

Hyolithellus micans and *Discinella* from the Kap Troedsson Formation (Cambrian Series 2) of North Greenland (Laurentia)

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The slender tubular conch and associated operculum comprising *Hyolithellus micans*, as originally proposed from the lower Cambrian of New York State, are described from the lower Cambrian Kap Troedsson Formation of North Greenland. Following a review of the nomenclative history, *Discinella*, also first described from New York State for the operculum without any assigned species, is regarded as a junior synonym of *Hyolithellus micans* as it was originally proposed. *Hyolithellus* and *Discinella* are generally employed as separate genera for just the conch and the operculum, respectively, a pragmatic approach since the operculum and conchs are rarely associated. The Kap Troedsson Formation samples are unusual on account of the collective occurrence of the phosphatic conchs and opercula with circular attachment scars and holdfasts, which supports their interpretation as comprising a single sedentary operculate annelid that was attached to hard substrates.

Keywords: Annelid, Kap Troedsson Formation, Cambrian, North Greenland, Laurentia

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The Cambrian fossils *Hyolithellus* and *Discinella* share a confused nomenclative history dating back to an acrimonious debate between their respective authors, Elkanah Billings (Montreal) and James Hall (Albany), concerning the priority of the articles in which they were described, and hence the status of the names themselves (Billings 1871a, b; Hall 1871, 1872, 1873). Interpretations of their evolutionary affinities are no less involved, with *Discinella* referred to as a brachiopod, bivalve, gastropod, monoplacophoran and the opercula of *Hyolithellus* or other similar organism, as summarized by Skovsted & Topper (2017), Topper & Skovsted (2017) and Demidenko & Parkhaev (2020), while the slender cone of *Hyolithellus* has been interpreted as a cnidarian, pogonophoran, hyolith, annelid or of uncertain taxonomic affinity, as listed by Novozhilova (2010, table 1) and Demidenko (2021).

Samples from the lower Cambrian (Cambrian Series 2) Kap Troedsson Formation of central North Greenland (Fig. 1) contain both conchs widely referred to *Hyolithellus* and opercula often identified as *Discinella* (Fig. 2). Following review of their nomenclative relationship, *Discinella* Hall, 1873 is here considered to

be a junior synonym of *Hyolithellus micans* (Billings 1871a, b), the type species of *Hyolithellus* as originally described to include both conch and operculum. The co-occurrence of conchs, opercula and attachment scars described here from North Greenland supports interpretation as a sedentary, tube-dwelling annelid with operculum. However, doubts concerning the lack of fossil evidence for the inlife association from other localities across several palaeocontinents argue against the simple extension of this model to all species of *Hyolithellus* and have promoted a pragmatic approach by many workers, for example (Poulsen 1932), with a formal systematic separation of operculate genera and their presumed hosts. In practice, *Discinella* based solely on the operculum has usually been excluded from *Hyolithellus micans*.

The scarcity of localities where *Discinella* (or the morphologically similar *Mobergella* Hedström, 1923) occurs together with the slender, tubular conch of *Hyolithellus* has been noted by several authors, most recently by Demidenko & Parkhaev (2020), as evidence that *Discinella* was not the operculum of *Hyolithellus*. Such taphonomic separation is not unique:

it also confronts hyolith workers on a daily basis, not least those who work with acid resistant micro-assemblages from the lower and middle Cambrian. Thus, while Bengtson *et al.* (1990) were successful in associating disarticulated opercula and conchs in the lower Cambrian of South Australia, Peel (2021) was confronted by a variety of phosphatized hyolith opercula in samples from the Aftenstjernesø Formation of North Greenland in which conchs were rare. The discrepancy involved diagenetic preservational differences and likely also size sorting of skeletal elements with different hydrodynamic properties, but also biases in preparation. It is also possible that opercula of some *Hyolithellus* species were organic and not phosphatic, thereby significantly reducing their fossilization potential.

As regards *Hyolithellus* and *Discinella*, the argument that the absence of co-occurrences of opercula and conchs indicates a lack of biological association is often overstated. For comparison, calcified and non-calcified opercula of calcified serpulid polychaetes are known back to the Permian (Sanfilippo *et al.* 2017). They may be locally abundant in swarms but are usually rare in the fossil record (Gatto & Radwanska 2000). Similarly, virtually all shelled fossil gastro-

pods represented in the Lower Palaeozoic possessed opercula, yet finds of opercula from the numerous, diverse gastropod assemblages described from this time interval are so uncommon that individual finds of operculate gastropods have often justified separate publication (Yochelson & Linsley 1972; Yochelson 1979; Gubanov & Yochelson 1994; Horný & Peel 1995; Peel & Horný 1996; Rohr & Yochelson 1999; Rohr *et al.* 2004; Peel 2015, 2018). Organic opercula are less likely to be preserved, but heavily calcified opercula postmortally isolated from their gastropod hosts may be relatively common locally, as in the Silurian limestones of Gotland, Sweden (Lindström 1884) and the Guelph Formation of Ontario (Whiteaves 1891). Massively calcified ceratopod opercula often dominate shallow water carbonates in Laurentian Lower Ordovician strata while the gastropod shells are inconspicuous (Yochelson & Bridge 1958). Similarly, isolated opercula of the coiled orthothecid hyolith *Protothenella flemingi* Runnegar & Jell, 1976 have not been recognized, with just a single operculum associated with the shell known from amongst several hundred specimens from North Greenland of the internationally widely distributed genus (Peel 2021b).

