

1 ***Saccorhytus* is an early ecdysozoan and not the earliest deuterostome**

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The early history of deuterostomes, the group composed of the chordates, echinoderms and hemichordates<sup>1</sup>, is still controversial, not least because of a paucity of stem-representatives to these clades<sup>2-5</sup>. The early Cambrian microscopic animal *Saccorhytus coronarius* was interpreted as an early deuterostome on the basis of purported pharyngeal openings, providing evidence for a meiofaunal ancestry<sup>6</sup> and an explanation for the temporal mismatch between palaeontological and molecular clock timescales of animal evolution<sup>6-8</sup>. Here we report new material of *Saccorhytus coronarius*, which is reconstructed as a millimetric and ellipsoidal meiobenthic animal with spinose armor and a terminal mouth but no anus. Purported pharyngeal openings in support of the deuterostome hypothesis<sup>6</sup> are shown to be taphonomic artifacts. Phylogenetic analyses indicate that *Saccorhytus coronarius* belongs to total-group Ecdysozoa, expanding the morphological disparity and ecological diversity of early Cambrian ecdysozoans.

The microscopic animal *Saccorhytus coronarius* was first reported from the early Cambrian (531.8–536.4 Ma<sup>9</sup>) Kuanchuanpu Formation at the Zhangjiagou section in South China<sup>6</sup>. It was interpreted as an anusless, meiobenthic deuterostome<sup>6</sup> largely based on the presence of pharyngeal openings, one of the few deuterostome

synapomorphies<sup>10</sup>. As such, *Saccorhytus coronarius* fills a critical gap in the deuterostome fossil record and represents an instance of loss of the anus in deuterostomes, which is known to have occurred several times independently in bilaterians<sup>11</sup>. However, it has also been speculated that *Saccorhytus coronarius* may be a stem-ecdysozoan or a primitive bilaterian<sup>12</sup>. To test these phylogenetic interpretations and evolutionary implications of *Saccorhytus coronarius*, we obtained new evidence on its morphology and ecology based on new material from the early Cambrian Kuanchuanpu Formation at the Zhangjiagou section<sup>13,14</sup> (Figs. 1–3; Extended Data Figs. 2–8) and Shizhonggou section<sup>15</sup> (Extended Data Fig. 9) in Shaanxi Province, South China (see Extended Data Fig. 1 for localities). We characterized *Saccorhytus coronarius* using both scanning electron microscopy and synchrotron X-ray tomography<sup>16</sup>, interpreted its morphology through a taphonomic lens, reconstructed its three-dimensional morphology and, on the basis of an expanded morphological database of metazoans, carried out a comprehensive phylogenetic analysis to establish its phylogenetic affinity<sup>6,12,13</sup>.

### **Anatomy of *Saccorhytus coronarius***

Most Zhangjiagou specimens are taphonomically flattened and subsequently abraded during transportation or sample preparation, but some are three-dimensionally preserved with a lesser extent of deformation (Extended Data Fig. 2a, b; Supplementary Video 1). Only the exterior body wall is preserved; no internal organs are observed (Extended Data Figs. 2c, 3c, f). The body wall is composed of two layers and represents

the preserved part of the integument (Figs. 1d, 2b; Extended Data Figs. 2d, 3c, 4a, 5e). No cilium insertion sites were observed on the integument, even in high-magnification SEM images. A chevron pattern is present in places of the integument (Fig. 3h; Extended Data Figs. 3h, 4e, 6f, 7a, c).

*Saccorhytus coronarius* is ellipsoidal in overall shape, with a polar aperture that can be closed or open (Figs. 1a, f, 2f; Extended Data Figs. 2a, d, 3d, 4a, h, 5c, 6a, d, 7f, 8b). The aperture has various appearances depending on the degree of compression and closure including as a flattened slit (Fig. 1b; Extended Data Figs. 7f, 8a), partially open with two V-shaped corners (Fig. 1f; Extended Data Figs. 2d, 3d, 4h, 5c, 6a) and, when fully open, approximately circular (Extended Data Figs. 6d, 8b). The closed polar aperture divides the body into two halves, with one half slightly wider than the other (Fig. 1a; Extended Data Fig. 2a, b; Supplementary Video 1).

