

Skeletal anatomy of the extinct shark *Paraorthacodus jurensis* (Chondrichthyes; Palaeospinacidae), with comments on synechodontiform and palaeospinacid monophyly

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The skeletal morphology of *Paraorthacodus jurensis*, a Late Jurassic neoselachian from Nusplingen, is described based on the incomplete holotype and a newly discovered almost complete specimen. For the first time, the postcranial skeleton could be investigated. *Paraorthacodus* is characterized by a monognath dental heterodonty and tearing-type dentition. The number of lateral cusplets in the lateral teeth differs between the holotype and the new specimen, possibly indicating sexual dimorphism. Clasper organs are not preserved in either of the two specimens. The notochord is sheathed by about 123 well-calcified vertebral centra. The posterior-most caudal vertebrae are lacking. The transition from monospondylous thoracic to diplospondylous abdominal vertebrae occurs at centra 48 and 49. The origin of the caudal fin is at the 80th centrum. Most conspicuous is the presence of a single spineless dorsal fin. In this respect, *Paraorthacodus* differs from most palaeospinacids, but resembles *Macrourogaleus*. *Palidiplospinax* possibly is sister to a group comprising *Synechodus*, *Paraorthacodus*, and *Macrourogaleus* (the Palaeospinacidae). A reinterpretation of dental and skeletal characters of synechodontiform taxa indicates that Synechodontiformes and Palaeospinacidae are monophyletic groupings of basal neoselachians. Synechodontiformes is probably sister to all living elasmobranchs.

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ADDITIONAL KEYWORDS: Kimmeridgian – late Jurassic – lithographic limestones – Neoselachii – Nusplingen – southern Germany – Synechodontiformes – systematic position.

INTRODUCTION

Neoselachii (sharks, skates, and rays) is a well-defined monophyletic clade representing one of the most successful and highly diverse groups of marine vertebrates. Its fossil history encompasses almost 300 million years and probably extends back into the Early Permian (e.g. Ivanov, 2005), although the oldest isolated remains such as teeth are very rare. Phylogenetic and fossil record analyses indicate a first

major radiation event and high taxonomic diversity in the Jurassic, when all major clades appeared with the exception of Squaliformes and Lamniformes (Kriwet & Klug, 2008; Kriwet *et al.*, 2008).

Nevertheless, our understanding of early neoselachian diversity is still very inadequate despite many recent advances (Thies & Candoni, 1998; Böttcher & Duffin, 2000; Underwood, 2002, 2006; Kriwet, 2003a, b; Kriwet & Klug, 2004; Maisey, Naylor & Ward, 2004; Underwood & Ward, 2004b). This is mainly related to the nature of preservation, because selachian skeletons are mostly cartilaginous and rarely preserved as fossils. Isolated material (e.g. teeth,

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placoid scales, or fin spines), conversely, are very resistant and easily become fossilized. As a basic principle, teeth are taxonomically and systematically useful. Similar trophic adaptations, however, might result in similar tooth morphologies in not closely related groups, just as many taxa show different degrees of ontogenetic and sexual dental variability. Only the precise study of tooth morphologies in combination with fossilized skeletal elements enables the establishment of systematically useful tooth characters for inferring interrelationships and diversity patterns through time.

Despite the fact that isolated teeth are very abundant in the fossil record, limited skeletal remains of neoselachians have been reported from the Lower Jurassic (200–175 Mya) of southern England and southern Germany, the Upper Jurassic lithographic limestones (160–145 Mya) of south-eastern France and southern Germany, and the Upper Cretaceous limestones (100–65 Mya) of Germany, Lebanon, southern England (Chalk) and the USA (Niobrara Chalk) up to now. Articulated skeletons are also known from the Eocene (56–34 Mya) of Bolca (Italy), the Eocene Green River Formation of the USA, and the Oligocene of Frauenweiler (southern Germany). In these localities, cartilaginous remains and soft-bodied structures are preserved, contributing to our understanding of morphological traits in early and/or extinct neoselachians.

The stratigraphically oldest known group within Neoselachii is the synechodontiforms, which are considered to be a monophyletic group of basal galeomorph sharks without any extant representatives (see below). Their fossil record ranges from the Early Permian (295 Mya) to the Eocene (34 Mya) (e.g. Capetta, 1973, 1992; Duffin & Ward, 1993; Underwood, Mitchell & Veltkamp, 1999; Böttcher & Duffin, 2000; Cuny, Rieppel & Sander, 2001; Delsate, Duffin & Weis, 2002; Kriwet & Klug, 2004, 2008; Maisey *et al.*, 2004; Ivanov, 2005; Klug & Kriwet, 2008). Nine genera have been described to date from the northern and southern hemispheres (e.g. Duffin, 1982, 1987, 1993a, b, c; Biddle, 1993; Cvancara & Hoganson, 1993; Johns, Barnes & Orchard, 1997; Underwood, 2002; Kriwet, 2003a, b; Underwood & Ward, 2004a, b; Klug & Kriwet, 2006). Within synechodontiforms, the Palaeospinacidae are considered the most diverse family with more than 30 described species in four genera: *Macrourogaleus* Fowler, 1947, *Paraorthacodus* Glikman, 1957, *Palidiplospinax* Klug & Kriwet, 2008, and *Synechodus* Woodward, 1888 (e.g. Kriwet & Klug, 2004; Klug, 2008, 2009; Klug & Kriwet, 2008; Klug *et al.*, 2008). The genera *Palidiplospinax* from the Early Jurassic (southern England, southern Germany), *Macrourogaleus* from the Late Jurassic (southern Germany), and *Synechodus* from the Late

Jurassic (southern Germany) and Late Cretaceous (Chalk, southern England) are represented by skeletal remains.

So far, the only known skeletal remain of the palaeospinacid *Paraorthacodus* is the holotype of *Paraorthacodus jurensis* (Schweizer, 1964; Dietl & Schweigert, 2001, 2004). This specimen lacks the postpectoral parts as well as the anterior tip of the skull. The intentions of this paper are: (1) to present a new and almost complete specimen of this taxon; (2) to give a detailed anatomical description of *Par. jurensis* based on the holotype and the new specimen; (3) to present an emended diagnosis for the genus and species; and (4) to discuss the systematic position of this shark and its relatives.

MATERIAL AND METHODS

The fossil material of the palaeospinacid shark *Par. jurensis* (Schweizer, 1964) described herein consists of two skeletal remains both coming from the locality of Nusplingen; the very incomplete skeleton of the holotype and a new, nearly completely preserved skeleton, which shows remarkable morphological details. The Upper Jurassic locality of Nusplingen is located in south-western Germany (Fig. 1) and has been famous for its exceptional preservation of fossils since the middle of the 19th century (e.g. Fraas, 1855; Quenstedt, 1855, 1857). These lithographic limestones are similar to those of the Solnhofen area in south-eastern Germany, which are, however, much richer and more diverse in their fossil content such as sharks (e.g. Kriwet & Klug, 2004, 2008; Carvalho, Kriwet & Thies, 2008; Klug, 2009). The Nusplingen Lithographic Limestone is of late Kimmeridgian age based on its characteristic ammonite fauna and belongs to the *Beckeri* zone, *Ulmense* subzone (see Schweigert, 1998, 2007; Schweigert & Zeiss, 1999).

The history of the finding of the holotype could not be reconstructed because of missing or imprecise available data, but the holotype might have been excavated in the 19th century. Although neither Schweizer (1964) nor Duffin (1993a) provided detailed information about the precise quarry, the holotype comes most probably from the finding bed G of the so-called Nusplingen quarry, where the Staatliches Museum für Naturkunde Stuttgart (SMNS) started excavating the Nusplingen Lithographic Limestone for scientific purposes again in 1994. The second specimen of *Par. jurensis* was discovered during the 2005 field campaign of the SMNS in bed L, which is slightly older than the finding bed G of the holotype (for stratigraphical age see Dietl *et al.*, 1998). The biostratigraphical age of both beds is the same (e.g. Schweigert, 1998). The most abundant fossil shark

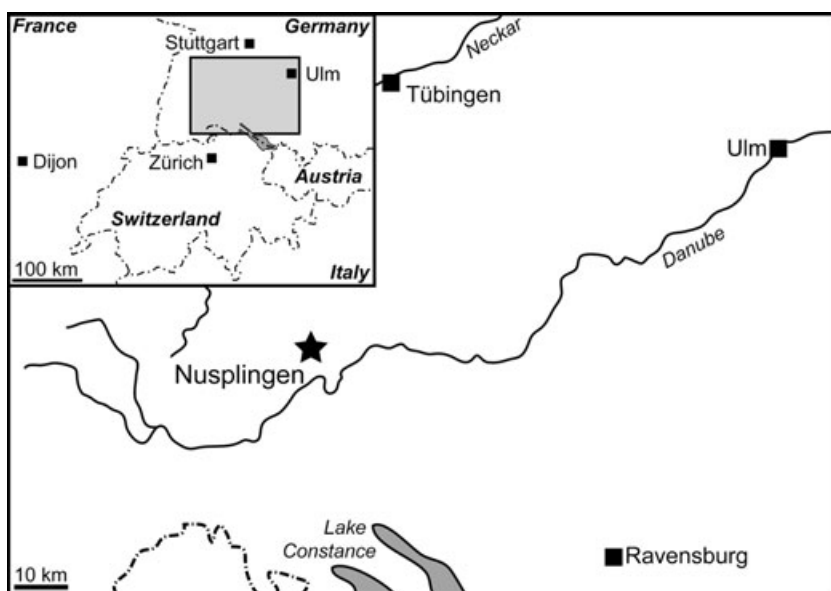


Figure 1. Map showing the geographical location of Nusplingen in south-western Germany.

from this limestone is the angel shark *Pseudorhina acanthoderma* (Fraas, 1854) and additional isolated remains of chondrichthyans, such as isolated teeth of *Sphenodus nitidus* Wagner, 1861 and *Notidanoides muensteri* Agassiz, 1843.

The photographs of teeth of the holotype were taken with a Leica MZ 95 stereomicroscope combined with the software Leica Application Suite [Version 2.8.1 (Build : 1554), Leica Microsystems (Switzerland) Limited, Leica Microsystems CMS GmbH]. The X-ray photographs of the holotype were performed by the 'Horse-Clinic' Kirchheim, Germany.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; BSPGM, Bayerische Staatssammlung für Paläontologie und Geologie München, Germany; GPIT, Geologisch-Paläontologisches Institut Tübingen, Germany; IRSNB, Institut royal des Sciences naturelles de Belgique; JME, Jura-Museum Eichstätt, Germany; MNHL, The Natural History Museum, London, United Kingdom (collection numbers under BMNH); SMF, Senckenberg-Museum Frankfurt, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

SYSTEMATIC PALAEOLOGY

The terminologies used for the skeletal morphology are those of Compagno (1984, 1999), Maisey (1986a,

b), and Iuliis & Pulerà (2007), and for the dental morphology follow Cappetta (1987), Siverson (1992) and Shimada (2002).

SUPERCLASS CHONDRICHTHYES HUXLEY, 1880
 CLASS ELASMOBRANCHII BONAPARTE, 1838
 COHORT EUSELACHII HAY, 1902
 SUBCOHORT NEOSELACHII COMPAGNO, 1977
 SUPERORDER GALEOMORPHII COMPAGNO, 1973
 ORDER SYNECHODONTIFORMES DUFFIN &
 WARD, 1993
 FAMILY PALAEOSPINACIDAE REGAN, 1906
 GENUS *PARAORTHACODUS* GLIKMAN, 1957

Type species: Synechodus recurvus Trautschold, 1877, Cenomanian (Late Cretaceous) of the Volga region, Russia.

Revised diagnosis: Palaeospinacid shark characterized by the following combination of features: orbital process lacking; two ventral (anteroventral and posteroventral) labial cartilages; pectoral girdle attached to sixth vertebra; coracoid bars not fused to each other but separated by a sternal cartilage; suprascapular processes present; vertebrae of astero-spondylic type; hook-shaped haemal arches present in diplospondylous precaudal vertebrae; single dorsal fin without fin spine; dorsal fin posteriorly located and inserts at 57th centrum; haemal arches and haemal spines not fused throughout caudal fin; dentition with gradient monognathic heterodonty; small parasymphysial teeth present; generally constant number of

lateral cusplet pairs in tooth families; cusp and cusplets deeply notched; linear decrease of cusp height from main cusp laterally; labial base of crown not jutting out above crown/root junction; cutting edges well developed; root vascularization pattern of distinct pseudopolyaulacorhize type with labial depression to which basally open nutritive grooves are restricted,

Differential diagnosis: *Paraorthacodus* differs most noteworthy (1) from all non-neoselachian chondrichthyans in having a reduced number of labial cartilages, a segmented notochord with well-calcified vertebral centra and a triple-layered tooth enameloid including a parallel-fibred layer; (2) from squalomorph sharks (including hexanchiforms, which also have a single dorsal spineless fin) in having five branchial arches and lacking an orbital process on the palatoquadrate; (3) from heterodontiforms and orectolobiforms in having a single dorsal spineless fin, in the distinct tooth morphologies, and a well-developed rostrum; (4) from lamniforms and carcharhiniforms in having labial cartilages and lacking a tripodal rostrum; (5) from *Sphenodus* in having teeth with well-developed lateral cusplets and well-developed nutritive grooves on the labial root face; (6) from *Palidiplospinax* in having small parasymphysial teeth and a single spineless dorsal fin; (7) from *Macrourogaleus*, in having comparably larger paired fins, no elongated anal fin, and a larger subtriangular dorsal fin and absent enlarged placoid scales on the dorsal caudal crest; (8) from *Synechodus* in having a single dorsal fin, comparably shorter dental laminae in relation to jaw length, teeth with central cusps at least twice as high as lateral cusplets, all teeth with symmetric number of lateral cusplets in all files (in *Synechodus*, the number of lateral cusplets is asymmetric in lateral files), cusplets deeply separated from main cusp, labial crown face not jutting out over root, linear decrease of crown height from tip of main cusp towards the most lateral cusplet in labial and lingual views, basal face of root comparably more horizontal in all tooth positions.

