Acta Geologica Polonica, Vol. 58 (2008), No. 2, pp. 235-241

A new species of extinct bullhead sharks, *Paracestracion viohli* sp. nov. (Neoselachii, Heterodontiformes), from the Upper Jurassic of South Germany

JÜRGEN KRIWET

Museum für Naturkunde, Department of Collections, Invalidentsr. 43, D-10115 Berlin, Germany.
E-mail: juergen.kriwet@museum.hu-berlin.de

ABSTRACT:

KRIWET, J. 2008. A new species of extinct bullhead sharks, *Paracestracion viohli* sp. nov. (Neoselachii, Heterodontiformes), from the Upper Jurassic of South Germany. *Acta Geologica Polonica*, **58** (2), 235-241. Warszawa.

The early history of heterodontid sharks is documented mainly by isolated teeth. So far, three different heterodontid genera have been recorded from the Jurassic: *Proheterodontus* from the Middle Jurassic of England (and probably Upper Jurassic of France), *Paracestracion* from the Early to Late Jurassic of England, Belgium and S. Germany, and *Heterodontus* from the Upper Jurassic of South Germany. *Paracestracion* is known by isolated teeth in the Early and Middle Jurassic and by articulated skeletons in the Late Jurassic. Recently discovered skeletal remains from the upper Kimmeridgian locality of Schamhaupten, S. Germany, represent a new, hitherto unknown extinct species of *Paracestracion*, *P. viohli* sp. nov., which documents further taxonomic diversity of early heterodontids. This new taxon is represented by a subadult individual as indicated by the absence of molariform lateral teeth; it shares with other species of *Paracestracion* the characteristic holaulacorize cuspidate teeth. It differs from all other species in having ornamented lingual crown faces. Teeth of *Proheterodontus* differ in a different tooth root vascularisation. *Proheterodontus* and *Paracestracion* vanished before or at the Jurassic/Cretaceous boundary with *Heterodontus* becoming progressively more diverse in the Cretaceous and Cenozoic.

Key words: Heterodontidae, Late Jurassic, Schamhaupten, Diversity.

INTRODUCTION

Modern bullhead sharks (Heterodontiformes) are represented by eight benthic species, which are confined to circumpacific waters (COMPAGNO 1999). Conspicuous characters are the very monognathic heterodont dentition, which is an adaptation to a durophagous feeding strategy, and the presence of fin spines supporting the two dorsal fins. Their fossil record extends well back into the Early Jurassic and consists primarily of isolated teeth. The oldest records are from the Toarcian (Early Jurassic), some 180 million years ago (e.g. THIES 1983; UNDERWOOD 2006). The fossil record of heterodontids and the remaining galeomorphs indicates that the split between both groups must have occurred in the earliest Jurassic (MAISEY & *al.* 2004). This corresponds well with age estimates on the divergence between both groups based on immunological distances indicating that the split must have occurred 240 ± 65 million years ago (DAVIES & *al.* 1987). MUSICK & *al.* (2004) consider fossil heterodontids to be congeneric with modern ones and assume that they were widespread over the eastern neritic Pangean margin. This and additional information (KRIWET & KLUG 2008) demonstrate that heterodontoids most probably originated in Europe, which was an archipelago in the western Tethys Sea. Consequently, the modern distribution might be the result of the vicariant break-up of Pangea. The presence of *Heterodontus* in the Late Jurassic was indicated by EASTMAN (1914), MAISEY (1982) and KRIWET & KLUG (2004). Jurassic heterodontids belong to three different genera, *Heterodontus*, *Paracestracion* and *Proheterodontus*, signifying that heterodontiform diversity was much greater in the Jurassic than in the Cretaceous and Cenozoic. Nonetheless, bullhead sharks of the order Heterodontiformes are quite rare in the Jurassic lithographic plattenkalks of the Solnhofen area and Nusplingen in South Germany (see KRIWET & KLUG 2004). The finding of new taxon from these plattenkalks is, therefore, of great importance.

