Redescription of *Yinostius major* (Arthrodira: Heterostiidae) from the Lower Devonian of China, and the interrelationships of Brachythoraci

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*Yinostius major* is a heterostiid arthrodire (Placodermi) from the Lower Devonian Jiucheng Formation of Yunnan Province, south-western China. A detailed redescription of this taxon reveals the morphology of neurocranium and visceral side of skull roof. *Yinostius major* shows typical heterostiid characters such as anterodorsally positioned small orbits and rod-like anterior lateral plates. Its neurocranium resembles those of advanced eubrachythoracids rather than basal brachythoracids, and provides new morphological aspects in heterostiids. Phylogenetic analysis based on parsimony was conducted using a revised and expanded data matrix. The analysis yields a novel scenario on the brachythoracid interrelationships, which assigns Heterostiidae (including *Heterostius ingens* and *Yinostius major*) as the sister group of *Dunkleosteus amblyodoratus*. The resulting phylogenetic scenario suggests that eubrachythoracids underwent a rapid diversification during the Emsian, representing the placoderm response to the Devonian Nekton Revolution. The instability of the relationships between major eubrachythoracid clades might have a connection to their longer ghost lineages than previous scenarios have implied.

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INTRODUCTION

The Arthrodira Woodward, 1891 is the largest and most diverse group within the Placodermi McCoy, 1848 (Carr, 1995; Young, 2010). The morphological disparity of arthrodirines is perhaps best illustrated by the Heterostiidae Jaekel, 1903, an enigmatic arthrodire taxon known for its large body size and extremely extended anterior lateral plates. The type genus of the family, *Heterostius* Asmuss, 1856, was among the first group of early vertebrates to be described scientifically. The highly visible, large bony plates from the soft matrix found in the Baltic states had long been noted by early palaeontologists. However, they were often misidentified and given names such as *Ichthyosauroides* Kutorga, 1835, *Astroplepis asmussi* Agassiz, 1844–45 and *Chelonicthys asmussii* Agassiz, 1844–45, Asmuss (1856) for the first time referred these Baltic specimens to fish correctly, and named them *Heterostius* and *Homostius*, respectively, under several specific names. Shortly thereafter, Pander (1857) gave a more detailed description of the Baltic species of *Heterostius* including a reconstruction of part of the head and thoracic armour.

Woodward (1891) redefined *Chelonicthys asmussii* as *Heterosteus asmussi*. Subsequently, the two names ‘*Heterostius’* and ‘*Heterosteus’* seemed to be used interchangeably. To give an incomplete list of examples, the name ‘*Heterosteus’* was applied in Heintz (1928), Denison (1978, 1984) and Janvier (1996), while ‘*Heterostius’* was applied in Heintz (1930), Gross (1933), Stensiö (1963)

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plates are fused. Yinosteus genus to the anterior dorsolateral plate, and possibly belongs or lateral plate, which is integrated but not fused to (Ørvig, 1969: fig. 4C) should be the extended anteri-longer central plates, thinner dermal bones, and much having a shorter and broader skull roof, broader and

Heintz (1928, 1930) described the Baltic specimens of Heterostius in detail. Gross (1933) described a heterostiid anterior lateral plate from Sötenich, Germany, and assigned it to Heterostius. Ørvig (1969) erected the second heterostiid genus, Herasmius, from the Wood Bay Group (upper Lower Devonian or lower Middle Devonian) in Spitsbergen. The only species of the genus, Herasmius granulatus, is represented by an incomplete skull roof. Herasmius granulatus Ørvig, 1969 differs from Heterostius ingens Asmuss, 1856 in having a shorter and broader skull roof, broader and longer central plates, thinner dermal bones, and much finer tubercular ornaments. The unidentified plate (Ørvig, 1969: fig. 4C) should be the extended anteri-or lateral plate, which is integrated but not fused to the anterior dorsolateral plate, and possibly belongs to Herasmius granulatus. In Heterostius ingens the two plates are fused.

Wang & Wang (1984) reported the third heterostiid genus Yinosteus from the South China block, which represents the first heterostiid outside Euramerica and illustrates the wide distribution of the group. The fusion of the dermal plates and relatively extensive ossification compared with most other brachythoracics suggest that the holotype of Yinosteus major Wang & Wang, 1984 belongs to an adult individual. Yinosteus differs from Heterostius and Herasmius in having a smaller body size, proportionately broader nuchal plate, larger nuchal gap and coarser tubercular ornaments. Part of the description in Wang & Wang (1984) needs to be properly illustrated. Also, characters that are phylogenetically informative were not fully exploited.

The members of the Heterostiidae show similarities to the basal brachythoracid Homostiidae Jaekel, 1903, such as the large body size, anteriorly placed orbits, elongated occipital region, anteriorly extended anterior lateral plate and reduction of ventral thorac-ic armour. However, heterostiids also resemble the ad-vanced eubrachythoracics in the position of the posterolateral corner of the skull roof, and the highly developed posterior carinal process of the ventral keel of the median dorsal plate (Stensiö, 1963; Denison, 1978; Young, 1981; Zhu & Zhu, 2013).

This mosaic character complement of heterostiids has resulted in competing hypotheses of their phylogenetic assignment. Stensiö (1963) discussed Heterostius in the chapter on pachyosteomorphs. However, he stated that Heterostius may turn out to be a coccosteomorph, based on its elongated occipital region shared with Homostius, which he assigned into Coccosteomorphi Stensiö 1944. Denison (1978) considered Heterostiidae as the sister group of all brachythoracids, although he acknowled- edged that the thoracic armour of Heterostiidae resembles that of Pachyosteina. He later moved the taxon to a higher phylogenetic position by including it in Brachythoraci Gross, 1932 (Denison, 1984), partly fol-low ing Young (1981), who provided a revised cladogram showing heterostiids among basal brachythoracics. Janvier (1996) described Heterostiidae as a eu brachythoracid taxon, but beyond that is of uncertain phylogenetic position.

In the first published attempt to include any heterostiid in a computerized analysis of brachythoracid phylogeny (Zhu & Zhu, 2013), Heterostius ingens is assigned to a much more crownward position. It is nested within Dunkleosteidae Stensiö, 1963, being the sister group of Dunkleosteus Lehman, 1956. However, the morphological evidence that supports this scenario is mostly confined to the external aspects of the skull roof.

Here we provide a detailed redescription of the holotype of Yinostius major, which yields new phylogenetically significant information, especially that of the neurocranium morphology. We then conduct an updated phylogenetic analysis, which for the first time includes basal brachythoracids in the ingroup. Also, new characters are defined based on the comparative anatomy of arthrodires, with particular emphasis on the visceral surface of the skull roof and neurocranium morphology. With a revised data matrix, we hope to render a more convincing scenario that could lead to a better understanding of not only the position of heterostiids, but also the brachythoracid phylogeny as a whole.

GEOLOGICAL BACKGROUND

The holotype material of Yinosteus major was collected from black shale near Wuding in 1979 (Fig. 1). The horizon was identified by Wang & Wang (1984) as the Black Shale Member of the Middle Devonian Haikou Formation. Shortly thereafter, Wang (1984) included the horizon within the newly erected Jiucheng Formation and maintained its Middle Devonian diagno-sis, which was supported by Liu (1994). The dating of the Jiucheng Formation was modified by Wang & Zhu (1995) to be late Emsian, Early Devonian, under the following arguments: first, the Jiucheng Formation and the Pojiao Formation below it were continuously deposited, and the latter is dated to be early Emsian based on the invertebrate evidence; second, the fish fauna from the Jiucheng Formation is comparable with European and Australian Emsian faunas.


