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# The oldest hyolithids (Cambrian Series 2, Montezuman Stage) from the Iapetan margin of Laurentia

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**Abstract.**—The recent description of the nevadioid trilobite *Buenellus chilhoweensis* Webster and Hageman, 2018 established the presence of early Cambrian Montezuman Stage (Cambrian Series 2, Stage 3) faunas in the Murray Shale of Chilhowee Mountain, Tennessee. The description recognized the oldest known age-diagnostic Cambrian trilobite from the Laurentian margin of the former Iapetus Ocean since *Buenellus* Blaker, 1988 is known otherwise only from the Sirius Passet Lagerstätte on the Innuitian margin of North Greenland. The bivalved arthropods *Isoxys chilhoweanus* Walcott, 1890 and *Indota tennesseensis* (Resser, 1938a) have also been described from the Murray Shale, but hyolithids appear to be the dominant body fossils in terms of diversity and abundance. Although poorly preserved, the hyolithids occurring together with *Buenellus chilhoweensis* are described to improve understanding of the Murray Shale biota. The hyolith assemblages of the Murray Shale and Sirius Passet Lagerstätte are not closely similar, although the poor preservation of both hinders comparison.

## Introduction

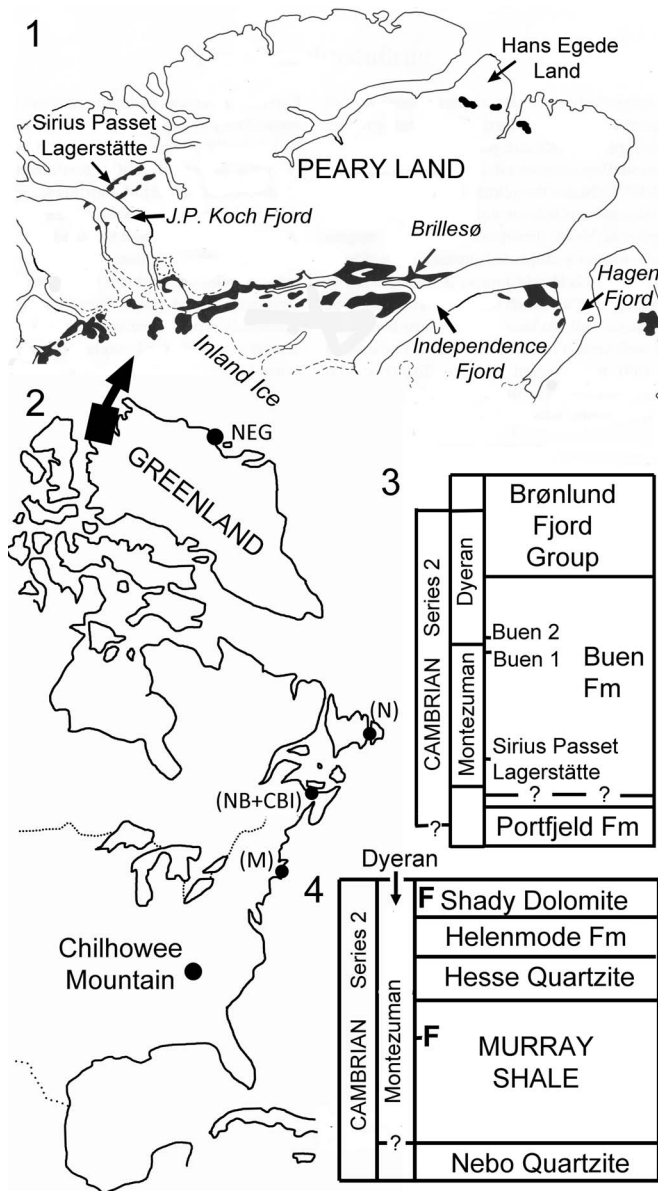
Outcrops of Laurentian lower Cambrian (Cambrian Series 2) strata extend from Alabama and Tennessee to North-East Greenland along the Eastern Seaboard of North America (Palmer, 1971; Hatcher et al., 1989; Williams, 1995; Derby et al., 2012; Torsvik and Cocks, 2016; Fig. 1). Traditionally, their age has been determined by occurrences of trilobites indicative of the Dyeran Stage of North American usage (Cambrian Stage 4), with widespread records of *Olenellus* Hall in Billings, 1861 and related trilobites in the literature (Resser, 1938a; Resser and Howell, 1938; Bird and Rasetti, 1968; Palmer, 1971; Skovsted, 2006; Stein, 2008; Webster and Hageman, 2018). By contrast, extensive faunas of older Cambrian trilobite faunas indicative of the Montezuman Stage (Cambrian Stage 3, but see Geyer, 2019), are well known from the opposite side of Laurentia, in the western United States (Hollingsworth, 2011). However, fossiliferous Avalonian successions in Rhode Island and Massachusetts, New Brunswick, Nova Scotia, and eastern Newfoundland (Fig. 1.2), comprising the Terreneuvian (Cambrian Series 1) of Landing et al. (2007) and Cambrian Series 2 to Lower Ordovician, are juxtaposed against the Laurentian of the Eastern Seaboard of present-day North America.

The recent description of the nevadioid trilobite *Buenellus* Blaker, 1988 from the upper Murray Shale of Chilhowee Mountain, eastern Tennessee (Fig. 1.2, 1.4) is significant in providing evidence of the Montezuman Stage in the Laurentian terrane of the eastern United States (Webster and Hageman, 2018). *Buenellus* is otherwise known only from its type locality in the Sirius Passet Lagerstätte (Fig. 1.1) of Peary Land, North Greenland

(Blaker and Peel, 1997; Babcock and Peel, 2007; Ineson and Peel, 2011; Peel and Willman, 2018).

The Sirius Passet Lagerstätte is the oldest known fossil assemblage within a succession of Montezuman–early Dyeran (Cambrian Stages 3–4) age assigned to the Buen Formation (Ineson and Peel, 1997; Peel and Willman, 2018; Fig. 1.3). The Lagerstätte is known only from a single locality, but the siliciclastic sediments of the Buen Formation are otherwise widely distributed in eastern North Greenland (Higgins et al., 1991a, b; Ineson and Peel, 1997, 2011; Peel and Willman, 2018; Fig. 1.1). The Buen Formation lies within the transarctic Innuitian Orogen, facing the Arctic Ocean (Higgins et al., 1991a, b). By contrast, the Murray Shale at Chilhowee Mountain, and other Laurentian outcrops along the Eastern Seaboard between Alabama and North-East Greenland (Fig. 1.2, 1.4), accumulated along the shore of the former Iapetus Ocean (Torsvik and Cocks, 2016). In Cambrian times, however, Laurentia occupied a tropical position, and this Iapetan margin faced to the south (Torsvik and Cocks, 2016).

