# First Record of *Petalodus* Owen, 1840 (Chondrichthyes, Petalodontidae) in the Lower Permian (Cisuralian) of China

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**Abstract:** The Petalodontiformes are a small intriguing group of Permo–Carboniferous chondrichthyans. *Petalodus* is the longest known petalodont genus generally considered representative of the order. The first definite fossil record of seven well-preserved *Petalodus* teeth has been found in the Qianshi limestone in the Lower Permian (Cisuralian) middle–upper Taiyuan Formation in Yangquan City, Shanxi Province, North China. The specimens are characterized by petal-shaped teeth with a spade-like crown, and a long, tongue-shaped root; the crown is circled with a band or cingulum composed of imbricated ridges at the base. All seven teeth are assigned to the species *P. ohioenesis* because of their vertically narrow cingulum and much longer root. *Petalodus* is a worldwide genus, with fossil localities mainly concentrated in the Laurussia supercontinent. The occurrence of *Petalodus* teeth in Yangquan not only is the first fossil record in China, but also only the second record in Asia. The Yangquan fossil site was part of the paleoequatorial North China Craton during the Early Permian, and was isolated from Laurusia and East Gondwana by the Paleo-Tethys Ocean. The successful dispersal of *Petalodus* from Laurusia to the North China Block along Paleo-Tethys may support the possibility that *Petalodus* taxa were active free-swimmers rather than bottom dwellers. The new finding increases the petalodont diversity in eastern Asia, and also sheds new light on the distribution and stratigraphic range.

**Key words:** vertebrate paleontology, *Petalodus*, Petalodontiformes, Yangquan, Taiyuan Formation, Paleo-Tethys Ocean, Asselian–Sakmarian, Shanxi Province

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## 1 Introduction

The Petalodontiformes are a small intriguing group of chondrichthyans, which ranged from the Carboniferous (late Mississippian) to the Permian. These 'sharks' can hardly be classified in either of the two major extant Elasmobranchii and Holocephali, but are part of the more basal Euchondrocephali (Janvier, 1996; Lund and Grogan, 1997; Ginter et al., 2010). They are characterized by petal-shaped teeth and possessed a symphysial tooth series (Hansen, 1985; Janvier, 1996; Lund and Grogan, 1997). Up to now, there are about 17 genera referred to Petalodontiformes, but most are known principally from isolated teeth (Lund et al., 2014) except for two complete fishes *Belantsea* from the Serpukhovian Bear Gulch fauna, Montana, USA (Lund, 1989; Grogan and Lund, 2002), and *Janassa* from the Middle Permian Kupferschiefer and Marl Slate of Germany and Durham, northern England (Woodward, 1889, p. 36; Malzahn, 1968; Ginter et al., 2010, p. 35). The cosmopolitan genus *Petalodus* is one of the longest known petalodonts and generally considered representative of Petalodontiformes since it was first described by Owen (Owen, 1840; Hansen, 1985). It is widely distributed in upper Mississippian to lower Permian (Cisuralian) marine deposits throughout the northern hemisphere, including Europe, North America, and Asia (Miller, 1957; Elliott et al., 2004; Goto and Okura, 2004; Brusatte, 2007). However, as yet, there has been no undoubted fossil record of *Petalodus* in China. Although two teeth from the Permian of China were described as *Petalodus shingkuoi* (Young, 1950) and *Petalodus* cf. *shingkuoi* (Liu and Hsieh, 1965), they are now recognized as the lower median teeth from another giant petalodontiform shark *Megactenopetalus* (Chondrichthyes, Pristodontidae) (Hansen, 1978).

Here, we describe the first definite fossil record of *Petalodus* teeth from the middle–upper Taiyuan Formation (Fm., Cisuralian, Lower Permian) in Yinying Town, Yangquan City, Shanxi Province, North China (Fig. 1a). The new finding not only increases the petaldont diversity in eastern Asia, but also sheds new light on the distribution and stratigraphic range of the petalodontiforms.

