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1 The early Cambrian *Saccorhytus* is a non-feeding larva of a scalidophoran 2 worm

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10 11 **Abstract**

12
13 With its bag-like appearance, spiny ornament and single opening *Saccorhytus coronarius* is
14 one of the most enigmatic animal of the early Cambrian Kuanchuanpu Formation (ca 535 Ma)
15 and has been at the heart of debates concerning the origin of two major animal lineages: the
16 deuterostomes and the ecdysozoans. Although Ecdysozoa is now the most plausible option,
17 key aspects of its palaeobiology have remained elusive. I suggest here that *Saccorhytus* was
18 the possible larval stage of one of the numerous scalidophoran worms that co-existed with it
19 in the Kuanchuanpu biota, especially those with bilateral pairs of broad-based sclerites such
20 as *Eokinorhynchus*. This new interpretation is mainly based on the development of extant
21 priapulid worms (Scalidophora). It would imply that *Saccorhytus* is a non-feeding larva and
22 that its enigmatic single aperture with a pleated structure is not a mouth but more likely the
23 opening through which the juvenile exited. Thus, the strange anatomy of *Saccorhytus* could
24 be explained in a simple way without involving complex evolutionary processes (e.g.
25 simplification, miniaturization, loss of anus, etc.). Instead of being a relatively basal member
26 of the total-group Ecdysozoa, *Saccorhytus* would find a more likely position among the total-
27 group Scalidophora.
28

29 **Key-words:** Scalidophora, Ecdysozoa, *Saccorhytus*, larva, early Cambrian
30
31

32 **Introduction**

33
34 *Saccorhytus coronarius* is one of the most enigmatic animal of the 535-million-year-old
35 Kuanchuanpu biota from China that is dominated by scalidophoran worms (body fossils and
36 exuviae; e.g. [1-5]), cnidarian larval stages (e.g. [6-10]) and countless tiny mollusk-like and
37 tubular animals (e.g. [11]). This bag-like organism was first interpreted as a microscopic
38 deuterostome based on the occurrence of a series of conical lateral perforations seen as body
39 openings and the possible functional analogues of pharyngeal gills [12]. However, a more
40 recent study by Liu et al. [13] using Synchrotron X-ray tomographic microscopy (SRXTM)
41 demonstrated that these conical features were actually broken spines and therefore
42 taphonomic artifacts that could no longer be considered as indicating deuterostome affinities.
43 Liu et al. [13] also provided remarkably detailed information on the external morphology of *S.*
44 *coronarius*, especially its complex cuticular symmetrical ornament and a single opening with
45 radial folds tentatively interpreted as the mouth (e.g. Supplementary Figure 1). Their cladistic
46 analysis resolved *S. coronarius* as a basal ecdysozoan, a basal panarthropodan or a basal
47 cycloneuralian [13]. The ecdysozoan affinities of *S. coronarius* are best supported by the

48 presence of broad-based cuticular elements that strongly recall the pointed sclerites of
49 Cambrian scalidophorans, although detailed comparisons with coeval worms are lacking [13].
50 The bilayered structure of the cuticle is also considered as an additional evidence to support
51 the ecdysozoan affinities of *Saccorhytus* although uncertainties remain (e.g. biological versus
52 taphonomic origin). Even though *Saccorhytus* is most likely an ecdysozoan, no explanation has
53 yet been found for the extreme originality of its body plan. Indeed, the bag-like shape of *S.*
54 *coronarius* has no equivalent in extinct and extant cycloneuralians (Nematoida + Scalidophora)
55 that typically have a tubular annulated shape (e.g. scalidophorans) or have a segmented body
56 and bear appendages (e.g. panarthropods). *S. coronarius* also lacks an introvert that plays a
57 vital role in the locomotion and feeding behaviour of extant cycloneuralians. Finally, its single
58 opening interpreted as the mouth [12, 13] is among the most puzzling issues concerning *S.*
59 *coronarius*. The absence of an anal opening is exceptional among modern ecdysozoans, being
60 limited to some shell-less cirripedes, mites, marine nematomorphs and male nematodes (see
61 refs in [14]) and seems to mainly result from secondary loss related to ecological specialization.
62 The atypical morphology found in *S. coronarius* (e.g. lack of introvert and anus, bag-like shape)
63 is clearly at odds with the idea of *S. coronarius* being the adult or subadult form of an
64 ecdysozoan animal, except if we assume that it is a highly derived microscopic (possibly
65 meiobenthic [12]) animal that underwent drastic anatomical simplification. We propose here
66 to test a radically different hypothesis, that of *S. coronarius* being the larval stage of one of
67 the scalidophoran worms present in the Kuanchuanpu biota. Our analysis is based on the re-
68 examination and re-interpretation of the fossil specimens figured by Han et al. [12] and Liu et
69 al. [13], in the light of the developmental characteristics of extant priapulid worms (e.g. [14-
70 15]).

