

1 **Convergent evolution of ventral adaptations for enrollment in trilobites and extant**
2 **euarthropods**

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9

10 **Abstract**

11 The ability to enroll for protection is an effective defensive strategy that has convergently
12 evolved multiple times in disparate animal groups ranging from euarthropods to mammals.
13 Enrollment is an evolutionary staple of trilobites, and their biomineralized dorsal exoskeleton
14 offers a versatile substrate for the evolution of interlocking devices. However, it is unknown
15 whether trilobites also featured ventral adaptations for enrolment. Here, we report ventral
16 exoskeletal adaptations that facilitate enrollment in exceptionally preserved trilobites from the
17 Upper Ordovician Walcott-Rust Quarry in New York State, USA. Walcott-Rust trilobites reveal
18 the intricate three-dimensional organization of the non-biomineralized ventral anatomy preserved
19 as calcite casts, including the spatial relationship between the articulated sternites (i.e., ventral
20 exoskeletal plates) and the wedge-shaped protopodites. Enrollment in trilobites is achieved by
21 ventrally dipping the anterior margin of the sternites during trunk flexure, facilitated by the
22 presence of flexible membranes, and the close coupling of the wedge-shaped protopodites.
23 Comparisons with the ventral morphology of extant glomerid millipedes and terrestrial isopods

24 reveal similar mechanisms used for enrollment. The wedge-shaped protopodites of trilobites
25 closely resemble the gnathobasic coxa/protopodite of extant horseshoe crabs. We propose that
26 the trilobites' wedge-shaped protopodite simultaneously facilitates tight enrollment and
27 gnathobasic feeding with the trunk appendages.

28

29 **Introduction**

30 The ability to completely enroll the body to form a tight protective ball to deter predatory attacks
31 represents an effective strategy that has evolved multiple times throughout bilaterian evolution,
32 including archetypical examples like xenarthan mammals (Superina and Loughry, 2012) and
33 several euarthropods such as myriapods (Hannibal and Feldmann, 1981; Shear et al., 2011),
34 terrestrial isopods (Brökeland et al., 2001; Hyžný and Dávid, 2017), and even some insect
35 lineages (Ballerio and Grebennikov, 2016). Among extinct species, enrollment has been
36 thoroughly documented in trilobites, a megadiverse group of marine euarthropods typified by the
37 presence of a biomineralized calcitic dorsal exoskeleton (Fig. 1). Trilobite evolutionary history
38 throughout the Paleozoic was heavily influenced by their ability to enroll effectively (e.g., Esteve
39 et al., 2013; Suárez and Esteve, 2021; Chipman and Drage, 2023). Early Cambrian species show
40 evidence of complete but imperfect (i.e. no encapsulating) enrollment, leaving open gaps
41 between the thoracic and pygidial spines (Ortega-Hernández et al., 2013), whereas more derived
42 groups evolved a diverse array of complex interlocking coaptive devices to make this defensive
43 strategy more effective (e.g., Esteve et al., 2011, 2017, 2018). Despite its significance for the
44 long-term evolutionary success of trilobites, enrollment is exclusively known from the
45 perspective of the dorsal exoskeleton due to the paucity of enrolled specimens with exceptionally
46 preserved non-biomineralizing ventral structures (Fig. 1). Thus, the precise physical mechanisms

47 by which the ventral surface of trilobites could accommodate their numerous biramous
48 appendages and other exoskeletal structures during enrollment remains enigmatic. Attempts to
49 explain how the limbs would be organized relative to each other during enrolment have focused
50 on hypothetical reconstructions of the non-biomineralized structures, like the exceptionally
51 preserved Ordovician trilobite *Placoparia cambriensis* (e.g., Whittington, 1993). Although this
52 reconstruction considered the position of the flexible intersegmental tendinous bars based on
53 fossil data, it did not account for the presence of sternites (i.e., ventral exoskeletal plates) that are
54 located in the medial space between each pair of limbs (Whittington, 1993). Moreover, trilobite
55 appendages are infrequently preserved, being only known from *Konservat-Lagerstätten* such as
56 the early Cambrian Chengjiang (e.g., Ramsköld and Edgecombe, 1996; Hou et al., 2008), mid-
57 Cambrian Burgess Shale (e.g., Whittington, 1975; Losso and Ortega-Hernández, 2022), and
58 Ordovician Beecher's Bed (e.g., Whittington and Almond, 1987; Hou et al., 2021). Trilobite
59 macrofossils from *Konservat-Lagerstätten* are typically highly compressed and their appendages
60 are only found in prone specimens, limiting our understanding of the three-dimensional
61 morphology and organization of the limbs during enrollment. In this context, the precise
62 morphology of trilobite appendages has also not been comprehensively considered in terms of
63 how they would fit in a completely enrolled position. The cross-section shape of the trilobite
64 protopodite, for example, has been illustrated as either oval (Whittington, 1975; Whittington and
65 Almond, 1987; Bruton and Haas, 1999; Bicknell et al., 2021; Schmidt et al., 2021) or square
66 (Hou et al., 2021), or authors have omitted them altogether because of the lack of available data -
67 (Whittington, 1993). While these differences may seem minor, shape plays a critical role in the
68 function of various body parts (e.g., Bicknell et al. 2021), and thus this represents a fundamental

69 gap of missing data when reconstructing the early autecology and functional morphology of one
70 of the first successful clades in the evolutionary history of euarthropods.

71 In this study, we describe the non-biomineralized three-dimensional ventral exoskeletal
72 morphology of trilobites from the Upper Ordovician (Mohawkian) Rust Formation of New York
73 state based on exceptionally preserved fossils with soft tissues replicated as calcite casts (Losso
74 et al., 2023). Trilobites from the Walcott-Rust Quarry are preserved in various stages of trunk
75 flexure, revealing the intricate coupling of the biramous appendages and sternites to maximize a
76 tight complete enrollment. Comparisons with the three-dimensional exoskeletal and appendicular
77 morphology of extant euarthropods, including a glomerid millipede, a terrestrial isopod, and the
78 Atlantic horseshoe crab *Limulus polyphemus*, indicate striking cases of convergent evolution in
79 terms of their ventral exoskeletal anatomy. The presence of these functionally similar adaptations
80 in phylogenetically disparate euarthropod lineages demonstrates a profound case of convergent
81 evolution towards a common method of body enrollment separated by over 500 million years.

82

83 **Materials and methods**

84 All studied specimens are housed at the Museum of Comparative Zoology (MCZ) at Harvard
85 University (Cambridge, Massachusetts, USA). Trilobites from the Walcott-Rust Quarry originate
86 from the Upper Ordovician Rust Formation, Trenton Group, in New York state. The
87 exceptionally preserved trilobite fossils are composed of three-dimensional calcite casts of non-
88 biomineralized tissues in a micritic limestone matrix from Layer 3 of the Rust Formation (see
89 Losso et al., 2023). The studied trilobites are mounted as thin sections, produced by Charles D.
90 Walcott in the 1870s (Yochelson, 1998). Fossil specimens were imaged at the Digital Imaging
91 Facility (DIF) at the MCZ using a Keyence microscope with transmitted light. Extant

92 euarthropod specimens sampled from the Invertebrate Zoology collections at the MCZ were
93 imaged to analyze their protopodite and sternite morphologies, including *Limulus polyphemus*
94 (MCZ:IZ:41112), a glomerid millipede (MCZ:IZ:165554) and a terrestrial isopod
95 (MCZ:IZ:90105). All three specimens were stained with iodine prior to micro-computed
96 tomographic scanning using a Bruker SkyScan 1173 micro-CT scanner at the DIF. Extant
97 specimens were stained in iodine to increase resolution of Micro-CT scanning (See Supplemental
98 Information for detailed staining method). Micro-CT imaging was performed at a voltage of 80
99 kV, wattage of 100 μ A, a resolution of 6 μ m, and with a 0.5 mm thick aluminum filter. Scans
100 were reconstructed as TIFF stacks in NRecon (Bruker Corporation) and visualized and
101 segmented in Dragonfly 2019 4.0 (Object Research Systems, Montreal, Canada).

102 One specimen of MCZ:IZ:165554 from the lot of six was dissected and photographed.
103 Dissections were performed using an Zeiss Stemi 305 microscope under direct light conditions,
104 and photographs were taken using a Zeiss Axiocam 208 color camera.

