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# 1 Interpreting fossilized nervous tissues

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## 22 **Abstract**

23 Paleoneuroanatomy is an emerging subfield of paleontological research with great potential  
24 for the study of evolution. However, the interpretation of fossilized nervous tissues is a  
25 difficult task and presently lacks a rigorous methodology. We critically review here cases  
26 of neural tissue preservation reported in Cambrian arthropods, following a set of  
27 fundamental paleontological criteria for their recognition. These criteria are based on a  
28 variety of taphonomic parameters and account for anatomical complexity. Application of  
29 these criteria shows that firm evidence for fossilized nervous tissues is less abundant and  
30 detailed than previously reported, and we synthesize here evidence that has strong support.  
31 We argue that the vascular system, and in particular its lacunae, is likely central to the  
32 understanding of many of the fossilized peri-intestinal features known across Cambrian  
33 arthropods. In conclusion, our results suggest the need for caution in the interpretation of  
34 evidence for fossilized neural tissue, which will increase the accuracy of evolutionary  
35 scenarios.

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37  
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## 39 **Keywords**

40 Paleoneuroanatomy, Cambrian, Burgess Shale-type, Taphonomy, Arthropoda,  
41 Lagerstätten, Morphoanatomy

42

44 **1. INTRODUCTION: EVIDENCE FOR FOSSILIZED BRAINS IN CAMBRIAN**  
45 **ARTHROPODS**

46 In the past decade, there has been a surge of studies presenting evidence of fossilized  
47 nervous tissues, mainly in fossil arthropods from Cambrian Konservat-Lagerstätten<sup>[1–10]</sup>,  
48 but also, more rarely, from more recent deposits<sup>[11]</sup>. The question of whether such labile  
49 tissues—that is, prone to rapid decay—as ganglia and nerves can be preserved in settings  
50 of BST deposits has been discussed at length before<sup>[12–14]</sup>. The possibility of direct  
51 fossilization of nervous tissues (as opposed to, e.g., skull endocasts<sup>[15]</sup>) rests on three key  
52 observations: (1) the experimental demonstration that nervous tissues in invertebrates can  
53 be persistent to decay, all other conditions being equal<sup>[14]</sup>, (2) the demonstration that the  
54 timing of decay observed under controlled experimentation does not correspond to the  
55 range of preservation seen in fossils<sup>[12]</sup>, particularly in BST deposits<sup>[16]</sup>, and (3) the well-  
56 established presence in these fossils of other labile tissues, such as muscles, digestive tracts,  
57 and even eggs<sup>[17]</sup>.

58         Some paleoneurological evidence has also been criticized on interpretative and  
59 taphonomic grounds<sup>[18–20]</sup>. Criticism has stemmed largely from inconsistency of either the  
60 fossil structure with its expected morphology or with the characteristics of preservation of  
61 compression fossils, or both. Insufficient consideration of such complexities in some  
62 studies has led to the reconstruction of the CNS in numerous Cambrian arthropods, which  
63 when integrated into synthetic reconstructions and evolutionary scenarios<sup>[3]</sup>, must remain  
64 open to question. Despite efforts to disambiguate observable tissues, fundamental aspects  
65 of BST preservation and of the internal morphoanatomy of arthropods have been  
66 overlooked.

67           Considering morphoanatomical features surrounding the gut is crucial because they  
68 are closely associated with neural tissues. Some common and long-known structures, such  
69 as “tonguelets”<sup>[2,21,22]</sup>, defined as sub-intestinal triangular projections, are particularly  
70 important in this context, but have rarely been considered when studying the CNS,  
71 specifically, the ventral nerve cord (VNC) that runs along the trunk. For this reason, it is  
72 important to reassess the peri-intestinal anatomy of Cambrian arthropods<sup>[19]</sup> based on  
73 robust criteria and clear methodology. Although fossilized nervous tissues have been  
74 discussed in a few non-arthropod BST fossils<sup>[23,24]</sup>, here we focus specifically on  
75 morphoanatomy and paleoneuroanatomical evidence in fossil arthropods. Our conclusions  
76 and methodological criteria, however, apply to all preserved nervous tissues.

77

## 78 **2. BURGESS-SHALE TYPE PRESERVATION AND TAPHONOMY**

79 *Implications of the fossilization process.* The leading question in the identification of  
80 fossilized CNS, as for other tissues, should be: What unambiguously constrains the identity  
81 a feature of interest in its specific taphonomic context? Below, we discuss the nature of  
82 BST preservation and caveats related to compression that must be accounted for when  
83 making interpretations. It should also be emphasized that a definitive interpretation is *not*  
84 always possible. In epistemological terms, uncertainty is a positive criterion. To consider  
85 uncertainty as valid information given the data is not trivial: it was historically important  
86 during the redescription of Burgess Shale fossils led by Harry Whittington<sup>[25,26]</sup>, and  
87 different conceptual views in more recent years—translating uncertainty into absence—  
88 have strongly impacted our view of early arthropod evolution<sup>[27]</sup>.

89           The taphonomy of exceptional preservation is governed by specific spatial and  
90 temporal parameters<sup>[28–30]</sup>. The defining characteristic of BST deposits is that soft-bodied  
91 organisms are preserved primarily as organic remains<sup>[31,32]</sup>. Fossils are strongly  
92 compressed parallel to bedding, however preparation and uneven splitting<sup>[e.g., 33]</sup> as well as  
93 tomographic techniques<sup>[e.g., 34]</sup>, where possible, reveal that a slight three dimensional  
94 expression of organic features persists. Over geologic time, organic matter comprising BST  
95 fossils is transformed into kerogen<sup>[32]</sup>. As a consequence, most individual tissues become  
96 indistinguishable compositionally and visually, although, under certain conditions, they  
97 can still be differentiated topologically (see also Supplementary Discussion). In  
98 unweathered BST fossils, original morphoanatomical features rich in carbon typically  
99 appear as reflective, compositionally homogeneous patches (Figs 1-6).

100           Although organic tissues are primarily preserved as carbon films, mineralization  
101 may also play a role, either as infill of anatomical cavities, as primary replacements of soft  
102 tissue during fossilization or as secondary products related to subsequent geologic history,  
103 specifically metamorphism and weathering. These phenomena have led to the precipitation  
104 of aluminosilicate minerals across organic remains of fossils from the Burgess Shale<sup>[31]</sup>  
105 and Sirius Passet<sup>[41]</sup>, and to the deposition of iron oxides within Chengjiang fossils<sup>[80]</sup>. We  
106 discuss these aspects in more detail in Supplementary Discussion, but, in the context of  
107 this study, it is particularly important to emphasize that elements of the arthropod digestive  
108 system, including the intestine, are often preserved as a combination of phases, with carbon  
109 representing the gut wall surrounding a mineralized fluorapatite filling of the intestinal  
110 cavity. Thus, the intestine of a BST fossil visible after a perfect coronal split of the  
111 specimen would display a central phosphatic tract bordered by two parallel carbon lines.

112 Typically, however, the split occurs along the surface of the relief of the gut infill. In  
113 addition, in a majority of cases, the carbonaceous gut wall is not distinct because it is  
114 included in a broader peri-intestinal film. In deposit feeders, the formation of intestinal  
115 apatite is prevented when the gut is filled, yielding instead a composition close to that of  
116 the matrix (see e.g., *Burgessia*<sup>[2]</sup>); heavy weathering, as in the case of early Cambrian BST  
117 deposits of China, is also likely responsible for the replacement of fluorapatite  
118 permineralization by aluminosilicates<sup>[35]</sup>.

119 Tonguelets commonly occur in a variety of BST arthropods and are dominantly  
120 preserved as carbon, although in the Burgess Shale aluminosilicate films occur in  
121 association. In certain groups, such as leaichoiliids, tonguelets co-occur with distinct  
122 midgut glands<sup>[21,35]</sup>. This evidence speaks against a digestive identity of these features. The  
123 vascular morphology of tonguelets in certain taxa<sup>[22]</sup> and their broad association with a  
124 circum-intestinal carbon film<sup>[2,21]</sup> suggest that these features are derived instead from  
125 hemocoelic cavities that played a role in gas and nutrient distribution.

126 It has been proposed that serial peri-intestinal ramifications, including tonguelets,  
127 could be formed as artefacts of bacterial activity during early stages of decay<sup>[36,18]</sup>. Limited  
128 autolysis under reducing conditions would favour colonization of tissues by invading  
129 bacteria and it is possible that microbial biofilms could also be preserved as organic carbon  
130 remains. The documented microbial colonization of the peri-intestinal cavity during early  
131 stages of decay<sup>[36]</sup> highlights the role that bacteria may play in the taphonomy of peri-  
132 intestinal tissues, specifically in the formation of various artefacts such as blackened  
133 cuticular linings and stains (Figs 1, 2). However, patterns of microbial replication require  
134 an original biological substrate, which is why it is important to stress that microbial

135 proliferation cannot be used to explain the entirety of internal features preserved in BST  
136 fossils as artefacts<sup>[18]</sup>. Fossils have been used to show that a wide range of symmetrical  
137 patterns indeed may be attributable to decay<sup>[18]</sup>, but such decay merely tends to transform  
138 original symmetrical biological features into irregular shapes with indistinct boundaries. In  
139 the specific case of *Fuxianhuia*, decay is clearly visible in imperfectly preserved tissues  
140 associated with the circum-digestive area and the masticatory elements of mandibles.

