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First Middle Devonian galeaspid from the Haikou Formation in Yunnan Province

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Abstract The Early Emsian Event (E'Em Event), the most significant bio-event for Chinese Devonian vertebrates, has significantly impacted on the diversity of galeaspids. The endemic Galeaspida almost became extinct after the Mid-Emsian Event (M'Em Event). Only few galeaspid taxa survived from these events, such as *Clarorbis apponomedianus* from the Eifelian of Guangxi, South China, and an indeterminate galeaspid from the Frasnian of Ningxia, Northwest China. Here, we report the first Middle Devonian galeaspid, *Dongfangaspis* sp., from the Haikou Formation in Wuding, Yunnan Province. The new material is more suggestive of the type species of *Dongfangaspis*, *D. major*, than *Laxaspis* and *Polybranchiaspis* in its suborbicular headshield with small inner cornual process, broad and nearly aequilate ventral rim, and about 45 pairs of branchial fossae. *Dongfangaspis* bears the largest number of branchial fossae ever recorded in galeaspids, which probably play an important role in *Dongfangaspis* surviving from the E'Em and M'Em events. The new finding represents the second Middle Devonian fossil record of galeaspids, and extends the chronological range of *Dongfangaspis* from the Pragian (Early Devonian) to the Eifelian (Middle Devonian).

Key words Wuding, Yunnan; Middle Devonian; Haikou Formation; galeaspid; E'Em Event

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1 Introduction

The Galeaspida is a group of 'ostracoderms' (jawless stem-gnathostomes) that thrived during the Siluro–Devonian period (Tarlo, 1967; Zhu, 1992; Janvier, 1996; Zhu and Gai, 2006; Janvier et al., 2009; Gai et al., 2018). The endemic galeaspids underwent quick radiation in South China soon after the Silurian-Devonian Boundary (S/D) Event, but were replaced by the cosmopolitan forms after the Early Emsian Event (E'Em Event), and almost disappeared

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after the Mid-Emsian Event (M'Em Event) (Zhu, 2000). To our knowledge, only two galeaspid species survived to Middle-Late Devonian. One is *Clarorbis apponomedianus* from the Eifelian of Guangxi, South China, which represents the first convincing record of the Middle Devonian galeaspids in China (Pan and Ji, 1993). The other is an indeterminate galeaspid from the Zhongning Formation in the Hongshiwan Section of Zhongwei, Ningxia, Northwest China (Pan et al., 1987), which is referred to as the Frasnian age (Jia et al., 2010). In Ningxia, the age of the Zhongning Formation ranges from late Frasnian to Famennian. The Late Devonian tetrapod *Sinostega* (Zhu et al., 2002), tetrapod-like fish *Hongyu* (Zhu et al., 2017), and the antiarchs including *Remigolepis* and *Ningxialepis* (Pan et al., 1987; Jia et al., 2010) were found from the uppermost part of the Zhongning Formation in the Shixiagou Section, Famennian in age. The Zhongning Formation in the Hongshiwan Section (about 100 km southwestern of the Shixiagou Section) is very thin and yields the youngest known galeaspid together with *Lepidophloeum rhombicum*, *Remigolepis zhongweiensis*, and *R. xiangshanensis.* The fish-bearing strata roughly correspond to the lower part of the Zhongning Formation in the Shixiagou and Dadaigou Sections (Jia et al., 2010). Here we report a new specimen of *Dongfangaspis* from the Haikou Formation (Eifelian, Middle Devonian) in Wuding, Yunnan Province. The Early-Middle Devonian strata are well developed in Wuding (Liu, 1994; Wang and Zhu, 1995) and rich in fossil fishes including galeaspids (Liu, 1973), placoderms (Liu and Wang, 1981; Wang and Wang, 1983; Wang, 1992; Wang and Zhu, 1995; Zhu et al., 2016; Pan et al., 2017), and sarcopterygians (Fan, 1992). However, galeaspid fossils have not been found in the Middle Devonian strata in the region. The youngest galeaspid record in Yunnan Province is *Wumengshanaspis cuntianensis* from the Soutoushan Formation (Emsian, Early Devonian) near the Cuntian village, Yiliang County, northeastern Yunnan (Wang and Lan, 1984). The new material of *Dongfangaspis* is not only the first Middle Devonian galeaspid record in Yunnan, but also the second one worldwide.

2 Geological setting

The specimen IVPP V 15926 was collected in the 1980s from the middle part of the Haikou Formation at a site between Longtan and Zhaojiazhuang villages near the county of Wuding, Yunnan Province (Fig. 1A). The Devonian strata, well developed and rich in fish fossils in Wuding County, comprise the Posongchong, Pojiao, Jiucheng, and Haikou formations in ascending chronological order (Fig. 1B). The first galeaspid fossil record in the region is *Huananaspis* (Liu, 1973) from the Lower Devonian Posongchong Formation, which overlies unconformitably the Lower Ordovician Hongshiya Formation (Fig. 1B). The new galeaspid material was collected from the yellow medium-thick bedded quartz sandstone of the middle part of the Haikou Formation, in which antiarchs and sarcopterygians are diverse and abundant, represented by *Dianolepis liui* and *Thursius wudingensis* (Chang, 1965; Fan, 1992; Ritchie et al., 1992). The vertebrate assemblage was also known from the lower part of

the Qujing Formation in Qujing and Zhaotong (Chang, 1965; Pan and Wang, 1978; Fan, 1992; Ritchie et al., 1992). Therefore, it was named the Qujing Assemblage and aged as the late Eifelian (Zhao and Zhu, 2010).