The polar aperture is surrounded by radial folds of the integument (Figs. 1b, e, f, 2f; Extended Data Figs. 2d, f, g, 3d, 4a, c, h, 6a, d, 8a). The radial folds are internally pleated (Fig. 2g, h) and surrounded by a circlet of about 25–30 circumapertural protuberances that are in close contact with each other (Fig. 1f; Extended Data Figs. 2d, 4h). The circumapertural protuberances are internally hollow (Figs. 1b, e, 2f-h), largest at the midline, but decrease in size toward the sides (Fig. 1f; Extended Data Figs. 2d, 4h, 5c). Each of the circumapertural protuberances is flattened and tridentate, with a larger main spine flanked by two smaller lateral spines (Fig. 1g; Extended Data Figs. 2f, g, 4g, 6c, 8e). In many specimens, the protuberances are broken at the base, leaving circular to rectangular openings on the integument (Figs. 1b, 2f). Abapertural of the

circumapertural protuberances is an array of large protuberances that, unlike the circlet disposition of the circumapertural protuberances, are arranged in one or two rows on only one side of the polar aperture; when the aperture is flattened, the large protuberances are always arranged in-line with but never at the corners of the flattened aperture. The number of large protuberances varies from one (Fig. 2a; Extended Data Figs. 3d, 5a), two (Figs. 1a, f, 2f; Extended Data Figs. 4a, h, 6a, d, 7f, 8b, c), three (Extended Data Fig. 2d), four (Extended Data Figs. 4c, 5c), to five (Extended Data Figs. 2a, 7d), possibly representing intraspecific or ontogenetic variations. They are arranged in one row if fewer than five, or in two rows if five. The large protuberances are also flattened and tridentate, with a main spine flanked by two lateral spines or denticles (Fig. 1j; Extended Data Figs. 4c, 6a, 8a, c, e). The circumapertural and large protuberances have similar morphology, and the only difference is that the latter are larger and longer.

Further abapertural, there are numerous integument folds that are radially arranged (Fig. 1a, e; Extended Data Figs. 2d, 4a, c, 5c, 6a, d, 7b, 8b), as well as nodes or tubercles close to the large protuberances (Fig. 1a, f; Extended Data Figs. 2d, e, 4a, c, h, 5c, 6a, d, 7d). These nodes are arranged in crescent semi-circlets or sets parallel to disposition of the large protuberances. The first set of nodes are in-line with the large protuberances and extend laterally (Fig. 1j; Extended Data Figs. 4a, c, 6a, d, 7d); the next two or three sets extend continuously to the sides, whereas the remaining two to three sets are more sparsely and less regularly arranged (Extended Data Figs. 4a, c, 7d), and further beyond are sometimes singularly disposed nodes (Extended Data Fig. 7d).

There are up to eight pairs of body cones around the body. Three pairs are arranged bilaterally in a row close to the side of the polar aperture opposite to the large protuberances (Figs. 1a, f, 2f, 3a; Extended Data Figs. 2d, 4a, i, 5c, d, 6d, 8b); of these, the medial pair (l/rc1) are the smallest, whereas the lateral-most pair (l/rc3) are the largest (Supplementary Table 1). Up to five additional pairs of body cones are found on the lateral and abapertural sides of the body. They are also arranged bilaterally (Fig. 3f, l; Extended Data Figs. 4b, j, 5c, d, 6e, 7b, e, g). The largest are the 6th pair (l/rc6; Supplementary Table 1), which are always present (Figs. 1f, 2a, c, 3b, f, j, l; Extended Data Figs. 2b, e, 3d, 4b, h, j, 5b, c, 6e, h, 7b, g, 8f), whereas the other body cones, particularly the 7th and 8th pairs (l/rc7 and l/rc8), may be absent (Fig. 1f; Extended Data Fig. 2e), probably reflecting intraspecific or ontogenetic variations.

Each body cone has an expanded conical base ornamented with longitudinal folds or ridges (Figs. 1c, h, i, 2a, b, 3c–e, h, k; Extended Data Figs. 3g, 4e, 5a, 6f, g, 8b). Completely preserved body cones have an apical spine with a closed tip (Figs. 2b, 3h, k; Extended Data Figs. 3i, 4k, 7a, 8d); however, most body cones are broken at the base or middle of the cone, at the junction between the conical base and the apical spine, or at the apical spine (Figs. 1c, h, i, 2a, 3c–e, j, l; Extended Data Figs. 2d, 4i, j, 7f, 8b). When preserved, apical spines are always adpressed on the body wall (thus protected from abrasion or breakage during fossil preparation), and they are about three to four times the height of the base in the 4th and 5th pairs of cones (Fig. 3h, k; Extended Data Figs. 3i, 4k), but can be proportionally shorter in the 1st–3rd and 6th pairs of cones (Figs. 2b, 3c–e). The 1st–3rd and 6th pairs of body cones are equivalent to the 1st–3rd

and 4th pairs of body cones of Han et al.<sup>6</sup>. SRXTM<sup>16</sup> analysis shows that the conical bases have mineral preservation consistent with the surrounding integument but exhibit a distinct X-ray attenuation profile from the underlying layer (Fig. 2d, e).

