1 **A possible Cambrian stem-group gnathiferan-chaetognath from the Weeks**

2 **Formation (Miaolingian) of Utah**

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4 Simon Conway Morris[1], Ru D. A. Smith[2], Jennifer F. Hoyal Cuthill[1,3], Enrico Bonino[4], and

5 Rudy Lerosey-Aubril[5]

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7 [1]Department of Earth Sciences, University of Cambridge, Downing Street, CB2 3EQ, UK

8 sc113@cam.ac.uk

9 [2]14906 Oak Bend Drive, Houston, TX 77079, USA ru.d.a.smith@gmail.com

10 [3]Institute of Analytics and Data Science and School of Life Sciences, University of Essex,

11 Wivenhoe Park, Colchester CO4 3SQ, UK j.hoyal-cuthill@essex.ac.uk

12 [4]Back to the Past Museum, Carretera Cancún, Puerto Morelos, Quintana Roo 77580, Mexico

13 e_bonino@yahoo.it

14 [5]Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street,

15 Cambridge, MA 02138, USA leroseyaubril@gmail.com

16 *Corresponding author: E-mail: sc113@cam.ac.uk (S.C.M.)

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18 **Running Header:** Possible stem-group gnathiferan-chaetognath

19

20 **Abstract—**In recent years the plethora of "weird wonders", the vernacular for the apparently

21 extinct major bodyplans documented in many of the Cambrian Lagerstätten, has been

22 dramatically trimmed. This is because various taxa have either been assigned to known phyla

23 or at least accommodated in larger monophyletic assemblages. Nevertheless, a number of

24 Cambrian taxa retain their enigmatic status. To this intriguing roster we add *Dakorhachis*

25 *thambus* n. gen. n. sp., from the Miaolingian (Guzhangian) Weeks Formation Konservat-

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26   Lagerstätte of Utah. Specimens consist of an elongate body lacking appendages, but which is

27   apparently segmented. A prominent feeding apparatus consists of a circlet of triangular teeth,

28   while posteriorly there are three distinct skeletal components. *D. thambus* n. sp. is interpreted

29   as an ambush predator and may have been partially infaunal. The wider affinities of this new

30   taxon remain conjectural but it is suggested that it may represent a stem-group member of the

31   Gnathifera, today represented by the gnathostomulids, micrognathozoans, rotifers, and

32   possibly with links also to the chaetognaths.

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34   UUID: http://zoobank.org/22113E6B-F79E-4D06-9483-144618A61327

35

36   **Introduction**

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38   Cambrian Konservat-Lagerstätten ("Lagerstätten" hereafter) provide exceptional insights into

39   early metazoan evolution, not least because of an abundance of lightly sclerotized and soft-

40   bodied taxa. Laurentian examples include the iconic Burgess Shale in British Columbia

41   (Canada), as well as a series of important deposits in Utah (Spence Shale, Wheeler Formation,

42   Marjum Formation; e.g. Muscente et al., 2017; also Fig. 1). In contrast the Weeks Formation

43   (Miaolingian), exposed near Notch Peak, Utah, only more recently has yielded an important

44   Burgess Shale-type fauna (Hesselbo, 1989; Lerosey-Aubril et al., 2013, 2014, 2015, 2018;

45   Lerosey-Aubril, 2015; Ortega-Hernández et al., 2015; Robison et al., 2015). Not only is this

46   latter assemblage important in extending our knowledge of Cambrian life, but its

47   chronological position close to the Miaolingian/Furongian boundary fills a significant gap in

48   the fossil record of non-biomineralizing animals and apparently corresponds to the onset of

49   major biotic changes (Lerosey-Aubril et al., 2018).

50   To the first approximation Burgess Shale-type faunas (e.g. Briggs et al., 1994; Hou et

51   al., 2004) have a well-established identity with a predominance of arthropods (both trilobites,

52   including agnostoids, as well as lightly skeletonized taxa), priapulids (and related

53   scalidophorans), and sponges. Somewhat more occasional there occur such groups as the

54   annelids, vetulicolians, wiwaxiids and other sclerite-bearing taxa. Such faunas remain a focus

55   of attention not only on account of their sheer diversity, but also because a number of hitherto

56   problematic taxa appear to belong to stem-groups that in principle are instrumental in our

57   understanding of the origin of phyla.