MATERIAL AND METHODS

The specimen that forms the focus of this study and which is assigned to a new extinct species comes from the upper Kimmeridgian of Schamhaupten in Bavaria (South Germany). The fossil-yielding layers consist of laminated and strongly silicified calcarenites and calcisiltites, which are coarser grained than the Solnhofen limestones. The specimen is housed in the Jura Museum Eichstätt, S Germany (JM Scha). Casts of the teeth were prepared and photographed under SEM.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes HUXLEY, 1880
Subclass Elasmobranchii BONAPARTE, 1838
Cohort Euselachii HAY, 1902
Subcohort Neoselachii COMPAGNO, 1977
Order Heterodontiformes BERG, 1940
Family Heterodontidae GRAY, 1851

Paracestracion KOKEN, in ZITTEL, 1911

TYPE SPECIES: *Cestracion falcifer* WAGNER, 1857, from the lower Tithonian of Solnhofen, S. Germany.

INCLUDED SPECIES: *P. sarstedensis* (THIES, 1983) from the Toarcian of Belgium and Aalenian of N. Germany; *P. bellis* UNDERWOOD & WARD, 2004 from the Bathonian of England; *P.* sp. from the Callovian of England (THIES 1983); *P. viohli* sp. nov. from the Kimmeridgian of S. Germany.

Paracestracion viohli sp. nov.

DIAGNOSIS: A species of *Paracestracion* represented by a single subadult (?) specimen and characterized by the following combination of dental characters: Cusps of all teeth symmetrical or slightly asymmetrical with cusps being bent lingually; cusps of lateral and posterior teeth feebly inclined distally; anterior and lateral teeth with robust central cusp flanked by two to three pairs of lateral cusplets with the first pair being well-developed; crown of anterior and antero-lateral teeth higher than wide, becoming wider towards commissure; teeth of posterior files with up to four pairs of broadly united lateral cusplets; cutting edge well-developed and continuous through the apices of the main cusp and lateral cusplets; labial crown face flat and smooth; basal labial edge faintly convex in anterior teeth, smoothly curved in lateral and posterior teeth; lingual face cambered displaying irregular and vertical folds.

ETYMOLOGY: The species name is dedicated to Günter VIOHL in recognition of his contribution to the geology and fossils of the Bavarian Late Jurassic lithographic limestones.

HOLOTYPE: JM Scha 728, anterior part of body with dentition.

AGE: Late Kimmeridgian, Late Jurassic.

TYPE LOCALITY AND HORIZON: Schamhaupten, Bavaria, Germany; Mörnsheim beds, Ulmense Zone, Rebouletianum Subzone.

DESCRIPTION: The holotype and single specimen, JME Scha 728, consists of an incompletely preserved specimen in ventral view (Text-fig. 1.1). The body posterior to the pelvic fins is lacking, thus providing no information of its gender. The preserved portion of the body measures 16 cm in total length. It is densely covered with placoid scales outlining the anterior body portion including most of the head, parts of the jaws with the dentition, the girdles, and the pectoral and pelvic fins in ventral view. The scales do not differ in their general morphology from those described for other Late Jurassic heterodontids (see KRIWET &

