**. CHVm03.641, paratype, posterior tooth in labial (S) and lingual (T) views, ×25.

two pairs of cusplets in anteriors and mesial laterals; (4) moderate labial protuberance supported by weak root buttress.

Description of teeth. The dentition of *P. celsucuspus* is characterized by high-cusped anterior teeth and considerably lower laterals and posteriors. There appears to be a gradual change in tooth height from laterals to posteriors, but a rapid shift between anteriors and laterals, resulting in a disjunct pattern of strong monognathic heterodonty. Anteriors are very close to symmetrical and have a high central cusp, ornamented with a central labial fold that is

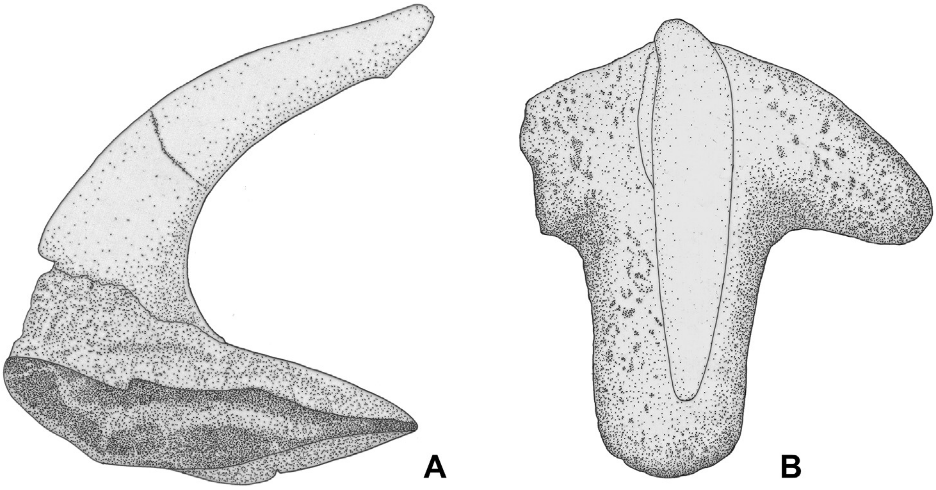

Fig. 4. A, **B**. Cephalic spine of *Parvodus celsucuspus* sp. nov. CHV03.006 in lateral (A) and dorsal (B) view, ×5.

enlarged basally to form a labial protuberance. Other anteriors have a slightly posteriorly inclined cusp and are somewhat more delicate. The cusp is circular to slightly oval in cross-section. All anteriors have two pairs of cusplets, where the inner pair is relatively high and the second pair constitutes the lateral extremities of the crown. The teeth are weakly and variably ornamented with a few folds on the cusp and cusplets often reaching the crown shoulder. Laterals are lower and possess two pairs of cusplets in the mesial rows, whereas more posteriorly situated laterals have three pairs. They also become increasingly lower towards the commissure of the jaw. Both cusp and cusplets are more triangular in outline. Posterior teeth have cusps that are only slightly higher than the cusplets and the crown may be lower than the root. Ornamentation of both laterals and posteriors comprises rather strong enameloid folds, which are widely spaced and seem to be more strongly developed on the lingual side of the teeth.

The root morphology is similar in all teeth regardless of position, with a very low labial shelf perforated by a single row of small circular foramina, a concave labial part of the basal surface where many foramina open, and a smooth, flat area by the lingual edge of the basal surface. The lingual surface is convex and numerous larger foramina open irregularly on the lower part of the surface. Small circular foramina are primarily confined to the area close to the somewhat incised crown–root junction. A few, presumably juvenile, teeth were recorded in the samples and these are similar in morphology, apart from being minute and having a smaller root. There were no pronounced high-cusped anterior teeth in the juvenile material and it is likely that this character only developed in larger or adult sharks. The largest anterior teeth measure 2.7 mm in width.

Description of cephalic spines. The basal plate of the cephalic spine is very slightly ‘arrow shaped’ in dorsal view, with the lateral lobes angled somewhat posteriorly. Compared to the robust, parallel-sided posterior lobe, the anterior lobes are rather small and thin. The entire basal plate has a smoothly rounded anterior edge. The crown is smooth with a small barb on the ventral side, slightly anterior to the apex, and a ridge on the anterior edge. It is recurved to an angle of approximately 130°. The figured specimen is worn and other, incomplete spines display a larger barb on the ventral side and more extensive ornamentation of strong folds on the lower parts of the crown as well as a single horizontal fold on the lateral side.

