

The Early Cambrian (Botomian) stem group brachiopod *Mickwitzia* from Northeast Greenland

CHRISTIAN B. SKOVSTED and LARS E. HOLMER



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The problematic brachiopod *Mickwitzia* Schmidt, 1888 is re-described based on new material of *M. cf. occidens* Walcott, 1908 from the Early Cambrian (Botomian) Bastion and Ella Island formations of Northeast Greenland. Etched material demonstrates that *Mickwitzia* has a lingulid-like juvenile (“larval”) shell with trails of nick-points, reflecting the movement of marginal setae. Juvenile and early mature ventral valves have a lingulid-like pseudointerarea with a pedicle groove. The shell of *M. cf. occidens* is only partially phosphatic, in particular around the juvenile–early mature shell in both valves. The phosphatic shell includes at least two types of cylindrical structures: (1) slender columns identical with the columns of acrotretoid brachiopods and (2) relatively thicker tubes which may be open to the exterior surface and have internal striations (on the ventral pseudointerarea). The striations are most likely imprints of microvilli and these tubes can be inferred to have contained setae. The thinner linguliform columns and thicker setigerous striated tubes are considered to be homologous with identical structures in the sellate and mitral sclerites of the problematic *Micrina*, which has been identified as a probable primitive stem group of the Brachiopoda. *Mickwitzia* represents a more derived member of the stem group Brachiopoda.

Key words: Brachiopoda, *Mickwitzia*, ontogeny, shell structure, Cambrian, Botomian, Greenland.

Christian B. Skovsted [Christian.Skovsted@geo.uu.se], Lars E. Holmer [Lars.Holmer@pal.uu.se], Institute of Earth Sciences, Department of Palaeobiology, Norbyvägen 22, S-752-36 Uppsala, Sweden.

Introduction

Mickwitzia is one of the largest known bivalved organisms from the Lower Cambrian; the width of the shell can reach 60–72 mm (Jensen 1993; Balthasar 2001). Although it has been referred to the paterinid brachiopods (subphylum Linguliformea, class Paterinata) (Schuchert and LeVene 1929; Rowell 1965), others have questioned its brachiopod affinity (e.g., see McMenamin 1992 and Laurie 2000 for reviews). Laurie (2000) tentatively excluded the genus from the phylum Brachiopoda in view of the enigmatic “punctate, three-layered phosphatic shell” as well as the lack of any unequivocal brachiopod characters beyond that of the simple bivalved shell.

The type species *Mickwitzia monilifera* (Linnarsson, 1869) from the Early Cambrian (?Tommotian–Atdabanian) of Baltoscandia is poorly understood and the most detailed available account of this taxon is still that of Walcott (1912; but see also Jensen 1993). The internal and external morphology of this and all other species have remained enigmatic due to their poor preservation. Both Jensen (1993) and Nemliher (2001) discussed the diagenetic history of the shells of *M. monilifera*, which have been strongly altered and phosphatized. The mickwitziid material described by McMenamin (1992) is preserved in a similar manner and did not allow a more detailed understanding of the phylogenetic relationships of *Mickwitzia*.

New material of *Mickwitzia cf. occidens* from the Lower Cambrian (Botomian) of Greenland, etched from limestones,

preserves previously unknown morphological details, in the light of which the general affinity and systematic position of the genus was discussed briefly by Skovsted and Holmer (2000) and Holmer (2001). Holmer et al. (2002) gave a brief account of the shell structure and the setigerous tubes in connection with a cladistic analysis and indicated that *Mickwitzia* is a derived member of the brachiopod stem group that also includes the problematic tommotiid *Micrina*. The objective of this paper is to give a more detailed account of the morphology and shell structure of *Mickwitzia cf. occidens* Walcott, 1908 based on the Greenland specimens.

