

A possible Cambrian stem-group gnathiferan-chaetognath from the Weeks Formation (Miaolingian) of Utah

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Abstract.—In recent years the plethora of ‘weird wonders,’ the vernacular for the apparently extinct major body plans documented in many of the Cambrian Lagerstätten, has been dramatically trimmed. This is because various taxa have been either assigned to known phyla or accommodated in larger monophyletic assemblages. Nevertheless, a number of Cambrian taxa retain their enigmatic status. To this intriguing roster we add *Dakorhachis thambus* n. gen. n. sp. from the Miaolingian (Guzhangian) Weeks Formation Konservat-Lagerstätte of Utah. Specimens consist of an elongate body that lacks appendages but is apparently segmented. A prominent feeding apparatus consists of a circle of triangular teeth, while posteriorly there are three distinct skeletal components. *D. thambus* is interpreted as an ambush predator and may have been partially infaunal. The wider affinities of this new taxon remain conjectural, but it is suggested that it may represent a stem-group member of the Gnathifera, today represented by the gnathostomulids, micrognathozoans, and rotifers and possibly with links to the chaetognaths.

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Introduction

Cambrian Konservat-Lagerstätten (‘Lagerstätten’ hereafter) provide exceptional insights into early metazoan evolution, not least because of an abundance of lightly sclerotized and soft-bodied taxa (Hagadorn, 2002). Laurentian examples include the iconic Burgess Shale in British Columbia (Canada) as well as a series of important deposits in Utah (Spence Shale, Wheeler Formation, Marjum Formation; e.g., Muscente et al., 2017; Fig. 1). By contrast, the Weeks Formation (Miaolingian), exposed near Notch Peak, Utah, only more recently has yielded an important Burgess Shale–type fauna (Hesselbo, 1989; Lerosey-Aubril et al., 2013, 2014, 2018; Lerosey-Aubril, 2015; Ortega-Hernández et al., 2015; Robison et al., 2015). Not only is this latter assemblage important in extending our knowledge of Cambrian life, but also its chronological position close to the Miaolingian–Furongian boundary fills a significant gap in the fossil record of non-biomineralizing animals and apparently corresponds to the onset of major biotic changes (Lerosey-Aubril et al., 2018).

To the first approximation, Burgess Shale–type faunas (e.g., Briggs et al., 1994; Hou et al., 2004) have a well-established identity with a predominance of arthropods (both trilobites, including agnostoids, and lightly skeletonized taxa), priapulids (and related scalidophorans), and sponges. Somewhat more occasional there occur such groups as the annelids,

vetulicolians, wiwaxiids, and other sclerite-bearing taxa. Such faunas remain a focus of attention not only on account of their sheer diversity but also because a number of hitherto problematic taxa appear to belong to stem groups that in principle are instrumental in our understanding of the origin of phyla.

Not all such taxa, however, can be accommodated in this fashion, and in one way or another, a number of them retain their enigmatic status. Broadly, these can be divided into three categories, although the boundaries that separate them are by no means absolute. Some, such as the vetulicolians, form a relatively diverse clade but their wider relationships within the deuterostomes continue to be controversial (e.g., Ou et al., 2012; García-Bellido et al., 2014). Others, such as *Nectocaris*, have deeply polarized opinion, in this case as to whether this animal is an early cephalopod (e.g., Smith and Caron, 2010; Kroger et al., 2011; Smith, 2013). Finally, there are singletons that for all intents and purposes remain in taxonomic limbo, and it is to this last category we add a remarkable new taxon, *Dakorhachis thambus* n. gen. n. sp. (Fig. 1). These three categories also have the heuristic value of providing a crude metric of relative phylogenetic ignorance, although in each case new fossil finds ultimately will ensure more secure placement within the metazoan tree. Moreover, properly interpreted, these enigmatic taxa may help to throw crucial light on key transitions between major groups. At this juncture, we are unable to assign *D. thambus* with confidence to any known group, but it is

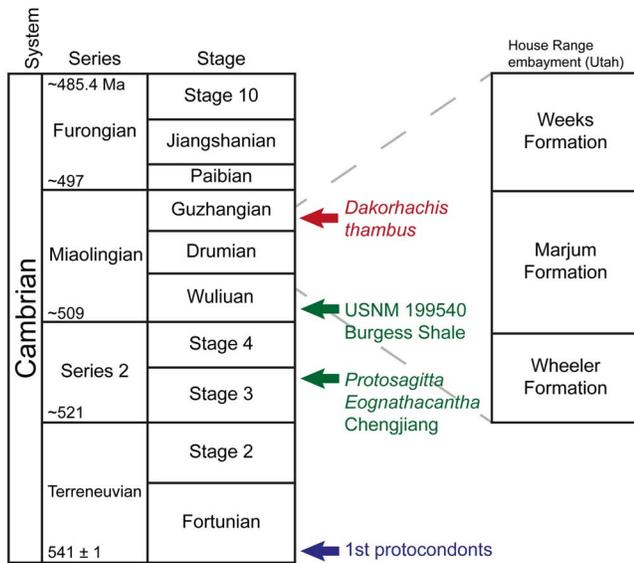


Figure 1. Stratigraphic occurrences of *Dakorhachis thambus* (in color version, red) and the oldest chaetognaths (in color version, green) and protoconodonts (in color version, blue). Cambrian chaetognaths *Eognathacantha*, *Protosagitta* and USNM 199540.

evidently a member of the Bilateria. In our opinion, this taxon is more likely to fall within the Spiralia (rather than the deuterostomes or ecdysozoans). In the following, we tentatively suggest that *D. thambus* might represent a stem-group gnathiferan.

Geological setting

The general setting of this Lagerstätte has been reviewed by Lerosey-Aubril et al. (2018). In brief, the Weeks Formation (Miaolingian, Guzhangian) is a relatively deepwater deposit, apart from the upper section (70 m) that records a substantial shallowing of the depositional environment associated with the end of basinal accumulation in the so-called House Range Embayment. Below this transitional interval, lithologies are alternating micrites and calcareous claystones. These are indicative of a low-energy, distal ramp environment, which was periodically disturbed by storm-induced gravity flows and episodes of oxygen depletion. Unlike the Burgess Shale, where much of the biota was introduced into a toxic environment by small turbidity flows (e.g., Conway Morris, 1986), transport in this Lagerstätte was evidently minimal. The exceptional preservation in the Weeks Formation is restricted to a 25 m interval about 205 m below the top of the unit. This interval has yielded a diverse fauna (~73 species), which according to agnostoids (*Proagnostus gibbus* Zone) and trilobites (*Cedaria* Zone) is of mid-Guzhangian age.

