

Meiofaunal deuterostomes from the basal Cambrian of Shaanxi (China)

Jian Han¹, Simon Conway Morris², Qiang Ou^{3,4}, Degan Shu¹ & Hai Huang⁵

Deuterostomes¹ include the group we belong to (vertebrates) as well as an array of disparate forms that include echinoderms², hemichordates³ and more problematic groups such as vetulicolians⁴ and vetulocystids⁵. The Cambrian fossil record is well-populated with representative examples, but possible intermediates^{6,7} are controversial and the nature of the original deuterostome remains idealized. Here we report millimetric fossils, *Saccorhytus coronarius* nov. gen., nov. sp., from an Orsten-like Lagerstätte from the earliest Cambrian period of South China, which stratigraphically are amongst the earliest of deuterostomes. The bag-like body bears a prominent mouth and associated folds, and behind them up to four conical openings on either side of the body as well as possible sensory structures. An anus may have been absent, and correspondingly the lateral openings probably served to expel water and waste material. This new form has similarities to both the vetulicolians⁴ and vetulocystids⁵ and collectively these findings suggest that a key step in deuterostome evolution was the development of lateral openings that subsequently were co-opted as pharyngeal gills^{2–4,8}. Depending on its exact phylogenetic position, the meiofaunal habit of *Saccorhytus* may help to explain the major gap between divergence times seen in the fossil record and estimates based on molecular clocks⁹.

Insights into the early evolution of deuterostomes¹ are critically dependent on the Cambrian fossil record, notably from Burgess Shale-type and Orsten-style Lagerstätten. By Cambrian Series 2–3 (around 510–520 million years ago (Ma)), this superphylum had diversified into echinoderms², hemichordates³, tunicates¹⁰ and vertebrates¹¹, as well as the more problematic cambroernids⁶, vetulicolians^{4,12}, vetulocystids^{5,13} and yunnanozoans⁷. This degree of disparity, combined with apparently rapid divergences, renders the identification of the various stem groups problematic and also frustrates reconstruction of the ur-deuterostome.

Here we describe a suite of phosphatized microfossils from the earliest Cambrian period of South China (Extended Data Fig. 1). These fossils throw new light on what appears to be an early stage in deuterostome evolution and reiterate the importance of Örsten-style Lagerstätten^{14–17} as a source of insights into the Cambrian metazoan radiations.

Deuterostomia Grobben, 1908

Saccorhytidida (new stem group) Han, Shu, Ou and Conway Morris, 2017

Saccorhytidae (new family) Han, Shu, Ou and Conway Morris, 2017

Diagnosis. Millimetric, ellipsoidal body, ventral mouth and multiple lateral openings.

Saccorhytus gen. nov. Han, Shu, Ou and Conway Morris, 2017

Saccorhytus coronarius gen et sp. nov. Han, Shu, Ou and Conway Morris, 2017

Etymology. Generic name reference to bag-like body (L. *saccus*) and wrinkled preservation (Gr. *rhytis*). Specific name in reference to crown-like mouth.

Diagnosis. Hemi-ellipsoidal, bilaterally symmetrical body. Integument bears chevron pattern. Ventral mouth defined by two circlets of radial folds, inner circlet with associated protuberances. Aborally and dorsally up to four nodulate rugae. Eight body openings, conical, defined by radial folds. In mid-region anteriorly directed spines. Smaller pores parallel to body cones and in posterior region, possibly housed setae. Holotype. XX45-20.

Other material. XX25-62 and another 43 specimens (Supplementary Table 1).

Locality. Zhangjiagou section, Hexi, Xixiang County, Shaanxi, China.

Stratigraphy. Kuanchuanpu Formation, Fortunian Stage of Terreneuvian Series.

Forty-five phosphatized specimens are available (Figs 1, 2, Extended Data Figs 2–6 and Supplementary Table 1). As with similar material from this horizon^{14–16} and co-eval deposits¹⁷, the phosphatic composition of the specimens is evidently the result of very early diagenesis. Extensive folding suggests that in life the integument was thin, flexible and only slightly sclerotized. The integument consists of two layers (Extended Data Figs 2b, c, h, 3c, g, 5k, 6c, d), and frequently exhibits a fine-scale, densely spaced chevron-like folding on both external and internal surfaces (Fig. 1b, Extended Data Figs 2f–i, 3h, 4g and Supplementary Table 1). If original, this suggests that the integument was bi-layered.

The body is hemi-ellipsoidal, with a maximum length of 1,300 µm, width 800 µm and height 900 µm (Extended Data Fig. 7). Most material is crushed but several specimens (Fig. 1g, h and Extended Data Figs 5g, h, 6a) confirm original bilateral symmetry. Otherwise, body orientations depend principally on identification of the mouth, and presumably the more dorsal and posterior location of the body cones and possibly sensory pores. Post-mortem deformation makes the precise dispositions of other structures more difficult to interpret. The most parsimonious conclusion, however, is that these features were also arranged bilaterally (Fig. 1g, h and Extended Data Figs 4f, h 6a).

The largest of the body openings (approximately 300–500 µm) is defined by a double circlet with prominent radial folds. The folds of the inner circlet are somewhat finer and this circlet also bears a series of oral protrusions, each consisting of an outer sheath and an inner peg-like structure (Figs 1a, d, e, g–i, 2a, b, d, e and Extended Data Figs 2c, 3f, 4a, c, f, 5a, c, d, g, i). This double circlet is interpreted as the oral region, while the protrusions, notably the most anterior pair (Extended Data Figs 5g, i, 6f, g), may represent sensilla. The flexibility of the oral region is evident from both its lateral compression and dorsal arching (Figs 1a, d, e, i, 2d and Extended Data Figs 4a, e, 5a, c, d, g).

Anterior to the oral region, the dorsal integument consists of up to four rugae with a nodular appearance (Figs 1a, d, 2a, b, d and Extended Data Figs 3d, 4a, c, 5a, f). These may be separated by intervening integument or (presumably as a result of contraction) are closely adpressed with the nodular regions interlocked. Behind the rugae, the

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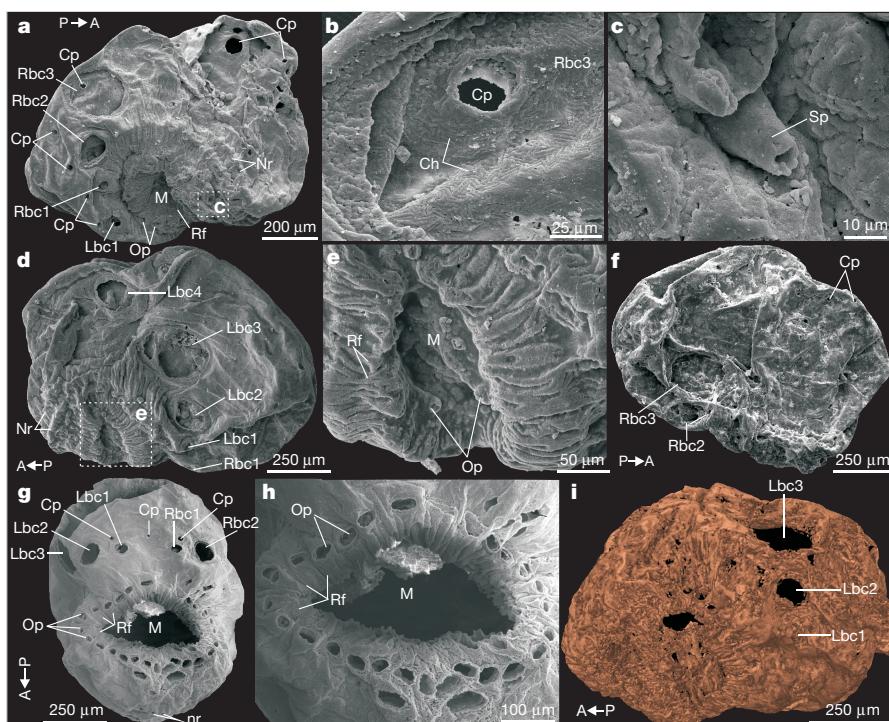


