
Supplementary information

***Urokodia* sheds light on the origin of chelicerae and book gills of Chelicerata**

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***Urokodia* illuminates the origin of chelicerae and book gills of Chelicerata**

Yu Liu^{1,2,3,4*†}, Lorenzo Lustri^{1,2†}, Huijuan Mai^{1,2}, Mark Williams^{2,3}, Liming Liu^{1,2}, Yani Tang^{1,2}, Thomas H.P. Harvey^{2,3}, Xianguang Hou^{1,2*}

¹Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University; Kunming, China.

²MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Institute of Palaeontology, Yunnan University; Kunming, China.

³School of Geography, Geology and the Environment, University of Leicester; Leicester, UK.

⁴Guilin University of Electronic Technology; Guilin, China.

† These authors contributed equally to this work.

*Corresponding authors. Emails: yu.liu@ynu.edu.cn; xghou@ynu.edu.cn

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Supplementary Text and References

Supplementary Table 1

Supplementary Text

Systematic palaeontology

Euarthropoda Lankester, 1904¹

Cheliceromorpha Boudreaux, 1979²

Included taxa. Jianfengiidae Aria, Zhao, Zeng, Guo and Zhu, 2020³; Leancoiliida Størmer 1944⁴; Habeliida Aria and Caron, 2017⁵; Mollisoniida Lerosey-Aubril et al., 2020⁶; Pycnogonida Latreille, 1810⁷; Offacolidae Sutton, Briggs, Siveter, Siveter and Orr, 2002⁸; Prosomapoda, Lamsdell 2013⁹.

Remarks. Our phylogenetic analyses retrieve a monophyletic Cheliceromorpha. We refrain from the usage of Cheiromorpha in ref. 10, in the included taxa section of Cheliceromorpha and instead use Jianfengiidae from ref. 3 and Leancoiliida from ref. 4, as Cheiromorpha is paraphyletic in our phylogenetic analyses and its validity remains uncertain.

Emended diagnosis. Deuteropods¹¹ with a cephalic shield encompassing a first pair of raptorial appendages (deutocerebral appendages) with a reduced number of articles (six or less) followed by three to five other pairs of appendages with well-developed endopods and exopods possibly reduced, tubulaceous, or secondarily lost, and the presence of exites with overlapping lamellae, secondarily evolved into the book gills lamellae

Remarks. Definition of lower and upper stem Chelicerata according to the evolution of chelicerae and book gills illustrated by *Urokodia*. We refrain from revising the definition of Chelicerata, which in its current form¹² remains valid for defining the crown group. Instead, we focus on discussing the implications of *Urokodia* for understanding the transition from lower to upper stem and to Chelicerata *sensu stricto*. The exceptional anatomy of *Urokodia* fills an important gap in the transition from lower stem megacheiran-like morphologies (Figs. 1–3) to habeliids, mollisoniids, and ultimately toward Chelicerata *sensu stricto*. *Urokodia* documents three key anatomical transformations in the group, allowing us to formally define them: the progressive tagmosis of the cephalic shield into a prosoma; the transformation of the first pair of raptorial appendages from great appendages to chelicerae; and the transition from megacheiran-like trunk appendages to book gills.

Here we characterize, based on these three features, what can be defined as the lower and upper stem chelicerates. In contrast, Chelicerata *sensu stricto* is exemplified by *Megachelicerax cousteau*¹³, which exhibits a modern-like organization, including a fully differentiated prosoma, true chelicerae, and lamellated gills. Although an operculum has not been described, it was likely present, and the number of lamellae greatly exceeds that observed in the overlapping flaps of the exites of megacheirans and mollisoniids.

According to this framework and our phylogenetic analyses, megacherians plus Chelicerata make a monophyletic Cheliceromorpha (equal to total-group Chelicerata in ref. 13). Megacheirans are lower stem Chelicerata (Fig. 3b). The lower stem is characterized by a relatively low degree of tagmosis, with 5–6 segments (including the ocular segment) incorporated beneath the head shield, and deutocerebral appendages being multichelate, bearing three or more likely functional chelae and a limited degree of post deutocerebral appendage specialization compared to more crown-ward groups. The trunk possesses exites with overlapping flaps (up to four), relatively small in surface area, associated with an exopod bearing well-developed lamellae and a functional endopod.

The upper stem chelicerates include Mollisoniida, *Urokodia* and habeliids. Due to the uncertainty regarding the morphology of habeliid chelicerae and the presence of exites, we have divided the upper stem into two grades.