Material, methods and geological setting

The samples of *Mickwitzia cf. occidens* were dissolved using 10% acetic acid from limestones in the Lower Cambrian Bastion and Ella Island formations (middle Dyeran Stage), Northeast Greenland. These rocks form part of a thick sequence of shallow-marine, upper Proterozoic to Ordovician stable shelf sediments (Fig. 1). Fossiliferous limestones in the middle and upper parts of the silt and shale-dominated Bastion Formation and in the overlying silt and lime-dominated Ella Island Formation (Cowie and Adams 1957; Stouge et al. 2001) were sampled. The majority of samples were collected in 1988 by J.S. Peel and M.P. Smith, then at the Geological Survey of Greenland, Copenhagen (GGU), in

the Albert Heim Bjerge region (GGU 314802, 804, 806–810, 814–816, 835–838) and C.H. Ostenfeld Nunatak (GGU 314901–910, 919, 923–924, 931, 933–934) of northern Hudson Land (Fig. 1). One additional limestone sample from museum collections was also included; it was collected from an unknown level within the upper Bastion Formation of Hyolithus Creek, Andrée Land by Christian Poulsen in 1929, and contained a single crack-out macroscopic specimen of *Mickwitzia* preserved in matrix. A diverse and well-preserved fauna of small shelly fossils accompanies *Mickwitzia* in the acid-resistant residues, including brachiopods (*Eoobolus prisca*, *Botsfordia caelata*, *Obolella congesta*, *Paterina mediocris*), hyoliths, arthropods (*Bradoria* sp., *Mongolotubulus henrikseni*), molluscs (*Anabarella australis*, *Stenotheca taconica*, *Pelagiella subangulata*) and problematic taxa including a mobergellan (*Discinella micans*) and an unidentified lapworthellid.

Etched specimens were coated with gold and studied using a Scanning Electron Microscope (SEM). A longitudinal thin-section of a single specimen was made and the elemental composition of the shell investigated using a Cameca electron microprobe. The section was later etched in 2% hydrochloric acid and studied under the SEM. All illustrated specimens have been deposited in the Geological Museum of Copenhagen, abbreviated MGUH. The samples collected by the Geological Survey of Greenland (GGU) are also housed in MGUH collections.

Terminology

The established terminology used to describe brachiopods (e.g., Williams et al. 1997) can also be applied to *Mickwitzia* with few exceptions. However, Cohen et al. (2003) and Williams and Holmer (2002) recently cast some doubt as to the generally accepted dorsal-ventral orientation of the brachiopod valves. It is clear that the correct anatomical orientation of brachiopods needs further study, but in the meantime the traditional usage of the dorsal-ventral valve orientation is retained. The bivalved shell of *Mickwitzia* invariably consists of a planar to slightly convex valve with a submarginal apex and a low conical valve with the apex at or near the posterior margin (Laurie 2000). It has been commonly assumed that the conical/planar valves correspond to the ventral/dorsal valves of brachiopods, but no clear interior or exterior characters supporting this assumption have ever been described from any pre-existing material of *Mickwitzia*.

Sutton (in Sutton et al. 1999: 22) suggested the new term “thickened platform” for a linguliform pseudointerarea formed by internal rather than marginal accretion. It is clear that this type of pseudointerarea, including a pedicle groove, is present in the conical valve of *M. cf. occidentis*, supporting the notion that it represents the ventral valve. However, the term “thickened platform” may be confused with the thickened platform that supports the visceral area of, e.g., elkaniid brachiopods (e.g., Holmer 1993: fig. 5). Although it is important to distinguish between the internally and marginally

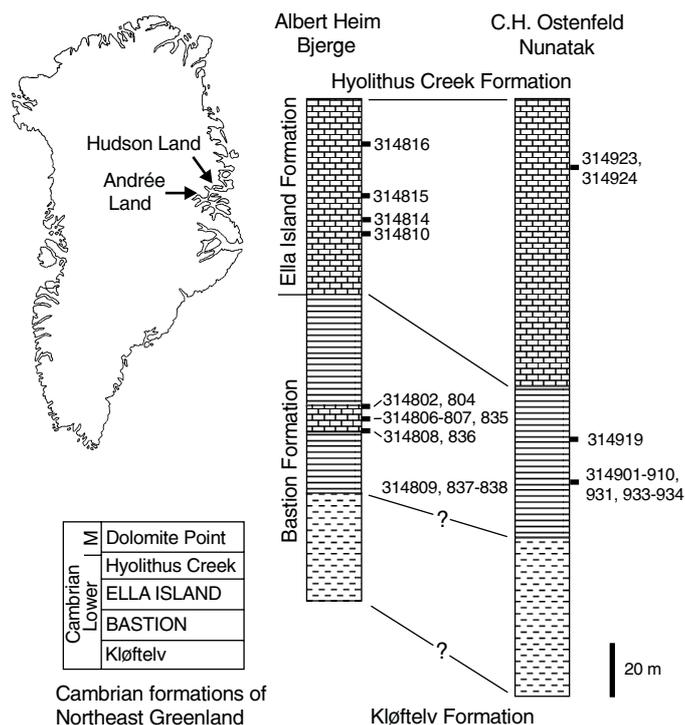


Fig. 1. Stratigraphical subdivisions of the Lower Cambrian and location map of Northeast Greenland, with simplified stratigraphical logs. Sample numbers and levels indicated.

accreted pseudointerarea in the description of these structures, it may not be necessary to use special terms and *pseudointerarea* is used here in the wide sense including both types.

