



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 Dunkleosteidae.

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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 arthrodires 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 Buchanosteoidea 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

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America, and Australia (Trinajstić & Hazelton, 2007; Trinajstić & Dennis-Bryan, 2009; Carr & Hlavin, 2010). Over the past few years, several early arthropods 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 arthropod groups such as phyllolepid and wuttagoonaspids. By contrast, the promising collections of Chinese eubranchyothoracids (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.

Kiangyosteus yohii Liu, 1955, from the Givetian Guanwushan Formation of Sichuan represents the first record of Chinese arthropods (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 arthropod genus *Kiangyosteus*. 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 *Kiangyosteus* 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 parasphenoid of an arthropod. This revision was followed by Denison (1978) and Dennis-Bryan (1995). Based on the similarities of the parasphenoid and anterior lateral plates between *Kiangyosteus* and *Dunkleosteus* Lehman, 1956, Denison (1978) also suggested *Kiangyosteus* as a primitive member of the Dinichthyidae Newberry, 1885. Since the 1990s, computerized phylogenetic analyses have been applied to branchyothoracid systematics (Carr, 1991; Carr & Hlavin, 1995, 2010; Lelièvre, 1995; Trinajstić & Dennis-Bryan, 2009). Initially, *Kiangyosteus* was omitted from the phylogenetic analysis of eubranchyothoracids (Carr, 1991). Carr & Hlavin (1995) later assigned it as *Pachyosteomorphi incertae sedis*. In a recent cladistic analysis of eubranchyothoracid arthropods by Carr & Hlavin (2010), the position of *Kiangyosteus* still remained ambiguous because of the large amount of missing data.

In this work we offer a detailed redescription of *Kiangyosteus yohii* (Fig. 2) and a renewed eubranchyothoracid cladistic analysis, which yields a novel phylogenetic hypothesis and clarifies the relationship of *Kiangyosteus* with other eubranchyothoracid arthropods.

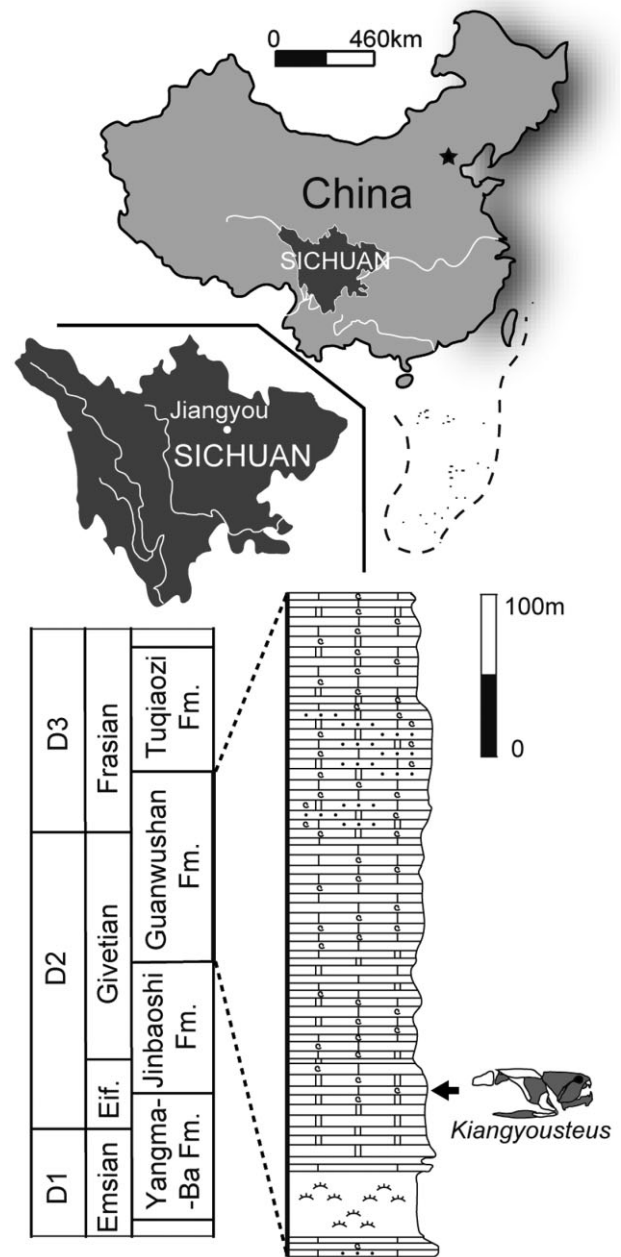


Figure 1. Middle Devonian sequence in Longmenshan area (Sichuan, China), showing the stratigraphical position of *Kiangyosteus yohii*. D1, Early Devonian; D2, Middle Devonian; D3, Late Devonian; Eif., Eifelian; Fm., Formation. Modified after Hou *et al.* (1988).

MATERIAL AND METHODS

ABBREVIATIONS

Institutional abbreviations

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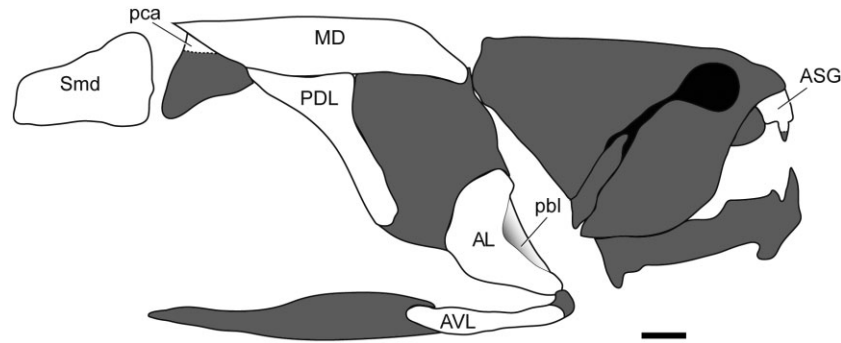


Figure 2. *Kiangyosteus yohii*. Head and trunk shield restored in right lateral view, the preserved parts are shown in white. Abbreviations: AL, anterior lateral plate; ASG, anterior supragnathal; AVL, anterior ventrolateral plate; MD, median dorsal plate; pbl, postbranchial lamina; pca, carinal process of median dorsal keel; PDL, posterior dorsolateral plate; Smd, submedian dorsal plate. Scale bar = 2 cm.