105

106 **Results**

107 **Sternite morphology and preservation**

108 Specimen MCZ:IP:158251, a thin section of the cheirurid trilobite *Ceraurus pleurexanthemus* in
109 a completely enrolled position (Fig. 2a), reveals the three-dimensional morphology of ventral
110 exoskeletal structures in exceptional detail. The presence of the hypostome and articulating half
111 rings on the same specimen indicates that the section follows the sagittal plane along the midline
112 of the body (Fig. 2a). In addition to showing the pattern of overlap and articulation of the
113 tergites, MCZ:IP:158251 also preserves non-biomineralized ventral exoskeletal structures bound
114 by the body wall as delimited by the presence of sparry and fibrous calcite (Losso et al., 2023).

115 MCZ:IP:158251 features five imbricating and serially arranged ventral structures that dip
116 anteriorly at a 50° angle relative to each other and nearly perpendicular to the dorsal exoskeleton
117 (Fig. 2b). Unlike the dorsal articulating half rings in the same specimen, the ventral structures do
118 not directly overlap each other (Fig. 2b) but are continuous between them based on the
119 distribution of the fibrous calcite. We interpret these ventral features as direct evidence of
120 sternites in *C. pleurexanthemus*, expressed as the thickened exoskeletal plates, connected on the
121 anterior and posterior margins by transverse series of flexible tendinous bars (Fig. 2b). Another
122 specimen of *C. pleurexanthemus* (MCZ:IP:158227) shows a similar sagittal section along the
123 midline of the body, but here the trunk is only partially enrolled, a position that informs the
124 position of the ventral structures under a different configuration (Fig. 2c). MCZ:IP:158227 also
125 preserves five sets of repeating structures, but because of the more abaxial position of the thin
126 section, as indicated by the protopodites seen posteriorly, the sternites are not visible. The
127 anterior ventral structures are underneath the slightly enrolled first five tergites and consist of
128 corrugated bulges with a shorter ventrally concave region between each (Fig. 2c, d). The lesser
129 degree of trunk flexure in MCZ:IP:158227 shows that the sternites would be parallel relative to
130 the dorsal exoskeleton in a fully prone position (Fig. 2c, d).

131 Comparisons with 3D datasets of partially and completely enrolled isopods and
132 millipedes supports the interpretation of the ventral morphology of *Ceraurus pleurexanthemus* as
133 all taxa display the same pattern of anterior imbrication of sternites during enrollment despite
134 their different morphologies (Figs. 2, 3). The terrestrial isopod displays a more complex sternite
135 morphology than trilobites, with a row of paired rectangular plates (Fig. 3a – c) rather than the
136 single row of hourglass shaped sternites (Whittington, 1993; Ortega-Hernández and Brena,
137 2012). The anterior edge of the isopod sternite dips ventrally during enrollment below the

138 posterior margin of the preceding plate (Figs. 2e, f, 3c). Glomerid millipedes have wish-bone-
139 shaped sternites (Fig. 3d – f) with limbs emerging from protopodite/coxa cavities between
140 adjacent ventral plates (Fig. 3f). The elongate lateral portions of each sternite align with the
141 adjacent pleurites (Fig. 3e; Supplemental Fig. 1) and imbricate anteriorly during enrollment (Fig.
142 3f).

143

144 **Protopodite morphology and preservation**

145 Exsagittal thin sections of Walcott-Rust trilobites such as MCZ:IP:158240 (*Ceraurus*
146 *pleurexanthemus*; Fig. 4a, b) and MCZ:IP:104956 (*Flexicalymene senaria*; Fig. 4c, d) show the
147 lateral ventral morphology in three-dimensions with exceptional detail. The hypostome and
148 articulating half rings of the tergites are visible in these specimens, similarly to the sagittal thin
149 section in MCZ:IP:158251 (Fig. 2a), but the posterior projections of the hypostome indicates that
150 the more abaxial position near the lateral margin of the axial lobe (Fig. 4a, c). In both
151 MCZ:IP:158240 and MCZ:IP:104956, a series of serially repeating wedge-shaped ventral
152 structures are associated with each of the tergites (Figs. 4a, 5c, d). The presence of fibrous calcite
153 defining these structures indicates that they were originally non-biomineralized (Losso et al.,
154 2023). The wedge-shaped ventral structures are widest dorsally and taper ventrally to a point at a
155 40-50° angle (Fig. 4b, d). Specimen MCZ:IP:104956 of *F. senaria* displays a series of 22 wedge-
156 shaped structures, four of which are associated with the cephalon, but none are visible beneath
157 the pygidium (Fig. 4c). MCZ:IP:104956 is 65% enrolled and the series of wedge-shaped
158 structures are angled slightly anteriorly (Fig. 4c). The anterior most wedges have a straight
159 anterior margin that gently curves anteriorly at their mid-section (Fig. 4d). The posterior margin
160 of the wedge is similarly curved, which allows for the succeeding wedges to fit snugly against

161 one another when in direct contact (Fig. 4d). The terminal tip of the wedge is slightly enlarged
162 and bulbous (Fig. 4d).

163 Based on their taphonomy and morphology, we interpret the serially repeating wedge-
164 shaped structures observed in both *C. pleurexanthemus* and *F. senaria* as direct evidence of
165 three-dimensionally preserved protopodites, namely the part of the arthropodized biramous
166 appendage that is in direct contact with the body wall (Boxshall, 2004), as observed in a cross-
167 sectional view from an exsagittal plane. This interpretation is supported by the precise
168 association of a wedge with each tergite (Fig. 4c) and the abaxial position relative to the axial
169 lobe of the dorsal exoskeleton which can also be seen in a transverse thin section of *C.*
170 *pleurexanthemus* showing an anterior view of the proximal portion of the appendage (Fig. 5a).

171 The repeating wedge-shaped structures are not part of the biomineralized dorsal
172 exoskeleton, such as muscle attachment sites or apodemes (Whittington et al., 1997; Edgecombe
173 and Sherwin, 2001; Siveter et al., 2021) as the original calcite would be clearly visible similar to
174 the tergites and sternites (Fig. 2b, c). Comparisons with additional thin section specimens of *C.*
175 *pleurexanthemus* further strengthen the interpretation of the wedges as protopodites. Specimen
176 MCZ:IP:110933 shows a clear and unobstructed view of one biramous appendage (Fig. 5a),
177 which shows that the laterally splayed protopodites of *C. pleurexanthemus* are subtriangular in
178 anterior view with a nearly vertical medial margin and horizontal ventral margin. The medial
179 margin is studded with gnathobasic spines, and the ventral edge is marked by elongate endites
180 (Fig. 5a). The exopodite is visible dorsally and the endopodite extends from the distal margin of
181 the protopodite (Fig. 5a). The protopodite of MCZ:IP:110933 extends from the lateral edge of
182 the dorsal exoskeleton's axial lobe and partially into the pleural lobe, which closely correlate
183 with the position of the wedge-shaped structures seen in exsagittal thin sections (Fig. 4a, c). One

184 specimen (MCZ:IP:110918) of *Flexicalymene senaria* sectioned in coronal view shows a series
185 of wedge-shaped structures whose apex points towards the midline of the body (Fig. 5c, d). The
186 position within the body and the comparison with the two other views (Fig. 4c, d), support the
187 interpretation of these structures also represent the protopodites as observed from a dorsal
188 section, which further confirms their wedge-shaped three-dimensional organization.

189 Comparisons with the 3D morphology of *Limulus polyphemus* supports the interpretation
190 of the ventral structures seen in *Ceraurus pleurexanthemus* and *Flexicalymene senaria* as
191 exsagittal and coronal views of protopodites based on the wedge-shaped morphology of the
192 coxa/protopodite (Fig. 4e, f). The coxa/protopodite of the walking legs in *L. polyphemus* are
193 dorsoventrally elongate with a large area of attachment to the body wall, the dorsal edge is broad
194 cross section decreasing in width ventrally (Fig. 4e, f). In cross section from an exsagittal view,
195 the coxae/protopodite are broadest dorsally, tapering ventrally (Fig. 4g, h). The
196 coxae/protopodite are also wedge-shaped in coronal view, narrowest near the body wall and
197 widening distally (Fig. 5e, f), a condition that is also seen in *Flexicalymene senaria* (Fig. 5c, d).

