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New records of Late Jurassic sharks teeth from Southern Germany

By Christopher J. Duffin, Morden (England)

With 5 figures and 2 tables



Abstract

Two small collections of Late Jurassic sharks teeth are briefly described. Samples from the *transversarium* Zone (Middle Oxfordian) of Reichenbach and the *planula* Zone (Upper Oxfordian) of Stuifen contain teeth of *Protospinax annectans* WOODWARD, *Synechodus riegrafi* (THIES) and *Sphenodus cf. longidens* AGASSIZ.

Résumé

Deux petites collections de dents de requins (Jurassique supérieure) sont décrites brièvement. Des exemples de la zone à *transversarium* (Oxfordien moyen) de Reichenbach et de la zone à *planula* (Oxfordien supérieur) de Stuifen contiennent des dents de *Protospinax annectans* WOODWARD, *Synechodus riegrafi* (THIES) et *Sphenodus cf. longidens* AGASSIZ.

Zusammenfassung

Zwei kleine Sammlungen von Zähnen oberjurassischer Haie werden kurz beschrieben. Proben der *transversarium*-Zone (Mitteloxfordium) von Reichenbach und der *planula*-Zone (Oberoxfordium) enthalten Zähne von *Protospinax annectans* WOODWARD, *Synechodus riegrafi* (THIES) und *Sphenodus cf. longidens* (AGASSIZ).

1. Introduction

Germany is famous for its Jurassic Conservat-Lagerstätten at Holzmaden (Toarcian: Early Jurassic) and Solnhofen (Tithonian: Late Jurassic). Amongst these faunas are beautifully preserved fully articulated chondrichthyans. Such specimens have been important for reference and comparison in the description of newly collected microvertebrate faunas (e. g. THIES, 1983).

In his study of Jurassic microvertebrate selachian faunas, THIES (1983) described sharks teeth obtained from washed and screened samples of German Hettangian (Egge), Pliensbachian (Gretenberg), Aalenian (Moorberg), Oxfordian (Buchsteige) and Kimmeridgian (Uppen, Oker and Holzmühle) age, together with a selachian fauna from the Callovian (Stewartby) of England.

The purpose of this short note is to describe two small selachian samples collected from the Oxfordian localities of Reichenbach and Stuifen by Dr. FEIFEL. His collection was purchased by the Staatliches Museum für Naturkunde in Stuttgart (SMNS) in 1947.

2. Geological background

The Weissjura (Oxfordian to Tithonian) of Southern Germany covers an area of over 10 000 square kilometers, forming the steep hills of the Swabian and Franconian Alb (ZIEGLER, 1977).

The Reichenbach section is located about 1 km east of the village of Reichenbach, and 3 km west of Geislingen (Fig. 1). According to the information accompanying the specimens collected by FEIFEL, the sample is of *transversarium* Zone age (Middle Oxfordian; Oxfordmergel ox1). More precise details are not available.

Stuifen is a prominent arcuate ridge situated 0.8 km north of Wissgoldingen and 3.5 km south of Schwäbisch Gmünd (Fig. 1). According to the information accompanying the specimens, the sample was also collected from the *Epipeltoceras transversarium* Zone. Referring to the geological map of the area, however, the section lies within an area of Upper Oxfordian rocks belonging to the *Idoceras planula* Zone. This is confirmed by HÖNIG (1984: 122), who gives a description of the section, placing it within the limestones and marls of the Oxfordkalk (ox2).

