

# Late Jurassic selachians (Chondrichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity

By  
Jürgen Kriwet\* & Stefanie Klug

Ludwig-Maximilians-Universität München, Department für Geo- und Umweltwissenschaften,  
Sektion Paläontologie, Richard-Wagner-Straße 10, 80333 Munich, Germany

Manuscript received 20 October 2004, revision accepted 24 November 2004

## Abstract

The record and taxonomy of Late Jurassic selachians from southern Germany is reviewed and discussed. The conservation lagerstätten of Nusplingen and the Solnhofen area are outstanding because they yielded numerous entire skeletons. Only a few studies of isolated teeth from localities elsewhere contributed to the knowledge of Late Jurassic selachian diversity of southern Germany. However, the current knowledge is still very incomplete. Bulk sampling of Kimmeridgian strata near the village of Mahlstätten (Baden-Württemberg) allows the study of a diverse selachian assemblage and significantly increases the number of selachian species from southern Germany. The Late Jurassic selachian fauna of southern Germany is amongst the most diverse known from the Jurassic of Europe, comprising at least 16 genera and 30 species. Hybodonts and synchodontiforms are comparably rare in Late Jurassic southern Germany faunas of whole-bodied specimens. Conversely, teeth of synchodontiforms dominate collections of isolated teeth. Completely articulated specimens of *Paraorthacodus* are presented from the lithographic limestones of Solnhofen for the first time. The validity of the hexanchiform genera *Eonotidanus* and *Paranotidanus* is discussed. The presence of two heterodontids, *Heterodontus* and *Paracestracion*, in the Late Jurassic is confirmed based on tooth morphologies and postcranial features. The composition of Late Jurassic selachian faunas indicate that the distribution of taxa is greatly influenced environmentally. Despite all recent advances, it is evident that the taxonomy of Late Jurassic selachians is still in urgent need of revision.

**Key words:** Hybodontiformes, Neoselachii, Upper Jurassic, Bavaria, Baden-Württemberg, diversity, faunal relationships.

## Kurzfassung

Oberjurassische Selachier sind hauptsächlich aus den Konservatagerstätten von Nusplingen und der Solnhofener Gegend bekannt. Die Exemplare liegen in vollständiger Erhaltung

vor. Bisher gab es nur wenige weitere Funde von Haifischresten aus anderen süddeutschen oberjurassischen Lokalitäten. Basierend auf neuen Funden aus dem Kimmeridgium sowie erneuter Untersuchungen der Exemplare aus Solnhofen und Nusplingen wird der derzeitige Kenntnisstand oberjurassischer Selachier Süddeutschlands (Bayern, Baden-Württemberg) zusammengefasst und ihre Taxonomie diskutiert. Die oberjurassischen Haifisch-Faunen Süddeutschlands gehören zu den diversesten Faunen dieser Zeit und umfassen mindestens 16 Gattungen und 30 Arten. Hybodontier sind im Oberjura Süddeutschlands allgemein sehr selten. Die häufigsten Reste stammen von synchodontiformen Haien, die durch mehrere Arten repräsentiert sind. Vollständig artikulierte Exemplare von *Paraorthacodus* aus den lithographischen Plattenkalken Solnhofens werden erstmalig vorgestellt. Die Validität der beiden hexanchiformen Gattungen *Eonotidanus* und *Paranotidanus* wird diskutiert. Das Vorkommen zweier heterodontider, *Heterodontus* und *Paracestracion*, im Oberjura Süddeutschlands wird bestätigt. Unterschiede zwischen *Heterodontus* und *Paracestracion* finden sich in der Morphologie der anterioren Zähne und in der postkranialen Anatomie. Es sind deutliche Unterschiede in den Faunen, basierend auf skelettalem Material oder isolierten Zähnen, als Resultat unterschiedlicher Ablagerungsbedingungen festzustellen. Trotz aller Fortschritte in den letzten Jahren sind oberjurassische Selachier nach wie vor unzureichend bekannt. Die faunistischen Beziehungen oberjurassischer Faunen Europas werden allgemein diskutiert.

**Schlüsselwörter:** Hybodontiformes, Neoselachii, Bayern, Oberjura, Baden-Württemberg, Diversität, faunistische Beziehungen.

## 1. Introduction

The Jurassic was an important period in the evolution and radiation of neoselachian sharks and rays because it was then when most groups of modern and extinct sharks and rays appeared first in the fossil record. Despite all progress accomplished in the last years, the completeness of the fossil record of

\* Author for correspondence and reprint requests; E-mail: j.kriwet@lrz.uni-muenchen.de

neoselachians is still disputed. Phylogenetic hypotheses of neoselachian interrelationships based on morphological data (e.g., SHIRAI 1992a) require long ghost lineages to be congruent with the fossil record. Conversely, phylogenetic analyses based on molecular data are in better accordance with the stratigraphic distribution of neoselachians, indicating that only few modern lineages were present in the Early Jurassic (MAISEY et al. 2004). This led to the conclusion that there was probably no modern neoselachian radiation event prior to the Early Jurassic, and that before this time there was no significant increase in the numbers of lineages (MAISEY et al. 2004), although the fossil record of neoselachians can be traced back into the Triassic with confidence (THIES 1982; CUNY & BENTON 1999). Palaeozoic remains of neoselachians (e.g., DUFFIN & WARD 1983; TURNER & YOUNG 1987; DUFFIN et al. 1996) are questionable because they lack a triple-layered enameloid ultrastructure, which is one of the best characters for identifying isolated neoselachian teeth (CUNY & BENTON 1999).

Our understanding of Jurassic neoselachian diversity is, however, still very inadequate despite many recent studies (e.g., THIES & CANDONI 1998; LEIDNER & THIES 1999; BÖTTCHER & DUFFIN 2000; DELSATE & CANDONI 2001; UNDERWOOD 2002; KRIWET 2003; UNDERWOOD & WARD 2004). 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 produced a well-preserved and diverse array of entire skeletons of selachians (e.g., HEINEKE 1906; KUHN 1961; SCHWEIZER 1964; LAMBERS 1999; DIETL & SCHWEIGERT 2001). Outside Germany, the Kimmeridgian lithographic limestones of Cerin (France) yielded a similar array of perfectly preserved fossil fishes (SAINT-SEINE 1949) although taxonomic differences exist and the diversity is considerably lower in the French deposits. THIES (1995) and LEIDNER & THIES (1999) examined the placoid scales and teeth of articulated Late Jurassic neoselachians and presented short taxonomic discussions. However, no detailed morphological analyses of Late Jurassic selachians from southern Germany have been carried out recently. The intention of this paper is to (1) review the selachian assemblages from the Upper Jurassic of Baden-Württemberg and Bavaria, (2) discuss their taxonomy, and (3) compare Late Jurassic selachian assemblages of Europe in general terms.

**Abbreviations:** Abbreviations used in this paper: BMNH, Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; JM-SOS, Jura Museum Eichstätt, Germany (SOS indicates specimens from the Solnhofen area); MB.f, Natural History Museum, Berlin, Germany; SMNS, Museum of Natural History, Stuttgart; PIMUZ, Palaeontological Institute and Museum of the University of Zürich, Switzerland.

## 2. The Localities

### 2.1. Solnhofen (Southern Franconian Alb, Southern Germany)

Late Jurassic sediments of the southern Franconian Alb were deposited on the Franconian-South Bavarian Carbonate Platform (Fig. 1). The development of this platform is related to the growth of coral-sponge-microbial biohermes, which started

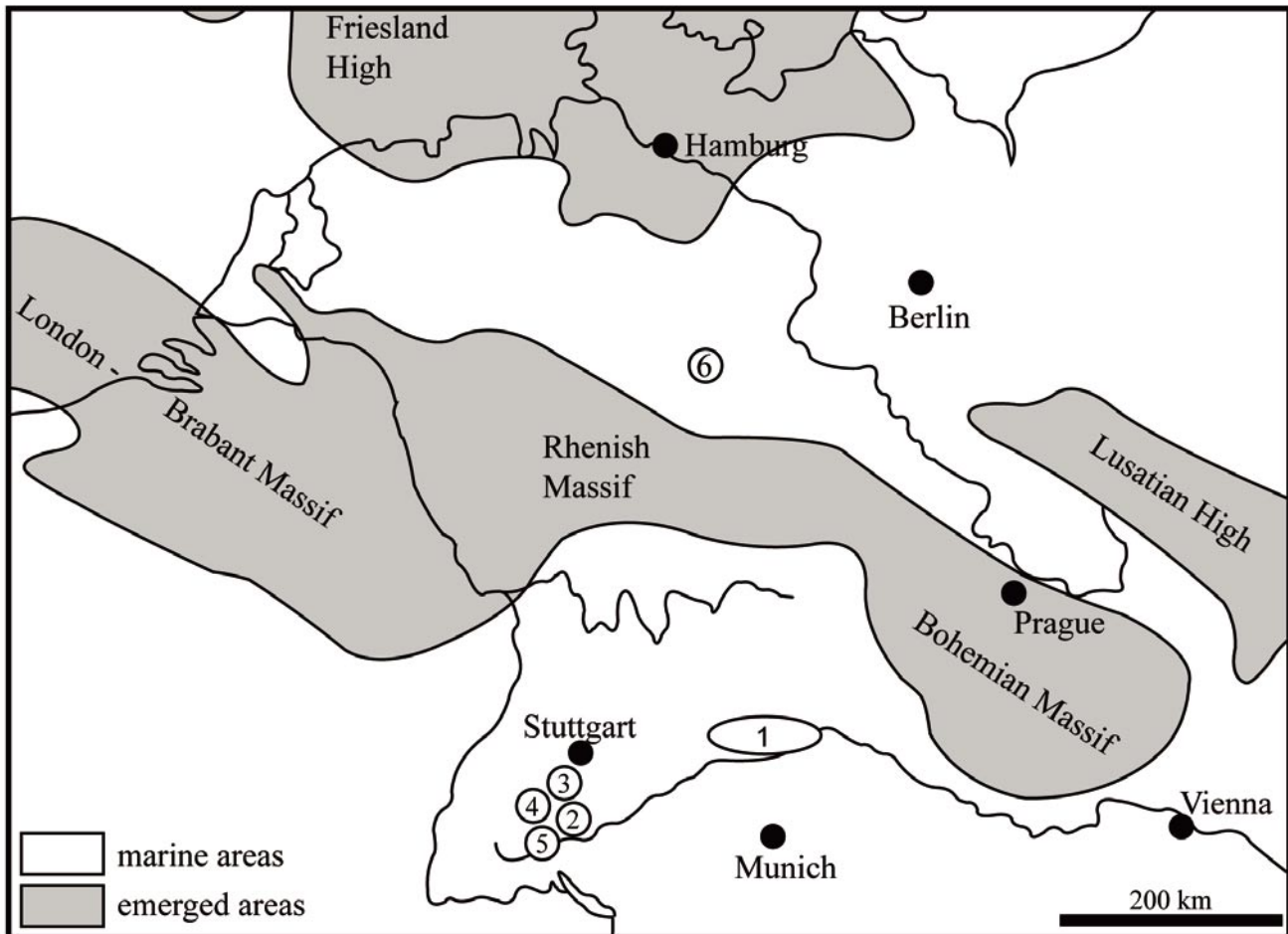
in the Oxfordian and resulted in the creation of submarine elevations and basins (KEUPP et al. 1993). The maximal extension of these structures occurred in the late middle Kimmeridgian, when progressive shallowing of the platform occurred (VIOHL 1996). Fine laminated plattenkalks (lithographic limestones) were deposited in the basins between sponge- and coral-covered build-ups. As a general term, the Solnhofen Limestones refer to the area between the cities of Solnhofen in the west and Regensburg in the east, including various localities of different ages, most important are Solnhofen, Eichstätt, and Kelheim. Industrial mining of the lithographic limestones started in the mid 19<sup>th</sup> century and continued until today. The plattenkalks are considered conservation lagerstätten because fossils are rare but perfectly preserved displaying even soft parts. Over the last 150 years they produced a large variety of vertebrate fossils including the nine specimens of the famous *Archaeopteryx*.

Unfortunately, most specimens in museum collections come from different sites or quarries, which were partly abandoned long ago so that the exact provenance and stratigraphic age of many specimens is unknown and difficult to establish. The oldest fish fossils were recovered from the middle Kimmeridgian of the Treuchtlingen Formation in the vicinity of Kelheim (VIOHL 1996). During the early Tithonian Solnhofen Formation (Malm Zeta 2), pure micrite without bioclasts and relatively little organic matter was deposited. Most selachians were recovered from this formation. The overlying Mörsenheim Formation (Malm Zeta 3) also yielded actinopterygians in perfect conservation but selachians are rare. According to LEIDNER & THIES (1999), the following taxa occur in the lithographic limestones of the Franconian Alb: *Notidanoides muensteri*, *Sphenodus macer*, *Synechodus* nov. sp., *Squatina alifera*, Squatinidae nov. gen., *Heterodontus falcifer*, *Phorcynis catulina*, *Corysodon cirinensis*, *Palaeoscyllium formosum*, *Palaeocarcharias stromeri*, and *Asterodermus platypterus*.

### 2.2 Nusplingen (Southern Germany, Southwestern Swabian Alb)

The famous plattenkalks of Nusplingen are located about 100 km southwest of Stuttgart and 12 km north of the river Danube in the southwestern Swabian Alb (Fig. 1). Here, fine laminated late Kimmeridgian (Ulmense Zone) limestones and marls were deposited in a small lagoon under tropical conditions (SCHWEIGERT et al. 1996; SCHWEIGERT 1998; DIETL & SCHWEIGERT 2001). The plattenkalks are restricted to an area of ca. 2 km<sup>2</sup>. Only a few small outcrops are still accessible; most quarries are abandoned. Small temporary quarries were used for the search of fossils and many of the older classic discoveries, such as large and complete crocodilian skeletons, pterosaurs, and fishes, were made during the initial period of exploration.

The most important recent outcrops are the Nusplingen and Egesheimer quarries. The latter was opened in the early 1980s and scientific excavations started in the 1990s. For a more complete historical review of the Nusplingen quarries and their floral and faunal contents see BÖTTCHER & DUFFIN (2000) and DIETL & SCHWEIGERT (2001). To date, two holoccephalans, nine elasmobranchs, two crossopterygians, and ca. 19 actinopterygians were discovered (DIETL & SCHWEIGERT 2001). The selachian assemblage was studied by SCHWEIZER



**Figure 1:** Late Jurassic palaeogeographic sketch map of central Europe showing localities discussed in the text. (1) Solnhofen area, Bavaria (Oxfordian to Tithonian). (2) Nusplingen, Baden-Württemberg (late Kimmeridgian). (3) Buchsteige, Baden-Württemberg (late Oxfordian). (4) Stuifen / Reichenbach, Baden-Württemberg (late Oxfordian). (5) Mahlstetten, Baden-Württemberg (Kimmeridgian). (6) Northwestern Germany (Oxfordian to Tithonian).

(1964). According to LEIDNER & THIES (1999) and DIETL & SCHWEIGERT (2001: p. 71) it comprises: *Notidanoides muensteri* (AGASSIZ, 1843), *Eonotidanus serratus* (FRAAS 1855), *Heterodontus falcifer* (WAGNER, 1857), *Palaeoscyllium* sp., *Sphenodus macer* (QUENSTEDT, 1852), *Paraorthacodus jurensis* (SCHWEIZER, 1964), *Squatina acanthoderma* FRAAS, 1854, and *Belemnobatis sismondiae* THIOLLIÈRE, 1854.

### 2.3 Buchsteige, Lochen (Southern Germany, Southwestern Swabian Alb)

Isolated teeth of neoselachians were presented by QUENSTEDT (1858) and THIES (1983) from Buchsteige, south of Tübingen (Fig. 1). The material is comprised of some 60 teeth of four selachian species from glauconitic marls of the lower Bimammatum Zone (late Oxfordian), including the synechodontiforms *Synechodus riegrafi* (THIES, 1983) and *Sphenodus longidens* (AGASSIZ, 1843), the squalomorph *Protospinax lochensteinensis* THIES, 1983, and the squatiniform *Squatina* sp. *Protospinax lochensteinensis*, which is known exclusively from this locality.

### 2.4. Reichenbach and Stuifen (Southern Germany, Southwestern Swabian Alb)

DUFFIN (1993) reported two small collections of isolated neoselachian teeth from the Oxfordian of Reichenbach and Stuifen respectively (Fig. 1). Both localities are situated between the cities of Schwäbisch Hall and Ulm in eastern Baden-Württemberg. The material comprises 11 selachian teeth, which were collected by an amateur palaeontologist. The Reichenbach specimens come from the Transversarium Zone (middle Oxfordian) whereas the Stuifen teeth were obtained from marls of the Planula Zone (late Oxfordian). The fauna consists of *Protospinax annectans* WOODWARD, 1918, *Synechodus riegrafi* (THIES, 1983), and *Sphenodus* cf. *S. longidens* AGASSIZ, 1843. Teeth of *S. longidens* are quite common in the Middle Jurassic of Europe.

### 2.5. Mahlstetten (Southern Germany, Southwestern Swabian Alb)

Greyish marls of Kimmeridgian age (Malm Delta 2) are exposed along the street between the villages of Mahlstetten and Mühlheim near Ravensburg in southern Baden-Württemberg (Fig. 1). This locality was discovered by E. UNGER



**Figure 2:** Holotype of *Hybodus fraasi* BROWN, 1900 (BSP 1899 I 2) from the lower Tithonian of Solnhofen (Bavaria). Scale bar = 10 cm.

(Aulendorf) in 1995 and the vertebrate bearing strata were explored for palaeontological reasons until recently. Teeth and placoid scales were recovered by bulk sampling of about 650 kg of sediment and screen-washing. So far, several hundred teeth of ca. 25 neoselachian species and a single hybodontoid taxon were identified. Most abundant are teeth of synechodontiforms (several species of *Sphenodus*, *Paraorthacodus*, and *Synechodus*). Squalomorphs (*Protospinax*) and several orectolobiforms (e.g., *Palaeobrachaelurus*) also are abundant, followed by hexanchiforms (*Notidanoides*) and scyliorhinids (e.g., *Palaeoscyllium*). Teeth of squatinids, heterodontids (*Paracestracion*), and batoids are comparably rare. A detailed taxonomic description of this fauna will be presented elsewhere (J.K., S.K. & E.U. in prep.).

### 3. Taxonomic Remarks

Several phylogenetic analyses have been attempted to resolve the interrelationships of neoselachians sharks, skates, and rays in recent years using morphological and molecular data (e.g., SHIRAI 1992a, 1996; BRITO & SERET 1996; CARVALHO 1996; CARVALHO & MAISEY 1996; DOUADY et al. 2003; WINCHELL et al. 2003; KRIWET 2004a; MCEACHRAN & ASCHLIMAN 2004; MAISEY et al. 2004). The most notable discrepancy between the hypotheses is the position of batoids, which are nested within modern sharks when morphological data are employed, but resolved as sister group to all modern sharks based on molecular data. Combining all data sets in a single hypothesis (phylogenetic supertree) also does not support the position of batoids within modern sharks (J.K. in prep.). On this basis we refute the clade Hynposqualea of SHIRAI (1992a) and CARVALHO (1996) that includes Squatiniformes, Pristiophoriformes, and Batoidea. Despite all progress that has been made in the last few years, the interrelationships of Late Jurassic selachians are still poorly resolved. A detailed systematic revision of these selachians is, however, beyond the scope of this paper.

#### 3.1 Hybodontoida

The interrelationships of hybodontoids are still obscure although the morphological understanding of these forms has improved in the last decades (e.g., MAISEY 1982a, 1983, 1987, 1989; KRIWET 2004b). Hybodonts are very rare in the Upper Jurassic of southern Germany when compared to contemporaneous localities (e.g., northwestern Germany, southern England). So far, no isolated teeth of hybodontoids have been found in any southern German locality considered here. MAISEY (1986a) and LEIDNER & THIES (1999) state that there is a single hybodontoid taxon, *Hybodus fraasi* BROWN, 1900, in the Upper Jurassic of southern Germany (Fig. 2). *Hybodus fraasi* is supposed to be represented by a single specimen in part and counterpart from the lower Tithonian of the Solnhofen area (BSP 1899 I 2). Fragmentary fin spines of *Hybodus* are also present in the oropharynx of *Paraorthacodus jurensis* SCHWEIZER, 1964 (MAISEY 1985). A second specimen of *H. fraasi* is housed in the fossil fish collection of the Museum of Natural History in Berlin (J.K. pers. obser.), and a third is in private possession (FRICKHINGER 1999, fig. 155).

*Hybodus* was not the only hybodontoid that thrived in the lagoons of Bavaria. An isolated fin spine of *Asteracanthus ornatissimus* AGASSIZ, 1837 from the Kimmeridgian of Kelheim (BSP AS XIX 503) (Fig. 3) indicates that hybodontoids might have been more abundant than commonly presumed (see also WAGNER 1861).

