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2 **Host specific infestation in early Cambrian worms**

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16 Keywords: Cambrian, Chengjiang Lagerstätte, commensal symbiosis, worms, *Cricocosmia*,

17 *Mafangscortex*, ecological diversification, aggregate infestation, host-specificity, host-shift

18

19 Abstract:

20 Symbiotic relationships are widespread in terrestrial and aquatic animals today, but evidence of
21 symbiosis in the fossil record between soft-bodied bilaterians where the symbiont is intimately
22 associated with the integument of the host is extremely rare. The radiation of metazoan life
23 apparent in the Ediacaran (~ 635 to 541 Ma) and Cambrian (~ 541 to 488 Ma) is increasingly
24 accepted to represent an ecological diversification resulting from earlier key genetic
25 developmental events and other innovations that occurred in the late Tonian and Cryogenian
26 periods (~ 850 to 635 Ma). The Cambrian has representative animals in each major ecospace
27 category, the early Cambrian in particular witnessing the earliest known complex animal
28 communities and trophic structures, including symbiotic relationships. Here we report on newly
29 discovered *Cricocosmia* and *Mafangsclex* worms that are host to aggregates of a new species of
30 tiny worm in the lower Cambrian (Series 2, Stage 3) Chengjiang Lagerstätte of Yunnan
31 Province, southwest China. The worm associations suggest the earliest known record of
32 aggregate infestation of the integument of a soft-bodied bilaterian, host-specificity and host-shift.

33

34 Bilateria

35 Protostomia

36 *Inquicus fellatus* gen. et sp. nov

37 **Etymology.** Latin, *inquilinus*, a lodger, a dweller in another's house, plus *priscus*, ancient;
38 and *fellator*, a sucker, plus *atus*, provided with, alluding to its lifestyle.

39 **Holotype.** YKLP13235 (part and counterpart), a complete specimen, 3.3 mm long, attached to
40 *Cricocosmia jinningensis* specimen YKLP13226 (Figs 1a-b, 2a-d; Supplementary Fig. 1a-b). Eleven
41 other specimens of *I. fellatus* (YKLP13236 - YKLP13246) are attached to this host (Figs 1a-b, 2f;
42 Supplementary Fig. 1a-d).

43 **Referred material.** At least 53 attached individuals and attachment discs lacking an attached
44 individual, associated with *Mafangsclex sinensis* and *C. jinningensis* specimens (Figs 1-3;
45 Supplementary Figs 1-3; see Supplementary Table 1 for localities).

46 **Locality.** Ercaicun (type locality), Haikou, Kunming, Yunnan Province, China.

47 **Horizon.** Yu'an-shan Member, Chiungchussu Formation, *Eoredlichia-Wutingaspis* trilobite biozone,
48 Nangaoan Stage of Chinese regional usage, Cambrian Series 2, Stage 3¹.

49 **Diagnosis for genus (monotypic) and species.** Small, 'bowling-pin'-shaped worm with a sub-
50 circular-shaped attachment disc at the posterior end of the body and a through gut that is funnel-
51 shaped anteriorly. At the end of the gut near the attachment disc there is a tiny sub-circular structure,
52 interpreted as the anus/urogenital opening.

53

54 **Morphology**

55 The body is elongate; well-preserved specimens are up to 3.3 mm long, 'bowling-pin'-shaped, with a
56 gently curved outline (Fig. 2a-b). Narrow annulations about 100 µm in width are evident along the
57 length of the body (Fig. 2a-b). The animal is attached to the host at one end (Fig. 2d). This is inferred

to be posterior, based on the interpretation of the constricted and expanded opposite end being a head, and an expansion of the gut at that end being a pharynx (Fig. 2c). The body is widest at a quarter length from the attached end, narrowest at approximately three-quarters length and is expanded distally into a free, elongate bulb with an acute tip (Fig. 2a-b, f; Supplementary Fig. 1c-d). The attachment area consists of a sub-circular-shaped disc (*circa* 200-300 μm diameter) that does not penetrate the cuticle in either *M. sinensis* or *C. jinningensis* (external annulation and cuticular ornamentation of the host are visible at the base of the attachment; Fig. 2e; Supplementary Fig. 3i-k). A swelling or depression along the edge of the attachment disc (Fig. 2e; Supplementary Fig. 3i-k) is the only indication of potential damage to the host's cuticle. A dark trace, presumed to be the gut, extends along the mid-line of the body (Figs 1a-b, 2a). At the end of the gut near the attachment disc there is a tiny sub-circular feature interpreted as the anus/urogenital opening (evident only in the well-preserved holotype; Fig. 2a-b, d). At the opposite, anterior end the gut widens to form a funnel-shaped structure that is interpreted to be the pharynx (Fig. 2c).

