# Current Biology

# A Tube-Dwelling Early Cambrian Lobopodian

## Highlights

- New specimens indicate *Facivermis* is a tube-dwelling lobopodian

- Phylogenetic analyses place *Facivermis* in Luolishaniidae (total group Onychophora)

- *Facivermis*' worm-like morphology resulted from adaptation to tube dwelling

- *Facivermis* was not intermediate between cycloneuralian worms and panarthropods

## Authors

Richard J. Howard, Xianguang Hou, Gregory D. Edgecombe, Tobias Salge, Xiaomei Shi, Xiaoya Ma

## Correspondence

xghou@ynu.edu.cn (X.H.),
x.ma2@exeter.ac.uk (X.M.)

## In Brief

*Facivermis* is an enigmatic worm from the early Cambrian Chengjiang Biota. Here, Howard et al. identify *Facivermis* as a tube-dwelling lobopodian and demonstrate that its worm-like appearance was a secondary adaptation. This shows that *Facivermis* was not a basal, ancestrally worm-like panarthropod, as some studies suggest.

CellPress

# A Tube-Dwelling Early Cambrian Lobopodian

Richard J. Howard,[1,3,4] Xianguang Hou,[1,2,*] Gregory D. Edgecombe,[1,4] Tobias Salge,[5] Xiaomei Shi,[1,2]
and Xiaoya Ma[1,2,3,6,*]
[1]MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, Chenggong Campus, Kunming 650500, China
[2]Yunnan Key Laboratory for Palaeobiology, Yunnan University, Chenggong Campus, Kunming 650500, China
[3]Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall TR10 9TA, UK
[4]Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
[5]Imaging and Analysis Centre, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
[6]Lead Contact
*Correspondence: xghou@ynu.edu.cn (X.H.), x.ma2@exeter.ac.uk (X.M.)
https://doi.org/10.1016/j.cub.2020.01.075

## SUMMARY

*Facivermis yunnanicus* [1, 2] is an enigmatic worm-like animal from the early Cambrian Chengjiang Biota of Yunnan Province, China. It is a small (<10 cm) bilaterian with five pairs of spiny anterior arms, an elongated body, and a swollen posterior end. The unusual morphology of *Facivermis* has prompted a history of diverse taxonomic interpretations, including among annelids [1, 3], lophophorates [4], and pentastomids [5]. However, in other studies, *Facivermis* is considered to be more similar to lobopodians [2, 6–8]—the fossil grade from which modern panarthropods (arthropods, onychophorans, and tardigrades) are derived. In these studies, *Facivermis* is thought to be intermediate between cycloneuralian worms and lobopodians. *Facivermis* has therefore been suggested to represent an early endobenthic-epibenthic panarthropod transition [6] and to provide crucial insights into the origin of paired appendages [2]. However, the systematic affinity of *Facivermis* was poorly supported in a previous phylogeny [6], partially due to incomplete understanding of its morphology. Therefore, the evolutionary significance of *Facivermis* remains unresolved. In this study, we re-examine *Facivermis* from new material and the holotype, leading to the discovery of several new morphological features, such as paired eyes on the head and a dwelling tube. Comprehensive phylogenetic analyses using parsimony, Bayesian inference, and maximum likelihood all support *Facivermis* as a luolishaniid in a derived position within the onychophoran stem group rather than as a basal panarthropod. In contrast to previous studies, we therefore conclude that *Facivermis* provides a rare early Cambrian example of secondary loss to accommodate a highly specialized tube-dwelling lifestyle.

## RESULTS AND DISCUSSION

### Systematic Paleontology

Superphylum Panarthropoda Nielsen, 1995 [9]

Phylum (stem group) Onychophora Grube, 1853 [10]
Family Luolishaniidae Hou and Bergström, 1995 [11]
Type genus and species *Luolishania longicruris* Hou and Chen, 1989 [1]

### *Emended Diagnosis*

Lobopodians with a non-annulated head region, annulated trunk, and anterior-posterior tagmatization of the lobopods. The head may bear paired dorso-lateral eyes and/or a pair of pre-ocular, non-sclerotized antenniform appendages. Anterior tagma comprises five or six pairs of slender, elongate lobopods with double rows of spines/setae in a chevron pattern on their ventral surface. Posterior tagma, where present, comprises 3–9 shorter, single-clawed lobopods. Dorsal sclerotization, where present, comprises median components as well as paired lateral components (emended from [6]).

### *Included Taxa*

*Luolishania longicruris* [11, 12] (*Miraluolishania haikouensis*) [13, 14], Cambrian stage 3, Yunnan (Chengjiang). *Facivermis yunnanicus* [1, 2], Cambrian stage 3, Yunnan (Chengjiang). *Collinsium ciliosum* [15], Cambrian stage 3, Yunnan (Xiaoshiba). An unnamed species [16], Cambrian stage 4, South Australia (Emu Bay Shale). *Ovatiovermis cribrosus* [6], Wuliuan stage, British Columbia (Burgess Shale). *Acinocricus stichus* [17, 18], Wuliuan stage, Utah (Spence Shale).

### *Remark*

The "Collins Monster" and another similar luolishaniid await formal description [19–22].

Genus and species *Facivermis yunnanicus*
1989 *Facivermis yunnanicus* Hou and Chen [1], Figures 1–4 and plates 1-2
2002 *Xishania longiscula* Hu [23], plate 17.4
2006 *Facivermis yunnanicus* Liu et al. [2], Figures 1–3

### *Type Material*

Holotype NIGPAS 108720 (part and counterpart), stored at Yunnan Key Laboratory for Palaeobiology. Holotype is figured here (Figures 2A, 2D, 3A, and 3C) and also in Hou and Chen [1] (Figures 1 and 2, plate 1), Chen et al. [3] (Figure 297, p. 198), and Hou et al. [24] (Figures 25.3c and 25.3d). Nine new specimens in total are figured here, and a full specimen list is provided (Table S1).