71

72

73 **Embryonic and larval development of extant priapulids**

74

75 Extant priapulids such as *Priapululus caudatus* develop through three post-embryonic larval
76 stages [15] (Figure 1a-d and Supplementary Figure 2a, b). The hatching larva that emerges
77 from the spherical embryonic case has a differentiated introvert crowned by scalids and a
78 bulbous trunk, and is able to burrow into mud. The gut is already formed (Anlagen) although
79 neither the anus nor the mouth shows any external opening yet. The molting of this non-
80 feeding larva gives rise to the first loricate larva that similarly lacks a functional mouth and
81 anus. The trunk is encased within a lorica composed of eight fused cuticular plates and more
82 scalids add to the protruding introvert. The second loricate larva has most of the
83 characteristics of the adult priapulids such as a proper mouth opening, a mouth armed with
84 several rows of pharyngeal teeth and a functional anal opening, and has the capacity to feed
85 on meiobenthic prey. Martín-Durán and Hejnal [14] provided more detailed information on
86 the embryonic development of *P. caudatus* and showed that the introvert differentiated from
87 the trunk via a symmetrical lateral constriction and a marked invagination at the animal pole
88 (Figure 1e-g). At the end of this developmental stage termed introvertula and before hatching,
89 the introvert and the mouth are strongly retracted into the trunk. Although the hatching and
90 first loricate larvae internally show a fully developed digestive system, their mouth remains
91 invaginated and their anus closed to exterior. As a result, the central closed pit at the top of
92 the introvert is not the mouth. The mouth opening *sensu stricto* only appears at the second
93 loricate larval stage through a “devagination” process that makes it fully functional. Martín-
94 Durán and Hejnal [14] also pointed out that the major transformation of the digestive system

95 that occurs between the embryonic and larval stages is accompanied by the development of
96 a muscle system (longitudinal, circular and retractor fibers) that plays a key role in the
97 introvert contraction (e.g. during ecdysis, burrowing of hatching larva). This set of information
98 on the development of extant priapulid worms is crucial to the new interpretation of *S.*
99 *coronarius* presented here -i.e. the possible larval stage of a scalidophoran worm.

102 **Results and discussion**

105 **Overall shape and size of *Saccorhytus***

107 *Saccorhytus coronarius* is commonly represented as a spiky inflated animal with a strong
108 bilateral symmetry underlined by paired cuticular elements [12, 13]. Its shape is roughly that
109 of an ellipsoid (length of semi-axes are a, b, c) with a and b approximately equal and c being
110 40% longer than a and b (see reconstruction in [13]). However, its three-dimensional original
111 aspect is very rarely preserved (e.g. [13], fig. 1a, suppl. fig. 6d), most specimens being
112 incomplete and strongly deflated, crumpled and folded (e.g. [13], suppl. figs 3a, b and 4d-f). I
113 tentatively measured the maximum length of the relatively complete specimens (N= 29)
114 figured by Han et al. [12] and Liu et al. [13], all from the Zhangjiagou Section, Kuanchuanpu
115 Formation. Eighty-nine percents of them fall between 949 and 1375 μm (the largest specimen
116 is ca 30% larger than the smallest one; Supplementary Table 1 and Supplementary Figures 3,
117 4). Because the majority of these specimens are affected by strong deformation, these
118 variations cannot be reliably used to determine whether *S. coronarius* had a continuous or
119 discontinuous growth (molting stages). These variations more likely result from the cuticular
120 deformation and folding that affected the flexible ellipsoidal body before phosphatic
121 mineralization took place. Although the body length varies, that of the polar aperture remains
122 fairly constant (Supplementary Figure 4), which suggests that the specimens studied so far
123 represent only one growth stage with little original variation in size between individuals.
124 Moreover, a simple model (Supplementary Figure 5) shows that comparable size variations
125 (up to ca 30% in maximal length) are obtained when applying deformation to Japanese paper
126 balloons that mimic the cuticular ellipsoidal case of *S. coronarius*.

129 **The mouth-like opening of *Saccorhytus***

131 *Saccorhytus coronarius* is characterized by a single slit-like opening (polar aperture; Liu et al.
132 2022) surrounded by numerous radial folds and a peripheral row of closely packed
133 circumapertural spiny protuberances. Most of these teeth-like hollow elements are tridentate
134 with a central longer spine and a shorter one on either side [13] (fig. 1g). They strongly recall
135 the pharyngeal teeth of extant priapulids such as *Priapulid caudatus* that have a comparable
136 symmetrical multidentate structure (Figure 2e-g). The re-examination of Liu et al.'s [13] high-
137 resolution images allow to determine the number of these circumapertural teeth in *S.*
138 *coronarius*. There are 27 of them (Figure 3c-h). The same number is also found in one
139 specimen figured by Han et al. ([12]; fig. 1g, h; Figure 3a, b) and collected from the same
140 locality and section (Kuanchuanpu Formation, Zhangjiagou section). Although poorly
141 preserved (circumapertural folds missing) this specimen clearly displays 27 holes roughly

142 aligned in an ellipse, that each corresponds to a basally broken spine (Figure 3a, b).
143 *Eopriapulites sphinx*, a scalidophoran worm from the Kuanchuanpu Formation has a circlet of
144 closely packed elements that seem to be closing the mouth and whose number is comparable
145 with that of *Saccorhytus*' apertural teeth (Figure 3i-k). Whether these radial elements seen in
146 a single specimen of *E. sphinx* are pharyngeal teeth [1] or instead represent a protective
147 closing feature is uncertain. In the second hypothesis, this feature might be the counterpart
148 of the circumapertural folds + teeth seen in *Saccorhytus*.