The description of *Buenellus chilhoweensis* brings into focus other faunal elements that have been known from the Murray Shale since the late nineteenth century. The history of research into these, and the geological setting of the Murray Shale, were described in detail by Hageman and Miller (2016) and Webster and Hageman (2018), the former providing a detailed description of the succession of trace fossil assemblages. In addition to *Buenellus*, the bivalved arthropod *Isoxys* Walcott, 1890 was proposed by Walcott (1890) with *Isoxys chilhoweanus* Walcott, 1890 as its type species, the latter illustrated also by Williams et al. (1996). The bradoriid *Indota tennesseensis* (Resser, 1938a) was established on the basis of material from



**Figure 1.** Localities and stratigraphy. (1) Peary Land region of North Greenland showing outcrops of the Buen Formation (black) and localities with Montezuman Stage fossil assemblages; (2) Eastern Seaboard of North America with Greenland displaced southward to its approximate position in the Cambrian. NEG indicates Dyeran occurrences in North-East Greenland. (M), (NB + CBI), and (N) locate Avalonian successions in Massachusetts, New Brunswick and Cape Breton Island, and eastern Newfoundland, respectively; (3) early Cambrian stratigraphy in southern Peary Land showing derivation of fossil assemblages with the Buen Formation; (4) early Cambrian stratigraphy at Chilhowee Mountain, Tennessee, indicating location of fossiliferous samples (F) in the Murray Shale (Montezuman Stage) and the established Dyeran Stage faunas of the Shady Dolomite in Virginia (Byrd et al., 1973; Fritz and Yochelson, 1988; McMenamin et al., 2000).

Chilhowee Mountain (Resser, 1938a), and it has been revised subsequently by Laurence and Palmer (1963), Siveter and Williams (1997), and Streng and Geyer (2019). Walcott (1890) first noted the occurrence of hyoliths, and Resser (1938a, pl. 4, figs. 30, 31) illustrated two specimens identified as *Hyolithes* sp. indet. Webster and Hageman (2018) reported numerous trace fossils from the fossiliferous samples (Hageman and Miller,

2016). Undescribed elements in the fauna include a possible pelagiellid mollusk, while numerous small (0.5 mm) circular tablets of unknown affinity that resemble specimens described by Peel and Willman (2018, fig. 16A–D) from Buen Assemblage 2 at Brillesø, southern Peary Land, North Greenland, have been observed on several shale surfaces.

Wood and Clendening (1982) described acritarchs from the lower part of the Murray Shale at Chilhowee Mountain, proposing *Medousapalla choanoklosma* as a new genus and species for acritarchs with hollow, closed, and distally funnel-shaped processes. The holotype of *M. choanoklosma* was described from Locality 1 in Wood and Clendening (1982), which is geographically closest to the material described herein. In total, Wood and Clendening (1982) described a dozen sphaeromorphic and acanthomorphic acritarchs from two localities. The same year, *Skiagia* was erected by Downie (1982) for acritarchs displaying the same morphology as *Medousapalla*. Zang (2001) consequently considered *Medousapalla* to be a junior synonym of *Skiagia* and included *M. choanoklosma* in *Skiagia ornata* (Volkova, 1968). *Skiagia ornata* is a geographically widespread early Cambrian taxon potentially marking a stratigraphic level earlier than ca. 531 Ma (Moczyłowska, 2002; see also Moczyłowska and Zang, 2006 for a longer, up-to-date discussion on the stratigraphic importance of *Skiagia* and its use in correlation).

This paper describes hyolithids that occur together with *Buenellus chilhoweensis* in the Murray Shale. Although poorly preserved and not individually age diagnostic, these hyolithids appear to be the most abundant and diverse element of the fauna. As such, they help establish a more complete picture of the Murray Shale biota during the Montezuman Stage. The hyolithid assemblage is compared with the hyolith fauna occurring together with *Buenellus higginsii* Blaker, 1988 in the Sirius Passet Lagerstätte (Peel, 2010; Peel and Ineson, 2011) and other Montezuman–early Dyeran horizons in North Greenland (Peel and Willman, 2018).