On the abapertural side, there are numerous short and slender spines with a sharp tip that may extend beyond the 8th body cones (Fig. 3g, i; Extended Data Figs. 2e, 3h, 4b, 6e). The number and distribution of these spines are not uniform among different specimens. They may be randomly distributed and are basally separate from each other. They vary in size, with those around the 8th body cones slightly smaller than others, but they are generally much smaller than the body cones (Supplementary Table 1) and are typically broken from the base (Extended Data Figs. 4b, 5d, 6e). More completely preserved spines tend to be adpressed against the integument (Fig. 3g, i) and thus were not abraded during fossil preservation or preparation.

Shizhonggou specimens (Extended Data Figs. 1b, 9) are similar to the Zhangjiagou specimens described above and in Han et al.<sup>6</sup>. They share key structures such as a polar aperture surrounded by radial folds (Extended Data Fig. 9e), two-layered integument (Extended Data Fig. 9b, d), body cones with a conical base and an apical spine (Extended Data Fig. 9a, c, e), and small abapertural spines (Extended Data Fig. 9a, c, f). These structures identify the Shizhonggou specimens to *Saccorhytus*.

## **Taphonomy and preservation**

Although no internal anatomy is preserved in the Zhangjiagou and Shizhonggou specimens, microstructures in the two-layered integument inform us about fossilization

processes and aid in biological and taphonomic interpretations. The two integument layers can be separated from each other by a gap (Fig. 1d) or tightly adpressed to each other with no gaps in between, as observed in both SEM (Extended Data Fig. 5e) and SRXTM<sup>16</sup> (Extended Data Fig. 3c). The tightly adpressed layers cannot be phosphatic coatings on both sides of a substrate that has since been lost, in which case a gap would be present between the layers. Rather, they likely represent two integumental sub-layers that were secondarily phosphatized through mineral impregnation. The mineralization may have occurred before and after the taphonomic detachment of the two sub-layers, resulting in both adpressed and separated integument layers. This interpretation is consistent with random orientation of the nanometer-scale apatite crystals that replicate the integument layer (Extended Data Fig. 5f), because phosphatic impregnation tends to be accomplished by randomly oriented nanocrystals whereas phosphatic encrustation results in apatite crystals that orient perpendicular to and grow away from the substrate<sup>17</sup>.

SRXTM analysis<sup>16</sup> shows that the outer integument layer has a lower X-ray attenuation profile and preserves surface wrinkles and spines across the body surface, and the inner integument layer exhibits a higher attenuation profile and is associated with, but not limited to, centripetal void-filling mineralization (Extended Data Fig. 9b). In places, the inner layer is detached from the outer layer (Extended Data Fig. 9d). The detached layers preserve complementary symmetry (Extended Data Fig. 9d) and can be virtually re-attached to restore their original configuration. There is no brittle deformation associated with this localized layer separation (Fig. 1d), indicating that it

occurred prior to mineralization, associated with decay, with the inner layer delaminating from the outer and collapsing inward. In some of the compressed specimens, instead of two clear layers there is a thick layer of homogeneous mineralization around the entire body, surrounded by centrifugal and centripetal infilling visible as concentric layers (Fig. 2e). The homogeneous layer is continuous with the radial folds and protuberances located around the polar aperture (Fig. 2g, h) as well as with the body cones, indicating that this mineral phase preserves original biological structure. In other specimens, there are few visible layers of mineralization, with most of the interior of the specimen displaying the same high X-ray attenuation profile (Extended Data Fig. 2c), but the key anatomical features are still present on the surface, indicating that they are endocasts of the surface integument layer which is either not preserved or has been lost after preservation.

The symmetry of *Saccorhytus coronarius* is anchored on the polar aperture. This aperture is the only body opening and is here interpreted as the mouth, with the radial folds controlling its opening and closure, whereas a distinct anus is absent. The terminal mouth defines an oral-aboral body axis, the symmetrical arrangement of the body cones imparts the animal with a bilateral symmetry (i.e., left and right sides), and the polarized distribution of large protuberances and nodes indicate the existence of a third body axis that is orthogonal to the oral-aboral and left-right axes. *Saccorhytus* thus has three main body axes. Guided by extant animals with three body axes, i.e., the bilaterians<sup>18</sup>, we identify the three main body axes in *Saccorhytus* as homologous to the anterior-posterior, dorsoventral and left-right axes of bilaterians. Therefore, *Saccorhytus* is

reconstructed as a sac-like bilaterian with spinose armor and a terminal mouth but no anus (Fig. 4a–c; Supplementary Video 2); this reconstruction is different from that of Han et al.<sup>6</sup> who placed the mouth ventrally.

