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The Late Jurassic neoselachian *Macrourogaleus* FOWLER, 1947 is a palaeospinacid shark (Elasmobranchii; Synechodontiformes)

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ABSTRACT:

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The taxonomy of palaeospinacid sharks (Chondrichthyes, Neoselachii) is reviewed. New skeletal material from the famous Late Jurassic lithographic limestones of southern Germany (Solnhofen area and Nusplingen) enables identification of the morphological and dental differences between *Synechodus* and *Paraorthacodus*. These taxa were hitherto known mainly by isolated teeth or a few mostly fragmentary skeletal remains from the Early and Late Jurassic and Late Cretaceous. Differences not only include dental features but also the presence of a single dorsal fin in *Paraorthacodus* compared to two in *Synechodus*. Fin spines are restricted to Early Jurassic specimens. A detailed examination of the small neoselachian shark, *Macrourogaleus hassei*, from the lithographic limestones of the Solnhofen area revealed that this taxon displays the characteristic synechodontiform tooth root morphology (pseudopolyaulacorhize) and a single dorsal fin as seen in *Paraorthacodus*. Consequently, *Macrourogaleus* is assigned to the Palaeospinacidae. It differs from *Paraorthacodus*, however, in the presence of a single row of enlarged placoid scales on the caudal crest.

Key words: Neoselachii, Palaeospinacidae, *Macrourogaleus*, Late Jurassic.

INTRODUCTION

Our understanding of Jurassic neoselachian systematics and taxonomy is still very inadequate despite many recent studies (e.g. LEIDNER & THIES 1999, BÖTTCHER & DUFFIN 2000, UNDERWOOD 2002, KRIWET 2003, KRIWET & KLUG 2004, UNDERWOOD & WARD 2004, KLUG & KRIWET 2006, KLUG & *al.* in press, KLUG & KRIWET 2008). The lithographic limestones of southern Germany (Nusplingen, Solnhofen area), which are late Kimmeridgian and early Tithonian in age, are amongst the most famous fossil fish localities world-wide because they have produced a well-preserved and diverse array of entire skeletons of selachians (e.g. SCHWEIZER 1964, THIES 1995, LEIDNER & THIES 1999, DIETL & SCHWEIGERT 2001, KRIWET & KLUG 2004). However, no detailed morphological analyses of most of these Late Jurassic selachians have been undertaken recently. For a summary of the selachians from the lithographic limestones see KRIWET & KLUG (2004). The intention of this paper is to summarize the current knowledge about synechodontiform sharks and to review the systematic position of the small neoselachian shark *Macrourogaleus* FOWLER, 1947 from the Late Jurassic lithographic limestones of southern Germany.

THE SYNECHODONTIFORM CONTROVERSY

The identity and monophyly of synechodontiform and palaeospinacid sharks was debated in the past (e.g. THIES 1991, 1993, CAPPETTA 1992, MAISEY & *al.* 2004). Nevertheless, I agree with DUFFIN & WARD (1993) and consider synechodontiform sharks to represent a monophyletic extinct basal group of neoselachians without extant representatives. Their fossil history ranges from the Early Triassic to the Late Palaeogene (e.g. THIES 1982, SIVERSON 1992, DUFFIN & WARD 1993). A few isolated teeth identified as *Synechodus antiquus* from the lower Permian of the Ural region most likely might represent the oldest documented record of any known synechodontiform, extending their fossil record back into the Palaeozoic (IVANOV 2005). Isolated teeth of synechodontiform sharks are quite abundant in Mesozoic and Palaeogene strata of the Northern Hemisphere, but less frequent in the Southern Hemisphere (KLUG & *al.* in press). Conversely, skeletal remains are rare and only few have been described from the Lower Jurassic and Upper Cretaceous of England, and the Lower and Upper Jurassic of southern Germany (MAISEY 1985, DUFFIN & WARD 1993, KRIWET & KLUG 2004).

