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A sea scorpion claw from the Lower Devonian of China (Chelicerata: Eurypterida)

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An isolated chelicera (claw) of a pterygotid eurypterid is described from the Lower Devonian Xitun Formation of Yunnan Province, China. It is different from chelicerae of other pterygotids in having four principal denticles and at least four intermediate denticles between the principal denticles on both rami. This Chinese pterygotid, estimated at about 70 cm long, was a top predator that probably hunted small, primitive fishes, such as galeaspids. This discovery represents the first record of Pterygotidae from Asia and the third fossil eurypterid from China.

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EURYPTERIDS (sea scorpions) are aquatic, predatory chelicerates that originated in the early Late Ordovician and became extinct during the Late Permian (Dunlop 2010, Tetlie 2007, Vrazo & Braddy 2011). The family Pterygotidae, comprising about 46 species within five genera, is the most speciose clade of eurypterids, and *Slimonia* is inferred to represent the sister group of this family (Tetlie & Briggs 2009). Pterygotidae originated in the late early Silurian and went extinct during the Middle Devonian (Tetlie 2007). They are a monophyletic group characterized by the possession of enlarged raptorial chelicerae, non-spiny appendages III–V, undivided medial appendages, laterally expanded pretelson and a broad, paddle-like telson (Tetlie & Briggs 2009). Pterygotids were formidable predators with keen binocular vision and chelicerae adapted for either cutting or crushing (Laub *et al*. 2010, Selden 1984). Some of them are among the largest arthropods, e.g., the largest individual is estimated as up to 350 cm in length (body length 250 cm plus about 100 cm for the extended chelicerae: Braddy *et al*. 2008). Pterygotidae were first discovered by quarrymen excavating Lower Devonian strata of Scotland (Poschmann & Tetlie 2006, Woodward 1866–1878). Subsequently, they have been described from North America, Europe, Bolivia and Australia (Lamsdell & Legg 2010, Miller 2007, Tetlie & Briggs 2009).

Eurypterids are extremely rare in China and, so far, only two unequivocal specimens have been described. The first Chinese eurypterid was described from the Lower Permian of Hebei (Grabau 1920). The second eurypterid was described based on an almost complete specimen from the lower Silurian Xiaoxiyu Formation of Hunan Province (Tetlie *et al*. 2007). In addition, three *Eurypterus* species were described by Chang (1957) based on several fragments from the Silurian of Hubei Province. However, the original descriptions of these specimens are problematic; thus, a re-examination is needed to confirm their taxonomic placement (Tetlie *et al*. 2007). Here, we report an isolated pterygotid chelicera from the Lower Devonian Xitun Formation of Yunnan, China. It is not only the first record of Pterygotidae from Asia, but also the third fossil eurypterid from China.

Materials and methods

The specimen IVPP-I4593 is an isolated chelicera with its two rami in articulation collected from the Lower Devonian Xitun Formation of Qujing City, Yunnan Province, southwestern China. The specimen is preserved as a carbonaceous compression in yellowish mudstone. Lower Devonian deposits are well developed in the Qujing area of Yunnan, and are assigned to the Xiaxishancun, Xitun, Guijiatun and Xujiachong formations in stratigraphically ascending order (Dupret & Zhu 2008). The Siluro-Devonian boundary is

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generally placed at the base of the Xiaxishancun Formation, based on comprehensive studies of spores, conodonts, ostracods, vertebrate assemblages, geochemical stratigraphy, amongst other criteria (Cai *et al*. 1994, Fang *et al*. 1994, Lamsdell *et al*. 2013, Wang *et al*. 1992, Zhao *et al*. 2011). However, Tian *et al*. (2011) recently re-analyzed the spore assemblages from the Xitun Formation, and argued that the Siluro-Devonian boundary should be placed in the middle of the Xitun Formation. The Xitun Formation, about 400 m thick, is considered to be Lochkovian in age (Cai *et al*. 1994, Xue 2012, Zhao & Zhu 2010). It is composed mainly of yellowish and greenish grey siltstone, mudstone and marl, and may represent the deposits of a river mouth and delta front (Cai *et al*. 1994, Fan & Liu 1995). This formation yields abundant fossils, including spores (Tian *et al*. 2011), bivalves and brachiopods (Fang *et al*. 1994), ostracods (Wang *et al*. 1992), land plants (Cai & Wang 1995, Xue 2012) and fishes (Dupret & Zhu 2008, Zhao *et al*. 2011).