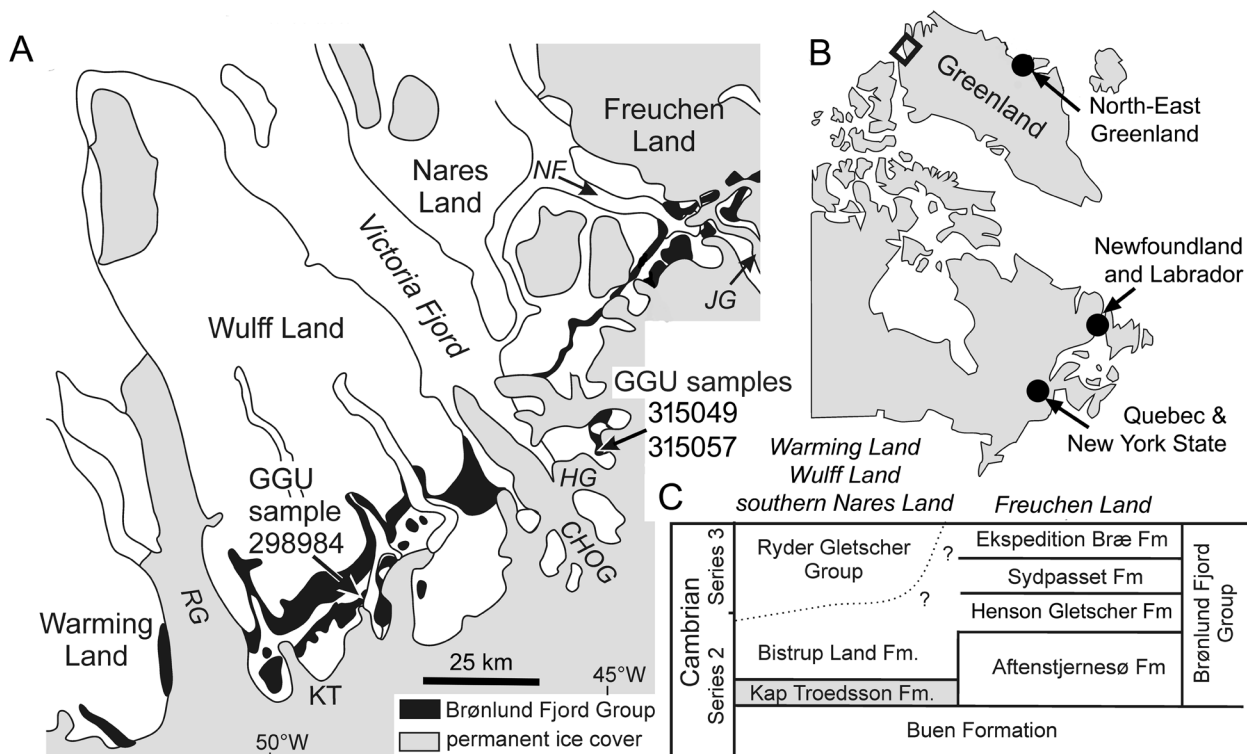


Fig. 1. **A:** Sample localities in central North Greenland. CHOG, C.H. Ostenfeldt Gletscher; HG, Harder Gletscher; JG, Jungersen Gletscher; KT, Kap Troedsson; NF, Nordenskiöld Fjord; RG, Ryder Gletscher. **B:** localities yielding *Discinella micans* and *Hyolithellus micans* (filled circles) and location of A. **C:** Cambrian stratigraphy in the southern Warming Land-Freuchen Land area.

Geological background

GGU samples 298984, 315049 and 315057 were collected from the lower Cambrian Kap Troedsson Formation of central North Greenland (Fig. 1A). GGU sample 298984 was collected by J.S. Peel on 4 August 1985 from south-west Wulff Land (81°24.5' N, 47°54.5' W) at about 25 m above the base of the formation. GGU samples 315049 and 315057 were collected by J.S. Peel on 11 July 1984 on the north side of Harder Gletscher, in the land area south of Nares Land (81°10.5' N, 44°36.8' W).

The Kap Troedsson Formation was proposed by Ineson & Peel (1997) for a distinctive unit of grey limestones and interbedded mudstones between the underlying black shales of the Buen Formation and the overlying brown dolostone crags of the Bistrup Land Formation (Fig. 1C). It thickens from 25 m at the type section in south-western Wulff Land to about 65 m around the head of Victoria Fjord. The Kap Troedsson Formation accumulated in a midramp setting and records the establishment of carbonate-dominated deposition during the early Cambrian (Higgins *et al.* 1991; Ineson & Peel 1997). It is richly fossiliferous, with many taxa in common with the Aftenstjernesø Formation (Peel 2021a; Oh *et al.* in press). Trilobite assemblages in which *Calodiscus lobatus* (Hall, 1847), *Ekvipagetic marginata* (Rasetti, 1967) and olenellids are conspicuous were described by Blaker & Peel (1997). Peel (2014) described epibionts and failed predation on the brachiopod *Botsfordia* Matthew, 1891, including attachment scars attributed to *Hyolithellus*, also discussed herein. Peel (2017a, b) described exceptionally well preserved bradoriid arthropods and grain selection by *Salterella*.

In North-East Greenland, GGU sample 314837 was collected by J.S. Peel on 6 July 1988 from the Bastion Formation on the western side of Albert Heim Bjerge, Hudson Land (Fig. 1B; 73°10' N, 23°40' W; Skovsted 2006, fig. 1). Cambrian outcrops and formations in North-East Greenland were described by Cowie & Adams (1957), Smith *et al.* (2004), Skovsted (2006) and Stouge *et al.* (2012). Thin limestone beds and nodules in the upper member of the formation have yielded an extensive lower Cambrian fauna documented by Skovsted (2006, including earlier references), Skovsted *et al.* (2010) and Peel (2025).

Comparative material of *Hyolithellus* is described from the Ekspedition Bræ Formation, middle Cambrian (Miaolingian Series, Drumian Stage): GGU sample 271573, was collected by J.S. Peel on 2 July 1978 at the head of Henson Gletscher in western Peary Land, North Greenland (82°10' N, 39°40' W); GGU sample 315119 was collected by J.S. Peel on 22 July 1984 in

southern Freuchen Land, North Greenland (82°10' N, 42°25' W).

