

## HYBODONTIFORM SHARK REMAINS (CHONDRICHTHYES, ELASMOBRANCHII) FROM THE LOWER TRIASSIC OF YUNNAN PROVINCE, CHINA, WITH COMMENTS ON HYBODONTIFORM DIVERSITY ACROSS THE PTB

WEN WEN,<sup>1,2\*</sup> JÜRGEN KRIWET,<sup>3</sup> QIYUE ZHANG,<sup>2</sup> MICHAEL J. BENTON,<sup>4</sup> CHRISTOPHER J. DUFFIN,<sup>5</sup>  
JINGYUAN HUANG,<sup>2</sup> CHANGYONG ZHOU,<sup>2</sup> SHIXUE HU,<sup>2</sup> and ZHIXIN MA<sup>2</sup>

<sup>1</sup>School of Earth Sciences and Engineering, Nanjing University, 163 Xianlin Road, Qixia District, Nanjing 210023, People's Republic of China;

<sup>2</sup>Chengdu Center of China Geological Survey, No. 2, N-3 Section, First Ring Road, Chengdu 610081, People's Republic of China, wenwen2020240@163.com;

<sup>3</sup>Department of Palaeontology, University of Vienna, Geozentrum UZA 2, Althanstrasse 14, 1090 Vienna, Austria, juergen.kriwet@univie.ac.at;

<sup>4</sup>School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK, mike.benton@bristol.ac.uk;

<sup>5</sup>Earth Sciences Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK, cduffin@blueyonder.co.uk

**ABSTRACT**—Hybodontiform shark teeth, cephalic and fin spines as well as placoid scales are reported here for the first time from the continental, Lower Triassic Dongchuan Formation near the village of Zhaojia (Huize County, Yunnan Province) in south-west China. The isolated teeth are assigned to three unidentified hybodontiforms but also to a new species of *Parvodus*, *P. huizodus* sp. nov., the oldest record of this small-toothed lonchidiid shark genus, extending its range well down into the Lower Triassic. This new species, together with additional hybodontiform remains, provides new evidence of shark occurrences in the aftermath of the end-Permian mass extinction event, when freshwater environments might have acted as centers of origin rather than refugia for sharks. A review of the species assigned to *Parvodus* and similar small hybodontiform sharks reveals two distinct ecomorphological groups. Group 1, which is characterized by clutched-type dentitions, includes eight species (three of which remain unnamed) ranging from the Middle Triassic to Lower Cretaceous, while group 2, characterized by cutting-crushing type dentitions, comprises 11 species (six of which remain unnamed) including the type-species, *P. rugianus* ranging from the Lower Triassic to the Lower Cretaceous. The new fossils documented here reveal that hybodontiforms were already adapted to freshwater environments in the Lower Triassic rather than in the Jurassic in China.

<http://zoobank.org/urn:lsid:zoobank.org:pub:9FA915B5-C838-4778-95C9-B851676751A4>

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP).

Citation for this article: Wen W., J. Kriwet, Q. Zhang, M. J. Benton, C. J. Duffin, J. Huang, C. Zhou, S. Hu, and Z. Ma. 2022. Hybodontiform shark remains (Chondrichthyes, Elasmobranchii) from the Lower Triassic of Yunnan Province, China, with comments on hybodontiform diversity across the PTB. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2022.2108712

### INTRODUCTION

Key uncertainties in shark evolution include the question of when hybodontiforms entered fresh waters, assuming that this might have happened several times independently after the Paleozoic as evidenced by the absence of a continuous freshwater record of hybodontiforms, and postulated responses to the end-Permian mass extinction on shark evolution. Hybodontiforms (sensu Coates and Gess, 2007) were the dominant sharks for much of the Mesozoic Era. They are the extinct sister group of the neoselachians (sensu Compagno, 1977; versus Elasmobranchii sensu Maisey, 2012), which include all extant sharks, rays, and skates and taxa nested phylogenetically within this clade. Both clades were present throughout the Triassic, with records from China, but sharks are much less well documented

than osteichthyan fishes, and this is especially true around the Permian–Triassic boundary (PTB; Benton et al., 2013).

The most basal and oldest hybodontiform sharks known from complete, unambiguous skeletal remains are *Tristychius* and *Onychoselache* from the Viséan (early Carboniferous), part of the early Carboniferous chondrichthyan radiation (Friedman and Sallan, 2012). However, isolated teeth of general hybodontiform morphology (Ginter et al., 2002) date back further, to the Famennian (Late Devonian), indicating that hybodontiform sharks might have evolved and radiated prior to the end-Devonian mass extinction event (Duffin, 2001; Coates and Gess, 2007). Early Carboniferous holomorphic hybodontiform fossils occur in near-coastal and lagoonal to even freshwater deposits, indicating that hybodontiforms might have evolved in shallow-marine environments; it appears that they were euryhaline early in their evolutionary history, being able to tolerate different salinity regimes (e.g., Duffin, 1997; Duffin and Thies, 1997; Rees and Underwood, 2006, 2008; Klug et al., 2010; Leuzinger et al., 2015, 2017; Stumpf and Kriwet, 2019; Stumpf et al., 2021a). Devonian dental records assigned to hybodontiforms from marine settings also

\* Corresponding author.

Color versions of one or more of the figures in the article can be found online at [www.tandfonline.com/ujvp](http://www.tandfonline.com/ujvp).

support this interpretation (Ginter et al., 2002). The Pennsylvanian (upper Carboniferous) hybodontiform *Hamiltonichthys*, represented by several holomorphic specimens and slightly more derived than *Onychoselache*, is known mostly from freshwater deposits (Maisey, 1989). While xenacanthiforms were the dominant sharks in freshwater environments during the Paleozoic, they seemingly were replaced by hybodontiforms after the Permian–Triassic mass extinction (PTME). Unambiguous Late Triassic xenacanthiforms have been reported from the UK (Woodward, 1889), Texas (Johnson, 1980), India (Bhat et al., 2018a), Germany (Seilacher, 1943, 1948), and Australia (Turner, 2011), which indicate that the group survived the PTME in freshwater environments, which might have acted as refugia.

During the Triassic and Jurassic, hybodontiforms repeatedly invaded freshwater environments such as lakes and rivers, and in the Cretaceous remains of hybodontiforms occur predominantly in continental deposits (Cuny, 2012). It is hard to identify obligate freshwater sharks (restricted exclusively to such environments) in the fossil record because of taphonomic and collecting biases. Therefore, stable isotopes are often used to establish the environmental settings of the fossil-bearing localities (Fischer et al., 2012, 2013). Here we present a new low-diversity hybodontiform shark assemblage from Lower Triassic freshwater deposits including a new lonchidiid species, *Parvodus huizodus* Wen and Kriwet sp. nov., and reconsider hybodontiform diversity patterns across the PTB on a regional scale.

#### GEOGRAPHIC AND STRATIGRAPHIC CONTEXT

The Dongchuan Formation of Huize County, Yunnan Province, consists of purple conglomerates, sandstones, siltstones, limestones, olive/gray sandstones and mudstones, interpreted as continental in origin. It is about 400–800 m thick, conformably overlies the Permian Emeishan basalt, and is followed upwards by the Middle Triassic (Anisian) Guanling Formation (Sun and Han, 1998). An Early Triassic age for the Dongchuan Formation is supported by a diverse array of bivalves marking the *Eumorphotis–Promyalina* zone according to the regional geological report (1:200000) for Dongchuan (Xiong, 1980).

The fossils come from the Shuanglongtan section located at Zhaojia village, in the south-west of Huize County, at the north-western margin of the Nanpanjiang basin (Fig. 1A, B). The Xuanwei Formation is composed mainly of olive/gray purple mudstone, siltstone, fine to coarse sandstone containing abundant plant fossils interbedded with a few coal seams, suggesting a fresh lake-swamp or river flat environment (Feng et al., 1994). The Dongchuan Formation here is divided into three members according to the regional geological report (1:50000) for Dongchuan (Lin et al., 2015). The first member is 95 m thick and comprises purple conglomerates intercalated with sandstones and mudstones (Fig. S1A in Supplemental Data), which imply typical alluvial fan sedimentation. The second member is 454 m thick, the lower part comprises purple thick sandstones interbedded with mudstones (Fig. S1B in Supplemental Data), with large-scale tabular cross bedding (Fig. S1C in Supplemental Data) and tough cross bedding (Fig. S1D in Supplemental Data), upward the sandstone becomes thinner, and small-scale cross bedding occurs, forming a fining-upward succession, suggesting pointbank deposits. The third member is 117 m thick and consists of yellow, olive/gray and purple mudstones intercalated with fine sandstones and a thin layer of limestone (Fig. S1E, F in Supplemental Data). Abundant spherical features (Fig. S1G, H in Supplemental Data) in the mudstone indicate intense weathering process in the mudstones, with infrequent horizontal bedding and fragments of plants. Small-scale cross beds are occasionally observable in the sandstones. Overall, the third member was deposited in a floodplain environment. All the

shark teeth reported here were recovered from the middle-upper part of the third member of the Dongchuan Formation. The fossiliferous layer is a 20 cm thick massive bioclastic limestone, bed 27 in the Shuanglongtan section (Fig. 1C). Except for shark teeth, the tooth plates of lungfish and scales and teeth of actinopterygians were also found in the bioclastic limestone. There is a bentonite layer just beneath the fossil layer, and its zircon LA-ICP-MS U-Pb age is  $249.3 \pm 1.4$  Ma (Supplemental Data), indicating Olenekian, Early Triassic.

In the Chahe and Lubei sections, the upper Permian to Lower Triassic units are the Xuanwei, Kayitou, Dongchuan, and Jialingjiang formations. In these sections, the Dongchuan Formation overlies the uppermost Permian Kayitou Formation and is overlain by the Jialingjiang Formation, which is Olenekian (Zhang et al., 2016, 2017). The exact age of the Kayitou Formation is debated, especially whether it is entirely latest Permian in age, or whether it spans the PTB, terminating in the earliest Triassic (Zhang et al., 2016; Shen et al., 2019). Either way, the overlying Dongchuan Formation is uniformly dated as Griesbachian, lower Induan (Shen et al., 2019). However, the Shuanglongtan section at Zhaojia village is hard to compare with the Chahe and Lubei sections because of sedimentary facies changes. So, we use the Dongchuan Formation for the whole succession of Early Triassic according to the regional geological report.

#### MATERIALS AND METHODS

**Material**—The studied material includes several dozen isolated hybodont teeth, cephalic spines, fin spines, placoid scales, and remains of actinopterygians. Some specimens from the shark horizon were surface-collected while bulk sampling from vertebrate-containing limestone blocks was also carried out.

**Terminology**—Here, we follow a rather conservative taxonomic concept and distinguish between Hybodontiformes and Neoselachii. The term Hybodontiformes is used for extinct taxa as defined by Coates and Gess (2007), with the following synapomorphies: posterior (otic) portion of palatoquadrate reduced; fin spines with large retrorse denticles; presence of calcified pleural ribs; trochlear foramen level with or anterior to optic foramen. The term Neoselachii identifies modern-grade sharks, rays, and skates and their extinct allies. Elasmobranchii is considered here to consist of the sister group of Hybodontiformes and Neoselachii (contra Maisey, 2012). The descriptive tooth terminology follows that of Cappetta (2012).

**Preparation and Documentation**—Limestone blocks containing fossil fish remains were collected in the field and preparation was conducted in the Chengdu Center of the China Geological Survey. While some specimens were mechanically prepared with needles under a stereomicroscope, additional rock samples (50 kg) were dissolved with buffered 10% acetic acid and the residues picked under a stereomicroscope down to a sieve fraction of 0.159 mm. All teeth were studied with a Leica M125 microscope. Digital images of teeth still embedded in the matrix were obtained using a Zeiss Smartzoom 5 to combine a stack of 20 images into a single microphotograph, with all parts of the specimen in focus. Acid prepared specimens were studied and digitally imaged with a Hitachi S-4800 SEM at the Chengdu Center of the China Geological Survey.

**Repositories and Institutional Abbreviations**—All specimens described here are deposited in the fossil collections of the Chengdu Center of the China Geological Survey (CDCGS), Chengdu, China, prefixed HZ indicating the location of the fossil site in Huize County.

#### SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880  
Subclass ELASMOBRANCHII Bonaparte, 1838

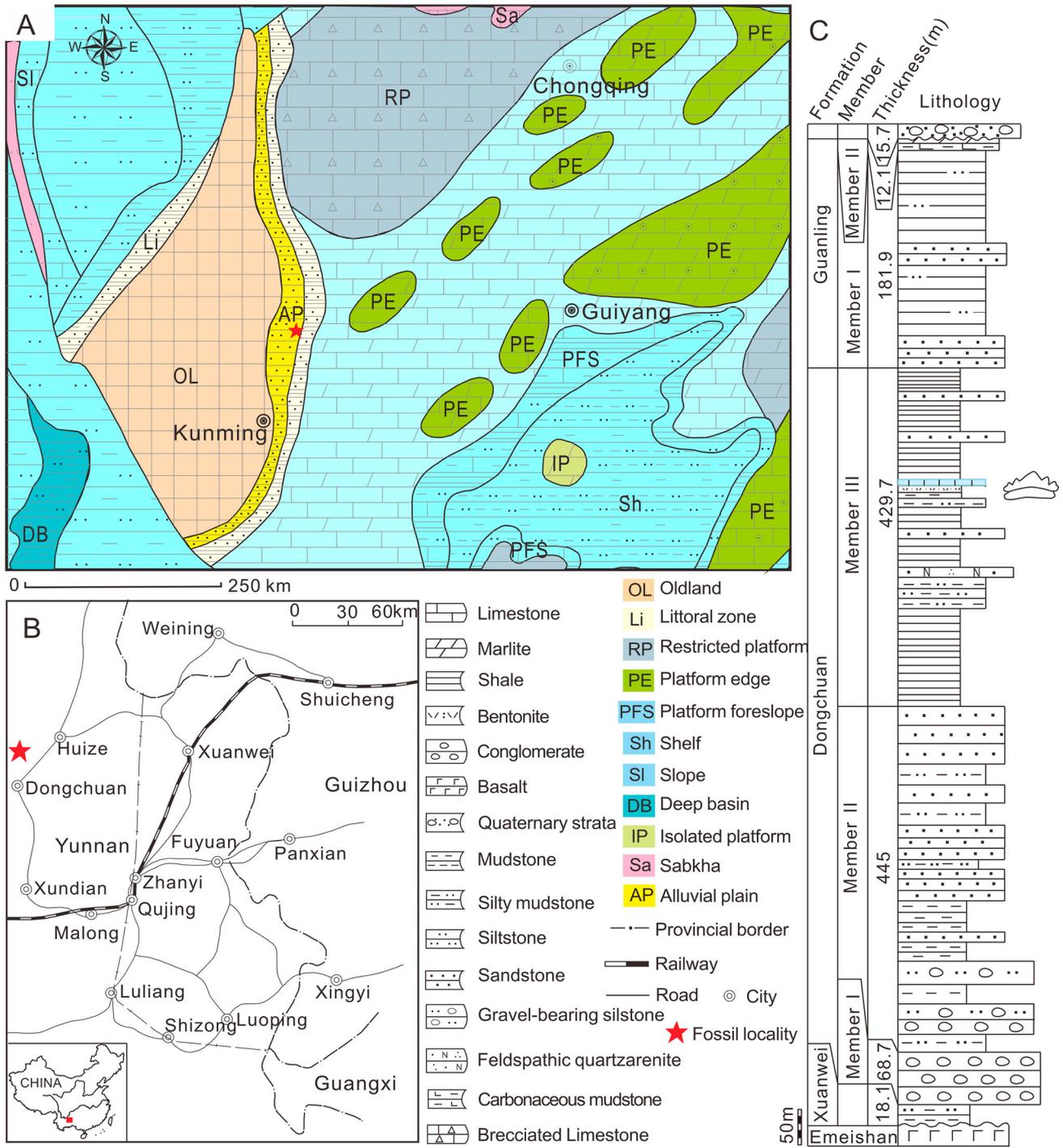


Figure 1. Location map: **A**, geological map of Yunnan and Guizhou Provinces with lithology (modified after Feng et al., 1997; Zhang et al., 2016); **B**, location map of Zhaojia village; **C**, profile of Shuanglongtan section.

Order HYBODONTIFORMES Maisey, 1987  
 Superfamily HYBODONTOIDEA Owen, 1846  
 Family LONCHIDIIDAE Herman, 1977, sensu Rees, 2008  
 Genus *PARVODUS* Rees and Underwood, 2002

**Type Species**—*Lissodus rugianus* Ansorge, 1990, from Wealden-type brackish-limnic clays of Berriasian–Valanginian age on the Island of Rügen, North Germany.

**Diagnosis**—Small lonchidiid shark characterized by cutting-/crushing-type dentition with teeth having a comparably low and mostly broad, almost triangular main cusp, which is not well separated from the lateral cusplets, and in which the lateral cusplets generally are broadly united.

*PARVODUS HUIZODUS* Wen and Kriwet, sp. nov.  
 (Figs. 2–5)

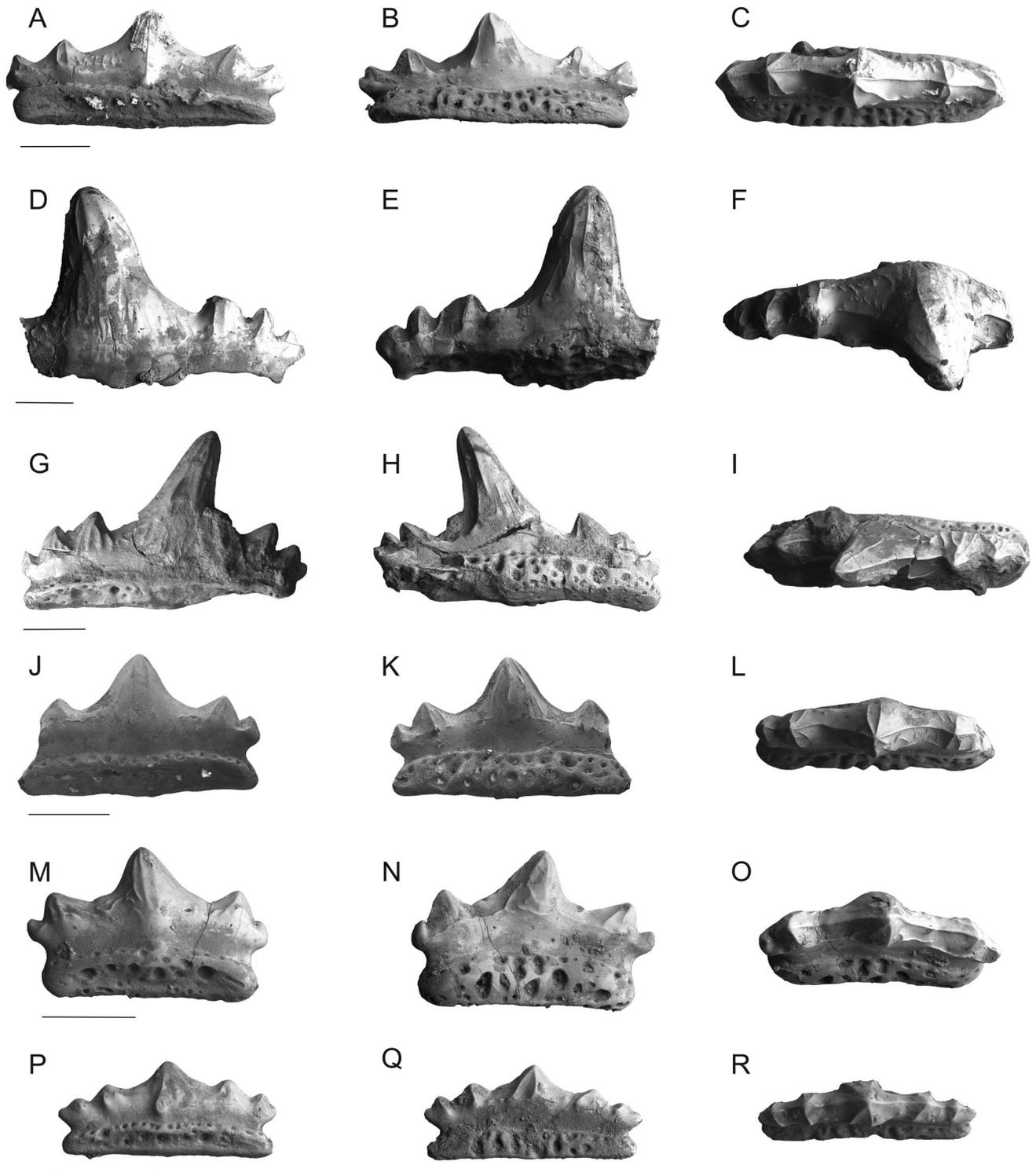


FIGURE 2. Teeth of *Parvodus huizodus* Wen and Kriwet, sp. nov. **A–C**, HZ-10, holotype, antero-lateral tooth in labial (**A**), lingual (**B**), and occlusal views (**C**); **D–F**, HZ-11, anterior tooth in labial (**D**), lingual (**E**), and occlusal views (**F**); **G–I**, HZ-12, anterior tooth in labial (**G**), lingual (**H**), and occlusal views (**I**); **J–L**, HZ-13, antero-lateral tooth in labial (**J**), lingual (**K**), and occlusal views (**L**); **M–O**, HZ-14, antero-lateral tooth in labial (**M**), lingual (**N**), and occlusal views (**O**); **P–R**, HZ-15, latero-posterior tooth in labial (**P**), lingual (**Q**), and occlusal views (**R**). Scale bars equal 1 mm.

**Holotype**—HZ-10, an antero-lateral tooth with root (Fig. 2A–C).

**Paratypes**—Eight teeth (HZ-1, HZ-2, HZ-3, HZ-4, HZ-5, HZ-6, HZ-11–HZ-20) (HZ-5, HZ-11–HZ-20 are complete) and three cephalic spines (HZ-21, HZ-22, HZ-23).

**Locality and Stratigraphic Age**—Zhaojia village, Huize County, Yunnan Province, China. Teeth of the new species were recovered from the upper part of the third member of the Dongchuan Formation; Olenekian, Lower Triassic. GPS: 103°6' 56"E, 26°28'25"N.

**Etymology**—The species name represents a combination of the name of the type locality and ‘odous’ (Greek) meaning ‘tooth’.

**Diagnosis**—A species of *Parvodus* characterized by the combination of the following dental characters (autapomorphic characters are indicated by an asterisk): main cusp moderately blunt, two to three pairs of low, broadly united and not very well-separated lateral cusplets, with vertical, more or less parallel ridges on the main cusp, starting just above the labial protuberance (labial peg) and ascending apically reaching the apex; rare vertical ridges on lateral cusplets usually originating at apices and continuing basally into a small node; short horizontal ridges present between main cusp and first lateral cusplets\*; short and very faint vertical ridges and small crenulae occasionally present between main cusp and first cusplets\*; labial protuberance small but well developed and rounded, not supported by a root buttress in latero-posterior teeth; labial protuberance very reduced to absent in anterior teeth; root fairly low, with a single row of small, rounded foramina present labially below crown-root junction and an additional row of large, oval foramina present basally on the recessed portion of the root, becoming smaller and circular below mesial and distal cusplets; incised lingual crown-root junction in posterior-lateral teeth.

**Description**—The holotype (HZ-10) represents an antero-lateral tooth with a mesio-distal length of 4 mm. In labial view, the main cusp is triangular with a distally inclined apex and flaring base. There are two well-developed lateral cusplets plus one incipient distal cusplet, whose axes diverge slightly from that of the main cusp. The crown is about twice as high as the root in labial view. The main cusp is relatively low and blunt, but twice as high as the first lateral cusplets. There are three low but well-developed ridges descending from the apex basally; only the middle one reaches the base of the cusp. A small and rounded labial peg, which is directed basally and slightly distally displaced, is developed in latero-posterior teeth. In anterior teeth, this labial peg is either very reduced (Fig. 2G) or completely absent (Fig. 2D). Additional small granulae and faint, short, impersistent vertical ridges are present between the main cusp and first mesial cusplet on the labial face of the crown. The vertical ridges on the lateral cusplets are prominent and elongated continuing basally into small nodes.

