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The dentition of *Hybodus hauffianus* Fraas, 1895 (Toarcian, Early Jurassic)

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With 12 Figures

Abstract

The dentition of *Hybodus hauffianus* Fraas, 1895 from the Posidonienschiefer (Toarcian, Early Jurassic) of Baden-Württemberg (southern Germany) is described in detail for the first time. Heterodonty is characterised and differential diagnosis confirms validity at the species level.

Zusammenfassung

Die Bezahnung von *Hybodus hauffianus* Fraas, 1895 aus dem Posidonienschiefer von Baden-Württemberg (Süddeutschland) wird zum ersten Mal detailliert beschrieben. Es besteht eine monognathe Heterodontie. Die Gültigkeit der Art wird anhand einer Differentialdiagnose bestätigt.

1. Introduction

Selachian microvertebrate remains have considerable potential in biostratigraphy; phosphatic teeth and scales have a high preservation potential. Since there is continuous replacement of the dentition and each selachian is covered by a dense shagreen of dermal denticles, one individual shark can give rise to large numbers of microvertebrate fossils. Furthermore, selachian teeth and scales are robust clasts which can be relatively easily identified from abraded fragments. They can be readily extracted without damage from a wide range of sediments – by acid treatment of limestones and clastic rocks with calcareous cements, disaggregation of organic-rich shales and mudrocks by treatment with kerosene and boiling water, breakdown of clays by treatment with hydrogen peroxide, and the washing and sieving of relatively unconsolidated sediments. They lend themselves to bulk sampling.

One of the problems encountered in identifying isolated microvertebrate remains is that of form genera or organ genera. Different teeth within the same dentition may be allocated to separate species unless heterodonty is adequately appreciated and dif-

Fig. 1. Map of Baden-Württemberg to show the geographical location of Holzmaden.

ferent skeletal elements from the same taxon may be allocated to different genera. The presence of articulated or associated material in Fossil Konservat-Lagerstätten are important in avoiding such problems and constructing appropriate synonymies. The bulk of such material was, in the cases of many localities, collected during the nineteenth or early twentieth centuries. Available specimens are often cursorily described or poorly figured, often in older, relatively inaccessible literature, or disseminated through the collections of a wide range of Institutions.

A considerable body of bulk sampled material from European Mesozoic rocks is beginning to be accumulated through the activities of a number of amateur and professional active researchers in France (e.g. Biddle, 1993; Cuny, 1993; Cappetta, 1990), Belgium (Herman, 1977; Delsate & Godefroit, 1994), Luxembourg (Delsate, 1994), Germany (Thies, 1983; Müller, 1989), Holland (Halter, 1995), Sweden (Siverson, 1993), Poland (Liszkowski, 1993) and Britain (Thies, 1983).

A number of taxa from Fossil Lagerstätten such as Lyme Regis (Hettangian to Sinemurian), Holzmaden (Toarcian) and Solnhofen (Kimmeridgian) have been recently redescribed or revised. These include the Early Jurassic synechodontiforms ("*Palaeospinax*", *Synechodus*, *Paraorthacodus* and *Sphenodus* – Duffin, 1993b; Duffin & Ward, 1993) and hybodontiforms (Duffin, 1993a; Maisey, 1987), plus Late Jurassic hybodonts (Maisey, 1986a) and various neoselachian genera (Maisey, 1977, 1985, 1986a; Duffin, 1988). This has helped to produce more confident identification of isolated selachian remains (e. g. Delsate & Duffin, 1993).

The anatomy of *Hybodus hauffianus* Fraas, 1896 from the German Posidonienschiefer (Toarcian, Early Jurassic) is apparently under review (Maisey, 1987: 23) as part of a larger study of hybodont sharks (Maisey, 1978, 1982, 1983, 1986, 1987). For that reason, the present paper is limited to a consideration of the dentitions of

the hybodont sharks of Holzmaden (Fig. 1), which have been largely ignored since the original description of FRAAS (1896). Available material of *Hybodus hauffianus* does include, however, some beautifully preserved articulated specimens (Figs. 11, 12a, b).

2. Systematic Palaeontology

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Cohort Euselachii HAY, 1902
Superfamily Hybodontoidea OWEN, 1846
Family Hybodontidae OWEN, 1846

Genus *Hybodus* AGASSIZ, 1837

Type species: *Hybodus reticulatus* AGASSIZ, 1837 from the Sinemurian ("Lower Lias") of Lyme Regis, Dorset, England.

Hybodus hauffianus FRAAS, 1895
Figures 2–9, 11–12

1858 *Hybodus reticulatus*. – QUENSTEDT, 222, pl. 27, fig. 1.
* 1895 *Hybodus Hauffianus* E. FRAAS. – FRAAS, 24–26, 1 fig.
1896 *Hybodus Hauffianus* E. FRAAS. – FRAAS, 1–25, pl. 1, figs. 1, 2; pl. 2, figs. 1–2, 4–9.
1900 *Hybodus Hauffianus* E. FRAAS. – BROWN, 159, text-figs. 3A, 4, 5B, 6D, 7; pl. 16, figs. 1–6.
1906 *Polyacrodus (Hybodus) Hauffianus*. – JAEKEL, 158–159, fig. 2.
1907 *Hybodus Hauffianus*. – KOKEN, 262, figs 1, 2, pls. 1–3.
1916 *Hybodus hauffianus*. – WOODWARD, fig. 1.
1977 *Hybodus hauffianus*. – RIETSCHEL, 129, fig. 7.
1982 *Hybodus hauffianus*. – MAISEY, 10, fig. 56.
1986 *Hybodus hauffianus*. – PROBST, 151, fig. 1, 55.
1987 *Hybodus* cf. *reticulatus*. – MAISEY, 23, figs. 15, 16A, 17.
1990 *Hybodus hauffianus*. – POLLARD, 364, fig. 2.
1992 *Hybodus hauffianus*. – DOYLE & MACDONALD, 69, 77, fig. 2.