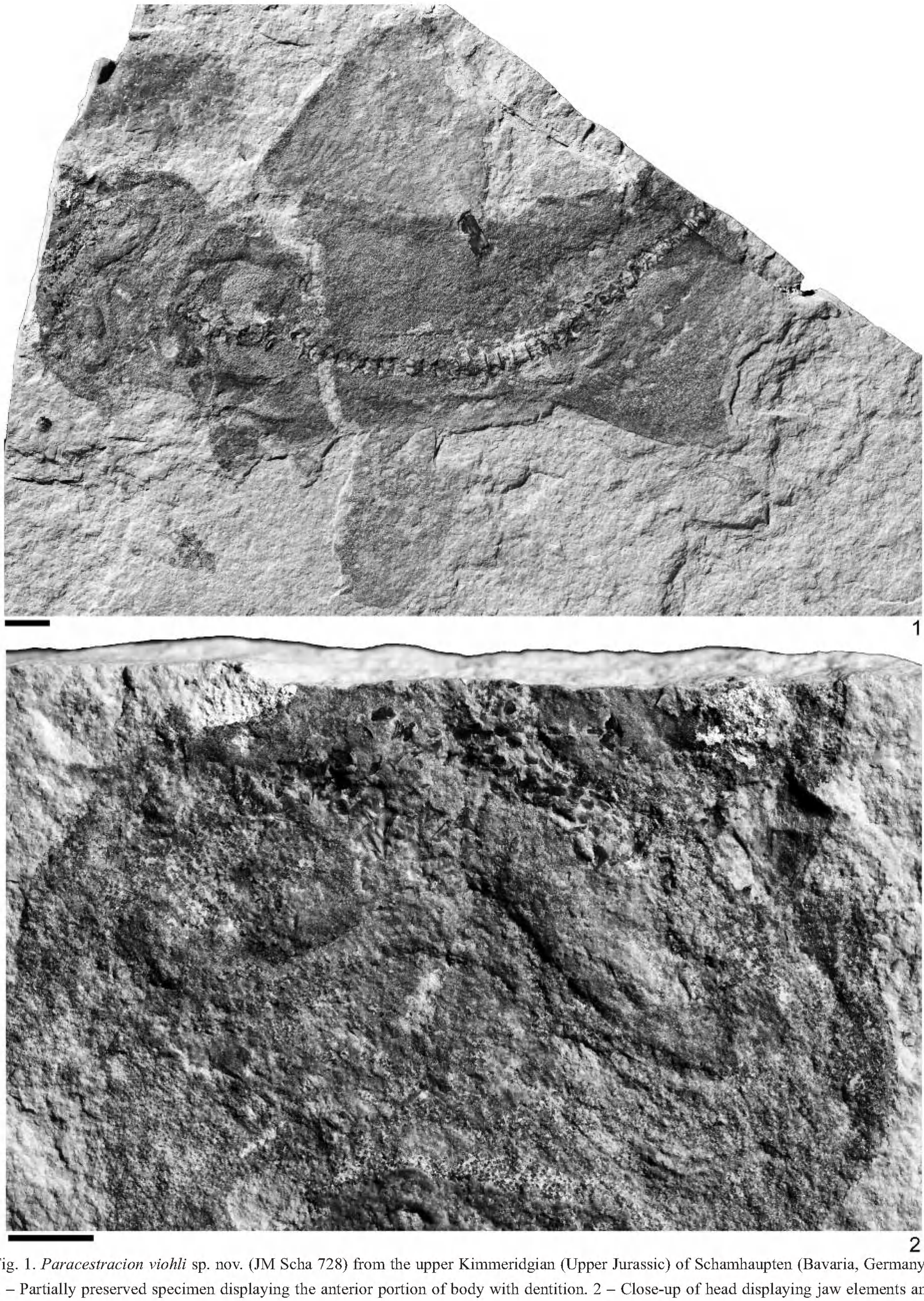

Fig. 1. *Paracestracion viohli* sp. nov. (JM Scha 728) from the upper Kimmeridgian (Upper Jurassic) of Schamhaupten (Bavaria, Germany). 1 – Partially preserved specimen displaying the anterior portion of body with dentition. 2 – Close-up of head displaying jaw elements and dentition. Scale bars equal 0.5 cm

KLUG 2004). Unfortunately, they are densely arranged and thus do not allow any detailed observation of skeletal features such as the neurocranium, the mandibular arches or the pectoral elements. The anterior tip of the snout and most of the palatoquadrate arcade are also missing.

