Mobergellans from the early Cambrian of Greenland and Labrador — new morphological details and implications for the functional morphology of mobergellans

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Running header: Mobergellans from Greenland and Labrador

Abstract.—New morphological features of the mobergellan *Discinella micans* (Billings, 1871) from the lower Cambrian (Stage 4) of North-East Greenland and southern Labrador are described. The new features include: (1) the morphology of the larval shell, which is shown to be cap-shaped, sub-circular and with impressions of the internal muscle attachment scars; (2) a range of unusual shell deformations (changes in growth direction resulting in thickened shells, partial detachment of shell laminae and subsequent regrowth, internal projections of shell material increasing the depth of the shell by up to 150%, disturbances and irregular fusion of muscle scars). In addition we provide new details about the variability in number and shape of the anteriormost internal muscle scars which often fuse and may vary in number from one to three (resulting in 9 to 11 scars in total). Together the new observations provide additional strength to the hypothesis that mobergellan shells represent opercula of an as yet unknown tubular organism.

Introduction

The fossil record of the earliest Cambrian (Terreneuvian and unnamed Cambrian Series 2) is dominated by a plethora of small shells, plates and sclerites, often collectively labeled Small Shelly Fossils (SSF; Matthews and Missarzhevsky, 1975; Bengtson et al., 1990). These fossils, usually extracted from carbonate rocks using acid treatment, represent some of the earliest undoubted metazoan body fossils and a vital component for our understanding of early animal evolution during the Cambrian Explosion. Many SSF taxa represent parts of larger skeletons (sclerites, spicules etc.) and their often unusual morphology lacks clearly identifiable counterparts among living metazoans. This has historically led to the placement of many SSF taxa among the problematica. However, detailed study of morphology, shell structure and partly articulated specimens have meant that we can now place many previously problematic SSFs in the stem groups of modern phyla. Examples include the net-like plates of *Microdictyon* that have been shown to belong to stem onychophorans (Chen et al., 1989) and the cap- or cone-shaped tommotiids that have been interpreted as members of the brachiopod stem group (Skovsted et al., 2008, 2009, 2011, 2014; Murdock et al., 2012, 2014). Yet, some SSF groups remain problematic in terms of both functional morphology and phylogenetic position. One such group is the mobergellans.

Mobergellans are highly problematic disc-shaped fossils from the first half of the Cambrian (Stages 3-5) that are widespread and may be locally very common (Lochman, 1956; Bengtson, 1968, Skovsted, 2003; Streng & Skovsted, 2006; Demidenko et al., 2016). The shell of mobergellans are phosphatic, presumably by original composition and grew by marginal accretion (Lochman, 1956; Bengtson, 1968). The most distinctive features of mobergellans are radiating sets of muscle scars and/or platforms on the supposedly internal surface. The exact nature and number of scars is variable (from eight to 14) but the scars are usually arranged in pairs on either side of a central line of bilateral symmetry. Mobergellans were first discovered almost 150 years ago (Billings, 1871) and their taxonomy and phylogenetic position have been discussed ever since. Originally considered to be the opercula of the phosphatic tubular fossil *Hyolithellus* (Billings, 1871, Fisher, 1962), mobergellans have also been interpreted as brachiopods (Hall, 1872; Moberg, 1892; Dzik, 2010), univalved molluscs (Hedström, 1923, 1930; Missarzhevsky, 1989; Conway Morris and Chapman, 1997) as well as the

opercula of an as yet unknown tubular organism (Bengtson, 1968; Rozanov and Zhuravlev, 1992; Topper and Skovsted, 2017).

Here, we illustrate and describe specimens from extensive collections of the mobergellan *Discinella micans* (Billings, 1871) from North-East Greenland and southern Labrador (Cambrian Stage 4). *Discinella micans* is known to occur along the present eastern palaeomargin of Laurentia (Fig. 1), from North Greenland (J.S. Peel, personal communication, 2016), North-East Greenland (Poulsen, 1932; Skovsted, 2003), through Labrador and western Newfoundland (Schuchert and Dunbar, 1934; herein), Quebec (Landing et al., 2002), the Taconic allochthons of Vermont and New York State (Walcott, 1886; Lochman, 1956) and into a cratonic setting within the Appalachian region of western New York (Palmer, 1971). The basic morphology of *D. micans* is relatively well known from previous studies (Lochman, 1956; Landing and Bartowski, 1996; Conway Morris and Chapman, 1997; Skovsted, 2003). However, important aspects of the morphology and variability of these problematic shells have never been described before and we will focus our work on new morphological details that may increase our understanding of the ontogeny and functional morphology of mobergellans. New observations described for the first time herein are the morphology of the larval shell, the variability of the anteriormost muscle scars and a range of different unusual shell morphologies and deformations that may constrain the functional morphology of mobergellans.