#### 3.2 Hexanchiformes

Extant hexanchiforms include two families, i.e. Chlamydoselachidae and Hexanchidae. Chlamydoselachids (frilled sharks) are very rare in the fossil record and the oldest remains come from Late Cretaceous times (M. GOTO, pers. comm. 2001). Hexanchids (cow sharks) comprise three extant genera, *Hexanchus*, *Heptarhynchus*, and *Notorhynchus* (the latter two are placed in their own family by some authors) with



**Figure 3:** Fragmentary dorsal fin-spine of *Asteracanthus ornatisimus* AGASSIZ, 1837 (BSP AS XIX 503) from the Kimmeridgian of Kelheim (Bavaria). Lateral view, anterior edge points to the left. Scale bar = 1.0 cm.

four species (COMPAGNO 1999). Hexanchiforms are *inter alia* characterized by a single dorsal fin without preceding spine and very characteristic dentitions.

The fossil record of hexanchiforms extends back into the Jurassic (e.g., DE BEAUMONT 1960a; UNDERWOOD & WARD 2004) with at least six fossil genera (WARD & THIES 1987). Prior to the work of SCHWEIZER (1964), descriptions of Late Jurassic hexanchids focused only on general patterns of gross morphology and, predominantly, teeth. Several nominal Jurassic taxa have been described so far. Early Jurassic species are *Notidanus arzoensis* DE BEAUMONT (1960) from the Lias of Switzerland, *Hexanchus? wiedenrothi* THIES, 1983 from the Lias of northwestern Germany, and *Notidanus amalthei* OPPEL, 1854 from the Lias of Baden-Württemberg (a fragmentary cusp). From the Middle Jurassic, a single species, *Notidanus contrarius* MÜNSTER 1843, was reported from Bajocian strata of Bavaria. Late Jurassic records are more numerous and include isolated teeth and entire skeletons: *Notidanus muensteri* AGASSIZ, 1843 (skeletal remains and isolated teeth) from the Oxfordian of Suisse, Kimmeridgian of Baden-Württemberg, and Tithonian of Bavaria (Fig. 4a, b), and *Notidanus eximius* WAGNER, 1861 and *Notidanus intermedius* WAGNER, 1861 from the Tithonian of Bavaria. However, the latter species is based solely on a pathological lower tooth that belongs to *Notidanus serratus* (SCHWEIZER 1964: p. 78) (Fig. 4c). Two species, *Notidanus huegeliae* MÜNSTER, 1843 and *Notidanus serratus* FRAAS, 1855 were reported from the Kimmeridgian of Baden-Württemberg.

Most of the taxa are based on isolated teeth (except *Notidanus muensteri*) and MAISEY (1986b) and WARD & THIES (1987) presented revisions. WARD & THIES (1987) identified a serrated and an unserrated Early Jurassic hexanchid, *Hexanchus? wiedenrothi* and *Notidanus arzoensis* respectively. Similarly, there is a hexanchid with serrated (*Notidanus serratus*) and unserrated teeth (*Notidanus muensteri*) in the Middle to Late Jurassic (Fig. 4b, c). PFEIL (1983) introduced the genus *Eonotidanus* based on *Notidanus contrarius* to include all Jurassic hexanchids. Because of the incomplete nature of the holotype, this view was refuted by MAISEY (1986b), WARD &

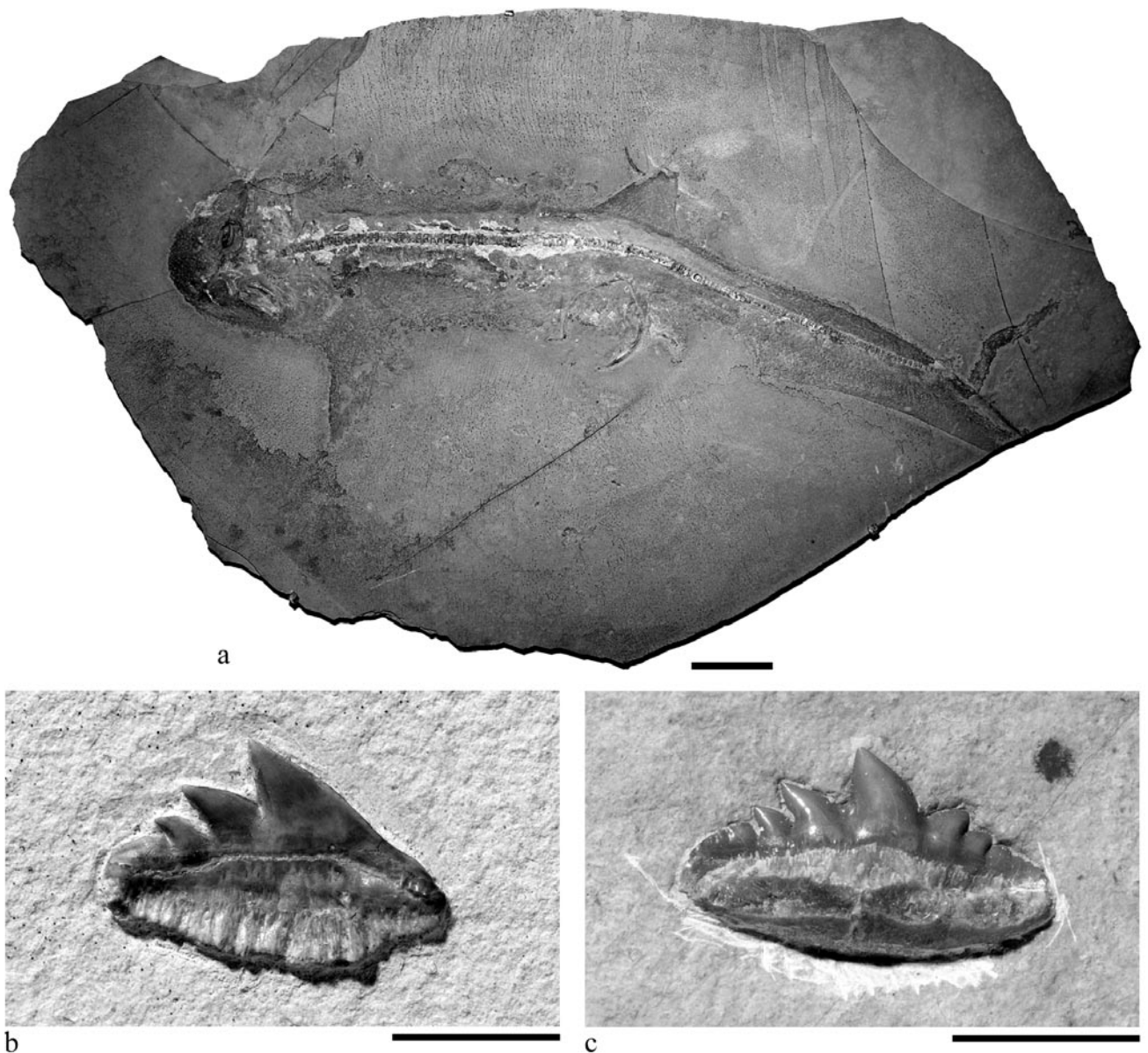
THIES (1987), and CAPPETTA (1990). These authors state that the morphology falls well within the expected range of heterodonty of all Jurassic hexanchids; furthermore, the morphology is plesiomorphic. Consequently, MAISEY (1986b) referred *N. muensteri*, which was assigned to *Eonotidanus* by PFEIL (1983), to the genus *Notidanoides* based on skeletal aspects. This view has been accepted by most authors (but see also discussion in CAPPETTA 1990: p. 47). *N. arzoensis*, *N. eximius*, *N. huegeliae*, and *N. daviesi* are considered to be junior subjective synonyms of *N. muensteri*.

The genus *Paranotidanus* was first mentioned in WARD & THIES (1987) but rejected by CAPPETTA (1990), because no holotype was designated and no diagnosis provided. Although this is correct, UNDERWOOD & WARD (2004) considered the passage in WARD & THIES (1987: p. 93) ‘... species differ from *Notidanoides* in having serrations on the base of the mesial cutting edge of the principle cusp ...’ to constitute a generic diagnosis and the first species listed by WARD & THIES (1987) to be the type species (*Notidanus serratus*). However, according to the rules of zoological nomenclature (ICZN, paragraphs 10, 11, and 15), this does not represent a valid diagnosis. Consequently, the name *Paranotidanus* is considered a *nomen nudum* and we use *Eonotidanus* for *N. serratus* in quotation marks pending further evaluation. Nevertheless, two hexanchids can be distinguished in the Upper Jurassic of southern Germany contrary to the view of LEIDNER & THIES (1999) and others: *Notidanoides muensteri*, which was based on isolated teeth but is also known by some skeletons from the Oxfordian of Switzerland, Kimmeridgian of Nusplingen, and lower Tithonian of Bavaria (Fig. 4a), and “*Eonotidanus*” *serratus* from the Kimmeridgian of Nusplingen and Tithonian of Mühlheim near Solnhofen. “*Eonotidanus*” *serratus* was also reported from the Oxfordian of England (WOODWARD 1866).

### 3.3. Protospinacidae

*Protospinax* is one of the most enigmatic and problematic selachians from the Upper Jurassic of southern Germany (CARVALHO & MAISEY 1996). This shark is represented not only by isolated teeth but also by several complete skeletons (Fig. 5). WOODWARD (1919) placed it in its own family, Protospinacidae, and indicated similarities to squalomorphs (= “Spinacidae”) but also to contemporaneous batoids (e.g., *Belemnobatis*). SAINT-SEINE (1949) regarded *Protospinax* as sister group of all living and fossil batoids. These views were retained to some extent by subsequent authors. For instance, COMPAGNO (1973) stated that *Protospinax* might represent a link between squalomorphs and batoids with *Protospinax* being a possible ancestor of batoids. MAISEY (1976) contributed to the confusion of the taxonomic affinities by transferring the type-specimen (BMNH P.8775) and a second specimen (BSP 1963 I 19) of *Protospinax annectans* WOODWARD 1919 (the type-species of *Protospinax*) to the batoid genus *Belemnobatis*. In addition, he erected a new genus, *Squalogaleus*, for a third specimen that is kept in the Natural History Museum, London, and was described and figured by WOODWARD (1919: p. 233, pl. 1, fig. 3, 3a).

The interpretation of the systematic position of *Protospinax annectans* was refuted by CAPPETTA (1987) who noted that the similarities in pectoral fin morphology between *Protospinax* and *Belemnobatis* represent convergent developments and



**Figure 4:** Hexanchiformes. **a:** *Notidanoides muensteri* AGASSIZ, 1843 (BSP 1964 XXIII 157) from the lower Tithonian of Eichstätt (Bavaria). Scale bar = 10 cm. **b:** Isolated teeth of *Notidanoides muensteri* AGASSIZ, 1843 (BSP 1989 XI 2) from the Kimmeridgian of Daiting (Bavaria). Labial view. Scale bar = 1.0 cm. **c:** Tooth of “*Eonotidanus*” *serratus* O. FRAAS, 1855 (BSP AS I 1159, holotype of *Notidanus intermedius* WAGNER, 1861) from the Tithonian of Mühlheim / Solnhofen (Bavaria). Lingual view. Scale bar = 1.0 cm.

are adaptations to a benthic life-style, a view subsequently accepted. *Squalogaleus* was considered to be a plesiomorphic galeomorph (MAISEY 1976), in which fin spines were retained, but was later interpreted as squalomorph (MAISEY 1980; CAPPETTA 1987). SHIRAI (1992a: p. 119) evaluated the relationships of squalomorphs with cladistic methods and a more detailed analysis was presented by CARVALHO & MAISEY (1996) using an improved data set of anatomical characters. They conclude that *Protospinax* must be placed high up in the squalan clade and represents the sister group of all extant hypnosqualeans (squatinooids, pristiophorooids, and batoids).

Although the systematic position of *Protospinax* might thus be regarded as resolved, problems emerge when molecular data are used to establish the relationships of extant sharks, skates, and rays (see above). Hypotheses derived from these data do not support a hypnosqualean clade. Furthermore, it is not

possible to resolve the phylogenetic position of *Protospinax* when combining the morphological and molecular data (J.K. in prep.). Consequently, we regard the systematic position of *Protospinax* as unresolved but agree that protospinacids are closely related to at least some squalomorphs.

The validity of *Squalogaleus* was strongly doubted by THIES (1983) who regarded it as a junior synonym of *Protospinax*. CAPPETTA (1987), on the other hand, accepted the validity of *Squalogaleus* and presented a range of dental characters to distinguish between the teeth of *Protospinax* and *Squalogaleus*. DUFFIN (1993) and KRIWET (1998, 2003) also supported retention of both *Protospinax* and *Squalogaleus*. UNDERWOOD (2002), on the contrary, supports THIES' (1983) interpretation and regards the holotype of *Squalogaleus* as a juvenile specimen of *Protospinax annectans*.

Because we were not able to identify skeletal characters in



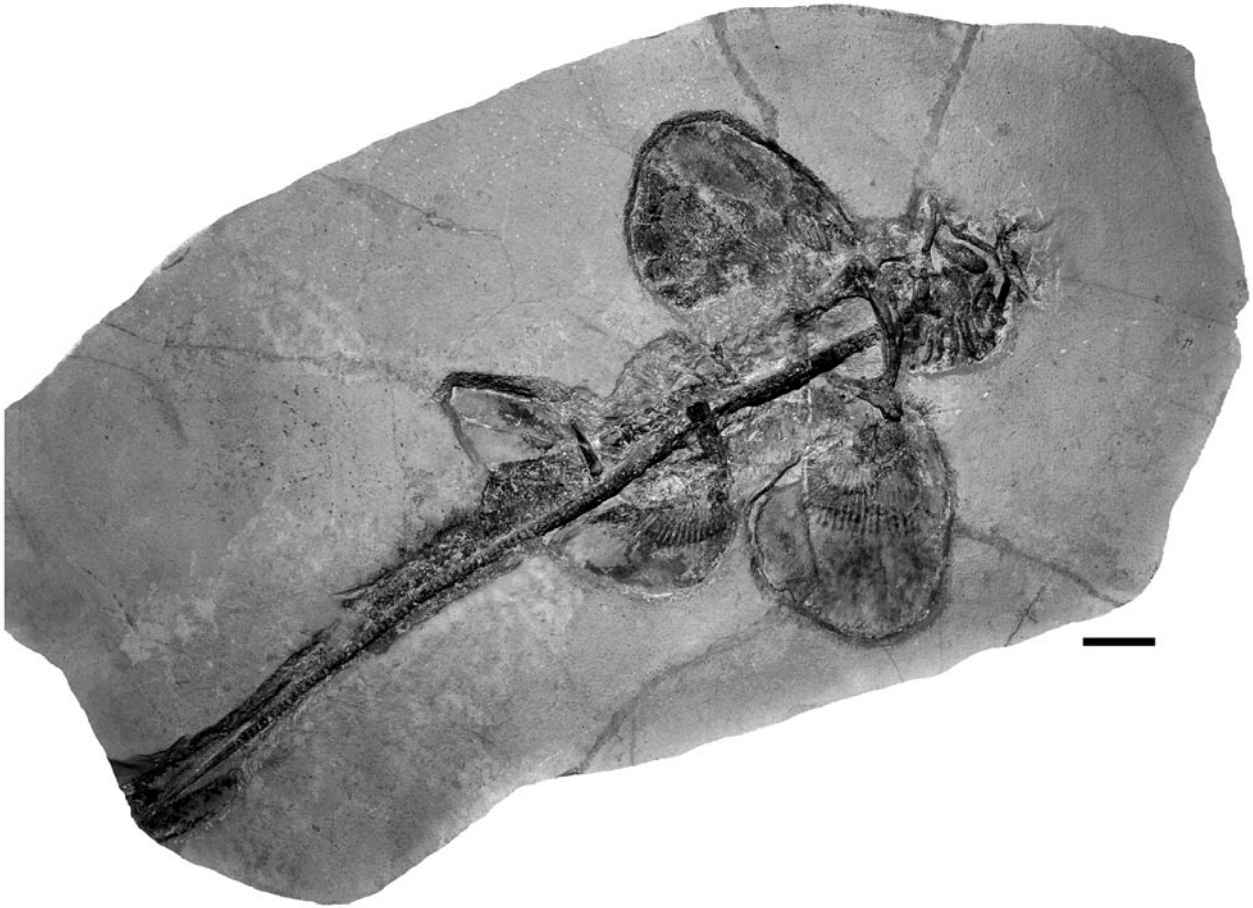


Figure 5: *Protospinax annectans* WOODWARD, 1919 (BSP 1963 I 19) from the lower Tithonian of Eichstätt. Ventral view. Scale bar = 10 cm.

the holotype of *Squalogaleus* (BMNH 37014) in order to exclude it from *Protospinax*, we tentatively agree with UNDERWOOD (2002) and submit that *Squalogaleus woodwardi* be treated as a junior synonym of *Protospinax annectans*.

Larger samples of isolated teeth render species differentiation difficult because of the extreme variability, especially in the morphology of the central vascular root canal. This character was used in the past to separate teeth of *Protospinax* (holaulacorhize) from teeth of *Squalogaleus* (hemiaulacorhize) (e.g., CAPPETTA 1987), a supposition that cannot be retained. According to UNDERWOOD & WARD (2004), the morphology of the vascular canal differs between species but also within species of *Protospinax* indicating ontogenetic variation. Isolated teeth of *Protospinax* are quite common in Jurassic sediments (e.g., DUFFIN 1993; KRIWET 1998; UNDERWOOD 2002; KRIWET 2003; UNDERWOOD & WARD 2004), but only seven species have been identified to date, four of which from Middle Jurassic strata. Late Jurassic species are: *P. lochensteinensis* THIES, 1983 from the Oxfordian of Buchsteige, Baden-Württemberg, *P. planus* UNDERWOOD, 2002 from the Kimmeridgian of England, and *P. annectans* from the Tithonian of Bavaria. *Protospinax annectans* is the only protospinacid known from entire skeletons. Teeth attributed to *P. annectans* from the Callovian of England (THIES 1983) and the Oxfordian of Baden-Württemberg (DUFFIN 1993) might represent a different species (UNDERWOOD 2002). Additional teeth of yet unnamed species occur in the Callovian of Poland (KRIWET 2003). In the new Kimmeridgian locality of Mahlsetten, teeth of *Protospinax* are amongst the most

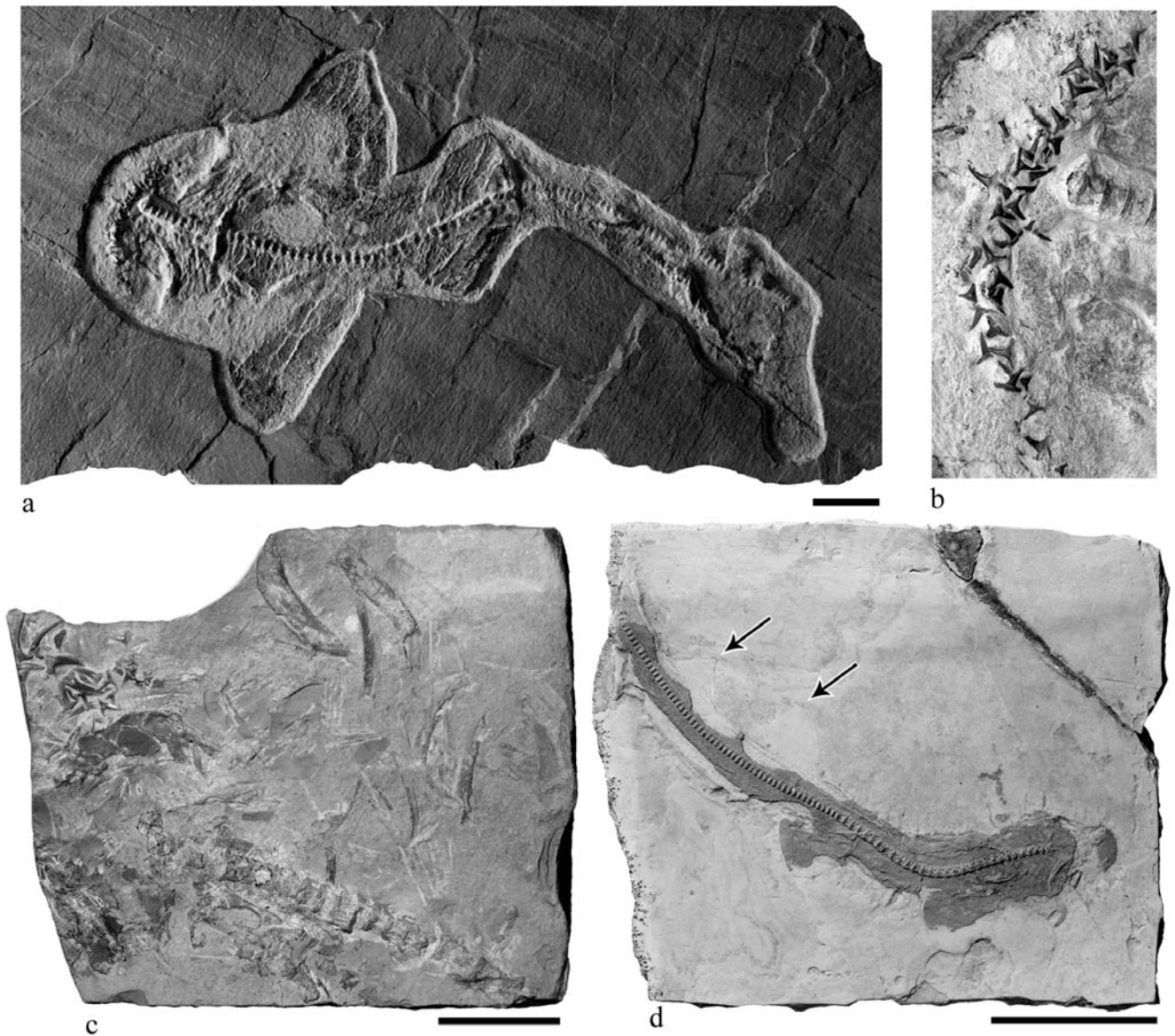
common and provably represent five distinct species.