Included species: *Paraorthacodus andersoni* (Case, 1978) from the Santonian and Campanian, *Paraorthacodus antarcticus* Klug *et al.*, 2008, from the Campanian, *Paraorthacodus clarkii* (Eastman, 1901) from the Thanetian, *Paraorthacodus conicus* (Davis, 1890) from the Coniacian to Campanian, *Paraorthacodus eocaenus* (Leriche, 1902) from the Thanetian to Ypresian, *Paraorthacodus jurensis* (Schweizer, 1964) from the Kimmeridgian, *P. nerviensis* (Leriche, 1929) from the uppermost Cretaceous, *Paraorthacodus patagonicus* (Ameghino, 1893) from the Coniacian, *Paraorthacodus recurvus* (Trautschold,

1877) from the Albian and uppermost Cretaceous, *Paraorthacodus sulcatus* (Davis, 1888) from the Campanian, *Paraorthacodus validus* (Chapman, 1918) from the Cretaceous.

PARAORTHACODUS JURENSIS (SCHWEIZER, 1964)

Synechodus jurensis; Schweizer, 1964: 63, pl. 7 figs 1–9, pl. 8 figs 5–6.

Synechodus jurensis; Reif, 1973a: 9, fig. 7e–k.

Synechodus jurensis; Reif & Goto, 1979: fig. 2e.

Synechodus jurensis; Maisey, 1985: 15.

Synechodus jurensis; Reif, 1985: text-fig. C(e).

Paraorthacodus jurensis; Duffin, 1993a: text-figs 2–4, pls 1–3.

Paraorthacodus cf. jurensis; Dietl *et al.*, 2006: pl. 5.

Paraorthacodus jurensis; Dietl *et al.*, 2007: pl. 5.

Holotype: Specimen described by Schweizer (1964) from the upper Kimmeridgian (Upper Jurassic) of the Nusplingen Lithographic Limestone of south-western Germany, bed G (see also Aldinger, 1930; Duffin, 1993a; Dietl *et al.*, 1998). The specimen is housed in the GPIT under collection number GPIT 1210/1.

Revised diagnosis: A species of *Paraorthacodus* characterized by the combination of the following skeletal and dental characters (upper and lower teeth are not distinguishable in preserved specimens): pelvic girdle inserts at 42nd to 43rd vertebra; transition from monospondylous abdominal to diplospondylous pre-caudal vertebral column between centra 48 and 49; diplospondylous caudal fin skeleton starts at 80th centrum. Sexual dimorphism in tooth morphology present by a different number of lateral cusplets in all tooth positions: number of cusplets of gender 1 (holotype) without brackets, of gender 2 (new specimen) with brackets; main cusp with high coronal profile in anterior and lateral teeth, with low coronal profile in posterior teeth; ornamentation of delicate nonbifurcating vertical ridges originating above crown/root junction in labial view, and above the prominent lingual neck lacking any ornamentation in lingual view. Single left and right small parasymphysial teeth with straight and slender main cusp flanked by two pairs of triangular cusplets diverging from main cusp, and U-shaped root in labial view. Anterior teeth with main cusp flanked by two(three) pairs of lateral cusplets; main cusp without distal inclination; parallel cutting-edges in the upper two-thirds of main cusp, lowest third expanding to the doubled width; cusplets inclined towards main cusp and staggered downwards laterally; ornamentation on lowest third of main cusp and lowest half of cusplets in labial view; in lingual view ornamentation on the lower half of the main cusp and lower two-thirds of cusplets; root lobes

slightly curved anteriorly in basal view; in labial view root lobes curved downwards. Lateral teeth with main cusp flanked by three(four) pairs of lateral cusplets; distally inclined main cusp in anterior-most teeth; mesial cusplets slightly distally inclined; distal cusplets straight and only most lateral inclined mesially; crown base of anterolateral teeth slightly curved downwards, of posterolateral teeth horizontal in labial view; parallel cutting-edges in the upper two-thirds of main cusp, lowest third expanding to the doubled width; expansion of ornamentation in labial and lingual view same as in anterior teeth; root lower than in anterior teeth; root lobes slightly curved downwards in anterolateral teeth in labial view; horizontal root base in other lateral positions; in basal view root lobes faintly curved labially with very deep and rectangular expansion. Posterior teeth with main cusp flanked by two(three) pairs of lateral cusplets, reduced to one(two) pairs to the commissure; main cusp slightly distally inclined; teeth decrease in width and height posteriorly; lateral cusplets almost reach same height as main cusp towards the commissure; ornamentation increases in height on labial face towards the commissure reaching apex in posterior-most teeth; lingual face ornamented throughout the crown; root with horizontally noncurved basis.

Comments: Maisey *et al.* (2004) assigned an incomplete skeleton of a Late Jurassic shark from the Solnhofen area, which is housed in the Senckenberg Museum Frankfurt (FSM P.4392) tentatively to *Paraorthacodus*. Unfortunately, this specimen, despite displaying a lot of morphological information, has no unpaired fins preserved. Based on dental structures, however, this specimen should be assigned to *Synechodus* (S. Klug, unpubl. data). Consequently, the two specimens of *Par. jurensis* and two small specimens of *Paraorthacodus* sp. (which might be juveniles to *Par. jurensis*) from the Solnhofen quarries (compare Kriwet & Klug, 2004: fig. 7; Klug & Kriwet, 2008: fig. 3a) are the only known skeletal remains of this genus that allow the identification of additional skeletal diagnostic characters in addition to dental features for comparison with and differentiation from other species of *Paraorthacodus*.

Referred specimen: A single specimen from the upper Kimmeridgian (Upper Jurassic) of the lithographic limestones of Nusplingen (south-western Germany), bed L. The specimen is housed in the SMNS under collection number SMNS 88987/1.

DESCRIPTION

In the holotype of *Par. jurensis* the anterior part of the vertebral column, the pectoral girdle, the branchial

apparatus, and the skull, which lacks the snout and the anterior-most tips of the jaws, are preserved in ventral view (Fig. 2). The new and much more complete skeleton of this species is preserved anteriorly in ventral view, whereas the posterior part is visible in lateral view because of the torsion of the vertebral column posterior to the pelvic girdle (Fig. 3). The preserved total length of the specimen is 1240 mm. The dentition with abundant teeth, the skull, the pectoral and pelvic girdles with fin-bases, the dorsal fin with its base, the caudal fin skeleton, the vertebral column, and several shagreened placoid scales are fossilized. Both specimens are about of the same size according to the similar size of the preserved skull elements.

In the following, we will not repeat in detail the description of the holotype, which was published by Schweizer (1964) and Duffin (1993a), but only provide additional information.

SKULL

Despite the fact that the anterior portions of both specimens of *Par. jurensis* are quite well preserved in ventral views, they do not display abundant cranial features, rendering the identification and reconstruction of most neurocranial parts impossible. This is mainly because the cranium is deeply imbedded in the sediment and because elements of the visceral arches additionally obscure the ventral aspect of the cranium.

The preserved parts of the holotype (GPIT 1210/1) are only slightly disarticulated. However, the anterior parts of the jaws and the right branchial apparatus are lacking (Fig. 2). The new, very well-preserved specimen (SMNS 88987/1) shows skeletal elements in different views such as the rostrum, jaws in lingual and labial views, the hyoid, and the branchial apparatus (Fig. 4). The basihyal is the only cartilaginous element of the mandibular and hyoid arches that is missing in both specimens. This median cartilage articulates anteroventrally with the ceratohyals and represents the mouth floor.

Neurocranium

The neurocranium is not accessible in the holotype. In the new specimen, portions of the ethmoidal region are visible in ventral view only. The orbital, otic, and occipital regions are obscured by silicified sediment and additionally the jaw and anterior branchial elements. The rostrum, which is the most anterior part of the neurocranium, is the only preserved element of the neurocranium. This structure supports the prenasal snout and generally encloses the anterior part of the precerebral fossa in neoselachians. It is spoon-shaped with a rounded blunt tip. It extends forward

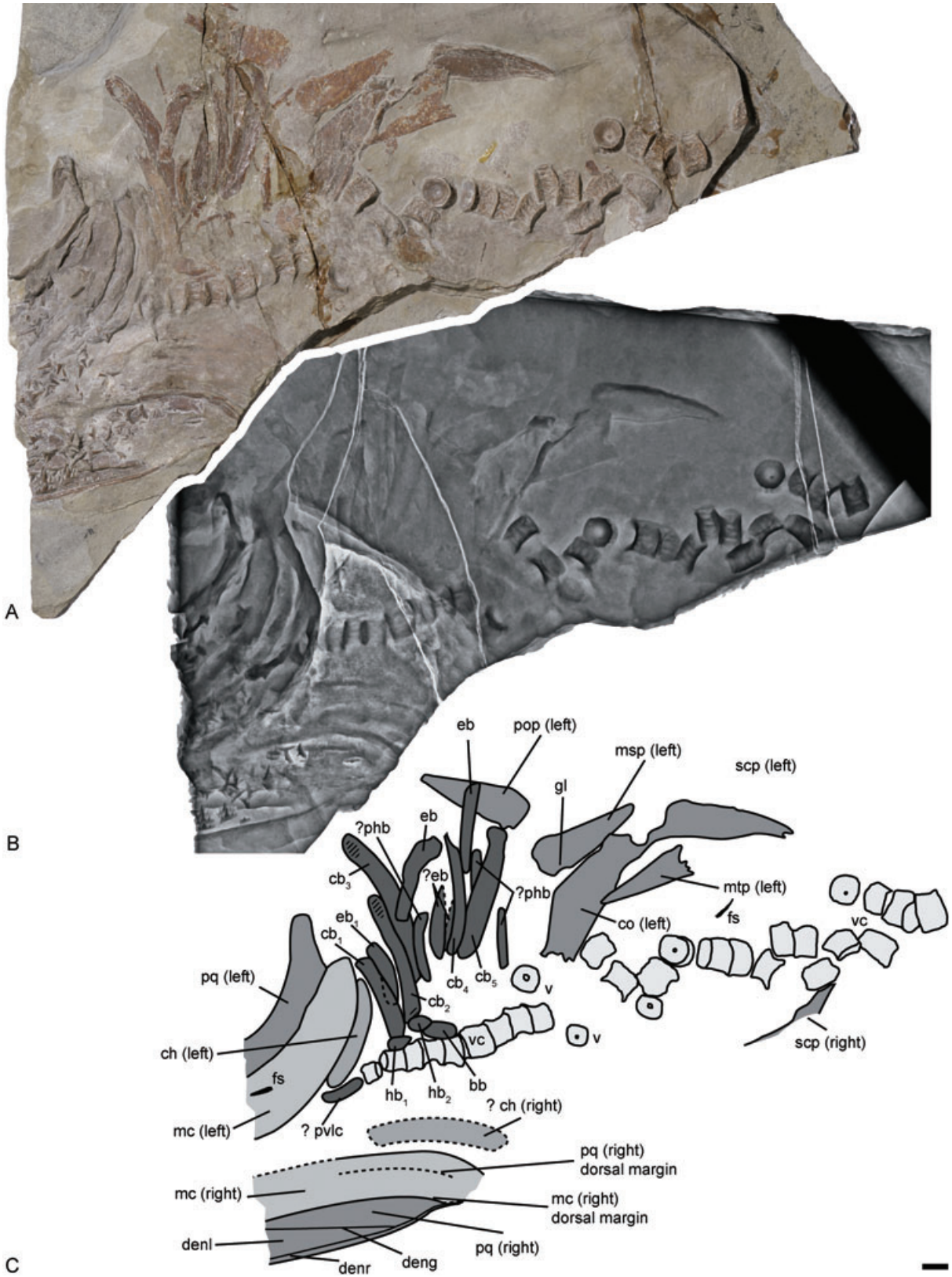


Figure 2. The holotype of *Paraorthacodus jurensis* (GPIT 1210/1). A, holotype as preserved including the skull, the left branchial apparatus, the pectoral girdle, and the anterior portion of the vertebral column. B, radiograph of the anterior portion of the holotype. C, camera-lucida drawing of the holotype. Scale bar = 10 mm. Abbreviations: bb, basibranchial; cb, ceratobranchial; ch, ceratohyal; co, coracoid bar; deng, dental groove; denl, dental lamina; denr, dental ridge; eb, epibranchial; fs, fin spine of a chimeroid; gl, glenoid surface; hb, hypobranchial; mc, Meckel's cartilage; msp, mesopterygium; mtp, metapterygium; phb, pharyngobranchial; pop, propterygium; pq, palatoquadrate; pvlc, posteroventral labial cartilage; scp, scapular process; v, vertebra; vc, vertebral column.