Specimens were recovered by the solution of limestone samples in 10% acetic acid, and hand picked from residues concentrated by wet sieving. Images of selected specimens were prepared by scanning electron microscopy (SEM) prior to montage using Adobe Photoshop.

Nomenclative history

Elkanah Billings first described the new species *Hyolithes? micans*, later assigned to the new genus *Hyolithellus*, in *The Canadian Naturalist*, but the dates of publication have been variously cited as 1871 and 1872. Volume 6 (parts 1–4) is dated 1872 on the front cover but publication dates of the individual parts are given beneath the text after the last article in each part. At the end of Billings' article proposing *Hyolithellus*, the final one in part 2, it is stated "Published December, 1871." Thus, the description by Billings of the slender, slowly expanding, tubular conch and associated (but not attached) operculum of *Hyolithes? micans* (Billings, 1871a, p. 213–222) was followed on the last page in the same journal part by his proposal of the new genus *Hyolithellus*, which also included both the conch and the operculum of *Hyolithes? micans* (Billings, 1871b, p. 240). The same text was republished by Billings (May 1872) where it was stated at the foot of the title page that publication was 'extracted from the Canadian Naturalist of December, 1871'.

James Hall proposed the new genus *Discinella* without designating a type species or making reference to any named species, considering it to be a brachiopod. He claimed that description of his name should be credited to a pre-publication pamphlet that he distributed in 1871. Horowitz *et al.* (2017, p. 83: Item 564) presented documentation of Hall's claim that these pre-publication copies were printed in March 1871 in an issue of 25 or 30 copies and some were distributed on the 7th April 1871. However, Hall (1873) listed just ten recipients. The copies lacked illustrations but Horowitz *et al.* (2017: Item 590) noted that a pamphlet distributed in March 1872 contained figures. In the formal publication (Hall 1873), the original text including added footnotes and rejoinders to published criticisms by Billings was published without illustrations and with a concluding date of "Albany, N. Y., May, 1872." In a footnote Hall (1873, p. 244) stated "Published March, 1871. Reprinted with explanation of figures, March 1872."

The confrontation between Billings and Hall was reviewed by Hedström (1930), but the disagreement focussed on the naming of brachiopods rather than

the material that Billings described as the new species *Hyolithes? micans* (later *Hyolithellus micans*) and that which Hall referred to his new genus *Discinella*. Surprisingly, the priority of Hall's (1871) pamphlet has been accepted by brachiopod workers with regard to the new brachiopod *Rhynobolus* (Ager *et al.* 1965) even though the distribution list of a mere 10 hand-chosen recipients makes a mockery of nomenclative requirements for ready accessibility. Additionally, Hall (1871, 1872, 1873) neither designated a type species for *Discinella* nor associated any species name with his genus.

Walcott (1886, p. 142, pl. 14, figs. 2, 2a–e) repeated Billings' and Hall's descriptions as quotations, but added new illustrations of *Hyolithellus micans*. He adopted the formal Hall (1873) publication date of *Discinella* and placed it as a junior synonym of *Hyolithellus*, commenting that it was undoubtedly the same as the operculum in Billings' material since they were both from Troy, New York State. In so doing, Walcott (1886) fixed the operculum of *Hyolithellus micans* as being the type species of *Discinella*; no type species was given by Hall (1871, 1872, 1873).

Holm (1893) strongly disagreed with the placement of *Discinella* as a junior synonym of *Hyolithellus*, but Walcott's (1886) opinion was followed by Shimer & Schrock (1944) and Lochman (1956). The latter gave a full description of the conch and operculum of *Hyolithellus micans* (Billings) from New York State, but with an erroneous 1872 date of authorship.

Fisher (1962, p. W132) noted that Hall (1871, 1872, 1873) failed to designate a type species but commented that "it is obvious that type is operculum of *Hyolithes micans* Billings, 1871". He incorrectly stated that *Discinella* was originally described as a gastropod whereas Hall (1871, 1872, 1873) had interpreted it as a brachiopod. Fisher (1962, p. W132) concluded that "*Discinella* is a senior synonym (March 1871) of *Hyolithellus* (Dec. 1871) but because of wide usage of latter name, the former should be suppressed." The statement concerning priority of *Discinella* as a senior synonym is refuted. The International Code of Zoological Nomenclature (2000) rules for suppression as a *nomen oblitum* are also not met since *Discinella* was used by Moberg (1892), Braastad (1915) and Hedström (1923, 1930). Fisher's (1962) call for suppression has also largely been ignored in later years (Missarzhevsky 1989, Landing & Bartowski 1996, Landing *et al.* 2002, Skovsted 2006, Skovsted & Topper 2017, Topper & Skovsted 2017).

Among the first assignments to *Discinella* were descriptions of *Discinella holsti* from the lower Cambrian of Sweden by Moberg (1892) and Wiman (1903), later extended to Norway by Braastad (1915). Hedström (1923, 1930) proposed a new genus *Mobergella* with type species *Mobergella holsti* for Moberg's (1892) ma-

terial, distinguishing it from *Discinella* on the number of muscle scars on the shell interior, but neither genus was considered to be an operculum. Initially, Hedström (1923) referred the North American operculum to *Mobergella micans* (Billings) but later he gave a description of *Discinella* as a patelline gastropod and also provided photographs of *Discinella micans* (Billings, 1871) based on material from the lower Cambrian of Schodack Landing, New York State that was supplied by Charles E. Resser of the Smithsonian Institution, Washington D.C (Fig. 3E, F; Hedström 1930, fig. 1). Åhman & Martinsson (1965) designated a lectotype of *Mobergella holsti* from Öland, eastern Sweden, and a detailed study by Bengtson (1968) added two new species of *Mobergella* to the type species.