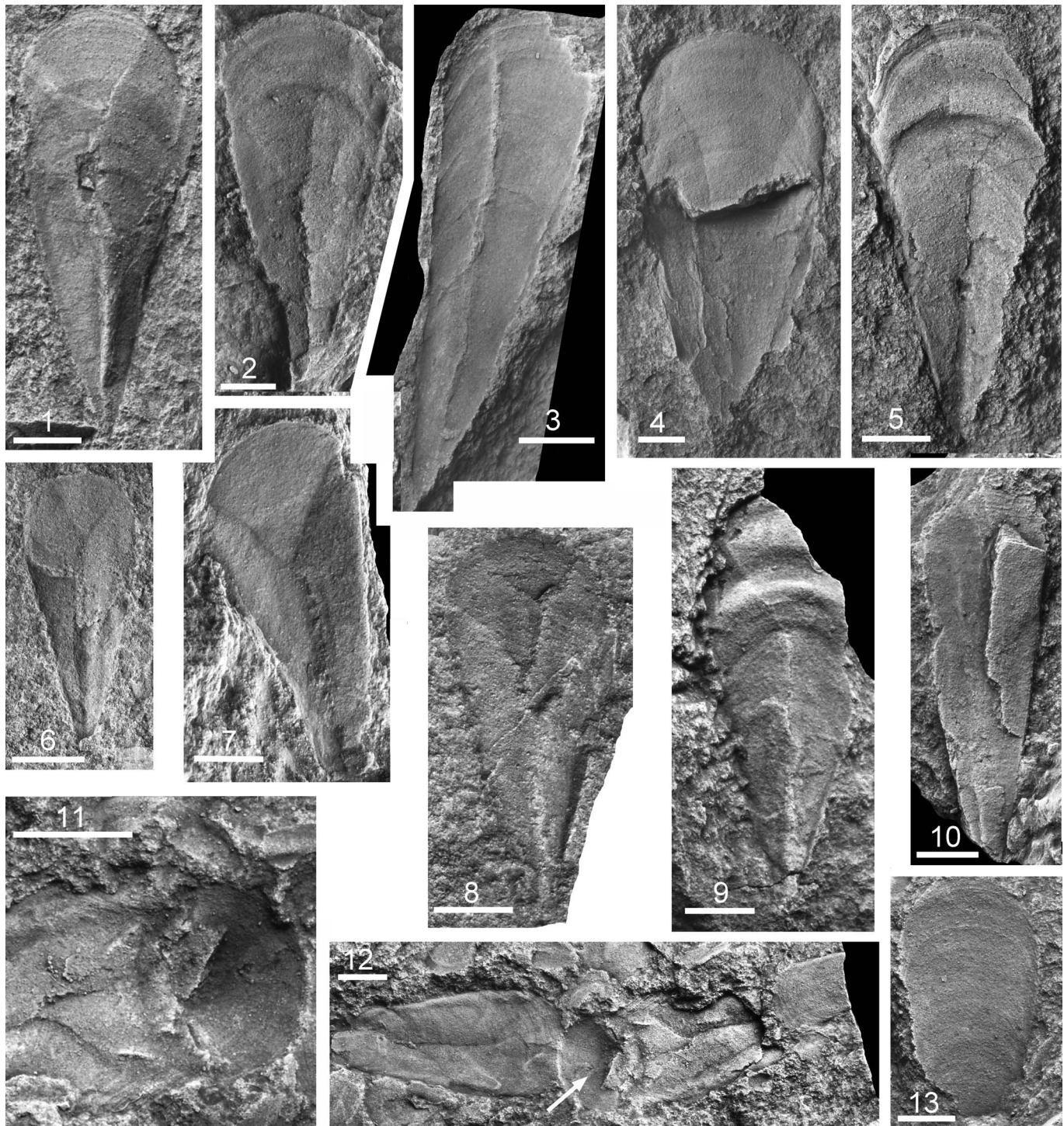
## Materials and methods

About 35 hyolithid specimens preserved in pale buff weathering shale were examined from locality CM3 of Webster and Hageman (2018) on Chilhowee Mountain (Fig. 1.2, 1.4) where they occur together with *Buenellus chilhoweensis* in the upper Murray Shale (Webster and Hageman, 2018, p. 457; 35°44.817'N, 083°48.446'W). The specimens are crushed, but not completely flattened, and some are preserved as external and internal molds. Conchs dominate but most are broken (Fig. 2). Opercula occur as isolated fossils (Fig. 3) and in rare partially articulated associations with conchs (Fig. 2.11). Rare broken fragments of the paired appendages (helens) have been observed as isolated fossils.

After painting with a thin coat of black colloidal carbon, all specimens were whitened with ammonium chloride sublimate before routine examination and photography. Images were captured using a Lumenera Infinity X32 high-resolution USB camera with attached Micro Nikkor 55 mm lens and assembled in Adobe Photoshop CS4.

Several samples were washed and cleaned in distilled water, rinsed in hydrochloric acid (HCl), and finally treated with hydrofluoric acid (HF). Residues were screened for organic-walled microfossils, but deep weathering of these samples has resulted





**Figure 2.** Hyolith conchs from the Murray Shale, Chilhowee Mountain, Tennessee. (1–4, 6–8) *Burithes?* sp. (1) PMU 35718, ventral surface; (2) PMU 35719, ventral surface; (3) PMU 35720, obliquely crushed ventral surface; (4) PMU 35721, central surface, above, with external mold of dorsal surface, below; (6) PMU 35722, crushed, with dorsal surface overlying internal surface of ventral surface with ligula; (7) PMU 35723, ventral surface with characteristic fractures; (8) PMU 35724, ventral surface. (5, 9) Hyolithid sp. 1, PMU 35725: (5) external and (9) internal molds showing prominent corrugation. (10) Hyolithid sp. 3, PMU 35726, dorsal view. (11–13) Hyolithid sp. 2: (11, 12) PMU 35727 with three fragmentary specimens in ventral aspect, probably within a gut fill, coprolite, or burrow; arrow in (12) locates external mold of operculum shown in detail in (11); (13) PMU 35728, external mold of ventral surface. Scale bars = 2 mm.

in destruction of original organic material and the introduction of contaminants.

*Repositories and institutional abbreviations.*—The prefix MGUH indicates a specimen deposited in the paleontological

type collection of the Natural History Museum of Denmark (formerly Geological Museum), Copenhagen. PMU indicates a specimen deposited in the paleontological type collection of the Museum of Evolution, Uppsala University, Sweden.

## Systematic paleontology

Order Hyolithida Syssoiev, 1957  
Family Angusticornidae Syssoiev, 1968

*Remarks.*—Angusticornids are characterized by the acutely angular lateral transition between the flattened ventral surface and the convex dorsal surface (Malinky and Geyer, 2019).

Genus *Burithes* Missarzhevsky, 1969

*Type species.*—*Lineivitus distortus* Syssoiev, 1962 from the Cambrian (late Terreneuvian) of the Aldan River, Siberia, by original designation.

*Remarks.*—Missarzhevsky (1969, 1981) proposed *Burithes* from the Tommotian and Atdabanian stages (Cambrian Stage 2 and 3) of Siberia, with type species *Lineivitus distortus* Syssoiev, 1962 from the Aldan River. The shallowly convex dorsum, considered ventral by Missarzhevsky (1969, 1981), passes by way of acute lateral angulations onto the almost flat ventral surface. Malinky (2014) noted that all specimens in Syssoiev's (1962) type material were internal molds and that details of ornamentation and the external expression of the lateral edges were not known. Consequently, Malinky (2014) recommended that the name should be restricted to the type material, and he further established *Haydenoconus*, in which the lateral edges on the shell exterior are sharp, keel-like. However, the type species, *Hyolithes gallatinensis* Resser, 1938b, was described from the Furongian of Wyoming although a second species, *Haydenoconus prolixus* (Resser, 1939), was described from the Miaolingian of Idaho. Malinky (2014) did not comment on the status of the other species that Missarzhevsky (1969, 1981), Meshkova (1974), Meshkova et al. (1983), and Rozanov et al. (2010) referred to *Burithes*. While acknowledging Malinky's (2014) recommendation, *Burithes* is employed in the present context on the basis of the descriptions and illustrations presented by Missarzhevsky (1969, 1981).

*Burithes?* sp.  
Figure 2.1–2.4, 2.6–2.8

*Description.*—Conch with incremental angle 20°–25° and ligula about one-sixth of total length (Fig. 2.1), with slight longitudinal curvature such that the ventral surface may have been shallowly convex (Fig. 2.3). Width of ligula about half its length, but length increasing proportionately with growth (Fig. 2.4). Shallow lateral sinuses for the likely passage of helens lie on the dorsal side of the angular transition from the convex dorsal surface to the almost flat ventral surface. Dorsal surface seemingly uniformly shallowly convex, but degree of inflation uncertain due to crushing. Ornamentation on ventral surface of fine comarginal growth lines with occasional growth halts that may appear periodic (Fig. 2.3). Ornamentation on dorsal surface poorly known, seemingly almost orthocline. Operculum and helens not certainly known, but associated isolated opercula are wider than long (Fig. 3), supporting the interpretation that the dorsal surface of the conch was not strongly inflated.

*Material.*—PMU 35719–PMU 35724, Murray Shale, Montezuman Stage (Cambrian Stage 3), Chilhowee Mountain, Tennessee.

*Remarks.*—All specimens are compressed, although a degree of separation between the dorsal and ventral surfaces may be maintained (Fig. 2.4). Crushing has often produced Y-shaped cracks that extend from the ligular margin down the median line as a raised, irregular ridge or angulation to near the apex (Fig. 2.1). The median fracture is commonly expressed as a ridge on the ventral surface, but this is a preservational artifact. However, a broad, rounded ridge in some specimens (Fig. 2.1) likely represents compaction around a solid object within the conch interior, possibly an early mineralized burrow or sediment-infilled section of gut (Devaere et al., 2014).