71

72 **Worm-host association**

I. fellatus individuals are each attached to respective *C. jinningensis* hosts in the central part of a single annulation (Figs 1a-b, 2f, 3a-b). Attachment in *M. sinensis* is similarly central or at the edge of an annulation or extends across the boundary of adjacent annulations (Fig. 3d; Supplementary Fig. 3a-k). From six to fifteen *I. fellatus* specimens are attached to individual *C. jinningensis* specimens; *M. sinensis* individuals have two to twelve attached (Supplementary Table 1). In some cases *I. fellatus* forms aggregates of six or more on the host; for example, YKLP13226 bears ten *I. fellatus* within a 12 mm section of the host (Fig. 1a-b), and YKLP13229 bears six *I. fellatus* within a 6 mm section (Fig. 3c; Supplementary Fig. 2c). Within these aggregates individuals can sometimes be evenly spaced (commonly by about 1 mm in YKLP13231, Fig. 3a-b). There is no consistent placement of aggregates relative to the anterior or posterior ends of the host worms. *I. fellatus* individuals are attached on the inner-coiled surface (interpreted to be the ventral, by comparison to other Cambrian cycloneuralians²) in five host worms (e.g. Fig. 1a; Supplementary Table 1). In one *C. jinningensis* host (Fig. 3a-b) and

one *M. sinensis* host (Fig. 3d, Supplementary Fig. 3), *I. fellatus* is attached to both ventral and dorsal surfaces. *I. fellatus* shows no evidence of bending or curving and their bodies are presumed to have been relatively stiff. Some are preserved perpendicular to the axis of the host, and others are sub-perpendicular, suggesting articulation at the attachment disc (e.g. Fig. 1a-b).

Discussion

There are insufficient morphological characters in *I. fellatus* to recognize the biological affinity of this taxon within Bilateria. Affinity with some vermiform phyla that are common symbionts is contradicted. A complete through gut negates affinities to Platyhelminthes, and a lack of external or internal segmentation is inconsistent with an assignment to the overwhelming majority of Annelida. The bowling-pin body shape and aboral attachment structure invite comparison with gastrotrichs and rotifers, though both of these conflict with fundamental characters of *I. fellatus*. Notably, gastrotrichs have marked dorsoventral differentiation, the flattened ventral surface bearing dense cilia that facilitate benthic locomotion, whereas *I. fellatus* exhibits no obvious dorsal and ventral sides. No modification corresponding to the diagnostic corona of rotifers is observed. An identity as immature representatives of the cycloneuralian hosts is contradicted by *I. fellatus* being associated with two different hosts, and the lack of an introvert, which is developed in Cambrian cycloneuralians even in embryonic stages³.

Supposed symbiotic associations of animals (parasitism, mutualism, commensalism^{4,5}) occur throughout the Phanerozoic fossil record⁶⁻¹¹, including the early Cambrian¹². For example, within Cambrian Lagerstätten there are examples of brachiopod epibionts on algae and on other brachiopods within the Chengjiang biota^{13,14}, and a case of commensalism involving brachiopods on a Burgess Shale *Wiwaxia* host¹⁵. In the exceptionally preserved Silurian Herefordshire biota, a more sophisticated relationship has been demonstrated by pentastomid arthropods parasitic on ostracods¹¹.

A parasitic relationship for *I. fellatus* with its host is unlikely, as the attachment disc is not associated with penetration of the host cuticle, the oral end of *I. fellatus* faces away from the host, and

I. fellatus appears to have been stiff, with no evidence that it could articulate backwards towards its host. Nevertheless, if *I. fellatus* were not feeding directly on its host, in those specimens with the most intensive infestation (Figs 1a,b, 3a,b), this may have substantially inhibited host locomotion and ultimately could have proved deleterious to its well-being. Alternatively, the relationship may have been commensal (used here in the sense of being beneficial to the colonizer but not the host), with *I. fellatus* using its host worm for attachment as an epibiont, or the attachment may have been temporary, and the relationship phoretic. Epibiontic or phoretic relationships commonly facilitate dispersal, protection or access to food sources. A chance association of *I. fellatus* with its host worm is the least parsimonious interpretation, given that some 53 individuals (or attachment discs) are associated with seven host specimens from three different Chengjiang localities (Supplementary Table 1). Furthermore, the style of attachment is consistent across these specimens.