141         One critical implication of these observations for BST fossils is that there is, as of  
142 yet, no established tissue-specific pathway for mineralized preservation outside of the  
143 digestive system and muscles. Tonguelets and perhaps other structures (gills, see below)  
144 can potentially also be identified via their 3D replication in phosphate, but a better  
145 disambiguation is required. The identification of all other tissues, including the CNS,  
146 depends almost exclusively on visual separation, topological (physical) separation and  
147 morphological consistency with the interpreted structure (Figs 1, 2). Given that BST fossils  
148 are strongly compressed, the difficulty lies in demonstrating such isolation, after  
149 considering the presence of all other fossilized morphological features and their  
150 taphonomic variations.

151 *Contextual taphonomy.* Taphonomy is also determined by parameters related to  
152 entombment and splitting. When reconstructing the morphoanatomy of BST animals, the  
153 main contextual aspects that must be considered are: orientation of the fossil relative to  
154 bedding, superimposition of features, artefacts related to compression and/or to the  
155 mudstone matrix (such as slickenides), degree of decay and incomplete preservation of  
156 features, unevenness in the plane of splitting that passes through fossils and may create  
157 positive and negative features between part and counterpart, and the layered, three-

158 dimensional distribution of features intersected by the plane of splitting<sup>[26,37,38]</sup>. In the latter  
159 case, we call three-dimensionality the degree of vertical distribution of fossil features  
160 across the matrix, perpendicular to the plane of splitting.

161         Although there are exceptions, these parameters imply that our ability to constrain  
162 feature identity or morphology ideally necessitates a sample of multiple specimens  
163 covering a range of orientations and taphonomic variations. This is also true for fully three-  
164 dimensional, shelly fossils, which are rarely complete and unaltered. A good understanding  
165 of taphonomic parameters for a particular species, in addition to the context of the entire  
166 deposit, is crucial to constructing a methodology of identification, because it informs signal  
167 versus possible noise (i.e., artefacts) in fossils. As a general rule, the more that fossils are  
168 altered, the more parameters must be considered to constrain the identity of internal  
169 features observed.

170         Obviously, accurate fossil interpretation also requires a coherent understanding of  
171 morphoanatomy between extant and fossil taxa. The distinction and reconstruction of  
172 internal features in BST material is a particularly complex task owing to (1) the  
173 preservation of most tissues as carbonaceous remains, (2) the merging of various tissues  
174 into a single kerogen film, and (3) the complexity and diversity of arthropod internal  
175 morphoanatomy. This is particularly evident in the head and peri-intestinal regions where  
176 the overlap of the eyes, brain tissues, esophagus, gut and gut glands, hemolymph cavities  
177 as well as limbs, segments and other cuticular outlines (Fig. 3A-C) may create an entangled  
178 assemblage of traces that are difficult to discriminate. In the cephalic region of extant  
179 arthropods, the CNS consists of three main units (protocerebrum, deutocerebrum,  
180 tritocerebrum) that have extensions into various sensory organs and head appendages.



181 Posteriorly, the body is innervated by the ventral nerve cord (VNC) and its numerous  
182 extensions (towards trunk organs and abdominal appendages), in close association with  
183 other organs systems, typically the circulatory system. Overlap patterns of these tissues  
184 when compressed, combined with potential decay prior to the stabilization of organic  
185 tissues, can lead to a disparity of shapes that do not accurately reflect the original biological  
186 configuration and could potentially yield incorrect interpretations (Fig. 2).

187 A prominent issue affecting research in systematic paleontology is also that fossil  
188 documentation in the literature is severely biased. Most of the time, only the best specimens  
189 of a given taxon are illustrated, which makes learning to interpret fossils based only on  
190 literature very arduous, if not impossible. Eye training is a long and demanding process  
191 which is critical to direct fossil observation but also to the interpretation of modern imagery  
192 techniques. Without background training providing knowledge of artefact ranges and  
193 taphonomic variations, or when interpretations are not critical enough, exceptional fossils  
194 can easily be overinterpreted.

195 *Three fundamental criteria and redundancy.* In consideration of the above, we propose to  
196 use three fundamental criteria for the identification and interpretation of fossilized nervous  
197 tissues. The first is *topological disambiguation*, the ability to visually distinguish the  
198 structure of interest and constrain it as biological in origin. The second is an *explicit*  
199 *taphonomic context*, whereby the conditions surrounding fossilization, including  
200 compaction, are known and favorable to a positive identification of the structure of interest.  
201 The third is *morphoanatomical consistency*, requiring that the identified feature be  
202 consistent in shape and location with the overall morphoanatomy of the fossil species and  
203 its group. Additionally, owing to the fact that taphonomic variations condition our

204 understanding of fossils, an interpretation will be stronger when there are replicates of the  
205 evidence in other specimens—which we call here *redundancy* of the evidence.

206

### 207 **3. CASE ANALYSES**

#### 208 **3.1. “Gilled lobopodians” and radiodontans**

209 Radiodontans, iconic early Paleozoic predators, are terminologically regarded as the  
210 earliest arthropods<sup>[27]</sup> or as early stem euarthropods<sup>[39]</sup>. Nomenclatural differences  
211 notwithstanding, the phylogenetic placement of radiodontans within Panarthropoda is  
212 consensual<sup>[40]</sup>. Their prominent frontalmost, arthrodized appendages been compared to and  
213 considered homologous with the antennae of onychophorans (velvet worms), which are,  
214 with tardigrades (water bears), the only extant sister groups to arthropods. Owing to the  
215 protocerebral innervation of antennae in onychophorans, some authors have concluded that  
216 the frontalmost appendages of radiodontans may not be homologous with the topologically  
217 equivalent limbs—chelicerae or antennulae—of true arthropods<sup>[39]</sup>, because the  
218 frontalmost appendages arguably connect to the deutocerebrum<sup>[41]</sup>. This hypothesis  
219 conflicts, however, with existing fossil and phylogenetic evidence suggesting structural  
220 homology between the frontalmost appendages of radiodontans and euarthropods<sup>[19]</sup>—  
221 termed the cheirae<sup>[27]</sup>—, and lacks support from direct fossil evidence.

222 In 2012, *Lyrarapax unguispinus*, from the Chengjiang Lagerstätte, China, was  
223 presented as preserving brain tissues demonstrating the protocerebral nature of radiodontan  
224 cheirae. There have been concerns<sup>[19,20]</sup>, however, that the key specimen *Lyrarapax*  
225 *unguispinus* YKLP13305 had been misinterpreted<sup>[9]</sup>. Originally, the authors described a  
226 large central brain mass from which two frontal lobes protruded, purportedly innervating the  
227 cheirae. The neural identification of the tissue is notably supported by the quality of the

228 specimen, isolation of the relevant carbon trace from other remains (mainly gut and  
229 appendages), morphology, and consistent counterpart. The frontal lobes have clear  
230 margins, are likely part of the CNS by exclusion (but see section 4 below) and connect to  
231 the central mass lying on the same plane, supporting interpretation as a brain, and, in the  
232 specific case of the frontal lobes, the protocerebrum (Fig. 4F).

233         However, the location, connection and identity of these features conflict with other  
234 aspects of the morphoanatomy of the fossil, which is particularly clear in YKLP13305. As  
235 confirmed by all other specimens of *Lyrarapax unguispinus*, the eye stalks in this animal  
236 are long, bent, and insert very fronto-laterally<sup>[9,42]</sup> (Fig. 4F). The frontal, arguably  
237 protocerebral lobes overlap the base of the eye stalks (as opposed to the misinterpreted base  
238 of the cheirae) and partially follow their bending. Lateral nerves posterior to these lobes  
239 and projecting from the central brain mass were originally interpreted to innerve the eyes.  
240 However, this is anatomically impossible, because these lateral nerves do not connect with  
241 the eye stalks, but instead project towards the lateral margins of the head, clearly delimited  
242 by cracks in the sediment caused by relief of lateral head margins (Fig. 4F). If indeed they  
243 are nerves, these extensions would be bound to the deutocerebral neuropil, and would  
244 connect to the bases of the cheirae, which in YKLP13305 are most likely located below  
245 them.

246         This reexamination aligns with the recent description of similar structures in  
247 another radiodontan, *Stanleycaris hirpex*<sup>[43]</sup>. This taxon satisfies the best scenario criteria  
248 for the identification of a fossilized brain for similar reasons as *Lyrarapax unguispinus*  
249 does, with the help of multiple, particularly well-preserved specimens. Although it is not  
250 entirely clear whether part of the foregut or esophagus could be associated with the remains

251 described as the CNS, the structures identified as brain, optic tracts and appendicular nerves  
252 form a coherent ensemble characterized by dense kerogen remains. Importantly,  
253 *Stanleycaris* also offers exceptional redundancy of evidence compared to other cases of  
254 fossilized CNS: many of the specimens taken alone would be insufficient to determine the  
255 morphology of these internal organs, and the wide range of variations in preservation  
256 illustrates the impact of taphonomy on the interpretation of such features.

257         A crucial aspect of taphonomy in this case is three-dimensionality, in the context  
258 of strong compression. In *Lyrarapax* and other paleoneuroanatomical examples (see  
259 below), anatomical interpretations are made almost always based on the information visible  
260 on the plane of splitting. Irrespective of whether the fossil itself retains some three-  
261 dimensional relief, original three-dimensionality strongly affects fossil structure—and, in  
262 mature living arthropods, brains have generally pronounced three-dimensional  
263 expression<sup>[44]</sup>. When strictly comparing with extant arthropods, a frontal, appendicular  
264 nerve inserted on the ventral side of the brain would identify it as deutocerebral, rather than  
265 protocerebral<sup>[43]</sup>; any other, plesiomorphic configuration would otherwise have to be  
266 justified. This is why a robust consideration of original three-dimensionality is generally  
267 critical to the accurate interpretation of head organs and resolving this type of detail is only  
268 possible with the highest fidelity of preservation, allowing for clear feature isolation.

