

NEOSELACHIAN SHARK AND RAY TEETH FROM THE VALANGINIAN, LOWER CRETACEOUS, OF WĄWAŁ, CENTRAL POLAND

by JAN REES

Karlstad University, Division for Environmental Sciences, SE-651 88 Karlstad, Sweden; e-mail: jan.rees@kau.se

Typescript received 12 May 2003; accepted in revised form 5 December 2003

Abstract: Valanginian strata at Wąwał in central Poland have yielded the oldest marine neoselachian assemblages from the Cretaceous of Europe. The faunas comprise seven taxa including *Heterodontus polonicus* sp. nov., an indeterminate orectolobiform, *Protolamna* sp., *Palaeoscyllium* sp., *Synechodus nitidus*, *Squatina cranei* and *Belemnobatis* sp. *Heterodontus polonicus* is recognized primarily by the high amount of reticulate ornamentation on the lower labial side of the anterior teeth. The faunas from Wąwał are numerically

dominated by neoselachian genera such as *Synechodus*, *Heterodontus* and *Belemnobatis* that were already well established in the Jurassic. More modern taxa include the oldest recorded occurrence of the true *Squatina*-lineage, and the presence of *Protolamna* is one of the earliest undoubted lamniform occurrences so far reported.

Key words: Cretaceous, Neoselachii, Poland, rays, sharks, teeth, Valanginian.

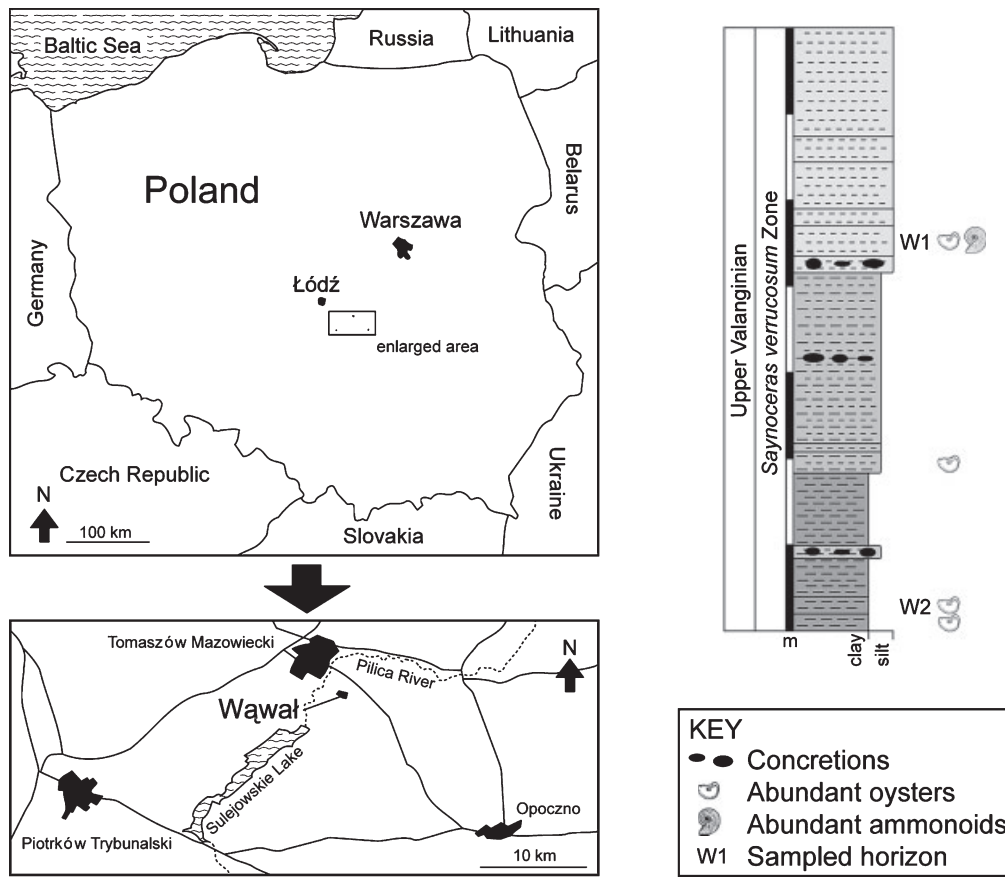
DURING the Jurassic, the diversity of neoselachian sharks and rays increased dramatically following low-diversity assemblages that characterized the Triassic. Recent investigations have shown that most extant neoselachian groups first occur in the Jurassic, constituting a major radiation (Cappetta *et al.* 1993; Candoni 1995; Underwood 2002). The composition of Jurassic faunas, however, appears to be quite different from that of Cretaceous assemblages, and the former are often numerically dominated by extinct groups (e.g. palaeospinacids) or by bottom-dwelling selachians (e.g. squatinids and batoids), although the faunas seem to be environmentally controlled (Underwood and Ward 2004). By the mid-Cretaceous, marine selachian assemblages have a considerably more modern composition, including lamniforms and several batoid groups unknown in the Jurassic. The earliest part of the Cretaceous is consequently a crucial period in the faunal evolution of neoselachians but marine faunas from this period are rare and have been described from only a few localities (e.g. Kriwet 1999; Underwood *et al.* 1999). The Valanginian strata of central Poland have yielded the first marine neoselachian fauna from this stage, thus expanding our knowledge of Early Cretaceous neoselachian distribution.

GEOLOGY

The sedimentary sequence at the Wąwał clay pit (Text-fig. 1) comprises large parts of the Valanginian Stage,

resting unconformably on Jurassic strata (Kutek *et al.* 1989). Sediments exposed in April 2001 were exclusively dark clays and silts (Text-fig. 1), deposited in a shallow-water environment probably in, or slightly beneath, the littoral zone (A. Kaim, pers. comm. 2002), corresponding to a global lowstand (Kutek *et al.* 1989). The marine palaeoenvironment is confirmed by the frequent presence of stenohaline echinoderms and ammonoids within the section. The recorded ammonoid fauna enables an accurate age determination, and the entire section described herein (Text-fig. 1) can be included in the upper part of the lower Upper Valanginian *Saynoceras verrucosum* Zone. Estimates of the palaeotemperature in the sea range from 13.5 to 16.5°C (A. Kaim, pers. comm. 2002). Several horizons in the Wąwał section are highly fossiliferous, being particularly rich in bivalves, gastropods, ostracods and foraminifera. Other frequent fossils include ammonoids, crustaceans, bryozoans, brachiopods and actinopterygian otoliths.

As the sea that covered central Poland during the Valanginian was connected to the North Sea through the German Basin (Kutek *et al.* 1989; Mutterlose 1992), the faunas recorded are primarily of Boreal composition. The Wąwał area was situated in a seaway connecting the Boreal and Tethyan realms (Kaim 2001) and during a short period in the earliest Late Valanginian, a highstand of the Carpathian Ocean allowed Tethyan faunas to migrate into the region (Mutterlose 1992). Boreal faunas reclaimed the area when the eustatic trend reversed later in the early Late Valanginian. A few Tethyan organisms, such as



TEXT-FIG. 1. Map of Poland with detailed map showing the locality at Wąwał and the strata exposed in late April 2001.

ammonoids and foraminifera, coexisted with the Boreal faunas in Poland during the greater part of the Late Valanginian (Mutterlose 1992), indicating that the seaway was open throughout this period. During fieldwork for this paper (April 2001), no parts of the lowest Upper Valanginian were exposed and the entire sampled sequence is considered to have been deposited in an ocean with major Boreal influence (Kaim 2001).