The bilateral symmetry with anterior-posterior, dorsoventral and left-right axes suggests that *Saccorhytus* is phylogenetically affiliated with the Bilateria<sup>18</sup>. *Saccorhytus* lacks an anus, but this condition may represent either primitive or secondary absence (loss), considering that a through gut with a terminal anus may have evolved independently in different bilaterian lineages<sup>19</sup> and loss of the anus has also occurred several times independently in different bilaterian groups<sup>11</sup>. The previously proposed deuterostome hypothesis<sup>6</sup> was based on similarities between the body cones of *Saccorhytus* and the body openings (interpreted as pharyngeal openings) of vetulicolians<sup>20</sup> and vetulocystids<sup>21</sup>. Better preserved specimens illustrated here (Figs. 1h, 2b, 3c, e, h, k; Extended Data Figs. 3i, 4k, 9e), however, show that the body cones in *Saccorhytus* have a closed apical spine and they are probably stiffened sclerites. *Saccorhytus* thus lacks homologs of pharyngeal openings<sup>18</sup> and, as such, cannot be considered as a deuterostome.

## **Phylogenetic analysis and affinity**

To resolve the phylogenetic affinity and evolutionary significance of *Saccorhytus*, we assembled a dataset of phenotypic characters from the diversity of metazoan phyla<sup>22–26</sup> which was subjected to Bayesian phylogenetic analysis in MrBayes<sup>27</sup>. Our dataset recovers monophyletic Bilateria, Protostomia, Ecdysozoa, Deuterostomia and

Coelenterata, with a partial constraint to resolve Lophotrochozoa (Extended Data Fig. 10a). Within this framework, *Saccorhytus* is resolved as a total-group ecdysozoan (Extended Data Fig. 10a).

To account for the uncertainties about the phylogenetic affinity of the Xenacoelomorpha (as a deuterostome or a basal bilaterian<sup>28</sup>), the monophyly of the Deuterostomia<sup>29</sup>, and the monophyly of the Coelenterata<sup>22,30,31</sup>, we conducted additional analyses with partial topology constraints (Supplementary Phylogenetic Analyses). In these analyses, *Saccorhytus* was consistently resolved as part of a polytomy at the base of total-group Ecdysozoa (Extended Data Fig. 10b, c). The topology of the phylogenetic results (Extended Data Fig. 10) indicates that *Saccorhytus* could be a basal ecdysozoan, a basal panarthropodan, or a basal cycloneuralian (Fig. 4d).

To test the robustness of the total-group ecdysozoan interpretation, we carried out stepping stone analyses to compare the Bayes factors of trees where *Saccorhytus* is constrained to Ecdysozoa, to Deuterostomia<sup>6</sup>, or to Coelenterata (a position that appeared in a small number of suggested trees from our Bayesian analyses). The model in which *Saccorhytus* is constrained to Ecdysozoa has overwhelmingly positive support compared with Deuterostomia (ln-Bayes factor of 11.915,  $2 \cdot \log_e B_{12}$  of 23.83) and Coelenterata models (ln-Bayes factor of 5.54,  $2 \cdot \log_e B_{12}$  of 11.08)<sup>32</sup>. We can therefore confidently rule out a deuterostome or coelenterate affinity for *Saccorhytus*. The ecdysozoan interpretation is consistent with the observation that most specimens are deflated, deformed, and preserved with integuments but no internal anatomy, indicating

that they may be cuticles or cuticular exuviae which are more decay-resistant than the soft internal tissues<sup>33</sup>. This interpretation is different from that of Han et al.<sup>6</sup> who coded the integumental layer as an epidermis in their character matrix.

## Conclusions

The small body size of *Saccorhytus* indicates a meiobenthic life style. The non-ciliated integument implies that it did not have cilia for locomotion or feeding. *Saccorhytus* also lacked setae or paired appendages, thus was unable to creep or crawl. Locomotion by hydrostatic skeletons is possible if its integument was flexible. *Saccorhytus* was likely a free epibenthic or interstitial meiofaunal animal living in a low Reynolds-number environment. It is also possible that muscles may have been attached to its body cones which may have provided leverage for locomotion. Whereas the two-layered integument may represent cuticular structures with two sub-layers, the circumapertural protuberances, large protuberances, body cones, and small abapertural spines are likely sclerotized cuticular structures and may have functioned as sensory and/or defense structures, whereas the mouth is the only body opening that must have functioned for feeding and excretion.