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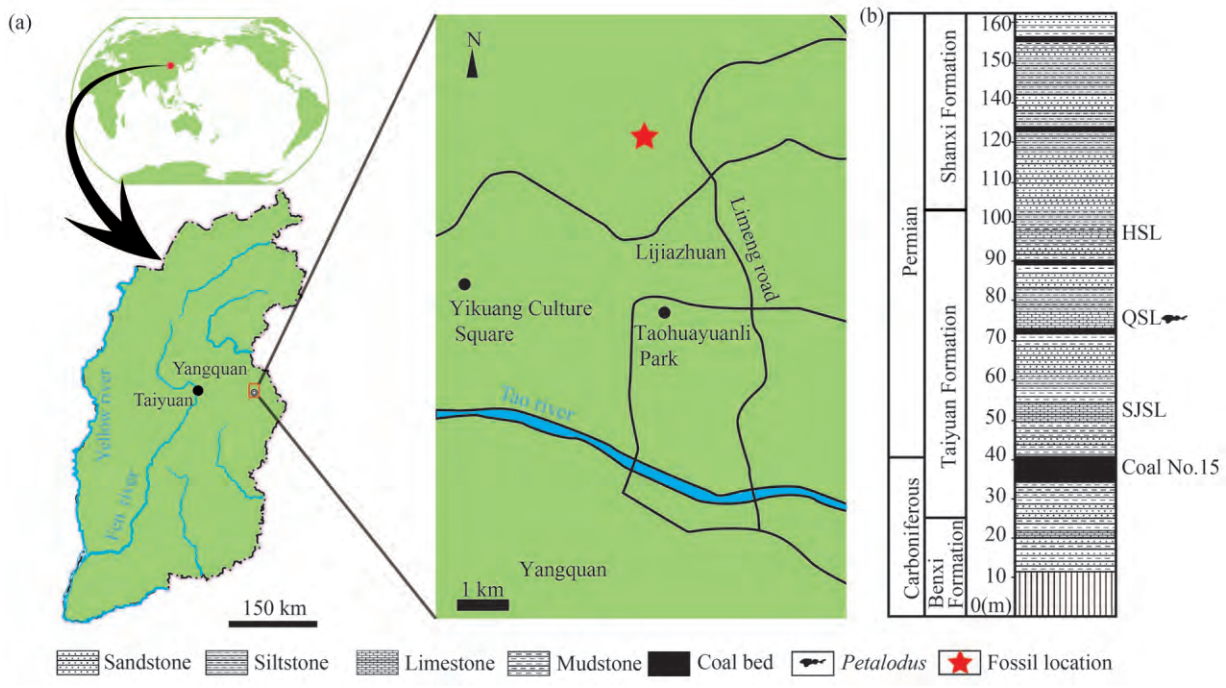


Fig. 1. Geological setting of *Petalodus ohioensis*.
(a) Maps of the fossil locality of *Petalodus ohioensis*; (b) fish-bearing lithological column in Yangquan, Shanxi Province, China. QSL, Qianshi limestone; HSL, Houshi limestone; SJSL, Sijieshi limestone.

## 2 Geological Setting

Seven well-preserved specimens were collected from the Qianshi limestone layer (a marker bed rich in crinoid stem fragments) of the middle–upper Taiyuan Fm., Yuemengou Group, in a coal pit at Yinying Town, Yangquan, Shanxi Province, North China (Fig. 1a). The Taiyuan Fm. is a set of deposits of continental–oceanic interaction facies, mainly consisting of coal, mudstone, limestone, and sandstone, which conformably overlies the Benxi Fm. and conformably underlies the Shanxi Fm. (Fig. 1b; Ge et al., 1985; Wang and Pfefferkorn, 2013; Wan et al., 2020). The middle and upper parts of the Taiyuan Fm. are dominated by deltaic and shoreface deposits, and yield the index fossil fusulinid *Sphaeroschwagerina* fauna and the conodont *Sweetognathus merrilli*, and thus probably belong to the Asselian–Sakmarian (Early Permian: Cisuralian) (Fan et al., 1999; Shen et al., 2019; Wan et al., 2020).

## 3 Samples and Methods

Seven complete teeth (YQZYJ003-009) were collected from the Qianshi Limestone (middle–upper Taiyuan Fm. (Cisuralian, Lower Permian) in Yinying Town, Yangquan, Shanxi Province. All the specimens were prepared mechanically using a vibro-tool with a tungsten-carbide bit or a needle, measured with a digital vernier caliper, and studied under an Olympus SZ61 zoom stereo microscope. They were photographed with a Canon EOS 5D Mark III camera coupled with a Canon macro photo lens EF 100 mm 1:2.8 L for general morphology and a Canon macro photo lens MP-E 65 mm 1:2.8 1–5× for the close-up of the microstructure. All fossils are permanently housed and accessible for examination in the collections of the Planning and Natural Resources Bureau of Yangquan, Yangquan City, Shanxi Province (YQZYJ). In addition, the holotype specimens of '*Petalodus*' *shingkuoi* (IVPP V 701) (Young, 1950) and '*Petalodus*' cf. *shingkuoi* (IVPP P.54.01) (Liu and Hsieh, 1965) housed in the museum of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, were reexamined and photographed for comparison.