Description of dorsal fin spines. A single dorsal fin spine is completely preserved but most of them lack the larger part of the base. The posterior wall is ornamented with a series of hook-like denticles, which extend approximately on the upper two-thirds of the posterior length of the mantle. They are set in a single alternate row, and are angled towards the centre. They decrease in size gradually towards the apex of the spine. The lateral sides of the mantle are ornamented with 3–5 costae. The intercostal trunk dentine is ornamented with intercostal grooves. The complete spine measures 79 mm in total length.

Remarks. A reconstructed dentition of *P. celsucuspus* would be easily separated from most closely related species, including *P. rugianus*, *P. curvidens* and *P. pattersoni*, by the presence of high-cusped anterior teeth. Isolated lateral and posterior teeth may be more difficult to separate, but those of *P. curvidens* are never as wide as teeth of *P. celsucuspus*, regardless of tooth position, and only possess two pairs of cusplets. Lateral teeth of *P. rugianus* are far lower than those of *P. celsucuspus* but anteriors of the former species can be similar to laterals of the latter. The crown–root junction is always close to horizontal in *P. rugianus* and the first pair of cusplets is situated further from the cusp (see Rees, 2002, fig. 8) than in teeth of *P. celsucuspus*. The Bathonian species *P. pattersoni* have a dentition with low and narrow anteriors, where the labial protuberance is supported by a strong root buttress, and mesio-distally wide laterals, lower than those of *P. celsucuspus*. Although anterior teeth of both the Kimmeridgian *P. lusitanicus* and the Berriasian *P. celsucuspus* are similar in having a high cusp, teeth of the former species are far more heavily built and robust, with more extensive ornamentation (Kriwet, 2004, fig. 2). Laterals of *P. lusitanicus* are more mesio-distally expanded with higher and more widely spaced cusplets. Further differences include wider posterior teeth and a greater degree of variation within the Kimmeridgian species. Teeth of *P. celsucuspus* may also be similar to those of *Hybodus parvidens* Woodward, 1916, an Early Cretaceous species of uncertain generic affinity (e.g. Rees, 2002). This species may in fact belong to *Parvodus*, but will herein be retained in *Hybodus*, as originally designated (Woodward, 1916), on the basis of a more complex ornamentation pattern, at least in the type material. Future studies are needed to establish the affinity of this species, but the teeth can nevertheless be separated from those of *P. celsucuspus* by the more strongly developed labial protuberance, mesio-distally wider appearance and less organized pattern of vascular foramina in the root.

The basal plate morphology of the cephalic spine found associated with teeth of *P. celsucuspus* as the sole hybodont (Fig. 4), and the spine figured by Hervat and Hervat (1993, fig. 5) from the same

Fig. 5. Fin spine of *Parvodus celsucuspus* sp. nov. MGUH 30420 in lateral view, ×2.

locality, is slightly 'arrow shaped' as opposed to the more common 'T-shape' among hybodonts, particularly larger species (e.g. Maisey, 1987; Antunes et al., 1990). More pronounced 'arrow shape' has previously been found in cephalic spines of *Lonchidion selachos* Estes, 1964. The similarity in cephalic spine morphology may imply a closer relationship between *Parvodus* and *Lonchidion* Estes, 1964 than between *Parvodus* and *Lissodus* Brough, 1935, as the latter genus has rather a unique cephalic spine morphology, including a 'T-shaped' basal plate (Rees, 2008). It is likely that details in the fin spine morphology may be used in the future to expand the diagnosis of *Parvodus*, but this is beyond the scope of this investigation as it requires restudy of fin spines within the entire hybodont clade.

High anterior teeth, as in *P. celsucuspus* and *P. lusitanicus*, indicate that these sharks inhabited a slightly different ecological niche than other species of the genus. The dentitional pattern would be of a more piercing nature, suggesting a diet more directed towards softer prey, such as smaller actinopterygians, rather than shelled invertebrates. The dentitional pattern of juvenile *P. celsucuspus* on the other hand was probably more similar to those of other species within the genus and implies a generalistic feeding behaviour and most likely a wider range of prey. This strategy would be advantageous for juvenile sharks that probably inhabited smaller geographic areas than adults of the species and were subject to more intense predation pressure.

Subcohort Neoselachii Compagno, 1977
Superorder Batomorphii Cappetta, 1980
Order Rajiformes Berg, 1940
Incertae familiae

Genus *Belemnobatis* Thiollière, 1854
Type species. *Belemnobatis sismondae* Thiollière, 1854 from the Upper Jurassic of Cerin, northern France.

Belemnobatis variabilis Underwood and Rees, 2002
Fig. 6

2002 *Belemnobatis variabilis*; Underwood and Rees, p. 94, pl. 3, figs. 1–11, pl. 4, figs. 1–4.

Material. 19 teeth and 33 dermal denticles, all from horizons C32 and C33 of the section of the *Carrière de Champblanc* (Cherves-de-Cognac, France), lower to middle Berriasian, Lower Cretaceous.