To summarize, *Saccorhytus* does not have pharyngeal openings and is not a deuterostome. It is instead a total-group ecdysozoan (Fig. 4d). Together with co-occurring cycloneuralians from the Zhangjiagou section<sup>34-36</sup> and equivalent strata in South China<sup>37,38</sup>, *Saccorhytus* testifies to the remarkable morphological disparity and ecological diversity of early Cambrian ecdysozoans, and it presents another case of

secondary absence of the anus in ecdysozoans<sup>11</sup>.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/XXXX>.

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370

## 371 **Methods**

372 The fossil specimens were recovered from the early Cambrian Kuanchuanpu  
 373 Formation at Zhangjiagou section<sup>14</sup> (specimen numbers with prefix UMCU or He)  
 374 and Shizhonggou section<sup>15</sup> (specimen numbers with prefix KYuan), China (Extended  
 375 Data Fig. 1). The key horizons at both sections yielding *Saccorhytus* specimens fall  
 376 within the small shelly fossil *Anabarites trisulcatus*-*Protohertzina anabarica*

377 Assemblage Zone<sup>14,39,40</sup> and have a time span of 531.8–536.4 Ma<sup>9</sup>, belonging to the  
378 Cambrian Fortunian Stage. Rock samples from these two sections were macerated  
379 using diluted acetic acid (10%), and microfossils were handpicked from residues  
380 under a binocular microscope. The UMCU (University Museum of Chang'an  
381 University) specimens were glued on pin-type aluminum stubs by diluted milk glue  
382 for observation under a LEO 1530VP field-emission environmental scanning electron  
383 microscope, a Hitachi SU3500 scanning electron microscope, and a field-emission  
384 scanning electron microscope TESCAN MAIA3 at the Nanjing Institute of Geology  
385 and Palaeontology, Chinese Academy of Sciences. The FUB (Freie Universität Berlin)  
386 specimens were rinsed in pure ethanol, mounted on aluminium sample stubs with  
387 adhesive carbon film and sputtered for 6 minutes with gold in a BioRad elemental  
388 SEM coating system, and then observed under a ZEISS Supra 40 VP Ultra at the  
389 Department of Earth Sciences, Freie Universität Berlin.

390 Synchrotron Radiation X-ray Tomographic Microscopy (SRXTM)<sup>16</sup> was conducted at  
391 the X02DA TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institut,  
392 Villigen, Switzerland. Projections were obtained with beam energies of 15–22.5 KeV,  
393 exposures of 150–860 ms, using a 20 µm LuAg:Ce scintillator, 10× and 20×  
394 objectives, yielding reconstructed tomographic data with voxel dimensions of 0.65  
395 µm and 0.325 µm, respectively. A total of 1501 projections were taken equi-angularly  
396 through 180° rotation within the beam. Projections were post-processed and  
397 rearranged into flat- and dark-field-corrected sinograms, and reconstruction was  
398 performed on a 60-core Linux PC farm, using a highly optimized routine based on the

Fourier transform method and a regridding procedure<sup>41</sup>. Slice data were analyzed and manipulated using VGStudioMax ([www.volumegraphics.com](http://www.volumegraphics.com)) and AVIZO ([www.thermofisher.com/avizo/software](http://www.thermofisher.com/avizo/software)).

Phylogenetic analyses were conducted based on updated description and reconstruction of *Saccorhytus coronarius*, a broad sampling of animal taxa, and a comprehensive coding of 134 morphological characters. The data matrix was subjected to Bayesian phylogenetic analysis under the Mk model<sup>42</sup> implemented in MrBayes3.2 (ref.<sup>27</sup>).

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#### **Data availability**

The data that support the findings of this study are available in the paper and its Supplementary Information, or from the corresponding authors upon reasonable request. All specimens illustrated in this paper are deposited at the University Museum of Chang'an University (accession numbers UMCU2014001–2014005, 2016006–2016010, 2018011–2018015, 2019016–2019020, and 2020021–2020025), and at the Department of Earth Sciences, Freie Universität Berlin (accession numbers He22-45, He22-57, He22-94, KYuan26, KYuan55, and KYuan102). Tomographic data are freely available from the University of Bristol data repository, data.bris, at <https://doi.org/10.5523/bris.2iha22zobeher2leh936xrktqx>.

#### **Code Availability**

The phylogenetic dataset, commands, and topological constraints necessary to run the MrBayes analyses are included as NEXUS formatted files in the Supplementary Information.

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**Author contributions** H.Z. and P.C.J.D. designed the research; Y.L., T.S., B.Y. and M.S. obtained the fossils; H.Z. and M.S. carried out SEM work; E.C., F.M., and P.C.J.D. collected SRXTM data; E.C. and B.D. analyzed SRXTM data; E.C. and P.C.J.D. conducted phylogenetic analyses; H.Z., E.C., S.X., M.S., and P.C.J.D. developed the interpretation; H.Z. wrote the first draft of the manuscript, with contributions from all other authors.

