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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 tennesseenensis (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 chilhoweana Walcott, 1890 as its type species, the latter illustrated also by Williams et al. (1996). The bradoriid Indota tennesseenstis (Resser, 1938a) was established on the basis of material from...
noted the occurrence of hyoliths, and Resser (1938a, pl. 4, 30, 31) illustrated two specimens identified as fossils from the fossiliferous samples (Hageman and Miller, 1997), and Streng and Geyer (2019). Walcott (1890) subsequently by Laurence and Palmer (1963), Siveter and Wil-bern (2018) reported numerous trace fossils. The holotype of M. chaoanoklosma 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. chaoanoklosma in Skiagia ornata (Volkova, 1968). Skiagia ornata is a geographically widespread early Cambrian taxon potentially marking a stratigraphic level earlier than ca. 531 Ma (Moczydłowska, 2002; see also Moczydłowska 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 higginsi 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 in 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 species Mouras skagia 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 (Moczydłowska, 2002; see also Moczydłowska and Zang, 2006 for a longer, up-to-date discussion on the stratigraphic importance of Skiagia and its use in correlation).

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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.**—*Linevitus 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 *Linevitus 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 gallatimensis* Resser, 1938b, was described from the Furongian of Wyoming although a second species, *Haydenoconus prolixus* (Resser, 1939), was described from the Miaoalingian 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 orthoclone. 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 ligual 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-filled 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 whieliet* (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 boeruglamensis* 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 *Grantititheca* 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

**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 orthoclone. 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 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).

**Burithes distortus** Syssoiev, 1962

**Remarks.**—Missarzhevsky (1969, 1981) proposed *Burithes* from the Tommotian and Atdabanian stages (Cambrian Stage 2 and 3) of Siberia, with type species *Linevitus 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 gallatimensis* Resser, 1938b, was described from the Furongian of Wyoming although a second species, *Haydenoconus prolixus* (Resser, 1939), was described from the Miaoalingian 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).
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 Trapezovitius sinicus (Sysoiev, 1958) and Burithes cuneatus Missarzhevsky, 1969, by Qian et al. (2003) in Nitoricornus wushimensis 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 Brilless, 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. Adaperturally, 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 ?Crestjathi tus danianus from New Brunswick, Canada, whereas the dorsal surface is ornamented with barely discernible fine growth lines.
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° 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 amblyogonal 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 boerglumensis and Kalaallitia myliusichrichseni 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°, 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 ?Crestjalithus 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 (Dyran Stage) to the genus, but the assignment was questioned by Streng and Geyer (2019). *Isothyx chilhoweanus* from the Murray Shale is similar to *Isothyx 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 nevadoid *Linniphascos 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. 11); they are not well known, but unidentifiable hyolith fragments are associated with poorly preserved trilobites (Peel and Willman, 2018).

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