As indicated by the pattern of decay, *I. fellatus* and hosts were attached in life, not via post-mortem colonization of a host carcass for scavenging. In cases where the host specimen is well preserved - presumed to be *in vivo* (e.g., *C. jinningensis* YKLP 13226, Fig. 1a) - or with minimal decay (e.g., *M. sinensis* YKLP 13230 and 13232), attached *I. fellatus* specimens are also well preserved (Fig. 2e; Supplementary Fig. 2b, d-e; Supplementary Table 1). Host specimens showing evidence of decay lose the pattern of their annulation and body outline (e.g. *C. jinningensis*, YKLP 13231), and attached *I. fellatus* are also poorly defined (Fig. 3a-b). The only specimen (*M. sinensis*, YKLP 13228) from a slowly deposited ‘Background Bed’ (interpreted as such by abundant algae in the sediment), rather than rapidly deposited ‘Event Bed’, shows more obvious decay and has the most poorly preserved *I. fellatus*, represented only by attachment discs (Fig. 3d; Supplementary Fig. 3a-k), or by specimens broken-off near their base (insets in Fig. 3d). In colonizing its host, *I. fellatus* may have responded to a specific chemical, environmental, or behavioral cue resulting in aggregates, with all individuals of similar size on one host. This suggests colonization might have occurred via rapid asexual reproduction from one initial colonizer¹⁶ or, given the similar size of *I. fellatus* on each host, via pelagic or benthic larvae¹⁷. Given that in some specimens the infestation is extensive, host individuals were at this time likely exposed on the seabed, rather than in burrows^{cf.18}.

I. fellatus represents the earliest probable example of host specificity in the fossil record. The association of *I. fellatus* with two host species is comparable with modern commensal ecologies. Of sixteen other priapulid, or possible priapulid-like species in the Chengjiang biota¹, none have *I. fellatus* associates, this in spite of collection of the Chengjiang biota for over three decades. This suggests a high-degree of host specificity that does not appear to have been mediated simply by attachment morphology, as several other Chengjiang worm species have a similar cuticular structure to *C. jinningensis* and *M. sinensis* but lack *I. fellatus*. The possibility that material of *I. fellatus* represents more than one species of similar infesting worm is unlikely, given the similarity of size, shape, gut, and attachment structure across the 53 specimens we have examined.

The relationship of *I. fellatus* with two host species also indicates a capacity for host-shift – the colonization of a new host species from an original host – and that this type of ecology was already developed in early Cambrian ecosystems. Host shift is regarded as an important mechanism for sympatric speciation across many organismal groups¹⁹⁻²¹.

Infestation rates of *I. fellatus* are comparable to living analogues. Though instances of attached *I. fellatus* are rare, they are within the rates of, for example, modern polychaete commensal infestations¹⁶, with *circa* 0.1%- infestation of *C. jinningensis* with *I. fellatus* (3 of 3098 specimens examined) and *circa* 0.8%-infestation of *M. sinicus* with *I. fellatus* (4 of 476 specimens examined). Although infestation is limited, it does not preclude this type of commensal ecology being more widespread in Cambrian marine ecosystems. Infestation rates vary in modern settings through environmental gradients such as water depth. The depositional basin of the Chengjiang biota extended over at least 1000 km² and had an eastwards sloping marine shelf^{22,23}. *I. fellatus* is unknown east of localities around Haikou, even though specimens of *Mafangsclex* are reported from the deeper shelf settings of the Chengjiang area.

Animal burrows, possibly of priapulid origin²⁴, define the Ediacaran-Cambrian System boundary²⁵, an isochronous surface some 20 million years earlier than the Chengjiang biota. Trace fossils, possibly attributable to priapulids, are also reported from the latest Ediacaran, in strata younger than ~ 560 - 550 Ma^{26, 27}. The development of complex host-specific ecologies, as

demonstrated by *I. fellatus*, might therefore have evolved over a protracted interval of late Precambrian and early Cambrian time, the main burst of ecological diversification of animals being during the Cambrian explosion^{28,29}. Previous work has shown that about one-third of the modes of life known from the Recent were occupied during the early and middle Cambrian³⁰. This compelling case of symbiosis documented herein identifies the earliest record of aggregate infestation, host-specificity and host-shift, and thus fills a gap in our knowledge of the complexity of Cambrian ecosystems.