**MATERIAL AND METHODS**

**ABBREVIATIONS**

*Institutional abbreviations*

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

*Anatomical abbreviations*

ADL, anterior dorsolateral plate or its corresponding portion of the anterior dorsolateral plate and anterior lateral plate complex; ADL-AL complex, anterior dorsolateral plate and anterior lateral plate complex; AL, anterior lateral portion of the anterior dorsolateral plate and anterior lateral plate complex; btr.sh, basitrabecular shelf; C, central plate or its impression on the neurocranium; c.p, posterior corner of the skull roof; ch.pr.sv, channel for the supravagal process of the neurocranium; d.end, endolymphatic duct; f.d.end, impression of the endolymphatic duct on the visceral surface of the skull roof; f.dm, median subnuchal depression; f.laf, impression of the lateral articular fossa for dermal neck joint; f.lcp, impression of the lateral consolidated part of skull roof; f.o, neurocranium fonsel; fo.pi, pineal fossa; fo.sg, subglenoid fossa; f.ppt, impression of the pineal pit; f.pr.pop, impression of the posterior postorbital process of the neurocranium; f.pr.pto, impression of the postocular ventral process of the skull roof; f.pr.sv, impression of the supravagal process of the neurocranium; f.pro.dpr, impression of the preorbital dermal process of the preorbital plate; f.pt.u, impression of the nuchal paired pits on the neurocranium; f.pto.dpr, impression of the postorbital dermal process of the postorbital plate; f.sov, impression of the supraorbital vault; f.th.n, impression of the posterior transverse nuchal thickening; f.th.pi, impression of the visceral thickening of the pineal plate; fr.ADL, fractured anterior dorsolateral plate; fr.MD, anterior corner fractured and separated from the median dorsal plate; gc, glenoid condyle; g.Nu, nuchal gap; laf, lateral articular fossa for dermal neck joint; lcp, lateral consolidated part of the skull roof; M, marginal plate; MD, median dorsal plate; MD.oa, overlap area of the median dorsal plate; orb, orbit; Nu, nuchal plate or its impression on the neurocranium; pca, posterior carinal

process of median dorsal keel; PDL, posterior dorsolateral plate; Pi, pineal plate; PL, posterior lateral plate; PM, postmarginal plate or its impression; PNu, paranuchal plate or its impression on the neurocranium; ppt, pineal pit; pr.ant, antorbital process of the neurocranium; pr.ect, ethmoid process; pr.gl, occipital glenoid process; pr.IX, neurocranium process that bears the glossopharyngeus canal ventrally; pr.mp, posterior median process of the nuchal plate or its impression; Pro, preorbital plate; pr.opa, occipital pararticular process; pr.poa, anterior postorbital process of the neurocranium; pr.pop, posterior postorbital process of the neurocranium; pr.pto, postocular ventral process of the skull roof; pr.sg, subglenoid process; pr.so, supraorbital process of the neurocranium; pr.sv, supravagal process of the neurocranium; pro.dpr, preorbital dermal process of the preorbital plate; Psp, parasphenoid; Pto, postorbital plate; pt.u, nuchal paired pits on the neurocranium; pt.o, postocular ventral process of the postorbital plate; R, rostral plate; r.sc, external ridge of the posterior semi-circular canal; ScI, sclerotic plate; sov, supraorbital vault; th.pi, the visceral thickening of the pineal plate.

**Phylogenetic abbreviations**
CI, consistency index; L, length of trees (in evolutionary steps); n, number of trees; RI, retention index.

**SYSTEMATIC PALEONTOLOGY**
**Placodermi** McCoy 1848
**Arthrodira** Woodward, 1891
**Brachythoraci** Gross, 1932
**Family Heterodeidae** Jaekel 1903
*Type genus: Heterostius* Asmuss, 1856.

*Diagnosis:* Moderately to very large arthrodires with the cranial and trunk shields broad and dorso-ventrally compressed. The skull roof narrows anteriorly, and the posterolateral corners of the skull roof are in line with the posterior margin. The orbits are small, anterodorsally positioned. The dermal plates on the posterior part of the skull roof are moderately long, while those on the anterior part are short. The condyles of the cranio-thoracic joint are strongly developed, but not transversely elongated. The lateral wall of the thoracic armour are much reduced, the antero- or lateral plate is fused with the anterior dorsolateral plate. The anteroventral part of the anterior lateral plate develops into an elongated, rod-like process. The ventral thoracic armour is reduced to a single plate that extends far anteriorly under the head.

**YINOSTIUS Wang & Wang, 1984**

*Type and only species: Yinostius major* Wang & Wang, 1984

*Diagnosis:* As for the type and only known species.

**Yinostius major** Wang & Wang, 1984

*Holotype:* Near-complete head and thoracic armour, slightly displaced but all plates occur on one slab (IVPP V7142, Fig. 2).

*Locality and horizon:* Wuding, Yunnan Province, China; Jiucheng Formation, Emsian, Lower Devonian.

*Emended diagnosis:* Medium to moderately large arthrodire, with the median dorsal plate having an estimated length of 16 cm. The skull roof shows typical heterostiid characters such as anteriorly tapered outline, anterodorsally positioned small orbits and posteriorly positioned posterolateral corners. The neurocranium resembles that of eubrachythoracids in the posteriorly positioned pineal foramen, long and narrow orbitotemporal region, laterally expanded supravagal process, and absence of subnasal shelf. The median dorsal plate is short and broad, with a length/breadth ratio of 0.52. The posterior carinal process of the median

![Figure 2. Yinostius major. Holotype IVPP V7142. Scale bar = 5 cm.](image-url)
dorsal plate is highly developed. The rod-like anterior or lateral and the anterior dorsolateral plates are completely fused to form a complex, with a spherical glenoid condyle. The dermal ornament consists of coarse tubercles.

MORPHOLOGICAL DESCRIPTION

SKULL ROOF

The skull roof is roughly isosceles trapezium in shape, with its posterior margin about four times as broad as its anterior margin. The posterolateral corner of the skull roof corresponds to the lateral corner of the postmarginal plate (PM; Figs 3B, 5, 6D, E). The corner is extremely posteriorly positioned to be behind the foremost point of the nuchal gap and the articular fossa for the neck joint, as in some advanced pachyosteomorphs, such as *Gorgonicthys clarki* Claypole, 1892 (Stensiö, 1963: fig. 112B). In *Heterostius ingens* (Heintz, 1930: fig. 2) and *Dunkleosteus intermedius* (synonymized to *D. terrelli* Newberry, 1873, see Denison, 1978) (Stensiö, 1963: fig. 112A) this corner is approximately level with the foremost point of the nuchal gap. Posteriorly, the lateral parts of the skull roof are curved downward, and the posterolateral corner corresponds to the subglenoid fossa on the visceral side of the ADL-AL complex (fo.sg, Fig. 6C–E) when articulated. We flatten the curving in the attempted reconstruction of the skull roof (Fig. 6D) for a better display of the neck articulation. The reconstructed skull roof of *Yinosteus major* is nonetheless still longer and narrower than those of *Heterostius ingens* and *Herasmius granulatus*.

The orbit (orb, Figs 3B, 5) is small and anteriorly placed, as in other heterostiids. The highly developed preorbital (pro.dpr, Fig. 3B) and postorbital dermal processes (pto.dpr, Fig. 3B) comprise approximately two-thirds of the orbital circle, indicating a dorsally placed orbit. The majority of brachythoracids have laterally positioned orbits, with the exception of *Homostius sulcatus* Kutorga, 1837, in which the preorbital and postorbital dermal processes are butted together to encircle the dorsally positioned orbit entirely (Heintz, 1934: fig. 1). However, this situation is not shared by other homostiids, such as *Antineosteus lehmani* Lelièvre, 1984. Dorsally positioned orbits might reflect an adaption to benthic living in parallel.

The left sclerotic ring is preserved in internal mould. The right sclerotic ring (Scl, Figs 5, 6D) is preserved but its anterior part is embedded deep in the matrix.

**Figure 3.** *Yinostius major.* A, latex peel of the holotype; B, interpretation of the latex peel. The boundaries of fragmental parts are shown as dotted lines. ADL-AL complex, anterior dorsolateral plate and anterior lateral plate complex; f.pr.pop, impression of the posterior postorbital process of the neurocranium; f.pr.sv, impression of the supravagal process of the neurocranium; fr.ADL, fractured anterior dorsolateral plate; fr.MD, anterior corner fractured and separated from the median dorsal plate; laf, lateral articular fossa for dermal neck joint; lcp, lateral consolidated part of the skull roof; MD, median dorsal plate; MD oa, overlap area of the median dorsal plate; pca, posterior carinal process of median dorsal keel; PDL?, possible posterior dorsolateral plate; PL?, possible posterior lateral plate; PM, postmarginal plate; pr.ppto, postocular ventral process of the skull roof; pro.dpr, preorbital dermal process of the preorbital plate; pt.u, nuchal paired pits on the neurocranium; pto.dpr, postorbital dermal process of the postorbital plate; sov, supraorbital vault; th.pi, the visceral thickening of the pineal plate. Scale bar = 5 cm.

The detail of the sclerotic ornaments is unknown, as only the visceral surface of the sclerotic plates is visible. A gap between the two preorbital dermal processes represents the rectangle-shaped rostral plate, which is not preserved. It is unlikely that the rostral is preserved in V7142 as described by Wang & Wang (1984), given that the preserved neurocranium is lacking a rhinocapsule normally associated with the rostral plate. The anterior-most impression along the midline (‘rostral’ in Wang & Wang, 1984) is here interpreted as left by visceral thickening of the pineal plate (th.pi, Fig. 3B; f.th.pi, Figs 4, 5) and the pineal pit (ppt, Fig. 3B; f.ppt, Figs 4, 5). The fractured lateral margin of the impression was produced when the pineal plate was peeled away from the neurocranium. The visceral thickening of the pineal plate resembles those of most pachyosteomorphs (e.g. Dunkleosteus ‘intermedius’, Stensiö, 1963: fig. 112A) in its narrow outline. In basal (e.g. Dhanguura johnstoni Young, 2004) and coccosteomorph (e.g. Compagopiscis croucheri Gardiner & Miles, 1994) brachythoracids this thickening is mostly short and broad.

