JOURNAL OF
PALEONTOLOGY
A PUBLICATION OF THE
Paleontological
S O C I E T Y

# A large pelagic lobopodian from the Cambrian Pioche Shale of Nevada

Christian R.A. McCall* 

Otterville, Ontario N0J 1R0, Canada <christianmccall23@yahoo.ca>

**Non-technical Summary.**—Lobopodians are an iconic group of animals from the Paleozoic that includes *Hallucigenia* and *Opabinia*, as well as living animals such as tardigrades and velvet worms. They would also eventually give rise to the first arthropods by developing a hard, sclerotized exoskeleton. During the Cambrian, a rare subset of lobopodians possessed large swimming flaps, sometimes alongside ventral walking limbs. A new, large-bodied pelagic lobopodian from the Cambrian of Nevada is described, possessing more swimming flaps than any other lobopodian or radiodont.

**Abstract.**—Lobopodians are an iconic and diverse group of animals from the Cambrian, which alongside radiodonts, present an important window into the evolution of arthropods and the development of Paleozoic ecosystems. Of these, a rare few species outside of Radiodonta possess lateral swimming flaps. The recent discovery of *Utahnax* provided much-needed insight into the evolution of swimming flaps, suggesting that the ventrolateral flaps of *Kerygmachela* evolved independently from other flap-bearing lobopodians and radiodonts. Here a new pelagic lobopodian species is described, *Mobulavermis adustus* new genus new species, the first lobopodian to be reported from the Cambrian-age Pioche Shale of Nevada. *Mobulavermis adustus* was large and possessed more ventrolateral flap pairs than any other known lobopodian or radiodont. It is found to be a close relative of both *Kerygmachela* and *Utahnax*, allowing the establishment of the new lobopodian family Kerygmachelidae new family. In addition, an indeterminate euarthropod fossil from the Pioche Formation is described in brief, and the recently described Chengjiang species *Parvibellus avatus* Liu et al., 2022, thought to have been related to the "gilled lobopodians," is reinterpreted as a juvenile siberiid lobopodian.

UUID: http://zoobank.org/759c4eb9-ec60-4d5a-8b20-4f115ab79575

## Introduction

Although popularly considered to be oddities of the Cambrian period that quickly disappeared from the fossil record (Gould, 1989), recent discoveries have clarified that lobopodians and radiodonts played a considerable role in Paleozoic ecosystems (Lerosey-Aubril and Ortega-Hernández, 2022). Lobopodians persisted all the way into the Carboniferous period in the form of marine and onychophoran-like forms from the Mazon Creek Fauna (Murdock et al., 2016) and persist today in the form of onychophorans (velvet worms) and tardigrades. *Schinderhannes bartelsi* Kühl et al., 2009, a diminutive peytoiid, is the youngest known radiodont fossil, dated to the Early Devonian. Radiodonts form a monophyletic group sister to Arthropoda (Moysiuk and Caron, 2022), while the term "lobopodian" has taken on a looser definition. By modern usage, "lobopodians" refers to a paraphyletic group of rare, vermiform, basal panarthropods with lobopodous limbs, or occasionally soft swimming flaps (Caron and Aria, 2020). Radiodonts, owing to their more easily preserved sclerotized appendages and cephalic carapace elements, are described more frequently (Wu et al., 2021b) and continue to be discovered at a mostly steady rate.

Among these discoveries, however, very few known nonradiodont taxa belong to the stem arthropods. These animals, known from only a small number of species, include the siberiids (three or four species), the "gilled lobopodians" (three species), and the opabiniids (three or four species). Siberiids, which essentially resemble their onychophoran-branch relatives but with more obvious adaptations for predation, may have been some of the first raptorial animals on the planet according to phylogenetic bracketing (Howard et al., 2022), while opabiniids, known only from a single species before the recent descriptions of *Utaurora comosa* Pates et al., 2022 (Pates et al., 2022a) and two specimens from the Ordovician of Wales (Pates et al., 2022b), are famously unique, even among other Cambrian taxa. The gilled lobopodians are perhaps some of the least well understood, being known only from two species from the Sirius Passet Lagerstätte of Greenland and, questionably, the recently described *Utahnax vannieri* Lerosey-Aubril and Ortega-Hernandez, 2022. The Sirius Passet species, *Pambdelurion whittingtoni* Budd, 1997 and *Kerygmachela kierkegaardi* Budd, 1993, were initially described as gilled lobopodians for their supposed possession of lobopodous ventral limbs and setal-gill bearing dorsal flaps. Since their descriptions in the 1990s, we have learned more about *Pambdelurion* and *Kerygmachela*, from numerous fossils of the former and relatively rare fossils of the latter (Lerosey-Aubril and Ortega-Hernandez, 2022). At the same time, the nature or presence of "gills" in

either taxa remains insufficiently demonstrated, as are the ventral lobopods of *Kerygmachela*. These taxa are of great importance to our understanding of arthropod evolution and yet remain poorly understood. Here a new "gilled lobopodian" related closely to *Kerygmachela* and *Utahnax* is described from the Pioche Shale of Nevada, representing the first and only known lobopodian from the formation.

## Geological setting

The lobopodian fossils described herein are recorded (Lieberman, 2003) as having originated from the same locality (the Ruin Wash locality, west side of Chief Range, 17 km west of Panaca) in the Comet Shale Member (Delamaran) strata of the Pioche Shale in Nevada, USA, within a depositional setting of the then equatorial southern Great Basin (Pates et al., 2021b) along the inner shelf of the paleocontinent Laurentia (Wotte and Sundberg, 2017). However, other non-lobopodian specimens recorded as having derived from the same locality within the Comet Shale Member have since been restudied and assigned to the slightly older, underlying Combined Metals Member (Dyeran) (Pates et al., 2021b). The lobopodian fossils described here are preserved in yellows, oranges, and dark red colors, which, on the basis of previous textural and elemental analyses of coeval soft-bodied specimens (Moore and Lieberman, 2009), suggests they are preserved as botryoidal hematite ($Fe_2O_3$), the expected mode of preservation for soft-bodied fossils in the Combined Metals Member. Soft-bodied faunal elements from the Comet Shale Member, which are preserved as a kerogenized carbon film, do not demonstrate the same dramatic reddish coloration. A previously described radiodont appendage belonging to *Anomalocaris magnabasis* Pates et al., 2021b and displaying a comparable coloration and mode of preservation, KUMIP 293605, was previously described by Lieberman (2003) as coming from the Comet Shale Member but is now known to have come from the Combined Metals Member (Pates et al., 2021b). Other soft-bodied taxa collected from Pioche Shale include *Canadaspis perfecta* Walcott, 1912, ?*Perspicaris dilatus* Robison and Richards, 1981, *Anomalocaris magnabasis* Pates et al., 2021 (Pates et al., 2021b), *Herpetogaster collinsi* Caron et al., 2010, *Alalcomenaeus* sp., *Hurdia* sp., *Tuzoia* spp., *Ottoia* sp., an indeterminate panarthropod (KUMIP 293606, see description in the following), and an indeterminate sclerotized tergite previously considered to be a radiodont flap (Lieberman, 2003; Foster, 2014; Kimmig et al., 2019; Ortega-Hernández et al., 2019; Pates et al., 2021b).

## Materials and methods

The two specimens of the new lobopodian were studied through numerous photographs (dry and under liquid immersion) taken and provided by KUMIP staff. Photographs of KUMIP material were taken using a Canon EOS 7D Mark II at a focal length of 50 mm and using a Canon EOS 500D at a focal length of 60 mm, all by KUMIP staff. Figures were prepared using Adobe Photoshop 23.2.2. Photographs of specimens were adjusted digitally for enhanced color and contrast.

*Phylogenetic methods.*—A phylogenetic matrix of 168 morphological characters for 69 taxa was compiled, referenced primarily from previous phylogenetic studies focusing on radiodont taxa and other basal panarthropods. Many characters were modified from previous studies or added, and in the case of the phylogenetic matrix used by Zeng et al. (2023), many characters were removed, as coding discrete characters for endites and podomeres with great specificity resulted in a tree topology far less precise than coding using a smaller, but still specific, set of characters that code for the frontal appendages more generally. The trees were rooted on the aysheaiid lobopodian *Aysheaia pedunculata* Walcott, 1911b, a consistently basal species (often recovered as basal to the total-group onychophoran/total-group arthropodan split) (Howard et al., 2020). *Kerygmachela* specifically was coded following the alternative flap origin hypothesis argued for in Lerosey-Aubril and Ortega-Hernandez (2022), which is further supported by the morphology of the new lobopodian described herein. The morphological matrix was assembled using Mesquite 3.70 (Maddison and Maddison, 2021), analyzed using TNT 1.5 (Goloboff and Catalano, 2016), using New Technology Search with Sectorial Search, Rachet, Drift, and Tree Fusing all enabled under standard settings, set to find the minimum length 500 times, under equal weights (concavity constant $k = 3$, 4, 10) and under implied weighting, and with the option to collapse trees after search enabled, and visualized using TreeGraph 2.15 (Stöver and Müller, 2010). The morphological matrix and list of taxa and characters, including notes on characters added or changed from previous studies, are included with the supplementary information.

*Repositories and institutional abbreviations.*—All Pioche Shale specimens are housed at the University of Kansas, Biodiversity Institute, Division of Invertebrate Paleontology collections (KUMIP). Material of *Kerygmachela* studied through photographs for comparison is deposited at the Geological Museum, Natural History Museum of Denmark, University of Copenhagen (MGUH). The holotype of *Parvibellus avatus* Liu et al., 2022 is deposited in the Early Life Institute (ELI) of Northwest University, Xi'an, China.

## Systematic paleontology

Superphylum Panarthropoda Nielsen, 1995
Family Kerygmachelidae new family

*Type genus.*—*Kerygmachela* Budd, 1993.

*Other taxa included.*—*Utahnax* Lerosey-Aubril and Ortega-Hernández, 2022, *Mobulavermis* n. gen.

*Diagnosis.*—Lobopodians with lobopod-derived ventrolateral swimming flaps and lacking dorsal flaps or setal blades; trunk elongate, roughly cylindrical, and annulated; paired frontal appendages large and raptorial.

*Remarks.*—Although formerly grouped together under the informal title "gilled lobopodians" (Young and Vinther, 2017), the morphological disparity between *Kerygmachela* and *Pambdelurion* is evident. Their anatomical differences extend from the caudal spine (one long telson-like caudal

spine in *Kerygmachela*, contrasted with *Pambdelurion*'s short pair of annulated cerci) to their heads, where they are perhaps most different. While their large frontal appendages are outwardly similar, the head of *Pambdelurion* is also dominated by a large ventral-facing extensible mouth, lined on either side with strongly sclerotized triangular teeth (Vinther et al., 2016). The mouth of *Kerygmachela*, by contrast, is small and forward set and opens anteriorly; it apparently lacks sclerotized teeth and possesses instead a pair of stylet-like spines on either side of the mouth, originating just behind it (Park et al., 2018). Despite these differences, however, they have long been isolated from the rest of the lobopodians, with their closest relatives being basal siberiids lacking swimming flaps and eyes, and the opabiniids, with numerous eyes and their frontal appendages conjoined up to their anterior into a fleshy, annulated proboscis (a notable exception is *Omnidens amplus* Hou et al., 2006, known only from the mouthparts, which bear tremendous similarity to those of *Pambdelurion*; comparison of the two suggests that *Omnidens* could reach sizes up to 1.5–1.7 m, making it the largest known Cambrian animal, awaiting confirmation from more-complete remains). For this reason, the term "gilled lobopodian" has continued to be used, in lieu of more taxa to clarify their relationships with other lobopodians. The description of *Utahnax* (Lerosey-Aubril and Ortega-Hernández, 2022) was a welcome and necessary addition to this grade of flap-bearing lobopodians and cast further doubt on the presence of ventral lobopods in *Kerygmachela*, and its relationship to *Pambdelurion*. The discovery of yet another new flap-bearing lobopodian closely related to *Kerygmachela* allows the formal establishment of a family clade containing *Kerygmachela*, and yet excluding *Pambdelurion*. Whether or not ventral lobopods are genuinely absent in the kerygmachelids (*Utahnax*, *Kerygmachela*, and the new lobopodian species) could still be considered ambiguous, particularly in the case of *Kerygmachela* from the often difficult-to-interpret fossils of the Sirius Passet; however, the available evidence strongly favors the alternative hypothesis presented by Lerosey-Aubril and Ortega-Hernández (2022).