This short review of *Protospinax* and *Squalogaleus* species exemplifies the problems we are dealing with momentarily. A detailed description of the dentition of articulated specimens of *Protospinax* housed in the Natural History Museum, London, and the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, will help in solving the problems.

### 3.4. Synechodontiformes

The taxonomy of *Palaeospinax*, *Synechodus*, and *Paraorthacodus* has been controversial and confusing (e.g., WOODWARD 1889; CAPPETTA 1973, 1987, 1992; HERMAN 1977; THIES 1991, 1992, 1993; LEIDNER & THIES 1999). 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 and demonstrated that the teeth of *Palaeospinax* and *Synechodus* display the same morphology and all material of *Palaeospinax* was consequently attributed to *Synechodus*.

Twenty-one species, ranging from the Late Triassic to Palaeocene, were attributed to *Synechodus* (DUFFIN & WARD 1993; UNDERWOOD 2002; KRIWET 2003; UNDERWOOD & WARD 2004). The validity of *Paraorthacodus* was confirmed by DUFFIN & WARD (1993) and SIVERSON (1992) who presented a range of dental characters to distinguish both and assigned at least 15 species to *Paraorthacodus*. A few additional, still undescribed species occur in the Late Jurassic and Cretaceous (SIVERSON



**Figure 6a:** *Sphenodus macer* (QUENSTEDT, 1851) (SMNS 80142/44) from the upper Kimmeridgian of Nusplingen (Baden-Württemberg). Scale bar = 10 cm. **b:** Close up of dentition of specimen SMNS 80142/44. **c:** Holotype of *Sphenodus nitidus* WAGNER, 1861 (BSP AS VII 647) from the lower Tithonian of Solnhofen (Bavaria). Scale bar = 5.0 cm. **d:** *Synechodus* sp. (BSP 1878 VI 6) from the lower Tithonian of Solnhofen (Bavaria). Arrows point to impressions of the two dorsal fins. Scale bar = 5.0 cm.

1997; S.K. & J.K. in prep.).

The main distinctive feature of the teeth of *Synechodus* is that the lateral cusplets are not as strongly separated from the main cusp as in *Paraorthacodus* and that the labial face is cambered and overhangs the crown/root junction. In addition, the teeth of *Paraorthacodus* possess rather high and acute lateral cusplets and more or less well-developed vertical ridges on the labial and lingual crown faces.

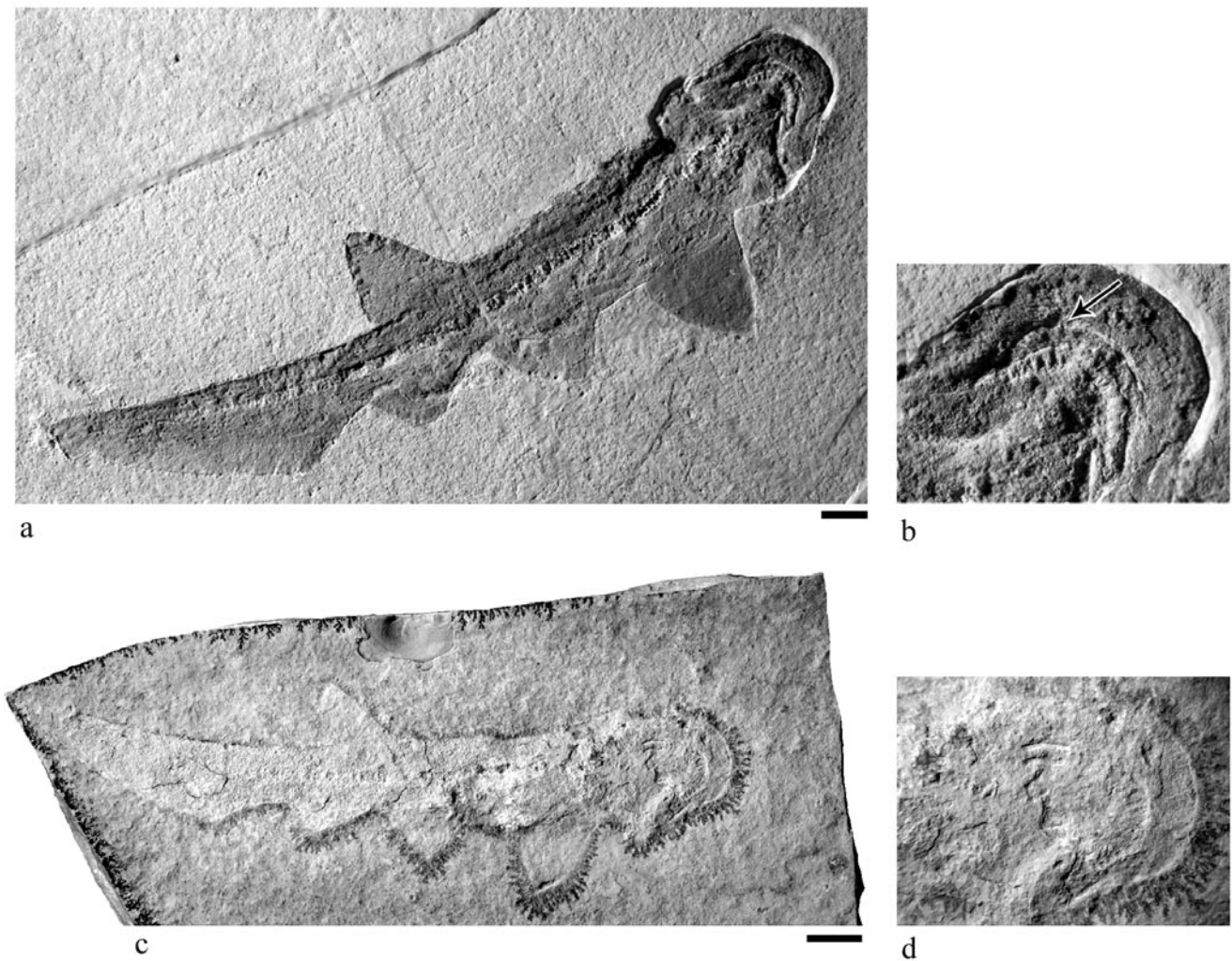
DUFFIN & WARD (1993) placed *Synechodus* and *Paraorthacodus* in the family Paraorthacodontidae, which in turn was united with the family Orthacodontidae (with its single genus *Sphenodus*) in the order Synechodontiformes. The assignment of the Middle Triassic selachian *Mucrovenator* CUNY et al., 2001 to the Synechodontiformes was disputed by KRIWET (2003) based on the absence of the very characteristic deep grooves that are separated by laminae on the labial root face and a less developed bulge of the labial crown face.

UNDERWOOD & WARD (2004) identified another possible Jurassic-Cretaceous synechodontiform, *Pseudonotidanus*, which combines dental features of both hexanchiforms (shape of the crown) and synechodontiforms (lingually expanded, flat-based root). Three species, *Palaeospinax politus* THIES, 1992 from the Toarcian of southern Germany, *Pseudonotidanus semirugosus* UNDERWOOD & WARD, 2004 from the Bathonian of England, and *Welcomia bodeuri* CAPPETTA, 1990 from the Valnginian of France were included in this genus. The skeleton of *Pseudonotidanus politus* differs from that of hexanchiforms in having at least one spine that supports the posterior dorsal fin.

We adopt the systematic scheme of DUFFIN & WARD (1993) and UNDERWOOD & WARD (2004) and consequently distinguish three synechodontiform genera, *Sphenodus*, *Synechodus*, and *Paraorthacodus* in the Upper Jurassic of southern Germany.

At least 24 species, ranging from the Early Jurassic to the Palaeocene, were referred to *Sphenodus* (DE BEAUMONT





**Figure 7:** *Paraorthacodus* sp. **a:** Specimen BSP 1996 I 31 from the lower Tithonian of Eichstätt (Bavaria). **b:** Close up of head of specimen BSP 1996 I 31. Ventral view. Arrows point to preserved lower and upper dentition. **c:** Specimen BSP 1894 X 5 from the lower Tithonian of Eichstätt (Bavaria) **d:** Close up from head of specimen BSP 1894 X 5. Ventral view. Scale bars = 1.0 cm.

1960a; DUFFIN & WARD 1993), most of which have been erected based on isolated teeth. Skeletal material of Late Jurassic taxa of southern Germany is known only from *S. macer* and *S. nitidus*. *Sphenodus macer* (Fig. 6a, b) is known from skeletal remains, isolated teeth, and a complete specimen from the middle Oxfordian and Kimmeridgian of Baden-Württemberg, e.g., Nusplingen (SCHWEIZER 1964; BÖTTCHER & DUFFIN 2000). The second species, *S. nitidus* (Fig. 6c) was instituted based on a partial skeleton from the lower Tithonian of Solnhofen (WAGNER, 1861). This species also occurs in the Oxfordian and Kimmeridgian of Baden-Württemberg, including Nusplingen (BÖTTCHER & DUFFIN 2000).

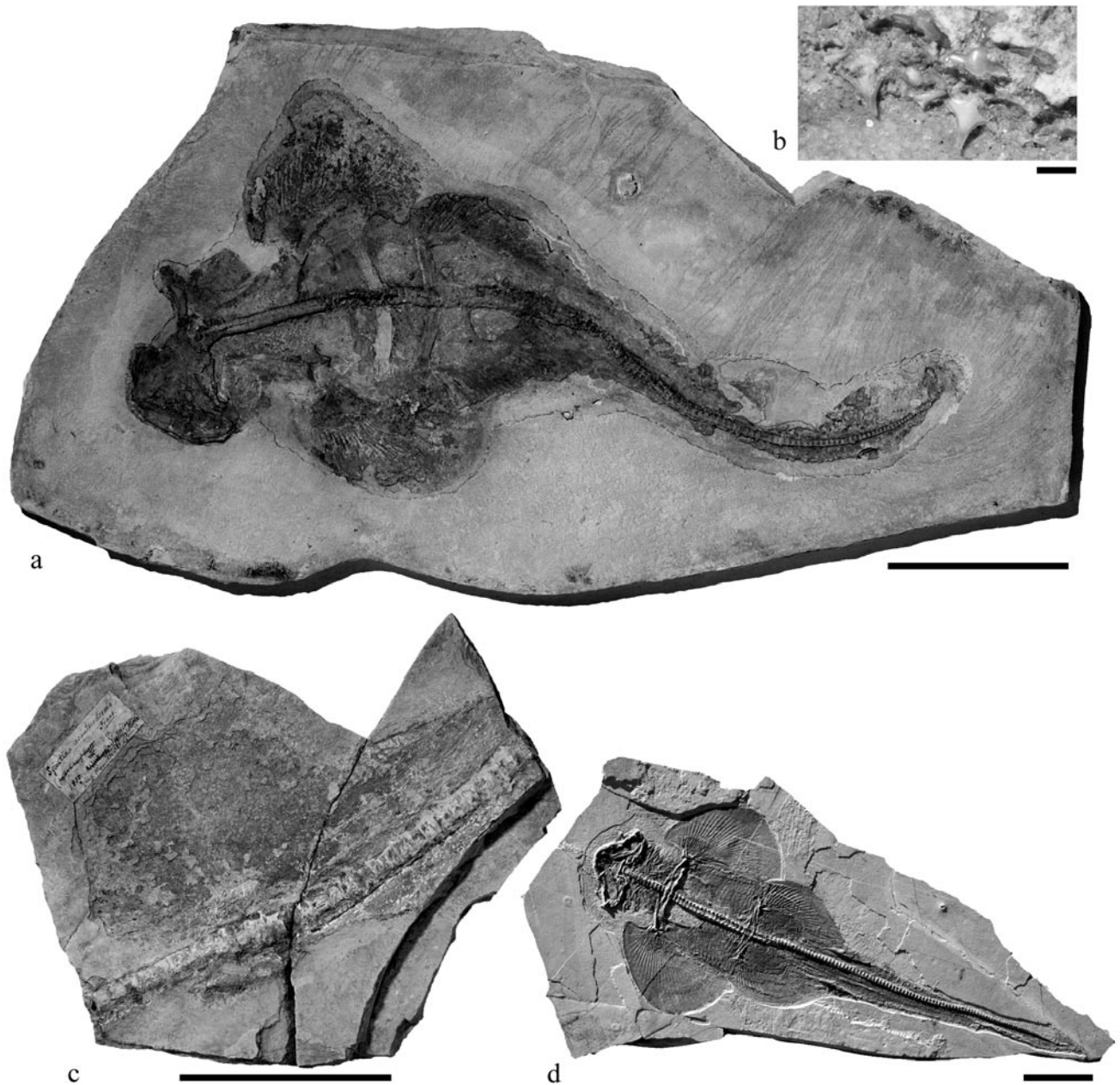
The body of *Sphenodus macer* is fusiform and bears two sub-triangular and well separated dorsal fins (Fig. 6a). The second dorsal fin is considerably smaller than the first one. The first dorsal fin inserts above and immediately behind the large and triangular pectoral fins, the second directly overlies the small anal fin. The pelvic fins lie just behind the first dorsal fin. Pectoral, pelvic, and anal fins decrease in size posteriorly. The anal fin is well separated from the caudal fin. The caudal fin is incompletely preserved but displays the asymmetrical outline with an elongated upper and shorter ventral lobe.

There are no dorsal fin spines. The vertebrae are of the astero-spondylic type.

*Sphenodus nitidus* WAGNER, 1861 differs from *S. macer* in dental features. The teeth are higher and have narrower roots, the distal cutting edge of the cusp is considerably shorter than the mesial one, and the cusp displays a stronger torsion in anterior view (Fig. 6b, c).

The differences in tooth and general morphology and geographic distribution of the two species indicate that *S. macer* with its clutching-type dentition was living very near to, or directly on, the bottom (BÖTTCHER & DUFFIN 2000). Conversely, *S. nitidus* with its tearing-type dentition and wider distribution was adapted to, free-swimming preying on teleosts and probably inhabited the mid- to surface waters.

Paraorthacodontids are comparably rare in the Upper Jurassic of southern Germany. Most species referred to *Synechodus* are mainly based on isolated teeth. Skeletal material has been presented only for three species up to date, *S. dubrisiensi* (the type-species) from the Lower Cretaceous of England, and *S. enniskilleni* and *S. occultidens* from the Lower Jurassic of England (e.g., MAISEY 1985; DUFFIN & WARD 1993). *Synechodus enniskilleni* possesses two dorsal fins that are rather narrow



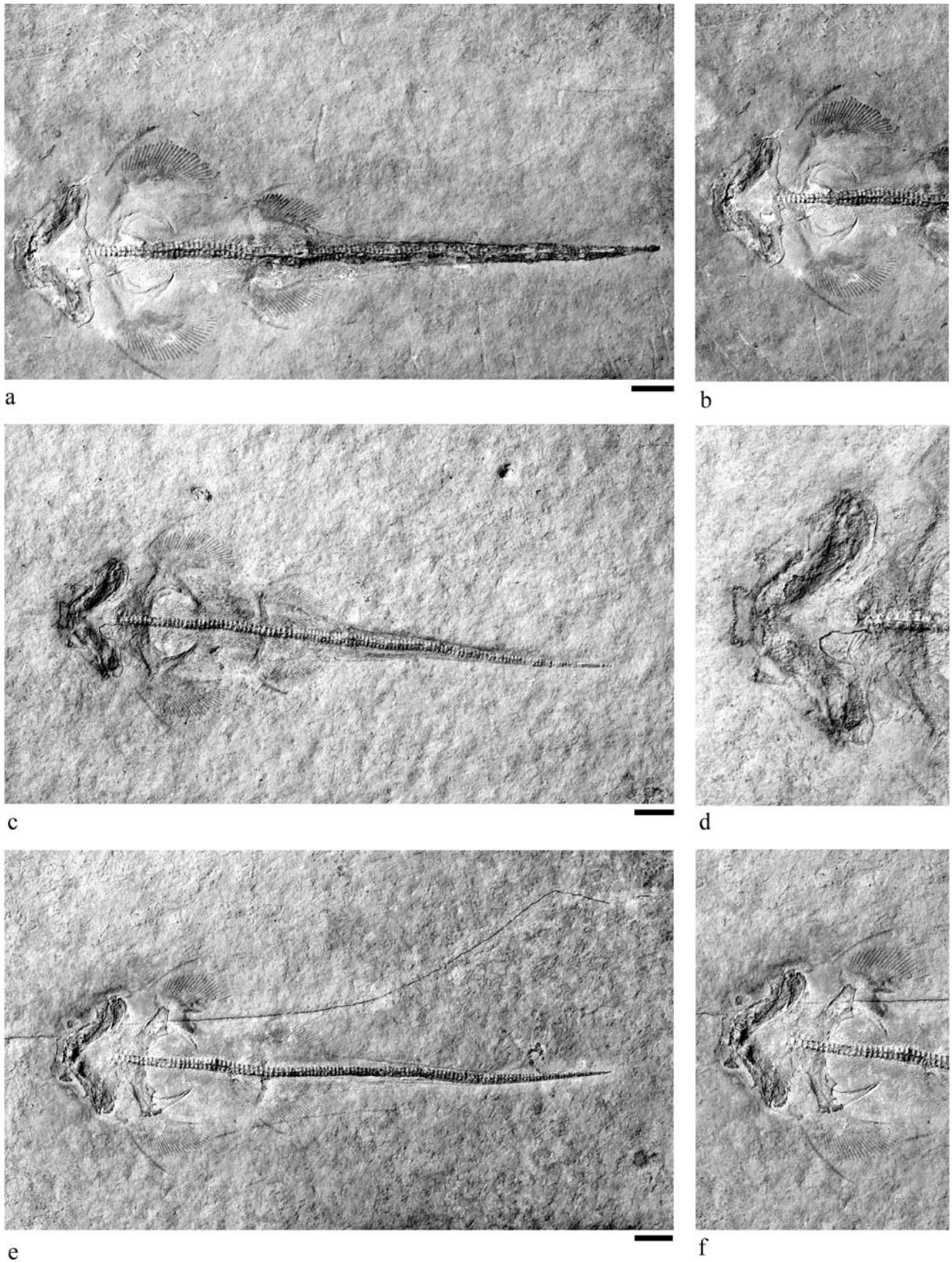
**Figure 8:** Adult specimens of *Squatina alifera* MÜNSTER, 1842. **a-b:** Holotype (BSP AS VII 3) from the lower Tithonian of Eichstätt (Bavaria). **a:** Ventral view of entire specimen. Scale bar = 10 cm. **b:** Close up of anterior-lateral teeth. Scale bar = 0.1 cm. **c:** Pectoral fin of specimen BSP AS I 1366 from the upper Kimmeridgian of Nusplingen (Baden-Württemberg). Scale bar = 10 cm. **d:** *Squatina acanthoderma* (O. FRAAS, 1854) (SMNS 80431/20) from the upper Kimmeridgian of Nusplingen (Baden-Württemberg). Scale bar = 10 cm.

and sub-equal in size. The first dorsal fin inserts above and just behind the rather large pectoral fin. The pelvic and anal fins insert well behind the first and second dorsal fins respectively. The caudal fin is rather short and heterocercal with comparably short upper and lower rounded lobes. The vertebrae are of the cyclospondylic to asterospondylic type (DUFFIN & WARD 1993).