269         The “gilled lobopodian” *Kerygmachela kierkegaardi* from the early Cambrian  
270 Sirius Passet Lagerstätte of Greenland was described with head and CNS entombed parallel  
271 to the sediment and showing, by contrast, limited relief. The “gilled radiodontans” are stem  
272 arthropods that lack arthrodization and resolve more basally than radiodontans, implying  
273 that their brain configuration might be both different and simpler. *Kerygmachela* MGUH

274 32049<sup>[10]</sup> (Fig. 5C, D) likewise presents a strong case for nervous tissue preservation: the  
275 size and shape of the anterior neuropil and its nerves are consistent with that of  
276 panarthropods in dorsal view and, importantly, are visually and compositionally distinct  
277 from the underlying pharynx, which shows relief and preservation in phosphate. In this  
278 instance, frontal appendages are spread out fronto-laterally and do not cause ambiguity  
279 with respect to the nerve extensions through them. Problematically, however, insertions of  
280 these nerves at the front of the putative brain can be interpreted as protocerebral, conflicting  
281 with the radiodontan evidence discussed above, because these enlarged frontal appendages  
282 are likely homologous between these groups. Implications are discussed further in section  
283 5.

284

### 285 **3.2. Megacheirans**

286 Three-dimensionality and topological consistency are also crucial factors for  
287 interpretations of putative CNS in megacheirans, mostly leanchoiliids. Leanchoiliid  
288 megacheirans are early euarthropods, possibly stem chelicerates<sup>[27]</sup>, characterized by  
289 flagellate and multi-chelate cheirae. It has been well documented that, in megacheirans,  
290 cheirae insert very anteriorly, close to the insertion of the eyes<sup>[19,21,45]</sup>. The eyes of certain  
291 leanchoiliid specimens, preserved in dorso-ventral compression, can appear to be ventral,  
292 but accounting for the much larger sample of specimens preserved in a variety of different  
293 positions, the eyes are more accurately fronto-lateral with the great appendages inserted  
294 almost underneath them<sup>[21,46]</sup>.

295 In several recent anatomical reconstructions based on remains interpreted as  
296 CNS<sup>[3,4,6]</sup>, cheirae are associated with a deutocerebral nerve but are placed in a more

297 posterior location. In these reconstructions, the designated “protocerebrum” lies at the level  
298 of the known frontalmost appendage insertion, while the “deutocerebrum” encompasses  
299 two post-frontal cephalic limbs (Figs 3D, E, 4B, D). The reconstructions are further  
300 complicated by the fact that the purported paleoneuroanatomical evidence itself in  
301 leanchoiliids does not account for critical taphonomic criteria.

302         Lan and colleagues<sup>[3]</sup> recently presented a detailed reconstruction of leanchoiliid  
303 brains based on two specimens of a *Leanchoilia*-like taxon from the middle Cambrian  
304 (Wuliuan stage) Kaili biota, arguing that a separate, asegmental part of the forebrain of  
305 arthropods called the prosocerebrum was expressed in these taxa. Relative to other BST  
306 fossil specimens for which CNS remains have been inferred, both Kaili leanchoiliid  
307 specimens are significantly altered by weathering and/or original decay, affecting  
308 observable features. Significant alteration complicates the interpretation of unconstrained  
309 patterns. The absence of counterparts further complicates the possibility of a strong  
310 interpretation. Suggested nervous tissues are not explicitly discriminated from surrounding  
311 tissues, perhaps because this is not possible given preservation quality, or perhaps because  
312 the distinction is based on morphoanatomical misinterpretation. Critically, the three-  
313 dimensionality, orientation and convex boundaries of purported nerves in GRCP15007 are  
314 consistent in size and shape with underlying basipods (Fig. 3D), opposing mesially, as  
315 previously documented in dorsally-preserved specimens of *Leanchoilia* and similar  
316 arthropods<sup>[47]</sup>. A pair of swellings located just behind the eyes (Fig. 3D) matches with the  
317 expected location of the insertion of cheirae<sup>[21]</sup> (Fig. 3A, B, E-F), often expressed in dorsal  
318 view by folds, markings and outlines associated with the base of the appendages<sup>[48, pl. 13,49,</sup>  
319 fig. 3B]. Impressions of frontal appendage insertions are known in *Leanchoilia*<sup>[47]</sup> and a

320 variety of other BST arthropods<sup>[50]</sup>, and in specimens in which these appendages do not  
321 project anteriorly, they are likely folded under the body<sup>[21]</sup>, thus potentially leaving paired  
322 imprints in the post-buccal area (Fig. 3).

323         The eye tracts illustrated in detail in GRCP 15007 are not visible on the higher-  
324 resolution image in (Fig. 3D, E). A small inter-ocular swelling, in the same specimen,  
325 might correspond to the location of the leanchoiiliid labrum (putative in adults), but may  
326 also represent another feature located at the junction of all optic tracts. Consequently, the  
327 trapezoidal outline situated behind the insertion of the frontalmost appendages in GRCP  
328 15007 (Fig. 3E) appears consistent with the shape of the mouth in these taxa<sup>[51]</sup>. There is a  
329 half-ringed area encompassing the space behind the eyes and overlapping the insertion of  
330 the frontalmost appendages (Figs 3D-F, 4A) that has been documented before<sup>[47]</sup> (plate 1,  
331 fig. 1, 3). The well-defined boundaries of this seemingly internal structure suggest it is also  
332 cuticular, rather than neural, and therefore could represent a large apodeme.

333         Elemental mapping data<sup>[3, fig. 2]</sup> show that the axial area in leanchoiiliid sp. GRCP  
334 15007 and 15009 is comprised of a polymorph of calcium phosphate (most likely  
335 fluorapatite as in other BST fossils) surrounded by carbon, even if large central chunks of  
336 intestinal apatite are missing in GRCP 15009. This is what is expected from the  
337 preservation of the internal aspect of the gut by mineralized infill and of the gut epithelium  
338 as kerogen (Figs 1, 2): the plane of splitting cuts through the gut, in cross-section showing  
339 the interior of the gut tube bound by two parallel lines. GRCP 15009 is severely altered,  
340 and the central lacuna of apatite was most likely created by loss at the time of splitting.  
341 Nodes and tracts preserved in carbon anterior to the remains of the gut tract repeat the serial  
342 pattern of latero-ventral tonguelets. Given these considerations, it appears likely that only

343 the anteriormost section at the level of eye insertion could represent parts of the CNS, but  
344 such an interpretation is speculative (see below).

345 ROMIP 57655 is comparable to GRCP 15007 in its angle of burial and in the  
346 features visible, though it is much more complete and detailed (Fig. 4A). This specimen  
347 likewise displays the eyes without any tract, as well as the underlying half-ringed structure  
348 underneath them, which seems to be internal. ROMIP 57655 also documents more clearly  
349 the complex peri-intestinal and ramifying kerogen film, showing how various remains of  
350 this film overlap in the medial area of GRCP 15007. Peri-intestinal ramifications mostly  
351 represent sub-intestinal tonguelets, but they can appear cut, flared out, filamentous or they  
352 can be fused altogether with the cuticular margins of limbs as a result of differences in the  
353 plane of splitting through specimens and in the extent of partial decay. ROMIP 57655 thus  
354 represents a typical general example of internal, peri-intestinal tissue preservation in BST  
355 fossils, and shows how variations on these patterns could recreate the appearance of a CNS  
356 (Fig. 6). More generally, patterns of folding in compressed cuticle or other carbon-rich  
357 tissues can easily produce structural shapes that are not readily interpretable. In *Actaeus*  
358 *armatus*, for instance, the manipulation of certain brightness and contrast settings can help  
359 isolate elements resembling the brain (Fig. 4G), but the distribution of carbon in the head  
360 of this very well-preserved specimen shows much greater complexity (Fig. 4H), notably  
361 cuticular collapse and folding. Manipulating these light settings can change the visible  
362 amount of carbon (or carbon-coated) film and therefore can reproduce lesser preservation  
363 or a different plane of splitting. Cheirae in this specimen could be easily interpreted as  
364 protocerebral if one were to disregard other fossil structures, or if the specimen was more  
365 poorly preserved.



366 To investigate *Alalcomenaeus* YKLP 11075—another leanchoilid—, Tanaka and  
367 colleagues interestingly combined two X-ray-based techniques: one based on X-ray  
368 fluorescence and used for elemental analysis, here of Fe, the other being tomographic—  
369 MicroCT scanning<sup>[4]</sup>. Comparing different sources of visualization could be a way to help  
370 disambiguate different structures in fossils. However, the authors interpreted overlapping  
371 signals from both techniques as remains of the CNS, without providing a taphonomic  
372 rationale as to why this should be the case. As explained earlier, there is, as of yet, no  
373 established tissue-specific mineralization pathway outside of some phosphate-based cases.  
374 A tomographic investigation sensitive to Fe will provide an incomplete tridimensional map  
375 of both internal and external remains, as is now shown for several Chengjiang taxa<sup>[51,52]</sup>,  
376 whereas elemental mapping of Fe will reveal a partly similar pattern, depending on  
377 differences in sensitivity. Should the CNS be preserved or secondarily coated in part by  
378 Fe-compounds, this approach is insufficient to discriminate it from all other existing  
379 internal and external structures. In addition, original imagery in Tanaka et al.<sup>[4]</sup> shows that  
380 both techniques largely recover 1) incompletely overlapping regions of the same structures,  
381 implying that the overlapping signal from both methods is an incomplete representation of  
382 the same feature, and 2) structures that are clearly separate; for instance, guts and  
383 appendage traces in both cases are confounded with tergo-pleural boundaries, thus ruling  
384 out the isolation of a discrete CNS. The patterns shown for *Alalcomenaeus* YKLP 11075  
385 therefore correspond to an overlap of the digestive system, the peri-intestinal cavity,  
386 appendages, and segment boundaries, with deformation resulting from partial decay and  
387 compaction of soft tissues against the cuticle. The “vertebrae”-like central structure in  
388 particular, resembling sternites, is likely the result of the impression of the gut

389 superimposed upon, and emphasizing segment boundaries. Interestingly, the features  
390 interpreted as neural in *Alalcomenaeus* were considered chelicerate-like in this study, but  
391 were instead presented as consistent with an ancestral brain configuration<sup>[3]</sup>: this  
392 emphasizes the uncertainty of interpretations based on insufficiently clear fossilized  
393 biological patterns.