149 The radial folds of *S. coronarius* represents a continuous pleated structure showing no gap
150 with the basal part of the circumapertural teeth (Supplementary Fig. 5). The width of most
151 teeth corresponds to three or four pleats ([13], fig. 1g; Supplementary Figure 6). The polar
152 aperture of *S. coronarius* has always been interpreted as a mouth [12, 13] although there is
153 little solid evidence to support it. This supposed mouth opening also raises functional issues.
154 The periapertural teeth have a centrifugal arrangement (e.g. [13], fig. 4a, b) that makes them
155 unlikely to have served as a prehensile let alone masticatory apparatus. In contrast, the
156 pharyngeal teeth of extant priapulids that catch and draw food into the gut have a much more
157 central position and are arranged in several rows (Figure 2e). Moreover, the teeth of
158 *Saccorhytus* are so tightly packed together that any mouth contraction (if we consider the
159 opening as a mouth) would have been virtually impossible or extremely limited. Alternatively,
160 the capacity for such opening to possibly suck nutrients suspended in water is equally
161 questionable and would have required a well-developed muscular network, possibly
162 comparable to that of cnidarians that have a single gastrovascular cavity (e.g. [16]). No muscle
163 system capable of oral contractions is present in *Saccorhytus*. However, it should be noted
164 that the absence of muscles may result from taphonomic bias. Under normal conditions,
165 muscle fibers usually decompose very rapidly after death. Muscle preservation is extremely
166 rare in the Kuanchuanpu fossils [9, 10] and probably results from exceptionally favorable
167 conditions that made muscle mineralization possible. In summary, neither the teeth nor the
168 pleated radial folds seem to have played any dynamic role in trapping food particles. The
169 supposed mouth of *Saccorhytus* is therefore more likely to be a passive closing structure.
170 Interestingly, a comparable closing circumoral apparatus is seen in extant kinorhynchs
171 (meiobenthic scalidophorans) in the form of platelet-like placids (see [16] fig. 18.2 and [17])
172 that protect the mouth opening.

173

174

175 **Cuticular structure of *Saccorhytus***

176

177 The integument of *Saccorhytus coronarius* has been described [13] (Liu et al. 2022) as being a
178 bilayered cuticular structure, mainly based on the thin concentric phosphatic layers that often
179 occur around the broken edge of the conical sclerites (e.g. [13], suppl. figs 5, 6). An assumed
180 delamination of these inner and outer layers is seen in one specimen ([13], fig. 1d and suppl.
181 fig. 5e). Electron microscopy (SEM) of the cuticular structure of *Priapulidus caudatus* (extant
182 Priapulida; Scalidophora) was performed to test whether this bilayered configuration is
183 original and also occurs in extant scalidophoran worms (Priapulida) or, on the contrary, may
184 represent a taphonomic artefact. The cuticle of *P. caudatus* is relatively thin (5-7 μ m; Figure
185 2c, d) and flexible along the trunk and secreted by underlying epidermal cells [4, 5]. Although
186 transmission electron microscopy (TEM) reveals 3 layers (epi-, exo- and endocuticle; see [18]),
187 the cuticle of *Priapulidus*, when observed under the SEM, shows a uniform series of sinuous
188 interwoven layers of chitin with no visible structural discontinuity (Figure 2c, d), thus

189 contrasting with the bilayered structure seen in *S. coronarius*. Similarly, the sclerotized scalds
190 and pharyngeal teeth of *P. caudatus* shows no subdivision either (see cross sections in SEM;
191 Figure 2h-l). The pharyngeal teeth of *P. caudatus* are lined internally by epithelial cells (Figure
192 2j, k). The only instance where a split can be observed within the cuticular structure of
193 scaldophorans [4, 5] is when the cuticle is being renewed just before ecdysis. A narrow gap is
194 then formed between the base of the old cuticle (endocuticle) and the newly secreted one
195 (see TEM in [18]). Molting may explain the delaminated structure seen along the body of *S.*
196 *coronarius* ([13], fig. 1d) and would confirm the ecdysozoan nature of this organism. However,
197 an alternative explanation may be considered. Experimental taphonomy (e.g. [19-22]) show
198 that, after death, microbial biofilms colonize all available biological substrates and at the same
199 time, act as nuclei to promote the precipitation of phosphate or calcite [23, 24], depending
200 on environmental parameters. In this context, the bilayered structure seen in *Saccorhytus*
201 might result from the deposition of phosphate on the inner and outer surface of the thin
202 cuticle and would not represent the original cuticular structure. However, these various
203 hypotheses (original bilayered structure, moulting or taphonomic artefact) remain open to
204 discussion.