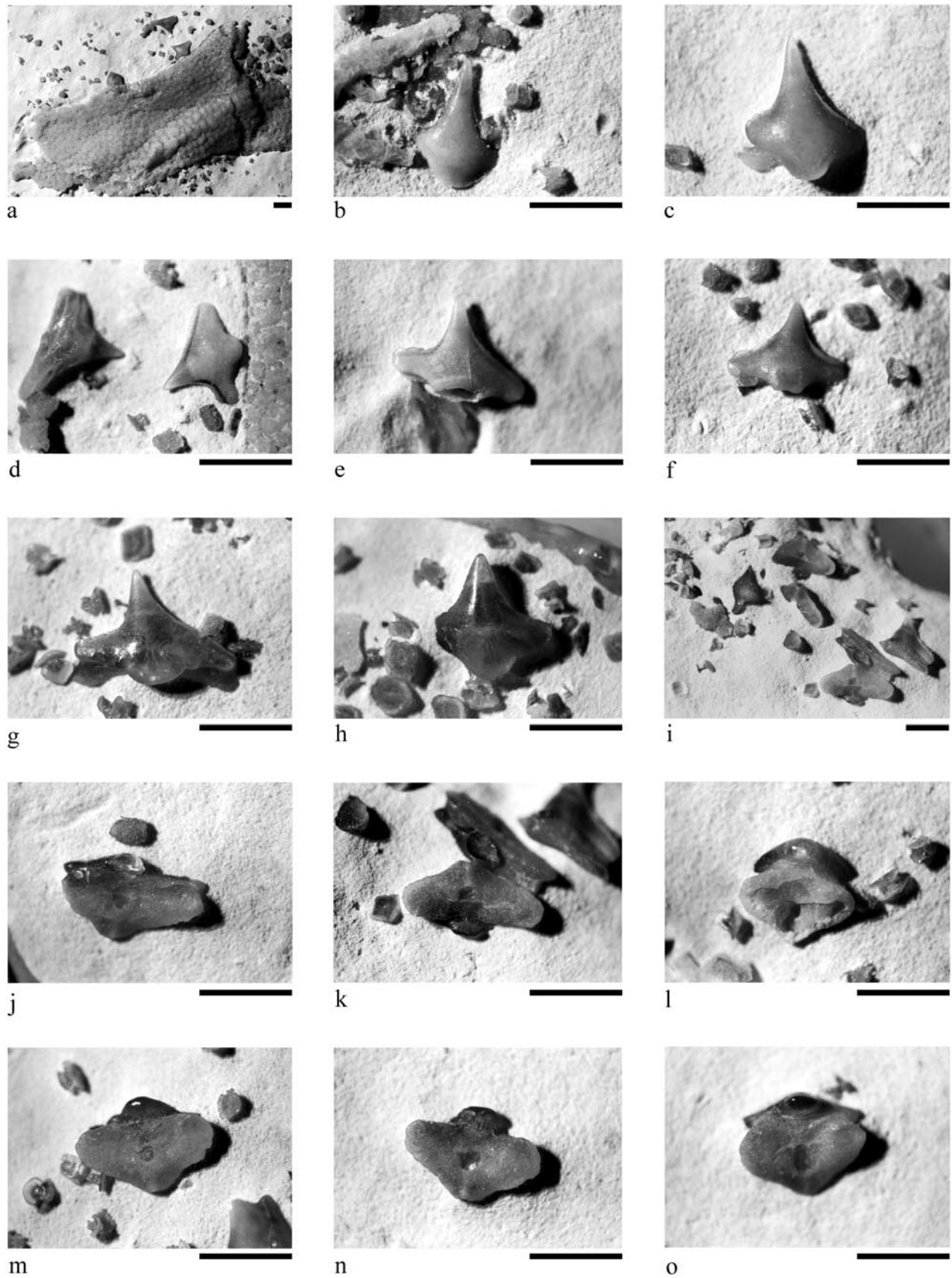
The occurrence of fin spines in *Synechodus* remains elusive. DUFFIN & WARD (1993) noted in their revised diagnosis of this genus that fin spines are present in some species contrary to MAISEY (1975), who did not find fin spines. UNDERWOOD & WARD (2004) indicated the possible presence of a smooth fin spine in a specimen of *S. dubrisiensis*. The fin spines of *S. enniskilleni* are, conversely, not completely smooth (DUFFIN

& WARD 1993: pl. 3).

No species of *Synechodus* has been named to date from the Upper Jurassic of southern Germany. LEIDNER & THIES (1999) were the first to figure a characteristic tooth from a complete specimen derived from the lower Tithonian of the Solnhofen area that represents a new species. In addition, a complete small specimen in Munich, BSP 1878 VI 6 (Fig. 6d), was also identified as *Synechodus* sp. (written information on label by D. THIES). Unfortunately, all teeth were removed from this specimen so that this identification cannot be confirmed at the moment. Remarkably, the specimen displays two dorsal fins without preceding spines (Fig. 6d). This discovery coincides with the statement of DUFFIN & WARD (1993) that fin spines are unequally distributed among the species of *Synechodus*,

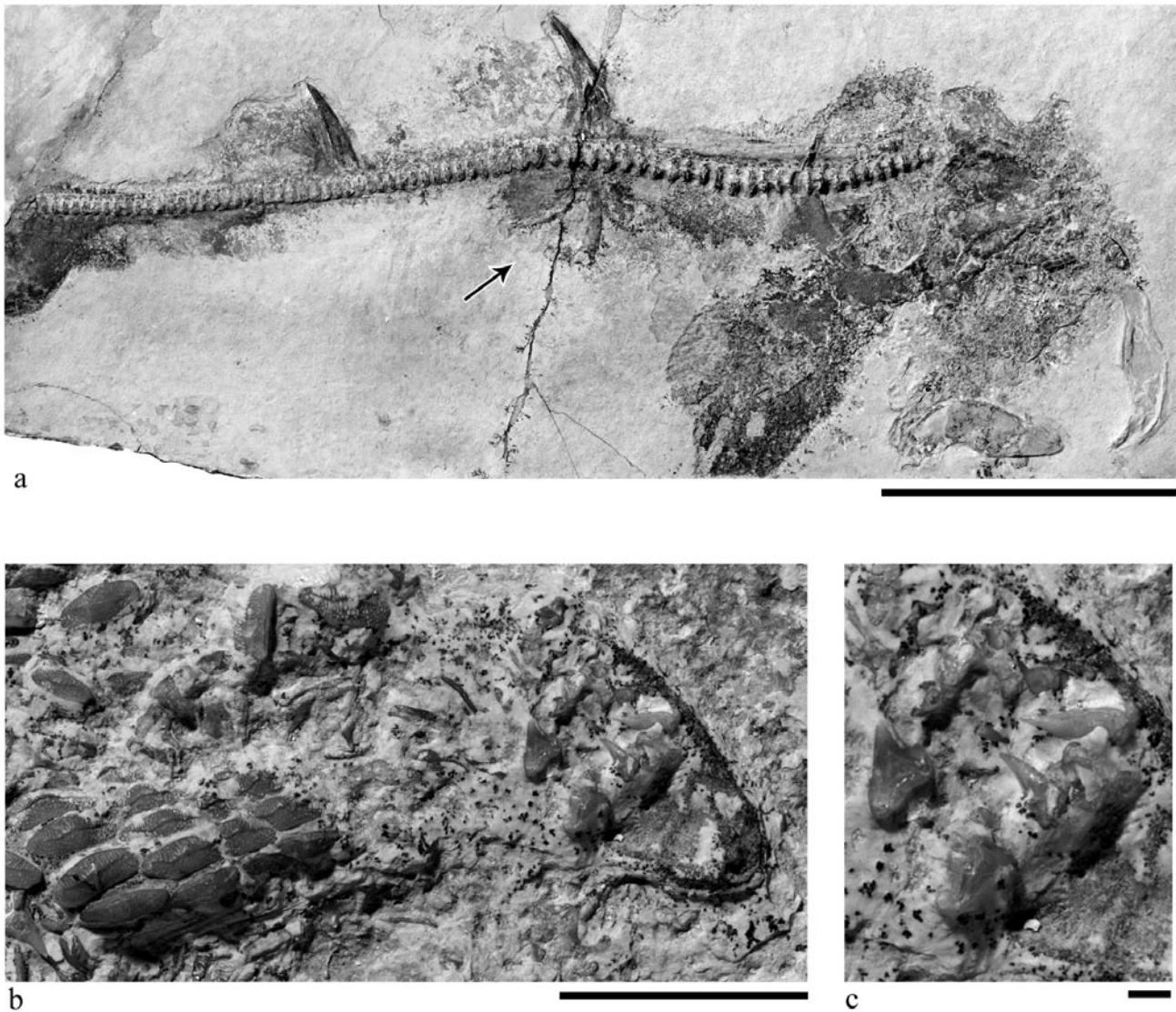


**Figure 9:** Juvenile specimens of *Squatina alifera* MÜNSTER, 1842 (syn. *S. speciosa*) from the lower Tithonian of Eichstätt (Bavaria). Ventral views. All scale bars = 1.0 cm. **a:** Specimen BSP AS I 1368. **b:** Close up of anterior portion of specimen BSP AS I 1368. **c:** Specimen BSP AS I 817. **d:** Close up of anterior portion of specimen BSP AS I 817. **e:** Specimen BSP AS I 1367. **f:** Close up of anterior portion of specimen BSP AS I 1367.



**Figure 10:** Disarticulated dentition of *Squatina alifera* MÜNSTER 1842 (PIMUZ AS II 3050) from the lower Tithonian of Eichstätt (Bavaria) displaying morphological variation. Scale bars = 0.1 cm. **a:** Portion of Meckelian cartilage with lower teeth. **b:** Anterior tooth, labial view. **c:** Antero-lateral tooth, labial view. **d:** Upper and lower lateral teeth, lingual view. **e:** Lower lateral tooth displaying incipient lateral cusplets, lingual view. **f:** Lateral tooth, labial view. **g-h:** Lateral teeth, labial view. **i:** Scattered lateral teeth. **j-k:** Lateral teeth, basal views. **l:** Posterior? tooth, basal view. **m-n:** Lateral teeth, basal views. **o:** Latero-posterior tooth, basal view.





**Figure 11:** Holotype of *Paracestracion falcifer* (WAGNER, 1861) (BSP AS VI 505) from the lower Tithonian of Solnhofen (Bavaria). Adult specimen. **a:** Lateral view. Arrow points to position of pelvic fin. Scale bar = 10 cm. **b:** Close up of the dentition displaying molariform and cuspidate anterior teeth. Scale bar = 1.0 cm. **c:** Close up of anterior teeth. Scale bar = 0.1 cm.

but also indicates that *Synechodus*, as currently understood, might represent a paraphyletic taxon.

A single species of *Paraorthacodus*, *P. jurensis* (SCHWEIZER, 1964), has been described from the lithographic limestones of southern Germany. This species is represented by the anterior disarticulated 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 synechodontiform teeth from the Kimmeridgian of Mahlstetten and a re-evaluation of dental characters of *Paraorthacodontidae* by one of us (S.K.) also support its assignment to *Paraorthacodus*. Two additional complete specimens of a new species of *Paraorthacodus* are kept in the collections of the Jura Museum Eichstätt and the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (Fig. 7).

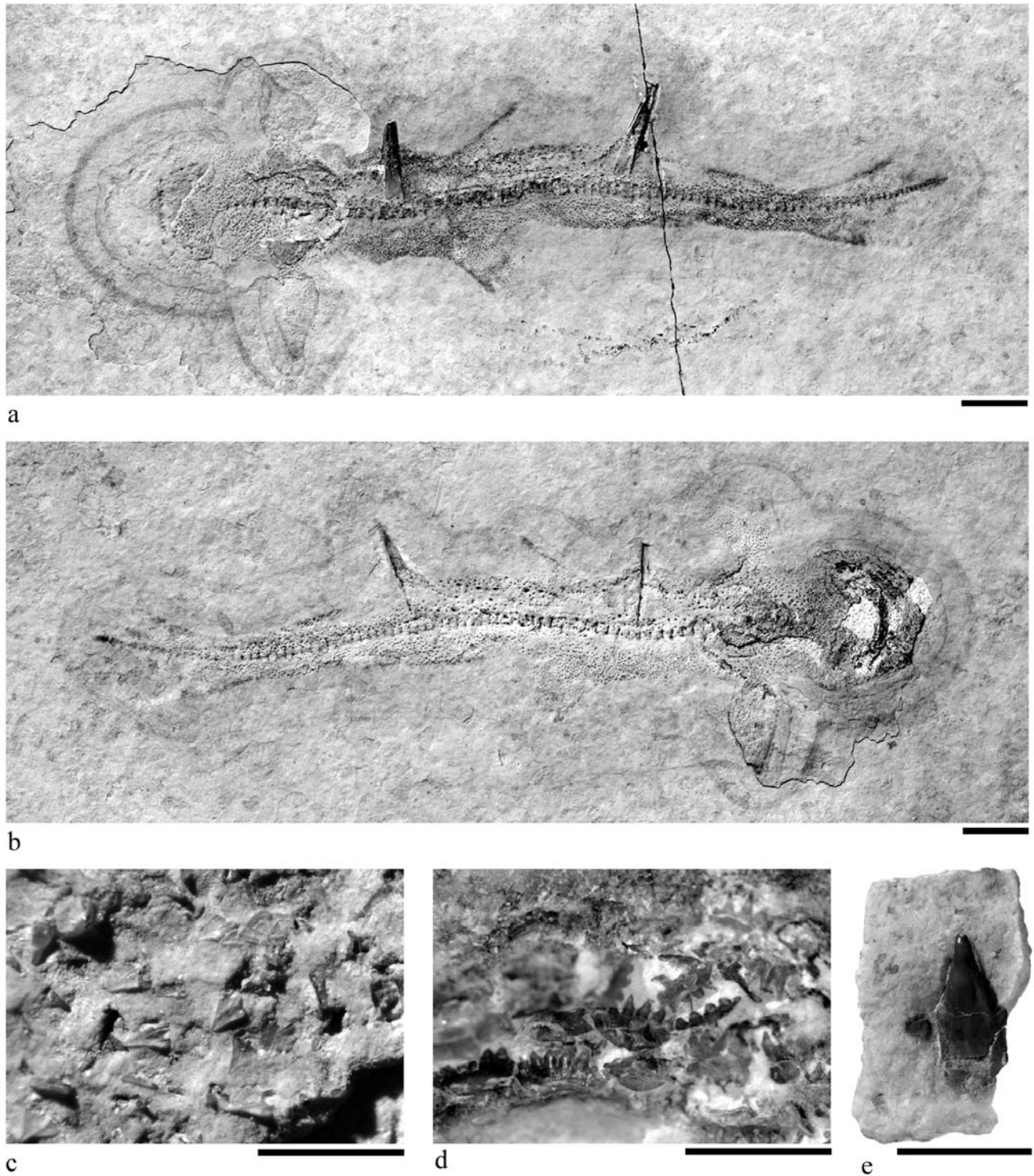
Both specimens are small (Fig. 7a, c) and display remnants of the dentition with high crowned and delicate teeth displaying up to three pairs of high, upright, and slender lateral cusplets (Fig. 7b, arrow). The ornamentation consists of numerous

vertical ridges on the labial and lingual crown faces. The most conspicuous differences to *P. jurensis* are the lack of expanded bases of the cusp and cusplets and that the enameloid is continuous basally between cusp and cusplets.

The body of the two specimens is fusiform and the rostrum is short and broad. There is a single dorsal fin that is large and triangular, and situated well back along the body just in front of the caudal fin (Fig. 7a, c). It inserts above and immediately behind the relatively big pelvic fin, which is rounded in outline. The pectoral fin is slightly larger than the dorsal fin and placed well in front of the pelvic fin. The anal fin resembles the pelvic one and is situated just in front of the caudal fin. The caudal fin is heterocercal and relatively broad without distinct subterminal notch and ventral lobe.

The carcharhiniform *Macrourogaleus* resembles the new paraorthacodontid with regard to the presence of a single dorsal fin, but differs in the position and size of the dorsal and anal fins, in having a more elongated body, and in tooth morphology (see below).





**Figure 12a-d:** *Paracestracion falcifer* (WAGNER, 1861) (BSP 1885 I 12a,b) from the lower Tithonian of Eichstätt (Bavaria). Juvenile specimen. **a-b:** Plate and counter plate. Scale bars = 1.0 cm. **c:** Close up of placoid scales from mouth corner. Scale bar = 0.1 cm. **d:** Close up of the dentition displaying anterior and antero-lateral pectinate teeth. Scale bar = 0.1 cm. **e:** Holotype of *Heterodontus semirugosus* PLIENINGER, 1847 (BSP AS I 1376) from the Kimmeridgian of Kelheim (Bavaria). Isolated anterior tooth, labial view. Scale bar = 1.0 cm.

### 3.5. Squatiniformes

Complete squatiniform skeletons are relatively abundant in the lithographic limestones of southern Germany (Figs 8, 9) and several dozen perfectly preserved specimens were recovered from Nusplingen in the last years. Three different species were identified in the 19<sup>th</sup> century.

Two species, *Squatina alifera* (MÜNSTER, 1842) (Fig. 8a, c)

and *S. speciosa* (VON MEYER, 1856) (Fig. 9), were described from the Solnhofen area and a single species, *Squatina acanthoderma* (O. FRAAS, 1854), occurs in the Nusplingen plattenkalks (Fig. 8d). *Squatina alifera* and *S. acanthoderma* differ in size, body proportions, and skeletal anatomy (DINKEL 1921). In addition, *S. alifera* has teeth with incipient lateral cusplets (Fig. 8b), which are absent in *S. acanthoderma*.

*Squatina speciosa*, the second species from the Solnhofen

area, differs from *S. alifera* primarily in being considerably smaller and more delicate (Fig. 9). Consequently, all small specimens from the Solnhofen area were attributed to this species. The validity of the three species was never seriously questioned. DINKEL (1921) was one of the few arguing that the small specimens named *S. speciosa* could be juveniles of *S. alifera* because of the small size, but eventually followed VON MEYER's (1859) opinion and concluded that they were actually adults.

Recently, LEIDNER (1997) and LEIDNER & THIES (1999) re-evaluated the dental and placoid morphology of Late Jurassic squatiniforms. They confirmed the differences in dental morphology between *S. alifera* and *S. acanthoderma* but did not find any differences in scale structure. The teeth of *S. speciosa* display lateral cusplets, and this taxon is accordingly identified as juvenile form of *S. alifera* by LEIDNER & THIES (1999). A re-examination of the specimens housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, supports this interpretation. LEIDNER & THIES (1999) indicate the presence of another, new squatinid genus in Solnhofen that is comparable to *S. acanthoderma* in tooth morphology but differs from all Late Jurassic squatinids in placoid scale morphology.

Squatinid teeth are rather rare in the Kimmeridgian of Mähle. The few teeth recovered to date so far resemble teeth of *S. acanthoderma* in their general appearance (e.g., lack of lateral cusplets). THIES (1983) indicated the presence of teeth of *Squatina* sp. in the Oxfordian of Buchsteige, Baden-Württemberg, and UNDERWOOD (2002) reported teeth of *S. alifera* and *S. ? frequens* from the Kimmeridgian of England.

Common features of all Jurassic teeth attributed to *Squatina* are the well-detached labial apron and lateral blades strongly overhanging the root (Fig. 10). These features are not found in modern *Squatina* spp. although their teeth are very similar, but this may be related to the fact that the tooth architecture of *Squatina* is rather simple and very conservative. Consequently many isolated *Squatina*-like teeth from the Jurassic and Cretaceous were assigned to squatinids (e.g., THIES 1983; BATCHELOR & WARD 1990; BIDDLE 1993; REES 2002; UNDERWOOD 2002), which resulted in taxonomic lumping of similar tooth types. Similar problems exist also in the case of the Cretaceous orectolobiform teeth. As a result, the true specific composition of orectolobiforms and squatiniforms in the Jurassic and Cretaceous is rather obscure. KRIWET (1998, 2003) and UNDERWOOD (2002) discussed this problem but did not provide any final solution. The teeth of extant squatinids and orectolobiforms share several significant characters. HERMAN et al. (1992) concluded that *Squatina* may in fact be an orectolobiform. A stable character of *Squatina* teeth could be the labial knob-like apron that is well-supported by the root in basal view and a flat basal root face. Conversely, in most (if not all) Jurassic teeth attributed to *Squatina*, the labial apron is more rectangular or broadly rounded, rather massive, and well detached from the root. In addition, the labial root depression is much more pronounced in orectolobiforms and Late Jurassic squatinids than in modern squatinids.