Material and methods

The material for the present contribution was derived from two areas of eastern Laurentia; the fjord area of North-East Greenland and the coastal region of southern Labrador. The Greenland material was derived from the lower Cambrian Bastion and Ella Island formations where *Discinella* was first reported by Poulsen (1932) and subsequently in greater detail by Skovsted (2003). A total of about 800 specimens of *D. micans* were found in acid resistant residues of limestone samples collected by J.S. Peel under the auspices of the Geological Survey of Greenland (GGU) from the upper Bastion Formation and the overlying Ella Island Formation of Albert Heim Bjerge and C.H. Ostenfeld Nunatak. Rare specimens of a second mobergellan, *Aktugaia?* sp., were reported from the Bastion

Formation by Skovsted (2006), but this material is too poorly preserved to be analyzed in detail herein. For detailed information on the geology, age and stratigraphical occurrence of *D. micans* in North-East Greenland see Skovsted (2003, 2006).

In southern Labrador (eastern Canada), *Discinella micans* occurs in the lower part of the Forteau Formation (Labrador Group). The species is relatively common in the basal Devils Cove member and in the overlying Middle Shale member (see Knight 2013; Knight and Boyce, 2015 and Skovsted et al., in press for detailed characterization of the Forteau Formation). In our material *D. micans* occurs in interreef limestones mainly composed of echinoderm shell debris adjacent to the archaeocyathid patch reefs which formed in an inboard shelf setting during a transgression (Spencer, 1980; Skovsted et al., in press). *Discinella micans* also occurs in the Devils Cove member of the Forteau Formation in western Newfoundland (CBS pers. observation 2016), but these specimens have not been closely studied in the present work. A total of over 900 specimens were recovered from a suit of samples derived mainly from beach cliffs along the Straights of Belle Isle, east of Forteau collected by A.R. Palmer and student in 1978 and 1979 (material now at the Institute for Cambrian Studies (ICS) at the University of Chicago) and by CBS in 2007. The majority of specimens were recovered from the section at Fox Cove (for details see Skovsted et al., in press).

Selected specimens from acid resistant residues (dissolved in 10% acetic acid) were gold-coated and investigated using SEM facilities at Uppsala University and Swedish Museum of Natural History in Stockholm. All illustrated specimens from Greenland are housed in the Swedish Museum of Natural History (SMNH) in Stockholm, Sweden while specimens from Labrador are housed at the Provincial Museum of Newfoundland and Labrador (NFM), St. John's, Newfoundland, Canada.

Taxonomic remark

The taxonomic status of the name *Discinella micans* (Billings, 1871) is somewhat uncertain following more than 100 years of unusual taxonomic practices in studies of mobergellans (e.g., Billings, 1871; Hall, 1872; Moberg, 1892; Hedström, 1923, 1930; Fisher, 1962; see also discussion in Bengtson, 1968 and Skovsted, 2003). However, a full taxonomic revision of the genus should in our view be

carried out in connection with a larger revision of the Family Mobergellidae and is thus outside the scope of the present contribution. We therefore adhere to the established use of the name *Discinella micans* in the present contribution awaiting future resolution of mobergellan taxonomy.

***Discinella micans* from North-East Greenland and southern Labrador**

The shells of *Discinella micans* from Greenland and Labrador are circular to sub-circular discs with flat or weakly convex or concave lateral profile (Skovsted, 2003). The external surface is ornamented by fine concentric growth lines at regular intervals, presumably reflecting growth of the shell through addition of fine laminae as previously documented for other mobergellans (Bengtson, 1968; Streng and Skovsted, 2006; Demidenko, 2016). The apex of the shell is subcentral but usually slightly shifted towards the anterior side of the shell. Internally, the shells are smooth, with the exception of a series of (usually) 10 paired muscle imprints (although some specimens may instead have nine or 11 scars), roughly arranged in a circle, slightly shifted towards the anterior of the shell. The size of the muscle scars increases towards the posterior resulting in a distinctive bilateral symmetry. Each muscle scar is a sub-circular to triangular depression often ornamented by low, roughly parallel ribs mirroring the shape of the muscle scar and presumably reflecting growth lines.