Description of teeth. Thirteen of the teeth have a somewhat cruciform shape of the crown in occlusal view and lack a central cusp or have only a minor elevation. The lingual uvula is narrow and parallel-sided with a rounded or pointed extremity, but it never reaches the lingual notch of the root. In juveniles, the uvula may be more tapering. It is flat or concave in lateral view. The protuberance of the labial apron overhangs the root without being basally inclined. It is often worn with a circular wear facet in labial view. The labial face of the crown is rather flat. In occlusal view, the labial face shows a moderate bulge on each side of the central labial protuberance. The longitudinal crest is well developed and close to straight. The teeth are almost devoid of ornamentation but there is a faint horizontal ridge near the base of the mesial and distal extremities of the crown, which sometimes extends on the labial side of the crown and is probably frequently removed by wear. Wear facets are often well developed on the labial protuberance and on the upper part of the lingual uvula, indicating that teeth from each file interlocked closely with each other. Facets can also be found labially and lingually near the mesial and distal extremities of the crown, which indicates that ranks of teeth were also set in staggered rows, as in recent *Rhinobatos* Linck, 1790.

Two teeth (Fig. 6A–C) differ from the morphology described above in showing a low central cusp and a basally inclined labial protuberance that overhangs the root. The lingual uvula is either short with a quite pointed extremity or very short with an angular extremity. The crown is broad and rounded at the mesial and distal parts.

The structure of the root is very similar in all teeth studied. It is moderately projected lingually with a broad and deep central groove in basal view (holaulacorhize vascularization pattern). In some teeth, the two lobes join, causing the central labio-lingual groove to be partially closed basally (hemiaulacorhize vascularization pattern). The groove opens in the continuation of the lingual uvula, except in one tooth where the aperture is displaced to the side, forming a notch at the lingual end of the root. In occlusal view, there is a pair of large nutritive margino-lingual foramina on either side of the uvula, and rarely, a second pair occurs. There are also