### *Locality and Stratigraphy*

Chengjiang Biota, Yunnan Province, People's Republic of China. Chiungchussu Formation, Yu'anshan Member
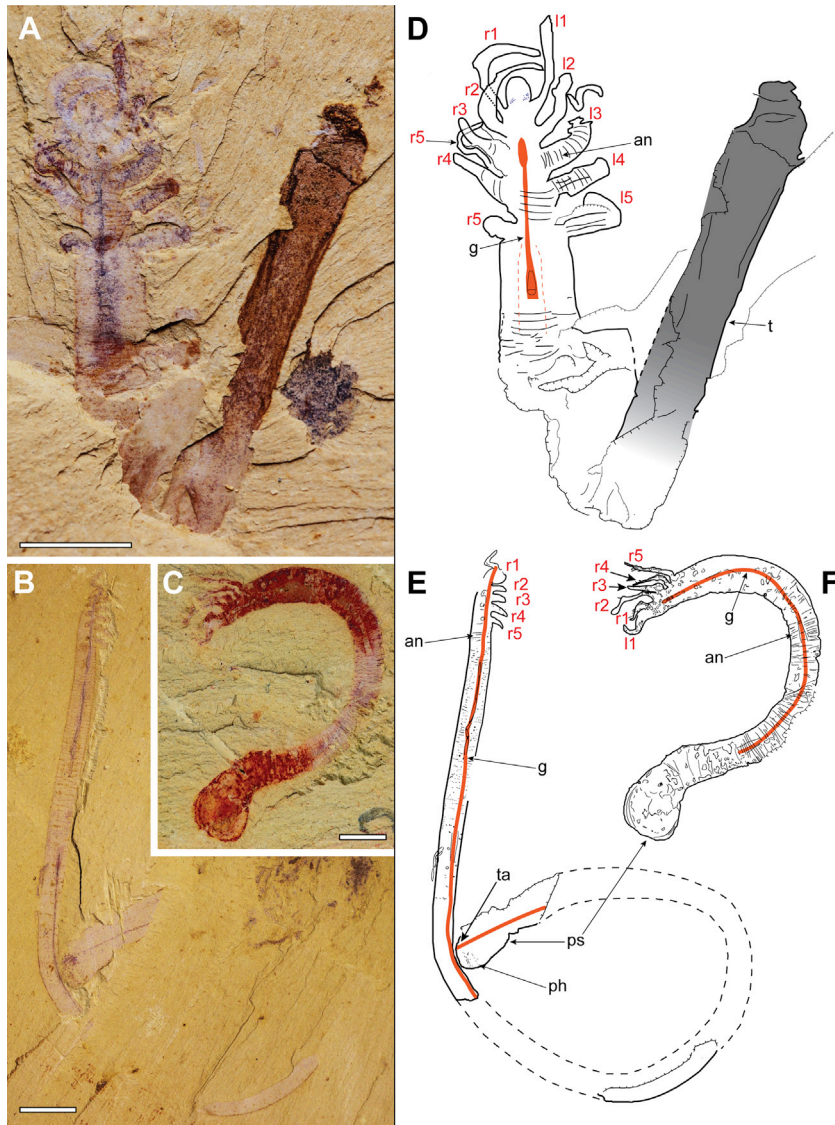
the mouth and pharynx (i.e., any radial elements characteristic of ecdysozoans) is not visible. The mouth is terminal, appearing to bend downward slightly (see Figures 2B and 2E, labeled "m"). Pre-ocular appendages appear to be present in YKLP 11378 (see Figures 2B and 2D, labeled "ant"), but fidelity of preservation is insufficient to confirm whether they are comparable to the antenniform appendages of *Luolishania longicruris* and *Collinsium ciliosum.* A cephalic sclerite, as in that of *L. longicruris*, *C. ciliosum*, and the Emu Bay Shale luolishaniid, is absent.

### *Anterior—Lobopods*

Five pairs of slender, annulated lobopods located ventro-laterally on the anterior-most trunk. Size ranging from around 3.5 mm in length in smaller specimens (e.g., YKLP 11375; Figures 1C and 1F) to 4 to 5 mm in larger specimens (e.g., NIGPAS 108720; Figures 2A and 2D). Lobopods are conical in overall shape, as indicated by circular bases (see Figures 2B, 2E, and S4B). Characteristic luolishaniid setae in a double row attach ventrally with a broader base (Figure S4D, arrows indicate the position of the setal bases; also see Figure 3g in Liu et al. [2]). Observed setae range in length from 0.198 to 0.335 mm in YKLP 11375 (Figure S4C) and from 1.162 to 1.844 mm in YKLP 11380 (Figure S4D). An average interspace of ~0.34 mm from seta base to base is recorded from the best preserved example (YKLP 11380; Figure S4D).

### *Middle Trunk*

Annulated, comprising the majority of the length of the animal. Total length, including anterior and posterior, ranges from ~2.8 to 9 cm. The trunk is greatly elongated, resulting in an overall vermiform appearance. Curved spines (see Figures 2B and 2E, labeled "ts," arrows indicating the position of trunk spines on the annuli) and papillae (Figures 2A and 2D, labeled "pap") characterize the trunk cuticle.

(*Eoredlichia-Wutingaspis* Biozone), Cambrian series 2, stage 3 [24]. Type material is from Maotianshan section; all other material studied here is from the Mafang and Jianshan sections in Haikou.

### *Emended Diagnosis*

Luolishaniid with three body regions: anterior; middle; and posterior. The anterior comprises head and setose lobopods (five pairs). A pair of simple ocellus-like eyes is positioned dorso-laterally on the head. The middle comprises a greatly elongated and limbless portion of the trunk. The trunk is adorned with papillae and short, curved spines/setae. The posterior comprises a pear-shaped terminal swelling with two or three rings of hooks and a terminal anus. The body is enclosed within a tube (emended from [2]).

### Description

### *Anterior—Head*

1–2.5 mm in length. Ovoid in overall shape, with paired dorso-lateral simple ocellus-like eyes preserved as dark pigment spots (see white triangles in Figures 3A and 3C). The fine structure of
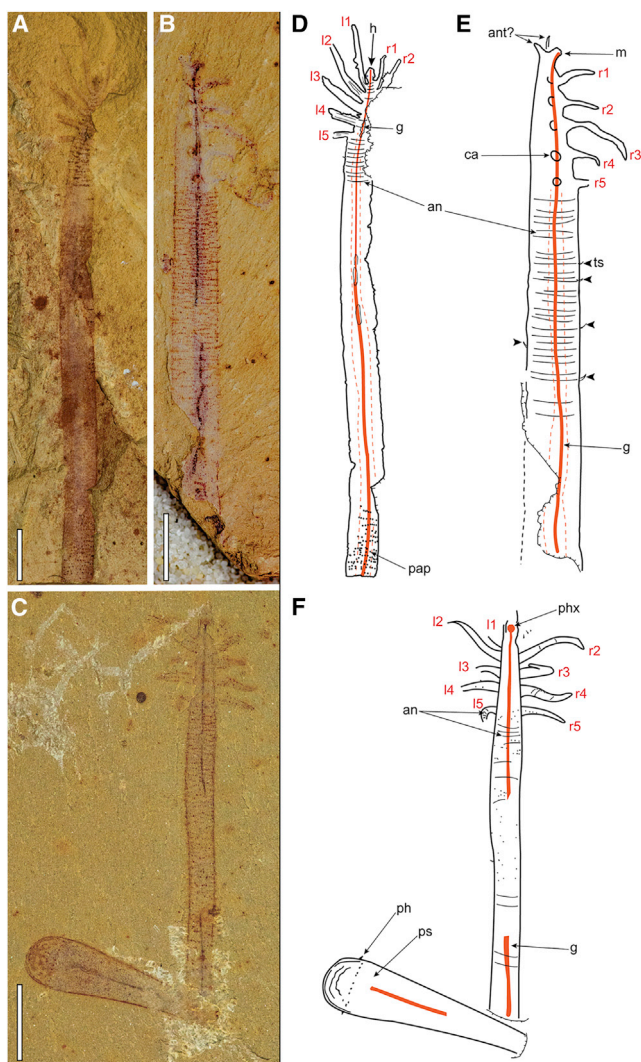
## Figure 2. Holotype and New Material of *Facivermis*

