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A new petalichthyid placoderm from the Early Devonian of Yunnan, China

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ARTICLE INFO

Article history:

Received 16 July 2014

Accepted after revision 13 October 2014

Available online 14 January 2015

Handled by Michel Laurin

Keywords:

Petalichthyida

Placodermi

Early Devonian

HRCT scanning

Morphology

Mots clés :

Petalichthyida

Placodermi

Dévonien inférieur

Tomodensitométrie haute résolution

Morphologie

ABSTRACT

Pauropetalichthys magnoculus, a new genus and species within the Petalichthyida (Gnathostomata; Placodermi), is described from the Late Emsian (Early Devonian) of Qujing, Yunnan, southwestern China. A three-dimensional reconstruction of the skull roof and neurocranium based on high-resolution computed tomography reveals the pattern of sensory canals, the visceral surface of the skull roof, and the profile of the endocranium. The perichondral lining of the nasal capsules provides the first hard evidence of nasal capsules in petalichthyids. A phylogenetic analysis resolves the new taxon as the most basal member of the Quasipetalichthyidae, an endemic group sister to the Macropetalichthyidae. In light of the newly revealed endocranial features, we discuss the morphological disparity of petalichthyid endocrania. The paleogeographic distribution of the Petalichthyida is summarized to show the group's center of origin and routes of dispersal.

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R É S U M É

Pauropetalichthys magnoculus, nouveaux genre et espèce de Petalichthyida (Gnathostomata; Placodermi) est décrit dans le tardi-Emsien (Dévonien inférieur) de Qujing, Yunnan, Sud-Ouest de la Chine. Une reconstitution tridimensionnelle du toit du crâne et du neurocrâne, basée sur la tomodensitométrie haute résolution révèle la configuration des canaux sensoriels, la surface viscérale du toit du crâne et le profil de l'endocrâne. Le revêtement périchondral des capsules nasales fournit la première évidence sérieuse de capsules nasales chez les pétalichthyidés. Une analyse phylogénétique caractérise le nouveau taxon comme étant le membre le plus basal des Quasipetalichthyidae, un groupe endémique frère des Macropetalichthyidae. À la lumière de ces traits endocrâniens récemment découverts, les auteurs discutent de la disparité morphologique des endocrânes de pétalichthyidé. La distribution paléogéographique des Petalichthyida est résumée pour montrer le lieu d'origine du groupe et les itinéraires de dispersion.

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1. Introduction

Placoderms are a diverse group of early vertebrates that underwent a highly successful radiation in the Devonian (Carr, 1995; Denison, 1978; Young, 2010). Recent studies regard placoderms as an assemblage of primitive jawed vertebrates, which form the paraphyletic crownward part of the gnathostome stem group (Brazeau, 2009; Brazeau and Friedman, 2014; Zhu et al., 2013). The Petalichthyida, a major group within the Placodermi, consists of the Macropetalichthyidae Eastman, 1898, the Quasipetalichthyidae Liu, 1991, and basal petalichthyids including *Diandongpetalichthys* (P'an and Wang, 1978), *Xinanpetalichthys* P'an and Wang, 1978 and *Neopetalichthys* Liu, 1973 (Liu, 1973; P'an and Wang, 1978; Zhu, 1991). The group displays a consistent overall morphology, characterized by sensory canals in an X-shaped pattern, two pairs of paranuchal plates and an elongated nuchal plate (Janvier, 1996). Among the Petalichthyida, only the Macropetalichthyidae is cosmopolitan, while the Quasipetalichthyidae and basal petalichthyids are endemic to China. The phylogenetic position of the Petalichthyida within the paraphyletic placoderm segment of the gnathostome stem is still in dispute (Brazeau, 2009; Davis et al., 2012; Goujet and Young, 1995; Young, 2010; Zhu et al., 2013), partly because *Macropetalichthys* was the only petalichthyid included in the relevant analyses. Knowledge of primitive petalichthyids, and particularly of their endocranial features, remains limited. Here we describe a primitive petalichthyid, *Pauropetalichthys magnoculus* gen. et sp. nov. from the Late Emsian (Early Devonian) of southwestern China, which represents the earliest quasipetalichthyid and sheds new light on the morphology and phylogeny of petalichthyids.

Endemic taxa play an important role in paleogeographic studies. Based on endemic fish taxa, Young (1981, 1993) divided the Devonian vertebrate fauna into five provinces. Walliser (1995) defined the Early Emsian Event (E'Em Event), and Zhu (2000) used Chinese fossil taxa to demonstrate that this event involved a faunal turnover in which endemic taxa were replaced by cosmopolitan ones in South China. A re-evaluation of the distribution of petalichthyids highlights a close connection between the long-distance dispersal of this group and the E'Em Event, and adds to current knowledge of the origin and early diversification of the Petalichthyida.

2. Materials and methods

Institutional Abbreviations: CAS, Chinese Academy of Sciences; IHEP, Institute of High Energy Physics (Beijing, China); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China).

Anatomical abbreviations: art.pq, articular surface for palatoquadrate; cap.n, nasal capsule; C, central plate; cr.PNu, paranuchal crista; dp.cu, cucullaris depression; eth.c, ethmoid commissure that connects supraorbital canals; fc, foramina cribrosa; f.dend.e, external opening for endolymphatic duct; f.dend.i, internal foramen for endolymphatic duct; f.gl, glenoid fossa; f.pi, pineal foramen; f.VII.hm, foramen for hyomandibular branch

of facial nerve; gr.cs, groove for ridge bordering semi-circular canals; ioc, infraorbital canal; Lio, infraorbital lobe; Lio.l, left infraorbital lobe; Lio.r, right infraorbital lobe; la.csp, posterior lamina of craniospinal process; la.crib, lamina cribrosa; lc, main lateral line canal; Mg, marginal plate; mpl, middle pit line; nla, anterior postorbital notch; nlp, posterior postorbital notch; Nu, nuchal plate; occ, occipital cross-commissure; orb, orbital cavity; pdl, posterior descending lamina; Pi, pineal plate; pmc, postmarginal canal; PNu.a, anterior paranuchal plate; PNu.p, posterior paranuchal plate; PrO, preorbital plate; ppl.a, anterior part of posterior pit line; ppl.p, posterior part of posterior pit line; pr.ant, antorbital process; pr.csp, craniospinal process; pr.dao, dermal antorbital process; pr.iNu, infranuchal process; pr.ma, mesial articular process; pr.pm, posterior median process; pr.poap, anterior postorbital process; pr.poap, complex formed by anterior and posterior postorbital processes; pr.pop, posterior postorbital process; pr.so, supraorbital process; pr.sv, supravagal process; PtO, postorbital plate; r.cs, ridge bordering anterior and posterior semicircular canals of the labyrinth; r.eth.c, ridge caused by ethmoid commissure that connects the supraorbital canals; r.ioc, ridge caused by infraorbital canal; r.lc, ridge caused by main lateral line canal; r.pmc, ridge caused by postmarginal canal; r.ppl, ridge caused by posterior part of posterior pit line; r.soc, ridge caused by supraorbital canal; Ro, rostral plate; sc, semicircular canal; soc, supraorbital canal; sov, supraorbital vault; th.Nu, nuchal thickening; th.PrO, thickening of preorbital plate; VII.hm, hyomandibular branch of facial nerve.

Phylogenetic analysis abbreviations: CI, consistency index; RI, retention index.

Geographic abbreviations: AF, Africa; ANT, Antarctica; ARB, Arabia; ARM, Armorica; AU, Australia; BAL, Baltica; G, Greenland; IN, India; KAZ, Kazakhstan; NA, North America; NC, North China; SA, South America; SC, South China; SIB, Siberia; TAR, Tarim.