394         A lack of feature discrimination also impacts interpretations of *Alalcomenaeus*  
395 MCZ IP-197956 and KUMIP 204782<sup>[6]</sup>. MCZ IP-197956 is poorly preserved, but with a  
396 general pattern commonly observed in megacheiran specimens<sup>[47,46,45,21]</sup>, namely a likely  
397 phosphatic gut trace surrounded by an originally carbon-rich peri-intestinal trace with  
398 ventral lobations and inconsistent filamentous remains—not limited to the ventral side and  
399 not consistently projecting into limbs, for instance as in *Surusicaris*<sup>[22]</sup>—which are signs  
400 of loss to decay. In KUMIP 204782, which is also poorly preserved, filamentous traces are  
401 serially repeated, but they are again similar to common linear artefacts in BST arthropods  
402 (Fig. 6E-H), and it is not possible to disambiguate them from tonguelets and cuticular lines,  
403 especially segment boundaries and appendage outlines, or, considering the quality of the  
404 specimen, even possible deformation of tissue margins through decay<sup>[36,18]</sup>. The anterior  
405 part of the head shows the impression of cheirae, and the “hypostome” is misinterpreted as  
406 a displaced part of the foregut (Fig. 4D).

407         Sub-intestinal tonguelets, or taphonomically-separated distal tips of them, were  
408 also annotated as nerves in the basal megacheiran-like *Kylinxia*<sup>[53]</sup>, without argument for  
409 this interpretation.

410

### 411 **3.3. Extant lineages**

412 **3.3.1. Mandibulata**

413 Among other euarthropods, fuxianhuiids have been a central focus of  
414 paleoneuroanatomical studies<sup>[5,8,13]</sup>—a conjunction of specimen availability, evidence and  
415 a long-standing view that these animals represent an ancestral stem euarthropod body  
416 plans<sup>[5,54]</sup>, even though there is evidence that they are in fact mandibulates<sup>[55]</sup>. The two  
417 cases are the description of optic neuropils and brain in *Fuxianhuia* on the one hand, and  
418 that of a VNC in *Chengjiangocaris* on the other.

419         Despite peculiar taphonomic conditions, under which no other soft internal tissue  
420 is preserved, the VNC of *Chengjiangocaris* YKLP 12026 benefits from a clear topological  
421 isolation—the split of the fossil passes through the nerve cord—and yields fine  
422 morphological details. Notwithstanding evolutionary implications for the number of  
423 interganglionic peripheral nerves<sup>[5,55]</sup>, YKLP 12026 satisfies the conditions of topological  
424 disambiguation and explicit taphonomic context described above, with each putative  
425 ganglion corresponding to a somite on the polypodous body (in which tergites correspond  
426 to the dorsal fusion of several segments). Nevertheless, YKLP 12324, preserved in dorsal  
427 aspect, and also interpreted to display a VNC, calls for caution. At cursory inspection, the  
428 chain-like medial structure is similar, but each successive node is in strong relief,  
429 suggesting greater sclerotization, each forms a single unit incompatible with paired ganglia,  
430 and, most importantly, each connects rigorously with the base of each adjoining limb.  
431 Shape and three-dimensionality would therefore be more consistent with a series of  
432 sternites (see, e.g., ref.<sup>[33]</sup>). This would not be exclusive of the presence of a VNC *per se*,  
433 because the carbonaceous trace observed on fossils and radiating filaments could  
434 correspond to the nerve cord overprinted onto the sternites. The morphology of the VNC

435 in YKLP 12026 suggests that taphonomic conditions leading to the preservation of this  
436 feature preserve an aspect close to the original VNC. The recognition that the VNC could  
437 preserve as poorly-defined trace under the best conditions (see also, e.g., ref.<sup>[23]</sup>) can  
438 facilitate disambiguation of the VNC from other structures<sup>[14]</sup>.

439 In *Fuxianhuia* YKLP 15006<sup>[8]</sup> and similar specimens<sup>[13]</sup>, optic neuropils are clearly  
440 laid out within the eye stalks, and are present in similar shapes on the counterpart. Thus,  
441 the evidence is redundant as well<sup>[13]</sup>. However, the post-ocular neural morphology of  
442 *Fuxianhuia* can only be partially disambiguated from the rest of the morphoanatomy,  
443 because the key specimens presented may have other internal tissues or appendages in the  
444 same area that are not distinguishable. For example, in YKLP 15006<sup>[13]</sup>, there is a broad  
445 darkening of the antennules clearly representing more than a single nerve outline, which  
446 points to a more complex taphonomic history and possibly the overlap of different tissues  
447 in the compression fossil.

448 The brain morphoanatomy of *Fuxianhuia* may be better constrained by looking at  
449 another early mandibulate, *Waptia*<sup>[2]</sup> (Fig. 5G). ROMIP 64293 and USNM 138231 show  
450 the same configurations of branching kerogen tracts, which are comparable to those  
451 documented in *Fuxianhuia*, and are of brain-like morphology: an anterior bridge  
452 connecting with optic tracts is also connected by lateral tracts to a posterior transversal  
453 trace, forming a roughly trapezoidal fenestra which, according to the known anatomy of  
454 the head, is located above the mouth. This opening is therefore a strong candidate for the  
455 stomodaeum<sup>[2]</sup>. As in *Fuxianhuia*, multiple overlapping elements indicate that other  
456 tissues—mostly the gut and appendages—are preserved together with the putative neural  
457 tissues, but the latter are distinct, consistent with expected morphoanatomy, and the fidelity

458 of preservation is relatively good, although redundancy proves to be crucial here (ROMIP  
459 64293 is in poor condition and would only be inconclusive on its own). Although we  
460 consider the evidence ambiguous in this specimen, our own tracing of GRCP15009 (Fig.  
461 5H, I) suggests that a comparable very anterior stomodaeum might be present in  
462 leanchoilids, which would also conform to their morphoanatomy, in particular the  
463 insertion of the cheirae.

464 Ma and colleagues revised their interpretation of the morphoanatomy of  
465 *Fuxianhuia*'s brain based on the counterpart of YKLP 15006 and two additional  
466 specimens<sup>[13]</sup>, preferring to consider the central “fenestrum” as a part of the brain that was  
467 taphonomically removed. Based on the configuration in *Waptia*, and the well-defined  
468 anterior margins of the deutocerebrum in YKLP 15006 (labelled “PRO” in ref.<sup>[13]</sup>), the  
469 fenestrum interpretation is well-grounded and the observed non-lacunar pattern YKLP  
470 11357 corresponds in fact to a more ventral layer, below the stomodaeal aperture, where  
471 the brain forms a compact mass. It is also possible that the fenestrum is an artefact caused  
472 by the compression of a thick protocerebrum with any frontalmost organs (see, e.g.,  
473 combined patterns of protocerebrum and naupliar ocellus in *Artemia*<sup>[56]</sup>), and therefore that  
474 the stomodaeum is more posterior, closer to the brain configuration of extant crustaceans,  
475 but this would make the location of the deutocerebrum and the innervation of frontalmost  
476 appendages less plausible.

477 In a way similar to some examples cited above, *Waptia fieldensis* ROMIP 64295  
478 also exhibits a cephalothoracic peri-intestinal tonguelet pattern that could, without context,  
479 be mistaken for a diagnostic chelicerate-like condensed CNS<sup>[57]</sup>, and other specimens (e.g.,  
480 ROMIP 64287<sup>[2]</sup>) show intestinal features that mimic ganglia and nerves (Fig. 5A, B).

481 Additional specimens (such as USNM 114259, see<sup>[2, SEM S17]</sup>) confirm the occasional rosary  
482 aspect of the gut based on location and calcium phosphate infill. This illustrates how a  
483 proper taphonomic sampling is essential to an accurate interpretation.

484

### 485 **3.3.2. Chelicerata**

486 The middle Cambrian euarthropod *Mollisonia*, recently reinterpreted as the earliest bona  
487 fide chelicerate<sup>[1]</sup>, was presented with three pairs of optic neuropils—a surprisingly  
488 “derived” condition suggesting in fact that a complex neuropil arrangement was ancestral  
489 in euarthropods, and that many extant lineages experienced secondary simplifications.  
490 Similar to *Fuxianhuia*, the outline of these neuropils is distinct, and their location makes  
491 an overlap with non-neural tissues unlikely, although the full evidence is provided by only  
492 a single specimen.