205

206

207 **Lack of internal organs**

208

209 None of the specimens studied by Han et al. [12] and Liu et al. [13] shows internal features
210 that may resemble a gut tract possibly attached to the polar aperture, or any other organ. One
211 of them (UMCU 2016009; [13], fig. 1a, d) keeps a well-preserved ellipsoidal shape and show a
212 large breach thus revealing details of the inner surface of the body (Supplementary Figure 7a,
213 b). The inner and outer surfaces communicate via perforations running through the conical
214 sclerites and the circumapertural teeth and no remains of internal organs can be seen. This
215 raises questions about the biological nature of *Saccorhytus*, with two possible options: 1)
216 either internal tissues and organs were present and decayed rapidly after death or 2) *S.*
217 *coronarius* was originally an empty cuticular case at the time it was mineralized in phosphate.
218 The second hypothesis seems to be the most plausible one because a number of fossilized
219 organisms associated with *Saccorhytus* in the Kuanchuanpu Formation have well-preserved
220 soft parts. For example, *Olivoides* (Cnidaria) displays secondarily phosphatized internal
221 structures such as muscles [24] and details of the digestive and reproductive systems (e.g. Han
222 et al. 2013, Wang X. et al. 2017, 2020). The absence of internal organs in *S. coronarius* seems
223 to have a biological rather than artefactual origin, and would suggest that this species is
224 overwhelmingly represented by exuviae (possibly a single molting stage; see paragraph 1 on
225 size range) and not body fossils (carcasses). This interpretation is also supported by the typical
226 crumpled and deflated appearance of most specimens (see [8, 12]).

227

228

229 ***Saccorhytus* the larval stage of a scaldophoran worm**

230

231 Based on the development of extant priapulids (three successive larval stages (hatching larva
232 + two loricate larvae; see [15] and Figure 1 and Supplementary Figure 2a, b), we interpret *S.*
233 *coronarius* as a non-feeding, possibly lecithotrophic hatching larva that further developed into
234 vermiform stages, thus finding a more natural explanation to its enigmatic anatomy and the
235 long-standing question of its unique opening [12, 13]. The polar aperture of *S. coronarius*
236 would not be a mouth but instead a closing structure and the opening through which the

237 assumed second larval stage would have exited (see transition from hatching larva to first
238 loricate larva in *Priapulius caudatus*, Figure 1). Again, the development of extant priapulids [14,
239 15] shed light on how *S. coronarius* might have developed. The transition from embryo to
240 hatching larva seen in *P. caudatus* is characterized by the development of the digestive system
241 and the differentiation between trunk and introvert. We suggest that *S. coronarius* developed
242 through a comparable process in which the introvert eversion gave rise to the vermiform
243 shape and functional mouth (Figure 4). This would imply that the internal anatomy of *S.*
244 *coronarius* was relatively simple and mainly consisted of an outer cuticular wall (possibly
245 associated with muscle fibers as in modern priapulids), an invaginated introvert and a
246 pseudocoelomic cavity filled with a fluid. This configuration would clearly make *S. coronarius*
247 unable to generate any active locomotion and feeding. As a result, and due to its microscopic
248 size, it may have remained concealed within the interstices of sediment as suggested by
249 previous authors (meiofaunal hypothesis; e.g. [12]). The enigmatic tridentate circumapertural
250 teeth of *S. coronarius* (Supplementary Figures 1 and 6) might correspond to a row of non-
251 functional pharyngeal teeth (see modern counterparts; Figure 2e-g) that fully developed later
252 in the course of morphogenesis (vermiform stages).

253 If we consider this hypothesis as valid, then we need to determine which animal this
254 supposed larva may belong to. Scalidophoran worms associated with *Saccorhytus* in the
255 Kuanchuanpu Formation seem to be the best potential candidates. Euarthropod remains are
256 absent from the Kuanchuanpu SSF-assemblages, the only known ecdysozoans known so far
257 being scalidophoran worms [1, 3]. These worms display most of the diagnostic features of
258 extant representatives of the group (e.g. priapulids), such as an elongated annulated trunk,
259 an introvert and a variety of cuticular spiny elements (e.g. scalids, pharyngeal teeth). Rare
260 remains of internal soft parts suggest that a gut ran from the mouth and pharyngeal area
261 through to the anus. At least seven scalidophoran species are known from the basal Cambrian
262 Kuanchuanpu Formation [1-3, 26-30]. Although usually preserved in 3D, their introvert,
263 pharynx and oral area are often missing. In most species (except *Eopriapulites sphinx*), the
264 trunk consists of a relatively small number of annulations each bearing a single row of small
265 spiny sclerites, more rarely platelets (*Eokinorhynchus rarus*), and in various number, large
266 sclerites with a broad base that straddles on at least two annuli. Some of these large pointed
267 sclerites are distributed in bilateral pairs along the trunk (e.g. *E. rarus*), others align
268 longitudinally in a single row (e.g. *Xinliscolex intermedius*). Thus, many of these worms display
269 a well-marked bilateral symmetry and dorsoventral polarity that is similarly expressed in *S.*
270 *coronarius* by large paired sclerites. Interestingly, *S. coronarius* has the same number (6
271 symmetrical pairs) of conical sclerites as *E. rarus* although their overall shape differs markedly
272 (ellipsoidic bag-like vs tubular and elongated). Although similarities have been noted with
273 *Eopriapulites sphinx* (possibly 27 radial elements; see Figure 3 and second paragraph of the
274 discussion), the closest resemblances are found with scalidophoran species bearing
275 symmetrical sclerites such as *E. rarus* [3]. Importantly, although their overall shape, again,
276 differs (elongated vs bag-like), *E. rarus* and *S. coronarius* have both 6 symmetrical pairs of
277 broad-based sclerites over their body (Figure 4a, b). *Xinliscolex intermedius* [30], although
278 incompletely known, had the same type of sclerites (7) distributed in a single dorsal row
279 (Figure 4c). The possible development from a bag-like larva to a vermiform juvenile is likely to
280 have been accompanied by the spatial redistribution of the paired sclerites (Fig. 4a, b).