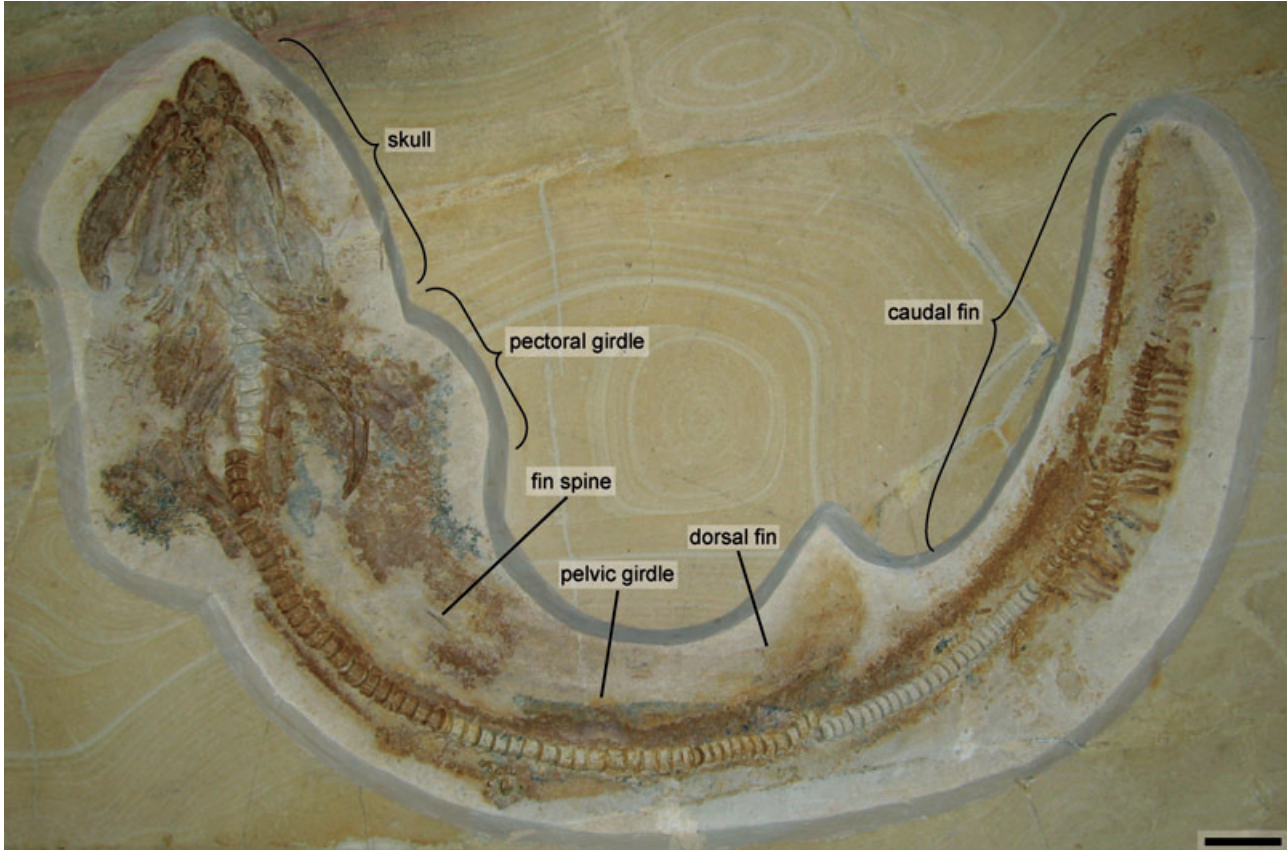


Figure 3. Complete articulated specimen of *Paraorthacodus jurensis* (SMNS 88987/1). Scale bar = 50 mm.

over a subterminal and crescentic mouth. Individual rostral cartilages or bars are not visible.

Jaws

The upper and lower jaws are very well preserved in the new specimen and are visible according to the disarticulation of the skull in different views (Fig. 5). The right palatoquadrate and Meckel's cartilage are preserved in lingual views and the left Meckel's cartilage in labial view. The posterior portion of the left palatoquadrate is also seen in labial, the anterior half conversely in ventral view. The weaker articulation of the symphysis resulted in the anterior disconnection of the lower and upper jaw elements, which are separated. The jaw suspension is of amphistylic type and this shark evinces the 'double' selachian-type jaw

articulation consisting of the lateral and medial quadratomandibular joints and which is preserved in life position in the left jaw.

Meckel's cartilage (Fig. 5A–B): The lower jaws of the new specimen measure 56 mm in total length. They taper anteriorly to the slender symphysis. The dental region expands posteriorly from the anterior tip of the symphysis and decreases along the jaw about two-thirds of the total length of the Meckel's cartilage. This region is subdivided into three specific structures with different functional morphologies. Teeth originate in the dental groove and are transported by the dental lamina to the dental ridge, where they reach their functional position. These structures are very well preserved in both lower jaws, but visible

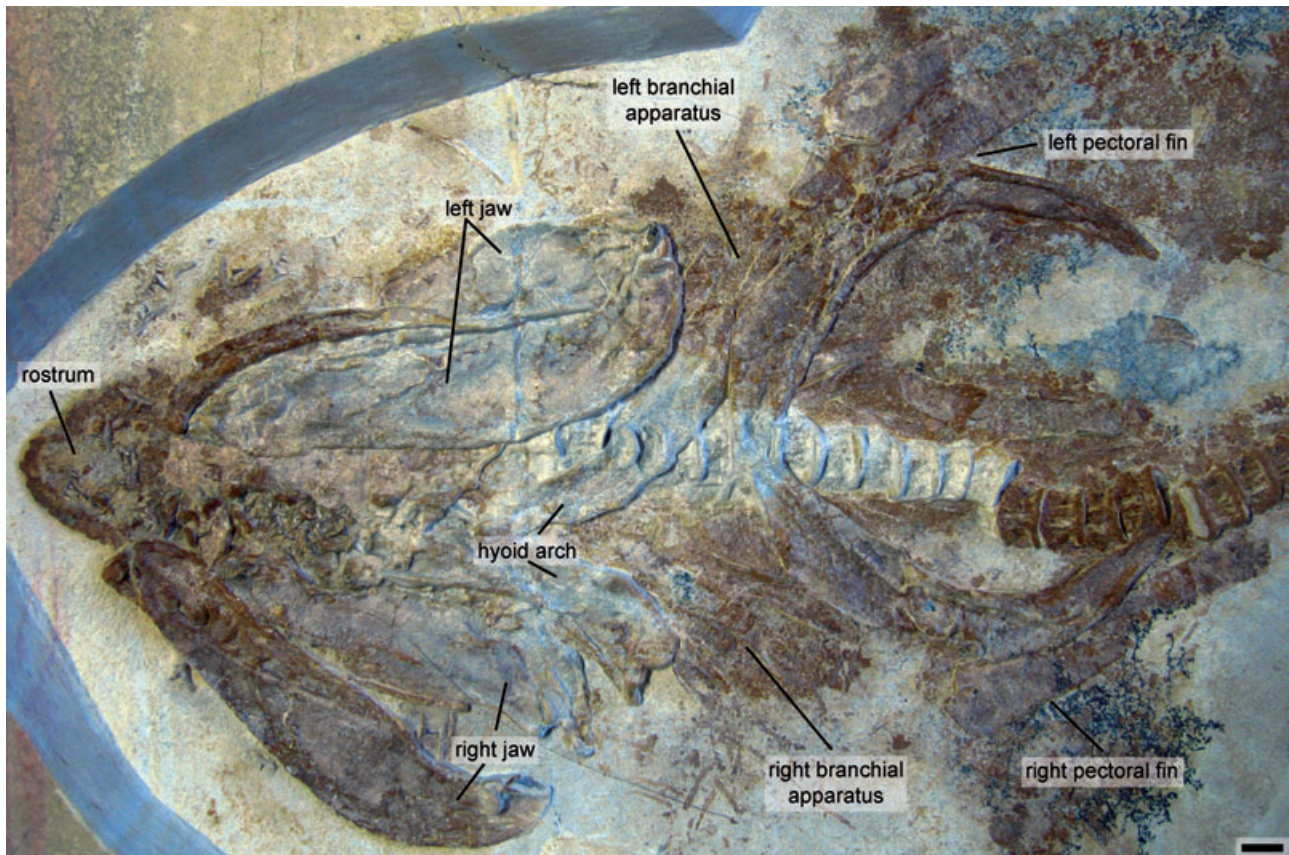


Figure 4. Skull and pectoral girdle of *Paraorthacodus jurensis* (SMNS 88987/1). Scale bar = 10 mm.

only as imprints on the left Meckel's cartilage because of its preservation in labial view. Especially the dental ridge is very prominent in the anterior part but diminishes towards the posterior. A subdivision of the dental lamina into two separate areas as is found in lamniform sharks is absent. The posterior margin of the Meckel's cartilage is perspicuously curved and the vertical margin is not flattened. The sigmoidal dual articulation is visible in the left lower jaw and consists of the lateral and medial quadratomandibular joints. The articulation surfaces are very well visible in the right lower jaw. The lateral quadratomandibular joint lies posterior to the medial joint and displays the articular cotylus in the lower jaw, which is of ellipsoid shape with its roll axis along the longitudinal axis of the lower jaw. The medial quadratomandibular joint lies anterior to the lateral articulation. It displays a small condyle in the Meckel's cartilage, the articular knob, which is very prominent in this shark and very well preserved in the right jaw apparatus. The prominent articular process of the palatoquadrate fits into the articular cotylus of the Meckel's cartilage. The articular knob of the lower jaw articulates with the quadrate cavity of the upper jaw. This characteristic articulation is specialized and

prevents lateral movements and displacement of the upper and lower jaws. The lingual mandibular ridge, which is present next to the articular knob, encloses the internal mandibular concavity wherein fits the lower hyoid arch element, the ceratohyal.

Palatoquadrate: The right palatoquadrate of the holotype of *Par. jurensis* displays the dental lamina with two tooth rows *in situ* (Fig. 2A). The anterior tooth row consists of three and the posterior one of two teeth. The functional series is not preserved in these tooth rows (Fig. 6F, H). All other characteristics and features are better preserved in the new specimen (Fig. 5C–D). The upper jaws are 60 mm in total length. The dental region extends from the symphyseal articulation posteriorly along the ventral margin of the jaws comprising approximately two-thirds of the total length of the jaw. The right palatoquadrate is preserved in lingual view, as is the right Meckel's cartilage, which overlaps the upper jaw in its anterior part. The left palatoquadrate articulates with the left Meckel's cartilage in life position and is visible in labial view in its posterior portion. However, the anterior part of the left upper jaw is fossilized in a different way and compacted in a lateral direction, so