Figure 1 | *Saccorhytus coronarius* gen. et sp. nov. from the Cambrian Kuanchuanpu Formation, South China. **a–c**, Holotype XX45-20.

a, Right side. The mouth (M) arched dorsally along the anterior–posterior axis. **b**, Chevron pattern (Ch) on the inner surface of the integument. **c**, A spine (Sp) close to the mouth. **d–f**, XX45-56. **d**, Left side. **e**, Detail of the dorsally arched and folded mouth with radial folds (Rf) and oral protrusions (Op) in **d**. **f**, Circular pores (Cp) on the dorsal, right side. **g–i**, XX48-64 with limited compression. **g**, Ventral view, showing body

integument grades into a zone with longitudinal folds, but the posterior body is relatively smooth. Otherwise the most prominent structures are a series of body cones (Figs 1a, d, g, i, 2a, c, d, f, g and Extended Data Figs 2a, b, d, h, 3a, c, d, g, 4b, d, f, h, 5a–c, e, g, k, 6). These vary in size (56–328 μm across), but all are formed of a series of ribs radiating from an unoccluded aperture. Up to eight body cones are visible, with the four body cones on the left and right sides extending in a more dorsal direction (Fig. 3a). The first body cone is located immediately behind the oral region, and the body cone behind it is somewhat larger. The third body cone is the largest, and the most dorsal one is smaller. There are also two sets of small circular pores (30 μm across). One set is widely separated and runs parallel to the body cones (Fig. 1a, g and Extended Data Figs 4f, h, 5g). The other set is more dorsal and consists of sub-linear arrays (Figs 1a, b, f, 2a, c, f, g and Extended Data Figs 2a, d, e, j, 3a, d, e, 4f, h, 5b, h, j). Finally there are occasional conspicuous spines, with a wide base and elongate anterior taper (Figs 1c, 2h and Extended Data Figs 3d, 5a, b, f, 6a). Strong folding makes the conclusion tentative, but no anus is evident (Fig. 3a).

The oral region could evidently distend, with its pleated arrangement accommodating changes in size. This, combined with dorsal arching, would allow ingestion of food particles and possibly somewhat larger prey¹⁸. The size of mouth also suggests that water was swallowed, with the body cones being interpreted as exhalant structures. The dorsal extension of the body cones suggests that the corresponding oral cavity was also elongate. The more dorsal set of circular pores may represent the insertion points of setae. The other set adjacent to the body cones may have had a sensory function, although alternatively they could have released internal contents such as adhesive mucus or gametes.

The millimetric size of *Saccorhytus* does not preclude a planktonic location, but its globular shape is consistent with a meiobenthic habit within what is now a phosphatic shelly limestone¹⁶. Although we

cones (Bc) bilaterally arranged around the anterior, including the mouth. Two circular pores are adjacent to the first body cones (Bc1) and a small circular pore is on the mid-ventral line of the body. **h**, Oral protrusions lacking distal ends and appearing as a circle of pores. **i**, Left view reconstructed by microcomputerized tomography data. Lbc1–Lbc4, left body cones; Nr, nodular rugae; Rbc1–Rbc4, right body cones; Rf, radial folds; Sc, sub-layer of cuticle; arrowed AP, anterior–posterior axis.

did not find exact counterparts amongst extant meiobenthic taxa, *Saccorhytus* shows a suite of features consistent with an interstitial habitat¹⁸. These include a thick but flexible cuticle, suitable for mechanical protection and wriggling between sediment grains, respectively (Extended Data Fig. 1c, d). The postulated setae, especially those towards the dorsal side, could perform a haptic role, including temporary attachment. Many meiobenthic taxa are progenetic and deciding whether *Saccorhytus* is best interpreted as a miniaturized adult or a larval stage has important implications for both potential life cycles and phylogenetic relationships. Evidence in favour of the former includes the observation that, despite a size range of 548–1,326 μm, the morphology is effectively invariant. More notable is that most extant larvae¹⁹ are ciliated and, although a few groups such as the bryozoans (cyphonautes) and loriciferans have thin cuticular coverings, they are unlike the relatively massive coat of *Saccorhytus*.

Irrespective of whether *Saccorhytus* is a progenetic relative of unknown macroscopic taxa, its closest relationships appear to lie with the vetulicolians and possibly vetulocystids. Forming part of a highly disparate suite of taxa, collectively they appear to represent early deuterostomes^{1,20}, albeit ones not easily assigned to particular stem groups²¹. Our phylogenetic analysis (Fig. 3b, Extended Data Fig. 8 and Supplementary Information) confirms both the monophyly of the deuterostomes²² and component groups including vetulicolians plus banffiids and vetulocystids, but the position of *Saccorhytus* remains less well constrained.

With respect to vetulicolians, similarities with *Saccorhytus* include the circum-oral radial structures and the body openings, interpreted as pharyngeal gills in the former group. In forms such as *Didazoon*¹² the gills also have a convex exterior, although here the openings are directed posteriorly. Moreover, in *Didazoon* the relative size of the openings in the posterior direction is similar to that seen in *Saccorhytus*, notably with the third opening being conspicuously larger. In *Didazoon*¹²,