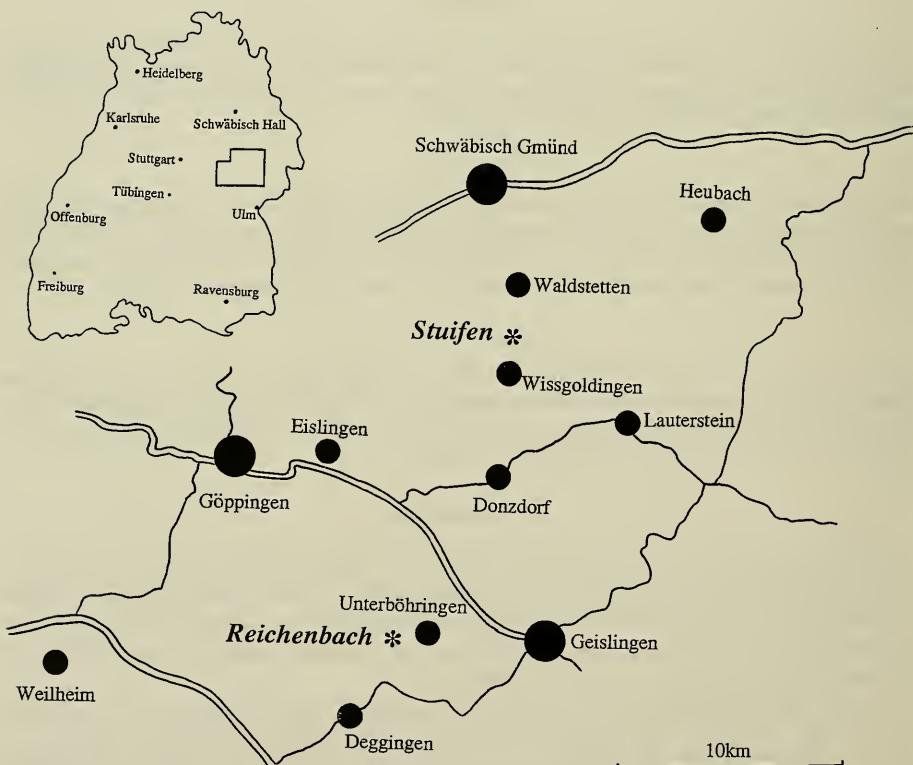


Fig. 1. Sketch map to show the locations of Reichenbach and Stuifen. Inset Baden-Württemberg.

2. Systematic palaeontology

Class Chondrichthyes
 Subclass Elasmobranchii
 Cohort Neoselachii
 Order incertae sedis
 Family Protospinacidae WOODWARD, 1918

Genus *Protospinax* WOODWARD, 1918

Type species: *Protospinax annectans* WOODWARD, 1918.

Comments: WOODWARD (1919) considered *Protospinax* to be the ancestor of the batoids. He based the genus and species on two specimens, BM (NH) P.8775 and 37014, believing the latter to be a juvenile. MAISEY (1976) considered the type specimen to be a true rhinobatoid referable to *Belemnobatis* THIOLIERE (1854), and the second specimen (BM(NH) 37014) to be a galeomorph shark of uncertain position. He made this specimen the holotype of *Squalogaleus woodwardi* MAISEY (1976).

Protospinax annectans WOODWARD, 1918

Figs. 2a-r, 3a-e

*1918 *Protospinax annectans* WOODWARD; WOODWARD, 232, pl. 1, figs. 2-3.

1976 *Belemnobatis annectans*; MAISEY, 733, pl. 111, text-figs. 1-4.

1983 *Protospinax annectans*; THIES, 21, pl. 3, figs. 2-6.

1987 *Protospinax annectans*; CAPPETTA, 67, figs. 62a-f.

1990 *Protospinax annectans*; BATCHELOR & WARD, 192, pl. 3, figs. 3a-b.

1991 ?*Protospinax*; MARTILL, pl. 38, fig. 7.

Holotype: BM(NH) P.8775, an almost complete fish from the Plattenkalk (Tithonian; Late Jurassic) of Solnhofen, Bavaria, southern Germany (WOODWARD, 1918).

New material: 4 isolated teeth from Reichenbach - SMNS 50967/1 (Figs. 2a-e), 50967/3 (Figs. 2f-h), 50967/4 (Figs. 2i-m), 50967/5 (Figs. 2n-r); 1 isolated tooth from Stuifen, 59112/3 (Fig. 3a-e).

Localities: Reichenbach; Stuifen. Fig. 1.