**Competing interests** The authors declare no competing interests.

**Inclusion and ethics** The research described in this study included local researchers from the initial stages of design through execution, analysis, interpretation and publication. All researchers who contributed to the study are recognized through authorship. We were provided with permission for sampling through formal agreements with the Nanjing Institute of Geology and Palaeontology (NIGPAS),

Chinese Academy of Sciences, extending back to 2000.

#### **Additional information**

**Supplementary information** is available for this paper at <https://doi.org/XXXX>

**Correspondence and requests for materials** should be addressed to H.Z., S.X., or P.C.J.D.

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**Figure 1. Anatomy of *Saccorhytus coronarius*.** **a–e**, UMCU2016009, with two large protuberances; **a**, apertural view; **b**, detail of polar aperture; **c**, detail of broken third right body cone, with jagged edge exposing two integument layers; **d**, opposite side of **a**, with abapertural integument missing, showing inner view of polar aperture and detached integument layers; **e**, detail of inner side of aperture, showing hollow nature of circumapertural protuberances; **f, g, j**, UMCU2019016, with two large protuberances; **f**, apertural lateral view; **g**, detail of circumapertural protuberances; **j**, detail of large protuberances; **h, i**, UMCU2018011; **h**, a fragment; **i**, detail of fifth right body cone, showing remnant of apical spine. Abbreviations: **b**, base of body cone; **ch**, chevron; **cp**, circumapertural protuberance; **i**, integument; **if**, integument folds; **i/ol**, inner/outer integument layer; **l/rc1–8**, first to eighth left/right body cone

(assuming an anterior mouth and dorsal large protuberances); lf, longitudinal folds; lp, large protuberance; ls, lateral spine; ms, main spine; n, node; pa, polar aperture; rf, radial folds; s, apical spine of body cone; sp, small abapertural spine. Scale bar: 200  $\mu\text{m}$  (**a, d, f, h**), 100  $\mu\text{m}$  (**b, c, e, g, j**), 20  $\mu\text{m}$  (**i**).

**Figure 2. Anatomy of *Saccorhytus coronarius*** *Saccorhytus coronarius*. **a, b**, He22-45, with a single large protuberance; **a**, lateral view; **b**, close-up view of sixth lateral body cone; **c–e**, He22-94, SRXTM images; **c**, surface model, lateral view; **d, e**, virtual sections through body cones as denoted in **c**; **f–h**, He22-57, with two large protuberances; **f**, apertural view; **g**, virtual section through radial folds as denoted in **f**, bisecting a circumapertural protuberance; **h**, virtual section through radial folds as denoted in **f**. Scale bar: 200  $\mu\text{m}$  (**a, c, f**), 110  $\mu\text{m}$  (**b**), 55  $\mu\text{m}$  (**d**), 80  $\mu\text{m}$  (**e**), 50  $\mu\text{m}$  (**g–h**). See Fig. 1 for abbreviations.

**Figure 3. Anatomy of *Saccorhytus coronarius***. **a–e**, UMCU2020021; **a**, lateral view; **b**, right view; **c–e**, detail of body cones tilted  $\sim 40^\circ$  from **a** and **b**, showing remnant of apical spine; **f, h**, UMCU2016008; **f**, lateral view; **h**, detail of fourth lateral body cone adpressed against body wall; **g, i**, UMCU2016010; **g**, abapertural view; **i**, detail of small abapertural spines adpressed against body wall; **j, k**, UMCU2018012; **j**, right view; **k**, detail of fifth right body cone adpressed against body wall; **l**, UMCU2019018, abapertural lateral view. Scale bar: 200  $\mu\text{m}$  (**a, b, f, g, j, l**), 60  $\mu\text{m}$  (**c–e, h, i, k**). See Fig. 1 for abbreviations.

**Figure 4. Reconstruction and phylogenetic interpretation of *Saccorhytus coronarius*.** **a–c**, reconstructions showing anterior or apertural (**a**), left (**b**), and posterior or abapertural (**c**) views; scale bar 500  $\mu\text{m}$ ; see Fig. 1 for abbreviations; **d**, phylogeny of Metazoa based on Extended Data Fig. 10, and possible position of *Saccorhytus*, based on Bayesian phylogenetic analysis of a phenotypic dataset using the Mk model implemented in MrBayes 3.2.7a<sup>27</sup> (see Supplementary Phylogenetic Analyses); animal icons from phylopic.org.