Lectotype: Orig. FRAAS, 1896, pl. 1, fig. 2, SMNS 8503. design. herein. Here refigured Fig. 2.
Type locality: Holzmaden, Baden-Württemberg, Southern Germany.
Type horizon: Schwarzjura εII4 (1.5 m above the "Fleins").
Age: *elegans* Subzone, Toarcian, Early Jurassic.
Range: upper part of the *semicelatum* Zone to the lower part of the *fibulatum* Zone (εII2 to εII12) (RIEGRAF, WERNER & LÖRCHER, 1984: 34).
Collector: BERNHARD HAUFF, 1894.

Remarks on type material. – In his original description, FRAAS (1895) mentioned two specimens, SMNS 8503 and SMNS 8663, figuring the latter (FRAAS, 1895: 24). On describing the material in more detail later (FRAAS, 1896: 4), he referred to SMNS 8663 as "Das Hauptstück bildet die Platte No. 1" – the 'main' specimen. It (a skull and dorsal fin spine) is still available but partially destroyed; no teeth are present on the surviving part of the slab. When describing the dentition, FRAAS (1896: 14) wrote "Das schönste Zahnmaterial liefert die Platte No. 2". This is SMNS 8503. MAISEY (1982: 28) states that SMNS 8503 is the holotype. However, FRASS did not formally identify a holotype; his description was initially compiled from the two

Fig. 2. SMNS 8503, the lectotype of *Hybodus hauffianus* Fraas (1895) from the Schwarzjura εII4 of Holzmaden, Baden Württemberg, southern Germany. Whole specimen.

specimens (Fraas, 1895) cited above, and later extended in a similar manner for a further two specimens (Fraas, 1896). Therefore SMNS 8663 and SMNS 8503 are syntypes. Following Article 74 of the ICZN, normal taxonomic practice demands designation of one of the syntypes as a lectotype. SMNS 8503 is here designated the lectotype of *Hybodus hauffianus* on the basis that, of the surviving parts of the original specimens, it is the most informative on which to define the species.

The specimen (Figs. 2–4) originally preserved parts of the dentition, Meckelian Cartilages, first dorsal fin spine and associated cartilages. Fragmentation of the Stuttgart Collections during the Second World War meant that some of the specimens were lost or damaged and SMNS 8503 was a casualty. The matrix is now baked to a reddish colour from the original grey/black of the Posidonia Shale due exposure to fire and only parts of the dentition, left Meckelian Cartilage, palatoquadrate and a

few associated fragmentary cartilages remain (compare Fig. 2 with FRAAS, 1896, pl. 1, fig. 2). The original figure of FRAAS (1896) shows a crack across the specimen and it is largely the block to the left of the fracture in that illustration which is now available.

Other specimens used in the present study:

- (i) SMNS 52458 – an articulated cranial fragment preserving the dentition, lower jaw, cephalic spines, palatoquadrate. Provenance – εII3 ("Fleins") of G. FISCHER Quarry, Holzmaden, collected in 1970 (Figs. 5–8).
- (ii) SMNS 10062 – a complete skeleton with belemnites in the gastric mass (Fig. 12a), collected from εII8 or 9 (2 m above the "Fleins") at Holzmaden in 1899 (cf. SCHMIDT, 1921; ABEL , 1927, 1935; HAUFF, 1933; DACQUÉ, 1930; WEIGELT, 1927; WEILER, 1934; WAGNER, 1950; POLLARD, 1968, 1990; RIETSCHEL, 1977; MUNDLOS, 1979; DUFFIN, 1983; JÄGER, 1985; ZIEGLER, 1986, 1988; PROBST, 1989; VAN DIGGELEN, 1986; BÖTTCHER, 1989; FRENTZEN, 1936; DOYLE & MACDONALD, 1993; URLICHS, WILD & ZIEGLER, 1994).
- (iii) SMNS 15150 – a complete skeleton with the dentition from εII2 of Ohmden (HAUFF, 1959; ZIEGLER, 1985, 1988; FRICKHINGER, 1991), collected by HAUFF in 1925 (Fig. 12b).
- (iv) SMNS 80594 – (in three parts) a small cranial fragment with at least 12 associated teeth, a partial skull with 1 tooth exposed in labial view and two other dental fragments, broken fragments of a dorsal fin spine, all from Gomaringen, W. LUDWIG collection, 1992.
- (v) SMNS 54048 – a disarticulated anterior part of a skeleton with well preserved teeth from εII10 of HAUSER Quarry, Ohmden, collected in 1968 (Fig. 9c).
- (vi) SMNS 51949 – a virtually complete specimen from the εII4 of G. FISCHER Quarry in Holzmaden, described by MAISEY (1987: 23, figs. 15, 16A, 17) as *Hybodus* cf. *reticulatus*. Collected in 1980.
- (vii) SMNS 52460 – a virtually complete skeleton with dentition (Fig. 10) from the εII6 ("Schieferklotz"), of P. KIRSCHMANN Quarry, Ohmden, collected in 1983.
- (viii) SMNS 51136 – a partial anterior skeleton with a single tooth exposed in labial view from the εII10 ("Falchen") of G. FISCHER Quarry, Holzmaden, collected in 1971.
- (ix) SMNS 50980 – an isolated tooth in lingual view from J. FISCHER Quarry, εII4, Ohmden.
- (x) SMNS 55628 – an isolated tooth in labial view from the εII12 ("Schlacken") of G. FISCHER Quarry, Holzmaden, collected in 1987.
- (xi) GPIT uncatalogued – a partial skull and articulated dentition which has been acid prepared from both sides, located in the Fisch Saal drawers.
- (xii) BMNH P.5880 – a disarticulated anterior part of a skeleton from Boll, figured as *Hybodus* cf. *reticulatus* by MAISEY (1987, figs. 14, 16B, C). Stratigraphical details are not available.