Additional information on the systematic position of Late Jurassic *Squatina*-like neoselachians comes from skeletal anatomy. The extant *Squatina* is characterized by many autapomorphies including skeletal and myological characters (COMPAGNO

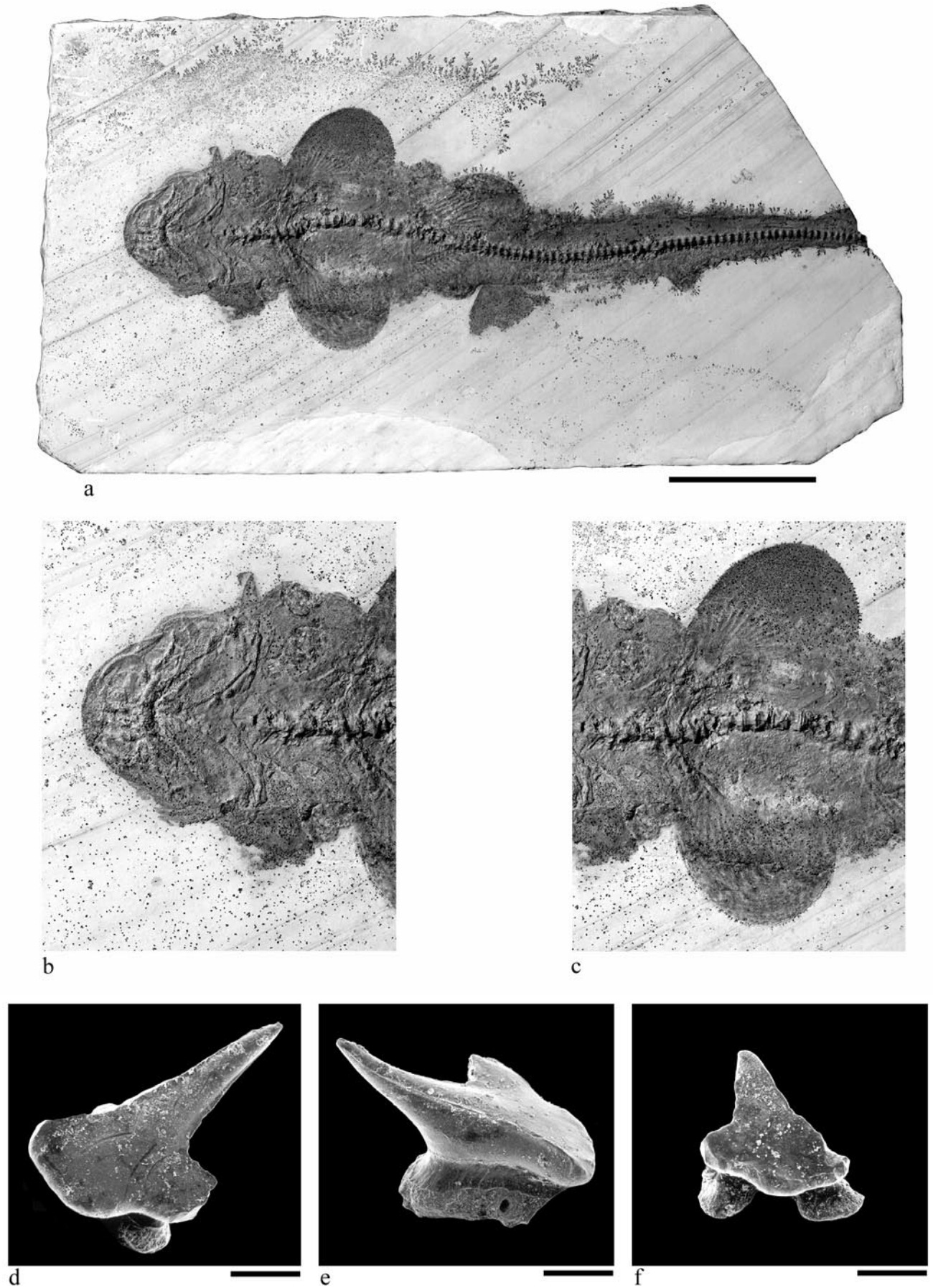
1973). Since then, several cladistic analyses of neoselachian interrelationships have been proposed providing additional information on the sister group relationships of *Squatina*. However, articulated fossils were not included in these analyses. DINKEL (1921) was one of the few who described the skeletal anatomy of fossil squatinids from the Upper Jurassic of southern Germany, but did not provide any deeper insight into their systematic position. The most conspicuous character, among others, is the morphology of the pectoral girdle and the articulation of the pectoral fin. In extant *Squatina* spp., the scapulocoracoid is strongly U-shaped (as in all sharks) with condyles that are not arranged horizontally but diagonally. The condyle for the propterygium and mesopterygium is bilobate (SHIRAI 1992b). In Late Jurassic *Squatina*-like specimens, the scapulocoracoid is less U-shaped but more angular similar to the condition found in extant and fossil batoids. In addition, the metapterygoid is posteriorly elongated. The condyles, as far as it can be ascertained, are arranged horizontal.

At the moment it remains uncertain whether all Late Jurassic *Squatina*-like species belong to the same group of neoselachians and whether they should be excluded from *Squatina* at present. The differences in dental and skeletal morphology of *S. alifera*, *S. acanthoderma*, and the still undescribed taxon (LEIDNER & THIES 1999), for instance, still have to be explained in a phylogenetic framework. Accordingly, we leave all these specimens within *Squatina* for the time being.

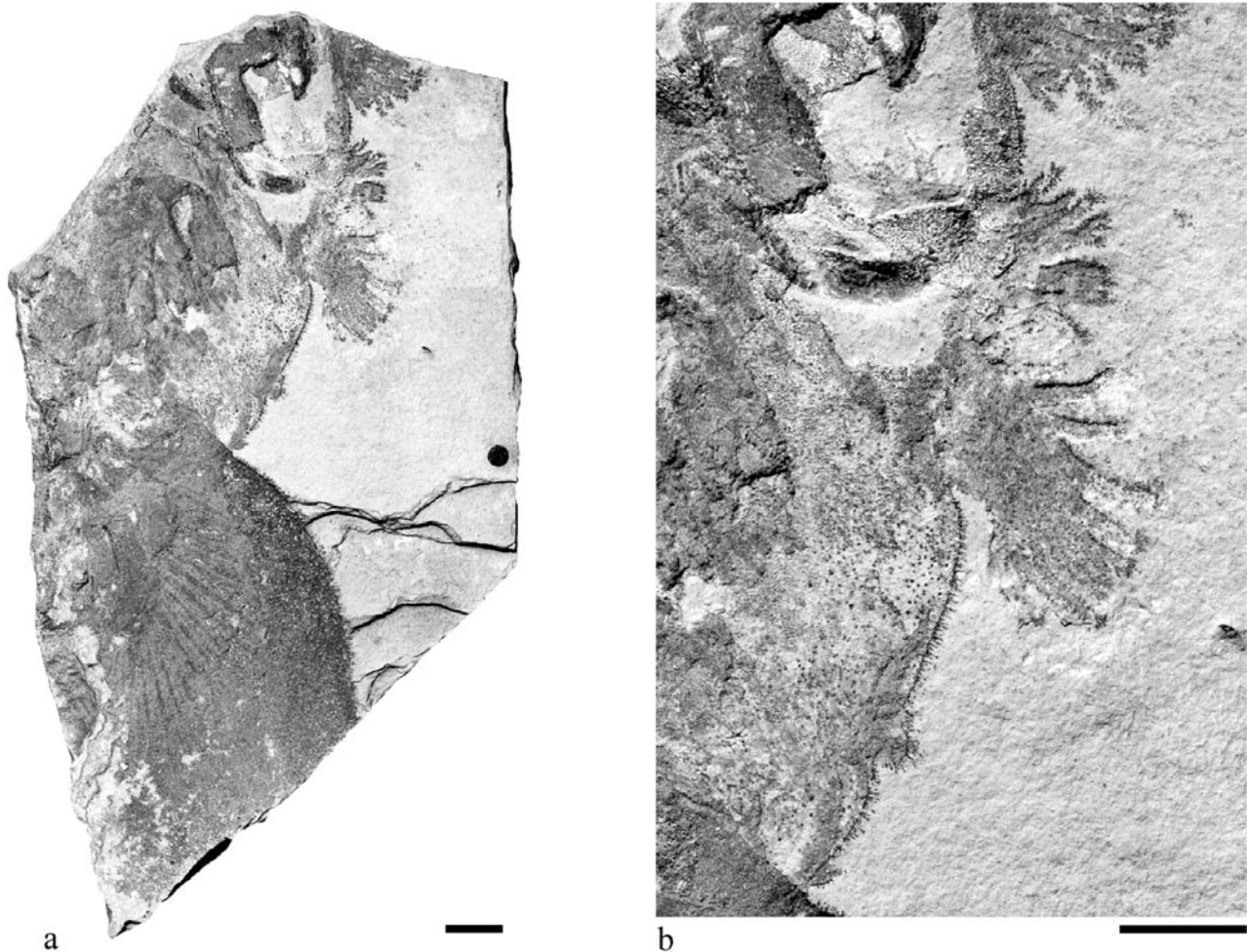
### 3.6. Heterodontiformes

Modern heterodontids (horn sharks) are represented by eight benthic species, which are confined to circum-Pacific waters (COMPAGNO 1999). Conspicuous characters are the very monognathic heterodont dentition, which is an adaptation to durophagous prey, and the presence of fin spines supporting the two dorsal fins. The fossil record of heterodontids extends back into the Jurassic and consists primarily of isolated teeth. Articulated skeletons were recorded from the Upper Cretaceous Chalk of England (e.g., WOODWARD 1889) and from the Upper Jurassic of Solnhofen (e.g., WAGNER 1857; SCHWEIZER 1964). WAGNER (1857) introduced the species *Heterodontus* (= *Cestracion*) *falcifer* for a skeleton with disarticulated head (Fig. 11). The dentition is well preserved and displays the typical heterodontid pattern. Anterior teeth have symmetrical, massive, and cuspidate crowns (Fig. 11c). The anterior teeth of juveniles are pectinate with up to six cusps. The prominent apron, which is basally concave and laterally constricted, labially overhangs the root. Lateral teeth are mesio-distally elongated, more or less curved, and lack a distinct cusp (Fig. 11b). The ornamentation of the occlusal surface is generally strong and consists of ridges and alveoli. A transverse crest is occasionally developed.

The dental characters and the presence of two dorsal fin spines in Late Jurassic heterodontids are in accordance with those seen in modern *Heterodontus* species. WAGNER (1861) incorrectly placed this specimen with the hybodontoid *Acrodus*, but the inclusion of this species in *Heterodontus* was generally accepted (e.g., WOODWARD 1889). Meanwhile, many specimens of *H. falcifer* were recovered from the lithographic limestones of the Solnhofen area and Nusplingen including numerous small exemplars (Fig. 12a-d).



**Figure 13a-c:** *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) from the lower Tithonian of Zandt near Denkendorf (Bavaria). Ventral view. Scale bar = 5.0 cm. **b:** Close up of head. **c:** Close up of shoulder girdle and pectoral fins. **d-f:** Isolated teeth of specimen BSP AS I 1364 from the lower Tithonian of Sonhofen area (Bavaria). Scale bars = 0.02 cm. **d:** Anterior-lateral tooth, labial view. **e:** Antero-lateral tooth, lateral view. **f:** Posterior tooth, labial view.



**Figure 14a:** *Corysodon cirinensis* SAINT-SEINE, 1949 (MB.f. 11191) from the lower Tithonian of Solnhofen (Bavaria). Ventral view. **b:** Close up of specimen MB.f. 11191 displaying lateral head barbels. Scale bars = 1.0 cm.

KOKEN (in ZITTEL 1911) erected the genus *Paracestracion* for *H. falcifer* based on characteristics of the fin spines (e.g., lateral tubercles) and teeth (presence of a median crest), which were subsequently recognized as unreliable (MAISEY 1982b). As a result, the validity of *Paracestracion* was not widely accepted (e.g., CAPPETTA 1987).

Nevertheless, there are important differences between extant *Heterodontus* species and Late Jurassic specimens. The pelvic fins insert almost beneath the fin spine of the first dorsal, and the pectorals are situated far anteriorly just behind the skull in most specimens of *H. falcifer* (Fig. 11a) except for one specimen that was attributed to a different species, *H. zitteli*, by EASTMAN (1914). Moreover, the fin spines are partly vascularized in *H. falcifer* (MAISEY 1982b). We therefore accept the genus *Paracestracion* as valid.

The most reliable features to distinguish isolated teeth of *Paracestracion* from those of the modern horn sharks are, apparently, dental characters. SCHWEIZER (1964: fig. 3) indicated an open nutritive groove of the root separating two narrow and mesio-distally elongated root lobes in anterior teeth of *H. falcifer* (see also UNDERWOOD 2002). Anterior teeth of juveniles and adults of *Heterodontus* always possess hemiaulacorhizan root vascularisation.

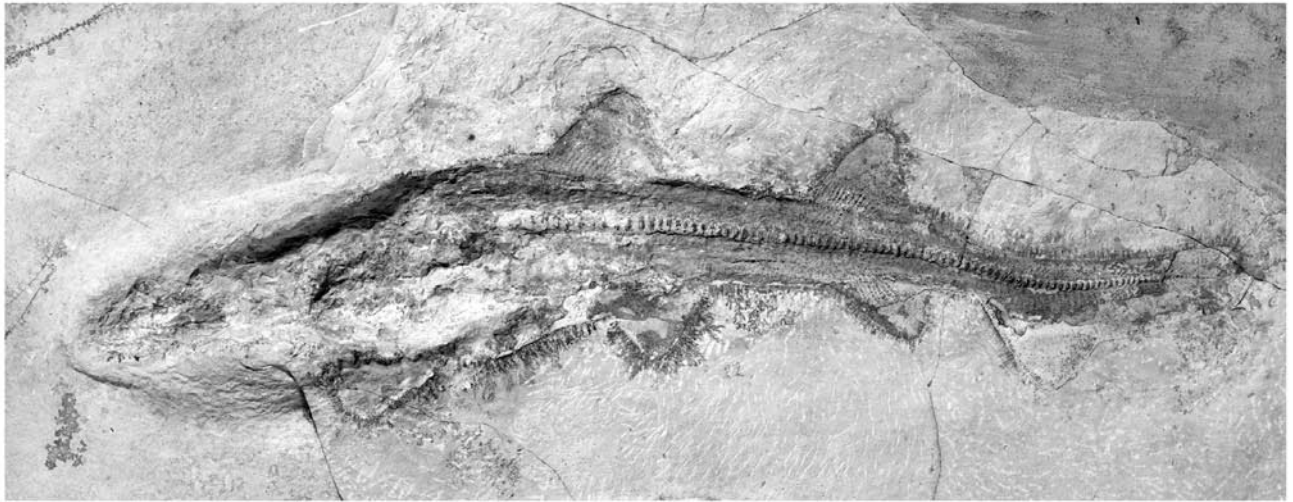
UNDERWOOD (2002) stated that the pectinate juvenile teeth are not replaced during ontogeny, but retained into

adulthood, and that molariform lateral teeth similar to those of *Heterodontus* are only found in large specimens (see also SCHWEIZER 1964). The absence of molariform teeth in several fossil assemblages led UNDERWOOD (2002) to the assumption that these tooth morphologies were never developed in some species. In modern neonate horn sharks, lateral molariform teeth are present but poorly mineralized (SUMMERS et al. 2004). It is possible to envisage that the lateral teeth in Late Jurassic juvenile heterodontids also were weakly mineralized and therefore inadequately represented in the fossil record.

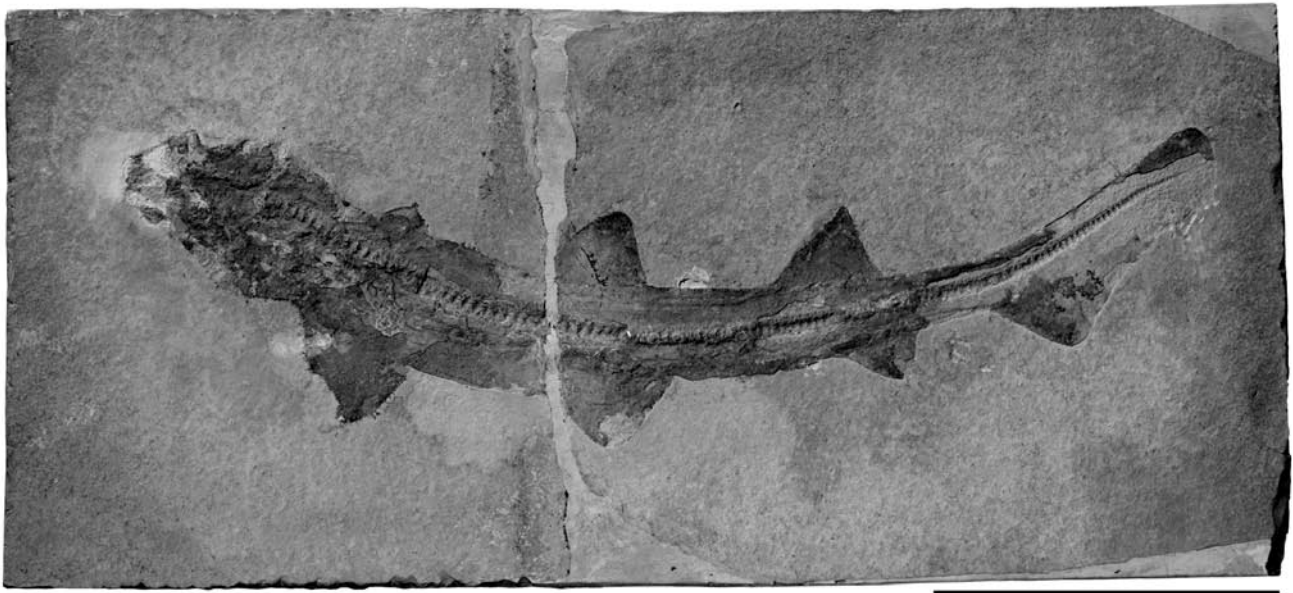
The examination of articulated juvenile and adult specimens revealed the presence of pectinate anterior and a lack of molariform lateral teeth in juveniles (Fig. 12d). However, the rather large holotype, which does not differ in skeletal anatomy from the smaller specimens, displays the predicted molariform lateral teeth but also typical anterior teeth of adult *Heterodontus* species; pectinate anterior teeth are missing. The adult dental pattern renders identification of *Paracestracion* difficult if the roots of the teeth are not visible (e.g., in articulated dentitions). In this case, the relative position of the fins provides the soundest character for differentiation.

We therefore agree with KOKEN (in ZITTEL 1911) and UNDERWOOD (2002) and refer those specimens that are characterized by anterior teeth with an open nutritive groove and pelvic fins situated far anteriorly below the first dorsal

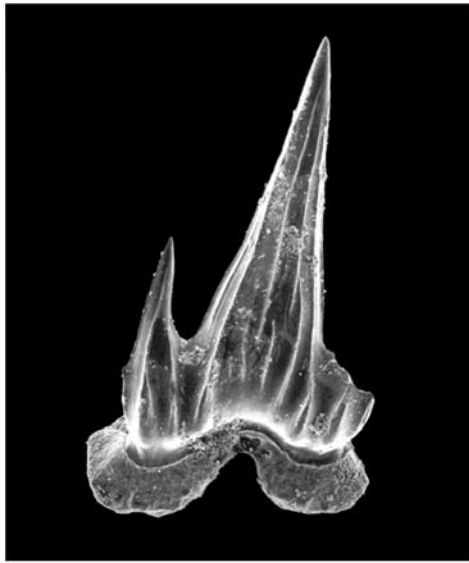




a



b



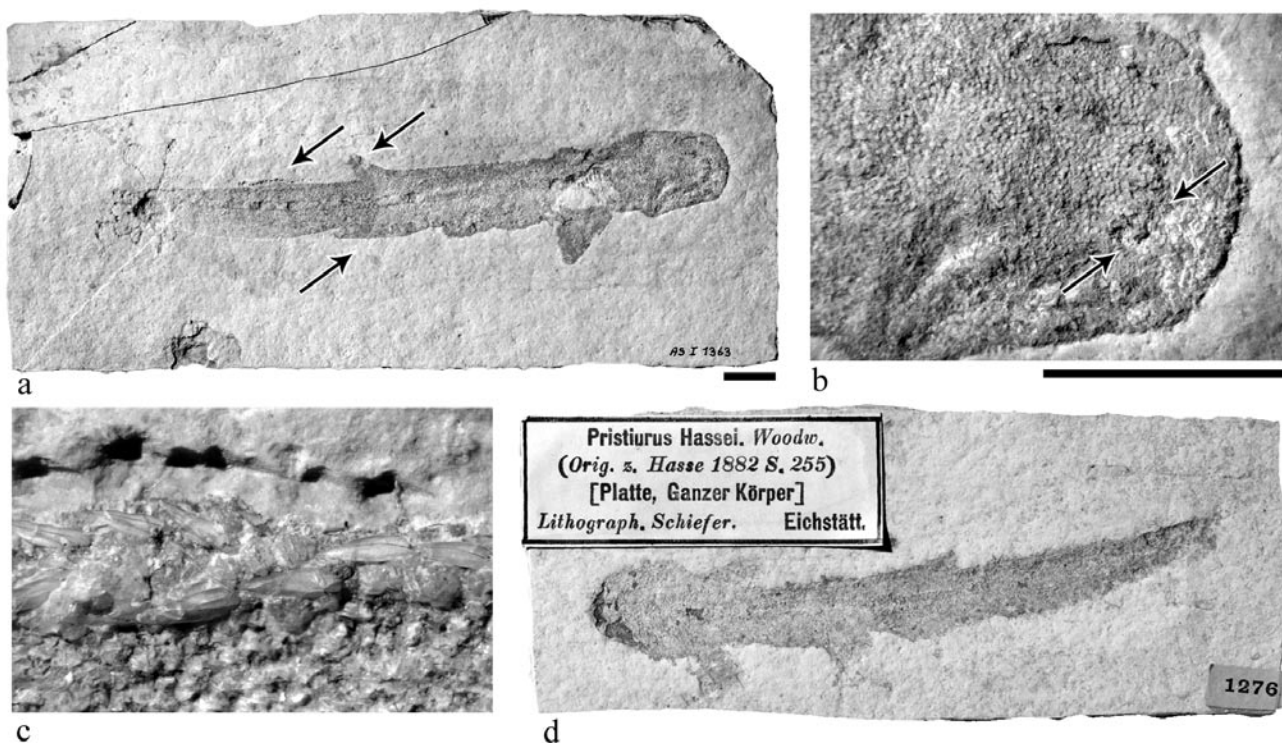
c



d

**Figure 15:** *Palaeoscyllium formosum* WAGNER, 1857. **a:** Holotype (BSP AS I 1365) from the lower Tithonian of Solnhofen (Bavaria). Lateral view. Scale bar = 10 cm. **b:** Specimen BSP AS I 589a from the lower Tithonian of Solnhofen (Bavaria). Lateral view. Scale bar = 10 cm. **c-d:** Anterior teeth of specimen BSP AS I 589a. Scale bars = 0.04 cm. **c:** Labial view. **d:** Lateral view.