281 The recent discovery [31] of a well-preserved, secondarily phosphatized hatching larva of
282 cycloneuralian (Scalidophora + Nematoida) in the middle Cambrian (Wulian Stage) of North
283 Greenland is worth being mentioned here. The unique specimen of *Inuitiplaskus kouchinskyi*

284 (Supplementary Figure 2c, d) is ca 1250 μm long and has a bottle-like shape with a
285 differentiated trunk and neck and a wrinkled outer surface. Although devoid of a lorica (plated
286 cuticular case around trunk), *I. kouchinskyi* shares close resemblances with the larval stages
287 of extant priapulids (Supplementary Figure 2a, b). Interestingly, its anterior end seems to be
288 closed by a central swelling, suggesting that its mouth was not open as seen in the hatching
289 and first loricate larva of extant priapulids (compare Supplementary Figure 2a, d). *I.*
290 *kouchinskyi* is likely to have been a non-feeding larva and a possible member of the stem-
291 group Priapulida [30]. This fossil suggests that some Cambrian cycloneuralians were indirect
292 developers as are, for example, modern priapulids. Finally and importantly, *I. kouchinskyi*
293 appears to be closely similar to the hypothetical developmental stage of our model (Figure 4d,
294 e) that would have followed *Saccorhytus*. This is a key fossil evidence that supports our general
295 interpretation. Other comparable vase-shaped larvae such as *Orstenoloricus shergoldii* (480-
296 950 μm in total length) are known from the mid-Cambrian of Australia [32].

297 In summary, although *Saccorhytus* lacks robust scalidophoran characters, the hypothesis that
298 it could represent the larval stage of an early Cambrian member of this group remains the
299 least speculative one. It should be noted that, similarly, the larval and adult stages of modern
300 priapulids are extremely different from each other. Alternatively, *Saccorhytus* could be the
301 larva of a hypothetical extinct group of ecdysozoans with no modern equivalent, that we are
302 presently unable to characterize because of the lack of fossil evidence.

303

304

305 ***Saccorhytus* in the ecdysozoan phylogenetic tree**

306

307 The cladistic analysis made by Liu et al. ([13], fig. 4) resolved *Saccorhytus coronarius* as part of
308 a polytomy at the base of the total-group Ecdysozoa, leaving its exact placement open -i.e.
309 either as a basal ecdysozoan, a basal panarthropodan or a basal cycloneuralian. These results
310 are based on the assumption that *S. coronarius* is a pre-adult or adult animal and is compared
311 as such with adults from other ecdysozoan groups. Our alternative view of making *S.*
312 *coronarius* no longer a weird animal with a single opening but the possible larval stage of one
313 of the scalidophoran worm of the Kuanchuanpu biota, would alter its position within the tree.
314 Since *Saccorhytus* may share affinities with some Cambrian scalidophorans (e.g.
315 *Eokinorhynchus*), it would be likely to occupy a less basal position within Ecdysozoa and
316 possibly join the total-group Scalidophora (Supplementary Figure 8). Intentionally, no new
317 phylogenetic analysis is made here because of the evident difficulty of integrating an assumed
318 larva (*Saccorhytus*) into a matrix dominated by adult or preadult forms (the rest of the coded
319 ecdysozoans). Lastly, the present study allows neither to resolve the relation between the
320 main lineages of Ecdysozoa (Scalidophora, Nematoida, Panarthropoda) and their order of
321 divergence in the evolutionary tree, nor to test recent phylogenies. For example, Howard et
322 al. [33] resolved Scalidophora as the sister-group of all other ecdysozoans (Nematoida +
323 Panarthropoda) whereas its monophyly is questioned by Laumer et al. [34].

324

325

326 **Possible lifestyle and habit**

327

328 Assuming that *Saccorhytus coronarius* was a non-feeding larva invite to reconsider its assumed
329 lifestyle [12, 13]. *S. coronarius* may have lived within the sediment, perhaps in interstitial
330 environments, its spiny ornament possibly playing the role of anchoring features. This would

331 reconcile with previous interpretations of *Saccorhytus* being a meiobenthic organism [12].
332 Since *Saccorhytus* had no functional introvert and developed musculature, it was most
333 probably unable to move through sediment. In contrast, one of the assumed larval stages that
334 would have followed *Saccorhytus* (Figure 4) may have had capacities to move actively and
335 feed (see development of modern priapulids) as it gradually transformed into a more
336 elongated and tubular organism (Figure 4e).