The crown area below the cusp and lateral cusplets (‘crown shoulder’) is low and devoid of any ornamentation. The occlusal crest (cutting edge) is well developed, runs the full mesiodistal length of the crown and is continuous between main cusp and all lateral cusplet apices.

In lingual view, three prominent ridges are present on the main cusp, starting at the apex and descending towards the base of the cusp but do not reach the crown-root junction. There is no lingual protuberance. A horizontal ridge is present basally between the main cusp and the first lateral cusplets. The area between the main cusp and first mesial cusplet displays three faint vertical ridges starting at the horizontal ridge, but not reaching the cutting edge. No distinct mesial or distal nodes can be observed lingually. The crown area below the cusp and lateral cusplets are devoid of any ornamentation. The root is extremely shallow in labial view. A row of small foramina is present below the main cusp and distal cusplets. The lingual root face is shallower than the crown and does not exceed the length of the crown mesially and distally. A row of small and rounded foramina occurs lingually below the crown-root junction and an additional row of larger foramina is developed below the main cusp and distal cusplets. Those foramina below the mesial cusplets are smaller and more rounded.

**Dental Variations**—The dentition of *Parvodus huizodus* Wen and Kriwet sp. nov. is of clutching-type and characterized by a linear gradient monognathic heterodonty (Figs. 2, 3, 4) with teeth ranging in mesio-distal length from 1–4 mm. The height

of the main cusp decreases gradually from anterior to posterior positions. The relative heights of the crown and the root vary through the dentition; in anterior teeth the crown forms around 80% of the total tooth height, whereas the crown and root are subequal in height in posterior teeth. The labial peg is weak in anterior teeth but is more strongly developed in lateral and posterior positions. The number of lateral cusplet pairs varies from two to three and crown ornamentation tends to become less complex distally through the dentition. The crown profile gets lower distally through the dentition. The basal horizontal ridge between the main cusp and first lateral cusplets is a consistent character and present in all teeth of this species. The occlusal crest is well-developed in all tooth positions. The root morphology also is similar in all teeth regardless of their position, with a very low concave labial shelf that is perforated by a single row of small circular foramina. The lingual surface is convex and higher, with larger foramina.

Specimens HZ-11 and HZ-12 are two anterior teeth (Fig. 2D–I), but HZ-11 lacks the root. It has a high main cusp with two to three lateral cusplets, whose axes diverge slightly from that of the main cusp. The height of the main cusp is three to four times the height of the first lateral cusplet. There is no labial peg but at the base of the main cusp, the vertical ridges of the lateral cusplets form small knob-like swellings.

Tooth HZ-12 also has a high main cusp, three lateral cusplets, and a low root. The main cusp, which is more slender than that of HZ-11 is inclined distally and is four times the height of the first lateral cusplets. The main cusp and lateral cusplets are variably ornamented with more vertical ridges in anterior teeth. A small labial peg is developed at the base of the main cusp.

The antero-lateral tooth HZ-1 has two well-developed distal plus one incipient distal cusplet (Fig. 3A). Short and very faint vertical ridges and small nodules are present labially between the main cusp and first distal cusplet.

The antero-lateral teeth (HZ-13, HZ-14) have two pairs of lateral cusplets (Fig. 2J–O). Tooth HZ-14 has only a small labial peg. Two to three ridges occupy the labial face of the main cusp starting at the apex and not reaching the base. Three ridges are displayed on the first pair of lateral cusplets. The mesial area between the main cusp and the first lateral cusplets is ornamented with small granulae. A horizontal ridge is developed between the main cusp and the first lateral cusplets in lingual view.

In labial view, the latero-posterior teeth HZ-2 and HZ-3 show a short horizontal ridge basally between the main cusp and the first lateral cusplets (Fig. 3B–D). Small nodules occur above the horizontal ridge.

In HZ-2 (Fig. 3B), a prominent vertical labial ridge is initiated about halfway up the main cusp, and descends basally, bifurcating just above the small labial peg giving it an almost triangular outline.

Tooth HZ-5 also is a complete latero-posterior tooth but only its lingual side can be observed (Fig. 3F). There are three pairs of lateral cusplets with the outermost pair being incipient. The main cusp is low but basally broad with the mesial cutting edge being longer than the distal one, giving the main cusp a slightly distally inclined appearance. A single prominent vertical ridge exists on the first two mesial cusplets, which are connected basally by a horizontal ridge. A short horizontal ridge connects the second and third mesial cusplets.

The lateral tooth HZ-15 also has three pairs of lateral cusplets, but a weak labial peg and less ornamentation on the crown (Fig. 2P–R).

The posterior teeth (HZ-18, HZ-19) have only two pairs of minute cusplets and weak labial pegs (Fig. 4A–F). The ornamentation seems to be less dense but more strongly developed on the lingual side in these teeth. Vertical ridge bifurcation takes place halfway down the main cusp lingually. There is also a horizontal

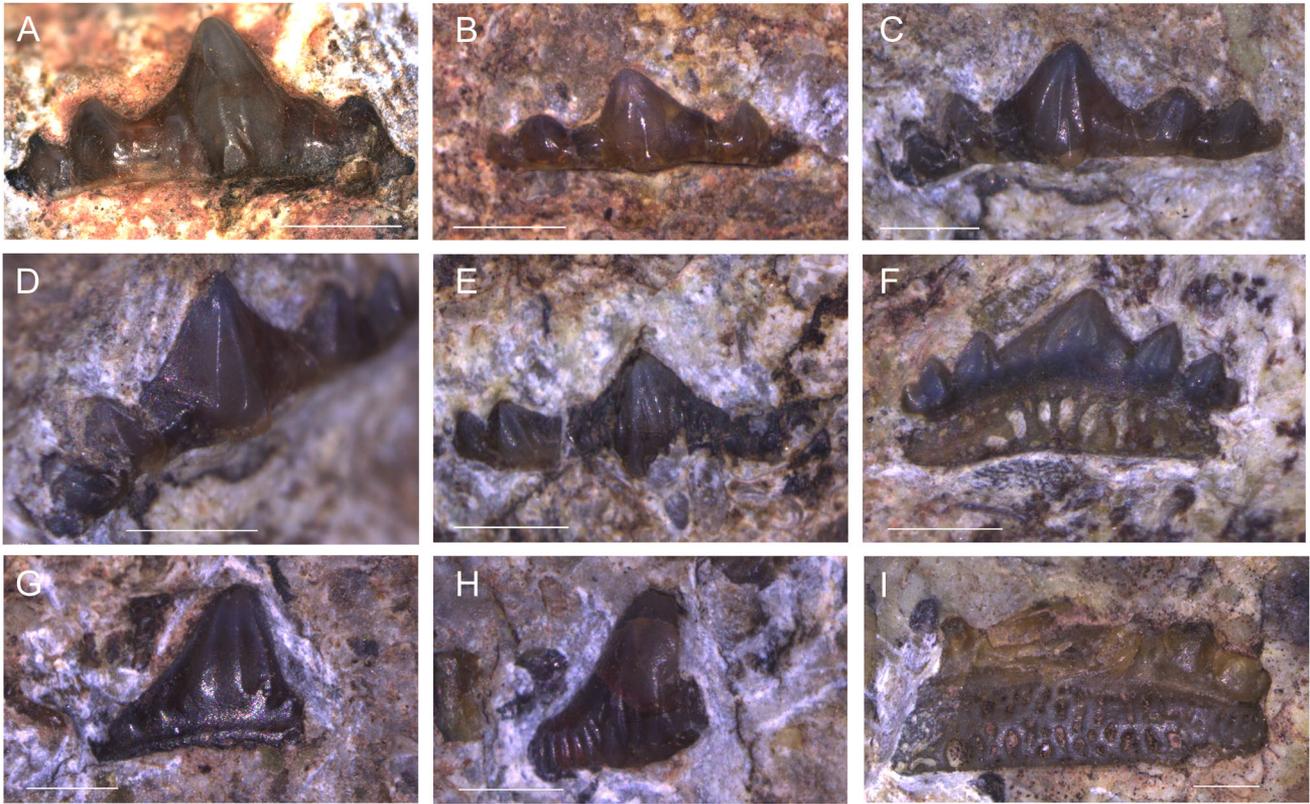


FIGURE 3. Teeth of *Parvodus huizodus* Wen and Kriwet, sp. nov. and Hybodontiformes fam., gen. et sp. indet. **A**, HZ-1, *Parvodus huizodus*, antero-lateral tooth, labial view; **B**, *Parvodus huizodus*, HZ-2, latero-posterior tooth, labial view; **C**, *Parvodus huizodus*, HZ-3, latero-posterior tooth, labial view; **D**, *Parvodus huizodus*, HZ-3, magnification of the horizontal ridge between the main cusp and lateral cusplet; **E**, *Parvodus huizodus*, HZ-4, latero-posterior tooth, labial view; **F**, *Parvodus huizodus*, HZ-5, latero-posterior tooth, lingual view; **G**, Hybodontiformes fam., gen. et sp. indet 1, HZ-7, labial view; **H**, Hybodontiformes fam., gen. et sp. indet 2, HZ-8, labial view; **I**, Hybodontiformes fam., gen. et sp. indet 3, HZ-9, incomplete tooth with complete root. Scale bars equal 1 mm.

ridge on the lingual face. The root is higher compared with the condition found in lateral teeth, being sub-equal to that of the crown.

The extreme posterior tooth HZ-20 has a conspicuous mesio-distally narrow crown (Fig. 4G–I). Ornamentation on the lingual side is stronger than on the labial side. The labial peg is not prominent, but the horizontal ridge also can be seen in lingual view. The root displays a similar morphology as the anterior teeth and also displays a strongly incised crown-root junction.

Teeth HZ-16 and HZ-17 are minute (1 mm in mesio-distal length) and interpreted here as representing juvenile individuals, which are characterized by comparably higher crowns and roots (Fig. 4J–O). The main cusp is also slightly higher with two pairs of lateral cusplets. The main cusp has one to three ridges in labial view. No ridge is developed on the lateral cusplets and the labial peg is faint. On the lingual crown face, one to two obvious ridges can be seen on the main cusp, which may bifurcate basally. One main ridge appears on the first pair of lateral cusplets. The mesial area between main cusp and first lateral cusplet is smooth. The mesial horizontal ridge is discontinuous. No ornamentation on the junction between the crown and the root is present. Note also that the crown/root junction is somewhat arched beneath the main cusp in labial view, whereas it is much straighter in larger teeth from all positions in the dentition. The root of the juvenile teeth seemingly is relatively higher than that of lateral adult teeth. A row of small circular foramina is present labially, whereas two rows occur on the lingual root face. The lower foramina are much larger and oval in shape

(long axes vertically longer than mesio-distally). Both teeth differ very slightly in the form and inclination of the main cusp and the morphology of lateral cusplets indicating that HZ-16 probably comes from an anterior, while HZ-17 derives from an antero-lateral jaw position. This could suggest that juvenile dentitions are more homodont than those of adults, where clear differences between anterior and antero-lateral teeth are developed.

**Remarks**—The general morphology of the teeth of the new species described here including the small size, the bilaterally symmetrical anterior teeth, comparatively low and broad main cusp, low and not well-separated lateral cusplets, the rounded, rather small labial protuberance, and the lingually displaced, low root allow their allocation to the genus *Parvodus* as defined by Rees and Underwood (2008). These authors originally assigned four species and an additional questionable occurrence to this genus resulting in a stratigraphic range from Lower Jurassic (Sinemurian) to Lower Cretaceous. In the following, two additional species were included in *Parvodus* so that six species (*Parvodus rugianus* [type-species], *P. curvidens*, *P. pattersoni*, *P. tikiensis*, *P. celsucuspus*, and *P. heterodon*) with a fossil range from the Upper Triassic (Carnian–Norian) to Lower Cretaceous (Valanginian) from Europe and India were considered valid (Rees, 2002; Rees and Underwood, 2002, 2006; Rees et al., 2013; Prasad et al., 2008; Sweetman et al., 2014). However, the Late Triassic Indian species *Parvodus tikiensis* was recently transferred to a new genus, *Pristisodus* (Bhat et al., 2018b).