**Figure 16:** *Macrourogaleus hassei* (WOODWARD, 1889). **a:** Holotype (BSP AS I 1363) from the lower Tithonian of Eichstätt. Arrows point to caudal crest of large denticles, single dorsal fin, and elongated anal fin. Lateral view. **b:** Close up of head of specimen BSP AS I 1363. Ventral view. Arrows point to position of preserved teeth. Scale bar = 1.0 cm. **c:** Close up of caudal crest of large denticles of specimen BSP AS I 1363. Scale bar = 0.1 cm. **d:** Specimen BSP AS I 1362 from the lower Tithonian of Eichstätt (Bavaria). Scale bar = 1.0 cm.

to *Paracestracion falcifer*. The fossil record of *Paracestracion* ranges from the Toarcian to the Tithonian with the following species (UNDERWOOD 2002; UNDERWOOD & WARD 2004): *Paracestracion sarstedensis* (THIES 1983) from the Toarcian of Belgium and Toarcian of northern Germany, *Paracestracion bellis* UNDERWOOD & WARD, 2004 from the Bathonian of England, *Paracestracion* sp. (THIES 1983) from the Callovian of England, and *Paracestracion falcifer* from the Kimmeridgian of Nusplingen and Tithonian of the Solnhofen area.

UNDERWOOD & WARD (2004) introduced another Jurassic heterodontid, *Probeterodontus sylvestris*, from the Bathonian of England. The dentition is characterized by cuspidate teeth with up to three pairs of lateral cusplets in all jaw positions and hemiaulacorhizan roots with very slender and elongated root lobes. Teeth of this morphology are not known from the Late Jurassic.

The holotype and only specimen of *Heterodontus zitteli* EASTMAN, 1914 is an adult with characteristic dental patterns that differs from *Paracestracion* in that the pelvic fin inserts behind the first dorsal fin.

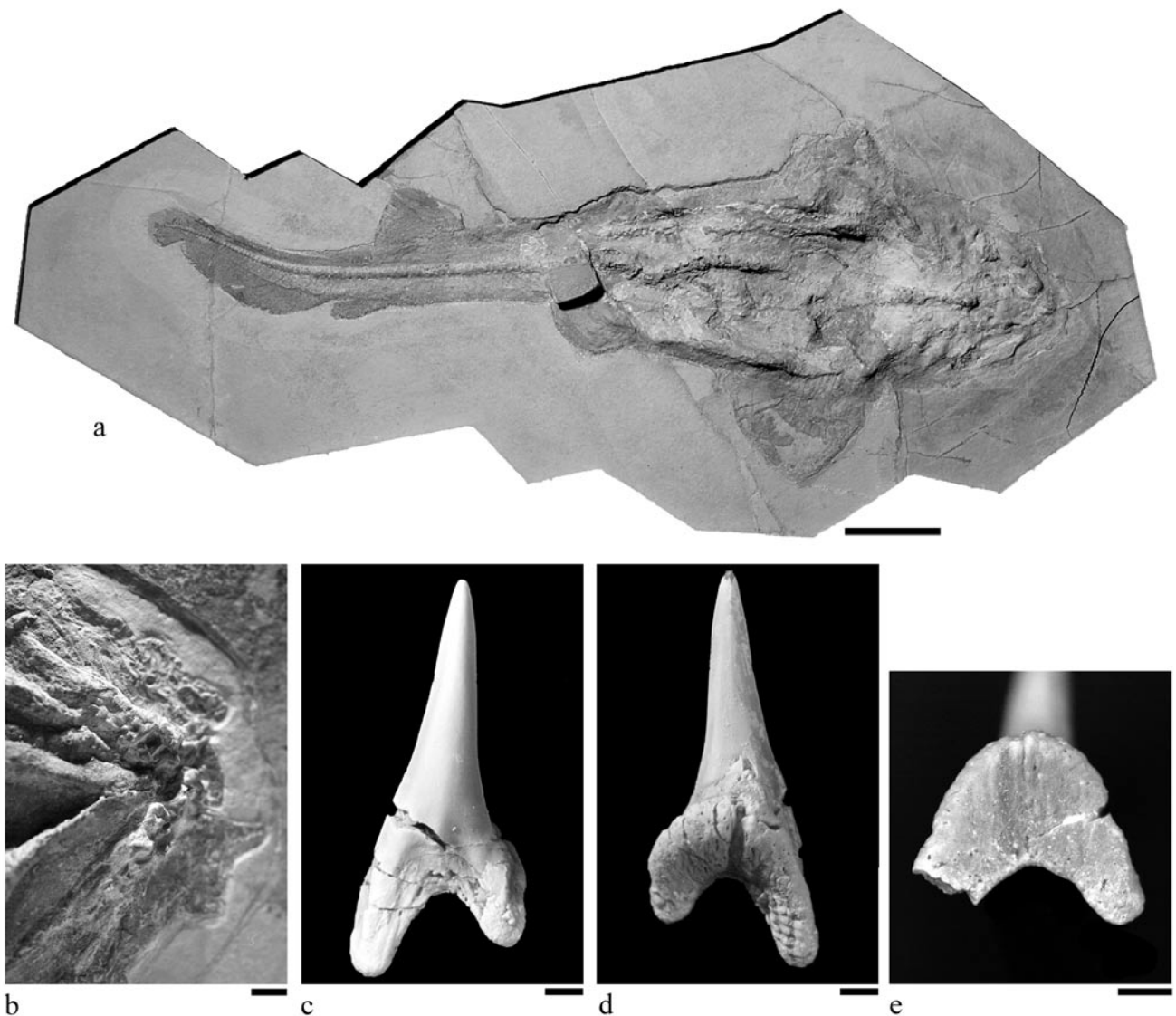
Isolated heterodontid teeth are rather rare in the Upper Jurassic of southern Germany and some specimens from the Tithonian of Kelheim were referred to *Acrodus semirugosus* PLIENINGER, 1847 and *Bidentia bidens* (QUENSTEDT, 1852) respectively (MUSPER 1920). SCHWEIZER (1961) re-analyzed those teeth and concluded that these teeth resemble those of modern *Heterodontus* species in the overall morphology and referred them to *H. semirugosus*. This conclusion is supported here. Teeth of this species display a rather high and hemiaulacorhize root and a single-cuspidate massive crown with incipient lateral cusplets (Fig. 12e).

Heterodontid remains other than those from Nusplingen have not been described from the Upper Jurassic of Baden-Württemberg so far. The new locality of Mahlstetten yielded six anterior but no molariform heterodontid teeth. The root is, unfortunately, barely preserved and does not provide unambiguous taxonomic evidence. The morphology of the crown is very similar to that seen in *Paracestracion* spp.

### 3.7. Orectolobiformes

The only orectolobiform that occurs in the conservation lagerstätten of southern Germany is *Phorcynis catulina* THIOLLIÈRE, 1854 (Fig. 13) from Solnhofen. This species was originally described from the Kimmeridgian of Cerin, France. CAPPETTA (1987) referred *Crossorhinops minus* (WOODWARD, 1889), *Crossorhinus jurassicus* WOODWARD, 1918, and *Palaeocrossorhinus* (type species: *Crossorhinus jurassicus*) to *Phorcynis catulina*. CAPPETTA (1987) also attributed the genera *Corysodon* SAINT-SEINE, 1949 and *Palaeoscyllium* WAGNER, 1857 to the Orectolobiformes. LEIDNER & THIES (1999) rejected this interpretation because the placoid and dental morphology of both is typical carcharhiniform (see below), whereas the placoid and scale pattern of *Phorcynis* is characteristic for orectolobiforms (LEIDNER & THIES 1999).

Several skeletons have been recovered that are housed in Paris (MHNL 15293), London (BMNH P.11211), and Munich (BSP 1990 XVIII 51, Fig. 13a-c). The overall morphology is orectolobiform with rather large and rounded pectoral and pelvic fins (Fig. 13c). The two dorsal fins are placed well back along the body, rather triangular, and subequal in size. The insertion of the pelvic fins is in front of the first dorsal. The



**Figure 17:** *Palaeocarcharias stromeri* DE BEAUMONT, 1960. **a:** Specimen BSBGM 1964 XXIII 156 from the lower Tithonian of Sonnhofen area (Bavaria). Scale bar = 10 cm. **b:** Mouth of specimen JM-SOS 2294 from the lower Tithonian of Solnhofen area (Bavaria). Ventral view. Scale bar = 1.0 cm. **c-e:** Isolated teeth of specimen JM-SOS 2216 from the lower Tithonian of Blumenberg / Eichstätt (Bavaria). Scale bars = 0.1 cm. **c:** Anterior tooth, labial view. **d:** Anterior tooth, lingual view. **e:** Anterior tooth, basal view.

caudal fin is elongated with a subterminal notch. The anal fin is small and rounded similar to those of extant parascylliids.

The tooth morphology was described by LEIDNER & THIES (1999) based on specimen BSP AS I 1364 (Fig. 13d-f) and is identical to those seen in the holotype from Cerin, France (SAINT-SEINE 1949: fig. 5). The broad labial apron that overhangs the root and the hemiaulacorhize vascularisation of the root demonstrates the orectolobiform affinity of *Phorcynis*.

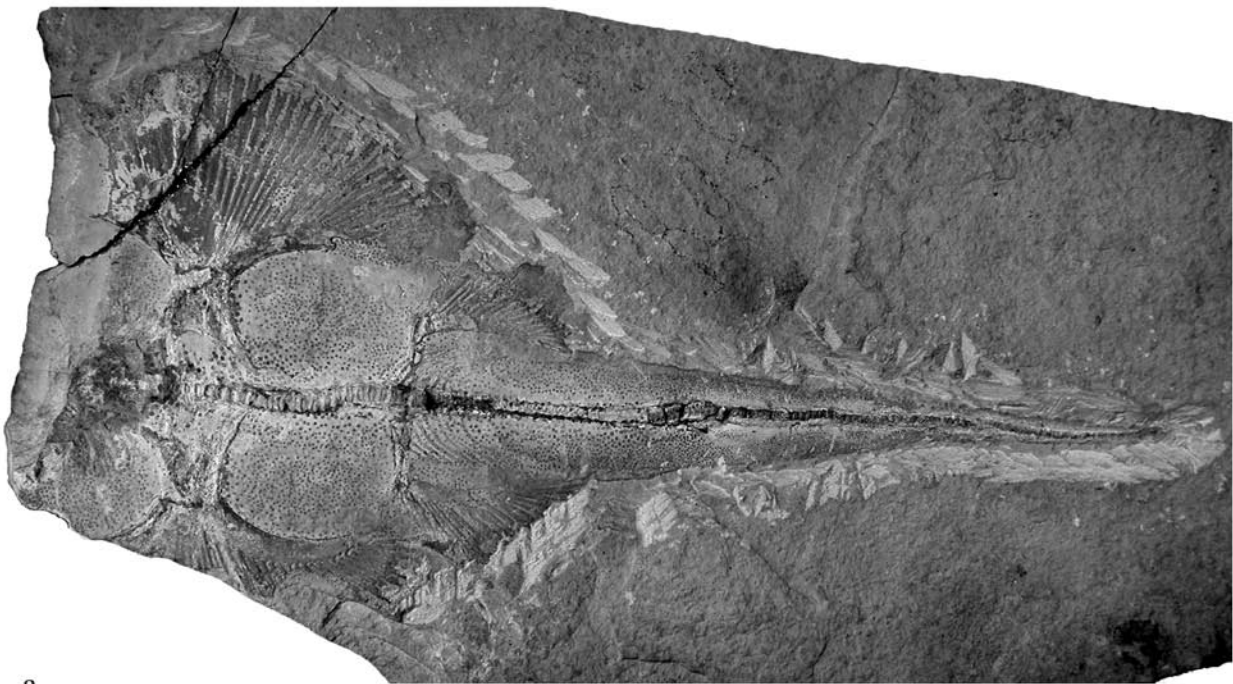
Orectolobiforms are relatively rare in the Upper Jurassic of Europe. Articulated or isolated remains of orectolobiforms have not been recovered from Nusplingen, Stuifen, Reichenbach, and Buchsteige in Germany. However, this is correct only if the Late Jurassic teeth attributed to *Squatina* are, in fact, not orectolobiform in origin. The Mahlstetten locality yielded several dozens of orectolobiform teeth including those of *Phorcynis* and *Palaeobrachaelurus*, but also other taxa hitherto unknown from southern Germany. *Phorcynis* occurs also in the Kimmeridgian of Spain (KRIWET 1998: pl. 4, fig. 3).

### 3.8. Carcharhiniformes

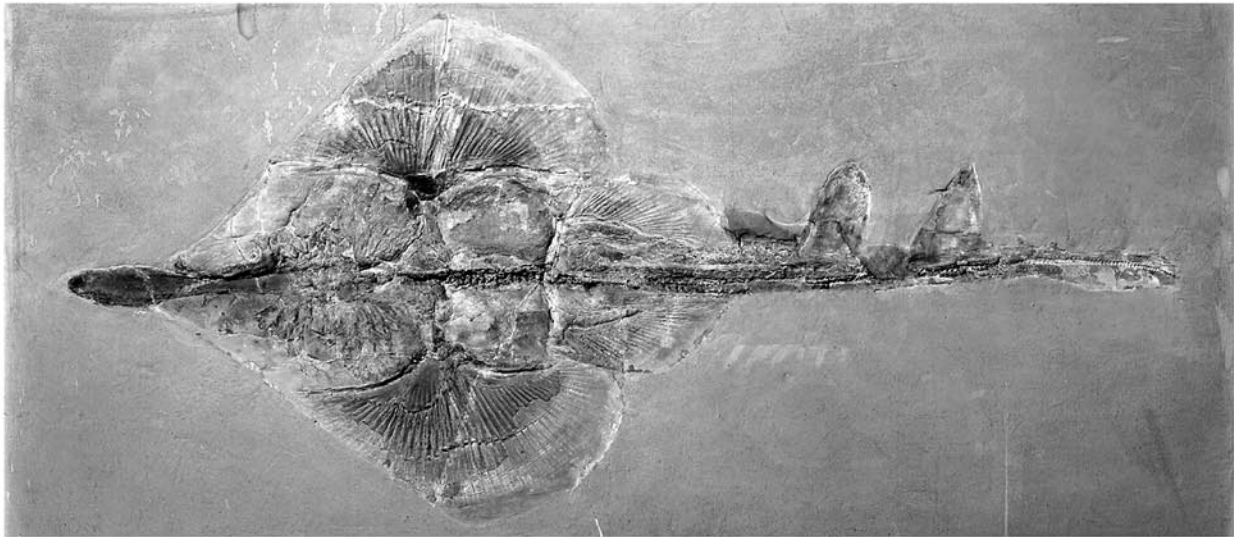
Carcharhiniforms are represented by at least three genera in Solnhofen: *Corysodon cirinensis* SAINT-SEINE, 1949, *Palaeoscyllium formosum* WAGNER, 1857, and *Macrourogaleus hassei* (WOODWARD, 1889). *Corysodon* was previously known only from the Kimmeridgian of Cerin, northwestern France, and northwestern Germany (THIES & CANDONI 1998), but specimen MB f.11191 (Fig. 14) displays the typical tooth morphology and indicates the presence of *Corysodon cirinensis* also in southern Germany.

Based on the similar form and position and size of the fins, CAPPETTA (1987) synonymized *Corysodon* with *Palaeoscyllium*, proportional differences were interpreted as due to post-mortem deformation.

The holo- and paratype of *Corysodon cirinensis* are rather well preserved (THIES & CANDONI 1998). The dorsal, pelvic, and anal fins are comparably large and triangular in outline. The



a

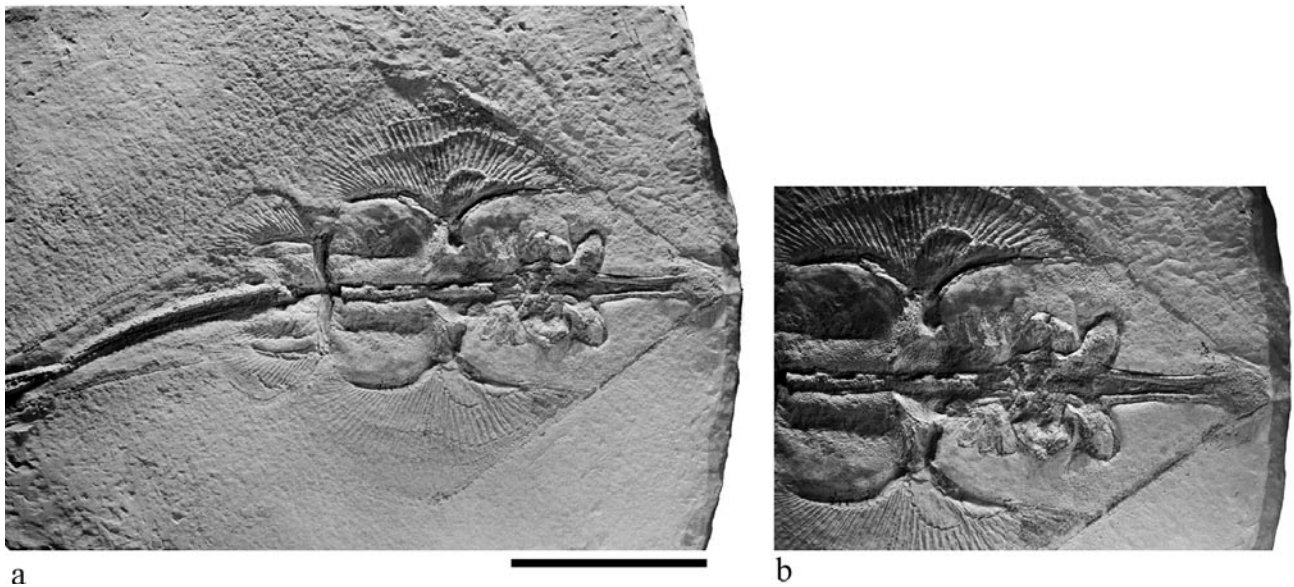


b



c

**Figure 18:** *Asterodermus platypteros* AGASSIZ, 1843. **a:** Holotype (BMNH P.12067) from the Kimmeridgian of Kelheim (Bavaria). Scale bar = 1.0 cm. **b:** Specimen BSP AS I 505 from the lower Tithonian of Eichstätt (Bavaria). Scale bar = 10 cm. **c:** Specimen BSP 1952 I 82 from the lower Tithonian of Langenaltheim / Solnhofen (Bavaria). Scale bar = 10 cm.



**Figure 19:** *Asterodermus platypteros* AGASSIZ, 1843 (JM-SOS 3647) from the lower Tithonian of Eichstätt (Bavaria). Juvenile specimen. Scale bar = 10 cm. **b:** Close up of the neurocranium displaying well-preserved articulation of pectoral fins, nasal capsules, and elongated rostrum.

two dorsal fins are of sub-equal size. The pelvic and anal fins insert almost below the hind end of the first and second dorsal fins respectively. The posterior part of the anal fin reaches the caudal fin. The skull is heavily crushed obscuring most details. Specimen MB f.11191 displays long and branched barbels at the anterior portion of the head (Fig. 14b) that are untypical for carcharhiniforms but resemble those seen in extant orectolobids (wobbegongs). A detailed anatomical investigation of all articulated material is necessary to reconstruct the systematic position of *Corysodon* with confidence.

*Palaeoscyllium formosum* generally resembles *Corysodon* but differs in that the second dorsal fin is considerably smaller than the first, and the pelvic and anal fins are placed further anteriorly with the anal fin inserting below the anterior half of the second dorsal fin (Fig. 15a, b). Additionally, there is a distinct gap between the anal and caudal fin. The teeth display scyliorhinid morphology with delicate and high central and lateral cusps with strong ornamentation (Fig. 15c, d). Similar teeth from the Kimmeridgian of northern France were described by CANDONI (1993) as *Parasymbolus octevillensis* but subsequently recognized as junior synonym of *Palaeoscyllium formosum* (LEIDNER & THIES 1999).

*Palaeoscyllium formosum* also occurs in the Kimmeridgian of Spain (KRIWET 1998) and Kimmeridgian of England (UNDERWOOD 2002). The oldest record of *Palaeoscyllium*, *P. tenuidens*, comes from the Bathonian of England (UNDERWOOD & WARD 2004), the youngest species, *P. reticularis*, is from the Albian of England (UNDERWOOD & MITCHELL 1999). The only record of *Palaeoscyllium* in Baden-Württemberg is from the Kimmeridgian of Mahlstätten.