Preservation

The fossils described here show the same style of preservation as most of the non-biomineralizing taxa of the fauna (Lerosey-Aubril et al., 2018, fig. 3b, c). This is the result of a series of chemical and physical alterations that occurred mostly at a

late stage of diagenesis. Such is very much a hallmark of the Weeks Formation fauna where evidence of diagenetic phosphatization is associated with strong taxonomic and histological controls. Indeed, all known instances of secondary phosphatization concern organs rich in phosphorus (e.g., arthropod guts) or tissues underneath primary phosphatic structures, such as aglaspidid cuticle or palaeoscolecid plates (Lerosey-Aubril, 2015; Lerosey-Aubril et al., 2012, 2018).

In the case of *D. thambus* n. gen. n. sp., these postmortem changes include the initial flattening of the carcasses and, much later, the replacement of the presumably carbonaceous material with pyrite and subsequent coating of this pyritic layer (now as oxidized pseudomorphs) by chlorite (in a fan-like arrangement) (Fig. 2). This strong diagenetic imprint is related to major igneous intrusions as well as more recent intense weathering. Scanning electron micrographs of specimens of *D. thambus* suggest that the trunk is composed chiefly of iron oxides and chlorite (Fig. 2), and this is consistent with compositional (energy-dispersive X-ray spectroscopy [EDS]) analyses (Supplemental Fig. 1).

The translucent teeth differ in composition from the trunk and appear to have a predominantly calcitic composition (Fig. 2.3–2.5). As discussed in the following, while an original composition cannot be excluded, it seems as likely that the calcite is also diagenetic. Micro-CT shows moderate three-dimensional (3D) preservation of the teeth at the specimen surface. However, due to the mode of fossil preservation (low-density contrast composition and compression), no further (e.g., internal or subsurface) 3D information was recovered.

Materials and methods

The material consists of nineteen specimens preserved flattened parallel to bedding. One slab bears two specimens (UU.15101.05, 15101.06), two slabs have three specimens each (UU15101.02, 15101.03, 15101.04 and 15101.12, 15101.13, 15104.14), while another slab has five superimposed specimens (UU15101.07, 15101.08, 15101.09, 15101.10, 15101.11); other specimens are isolated. This material was examined under a binocular microscope with a drawing tube employed to prepare camera-lucida interpretative drawings. Specimens UU17122.03, 18056.27, and 18056.28 were photographed immersed in dilute ethanol using a Leica IC80 HD camera mounted on a Leica M80 microscope. Specimen UU17122.03 was studied uncoated (low vacuum mode) using a scanning electron microscope (SEM) JEOL JSM-6010LV equipped with an EDS module JEOL EX-94410TIL11 at the University of New England. Similar SEM and EDS investigations were performed on both entire specimens (UU15101.01, UU15101.07) and polished sections using a QEMSCAN 650F SEM at the University of Cambridge. Last, computed tomography (CT) scans of specimen UU15101.01 (holotype) were obtained using a Nikon XTH225 ST CT scanner at the Cambridge Biotomography Centre.

Repositories and institutional abbreviations.—Types, figures, and other specimens (including petrographic sections) examined in this study are deposited in the Department of

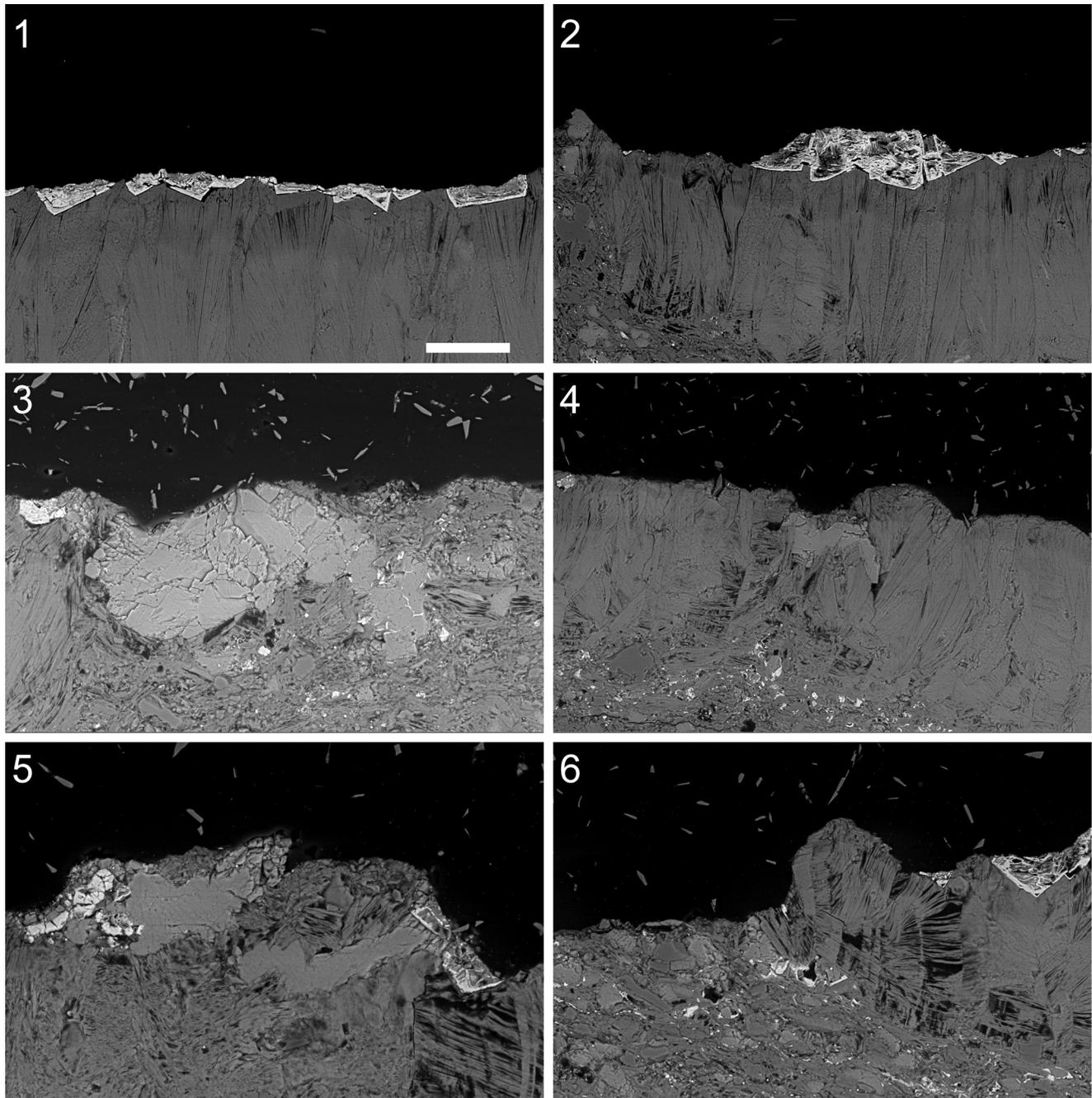


Figure 2. *Dakorhachis thambus* n.gen. n.sp. from the Weeks Formation (Miaolingian, Guzhangian), Utah, USA. Scanning electron micrographs in backscatter mode of polished sections. (1, 2) UU15101.07: (1) fossil body composed of radiating fans of a chloritic mineral with pseudomorphs of pyrite across upper surface; (2) detail of fossil body and pseudomorphs. (3–6) UU15101.08: (3) tooth, composed of calcite; (4) tooth and surrounding fossil body; (5) two teeth and surrounding fossil body, including pyrite pseudomorphs; (6) fossil body with stacked chloritic mineral. Scale bar = 50 μ m.

