

Fossils from South China redefine the ancestral euarthropod body plan

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SUPPLEMENTARY TEXT

Systematic palaeontology

Superphylum Panarthropoda Nielsen, 1995

Phylum Euarthropoda Lankester, 1904

Clade Heptopodomera Aria, Caron and Gaines, 2015

Class Megacheira Hou and Bergström, 1997

Diagnosis (emended from Hou and Bergström, 1997). Heptopodomeran euarthropods with the following characters: large and prominent pair of multi-chelate frontalmost appendages made of five podomeres; a simple cephalic shield covering two to three pairs of appendages with little to no morphological differentiation for food processing; series of homonomous trunk tergo-pleurae folded around the sub-cylindrical body; simple biramous trunk appendages with non enditic heptopodomerous endopods, robust basipods, and paddle-shaped exopods fringed at least medio-distally with contiguous oblanceolate lamellae. Tailpiece a telson.

Remark. We reuse the Class Megacheira to simplify the diagnosis of our new genus, but the monophyly of this taxon remains uncertain (see discussion herein on phylogenetic results). We consider that *Parapeytoia* should belong to this group and thus leave open any statement about the differentiation of basipods, in this case as masticatory gnathobases.

Family Jianfengiidae Aria, Zhao, Zeng, Guo and Zhu, fam. nov.

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Diagnosis. Megacheirans with the following characters: lateral eyes pedunculate; head shield formed by at least the first four anterior somites; well-marked traces of segmental boundaries in head shield; multisegmented trunk (segment number ≥ 20); trunk appendages long: exopod elongate, endopods made of elongate podomeres.

Type genus. *Jianfengia* Hou, 1987.

Other included taxa. *Fortiforceps foliosa* Hou and Bergström, 1997; *Sklerolibyon maomima* gen. et. sp. nov. Possibly includes *Parapeytoia yunnanensis* Hou et al., 1995.

Remark. It is uncertain whether *Parapeytoia* should belong to this family. The presence of *Fortiforceps*-like frontal appendages combined with many morphological uncertainties (e.g. head anatomy, number of trunk segments) is optimized in our phylogeny as an inclusion of *Parapeytoia* within Jianfengiidae with strong support. However, the presence of masticatory gnathobases and the lack of elongate endopod podomeres suggest this taxon is more derived, perhaps sister to Arachnomorpha (sensu Aria 2019). To clarify this, a reexamination of the holotype and additional specimens would be much needed. We note that Hou and Bergström (1997) erected the monospecific family Fortiforcipidae and order Fortiforcipida based on *Fortiforceps foliosa*. These taxonomic ranks are redundant and were not justified with respect to close megacheiran relatives, including the previously described *Jianfengia*. We therefore do not make use of them in this study.

Genus *Sklerolibyon* Aria, Zhao, Zeng, Guo and Zhu, gen. nov.

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Etymology. From the Greek *σκληρός* (sklēros) and *λίβυον* (líbyon), meaning respectively “hard” and “wild lotus,” owing to the flower-shaped frontal appendages and armoured body of this fossil arthropod from South China.

Type and only species. *Sklerolibyon maomima* (see below).

Diagnosis. Jianfengioid megacheiran with the following characteristics: Body length 25 mm (without frontal appendages and telson); frontalmost appendages with long (ca. twice as long as anterior section of head shield), curved basal podomere and stout chalice-shaped peduncle; short armoured head shield representing the fusion and compression of the first three segments (or first four somites) and part of segment 4; antero-lateral margins of head shield produced into prominent gladius-shaped lateral spines; segment 5 shorter than trunk segments but with similar dorsal armature, seemingly also fused to the anterior shield; appendages of segment 5 biramous, likely smaller than further posterior appendages; appendages of segments 2-4 smaller than appendages of segment 5, seemingly $2/3^{\text{rd}}$ of length of cephalic spine; trunk 33-segmented; each trunk segment divided out by two cuticular half-rings: one of these elevated cuticular ridges placed posteriorly at the points of articulation and contiguous with adjacent segments, while the other divides the segment transversally into a longer anterior part and shorter posterior part; intermediary half-ring with medial effacement interrupting the closure of the ring, although said effacement is somewhat attenuated in posteriormost segments; trunk pleurae likely short and little developed.

Remark. The delimitation of the head tagma is somewhat ambiguous, because segment boundaries are confounded with their marginal armature, also present in the head shield. The fifth pair of cephalic appendages and corresponding segment seem to be part of the cephalon, which would therefore result in a five-segmented head tagma. The posterior margin of the “genal” spines of the head shield, however, are located within segment 4, which would imply an anatomy that is more consistent with the known megacheiran body plan. For simplicity and to facilitate comparison with *Jianfengia*, we consider segment 5 as part of the trunk (but see main text).