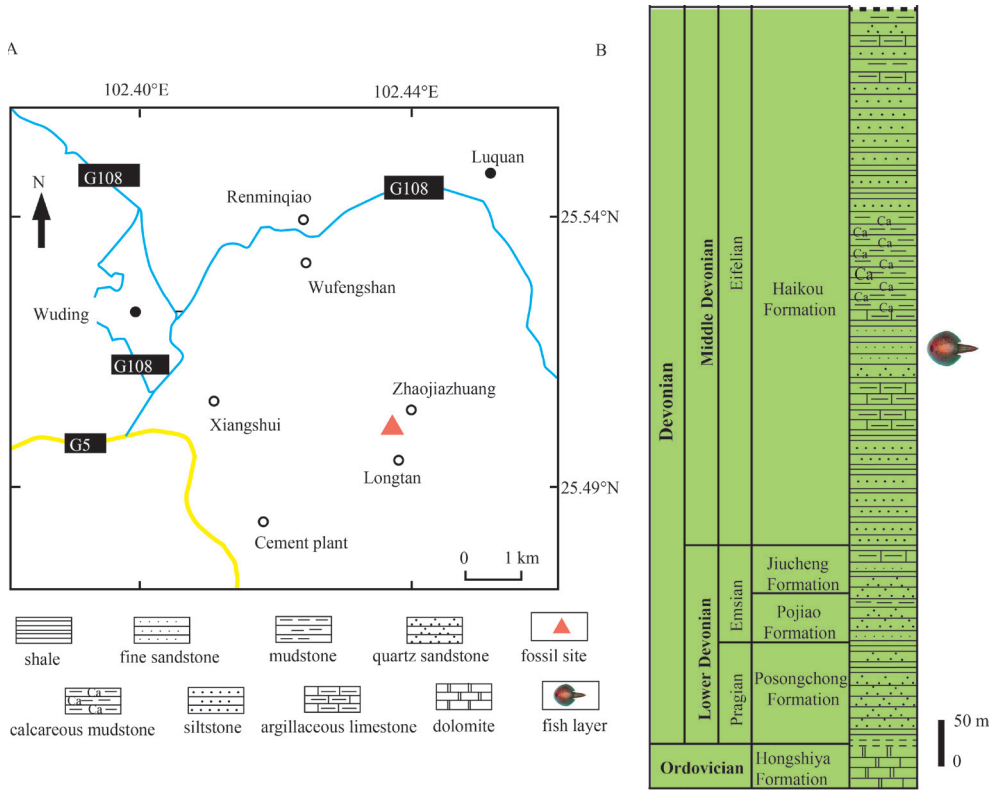

Fig. 1 Maps of the fossil locality of *Dongfangaspis* sp. (A) and the fish-bearing lithological column (B) in Wuding, Yunnan Province, China

3 Material and methods

The new material of *Dongfangaspis* sp. is an incomplete headshield (IVPP V 15926), which is permanently housed and accessible for examination in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences. The holotype of *Dongfangaspis major* (IVPP V 4421) housed in IVPP, and the holotype of '*Dongfangaspis qujingensis*' (GMC V1753) and the referred specimen of *Laxaspis* cf. *L. qujingensis* (GMC V2072) housed in the Geological Museum of China (GMC) are reexamined and photographed for comparative study. The fossils were prepared mechanically using a vibro tool with a tungsten-carbide bit or a needle. All measurement data were obtained via a digital vernier caliper. In addition, the specimens were examined under the Olympus SZ61 zoom stereo microscope and photographed with a Canon EOS 5D Mark III camera. The pictures for the general morphology were conducted by the Canon macro photo lens EF 100 mm 1:2.8L, while the close-up of the ornamentation was acquired with the Canon macro photo lens MP-E 65 mm 1:2.8 1–5×.

4 Systematic paleontology

Subclass Galeaspida Tarlo, 1967
Supraorder Polybranchiaspidida Janvier, 1996
Order Polybranchiaspiformes Liu, 1965
Family Polybranchiaspidae Liu, 1965
Genus *Dongfangaspis* Liu, 1975

Type species *Dongfangaspis major* Liu, 1975 (Fig. 2A, B).

Diagnosis (emended) Large-sized polybranchiaspid fish; headshield sub-circular, about 230 mm in length, 250 mm in width, slightly wider than long; rostral margin round, blunt; inner cornual process leaf-shaped; ventral rim broad, nearly aequilate with a width of 20 mm; the inner margin of the ventral rim nearly parallel with the lateral margin of the headshield; median dorsal opening transversely elongated oval in shape, with a convex posterior margin; orbital opening round, dorsally positioned; pineal opening almost level with the posterior margin of the orbital openings; about 45 pairs of branchial fossae; eight pairs of lateral transverse canals with branched distal ends; ornamentation of the headshield composed of tiny-granular tubercles.

Remarks *Dongfangaspis* is a monospecific genus, which was erected by Liu (1975) based on the holotype of *Dongfangaspis major* from the Guanshanpo Formation of the Pingyipu Group in Jiangyou, Sichuan (Fig. 2A). The holotype is the only specimen and incomplete, which results in the diagnosis of *Dongfangaspis* being not distinctive enough to separate it from *Laxaspis* and *Polybranchiaspis*. For example, three species, *D. paradoxus*, *D. yunnanensis* (Fang et al., 1985), and '*D. qujingensis*' (Pan and Wang, 1981; Pan, 1992) were once referred to *Dongfangaspis*. However, *D. paradoxus* and *D. yunnanensis* (Fang et al., 1985) from the Xishancun Formation in Qujing, Yunnan, were later recognized as the junior synonyms of *Polybranchiaspis liaojiaoshanensis*, whereas '*D. qujingensis*' is more suggestive of *Laxaspis qujingensis* than *D. major* (Zhu and Gai, 2006). Another specimen GMC V2072, which was initially classified as '*D. qujingensis*', differs from the holotype of '*D. qujingensis*' on the broader headshield and round, blunt rostral margin. Therefore, it probably represents a new species of *Laxaspis* and was temporarily denominated as *Laxaspis* cf. *L. qujingensis* (Zhu et al., 2015).