493 Two *Mollisonia* specimens were later reexamined in that context, with description  
494 of nervous tissues<sup>[7]</sup>. The interpretations of *Mollisonia* MCZ 1811 and USNM 305093<sup>[7]</sup>  
495 exhibit issues similar to leanchoilid examples discussed before. USNM 305093 is a poorly  
496 preserved specimen with generic patterns of preservation of internal tissues. Only a central  
497 internal tube is visible with reflective ventral ramifications as well as segment boundaries.  
498 This central tube is the gut, surrounded by the typical carbon-rich peri-intestinal cavity  
499 (Fig. 4E), whose impression connects with the generally carbon-rich eyes, and ventral  
500 ramifications. The ventral ramifications correspond to the dorsal margin of the two main  
501 diverging rami of the limbs, as evidenced for instance by ROMIP 65015, showing likely  
502 further decay (Fig. 6G, H), and in other taxa. MCZ 1811 is of better quality, but the  
503 specimen contains only indistinct carbon traces anteriorly and a typical circum-intestinal

504 carbon patch. Features interpreted as a “segmental nerve” and “gut diverticula” are  
505 identified by elemental mapping where C, P and Ca overlap, although neither of these  
506 features can be discriminated or confirmed by the rest of the fossil evidence<sup>[1]</sup>. Consistent  
507 with the antero-posterior configuration, the “gut diverticulum” in dorsal view is a tonguelet  
508 that the authors interpret as nerve in lateral view.

509 Interpretative consistency is also paramount, even when known morphoanatomy is  
510 thoroughly considered, especially in the case of well-studied taxa. For instance, ROMIP  
511 57655 illustrates that the alleged esophageal foramen in *Alalcomenaeus* sp. YKLP 11075<sup>[4]</sup>  
512 (Fig. 4B) can preserve as reflective patch (Fig. 4A), a fenestra (Fig. 4B) or a three-  
513 dimensional gut tract swelling (Fig. 4E). This is incompatible with an interpretation of all  
514 the reflective traces as neural<sup>[3,4]</sup>, in which case the foramen itself would not be reflective  
515 or swollen, but instead is consistent with an hemocoelo-digestive hypothesis. Given the  
516 evidence, this area more likely represents a differentiated foregut, perhaps a stomach.

517

### 518 **3.4. Other panarthropods**

519 Recent claims were made about the discovery and identification of a brain in the  
520 lobopodian *Cardiodictyon*, presented as a tripartite protocerebrum, as well as a VNC<sup>[58]</sup>.  
521 Lobopodians being the paraphyletic sister lineage to arthropods, the presence of a tripartite  
522 protocerebrum in these animals would have important implications for head evolution in  
523 the entire group<sup>[59]</sup>. Here again, however, we find nothing convincing in terms of  
524 taphonomy, morphoanatomical consistency, or disambiguation power. Taphonomically,  
525 the magenta-to-purple Fe-oxide stains on which the argument is based are well known to  
526 be present throughout Chengjiang fossils, with no demonstrated organ affinity (see, e.g.,

527 their fig. S1). They represent Fe-stains derived from oxidation of original pyrite, however,  
528 it is not clear that these stains track the original distribution of pyrite, or that pyrite  
529 originally replicated the structures in question. In the absence of crystal molds or  
530 pseudomorphs that provide evidence for the original distribution of pyrite, as conclusively  
531 demonstrated before<sup>[14,60]</sup>, the colored patches may be entirely secondary in origin, in  
532 which case their morphoanatomical significance would be non-specific—as suggested by  
533 their uneven distribution and overlap with other oxidized parts of the fossil (Supp. Fig. 3).  
534 In general, the distinctly colored phases picked out by chromatic filtering represent the  
535 complex post-Cambrian weathering history of Chengjiang fossils<sup>[61]</sup>. A careful taphonomic  
536 study and model are required to establish the structures as biological in origin.

537 Correlatively, the colored patches isolate neither brain nor nerve cord specifically. We  
538 conducted a similar “chromatic isolation” (consisting in selective isolation of color ranges  
539 from an image) on the main specimen presented with nerve tissues (YKLP11422) as well  
540 as YKLP11418 and YKLP11419 (Supp. Fig. 3). Coloration occurs clearly over the entire  
541 surface of the fossil, and patterns—especially in the head—are influenced by cracks or  
542 fractures in the matrix (Supp. Fig. 3). Density of this particular stain increases over limbs  
543 and in the sclerotic interspace, as well as on the contour of the head. There is neither  
544 tripartite consistency nor clear internal topology that would identify any part of these traces  
545 as a separate CNS. Fig. S5<sup>[58]</sup> in the original publication shows the extent of image  
546 manipulation required, including deletion of all surrounding elements, to produce a vague  
547 tripartite patch of color. A thorough investigation of these fossils is warranted.

548



549 **4. NATURE AND DISPARITY OF LATERO-VENTRAL ‘TONGUELETS,’ AND**  
550 **OTHER POSSIBLE MANIFESTATIONS OF THE LACUNAR CIRCULATORY**  
551 **SYSTEM**

552 As we have shown (Figs 1, 2, 4A-E, 5A, B, H, I, 6), latero-ventral tonguelets are of central  
553 importance in the disambiguation of the CNS in BST arthropods. The term ‘tonguelet’  
554 itself is assigned broadly to all latero-ventral extensions of the peri-intestinal area,  
555 encompassing a variety of shapes and possibly tissular identity. As primary distinctions,  
556 tonguelets occur with well-defined boundaries as single lobes (Figs 5A, B, 6D) or  
557 ramifying structures<sup>[22]</sup>, but also as variations of those types with more diffuse boundaries  
558 (Figs 4A-E, G, H, 5A, 6A, E, G).

559 The ramification of tonguelets into two or three branches is common in BST  
560 arthropods (Figs 4A, C, D, 6E-G). Based on taphonomic processes discussed above and a  
561 possible hemocoelic affinity advocated previously<sup>[2,22,62,63]</sup>, such ramifications arguably  
562 replicate an original subdivision of the cavity when present across somites in well-  
563 preserved specimens. In *Surusicaris*<sup>[22]</sup>, where tonguelets are arguably consistent with an  
564 original biological feature, branching of the carbon film is specifically associated with the  
565 exopods. In *Opabinia*, tonguelets often connect with the base of gill blades, and they are  
566 also particularly well-developed inside the shaft of respiratory appendages of *Waptia* (Fig.  
567 5A, B). This evidence points to a relationship of these tonguelets with a respiratory and  
568 more generally gas and nutrient-exchange function<sup>[2,21]</sup>. In the context of the peri-intestinal  
569 hemocoel model, tonguelets would therefore specifically represent cavities connecting  
570 permeable organs with the main hemolymphatic system—the ventral hemolymph  
571 reservoirs of the circulatory lacunar system (Supp. Fig. 1).

572 In *Alalcomenaeus* sp. ROMIP 62968 from the Marble Canyon locality (Fig. 6B-D),  
573 typical tonguelets expand into the proximalmost bundle of short lamellae. This  
574 configuration is consistent with recent tomographic information from Chengjiang fossils  
575 demonstrating the presence of proximal lamellate features in arachnomorphs<sup>[52]</sup>. This  
576 additional evidence further suggests that latero-ventral tonguelets are hemocoelic  
577 connections between the peri-intestinal cavity and respiratory appendages, and,  
578 occasionally, the gills themselves. The exact correspondence between the circulatory  
579 system and tonguelets is beyond the scope of this study but is currently under investigation  
580 by the authors.

581 In any case, the similarity in topology and morphology with the ventral lacunar  
582 system<sup>[64]</sup>, as well as the body of evidence showing that ramifications are tightly associated  
583 with gills and other gas exchange areas, constrains the identity of sub-intestinal tonguelets  
584 as hemocoelic cavities. Not only does this have clear consequences for the interpretation  
585 of all comparable tonguelet elements across BST arthropods, but this also calls into  
586 question the accuracy of reconstructed brains. If, as tonguelets currently suggest, the  
587 lacunar circulatory system is preserved, then this system would also potentially preserve in  
588 the cephalic region. In certain cases, such as in horseshoe crabs, the enclosing lacunar  
589 circulatory system can replicate the gross morphology of the brain, while the vascular  
590 system, closely surrounding the prosomal synganglion, is virtually identical in shape<sup>[65]</sup>.  
591 The recently documented syncerebron of *Euproops*<sup>[11]</sup> shows clearly that there was no  
592 original mineralization of nervous tissues, but instead a mold of a central cavity which, in  
593 xiphosurans, is indistinguishable from the cavity of the circulatory system tightly enclosing  
594 the brain<sup>[65]</sup>. However, cephalic lacunar systems are poorly known in general, in part due

595 to technical difficulties in keeping them intact experimentally. Derived pancrustaceans  
596 have shown so far a great complexity of cavities connected to cephalic organs, as well as  
597 eye stalks (Torben Göpel, pers. comm.), which could create patterns interpretable as  
598 neuropils and commissures that do not accurately replicate the CNS.

599         Therefore, the preservation of a cardiovascular system in *Fuxianhuia protensa*  
600 YKLP 11336 would represent preservation of a unique type of tissue among BST fossils.  
601 Similar to our assessments of putative neural remains, it should be noted that the specimen  
602 is poorly preserved, (1) not allowing for clear disambiguation with other tissues, and (2)  
603 increasing the likelihood of deformation via decay. Darkening of the intermandibular area  
604 is quite common<sup>[18,55]</sup>, whereas serial lobate patterns could correspond to outlines of the  
605 limb bases, peculiarly-preserved tonguelets, or a combination of both. Based on the same  
606 validation criteria we put forward for brain tissues (see below), the evidence shown in  
607 YKLP 11336 should be considered incomplete.