## 4 Systematic Paleontology

Class **Chondrichthyes** Huxley, 1880
Subclass **Euchondrocephali** Lund and Grogan, 1997
Order **Petalodontiformes** Patterson, 1965
**Petalodontida** Zangerl, 1981
Family **Petalodontidae** Newberry and Worthen, 1866
Genus ***Petalodus*** Owen, 1840

**Diagnosis** (modified from Hansen, 1996): A large shark-like fish with a symphysial tooth series, petal-shaped teeth with a spade-like crown, and a long, tongue-shaped root; the crown labio-lingually compressed, convex labially and concave lingually; the crown thicker at the base with a band or cingulum composed of imbricated ridges, and thinner toward the top to form a crescent-shaped cutting edge with vertical furrows along the entire coronal margin.

***Petalodus ohioensis*** Safford, 1853

**Diagnosis:** Tooth crown with vertically narrow cingulum and longer root.

**Material:** Seven teeth (YQZYJ003-009) from the Qianshi limestone layer, Taiyuan Fm., Yuemengou Group, Asselian–Sakmarian age, Cisuralian, Early Permian, in a coal pit at Yinying Town, Yangquan, Shanxi Province.

**Measurements:** see Table 1.

**Description:** The collection includes seven isolated symmetrical teeth from at or near the symphysis of the jaw. Specimens YQZYJ008 (Fig. 2a) and YQZYJ006 (Fig. 2b) are two complete teeth that provide the labial (Fig. 2a1, b1), lateral (Fig. 2a2, b2), and lingual (Fig. 2a3, b3) views; specimens YQZYJ003 (Fig. 2e), YQZYJ004 (Fig. 2f), YQZYJ007 (Fig. 2c), YQZYJ009 (Fig. 2g) are four relatively complete teeth adhering to matrix that provide a labial view only. In contrast, specimen YQZYJ005 (Fig. 2d) is an incomplete tooth embedded in matrix that offers a lingual view only. Specimen YQZYJ006 (Fig. 2b) is the largest tooth with an extreme height of 55.3 mm (21.4 mm crown +33.9 mm root on the labial side; 28.3 mm crown +27.0 mm root on the lingual side) and the maximum width of the crown being 46.5 mm (Table 1). Specimen YQZYJ008 (Fig. 2a) is the smallest tooth, probably from a juvenile, which measures approximately 17.9 mm wide, 21.8 mm high (11.6 mm crown +10.2 mm root on the labial side; 14.0 mm crown +7.8 mm root on the lingual side) (Table 1). The sizes of the other five teeth (Fig. 2c–g) are close to those of