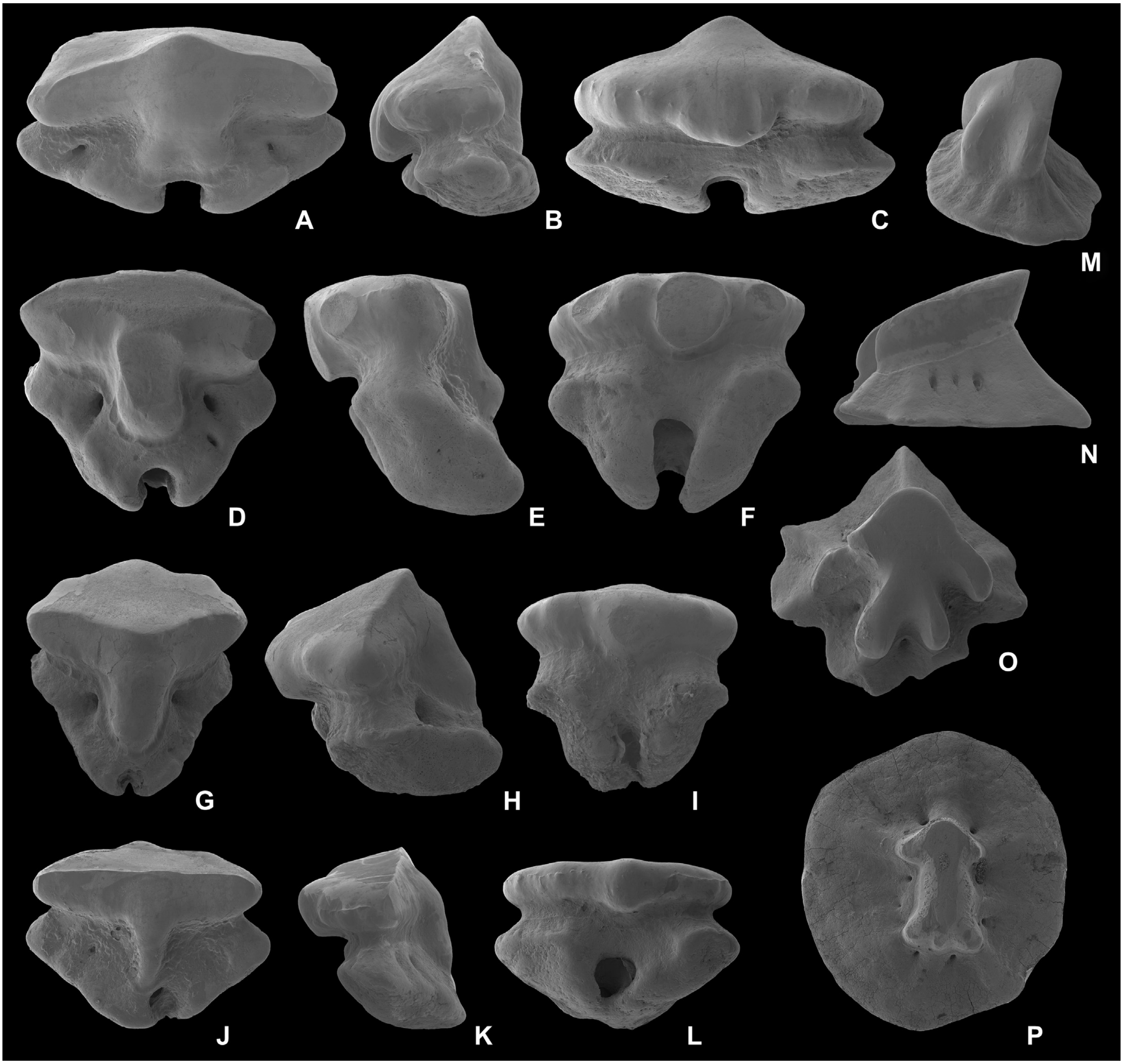

Fig. 6. Teeth and scales of *Belemnobatis variabilis* Underwood and Rees, 2002. **A**–**C**. CHVm03.642, anterior, possibly male, tooth in lingual-occlusal (A), lateral (B) and labial (C) views, ×60. **D**–**F**. CHVm03.643, lateral tooth in lingual-occlusal (D), lateral (E) and labial (F) views, ×60. **G**–**I**. CHVm03.644, anterior, possibly female, tooth in lingual-occlusal (G), lateral (H) and labial (I) views, ×60. **J**–**L**. CHVm03.645, juvenile tooth in lingual-occlusal (J), lateral (K) and labial (L) views, ×80. **M**. CHVm03.646, placoid scale in oblique apical view, ×70. **N**, **O**. CHVm03.647, placoid scale in lateral (N) and apical (O) views, ×60. **P**. CHVm03.247, placoid scale in apical view, ×40.

smaller foramina close to the lingual notch in some teeth. The mesial and distal margins of the root are either straight or concave. When concave, the maximum concavity is at the height of the margino-lingual foramina. The teeth range in mesio-distal width from 0.5 to 1.0 mm.

Description of dermal denticles. The crowns of the dermal denticles are elongated antero-posteriorly and most show an arrow-head shape with two branches diverging anteriorly. The anterior extremity also possesses two diverging branches, leading to a posteriorly pointing arrow-shape of the entire crown. The lateral branches are variously developed so that from one dermal denticle to another, the crown shape can be simply elongated with two somewhat bulbous extremities to the shape of a fully formed arrow. The crown may be parallel to the root surface, or more erect, where the posterior end is variously elevated compared to the anterior one. The most erect crowns belong to the smallest denticles.

In apical view, the base has a variable outline and it can be circular, quadrangular, pentagonal, or irregular, but it is always wider than the crown. It is often ornamented with strong radiating ridges, up to ten on a single denticle. Between the ridges, just below the neck of the crown, there are several nutritive foramina. The basal face is flat to slightly convex, with a large central foramen that may be lacking in some specimens. The diameter of the largest scales is 1.4 mm.

Remarks. The low and transversely expanded crown, as well as the narrow lingual uvula, suggests that the teeth from Cherves-de-Cognac belong to the genus *Belemnobatis* rather than *Spathobatis* (e.g., Cavin et al., 1995; Underwood et al., 1999; Underwood and Rees, 2002; Rees, 2005; Cappetta, 2012). Only one cuspidate tooth in the material described above possesses a wide lingual uvula similar to that found in teeth of *Spathobatis*, but this specimen shares the faint horizontal ridge at the mesial and distal extremities of the crown with the other teeth from Cherves-de-Cognac. The appearance of a cusp in some teeth is thus probably linked to monognathic, or perhaps more likely gynandric, heterodonty as was previously found in *Belemnobatis variabilis* (Underwood and Rees, 2002). The teeth from Cherves-de-Cognac are very similar to the contemporary English teeth of *B. variabilis* (Underwood and Rees, 2002) and the only unique character recorded in the French material is the weak horizontal ridge on the crown, a feature that could easily have been lost by wear in the English material, where most teeth are slightly worn. As the French teeth are both extremely similar and contemporary, we refer them to *B. variabilis*.