58   Not all such taxa, however, can be accommodated in such a fashion and in one way or

59   another a number of them retain their enigmatic status. Broadly these can be divided into

60   three categories, although the boundaries that separate them are by no means absolute. There

61   are those, such as the vetulicolians, that form a relatively diverse clade but whose wider

62   relationships within the deuterostomes continue to be controversial (e.g. Ou et al., 2012;

63   García-Bellido et al., 2014). Then there are such taxa as *Nectocaris* that have deeply

64   polarized opinion, in this case as to whether or not this animal is an early cephalopod (e.g.

65   Kroger et al., 2011; Smith, 2013). Finally there are singletons that for all intents and purposes

66   remain in taxonomic limbo, and it is to this last category we add a remarkable new taxon,

67   *Dakorhachis thambus* n.gen. n.sp. (Fig. 1). These three categories also have the heuristic

68   value of providing a crude metric of relative phylogenetic ignorance, although in each case

69   new fossil finds ultimately will ensure more secure placement within the metazoan tree.

70   Moreover, properly interpreted these enigmatic taxa may help to throw crucial light on key

71   transitions between major groups. At this juncture we are unable to assign *D. thambus* n. sp.

72   with confidence to any known group, but it is evidently a member of the Bilateria. In our

73   opinion this taxon is more likely to fall within the Spiralia (rather than the deuterostomes or

74   ecdysozoans). Below we tentatively suggest that *D. thambus* n. sp. might represent a stem-

75   group gnathiferan.

76

77   **Geological setting**

78

79   The general setting of this Lagerstätte has been reviewed by Lerosey-Aubril et al., (2018). In

80   brief, the Weeks Formation (Miaolingian; Guzhangian) is a relatively deep-water deposit,

81   apart from the upper section (70 m) that records a substantial shallowing of the depositional

82   environment associated with the end of basinal accumulation in the so-called House Range

83   Embayment. Below this transitional interval, lithologies are alternating micrites and

84   calcareous claystones. These are indicative of a low-energy, distal ramp environment, which

85   was periodically disturbed by storm-induced gravity flows and episodes of oxygen depletion.

86   Unlike the Burgess Shale, where much of the biota was introduced into a toxic environment

87   by small turbidity flows (e.g. Conway Morris, 1986), in this Lagerstätte transport was

88   evidently minimal. The exceptional preservation in the Weeks Formation is restricted to a 25-

89   meter-interval about 205 m below the top of the unit. This interval has yielded a diverse

90   fauna (c. 73 species) which according to agnostoids (*Proagnostus gibbus* Zone) and trilobites

91   (*Cedaria* Zone) is of mid-Guzhangian age.

92

93   **Materials and Methods**

94

95   The material consists of nineteen specimens preserved flattened parallel to bedding. One slab

96   (UU.15101.05, 15101.06) bears two specimens, two slabs (UU15101.02, 15101.03, 15101.04

97   and 15101.12, 15101.13, 15104.14) have three specimens each, while another slab

98   (UU15101.07, 15101.08, 15101.09, 15101.10, 15101.11) has five superimposed specimens;

99   other specimens are isolated. This material was examined under a binocular microscope, with

100   a drawing tube employed to prepare camera-lucida interpretative drawings. Specimens

101   UU17122.03, 18056.27, 18056.28 were photographed immersed in dilute ethanol using a

102   Leica IC80 HD camera mounted on a Leica M80 microscope. Specimen UU17122.03 was

103   studied uncoated (low vacuum mode) using a scanning electron microscope (SEM) JEOL

104   JSM-6010LV equipped with an energy-dispersive X-ray spectroscopy (EDS) module JEOL

105   EX-94410T1L11 at the University of New England. Similar SEM and EDS investigations

106   were performed on both entire specimens (UU15101.01, UU15101.07) and polished sections

107   using a QEMSCAN 650F SEM at the University of Cambridge. Lastly, computed

108   tomography (CT) scan of specimen UU15101.01 (holotype) were obtained using a Nikon

109   XTH225 ST CT scanner at the Cambridge Biotomography Centre.

110

111   *Repository and institutional abbreviations.*—Types, figures, and other specimens (including

112   petrographic sections) examined in this study are deposited in the Department of Geology and

113   Geophysics (Research Collections), University of Utah, USA (UU) and Back to the Past

114   Museum, Cancún, Mexico (BPM).

115

116   **Preservation**

117

118   The fossils described here show the same style of preservation as most of the non-

119   biomineralizing taxa of the fauna (Lerosey-Aubril et al., 2018, fig. 3b, c). This is the result of

120   a series of chemical and physical alterations that occurred mostly at a late stage of diagenesis.

