A redescription of *Kiangyousteus yohii* (Arthrodira: Eubrachythoraci) from the Middle Devonian of China, with remarks on the systematics of the Eubrachythoraci

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*Kiangyousteus yohii* Liu, 1955, is a eubrachythoracid arthrodire fish (Placodermi) from the Middle Devonian Guanwu Formation of south-western China. Although *Kiangyousteus* was the first arthrodire described in China, its phylogenetic position within the Eubrachythoraci remained uncertain because of a lack of diagnostic data in previous studies. A detailed redescription of this taxon reveals similarities to *Dunkleosteus terrelli* in the possession of transverse articular facets on the parasphenoid and the lack of adsymphyseal denticles on the anterior supragnathal. Our phylogenetic analysis assigned *K. yohii* to the family Dunkleosteidae, which includes *Eastmanosteus calliaspis*, *Eastmanosteus pustulosus*, *Golshanichthys asiatica*, *Heterostius ingens*, *Xiangshuiosteus wui*, and *Dunkleosteus*. The analysis also yielded several new scenarios on eubrachythoracid interrelationships, notably the sister-group relationship between Coccosteomorphi and Aspinothoraci, the polyphyly of the referred species of *Eastmanosteus*, and the assignment of *Heterostius* and *Xiangshuiosteus* within the Dunkleosteidea.

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INTRODUCTION

The Arthrodira Woodward, 1891, is the most diverse group of placoderm fishes (Denison, 1978; Carr, 1995; Young, 2010) and a predominant component of many Devonian vertebrate faunas (Lebedev & Zakharenko, 2010). The interrelationships of arthrodirines and their relationship to the other placoderms form a recurrent topic in early gnathostome evolution (Denison, 1984; Goujet, 1984b; Goujet & Young, 2004; Brazeau, 2009; Davis, Finarelli & Coates, 2012). The Arthrodira is conventionally divided into the paraphyletic Actinolepida Miles, 1973, the Phlyctaenii Fowler, 1947, and the Brachythoraci Gross, 1932 (Miles, 1973; Young, 1979; Dupret, 2004; Dupret, Goujet & Mark-Kurik, 2007; Dupret & Zhu, 2008; Dupret, Zhu & Wang, 2009). The Brachythoraci is further subdivided into several basal groups (including Holonematidae Obruchev, 1932, Homosteoidea Jaekel, 1903, and Buchanosteoida White, 1952), and a derived clade, the Eubrachythoraci Miles, 1971, in which the Coccosteomorphi Stensiö, 1944 and the Pachyosteomorphi Stensiö, 1944 can be identified (Stensiö, 1944, 1959; Miles & Dennis, 1979; Lelièvre, Janvier & Goujet, 1981; Carr, 1991; Carr & Hlavin, 2010). Current investigations of eubrachythoracid phylogeny are mainly based on fossils from Europe, North
Over the past few years, several early arthrodires from China have been described in detail (Dupret, 2008; Dupret & Zhu, 2008; Dupret et al., 2009; Zhu, Wang & Wang, 2010), shedding new light on the origin and early evolution of basal arthrodire groups such as phyllolepids and wuttagoonaspids. By contrast, the promising collections of Chinese eubrachythoracids (Liu, 1955; Wang, 1979, 1982; 1991, 1992a, b, 1996; Wang & Wang, 1983, 1984, 1999; 2000; Wang & Zhu, 2004) have not yet been fully appreciated. The absence of a comprehensive and detailed study of this material remains an impediment to our profound understanding of placoderm diversity and evolution.

*Kiangyousteus yohii* Liu, 1955, from the Givetian Guanwushan Formation of Sichuan represents the first record of Chinese arthrodires (Fig. 1). The fossils were collected by Professor S. H. Yoh from Peking University during his 1953 field trip to Mount Guanwushan (formerly ‘Kuan-Wu-Shan’) of Jiangyou (formerly ‘Kiangyou’) district, Sichuan Province. Liu (1955) later described the material and erected the arthrodire genus *Kiangyousteus*. He assigned the taxon as a primitive member of the Coccosteidae Traquair, 1888, and thought it related to the ancestral form of either *Dinichthys* Newberry, 1868 or *Titanichthys* Newberry, 1885 (Liu, 1955). Obruchev (1964) catalogued *Kiangyousteus* in his handbook, and pointed out that specimen IVPP V801.1, which was identified as a pineal plate by Liu (1955), was in fact the parapleural of an arthrodire. This revision was followed by Denison (1978) and Dennis-Bryan (1995). Based on the similarities of the parapleural and anterior lateral plates between *Kiangyousteus* and *Dunkleosteus* Lehman, 1956, Denison (1978) also suggested *Kiangyousteus* as a primitive member of the Dinichthyidae Newberry, 1885. Since the 1990s, computerized phylogenetic analyses have been applied to brachythoracid systematics (Carr, 1991; Carr & Hlavin, 1995, 2010; Lelièvre, 1995; Trinajstic & Dennis-Bryan, 2009). Initially, *Kiangyousteus* was omitted from the phylogenetic analysis of eubrachythoracids (Carr, 1991). Carr & Hlavin (1995) later assigned it as Pachyosteomorphi incertae sedis. In a recent cladistic analysis of eubrachythoracoid arthrodires by Carr & Hlavin (2010), the position of *Kiangyousteus* still remained ambiguous because of the large amount of missing data.

In this work we offer a detailed redescription of *Kiangyousteus yohii* (Fig. 2) and a renewed eubrachythoracid cladistic analysis, which yields a novel phylogenetic hypothesis and clarifies the relationship of *Kiangyousteus* with other eubrachythoracid arthrodires.
Anatomical abbreviations
- a.con, anterior concave region for the articulation with anterior supragnathal
- ADL.cf, contact face for anterior dorsolateral plate
- AL, anterior lateral plate
- ala, anterior lamina of anterior supragnathal
- ASG, anterior supragnathal
- a.th, anterior thickening of parasphenoid
- AVL, anterior ventrolateral plate
- AVL.th, ventral thickening of anterior ventrolateral plate
- bhy.th, buccohypophysial thickening on the parasphenoid
- C, central plate
- ch.eth, channel for neurocranial ethmoid region
- cr.m, ventral median crest of parasphenoid
- csc, central sensory line groove
- cusp.th, lateral thickening for anterior supragnathal cusp
- dlia, dorsal lamina of anterior supragnathal
- em.arc, embayment for vertebral arch
- em.pb, postbranchial embayment
- f.bhy, buccohypophysial foramen
- f.pca, fractured face of the carinal process of median dorsal keel
- gr.a.com, transverse ventral groove of parasphenoid
- IL.oa, overlap area for the interolateral plate
- ioc.ot, otic branch of infraorbital line groove
- ioc.pt, postorbital branch of infraorbital line groove
- kv, ventral keel of median dorsal plate
- lam.dent, denticles on the postbranchial lamina
- lc, main lateral line groove
- ld, dorsal branch of main lateral line
- lla, lateral lamina of anterior supragnathal
- lr.cusp, lateral cusp of anterior supragnathal
- M, marginal plate
- MD, median dorsal plate
- MD.oa, overlap area for median dorsal plate
- MD.th, posterior thickening of median dorsal plate
- Nu, nuchal plate
- obst.pr, obstantic process of anterior lateral plate
- P, pineal plate
- pbl, postbranchial lamina
- pca, carinal process of median dorsal keel
- PDL, posterior dorsolateral plate
- PDL.cf, contact face for posterior dorsolateral plate
- PL.cf, contact face for posterior lateral plate
- PL.oa, overlap area for posterior lateral plate
- pmc, postmarginal line groove
- PNU, paranuchal plate
- PrO, preorbital plate
- pr.occ, occlusal shelf posterior to the lateral cusp
- PtO, postorbital plate
- R, rostral plate
- s.e, subpectoral emargination
- sec.th, second thickening posterior to the buccohypophysial thickening
- Smd, submedian dorsal plate
- soc, supraorbital sensory line groove
- vts, transverse ventral sensory line