The supraorbital vault is preserved as an impression on the natural mould of the skull roof (sov, Fig. 3B; f.sov, Fig. 5). It is moderately developed, wider than that of the basal brachythoracids such as Holonema westolli Miles, 1971 and Buchanosteus confertituberculatus Young, 1979, but is not as well developed as that of most eubrachythoracids in terms of both breadth and depth.

The paired impressions immediately posterior to the supraorbital vaults were left by the postocular ventral processes of the skull roof (pr.pto, Fig. 3B; f.pr.pto, Fig. 5). Judging from the impressions, the postocular ventral process is well developed, but not as prominent as that in taxa such as Dunkleosteus raveri Carr & Hlavin, 2010. The mould of the skull roof in this region suggests that the triangular depression posterior to the supraorbital vault in taxa such as Dhanguura johnstoni (Young, 2004: fig. 4) is missing in Yinosteus.

Posterior to the postocular ventral processes are the paired lateral consolidated parts of the skull roof (lc.p, Fig. 3B; f.lcp, Fig. 5). They are represented by two elongated impressions along the lateral margin of the mould, extending from the posterior wall of the supraorbital vault to the posterolateral corners of the skull roof. The consolidated parts are simple thickenings, lacking the lateral and mesial grooves along the lateral margin of the skull roof (Young, 2004: fig. 4) in Dhanguura johnstoni.

Judging from the mould of the skull roof, a well-developed transverse nuchal thickening (f.th.n, Fig. 5) runs continuously along the entire posterior skull roof border, reaching as far as the two posterolateral corners of the skull roof. A pair of nuchal pits (pt.u, Fig. 3B; f.p.t.u, Fig. 5) is present anterior to the middle portion of the nuchal thickening. The pits are represented by two circular concave regions that open ventrally and are well separated by a median septum. This septum does not extend continuously to the median posterior nuchal process (pr.mp, Fig. 5) at the middle of the posterior nuchal border.

The articular fossa (laf, Fig. 3B; f.laf, Fig. 5) for the neck articulation, similar to that of Heterostius ingens,
is extremely laterally positioned, closer to the posterolateral corner of the skull roof than that of most other arthrodires. The articular fossa is represented by a simple and relatively small facet, preserved as an impression. The para-articular process is missing in *Yinosteus major*, or not developed enough to leave any impression.

Only limited sutures of the plates are discernible from their impressions on the neurocranium, including the suture between the two central plates, the anterior boundary of the nuchal plate, the anterior boundary of the paranuchal plate, the suture between the nuchal and paranuchal plates, and the mesial boundary of the postmarginal plates. Note that these sutures are the visceral ones and cannot be readily used to infer the external geometry of the skull roof plates. For example, the visceral anterior margin of the nuchal plate is convex in most brachythoracids, while the external anterior margin of the nuchal plate can be convex, straight or concave.

Even so, it is feasible to infer the nuchal or skull roof occipital elongation from the visceral suture between the nuchal and central plates. In *Yinosteus major*, the length ratio between the nuchal plate in visceral view and the skull roof is 0.54, approximately the same proportion as that of *Heterostius ingens*, in which the length ratio between the nuchal plate in external view and the skull roof is 0.50 (measured from Heintz, 1930: fig. 2). The above two length ratios representing the extent of the elongation of the heterostiid nuchal plates are significantly smaller than that of *Homostius sulcatus*, in which the length ratio between the nuchal plate in visceral view and the skull roof is 0.67 (measured from Heintz, 1934: figs 1, 2). In comparison, in *Coccosyteus cuspidatus* Miller, 1841 the length ratio between the nuchal plate and the skull roof is 0.39 and 0.46, in external and visceral view, respectively (Miles & Westoll, 1968: fig. 2). In *Dunkleosteus ‘intermedius’*, the ratio is 0.28 in external view and 0.32 in visceral view (Stensiö, 1963: figs 99A, 112A).

**NEUROCRANIUM**

The neurocrania of brachythoracids are usually poorly ossified. Only a few complete or near-complete brachythoracid neurocrania (Stensiö, 1963, 1969; Young, 1979) and several partly preserved ones (Dennis & Miles, 1979b, 1981; Long, 1988a; Otto, 2005) are described. The most well-preserved neurocranium among brachythoracids, that of *Tapinoestes heintzi*, lacks its occipital part. It is rare that the entire profile of the neurocranium is preserved as in *Yinosteus major*.

Only the dorsal aspect of the neurocranium can be observed in *Yinosteus major*. The neurocranium is flat and large. The endoskeletal rhinocapsule is lost along with the rostral plate. The M-shaped anterior margin of the neurocranium possibly outlines the area for the paired olfactory tracts, olfactory bulbs and extracribrosal regions of postnasal walls. The antorbital process of the neurocranium (pr.ant, Figs 5, 8C) is more developed than that of most arthrodires with neurocrania preserved, corresponding to the highly developed preorbital dermal process, which in turn reflects the mesial position of the eye capsule.
At the level of the supraorbital dermal process, the neurocranium is poorly preserved with a large area cracked and missing. There is no evidence of a subocular process. If the subocular process is not protruding laterally, it is invisible in dorsal view as in our specimen.

At the right side where the missing area is smaller, the neurocranium shows a dorsolateral process. This process is located posterior to the level of the postocular ventral process of the skull roof. We interpret this process as the supraorbital process sensu Stensiö, 1963 (pr.so; Figs 5, 8C). The process is represented by a vestigial swelling, similar to that of Tapinosteus heintzi Stensiö, 1963 and Dunkleosteus ‘intermedius’ (Stensiö, 1963: figs 47A, 89A).

Posterior to the supraorbital process, the trabecular structure of the neurocranium emerges laterally in dorsal view. Stensiö (1963) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf, a term borrowed from chondrichthyan cranial anatomy, while Dupret (2010) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf, a term borrowed from chondrichthyan cranial anatomy, while Dupret (2010) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf, a term borrowed from chondrichthyan cranial anatomy, while Dupret (2010) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf, a term borrowed from chondrichthyan cranial anatomy, while Dupret (2010) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf, a term borrowed from chondrichthyan cranial anatomy, while Dupret (2010) named the laterally protruding trabecular region of arthrodires as the basitrabecular shelf.

The posterior right part of the neurocranium is mostly concealed by the displaced ADL plate (ADL, Fig. 5). The maximum breadth measures 31 cm. The maximum length along the midline of the plate (not counting the protruding carinal process) measures 16 cm, giving a length/breadth ratio of 0.52. In comparison, the MD of Homostius sulcatus has a length/breadth ratio of 0.41 (measured from Heintz, 1934: fig. 32).

The general shape of the plate resembles that of Heterostius ingens and many pachyosteomorphs. The plate is slightly arched. Its anterior margin is strongly concave, corresponding to the large nuchal gap. The lateral margin is also slightly concave, resulting in lat-
erally extended antero-lateral corners. The posterior margin is roughly circular and without a posterior spine. The dorsal surface of the plate is ornamented with coarse tubercles. The visceral aspect is unknown, except the carinal process, which extends beyond the posterior margin of the dorsal surface. This situation resembles advanced pachyosteomorphs such as *Dunkleosteus terrelli* and differs from that of *Homostius sulcatus*, in which the ventral keel is protruding anteriorly rather than posteriorly. The posteriorly protruding part of the carinal process measures 7 cm in length. The posterior face of the carinal process is smooth and convex, not spatulate. No dorsal branch of the main lateral line is visible.

**Anterior dorsolateral plate and anterior lateral plate complex (ADL-AL complex, Figs 3B, 6B–D)**

The ADL and AL plates of *Yinosteus major* are fused, as in *Heterostius ingens*. Both sides of the ADL-AL complex are preserved as the moulds: the left side is near-complete, while the right is fractured, with its upper part displaced to overlap the lateral corner of the skull roof (fr.ADL; Figs 3B, 5, 6B), and with an area overlapped by the right anterior lateral corner.
of the MD (MD.oa; Figs 3B, 6B). The rest of the right ADL-AL complex is located at the right side of the MD, with most of the anterior rod-like extension missing (right ADL-AL complex, MD.oa; Fig. 3B).

The visceral surface of the left complex features a fossa just below the glenoid condyle (fo.sg; Fig. 6C), as well as a ridge (rdg.ADL-AL; Fig. 6C). In life the fossa is so positioned that it could receive the posterolaterally extended posterolateral corner of the skull roof, when the skull roof is raised and the posterolateral corner is depressed (Fig. 6D). In Dunkleosteus terrelli, a similar subglenoid fossa is present, but in this case it is in the position to receive the highly developed para-articular process on the paranuchal plate (Dinichthys Newberry, 1868 in Heintz, 1932: fig. 73).