121   Such is very much a hall-mark of the Weeks Formation fauna where evidence of diagenetic

122   phosphatization is associated with strong taxonomic and histological controls. Indeed, all

123   known instances of secondarily phosphatization concern organs rich in phosphorus (e.g.

124   arthropod guts) or tissues underneath primary phosphatic structures, such as aglaspidid cuticle

125   or palaeoscolecid plates (Lerosey-Aubril, 2015; Lerosey-Aubril et al., 2012, 2018).

126   In the case of *D. thambus* n. sp. these post-mortem changes include the initial

127   flattening of the carcasses, and much later the replacement of the presumably carbonaceous

128   material with pyrite and subsequent coating of this pyritic layer (now as oxidized

129   pseudomorphs) by chlorite (in a fan-like arrangement) (Fig. 2). This strong diagenetic

130   imprint is related to major igneous intrusions as well as more recent intense weathering.

131   Scanning electron micrographs of specimens of *D. thambus* n. sp. suggest that the trunk is

132   chiefly composed of iron oxides and chlorite (Fig. 2), and this is consistent with

133   compositional (EDS) analyses (Fig. S1).

134   The translucent teeth differ in composition from the trunk, and appear to have a

135   predominantly calcitic composition (Fig. 2.3-2.5). As discussed below whilst an original

136   composition cannot be excluded, it seems as likely that the calcite is also diagenetic. Micro-

137   CT shows moderate 3D preservation of the teeth at the specimen surface (Fig. 5). However,

138   due to the mode of fossil preservation (low density-contrast composition and compression),

139   no further (e.g. internal or subsurface) 3D information was recovered.

140

141   **Systematic paleontology**

142

143   ?Superphylum Spiralia

144   ?Gnathifera-Chaetognatha

145   Family Dakorhachiidae new family

146

147   *Type genus (by monotypy).—Dakorhachis* n. gen. from the Miaolingian (Guzhangian) Weeks

148   Formation of the House Range, Utah, USA.

149

Diagnosis.—Vermiform, segmented body anteriorly bearing prominent ?calcitic teeth.

151

Remarks.—Chaetognatha is currently treated as a distinct phylum, and recent molecular

evidence (Fröbius and Funch, 2017; Marlétaz et al., 2019) links them to the Gnathifera whose

component phyla are Gnathostomulida, Micrognathozoa and Rotifera (with parasitic

Acanthocephala). Phylum status denotes their morphological distinctiveness, but all these

phyla are united by the possession of an anterior basket of chitinous teeth. As discussed

below *D. thambus* n. sp. is tentatively interpreted as a stem-group representative of a

Gnathifera-Chaetognatha clade (we suggest the colloquial moniker chaetognathiferans).

159

Genus *Dakorhachis* new genus

161

Type species (by monotypy).—Dakorhachis thambus n. gen. n. sp.

163

Diagnosis.—As for type species by monotypy.

165

Etymology.—A combination of *dakos* (Greek) a biter and *rachis* (Greek) ridge.

167

Remarks.—A new genus that amongst other taxa from the Cambrian finds no close

counterpart, nor appears to have known equivalents elsewhere.

170

Dakorhachis thambus new species

Figures 3–7, S2

173

174   2018 "Enigmatic organism" Lerosey-Aubril et al., fig. 3a–c

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176   *Holotype.*—Complete specimen (UU15101.01), Department of Geology and Geophysics

177   (Research Collections), University of Utah, Salt Lake City, Utah.

178   *Diagnosis.*—Elongate and robust body. Feeding apparatus comprising at least six hollow

179   teeth, characterized by gently convex outer side with prominent central ridge and concave

180   inner side with narrow ridge-like margins, and in posterior direction associated skeletal

181   elements in form of hook-like elements, inverse v-shaped sclerites, and elongate rods. Trunk

182   composed of 30 segments, gently tapering posteriorly, terminating in blunt tip.