The specimen is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. The photograph of the specimen was taken using a Nikon D3X camera, and line drawings were finalized using photographs and image-editing software (CorelDRAW X4 and Adobe Photoshop CS). The denticle terminology follows Miller (2007). Abbreviations: td, terminal denticle on fixed ramus; d1–d4, principal denticles on fixed ramus, d1, primary denticle; td′, terminal denticle on free ramus; d1′–d4′, principal denticles on free ramus, d1′, primary denticle. The higher classification of eurypterids is based on the phylogenetic analyses of Tetlie & Cuggy (2007) and Braddy *et al*. (2008).

Systematic palaeontology

Order EURYPTERIDA Burmeister, 1843

Family PTERYGOTIDAE Clarke & Ruedemann, 1912

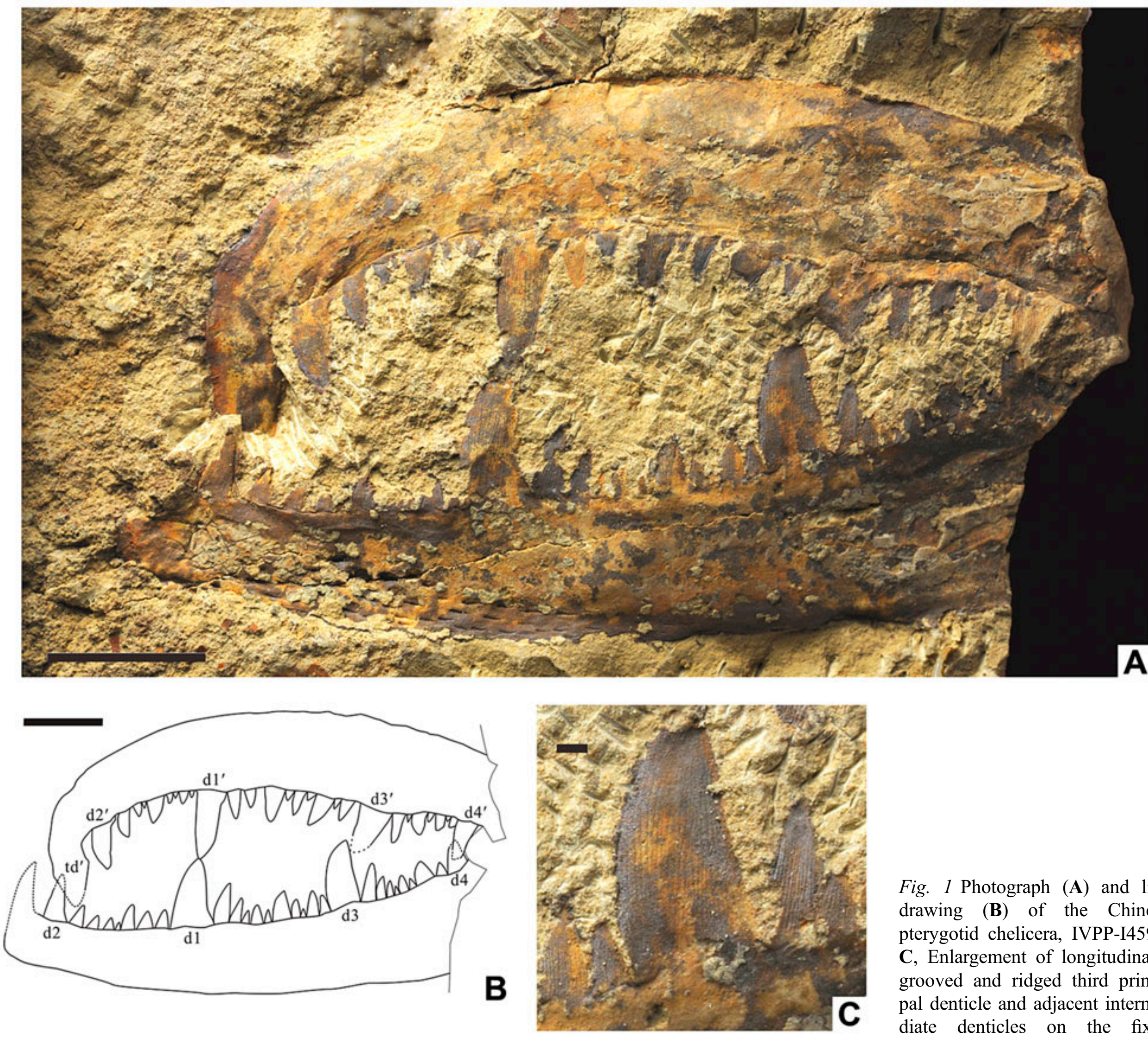

Fig. 1 Photograph (**A**) and line drawing (**B**) of the Chinese pterygotid chelicera, IVPP-I4593. **C**, Enlargement of longitudinally grooved and ridged third principal denticle and adjacent intermediate denticles on the fixed ramus. Scale bar = 10 mm for A and B, 1 mm for C.