Mollisoniida and *Urokodia* represent the upper stem grade 1. Within this upper stem, the deutocerebral appendages exhibit a reduction and consolidation from multiple chelae into a single pair, as seen in the short pincer-like great appendages of *Urokodia*. This transformation represents a key step toward the chelicerate condition observed in Chelicerata *sensu stricto* such as *Megachelicerax*¹³. The chelicerate anatomy of *Mollisonia* has been questioned by several authors^{14,15}; further study of the material is needed to determine whether mollisoniids possessed appendages more similar to the single pincer-like structures with vestigial segmentation of *Urokodia* or to more crown-ward chelicerae by lacking any trace of vestigial segmentation. The transition of upper stem grade 1 toward the chelicerae of Chelicerata *sensu stricto* is accompanied by an advanced degree of tagmosis, with one ocular segment and six appendage-bearing segments incorporated beneath the head shield and a moderate level of appendage specialization. The trunk appendages further reflect this intermediate status.

Habeliids represent the upper stem grade 2. Their deutocerebral appendages remain unknown, but are likely short and uniramous, representing a potentially apomorphic condition within the group. It is interesting to note that the deutocerebral appendages of mollisoniids, habeliids, and *Urokodia* may all differ. If this is the case, the lower stem phase of chelicerate evolution may have been characterized by a period of extensive evolutionary experimentation. To assess this possibility, further study is needed to provide a better understanding of the anatomy of these crucial appendages in mollisoniids and habeliids. Despite this uncertainty, habeliids exhibit a markedly advanced degree of prosomal tagmosis, with one ocular segment and six appendage-bearing segments incorporated beneath the prosomal shield and a clear differentiation between post-deutocerebral prosomal appendages and those of the opisthosoma. Their opisthosomal appendages are poorly known, and exites have never been observed, but they appear to be strongly derived,

notably displaying a paddle-like exopodial morphology that has been suggested to be homologous to the seventh appendage pair of offacolids; however, this homology is rendered uncertain under the present phylogenetic framework. Their placement within the upper stem chelicerates (Fig. 3b) is primarily grounded in their prosomal tagmosis, which is considered more crown-ward than that of *Urokodia* and Mollisoniida due to the presence of truly specialized prosomal appendages. These include biramous appendages with tubuliaceous exopodal rami (see supplementary material in ref. 13, their table 1 for a summary of the nomenclature of this type of appendage in chelicerates), which are also found in more derived Chelicerata *sensu stricto*, such as the Offacolids. The absence of certain information regarding the morphology of the key character for this grade, like deutocerebral appendage morphology and thoracic appendages, is a major source of uncertainty and likely explains its different position among all our phylogenetic analyses iterations.

In contrast, Chelicerata *sensu stricto* displays a fully derived anatomical organization. The deutocerebral appendages are unichelate, with chelae lacking segmentation, corresponding to true chelicerae. The degree of tagmosis is similarly high, with seven segments incorporated beneath the head shield, but with a clear and consistent differentiation between post-deutocerebral prosomal appendages and those of the opisthosoma, going from the presence of tubuliaceous exopodal rami to uniramous appendages in their prosoma. The opisthosomal appendages bear fully developed book gills, in which the exites are organized as well-defined lamellae in number exceeding those of *Urokodia* and mollisoniids, while endopods are strongly reduced and vestigial.

Urokodia aequalis Hou, Chen, and Lu, 1989¹⁶

Emended Diagnosis. Cheliceromorpha with prosomal shield sub-rectangular in dorsal view, carrying a pair of anterior spines followed by three pairs of lateral spines, each corresponding to a transverse ridge on the lateral region of the prosomal shield. Robust single pincer-like first pair of appendages consisting of one peduncle and four distal podomeres each bearing one spine. Trunk somite number may be subject to ontogenetic changes, 15 are present in the studied material, each expressing a tergite devoid of axial region dorsally and a pair of biramous limbs ventrally. The exopods and exites form book gills, endopods are multipodomerous. Tail shield trapezoid in outline, bearing a pair of posterior spines and numerous small spines on the straight posterior margin. Several somites incorporated in the pygidial shield, dorsally expressing only the axial region of the tergites, ventrally expressing several pairs of close-together exopods (i.e. pretelsonic processes) without endopods or exites.

Remarks. In a recent study, a closed chelicera was misinterpreted as an antenna of *Urokodia* (figs. 1C, 3E in ref. 17), misleading the authors to assign the animal to Artiopoda. This bears directly on a recurring problem in Cambrian datasets: when frontal-most appendages are preserved in

overlapping positions and with strong compression, the same structure can be misidentified (e.g., as antenniform) and consequently drive erroneous placement and character coding¹⁷.