(A) NIGPAS 108720 (holotype), dorsal orientation.
(B) YKLP 11378, lateral orientation, showing trunk spines/setae on dorsal and ventral trunk.
(C) YKLP 11403, in possible dorsal orientation.
(D) Drawing of NIGPAS 108720.
(E) Drawing of YKLP 11378.
(F) Drawing of YKLP 11403.
ant?, possible antenniform appendages; ca, circular attachments; h, head; m, mouth; pap, papillae; phx, pharynx; ts, trunk spines. The alimentary canal is highlighted in orange where visible, with the surrounding body cavity in dashed lines. Scale bars, (A and B) 2.5 mm; (C) 2 mm.
See also Figures S3 and S4 for additional *Facivermis* specimens and morphological features and Table S1 for complete list of referred material.

### Posterior

The swollen posterior is pear shaped and present in three specimens studied here (YKLP 11374, 11375, and 11403). YKLP 11374 shows the terminal anus (Figures 1B and 1E, labeled "ta"), and YKLP 11403 shows the rows of hooks (Figures 2C and 2F, labeled "phx"), which are also figured elsewhere [2, 23].

### Alimentary Canal

Through gut runs between a terminal mouth and anus, with no diverticula. The gut is narrow, preserved as black carbonaceous film, occasionally with sediment infills. The alimentary canal is highlighted in all specimens in Figures 1, 2, and S3.

### Tube

Preserved as flat and oblong, but presumably cylindrical in life. The cuticle and soft tissues of *Facivermis* are preserved in a range of reds and purples, whereas the tube obscures the trunk morphology and is clearly distinguishable as a brown rusty color with a coarse texture and a straight and rigid margin (see Figures 1A, 1D, and S4A). Only two specimens exhibit the tube out of 30 known specimens (Table S1). YKLP 11377 shows the trunk, lobopods, and head extending from the tube, whereas YKLP 11379 shows only the lobopods extending from the tube (Figure S4A).

### Remarks

Chen [3] reported occasional parapodia-like structures extended out from the trunk, which was not observed in any of our specimens. However, we do observe fine spines/setae along the annulations (see "Middle Trunk" above and Figures 2B and 2D, arrows pointing to trunk spines), which appear comparable to cuticular elements of *Collinsium ciliosum*. These spines are not equivalent to the metameric sclerotized armament seen in other luolishaniids, hallucigeniids, *Onychodictyon*, etc.

### *Facivermis* as a Lobopodian

Lobopodians are an evolutionary grade that encompasses the stem groups to the three panarthropod phyla—Arthropoda, Onychophora, and Tardigrada [25, 26]. Cambrian *Konservat-Lagerstätten*, such as the Chengjiang Biota [11, 12, 14, 27–33], Sirius Passet [34–37], Burgess Shale [6, 38–40], and Emu Bay Shale [16], yield the majority of lobopodian material (though isolated elements also occur as microfossils) [41–43], and a mosaic of panarthropod characters are mapped across the various taxa. As such, Cambrian lobopodians are crucial to interpreting the early evolution and deep genealogical relationships of panarthropods, as they yield uniquely informative character combinations in phylogenetic analyses [15, 39, 40, 44–48]. New morphological and phylogenetic work here supports a lobopodian affinity for *Facivermis*, as suggested by some earlier studies [2, 6], and refutes an annelid [1, 3], lophophorate [4], or pentastomid [5] affinity.

A number of lobopodian features are identifiable in *Facivermis*. The head bears paired, dark spots in a dorso-lateral position (Figures 3A and 3C). We interpret these as ocular structures based on the presence of consistent structures in the coeval lobopodian *Luolishania longicruris* [11–14] (Figures 3B and 3D)—which were interpreted as eyes preserved as residual carbon-rich visual pigments in elemental mapping analyses [49]. The positional consistency of these structures (i.e., paired, symmetrical, and located dorso-laterally on the head) between *Facivermis* and *Luolishania*, as well as numerous other lobopodians [6, 14, 32, 33, 39, 49], supports this. These visual organs contradict a pentastomid or lophophorate affinity.

Hou and Chen [1] compared *Facivermis'* appendages to the five pairs of head tentacles in nereid polychaetes to support an annelid affinity. However, they conceded they are not consistent in position with those of nereids—which are all on the head,
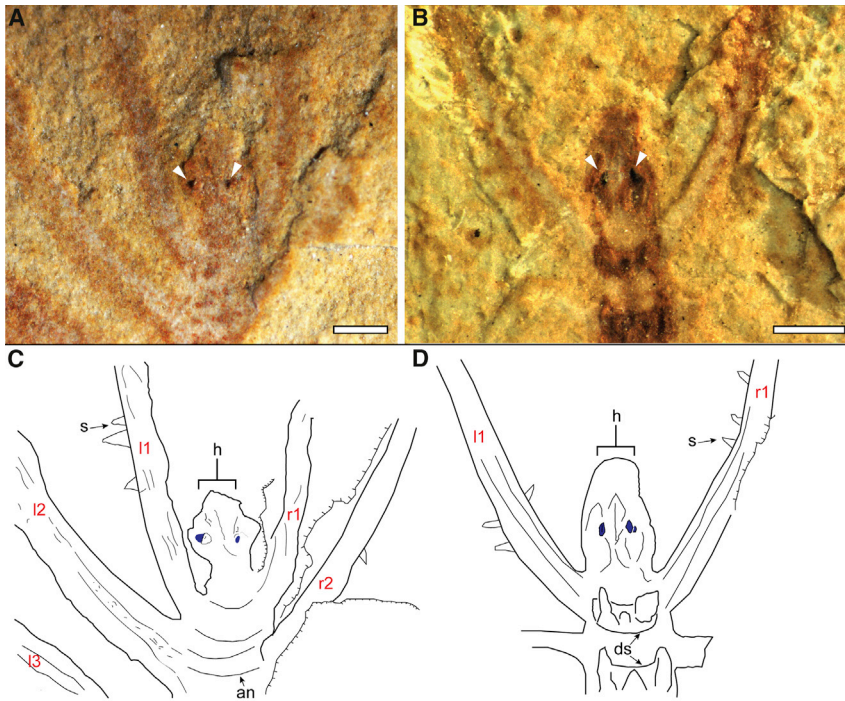
**Figure 3. Head and Ocular Structures of *Facivermis* and *Luolishania***

