Neoselachian remains (Chondrichthyes, Elasmobranchii) from the Middle Jurassic of SW Germany and NW Poland

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New neoselachian remains from the Middle Jurassic of SW Germany and NW Poland are described. The locality of Weilen unter den Rinnen in SW Germany yielded only few orectolobiform teeth from the Aalenian representing at least one new genus and species, *Folipistrix digitulus*, which is assigned to the orectolobiforms and two additional orectolobiform teeth of uncertain affinities. The tooth morphology of *Folipistrix* gen. nov. indicates a cutting dentition and suggests specialised feeding habits. Neoselachians from Bathonian and Callovian drill core samples from NW Poland produced numerous selachian remains. Most teeth are damaged and only the crown is preserved. Few identifiable teeth come from uppermost lower to lower middle Callovian samples. They include a new species, *Synechodus prorogatus*, and rare teeth attributed to *Palaeobrachaelurus* sp., *Pseudospinax*? sp., *Protospinax* cf. *annectans* Woodward, 1919, two additional but unidentifiable *Protospinax* spp. and *Squalogaleus* sp. Scyliorhinids are represented only by few isolated tooth crowns. No batoid remains have been recovered. The two assemblages contribute to the knowledge about early neoselachian distribution and diversity.

Key words: Chondrichthyes, Neoselachii, Jurassic, Germany, Poland, taxonomy, diversity.

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Introduction

Neoselachii is a well-defined monophyletic clade and represents one of the most successful groups of selachians. The fossil history of neoselachians encompasses almost 250 million years and extends back at least to the Early Triassic (Thies 1982) although rare isolated teeth from Palaeozoic strata may represent plesiomorphic members of this group (e.g., Duffin and Ward 1983; Turner and Young 1987). The first major radiation and diversification event of neoselachians is related to the Rhaetian transgression that produced extensive shallow epicontinental seas over most of western Europe (Cuny and Benton 1999). The Early to Middle Jurassic radiation of neoselachians heralds the first appearance of many extant groups. In the Late Jurassic almost all neoselachian clades were present. During the latest Jurassic and the beginning of the Cretaceous they rapidly diversified and in the Early Cretaceous shark faunas of modern character appeared. Parallel to the radiation of modern sharks, the hybodonts decreased and at the end of the Cretaceous period they became extinct. Batoids are known since the Toarcian, Early Jurassic (Thies 1983; Delsate and Candoni 2001). They are the sister-group to the neoselachian sharks (Carvalho 1996). In the Late Jurassic they became more abundant in the fossil record.

European Early and Middle Jurassic selachian records have been reported from Sweden (Rees 2000), Denmark (Rees 1998), Northern Germany (Thies 1983, 1989, 1993; Cappetta 1987), Southern Germany (Quenstedt 1852, 1885; Woodward 1889; Frass 1896; Thies 1992, 1993), Northern France (Duffin and Ward 1993), Luxembourg (Delsate 1995), Belgium (Delsate and Thies 1995; Delsate and Godefroit 1995; Delsate et al. 2002), and England (Duffin and Ward 1983). Most of these faunas are, however, dominated by hybodonts. The most diverse Middle Jurassic neoselachian fauna occurs in England (Underwood and Ward in press). This fauna elucidates the rapid diversification of early neoselachians and shows how poor our knowledge concerning these selachians still is.

In this paper, I will present new selachian records from the Middle Jurassic of Germany and Poland. Although the collection is rather small, it contributes to the knowledge about early neoselachian distribution and diversity.

Localities and material

The material described herein comes from two localities in SW Germany and NW Poland (Fig. 1A). The SW German site is located near the small village of Weilen unter den Rinnen in Baden-Württemberg (Fig. 1B). Here, fossil-bearing strata of the so-called "Opalinuston" (Dogger α) are exposed, which are assigned to the lower Aalenian based on the occurrence of the ammonite *Leioceras opalinum*. Unfortunately, no other ammonites have been found so that it is not clear whether the selachian remains come from the lower or upper parts of the lower Aalenian. The thickness of the Dogger α reaches almost

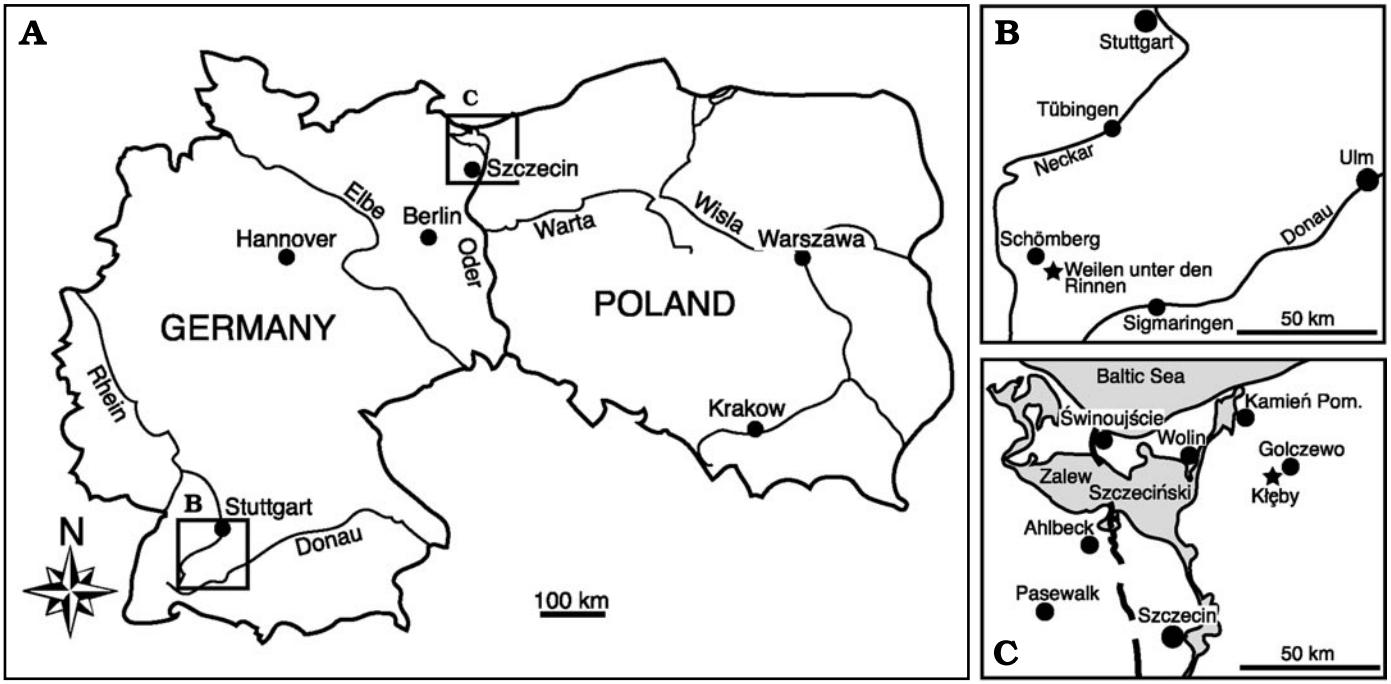

Fig. 1. Map of Germany and Poland (**A**) showing localities of Weilen unter den Rinnen (**B**) and Kłęby 1/37 (**C**) that yielded the selachian material described in this paper.