Poulsen (1932) described *Discinella micans* and erected *Discinella brastadi* for material from North-East Greenland, which he considered identical to that described by Braastad (1915) from Norway. Importantly, he separated *Discinella micans* and *Hyolithellus micans* taxonomically, interpreting the former as a patelliform gastropod and the latter as a possible pteropod. Missarzhevsky (1989) established a new genus *Brastadella* based on Poulsen's *Discinella brastadi* from Greenland, but Skovsted (2003) assigned Poulsen's (1932) *Discinella brastadi* to *Discinella micans* (see also Skovsted 2006) while also describing new species and combinations of *Mobergella* from Siberia.

Landing & Bartowski (1996), Landing *et al.* (2002), Skovsted (2006), Skovsted & Topper (2017) and Topper & Skovsted (2017) referred specimens from north-eastern USA, eastern Canada (Fig. 3G–H) and North-East Greenland (Fig. 3A–D) to *Discinella micans* with various combinations of author and date.

More than 20 described species of *Hyolithellus* conchs have been described from the lower and middle Cambrian of Laurentia, Eurasia and Australia (Demidenko & Parkhaev 2020), most notably from Siberia (Rozanov & Missarzhevsky 1966; Rozanov *et al.* 1969; Missarzhevsky & Mambetov 1981; Parkhaev & Demidenko 2010; Demidenko & Parkhaev 2020), but Devaere *et al.* (2019) commented on the poor taxonomic resolution of the genus. Specimens are usually preserved as tubular fragments broken at both ends but holdfasts and holdfast scars were described by Peel (2014, 2025, also Fig. 4 herein) from the lower Cambrian Kap Troedsson Formation and the middle Cambrian upper Henson Gletscher Formation of North Greenland, and by Skovsted *et al.* (2021) from the lower Cambrian Mural Formation of western Canada. The characteristic transverse ornamentation of the phosphatic tubes is often highly variable both within and between individuals.

The distribution of pre-publication pamphlets was a characteristic feature of James Hall's publication strat-

egy (Horowitz *et al.* 2017). When widely distributed, many of these pamphlets have been accepted as the valid source of new taxa prior to their official publication despite the nomenclative chaos that has often followed; Peel (2018) provided an example. However, the unacceptably low distribution of Hall's (1871) pamphlet to a mere ten recipients requires rejection of claims of priority for *Discinella* over *Hyolithellus* from the point of view of a lack of general availability. Hall's (1871, 1872, 1873) failure to associate a species name with the proposal of *Discinella* is an aggravating circumstance. Hall (1872, 1873) were clearly published later than Billings (1871a, b), indicating that *Hyolithellus* has priority. Recall, however, that Poulsen's (1932) separation of *Discinella micans* from *Hyolithellus micans* established a pragmatic solution to the handling of nonassociated material even though based on scientific arguments that are not accepted.

Institutional abbreviations. GGU prefix indicates a sample collected by Grønlands Geologiske Undersøgelse (GGU; Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. MGUH: Natural History Museum of Denmark, Copenhagen. NFM: Provincial Museum of Newfoundland and Labrador, St. John's, Newfoundland, Canada. PMU: palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden. SGU: Swedish Geological Survey, type collection permanently housed in the Museum of Evolution, Uppsala University. SMNH: Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden.

Systematic descriptions

Phylum Annelida Lamarck, 1802

Order Hyolithelminthida Fisher, 1962

Family Hyolithellidae Walcott, 1886

Remarks. Walcott (1886, p. 131) introduced the family Hyolithellidae for *Hyolithellus* and a variety of fossils including hyolithids. Fisher (1962) restricted the family to *Hyolithellus* and the opercula *Barella* Hedström, 1930, *Discinella* and *Mobergella*, but this general inclusion of the opercula is rejected; Hyolithellidae is based on the conch of *Hyolithellus*.

An alternative classification by Missarzhevsky (1989, p. 187) proposed the new family Mobergellidae, questionably placed within the molluscs, to include *Mobergella*, *Brastadella* and *Discinella*. Demidenko & Parkhaev (2020) maintained Mobergellidae as a family, extending its content and presenting an

exhaustive overview of mobergellid species. This is a practical approach since most described mobergellids lack established associations with other fossils. They transferred the family from the molluscs to the annelids, considering the phosphatic mobergellid shells to be the caudal shields of sipunculids, which lack a mineralized tube dwelling. The shields block the entrance to sipunculid burrows and may have facilitated their excavation (Rice 1969; Wisshak *et al.* 2017). Sipunculids have a geological record extending back to the early Cambrian (Huang *et al.* 2004) but without caudal shields.

Genus *Hyolithellus* Billings, 1871b

1871b *Hyolithellus* Billings, 1871b, p. 240.

1873 *Discinella* Hall, p. 246.

1886 *Hyolithellus*; Walcott, p. 141.
(only partial synonymy)

Type species. *Hyolithes? micans* Billings, 1871a [= *Hyolithellus micans* (Billings, 1871b)], from the lower Cambrian of New York State.

Remarks. Hall's (1871) naming of *Discinella* does not meet the criteria for availability for it to be regarded as a senior synonym of *Hyolithellus* as originally defined (conch+operculum) by Billings (1871b). The status of Hall (1872) in this respect is not known but it is a junior synonym of Billings' (1871a, b) genus on account of its publication date, as is Hall (1873).

Billings' (1871a, b) original concept of *Hyolithellus micans* (conch+operculum) is maintained here since it is supported by the described material from the Kap Troedsson Formation. However, following Walcott's (1886) fixation of the type of *Discinella*, Poulsen (1932, p. 17, 19) formally separated *Discinella micans* (Billings), based on the operculum alone, from *Hyolithellus micans* Billings, based on the tubular conch. Use of *Discinella micans* and *Hyolithellus micans* in this sense offers a practical approach in many settings and is not affected by the issue of initial priority.

Hyolithellus micans (Billings, 1871a)

Figs. 2, 3

1871a *Hyolithes? micans* Billings, p. 215–216, fig. 1, 3a, b.

1871b *Hyolithellus micans*; Billings, 1871b, p. 240.

1872 *Hyolithes? micans* + *Hyolithellus micans*; Billings, p. 352–360.

1873 *Discinella* Hall, p. 246.