608         Broader support for the identification of peri-intestinal traces as hemocoelic  
609 cavities also comes from additional evidence often overlooked in this context. This  
610 evidence is comprised of traces of biological origin contrasting body cavity with cuticular  
611 margins and in particular doublures, and of long traces inside tailpieces or other extended  
612 cuticular features. Interpretations of the thin reflective filament throughout the long telsons  
613 of *Burgessia* or *Molaria* (Fig. 6F) have only been tentative, yet this trace is equivalent in  
614 size, extent and location to the xiphosuran caudal artery<sup>[65]</sup>. This correspondence also led  
615 some authors, almost two decades ago, to interpret the peri-intestinal trace and its long  
616 ramifications into the cephalic spines of *Marrella* as remains of the circulatory system<sup>[62]</sup>.  
617 Distinctly, but complementarily, broad internal patterns single out the extent of the body

618 doublure, for instance in naraoids<sup>[63, fig. 4]</sup>, or the doublure of the tailpiece, as in *Waptia*<sup>[2,</sup>  
 619 fig. 18]

620

621 **5. WHAT DO WE REALLY KNOW ABOUT NERVOUS SYSTEMS IN EARLY**  
 622 **ARTHROPODS?**

623

624

Genus	Specimen	TD	MAC	ETC	R
<i>Alalcomenaeus</i>	MCZ IP-197956	N	N	N	NA
	MCZ IP-197956	N	Y	N	NA
	YKLP 11075	N	N	N	NA
<i>Chengjiangocaris</i>	YKLP 12024, 12026	Y	P	Y	?
<i>Fuxianhuia</i>	YKLP 15006, YKLP 11357, YKLP 11358	P	Y	P	Y (3)
<i>Kerygmachela</i>	MGUH 32048- 57	Y	Y	Y	Y (10)
<i>Kylinxia</i>	NIGP 171304	N	Y	N	NA
Leanchoiliid indet.	GRCP15007	N	P	N	NA
	GRCP15009	N	P	N	NA
<i>Lyrarapax</i>	YKLP13304-6	Y	P	Y	P
<i>Cardiodictyon</i>	YKLP11434	N	N	N	NA
<i>Mollisonia</i>	MCZ 1811	N	P	N	NA
	USNM 305093	N	P	N	NA
	ROMIP 62978	Y	Y	Y	P (3)
<i>Stanleycaris</i>	ROMIP 65674, 65756-59, 65761, 65763, 65777	P	Y	Y	Y (8)
<i>Waptia</i>	USNM 138231, ROMIP 64293	Y	Y	Y	Y (2)
<i>Yawunik</i>	ROMIP 63067	Y	P	P	P

625

626 **Table 1. Assessment of key specimens discussed in this study and used as**  
 627 **paleoneuroanatomical references, based on our methodological criteria.** These criteria

628 are assessed relative to the evidence at hand and the interpretation put forward: in some  
629 cases, they evaluate the entire brain or CNS, in others, only parts of it. Numbers under the  
630 Redundancy column indicate the total number of specimens replicating the relevant  
631 evidence. Abbreviations: ETC, Explicit taphonomic context; MAC, Morphoanatomical  
632 consistency; N, no; NA, non-applicable (whenever one or more criteria are not fulfilled);  
633 P, partial; R, redundancy of evidence (that is, replication in other specimens); TD,  
634 topological disambiguation; Y, yes; See also main text and Fig. 7.

635

636 In light of these reassessments, we used the three criteria explicated earlier in this  
637 specific context (Fig. 7), as well as redundancy of evidence, to evaluate the robustness of  
638 the arthropod paleoneuroanatomical evidence published thus far from Cambrian fossils  
639 (Table 1, Supplementary Discussion). Additionally, the outcome of our revision is  
640 summarized diagrammatically in Fig. 8, using a phylogenetic framework recovered from  
641 recent cladistic analyses<sup>[1,55,66]</sup>.

642 When a more rigorous approach to tissue interpretation is applied and various  
643 extrapolations are subtracted, paleoneurological evidence provides a far less complete  
644 scenario than depicted by a number of recent studies, especially regarding the  
645 arachnomorph CNS<sup>[3,6,7]</sup>. In addition, we present here ideal situations where cephalic  
646 lacunae were not misinterpreted as nervous tissues, but this possibility should be  
647 considered as well.

648 *Stanleycaris* together with a reexamined *Lyrarapax* provide some reliable anterior  
649 CNS morphological evidence in radiodontans (Table 1) that is important both in  
650 documenting brain organization before the rise of euarthropods, and in connecting with the

651 condition of *Kerygmachela*. The simple brain of *Kerygmachela*, bearing similarities with  
652 the dorsal commissure and possibly the frontal nerve ring of tardigrades as seen from dorsal  
653 view<sup>[67]</sup> (but see [72]), contrasts with the antero-posterior differentiation of the putative  
654 radiodontan brains, which appear to have a separate deutocerebrum and well-defined  
655 stomodaeum. This lends support to the view that the pre-radiodontan brain was a  
656 metaneuropil that later subdivided<sup>[27,53]</sup>, as the separate identity of pre-gnathal segments  
657 from posterior ones would suggest<sup>[68]</sup>.

658         By contrast, any brain morphoanatomies remain to be clearly demonstrated in both  
659 leanchoilids and mollisoniids (Table 1), outside of the optic neuropils in *Mollisonia*  
660 *plenovenatrix*<sup>[1]</sup>. *Yawunik kootenayi* ROMIP 63067<sup>[21]</sup> (Fig. 5E, F) distinctly shows all four  
661 eyes with optic tracts connecting to a central rectangular structure at the very front of the  
662 animal, without overlap with the gut, circum-digestive structures or appendages. The  
663 central rectangular element could be part of the protocerebrum, but it is also very similar  
664 to the inter-ocular element in relief in GRCP15007 that we compared topologically with  
665 the labrum (Fig. 3D, E). Hence, at this time, the identity of this feature remains uncertain.

666         Within total-group Mandibulata, optic neuropils and possible brain  
667 morphoanatomies would also benefit from more robust evidence. Apart from the arguable  
668 nerve cord documented in *Chengjiangocaris*, the post-frontal CNS remains elusive, and  
669 additional evidence based on the methodological criteria developed above will be needed  
670 to make firm interpretations.

671         It is also important to reexamine existing interpretations in light of the total  
672 evidence. In *Fuxianhuia* YKLP 11358<sup>[13]</sup>, for instance, the proximal part of the eye  
673 connectives, including the first pair of optic neuropils, appears short and round (without

674 more distal neuropils) because of the angle of splitting, and yields a morphology very  
675 similar to the frontal lobes of *Lyrarapax* (Fig. 4F), which also insert into the base of the  
676 eye stalks. This would therefore support an optic neuropil identity for the radiodontan  
677 ‘frontal lobes,’ with the base and first neuropil possibly lying on a slightly different plane  
678 than the distal neuropils. Based on *Stanleycaris*, it was recently proposed that these lobes  
679 could be related to a large ancestral median eye<sup>[43]</sup>, but the connection between the median  
680 eye and the rest of the protocerebrum in this taxon is not clearly preserved as it is in the  
681 anterior lobes of *Lyrarapax* or the proximal optic neuropils of *Fuxianhuia*.

682         One of the strongest outcomes of arthropod paleoneuroanatomy is therefore that  
683 complex visual systems based on three separate nested optic neuropils either convergently  
684 evolved in mollisoniids and fuxianhuiids, or, more likely, were present at the origin of  
685 Euarthropoda<sup>[1,27]</sup>—and perhaps even Arthropoda<sup>[69]</sup>. Our reinterpretations also suggest  
686 that a deutocerebrum was already present in radiodontans, in line with recent evidence<sup>[43]</sup>.  
687 There is also evidence for a very anterior stomodaeum in early mandibulates, and a more  
688 three-dimensionally shaped brain accommodating a more ventral deutocerebrum, but this  
689 was possibly already the case in radiodontans. The location and shape of the stomodaeum  
690 in leanchoiliids might be similar to what is observed in early mandibulates (Fig. 5H, I), but  
691 this is conjectural. Based on the condition seen in *Kerygmachela*, it appears nonetheless  
692 that the origin of Arthropoda involved a significant structural change cumulating in the  
693 arthrodization of the frontalmost appendages, the sclerotization of the mouth, the  
694 development of compound eyes and, as perhaps would be expected, the physical expansion  
695 of the brain.

696

697 **6. CONCLUSIONS**

698 Although considerable effort and progress have been made to consolidate the scientific  
699 basis of paleoneuroanatomy<sup>[14]</sup>, a careful approach to such evidence, more inclusive of the  
700 diversity of preservation states and taphonomic variations, and subject to specific criteria  
701 of validation, is essential. A critical analysis of the existing evidence in this area and the  
702 contribution of additional material constrains a less detailed but more robust basis for  
703 understanding paleoneuroanatomical evidence in early arthropods. The evolutionary  
704 aspects that we consider here to be well documented are: the structural development of the  
705 brain, possibly associated with an early ventralization of the deutocerebrum at the origin  
706 of Arthropoda, and the likely presence of a complex visual system involving three distinct  
707 optic neuropils occurring with the rise of euarthropods, and perhaps even closer to the  
708 origin of compound eyes itself.

709

710 **Institutional abbreviations.** BST, Burgess Shale-type; CNS, central nervous system;  
711 GRCP, Museum of Guizhou Research Center for Palaeobiology; ROMIP, Royal Ontario  
712 Museum Invertebrate Palaeontology; VNC, ventral nerve cord; YKLP, Yunnan Key  
713 Laboratory for Palaeobiology.