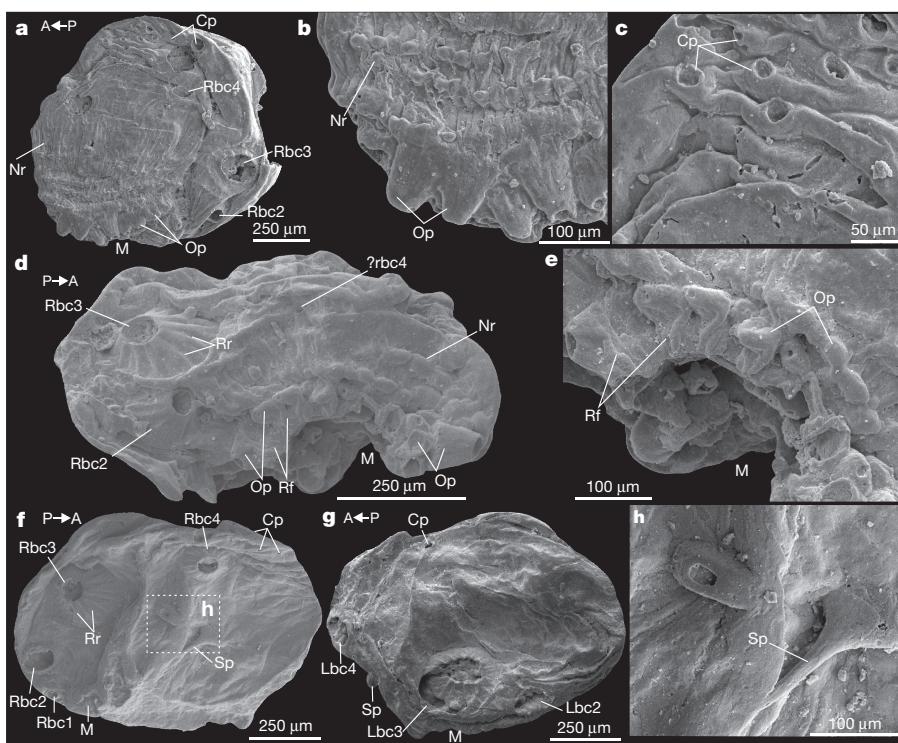


Figure 2 | *Saccorhytus coronarius* gen. et sp. nov. **a–c**, XX45-1. **a**, Left side. **b**, Detail of mouth with nodular rugae and oral protrusions in **a**. **c**, Circular pores on the dorsal side of **b**. **d, e**, XX36-22. **d**, Right view. Nodular rugae visible on ventral posterior part of the body, and body cones with radial ribs (Rr). **e**, Detail of mouth with radial folds and oral

protrusions of which those on the middle line are largest. **f–h**, XX34-298. **f, g**, Right and left, respectively; four body cones with radial ribs on either side of the specimen with circular pores on the dorsal side. **h**, Anterior body showing spine and unidentified structure with a sub-rectangular base and pore.

Pomatrum, *Xidazoon*^{1,12} and *Banffia*²³ the oral region shows variably developed pleating (Extended Data Fig. 9), similar to *Saccorhytus*. Similarities to the vetulocystids⁵ include body openings defined as

truncated cones with well-developed radial ribs, albeit more numerous. The anterior body of vetulocystids is also strongly convoluted, and so reminiscent of *Saccorhytus*.

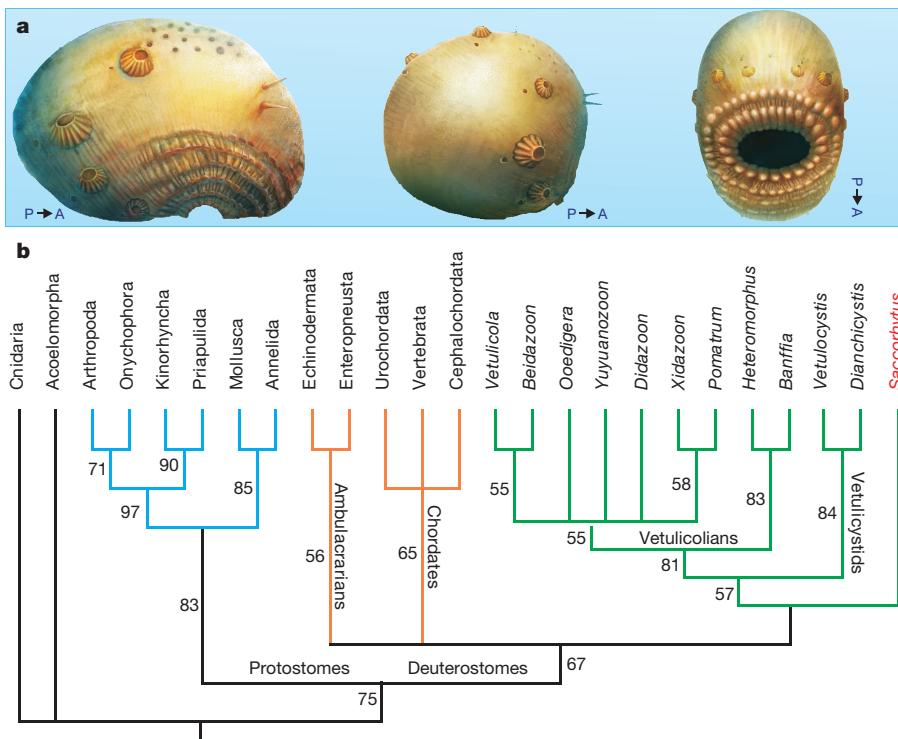


Figure 3 | Reconstruction of *Saccorhytus coronarius* gen. et sp. nov. **a**, and the phylogeny of early deuterostomes. **a**, Lateral, hind and ventral views. **b**, The most parsimonious tree (tree length, 96; consistency index, 0.6771; retention index, 0.8394; rescaled consistency index, 0.5683) arising from a matrix of 25 taxa and 61 characteristics. The values at nodes indicate bootstrap support greater than 50% (see Supplementary Information for details).

Very few characters unite the deuterostomes^{8,22,24}, and only the pharyngeal openings are potentially fossilizable. In this context the body cones of *Saccorhytus* are more similar to the apparently equivalent structures found in the vetulicolians and vetulocystids than they are to the pharyngeal structures of other deuterostomes^{1,3,7,11}. Early deuterostomes have a through gut, so the apparent absence of an anus in *Saccorhytus* could be secondary, as in brachiopods and ophiuroids. It remains possible, however, that this feature was inherited from more primitive bilaterians²⁵, possibly linked to the acoels and xenoturbellids^{24,26}.

We draw two main conclusions. First, some of the earliest deuterostomes were meiofaunal, and this finding complements proposals that such animals were benthic worms²⁷. In contrast, however, to the suggestions that early deuterostomes possessed an indirect life cycle with a feeding larva²⁴, the biology of *Saccorhytus* seems more consistent with direct development²⁸. Previous work had emphasized the possible importance of the first stages of metazoan evolution occurring in a meiofaunal context²⁹. The discrepancy between the known fossil record of early metazoans and their estimated times of divergence³⁰ as based on molecular clocks suggests that such miniaturized forms could slip through the nets of most fossilization pathways and so help to explain this cryptic history⁹. Second, the body cone openings of *Saccorhytus* are consistent with deuterostome body openings being very primitive^{8,24}. In *Saccorhytus*, however, diffusion across the body surface would have met any respiratory needs, suggesting that a transformation to specifically pharyngeal gills was linked to an increase in body size. If *Saccorhytus* lacked an anus, body openings may have originated to dispose of waste material.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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(see full-text HTML version for details).

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Supplementary Information is available in the online version of the paper.

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Author Contributions J.H. and D.S. conceived the project. J.H., S.C.M. and Q.O. wrote early drafts of paper and assessed initial results. J.H. prepared photographs and phylogenetic analysis. H.H. undertook computerized tomography restoration. All authors discussed results, and developed observations and conclusions.