Larval shell morphology.—The initial shell of *Discinella micans* is a low, cap shaped subcircular structure at or close to the center of the shell (Fig. 2). Its placement is usually slightly shifted from the center towards the anterior (Fig. 2.1, 2.3, 2.5, 2.7). In well preserved specimens the initial shell is defined and clearly delineated by the onset of commarginal growth as the initial shell itself lacks growth lines. The initial shell is always convex in lateral profile, even in specimens where growth direction later changes resulting in a concave adult shell. The structure has a maximum diameter of 210 μm (average from 22 specimens) and its height typically represent 38% of the diameter (average from 8 specimens). The initial shell is similar in shape and general morphology to the larval shells of various invertebrates (such as gastropods, brachiopods, hyolith opercula etc.; see Demidenko, 2016)

and likely represents the first mineralized growth stage which may have been formed at or slightly before settling of the larvae on the sea floor.

The cap-shaped larval shell of *Discinella micans* consists of a central ridge oriented along the anterior-posterior line of symmetry (Fig. 2.2, 2.4, 2.6, 2.8). The ridge is widest in the center and sometimes divided in a series of distinct rounded lobes (Fig. 2.6). From the central ridge extends on both sides a set of six to eight fine ribs separating slightly depressed areas forming a radial pattern (Fig. 2.2, 2.4, 2.6).

The larval shell is commonly preserved in specimens from samples with generally good preservation of phosphatic fossils but it is not observable in all specimens. This is potentially the reason why this feature has not been noted in previous investigations (Lochman, 1956; Landing & Bartowski, 1996; Conway Morris & Chapman, 1997; Skovsted 2003).

Anterior muscle scars.—The characteristic muscle scars on the interior surface of *Discinella micans* are variable in number (Fig. 3). Although 10 scars are usually reported in the literature, the anteriormost pair of scars are often fused, resulting in 9 obvious scars. Conway Morris and Chapman (1997) implied that fusion of the anteriormost scars may be a feature of late growth stages in *D. micans*. However, in our material fusion of the anteriormost muscle scars appear to affect specimens of all sizes. Large specimens sometimes express fused scars (Fig. 3.1-3.4, 3.11-3.12) and sometimes separate scars (Fig. 3.5-3.6, 3.9-3.10). The same pattern is obvious in the smallest specimens recovered where both fused (Fig. 3.17-3.18) and separate scars (Fig. 3.19-3.20) occur.

Conway Morris and Chapman (1997) reported an extra scar-like feature on the shell interior close to the fused anteriormost scars in a large and unusually thick-shelled specimen from New York State and Skovsted (2003) noted that similar extra scars are also present in specimens from Greenland. In our material extra scars between or behind the anteriormost pair of scars are present in a large number of specimens from both Greenland and Labrador (Fig. 3.6, 3.10, 3.12, 3.14, 3.16). The position of the extra scar is typically between (Fig. 3.6) and slightly behind (i.e., closer to the center of the shell; Fig 3.14, 3.16) the normal anteriormost muscle scars. It is variable in size relative to the other scars of the shell interior but is typically much smaller than the smallest of the anteriormost scars

(about 10-50 μm in diameter). The extra scar is sub-circular to transversely oval and of variable depth but often appears to be deeper than the normal anteriormost scars (Fig. 3.10, 3.14).

Anomalous muscle scars.—A few otherwise unremarkable specimens of *Discinella micans* exhibit unusual configurations of muscle scars, here exemplified by a shell from North-East Greenland (Fig. 4.10). This specimen has a normal set of five muscle scars of increasing size on the right hand side but on the left hand side only four scars are apparent, and only the posteriormost two are of normal morphology. In the anteriormost position is a single large, heart-shaped scar. Based on the position of this scar compared to the scars of the right hand side, it presumably represents the fused first and second muscle scar of the left hand side. The following scar on the left hand side is reduced to a narrow slit-like feature between the unusually large combined first and second scar and the normal posteriormost two scars.