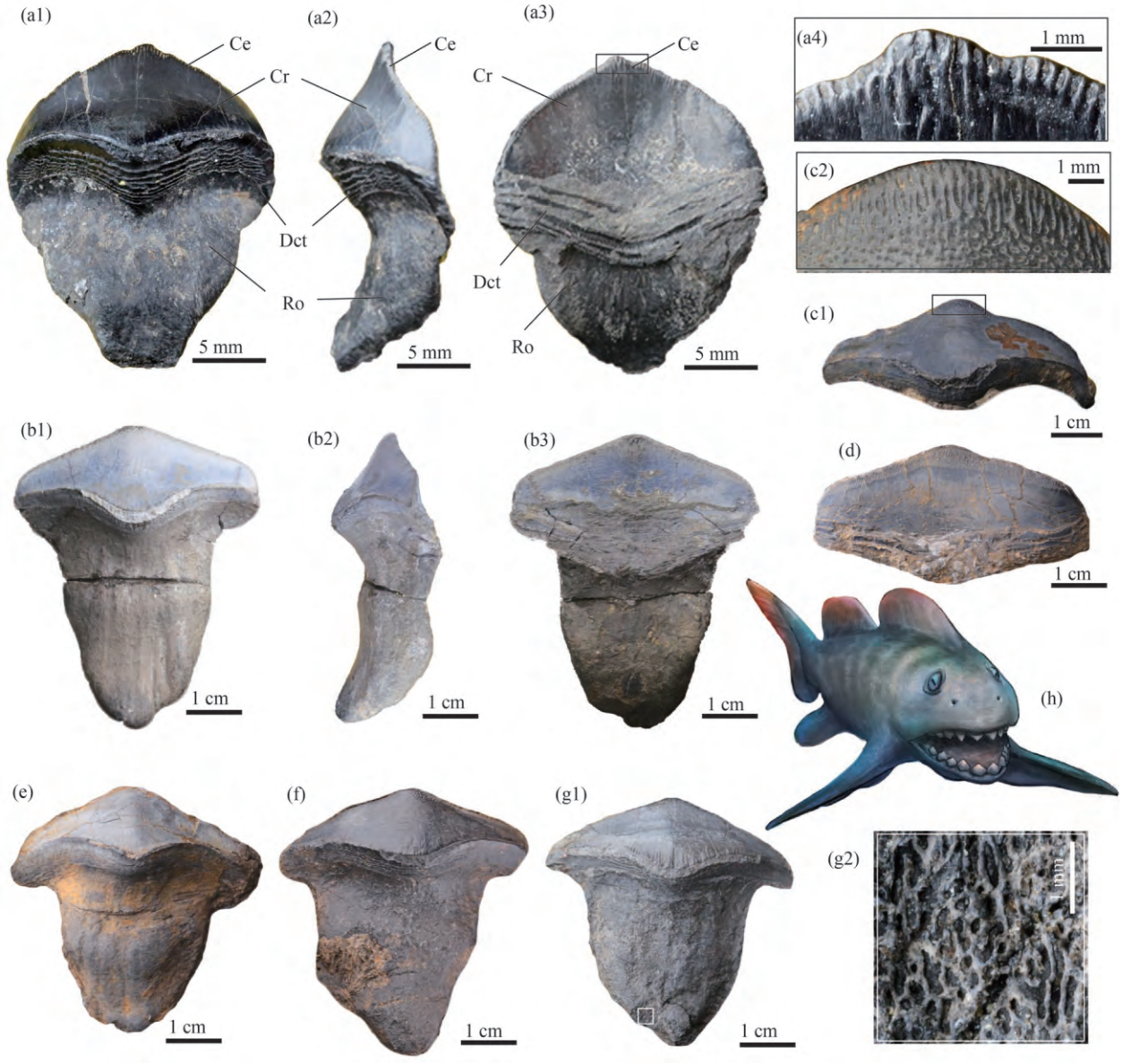


Fig. 2. Photographs and restoration of *Petalodus ohioensis*.

(a) Photograph of specimen YQZYJ008, in (a1) labial, (a2) lateral, and (a3) lingual views, (a4) close-up of the box region of (a3), showing vertical furrows on cutting edge; (b) photograph of specimen YQZYJ006, in (b1) labial, (b2) lateral, and (b3) lingual views; (c) photograph of specimen YQZYJ007, in (c1) labial view, and (c2) close-up of the box region of (c1), showing furrows on cutting edge; (d) photograph of specimen YQZYJ005, in lingual view; (e-f) photograph of specimen YQZYJ003, YQZYJ004, in labial view; (g) photograph of specimen YQZYJ009, in (g1) labial view, and (g2) close-up of the box region of (g1), showing the vascular pattern of the osteodentine; (h) possible life restoration drawn by Dinghua Yang. Ce, cutting edge; Cr, crown; Dct, distal crown tongue; Ro, root.

**Table 1 Measurements for *Petalodus* specimens used in this study (in mm)**

| Taxon (catalog number) | Crown side | *Petalodus ohioensis* | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | YQZYJ003 | YQZYJ004 | YQZYJ005 | YQZYJ006 | YQZYJ007 | YQZYJ008 | YQZYJ009 |
| Maximum tooth height | Labial | 46.1 | 48.0 | – | 55.3 | – | 21.8 | 47.8 |
| Maximum crown width | Labial | 44.5 | 46.1 | 45.4 | 46.5 | 42.1 | 17.9 | 46.1 |
| Maximum crown height | Labial | 17.4 | 17.2 | – | 21.4 | 18.8 | 11.6 | 18.6 |
| | Lingual | – | – | 24.1 | 28.3 | 24.4 | 14.0 | – |
| Maximum cingulum height | Labial | 5.5 | 5.1 | – | 4.0 | 5.5 | 3.6 | 5.0 |
| | Lingual | – | – | 10.2 | 14.8 | – | 4.5 | – |
| Maximum root height | Labial | 28.7 | 30.8 | – | 33.9 | – | 10.2 | 29.2 |
| | Lingual | – | – | – | 27.0 | – | 7.8 | – |