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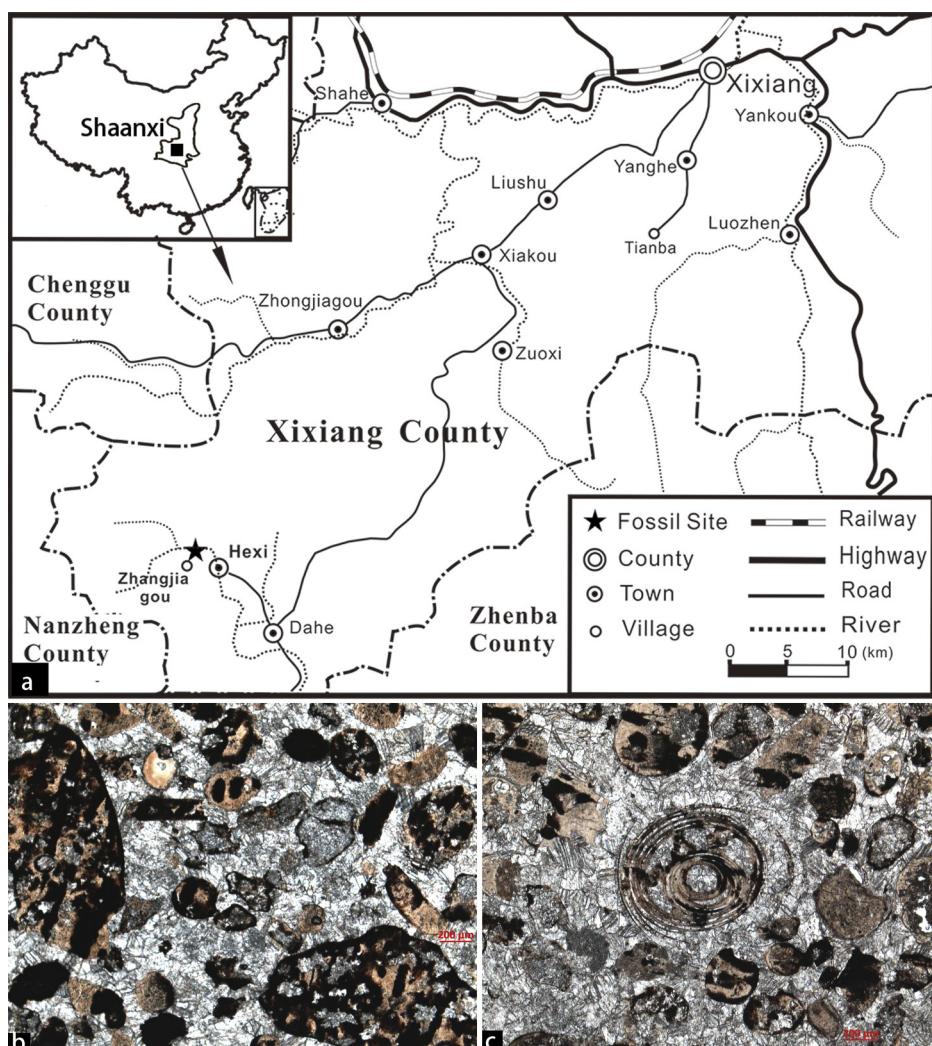
METHODS

Most of the rock samples were treated with 8% acetic acid solution, with the insoluble component being examined with a binocular microscope. Coated with gold, the specimens were imaged under high vacuum in a scanning mode using secondary electrons with an of FEI Quanta 400 FEG scanning electron microscope. Internal anatomy of specimens was examined using microcomputed tomography (micro-CT) with a ZEISS Xradia-510 in Xian Shiyou University, China with settings: source voltage ~40kV, target current ~74 μ A. For a single microfossil we acquired 990 successive pictures each with a resolution of 1,013 \times 1,013 pixels, and each pixel was about 1 μ m. Micro-CT data were processed using VG Studio 2.2 Max for 3D reconstructions. All specimens are deposited at the Early Life Institute (ELI),

Northwest University, Xi'an, China. Forty-five specimens are assigned to *Saccorhytus coronarius* gen. nov., sp. nov.: XX23-248, XX25-62, XX26-170, XX26-168, XX34-298, XX35-228, XX36-22, and so on.

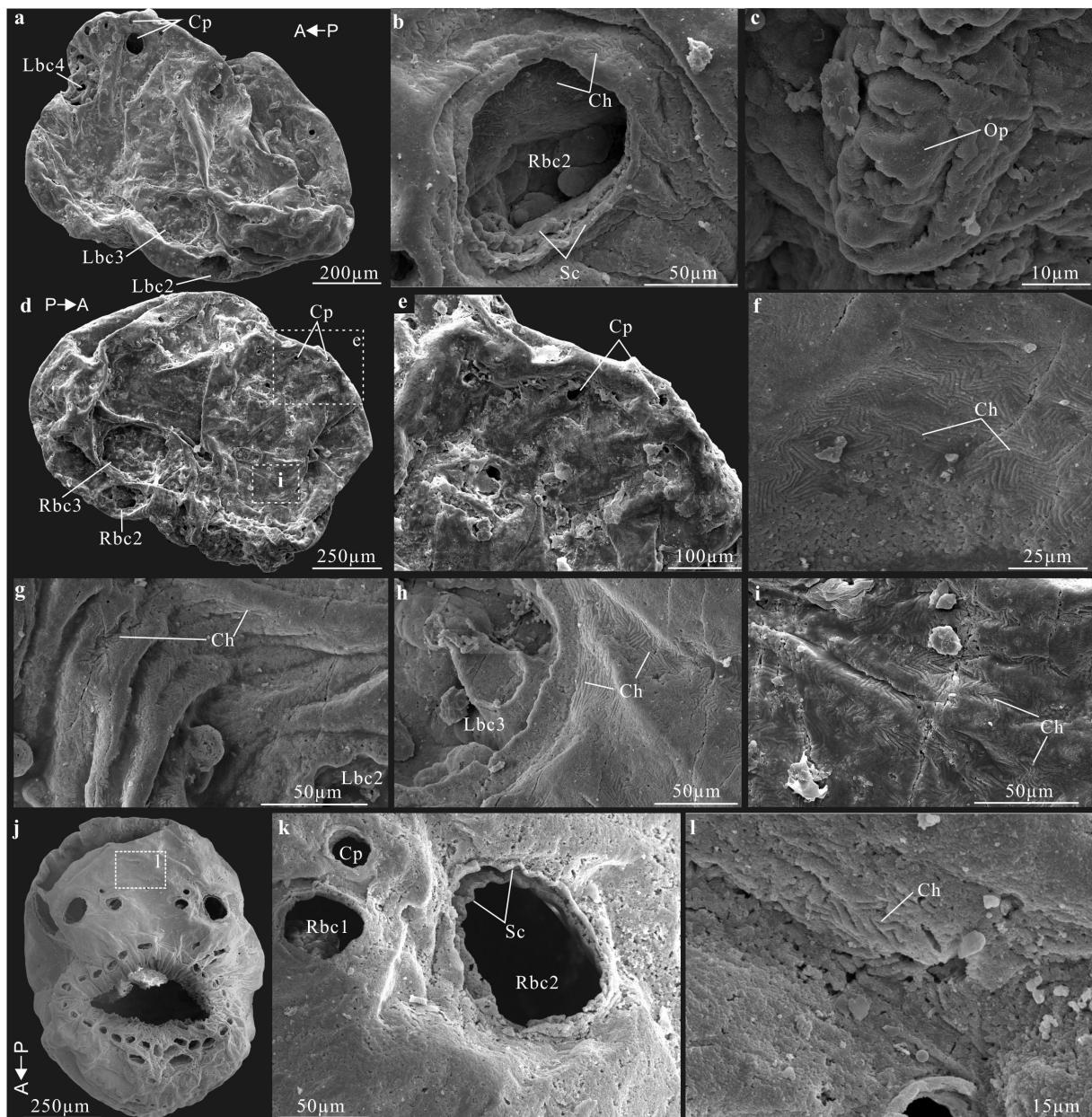
Data availability. Source data for all figures are provided with the paper. The phylogeny in Fig. 3 is provided in the Supplementary Information.