2.1. Material

The holotype and only known specimen of *Pauropetalichthys magnoculus* was collected from yellowish siltstone of the Chuandong Formation exposed on the slope of a hill close to Shuanghe Village, about 7 km southwest of Zhanyi township, Qujing, Yunnan. From the same layer of the same site were found fossils of *Kenichthys campbelli* Chang and Zhu, 1993, *Heimenia Ørvig, 1969* and *Tarachomyx multicostatus* Qiao and Zhu, 2008 (Chang and Zhu, 1993; Qiao and Zhu, 2008; Wang, 1986; Zhu et al., 2002). The Early Devonian non-marine strata of Qujing can be divided from bottom to top into the Xishancun, Xitun, Guijiatun, Xujiachong, and Chuandong formations. Biostratigraphic correlations involving spore, fish and bivalve fossils imply that the Lower-Middle Devonian boundary is located in the upper part of the Chuandong Formation, and that the fish-bearing horizon is Late Emsian in age (Liu et al., 2004; Zhu and Wang, 1996a; Fig. 1). The specimen is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, in Beijing.

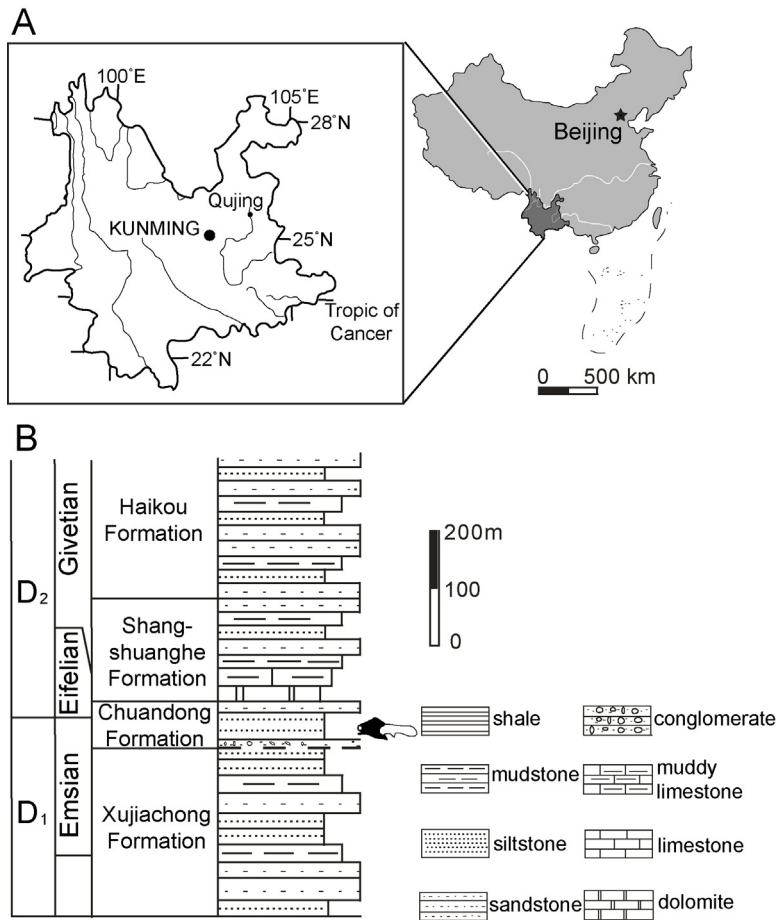


Fig. 1. A. Map of China, with emphasis on Yunnan province. B. Early Devonian sequence in Zhanyi area (Qujing, Yunnan, China), showing the stratigraphic position of *Pauropetalichthys magnoculus*. D₁, Early Devonian; D₂, Middle Devonian.

Fig. 1. A. Carte de la Chine, avec l'accent mis sur la province du Yunnan. B. Séquence Dévonien inférieur dans la région de Zhanyi (Qujing, Yunnan, Chine), montrant la position stratigraphique de *Pauropetalichthys magnoculus*. D₁, Dévonien inférieur ; D₂, Dévonien moyen.

2.2. Methods

The specimen was prepared mechanically using pneumatic air scribes and needles under stereomicroscopes. To enhance contrast, the specimen was coated with ammonium chloride sublimate before it was photographed using Nikon D3X. We scanned the specimen using the 225 kV high-resolution computed tomography apparatus (developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins of the CAS. The specimen was scanned with a beam energy of 130 keV and a flux of 100 μ A at a detector resolution of 8.6 μ m per pixel, using a 720° rotation with a step size of 0.5° and an unfiltered aluminum reflection target. The same settings were used in a previous study carried out by Zhu et al. (2013). A total of 1440 transmission images were reconstructed in a matrix of 1608 slices each measuring 2048 \times 2048 pixels, by means of two-dimensional reconstruction software (IVPP225KVCT_Reconstruction) developed by the Institute of High Energy Physics, CAS. Three-dimensional reconstructions were then generated using Mimics (Materialize

version 16), and images exported from Mimics were processed in Adobe Photoshop and Adobe Illustrator.

The data matrix was composed with Mesquite version 2.73 (Maddison and Maddison, 2008). Phylogenetic analysis was performed with PAUP* v4.0b10 (Swofford, 2003). All characters were unordered and unpolarized *a priori*, and two arthrodire taxa were used as outgroups for state character polarization. The exhaustive search function was used, and synapomorphies were assigned to nodes according to DELTRAN (delayed transformation) optimization.

3. Systematic paleontology

Class PLACODERMI McCoy, 1848
Order PETALICHTHYIDA Jaekel, 1911
Family **Quasipetalichthyidae** Liu, 1991
Genus ***Pauropetalichthys*** nov.

Pauropetalichthys magnoculus sp. nov.

Holotype: IVPP V 20160 (Fig. 2), skull roof and partially preserved endocranium. No referred material is known.

Etymology: Genus name from *pauros* (Greek, small), *petalon* (Greek, thin plate) and *ichthys* (Greek, fish). The

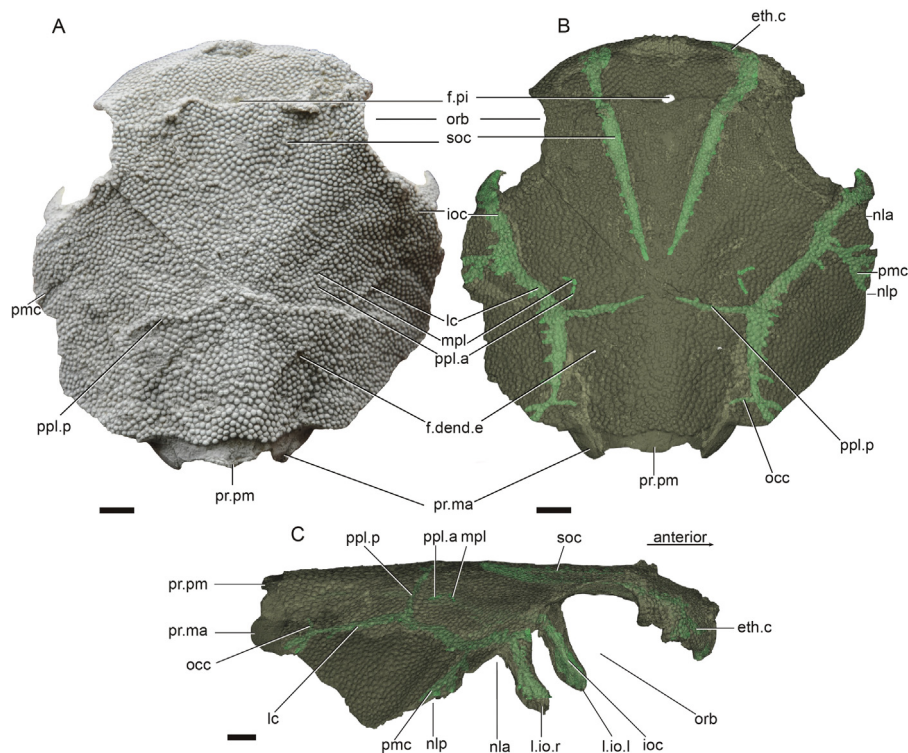


Fig. 2. (Color online.) *Pauropetalichthys magnoculus* gen. et sp. nov., Zhanyi area, Qujing, Yunnan, China, Late Emsian. Holotype IVPP V 20160. A. Photograph of the skull roof in dorsal view. B. Digital reconstruction of the skull roof in dorsal view. C. Digital reconstruction of the skull roof in right lateral view. Scale bars: 1 mm.