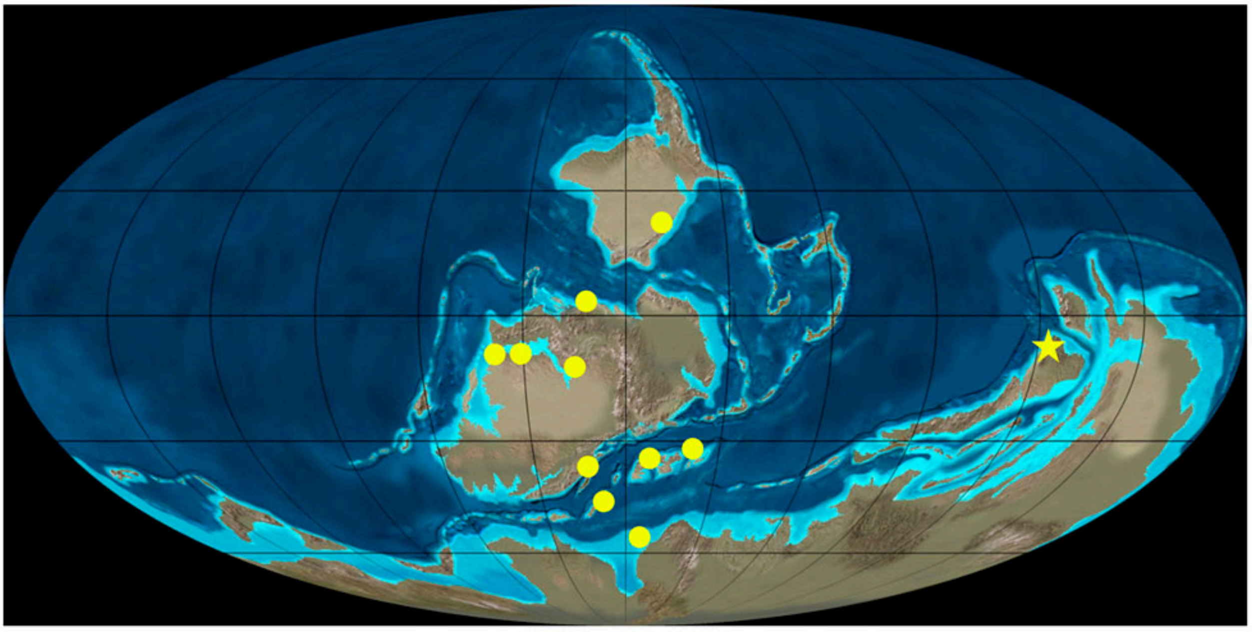

Fig. 2. Palaeogeographic distribution of Devonian Pterygotidae. Global palaeogeographic reconstruction for the Early Devonian (400 Ma) is after Blakey (2005). Circles represent localities of previously described Devonian Pterygotidae (Tetlie 2007). Star shows the location of the Chinese pterygotid.

Pterygotidae gen. et sp. indet. (Fig. 1)

Description. A chelicera comprising the fixed and free ramus (Fig. 1A, B). Denticles densely aligned, with fine longitudinal striations (Fig. 1C), without marginal serrations. Several rows of longitudinally elongate pits preserved on distal end of ventral margin of fixed ramus (Fig. 1A).

Fixed ramus preserving four principal denticles, with base not preserved. Preserved length about 65 mm. Denticles curved posteriorly. Terminal denticle (td) missing. Primary denticle (d1) robust, length 7.7 mm, width at base 4.6 mm, curved posteriorly, Anterior principal denticle (d2) length 4.6 mm, width at base 2.3 mm, curved posteriorly along anterior edge, close to terminal denticle. No intermediate denticle before anterior principal denticle (d2). Third principal denticle (d3) length 7.7 mm, width at base 4.1 mm, oriented at a right angle to the ramus, with anterior margin curved posteriorly. Posterior principal denticle (d4) partly preserved, estimated length 4.1 mm. Five intermediate denticles located between anterior principal denticle (d2) and primary denticle (d1); six or seven intermediate denticles between third principal denticle (d3) and primary denticle (d1); four intermediate denticles between third principal denticle (d3) and posterior principal denticle (d4).

Free ramus curved, with terminal and four principal denticles. Preserved length about 58 mm; total length estimated about 80 mm, indicating an animal with a total body length of 700 mm. Terminal denticle (td′) robust, angled slightly away from the ramus. Denticle morphology on free ramus is similar to that of fixed ramus.