WOODWARD (1889) proposed the species *Pristiurus hassei* for a small shark that was figured by HASSE (1882) under the name *Pristiurus* (junior synonym of *Galeus*). FOWLER (1947) referred the Late Jurassic specimens to *Macrourogaleus*, based on the apparent discrepancies, 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 (Fig. 16). The presence of large denticles

on the caudal crest in *P. hassei* (Fig. 16a, c) and *Galeus* most likely represents convergent developments. In both groups, these denticles are present on the upper margin of the caudal fin. *Macrourogaleus* resembles extant hexanchiforms and the scyliorhinid *Pentanchus*, but also the fossil synechodontiform *Paraorthacodus* in having a single dorsal fin.

The dentition is partly preserved in specimen BSP AS I 1363 (Fig. 16b) with teeth showing the characteristic scyliorhinid morphology (J.K. & S.K. in prep.). The teeth are delicate, multicuspate, and ornamented with numerous vertical ridges. The root resembles those seen in *Galeus*.

THIES (in press) reports the first unambiguous species of the family Scyliorhinidae from the Tithonian of the Solnhofen area based on fin proportions. The teeth of this new taxon differ significantly from all other carcharhiniforms.

### 3.9. *Palaeocarcharias*

The single species of *Palaeocarcharias*, *P. stromeri*, was based on three articulated specimens from the lower Tithonian of Bavaria (DE BEAUMONT 1960b). Additional specimens were subsequently recovered and are located in several museums and private collections (Fig. 17).

The holotype of *Palaeocarcharias stromeri*, a complete specimen, is housed in the Jura Museum, Eichstätt (JM-SOS 2294). Isolated teeth of *Palaeocarcharias* have not been reported to date. A tooth from the Upper Jurassic of the Moscow region figured by KIPRIJANOFF (1880: pl. 1, fig. 4) could belong to a lamniform, probably even to *Palaeocarcharias* (CAPPETTA 1987: p. 111), but no additional records exist. Moreover, there is no indication of *Palaeocarcharias* teeth in larger collections of isolated teeth from northern Germany (e.g., THIES 1983), southern Germany (this study) or elsewhere in Europe. So far, *P. stromeri* is only known from the lithographic limestones of the Solnhofen area.

The body of *Palaeocarcharias* is reaching one meter total length, is fusiform and dorso-ventrally flattened (Fig. 17a). The rostral cartilage is very short. The two dorsal fins are of

<b>Taxon</b>	<b>S Germany</b>	<b>NE Germany</b>	<b>S England</b>	<b>N France</b>	<b>W France</b>	<b>E France</b>	<b>NE Spain</b>
<i>Asteracanthus</i>	X	X	X	X			
<i>Hybodus</i>	X	X		X	X		
<i>Polyacrodus</i>		X		X	X		
<i>Lissodus</i>				X			
<i>Notidanoides</i>	X						X
“ <i>Eonotidanus</i> ”	X						
<i>Protospinax</i>	X	X	X	X	X		X
<i>Pseudospinax</i>			X				
<i>Sphenodus</i>	X	X	?	X			
<i>Synechodus</i>	X	X	X	X			X
<i>Paraorthacodus</i>	X			X			
<i>Squatina</i>	X		X	X			X
<i>Paracestracion</i>	X		X	?			
<i>Heterodontus</i>	X	X	X	X	X		
<i>Phorcynis</i>	X	X			X	X	X
<i>Cantioscyllium</i>			X				
<i>Palaeobrachaelurus</i>				X			
<i>Orectolobif. indet.</i>			X				
<i>Corysodon</i>	X	X				X	
<i>Palaeoscyllium</i>	X	X	X				X
<i>Macrourogaleus</i>	X						
<i>Ctenascyllum</i>				X			
<i>Asterodermus</i>	X	X		X			
<i>Belemnobatis</i>		X		X		X	
<i>Spathobatis</i>		?	X	X	X	X	X

**Table 1:** Occurrences of selachians (Hybodontidae, Neoselachians) in the Upper Jurassic (Oxfordian – Tithonian) of Europe. N France refers to the localities of the Boulonnais, W France to the La Rochelle area, and E France to the locality of Cerin. Data from: CANDONI (1995); DUFFIN & THIES (1997); KRIWET (1998); THIES & CANDONI (1998); LEIDNER & THIES (1999); MUDROCH (2001); UNDERWOOD (2002); this study.



Taxon	Stuifen/Reichenbach	Buchsteige	Mahlstetten	Nusplingen	Solnhofen
<i>Asteracanthus</i>					X
<i>Hybodus</i>					X
<i>Lissodus</i>			X		
<i>Notidanoides</i>			X	X	X
“ <i>Eonotidanus</i> ”				X	X
<i>Protospinax</i>	X	X	X	?	X
<i>Sphenodus</i>	X	X	X	X	X
<i>Synechodus</i>	X	X	X		X
<i>Paraorthacodus</i>			X	X	X
<i>Squatina</i>		X	X	X	X
<i>Paracestracion</i>				X	X
<i>Heterodontus</i>			?		X
<i>Phorcynis</i>					X
<i>Palaeobrachaelurus</i>			X		
<i>Batoidea</i> indet.			X		
<i>Corysodon</i>					X
<i>Palaeoscyllium</i>			X	X	X
<i>Macrourogaleus</i>					X
<i>Asterodermus</i>			X		X

**Table 2:** Occurrences of selachians (Hybodontoidae, Neoselachii) in the Upper Jurassic of southern Germany. Solnhofen area: lower Tithonian; Nusplingen: upper Kimmeridgian; Stuifen: middle Oxfordian; Reichenbach: upper Oxfordian; Buchsteige: upper Oxfordian; Mahlstetten: Kimmeridgian.

sub-equal size and the caudal fin is heterocercal with a rounded top, subterminal notch, and a rather deep lower lobe. The pelvic and anal fins insert below the hind end of the first and second dorsal fins respectively.

The dentition displays a gradient monognathic heterodonty with high-cusped anterior and low-crowned postero-lateral

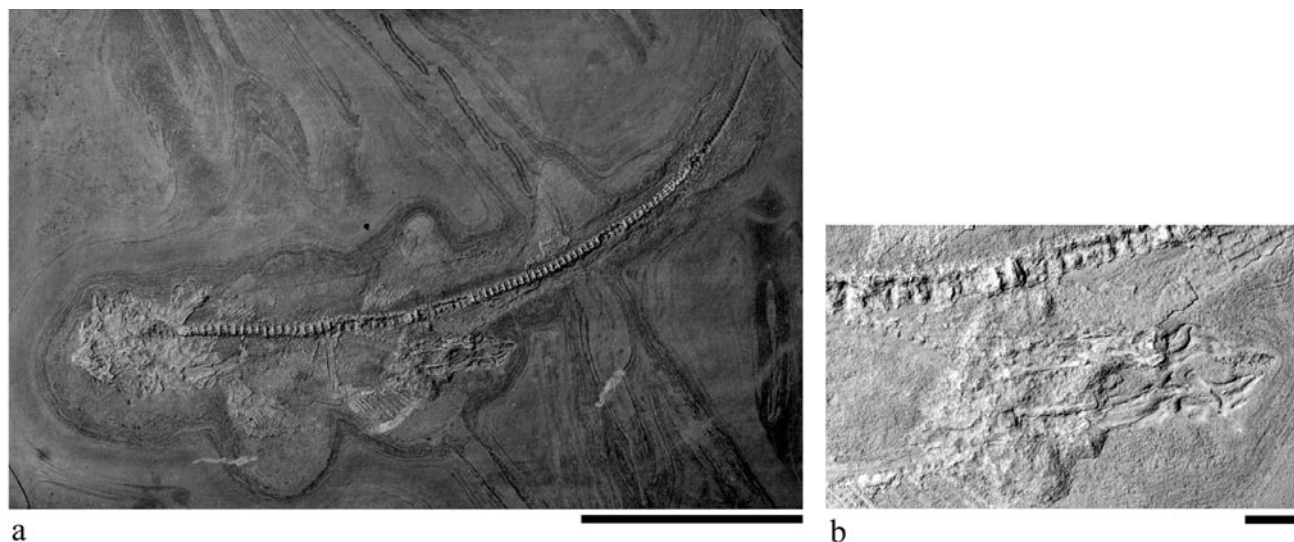
teeth. All teeth have a rather massive, lingually inclined crown with a central cusp but no lateral cusplets (Fig. 17c, e). The lingual crown face is rather convex, the labial face is more flattened. The cutting crest is well-developed and continuous. The labial crown extends over the surfaces of the root prongs. Very short, vertical striations occur along the basis of the labial face in some teeth. A narrow and short bulge is developed at the base of the labial face (Fig. 17c). Fine and short striations arise lingually from a distinct crown collar. Parasymphyseal and anterior tooth crowns are slightly asymmetric with an elongated mesial root lobe (Fig. 17b, c). Teeth of more lateral positions have a straight cusp with equally long root lobes (Fig. 17e). The root vascularisation is holaulacorhize with a more or less deep central groove that separates the two root lobes in most teeth (Fig. 17d). This canal, however, can be closed secondarily in lateral teeth (Fig. 17e).

Despite the complete nature of the specimens only few studies have been carried out to settle the systematic position of *Palaeocarcharias*. DE BEAUMONT (1960b) placed *Palaeocarcharias* at the base of lamniforms (“basal Isuridae”). DUFFIN (1988), in re-examining the specimens of *Palaeocarcharias*, concluded that the body form is similar to oreotolobiforms, the tooth morphology, on the contrary, typical for lamniforms (mackerel sharks). He consequently interpreted this shark as a benthonic stem group representative of lamniforms and noted that lamniforms arose from oreotolobiforms ancestors. CAPPETTA (1987) underlined the lamniform tooth morphology of *Palaeocarcharias* and placed it in the vicinity of lamniforms. APPLGATE (2001) also found *Palaeocarcharias* to be a transitional taxon between Oreotolobiformes and Lamniformes and suggests that it warrants its own family, Palaeocarcharidae, and order, Palaeocarchariformes, names that were never officially published and are therefore not available. A re-evaluation of the systematic position employing cladistic principles and using dental and cranial/postcranial characters indicates that *Palaeocarcharias* is the basal sister group of lamniforms but no member of oreotolobiforms (J.K. & D. THIES in prep.). This hypothesis supports APPLGATE’s interpretation.

### 3.10. Batoidea

The taxonomy of Late Jurassic batoids is in a disastrous state. Detailed anatomical revisions have to be performed prior to a recon of their systematic position is possible with any confidence despite several recent attempts. Unfortunately, the holotype of *Asterodermus platypterus* AGASSIZ, 1843 from the Tithonian of southern Germany lacks the skull so that it is not possible to establish its dental morphology (Fig. 18a). Two additional batoids, *Belemnobatis sismondæ* THIOLLIÈRE, 1854 and *Spathobatis bugesiacus* THIOLLIÈRE, 1854, occur in the Kimmeridgian lithographic limestones of Cerin, France. *Belemnobatis sismondæ* was also reported from the Kimmeridgian of Nusplingen (SCHWEIZER 1964).

LEIDNER & THIES (1999) were able to identify additional specimens of *Asterodermus platypterus* based on scale morphology. Although *A. platypterus* resembles *Spathobatis bugesiacus* in scale morphology, the teeth differ significantly and are more similar to those of *Belemnobatis*. CAVIN et al. (1995) and LEIDNER & THIES (1999) listed several dental features to distinguish the three genera. Identifying *Asterodermus* on the basis of pla-



**Figure 20:** *Palaeoscyllium formosum* WAGNER, 1857 (BSP AS I 1375) from the Kimmeridgian of Cerin (France). **a:** Complete specimen in lateral view. Scale bar = 10 cm. **b:** Close up of specimen BSP AS I 1375 displaying detailed morphology of clasper cartilages. Scale bar = 1.0 cm.

coid scale and tooth morphology approved finding additional characters to differentiate the three genera. For instance, the rostrum is long in *Asterodermus* (Figs 18a, b, 19) and *Spathobatis* but rather short and blunt in *Belemnobatis sismondæ*. The rostrum of *Belemnobatis morinicus*, however, is also long and comparable to that of *Spathobatis* and *Asterodermus* (CAVIN et al. 1995). LEIDNER & THIES (1999) tentatively identified all Late Jurassic batoids from the lithographic limestones of southern Germany as belonging to *Asterodermus*.

Many isolated teeth have been assigned to different species in the past (e.g., THIES 1983; CANDONI 1995). The impossibility to identify these species when larger samples of isolated teeth are examined indicates that species of *Spathobatis* (e.g. *S. bugesiacus*) are characterized by a high degree of heterodonty (UNDERWOOD 2002). This author agrees with CAVIN et al. (1995) that teeth of *Belemnobatis* may be separated from teeth of *Spathobatis* in having a gracile lingual uvula and slightly flared lateral edges of the crown and root. Subsequently, UNDERWOOD & WARD (2004) identified several additional species of *Belemnobatis* and *Spathobatis* from the Bathonian of England stating that *Asterodermus* should be restricted to the holotype until the tooth morphologies of specimens referred to this species are better known.

All three batoids possess vestigial spines in front of the two dorsal fins, which are rarely preserved. SCHWEIZER (1964) described and figured a skeletal fragment that he referred to *Belemnobatis sismondæ*. The specimen consists of parts of the vertebral column but it does not preserve the head and fins. It displays rather massive and large dorsal fin spines, which are unusual for Late Jurassic batoids and the specimen more probably belongs to *Protospinax*.

Although we agree with UNDERWOOD (2002) that the heterodonty of *Spathobatis* might still be poorly established we also agree with LEIDNER & THIES (1999) that the tooth morphology of *Asterodermus*-like specimens from the Upper Jurassic of southern Germany allows to distinguish it from the other two genera (J.K. & D. THIES in prep.). Therefore, we consider that all Late Jurassic batoids from southern Germany can be assigned

to *Asterodermus platypterus*. This interpretation is also supported by the skeletal anatomy of specimens examined in the course of this project (Figs 18, 19).

A few isolated *Asterodermus*-like teeth from the Kimmeridgian of Mahlstetten are the first unambiguous evidence of Late Jurassic batoids in Baden-Württemberg (J.K., S.K. & E.U. in prep.). Late Jurassic batoid records from outside Germany include specimens from the Kimmeridgian of France, Spain, and England (CANDONI 1995; CAVIN et al. 1995; KRIWET 1998; UNDERWOOD 2002).

#### 4. Diversity and Faunal Relationships

The selachian fauna of the Upper Jurassic (Oxfordian – Tithonian) of southern Germany is amongst the most diverse known from the Jurassic of Europe and include at least 30 species belonging to 16 genera (Tab. 1). Many genera occur also in other Late Jurassic European localities. In many ways, the generic diversity is similar to that from the Middle Jurassic (KRIWET 2003; UNDERWOOD & WARD 2004).

European Late Jurassic selachian faunas comprise at least four hybodontoids, about 18 neoselachian sharks, and three batoid genera. The only hybodontoid record from the Upper Jurassic of north-eastern Spain is a very fragmentary tooth from the Oxfordian bearing resemblances to teeth of *Acrodus* and would consequently bring the total number of hybodontoid genera to five. Moreover, the Kimmeridgian fauna of Mahlstetten contains several yet unidentified genera of different clades (e.g., orectolobiform).

Separating the faunal components listed in Tab. 1 according to their stratigraphic age reveals that faunas represented by isolated teeth of Oxfordian and Kimmeridgian age from northern Germany, southern England and northern France are actually more diverse than those from southern Germany.

The most diverse Tithonian selachian fauna comes from the lithographic limestones of the Solnhofen area and is represented by entire specimens. Only a few additional Tithonian selachian

faunas were described to date (e.g., CUNY et al. 1991; CANDONI 1995). The scarcity of selachians of this age in Europe is due rather to a collecting bias than representing, a biological or ecological signal.

Late Jurassic European (Tab. 1) and southern German (Tab. 2) faunal variations are mainly related to different environmental settings. For instance, the Kimmeridgian faunas of northern France, north-eastern Spain, and England are considered to be typical for neritic environments (CANDONI 1995; KRIWET 1998; UNDERWOOD 2002), whereas the Tithonian fauna of northern France characterizes an inner shelf fauna (CANDONI 1995). The plattenkalks of southern Germany were deposited in shallow marine and restricted environments and contain the typical suite of Late Jurassic selachians with hexanchiforms, squatinids, and batoids being quite abundant. Less numerous are hybodonts, synechodontiforms, protospinacids, and lamniforms. Teeth of synechodontiforms are very abundant in collections of isolated teeth from the Upper Jurassic of southern Germany. In the Kimmeridgian of Mähle, isolated teeth of *Paraorthacodus* are the most numerous selachian remains. Conversely, teeth of *Synechodus*, heterodontids, and batoids are extremely rare. *Squatina* is by far the most abundant selachian in the Kimmeridgian plattenkalks of Nusplingen with batoids being completely absent. Batoids are the most frequent selachians in the Kimmeridgian limestones of Cerin in France, almost to the exclusion of other selachians. *Palaeoscyllium* displays the widest geographic distribution amongst carcharhiniforms and occurs in almost all Late Jurassic localities. Complete skeletons of this genus do not only occur in Solnhofen but also in Cerin, France (Fig. 20).

Hybodonts are scarce in neritic and inner-shelf to lagoonal environments but occur with teeth of batoids occasionally in high numbers in environments with reduced salinities in northern Germany (THIES 1983; DUFFIN & THIES 1997; MUDROCH 2001) (Fig. 1). In near freshwater environments, batoids are absent.

The similarities between the Late Jurassic selachian associations of Europe, including several marine and wide-spread taxa (e.g., protospinacids, batoids, *Phorcynis*, *Palaeoscyllium*), indicate continuous faunal exchanges at the end of the Jurassic period. These exchanges were facilitated by open sea-ways between the areas under consideration. The high abundance of squatinids and heterodontids in near-coastal to lagoonal environments of carbonate shelves in southern Germany may suggest close affinities of these selachians with the reef habitats (UNDERWOOD 2002).

## 5. Conclusions

Although sporadic research concerning Late Jurassic selachians has been carried out and the dental patterns of several groups from the plattenkalks of southern Germany have been restudied in recent years, the taxonomy and systematics of many selachians remains exclusive and most faunas remain poorly understood. This is mainly due to the lack of comprehensive morphological studies including the cranial and postcranial anatomy. New studies of Late Jurassic selachians from different localities including entire skeletons from southern Germany will provide much new information concerning the

systematic position, interrelationships, and faunal affiliations of Late Jurassic neoselachians. Entire skeletons of selachians from the Solnhofen area represent a unique source of information but the taxonomic diversity of selachians from the Solnhofen area is still not established despite all recent advances (e.g., LEIDNER & THIES 1999). In the present study, two hybodontoid and at least 28 neoselachian species were identified in Upper Jurassic localities of southern Germany. However, the current knowledge as summarized here poses more questions at present than can it provide solutions.

## Acknowledgments

We would like to thank the following persons for granting access to specimens under their care: G. ARRATIA (Museum of Natural History Berlin, Germany), R. BÖTTCHER (Staatliches Museum für Naturkunde, Stuttgart, Germany), P. FOREY and A. LONGBOTTOM (The Natural History Museum London, UK), M. KÖBLER-EBERT and G. VIOHL (Jura Museum Eichstätt, Germany), and M. PHILIPPE (Collection des Facultés Catholiques, Lyon, France). H. FÜRER (Paläontologisches Institut und Museum der Universität Zürich, Switzerland) generously provided the specimen of Figure 10, J.K. is deeply indebted to D. THIES (Hanover, Germany) for sharing his knowledge about fossil selachians with him and for providing SEM figures of *Phorcynis*. A. MUDROCH (Hanover, Germany) is acknowledged for discussions and information. G. JANßEN (Ludwig-Maximilians-Universität, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie, Munich, Germany) is thanked for preparing most of the photos. We thank R. BÖTTCHER (Stuttgart) for providing photos of *Sphenodus macer* and *Squatina acanthoderma* from Nusplingen. Photos of *Palaeocarcharias* teeth are by the authors. We are indebted to J. ERL (Bayerische Staatssammlung für Paläontologie und Geologie Munich, Germany) who checked the reference section and helped locating literature. L. SCHMITZ (Davies, California, U.S.A.) is acknowledged for proof reading of the manuscript. M. KRINGS (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany) and M. MAISCH (Eberhard Karls Universität Tübingen, Germany) are thanked for their constructive reviews and helpful suggestions. W. WERNER (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany) is thanked for all his patience and support during the preparation of this manuscript.