***Dongfangaspis* sp.**

(Fig. 3A–E)

Material An incomplete headshield, IVPP V 15926.

Locality and horizon A site between Longtan and Zhaojiazhuang villages in Wuding County, Yunnan; Haikou Formation, Eifelian, Middle Devonian.

Diagnosis Large-sized polybranchiaspid fish; broad and nearly aequilate ventral rim with a width of 35–37 mm; more than 37, and estimated 45 pairs of branchial fossae; at least three lateral transverse canals; ornamentation of the headshield composed of tiny-granular tubercles.

Remarks The new material from the Haikou Formation in Wuding County is more suggestive of *D. major* than *Laxaspis* and *Polybranchiaspis* in its small inner cornual process, broad and nearly aequilate ventral rim, and about 45 pairs of branchial fossae. However, the lack of data on the median dorsal opening precludes erecting a new species for the new specimen.

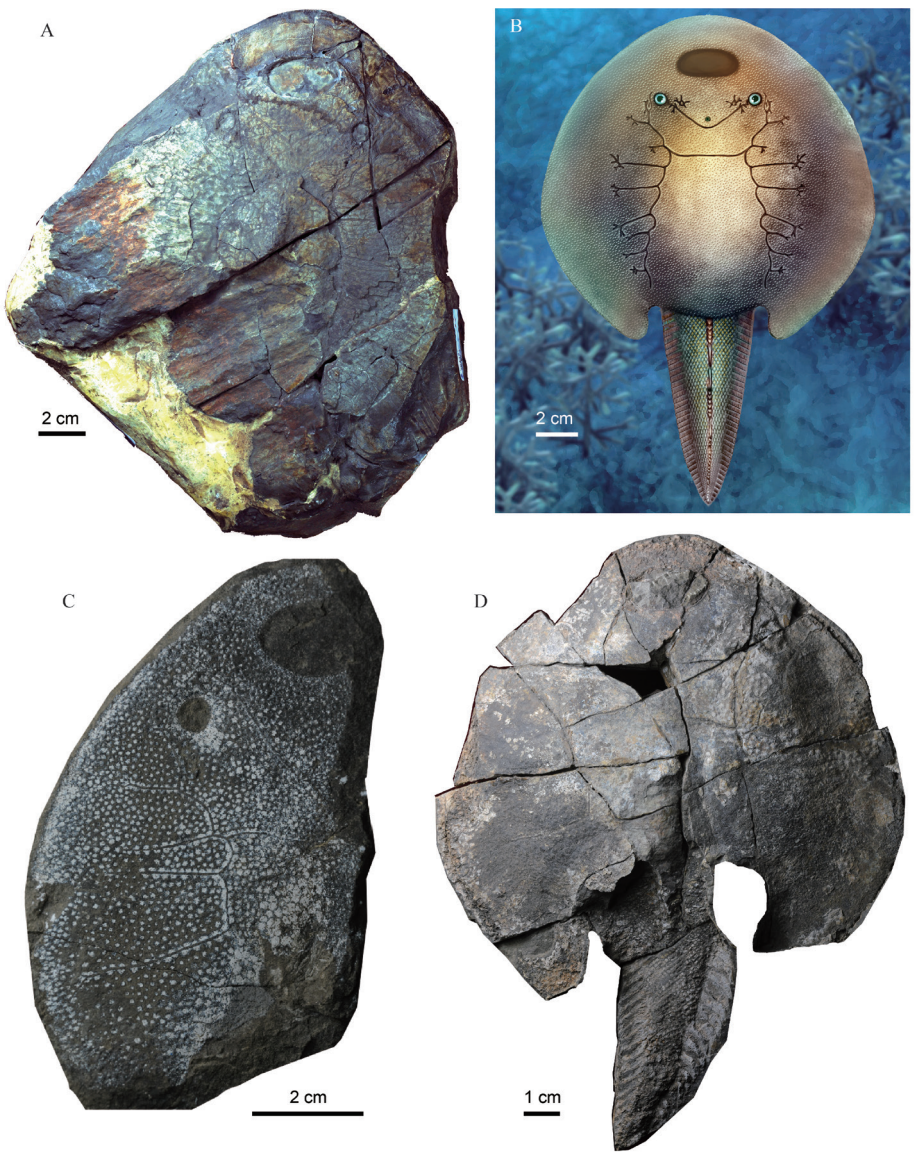

Fig. 2 Photographs and restoration of *Dongfangaspis* and *Laxaspis*
A. the holotype IVPP V 4421 of the type species of *Dongfangaspis*, *D. major* Liu, 1975 from the Guanshanpo Formation, Pingyipu Group, Yanmenba, Jiangyou, Sichuan, in dorsal view; B. restoration of *D. major*; C. '*Dongfangaspis qujingensis*' from the Xishancun Formation, Qujing, Yunnan Province, Early Devonian (early Lochkovian), GMC V1753, in ventral view; D. GMC V2072 from the upper part of the Xishancun Formation, Qujing, Yunnan Province was referred to '*Dongfangaspis qujingensis*', but was recognized as *Laxaspis* cf. *L. qujingensis*