MATERIAL AND METHODS

Wąwał is a small village situated close to the town of Tomaszów Mazowiecki in central Poland, some 110 km south-west of Warszawa (Text-fig. 1). An abandoned clay pit (active in 2001) is located on the outskirts of the village. Most of the selachian material described herein is derived from bulk samples collected in April 2001 from two horizons containing abundant molluscan macrofossils (W1 and W2; see Text-fig. 1). Sediments from the Wąwał section are largely un lithified and the samples, each weighing approximately 100 kg, were dried and left in a solution of hot water and washing detergent for a few hours. The disintegrated sediment was washed through a large sieve

with a mesh aperture of 0.355 mm and the residues, mainly comprising mollusc shells and representing close to 10 per cent of the original sample weight, were dissolved in buffered acetic acid. In order to remove glauconite grains, comprising 95 per cent of the 0.355–0.500 mm fraction of W1, this residue was fed through a magnetic separator. The insoluble and non-magnetic residues were sorted under a binocular microscope and yielded 127 neoselachian teeth and 164 scales. During a previous investigation of the gastropod fauna at this locality (Kaim 2001, 2002), 11 neoselachian teeth and a single scale were recovered. Precise correlation of horizons previously yielding shark teeth to beds sampled for the present paper is somewhat complicated as layers may not be laterally persistent.

The illustrated teeth, together with the rest of the material, are housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warszawa (ZPAL).

SYSTEMATIC PALAEOLOGY

Higher relationships of the Neoselachii follow that of Shirai (1996) with the Synechodontiformes included in the *Squalea* because of their close affinity to

the Hexanchiformes (Duffin and Ward 1993). Descriptive tooth terminology follows that of Cappetta (1987).

Subcohort NEOSELACHII Compagno, 1977

Superorder GALEA Shirai, 1996

Order HETERODONTIFORMES Berg, 1940

Family HETERODONTIDAE Gray, 1851

Genus HETERODONTUS Blainville, 1816

Type species. *Squalus philippi* Schneider, 1801 (junior synonym of *Squalus portusjacksoni* Meyer, 1793), Recent in Australian temperate to subtropical waters to a depth of at least 172 m (Compagno 1984).

Heterodontus polonicus sp. nov.

Plate 1, figures 1–14

Derivation of name. Latinization of Poland, the country of origin.

Type material. Holotype, ZPAL P.10/1, Pl. 1, figs 1–3, complete anterior tooth; paratypes, ZPAL P.10/2, Pl. 1, figs 4–6, 14, incomplete anterior tooth and ZPAL P.10/4, Pl. 1, figs 10, 12–13, complete lateral tooth.

Type stratum. Horizon W1 in the Upper Valanginian (*verrucosum* Zone) sequence at the Wąwał clay pit, central Poland (Text-fig. 1).

Additional material. 24 incomplete teeth (ZPAL P.10/3, ZPAL P.10/5 and unnumbered), all of which are considered to originate from subadult or adult individuals. This species occurs mainly in W1 with only a single tooth recovered from W2.

Diagnosis. Anterior teeth of this species are highly ornamented with irregular folds forming a reticulate surface on the basal labial part of the crown. Large lateral teeth possess equal-sized enlarged depressions situated in two rows on either side of the longitudinal ridge.

Description. Anterior teeth have a moderately high central cusp with well-developed cutting edges. A single pair of minute elevations in these cutting edges may occur at the base of the cusp. The anterior teeth possess irregular folds in the enameloid on the lower labial part of the crown, forming a reticulate ornamentation. On the lingual side, the crown displays a central protuberance entirely supported by the root. The root is smaller than the crown with a V-shaped basal outline, the V opening to the labial side. A horizontal labio-lingual canal is formed in the lingual part of the root and a few smaller foramina open on each side of the lingual protuberance. The largest anterior tooth measures 3.7 mm in mesio-distal width. Lateral teeth are low, non-cuspidate and mesio-distally expanded. Reticulate ornamentation covers the entire crown and is differentiated to form a

moderately well-developed longitudinal ridge on the highest part of the crown. In large lateral teeth, there are two rows of expanded depressions on either side of this ridge whereas smaller laterals possess both depressions and folds on the occlusal surface. The root is low and smaller than the crown and has minute foramina irregularly placed on both the lingual and the labial root faces. The largest lateral tooth measures 14.5 mm in width.

Remarks. The teeth of *Heterodontus polonicus* recovered have a morphology that strongly indicates adult and subadult origin, including a near absence of cusplets in the anterior teeth and well-developed enlarged lateral teeth. The size of the largest anterior tooth is equivalent to those of a Recent *H. portusjacksoni* approximately 1 m long (see Reif 1976).

Late Jurassic and Early Cretaceous heterodontids are known from several localities across Europe. Three nominal species have been described from the Upper Jurassic lithographic limestones of southern Germany. The Kimmeridgian *Heterodontus falcifer* (Wagner, 1857) was designated type species of *Paracestracion* by Koken (1911) and is retained in this genus by some authors (Maisey 1982; Underwood 2002), although others regard *Paracestracion* as a junior synonym of *Heterodontus* (e.g. Cappetta 1987). A number of juvenile specimens of *H. falcifer* are known, but it is doubtful whether there is any adult shark with visible dentition in the material referred to this species. The largest specimen of *H. falcifer* with preserved teeth that was found in the survey by Schweizer (1964) has a total body length of 0.5 m. It is likely that adult sharks grew larger, as is indicated by a 1-m-long specimen without visible dentition that was assigned to *H. falcifer* by the same author. Anterior teeth of this species lack any ornamentation and if fossil species follow the same pattern as the Recent *H. portusjacksoni* (see Reif 1976), ornamentation would occur on teeth of subadult individuals; thus, *H. falcifer* cannot be conspecific with *H. polonicus*. Another species from the Upper Jurassic of southern Germany, *H. semirugosus* (Plieninger, 1847), possesses anterior teeth with a higher and more slender cusp, larger cusplets and ornamentation that only comprises simple folds (Schweizer 1961), in contrast to the reticulate ornamentation pattern of *H. polonicus*. Large lateral teeth of *H. semirugosus* possess a number of almost parallel folds on one side of the central ridge while the entire crown in large laterals of *H. polonicus* is covered with reticulate ornamentation. The third nominal species of the Heterodontidae from the Upper Jurassic of southern Germany is *H. zitteli* Eastman, 1914, known only from a single, very juvenile individual (150 mm in total length) and considered to be synonymous with *H. falcifer* (Schweizer 1964). The extensive ornamentation on the anterior teeth of *H. polonicus* separates this species from the Early Cretaceous *H. carerens* Kriwet, 1999 from the Barremian of Spain, *H. canaliculatus* (Egerton, in Dixon 1850) from the

Albian–Turonian of England and France and *H. upnikensis* (Dalinkevičius 1935) from the Albian and Cenomanian of Lithuania and France. *Heterodontus carerens* is further characterized by anterior teeth with prominent lateral blades on the labial side of the crown and a low root. Additionally, lateral teeth of *H. carerens* are higher and the ornamentation is less reticulate and more irregular compared with lateral teeth of *H. polonicus*. Anterior teeth of *H. upnikensis* possess a low root and a markedly higher cusp than in *H. polonicus*, while *H. canaliculatus* has anteriors with widely separated cusplets and laterals with a more pronounced longitudinal crest. Lateral teeth of the Aptian *H. sulcatus* Woodward, 1889 (a species known only from lateral teeth) from England can be separated from those of *H. polonicus* in being more mesio-distally expanded, often with narrow distal and mesial parts, and by a more symmetrical ornamentation in smaller teeth. A single anterior tooth from the Albian of north-east France referred to *Heterodontus* sp. by Biddle (1993) displays some labial ornamentation but considerably less than in teeth of *H. polonicus*. This French tooth also possesses extremely well-developed cutting edges and a root morphology quite different from that of *H. polonicus*.

Order ORECTOLOBIFORMES Applegate, 1974

Family uncertain

Gen. et sp. indet.

Text-figure 2J–M

Material. 22 incomplete teeth, ZPAL P.10/6, ZPAL P.10/7 and unnumbered.

Description. These small teeth possess a moderately high and slender central cusp, usually flanked by a single pair of minute lateral cusplets. The entire crown is labio-lingually compressed, covered with smooth enameloid, and equipped with moderately well-developed cutting edges. A labial apron descends from the crown and would overhang the root, but the root is not preserved in any specimen. The largest tooth-crown measures 1.0 mm in mesio-distal width.

Remarks. The morphology of these tooth-crowns is somewhat similar to that of certain hemiscyliids (e.g. *Pseudospinax* Müller and Diedrich, 1991) but the poor

state of preservation does not allow any closer systematic determination.