Referred material:

- (i) SMNS 10062a-d – isolated parts of a skull from the εII8 or 9 of Holzmaden, including postorbital processes and the base of a cephalic spine (BROWN, 1900).
- (ii) SMNS 8663 – a partial skeleton from the εII3 ("Fleins"), collected by B. HAUFF in 1893. This is specimen number 1 (the "main specimen") of FRAAS (1896: 4, pl. 1, fig. 1).
- (iii) SMNS 80595 – dorsal fin spine and scapulocoracoids plus associated skin and other cartilages from Holzmaden (FRAAS, 1896 : 7).
- (iv) SMNS 51135 – the partial skeleton of a juvenile from the εII3 of G. FISCHER Quarry, Holzmaden, collected in 1974.
- (v) SMNS 7276 – an isolated dorsal fin spine from Ohmden, collected in 1887.
- (vi) SMNS 52342 – an isolated dorsal fin spine from the εII3 ("Fleins") of J. FISCHER Quarry, Ohmden, collected in 1983. Note that this spine is much more slender with fewer longitudinal ridges than is the case in the other hybodont dorsal fin spines examined from the Posidonienschiefer.
- (vii) SMNS 52459 – an isolated dorsal fin spine, collected from the εII12 ("Schlacken") of G. FISCHER Quarry, Holzmaden before 1969.
- (viii) SMNS 4550 – an isolated dorsal fin spine from εII4 ("Unterer Schiefer") of Ohmden, MANDELSLOHE collection, 1864 (FRAAS, 1910: 189, pl. 57, fig. 17).

- (ix) SMNS 58749 – an unprepared, virtually complete skeleton from εII4 of Holzmaden (G. Fischer Quarry, 1988).
- (x) SMNS 58748 – a fragment of a hyomandibula from εIII1 (G. Fischer Quarry, Holzmaden, collected in 1988).
- (xi) SMNS 52222 – a partial skeleton with both dorsal fin spines from the εII12 ("Schlacken") of A. Fischer Quarry, Aichelberg, collected in 1982.
- (xii) SMNS 50804 – a partial skeleton with both dorsal fin spines from εII3 ("Fleins") of J. Fischer Quarry, Zell, collected in 1976.
- (xiii) GPIT uncatalogued – a complete wall mounted specimen in left lateral view, but lacking the dentition. The specimen was described and figured by Koken (1907).
- (xiv) GPIT uncatalogued – a skull in dorsal view (Koken, 1907, fig. 2).

Description of SMNS 8503

At least 35 teeth are preserved on the surviving part of this specimen (Fig. 2). It has been fairly coarsely prepared by mechanical means. This, fire damage and breakage means that, although the teeth are clearly visible, many lack details or are damaged (Fig. 3). The teeth lie mostly in the space between the left Meckelian cartilage and the palatoquadrate fragment (although a few overlie and are scattered over the margins of both cartilages) and are preserved in a variety of views, sufficient to allow characterisation of the species. The teeth are disassociated and difficult to assign with confidence to any particular jaw. The best individual teeth are illustrated in Figure 4.

The teeth in this specimen measure from 11 mm to 15 mm mesiodistally and up to 9 mm high. A moderately high, upright or slightly distally inclined central cusp is flanked by up to 4 pairs of lateral cusplets. The central cusp is sharply pointed with well developed cutting edges and a height to base length ratio of between 1.28 and 1.6. The lateral cusplets decrease in height mesially and distally with the highest pair being just less than 50 % of the height of the central cusp. The first lateral cusplet axis diverges from that of the central cusp mesially and distally (Fig. 4a).

The crown is strongly ornamented both labially and lingually. The central cusp has a series of vertical ridges extending basally from near the cusp apex, terminating around 75 % of the way down the cusp. They do not extend to the crown/root junction. Since virtually all cusp apices are either broken or obscured it is impossible to determine whether the vertical ridges attain them. The ridges on the central cusp do not anastomose or bifurcate. They may extend for their whole length without a break, or may be represented as short, isolated strips (Fig. 4b). There is a maximum density of 2 vertical ridges per millimetre.

In some teeth the lingual vertical ridges coalesce basally to form a moderate, impersistent longitudinal ridge at the crown shoulder. This may give rise to further, very short, impersistent ridges apically and basally. The lateral cusplets also possess non-bifurcating, slightly stronger vertical ridges which attain the cusplet apices (Fig. 4a). These, too, may coalesce at their bases giving rise to a longitudinal ridge which may break up into a reticulate, anastomosing pattern (Fig. 4c).

No one tooth is sufficiently well preserved in labial view to warrant illustration. Coarse vertical ridges descend the central cusp from the apex without branching. These vertical ridges are entire; it is most unusual for short lengths of vertical ridge to be present on the central cusp. They are not confluent at their bases, but remain separate. No longitudinal ridge is developed labially. A prominent labial node is de-

Fig. 3. SMNS 8503, the lectotype of *Hybodus hauffianus* FRAAS (1895) from the Schwarzjura εII4 of Holzmaden, Baden Württemberg, southern Germany. Detail of the dentition.

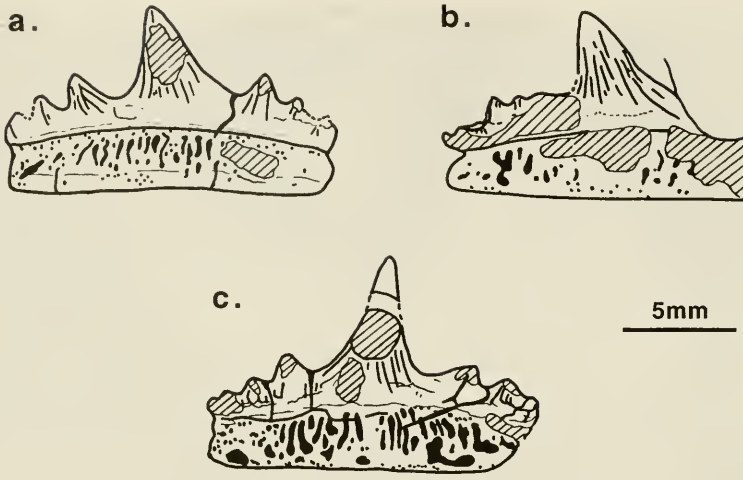

Fig. 4. Camera lucida drawing of the best preserved teeth of *Hybodus hauffianus* on the lectotype (SMNS 8503; Schwarzjura εII4 of Holzmaden, Baden Württemberg, southern Germany).
a: Tooth from the tip of the Left Meckelian cartilage in lingual view; b: Tooth chosen from the cluster lying between the Meckelian cartilages, in lingual view; c: Tooth from close to the crest of the left Meckelian cartilage in lingual view.

veloped on the coarsest central vertical ridge and is crested by it. The lateral cusplets are ornamented in similar fashion and may develop labial nodes.