This group includes at least three families, Orthacodontidae, Palaeospinacidae and Pseudonotidanidae, with two additional taxa of uncertain systematic position, which are known only by rare isolated teeth from the Late Triassic and Middle Jurassic (DUFFIN & WARD 1993). Six genera, *Palidiplospinax* (with three species), *Pseudonotidanus* (with one species), *Paraorthacodus* (with 17 species), *Rhomphaiodon* (with one species), *Sphenodus* (with 23 species), *Synechodus* (with 15 species), and *Welcommia* (with two species) have been reported from Permian? to Palaeogene strata to date. According to our current knowledge, they had their greatest taxonomic diversity in the Jurassic. However, the taxonomy of Palaeospinacidae (including *Palaeospinax*, *Synechodus* and *Paraorthacodus*) has been the subject of controversy and remains confusing despite the high abundance of synechodontiform remains, including some skeletal fragments (e.g. WOODWARD 1889, CAPPETTA 1987, KRIWET & KLUG 2004). Most Jurassic teeth are traditionally referred to *Palaeospinax* and those from the Cretaceous and Palaeogene to *Synechodus* or *Paraorthacodus*. DUFFIN & WARD (1993) reviewed the dental and skeletal anatomy of these taxa by comparison with skeletal remains from the Lower Jurassic of Lyme Regis and demonstrated that the teeth of *Palaeospinax* and *Synechodus* display very similar morphologies, consequently transferring all material of *Palaeospinax* to *Synechodus*. The validity of *Paraorthacodus* was questioned repeatedly in the past and most species were assigned to *Synechodus* by various authors. Nevertheless, SIVERSON (1992), DUFFIN & WARD (1993) and KRIWET (2003) presented an array of dental characters to distinguish teeth of *Paraorthacodus* from those of *Synechodus,* including rather high and acute lateral cusplets with more or less well-developed vertical ridges on the labial and lingual crown faces, lateral cusplets well-defined and strongly separated from the main cusp and a labial crown face not overhanging the crown-root junction. Conversely, teeth of *Synechodus* are characterized by broadly united lateral cusplets and main cusp, and an irregular number of mesial and distal cusplets. DUFFIN & WARD (1993) placed *Synechodus* and *Paraorthacodus* into the family Palaeospinacidae. The re-examination of articulated neoselachian skeletons from the Lower and the Upper Jurassic of southern Germany by myself enables a re-evaluation of dental and skeletal characters in palaeospinacid genera (see in detail KLUG & KRIWET 2008). These specimens indicate that the number of dorsal fins and the presence or absence of dorsal fin spines represent important skeletal features for identifying palaeospinacids. *Synechodus* bears two dorsal fins without fin spines, whereas *Paraorthacodus* has only a single dorsal fin lacking a fin spine directly in front of the caudal fin. All palaeospinacids from the Early Jurassic, conversely, have two spines supporting the dorsal fins and are consequently assigned to a new genus, *Palidiplospinax* (KLUG & KRIWET 2008), comprising three species (*P. enniskilleni, P. occultidens* and *P. smithwoodwardi*). Diagnostic dental characters distinguishing the three palaeospinacid genera are the form of the main cusp, cusplet symmetry on each side of the main cusp, gradual or exponential decrease of cusplet heights and the shape of the root face in basal and labial views (KLUG & KRIWET 2008).

UNDERWOOD & WARD (2004) identified an additional possible Jurassic–Cretaceous synechodontiform, *Pseudonotidanus* (with two species), which combines dental features of both hexanchiforms (shape of the crown) and synechodontiforms (lingually expanded, flat-based root), but is established as a synechodontiform because of the diagnostic tooth-root morphology. The orthacodontid shark *Sphenodus* is represented by at least 23 species ranging from the Early Jurassic to the Palaeocene (DUFFIN & WARD 1993). Most of these taxa are based on isolated teeth and skeletal material is known only from *Sphenodus macer* and *S. nitidus* from the Upper Jurassic of southern Germany (BÖTTCHER & DUFFIN 2000).

LATE JURASSIC PALAEOSPINACID SHARKS

KRIWET & KLUG (2004) presented a detailed discussion on Late Jurassic synechodontiforms from southern Germany. In this section, only palaeospinacids are considered, albeit orthacodontids (*Sphenodus macer* and *S. nitidus*) are quite common in Late Jurassic marine strata. Palaeospinacid sharks currently include the genera *Synechodus, Paraorthacodus* and *Palidiplospinax*. Most species referred to this family are based mainly on isolated teeth, skeletal material having been described for only a few species to date.

Three species of *Palidiplospinax* are represented by skeletal material from the Lower Jurassic of England and southern Germany, *P. enniskilleni, P. occultidens* and *P. smithwoodwardi* (e.g. MAISEY 1985, DUFFIN & WARD 1993, KLUG & KRIWET 2006, 2008).