Phylogenetic abbreviations
- CI, consistency index
- CIsct, consistency index of the strict consensus tree
- L, length of trees (in evolutionary steps)
- Lsct, length of the strict consensus tree
- n, number of trees
- RI, retention index
- RIsct, retention index of the strict consensus tree

SYSTEMATIC PALAEONTOLOGY
PLACODERMI McCoy, 1848
ARTHRODIRA Woodward, 1891
BRACHYTHORACI Gross, 1932
EUBRACHYTHORACI Miles, 1971
PACHYOSTEOMORPHI Stensiö, 1944
(suborder Brachythoraci Gross, 1932, in part; suborder Pachyosteina Stensiö, 1944; suborder Pachyosteomorphi Stensiö, 1944, in part; Pachyosteomorphi Stensiö, 1959; order Pachyosteida Obruchev, 1964; suborder Pachyostei Stensiö, 1969)

FAMILY DUNKLEOSTEIDAE Stensiö, 1963
Type genus
Dunkleosteus Lehman, 1956.

Diagnosis (modified after Carr & Hlavin, 2010)
Pachyosteomorphi in which the interolateral plate contacts the spinal plate laterally; the spinal plate does not bear a spinal pit; the posterior ventrolateral plate bears a small postpectoral lamina; the anterior supragnathal plate in dorsal view forms an open ring
with an angle of about 90°; and the parasphenoid bears a pair of posterolateral processes. The clade Dunkleosteidae includes Dunkleosteus as its type genus and all other genera in Dunkleosteoidea Vézina, 1990 more closely related to Dunkleosteus than to Panxiosteus.

**Kiangyousteus Liu, 1955**

Type and only included species


Diagnosis

As for the type and only known species.

**Kiangyousteus yohii** Liu, 1955

Holotype

IVPP V801, displaced plates in association, including a right anterior supragnathal (IVPP V801.8, Fig. 3), a parasphenoid (IVPP V801.1, Figs 4, 5E), a median dorsal (IVPP V801.4, Fig. 6A–C), a submedian dorsal (IVPP V801.6, Fig. 6D, E), a right anterior lateral (IVPP V801.2, Fig. 7), a right anterior ventrolateral (IVPP V801.5, Fig. 8A, B) and a right posterior dorsolateral (IVPP V801.3, Fig. 8C, D).

Type locality and horizon

Mount Guanwushan of Jiangyou, Sichuan Province, China; Guanwushan Formation, Givetian, Middle Devonian.

Emended diagnosis

Dunkleosteid species in which the parasphenoid bears an articulation with the anterior supragnathal; the median dorsal plate bears a dorsal branch of the main lateral line; and the anterior supragnathal bears an occlusal shelf posterior to the lateral cusp.

**Morphological description**

Head shield: Anterior supragnathal (IVPP V801.8, Fig. 3): The right anterior supragnathal, comprising anterior, lateral, and dorsal laminae (ala; Fig. 3C, lla, dla; Fig. 3A, B), closely resembles that of Dunkleosteus and Gorgonichthys in shape (Dunkle & Bungart, 1946). The lateral lamina possesses only one lateral cusp (lr.cusp; Fig. 3A, B; Dunkle & Bungart, 1946: fig. 1, anteroventral cusp). Two ridges or thickenings (cusp.th; Fig. 3B, C) reinforce the cusp on both labial and lingual sides. Posteriorly to the inner cusp ridge a depressed occlusal accommodation (pr.occ; Fig. 3B) for the cusp of infragnathal plate is visible. The arrangement differs from that of Dunkleosteus terrelli Newberry, 1873, in which the occlusal accommodation for the infragnathal cusp lies anterior to the supragnathal cusp (Stensiö, 1963: fig. 118a–c). The incised occlusal surface extends mesially to the inner surface of the anterior lamina.

The possible posterior process and the contact region to the parasphenoid on the posterior part of the dorsal lamina of the plate are missing. A depression (ch.eth; Fig. 3C) for the articulation with subnasal elements as defined in Dunkle & Bungart (1946) is present on the outer face, although obscure because of poor preservation. No tubercle or adsymphyseal denticle is present on the plate.

Parasphenoid (IVPP V801.1, Fig. 4): This plate, initially described by Liu (1955) as the pineal plate, was later identified by Obruchev (1964) as the parasphenoid. It is roughly pentagram-shaped, and

![Figure 3. Kiangyousteus yohii. Right anterior supragnathal plate (IVPP801.8) in A, labial, B, lingual, and C, anterior views. Abbreviations: ala, anterior lamina of anterior supragnathal; ch.eth, channel for neurocranial ethmoid region; cusp.th, lateral thickening for anterior supragnathal cusp; dla, dorsal lamina of anterior supragnathal; lla, lateral lamina of anterior supragnathal; lr.cusp, lateral cusp of anterior supragnathal; pr.occ, occlusal shelf posterior to the lateral cusp. Scale bars = 1 cm.](image-url)
Kiangyousteus yohii. Parasphenoid (IVPP801.1) in A, dorsal, and B, ventral views. Abbreviations: a.con, anterior concave region for the articulation with anterior supragnathal; a.th, anterior thickening of parasphenoid; bhy.th, buccohypophysial thickening on the parasphenoid; cr.m, ventral median crest of parasphenoid; f.bhy, buccohypophysial foramen; gr.a.com, transverse ventral groove of parasphenoid; pl.pr, posterolateral process of parasphenoid; sec.th, second thickening posterior to the buccohypophysial thickening. Scale bar = 2 cm.
the parasphenoid can be useful for the investigation of eubrachythoracid phylogeny and the systematic position of *Kiangyousteus*.