(A) Close up of the anterior region of *Facivermis yunnanicus*, showing the head (NIGPAS 108720). White triangles point to the simple ocellus-like eyes.

(B) Close up of the anterior region of *Luolishania longicruris*, showing the head (YKLP 11272). White triangles point to the eyes.

(C) Drawing of the anterior region of *Facivermis yunnanicus* (NIGPAS 108720). Eyes are highlighted in blue.

(D) Drawing of the anterior region of *Luolishania longicruris* (YKLP 11272). Eyes are highlighted in blue.

ds, dorsal sclerites; s, setae. Scale bars, (A) 0.5 mm; (B) 0.3 mm.

See also Figures S3 and S4 for additional *Facivermis* specimens and morphological features and Table S1 for complete list of referred material.

unlike the metameric sequence of *Facivermis*' appendages on the anterior part of the trunk. An annelid affinity is inconsistent with the structure of *Facivermis*' appendages, which exhibit circular attachments to the trunk (Figures 1B, 1E, 2B, 2E, and S4B) in a ventro-lateral position. This indicates that the lobopods were conical structures rather than parapodia—which typically comprise both a dorsal notopodium and ventral neuropodium. Such circular attachments are widely documented in lobopodians in Burgess Shale-type preservation, e.g., *Paucipodia* (Hou et al. [31], Figures 4A, 4C, 4E, and 4F), *Onychodictyon* (Liu et al. [28], Figure 1B¹), and *Aysheaia* (Whittington [38], Figure 30). Liu et al. [2] recognized the similarity of *Facivermis*' appendages to the anterior lobopods of *Luolishania*, and Caron and Aria [6] resolved *Facivermis* as outgroup to Luolishaniidae (albeit with low support). Our study corroborates the interpretations of these authors that *Facivermis* is a lobopodian.

### Lifestyle of *Facivermis*—Ecological Interpretations

The unique aspects of *Facivermis* compared to other lobopodians are its elongated worm-like (vermiform) body lacking posterior appendages, its hook-bearing posterior, and its dwelling tube. Combined with the suspension-feeding function of the anterior setose lobopods [6], we predict that *Facivermis* was most likely similar to extant (but only distantly related) feather duster worms [50, 51], which are also tube dwelling, and suspension feed using anterior setose food-gathering appendages. Our interpretation contradicts previous hypotheses that *Facivermis* was an ambush-style predator [2] but endorses the idea that the appendages were not used for locomotion and that the posterior hooks represent an anchoring mechanism.

Although the dwelling tube fits the morphological adaptations exhibited by *Facivermis*, the tube's rarity presents a puzzling preservation aspect. As it is unknown whether the tube was biogenic or built from sediment, it is possible that the tube had a lower preservation potential than the rest of the body. An alternative explanation is that specimens of the tube lacking a body fossil association would not have been recognized as *Facivermis* previously, indicating that *Facivermis* may have been relatively mobile (e.g., if tubes were discarded periodically).

### Luolishaniid and Lobopodian Phylogeny

Phylogenetic analyses using parsimony, Bayesian inference, and maximum likelihood (Figures 4, S1, and S2) recovered *Facivermis* within the Luolishaniidae [6, 11–16]. The only previous phylogenetic analysis to include *Facivermis* [6] found it to be the poorly supported outgroup to Luolishaniidae, at the most basal position within the panarthropod stem group, leaving open the possibility that the vermiform morphology of *Facivermis* was an ancestral trait (a plesiomorphy). By contrast, our phylogenetic results—which receive higher support values based on new morphological observations—show *Facivermis* branching within Luolishaniidae, with Luolishaniidae in the onychophoran stem group (as in other iterations of this matrix) [15, 39, 40, 47]. Our phylogeny supports the vermiform body plan of *Facivermis* as a derived state (an autapomorphy), the result of secondary modification rather than a basal phylogenetic position.