## 6. References

- AGASSIZ, J. L. R. (1833-44): Recherches sur les Poissons Fossiles. 5 vols., with supplements; Neuchâtel et Soleure (Petitpierre), 1420 pp.
- APPLEGATE, S. P. (2001): The Origin of the Lamniform Sharks – a Study in Morphology and Paleontology of Recent and fossil genera. – American Elasmobranch Society 2001. Annual Meeting, Abstracts.
- BATCHELOR, T. J. & WARD, D. (1990): Fish remains from a temporary exposure of the Hythe Beds (Aptian – Lower Cretaceous) near Godstone, Surrey. – Mesozoic Research, 2: 181-203.
- BEAUMONT, G. DE (1960a): Contributions à l'Etude des Genres *Orthacodus* Woodw. Et *Notidanus* Cuv. (Selachii). – Mémoires suisses de Paléontologie, 77: 1-46.
- BEAUMONT, G. DE (1960b): Observations préliminaires sur trois Séla-

- ciens nouveaux du Calcaire lithographique d'Eichstätt (Bavière). – *Eclogae Geologicae Helvetiae*, **53**: 315-329.
- BIDDLE, J.-P. (1993): Les elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute Marne (France). – *Professional Papers of the Geological Survey of Belgium*, **264**: 191-240.
- BÖTTCHER, R. & DUFFIN, C. J. (2000): The neoselachian shark *Sphegnodus* from the Late Kimmeridgian (Late Jurassic) of Nusplingen and Egesheim (Baden-Württemberg, Germany). – *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, **283**: 1-31.
- BRITO, P. M. & SERET, B. (1996): The new genus *Iansan* (Chondrichthyes, Rhinobatoidea) from the Early Cretaceous of Brazil and its phylogenetic relationships. – In: ARRATIA, G. & VIOHL, G. (Eds): *Mesozoic Fishes – Systematics and Paleocology*; Munich (Pfeil), 47-62.
- BROWN, C. (1900): Über das Genus *Hybodus* und seine systematische Stellung. – *Palaeontographica*, **A 46**: 149-174.
- CANDONI, L. (1993): Découverte de *Parasymbolus* gen. et sp. nov. (Scyliorhinidae – Elasmobranchii) dans le Kimméridgien de Normandie, France. – *Professional Papers of the Geological Survey of Belgium*, **264**: 147-156.
- CANDONI, L. (1995): Deux faunes inédites de sélaciens dans le Jurassique terminal français – premiers resultants stratigraphiques. – *Bulletin trimestriel de la Société Géologique de Normandie et Amis Muséum du Havre*, **82**: 29-49.
- CAPPETTA, H. (1973): Selachians from the Carlile Shale (Turonian) of South Dakota. – *Journal of Paleontology*, **47**: 504-514.
- CAPPETTA, H. (1987): Mesozoic and Cenozoic Elasmobranchii. – In: SCHULTZ, H.-P. (Ed): *Handbook of Palaeoichthyology, Chondrichthyes II*, Vol. 3B; Stuttgart (Gustav Fischer), 1-193.
- CAPPETTA, H. (1990): Hexanchiforme nouveau (Neoselachii) du Crétacé inférieur du Sud de la France. – *Palaeovertebrata*, **20**: 33-54.
- CAPPETTA, H. (1992): New observations on the palaeospinacid dentition (Neoselachii, Palaeospinacidae). – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **9**: 565-570.
- CARVALHO, M. R. (1996): Higher-level elasmobranch phylogeny, basal squalans, and paraphyly. – In: STIASNY, M. L. J., PARENTI, L. R. & JOHNSON, G. D. (Eds): *Interrelationships of Fishes*; San Diego (Academic Press), 35-63.
- CARVALHO, M. R. & MAISEY, J. G. (1996): Phylogenetic relationships of the Upper Jurassic shark *Protospinax* WOODWARD 1919 (Chondrichthyes: Elasmobranchii). – In: ARRATIA, G. & VIOHL, G. (Eds): *Mesozoic Fishes – Systematics and Paleocology*, Munich (Pfeil), 9-49.
- CAVIN, L., CAPPETTA, H. & SÉRET, B. (1995): Révision de *Blemmobatis morinicus* (SAUVAGE, 1873) du Portlandien du Boulonnais (Pas-de-Calais, France). Comparaison avec quelques Rhinobatidae Jurassiques. – *Geologica et Palaeontologica*, **29**: 245-267.
- COMPAGNO, L. J. V. (1973): Interrelationships of living elasmobranches. – In: GREENWOOD, P. H., MILES, R. S. & PATTERSON, C. (Eds): *Interrelationships of Fishes*. – *Zoological Journal of Linnean Society, Supplement 1*, **53**: 15-61.
- COMPAGNO, L. J. V. (1999): Checklist of Living Elasmobranchs. – In: HAMLETT, W. C. (Ed): *Sharks, Skates, and Rays – The Biology of Elasmobranch Fishes*; Baltimore, London (Johns Hopkins University Press), 471-498.
- CUNY, G. & BENTON, M. (1999): Early radiation of neoselachian sharks in western Europe. – *Geobios*, **32**: 193-204.
- CUNY, G., BUFFETAUT, E., CAPPETTA, H., MARTIN, M., MAZIN, J. M. & ROSE, J. M. (1991): Nouveaux restes de Vertébrés du Jurassique terminal du Boulonnais (Nord de la France). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **180**: 323-347.
- CUNY, G., RIEPPEL, O. & SANDER, M. (2001): The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada. – *Zoological Journal of the Linnean Society*, **133**: 285-301.
- DELSATE, D. & CANDONI, L. (2001): Description de nouveaux morphotypes dentaires de Batomorphii toarciens (Jurassique inférieur) du Bassin de Paris: Archaeobatidae nov. fam. – *Bulletin de la Société naturelle de Luxembourg*, **102**: 131-143.
- DIETL, G. & SCHWEIGERT, G. (2001): Im Reich der Meerengel: der Nusplinger Plattenkalk und seine Fossilien; Munich (Pfeil), 144 pp.
- DINKEL, H. (1921): Untersuchung der Squatinen im Weissen Jura Schwabens; unpublished Dr. Thesis, University of Tübingen, 78 pp.
- DOUADY, C. J., DOSAY, M., SHIVJI, M. & STANDHOPE, M. J. (2003): Molecular and phylogenetic evidence refuting the hypothesis of Batoidea (rays and skates) as derived sharks. – *Molecular Phylogenetics and Evolution*, **26**: 215-221.
- DUFFIN, C. J. (1988): The Upper Jurassic selachian *Palaeocarcharias* DE BEAUMONT (1960). – *Zoological Journal of the Linnean Society*, **94**: 271-286.
- DUFFIN, C. J. (1993): New records of Late Jurassic sharks teeth from Southern Germany. – *Stuttgarter Beiträge zur Naturkunde, Serie B*, **193**: 1-13.
- DUFFIN, C. J., RICHTER, M. & NEIS, P. A. (1996): Shark remains from the Late Carboniferous of the Amazon Basin, Brazil. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **4**: 232-256.
- DUFFIN, C. J. & THIES, D. (1997): Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. – *Geologica et Palaeontologica*, **31**: 235-256.
- DUFFIN, C. J. & WARD, D. J. (1983): Teeth of a Neoselachian shark from the British Lower Jurassic. – *Palaeontology*, **26**: 839-844.
- DUFFIN, C. J. & WARD, D. J. (1993): The Early Jurassic Palaeospinacid sharks of Lyme Regis, southern England. – *Professional Paper of the Geological Survey of Belgium*, **264**: 53-102.
- EASTMAN, C. R. (1914): Catalog of the fossil fishes in the Carnegie Museum, Part IV. – *Memoires of the Carnegie Museum*, **6**: 389-449.
- FOWLER, H. W. (1947): New Taxonomic names of fish-like vertebrates. – *Notulae Naturae*, **187**: 1-16.
- FRAAS, O. (1854): *Squatina acanthoderma*. Der Meerengel von Nusplingen. – *Zeitschrift der Deutschen Geologischen Gesellschaft*, **6**: 782-799.
- FRAAS, O. (1855): Beiträge zum obersten weissen Jura in Schwaben. – *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, **11**: 76-107.
- FRICKHINGER, K. A. (1999): Die Fossilien von Solnhofen 2; Korb (Goldschneek), 190 pp.
- HASSE, C. (1882): Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule. Besonderer Theil; Jena (Gustav Fischer), 285 pp.
- HEINEKE, E. (1906): Die Ganoiden und Teleostier de Lithographischen Schiefers von Nusplingen. – *Geologische und Palaeontologische Abhandlungen, Neue Folge*, **8**: 159-214.
- HERMAN, J. (1977): Les Sélaciens des néocétacés 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*, **15**: 1-450.
- HERMAN, J., HOVESTADT-EULER, M. & HOVESTADT, D. C. (1992): Part A: Selachii. No. 4: Order Orectolobiformes – Families: Brachaeluridae, Ginglymostomidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomidae. Order Pristiophoriformes – Families: Pristiophoridae. Order Squatiniformes – Family: Squatinidae. – *Bulletin de l'Institut Royal des Sciences naturelles de Belgique*, **15**: 193-254.
- KEUPP, H., JENISCH, A., HERRMANN, R., NEUWEILER, F. & REITNER, J. (1993): Microbial Carbonate Crusts – a Key to the Environmental Analysis of Fossil Spontiolites? – *Facies*, **29**: 41-54.
- KIPRIJANOFF, V. A. (1980): Über fossile Fische des Moskauer Gouvernements. – *Bulletin de la Société Impériale des Naturalistes de Moscou* **55**: 1-7.
- KOKEN, E. (1911): Pisces. – In: ZITTEL, K. A. (Ed): *Grundzüge der Paläontologie. Zweite Abteilung, Vertebrata*; München, Berlin (Oldenbourg), 142 pp.
- KRIWET, J. (1998): Late Jurassic elasmobranch and actinopterygian fishes from Portugal and Spain. – *Cuadernos de Geología Ibérica*, **24**: 241-260.
- KRIWET, J. (2003): Neoselachian remains (Chondrichthyes, Elasmobranchii) from the Middle Jurassic of SW Germany and NW Poland. – *Acta Palaeontologica Polonica*, **48**: 583-594.
- KRIWET, J. (2004a): The systematic position of the Cretaceous sclerorhynchid sawfishes (Elasmobranchii, Pristiogalea). – In: ARRATIA, G. & TINTORI, A. (Eds): *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*; Munich (Pfeil). 57-74.

- KRIWET, J. (2004b): Late Jurassic selachians (Chondrichthyes: Hybodontiformes, Neoselachii) from Central Portugal. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **2004**: 233–256.
- KUHN, O. (1961): Die Tier- und Pflanzenwelt des Solnhofener Schiefers. Mit vollständigem Arten- und Schriftenverzeichnis. – Geologica Bavarica, **48**: 1–68.
- LAMBERS, P. H. (1999): The actinopterygian fish fauna of the Late Kimmeridgian and Early Tithonian 'Plattenkalke' near Solnhofen (Bavaria, Germany): state of the art. – Geologie en Mijnbouw, **78**: 215–229.
- LEIDNER, A. (1997): Schuppen oberjurazeitlicher Elasmobranchier; unpublished Masters Thesis, University of Hanover, 36 pp.
- LEIDNER, A. & THIES, D. (1999): Placoid scales and oral Teeth of Late Jurassic elasmobranchs from Europe. – In: ARRATIA, G. & SCHULTZE, H.-P. (Eds): Mesozoic Fishes 2 – Systematics and Fossil Record; Munich (Pfeil), 29–40.
- MAISEY, J. G. (1975): The interrelationships of phalacanthous selachians. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **9**: 563–567.
- MAISEY, J. G. (1976): The Jurassic selachian fish *Protospinax* WOODWARD. – Palaeontology, **19**: 733–747.
- MAISEY, J. G. (1980): An evaluation of jaw suspension in sharks. – American Museum Novitates, **2706**: 1–17.
- MAISEY, J. G. (1982a): The anatomy and interrelationships of Mesozoic hybodont sharks. – American Museum Novitates, **2724**: 1–48.
- MAISEY, J. G. (1982b): 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. (1983): Cranial anatomy of *Hybodus basanus* EGERTON from the Lower Cretaceous of England. – American Museum Novitates, **2758**: 1–64.
- MAISEY, J. G. (1985): Cranial Morphology of the Fossil Elasmobranch *Synechodus dubrisiensis*. – American Museum Novitates, **2804**: 1–28.
- MAISEY, J. G. (1986a): Anatomical Revision of the Fossil Shark *Hybodus fraasi* (Chondrichthyes: Elasmobranchii). – American Museum Novitates, **2857**: 1–16.
- MAISEY, J. G. (1986b): The Upper Jurassic Hexanchoid Elasmobranch *Notidanoidea* n. g. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **172**: 83–106.
- MAISEY, J. G. (1987): Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with comments on hybodontid systematics. – American Museum Novitates, **2878**: 1–39.
- MAISEY, J. G. (1989): *Hamiltonichthys mapei*, g. & sp. nov. (Chondrichthyes, Elasmobranchii), from the Upper Pennsylvanian of Kansas. – American Museum Novitates, **2931**: 1–42.
- MAISEY, J. G., NAYLOR, G. J. P. & WARD, D. J. (2004): Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. – In: ARRATIA, G. & TINTORI, A. (Eds): Mesozoic Fishes 3 – Systematics, Palaeoenvironments and Biodiversity; Munich (Pfeil), 17–56.
- MCEachran, J. D. & ASCHLIMAN, N. (2004): Phylogeny of Batoidea. – In: CARRIER, J. C., MUSICK, J. A. & HEITHAUS, M. R. (Eds): Biology of sharks and their relatives; Boca Raton, London, New York, Washington DC (CRC Press), 79–114.
- MEYER, H. VON (1856): Mittheilungen an Professor Bronn gerichtet. – Neues Jahrbuch für Mineralogie und Petrefactenkunde, **1856**: 418–420.
- MEYER, H. VON (1859): Squatina Thaumasia speciosa aus dem lithographischem Schiefer von Eichstätt. – Palaeontographica, **7**: 3–8.
- MUDROCH, A. (2001): Fischzähne aus dem Oberjura Nordwesteuropas – Systematik, Biogeochemie und Palökologie; unpublished Dr. Thesis, University of Hanover, 142 pp.
- MÜNSTER, G. (1842): Beschreibung einiger neuen Fische aus der Jura-Formation von Bayern und Württemberg. – Beiträge zur Petrefacten-Kunde, **5**: 55–64.
- MÜNSTER, G. (1843): Beitrag zur Kenntnis einiger neuer seltener Versteinerungen aus den lith. Schiefen in Bayern. – Beiträge zur Petrefactenkunde, **6**: 1–54.
- MUSPER, F. (1920): Der Brenztaloolith, sein Fossilgehalt und seine Deutung. – Württembergisches Jahrbuch, **76**: 1–35.
- OPPEL, A. (1854): Der mittlere Lias Schwabens. – Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, **10**: 43–136.
- PFEIL, F. H. (1983): Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. – Palaeoichthyologica, **1**: 1–315.
- PLIENINGER, T. (1847): Die Wirbeltierreste im Korallenkalk von Schnaitheim. – Württemberg Jahrbuch, **3**: 227.
- QUENSTEDT, F. A. (1851/52): Handbuch der Petrefactenkunde; Tübingen (Laupp), 1239 pp.
- QUENSTEDT, F. A. (1858): Der Jura; Tübingen (Laupp), 842 pp.
- REES, J. (2002): Shark fauna and depositional environment of the earliest Cretaceous Vitabck Clays at Eridskal, southern Sweden. – Transactions of the Royal Society of Edinburgh, Earth Science, **93**: 59–71.
- SAINT-SEINE, P. DE (1949): Les poisons des calcaires lithographiques de Cerin (Ain). – Nouvelles Archives du Muséum d'Histoire naturelle de Lyon, **2**: 159–276.
- SCHWEIGERT, G. (1998): Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, *Bekkeri*-Zone, *Ulmense*-Subzone, Schwäbische Alb). – Stuttgarter Beiträge zur Naturkunde, **267**: 1–61.
- SCHWEIGERT, G., DIETL, G., KAPITZKE, M., RIETER, M. & HUGGER, R. (1996): Libellen aus dem Nusplinger Plattenkalk (Oberjura, Ober-Kimmeridgium, Baden-Württemberg). – Stuttgarter Beiträge zur Naturkunde, Serie B, **236**: 1–12.
- SCHWEIZER, R. (1961): Über die Zähne von *Heterodontus semirugosus* (PLIENINGER) aus dem Brenztaloolith von Schnaitheim und dem Diceraskalk von Kelheim (Malm  $\xi$ ). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **113**: 95–109.
- SCHWEIZER, R. (1964): Elasmobranchier und Holocephalen aus den Nusplinger Plattenkalken. – Palaeontographica, **A 123**: 58–110.
- SHIRAI, S. (1992a): Squalan Phylogeny, a new Framework of "Squaloid" Sharks and related Taxa; Sapporo (Hokkaido University Press), 151 pp.
- SHIRAI, S. (1992b): Phylogenetic relationships of the angel sharks, with comments on elasmobranch phylogeny (Chondrichthyes, Squatinidae). – Copeia, **1992**: 505–518.
- SHIRAI, S. (1996): Phylogenetic interrelationships of Neoselachians (Chondrichthyes: Euselachii). – In: STIASNY, M. L. J., PARENTI, L. R. & JOHNSON, G. D. (Eds): Interrelationships of Fishes; San Diego (Academic Press), 9–43.
- SIVERSON, M. (1992): Late Cretaceous *Paraorthacodus* (Palaeospinacidae, Neoselachii) from Sweden. – Journal of Vertebrate Paleontology, **66**: 994–1001.
- SIVERSON, M. (1997): Sharks from the Mid-Cretaceous Gearle Siltstone, southern Carnarvon Basin, Western Australia. – Journal of Vertebrate Paleontology, **17**: 453–465.
- 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. (1982): A neoselachian shark tooth from the Lower Triassic of the Kocaeli (= Bithynian) Peninsula. W Turkey. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1982**: 272–278.
- THIES, D. (1983): Jurazeitliche Neoselachier aus Deutschland und S-England (Jurassic Neoselachians from Germany and S-England). – Courier Forschungsinstitut Senckenberg, **58**: 1–116.
- THIES, D. (1991): *Palaeospinax*, *Synechodus* and/or *Paraorthacodus*? The problem of palaeospinacid genera (Pisces, Neoselachii). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **9**: 549–552.
- THIES, D. (1992): A new species of *Palaeospinax* (Chondrichthyes, Neoselachii) from the Lower Jurassic *Posidonia* Shale of Southern Germany. – Paläontologische Zeitschrift, **63**: 137–146.
- THIES, D. (1993): *Palaeospinax*, *Synechodus* and/or *Paraorthacodus*. Is the problem of palaeospinacid genera (Pisces, Neoselachii) solved? – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **12**: 724–732.
- THIES, D. (1995): Placoid Scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of northern Germany.



- Journal of Vertebrate Paleontology, **15**: 463-481.
- THIES, D. (in press): A catshark (Neoselachii, Carcharhiniformes, Scyliorhinidae) from the Late Jurassic of Germany. – *Paläontologische Zeitschrift*.
- THIES, D. & CANDONI, L. (1998): *Corysodon* SAINT-SEINE 1949 – a valid genus of Mesozoic neoselachian sharks. – *Geologica et Palaeontologica*, **32**: 221-233.
- THIOLLIÈRE, V. J. (1854): Description des poisons fossils provenant des geissements corallines du Jura dans le Bugey, Vol. I; Paris (J. B. Bailliere), 28 pp.
- TURNER, S. & YOUNG, G. C. (1987): Shark teeth from the early Middle Devonian Cravens Peak Beds, Geogina Basin, Queensland. – *Alcheringa*, **11**: 233-244.
- UNDERWOOD, C. J. (2002): Sharks, rays and a chimaeroid from the Kimmeridgian (Late Jurassic) of Ringstead, Southern England. – *Palaeontology*, **45**: 297-325.
- UNDERWOOD, C. J. & MITCHELL, S. F. (1999): Albion and Cenomanian selachian assemblages from North-East England. – *Special Papers in Palaeontology*, **60**: 9-56.
- UNDERWOOD, C. J. & WARD, D. J. (2004): Neoselachian Sharks and Rays from the British Bathonian (Middle Jurassic). – *Palaeontology*, **47**: 447-501.
- VIHOL, G. (1996): The palaeoenvironment of the Late Jurassic fishes from the southern Franconian Alb (Bavaria, Germany). – In: AR-RATIA, G. & VIOHL, G. (Eds): *Mesozoic Fishes – Systematics and Paleoecology*; Munich (Pfeil), 513-528.
- 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.
- WAGNER, J. A. (1861): Monographie der fossilen Fische aus den Lithographischen Schiefern Bayerns. – *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften*, **9**: 16-20.
- WARD, D. J. & THIES, D. (1987): Hexanchid shark teeth (Neoselachii, Vertebrata) from the Lower Cretaceous of Germany and England. – *Mesozoic Research*, **1**: 89-106.
- WINCHELL, C. J., MARTIN, A. P. & MALLATT, J. (2003): Phylogeny of elasmobranchs based on LSU and SSU ribosomal RNA genes. – *Molecular Phylogenetics and Evolution*, **31**: 214-224.
- WOODWARD, A. S. (1866): On the Paleontology of the Selachian Genus *Notidanus*, CUVIER. – *Geological Magazine, New Series*, **3**: 205-217.
- WOODWARD, A. (1889): Catalogue of the fossil Fishes in the British Museum. Part I; London (British Museum, Natural History), 474 pp.
- WOODWARD, A. S. (1918): The fossil fishes of the English Wealden and Purbeck formations, Part II. – *Monographs of the Palaeontographical Society*, **70**: 49-104.
- WOODWARD, A. (1919): On two new elasmobranch fishes (*Crossorhinus jurassicus*, sp. nov. and *Protospinax annectans*, gen. et sp. nov.) from the Upper Jurassic lithographic stone of Bavaria. – *Proceedings of the Zoological Society of London*, **13**: 231-235.
-