337

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341 support (Pack Ambition International grant) and the anonymous reviewers for their
342 constructive remarks.

343

344 **Material and methods**

345 Our study and re-interpretation of *Saccorhytus coronarius* is mainly based on the high-
346 resolution images shown in [13] (both figures and supplementary figures in Extended data).
347 Line-drawings from these images were made by using Adobe Illustrator and Photoshop CS6.
348 The fossil specimens originally described by Liu et al. 2022 are all from the early Cambrian
349 Kuanchuanpu Formation, more precisely, horizons falling within the Small Shelly Fossil (SSF)
350 *Anabarites trisulcatus-Protohertzina anabarica* Assemblage Zone (531.8-536.4 Ma; Fortunian
351 age), The original images [13] were obtained by using scanning electron microscopy (SEM) and
352 synchrotron radiation X-ray tomographic microscopy (SRXTM) and provide exceptional details
353 on the 3D-structure and external ornament of *Saccorhytus coronarius*. Extant priapulid worms
354 (*Priapululus caudatus*) were collected from the Gullmar Fjord near the Kristineberg Marine
355 Station (University of Göteborg, Sweden), fixed with glutaraldehyde, transferred in 100%
356 ethanol, dried (Critical Point with a Leica EM CPD 300) and mounted for SEM (FEI Quanta 250
357 FEG at CT μ , Université Claude Bernard, Lyon).

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473 **EXPLANATION OF TEXT-FIGURES**

474

475 **Figure 1. Post-embryonic development of *Priapulius caudatus*** (Scalidophora, Priapulida). (*a-*
 476 *d*) External morphology based on SEM images [15]; after hatching, the larva (light yellow)
 477 molts and gives rise to the first loricate larva (light orange). (*e-g*) Internal morphology (cross-
 478 sections from [14], fig. 2) showing the pre-hatching embryo, the post-hatching larva and the
 479 first loricate larva, respectively; both larvae are non-feeding and lack a mouth and anus
 480 cuticular opening. Small black arrows indicate the introvert-trunk boundary. (*d*) and (*g*) show
 481 an everted and inverted state respectively. Abbreviations are as follows: 1ll, 1st loricate larva;
 482 an, anus; dg, digestive tract; em, embryo; es, egg shell; ex, exuvia of hatching larva; hl,
 483 hatching larva; in, introvert; lo, lorica; mo, mouth.; ne, neck; pc, pseudocoelomic cavity filled
 484 with fluid; sc, scalid; tr, trunk.

485

486 **Figure 2. Cuticular features of extant *Priapulius caudatus*** (Priapulida) from Sweden. (*a, b*)
 487 Fragment of body wall showing longitudinal and circular bundles of muscle fibers, underlying
 488 cuticle; general view and details. (*c*) Cross-section through body wall showing cuticle secreted
 489 by underlying epidermal cells. (*d*) Cross-sections through cuticle showing wavy chitinous
 490 layers. (*e*) Pharyngeal teeth around mouth. (*f, g*) Details of multidentate pharyngeal teeth. (*h,*
 491 *i*) Broken pharyngeal tooth showing sclerotized cuticle in section, general view and details.
 492 (*j, k*) Broken pharyngeal tooth showing internal tissue (epidermal cells). (*l*) Broken pharyngeal
 493 tooth. All SEM images. Abbreviations are as follows: ba, boundary between annuli; cf, chitin
 494 fiber; cm, circular muscle; cs, central spine; cu, cuticle; ec, epidermal cells; in, introvert; is,
 495 internal surface; lm, longitudinal muscle; os, outer surface; ph, pharynx; pt, pharyngeal tooth;
 496 sc, scalid; ss, secondary spine. Scale bars: 500 μm in A, E; 200 μm in B, G; 100 μm in F, J; 50 μm
 497 in H; 10 μm in C, K, L; 5 μm in I; 2 μm in D.

498

499 **Figure 3. Distribution of cuticular teeth around the apertural area of *Saccorhytus coronarius***
 500 and *Eopriapulites sphinx* (Scalidophora), both from the early Cambrian Kuanchuanpu
 501 Formation, China. Line drawings from original photographs. (*a, b*) Specimen ELIXX-48-64
 502 figured by Han et al. [12] (fig. 1g, h); teeth truncated near their basis. (*c, d*) Specimen UMCU
 503 2014001 figured by Liu et al. [13] (Suppl. fig. 2d) (see also Supplementary Figure 1e). (*e, f*)
 504 Specimen UMCU 2019019 figured by Liu et al. [13] (Suppl. fig. 6d) (see also Supplementary
 505 Figure 1f). (*g, h*) Specimen UMCU 2016009 figured by Liu et al. [13] (fig. 1a) (see also
 506 Supplementary Figure 1a-d). (*i-k*) Specimen CGM 16 figured by Liu et al. [1] (fig. 3a, b). The
 507 circumapertural teeth, radial folds and other external cuticular features of *S. coronarius*, are
 508 represented in light yellow, orange and gray, respectively. The pharyngeal teeth and other
 509 cuticular features of *E. sphinx*, are represented in light yellow and green, respectively. The
 510 number of circumapertural teeth is 27 in *S. coronarius* and probably the same in *E. sphinx*,
 511 suggesting that the radial folds + circumapertural teeth of *S. coronarius* have a possible
 512 counterpart in *E. sphinx*. Same scale for (*a*), (*c*), (*e*), (*g*), (*j*) and for (*b*), (*d*), (*f*), (*h*), (*k*).
 513 Abbreviations are as follows: an, annulation; cs, conical broad-based sclerite; ct,
 514 circumapertural tooth; ls, large spines; m, mouth; pa, polar aperture; pt, pharyngeal tooth; rf,
 515 radial folds; sc, scalid; tr, trunk.