*Facivermis*' derived nature is bolstered by its sister-group relationship. Within Luolishaniidae, *Facivermis* was recovered as sister taxon to *Ovatiovermis* in three of four analyses (equal and implied weights parsimony; Figure S1) and maximum likelihood (Figure S2)—but not Bayesian inference (Figure S2), which failed to resolve a polytomy of *Ovatiovermis*, *Facivermis*, and a clade comprising all other luolishaniids. *Facivermis* and *Ovatiovermis* are similar and appear to show a transitional series toward a progressively less mobile lifestyle in contrast to more errant luolishaniids (e.g., *Luolishania* and *Collinsium*). Both *Facivermis* and *Ovatiovermis* show a reduction in the number
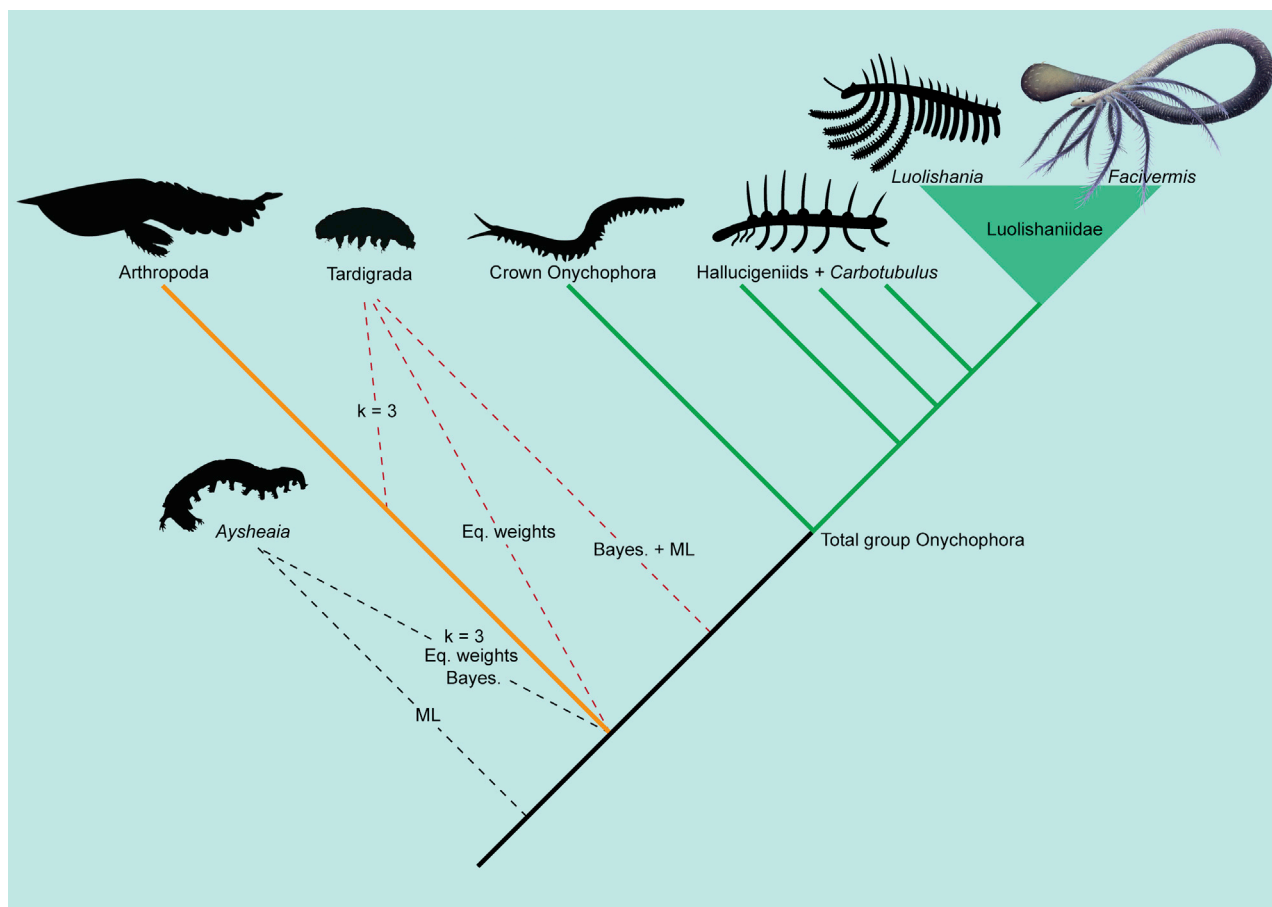
**Figure 4. Phylogenetic Position of *Facivermis***
Summary tree showing relationships inferred under both parsimony and probabilistic methods (see STAR Methods). Dashed lines indicate the labile branching of taxa according to different optimality criteria. The positions of *Facivermis* and Luolishaniidae were robust to alternative optimality criteria. Bayes, Bayesian inference; eq. weights, maximum parsimony under equal character weighting; k = 3, maximum parsimony under implied character weighting; ML, maximum-likelihood.
See Figures S1 and S2 for full tree topologies and Data S1A and S1B for phylogenetic characters and matrix, respectively.

of posterior lobopods. *Ovatiovermis* has just three pairs, and *Facivermis* has none, compared with the nine pairs possessed by *Luolishania* and *Collinsium*. Furthermore, the three posterior pairs of *Ovatiovermis* are stout and equipped with a single hook-like claw. Caron and Aria [6] inferred that these limbs were better adapted to anchoring than walking, as did Yang et al. [15] in the case of *Collinsium* and Ma et al. for *Luolishania* [12], and this is certainly also the case for the hook-bearing posterior of *Facivermis* [2]. Loss of limbs and locomotory function in the *Facivermis-Ovatiovermis* lineage is coupled with a lack of sclerotized armor seen in other luolishaniids (and outgroups, such as *Hallucigenia*). A loss of armor would suggest these animals were out of reach of epibenthic and nektonic predators—further supported by the tube-dwelling lifestyle of *Facivermis* reported here.

**Evolutionary Significance of *Facivermis***
Within Ecdysozoa [52, 53], molecular phylogenies typically recover the cycloneuralians (nematoids and scalidophorans) as paraphyletic toward panarthropods [53]. As such, whether

more nematoid-like or scalidophoran-like, at least the very earliest diverging members of the panarthropod stem group are likely to have been vermiform animals. There are many shared characters between lobopodians and cycloneuralian worms (i.e., ancestral characters of Ecdysozoa) to support this molecular hypothesis. Radial pharyngeal teeth reminiscent of scalidophorans are known among lobopodians [34, 39], and the phosphatic sclerites of the cycloneuralians *Tabelliscolex hexagonus* and *Cricocosmia jinningensis* are potentially homologous to lobopodian sclerites [54, 55]. However, as phylogenetic analyses have consistently supported a derived affinity among priapulans for worms like *Cricocosmia* and *Tabelliscolex* [56–59], these characters are uninformative plesiomorphies with regard to the origin of Panarthropoda. For this reason, *Facivermis* represents an interesting taxon for panarthropod evolution, as its combination of paired appendages and a vermiform appearance makes it appear transitional between cycloneuralians and lobopodians [2, 6]. Previously, the vermiform appearance and lack of posterior limbs in *Facivermis* were considered to be ancestral [6], and authors advocated that *Facivermis*

represents a candidate system to explore the origins of paired appendages [2]. However, our phylogenetic analyses all indicate that *Facivermis* was a derived panarthropod and not phylogenetically intermediate between cycloneuralians and lobopodians. Therefore, *Facivermis* instead represents an early Cambrian example of secondary adaptation to a highly specialized ecology (i.e., as a tube-dwelling suspension feeder).

That the vermiform condition in *Facivermis* was autapomorphic is significant because it rules out luolishaniid-style suspension feeding as being associated with the origin of paired appendages. Indeed, it was suggested by Caron and Aria [6] that *Facivermis* may represent a transition between endobenthic vermiform panarthropods and errant epibenthic panarthropods (i.e., lobopodians). In this scenario, paired appendages evolved as a feeding adaptation rather than a locomotory one, and the distinctive luolishaniid ecology is plesiomorphic. Our findings here show that this is not the case, and *Facivermis* does not fit the criteria of an ancestrally vermiform panarthropod.