In terms of its overall shape, the Murray Shale conchs are similar to *Burithes erum* Missarzhevsky, 1969 from the Tommotian of the Anabar Massif of Siberia (Missarzhevsky, 1969, 1981). *Nevadotheca whitei* (Resser, 1938b) from the Pioche Shale (Cambrian Series 2) of Nevada, the type species of *Nevadotheca* Malinky, 1988, differs in having a high, inflated dorsum and narrowly rounded lateral margins. This is also the case in *Nevadotheca boerghumensis* Peel and Willman, 2018 and *Kalaallitia myliuserichseni* Peel and Willman, 2018, described from the early *Olenellus* Biozone (Dyeran, Cambrian Stage 4) of the Buen Formation of southern Peary Land, North Greenland, but *Kalaallitia* is distinguished by its fine longitudinal lirae and longer ligula. Opercula referred to these Peary Land species are proportionately longer than Murray Shale specimens, suggesting that the dorsal surface of their conchs was more strongly inflated than in *Burithes?* sp.

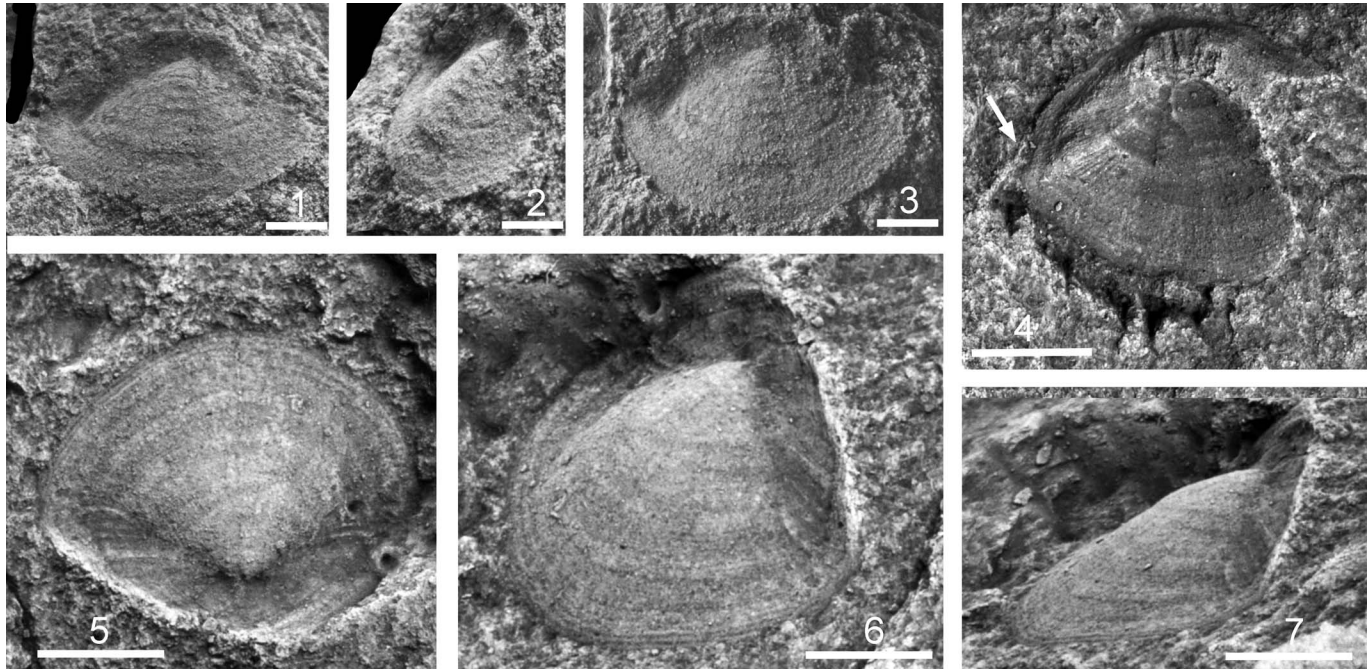
Malinky and Skovsted (2004) noted some similarity between specimens from the Dyeran of North-East Greenland and *Burithes*, but the acute dorsum of their material suggested assignment to *Grantitheca* Malinky, 1989 by Peel and Willman (2018). In contrast to material from the Murray Shale and Buen Formation, hyoliths from North-East Greenland are preserved mainly as internal molds in limestone or as phosphatic residues from limestones (Malinky and Skovsted, 2004; Skovsted, 2006).

Family uncertain  
Hyolithid sp. 1  
Figure 2.5, 2.9

*Material.*—PMU 35725, internal mold and corresponding external mold of the ventral surface, Murray Shale, Montezuman Stage (Cambrian Stage 3), Chilhowee Mountain, Tennessee.

*Remarks.*—This species, known from the illustrated specimens and two additional fragments, is characterized by two or three prominent transverse folds or corrugations on the adapertural part of the shallowly convex ventral surface of the conch and ligula (Fig. 2.5, 2.9). The incremental angle is about 30°, and the length of the ligula is slightly more than half its width. Lateral sinuses are present at the transition from the shallowly convex ventral surface to the dorsal surface, but the degree of inflation of the latter is not known. Ornamentation consists of fine comarginal growth lines, although these are more strongly developed at the preserved aperture (Fig. 2.5).





**Figure 3.** Hyolithid opercula from the Murray Shale, Chilhowee Mountain, Tennessee. (1–3) PMU 35729: (1) oblique apertural, (2) dorso-lateral, and (3) dorsal views. (4) PMU 37730 external mold with arrow indicating lateral sinus for passage of helen; (5–7) PMU 35731: (5) dorsal, (6) dorso-lateral, and (7) lateral views. (1–3) Scale bars = 1 mm; (4–7) scale bars = 2 mm.

Corrugation of the latest growth stage of the ventral surface and ligula is common in hyolithids, but not with the high degree of emphasis seen in the Murray Shale specimen (Fig. 2.9). Examples were illustrated by Missarzhevsky (1969, 1981) in specimens from Siberia referred to *Trapezovitus sinscus* (Sysoiev, 1958) and *Burithes cuneatus* Missarzhevsky, 1969, by Qian et al. (2003) in *Nitoricornus wushiensis* Qian et al., 2003 from the lower Cambrian of Xinjiang, China, and by Malinky (1990, fig. 1.6) in specimens from New Brunswick.

Simpson and Sundberg (1987) interpreted a specimen from the Hampton Formation of southwestern Virginia as a rugose hyolith compared to *Tuojdachithes? biconvexus* (Cobbold, 1919), but Hageman and Miller (2016) considered that it was not a fossil. Peel and Willman (2018, fig. 13G) illustrated a more-slender, unnamed hyolithid from Buen Assemblage 1 at Brillesø, southern Peary Land (Fig. 1.1) with rugose comarginal ornamentation on the ventral surface of the ligula, but this is much less prominent than in the Murray Shale specimens.