198

199 **Discussion**

200 Walcott-Rust trilobites reveal new insights into the ventral morphology of trilobites, with direct
201 implications for understanding their adaptations for enrollment. A single row of hour-glass
202 shaped sternites are known throughout Trilobitomorpha such as *Arthroaspis bergstroemi* (Stein
203 et al., 2013), *Misszhouia longicaudata* (Zhang et al., 2007; Mayers et al., 2019), and *Sinoburius*
204 *lunaris* (Chen et al., 2019). The pyritized olenid trilobite *Triarthrus eatoni* preserves appendages,
205 sternites and tendinous bars (Whittington and Almond, 1987), which closely resemble those
206 found in the pliomerid *Placoparia cambriensis* (Whittington, 1993). These examples of

207 preserved sternites are only observable in either ventral or dorsal view due to their preservation
208 in compacted body fossils, therefore not providing information about the three-dimensional
209 morphology, position within the body or movement during enrollment. The Walcott-Rust
210 specimens provide complementary views of the sternites and protopodites that allow to
211 reconstruct their three-dimensional overall morphology.

212

213 **Sternite position during enrollment**

214 All known cases of sternite preservation in trilobites and non-biomineralized trilobitomorphs
215 point towards the same broad pattern of morphological organization, in which the sternites are
216 successively arranged in an axial row that runs parallel to the dorsal exoskeleton, and which are
217 separated by flexible tendinous bars (Fig. 2c, d) (Whittington, 1993; Zhang et al., 2007; Stein et
218 al., 2013; Mayers et al., 2019; Chen et al., 2019). The sternites are cuticular and have a thinner
219 constitution than the dorsal exoskeleton; however, the ventral side of the body would not be able
220 to physically accommodate the entire sternite series during complete enrollment while
221 maintaining their outstretched disposition without producing excessive tension on either the
222 ventral side, due to over compression, or the dorsal side, due to over extension (Fig. 5f). Instead,
223 the ventral data from Walcott-Rust trilobites demonstrate that the sternites and tendinous bars
224 become corrugated in the transition between prone position to partial and complete enrollment
225 (Fig. 2a, b), with the anterior edge of the sternite angling ventrally and the flexible tendinous bar
226 bulging (Fig. 6a-d). Critically, the same configuration between the sternites and arthrodistal
227 membranes are also observed in isopods (Fig. 3a – c) and millipedes (Fig. 3d – f), with the
228 anterior edge of the sternites dipping ventrally to accommodate tight and complete enrollment.
229 These comparisons indicate that despite the distant phylogenetic relationships between trilobites

230 (extinct stem-group chelicerates), isopods (extant crustaceans) and millipedes (extant
231 myriapods), these euarthropods share fundamentally similar exoskeletal ventral adaptations that
232 facilitate protective enrollment. These findings evidence a striking case of convergent evolution
233 that is heavily influenced by the mechanical requirements and limitations necessary to achieve
234 complete encapsulations in euarthropods, which have been extensively investigated in terms of
235 their dorsal exoskeletal morphology (e.g., Esteve et al., 2011, 2017, 2018; Chipman and Drage,
236 2023), but never from the perspective of the ventral anatomy until now. Repeated convergent
237 evolution of the same mechanism in three distantly related euarthropods demonstrates the
238 constraints of achieving complete enrollment with a rigid exoskeleton, and simultaneously the
239 evolutionary advantages that this strategy must confer. Even more notably sternite morphology
240 varies between the three taxa, from a single row of hourglass-shaped plates in trilobites (Fig. 2a),
241 paired rectangular plates in isopods (Fig. 3c), to wish-bone-shaped sternites in glomerids (Fig.
242 3f), yet all species enroll utilizing the same basic mechanism.

243

244 **Functional implications for trilobite musculature during enrollment**

245 The new insights into the ventral exoskeletal organization of the trilobite exoskeleton have direct
246 implications for understanding the functional morphology of the trunk musculature during
247 enrollment (Fig. 6). Three proposed dorsal-ventral muscles would attach from tergites to sternites
248 based on crustacean analogs; the anteriorly descending muscle, the vertically descending muscle
249 and the posteriorly descending muscle (Cisne, 1981; Whittington, 1993). Longitudinal ventral
250 muscles have been proposed to be on either side of the body of trilobites, attaching to the
251 tendinous bar (Beecher, 1902; Størmer, 1939; Hupe, 1953; Whittington, 1993). The
252 reconstruction of an exceptionally preserved specimen of *Placoparia cambriensis* with soft

253 tissues in sagittal cross section (Whittington, 1993) bears striking similarities to MCZ:IP:158227
254 which is not fully enrolled (Fig. 2c). However, the fully enrolled reconstruction illustrates the
255 ventral anatomy exactly the same as in the prone position (Whittington, 1993) despite the
256 Walcott-Rust trilobites and MCZ:IP:158251 having been published nearly 100 years before with
257 the corrugated ventral structures highlighted (Walcott 1881). A proposed mechanism of
258 enrollment and extension for trilobites relied on the contraction of the longitudinal ventral
259 muscle would bring the sternites closer together, enrolling of the body versus contraction of the
260 dorsal longitudinal muscle that would extend the body to a prone position (Whittington, 1993)
261 (Fig 6).

262 In extant euarthropods that completely enroll their body similarly to trilobites, such as
263 glomeriid millipedes and terrestrial isopods, contraction of the longitudinal ventral muscle flex
264 the body ventrally (Manton, 1961). However, the sternites are too long (sag.) to allow complete
265 enrollment without substantial overlap between them (Fig. 3c, f). In this context, the sagittal thin
266 section of *C. pleurexanthemus* (MCZ:IP: 158251) demonstrates that trilobite enrollment was
267 accomplished by ventrally dipping the anterior margin of the sternites, producing a corrugated
268 outline of sternites and arthrodistal membrane (Fig. 3c, f). Based on their basic functional
269 morphology, euarthropod enrollment is achieved through contraction of the longitudinal ventral
270 muscle and the vertically descending muscle, bringing sternites closer together and raising the
271 posterior margin dorsally (Fig. 6b, c). Returning to the prone position is accomplished through
272 contraction of the longitudinal dorsal muscle and anteriorly descending muscle, which brings the
273 tergites closer together and raises the anterior margin of the sternite to a horizontal position (Fig.
274 6d).

275

276 **Functional implications of wedge-shaped protopodites**

277 The overall morphological organization of the trilobite protopodite has been elusive because of
278 its non-biomineralized nature and proximity to the midline, with three-dimensional structure
279 being especially difficult to reconstruct because of a lack of suitable trilobite fossils that clearly
280 show this structure (Whittington, 1975; Zeng et al., 2017; Holmes et al., 2020; Bicknell et al.,
281 2021; Hou et al., 2021; Siveter et al., 2021). This has left a gap in our understanding of
282 locomotion, enrollment, and feeding autecology because of the crucial role of the protopodite
283 (Bruton and Haas, 1999; Ortega-Hernández and Brena, 2012; Bicknell et al., 2018, 2021).
284 Appendages are most frequently preserved in highly compressed anterior or posterior views such
285 as *Olenoides serratus* from the Burgess Shale (Whittington, 1975; Hou et al., 2021), *Redlichia*
286 *rex* (Holmes et al., 2020) from Emu Bay, or *Hongshiyanaspis yiliangensis* (Zeng et al., 2017).
287 The lack of detailed information regarding the cross section of the trilobite protopodite has
288 resulted a variety of hypothetical morphological interpretations. For instance, the cross section
289 the trilobite protopodite has been reconstructed as having disparate shapes, including oval (e.g.
290 Whittington, 1975; Whittington and Almond, 1987; Bruton and Haas, 1999; Ortega-Hernández
291 and Brena, 2012; Bicknell et al., 2021; Schmidt et al., 2021), square (Hou et al., 2021), or this
292 aspect has been omitted them altogether because of the lack of available data (Whittington,
293 1993).

294 Wedge-shaped protopodites may be common across Trilobita and even more broadly
295 within euarthropods. Specimens of *Isotelus* (DeKay, 1824) are preserved with ventral views of
296 three-dimensional protopodites (Mickleborough, 1883; Raymond, 1920) which appear as thin
297 transverse to anterolateral bars, a similar condition to that seen in *Triarthrus eatoni* (Hall, 1838)
298 (Whittington and Almond, 1987). Wedge-shaped protopodites can explain this view, as the

299 *Isotelus* specimens show a coronal cross section similar to *Flexicalymene senaria*
300 MCZ:IP:110918 (Fig. 4C). The thin and elongate appears of protopodites in *Isotelus* and *T.*
301 *eatoni* is the result of the coronal view through the ventral edge or middle of the structure
302 resulting in a superficially noodle like appearance. The Silurian trilobite *Dalmanites* sp. from the
303 Herefordshire Biota is preserved as three-dimensional calcite casts visualized through serial
304 sectioning (Siveter et al., 2021) similar to the preservation seen in the Walcott-Rust fossils
305 (Losso et al., 2023). This allows segmentation of individual appendages which display wedge-
306 shaped protopodites resembling those of *Flexicalymene senaria* and *Ceraurus pleurexanthemus*
307 (Fig. 4a-d). Wedge-shaped protopodites are also found in other trilobitomorpha, such as
308 xandarellids based on a specimen preserved as a three-dimensional external mold in displaying a
309 coronal view of the appendages which plunge into the matrix (Ortega-Hernández et al., 2017).
310 The protopodites appear elongate and slender, similar to *Isotelus* and *T. eatoni* discussed above.
311 Given the similar orientation to those specimens, the wedge-shaped protopodite morphology can
312 also account for this specimen with only a 2D view of the structures being visible from the
313 surface. An exception to this appears to be *Agnostus pisiformis* (Linnaeus, 1747) which has an
314 oval coronal cross section (Müller and Walossek, 1987), but determining protopodite cross
315 section from the published literature is difficult because the required views are rarely illustrated
316 for extant species and rarely preserved in fossil specimens.