Fig. 2. (Couleur en ligne.) *Pauropetalichthys magnoculus* gen. et sp. nov., région de Zhanyi, Qujing, Yunnan, Chine, Tardi-Emsien. Holotype IVPP V 20160. A. Photographie du toit du crâne en vue dorsale. B. Reconstitution numérique du toit du crâne en vue dorsale. C. Reconstitution numérique du toit du crâne en vue latérale droite. Barres d'échelle = 1 mm.

specific epithet is derived from *magnus* (Latin, large) and *oculus* (Latin, eye), referring to the large orbits of the species.

Type locality and horizon: Shuanghe Village, Zhanyi district, Qujing, Yunnan Province, China; Chuandong Formation; Late Emsian, Early Devonian.

Diagnosis: Small petalichthyid with broad head; nuchal plate elongate, and in contact with preorbital and pineal plates anteriorly; two pairs of paranuchal plates; anterior paranuchal plate bearing junction of main lateral line canal with posterior pit line canal; postmarginal plate absent; pineal plate large and round, with pineal opening; orbits about one-third of skull roof length, and positioned at anterolateral margin of skull roof rather than being enclosed by skull roof bones; central plate small and far posterior to orbit, rather than entering orbital margin; posterior descending lamina of nuchal plate well developed; glenoid fossa and mesial articular process on posterior paranuchal plate longitudinally extended; ornament on skull roof consisting of concentric or irregularly arranged tubercles; sensory canals enclosed within dermal bones, communicating with surface by pores arranged in uniserial rows; posterior pit line canals and supraorbital canals converging to ossification center of nuchal plate, forming an incomplete X-shaped pattern; occipital cross-commissure extending medially; lateral segments of ethmoid commissure not in

mutual contact; external opening for endolymphatic duct between posterior pit line and occipital cross-commissure; nasal capsule ellipsoidal in shape, comparatively large and opening downward; articular facet for palatoquadrate on ventral side of preorbital plate; foramen for hyomandibular branch of facial nerve (f.VII.hm) in distal part of anterior postorbital process; and posterior face of craniospinal process bears circular depression.

4. Description

4.1. Skull roof

The length of the skull roof (from the anterior margin to the mesial articular process) is 13.6 mm. The maximum breadth, which occurs between the apexes of the arched lateral margins of the marginal plates, is 12.9 mm. The skull roof is broad, with a length-width ratio of 1.05. The orbit is anteriorly placed and not enclosed laterally by the skull roof. The length of the orbit is 4.4 mm, almost one third of the skull roof length. The orbit/skull roof length ratio varies from 0.12 (*Macropetalichthys rapheidolabis*; Norwood and Owen, 1846) to 0.16 (*Lunaspis broilii*; Gross, 1961) among previously described petalichthyids, so the value for *Pauropetalichthys* (Fig. 3) is the largest known within the group. The preorbital region is short, similar to those of arthrodires, quasipetalichthyids and *Diandongpetalichthys*.

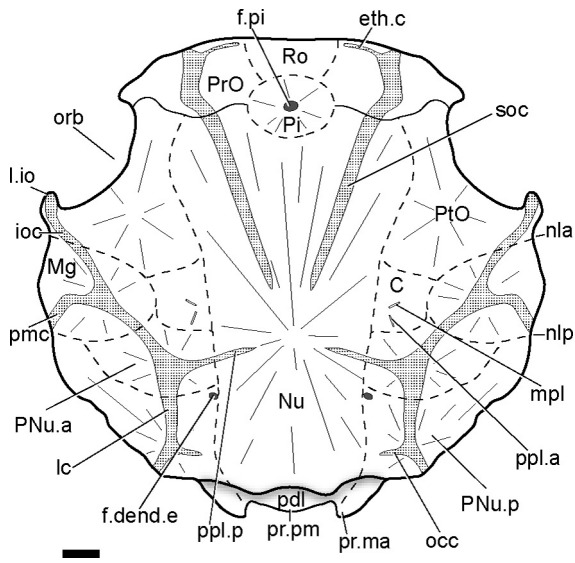


Fig. 3. *Pauropetalichthys magnoculus* gen. et sp. nov., Zhanyi area, Qujing, Yunnan, China, Late Emsian. Holotype IVPP V 20160; interpretative drawing of the skull roof in dorsal view. Scale bars: 1 mm.
Fig. 3. *Pauropetalichthys magnoculus* gen. et sp. nov., région de Zhanyi, Qujing, Yunnan, Tardi-Emsien. Holotype IVPP V 20160; dessin interprétatif du toit du crâne en vue dorsale. Barres d'échelle = 1 mm.

In contrast, macropetalichthyids have significantly longer preorbital regions (Liu, 1991; Stensiö, 1925, 1969; Zhu, 1991). The skull roof is arched along the midline, its summit lying at the center of the nuchal plate (Fig. 2C).

The skull roof is thinner along the midline than along the margin. The skull roof plates are mostly fused, and few

bone sutures can be traced. The restored dermal bone pattern (Fig. 3) is inferred from the positions of the sensory canal intersections, which are assumed to correspond to those of ossification centers, and from the concentrically arranged ornament. The skull roof consists of three median bones (the rostral, pineal, and nuchal plates) and six pairs of laterally located bones (the preorbital, postorbital, central, marginal, anterior paranuchal and posterior paranuchal plates). A similar pattern can be seen in *Quasipetalichthys* and *Eurycaraspis* (Liu, 1991; Fig. 4).

The rostral plate (Ro, Fig. 3) is situated at the front of the skull, and curves downward anteriorly. However, its sutures with adjoining plates are indistinct. Together with the downward-curving preorbital plates, the anterior part of the skull roof envelopes the nasal capsules. In *Macropetalichthys* and *Eurycaraspis*, by comparison, the anterior part of the skull roof is flat and lacks a downward-curving lamina (Liu, 1991; Stensiö, 1925).

Although the boundaries of the pineal plate (Pi, Fig. 3) are not clear, both the position of this plate and the approximate position of the pineal organ can be inferred from the location of the pineal foramen and fossa on the visceral surface of the plate. A pineal opening is absent in both *Quasipetalichthys haikouensis* (Liu, 1973) and *Eurycaraspis incilis* (Liu, 1991; Fig. 4).

The nuchal plate (Nu, Fig. 3) is the largest bone in the skull roof. The ratio of its length to the total skull roof length is 0.72. The dermal ornament on the nuchal plate shows more tiny tubercles, interspersed between the larger ones, than are present on the other skull roof bones. The ossification center of the nuchal plate is located near the posterior point of trisection of the plate midline.