183

184   *Occurrence.*—Exposures in North Canyon, adjacent to Notch Peak, House Range, Utah.

185   Weeks Formation (Cambrian Series 3, Guzhangian).

186

187   *Description.*—Apart from minor preservational variants, the material is united in showing a

188   body consisting of a relatively elongate trunk (Figs. 3, 5, S3) which at its anterior bears a

189   prominent feeding apparatus (Figs. 4, 5.3). Total length can reach 28 mm, and maximum

190   width of trunk 7 mm (Fig. S3). The feeding apparatus bears at least six prominent teeth, of

191   which about half are exposed in outer aspect and the remainder in inner aspect, suggesting

192   that originally they formed a circum-oral circlet (Fig. 4.1,4.3). Each tooth (c. 3 mm long) has

193   a narrow triangular form, and in outer aspect is gently convex and bears a prominent and

194   relatively narrow longitudinal ridge. In inner aspect the tooth is concave, but the margins are

195   defined by very narrow ridges. The teeth have a fibrous texture, while the broken margin of

196   one tooth shows what may be a hollow interior (Fig. 6). Elemental analyses indicate that the

197   teeth to have a predominantly calcitic composition (see above and Dryad file). Posterior to the

198   teeth are three other skeletal components, evidently with a similar composition to the teeth

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199   (Fig. 4.2, 4.4). Immediately to the posterior of the teeth are small hook-like structures, while

200   behind them are a series of inverse V-shaped units. Most likely these units also formed

201   circlets. Finally adjacent to, or superimposed on, the anteriormost trunk are rod-like

202   structures, usually straight but occasionally with a sinuous shape.

203   The trunk is relatively featureless and lacks appendages or other extensions. In some

204   specimens the configuration is somewhat sinuous (Fig. 3.3; see also Lerosey-Aubril et al.,

205   2018, fig. 3a), suggesting an original degree of flexibility (also Fig. 3.7). The width is more

206   or less uniform and although most specimens have a rounded termination, it occasionally

207   appears to be acute. Broad transverse folds (c. 0.8 mm) may be surficial annulations but here

208   are interpreted as segments (Figs. 3, 1., 3.2, 5. 1., 5.2, 7). In life these would have totalled

209   about 30. That these structures are original rather than post-mortem (or tectonic) is supported

210   by three lines of evidence. First, these transverse bands are evidently three-dimensional (Fig.

211   S2) and sometimes match a corrugated body margin. In addition, associated specimens with

212   different orientations have folds transverse to their respective bodies rather than parallel to

213   any rock fabric (Fig. S3).

214

215   *Etymology.—thambos* (Greek). an astonishment.

216

217   *Materials*.—UU15101.02–15101.15, 17122.03, 18056.27, 18056.28; BPM-1090.

218

219   DISCUSSION

220

221   *Paleoecology and mode of life.— D. thambus* n. sp. lacks fins or other anatomical features

222   consistent with a pelagic mode of life and therefore is interpreted as benthic. Co-association

223   of specimens indicates a gregarious habit, although the case of parallel stacking

224 (UU15101.07-15101.11) is most likely post-mortem. Locomotory organs are not evident but

225 presumably this animal could have moved across or within the sea-floor by peristaltic

226 contractions. Given, however, the arrangement of the teeth is in the form of a sort of basket it

227 may have captured its prey as an ambusher and as such the animal may have been semi-

228 sessile and partially concealed in the sea-floor. The attitude of the teeth varies from parallel to

229 an anterior convergence, but in life they presumably opened wider to tackle larger prey. The

230 function of the skeletal elements posterior to the teeth is more conjectural. One suggestion is

231 that they served for insertion of muscles associated with protrusion and subsequent closure of

232 the teeth.

233 *Phylogenetic affinities.*—The wider relationships of *D. thambus* n. sp. are necessarily

234 problematic given its lack of close identity to any known group. Such evidence as there is

235 must look to the feeding apparatus. A potentially important clue might be the calcitic

236 composition of the teeth, although as noted this may well be diagenetic. Certainly amongst

237 metazoans calcitic teeth are unusual, with the most notable instances being in the echinoids

238 (e.g. Wang et al., 1997; Stock et al., 2014) and extinct ophiocistioids (e.g. Reich et al., 2018).