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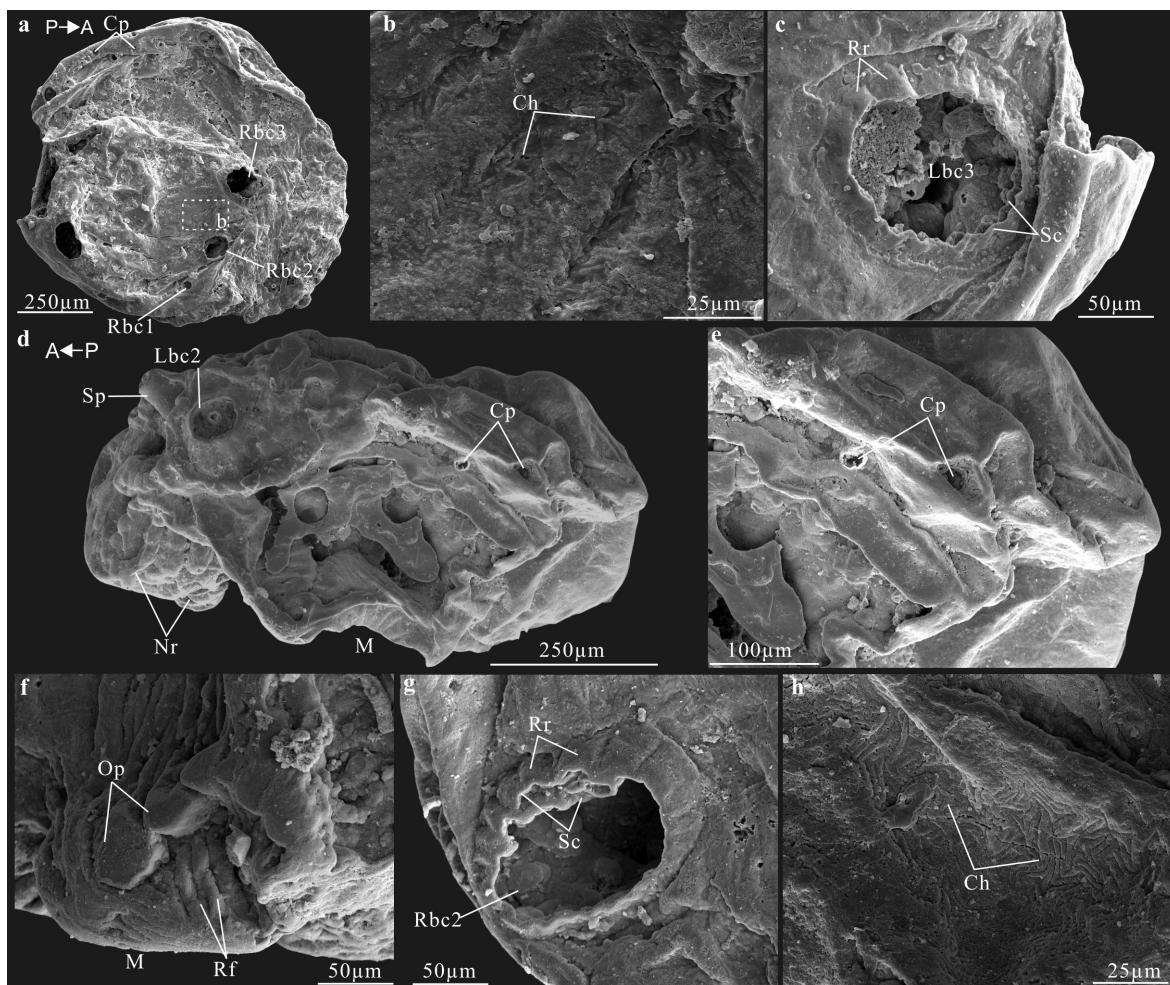
Extended Data Figure 1 | Geographical location of horizon and its petrography. **a,** Locality map of the Zhangjiagou section, Xixiang, Shaanxi Province, China. In addition to *Saccorhytus*, the phosphatic limestone of Bed 2 of the Kuanchuanpu Formation in the Zhangjiagou section

(see ref. 16) contains numerous small shelly fossils. **b, c,** Petrographic sections (plane-polarized light) of Bed 2 showing the phosphatic bioclastic grains, carbonate matrix and cements.



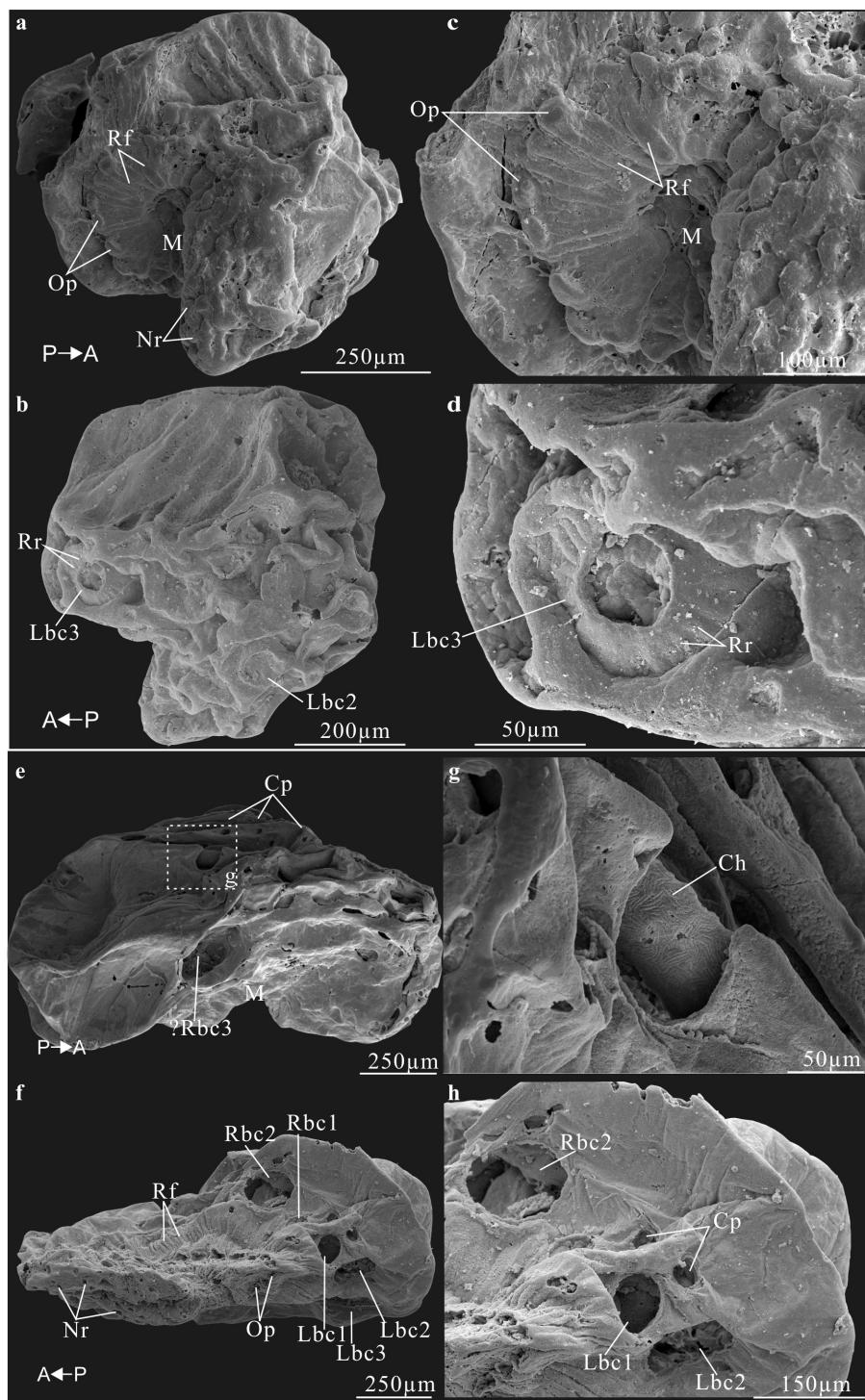
Extended Data Figure 2 | *Saccorhytus coronarius* gen. et sp. nov.
a–c, Holotype XX45-20. **a**, Left side, showing the body cones and circular pores. **b**, Two sub-layers of the integument around a body cone (Rbc2), with chevron pattern on the external and inner surfaces in Fig. 1a. **c**, Close-up of an oral protrusion in Fig. 1a. **d–i**, XX45-56.