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; dla, dorsal lamina of anterior supragnathal; em.arc, embayment for vertebral arch; em.pb, postbranchial embayment; f.bhy, buccohypophysial foramen; ff.pca, fractured face of the carinal process of median dorsal keel; f.pca, fossa for 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; pl.pr, posterolateral process of parasphenoid; PM, postmarginal 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; CI_{st}, consistency index of the strict consensus tree; L, length of trees (in evolutionary steps); L_{st}, length of the strict consensus tree; n, number of trees; RI, retention index; RI_{st}, retention index of the strict consensus tree.

SYSTEMATIC PALAEOONTOLOGY

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 Dunkleosteioidea Vézina, 1990 more closely related to *Dunkleosteus* than to *Panxiosteus*.

KIANGYOUSTEUS LIU, 1955

Type and only included species

Kiangyousteus yohii Liu, 1955.

Diagnosis

As for the type and only known species.

KIANGYOUSTEUS YOHII LIU, 1955

Holotype

IVPP V801, displaced plates in association, including a right anterior supraghnathal (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 supraghnathal; the median dorsal plate bears a dorsal branch of

the main lateral line; and the anterior supraghnathal bears an occlusal shelf posterior to the lateral cusp.

Morphological description

Head shield: *Anterior supraghnathal* (IVPP V801.8, Fig. 3): The right anterior supraghnathal, 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 supraghnathal 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

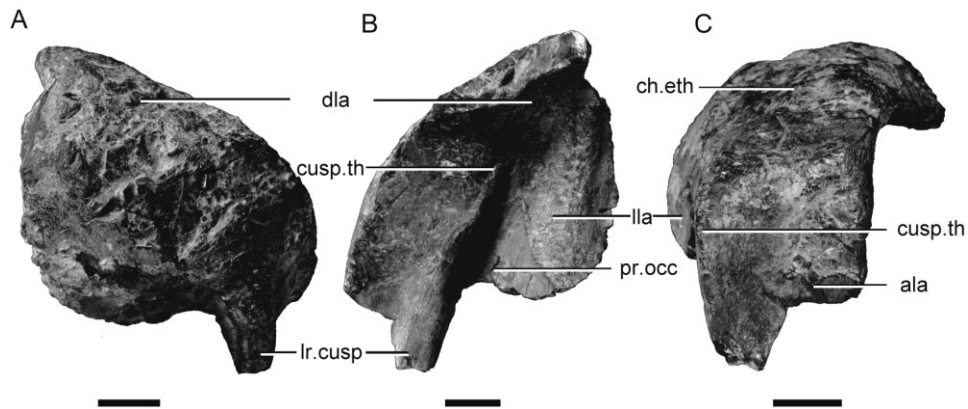


Figure 3. *Kiangyousteus yohii*. Right anterior supraghnathal plate (IVPP801.8) in A, labial, B, lingual, and C, anterior views. Abbreviations: ala, anterior lamina of anterior supraghnathal; ch.eth, channel for neurocranial ethmoid region; cusp.th, lateral thickening for anterior supraghnathal cusp; dla, dorsal lamina of anterior supraghnathal; lla, lateral lamina of anterior supraghnathal; lr.cusp, lateral cusp of anterior supraghnathal; pr.occ, occlusal shelf posterior to the lateral cusp. Scale bars = 1 cm.

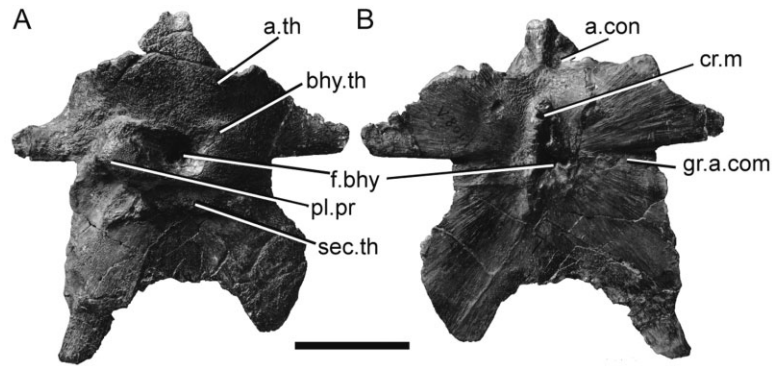


Figure 4. *Kiangyosteus yohii*. Parasphenoid (IVPP801.1) in A, dorsal, and B, ventral views. Abbreviations: a.con, anterior concave region for the articulation with anterior supragnathal; a.th, anterior thickening of parasphenoid; bhy.th, buccohypophysial thickening of the parasphenoid; cr.m, ventral 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.

can be divided into pre- and posthypophysial divisions by the level of the buccohypophysial foramen (f.bhy; Fig. 4A, B). Unlike most arthrodires, the prehypophysial division is short and heavily thickened (a.th; Fig. 4A), with two concave facets for the contact with anterior supragnathals (a.con; Fig. 4B) at its anterior extreme. Amongst the genus *Dunkleosteus*, Carr & Hlavin (2010) identified two contact types between the parasphenoid and supragnathal plates: transverse articular facets in *D. terrelli* and *Dunkleosteus raveri* Carr & Hlavin, 2010, and thickened anterolateral contact face in *Dunkleosteus amblyodoratus* Carr & Hlavin, 2010. *Kiangyosteus* shows transverse facets resembling those of *D. terrelli* and *D. raveri*. The septum between the contact facets forms the anterior process of the 'pentagram'. The posthypophysial division is larger and thinner than the prehypophysial division, with two posterior processes of the 'pentagram' separated by a large gap. A similar posterior profile can also be seen on the parasphenoid of *Dunkleosteus* (Carr & Hlavin, 2010).

Dennis-Bryan (1995) reversed the pre- and posthypophysial regions of the parasphenoid of *Kiangyosteus* from the earlier interpretation by Denison (1978). Carr & Hlavin (2010) followed Denison (1978) regarding the orientation of the plate and suggested an alternative interpretation that the anterior part of the prehypophysial region was incomplete, according to which the restored parasphenoid might resemble the typical pachyosteomorph condition with a longer and thinner-built prehypophysial region. However, based on the comparison with the parasphenoid of *D. terrelli*, we consider that the prehypophysial region is short and almost complete.