Trunk shield: Median dorsal plate (IVPP V801.4, Fig. 6A, B, C): The median dorsal plate (MD) is shovel-shaped and is arched transversely. The anterior border is emarginated, and forms two anterolateral horn-like processes together with the slightly concave lateral edges. The posterior border is rounded. The right half of the plate is heavily deformed. A reconstruction based on the intact left half reveals that the median dorsal plate of *Kiangyousteus* is shorter and broader than former interpretations by Liu (1955) and Denison (1978). However, with a length/width ratio of 1.2, the median dorsal plate of *Kiangyousteus* is still coded as 'long and narrow' in the current data matrix (Appendix 1, character 26).

In comparison, most members of the Pachyosteomorphi have a short and broad median dorsal plate (length/breadth ratio < 1), with the exception of *E. calliaspis*, whose median dorsal plate has a length/breadth ratio of 1.5. *Belosteus elegans* Jaekel 1919 (Stensiö, 1963) also has a narrow median dorsal plate, but in this particular case it is probably a derived state owing to the lateral compression of the entire body.
In visceral view, a well-developed ventral keel (kv; Fig. 6B) goes along the midline. Most of its rear part is missing. Judging from the fracture face of the missing carinal process (ff.pca; Fig. 6B), the keel bears a stout posterior carinal process at its end. The carinal process does not go beyond the posterior border of the median dorsal plate. Two ventral transverse thickenings (MD.th; Fig. 6B) extend from the base of the carinal process to the lateral edges.

The dorsal surface of the plate is covered with densely distributed small tubercles. The dorsal branch of the main lateral sensory line (ld; Fig. 6A) is visible on the dorsal surface of the median dorsal plate as a shallow groove.

Anterior lateral plate (IVPP V801.2, Fig. 7): The anterior lateral plate (AL) is a thick triangular plate with an obstantic process (obst.pr; Fig. 7A, B). The large upper part restored by Liu (1955: fig. 4a), referring the plate to the type of *Dinichthys* (possibly *Dunkleosteus* here), does not exist. Nor does it resemble the near-equilateral triangular AL shape of coccosteomorphs, as the postbranchial embayment (em.pb; Fig. 7A) on the anterior border is clearly developed, and the anterior ventral part of the anterior lateral plate is moderately long.

In general shape, the anterior lateral plate of *K. yohii* can be compared to that of *E. calliaspis* (Dennis-Bryan, 1987: fig. 22c, d), except that the former possesses an exceptionally developed postbranchial lamina (pbl; Fig. 7B, C), which extends down and beyond the anteroventral corner on the external surface of the anterior lateral plate. The extension of the postbranchial lamina on the anterior lateral plate indicates that the interolateral plate possesses a branchial lamina as well. A tubercular ornament is present both on the exposed surface of the plate and on the postbranchial lamina (lam.dent; Fig. 7C). The postbranchial lamina ornament would extend to the postbranchial lamina of the interolateral plate.

Anterior ventrolateral plate (IVPP V801.5, Fig. 8A, B): This is an almost flat triangular plate, with a Y-shaped thickening (AVL.th; Fig. 8B) on the anterior part of the inner surface. Anteriorly, there is an overlap area for the interolateral plate (IL.oa; Fig. 8A). A moderate lateral embayment forms the subpectoral emargination (s.e; Fig. 8A). The existence of an overlap area along the embayment described by Liu (1955) is doubtful.

A tubercular ornament is present on the external surface of the plate. The tubercles in the middle are slightly larger than those along the margins, opposite to the ornament pattern of the median dorsal plate. The transverse ventral sensory line groove (vts; Fig. 8A) is present.

Posterior dorsolateral plate (IVPP V801.3, Fig. 8C, D): The anterior part of the posterior dorsolateral plate (PDL) is missing. The missing part was reconstructed with plaster on the current specimen before this study. The posterior margin of the plate is very long and slightly concave. A poorly preserved portion of the area overlapped dorsally by the median dorsal plate is clearly identifiable (MD.oa, Fig. 8A), and shows the extension and angle of the contact between the two plates. The lower part of the plate is reinforced by an internal thickening. A developed socket-like overlap area (PL.oa; Fig. 8A) is present for the posterior lateral plate. A tubercular ornament is present on the external surface of this plate.

Figure 7. *Kiangyousteus yohii*. Right anterior lateral plate (IVPP801.2) in A, lateral, B, visceral, and C, anterior views, detailing the denticulated area of postbranchial lamina. Abbreviations: ADL.cf, contact face for anterior dorsolateral plate; em.pb, postbranchial embayment; lam.dent, denticles on the postbranchial lamina; obst.pr, obstantic process of anterior lateral plate; pbl, postbranchial lamina; PL.cf, contact face for posterior lateral plate. Scale bar = 2 cm.
Endoskeleton: Submedian dorsal plate (IVPP V801.6, Fig. 6D, E): The submedian dorsal plate of Kiangyousteus differs from the oval-shaped submedian dorsal plate of Coccosteus cuspidatus Miller, 1841 (Miles & Westoll, 1968: fig. 48) in its right trapezoid outline, resembling more that of E. calliaspis, although proportionally larger and sturdier. The plate is a perichondrally ossified element. It is triangular in cross-section and devoid of ornament, with thickenings visible along its anterior and ventral sides. The anterior face shows a fossa for the carinal process of the median dorsal keel (f.pca; Fig. 6D, E). An embayment for the neural arches (em.arc; Fig. 6E) is visible on the ventral face.

Figure 8. Kiangyousteus yohii. Right anterior ventrolateral plate (IVPP801.5) in A, ventral, and B, dorsal (visceral) views. Right posterior dorsolateral plate (IVPP801.3) in C, lateral, and D, mesial views. Abbreviations: AVL.th, ventral thickening of anterior ventrolateral plate; IL.oa, overlap area for the interolateral plate; MD.oa, overlap area for median dorsal plate; PL.oa, overlap area for posterior lateral plate; s.e, subpectoral emargination; vts, transverse ventral sensory line. Scale bars = 2 cm.

Endoskeleton: Submedian dorsal plate (IVPP V801.6, Fig. 6D, E): The submedian dorsal plate of Kiangyousteus differs from the oval-shaped submedian dorsal plate of Coccosteus cuspidatus Miller, 1841 (Miles & Westoll, 1968: fig. 48) in its right trapezoid outline, resembling more that of E. calliaspis, although proportionally larger and sturdier. The plate is a perichondrally ossified element. It is triangular in cross-section and devoid of ornament, with thickenings visible along its anterior and ventral sides. The anterior face shows a fossa for the carinal process of the median dorsal keel (f.pca; Fig. 6D, E). An embayment for the neural arches (em.arc; Fig. 6E) is visible on the ventral face.