Skeletal remains of *Synechodus* are only known of a single species, *S. dubrisiensis* (the type-species) from the Upper Cretaceous of England. These specimens, however, lack the postcranial skeleton in most cases. Consequently, the presence or absence of fin spines in *Synechodus* was unknown until now. DUFFIN & WARD (1993) noted in their revised diagnosis of this genus that fin spines are present in some species, contrary to MAISEY (1975), who did not find fin spines. UNDERWOOD & WARD (2004) indicated the possible presence of a smooth fin spine in a specimen of *S. dubrisiensis*. This statement cannot be maintained based on my own studies of all known specimens of *S. dubrisiensis* housed in several English collections. So far, no species of *Synechodus* from the Upper Jurassic of southern Germany was described in detail or named, although LEIDNER & THIES (1999) figured a characteristic tooth from a complete skeleton from the lower Tithonian of the Solnhofen area that represents a new species (KLUG in prep.). Another complete small skeleton in the collection of the Bavarian palaeontological state collections in Munich, BSP 1878 VI 6, was also identified as *Synechodus* sp. (written information on label by D. Thies; see KRIWET & KLUG 2004: fig. 6d). Unfortunately, all the teeth were removed from this specimen so that this identification cannot be confirmed here. Remarkably, this specimen displays two dorsal fins without preceding spines (KRIWET & KLUG 2004, fig. 6d; KLUG & KRIWET 2008). This discovery agrees with the statement of DUFFIN & WARD (1993) that fin spines are unequally distributed among the palaeospinacid species. Additional new material from the lithographic limestones supports this interpretation.

A single skeletal remain of *Paraorthacodus*, *P. jurensis* (SCHWEIZER, 1964), was described from the Late Jurassic lithographic limestones of southern Germany. It is represented by the anterior portion of a skeleton that was originally referred to *Synechodus*. The teeth display, however, the characteristic *Paraorthacodus* morphology according to CAPPETTA (1987) and DUFFIN & WARD (1993) (contrary to LEIDNER & THIES 1999). Examination of a new and complete skeleton of this taxon from Nusplingen (KLUG & *al.* in prep.) and a re-evaluation of the dental characters of palaeospinacids also support its assignment to *Paraorthacodus*. This specimen and additional skeletal material of juvenile specimen from the lithographic limestones of the Solnhofen area (KRIWET & KLUG 2004, fig. 7) display a single dorsal fin just in front of the caudal fin. The caudal fin is heterocercal and relatively broad, with a distinct subterminal notch and ventral lobe.

THE IDENTITY AND SYSTEMATIC POSITION OF *MACROUROGALEUS* FOWLER, 1947

HASSE (1882) figured a small shark specimen from the lithographic limestones of the Solnhofen area under the name *Pristiurus* (junior synonym of *Galeus*), which was assigned to a new species, *P. hassei* by WOODWARD (1889) (Text-fig. 1). Subsequently, FOWLER (1947) referred this and similar specimens to the new taxon *Macrourogaleus*, based on the apparent discrepancies but also similarities to *Galeus*. The most obvious differences between *P. hassei* and *Galeus* are the presence of a single, rather small dorsal fin just in front of the caudal fin and a low and elongated anal fin. In addition, *Macrourogaleus* is characterized by a single row of enlarged placoid scales on the caudal crest (Text-fig. 1.4), which is similar to the condition found in the extant *Galeus*. The dentition is not preserved or is covered by placoid scales in most specimens studied. Only a few specimens, including the holotype, display a few teeth in different aspects, enabling an account of dental morphologies and a comparison with other neoselachians. Generally, *Macrourogaleus* is considered to be a carcharhiniform with affinities to scylioirhinids. However, THIES & LEIDNER (1999) did not list or discuss this taxon in their short review of Late Jurassic sharks and batoids from southern Germany. KRIWET & KLUG (2004) stated that the teeth might resemble those of *Galeus*, based on very uninformative material. Meanwhile, some more specimens were prepared to display additional teeth and new material (e.g. in the American Museum of Natural History, AMNH) has been studied (see Text-fig. 1.6). The teeth of all the specimens examined are delicate and multi-