#### Hyolithid sp. 2 Figure 2.11–2.13

**Material.**—PMU 35727–PMU 35728, Murray Shale, Montezuman Stage (Cambrian Stage 3), Chilhowee Mountain, Tennessee.

**Remarks.**—The coincidence of the long axes of three overlapping incomplete specimens in ventral aspect (Fig. 2.12) suggests that they may form part of a gut fill or coprolite (Vannier, 2012). One of the specimens preserves the operculum in place (Fig. 2.11, arrow in 2.12). The incremental

angle is about 20°, and the ligula is short. The ventral surface is shallowly convex, but the lateral edges are rounded and delimited on their axial edge by a shallow longitudinal furrow. The dorsal surface is not known, but lateral sinuses seem to be well developed (Fig. 2.11). The impression of the dorsal exterior of the operculum shows comarginal growth lines and a suggestion of a radial furrow. While similar in shape to that illustrated in Figure 3.5–3.7, it is too poorly preserved for closer comparison.

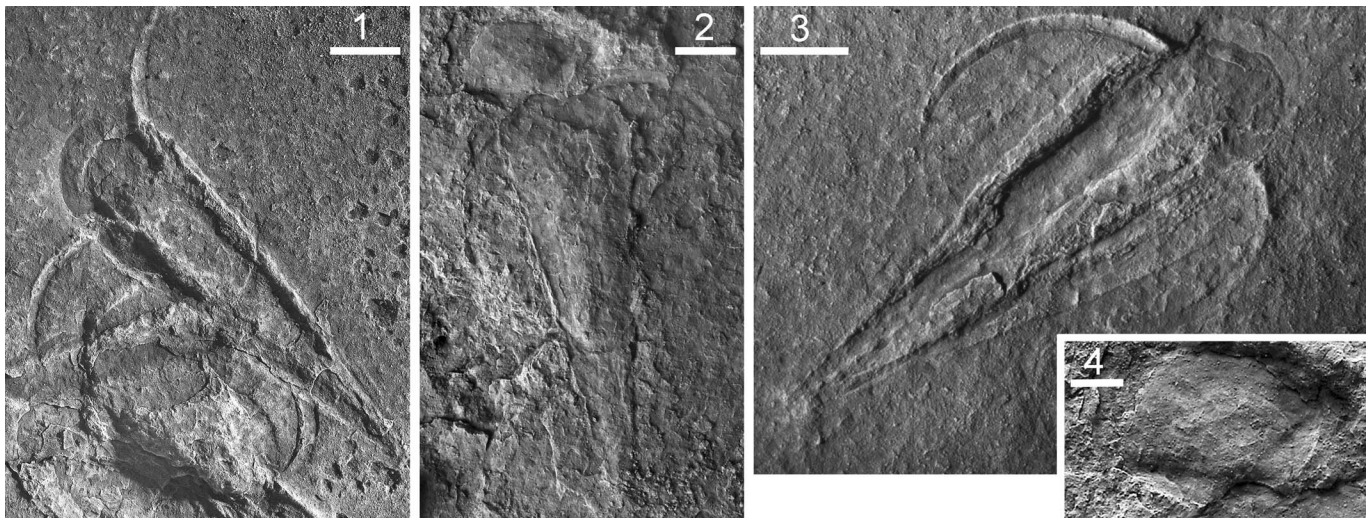
#### Hyolithid sp. 3 Figure 2.10

**Material.**—PMU 35726, Murray Shale, Montezuman Stage (Cambrian Stage 3), Chilhowee Mountain, Tennessee.

**Remarks.**—This poorly preserved specimen has an incremental angle of 15° and appears to have an oxygonal aperture. Aperturally, shallowly convex comarginal growth lines on the ventral surface are cord-like and laterally discontinuous, resembling the pattern illustrated by Malinky (1990) as *Nitoricornus danianum* (Matthew in Walcott, 1884) and by Kruse and Hughes (2016) as *?Crestjahitus danianus* from New Brunswick, Canada, whereas the dorsal surface is ornamented with barely discernible fine growth lines.

#### Hyolithid opercula Figure 3

**Material.**—PMU 35729–PMU 35731, Murray Shale, Montezuman Stage (Cambrian Stage 3), Chilhowee Mountain, Tennessee.



**Figure 4.** Articulated hyolithids from the Sirius Passet Lagerstätte, Buen Formation, Peary Land, North Greenland. (1) MGUH 29260; (2, 4) MGUH 29691: (2) ventral surface with operculum displaced and inverted to show conical surface; (4) enlarged view. (3) MGUH 29258, ventral surface. (1–3) Scale bars = 2 mm; (4) scale bar = 1 mm.

**Remarks.**—Three poorly preserved specimens of partially articulated hyolithid skeletons occur (Fig. 2.11, 2.12), but several isolated opercula are known (Fig. 3). The length of the best-preserved specimen is about four-fifths of its width (Fig. 3.5). Following terminology employed by Malinky and Berg-Madsen (1999, text-fig. 2), its conical shield is hemispherical in plan view, and the summit lies at about one-quarter of the distance from the adapical margin to the adapertural margin (Fig. 3.5). The folds separating the conical and cardinal surfaces delimit an angle of about  $130^\circ$  in plan view (Fig. 3.5). In lateral perspective (Fig. 3.7), the cardinal shield rises high above the summit of the operculum, with the inclination of its adapical margin (right in Fig. 3.7) suggesting that the conch had an amblyogon margin. The cardinal area is ornamented with radial ridges transverse to the comarginal growth lines present over the entire conch. The latter are most conspicuous on the conical shield where radial ornamentation consists of fine lines (Fig. 3.5, 3.6).

A second specimen, preserved as an external mold, has a well-defined convex adapical border with prominent coarse ridges between the summit and the adapical margin (Fig. 3.4). A broad shallow sinus in the margin (Fig. 3.4, arrow) marks the exit point for the helen. A third specimen (Fig. 3.1–3.3) has a more elliptical shape than the other two specimens and develops a series of short comarginal rugae located medially on the conical shield.

The cardinal surface is proportionately longer in opercula of *Nevadotheca boerghumensis* and *Kalaallitia myliuserichseni* from the early *Olenellus* Biozone (Buen Assemblage 2) at Brillesø, southern Peary Land (Peel and Willman, 2018, fig. 14), and the folds separating the conical and cardinal surfaces delimit an angle of about  $90^\circ$ , much smaller than in the specimens from the Murray Shale. In this respect, the opercula from the Murray Shale more closely resemble the opercula associated with articulated specimens from the Sirius Passet Lagerstätte (Fig. 4.2, 4.4), but these are too poorly preserved for close comparison. A similar wide angle is seen in *Nitoricornus danianum* illustrated

by Malinky (1990, fig. 1.1) from New Brunswick and assigned to *?Crestjahitus danianus* by Kruse and Hughes (2016).