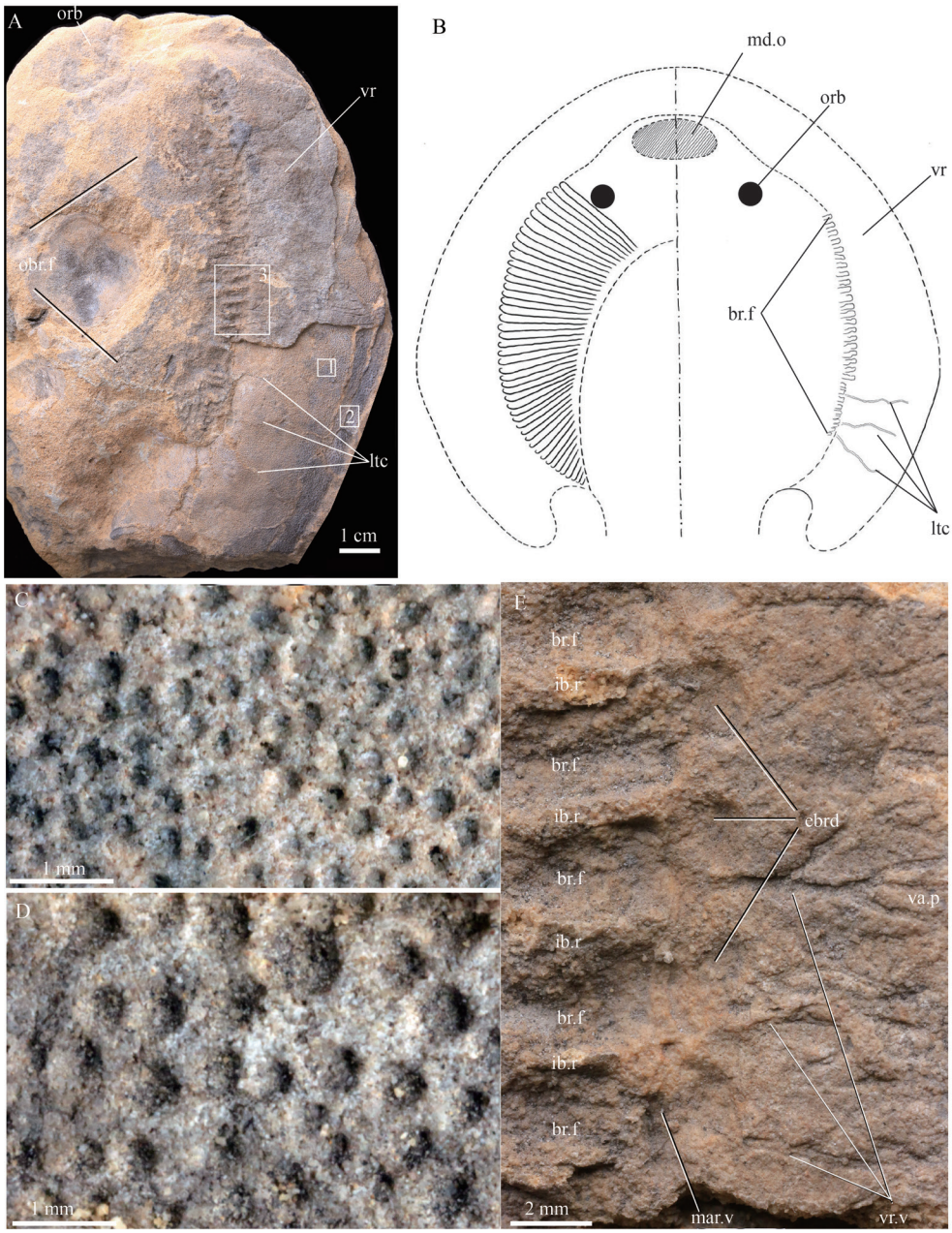

Fig. 3 Photographs, interpretive drawing and restoration of *Dongfangaspis* sp. from Wuding, Yunnan
A. an incomplete headshield, holotype, IVPP V 15926, in ventral view;
B. interpretive drawing (right half) and restoration (left half), in dorsal view;
C. close-up of granular tubercles on the headshield (box region 1 of Fig. 3A);
D. close-up of granular tubercles on the ventral ring (box region 2 of Fig. 3A);
E. close-up of the branchial fossae (box region 3 of Fig. 3A)
Abbreviations: br.f, branchial fossa; ebrd, impression of extrabranchial division of the branchial fossa; ib.r, interbranchial ridge; ltc, lateral transverse canal; mar.v, marginal vein; md.o, median dorsal opening; obr.f, oralo-branchial fenestra; orb, orbital opening; va.p, plexus of subcutaneous vascular canals; vr, ventral rim; vr.v, ventral rim vein

Description The new specimen V 15926 is an incomplete headshield, representing a large-sized polybranchiaspid fish. The preserved length of the headshield is 155 mm, and the maximum length is estimated to be 200 mm. The length of headshield in the holotype of *Dongfangaspis major* is about 200 mm, while about 60 mm in *Polybranchiaspis*, and about 130 mm in *Laxaspis* (Zhu et al., 2015). Obviously, the length of the new headshield is close to that of *D. major*. The dorsal part of the headshield can only be observed ventrally, showing a dorsally convex 'dome'. A round impression with a diameter of 10 mm, preserved in the anterior part of the headshield, probably represents the orbital opening (orb, Fig. 3A, B), which is closer to the midline than the lateral margin of the headshield. Three sensory canals probably for the lateral transverse canal (ltc, Fig. 3A, B) are observed on the internal surface of the headshield. The ornamentation of the headshield exhibits numerous tiny, dense granular tubercles (Fig. 3C). There are about 8–10 tubercles per square millimetre.