Geology and Geophysics (Research Collections), University of Utah, USA (UU,) and Back to the Past Museum, Cancún, Mexico (BPM).

Systematic paleontology

?Superphylum Spiralia
 ?Gnathifera-Chaetognatha
 Family Dakorhachiidae new family

Type genus (by monotypy).—*Dakorhachis* n. gen. from the Miaolingian (Guzhangian) Weeks Formation of the House Range, Utah, USA.

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

Remarks.—Chaetognatha is currently treated as a distinct phylum, and recent molecular evidence (Fröblius 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 in the following, *D. thambus* n. gen. n. sp. is tentatively interpreted as a stem-group representative of a Gnathifera-Chaetognatha clade (we suggest the colloquial moniker chaetognathiferans).

Genus *Dakorhachis* new genus

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

Diagnosis.—As for type species by monotypy.

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

Remarks.—A new genus that appears to have no known equivalents elsewhere.

Dakorhachis thambus new species Figures 3–7, Supplemental Figure 2

2018 ‘Enigmatic organism’ Lerosey-Aubril et al., fig. 3a–c.

Holotype.—Complete specimen (UU15101.01), Department of Geology and Geophysics (Research Collections), University of Utah, Salt Lake City, Utah.

Diagnosis.—Elongate and robust body. Feeding apparatus comprising at least six hollow teeth, characterized by gently convex outer side with prominent central ridge and concave inner side with narrow ridge-like margins, and in posterior direction associated skeletal elements in form of hook-like elements, inverse V-shaped sclerites, and elongate rods. Trunk composed of 30 segments, gently tapering posteriorly, terminating in blunt tip.

Occurrence.—Exposures in North Canyon, adjacent to Notch Peak, House Range, Utah. Weeks Formation (Cambrian Series 3, Guzhangian).

Description.—Apart from minor preservational variants, the material is united in showing a body consisting of a relatively elongate trunk (Figs. 3, 5, Supplemental Fig. 3) that, at its anterior, bears a prominent feeding apparatus (Figs. 4, 5.3). Total length can reach 28 mm, and maximum width of trunk is 7 mm (Supplemental Fig. 3). The feeding apparatus bears at least six prominent teeth, of which about half are exposed in outer aspect and the remainder in inner aspect, suggesting that, originally, they formed a circum-oral cirlet (Fig. 4.1, 4.3). Each tooth (~3 mm long) has a narrow triangular form and in outer aspect is gently convex and bears a prominent and relatively narrow longitudinal ridge. In inner aspect, the tooth is concave, but the margins are defined by very narrow ridges. The teeth have a fibrous texture, while the broken margin of

one tooth shows what may be a hollow interior (Fig. 6). Elemental analyses indicate that the teeth have a predominantly calcitic composition (see the preceding and Dryad file). Posterior to the teeth are three other skeletal components, evidently with a composition similar to the teeth (Fig. 4.2, 4.4). Immediately to the posterior of the teeth are small hook-like structures, and behind them is a series of inverse V-shaped units. Most likely these units also formed cirlets. Finally, adjacent to, or superimposed on, the anteriormost trunk are rod-like structures, usually straight but occasionally with a sinuous shape.

The trunk is relatively featureless and lacks appendages or other extensions. In some specimens, the configuration is somewhat sinuous (Fig. 3.3; see also Lerosey-Aubril et al., 2018, fig. 3a), suggesting an original degree of flexibility (also Fig. 3.7). The width is more or less uniform, and although most specimens have a rounded termination, it occasionally appears to be acute. Broad transverse folds (~0.8 mm) may be surficial annulations but here are interpreted as segments (Figs. 3.1, 3.2, 5.1, 5.2, 7). In life these would have totaled about 30. That these structures are original rather than post-mortem (or tectonic) is supported by three lines of evidence. First, these transverse bands are evidently three dimensional (Supplemental Fig. 2) and sometimes match a corrugated body margin. In addition, associated specimens with different orientations have folds transverse to their respective bodies rather than parallel to any rock fabric (Supplemental Fig. 3).

Etymology.—From *thambos* (Greek), an astonishment.

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

Remarks.—A new species that has no close counterpart among other Cambrian taxa.

Discussion

Paleoecology and mode of life.—*D. thambus* n. gen. n. sp. lacks fins or other anatomical features consistent with a pelagic mode of life and therefore is interpreted as benthic. Co-association of specimens indicates a gregarious habit, although the case of parallel stacking (UU15101.07–15101.11) is most likely postmortem. Locomotory organs are not evident, but presumably this animal could have moved across or within the seafloor by peristaltic contractions. Given, however, that the arrangement of the teeth is in the form of a sort of basket, it may have captured its prey as an ambusher, and as such the animal may have been semi-sessile and partially concealed in the seafloor. The attitude of the teeth varies from parallel to an anterior convergence, but in life they presumably opened wider to tackle larger prey. The function of the skeletal elements posterior to the teeth is more conjectural. One suggestion is that they served for insertion of muscles associated with protrusion and subsequent closure of the teeth.

Phylogenetic affinities.—The wider relationships of *D. thambus* are necessarily problematic given its lack of close identity to any known group. Such evidence as there is must look to the feeding