The ridge on the visceral surface of the left complex probably represents the position where the ADL and AL are sutured. This is based on the observation that a similar ridge is present in many euibrachythoracids such as Eastmanosteus calliaspis Dennis-Bryan, 1987 and Dunkleosteus terrelli (Heintz, 1932: fig. 52) in which the area posterior to the ridge is the overlapped area for the ADL.

The ADL-AL complex of Yinosteus major resembles that of Heterostius rhenanus Gross, 1933 in possessing a highly developed glenoid condyle, a fossa anterior to the glenoid condyle and a ridge along the rod-like extension of the AL. These distinctive states are possibly the synapomorphies of Heterostiidae.

The dural neck joints in arthrodires underwent considerable evolutionary modifications and hold phylogenetic significance (Miles, 1969; Miles & Young, 1977). In many basal brachythoracids such as Parabuchanosteus murrumbridgeensis White, 1952, the movement of the neck articulation is confined by the presence of both a para-articular process and a subglenoid process (Jarvik, 1980: fig. 295). In most euibrachythoracids such as Compagopiscis croucheri (Gardiner & Miles, 1994: fig. 6) and Dunkleosteus terrelli (Heintz, 1932: fig. 68: pp. 70, 71), the condyle is directed inward to form a traverse cylinder, and is articulated to the matching rectangular articular facet, allowing limited dimension of movement. In heterostiids, the condyle is much more spherical without limiting the para-articular process, the most kinetic structure among arthrodire neck joints, which might be linked to the peculiar feeding mechanism in Heterostiidae.

Posterior dorsolateral plate (PDL?; Fig. 3)
A mould of a triangular plate posterior to the mould of the MD is interpreted as the posterior dorsolateral plate. It is poorly preserved as a natural mould of its external surface, providing limited morphological information. Tubercles are visible and are significantly finer than those on the median dorsal plate and the posterior lateral plate.

Posterior lateral plate (PL?; Fig. 3)
An indistinct triangular mould next to the PDL is interpreted as the posterior lateral plate. It is poorly preserved and the current shape may not represent the actual outline of the plate. Coarse tubercles are visible.

DISCUSSION
THE DIMENSION OF THE OCCIPITAL REGION OF NEUROCRANIUM IN ARTHRODIRES

In the gnathostome neurocrania, the occipital region is located posterior to the otic–occipital fissure (Jarvik, 1980). In those taxa that lack the otic–occipital fissure, the boundary between otic and occipital regions is marked by the aperture of the vagus canal, as this aperture always corresponds to the otic–occipital fissure whenever the latter is present (Schultz, 1993). However, in Yinosteus major and many other arthrodires, the otic–occipital fissure is not discernible. In this case, the impression of the endolymphatic duct can be used to mark the otic–occipital boundary.

In arthrodires, as in most other placoderms, the endolymphatic duct penetrates out of the neurocranium and extends posteriorly into the skull roof. The otic region is often swelled to accommodate the labyrinth, forming a posterior wall. This posterior wall is deduced to be the posterior end of the otic region. When the endolymphatic duct penetrates this wall posterodorsally, the aperture marks the otic–occipital boundary. As the neurocranium is attached tightly to the skull roof, the beginning of the endolymphatic duct in the skull roof is in approximately the same position with the aperture of the endolymphatic duct in the neurocranium. As a result, when other landmarks, namely the otic–occipital fissure or the aperture of the vagus canal are not available, the beginning of the endolymphatic duct on the visceral surface of the skull roof can be used to denote the otic–occipital boundary in the neurocranium.

The elongated posterior part of the skull roof, especially the long nuchal plate, was considered to be a synapomorphy shared by heterostiids and homostiids (Denison, 1978; Young, 1981). As stated above, the nuchal plate in heterostiids is significantly shorter in proportion than that in most homostiids. Moreover, in homostiids such as Antineosteus lehmani (Fig. 8B), the beginning of the endolymphatic duct on the visceral surface of the skull roof is close to the anterior extremity of the nuchal plate, implying that the occipital part of the neurocranium in homostiids is elongated, as well as the nuchal plate. In most other brachythoracids such as Coccosteus cuspidatus, the be-
ginning of the endolymphatic duct on the visceral surface of the skull roof is also close to the anterior extremity of the nuchal plate (Fig. 8C), implying that both the occipital part of the neurocranium and the nuchal plate are not elongated. In heterostiid Yinosteus major, the nuchal plate is considerably elongated, but the beginning of the endolymphatic duct on the visceral surface of the skull roof is significantly posterior to the anterior extremity of the nuchal plate, indicating a normalized occipital part of the neurocranium (Fig. 8A).

Based on the above observation, the elongation of the posterior part of the skull roofs in heterostiids and homostiids can be independently acquired, and whether it is a synapomorphy shared by the two groups needs to be tested by a parsimony analysis incorporating additional characters. The above observation also demonstrates that among placoderms the visceral aspect of the skull roof can reveal important morphological information regarding the neurocranium.

**COMPARISON OF EXTERNAL ASPECTS OF THE NEUROCRANIA IN ARTHRODIRE**

The complexity of the vertebrate neurocrania yields a considerable amount of morphological characters for phylogenetic analyses (Stensiö, 1925, 1963; Young, 1979, 1980; Maisey, 2005; Brazeau, 2009; Davis, Finarelli & Coates, 2012). However, in brachythoracid arthrodires the neurocranial characters have received less attention phylogenetically. This is due to the fact that few brachythoracids possess a well-preserved neurocranium, and a lack of comparisons between available brachythoracid neurocrania.

The neurocranium of Yinosteus major is preserved with its dorsal outline. Comparison of the current specimen with other published information on arthrodire neurocrania can shed light on the character evolution of the brachythoracid neurocranium, contributing to a better supported scenario of brachythoracid phylogeny. Taxa used in the comparison include: 'phlyctaenid' Dicksonosteus arcticus Goujet, 1975 as the outgroup of brachythoracids, Parabuchanosteus murrumbidgeenis as the most thoroughly studied basal brachythoracid, Yinosteus major, Tapinosteus heintzi with neurocranium and brain cavity studied using serial grinding, and another eu brachythoracid taxon Trematosteus fontanellus.

The following characters that are potentially able to contribute to a better-supported phylogenetic scenario can be identified from the comparison.

1. The presence or absence of the subnasal shelf. In Dicksonosteus arcticus and Parabuchanosteus murrumbidgeenis, the ventral wall of the orbitotemporal extends anteriorly to develop a subnasal shelf, with a protruding ectethmoid processes that can be seen in dorsal view (pr.ect, Fig. 7A, B), while in Yinosteus major, Tapinosteus heintzi and Trematosteus fontanellus and all eubrachythoracids described to date the subnasal shelf is lost (Dennis & Miles, 1979b, 1981; Long, 1988a; Otto, 2005; Stensiö, 1963).

2. The position of the pineal foramen. In Dicksonosteus arcticus and Parabuchanosteus murrumbidgeenis, the pineal foramen is positioned between the ethmoid capsule and the anterior margin of the orbitotemporal (fo.pi, Fig. 7A, B), while in Yinosteus major, Tapinosteus heintzi and Trematosteus fontanellus, the pineal foramen is positioned posteriorly in the middle section of the orbitotemporal region (fo.pi, Fig. 7C–E).

3. The length/breadth ratio of the orbitotemporal. In Dicksonosteus arcticus and Parabuchanosteus murrumbidgeenis, the orbitotemporal is very short compared with the otic, and is broad when compared both with the otic and with the supraorbital vault beside it (Fig. 7A, B), while in Yinosteus major, Tapinosteus heintzi and Trematosteus fontanellus, the orbitotemporal is narrow and longitudinally comprises a significantly larger portion of the neurocranium (in the latter two taxa the elongation of orbitotemporal may be linked to the large orbit, but Yinosteus major possesses both a small orbit and an elongated orbitotemporal, Fig. 7C–E).

4. The longitudinal proportion of the occipital. In Dicksonosteus arcticus (Fig. 7A), as well as other basal arthrodires, the occipital is short, while in most brachythoracids, such as Parabuchanosteus murrumbidgeenis, Yinosteus major and Tapinosteus heintzi, the occipitals are elongated (Fig. 7B–D). In Trematosteus fontanellus and some aspinothoracids, the occipital is shortened (Fig. 7E), presumably an autapomorphy in Aspinothoraci sensu Miles and Dennis (1979).

5. Shape of the supravagal process outline. In Dicksonosteus arcticus the supravagal process is approximately right-angled (pr.sv, Fig. 7A), while in brachythoracids the supravagal process is more acute-angled. Among brachythoracids, Parabuchanosteus murrumbidgeenis possesses a relatively blunt supravagal process (pr.sv, Fig. 7B), which in Trematosteus fontanellus (pr.sv, Fig. 7E) is extremely acute. The shape of the supravagal process is possibly linked to the shape of the nuchal plate.