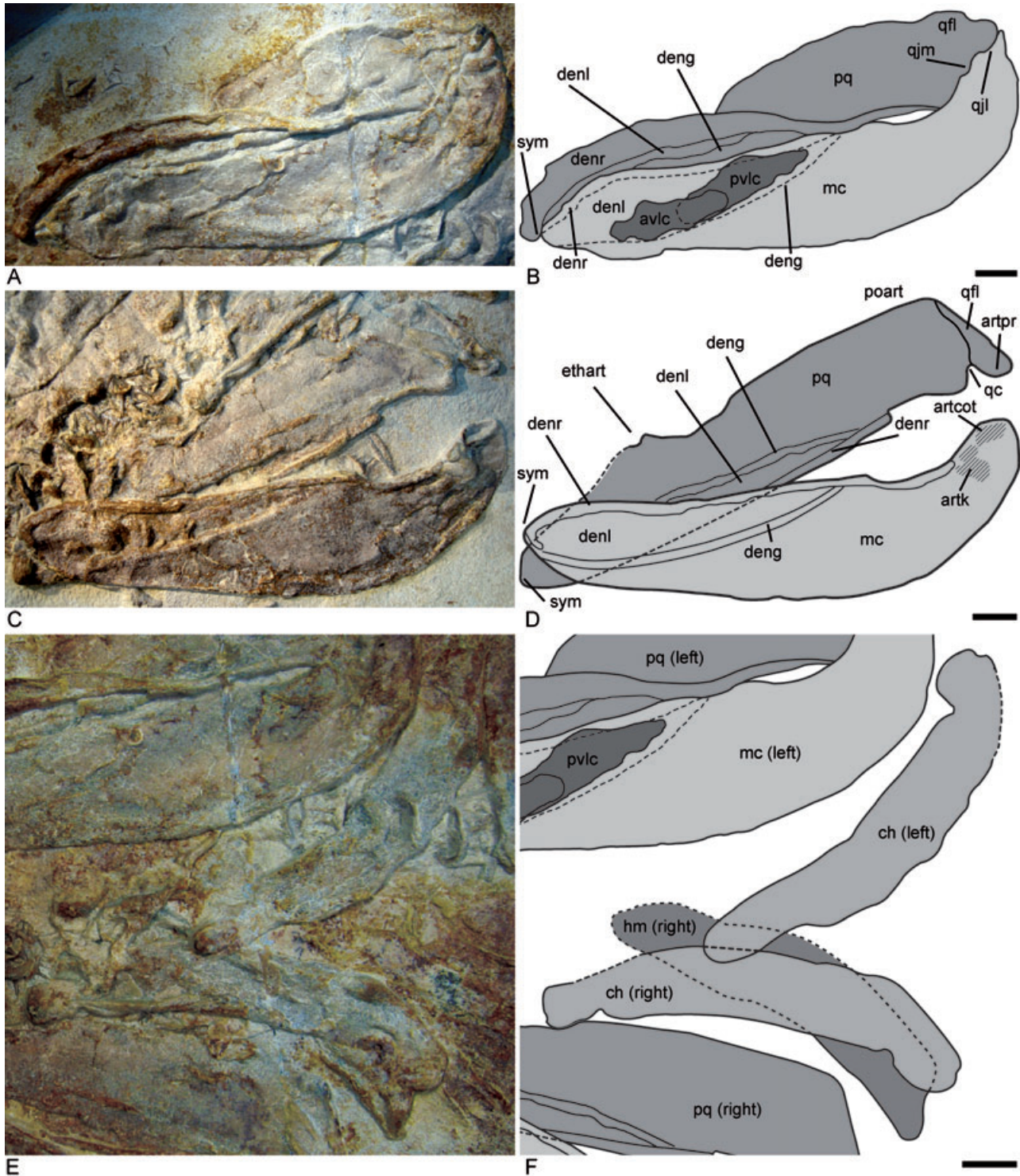


Figure 5. Jaws and hyoid apparatus of *Paraorthacodus jurensis* (SMNS 88987/1). A, left jaws as preserved. B, camera-lucida drawing of left jaws. C, right jaws as preserved. D, camera-lucida drawing of right jaws. E, hyoid apparatus as preserved. F, camera-lucida drawing of hyoid apparatus. Scale bars = 10 mm. Abbreviations: artcot, articular cotylus; artk, articular knob; artpr, articular process; avlc, anteroventral labial cartilage; ch, ceratohyal; deng, dental groove; denl, dental lamina; denr, dental ridge; ethart, ethmoidal articulation; hm, hyomandibular; mc, Meckel's cartilage; poart, postorbital articulation; pq, palatoquadrate; pvlc, posteroventral labial cartilage; qc, quadrate cavity; qfl, quadrate flange; qjl, lateral quadratomandibular joint; qjm, medial quadratomandibular joint; sym, symphysis.

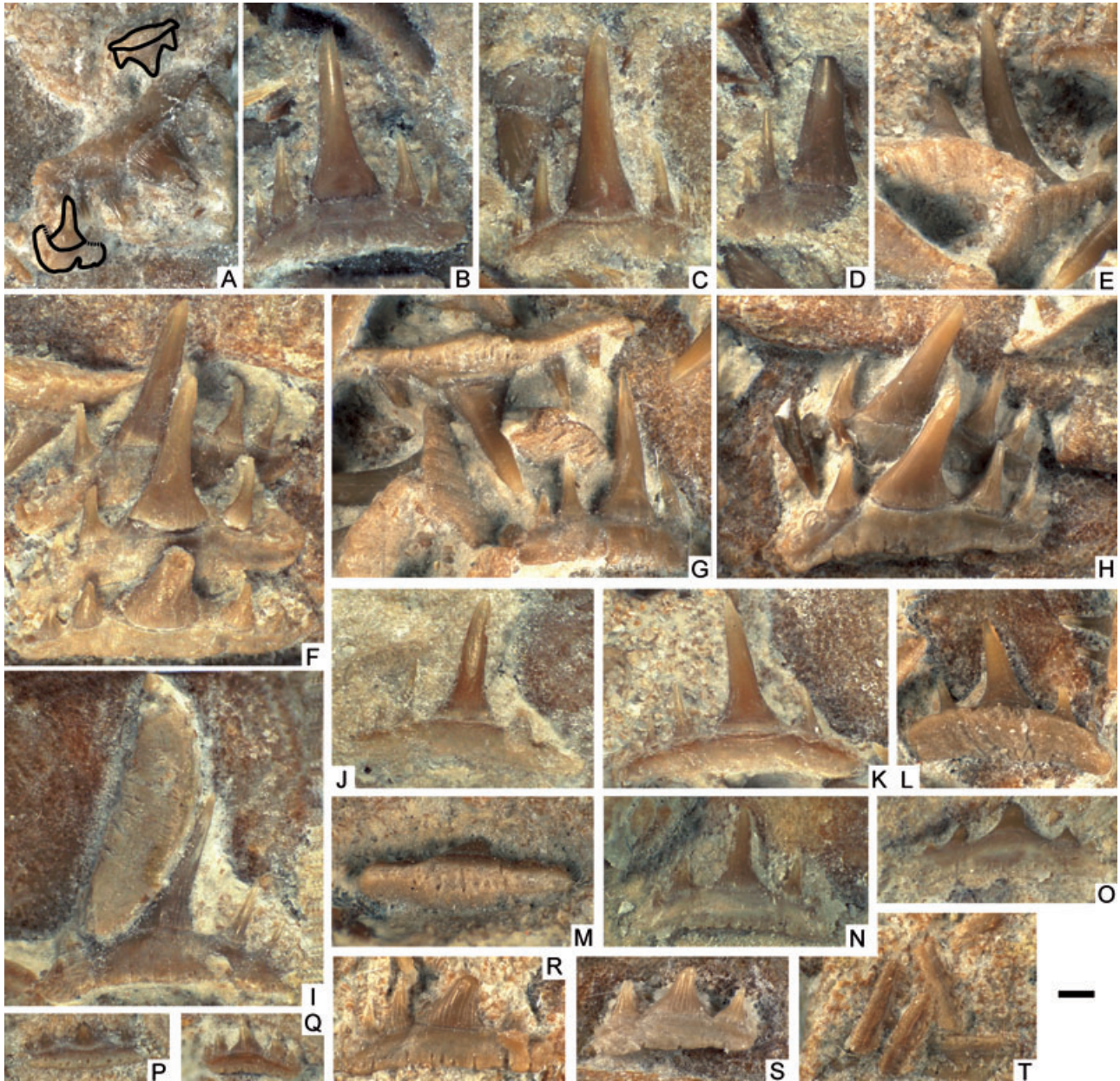


Figure 6. Teeth of the holotype of *Paraorthacodus jurensis* (GPIT 1210/1). A, parasymphysial teeth (outlined) in labial (bottom) and lingual (top) views. B–D, anterior teeth in labial views. E, anterior tooth in laterobasal view. F, lateral teeth of a single row in labial views. G, lateral teeth in laterobasal, lingual, and labial views (from left to right). H, lateral teeth of a single row in labial views. I, lateral teeth in basal (top) and labial (bottom) views. J–K, lateral teeth in labial views. L–M, anteroposterior teeth in linguobasal views. N, anteroposterior tooth in labial view. O, anteroposterior tooth in labiobasal view. P–Q, posterior teeth in lingual views. R–S, posterior teeth in labial views. T, four posterior-most teeth next to the commissure in labial view. Scale bar = 1 mm.

that it is not visible in labial but in ventral view. This orientation displays the slightly curved dental region with the dental groove and a very prominent dental ridge that tapers towards the commissure (Fig. 5A–B). The compression caused by taphonomic processes resulted in compaction of the dental lamina, which is

only present as a narrow strip. The dorsal processes are not very well preserved according to the orientation of the jaws. The ethmoidal articulation is only visible in the right upper jaw. However, the precise anterior outline of this neurocranial articulation process is not traceable because of the overlapping of

the teeth in this region. An orbital process is not present in *Par. jurensis* as it is also absent in all other galeomorph sharks. The dorsal margin of the palatoquadrates continues posteriorly towards the postorbital articulation process, which is located directly posterior to the dental groove. In the upper jaws, this process is not very well preserved because of the orientation impeding a straight view. The quadrate flange is present in both palatoquadrates expanding ventrally to the posterolateral extremity, where the articular process of the Meckel's cartilage is located.

Labial cartilages: Labial cartilages are paired elements that are located external to the mandibular arch. They are common in modern sharks and vary in size and number. These structures reduce the size of the mouth gape preventing food items from escaping before being swallowed. Lamniform and carcharhinoid sharks and some batoids are the only groups lacking labial cartilages. Most sharks display two dorsal (anterodorsal and posterodorsal) and one to two ventral (anteroventral and posteroventral) labial cartilages.

The holotype and the new specimen only have ventral labial cartilages preserved. The dorsal labial cartilages are not visible because of the orientation of the jaws and the faint condition of these elements avoiding the conspicuousness as imprint. The holotype displays only a single labial cartilage, which is dislocated ventrally towards the lower margin of the left ceratohyal (Fig. 2). This position and the faintly curved shape of this cartilage support its identification as the posteroventral labial cartilage. In the new specimen, two ventral labial cartilages are preserved almost in their original position external to the left Meckel's cartilage (Fig. 5A–B). They are elongated and expand in their central part tapering to their ends. The slightly shorter anteroventral labial cartilage overlaps the anterior portion of the posteroventral labial cartilage. They are dorsally located next to the dental groove and extend from the ventral margin of the Meckel's cartilage to the posterior end of the dental lamina.

Hyoid apparatus

The hyoid apparatus is the second arch of the visceral skeleton posterior to the mandibular arch. It is modified to suspend the jaw apparatus from the neurocranium, support the mouth floor and to assist in closing and opening of the jaws. The hyoid apparatus is located posterolingually to the Meckel's cartilage and the palatoquadrate and is articulated to different surfaces of the jaws and the neurocranium.

Ceratohyal: The right ceratohyal of the holotype is only visible in the radiograph because of sediment cover (Fig. 2B). The left ceratohyal is preserved

directly below the posteroventral margin of the left Meckel's cartilage and is partly overlapped by the ventral margin of the lower jaw. They are visible in labial view and display the same curvature as the ventral margin of the Meckel's cartilage. The ceratohyals of the new specimen are still preserved almost in their original position (Fig. 5E–F). Only the disarticulation of the jaws especially at their symphyseal articulation area enables the view on the labial face of these elements. They measure about two-thirds of the total length of the Meckel's cartilage and were connected to the mandibular arch by ligaments that attached next to the articulation surfaces of the lower and upper jaws. The ventral margin of the ceratohyals is regularly curved. The dorsal margin faintly tapers anteriorly and posteriorly and shows distinct indentations near the proximal ends. The posterior edge is rounded and represents a small notch at the posterior-most dorsal edge. The anterior edge of the ceratohyal is angled and displays a very distinct ligament facet of ellipsoid shape. This ligament jointed the ceratohyal to the not preserved basihyal.

Hyomandibula: Only the right hyomandibula is preserved in the new specimen (Fig. 5E–F). This element is visible in lingual view and displays the same curvature as the posterodorsal margin of the palatoquadrate. It measures about 60% of the total length of the palatoquadrate. The hyomandibula is obscured in most parts by the ceratohyals. The exposed posterior-most edge distinctly tapers. The anterior portion is more expanded and displays a drop-shaped, shallow depression. This depression represents the attachment area of ligaments that connect the hyomandibula to the postorbital region of the neurocranium.

Dentition

The dentition is characterized by a gradient monognathic heterodonty and is subdivided into parasymphysial, anterior, lateral, and posterior teeth. We identified parasymphysial and anterior teeth conversely to Duffin (1993a), who declared the anterior teeth described herein as symphyseal teeth. The holotype displays about 60 (Fig. 6) and the new specimen about 40 teeth (Fig. 7).

Parasymphysial teeth: Parasymphysial teeth are characterized by their position next to the symphysis and differ in size and/or morphology from all other teeth. Only the holotype of *Par. jurensis* displays two teeth of this type (Fig. 6A). They measure 2.1 mm in width and are very small compared to the teeth in anterior and lateral positions. The height of the tooth preserved in labial view is 2.2 mm. The height of lingually exposed tooth measures only 1.5 mm. A single main cusp flanked by a pair of lateral cusplets



Figure 7. Teeth of *Paraorthacodus jurensis* (SMNS 88987/1). A–B, anterior teeth in labial views. C, anterior teeth in labial (left) and lingual (right) views. D, anterior teeth in lingual views. E–H, lateral teeth in labial views. I–N, lateral teeth in lingual views. O, lateral tooth in basal view. P, lateral tooth in lingual view (left) and posterior tooth in labial view (right). Q–R, posterior teeth in lingual views. S, posterior tooth in labial view (scale bar only for S). All scale bars = 1 mm.

characterizes these teeth. The main cusp is straight and slender and expands in its lower third. The lateral cusplets are only present in the lingually exposed tooth and are lacking in the labially exposed tooth. The cusplets are very small, triangular, and their apices abandon the main cusp. The characteristic and pronounced separation of the main cusp and the lateral cusplets from each other is very distinct in labial view. There is no ornamentation visible or preserved on the labial or lingual faces of the crown. The root is U-shaped in labial view displaying the characteristic pseudopolyaulacorhize vascularization pattern with basally open nutritive grooves, which extend lingually at most to the middle of the root in basal view.

Anterior teeth: The anterior teeth of *Par. jurensis* are characterized by a high coronal profile with a slender upright central cusp flanked by up to three pairs of lateral cusplets. The ratio of crown width to crown height above the crown/root junction is about 0.85 in the anterior-most teeth (Fig. 7A–C) and continuously increases up to 1.1 in the last anterior position (Fig. 6B–D). The contour of most teeth, especially the apex, is often obscured and covered by sediment, which hampers the reconstruction of the precise ratio.