Methods

Data availability. All specimens (YKLP 13226-13232, YKLP 13235-13288) are deposited at the Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China. Some specimens were prepared mechanically with needles under a stereomicroscope. The authors declare that all data supporting the findings of this study are available within the paper and its supplementary information files.

Photography. Host specimen YKLP 13226 and the attached *I. fellatus* specimens were photographed with a Nikon D3X camera equipped with an AF-S VR Micro-Nikkor 105mm lens. Host specimens YKLP 13227-13228 and *I. fellatus* specimens were photographed with a Canon 650D camera mounted with a Canon EF-S 60 mm macro lens or a Canon MP-E 65 mm (1-5X) macro lens. Host specimens YKLP 13229-13232 and *I. fellatus* specimens were photographed with a Canon 5D DSLR camera on Nikon Multiphot macrophotographic equipment, including bellows extensions and Macro-Nikkor 6.5 cm or 12 cm lenses. Details of the holotype of *I. fellatus* (YKLP 13236) were captured with a Leica DFC5000 camera mounted to a Leica M205C stereomicroscope. Specimens were photographed in polarized or normal incident fibre-optic light. Camera lucida drawings were produced with a Meiji Techno RZ stereomicroscope and traced in Adobe Illustrator CC 2014.2.2.

SEM and EDX. Scanning electron microscope (SEM) images were obtained using a LEO 1455VP at 12 kV accelerating voltage and 16-18 Pa chamber pressure. Energy dispersive X-ray spectroscopy (EDX) was performed using a FEI Quanta 650 FEG instrument at 15 kV accelerating voltage and 20

191 Pa chamber pressure. The EDX images were prepared with selected colour within Adobe Photoshop

192 CC 2014.2.2.

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261 **Acknowledgements**

262 The reconstruction was made by B. Nicholls (<http://paleocreations.com>). This research is funded by
263 NSFC (41572015, U1302232), NERC Independent Research Fellowship (NE/L011751/1), the
264 Leverhulme Trust grants (RPG-2015-441, EM 2014-068), the Royal Society International Joint
265 Project (IE131457), and the Yunnan Innovation Research Team grant (2015HC029).

266

267 **Author Contributions**

268 P.C., X.M., X.H. and D.Z. collected and prepared all specimens. P.C. and X.M. conceived the project
269 and led the team. All authors interpreted the data. M.W. and David S. wrote the initial draft with
270 scientific and editorial input from all authors. T.G., S.E.G. and P.C. conducted SEM and element
271 mapping analyses. Derek S. and P.C. photographed the specimens and prepared figures. M.W. and
272 P.C. made the camera-lucida drawings. X.M. calculated infestation rates.

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274 **Additional information**

275 **Supplementary information** is available for this paper.

276 **Correspondence and requests for materials** should be addressed to X.M. (xma407@nhm.ac.uk).

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279 **Competing Financial Interests**

280 The authors declare no competing financial interests.

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Figure Legends

Figure 1 | Cluster of *Inquicus fellatus* attached to *Cricocosmia jinningensis*. **a**, *C. jinningensis* (YKLP13226a) with a minimum of 12 attached *I. fellatus* (YKLP13235-13246, see Supplementary Fig. 1a for specimen numbering) on the ventral side. **b**, interpretative drawing. Scale bar, 3 mm.

Figure 2 | Morphology of *I. fellatus*. **a-b**, holotype (YKLP 13235a), showing attachment disc (ad), annulation, anus or urogenital opening (uo), and trace of gut, and element map (Fe), showing concentration of Fe at the attachment disc, the urogenital opening/anus and the anterior end. **c-d**, detail of the anterior (c) and posterior (d) of the holotype, note the bilobed shape (hollow arrows) of the urogenital opening/anus as in (b); **e**, Scanning electron micrograph showing heavily pyritized remains of an attachment disc (YKLP 13274) on host *M. sinensis* (see Fig. 3d and Supplementary Fig. 3), note the cuticle of the worm beneath the attachment is undamaged. **f**, element map (Fe) of several individuals of *I. fellatus* on *C. jinningensis* host (YKLP13226a), showing the attachment disc positioned centrally on each annulation (hollow arrows). For details of the role of iron in preservation see⁴. Scale bars, **a-b**, 400 μ m; **c-e**, 100 μ m; **f**, 1mm.