Genus *Mobulavermis* new genus

*Type species.*—*Mobulavermis adustus*, by monotypy.

*Diagnosis.*—As for type species, by monotypy.

*Etymology.*—From *Mobula*, the genus name of extant manta rays and devil rays, drawing comparison to the elongate flexible caudal spines and broad swimming flaps of *Mobula* rays, which resemble the outline of the new taxon, combined with the Latin *vermis*, meaning "worm."

*Remarks.*—As for species.

*Mobulavermis adustus* new species
Figures 1, 2, 3.1–3.4, 3.6, 4

2003 Anomalocaridid gen. indet. sp. indet.; Lieberman, p. 683, fig. 6.4.
2022 indeterminate anomalocaridid; Lerosey-Aubril and Ortega-Hernández, p. 15.

*Type specimens.*—Holotype: KUMIP 298510, part and counterpart, a large, incomplete individual preserving the posterior portion of the body, including a caudal spine. Paratype: KUMIP 298511, part and counterpart, a smaller, also incomplete individual preserving the posterior portion of the body.

*Diagnosis.*—Lobopodian with vermiform body terminating in an elongate, flexible caudal spine; numerous broad, densely packed, lobopod-derived ventrolateral body flaps strongly overlapping successively; posterior ventrolateral body flaps decreasing in size linearly toward base of caudal spine until becoming flush with trunk; ventrolateral body flap posterior margins convex, anterior margin begins perpendicular to body wall before gradually curving posteriorly.

*Occurrence.*—Pioche Formation, Combined Metals Member (Cambrian Series 2, Stage 4, *Nephrolenellus multinodus* Biozone), Lincoln County, Nevada; Ruin Wash locality, 17 km west of Panaca, west side of Chief Range, NW 1/4, SW 1/4, Sec 15, R65E TS2.

*Description.*—The holotype specimen (KUMIP 298510) of *Mobulavermis adustus* n. gen. n. sp. is a probably ventrally exposed specimen, following the interpretation of Budd (1999) where the flaps are imbricated normally; see also MGUH 32.061, which demonstrates the normal imbrication of the swimming flaps (Park et al., 2018, supp. fig. 9d, e), unlike the reverse imbrication of radiodont flaps (Daley and Edgecombe, 2014), preserving the posterior portion of the body (Fig. 1). The specimen is dark red to yellowish due to a high concentration of weathered hematite. The total length of the body is unknown, but the preserved portion of the holotype measures 80.60 mm (measured along the sagittal curve of the trunk) long and 11.5 mm at the greatest width of the trunk, excluding the ventrolateral flaps, which are easily distinguished from the trunk by a strong and steep shift in color, seen as a bright orange-yellow border on each side of the body, with little preserved between. In some places, evidence of annulation may be present (Fig. 1.1, 1.4), although little of the actual trunk surface is preserved. On either side of the preserved portion of the body are at least 11 or 12 ventrolateral swimming flaps visible (red to dark red), although they are often poorly delineated. The flaps are broad and strongly imbricated and show no evidence of annulation, ruling out the possibility that they represent large lobopodous appendages. The posterior margins of the flaps are typically more clearly visible and show a gently convex outline (Fig. 1.1, 1.2). The anterior margins of the flaps are preserved less often but are apparently perpendicular to the body wall for much of the length of the flap before also developing a slight convex curve. The maximum length of the longest exposed ventrolateral flap (close to the anterior of the body; Fig. 1.1, 1.2, 1.5) is 19.1 mm, although the flap appears to continue beyond this. The flaps appear uniformly flat and apparently without any kind of anterior zone or radiodont-like strengthening rays. The largest of the flaps, previously mentioned, perhaps shows traces of wrinkled ornamentation running distally and slightly posteriorly, similar to that
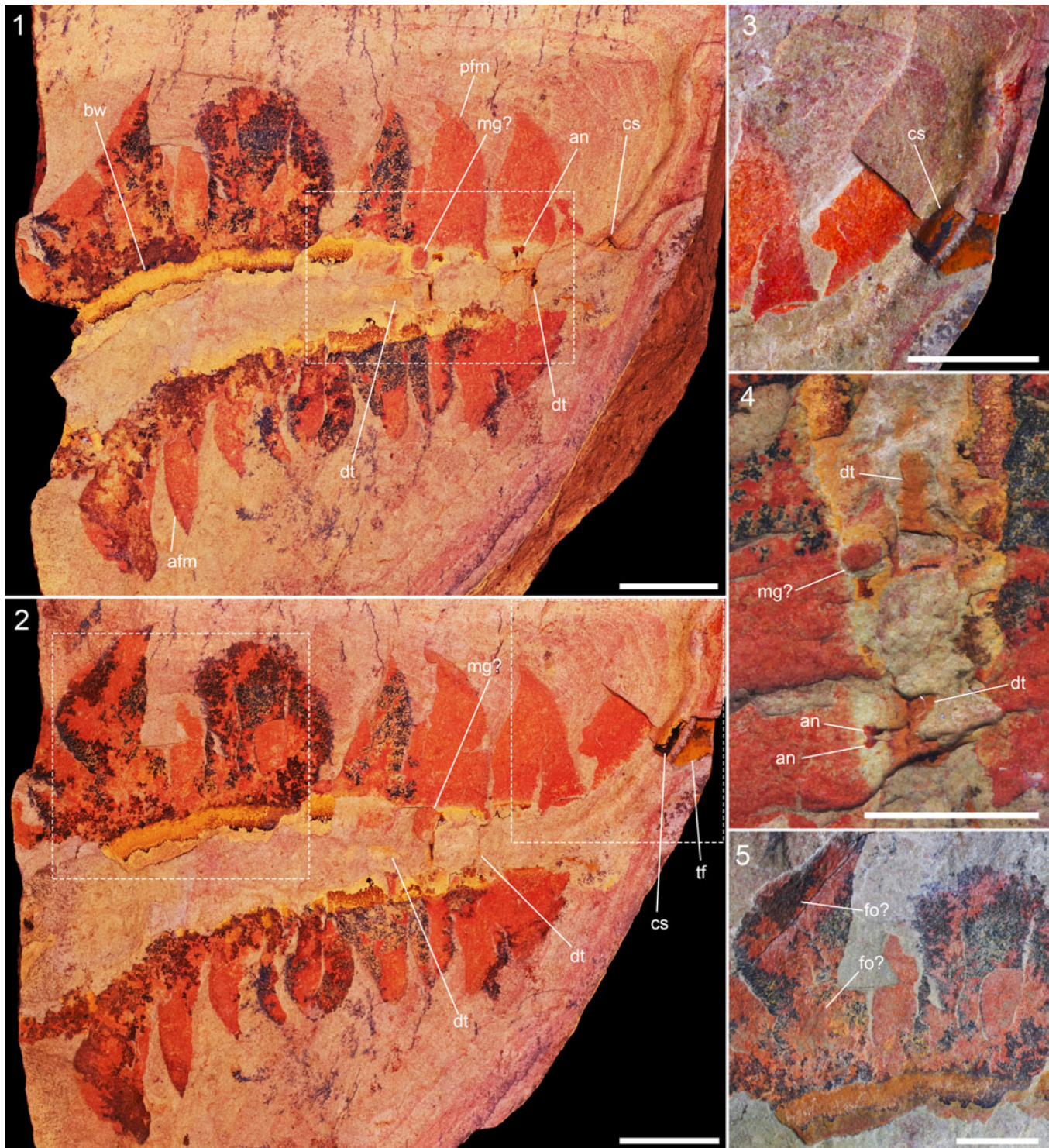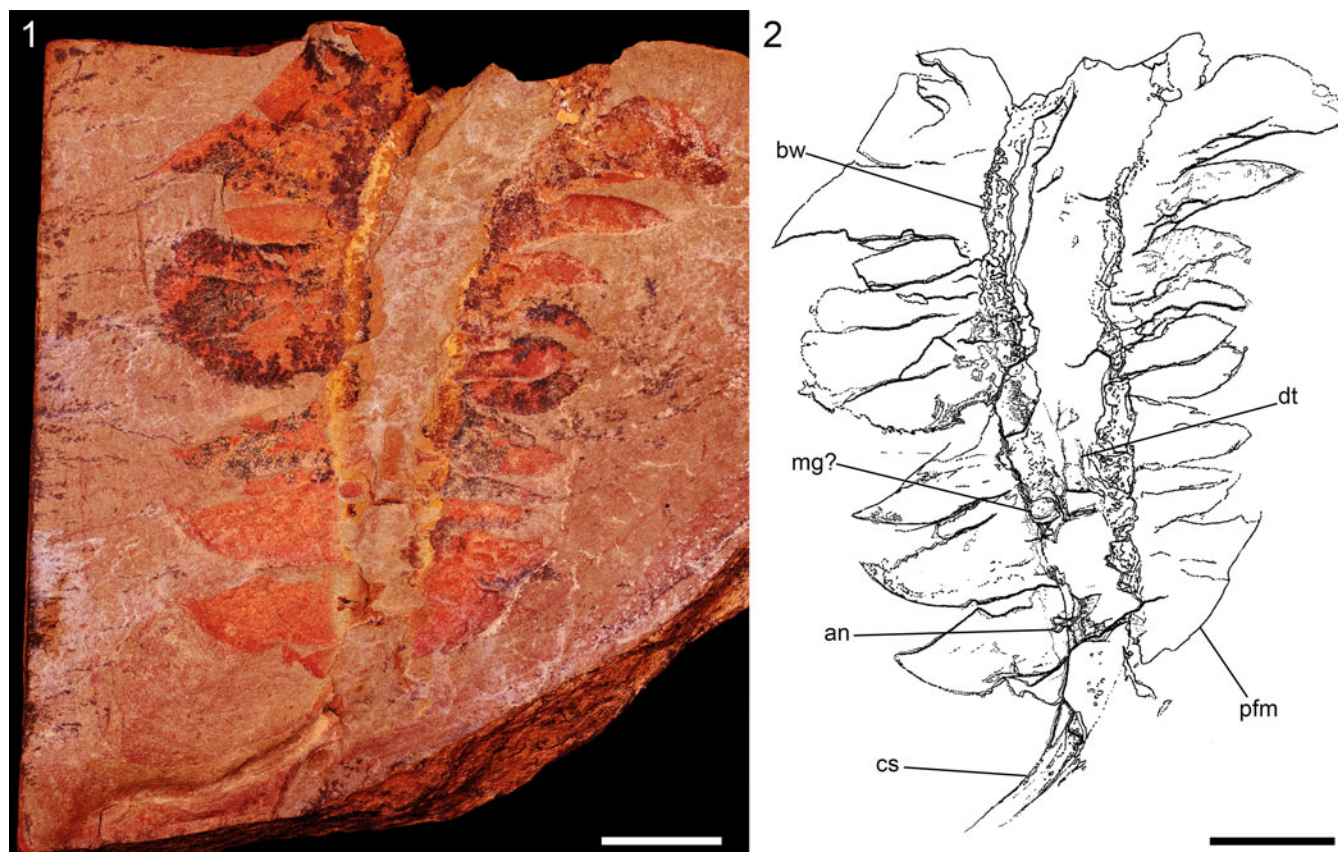
**Figure 1.** *Mobulavermis adustus* KUMIP 298510 (holotype) from the Pioche Shale, middle Cambrian, Nevada: (**1**) KUMIP 298510a (part), immersed, showing curving body and caudal spine preserved in negative relief; (**2**) KUMIP 298510b (counterpart), immersed, with caudal spine in strong positive relief; (**3**) KUMIP 298510b (counterpart), dry, closeup of caudal spine in positive relief and some reduced terminal flaps; (**4**) KUMIP 298510a (part), immersed, closeup of trunk interior, showing digestive tract, possible gut gland, and possible evidence of strong trunk annulation; (**5**) KUMIP 298510b (counterpart), dry, closeup of flap surfaces near anterior of specimen. Scale bars = 10 mm. afm = anterior flap margin; an = annulations; bw = body wall; cs = caudal spine; dt = digestive tract; fo = flap ornamentation; mg = midgut gland; pfm = posterior flap margin; tf = terminal reduced flaps.

observed in *Kerygmachela* and *Utahnax* (Lerosey-Aubril and Ortega-Hernández, 2022); however, this could also be taphonomic wrinkling.