Several species of *Belemnobatis* occur in the Jurassic, both as isolated teeth and as more complete fossil fishes. Three species have been recorded in the English Middle Jurassic (Thies, 1983; Underwood and Ward, 2004). Teeth of the Bathonian *B. kermacki* Underwood and Ward, 2004 and *B. stahli* Underwood and Ward, 2004 differ from those of *B. variabilis* in that the lingual uvula often reaches the notch of the root and that most teeth are mesiodistally wider. In *B. kermacki*, the labial edge of the crown is more smoothly rounded and almost without a labial protuberance, whereas teeth of *B. stahli* seem to have a well developed protuberance, larger and more strongly defined than in teeth of *B. variabilis*. Both Bathonian species have dentitions that seem to be devoid of strongly cuspidate teeth. Contrary to the teeth from Cherves-de-Cognac, the delicate teeth of *B. werneri* (Thies, 1983) from the Callovian of England show a protruding and narrower labial protuberance as well as faint lateral lingual uvulae and a weaker central lingual uvula (Thies, 1983). The teeth described herein differ from those of *B. sismondae* from the Kimmeridgian of France in possessing a higher crown and a labial apron that does not protrude labially as much as in the teeth of the latter species (see Cavin et al., 1995). The large lingual foramina on either side of the uvula form a groove in teeth of *B. sismondae*, but in *B. variabilis* they are more rounded and situated closer to the crown–root junction. Additionally, the lingual uvula is narrower in the Jurassic species. The teeth from Cherves-de-Cognac share with those of *B. morinicus* from the Tithonian of France a rather high crown, an irregular outline of the labial apron in occlusal view (without being as crenulated as in *B. picteti* Cappetta, 1975, see below) and a labial protuberance with a circular outline in baso-labial view (Cavin et al., 1995, pl. 1, fig. 4c, pl. 2, fig. 1c). The uvula in *B. morinicus* tends to be longer than in the teeth of *B. variabilis*, reaching the lingual notch of the root, and the basal groove in the teeth of *B. morinicus* has not been reported to be closed, contrary to what can be observed in some teeth of *B. variabilis*. Additionally, the heterodonty of *B. morinicus* does not seem to include any particularly wide teeth. The teeth from Cherves-de-Cognac are very similar to those of *Belemnobatis* sp. from the Valanginian of Poland, but Rees (2005) did not find any traces of a horizontal ridge at the base of the mesial and distal extremities of the crown on the Polish teeth. The foramina on either side of the lingual uvula are more rounded in *B. variabilis* than in the Polish material. Teeth of *B. variabilis* differ from those of *B. picteti* from the Aptian of France by lacking a crenulated labial edge and showing a partially roofed basal groove (Cappetta, 1975).

Dermal denticles with a smooth arrow-shaped crown are found in the posterior dorsal skull region of *Belemnobatis sismondae* (Leidner and Thies, 1999, fig. 2F, G), while denticles referred to *Asterodermus* sp. and *Spathobatis bugesiacus* Thiollière, 1854 (most likely the same species, see Underwood [2002] and Rees [2005]) lack a lobate anterior part of the crown (Leidner and Thies, 1999). Dermal denticles with lobate anterior and posterior parts of the crown from the Kimmeridgian of northern Germany were attributed to *Asterodermus* by Thies (1995) even though the same sediments yielded teeth referable to *Spathobatis* (see Thies, 1983). The denticles can easily be separated from those of *Belemnobatis* by the presence of a marginal band of small tubercles around the crown (Thies, 1995). It is therefore likely that both teeth and dermal denticles from Cherves-de-Cognac belong to the same species (i.e. *B. variabilis*). Dermal denticles with an arrow-shaped crown were also found in the Aptian of England (Underwood, 2004a), but contrary to those from Cherves-de-Cognac, the crown is ornamented with branching ridges. According to Underwood (2004a), these scales are very similar to those of recent *Heterodontus* de Blainville, 1816 and *Squatina* Duméril, 1806.

5. Faunal discussion

Non-marine selachian assemblages from the Lower Cretaceous occur in many areas of western and northern Europe (e.g., Patterson, 1966; Ansorge, 1990; Underwood and Rees, 2002; Rees, 2002; Bermúdez-Rochas, 2009), in the extremely extensive lagoonal system that prevailed at the time. All previously described faunas have a more diverse hybodont component, often with several species of different size and ecological adaptation. Neoselachian diversity is particularly low over the entire area in these kinds of environments and members of this clade may also be completely lacking.

As the assemblage from Cherves-de-Cognac includes *P. celsucuspus* as the only hybodont, despite sampling of many horizons and recovery of a large number of teeth, it is likely that the environment was particularly well suited for this species, and possibly hostile to other taxa. Different species of *Parvodus* are commonly found only in a restricted area, *P. rugianus* being an exception and occurring from England in the west to Germany in the east, but this has been interpreted as a sampling bias. Perhaps these small hybodont sharks were not able to migrate large distances but slowly spread close to the shoreline and in very shallow lagoons. Teeth from several species of *Belemnobatis* have been recorded in sediments representing environments with reduced salinity (Underwood and Rees, 2002), as well as fully marine strata (Cavin et al., 1995; Underwood, 2004b; Rees, 2005), but never in freshwater deposits. It is likely that these rays were better adapted to life in the marine realm, which would explain the presence of the same species in southern England and Cherves-de-Cognac.