d, e, Close-ups of circular pores on the right, dorsal side. **f–i**, Chevron pattern on integument surface of dorsal side. **j–l**, XX48-64. **j**, Ventral view. **k**, Radial ribs of body cones defined as wavy margin, with integument composed of two sub-layers. **l**, Chevron pattern on integument surface.


Extended Data Figure 3 | *Saccorhytus coronarius* gen. et sp. nov.

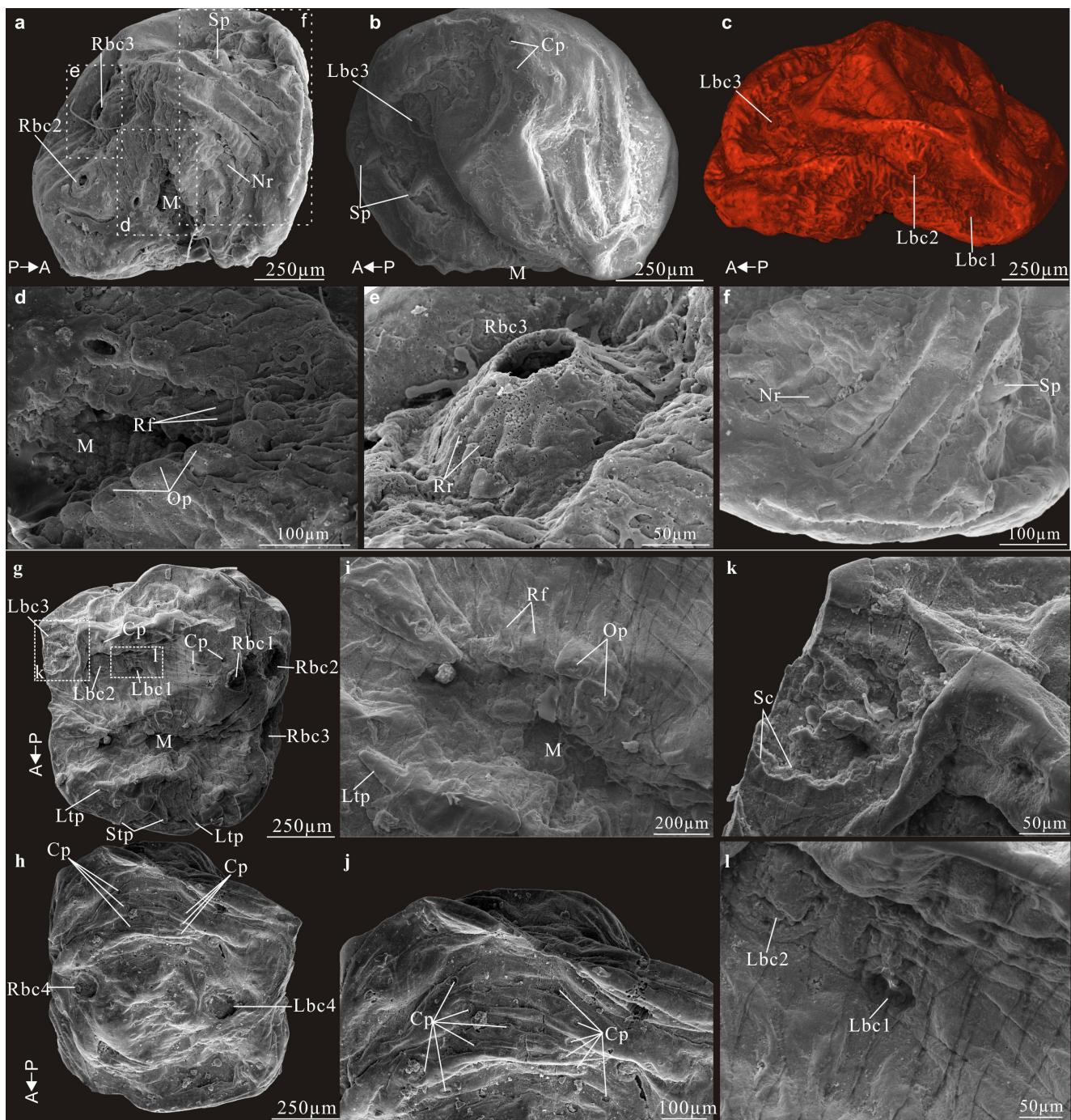
a–c, XX45-1. **a**, Right side. **b**, Chevron pattern on integument surface. **c**, Two sub-layers of the integument on the third, left body cone (Lbc3) in Fig. 2a. **d**, XX36-22. **d**, Left view. A spine close to the second, left body cone (Lbc2); ventral part with nodular rugae. **e**, Circular pores on the

dorsal side of **d**. **f–h**, XX34-298. **f**, Close-up of closed mouth with radial folds and oral protrusions in Fig. 2f. **g**, Two sub-layers of the integument on the second, right body cone (Rbc2) with radial ribs in Fig. 2g. **h**, Chevron pattern on integument surface.