The exposed portion of the digestive tract (Fig. 1.4), orange in color, measures 2.1 mm in width and, judging from the paratype, probably terminates at the base of the caudal spine, where
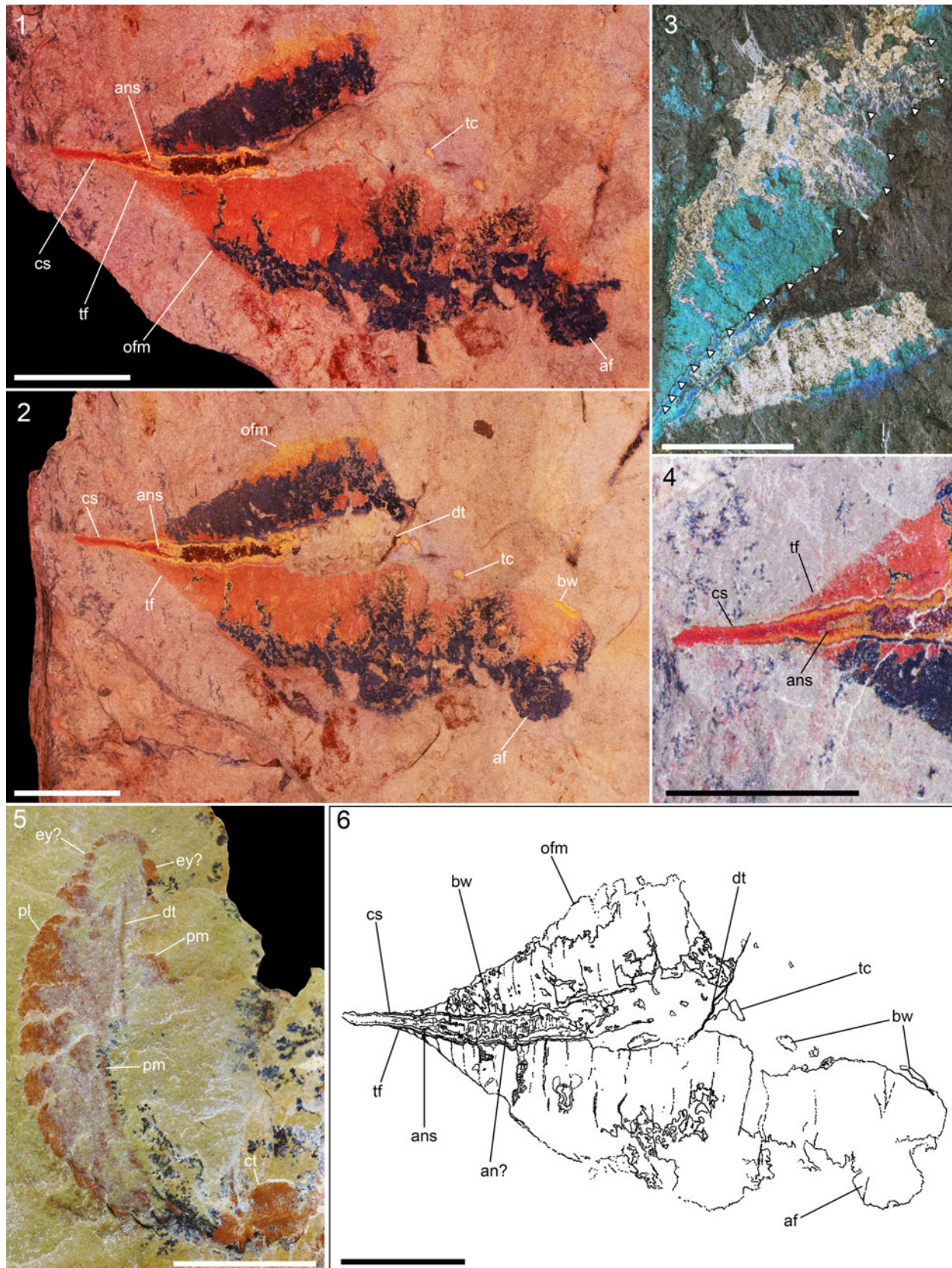
**Figure 2.** *Mobulavermis adustus* KUMIP 298510 (holotype) from the Pioche Shale, middle Cambrian, Nevada: (**1**) KUMIP 298510a (part), dry; (**2**) interpretative drawing of *Mobulavermis adustus* KUMIP 298510. Scale bars = 10 mm. Abbreviations as in Figure 1.

the flaps end. The caudal spine is elongate, unsegmented, and probably flexible and transitions smoothly from the trunk-bearing portion of the body with no marked change in width or shape, unlike what is seen in *Kerygmachela*, where the caudal spine reduces to nearly half the width of the trunk at the anus (Park et al., 2018). Notably, there is a fair degree of three-dimensional preservation to the caudal spine. The caudal spine is shorter than that of *Kerygmachela*, at least in this specimen, and probably somewhat flexible judging from the slight curve of the caudal spine seen in both the holotype and paratype, in contrast to the entirely stiff caudal spine of *Kerygmachela* (Fig. 4.7). Toward the posterior of the trunk, close to the body wall, is a single reddish subcircular structure (2.3 mm at its widest) with flat relief (Fig. 1.1, 1.2, 1.4). The structure is incomplete, unlikely to represent the insertion point of a walking limb, but could represent a gut gland or, less likely, a dorsal tubercule (Fig. 2).

The paratype specimen (KUMIP 298511) is of a smaller individual (∼ 50.7 mm along the sagittal curve of the trunk), also preserving only the posterior portion of the body (Fig. 3). The trunk in this specimen is perhaps faintly annulated and, perhaps due to its smaller size (3.3 mm at its widest), is more completely preserved, although the trunk disappears almost entirely a short distance anteriorly. Small and isolated portions of the bright orange trunk region are still present down the length of the whole specimen (Fig. 3.1, 3.2), showing that the trunk follows a gentle sinusoidal curve and probably changes little in width anteriorly. The trunk displays the same banded coloration of oranges, yellows, and dark reds observed in the holotype specimen. The posterior portion of the digestive tract (the preserved portion of which is 2.3 mm long and 0.5 mm wide) is visible as a much lighter-colored stripe in the middle of the trunk, tapering posteriorly, in contrast to the dark reds and blacks that overlie it down most of the trunk length. Where the digestive tract tapers and abruptly terminates may indicate the position of the anus, around where the ventrolateral flaps are at their smallest but just before the flaps disappear entirely, giving way to the caudal spine. The paratype specimen better illustrates the general outline of the animal. The outline, including all observable ventrolateral flaps, could be described as cordate or acuminate posteriorly, where the ventrolateral flaps are widest in the middle of the body, gently tapering toward the posterior. The tapering of the posterior flaps then becomes more gradual, such that the distal outline of the ventrolateral flaps joins smoothly to the outline of the caudal spine. The distance between successive flaps shrinks posteriorly along with their size. The caudal spine is mostly straight and appears to be incompletely preserved posteriorly. The distal outline of the ventrolateral flaps is essentially smooth and unbroken down its entire length, excluding areas where parts of the flap surface are missing. The ventrolateral flaps are mostly orange red or very dark red/black, darkening at the edges. In some places along these edges, yellowish preserved organic material appears to bleed out of the edge of the orange-red flaps (Fig. 3.2). These areas of yellow staining may

**Figure 3.** *Mobulavermis adustus* KUMIP 298511 (paratype) and indeterminate euarthropod KUMIP 293606 from the Pioche Shale, middle Cambrian, Nevada: (**1**) *Mobulavermis adustus* KUMIP 298511a (part), immersed, showing extent and outline of flaps in the posterior and middle of the body; (**2**) *Mobulavermis adustus* KUMIP 298511b (counterpart), immersed; (**3**) *Mobulavermis adustus* KUMIP 298511a (part), dry, colors inverted for clarity, with white arrows indicating approximate topographic changes between distinct lateral flaps; (**4**) *Mobulavermis adustus* KUMIP 298511b (counterpart), immersed, closeup of caudal spine and terminal reduced flaps; (**5**) Pioche euarthropod KUMIP 293606, normal color, dry; (**6**) interpretative drawing of *Mobulavermis adustus* KUMIP 298511 (paratype). Scale bars = 10 mm. af = anterior flap; ans = anus; ct = expanded caudal tergite; ey = eye; pl = pleura of tergite; pm = proximal margin of pleural region; ofm = outer flap margin; tc = trunk cuticle; other abbreviations as in Figure 1.

represent the original distal boundaries of the ventrolateral flaps or may be a taphonomic artifact. Steep changes in elevation that occur down the length of the specimen demarcate new flap surfaces, demonstrating that this is not a continuous structure but instead densely arranged flaps taking on the appearance of a continuous surface (Fig. 3.3). The preserved portion of the trunk appears to bear at least 18 or 20 ventrolateral trunk flap pairs, more than observed in any other known gilled lobopodian (Budd, 1997), radiodont (Pates et al., 2021a; Zeng et al., 2023), or opabiniid (Pates et al., 2022a). Like the holotype, the total length of the body in this specimen cannot be reliably estimated, but there were likely more flap pairs on the remainder of the body that are not preserved here.

Considering that the preserved portions of KUMIP 298510 and KUMIP 298511 are similar in overall size (80.6 mm and 50.7 mm long along the trunk, respectively), the mismatch of their relative proportions is problematic. The trunk region of KUMIP 298510 is ~3.5 times wider than that of KUMIP 298511, and the posteriormost flaps of KUMIP 298510 appear much larger and more developed than the gradually reducing flaps at the base of the caudal spine region in KUMIP 298511. While the trunk region could have grown wider proportionally through ontogeny, comparison between the two specimens, including caudal spine length and ventrolateral flap pair count, still suggests that the larger KUMIP 298510 represents the equivalent of only the posterior half of the smaller KUMIP 298511. If the trunk flap count for each specimen is correct, or close, this suggests that the complete trunk length of KUMIP 298510 may have been around 20 cm (representing only half the body portion shown in the paratype), not including the reconstructed head or frontal appendages and not considering the likely possibility that the trunk continues beyond the 18–20 flaps preserved in KUMIP 298511. At their longest from base to tip, the frontal appendages of *Kerygmachela kierkegaardi* are roughly equal in length to the flap-bearing trunk section (Park et al., 2018). By direct comparison, the frontal appendages of *Mobulavermis* could have reached up to ~20 cm, although the frontal appendages of *Mobulavermis* may have been considerably shorter (perhaps closer to only ~10 cm), as the frontal appendages of *Kerygmachela* bear extremely elongate terminal spines (the "outermost frontal processes" of Park et al. [2018]) and may represent an extreme among the group. Regardless, *Mobulavermis adustus* may have been among one of the largest known lobopodians. A conservative estimate for the total body length of *Mobulavermis*, from tail spine to the end of the frontal appendages, could be ~30 cm, and more maximally ~50 cm, assuming the holotype is fully grown.

*Etymology.*—From the Latin *adustus*, meaning "burnt," "singed," or "sun-burnt," in reference to the dramatic yellow, red, and black coloration of the two known specimens and to the arid conditions of the type locality.