specimen YQZYJ006 (Fig. 2b) and much larger than specimen YQZYJ008 (Fig. 2a; Table 1). All measurements are given in Table 1.

The crown (Cr, Fig. 2a1, a2, a3, b, c1, d, e, f, g1) is spade-shaped with a broad coronal margin. It is labio-lingually compressed and looks like a booted foot in lateral view (Fig. 2a2, b2). It is convex on the labial side (Fig. 2a1, b1, c1, e, f, g1) and concave on the lingual side (Fig. 2a3, b3, d). The crown is thicker toward the base, where it is circled by a band or cingulum composed of 6–8 horizontal imbricated ridges, which is called the distal crown tongue (Dct, Fig. 2a1, a2, a3, b, c1, d, e, f, g1). The cingulum is present both on the lingual and labial surface but more expanded on the lingual side (Fig. 2a1, a3, b1, b3). A faint wavy pattern is present at the crown–root contact on the labial side (Fig. 2a1, b1, c1, e, f, g1). The crown is thinner toward the top, where it becomes a crescent-shaped cutting edge (Ce, Fig. 2a1, a3, b1, b3, c1, d, e, f, g1). Numerous vertical fine grooves or furrows extend 1–5 mm down from the edge on both the lingual and labial side along the entire coronal margin (Fig. 2a4, c2, d). These vertical cutting edge furrows (Fig. 2a4, c2, d) have been interpreted as dentinal tubules within the orthodentine exposed after the superficial enameloid (vitrodentine) abraded in long-term predation (Robb III, 2003). The root (Ro, Fig. 2a1, a2, a3, b1, b2, b3, e, f, g1) is tongue-shaped and comes to a rounded point distally. It is relatively thicker and longer than the crown, which is approximately 1.5 times longer than the crown (Table 1). The slight post-preservational damage to the distal root exposes the vascular pattern of the osteodentine ('trabecular' dentine) (Fig. 2g2) in specimen YQZYJ009 (Fig. 2g1) as in the petalodont specimen (KUVP 13322) from the Upper Pennsylvanian rocks of northeastern Kansas (Robb III, 2003).

## 5 Discussion and Conclusion

*Petalodus* is a long-known genus of the Petalodontiformes for more than 180 years since the eminent British anatomist Owen defined it in 1840 based on a tooth that he named *Petalodus hastingsii* (Fig. 3c1, c2) from the upper Middle Mississippian Ticknall Limestone, South Derbyshire, England (Owen, 1840). However, the type species *Petalodus hastingsii* was later recognized as a junior synonym of a tooth that Agassiz had named '*Chomatodus*' *acuminatus* Agassiz, 1838 (Fig. 3a) making Agassiz's specimen the type for the genus (in Agassiz, 1833–43). Safford (1853) named a second species "*Getalodus*" *ohioensis* (Fig. 3b) from the Upper Pennsylvanian Cambridge Limestone of Guernsey County, Ohio; the genus name later recognized as a typographical error for *Petalodus*. There are now about 35 species of *Petalodus* named based on subtle shape differences. However, most of the later named species are assumed to be junior synonyms of *P. acuminatus* Agassiz, 1838 (Fig. 3c1, c2) and/or *P. ohioensis* Safford, 1853 (Fig. 3d1, d2). The type species *P. acuminatus* was the dominant Mississippian species in England and Scotland, whereas *P. ohioensis* was the dominant Pennsylvanian to Cisuralian species in North America (see review Harper, 2018; Fig. 4). The teeth of *P. ohioensis* closely resemble those of *P. acuminatus*, but differ in the narrow, lingually-ridged band and in their larger tooth size (Hansen, 1996; Zidek and Kietzke, 1993). In addition, *P. acuminatus* has an equally short crown and base (Zidek and Kietzke, 1993). Our specimens are assigned to the species *P. ohioenesis* because of their vertically narrow cingulum and much longer root (Table 1). The cingulum circling the crown is generally regarded as a critical differential diagnostic between the two species. Usually, there are 4–8 horizontal imbricated ridges in *P. ohioensis* (Fig. 2a3, b3, d, 3d2), whereas there are about 10–14 imbricated ridges in *P. acuminatus* (Fig. 3c1).