130 m in Baden-Württemberg (Swabian Alb) and consists of alternating layers of clays, clayish marls with occasional layers of marls and calcareous concretions. Generally, the "Opalinuston" is not very fossiliferous. The selachian material in this study and additional microfossils were obtained by bulk sampling, processing and microscope picking. In addition to the rare selachian teeth, numerous otoliths of actinopterygians and statoliths of teuthids were recovered. This material will be housed in the fossil fish collection of the Staatliches Museum für Naturkunde, Stuttgart.

The Polish locality is situated within the northern German-Polish trough. Here, Late Jurassic strata are exposed while Middle Jurassic sediments are only known from drill cores. The Middle Jurassic selachian remains reported on herein were recovered from an ore drill core (Klemmen 1/37 referred to as Kłęby 1/37 in the following), which comes from Kłęby, S of the city of Kamień Pomorski, E of Wolin, NW Poland (Fig. 1C). The drill core samples and the material described herein will be housed in the collections of the Bundesanstalt für Geowissenschaften und Rohstoffe in Berlin. The drill core samples were partially (about 500 g) processed with H_2O_2 and screen washed for microfossils in the course of an extensive study of gastropods (e.g., Gründel 1998). The stratigraphy of the drill core is based on ostracodes (Gründel 1999; Table 1). The remaining residues contain abundant ostracodes, otoliths, and fish teeth. The selachian material consists mainly of isolated teeth of neoselachians and a single find of a very fragmentary hybodont remain (Fig. 2A–C). Fish remains are rather rare in Bathonian samples but more abundant in Callovian ones of the drill core while Bajocian sediments have not yielded any vertebrate remains so far. Bathonian selachians are represented by two dozens isolated, mainly very fragmentary tooth crowns of unidentified taxa only. The Callovian material contains about 50 teeth most of which are damaged or lacking the root. Most fish remains are confined to samples

Table 1. Stratigraphy of Kłęby 1/37 drill core (revised after Gründel 1999) and distribution of vertebrate remains.

Depth	
240.5–249.5 m	uppermost lower to lower middle Callovian Numerous actinopterygian teeth and otoliths. Selachians: *Pseudospinax*? sp., *Palaeobrachaelurus* sp., *Synechodus prorogatus* sp. nov., *Protospinax* cf. *annectans*, *Protospinax* sp. 1, *Protospinax* 2, *Squalogaleus* sp.
249.5–252.5 m	middle Callovian? (no ostracodes) No vertebrate remains
253.6– ~265 m	upper Callovian Highest abundance of selachian and actinopterygian teeth and otoliths. Fragmentary remains of Hybodontiformes indet. All neoselachian teeth fragmentary and unidentifiable
265–291.6 m	uppermost lower to upper Bathonian Selachian and rare actinopterygian teeth, some otoliths. All selachian teeth fragmentary and unidentifiable.
291.1–316.5 m	? (no ostracodes) No vertebrate remains
316.5–370.0 m	upper Bajocian No vertebrate remains

of Callovian age (see below). Almost all taxonomically identifiable teeth come from samples of uppermost lower to lower middle Callovian age. Here, the highest taxonomic diversity is identifiable. Unfortunately, the material is not very abundant and most specimens lack the root partially or completely. Thus, a specific identification of many specimens is not possible. Otoliths and isolated teeth of actinopterygians occur in rather high numbers in all vertebrate-bearing samples (Table 1).

Institutional abbreviations.—BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Systematic palaeontology

Remark.—The tooth terminology follows that of Cappetta (1987).

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Superorder Galeoidea Carvalho, 1996
Order Orectolobiformes Applegate, 1972
Family Hemiscylliidae Gill, 1862
Genus *Pseudospinax* Müller and Diedrich, 1991

Type species: *Pseudospinax pusillus* Müller and Diedrich, 1991 from the Cenomanian of NW Germany.

Pseudospinax? sp.

Fig. 2B.

Material.—Two isolated teeth lacking roots (BGR X 12500, BGR X 12501), Kłęby 1/37: 244.8–245.7 m. Callovian.

Description.—The crown of both teeth is very flat labio-lingually and completely smooth on both lingual and labial crown faces. The labial crown face is plane and mesio-distally expanded with a cordiform outline. The basal edge is regularly convex. In lateral view, the labial face is also more or less flat without any concavity between central cusp and crown shoulder. The central cusp is slender, pointed and bent lingually. The transverse cutting edge is distinct and is continuous between the central cusp and the lateral heels. The cutting edge of the distal heel is angled forming an incipient, rudimentary cusplet whereas the mesial one is convex without any cusplet. The lingual face is much reduced and more convex. The lingual protuberance is prominent and supports a tapering and rather short lingual uvula. The root is completely missing.

Remarks.—The genus *Pseudospinax* was erected for isolated teeth from the Cenomanian of NW Germany by Müller and Diedrich (1991). Underwood and Mitchell (1999) attributed material from the Albian of England to this genus and presented an amended diagnosis. The main distinguishing feature from similar teeth of *Protospinax* is mainly the absence of a basal concave labial crown edge, a lower root and a less well defined uvula. Subsequently, Underwood (2002) attributed an isolated tooth crown from the Kimmeridgian of England to this genus expanding its range into the Jurassic. The specimens from Kłęby exhibit the typical crown morphology of teeth of *Pseudospinax*. However, the character "round and not concave labial crown edge" seems to vary within *Protospinax* from being absent to present. Consequently, the attribution of the specimen to *Pseudospinax* is provisional until additional material is available to study its morphology in more detail.

Family Brachaeluridae Applegate, 1972
Genus *Palaeobrachaelurus* Thies, 1983

Type species: *Palaeobrachaelurus bedfordensis* Thies, 1983 from the Middle Jurassic of southern England.

Palaeobrachaelurus sp.

Fig. 2C.

Material.—A single tooth (BGR X 12502), Kłęby 1/37: 244.8–245.7 m. Callovian.

Description.—The single specimen is rather small. The main cusp is bulky, upright and bent lingually with an abraded apex. The tooth crown is mesio-distally expanded and displays well-developed lateral heels with two pairs of lateral cusplets. The first pair of cusplets is distinctly separated from the main cusp. The outer lateral cusplets are only rudimentary. The labial face of the tooth crown is convex in both apico-basal and mesio-distal directions. The base of the crown overhangs the root labially with a prominent apron. The apron is broad and rectangular in labial view with divergent margino-lateral margins and a slightly centrally concave labial margin. The lingual face of the crown is very convex and continues into a short but broad and tongue-shaped uvula covering the lingual protuberance of the root almost completely. The occlusal surface of the uvula is flat. The crown-root junction is slightly furrowed and marked by a neck collar. The tooth crown is completely smooth without any ornamentation or sculpture.