714

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717

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719



720 **Data availability.** All data used in this study are provided upon publication.

721

722 Author contributions. CA designed the study, wrote the first draft of the manuscript and  
723 made the figures; all authors contributed to the critical discussion and to the final version  
724 of the manuscript.

725

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916

917 **Figure captions**

918 **Figure 1.** Explanatory diagrams for peri-intestinal preservation in Burgess-Shale type  
919 arthropods. Top: Transverse cross-sections representing different preservation types and  
920 two different original conditions for the ventral lacunar system (left and right). Bottom:  
921 Coronal sections in dorsal view corresponding to Top diagrams. A. Specimen close to time  
922 of entombment, unflattened, with phosphate-filled gut and distinct internal features,  
923 including heart (he), gut (gt), gut epithelium (ge), ventro-lateral hemocoelic cavities, part  
924 of the lacunar circulatory system (tg for “tonguelets”), ventral nerve cord (vnc) and ventral  
925 vascular system (vvs). Contrary to the vascular network, the lacunar circulatory system is  
926 not bounded by membranes and is shown in dotted lines. On the right side, intra-  
927 appendicular channels (tg) are not well developed; on the left, hemolymph channels branch  
928 out from the main lacunar cavity into endopod and exopod rami, and a third, additional  
929 cavity projects into a separate gill. On the dorsal view (bottom), depending on orientation  
930 and plane of observation, 1, 2 or 3 tonguelets might be visible. In this same view, the ventral

931 nerve cord is here represented by transparency, but not expected to be visible. B. Specimen  
932 with limited deformation and minimal to no decay. Membranes and cavities now uniformly  
933 preserved as kerogen films, mediated by limited microbial activity. Theoretically, in some  
934 conditions, remains of the ventral nerve cord may remain isolated from the peri-intestinal  
935 carbon film (right side), although the evidence for this is debatable in fossils. Phosphate  
936 formation sometimes invades tonguelets (right side, asterisk). C. Specimen with significant  
937 decay and diagenetic alterations. The combination of these alterations produces a variety  
938 of peri-intestinal shapes (right side) that can secondarily mimic genuine branching of the  
939 hemolymph system (left side), or, to an extent, ganglia and nerves.

940

941 **Figure 2. Explanatory diagrams for general preservation in Burgess-Shale type**  
942 **arthropods.** Top: Sagittal sections representing different preservation types of a fictional  
943 *Fortiforceps*-like megacheiran. Bottom: Coronal sections in dorsal view corresponding to  
944 Top diagrams. A. Specimen close to time of entombment, with phosphate-filled gut and  
945 distinct internal features shown as outlines. Nervous tissues in green, apatite in blue,  
946 cuticular and gut boundaries in black, sub-intestinal tonguelets in orange. Phosphate  
947 formation sometimes invades tonguelets. B. Specimen with limited deformation and  
948 minimal to no decay. Membranes and cavities now uniformly preserved as kerogen films,  
949 mediated by limited microbial activity. C. Specimen with significant decay and diagenetic  
950 alterations. Note merging of carbon films from anterior cephalic area posteriad. Disparity  
951 of tonguelet shapes is exaggerated to show range of possible shapes, a number of which is  
952 illustrated in this study: BR, branching type (here, secondary); DI, diffuse type; MCa,  
953 merged cuticular, appendicular type (peri-intestinal trace merged with cuticular outlines at

954 base of limbs); MCt, merged cuticular, tergo-pleural type (peri-intestinal trace merged with  
955 cuticular outlines of tergo-pleurae); SP, split type. Early taphonomic phases are also  
956 commonly associated with a ventralization of the gut tract, not shown here. See Figure 1  
957 for abbreviations; other abbreviations: ey, eye; fa, frontal appendages; mo, mouth; os,  
958 ocular sclerite.

959

960 **Figure 3. Leanchoiliid taphonomy and morphoanatomy.** A-C, Diagrammatic cross-  
961 sections of a generalized leanchoiliid; nervous system in green, eyes in dark blue,  
962 simplified peri-intestinal lacunar vascular system in light blue, digestive system in red,  
963 heart in purple. A, Section at the front of great appendage insertion, showing main brain  
964 mass and optic tracts; shape of protocerebrum follows P-S; dotted line represents possible  
965 protocerebral fenestra, see text for explanations. B, Section at the back of great appendage  
966 insertion, showing looping foregut and mouth opening. C, Section through trunk, with large  
967 ventral hemocoelic system connecting to gills and exopods. D, E, *Leancoilia* sp.  
968 GRCP15007, close-up of cephalic area (see Lan et al.<sup>[3]</sup> fig. 1A, B). Underlying horseshoe  
969 structure as in E in dashed line; circular swellings marking likely frontalmost appendage  
970 insertion in dotted lines. F, *L. superlata* ROMIP 57655, close-up of cephalic area, grayscale  
971 and inverted lightness. Post-ocular semi-circular structure as in D, E. Double arrow indicate  
972 width of branching peri-intestinal carbon pattern. See also Fig. 3A for full specimen.  
973 Picture courtesy of Jean-Bernard Caron. G, H, *Leancoilia* sp. GRCP15009. G, Picture  
974 provided from Supplementary Material in Lan et al.<sup>[3]</sup> H, Tracing of main carbon linings  
975 in G superimposed onto the main feature signal presented in the specimen in Lan et al. fig.  
976 2A. Arrowheads mark in: D, E, pyritised cuticular outlines; sides of the post-ocular

977 structure overlapping frontalmost appendage insertion. Asterisks mark in: D, E, small  
978 swelling of interocular, pre-oral structure, possibly labral; F, G, areas in relief from each  
979 side of the buccal region, possibly related to frontalmost appendages folded under the body.  
980 Colour coding: In A-C, nervous system in green, eyes in dark blue, dorsal artery in purple,  
981 lacunar circulatory system and peri-intestinal hemocoelic cavity in light blue, digestive  
982 system in red; in H, morphological feature lining in red, cuticular folds in red dashed line,  
983 cracks in sediment layer in yellow dashed line, oesophagal/post-oesophagal area in purple.  
984 Abbreviations: ba, basipod; fai, insertion of frontal appendage; fg, foregut; mo, mouth.  
985 Scale bars: 2 mm.

986

987 **Figure 4. Taphonomic variations in the preservation of internal structures among**  
988 **Cambrian arthropods.** A, *L. superlata* ROMIP 57655, photo courtesy of Jean-Bernard  
989 Caron. Full specimen, wet, polarized light. The branching reflective pattern (typically  
990 highly carbonaceous) surrounds the entire digestive tract, including midgut glands and is  
991 not limited to ventral pairs of closely associated swellings, like ganglia. B, C,  
992 *Alalcomenaeus* sp. YKLP 11075. B, Cephalic area from Tanaka et al.<sup>[4]</sup> Extended Data fig.  
993 1, with expected location of appendages based on leaichoiliid literature. C, Elemental and  
994 tomographic imagery methods capture parts of the same peri-intestinal system, which  
995 largely overlap, but do not isolate any structure identifiable with a VNC. D, *Alalcomenaeus*  
996 sp. KUMIP 204782 cephalic area from Ortega-Hernández et al.<sup>[6]</sup> fig. 2a, showing expected  
997 insertion of anterior appendages. Anterior hexagonal piece is a displaced fragment of the  
998 foregut. E, *Alalcomenaeus* sp. MCZ IP-197956 trunk section from Ortega-Hernández et  
999 al.<sup>[6]</sup> fig. 1a. Gut tract likely apatitic with broad peri-intestinal patch and subtriangular

1000 extensions (“tonguelets”). F, *Lyrarapax unguispinus* YKLP13305 anteriormost head  
1001 region from Cong et al.<sup>[9]</sup> fig. 2h. Internal frontal lobes lie on top of the base of the eye  
1002 stalks, and lateral extensions of putative brain are not optical nerve tracts. Double red lines  
1003 indicate connection of the eyes with the eye stalks. G, H, *Actaeus armatus* holotype USNM  
1004 155597. G, Anteriormost portion of the cephalon, wet specimen with cross-polarized  
1005 lighting. Note cuticular collapse in right frontalmost appendage and widespread fold lines.  
1006 H, Same as P with low brightness and enhanced contrast. Arrowheads mark in: A, peri-  
1007 intestinal tonguelet traces with various shapes; E, probable patches of apatite; G, cuticular  
1008 collapse. Asterisks mark in: E, circum-intestinal carbon trace. Abbreviations: *cn*, cephalic  
1009 appendage *n*; *es*, eye stalk; *fai*, insertion of frontal appendage; *fl*, frontal lobe; *gt*, gut tract;  
1010 *le*, lateral eye; *PC*, protocerebrum; *tg*, sub-intestinal tonguelet; *vr*, various remains. Scale  
1011 bars: 2 mm.