In the posterior half of the skull roof, a pair of foramina is identified as the external openings of the endolymphatic

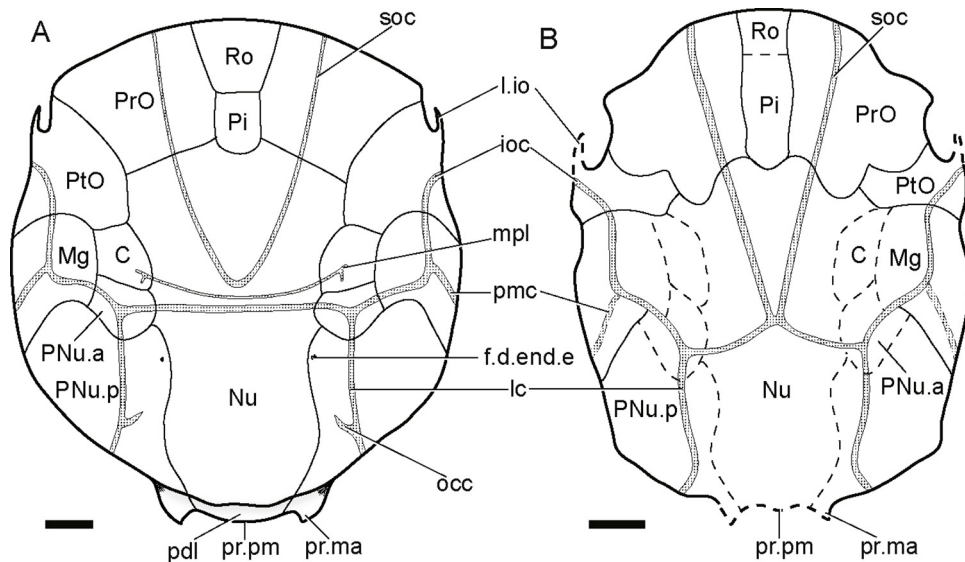


Fig. 4. A. Restoration of the skull roof of *Eurycaraspis* in dorsal view. B. Restoration of the skull roof of *Quasipetalichthys* in dorsal view. Both redrawn after Liu (1991). Scale bars: 10 mm.
Fig. 4. A. Restauration du toit du crâne d'*Eurycaraspis* en vue dorsale. B. Restauration du toit du crâne de *Quasipetalichthys* en vue dorsale. Les deux sont redessinés d'après Liu (1991). Barres d'échelle = 10 mm.

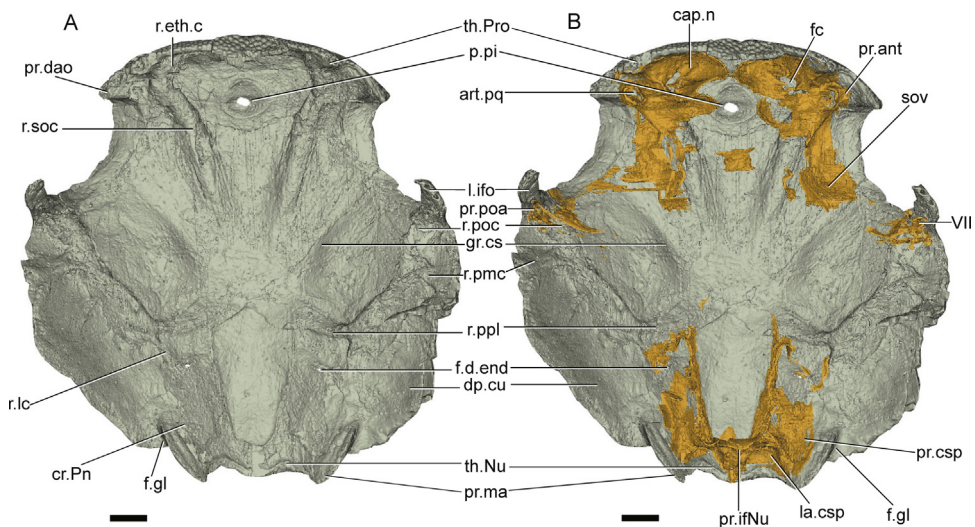


Fig. 5. (Color online.) *Pauropetalichthys magnoculus* gen. et sp. nov., Zhanyi area, Qujing, Yunnan, China, Late Emsian. A. Digital reconstruction of the skull roof in visceral view. B. Digital reconstruction of the skull roof and the perichondral bone in visceral view. Scale bars: 1 mm.

Fig. 5. (Couleur en ligne.) *Pauropetalichthys magnoculus* gen. et sp. nov., région de Zhanyi, Qujing, Yunnan, Chine, Tardi-Emsien. A. Reconstitution numérique du toit du crâne en vue viscérale. B. Reconstitution numérique du toit du crâne et de l'os périchondral en vue viscérale. Barres d'échelle = 1 mm.

ducts (f.dend.e, Figs. 2 and 3). In visceral view, corresponding foramina that represent the internal openings of the ducts are apparent. Similar duct openings are also present in *Eurycaraspis*, but were formerly misinterpreted as foramina for cutaneous sensory cells (Liu, 1991).

The suture between the preorbital and postorbital plates is clearly visible. The preorbital plate (PrO, Fig. 3) curves downward anteriorly, and its mesial margin is in contact with the rostral plate anteriorly and the pineal plate posteriorly. A dermal antorbital process (pr.dao, Fig. 5A) forms the anterior margin of the orbit. Moreover, a dermal eminence (th.PrO, Fig. 5) can be seen at the anterior part of the preorbital plate. The HRCT scan shows that the dermal eminence encloses the supraorbital canal (Fig. 5).

The suture between the postorbital (PtO, Fig. 3) and marginal plates (Mg, Fig. 3) is difficult to distinguish. The outline of the postorbital plate is inferred from its radiating ornament. Similarly, the point where the posterior pit line converges with the infraorbital canals is assumed to coincide with the ossification center of the marginal plate. The anterior postorbital notch (nla, Fig. 3) might indicate the position of the suture between the postorbital and marginal plates, whereas the posterior postorbital notch (nlp, Fig. 3) might indicate that of the suture between the marginal and posterior paranuchal plates. The mesial margin of the marginal plate contacts the central and anterior paranuchal plates.

The infraorbital lobe (l.io, Fig. 2C) of the postorbital plate is well developed and extends anteroventrally, but does not enclose the orbit. The tip of the lobe is slightly enlarged. In contrast, the lobe tapers gently in *Eurycaraspis* and *Quasipetalichthys* (Fig. 4). The infraorbital sensory canal passes through the infraorbital lobe, and exits at its anterior end (Figs. 2C and 3).

Both the central and the anterior paranuchal plates are proportionally small. The suture between the central plate

(C, Fig. 3) and the anterior paranuchal plate (PNU.a, Fig. 3) is unclear. The central plate bears the middle pit line (mpl, Fig. 3) and the anterior part of the posterior pit line (ppl.a, Fig. 3). The point of convergence of the posterior part of the posterior pit line (ppl.p, Fig. 3) and the main lateral line canal (mpl, Fig. 3) coincides with the ossification center of the anterior paranuchal plate.

The posterior paranuchal plate (PNU.p, Fig. 3) forms the posterolateral part of the skull roof. Its ossification center is located where the main lateral line canal meets the occipital cross-commissure. On the visceral side of the posterior paranuchal plate, a smooth cucullaris depression (dp.cu, Fig. 5) is delimited by the ridge of the main lateral line canal anteriorly and the paranuchal crista (cr.PNU, Fig. 5A) laterally.

The posterior descending lamina of the nuchal plate (pdl, Fig. 3), which is known only in *Pauropetalichthys* and *Eurycaraspis*, is at the posterior end of the skull roof. It is a thin structure with a distinct posterior median process (pr.pm, Figs. 2 and 3). Lateral to the posterior descending lamina, the mesial articular process (pr.ma, Figs. 5B and 3) is well developed. The mesial articular process forms an angle of approximately 120° with the posterior margin of the posterior paranuchal plate in dorsal view.