Most of the left ventral rim of the headshield is preserved in the holotype. The headshield curves ventrally to form a flat ventral rim. The ventral rim is wide and elongate, with a preserved length of 155 mm. The ventral rim is nearly aequilate, with the maximum width of 37 mm in the middle part, and the minimum width of 35 mm in the posterior part. The lateral edge of the ventral rim is strengthened by a thickening dermal ring with a width of 5 mm, where the dorsal part of the headshield curves ventrally. The ornaments on the thickened ring are much larger than those on the dorsal part of the headshield, with about 4 tubercles per square millimetre (Fig. 3D).

The ventral rims embrace a large oralo-branchial fenestra (obr.f, Fig. 3A), under which a large oralo-branchial chamber exists. The oralo-branchial fenestra is probably covered by one or two dermal ventral plates, but not preserved in our specimen. Numerous branchial fossae can be observed along the lateral margin of the oralo-branchial fenestra. The branchial fossae, separated by thin interbranchial ridges (ib.r, Fig. 3E), are reduced to slender and parallel grooves. The width of branchial fossa is about 3.0 mm. There are about 37 branchial fossae observed along the lateral margin of the oralo-branchial fenestra in a length of 11.0 cm. The total length of the lateral margin of the oralo-branchial fenestra is about 13.5 cm with an average of one external branchial opening per 3.0 mm. As such, the total number of the branchial fossae may have been about 45 pairs as that of *Dongfangaspis major* estimated by Janvier (2004). There exists a round, small pit at the distal extremity of each branchial fossa, which is interpreted as the extra-branchial division of the branchial fossa (ebrd, Fig. 3E) lying dorsally to each external branchial opening (Janvier, 2004).

An elongate canal probably for the marginal vein (mar.v, Fig. 3E) flanks the oralo-branchial fenestra. Along its course, the canal of the marginal vein projects a small canal extending laterally to the ventral rim, probably for the ventral rim vein (vr.v, Fig. 3E) (Gai et al., 2019). Each canal of the ventral rim vein ramifies into 3–5 branches at its distal extremity. Numerous rami from adjacent ventral rim veins intersect each other to form a rich network or plexus of subcutaneous vascular canals (va.p, Fig. 3E) at the boundary between the exo- and endo-skeletons.

5 Discussion and conclusion

Dongfangaspis can be assigned to the Polybranchiaspidae (Zhu and Gai, 2006; Gai et al., 2018; Shan et al., 2020; Jiang et al., 2021; Meng and Gai, 2021), which was established by Liu (1965) and includes *Bannhuanaspis*, *Dongfangaspis*, *Polybranchiaspis*, *Laxaspis*, and *Damaspis*. However, the diagnostic features of *Dongfangaspis* are not clear enough to distinguish it from *Laxaspis* and *Polybranchiaspis* because of the poorly preserved specimen. The new specimen of *Dongfangaspis* is more suggestive of *D. major* than *Laxaspis* and *Polybranchiaspis* in its subcircular headshild with small inner cornual process, broad and nearly aequilate ventral rim, and about 45 pairs of branchial fossae (Fig. 4A). By contrast, *Laxaspis* (Fig. 4B) and *Polybranchiaspis* (Fig. 4C) are oval with developed inner cornual process and median dorsal spine. The ventral rim of *Laxaspis* is broad, but nonuniform in the width showing a pointed front end and a much wider rear end (Fig. 4B). The ventral rim of *Polybranchiaspis* (Fig. 4C) is aequilate as that of *Dongfangaspis*, but much narrower than that of *Dongfangaspis* (Fig. 4A). Last but the most important, *Dongfangaspis* exhibits the largest number of branchial fossae, possibly up to 45 pairs, ever recorded in galeaspids. The branchial fossae in *Laxaspis* (Fig. 4B) and *Polybrabchiaspis* (Fig. 4C) are 18 and 12 pairs respectively. The Silurian galeaspids Dayongaspidae, Xiushuiaspidae, Hanyangaspidae, Eugaleaspiformes and the oldest polybranchiaspiform *Platylomaspis* have the least branchial fossae (6–7 pairs), probably representing the most general condition (Janvier, 2004). The "polybranchic" (more than ten pairs of branchial fossae) condition began with the radiation of Polybranchiaspiformes in the lower Lochkovian Xishancun Formation in Qujing, Yunnan Province. However, the branchial fossae of the galeaspids during this stage are less than 20 pairs, e.g., 12 pairs in *Polybranchiaspis*, and 18 pairs in *Laxaspis*. In the Pragian of Early Devonian, the branchial fossae burst into more than 30 pairs in some taxa, such as 32 pairs in *Lopadaspis* (Wang et

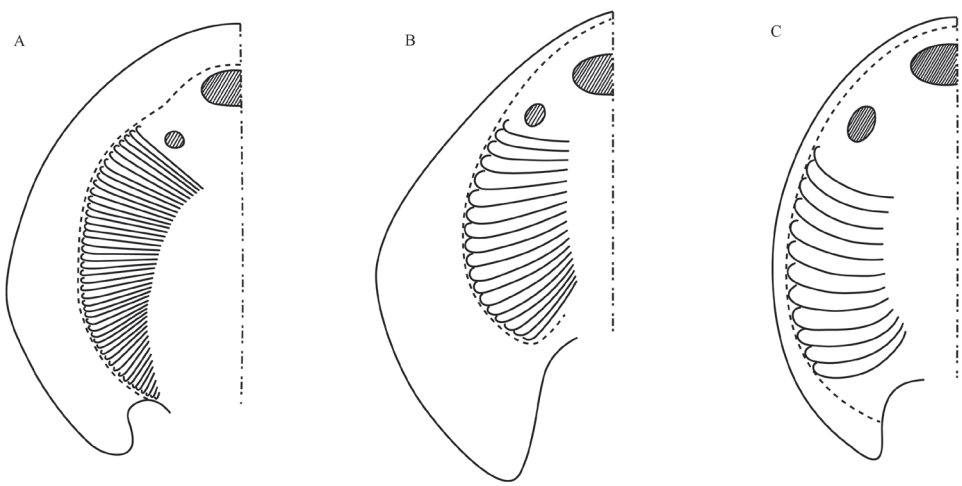

Fig. 4 The diagnostic differences of *Dongfangaspis* (A), *Laxaspis* (B), and *Polybranchiaspis* (C)
A–C, left half part of the headshield, in dorsal view, not to scale