Shell malformations.—Shell growth in *Discinella micans* is typically very regular with slow increase in shell diameter in concert with the addition of new shell layers. The variation in width of growth increments (i.e., the distance between adjacent growth lines) appears to be small and the growth rate seem to have changed very little through ontogeny in most specimens (Fig. 2.1, 2.5, 2.7). However, some specimens in our collections show evidence of disruption of the normal growth regimen. In some specimens the growth vector changes and new shell layers are added without increase in diameter resulting in thick shells with pronounced marginal rims (Fig. 4.1-4.2). Other specimens exhibit traces of disruption in shell formation with new shell layers partly detached from the older shell (Fig. 4.7-4.9). In such specimens new shell material was sometimes added at an angle or slightly off-center compared to previously formed shell (Figs 2.3, 4.7). Growth lines in the new shell layers inserted below the previous shell seem to indicate a reduction in the diameter of the shell secreting tissue before the new shell was formed (Fig. 4.8), partly at an angle to the older shell (visible as a narrow slot between the old and new shell; Fig. 4.9). The newly formed shell in such regrown specimens shows no other signs of disruption of the shell secreting tissue. The growth increments are of normal width and although the new growth may be slightly off-center, the shape of the disc only changes marginally.

A single specimen of *Discinella micans* from Labrador exhibits a gross malformation of the shell in the form of a high dome-shaped growth on the internal surface, close to the edge of the shell in the area adjacent to one of the last muscle scars (Fig 4.3- 4.6). This specimen is otherwise unremarkable among specimens of *D. micans* in our collections. The shell is large but not unusually large (diameter 2.04 mm), except for the anomalous growth it is almost flat and the anteriormost pair of muscle scars is fused. The growth pattern appears to be perfectly normal except for the formation of this distinct dome-like structure. The dome is smoothly rounded, 0.48 mm high and is 0.3 mm wide near its apex. The abnormal growth though has flared the shell margin on either side of the dome by 0.3 mm and in total affects about 44% of the diameter of the shell and increases the total height of the sclerite by 150% (shell height – 0.32mm). The surface of the dome is continuous with the shell interior and a fracture along the shell edge reveals that the anomalous growth affected a series of shell layers (Fig. 4.6).

Discussion

The Mobergellidae is characterized by disc-shape shells with an internal surface bearing a variable number of muscle attachment structures. Although these features are fluid across the group, the morphology of the larval shell appears to be relatively consistent, represented by a sub centrally positioned, low, flat or cap shaped subcircular structure that frequently exhibit features that reflect the configuration of the muscle scars on the interior surface (Fig. 2). Slight variation does exist, for example in the Siberian species of *Mobergella* (Skovsted, 2003; Demidenko, 2016), the larval shell is sometimes flat and ornamented by radial rows of pores, reflecting the porous surface of muscle scars on the inside of the adult shell. The larval shell structures in *D. micans* described here reflects the imprints of the internal muscles on the larval shell as depressed areas between radiating ribs. These areas probably represent the attachment sites of the larval muscles to the shell interior and formed by the deformation of the thin shelled (and possibly poorly mineralized) cap-shaped larval shell by the forces induced by muscular contraction. The problematic fossil *Hippoklosma mongolica* Conway Morris and Chapman, 1997 from the lower Cambrian of Mongolia has been compared to mobergellans

(Missarzhevsky, 1989; Conway Morris and Chapman, 1997), but the lack of distinct muscle scars and the peculiar radiating fields of fibrous bundles (fibroplacodes) on the external surface of the shell seems at odds with the typical morphology of mobergellans and this taxon has sometimes been excluded from the group (Streng and Skovsted, 2006; Demidenko, 2016). However, the cap-shaped larval shell of *H. mongolica* is composed of a central axis with arcuate furrows extending on both sides. This configuration of structures is strikingly similar to the larval shell morphology of *D. micans* described here and may lend further support for the hypothesis that *H. mongolica* is closely related to the Mobergellidae.