Order LAMNIFORMES Berg, 1958

Family CRETOXYRHINIDAE Glikman, 1958

Genus PROTOLAMNA Cappetta, 1980

Type species. *Protolamna sokolovi* Cappetta, 1980 from the Upper Aptian, Lower Cretaceous, of southern France.

Protolamna sp.

Text-figure 2A–G

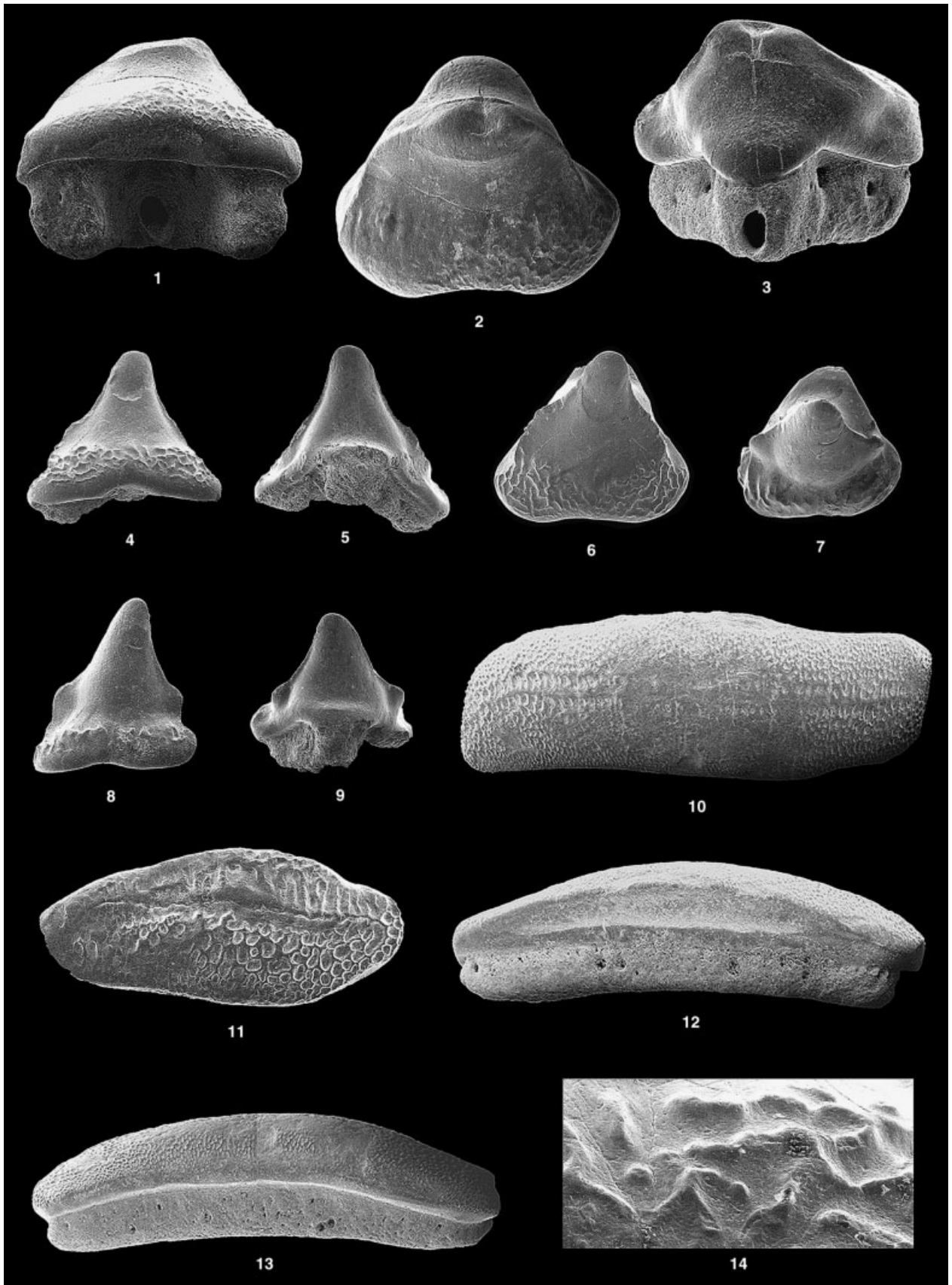
Material. One complete (ZPAL P.10/8) and nine incomplete teeth including ZPAL P.10/9 and ZPAL P.10/10.

Description. A high and slender central cusp flanked by a single pair of lateral cusplets characterizes these teeth. Anterior and antero-lateral teeth are close to symmetrical while the crown of lateral teeth is posteriorly inclined. The ornamentation comprises coarse vertical folds on the lower labial side of the crown, generally being more closely spaced in smaller and lateral teeth. The amount of ornamentation on the lingual side is highly variable but usually includes a few weaker folds on the cusplets and lower half of the cusp. A well-developed lingual neck is present at the base of the cusp but the height of this neck is somewhat variable. The root is high, with long lobes, and a prominent lingual bulge. In the centre of this bulge, there is a wide nutritive groove. Additionally, a few small foramina open on each side of the lingual bulge and in the centre of the low labial root-face. The largest tooth measures 8.1 mm in height.

Remarks. These Polish teeth of *Protolamna* differ slightly from those of the type species, *P. sokolovi*, from the Aptian of southern France. The root is somewhat less bulky and the groove in the centre of the root bulge is more prominent than in teeth of *P. sokolovi*. The teeth from Wąwał also possess more strongly developed ornamentation, particularly on the labial side. Teeth from the Barremian referred to *P. cf. sokolovi* by Biddle (1988), Canudo *et al.* (1995) and Kriwet (1999) have a more prominent ornamentation, with coarse folds that cover most of the crown. This difference may, however, be explained by the small size of these French and Spanish

EXPLANATION OF PLATE 1

Figs 1–14. *Heterodontus polonicus* sp. nov. 1–3, holotype, ZPAL P.10/1, complete anterior tooth, horizon W1, labial, occlusal and lingual views; $\times 13$. 4–6, 14, paratype, ZPAL P.10/2, anterior tooth-crown, horizon W1, labial, lingual and occlusal views; $\times 13$, detail of ornamentation; $\times 64$. 7–9, ZPAL P.10/3, anterior tooth-crown, horizon W1, occlusal, labial and lingual views; $\times 13$. 10, 12–13, paratype, ZPAL P.10/4, enlarged lateral tooth, horizon W1, occlusal, lingual and labial views; $\times 5$. 11, ZPAL P.10/5, lateral tooth, horizon C3 of Kaim (2001), \approx horizon W2, occlusal view; $\times 13$.



specimens. It is possible that the Polish teeth may be included in a new species but owing to the scarcity of the material and poorly understood dental variation of early species of *Protolamna*, they are at present left in open nomenclature. Being from deposits of early Late Valanginian age, these teeth represent one of the oldest occurrences of undoubted lamniforms so far reported.

Order CARCHARHINIFORMES Compagno, 1973
Family SCYLORHINIDAE Gill, 1862

Genus PALAEOSCYLLIUM Wagner, 1857

Type species. *Palaeoscyllium formosum* Wagner, 1857 from the Tithonian, Upper Jurassic of Solnhofen, southern Germany.

Palaeoscyllium sp.
Text-figure 2H-I

Material. One antero-lateral tooth-crown, ZPAL P.10/11.

Description. This tooth-crown possesses a high and slender central cusp flanked by two lateral cusplets on the mesial side and one on the distal side. The entire tooth-crown is posteriorly inclined. Cutting edges are well developed and coarse folds cover the enameloid on the lower part of the labial side. Lingual ornamentation is limited to a few weaker folds on the cusplets and lower half of the cusp. Nothing is preserved of the root. The tooth-crown measures 1.2 mm in width.