The root is hemiaulacorhize with a central foramen that is connected to a second smaller one via a shallow canal on the surface of the root. There is a rather distinct medio-lingual foramen that opens onto the lingual face of the protuberance just below the neck collar. The root lobes are flared and jut out below the crown marginally in labial view. Lingually, they meet to form the protuberance, which is broad in basal view. The area enclosed by the root lobes is flat and of V-shaped outline. The central foramen opens into the area between the root lobes. The basal surfaces of the root lobes are flat. Two margino-lingual foramina are present on one side of the root, while there is only a single on the other.

Remarks.—The tooth from Kłęby displays all characteristic features of orectolobiform teeth (e.g., bilaterally symmetrical, overall crown morphology, hemiaulacorhize root). The morphology matches perfectly the one of teeth attributed to *Palaeobrachaelurus* from the Early and Middle Jurassic of Germany, Belgium, and England (e.g., Thies 1983, 1989; Delsate and Lepage 1990). The lack of any ornamentation or

sculpture differentiates it easily from other contemporaneous orectolobiforms (e.g., *Annea*, *Orectoloboides*). The dentition of *Palaeobrachaelurus* is slightly heterodont expressed by the presence or absence of lateral cusplets and the form of the labial apron (Thies 1983; Cappetta 1987). The labial margin of the apron is rounded in anterior to antero-lateral files, while it is straighter or even concave in lateral to posterior rows. The cusplets are completely reduced in posterior rows. Consequently, the tooth from Kłęby comes from a lateral tooth row.

Palaeobrachaelurus is known from the Toarcian of Germany (*P. aperizosteus* Thies, 1983) and Belgium (*P.* sp., Delsate and Lepage 1990), from the Aalenian of Germany (*P.* spp., Thies 1983), from the Bathonian of England (Charlie J. Underwood personal communication 2002), and from the Callovian of England (*P. alisonae* and *P. bedfordensis*, Thies 1983). Candoni (1995) indicates the presence of *Palaeobrachaelurus* in the Kimmeridgian of northern France, which would represent the stratigraphic youngest record. Teeth of *P. asperizosteus* differ in the much more expanded crown base with four lateral cusplets in lateral teeth and a less well-developed, rectangular apron. The contemporaneous specimen from Belgium resembles teeth of *P. alisonae* Thies, 1983. The main distinctive character of *P. alisonae* is the morphology of the crown base and the apron. The apron in *P. alisonae* is tongue-like with concave margino-labial margins. Lateral teeth of *P. bedfordensis* from the Callovian of England also differ in the morphology of the apron and in the presence of two pairs of well-developed and distinct lateral cusplets from *P. alisonae*. The specimens described by Thies (1989) from the Aalenian of Germany disagree in the morphology of the crown, especially of the apron, and in the form and number of lateral cusplets compared to *P. alisonae*. The teeth from the Bathonian of England differ in the overall morphology of the cusp and cusplets and in the form of the apron (Charlie J. Underwood personal communication 2002). The specimen from Kłęby might represent a new species of *Palaeobrachaelurus*. However, it seems premature to attribute it to a new or already known species since the tooth morphologies of different species are very similar and only a single tooth has been recovered from Poland so far.

Family indet.

Genus *Folipistrix* nov.

Type species: *Folipistrix digitulus* sp. nov.

Etymology: The generic name is derived from *folium* (n.), the Latin word for leaf, in reconsideration of the outline of the tooth crown and *pistrix* (f.), the Latin word for sea monster or shark.

Diagnosis.—Neoselachian characterised by very small, hemiaulacorhize teeth. Tooth crown high and triangular. No lateral heels or lateral cusplets. Cutting edge well developed, continuous and irregular jagged. Broad, well-developed rectangular labial protuberance present. Labial protuberance protruding almost horizontally, not being supported by root and well detached from labial root depression. No lingual uvula or ornamentation. Central root foramen small, incipient. Two pairs of margino-lateral foramina. Medio-lingual foramen small.

Differential diagnosis.—The teeth of *Folipistrix* gen. nov. differ from similar teeth of other neoselachians such as *Squatina* in the absence of lateral heels and the well-detached and not root-supported protuberance. They differ from teeth of all other Jurassic orectolobiforms in the absence of lateral cusplets (e.g., *Palaeobrachaelurus*, *Annea*, *Orectoloboides*) or in the absence of crown ornament (e.g., *Annea*, *Orectoloboides*). From teeth of the agaleid *Agaleus* they are distinguished by the absence of a labial horizontal ridge and a root buttress supporting the labial protuberance. The combination of triangular labio-lingually compressed tooth crown, absent lateral heels and lateral cusplets, jagged cutting edges and absent lingual uvula distinguishes the teeth of the new genus easily from all known orectolobiform and carcharhiniform taxa.

Folipistrix digitulus sp. nov.

Figs. 2D, 3A.

Holotype: SMNS 87861.

Paratype: SMNS 87862.

Type locality: Weilen unter den Rinnen, SW Germany.

Type horizon: "Opalinuston", Dogger α, lower Aalenian, Middle Jurassic.

Etymology: The species name is derived from *digitulus* (m.), the Latin word for a little finger in reconsideration of the finger-like projected labial protuberance.

Occurrence: Only known from the type locality.

Diagnosis.—Same as for genus.

Description.—The holotype (Fig. 2D) is a small tooth with preserved crown and root. The crown is relatively high and triangular in labial view without lateral cusplets. There are also no lateral heels. The crown is rather compressed labio-lingually. The labial face is almost flat and only slightly cambered toward the lower part of the crown. There is a distinct, labially projecting protuberance with rectangular outline in labial view. A root buttress or the root itself does not support the protuberance. In lateral view, the well-developed protuberance juts labially being almost horizontal. The base of the tooth crown is concave in labial view and overhangs the root slightly. The cutting edge is well developed. It displays a few very coarse, irregular indentations giving the cutting edge a coarsely serrated, leaf-like appearance. The serrations are very coarse basally. The lingual face is more convex. There is no median uvula and the neck collar is very thin, nearly absent. There is no crown ornament or sculpture developed.