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References

Ansorge, J., 1990. Fischreste (Selachii, Actinopterygii) aus der Wealdentonscholle von Lobber Ort (Münchgut/Rügen/DDR). Paläontologische Zeitschrift 64, 133–144.
Antunes, M.T., Maisey, J.G., Marques, M.M., Schaeffer, B., Thomson, K.S., 1990. Triassic fishes from the Cassange Depression (R. P. de Angola). Ciências da Terra (UNL), Número Especial 1990, 1–64.

Berg, L.S., 1940. Classification of fishes, both recent and fossil. Travaux de l'Institut Zoologique de l'Académie des Sciences de l'URSS 5, 85–517 (in Russian).

Bermúdez-Rochas, D.D., 2009. New hybodont shark assemblage from the Early Cretaceous of the Basque–Cantabrian Basin. Geobios 42, 675–686.

de Blainville, H.M.D., 1816. Prodrome d'une distribution systématique du règne animal. Bulletin de la Société Philomatique de Paris 8, 105–124.

Brough, J., 1935. On the structure and relationships of the hybodont sharks. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 79, 35–50.

Buffetaut, E., Pouit, D., Rigollet, L., Archambeau, J.-P., 1989. Poissons et reptiles continentaux du Purbeckien de la région de Cognac (Charente). Bulletin de la Société Géologique de France 5, 1065–1069.

Cappetta, H., 1975. Sélaciens et holocéphale du Gargasien de la région de Gargas (Vaucluse). Géologie Méditerranéenne 2, 115–134.

Cappetta, H., 1980. Les Sélaciens du Crétacé supérieur du Liban. 2. Batoides. Palaeontographica Abteilung A 168, 149–229.

Cappetta, H., 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Handbook of Paleoichthyology, 3E. Verlag Dr. Friedrich Pfeil, München, 512 pp.

Cappetta, H., Buffetaut, E., Suteethorn, V., 1990. A new hybodont from the Lower Cretaceous of Thailand. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1990, 659–666.

Cappetta, H., Buffetaut, E., Cuny, G., Suteethorn, V., 2006. A new elasmobranch assemblage from the Lower Cretaceous of Thailand. Palaeontology 49, 547–555.

Cavin, L., Cappetta, H., Séret, B., 1995. Révision de *Belemnobatis morinicus* (Sauvage, 1873) du Portlandien du Boulonnais (Pas-de-Calais, France). Comparaisons avec quelques Rhinobatidae Jurassiques. Geologica et Palaeontologica 29, 245–267.

Chen, L., Cuny, G., Wang, X., 2007. The chondrichthyan fauna from the Middle–Late Triassic of Guanling (Guizhou province, SW China). Historical Biology 19, 291–300.

Colin, J.-P., El Albani, A., Fürsich, F.T., Martin-Closas, C., Mazin, J.-M., Billon-Bruyat, J.-P., 2004. Le gisement "Purbeckien" de vertébrés de Cherves-de-Cognac, Charente (SW France): nouvelles données biostratigraphiques. Comptes Rendus Palevol 3, 9–16.

Compagno, L.J.V., 1977. Phyletic relationships of living sharks and rays. American Zoologist 17, 303–322.

Coquand, H., 1860. Description physique, géologique, paléontologique et minéralogique du département de la Charente. Tome deuxième. Barlatier-Feissat et Demonchy, Marseille, 420 pp.

Cuny, G., Ouaja, M., Srarfi, D., Schmitz, L., Buffetaut, E., Benton, M.J., 2004. Fossil sharks from the Early Cretaceous of Tunisia. Revue de Paléobiologie volume spécial 9, 127–142.

Cuny, G., Suteethorn, V., Kamha, S., Buffetaut, E., Philippe, M., 2006. A new hybodont shark assemblage from the Lower Cretaceous of Thailand. Historical Biology 18, 21–31.

Cuny, G., Suteethorn, V., Kamha, S., Buffetaut, E., 2008. Hybodont sharks from the Lower Cretaceous Khok Kruat Formation of Thailand, and hybodont diversity during the Early Cretaceous. In: Cavin, L., Longbottom, A., Richter, M. (Eds.), Fishes and the break-up of Pangaea. Geological Society, London, Special Publications 295, pp. 93–107.

Cuny, G., Cavin, L., Suteethorn, V., 2009a. A new hybodont with a cutting dentition from the Lower Cretaceous of Thailand. Cretaceous Research 30, 515–520.