239 Moreover, in the former group they can on occasion show a fibrous microstructure (Reich and

240 Smith, 2009, text-Fig. 9C, D). There is, however, no other feature of *Dakorhachis* n. gen. that

241 would indicate an affinity to either the echinoids or any other echinoderm, especially if the

242 principal teeth totalled six, an obvious departure from the characteristic pentaradial symmetry

243 of this phylum.

244   In passing, it is worth noting that *D. thambus* n. sp. shows some broad similarities in

245 overall shape to the unusual sponge *Takakkawia lineata* from the Burgess Shale, which has

246 marginal "fins" extending from a conical body (Botting, 2012). However, numerous detailed

247 differences in morphology indicate that the resemblance between these taxa is superficial.

248 Specifically, there are differences in the size, shape and annulation of the body in *D. thambus*

249 (which averages 2.1 cm long, is vermiform and has transverse annulations) versus *T. lineata*

250 (which is longer (Botting, 2012, Fig. 1), more vasiform and displays diagnostic lengthwise

251 lineations). Furthermore, there are major differences in the shape and organisation of the

252 teeth of *Dakorhachis* (which are elongate, sharply pointed and restricted to the anterior body

253 margin) versus the "fins" of *T. lineata* (which are wider, flat topped, and accompanied by

254 broad spicules extending down the length of the body). Whilst there is no other reason to

255 interpret *D. thambus* n. sp. as any sort of sponge, the potential complexities of assigning

256 Cambrian taxa to particular groups and the consequent phylogenetic implications are apparent

257 from Botting and Muir's (2018) proposed linkage of *Takakkawia* to the putative ctenophore

258 *Thaumactena*. That said there is no evidence for comparing *D. thambus* n. sp. to any of the

259 Cambrian ctenophores (e.g. Ou et al., 2015).

260 Notwithstanding such comparisons, *D. thambus* n. sp. is evidently a bilaterian rather

261 than a representative of the diploblasts (let alone a sponge). There appears to be no particular

262 similarity to either the deuterostomes or ecdysozoans. Although, in the latter case, it is true

263 that the priapulids and related scalidophorans typically have an introvert equipped with

264 circlets of teeth, these and associated structures show a complex zonation and diversity of

265 forms (e.g. Smith et al., 2015) that find no counterpart in the array of teeth seen in *D. thambus*

266 n. sp. or its ancillary skeletal structures. Most likely *D. thambus* n. sp. is a member of the

267 Spiralia.

268 Amongst the spiralians the most fruitful comparisons may possibly lie with the

269 Gnathifera. This monophyletic group (e.g. Laumer et al., 2015) comprises the

270 gnathostomulids (e.g. Herlyn and Ehlers, 1997; Sørensen et al., 2006), its sister group the

271 micrognathozoans (e.g. Bekkouche and Worsaae, 2016; Bekkouche et al., 2014), and the

272 syndermatans (the group encompassing the rotifers and endoparasitic acanthocephalans; e.g.

273 Rieger and Tyler, 1995; Wulfken and Ahlrichs, 2012). Gnathiferans are millimetric and

274   typically meiofaunal, but despite this all possess intricate jaw apparatuses that reaches an

275   apogee in the complex array found in the micrognathozoans (e.g. Kristensen and Funch, 2000;

276   De Smet, 2002; Sørensen, 2003). Current phylogenetic schemes place the gnathiferans as

277   sister to all other spiralians (e.g. Bekkouche and Worsaae, 2016; Laumer et al., 2015), which

278   in turn are broadly divided into the "platyozoans" and the more securely identified

279   lophotrochozoans.

280   The disparity of extant gnathiferans, combined with an almost non-existent fossil

281   record (e.g., Poinar and Ricci, 1992; Waggoner and Poinar, 1993; Jha et al., 2011), and their

282   still poorly resolved systematic position within the bilaterians, pose a series of evolutionary

283   questions. Amongst the most problematic is the visualization of a stem-group form and its

284   corresponding recognition in the fossil record. This question may be further exacerbated if

285   the millimetric size of the extant gnathiferans is the result of secondary miniaturization from

286   macroscopic predecessors, rather than a primitive state.