6. The presence or absence of a neurocranial fontanelle. In several aspinothoracids the neurocranium possesses one or more dorsal fontanels (fo, Fig. 7D, E). The lack of a fontanelle in basal brachythoracids such as Parabuchanosteus murrumbidgeenis and in basal arthrodires such as Dicksonosteus arcticus indicates that the fontanelle in advanced
eubrachythoracids is not homologous to the similar fontanelle in elasmobranchs, unless the elasmobranchs originated from Eubrachythoraci, as implied by Stensiö (1963, 1969).

Based on the above comparison, the neurocranium of *Parabuchanosteus murrumbidgeensis* possesses typical brachythoracid characters such as the non-forked posterior postorbital process and elongated occipital, as well as basal arthrodire characters such as the presence of the subnasal shelf and the short and broad orbitotemoral. The neurocranium of *Yinosteus major* resembles those of the typical eubrachythoracids and differs from those of basal brachythoracids in the absence of a subnasal shelf, long and narrow orbitotemoral and posteriorly positioned pineal foramen.

**Figure 7.** Comparison of five arthrodire neurocrania in dorsal view. A, *Dicksonosteus arcticus*, after Goujet (1984); B, *Parabuchanosteus murrumbidgeensis*, after Young (1979); C, *Yinosteus major*; D, *Tapinosteus heintzi*, after Stensiö (1963); E, *Trematosteus fontanellus*, after Stensiö (1963). The vertical bar shows the longitudinal proportions of the various regions of the neurocranium, with the black part corresponding to the occipital region, and the small circle representing the location of the pineal foramen. btr.sh, basitrabecular shelf; d.end, endolymphatic duct; f.dm, median subnuchal depression; fo, neurocranium fontanel; fo.pi, pineal fossa; pr.ant, antorbital process of the neurocranium; pr.ect, ectethmoid process; pr.gl, occipital glenoid process; pr.IX, neurocranium process that bears the glossopharyngeus canal ventrally; pr.poa, anterior postorbital process of the neurocranium; pr.pop, posterior postorbital process of the neurocranium; pr.so, supraorbital process of the neurocranium; pr.sv, supravagal process of the neurocranium; r.sc, external ridge of the posterior semicircular canal. Not to scale.
PHYLOGENETIC ANALYSIS

The previous phylogenetic analyses of brachythoracids (Carr, 1991; Lelièvre, 1995; Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010; Zhu & Zhu, 2013) focused on eubrachythoracids and used basal brachythoracids such as Buchanosteus confertituberculatus as outgroups. Also, the characters in these analyses are mainly from skull roof and thoracic armour. We here perform a phylogenetic analysis based on an enlarged and revised data matrix, in which basal brachythoracids are included in the ingroup. The new matrix includes 60 taxa and 121 characters, in which 23 characters are new and are listed in Appendix 2.

The new matrix was treated with MESQUITE v. 2.73 (Maddison & Maddison, 2008). The analysis based on parsimony was performed with PAUP* v. 4.0b10 (Swofford, 2003) using the heuristic algorithm. Kujdanowiaspis podolica Brotzen, 1934 was designated the outgroup. We set 1000 random addition sequence replicates, and ‘maxtrees’ to ‘automatically increase’. The analysis gave 540 equally most parsimonious trees of 496 steps each (CI = 0.2843; RI = 0.6629). The strict consensus tree is presented in Figure 9. The synapomorphies listed in Appendix 4 were obtained under DELTRAN (delayed transformation) optimization. The Bremer decay indices were obtained using command files composed by TreeRot (Sorenson, 1999) in conjunction with the heuristic search algorithm in PAUP*.

Based on the analysis, 13 taxa are positioned between the outgroup Kujdanowiaspis podolica and the Eubrachythoracii Miles, 1971 (node 10, Fig. 9). We set node 2 to define Phlyctaenioidei Miles, 1973, and node 3 (including Homostius sulcatus plus Antineosteus lehmani and all the taxa crownward of them) to define Brachythoraci (node 3, Fig. 9), as it is the best supported node among the array (supported by nine synapomorphies and a Bremer decay index of 3).

Elvapis tuberculata Young, 2009, Dicksonosteus arcticus, Turrisaspis elektor Daeschler, Frames & Mullison, 2003, Groenlandaspis antarcticus Ritchie, 1975 and Holonema westolii are assigned in a polychotomy with Brachythoraci. The assignment of the williamsaspid Elvapis tuberculata agrees with Denison (1978) who placed Williamsaspidae White, 1952, then including only one species Williamsaspis bedfordi White, 1952, in the infraclass Phlyctaeniidae Miles, 1973, and disagrees with Young (2009) who suggested that the williamsaspid belong to the Brachythoraci. Also, the exclusion of taxa both from Groenlandaspidae Obruchev, 1964 and Holonematidae Obruchev, 1932 from Brachythoraci supports the scenario proposed by Denison (1978) and is contrary to the other arguments that the Holonematidae belongs to the Brachythoraci (Miles, 1971; Lelièvre, 1995).

Under the current scenario, Antineosteus lehmani, Homostius sulcatus, Buchanosteus confertituberculatus, Goodradigbeoon australianum White, 1978, Parabuchanosteus murrumbidgeeni, Dhanguura johnstoni, Gemuendenaspis angusta Traquair, 1903 and Xiangshuiosteus wui comprise the paraphyletic array of basal brachythoracids. Antineosteus lehmani and Homostius sulcatus are included in a monophyletic group (Fig. 9, node 4, supported by four synapomorphies and a Bremer decay index of 1) comparable to the family Homostiidae, supporting the original assignment of Antineosteus lehmani by Lelièvre (1984). The original identification of Dhanguura johnstoni as a homostiid by Young (2004) is not supported by the current analyses, despite several shared characters between them, such as the anteriorly pointed paranuchal plates. Buchanosteus confertituberculatus, Goodradigbeoon australianum and Parabuchanosteus murrumbidgeeni are placed in a monophyletic group (Fig. 9, node 6, supported by one synapomorphy and a Bremer decay index of 4), which can be compared with the superfamly Buchanosteoiidea Denison, 1978.
Xiangshuiosteus wui is assigned as the sister group of Eubrachythoraci. This assignment differs from both the original coccosteid assignment of Xiangshuiosteus wui by Wang (1992) and the dunkleosteid assignment by Zhu & Zhu (2013), and is better supported by the addition of new characters regarding the distinction between basal brachythoracids and eubrachythoracids.

Eubrachythoraci is traditionally subdivided into Coccosteomorphi and Pachyosteomorphi Stensiö, 1944, the latter being further subdivided into Dunkleosteoida and Aspinothoracidi sensu Miles & Dennis, 1979 (Carr, 1991; Gardiner & Miles, 1994; Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010). The previous analysis by Zhu & Zhu (2013) challenged the monophyly of Pachyosteomorphi in placing the Coccosteomorphi, rather than Dunkleosteoida, as the sister group of Aspinothoracidi. However, the low Bremer decay index and subset analyses indicate that this scenario is weakly supported and could be subject to further modifications. In the current analysis, the scenario of eubrachythoracid phylogeny resembles the traditional ones with both Coccosteomorphi (node 11, Fig. 9, supported by nine synapomorphies and a Bremer decay index of 1) and Pachyosteomorphi (node 27, Fig. 9, supported by three synapomorphies and a Bremer decay index of 1) being monophyletic. In the Pachyosteomorphi all the taxa crownward of Rhachiosteus pterygiatus Gross, 1938 are assigned to a monophyletic Dunkleosteoida (node 29, Fig. 9, supported by nine synapomorphies and a Bremer decay index of 1) and Aspinothoracidi (node 38, Fig. 9, supported by four synapomorphies and a Bremer decay index of 1), respectively.

With the addition of taxa in the current data matrix, the analysis yields a more detailed coccosteomorph phylogeny, subdividing Coccosteomorphi into two monophyletic groups that are comparable to the superfamily Coccosteoida Denison, 1978 and Incisocutoidea Trinajstic & Dennis-Bryan, 2009, respectively. The latter clade (node 17, Fig. 9, support-
ed by five synapomorphies and a Bremer decay index of 1) is in turn composed almost exclusively of taxa from the Gogo Formation with the only exception being Trematoosteus fontanellus, and all coccosteids morphs from the Gogo Formation in the current analysis are in turn included in Incisocutoidea. This scenario suggests the endemism of coccosteomorphs from the Gogo Formation, which make up the majority of arthrodires there. This argument also matches the general endemic nature of the Gogo vertebrate fauna (Long & Trinajstic, 2010; Trinajstic et al., 2014).