Sklerolibyon maomima Aria, Zhao, Zeng, Guo and Zhu, sp. nov.

Figs. 1c, d, 3d, Extended Data Fig. 1a, b

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Synonymy

“*Pseudoiulia cambriensis*”, 2016 Strausfeld et al. p. 160, fig. 5B

Etymology. A combination of the Chinese 矛 (Máo) and the Latin “mimus,” together meaning “spear-like,” owing to the elongate and tapering antero-posterior silhouette of the animal, with long and adorned limbs giving a feathery aspect not unlike the collar of ancient Chinese spears.

Holotype. NIGPAS 169962.

Other material. YKLP 11350.

Occurrence. Locality of Mafang, Haikou A.D., district of Xishan, city of Kunming, Yunnan Province, China, within the Maotianshan Shale Member of the Yu’anshan Formation (Cambrian Series 2, Stage 3, *Eoredlichia-Wutingaspis* Trilobite Assemblage Zone).

Diagnosis. As per genus.

Description. *Habitus and tagmatization.* Small (25 mm without frontal appendages and tailpiece), very elongate and multisegmented arthropod with biramous limbs and prominent, raptorial frontal appendages. Body composed of 39 somites arranged into a five-somitic head and a 34-somitic trunk. Well-developed lateral spines on the anterior portion of the cephalic

shield and markedly reinforced trunk segments. Pleurae poorly developed, body a narrow, posteriad-tapering tube with sub-quadratic section.

Frontalmost appendages. Five-podomorous “great appendages” of the yohoiid type, i.e., ending in four imbricated podomeres produced ventro-distally into elongate spines. Basis (podomere 1) very elongate (width ca. $1/5^{\text{th}}$ of length of frontal head shield; length $4/3^{\text{rd}}$ of that of frontal head shield), slightly curving dorsally. Peduncle (podomere 2) remarkably large, chalice-shaped, articulated with the basis so that the multi-chelate portion of the appendage is oriented dorsally; ventro-distal spine likely aligned with spine tips of more distal podomeres, reaching ca. the same length as the peduncle, i.e., $2/3^{\text{rd}}$ of basis length.

Eyes and inter-ocular area. One pair of well-developed, pedunculate lateral eyes. Eyes large, elliptical (major axis slightly inferior to half of cephalic width [without lateral spines]), protruding latero-frontally beneath head shield. Peduncles short. Median structures and presence of median eyes unknown.

Cephalon. Head tagma encompassing the first five somites. Tergites of segments 1 to 3 (=somites 2 to 4) fused into a ventrally bent almond-shaped shield, with long (ca. equal to width of shield proper) gladius-like spines produced on each side. Tergite of segment 4 expressed as a pseudo-segment with first half integrated to the anterior, spine-bearing portion of the head shield, and second half contiguous with the posterior margin of the cephalic spines and the anterior margin of segment 5. The frontal shield is shaped by a complex set of grooves and ridges: a frontal lip is followed centrally by a depression marking the anterior limit of the shield’s dome; laterally, the frontal rim extends into the elevated medial axis of the lateral spines, and projects continuously behind the central dome to form the occipital margin of the frontal shield; an additional, less pronounced depression precedes the occipital lip of the shield. At a distance approximately equal to $1/5^{\text{th}}$ of the frontal shield, posterior to the occipital lip of this shield, is another ridge delimiting the posterior margin of segment 4 (somite 5); posterior to this ridge lies segment 5, delimited posteriorly by a more or less rounded transverse carina and with an intermediate carina akin to those of trunk segments but only slightly closer to the posterior margin.

Cephalic appendages. Appendages of segment 5 biramous and likely similar in structure to trunk appendages, although seemingly shorter by a fourth or a fifth of their length. Appendages of segment 4 about $2/3^{\text{rd}}$ shorter than appendages of segment 5; proximally, the limb bears a typically enlarged and undifferentiated basipod, and likely also an exopod. The exact podomere count for cephalic endopods is unknown; however, in comparison to what is known in *Jianfengia*, *Fortiforceps* and other megacheirans, we construe that, in the head, endopods of at least segment 4 are likely heptapodomorous.

