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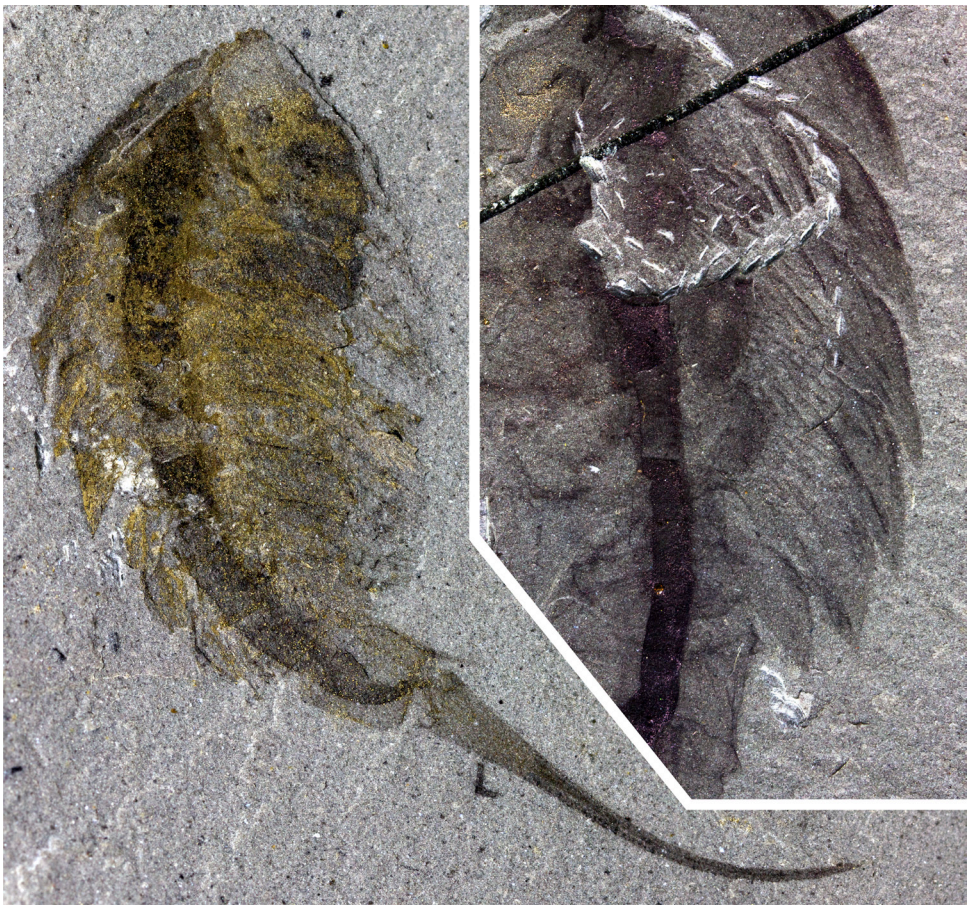

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A NEW CAMBRIAN ARTHROPOD, *EMERALDELLA BRUTONI*, FROM UTAH

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ABSTRACT

Emeraldella is a rare arthropod of relatively large body size that belongs with the trilobite-like arthropods, Artiopoda. *E. brutoni* n. sp. from the Wheeler Formation of west-central Utah is the second species described and marks the first confirmed occurrence of *Emeraldella* outside the Burgess Shale of British Columbia. An articulated, flagelliform telson, similar to that of the Burgess Shale taxon *Molaria*, is recognized in *Emeraldella*. Evidence for the presence of lamellae on the exopods of *Molaria* is presented, supporting affinity of that taxon with Artiopoda. A close relationship between *Emeraldella* and *Molaria* is tentatively suggested, based on the morphology of tergites and telson.

Keywords: Wheeler Formation, Drum Mountains, exceptional preservation, Arthropoda

INTRODUCTION

The Wheeler Formation of west-central Utah is well known for its diverse and exceptionally preserved biota, which was reviewed by Robison (1991). Briggs and others (2005, 2008), and Rigby, Church, and Anderson (2010) have described additional fauna. A new emeraldellid arthropod (Emeraldellidae Raymond, 1935; Artiopoda Hou & Bergström, 1997) is here described from the upper Wheeler in the Drum Mountains. Although the formation was previously assigned to the Middle Cambrian Series, it now falls mostly within the lower Drumian Stage (Babcock & others, 2007; Babcock, Robison, & Peng, 2011; Peng & Babcock, 2008), provisional Series 3, of the new global chronostratigraphic scale being developed by the International Commission on Stratigraphy. The new emeraldellid is associated with diagnostic trilobites of the upper *Ptychagnostus atavus* Biozone (Robison, 1976, 1984).

The Wheeler Formation accumulated in low-latitude, open-marine ramp and basin environments on the seaward side of broad, shallow-water carbonate platforms. Hintze and Robison (1975) reviewed regional stratigraphic relationships of the formation. Rees (1986), Gaines and Droser (2005), Gaines, Kennedy, and Droser (2005), Howley, Reese, and Jiang (2006), Babcock and others (2007), Elrick and Hinnov (2007), Brett and others (2009), Halgedahl and others (2009), and Howley and Jiang (2010), have provided more detailed information about its stratigraphy and depositional environments. One of us (S.B.C.) collected the fossil described here from the 6-meter-thick so-called hot-zone midway between sections W and C of Halgedahl and others (2009), which is characterized by high magnetic susceptibility, high gamma ray values, high clay content, and a bulk carbonate content ranging from about 4 to 20 percent. In the contexts of relative sea level changes and a sequence stratigraphic model, they identified a maximum flooding surface near the base of the hot zone and about 42 meters below the top of the formation. Some stratigraphers define the boundary between the Wheeler and overlying Pierson Cove Formation in the Drum Mountains at a stratigraphic level about 30 meters higher than that cited by Halgedahl and others (2009).