The fin spine is embedded in the body and only its basal fractured portion is visible. Consequently, it is not possible to establish any ornamentation pattern of the fin spine cap. The broken portion of the fin spine of *Foretikodontus* gen. nov. exposes a specialized layer of osteodentine.

The most conspicuous and distinguishing character is the dentition. The jaw apparatus is visible in ven-

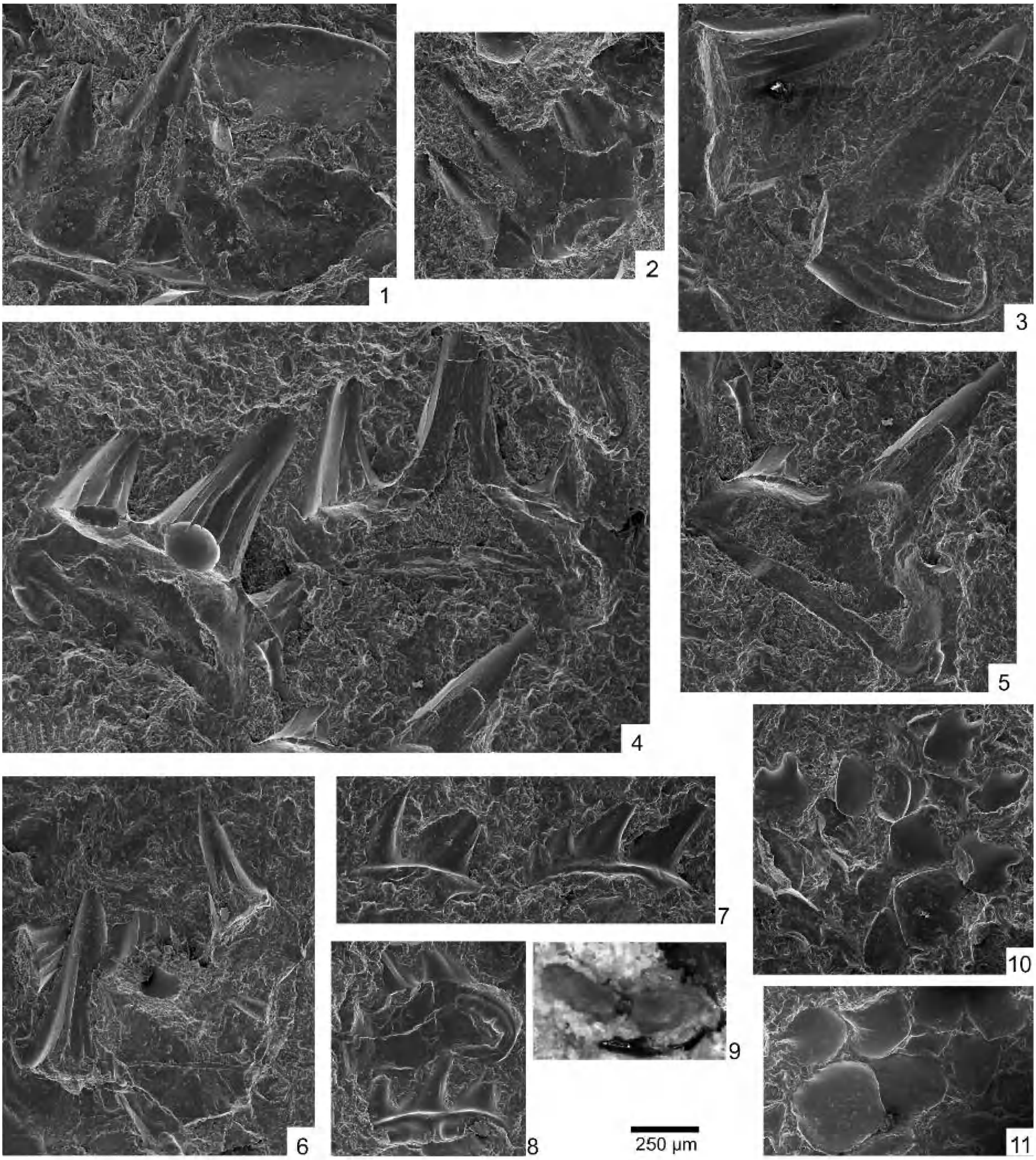

Fig. 2. *Paracestracion viohli* sp. nov. (JM Scha 728). SEM figures of teeth (casts). 1-2 – Anterior to antero-lateral teeth, labial views. 3 – Lateral tooth, labial view. 4 – Lateral teeth, lingual views. 5 – Anterior tooth, lingual view. 6-7 – Lateral to posterior teeth, lingual views. 8 – Posterior tooth, lingual view. 9 – Lateral tooth, basal view. 10-11 – Placoid scales

tral view. However, the anterior part of the skull and the palatoquadrates are lacking so that only the upper right dentition is preserved with some scattered teeth of the upper left jaw. The lower jaws are completely preserved but covered with shagreen so that only the outlines are recognizable. The shagreen covering the teeth, on the other hand, was mechanically removed (Text-fig. 1.2). In addition, casts of individual teeth were prepared for SEM examination (Text-figs 2.1-2.9). The teeth, which all show a massive cusp with several lateral cusplets, are broadly united and range in size from 1.5 cm height in the anterior teeth to 0.35 cm in the posterior teeth, strongly indicating that it represents a subadult specimen. Interestingly, no specialized, molariform lateral teeth are developed.

The anterior teeth are symmetrical, higher than wide, with a triangular crown and a slightly convex basal labial edge similar to the condition found in many post-Jurassic heterodontids. Three pairs of lateral cusplets flank the main cusp. The first pair of lateral cusplets is well-developed with high and acute apices, whereas the other two pairs of lateral cusplets are incipient and broadly united with the first pair of lateral cusplets, forming a saw blade pattern. The labial face of the crown is flat, completely smooth without any ornamentation, and juts out over the root. The lingual face is cambered and displays vertical and flexuous folds reaching far up the lateral cusplets and