### 5.1 *Petalodus* in China

The petalodontiform fossil record in China is sparse except *Chomatodus* (Petalodontidae) from the Lower Carboniferous of Guizhou (Ginter and Sun, 2007) and *Megactenopetalus* (Pristodontidae) (Fig. 3f1, f2, g1, g2) from the middle-upper Permian of Chongqing and Shanxi (Young, 1950; Liu and Hsieh, 1965). The two single-cusped teeth of *Megactenopetalus* in China were initially described as *Petalodus shingkuoi* (Fig. 3g1, g2) and *Petalodus cf. shingkuoi* (Fig. 3f1, f2). However, they obviously differ from the petal-shaped teeth of *Petalodus* and the bar-shaped teeth of *Chomatodus*, so they were reinterpreted as the lower median teeth of *Megactenopetalus* (Fig. 3h), another giant petalodontiform (Pristodontidae) by Hansen (1978). Wang and Turner (1985) described several *Petalodus*-like scales (not teeth) that were tentatively identified as a new species '*Petalodus*?' *daihuaensis* from the Upper Devonian (Famennian) Daihua Formation of Guizhou Province. These columnar specimens are fairly similar to those from the Late Pennsylvanian of the USA (Tway and Zidek, 1983, figs. 67, 69, 71, 73), but no histological examination was made on them because of the scarcity of the