The root is hemiaulacorhize with two broad, flattened lobes. In lateral view the root is more or less perpendicular to the tooth crown. The root lobes are slightly flared creating a faintly notched crown/root junction in labial view. In basal view, the root is V-shaped with a well-marked labial depression. The root lobes meet lingually to form a massive and broad lingual protuberance. A rather large medio-lingual foramen is present opening in the basal portion of the protuberance. The central foramen is small. There are two pairs of

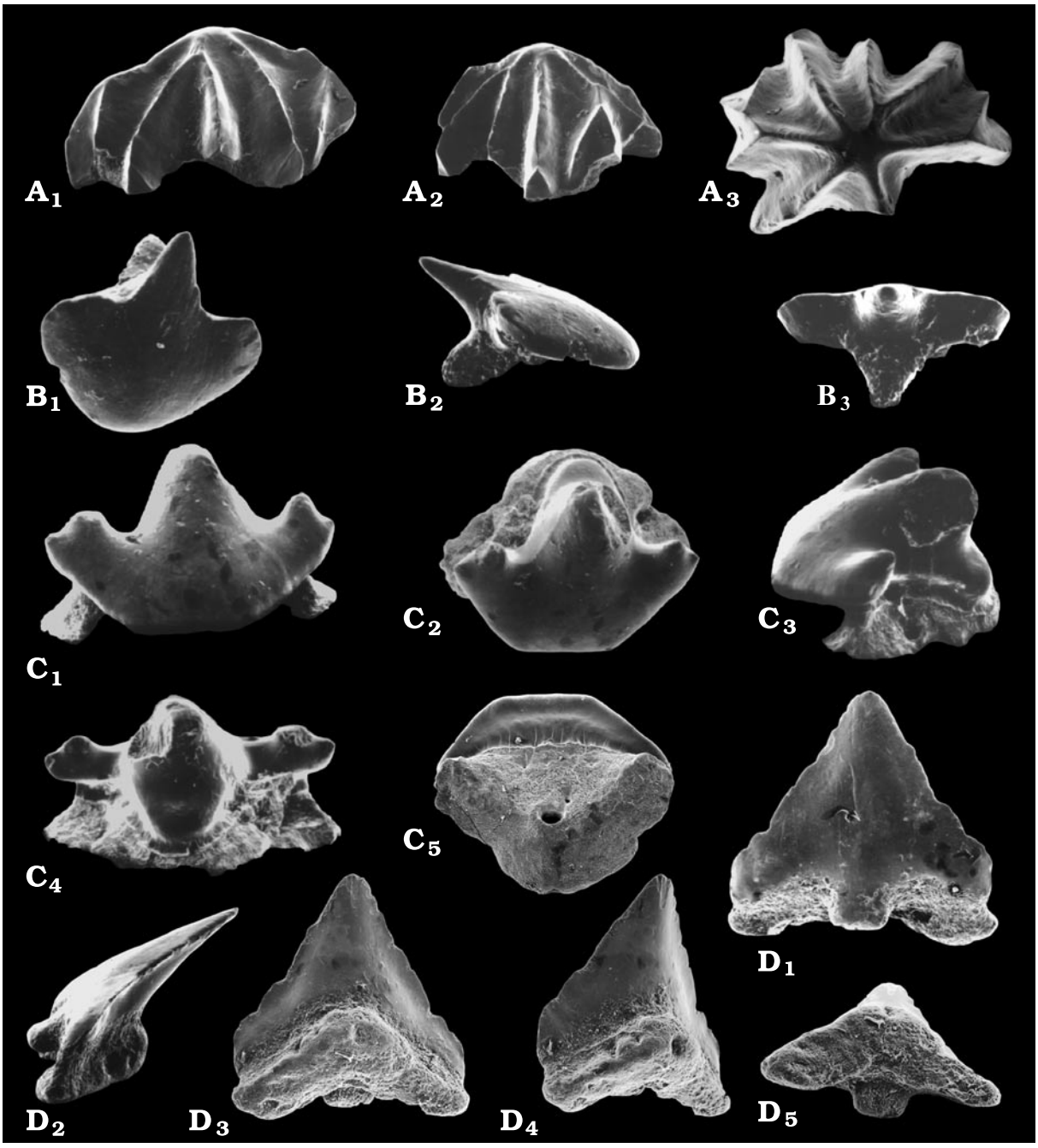

Fig 2. **A**. Hybodontiformes indet. BGR X 12499; in lateral (A_1, A_2) and occlusal (A_3) views. All × 40. **B**. *Pseudospinax*? sp. BGR X 12500, Kłęby 1/37: 244.8–245.7 m, Callovian; in occlusal (B_1), lateral (B_2), and lingual (B_3) views. All × 80. **C**. *Palaeobrachaelurus* sp. BGR X 12502, Kłęby 1/37: 244.8–245.7 m, Callovian in labial view (C_1), × 55, occlusal view (C_2), × 55, lateral view C_3, × 55, lingual view (C_4), × 55, and basal view (C_5), × 40. **D**. Holotype of *Folipistrix digitulus* gen. et sp. nov. SMNS 87861, Weilen unter den Rinnen, SW Germany, Dogger α, lower Aalenian; in labial view (D_1), × 50, lateral view (D_2), × 50. lingual view (D_3), × 45, latero-lingual view (D_4), × 45, and basal view (D_5), × 45.

margino-lateral foramina. A rather large foramen opens basally on the surface of one of the root lobes.

The paratype (Fig. 3A) is a fragmentary tooth. Most of the root as well as the basal parts of the crown are heavily damaged. However, the remaining part of the tooth exhibits the general morphology of the holotype, although the serration-like appearance of the cutting edges is less pronounced.

Discussion.—The overall morphology of the teeth is similar to that of orectolobiforms, e.g., hemiaulacorhize vascularisation pattern, well-developed labial root depression, well-developed labial protuberance not supported by the root. However, the absence of a lingual uvula is unusual for extant orectolobiforms, in which the uvula is supported by the lingual protuberance of the root (Herman et al. 1992). In the general tooth morphology the above-described specimens also resemble teeth of *Squatina* to some extend. However,

the tooth morphology of *Squatina* is rather simple and very conservative. Consequently many isolated *Squatina*-like teeth from the Cretaceous and Jurassic have been assigned to squatinids (e.g., Thies 1983; Batchelor and Ward 1990; Biddle 1993; Rees 2002; Underwood 2002). This resulted in a taxonomic lumping of similar morphotypes. Leidner and Thies (1999) already pointed out that there might be more genera of squatiniforms present in the Late Jurassic. But the identification of isolated orectolobiform teeth from the Cretaceous and Jurassic also might cause problems. As a result, the true specific composition of orectolobiforms and squatiniforms in the Jurassic and also in the Cretaceous is probably obscured. The teeth of extant squatiniforms and orectolobiforms share some very important features so that Herman et al. (1992) concluded that *Squatina* could represent an orectolobiform. A very characteristic feature of teeth of *Squatina* is the morphology of the protuberance, which is rounded in basal view and well supported by the root. This pattern is also found in several Cretaceous species. However, in most if not all Jurassic *Squatina* spp., the labial protuberance is more rectangular and massive and well detached from the root. In addition, the labial root depression is much more pronounced in orectolobiforms than in extant *Squatina* species. The taxonomy of Late Jurassic specimens and species referred to *Squatina* is still in need of revision. The main difference between teeth of *Squatina* and the new taxon is the absence of lateral heels, the presence of a well-developed labial root depression and the labial protuberance, which is not supported by the root but well detached from the root depression. Unfortunately, the taxonomy of Jurassic orectolobiforms is still not fully understood. Consequently, the new genus is assigned to Orectolobiformes as incertae familiae.

The teeth resemble those of some carcharhiniforms in the absence of a lingual uvula. However, the overall crown morphology and root vascularisation pattern suggests closer relationships with orectolobiforms.