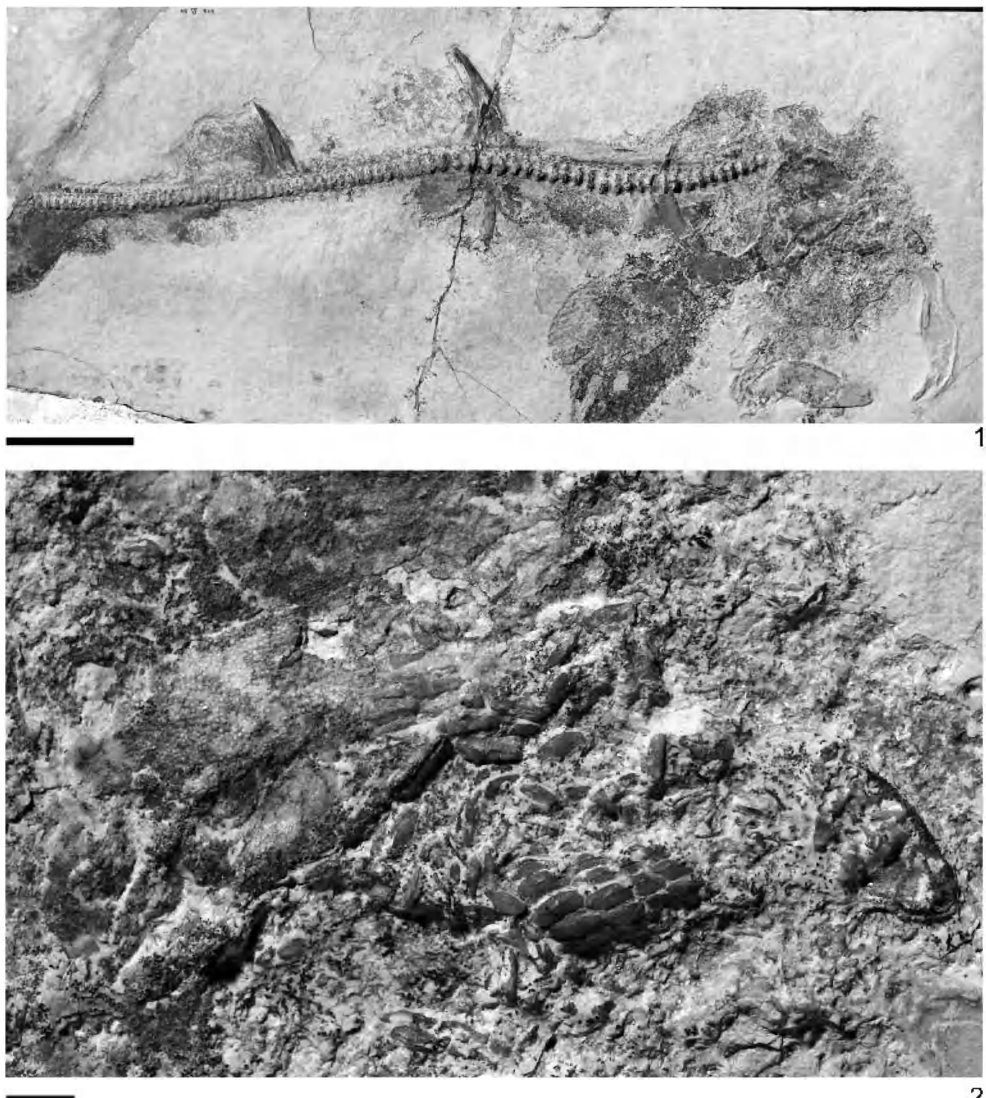

Fig. 3. Adult specimen of *Paracestracion falcifer* (WAGNER, 1857) (holotype, BSPG AS VI 505), from the lower Tithonian of Solnhofen, S. Germany. 1 – Complete specimen. Scale bar equals 5.0 cm. 2 – Close-up of disarticulated dentition displaying cuspidate anterior and molariform lateral teeth. Scale bar equals 0.5 cm.

main cusp. Basally, a short uvula is developed. The lateral teeth differ only in the basal labial edge being smoothly curved and with cusplets and cusp being slightly inclined distally. Distally, the teeth become wider than high with very well-developed first lateral cusplets, which are separated from the main cusp by a deep incision. The crown of all teeth is separated from the root by a constriction.

The root is low and V-shaped in basal view in anterior teeth but elongated in teeth of more posterior positions. The vascularisation is of the holaulacorhize type, with a well defined nutritive groove separating two root lobes (Text-figs 2.8-2.9). The number or form of nutritive foramina opening into the groove or on the lateral faces of the root lobes is not ascertainable.

DISCUSSION: So far, three different heterodontid genera have been recorded from the Jurassic, *Heterodontus*, *Paracestracion* and *Proheterodontus* (KRIWET & KLUG 2004; UNDERWOOD & WARD 2004). *Proheterodontus* was based on isolated teeth from the Bathonian of England by UNDERWOOD & WARD (2004). Adult dentitions are characterized by cuspidate teeth with up to three pairs of