The chelicerate status of Pycnogonida under the chelicera evolution model suggested by *Urokodia*

The chelicerate anatomy of *Urokodia* clarifies the evolutionary transition from multichelate to unichelate chelicerae and supports Megacheira as the sister group of Chelicerata. The transitional condition observed in *Urokodia* also provides new insight into the evolution of pycnogonid chelifores, reinforcing the homology of the first pair of appendages that unite crown chelicerates.

The monophyly of Crown Chelicerata, comprising Pycnogonida and Euchelicerata, is mainly supported by phylogenomic analyses^{18–22}, but also by the homology between chelicerae and chelifores. This homology is supported by neurological²³ and muscular evidence^{24,25}.

The presence of four²⁶ or five podomeres²⁷ in the chelifores of the Devonian pycnogonid *Palaeoisopus problematicus*, previously difficult to reconcile with three-segmented chelicerae ground plans, is instead consistent with an evolutionary scenario in which both chelicerae and chelifores evolved from a *Urokodia*-like multisegmented condition.

The chelicerae of *Urokodia* consist of four clearly differentiated elements. Three form one chela, while the fourth forms the opposing chela. A fifth proximal element may have supported the chelae, although its presence is uncertain.

In this context, *Urokodia* defines a basal chelicerate condition with a four-segmented chelicera, contrasting with previous models proposing a three-segmented ground pattern²⁷. The three-segmented chelicera is therefore more likely derived within Euchelicerata, and, independently, Pycnogonida.

Developmental data from pycnogonids further support this interpretation. Podomere count reduction during ontogeny has been documented in *L. illecebrosa*²⁸, suggesting that heterochronic shifts in podomere fusion could explain the reduction of segments from megacheirans to chelicerates. Larvae of several extant pycnogonids present a prominent spinning spine on the chelifores. This structure is present on the pre-chela podomeres at the protonymphon stage and is reduced during later development^{29,30}. Although functionally involved in host attachment during parasitic stages, this hypertrophic spine may represent a vestige of a previously multichelate chelicerae inherited from great appendage-like ancestors.

Despite these advances, some aspects of chelicera evolution remain unresolved. In particular, the nature of the first pair of appendages in Habeliida remains problematic under the evolutionary framework proposed here. This condition may reflect incomplete preservation, ontogenetic

variation, alternative systematic placement, or secondary loss of chelicerae. The proposed affinity of Habeliida with Offacolidae^{5,31} tentatively supports the hypothesis that its anterior appendages represent incompletely preserved elongated chelicerae.

Appendicular derivatives in *Urokodia*

Appendicular derivatives are variably modified appendages located on the preterminal trunk tergites across a wide range of arthropods^{31–35}. The group most prominently characterized by these structures is Vicissicaudata^{34,35}, but potential homologous appendages have also been reported in taxa such as Offacolida and Habeliida^{31,36}.

These derivatives are typically expressed as ventral plates, furcae, or flap-like appendages below the terminal tergites^{31,32}. Comparisons among taxa including vicissicaudates, habeliids, and offacolids suggest that these features may originate from modified trunk appendages; however, their exact relationships remain debated^{31–35}. Appendicular derivatives have also been proposed as a synapomorphy supporting a broader arachnomorph-grade hypothesis^{31,32}. Currently, the origin, homology and function of appendicular derivatives remain poorly resolved, largely because no living taxa (apart from the possible exception of extant crustaceans such as *Nebalia*) exhibit appendages inserted in comparable posterior positions³⁰. The absence of modern analogues for these anatomical features constrains the effective application of the developmental criterion used to assess homology³⁷. Consequently, researchers are limited to relying solely on a highly unstable phylogenetic framework to infer homology by ancestral state reconstruction or the less informative association criterion^{31,37}.

In this context, the posteriormost appendages of *Urokodia*, which differ from the more anterior ones by lacking exites and endopods (Extended Data Fig. 4), may represent an early stage in the differentiation of a character that could have evolved independently in both Artiopoda and Cheliceromorpha, thus with a common root of lacking endopods in the terminal tergites. This supports an exopodial origin for these widespread uniramous appendages. One possible explanation for the broad distribution of this feature is that its evolution reflects repeated responses to similar functional demands, such as stabilization and steering, which may account for its occurrence across a wide range of euarthropods. According to our phylogenetic framework (Extended Data Fig. 8), future investigations on megacheirans are needed to bridge the gap in the presence of this character between Artiopoda and Chelicerata.