1886 *Hyolithellus micans*; Walcott, p. 142–143, pl. 14, figs 2, 2a–e.

1930 *Discinella micans*; Hedström, p. 5–6, fig. 1.

1932 *Discinella micans*; Poulsen, p. 17–18, pl. 2, figs 7–8; p. 31, pl. 7, fig. 5.

1932 *Discinella bråstadi* Poulsen, p. 30–31, pl. 7, figs 6–9.
 1932 *Hyolithellus micans*; Poulsen, p. 31–32, pl. 7, fig. 10.
 1956 *Hyolithellus micans*; Lochman, p. 1369, pl. 2, figs. 1–21.
 1996 *Discinella micans*; Landing & Bartowski, fig. 9.13.
 2002 *Discinella micans*; Landing *et al.*, fig. 4.14.

2003 *Discinella micans*; Skovsted, p. 432, fig. 2A–I, , fig. 3A–C.
 2017 *Discinella micans*; Skovsted & Topper, p. 2–7, figs. 2.1–2.8, 3.1–3.20 4.1–4.9.
 2017 *Discinella micans*; Topper & Skovsted, figs. 1B, 2, 4E–G. (only partial synonymy)

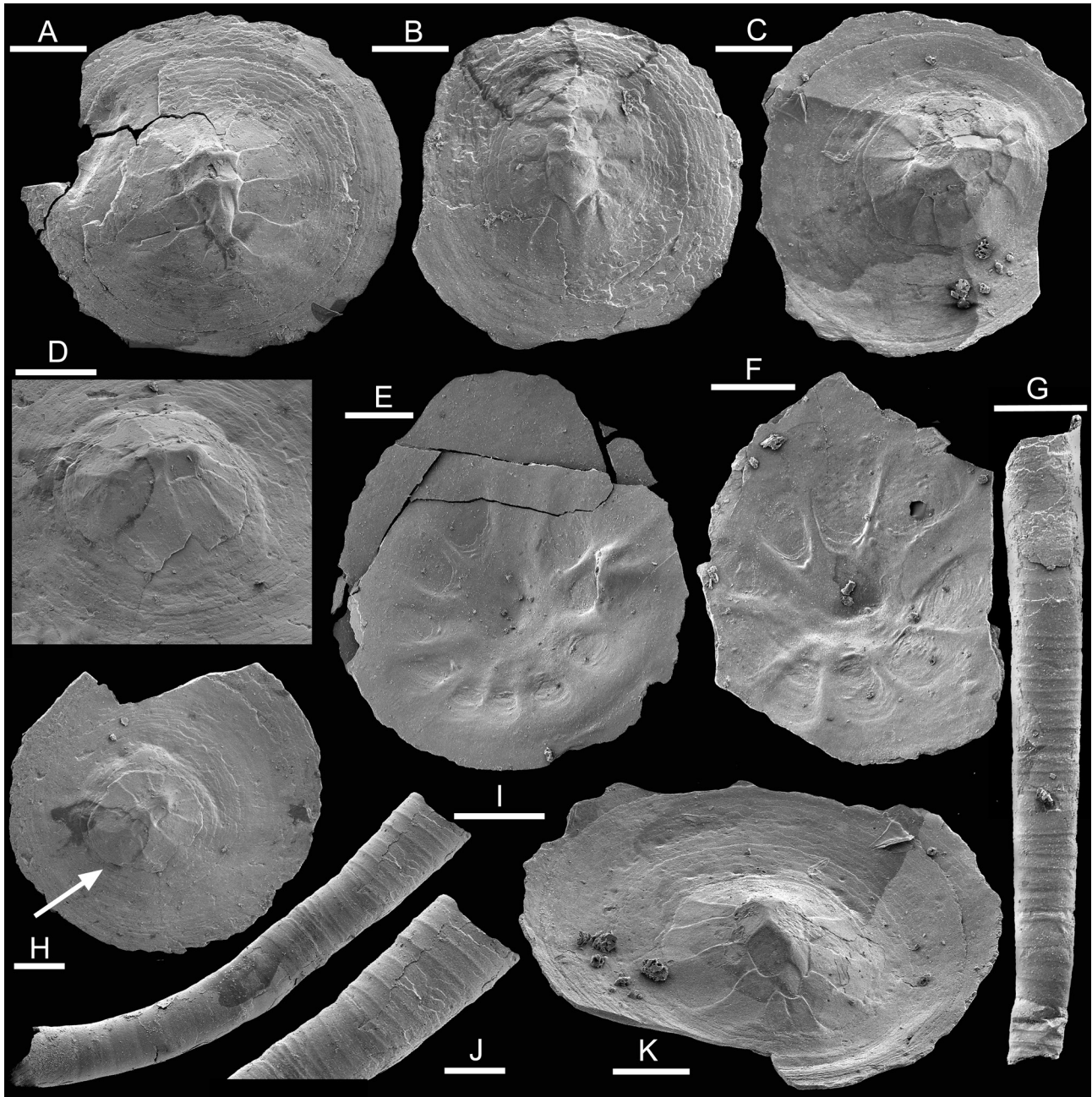


Fig. 2. *Hyolithellus micans* (Billings, 1871a), GGU sample 315049, Kap Troedsson Formation, Cambrian Series 2, North Greenland. **A–F, H, K:** opercula. **A:** PMU 31494, outer surface of juvenile showing plate-like structures of the exfoliated initial shell. **B:** PMU 31495, outer surface of juvenile with thin phosphate encrustation (lower left). **C, K:** PMU 31496 outer surface of concave specimen in apical (C) and oblique anterior (K) views. **D, H:** PMU 31497, outer surface showing repaired shell injury, arrowed in H, with detail (D). **E:** PMU 31498, inner surface with depressed apex and muscle attachment scars. **F:** PMU 31499, inner surface with depressed apex and muscle attachment scars. **G, I, J:** tubular conchs, broken at both ends. **G:** PMU 31500. **I, J:** PMU 31501, with detail of ornamentation (J). Scale bars: 50 µm (J); 100 µm (A–F, H, I, K); 200 µm (G).