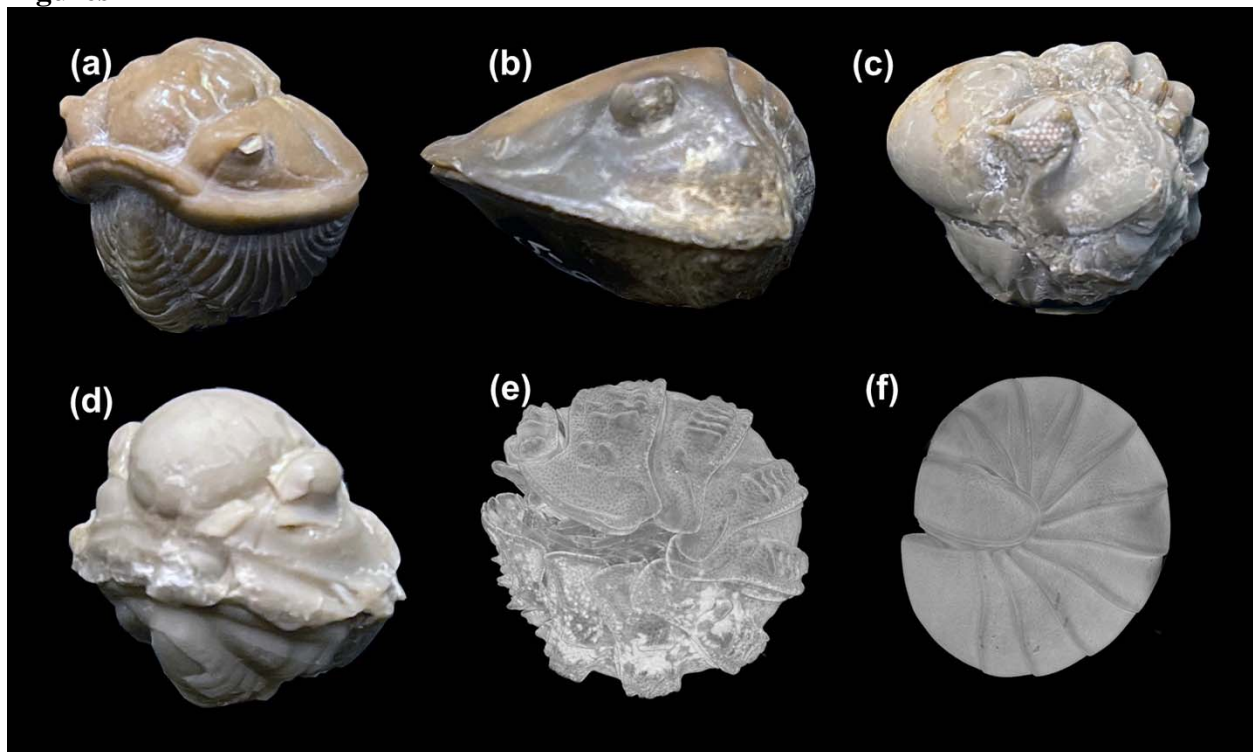
317 The widely reproduced oval cross section for the protopodite (Whittington, 1975;
318 Whittington and Almond, 1987; Bruton and Haas, 1999; Ortega-Hernández and Brena, 2012;
319 Bicknell et al., 2021; Schmidt et al., 2022) would severely hamper the ability of trilobites enroll
320 effectively. The oval protopodite would make it impossible for trilobites to achieve complete
321 enrollment under the normal observed range of motion of the tergites (Fig. 6E), or alternatively,

322 would require the dorsal side of the body to overextend significantly, leaving open gaps between
323 the articulating tergites and exposing the delicate arthroal membrane to predators (Fig. 6F). In
324 this context, the distinctively wedge-shaped protopodites of *Flexicalymene senaria* and *Ceraurus*
325 *pleurexanthemus* (Fig. 3A – D) would play a critical role during enrollment by facilitating a tight
326 body flexure, but without causing dorsal over extension thanks to their narrow ventral margin
327 and form-fitting shape relative to each other (Fig. 6G). Comparisons with the three-dimensional
328 appendage morphology of glomerid millipedes and terrestrial isopods indicate that these extant
329 taxa do not have a wedge-shaped protopodite but differ from trilobites in having medially-
330 (Supplemental Figs. 1, 2a – c) or laterally- (Supplemental Fig. 2d – f) attached appendages as
331 opposed to intermediate condition as in trilobites (Fig. 4a) and other extinct trilobitomorphs. A
332 critical difference between these extant taxa and trilobites, however, is the fact that the former do
333 not utilize the trunk appendages for food processing, but instead employ the modified mandibles
334 as mouthparts (Köihler and Alberti, 1990), whereas the entire limb series of trilobites has an
335 active role in feeding based on the presence of well-developed gnathobasic spines along the food
336 groove (Hegna, 2009; Bicknell et al., 2021). By contrast, the three-dimensional morphology of
337 the trilobite protopodite is more similar to that of *Limulus polyphemus* both in terms of its
338 transverse and dorsal sections (Fig. 3E-H; Fig. 4F, G), which does engage in aquatic gnathobasic
339 feeding with the entire prosomal limb series (Bicknell et al., 2018, 2021). Based on these
340 comparisons, we propose that the wedge shape of the trilobite protopodite reflects a unique
341 functional tradeoff between the physical constraints required for tightly accommodating the
342 appendages during complete enrollment (Fig. 6G), coupled with their pivotal role in food
343 processing during gnathobasic feeding through the ventral groove of the body.

344 The ability of trilobites to enroll for protection represents an iconic adaptation that
345 heavily influenced the long and successful evolutionary history of these extinct euarthropods.
346 Our new data from the Walcott-Rust Quarry reveal for the first time that, in addition to the
347 coaptative devices on the dorsal calcitic exoskeleton, trilobites also featured ventral
348 morphological adaptations of the non-biomineralized sternites and biramous appendages that
349 played a critical and multifaceted role in their mode of life. We find direct evidence that the
350 fundamental mechanism of sternite corrugation that facilitate complete enrolment in trilobites is
351 also expressed in extant glomerid millipedes and terrestrial isopods, showing a striking case of
352 convergent evolution in phylogenetically distant euarthropod clades separated by hundreds of
353 millions of years.