lateral cusplets in all jaw positions and hemiaulacorhize roots with very slender and elongated root lobes, but no lateral molariform teeth. This taxon might also occur in the lower Kimmeridgian of France (R. VULLO, personal communication). Articulated skeletons of fossil heterodontids are known only from the Upper Jurassic of Solnhofen and Nusplingen (e.g., WAGNER 1857; SCHWEIZER 1964) and from the Upper Cretaceous Chalk of England (e.g. WOODWARD 1889). *Paracestracion* is represented by four different species (one not identified at species level), ranging from the Toarcian to the Tithonian (UNDERWOOD 2002; KRIWET & KLUG 2004; UNDERWOOD & WARD 2004; this paper). So far, a single species of *Paracestracion*, *P. falcifer*, has been described from the Late Jurassic lithographic limestones of Nusplingen and the Solnhofen area (Text-fig. 3), represented by both juvenile and adult specimens (KRIWET & KLUG 2004). Important differences between extant *Heterodontus* and extinct *Paracestracion* species are the pelvic fins inserting almost beneath the fin spine of the first dorsal fin, and the pectorals that are situated far anteriorly just behind the skull in most specimens of *Paracestracion falcifer*. The fin spines are partly vascularised in *P. falcifer* in contrast to the situation found in modern *Heterodontus* spp. (MAISEY 1982). In adult specimens of *Paracestracion*, the fin spine cap is tuberculated, whereas the cap is smooth in juveniles under 25 cm body length (MAISEY 1982; personal observation).