The morphological similarity of the larval shell however, does not unfortunately assist greatly in revealing the functional morphology or biological affinity of these enigmatic sclerites. To resolve the functional morphology of mobergellans Topper and Skovsted (2017) compared the relative size of the prominent muscle scars of two mobergellans (*Mobergella holsti* and *Discinella micans*) to muscle attachment areas of modern and fossil invertebrate shells of differing function (eg. bivalves, brachiopods, monoplacophorans, polyplacophorans, annelid elytra, hyolith and gastropod opercula). The analysis showed that mobergellan muscle scars occupy about 20% of the area of the shell interior, which is very high compared to muscle attachment sites in most invertebrate shells, being only compatible with the muscle attachment area of the opercula of neritic gastropods. Hence, an opercular hypothesis as the function of mobergellan shells for a tube dwelling organism was considered most likely (Topper and Skovsted, 2017) although the nature of the associated tube and its phylogenetic affinity remain elusive. In North-East Greenland and Labrador, *Discinella micans* occur together with the phosphatic tubes of *Hyolithellus* Billings, 1871 as well as hyoliths and other calcareous tubes (Skovsted, 2006; Skovsted & Peel 2010; CBS personal observation 2016). However, the size and morphology of these tubes do not fit with the size and morphology of co-occurring *D. micans*.

Following Bengtson (1968), Topper and Skovsted (2017) hypothesized that the corresponding tube was cemented or firmly attached to the substrate and after the death of the animal the opercula were transported away by prevailing currents. The tendency for mobergellan sclerites to be recovered in high numbers from reworked transported sediments was used as evidence to support this hypothesis (Topper and Skovsted, 2017). *Discinella micans* material from Labrador was originally documented

from debris surrounding archaeocyathan bioherms (Spencer, 1980). Spencer (1980) also noted a decrease in the relative abundance of *D. micans* away from the archaeocyathan bioherms, contrasting to the simultaneously increasing abundance of the co-occurring brachiopod *Hadrotreta* (with shells of similar size, shape and composition), and it is possible that the mobergellan animal inhabited shallow water archaeocythid buildups and upon death the dissociated opercula accumulated at the base of the biohermal structures. Topper and Skovsted (2017) noted a trend of recovering mobergellan sclerites from reworked sediments including *Mobergella holsti* that has been documented from shallow water clastic sediments, associated with paleoislands in Baltica (Bengtson, 1968) and it is plausible that mobergellans preferred inhabiting shallow water, high-energy environments.

The material of *Discinella micans* described herein yields new information that may be important to further constrain the functional morphology of mobergellans. The unusual configuration of fused muscle scars in specimens of *D. micans* (Fig. 4.10) points to a considerable plasticity in the muscular system of mobergellans where unusual configurations of muscles appear to have been fully functional. The flat to concave lateral profile of the shells illustrated here (Fig. 5) is, as also noted by Topper and Skovsted (2017), not consistent with representing a univalved or a two-valved organism. This is of course assuming, in a two-valved scenario that both valves are morphologically recognizable as mobergellan sclerites. But perhaps most importantly is the unusual specimen documented herein with an internal anomalous growth (Fig. 4. 3-4.6). The anomalous growth of this unique specimen is reminiscent to the formation of pearls on the interior of shells of bivalves (e.g., Jacob et al., 2008) and to internal growth malformations in bivalves as a response to exposure to parasites (e.g., Kefi et al., 2012). Both are a defensive response to a foreign object or organism that disturbs the secretory tissues and results in the formation of new shell layers that drape over and encapsulate the foreign body. However, in these examples the height of the internal shell malformation is small relative to the height of the valves and does not prevent the closure of the valves (Kefi et al., 2012). The anomalous growth exhibited in the specimen illustrated here (Fig. 4.3-4.6) affected a series of shell layers and must have been a constant feature of the shell interior for a substantial portion of the life of the animal. The growth also increases the height of the sclerite by 150% and indicates that there must have existed a substantial cavity beneath the shell of this mobergellan to accommodate the

soft parts of the animal during growth. This observation presents further evidence that the mobergellid animal was substantially larger than the preserved shell itself and speaks against an interpretation of mobergellans as a two valved organism or a limpet-like univalved animal.

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Figure captions

Figure 1.—Map of North America showing known distribution of *Discinella micans* (Billings, 1871). Red stars indicate approximate locations in North Greenland, western Newfoundland, southern Quebec and New York State. Yellow stars indicate locations in North-East Greenland and southern Labrador sampled for the present investigation.