MATERIAL AND METHODS

The specimens were photographed both dry and immersed in alcohol (see figure captions). All photographs were taken under polarized light (Bengtson, 2000) with a Canon EOS 5D Mk II and Canon EF 50 mm f/2.5, Canon EF 100 mm f/2.8 L IS USM, and

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MP-E 65 mm f/2.8 Macro lenses with a circular polarizer. Where necessary, extended depth of field images (cf. Haug & others, 2009) were created from stacks of photographs with Adobe Photoshop CS5 Extended using layer auto-blending. Measurements were taken on the photographs with Orbicule Macnification 1.8. A composite line drawing was created by stacking photographs of part and counterpart in vector drawing software and tracing features on a separate drawing layer with a WACOM Intuos2 graphics tablet.

Figured specimens are deposited in the University of Kansas Museum of Invertebrate Paleontology (KUMIP), Lawrence, Kansas, and the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Terminology

The term caudal tergite refers to the posteriormost tergite, which lacks tergopleurae and articulates with the telson; caudal portion refers to the posterior part of the trunk, including the caudal flaps, because the preservation does not allow confident distinction of some features. The term prehypostomal sclerite is adopted from Paterson and others (2010) for the sclerite found in a number of fossil taxa between the hypostome and the head shield. Abbreviations used in the figures are: *ar*, articulating ridge; *atl*, antennula; *cf*, caudal flaps; *dl*, distal lobe of exopod; *g*, gut; *gd*, midgut diverticula; *hs*, head shield; *lm*, lamellae of exopod; *msp*, marginal spine on caudal tergite; *ps*, prehypostomal sclerite; *t10pm*, posterior margin of tenth tergite; *tg1–10*, tergites 1 through 10; *tgc*, caudal tergite; *tgc/tl*, border between caudal tergite and telson; *tl*, telson; *tlj*, telson joint. A question mark indicates a structure whose identification is tentative; subscript l or r indicates left or right in paired structures, and subscript pm indicates posterior margin.

SYSTEMATIC PALEONTOLOGY

Artiopoda Hou & Bergström, 1997

Discussion.—Stein and Selden (2011) provided an emended diagnosis for Artiopoda. We here present evidence that *Molaria spinifera* Walcott, 1912, belongs to Artiopoda, based on exopod structure, which is one of the diagnostic characters, but it does not share the diagnostic character of filiform antennulae. Characters like a flagelliform telson and an elongate caudal tergite without tergopleurae, as well as articulating ridges parallel with the anterior margin of the tergites suggest affinity of *M. spinifera* with *Emeraldella brocki* Walcott, 1912, a basal artiopod (Stein & Selden, 2011). Unless those characters can be shown to be symplesiomorphies present in basal artiopods, the antennular morphology of *M. spinifera* has to be considered autapomorphic for that taxon.

Emeraldellidae Raymond, 1935

The type genus, *Emeraldella* Walcott, 1912, is the only included genus.

Emeraldella Walcott, 1912

Type species.—*Emeraldella brocki* Walcott, 1912, p. 203–205.

Other included species.—*Emeraldella brutoni* n. sp.

Emended diagnosis.—Artiopod with head containing one antennular and three limb-bearing postantennular segments (plesiomorphy); antennulae long (about same length as trunk), containing more than 80 articles; first pair of postantennular limbs having reduced number of podomeres and no exopod. Trunk including 10 to 11 segments, and 1 elongate caudal segment with reduced tergopleurae and pair of ventral caudal flaps. Proportions of endopod podomeres strongly differentiated along body. Endopod curving outward proximally, downward at short, knee-like, fifth podomere; sixth podomere long, distinctly stenopodous. Exopod tripartite, proximal and middle parts articulating with basipod and first podomere, respectively. Lamellae on proximal part wide, with fine setules distally. Telson flagelliform, jointed, about same length as trunk, lateroventrally flanked by caudal flaps.

Discussion.—Stein and Selden (2011) emended the diagnosis of *Emeraldella* as given by Bruton and Whittington (1983). The inclusion of another species with different trunk segment count, as well as recognition of a flagelliform telson necessitates further emendation, given above.

Emeraldella is known with confidence from only its type locality in the Burgess Shale of British Columbia and the Wheeler Formation in the Drum Mountains, Utah, as described here. Briggs and Robison (1984) questionably assigned a specimen from the younger Marjum Formation of the House Range, Utah, to *Emeraldella* based mainly on the presence of 11 trunk tergites in combination with ill-defined characters of tergites and head shield. Other diagnostic characters are not discernible in that specimen. Stein and Selden (2011) showed that *Emeraldella brocki* has 12 rather than 11 tergites, whereas *Emeraldella brutoni* n. sp. has 11 trunk tergites, diminishing the utility of trunk-segment count as a diagnostic character of *Emeraldella*. It further appears that the tergite count in the Marjum specimen rests on the inferred boundaries between the head shield and the first thoracic tergite, in combination with a count of questionable limb traces in the trunk. Thus, there is no clear evidence of an eleventh limb pair, and the caudal end of the specimen is ill preserved. Following Stein and Selden (2011), the Marjum specimen is here regarded to be an indeterminate arthropod.

Emeraldella brutoni n. sp.

Figures 1–3

Diagnosis.—Large species of *Emeraldella* with ten trunk tergites with well-developed tergopleurae.

Description.—Body 70.8 mm long from anterior margin of head shield to base of telson. Maximum measurable length about 100 mm, with telson being incomplete. Maximum body width 43.5 mm between posterolateral tips of second trunk tergite.

Head shield semielliptical, about 14–16 mm long (sag.) and 41.4 mm wide (tr.); shield, including posterior border, not preserved axially, rendering exact length unknown. Anterior edge of head shield likely extended axially (Fig. 2.1–2.2), being unclear whether it represents part of head shield, a prehypostomal sclerite, or anterior of displaced hypostome.