With Chengjiang (518 Ma, Cambrian series 2, stage 3) [60] dating to just a few million years later than the oldest panarthropod body fossils [61], the tube-dwelling *Facivermis* was, despite its extreme antiquity, adapted to a highly specialized ecology that is atypical of other total-group Onychophora and lobopodians as a whole. This was achieved through a series of secondary character losses—particularly the loss of posterior legs. This amplifies an idea formulated by previous studies [6, 15] that the ancient marine stem group of Onychophora occupied a considerably larger amount of morphospace relative to the extant terrestrial crown group.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - ○ Fossil microscopy and photography
  - ○ Interpretative drawings
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Phylogenetic analyses
- DATA AND CODE AVAILABILITY

### REFERENCES

1. Hou, X.-G., and Chen, J.-Y. (1989). Early Cambrian tentacled worm-like animals (*Facivermis* gen. nov.) from Chengjiang, Yunnan. Acta Palaeo. Sinica *28*, 32–41.

2. Liu, J., Han, J., Simonettaa, M., Hu, S., Zhang, Z., Yao, Y., and Shu, D. (2006). New observations of the lobopod-like worm *Facivermis* from the early Cambrian Chengjiang Lagerstätte. Chin. Sci. Bull. *51*, 358–363.

3. Chen, J.-Y. (2004). The Dawn of the Animal World (Jiangsu Science and Technology Press).

4. Chen, J.-Y. (1997). Biology of the Chengjiang fauna. Bull. Natl. Museum Nat. Sci. *10*, 11–106.

5. Delle Cave, L., Insom, E., and Simonetta, A.M. (1998). Advances, diversions, possible relapses and additional problems in understanding the early evolution of the Articulata. Ital. J. Zool. (Modena) *65*, 19–38.

6. Caron, J.-B., and Aria, C. (2017). Cambrian suspension-feeding lobopodians and the early radiation of panarthropods. BMC Evol. Biol. *17*, 29.

7. Dzik, J. (2011). The xenusian-to-anomalocaridid transition within the lobopodians. Boll. Soc. Paleontol. Ital. *50*, 65–74.

8. Xianguang, H., Ramsköld, L., and Bergström, J. (1991). Composition and preservation of the Chengjiang fauna - a Lower Cambrian soft-bodied biota. Zool. Scr. *20*, 395–411.

9. Nielsen, C. (1995). Animal Evolution: Interrelationships of the Living Phyla (Oxford University Press).

10. Grube, E. (1853). Untersuchungen Über den Bau von Peripatus edwardsii. Müller's Arch. Anat. Physiol. *20*, 322–360.

11. Hou, X.-G., and Bergström, J. (1995). Cambrian lobopodians - ancestors of extant onychophorans? Zool. J. Linn. Soc. *114*, 3–19.

12. Ma, X., Hou, X., and Bergström, J. (2009). Morphology of *Luolishania longicruris* (Lower Cambrian, Chengjiang Lagerstätte, SW China) and the phylogenetic relationships within lobopodians. Arthropod Struct. Dev. *38*, 271–291.

13. Liu, J.N., Shu, D.G., Han, J., and Zhang, Z.F. (2008). Comparative study of Cambrian lobopods *Miraluolishania* and *Luolishania*. Chin. Sci. Bull. *53*, 87–93.

14. Liu, J., Shu, D., Han, J., and Zhang, Z. (2004). A rare lobopod with well-preserved eyes from Chengjiang Lagerstätte and its implications for origin of arthropods. Chin. Sci. Bull. *49*, 1063–1071.

15. Yang, J., Ortega-Hernández, J., Gerber, S., Butterfield, N.J., Hou, J.-B., Lan, T., and Zhang, X.-G. (2015). A superarmored lobopodian from the Cambrian of China and early disparity in the evolution of Onychophora. Proc. Natl. Acad. Sci. USA *112*, 8678–8683.

16. García-Bellido, D.C., Edgecombe, G.D., Paterson, J.R., and Ma, X. (2013). A 'Collins' monster'-type lobopodian from the Emu Bay Shale Konservat-Lagerstätte (Cambrian), South Australia. Alcheringa *37*, 474–478.

17. Conway Morris, S., and Robison, R.A. (1988). More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. Univ. Kansas. Paleo. Contrib. *122*, 1–48.

18. Ramsköld, L., and Chen, J.-Y. (1998). Cambrian lobopodians: morphology and phylogeny. In Arthropod Fossils and Phylogeny, G.D. Edgecombe, ed. (Columbia University Press), pp. 107–150.

19. Collins, D. (1986). Paradise revisited. Rotunda *19*, 30–39.

20. Collins, D. (2001). Three new onychophorans from the Burgess Shale of British Columbia. In Third International Conference on Trilobites and Their Relatives (The National Museum of Wales), p. 9.

21. Delle Cave, L., and Simonetta, A.M. (1991). Early Palaeozoic arthropods and problems of arthropod phylogeny; with some notes on taxa of doubtful affinities. In The Early Evolution of Metazoa and the Significance of Problematic Taxa, A.M. Simonetta, and S. Conway Morris, eds. (Cambridge University Press), pp. 189–244.

22. Simonetta, A.M. (2004). Are the traditional classes of arthropods natural ones? Recent advances in palaeontology and some considerations on morphology. Ital. J. Zool. (Modena) *71*, 247–264.

23. Chen, L.-Z. (2002). Early Cambrian Chengjiang Fauna in Eastern Yunnan China (Yunnan Science and Technology Press).

24. Hou, X.-G., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P.-Y., Gabbot, S.E., Ma, X.-Y., Purnell, M.A., and Williams, M. (2017). The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition (Wiley Blackwell).

25. Liu, J., and Dunlop, J.A. (2014). Cambrian lobopodians: a review of recent progress in our understanding of their morphology and evolution. Palaeogeogr. Palaeoclimatol. Palaeoecol. *398*, 4–15.

26. Ortega-Hernández, J. (2015). Lobopodians. Curr. Biol. *25*, R873–R875.

27. Liu, J., Steiner, M., Dunlop, J.A., Keupp, H., Shu, D., Ou, Q., Han, J., Zhang, Z., and Zhang, X. (2011). An armoured Cambrian lobopodian from China with arthropod-like appendages. Nature *470*, 526–530.

28. Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X. (2008). The lobopod *Onychodictyon* from the Lower Cambrian Chengjiang Lagerstätte revisited. Acta Palaeontol. Pol. *53*, 285–292.

29. Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X. (2006). A large xenusiid lobopod with complex appendages from the Lower Cambrian Chengjiang Lagerstätte. Acta Palaeontol. Pol. *51*, 215–222.

30. Vannier, J., Liu, J., Lerosey-Aubril, R., Vinther, J., and Daley, A.C. (2014). Sophisticated digestive systems in early arthropods. Nat. Commun. *5*, 3641.