al., 2001), 35 pairs in *Zhaotongaspis* (Wang and Zhu, 1994), and 45 pairs in *Dongfangaspis* (Janvier, 2004). This indicates that the number increase of branchial fossae in galeaspids is an evolutionary trend throughout the geological time and has occurred independently in different lineages. Janiver (2004) considered that galeaspids probably adopted a strategy to compensate for the flattening of their headsheild and branchial fossae by increasing the number of branchial fossae.

The Devonian global events were characterized by sea-level rise and fall, ocean anoxic/hypoxic events, and biological extinctions/turnovers (Walliser, 1996; Becker et al., 2012; Qie et al., 2018). The Early Emsian Event (E'Em Event) is characterized by a changeover from strong endemic fauna to cosmopolitan fauna in South China (Fig. 5) (Zhu, 2000). The Mid-Emsian Event (M'Em Event) refers to the Daleje Event connected with a transgression, which is named after the changes in lithology (from carbonates to shales) and fauna (most species of Mimosphinctidae vanished) near the base of the Daleje Formation in Bohemia (Walliser, 1996). Except for the faunal changes mentioned above, galeaspids can also be used to signify the Devonian events (Fig. 5). As one of the three major groups of Galeaspida, the oldest fossil record of Polybranchiaspiformes can be traced back to the early Telychian of Llandovery, Silurian (Gai et al., 2018). However, they did not undergo their radiation until the beginning of the Early Devonian, known as the *Polybranchiaspis–Laxaspis* assemblage (Assemblage I) (Zhu and Wang, 2000) or the Xishancun Assemblage (Zhao and Zhu, 2010) from the lower Lochkovian Xishancun Formation in Qujing, Yunnan Province. The galeaspids in the Xishancun Formation are characterised by the radiation of Polybranchiaspiformes, which consists of 11 polybranchiaspid species (Liu et al., 2018). However, the diversity of Polybranchiaspiformes suddenly declined by the Pragian of Early Devonian (Gai et al., 2018) (Fig. 5). Compared to the high diversity of Huananaspiformes, only two unusually large-sized polybranchiaspiforms survived in Pragian in China. One is *Nanningaspis zengi* from the Nakhaoling Formation of Guangxi (Gai et al., 2018), the other is *Dongfangaspis major* from the Guanshanpo Formation of Sichuan (Liu, 1975) (Fig. 5). After the middle Emsian of Early Devonian, the near-shore, shallow-water environment with muddy substratum and rich terrigenous clastics disappeared in South China (Qie et al., 2019). The endemic galeaspids almost became extinct after the Mid-Emsian event, i.e., Huananaspiformes and Eugaleaspiformes had gradually declined and only *Wumengshanaspis cuntianensis* survived into the late Emsian (Zhu, 2000) (Fig. 5). By the Eifelian of Middle Devonian, only few taxa of Polybranchiaspiformes can be found in China, such as *Clarorbis apponomedianus* from the Eifelian of Guangxi, South China (Pan and Ji, 1993) and an indeterminate galeaspid from the Frasnian of Ningxia, Northwest China (Pan et al., 1987) (Fig. 5). The discovery of the first Middle Devonian galeaspid from the Haikou Formation in Wuding, Yunnan Province reveals that *Dongfangaspis* also survived from the E'Em and M'Em events, which extends its chronological range from the Pragian of Early Devonian to the Eifelian of Middle Devonian. These latest occurrences of Polybranchiaspiformes are distributed from the Middle Devonian

of Yunnan and Guangxi in South China to the Upper Devonian of Ningxia in Northwest China. However, when and how did they start to migrate from the South China Block to the North China Block remains unknown and should be further explored in the future.