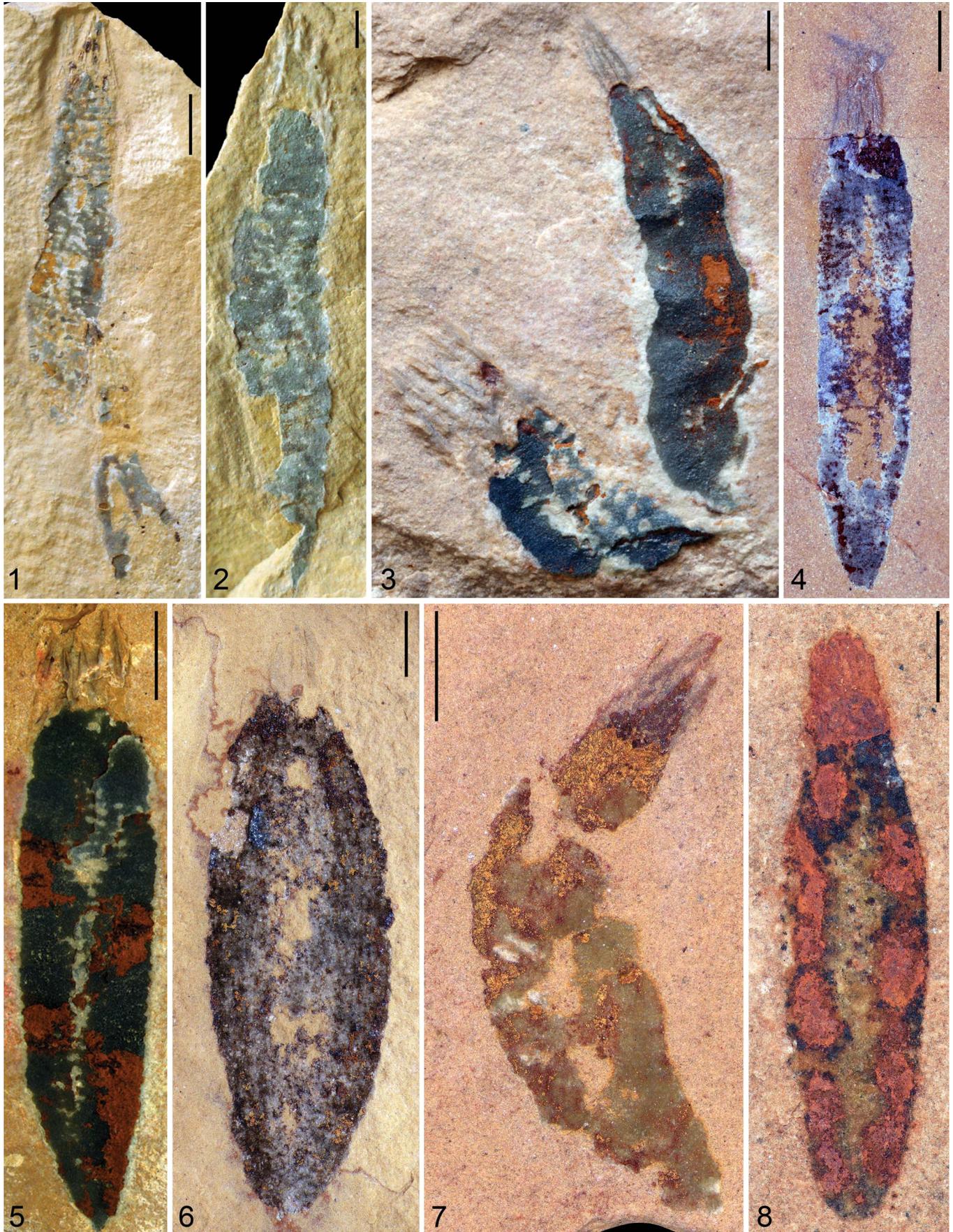


Figure 3. *Dakorhachis thambus* n. gen. n. sp. from the Weeks Formation (Miaolingian, Guzhangian), Utah, USA. (1) UU15101.02 (upper) and UU15101.03 (lower); (2) UU15101.04; (3) UU15101.05 (upper) and UU15101.06 (lower); (4) BPM1090; (5) UU15101.01 (holotype); (6) UU18056.27; (7) UU17122.03; (8) UU18056.28. (1–5) Specimens photographed dry. (6–8) Specimens immersed in dilute ethanol. (1, 5) Scale bars = 5 mm; (2–4, 6–8) scale bars = 2 mm.

apparatus. A potentially important clue might be the calcitic composition of the teeth, although as noted this may well be diagenetic. Certainly among metazoans, calcitic teeth are unusual, with the most notable instances being in the echinoids (e.g., Wang et al., 1997; Stock et al., 2014) and extinct ophiocystioids (e.g., Reich et al., 2018). Moreover, in the former group, the teeth can on occasion show a fibrous microstructure (Reich and Smith, 2009, text-fig. 9C, D). There is, however, no other feature of *Dakorhachis* that would indicate an affinity to either the echinoids or any other echinoderm, especially if the principal teeth totaled six, an obvious departure from the characteristic pentaradial symmetry of this phylum.

In passing, it is worth noting that *D. thambus* shows some broad similarities in overall shape to the unusual sponge *Takakkawia lineata* Walcott, 1920 from the Burgess Shale, which has marginal ‘fins’ extending from a conical body (Botting, 2012). However, numerous detailed differences in morphology indicate that the resemblance between these taxa is superficial. Specifically, there are differences in the size, shape, and annulation of the body in *D. thambus* (which averages 2.1 cm long, is vermiform, and has transverse annulations) versus *T. lineata* (which is longer [Botting, 2012, fig. 1], more vasiform, and displays diagnostic lengthwise lineations). Furthermore, there are major differences in the shape and organization of the teeth of *Dakorhachis* (which are elongate, sharply pointed, and restricted to the anterior body margin) versus the ‘fins’ of *T. lineata* (which are wider, flat topped, and accompanied by broad spicules extending down the length of the body). While there is no other reason to interpret *D. thambus* as any sort of sponge, the potential complexities of assigning Cambrian taxa to particular groups and the consequent phylogenetic implications are apparent from Botting and Muir’s (2018) proposed linkage of *Takakkawia* to the putative ctenophore *Thaumactena*. That said, there is no evidence for comparing *D. thambus* with any of the Cambrian ctenophores (e.g., Ou et al., 2015).

Notwithstanding such comparisons, *D. thambus* is evidently a bilaterian rather than a representative of the diploblasts (let alone a sponge). There appears to be no particular similarity to either the deuterostomes or ecdysozoans. Although, in the latter case, it is true that the priapulids and related scalidophorans typically have an introvert equipped with circllets of teeth, these and associated structures show a complex zonation and diversity of forms (e.g., Smith et al., 2015) that find no counterpart in the array of teeth seen in *D. thambus* or in its ancillary skeletal structures. Most likely, *D. thambus* is a member of the Spiralia.

Among the spiralian, the most fruitful comparisons may possibly lie with the Gnathifera. This monophyletic group (e.g., Laumer et al., 2015) comprises the gnathostomulids (e.g., Herlyn and Ehlers, 1997; Sørensen et al., 2006), its sister group the micrognathozoans (e.g., Bekkouche et al., 2014; Bekkouche and Worsaae, 2016), and the syndermatans (the group encompassing the rotifers and endoparasitic acanthocephalans; e.g., Rieger and Tyler, 1995; Sørensen, 2002a; Wulfken and

Ahrlrichs, 2012). Gnathiferans are millimetric and typically meiofaunal, but despite this, all possess intricate jaw apparatuses that reach an apogee in the complex array found in the micrognathozoans (e.g., Kristensen and Funch, 2000; De Smet, 2002; Sørensen, 2003). Current phylogenetic schemes place the gnathiferans as sister to all other spiralian (e.g., Laumer et al., 2015; Bekkouche and Worsaae, 2016), which in turn are broadly divided into the ‘platyozoans’ and the more securely identified lophotrochozoans.

