

A NEW CHONDRICHTHYAN FAUNA FROM THE LATE JURASSIC OF THE SWISS JURA (KIMMERIDGIAN) DOMINATED BY HYBODONTS, CHIMAEROIDS AND GUITARFISHES

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Abstract: The fossil record of chondrichthyans (sharks, rays and chimaeroids) principally consists of isolated teeth, spines and dermal denticles, their cartilaginous skeleton being rarely preserved. Several Late Jurassic chondrichthyan assemblages have been studied in Europe based on large bulk samples, mainly in England, France, Germany and Spain. The first study of this kind in Switzerland is based on controlled excavations in Kimmeridgian deposits related to the construction of the A16 motorway in the Swiss Jura (Porrentruy, NW Switzerland). This study is based on more than 2000 isolated chondrichthyan remains (teeth, dental plates, spines and dermal denticles) and adds to our knowledge of the chondrichthyan distribution at a regional scale in Europe. We describe and identify this new fauna, define a new species of hybodont with crushing-type dentition (*Asteracanthus udufensis* sp. nov.) and report for the first time the carcharhiniform *Corysodon cirinensis* in Switzerland. By the Late

Jurassic, modern neoselachian sharks had overtaken hybodonts in European marine realms, the latter being gradually confined to brackish or freshwater environments. However, while the associated fauna of the Porrentruy platform indicates marine conditions, neoselachian sharks are surprisingly rare. The chondrichthyan assemblage is largely dominated by hybodonts, guitarfishes (rays) and chimaeroids that are all known to be euryhaline. This unexpected chondrichthyan faunal composition questions the presence of fresh to brackish water in the vicinity of the platform, and the occurrence of salinity fluctuations within a general context marine. This could explain the scarcity of neoselachian sharks and the extended success of hybodonts in the Porrentruy area as late as the Late Jurassic.

Key words: chondrichthyan, Swiss Jura, Kimmeridgian, hybodont, *Asteracanthus*, water salinity.

RECENTLY, numerous studies focusing on isolated chondrichthyan remains (teeth, dermal denticles, spines) have demonstrated their usefulness for faunal and palaeoenvironmental reconstructions (e.g. Underwood 2002, 2004; Rees 2005; Cuny *et al.* 2006; Klug & Kriwet 2013a). Until the second part of the twentieth century, studies of chondrichthyans focused mainly on macroremains; but more recently the consideration of small-sized, sometimes submillimetric fossils and of large bulk sampling have given a new dimension to the chondrichthyan picture (Underwood 2006; Underwood *et al.* 2016).

Late Jurassic chondrichthyan assemblages of Europe are generally characterized by the reduced presence of

hybodont sharks in marine deposits (e.g. Duffin & Thies 1997; Kriwet & Klug 2004) gradually replaced by the so-called modern sharks and rays (Neoselachii) (Cuny & Benton 1999) that underwent a strong diversification in the Middle Jurassic, an epoch when most of their groups emerged (Underwood 2006; Kriwet *et al.* 2009). Along with this neoselachian radiation and hybodont decline in marine realms, a diversification and great abundance of hybodonts is observed in restricted, reduced salinity and freshwater environments, especially by the Cretaceous (Cuny 2012). The Jurassic is thus a key period for the understanding of the interrelationship between hybodonts and neoselachians, both dominant at a certain point of

the chondrichthyan evolutionary history (Underwood & Ward 2004a).

With respect to Swiss chondrichthyan faunas from the Late Jurassic, large datasets from bulk samples had never been acquired, and few publications are available on the topic (Agassiz 1843 *in* 1833–1844; Peyer 1946; Müller 2011). Swiss Late Jurassic chondrichthyan faunas were therefore poorly known until now and represent an important missing piece in the chondrichthyan picture of Europe (Kriwet & Klug 2008). Here we report over 2000 isolated chondrichthyan remains, discovered in Kimmeridgian shallow-water platform deposits, in the vicinity of Porrentruy (Swiss Jura). The description and identification of this material, coming from a carbonate platform straddling Boreal and Tethyan ammonite provinces, will add to the knowledge of the geographical distribution of chondrichthyans in Europe during the Kimmeridgian, and qualify the general trend observed throughout the Jurassic, namely the diversification of neoselachians to the detriment of hybodonts.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

This study is based on fossil material discovered by the ‘Paléontologie A16’ team (PAL A16, Porrentruy, canton of Jura, NW Switzerland) in the framework of the building of the A16 motorway. Between 2000 and 2011, numerous sites of palaeontological interest were uncovered in the Ajoie region, around the locality of Porrentruy (Fig. 1).

The study region is part of the Tabular Jura (Marty *et al.* 2007) and is composed of a subhorizontal succession of limestone and more marly intervals of the

Reuchenette Formation. Chronostratigraphically, the section from the Banné Marls up to the *Virgula* Marls corresponds to the early Kimmeridgian to late Kimmeridgian respectively (Fig. 2) (Comment *et al.* 2015). Palaeogeographically, Porrentruy was a shallow-marine carbonate platform, located at about 30°N (Marty 2008) and rimmed by the Rhenish and London–Brabant massifs to the north, the Tethys to the south-east, the Central massif to the south and the Paris basin to the north-west (Fig. 3). The platform was a complex system of bulges and depressions locally inducing lateral changes in water depth. Numerous theropod and sauropod dinosaur tracks and hardgrounds indicate episodes of emergence (e.g. Marty 2008; Waite *et al.* 2013). A food source for the herbivorous dinosaurs was presumably present, and thus firm ground and freshwater must have been present in the vicinity. Several lines of evidence suggesting that a palaeosol was present in the region, and subsequently eroded, were presented by Waite *et al.* (2013). The presence of *Protocupressinoxylon purbeckensis* is recorded, a tree that can grow as high as 13 m and forms closed forests (Philippe *et al.* 2010) thus indicating a firm ground of considerable extent. The semi-arid climate was characterized by a high seasonality with long, dry summers and short, wet winters (Philippe *et al.* 2010; Waite *et al.* 2013). The study area presents affinities with the Boreal, as well as with the Tethyan realm in its ammonite association, albeit with a stronger Boreal influence (Schudack *et al.* 2013).

MATERIAL AND METHOD

The Mesozoic chondrichthyan material of Porrentruy is the result of controlled excavations conducted by the

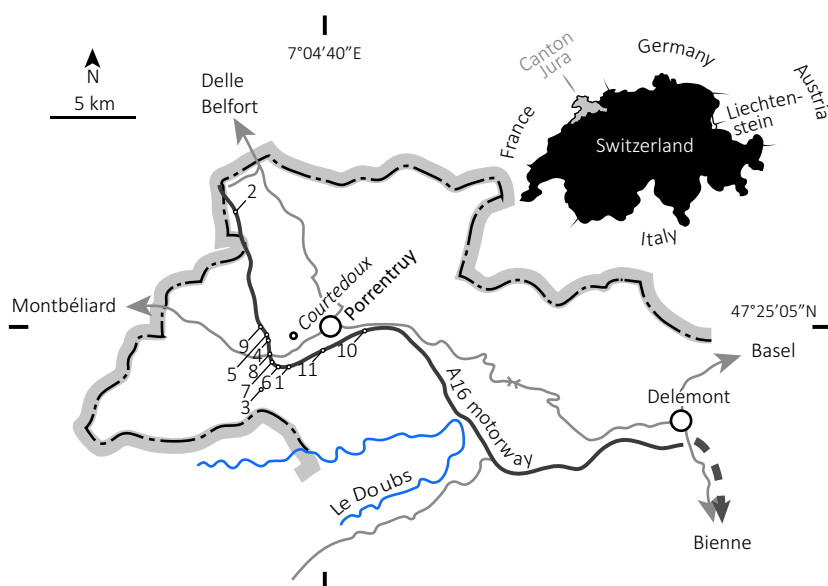


FIG. 1. Geographical map of the Ajoie region, Canton Jura, Switzerland (modified from Püntener *et al.* 2015). Excavation sites yielding chondrichthyan remains are marked, most of them along the track of the A16 motorway. See Site Abbreviations in text for details of locality names. 1, Bois de Montaigne (BDM); 2, Neu Bois (NBO); 3, Chevèze (CHV); 4, Bois d’Estai (BES); 5, Bois de Sylleux (BSY); 6, Creugénat (CRE); 7, Sur Combe Ronde (SCR); 8, Tchâfouè (TCH); 9, Vâ Tche Tchâ (VTT); 10, Roche de Mars (RDM); 11, Tunnel du Banné (TLB). Colour online.

Paléontologie A16 team (PAL A16) and comprises a large dataset: 2264 fossils, of which 1941 are elasmobranch teeth, 34 chimaeroid tooth plates, 245 dermal denticles, 34 fin spines and three cephalic spines. Several centra are recorded but were not used for identification due to their poor taxonomic value compared to dental remains (Kozuch & Fitzgerald 1989). The faunal spectrum is here exclusively based on teeth, but dermal denticles and spines are also described and identified. The micro-remains (millimetre or submillimetre) result from the screen washing of more than 3500 kg of sediment, while the macroremains (centimetre to decimetre) were sampled directly in the field (surface collecting). The sediment intended for sieving went systematically through different mesh sizes, down to 63 µm. All the material is currently housed in the PAL A16 fossil collection (Porrentruy, Swiss Jura) but will be permanently stored in the JURASSICA Museum (MJSN) in the same locality. Fossil collection numbers include the acronym of the locality of provenance.

Institutional abbreviations. NHMUK, Natural History Museum, London; MJSN, JURASSICA Museum (formerly Musée Jurassien des Sciences Naturelles), Porrentruy, Switzerland; PAL A16, Paléontologie A16, Porrentruy, Switzerland.

Site abbreviations. BDM, Courtedoux, Bois de Montaigne; BES, Courtedoux, Bois d'Estai; BSY, Courtedoux, Bois de Sylleux; CHV, Chevenez, La Combe; CRE, Courtedoux, Creugenat; NBO, Boncourt, Neu Bois; RDM, Porrentruy, Roche de Mars; SCR, Courtedoux, Sur Combe Ronde; TCH, Courtedoux, Tchèfouè; TLB, Porrentruy, Tunnel du Banné; VTT, Courtedoux, Vâ Tchè Tchâ.

SYSTEMATIC PALAEOLOGY

Elasmobranch teeth and spines

The terminology used for the description of teeth mainly follows Cappetta (2012). The nomenclature used for the spines follows Maisey (1982a).

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Cohort EUSELACHII Hay, 1902
 Order HYBODONTIFORMES Patterson, 1966
 Superfamily HYBODONTOIDEA Owen, 1846
 Hybodontoides indet.

Figure 4A–M

Material. 3 isolated cephalic spines; 16 isolated fin spines.

Description of the cephalic spines. Posteriorly curved crown (c) with enameloid coating (Fig. 4A–D) on a porous, three-lobed basal plate (bp) (Fig. 4E–G). The posterior lobe (lp) of the basal plate is broader than the lateral (ll) and mesial (lm) lobes and shows a more rounded outline. One cephalic spine shows a partly preserved crown on an incomplete basal plate (Fig. 4A–D). The two other specimens (e.g. Fig. 4E–G) lack the crown but have a complete basal plate with mesial and lateral lobes preserved: the lateral marginal indentation (mil) forms a near perpendicular angle with the posterior lobe, while the mesial marginal indentation (mim) is much smoother. Also, the lateral lobe is located more anteriorly relative to the mesial one. The angle between the anterior edge of the basal plate and its basal surface is obtuse in lateral view (Fig. 4F). The basal, anterior part of the crown is never preserved. Growth rings in the crown of the spine are visible in each specimen, all of them showing an entire or partial section of the crown.

Description of the fin spines. We can separate two groups of hybodont fin spines according to their ornamentation: those with thin, longitudinal ridges on one side (Fig. 4H–J), and those with star-shaped tubercles on the other side (Fig. 4K–M). We counted 11 fin spines of the first kind. They show a straight, vertical base and an upper half that gently curves posteriorly. The ornamentation consists of longitudinal, thin ridges on the lateral and anterior surfaces (Fig. 4H–I) and two vertical rows of alternating hooks on the posterior side (Fig. 4J). The ridge ornamentation is continuous on the anterior face but fades before the posterolateral edge on the lateral faces. The posterior hooks point ventrally and are arranged in two alternating rows that join at the very tip of the spine. The posterior surface opens in its lower part below the last hooks, and the inside of the spine is hollow. Most of the material is laterally flattened and broken just below the posterior tubercles or hooks. The best preserved specimens show an enameloid cover on the posterior hooks.

The fin spines of the second kind are massive and are five in number. They all show star-shaped tubercles (Cappetta 1987) organized in longitudinal rows on the lateral and anterior surfaces (Fig. 4K–L). The tubercles are of different sizes without a precise distribution, with low parallel ridges connecting most of the tubercles of a same row. In lateral view, the lower limit of the ornamented part of the spine is inclined anteriorly. The tubercles are not present on the posterior surface (Fig. 4M). The posterior edge is straight, while the anterior edge is curved. The best-preserved fin spine (MJSN TCH007-89, Fig. 4K–M) shows that the anterior and lateral tubercles cover more than half of its length. The ornamented surface of this latter specimen is damaged in its lowermost, anterior part. The spine opens in a deep, wide groove on its posterior side, making it hollow along its entire length. This groove closes as it approaches the tip but only superficially, so that the cavity remains underneath. The uppermost, posterior side of the spine shows two rows of alternating, star-shaped tubercles that become closer towards the tip. It is difficult to assess whether those two rows eventually join, since the tubercles are never preserved up to the very tip of the spine. The posterior tubercles are completely or partly abraded in most specimens. The enameloid covering is still visible on few tubercles. The largest fin spine (and also the largest chondrichthyan specimen in

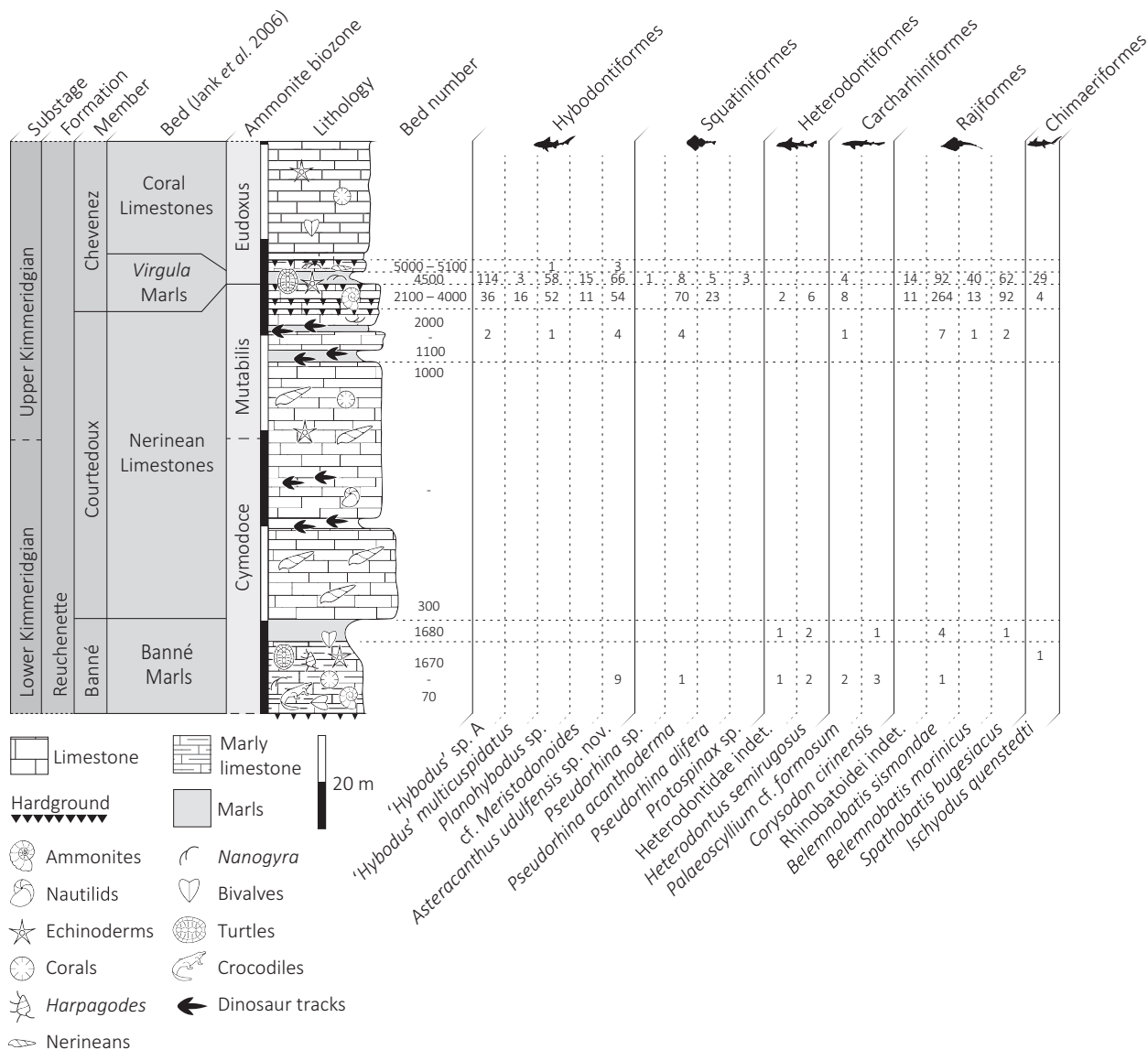


FIG. 2. Stratigraphical profile of the Porrentruy area with indication of the fossil content, and stratigraphic repartition of the chondrichthyan taxa (based on number of isolated dental remains). Differences in the total number of teeth between this figure and the faunal spectrum (Fig. 17) are due to material coming from unknown beds, mainly from tunnel fills. Modified from Comment *et al.* (2015).

the Porrentruy material) has a length of 26.5 cm, probably reaching about 30 cm when unbroken.

Remarks on the cephalic spines. Cephalic spines are a typical feature of Hybodontoidea male specimens, as indicated by their presence in articulated fossils possessing claspers (Maisey 1989; Maisey *et al.* 2004; Rees 2008). Our material differs from cephalic spines identified as *Planohybodus* (Rees & Underwood 2008) by having a basal plate with a more curved anterior edge, and a crown less curved posteriorly. The lobes of the basal plate are less elongated than in the material of Hybodontidae

indet. described by Cupello *et al.* (2012), but more than in lonchidiid cephalic spines of the same reference. Based on the co-occurrence of 'Hybodus' and *Asteracanthus* teeth within the Hybodontoidea material of Porrentruy, the cephalic spines could belong to either of these genera.