The crown morphology resembles those of some other extant galeomorphs to some extent (e.g., *Isistius*, *Carcharodon*, *Pterolamiops*) and is indicative for a cutting-type dentition. A cutting-type dentition also occurs in larger extant orectolobiforms (Cappetta 1987).

Fam. gen. et sp. indet.

Fig. 3B, C.

Material.—Two isolated tooth crowns (SMNS 87863, SMNS 87864), "Opalinuston", Dogger α, lower Aalenian, Middle Jurassic, Weilen unter den Rinnen, SW Germany.

Remarks.—Two very small isolated tooth crowns resemble those found in orectolobiform sharks. Both specimens are damaged and completely lack the root. The crowns are broadened mesio-distally with a very convex basal edge in labial view giving specimen SMNS 87863 a dagger-like appearance. The main cusp of this specimen is rather short and slender. There is a pair of small, slender and pointed lateral cusplets diverging slightly from the main cusp. The cutting edge is continuous between main and lateral cusplets. The labial crown face is narrow in lateral aspect.

The second specimen (SMNS 87864), as far as can be reconstructed, resembles the first specimen. However, the basal edge of the labial face seems to be straighter and the main cusp is slightly bent distally. This may indicate a lateral jaw position whereas specimen SMNS 87863 might come from an anterior to antero-lateral position. Both tooth crowns are completely smooth.

Identification on familiar, generic or even specific level of both specimens is impossible. Both specimens are very small and have been recovered only because of using a very small mesh width during sieving. Whether they represent teeth of juvenile or adult specimens is not discernable. Because of the small size, at least specimen SMNS 87864 may represent a juvenile specimen.

Subcohort Squalea White, 1937
Superorder Notidanoidea Carvalho, 1996
Order Synechodontiformes Duffin and Ward, 1993
Family Palaeospinacidae Regan, 1906
Genus *Synechodus* Woodward, 1888

Type species: *Hybodus dubrisiensis* Mackie, 1863 from the Upper Cretaceous of southern England.

Synechodus prorogatus sp. nov.

Fig. 3D, E, L.

Holotype: An antero-lateral tooth, BGR X 12503, Fig. 3D.

Additional material: A tooth crown fragment (lateral cusplet), BGR X 12504, as well as bioeroded crown, BGR X 12510, attributed to this species.

Type locality: Kłęby near Golczewo, NW Poland.

Type horizon: Drill core Kłęby 1/37: 244.8–245.7 m, Callovian.

Etymology: The species name is derived from *prorogatio*, the Latin word for prolongation in reconsideration of the labial enameloid expansions. The name is masculine in gender.

Occurrence.—Only known from the type locality.

Diagnosis.—A species of *Synechodus* characterised by very small teeth. Antero-lateral teeth asymmetrical with elongated mesial and shorter distal heel. Main cusp labio-lingually flattened. First pair of lateral cusplets pointed and high. Up to three small and widely fused lateral cusplets on mesial heel. Second distal cusplet very small. Labial ornamentation consisting of a mesio-distal fold parallel to the cutting edge. Additional horizontally orientated, irregular folds below lateral heels present and in contact with the main labial sculpture creating a narrow band of reticulate-like ornament. Two labial enameloid prolongations extending basally on labial root laminae. Lingual face with short, vertical folds not reaching the base of the crown.

Differential diagnosis.—The new species differs from all other *Synechodus* species:

– in the presence of vertical, basally directed labial enameloid prolongations at the basal margin of the crown. The