*Remarks.*—*M. adustus* represents the first, and currently only, described species of lobopodian from the Pioche Shale of Nevada. The description of this new taxon is based on two specimens collected from the Ruin Wash locality in the late 1990s by Allison Palmer. Lieberman (2003) presented a report on the soft-bodied fauna of the Pioche Shale, which included a number of anomalocaridid remains, since interpreted as belonging mostly to *Anomalocaris magnabasis* (Pates et al., 2021b). Among these, three possible anomalocaridid body fossils were briefly described, the first of which was figured while the second was only discussed. The first two body fossils are here described under a new genus, while the final body specimen mentioned, KUMIP 293606, is better interpreted as a euarthropod and is inconsistent with either fossil of the species described herein or with any radiodont body fossil. This new taxon represents one of only a handful of flap-bearing lobopodians known around the world (*Pambdelurion whittingtoni*, *Kerygmachela kierkegaardi*, *Utahnax vannieri*, and *Omnidens amplus*, which is known only from the mouth [Vinther et al., 2016], which is similar enough to the smaller *Pambdelurion* that some authors consider *Omnidens* to be *Pambdelurion* sp. rather than a distinct genus [Du et al., 2020]), and even fewer in which the swimming flaps are derived from the ventrolateral lobopods (Lerosey-Aubril and Ortega-Hernández, 2022) rather than being paired with them, providing further insight into the problem of ventral lobopods in *Kerygmachela*.

<div align="center">

Phylum Euarthropoda Lankester, 1904
Class, Order, and Family uncertain
Pioche euarthropod KUMIP 293606
Figure 3.5

</div>

2003    Anomalocaridid gen. indet. sp. indet.; Lieberman, p. 683, fig. 6.3.
2009    *Anomalocaris*; Moore and Lieberman, p. 58.

*Occurrence.*—Pioche Formation, Combined Metals Member (Cambrian Series 2, Stage 4, *Nephrolenellus multinodus* Biozone), Lincoln County, Nevada; Ruin Wash locality, 17 km west of Panaca, west side of Chief Range, NW 1/4, SW 1/4, Sec 15, R65E TS2.

*Description.*—KUMIP 293606 (Fig. 3.5) is a small soft-bodied panarthropod fossil, incomplete along the right side of the trunk. The animal is curved, with the intensity of the curve increasing toward the posterior. The outline of the animal is oblong, with the widest point slightly anterior to the middle of the body. The head is preserved mostly along its margins, with a large empty space of exposed matrix occupying the middle of the cephalic region. On the left side of the head is a possible diminutive eye tucked into the margin of the head; a similar structure on the right side of the head may represent the other eye, but the differentiation from the rest of the cephalic carapace on this side is less clear. The entire specimen is a uniform orange-red color, which becomes desaturated or obscured toward the middle of the specimen, except for a distinct linear structure in the axial region, which corresponds to a thin, central gut without any obvious extensions and which terminates at about the widest point of the body, and a second linear trace that probably represents a deviation or fold in the shape of the carapace. This second trace is mirrored on the right side in a single well-preserved pleural structure. At the anterior of the specimen is a large and flat structure with a

linear trace running through its middle anteroposteriorly, probably a raised midline of the carapace. Assuming the specimen is preserved in ventral, the pleural regions imbricate normally. The distal margins of each pleural structure are mostly straight and smooth parallel to the axial region, and the anterior and posterior margins of the pleural structures are also apparently straight.

*Material.*—KUMIP 293606, a mostly complete but poorly preserved body fossil, without an accompanying counterpart.

*Remarks.*—KUMIP 293606 has been included here as it has been previously attributed to the Radiodonta alongside the two specimens of *Mobulavermis* described here (Lieberman, 2003; Moore and Lieberman, 2009) and thus warrants a comparison. However, this specimen is inconsistent with the two *Mobulavermis* specimens. The pleural structures, assumedly tergite pleura, have a broadly rectangular shape, with a sharper corner posteriorly. The preservation of the head is also inconsistent with a flap-bearing lobopodian or radiodont as, although the margins of the head are preserved, it lacks any large frontal appendages, sclerotized or not, and lacks distinct cephalic sclerites found in radiodonts, both of which should preserve more readily than the margin of the head itself. The flattened caudal tergite is also more consistent with a euarthropod than with a radiodont or lobopod. However, as the specimen is still rather poorly preserved, its exact affinities are harder to identify; the overall shape of the specimen resembles arthropods such as *Mollisonia* Walcott, 1912 and *Leanchoilia* Walcott, 1912 but matches neither exactly. *Alalcomenaeus* sp. is known from the Pioche formation by a well-preserved lateral specimen, but this specimen and a dorsoventrally preserved specimen from the Marjum show a very different carapace shape, particularly in the expansive, trapezoidal cephalon (Ortega-Hernández et al., 2019), which this specimen does not appear to have. KUMIP 293606 is left in open nomenclature.

## Discussion

*Comparisons with other flap-bearing panarthropods.*—The species most morphologically similar to *Mobulavermis adustus* n. gen n. sp. is *Kerygmachela kierkegaardi* (Fig. 4.3–4.7), with both taxa bearing broad ventrolateral swimming flaps, a roughly cylindrical body, and an elongate caudal spine devoid of flaps (Park et al., 2018). The similarity of the two genera allows for inferences on the anterior morphology of *Mobulavermis*, such as the very likely presence of sessile, ventrally situated compound eyes, a forward-facing mouth, and large raptorial frontal appendages. These inferred features, in addition to the broad flaps and the absence of walking limbs, suggest that like *Kerygmachela*, *Mobulavermis* was primarily or exclusively pelagic, although more discussion of its ecology awaits the discovery of specimens preserving the anterior morphology. *Mobulavermis* differs from *Kerygmachela* in a few aspects, however, such as *Mobulavermis* bearing many more pairs of flaps, which are densely spaced and more broadly shaped. In addition, the flaps of *Mobulavermis* gradually reduce in size until they become essentially flush with the caudal spine, which is much shorter and possibly more flexible than that of *Kerygmachela*. Compared with *Utahnax*, the swimming flaps of *Mobulavermis* appear much more derived—*Utahnax* may represent a kind of transitional form between the cylindrical limbs of siberiids and the expanded flaps of later kerygmachelids. The anterior regions of the flaps in *Utahnax* show evidence of evaginations of the body cavity (shown as darker staining of the surface) extending deep into the anterior of the flap, similar to the condition in the lobopodous limbs of siberiids and *Opabinia regalis* Walcott, 1912 (Lerosey-Aubril and Ortega-Hernández, 2022). In addition, the anterior region of the flaps in *Utahnax* preserve some three-dimensionality, suggesting that the anterior region may have been thicker than the posterior region (they also merge onto the same plane before the merge with the body, suggesting this topographic change is not evidence of a separate, hidden structure), which is essentially flat and unornamented. Thus, it could be proposed that in the Kerygmachelidae, ventrolateral flaps were developed not by uniform dorsoventral compression of the lobopod limbs, but by the extension of a flattened flap-like posterior margin, alongside the more gradual flattening of the lobopodous limb as a whole, such that the surface would be essentially flat in later genera (*Kerygmachela* and *Mobulavermis* show no obvious signs of a differentiated anterior region or any indication of the extent of the body cavity into the flaps).

The description of *Mobulavermis* lends further credibility to the hypothesis that the flaps of *Kerygmachela* and *Utahnax* are unrelated to the dorsal flaps of *Pambdelurion*, Opabiniidae, and a number of peytoiid radiodonts (Lerosey-Aubril and Ortega-Hernández, 2022). Studies on preserved musculature in panarthropods from the Sirius Passet of Greenland have suggested that musculature was absent in the flaps of *Pambdelurion* but present in the lobopodous ventral limbs (Young and Vinther, 2017). This casts doubt on the swimming capabilities of *Pambdelurion* and, by extension, the Opabiniidae, which share homologous dorsal flaps and the controversial ventral lobopods (Budd and Daley, 2012); recent discoveries, including the ventral lobopods of *Mieridduryn bonniae* Pates et al., 2022b, and small, enigmatic structures possibly attributable to lobopodous legs in the holotype of *Utaurora comosa* Pates et al., 2022a, suggest that the lobopods of *Opabinia* are genuine. That the dorsal flaps are homologous to the dorsal flaps of *Pambdelurion* also suggests *Opabinia* may have moved primarily by walking on its lobopod legs rather than as an active swimmer, as previously believed. However, the same study (Young and Vinther, 2017) on the musculature of *Pambdelurion* also failed to identify flap musculature in *Kerygmachela* (the sole specimen cited in the study as belonging to *Kerygmachela* more closely resembles *Pambdelurion* judging from its broad, anteroposteriorly tapering trunk, lack of dorsal trunk nodes, large and anteriorly widened pharynx, and wide gap between the bases of the frontal appendages).

There is at least one specimen of *Kerygmachela*, MGUH 25.053, which undoubtedly preserves muscle tissue, attributable to *Kerygmachela* by the large trunk tubercules and the mostly cylindrical trunk. In this specimen, elongate bundles of muscle fibers are found outside the boundaries of the trunk, tapering outwardly (Budd, 1999). For each metameric segment of the body, two of these bundles are developed on either side of the

body, with one pair associated with the dorsal tubercules and the other offset behind, set between successive sets of dorsal tubercules. Some of these bundles are slightly curved posteriorly. Their exact origin on the body is undetermined, but they appear to originate laterally from the body. Comparison of these muscle fiber bundles with the elongate high-relief structures, supposedly lobopodous ventral limbs in the holotype and paratype of *Kerygmachela*, shows that some of these limb-like structures are associated with the dorsal tubercules (holotype, Fig 4.3, 4.4), while in other specimens (paratype, Fig. 4.6), they are set between the dorsal tubercule rows. This would make little sense if they were interpreted as lobopodous limbs, both their inconsistent position and the apparently doubled number of limbs per segment. Triangular limb-like structures with positive relief are also found in MGUH 32.059 (Park et al., 2018, supp. fig. 8f–h), where they are associated with the dorsal tubercules, oriented perpendicular to the body, and apparently more elongate than those of the holotype and paratype of *Kerygmachela*.

In the complete specimen MGUH 32.048, comparable structures are seen in relief (although they are particularly shallow in this specimen) and under high-angle polarized light. In this specimen, both positional modes of these structures can be identified, associated with the dorsal tubercules and offset between them; these "non-neural impressions" (Park et al., 2018) extend far into the pleural region, beyond the extent of the supposed diminutive lobopod limbs (Budd, 1993, 1999). Non-neural impressions are further identified in other specimens under high-angle polarized lighting, showing reflective patches that connect to the trunk and extend a great distance into the pleural region (Park et al., 2018, supp. fig. 6). While the suggestion that one or all of these high-relief triangular structures in the holotype and paratype of *Kerygmachela* represent lobopodous ventral limbs, the deep pleural extension of the "non-neural impressions," which appear to correspond to the supposed "lobopod limbs," suggests that all of these structures may be better interpreted as muscular extensions into the ventrolateral flaps rather than distinct ventral legs. The interpretation that these two muscle-fiber bundles power a single flap rather than a pair of structures on either side of the body aligns with the known intrinsic limb musculature of *Pambdelurion*, which consists of a distinct promotor and remotor muscle which taper anteriorly, extending distally from the trunk (Young and Vinther, 2017, fig. 9). Considering the limbs of *Pambdelurion* are homologous to either the flaps or the proposed ventral lobopods of *Kerygmachela*, a similar musculature should be expected, and available material suggests that these muscles belonged to the flaps. Restudy of the type material of *Kerygmachela* also elucidated further detail on the structures originally interpreted as setal-blade gills. While Lerosey-Aubril and Ortega-Hernández (2022) described these striations as confined mostly to the distal parts of the body flaps, the holotype and paratype material show no such preference (Fig. 4.3, 4.4, 4.6). The striations, or wrinkles, are present down the entire length of the flap, ending at the trunk, directed mostly anteroposteriorly rather than posterodistally. These wrinkles overlying the paired limb-like structures (which are here interpreted as internal flap musculature) may be responsible for the appearance of "annulations" on limbs (labeled "striated limb tip" in Budd, 1999). These wrinkles are unlikely to be related to, or analogous to, the strengthening

rays of radiodonts, which must have evolved later. Their exact function is unknown, but they perhaps served a similar respiratory role to the setal-blade gills of radiodonts.