Remarks on the fin spines. Hybodontiform fin spines can be differentiated from neoselachian ones by the presence of posterior tubercles (Maisey 1978). For an identification at a lower taxonomic level, isolated fin spines generally are of limited value (Bermúdez-Rochas 2009; Cuny 2012). Maisey (1978) separated two groups of fin spines based

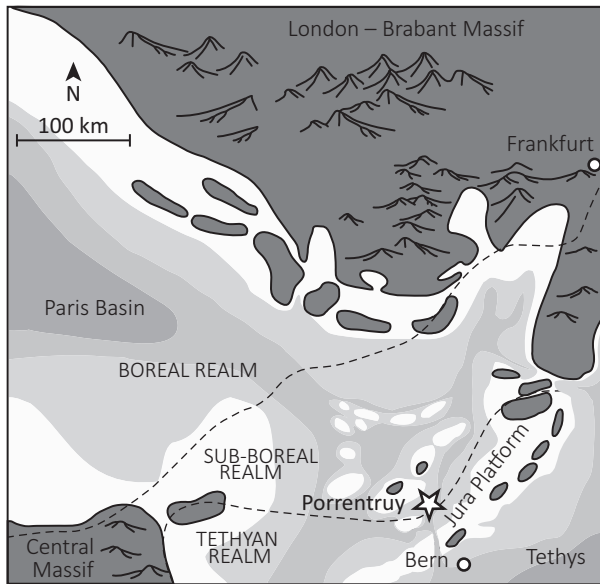


FIG. 3. Palaeogeographical map of the Porrentruy area and surroundings, modified from Comment *et al.* (2011). Emerged land is outlined, deeper water is indicated by a darker shade. The Jura platform is influenced by both the Tethyan and Boreal realms. Porrentruy has a palaeolatitude of 30°N.

on the ornamentation, as in the description above: *Asteracanthus* on one hand and *Hybodus*, *Acrodus* and *Lissodus* on the other. Since then, new genera of hybodonts have been erected (e.g. *Planohybodus*, *Meristodonoides*) (Rees & Underwood 2008; Underwood & Cumbaa 2010) some including species previously described as belonging to the genus *Hybodus*. Fin spines with star-shaped tubercles are classically attributed to *Asteracanthus* (Egerton 1854; Woodward 1888; Peyer 1946; Maisey 1978; Kriwet & Klug 2004; Pfeil 2011) the etymology of the genus referring to that feature (*astera* = star, *acanthus* = spine). However, this kind of fin spine has rarely been found in unambiguous association with *Asteracanthus* teeth (Woodward 1888), and in the presence of disarticulated material only, its attribution to any genus is generally considered to be dubious (Underwood & Rees 2002; Rees & Underwood 2008; Rigal & Cuny 2016). For these reasons, hybodont fin spines of the Porrentruy material are all identified as *Hybodontoides* indet.

Family HYBODONTIDAE Owen, 1846
Subfamily HYBODONTINAE Owen, 1846

Genus HYBODUS Agassiz, 1837 in 1833–1844

Type species. *Hybodus reticulatus* Agassiz, 1837, Lower Jurassic, southern England.

Remarks. The genus *Hybodus* has been used to identify a wide range of material that does not always correspond to the description and illustrations originally given in the work of Agassiz (1833–1844). Cappetta (2012) characterized this genus as ‘broadly polyphyletic’, and other authors have highlighted this nomenclatural vagueness (e.g. Underwood 2002; Rees & Underwood 2006). For these reasons, the genus name ‘*Hybodus*’ is here given in quotation marks. We chose to maintain the identification at the genus level for material differing slightly from previously described species to avoid further confusion until a revision is undertaken.

‘*Hybodus*’ sp. A
Figure 5A–F

Material. 101 teeth from different parts of the jaw, of which 4 teeth have roots (MJSN BSY009–970, MJSN TCH006–1150 (Fig. 5E–F), MJSN TCH006–1703 and MJSN SCR010–571).

Description. These multicuspitate teeth bear at least one, and up to three, pairs (Fig. 5D) of lateral cusplets, two pairs being the most common configuration. The cusplets are almost as high as the main cusp in posterior files, where the tooth crowns are rather low. Teeth of anterior files show a higher main cusp, with a triangular outline in labial or lingual view, and their cusplets reach halfway up the height of the main cusp. The number of cusplets is the same on the mesial and distal sides, and cusplets are circular in section. The asymmetry of more posterior teeth lies in the degree of inclination of the main cusp that is straight in anterior teeth, but mesially curved in more posterior ones. In some cases, the main cusp is also curved lingually. In symmetrical teeth, the cusplets diverge slightly from the main cusp (Fig. 5C), whereas they point to the same direction as the main cusp in asymmetrical ones. The first pair of cusplets is more distant from the main cusp than from the other cusplets. Mesiodistally, strongly elongated teeth show a lingual curvature in occlusal view, following that of the jaw. The ornamentation consists of strong folds that rarely divide towards the base of the crown. They cover the whole crown surface and converge towards the tip of the cusps and cusplets with the exception of large main cusps, where the ornamentation diminishes below the apex. These folds are visible equally well on the lingual and labial sides. A very well-developed, sharp cutting edge runs through the whole width of the tooth, connecting the cusp and cusplets.

There is a mesiodistal constriction at the crown-root junction (Fig. 5E–F). The root is projected lingually and its base is flat or gently curved, following the base of the crown. It is high, but not higher than the crown and presents an anaulacorhize vascularization stage (see Cappetta 2012). Complete teeth can reach 5 mm in mesiodistal length but the largest isolated main cusps suggest that they can be even longer.

Remarks. Several small hybodont teeth lacking nodes or protuberances on their labial and/or lingual sides share



characteristics with the material described above. Teeth of *'Hybodus' lusitanicus* Kriwet, 2004, considered as belonging to the genus *Parvodus* by some authors (Rees *et al.* 2013), are comparable to our material in their shape and very similar in their ornamentation. However, they can reach larger sizes (up to 8 mm mesiodistally; Kriwet 2004) and their main cusp is slender, while it is rather blunt in our specimens. Blunt cusps are present in *'Hybodus' gramanni* Duffin & Thies, 1997 (originally assigned to *Polyacrodus*, see Rees 2008), a low-crowned species from the Kimmeridgian of north-western Germany with an ornamentation similar to that of *'H.' lusitanicus*. Low-cusped teeth from our material are very similar to *'H.' gramanni*, but higher-cusped specimens, abundant in our assemblage, are not described for this species. The root morphology cannot be fully determined in our case, since the only specimen preserved with its root is strongly abraded (Fig. 5E–F). Features such as the degree of constriction of the root at the crown-root junction might have been blurred and are thus difficult to compare. Finally, while posterior teeth of *'Hybodus' sp. 1 sensu* Rees & Underwood (2006) are low-crowned and resemble our material, teeth of more anterior files differ by having a much higher main cusp that is not completely covered by ornamentation folds. We cannot separate low-cusped from high-cusped teeth in our material since specimens displaying cusps of intermediate height are present. It is likely that all of the material belongs to a single species with a gradient monognathic heterodonty. We retain this material in open nomenclature as *'Hybodus' sp. A*.

'Hybodus' multicuspidatus Duffin & Thies, 1997

Figure 5G–J

Material. 19 teeth, more or less fragmented.

Description. Narrow and broad crown in apical view with several pyramidal cusplets (up to three visible in the fragmented material) and narrower, lingual and/or labial nodes. When these latter appear only on one side, it is on the labial one (Fig. 5I–J). When present on both sides, they are larger on the labial side (Fig. 5H). There is almost no height difference between the cusplets.

The ornamentation consists of very strong folds which are much stronger than those in *cf. Meristodonoides* (see below) and

'Hybodus' sp. A described above; most point towards the apices. However, contrary to the previously described material, the folds do not all join at the apices and sometimes meet below. Some folds branch out from the apical crest and several fade before they reach the base of the crown. Some others appear at the base, and do not reach the top of the crown. A single apical crest between the cusps and cusplets is visible in occlusal view in all but one specimen that presents one fold on each side of the crown's longitudinal axis, connecting the apices of two cusplets (Fig. 5G). The root is never preserved.

Remarks. This material is very similar to *Polyacrodus brevicostatus* (Cappetta 2012, redrawn from Patterson 1966), *'Hybodus' obtusus* (Rees & Underwood 2008) and *Polyacrodus multicuspidatus* Duffin & Thies, 1997, insofar as these are hybodont species showing basal nodes. Strong folds and well-developed lateral nodes make this latter species the closest to our material. Moreover, its distribution, thus far limited to the Kimmeridgian of Germany, also corresponds to our context. The genus *Polyacrodus* must probably be considered a *nomen dubium* (Rees 2008) and referred to as *'Hybodus'*. We therefore identify the material as *'Hybodus' multicuspidatus*, this species presenting more and better-defined basal nodes than the *'H.' obtusus*. The position and size of the nodes seem to indicate that they first emerge labially.

Genus MERISTODONOIDES Underwood & Cumbaa, 2010

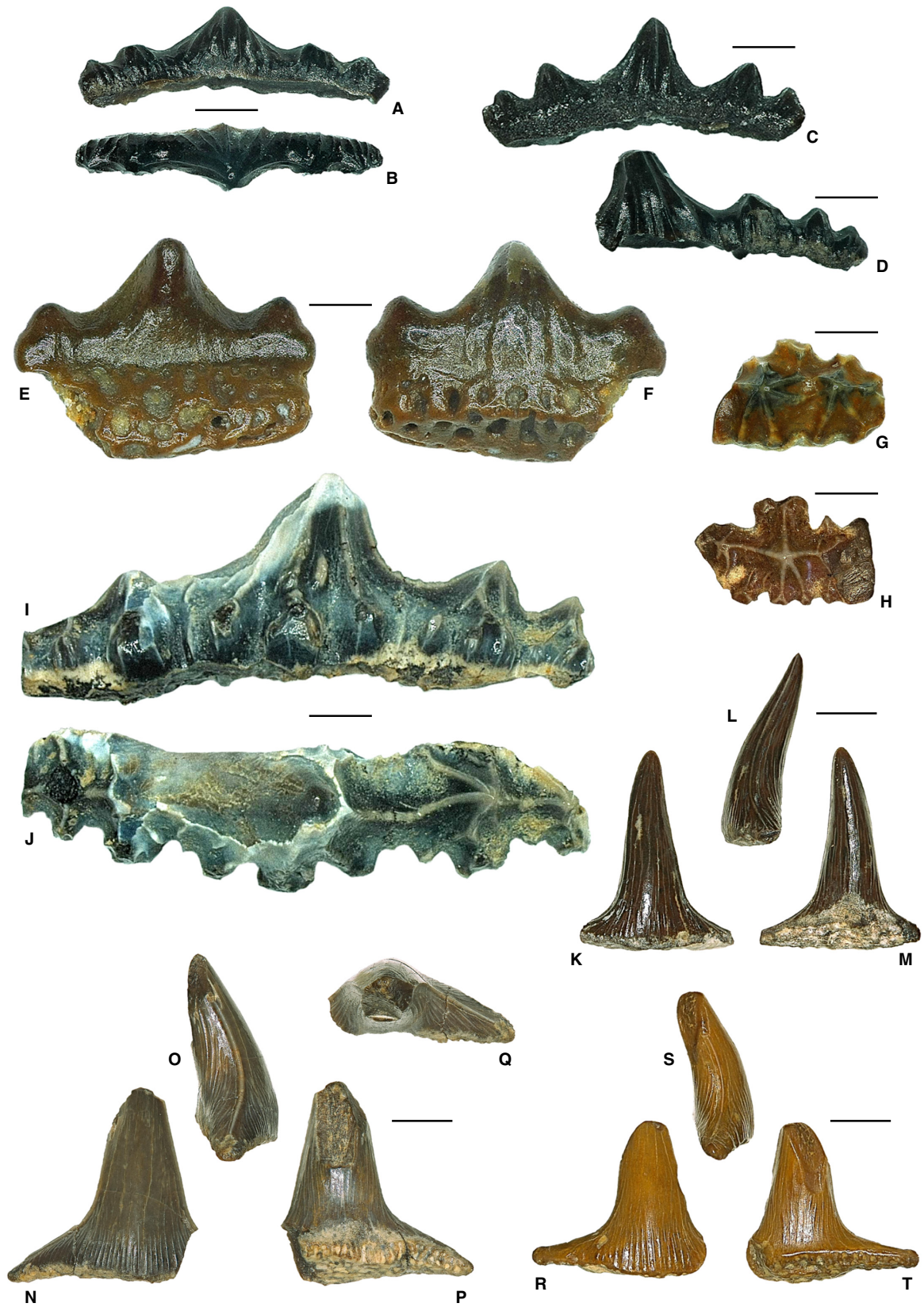
cf. Meristodonoides

Figure 5K–T

Material. 22 teeth.

Description. Teeth apparently devoid of lateral cusplets, with the cusp extending into mesiodistally elongated heels at its base, at least on one side. No tooth crown shows its labial and mesial ends preserved together. On fully preserved heels, lateral cusplets are never observed (e.g. Fig. 5R). The heels are low and the angle between them and the cusp is much higher than in the above described material. The crown can be slightly sigmoid in mesiodistal view (e.g. Fig. 5L). A cutting edge is present along the whole tooth crown. The ornamentation consists of thin, parallel ridges that are well marked, but always restricted to the very base of the single cusp, which is much more slender than in *Planohybodus* teeth described above.

FIG. 4. A–M, Hybodontoida indet., fin and cephalic spines, upper Kimmeridgian; A–D, cephalic spine, MJSN BSY006-428: A, right lateral; B, apical; C, anterior; D, posterior view; E–G, cephalic spine, MJSN SCR011-379: E, apical; F, left lateral; G, posterior view; H–J, fin spine, MJSN TCH006-1535: H, right lateral; I, anterior; J, posterior view; K–M, fin spine, upper Kimmeridgian, MJSN TCH007-89: K, right lateral; L, anterior; M, posterior view. N–P, Heterodontidae indet., fin spine fragment, upper Kimmeridgian, MJSN SCR011-347: N, left lateral; O, anterior; P, posterior view. Q–S, *?Paracestracion* sp., fin spine, upper Kimmeridgian, MJSN BSY009-199: Q, left lateral; R, anterior; S, posterior view. *Abbreviations:* bp, basal plate; c, crown; ll, lateral lobe of the basal plate; lm, mesial lobe of the basal plate; lp, posterior lobe of the basal plate; mil, lateral marginal indentation; mim, mesial marginal indentation. Scale bars represent: 2 cm (A–M, Q–S); 1 cm (N–P). Colour online.



Remarks. The Porrentruy material is close to *Planohyodus* but differs by possessing a more slender cusp. The genus *Meristodon* Agassiz, 1837 shows great similarities to the described material in the apparent lack of cusplets, the slightly labiolingually flattened cusp and the low ornamentation. Underwood & Cumbaa (2010) included some Cretaceous *Hybodius* species and material formerly referred to as *Meristodon* sp. within a new genus, *Meristodonoides*. Our material is also comparable to ‘*Hybodius*’ sp. 1 described by Underwood (2002), although this was not synonymized with *Meristodonoides* in that work. Our material matches the diagnosis of this latter genus, except that its fragmented nature makes it impossible to confirm the absence of well-developed lateral cusplets. We therefore assign our material to cf. *Meristodonoides*, potentially extending the stratigraphic range of this genus back to the Late Jurassic.

Genus PLANOHYBODUS Rees & Underwood, 2008

Type species. *Planohyodus peterboroughensis* Rees & Underwood, 2008, Middle Jurassic (Callovian), England.

Planohyodus sp.

Figure 6A–Q

Material. 22 teeth.

Description. Labiolingually compressed teeth with high and broad principal cusp. A well-developed, sharp cutting edge forms an unbroken crest over the whole long axis of the tooth in occlusal view. The main cusp can be either straight, slightly curved or sigmoid in mesiodistal view, and points more or less mesially, probably depending on the file. The crown is flanked by one to two pairs of cusplets that are much smaller but still show a well-developed cutting-edge.

The ornamentation is composed of very fine folds that sometimes branch at the base of the lateral cusplets. Some short folds on the main cusp do not reach its base but are rather isolated on the higher part of the crown. The ornamentation covers the whole lateral cusplets but does not meet at the apex like they do in ‘*Hybodius*’ sp. A, so that the occlusal, sharp cutting-edge is the only feature visible at the top of the cusplets. On the main cusp, the ornamentation fades away at the height of the tip of lateral cusplets or even lower. Crowns are usually slender but can also

look broader and more triangular in shape in labiolingual view (Fig. 6I–Q).

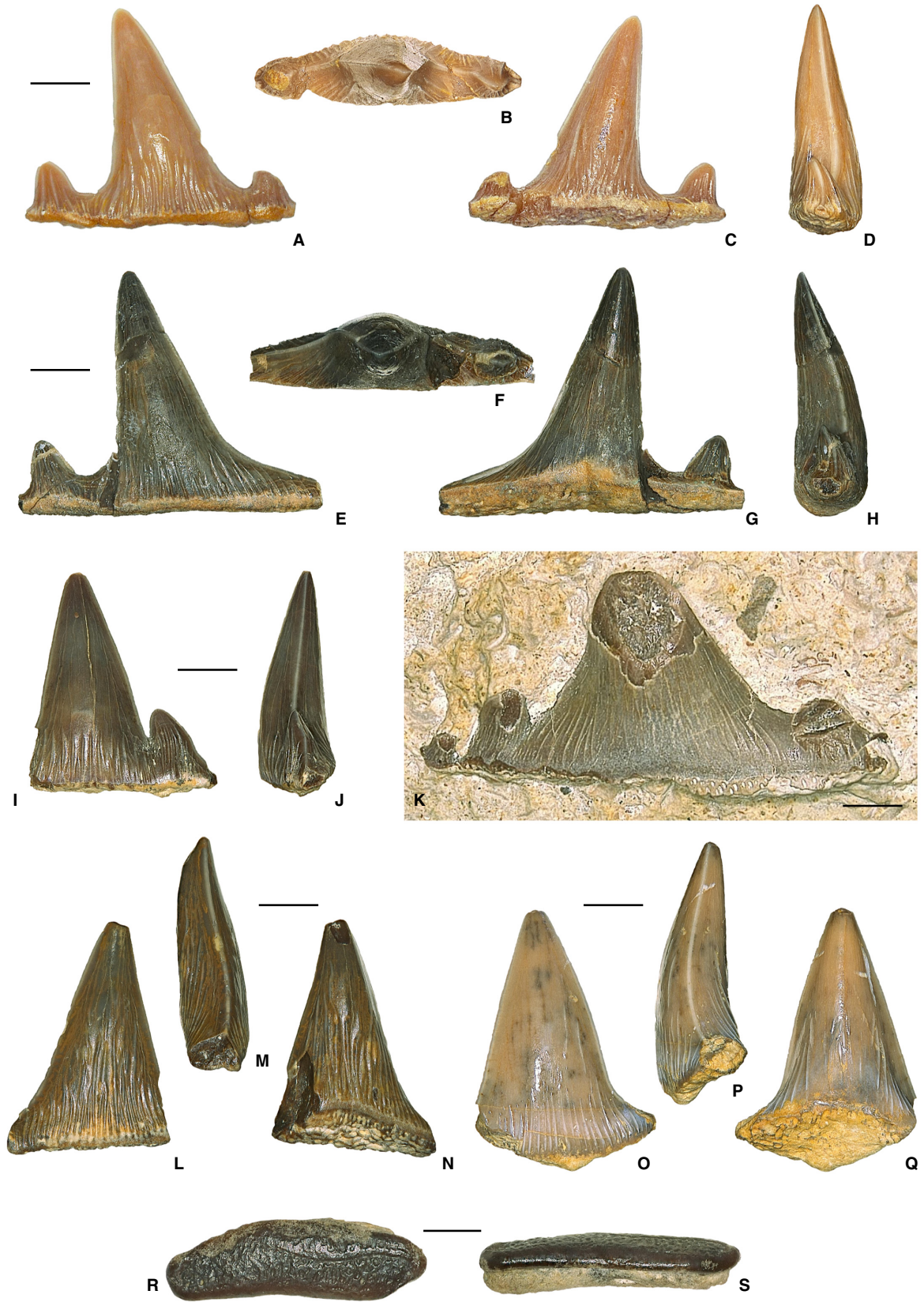
Remarks. In lateral view, the teeth look like those of *Egertonodus basanus* but can be differentiated in occlusal view by their labiolingually flattened central cusp. Our material is assigned to *Planohyodus* sp. (Rees & Underwood 2008) and possibly corresponds to the species *P. ensis* or *P. grossiconus*. The difference between the two species lies in the number of lateral cusplets (not more than a pair for *P. ensis*) and that the ornamentation is slightly stronger in *P. grossiconus*. In our case, the number of pairs of cusplets is difficult to assess since most of the teeth are broken. Regarding the ornamentation, the folds are shorter in some broken teeth where the number of lateral cusplets cannot be observed and generally all intermediates between the shortest and highest folds can be observed on the labial surface of the main cusp (Fig. 6A, E, I, L). As discussed above, hybodont species with high cusped teeth such as *Hybodius* and *Planohyodus* are difficult to separate based on isolated teeth and some descriptions contradict each other (e.g. Rees & Underwood (2008) vs Bermúdez-Rochas (2009) on the number of lateral cusplets in *P. ensis*). Our material could correspond to a new species with a dignathic heterodonty comprising a variation in the height of the ornamentation, the number of lateral cusplets and the slenderness of the main cusp, but this is difficult to demonstrate with the material currently at hand. *Planohyodus peterboroughensis* Rees & Underwood, 2008 also possesses two to three pairs of lateral cusplets but shows an ornamentation up to half of the main cusp (Pinheiro *et al.* 2013). Also, large teeth of our assemblage differ from *P. ensis* in being devoid of a weak serration at the base of the main cusp (Underwood & Rees 2002). Our specimens are easily differentiated from *P. marki* Pinheiro *et al.*, 2013, which possesses divergent lateral cusplets and a stronger ornamentation. We therefore maintain our material in open nomenclature as *Planohyodus* sp.