Coccosteoidae (node 12, Fig. 9, supported by five synapomorphies and a Bremer decay index of 1) is subdivided into two monophyletic groups, one (node 13, Fig. 9, supported by six synapomorphies and a Bremer decay index of 1) which includes Coccoosteus cuspidatus and several taxa that are traditionally assigned to the namesake Coccosteidae Traquair, 1888, namely Millerosteus minor Stensiö, 1959, Dickosteus throiplandi Miles & Westoll, 1963, Watsonosteus fletti Watson, 1992 and Protitanichthys rockportensis Eastman, 1907. Another monophyletic group (node 16, Fig. 9, supported by five synapomorphies and a Bremer decay index of 1) is composed of Plourdosteus canadensis Woodward, 1892, Janioosteus timanicus Ivanov, 1989 and Panxiososteus oculus Wang, 1979, and can be compared with the family Panxiososteidae Wang, 1979. When Wang (1979) erected this family, he considered it as ‘an intermediate between the Pholidosteidae and the Dinichthyidae’. Members of this family show a morphologically intermediate condition between coccosteids and dunkleosteids. This situation is demonstrated by the phylogenetic shift that Plourdosteus Örvig, 1951 has undergone. It was initially considered as a coccosteid with coccosteomorph characters such as a posteriorly enclosed pectoral fenestra (Stensiö, 1942; Örvig, 1951; Miles & Westoll, 1968). Vezina (1990) erected the family Plourdosteidae and placed it as the sister group of Dunkleosteidae. Gardiner & Miles (1994) and Long (1995) later assigned Plourdosteidae to Coccosteomorphi rather than Pachyosteomorphi. Carr & Hlavin (2010) proposed that Plourdosteus could be referred to a better-established Panxiososteidae, and placed the family as the most basal clade of Dunkleosteidae. In the current scenario, the phylogenetic position of Panxiososteidae is resolved as the sister group of Coccosteidae in Coccosteoidea, instead of being the most basal clade of Dunkleosteidae. The phylogenetically unstable condition of Panxiososteidae calls for further morphological description of Panxiososteus oculus and Plourdosteus canadensis.

Tapinosteus heintzi and a clade (node 40, Fig. 9, supported by three synapomorphies and a Bremer decay index of 1) containing three durophagous taxa from the Gogo Formation, namely Bruntonichthys multidentis Dennis & Miles, 1980, Bullerichthys fascidens Dennis & Miles, 1980 and Kendrickichthys cavernosus Dennis & Miles, 1980 are placed in the basal position of Aspinothoracidi. The newly added Melanosteus occitanus Lelièvre et al., 1987 is assigned as the sister group of Rhinosteus parvulus Jaekel, 1911. Together with Brachyosteus dietrichi Gross, 1932, Stenosteus angustopectus Carr, 1996, Gymnotrachelus hydei Dunkle & Bungart, 1939, Pachyosteus bulla Jaekel, 1903 and Heintzichthys gouldii Newberry, 1885 they compose a monophyletic group comparable to the family Selenosteidae Dean, 1901 (node 45, Fig. 9, supported by seven synapomorphies and a Bremer decay index of 1). The inclusion of Heintzichthys gouldii into Selenosteidae is in agreement with other analyses on the interrelationship of Aspinothoracidi (Carr & Hlavin, 2010; Rücklin, Long & Trinajstic, 2015). Whether Gorgonichthys clarki should be included in Selenosteidae can be left to future studies to answer.

The phylogeny of Dunkleosteidae is better resolved in the current analysis than in Zhu & Zhu (2013). Notable differences between current and previous scenarios include the assignment of Westralichthys uwagedensis Long, 1987 within a more advanced position, being the sister group of the clade (node 34, Fig. 9, supported by five synapomorphies and a Bremer decay index of 3) comprising Dunkleosteus terrelli, D. raveri, D. amblyodoratus, Heterostius ingens and Yinosteo major; and the assignment of Eastmanosteus calliaspis Dennis-Bryan, 1987 rather than Westralichthys uwagedensis, to the most basal position of Dunkleosteidae.

All members of Heterostiiidae are Early or Middle Devonian in age. The grouping of heterostids in the current scenario with Dunkleosteus, a Late Devonian and phylogenetically crownward genus, considerably extends the length of the ghost lineages in Dunkleosteidae. In light of the current scenario, the timing of the brachythoracid evolution (Fig. 10) shows a rapid evolutionary phase during the Emsian, Early Devonian, when the major eubrachythoracid clades emerged. The longer than previously conceived ghost lineages of eubrachythoracid clades partly explain the instability of the relationship between major eubrachythoracid clades, which is demonstrated by the low Bremer decay index support and the shifting scenarios between different analyses.

The eubrachythoracids possess distinctive features among placoderms such as laterally compressed body and reduced dermal shield, both suitable for a freeswimming nektonic lifestyle (Denison, 1978; Carr, 1995; Janvier, 1996). The emergence of this type of body plan corresponds to the so-called Devonian Nekton Revolution, triggered possibly by saturated demersal niches and by the flourishing of microplankton supplied by nutrients from the newly evolved terrestrial biomass (Klug et al., 2010). Both these events would have occurred during the Early Devonian. The earlier diversification of eubrachythoracid arthrodires indicates that
the placoderms, the dominant gnathostome group during the Early to Middle Palaeozoic, responded to environmental and ecological changes more rapidly than previous scenarios suggest.

CONCLUSIONS

The holotype of *Yinosteus major*, an Emsian heterostiid arthrodira from Wuding, Yunnan, China, shows previously undescribed neurocranial and visceral skull roof morphology. The exoskeleton of *Yinosteus major* shows typical heterostiid characters such as the anteriorly tapered skull roof, the small and anteriorly placed orbits, and the rod-like anterior lateral plates. The neurocranium resembles the advanced eubrachythoracids rather than the basal brachythoracids in the absence of the subnasal shelf, the posteriorly positioned pineal foramen, the long and narrow orbitotemporal region of the neurocranium and short occipital region of the neurocranium.
The occipital portion of the neurocranium in *Yinosteus major* is relatively short. This contrasts with the situation in the corresponding dermal bone, the elongated nuchal plate, which was previously considered as a possible synapomorphy shared with the basal brachythoracid homostiids.

The character evolution of the dorsal morphology in arthrodire neurocrania is summarized based on the comparison between five taxa including *Yinosteus major*. We recognize six new neurocranial characters that hold phylogenetic significance. With an expanded and revised data matrix, the current phylogenetic analysis yields a new scenario regarding brachythoracid phylogeny, in which Brachythoraci is composed of a paraphyletic array of basal taxa and a monophyletic Eubrachythoraci. Among the basal taxa, *Holonema westolli* and *Elvaspis tuberculata* were excluded from Brachythoraci. *Xiangshuiosteus wui* is placed as the sister group of Eubrachythoraci. Eubrachythoraci is divided into six monophyletic groups, namely Coccosteomorphi and Pachyosteomorphi. Coccosteomorphi is subdivided into Coccosteoeidea and Incisocutoidea. The majority of eubrachythoracids from the Gogo Formation are included in an endemic Incisocutoidea. Pachyosteomorphi is composed of *Rhachiosteus pterygiatus*, Dunkleosteoeidea and Aspinothoraci. Tapinosteus heintzi and a clade containing three durophagous taxa from the Gogo Formation are assigned a basal position of Aspinothoraci. Heterostiidae including *Heterostius ingens* and *Yinosteus major* are placed as the sister group of Dunkleosteus amblyodoratus.

When integrated into the chronontological framework, the current scenario shows that the major eubrachythoracid clades have significantly longer ghost lineages than previous scenarios would have shown, suggesting a rapid diversification phase of eubrachythoracids during Emsian times. The rapid diversification and long ghost lineage partly explain the instability of the relationship between major eubrachythoracid clades. The Early Devonian diversification of eubrachythoracids as nektonic predators and suspension feeders (Carr, 1991; Anderson et al., 2011) demonstrates that the placoderms may have responded to the Devonian Nekton Revolution more rapidly than previously thought.

The current study shows that the brachythoracid phylogeny benefits from a more comprehensive data matrix, with both new taxa and new characters. Visceral morphologies of the dermal bones were previously overlooked in several taxa with articulated specimens preserved. Recent advances in non-destructive technologies of fossil investigation, such as high-resolution computed tomography scanning and X-ray synchrotron radiation microtomography, have allowed researchers to extract further morphological information (Burrow, Jones & Young, 2005; Dupret et al., 2014; Gai & Zhu, 2014). The re-investigation of key taxa using these techniques is imperative for a better understanding of the evolution of brachythoracids, arthrodires and placoderms as a whole.

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REFERENCES


**APPENDIX 1**

**Data Matrix**

For characters 1–91 and characters 94–98, see Carr & Hlavin (2010); for characters 92 and 93, see Zhu Y-A. & Zhu M. (2013); for characters 99–121, see Appendix 2. The codings that differ from Zhu Y-A. & Zhu M (2013) are underlined.

**Antineosteus lehmani**

10000 0-100 00012 ?0101 01110 0-011 01010 00?? ?000 ???0?010 01110 00100 ????0 01010 00000 ????1 12001 -0?0 00001 00000 ?000 00??1 1

**Brachyosteus dietrichi**

11001 0-00(01) 21110 01100 10110 -201 11(01)1? 000?- 10-00 -?0?- 01111 11?10 01100 10101 ????- -0100 00-10 ??01 11201 -1110 11?11 01101 ?0?1! 00100 ?