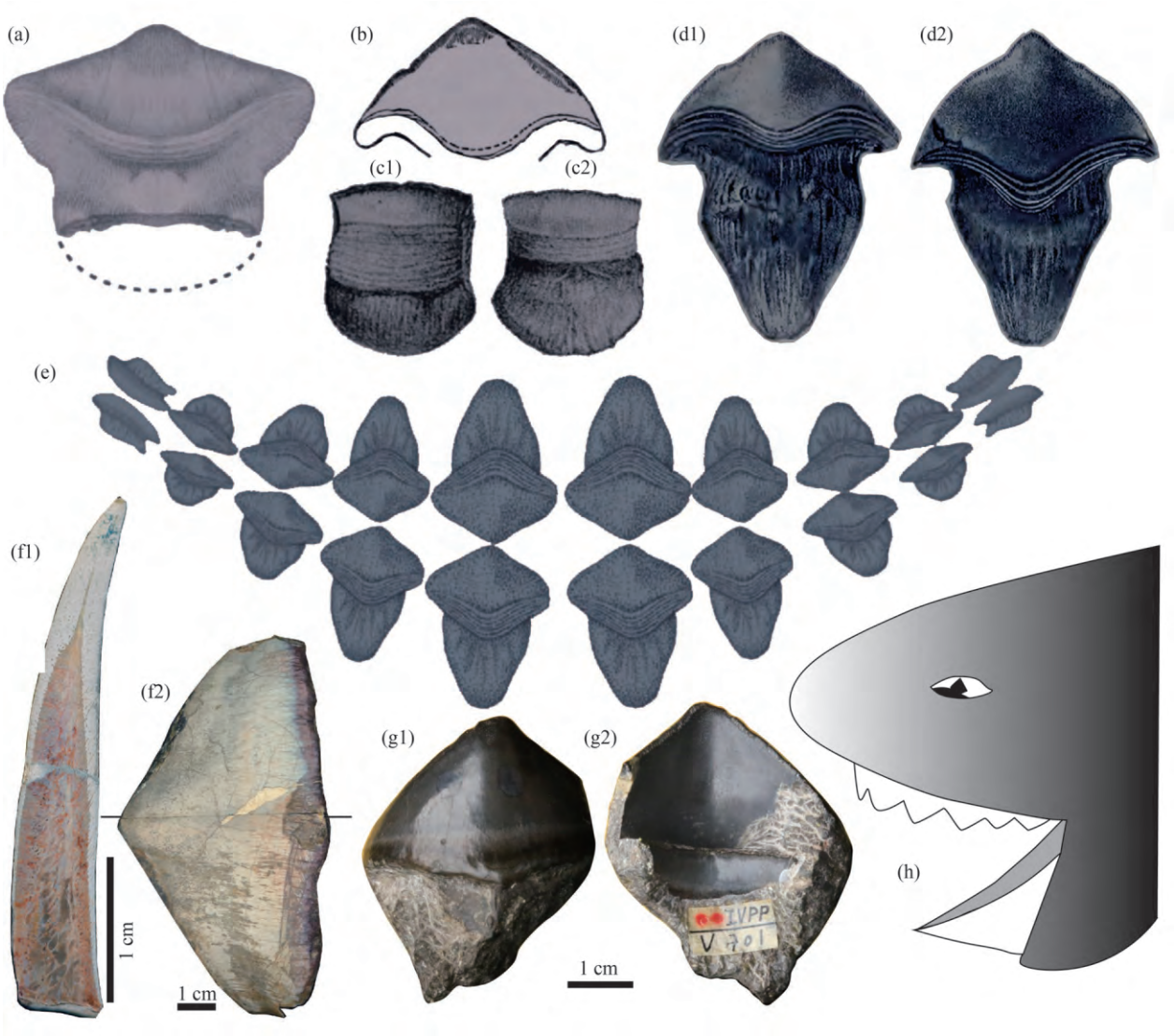


Fig. 3. Drawings and photographs of *Petalodus* and *Megactenopetalus*.
(a) Drawing of the holotype of *Petalodus acuminatus* (as '*Chomatodus*' *acuminatus*) as illustrated by Agassiz (1838, pl. 19, figs. 11, 13); (b) drawing of the holotype of *Petalodus ohioensis* (as *Getalodus ohioensis*) from the Cambridge Limestone, Upper Pennsylvanian, from Guernsey County, Ohio, as illustrated by Safford (1853, p. 142), in labial view; (c) drawing of the holotype of *Petalodus hastingsii* from the Mississippian Ticknall Limestone Fm., Ticknall, South Derbyshire, England, later recognized as a junior synonym of *Petalodus acuminatus* Owen (1840–1845), in lingual (c1) and labial (c2) views; (d) drawings of the most complete of the teeth of *Petalodus destructor* from the Pennsylvanian limestones of Illinois, later recognized as a junior synonym of *Petalodus ohioensis*, from Newberry and Worthen (1866, pl. 2), in labial (d1) and lingual (d2) views; (e) revised dental reconstruction of the jaw arrangement of *Petalodus* (modified from Harper, 2018); (f) photographs of the holotype of '*Petalodus*' *cf. shingkuoi* from the Maokou Limestone,Yangsin Series (Middle Permian), near Liangshan, Hanchun, southern Shanxi Province, in midsagittal (f1) and labial (f2) views; (g) photographs of the holotype of '*Petalodus*' *shingkuoi* from the top Lopingian Series (Late Permian) of Chongqing, in labial (g1) and lingual (g2) views; (h) restoration of *Megactenopetalus* (redrawn from Hansen, 1978); the teeth of (f) and (g) were later recognized as the lower median teeth of *Megactenopetalus.*

specimens. These Guizhou specimens were later considered to be a junior synonym of *Mitrellataxis dombrowskae* (Wang and Klapper, 1987) or at least should be refered to *Mitrellataxis* (Ji and Ziegler, 1992), which was regarded as a multielement genus of conodont firstly described in the upper Devonian of Maple Mill Shale in southeastern lowa and the Sulphur Springs Formation in east-central Missouri (Chauff and Price, 1980). It still remains controversial to be a conodont-like animal (Conodontophorida) (Chauff and Price, 1980) or scale-like fish (Wang and Turner, 1995). Therefore, the seven teeth from the Taiyuan Formation of Yangquan, Shanxi, are the first definite fossil record of *Petalodus* in China. *Petalodus* is a cosmopolitan genus widely distributed in upper Mississippian to lower Permian (Cisuralian) marine deposits throughout the northern hemisphere, including Europe: England (e.g. Agassiz, 1838), Scotland (e.g. Agassiz, 1838), Ireland (e.g. Woodward, 1889), Belgium (Miller, 1957), Italy (Dalla Vecchia, 1988; Sirna et al., 1994), Slovenia (Ramovs, 1997), Russia (Chabakov, 1927; Zittel, 1913); North America, including Illinois (e.g. Newberry and Worthen, 1866; Hay, 1895; Brusatte, 2007),