On the visceral side of the posterior descending lamina, a nuchal thickening (th.Nu, Fig. 5) is present, bordering the posterior portion of the craniospinal process (pr.csp, Figs. 5B and 6). Lateral to the mesial articular processes are situated a pair of glenoid fossae (f.gl, Fig. 5) comparable to those of *Eurycaraspis*, *Macropetalichthys* and *Wijdeaspis* (Liu, 1991; Stensiö, 1969; Young, 1978).

The ornamentation on the dorsal surface of the skull roof consists of densely set, spheroidal tubercles. In some areas, these tubercles are concentrically arranged, highlighting the ossification centers of the dermal bones on which they

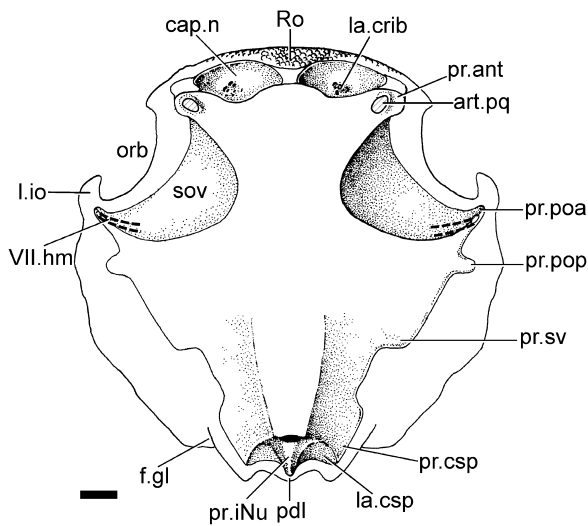


Fig. 6. *Pauropetalichthys magnoculus* gen. et sp. nov., Zhanyi area, Qujing, Yunnan, China, Late Emsian. Interpretative drawing of the endocranium in ventral view. Scale bar: 1 mm.

Fig. 6. *Pauropetalichthys magnoculus* gen. et sp. nov., région de Zhanyi, Qujing, Yunnan, Chine, Tardi-Emsien. Dessin interprétatif de l'endocrâne en vue ventrale. Barre d'échelle = 1 mm.

occur. The size of the tubercles varies across different areas. On the nuchal plate, the tubercles grow smaller near the ossification centers. Moreover, the tubercles along the skull roof margins are generally smaller than those located more centrally.

4.2. Sensory canal system

The sensory canals are enclosed within the dermal bones, with pores opening on the external surface. The pores along each canal are arranged in a single line. The sensory canals decrease in diameter near their exits, and taper to points where they end blindly with the bone of the skull roof. The sensory canals on the nuchal plate are arranged in an incomplete X-shaped pattern (Fig. 3): the supraorbital canals and posterior pit line canals converge toward the ossification center of the nuchal plate as in *Eurycaraspis*, but taper to points well before reaching the ossification center.

The supraorbital canal (soc, Fig. 3) begins at the anterior margin of the preorbital plate and extends posteromedially without meeting its counterpart on the opposite side. The supraorbital canal shows three moderate inflections. The anterior inflection is at the intersection with the ethmoid commissure, which coincides with the ossification center of the preorbital plate. The middle inflection occurs at the point of maximum curvature of the preorbital plate. The posterior inflection lies on the boundary between the preorbital and nuchal plates.

The ethmoid commissure (eth.c, Fig. 3) is situated on the anterior portion of the preorbital plate. The ethmoid commissure extends medially, but ends at the margin of the rostral plate. The commissure has been reported in some antiarchs, like *Dianolepis liui* Chang, 1965 and *Byssacanthus dilatatus* (Eichwald, 1844; see also Karatajūte-Talimaa,

1960), and thus seems likely to represent a primitive gnathostome feature.

The posterior part of the posterior pit line (ppl.p, Fig. 3) extends transversely and converges with its opposite counterpart and both supraorbital canals, similar to the condition in *Quasipetalichthys*, *Eurycaraspis* (Fig. 4) and *Diandongpetalichthys* (Liu, 1991; Zhu, 1991). As in *Lunaspis broilii*, Gross, 1961, the left and right posterior pit lines fail to contact each other.

The infraorbital canal (ioc, Fig. 3) begins at the infraorbital lobe of the preorbital plate and is directed posteromedially. This canal shows an inflection just posterior to infraorbital lobe.

The main lateral line canal (lc, Fig. 3) bends through an angle of 140° in the middle of its course. The diameter of the lateral line canal is greatest near the junction with the posterior part of the posterior pit line, and gradually decreases in both directions. The posterior portion of the main lateral line canal and the posterior part of the posterior pit line meet at an angle of 90°.

The postmarginal canal (pmc, Fig. 3) extends posterolaterally from the intersection between the infraorbital and main lateral line canals. The postmarginal canal has multiple wide branches that exit the skull. The postmarginal and main lateral line canals are both comparatively narrow near the point where they converge.

The occipital cross-commissure (occ, Fig. 3) is short, a feature that is common in Arthrodira and Acanthothoraci but has not been reported in any petalichthyid other than *Diandongpetalichthys* (Zhu, 1991). Two pairs of short grooves, representing the middle pit line and the anterior part of the posterior pit line (mpl, ppl.a, Figs. 2 and 3), are clearly discernable on the central plates.

4.3. Endocranium

Based on the HRCT scan of the holotype, we reconstructed part of the endocranium. The endocranium of *Pauropetalichthys* is platybasic and perichondrally ossified as in other petalichthyids and indeed most placoderms (Janvier, 1996). There is no trace of either endochondral ossification or calcified cartilage. We can infer the contours of the endocranium from depressions on the visceral side of the skull roof, which is in intimate contact with the dorsal wall of the endocranium (Fig. 6).

The endocranial processes of *Pauropetalichthys* include, on each side of the skull, an antorbital process (pr.ant, Fig. 6), an anterior postorbital process (pr.poa, Figs. 5B and 6), a posterior postorbital process (pr.pop, Fig. 6), a supravagal process (pr.sv, Fig. 6) and a craniospinal process (pr.csp, Figs. 5B and 6). However, the supraorbital process is almost impossible to trace on the visceral side of the skull roof. In general, the processes can be closely compared to those of *Eurycaraspis* (Liu, 1991). The very short distance between the anterior and posterior postorbital processes is a noteworthy feature.

The endocranium consists of the ethmoid division and the postethmo-occipital bone, but the suture between these components is not traceable by HRCT scanning. The postethmo-occipital bone can be subdivided into orbitotemporal, otic and occipital regions.