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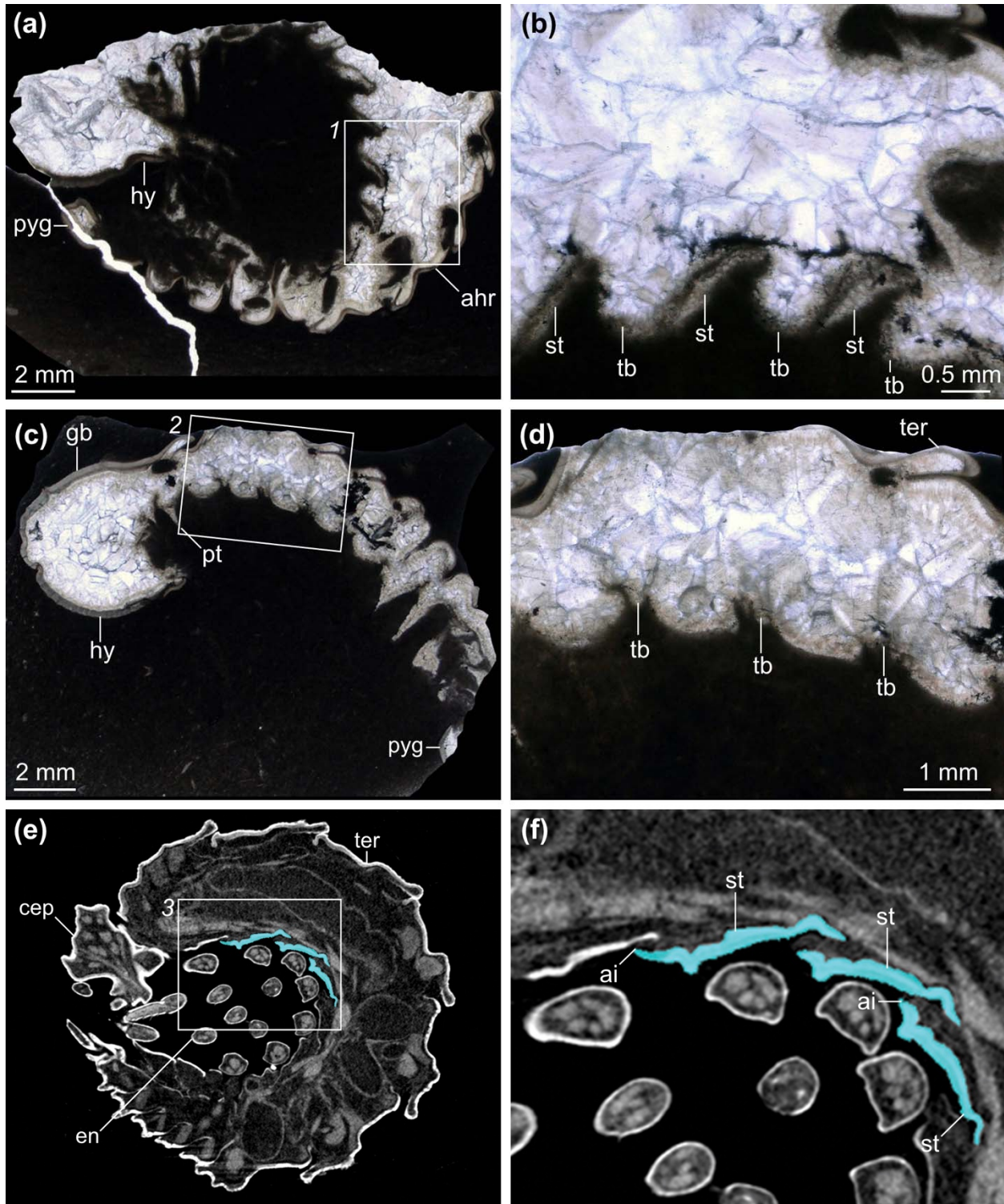
355 **Figures**



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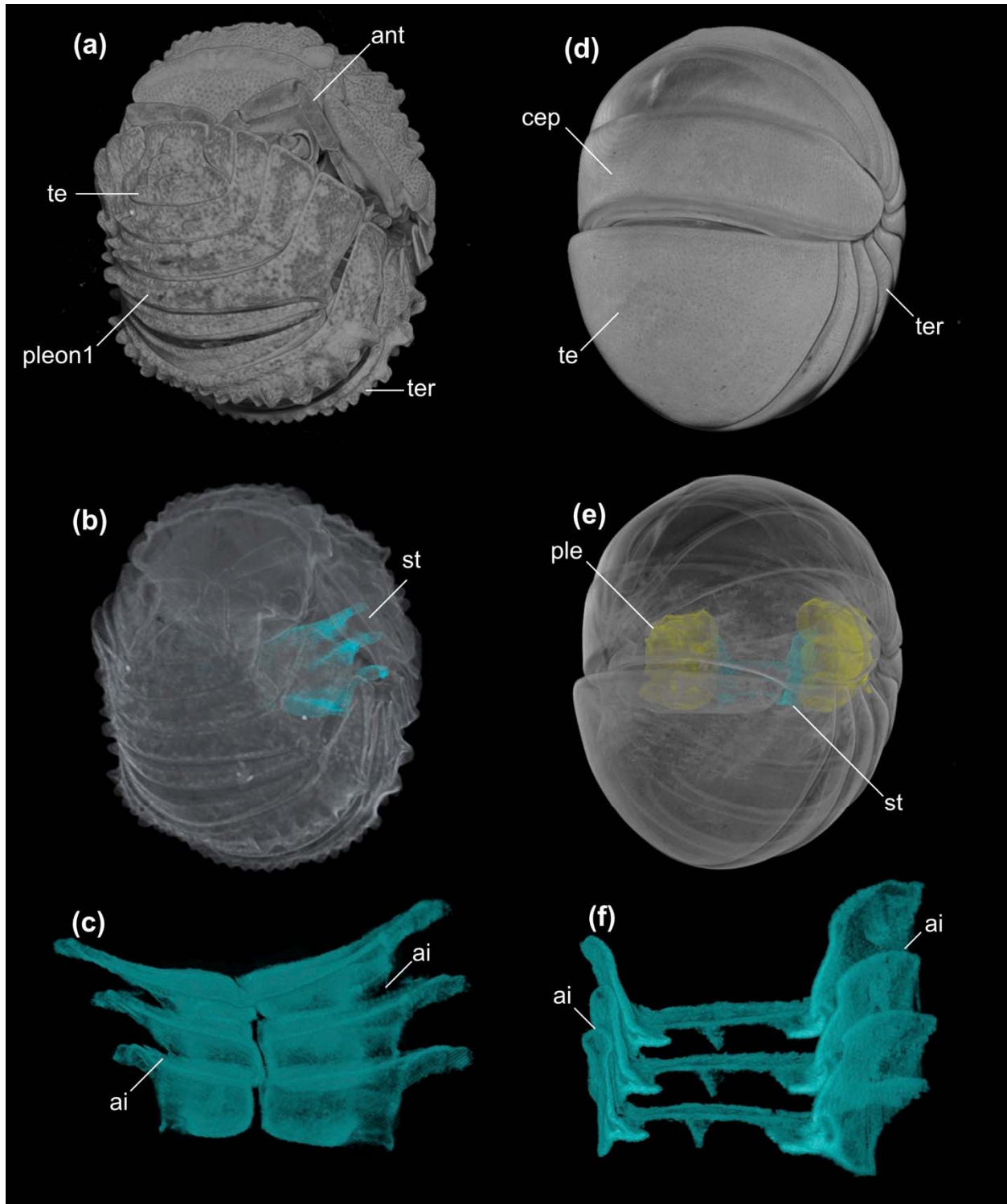
357 **Figure 1. Protective enrollment in trilobites and extant euarthropods.** (a) *Calymene fayettens*
358 (MCZ:IP:5112). (b) *Isotelus maximus* (MCZ:IP:58). (c) *Phacops foecundus* (MCZ:IP:201074).