The cross section of the slender central cusp is subcircular to elliptical, with a more convex lingual than labial face. The central cusp is only slightly bent lingually with no perceivable sigmoidal curvature and no distal inclination. In all anterior tooth positions, two (in the holotype) to three (in the new specimen) pairs of lateral cusplets flank the main cusp. The distinct cutting edges are nearly parallel in the upper two-thirds of the main cusp. In the lowest third the main cusp expands to the doubled width. Deep notches distinctly separate the central cusp and the lateral cusplets from each other, which is characteristic for the genus *Paraorthacodus*.

The first pair of cusplets is half of the size of the central cusp's height. Adjacent lateral cusplets of teeth linearly decrease in size mesially and distally (Fig. 8). The slender and acute lateral cusplets resemble the main cusp's form. They are inclined towards the main cusp. This feature is more distinct in anterior-most than in adjacent tooth positions. The cross sections of the lateral cusplets are subcircular to circular. The cusplets are staggered downwards laterally in anterior-most teeth inchoate at the first pair and followed by the second and third pair. This feature is also more distinctive in anterior-most tooth positions.

The cutting edges are well developed and continuous through cusp and lateral cusplets. The ornamentation consists of very delicate, nonbifurcating vertical ridges. These ridges originate above the

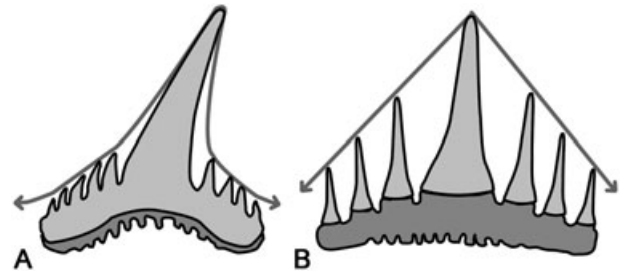


Figure 8. Generalized diagrams depicting the different decreases in crown heights of lateral cusplets. A, exponential decrease (*Synechodus*). B, linear decrease (*Paraorthacodus*).

crown/root junction and are not evenly distributed. This ornamentation covers at least the lower third of the labial face of the main cusp and the lower half of the labial face of the lateral cusplets. On the lingual face of the tooth crown, the ridges are more distinct and densely arranged. These ridges reach up to the middle of the central cusp's height and the lower two-thirds of the crown height of the lateral cusplets. Additionally, a very prominent lingual neck is developed lacking any ornamentation.

The roots of the anterior teeth are relatively high and the root lobes are slightly curved labially in basal view. In labial view, the root lobes are curved downwards, which is more distinct in the anterior-most teeth but less pronounced in posterior positions of anterior teeth. The vascularization pattern is of the characteristic palaeospinacid pseudopolyaulacorhize type displaying several nutritive groove openings exposed on the labial face, which open basally and extend lingually almost to the middle of the root base. These grooves vary in number and size. In lingual view, horizontally aligned foramina varying in number and size open onto the surface of the root.

Lateral teeth: Lateral teeth are characterized by a high coronal profile. The slender central cusp is maximally twice as high as the first pair of lateral cusplets. The general height of the lateral teeth decreases in posterior positions. The ratio of crown width to crown height is about 1.8 to 1.85 in the holotype, whereas the ratio of the new specimen ranges from 2.2 to 1.8. The additional pair of lateral cusplets in all lateral teeth in the latter specimen causes this variation. It is difficult to ascertain the precise ratio because of the embedding of teeth in the sediment matrix as for the anterior teeth.

The main cusp is bent lingually without any sigmoidal curvature. In anterior-most lateral teeth the main cusp is faintly distally inclined. Teeth of latero-posterior positions, conversely, display only very slightly distally inclined main cusps if at all. The

cross section of the main cusp and lateral cusplets is subcircular to rounded with convex labial and lingual crown faces. The holotype presents three and the new specimen four pairs of lateral cusplets. The height of the central cusp and lateral cusplets linearly decreases distally and mesially (Fig. 8). Mesial cusplets are slightly distally inclined. Distal cusplets are straight and only the most lateral ones are inclined towards the main cusp if at all. All lateral cusplets decrease in width at their bases. The cusp and all cusplets are well separated from each other by a deep notch reaching to the base of the crown. In anterolateral teeth the crown base is slightly curved downwards compared to posterolateral teeth, in which the crown base is horizontal in labial view.

The cutting edge is well developed and continuous through all cusp and cusplet apices. The ornamentation of the labial face resembles that of anterior teeth. The main cusp displays nonbifurcating, faint vertical ridges never exceeding the lower first third of the total height, whereas the cusplets bear the same ornamentation pattern with ridges reaching at least half of their height. The lingual face of the tooth crown shows the same ornamentation and the same morphology as the lingual neck as described above for anterior teeth. The roots are lower than in anterior teeth and the root lobes are only slightly curved downwards in anterolateral tooth positions in labial view. In all other tooth positions, the root has a horizontal base. In basal view, the root lobes are faintly curved labially. The vascularization pattern is of the same type as in anterior teeth displaying the same basally open nutritive grooves not extending far lingually. On the lingual root face numerous horizontally aligned foramina are visible, varying in size and number.

Posterior teeth: Posterior teeth can be subdivided into posterior teeth *sensu stricto* and teeth near the commissure. This distinction might be quite subjective but is supported by their general morphology and ornamentation pattern. Both types are preserved in the holotype, whereas the new specimen only displays teeth of the posterior positions *sensu stricto* (Fig. 7P–S). Posterior teeth are characterized by a very low coronal profile and only have a single to three pairs of lateral cusplets, converse to the condition in anterior and lateral teeth. The holotype displays a single or two pairs of lateral cusplets and the new specimen two to three. The ratio of crown width to crown height ranges from two to three. However the measurement conditions are the same as described in anterior and lateral teeth and therefore the size of teeth might be obscured.

The cross section of the main cusp and the cusplets is roughly circular displaying convex lingual and

labial faces. The main cusp is slightly inclined distally and lingually bent. The main cusp is flanked in anteroposterior tooth positions by two pairs of cusplets in the holotype and three pairs in the new specimen. Towards the commissure, the number of cusplet pairs is evenly reduced to a single in the holotype and two in the new specimen. All teeth decrease in width and height posteriorly. The main cusp displays the highest reduction of the height ratio in its upper part, distinguishable by the still present expanding base. The main cusp is less than twice as high as the first pair of cusplets. The lateral cusplets almost reach the same height as the main cusp towards the commissure. The cusps are also strictly separated from each other as described in anterior and lateral teeth.

The cutting edges are less well developed and the ornamentation pattern consists of the described faintly, nonbifurcating vertical ridges. These ridges increase in height on the labial face of posterior teeth towards the commissure and reach the apex in the posterior-most teeth. The lingual face displays the same pattern throughout the crown with the exception of the plain lingual neck.

The posterior teeth have a horizontally, in basal and labial views, noncurved root. These teeth display the characteristic vascularization pattern of the pseudopolyaulacorhize type with distinct visible nutritive grooves in labial view and numerous horizontally aligned foramina in lingual view, which vary in size and number.

The holotype presents very uncommon teeth of the position next to the commissure in addition to the described posterior teeth (Fig. 6T). These teeth display a very low crown but relatively high root and resemble the posterior-most crushing-like teeth in extant hexanchiforms to some extent. They measure 3.0 mm in total length and only 0.8 mm in maximum height. The main cusp and lateral cusplets are reduced to low and rounded bases, which are not deeply separated from each other in this tooth position. The distal cusplets are sometimes fused to a blade-like structure. The posterior-most commissural teeth display a very low tooth crown not separated into a main cusp and lateral cusplets. Faint ornamentation is present on the complete tooth crown.

Branchial apparatus

The branchial apparatus consists of five to seven branchial arches supporting the gills in living sharks. The most common number is five pairs of branchial arches. They consist of different elements. The most dorsal cartilages are homologous to the hyomandibula and consist of the pharyngobranchial element ventrally followed by the epibranchial element. The ventral cartilages representing the homologous

structure to the ceratohyal are the ceratobranchial and the hypobranchial elements. The hypobranchials sometimes differ in number and are connected to the unpaired basibranchials, which also differ in size, form, and number. The holotype has only parts of the left branchial apparatus preserved (Fig. 2). In the new specimen, parts of the left and right branchial apparatus are preserved (Fig. 9). The assignment of the different elements is partially difficult because of the delicate structure and the high dislocation of the branchial elements.

Pharyngobranchial elements: Three pharyngobranchial elements are preserved in the holotype and a single one in the new specimen (Figs 2, 9). They are slightly curved and display a more distinct curvature at the dorsal edge (Fig. 2). Two pharyngobranchials of the holotype are preserved in total length. The more anteriorly located cartilage is dedicated to the third branchial arch and is 28 mm long. The other element belongs to the fourth or fifth branchial arch and measures 25 mm in total length. The posterior part of the branchial apparatus is, unfortunately, too incomplete to detect any possible fusion of pharyngobranchials 4 and 5 to the fifth epibranchial element (pharyngobranchial blade, 'gill pickax'), which is characteristic of galeomorph sharks (plesiomorphically not present in heterodontids).

Epibranchial elements: Five epibranchial elements of the holotype and two of the new specimen are present (Figs 2, 9). The first epibranchial of the holotype is preserved in the original position overlapped by the first ceratobranchial element. It is slightly curved, faintly damaged along the ventral margin and measures 25 mm in total length. The best-preserved epibranchial is 36 mm long and covers partially the third ceratobranchial element. The dorsal portion of the epibranchial is pole-like, whereas the ventral portion is curved and club-shaped. The other epibranchial elements are incompletely preserved and yield no additional information.

Ceratobranchial elements: The majority of preserved branchial elements in both specimens are the ceratobranchials, which are completely present in the holotype (Fig. 2). The ceratobranchials are the longest elements of the branchial apparatus and increase posteriorly in length. Ceratobranchial 1 measures 3.5 cm, 2 is 52 mm, 3 is 65 mm, and 5 is 49 mm. The fourth ceratobranchial cartilage is incompletely preserved. The new specimen displays ceratobranchials 1–4 of the right and 1–3 of the left branchial apparatus. The fifth right and the fourth and fifth left ceratobranchial elements are partially covered by the pectoral girdle (Fig. 9). Only the right third and

fourth ceratobranchials are preserved in total length, and measure 48 and 49 mm, respectively. All ceratobranchials are slightly curved anteriorwards and have rounded edges, where ellipsoid-shaped ligament facets are located. The maximum width measures 7.5 mm.

Hypobranchial elements: Two hypobranchials are present in the holotype and the new specimen (Figs 2, 9). These cartilages are the most ventral paired branchial elements. The hypobranchials are triangle-shaped and taper towards the vertebral column. The holotype displays two elements belonging to the first and second left branchial arch. The new specimen represents the third and fourth hypobranchial element of the right branchial apparatus. The total lengths of these cartilages are 9 mm (first) and 8 mm (second) in the holotype, and 10 mm (third) and 8 mm (fourth) in the new specimen.

Basibranchial elements: Basibranchials are preserved in the holotype and in the new specimen. The holotype represents a single cartilage, which articulates with the second hypobranchial element. This elongated cartilage measures about 10 mm in length and 5.0 mm in width and is probably the first basibranchial element (Fig. 2). In the new specimen two basibranchials are visible. They are of longitudinal expansion and arranged successively. The posterior element is about one-third longer than the anterior one (Fig. 9). These cartilages represent the enlarged posterior-most basibranchial elements compared to the small anterior basibranchial elements described above.