Extended Data Figure 4 | *Saccorhytus coronarius* gen. et sp. nov.
a–d, XX25-62, highly compressed. **a, b**, Right and left sides, respectively. **c**, Close-up of mouth with radial folds and oral protrusions in **a**; note nodular rugae on ventral anterior of body. **d**, Third body cone with radial

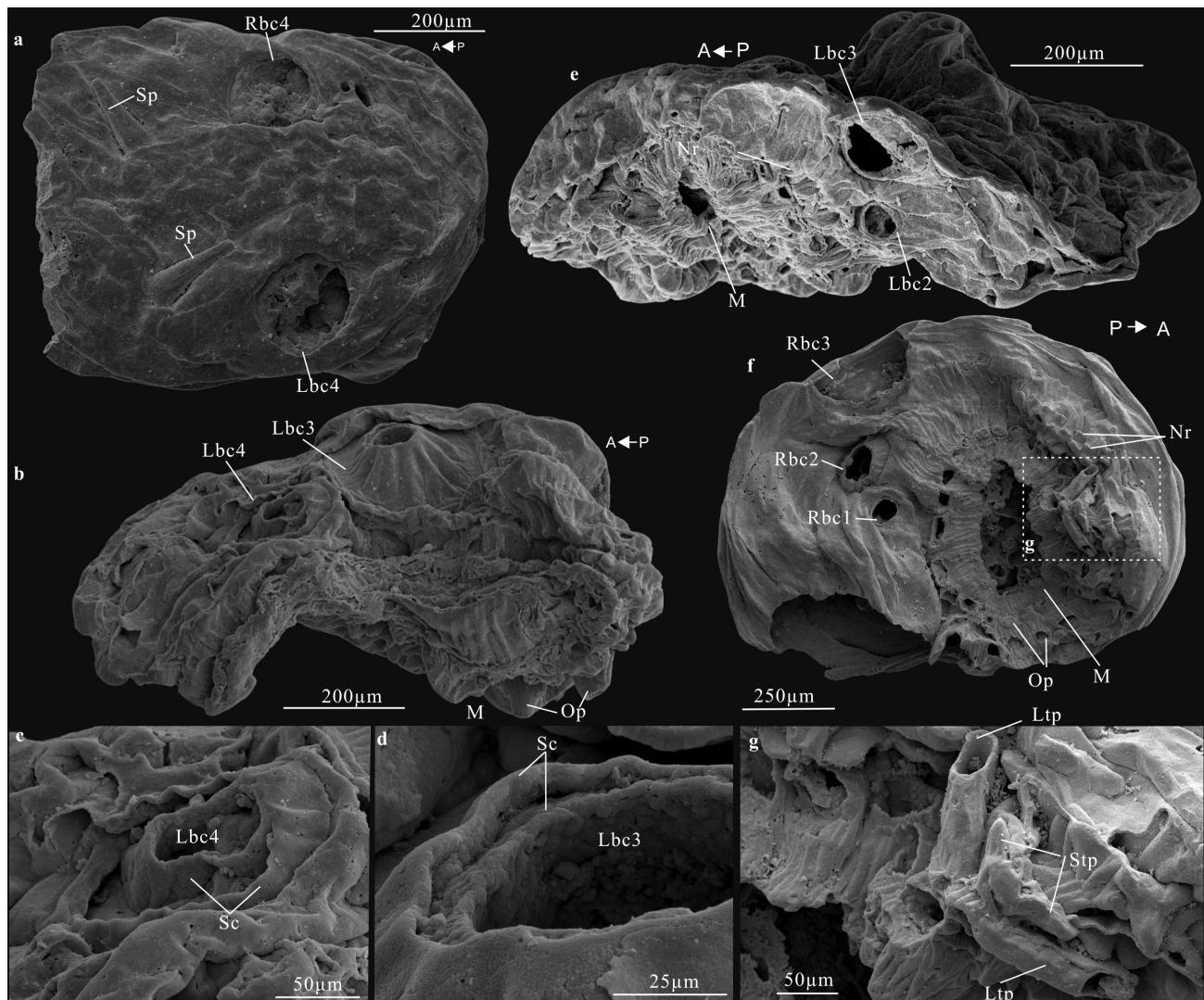
ribs. **e–h**, XX27-160. **e**, Right view. **f**, Ventral view showing ventral mouth with radial folds and anterior nodular rugae. **g**, Chevron pattern on inner surface of integument. **h**, Two circular pores to posterior of first body cone.



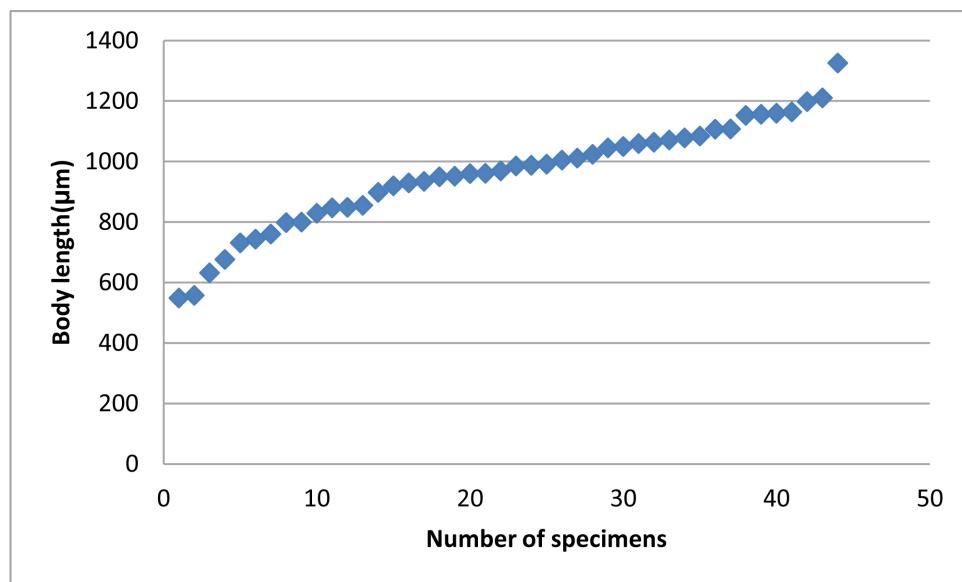
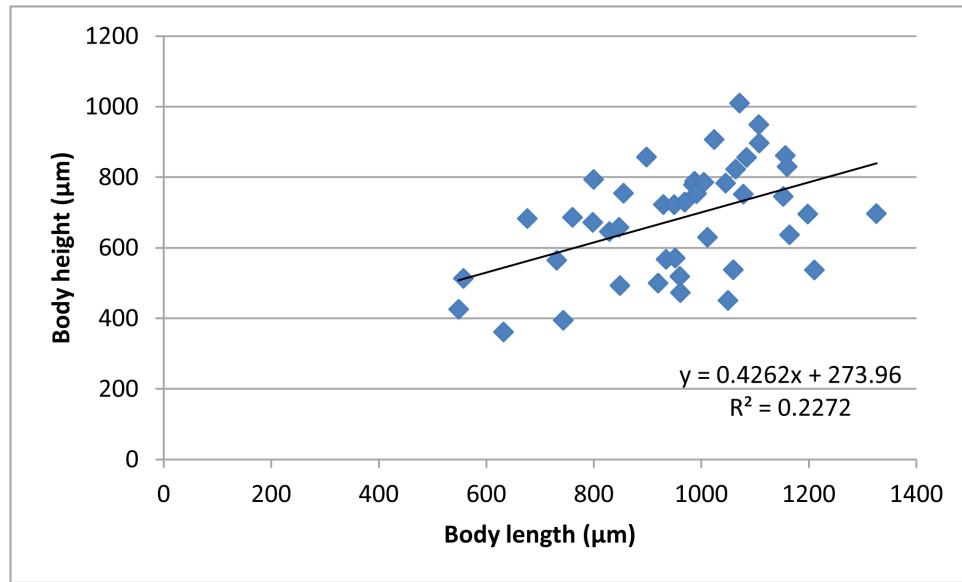
Extended Data Figure 5 | *Saccorhytus coronarius* gen. et sp. nov.