Age: Reichenbach - Oxfordmergel ox1, *transversarium* Zone, Weissjura α, Middle Oxfordian, Late Jurassic; Stuifen - Oxfordkalk ox2, *planula* Zone, Weissjura β, Upper Oxfordian, Late Jurassic.

Description. - Each tooth is less than 2 mm in length (mesiodistally), and longer than it is broad (labiolingually). The dimensions of the specimens are given in Table 1:

Tab. 1. Teeth of *Protospinax annectans* from Reichenbach and Stuifen (Late Jurassic, Germany), dimensions in mm.

Specimen number	Length	Breadth	Height
50 967/1	1.32	0.80	0.80
50 967/3	1.51	0.83	0.83
50 967/4	1.58	1.03	1.06
50 967/5	1.38	1.03	0.67
59 112/3	1.70	1.35	1.22

The descriptive terms used here largely follow that employed by CAPPETTA (1987). The coronal profile is low. A low central cusp with circular basal cross-section may be upright (e. g. 59112/3) or slightly inclined (e. g. 50967/4). There are no lateral cus-

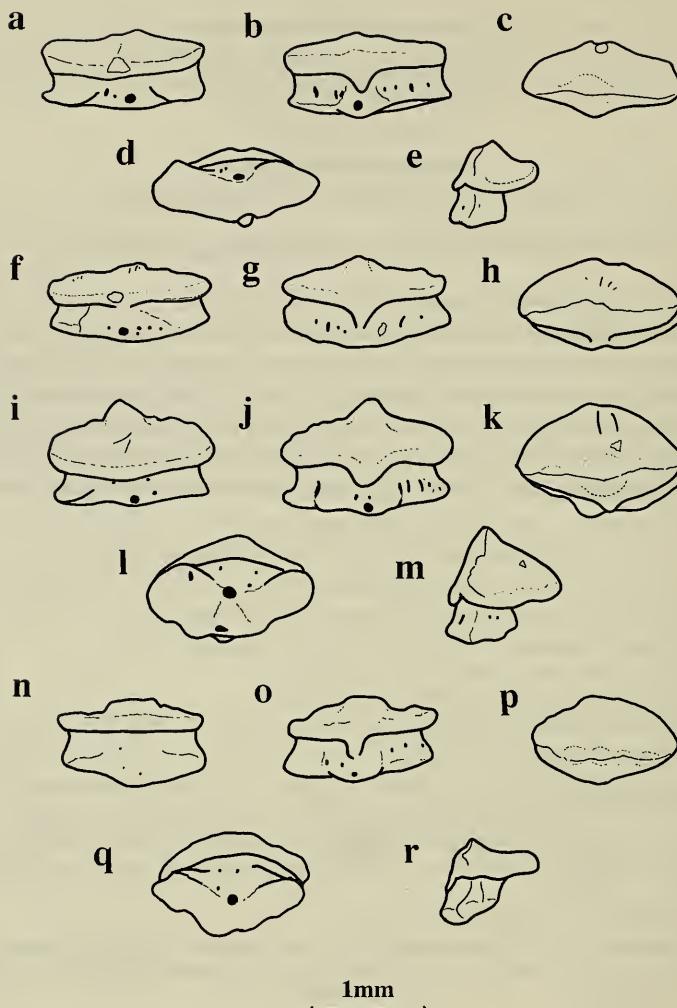


Fig. 2. Teeth of *Protospinax annectans* WOODWARD from the Lower Oxfordian of Reichenbach, southern Germany. Figs. a-e: 50967/1; Figs. f-h: 50967/3; Figs. i-m: 50967/4; Figs. n-r: 50967/5. Figs. a, f, i, n in labial view; Figs. b, g, j, o in lingual view; Figs. c, h, k, p in occlusal view; Figs. d, l, q in basal view; Figs. e, m, r in lateral view. All specimens held in SMNS.

plets, but the transverse or occlusal crest is strongly crenulated (Figs. 2f, i). The labial face of the crown projects strongly over the crown/root junction forming a visor (Figs. 2e, m, r; 3e). Occasional short, isolated, non-bifurcating ridges may be present on the labial face of the central cusp (Fig. 2f) and the occlusal surface of the visor (Fig. 2i). A pressure scar due to contact with the lingual apron of the preceding tooth in the file may be developed in a central position on the labial margin of the visor (Figs. 2a, f; 3a).