PHYLOGENETIC SYSTEMATICS
DATA SET COMPILATION AND METHODOLOGY
To elucidate the systematic position of K. yohii and its potential impacts on eubrachythoracid interrelationships, we performed a parsimony-based phylogenetic analysis. The outgroup taxa include a phlyctaeniid Dicksonosteus arcticus Goujet, 1975 (Goujet, 1975, 1984a) and three basal brachythoracids, namely Holonema westoli Miles, 1971, Homosteus sulcatus Kutorga, 1837 (Heintz, 1934), and Buchanosteus confertituberculatus Stensiö, 1945 (Young, 1979). The ingroup contains 33 taxa, entirely from the matrices of Carr (1991), Trinajstic & Dennis-Bryan (2009), and Carr & Hlavin (2010), with the exception of a Chinese taxon Xiangshuiosteus wui Wang, 1992a. The 98 characters in our data matrix were sourced from Carr & Hlavin (2010). Amongst the 98 characters, 85 characters were first formulated by Carr (1991). Carr & Hlavin (2010) updated or modified six out of 85 characters of Carr (1991), and added the remaining 13 characters.

In the matrix of Carr & Hlavin (2010), characters 92 and 93 were used to reveal the relative position of the posterolateral corner of the skull roof, and the
The extension of the anterior part of the skull roof, respectively. The transformation series of these two characters denotes some phylogenetic signals (Long, 1987; Carr, 1991); however, the formulations of these two transformation series by Carr & Hlavin (2010) rendered these two characters uninformative because most of the ratios calculated are far less than the smallest discriminant value (in both cases, 3.0). Another weakness of the original formulations is that these two characters are mutually dependent to a large extent (Fig. 9B) because of the following facts: first, distance a (Fig. 9A, used in character 92 of Carr & Hlavin, 2010) is in large proportion composed by distance b (used in character 93 of Carr & Hlavin, 2010), resulting in the correlation of these two numerators; second, distance c shared by both characters as the denominator fluctuates amongst the referred taxa as a result of shifting of the posterolateral corner, which should only be evaluated by one character, not both.

To make characters 92 and 93 less correlative, we modified their formulations. All three landmarks (the lateral articular fossa, the junction of sensory line grooves for the central line, otic and postorbital branches of the infraorbital line, and the pineal aperture or its position beneath the plate) from Carr & Hlavin (2010) were retained. We adopted distance b as the denominator in both calculations. Distance b is relatively stable, not fluctuating amongst the different taxa because of the shifting of the posterolateral corner or the extension of the anterior portion of the skull roof, and the enlargement of the orbit. Numerators were chosen according to the purposes of the character formulations. As character 92 reveals the position of the posterolateral corner, we used distance c as the numerator. To evaluate the extent of the anterior part of the skull roof, we used distance d, which is distance a minus distance b, to avoid the correlation of the two characters.

For a more objective discrimination between character states, we conducted a cluster analysis. Out of all 35 taxa analysed, we measured 33 taxa possessing skull roof information from original references (Appendix 2). The r1 and r2 ratios ($r1 = \frac{c}{b}$; $r2 = \frac{d}{b}$; Fig. 9A) were then Q-cluster analysed using SPSS v. 18.0. We
We rescaled the resulting dendrogram into eight clusters, which were constructed into a scatter plot (Fig. 9C). We drew the lines to reflect the discriminations between these clusters, and to reformulate the characters as follows: character 92 – position of the posterolateral corner of the skull roof judged from the ratio \((r1)\) of the posterior sensory line junction–fossa distance (distance c) divided by the anterior sensory line junction–fossa distance (distance b), \(r1 < 0.45\) (0), \(0.45 < r1 = < 0.58\) (1), \(r1 > 0.58\) (2); character 93 – extension of the anterior skull roof judged from the ratio \((r2)\) of the anterior sensory line junction–pineal foramen distance (distance d) divided by the anterior sensory line junction–fossa distance (distance b), \(r2 < 0.3\) (0), \(0.3 < r2 = = < 0.5\) (1), \(r2 > 0.5\) (2).

The description of the other characters used in our analysis can be found in Carr & Hlavin (2010). All characters were unweighted and unordered.

We also modified the codings of some taxa, including Camuropiscis laidlawi Dennis & Miles, 1979a, Coccosteus cuspidatus, E. calliaspis, Fallococestus turneri Long, 1990, Gorgonichthys elegans Long & Miles, 1978, Gymnotrachelus hydei Dunkle & Bungart, 1939, Hadrosteus rapax Gross, 1932, Harrytoombsia turneri Long, 1995, Incisoscutum sarahae Miles & Dennis, 1979, Incisoscutum ritchiei Dennis & Miles, 1981, Jacniosteus timanicus Miles & Dennis, 1979, Janiosteus timanicus Ivanov, 1989, Kiangyosteus yohii, Latocamarus couthardii Long, 1994, Mepanamaraspis kaprios Long, 1995, Pachyosteus bulla Jaekel, 1903, Panxiosteus occulus Wang, 1979, Plourdosteus canadensis Woodward, 1892, Protitanichthys rockportensis Case, 1931, Rhinosteus parvulus Gross, 1932, Rolfsteus camingensis Dennis & Miles, 1979b, Stenosteus angustoperpectus Carr, 1996, and Tubonanus lennardensis Dennis & Miles, 1979b (see Appendix 1). The revised matrix was compared with MESQUITE v. 2.73 (Maddison & Maddison, 2008), and the analysis was performed with PAUP* v. 4.0b10 (Swofford, 2003) using the heuristic algorithm. We set 1000 random addition sequence replicates, and ‘mactrees’ to ‘automatically increase’. The analysis gave 220 equally parsimonious trees of 344 steps each (CI = 0.3459; RI = 0.6193). The strict consensus tree is presented in Figure 10A with ten nested monophyletic groups as named nodes. The length of the strict consensus tree is 353 steps (CIcst = 0.3371; Rlcst = 0.6041). The synapomorphies listed (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*.

**Phylogenetic Results**

The result of the parsimony analysis significantly differs from the scenario of eubrachythoracid phylogeny previously proposed by Carr & Hlavin (2010) in the assignment of Coccosteomorphi and Aspinothoraci as sister groups, rather than Aspinothoraci sensu Miles & Dennis, 1979, and Dunkleosteidea as sister groups. In this topology, ‘Pachyosteomorphi’ appears paraphyletic. Heterostiostus ingens Asmuss, 1856, K. yohii and the newly added X. wui are assigned into the Dunkleosteidae, and Het. ingens is placed as the sister group of the genus Dunkleosteus.

The referred species of Eastmanosteus Obручев, 1964 (i.e. E. calliaspis and E. pustulosus) turn out to be not monophyletic.

The Eubrachythoraci (Fig. 10, node A) is traditionally classified into two major groups – the Coccosteomorphi and the Pachyosteomorphi (Stensiö, 1944). The two groups were considered to bear an ancestor-descendant relationship (Denison, 1984), or to represent successive evolutionary ‘levels of organization’ (Miles, 1969; Moy-Thomas & Miles, 1971). However, recent analyses agree on the sister-group relationship between the Coccosteomorphi and the Pachyosteomorphi, and the bisection of the Pachyosteomorphi into two monophyletic groups, Dunkleosteidea and Aspinothoraci (Carr, 1991; Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010). Carr & Hlavin (2010) suggested five synapomorphies for the Pachyosteomorphi: (1) the length of central-nuchal plate contact is increased; (2) the median dorsal plate is short and broad; (3) a lateral contact is developed between the suborbital and preorbital plates; (4) the paraphenoid bears a pair of posterolateral processes; and (5) the groove for the ventrolateral sensory line on the anterior lateral plate is lost.