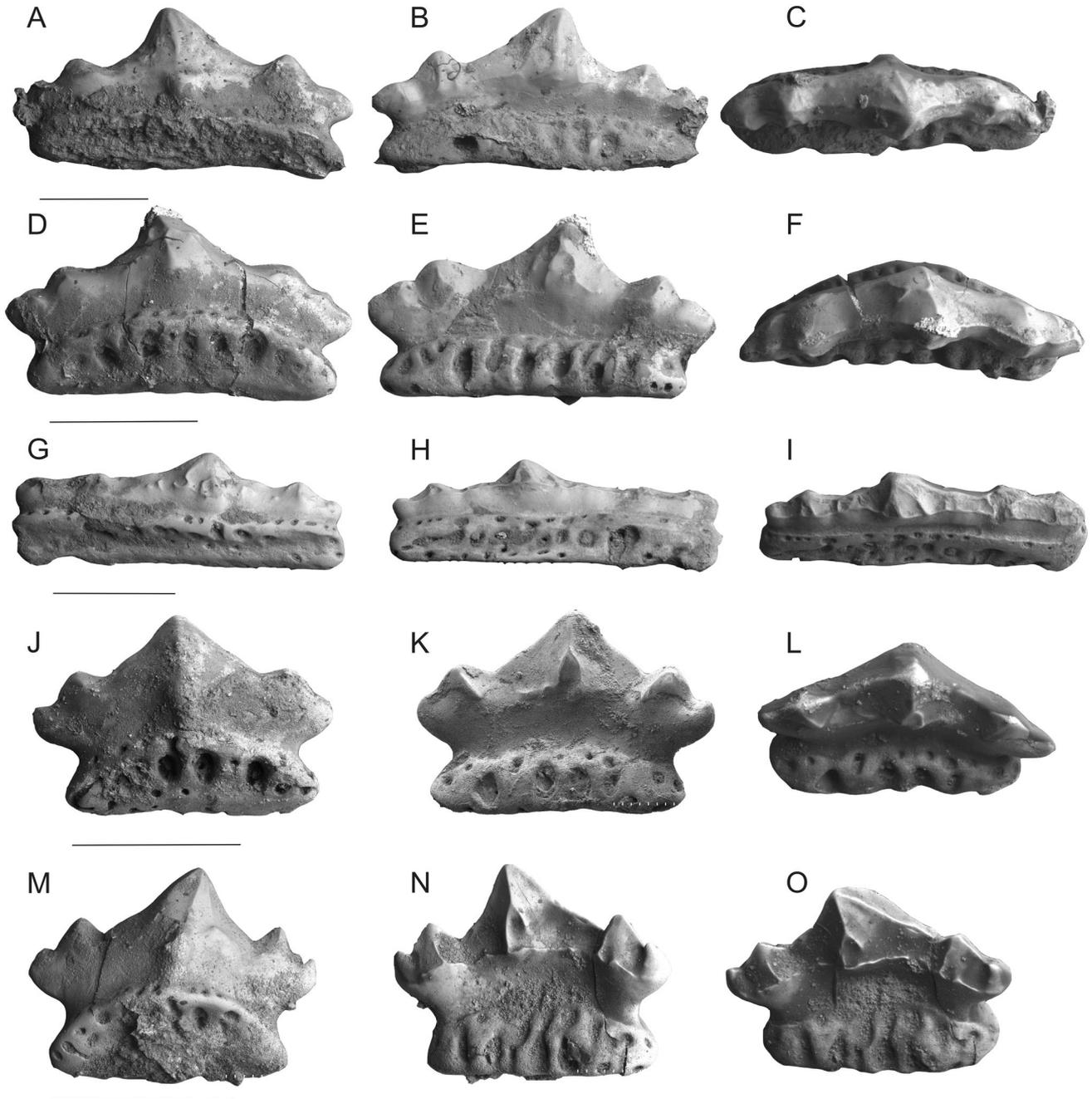


FIGURE 4. Teeth of *Parvodus huizodus* Wen and Kriwet, sp. nov. **A–C**, HZ-18, posterior tooth in labial (**A**), lingual (**B**), and occlusal views (**C**); **D–F**, HZ-19, posterior tooth in labial (**D**), lingual (**E**), and occlusal (**F**) views; **G–I**, HZ-20, extremely posterior tooth in labial (**G**), lingual (**H**), and occlusal (**I**) views; **J–L**, HZ-16, juvenile tooth in labial (**J**), lingual (**K**), and occlusal (**L**) views; **M–O**, HZ-17, juvenile tooth in labial (**M**), lingual (**N**), and occlusal (**O**) views. Scale bars equal 1 mm.

A literature review conducted during this study reveals, however, that *Parvodus* is significantly more diverse than was previously supposed, comprising at least 11 species, five of which have been named to date. These species range from the Lower Triassic to Lower Cretaceous (in stratigraphic order):

- a. *P. huizodus* Wen and Kriwet sp. nov. from the Olenekian of China (this study)
- b. ?*Pristrisodus* sp. from the Anisian Yangliujing Fm. of China (Chen et al., 2007)
- c. *Pristrisodus* sp. aff. *P. parvidens* from the lower Middle Jurassic Xietan Fm. of China (Shang et al. 2008)
- d. cf. *Pristrisodus* sp. from the lower Middle Jurassic Xietan Fm. of China (Shang et al., 2008)
- e. *P. duffini* from the Bathonian of England (Rees and Underwood, 2008)
- f. *P. pattersoni* from the Bathonian of England and Scotland (Rees and Underwood, 2006, 2008)
- g. *Pristrisodus* sp. from the Bathonian of Scotland (Rees and Underwood, 2006)

- h. *P. balabansaiensis* in part from the Callovian, Uzbekistan (Nessov and Kaznyshkin, 1988)
- i. *P. curvidens* from the Kimmeridgian of NW Germany (Duffin and Thies, 1997)
- j. *P. lusitanicus* from the Kimmeridgian of Portugal and the lower Tithonian of England (Kriwet, 2004)
- k. “*P. parvidens*” from the Upper Jurassic of Sweden (Rees, 1996)
- l. *P. celsucuspus* from the Berriasian (Lower Cretaceous) of western France (Rees et al., 2013)
- m. *P. heterodon* from Valanginian, England (Sweetman et al., 2014)
- n. *P. parvidens*, which probably is the most widespread species being reported from the Berriasian–Barremian of England (Purbeck and Wealden), France, Spain, northern Germany, Sweden, and the NW U.S.A. (Bermúdez-Rochas, 2009; Rees, 2002; Oreska et al. 2013)
- o. *P. rugianus*, which represents the type-species occurring from the Berriasian–Valanginian of N. Germany, England, Denmark, Sweden (Ansoerge, 1990; Rees, 2002)
- p. *Pristrisodus* sp. from the Hauterivian–Barremian of N Spain (Bermúdez-Rochas, 2009)
- q. *Pristrisodus* sp. from the Aptian of Thailand (Cuny et al., 2006)
- r. *Pristrisodus* sp. from the Aptian of northern U.S.A. (Oreska et al., 2013)
- s. *Pristrisodus* sp. from pre-Aptian deposits of NW Brazil (Cupello et al., 2012).

The different species can be grouped into two morphologically distinct groups based on tooth crown traits (Fig. 5). The first group (group 1 in the following) includes species with teeth characterized by rather high central cusps that are well separated from the lateral cusplets and form a clutching-type dentition (species b, c, e, h, j, k, l, n), while the second group (group 2 in the following), conversely, is characterized predominantly by teeth with a comparably low and mostly broad, almost triangular main cusp, which is not well separated from the lateral cusplets, and in which the lateral cusplets generally are broadly united forming a cutting-crushing dentition *sensu* Rees and Underwood (2002) (species d, f, g, i, m, o, p, q, r, s). The different tooth morphologies indicate that *Parvodus* as currently understood might represent an unnatural grouping of at least two different hybodontiforms. We, nevertheless, refrain from introducing new taxon names here, because a detailed dental morphological analysis and revision of all species is beyond the scope of this study. Consequently, we employ a conservative approach and assign the new species from the Lower Triassic of China tentatively to *Parvodus* pending further morphological studies on small-toothed hybodontiforms.

The new species described here undoubtedly belongs to group 2 (comparatively low and broad main cusp, low and not well-separated lateral cusplets), which also includes the type species of *Parvodus*. The character combination and especially the ornamentation of *P. huizodus* Wen and Kriwet sp. nov. consisting of a few vertical ridges starting above the labial peg and ascending apically without reaching the main cusp apex, vertical ridges on lateral cusplets usually originating at the apices descending basally and ending in small nodes, and the presence of a short horizontal ridge or small crenulae between the main cusp and lateral cusplets on the labial crown face readily distinguishes teeth of the new species from all other taxa in this group, but also from teeth of all other known hybodontiforms. Similar labial horizontal ridges also might occur in anterior teeth of *Parvodus heterodon* and *Pristrisodus tikiensis*, which are, however, continuous transversally, whereas they are restricted to the area between the main cusp and the lateral cusplets in the new species described

here. The anterior teeth are comparably high-crowned (if compared with latero-posterior teeth) and the labial peg might be very reduced (Fig. 2G) or even completely reduced (Fig. 2D). Nevertheless, the general ornamentation pattern of these anterior teeth unambiguously allows assignment of these teeth to the new species of *Parvodus* rather than to the other hybodontiforms presented here. Moreover, the species *P. celsucuspus* and *P. lusitanicus*, for example, also display rather high-crowned anterior and low-crowned latero-posterior teeth. The crown of *Parvodus* is similar to some extent to that of some Devonian euselachian sharks such as protacrodontids from the upper Famennian or Utah, Nevada and Middle Tournaian of Muhua, China. However, protacrodont teeth are characterized by a wider base, which is significantly extended lingually with larger nutritive foramina (Ginter, 2001; Ginter and Sun, 2007).

The evolutionary lineage that is characterized by a clutching-type dentition (group 1) shows that it was contemporaneous with group 2, with this group originating ca. 4.6 Ma earlier and vanishing ca. 8.2 Ma later than group 1 according to our present knowledge of their stratigraphic distribution. But it needs to be stressed that this statement is based on a rather small sample size. The differences in tooth architecture suggest that the two groups were adapted to different food resources. Species of *Parvodus* with high-crowned teeth, the preferred prey, nevertheless, might have included predominantly soft-bodied invertebrates and small fish, while species *Parvodus* with low and more massive crowns might have targeted shelled prey, thus reducing intra-species competition.

HYBODONTIFORMES fam., gen. et sp. indet. 1  
(Fig. 3G)

**Material**—A single fragmentary tooth, HZ-7.

**Locality and Stratigraphic Age**—Zhaojia village (GPS: 103°6′ 56″E, 26°28′25″N), Huize County, Yunnan Province, China. Upper part of the third member of Dongchuan Formation, Olenekian, Lower Triassic.

**Description**—Tooth HZ-7 is very incomplete preserving only the central main cusp, which is still embedded in the matrix and only displays the labial side. The cusp appears almost pyramidal due to three strong vertical ridges with somewhat swollen bases, that extend from the apex downwards but not reaching the base of the crown. Additional short oval and obliquely arranged crenulae can be observed on the preserved areas mesial and distal to the main cusp.

**Remarks**—The ornamentation of this tooth differs significantly from that of the other hybodontiforms from this locality. Its incomplete nature, however, does not allow any specific identification or assignment.

HYBODONTIFORMES fam., gen. et sp. indet. 2  
(Fig. 3H)

**Material**—A single fragmentary tooth, HZ-8. Only the main cusp is preserved.

**Locality and Stratigraphic Age**—Zhaojia village (GPS: 103°6′ 56″E, 26°28′25″N), Huize County, Yunnan Province, China. Upper part of the third member of Dongchuan Formation, Olenekian, Lower Triassic.

**Description**—The tooth HZ-8 also is fragmentary and lacks the mesial and distal parts of the crown as well as the root. The main cusp displays strong and short vertical ridges along the crown base that extend only a short distance apically. The ridges are not so strong as in HZ-7, but they are more densely packed.