The disparity of extant gnathiferans, combined with an almost nonexistent fossil record (e.g., Poinar and Ricci, 1992; Waggoner and Poinar, 1993; Jha et al., 2011), and their still poorly resolved systematic position within the bilaterians pose a series of evolutionary questions. Among the most problematic is the visualization of a stem-group form and its corresponding recognition in the fossil record. This question may be further exacerbated if the millimetric size of the extant gnathiferans is the result of secondary miniaturization from macroscopic predecessors rather than a primitive state.

Intriguingly, there is also phylogenomic evidence for a link between the gnathiferans and chaetognaths (Fröblius and Funch, 2017; Marlétaz et al., 2019). The latter are equipped with a formidable feeding apparatus consisting of prominent grasping spines and associated teeth (e.g., Bone et al., 1991), although at first sight there is no obvious macroscopic connection to any of the considerably more complex gnathiferan jaws. The phylogenetic position of the chaetognaths has long been regarded as basal among the bilaterians (Perez et al., 2013) but with conflicting views suggesting either a place among the most primitive protostomes (e.g., Marlétaz et al., 2006; Marlétaz and Le Parco, 2008; Shen et al., 2016) as opposed to a position among the basal lophotrochozoans (e.g., Matus et al., 2007; Dunn et al., 2008; Bernt et al., 2013).

The contribution of the Cambrian fossil record to the early evolution of the chaetognaths and gnathiferans to date has focused almost entirely on the former group. Here the protoconodonts, which apart from occasional fused clusters are effectively dispersed as small shelly fossils (Szaniawski, 1982, 2002), are complemented by several soft-bodied taxa similar to extant chaetognaths (Chen and Huang, 2002; Hu et al., 2007; Vannier et al., 2007; Shu et al., 2017) and what appear to be two more primitive representatives (*Ankalodus sericus* Shu et al., 2017 and *Capinatator praetermissus* Briggs and Caron, 2017) characterized by supernumerary teeth (Briggs and Caron, 2017) or a multi-jawed morphology (Shu et al., 2017) (Supplemental Fig. 1). It is now clear, however, that the hitherto enigmatic *Amiskwia* (Conway Morris, 1977) possesses a jaw apparatus that supports some sort of connection to the gnathiferans and/or chaetognaths (Caron and Cheung, 2019; Vinther and Parry, 2019).

Although the record of relevant soft-bodied taxa (*Amiskwia*, *Ankalodous*, *Capinatator*) is meager, as potential stem-group chaetognathiferans they hint at both morphological disparity and a range of ecologies from swimming to benthic. To this roster we tentatively propose to add *D. thambus*. As is the case with a

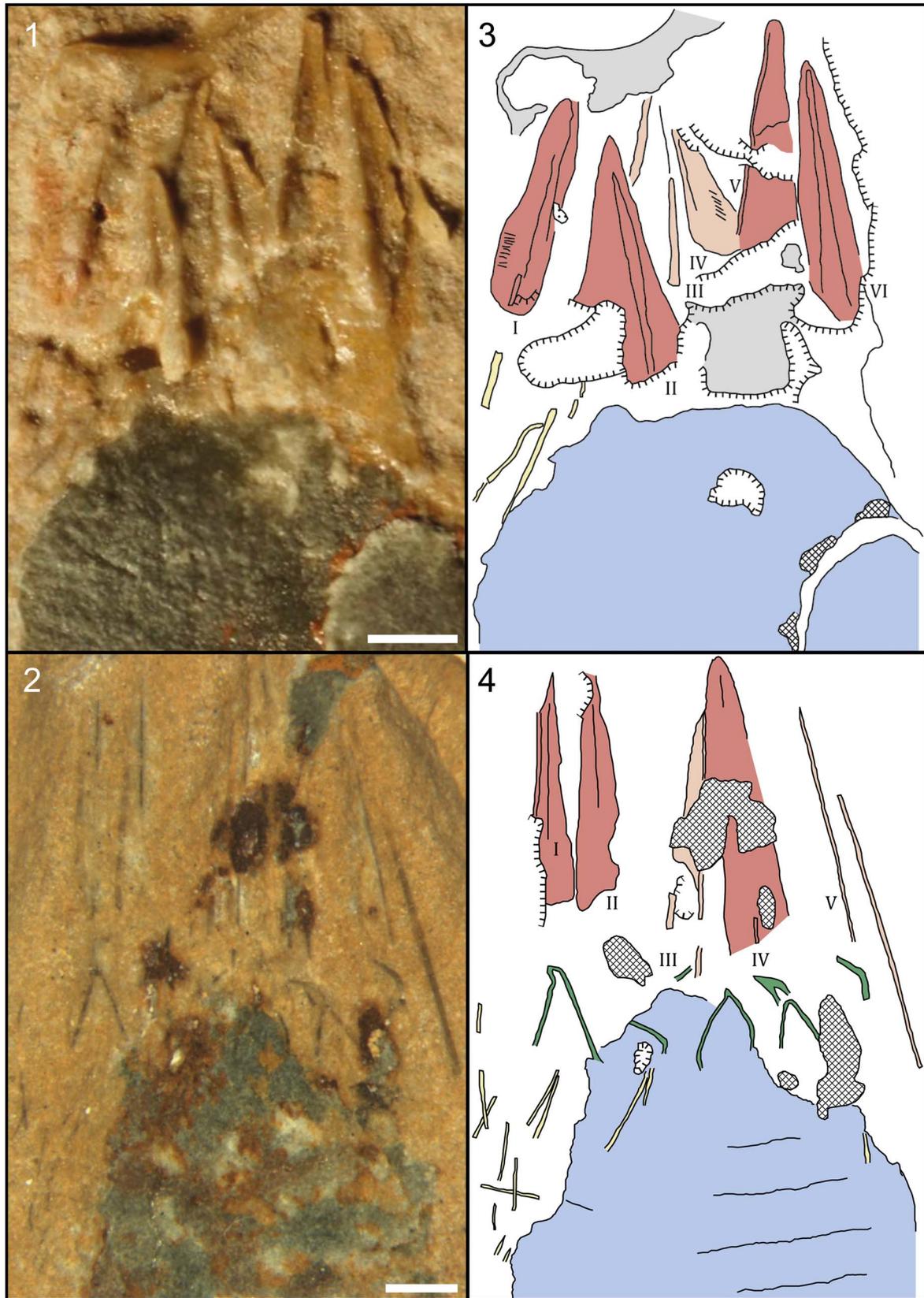


Figure 4. (1, 3) Feeding apparatus of *Dakorhachis thambus* n. gen. n. sp.: (1) UU15101.01 (holotype; CT images, Fig. 5); (3) UU15101.02. (2, 4) Corresponding camera lucida drawings. Body (blue/light gray), teeth exterior view (red/very dark gray), interior view (pink/fairly dark gray), V-shaped units (green/dark gray), rods (yellow/very pale gray), adhesive (grey/darkish gray), oxides (hatched), sediment (white). Scale bars = 1 mm.