In our scenario, the Coccosteomorphi (Fig. 10, node C), Aspinothoraci (Fig. 10, node J), and Dunkleosteidea (Fig. 10, node Q) remain monophyletic. However, Aspinothoraci and Coccosteomorphi are more closely related to each other than either is to Dunkleosteidea, making Pachyosteomorphi (i.e. Aspinothoraci plus Dunkleosteidea) paraphyletic. The four synapomorphies supporting the sister-group relationship between Coccosteomorphi and Aspinothoraci are: (1) the orbit size is intermediate (character 28, state 1); (2) the ventral lamina of the posterior lateral plate is present (character 44, state 1); (3) the ratio of the anterior sensory line junction–pineal foramen distance divided by the anterior sensory line junction–fossa distance is not less than 0.3 and not greater than 0.5 (character 93, state 1); and (4) the position of the junction of the postorbital, marginal, and central plates lies posterior to the anterior margin of the nuchal plate (character 94, state 1).

Nearly all the cladistic analyses suggest that the Coccosteomorphi is monophyletic (Dennis-Bryan & Miles, 1983a; Carr, 1991, 2004; Trinajstic &
This is corroborated by the current analysis. The majority of the coccosteomorph taxa in our analysis are found in Australia, where complete and articulated specimens are exquisitely preserved (Trinajstic & Hazelton, 2007; Trinajstic et al., 2007; Long & Trinajstic, 2010) and thus a comprehensive character coding is available. The monophyly of the Coccosteomorphi is supported by the following 12 synapomorphies: (1) the paranuchal plate embayment of the central plate is developed (character 14, state 2); (2) the postnasal plate infrafenestral process is present (character 16, state 1); (3) the median preorbital plate contact is short (character 19, state 0); (4) the postorbital plate embayment of the central plate is shallow (character 20, state 1); (5) the marginal plate extends longer than half the lateral border of the skull roof (character 24, state 1); (6) the ventral lamina of the interlateral plate is small or absent (character 48, state 0); (7) the suborbital plate overlaps the postorbital plate (character 53, state 1); (8) the suborbital plate does not contact the preorbital plate (character 54, state 0); (9) the dorsal process of the anterior superognathal plate forms an open ring with an angle of about 90° (character 69, state 1); (10) the central groove meets the supraorbital groove (character 76, state 1); (11) the dorsal branch of the main lateral line is present on the posterior dorsolateral plate (character 78, state 1); and (12) the dorsal branch of the main lateral line is present on the median dorsal plate (character 80, state 1).

Figure 10. Strict consensus tree of 220 most parsimonious trees using a revised data set of 98 characters and 37 taxa. Numerical values in the right side of the nodes denote Bremer decay indices. Named nodes: A, Eubrachythoraci; C, Coccosteomorphi; F, Incisoscutoidea; H, Camuropiscidae; J, Aspinothoraci; N, Selenosteidae; Q, Dunkleosteidea; T, Panxiosteidae; U, Dunkleosteidae. Abbreviations: CI, consistency index; CIsct, consistency index of the strict consensus tree; L, length of trees (in evolutionary steps); Lsct, length of the strict consensus tree; n, number of trees; RI, retention index; RIsct, retention index of the strict consensus tree.
by Long (1995), it was later placed amongst the basal Coccosteomorphi (Trinajstic & Dennis-Bryan, 2009; Anderson, 2010), a reassignment corroborated in our analysis.

The Camuropiscidae Dennis & Miles, 1979a (Fig. 10, node H) is a group of Australian eubrachythoracids with a protruding rostrum (Dennis & Miles, 1979a; Denison, 1984; Long, 1988; Gardiner & Miles, 1990; Carr, 1991; Trinajstic & Dennis-Bryan, 2009). In our analysis the monophyly of the Camuropiscidae is characterized by the following six synapomorphies: (1) the rostral plate is not developed posteriorly (character 5, state 0); (2) the central plate tapers anteriorly (character 22, state 0); (3) the extent of the marginal plate along the lateral border of the skull roof is greater than half the length measured from the postorbital process to the postero-lateral corner of the skull roof (character 24, state 1); (4) broad submarginal plate (character 60, state 0); (5) cheek and skull roof overlap well bound (character 62, state 1); and (6) postmarginal without groove (character 85, state 0).

A monophyletic group (Fig. 10, node F) comparable to the superfam-ily Incisoscutoidea Trinajstic & Dennis-Bryan, 2009 is also recognized in our analysis. The group is composed of Incisoscutum, Compagopiscis, and the Camuropiscidae, and is supported by five synapomorphies: (1) the lateral consolidated arch extended laterally (character 2, state 1); (2) the border of the posterior nuchal plate is concave (character 11, state 2); (3) the suborbital plate does not contact with the preorbital plate (character 54, state 0); (4) the width of the prehypophysial shelf of parasphenoid is less than the length, the width of the posthypophysial shelf is greater than the length (character 71, state 1); and (5) the parasphenoid bears a ventromedian crest (character 74, state 1). Incisoscutum or the family Incisoscutoidea Denison, 1984 was considered to be either the sister group of the Camuropiscidae (Denison, 1984; Long, 1988) or in the Pachyosteo-morphi (Dennis & Miles, 1981). In our analysis, Incisoscutum, Compagopiscis, and Camuropiscidae are in polytomy. Compagopiscis was formerly considered to form a monophyletic group with Harrytoombsia and Menamaraspis (Plourdosteidae Gardiner & Miles, 1994; Long, 1995). It is currently nested within the Incisoscutoidea, as in Trinajstic & Dennis-Bryan (2009).

The monophyly of Aspinothoraci is characterized by three synapomorphies: (1) the lateral face of the anterior superognathal plate is enclosed (character 67, state 1); (2) the lateral face of the anterior superognathal bears an occlusal shelf posterior to the lateral cusp (character 88, state 1); and (3) the paired pits on the internal side of the nuchal plate are separated by a median septum (character 97, state 1). Dinichthys herzeri and Hadrosteus rapax are identified to be the basal members of the Aspinothoraci, as in Carr & Hlavin (2010). In the Aspinothoraci, the Selenosteidae Dean, 1901 (Fig. 10, node N) was formerly recognized as a monophyletic group (Lelièvre et al., 1987; Rücklin, 2011). In the current analysis, it includes four taxa: Stenosteus angustopterus, Gymnotrachelus hydei, Rhinosteus parvulus, and Pachyosteus bulla, arranged differently from the scenario of Rücklin (2011). The clade is supported by a Bremer decay index of 3 and by the following seven synapomorphies: (1) the ventral ridge of the median dorsal plate bears a posterior process, but is not spatulate (character 35, state 1); (2) the submarginal plate is loosely associated with the hyomandibular (character 59, state 0); (3) the submarginal plate is broad (character 60, state 0); (4) the inferognathal plate bears an anterior dental field (character 64, state 1); (5) the adsymphyseal denticles are present (character 65, state 1); (6) the posterior supragnathal plate does not bear a dorsal process (character 70, state 0); and (7) the angle between the postorbital and otic branches of the intraorbital sensory line groove is less than 45° (character 75, state 2).