### Faunal comparison

The Murray Shale hyolithids are the oldest hyoliths known from present-day eastern Laurentia but not from eastern North America. Hyoliths considered to be of Terreneuvian and younger age were reported from Avalonian terranes (Fig. 1.2) by Landing (1988, 1991, 1995), Landing et al. (1989), Landing and Murphy (1991), and Landing and Kröger (2012). Malinky and Geyer (2019, fig. 2) referred some of this material to the Montezuman, citing the occurrence of *Aimitus* Syssoiev, 1966 and *Notabilitus* Syssoiev, 1968.

Peel (2010) and Peel and Ineson (2011) described hyolithids and orthothecids from the Sirius Passet Lagerstätte occurring together with *Buenellus higginsi*. Orthothecids have not been recognized from the Murray Shale. Although several hyolithid specimens from the Sirius Passet Lagerstätte preserve the operculum and paired helens together with the conch, their poor state of preservation precludes more precise identification. However, opercula from the Murray Shale are similar in shape to a Sirius Passet operculum (Fig. 4.2, 4.4) and unlike those occurring in the Dyeran Buen Assemblage 2 from southern Peary Land (Peel and Willman, 2018). Variation in the incremental angle of the conch suggests that several taxa may be present in the Sirius Passet articulated material. Some Sirius Passet specimens have an angular dorsum not seen in Murray Shale material and thereby resemble *Grantitheca* Malinky, 1989, although this genus was not recognized by Landing and Bartowski (1996, p. 757). The articulated specimens are associated with longitudinally ribbed conchs assigned to *Trapezovitus* Syssoiev, 1958 and an orthothecid, but specimens similar to these have not been observed from the Murray Shale.

The bradoriid *Indota* Öpik, 1968, represented by *Indota tennesseensis* in the Murray Shale, has not been described



from the Sirius Passet Lagerstätte. Peel and Willman (2018) tentatively referred poorly preserved specimens from the upper Buen Formation (Dyeran Stage) to the genus, but the assignment was questioned by Streng and Geyer (2019). *Isoxys chilhoweana* from the Murray Shale is similar to *Isoxys volucris* Williams, Siveter, and Peel, 1996, which is the most abundant fossil in the Sirius Passet Lagerstätte (Williams et al., 1996; Stein et al., 2010; Nielsen et al., 2017).

Peel and Willman (2018) illustrated two crushed hyolithids from Buen Assemblage 1 at Brillesø, southern Peary Land, in association with the nevadioid *Limniphacos perspicillum* Blaker and Peel, 1997 of presumed Montezuman age (Hollingsworth, 2011). The rugose growth ornamentation of one of these (Peel and Willman, 2018, fig. 13G) is reminiscent of Hyolithid sp. 1 from the Murray Shale but is much less strongly expressed. Strata within the Buen Formation of probable Montezuman age occur in Hans Egede Land, eastern Peary Land (Fig. 1.1); they are not well known, but unidentifiable hyolith fragments are associated with poorly preserved trilobites (Peel and Willman, 2018).