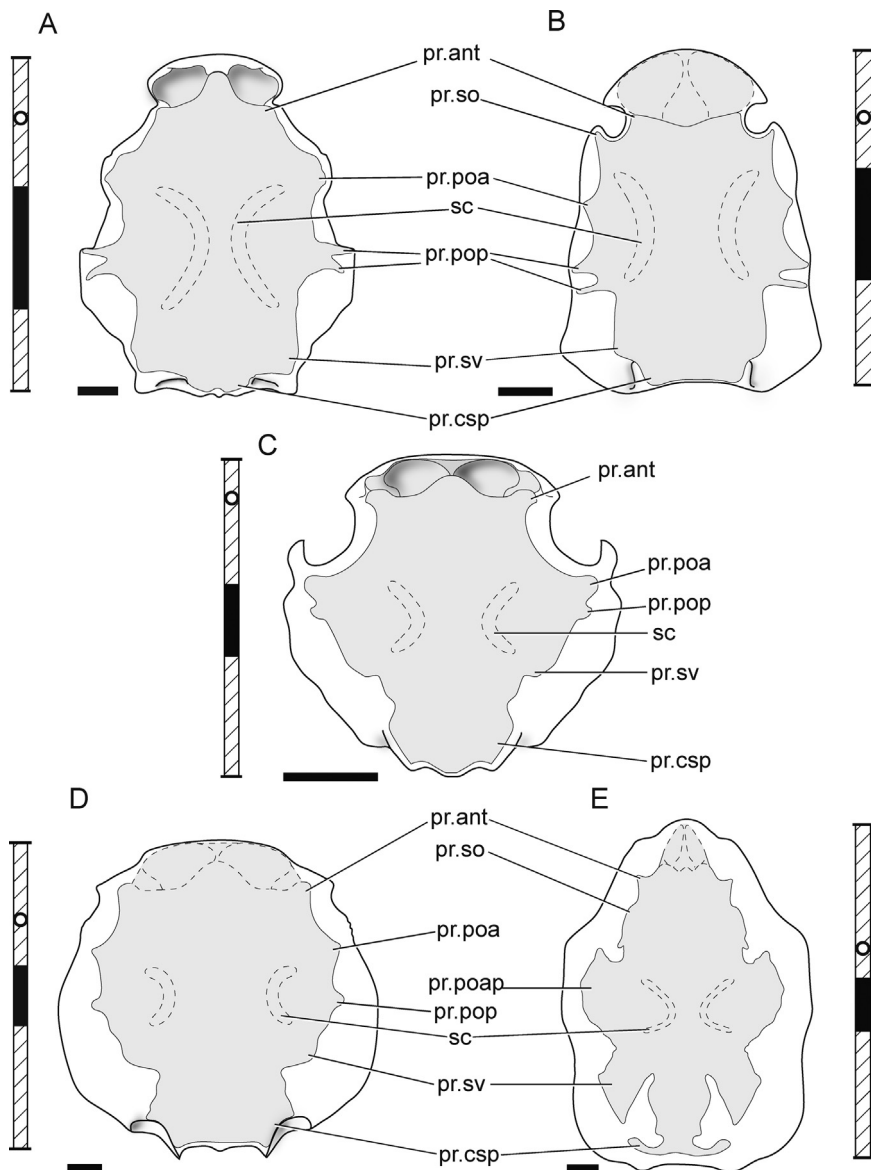


Fig. 7. Comparison of the endocranium in Petalichthyida and Arthrodira. A. *Dicksonosteus arcticus* (after Goujet, 1984). B. *Diandongpetalichthys liaojiaoshanensis* (after Zhu, 1991). C. *Pauropetalichthys magnoculus* gen. et sp. nov. D. *Eurycaraspis incilis* (after Liu, 1991). E. *Macropetalichthys rapheidolabis* (after Stensiö, 1963). The endocranium (in gray) is shown in visceral view. The vertical bar shows the relative lengths of the regions that make up the endocranium, with the black area corresponding to the otic region, and the small circle showing the location of the pineal opening. Scale bar: 5 mm.

Fig. 7. Comparaison de l'endocrâne entre Petalichthyida et Arthrodira. A. *Dicksonosteus arcticus* (d'après Goujet, 1984). B. *Diandongpetalichthys liaojiaoshanensis* (d'après Zhu, 1991). C. *Pauropetalichthys magnoculus* gen. et sp. nov. D. *Eurycaraspis incilis* (d'après Liu, 1991). E. *Macropetalichthys rapheidolabis* (d'après Stensiö, 1963). L'endocrâne (en grisé) est présenté en vue viscérale. La barre verticale indique les longueurs relatives des régions qui constituent l'endocrâne, avec la zone noire correspondant à la région otique et le petit cercle montrant la localisation de l'orifice pinéal. Barre d'échelle = 5 mm.

The ethmoid division bears a pair of nasal capsules (cap.n, Fig. 6), a structure that has not been previously reported in any petalichthyid. Each nasal capsule opens ventrally as in the arthrodires *Buchanosteus* (Young, 1979) and *Dicksonosteus* (Goujet, 1984). An irregular foramen piercing the dorsomedial surface of the nasal capsule represents the foramina cribrosa (fc, Fig. 5B).

Behind the nasal capsule, the articular surface for the palatoquadrate (art.pq, Figs. 5B and 6) forms a hole in the perichondral envelope as in *Romundina* (Dupret et al.,

2010, 2014; Goujet, 2001). Behind the articular surface, the perichondral bone around the orbital cavity forms a supraorbital vault (sov, Figs. 5B and 6). Beneath the infraorbital lobe, the perichondral bone encloses a canal for the hyomandibular branch of the facial nerve (VII.hm, Fig. 6). The hyomandibular branch of the facial nerve is not directed along the infraorbital lobe, and its foramen is at the tip of the antorbital process. The orbitotemporal region extends from the articular surface for the palatoquadrate to the front end of the ridge bordering the semicircular canals.

The otic region is characterized by a pair of depressions on the visceral side of the skull roof, corresponding to the ridges bordering anterior and posterior semicircular canals of the labyrinth (r.cs, Fig. 5). As in other petalichthyids, the otic region is moderately short. It is noteworthy that the anterior and posterior postorbital processes, and the otic region, vary among petalichthyids in their shapes and positions (Fig. 7).

The occipital region is the posterior part of the endocranium. The supravagal process (pr.sv, Fig. 6) is located posterior to the posterior extremity of the ridge bordering anterior and posterior semicircular canals.

The craniospinal process (pr.csp, Figs. 5B and 6) lies behind the supravagal process, as in *Macropetalichthys* (Stensiö, 1963). The paranuchal crest, which was described by Young (1978) as a ventral thickening developed beneath the ossification center of the posterior paranuchal plate in *Wijdeaspis*, contacts to the lateral wall of the craniospinal process. At the posterior extremity of the endocranium, the perichondral bone forms an infranuchal process (pr.iNu, Fig. 5B). On both sides of the infranuchal process, the craniospinal processes (Figs. 5B and 6) display subcircular depressions on their posterior walls (la.csp, Figs. 5B and 6) as in *Macropetalichthys* (Stensiö, 1969). These depressions represent articular facets for the trunk armor.

5. Comparisons and discussion

5.1. Phylogenetic analysis

In order to resolve the systematic position of *Pauropetalichthys magnoculus* within the Petalichthyida, a computer-based phylogenetic analysis was performed. The ingroup consisted of six taxa including *Diandongpetalichthys liaojiaoshanensis* (P'an and Wang, 1978; Zhu, 1991), *Macropetalichthys rapheidolabis* (Norwood and Owen, 1846; Stensiö, 1969), *Lunaspis broilii* (Gross, 1937, 1961), *Pauropetalichthys magnoculus* gen. et sp. nov., *Quasipetalichthys haikouensis* (Liu, 1973) and *Eurycaraspis incilis* (Liu, 1991). The outgroup consisted of the arthrodires *Dicksonosteus arcticus* (Goujet, 1975, 1984) and *Kujdanowiaspis podolica* (Brotzen, 1934; Dupret, 2010). The full list of 22 characters is given in Appendix 1 (character state coding does not indicate any *a priori* designation of particular states as primitive or derived). The data matrix is given in Appendix 2.