Syntypes. Billings (1871a, fig. 1, 3a, b) illustrated a conch and operculum but their location is not known. The syntypes were separated in the description of *Hyalithellus micans* (the conch) and *Discinella micans* (the operculum) by Poulsen (1932).

Material. Kap Troedsson Formation; conchs PMU 31500 and PMU 31501; opercula PMU 31494–PMU 31499, all from GGU sample 315049. Bastion Formation, Hudson Land, North-East Greenland: opercula, MGUH 26733, MGUH 27608, SMNH PZ x 6469 and PMU 31502, all from GGU sample 314837. Forteau Formation, southern Labrador, Canada; opercula NFM F-2472 and NFM F-2474 from Institute of Cambrian Studies sample ICS1575.

Description. The tubular conch is preserved in calcium phosphate, with a finely lamellar structure evident on the outer surface in the illustrated opercula (Fig. 2A–C, K). Lamellar structure in the tubular conch was

described by Skovsted & Peel (2011) and by Demidenko (2021).

The largest fragment of the conch occurring in GGU sample 315049 has a length of 1.4 mm during which its diameter increases from 120 μm to 180 μm (Fig. 2G). It is almost straight, with a circular cross-section and thin wall; it is partly exfoliated. A second specimen is curved near the base, with obscure transverse growth lines, but straightens distally during which irregularly spaced, rounded transverse ribs separated by shallowly concave to flat interspaces of up to 20 μm distally become more prominent. (Fig. 2I, J). Adjacent samples from the same locality yield conch fragments up to 3 mm in length with fine growth lines.

Opercula from GGU sample 315049 are thin translucent discs that range in diameter from about 450 μm to 650 μm (Fig. 2A–C, H, K), which is substantially larger than the diameter of tubular conchs of *Hyalithellus* in the same collection (Fig. 2G, I, J). The apical area of the outer surface is always elevated above the

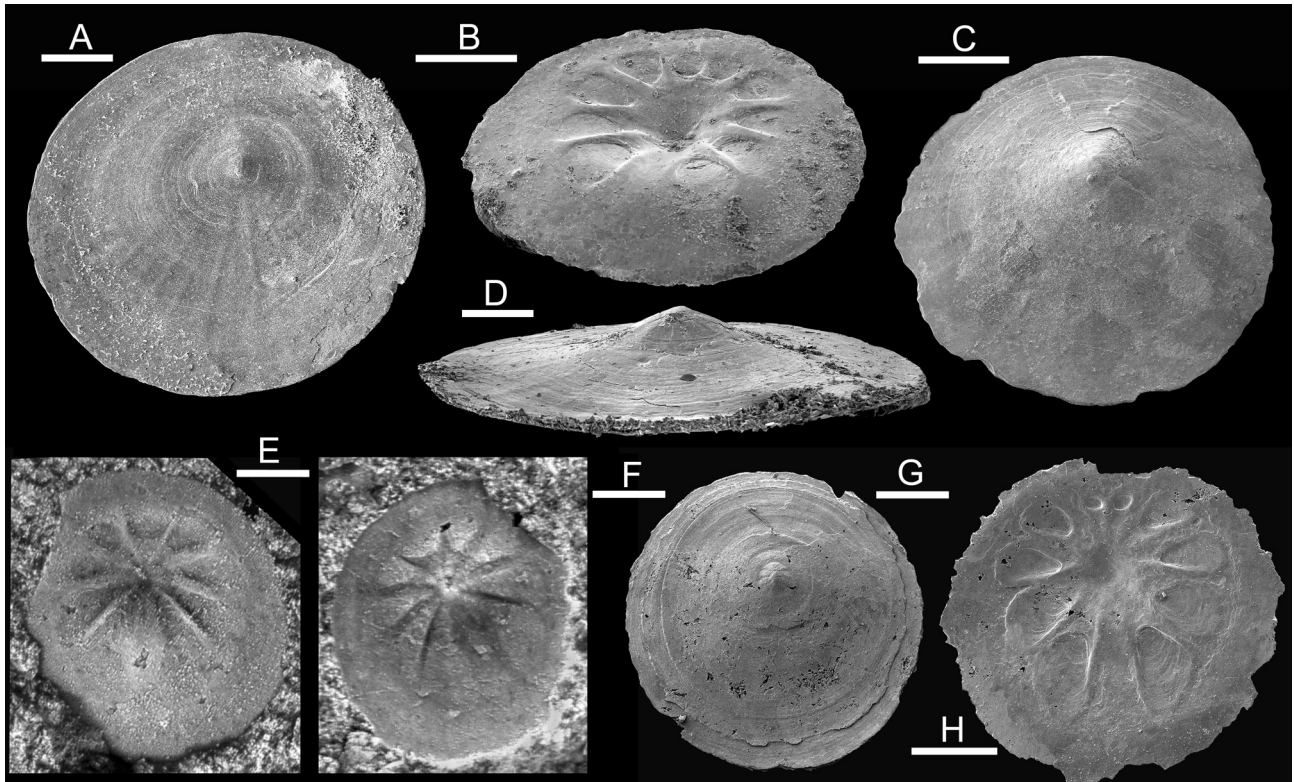


Fig. 3. Opercula of *Hyolithellus micans* (Billings, 1871a). **A–D:** Bastion Formation, North-East Greenland, GGU sample 314837. **A:** MGUH 26733, outer surface, with local radial ribs. **B:** SMNH PZ X 6469, inner surface of concave operculum with depressed apex and muscle scars. **C:** MGUH 27608, outer surface of conical specimen. **D:** PMU 31502, oblique lateral view. **E, F:** internal surface, part and counterpart of SGU 7614a, b, the specimen illustrated by Hedström (1930, fig. 1a, b), collected 1 mile below N.Y. Central Railroad Station, Schodack Landing, New York. Presented to Hedström by Charles E. Resser from the collection of U.S. National Museum, Washington D.C. **G, H:** Forteau Formation, Labrador, specimens collected by A.R. Palmer in 1979 from sample ICS1575 (Institute for Cambrian Studies), Middle Shale member, Forteau Formation, Fox Cove, southern Labrador (after Skovsted & Topper, 2017). **G:** NFM F-2472, outer surface. **H:** NFM F-2478, inner surface with muscle attachment scars. Scale bars: 200 μm (D); 400 μm (B); 500 μm (A, C–H).