31. Hou, X.-G., Ma, X.-Y., Zhao, J., and Bergström, J. (2004). The lobopodian *Paucipodia inermis* from the Lower Cambrian Chengjiang fauna, Yunnan, China. Lethaia *37*, 235–244.

32. Ou, Q., Shu, D., and Mayer, G. (2012). Cambrian lobopodians and extant onychophorans provide new insights into early cephalization in Panarthropoda. Nat. Commun. *3*, 1261.

33. Ou, Q., Liu, J., Shu, D., Han, J., Zhang, Z., Wan, X., and Lei, Q. (2011). A rare onychophoran-like lobopodian from the Lower Cambrian Chengjiang Lagerstätte, Southwestern China, and its phylogenetic implications. J. Paleontol. *85*, 587–594.

34. Vinther, J., Porras, L., Young, F.J., Budd, G.E., and Edgecombe, G.D. (2016). The mouth apparatus of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*. Palaeontology *59*, 841–849.

35. Young, F.J., and Vinther, J. (2017). Onychophoran-like myoanatomy of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*. Palaeontology *60*, 27–54.

36. Budd, G.E. (1998). The morphology and phylogenetic significance of *Kerygmachela kierkegaardi* Budd (Buen Formation, Lower Cambrian, N Greenland). Trans. R. Soc. Edinb. Earth Sci. *89*, 249–290.

37. Park, T.S., Kihm, J.-H., Woo, J., Park, C., Lee, W.Y., Smith, M.P., et al. (2018). Brain and eyes of *Kerygmachela* reveal protocerebral ancestry of the panarthropod head. Nat. Commun. *9*, 1019.

38. Whittington, H.B. (1978). The Lobopod Animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. Philos. Trans. R. Soc. Lond. B Biol. Sci. *284*, 165–197.

39. Smith, M.R., and Caron, J.B. (2015). *Hallucigenia*'s head and the pharyngeal armature of early ecdysozoans. Nature *523*, 75–78.

40. Smith, M.R., and Ortega-Hernández, J. (2014). *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. Nature *514*, 363–366.

41. Maas, A., Mayer, G., Kristensen, R.M., and Waloszek, D. (2007). A Cambrian micro-lobopodian and the evolution of arthropod locomotion and reproduction. Chin. Sci. Bull. *52*, 3385–3392.

42. Caron, J.-B., Smith, M.R., and Harvey, T.H.P. (2013). Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. Proc. Biol. Sci. *280*, 20131613.

43. Pan, B., Topper, T.P., Skovsted, C.B., Miao, L., and Li, G. (2018). Occurrence of *Microdictyon* from the lower Cambrian Xinji Formation along the southern margin of the North China Platform. J. Paleontol. *92*, 59–70.

44. Legg, D.A., Sutton, M.D., and Edgecombe, G.D. (2013). Arthropod fossil data increase congruence of morphological and molecular phylogenies. Nat. Commun. *4*, 2485.

45. Legg, D.A., Ma, X., Wolfe, J.M., Ortega-Hernández, J., Edgecombe, G.D., and Sutton, M.D. (2011). Lobopodian phylogeny reanalysed. Nature *476*, E2–E3, discussion E3–E4.

46. Mounce, R.C.P., and Wills, M.A. (2011). Phylogenetic position of *Diania* challenged. Nature *476*, E1 discussion E3–E4.

47. Zhang, X.-G., Smith, M.R., Yang, J., and Hou, J.-B. (2016). Onychophoran-like musculature in a phosphatized Cambrian lobopodian. Biol. Lett. *12*, 20160492.

48. Siveter, D.J., Briggs, D.E.G., Siveter, D.J., Sutton, M.D., and Legg, D. (2018). A three-dimensionally preserved lobopodian from the Herefordshire (Silurian) Lagerstätte, UK. R. Soc. Open Sci. *5*, 172101.

49. Ma, X., Hou, X., Aldridge, R.J., Siveter, D.J., Siveter, D.J., Gabbott, S.E., Purnell, M.A., Parker, A.R., and Edgecombe, G.D. (2012). Morphology of Cambrian lobopodian eyes from the Chengjiang Lagerstätte and their evolutionary significance. Arthropod Struct. Dev. *41*, 495–504.

50. Licciano, M., Terlizzi, A., Giangrande, A., Cavallo, R.A., and Stabili, L. (2007). Filter-feeder macroinvertebrates as key players in culturable bacteria biodiversity control: a case of study with *Sabella spallanzanii* (Polychaeta: Sabellidae). Mar. Environ. Res. *64*, 504–513.

51. Giangrande, A., Cavallo, A., Licciano, M., Mola, E., Pierri, C., and Trianni, L. (2005). Utilization of the filter feeder polychaete *Sabella*. Aquacult. Int. *13*, 129–136.

52. Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., Rivera, M.C., Garey, J.R., Raff, R.A., and Lake, J.A. (1997). Evidence for a clade of nematodes, arthropods and other moulting animals. Nature *387*, 489–493.

53. Giribet, G., and Edgecombe, G.D. (2017). Current understanding of Ecdysozoa and its internal phylogenetic relationships. Integr. Comp. Biol. *57*, 455–466.

54. Steiner, M., Hu, S., Liu, J., and Keupp, H. (2012). A new species of *Hallucigenia* from the Cambrian Stage 4 Wulongqing Formation of Yunnan (South China) and the structure of sclerites in lobopodians. Bull. Geosci. *87*, 107–124.

55. Han, J., Liu, J., Zhang, Z., Zhang, X., and Shu, D. (2007). Trunk ornament on the palaeoscolecid worms *Cricocosmia* and *Tabelliscolex* from the Early Cambrian Chengjiang deposits of China. Acta Palaeontol. Pol. *52*, 423–431.

56. Wills, M.A., Gerber, S., Ruta, M., and Hughes, M. (2012). The disparity of priapulid, archaeopriapulid and palaeoscolecid worms in the light of new data. J. Evol. Biol. *25*, 2056–2076.

57. Ma, X., Aldridge, R.J., Siveter, D.J., Siveter, D.J., Hou, X., and Edgecombe, G.D. (2014). A new exceptionally preserved Cambrian Priapulid from the Chengjiang Lagerstätte. J. Paleontol. *88*, 371–384.

58. Zhang, H., Xiao, S., Liu, Y., Yuan, X., Wan, B., Muscente, A.D., Shao, T., Gong, H., and Cao, G. (2015). Armored kinorhynch-like scalidophoran animals from the early Cambrian. Sci. Rep. *5*, 16521.