The analysis yielded a single most parsimonious tree (Fig. 8). Among the monophyletic Quasipetalichthyidae, *Pauropetalichthys* is the sister group of *Quasipetalichthys* plus *Eurycaraspis*. Synapomorphies of the Quasipetalichthyidae (Node 4, Fig. 8) include the presence of a posterior descending lamina, the absence of a supraorbital process, the posterior position of the ossification center of the nuchal plate, the presence of a mesial articular process and the eminence of the preorbital plate. Synapomorphies of the *Quasipetalichthys* - *Eurycaraspis* clade (Node 5, Fig. 8) include contact between the contralateral posterior pit lines, and between the contralateral supraorbital canals. Synapomorphies of the quasipetalichthyid-macropetalichthyid clade (Node 2, Fig. 8) include the fact that the postnasal plate does

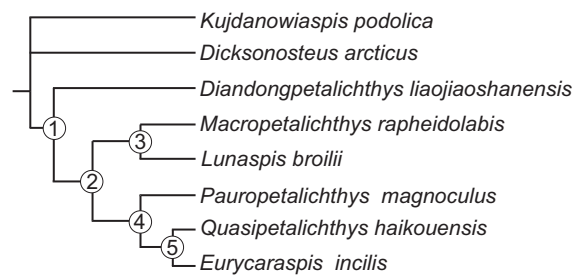


Fig. 8. The most parsimonious tree from an analysis of 22 characters and 8 placoderm taxa, with node numbers designating various clades (tree length = 30; CI = 0.7333; RI = 0.7241). Character states supporting the clades include: node 1: 2(0), 17(1), 19(1); node 2: 10(0), 12(0), 14(1); node 3: 9(1), 13(1); node 4: 6(1), 11*(1), 16(0), 20(1), 22(1); node 5: 3(1), 4(1). Asterisks indicate ambiguous character states resolved using DELTRAN.

Fig. 8. Arbre le plus parcimonieux obtenu à partir de 22 caractères et 8 taxons de placodermes, avec les nombres de nœuds désignant les divers clades (longueur de l'arbre = 30; CI = 0,7333; RI = 0,7241). Les états de caractères appuyant les clades comportent : nœud 1: 2(0), 17(1), 19(1); nœud 2: 10(0), 12(0), 14(1); nœud 3: 9(1), 13(1); nœud 4: 6(1), 11*(1), 16(0), 20(1), 22(1); nœud 5: 3(1), 4(1). Les astérisques indiquent les états de caractères ambigus établis en utilisant DELTRAN.

not form part of the orbital margin, the absence of the postnasal plate, and the unforked morphology of the posterior postorbital process.

5.2. Some endocranial features in petalichthyids

Pauropetalichthys presents many primitive characters with the potential to contribute to our understanding of petalichthyid interrelationships. Thus, we comment further on the morphology of petalichthyid endocrania with special reference to *Pauropetalichthys*.

The pineal foramen is positioned more posteriorly in *Eurycaraspis* and *Macropetalichthys* than in *Dicksonosteus* and *Diandongpetalichthys* (Goujet, 1984; Zhu, 1991; Fig. 7). *Pauropetalichthys* retains the primitive state, having an anteriorly positioned pineal foramen. In most placoderms, the position of the pineal foramen roughly corresponds to the site where the pineal organ emerges from the diencephalon, because the flattened endocranium is close to the visceral surface of the skull roof. Accordingly, the posteriorly positioned pineal foramen seen in some taxa suggests a posteriorly placed diencephalon. In *Macropetalichthys* the posterior position of the diencephalon is inferred to have resulted mainly from elongation of the olfactory tract (fig. 31, Stensiö, 1963). Because of a lack of endocranial preservation, it remains uncertain whether the olfactory tract was also elongated in *Eurycaraspis*.

The position of the supravagal process varies in petalichthyids (pr.sv, Fig. 7). In *Diandongpetalichthys*, the process is close to the posterior extremity of the endocranium, similar to the morphology in arthrodires such as *Dicksonosteus*. By comparison, a significantly longer occipital part of the endocranium is situated posterior to the supravagal process in *Pauropetalichthys*, a condition reminiscent of that seen in *Macropetalichthys* and *Eurycaraspis*. The supravagal process itself also varies in shape, being nearly right-angled in *Diandongpetalichthys* and the arthrodire *Dicksonosteus* but forming

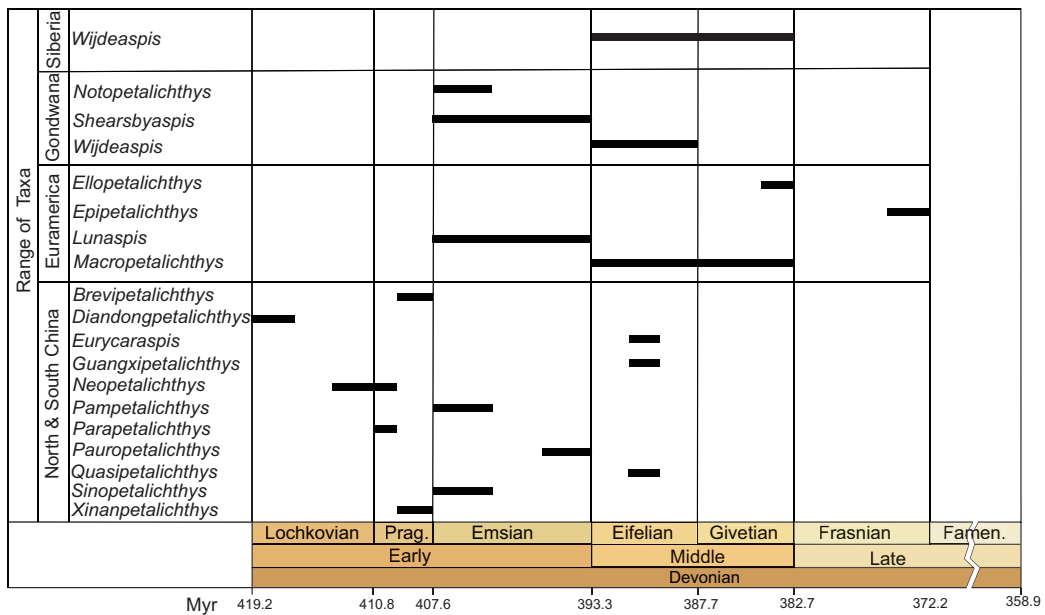


Fig. 9. (Color online.) Temporal and paleogeographic ranges of various petalichthyids. References in Appendix 3.

Fig. 9. (Couleur en ligne.) Gammes temporelles et paléogéographiques de pétalichthyidés variés. Références dans l'Appendice 3.

an obtuse angle in *Pauropetalichthys*, *Eurycaraspis* and *Macropetalichthys*.

The posterior postorbital process is forked in *Diandongpetalichthys* (Zhu, 1991), but unforked and somewhat underdeveloped in *Pauropetalichthys*, *Eurycaraspis* and *Macropetalichthys* (Liu, 1991; Stensiö, 1963). Outgroup comparison shows that the forked process is also present in primitive arthrodires such as *Dicksonosteus* (Goujet, 1984), and should therefore be considered a plesiomorphy. In addition, the posterior postorbital process is much closer to the anterior postorbital process in *Pauropetalichthys* than in *Dicksonosteus* and *Diandongpetalichthys* (Goujet, 1984; Zhu, 1991). The short distance between anterior and posterior postorbital processes also appears in *Eurycaraspis* but to a lesser extent (Liu, 1991). In *Macropetalichthys*, the anterior and posterior postorbital processes are completely fused into a single complex (pr.poap, Fig. 8; Stensiö, 1963).

The extent of the otic region can be inferred from that of the labyrinths, or that of their imprints on the visceral surface of the skull roof. In *Dicksonosteus* and *Diandongpetalichthys*, the otic region is relatively long, forming 36 percent and 31 percent of the total length of the endocranium respectively (Goujet, 1984; Zhu, 1991). In *Pauropetalichthys* and *Eurycaraspis*, the otic region is considerably shorter, forming 23 percent and 18 percent of the total length of the endocranium respectively (Liu, 1973, 1991). The otic region of *Macropetalichthys*, forming only 15 percent of the total length of the endocranium, is the shortest of any petalichthyid (Stensiö, 1925, 1963). Proportional shortening of the otic region in petalichthyids may actually reflect general elongation of both the orbitotemporal and occipital parts of the endocranium.