**Bruntonichtys multidens**


**Buchanosteus confertituberculatus**


**Bullerichtys fasciendus**


**Camuropiscis laidlawi**

11110 10000 21111 1?11? 00010 11011 10002 101?0 0?011 1110? 71110 11??0 01101 00101 ?0?1?1 01000 00110 ?0??1 122- 00?0 11-01 00000 ???100 000-0 0
**APPENDIX 2**

**NEW CHARACTERS**

**SKULL ROOF**

99. Development of the crista supraethmoidalis at the visceral surface of the skull roof: underdeveloped, absent or present but not convergent in the midline (0); developed, horizontally across the visceral surface of the skull roof (1).

The developed crista supraethmoidalis is present in basal arthrodires such as *Dicksonosteus arcticus* and in basal brachythoracids such as *Parabuchanosteus murrumbidgeenis* and *Dhanguura johnstoni*. The similar structure is also present in Aspinothoracidi such as *Enseosteus jaekeli*. In Aspinothoracidi the crista supraethmoidalis is positioned anterior to the pineal pit, while in basal arthrodires and basal brachythoracids the crista supraethmoidalis is posterior to the pineal pit.

100. Rostral and pineal plates fused into one plate: absent (0); present (1).

101. Shape of the pineal plate on the external surface of the skull roof: short and broad (0); long and narrow (1).

This character may be linked to the elongation and narrowing of the orbitotemporal region of the neurocranium.

102. Lateral development of the supraorbital vault compared with the breadth of the skull roof at the level immediately behind the supraorbital vault.
This definition of the skull roof breadth is to make this character independent to character 113: underdeveloped, indicated by the ratio of the breadth of both sides of the lateral expansion of the supraorbital vaults/the breadth of the skull roof at the level immediately behind the supraorbital vault less than 0.3 (0); developed, indicated by the ratio of the breadth of the lateral expansion of the supraorbital vaults/the breadth of the skull roof larger than 0.3 (1).

103. Development of the postorbital process of the postorbital plate: moderately developed (0); highly developed, defined as the postorbital process composing one-quarter of the orbit (1).

104. Position of the anterior end of the endolymphatic duct on the visceral surface of the skull roof, indicating the neurocranial aperture of the endolymphatic duct: anteriorly positioned, defined as positioned anterior to the nuchal thickening (0); posteriorly positioned, on the nuchal thickening.

105. Posterior lateral shape of the nuchal plate: nuchal straight, not expanded laterally (0); nuchal trapezoid, expanded laterally (1).

Modified after Gardiner & Miles (1990: character 22.36). This character not being included in several previous analyses (Carr, 1991; Carr & Hlavin, 2010; Zhu & Zhu, 2013) was due to all eubrachythoracids to date possessing posterolaterally expanded nuchal plates, rendering this character uninformative if only eubrachythoracids are included as the ingroup.

106. Median ridge on the visceral surface of the nuchal plate, corresponding to the median depression on the occipital region of the neurocranium: absent (0); present (1).

107. Position of the paired nuchal pits: anteriorly positioned, defined by position anterior to or on the transverse nuchal thickening (0); posteriorly positioned, defined by position posterior to the transverse nuchal thickening (1).

Nuchal pits positioned posterior to the transverse nuchal thickening is present in several aspinothoracids such as *Dinichthys herzeri* (Carr & Hlavin, 2010: fig. 1).

108. Position of the skull roof and thoracic armour articulation: not close to posterolateral corner of the skull roof (0); close to posterolateral corner of the skull roof (1).

109. Skull roof fenestra: absent (0); present (1).

**Gnathal Plates and Parasphenoid**

110. Shape of the infragnathal plate, defined by the depth of the occlusal portion and posterior blade portion, respectively: blade portion significantly deeper (0); occlusal portion deeper, or nearly equal between these two parts of the infragnathal plate (1).

Anderson (2008) identified two distinct morphotypes in eubrachythoracids indicating different feeding niches. The deep blade and narrow dental portion in most coccosteomorphs implies a scissor-like occlusion, while the narrow blade and deep dental portion in most pachyosteomorphs implies a vice-like occlusion.

111. Parasphenoid thickened around the buccohypophysial foramen: absent (0); present (1). Parasphenoid thickened around the buccohypophysial foramen is to date the synapomorphy of Eubrachythoraci. In basal arthrodires such as *Turrisaspis elector* and basal brachythoracids such as *Parabuchanosteus murrumbidgeensis* and *Antinoeoteus lehmani*, the parasphenoid is thinner and not thickend around the buccohypophysial foramen.

112. Stem-like prehypophysial region of the parasphenoid: absent (0); present (1). The stem-like prehypophysial region of the parasphenoid is present in several aspinothoracids such as *Gymnortachelus hydei* (Carr, 1994: fig. 9). *Trematosteus fontanellus* is coded as possessing stem-like prehypophysial region of the parasphenoid because it is significantly narrower than the postohypophysial region, although its prehypophysial region is very unusual in being considerably elongated and anteriorly broadened into a sword-shape.

**Neurocranium**

113. Breadth of the orbitotemporal neurocranium, indicated by the breadth between the two inner margins of the supraorbital vaults: wide, defined by the ratio of the breadth of the orbitotemporal neurocranium/the breadth of the skull roof at the level immediately behind the supraorbital vault larger than 0.4 (0); narrow, defined by the ratio of the breadth of the orbitotemporal neurocranium/the breadth of the skull roof less than 0.4 (1).

114. Shape of the supravagal process of the neurocranium, indicated by the impression of the channel left by the supravagal process on the visceral surface of the skull roof when the neurocranium is not preserved: near right-angled (0); developed laterally to form an acute angle (1).

This character may be linked to the posterolateral expansion of the dermal nuchal plate (character 104). The right-angled supravagal process is primarily present in basal arthrodires such as *Kujdanowiaspis podolica*, *Dicksonosteus arcticus*
and Holonema westolli. Several basal brachythoracids such as Antineosteus lehmani also possess a near right-angled supravagal process.

**THORACIC ARMOUR**

115. Posterior development of the posterior carinal process of the keel on the visceral surface of the median dorsal plate: posteriorly developed, beyond the posterior margin of the median dorsal plate in dorsal view (0); not posteriorly developed, not beyond the posterior margin of the median dorsal plate in dorsal view (1).

This character definition is different from Carr & Hlavin (2010: cha. 35) in that the latter only discriminated the presence and absence of posterior carinal process, but did not indicate its extent of development. The posterior carinal process beyond the posterior margin of the median dorsal plate is the result of both the development of itself and the shortening of thoracic armour.

116. Median dorsal plate elevated dorsally into a median crest: (0) absent; present (1).

The median dorsal crest is only present in basal arthrodires, including holonematids and groenlandaspids, as well as the basal brachythoracid Gemuendenaspis angusta.

117. Anterior dorsolateral plate and anterior lateral plate fused into one complex: not fused (0); fused (1).

118. Anterior ventral corner or anterior ventral wing (sensu Carr, 1996) of the anterior lateral plate extends anterolaterally: not extending anterolaterally, the lateral profile of the anterior lateral plate is sub-triangular or rhomboid (0); extending anterolaterally, making the lateral profile of the anterior lateral plate 'boomerang'-shaped (1).

Homosteids such as Homostius sulcatus and Antineosteus lehmani also possess an elongated anterior lateral plate. However, in homosteids the elongation in most part applies to the upper lamina rather than the anterior ventral corner of the anterior lateral plate and does not fit the above definition. Therefore, in the current data matrix Homostius sulcatus and Antineosteus lehmani are coded as ‘0’ in character 116.

119. In those taxa that possess an anterolaterally extended anterior lateral plate, the extent of the extension: extended normally (0); extended into a rod-like structure (1). In those taxa that do not possess an anterolaterally extended anterior lateral plate, this character is scored as ‘not applicable’.

120. External surface of the anterior lateral plate quadrated by four ridges radiating from the ossification centre of the plate: absent (0); present (1).

121. Anteroventral groove on the ventral surface of the interolateral plate: absent (0); present (1). Miles (1965) considered that the anteroventral groove accommodated the neuromasts. This groove is present in most basal arthrodires and lost in most eubrachythoracids, retained only in Coccosteus cuspidatus.

**APPENDIX 3**

**TAXA LIST AND SOURCE REFERENCES**

Name: Antineosteus lehmani Lelièvre, 1984
Locality and horizon: Akka-N-Arrouch, Morocco. Late Emsian, Early Devonian.

Name: Brachyosteus dietrichi Gross, 1932
Locality and horizon: Bad Wildungen, Germany. Late Frasnian, Late Devonian.

Name: Bruntonichthys multidens Dennis & Miles, 1980
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.

Name: Buchanosteus confertituberculatus Young, 1979
Locality and horizon: Buchan, Australia. Emsian, Early Devonian.