The revised descriptive terminology for the growth stages of the brachiopod shell elaborated by Williams (2003) is adopted here. Thus the *first-formed shell* is used for a mineralised coat, lacking signs of accretionary growth at the mantle lobe; it corresponds to what has been termed previously “protegulum” and “embryonic shell”. The *brephic shell* is used for a circular to oval shell showing signs of accretionary growth (with e.g., *fila*) and which is bounded by an outer major disturbance and change in growth (most probably related to settling); it corresponds largely to the so-called “larval shell” described from living and fossil linguliform brachiopods. Williams (2003) also proposed that *juvenile shell* might be used in a wider sense, lumping these two stages together if they are not clearly differentiated.

Systematic palaeontology

“Stem group Brachiopoda”

Family Mickwitziidae Gorjansky, 1969

Revised diagnosis.—Shell ventribiconvex, inequivalved, ovate to subcircular; apex of both valves commonly submarginal and erect; ventral apex may be curved over posterior margin; lingulid-like juvenile (“larval”) shell may be present; mature shell pustulose; pseudointerareas of both valves usually poorly defined; ventral pseudointerarea rarely

anacline (in early growth stages), more commonly apsacline to procline (in adults), and sometimes with narrow pedicle groove in juveniles; interior of both valves inadequately known; shell organophosphatic, but may generally have been poorly mineralized; shell structure with slender acrotretoid-type columns and thicker tubes that are usually orthogonal, but also may be parallel with and open to external surface; inferred setigerous thicker tubes on ventral pseudointerarea preserve internal striations (imprints of microvilli) and cause cylindrical depressions around aperture.

Phylogenetic remarks.—The stem and crown group concept (see Budd and Jensen 2000) has not been widely used for analysing phylogenetic relationships within the Brachiopoda (Holmer 2001). The mickwitziids clearly can be referred to a stem group of the Brachiopoda (Balthasar 2001; Holmer 2001). In the cladistic analysis of Holmer et al. (2002: text-fig. 4) they are the closest sister group to the crown group Brachiopoda (as represented by all living and most extinct taxa of brachiopods). The monophyletic combined group of mickwitziids + crown group Brachiopoda does not correspond currently to any named taxon at any systematic level. As proposed by Conway Morris and Peel (1995; see also Conway Morris 1998: fig. 86), some halkieriids also can be considered as stem group brachiopods, and cladistic analyses (Williams and Holmer 2002; Holmer et al. 2002) indicate that the phosphatic sclerite-bearing problematical tommotiid *Micrina* (Williams and Holmer 2002) belongs to this paraphyletic group. The exact relationships of the taxa within the brachiopod stem lineages have yet to be worked out in more detail.

Genera included.—*Mickwitzia* Schmidt, 1888 [= *Causea* Wiman, 1902; ?*Microschedia* Geyer, 1994].

Stratigraphic and geographic distribution.—Lower Cambrian (?Tommotian, Atdabanian–Toyonian, ?Middle Cambrian) of Baltica (Sweden, Finland, Estonia, Lithuania), Laurentia (USA, Canada, Greenland), and possibly north Gondwana (Morocco; McMenamin 1992, Geyer 1994).

Genus *Mickwitzia* Schmidt, 1888

Type species: *Lingula monilifera* Linnarsson, 1869; Lower Cambrian (?Tommotian–Atdabanian) Mickwitzia beds (File Haidar Formation), Västergötland, Sweden.

Diagnosis.—As for family.