Remarks. The genus *Palaeoscyllium* was originally described on the basis of an incomplete fish lacking the head (Wagner 1857). Recently, Leidner and Thies (1999), using placoid scale morphology, were able to identify other, more complete, specimens of this genus from the Upper Jurassic of southern Germany. The teeth of *Palaeoscyllium* are extremely similar to those of the contemporary scylorhinid *Parasymbolus* Candoni, 1993, and the two genera are now considered synonymous (Leidner and Thies 1999; Underwood 2002) as *Parasymbolus octevillensis* Candoni, 1993 is a junior synonym of *Palaeoscyllium formosum* (Underwood 2002). The Polish tooth-crown is similar to teeth of *P. formosum* although it is mesio-distally wider, more posteriorly inclined and slightly less ornamented. Teeth of another species, *P. reticularis* (Underwood and Mitchell, 1999) from the English Albian, are generally lower and possess a wider central cusp than those of *P. formosum* and the Polish species. The English teeth are also ornamented with a more reticulate pattern on the labial side.

The Polish tooth-crown was collected during previous fieldwork and is derived from the lower part of the *Saynoceras verrucosum* Zone, when the Wąwał strata were deposited under major Tethyan influence (Bed C2 of

Kaim 2001). The Polish occurrence of *Palaeoscyllium* extends the palaeogeographical distribution of the genus to the east.

Superorder SQUALEA Shirai, 1996
Order SYNECHODONTIFORMES Duffin and Ward, 1993
Family PALAEOSPINACIDAE Regan, 1906

Genus SYNECHODUS Woodward, 1888b

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

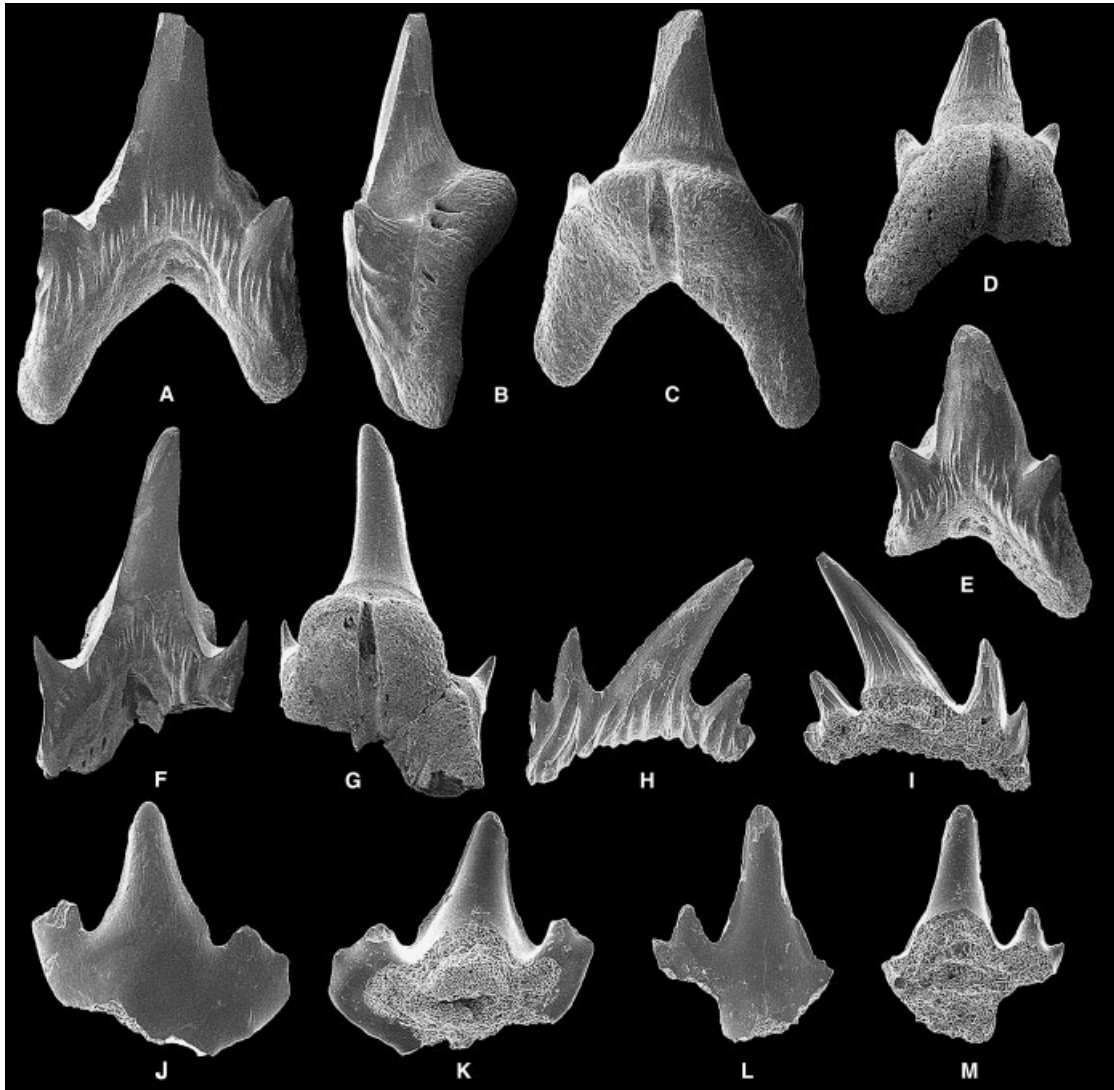
Synechodus nitidus Woodward, 1911
Plate 2, figures 6–15

- 1911 *Synechodus nitidus* Woodward, p. 219, pl. 46, figs 3–4.
1935 *Synechodus nitidus* Woodward; Dalinkevičius, p. 257, pl. 2, figs 39–49.
1975 *Synechodus nitidus* Woodward; Cappetta, p. 117, fig. 3, pl. 2, figs 8–12.
1987 *Synechodus nitidus* Woodward; Cappetta, p. 130.
1999 *Synechodus nitidus* Woodward; Underwood and Mitchell, p. 15, pl. 2, fig. 6.

Material. The material from Wąwał comprises seven complete and 33 incomplete teeth including ZPAL P.10/12–ZPAL P.10/16. This species occurs in both sampled beds.

Description. The anterior teeth have a high and slender central cusp with a comparably wide base. Two to three pairs of equal-sized lateral cusplets flank the cusp. The ornamentation on the labial side comprises weak folds, primarily on the cusplets and sides of the cusp, while the centre of the cusp is completely smooth. Reticulate ornamentation may occur on the mesial and distal heels. On the lingual side, most teeth have an ornamentation of fine folds covering the cusplets and reaching to at least one-third of the cusp height. A thin lingual neck is clearly visible in anterior teeth. Lateral teeth are lower and more ornamented, with folds often covering the entire crown. Posterior teeth are very low-crowned, without well-demarcated cusp or cusplets. These teeth are ornamented with densely spaced irregular folds covering the entire crown and forming a reticulate pattern. This type of ornamentation can also be found on large parts of juvenile tooth-crowns. The root morphology is very similar in teeth of different files and is characterized by a low labial root-face and a lingually projected root. A few prominent grooves on the labio-basal edge form the pseudo-polyaulacorhize root vascularization pattern. The largest anterior tooth measures 4.4 mm in mesio-distal width.

Remarks. Teeth of the holotype of *Synechodus nitidus* appear to be slightly more asymmetrical, with a higher



TEXT-FIG. 2. A–G, *Protolamna* sp. A–C, ZPAL P.10/8, anterior tooth, \approx horizon W2, labial, lateral and lingual views; $\times 7$. D–E, ZPAL P.10/10, anterior tooth, horizon C3 of Kaim (2001), \approx horizon W2, lingual and labial views; $\times 7$. F–G, ZPAL P.10/9, incomplete tooth, horizon W2, labial and lingual views; $\times 7$. H–I, *Palaeoscyllium* sp., ZPAL P.10/11, antero-lateral tooth-crown, horizon C2 of Kaim (2001), labial and lingual views; $\times 30$. J–M, *Orectolobiformes* gen. et sp. indet. J–K, ZPAL P.10/6, tooth-crown, horizon W1, labial and lingual views; $\times 35$. L–M, ZPAL P.10/7, tooth-crown, horizon W1, labial and lingual views; $\times 35$.

number of mesial cusplets, than the teeth from Wąwał. This is regarded herein as being within the normal range of intraspecific variation. It is further possible that the Aptian *S. tenuis* Woodward, 1889 from southern England could fall within this range as the general morphology and ornamentation pattern of the holotype (Woodward 1889, pl. 11, fig. 21) is very similar to teeth of *S. nitidus*. As previously noted by Batchelor and Ward (1990), the two species may be synonymous. Separating teeth of *S. nitidus* from those of the contemporary *S. dubrisiensis* is seldom problematic. Teeth of the latter species are mesio-distally wider than corresponding teeth of

S. nitidus and possess more extensive ornamentation covering most of the tooth-crown.

It is evident that *Synechodus* evolved slowly during the Early Cretaceous, as indicated by the two long-lived species *S. dubrisiensis*, ranging from the Hauterivian (Underwood *et al.* 1999) to the Cenomanian (Underwood and Mitchell 1999), and *S. nitidus*, with a stratigraphical distribution from the Valanginian (herein) to the Coniacian (Dalinkevičius 1935). The presence of *S. nitidus* in the Polish Valanginian is the oldest reported occurrence, and it expands the palaeogeographical distribution of this species to the south-east.