The lingual face of the crown descends steeply from the occlusal crest in lateral view, forming a slight convex bulge at the base of the central cusp (Fig. 3e). The lin-

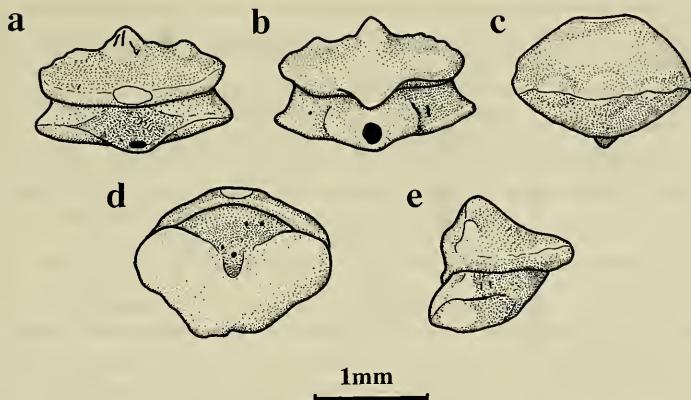


Fig. 3. Tooth of *Protospinax annectans* WOODWARD (SMNS 59112/3) from the Upper Oxfordian of Stuifen, southern Germany. a: labial view; b: lingual view; c: occlusal view; d: basal view; e: lateral view.

gual apron is quite short, triangular in occlusal view, and has a slightly rounded tip (Fig. 2k).

The root is lingually displaced beneath the crown (Figs. 2e, m, r; 3e). The basal face of the root is flat and V-shaped, with the apex directed lingually. The vascularisation is hemiaulacorhizic; a fully roofed central canal extends between prominent medio-internal and medio-external foramina. Lateral foramina are developed lingually, and additional smaller foramina are scattered over the central region of the labial root face (Figs. 2a, b, j, l).

Discussion

As mentioned above, one of the two articulated specimens of *Protospinax annectans* described by WOODWARD (1918) was made the holotype of the galeomorph shark *Squalogaleus woodwardi* MAISEY (1976), a move recently accepted by CAPPETTA (1987). THIES (1983: 23) has argued, however, that *S. woodwardi* is a junior synonym of *P. annectans* on the basis that the enameloid ultrastructures are identical; it is the typical autapomorphic condition (i. e. triple-layered, possessing a central parallel-fibred enameloid) of neoselachian sharks, rather than the specialised type (lacking a parallel-fibred layer) characteristic of batoids. Furthermore, THIES considered the differences in tooth morphology between the two genera to be trivial.

Certainly, those dental characters used by MAISEY (1976: 744) to distinguish the two genera are inappropriate, since he has misidentified the orientation of the teeth in *P. annectans*; labial and lingual sides of the teeth were confused. CAPPETTA (1987), however, was able to find a range of dental characters which seem to support the anatomical evidence forwarded by MAISEY for the generic distinction of *Protospinax* and *Squalogaleus*. I tentatively accept the overall conclusions of MAISEY (1976) and CAPPETTA (1987) as to the validity of *Protospinax* and *Squalogaleus*. Isolated teeth of these two genera remain difficult to tell apart from each other and are very similar to those of *Spathobatis* in microvertebrate faunas. A summary of the distinguishing characters, largely distilled from CAPPETTA (1987), is given in Fig. 4 and Tab. 2.