The dorsal surface of the plate is coarse. The buccohypophysial thickening (bhy.th; Fig. 4A) bears a

pituitary depression, which accommodates the paired buccohypophysial foramen. The right extremity of the thickening develops a rounded lateral (posterolateral) process (pl.pr; Fig. 4A) as defined by Gardiner & Miles (1990). The absence of process on the left counterpart and the asymmetry of the buccohypophysial thickening may be the result of post-mortem deformation or weathering, as the dorsal surface was exposed when discovered (Liu, 1955). There is no sign of a median hypophysial vein foramen. Posterior to the buccohypophysial thickening is a second weak thickening (sec.th; Fig. 4A), forming two steps. No visible dorsal median groove is present.

The ventral surface is relatively plain and smooth, with only radiation textures visible. The transverse ventral groove (gr.a.com; Fig. 4B) is very shallow, disappearing near the mid-line. Two deep notches are visible at the lateral edges of the plate, giving the plate a pentagram-like outline. An inverted V-shaped prehypophysial ventral median crest (cr.m; Fig. 4B) is present. The anterior end of the crest, forming a downward process, does not reach the anterior edge of the plate, contrary to the conditions observed in *Eastmanosteus pustulosus* Eastman, 1897, and *Eastmanosteus calliaspis* Dennis-Bryan, 1987 (Fig. 5). No tubercular or denticulate ornament is present on any part of the plate. Dennis-Bryan (1995) stated that the parasphenoid of placoderms is species-specific, lacking synapomorphies useful in phylogenetic analysis. Whereas the parasphenoid of *Kiangyosteus* bears specialized features such as the pentagram shape, the extremely shallow ventral groove, and the short inverted V-shaped median crest, it shows definitive similarities to the 'dunkleosteid type' parasphenoid as defined in Stensiö (1963) in possessing articular facets. As will be studied in the following phylogenetic analysis, certain characters of

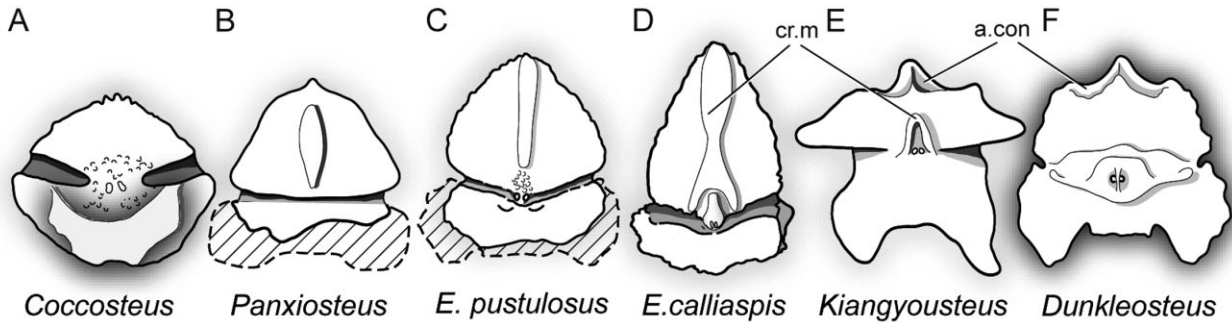


Figure 5. Comparison of eubrachythoracid parasphenoids. Modified after Dennis-Bryan, 1995; Kulczycki, 1956; and Wang, 1979. A, *Coccosteus cuspidatus*, B, *Panxiosteus oculus*, C, *Eastmanosteus pustulosus*, D, *Eastmanosteus calliaspis*, E, *Kiangyousteus yohi*, in ventral views; F, *Dunkleosteus terrelli*, in dorsal view. Abbreviations: a.con, anterior concave region for the articulation with anterior supragnathal; cr.m, ventral median crest of parasphenoid. Not to scale.

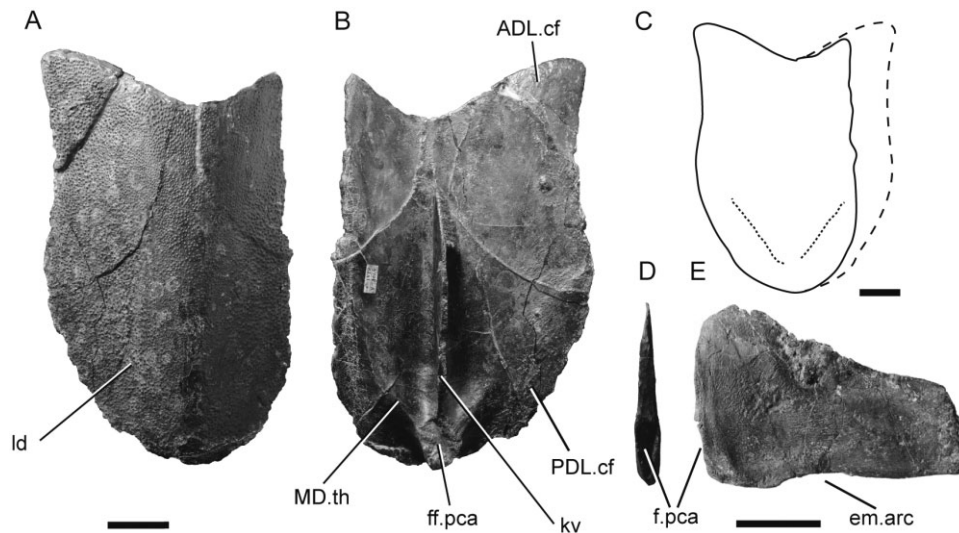


Figure 6. *Kiangyousteus yohii*. Median dorsal plate (IVPP801.4) in A, dorsal, and B, ventral views. C, median dorsal plate in dorsal view with the right part restored by dashed line. Submedian dorsal plate (IVPP801.6) in D, anterior, and E, lateral views. Abbreviations: ADL.cf, contact face for anterior dorsolateral plate; em.arc, embayment for vertebral arch; ff.pca, fractured face of the carinal process of median dorsal keel; f.pca, fossa for the carinal process of median dorsal keel; kv, ventral keel of median dorsal plate; ld, dorsal branch of main lateral line; MD.th, posterior thickening of median dorsal plate; PDL.cf, contact face for posterior dorsolateral plate. Scale bars = 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.