Order SQUATINIFORMES Buen, 1926
Family SQUATINIDAE Bonaparte, 1838

Genus SQUATINA Duméril, 1806

Type species. *Squalus squatina* Linnaeus, 1758, Recent in temperate European and North African waters in depths to at least 150 m (Compagno 1984).

Remarks. Identifying isolated teeth of this genus to specific level is difficult (Cappetta 1987) as the tooth morphology is extremely conservative and has remained virtually the same since the Aptian (Cappetta 1975; Siverson 1995). A few Jurassic squatinid taxa included in *Squatina* [e.g. '*S.* *alifera* (Münster, 1842) and *S.?* *frequens* Underwood, 2002] have a dental morphology quite different from Aptian and younger species (Rees 2002; Underwood 2002). The teeth of these Jurassic taxa can be distinguished by their development of lateral blades possessing cusplets, a more prominent labial protuberance unsupported by the root and a root divided in two separate lobes. As suggested by Underwood (2002), it is likely that a new genus is needed to include most Jurassic species referred to *Squatina* but that is beyond the scope of this paper.

Squatina cranei Woodward, 1888a
Plate 2, figures 1–5

- 1888a *Squatina cranei* Woodward, p. 144, pl. 7, figs 1–6.
1889 *Squatina cranei* Woodward; Woodward, p. 70.
1911 *Squatina cranei* Woodward; Woodward, p. 224, pl. 47, figs 7–12.
1975 *Squatina cranei* Woodward; Cappetta, p. 124, fig. 8.
1977 *Squatina cranei* Woodward; Herman, p. 123, pl. 5, fig. 2.
1991 *Squatina cranei* Woodward; Müller and Diedrich, p. 21.
1993 *Squatina cranei* Woodward; Biddle, p. 199, pl. 1, fig. 2.

Material. Four complete and 14 incomplete teeth including ZPAL P.10/17 and ZPAL P.10/18.

Description. The teeth possess a high central cusp with prominent cutting edges continuing on the mesial and distal heels of the tooth. Most teeth have a straight cusp; it is slightly inclined to the posterior in two specimens only. The labial protuberance is well developed and partly supported by the root. The shape is somewhat variable, from parallel-sided to drop-shaped. A median lingual uvula is present in three teeth only, where it is clearly developed and parallel-sided. The low and lingually projected root displays a number of small foramina on the upper part of the lingual root-face and commonly a single, large foramen in the centre of the lingual root protuberance. Additionally, a single large foramen in the central part of the basal surface confirms the hemiaulacorhize stage of root vascularisation. The teeth range from 3.6 to 6.5 mm in mesio-distal width.

Remarks. These Polish teeth are identical to those of *Squatina cranei* Woodward, 1888a from the Albian and Cenomanian of southern England and are thus included in this species. The conservative tooth morphology of this genus (see above) may lead to unnaturally long-ranging species but this may also be a result of a slowly evolving lineage. *Squatina decipiens* from the Cenomanian of Lithuania is separated from *S. cranei* on tooth size only (Dalinkevičius 1935) and is probably a junior synonym of the latter. The presence of both nominal taxa in the Albian and Aptian of France (Cappetta 1975; Biddle 1993) supports this interpretation. The occurrence of *S. cranei* in the Polish Valanginian represents the oldest record of the true *Squatina*-lineage reported so far.

Order RAJIFORMES Berg, 1940
Family uncertain

Genus BELEMNOBATIS Thiollière, 1854

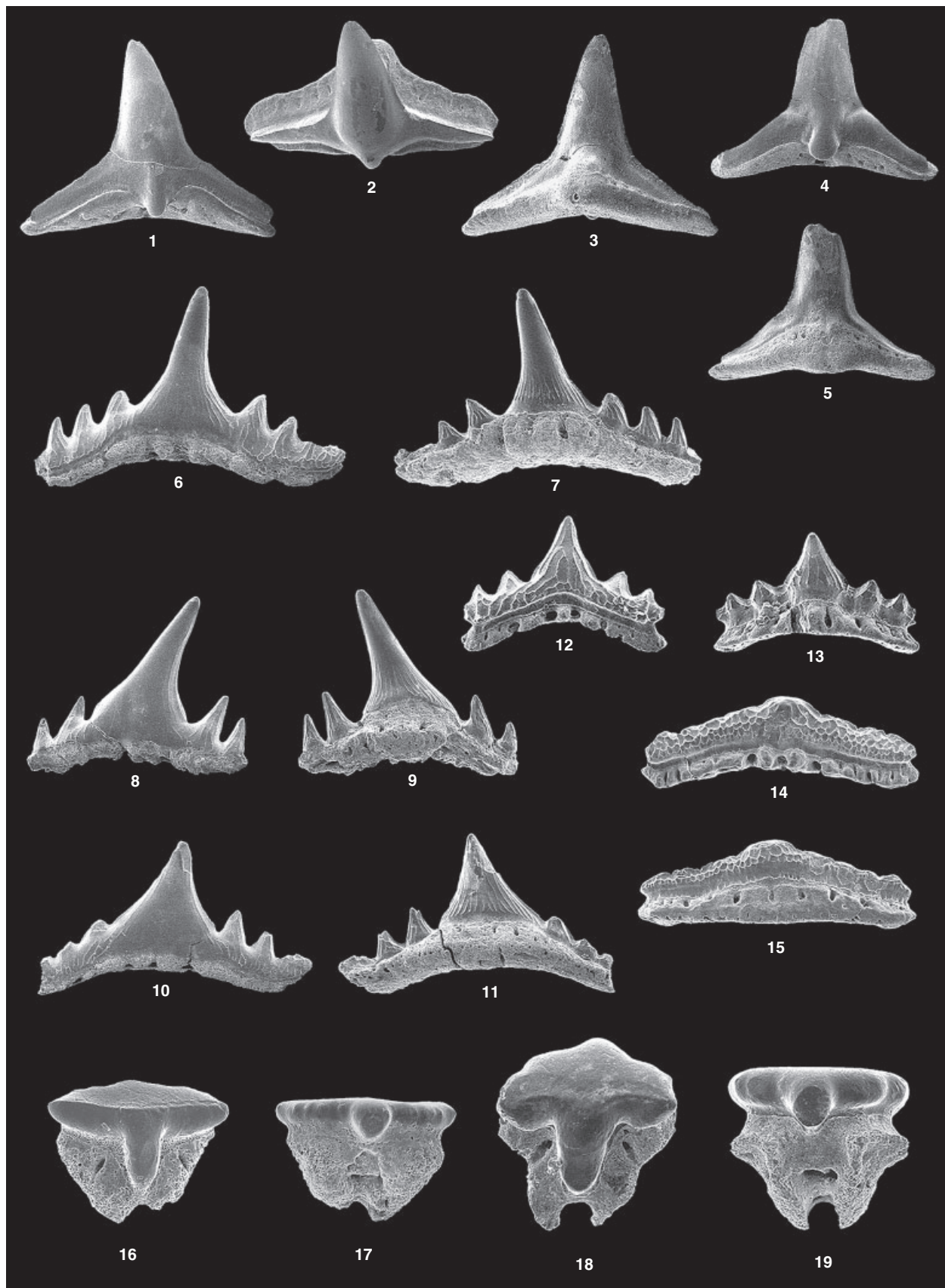
Type species. *Belemnobatis sismondæ* Thiollière, 1854 from the Upper Kimmeridgian, Upper Jurassic of Cérin, northern France.