Trunk, excluding caudal portion, composed of 10 tergites with well-developed tergopleurae, which become more falcate rearward. Tergite arch also increases rearward. Most tergite boundaries only discernible laterally (Fig. 1, Fig. 3), but overlap seems to be substantial, up to one-third of tergite length (sag.). Traces of articulating ridge preserved parallel to anterolateral margin on

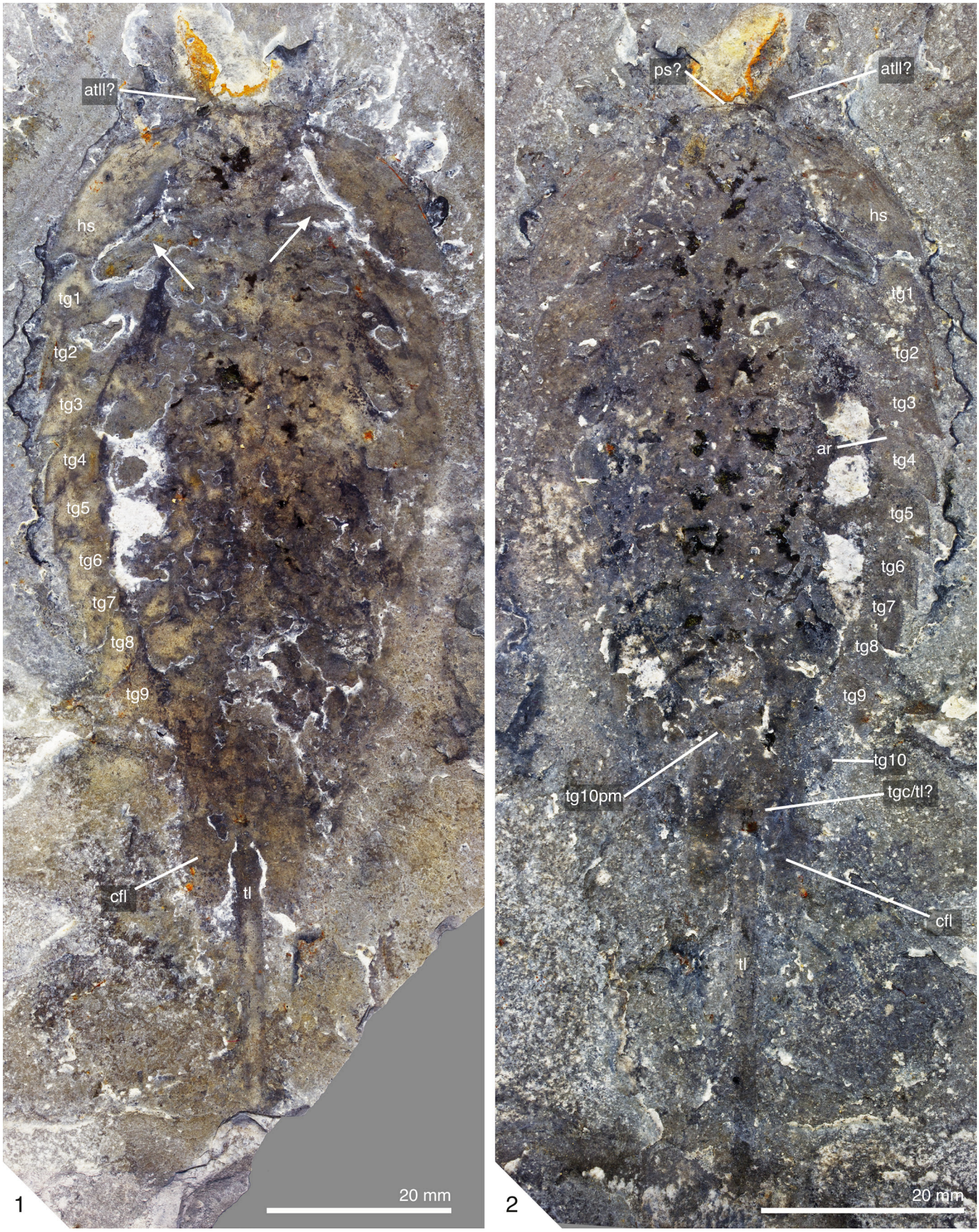

Figure 1. *Emeraldella brutoni* n. sp., KUMIP 321500, immersed in alcohol, using crossed polarizers. *1,* Part, overview of specimen, *arrows* indicate possible remnants of limbs; *2,* counterpart, overview of specimen (new).