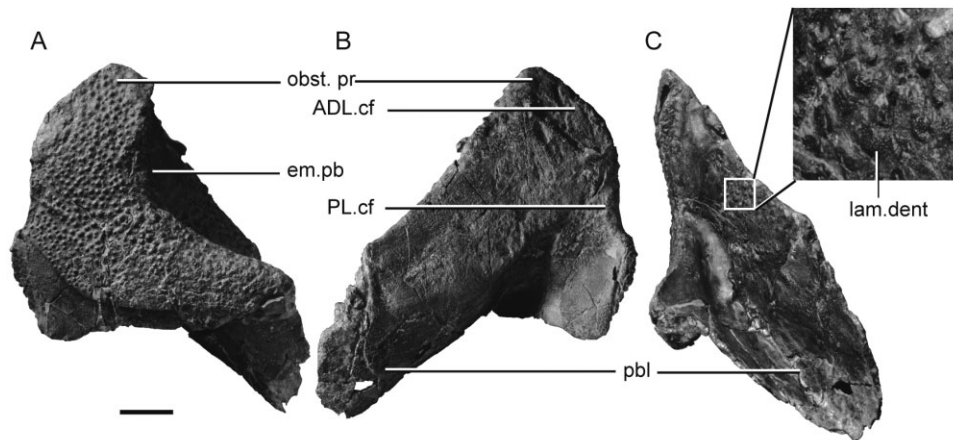


Figure 7. *Kiangyosteus yohii*. Right anterior lateral plate (IVPP801.2) in A, lateral, B, visceral, and C, anterior views, detailing the denticulated area of postbranchial lamina. Abbreviations: ADL.cf, contact face for anterior dorsolateral plate; em.pb, postbranchial embayment; lam.dent, denticles 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.

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.

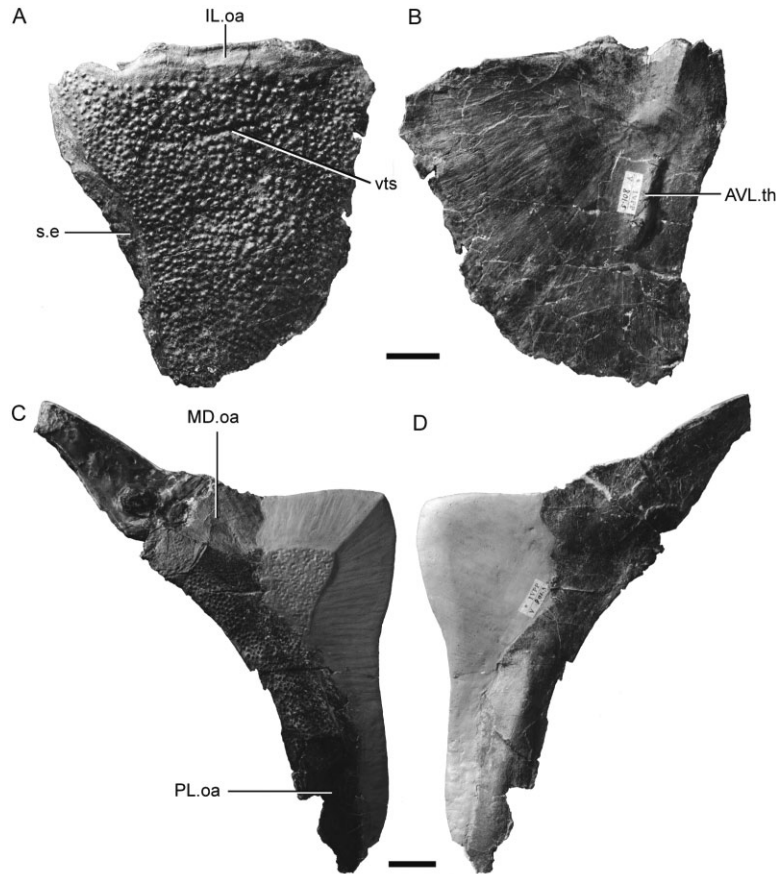


Figure 8. *Kiangyousteus yohii*. Right anterior ventrolateral plate (IVPP801.5) in A, ventral, and B, dorsal (visceral) views. Right posterior dorsolateral plate (IVPP801.3) in C, lateral, and D, mesial views. Abbreviations: AVL.th, ventral thickening of anterior ventrolateral plate; IL.oa, overlap area 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 interrelation-

ships, 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 westolli* 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), Trinajstić & Dennis-Bryan (2009), and Carr & Hlavín (2010), with the exception of a Chinese taxon *Xiangshuiosteus wui* Wang, 1992a. The 98 characters in our data matrix were sourced from Carr & Hlavín (2010). Amongst the 98 characters, 85 characters were first formulated by Carr (1991). Carr & Hlavín (2010) updated or modified six out of 85 characters of Carr (1991), and added the remaining 13 characters.

In the matrix of Carr & Hlavín (2010), characters 92 and 93 were used to reveal the relative position of the posterolateral corner of the skull roof, and the

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, *Cocosteus cuspidatus*, *E. calliaspis*, *Fallocosteus turneri* Long, 1990, *Gorgonichthys clark* Claypole, 1892, *Gymnotrachelus hydei* Dunkle & Bungart, 1939, *Hadrosteus rapax* Gross, 1932, *Harrytoombsia elegans* Miles & Dennis, 1979, *Incisoscutum ritchiei* Dennis & Miles, 1981, *Incisoscutum sarahae* Long, 1994, *Janiosteus timanicus* Ivanov, 1989, *Kiangyosteus yohii*, *Latocamurus coulthardi* Long, 1988, *Mcnamaraspis kaprios* Long, 1995, *Pachyosteus bulla* Jaekel, 1903, *Panxiosteus occullus* Wang, 1979, *Plourdosteus canadensis* Woodward, 1892, *Protitanichthys rockportensis* Case, 1931, *Rhinosteus parvulus* Gross, 1932, *Rolfosteus canningensis* Dennis & Miles, 1979b, *Stenosteus angustopectus* Carr, 1996, and *Tubonasus lennardensis* Dennis & Miles, 1979b (see Appendix 1). The revised matrix was treated 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 ‘maxtrees’ 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 (CI_{st} = 0.3371; RI_{st} = 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 phylog-

eny previously proposed by Carr & Hlavin (2010) in the assignment of Cocosteomorphi and Aspinothoraci as sister groups, rather than Aspinothoraci *sensu* Miles & Dennis, 1979, and Dunkleosteioidea as sister groups. In this topology, ‘Pachyosteomorphi’ appears paraphyletic. *Heterostius 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* Obruchev, 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 Cocosteomorphi 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 Cocosteomorphi and the Pachyosteomorphi, and the bisection of the Pachyosteomorphi into two monophyletic groups, Dunkleosteioidea and Aspinothoraci (Carr, 1991; Trinajstić & 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 parasphenoid 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 Cocosteomorphi (Fig. 10, node C), Aspinothoraci (Fig. 10, node J), and Dunkleosteioidea (Fig. 10, node Q) remain monophyletic. However, Aspinothoraci and Cocosteomorphi are more closely related to each other than either is to Dunkleosteioidea, making Pachyosteomorphi (i.e. Aspinothoraci plus Dunkleosteioidea) paraphyletic. The four synapomorphies supporting the sister-group relationship between Cocosteomorphi 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 Cocosteomorphi is monophyletic (Dennis-Bryan & Miles, 1983a; Carr, 1991, 2004; Trinajstić &