lateral areas that vary from shallowly convex to concave (Fig. 2C, K). The inner surface shows a depressed apical area with five prominent muscle attachment scars located symmetrically on each side of the median plane and impressed into the smooth surface (Fig. 2E, F). Each of the muscle scars preserves a series of arcuate growth lines paralleling the abaxial margin of the scar (Figs 2F, 3H).

The outer surface of the operculum is divided into two distinct zones. The raised, slightly excentric apical area is interpreted as the larval shell. It is circular to oval (length about 250 μm) and bilaterally symmetrical, with growth lines restricted to the narrow transitional zone to surrounding lateral areas (Fig. 2A–C, K). The lateral areas are ornamented with fine, closely spaced, lamellose comarginal growth lines and peri-

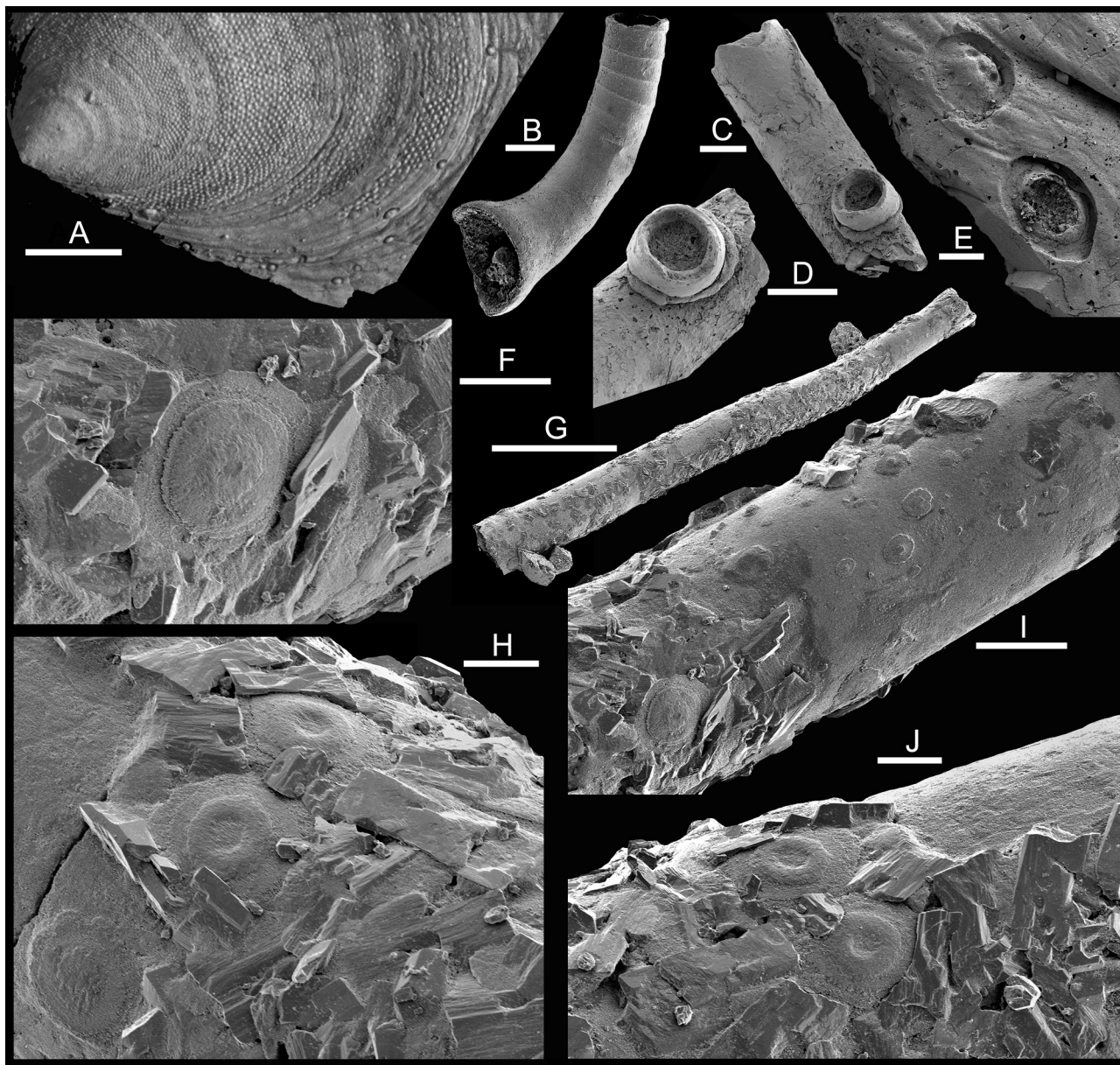


Fig. 4. Holdfasts and attachment scars, Kap Troedsson Formation unless stated. **A:** MGUH 30872 from GGU sample 315057, ventral valve of *Botsfordia* with numerous circular holdfasts on the lateral margin. **B:** PMU 31503 from GGU sample 315119, tubular conch with expanded basal margin, Ekspedition Bræ Formation, Miaolingian Series. **C, D:** PMU 31504 from GGU sample 271573, holdfast cemented to exfoliated conch of *Hyolithellus*, Ekspedition Bræ Formation, Miaolingian Series. **E:** MGUH 30884 from GGU sample 315057, attachment surfaces etched into valve of *Botsfordia*. **F–J:** PMU 31505 from GGU sample 298984, holdfasts; note the great variation in size (I). Scale bars: 20 μm (F, H, J); 50 μm (E, I); 100 μm (B–D); 200 μm (G); 1 mm (A).

odic growth halts (Fig. 2A, C).