Subfamily ACRODONTINAE Casier, 1959 *sensu* Maisey, 1989

Genus ASTERACANTHUS Agassiz 1837 *in* 1833–1844

Type species. *Asteracanthus ornatissimus* Agassiz, 1837, Kimmeridgian, Oxford, England.

FIG. 5. A–F, ‘*Hybodius*’ sp. A, teeth, upper Kimmeridgian; A–B, MJSN TCH005-1036: A, lingual; B, apical view; C, MJSN TCH005-1750 in lingual view; D, MJSN TCH005-1751 in lingual view; E–F, MJSN TCH006-1150: E, lingual; F, labial view. G–J, ‘*Hybodius*’ *multicuspidatus*, teeth, upper Kimmeridgian; G, MJSN TCH006-1552 in apical view; H, MJSN TCH006-1605 in apical view; I–J, MJSN TCH005-626: I, labial; J, apical view. K–T, cf. *Meristodonoides*, teeth, upper Kimmeridgian; K–M, MJSN SCR002-1468: K, labial; L, mesiodistal; M, lingual view; N–Q, MJSN SCR010-371: N, labial; O, mesiodistal; P, lingual; Q, apical view; R–T, MJSN TCH004-622: R, labial; S, mesiodistal; T, lingual view. Scale bars represent: 0.5 mm (A–F); 1 mm (G–J); 2 mm (K–T). Colour online.



Remarks. Rees & Underwood (2008) included the genus *Asteracanthus* in the family Hybodontidae and the sub-family Acrodontinae. This genus was first erected by Agassiz (1837 in 1833–1844) to identify fin spines presenting a very characteristic ornamentation composed of star-shaped tubercles. Later, a clear association between *Strophodus* teeth and *Asteracanthus* fin spines allowed the assignment of part of the *Strophodus* dental material to *Asteracanthus*, under the species *A. ornatissimus* (Woodward 1888), *Strophodus* being a junior synonym. Although isolated ‘*Strophodus*’ teeth commonly co-occur with *Asteracanthus* fin spines of species other than *A. ornatissimus*, there are some localities where fin spines are abundant without any ‘*Strophodus*’ tooth being recorded. This has made several authors refrain from assigning fin spines to the genus *Asteracanthus* until they are found in unambiguous association with teeth (e.g. Rees & Underwood 2008) although the genus is still widely used to refer to dental material. Since *Asteracanthus* was originally described based on fin spine material, the genus *Strophodus* should be restricted to the dental material where teeth and fin spines are not considered to be related. Here, we maintain the genus *Asteracanthus* for our dental material to avoid further confusion in hybodont systematics.

Asteracanthus udulfensis sp. nov.

Figures 7, 8

- 1946 *Asteracanthus* sp. indet.; Peyer, table p. 65 and pl. 4, fig. 9; table p. 65 and pl. 4, fig. 13; table p. 66 and pl. 4, fig. 16.
2001 *Asteracanthus* cf. *ornatissimus*; Mudroch, p. 177 (appendix), pl. 1, fig. 1A.

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Derivation of name. From one of the localities that yielded a large part of the material, Courtedoux (see Fig. 1), in Latin *Curtis udulfi*.

Type specimen. Holotype, MJSN TCH005-640 (Fig. 8C–G), complete posterior tooth.

Type stratum. *Virgula* Marls (Reuchenette Formation), upper Kimmeridgian, Ajoie region, canton of Jura, Switzerland.

Material. 149 teeth from one of the following positions in the jaw: symphyseal, anterior (first and second file), lateral (third and fourth file) and posterior.

Diagnosis. Shark with crushing-type, strongly ornamented dentition differing from other *Asteracanthus* (or previously ‘*Strophodus*’) species by the combination of the following characters: symphyseal file in at least one of the jaws with asymmetrical and strongly arched teeth, showing a folded ornamentation on the lingual side and a more reticulated pattern on the labial side of the crown; teeth of the first anterior file asymmetrical, high and strongly arched, with a well-developed apical crest, a folded ornamentation on the lingual side and a reticulated one on the labial side; teeth of the first lateral file domed mesially rather than at their centre; teeth of the second lateral file entirely reticulated, parallelogram-shaped and broader than the teeth of the first lateral file; teeth of the posterior file of a very characteristic, somewhat polygonal shape with a concave, lingual edge and a root projected distally. The root is pierced by large and small foramina. Large foramina exclusively open on the labial and lingual surfaces.

Associated teeth and articulated dentition of *Asteracanthus* show that the dental pattern is composed of two files of anterior, lateral and posterior teeth respectively. Additionally, a symphyseal file can be present, possibly reflecting a dignathic variation since it is absent in some articulated dentitions (Rees & Underwood 2008).

Description. Teeth of symphyseal, anterior, lateral and posterior positions are recorded in the Porrentruy material. The symphyseal teeth show a strongly worn cusp, but the remains of a crest can be distinguished mesially and distally on the unworn portion of the crown (Fig. 7A). The ornamentation is composed of folds on the lingual half of the crown and is reticulated on its labial half. In occlusal view, the outline of the crown is nearly hexagonal. In labiolingual view, the crown is symmetrical with its centre strongly bent, and the mesial and distal extremities bend back to form a concave curvature on each side of the crown on their lingual edge (Fig. 7B). The root is partially preserved in one specimen (MJSN TCH005-617) and presents a concave labial surface hidden by the overhanging crown in occlusal view, while the lingual surface of the root forms a bulge that makes it slightly visible in occlusal view. The mesiodistal edges of the root do not extend beyond the crown and have a concave outline in labiolingual view. Foramina of different sizes seem to be randomly distributed, especially on the labial surface.

FIG. 6. A–Q, *Planohybodus* sp., teeth, upper Kimmeridgian; A–D, MJSN CHV010-6: A, labial; B, apical; C, lingual; D, mesiodistal view; E–H, MJSN TCH005-477: E, labial; F, apical; G, lingual; H, mesiodistal view; I–J, MJSN TCH004-65: I, labial; J, mesiodistal view; K, MJSN TCH003-34 in lingual view; L–N, MJSN TCH006-998: L, labial; M, mesiodistal; N, lingual view. O–Q, MJSN SCR002-150: O, labial; P, mesiodistal; Q, lingual view. R–S, Heterodontidae indet., posterior tooth, lower Kimmeridgian, MJSN VTT006-1331: R, occlusal; S, labiolingual view. Scale bars represent: 2.5 mm (A–Q); 1 mm (R–S). Colour online.



Teeth of the first anterior file (Fig. 7D–G) have a strongly curved, asymmetrical crown that forms an acute angle at the apex in labiolingual view. An apical, sigmoid crest mesiodistally crosses the whole length of the crown. In occlusal view, the teeth have the shape of a labiolingually flattened hexagon with one edge longer than the other, the long edge being the labial one (see Rees & Underwood 2008). The rich ornamentation of the crown consists of strong folds that spread radially from the apex, branching at the edge of the crown on the lingual side, or converted into a reticulated pattern on the labial side. The root, only partially visible in one specimen (MJSN SCR010–389, Fig. 7D–G), is high and perforated by randomly distributed small and large foramina labially and lingually, the largest being confined to the base of the root. Densely packed, small foramina are arranged in a line that follows the base of the crown (Fig. 7E). In labiolingual view, the outline of the root roughly forms a pentagon whose basal edge is concave and slightly curved towards the apex. The crown overhangs the root, both mesiodistally and labiolingually.

Anterior teeth of the second file (Fig. 7H–J) are more elongated mesiodistally but still show a well-defined sigmoidal crest across their whole length that is however more developed on the mesial side. The crown forms a dome that is shifted distally. The distal part of the crown forms two clear corners in occlusal view, while its mesial extremity becomes gradually constricted. The ornamentation comprises radial folds originating at the central dome and a more or less defined, reticulated pattern on the mesial and labial ends. No tooth preserves the root.

Lateral teeth of the first file (Fig. 7K–X) are domed mesially. In labial and lingual view, the base of the crown is curved. In occlusal view, the crown has the shape of a parallelogram (Fig. 7T), or can be rather comma-shaped with a beveled distal end (Fig. 7N, W), most likely depending on the tooth row. Again, the ornamentation is reticulated distally and composed of radial, frequently branching folds around the dome. A weak crest is visible in some specimens and is displaced lingually (Fig. 7K, Q, T). One lateral tooth (MJSN SCR003–576, Fig. 7T–V) shows a pathological deformation. The root is poorly preserved. Lateral teeth of the second file (Fig. 8A, B) show the largest labiolingual width, with labial and lingual edges parallel to each other. The mesial part is slightly domed but the base of the crown shows almost no curvature in a labiolingual view, contrary to lateral teeth of the first file. No crest is visible and the ornamentation is entirely reticulated. In occlusal view, the reticulated pattern is smaller and more densely packed along the outline of the crown. It becomes slightly elongated on the labial part of the crown. The root, preserved in two specimens (MJSN SCR011–281 and MJSN SCR010–303; Fig. 8A, B), is thick, and does not show any constriction at its junction with the crown. Its basal edge is slightly sigmoid in labiolingual view, and the

labial and lingual faces are perforated by large foramina arranged in a horizontal line. Numerous small foramina are randomly distributed all over the root. As in teeth of the first anterior file, a line of small foramina follow the base of the crown.

Only one posterior tooth (Fig. 8C–G) has been recorded, but its completeness and singular shape allow it to be differentiated from any other posterior tooth of *Asteracanthus* species described so far. It is nearly square in occlusal view but with the two mesial corners truncated and a concave, distal edge. Strong folds radiate from an inconspicuous apex displaced mesially, and branch towards the lingual, distal and labial edges. Towards the mesial edge, the ornamentation becomes reticulated. The root is thick and follows the shape of the crown, except labially where it projects diagonally beyond the crown and towards the back of the jaw. On the distal and mesial faces, large foramina open randomly (Fig. 8D) but are nonetheless confined to the mid-height of the root. Only small foramina are present on the basal surface of the root (Fig. 8G).

Remarks. *Asteracanthus* teeth have a wide size range in the material from Porrentruy. As an example, lateral teeth can be from 8 mm long and 3 mm wide (MJSN SCR004–221, Fig. 8N) to 31 mm long and 16 mm wide (MJSN SCR010–303, Fig. 8A). These variations are likely to reflect different ontogenetic stages, since they are observed in several teeth of similar positions. Underwood & Rees (2008) described in detail several species of Jurassic *Asteracanthus* that show similarities with the Porrentruy material, none of them matching entirely:

1. Teeth of the middle Jurassic *Asteracanthus medius* (Owen, 1869), represented by an articulated dentition from the Bathonian–Callovian of Normandy (Rees & Underwood 2008), are similar in shape to our material, however the ornamentation is generally less reticulated and more folded in our case. Anterior teeth of *A. medius* are described as ‘weakly arched’ (Rees & Underwood 2008), thereby differing from our material. In contrast, lateral teeth of the first file are much more arched in *A. medius*. Also, teeth of this position are domed at their centre in *A. medius*, whereas the dome area is displaced mesially in our material. Posterior teeth of *A. medius* show an outline different from our material (oval compared to polygonal, respectively).
2. Lateral teeth of the middle Jurassic *Asteracanthus tenuis* Agassiz, 1838 show a strong, sigmoid curvature in occlusal view, a feature never found in our

FIG. 7. *Asteracanthus udulfensis* sp. nov., adult to subadult teeth, upper Kimmeridgian. A–C, symphyseal tooth MJSN TCH007-660: A, apical; B, lingual; C, labial view. D–G, first anterior tooth, MJSN SCR010-389: D, apical; E, labial; F, mesial; G, distal view. H–J, second anterior tooth MJSN SCR011-285: H, apical; I, lingual; J, labial view. K–X, first lateral teeth; K–M, MJSN SCR002-80: K, occlusal; L, lingual; M, labial view. N–P, MJSN CHV000-126: N, occlusal; O, lingual; P, labial view. Q–S, MJSN BSY008-950: Q, occlusal; R, lingual; S, labial view. T–V, MJSN SCR003-576: T, occlusal; U, lingual; V, labial view. W–X, MJSN SCR010-1125: W, occlusal; X, lingual view. Scale bar represents 2.5 cm. Colour online.



material. Only the mesial and distal extremities of the crown can point lingually or labially, while the major part of the crown is straight. No posterior tooth is known for *A. tenuis*.

3. *Asteracanthus magnus* Agassiz, 1838 from the middle Jurassic can be excluded, with lateral teeth of triangular outline (previously considered to be anterior teeth; cf. Rees & Underwood 2008; Rigal & Cuny 2016) being clearly different. Also, lateral teeth of the second file are broader than in our material.
4. *Asteracanthus smithwoodwardi* Peyer, 1946 from the Lower Jurassic of Switzerland differs by its very broad lateral teeth from the second file in occlusal view (Peyer 1946).
5. Teeth of *A. ornatissimus* Agassiz, 1837 from the Middle–Late Jurassic generally show a stronger ornamentation than the Porrentruy material (Underwood & Rees 2008). The ornamentation can also be somewhat weaker, as in the associated dentition of *A. ornatissimus* (NHMUK PV P6831). However, posterior teeth of this latter specimen have a more oval outline in occlusal view and do not present any concave edge. Moreover, lateral teeth of the first file of the Porrentruy material do not show a crest, as developed in teeth of *A. ornatissimus*, and have their domed area displaced mesially. Teeth of the Etches Collection from the lower Kimmeridgian and identified as *A. ornatissimus* could belong to the new species we describe here. Only one lateral tooth is well-preserved (C. Underwood pers. comm. 2017) and is very similar in its ornamentation and general proportions to lateral teeth of the first file of our material (see Fig. 7Q, X).

Teeth identical to our material are described and illustrated in Peyer's work reviewing Swiss occurrences of *Asteracanthus* (1946), but are not identified below genus level. Rees & Underwood (2008) stated that 'material figured by Peyer (1946) ... and originating from the Upper Jurassic of Switzerland probably represents an undescribed species dentally similar to *A. ornatissimus*', which is classically the only species recorded in the Kimmeridgian. This supports the definition of a new species for the Kimmeridgian, *Asteracanthus udulfensis* sp. nov. The variation is considered intraspecific and is especially marked in teeth of the first lateral file. This could reflect differences between functional and non-functional teeth, i.e. teeth of different rows.

Occurrence. The distribution of the new species *Asteracanthus udulfensis* is so far restricted to the Kimmeridgian of the Swiss Jura. All the present material comes from the Porrentruy area (canton of Jura) and specimens identified by Peyer (1946) as *Asteracanthus* sp. can be included in the new species, extending its occurrence to the cantons of Solothurn (Oberbuchsiten), Bern (Twann) and Neuchâtel (unspecified location).

Subcohort NEOSELACHII Compagno, 1977

Order SQUATINIFORMES de Buen, 1926

Family PSEUDORHINIDAE Klug & Kriwet, 2013b

Remarks. As noted by Underwood (2002), extant Squatiniformes (genus *Squatina* Duméril, 1806) and their Jurassic ancestors have a dental morphology that differs enough to assign Jurassic representatives to a new genus, this genus being *Pseudorhina* following the revision of Late Jurassic Squatinidae by Carvalho *et al.* (2008). During the Jurassic, neoselachians underwent a radiation and many forms with similar primitive characters arose, which makes it difficult to differentiate between taxa. Four main orders of Chondrichthyes may grow teeth with a labial apron or comparable structures: Hybodontiformes, Squatiniformes, Orectolobiformes and Heterodontiformes.

Genus PSEUDORHINA Jaekel, 1898

Type species. *Thaumas alifera* Münster, 1842, lower Tithonian, Solnhofen–Eichstätt, Bavaria, Germany.

Description. Teeth with a high, robust central cusp, lateral heels (blades) on each side and a labial apron. The crown surface is very smooth and devoid of any ornamentation. The teeth are cross-shaped in labial view because of the labial apron that is as wide as the main cusp. The crown is labially swollen, forming a curve from the apron up to the apex of the main cusp in mesiodistal view, and it is strongly concave in lingual view. A lingual uvula is located just below the main cusp. Therefore, the basal outline of the crown is strongly convex on each side of this uvula in lingual view. The main cusp is slender and points lingually, with a cutting-edge that continues onto the lateral heels. It is displaced and curved distally in more posterior files, where teeth are asymmetrical (Carvalho *et al.* 2008). The root is heart-shaped, hemiaulacorhize, and displaced lingually (Fig. 9). The root is composed of two rounded lobes that join in a lingual protuberance and together

FIG. 8. *Asteracanthus udulfensis* sp. nov., adult and juvenile teeth, upper Kimmeridgian. A–G, adult teeth; A–B, second lateral tooth, MJSN SCR010-303: A, occlusal; B, lingual view; C–G, posterior tooth, holotype, MJSN TCH005-640: C, occlusal; D, distal; E, lingual; F, labial; G, basal view. H–Q, juvenile teeth; H–J, ?first anterior tooth MJSN TCH005-338: H, occlusal; I, lingual; J, labial view; K–M, first or second lateral tooth, MJSN SCR011-516: K, occlusal; L, lingual; M, labial view; N–O, first or second lateral tooth, MJSN SCR004-221: N, occlusal; O, lingual view; P–Q, first or second lateral tooth, MJSN SCR010-104: P, occlusal; Q, lingual view. Scale bar represents: 2.5 cm (A–G); 1 cm (H–Q). Colour online.