359 (d) *Proetus bohemicus* (MCZ:IP:5264). (e) Terrestrial isopod (MCZ:IZ:90105). (f) Glomerid
360 millipede (MCZ:IZ:165554).
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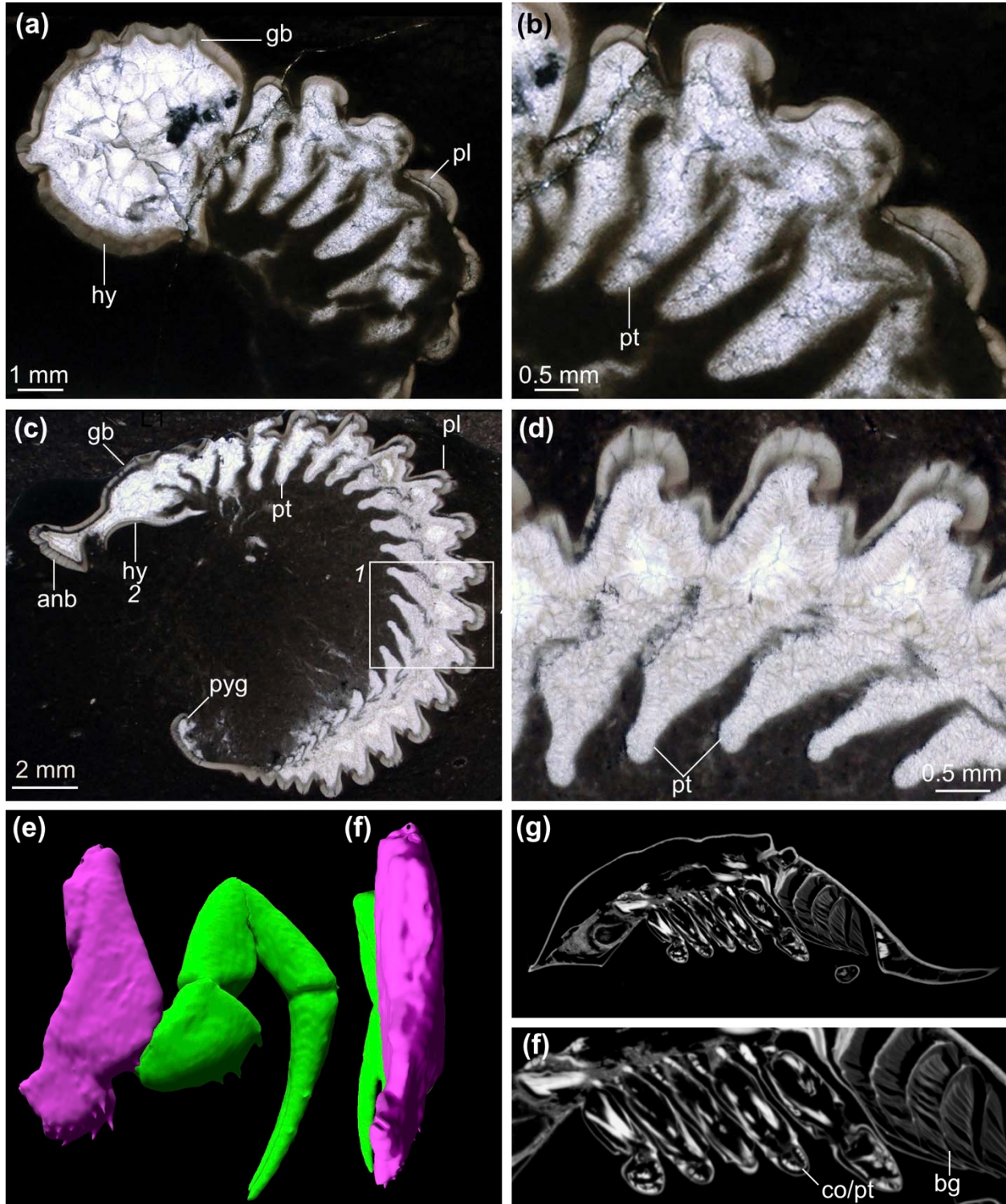
362
363 **Figure 2. Comparison of sternites and tenuous bars in *Ceraurus pleurexanthemus* and**
364 **terrestrial isopod in lateral exsagittal section. (a) Photomicrograph of MCZ:IP:158251, a**
365 **sagittal thin section of a nearly completely enrolled specimen with preserved sternites and**

366 tendinous bars. (b) Photomicrograph of MCZ:IP:158251 showing magnification of sternites box
367 1 of (a). (c) Photomicrograph of MCZ:IP:158227, a sagittal thin section showing tendinous bars
368 in partial enrollment. (d) Photomicrograph of MCZ:IP:158227 showing magnification of
369 tendinous bars box 2 of (c). (e) Tomographic slice of isopod MCZ:IZ:90105 showing corrugation
370 of sternites (blue highlight). (f) Magnification of sternites (MCZ:IP:90105). Abbreviations: ahr,
371 articulating half ring; cep, cephalon; en, endopodite; gb, glabella; hy, hypostome; pyg, pygidium;
372 st, sternite; tb, tenuous bar.
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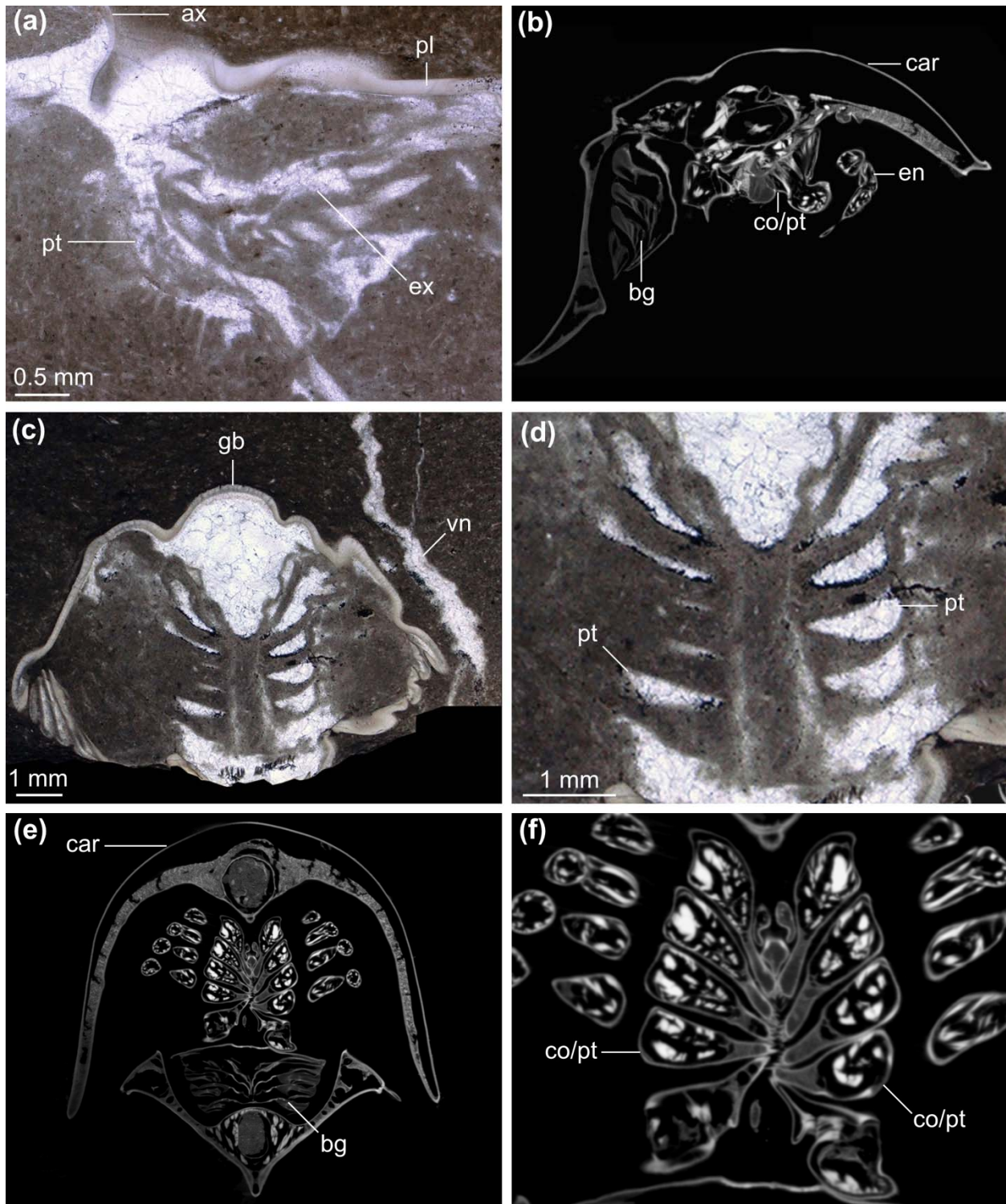
374
375 **Figure 3. Sternite organization during enrolment in terrestrial isopods and glomerid**
376 **millipedes.** (a – d) Micro-CT scan of terrestrial isopod MCZ:IZ:90105. (a) Reconstruction of
377 90% enrolled specimen. (b) Micro-CT of full specimen with three segmented sternites (blue
378 highlight). (c) Micro-CT segmented sternites from three segments. (d – f) Micro-CT scan of
379 glomerid millipede MCZ:IZ: 165554. (d) Reconstruction of completely enrolled specimen. (e)
380 Reconstruction of full specimen with three segmented sternites (blue highlight) and pleurites