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## References

- Babcock, L.E., and Peel, J.S., 2007, Palaeobiology, taphonomy and stratigraphic significance of the trilobite *Buenellus* from the Sirius Passet Biota, Cambrian of North Greenland: *Memoirs of the Association of Australasian Palaeontologists*, v. 34, p. 401–418.
- Billings, E., 1861, On some new or little known species of lower Silurian fossils from the Potsdam Group (Primordial Zone), in Hitchcock, E., Hitchcock, E., Jr., Hager, A.D., and Hitchcock, C.H., eds., *Report on the Geology of Vermont: Descriptive, Theoretical, Economical, and Scenographical*, Volume 2: Claremont, New Hampshire, Claremont Manufacturing Company, p. 942–955.
- Bird, J.M., and Rasetti, F., 1968, Lower, middle, and upper Cambrian faunas in the Taconic sequence of eastern New York: Stratigraphic and biostratigraphic significance: *Geological Society of America Special Paper*, v. 113, 66 p.
- Blaker, M.R., 1988, A new genus of nevadiid trilobite from the Buen Formation (early Cambrian) of Peary Land, central North Greenland: *Grønlands Geologiske Undersøgelse Rapport*, v. 137, p. 33–41.
- Blaker, M.R., and Peel, J.S., 1997, Lower Cambrian trilobites from North Greenland: *Meddelelser om Grønland, Geoscience*, v. 35, p. 1–145.
- Byrd, W.J., Weinberg, E.L., and Yochelson, E.L., 1973, *Salterella* in the lower Cambrian Shady Dolomite of southwestern Virginia: *American Journal of Sciences*, v. 273-A, p. 252–260.
- Cobbold, E.S., 1919, Cambrian Hyolithida, etc., from Hartshill in the Nuneaton district, Warwickshire: *Geological Magazine*, v. 6, p. 149–158.
- Devaere, L., Clausen, S., Álvaro, J.J., Peel, J.S., and Vachard, D., 2014, Terreneuvian Orthothecid (Hyolitha) Digestive Tracts from Northern Montagne Noire, France: Taphonomic, Ontogenetic and Phylogenetic Implications: *PLoS ONE*, v. 9, e88583.
- Derby, J.R., Fritz, R., Longacre, S., Morgan, W., and Sternbach, C., eds., 2012, *The Great American Carbonate Bank: The Geology and Economic Resources of the Cambrian–Ordovician Sauk Megasequence of Laurentia*: American Association of Petroleum Geologists Memoir 98, 1,206 p.
- Downie, C., 1982, Lower Cambrian acritarchs from Scotland, Norway, Greenland and Canada: *Transactions of the Royal Society of Edinburgh, Earth Science*, v. 72, p. 257–295.
- Fritz, W.H., and Yochelson, E.L., 1988, The status of *Salterella* as a lower Cambrian index fossil: *Canadian Journal of Earth Sciences*, v. 25, p. 403–416.
- Geyer, G., 2019, A comprehensive Cambrian correlation chart: *Episodes*, v. 42, p. 1–12.
- Hageman, S.J., and Miller, W., III, 2016, New fossil discoveries in the Chilhowee Group (southern Appalachians, USA): Evidence for the Ediacaran–Cambrian transition, ‘Cambrian Agronomic Revolution’, and earliest trilobites at the southern margin of Laurentia: *Neues Jahrbuch für Geologie und Paläontologie Abh.*, v. 281, p. 135–154.
- Hatcher, R.D., Jr, Thomas, W.A., and Viele, G.W., 1989, *The Appalachian–Ouachita Orogen in the United States*: Boulder, Colorado, Geological Society of America, 767 p.
- Higgins, A.K., Ineson, J.R., Peel, J.S. Surlyk, F.S., and Søndersholm, M., 1991a, Lower Palaeozoic Franklinian Basin of North Greenland: *Bulletin Grønlands Geologiske Undersøgelse*, v. 160, p. 71–139.
- Higgins, A.K., Ineson, J.R., Peel, J.S. Surlyk, F.S., and Søndersholm, M., 1991b, Cambrian to Silurian basin development and sedimentation, North Greenland, in Trettin, H.P., ed., *Geology of the Innuitian Orogen and Arctic Platform of Canada and Greenland*: Ottawa, Geological Survey of Canada, p. 109–161.
- Hollingsworth, J.S., 2011, Lithostratigraphy and biostratigraphy of Cambrian Stage 3 in western Nevada and eastern California, in Hollingsworth, J.S., Sundberg, F.A., and Foster, J.R., eds., *Cambrian Stratigraphy and Paleontology of Northern Arizona and Southern Nevada*: Museum of Northern Arizona Bulletin, v. 67, p. 26–42.
- Ineson, J.R., and Peel, J.S., 1997, Cambrian shelf stratigraphy of North Greenland: *Geology of Greenland Survey Bulletin*, v. 173, p. 1–120.
- Ineson, J.R., and Peel, J.S., 2011, Geological and depositional setting of the Sirius Passet Lagerstätte (early Cambrian), North Greenland: *Canadian Journal of Earth Sciences*, v. 48, p. 1259–1281.
- Kruse, P.D., and Hughes, N.C., 2016, Himalayan Cambrian hyoliths: *Papers in Palaeontology*, v. 2, p. 323–341.
- Landing, E., 1988, Lower Cambrian of eastern Massachusetts: Stratigraphy and small shelly fossils: *Journal of Paleontology*, v. 62, p. 661–695.
- Landing, E., 1991, Upper Precambrian through lower Cambrian of Cape Breton Island: Faunas, paleoenvironments, and stratigraphic revision: *Journal of Paleontology*, v. 65, p. 570–595.
- Landing, E., 1995, Upper Placentian–Branchian Series of mainland Nova Scotia (middle-upper lower Cambrian): Faunas, paleoenvironments, and stratigraphic revision: *Journal of Paleontology*, v. 69, p. 475–495.
- Landing, E., and Bartowski, K.E., 1996, Oldest shelly fossils from the Taconic allochthon and late early Cambrian sea-levels in eastern Laurentia: *Journal of Paleontology*, v. 70, p. 741–761.
- Landing, E., and Kröger, B., 2012, Cephalopod ancestry and ecology of the hyolith “*Allathea*” *degeeri* s.l. in the Cambrian evolutionary radiation: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 353–355, p. 21–30.
- Landing, E., and Murphy, J.B., 1991, Uppermost Precambrian(?)–lower Cambrian of mainland Nova Scotia: Faunas, depositional environments, and stratigraphic revision: *Journal of Paleontology*, v. 65, p. 382–386.
- Landing, E., Myrow, P., Benus, A.P., and Narbonne, G.M., 1989, The Placentian Series: Appearance of the oldest skeletalized faunas in southeastern Newfoundland: *Journal of Paleontology*, v. 63, p. 739–769.
- Landing, E., Peng, S., Babcock, L.E., Geyer, G., and Moczydlowska-Vidal, M., 2007, Global standard names for the lowermost Cambrian series and stage: *Episodes*, v. 30, p. 287–289.
- Laurence, R.A., and Palmer, A.R., 1963, Age of the Murray Shale and Hesse Quartzite on Chilhowee Mountain, Blount County, Tennessee: *United States Geological Survey Professional Paper* 475-C, p. C53–C54.
- Malinky, J.M., 1988, Early Paleozoic Hyolitha from North America: Reexamination of Walcott’s and Resser’s type specimens: *Journal of Paleontology*, v. 62, p. 218–233.
- Malinky, J.M., 1989, New Early Paleozoic Hyolithida and Orthothecida (Hyolitha) from North America: *Journal of Paleontology*, v. 63, p. 302–319.
- Malinky, J.M., 1990, Cambrian Hyolitha from Northeast Canada: Reappraisal of the hyolith orders Camerothecida and Diplotheceida: *Journal of Paleontology*, v. 64, p. 587–595.
- Malinky, J.M., 2014, Cambrian Hyolitha and problematica from West Laurentian North America: Taxonomy and palaeobiogeography: *Alcheringa*, v. 38, p. 338–363.
- Malinky, J.M., and Berg-Madsen, V., 1999, A revision of Holm’s early and early mid Cambrian hyoliths of Sweden: *Palaeontology*, v. 42, p. 25–65.
- Malinky, J.M., and Geyer, G., 2019, Cambrian Hyolitha of Siberian, Baltican and Avalonian aspect in east Laurentian North America: Taxonomy and palaeobiogeography: *Alcheringa*, v. 43, p. 171–203.
- Malinky, J.M., and Skovsted, C.B., 2004, Hyoliths and small shelly fossils from the lower Cambrian of North-East Greenland: *Acta Palaeontologica Polonica*, v. 49, p. 551–578.
- McMenamin, M., Debrenne, F., and Zhuravlev, A., 2000, Early Cambrian Appalachian archaeocyaths: Further age constraints from the fauna of New Jersey and Virginia, USA: *Geobios*, v. 33, p. 693–708.
- Meshkova, N.P., 1974, Lower Cambrian hyoliths of the Siberian Platform: *Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie Akademii Nauk SSSR*, v. 97, p. 1–110. [in Russian]