Belemnobatis sp.
Plate 2, figures 16–19

Material. Two complete teeth (ZPAL P.10/19 and ZPAL P.10/20) and 18 tooth-crowns.

EXPLANATION OF PLATE 2

- Figs 1–5. *Squatina cranei* Woodward 1888a. 1–3, ZPAL P.10/17, antero-lateral tooth, horizon W1, labial, occlusal and lingual views. 4–5, ZPAL P.10/18, anterior tooth, horizon W2, labial and lingual views. Both $\times 6.5$.
Figs 6–15. *Synechodus nitidus* Woodward, 1911. 6–7, ZPAL P.10/12, anterior tooth, horizon W1, labial and lingual views; $\times 12$. 8–9, ZPAL P. 10/13, anterior tooth, horizon W1, labial and lingual views; $\times 12$. 10–11, ZPAL P. 10/14, antero-lateral tooth, horizon W2, labial and lingual views; $\times 12$. 12–13, ZPAL P. 10/15, juvenile tooth, horizon W1, labial and lingual views; $\times 20$. 14–15, ZPAL P. 10/16, posterior tooth, horizon W2, labial and lingual views; $\times 20$.
Figs 16–19. *Belemnobatis* sp. 16–17, ZPAL P.10/19, lateral tooth, horizon W2, lingual-occlusal and labial views. 18–19, ZPAL P.10/20, antero-lateral tooth, horizon W2, lingual-occlusal and labial views. Both $\times 44$.



REES, neoselachian teeth

Description. The dentition of this species is characterized by a high degree of monognathic, and possibly gynandric heterodonty. Anterior teeth may have a small but demarcated cusp and are rather stout, while lateral teeth are lower, mesio-distally expanded and possess a prominent transverse crest. In occlusal view, this crest is either straight or sinuous. The teeth have a rather narrow and tapering median lingual uvula while rudimentary marginal lingual uvulas are displayed in only a few teeth. The labial projection of the crown is moderate but there may be a well-developed knob-like labial protuberance. Only a few teeth display any ornamentation, comprising weak folds on the labial rim of the crown. Below the median lingual uvula there is a prominent notch in the root, and on either side of the uvula a large foramen opens. The root is divided into two well-separated lobes by a large, basal groove with one or two nutritive foramina in the centre. The teeth range from 0.5 to 0.9 mm in width.

Remarks. The taxonomy of Late Jurassic and Early Cretaceous batoids of the three nominal genera *Belemnobatis*, *Spathobatis* Thiollière, 1854 and *Asterodermus* Agassiz, 1843 is currently in a state of confusion. The dentitional distinction between *Belemnobatis* and *Spathobatis* is somewhat unclear, although skeletal characteristics clearly justify the two genera (Cavin *et al.* 1995). The dentitions of species usually referred to *Spathobatis* include anterior teeth with a high central cusp and lateral teeth in which the cusp is smaller, but clearly marked. The median lingual uvula is strongly developed, often wide and expanding towards the root, while the root itself has a rather robust morphology. Teeth referred to *Belemnobatis* are lower, more mesio-distally expanded and often possess a tapering median lingual uvula. Clearly developed cusps are rarely found but distinctive transverse crests are common (Cavin *et al.* 1995). However, many of the separating characters differ gradually and it may be difficult to refer isolated teeth to either of these genera. It is evident that many teeth, representing several individuals and different tooth positions, are needed to determine the generic affinity of any tooth-based species. As the holotype of *Asterodermus platypterus* Agassiz, 1843, the type species of *Asterodermus*, is a partial fish lacking the head, neither teeth nor rostral length (as in Leidner and Thies 1999) can be used to diagnose this genus unless other characters are found to distinguish this specimen from complete skeletons of *Spathobatis* and *Belemnobatis*. The holotype of *A. platypterus* is housed in The Natural History Museum, London (P.12067) and, contrary to the claims of Arratia *et al.* (2002), the placoid scale morphology has been studied on several occasions by the author. Scales identical to those of the holotype, and scales referred to *Asterodermus* by Thies (1995) and Leidner and Thies (1999), have been recorded from Late Jurassic and Early Cretaceous deposits yielding teeth of *Spathobatis* and/or *Belemnobatis* (e.g. Underwood 2002; Underwood and Rees 2002). Furthermore, Leidner and Thies (1999) found that

the placoid scale morphology of the holotype of *A. platypterus* is identical to that of the holotype of *S. bugesiacus* Thiollière, 1854, the type species of *Spathobatis*. Despite recent claims by Leidner and Thies (1999) and Arratia *et al.* (2002), no characters have so far been provided for a generic diagnosis of *Asterodermus*. Although it is likely that *A. platypterus* is conspecific with *S. bugesiacus* (Underwood 2002), a thorough investigation of the skeletal morphology of the holotype of *A. platypterus* is needed to resolve this issue.

The low crown profile and near absence of clearly demarcated cusps warrant the inclusion of the Polish teeth in *Belemnobatis*, at least for the time being (see below). The Polish teeth differ from those of *B. morinicus* (Sauvage, 1873) from the Tithonian of France, in being mesio-distally wider and having a larger crown with a less developed labial projection. A knob-like labial protuberance, which can be found in some of the Polish teeth, separate them from those of the type species, *B. sismondæ* from the Kimmeridgian of France. Teeth of the latter species are also characterized by a wider basal notch and a more prominent labial crown projection. Teeth of *B. weneri* Thies, 1983 from the Callovian of England possess both extreme labial protuberance and crown projection. By contrast to the Polish specimens, the root in teeth of *B. weneri* is both wider and higher than the crown. The general morphology and, in particular, the high degree of heterodonty where anterior teeth approach a *Spathobatis*-like morphology indicate that the Polish species is more closely related to the Early Cretaceous *B. variabilis* Underwood and Rees, 2002 and *B. picteti* (Cappetta, 1975) than to the Jurassic species of *Belemnobatis*. The median lingual uvula in teeth of *B. variabilis* from southern England is larger and parallel-sided as opposed to the tapering uvula in the Polish specimens. The more strongly developed labial crown projection in teeth of both *B. variabilis* and *B. picteti* separates these species from the Polish one. It is possible that this Valanginian occurrence represents an undescribed species but it is left in open nomenclature as the material only comprises two complete teeth. Arratia *et al.* (2002) claimed, without presenting any supporting evidence, that *B. variabilis* must be placed within another batoid genus that would also include some Early Cretaceous teeth referred to *Spathobatis*. It is herein agreed that the high degree of heterodonty may warrant the erection of a new genus including *B. variabilis*, *B. picteti* and the Polish material but not, as suggested, the bulky and rounded teeth referred to *Spathobatis* by Biddle (1993) and Kriwet (1999). At our present state of knowledge about these batoids, however, it would be premature to erect new genera before the existing genera are properly understood.

EARLY CRETACEOUS NEOSELACHIAN DISTRIBUTION

Selachian faunas from the first half of the Early Cretaceous (Berriasian–Barremian) are known from many localities in northern and western Europe but the majority of these assemblages are derived from non-marine deposits and include almost exclusively hybodont sharks (e.g. Patterson 1966; Ansorge 1990; Rees 2002; Underwood and Rees 2002). Neoselachian assemblages of the Berriasian–Barremian are so far limited to a few localities and have recently been recorded in the Hauterivian of England (Underwood *et al.* 1999), the Lower and Upper Barremian of Spain (Canudo *et al.* 1995; Kriwet 1999) and the Upper Barremian of France (Biddle 1988). Additionally, a number of isolated neoselachian occurrences have been recorded in the Hauterivian and Barremian of Germany (Thies 1979, 1981; Ward and Thies 1987) and the Valanginian and Hauterivian of France (Leriche 1910; Cappetta 1990). Selachian teeth from the Late Barremian assemblage of France were concentrated in a bone-bed (Biddle 1988) and do not represent a natural assemblage. The frequent hybodont teeth and the composition of the neoselachian assemblage, including almost exclusively lamniforms and batoids, suggest that the Late Barremian fauna from Spain (Canudo *et al.* 1995) perhaps originates from a marginal marine setting. Most hybodonts were at this time primarily restricted to non-marine habitats and many batoids are known to occur in settings with lower salinity. In the open marine assemblages, neoselachians constitute the main portion of the fauna, both regarding the number of specimens and species diversity. As with their Late Jurassic analogues, the assemblages are dominated either by neoselachian groups that were already well established in the Jurassic (palaeospinacids; Underwood *et al.* 1999) or by bottom-dwellers (heterodontids and rajiforms; Kriwet 1999). Noteworthy, however, is an increased diversity of batoids, particularly on a higher systematic level, including early appearances of the Hypsobatidae and the Sclerorhynchidae (Kriwet 1999). Lamniforms, with an undoubted record ranging from the Valanginian, appear to have been slightly more diverse in the Barremian (Canudo *et al.* 1995; Kriwet 1999), an early indication of their coming success as large predatory sharks in the Late Cretaceous. Aptian and Albian neoselachian assemblages are more similar to their Late Cretaceous counterparts and include a wide range of lamniforms and rajiforms (e.g. Biddle 1993; Underwood and Mitchell 1999).