Name: Bullerichthys fascidens Dennis & Miles, 1980
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.

Name: Camuropiscis laidlawi Dennis & Miles, 1979a
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.

Name: Coccosteus cuspidatus Miller, 1841
Locality and horizon: Lower Caithness Flagstone Group, Scotland. Eifelian, Middle Devonian.

Name: Compagopiscis croucheri Gardiner & Miles, 1994
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.

Name: Dhanguura johnstoni Young, 2004
Locality and horizon: New South Wales, Australia.

Name: Dicksonosteus arcticus Goujet, 1975

Locality and horizon: Dickson land, Spitsberg. Pragian
to Emsian, Early Devonian.
Source reference: Carr & Hlavin, 2010; Goujet, 1975,
1984.
Name: Dickosteus threiplandi Miles & Westoll,
1963
Locality and horizon: Orkneys and Caithness,
Scotland. Late Eifelian to Early Givetian, Middle
Devonian.
Name: Dinichthys herzeri Newberry, 1868
Locality and horizon: Delaware County, Ohio, USA.
Famennian, Late Devonian.
Name: Dunkleosteus amblyodoratus Carr & Hlavin,
2010
Locality and horizon: Ontario, Canada. Frasnian or
Famennian, Late Devonian.
Name: Dunkleosteus raveri Carr & Hlavin, 2010
Locality and horizon: Erie County, Ohio, USA. Early
Famennian, Late Devonian.
Name: Dunkleosteus terrelli Newberry, 1873
Locality and horizon: Ohio, Tennessee, Pennsylva-
nia and California, USA. Late Frasnian to Famennian,
Late Devonian.
Name: Eastmanostes calliaspis Dennis-Bryan, 1987
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Source reference: Carr & Hlavin, 2010; Dennis-Bryan,
1987.
Name: Eastmanostes pustulosus Eastman, 1897
Locality and horizon: Wisconsin, New York, and Iowa,
USA, and Holy Cross Moutain, Poland. Givetian, Middle
Devonian to Early Famennian, Late Devonian.
Source reference: Carr, 1991; Carr & Hlavin, 2010;
Name: Elvaspis tuberculata Young 2009
Locality and horizon: New South Wales, Australia.
Emsian, Early Devonian.
Name: Fallocosteus turneri Long, 1990
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Source reference: Long, 1990; Trinajstic &
Dennis-Bryan, 2009.
Name: Gemuendenaspis angusta Traquair, 1903
Locality and horizon: Hunsrückschiefer, Germany,
Early Emsian, Early Devonian.
Name: Golshanichthys asiatica Lelièvre, Janvier &
Goujet, 1981
Locality and horizon: Kerman, Iran. Early Frasnian,
Late Devonian.
Source reference: Carr & Hlavin, 2010; Lelièvre,
Janvier & Goujet, 1981.
Name: Goodradigbeeon australianum White, 1978
Locality and horizon: Murrumbidgee, Australia, Emsian, Early Devonian.
Name: Gorgonichthys clarkei Claypole, 1892
Locality and horizon: Ohio, USA. Famennian, Late
Devonian.
Source reference: Carr & Hlavin, 2010; Dunkle &
Bungart, 1940; Denison, 1978; Stensiö, 1963.
Name: Groenlandaspis antarcticus Ritchie 1975
Locality and horizon: Aztec siltstone, Victorian Land,
Antarctica. Givetian according to Young (1989), originally identified by Ritchie (1975) as Late Devonian.
Name: Gymnotrachelus hydei Dunkle & Bungart, 1939
Locality and horizon: Ohio, USA. Famennian, Late
Devonian.
Source reference: Carr, 1994; Carr & Hlavin, 2010;
Dunkle & Bungart, 1939.
Name: Hadrosteus rapax Gross, 1932
Locality and horizon: Bad Wildungen, Germany. Late
Frasnian, Late Devonian.
Name: Harrytoombsia elegans Miles & Dennis, 1979
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Source reference: Miles & Dennis, 1979; Trinajstic
Name: Heintzichthys gouldii Newberry, 1885
Locality and horizon: Ohio, USA. Famennian, Late
Devonian.
Name: Heterostius ingens Asmuss, 1856
Locality and horizon: Aruküla beds, Estonia. Eifelian,
Middle Devonian.
Source reference: Carr & Hlavin, 2010; Miles, 1971
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Name: Holonema westoii Miles, 1971
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Name: Homostius sulcatus Kutorga, 1837
Locality and horizon: Aruküla beds, Estonia. Eifelian,
Middle Devonian.
Name: Incisoscutum ritchiei Dennis & Miles, 1981
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Source reference: Dennis & Miles, 1981; Trinajstic
Name: Incisoscutum sarahae Long, 1994
Locality and horizon: Kimberley, Australia. Early
Frasnian, Late Devonian.
Name: Janiosteus timanicus Ivanov, 1989
Locality and horizon: Timan, Russia. Late Givetian, Middle Devonian.
Name: Kendrickichthys cavernosus Dennis & Miles, 1980
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Kiangyousteus yohii Liu, 1955
Locality and horizon: Sichuan, China. Givetian, Middle Devonian.
Name: Kujdanowiaspis podolica Brotzen, 1934
Locality and horizon: Podolica, Ukraine. Lochkovian, Early Devonian.
Name: Latocamurus coulthardi Long, 1988a
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Mcnamaraspis kaprios Long, 1995
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Melanosteus occitanus Lelièvre et al., 1987
Locality and horizon: Montagne Noire, France. Late Frasnian, Late Devonian.
Name: Millerosteus minor Stensiö, 1959
Locality and horizon: Orkneys and Caithness, Scotland. Early Givetian, Middle Devonian.
Name: Parabuchanosteus murrumbidgeensis White, 1952
Locality and horizon: Murrumbidgee, Australia, Emsian, Early Devonian.
Name: Pachyosteus bulla Jaekel, 1903
Locality and horizon: Bad Wildungen, Germany. Late Frasnian, Late Devonian.
Name: Protitanichthys rockportensis Eastman, 1907
Locality and horizon: Michigan, USA. Early Givetian, Middle Devonian.
Name: Rhachiosteus pterygiatus Gross, 1938
Locality and horizon: Bergisch-Gladbach, Germany. Late Givetian, Middle Devonian to Early Frasnian, Late Devonian.
Source reference: Gross, 1938; Miles, 1966a.
Name: Stenosteus angustopectus Carr, 1996
Locality and horizon: Ohio, USA. Famennian, Late Devonian.
Name: Tapinosteus heintzi Stensiö, 1963
Locality and horizon: Bad Wildungen, Germany. Late Frasnian, Late Devonian.
Name: Torosteus tuberculatus Gardiner & Miles, 1990
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Torosteus pulchellus Gardiner & Miles, 1990
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Tubonasus lennardensis Dennis & Miles, 1979b
Locality and horizon: Kimberley, Australia. Early Frasnian, Late Devonian.
Name: Turrisaspis elektor Daeschler, Frumes & Mullison, 2003
Locality and horizon: Pennsylvania, USA. Famennian, Late Devonian.
Name: Watsonosteus fletti Watson, 1932
Locality and horizon: Orkney Isles, Scotland, UK. Late Givetian, Middle Devonian.
Name: Westralichthys uwagedensis Long, 1987
Locality and horizon: Western Australia, Australia. 
Middle Famennian, Late Devonian.
Name: *Xiangshuiosteus wui* Wang, 1992
Locality and horizon: Yunnan, China. Emsian, Early Devonian.
Name: *Yinosteus marjor* Wang & Wang, 1984
Locality and horizon: Yunnan, China. Emsian, Early Devonian.

**APPENDIX 4**

**List of Synapomorphies That Define the Clades Shown in Figure 9**

Asterisks indicate ambiguous character states resolved using DELTRAN (delayed transformation) optimization. Character state is ‘1’ unless marked otherwise.

| Node 2: 34, 14, 17, 26 (0), 71, 95*, 106 (0) |
| Node 3: 1, 10 (0), 24, 29, 60, 63*, 90, 105, 116 (0)* |
| Node 4: 2 (0), 31 (0)*, 36 (0), 55* |
| Node 5: 4, 16*, 30*, 54, 79 (0), 114, 120 (0) |
| Node 6: 100 |
| Node 7: 9, 18 (2)*, 98*, 102 |
| Node 8: 29 (0), 83*, 84* |
| Node 9: 13, 14 (0), 24 (0) |
| Node 10: 2*, 5*, 8 (0)*, 12*, 15 (0), 22, 28, 35 (2)*, 57*, 58*, 65*, 68*, 70*, 74*, 99 (0)*, 101, 111*, 113* |
| Node 11: 37, 39, 43*, 44, 50 (0)*, 51 (2), 71 (0), 73, 93 |
| Node 12: 10, 13 (2)*, 76, 78, 80 |
| Node 13: 4 (0), 20*, 22, 53, 99, 113 (0) |
| Node 14: 9 (0), 43 (0) |