The root is displaced lingually from the crown undersurface. The basal face is flat and rectangular, perforated by many small foraminae. The lingual face of the root is convex labiolingually. Smaller foraminae enter the root more or less horizontally close to the crown/root junction and toward the baso-labial root border, while those in the central part of the root are much larger and elongate apico-basally. The vascularisation is somewhat similar to that illustrated for *Hybodus reticulatus* (Sinemurian, Early Jurassic of Britain) by Maisey (1987, fig. 18).

The labial face of the root is poorly presented in teeth from this specimen. Apart from the fact that its topography is fairly generalised for hybodont sharks teeth with a thin horizontal shelf beneath the crown/root junction giving way to a concave surface angled basally, there is little detail available.

Description of SMNS 52458

This specimen, discovered much more recently than SMNS 5803, has the advantage of having been prepared by an air abrasive. Its dentition is the best preserved of all of the remaining specimens which I have studied, and some of the individual teeth are illustrated in Figs. 5a-e, 7a-b and 9a. The teeth of all other specimens listed above conform to those of this specimen (see also Figs. 9b, c).

In SMNS 52458 the jaws and teeth are minimally disarticulated. The right Meckelian Cartilage (exposed in outer lateral view) lies above the left (exposed in inner lateral view) overlapping part of the articular condyle (Fig. 6). The right palato-

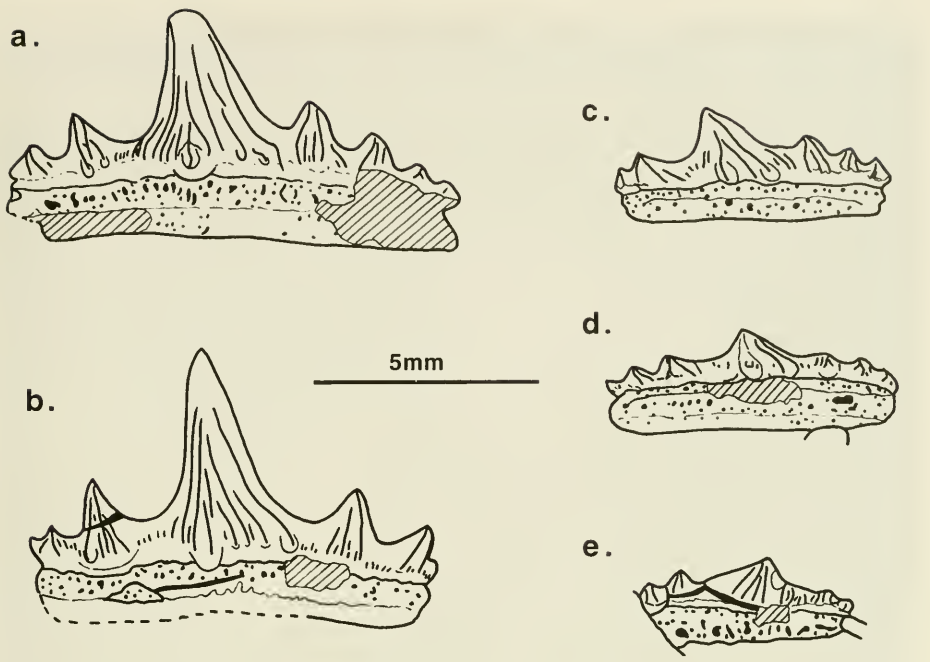

Fig. 5. Camera lucida drawing of the best preserved teeth of *Hybodus hauffianus* FRAAS (1895) from SMNS 52458 (Schwarzjura εII3 of Holzmaden).
a: anterior tooth in labial view from the right lower dentition, approximately Row II, counting from the symphysis; b: lateral tooth in labial view from about Row VI of the right lower dentition (mid way along the Meckelian Cartilage); c: posterolateral tooth in labial view from about Row VIII of the right lower dentition; d: posterolateral tooth in labial view from about Row X of the right ?lower dentition; e: extreme posterolateral tooth in lingual view from about Row XII of the right ?lower dentition.

quadrate and hyomandibula are very close to life position and part of the ventral margin of the left palatoquadrate is near the corner of the block. The dental laminae have become detached from the jaws but the orientation of the teeth within the sediment permits confident assignation to upper and lower dentitions in most cases, and sometimes to right or left sides. Most of the teeth are exposed in labial view.

The dentition would have comprised approximately twelve tooth rows in each upper and lower jaw. The individual represented by SMNS 52458 was smaller and therefore younger than SMNS 8503. The Meckelian cartilage length in SMNS 52458 is around 60 % of that in SMNS 8503. Tooth length ranges from 10.5 mm close to the symphysis to 5 mm in posterolaterals. The teeth in this specimen agree well with those of SMNS 8503 and the better exposure allows supplementary observations to be made.

Vertical ridges on the labial face of the central cusp rarely bifurcate. Occasional ridges may extend to the central cusp apex in posterolateral teeth, but tend to be restricted to the basal 85 % of the cusp in anterior teeth. Fine, short vertical ridges may intervene between the longer, coarser ridges at the crown shoulder (Fig. 5b).

The teeth are generally slightly asymmetrical (Fig. 5). The most symmetrical teeth seen occupy row ?6 in the lower dentition (Fig. 5b). Upper teeth seem to be very