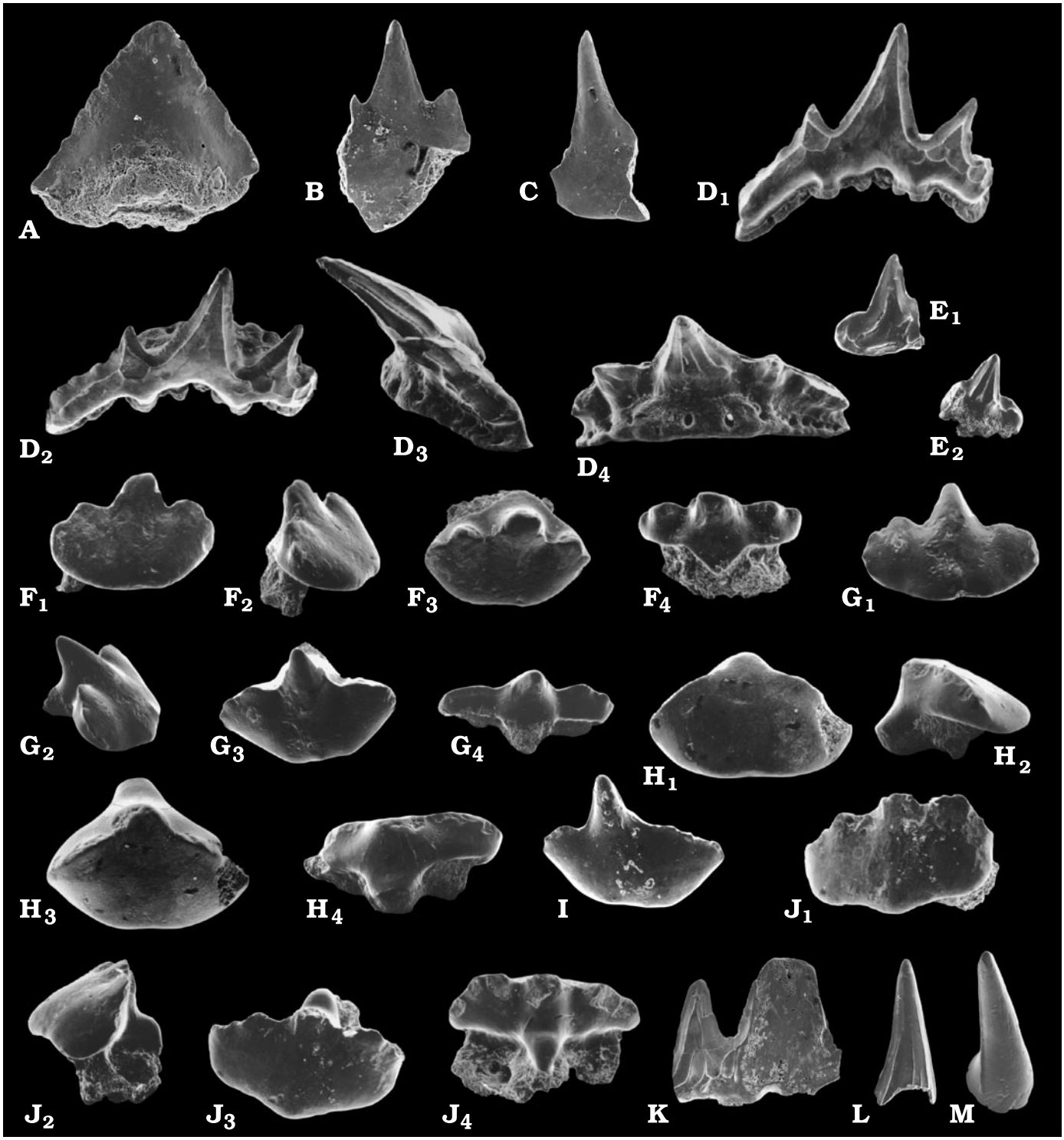

Fig. 3. **A**. Paratype of *Folipistrix digitulus* gen. et sp. nov. SMNS 87862, Weilen unter den Rinnen, SW Germany, Dogger α, lower Aalenian; in labial view, × 52. **B**–**C**. Orectolobiformes, fam. gen. et sp. indet. Weilen unter den Rinnen, SW Germany, Dogger α, lower Aalenian. **B**. Specimen SMNS 87863; in labial view, × 85. **C**. Specimen SMNS 87864; in labial view, × 115. **D**. Holotype of *Synechodus prorogatus* sp. nov. BGR X 12503, Kłęby 1/37: 244.8–245.7 m, Callovian; in labial (D_1), occlusal (D_2), lateral (D_3), and lingual (D_4) views. All × 40. **E**. Isolated lateral cusplet of *Synechodus prorogatus* sp. nov., BGR X 12504, Kłęby 1/37: 244.8–245.7 m, Callovian; in labial (E_1) and lingual (E_2) views. Both × 30. **F**. *Protospinax* cf. *annectans* Woodward, 1919. Specimen BGR X 12505, Kłęby 1/37: 244.8–245.7 m, Callovian; in labial (F_1), lateral (F_2), occlusal (F_3), and lingual (F_4) views. All × 65. **G**. *Protospinax* cf. *annectans* Woodward, 1919. Specimen BGR X 12506, Kłęby 1/37: 244.8–245.7 m, Callovian; in labial (G_1), lateral (G_2), occlusal (G_3), and lingual (G_4) views. All × 32. **H**. *Protospinax* sp. 1. BGR X 12507, Kłęby: 244.8–245.7 m, Callovian; in labial (H_1), lateral (H_2), occlusal (H_3), and lingual (H_4) views. All × 40. **J.** *Protospinax* sp. 2. BGR X 12508, Kłęby 1/37: 244.8–245.7 m, Callovian. Labial view. **K**. *Squalogaleus* sp. BGR X 12509, Kłęby 1/37: 244.8–245.7 m, Callovian; in labial (K_1), lateral (K_2), occlusal (K_3), and lingual (K_4) views. All × 50. **L**. *Synechodus prorogatus* sp. nov.? BGR X 12510, Kłęby 1/37: 253.6–~265 m, Callovian. Labial view, × 28. **M**. Scyliorhinidae indet. BGR X 12511, Kłęby 1/37: 253.6–~265, Callovian; in labial view, × 14. **N**. Neoselachii indet. BGR X 12512, Kłęby 1/37: 253.6–~265, Callovian; in labial view, × 22.

labial margin in all other species is straight to concave and continuous.
– in the presence of a labial fold, which is continuous mesio-distally and parallel to the well-developed cutting edge.
– in the horizontal, irregular folds below the lateral heels creating a narrow band of anastomosing- and reticulated-like ornamentation on the labial face and forming a crest-like structure on the lingual heels.

Description.—The single complete tooth is rather small measuring only 1.22 mm mesio-distally and 0.67 mm in height. The crown base is considerably mesio-distally elongated and high, and slightly asymmetrical with the mesial heel being longer than the distal one. The main cusp is slender, triangular in labial view but compressed labio-lingually to some extend and slightly curved lingually. The apex is pointed and slightly bent distally. There is one pair of well developed, pointed and slightly divergent lateral cusplets. The distal cusplet is larger than the mesial one. A second, rudimentary cusplet accompanies the distal one at its base. The mesial heel is significantly elongated and marked by three very small, strongly fused cusplets. The transverse cutting edge is well developed and continuous between the cusplets and the cusp. The labial face of the crown is rather flat but cambered at the base of the main cusp. The basal margin of the labial face is concave in labial view and overhangs the root with a prominent and round bulge. Two enameloid-covered, tongue-like expansions extend ventrally and cover two of the root laminae. These expansions are more or less located in the prolongation of the notches between main cusp and first lateral cusplets. The ornamentation consists of a continuous fold reaching over the entire mesio-distal width and being more or less parallel to the cutting edge. This fold is joint by horizontally oriented, irregular and fainter ridges below the lateral heels creating a narrow band of almost reticulated ornament, which is restricted to the upper half of the crown shoulder. A short, more or less vertical, very faint fold is present in the upper third of the main cusp. Otherwise, the labial face is smooth. None of the ornamentation elements reach the basis of the tooth crown.

The lingual face is much more convex than the labial one and much less developed below the lateral heels. The ornamentation consists of four vertical, slightly irregular ridges on the main cusp and three on the first pair of lateral cusplets. The folds do not reach the base of the crown or onto the lateral heels and do not bifurcate. There are two horizontal crests below the lateral heel giving the crown shoulder an almost angular appearance in lateral view.

The root is low, rather flared laterally and arched in labial view. The angle between crown and root is about 20°. The basal face of the root is flat lingually but almost hollowed labially. Here, some irregular short but deep grooves separated by thick laminae are present on the labial face giving the root a pseudopolyaulacorhize pattern. The lingual face is broad. There is a weakly developed lingual protuberance. There are six margino-lingual foramina mesially and four distally. The medio-lingual foramen is of the same size as the margino-lingual foramina and in line with them. Some similar large foramina open labially and are continuous with the corresponding margino-lingual foramina.

The second specimen attributed to this species represents a broken-off lateral cusplet, probably from the distal part. It shows the characteristic labial and lingual ornamentation.

A single, isolated and fragmentary, bioeroded tooth crown (see below) is provisionally attributed to this species because of the distinctive crown ornamentation.

Discussion.—There has been a long dispute and controversy over the taxonomic distinction between *Palaeospinax*, *Synechodus*, and *Paraorthacodus* (e.g., Woodward 1889; Cappetta 1973; Herman 1977; Cappetta 1987, 1992; Thies 1991, 1992, 1993). According to Duffin and Ward (1993) *Palaeospinax* might be a synonym of *Synechodus*. Consequently previous concepts (e.g., Glickman 1957; Cappetta 1973) seem to be basically valid. Two distinct groups based on their tooth morphologies are then recognizable within palaeospinacid neoselachians: *Paraorthacodus* and *Synechodus*. The main feature of *Synechodus* teeth is that the lateral cusplets are not as strongly separated from the main cusp as in *Paraorthacodus* and that the labial face is cambered and overhangs the crown/root junction with a bulge. Because of these features, the new species from Kłęby is attributed to *Synechodus*. Cuny et al. (2001) erected the synechodontiform genus *Mucrovenator* for isolated teeth from the Middle Triassic of North America and "*Hybodus*" *minor* from the Late Triassic of Europe. Teeth of this genus differ mainly in the absence of the very characteristic deep grooves separated by laminae on the labial root face and a less developed bulge of the labial face. The ornamentation consists of very strong and long vertical folds. The attribution of this genus to synechodontiforms seems questionable because of the root morphology.