- Meshkova, N.P., Missarzhevsky, V.V., Syssoiev, V.A., and Valkov, A.K., 1983, Phylum Hyolithozoa, in Sokolov, B.S., and Zhuravleva, I.T., eds., Lower Cambrian Stage Subdivision of Siberia. Atlas of Fossils: Trudy Instituta Geologii i Geofiziki Sibirskoe Otdelenie Akademii Nauk SSSR, v. 558, p. 54–96. [in Russian]
- Missarzhevsky, V.V., 1969, Descriptions of hyoliths, gastropods, hyolithelminths, camenids, and forms of an obscure systematic position. The Tommotian Stage and the problem of the lower boundary of the Cambrian: Trudy Ordena Trudovogo Krasnogo Znameni Geologicheskii Institut, Akademiya Nauk SSSR, v. 206, p. 105–175. [in Russian]
- Missarzhevsky, V.V., 1981, Descriptions of hyolithids, gastropods, hyolithelminths, camenids and forms of an obscure systematic position, in Raaben, M.E., ed., The Tommotian Stage and the Cambrian Lower Boundary Problem: New Delhi, India, Amerind Publishing Company, p. 117–205. [translation of Missarzhevsky, V.V., 1969]
- Moczyłowska, M., 2002, Early Cambrian phytoplankton diversification and appearance of trilobites in the Swedish Caledonides with implications for coupled evolutionary events between primary producers and consumers: Lethaia, v. 35, p. 191–214.
- Moczyłowska, M., and Zang, W., 2006, The early Cambrian acritarch *Skiagia* and its significance for global correlation: Palaeoworld, v. 15, p. 328–347.
- Nielsen, M.L., Rasmussen, J.A., and Harper, D.A.T., 2017, Sexual dimorphism within the stem-group arthropod *Isoxys volucris* from the Sirius Passet Lagerstätte, North Greenland: Bulletin of the Geological Society of Denmark, v. 65, p. 47–58.
- Öpik, A.A., 1968, Ordian (Cambrian) Crustacea Bradoriida of Australia: Bureau of Mineral Resources of Australia Bulletin, v. 103, p. 1–46.
- Palmer, A.R., 1971, The Cambrian of the Appalachian and eastern New England regions, eastern United States, in Holland, C.H., ed., Lower Palaeozoic Rocks of the World, Volume 1. Cambrian of the New World: London, UK, Wiley, p. 169–217.
- Peel, J.S., 2010, Articulated hyoliths and other fossils from the Sirius Passet Lagerstätte (early Cambrian) of North Greenland: Bulletin of Geosciences, v. 85, p. 385–394.
- Peel, J.S., and Ineson, J.R., 2011, The extent of the Sirius Passet Lagerstätte (early Cambrian) of North Greenland: Bulletin of Geosciences, v. 86, p. 535–543.
- Peel, J.S., and Willman, S., 2018, The Buen Formation (Cambrian Series 2) biota of North Greenland: Papers in Palaeontology, v. 4, p. 381–432.
- Qian, Y., Li, G., Zhu, M., and Yin, G., 2003, Hyoliths from the lower Cambrian Xiaerbulake Formation of Wushi, Xinjiang: Acta Micropalaeontologica Sinica, v. 24, p. 350–357.
- Resser, C.E., 1938a, Cambrian System (restricted) of the southern Appalachians: Geological Society of America Special Papers, v. 15, p. 1–140.
- Resser, C.E., 1938b, Fourth contribution to the nomenclature of Cambrian fossils: Smithsonian Miscellaneous Collections, v. 97, p. 1–43.
- Resser, C.E., 1939, The *Ptarmigania* strata of the northern Wasatch Mountains: Smithsonian Miscellaneous Collections, v. 98, p. 1–71.
- Resser, C.E., and Howell, B.J., 1938, *Olenellus* zone of the Appalachians: Bulletin of the Geological Society of America, v. 49, p. 195–248.
- Rozanov, A.Yu., et al., 2010, Fossils from the lower Cambrian Stage Stratotypes: Russian Academy of Sciences Transactions of the Palaeontological Institute, 228 p. [in Russian]
- Simpson, E.L., and Sundberg, F.A., 1987, Early Cambrian age for synrift deposits of the Chilhowee Group of southwestern Virginia: Geology, v. 15, p. 123–126.
- Siveter, D.J., and Williams, M., 1997, Cambrian bradoriid and phosphatocopid arthropods of North America: Special Papers in Palaeontology, v. 57, p. 1–69.
- Skovsted, C.B., 2006, Small shelly fauna from the upper lower Cambrian Bastion and Ella Island Formations, North-East Greenland: Journal of Paleontology, v. 80, p. 1087–1112.
- Stein, M., 2008, *Fritzenellus lapworthi* (Peach and Horne, 1892) from the lower Cambrian (Cambrian Series 2) Bastion Formation of North-East Greenland: Bulletin of the Geological Society of Denmark, v. 56, p. 1–10.
- Stein, M., Peel, J.S., Siveter, D.J., and Williams, M., 2010, *Isoxys* (Arthropoda) with preserved soft anatomy from the Sirius Passet Lagerstätte, lower Cambrian of North Greenland: Lethaia, v. 43, p. 258–265.
- Streng, M., and Geyer, G., 2019, Middle Cambrian Bradoriida (Arthropoda) from the Franconian Forest, Germany, with a review of the bradoriids described from West Gondwana and a revision of material from Baltica: PalZ, v. 93, p. 567–591.
- Syssoiev, V.A., 1957, To the morphology, systematics and systematic position of the Hyolithoidea: Doklady Akademii Nauk SSSR, v. 116, p. 304–307. [in Russian]
- Syssoiev, V.A., 1958, Superorder Hyolithoidea, in Orlov, Yu.A., Luppov, N.P., and Drushchits, V.V., eds., Osnovy paleontologii. Molluski-golovongie P. Ammonoidei (Tseratity i ammonity), Vnutrirakovinnye, Prilozhenie: Koniknkhii: Moscow, Gosgeoltekhizdat, p. 184–190.
- Syssoiev, V.A., 1962, Cambrian hyolithids from the northern slope of the Aldan shield: Moscow, Nauka, 65 p. [in Russian]
- Syssoiev, V.A., 1966, On the hyoliths of the Yudom suite of the northeastern part of Aldan anticline: Doklady Akademii Nauk SSSR, v. 166, p. 951–954. [in Russian]
- Syssoiev, V.A., 1968, Stratigraphy and hyoliths of the oldest lower Cambrian beds of the Siberian Platform: Yakutsk, Yakutskiy filial Sibirskogo Otdeleniya Instituta Geologii, Akademiya Nauk SSSR, 67 p. [in Russian]
- Torsvik, T.H., and Cocks, L.R.M., 2016, Earth History and Palaeogeography: Cambridge, UK, Cambridge University Press, 317 p.
- Vannier, J., 2012, Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem: PLoS ONE, v. 7, e52200.
- Volkova, N.A., 1968, Acritarchs of the Precambrian and lower Cambrian of Estonia, in Volkova, N.A., Zhuravleva, Z.A., Zabrodin, V.E., and Klinger, B.Sh., eds., Problematika pograniichnykh sloev rifeya i kembriya Russkoy platformy, Urala i Kazakhstana: Moscow, Trudy Geologicheskii Institut, Akademiya Nauk SSSR, p. 8–36. [in Russian]
- Walcott, C.D., 1884, On the Cambrian faunas of North America: Bulletin of the United States Geological Survey, v. 10, p. 1–55.
- Walcott, C.D., 1890, The fauna of the lower Cambrian or Olenellus Zone, in Tenth Annual Report of the Director, 1888–1889: United States Geological Survey, p. 509–774.
- Webster, M., and Hageman, S.J., 2018, *Buenellus chilhoweensis* n. sp. from the Murray Shale (lower Cambrian Chilhowee Group) of Tennessee, the oldest known trilobite from the Iapetan margin of Laurentia: Journal of Paleontology, v. 92, p. 442–458.
- Williams, H., 1995, Geology of the Appalachian–Caledonian Orogen in Canada and Greenland: Boulder, Colorado, Geological Society of America, 944 p.
- Williams, M., Siveter, D.J., and Peel, J.S., 1996, *Isoxys* (Arthropoda) from the early Cambrian Sirius Passet Lagerstätte, North Greenland: Journal of Paleontology, v. 70, p. 947–954.
- Wood, G.D., and Clendening, J.A., 1982, Acritarchs from the lower Cambrian Murray Shale, Chilhowee Group, of Tennessee, USA: Palynology, v. 6, p. 255–265.
- Zang, W.-l., 2001, Acritarchs, in Alexander, E.M., Jago, J.B., Rozanov, A. Yu., and Zhuravlev, A. Yu., eds., The Cambrian Biostratigraphy of the Stansbury Basin, South Australia: Transactions of the Palaeontological Institute, Russian Academy of Sciences, v. 282, p. 74–85.

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