Cuny, G., Srisuk, P., Khamha, S., Suteethorn, V., Tong, H., 2009b. A new elasmobranch fauna from the Middle Jurassic of southern Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society, London, Special Publications 315, pp. 97–113.

Cupello, C.D., Bermúdez-Rochas, D.D., Martill, D.M., Brito, P.M., 2012. The Hybodontiformes (Chondrichthyes, Elasmobranchii) from the MissãoVelha Formation (?Lower Cretaceous) of the Araripe Basin, North-East Brazil. Comptes Rendus Palevol 11, 41–47.

Delsate, D., Duffin, C.J., 1993. Chondrichthyens du Sinémurien de Belgique. Belgian Geological Survey Professional Paper 264, 103–136.

Duffin, C.J., 1985. Revision of the hybodont selachian genus *Lissodus* Brough (1935). Palaeontographica Abteilung A 188, 105–152.

Duffin, C.J., 2001. The hybodont shark, *Priohybodus* d'Erasmo, 1960 (Early Cretaceous, northern Africa). Zoological Journal of the Linnean Society 133, 303–308.

Duffin, C.J., Cuny, G., 2008. *Carcharopsis prototypus* and the adaptations of single crystallite enameloid in cutting dentitions. Acta Geologica Polonica 58, 181–184.

Duffin, C.J., Thies, D., 1997. Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. Geologica et Palaeontologica 31, 235–256.

Duméril, A.M.C., 1806. Zoologie analytique ou méthode naturelle de classification des animaux. Paris, 344 pp.

El Albani, A., Fürsich, F.T., Colin, J.-P., Meunier, A., Hochuli, P., Martin-Closas, C., Mazin, J.-M., Billon-Bruyat, J.-P., 2004. Palaeoenvironmental reconstruction of the basal Cretaceous vertebrate bearing beds in the northern part of the Aquitaine Basin (SW France): sedimentological evidence. Facies 50, 195–215.

d'Erasmo, G., 1960. Nouvi avanzi ittiolitici della "serie di Lugh" in Somalia conservati nel Museo Geologico di Firenze. Palaeontographica Italia 55, 1–23.

Estes, R., 1964. Fossil vertebrates from the Lance Formation. University of California Publications in Geological Sciences 49, pp. 1–187.

Ginter, M., Hampe, O., Duffin, C.J., 2010. Chondrichthyes. Palaeozoic Elasmobranchii: Teeth. Verlag Dr. Friedrich Pfeil, München, 168 pp.

Hay, O.P., 1902. Bibliography and catalogue of the fossil vertebrata of North America. Bulletin of the United States Geological Survey 179, 1–868.

Herman, J., 1977. Les sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphique intercontinentale. Mémoires pour servir à l'explication des Cartes Géologiques et Minières de la Belgique. Service Géologique de Belgique 15 (for 1975), 1–401.

Hervat, P., Hervat, M., 1993. Découverte de *Polyacrodus parvidens* (Woodward, 1916) (Elasmobranchii, Hybodontoidea) dans un faciès Purbeckien (Tithonien supérieur) du Charentais (France). Cossmanniana 2, 43–48.

Jeppsson, L., Anehus, R., Fredholm, D., 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. Journal of Paleontology 73, 964–972.

Klug, S., Tütken, T., Wings, O., Pfretzschner, H.-U., Martin, T., 2010. A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China. Palaeobiodiversity and Palaeoenvironments 90, 241–257.

Kriwet, J., 2004. Late Jurassic selachians (Chondrichthyes: Hybodontiformes, Neoselachii) from Central Portugal. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2004, 233–256.

Kriwet, J., Kiessling, W., Klug, S., 2009. Diversification trajectories and evolutionary life-history traits in early sharks and batoids. Proceedings of the Royal Society B 276, 945–951.

Leidner, A., Thies, D., 1999. Placoid scales and oral teeth of Late Jurassic elasmobranchs from Europe. In: Arratia, G., Schultze, H.-P. (Eds.), Mesozoic fishes 2-systematics and the fossil record. Verlag Dr. Friedrich Pfeil, München, pp. 29–40.

Le Loeuff, J., Buffetaut, E., Merser, C., 1996. Découverte d'un dinosaure sauropode tithonien dans la région de Cognac (Charente). Géologie de la France 2, 79–81.

Linck, H.F., 1790. Versuch einer Eintheilung der Fische nach den Zähnen. Magazin für das Neueste aus der Physik und Naturgeschichte 6, 28–38.

Maisey, J.G., 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. American Museum Novitates 2878, 1–39.