Trunk. Post-cephalic tagma 34-segmented. Trunk segments are delimited by carinate half-rings at the points of articulation. Additionally, each trunk segment is divided into asymmetric anterior and posterior halves by another half-ring; anterior segmental interval ca. 2.5 times length of posterior part in anterior segments, and reduced to less than twice in posteriormost segments; medial effacement of the intermediary half-rings from the back of the frontal shield to last trunk tergite interrupting the closure of the rings dorsally, although said effacement is attenuated in posteriormost segments. Trunk pleurae likely short and little developed, with body forming a narrow, posteriad-tapering tube with sub-quadratic section.

Trunk appendages. Trunk appendages of general megacheiran structure: biramous, with large undifferentiated basipod bearing elongate endopods and paddle-shaped exopods fringed with likely oblancheolate lamellae. Endopods and exopods remarkably long and elongate, with endopods reaching up to four times the height of the corresponding segment, and exopods up to four times as long as wide. Whether the basis is composed of a single podomere is unknown; exopod attachment also unknown.

Tailpiece. Tailpiece unknown.

Remark. YKLP 11350 was previously assigned to *Pseudoiulia cambriensis* Hou and Bergström, 1998 [3]; however, *Pseudoiulia* has wide tergites with short but well-developed pleurae and segments lack strong ornamentation [2, 4]. YKLP 11350 instead presents all the characteristics of *Sklerolibyon maomima* as described above, including the characteristic segmental ornamentation. YKLP 11352 in ref. [3] was also referred to as *Pseudoiulia*, but the original documentation is insufficient to confidently identify this specimen. Based on the presence of anterior cephalic spines (see main text), it would seem to belong instead to *Jianfengia*.

Owing to the very small size of the last visible segments on the part of the holotype, we consider very likely that they terminate the body and that the posteriormost piece of cuticle broken through by the fracture in the sample is in fact part of the telson. Thus the total somite count is probably accurate, despite the specimen being technically incomplete. The unusual modification and thickening of the exoskeleton indicate that, in spite of a lack of biomineralization, the cuticle was likely hardened by polymers of chitin and other proteins.

Supplementary Discussion

Neural tissues in *Lyrarapax*. Cong and colleagues [5] introduced a new radiodontan from the Chengjiang biota in China with compact body and atypical frontal appendages. They also described carbon-rich patches in the eyes and anterior portion of the head. A single specimen (YKLP 13305) preserves such patches at the very front of the head that the authors interpreted as nerves originating from the protocerebrum and innervating the frontal appendages. Good candidates for arthropod nerves have now been described in several taxa from either the Burgess Shale [6, 7] or the Chengjiang Lagerstätten [8], and, as nerves, consistently preserve as filaments running through podomeres or body segments. In the case of *Lyrarapax*, the features documented are large, bulbous, and have delimited extents on both left and right sides, strongly suggesting they do not project further into the appendages but remain in or overlap their bases. These structures thus clearly differ from known preserved nerves in BST deposits. Being internal, prominent, paired and projecting from an anteriormost carbon patch, there is however little doubt that they are organs related to the central nervous system. It is also important to note that they are located underneath the rounded frontal sclerite, which is slightly displaced anteriorly in YKLP 13305. A much more plausible interpretation to us is therefore that these structures are sensory organs (and their tracts) of the inter-ocular complex as described in many early euarthropods [7, 9-11]. Alternatively, based on the relief patterns documented in their Fig. 2b, as well as the margin delimitations of the overall frontal structures, it is also possible that these traces are simply more reflective parts of the central ocular tract, with posterior carbon imprints related to the frontal appendages and/or the mouth. The absence of replication of this evidence in the form of additional specimens renders a final assessment difficult.

Brain morphology in cf. *Alalcomenaeus*. Tanaka et al. [12] provided a detailed description of internal remains in a small leptochoeliid possibly related to *Alalcomenaeus*. It is clear from the distribution of pyrite analyzed both through the elemental mapping of Fe and Micro-CT scanning that the traces highlighted in YKLP 11075 are overlapping features from the outer cuticle, the appendages and internal organs including the gut and, possibly, the CNS as well as other tissues originally compressed into the same kerogen layer. There is no clear rationale to explain why the mapping of iron and the Micro-CT (with these specific settings) could have isolated the CNS better than other elements or methods. The lack of redundancy for such evidence points to a possible taphonomical bias. While neural tissues may well be preserved in this specimen, it has not been clearly discriminated from other tissues, most probably because it is simply not possible based on an original dorso-ventral compression followed by non-

specific replacement by clay minerals and pyrite. Further tentative interpretations regarding the morphology of the brain are thus equally dubious.

Supplementary references

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