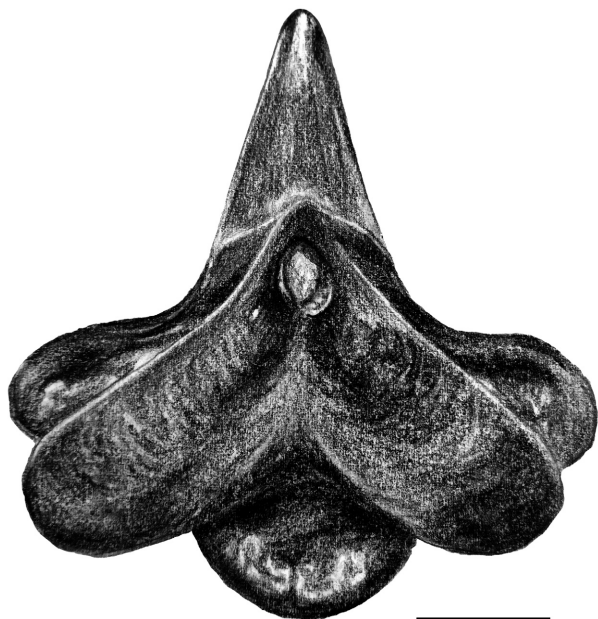


FIG. 9. Basal view of *Pseudorhina acanthoderma* (MJSN TCH004-1214) showing a hemiaulacorhize vascularization type. Scale bar represents 0.5 mm.

form a widely opened V-shape. There are two main foramina visible, one in the centre of the basal face of the root, the other in the centre of the lingual protuberance, just below the uvula.

Remarks. According to Carvalho *et al.* (2008), the shape and size of the labial apron varies between species and position in the jaw, heterodonty is thus a common feature in *Pseudorhina*. It is noteworthy that Underwood (2002) described a Kimmeridgian fauna from Ringstead, southern England, very similar to the one from the Ajoie region, including two types of Squatiniformes, one dominating the other, as in our material.

Pseudorhina acanthoderma Fraas, 1854
Figures 9, 10A–B

1983 *Pseudorhina* sp.; Thies, pl. 11, fig. 6.

Material. 69 teeth from different parts of the jaw.

Description. The lateral heels are convex at their basal edge but straight to concave on their occlusal edge. They are devoid of

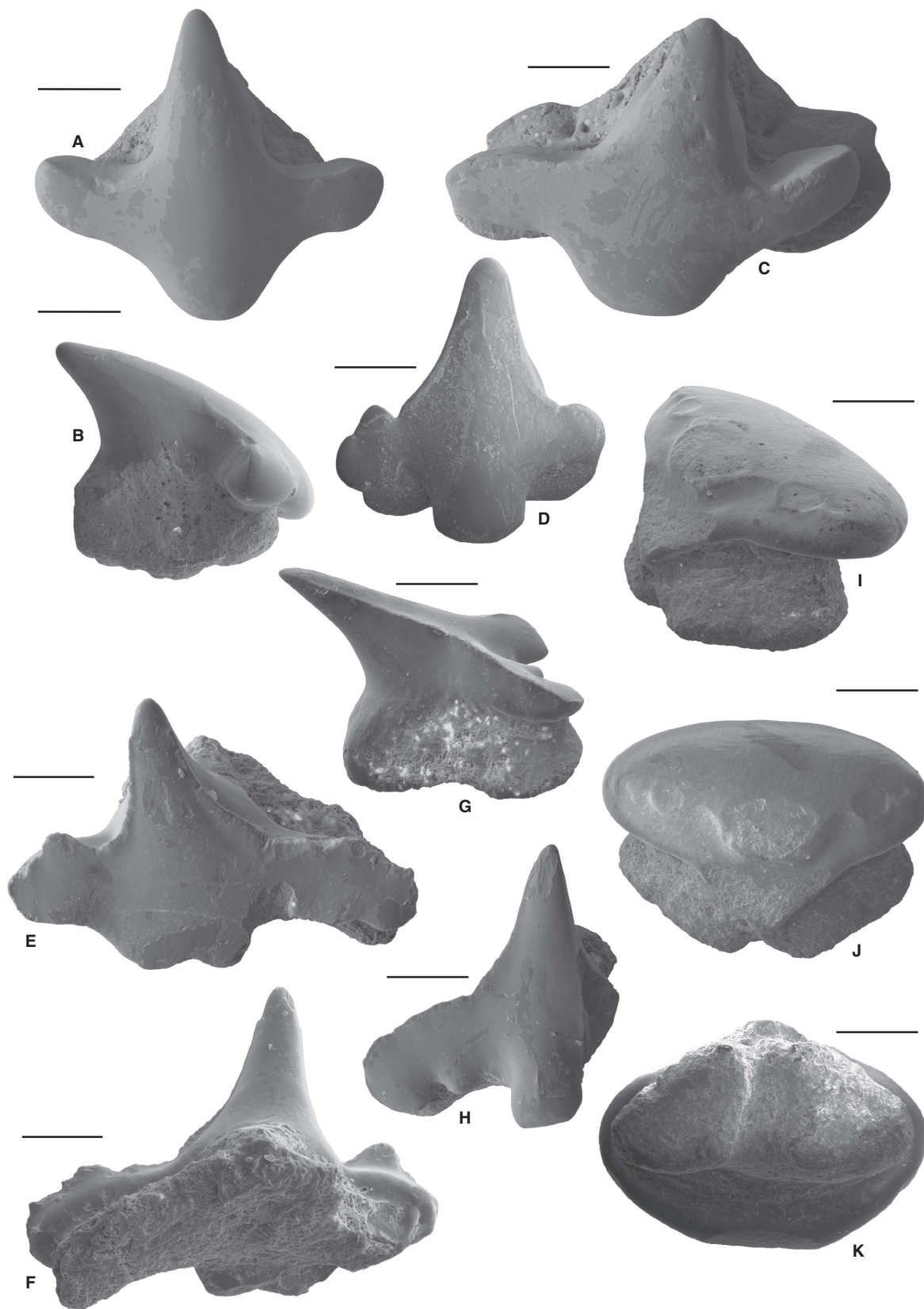
lateral cusplets and show a rounded apron. In some teeth, a crenulation is visible on the occlusal edge of the lateral heels (MJSN TCH005-1100), but this feature remains very weak. The labial apron can be of irregular and sinuous outline in very asymmetrical teeth (MJSN TCH004-1262 and MJSN TCH006-1386). The root is pierced by up to four (and most commonly three) marginolingual foramina on each side of the main cusp.

Remarks. Almost all teeth show an abraded cusp and it is thus difficult to assess the more slender character of the cusp compared to *P. alifera*. Moreover, the cusplets on the lateral heels present in *P. alifera* can be incipient in adult specimens (Carvalho *et al.* 2008), a feature that could possibly be erased by post mortem transport. Nevertheless, all teeth described above show a rounded apron, a character distinguishing *P. acanthoderma* from *P. alifera*, where it is more rectangular in shape (Carvalho *et al.* 2008; Thies & Leidner 2011). According to these authors, the crenulated heel edge observed in some of the *P. acanthoderma* teeth described above are only ‘simulating lateral cusplets’. Our material can be distinguished from *Pseudorhina* sp. teeth figured in Thies & Leidner (2011) by a higher angle between the lateral heels and the main cusp. One fragmentary tooth of *Pseudorhina* sp. figured in Thies (1983, pl. 11, fig. 6) probably belongs to *P. acanthoderma* and comes from a more lateral position than the one figured here (Fig. 10A). The other tooth figured in this reference (Thies 1983, pl. 11, fig. 5) resembles *P. acanthoderma* by its rounded apron, but differs from our material by having a much more flattened crown in mesiodistal view and lateral heels, the basal edge of which is concave. Contrary to our material, *Pseudorhina speciosa* has its lateral heels developed in clear cusplets (Thies & Leidner 2011). *Squatina? frequens* Underwood, 2002 (which probably also belonging to *Pseudorhina*, see Guinot *et al.* 2014) shows a great variation in the extension of its lateral heels. Teeth with crown proportions resembling our material differ in the shape of their heel extremities. The number of marginolingual foramina is an additional feature that allows us to identify our material as *P. acanthoderma*, as this taxon can show up to six pairs of foramina (Carvalho *et al.* 2008).

Pseudorhina alifera Münster, 1842
Figure 10C–F

Material. 27 teeth from different parts of the jaw.

FIG. 10. A–H, *Pseudorhina*, teeth, upper Kimmeridgian; A–B, *Pseudorhina acanthoderma*, MJSN TCH006-1588: A, labial; B, mesiodistal view; C–F, *Pseudorhina alifera*; C, lateral tooth TCH006-1802 in labial view; D, MJSN TCH005-1117 in labial view; E–F, MJSN SCR010-567: E, labial; F, lingual view; G–H, *Pseudorhina* sp., MJSN TCH005-1137: G, mesiodistal; H, labial view. I–K. *Protospinax* sp., tooth, upper Kimmeridgian, MJSN TCH005-1080: I, linguo-lateral; J, lingual; K, basal view. Scale bars represent: 0.5 mm (A–B, D, I–K); 0.25 mm (C, E–H).



Description. These teeth resemble the *P. acanthoderma* specimens, except for the following characters: they can show low but clear cusplets on the lateral heels (Fig. 10D–F); the apron is rectangular in labial view and relatively flat in mesiodistal view; and the number of marginolingual foramina of the root is limited to one or two pairs. The cusplets are narrow but well defined and composed of very thin enameloid that makes them look translucent. A cusplet is sometimes present only on one of the sides of the main cusp.

Remarks. The mediolingual foramen of the root is much larger and displaced lingually compared to *Pseudorhina frequens* Underwood, 2002. Teeth of our material show clear cusplets and/or a rectangular apron, thereby differing from the above described *P. acanthoderma*, are assigned to *Pseudorhina alifera* (Carvalho *et al.* 2008; Thies & Leidner 2011). The number of marginolingual foramina also matches with this species (Carvalho *et al.* 2008). Cusplets in *Squatina? frequens* Underwood, 2002 are located at the very extremities of the heels, giving them an angular aspect not observed in our material. Teeth of our material showing two pairs of marginolingual foramina also differ from this latter species, in which they are limited to a single pair. Variations in tooth size in our material most probably reflect ontogenetic stages.

Pseudorhina sp.
Figure 10G–H

Material. One partial tooth (MJSN TCH005-1137).

Description. Tooth differing from the previously described *Pseudorhina* species in showing a heel with a very strongly pectinate basal edge. The occlusal edge is slightly sinuous, the labial apron is clearly rectangular and the uvula is well developed. The tooth is incomplete, one of the two lateral heels is lacking.

Remarks. Teeth displaying this morphology have not been previously described. The strongly pectinate basal edge of the heels suggests the assignment to a new species. However, based on this single and fragmentary tooth, we simply ascribe it to *Pseudorhina* sp.

Superorder SQUALOMORPHII Compagno, 1973
Family PROTOSPINACIDAE Woodward, 1918

Genus PROTOSPINAX Woodward, 1918

Type species. *Protospinax annectans* Woodward, 1918, lower Tithonian, Solnhofen, Germany.

Protospinax sp.

Figure 10I–K

Material. Three teeth (MJSN TCH007-732 and MJSN TCH005-1080).

Description. These small teeth do not exceed 2 mm in length and their crown is ovoid in occlusal view. Their labial face is flat and smooth, without any ornamentation, and with a rounded to very slightly convex labial edge. The crown extends on its lingual side into an uvula, or apron, that reaches half of the height of the root. The smallest tooth is very asymmetrical and is most likely to come from a more posterior file. No cusp is visible but the three teeth show abraded surfaces in the form of circular areas on the lateral edge (Fig. 10J), on both sides of the uvula. The root is holaulacorhize (Fig. 10K) and much more expanded at the basal part of the tooth than at its junction with the crown. It represents approximately two-thirds of the total height of the tooth. The root of the larger tooth shows two lobes of triangular shape with rounded angles and a deep, straight groove between them. The smaller tooth, because of its asymmetry, shows lobes of different sizes, contrary to the other teeth that are symmetrical. They are not parallel to each other so that the nutritive groove is not straight but triangular in shape.

Remarks. According to their general shape, these teeth can be ascribed to the genus *Protospinax*. Teeth of this genus can show cusplets at the same positions as the abraded circular surfaces described above (Underwood & Ward 2004a). A line runs around these abrasion marks and probably corresponds to the ‘faint convex ridges at the base of the cusps’ described by Underwood & Ward (2004a). The part of the crown just above the uvula shows a broken surface that has been worn and which was probably bearing the main cusp. This feature is visible only on the largest tooth, suggesting either the absence of a larger cusp on the small tooth or its higher degree of wear. The crown strongly overhangs the root in all directions, but more so labially, so that it looks like a plateau with rounded edges. Intraspecific variations of the root vascularization type have been reported for *Protospinax* (Underwood 2002) and such variations are difficult to assess based on three teeth only. Our material is similar to the tooth figured in Weis & Bei (2015), not identified at the species level, to *Protospinax* sp. 1 described by Underwood & Ward (2004b) and to *Protospinax? muftius* (Thies 1983, pl. 5, fig. 2 only; pl. 6). It differs from *P. annectans* Woodward, 1919, and *Protospinax* sp. 1 *sensu* Kriwet (2003) by its presence of lateral cusplets, and from *P. cf. annectans* and *Protospinax* sp. 2 *sensu* Kriwet (2003) by its absence of crenulated cutting edge (Duffin 1993; Kriwet 2003; Thies & Leidner 2011). Middle Jurassic species such as *P. carvalhoi* and *P. magnus* Underwood & Ward, 2004a, differ in their root lobes and root vascularization stage respectively. Moreover, this

latter species is not found in platform and lagoon facies (Underwood & Ward 2004a). Due to the low number of specimens and the high degree of wear, these teeth are not identified at species level.

Superorder GALEOMORPHII Compagno, 1973

Order HETERODONTIFORMES Berg, 1940

Family HETERODONTIDAE Gray, 1851

Heterodontidae indet.

Figures 4N–P, 6R–S, 11

Material. One fragment of a fin spine (MJSN SCR011-347, Fig. 4N–P), one incomplete, anterolateral tooth (MJSN VTT006-1500, Fig. 11) and four posterior teeth (e.g. MJSN VTT006-1331, Fig. 6R–S).

Description of the spine. Fragment of a fin spine showing an enameloid coating on its upper part. Longitudinal growth lines are visible on the whole surface, including the enameloid coating. Growth lines of the enamel cap are more or less parallel to its lower limit. The limit of the enameloid coating gently slopes downwards from the posterior to the anterior edge and is not regular. The posterior surface is concave and bears no hooks. The entire fragment is 10 mm long, of triangular section and devoid of tubercles.

Description of the teeth. The small, anterior tooth (Fig. 11) of about 1 mm shows one main cusp, and two mesial and one distal cusplets. The cusp and the cusplets are inclined in the same direction, pointing distally towards the commissure of the jaw. All cusplets present a cutting edge which is especially well developed in the broader cusp. Their bases are broadly united and a discrete furrow is visible between them. The base of the crown is flat. The root is also broken and only an asymmetrical, strong V-shape can be described, with no information about its entire shape. Features often used to characterize a root, such as the foramina or the swelling between root lobes are not visible.

The posterior teeth (Fig. 6R–S) are molariform and mesiodistally elongated. A sigmoid, longitudinal crest is present, appearing as a simple line in worn-out teeth. The crown shows an ornamentation that differs in the labial and lingual parts. The ornamentation of the labial part consists of a series of grooves

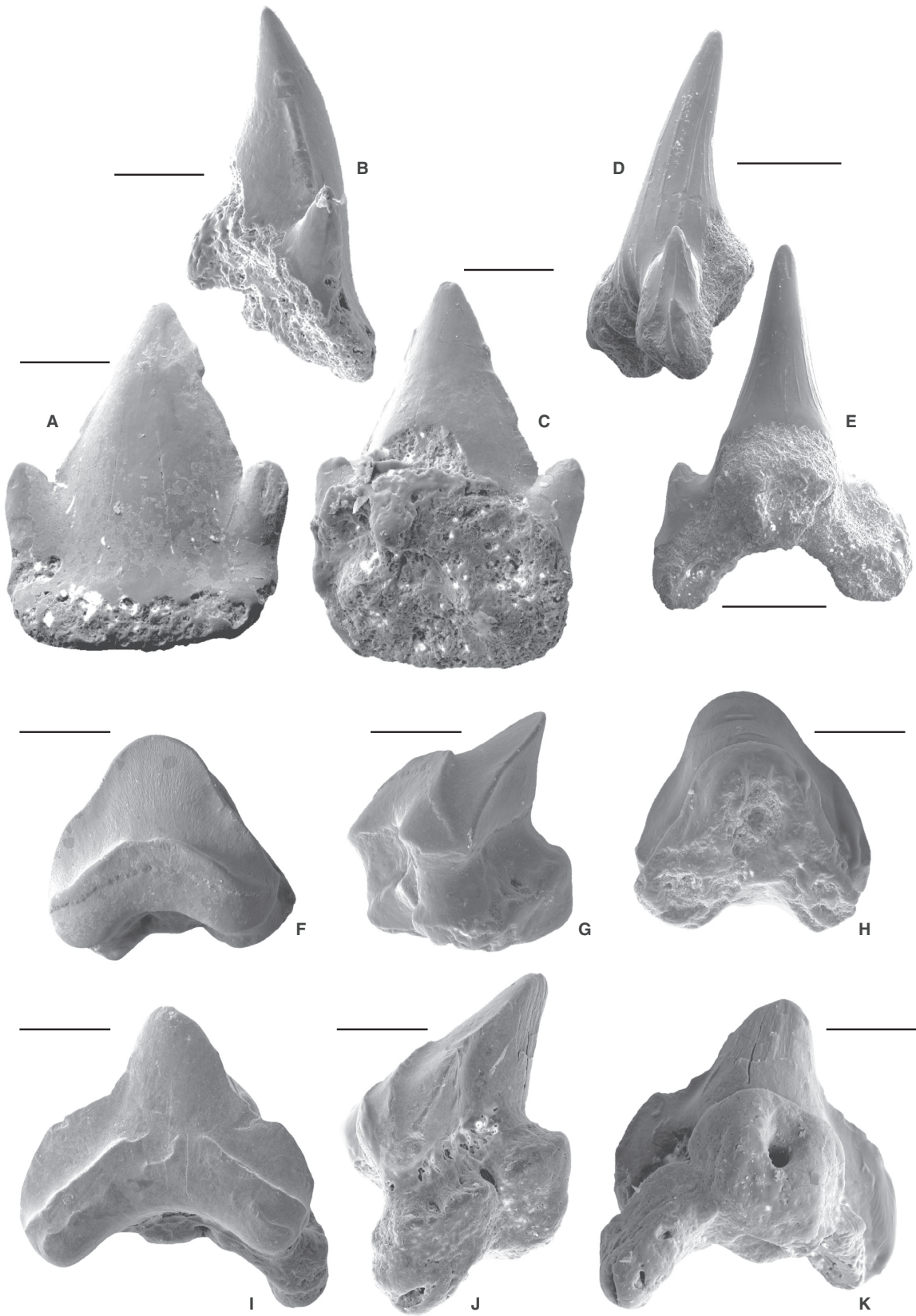
of different sizes and lengths, round or oval in shape, while the lingual part displays wrinkles perpendicular to the crest. The lingual ornamentation can be partly distinguished in two specimens only. It is smooth and unornamented in other specimens, probably abraded. The crest is not always located in the centre of the crown and is sometimes strongly shifted linguallly. The root is not well preserved.