59. Harvey, T.H.P., Dong, X., and Donoghue, P.C.J. (2010). Are palaeoscolecids ancestral ecdysozoans? Evol. Dev. *12*, 177–200.

60. Yang, C., Li, X.-H., Zhu, M., Condon, D.J., and Chen, J. (2018). Geochronological constraint on the Cambrian Chengjiang biota, South China. J. Geol. Soc. *175*, 659–666.

61. Daley, A.C., Antcliffe, J.B., Drage, H.B., and Pates, S. (2018). Early fossil record of Euarthropoda and the Cambrian Explosion. Proc. Natl. Acad. Sci. USA *115*, 5323–5331.

62. Nguyen, L.T., Schmidt, H.A., von Haeseler, A., and Minh, B.Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. *32*, 268–274.

63. Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., and Huelsenbeck, J.P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. *61*, 539–542.

64. Goloboff, P.A., and Catalano, S.A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics *32*, 221–238.

65. Terborg, R., Kaeppel, A., Yu, B., Patzschke, M., Salge, T., and Falke, M. (2017). Advanced chemical analysis using an annular four-channel silicon drift detector. Micros. Today *25*, 30–35.

66. Goloboff, P., Farris, S., and Nixon, K. (2000). TNT (tree analysis using new technology). http://www.zmuc.dk/public/phylogeny/tnt/.

67. Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2008). TNT, a free program for phylogenetic analysis. Cladistics *24*, 774–786.

68. Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D., and Kluge, A.G. (1996). Parsimony jackknifing outperforms neighbor-joining. Cladistics *12*, 99–124.

69. Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramirez, M.J., and Szumik, C.A. (2003). Improvements to resampling measures of group support. Cladistics *19*, 324–332.

70. Lewis, P.O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. *50*, 913–925.

71. Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q., and Vinh, L.S. (2018). UFBoot2: improving the ultrafast bootstrap approximation. Mol. Biol. Evol. *35*, 518–522.

72. Minh, B.Q., Nguyen, M.A., and von Haeseler, A. (2013). Ultrafast approximation for phylogenetic bootstrap. Mol. Biol. Evol. *30*, 1188–1195.

# STAR★METHODS

## KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
| --- | --- | --- |
| Biological Samples | | |
| *Facivermis yunnanicus* | Yunnan Key Laboratory for Palaeobiology | YKLP |
| Software and Algorithms | | |
| IQ-TREE | [62] | http://www.iqtree.org/ |
| MrBayes 3.2 | [63] | http://nbisweden.github.io/MrBayes/index.html |
| TNT | [64] | http://www.lillo.org.ar/phylogeny/tnt/ |
| Adobe Illustrator | Adobe Systems Incorporated | https://www.adobe.com/products/illustrator.html |
| Adobe Photoshop | Adobe Systems Incorporated | https://www.adobe.com/products/photoshop.html |
| Zeiss Zen | Carl Zeiss AG | https://www.zeiss.com/microscopy/int/products/microscope-software/zen.html |

## LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for fossil resources should be directed to and will be fulfilled by the Lead Contact, XM (x.ma2@exeter.ac.uk). This study did not generate any new data that is not included as supplemental data (see Data S1A and S1B).

## EXPERIMENTAL MODEL AND SUBJECT DETAILS

All new material of *Facivermis yunnanicus* Hou and Chen, 1989 [1] was collected by Yunnan Key Laboratory for Palaeobiology from the Mafang and Jianshan sections (Cambrian Series 2, Stage 3) in Haikou, Yunnan Province, People's Republic of China [24], and housed at Yunnan Key Laboratory for Palaeobiology. See referred material in Table S1.

## METHOD DETAILS

### Fossil microscopy and photography
*Facivermis yunnanicus* specimens were examined under normal and polarized light using a Zeiss SteREO Discovery light microscope. Photographs were taken using the microscope's mounted scope, as well as with a Canon EOS 750D DSLR camera equipped with a Sigma 105 mm 1:2.8 DG Macro lens. The head region of the holotype was examined under a FEI Quanta 650 FEG scanning electron microscope at the Natural History Museum, London, UK. One specimen was mapped for elemental concentration using energy-dispersive X-ray spectroscopy (EDX) at 9 kv accelerating voltage with an annular SSD EDX detector [65].

### Interpretative drawings
Interpretative drawings were produced by tracing fossil specimens under a camera lucida equipped on a Zeiss SteREO Discovery light microscope. Tracings were digitized using Adobe Photoshop and Illustrator.

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Phylogenetic analyses
We used the panarthropod character matrix of Smith and Caron [39] (based on Smith and Ortega-Hernández [40]), recoding to include *Facivermis yunnanicus*, *Collinsium ciliosum* and *Ovatiovermis cribrosus*. See Data S1A and S1B for the full character list and matrix respectively. We also recoded head sclerites to be present in *Luolishania longicruris* based on other studies' interpretation of this taxon [12], and removed the unstable taxa *Orstenotubulus evamuellerae* and *Hadranax augustus.* In total, the matrix comprised 41 taxa and 84 characters. Phylogenetic analyses were performed using parsimony, maximum likelihood and Bayesian optimality criteria.

Four maximum-parsimony analyses were conducted using the New Technology search in TNT 1.5 [64, 66, 67], first under equal character weighting (producing a strict consensus of 7 trees, see Figure S1), and then under implied weighs with a concavity constant of $k = 3$ (producing a strict consensus of 5 trees, see Figure S1). Extensive discussion of character weighting strategies using this

dataset can be found in Smith and Ortega-Hernández [40]. Parsimony tree searches were then repeated using appropriate resampling strategies (1000 replicates) under default conditions to assess nodal support (jackknife resampling for equal weights [68], symmetric resampling for implied weights [69] – see Figure S1).

Probabilistic tree searches used two alternative implementations of the MK model [70]: maximum-likelihood and Bayesian inference. The maximum-likelihood tree search was conducted in IQ-TREE [62], and support was assessed using the ultrafast phylogenetic bootstrap replication method [71, 72] to run 300,000 replicates (Figure S2). Bayesian analyses were performed in MrBayes 3.2.7 [63] using the MK + gamma mode [70], with convergence after 3,000,000 generations. Convergence was assessed using the sump command in MrBayes (standard deviation of split frequencies < 0.01, ESS scores > 200, PSRF ~1.0 across all parameters). 25% of samples were discarded as burnin, and tree samples summarized as a majority rule consensus (Figure S2).

## DATA AND CODE AVAILABILITY

The phylogenetic dataset compiled for this study is included (Data S1B), and no other datasets or code were analyzed.