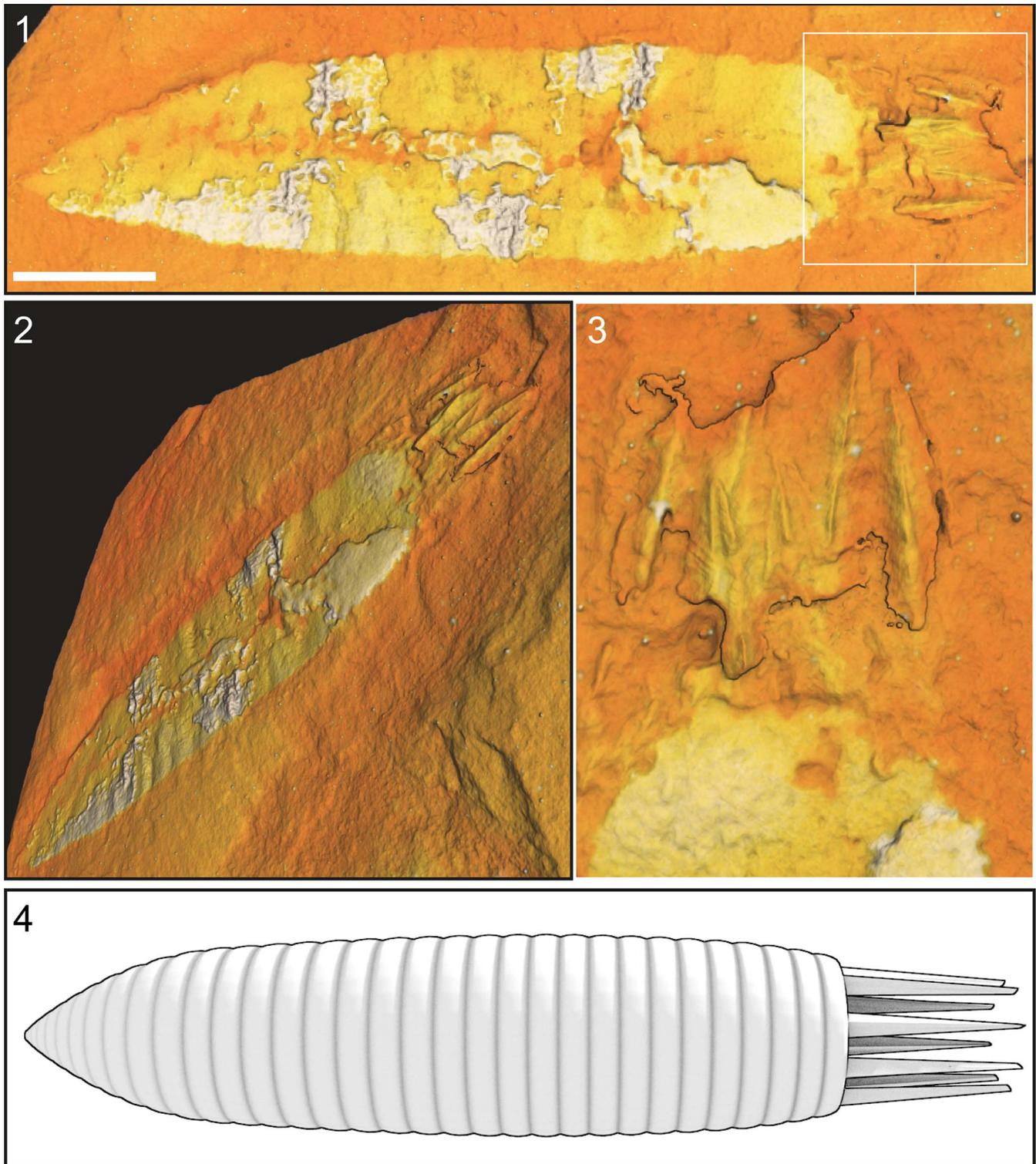


Figure 5. Holotype (UU15101.01) of *Dakorhachis thambus* n. gen. n. sp. (1) micro-CT volume rendering; false color represents specimen density. (2) Rotated view showing 3D transverse banding on the trunk, perpendicular to the long axis. (3) Detail of teeth. (4) Simplified reconstruction. Scale bar = 5 mm.

number of other controversial Cambrian groups, a convincing phylogenetic analysis is frustrated by the paucity of available character-states and the added possibility that those available for tabulation in reality are convergent. Our assignment relies on a tentative interpretation of the feeding apparatus of *D.*

thambus as a precursor to the much more complex jaws seen in extant gnathiferans as well as the possible equivalent in the chaetognaths. Here, therefore, we sketch a possible set of transitions (Fig. 8) that might link the feeding apparatus of *Dakorhachis* n. gen to those of the gnathiferans and chaetognaths.

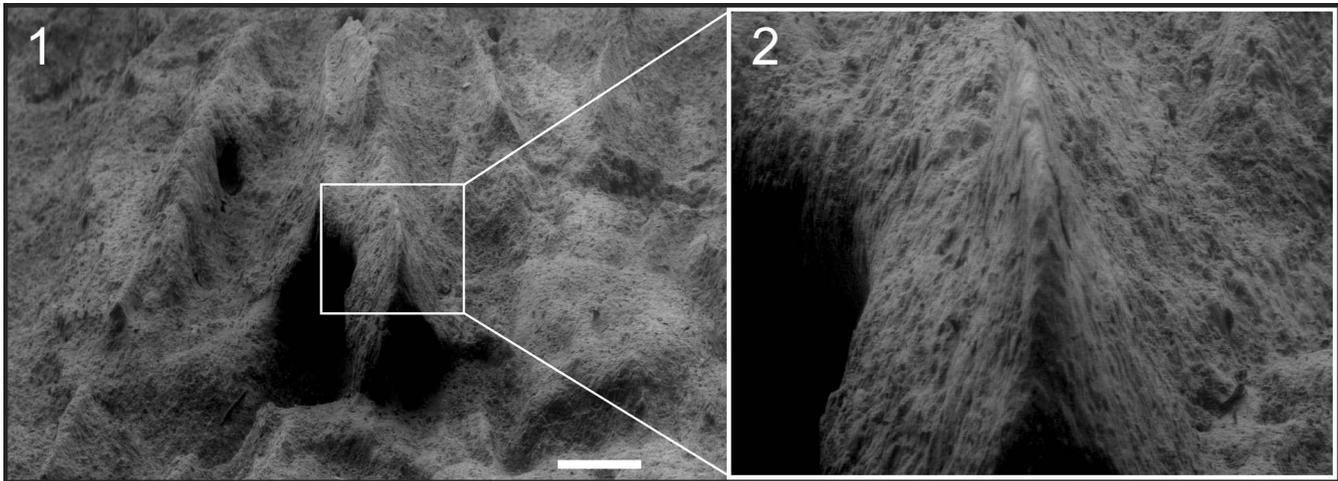


Figure 6. Electron micrographs of the feeding apparatus of the holotype (UU15101.01) of *Dakorhachis thambus* n. gen. n. sp. (1) Overview; (2) detail showing the hollow tooth interior and fibrous microstructure. Scale bar = 500 μ m.