GIRDLES AND PAIRED FINS

Pectoral girdle and fins: The holotype displays an incompletely preserved left and a very small part of the right pectoral girdle. The left basal elements of the pectoral fin are present but dislocated. The fin base articulation area of the scapulacoracoid is missing, as is the right coracoid bar, the right basal fin elements, and the majority of the right scapular process (Fig. 2). The new specimen presents the complete U-shaped pectoral girdle in ventral view (Fig. 9). The oval-shaped sternal cartilage is located at the sixth vertebra and forms ventrally the connection of the scapulacoracoids. These are the main parts of the pectoral girdle and are subdivided into the coracoid bar, the scapular processes, and the suprascapulars. The coracoid bars expand in the first half of their total length to a maximum diameter of 20 mm and decrease towards the articulation region of the basal elements of the pectoral fin. The scapular process measures at its maximum 14.5 mm in diameter

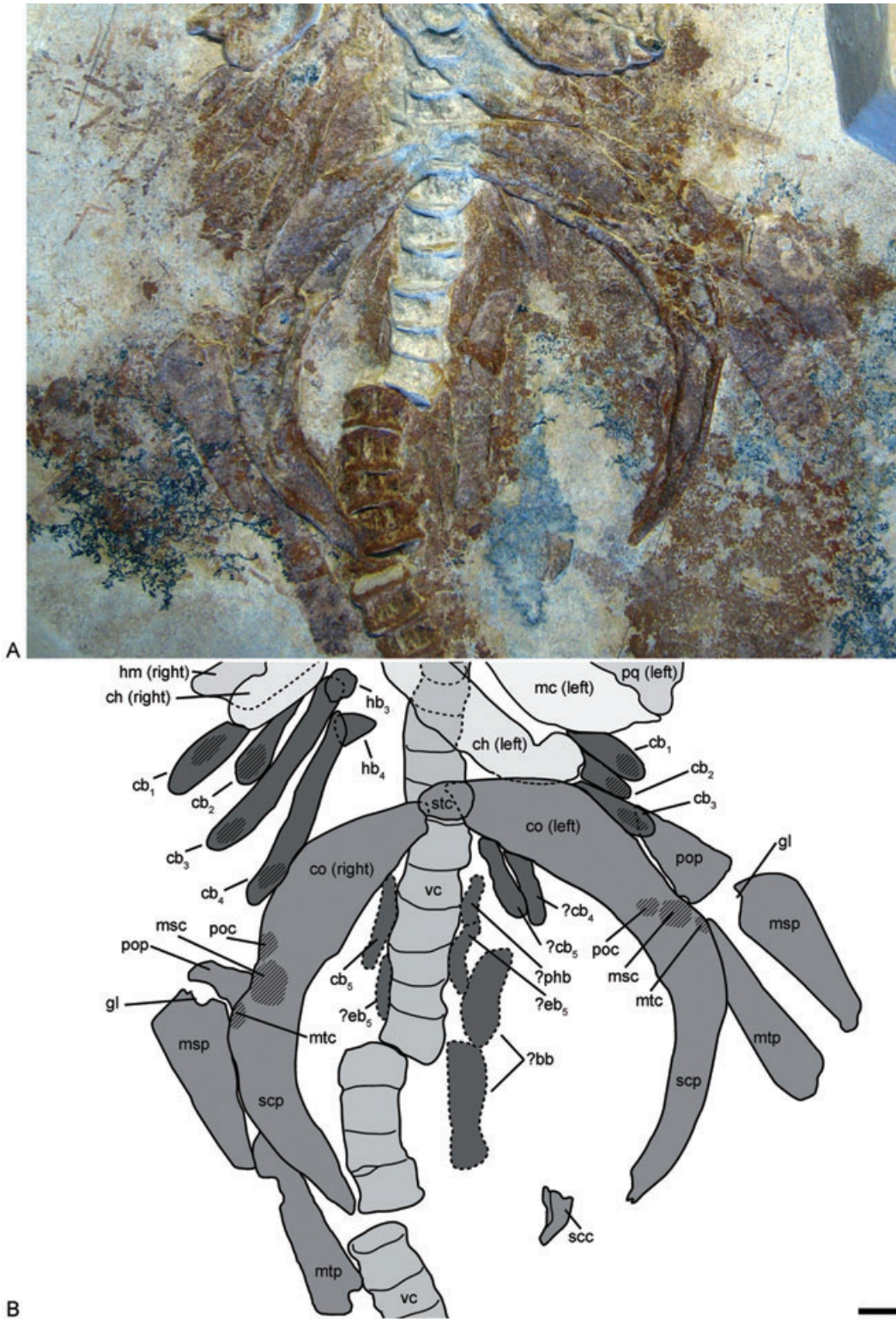


Figure 9. Branchial apparatus and pectoral girdle of *Paraorthacodus jurensis* (SMNS 88987/1). A, specimen as preserved. B, camera-lucida drawing. Scale bar = 10 mm. Abbreviations: bb, basibranchial; cb, ceratobranchial; ch, ceratohyal; co, coracoid bar; eb, epibranchial; gl, glenoid surface; hb, hypobranchial; hm, hyomandibular; mc, Meckel's cartilage; msc, mesocondyle; msp, mesopterygium; mtc, metacondyle; mtp, metapterygium; phb, pharyngobranchial; poc, procondyle; pop, propterygium; pq, palatoquadrate; scc, suprascapular cartilage; scp, scapular process; stc, sternal cartilage; vc, vertebral column.

posterior to this articulation area and tapers regularly to its edge. Only the left suprascapular cartilage is preserved, which is, however, slightly dislocated. This element is distinctly flexed with a very slender tip. The largest articulation surface of the scapulacoracoid is the rounded mesocondyle, which forms the articulation facet for the mesopterygium. The smaller, also rounded procondyle is ventrally located and displays the joint to the propterygium. The metapterygium connects to the smallest articulation surface, the oval-shaped metacondyle lying dorsally to the mesocondyle. The distance between the mesocondyle and procondyle is about half of the distance between the mesocondyle and metacondyle.

The three basal elements of the pectoral fin are clearly visible in the more complete specimen with the right propterygium being fragmentary (Fig. 9). The triangular-shaped propterygium measures 27 mm in length and 23 mm in maximum width next to the articulation surface. This surface is developed as a slight notch and located at the inner edge of the propterygium. The largest basal element is the mesopterygium, which displays the large glenoid surface joining the mesocondyle. The mesopterygium measures 46 mm in total length, tapers to its rounded tip, and displays a very straight internal margin. The external margin is distinctly angled at the widest part (18 mm), which is very well preserved on the right side of the pectoral girdle. The metapterygium is the most slender element with 14 mm in maximum width and the longest element with 48 mm in total length. The articulation surface of the metapterygium to the metacondyle is not visible, because the scapular processes overlap the right and left metapterygia. The metapterygium of the holotype is pointed and tapers towards the articulation area. The posterior part is not preserved in the holotype but present in the new specimen and displays a broadly rounded edge.

Pelvic girdle and fins: The pelvic fin is not preserved in the holotype because of the absence of the posterior part of the skeleton. The new specimen displays the pelvic girdle, which inserts at vertebrae 42–43. It is especially dislocated in its right part (Fig. 10). The vertebral column overlaps the puboischiadic bars and the propterygia, which are very poorly preserved. The poor preservation does not allow a precise reconstruction of the outline of the left metapterygium. The right metapterygium is missing. The slightly curved metapterygium is well preserved and measures 33 mm in length and 12 mm in width. The length of the propterygia is not identifiable, because the posterior edges are incompletely preserved. The puboischiadic bars display the characteristic angled shape in the posterior-most portions. The left puboischiadic

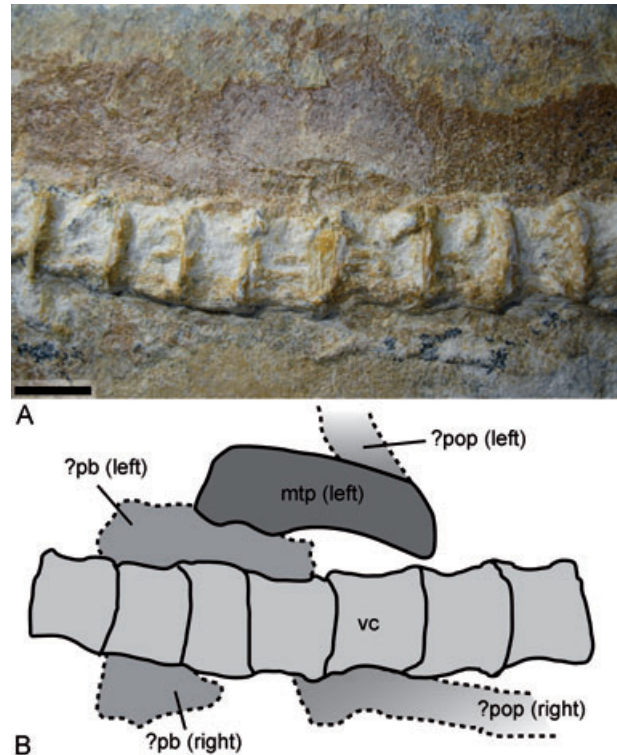


Figure 10. Pelvic girdle of *Paraorthacodus jurensis* (SMNS 88987/1). A, specimen as preserved. B, camera-lucida drawing. Scale bar = 10 mm. Abbreviations: mtp, metapterygium; pb, puboischiadic bar; pop, propterygium; vc, vertebral column.

bar is preserved in total length, although its outline is poorly defined. The right puboischiadic bar is incomplete in the posterior part. No cartilaginous elements of the clasper organs are discernible.

VERTEBRAL COLUMN

Schweizer (1964) and Duffin (1993a) have already described the 29 preserved vertebrae of the holotype in detail. Here a single vertebra, which is fossilized in transverse section, is described and figured to elucidate the chondrification pattern of the vertebrae (Fig. 11A). This vertebra measures 10 mm in diameter and displays the characteristic palaeospondylic calcification pattern of the asterospondylic type, named after the conspicuously visible cross-like pattern.

The vertebral column of the new specimen is incomplete, with 123 vertebrae being preserved. The posterior-most vertebrae are disarticulated but we assume that only few caudal fin vertebrae are missing (Fig. 3). The first and probably the second vertebra are obscured by the skull and are consequently not visible (Fig. 4). The centra of the vertebral column are



Figure 11. Vertebral column of *Paraorthacodus jurensis*. A, vertebra in transverse section displaying the characteristic palaeospinacid calcification of the asterospondylic type (holotype, GPIT 1210/1). Scale bar = 5 mm. B, abdominal vertebrae with preserved haemal arches (SMNS 88987/1). Scale bar = 10 mm.

faintly hourglass shaped and are one-third to one-quarter wider than deep. They are medially constricted and display distinct concave anterior and posterior faces. In addition, a few horizontal ridges are present on the lateral walls of the centra. These ridges are determined by the secondary calcification. Some centra represent faint diagonal ridges on the lateral walls. The measurements of the vertebrae differ throughout the vertebral column. The width of centra 1 to 35 measures constantly 13.4 mm and decreases to 11.3 mm between centra 36 and 48. The reduction in width continues from centra 49 to 80 from 11.3 to 10.6 mm. The depth measures constantly 7.7 mm between centra 1 to 20, but increases from 9.2 to 10.6 mm between centra 21 to 48. Posterior to the 48th centrum (centra 49 to 80) the vertebrae display a constant depth of 6.1 mm. Consequently, the transition from the monospondylous thoracic to the diplospondylous precaudal (abdominal) vertebral column is between centra 48 and 49.

The diplospondylous caudal fin skeleton originates at the 80th centrum. Its anterior part is distinguished by a constant width of 10.6 mm and a decreasing depth from 6.1 to 5.4 mm (centra 80 to 90). The following centra (> 90) display a constant decrease in depth and width towards the smallest measurable centrum, which is 4.8 mm in depth and 5.7 mm in width.

Haemal arches are only fragmentarily preserved throughout the precaudal part of the skeleton of the new specimen, with the exception of the caudal fin, where they are abundantly present. The first recognizable but imperfect haemal arch is located at vertebra 49, where the diplospondylous precaudal vertebral column commences. There are a few additional haemal arches present, which are nearly complete and located anterior to the single dorsal fin next to centrum 56 (Fig. 11B). They have a broad base

measuring the same length as their corresponding vertebra. In addition, they display posteriorwards the characteristic slightly hook-shaped form. Haemal spines are only present in the caudal skeleton.

UNPAIRED FINS

The incomplete preservation of the holotype of *Par. jurensis* prevents the identification and description of the unpaired fins. The new specimen, conversely, displays a single dorsal fin and the very well-preserved caudal fin. However, the anal fin is also lacking in this specimen.

Dorsal fin: Two dorsal fins are common for modern sharks. Differences in size are very variable. In a few extant sharks the first dorsal fin is absent, e.g. Hexanchiformes, *Pentanchus*, and some batoids. *Paraorthacodus jurensis* displays this pattern and the single dorsal fin inserts at the 57th vertebra by the anterior-most edge of the basal pterygophore (Fig. 12). The body outline of the new specimen is indicated by the preserved dermal scale covering and is thus clearly perceptible, documenting the absence of a second dorsal fin without any doubt. This is also supported by two other specimens of *Paraorthacodus* from the Upper Jurassic of the Solnhofen area (Kriwet & Klug, 2004; Klug & Kriwet, 2008).

The posterior situated dorsal fin extends for five vertebrae and is 34 mm long. The maximum height measures 17 mm. The anterior margin increases fast and reaches the maximum height after the 58th vertebra and then decreases slightly to its posterior tip. Additionally preserved elements of the dorsal fin are four radial pterygophores, which are slightly dislocated. These obliquely arranged elements are more delicate and less calcified than the basal pterygophore, so they are not as well fossilized as other

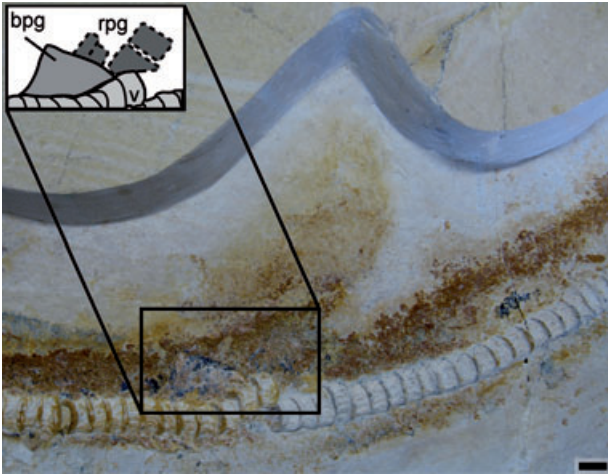


Figure 12. Dorsal fin of *Paraorthacodus jurensis* (SMNS 88987/1) as preserved and camera-lucida drawing (inset). Scale bar = 10 mm. Abbreviations: bpg, basal pterygophore; rpg, radial pterygophore.

elements. Posterior to the basal pterygophore, the radial pterygophores are arranged in one row to which numerous ceratotrichia are sutured, composing the dorsal fin. The form and exact size of the dorsal fin cannot be reconstructed in detail because several skeletal elements are not preserved, such as the ceratotrichia and several radial pterygophores. The shagreen of the skin also displays an ill-defined outline and yields no further information.