Remarks on the fin spine. Among the taxa identified in our assemblage based on teeth, several have fin spines: hybodonts, heterodontids, *Protospinax*, rhinobatids (*Belemnobatis* and *Spathobatis*) and Holocephali (*Ischyodus*) (Maisey 1976, 1978, 1979; Stahl 1999). The fragment of the fin spine described here (Fig. 4N–P) is distinguishable from those of Hybodontiformes and *Ischyodus* by the lack of posterior hooks and its continuous enameloid cover (Maisey 1978; Stahl 1999). It differs from rhinobatid and *Protospinax* fin spines that are round in cross-section and show an enameloid cover only at the very tip of their spine, if at all (Maisey 1976). On the other hand, it corresponds well to the Heterodontidae described by Maisey (1982a) who indicated that an enameloid cover is present in *Heterodontus* and *Paracestracion*. The absence of tubercles is common in fin spines of *Heterodontus* but fin spines of juvenile *Paracestracion* can also be devoid of such ornamentation. Still, since the fragment described here shows the edge of the enameloid cover, its size is easily comparable with a much more complete fin spine of *Paracestracion* showing a tuberculate ornamentation (Fig. 4Q–S) and thus corresponding to an adult specimen. The sizes being similar, it is unlikely that our fin spine fragment belongs to a juvenile specimen of *Paracestracion*. Since it is far from being complete and is the only one of its kind in the Porrentruy material, it has not been identified to a lower taxonomic level than the family Heterodontidae.

Remarks on the teeth. The lack of features preserved in the only anterolateral tooth makes its identification very difficult. The incomplete root with a strong V-shape is reminiscent of both *Proheterodontus* Underwood & Ward, 2004a and *Paracestracion* Koken in Zittel, 1911, but the well-developed cutting edge of the broader cusplet

FIG. 11. Incomplete anterolateral tooth of a Heterodontidae sp. (MJSN VTT006-1500) in labial (left) and lingual (right) view. Scale bar represents 0.2 mm.





resembles that latter genus. The root vascularization type is different in these two genera (holaulacaurhize and hemiaulacaurhize respectively) and would allow their differentiation, but no foramina could be observed. This tooth could belong to a juvenile specimen. The root does not seem larger than the crown which is again more similar to *Paracestracion*, but that character also appears in juvenile *Proheterodontus* (Underwood & Ward 2004a).

The posterior teeth (Fig. 6R–S) resemble those of *Paracestracion falcifer* Wagner, 1857 illustrated in Underwood (2002) as well as those of *Heterodontus semirugosus* Plieninger, 1847. Molariform teeth of those two genera are known to be similar. Some teeth show ornamentation on their labial half only, probably due to wear. Since part of the material has been assigned to both *Heterodontus semirugosus* (several anterior teeth, one fin spine) and *Paracestracion* (one anterior tooth and one fin spine, see below), these molariform teeth could be attributed to any of the two genera, according to the faunal composition, and are therefore kept in open nomenclature.

Genus HETERODONTUS Blainville, 1816

Type species. *Squalus philippi* Bloch & Schneider, 1801, Recent.

Heterodontus semirugosus Plieninger, 1847 Figure 12A–C

Material. Six anterior teeth.

Description. The anterior teeth are high and composed of one central, main cusp representing almost the whole width of the crown. Two much smaller and thinner cusplets are not well-separated from the main cusp. The cutting edge of the cusps is sharp, better developed at the base, and fades towards the apices, probably because of wear. In labial view, the large teeth show a triangular main cusp, whereas its outline is somewhat more sinuous and swollen at its base in smaller teeth. The crown surface is smooth without any ornamentation. The cusplets do not diverge much from the main cusp and are fused to it in some cases. At least two specimens (MJSN TCH006-1581) show a second cusplet that is still fused to the other one at one side of the main cusp. The cusplets share a robust and wide common base with the main cusp from which they are separated quite high in the crown. One specimen (MJSN TCH006-1383) shows a slight crenulation on the edge of the cusplets and at the base of the main cusp.

The root is of a hemiaulacorhize vascularization type and is completely hidden by the crown in labial view (Fig. 12A). In lingual view, it forms a V-shape pointing towards the apex and with a protuberance at its junction with the crown, just below the main cusp. This lingual protuberance is pierced by a foramen and a second foramen opens just under this lingual bulge. The crown–root junction is strongly concave on the mesial and distal sides.

Remarks. As the name indicates, representatives of the family Heterodontidae are characterized by a very heterodont dentition, a character that can be monognathic and ontogenetic (Cappetta 2012). The family Heterodontidae is represented by the genera *Heterodontus*, *Paracestracion* and *Proheterodontus* in the Jurassic (Kriwet 2008). Our material differs from *Paracestracion* in its much wider main cusp and a generally less gracile aspect of its cusp and cusplets. Also, the cusplets are more separated from the main cusp in this latter genus (Underwood 2002; Kriwet 2008; Guinot *et al.* 2014) and the root vascularization is of holaulacorhize type in *Paracestracion* (Kriwet 2008). Teeth of *Proheterodontus* differ from our material by having a much more gracile aspect and flattened cusps. They can bear up to three pairs of lateral cusplets and are not associated with molariform, posterior teeth (Underwood & Ward 2004a). Regarding *Heterodontus*, the last publication illustrating the only species known in the Jurassic, *H. semirugosus*, was by Schweizer (1961). Since only a few anterior teeth are figured, some of which are broken, the comparison is difficult. Moreover, the illustration and description of the dental material in the reference publication for this species (first identified as *Acrodus semirugosus*) is of little help (Plieninger 1847). The labial side of the holotype was figured by Kriwet & Klug (2004). However, since this species is by now the only one recorded in the Kimmeridgian and its description matches our material, we assign our *Heterodontus* material to the species *H. semirugosus*. According to Cappetta (2012), more than two pairs of lateral cusplets characterize young individuals. Our material is therefore likely to belong to an adult specimen.

Genus PARACESTRACION Koken *in* Zittel, 1911

?*Paracestracion* sp. Figure 4Q–S

Material. One fin spine (MJSN BSY009-199).

FIG. 12. A–C, *Heterodontus semirugosus*, anterior tooth, lower Kimmeridgian, MJSN VTT006-1362: A, labial; B, mesiodistal; C, lingual view. D–E, *Palaeoscyllium* cf. *formosum*, MJSN TCH007-628: D, mesiodistal; E, lingual view. F–K, *Corysodon cirinensis*, teeth, lower Kimmeridgian; F–H, MJSN VTT006-1373: F, labial; G, labiolateral; H, lingual view; I–K, MJSN VTT006-1372: I, labial; J, mesiodistal; K, lingual view. Scale bars represent: 0.5 mm (A–E); 0.2 mm (F–K).

Description. Fin spine with straight edges, an enameloid cap at the tip and a tuberculate ornamentation on most of the surface. The overall surface shows longitudinal, parallel growth lines except for the upper part of the posterior surface where the growth lines are hidden by a central groove. The ornamentation covers the lateral surfaces, except at their base and tip, and consists of regularly distributed tubercles covered by enameloid (Fig. 4Q). Those overlap the growth line pattern. The tip of the spine is also covered by enameloid, under which the growth lines are still visible. The limit of the enameloid cover is inclined forwards, so that a closed V of enameloid is visible in anterior view (Fig. 4R). The centre of the posterior surface is slightly concave and naked (Fig. 4S), while the sides present some tubercles. The base of the spine is broken off, so that it is not possible to assess whether a posterior opening was present or not. As for all the previously described spines, the inner part is hollow and the walls are thin (down to 1 mm), features visible in basal view. The wall is thicker at the anterior side and reaches 3 mm. Growth rings are visible on the basal, broken-off surface of the wall. The spine has a maximal length of 73 mm and a maximal width of 20 mm.

Remarks. This fin spine shows several features typical of Heterodontiformes, such as straight edges and growth lines following the long axis of the spine (Maisey 1982b). The absence of posterior hooks or tubercles contributes to differentiate it from Hybodontiformes ones. A basal opening is present on Heterodontiformes but only at the very base of the spine. Our specimen corresponds to the description of *Paracestracion* sp. (Maisey 1982b). However, it seems difficult to differentiate the several early Heterodontidae genera based on fin spines only: the presence of tubercles is not diagnostic for any genus, since they may be absent on juvenile specimens of *Paracestracion* and become more and more frequent during growth in *Heterodontus tuberculatus*. Maisey (1982b) suggested that the tubercles may represent a primitive character. According to him, the difference between *Heterodontus* and *Paracestracion* fin spines lies in the fact that *Heterodontus* fin spines lack trabecular dentine, while *Paracestracion* spines do not. No microscopic analysis of the fin spine dentine has been conducted, but small cavities are visible in the broken section of the wall under a binocular microscope. Whether this corresponds to trabecular dentine is questionable.

The tuberculate ornamentation of the Porrentruy specimens is widespread when compared to the enameloid cover (Fig. 4Q). The tubercles are thought to appear early in *Paracestracion* development. In *H. reticulatus*, however, they seem to be more prominent in older specimens. Comparing the size of this material with the fragmentary fin spine identified as Heterodontidae indet. (Fig. 4N–P) indicates similar sizes (see the above remarks on the heterodontid fin spine). It is unlikely that specimens of comparable sizes would show such discrepancies in their tubercle ornamentation, since this feature varies with

ontogeny. The presently described specimen thus probably belongs to a different taxon. Also, the largest part of the spine surface is covered by tubercles in the Porrentruy specimen and such an important tubercle ornamentation is not mentioned for *Heterodontus* in the literature. This fin spine is therefore identified as ?*Paracestracion* sp.

Order CARCHARHINIFORMES Compagno, 1973
Family SCYLIORHINIDAE Gill, 1862

Genus PALAEOCYLLIUM Wagner, 1857 *non* Marck, 1863

Type species. *Palaeoscyllium formosum* Wagner, 1857, Upper Jurassic of Germany.

Palaeoscyllium cf. *formosum* Wagner, 1857
Figures 12D–E, 13

Material. 15 teeth from different positions in the jaw, including 2 with preserved root (MJSN TCH007-628 (Fig. 12D–E) and MJSN VTT006-1335).

Description. Small teeth (up to 2 mm high), higher than broad, bearing a long, gracile, sharp main cusp pointing slightly

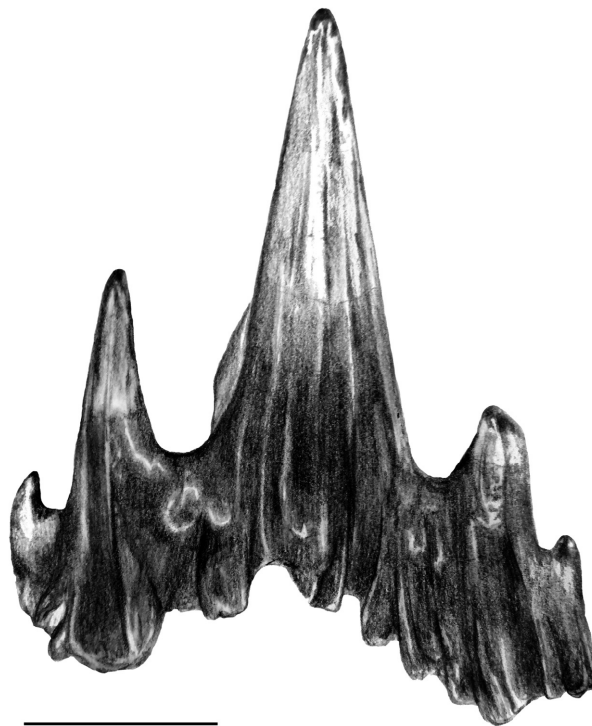


FIG. 13. Tooth of *Palaeoscyllium* cf. *formosum* (MJSN TCH006-1174) in labial view. Scale bar represents 0.25 mm.

towards the lingual side. The tooth is thus concave in lingual view whereas the labial face is generally flat, sometimes curved lingually at the very end of the main cusp. Two much more reduced (about a quarter of the main cusp) but still sharp cusplets show a more massive, almost nodulous base. Those either rise straight up or slightly converge towards the main cusp. In apical view, the cusplets are arranged in a straight line together with the main cusp. The labial face of the crown is covered by strong folds at its base, which gradually diminish towards the apices and build a bulge at the crenate base of the crown. In lingual view, the ornamentation is reduced to very fine, inconspicuous lines on the main cusp.

The root is pseudohemiaulacorhize and strongly curved with a very well-defined reversed V-shape in lingual (Fig. 12E) and labial view. The base of the crown follows the same curvature. The root is low and composed of three lobes, the central one showing a well-developed foramen. Additional foramina are present on the lateral root lobes. The lingual face of the root forms a protuberance in its central part, just below the main cusp. Only two teeth, a small and a larger one, still have their root preserved. The root is clearly wider than the crown on the very small specimen but not on the larger one. The larger tooth looks transported and rolled and its root has probably also been rounded.

Remarks. The fragile, gracile aspect of these teeth is typical for the family Scyliorhinidae (Cappetta 2012). The cusp and cusplets are curved mesiodistally in some teeth, corresponding to a more posterior position in the jaw (Underwood & Ward 2004a). The extreme case in this material is represented by MJSN VTT006-1335 where the lateral cusplet is developed on the distal side only. The small size of that tooth (<0.5 mm) indicates that it might represent a juvenile. Another tooth in the same sample is of the same size but does not show any lateral cusplet. One tooth (MJSN TCH006-1174, Fig. 13) shows two pairs of lateral cusplets and probably corresponds to a more posterior position in the jaw (Underwood & Ward 2004a). The first pair is much higher than in the other teeth and reaches half of the height of the main cusp.

The lingual protuberance of the root allows an assignment to the order Synechodontiformes to be excluded. The teeth are very similar to the ones described by Candoni (1993) for *Parasymbolus octevillensis*, which is now considered to be a synonym of *Palaeoscyllium formosum* (Underwood 2002; Cappetta 2012). These additional cusplets are much better developed than the 'vestigial pair' of *P. formosum* (Candoni, 1993) and are not restricted to the distal side of the tooth. The angle between the root lobes should help differentiate *P. tenuidens* from *P. formosum* (Underwood & Ward 2004a), but this character appears difficult to use since both *P. formosum* and *P. tenuidens* teeth show a considerable variation in this feature. The two pairs of lateral cusplets of the specimen MJSN TCH006-1174 resemble those of *Palaeoscyllium tenuidens* (Underwood & Ward 2004a) but the

stratigraphic distribution of this species is so far restricted to the Bathonian, while *P. formosum* is known in the Kimmeridgian. We identify our specimens as *Palaeoscyllium* cf. *formosum*, with some reserve because of the two pairs of well-developed cusplets of the specimen MJSN TCH006-1174 (Fig. 13).

Family INCERTAE SEDIS

Genus CORYSODON Saint-Seine, 1949

Type species. *Corysodon cirinensis* Saint-Seine, 1949.

Corysodon cirinensis Saint-Seine, 1949

Figure 12F–K

Material. Four teeth.

Description. Small teeth (about 0.5 mm wide) with blunt crown of triangular outline in labial view. The basal edge of the crown is curved and concave. A labial bulge is present at the base of the crown and draws a crest parallel to the crown base in labial view (Fig. 12F). A secondary crest runs just below, in a flatter line. Anterolateral teeth are symmetrical, while lateral ones show a distally inclined crown (Cappetta 2012). The outline of the lateral tooth crown is concave on both sides of the apex. The root is composed of two lobes and a prominent lingual bulge that is pierced by a foramen (Fig. 12H, K). It is symmetrical in anterolateral teeth and shows an elongated mesial lobe in lateral ones.

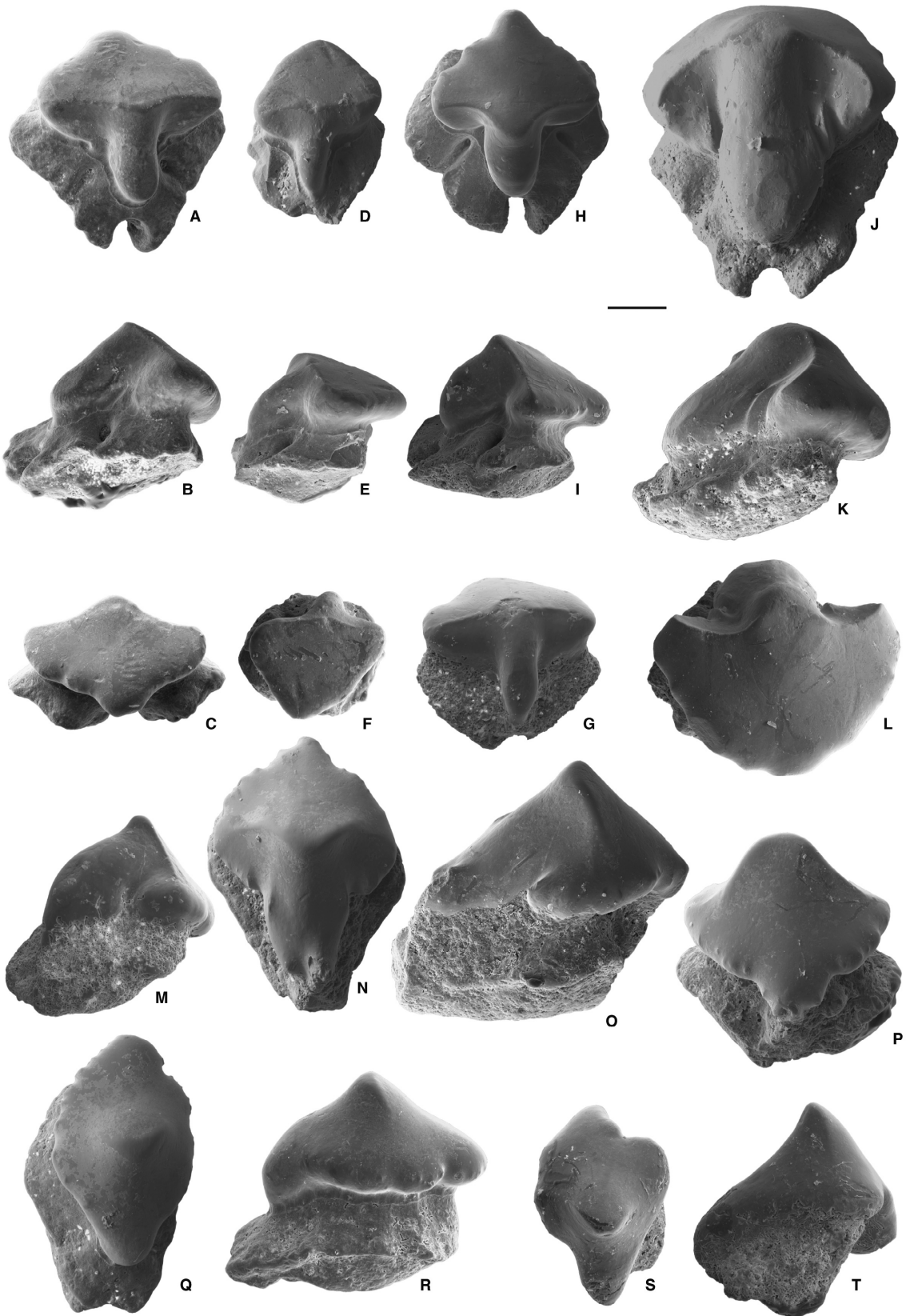
Remarks. After having been disputed (see Cappetta 1987), the validity of the genus *Corysodon* described by Saint-Seine is now well established. However, its systematic position remains dubious and a thorough study of the genus is needed to assign it with certainty to a family (Thies & Candoni 1998; Kriwet & Klug 2004; Cappetta 2012). Our material closely resembles teeth figured by Thies & Candoni (1998). They belong to the only species of the genus: *Corysodon cirinensis*. This species has already been recorded in the Upper Jurassic of France and Germany (Thies & Candoni 1998; Mudroch 2001; Kriwet & Klug 2004; Thies & Leidner 2011). This is the first record of the genus *Corysodon* in Switzerland.