287   Intriguingly there is also phylogenomic evidence for a link between the gnathiferans

288   and chaetognaths (Fröbius and Funch, 2017; Marlétaz et al., 2019). The latter are equipped

289   with a formidable feeding apparatus consisting of prominent grasping spines and associated

290   teeth (e.g. Bone et al., 1991), although at first sight there is no obvious macroscopic

291   connection to any of the considerably more complex gnathiferans jaws. The phylogenetic

292   position of the chaetognaths has long been regarded as basal amongst the bilaterians (Perez et

293   al., 2013), but with conflicting views suggesting either a place amongst the most primitive

294   protostomes (e.g. Marlétaz et al., 2006; Marlétaz and Le Parco, 2008; Shen et al., 2016) as

295   against a position amongst the basal lophotrochozoans (e.g. Matus et al., 2007; Dunn et al.,

296   2008; Bernt et al., 2013).

297   The contribution of the Cambrian fossil record to the early evolution of the

298   chaetognaths and gnathiferans to date has almost entirely focused on the former group. Here

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299 the protoconodonts, which apart from occasional fused clusters, are effectively dispersed as

300 small shelly fossils (Szaniawski, 1982, 2002), are complemented by several soft-bodied taxa

301 similar to extant chaetognaths (Chen and Huang, 2002; Hu et al., 2007; Vannier et al., 2007;

302 Shu et al., 2017), and what appear to be two more primitive representatives (*Ankalodus*

303 *sericus* and *Capinator praetermissus*) characterized by supernumerary teeth (Briggs and

304 Caron, 2017) or a multi-jawed morphology (Shu et al., 2017) (Fig. S1). It is now clear,

305 however, that the hitherto enigmatic *Amiskwia* (Conway Morris 1977) possesses a jaw

306 apparatus that supports some sort of connection to the gnathiferans and/or chaetognaths

307 (Vinther and Parry, 2019; Caron and Cheung, 2019).

308   Although the record of relevant soft-bodied taxa (*Amiskwia*, *Ankalodous*, *Capinator*)

309 is meagre, as potential stem-group chaetognathiferans they hint as both morphological

310 disparity and a range of ecologies from swimming to benthic. To this roster we tentatively

311 propose to add *D. thambus* n. sp. As is the case with a number of other controversial

312 Cambrian groups, a convincing phylogenetic analysis is frustrated by the paucity of available

313 character-states and the added possibility that those available for tabulation in reality are

314 convergent. Our assignment relies on a tentative interpretation of the feeding apparatus of *D.*

315 *thambus* n. sp. as a precursor to the much more complex jaws seen in extant gnathiferans as

316 well as the possible equivalent in the chaetognaths. Here, therefore, we sketch a possible set

317 of transitions (Fig. 8) that might link the feeding apparatus of *Dakorhachis* n. gen to those of

318 the gnathiferans and chaetognaths.

319   There is agreement that some of the elements of gnathiferan apparatuses are

320 homologous (e.g., Sørensen, 2002; Sørensen et al., 2006), but nevertheless collectively the

321 clade shows a wide diversity of forms. Interestingly, the more basal gnathostomulids possess

322 a somewhat less elaborate jaw (e.g., Riedl and Rieger, 1972) and within this group there are a

323 number of trends that can be traced from what appears to be the most primitive arrangement

324   (e.g., Sterrer, 1972; Sørensen, 2002). Thus, despite various elaborations, the basic

325   configuration of the jaw is as a forceps-like unit joined to a proximal base and a basal plate.

326   Derivation of this arrangement from something similar to *D. thambus* n. sp. via an amiskwiid

327   (Caron and Cheung, 2019) would, in principle, involve a shift from an effectively radial

328   symmetry to a bilateral configuration, reduction from six teeth to three (along with substantial

329   miniaturization), and possibly incorporation of the more proximal skeletal elements in *D.*

330   *thambus* n. sp. into the jaw apparatus.

331   The likely phylogenetic relationship between chaetognaths and gnathiferans (Fröbius

332   and Funch, 2017; Marlétaz et al., 2019) may also find some support in the morphology

333   exhibited by *D. thambus* n. sp. Whilst there is little obvious similarity between the jaw

334   configurations of the gnathiferans versus chaetognaths, in both cases the principal

335   composition is chitinous (e.g., Bone et al., 1983; Sørensen and Sterrer, 2002). The distinctive

336   rod-like microstructures of most gnathiferan teeth (e.g., Riemann and Ahlrichs, 2008) is

337   presumably a synapomorphy of the group, but in *D. thambus* n. sp. the fibrous microstructure

338   and possible hollow interior find a possible counterpart in the protoconodonts (e.g.