**Remarks**—The ornamentation pattern distinguishes it from the other hybodontiforms in this site, but the fragmentary

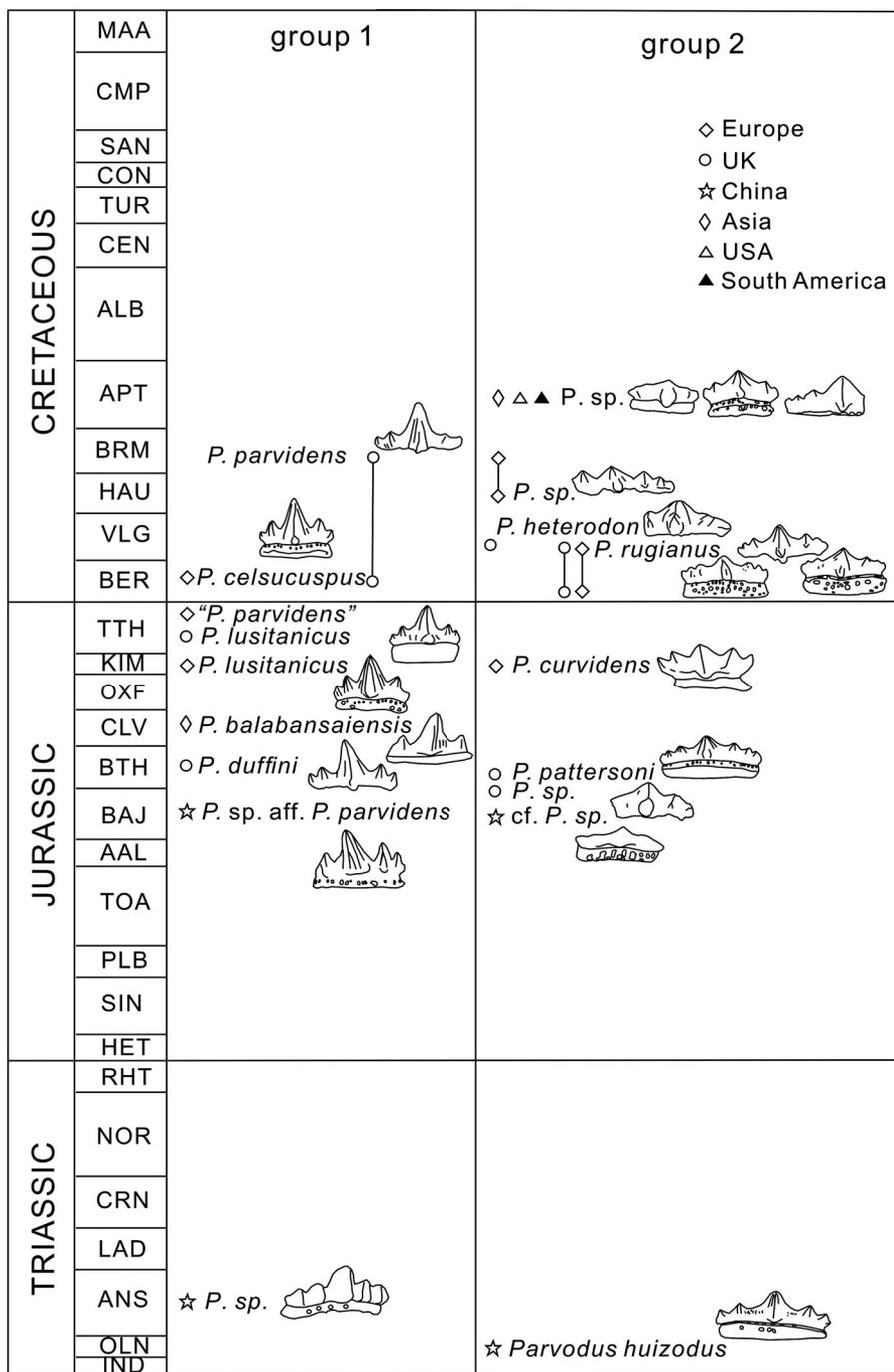


FIGURE 5. Two morphologically distinct groups with the new species in the second group. **Abbreviations:** AAL, Aalenian; ALB, Albian; ANS, Anisian; APT, Aptian; BAJ, Bajocian; BER, Berriasian; BRM, Barremian; BTH, Bathonian; CEN, Cenomanian; CLV, Callovian; CMP, Campanian; CON, Coniacian; CRN, Carnian; HAU, Hauterivian; HET, Hettangian; IND, Induan; KIM, Kimmeridgian; LAD, Ladinian; MAA, Maastrichtian; NOR, Norian; OLN, Olenekian; OXF, Oxfordian; PLB, Pliensbachian; RHT, Rhaetian; SAN, Santonian; SIN, Sinemurian; TOA, Toarcian; TTH, Tithonian; TUR, Turonian; VLG, Valanginian.

preservation prevents any taxonomic assignment beyond the order level.

HYBODONTIFORMES fam., gen. et sp. indet. 3 (Fig. 3I)

**Material**—An incomplete tooth, HZ-9.

**Locality and Stratigraphic Age**—Zhaojia village (GPS: 103°6' 56"E, 26°28'25"N), Huize County, Yunnan Province, China. Upper part of the third member of Dongchuan Formation, Olenekian, Lower Triassic.

**Description**—The single tooth of this taxon is also incomplete but preserves the root and the basal part of the crown including remnants of the lateral cusplets. It is still embedded in the rock and displays only the lingual side. The mesial portion of the tooth is largely missing. There are two distal lateral cusplets preserved that appear rather blunt. Mesially, remnants of a lateral cusplet are present. The root is highest mesially decreasing in height distally. The crown-root junction is almost completely straight and only a little arched. A well-defined row of small, circular foramina is present directly below the crown-root junction. Four additional irregular rows of larger and oval foramina

accompany the row of small foramina basally. Additional larger rounded to oval-shaped foramina are arranged below this row in four rather irregular rows.

**Remarks**—This tooth resembles those of *Parvodus huizodus* Wen and Kriwet sp. nov. to some extent, but the remaining lateral cusplets are seemingly more blunt and massive in HZ-9. The most conspicuous difference, however, is the presence of four irregular rows of nutritive foramina below the regular row of foramina on the lingual root face. Due to the poor presentation, it is nevertheless impossible to assign the specimen to any hybodontiform group.

#### ADDITIONAL MATERIAL

Additional but rare cranial and postcranial material was discovered together with the dental material described above. However, it is not possible to allocate this material to any of the tooth-based taxa because none of these specimens was found directly associated with the dental remains.

**Cephalic Spines**—This material includes four cephalic spines, HZ-21, HZ-22, HZ-23, and HZ-32 (Fig. 6), of which specimen HZ-21 measures 5 mm in length (Fig. 6A–D). Its crown is massive, curves posteriorly and is devoid of any ornamentation. The apex of the crown, unfortunately, is broken off, so it is impossible to identify whether a posterior barb was present. Its basal plate is very porous and displays a lateral, mesial, and posterior lobe. The posterior lobe is parallel sided, short and rectangular in outline. The mesial and lateral lobes are not completely preserved. Based on the morphology of the preserved part, the main shape of the basal plate was T-shaped in dorsal view.

The cephalic spine HZ-22 is slightly larger and measures 5.5 mm in length, but lacks the mesial lobe and tip of the cusp (Fig. 6E–H). The lateral lobe is well extended and angled posteriorly. The basal plate is essentially “arrow shaped.” The triangular parts of the lateral and mesial lobes, however, are very fragile and easily broken off, resulting in the specific shape of the basal plate in specimen HZ-22. A small and accentuated accessory cusplet is present between the lateral lobe and the main cusp. The posterior lobe is rectangular with posterior end rounded.

The cephalic spine HZ-23 is the largest one recovered and measures 9 mm in length, but also lacks the cusp and lateral lobe (Fig. 6I–L). The mesial lobe is angled posteriorly. The accessory cusp can also be observed although it is not complete. The posterior lobe is robust and parallel-sided.

The cephalic spine HZ-32 is the most complete one and measures 7 mm in length (Fig. 6M–P). The crown is complete and curves posteriorly without any ornament. The tip is pointed without barb. The robust mesial lobe and lateral lobe are well extended and angled posteriorly. The angle between the lateral lobe and the main cusp is bigger than that of HZ-22 and smaller than that of HZ-23. A moderate accessory cusplet appears between the main cusp and mesial lobe. The posterior lobe is short with a swelling end. The basal plate is very porous with many short ridges beneath the crown.

These cephalic spines were recovered in the same fossiliferous layer as the hybodontiform teeth including those of *P. huizodus* Wen and Kriwet sp. nov. The four cephalic spines except HZ-21 resemble those assigned to other species of *Parvodus* such as *P. celsucuspus* and *P. parvidens*, but also *Lonchidion selachos*, for example, in the “arrow shaped” basal plate (see Rees, 2002, 2008; Rees and Underwood, 2002; Rees et al., 2013), rather than having the “T-shaped” basal plate found in other hybodontiforms. The Chinese specimens differ from those assigned to *P. celsucuspus* by Rees et al. (2013), nevertheless, in lacking any crown ornamentation. There is a

small pointed accessory cusp between the lateral lobe and the main cusp, which differs from cephalic spines previously assigned to *Parvodus* spp. and *Lonchidion* spp. An accessory cephalic spine cusp was described in *Hybodus reticulatus* and *Lissodus cassangensis* (Maisey, 1987; Antunes et al., 1990). However, the accessory cusps are rounded in *Hybodus reticulatus* and divergent from the main cusp in *Lissodus cassangensis*. Furthermore, *Hybodus reticulatus* has a “T-shaped” basal plate and *Lissodus cassangensis* has an extended posterior lobe and broad lateral lobe.

**Fin Spines**—Two nearly complete, but small fin spines, HZ-24, HZ-25 (Fig. 7) were also obtained from the fossiliferous layer in the upper part of the third member of Dongchuan Formation. They measure 4 and 5 cm in apico-basal length, respectively. The lateral walls of the spines are ornamented with six vertical, slightly meandering costae. The intercostal trunk dentine is ornamented with intercostal grooves. No posterior denticles are preserved.

The general morphology of these fin spines agrees with that generally found in hybodontiform sharks. Unfortunately, however, the preservation and the occurrence of several different tooth-based hybodontiforms in the locality preclude assignment to any particular taxon.

**Placoid Scales**—Four different morphotypes of hybodontoid placoid scales, HZ-26, HZ-27, HZ-28, HZ-29, HZ-30, HZ-31 (Fig. 8), were recovered from the same fossiliferous horizon. The most common scales belong to morphotype 1, with diameters measuring 1.5–2.2 mm (Fig. 8A–F). Placoid scales of this type are stud-like, virtually symmetrical and ornamented with coarse, mostly non-bifurcating ridges that extend from the apex to the base. The apex is situated centrally above the base, which has a convex underside. A set of radial ridges is present on the margins of the base upper surface. Placoid scales of morphotype 2 are similar to those of morphotype 1, but some vertical ridges are curved posteriorly in apical view and the apex is displaced posteriorly but not beyond of the basal plate (Fig. 8G, H). Unlike morphotype 1, the vertical ridges show several orders of basal bifurcation. These scales are up to 1.2 mm in basal width, have a strongly convex undersurface and a higher density of finer radial ridges on the marginal areas of the base upper surface.

Placoid scales of morphotype 3 have laterally compressed crowns, which are acuminate, posteriorly inclined, and beyond the basal plate (Fig. 8I, J). Two lateral ridges flank a strong anterior ridge, all three merging at the posteriorly directed crown apex. All ridges show several orders of basal bifurcation. The base has radial ridges on the margins of the upper surface, and a slightly flatter undersurface than those of morphotypes 1 and 2.

The single scale assigned to morphotype 4 is minute and measures only 0.7 mm in width (Fig. 8K, L). It is symmetrical and spike-like and the vertical ridges starting from the apex are irregular; most reach the base of the crown, but some are very short and extend only a short distance from the apex (Fig. 8L). The basal plate is very narrow compared with that of the other morphotypes, almost not protruding below the cusp in apical view and rather high. The apex of the cusp is situated centrally.