1012

1013 **Figure 5. Disambiguation between latero-ventral tonguelets and putative nervous**  
1014 **remains.**

1015 A, B, G, *Waptia fieldensis*. A, ROMIP 64287, latero-oblique view, close-up of  
1016 cephalothoracic area. B, ROMIP 64295, dorsal view, close-up of thoracic area. C, D,  
1017 *Kerygmachela kirkegaardi*, from the lower Cambrian Sirius Passet, frontal area showing  
1018 phosphatized muscular pharynx and distinct nervous tissues. C, MGUH 32048, high-angle  
1019 polarized lighting. D, MGUH 32049, wavelength dispersive X-ray elemental map of  
1020 carbon. E, F, *Yawunik kootenayi* ROMIP 63067. E, Close-up of cephalic area, inverted  
1021 brightness. F, Inset in R. G, USNM 138231, close-up of frontal area, with putative brain  
1022 remains. H, Tracing of main carbon linings in the frontal area of GRCP15009

1023 superimposed onto the main feature signal presented in the specimen in Lan et al. fig. 2A  
1024 <sup>[3]</sup> I, Separate interpretative drawing, showing conjectural neural configuration. Line colour  
1025 coding: In H, morphological feature lining in red, cuticular folds in red dashed line, cracks  
1026 in sediment layer in yellow dashed line, oesophagal/post-oesophagal area in purple; in I,  
1027 digestive tract in blue, gut epithelium in magenta, speculative neural tissues in green, with  
1028 denser carbon masses as disks or ellipses, and tonguelet/lacunar system in orange, cuticular  
1029 folds in grey. Arrowheads mark in: A, filaments projecting from an intestinal swelling; F,  
1030 putative optical nerve tracts; G, H, separate rami of the appendages. Asterisks mark in: G,  
1031 I, stomodaeum or protocerebral foramen. Abbreviations: DC, deutocerebrum; fo, frontal  
1032 organ; gt, gut; le, lateral eye; me, median eye; nv, nerve; PC; ph, pharynx; oe, oesophagus;  
1033 tg, sub-intestinal tonguelet; vs, visual surface. Scale bars: A, B, 1 mm; C, 5 mm; D-H, 2  
1034 mm.

1035

1036 **Figure 6. Circum-digestive preservation and anatomical identity.** A, E, *Alalcomenaeus*  
1037 *cambricus*. A, ROMIP 45613, Close-up of middle section of trunk, showing circum-  
1038 intestinal black pattern with dorsal limb extensions. B-D, *Alalcomenaeus* sp. ROMIP  
1039 62968. B, D, Close-ups of middle section of trunk with parallel (B) and perpendicular (D)  
1040 polarization, showing carbonaceous preservation of proximal gill bundles (white reflective  
1041 areas in D). The gut tract is preserved as apatite (black in D, tridimensional), and additional  
1042 apatitic subintestinal elements may represent distal extensions of the hemocoelic cavities  
1043 invading the exopods. C, Close-up of gill bundle in B. E, ROMIP 45616, photograph with  
1044 inverted brightness, showing web pattern of denser kerogen or kerogen-coated features,  
1045 including eyes, gut outline, possible gill bundles, tergite boundaries, and long, ramified

1046 filamentous elements invading the endopods. Arrows point to diffuse reflective areas inside  
1047 endopods. Asterisk indicates endopod whose reflective lining clearly represents cuticular  
1048 boundaries. F, *Molaria spinifera* USNM 57688, photographed with perpendicular  
1049 polarization, showing patterns similar to E. Here, an outstanding carbonaceous trace also  
1050 runs through the long telson, and ends relatively widely. G, H, *Mollisonia plenovenatrix*  
1051 ROMIP 65015, wet specimen; see Aria and Caron<sup>[1]</sup> for details of the counterpart. G, Cross-  
1052 polarized light, showing broad peri-intestinal reflective area with bifurcating ventral  
1053 tonguelets. H, Direct light. Arrowheads point to in: A, tonguelet extensions on the dorsal  
1054 margin of exopods; B, D, apatitic fragments, likely from distal portions of tonguelets; C,  
1055 finger-shaped gill bundle elements; E, F, various carbonaceous linings, G, H, tonguelet  
1056 bifurcations corresponding to split appendicular lobes. Abbreviations: gt; gut tract; pic,  
1057 peri-intestinal cavity; tg, tonguelet; xpl, primary lobe of exopod; xtl, tertiary lobe of  
1058 exopod. Scale bars: A, G, H, 2.5 mm; B, D, 1 mm; C, 0.25 mm; E, F, 5 mm.

1059

1060 **Figure 7. Synthetic diagram of proposed methodological criteria for fossilized CNS**  
1061 **disambiguation.** Abbreviations: IDed, identified.

1062

1063 **Figure 8. Revised summary of arguable paleoneurological evidence among early**  
1064 **arthropods.** An expanded brain appears to emerge with Arthropoda. A complex visual  
1065 system involving three optic neuropils could be present at least in the common ancestor of  
1066 euarthropods. The identity of the main brain mass in *Kerygmachela* relative to more  
1067 derived taxa is uncertain, as it may correspond to a “metaprotocerebrum”<sup>[70,27,68]</sup>.  
1068 Phylogenetic relationships based on ref.<sup>[55]</sup>, nomenclature based on ref.<sup>[71]</sup>. On brain

1069 configuration diagrams (top): protocerebral structures in light green, deutocerebral  
1070 structures in dark green, stomodaeum in blue and magenta. On fossil diagrams (middle):  
1071 Nervous tissues in green, digestive tract in blue-grey, appendicular outlines in grey, all  
1072 other cuticular outlines in black; numbers represent optic neuropils. Curved arrows denote  
1073 cases where frontal appendage innervation is likely affected by topology and runs beneath  
1074 the rest of the brain, potentially creating compression artefacts. See Supplementary Figure  
1075 2 for enlarged diagrams. Abbreviations: APc, anterior protocerebrum; da, deutocerebral  
1076 appendage; Dc, deutocerebrum; n, optic neuropil; pc, main protocerebral commissure;  
1077 MPc, median protocerebrum; so, sensory organ; st, stomodaeum; T.-G., total-group  
1078 (evolutionary group including extinct and extant representatives of a lineage).

1079

1080 **Supplementary Discussion.** Complementary comments on BST mineralization and  
1081 recommendations regarding interpretations of fossilized putative nervous systems.

1082

1083 **Supplementary Figure 1. Anatomical complexity of organ systems exemplified by**  
1084 **extant crustaceans.** A, B. Histological sections through the anterior part of *Vargula*  
1085 *hilgendorffii* (Crustacea, Ostracoda) showing the circulatory and nervous (peri-oesophageal  
1086 ring) systems in A and part of the hemolymphatic network in B (see sections location in  
1087 C). C. Lateral view of an adult female of *Vargula hilgendorffii*. D. Idealized section  
1088 showing hemolymph circulation (blue arrows). E, F. Lateral view of *Nebalia bipes*  
1089 (Crustacea, Leptostraca) and details of foliaceous thoracopods (carapace removed). G-I,  
1090 *Dahlella caldarensis* (Crustacea, Leptostraca), thoracopods in transmitted light showing  
1091 afferent (red arrows) and efferent (blue arrows) hemolymph canals and sinuses running



1092 through thoracopods. A and B are microtome paraffin sections stained with hematoxylin  
1093 and eosin. F is an SEM image. Extant arthropods have an extensive network of vessels and  
1094 internal hemocoelic cavities filled with hemolymph. Their “open” circulatory system  
1095 consists of the vascular system, made of dorsal heart and arteries (e.g. aorta) that deliver  
1096 hemolymph to various body regions, and of the relatively understudied lacunar system<sup>[64]</sup>.  
1097 The cardiovascular unit pumps hemolymph into the lacunar system that bathes all tissues  
1098 and organs and supplies them with oxygen and nutrients. Oxygen is transported by the  
1099 metalloproteins hemocyanin or hemoglobin circulating in the hemolymph from gas  
1100 exchange areas, such as gills in marine taxa, or from direct aerial openings in terrestrial  
1101 tracheate arthropods, to the heart. The supramillimetric size of most Cambrian arthropods  
1102 implies the presence of a comparable circulatory system without which the distribution of  
1103 oxygen and nutrients to tissues would be impossible. Abbreviations are as follows: ac,  
1104 afferent channel; ao, aorta; ap, appendage; ec, efferent channel; ft, foliaceous thoracopods;  
1105 hc, hemocyte; he, heart; mu, muscle; my, myocardium; nt, neural tissue; oe, oesophagus;  
1106 por, peri-oesophageal ring. Scales bars: A, B, H, 100  $\mu\text{m}$ ; C, E, 1 mm; F, 500  $\mu\text{m}$ ; G, 200  
1107  $\mu\text{m}$ ; H, 100  $\mu\text{m}$ ; I, 50  $\mu\text{m}$ .

1108

1109 **Supplementary Figure 2. Early arthropod diagrams with arguable neural tissue**  
1110 **evidence.** A, *Kerygmachela*. B, Generalized anomalocaridid. C, Leanchoiliid. D,  
1111 *Mollisonia*. E, Waptiid. F, Fuxianhuiid. Nervous tissues in green, digestive tract in blue-  
1112 grey, appendicular outlines in grey, all other cuticular outlines in black; numbers represent  
1113 optic neuropils. Numbers count optic neuropils. Abbreviations: pc, main protocerebral  
1114 commissure; st, stomodaeum.

1115

1116 **Supplementary Figure 3. Anterior region of *Cardiodictyon catenulum* (from**  
1117 **Strausfeld et al.<sup>[58]</sup>).** A-C, YKLP11419. D-F, YKLP11418. G-I, YKLP11434. A, D, G,  
1118 original plain light photographs. B, E, H, same as A, D, G with color desaturation, except  
1119 for the magenta-purple range. C, F, I, isolated magenta-purple coloration from B, E, H on  
1120 black background. Yellow dashed lines represent cracks or major relief over the fossil.  
1121 Other arrows and annotations are from original publication. Note broad variations in  
1122 staining patterns within and among specimens, and how patterns in the head are affected  
1123 by cracks and relief. The “eye” is another crack through the superficial oxidized layer and  
1124 not a clear biological feature. Scale bars in A and G: 0.5mm. Scale bar for YKLP11418  
1125 missing in original publication.

1126