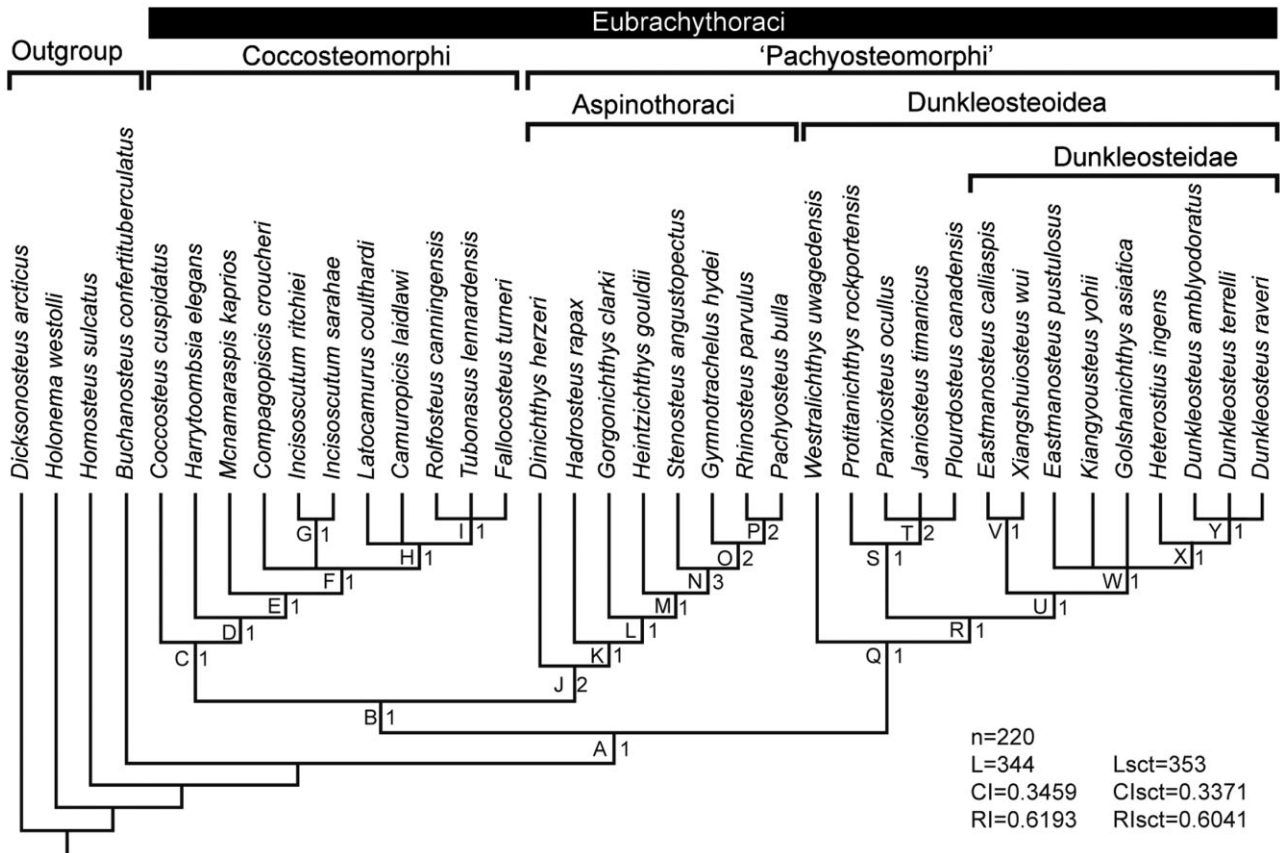


Figure 10. Strict consensus tree of 220 most parsimonious trees using a revised data set of 98 characters and 37 taxa. Numerical values in the right side of the nodes denote Bremer decay indices. Named nodes: A, Eubrachythoraci; C, Coccosteomorphi; F, Incisoscutoidea; H, Camuropiscidae; J, Aspinothoraci; N, Selenosteidae; Q, Dunkleosteioidea; T, Panxiosteidae; U, Dunkleosteidae. Abbreviations: CI, consistency index; CIsc, 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; RIsc, retention index of the strict consensus tree.

Dennis-Bryan, 2009; Carr & Hlavin, 2010). 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 (Trinajstić & Hazelton, 2007; Trinajstić *et al.*, 2007; Long & Trinajstić, 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).

Coccosteus is currently the most basal member in the Coccosteomorphi. The two successive coccosteomorph taxa are *Harrytoombsia* and *Mcnamaraspis*. The basal position of *Harrytoombsia* matches its primitiveness diagnosed by Miles & Dennis (1979), contrary to the statement that it belongs to the more advanced Pachyosteomorphi (Vézina, 1990). Although *Mcnamaraspis* was initially assigned into the Plourdosteidae

by Long (1995), it was later placed amongst the basal Coccosteomorphi (Trinajstić & 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 eubranchyothoracids with a protruding rostrum (Dennis & Miles, 1979a; Denison, 1984; Long, 1988; Gardiner & Miles, 1990; Carr, 1991; Trinajstić & 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 posterolateral 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 superfamily Incisoscutoidea Trinajstić & 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 Incisoscutidae Denison, 1984 was considered to be either the sister group of the Camuropiscidae (Denison, 1984; Long, 1988) or in the Pachyosteomorphi (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 *Mcnamaraspis* (Plourdosteidae Gardiner & Miles, 1994; Long, 1995). It is currently nested within the Incisoscutoidea, as in Trinajstić & 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 angustopectus*, *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 infraorbital sensory line groove is less than 45° (character 75, state 2).