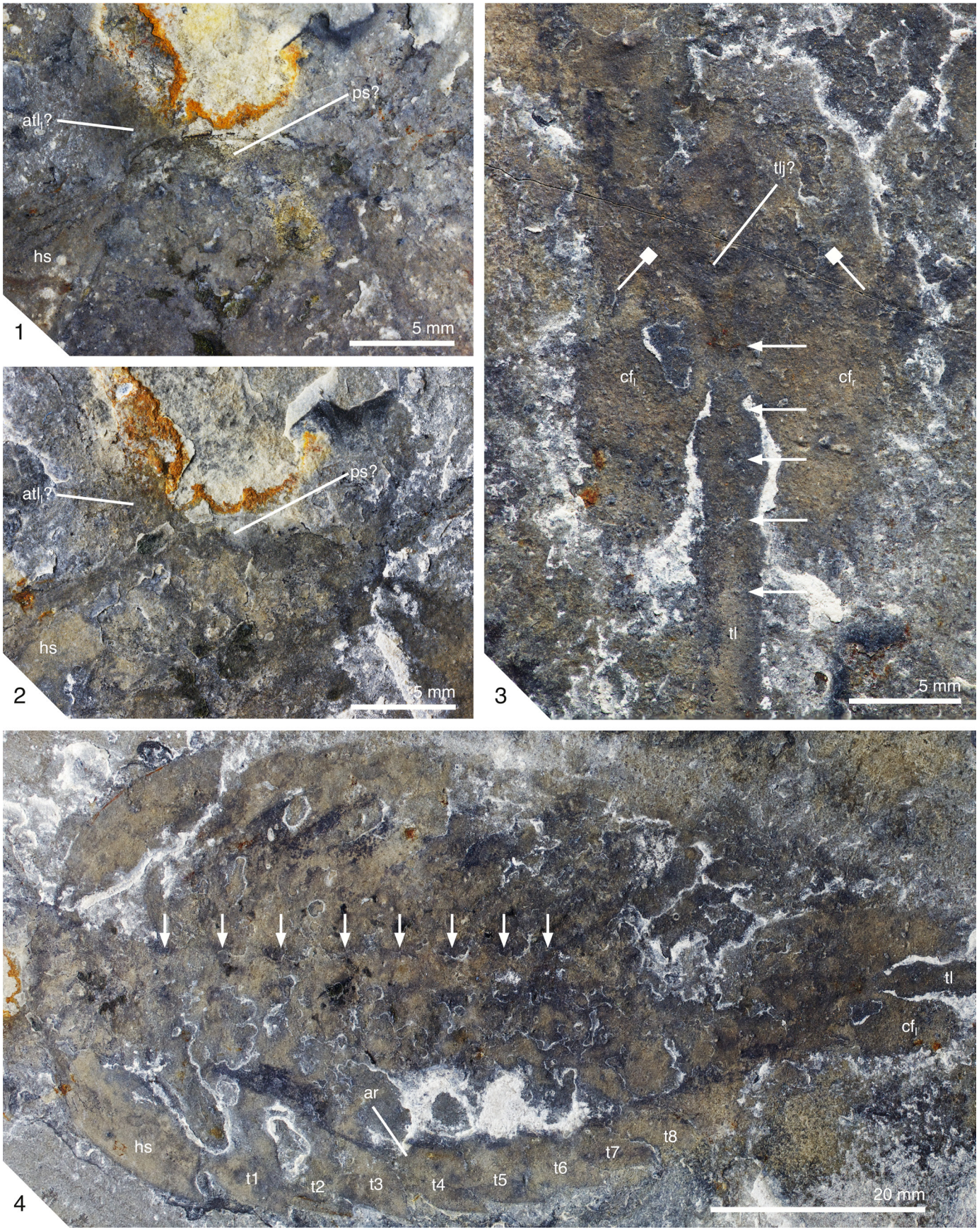

Figure 2. *(For explanation, see facing page).*

fourth tergite (Fig. 1.2, Fig. 2.4). Because the axial region of the tergites is not preserved, evidence of possible trilobation is lacking. Tergite count is based on lateral extremities of tergopleurae, which are best preserved on left side of trunk in the part (Fig. 1.1) and right side in the counterpart (Fig. 1.2). Tenth tergopleura, seen on right side of counterpart, is in immediate proximity to lateral edge of caudal portion. Posterior margin of tenth tergite is faintly visible as dark band in counterpart (Fig. 1.2). Evidence of tergopleurae in caudal portion is lacking.

Features in the caudal portion are difficult to discern (Fig. 2.3). The telson is on a layer of sediment that is flaking off proximally, exposing the caudal flaps onto which the outline of the telson is faintly impressed. A transverse dark stain crosses the center, coinciding with a fold traversing most of the caudal portion, which could mark the trunk-telson boundary, but the lateral margins of the caudal flaps appear to be continuous with the rest of the caudal portion. Immediately posterior to the transverse dark stain, a crescentic impression arches backward axially. A number of additional transverse marks, all indistinct, are posterior to that but are expressed as nicks rather than impressions (Fig. 2.3, arrows).

Caudal flaps are poorly preserved, with relation to remaining caudal portion being barely discernible. Fringing spines laterally and posteriorly are vaguely visible. Internal flap margins are visible as longitudinally arched dark stains. Diagonal lines run from anterolateral corner of caudal portion to the telson; it is unclear whether they are joints in the caudal flaps.

The part shows paired dark patches in the axial region. They are more faint than the prominent black stains on the counterpart and to some extent in the part, being best seen under crossed polarizers when the specimen is dry (Fig. 2.4, arrows). They appear to be segmental, although those of trunk segments six and seven are confluent on the left side. Posterior to trunk segment seven, they are no longer discernible. The patches may represent midgut diverticula, which are commonly preserved in fossil arthropods (Butterfield, 2002). Other, darker patches occurring axially on both part and counterpart and abaxially on the part are more difficult to associate with any particular structure (Fig. 1, only the abaxial ones drawn in Fig. 3, diagonal hatching).

The head shield is flaked off axially, revealing cuticular structures abaxially under the head and the head-trunk boundary, best seen in the part (Fig. 1.1, arrows). These are likely remnants of appendages, but the poor preservation does not allow further description. Apart from that, appendage preservation is only present in the proximal part of the left antennule, which is too poorly preserved for further description.

The cuticle carried a reticulate pattern, best seen on the right side of the head shield and first trunk tergite of the counterpart (Fig. 1.2).

Etymology.—After Professor David L. Bruton, University of Oslo, for advancing knowledge of *Emeraldella*.

Holotype.—KUMIP 321500, part (Fig. 1.1) and counterpart (Fig. 1.2). The tergites overlap from anterior to posterior in the part and the axial portions of at least the head shield are flaked off, exposing ventral structures beneath it. This is taken to indicate that the specimen is preserved in dorsal aspect.

Discussion.—Specimen USNM 136642 of *Emeraldella brocki* (Bruton & Whittington, 1983, fig. 22–23; Stein & Selden, 2011, fig. 4A) shows a median extension similar to that of KUMIP 321500. Stein and Selden (2011) tentatively interpreted the structure in *E. brocki* to be a prehypostomal sclerite (using the term rostral plate). Specimen USNM 136440 of *E. brocki* (Bruton & Whittington, 1983, fig. 11, plate 3; Stein & Selden, 2011, fig. $10A_1$) also shows a distinct median extension, but the anterior of that specimen is folded, presenting the posterior of the head shield in cross section. The median projection is therefore rather dorsal and covers the width of the thoracic axis. Trilobation of the head shield may have been expressed posteriorly in *E. brocki* (Stein & Selden, 2011), but whether it could account for the extent seen in this specimen is questionable. A possible cause for the extent might be stabilization of the axial region against compaction through early permineralization (Bruton & Whittington, 1983; Butterfield, 2002).