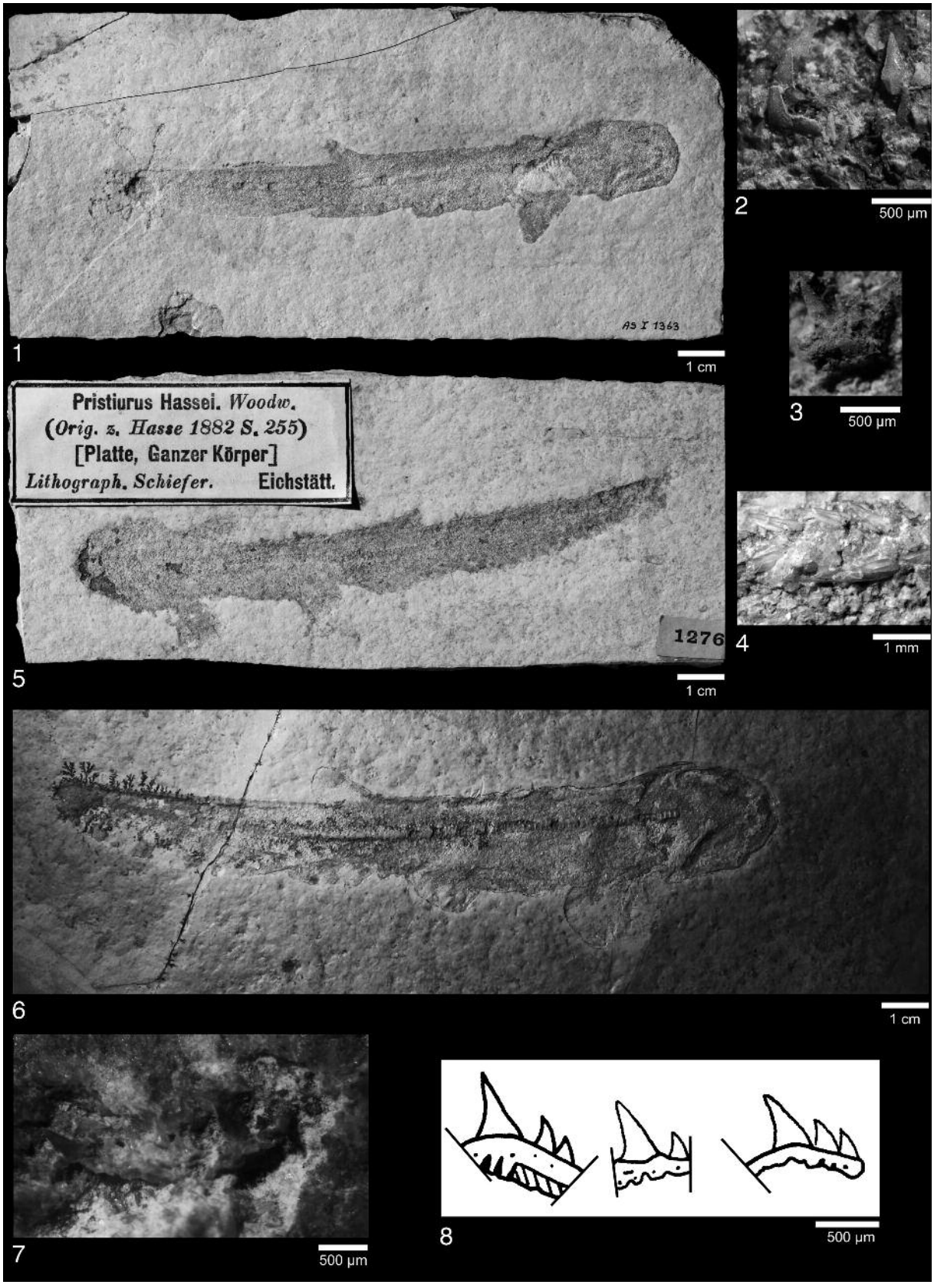

Fig. 1. *Macrourogaleus hassei* (WOODWARD, 1889) from the Late Jurassic lithographic limestones of the Solnhofen area. 1-4 – Holotype (BSP AS 1363). 1 – Lateral view. 2-3 – Close-ups of teeth. 4 – Close-up of enlarged caudal placoid scales. 5 – Specimen BSP AS 1362. 6-8 – Specimen AMNH 7498. 6 – Specimen in lateral view. 7 – Close-up of tooth. 8 – Camera lucida drawing of three teeth. From left to right: lingual, labial and lingual view

cuspidate and display the characteristic root morphology (pseudopolyaulacorhize) of synechodontiforms (Text-fig. 1.2, 1.3, 1.7, 1.8). Additionally, *Macrourogaleus* resembles specimens of *Paraorthacodus* with regard to the presence of a single dorsal fin, but differs considerably from this genus in the position and size of the dorsal and anal fins, in having a more elongated body, and in the presence of a single row of enlarged denticles on the caudal crest posterior to the dorsal fin. Consequently, *Macrourogaleus* is considered to represent a valid genus that must be assigned to the Palaeospinacidae. The exact systematic position of *Macrourogaleus* within the Synechodontiformes is currently being explored by me but most probably it is the sister taxon to *Paraorthacodus*.

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