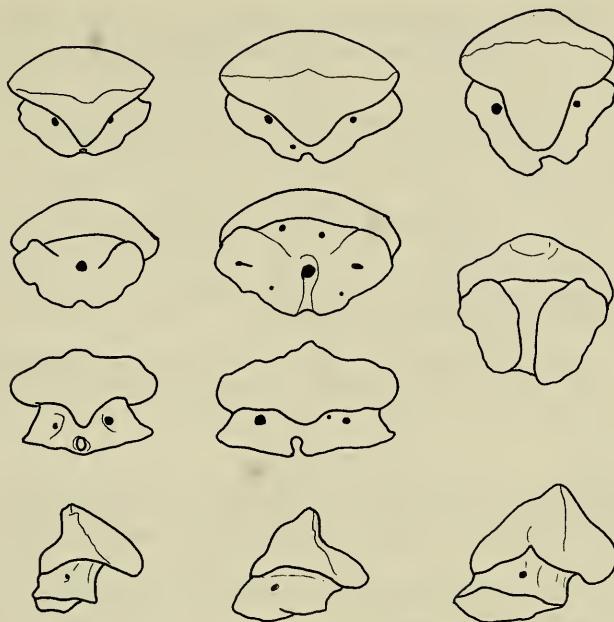
Genus Character	<i>Squalogaleus</i>	<i>Protospinax</i>	<i>Spathobatis</i>
Proportions	Mesiodistal > labiolingual	Mesiodistal > labiolingual	Mesiodistal = labiolingual
Visor	Very strong	Moderate	Very strong
Uvula	Moderately long Fairly pointed tip Moderate base	Long Rounded tip Broad base	Very long Rounded tip Broad base
Upper labial face of crown	Convex	Strongly concave	Mildly concave
Lingual face of crown	Smooth Concave	Strongly humped Convex	Small hump Convex
Foramina on basal face of root	Absent	Present	Absent
Central vascular canal	Open in anterior teeth Partially closed in posterior teeth	Open with a central foramen	Open

Tab. 2. Table to compare morphological features of the teeth of *Squalogaleus*, *Protospinax* and *Spathobatis* (information from CAPPETTA 1987).

The Oxfordian teeth described here are referred to *Protospinax* for the following reasons. The upper part of the labial face of the crown is concave as it ascends the central cusp, the upper lingual crown face is not concave but straight or convex at the central cusp base, and the lingual apron is quite short. This contrasts with the condition in *Squalogaleus* teeth, where the upper lingual face is concave, the upper labial crown face is straight and the lingual apron is relatively long. *Spathobatis* has an even longer lingual apron.

CAPPETTA (1987: 67) describes the roots of *P. annectans* teeth from the holotype as having a centrally placed open vascular groove on the basal face whose floor is punctuated by a well developed central foramen. A basal foramen perforates each lobe of the root basal face and lateral foramina are present on the lingual face of the root.

Oxfordian teeth of Reichenbach and Stuifen have a fully roofed central vascular canal, and none of them shows the development of basal foramina on the lobes of the basal face of the root. This condition more closely resembles that in *Squalogaleus*, where the central canal is often roofed, and basal foramina are lacking. It must be appreciated that roofing of the median vascular canal tends to be a variable feature in hemiaulacorhizid teeth, depending on maturity of the individual and degree of abrasion sustained by the teeth during transportation and deposition. Much further material of both genera is necessary before the significance of closed or open vascular canals in the root can be adequately assessed. Thus, it would appear that *Protospinax* is the best generic candidate for the German Oxfordian teeth.



Squalogaleus *Protospinax* *Spathobatis*

Fig. 4. Diagram to compare teeth of *Squalogaleus*, *Protospinax* and *Spathobatis*. Views from top to bottom – occlusal, basal, lingual, lateral. Diagrams not to scale.

Three species of *Protospinax* have been reported in the literature: *P. annectans* (Tithonian, Late Jurassic of Solnhofen, Germany), *P. lochensteinensis* THIES (1983) (Upper Oxfordian to ?Lower Kimmeridgian, Late Jurassic of Buchsteige, Germany) and *P.? muf-tius* THIES (1983) (Callovian, Middle Jurassic of Rookery Pit, England).