The Wąwał faunas are numerically dominated by neoselachian genera typical of Late Jurassic assemblages, such as *Synechodus*, *Heterodontus* and *Belemnobatis*. There is also a striking component of taxa more commonly

found in mid-Cretaceous and later faunas, including early occurrences of the true *Squatina*-lineage and the lamni-form *Protolamna*. The Wąwał faunas are not particularly similar in composition to the Berriasian–Barremian faunas previously described and it is evident that the depositional environment was an important factor. The Hauterivian assemblage from Speeton in north-east England (Underwood *et al.* 1999, Bed C7H) is stratigraphically closest to the Wąwał assemblages and this fauna is numerically dominated by a palaeospinacid (*Synechodus dubrisiensis*, similar to that of Wąwał W2). The Speeton and Wąwał faunas are also the only pre-Albian assemblages recorded from the Boreal realm.

Acknowledgements. I am indebted to Andrzej Kaim, Warszawa, for introducing me to the locality, assisting in the fieldwork and sharing his vast knowledge of the Polish Lower Cretaceous. Discussions with Mikael Siverson, Kävlinge, and Gilles Cuny, Copenhagen, further improved the content of this paper. The Royal Physiographical Society of Sweden contributed with a travel and fieldwork grant for which I am very grateful. The Institute of Paleobiology at the Polish Academy of Sciences in Warszawa and the Department of Geology at Lund University kindly provided laboratory facilities. SEM work was carried out at the Geological Institute, Copenhagen University, and I am particularly grateful for the assistance provided by Kurt Nielsen, Copenhagen. I also thank Charlie Underwood, London, for providing photographs of type material housed in The Natural History Museum, London, and Euan Clarkson, Edinburgh, for correcting my English.

REFERENCES

- AGASSIZ, L. J. R. 1833–43. *Recherches sur les poissons fossiles*, 3. Imprimerie de Petitpierre, Neuchâtel, 390 + 32 pp.
- ANSORGE, J. 1990. Fischreste (Selachii, Actinopterygii) aus der Wealdentonscholle von Lobber Ort (Müch-gut/Rügen/DDR). *Paläontologische Zeitschrift*, **64**, 133–144.
- APPLEGATE, S. P. 1974. A revision of the higher taxa of orectolobids. *Journal of the Marine Biological Association of India*, **14** (for 1972), 743–751.
- ARRATIA, G., KRIWET, J. and HEINRICH, W.-D. 2002. Selachians and actinopterygians from the Upper Jurassic of Tendaguru, Tanzania. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe*, **5**, 207–230.
- BATCHELOR, T. J. and WARD, D. J. 1990. Fish remains from a temporary exposure of Hythe Beds (Aptian–Lower Cretaceous) near Godstone, Surrey. *Mesozoic Research*, **2**, 181–203.
- BERG, L. S. 1940. Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique de l'Académie des Sciences de l'URSS*, **5**, 85–517. [In Russian].
- 1958. *System der rezenten und fossilen Fischartigen und Fische*. Deutscher Verlag Wissenschaft, Berlin, 310 pp.

- BIDDLE, J. P. 1988. Contribution à l'étude des séliaciens du Crétacé du Bassin de Paris. Découverte de quelques nouvelles espèces associées à une faune de type wealdien dans le Barrémien supérieur (Crétacé inférieur) des environs de Troyes (Aube). *Publications, Musée de Saint-Dizier*, **2**, 1–22.
- 1993. Les elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France). *Belgian Geological Survey, Professional Paper*, **264**, 191–240.
- BLAINVILLE, H. M. D. DE 1816. Prodrome d'une distribution systématique du regne animal. *Bulletin de la Société Philomatique de Paris*, **8**, 105–124.
- BONAPARTE, C. L. J. L. 1838. Synopsis vertebratorum systematis. *Nuovi Annali delle Scienze Naturali*, **2**, 105–133.
- BUEN, F. DE 1926. Catalogo ictiologico del Mediterraneo Español y de Marruecos, recopilando lo publicado sobre peces de las costas mediterraneas y proximas del Atlantico (Mar de España). *Resultados de las Campañas Realizadas por Acuerdos Internacionales, Instituto Español de Oceanografía*, **2**, 1–221.
- CANDONI, L. 1993. Découverte de *Parasymbolus octevillensis* gen. et sp. nov. (Scyliorhinidae-Elasmobranchii) dans le Kiméridgien de Normandie, France. *Belgian Geological Survey, Professional Paper*, **264**, 147–156.
- 1995. Deux faunes inédites de séliaciens dans le Jurassique terminal Français - premiers résultats stratigraphiques [sic]. *Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre*, **82**, 29–49.
- CANUDO, J. I., CUENCA-BESCÓS, G. and RUIZ-OMENACA, J. I. 1995. Tiburones y rayas (Chondrichthyes, Elasmobranchii) del Barremiense superior (Cretacico inferior) de Vallipón (Castellote, Teruel). *Beca del Museo de Mas de las Matas Año*, **1995**, 35–57.
- CAPPETTA, H. 1975. Séliaciens et holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géologie Méditerranéenne*, **2**, 115–134.
- 1980. Modification du statut générique de quelques espèces de séliaciens Crétacés et Tertiaires. *Palaeovertebrata*, **10**, 29–42.
- 1987. *Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii*. Gustav Fischer Verlag, Stuttgart, 193 pp.
- 1990. Hexanchiforme nouveau (Neoselachii) du Crétacé inférieur du sud de la France. *Palaeovertebrata*, **20**, 33–54.
- DUFFIN, C. J. and ŽIDEK, J. 1993. Chondrichthyes. 593–609. In BENTON, M. J. (ed.). *The fossil record 2*. Chapman & Hall, London, 845 pp.
- CAVIN, L., CAPPETTA, H. and SÉRET, B. 1995. Révision de *Belemnobatis morinicus* (Sauvage, 1873) du Portlandien du Boulonnais (Pas-de-Calais, France). Comparisons avec quelques Rhinobatidae Jurassiques. *Geologica et Palaeontologica*, **29**, 245–267.
- COMPAGNO, L. J. V. 1973. Interrelationships of living elasmobranchs. 15–61. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). *Interrelationships of fishes*. Zoological Journal of the Linnean Society, **53** (Supplement), 536 pp.
- 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**, 303–322.
- 1984. FAO species Catalogue, Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. *FAO Fisheries Synopsis* (125), **4**, 1–655.
- DALINKEVIČIUS, J. A. 1935. On the fossil fishes of the Lithuanian chalk. I. Selachii. *Mémoires de la Faculté des Sciences de l'Université de Vytautas le Grand*, **9**, 274–305.
- DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. London, 408 pp.
- DUFFIN, C. J. and WARD, D. J. 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Belgian Geological Survey, Professional Paper*, **264**, 53–102.
- DUMÉRIL, A. M. C. 1806. *Zoologie analytique, ou méthode naturelle de classification des animaux*. Allais, Paris, 344 pp.
- EASTMAN, C. R. 1914. Catalogue of the fossil fishes in the Carnegie Museum, Part IV. *Memoirs of the Carnegie Museum*, **6**, 389–449.
- GILL, T. 1862. Analytical analysis of the order of Squali and revision and nomenclature of genera. *Annals of the Society of Natural History of New York*, **1862**, 367–408.
- GLIKMAN, L. S. 1958. Rates of evolution in lamnoid sharks. *Doklady Akademii Nauk SSSR*, **123**, 568–571. [In Russian].
- GRAY, J. E. 1851. *List of the specimens of fish in the collection of the British Museum, Part 1. Chondropterygii*. British Museum (Natural History), London, 160 pp.
- HERMAN, J. 1977. Les séliaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphie intercontinentale. Mémoires pour servir à l'explication des Cartes Géologiques et Minières de la Belgique. *Service Géologique de Belgique*, **15** (for 1975), 1–401.
- KAIM, A. 2001. Faunal dynamics of juvenile gastropods and associated organisms across the Valanginian transgression-regression cycle in central Poland. *Cretaceous Research*, **22**, 333–351.
- 2002. Gradual evolution of the Early Cretaceous marine gastropod *Rissoina* lineage in central Poland. *Acta Palaeontologica Polonica*, **47**, 667–672.
- KOKEN, E. 1911. Pisces. 3–142. In ZITTEL, K. A. (ed.). *Grundzüge der Paläontologie. Zweite Abteilung, Vertebrata*. Second edition. Oldenburg, München and Berlin, 142 pp.
- KRIWET, J. 1999. Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaïne (Spanien, Provinz Teruel). *Palaeo Ichthyologica*, **9**, 113–142.
- KUTEK, J., MARCINOWSKI, R. and WIEDMANN, J. 1989. The Wąwał section, central Poland – an important link between Boreal and Tethyan Valanginian. 717–754. In WIEDMANN, J. (ed.). *Cretaceous of the Western Tethys. Proceedings of the 3rd International Cretaceous Symposium, Tübingen 1987*. Schweizerbart, Stuttgart, 1005 pp.
- LEIDNER, A. and THIES, D. 1999. Placoid scales and oral teeth of Late Jurassic elasmobranchs from Europe. 29–40. In ARRATIA, G. and SCHULTZE, H. P. (eds). *Mesozoic fishes 2 - systematics and the fossil record*. Verlag Dr Friedrich Pfeil, München, 608 pp.
- LERICHE, M. 1910. Sur quelques Poissons du Crétacé du Bassin de Paris. *Bulletin de la Société de France*, **10**, 455–471.
- LINNAEUS, C. 1758. *Systema naturae*. Tenth edition. Salvi, Stockholm, 824 pp.