Discussion

Pterygotidae comprises five genera: *Acutiramus* Ruedemann, *Ciurcopterus* Tetlie & Briggs, *Erettopterus* Salter, *Jaekelopterus* Waterston and *Pterygotus* Agassiz (Lamsdell & Legg 2010, Laub *et al*. 2010, Miller 2007, Poschmann & Tetlie 2006, Tetlie & Briggs 2009, Waterston 1964). *Ciurcopterus* is thought to be the sister taxon to the remaining pterygotids, but the chelicerae are unknown in this taxon (Tetlie & Briggs 2009). The Chinese specimen is different from the chelicera of *Erettopterus* in that the latter has less differentiated denticles (Tetlie & Briggs 2009); from the chelicera of *Acutiramus* in lacking the long, anterior oblique denticle on the fixed ramus (Laub *et al*. 2010); from the chelicera of *Pterygotus* in the latter having seven principal denticles on a free ramus (Miller 2007); from the chelicera of *Jaekelopterus* in the latter having the free ramus with three large principal denticles, and two intermediate denticles before the anterior principal denticle, with two more between the anterior and primary principal denticles (Lamsdell & Legg 2010).

Chelicerae are the most commonly preserved pterygotid remains because of their robust nature (Braddy *et al*. 2008). Several pterygotid species have been erected based on isolated chelicerae (Lamsdell & Legg 2010). Phylogenetic relationships within the Pterygotidae have been discussed by Braddy *et al*. (2008), Tetlie & Briggs (2009), Lamsdell & Legg (2010) and Lamsdell & Selden (2013). However, phylogenetic relationships based on the morphology of pterygotid chelicerae remain unclear. The characters of pterygotid chelicera are too few to support a robust cladistic analysis. The chelicera of pterygotids can be highly variable, as shown within *Erettopterus* (Waterston 1964, Ciurca & Tetlie 2007), and its morphology is in some cases dependent on mode of life and stage of ontogeny (Lamsdell & Legg 2010, Waterston 1964). The morphology of the chelicerae is thus not suitable for generic-level taxonomy (Lamsdell & Legg 2010). Therefore, the Chinese specimen is provisionally assigned to gen. et. sp. indet. until more complete specimens are discovered.

The total length of the Chinese pterygotid possessing this chelicera is estimated to have been about 70 cm based on the typical chelicera:body ratios (Braddy *et al*. 2008). However, the adult may have been larger, if the specimen is a juvenile. The pterygotids were at the top of the food chain because their powerful chelicerae were developed into enlarged raptorial, prey-catching organs (Braddy *et al*. 2008, but see Laub *et al*. 2010). The Chinese pterygotid was found in association with some small, primitive fish, such as Galeaspida and Phyllolepida (Dupret & Zhu 2008, Zhao *et al*. 2011), and it probably fed on the latter. Romer (1933) argued that the development of dermal armour in certain groups of jawless vertebrates was a response to predation pressure exerted by pterygotids, and that the demise of pterygotids in the Devonian was due to jaw development and increased mobility in vertebrates. The relationship between the rise of pterygotids and the evolution of dermal armour in vertebrates remains unclear, but the decline of pterygotids coincided with the radiation of Placodermi, providing circumstantial evidence that the demise of pterygotids was due to increased competition from vertebrates (Lamsdell & Braddy 2010).

Pterygotids ranged from the late early Silurian to the Middle Devonian, around 37 myrs (Tetlie & Briggs 2009). Most previously described Pterygotidae are from the Silurian of Euramerica. Only ten Devonian species have been described and are restricted to the USA (Kjellesvig-Waering 1964), Australia (Burrow *et al*. 2002), Scotland (Tetlie 2007), Germany (Poschmann & Tetlie 2006), France (Waterlot 1966), Spain (Chlupáč *et al*. 1997), Belgium (Leriche 1925), Norway (Tetlie 2007), the Czech Republic and Bolivia (Chlupáč 1994, Tetlie 2007; Fig. 2). Our discovery represents the first record of Pterygotidae from Asia, and further suggests that they had a cosmopolitan distribution (Tetlie 2007). This wide dispersal is probably a result of their substantial swimming abilities (Tetlie 2007). Furthermore, our recent collection of new eurypterids from China (including some undescribed Silurian specimens) confirms the previous viewpoint that the apparent lack of eurypterids outside Europe and North America is just a collecting bias (Tetlie 2007). The specimens from China will greatly improve our knowledge of the evolutionary history and palaeogeographic distribution of these bizarre animals.

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