Poor preservation does not allow detailed morphological assessment of the caudal portion in *Emeraldella brutoni*. The caudal flaps of *E. brocki* insert beneath the anterior part of the caudal tergite, and their structure appears to be complex (Stein & Selden, 2011). Judging from the extent of the lateral margins and diagonal lines traversing them, the caudal flaps of *E. brutoni* also appear to extend almost to the anterior margin of the caudal portion. Specimen USNM 136640 (Stein & Selden, 2011, fig. $10A_2$) shows features similar to the diagonal lines observed in *E. brutoni*, and in similar orientation. Unfortunately, preservation does not allow assessment as to whether the features represent joints in the flaps of either species. Compared with *E. brocki*, presence of a caudal tergite is inferred in *E. brutoni*, but there is little direct evidence other than the transverse fold and dark stain, which may indicate the posterior border of such a tergite. It is not clear whether the backward arching crescentic impression marks the trunk-telson joint. Stein and Selden (2011) interpreted a crescentic backward arch in the anterior part of the telson of *E. brocki* to bound membranous cuticle surrounding the anus. Without preservation of a gut tract in the specimen of *E. brutoni,* the crescentic impression cannot be positively identified as a similar structure.

The transverse marks on the telson of KUMIP 321500, although they might be interpreted as taphonomic artifacts (e.g., creases due to physical impact, cuticular features, or irregularities), are most likely joints. A jointed, flagellum-like telson is known from *Molaria spinifera* Walcott, 1912 (Fig. 4.1, arrows; see also Whittington, 1981). The telson of *E. brocki* was described as styliform (Bruton & Whittington, 1983; Stein & Selden, 2011), but further investigation shows evidence of a jointed telson, even

Figure 2. *Emeraldella brutoni* n. sp., KUMIP 321500. *1–2,* Detail of anterior part of head shield showing anterior median extension of head shield, the possible prehypostomal sclerite; *1,* counterpart (immersed in alcohol), image is mirrored for comparison with part; *2,* part (dry); *3,* detail of caudal flaps and telson of part (dry, crossed polarizers), *arrows* indicate articulations in telson; *4,* trunk showing biserial dark stains (*arrows*) of possible midgut diverticula in the part (dry) (new).

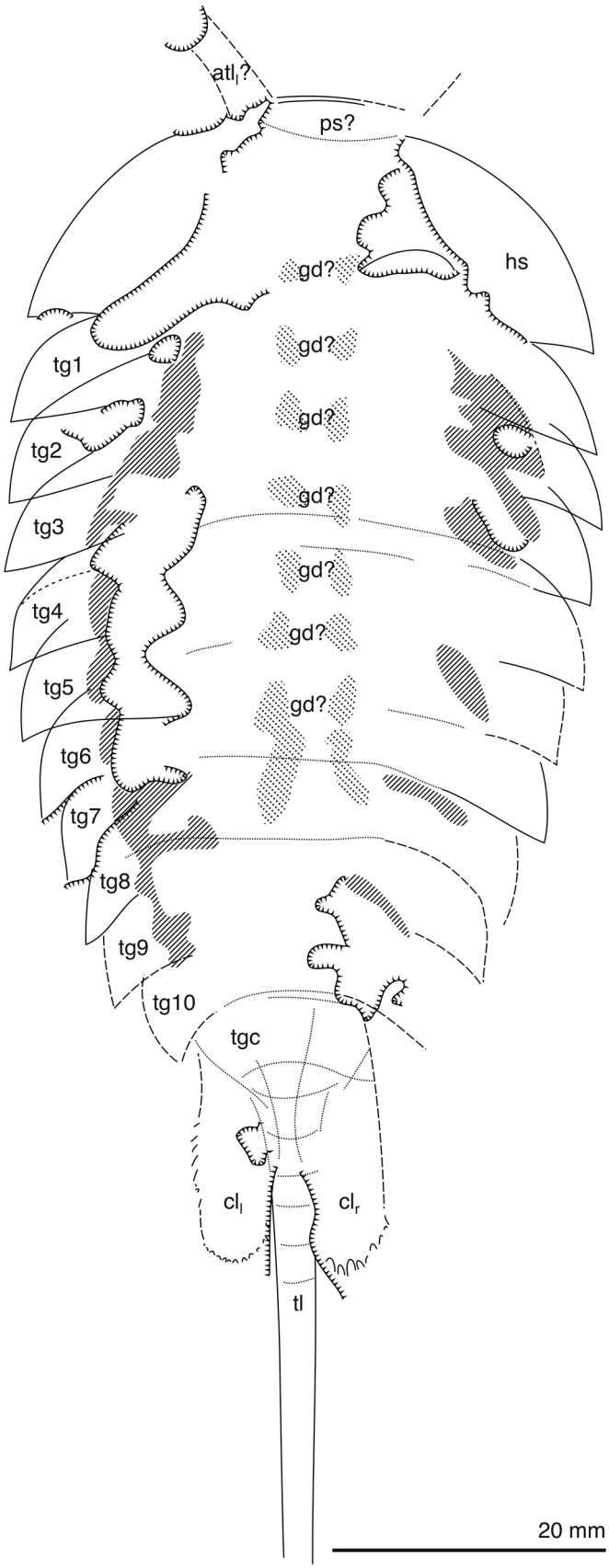

Figure 3. *Emeraldella brutoni* n. sp. Interpretative composite line drawing from both part and counterpart of KUMIP 321500 (new).

in that species. The telson is more or less fully preserved in only 9 of the 24 specimens (USNM 57702, 136439, 136441, 144917, 144919, 144923, 144928, 144929, 250230), and two additional specimens (USNM 144918 and 250227) have the proximal part preserved. Although overlooked in previous studies (Bruton & Whittington, 1983; Stein & Selden, 2011), the lectotype (USNM 57702) shows articulations in the telson (Fig. 4.3, arrows), which slightly bends at each articulation. USNM 136641, 144918, 144919, 250227, and 250230 show good evidence for similar articulations. The thirteenth segment identified by Bruton and Whittington (1983) is the most proximal article of the telson. Stein and Selden (2011) identified the anus at the base of this article and considered the article to be part of the telson, but failed to recognize articulations along the entire telson. An articulated, flagelliform telson is present also in *Retifacies abnormalis* Hou, Chen, & Lu, 1989, and has more recently been reported from *Pygmaclypeatus daziensis* Zhang, Han, & Shu, 2000 (Xu, 2004). In these taxa, the telson does not articulate with a caudal tergite, but a well-developed pygidium-like shield. Lin (2009) described flexibility of the telson in *Burgessia bella* Walcott, 1912, which was initially considered to be flagelliform and later to be styliform (see Lin, 2009, and references therein). Lin (2009) assumed a flexible styliform telson that could be stiffened by hydrostatic pressure. Given that telson articulation can be elusive in *E. brocki*, the material of *B. bella* should be restudied.