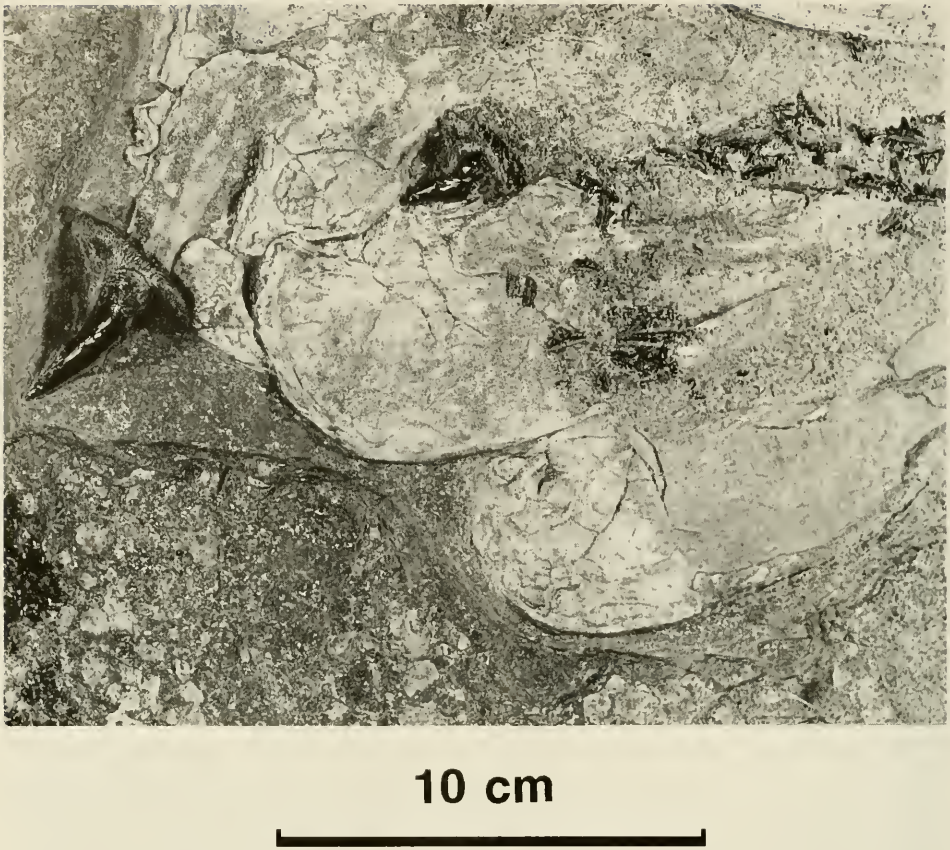

Fig. 6. Part of SMNS 52458 (*Hybodus hauffianus* Fraas, 1895; Schwarzjura εII3 of Holzmaden) showing the proximal parts of the Meckelian Cartilages, cephalic spines and posterior parts of the dentition.

slightly larger than corresponding lower teeth, and to have rather more distally inclined central cusps.

Changes taking place distally through the dentition include the following:

- (i) Decrease in mesiodistal tooth length to around 50 % of the length of anterior teeth in posterolaterals.
- (ii) Decrease in central cusp height by about 60 % in posterolaterals.
- (iii) Increase in relative depth of the root from 25 % of the tooth height to 50 % of the tooth height.
- (iv) Anterior teeth have distally inclined central cusps becoming more upright in laterals, then progressively more distally inclined in posterolaterals.
- (v) Lateral cusplets change from 2 distal and 4 mesial cusplets in anterior teeth (Fig. 5a), through 3 mesially and distally in laterals (around row 6; Fig. 5b) to 3 mesial and 2 or 3 distal cusplets in posterolateral teeth (Fig. 5d).
- (vi) Decrease in extent of the fine vertical ridges intervening between the longer, coarse vertical ridges on labial and lingual faces of the crown.

– (vii) Increase in length of vertical ridges on the crown from around 75 % of the cusp height in anterior and lateral teeth to 100 % in posterolaterals.

SMNS 52458 also preserves the 2 cephalic spines from the right side (Figs. 6, 8). The larger of the two (Figure 7b) is derived from the otic region and the smaller, more anterior cephalic spine (Figure 8a) is from the supratemporal region. Note that no accessory lateral or accessory medial cusps are developed at the base of the spine. There is a strong posterior barb. The anterior face of the spine is ornamented by sparse vertical ridges and a relatively short mesial crest. The tripartite base is quite strongly asymmetrical.

3. Discussion

The more detailed description of the dentition of *Hybodus hauffianus* given above now permits comparison with the teeth of other Mesozoic hybodont sharks. I disagree with Maisey (1987: 23) who commented that two specimens (SMNS 51949 and BMNH P5880) have "tooth morphology (which) resembles that of *H. reticulatus* rather more than *H. hauffianus* from the same locality". In my opinion, the dentitions of these two specimens fall within the range of morphology defined above for *H. hauffianus*, which clearly differs from the dental architecture of *H. reticulatus* (Fig. 10).

All of the specimens of *H. hauffianus* exposing dentitions available to me (Figs. 4, 5, 7, 9; Maisey, 1987, fig. 16) and listed above differ in dental morphology to *H. reticulatus* (see Maisey 1987, figs. 1, 10, 18; Duffin, 1993a, fig. 1d) in the following ways:

– (i) Labial nodes developed as swellings at the base of strong vertical ridges on the central cusp and lateral cusplets of *H. hauffianus* (e.g. Fig. 9c) are absent in *H. reticulatus* (Fig. 10).
– (ii) Coalescence of vertical ridge bases to form an impersistent longitudinal ridge on the lingual crown shoulder in *H. hauffianus* is absent in *H. reticulatus*.
– (iii) The lingual shelf developed in larger teeth of *H. reticulatus* (Duffin, 1993a: 49) is absent in *H. hauffianus*.
– (iv) Vertical ridges in *H. reticulatus* are usually entire, rather than being occasionally broken into shorter lengths as in *H. hauffianus*.
– (v) Considering the dentition as a whole, more teeth are symmetrical in *H. reticulatus* than is the case with *H. hauffianus*.

If the cephalic spines are also considered:

– (vi) Cephalic spines of *H. reticulatus* possess lateral and mesial accessory cusps (Maisey, 1987, figs. 12, 13) whereas *H. hauffianus* does not (Figure 8).
– (vii) Spine bases of *H. reticulatus* are more densely ornamented than those of *H. hauffianus* (compare Figure 8 with Maisey, 1987, figs. 12, 13).
– (ix) The dorsal crest is less well developed in *H. hauffianus* than in *H. reticulatus*.