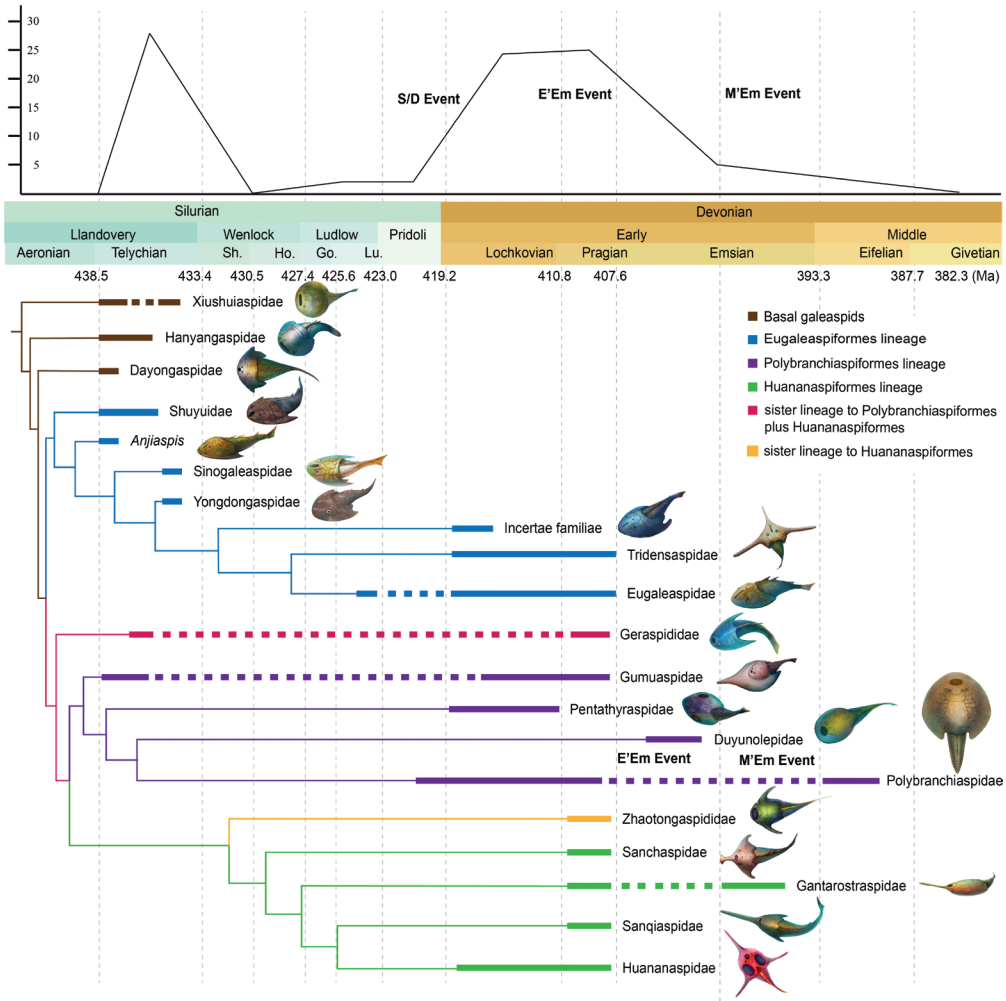

Fig. 5 Diversity at genus level and phylogenetic tree of galeaspids projected against stratigraphy in the Silurian-Devonian of China

Abbreviations: Go. Gorstian; Ho. Homerian; Sh. Sheinwoodian; Lu. Ludfordian

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云南中泥盆统海口组盔甲鱼类的首次发现

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摘要：早埃姆斯期生物事件是中国泥盆纪脊椎动物演化过程中最重要的生物事件，对盔甲鱼类的生物多样性产生了重大影响。在埃姆斯期之后，具有浓厚区域性色彩的盔甲鱼类几乎灭绝，只有少数属种遗存，如发现于华南广西中泥盆统艾菲尔阶的近中显眶鱼(*Clarorbis apponomedianus*)以及西北宁夏上泥盆统弗拉阶的一个多鳃鱼类未定种。首次报道了产自云南省武定县海口组的第一个中泥盆世盔甲鱼——东方鱼未定种(*Dongfangaspis* sp.)。与宽甲鱼(*Laxaspis*)和多鳃鱼(*Polybranchiaspis*)相比，这件新标本呈现出明显的东方鱼属的特征：近圆形的头甲，内角小，腹环宽且近乎等宽，约有45对鳃囊。东方鱼具有有史以来数目最多的鳃囊，这可能帮助它们在早、中埃姆斯期生物事件中幸存下来。这一新发现也是第二个中泥盆世盔甲鱼类化石记录，并将东方鱼属的生存时代从早泥盆世布拉格期扩展到了中泥盆世艾菲尔期。

关键词：云南武定，中泥盆世，海口组，盔甲鱼类，早埃姆斯期生物事件

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References

Becker R T, Gradstein F M, Hammer O, 2012. The Devonian Period. In: Gradstein F M, Ogg J G, Schmitz M D et al. eds. The Geologic Time Scale 2012, Vol 2. Amsterdam: Elsevier. 559–601

Chang K J, 1965. New antiarchs from the Middle Devonian of Yunnan. Vert PalAsiat, 9: 1–9

Fan J H, 1992. A new species of *Thursius* from Wuding, Yunnan. Vert PalAsiat, 30: 195–209

Fang R S, Jiang N R, Fan J C et al., 1985. The Middle Silurian and Early Devonian Stratigraphy and Palaeontology in Qujing District, Yunnan. Kunming: Yunnan People's Publishing House. 1–171

Gai Z K, Lu L W, Zhao W J et al., 2018. New polybranchiaspiform fishes (Agnatha: Galeaspida) from the Middle Palaeozoic of China and their ecomorphological implications. PLoS One, 13: e0202217

Gai Z K, Zhu M, Donoghue P C J, 2019. The circulatory system of Galeaspida (Vertebrata; stem-Gnathostomata) revealed by synchrotron X-ray tomographic microscopy. Palaeoworld, 28: 441–460

Janvier P, 1996. Early Vertebrates. Oxford: Clarendon Press. 1–393

Janvier P, 2004. Early specializations in the branchial apparatus of jawless vertebrates: a consideration of gill number and size. In: Arratia G, Wilson M V H, Cloutier R eds. Recent Advances in the Origin and Early Radiation of Vertebrates. München: Verlag Dr. Friedrich Pfeil. 29–52

Janvier P, Thanh T D, Phuong T H, 2009. Occurrence of *Sanqiaspis*, Liu, 1975 (Vertebrata, Galeaspida) in the Lower Devonian of Vietnam, with remarks on the anatomy and systematics of the Sanqiaspididae. C R Palevol, 8: 59–65

Jia L T, Zhu M, Zhao W J, 2010. A new antiarch fish from the Upper Devonian Zhongning Formation of Ningxia, China. Palaeoworld, 19: 136–145

Jiang W Y, Zhu M, Shi X D et al., 2021. *Qushiaspis*, a new genus of gantarostrataspid fish (Galeaspida, stem-gnathostomata) from the Lower Devonian of Yunnan, China. Hist Biol, doi: 10.1080/08912963.2021.1888086

Liu S F, 1994. On the Middle Devonian series of Wuding, Yunnan. Vert PalAsiat, 32: 32–40