a–f, XX27-168. a, b, Right and left sides, respectively. Two body cones on right in a; two spines close to third left body cone in b. c, Left view of specimen reconstructed by micro-CT showing concealed body cones (Lbc1 and Lbc2). d, Close-up of arched mouth with radial folds and oral protrusions in a. e, Third body cone (Rbc3) with radial ribs and truncated opening. f, Nodular rugae and anterior spine in a. g–l, XX47-498. g, Ventral view, mouth arched; body cones arranged with bilateral

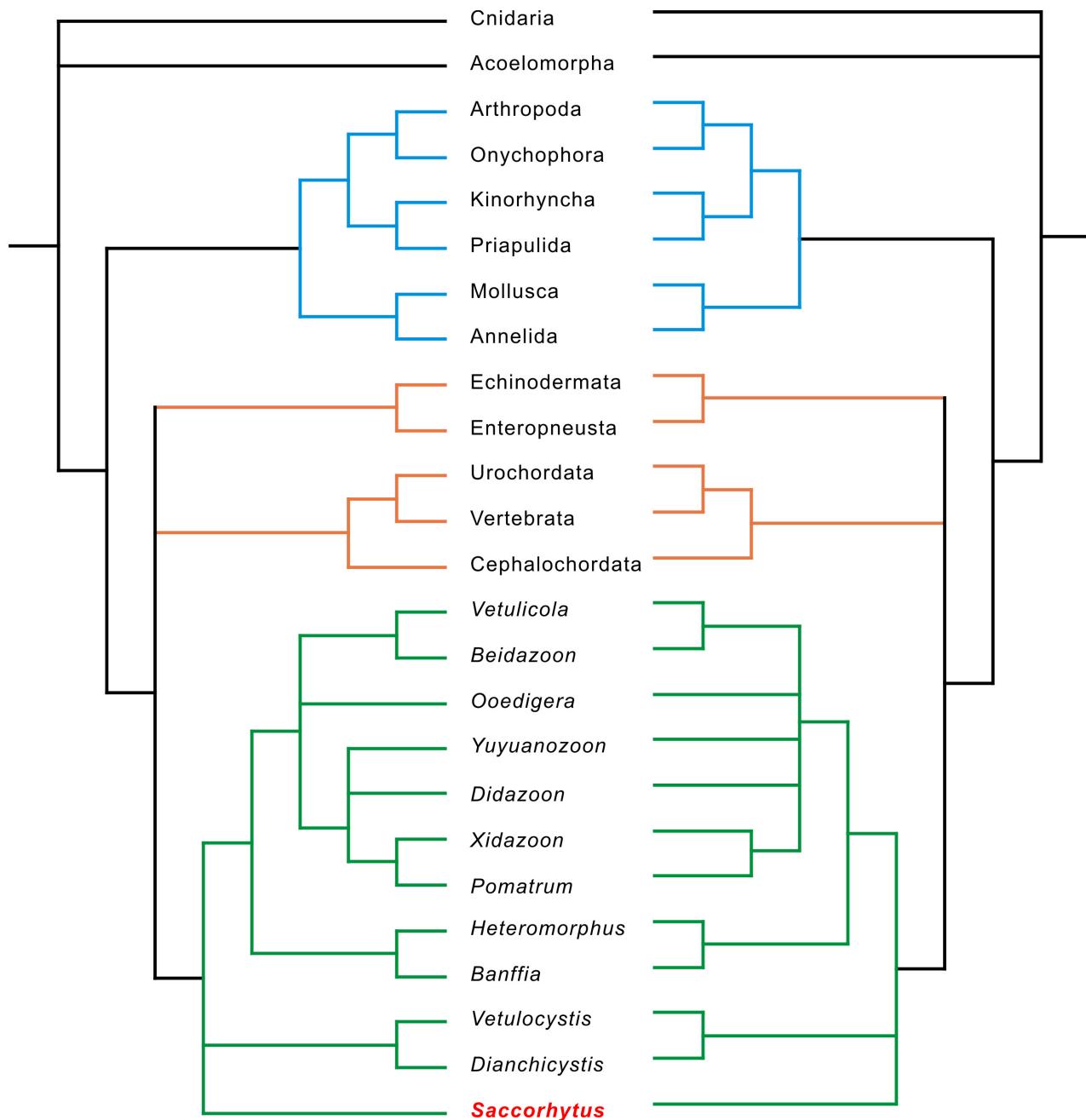
symmetry, delimited by a circular pore at the mid-ventral line. A pair of large and small tubular protrusions (Ltp and Stp, respectively) are visible at the anterior, mid-ventral line of the mouth. h, Dorsal view with body cones arranged bilaterally. i, Close-up of mouth with radial folds and elongate oral protrusions most prominent along the middle line. j, At least 12 circular pores arranged bilaterally in two longitudinal rows. k, Third left body cone with broken scars (Sc) of radial ribs. l, Inconspicuous first and second left body cones.



Extended Data Figure 6 | *Saccorhytus coronarius* gen. et sp. nov. **a**, XX54-354. Dorsal view showing a pair of spines and bilaterally arranged fourth body cones. **b–d**, XX56-192. **b**, Lateral view of the body. **c, d**, Integument of body cones consisting of two sublayers. **e**, XX59-253, showing the ventral anterior location of the mouth. **f, g**, XX61-27, showing two pairs of tubular projections (Ltp and Stp) at the anterior end of the mouth.

**a****b**

Extended Data Figure 7 | Body dimensions of 44 specimens. **a**, Rank order of lengths. **b**, Bivariate plot of height versus length. Despite a positive correlation in **b**, the low goodness of fit probably reflects the extensive crushing of most of the specimens.



Extended Data Figure 8 | Consensus trees. Left, produced by PAUP4.0; right, produced by TNT 1.1. The consensus tree from TNT 1.1 used New Technology Search with default options.



Extended Data Figure 9 | Deuterostomes from the Chengjiang fauna (Stage 3, Series 2), south China. **a,** *Xidazoon stephanus* Shu *et al.*, 1999 (ref. 31) (ELI0000194). **b,** *Didazoon haoae* Shu *et al.*, 2001 (ref. 32) (ELI0000194). **c,** *Pomatrum ventralis* Luo *et al.*, 1999 (ref. 32) (ELIJS010B). **d, e,** *Beidazoon venustum* Shu 2005 (ref. 33) (ELIJS454A, B). **f,** *Vetulocystis catenata* Shu *et al.*,

2004 (ELISK016A). Double-circlet mouth as seen in *Saccorhytus* is present in *Xidazoon* and *Pomatrum*; gill pouches are visible in *Didazoon*, *Pomatrum* and *Beidazoon*; two body cones similar to those of *Saccorhytus* can be seen in *Vetulocystis*; and gill pouches with radial ribs that resemble those of *Saccorhytus* can also be seen on *Beidazoon*.