381 (yellow highlight). (f) Micro-CT segmented sternites from three segments. Abbreviations: ai,
382 anterior imbrication; ant, antenna; cep, cephalon; ple, pleurite; st, sternites; te, telson; ter, tergite.
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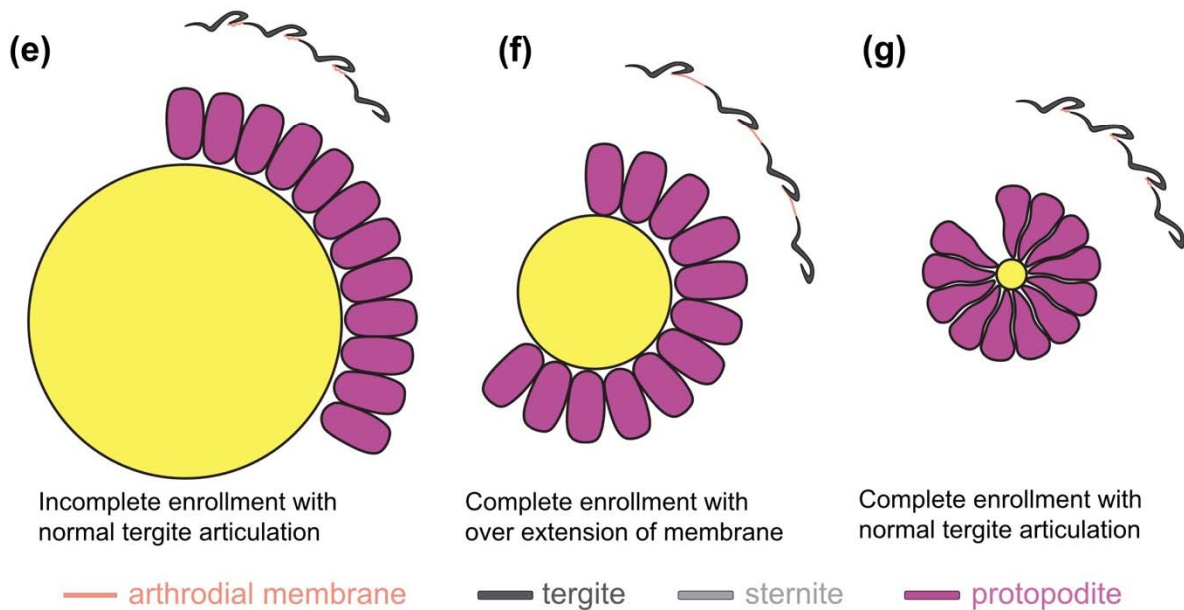
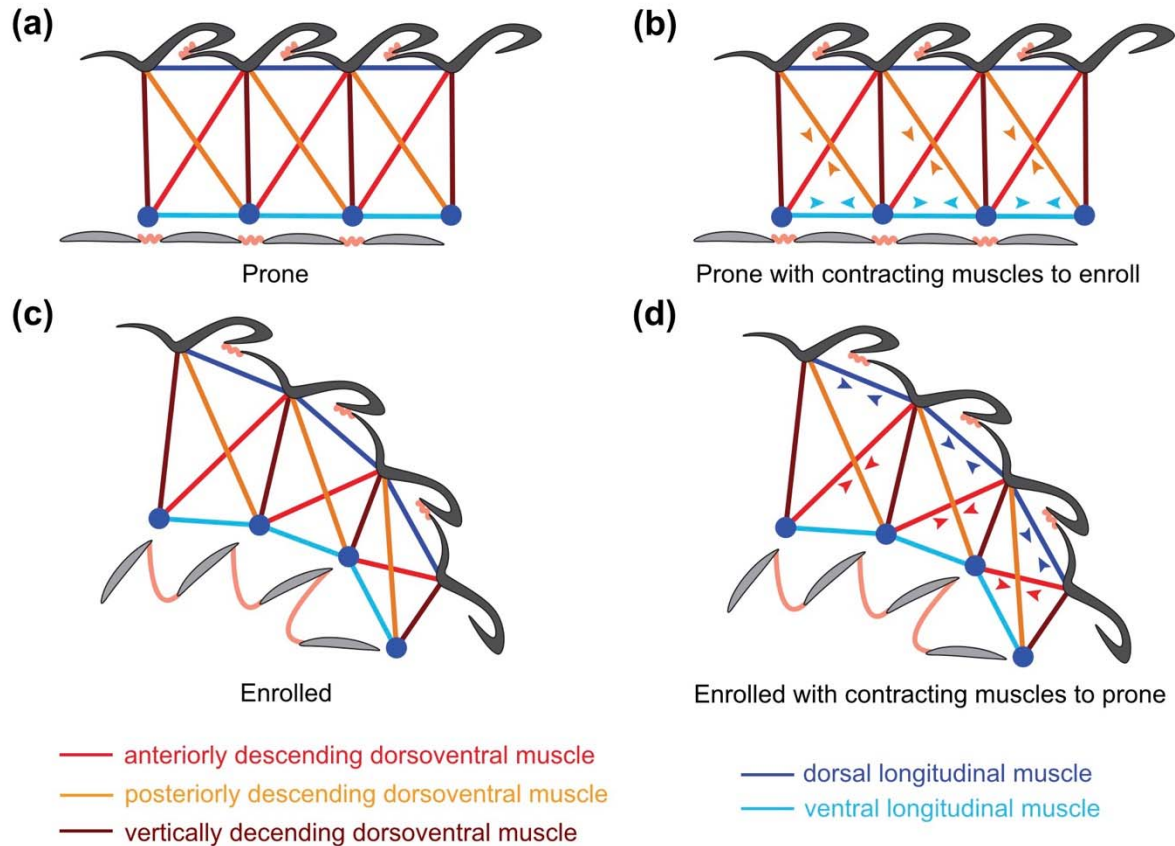
384
385 **Figure 4. Comparison of coxa/protopodite morphology in Walcott Rust trilobites and**
386 ***Limulus polyphemus* in lateral section.** (a) Photomicrograph of *Ceraurus pleurexanthemus*, an
387 exsagittal thin section of showing protopodites in cross section from a lateral view

388 (MCZ:IP:158240). (b) Magnification of protopodites. (c) Photomicrograph of *Flexycalymene*
389 *senaria*, a transverse thin section of showing protopodites in dorsal view (MCZ:IP:110918). (d)
390 Magnification of protopodites in box 1 of (c). (e) Micro-CT segmentation of *Limulus*
391 *polyphemus* (MCZ:IZ: 41112) showing anterior view of walking leg two including
392 coxa/protopodite (purple highlight) and endopodite (green highlight). (f) Micro-CT segmentation
393 of *Limulus polyphemus* (MCZ:IZ: 41112) showing medial view of walking leg two. (g)
394 Tomographic slice of *Limulus polyphemus* (MCZ:IZ: 41112) in exsagittal view showing lateral
395 section of protopodite. (h) Magnification of coxa/protopodite in lateral section. Abbreviations:
396 anb, anterior band of cranium; co, coxa; gb, glabella; hy, hypostome; pl, pleural lobe; pt,
397 protopodite; pyg, pygidium.
398



399
400 **Figure 5. Comparison of coxa/protopodite morphology in Walcott-Rust trilobites and**
401 ***Limulus polyphemus* in anterior and coronal sections.** (a) Photomicrograph of *Ceraurus*
402 *pleurexanthemus*, a transverse thin section of showing an anterior-posterior view of the
403 protopodite (MCZ:IP:110933). (b) Tomographic slice of *Limulus polyphemus* (MCZ:IZ:41112)
404 showing anterior view of coxa/protopodite. (c) Photomicrograph of *Flexicalymene senaria*, a
405 transverse thin section showing coronal view of four protopodites (MCZ:IP:110918). (d)

406 Magnification of protopodites of MCZ:IP:110918. (e) Tomographic slice of *Limulus polyphemus*
 407 (MCZ:IZ: 41112) showing coronal view of coxae/protopodites. (f), Magnification of coxae of
 408 MCZ:IZ:41112. Abbreviations: ax, axial lobe; car, carapace; co/pt, coxa/protopodite; bg, book
 409 gill; ex, exopodite; gb, glabella; pl, pleural lobe; pt, protopodite; vn, calcite vein.