The larval shell has an elevated spindle-shaped median axis also described by Skovsted & Topper (2017). In the present material it is bounded on each side by the impressions of five imbricated plate-like structures which step down towards the posterior (Fig. 2A–C). Views in Figure 2A, B are therefore oblique anterior views. The plates are most clearly visible in slightly exfoliated specimens (compare Fig. 2A with 2B). The central spindle is crossed by prominent acute ridges (Fig. 2A, K) interpreted as plate margins. A median anterior plate is followed by paired lateral plates (Fig. 2A, K).

Surface attachment. Almost all specimens of the tubular conchs of *Hyolithus* described in the literature and in Greenland collections are broken at each end and they are often worn. Rare specimens of *Hyolithellus* showing an expanded base indicating attachment to a hard surface were described by Skovsted *et al.* (2021) from the lower Cambrian Mural Formation of western Canada and by Peel (2025) and Willman & Peel (2026) from the Henson Gletscher Formation (Drumian) of North Greenland. A specimen from the Ekspedition Bræ Formation (Drumian) shows that the expanded base of the tube is hollow without an attachment plate (Fig. 4B), while a second specimen from the same formation preserves the attachment of a broken tubular conch to a fragment of a partly exfoliated specimen of *Hyolithellus*, with a collar of phosphate sealing the junction (Fig. 4C, D). The expansion towards the base is gradual, in contrast to the abrupt expansion seen in *Sphenothallus* Hall, 1847 (Peel 2021c).

Linguliformean brachiopod valves from the Kap Troedsson Formation show circular attachment scars (diameter about 100 µm) etched into their outer surface that conform to the margin of the *Hyolithellus* tubular conchs and are of similar diameter (Fig. 4A, E; Peel 2014). Circular scars from the Kap Troedsson Formation attached to a diagenetically mineral encrusted rod (Fig. 4F–J) are much smaller (diameter 10–40 µm) than the rings etched into the brachiopods (about 100 µm). They differ also in preserving a circular pit at the centre of the raised inner part of the scar (Fig. 4H, J) and cannot be referred to *Hyolithellus micans* with confidence.

Remarks. Skovsted & Peel (2011) described unusually large specimens of *Hyolithellus* in life position from the basal member of the Aftenstjernesø Formation in North Greenland, laterally equivalent to the Kap Troedsson Formation in more eastern areas. The straight or slightly undulating tubes are up to 75 mm long and 600 µm to 4.2 mm in diameter, with an aver-

age expansion rate of 2.7°. Almost half of the observed specimens were oriented passing through the sediment vertically, always tapering downwards. Opercula have not been observed in samples from the Aftenstjernesø Formation.

The fine growth lines between the transverse ribs of the conch of *Hyolithellus micans* from the Kap Troedsson Formation are also seen in a specimen from New York State assigned to the species by Walcott (1890, pl. 79, fig. 1). Landing & Bartowski (1996) illustrated conchs with the same ornamentation from the lower Cambrian Browns Pond Formation of eastern New York State, often in samples also yielding opercula. Skovsted (2006) reported conchs of *Hyolithellus micans* from most samples from the Bastion and Ella Island formations in North-East Greenland, commenting on the variation in transverse ornamentation, but illustrated specimens from the upper member of the Bastion Formation have more widely spaced ribs. Robust opercula are also widely distributed in North-East Greenland (Skovsted 2006; Skovsted & Topper 2017). The large specimens illustrated by Skovsted & Peel (2011) from the Aftenstjernesø Formation are often partly exfoliated but show similar ribbing.

In GGU sample 315049, the opercula have a larger diameter than the tubular conchs and the attachment scars. While likely reflecting differences in hydrodynamic properties and differential post-depositional sorting, specimen size in the examined residues is strongly influenced by preparation techniques involving routine wet sieving into specific size categories (usually 250 µm and 500 µm).

The circular shape and concave outer surface provide the strongest evidence in support of interpretation as opercula within some form of tubular conch (Figs. 2K, 3B, H), although the analysis of musculature by Topper & Skovsted (2017) is also a significant contribution. As with many gastropods, opercula with this concave shape can be withdrawn deep into the host tube providing improved defence against predatory attacks that otherwise might target the vulnerable suture between the conch and operculum (Vermeij 1987; Checa & Jiménez-Jiménez, 1998; Peel 2015, 2018). An interesting corollary was provided by Hadfield (1970) who noted that a sedentary tube-dwelling vermetid gastropod from California, similar in its mode of life to that envisaged for *Hyolithellus micans*, periodically moulted its operculum and generated a new one.

Almost all of the delicate opercula show broken margins, in part caused during specimen preparation. However, one specimen shows a repaired non-lethal injury to the outer surface of the larval shell, likely caused by a failed predatory attack, that was repaired prior to subsequent shell growth (Fig. 2D, arrow in H).

Conclusions

Discinella Hall, 1873 is a junior synonym of *Hyolithellus micans* as originally described by Billings (1871a, b). However, Poulsen (1932) separated the operculum and tubular conch placed together in Billings' (1871a, b) descriptions and established *Discinella micans* and *Hyolithellus micans* as separate taxa, for the operculum and the conch respectively. This is a pragmatic approach followed by most workers, based on varied interpretations of two skeletal elements that often do not occur together.

The concurrence of the tubular phosphatic conchs, opercula and attachment structures in samples from the Kap Troedsson Formation (Cambrian Series 2) supports interpretation of *Hyolithellus micans* in the original sense of Billings (1871a, b) as a sedentary, operculate annelid attached to hard surfaces.

Apart from the present example, the relationships, if any, between the eight mobergellan opercula and the 22 species of *Hyolithellus* listed by Demidenko & Parkhaev (2020, figs 1, 2) are not known.

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