339   Szianiawski, 2002). If there is an evolutionary connection between *D. thambus* n. sp. and the

340   chaetognaths then in parallel to the gnathiferans this would involve a transition between the

341   apparently radial configuration of the teeth in the former taxon to the bilateral arrangement on

342   the chaetognaths. Although very different to the trajectory of the gnathiferans that led

343   towards a meiofaunal existence, this proposed evolutionary path would also be a consequence

344   of a major ecological shift, from a perhaps semi-sessile benthic life style to a more motile

345   pelagic one.

346   It is worth pointing out that whilst the fused clusters of protoconodonts (e.g.,

347   Szaniawski, 1982, 2002) are convincingly compared to the bundles of feeding spines in the

348   chaetognaths, in contrast most protoconodont taxa are never recovered as fused clusters.

349 Whilst this disaggregation may be the consequence of standard processing of samples by acid

350 digestion, it seems equally possible that in such taxa the arrangement of the feeding apparatus

351 was either more open and/or arranged as a multiple series (Shu et al., 2018). An alternative

352 option might be that some of these feeding spines actually belonged to animals closer to *D.*

353 *thambus* n. sp., where the teeth were not clustered, but radially organised around a terminal

354 mouth. In terms of similarities of the teeth of *D. thambus* n. sp. and supposed

355 protoconodonts, two possible candidates are some specimens of *Protohertzina robusta* (Pyle

356 et al., 2006, fig. 6.8) and an unnamed taxon described by Kouchinsky et al. (2015, fig. 53M,

357 their 'undetermined form 4'). Our knowledge of early chaetognath evolution may also be

358 incomplete. Thus the otherwise distinctive coelocerodonts (Szaniawski, 2015) have a

359 chaetognath-like arrangement of the teeth, while the possible protoconodont *Huayuanodontus*

360 has a tooth histology distinct from other taxa (Dong, 2007).

361   If we are correct in regarding *D. thambus* n. sp. as a sister-taxon of the clade

362 gnathiferans-chaetognaths, this suggests that their common ancestor was macroscopic, semi-

363 sessile and segmented. Thus, the miniaturization and largely meiofaunal existence would

364 have been secondarily acquired in the evolutionary history of gnathiferans, in contrast to the

365 general assumption that it is a plesiomorphic condition for the group (e.g., Laumer et al.,

366 2015). As to the chaetognaths, our discovery cannot resolve more precisely their position to

367 other early bilaterians (e.g. Marlétaz et al., 2008, 2019; Shen et al., 2016). It supports,

368 however, the idea, that notwithstanding subsequent loss and redeployment (Blair, 2008),

369 segmentation amongst the bilaterians is primitive. Moreover, in extant chaetognaths the

370 progenitor neural cells of the trunk are not only highly organized but form 30-35 rows (Perez

371 et al., 2013), comparable to the segment total in *D. thambus* n. sp.. Primitive chaetognaths

372 such as *Ankalodous* (Shu et al., 2017) may have also had relatively limited motility, but

373 overall there was evidently a shift to a much more active mode of life (e.g. Vannier et al.,

15

374 2007). Evidence for a migration to a pelagic mode of life (Vannier et al., 2007; Casenove et

375 al., 2011; Hu et al., 2007) is supported both by the evolution of chaetognath musculature

376 (Casanova and Duvert, 2002) and molecular data (Papillon et al., 2006). Significantly this

377 shift may have been via benthoplanktonic intermediates, although the few truly benthic

378 chaetognaths extant are very derived (Casanova and Duvert, 1996) and show no significant

379 similarities to *D. thambus* n. sp. This transition to the pelagic realm would also have been

380 marked by the separation of the teeth into two separate grasping bundles (along with smaller

381 teeth adjacent to the mouth), changes in the patterns of their replacement (Moreno and Kapp,

382 2003), and loss of mineralization to assist buoyancy. This would have been combined with

383 extensive re-organization of the head musculature. Further changes would have included

384 narrowing of the body, reduction to an oligomeric (tripartite) segmentation (Balavoine and

385 Adoutte, 2003), as well as the development of prominent fins and complex eyes.

386

387 **Accessibility of supplemental data**

388

389 Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.p5hqbzkkz

390

391 **Acknowledgments**

392

399

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604

605 **FIGURE CAPTIONS**

606

607 **Figure 1.** Stratigraphic occurrences of *Dakorhachis thambus* (in color version, red) and the

608 oldest chaetognaths (in color version, green) and protoconodonts (in color version, blue).