Bearing in mind the discussion above as to the distinction between *Squalogaleus* and *Protospinax* on the grounds of dental morphology, it would appear that *P.? muf-tius* is best accommodated in *Squalogaleus* (note its strongly concave upper lingual crown face).

The teeth of *P. lochensteinensis* have a prominent vertical ridge directly above the visor, whereas those of *P. annectans* have a smooth crown. The Oxfordian teeth from Reichenbach and Stuifen have occasional fine ridges in various positions on both labial and lingual faces of the crown, but do not develop the strong ridge so typical of *P. lochensteinensis*. The specimens described here are therefore suggested as belonging to *P. annectans*, which is also known from the Callovian of Britain and the Tithonian of Germany.

Order Synechodontiformes DUFFIN & WARD, 1993
 Family Palaeospinacidae REGAN, 1906

Genus *Synechodus* WOODWARD, 1888

Type species: *Synechodus dubrasiensis* (MACKIE, 1863).

Synechodus riegrafi (THIES, 1983)
 Figs. 5d-j

*1983 *Palaeospinax riegrafi*; THIES, 16, pl. 2, figs. 1-2.

1987 *Palaeospinax riegrafi*; DUFFIN, fig. 6D.

Material: 3 isolated, fragmentary teeth; 1 specimen from Reichenbach – 50967/6 (Figs. 5d-e); 2 specimens from Stuifen – 59112/1 (Figs. 5h-j), 59112/2 (Figs. 5f-g).

Description

All three specimens are broken, and comprise the central cusp and badly eroded parts of the root. Only one specimen (59112/1) preserves any sign of lateral cusplets (Figs. 5h, i).

The central cusp is lingually inclined but shows no mesial or distal inclination in the specimens available. The ratio of cusp height to cusp base length varies from 1 : 1.26 in 59112/1 to 1 : 2.2 in 59112/2.

There is evidence of one pair of lateral cusplets in 59112/1. The upright lateral cusplets are approximately one fifth of the height of the central cusp. They are confluent with the base of the central cusp. Both the central cusp and lateral cusplets are ornamented by fairly coarse vertical ridges on both labial and lingual faces. The ridges are initiated just above the crown/root junction and ascend the crown toward the occlusal crest. Approximately half of the vertical ridges on the labial face of the crown are confined to the lower half while the remainder terminate some distance from the cusp apex (Fig. 5h). The ridges on the lingual face are confined to the basal two thirds of the central cusp (Fig. 5g). Few of the ridges show bifurcation basally. An impermanent horizontal ridge connects some vertical ridge bases in 59112/1.

Details of the root morphology are lacking. The root projects lingually from the crown underside.

Discussion

The overall morphology of the tooth fragments is consistent with that of palaeospinacid sharks. DUFFIN & WARD (1993) have recently reviewed this group of neoselachians and have recognized only two valid genera – *Paraorthacodus* and *Synechodus*. „*Palaeospinax*“ is considered to be a *nomen nudum*, being based upon a single specimen demonstrating no features of taxonomic significance. See THIES (1991; 1993, in press) and CAPPETTA (1992) for other points of view.

The confluence of lateral cusplet and central cusp bases in the German Oxfordian material indicates that the specimens should be allocated to *Synechodus*; lateral cusplets and central cusp bases are separate on the crowns of *Paraorthacodus* spp.

Palaeospinax kruckowi THIES (1983) (Upper Aalenian of Moorberg, Germany) and *Synechodus jurensis* SCHWEIZER (1964) (Tithonian of Nusplingen, Germany) have both been reassigned to *Paraorthacodus* (DUFFIN 1993, DUFFIN & WARD 1993).