*Mobulavermis* can be differentiated from the radiodonts by its nearly cylindrical, extremely elongate trunk (judging from the portion of the trunk that is preserved), contrasted with the strongly posteriorly or anteroposteriorly tapering, rather compact bodies of radiodonts (Potin and Daley, 2023); by the absence of any associated sclerotized appendages, carapace elements, or mouthparts; and by the absence of any ornamentation on its relatively well-preserved flaps (some peytoiids with dorsal flaps such as *Aegirocassis* Van Roy et al., 2015, have trunks that are blocky in cross section and only weakly tapering posteriorly, but this condition is very dissimilar to the present fossils and always accompanied by obvious setal blades). Radiodonts exhibit a diverse array of flap morphologies, which can be separated into a few different archetypes. Anomalocaridid and amplectobeluid radiodonts have elongate, mostly lobate flaps divided into a clear anterior zone, which is robust and strengthened by vein-like strengthening rays running anterodistally from the median of the flap to the anterior margin, and a posterior zone, which is mostly smooth and featureless (Zeng et al., 2023). In *Ramskoeldia platyacantha* Cong et al., 2018 and a number of isolated body flaps from the Emu Bay Shale (Daley et al., 2013), the flaps are broad and roughly triangular, with a posterior margin essentially perpendicular to the trunk axis, with a wide anterior zone ornamented with strongly anterodistally directed strengthening rays. This occasionally leads to their confusion with the body flaps of peytoiids (Zhu et al., 2021). In peytoiids, flaps are generally short, either subcircular or triangular, and may be paired with dorsal flaps (Van Roy et al., 2015). The ventrolateral flaps of peytoiids are uniformly ornamented with strengthening rays that run from the base of the flap to the outer margin; in at least *Peytoia* Walcott, 1911a, there is also a posterior zone where the strengthening rays are absent or weak. The strengthening rays of peytoiids are well defined, while no such structures are observed in the fossils of *Mobulavermis*, nor do they match the morphology of anomalocaridid/amplectobeluid flaps with their clearly divided anterior and posterior zones. In addition, the condition of an elongate, unpaired caudal spine lacking an associated tail fan is not known in any known radiodont.

*Alternative interpretation of* Parvibellus.—The recently discovered lobopodian *Parvibellus avatus* Liu et al., 2022 from the Chengjiang Fauna of Yunnan, China, was initially interpreted as a lower stem group arthropod bearing at least 11 pairs of ventrolaterally protruding, slightly overlapping trunk flaps (Fig. 4.8) described as similar to the dorsal flaps of other Cambrian lobopodian genera such as *Opabinia* and unlike the clawed walking legs of lobopodians such as *Aysheaia*. The single known specimen of *Parvibellus* (total length 5.25 mm) also preserved a distinct, rounded head region with a large, ventrally projecting circular mouth lined with sclerotized tooth plates, no evidence supporting the presence of eyes, and two small, unsclerotized, antennae-like frontal appendages. The trunk of the specimen is wide and preserves a simple gut running from the mouth to between the terminal pair of trunk outgrowths, described as diminutive furcae. The authors
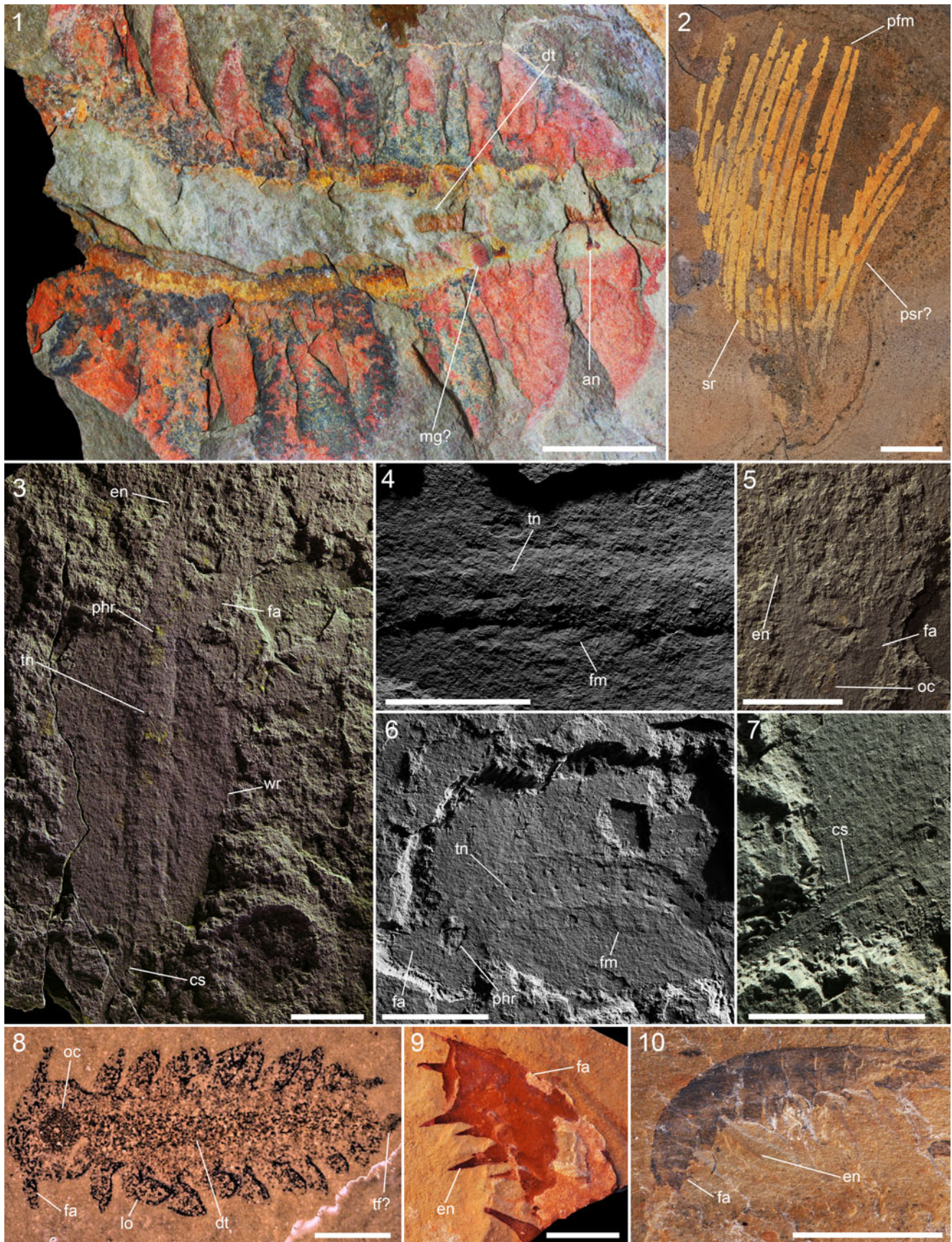
**Figure 4.** Comparison between *Mobulavermis adustus* and other lobopodian taxa: (**1**) *Mobulavermis adustus* KUMIP 298510a (holotype, part), dry, showing steep changes in elevation between successive flaps; (**2**) *Hurdia* sp. KUMIP 314057a (part) from the Spence Shale (Cambrian, Utah, USA), immersed, showing the construction of the peytoiid lateral flap as composed of numerous tightly spaced strengthening rays running the total length of the flap (note the overlapping, angled strengthening rays in the posterior of the flap); (**3**) *Kerygmachela kierkegaardi* MGUH 22.083 (holotype) from the Sirius Passet (Cambrian, Greenland); (**4**) *Kerygmachela kierkegaardi* MGUH 22.083 (holotype) from the Sirius Passet (Cambrian, Greenland), showing detail of flap wrinkles and limb-like structures; (**5**) *Kerygmachela kierkegaardi* MGUH 22.083 (holotype) from the Sirius Passet (Cambrian, Greenland), showing detail of head region; (**6**) *Kerygmachela kierkegaardi* MGUH 22.085 (paratype) from the Sirius Passet (Cambrian, Greenland); (**7**) *Kerygmachela kierkegaardi* MGUH 22.085 (paratype) from the Sirius Passet (Cambrian, Greenland), showing detail of caudal region; (**8**) *Parvibellus avatus* ELI-EJ 048A (holotype, part) from the Chengjiang Biota, Chiungchussu Formation (Cambrian, Yunnan, China) (**9**) *Anomalocaris magnabasis* KUMIP 293605 frontal appendage, immersed, from the Combined Metals Member, showing a deep red coloring, owing to heavy hematite concentration; (**10**) *Anomalocaris magnabasis* KUMIP 307022 frontal appendage, immersed, from the Comet Shale Member, which is not associated with hematitic preservation, showing a desaturated blueish hue. Photographs of *Kerygmachela* were provided by M. L. Nielsen on behalf of the Natural History Museum of Denmark. The photograph of *Parvibellus* is adapted from Liu et al. (2022), under CC BY 4.0. Scale bars = 10 mm. en = endite; fa = frontal appendage; fm = flap musculature; lo = lobopodous limbs; oc = oral cone; pfm = proximal flap margin; phr = pharynx; psr = posterior strengthening ray; sr = strengthening ray; tf = tail fan; tn = trunk dorsal node; wr = wrinkled surface of flap. Other abbreviations as in Figures 1 and 3.

excluded the possibility of the specimen representing a juvenile or larval radiodont by comparisons with known juvenile specimens of *Lyrarapax unguispinus* Cong et al., 2014, which are virtually identical to adult specimens (Liu et al., 2018) (a suite of juvenile *Stanleycaris hirpex* Pates et al., 2018 fossil specimens show that the overall shape of the radiodont body remains largely unchanged through ontogeny, with the eyes developing precociously, although there is a period of anamorphic growth where trunk segments were added posteriorly [Moysiuk and Caron, 2023]). This is highly inconsistent with an interpretation of *Parvibellus* as a radiodont. *Parvibellus* as a total-group Onychophoran lobopodian or as belonging to the more basal aysheaiids was also rejected as the trunk of *Parvibellus* is short, with stout, laterally projecting limbs lacking claws or obvious annulation. In addition, while the overall shape of *Parvibellus* could be consistent with an aysheaiid, the mouth of *Parvibellus* is obviously ventral and lined with large triangular tooth plates, while the mouth openings of aysheaiids are devoid of obvious sclerites and directed far anteriorly (Whittington, 1978).

With these groups excluded, the authors allied *Parvibellus* with the "APOK" group (Anomalocaridids, *Pambdelurion*, *Opabinia*, *Kerygmachela*). As evidence toward this placement, the authors compared the lack of eyes in their specimen with traditional reconstructions of *Pambdelurion* and *Kerygmachela*, which were both originally described as lacking eyes. However, recent evidence has demonstrated that both *Kerygmachela* and *Pambdelurion* possessed large, ventral, sessile compound eyes—long and sickle-shaped in *Kerygmachela* (Park et al., 2018) and more bulbous in *Pambdelurion* (Fleming et al., 2018). These eyes are evidenced by paired and consistently shaped reflective patches on the undersides of the head region, just posterior to the bases of the frontal appendages (in *Pambdelurion*, they flank the large ventral mouth on either side), making the argument that the lack of eyes is shared between *Parvibellus* and the traditionally defined gilled lobopodians unconvincing. This also excludes *Parvibellus* from aligning with the opabiniids *Opabinia* and *Utaurora*, while the paired and unfused frontal appendages exclude it from the possibly eyeless taxa recently described from the Castle Bank fauna of Wales (Pates et al., 2022b). The comparison between the appendages of *Parvibellus* and the dorsal flaps of opabiniids and gilled lobopodians is also in opposition with the emerging view that the dorsal flaps of *Pambdelurion* and *Opabinia* were simple extrusions of the body wall lacking muscular control and that the flaps of the kerygmachelids evolved swimming flaps independently.