**Extended Data Figure 1** | Location map and stratigraphic column. **a**, map of Shaanxi Province, South China, with star marking Zhangjiagou section and hexagon marking Shizhonggou section where fossils of *Saccorhytus coronarius* were collected; **b**, detailed map of southern Shaanxi Province showing Zhangjiagou section (star) and Shizhonggou section (hexagon); **c**, stratigraphic column of Zhangjiagou section showing key horizon (arrow) where fossils of *Saccorhytus coronarius* were collected.

**Extended Data Figure 2** | *Saccorhytus coronarius*. **a–c**, UMCU2014005, with five large protuberances; **a**, apertural or anterior view; **b**, abapertural or posterior view; **c**, SRXTM image, virtual transverse section marked in **b**; **d–g**, UMCU2014001, with three large protuberances; **d**, apertural or anterior view; **e**, abapertural or posterior view; **f**, **g**, detail of circumapertural protuberances. Scale bar: 200  $\mu\text{m}$  (**a–e**), 50  $\mu\text{m}$  (**f**), 40  $\mu\text{m}$  (**g**). See Fig. 1 for abbreviations.

**Extended Data Figure 3** | *Saccorhytus coronarius*. **a–c**, UMCU2014001, same specimen as in Extended Data Fig. 2**d**; **a**, dorso-anterior view (assuming an anterior mouth and dorsal large protuberances); **b**, ventral view (assuming an anterior mouth and dorsal large protuberances); **c**, SRXTM image, virtual longitudinal section marked in **a**, with arrows marking boundary between two integument layers; **d–i**, UMCU2014002; **d**, left view; **e**, right view; **f**, SRXTM image, virtual tangential coronal section marked in **d**; **g**, close-up of sixth left body cone in central right of **d**; **h**, detail of small abapertural spines and chevron patterns in lower right of **d**; **i**, detail of fourth, fifth, and sixth right body cones in upper central of **e**. Scale bar: 200  $\mu\text{m}$  (**a**, **b**, **d**, **e**); 100  $\mu\text{m}$  (**c**, **f**); 40  $\mu\text{m}$  (**g**, **h**), 60  $\mu\text{m}$  (**i**). See Fig. 1 for abbreviations.

**Extended Data Figure 4** | *Saccorhytus coronarius*. **a**, **b**, UMCU2019017, with two large protuberances; **a**, apertural or anterior view; **b**, abapertural or posterior view; **c**, UMCU2016006, with four large protuberances, antero-left view; **d**, **e**, UMCU2020022; **d**, left view; **e**, detail of seventh right body cone and chevron pattern in central right of **d**; **f**, **g**, UMCU2020023; **f**, left view; **g**, detail of circumapertural protuberances in central left of **f**; **h**, UMCU2018013, with two large protuberances, antero-left view; **i–k**, UMCU2020024; **i**, right ventral view (assuming an anterior mouth and dorsal large protuberances); **j**, left dorsal view (assuming an anterior mouth and dorsal large protuberances); **k**, detail of fourth left body cone in central of **j**. Scale bar: 200  $\mu\text{m}$  (**a–d**, **f**, **h–j**), 40  $\mu\text{m}$  (**e**, **g**, **k**). See Fig. 1 for abbreviations.

**Extended Data Figure 5** | *Saccorhytus coronarius*. **a, b**, UMCU2014004, with only one large protuberance; **a**, anterior dorsal view (assuming an anterior mouth and dorsal large protuberances); **b**, abapertural or posterior view; **c, d**, UMCU2018014, with four large protuberances; **c**, right view; **d**, left view; **e, f**, same specimen as shown in Fig. 1**a–e**, UMCU2016009; **e**, close-up view of central right of Fig. 1**d**, with arrow indicating the two tightly adpressed integument layers and rectangle marking area enlarged in **f**, which illustrates randomly oriented nanometer-scale apatite crystals. Scale bar: 200  $\mu\text{m}$  (**a–d**), 25  $\mu\text{m}$  (**e**), 1  $\mu\text{m}$  (**f**). See Fig. 1 for abbreviations.

**Extended Data Figure 6** | *Saccorhytus coronarius*. **a–c**, UMCU2016007, with two large protuberances; **a**, apertural or anterior view; **b**, abapertural or posterior view; **c**, detail of circumapertural protuberances in central right of **a**; **d–g**, UMCU2019019, with two large protuberances; **d**, apertural or anterior view; **e**, abapertural or posterior view; **f, g**, detail of fourth and fifth right body cones in central upper and upper right of **e**; **h, i**, UMCU2018012, same specimen as in Fig. 3**j**; **h**, left view; **i**, detail of fourth, fifth, and sixth left body cones in upper left of **h**. Scale bar: 200  $\mu\text{m}$  (**a, b, d, e, h**), 20  $\mu\text{m}$  (**c, f, g, i**). See Fig. 1 for abbreviations.