5.3. Paleogeographic distribution of petalichthyids

Before *Pauropetalichthys* was discovered, 17 petalichthyid genera had been reported from China, Iran, Australia, Siberia and Euramerica, ranging in age from Lochkovian to Late Frasnian (Fig. 9; Denison, 1978; Zhu, 2000). A complete list of taxa and localities is given in Appendix 3.

Outside China, petalichthyids are known from the Emsian (Early Devonian) to the Late Frasnian (Late Devonian), and belong to the *Macropetalichthyidae* exclusively. By comparison, the Chinese petalichthyids appear earlier (Lochkovian, Earliest Devonian) and show a higher diversity. In Lochkovian - Pragian (Early Devonian) deposits, petalichthyids are restricted to the South China Block. The discovery of *Quasipetalichthys* in both North China and South China suggests paleogeographic proximity between the two blocks (Jia et al., 2010; Ritchie et al., 1992). Although several Chinese petalichthyids are endemic, such as *Diandongpetalichthys* (Pan and Wang, 1978; Zhu, 1991), *Quasipetalichthys* (Liu, 1973; Pan et al., 1987) and *Eurycaraspis* (Liu, 1991), Chinese deposits have also yielded such macropetalichthyids as *Xinanpetalichthys* (Pan and Wang, 1978), *Pampetalichthys* (Zhu and Wang, 1996b; Zhu, 2000), and *Guangxipetalichthys* (Ji and Pan, 1997). However, the purported discoveries of *Lunaspis* sp. (Liu, 1981) and *Macropetalichthyidae* gen. et sp. indet. (Wang and Cao, 1988) from China are doubtful. The former report is based on a partial coat of trunk armor that may belong to an arthrodire, while the latter is based on material that is too fragmentary to be assigned to the *Macropetalichthyidae* with certainty.

Plotting the distribution of petalichthyids on an Early Devonian global reconstruction (Fig. 10) indicates that

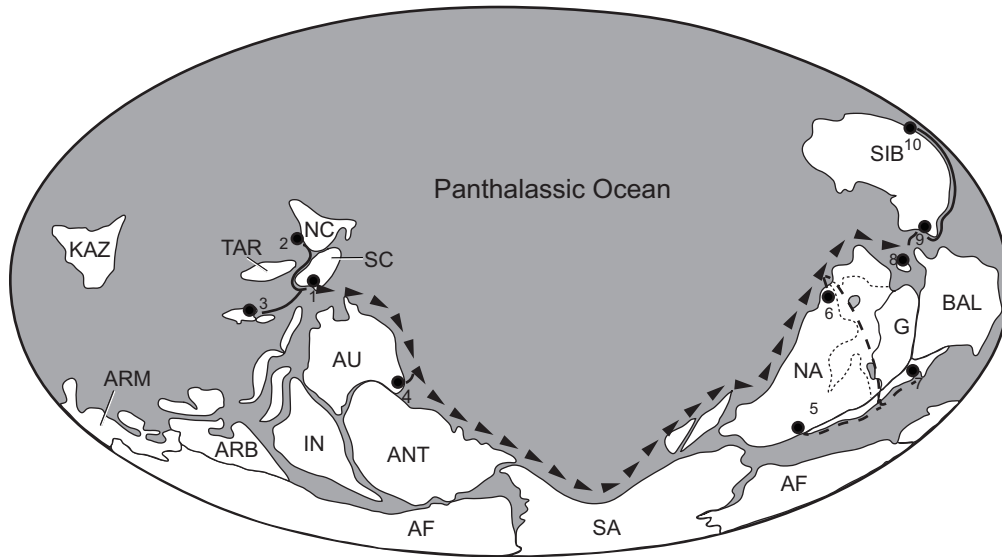


Fig. 10. Global distribution of the Petalichthyida, plotted on a paleogeographic reconstruction of the Devonian (map after Zhu and Zhao, 2006). Localities: 1. Southern and southwestern China; 2. Northern China; 3. Iran; 4. New South Wales, Australia; 5. New York, USA; 6. Northern Canada; 7. Germany; 8. Spitsbergen; 9. Severnaya Zemlya, Russia; 10. Northwestern Siberia.

Fig. 10. Distribution globale des Petalichthyida, rassemblés dans une reconstitution paléogéographique du Dévonien (carte d'après Zhu et Zhao, 2006). Localisation : 1. Chine du Sud et du Sud-Ouest ; 2. Chine du Nord ; 3. Iran ; 4. Nouvelle-Galles du Sud, Australie ; 5. New York, États-Unis ; 6. Nord du Canada ; 7. Allemagne ; 8. Spitzberg ; 9. Severnaya Zemlya, Russie ; 10. Sibérie nord-occidentale.

macropetalichthyids may have dispersed along the nearly continuous coastline from South China to eastern Gondwana, Euramerica and Siberia, as may also have been true of sarcopterygians (Zhu and Zhao, 2006). The occurrence of *Wijdeaspis* in areas as widely separated as Spitsbergen, Severnaya Zemlya, Siberia and Iran (Denison, 1978; Heintz, 1929, 1937) suggests that macropetalichthyids might have possessed a strong dispersal capacity.

Two major bio-events affected Chinese petalichthyids. The first was the E'Em Event, which can be recognized as a faunal turnover from endemic taxa to more cosmopolitan ones (Walliser, 1995; Zhu, 2000). The second was the Late Eifelian Event (Walliser, 1995), which resulted in the extinction of petalichthyids in China. Based on the analysis of Zhu and Wang (1996b), the Petalichthyida originated in the Lochkovian of South China and diversified in South China before the E'Em Event, and macropetalichthyids subsequently dispersed to other regions in the Early Emsian. Primitive arthrodiroids underwent a similar long-dispersal history from South China to Gondwana and Euramerica, but at an earlier time (Dupret, 2008; Dupret and Zhu, 2008).

6. Conclusion

Paupropetalichthys magnoculus gen. et sp. nov. from Zhanyi, Yunnan, China represents the earliest known member of the Quasipetalichthyidae. Study of the holotype of this new species reveals important information regarding petalichthyid anatomy, particularly pertaining to the nasal capsules, and confirms that the Quasipetalichthyidae are a monophyletic group.

Based on the comparisons between the endocrania of petalichthyids and those of primitive arthrodiroids (Actinolepidoidei and Phlyctaenii), we tentatively suggest that the obtusely angled supravagal process, unforked posterior postorbital process and fused postorbital processes seen in some petalichthyids are derived characters. Proportional shortening of the otic region in petalichthyids may be a function of general elongation of the orbitotemporal and occipital parts of the endocranium. However, caution in interpreting these features is warranted because only two groups of placoderms (arthrodiroids and petalichthyids) are considered here. The paleogeographic distribution of the Petalichthyida reveals a Chinese origin of the group, and a long-distance dispersal of macropetalichthyids after the E'Em Event.

Acknowledgements

This research was funded by Major Basic Research Projects of China (2012CB821902), and National Major Scientific Instrument and Equipment Development Project of China (2011YQ03012). We thank W.-J. Zhao, Z.-K. Gai and M. Castiello for discussion, C.-H. Xiong for specimen preparation, and Y.-M. Hou for CT scanning.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2014.10.006>. Additional citations in supplementary data: Broili, 1929; Dupret et al., 2007; Ji, 1996; Johnson et al., 2000; Kayser, 1880; Kiaer, 1915; Pan et al.,

1975; Young, 1985; Wang, 1988; Woodward, 1941; Zhao and Zhu, 2010.

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