Figure 2.—*Discinella micans* (Billings, 1871) in external view. Specimens in 1-6 from sample ICS1575, Middle Shale member, Forteau Formation, Fox Cove, southern Labrador. Specimen in 7-8 from sample GGU 314837, upper Bastion Formation, Albert Heim Bjerge, North-East Greenland. **(1, 2)** NFM F-2472; **(1)** dorsal side, anterior and posterior directions indicated; **(2)** detail of larval shell in oblique view. **(3, 4)** NFM F-2473; **(3)** dorsal side; **(4)** detail of larval shell in oblique view. **(5, 6)** NFM F-2474; **(5)** dorsal side; **(6)** detail of larval shell in oblique view. **(7, 8)** SMNH PZ X 6465; **(7)** dorsal side; **(8)** detail of larval shell. Scale bars equals 500 µm in 1, 3, 5, 7 and 100 µm in 2, 4, 6, 8.

Figure 3.—*Discinella micans* (Billings, 1871) in internal view. Specimens in 1-8 from sample GGU 314837, upper Bastion Formation, Albert Heim Bjerge, North-East Greenland. Specimens in 9-20 from sample ICS1575, Middle Shale member, Forteau Formation, Fox Cove, southern Labrador. **(1, 2)** SMNH PZ X 6466; **(1)** internal view; **(2)** detail of anteriormost muscle scars. **(3, 4)** SMNH PZ X 6467; **(3)** internal view; **(4)** detail of anteriormost muscle scars. 5-6, SMNH PZ X 6468. **(5)** internal view. **(6)** detail of anteriormost muscle scars. **(7, 8)** SMNH PZ X 6469; **(7)** internal view; **(8)** detail of anteriormost muscle scars. **(9, 10)** NFM F-2475; **(9)** internal view; **(10)** detail of anteriormost muscle scars. **(11, 12)** NFM F-2476; **(11)** internal view; **(12)** detail of anteriormost muscle scars. **(13, 14)** NFM F-2477; **(13)** internal view; **(14)** detail of anteriormost muscle scars. **(15, 16)** NFM F-2478; **(15)** internal view; **(16)** detail of anteriormost muscle scars. **(17, 18)** NFM F-2479; **(17)** internal view; **(18)** detail of anteriormost muscle scars. **(19, 20)** NFM F-2480; **(19)** internal view; **(20)** detail of

413 anteriormost muscle scars. Scale bars equals 200 μm in 1, 3, 5, 7, 9, 11, 13, 15, 17, 19 and 20 μm in 2,
414 4, 6, 8, 10, 12, 14, 16, 18, 20.

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416 **Figure 4.**—*Discinella micans* (Billings, 1871), malformed specimens. Specimens in 1-9 from sample
417 ICS1575, Middle Shale member, Forteau Formation, Fox Cove, southern Labrador. Specimen in 10
418 from sample GGU 314837, upper Bastion Formation, Albert Heim Bjerge, North-East Greenland. (1,
419 2) NFM F-2481; (1) internal view; (2) oblique, lateral view showing thick shell along anterior margin.
420 (3-6), NFM F-2482; (3) internal view; (4) oblique lateral view showing posterior growth
421 malformation; (5) oblique anterior view showing growth malformation; (6) detail of growth
422 malformation in posterior view showing multiple shell layers. (7-9) NFM F-2483; (7) dorsal view; (8)
423 detail of posterior shell showing growth lines and detachment of shell laminae; (9) detail of posterior
424 shell edge in oblique view showing slit between shell laminae formed before and after malformation.
425 (10) SMNH PZ X 6470, oblique, internal posteriolateral view showing fusion of muscle scars on left
426 side. Scale bars equal 500 μm in 1-5, 7, 10 and 100 μm in 6, 8, 9.

427

428 **Figure 5.**—*Discinella micans* (Billings, 1871), showing variability in concavity. All specimens from
429 sample ICS1575, Middle Shale member, Forteau Formation, Fox Cove, southern Labrador. (1, 2)
430 NFM F-2484; (1) lateral view of convex specimen, apex up; (2) internal view. (3, 4), NFM F-2485; (3)
431 lateral view of flat specimen, apex up; (4) internal view. (5, 6) NFM F-2486; (5) lateral view of
432 concave specimen, apex up; (6) internal view. Scale bar equals 1 mm for all images.

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