609 Cambrian chaetognaths *Eognathacantha*, *Protosagitta* and USNM 199540.

610

611 **Figure 2**. *Dakorhachis thambus* n.gen. n.sp. from the Weeks Formation (Miaolingian,

612 Guzhangian), Utah, USA. Scanning electron micrographs in backscatter mode of polished

613 sections (uncoated) of UU15101.07 (**1**, **2**) and UU15101.08 (**3-6**). (**1**) Fossil body composed

614 of radiating fans of a chloritic mineral with pseudomorphs of pyrite across upper surface. (**2**)

615 Detail of fossil body and pseudomorphs. (**3**) Tooth, composed of calcite. (**4**) Tooth, and

616   surrounding fossil body. (**5**) Two teeth, surrounding fossil body including pyrite

617   pseudomorphs. (**6**) Fossil body with stacked chloritic mineral. Scale bar for all figures 50

618   μm.

619

620   **Figure 3.** *Dakorhachis thambus* n. gen. n. sp. from the Weeks Formation (Miaolingian,

621   Guzhangian), Utah, USA. (**1**) UU15101.02 (upper) and UU15101.03 (lower); (**2**)

622   UU15101.04; (**3**) UU15101.05 (upper) and UU15101.06 (lower); (**4**) BPM1090; (**5**)

623   UU15101.01 (holotype); (**6**) UU18056.27; (**7**) UU17122.03; (**8**) UU18056.28. Specimens

624   photographed (1-5) dry or (6-8) immersed in dilute ethanol. Scale bars are (**1, 5**) 5 mm; (**2-4,**

625   **6-8**) 2 mm.

626

627   **Figure 4.** Feeding apparatus of *Dakorhachis thambus* n. gen. n. sp. in specimens (**1**)

628   UU15101.01 (holotype; CT images, Fig.5) and (**3**) UU15101.02 with (**2, 4**) corresponding

629   camera lucida drawings. Body (blue/light gray), teeth exterior view (red/very dark gray),

630   interior view (pink/fairly dark gray), V-shaped units (green/dark gray), rods (yellow/very pale

631   gray), adhesive (grey/darkish gray), oxides (hatched), sediment (white). Scale bars (**1, 3**) are 1

632   mm.

633

634   **Figure 5.** Holotype (UU15101.01) of *Dakorhachis thambus* n. gen. n. sp. (**1**) micro-CT

635   volume rendering, false color represents specimen density. (**2**) Rotated view showing 3-

636   dimensional transverse banding on the trunk, perpendicular to the long-axis. (**3**) Detail of

637   teeth. (**4**) Simplified reconstruction. Scale bar is 5 mm.

638

639 **Figure 6.** Electron micrographs of the feeding apparatus of the holotype (UU15101.01) of

640 *Dakorhachis thambus* n. gen. n. sp.. **(1)** overview and **(2)** detail showing the hollow tooth

641 interior and fibrous microstructure. Scale bar is 500 µm.

642

643 **Figure 7.** SEM of the body trunk surface of *Dakorhachis thambus* n. gen. n. sp. specimen

644 UU15101.01 showing iron oxides layer (black arrow) and the imprints of pseudomorphs of

645 iron oxides after pyrite on the segmented chloritic surface (white arrows). Scale bar 0.5 mm.

646

647 **Figure 8.** Hypothetical transitions between the jaw apparatus of *Dakorhachis thambus* n. gen.

648 n. sp. and (a) those of the chaetognaths (and protoconodonts) via forms similar to *Ankalodous*

649 *sericus* Shu et al. and (b) the gnathiferans (as represented by the gnathostomulids) via forms

650 similar to *Amiskwia sagittiformis* Walcott.