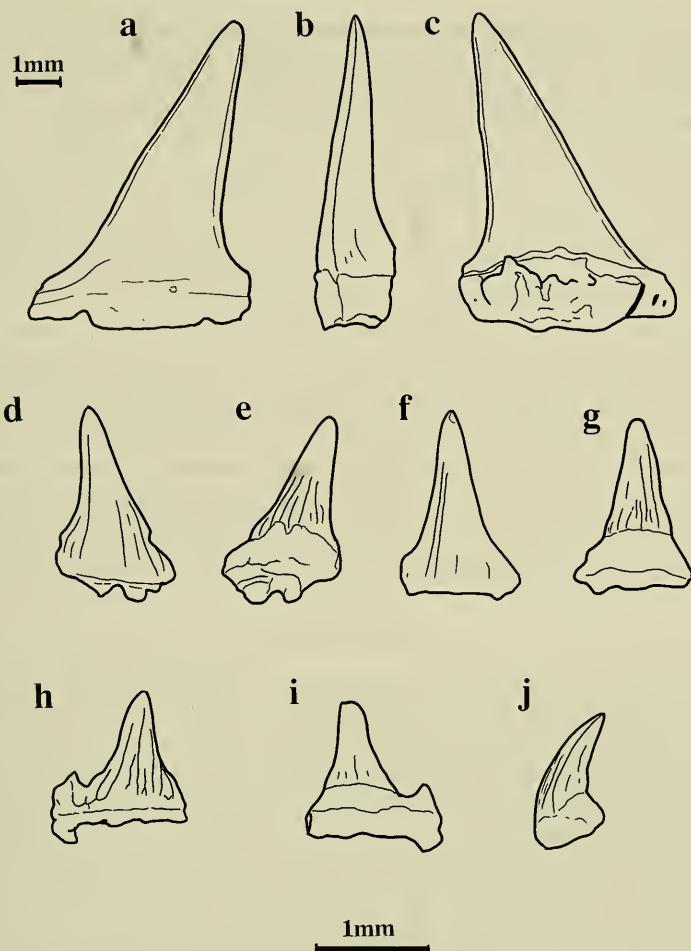


Fig. 5. Teeth of Oxfordian selachians from Reichenbach and Stuifen. Fragmentary tooth of *Sphenodus cf. longidens* (AGASSIZ) (SMNS 50967/2; Reichenbach) in a: labial; b: distal; c: lingual views. Teeth of *Synechodus riegrafi* (THIES); SMNS 50967/6 (Reichenbach) in d: labial view; e: lingual view; SMNS 59122/2 (Stuifen) in f: labial view; g: lingual view; SMNS 59122/1 (Reichenbach) in h: labial; i: lingual; j: lateral view.

Unless the German material described above is a new species, that leaves only one other palaeospinacid species as a possible candidate for the Oxfordian material: *Palaeospinax riegrafi* THIES (1983). This species has been assigned to *Synechodus* by DUFFIN & WARD (1993) and compares well with the specimens described above. Teeth of *S. riegrafi* measure up to 2.7 mm in length (mesiodistally), and have up to four lateral cusplet pairs, the largest of which measures up to one third of the height of the central cusp. Coarse, seldom bifurcating vertical ridges ascend the crown, terminating below the central cusp apex as in the Reichenbach and Stuifen specimens.

Family Orthacodontidae (GLYCKMAN 1957)

Genus *Sphenodus* AGASSIZ, 1843

Type species: *Sphenodus longidens* AGASSIZ (Corallian to Oxfordian).

Sphenodus cf. *longidens*

Figs. 5a-c

Material: 1 isolated fragmentary crown from Reichenbach (50967/2; Figs. 5a-c).

Description

The specimen consists of the central cusp, measuring 10 mm in height, surmounting a badly eroded fragmentary root, measuring 7 mm mesiodistally. The sharply pointed central cusp is upright labiolingually, but inclined distally. The occlusal crest forms well developed cutting edges. The crown is completely smooth, lacking ornamentation entirely. The greater part of the mesial lateral flange can be discerned, plastered onto the root surface, while only the proximal part of the distal lateral flange remains. The root is too incomplete to discern any useful morphological features.