**Extended Data Figure 7** | *Saccorhytus coronarius*. **a–c**, UMCU2016008, same specimen as in Fig. 3**f**, with three large protuberances; **a**, detail of fourth, fifth, and sixth left body cones in central upper of Fig. 3**f**; **b**, right view; **c**, detail of fifth and sixth right body cones in upper left of **b**; **d**, UMCU2019020, a fragment with five

large protuberances, dorsal anterior view (assuming an anterior mouth and dorsal large protuberances); **e, h**, UMCU2020025; **e**, left view; **h**, detail of fourth and fifth left body cones, exhibiting round conical bases with longitudinal folds; **f, g**, UMCU2018015, with two large protuberances; **f**, apertural or anterior view; **g**, abapertural or posterior view. Scale bar: 60  $\mu\text{m}$  (**a**), 200  $\mu\text{m}$  (**b, d–g**), 50  $\mu\text{m}$  (**c, h**). See Fig. 1 for abbreviations.

**Extended Data Figure 8** | *Saccorhytus coronarius*. **a**, UMCU2018015, same specimen as in Extended Data Fig. 7f, exhibiting radial folds and large protuberances; **b, d**, UMCU2019018, same specimen as in Fig. 3l, with two large protuberances; **b**, ventral anterior view (assuming an anterior mouth and dorsal large protuberances); **d**, detail of fourth and fifth right body cones in central upper of Fig. 3l; **c, e, f**, UMCU2014003, a fragment with two large protuberances; **c**, apertural or anterior view; **e**, detail of circumapertural protuberances and large protuberances; **f**, abapertural or posterior view. Scale bar represents 100  $\mu\text{m}$  in all images. See Fig. 1 for abbreviations.

**Extended Data Figure 9** | *Saccorhytus coronarius* from Kuanchuanpu Formation at Shizhonggou section. **a–d**, body surface with regular rows of small abapertural spines; **a, b**, KYuanH102; **a**, abapertural or posterior view; **b**, virtual section through a body cone as denoted in surface model, showing inner and outer integument layers; **c, d**, KYuan26; **c**, lateral view; **d**, virtual section through a body cone as denoted in surface

model; **e, f**, KYuan55; **e**, anterior ventral view (assuming an anterior mouth and dorsal large protuberances); **f**, close-up view, showing small abapertural spines and chevron patterns. Scale bar: 200  $\mu\text{m}$  (**a, c, e**), 50  $\mu\text{m}$  (**b**), 100  $\mu\text{m}$  (**d**), 40  $\mu\text{m}$  (**f**). See Fig. 1 for abbreviations.

**Extended Data Figure 10** | Phylogenetic positioning of *Saccorhytus*. **a**, partially constrained tree where constraint is compatible with monophyletic Lophotrochozoa; **b**, partially constrained tree where constraints are compatible with monophyletic Lophotrochozoa, paraphyletic Coelenterata and monophyletic Deuterostomia + Xenacoelomorpha; **c**, partially constrained tree where constraints are compatible with monophyletic Lophotrochozoa, paraphyletic Coelenterata and paraphyletic Deuterostomia. Nodal supports are posterior probabilities. In all trees, *Saccorhytus* is resolved as part of a polytomy at the base of Ecdysozoa. Animal icons from phylopic.org.

**Extended Data MrBayes NoConstraints** | MrBayes command block and matrix for unconstrained phylogenetic analysis.

**Extended Data MrBayes Combined Constraints** | MrBayes command block and matrix implementing combined topological constraints.

**Extended Data MrBayes ParaDeutConstraints** | MrBayes command block and

623 matrix implementing a paraphyletic Deuterostomia topological constraint.

624

625 **Extended Data MrBayes Stepping-stone Coelenterata** | MrBayes command block

626 and matrix implementing a stepping stone analysis assuming a coelenterate affinity

627 for *Saccorhytus*.

628

629 **Extended Data MrBayes Stepping-stone Deuterostomia** | MrBayes command block

630 and matrix implementing a stepping stone analysis assuming a deuterostome affinity

631 for *Saccorhytus*.

632

633 **Extended Data MrBayes Stepping-stone Ecdysozoa** | MrBayes command block and

634 matrix implementing a stepping stone analysis assuming an ecdysozoan affinity for

635 *Saccorhytus*.

636

637 **Supplementary Information** includes Systematic Palaeontology; Phylogenetic

638 Analyses; Characters Descriptions; Animations; Table 1; and a separate file in excel

639 format including the selected characters, character description, taxa, and command

640 lines in MrBayes.

641



