The teeth of *H. hauffianus* possess labial nodes, which distinguish them from those of the following species in which labial nodes are absent:

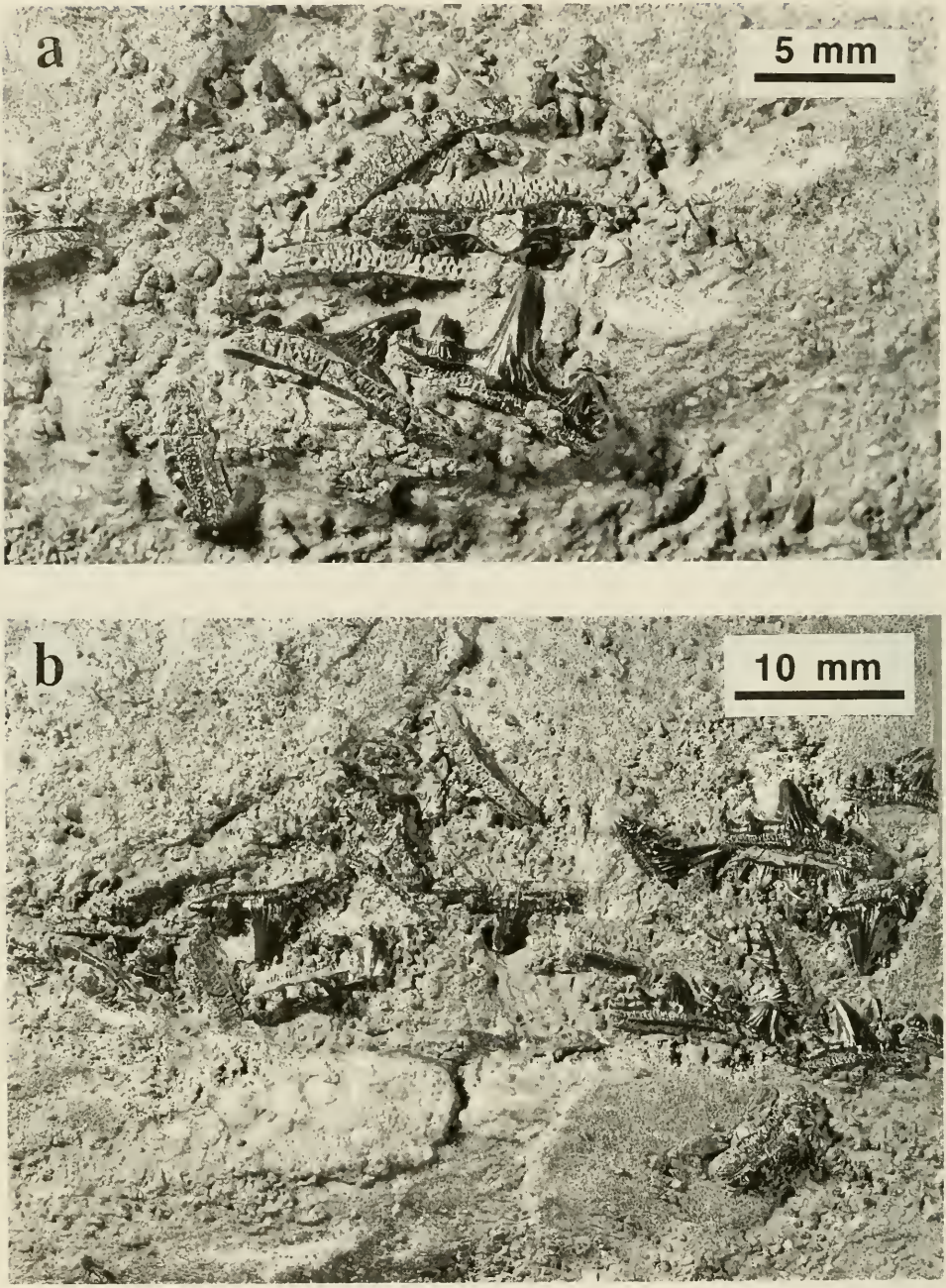

Fig. 7. SMNS 52458 (*Hybodus hauffianus* Fraas, 1895; Schwarzjura ε II3 of Holzmaden). a: parts of the right lower dentition from the proximal part of the right Meckelian cartilage; b: parts of the right ?upper dentition overlying the Meckelian cartilages at the point of their crossing over on the specimen.

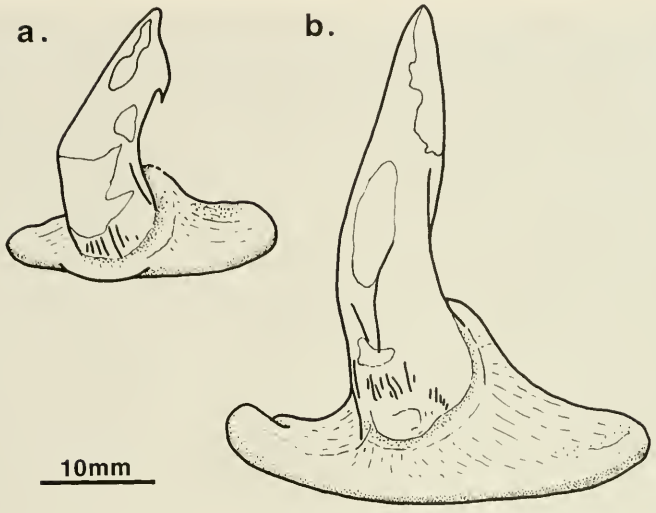

Fig. 8. Camera lucida drawings of cephalic spines from SMNS 52458 (*Hybodus hauffianus* FRAAS, 1895; Schwarzjura εII3 of Holzmaden).
a: spine from the supratemporal region in oblique anterior view; b: spine from the otic region in oblique anterior view.