Historically, the superfam-ily Dunkleosteoida can be interchangeable with the family Dinichthyidae (e.g. Janvier, 1996), a basket taxon for various advanced predatory pachyosteomorph arthrodires. The Dinichthyidae, however, has been dismissed after detailed investigation, with its members assigned into the Dunkleosteoida or the Aspinothoraci. Most materials of its type genus Dinichthys are redescribed as belonging to other pachyosteomorph species. The redefined Dinichthys based on fragmental materials is assigned into the Aspinothoraci (Carr & Hlavin, 1995; Carr & Hlavin, 2010). The Dunkleosteoida in the current analysis remains monophyletic, supported by two synapomorphies: (1) the preorbital plate em-bayment of the central plate is developed (character 13, state 2); and (2) the paranuchal plate em-bayment of the central plate is developed (character 14, state 2).

Westralichthys uvagedensis Long, 1987 was originally diagnosed as a ‘dinichthyd’ arthrodire more derived than Eastmanosteus and Golshanichthys (Long, 1987). It is moved to the most basal position of the Dunkleosteoida, being the sister group of all the other members in this superfamily.

Amongst basal Dunkleosteoida, Wang (1979) erected the family Panxiosteidae as an intermediate between the Pholiodsteidae Gross, 1932 and the Dinichthyidae. Recent analyses (Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010) referred the Russian taxa Janiosteus to the monophyletic Panxiosteidae. The close relationship of Panxiosteus with the genus Plourdosteus Ørvig, 1951 was also
revealed by recent analyses (Vézina, 1990; Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010). The phylogenetic position of Plourdosteus has nevertheless undergone several changes. Plourdosteus was initially considered as a coccosteid because it has diagnostic coccosteomorph characters such as a posteriorly enclosed pectoral fenestra (Stensiö, 1942; Örwig, 1951; Miles & Westoll, 1968). Vézina (1990) erected the family Plourdosteidae to include the following genera: Plourdosteus, Panxiosteus, Harrytoombsia, Kimberleyichthys Dennis-Bryan & Miles, 1983b, Janiosteus, and Eldenosteus Miles, 1964, and placed the family as the sister group of the Dunkleosteidae. Gardiner & Miles (1994) later assigned the Plourdosteidae including Gogopiscis, Compagopiscis, Torosteus, Harrytombsia, Plourdosteus, and Kimberleyichthys into the Coccososteomorphi rather than the Pachyosteomorphi. Into this family Long (1995) subsequently added Menamaraspis, which, together with Harrytombsia, is currently assigned into the Coccososteomorphi. Carr & Hlavin (2010) proposed that Plourdosteus could be referred to a better-established Panxiosteidae. Accordingly, the family Plourdosteidae should be dismissed. This taxon cluster is confirmed by the current analysis with five synapomorphies and a Bremer decay index of 2 supporting the clade (Panxiosteidae, Fig. 10, node T). The synapomorphies are as follows: (1) the central plate tapers anteriorly (character 22, state 0); (2) the marginal plate does not contact with the central plate (character 23, state 0); (3) the paranuchal plate does not bear a postnuchal process (character 30, state 0); (4) the ratio of the anterior sensory line junction–pineal foramen distance divided by the anterior sensory line junction–fossa distance is not less than 0.3 and not greater than 0.5 (character 93, state 1); and (5) the position of the junction between the postorbital, paranuchal, and central plates is even to the anterior margin of the nuchal plate (character 96, state 2).

Our analysis also reveals that Protitanichthys and the Panxiosteidae form a clade (Fig. 10, node S), which is supported by four synapomorphies: (1) the lateral consolidated arch is extended laterally (character 2, state 1); (2) the posterior edge of the pineal plate lies posterior to the orbit (character 9, state 1); (3) the posterior border of the median dorsal plate is spinous (character 37, state 1); and (4) the central groove meets the supraorbital groove (character 76, state 1).

The newly added Chinese taxa X. wui and the Australian member of Eastmanosteus (i.e. E. calliaspis) are clustered into a monophyletic clade, nested immediately above the clade comprising the Panxiosteidae and Protitanichthys. This assignment updates the previous coccosteoid placement of X. wui (Wang, 1992a). The three synapomorphies supporting their sister-group relationship (Fig. 10, node V) are: (1) the posterior edge of the pineal plate lies posterior to the orbit (character 9, state 1); (2) the preorbital plate embayment of the central plate is shallow (character 13, state 1); and (3) the ratio of the posterior sensory line junction–fossa distance divided by the anterior sensory line junction–fossa distance is greater than 0.58 (character 92, state 2).

Under the current phylogeny, E. calliaspis does not form a monophyletic group with E. pustulosus, the type species of Eastmanosteus. Future studies will probably result in a new genus for the Australian species. As pointed out by Dennis-Bryan (1987), most of the other species in Eastmanosteus are too poorly known to be taxonomically catalogued with confidence. A detailed phylogenetic review of the genus is hence required, which is, however, beyond the scope of this work.

Kiangyousteus yohii, formerly a Pachyosteomorphi incertae sedis (Carr & Hlavin, 1995; Carr & Hlavin, 2010), can now be nested within the Dunkleosteidea with confidence. It is feasible to define the family Dunkleosteidae to include all other genera in the Dunkleosteidea more closely related to Dunkleosteus than to Panxiosteus. In our analysis, the Dunkleosteidae (Fig. 10, node U, including E. calliaspis, E. pustulosus, X. wui, K. yohii, Golshanichthys asiatica Lelièvre et al., 1981, Het. ingens, and Dunkleosteus) is supported by following five synapomorphies: (1) the interolateral plate contacts the spinal plate laterally (character 40, state 0); (2) the spinal plate does not bear a spinal pit (character 46, state 0); (3) the posterior ventrolateral plate bears a small postpectoral lamina (character 51, state 1); (4) the anterior supragnathal plate in dorsal view forms an open ring approximately with an angle of 90° (character 69, state 1); and (5) the parasphenoid bears a pair of postrolateral process (character 72, state 1).