Not discussed by the authors, or included within the phylogenetic analysis and matrix accompanying the description, is the possibility that the specimen represents one of the slightly more basal siberiid lobopodians, more closely related to the gilled lobopodians and radiodonts than to the total-group onychophoran lobopodians such as *Hallucigenia* Conway Morris, 1977 or *Microdictyon* Bengston et al., 1986 (Smith and Ortega-Hernández, 2014). Siberiids are very uncommon among lobopodians but easily identified by their broad, mostly uniform trunk regions, paired lobopodous limbs projecting ventrolaterally, absence of any claws on the trunk limbs, large raptorial frontal appendages, ventrally projecting mouth bearing a circumoral ring of triangular sclerites, and lack of eyes. This is in addition to the differences in preservation between Burgess Shale fossils and other Chengjiang fossils, which make some direct comparisons between *Parvibellus* and fossils of *Opabinia* problematic. Whereas in *Opabinia* the flaps lie on different bedding planes, with individual flaps marked by small and sudden changes in elevation (Whittington, 1975), the fossil of *Parvibellus* is preserved on a single bedding plane. In *Parvibellus*, dark outlines trace the shapes of the appendages and, although they may have been slightly warped taphonomically, show that the overlapping of the appendages, and overall shape and flexibility, are much more in line with the interpretation of these appendages as siberiid-like lobopodous walking legs rather than flattened, reverse-imbricated swimming flaps. The appendages of *Parvibellus* are elongate and highly flexible, preserved orientated at inconsistent angles; they mostly overlap each other by the curling and compression of appendages over-top of one another, not overlapping at their bases as is observed in gilled lobopodians and most radiodont taxa.

*Parvibellus* differs from the siberiids in a few notable ways, however. The lobopods of the siberiids bear repeated elongate papillae lining the posterior margin of the trunk appendages (Dzik, 2011), which perhaps served a respiratory function to support a more active, predatory lifestyle more comparable to the gill-bearing opabiniids and radiodonts, while *Parvibellus* lacks any such structures. The largest of the siberiids, *Jianshanopodia*, capable of reaching over 30 cm long judging from comparisons of ELI−J0005A to complete specimens of *Jianshanopodia* and *Megadictyon*, has elongate, tree-like papillae projecting from the posterior margins of its lobopods (Liu et al., 2006; Dzik, 2011). These additional branches to the main structure could have greatly increased the surface area if these papillae served a respiratory function, similar to the convoluted surface of the respiratory setal blades in *Aegirocassis*.

Regarding the digestive tract observed in *Parvibellus*, it appears to lack any kind of diverticula structures, in contrast to the well-developed digestive tracts of other Chengjiang siberiids (Vannier et al., 2014) (although gut glands may be absent in *Siberion*). Finally, the frontal appendages of *Parvibellus* are small and undeveloped, while the frontal appendages of known siberiids are robust and bear raptorial endites or even claws at their tips (Vannier et al., 2014). The lack of these features in *Parvibellus* could, however, be explained by ontogenetic changes. The smallest known siberiid, *Siberion lenaicus* Dzik, 2011, is thought to have reached a maximum length of approximately 50–60 mm, judging from the more complete of the two known specimens (Dzik, 2011), while the sole specimen of *Parvibellus* measures only just over 5 mm, ~10 times smaller than *Siberion*. The diminutive size of the specimen would not immediately demand the growth of respiratory papillae as the existing surface area of the body would satisfy oxygen requirements. Restricting comparisons to only the Chengjiang Fauna, from which *Parvibellus* and the majority of siberiid species derive, possible adult forms become much larger, suggesting that *Parvibellus* could be a very early instar. The size and probably early developmental stage of the specimen could also explain the lack of any raptorial adaptations to the frontal appendages as individuals at this stage must have depended on a very different food source or prey than their large adult counterparts. The posteriormost portion of the specimen is poorly preserved, and a large area of it is missing. What is interpreted as a presumably paired furca-like structure may be interpreted as a reduced limb or part of a caudal fan, as observed in *Jianshanopodia* (Liu et al., 2006), or it may represent part of a medial lobe-like structure as seen in both *Jianshanopodia* and *Siberion* (Dzik, 2011). The interpretation of this structure as one of two paired furcae may also be correct. Because it probably represents a larval individual of an existing genus or species of siberiid lobopodian, and otherwise cannot be identified conclusively due to its probable immaturity, *Parvibellus* is here considered a nomen dubium and has not been included in the present phylogenetic analysis.

*Phylogenetic relationships.*—The tree topology (Fig. 5) recovered by analysis of the modified matrix is broadly similar to previously recovered topologies from other studies on radiodont systematics. The trees were rooted with *Aysheaia*, a consistently basal panarthropod (Howard et al., 2020). The most-basal clade of total-group Euarthropoda, the Siberiidae (Dzik, 2011), contains *Jianshanopodia* Liu et al., 2006, *Siberion* Dzik, 2011, and *Megadictyon* Luo and Hu in Luo et al., 1999. *Megadictyon* is more poorly understood than the former two genera, with the type species initially known only from a section of the trunk bearing large, robust limbs and diverticulae, missing both the anterior and posterior sections of the body. Because of this ambiguity in the holotype, all subsequent, more-complete specimens have been attributed only tentatively to the genus, under *Megadictyon* cf. *M. haikouensis* (Liu et al., 2007). There are several more indeterminate siberiid lobopodian fossils from the Chengjiang Fauna (Vannier et al., 2014), but these were not included in the study. A new clade of three taxa, including *Utahnax vannieri*, *Kerygmachela kierkegaardi*, and *Mobulavermis adustus* n. gen. n. sp., is

recovered in all trees under both equal weighting and implied weighting. In past studies, the informal name gilled lobopodians was used to join *Kerygmachela* and *Pambdelurion*. No formal name was established to unite the two genera, however, as the two genera formed a grade basal to the opabiniids, radiodonts, and arthropods rather than a distinct clade of closely related animals. The descriptions of *Utahnax vannieri* and of *Mobulavermis adustus* (Fig. 6) allow a more confident separation of *Pambdelurion whittingtoni* (and by extension, *Omnidens amplus*, which clades with *Pambdelurion*) from *Kerygmachela* and the establishment of a new formal clade between Siberiidae and the Opabiniidae (a monophyletic clade of *Opabinia regalis* and *Utaurora comosa* is present in all recovered trees, while the inclusion of the Castle Bank taxa is uncertain).

Deuteropoda is recovered as sister to Radiodonta and is rooted in a polytomy of the recently described *Erratus sperare* Fu et al., 2022 and (under equal weighting) the much earlier discovered *Cucumericrus decoratus* Hou et al., 1995. Both possess elongate unsclerotized trunk regions (save for the single large tergite that covers the head and much of the body in *Erratus*; a similar tergite is assumed to be present in *Cucumericrus* by phylogenetic bracketing but is not known from direct fossil evidence), with biramous appendages consisting of a lobopodous or distally sclerotized (Simonetta, 2004) walking limb and a soft dorsolateral flap. They are followed by the Isoxyidae and then by the euarthropods, including *Kylinxia zhangi* Zeng et al., 2020 (Izquierdo-López and Caron, 2022). A probable group of "paranomalocaridids", composed of *Paranomalocaris* and a recently figured undescribed species from the Kinzers Formation, were excluded from the matrix due to a relative absence of relevant applicable characters and the lack of any known remains besides the frontal appendages. The paranomalocaridids were similarly excluded from the analysis by Zeng et al. (2023) with the additional reason of their radiodont affinities being questionable overall. *Caryosyntrips* Daley and Budd, 2010, typically classed as a basal radiodont, is here recovered as basal to both Radiodonta and Deuteropoda. *Caryosyntrips* is recovered in a similar position by Moysiuk and Caron (2019) and found in a polytomy with Deuteropoda and Radiodonta by Lerosey-Aubril and Pates (2018) and by Moysiuk and Caron (2021). The analysis by Zeng et al. (2023) found *Caryosyntrips* as within Euarthropoda, rather than sister to it, or within Radiodonta.

A monophyletic Peytoiidae is rooted under equal weighting at two recently discovered fossils from the Chengjiang Fauna (Wu et al., 2022) attributed to Peytoiidae, but which both possess posteriorly oriented pectinate auxiliary spines, in contrast to the forward-facing or mesially oriented pectinate endites of all other peytoiids. The family name Peytoiidae is employed rather than "Hurdiidae" because, as pointed out by Greenfield (2023), the family name Hurdiidae has yet to be properly established following ICZN standards, and the name Peytoiidae (Conway Morris and Robison, 1982) is, as the oldest and only available name for the clade, the correct name to use. The known members of the Tamisiocarididae all form a polytomy with the base of Peytoiidae. Notably, *Houcaris saron* Hou et al., 1995, as well as "*Ramskoeldia*" *consimilis* Cong et al., 2018, which is here included under the genus *Houcaris* (see Supplementary Information), are not recovered as
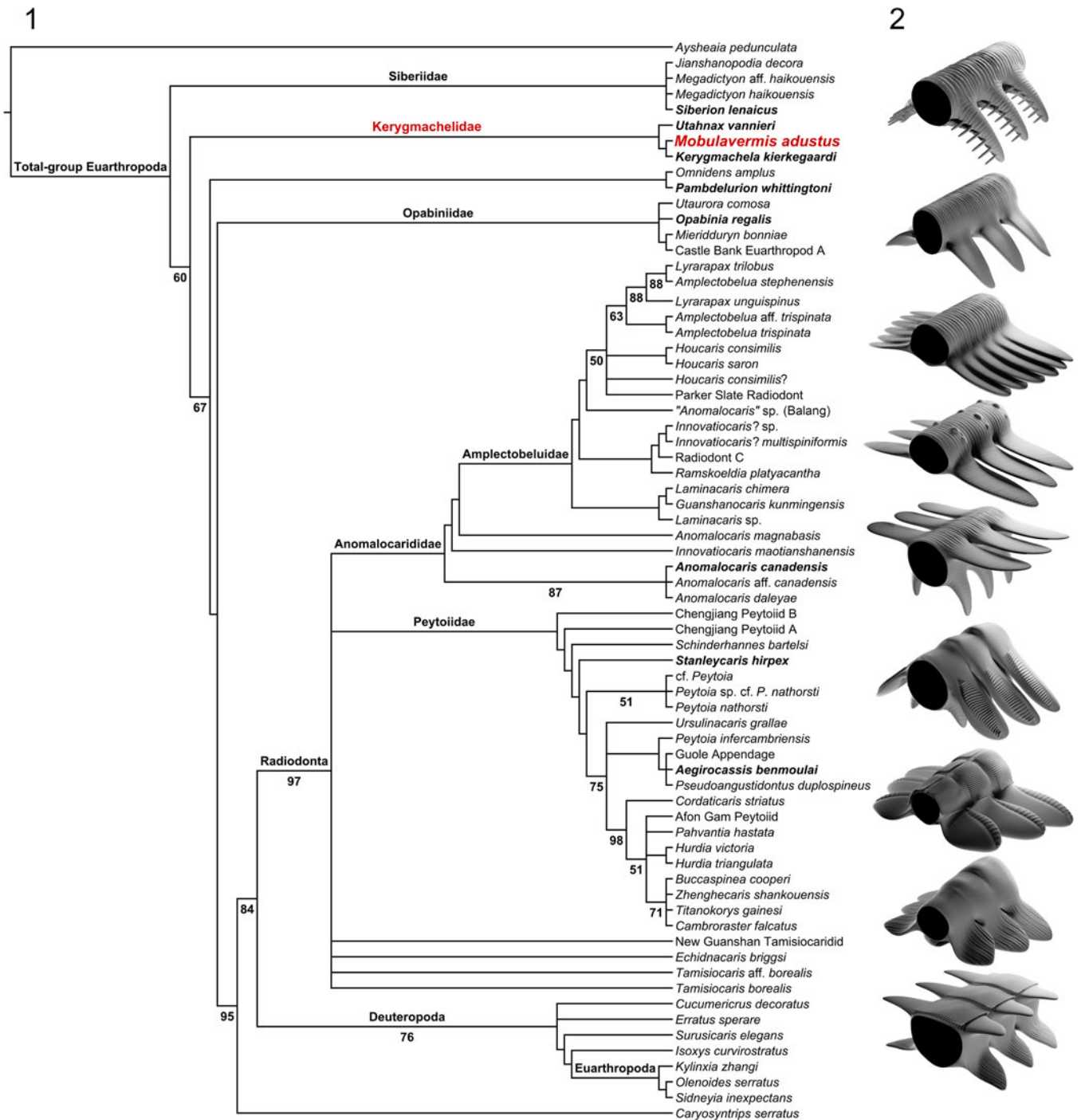
**Figure 5.** Phylogenetic results. (**1**) Majority-rule (50%) consensus of 299 most parsimonious trees under equal weighting (CI = 0.518, RI = 0.820), with newly named taxa highlighted and representative taxa bolded. Numbers beneath branches represent the percentage of trees in which that node was recovered, while branches without percentages are present in all trees. (**2**) Simplified trunk body plans of representative lobopodian and radiodont taxa (showing arrangements of annulation, setal blades, and limbs), in same order as bolded names. Models are shown facing away and to the right.

tamisiocaridids as recently described (Wu et al., 2021a) but consistently as members of Amplectobeluidae.