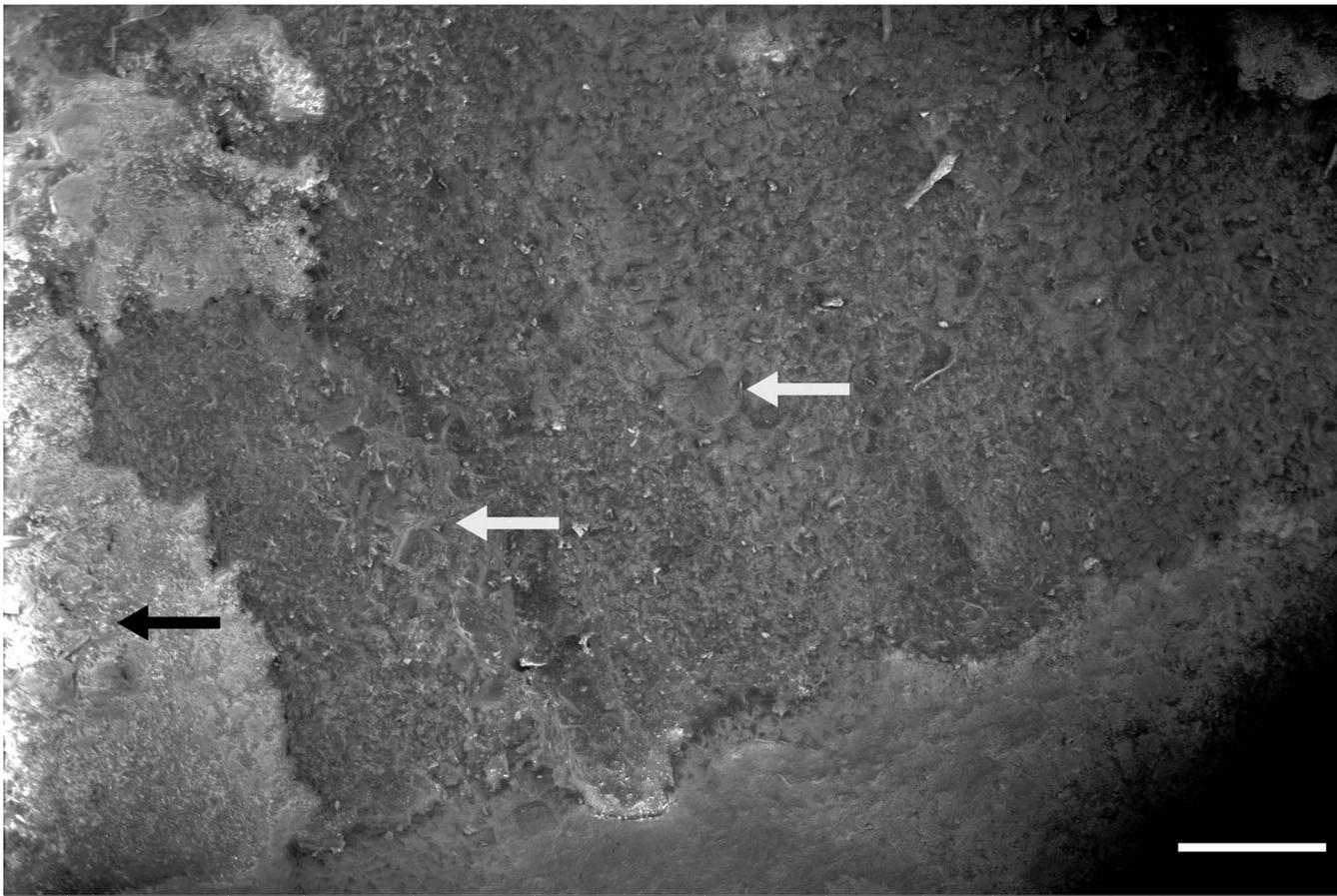


Figure 7. SEM of the body trunk surface of *Dakorhachis thambus* n. gen. n. sp. specimen UU15101.01 showing iron oxides layer (black arrow) and the imprints of pseudomorphs of iron oxides after pyrite on the segmented chloritic surface (white arrows). Scale bar = 0.5 mm.

There is agreement that some of the elements of gnathiferan apparatuses are homologous (e.g., Sørensen, 2002b; Sørensen et al., 2006), but nevertheless collectively the clade shows a wide diversity of forms. Interestingly, the more basal gnathostomulids possess a somewhat less elaborate jaw (e.g., Riedl and

Rieger, 1972), and within this group there are a number of trends that can be traced from what appears to be the most primitive arrangement (e.g., Sterrer, 1972; Sørensen, 2002b). Thus, despite various elaborations, the basic configuration of the jaw is as a forceps-like unit joined to a proximal base and a basal