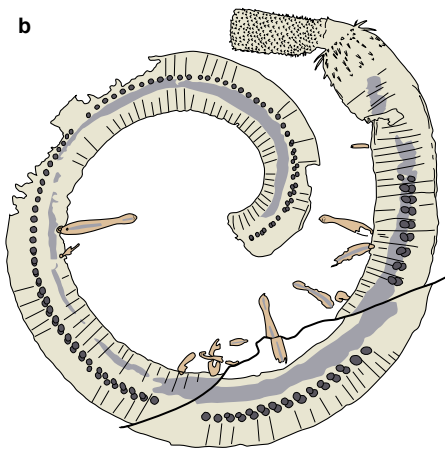
Figure 3 | Host worms and attached *I. fellatus* from the Chengjiang biota. **a-b**, *Cricocosmia jinningensis*, YKLP13231, with a minimum of 15 *I. fellatus* attached to both the ventral and dorsal sides of the host; both the host and the attached worms are partially decayed, evidenced by less well-defined outlines (compare with Figs. 1a, 2a), inset shows detail of two partially decayed *I. fellatus* (a) and the annulation of the host (b). **c**, *C. jinningensis*, YKLP13229a, decayed host (with loss of annulation) with a minimum of six poorly preserved *I. fellatus* attached to the ventral side. **d**, *M. sinensis*, YKLP13228a, decayed specimen from a ‘background’ mudstone, with multiple poorly preserved *I. fellatus* (insets) represented only by the posterior extremity of the body (hollow arrows) and its attachment disc (white arrows) (see also Supplementary Fig. 3). **e**, *M. sinensis*, YKLP 13230,

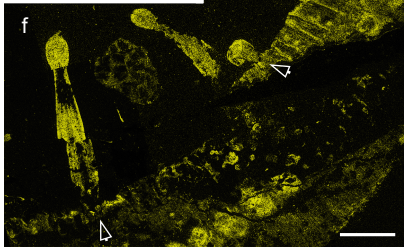
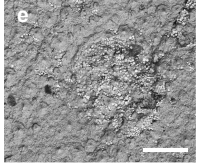
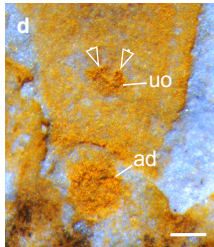
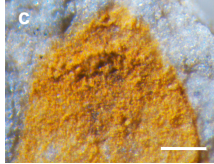
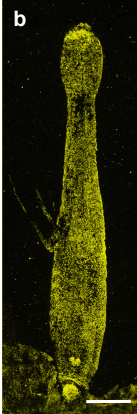
310 incomplete specimen with two *I. fellatus* with less well-defined outlines (inset). **f**, *M. sinensis*, YKLP
311 13227, well-preserved specimen with one incomplete *I. fellatus* (inset, YKLP 13288) attached at the
312 posterior end of the body. See Supplementary Figs 2-3 for registration numbers of *I. fellatus* on each
313 host worm. Scale bars, **a-f**, 5mm; inset in **a**, **b** and large inset in **d**, 1mm; small inset in **d** and **e**, 500
314 μm ; inset in **f**, 200 μm .