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Supplementary Table 1

Cheliceromorpha (= Total-group Chelicerata)									
Nature of the first raptorial appendages	First pair of raptorial appendages with a reduced number of articles (six or less)								
Degree of tagmosis	Cephalic shield encompassing the raptorial appendages followed by three to five other pairs of appendages with well-developed endopods and exopods possibly reduced or tubulaceous, or secondarily lost.								
Nature of thoracic appendages	Presence of exites with more than 5 overlapping big lamellae, secondarily evolved into the book gills lamellae.								
	Chelicerata sensu stricto	upper stem (grade 2)	upper stem (grade 1)	lower stem					
Nature of the first raptorial appendages	First pair of raptorial appendages unichelate and chelae devoid of segmentation.	As for Habeliids, they coincide.	First pair of raptorial appendages multiple chelae fused into a single pair of short pincer-like great appendage, and possibly more advanced morphology.	As for megacheirans, they coincide.					
Degree of tagmosis	Full tagmosis, with 7 segments incorporated under the head shield and clear differentiation between post-raptorial cephalic appendages and thoracic appendage.	As for Habeliids, they coincide.	Degree of tagmosis more advanced compared to the lower stem, with 7 segments incorporated under the head shield and a moderate degree of appendage specialization.	As for megacheirans, they coincide.					
Nature of thoracic appendages	Postcephalic appendages bearing book gills, with the exopods as opercula, the overlapping flaps of the exites now forming proper lamellae and greatly reduced endopods.	As for Habeliids, they coincide.	Trunk appendages composed of a larger flap-like, setae-bearing exopod with a low number (less than 5) of medium setae-free flaps stacked on its dorsal back side to form the exite.	As for megacheirans, they coincide.					
	Pycnogonids	Subhosurans	Offacolids	Megachelicerans	Habeliids	Mollisoniida	Erobodini	megacheirans	
Nature of the first raptorial appendages	Chelifores made of two spine and two articles. Larvae of some species presenting three spines (dipetrotrophic spine of protonymphon stage, see supplementary discussion).	Cheliceratae made of two spine and two articles.	Cheliceratae made of two spine and two articles.	Cheliceratae made of two spine and two articles.	Short uniramous appendages of no better identified nature(?).	Short chelicerate (?) made of two spine and two articles (?).	Pincer-like SGAs made of only two spines, but more than two articles forming a single chelae (vestigial).	Multichelate SGAs made of more than two spines and article.	
Degree of tagmosis	Derived. Reduced number of somites (three). All appendages uniramous and highly specialized (origet, pnp).	High. Five post raptorial appendages below the headshield. All of which are uniramous except for the presence of the flabelum.	High. Five post raptorial appendages below the headshield. All of which are differentiated with tubulaceous exopods.	High. Five post raptorial appendages below the headshield. All of which are differentiated with tubulaceous exopods.	High. Five post raptorial appendages below the headshield. All of which are differentiated with tubulaceous exopods.	Moderate. Five (six proposed) post raptorial appendages below the headshield. At least post raptorial appendages six differentiated with tubulaceous exopods.	Low. Five post raptorial appendages below the headshield. Post raptorial appendages undifferentiated.	Lowest. Three to four post raptorial appendages below the headshield. Post raptorial appendages undifferentiated.	
Nature of thoracic appendages	/	Bookgills. Reduced or absent endopods, exopods modified into operculum, fully developed bookgills lamellae from exites broad and numerous.	Bookgills. Reduced or absent endopods, exopods modified into operculum, fully developed bookgills lamellae from exites broad and numerous.	Uniramous. Exite so broad and numerous to be recognized as fully developed bookgills lamellae. Presence of a sclerite homologous to the exopod and the operculum.	Biramous. Well-developed endopods and paddle-like exopods. No trace of exite.	Possibly uniramous proto-book gills made of a larger flap-like, setae-bearing exopod with a low number (less than 5) of medium setae-free flaps stacked on its dorsal back side to form the exite.	Biramous trunk appendages made of a larger flap-like, setae-bearing exopod with a low number (less than 5) of medium setae-free flaps stacked on its dorsal back side to form the exite.	Biramous appendages made of an endopod, a larger flap-like, setae-bearing exopod with a lower number (less than 4) of smaller setae-free flaps stacked on its dorsal back side to form the exite.	

Supplementary Table 1. Summary of characters used to define the different groups of Cheliceromorpha, following the Bayesian and 5K parsimony topologies.