Historically, the superfamily Dunkleosteioidea 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 Dunkleosteioidea 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 Dunkleosteioidea in the current analysis remains monophyletic, supported by two synapomorphies: (1) the preorbital plate embayment of the central plate is developed (character 13, state 2); and (2) the paranuchal plate embayment of the central plate is developed (character 14, state 2).

Westralichthys uwagedensis Long, 1987 was originally diagnosed as a 'dinichthyid' arthrodire more derived than *Eastmanosteus* and *Golshanichthys* (Long, 1987). It is moved to the most basal position of the Dunkleosteioidea, being the sister group of all the other members in this superfamily.

Amongst basal Dunkleosteioidea, Wang (1979) erected the family Panxiosteidae as an intermediate between the Pholidosteidae Gross, 1932 and the Dinichthyidae. Recent analyses (Trinajstić & 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; Trinajstić & 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; Ørving, 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*, *Harrytoombsia*, *Plourdosteus*, and *Kimberleyichthys* into the Coccosteomorphi rather than the Pachyosteomorphi. Into this family Long (1995) subsequently added *Mcnamaraspis*, which, together with *Harrytoombsia*, is currently assigned into the Coccosteomorphi. 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 coccosteid 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.

Kiangyosteus yohii, formerly a Pachyosteomorphi *incertae sedis* (Carr & Hlavin, 1995; Carr & Hlavin, 2010), can now be nested within the Dunkleosteidae with confidence. It is feasible to define the family Dunkleosteidae to include all other genera in the Dunkleosteidae 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 posterolateral 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 *Heterosteus* resembles that of 'Pachyosteina'. Later, he (Denison, 1984) moved the taxa to a higher phylogenetic position by including it in the Brachythoraci, partly convinced by Young (1981), who proposed a revised cladogram showing heterostiids amongst basal brachythoracids. 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

(character 10, state 1); (2) the preorbital plate embayment of the central plate is absent (character 13, state 0); (3) the paranuchal plate embayment of the central plate is absent (character 14, state 0); (4) the postnuchal process of the paranuchal plate on the dermal surface is absent (character 30, state 0); (5) the median dorsal plate is short and broad to equidimensional (character 36, state 0); and (6) the ratio of the posterior sensory line junction–fossa distance divided by the anterior sensory line junction–fossa distance is less than 0.45 (character 92, state 0).

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 Dunkleosteidea (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 Dunkleosteidea), 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 aspinothoracids 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 Dunkleosteidea 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 Trinajstić & 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 Dunkleosteidea. The internal topologies within these three major groups of the Eubrachythoraci are mostly stable from subset to subset.

CONCLUSIONS

Kiangyosteus 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*, *Het. ingens*, and *Dunkleosteus*.

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

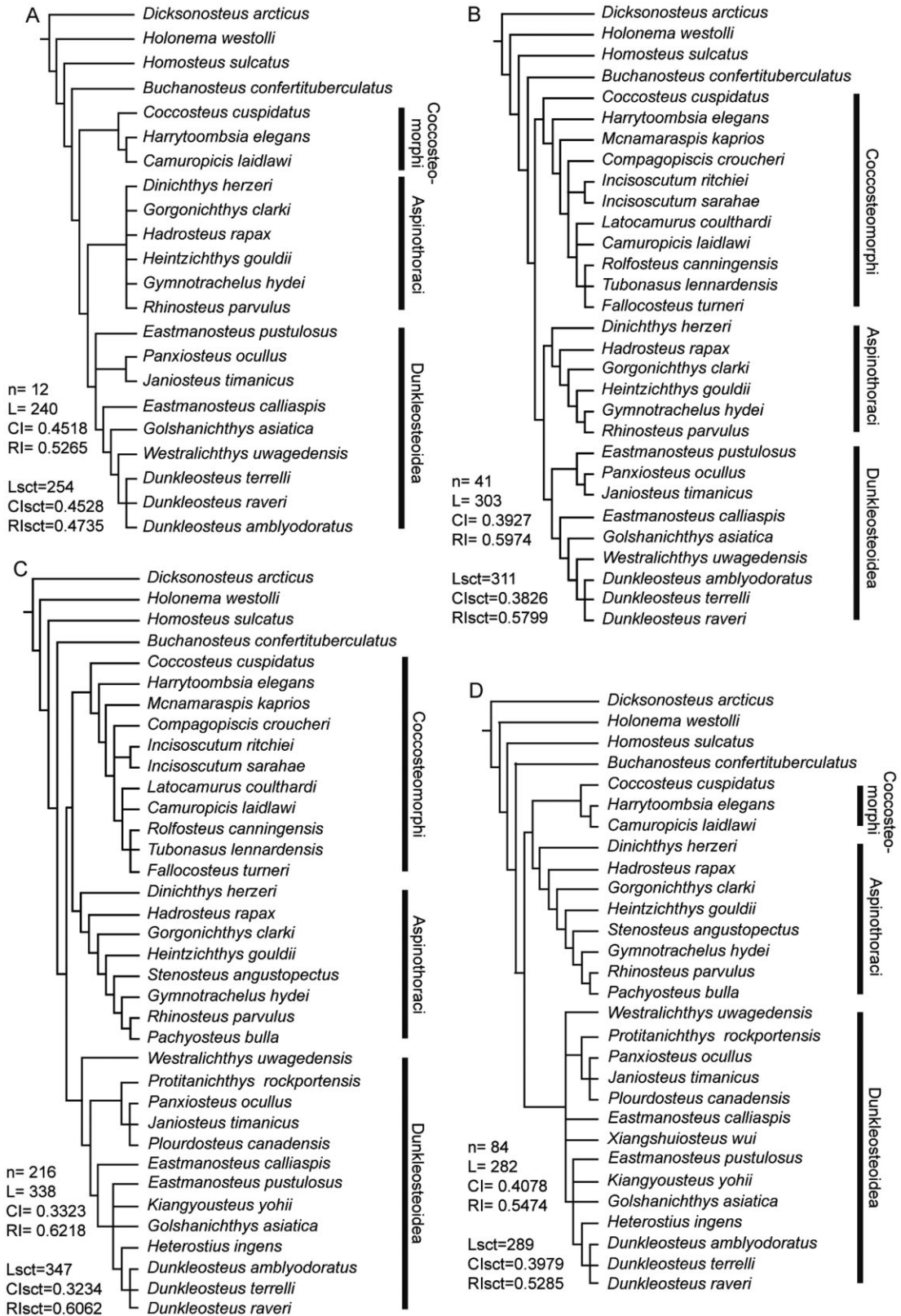


Figure 11. Cladograms of Eubrachythoraci relationships based on the subsets of the full data set. A, strict consensus tree based on the subset with taxa chosen by Carr & Hlavin (2010) and modified codings. B, strict consensus tree based on the subset with new taxa from Coccosteomorphi added. C, strict consensus tree based on the full data set excluding *Xiangshuiosteus wui*. D, strict consensus tree based on the subset with new taxa from Aspinothoraci and Dunkleosteidae added. Abbreviations: CI, consistency index; CI_{st}, consistency index of the strict consensus tree; L, length of trees (in evolutionary steps); L_{st}, length of the strict consensus tree; n, number of trees; RI, retention index; RI_{st}, retention index of the strict consensus tree.