Superorder BATOMORPHII Cappetta, 1980

Order RAJIFORMES Berg, 1940

Suborder RHINOBOATOIDEI Fowler, 1941

Remarks. Despite the fact that Cappetta (2012) and other authors included the ray genera identified below



(*Belemnobatis* and *Spathobatis*) in the family Rhinobatidae, no family name but the suborder Rhinobatoidei will be given here. Indeed, as mentioned in Underwood (2002), the family Rhinobatidae might represent a paraphyletic group, an assertion recently demonstrated based on molecular phylogenetic studies undertaken on modern specimens of this family (Last *et al.* 2016). This taxon shows a wide range of variations and their representatives are difficult to identify (a problem already mentioned by Kriwet & Klug 2004). Only two genera are known in the Kimmeridgian: *Spathobatis* and *Belemnobatis*. Those are morphologically close and the several descriptions available in the literature rarely fully converge (see Kriwet *et al.* 2009). As mentioned by Thies & Leidner (2011), a revision of the genera occurring in the Late Jurassic (*Belemnobatis*, *Spathobatis* and *Asterodermus* from the Tithonian) is needed. The descriptive terminology is largely based on Cavin *et al.* (1995) who proposed a precise description of *Spathobatis* and *Belemnobatis* specimens.

Genus BELEMNOBATHIS Thiollière, 1852

Type species. *Belemnobatis sismondae* Thiollière, 1852, upper Kimmeridgian, Cerin, Jura, Eastern France.

Belemnobatis sismondae Thiollière, 1852

Figure 14A–G

Material. 339 teeth from different positions in the jaw.

Description. Small teeth (0.5–1 mm) mesiodistally expanded with a moderately marked transversal crest and narrow lingual median uvula. The crown is mesiodistally wider than it is labiolingually, due to well-developed shoulders. The transverse crest commonly forms a straight line in occlusal view, but can be slightly curved labially in some cases. The lingual face is narrow but wide and the shoulders form a perpendicular angle with it. The uvula base is as broad as the base of the shoulders or thinner, so that it does not reach half of the lingual face width (Fig. 14A, D, G). The labial face is flat in mesiodistal view, triangular in occlusal view, and the labial visor is pointed. The angle formed by the labial and lingual

faces of the crown is rather obtuse (Fig. 14B, E). The lingual notch of the root clearly forms a furrow in some teeth (Fig. 14A), whereas the lingual part of the two lobes of the notch are fused in some others, making it look like a foramen rather than a furrow. It continues on the basal face in a nutritive groove which opens labially. A foramen is present at each side of the uvula on the lingual face (Fig. 14A). Most specimens lack the root.

Remarks. Teeth of *Belemnobatis* and *Asterodermus* (Thies & Leidner 2011) are very close morphologically and difficult to distinguish. Some authors consider *Asterodermus* to be *nomen dubium* (Underwood & Rees 2002) and this genus is only recorded in the Tithonian (Klug & Kriwet 2013a). Additionally, the absence of lingual marginal uvulae and an obtuse angle between the labial and lingual face allowed identification as *Belemnobatis*. Teeth of *Belemnobatis sismondae*, the classical species of the Kimmeridgian, match well with the Porrentruy material. Teeth from different positions in the jaw described by Cavin *et al.* (1995, pl. 3, all figs) and Thies & Leidner (2011, pl. 90, figs A–D) are found in our assemblage. Some additional variations can be highlighted from our specimens: most posterior teeth have a very narrow crown and are strongly asymmetrical with the distal shoulder becoming much longer than the mesial one; some teeth show a fusion of the root lobes; and few specimens have a very long lingual median uvula. This last feature is visible in Bathonian species of *Belemnobatis* (Underwood & Ward 2004a). The lingual closure of the root is a feature already reported by Klug & Kriwet (2013a) for *Belemnobatis* sp. and is due to monognathic heterodonty. The cusped teeth most probably belonged to males (Figs 14A–C). Male *Belemnobatis* teeth from anterior positions (i.e. with quite reduced shoulders) are the most difficult to separate from *Spathobatis* described below.

Belemnobatis morinicus Sauvage, 1873

Figure 14H–I

Material. 55 teeth.

Description. Small teeth (~0.5 mm) just a little more expanded mesiodistally than labiolingually with a thin uvula and a well-

FIG. 14. A–G, *Belemnobatis sismondae*, teeth, upper Kimmeridgian; A–C, MJSN BSY009-926a: A, occlusal view; B, mesiodistal; C, labial view; D–F, lateral tooth, MJSN BSY009-926b: D, occlusal; E, mesiodistal; F, labial view; G, MJSN TCH005-974 in lingual view. H–I, *Belemnobatis morinicus*, tooth, upper Kimmeridgian, MJSN TCH004-1286: H, occlusal; I, mesiodistal view. J–M, *Spathobatis bugesiacus*, teeth, upper Kimmeridgian; J–L, MJSN BSY009-936: J, linguo-occlusal; K, mesiodistal; L, labial view; M, MJSN TCH006-1396 in mesiodistal view. N–T, *Belemnobatis* or *Spathobatis*, teeth, upper Kimmeridgian; N–P, MJSN BSY009-271: N, occlusal; O, mesiodistal; P, labial view; Q–R, MJSN BSY009-273: Q, occlusal; R, mesiodistal view; S–T, MJSN SCR011-2501: S, occlusal; T, mesiodistal view. Scale bar represents 0.25 mm.

marked transversal crest. The teeth differ from *B. sismondæ* in having a higher crown, a better defined transversal crest, mesiodistally less expanded shoulders and an irregular outline of the labial face. This irregular outline varies from a gently hummocky line to angular protuberances. The labial edge of the labial face is pointed or rectangular in shape.

Remarks. The species *Belemnobatis morinicus* was revised by Cavin *et al.* (1995) and compared to *Belemnobatis sismondæ* and *Spathobatis bugesiacus*. All characters described in *B. morinicus* match with our specimens, the irregular outline of the labial face of the crown and the relatively short shoulders being especially distinctive.

Genus SPATHOBATIS Thiollière, 1852

Type species. *Spathobatis bugesiacus* Thiollière, 1852, upper Kimmeridgian, Cerin, Jura, Eastern France.

Spathobatis bugesiacus Thiollière, 1852

Figure 14J–M

Material. 157 teeth from different parts of the jaw.

Description. Small teeth (0.7–1 mm) with high crown, well-defined transverse crest and very broad median uvula. The crown is extended more labiolingually than mesiodistally and it is crossed by a transversal crest. The crest is gently curved lingually at the extremities in occlusal view. In high-cusped teeth, it can also gently point lingually at the level of the cusp. The lingual face shows a massive, very well-developed uvula that represents half of the tooth width in linguo-occlusal view (Fig. 14J). The edges of this median lingual uvula commonly converge into a slightly rounded point. The outline of the lingual face forms an obtuse angle between the basal line of the shoulders and the median lingual uvula. The latter is separated from the shoulders by a furrow (MJSN TCH006-1601). In some cases, a thin bulge forms between the median uvula and a secondary furrow (MJSN BSY009-936, Fig. 14J). The lingual marginal edges can be simple or show marginal uvulae. These edges can be more or less developed, as can the furrows. In high-cusped teeth, the outline of the median uvula becomes concave just before the cusp in mesiodistal view, while it is rather straight in lower-cusped teeth. In mesiodistal view, the lingual and labial faces form a right to acute angle at the apex (Fig. 14K, M). The labial face is straight or slightly concave in profile and overhangs the root. In occlusal view, the outline of the labial visor varies a lot and can be rather rounded, convex and of smooth or irregular outline, or quite triangular with concave edges. In any case, the basal edge of the labial visor is hummocky.

The root is clearly holaulacorhize and shifted lingually (Fig. 14K, M). A large foramen is present on each side of the uvula, sometimes opening into a furrow (MJSN TCH006-1601).

The lingual notch of the root is clearly visible between the two lobes of the root that are separated by a nutritive groove in the basal face. The nutritive groove widens towards the labial face. Mesiodistally, the root is not wider than the crown but lingually, it slightly extends over the median uvula. Many specimens lack the root.

Remarks. This material is assigned to the genus *Spathobatis* based on the combination of the following characters: the well-marked transversal crest, the broad lingual median uvula commonly representing half of the lingual width, the root shifted lingually and an angle of 90° or less between the labial and lingual faces in mesiodistal view. Additionally, a very well-developed cusp pointing lingually can be present in some teeth that probably belonged to male individuals (Underwood 2002). Assigning our material to a species is more difficult, mainly because the material of *Spathobatis* is limited to a few teeth in several publications, so that possible intraspecific variations may not be discernible. Our material shows notable variation in shape, which is principally due to wear that occurs on the lingual face of the crown and planes the crest and the cusp down, modifying the form of the tooth profile. The very massive lingual median uvula, as well as the presence of lateral furrows and lingual marginal uvulae, are characters that remain, even in strongly worn teeth. The more cusped the teeth, the more visible the furrows and the marginal uvulae. Our material differs from the *S. bugesiacus* figured in Thies & Leidner (2011) in having a much wider median uvula and a higher angle between the labial and lingual faces. These two latter features make our teeth resemble the *S. bugesiacus* material described by Cavin *et al.* (1995, pl. 2, figs 2–6) and Underwood (2002, text-fig. 5, all figs). Additional features are visible in our material, namely furrows often flanking the base of the lingual median uvula and the common presence of lingual marginal uvulae (Fig. 14J). Our material differs from the Oxfordian one identified by Klug & Kriwet (2013a) as *Spathobatis* sp. that might correspond to a new, undescribed species. In our case, teeth rarely show a lingual median uvula with edges as parallel as the ones described in this latter reference (fig. 5m), the basal end of the uvula is usually pointed instead of finger-shaped, and the labial face of the crown is more developed and often triangular. According to the same authors, the species *Spathobatis bugesiacus* (Thiollière, 1852) shows a strong heterodonty (monognathic and gynandric) and includes the species *S. uppensis* and *S. mutterlosei*, remaining the only valid species of this genus for the Kimmeridgian. Therefore, we assign our material to *S. bugesiacus* and add further dental variations within the species, especially regarding the development of the cusp and the well-developed marginal lingual uvulae. This latter feature is found in teeth of

Spathobatis sp. figured by Mudroch (2001) that can be assigned to *S. bugesiacus*.

Belemnobatis or *Spathobatis*

Figure 14N–T

Material. 25 teeth.

Description. Diamond-shaped teeth in occlusal view with extremely reduced shoulders compared to the lingual median uvula. The distal edges of the labial face are hummocky to very strongly indented (Fig. 14N). This indentation extends in some cases on the basal part of the shoulders until the median uvula. The angle between the median uvula and the basal edge of the shoulders is obtuse to very obtuse. In some cases, the lingual median uvula is linked to the lateral angles of the crown in a single, oblique line (Fig. 14S). The labial face is extremely extended labially and the labial visor is triangular in shape. It closes labially in an acute angle. In cusped specimens, the cusp is very high (Fig. 14T).

Remarks. The mesiodistally reduced extension of these teeth would match very well with a symphyseal position (i.e. on the central file of the jaw). However, a single record of a ‘symphyseal?’ tooth can be found in the literature for one of the two batoid genera present in our assemblage, namely *Belemnobatis* (see Underwood & Rees 2002). This hypothetical symphyseal tooth of *Belemnobatis variabilis* from the Lower Cretaceous shows a similar gross structure to our material, namely extremely reduced lateral shoulders, very high cusp and obtuse angle between the lingual median uvula and the base of the shoulders. However, symphyseal teeth are not reported in articulated specimens of *Belemnobatis* nor *Spathobatis* and our material is more likely to represent intraspecific variation in the dentition of the rhinobatid species identified above. The strongly indented crown of some of our teeth (e.g. MJSN BSY009-271, Fig. 14N–P) is reminiscent of *B. morinicus* but our material is much narrower mesiodistally. Reduced lateral shoulders make it difficult to discriminate between *Belemnobatis* and *Spathobatis*, this material is therefore identified as potentially belonging to either genus.

Chimaeroid (Holocephali) dental plates and fin spines

High-level taxonomy of chimaeroid fishes (superfamily and above) follows Nelson (2006). The family ‘Edaphodontidae’ Owen, 1845, is here considered to represent a collective unit in need of revision that would be beyond the scope of the present paper (see also discussion in Popov & Beznosov 2006; Popov & Machalski 2014).

Subclass HOLOCEPHALI Bonaparte, 1832 in 1832–1841

Superorder HOLOCEPHALOMORPHA Nelson, 2006

Order CHIMAERIFORMES Obruchev, 1953

Suborder CHIMAEROIDEI Patterson, 1965

Superfamily CALLORHYNCHOIDEA Garman, 1901

Family ‘EDAPHODONTIDAE’ Owen, 1845

Genus ISCHYODUS Egerton, 1843

Type species. *Chimaera townsendi* Buckland, 1835, Upper Jurassic (Tithonian), southern England.

Remarks. The descriptive terminology is based on Popov & Machalski (2014, fig. 3), some terms used are abbreviated in Fig. 15. Measurements include mesiodistal length of specimen (L) and ‘reference width’ of mandibular and palatine plates (Km, Kp, respectively), which can be described as the ‘incomplete width of a dental plate, measured perpendicular to the medial termination of this tritor, which is most commonly preserved in fossils – the outer tritor in palatine plates (Kp), the antero-outer tritor in mandibular plates (Km)’ (see Popov & Machalski, 2014, p. 6).

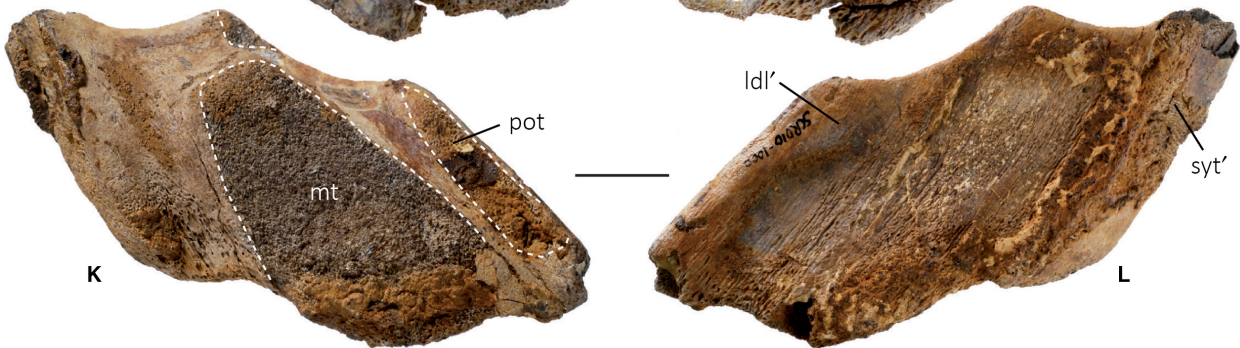
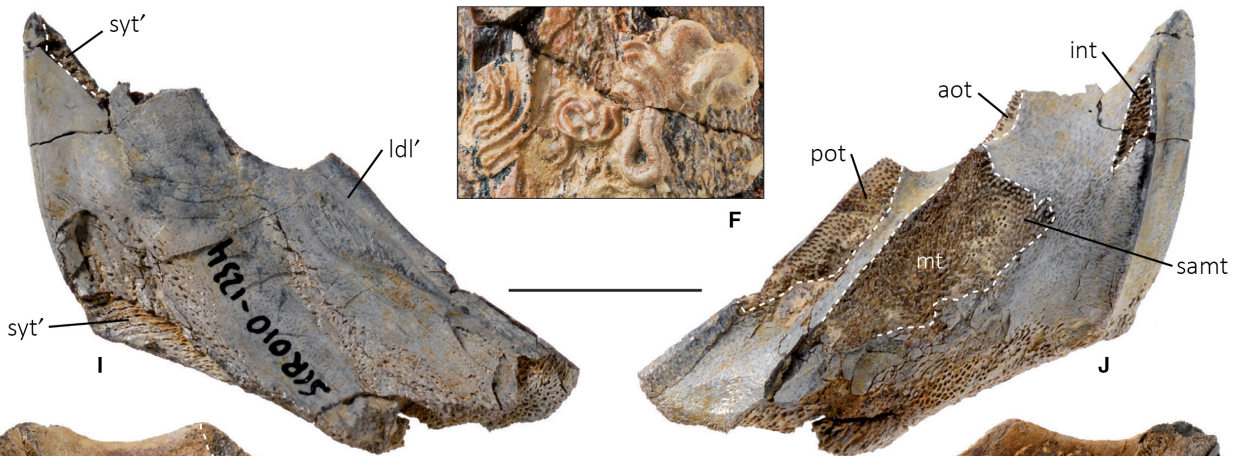
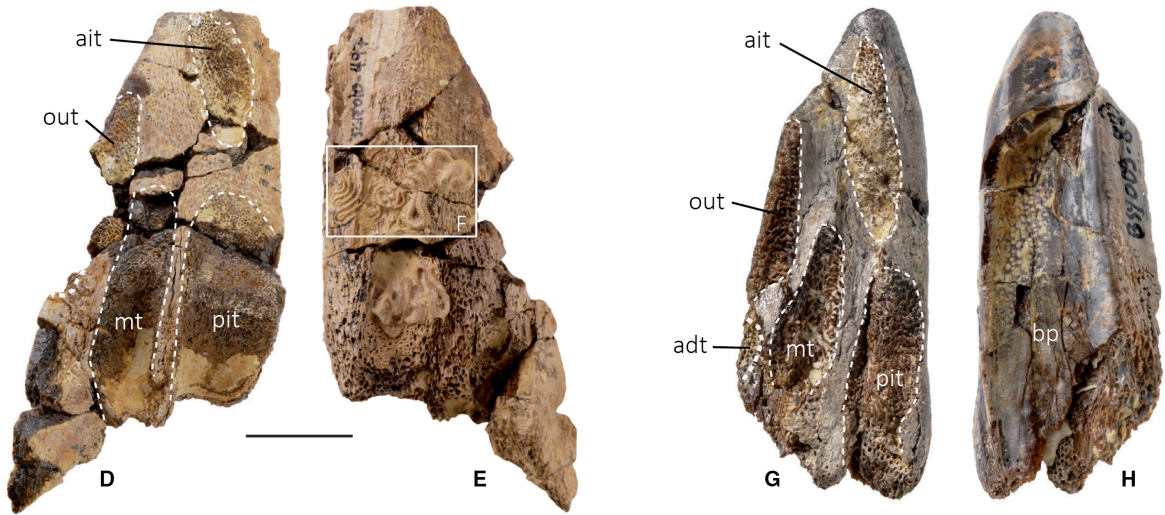
Ischyodus quenstedti Wagner, 1857

Figure 15A–L

Material. 16 fin spines. 34 dental plates from different positions in the jaw (mandibular and palatine): 9 palatine plates (3 left, 6 right) and 25 mandibular plates (12 right, 13 left).