Heterostius, an enigmatic arthrodire possessing an extremely extended anterior lateral plate, is phylogenetically in a state of flux. Denison (1978) considered it as the sister group of all brachythoracid arthrodires, although he acknowledged that the trunk shield of Heterosteina resembles that of ‘Pachyosteina’. Later, he (Denison, 1984) moved the taxa to a higher phylogenetic position by including it in the Brachythoracii, partly convinced by Young (1981), who proposed a revised cladogram showing heterostiids amongst basal brachythoracid. In our analysis, Heterostius is moved to a much more derived position. It is nested within the Dunkleosteidae, being the sister group of Dunkleosteus. The Heterostius–Dunkleosteus cluster (Fig. 10, node X) is supported by the following six synapomorphies: (1) the external anterior nuchal border is convex...
the full data set (Fig. 10). Compared with the topology of Carr & Hlavin (2010) while retaining their selection of 19 ingroup taxa. Compared with the topology of Carr & Hlavin (2010: fig. 9b), the Aspinothoraci was rendered as a polychotomy; *E. pustulosus*, the Dunkleosteidae (*sensu* Carr & Hlavin, 2010), and the Panxiosteidae are unresolved. However, the modification of codings did not alter the relationship amongst the Coccosteomorphi, the Aspinothoraci, and the Dunkleosteoida (Fig. 11A).

Second, we added eight coccosteomorph taxa into the modified matrix of Carr & Hlavin (2010). The resultant cladogram (Fig. 11B) still favoured the monophyly of the Pachyosteomorphi (Aspinothoraci plus Dunkleosteidae), as in Carr & Hlavin (2010). The internal topology of the Coccosteomorphi is the same as in the cladogram based on the full data set (Fig. 10). Compared with the topology of Carr & Hlavin (2010: fig. 9b), *E. pustulosus* was combined with the Panxiosteidae, forming a monophyletic group that bore a sister-group relationship with the Dunkleosteidae (*sensu* Carr & Hlavin, 2010).

Third, we added seven pachyosteomorph taxa (two aspinothoracoids and five dunkleosteoids) into the modified matrix of Carr & Hlavin (2010). The resultant cladogram (Fig. 11D), like that from the full data set (Fig. 10), combined the Coccosteomorphi and the Aspinothoraci, rather than the Dunkleosteoida and the Aspinothoraci, as sister groups. However, the relationships of dunkleosteoid groups were less well resolved compared with the cladogram obtained from the full data set (Fig. 10).

Finally, as *X. wui* (Wang, 1992a) is the only taxon not included in either Trinajstic & Dennis-Bryan (2009) or Carr & Hlavin (2010), we deleted it from the full data set to detect its potential impact on eubrachythoracid phylogeny. The resulted cladogram (Fig. 11C) showed no difference to that obtained from the full data set (Fig. 10).

Based on the analyses above, the addition of taxa, especially the dunkleosteoid and aspinothoracid arthrodires, rather than the modifications of the codings, played the critical role in the shift of the relationships amongst the Coccosteomorphi, the Aspinothoraci, and the Dunkleosteoida. The internal topologies within these three major groups of the Eubrachythoraci are mostly stable from subset to subset.

**DISCUSSION**

The differences of the current scenario from those obtained in previous analyses may result from either the addition of new taxa or the modifications of the character codings. To detect the impact of these factors on the eubrachythoracid phylogeny respectively, we conducted complementary analyses using different subsets of our full data set.

First, we modified the codings of the matrix in Carr & Hlavin (2010) while retaining their selection of 19 ingroup taxa. Compared with the topology of Carr & Hlavin (2010: fig. 9b), the Aspinothoraci was rendered as a polychotomy; *E. pustulosus*, the Dunkleosteidae (*sensu* Carr & Hlavin, 2010), and the Panxiosteidae are unresolved. However, the modification of codings did not alter the relationship amongst the Coccosteomorphi, the Aspinothoraci, and the Dunkleosteoida (Fig. 11A).

**CONCLUSIONS**

*Kiangyousteus yohii*, a Givetian dunkleosteoid arthrodire from Sichuan (south China), shows a unique character complement with a parasphenoid bearing *Dunkleosteus*-like anterior supragnathal articulations whereas the trunk shield shows resemblances to the Coccosteomorphi. A phylogenetic analysis nested *K. yohii* within the family Dunkleosteidae, which also contains *E. calliaspis*, *X. wui*, *E. pustulosus*, *G. asiatica*, *H. ingens*, and *Dunkleosteus*.

The major difference between the current and several former scenarios of eubrachythoracid phylogeny (Carr, 1991; Trinajstic & Dennis-Bryan, 2009; Carr & Hlavin, 2010) is the combination of Coccosteomorphi and Aspinothoraci, rather than Dunkleosteida and Aspinothoraci, resulting in the paraphyly of the Pachyosteomorphi. We recognized three family-level groups (Camurupiscidae, Selenosteiidae, and Panxiosteidae) as monophyletic clades. New scenarios are proposed. *Westralichthys uwaredensis* is placed as the most basal member of the Dunkleosteidae; *X. wui* is placed as the sister group of *E. calliaspis*, which should be excluded from the genus *Eastmanosteus*; *H. ingens* is nested as the sister group of *Dunkleosteus*.

Our analyses of eubrachythoracid arthrodires reveal the benefits of adding more taxa from different groups and regions. Additionally, the application of cluster analysis in the definition of quantitative characters has been demonstrated to be feasible. In the near future, a more comprehensive matrix, with data from taxa both newly discovered and published but not yet included in cladistic analyses, is essential for the ever-improved understanding of eubrachythoracid phylogeny.

Most eubrachythoracid arthrodires are considered as pelagic long-distance swimmers (Ivanov & Ginter, 1997; Anderson, 2010) and became naturally polydemic at least from the Middle Devonian. Chinese fossils contribute to a number of Middle and Late
Devonian eubrachythoracid taxa; some are not published yet, or were not described in full detail, like *K. yohii*. Further investigations of Chinese eubrachythoracid faunas, in comparison with their counterparts from the rest of the world, could well enhance our knowledge of the origin and dispersal of this group.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


Carr RK. 1996. *Stenosteus angustopectus* sp. nov. from the Cleveland shale (Famennian) of northern Ohio with a review of selenosteid (Placodermi) systematics. *Kirtlandia* 49: 19–43.


Carr RK, Hlavin WJ. 2010. Two new species of *Dunkleosteus* Lehman, 1956, from the Ohio Shale Formation (USA, Famennian) and the Kettle Point Formation (Canada, Upper Devonian), and a cladistic analysis of the Eubrachythoraci (Placodermi, Arthrodira). *Zoological Journal of the Linnean Society* 159: 195–222.


APPENDIX 1

DATA MATRIX

For the character list, see Carr & Hlavin (2010). The codings that agree with Carr & Hlavin (2010) but differ from Trinajstic & Dennis-Bryan (2009) are marked with *; the codings that agree with Trinajstic & Dennis-Bryan (2009) but differ from Carr & Hlavin (2010) are underlined; those differing from both Carr & Hlavin (2010) and Trinajstic & Dennis-Bryan (2009) are marked with ¦ and underlined.