All recovered placoid scales belong to the non-growing hybodontid type sensu Reif (1978) and display the typical features of hybodontiform placoid scales such as high and either conical crown with a ridged crown and absence of a defined neck between crown and basal plate. An assignment to any of the taxa represented by teeth in the Huize locality fauna is not possible; also, assignment of the scales to any particular body part remains difficult since different areas seemingly are occupied by different morphotypes. Nevertheless, Reif (1978) and Maisey (1982, 1986) presented very thorough accounts of

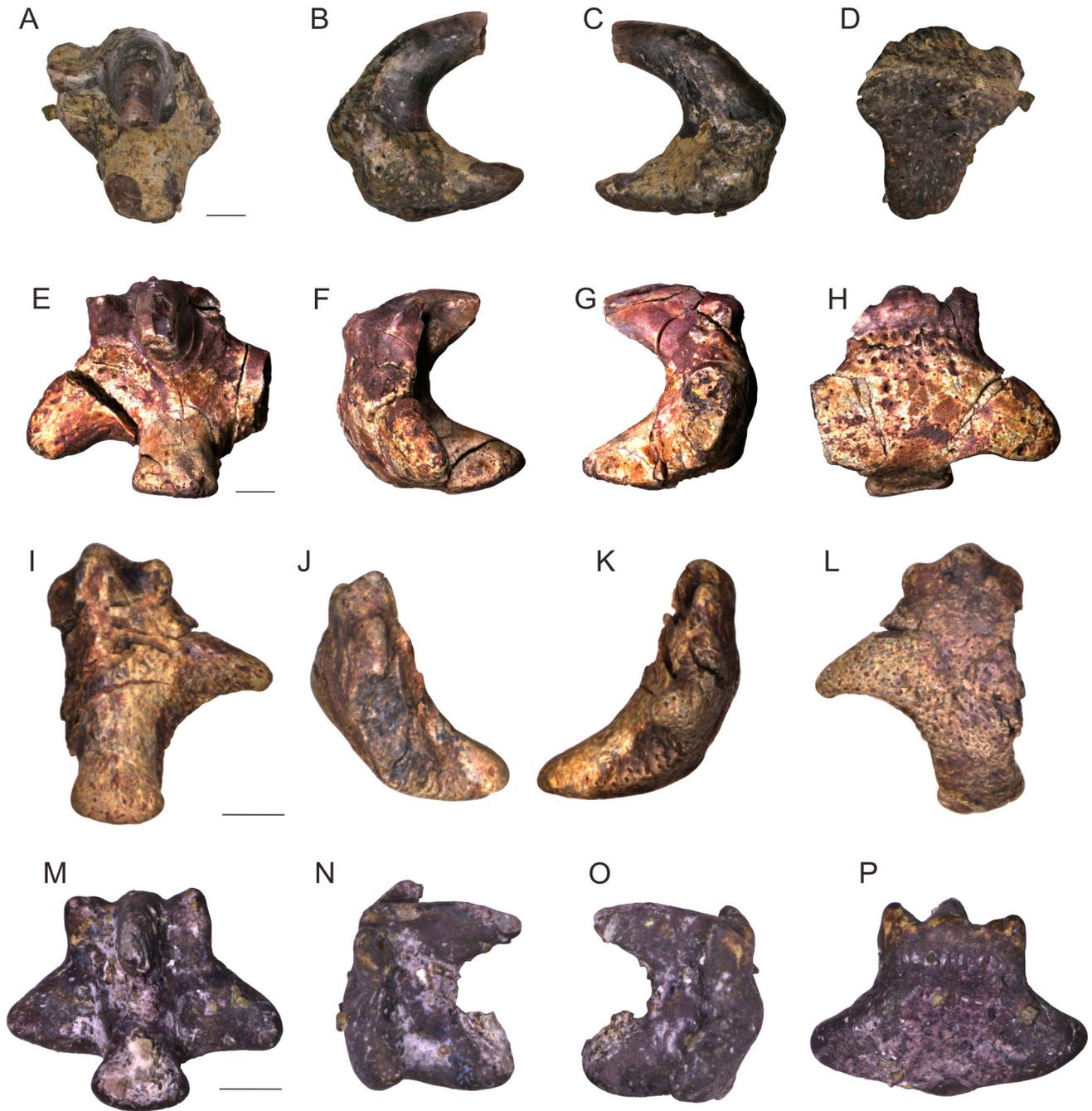


FIGURE 6. Hybodontiform cephalic spines. **A–D**, HZ-21, cephalic spine in dorsal (**A**), lateral (**B**), mesial (**C**), and basal (**D**) views; **E–H**, HZ-22, cephalic spine in dorsal (**E**), lateral (**F**), mesial (**G**), and basal (**H**) views; **I–L**, HZ-23, cephalic spine in dorsal (**I**), lateral (**J**), mesial (**K**), and basal (**L**) views; **M–P**, HZ-32, cephalic spine in dorsal (**M**), lateral (**N**), mesial (**O**), and basal (**P**) views. Scale bars for **A–H** equal 1 mm, scale bars for **I–P** equal 2 mm.

placoid scale morphology variations across the body of hybodontiforms, allowing a tentative assignment of the placoid scales described here to a specific body area. Accordingly, scales of morphotype 3 occur dorsally on the head, laterally over the upper jaws, across the postcranial body and the trailing edges of the fins, whereas cone-shaped placoid scales (morphotypes 1 and 2) cover the lower jaws laterally but also occur on the body posterior to the dorsal fin. Scale of morphotype 4 probably also originated from the head.

## DISCUSSION

### Taxonomy and Systematics

According to Cappetta (2012), hybodontiform sharks are arranged in seven families, the Hybodontidae, Distobatidae, Acrodontidae, Polyacrodontidae, Lonchidiidae, Steinbachodontidae, and Pseudodalatiidae. Here, we follow Kriwet (2004) and Rees and Underwood (2008) in considering the taxonomic and systematic status of *Polyacrodus* as ambiguous and *P. polycyphus* as a nomen dubium. Consequently, we also

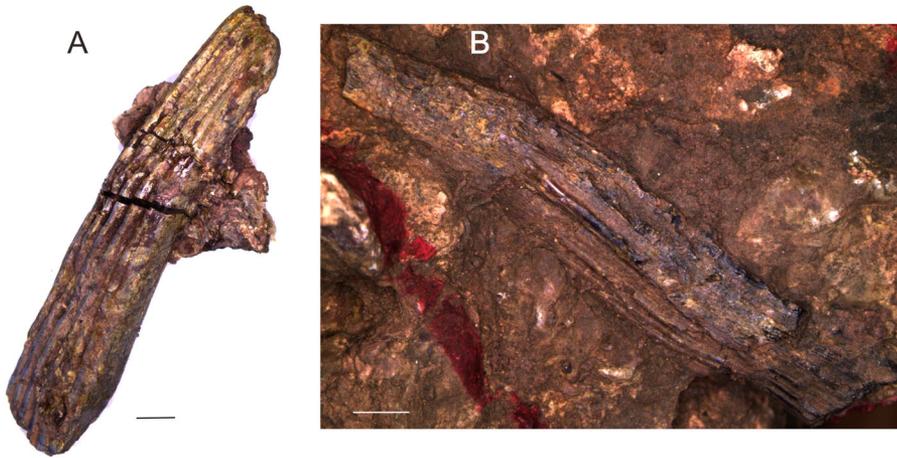


FIGURE 7. Hybodontiform fin spines. **A**, HZ-24, **B**, HZ-25 incomplete fin spines. Scale bars equal 3 mm.

reject the family Polyacrodontidae, which includes *Polyacrodus* and *Palaeobates*, in agreement with Cappetta (2012). The systematic scheme of Cappetta (2012) is also controversial, because it rests on descriptive morphological terms. Only Rees (2008), conversely, provided a different scheme based on cladistic principles using dental characters. According to this author, two families can be distinguished, Lonchidiidae (*Hylaeobatis*, *Lonchidion*, *Parvodus*, *Vectiselachos*, *Diplolonchidion*, *Pristrisodus*, *Jiaodontus*, *Bahariyodon*) and Hybodontidae (Acrodontinae: *Acrodus*, *Asteracanthus*, *Palaeobates*; Hybodontinae: *Hybodus*, *Egertonodus*; unnamed subfamily: *Planohybodus*, *Secarodus*, *Priohybodus*). *Lissodus* is excluded from the Lonchidiidae in this study because it also shares many characters with Acrodontinae such as heterodonty pattern, although the labial

protuberance is very reminiscent of some Lonchidiidae, in particular *Vectiselachos* (Rees, 2008). Recently, it was shown that the hybodontiforms *Asteracanthus* and *Strophodus*, which were considered synonymous for a long time, actually represent two well-separated genera distinct from all other known hybodontiforms (Stumpf et al., 2021b). *Strophodus* is characterized by specialized teeth that were well-adapted to a durophagous diet, whereas *Asteracanthus* had multicuspoid teeth quite similar to those of *Hybodus* and *Egertonodus*, suggesting closer phylogenetic relationships. Nevertheless, the systematic position of both *Asteracanthus* and *Strophodus* within Hybodontiformes remains ambiguous for the moment.

The small teeth described here and assigned to a new species are quite different from those of hybodontids and rather

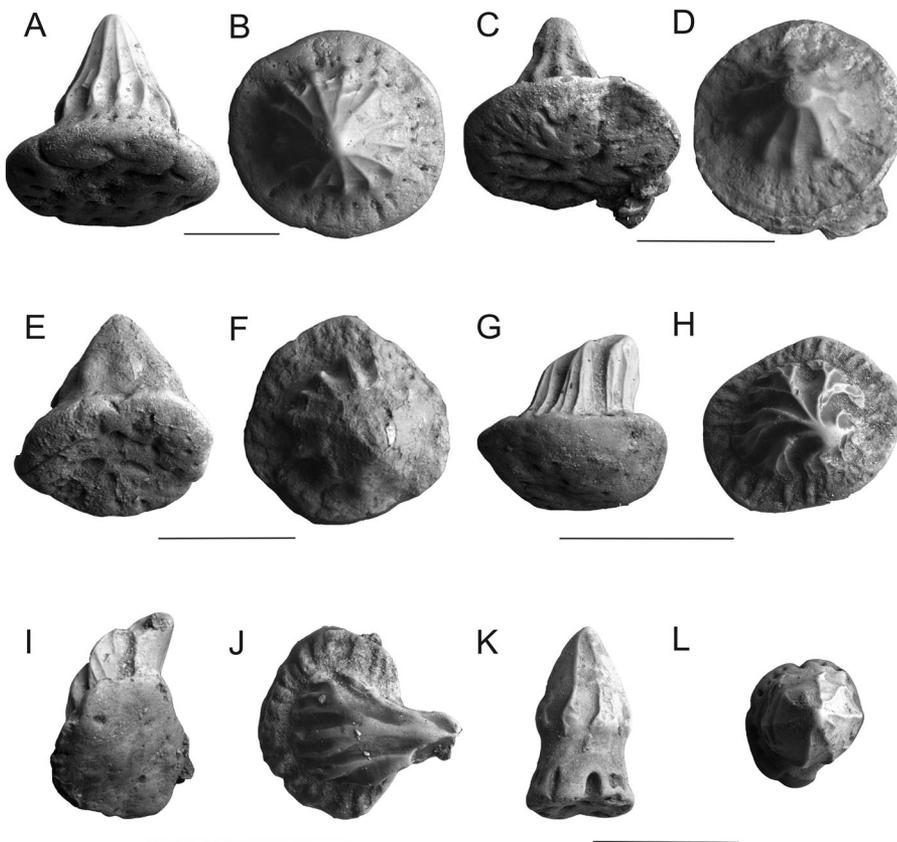


FIGURE 8. Hybodontiform placoid scales. **A–B**, HZ-26, morphotype I, in lateral (**A**) and apical (**B**) views; **C–D**, HZ-27, morphotype I, in lateral (**C**) and in apical (**D**) views; **E–F**, HZ-28, Morphotype I, in lateral (**E**) and in apical (**F**) views; **G–H**, HZ-29, morphotype II, in lateral (**G**) and in apical (**H**) views; **I–J**, HZ-30, morphotype III, in lateral (**I**) and in apical (**J**) views; **K–L**, HZ-40, morphotype IV, in lateral (**K**) and in apical (**L**) views. Scale bars equal 1 mm.

display the characteristic dental features of lonchidiid sharks such as a mesio-distally elongated crown, a labial protuberance, and a low root with a single row of rather circular nutritive foramina along the labial root face below the crown. Lonchidiidae currently includes eight genera that are all restricted to the Mesozoic (in stratigraphic order): *Parvodus* (Early Triassic–Early Cretaceous), *Lonchidion* (Middle Triassic–Late Cretaceous), *Diplolonchidion* (Late Triassic), *Pristisodus* (Late Triassic), *Vectiselachos* (Middle Jurassic–Early Cretaceous), *Jiaodontus* (Late Jurassic), *Hylaeobatis* (Early Cretaceous), and *Bahariyodon* (Early–Late Cretaceous). The genus *Lissodus*, which is excluded here from Lonchidiidae following Rees (2008), has also been reported from the Devonian, Carboniferous, and Permian (Fischer, 2008), indicating that lonchidiid sharks evolved after the Permian–Triassic extinction event.