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.

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APPENDIX 1

DATA MATRIX

For the character list, see Carr & Hlavin (2010). The codings that agree with Carr & Hlavin (2010) but differ from Trinajstić & Dennis-Bryan (2009) are

marked with *; the codings that agree with Trinajstić & Dennis-Bryan (2009) but differ from Carr & Hlavin (2010) are underlined; those differing from both Carr & Hlavin (2010) and Trinajstić & Dennis-Bryan (2009) are marked with * and underlined.

Buchanosteus confertituberculatus

?0?0? 0-?00 10012 ?0010 0?110 ??001 01012 1?00?
 ????1 ????? ?1100 00?11 00??? ????? 1??00 01??0
 1(0 1)011 0-??1 11001 -01

Camuropiscis laidlawi

01110 10000 21111 1?11? 00010 11101 1*10?? 111?1
 0?*011 11?0? ?1*110 10?20 011*01* 0*0*1*0*1* ?????1*
 0*1*0*0*0* 0*0*1*1*0* ?????1* 1*2*2*-.* 0*0*?

Coccosteus cuspidatus

10002 0-00(02)* 01120 11(02)*01* 01110 0-101 11012
 11001 00011 110?0 21100 01?11 00101 ?0111 001?0
 11101 00111 0-001 12111 -?1

Compagopiscis croucheri

11112* 00000 2*1111* 012-*0 01000 0-*2*01 1*100*2
 11011 00111 111*10 210*0*0 01111 001*01 01101
 11111 00000 00111 ?????1* 1*2*1*-*.* 0*0*1*

Dicksonosteus arcticus

12000 0-101 00002 00010 1?100 11000 11010 11000
 00001 11110 01000 0??10 00??? ?????0 00000 00010
 00001 0-??0 12000 -?0

Dinichthys herzeri

1???? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ????? ?1101 11101 ????? ????? ????? ?1?? 1???? ?1?

Dunkleosteus amblyodoratus

???? ????
 21??? ????? ????? ????? ????? ????? ????? ????? ?????
 ????? ????? ????? ????? ????? 10??1 1???? ?0?

Dunkleosteus raveri

?0022 0-01? ????? ?12-1 1?1??
 0-00? ?11? ????? ????? ????? ?1?1? ????? ?0??? ?????
 0??00 ????? ?111 11??1 1???? ?1?

Dunkleosteus terrelli

10021 0-011 21000 112-1 11110 0-000 11012 00000
 11-01 0101- 1101011?11 00100 20111 01000 00??0
 00111 11011 00001 -01

Eastmanosteus calliaspis

10102 0-012 01120 112-0* 11100 0-101 11012 10000
 11-01 0111- 11010 11111 00101 (1 2)*0111 11110 00010
 00111 0-0?1 121*0*1* -*01

Eastmanosteus pustulosus

10?02 0-002 01220 ?1000 11110 ???0? 11012
00??? ????? ????? ????? ????? ?010? ?1?? ????? 001?1
????1 ????? 11201 -01

Fallocosteus turneri

01110 10002 0*1111 11110* 00010 11101 11112 10110
00111 ?1111 21101 0???0 01100 00101 ?????*
0*1*0*0*0* 0*0*0*1*0* ?????1 121- 0??

Golshanichthys asiatica

1??0? ?????2 01220 ?1??0 1?1?0 0-?01 1101? ????? ?????
????? ???1? ????? ?0100 2???? ????? 0???? ????11 ????11
11001 -01

Gorgonichthys clarki

11001 0?101 01000 ?12-0 11000 ??101 11112 0000-
1?-?0 -??- ????? ????? ?0100 1110? ????? 00??0 ????1
0-1?1 001*- 011

Gymnotrachelus hydei

10001 0-000 21000 -12-1 00010 -201 11101 0000-
11-00 -??- 01?1?0?00 ?0111 000-0 3???? 00000 00010
0-001 011— 1*11

Hadrosteus rapax

????? ??101 (02)?010 ?12-0 1(01)100 0-101 1110? 00???
1???? ????? ?1?11 0???1 00100 11102 ????? 00??0 00-11
0-?01 01*2*11 -??

Harrytoombsia elegans

10112 0-000 01110 012-0 00000 0-101 10012 11011
0?111 11?10 21?10 011?1 00101 00101 00100 01000
00111 ????? 12*1*- 0*0*1

Heintzichthys gouldi

11?01 0-001 21002 -12-2 10010 -200 11102 0000-
10-10 -010- 11010 01111 10100 11101 01?01 00000
00011 0-101 011—111

Heterostius ingens

1000? 00001 0?002 ?1010 11110 ??0?0 11012 00???
11?00 ????? ?1000 0??11 00??? ????? ????? 00010 00111
????1 10011 -??

Holonema westolli

02002 0-011 10110 ?02-0 00000 0-100 110?1 10011
00101 11010 10000 00010 000?? ?00?0 ????? 01(0 1)1(0
1) 10011 ????? 12*0*- 000

Homosteus sulcatus

10000 0-100 00012 ?12-0 00110 ??010 01??0 00001
1?-?1 01?1- ?1001 0???1 001?? ????? ????? 01?00 11001
????1 11001 -?0

Incisoscutum ritchiei

11112* 0-000 0*1110 011*1*0 01000 1*0100 11012
11011 1*-?1 1101- 01000 01111 00101 00101 10111
10*001 00011 ????? 12*2*-* 0*0*1

Incisoscutum sarahae

11112* 0-000 21110 011*1*0 01000 12100 11012 11011
1?-?1 1101- 01000 01111 00101 00101 10111 10001
00011 ????? 11*1*-* 0*0*1

Janiosteus timanicus

????? ?012 ?22? ????? 000?0 ????0
110?? ????? ????? ????? ????? ????? ?0??? ????? ?????
1???? ????1 ????? 11*1*- 2??