**Buchanosteus confertituberculatus**

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**Camupropiscis laidlaiwi**

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**Coccosteus cuspidatus**

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**Dicksonosteus arcticus**

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**Dinichthys herzeri**

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**Dunkleosteus amblyodoratus**

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**Dunkleosteus raveri**

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**Dunkleosteus terrelli**

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**Eastmanosteus calliaspis**

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APPENDIX 2

TAXA LIST AND SOURCE REFERENCES OF CODING MODIFICATIONS

Buchanosteus confertituberculatus (Young, 1979)
Camuropiscis laidlawi (Dennis & Miles, 1979a)
Coccosteus cuspidatus (Miles & Westoll, 1968)
Compagopiscis croucheri (Gardiner & Miles, 1994)
Dicksonosteus arcticus (Goujet, 1975)
Dinichthys herzeri (Carr & Hlavin, 2010)
Dunkleosteus amblyodoratus (Carr & Hlavin, 2010)
Dunkleosteus raveri (Carr & Hlavin, 2010)
Dunkleosteus terrelli (Denison, 1978)
Eastmanosteus calliaspis (Dennis-Bryan, 1987)
Eastmanosteus pustulosus (Denison, 1978)
Fallocosteus turneri (Long, 1990)
Golshanichthys asiatica (Lelièvre et al., 1981)
Gorgonichthys clarki (Denison, 1978)
Gymnotrachelus hydei (Carr, 1994)
Hadroosteus rapax (Stensiö, 1963)
Harrytoombsia elegans (Miles & Dennis, 1979)
Heintzichthys gouldi (Carr, 1991)
Heterostius ingenus (Örvig, 1969)
Holonema westolli (Miles, 1971)
Homosteus sulcatus (Heintz, 1934; Heintz, 1968)
Incisoscutum ritchiei (Dennis & Miles, 1981)
Incisoscutum sarahae (Long, 1994)
Janioosteus timanicus (Ivanov, 1989)
Kiangyousteus yohii (this paper)
Latocamurus coulthardi (Long, 1988)

Mcnamaraspis kaprios (Long, 1995)
Pachysteus bulla (Stensiö, 1963)
Panxiosteus ocellus (Wang, 1979)
Plourdosteus canadensis (Miles, 1966)
Protitanicthys rockportensis (Miles, 1966)
Rhinosteus parvulus (Stensiö, 1963)
Rolfosteus cainingensis (Dennis & Miles, 1979b)
Stenosteus angustopectus (Carr, 1996)
Tubonasus lennardensis (Dennis & Miles, 1979b)
Westralichthys uwagedensis (Long, 1987)
Xiangshuiosteus wui (Wang, 1992a)

APPENDIX 3

CALCULATION DATA FOR CHARACTERS 92 AND 93 AND SOURCE REFERENCES

Buchanosteus confertituberculatus: r1 (distance c / distance b; Fig. 9A) = 0.56, r2 (distance d / distance b; Fig. 9A) = 0.16; Young, 1979
Camuropiscis laidlawi: r1 = 0.64, r2 = 0.51; Dennis & Miles, 1979b
Coccosteus cuspidatus: r1 = 0.62, r2 = 0.46; Miles & Westoll, 1968
Compagopiscis croucheri: r1 = 0.67, r2 = 0.42; Gardiner & Miles, 1994
Dicksonosteus arcticus: r1 = 0.61, r2 = 0.16; Goujet, 1975
Dunkleosteus terrelli: r1 = 0.41, r2 = 0.16; Denison, 1978
Eastmanosteus calliaspis: r1 = 0.67, r2 = 0.42; Dennis-Bryan, 1987
Eastmanosteus pustulosus: r1 = 0.56, r2 = 0.60; Denison, 1978
Fallocosteus turneri: r1 = 0.63, r2 = 0.39; Long, 1990
Golshanichthys asiatica: r1 = 0.57, r2 = 0.25; Lelièvre et al., 1981
Gorgonichthys clarki: r1 = 0.35, r2 = 0.45; Denison, 1978
Gymnotrachelus hydei: r1 = 0.51, r2 = 0.39; Carr, 1994
Hadroosteus rapax: r1 = 0.47, r2 = 0.75; Stensiö, 1963
Harrytoombsia elegans: r1 = 0.64, r2 = 0.36; Miles & Dennis, 1979
Heintzichthys gouldi: r1 = 0.49, r2 = 0.48; Carr, 1991
Heterostius ingenus: r1 = 0.44, r2 = 0.12; Örvig, 1969
Holonema westolli: r1 = 0.75, r2 = −0.05; Miles, 1971
Homosteus sulcatus: r1 = 0.52, r2 = 0.23; Heintz, 1934
Incisoscutum ritchiei: r1 = 0.64, r2 = 0.54; Dennis & Miles, 1981
Incisoscutum sarahae: r1 = 0.52, r2 = 0.38; Long, 1994
Janioosteus timanicus: r1 = 0.52 r2 = 0.38; Ivanov, 1989
Latocamurus coulthardi: r1 = 0.69, r2 = 0.62; Long, 1988
Menamaraspis kaprios: r1 = 0.68, r2 = 0.41; Long, 1995
**APPENDIX 4**

Characters and character states defining major clades shown in Figure 10

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

Node A: 5 (2), 12*, 15 (0)*, 17, 22, 31, 54*, 57*, 58, 68 (1), 81 (0) *

Node B: 28*, 44*, 93*, 94*;
Node C: 13*, 37*, 41 (0) *, 51 (2) *, 73*, 83, 92 (2) *;
Node D: 3*, 4*, 23 (0) *, 39*, 43*, 66 (0);
Node E, 75*;
Node F, 2*, 11 (2) *, 54 (0) *, 71*, 74*;
Node G, 30 (0), 41*, 48 (0), 51 (0) *, 76*, 77 (0), 80*, 83 (0) *;
Node H, 5 (0) *, 22 (0) *, 24*, 60 (0) *, 62*, 85*, (0) *;
Node I, 37 (0) *, 40 (0) *, 55, 83 (0) *;
Node J, 37 (0) *, 40 (0) *, 55, 83 (0) *;
Node K, 10, 21, 33, 36 (0), 65 (0), 75*, 77 (0), 91 (0);
Node L, 2, 5, 14 (0) *, 23 (0) *, 45 (0) *;
Node M, 11 (2) *, 15 (2) *, 22 (0) *, 24*, 28 (2) *, 34 (0), 61;
Node N, 35*, 59 (0) *, 60 (0) *, 64*, 65*, 70 (0) *, 75 (2) *;
Node O, 20*, 44 (0) *;
Node P, 14*, 25*;
Node Q, 13 (2) *, 14 (2) *;
Node R, 10 (2) *, 16, 21*, 42, 56, 74, 77 (0), 79, 83;
Node S, 2*, 9, 37*, 76*;
Node T, 22 (0) *, 23 (0) *, 30 (0) *, 93*, 96 (2);
Node U, 40 (0) *, 46 (0) *, 51, 69*, 72*;
Node V, 9, 13*, 92 (2) *;
Node W, 24*, 65 (0*), 86*;
Node X, 10*, 13 (0) *, 14 (0) *, 30 (0) *, 36 (0), 92 (0) *;
Node Y, 4 (2) *, 9*, 11 (2) *, 20*, 74 (0).