Fig. 4. The distribution of *Petalodus* species in the Upper Mississippian to Lower Permian (Cisuralian) marine deposits (around 280 Ma) throughout the northern hemisphere (picture courtesy of Baochun Huang).
1, Yangquan; 2, Utah; 3, Arizona; 4, Colorado; 5, New Mexico; 6, Kansas; 7, Oklahoma; 8,Texas; 9, Illinois; 10, Ohio; 11; Ireland; 12, Scotland; 13, England;14, Belgium; 15, Italy; 16, Slovenia; 17, Russia; 18, Japan. Abbeviations: IC, MOB, NCB, NQ, Qm, SCB, Si, and SQ represent the Indochina, Mongolian, North China, North Qiangtang, Qaidam, South China, Sibumasu, and South Qiangtang blocks/terranes, respectively.

Arizona (Elliott et al., 2004), New Mexico (Zidek and Kietzke, 1993; Lucas and Estep, 2000; Ivanov et al., 2009; Lucas et al., 2011), Kansas (Miller, 1957; Robb, 2003; Hamm and Cicimurri, 2005), Colorado (Lockley, 1984; Itano et al., 2003), Texas (Mcnulty, 1963), Oklahoma (Zidek, 1973), Ohio (Safford, 1853; Hansen, 1986), and Utah (Carpenter and Ottinger, 2018). Most of these fossil localities of *Petalodus* are concentrated in the former Laurussia supercontinent (Fig. 4), but is scarce in the East Asian blocks except for a report from a gray-green limestone of the Mizuyagadani Formation (Asselian, Early Permian) in central Japan (Goto and Okura, 2004; Fig. 4, site 18). Therefore, the occurrence of *Petalodus* teeth in Yangquan is not only the first fossil record in China, but also only the second record in Asia. This indicates that *Petalodus* has a wider-ranging habit and a longer geologic history than previously thought.

### 5.2 Paleobiology and paleogeography

The unique morphology of the symphysial tooth series of petalodonts probably indicates a specialized lifestyle (Elliott et al., 2004) (Fig. 3e, 2h). The classic view assumed that most petalodonts, including *Petalodus*, were bottom dwellers, ray-like fish with a depressed body and greatly enlarged pectoral fins (Romer, 1945, p. 7; Zangerl, 1981; Schaumberg, 1979). They were probably "opportunistic feeders" and "shell crunchers" that chewed up bivalves and brachiopods lying on the seafloor (Hamm and Cicimurri, 2005; Hodnett et al., 2011) because stomach residues from petalodont *Janassa* included brachiopods, crinoids, foraminifera, and crustaceans (Malzahn, 1968). Hansen and Mapes (1990) also described a cephalopod that appears to have been bitten by a petalodont. However, the sharp cutting ridges with numerous vertical fine grooves and the large occlusal surface of the teeth in *Petalodus* are suggestive of adaptations for biting and slicing soft tissues (Elliott et al., 2004). Therefore, Harper (2018) thought that *Petalodus* species probably were shark-like fishes living an active predatory lifestyle in the Late Paleozoic seas. Nevertheless, a possible function of the horizontal imbricated ridges embracing the base crown of the teeth in *Petalodus* may prevent the prey from escaping by increasing friction once the teeth pierce into the soft tissues.

During the Carboniferous and Permian periods, the fossil site of Yangquan was part of the North China Craton at paleoequatorial areas of the Palaeo-Tethys Ocean and experienced a wet tropical climate (Wang and Pfefferkorn, 2013; Huang et al., 2018; Wan et al., 2020). A great diversity of invertebrate fossils, including crinoids, bryozoans, brachiopods, gastropods, cephalopods, corals, fusulinids, ostracods, and trilobites, have been reported associated with the teeth of *Petalodus ohioensis* in this region (cover image), which would have provided an abundant food source for the diet of *Petalodus ohioensis*. The isolated position of the North China Block separated from the Laurusia and East Gondwana by the Paleo-Tethyan, and Paleo-Pacific oceans (Panthalassic) would undoubtedly act as a barrier for the dispersal of most vertebrates, including *Petalodus* (Fig. 4). The successful dispersal of *Petalodus* from Laurusia to the North China Block along the Paleo-Tethys Ocean might support the contention that *Petalodus* was an active free-swimmer rather than a bottom dweller.

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