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

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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 lonchidid 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-Permain 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 clutching-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-sppecies, *P. rugians* 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.

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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 Elasmobranchi 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 *Tristychus* 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...
support this interpretation (Ginter et al., 2002). The Pennsylva-
nian (upper Carboniferous) hybodontiform *Hamiltonichthys*, rep-resented by several holomorphic specimens and slightly more derived than *Onychoselache*, is known mostly from freshwater deposits (Maisey, 1989). While xenacanthiforms were the domi-nant 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 predomi-nantly in continental deposits (Cuny, 2012). It is hard to identify obligate freshwater sharks (restricted exclusively to such environ-ments) 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 hybodon-tiform shark assemblage from Lower Triassic freshwater deposits including a new lonchidid 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 Pro-vince, 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 *Eumor-phopsis–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. All the vertebrate-containing limestone blocks was also carried out. 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, 2017). The term *Kayitou* 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 iso-lated hybodont teeth, cephalic spines, fin spines, placoid scales, and remains of actinopterygians. Some specimens from 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 limesto-nite, 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 limesto-nite. There is a bentonite layer just beneath the fossil layer, and its zircon LA-ICP-MS U-Pb age is 249.3 ± 1.4 Ma (Sup-plemental 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 over-lain by the Jialingjiang Formation, which is Olenekian (Zhang et al., 2016, 2017). The term *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.

**Preparation and Documentation**—Limestone blocks contain-ing 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

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**SYSTEMATIC PALEONTOLOGY**

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
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)
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, impermanent 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 clumping-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
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. celsiuspus, 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, Pristrisodus (Bhat et al., 2018b).
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. aff. *P. parvidens* from the lower Middle Jurassic Xietan Fm. of China (Shang et al., 2008)
c. *Pristrisodus* sp. aff. *P. parvidens* from the lower Middle Jurassic Xietan Fm. of China (Shang et al., 2008)
d. *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)
g. *Pristrisodus* sp. from the Bathonian of Scotland (Rees and Underwood, 2006)

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.
h. *P. balabansaiensis* in part from the Callovian, Uzbekistan (Nessov and Kazneshkin, 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. celscuspus* 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 Wealdien), 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 (Ansorge, 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) is 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

**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, Olekniak, 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

**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, Olekniak, 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
preservation prevents any taxonomic assignment beyond the order level.

**HYBODONTIFORMES** fam., gen. et sp. indet. 3

**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

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<th>CRETACEOUS</th>
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<td>P. balabansiensis</td>
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<td>P. sp.</td>
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<td>⬤ Parvodus huizodus</td>
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**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, Rhaetic; SAN, Santonian; SIN, Sinemurian; TOA, Toarcian; TTH, Tithonian; TUR, Turonian; VLG, Valanginian.
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...
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.

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.

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 Polyacodus as ambiguous and P. polycyphus as a nomen dubium. Consequently, we also
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 multicuspid 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...
display the characteristic dental features of lonchidid 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), Pristisridos (Late Triassic), Vectiselachos (Middle Jurassic–Early Cretaceous), Jiaodontus (Late Jurassic), Hylaebatis (Early Cretaceous), and Baharyiyodon (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 lonchidid 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-PTB 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-PTB hybodontiform records in China, for which a paratonic 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 PTB. 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 PTB, whereas Hybodus and Parvodus seemingly are the dominant faunal elements of post-PTB 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 (Fragilicorona) 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, Liu 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, Acroodus, Parvodus, Polyacrodus, Hubiotodus, and Jiaodon tus 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 assembly 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 chondrichthians 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 Hancock, 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 reports 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.

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