The most reliable feature to distinguish isolated teeth of *Paracestracion* from those of the modern bullhead sharks is, however, an open nutritive groove of the root separating two mesio-distally elongated root lobes in anterior teeth of *Paracestracion*. Anterior teeth of juveniles and adults of *Heterodontus* always possess hemiaulacorhizan root vascularisation patterns. The dentition of juveniles of *Paracestracion* is characterized by pectinate teeth and the absence of molariform lateral teeth. In modern neonate bullhead sharks, molariform lateral teeth are present but poorly mineralized (SUMMERS & *al.* 2004). Consequently, it seems possible that lateral teeth in Jurassic juveniles of *Paracestracion* might also have been weakly mineralized and therefore inadequately represented in fossil assemblages. In adults, the molariform lateral teeth are well-mineralized, as exemplified by the holotype of *P. falcifer* (see KRIWET & KLUG 2004; Text-fig. 3.2). This specimen also displays the characteristic tuberculated fin spines. Its estimated total body length is about 42 cm. A comparison of mandibular cartilage and vertebrae length between the holotype of *P. falcifer* and that of the new species indicates that *P. viohli* sp. nov. was about 30 cm long, supporting the interpretation that the holotype represents a subadult individual.

The dentition of *P. viohli* sp. nov. is characterized by tooth morphologies and tooth sizes very similar to those of teeth of adult *Paracestracion* and *Heterodontus* spp., but differs significantly from that of very juvenile individuals in that the teeth are not pectinate. Despite the superficial similarities of tooth morphologies between the new species and *Paracestracion falcifer* (e.g. holaulacorhize root vascularisation), the dentition of *P. viohli* gen. nov. is easily distinguishable from all known species assigned to *Paracestracion* by the smooth labial crown faces, whilst vertical ridges ornament the lingual crown face. Teeth of several fossil and extant *Heterodontus* spp. occasionally display a characteristic ornamentation near the basal labial edge or short labial ridges.

The new species adds further information to past diversity patterns of heterodontids. The diversity at generic and species level was obviously considerably higher than in the Cretaceous or Cenozoic (KRIWET & KLUG 2008). *Proheterodontus* and *Paracestracion* vanished before or at the Jurassic/Cretaceous boundary, with *Heterodontus* becoming progressively more diverse in the Cretaceous. Nevertheless, the species diversity of past communities is less than the modern one, implying either collecting biases or difficulties in identifying isolated teeth at species level. The new species, *P. viohli* sp. nov., described in this paper is so far only known from the Kimmeridgian.

Acknowledgments

I am deeply indebted to G. VIOHL (Eichstäät, Germany), who drew my attention to this specimen and for information on the locality and geology of the lithographic limestones. I thank S. KLUG (Berlin, Germany) for preparing the casts and SEM pictures of the teeth. J. REES (Karlstad, Sweden) is acknowledged for his very helpful review.

REFERENCES

BERG, L.S. 1940. Classification of fishes, both recent and fossil. *Transactions of the Institute of Zoology, Academy of Sciences USSR*, **5**, 85-517.

BONAPARTE C.L.J.L. 1832-38. Selachorum tabula analytica. *Nuovi Annali delle Scienze Naturali*, **1**, 195-214.