Kiangyousteus yohii

????? ????? ????? ????? ????? ????? ????? 10??? ?1??1
?1?1? ????? ????? ????? ?1?-1 0101? ?0?1 ????? 111??
1???? ???

Latocamurus coulthardi

11110 0-102 2111? 01100 00010 11100 11102 11011
0?011 ????? 21?01 011?0 01100 00101 31111 01000
00110 ????? 12*2*-* 1*0*1

Mcnamaraspis kaprios

10112 00000 01110 012-*0 01000 0?1*0*1* 11*0*1*2
11011 00111 11010 210*10 01111 001*01 00*101
0*110*1 01000 00111 ?????* 1*2*1*-* 0*0*1

Pachyosteus bulla

?1??1 0-001 2?012 ?12-1 100?1 0-201 1110? ????- 1?-??
????- ?1?100???? 1?1?? ????? 1*?00*2 0???? 0??11 0-??1
012- 0?1

Panxiosteus ocullus

1*1*0*1*2 0-002 1*1*220 ?12-0 10010 0-000 11012*
?1*??? ????? ????? ?1*0*?? 1???? ?0??? ?0101 0??10
1????* 0*0*1*11 0-0?1 111- 20*1*

Plourdosteus canadensis

????2 0-012 01220 ?12-1 10000 0-000 1001? 110??
01-?1 ????- 010110???? 00101 20101 ????? 1???? 00111
0-001 11*1*-* 2*01

Protitanichthys rockportensis

111?2 00012 11220 112-*1 11100 0?00*1 11011 11001
11001 1111? 01010 1??01 00111 10102 ????? 10010
?*0110 0?0?1 11*0*0*1* -???

Rhinosteus parvulus

1???? 0-001 2?012 ?1112 10111 0-201 1010? 0000-
1?-00 -??- ?1?11 ????? 11111 ?????2 ?????2 00000 00111
????1 021*01 -??

Rolfosteus canningensis

?*1110 11000 01101 01110 00000 11101 110?2 10110
0?*111 11?*?0 21101 011?0 0110? ?0101 —11 01101
00010 -???1 12*1*- 0?1

Stenosteus angustopectus

11001 0-001 21002 -12-0 101?? -201 11101 0000-
10-10 -???- 01?1? 01?00 10111 ???0? ???2? ?0000 00-1?
0-?01 01*1*1*1* -*?1

Tubonasmus lennardensis

?*1?*?0 11002 21111 01110 000?0 11101 111?2 ??110
0?*111 1??0 21?01 ???*0 0110? ?0101 ?00?1 01000
00010 -???1 121*- 0?1

Westralichthys uwagedensis

?002? ???0 0122? ?1?0 0?100 ??001 1101? ????? ?????
????? ???1? ????? 00?? ???? ???? 0???? ????1 ?????1
00001 -01

Xiangshuiosteus wui

????0 0-112 0?122 ?12-1 10100 ??001 1101? ????? ?????
????? ????? ????? ????? ????? ???? 0???? ????1 ?????1
12000 -??

APPENDIX 2

TAXA LIST AND SOURCE REFERENCES OF
CODING MODIFICATIONS

Buchanosteus confertituberculatus (Young, 1979)
Camuropiscis laidlawi (Dennis & Miles, 1979a)
Cocosteus 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)
Fallicosteus turneri (Long, 1990)
Golshanichthys asiatica (Lelièvre *et al.*, 1981)
Gorgonichthys clarki (Denison, 1978)
Gymnotrachelus hydei (Carr, 1994)
Hadrosteus rapax (Stensiö, 1963)
Harrytoombsia elegans (Miles & Dennis, 1979)
Heintzichthys gouldi (Carr, 1991)
Heterostius ingens (Ørvig, 1969)
Holonema westolli (Miles, 1971)
Homosteus sulcatus (Heintz, 1934; Heintz, 1968)
Incisoscutum ritchiei (Dennis & Miles, 1981)
Incisoscutum sarahae (Long, 1994)
Janiosteus timanicus (Ivanov, 1989)
Kiangyousteus yohii (this paper)
Latocamurus coulthardi (Long, 1988)

Mcnamaraspis kaprios (Long, 1995)

Pachyosteus bulla (Stensiö, 1963)
Panxiosteus ocullus (Wang, 1979)
Plourdosteus canadensis (Miles, 1966)
Protitanichthys rockportensis (Miles, 1966)
Rhinosteus parvulus (Stensiö, 1963)
Rolfosteus canningensis (Dennis & Miles, 1979b)
Stenosteus angustopectus (Carr, 1996)
Tubonasmus 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
Cocosteus 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
Fallicosteus 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
Hadrosteus 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 ingens: $r1$ = 0.44, $r2$ = 0.12; Ørvig, 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
Janiosteus timanicus: $r1$ = 0.52, $r2$ = 0.38; Ivanov, 1989
Latocamurus coulthardi: $r1$ = 0.69, $r2$ = 0.62; Long, 1988
Mcnamaraspis kaprios: $r1$ = 0.68, $r2$ = 0.41; Long, 1995

Pachyosteus bulla: $r1 = 0.56$, $r2 = 0.70$; Stensiö, 1963
Panxiosteus ocellus: $r1 = 0.48$, $r2 = 0.39$; Wang, 1979
Plourdosteus canadensis: $r1 = 0.54$ $r2 = 0.42$; Miles, 1966

Protitanichthys rockportensis: $r1 = 0.58$, $r2 = 0.23$; Miles, 1966

Rhinosteus parvulus: $r1 = 0.64$, $r2 = 0.38$; Stensiö, 1963

Rolfosteus canningensis: $r1 = 0.59$, $r2 = 0.43$; Dennis & Miles, 1979a

Stenosteus angustopectus: $r1 = 0.46$, $r2 = 0.50$; Carr, 1996

Tubonasus lennardensis: $r1 = 0.61$, $r2 = 0.41$; Dennis & Miles, 1979a

Westralichthys uwagedensis: $r1 = 0.43$ $r2 = 0.13$; Long, 1987

Xiangshuiosteus wui: $r1 = 0.66$ $r2 = 0.11$; Wang, 1992a

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, 67*, 88*, 97*;

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).