Liu Y H, 1965. New Devonian agnathans of Yunnan. Vert PalAsiat, 9: 125–134

Liu Y H, 1973. On the new forms of Polybranchiaspiformes and Petalichthyida from Devonian of Southwest China. Vert PalAsiat, 11: 132–143

Liu Y H, 1975. Lower Devonian Agnathans of Yunnan and Sichuan. Vert PalAsiat, 13: 202–216

Liu Y H, Wang J Q, 1981. On three new arthrodires from Middle Devonian of Yunnan. Vert PalAsiat, 19: 296–304

Liu Y H, Gai Z K, Zhu M, 2018. New findings of galeaspids (Agnatha) from the Lower Devonian of Qujing, Yunnan, China. Vert PalAsiat, 56: 1–15

Meng X Y, Gai Z K, 2021. *Falxcornus*, a new genus of Tridensaspidae (Galeaspida, stem-Gnathostomata) from the Lower Devonian in Qujing, Yunnan, China. Hist Biol, doi: 10.1080/08912963.2021.1952198

Pan J, 1992. New Galeaspids (Agnatha) from the Silurian and Devonian of China. Beijing: Geological Publishing House. 1–77

Pan J, Ji S A, 1993. First discovery of Middle Devonian galeaspids in China. Vert PalAsiat, 31: 304–307

Pan J, Wang S T, 1978. Devonian Agnatha and Pisces of South China. In: Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences ed. Symposium on the Devonian System of South China. Beijing: Geological Publishing House. 298–333

Pan J, Wang S T, 1981. New discoveries of polybranchiaspids from Yunnan Province. Vert PalAsiat, 19: 113–121

Pan J, Huo F C, Cao J X et al., 1987. Continental Devonian System of Ningxia and its Biotas. Beijing: Geological Publishing House. 1–237

Pan Z H, Zhu M, Zhu Y A et al., 2017. A new antiarch placoderm from the Emsian (Early Devonian) of Wuding, Yunnan, China. Alcheringa, 42: 10–21

Qie W K, Ma X P, Xu H H et al., 2018. Devonian integrative stratigraphy and timescale of China. Sci China Earth Sci, 62: 112–134

Qie W K, Liang K, Königshof P, 2019. Devonian palaeoecosystems and palaeoenvironments of South China. Palaeobio Palaeoenv, 99: 1–5

Ritchie A, Wang S T, Young G C et al., 1992. The Sinolepidae, a family of antiarchs (placoderm fishes) from the Devonian of South China and eastern Australia. Rec Aust Mus, 44: 319–370

Shan X R, Zhu M, Zhao W J et al., 2020. A new genus of sinogaleaspids (Galeaspida, stem-Gnathostomata) from the Silurian Period in Jiangxi, China. PeerJ, 8: e9008

Tarlo L B H, 1967. Chapter 25 Agnatha. In: Harland W B, Holland C H, House M R et al. eds. The Fossil Record. London: The Geological Society of London. 629–636

Walliser O H, 1996. Global events in the Devonian and Carboniferous. In: Walliser O H eds. Global Events and Event Stratigraphy in the Phanerozoic. Berlin, Heidelberg, New York: Springer. 225–250

Wang J Q, 1992. New discovery of early Middle Devonian brachythoracid (placoderm fish) from Wuding Region of Yunnan. Vert PalAsiat, 30: 111–119

Wang J Q, Wang N Z, 1983. A new genus of Coccosteidae. Vert PalAsiat, 21: 1–8

Wang J Q, Zhu M, 1994. *Zhaotongaspis janvieri* gen. et sp. nov., a galeaspid from Early Devonian of Zhaotong, northeastern Yunnan. Vert PalAsiat, 32: 231–243

Wang J Q, Zhu M, 1995. Age of the Jiucheng Formation of Wuding, Yunnan. J Stratigr, 19: 20–24

Wang S T, Lan C H, 1984. New discovery of polybranchiaspids from Yiliang County, Northeast Yunnan Province. Bull Geol Inst, 9: 113–120

Wang S T, Wang J Q, Wang N Z et al., 2001. A new genus of Galeaspida from the late Early Devonian of eastern Guangxi, South China. Vert PalAsiat, 39: 157–167

Zhao W J, Zhu M, 2010. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. Palaeoworld, 19: 4–26

Zhu M, 1992. Two new eugaleaspids, with a discussion on eugaleaspid phylogeny. Vert PalAsiat, 30: 169–184

Zhu M, 2000. Catalogue of Devonian vertebrates in China, with notes on bio-events. Cour Forsch-Inst Senckenberg, 223: 373–390

Zhu M, Gai Z K, 2006. Phylogenetic relationships of galeaspids (Agnatha). Vert PalAsiat, 44: 1–27

Zhu M, Wang J Q, 2000. Silurian vertebrate assemblages of China. Cour Forsch-Inst Senckenberg, 223: 161–168

Zhu M, Ahlberg P E, Zhao W J et al., 2002. First Devonian tetrapod from Asia. Nature, 420: 760–761

Zhu M, Qiu Z X, Gai Z K et al., 2015. Palaeovertebrata Sinica, Vol. I, Fishes, Fascile 1, Agnathans. Beijing: Science Press. 1–272

Zhu M, Ahlberg P E, Zhao W J et al., 2017. A Devonian tetrapod-like fish reveals substantial parallelism in stem tetrapod evolution. Nat Ecol Evol, 1: 1470–1476

Zhu Y A, Zhu M, Wang J Q, 2016. Redescription of *Yinostius major* (Arthrodira: Heterostiidae) from the Lower Devonian of China, and the interrelationships of Brachythoraci. Zool J Linn Soc, 176: 806–834