Caudal fin: The caudal fin skeleton of sharks consists of dorsal epichordal and ventral hypochordal rays. The epichordal rays are composed of neural arches to which the neural spines are attached. Ventrally the haemal arches and the haemal spines form the hypochordal rays. The caudal fin of *Par. jurensis* is heterocercal with a very elongated upper lobe. The exact outline, however, remains ambiguous. The cartilaginous skeleton of the caudal fin is very well preserved showing remarkable details of these elements (Fig. 13). The first preserved haemal arch of the caudal fin articulates with the 83rd vertebra,

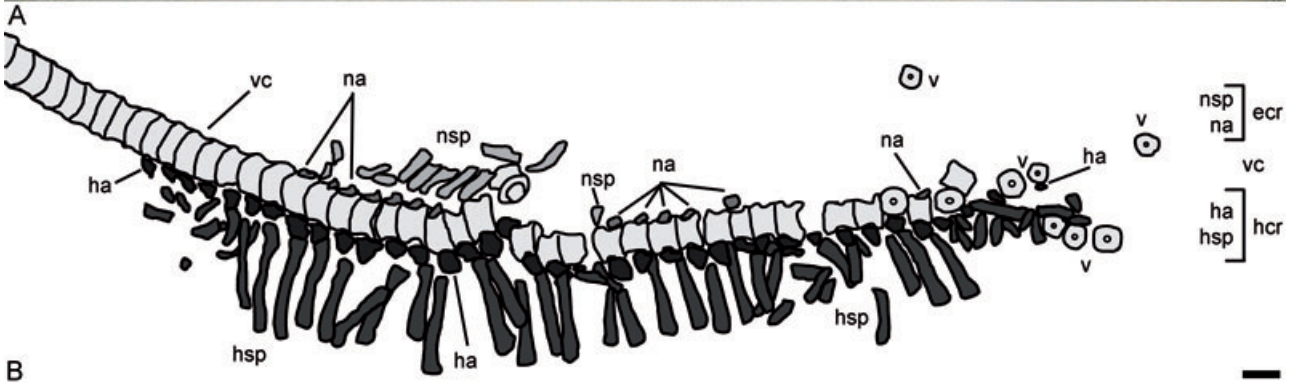


Figure 13. Caudal fin of *Paraorthacodus jurensis* (SMNS 88987/1). A, specimen as preserved. B, camera-lucida drawing. Scale bar = 10 mm. Abbreviations: ecr, epichordal rays; ha, haemal arch; hcr, hypochordal rays; hsp, haemal spine; na, neural arch; nsp, neural spine; v, vertebra; vc, vertebral column.

posteriorly followed by 36 haemal arches. The base of the arches is almost as wide as the corresponding vertebra and of triangular shape and tapers anteriorly. The maximum height of the arches never exceeds their maximum length. Throughout the caudal fin, the haemal arches are not fused to the haemal spines. The first haemal spines are comparatively short and their length increases posteriorly. They reach their maximum length of 29.4 mm at about the 89th to 90th vertebrae and decrease towards the posterior-most tip of the caudal fin, which is not preserved in this specimen. The bases of the haemal spines are as wide as the corresponding haemal arch. The anterior-most, long haemal spines have a slightly sigmoidal shape. All others display a straight and elongated anterior margin. The epichordal rays are not as well preserved as the hypochordals. However, several neural arches are located in the anterior and middle portion of the caudal fin in their original position. In contrast, only a few arches are present in the posterior part. They are very low and never exceed half of their anteroposterior length in height. The bases of the neural arches are as long as the corresponding vertebrae, similar to the haemal arches. The neural spines are only preserved in the anterior part of the caudal fin and are slightly dislocated in relation to the corresponding neural arches. The preserved maximum length of the neural spines measures 12.6 mm. The dorsal and ventral edges are also angled and slightly rhomboid shaped.

DISCUSSION AND CONCLUSION

SYSTEMATIC POSITION

Elasmobranchian affinities: *Paraorthacodus jurensis* (and its relatives such as *Palidiplospinax*, *Synechodus*, and *Macrourogaleus*) is easily recognized as a member of Elasmobranchii by the 'double' selachian-type jaw articulation with lateral and medial quadrato-mandibular joints, the lingual ridge on Meckel's cartilage, the presence of dermal placoid scales covering the body, a free palatoquadrate with amphistylic suspension, and characteristic permanent tooth replacement (teeth follow one another within a single tooth row revolver).

Neoselachian affinities: Living sharks, rays, skates, and all their extinct relatives form a monophyletic group, the Neoselachii [Euselachii of Moy-Thomas (1939), Reif (1977); Schaeffer & Williams (1977); Euselachiformes of Maisey (1975)], which is well supported by morphological and molecular data. Even though the monophyly of Neoselachii is thus beyond any dispute, the diagnosis of this group varies (Compagno, 1973, 1977; Reif, 1977; Schaeffer

& Williams, 1977; Schaeffer, 1981; Maisey, 1984a, 1986b, 1994; Thies & Reif, 1985; Cappetta, 1987; Gaudin, 1991; Carvalho, 1996; Shirai, 1996) and remains intricate. According to Carvalho (1996), neoselachians are characterized by four homoplastic features including fused but not coalesced left and right coracoids, which is the only character preserved in the new specimen of *Par. jurensis*. The conclusion of Maisey (1977) and Carvalho (1996) that no single coracoid bar is present in *Palidiplospinax* [formerly assigned to *Palaeospinax* Egerton, 1872, which is considered a *nomen dubium* (Duffin & Ward, 1993; Klug & Kriwet, 2008)], which is considered a member of Palaeospinacidae and which is sister to *Synechodus* and *Paraorthacodus*, is not supported. The remaining characters provided by Carvalho (1996) and Shirai (1996) for identifying neoselachians are not preserved in the two specimens of *Par. jurensis*.

Maisey (1975, 1976, 1977, 1985), Compagno (1977), Reif (1978), Thies (1983), and Maisey *et al.* (2004) presented additional neoselachian plesiomorphic features (nongrowing placoid scales, pectoral fins consisting of propterygium, mesopterygium, and metapterygium, amphistylic palatoquadrate connection) and apomorphic traits (nonlunate caudal fin, elongated metapterygium in pelvic fin, well-calcified vertebral centra constricting the notochorda segmentally), which are preserved in the specimens presented here and also support the placement of *Paraorthacodus* within Neoselachii.

The holotype and the new specimen of *Par. jurensis* display a single and two ventral labial cartilages, respectively. Dorsal labial cartilages are not preserved because of the preservation condition of both individuals. The presence of a reduced number of labial cartilages in comparison with hybodonts, which are the sister group of Neoselachii, moreover provides evidence that this taxon belongs to the neoselachians. The presence of two dorsal and two ventral labial cartilages might be considered plesiomorphic for neoselachians. Heterodontiforms have two dorsal and a single ventral labial cartilage, whereas the number of ventral cartilages in orectolobiforms varies from one to two. Lamniforms and carcharhiniforms are devoid of any labial cartilages. Squaliform and squatiniform sharks differ from *Paraorthacodus* in having two dorsal but a single ventral labial cartilage. The single, fused labial cartilage of hexanchiforms is a uniquely achieved condition.

The synechodontiform *Palidiplospinax*, which might represent the sister group to *Paraorthacodus* (Klug & Kriwet, 2008), displays the plesiomorphic condition of this group by having two dorsal fin spines of neoselachian composition and external appearance (Maisey, 1977; Maisey *et al.*, 2004).

Teeth of chondrichthyans are especially important in the fossil record, because of the predominantly cartilaginous nature of skeletal structures. These teeth display much morphological variation amongst taxa so that they are widely used for taxonomic and systematic purposes. In recent years, evidence has emerged that much intraspecific, sexual, and ontogenetic variation in tooth morphologies exist in living neoselachians, rendering identification of isolated teeth more difficult. However, numerous studies in the past decades have convincingly demonstrated that the ultrastructure of neoselachian tooth enameloid differs from that of other elasmobranchs (e.g. Reif, 1973b, 1977; Duffin, 1980, 1993b; Thies, 1982; Cuny, 1998; Cuny *et al.*, 1998, 2000, 2001; Cuny & Benton, 1999; Kriwet, 2004; Gillis & Donoghue, 2007) in that it consists of three layers with different crystallite orientations (internal tangled-bundled; middle parallel-bundled, PBE; external shiny layer) arranged into two units (Cuny & Risnes, 2005). The middle layer comprising the parallel-bundled enameloid is considered a synapomorphy of neoselachians (e.g. Reif, 1977; Thies, 1982; Maisey, 1984a, b, 1985; Thies & Reif, 1985), which is secondarily lost in posterior teeth of heterodontids. Palaeospinacidae including *Paraorthacodus* have the characteristic PBE layer of neoselachians (Cuny & Risnes, 2005), even though the degree of crystallite arrangement differs between Triassic and post-Triassic forms.

Galeomorph affinities: The higher classification of neoselachians has a long tradition resulting in different hypotheses of systematic arrangement. The most inclusive and recent ones are those of Carvalho (1996), Shirai (1996), Carvalho & Maisey (1996), and Maisey *et al.* (2004). Even though the interpretations of the first three studies do not fully agree with molecular analyses, especially in the position of rays and skates (e.g. Douadéy *et al.*, 2003; Winchell, Martin & Mallat, 2004), they provide a framework for discussing the systematic position of *Paraorthacodus* (and consequently its closest relatives) within neoselachians.

Carvalho (1996) provided seven characters, two of which are devoid of homoplasy, for characterizing Galeomorphii. Three characters consider skeletal features, which are, unfortunately, either not preserved [pharyngobranchial blade ('gill pickax' of Shirai, 1992): this element is not present in heterodontiforms] or ascertainable (ethmoidal region of neurocranium downcurved, hyomandibular fossa located anteriorly in otic region) in the two specimens of *Par. jurensis* presented here. Maisey (1985) identified the ethmoidal region of the closest relatives of *Paraorthacodus*, *Synechodus*, and *Sphenodus* to be downcurved. Consequently, it is most

parsimonious to assume that this region also was downcurved in *Paraorthacodus*.

Maisey (1980, 1984a, b) united squaliform, pristiophoriform, hexanchiform, and squatiniform sharks in a clade named 'orbitostylic sharks' based on the presence of a distinct palatoquadrate process that extends into the orbit. A similar process is present in batoids and was used *inter alia* to justify the systematic position of rays and skates within derived neoselachians, the Hypnosqualea (Shirai, 1992, 1996; Carvalho, 1996). Recent molecular genetic analyses, however, suggest that the presence of this process was achieved convergently in squalomorph sharks and batoids. This special palatoquadrate process is absent in *Paraorthacodus*, *Synechodus*, and *Palidiplospinax* as it is not developed in any galeomorph shark, supporting closer relationships of palaeospinacids with galeomorphs.

Squalomorph and batoid affinities: Neither in *Synechodus* (Maisey, 1985) nor in *Sphenodus* (Böttcher & Duffin, 2000), *Palidiplospinax* (Klug & Kriwet, 2008), or *Paraorthacodus* (this study) has any character supporting closer relationships between these extinct taxa and squalomorph sharks and batoids been identified to date.

Systematic position of Paraorthacodus and monophyly of Synechodontiformes: The skeletal morphology of *Palidiplospinax*, *Paraorthacodus*, *Macrourogaleus*, *Sphenodus*, and *Synechodus* indicates closer relationships to galeomorphs than to squalomorphs and batoids. Nevertheless, the monophyly of Palaeospinacidae and Synechodontiformes and their systematic position within Neoselachii has been repeatedly argued. Recently, Maisey *et al.* (2004) stated that the four taxa *Sphenodus*, *Paraorthacodus*, *Synechodus*, and '*Palaeospinax*' represent an 'assortment of different stem neoselachians and / or galeomorphs', because of the incongruent distribution of the pseudopolyaulacorhize tooth root pattern, which they considered not to be developed in *Sphenodus* (contrary to Böttcher & Duffin, 2000). Moreover, Böttcher & Duffin (2000) reconstructed the dentition of *Sphenodus macer* (Quenstedt, 1851) as having a single row of upper intermediate teeth, which is a characteristic feature of lamniform sharks. Consequently, Maisey *et al.* (2004) argued that *Sphenodus* might be a member of the lamniforms based on the presence of intermediate upper teeth, absence of distinct pseudopolyaulacorhize root pattern, and tooth crown morphology. However, tooth crown morphology is a problematic character, because it strongly depends on feeding adaptations and similar tooth morphologies are convergently developed in different neoselachian lineages. A re-investigation of the dentition of the

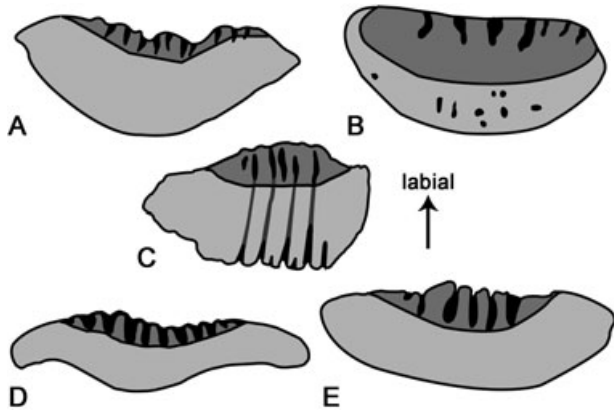


Figure 14. Diagrammatic sketch of tooth roots of selected synechodontiform sharks in basal view displaying the pseudopolyaulacorhize vascularization pattern (black) and labial root depression (dark grey). A, *Welcommia bodeuri*, IRSNB P6329. B, *Rhomphaidon minor*, GPIT without number. C, *Sphenodus nitidus*, SMNS 80144/5. D, *Synechodus dubrisiensis*, BMNH 36908 (holotype). E, *Paraorthacodus jurensis*, GPIT 1210/1 (holotype). Figures not to scale.

single more or less complete specimen of *Sphenodus macer* and the holotype of *Sphenodus nitidus* by two of us (S. K., J. K.) did not provide any evidence of an upper intermediate tooth row, leaving no evidence of any closer relationships between *Sphenodus* and Lamniformes. The small tooth identified as a possible intermediate upper tooth by Böttcher & Duffin (2000: pl. 1, fig. 2) most probably represents a small parasymphysial tooth. Moreover, the root of *Sphenodus* (and other supposedly basal synechodontiforms such as *Rhomphaidon* Duffin, 1993b and *Welcommia* Capetta, 1990) displays the pseudopolyaulacorhize vascularization pattern of the root with the distinct labial root depression to which basally open nutritive grooves are restricted, even if the vascularization pattern is not always distinctly developed in all tooth positions (Fig. 14). Secondary closure of nutritive tooth root grooves within any given neoselachian jaw is very common (J. K., pers. observ.).