Assignment of KUMIP 321500 to *Emeraldella* is based upon the presence of a caudal portion without tergopleurae and caudal flaps anteroventrally to a flagelliform telson. A further similarity is the presence of articulating ridges parallel to the anterior margin of the tergites. The specimen has only 10 trunk tergites with developed tergopleurae, rather than 11 plus the caudal tergite found in *Emeraldella brocki*. As the Wheeler specimen is larger than known specimens of *E. brocki,* it is not an early instar of that species, but represents a separate species. *E. brutoni* n. sp. further differs from *E. brocki* by having tergites that overlap by about one-third of their length (sag.) rather than by one-quarter (cf. Stein & Selden, 2011).

Several authors suggested a close relationship between *Molaria spinifera* and *Emeraldella brocki* (see Whittington, 1981, for references). *M. spinifera* is similar to species of *Emeraldella* in tergite morphology, presence of a caudal tergite without tergopleurae, and a flagelliform telson. It has only eight trunk segments, and despite the large number of known specimens, caudal flaps are not known from the species. The caudal tergite carries posterolateral marginal spines, which are not known from *Emeraldella*. The antennula of *M. spinifera* is minute, slender, and composed of only a few articles (Whittington, 1981), which is unlike the filiform antennulae of other artiopods (Stein & Selden, 2011), including *E. brocki*. Evidence indicates that the exopods of *M. spinifera* are

Figure 4. *1–2, Molaria spinifera* Walcott, 1912. *1,* USNM 272195, showing the articulation between the caudal tergite and the flagelliform telson; *2,* USNM 268930, showing evidence of artiopod-type exopod lamellae; *3, Emeraldella brocki* Walcott, 1912, lectotype, USNM 57702, detail of telson; *arrows* indicate articulations in telson. All specimens immersed in alcohol (new).

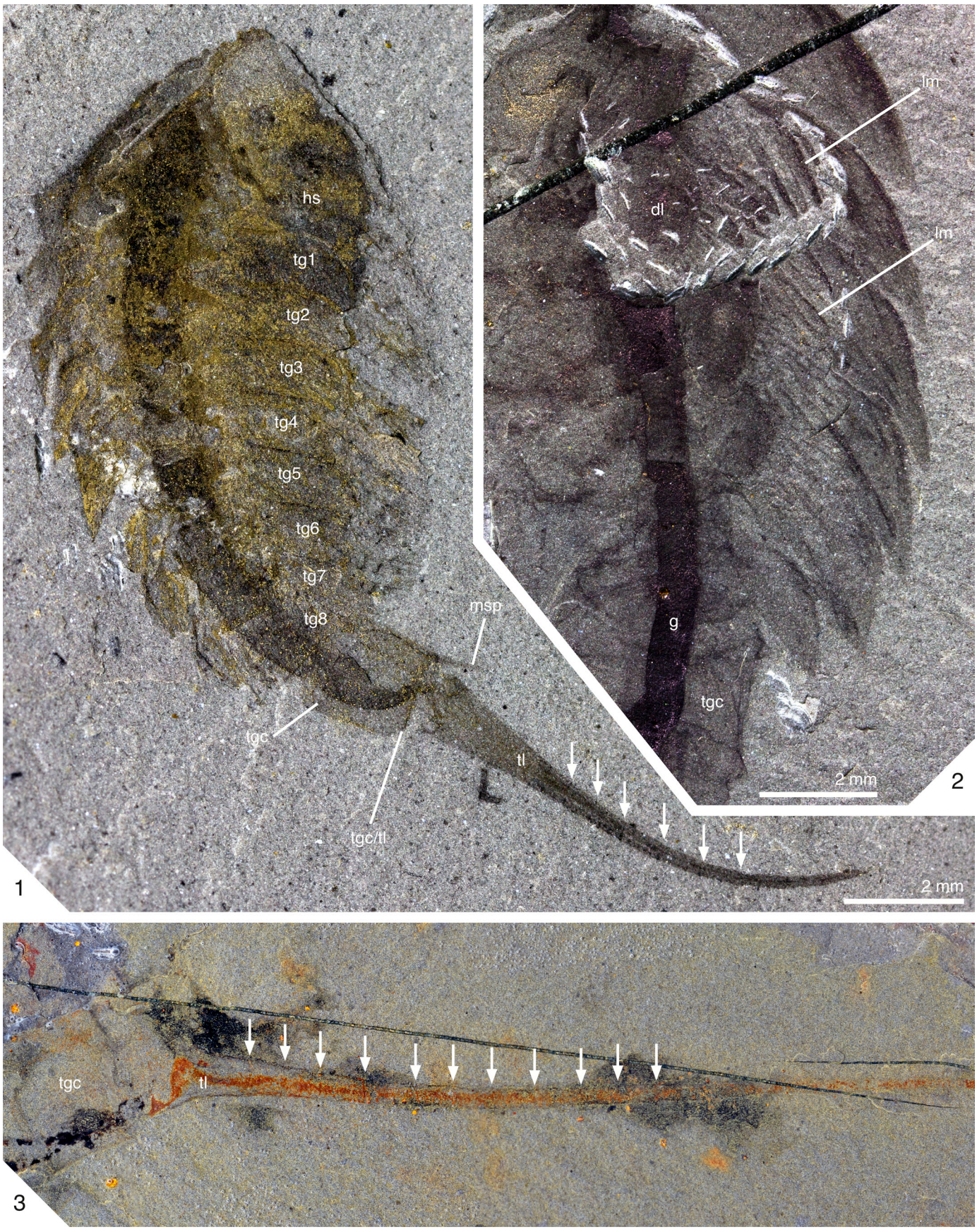

Figure 4. *(For explanation, see facing page).*

of the distinct artiopod type, with a proximal shaftlike, lamella-bearing part and a distal lobe fringed with setae. The distal lobe was figured by Whittington (1981, e.g., fig. 34–35) and is the most commonly preserved part of the exopod. Although Whittington (1981) did not observe lamellae and considered their absence as an argument against close affinities with *Emeraldella*, they are well exposed in USNM 268930 (Fig. 4.2), but there is also evidence in USNM 268923. A close relationship between *Emeraldella* and *Molaria* seems likely, but a comprehensive phylogenetic analysis is needed to further corroborate this.