COMPAGNO L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist,* **17**, 303-322.

— 1999. Checklist of Living Elasmobranchs. *In*: HAMLETT, W.C. (*Ed.*), Sharks, Skates, and Rays – The Biology of Elasmobranch Fishes, pp. 471-498. *Johns Hopkins University Press*; Baltimore and London.

DAVIES, D.H., LAWSON, R., BURCH, S.J. & HANSON, J.E. 1987. Evolutionary relationships of a "primitive" shark (*Heterodontus*) assessed by micro-complement fixation of serum transferring. *Journal of Molecular Evolution*, **25**, 74-80.

EASTMAN, C.R. 1914. Catalog of the fossil fishes in the Carnegie Museum, Part IV. *Memoires of the Carnegie Museum*, **6**, 389-449.

GRAY J.E. 1851. List of specimens of fish in the collection of the British Museum, Part. I; pp. 1-160. British Museum (Natural History); London.

HAY, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *United States Geological Survey*, *Bulletin,* **179**, 1-868.

HUXLEY J.T. 1880. On the application of the laws of evolution to the arrangement of Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880**, 649-662.

KOKEN, E. 1911. Pisces. *In*: ZITTEL, K.A. (*Ed.*), Grundzüge der Paläontologie. Zweite Abteilung, Vertebrata, pp. 1-142. *Oldenbourg*; München–Berlin.

KRIWET, J. & KLUG, S. 2004. Late Jurassic selachians (Chondrichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity. *Zitteliana*, **A 44**, 67-95.

KRIWET, J. & KLUG, S. 2008. Diversity and biogeography pattern of Late Jurassic neoselachians (Chondrichthyes, Elasmobranchii). *In*: CALIN, L., LONGBOTTOM, A. & RICHTER, M. (*Eds*), Fishes and the break-up of Pangea. *Geological Society of London, Special Publication*, **295**, 55-69.

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.

MAISEY, J.G., NAYLOR, G.J.P. & WARD, D.J. 2004. Mesozoic elasmobranches, neoselachian phylogeny and the rise of modern elasmobranch diversity. *In*: ARRATIA, G. & TINTORI, A. (*Eds*), Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity, pp. 17-56. *Dr. Friedrich Pfeil*; Munich.

MUSICK, J. A., HARBIN, M.M. & COMPAGNO, L.J.V. 2004. Historical zoogeography of the Selachii. *In*: CARRIER, J.C., MUSICK, J.A. & HEITHAUS, M.R. (*Eds*), Biology of sharks and their relatives, pp. 33-78. *CRC Press*; Boca Raton, Florida.

SCHWEIZER, R. 1964. Elasmobranchier und Holocephalen aus den Nusplinger Plattenkalken. *Palaeontographica*, **A123**, 58-110.

SUMMERS, A.P., KETCHAM, R.A. & ROWE, T. 2004. Structure and Function of the Horn Shark (*Heterodontus francisci*) Cranium Through Ontogeny: Development of an Hard Prey Specialist. *Journal of Morphology*, **260**, 1-12.

THIES, D. 1983. Jurazeitliche Neoselachier aus Deutschland und S-England (Jurassic Neoselachians from Germany and S-England). *Courier Forschungsinstitut Senckenberg*, **58**, 1-116.

UNDERWOOD, C. J. 2002. Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, Southern England. *Palaeontology*, **45**, 297-325.

— 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology*, **32**, 215-235.

UNDERWOOD, C.J. & 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 Schiefern der Umgegend von Solnhofen. *Gelehrter Anzeiger der Bayerischen Akademie der Wissenschaften*, **44**, 288-293.

WOODWARD, A.S. 1889. Catalogue of the fossil Fishes in the British Museum. Part I; pp. 1-474. *British Museum, (Natural History)*; London.

Manuscript submitted: 20th October 2007
Revised version accepted: 15th April 2008