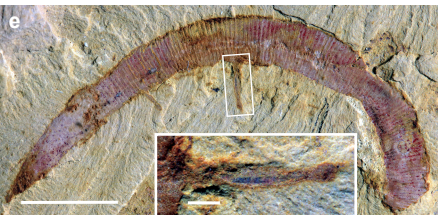
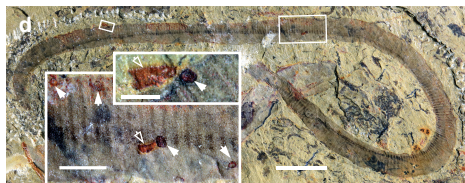
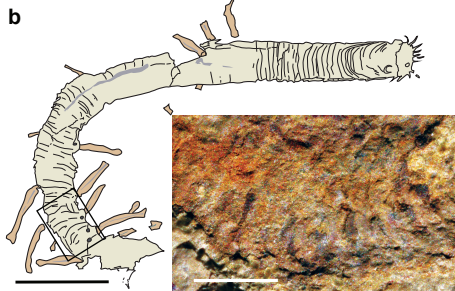
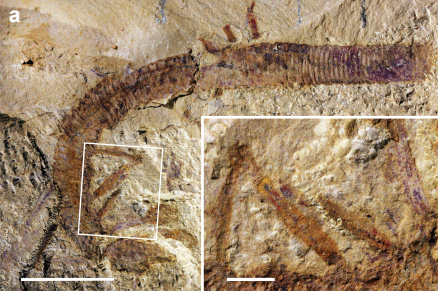
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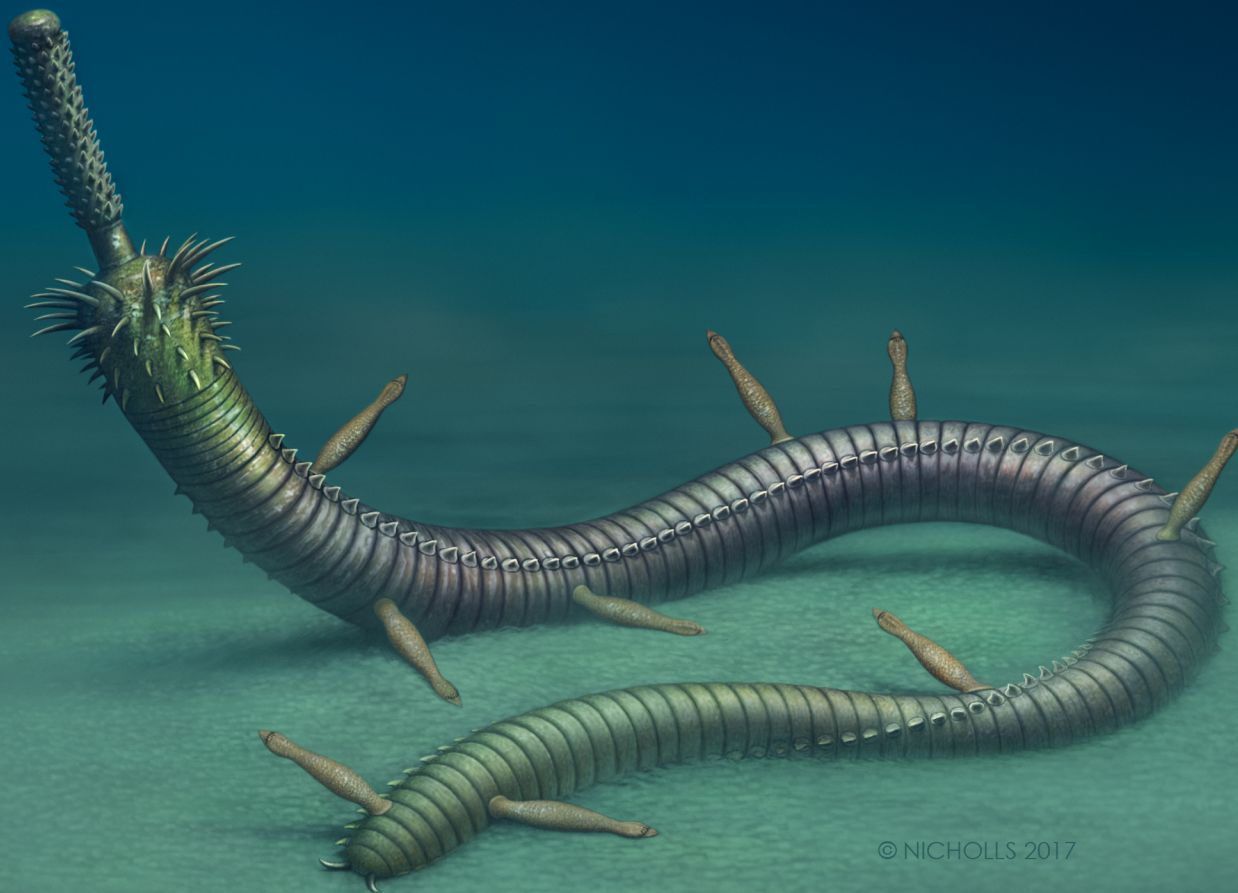
316 **Figure 4 | Artist's reconstruction of *Inquicus fellatus* infesting *Cricocosmia jinningensis*.**

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a**b**







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