### Regional Hybodontiform Diversity Patterns Across the PTB

In China, hybodontiform sharks are very common components of pre- and post-PTME chondrichthyan faunas, both in marine and freshwater environments, although their taxonomic diversity is quite low when compared with, for example, Europe (Rees and Underwood, 2008) (Supplemental Data). Interestingly, isolated placoid scales represent most pre-PTME hybodontiform records in China, for which a parataxonomic scheme was introduced (Wang et al., 2004, 2007; Ji et al., 2009).

Rare, isolated teeth from the Changhsingian (upper Permian) of China were assigned to *Lissodus* and *Polyacrodus* by Wang et al. (2007), and Wang et al. (2009) described the only known articulated hybodontiform skeleton (*Gansuselache tungshengi*) from China to date. This hybodontiform, whose relationships are unresolved, comes from sediments of Lopingian age and thus represents the only hybodontiform record directly below the PTME. In the Changhsingian, conversely, hybodontiforms including taxa based on placoid scales are most diverse even though the taxonomic assignment of some remains ambiguous (e.g., *Polyacrodus*). The absence of tooth-based hybodontiforms in the Lopingian most likely represents a taphonomic bias.

The taxonomic diversity of hybodontiforms seemingly increased during the Olenekian with four hybodontiform taxa, three of which are unidentified, and a new species of *Parvodus* and simultaneously representing the oldest record of this hybodontiform worldwide (this study). Additionally, a new lineage of *Parvodus* species with high-crowned teeth seemingly originated in marine settings at the beginning of the Middle Triassic. ‘*Polyacrodus*’ is apparently the only hybodontiform based on dental remains that crossed the PTME, whereas *Hybodus* and *Parvodus* seemingly are the dominant faunal elements of post-PTME hybodontiform assemblages in China.

From the Carnian of China, a diverse elasmobranch placoid scale fauna was described (Chen, 2002; Chen and Cuny, 2003), including one form-taxon (*Fragillicorona*) that also occurs in the Permian of China. The placoid scales described here cannot easily be ascribed to any of the taxa based on dermal denticles raised by Johns et al. (1997), whose work forms the foundation for taxonomic assignment of placoid scales from the Permian and Triassic of China. Moreover, placoid scales display different morphologies across the body and the number of placoid scale-based genera and species might significantly surpass the actual number of taxa (Naylor et al., 2021). Nevertheless, the placoid scales in this study display the characteristic features found in hybodontiform rather than neoselachian sharks, supporting our general taxonomic assignment here.

### Origins of Freshwater Hybodontiforms

During the Triassic and Jurassic, hybodontiforms repeatedly invaded freshwater environments such as lakes and rivers, and

not nearly exclusively marine until the Late Cretaceous. Indeed, Lu et al. (2005) suggested that hybodontiform sharks did not adapt to continental environments until the Jurassic in China, based on rich records of tooth-based taxa, including *Hybodus*, *Acrodus*, *Parvodus*, *Polyacrodus*, *Hubeiodus*, and *Jiaodontus* from Gansu, Yunnan, Sichuan, Shanxi, Hunan, Hubei provinces, and Junggar Basin (Young, 1935, 1941, 1942; Liu, 1962; Wang, 1977; Xue, 1980; Shang et al., 2008; Klug et al., 2010; Sun et al., 2018).

Our new findings suggest the switch to continental habitats might date back to the Early Triassic, although not all lineages were exclusively freshwater at that time. Already noted are the continental *Gansuselache tungshengi* (Wang et al., 2009) and *Hybodus youngi* (Liu, 1962). Our new assemblage of four taxa from the Dongchuan Formation, including the new species of *Parvodus* and three unidentified hybodontiforms, also comes from a continental setting of Early Triassic age. Whether this represents a typical Lower Triassic occurrence and that the PTME reset hybodontiform habitats, or whether this ichthyofauna is atypical in comparison to other sharks of the time (Lucifora et al., 2015) cannot be said at present because of limited sampling of coeval shark faunas. As noted by Koot et al. (2014), Early Triassic chondrichthyans have an average richness per locality of just over two genera and a maximum of six (Koot et al., 2014). Freshwater hybodontiforms are rare worldwide, with just one record of *Lissodus* sp. from the Scythian (Lower Triassic) in the Karoo Basin of South Africa (Bender and Hancox, 2004) apart from the Dongchuan ichthyofauna. Further collecting thus is required.

### CONCLUSIONS

In this study, we present the first Early Triassic sharks from the continental Dongchuan Formation in China and identify four hybodont dental morphotypes, which might represent distinct taxa. The small fauna importantly includes the earliest record and a new species, which represents the earliest record of the small-sized, durophagous hybodontiform, *Parvodus*. The rather rich fossil record of *Parvodus* indicates that it predominantly inhabited continental aquatic environments. In China, previous records of *Parvodus* come from the Jurassic Xietan Formation in the Three Gorges area (Shang et al., 2008). All these records of the second morphological group indicate that this shark occupied a rather wide range of environmental settings but never adapted to fully marine environments. The oldest record of the first morphologically distinct group which is of early Middle Triassic age also comes from China, but from marine sediments.

### ACKNOWLEDGMENTS

We thank G. M. Ren, X. Z. Cui, Z. B. Gou for the Zircon U-Pb analysis, G. Wang for help with using the SEM, S. L. Lin and Y. D. Qin for measuring the section. We thank C. Underwood and A. López-Arbarelo for editorial assistance, and J. Fischer and an anonymous reviewer for constructive suggestions. This work is supported by National Natural Science Foundation of China (No. 42102019, 41772022, and 41661134047), projects from China Geological Survey (DD20190054, DD20160020, DD20221635) and Observation and Research Station, Ministry of Natural Resources of the People’s Republic of China.

### ORCID

Wen Wen  <http://orcid.org/0000-0002-9661-9558>

Jürgen Kriwet  <http://orcid.org/0000-0002-6439-8455>

Michael J. Benton  <http://orcid.org/0000-0002-4323-1824>

## LITERATURE CITED

- Ansorge, J. 1990. Fischreste (Selachii, Actinopterygii) aus der Wealdentonscholle von Lobber Ort (Mönchgut/Rügen/DDR). *Paläontologische Zeitschrift* 64:133–144.
- Antunes, M. T., J. G. Maisey, M. M. Marques, B. Schaeffer, and K. S. Thomson. 1990. Triassic fishes from the Cassange Depression (R. P de Angola). *Ciências da Terra (UNL)* 1:1–16.
- Bender, P.A., and P. J. Hancox. 2004. Newly discovered fish faunas from the Early Triassic, Karoo Basin, South Africa, and their correlative implications. *Gondwana Research*. 7(1): 185–192.
- Benton, M. J., Q. Y. Zhang, S. X. Hu, Z. Q. Chen, W. Wen, J. Liu, J. Y. Huang, C.Y. Zhou, T. Xie, J. N. Tong, and B. Choo. 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Science Reviews* 125:199–243.
- Bermúdez-Rochas, D. D. 2009. New hybodont shark assemblage from the Early Cretaceous of the Basque-Cantabrian Basin. *Geobios* 42:675–686.
- Bhat, M. S., S. Ray, and P. M. Datta. 2018a. A new assemblage of freshwater sharks (Chondrichthyes: Elasmobranchii) from the Upper Triassic of India. *Geobios* 51:269–283.
- Bhat, M. S., S. Ray, and P. M. Datta. 2018b. A new hybodont shark (Chondrichthyes, Elasmobranchii) from the Upper Triassic Tiki Formation of India with remarks on its dental histology and biostratigraphy. *Journal of Paleontology* 92:221–239.
- Bonaparte, C. L. 1838. *Iconografia della fauna italiana per le quarto classi degli animali vertebrati*. Tomo III: Pesci. Salviucci, Roma, 266 pp.
- Cappetta, H. 2012. Chondrichthyes Mesozoic and Cenozoic Elasmobranchii: Teeth; in: H.-P. Schultze (ed.). *Handbook of Paleichthyology*, Vol. 3E. Verlag Dr. Friedrich Pfeil, München, 512 pp.
- Chen, L. D. 2002. New data of Middle- Late Triassic elasmobranch ichthyoliths from “Falang Formation” in Guanling, Guizhou. *Acta Micropalaeontologica Sinica* 19:276–287.
- Chen, L. D., and G. Cuny. 2003. Discovery of the Middle-Late Triassic elasmobranch ichthyoliths from the Guanling area, Guizhou, SW China. *Geological Bulletin of China* 22:236–247.
- Chen, L. D., G. Cuny, and X. F. Wang. 2007. The chondrichthyan fauna from the Middle-Late Triassic of Guanling (Guizhou province, SW China). *Historical Biology* 19:291–300.
- Coates, M. I., and R. W. Gess. 2007. A new reconstruction of *Onychoselache traquairi*, comments on early chondrichthyan pectoral girdles and hybodontiform phylogeny. *Palaeontology* 50:1421–1446.
- Compagno, L. J. 1977. Phyletic relationships of living sharks and rays. *American Zoologist* 17:303–322.
- Cuny, G. 2012. Freshwater hybodont sharks in Early Cretaceous ecosystems: A review; pp. 519–529 in: P. Godefroit (ed.). *Bernissart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press, Bloomington.
- Cuny, G., V. Suteethorn, S. Kamba, E. Buffetaut, and M. Philippe. 2006. A new hybodont shark assemblage from the Lower Cretaceous of Thailand. *Historical Biology* 18:21–31.
- Cupello, C. D., D. D. Bermúdez-Rochas, D. M. Martill, and P. M. Brito. 2012. The Hybodontiformes (Chondrichthyes: Elasmobranchii) from the Missão Velha Formation (?Lower Cretaceous) of the Araripe Basin, North-East Brazil. *Comptes Rendus Palevol* 11:41–47.
- Duffin, C. J. 1997. The dentition of *Hybodus hauffianus* Fraas, 1895 (Toarcian, Early Jurassic). *Stuttgarter Beiträge zur Naturkunde, Serie B* 256:1–20.
- Duffin, C. J. 2001. Synopsis of the selachian genus *Lissodus* Brough, 1935. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221:145–218.
- Duffin, C. J., and D. Thies. 1997. Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. *Geologica et Palaeontologica* 31:235–253.
- Feng, Z. Z., Z. D. Bao, and S. W. Li. 1997. Lithofacies Palaeogeography of Middle and Lower Triassic of South China. *Petroleum Industry Press, Beijing*.
- Feng, Z. Z., Z. K. Jin, Y. Q. Yang, Z. D. Bao, and W. J. Xin. 1994. Lithofacies Paleogeography of Permian of Yunnan–Guizhou–Guangxi Region. *Geological Publishing House Beijing*.
- Fischer, J. 2008. Brief synopsis of the hybodont form taxon *Lissodus* Brough, 1935, with remarks on the environment and associated fauna. *Freiberger Forschungshefte C* 528:1–23.
- Fischer, J., J. W. Schneider, S. Voigt, M. M. Joachimski, M. Tichomirowa, T. Tütken, J. Götze, and U. Berner. 2013. Oxygen and strontium isotopes from fossil shark teeth: Environmental and ecological implications for Late Palaeozoic European basins. *Chemical geology* 342(1): 44–62.
- Fischer, J., S. Voigt, M. Franz, J. W. Scheider, M. M. Joachimski, M. Tichomirowa, J. Götze, and H. Furrer. 2012. Palaeoenvironments of the late Triassic Rhaetian Sea: Implications from oxygen and strontium isotopes of hybodont shark teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* 353–355:60–72.
- Friedman, M., and L. C. Sallan. 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* 55:707–742.
- Ginter, M. 2001. Chondrichthyan biofacies in the Late Famennian of Utah and Nevada. *Journal of Vertebrate Paleontology* 21:714–729.
- Ginter, M., Y. L. Sun. 2007. Chondrichthyan remains from the Lower Carboniferous of Muhua, Southern China. *Acta Palaeontologica Polonica* 52:705–727.
- Ginter, M., V. Hairapetian, and C. Klug. 2002. Famennian chondrichthyan from the shelves of North Gondwana. *Acta Geologica Polonica* 52:169–215.
- Herman, J. 1977. Les séliaciens des terrains néocrétacés & paléocènes de Belgique & des contrées limitrophes. *Éléments d’une biostratigraphie intercontinentale. Mémoires pour servir à l’explication de Cartes Géologiques et Minières de la Belgique*. Service Géologique de Belgique 15:1–401.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 43:649–662.
- Ji, Q., X. X. Ji, and H. Z. Feng. 2009. Middle Permian fish microremains from the Sidazhai Area, Ziyun County, Guizhou Province. *Geological Review* 55(5):609–613.
- Johns, M. J., C. R. Barnes, and M. J. Orchard. 1997. Taxonomy and biostratigraphy of Middle and Late Triassic elasmobranch ichthyoliths from Northeast British Columbia. *Geological Survey Canada Bulletin* 502:1–235.
- Johnson, G. D. 1980. *Xenacanthoidii* (Chondrichthyes) from the Tecovas Formation (Late Triassic) of west Texas. *Journal of Paleontology* 54:923–932.
- Klug, S., T. Tütken, O. Wings, H. U. Pfretzschner, and T. Martin. 2010. A Late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China. *Palaeobiodiversity & Palaeoenvironments* 90:241–257.
- Koot, M. B., G. Cuny, M. J. Orchard, S. Richo, M. B. Hart, and R. J. Twitchett. 2014. New hybodontiform and neoselachian sharks from the Lower Triassic of Oman. *Journal of Systematic Palaeontology* DOI: 10.1080/14772019.2014.963179.
- Kriwet, J. 2004. Late Jurassic selachians (Chondrichthyes: Hybodontiformes, Neoselachii) from Central-Portugal. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2004:233–256.
- Leuzinger, L., G. Cuny, E. Popov, and J. P. Billon-Bruyat. 2017. A new chondrichthyan fauna from the Late Jurassic of the Swiss Jura (Kimmeridgian) dominated by hybodonts, chimaeroids and guitarfishes. *Papers in Palaeontology* 3:471–511.
- Leuzinger, L., L. Kocsis, J. P. Billon-Bruyat, S. Spezzaferri, and T. Vennemann. 2015. Stable isotope study of a new chondrichthyan fauna (Kimmeridgian, Porrentruy, Swiss Jura): an unusual freshwater-influenced isotopic composition for the hybodont shark *Asteracanthus*. *Biogeosciences* 12:6945–6954.
- Liu, X. T. 1962. Two new *Hybodus* from North Shensi, China. *Vertebrata Palasiatica* 6:150–156.
- Lin, S. L., Y. J. Gao, Y. D. Qin, and X. Y. Lou. 2015. Chengdu Center of China Geological Survey. Regional Geological Survey Report of the People’s Republic of China 1:50000 Baiwujie G48E010005. China Geological Survey.
- Lu, L. W., Y. G. Jin, and X. S. Fang. 2005. A revision of Middle Jurassic *Hybodus houtienensis* Young (Chondrichthyes: Hybodontidae) from Yunnan. *Geological Bulletin of China* 24:145–148.