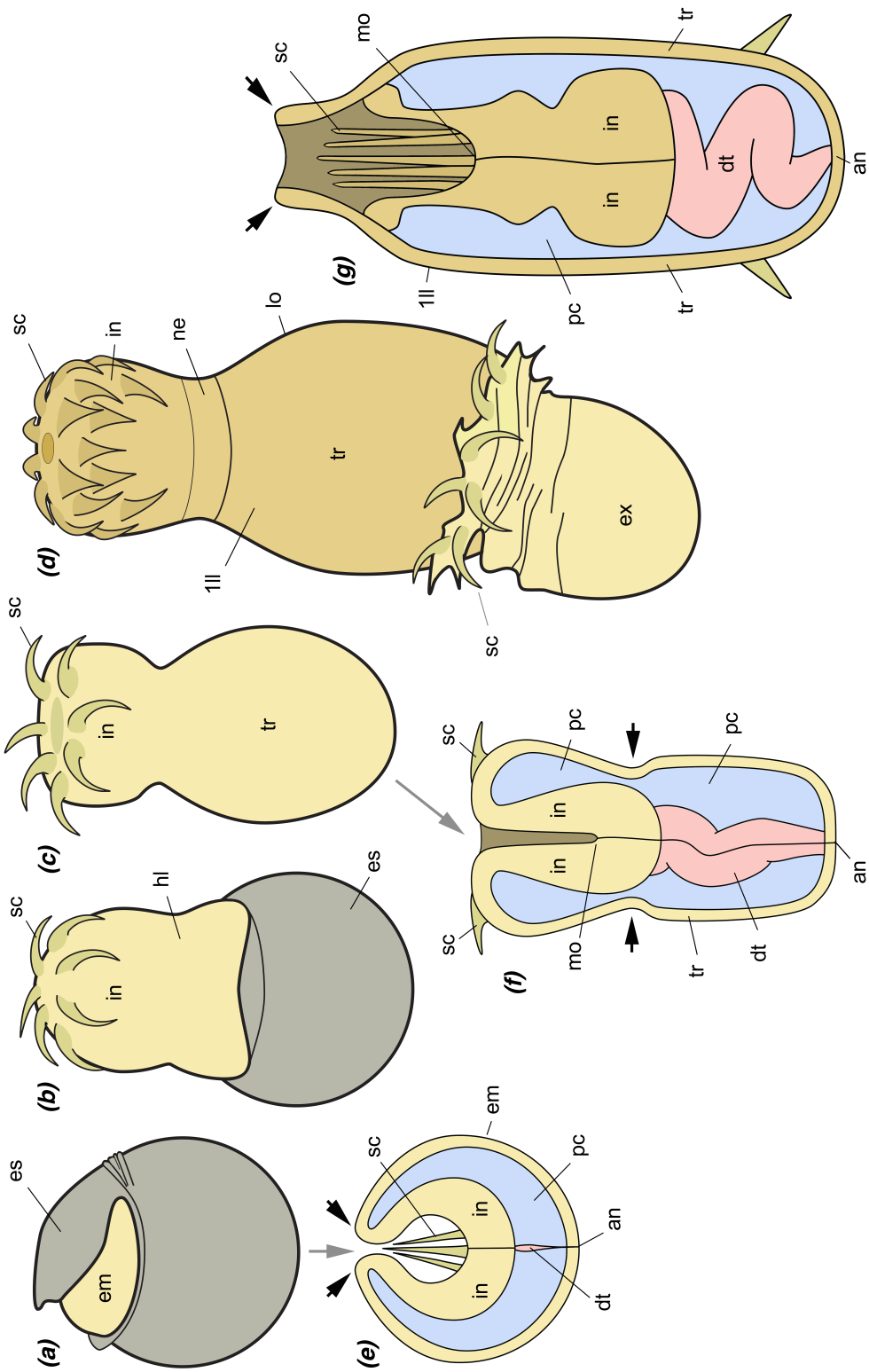
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517 **Figure 4. *Saccorhytus coronarius* (early Cambrian Kuanchuanpu Formation, China) as a non-**
 518 **feeding larva of a scalidophoran worm.** (*a, b*) Reconstruction based on [13] in apertural and
 519 side view, respectively. (*c*) Hypothetical internal anatomy of the larva, based on the larval

520 development of *Priapulid caudatus* (see [14]). (d) Hypothetical development of *S. coronarius*
521 showing the first vermiform stage coming out through the aperture and area bearing radial
522 folds (number and distribution of sclerites hypothetical), via molting. Abbreviations are as
523 follows: an, anus; cs, conical broad-based sclerite; ct, circumapertural tooth; cu, cuticle; dg,
524 digestive tract; ex, exuvia; in, introvert; ls, large spine; mo, mouth; pc, pseudocoelomic cavity
525 filled with fluid; rf, radial folds.