A preliminary phylogenetic analysis of taxa previously assigned to Synechodontiformes employing robust cladistic principles indeed suggests the monophyly of this group, which is supported by several homoplastic characters (S. Klug, unpubl. data). So far, the family Palaeospinacidae is supposed to comprise *Palidiplospinax*, *Paraorthacodus*, and *Synechodus* (Klug & Kriwet, 2008). *Palidiplospinax*, however, displaying two dorsal fins with spines, might represent the sister group to *Paraorthacodus* and *Synechodus*. A revision of carcharhinoid sharks from the Late Jurassic demonstrated that the small shark *Macrourogaleus*, which is also characterized by a

single dorsal fin, also belongs to the Palaeospinacidae and is very closely related to *Paraorthacodus* (Klug, 2008).

The clade Synechodontiformes, as currently understood, consists of two groups. One group comprises forms in which the distinct pseudopolyaulacorhize root pattern is less well developed in that the nutritive grooves might be comparably short and not so marked. In some taxa of this group, the roots also might convergently resemble that of basal hexanchiforms. The weak and irregular infolding of the labial root face for example in *Sphenodus* superficially resembles the root pattern in early hexanchiforms (C. Underwood, pers. comm.). However, this pattern is independently achieved and does not imply any closer relationships between palaeospinacids and hexanchiforms, because the hexanchiform tooth vascularization pattern is not pseudopolyaulacorhize but strictly anaulacorhize (Herman, Hovestadt-Euler & Hovestadt, 1987). The other group is characterized by well-developed pseudopolyaulacorhize tooth root patterns. The systematic position of several Triassic forms (e.g. *Mucrovenator* Cuny *et al.*, 2001) remains unresolved for the moment. All skeletal remains of synechodontiform sharks display vertebrae of the asterospondylic type, which is seen for example in the type material of *Palidiplospinax* and *Paraorthacodus* (e.g. Schweizer, 1964; Klug & Kriwet, 2008).

Accordingly, we consider Synechodontiformes and Palaeospinacidae to be monophyletic groups of neoselachians. Nevertheless, it is momentarily impossible to identify the systematic placement of synechodontiforms within Neoselachii and within any modern elasmobranch group (Galeomorphii, Squalomorphii, Batoidea) satisfactorily and they consequently might be sister to all modern elasmobranchs, a hypothesis already implied by Maisey (1985).

Conclusions

There is compelling evidence that *Par. jurensis* and its allies (e.g. *Palidiplospinax*, *Sphenodus*, *Synechodus*, *Macrourogaleus*), which are considered here to form a monophyletic group, the Synechodontiformes (see also Klug & Kriwet, 2008) pending further phylogenetic analyses, represent an extinct clade of Neoselachii. Living elasmobranchs consist of three closely related groups, the Galeomorphii, Squalomorphii, and Batoidea. The latter two were considered to represent a monophyletic group, the Squalea, by Shirai (1996) and Carvalho (1996). However, recent molecular analyses show that Batoidea is sister to all sharks, which is in better accordance with the fossil record of sharks and batoids (e.g. Maisey *et al.*, 2004), reducing the length of the ghost-lineages that result from Carvalho's (1996) analysis. This indicates reliably that morphological features supporting a monophyletic

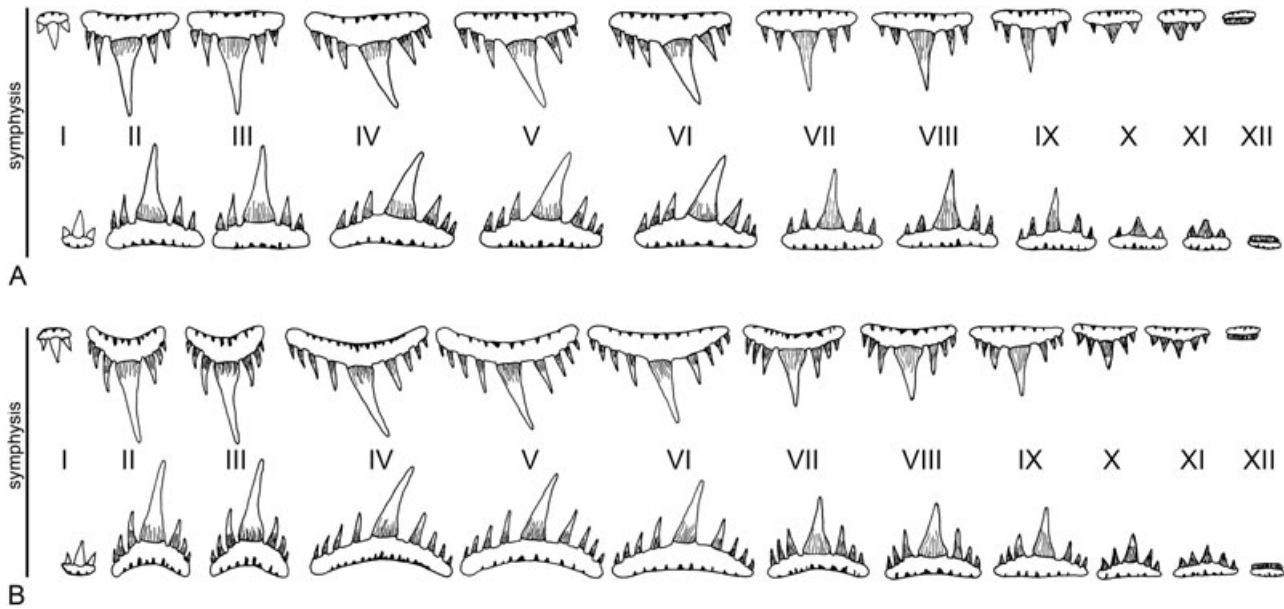


Figure 15. Tentative reconstruction of upper and lower dentition of *Paraorthacodus jurensis* displaying the dentition pattern, heterodonty, and sexual dimorphism. A, gender 1 (GPIT 1210/1, holotype). B, gender 2 (SMNS 88987/1). I, parasympyseal tooth; II–III, anterior teeth; IV–VI, lateral teeth; VII–XI, posterior teeth; XII, commissural tooth. Figures not to scale.

group consisting of Squalomorphii and Batoidea are homoplastic and/or plesiomorphic. There is strong evidence that Palaeospinacidae and Synechodontiformes as generally conceived form monophyletic groupings of neoselachians. Despite the fact that Synechodontiformes displays several characters, which might relate these sharks more to galeomorphs than to squalomorphs, no compelling interpretation of their systematic placement within Neoselachii is possible at the moment pending further phylogenetic analyses.

Defining neoselachians depends strongly on the interpretation of which taxa form the Neoselachii. Consequently, two alternative interpretations of the systematic position of *Paraorthacodus* and its relatives are conceivable. (1) *Paraorthacodus* is a stem-group representative of neoselachians, if Neoselachii is restricted to living forms and those extinct taxa, which are placed phylogenetically well within modern groups alone (crown-group); (2) *Paraorthacodus* is a 'true' neoselachian, if Neoselachii is defined to incorporate all living forms and extinct groups that fall just outside extant groups. Whatever definition is employed, there is strong evidence indicating that Synechodontiformes is sister to all living sharks and batoids.

SEXUAL DIMORPHISM

Sexual dimorphism is a common feature found in living sharks and batoids, including external and skeletal features. The most obvious difference between females and males is the presence of clasper organs in males, which represent modified pectoral fin cartilages. Unfortunately, the holotype of *Par. jurensis* is very incomplete, lacking almost all postcranial portions. The new specimen, regardless of its almost complete preservation, does not allow reconstruction of the pelvic girdle and pelvic fins in detail because of the very incomplete preservation of this region.

However, both specimens display differences in the number of lateral tooth cusplets adjunct to the main cusp. There is always one more pair of lateral cusplets present in the new and more complete specimen than in the corresponding tooth positions of the holotype (Fig. 15). We exclude the possibility that this represents ontogenetic variation because the cranial elements and anterior vertebral centra of both specimens are of similar size. Sexual dimorphism in tooth morphologies of living elasmobranchs is still very incompletely known and even less understood. Such variation is known to occur in several living deep-water sharks (number of lateral cusplets in upper

teeth of males higher and more variable than in females; Straube, Schliewen & Kriwet, 2008), batoids (periodic change of tooth crown morphology of males related to reproduction cycles; Kajiura & Tricas, 1996), and other sharks (some carcharhiniforms, *Hexanchus*; Herman, Hovestadt-Euler & Hovestadt, 1991; Underwood & Ward, 2008). Other skeletal differences indicating sexual dimorphism in the two examined specimens were not noted.

AUTECOLOGY

Feeding

The dentition of *Par. jurensis* resembles that of modern sand tiger sharks (family Odontaspidae) in that teeth have large and slender main cusps in anterior and lateral tooth rows with well-developed cutting edges and several lateral cusplets. Lateral cusplets are still present in the posterior-most teeth. There are multiple replacement tooth rows but only a single functional row, converse to the condition seen in the living *Odontaspis ferox* (Risso, 1810). The dental pattern of *Par. jurensis* corresponds to the tearing-type dentition of Cappetta (1987) and indicates that *Paraorthacodus* might have been an opportunistic predator feeding on a wide array of prey including probably soft-shelled invertebrates as well as fishes and other chondrichthyans.

Both specimens studied here preserve food items from previous meals. In the holotype, two fin-spine fragments are located in the mouth cavity, where they were embedded in the dermal tissue between teeth and a single one near the 15th vertebral centrum. Additionally, a distinct denticle-like structure is located in the mouth cavity (Duffin, 1993a). These remains were interpreted as belonging to *Ischyodus avitus* (Meyer, 1863; Schweizer, 1964; Duffin, 1993a). We confer with this assignment conversely to the interpretation of Maisey (1985), who considered these fin-spines to be the sole indication of hybodont sharks in the Nusplingen lithographic limestone. A fragmentary fin-spine of *I. avitus* is also present in the area of the alimentary tract of the new specimen. The preservation of chimeroid remains as the only food items in *Par. jurensis* indicates that these chondrichthyans might have constituted a major food resource and supports the interpretation that this shark occupied an upper trophic position within this ancient environment.

Lifestyle

The lifestyle of *Par. jurensis* was probably similar to that of the extant *Odontaspis ferox* as inferred from the general body outline and form of the caudal fin; nonetheless, the body of the living sand tiger shark is

more robust and shorter. The pectoral fins of *Paraorthacodus* are large and rounded and resemble to some extent those of the extant *Orectolobus* spp. but also *Odontaspis ferox*. These large pectorals, which stabilized the animal after its death, are the reason for the dorsoventral preservation of the anterior body portion in both specimens. A major difference between living sand tiger sharks and *Paraorthacodus* is the presence of a single dorsal fin in the latter, probably indicating slightly different locomotion patterns. The single posteriorly placed dorsal fin serves for rear locomotion. In that, *Par. jurensis* externally resembles living hexanchiforms, which are benthodermesal deepwater sharks of the outer continental and insular shelves and upper slopes characterized by very disjunct dental heterodonties and thus might not be the best comparative model for reconstructing the habits and adaptations of the extinct shark.

Modern sand tiger sharks are benthopelagic and found on or near the bottom of continental and insular shelves and upper slopes in shallow to 420 m deep waters (Last & Stevens, 1994; Mundy, 2005). *Paraorthacodus jurensis* most probably had a similar lifestyle and we consider this shark to be benthopelagic. Its very rare occurrence in the lithographic limestones of southern Germany implies that this predaceous shark predominately lived outside the reefs that developed in southern Germany during the Late Jurassic in open water and entered lagoonal areas only occasionally in the pursuit of prey.

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