Mazin, J.-M., Billon-Bruyat, J.-P., Pouech, J., 2006. The Purbeckian site of Cherves-de-Cognac (Berriasian, Early Cretaceous, Southwest France): a continental ecosystem accumulated in an evaporitic littoral depositional environment. In: Barrett, P.M., Evans, S.E. (Eds.), Ninth International Symposium on Mesozoic Terrestrial Ecosystem and Biota. Natural History Museum, London, UK, pp. 84–88.

Mazin, J.-M., Pouech, J., Hantzpergue, P., Lenglet, T., 2008. The Purbeckian site of Cherves-de-Cognac (Berriasien, Early Cretaceous, SW France): a first synthesis. Documents du Laboratoire de Géologie de Lyon, Mid-Mesozoic Life and Environments 164, 68–71.

Owen, R., 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. Longman, London, 308 pp.

Patterson, C., 1966. British Wealden sharks. Bulletin of the British Museum (Natural History) 11, 283–350.

Pouech, J., 2008. Position des mammifères dans les écosystèmes mésozoïques d'Europe Occidentale. Le gisement de Cherves-de-Cognac (Berriasien, Charente, France). Unpublished PhD thesis. University of Lyon 1, 274 pp, 93 plates.

Pouech, J., Mazin, J.-M., Billon-Bruyat, J.-P., 2006. Microvertebrate biodiversity from Cherves-de-Cognac (Lower Cretaceous, Berriasian, Charente, France). In: Barrett, P.M., Evans, S.E. (Eds.), Ninth International Symposium on Mesozoic Terrestrial Ecosystem and Biota. Natural History Museum, London, UK, pp. 96–100.

Prasad, G.V.R., Singh, K., Parmar, V., Goswami, A., Sudan, C.S., 2008. Hybodont shark teeth from the continental Upper Triassic deposits of India. In: Arratia, G., Schultze, H.P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 4-Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, München, pp. 413–432.

Rees, J., 2001. Jurassic and Early Cretaceous selachians – focus on southern Scandinavia. Lund Publications in Geology 153, 1–19.

Rees, J., 2002. Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden. Transactions of the Royal Society of Edinburgh: Earth Sciences 93, 59–71.

Rees, J., 2005. Neoselachian shark and ray teeth from the Valanginian, Lower Cretaceous, of Wąwał, central Poland. Palaeontology 48, 209–221.

Rees, J., 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results. Acta Geologica Polonica 58, 217–221.

Rees, J., Underwood, C.J., 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (Selachii). Journal of Vertebrate Paleontology 22, 471–479.

Rees, J., Underwood, C.J., 2008. Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). Palaeontology 51, 117–147.

Shang, Q., Cuny, G., Chen, L., 2008. Early Middle Jurassic vertebrate microremains from the Three Gorges area, southern China. Historical Biology 20, 87–99.

Thies, D., 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. Courier Forschungsinstitut Senckenberg 85, 1–117.

Thies, D., 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of northern Germany. Journal of Vertebrate Paleontology 15, 463–481.

Thiollière, V., 1854. Description des poissons fossiles provenants des gisements coralliens du Jura dans le Bugey. Annales des Sciences Physiques et Naturelles, 2ième Série 4, 1–27.

Underwood, C.J., 2002. Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, southern England. Palaeontology 45, 297–325.

Underwood, C.J., 2004a. Barremian and Aptian (Cretaceous) sharks and rays from Speeton, Yorkshire, NE England. Proceedings of the Yorkshire Geological Society 55, 107–118.

Underwood, C.J., 2004b. Environmental controls on the distribution of neoselachian sharks and rays within the British Bathonian (Middle Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 203, 107–126.

Underwood, C.J., 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. Paleobiology 32, 215–235.

Underwood, C.J., Mitchell, S.F., Veltkamp, K.J., 1999. Shark and ray teeth from the Hauterivian (Lower Cretaceous) of north-east England. Palaeontology 42, 287–302.

Underwood, C.J., Rees, J., 2002. Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England. Special Papers in Palaeontology 68, 83–101.

Underwood, C.J., Ward, D.J., 2004. Neoselachian sharks and rays from the British Bathonian (Middle Jurassic). Palaeontology 47, 447–501.

Vignaud, P., De Broin, F., Brunet, M., Cariou, E., Hantzpergue, P., Lange-Bardre, B., 1994. Les faunes de vertébrés jurassiques de la bordure nord-orientale du Bassin d'Aquitaine (France): biochronologie et environnements. Geobios 17, 493–503.

Woodward, A.S., 1916. The fossil fishes of the English Wealden and Purbeck Formations. Part 1. Monograph of the Palaeontological Society 69, 1–48.

Zangerl, R., 1981. Chondrichthyes I. Paleozoic Elasmobranchii. Gustav Fischer Verlag, Stuttgart, 115 pp.