Two species tentatively attributed to *Innovatiocaris*? in the description of *Innovatiocaris maotianshanensis* Zeng et al., 2023 form a monophyletic group within lower Amplectobeluidae, distant from the type species in Anomalocarididae, indicating they probably belong to a distinct genus. They are similar to the type species in their lack of posteriorly oriented auxiliary spines but easily differentiated by the outward kink separating the shaft and distal articulated regions, the hypertrophied first distal articulated zone endite pair, and the highly reduced or absent shaft endites in *Innovatiocaris*? *multispiniformis* Zeng et al., 2023 and *Innovatiocaris* sp., all distinctive traits of amplectobeluids. This morphological disparity warrants the
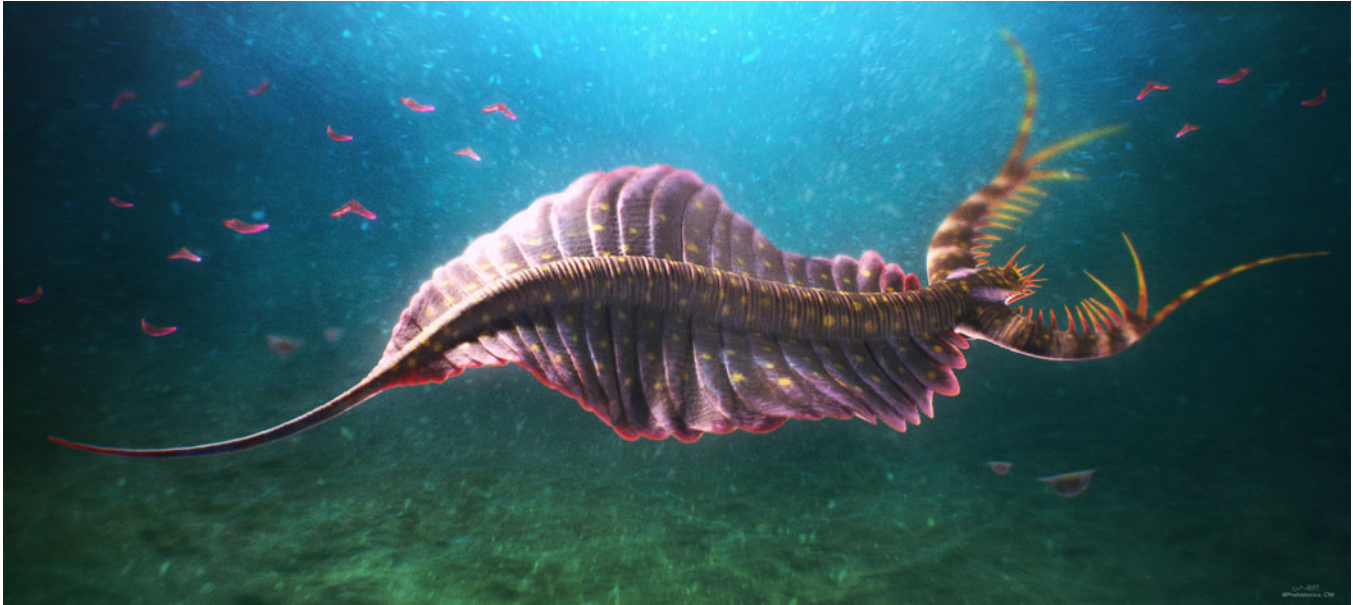
**Figure 6.** Digital life reconstruction of *Mobulavermis adustus,* shown swimming in a Cambrian ocean alongside small bivalved arthropods and early chordates (speculative anterior morphology based on *Kerygmachela kierkegaardi*).

establishment of a new genus, but this is outside the scope of the current study. *Laminacaris* Guo et al., 2019 is recovered as a basal amplectobeluid alongside *Guanshancaris kunmingensis* Wang et al., 2013, alongside "*Anomalocaris*" sp. from the Balang Formation (Liu, 2013), although the placement of "*Anomalocaris*" sp. should be viewed with caution until more complete material is described.

## Acknowledgments

## Declaration of competing interests

The author declares no competing interest.

## Data availability statement

The morphological matrix used for the phylogenetic analyses performed for this study, as well as an explanatory document detailing the matrix with notes on the coding of certain taxa, are available from MorphoBank (www.morphobank.org) doi:10.7934/P4884, at the permalink: https://morphobank.org/permalink/?P4884.

## References

Budd, G., 1993, A Cambrian gilled lobopod from Greenland: Nature, v. 364, p. 709–711.

Budd, G.E., 1997, Stem group arthropods from the Lower Cambrian Sirius Passet fauna of North Greenland, in Fortey, R.A. and Thomas, R.H., eds., Arthropod Relationships: Dordrecht, Springer Netherlands, p. 125–138.

Budd, G.E., 1999, The morphology and phylogenetic significance of Kerygmachela kierkegaardi Budd (Buen Formation, Lower Cambrian, N Greenland): Earth and Environmental Science Transactions of The Royal Society of Edinburgh, v. 89, p. 249–290.

Budd, G.E., and Daley, A.C., 2012, The lobes and lobopods of *Opabinia regalis* from the middle Cambrian Burgess Shale: Lethaia, v. 45, p. 83–95.

Caron, J., and Aria, C., 2020, The Collins' monster, a spinous suspension-feeding lobopodian from the Cambrian Burgess Shale of British Columbia: Palaeontology, v. 63, p. 979–994.

Caron, J.-B., Morris, S.C., and Shu, D., 2010, Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes: PLoS ONE, v. 5, n. e9586, https://doi.org/10.1371/journal.pone.0009586.

Cong, P., Ma, X., Hou, X., Edgecombe, G.D., and Strausfeld, N.J., 2014, Brain structure resolves the segmental affinity of anomalocaridid appendages: Nature, v. 513, p. 538–542.

Cong, P.-Y., Edgecombe, G.D., Daley, A.C., Guo, J., Pates, S., and Hou, X.-G., 2018, New radiodonts with gnathobase-like structures from the Cambrian Chengjiang biota and implications for the systematics of Radiodonta: Papers in Palaeontology, v. 4, p. 605–621.

Conway Morris, S, 1977, A new metazoan from the Cambrian Burgess Shale of British Columbia: Palaeontology, v. 20, p. 623–640.

Conway Morris, S.C., and Robison, R.A., 1982, The enigmatic medusoid *Peytoia* and a comparison of some Cambrian biotas: Journal of Paleontology, v. 56, p. 116–122.

Daley, A.C., and Budd, G.E., 2010, New anomalocaridid appendages from the Burgess Shale, Canada: Palaeontology, v. 53, p. 721–738.

Daley, A.C., and Edgecombe, G.D., 2014, Morphology of *Anomalocaris canadensis* from the Burgess Shale: Journal of Paleontology, v. 88, p. 68–91.

Daley, A.C., Paterson, J.R., Edgecombe, G.D., García-Bellido, D.C., and Jago, J.B., 2013, New anatomical information on Anomalocaris from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits: Palaeontology, v. 56, p. 971–990.

Du, K., Ortega-Hernández, J., Yang, J., Yang, X., Guo, Q., et al., 2020, A new early Cambrian Konservat-Lagerstätte expands the occurrence of Burgess Shale-type deposits on the Yangtze Platform: Earth-Science Reviews, v. 211, n. 103409, https://doi.org/10.1016/j.earscirev.2020.103409.

Dzik, J., 2011, The xenusion-to-anomalocaridid transition within the lobopodians: Bollettino della Società Paleontologica Italiana, v. 50, p. 65–74.

Fleming, J.F., Kristensen, R.M., Sørensen, M.V., Park, T.-Y.S., Arakawa, K., et al., 2018, Molecular palaeontology illuminates the evolution of ecdysozoan vision: Proceedings of the Royal Society B: Biological Sciences, v. 285, n. 20182180, https://doi.org/10.1098/rspb.2018.2180.

Foster, J., 2014, Cambrian Ocean World: Ancient Sea Life of North America: Bloomington, Indiana, Indiana University Press.

Fu, D., Legg, D.A., Daley, A.C., Budd, G.E., Wu, Y., and Zhang, X., 2022, The evolution of biramous appendages revealed by a carapace-bearing Cambrian arthropod: Philosophical Transactions of the Royal Society B: Biological Sciences, v. 377, n. 20210034, https://doi.org/10.1098/rstb.2021.0034.

Goloboff, P.A., and Catalano, S.A., 2016, TNT version 1.5, including a full implementation of phylogenetic morphometrics: Cladistics, v. 32, p. 221–238.

Gould, S.J., 1989, Wonderful Life: The Burgess Shale and the Nature of History (first edition): New York, W.W. Norton, 347 p.

Greenfield, T., 2023, "Hurdiidae" versus Peytoiidae: Incertae Sedis, https://incertaesedisblog.wordpress.com/2023/01/ (accessed Mar 2023).

Guo, J., Pates, S., Cong, P., Daley, A.C., Edgecombe, G.D., Chen, T., and Hou, X., 2019, A new radiodont (stem Euarthropoda) frontal appendage with a mosaic of characters from the Cambrian (Series 2 Stage 3) Chengjiang biota: Papers in Palaeontology, v. 5, p. 99–110.

Hou, X.G., Bergström, J., and Ahlberg, P., 1995, *Anomalocaris* and other large animals in the lower Cambrian Chengjiang fauna of southwest China: GFF, v. 117, p. 163–183.

Hou, X.G., Bergström, J., and Jie, Y., 2006, Distinguishing anomalocaridids from arthropods and priapulids: Geological Journal, v. 41, p. 259–269.

Howard, R.J., Hou, X., Edgecombe, G.D., Salge, T., Shi, X., and Ma, X., 2020, A tube-dwelling early Cambrian Lobopodian: Current Biology, v. 30, p. 1529–1536.e2.

Howard, R.J., Giacomelli, M., Lozano-Fernandez, J., Edgecombe, G.D., Fleming, J.F., et al., 2022, The Ediacaran origin of Ecdysozoa: integrating fossil and phylogenomic data: Journal of the Geological Society, v. 179, n. jgs2021-107, https://doi.org/10.1144/jgs2021-107.

Izquierdo-López, A., and Caron, J.-B., 2022, The problematic Cambrian arthropod Tuzoia and the origin of mandibulates revisited: Royal Society Open Science, v. 9, n. 220933, https://doi.org/10.1098/rsos.220933.