Description of the fin spines. The fin spines are curved posteriorly with a concave posterior surface ornamented by two rows of tubercles, one on each edge of the posterior wall. The centre of the posterior surface shows a longitudinal ridge at its very base that transforms dorsally into a groove. The tubercles are present on the three upper quarters of the spine length and located on the latero-posterior edges. In one specimen (MJSN BSY008-612), an additional series of five pairs of tubercles very close to each other is present more basally, separated from the other series of tubercles. The largest and best preserved fin spine (MJSN SCR011-139, Fig. 15A–C) with a total length of 134.5 mm shows a denticulate part of 97 mm long. The spine thickness at the most proximal denticle of denticulate part of the spine equals 12.5 mm. The lateral faces of the spines are gently striated longitudinally (Fig. 15A).

Description of the dental plates. Mandibular plates showing the typical construction of the genus, i.e. occlusal tritors of vascular pleromin with large and centrally placed median tritor (mt), flanked labially by short antero-outer (aot) and longer postero-outer (pot) tritors, as well as a moderate inner tritor (int) that may be absent in large plates. The beak tip formed by the symphyseal tritors of laminated pleromin (Stahl (1999), ‘laminated beak tritors’) is not visible in occlusal view but the



laminated structure of the pleromin body is visible in apical or basal view, as well as on the abraded symphyseal part of basal surfaces (Fig. 15I, L, *syt'*). A median tritor tapers mesially and has a rounded mesial outline in large plates (Km = 22 mm), with a slight bifurcation in smaller plates (Km = 5–15 mm) and a symphyseal appendix, not necessarily developed though (Fig. 15J, *samt*). Small plates also show a larger inner tritor (MJSN SCR010-1234, Fig. 15J, *int*) or two parallel tritors of smaller size (MJSN BSY009-434; Km = 5.3 mm). Only the flat basal surfaces of the plates are well-preserved enough to show the abraded lateral descending lamina as a sectorial ledge (Fig. 15I, L, *ldl'*).

Palatine plates are triangular in oral view with four occlusal elongated tritors of vascular pleromin: the postero-inner (*pit*), antero-inner (*ait*), outer (*out*) and median (*mt*) tritors. In smaller plates (Kp = 7–12 mm) all tritors are almost equal in width, the median tritor being displaced mesially over the postero-inner tritor, and a small additional outer tritor is occasionally present (Fig. 15G, *adt*). Larger plates (Kp = 16–20 mm) show a relatively larger postero-inner tritor, as well as smaller sized median tritor occasionally displaced distally (MJSN TLB003-666, Kp = 20 mm). The basal surface is abraded in all dental plates, so that the lateral descending lamina cannot be observed, except in the mesial sector of basal pocket (Fig. 15H, *bp*). No vomerine plate has been found in the assemblage.

Remarks. The difference in size, shape and distribution of the tritors between small and large plates, both mandibular and palatine, suggests the presence of an ontogenetic series. The size difference of the plates themselves also indicates different ontogenetic stages and varies from Km = 17–24 mm and Kp = 16–20 mm for adult specimens down to Km = 5–8 mm and Kp = 7–12 mm for possible juveniles. In terms of functional morphology, small plates of juveniles show a grinding dentition, while the larger plates of adults fulfill a crushing function.

Ischyodus quenstedti is probably a junior synonym of *I. egertoni* (Buckland, 1835) from the Callovian and Kimmeridgian of southern England, as proposed by Popov *et al.* (2009), but the first nominal species is used in this work until a formal revision is published. *Ischyodus quenstedti* is the only species of this genus known in central Europe, so far in Germany (Wagner 1857; Popov *et al.* 2013). Other *Ischyodus* specimens from Switzerland were reported by Müller (2011) from the upper Kimmeridgian

Solothurn Turtle Limestones (NW Switzerland), without any assignment to a species because of the fragmentary nature of the material. However, they look very similar to our specimens and can be identified as *I. quenstedti* as well.

The fin spines are typical of the suborder Chimaeroidei (Stahl 1999) and differ from the fin spine material assigned to Hybodontoida in the absence of posterior opening at the base and two opposing rows of posterior denticles. We assign the fin spines to *Ischyodus quenstedti*, the only chimaeroid species identified in our assemblage based on dental plates.

Dermal denticles

We present the isolated dermal denticles separately, since their taxonomic value is very limited. Dermal denticles have different shapes depending on their position on the body and thus on their function (e.g. protection against abrasion, hydrodynamic; Cappetta 2012). Even so, some dermal denticle morphologies can be typical of certain taxa, allowing an identification, but only at a high taxonomic level. Here, we describe morphotypes, mainly following Thies & Leidner (2011) for the descriptive terminology and for the identification if no other reference is mentioned. Thies & Leidner (2011) provided a rich illustration of teeth and dermal denticles from articulated specimens.

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Superfamily HYBODONTOIDEA Owen, 1846
Morphotype 1
Figure 16A, B

Material. 12 dermal denticles.

Description. Massive denticles with a high crown and narrow, circular base. The crown is hook-shaped, pointing posteriorly. Ridges cover the whole crown and converge towards the apex.

FIG. 15. *Ischyodus quenstedti*, fin spine and dental plates, upper Kimmeridgian. A–C, fin spine (L = 134.5 mm), MJSN SCR011-139: A, right lateral; B, anterior; C, posterior view; arrow in C indicates position of most proximal denticle of denticulate part of the spine. D–F, right palatine (Kp = 16 mm, L = 60 mm), MJSN SCR010-497: D, oral; E, aboral view; F, enlarged detail of the aboral view of Fig. 15E showing epibionts (sabeliid tubes of *Glomerula gordialis*). G–H, right palatine (Kp = 7 mm, L = 26.5 mm), MJSN BSY009-883: G, oral; H, aboral view. I–J, left mandibular (Km = 6.6 mm; L = 34 mm), MJSN SCR010-1234: I, aboral; J, oral view. K–L, right mandibular (Km = 16 mm, L = 68 mm), MJSN SCR010-1000: K, oral; L, aboral view. **Abbreviations:** *adt*, additional tritor (inner or outer); *ait*, antero-inner tritor; *aot*, antero-outer tritor; *bp*, basal pocket; *int*, inner tritor; Km, 'reference width' of mandibular plate; Kp, 'reference width' of palatine plate; L, mesiodistal length; *ldl'*, preserved sectorial ledge of abraded lateral descending lamina; *mt*, median tritor; *out*, outer tritor; *pit*, postero-inner tritor; *pot*, postero-outer tritor; *samt*, symphyseal appendix of median tritor; *syt'*, laminated pleromin body of symphyseal tritor. All scale bars represent 1 cm. Colour online.

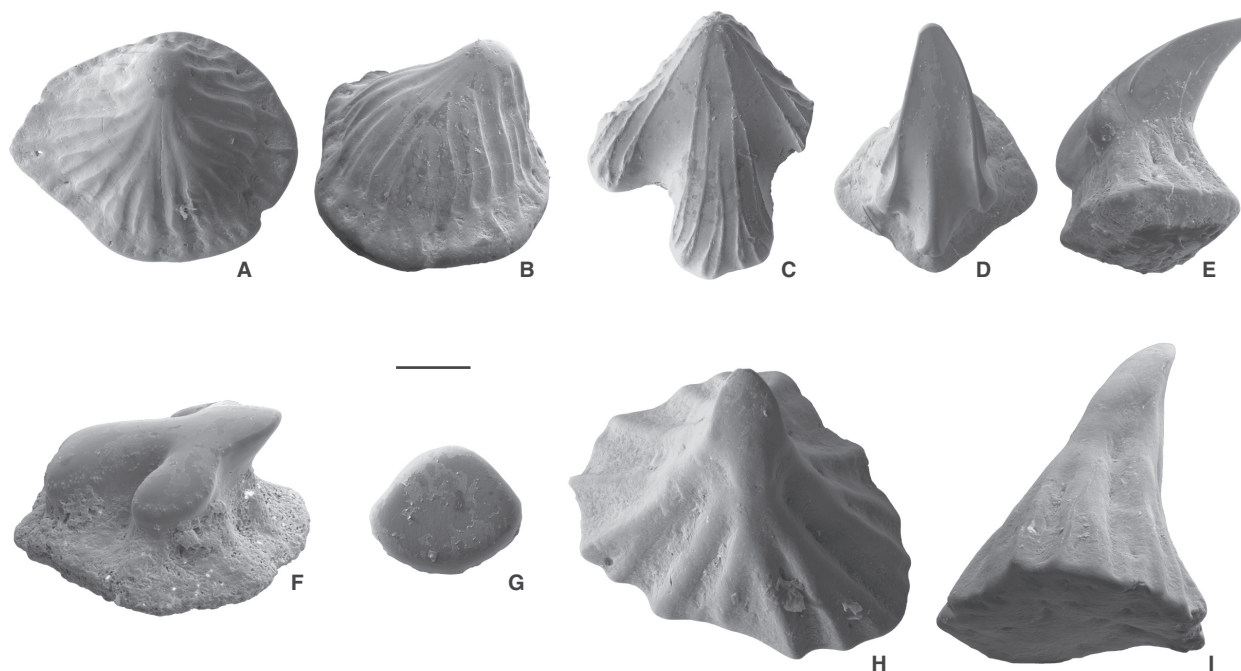


FIG. 16. Isolated dermal denticles, upper Kimmeridgian. A–B, morphotype 1, Hybodontoidea, MJSN TCH006-1814: A, apical; B, anterolateral view. C, morphotype 2, Neoselachii, MJSN BSY009-924 in occlusal view. D–E, morphotype 4, Squatinidae, MJSN TCH006-1613: D, apical; E, lateral view. F, morphotype 5, Rhinobatoidei, MJSN TCH006-1710 in lateral view. G, morphotype 6, Rhinobatoidei, MJSN TCH006-1558 in occlusal view. H–I, morphotype 8, Rhinobatoidei, MJSN BSY009-947: H, occlusal; I, lateral view. Scale bar represents 0.25 mm.

Remarks. Those denticles are typical of hybodonts. Their relatively small number compared to the high number of hybodont teeth found probably reflects a low replacement rate of their dermal denticles. This kind of thick, massive denticle is likely to play a protective role and be found on the ventral side of hybodonts with benthic habit.

Subcohort NEOSELACHII Compagno, 1977

Morphotype 2 Figure 16C

Material. Five dermal denticles.

Description. This morphotype never shows a preserved base but the crown is arrow-shaped. The crown is not smooth but ridges are present on the surface.

Remarks. Arrow-shaped denticles, more or less elongated, are found in several selachimorph genera, such as *Pseudorhina*, *Palaeoscyllium* and *Paracestracion* (Thies & Leidner 2011). They have not been observed on batoid taxa, so are here identified as Neoselachii indet. They can be found on the middle trunk, dorsal cranial and pectoral girdle regions.

Morphotype 3

Material. 27 dermal denticles.

Description. Undifferentiated denticles resembling morphotype 6 (see below and Fig. 16G) but with a tilted crown compared to the base and a low relief at its central, lower part. The crown is translucent in our material and higher posteriorly than anteriorly.

Remarks. This morphology seems widespread among neoselachians and is found in many genera (e.g. *Pseudorhina*, *Paracestracion*, *Phorcynis*, *Crossorhinus*, *Palaeocarcharias*) (Thies & Leidner 2011, e.g. pl. 17, fig. B2; pl. 19, fig. B–C).

Order SQUATINIFORMES de Buen, 1926

Family SQUATINIDAE Bonaparte, 1838

Morphotype 4 Figure 16D–E

Material. 38 dermal denticles.

Description. Denticles with a high base and elongated, gracile crown showing a central relief at its base. On both sides of this relief, the crown extends more posteriorly. The apex is flattened

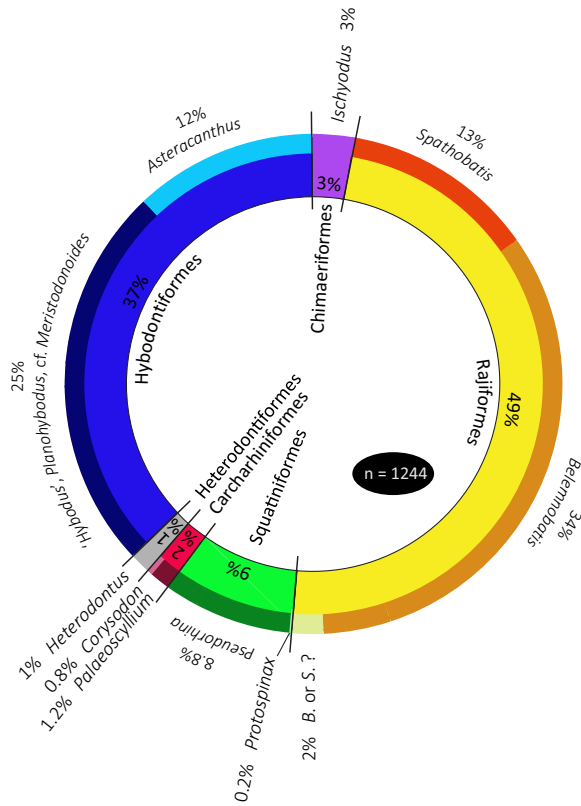


FIG. 17. Faunal spectrum at the genus level, based on teeth only and showing a strong dominance of Hybodontiformes and Rajiformes. The Chimaeriformes are also considered as one of the dominant taxa but are strongly underrepresented compared to other chondrichthyans because of their dentition limited to six non-renewable dental plates (Stahl 1999). Teeth fragments of 'Hybodus' sp. A were counted only when presenting the main cusp to limit bias induced by a high amount of isolated lateral cusplets. The record of the neoselachian shark *Paracestracion* is not visible in this graph but its presence in the faunal composition, probably very limited, is attested by a fin spine (MJSN BSY009-199, see Fig. 4Q–S). Abbreviation: B. or S., *Bellemnobatis* or *Spathobatis*.

in lateral view and the crown is translucent. In apical view, the crown shape resembles an elongated spade.

Remarks. This morphotype seems to be typical of the trunk and pelvic regions of *Pseudorhina* (Thies & Leidner 2011).

Superorder BATOMORPHII Cappetta, 1980
 Order RAJIFORMES Berg, 1940
 Suborder RHINOBAIDOIDEI Fowler, 1941
 Morphotype 5
 Figure 16F

Material. 46 dermal denticles.

Description. Narrow denticles with a knob-like to arrow-like crown. The base is circular in occlusal view and shows ridges arranged radially around the crown. The basal surface of the denticle is not flat, but convex. Contrary to morphotype 2, the surface is smooth and devoid of ridges.

Remarks. These denticles are found in all batoids illustrated by Thies & Leidner (2011) and are never attributed to shark taxa. Similar denticles identified as *Bellemnobatis* and *Spathobatis* are reported in the same publication. Since those two batoid taxa are the only ones identified based on teeth in the Porrentruy material, the dermal denticles can be assigned to both of them and are thus identified as Rhinobatoidei. They can be found at the level of the rostrum, at the centre of the disc and on the anterior edge of the wings.

Morphotype 6
 Figure 16G

Material. 98 dermal denticles.

Description. Undifferentiated denticles (see Thies & Leidner, 2011), flat with a crown overhanging the neck and of oval shape, triangular or diamond-shaped with rounded edges. Most specimens show a very translucent crown.

Remarks. Similar denticles were observed in many genera such as *Phorcynis*, *Palaeocarcharias*, *Corysodon*, *Sphenodus*, as well as in batoids. Since only four teeth of *Corysodon* have been identified in our material, those denticles are more likely to belong to Rhinobatoidei.

Morphotype 7

Material. 14 dermal denticles.

Description. This morphotype closely resembles morphotype 5 except that the base is high with a flat and stellate basal surface. The crown is smooth, often developed in an arrow shape and is higher on its posterior end.

Remarks. Again, these denticles are typical of batoids and identified as Rhinobatoidei.

Morphotype 8
 Figure 16H–I

Material. Five dermal denticles.

Description. Thorn-like denticles with a high base and a pointed crown that grows from the neck. The limit between the base and

the crown is sometimes unclear. The denticle points gently posteriorly.

Remarks. This dermal denticle morphology seems to be typical for batoids. Thies & Leidner (2011) found this morphotype only in *Belemnobatis sismondae*. However, we do not exclude the possibility that it could occur in other batoid genera and it will thus be identified as *Rhinoba-toidei*.

FAUNAL COMPOSITION

As mentioned in Material and Method above, the faunal spectrum (Fig. 17) is based on dental material only. In the case of '*Hybodus*' sp. A, a strong bias is induced by an important number of tooth fragments and isolated lateral cusplets, representing 731 fragments in total. Several of them might have originally belonged to the same tooth, given the large number of lateral cusplets (up to six) present in teeth of this taxon. Without those fragments, Hybodontidae represent 25% of the faunal spectrum. When included, the percentage of this group more than doubles and reaches 53%. To limit this bias, we excluded those fragments from the faunal spectrum and record only complete teeth, or fragments clearly displaying the main cusp, keeping in mind that the effective percentage of the Hybodontidae dental material lies somewhere between 25 and 53%.

Hybodont sharks (Hybodontiformes) and rays (Rajiformes) are the best represented groups, with their dental remains making up 86% of the total amount of dental material. The chimaeroid fishes (Holocephali), represented by a single species (*Ischyodus quenstedti*), correspond to a small percentage of the material (3%). However, *Ischyodus* individuals grow a limited number of six dental plates (statodont dentition *sensu* Patterson 1992), against hundreds to thousands of continuously renewed teeth for sharks and rays (lyodont dentition; see also Stahl 1999), and are thus comparatively underrepresented when only isolated remains are considered. The same applies to the hybodont *Asteracanthus*, which possesses significantly fewer teeth than other sharks (see the articulated dentition of *Asteracanthus* in Rees & Underwood 2008, p. 136). The Squatiniformes (angel sharks) are the most common modern sharks (75% of Squalomorpha, 9% of all dental material), whereas Heterodontiformes and Carcharhiniformes represent only 3% of the total dental remains. Regarding the fin spine material, 47% ($n = 16$) is composed of chimaeroid fin spines, indicating a marked presence of holocephalians in the Porrentruy palaeoenvironment. Hybodontiform fin spines represent 47% ($n = 16$) of the fin spine material, while neoselachian shark fin spines constitute the remaining 6% ($n = 2$).