Discussion

Sphenodus (= *Orthacodus*) is a long-ranging genus (Early Jurassic to Early Palaeocene) of synchondontiform shark containing a plethora of ill-defined species, amongst which much synonymy almost certainly exists. *S. longidens* was originally described from the Bajocian of Rabenstein (Bavaria; AGASSIZ, 1843, DE BEAUMONT, 1960) and has subsequently been tentatively recorded from the Early Jurassic of Bamberg (KUHN, 1935), the Bajocian of Sicily (KUHN, 1935), the Bathonian of north-west France (PRIEM, 1912), the Callovian of Germany and France (PRIEM, 1908, 1912; QUENSTEDT, 1858), the Oxfordian of France (PRIEM, 1912), Sicily (SEGUENZA, 1900) and Germany (including from Reichenbach – DE BEAUMONT, 1960), the Kimmeridgian of Normandy (France, SAUVAGE, 1880) and Germany (DE BEAUMONT, 1960; FAVRE, 1877) and the latest Jurassic of Normandy (SAUVAGE, 1867), Russia (TRAUTSCHOLD, 1860) and the Carpathians (ZITTEL, 1870), as well as the Senonian (Late Cretaceous) of Italy (BASSANI, 1881, 1888). For a guide to other species of *Sphenodus* see DE BEAUMONT (1960) and DUFFIN & WARD (1993).

The only articulated material of the genus known to date is that of *Sphenodus nitidus* (WAGNER, 1863) from which it is obvious that some heterodonty exists within the dentition; parasympphyseal and anterolateral teeth have upright crowns with high, slender, lanceolate central cusps, while posterolateral teeth are lower crowned with distally inclined central cusps having a longer base. This is the case with the specimen described above from Reichenbach, which is tentatively allied to *S. longidens*, pending a comprehensive review of the genus.

4. Discussion

The study of microvertebrate samples from Jurassic rocks is still in its infancy, but recent publications have already considerably modified our views on selachian biostratigraphy.

There are few selachian faunas available from comparison. The fauna closest in both age and location to the Stuifen collection described above comes from the Upper Oxfordian (and possibly Lower Kimmeridgian) of Buchsteige (Lochen; THIES, 1983). Here, glauconitic marls have yielded the following taxa (THIES, 1983; QUENSTEDT, 1858):

- Synechodus riegrafi* (THIES)
- Protospinax lochensteinensis* THIES
- Squatina* sp.
- Sphenodus longidens* (AGASSIZ)

The Oxford Clay (Callovian) of Britain is slightly older than the Reichenbach fauna, and has yielded the following selachian taxa (THIES, 1983; MARTILL, 1991):

- Hybodus obtusus* AGASSIZ
- Hybodus dawni* MARTILL
- Asteracanthus ornatus* AGASSIZ
- Asteracanthus acutus* AGASSIZ
- Notidanus muensteri* AGASSIZ
- Protospinax muftius* THIES
- Protospinax annectans* WOODWARD
- Paracestracion falcifer* WAGNER
- Heterodontus* sp.
- Palaeobrachaelurus bedfordensis* THIES
- Palaeobrachaelurus alisonae* THIES
- Orectoloboides pattersoni* THIES
- Sphenodus longidens* AGASSIZ
- Spathobatis wernerii* THIES

It is not clear at present whether the reduction in diversity from Callovian to Oxfordian, with loss of representation of hybodonts and orectolobids, plus dramatic decrease in diversity is a function of sedimentary facies and selachian ecology, or an artefact of sampling. THIES & REIF (1985) envisage palaeospinacids as slow-swimming, near bottom hunters in coastal waters, preying on fishes, crustaceans and molluscs. Protospinacids are presumed to have been sluggish swimmers, often resting on the bottom. They cruised both muddy and calcareous substrates and have been suggested as feeding on thin shelled benthonic invertebrates.

The above descriptions of isolated selachian teeth from the German Jurassic serve to extend the range of *Synechodus riegrafi* into the Middle Oxfordian, and add to the known palaeogeographical distribution of *Protospinax annectans*.

Acknowledgements

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Address of the author:

Dr. C. Duffin, 146, Church Hill Road, Sutton, Surrey SM3 8NF, England.

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