Kimmig, J., Meyer, R.C., and Lieberman, B.S., 2019, Herpetogaster from the early Cambrian of Nevada (Series 2, Stage 4) and its implications for the evolution of deuterostomes: Geological Magazine, v. 156, p. 172–178.

Kühl, G., Briggs, D.E.G., and Rust, J., 2009, A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany: Science, v. 323, p. 771–773.

Lankester, E.R., 1904, Memoirs: the structure and classification of the Arthropoda: Quarterly Journal of Microscopical Science, v. 47, p. 523–582.

Lerosey-Aubril, R., and Ortega-Hernández, J., 2022, A new lobopodian from the middle Cambrian of Utah: did swimming body flaps convergently evolve in stem-group arthropods? Papers in Palaeontology, v. 8, n. e1450, https://doi.org/10.1002/spp2.1450.

Lerosey-Aubril, R., and Pates, S., 2018, New suspension-feeding radiodont suggests evolution of microplanktivory in Cambrian macronekton: Nature Communications, v. 9, n. 3774, https://doi.org/10.1038/s41467-018-06229-7.

Lieberman, B.S., 2003, A new soft-bodied fauna: the Pioche Formation of Nevada: Journal of Paleontology, v. 77, p. 674–690.

Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X., 2006, A large xenusiid lobopod with complex appendages from the lower Cambrian Chengjiang Lagerstätte: Acta Palaeontologica Polonica, v. 51, p. 215–222.

Liu, J., Shu, D., Han, J., Zhang, Z., and Zhang, X., 2007, Morpho-anatomy of the lobopod *Magadictyon* cf. *haikouensis* from the early Cambrian Chengjiang Lagerstätte, South China: Acta Zoologica, v. 88, p. 279–288.

Liu, J., Lerosey-Aubril, R., Steiner, M., Dunlop, J.A., Shu, D., and Paterson, J.R., 2018, Origin of raptorial feeding in juvenile euarthropods revealed by a Cambrian radiodontan: National Science Review, v. 5, p. 863–869.

Liu, J., Dunlop, J.A., Steiner, M., and Shu, D., 2022, A Cambrian fossil from the Chengjiang fauna sharing characteristics with gilled lobopodians, opabiniids and radiodonts: Frontiers in Earth Science, v. 10, https://doi.org/10.3389/feart.2022.861934.

Liu, Q., 2013, The first discovery of anomalocaridid appendages from the Balang Formation (Cambrian Series 2) in Hunan, China: Alcheringa: An Australasian Journal of Palaeontology, v. 37, p. 338–343.

Luo, H.L., Hu, S.X., Chen, L.Z., Zhang, S.S., and Tao, Y.H., 1999, [Early Cambrian Chengjiang Fauna from Kunming region, China]: Kunming, China, Yunnan Science and Technology Press, 129 p. [In Chinese with English summary]

Maddison, W.P., and Maddison, D.R., 2021, Mesquite: a modular system for evolutionary analysis, v. 3.70: http://www.mesquiteproject.org (accessed Mar 2023).

Moore, R.A., and Lieberman, B.S., 2009, Preservation of early and middle Cambrian soft-bodied arthropods from the Pioche Shale, Nevada, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 277, p. 57–62.

Moysiuk, J., and Caron, J.-B., 2019, A new hurdiid radiodont from the Burgess Shale evinces the exploitation of Cambrian infaunal food sources: Proceedings of the Royal Society B: Biological Sciences, v. 286, n. 20191079, https://doi.org/10.1098/rspb.2019.1079.

Moysiuk, J., and Caron, J.-B., 2021, Exceptional multifunctionality in the feeding apparatus of a mid-Cambrian radiodont: Paleobiology, v. 47, p. 704–724.

Moysiuk, J., and Caron, J.-B., 2022, A three-eyed radiodont with fossilized neuroanatomy informs the origin of the arthropod head and segmentation: Current Biology, v. 32, p. 3302–3316.e2.

Moysiuk, J., and Caron, J.-B., 2023, A quantitative assessment of ontogeny and molting in a Cambrian radiodont and the evolution of arthropod development: Paleobiology, https://doi.org/10.1017/pab.2023.18.

Murdock, D.J.E., Gabbott, S.E., and Purnell, M.A., 2016, The impact of taphonomic data on phylogenetic resolution: *Helenodora inopinata* (Carboniferous, Mazon Creek Lagerstätte) and the onychophoran stem lineage: BMC Evolutionary Biology, v. 16, n. 19, https://doi.org/10.1186/s12862-016-0582-7.

Nielsen, C., 1995, Animal Evolution: Interrelationships of the Living Phyla: Oxford, Oxford University Press, 402 p.

Ortega-Hernández, J., Lerosey-Aubril, R., and Pates, S., 2019, Proclivity of nervous system preservation in Cambrian Burgess Shale-type deposits: Proceedings of the Royal Society B: Biological Sciences, v. 286, n. 20192370, https://doi.org/10.1098/rspb.2019.2370.

Park, T.-Y.S., Kihm, J.-H., Woo, J., Park, C., Lee, W.Y., Smith, M.P., Harper, D.A.T., Young, F., Nielsen, A.T., and Vinther, J., 2018, Brain and eyes of *Kerygmachela* reveal protocerebral ancestry of the panarthropod head: Nature Communications, v. 9, n. 1019, https://doi.org/10.1038/s41467-018-03464-w.

Pates, S., Daley, A.C., and Ortega-Hernandez, J., 2018, Reply to comment on "*Aysheaia prolata* from the Utah Wheeler Formation (Drumian, Cambrian) is a frontal appendage of the radiodontan *Stanleycaris*" with the formal description of *Stanleycaris*: Acta Palaeontologica Polonica, v. 63, p. 105–110.

Pates, S., Lerosey-Aubril, R., Daley, A.C., Kier, C., Bonino, E., and Ortega-Hernández, J., 2021a, The diverse radiodont fauna from the Marjum Formation of Utah, USA (Cambrian: Drumian): PeerJ, v. 9, n. e10509, https://doi.org/10.7717/peerj.10509.

Pates, S., Daley, A.C., Edgecombe, G.D., Cong, P., and Lieberman, B.S., 2021b, Systematics, preservation and biogeography of radiodonts from the southern Great Basin, USA, during the upper Dyeran (Cambrian Series 2, Stage 4): Papers in Palaeontology, v. 7, p. 235–262.

Pates, S., Botting, J.P., Muir, L.A., and Wolfe, J.M., 2022a, Ordovician opabiniid-like animals and the role of the proboscis in euarthropod head evolution: Nature Communications, v. 13, n. 6969, https://doi.org/10.1038/s41467-022-34204-w.

Pates, S., Wolfe, J.M., Lerosey-Aubril, R., Daley, A.C., and Ortega-Hernández, J., 2022b, New opabiniid diversifies the weirdest wonders of the euarthropod stem group: Proceedings of the Royal Society B: Biological Sciences, v. 289, n. 20212093, https://doi.org/10.1098/rspb.2021.2093.

Potin, G.J.-M., and Daley, A.C., 2023, The significance of Anomalocaris and other Radiodonta for understanding paleoecology and evolution during the Cambrian explosion: Frontiers in Earth Science, v. 11, https://doi.org/10.3389/feart.2023.1160285.

Robison, R.A., and Richards, B.C., 1981, Larger bivalve arthropods from the middle Cambrian of Utah: The University of Kansas Paleontological Contributions Paper 106, http://hdl.handle.net/1808/3757.

Simonetta, A.M., 2004, Are the traditional classes of arthropods natural ones? Recent advances in palaeontology and some considerations on morphology: Italian Journal of Zoology, v. 71, p. 247–264.

Smith, M.R., and Ortega-Hernández, J., 2014, Hallucigenia's onychophoran-like claws and the case for Tactopoda: Nature, v. 514, p. 363–366.

Stöver, B.C., and Müller, K.F., 2010, TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses: BMC Bioinformatics, v. 11, n. 7, https://doi.org/10.1186/1471-2105-11-7.

Vannier, J., Liu, J., Lerosey-Aubril, R., Vinther, J., and Daley, A.C., 2014, Sophisticated digestive systems in early arthropods: Nature Communications, v. 5, n. 3641, https://doi.org/10.1038/ncomms4641.

Van Roy, P., Daley, A.C., and Briggs, D.E.G., 2015, Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps: Nature, v. 522, p. 77–80.

Vinther, J., Porras, L., Young, F.J., Budd, G.E., and Edgecombe, G.D., 2016, The mouth apparatus of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*: Palaeontology, v. 59, p. 841–849.

Walcott, C.D., 1911a, Middle Cambrian holothurians and medusae: Smithsonian Miscellaneous Collections, v. 57, p. 41–68.

Walcott, C.D., 1911b, Middle Cambrian annelids; Smithsonian Miscellaneous Collection, v. 57, p. 109–144.

Walcott, C.D., 1912, Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata: Smithsonian Miscellaneous Collections, v. 57, p. 145–228.

Wang, Y., Huang, D., and Hu, S., 2013, New anomalocardid frontal appendages from the Guanshan biota, eastern Yunnan: Chinese Science Bulletin, v. 58, p. 3937–3942.

Whittington, H.B., 1975, The enigmatic animal *Opabinia regalis*, middle Cambrian, Burgess Shale, British Columbia: Philosophical Transactions of the Royal Society of London B, Biological Sciences, v. 271, p. 1–43.

Whittington, H.B., 1978, The lobopod animal *Aysheaia pedunculata* Walcott, middle Cambrian, Burgess Shale, British Columbia: Philosophical Transactions of the Royal Society of London B, Biological Sciences, v. 284, p. 165–197.

Wotte, T., and Sundberg, F.A., 2017, Small shelly fossils from the Montezuman–Delamaran of the Great Basin in Nevada and California: Journal of Paleontology, v. 91, p. 883–901.

Wu, Y., Fu, D., Ma, J., Lin, W., Sun, A., and Zhang, X., 2021a, *Houcaris* gen. nov. from the early Cambrian (Stage 3) Chengjiang Lagerstätte expanded the palaeogeographical distribution of tamisiocaridids (Panarthropoda: Radiodonta): PalZ, v. 95, p. 209–221.

Wu, Y., Ma, J., Lin, W., Sun, A., Zhang, X., and Fu, D., 2021b, New anomalocaridids (Panarthropoda: Radiodonta) from the lower Cambrian Chengjiang Lagerstätte: biostratigraphic and paleobiogeographic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 569, n. 110333, https://doi.org/10.1016/j.palaeo.2021.110333.

Wu, Y., Pates, S., Ma, J., Lin, W., Wu, Y., Zhang, X., and Fu, D., 2022, Addressing the Chengjiang conundrum: a palaeoecological view on the rarity of hurdiid radiodonts in this most diverse early Cambrian Lagerstätte: Geoscience Frontiers, v. 13, n. 101430, https://doi.org/10.1016/j.gsf.2022.101430.

Young, F.J., and Vinther, J., 2017, Onychophoran-like myoanatomy of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*: Palaeontology, v. 60, p. 27–54.

Zeng, H., Zhao, F., Niu, K., Zhu, M., and Huang, D., 2020, An early Cambrian euarthropod with radiodont-like raptorial appendages: Nature, v. 588, p. 101–105.

Zeng, H., Zhao, F., and Zhu, M., 2023, *Innovatiocaris*, a complete radiodont from the early Cambrian Chengjiang Lagerstätte and its implications for the phylogeny of Radiodonta: Journal of the Geological Society, v. 180, n. jgs2021-164, https://doi.org/10.1144/jgs2021-164.

Zhu, X., Lerosey-Aubril, R., and Ortega-Hernández, J., 2021, Furongian (Jiangshanian) occurrences of radiodonts in Poland and South China and the fossil record of the Hurdiidae: PeerJ, v. 9, n. e11800, https://doi.org/10.7717/peerj.11800.