- Lucifora, L. O., M. R. de Carvalho, M. K. Peter, and W. T. White. 2015. Freshwater sharks and rays. *Current Biology* 25:971–973.
- Maisey, J. G. 1982. The anatomy and interrelationships of Mesozoic hybodont sharks. *American Museum Novitates* 2724:1–48.
- Maisey, J. G. 1986. Heads and tails: a chordate phylogeny. *Cladistics* 2:201–256.
- 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*, gen. et sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates* 2931:1–42.
- Maisey, J. G. 2012. What is an “elasmobranch”? The impact of palaeontology in understanding elasmobranch phylogeny and evolution. *Journal of Fish Biology* 80:918–951.
- Naylor, G. J. P., A. de Lima, J. I. Castro, G. Hubbell, and M. C. C. de Pinna. 2021. Comment on “An early Miocene extinction in pelagic sharks”. *Science* 374(6573): eabj8723. Doi: [10.1126/science.abj8723](https://doi.org/10.1126/science.abj8723).
- Nessov, L. A., and M. N. Kaznyshkin. 1988. Late Jurassic cartilaginous fishes of northern Fergana. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva* 31:160–178.
- Oreska, M. P. J., M. T. Carrano, and K. M. Dzikiewicz. 2013. Vertebrate paleontology of the Cloverly Formation (Lower Cretaceous), I: faunal composition, biogeographic relationships, and sampling. *Journal of Vertebrate Paleontology* 33:264–292.
- Owen, R. 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. Longman Publishers, London, 308 pp.
- Prasad, G. V. R., K. Singh, V. Parmar, A. Goswami, and C. S. Sudan. 2008. Hybodont shark teeth from the continental Upper Triassic deposits of India; pp. 413–432 in G. Arratia, H. P. Schultze, and M. V. H. Wilson (eds.), *Mesozoic Fishes 4- Homology and Phylogeny*. Verlag Dr. Friedrich Pfeil, München.
- Rees, J. 1996. A new hybodont shark fauna from the Upper Jurassic Vitabäck Clays at Eriksdal, Scania, southern Sweden. *Examensarbete i geologi vid Lunds universitet. Historisk geologi och paleontology* 74:1–20.
- Rees, J. 2002. Shark fauna and depositional environment of the earliest Cretaceous Vitabäck Clays at Eriksdal, southern Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 93:59–71.
- Rees, J. 2008. Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology - preliminary results. *Acta Geologica Polonica* 58:217–221.
- Rees, J., and C. J. Underwood. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontidea (Selachii). *Journal of Vertebrate Paleontology* 22:471–479.
- Rees, J., and C. J. Underwood. 2006. Hybodont sharks from the Middle Jurassic of the Inner Hebrides, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 96:351–363.
- Rees, J., and C. J. Underwood. 2008. Hybodont sharks of the English Bathonian and Callovian (Middle Jurassic). *Palaeontology* 51:117–147.
- Rees, J., G. Cuny, J. Pouech, and J. M. Mazin. 2013. Non-marine selachians from the basal Cretaceous of Charente, SW France. *Cretaceous Research* 44:122–131.
- Reif, W. E. 1978. Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologische Zeitschrift* 52:110–128.
- Seilacher, A. 1943. Elasmobranchier-Reste aus dem oberen Muschelkalk und dem Keuper Württembergs. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte* 1943:256–271.
- Seilacher, A. 1948. Ein weiterer altertümlicher Elasmobranchier (*Phoebodus keuperinus* n. sp.) aus dem württembergischen Gipskeuper. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1948:24–27.
- Shang, Q. H., G. Cuny, and L. D. Chen. 2008. Early Middle Jurassic vertebrate microremains from the Three Gorges area, southern China. *Historical Biology* 20:87–99.
- Shen, J., J. Yu, J. Chen, T. J. Algeo, G. Xu, Q. Feng, X. Shi, N. J. Planavsky, W. Shu, and S. Xie. 2019. Mercury evidence of intense volcanic effects on land during the Permian-Triassic transition. *Geology* 47:1117–1121.
- Stumpf, S., and J. Kriwet. 2019. A new Pliensbachian elasmobranch (Vertebrata, Chondrichthyes) assemblage from Europe, and its contribution to the understanding of late Early Jurassic elasmobranch diversity and distributional patterns. *PalZ* 93:637–658.
- Stumpf, S., S. Etches, C. J. Underwood, and J. Kriwet. 2021a. *Durnonovariaodus maiseyi* gen. et sp. nov., a new hybodontiform shark-like chondrichthyan from the Upper Jurassic Kimmeridge Clay Formation of England. *PeerJ* 9:e11362.
- Stumpf, S., F. A. López-Romero, R. Kindlimann, F. Lacombat, B. Pohl, and J. Kriwet. 2021b. A unique hybodontiform skeleton provides novel insights into Mesozoic chondrichthyan life. *Papers in Palaeontology* 7:1479–1505. <https://doi.org/10.1002/spp2.1350>.
- Sun, B. D., W. Wang, J. P. Liu, D. H. Song, B. Y. Lü, Y. F. Xu, and L. Wang. 2018. New fossil materials of *Hybodus* (Chondrichthyes) in the Middle Jurassic found in Chuanjie Basin of central Yunnan Province. *Geological Bulletin of China* 37:1991–1996.
- Sun, Z. P., and Y. P. Han. 1998. Significance of Early Triassic Dongchuan Formation in Western Weining County of Guizhou. *Guizhou Geology* 15:115–118.
- Sweetman, S. C., J. Goedert, and D. M. Martill. 2014. A preliminary account of the fishes of the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England. *Biological Journal of the Linnean Society* 113:872–896.
- Turner, S. 2011. The survivors: Triassic xenacanthiform sharks in Australia. 12th International Symposium on Early Vertebrates/Lower Vertebrates, Dallas, Texas, June 11–14, 2011, *Ichthyolith Issues*.
- Wang, N. Z. 1977. Jurassic fishes from Lingling-Hengyang, Hunan and its stratigraphical significance. *Vertebrata Palasiatica* 15:233–243.
- Wang, N. Z., F. Jin, and W. Wang. 2004. Early Carboniferous fishes (acanthodian, actinopterygians and Chondrichthyes) from the east sector of North Qilian Mountain, China- Carboniferous fishes sequence from the east sector of North Qilian Mountain. *Vertebrata Palasiatica* 42:89–110.
- Wang, N. Z., X. S. Zhu, and F. Jin. 2007. Chondrichthyan microremains under Permian-Triassic boundary both in Zhejiang and Jiangxi provinces, China-fifth report on the fish sequence study near the Permian-Triassic boundary in South China. *Vertebrata Palasiatica* 45:13–36.
- Wang, N. Z., X. Zhang, M. Zhu, and W. J. Zhao. 2009. A new articulated hybodontoid from Late Permian of northwestern China. *Acta Zoologica* 90 (Suppl. 1):159–170.
- Woodward, A. S. 1889. Palaeichthyological notes - I. On the so-called *Hybodus keuperinus* Murch. and Strickl. - II. On *Diplodus moorei* sp. nov., from the Keuper of Somersetshire. - III. On a symmetrical hybodont tooth from the Oxford Clay of Peterborough. - IV. On a maxilla of *Saurichthys* from the Rhaetic of Aust Cliff, near Bristol. *Annals and Magazine of Natural History (Series 6)* 3:297–299.
- Xiong, J. Y., 1980. The eighth team of Regional Geological Investigation Team, Geological Bureau of Yunnan Province. *Regional Geological Survey Report of the People's Republic of China 1:200000 Dongchuan G-48-XIV*. Geological Bureau of Yunnan Province (In Chinese).
- Xue, X. X. 1980. New materials of Hybodontidae in Gansu and Shanxi. *Vertebrata Palasiatica* 18:9–14.
- Young, C. C. 1935. On a dorsal fin spine of *Hybodus* from N W Kansu (Gansu). *Bulletin of the Geological Society of China* 14 (1):53–54.
- Young, C. C. 1941. On two new fossil fishes from Southwestern China. *Bulletin of the Geological Society of China* 21:91–95.
- Young, C. C. 1942. Fossil vertebrates from Kuangyuan, N Szechuan (Sichuan). *Bulletin of the Geological Society of China* 22:293–308.
- Zhang, H., C. Q. Cao, X. L. Liu, L. Mu, Q. F. Zheng, F. Liu, L. Xiang, L. J. Liu, and S. Z. Shen. 2016. The terrestrial end-Permian mass extinction in South China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 448:108–124.
- Zhang, L. J., L. A. Buatois, M. G. Mángano, Y. A. Qi, X. Zhang, S. Sun, and C. Tai. 2017. Early Triassic estuarine depauperate *Cruziana* ichnofacies from the Sichuan area of South China and its implications for the biotic recovery in brackish-water settings after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 485:351–360.

Submitted December 20, 2021; revisions received July 3, 2022;

accepted July 9, 2022.

Handling Editor: Charlie Underwood.