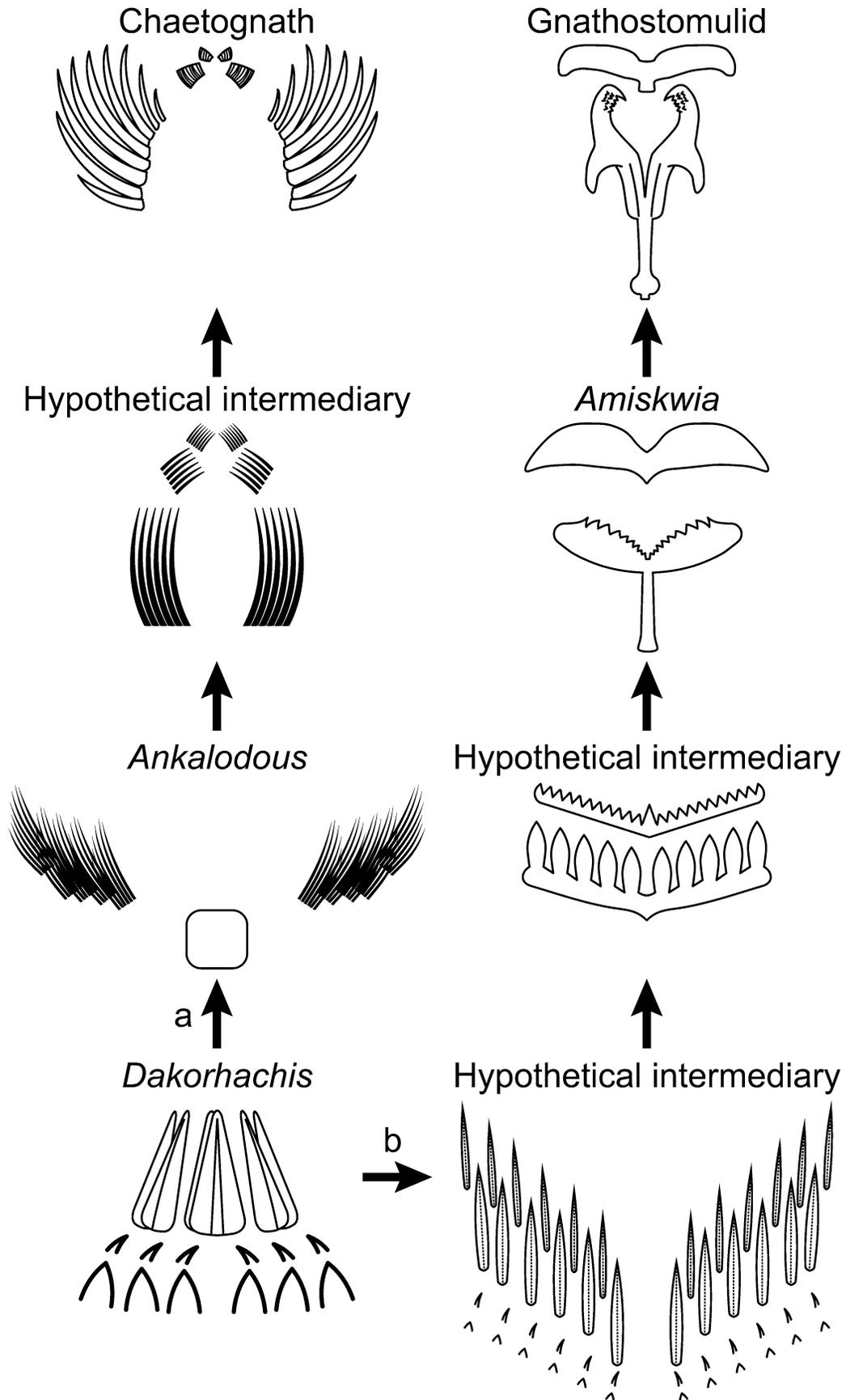


Figure 8. Hypothetical transitions between the jaw apparatus of *Dakorhachis thambus* n. gen. n. sp. and (a) those of the chaetognaths (and protoconodonts) via forms similar to *Ankalodous sericus* and (b) the gnathiferans (as represented by the gnathostomulids) via forms similar to *Amiskwia sagittiformis* Walcott, 1911.

plate. Derivation of this arrangement from something similar to *D. thambus* via an amiskwiid (Caron and Cheung, 2019) would, in principle, involve a shift from an effectively radial symmetry to a bilateral configuration, reduction from six teeth to three (along with substantial miniaturization), and possibly incorporation of the more proximal skeletal elements in *D. thambus* into the jaw apparatus.

The likely phylogenetic relationship between chaetognaths and gnathiferans (Fröblius and Funch, 2017; Marlétaz et al., 2019) may also find some support in the morphology exhibited by *D. thambus*. While there is little obvious similarity between the jaw configurations of the gnathiferans and chaetognaths, in both cases the principal composition is chitinous (e.g., Bone et al., 1983; Sørensen and Sterrer, 2002). The distinctive rod-like microstructures of most gnathiferan teeth (e.g., Riemann and Ahlrichs, 2008) is presumably a synapomorphy of the group, but in *D. thambus* the fibrous microstructure and possible hollow interior find a possible counterpart in the protoconodonts (e.g., Szaniawski, 2002). If there is an evolutionary connection between *D. thambus* and the chaetognaths, then in parallel to the gnathiferans this would involve a transition from the apparently radial configuration of the teeth in the former taxon to the bilateral arrangement on the chaetognaths. Although very different to the trajectory of the gnathiferans that led toward a meiofaunal existence, this proposed evolutionary path would also be a consequence of a major ecological shift, from a perhaps semi-sessile benthic lifestyle to a more motile pelagic one.

It is worth pointing out that while the fused clusters of protoconodonts (e.g., Szaniawski, 1982, 2002) are convincingly compared to the bundles of feeding spines in the chaetognaths, by contrast most protoconodont taxa are never recovered as fused clusters. While this disaggregation may be the consequence of standard processing of samples by acid digestion, it seems equally possible that in such taxa the arrangement of the feeding apparatus was more open and/or arranged as multiple series (Shu et al., 2017). An alternative option might be that some of these feeding spines actually belonged to animals closer to *D. thambus*, where the teeth were not clustered but radially organized around a terminal mouth. In terms of similarities of the teeth of *D. thambus* and supposed protoconodonts, two possible candidates are some specimens of *Protohertzina robusta* Qian, 1977 (Pyle et al., 2006, fig. 6.8) and an unnamed taxon described by Kouchinsky et al. (2015, fig. 53M, their ‘undetermined form 4’). Our knowledge of early chaetognath evolution may also be incomplete. Thus, the otherwise distinctive coeloceroconodonts (Szaniawski, 2015) have a chaetognath-like arrangement of the teeth, while the possible protoconodont *Huayuanodontus* has a tooth histology distinct from other taxa (Dong, 2007).

If we are correct in regarding *D. thambus* as a sister taxon of the clade gnathiferans-chaetognaths, this suggests that their common ancestor was macroscopic, semi-sessile, and segmented. Thus, the miniaturization and largely meiofaunal existence would have been secondarily acquired in the evolutionary history of gnathiferans, in contrast to the general assumption that it is a plesiomorphic condition for the group (e.g., Laumer et al., 2015). As to the chaetognaths, our discovery cannot resolve more precisely their position relative to other early bilaterians (e.g., Marlétaz and Le Parco, 2008; Shen et al., 2016; Marlétaz et al., 2019). It supports, however, the idea that,

notwithstanding subsequent loss and redeployment (Blair, 2008), segmentation among the bilaterians is primitive. Moreover, in extant chaetognaths, the progenitor neural cells of the trunk not only are highly organized but also form 30–35 rows (Perez et al., 2013), comparable to the segment total in *D. thambus*. Primitive chaetognaths such as *Ankalodous* (Shu et al., 2017) may have also had relatively limited motility, but overall there was evidently a shift to a much more active mode of life (e.g., Vannier et al., 2007). Evidence for a migration to a pelagic mode of life (Hu et al., 2007; Vannier et al., 2007; Casanova et al., 2011) is supported by both the evolution of chaetognath musculature (Casanova and Duvert, 2002) and molecular data (Papillon et al., 2006). Significantly, this shift may have been via benthoplanktonic intermediates, although the few truly benthic chaetognaths extant are very derived (Casanova and Duvert, 1996) and show no significant similarities to *D. thambus*. This transition to the pelagic realm would also have been marked by the separation of the teeth into two separate grasping bundles (along with smaller teeth adjacent to the mouth), changes in the patterns of their replacement (Moreno and Kapp, 2003), and loss of mineralization to assist buoyancy. This would have been combined with extensive reorganization of the head musculature. Further changes would have included narrowing of the body, reduction to an oligomeric (tripartite) segmentation (Balavoine and Adoutte, 2003), and the development of prominent fins and complex eyes.

Accessibility of supplemental data

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

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