- MACKIE, S. J. 1863. On a new species of *Hybodus* from the Lower Chalk. *Geologist*, **6**, 241–246.
- MAISEY, J. G. 1982. Fossil Hornshark finspines (Elasmobranchii; Heterodontidae) with notes on a new species (*Heterodontus tuberculatus*). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **164**, 393–413.
- MEYER, F. A. A. 1793. *Systematisch-summarische übersicht der neuesten zoologischen entdeckungen in Neuholland und Afrika*. Leipzig, 161 pp.
- MÜLLER, A. and DIEDRICH, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoburger Wald (Nordrhein-Westfalen, NW Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.
- MÜNSTER, G. 1842. Beschreibung einiger neuen Fische aus der Jura-Formation von Bayern und Württemberg. *Beiträge zur Petrefacten-Kunde*, **6**, 53–56.
- MUTTERLOSE, J. 1992. Migration and evolution patterns of floras and faunas in marine Early Cretaceous sediments of NW Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **94**, 261–282.
- PATTERSON, C. 1966. British Wealden Sharks. *Bulletin of the British Museum (Natural History), Geology*, **11**, 283–350.
- PLIENINGER, T. 1847. Die Wirbeltierreste im Korallenkalk von Schnaitheim. *Wuttberg Jahrbuch*, **3**, 227.
- REES, J. 2002. Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 59–71.
- REGAN, C. T. 1906. A classification of selachian fishes. *Proceedings of the Zoological Society of London*, **2**, 722–758.
- REIF, W.-E. 1976. Morphogenesis, pattern formation and function of the dentition of *Heterodontus* (Selachii). *Zoomorphologie*, **83**, 1–47.
- SAUVAGE, H. E. 1873. Notice sur un spathobate du terrain portlandien de Boulogne-sur-Mer. *Bulletin de la Société Académique de Boulogne-sur-Mer*, **2**, 94–103.
- SCHNEIDER, J. G. 1801. *Systema ichthyologiae iconibus CX illustratum*. Berolini, 584 pp.
- SCHWEIZER, R. 1961. Über die zähne von *Heterodontus semirugosus* (Plieninger) aus dem Brenztaloolith von Schnaitheim und dem Diceraskalk von Kelheim (Malm ζ). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **113**, 95–109.
- 1964. Die elasmobranchier und holocephalen aus den Nusplinger plattenkalken. *Palaeontographica, Abteilung A*, **123**, 58–110.
- SHIRAI, S. 1996. Phylogenetic interrelationships of Neoselachians (Chondrichthyes: Euselachii). 9–34. In STIASSEY, M. L. J., PARENTI, L. R. and JOHNSON, G. D. (eds). *Interrelationships of fishes*. Academic Press, San Diego, 575 pp.
- SIVERSON, M. 1995. Revision of *Cretorectolobus* (Neoselachii) and description of *Cederstroemia* n. gen., a Cretaceous carpet shark (Orectolobiformes) with a cutting dentition. *Journal of Paleontology*, **69**, 974–979.
- THIES, D. 1979. Selachierzähne aus der nordwestdeutschen Unterkreide. *International Union of Geological Sciences, Series A*, **6**, 211–222.
- 1981. Vier neue Neoselachier-Haiarten aus der NW-deutschen Unterkreide. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1981**, 475–486.
- 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. *Courier Forschungsinstitut Senckenberg*, **58**, 1–117.
- 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of northern Germany. *Journal of Vertebrate Paleontology*, **15**, 463–481.
- THIOLLIÈRE, V. 1854. Description des poissons fossiles provenants des gisements coralliens du Jura dans le Bugey. *Annales des Sciences Physiques et Naturelles, 2ème Série*, **4**, 1–27.
- UNDERWOOD, C. J. 2002. Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, southern England. *Palaeontology*, **45**, 297–325.
- and MITCHELL, S. F. 1999. Albian and Cenomanian selachian assemblages from north-east England. *Special Papers in Palaeontology*, **60**, 9–56.
- MITCHELL, S. F. and VELTKAMP, K. J. 1999. Shark and ray teeth from the Hauterivian (Lower Cretaceous) of north-east England. *Palaeontology*, **42**, 287–302.
- and REES, J. 2002. Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England. *Special Papers in Palaeontology*, **68**, 83–101.
- and WARD, D. J. 2004. Neoselachian sharks and rays from the British Bathonian (Middle Jurassic). *Palaeontology*, **47**, 447–501.
- WAGNER, J. A. 1857. Charakteristik neuer Arten von Knorpelfischen aus den lithographischen Schieferen der Umgegend von Solnhofen. *Gelehrte Anzeiger Bayer Akademie Wissenschaft*, **44**, 288–293.
- WARD, D. J. and THIES, D. 1987. Hexanchid shark teeth (Neoselachii, Vertebrata) from the Lower Cretaceous of Germany and England. *Mesozoic Research*, **1**, 89–106.
- WOODWARD, A. S. 1888a. On some remains of *Squatina cranei*, sp. nov., and the mandible of *Belonostomus cinctus*, from the chalk of Sussex, preserved in the collection of Henry Willett, Esq., F. G. S., Brighton Museum. *Quarterly Journal of the Geological Society of London*, **44**, 144–148.
- 1888b. On the Cretaceous selachian genus *Synechodus*. *Geological Magazine*, **3**, 496–499.
- 1889. *Catalogue of the fossil fishes in the British Museum (Natural History). Part I. Elasmobranchii*. Taylor & Francis, London, 474 pp.
- 1911. The fossil fishes of the English Chalk. Part 6. *Monograph of the Palaeontographical Society*, **64**, 185–224.