Synechodus is rather widespread and ranges from the Late Triassic (Rhaetian) to the Danian (Palaeocene) (Cappetta 1987; Duffin and Ward 1993). Jurassic species are *S. streitzi* and *S. paludinensis* from the Hettangian, *S. enniskilleni* and *S. occultidens* from the Hettangian and Sinemurian, *S. pinnai* from the Sinemurian, *S. egertonia* from the Toarcian, *S riegrafi* from the Oxfordian and *S. plicatus* from the Kimmeridgian (e.g., Thies 1983; Duffin and Ward 1993; Delsate et al. 2002). Teeth of *Synechodus* also occur in the Bathonian (Charlie J. Underwood personal communication 2002). The anterior to lateral teeth of *S. occultidens* and *S. paludinensis* also occasionally lack vertical folds or ridges on the labial face. However, teeth of these two species differ from the new species in the presence of very weak lateral cusplets, which are absent in certain tooth files, and in the labial crown face ornament. The ornamentation is of anastomosing, reticulated pattern that is restricted to the lower parts of the crown in *S. occultidens* while it consists of a reticulate ornament pattern at the base of the crown and additional longitudinal, vertical ridges in *S. paludinensis*. The holotype of the new species resembles antero-lateral teeth of *S. plicatus* Underwood, 2002 to some extent. How-

ever, they are easily distinguishable on the basis of the labial enameloid prolongations in the new species. Conversely, the base of the labial crown face is straight and only slightly curved in *S. plicatus*.

The characteristic ornamentation and the labial enameloid prolongations distinguish the Kłęby species from all known species and allow the creation of a new species despite the small sample size. Consequently, important features such as the heterodonty of the new species could not be reconstructed. The holotype may be attributed to an antero-lateral jaw position because of the asymmetrical form.

The new record from the Callovian of Poland fills the gap between the earlier Middle and Late Jurassic occurrences of *Synechodus*.

An isolated tooth crown that might be attributed to the new species exhibits evidence of bioerosion by the hyphate boring *Mycelites* (Fig. 3L).

Superorder Hypnosqualea Carvalho and Maisey, 1996

Family Protospinacidae Woodward, 1919

Genus *Protospinax* Woodward, 1919

Type species: *Protospinax annectans* Woodward, 1919 from the Upper Jurassic of southern Germany.

Protospinax cf. *annectans* Woodward, 1919

Fig. 3F, G.

Material.—A complete tooth, BGR X 12505 (Fig. 3F), and an additional tooth crown, BGR X 12506 (Fig. 3G), Kłęby 1/37: 244.8–245.7 m. Callovian.

Description.—The complete tooth is small, less than 2.0 mm in mesio-distal width. The crown is mesio-distally expanded. The central cusp is low, rather broad and oval in cross section. It is slightly displaced distally and bent lingually. The labial face projects strongly over the crown/root junction forming a moderate visor. The basal edge of the labial face is rounded with a faint central concavity. The upper labial crown face is concave in lateral view. The lateral heels are unequally long with the distal one being shorter. There are two notches on either side of the main cusp separating it from the lateral heels. There are no distinct lateral cusplets but the cutting edge is strongly crenulated forming two pairs of very blunt and low cusplets. The cutting edge is continuous along the mesio-distal width of the crown.

The lingual face is steep and concave in lateral view. The lingual uvula is short, triangular in occlusal view and pointed. Both lingual and labial crown faces are completely smooth without any ornament.

The root is slightly lingually displaced. The vascularisation is of hemiaulacorhize type with two V-shaped lobes. The basal surfaces of the lobes are flat. The lingual protuberance is weak and damaged in its basal part where a medio-lingual foramen opens. A central foramen opens into the angle where both lobes are fused. The outline of the root is cordiform in basal view. There is one pair of margino-lingual foramina.

The second specimen is slightly larger and more mesio-distally elongated. The morphology of the tooth crown is almost identically to that of the other specimen. However, the upper labial crown face is only slightly concave in profile view. The overall morphology suggests a lateral position of this tooth.

Discussion.—The identification of teeth of *Protospinax* and *Squalogaleus* is often very difficult because of very similar morphologies. There exist some controversies about the validity of *Squalogaleus*, a taxon erected by Maisey (1976) for one articulated specimen attributed to *P. annectans* by Woodward (1919). This was strongly argued by Thies (1983) who regarded *Squalogaleus* a junior synonym of *Protospinax*. However, Cappetta (1987) accepted the validity of *Squalogaleus* presenting a range of dental characters for identifying teeth of *Protospinax* and *Squalogaleus*. Duffin (1993) also supported two different genera *Protospinax* and *Squalogaleus* respectively based on tooth morphologies. The tooth from Kłęby corresponds well to the characters indicated by both authors for *Protospinax*: moderate labial visor, triangular and elongated lingual uvula, upper labial crown face concave, and central foramen present. However, it differs slightly in the absence of a humped and convex upper lingual crown face. But this character seems to vary within a single species and might depend on the jaw position. The teeth figured by Thies (1983) as *P. annectans* also does not exhibit this hump-like structure but a concave lingual crown face in lateral view, which is very similar to the condition found in the Polish specimens.

Protospinax annectans is known from the Callovian of Germany (Thies 1983) Oxfordian of Germany (Duffin 1993), Kimmeridgian of France (Candoni 1995) and Tithonian of Germany (Woodward 1919). The occurrence of a species at least closely related to *P. annectans* in the Callovian of Poland extends the geographic range of *Protospinax* further to the east. *Protospinax* is also known from the Toarcian (Thies 1983) and the Bathonian (Charlie J. Underwood personal communication 2002).

Protospinax sp. 1

Fig. 3H.

Material.—A single isolated tooth crown, BGR X 12507, Kłęby 1/37: 244.8–245.7 m. Callovian.

Remarks. —The specimen differs from the previous in the more robust crown. The cusp is small and blunt. The cutting edge is continuous and rectilinear without any crenulations or serrations. There are no lateral cusplets. The labial face is triangular in labial view and is more or less flat without a concavity of the upper crown face. The basal edge of the labial face is concave. The uvula is rather massive and a hump-like structure is indicated just below the apex on the lingual face. The root is not preserved.

The combination of the crown characters indicates its affiliation to *Protospinax*. It resembles slightly teeth figured by Thies (1983) as *P. annectans*. However, a specific attribution is not possible.

Protospinax sp. 2

Fig. 3J.

Material.—A single isolated tooth crown, BGR X 12508, Kłęby: 244.8–245.7 m. Callovian.

Remarks.—This specimen is characterised by a mesio-distally elongated crown with a slender but well-developed cusp that is displaced distally. The crown is asymmetrical resulting in an elongated mesial heel. The cutting edge is strongly crenulated and a very low, blunt and rudimentary cusplet is developed on the distal heel. The basal margin of the labial face is concave. This specimen is very similar to a tooth from the Bathonian of England (Charlie J. Underwood personal communication 2002).