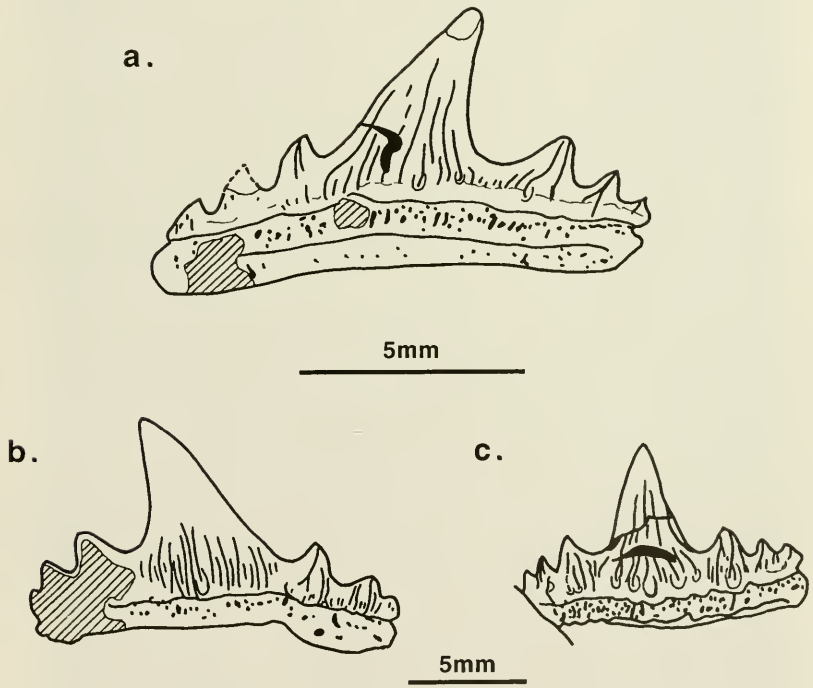

Fig. 9. Camera lucida drawings of teeth from *Hybodus hauffianus* FRAAS, 1895.
a: upper lateral tooth from about Row IX of SMNS 52458 (Schwarzjura εII3 of Holzmaden) in labial view; b: tooth in labial view from SMNS 80594 (Schwarzjura ε of Gomaringen); c: tooth in labial view from SMNS 54048.

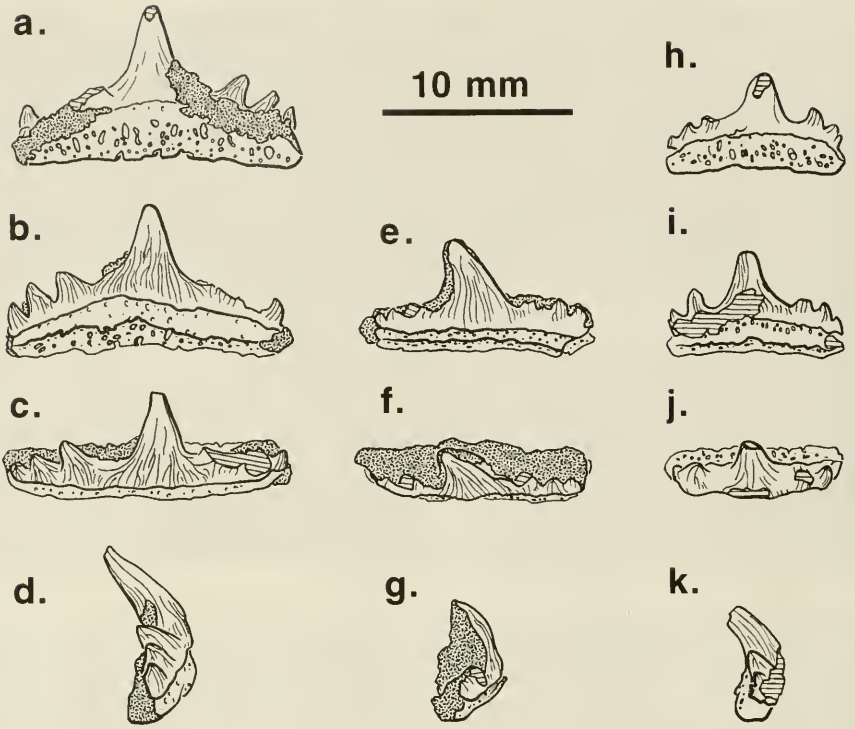

Fig. 10. Teeth of *Hybodus reticulatus* Agassiz, 1837 (Sinemurian, Early Jurassic of Lyme Regis, Dorset, England).
a-d: MCZ780; e-g: MCZ816; h-k: BM(NH) P2203D. a, h – lingual view; b, e, i – labial view; c, f, j – occlusal view; d, g, k, – lateral view. Diagrams after Maisey (1987).

- *Hybodus youngi* Liu, 1962 from the Triassic of China.
- *Hybodus plicatilis* Agassiz, 1837 from the Middle Triassic (Muschelkalk) of north west Europe.
- *Hybodus multiplicatus* Jaekel, 1889 from the Muschelkalk of Germany.
- *Hybodus angustus* Agassiz, 1837 from the European Muschelkalk.
- *Hybodus cuspidatus* Agassiz, 1837 from the late Triassic of Germany.
- *Hybodus longiconus* Agassiz, 1837 from the European Muschelkalk.
- *Hybodus multiconus* Jaekel, 1889 from the European Muschelkalk.
- *Hybodus mougeoti* Agassiz, 1843 from the European Muschelkalk.
- *Hybodus keuperianus* Winkler, 1880 from the Norian of Germany.
- *Hybodus nonstriatus* Winkler, 1880 from the Norian of Germany.
- *Hybodus minor* Agassiz, 1837 from the Late Triassic of Europe (see Duffin, 1993a for discussion of range).
- *Hybodus lawsoni* Duff, 1842 from the Late Triassic of Scotland.
- *Hybodus* sp. from the Bathonian (Middle Jurassic) of the western USA (Schaeffer & Patterson, 1984)
- *Hybodus grossiconus* Agassiz, 1843 from the Bathonian and Oxfordian of Europe (Woodward, 1889; Priem, 1911).
- *Hybodus antingensis* Liu, 1962 from the Middle Jurassic of China.
- *Hybodus songaensis* Saint-Seine & Casier, 1962 from the ?Late Jurassic/ Early Cretaceous of the Congo.
- *Egertonodus basanus* (Egerton, 1845) from the Weald Clay (Valanginian to Aptian, Early Cretaceous of Britain (Maisey, 1983), France (Biddle & Landemaine, 1988) and Morocco (Duffin & Sigogneau-Russell, 1993).

Fig. 11. Whole specimen of *Hybodus hauffianus* FRAAS, 1895 from the Schwarzjura εII6 of Ohmden (SMNS 52460).