Occurrence.—The holotype of *Emeraldella brutoni* n. sp. was collected from an outcrop of brown calcareous shale about 40 meters below the top of the Wheeler Formation, as identified by Halgedahl and others (2009). The locality is about 100 meters east of a broad, dry stream gully in the center S½NE¼ sec. 20, T. 15 S., R. 10 W., Drum Mountains Well 7.5' topographic quadrangle map (United States Geological Survey, 1971). A diverse associated biota includes trilobites [*Asaphiscus wheeleri* Meek, 1873, *Brachyaspidion sulcatum* Robison, 1964, *Elrathia kingii* (Meek, 1870), *Olenoides nevadensis* Meek, 1870], other arthropods (*Branchiocaris* ?*pretiosa* Resser, 1929, *Canadaspis* cf. *perfecta* Walcott, 1912, *Mollisonia symmetrica* Walcott, 1912), vetulicolians (*Skeemella clavula* Briggs & others, 2005), worms (*Selkirkia willoughbyi* Conway Morris & Robison, 1986, *Selkirkia* sp. Conway Morris & Robison, 1986, and undetermined taxa), undetermined hyoliths, undetermined lingulide brachiopods, sponges (*Choia carteri* Walcott, 1920, *Choia ridleyi* Walcott, 1920, *Diagoniella hindei* Walcott, 1920, *Hamptonia bowerbanki* Walcott, 1920, *Hamptonia parva* Rigby, Church, & Anderson, 2010, *Hintzespongia bilamina* Rigby & Gutschick, 1976, *Ratcliffespongia wheeleri* Rigby & Church, 1990, *Sentinella*? *draco* Walcott, 1920, *Vauxia bellula* Walcott, 1920), chancelloriids (*Chancelloria* sp.), and algae (*Margaretia dorus* Walcott, 1931, *Marpolia spissa* Walcott, 1919, *Yuknessia simplex* Walcott, 1919).

The prominent dry stream gully to the west provides limited vehicle access to the Global Standard Stratotype-section and Point of the Drumian Stage, which is 62 m above the base of the Wheeler Formation on a ridge crest about a kilometer north of the emeraldellid locality.

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Paul Selden (Lawrence) provided funding for MS to study the Burgess Shale material in the National Museum of Natural History. Mark Florence and Gene Hunt (both Washington) facilitated access to the collections of the NMNH. Loren Babcock (Columbus) read an early draft of the manuscript and provided helpful comments. David Bruton (Oslo) and Gregory Edgecombe (London) critically reviewed the manuscript and helped improve its quality.

REFERENCES

Babcock, L. E., R. A. Robison, & S. C. Peng. 2011. Cambrian stage and series nomenclature of Laurentia and the developing global chronostratigraphic scale. Museum of Northern Arizona Bulletin 67:12–26.

Babcock, L. E., R. A. Robison, M. N. Rees, S. Peng, & M. R. Saltzman. 2007. The Global boundary Stratotype Section and Point (GSSP) of the Drumian Stage (Cambrian) in the Drum Mountains, Utah, USA. Episodes 30:85–95.

Bengtson, S. 2000. Teasing fossils out of shales with cameras and computers. Palaeontologia Electronica 3:1–14.

Brett, C. E., P. A. Allison, M. K. DeSantis, W. D. Liddell, & A. Kramer. 2009. Sequence stratigraphy, cyclic facies, and *lagerstätten* in the Middle Cambrian Wheeler and Marjum Formations, Great Basin, Utah. Palaeogeography, Palaeoclimatology, Palaeoecology 277:9–33.

Briggs, D. E. G., B. S. Lieberman, S. L. Halgedahl, & R. D. Jarrard. 2005. A new metazoan from the Middle Cambrian of Utah and the nature of the Vetulicolia. Palaeontology 48:681–686.

Briggs, D. E. G., B. S. Lieberman, J. R. Hendricks, S. L. Halgedahl, & R. D. Jarrard. 2008. Middle Cambrian arthropods from Utah. Journal of Paleontology 82:238–254.

Briggs, D. E. G., & R. A. Robison. 1984. Exceptionally preserved non-trilobite arthropods and *Anomalocaris* from the Middle Cambrian of Utah. The University of Kansas Paleontological Contributions, Paper 111:1–24.

Bruton, D. L., & H. B. Whittington. 1983. *Emeraldella* and *Leanchoilia*, two arthropods from the Burgess Shale, Middle Cambrian, British Columbia. Philosophical Transactions of the Royal Society B: Biological Sciences 300:553–582.

Butterfield, N. J. 2002. *Leanchoilia* guts and the interpretation of three-dimensional structures in Burgess Shale–type fossils. Paleobiology 28:155–171.

Conway Morris, S., & R. A. Robison. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. The University of Kansas Paleontological Contributions, Paper 117:1–22.

Elrick, M., & L. A. Hinnov. 2007. Millennial-scale paleoclimate cycles recorded in widespread Palaeozoic deeper water rhythmites of North America. Palaeogeography, Palaeoclimatology, Palaeoecology 243:348–372.

Gaines, R. R., & M. L. Droser. 2005. New approaches to understanding the mechanics of Burgess Shale–type deposits. The Sedimentary Record 3:4–8.

Gaines, R. R., M. J. Kennedy, & M. L. Droser. 2005. A new hypothesis for organic preservation of Burgess Shale taxa in the middle Cambrian Wheeler Formation, House Range, Utah. Palaeogeography, Palaeoclimatology, Palaeoecology 220:193–205.