526
527 **Figure 5. Symmetrical arrangement of large trunk sclerites in *Saccorhytus* and**
528 **scalidophorans, all from the early Cambrian Kuanchuanpu Formation. (a) *Saccorhytus***
529 ***coronarius*, reconstruction simplified after [13]. (b, c) *Eokinorhynchus rarus* and *Xinliscolex***
530 ***intermedius*, reconstructions in assumed dorsal view, simplified after [3, 29], respectively. Not**
531 **to scale. Abbreviations are as follows: es, elongated posterior spine; in, introvert; ls, large**
532 **(broad-based) sclerite; mo, mouth; ph, pharynx; sp, sagittal symmetry plane (red line); tr,**
533 **trunk; 1-7, number of paired sclerites (not homologous in these three forms).**

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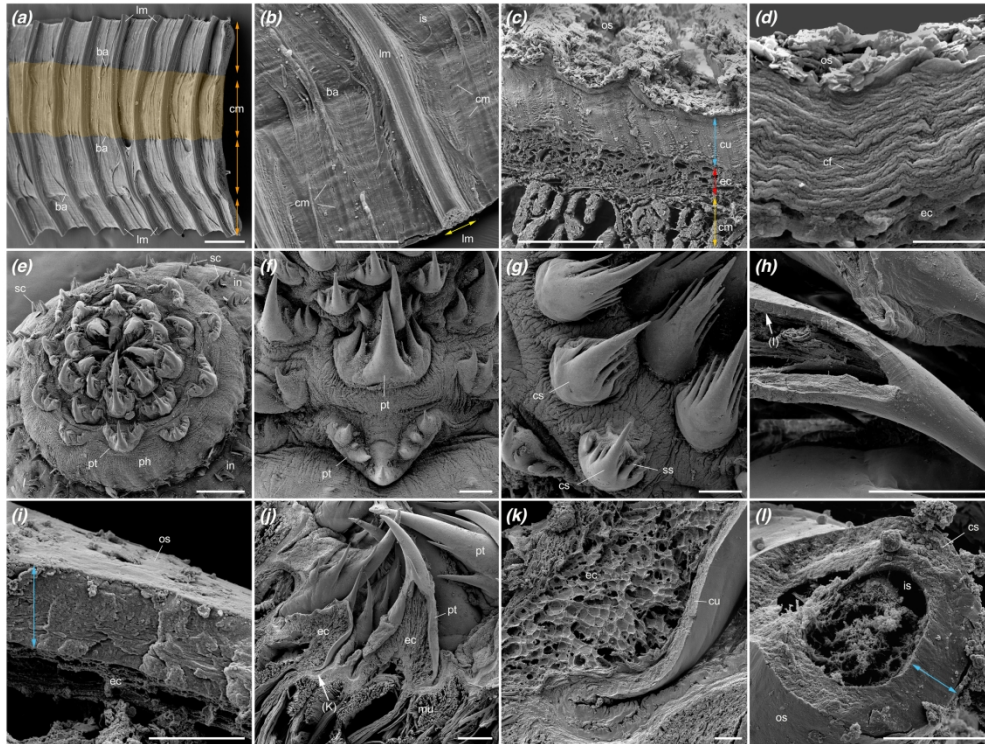


Figure 2. Cuticular features of extant *Priapulus caudatus* (Priapulida) from Sweden. (a, b) Fragment of body wall showing longitudinal and circular bundles of muscle fibers, underlying cuticle; general view and details.

(c) Cross-section through body wall showing cuticle secreted by underlying epidermal cells. (d) Cross-sections through cuticle showing wavy chitinous layers. (e) Pharyngeal teeth around mouth. (f, g) Details of multidentate pharyngeal teeth. (h, i) Broken pharyngeal tooth showing sclerotized cuticle in section, general view and details.

(j, k) Broken pharyngeal tooth showing internal tissue (epidermal cells). (l) Broken pharyngeal tooth. All

SEM images. Abbreviations are as follows: ba, boundary between annuli; cf, chitin fiber; cm, circular muscle; cs, central spine; cu, cuticle; ec, epidermal cells; in, introvert; is, internal surface; lm, longitudinal muscle; os, outer surface; ph, pharynx; pt, pharyngeal tooth; sc, scolid; ss, secondary spine. Scale bars: 500 μm in A, E; 200 μm in B, G; 100 μm in F, J; 50 μm in H; 10 μm in C, K, L; 5 μm in I; 2 μm in D.

209x157mm (300 x 300 DPI)