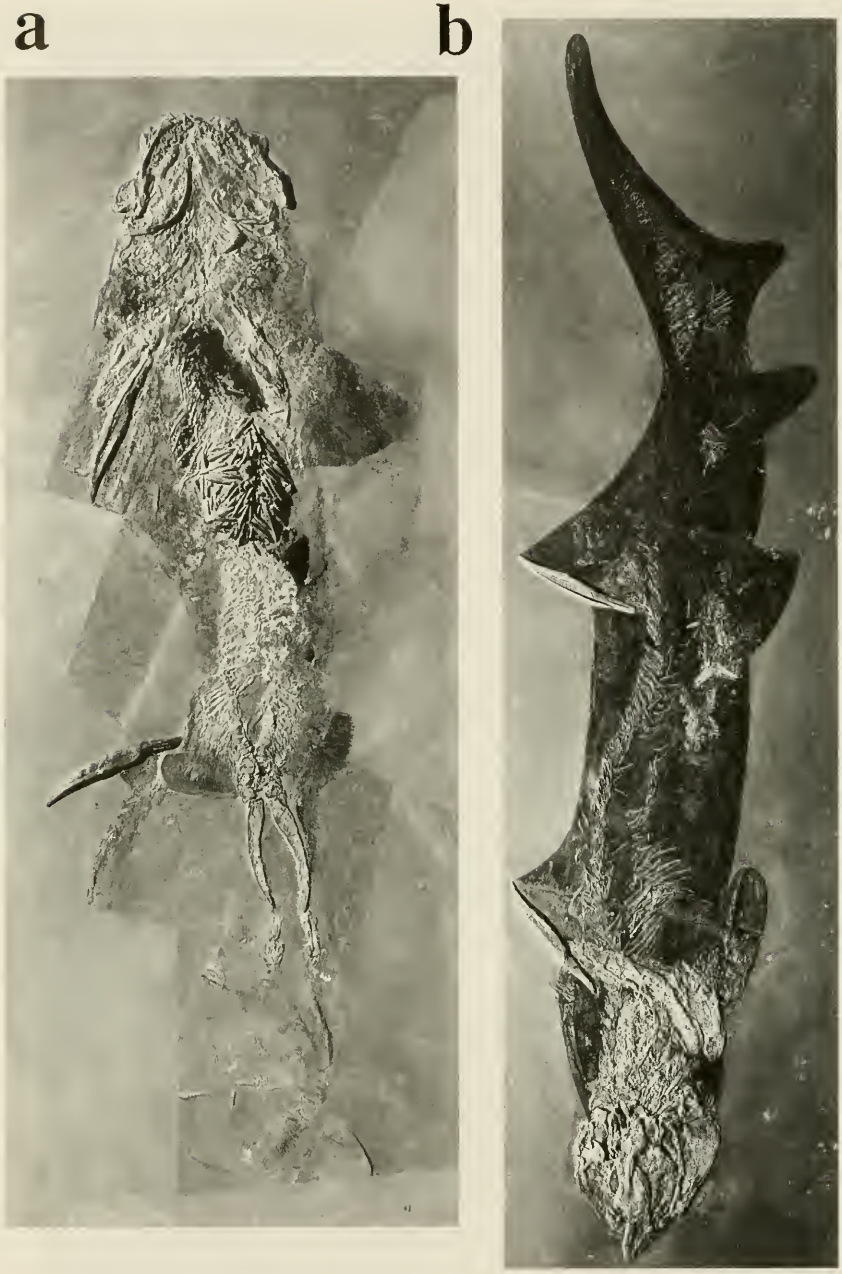

Fig. 12. Articulated, whole bodied specimens of *Hybodus hauffianus* Fraas, 1895 from the Early Jurassic of Holzmaden. – a: SMNS 10062; b: SMNS 15150.

- *Hybodus ensis* WOODWARD,1916 from the Middle Purbeck Formation to Grinstead Clay (Late Jurassic to Early Cretaceous) of Britain (PATTERSON, 1966).
- *Hybodus* sp. from the Campanian (Late Cretaceous) of Aachen (ALBERS & WEILER, 1964).
- *Hybodus butleri* THURMOND, 1972 from the ?Aptian to Albian (Early Cretaceous) of Texas.
- *Hybodus* sp. 1 and *Hybodus* sp. 2 from the Campanian to Maastrichtian (Late Cretaceous) of New Jersey, USA (CAPPETTA & CASE, 1975).
- *Hybodus montanensis* CASE, 1978 from the Campanian (Late Cretaceous) of the USA.
- *Hybodus wyomingensis* CASE, 1987 from the Campanian (Late Cretaceous) of the USA.

Amongst those hybodont sharks which develop labial nodes, the teeth of *H. hauffianus* can be distinguished from the following species since it lacks a lingual shelf:

- *Hybodus delabechei* (CHARLESWORTH, 1839) from the Hettangian to Sinemurian (Early Jurassic of Britain (DUFFIN, 1993a).
- *Hybodus raricostatus* AGASSIZ, 1843 from the Hettangian to Sinemurian (Early Jurassic of Britain (DUFFIN, 1993a).
- *Hybodus obtusus* AGASSIZ, 1837 from the Callovian to Oxfordian of Britain (see MARTILL, 1991 pl. 36 fig. 7).

H. hauffianus has non-bifurcating vertical ridges, which distinguishes it from the following species, in which strongly bifurcating vertical ridges are developed:

- *Hybodus cloacinus* QUENSTEDT, 1885 from the Rhaetian and ?Sinemurian of Britain, Belgium and Germany (DUFFIN, 1993a).

Teeth of *H. medius* AGASSIZ, 1843 from the Sinemurian of Britain (DUFFIN, 1993) have a squat, expanded central cusp in contrast to the higher, more slender condition in *H. hauffianus*.

The teeth of *Hybodus parvidens* WOODWARD, 1889 from the Early Cretaceous of Britain and the Paris Basin are generally smaller than those of *H. hauffianus*, seldom have vertical ridge bifurcation, and the vertical ridges usually attain the central cusp and lateral cusplet apices. It is unusual for labial nodes to be developed at the base of any but the central cusp in the Cretaceous species.

The teeth of *H. polycyphus* AGASSIZ, 1837 (the type species of *Polyacrodus*; Middle Triassic of Germany) has a much stronger node on the labial base of the central cusp than is the case in *H. hauffianus*, and a lower, much more inflated crown.

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