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412 **Figure 6. Functional morphology of trilobite enrollment.** (a – d), Hypothesized muscle
413 attachment in trilobites with contraction indicated by arrow heads. (a) Prone position. (b) Prone
414 position showing contraction along the VLM and DVP to enroll. (c) Enrolled position with
415 corrugation sternites dipping anteriorly and extended tenuous bars. (d) Enrolled position showing
416 contraction of DLM and DVA to extend the body. (e – g) Diagram showing impact of
417 protopodite morphology on complete and tight enrollment. (e) Oval protopodites restrict
418 complete enrollment under normal tergite extension. (f) Oval protopodites with maximum
419 contraction of the ventral edge cause excessive dorsal extension, exposing the arthrodistal
420 membrane. (g) Wedge-shaped protopodites based on MCZ:IP:104956 facilitate complete and
421 tight enrollment without over extension of dorsal arthrodistal membrane.
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426 USA) for facilitating access to specimens.
427
428

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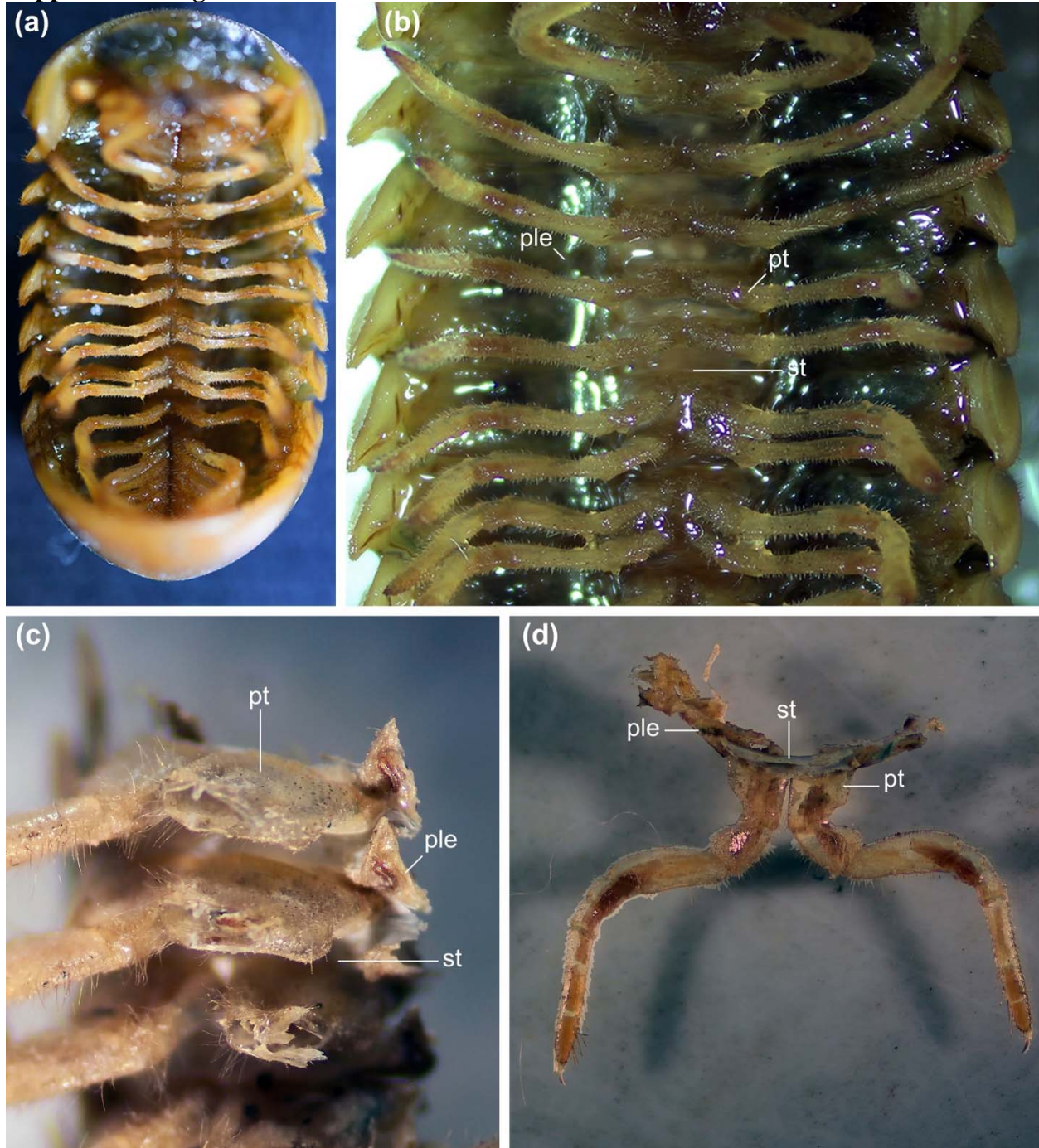
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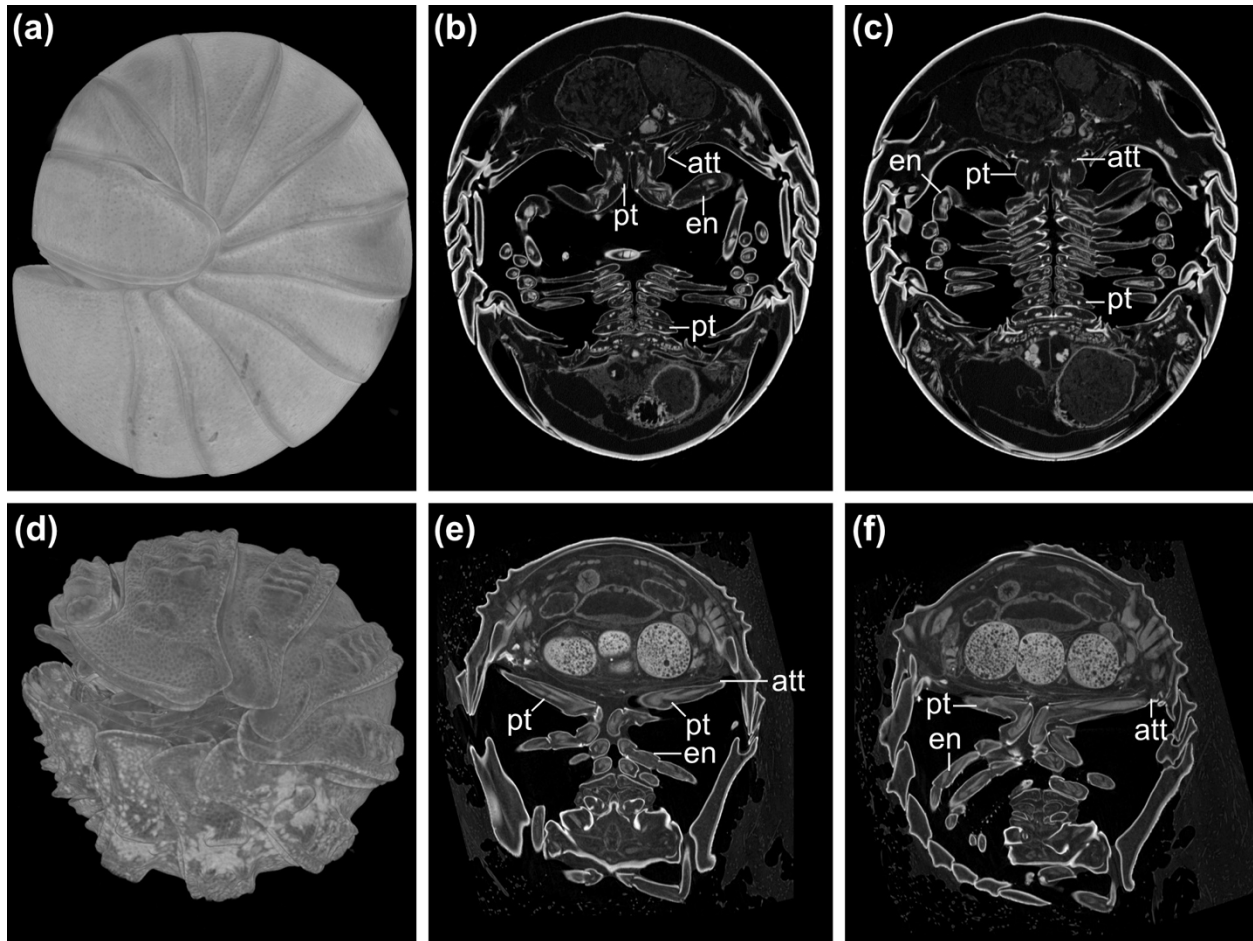
593

594 **Supplemental Figures**



595
596 **Figure 1. Dissection of terrestrial glomerid millipede.** (a) Ventral view of complete specimen
597 showing medial appendage attachment. (b) Ventral view of appendages. (c) Dissection of
598 sternites and appendages with endopodites of right side removed. (d) Anterior view of dissected
599 appendage pair with sternite and medial part of pleurite. Abbreviations: ple, pleurite; pt,
600 protopodite; st, sternite.

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Figure 2. Comparison of appendage attachment of glomerid millipede and terrestrial isopod. (a – c) Micro-CT of fully enrolled glomerid millipede (MCZ:IZ:165554). (a) Three-dimensional volume rendering. (b) Tomographic slice showing medial appendage attachment. (c) Tomographic slice showing appendage orientation during enrollment. (d – f) Micro-CT of fully enrolled terrestrial isopod (MCZ:IZ:90105). (d) Three-dimensional volume rendering. (e) Tomographic slice showing lateral appendage attachment. (f) Tomographic slice showing appendage orientation during enrollment. Abbreviations: att, attachment of appendage to body wall; en, endopodite; pt, protopodite.