Halgedahl, S. L., R. D. Jarrard, C. E. Brett, & P. A. Allison. 2009. Geophysical and geological signatures of relative sea level change in the upper Wheeler Formation, Drum Mountains, West-Central Utah: A perspective into exceptional preservation of fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 227:34–56.

Haug, C., J. T. Haug, D. Waloszek, A. Maas, R. Frattigiani, & S. Liebau. 2009. New methods to document fossils from lithographic limestones of southern Germany and Lebanon. Palaeontologia Electronica 12:12 p.

Hintze, L. F., & R. A. Robison. 1975. Middle Cambrian stratigraphy of the House, Wah Wah, and adjacent ranges in western Utah. Geological Society of America Bulletin 86:881–891.

Hou X., & J. Bergström. 1997. Arthropods of the Lower Cambrian Chengjiang Fauna, southwest China. Fossils and Strata 45:1–116.

Hou X., J. Chen, & H. Lu. 1989. Early Cambrian new arthropods from Chengjiang, Yunnan. Acta Palaeontologica Sinica 28:42–57.

Howley, R. A., & G. Q. Jiang. 2010. The Cambrian Drumian carbon isotope excursion (DICE) in the Great Basin, western United States. Palaeogeography, Palaeoclimatology, Palaeoecology 296:138–150.

Howley, R. A., M. N. Rees, & G. Q. Jiang. 2006. Significance of middle Cambrian mixed carbonate-siliciclastic units for global correlation: Southern Nevada, USA. Palaeoworld 15:360–366.

Lin, J. 2009. Function of hydrostatics in the telson of the Burgess Shale arthropod *Burgessia.* Biology Letters 5:376–379.

Meek, F. B. 1870. Descriptions of fossils collected by the U.S. Geological Survey. Proceedings of the Academy of Natural Sciences of Philadelphia 12:54–64.

Meek, F. B. 1873. Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the rocks in which they were found. *In* Sixth Annual Report of the United States Geological Survey of Territories. p. 431–518.

Paterson, J. R., G. D. Edgecombe, D. C. García-Bellido, J. B. Jago, & J. G. Gehling. 2010. Nektaspid arthropods from the lower Cambrian Emu Bay Shale lagerstätte, South Australia, with a reassessment of lamellipedian relationships. Palaeontology 53:377–402.

Peng S., & L. E. Babcock. 2008. Cambrian Period. *In* J. G. Ogg, G. Ogg, & F. M. Gradstein, eds., The Concise Geologic Time Scale. Cambridge University Press. p. 37–46.

Raymond, P. E. 1935. *Leanchoilia* and other Mid-Cambrian Arthropoda. Bulletin of the Museum of Comparative Zoology at Harvard College 76:205–230.

Rees, M. N. 1986. A fault-controlled trough through a carbonate platform: The Middle Cambrian House Range embayment. Geological Society of America Bulletin 97:1054–1069.

Resser, C. E. 1929. New Lower and Middle Cambrian Crustacea. Proceedings of the United States National Museum 76:1–18.

Rigby, J. K., & S. B. Church. 1990. A new Middle Cambrian hexactinellid, *Ratcliffespongia wheeleri*, from western Utah, and skeletal structure of *Ratcliffespongia.* Journal of Paleontology 64:331–334.

Rigby, J. K., S. B. Church, & N. K. Anderson. 2010. Middle Cambrian sponges from the Drum Mountains and House Range in Western Utah. Journal of Paleontology 84:66–78.

Rigby, J. K., & R. C. Gutschick. 1976. Two new Lower Paleozoic hexactinellid sponges from Utah and Oklahoma. Journal of Paleontology 50:79–85.

Robison, R. A. 1964. Late Middle Cambrian faunas from western Utah. Journal of Paleontology 38:510–566.

Robison, R. A. 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. Brigham Young University Geology Studies 23:93–109.

Robison, R. A. 1984. Cambrian Agnostida of North America and Greenland, Part I, Ptychagnostidae. University of Kansas Paleontological Contributions, Paper 109:1–59.

Robison, R. A. 1991. Middle Cambrian biotic diversity: Examples from four Utah Lagerstätten. *In* A. M. Simonetta & S. Conway Morris eds., The Early Evolution of Metazoa and the significance of problematic taxa. Cambridge University Press. Cambridge, UK. p. 77–98.

Stein, M., & P. A. Selden. 2011. A restudy of the Burgess Shale (Cambrian) arthropod *Emeraldella brocki* and reassessment of its affinities. Journal of Systematic Palaeontology, iFirst 2011:123, doi: 10.1080/14772019.2011.566634.

United States Geological Survey. 1971. Drum Mts. Well Quadrangle, Utah, 7.5 minute series (topographic). USGS. Washington, D.C. 1 sheet.

Walcott, C. D. 1912. Cambrian geology and paleontology II. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. Smithsonian Miscellaneous Collections 57:145–229.

Walcott, C. D. 1919. Cambrian Geology and Paleontology IV, no. 5—Middle Cambrian algae. Smithsonian Miscellaneous Collections 67:217–260.

Walcott, C. D. 1920. Cambrian Geology and Paleontology IV, no. 6—Middle Cambrian Spongiae. Smithsonian Miscellaneous Collections 67:261–364.

Walcott, C. D. 1931. Addenda to descriptions of Burgess Shale fossils. Smithsonian Miscellaneous Collections 85:1–46.

Whittington, H. B. 1981. Rare arthropods from the Burgess Shale, Middle Cambrian, British Columbia. Philosophical Transactions of the Royal Society B, Biological Sciences 292:329–357.

Xu G. 2004. New specimens of rare arthropods from the early Cambrian Chengjiang Fauna, Yunnan, China. Acta Palaeontologica Sinica 43:325–331.

Zhang X., J. Han, & D. Shu. 2000. A new arthropod *Pygmaclypeatus daziensis* from the Early Cambrian Chengjiang Lagerstätte, South China. Journal of Paleontology 74:979–983.