Superorder Squaloidea Carvalho, 1996
Order Squaliformes Goodrich, 1909
Family Squalidae Bonaparte, 1838
Genus *Squalogaleus* Maisey, 1976

Squalogaleus sp.

Fig. 3K.

Material.—A single tooth, BGR X 12509, Kłęby 1/37: 244.8–245.7 m. Callovian.

Description.—The single tooth is very small, the labial face being mesio-distally elongated. The crown is much broader than deep. The labial face is completely smooth and projects out over the root forming a very strong, almost horizontally directed visor. The labial contour of the visor is slightly concave with a central protuberance. In lateral view, the labial face is rectilinear and oblique. There is a rather broad central cusp, which is heavily abraded. The transverse cutting edge is well developed and forming two pairs of very low, blunt and rounded pairs of lateral cusplets.

The lingual face is much less developed but more convex than the labial face. It is strongly concave in its upper part in lateral view. The lingual face extends downwards to form a well developed but narrow uvula that tapers consistently towards the base edge that supported by the lingual root protuberance. The uvula is quite high in lateral aspect. The crown/root junction is well marked by a constriction. The tooth crown also juts out over the root laterally.

The root is high and somewhat displaced lingually. The vascularisation is of hemiaulacorhize type. The root lobes are arched and V-shaped in basal view. A well-developed labial root depression is present. A large central foramen opens into the labial depression. The lingual root protuberance is damaged so that the morphology of the medio-lingual foramen is not visible. Two margino-lateral foramina are present on one side of the root. Smaller foramina open onto the labial area of the root depression.

Remarks.—The main characters of *Squalogaleus* teeth are: a very strong and labially elongated visor, a moderately developed uvula with pointed lingual extremity, a rectilinear to convex upper labial crown face and a concave lingual face in lateral view. The root is comparably high with rather large foramina compared to teeth of *Protospinax*. The main difference to teeth of *Protospinax* is the convex labial edge, which forms almost a labial protuberance. Conversely, the labial edge is concave in *Protospinax*. The overall morphology of the single tooth from Kłęby matches these characters and is therefore assigned to *Squalogaleus*. So far, skeletal remains are only known from a single species from the Tithonian (*S. woodwardi* Maisey, 1976). Teeth of *Squalogaleus* also occur in the Kimmeridgian of Spain (Kriwet 1998) and Toarcian of the Paris Basin (Laurent Candoni personal communication 1999). The record from the Callovian of Poland closes the gap between the known Early and Late Jurassic records. The tooth figured by Delsate and Lepage (1990) as *Protospinax*? or *Squalogaleus*? from the Toarcian of Belgium might represent another taxon. The teeth described as *Protospinax lochensteinensis* by Thies (1983) are transferred to *Squalogaleus* (Candoni 1995) and its presence indicated in the Kimmeridgian of France.

Superorder, order, family, genus and species indet.

Fig. 3M, N.

Material.—Numerous isolated and fragmentary tooth crowns, BGR X 12510–12512, Kłęby 1/37.

Remarks.—Isolated tooth crowns or tooth fragments are rather abundant in several layers of the drill core (Table 1). Isolated tooth crowns occur in every vertebrate-bearing sample sometimes in rather high numbers (Fig. 3L–N). This mostly taxonomically unidentifiable material is more numerous than the identifiable specimens indicating that the preservation of selachian material in the drill core is on the whole rather poor. Some of these tooth crowns resemble teeth of *Parasymbolus* and might indicate the presence of scyliorhinids (Fig. 3M). A few other neoselachian tooth types also occur (Fig. 3N). The presence of the relatively high number of isolated tooth crowns might be related to fungal borings since *Mycelites* attacks predominantly the roots resulting in their complete destruction. However, Martill (1989) also described selachian teeth from the Callovian of England with borings in the enameloid of the tooth crowns caused by *Mycelites*-like organisms.

Diversity and palaeoecology of Jurassic neoselachians

The knowledge about the diversity and ecology of Jurassic selachians is still very patchy although some systematic sampling of Jurassic strata has been carried out in the last decades. Exceptions are the studies mentioned throughout this text. Pre-Toarcian neoselachian assemblages display low diversities of palaeospinacids, hexanchids and agaleids (e.g., Biddle 1993; Rees 1998, 2000). The diversity seems to increase from the Toarcian to Bajocian (e.g., Delsate and Thies 1995; Thies 1983, 1989, 1993). Heterodontiforms, orectolobiforms, and

rajiforms represent new and rather common Bajocian neoselachians. Batoids are represented by an archaic group named Archaeobatidae (Delsate and Candoni 2001). Toarcian and Bajocian assemblages mainly differ from those of Bathonian age in the absence of carcharhiniform taxa (personal observation). Callovian neoselachian assemblages are dominated by *Protospinax* and *Paracestracion*, several orectolobiforms and the batoid *Belemnobatis* with rare taxa of hexanchids and palaeospinacids (Underwood and Ward in press). From the Oxfordian onwards, the diversity of neoselachians increased steadily (see introduction).

Middle Jurassic neoselachians from southwestern Germany are not well known. Toarcian remains have been described by Fraas (1896), Reif (1974) and Thies (1992). The new neoselachian records from the Aalenian of SW Germany all belong to orectolobiforms and represent at least one new taxon. Jurassic orectolobiforms are generally regarded as unspecialised, bottom-dwelling predators living in shallow marine environments (Thies and Reif 1985). However, the tooth morphology of *Folipistrix* gen. nov. indicates a cutting dentition and suggests a more specialised feeding habit.

The neoselachian assemblage from the Middle Jurassic of Kłęby is rather low in diversity and abundance. The low specimen number is certainly related to the nature of the sample size (drill core) and consequently a higher diversity might have been present in this area of the Callovian Sea, which was connected to the Tethys. Two orectolobiforms are present. *Palaeobrachaelurus* is widespread in Middle Jurassic sediments of Europe. A recent analysis of the ecology of Bathonian neoselachians from Britain revealed that orectolobiforms are very abundant in very shallow coastal to lagoonal waters although some taxa, including *Palaeobrachaelurus*, were only recovered from neritic facies (Underwood and Ward in press). Palaeospinacids are also most commonly found in open-marine environments inhabiting mostly shelf regions (Underwood and Ward in press). Those palaeospinacids are interpreted as fast swimming predators (Thies and Reif 1985). The most common neoselachian genus of Kłęby, both numerically and in the species diversity, is *Protospinax*. *Protospinax* is also the dominant neoselachian taxon in most, if not all, Middle Jurassic selachian assemblages ranging from lagoonal to near-coastal and neritic environments (Thies and Reif 1985; Underwood and Ward in press). They represent sluggish swimmers (Thies and Reif 1985). The occurrence of *Squalogaleus* also indicate a near coastal to neritic environment (e.g., Candoni 1995). According to these reflexions the neoselachian assemblage from Kłęby might represent a near coastal but open-marine association with Tethyan rather then Boreal influences. This interpretation is also supported by the rather high number of statoliths of teuthids.

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