Stratigraphically, beds 2100 to 4500 (Nerinean Limestones and *Virgula* Marls, *Mutabilis* and *Eudoxus* ammonite zones respectively, see Fig. 2) yielded more than 90% of the chondrichthyan remains. In fact, bed 2100 has been nicknamed the 'fish beds'. Vertebrates are not common in the extensively excavated Banné Marls (lower Kimmeridgian), whose rich fossil content largely consists of invertebrates. The absence of hybodonts other than *Asteracanthus* in the Banné Marls could be explained by differences in their diet and lifestyle, since vertebrates and thus prey items such as fish are generally scarce in this section. Durophagous chondrichthyans and/or bottom-dwellers might have been favoured by a rich benthic invertebrate fauna, but the abundance of chondrichthyans in the Banné Marls remains very low.

In the upper Kimmeridgian, the stratigraphical distribution reflects a sampling bias, with marly and/or more intensively excavated beds (beds 2100–4000 and 4500) clearly standing out. Still, it is noteworthy that neoselachians decrease in the marly layer 4500, while the presence of hybodonts and chimaeras increases. The abundance of *Pseudorhina* in particular becomes comparatively low in bed 4500, indicating that angelsharks might have been more sensitive to terrigenous input and resulting water turbidity than rays for instance. Spatially, the dominance of Hybodontiformes and their association with Rajiformes is confirmed in the *Virgula* Marls over the three sites that yielded more than 90% of the chondrichthyan remains (i.e. BSY, TCH and SCR; Fig. 1). Those two taxa represent 80–90% of the chondrichthyan remains in each of these three localities. It is noteworthy that the genus *Corysodon* (Carcharhiniformes) is reported for the first time in Switzerland.

COMPARISON WITH OTHER EUROPEAN FAUNAS

During the Jurassic, neoselachians underwent an impressive radiation and colonized all marine realms. In parallel, the thus far dominant hybodont sharks were declining, confined to more and more restricted environments of reduced salinity or even freshwater, until their extinction at the end of the Cretaceous (Cuny & Benton 1999). European chondrichthyan faunas from the Kimmeridgian have already been studied in several localities: Ringstead in southern England, Oker and Uppen in northern Germany, Solnhofen and the Nusplingen area in southern Germany, Solothurn in north-western Switzerland, Cerin in central eastern France, etc. (Wenz *et al.* 1993; Thies 1995; Duffin & Thies 1997; Underwood 2002; Kriwet & Klug 2004; Müller 2011). The chondrichthyan fauna of Ringstead is the most similar to Porrentruy insofar as all genera identified in the Porrentruy material are present in

the Ringstead assemblage, except for the genera *Asteracanthus* (Hybodontiformes), *Corysodon* (Carcharhiniformes) and *Belemnobatis* (Rajiformes). According to Klug & Kriwet (2013a) the absence of the former could be due to the open marine palaeoenvironment of Ringstead, where hybodonts are not common. The rays are represented in Ringstead only by *Spathobatis*, a genus that is closely related to *Belemnobatis*. The neoselachian shark diversity is greater in Ringstead but all taxa absent from our assemblage are also associated with deeper water conditions (Underwood 2002). An exception is *Protospinax* that is described as very cosmopolitan and represented by only three teeth in our material.

Asteracanthus remains are common in England (Underwood 2002), but scarce in Germany or France, except in Normandy (Furic 2016; Rigal & Cuny 2016). The record of numerous hybodonts in Porrentruy is reminiscent of the fauna of northern Germany but contrasts with the fauna of southern Germany (Nusplingen, Solnhofen), where they are scarce, and with central eastern France (Cerin), where hybodonts apparently are absent (Duffin & Thies 1997; Kriwet & Klug 2004). On the other hand, our assemblage resembles Cerin, and Moorberg and Uppen in northern Germany (Thies 1983) insofar as rays are the dominant neoselachians, contrary to the fauna recorded in southern Germany (Kriwet & Klug 2004).

The association of hybodonts and rays is also found in the fossil assemblage of north-western Germany, where it corresponds to a palaeoenvironment of reduced salinity (Duffin & Thies 1997; Underwood 2002) but the dominance of those two taxa could also be related to near- and in-shore palaeoenvironments (Klug & Kriwet 2013a). In the Purbeck Group of Dorset (southern England), a marked dominance of rays and hybodonts has also been reported, in a context of fluctuating salinity (Underwood & Rees 2002). The fauna of the neighbouring locality of Solothurn is comparable to Ajoie, but lacks batoids, which might reflect a sampling bias detrimental to millimeter-sized remains. Our assemblage is characterized by the clear dominance of the hybodonts and rays, not observed in neighbouring localities such as Solnhofen or Cerin.

This faunal comparison must be considered carefully, since sampling methods differ from those used in the lithographic limestones (i.e. Solnhofen, Nusplingen, Solothurn, Cerin) and more marly rocks. Especially small material can be sampled in large amounts much more easily from a looser lithology. While the most important part of the material of Porrentruy comes from two marly intervals ('fish beds' and bed 4500), the material of southern Germany and central eastern France was yielded by lithographic limestones and consists mostly of articulated material (Duffin & Thies 1997). A quantitative comparison between these sites can easily be biased by the

differences in lithology and nature of the fossils (isolated vs articulated remains).

Chimaeroid fishes are represented by a single species (*Ischyodus quenstedti*) in Porrentruy. The chimaeroid diversity is thus poor when compared to other Kimmeridgian European assemblages in both marine (England and France) and lagoonal (Germany) environments, where up to five genera and about seven species are recorded, in addition to a relict species of a myriacanthid fish (Popov *et al.*, 2009). This could be due to not strictly marine conditions on the Porrentruy platform, since the genus *Ischyodus* is known to be relatively more euryhaline than other Mesozoic chimaeroids (Nessov & Averianov 1996; Nessov 1997).

TAPHONOMY

Transportation bioerosion

The chondrichthyan dental material is considered to be largely autochthonous. While rounded crowns and roots (Fig. 5E–F) suggest transportation of part of the material, teeth generally have better conserved ornamentation (e.g. Figs 5A–D, G–H, 6A–S, 7D–X, 8), cutting edges or pointed cusps (e.g. Figs 5K–Q, 6A–S, 13, 14A–C, M–P). Also, the presence of fin spines with well-preserved ornamentation supports the autochthonous character of several chondrichthyan groups in the assemblage. Several *Asteracanthus* teeth still display the root (see Figs 7D–G, K–M, 8A–G) and it has been proposed that hybodonts, contrary to neoselachians, only shed the crown during tooth replacement, the root being naturally resorbed (Rees & Underwood 2006; Underwood & Cumbaa 2010). Complete teeth would thus be a sign of post mortem deposition in Hybodontiformes, as opposed to the teeth shed during their life in the tooth replacement process. However, this capacity for resorption is not mentioned by other authors and is only based on the low number of root-bearing hybodont teeth in fossil assemblages. The preservation of the root of several *Asteracanthus* teeth is probably due to its greater robustness. Teeth most commonly displaying the root in our assemblage belong to rhinobatids that show a more rounded and compact design, making the root more resistant to mechanical damage through transportation. Bioerosion is the most probable cause of loss of the root in many chondrichthyan teeth. Indeed, traces identified as the ichnospecies *Mycelites ossifragus* Roux, 1887 (see Underwood *et al.* 1999; Cappetta 2012) and attributed to a green algae that attacks the dentine (Bernhauser 1953), are visible in SEM pictures of teeth (Fig. 14K) and dermal denticles. Larger marks, probably modern, affect the enameloid of several teeth (Fig. 18).

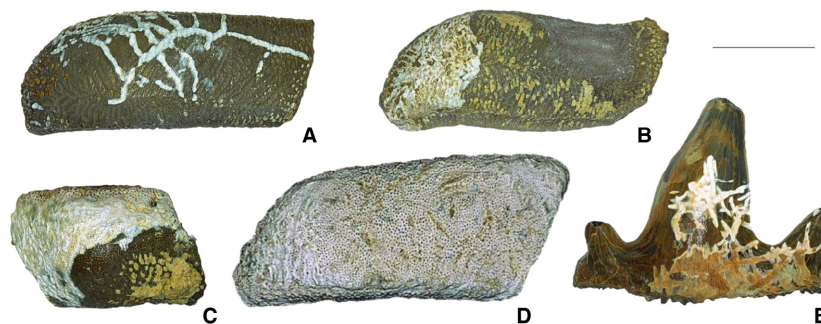


FIG. 18. Different types and extents of bioerosion on hybodont teeth, resulting in white traces in the enameloid layer. A–D, *Asteracanthus* sp., lateral teeth in occlusal view; A, MJSN SCR002-672; B, MJSN SCR002-1150, abraded area on the right side of the tooth is due to enameloid sampling for geochemical analysis; C, MJSN SCR003-1445; D, MJSN SCR008-23. E, *Planohybodus* sp., MJSN SCR008-12 in labial view. Scale bar represents 1 cm for *Asteracanthus* (A–D), 5 mm for *Planohybodus* (E). Colour online.

Within the chimaeroid dental material, mandibular plates predominate ($n = 25$; 74%) and palatine plates are less common ($n = 9$; 26%), while vomerine plates are totally absent. This numerical regression is typical of chimaeroid assemblages known from Mesozoic concentrate-type deposits (e.g. Popov & Machalski 2014) and seems to correlate mainly with a reduction in size and sturdiness from mandibular, to palatine and finally vomerine plates (EVP, pers. obs.). As a result, smaller and less resistant vomerine plates are probably preferentially lost during taphonomic and/or sampling processes. The chimaeroid dental plates show different degrees of alteration (Fig. 15D–J) and the fin spines preservation is generally much better, indicating that at least a part of the chimaeroid material is probably autochthonous. The dental plates show a total loss of the superficial ‘compact glossy tissue’ that usually covers the unworn part of both oral and aboral surfaces. Superficial structures such as the descending lamina are barely visible and the trabecular dentine of the plates is strongly abraded. The larger plates show a stronger degree of corrosion than the smaller ones (compare Fig. 15I–L) and sometimes display epibiont traces (Fig. 15E–F) determined as sabelliid tubes of *Glomerula gordialis* von Schlotheim, 1820 (A. P. Ippolitov pers. comm. 2016). Thus all chimaeroid dental material could have been transported over a short distance and exposed for longer periods of time on the sea floor.

PALAEOECOLOGY

Tooth morphology and inferences of diet

Fish tooth morphology is traditionally used to infer diet (Cappetta 2012). However, direct evidence of predation in the fossil record (Vullo 2011), stomach content of extant chondrichthyans (Collins *et al.* 2007) as well as biomechanical studies (Whitenack & Motta 2010;

Whitenack *et al.* 2011) have shown that tooth morphology alone can only give a broad idea of the diet. Since teeth can perform several functions (e.g. different movements during the feeding process, gripping of the female during mating), their morphology is not necessarily related to the prey item only (Whitenack & Motta 2010). The diet proposed below based on tooth morphology is thus potentially much more diverse.

Lifestyle and diet

The fauna described above is dominated by benthic and/or potentially durophagous taxa, indicating a well-oxygenated sea bottom, compatible with the rich invertebrate associated fauna recorded (Koppka 2015). Adaptation to a benthic lifestyle can be recognized in the morphology of the angelshark *Pseudorhina* and the batoids *Belemnobatis* and *Spathobatis*, all showing a dorso-ventrally flattened body (Kriwet & Kussius 1996; Rees 2012). The rays *Belemnobatis* and *Spathobatis* have a so-called crushing-type dentition, adapted to a durophagous diet, whereas *Pseudorhina* was rather piscivorous and is described as a probable ambush predator, like its extant relative *Squatina* (Underwood 2002; Guinot *et al.* 2012). It is most likely that heterodontiformes lived near the sea bottom with a diet composed of small, hard prey, such as crustaceans, molluscs and echinoderms, just like their extant representatives (Compagno 1999; Bone & Moore 2008). A similar diet is possible for the chimaeroid *Ischyodus* based on its dentition. This genus is also recorded in several shallow water environments (Hoganson & Erickson 2005).

Regarding the small amount of neoselachian shark teeth in the material, these were probably more abundant in other ecological niches and only occasional visitors to the Porrentruy carbonate platform. The selachimorph taxa recorded in Porrentruy are indeed primarily related

to coral reefs (Carrier *et al.* 2010), which are not common in our settings. Hybodontid sharks ('*Hybodus*', *Planohyodus*) display a wide range of tooth morphology and possible associated diet. They are known in almost all marine palaeoenvironments (Underwood 2002), and tolerate restricted settings such as reduced salinity (e.g. Fischer *et al.* 2011; Klug *et al.* 2010). The *Asteracanthus* dentition is typically associated with a durophagous diet, indicating that it could easily feed on bivalves, small ammonites and crustaceans. In the literature, *Asteracanthus* is alternately assumed to be a surface or bottom-dweller, based on its possible diet (Cuny 2002; Rees & Underwood 2008) and the temperature reflected by the stable isotope composition of its teeth (Lécuyer *et al.* 2003). Leuzinger *et al.* (2015) demonstrated with stable isotope analyses that this genus tolerated reduced salinity, broadening the range of potential ecological niches and prey items.

Regarding the chimaeroid fishes, the relationship between the mesiodistal length of the mandibular plate (L) and total body length (TL) corresponds to 4–6% in all Recent families of holocephalians (EVP pers. obs.). By correlation, the size differences observed in *I. quenstedti* mandibular plates of Porrentruy (L = 25 mm and Km = 5.3 mm for MJSN BSY009-434, to L = 105 mm and Km = 24 mm for MJSN SCR010-22) could indicate specimens differing in body size by a factor of four to five (TL = 400–600 mm against TL = 1700–2600 mm). The Porrentruy platform could have been a place of spawning and/or fattening for *Ischyodus*, just like nearshore sandy bays and large estuaries for the extant *Callorhinchus* (Last & Stevens 2009). According to current reconstructions of *Ischyodus quenstedti*, the genus *Callorhinchus* shows the most comparable morphology among extant chimaeroid fishes (Popov *et al.* 2013).

WATER SALINITY

The Porrentruy platform might have undergone salinity fluctuations because of its complex topography causing lateral variations in water depth, and creating semi-confined lagoons in which freshwater could have been trapped during the wet winters. However, the environment is generally considered to have been marine.

Salinity indications of the associated fauna

The invertebrate fauna of Porrentruy generally indicates marine conditions with the presence of numerous marine bivalve taxa (Koppka 2015), foraminifera (Gretz *et al.* 2010), echinoderms and corals. The last two are scarce, however, and the corals probably only built small patches

rather than large barrier structures (Gretz *et al.* 2010). More than 600 ammonites have also been discovered and support a marine setting (Comment 2012). However, the ostracod fauna indicates salinity variations in time, ranging from pliohaline to brachyhaline conditions (i.e. brackish to marine). These variations correlate well with the alternate presence/absence of ammonites in the stratigraphic section. The stratigraphic origin of all chondrichthyan remains also matches the brachyhaline conditions (i.e. marine) indicated by the ostracods (Schuckack *et al.* 2013).

Abundant and diverse marine reptiles have been reported in the same deposits in Porrentruy, including turtles (e.g. Plesiochelyidae, Thalassemydidae; Anquetin *et al.* 2014, 2015; Püntener *et al.* 2015) and crocodylians (Teleosauridae, Metriorhynchidae; Schaefer 2012). Their presence is consistent with a coastal marine environment in the Porrentruy area (Marty & Billon-Bruyat 2009). Within bony fish, the dominating taxa are marine caturids, as well as pycnodonts and *Scheenstia* (lepisosteiform), both euryhaline (LL pers. obs. 2015).

Salinity indications of the chondrichthyan fauna

All the chondrichthyan taxa recorded in the Kimmeridgian of Porrentruy are consistent with marine conditions. However, the following elements may indicate reduced salinity:

1. Presence of several taxa considered to be cosmopolitan (rays, protospinacids, *Palaeoscyllium*) (Underwood 2002; Kriwet & Klug 2004) and within those, a clear dominance of rays.
2. Within the subcohort Neoselachii, clear dominance of rhinobatid rays, described as being more tolerant to restricted conditions than other neoselachians (Underwood 2002).
3. Extremely reduced number of neoselachian sharks, considered stenohaline in the Jurassic.
4. Presence of *Palaeoscyllium*, considered to be the oldest known neoselachian shark to tolerate freshwater, so far only in Early Cretaceous deposits (Sweetman & Underwood 2006).
5. Dominance of rays, hybodonts and *Ischyodus*, all known to tolerate reduced salinity (Nessov & Averianov 1996; Nessov 1997; Rees & Underwood 2008). Jurassic *Ischyodus* could also tolerate freshwater conditions (Popov & Shapovalov 2007).
6. Absence of chimaeroid taxa other than the euryhaline *Ischyodus*, contrary to other Kimmeridgian assemblages known in Europe (Popov *et al.* 2009).
7. Dominance of rays and hybodonts potentially linked to reduced salinity conditions (Duffin & Thies 1997; Underwood & Rees 2002; Rees *et al.* 2013).

8. Euryhaline character of the hybodont *Asteracanthus*, recently demonstrated through stable isotope analyses, so far only in the study area (Leuzinger *et al.* 2015).

CONCLUSION

This is the first study of Kimmeridgian chondrichthyans using a large and diverse dataset from a Swiss locality. Until now, this has been one of the regions missing from our knowledge of Late Jurassic chondrichthyan faunas at the regional scale of Europe. It will surely provide important clues for the analysis of more global palaeobiogeographical patterns in an area influenced by both the Tethyan and Boreal realms. This new chondrichthyan assemblage from Porrentruy stands out with its abundance of hybodonts and rays, and its scarcity of modern sharks. While some similarities between our assemblage and other localities (especially the nearby locality of Solothurn) can be highlighted, the dominance of hybodonts observed in Porrentruy is more reminiscent of the assemblages of northern Germany and southern England (Duffin & Thies 1997; Underwood 2002). A striking difference with closer localities (Cerin, Nusplingen, Solnhofen) is the very low abundance of neoselachian sharks in Porrentruy, whereas these experienced a strong radiation in Jurassic marine realms of western Europe. It is not clear in what terms the Porrentruy environment was different and could have acted as a shelter for hybodonts, rare or completely absent from the contemporaneous and neighbouring lagoonal environments of Nusplingen and Cerin. Salinity fluctuations might have regularly occurred in the platform, preventing modern sharks from spreading into the Porrentruy area (assuming those were stenohaline), and allowing hybodonts to thrive.

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This published work and the nomenclatural act it contains, have been registered in ZooBank: <http://zoobank.org/References/25637E2D-F26A-4BBF-AFDA-119A63FEC61F>

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