Remarks.—The most important distinguishing character of *Mickwitzia* is its shell structure, which has usually been described simply as “punctate” and “three-layered” due to the poor preservation of all previously available material (e.g., Walcott 1912; McMenamin 1992; Laurie 2000). However, it is now clear that most aspects of the shell structure conform with the columnar shell of linguliform brachiopods; the most important and unique aspects of the shell structure that set *Mickwitzia* apart from the linguliforms are connected with the thicker tubes, and in particular the setigerous tubes that penetrate the shell on the ventral pseudointerarea (see further below). Specific discriminations and definitions within the genus are difficult due to the general lack of preserved dis-

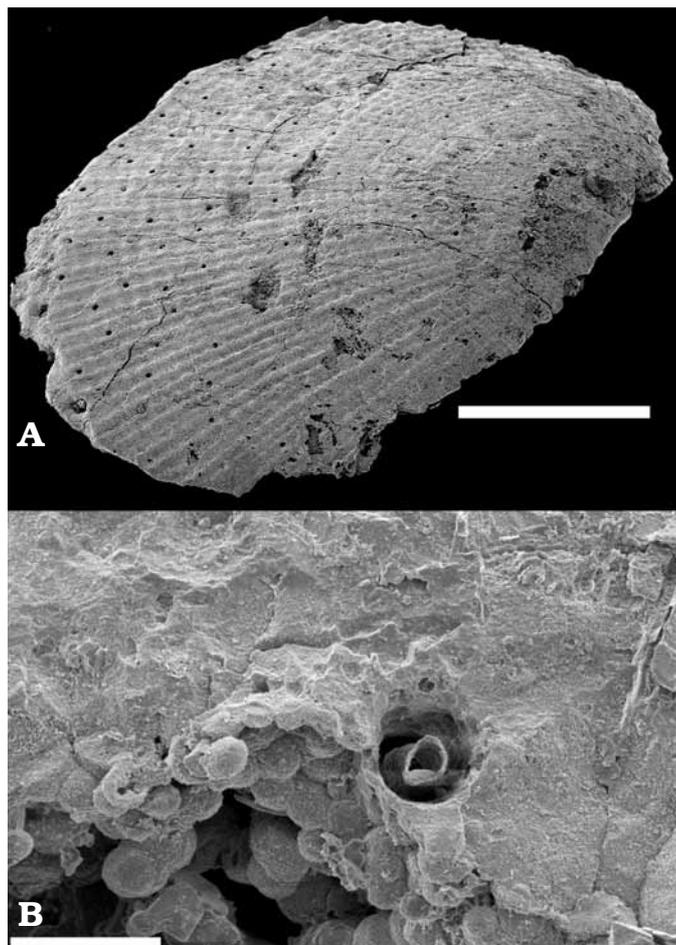


Fig. 2. *Mickwitzia occidens* Walcott. A. Ventral valve MGUH 26294, lateral view of exterior; scale bar 500 μ m. B. Ventral valve MGUH 26295, detail of exfoliated exterior with large tube and cocci; scale bar 20 μ m. All specimens from the middle member of the Poleta Formation in Indian Springs Canyon, northern Montezuma Range, Esmeralda County, Nevada.

tinctive characters (apart from differences in size) in most described species (see McMenamin 1992; Jensen 1993), and a full revision and list of species referred to the genus are outside of the scope of this paper.

Mickwitzia cf. *occidens* Walcott, 1908

Figs. 3–5, 7–14.

cf. *Mickwitzia occidens*; Walcott 1908: 54, pl. 7: 1.

cf. *Mickwitzia occidens* Walcott; Walcott 1912: 331, pl 4: 1.

?*Mickwitzia* sp.; Cowie and Adams 1957: 26.

cf. *Mickwitzia occidens* Walcott; Rowell 1977: 79, pl. 1: 12.

?*Mickwitzia multipunctata* sp. nov; McMenamin 1992: 180, figs. 1.1, 1.7, 4.3–4.6, 5.1–5.3.

?Perforate plate; Landing and Bartowski 1996: 759, figs. 9.16, 9.17.

Material.—Total of 410 ventral and 4 dorsal valves in addition to an undetermined number of fragments.

Taxonomic remarks.—*M. occidens* Walcott, 1908 from the Lower Cambrian of Nevada and California remains a very poorly understood species (Rowell 1977; see also McMenamin 1992). Rowell (1977) re-described the type material

which, as noted by him, comprises a single poorly preserved indeterminate fragment of a valve and four smaller fragments. Additional specimens referable to the species occur in the acid resistant residue of a limestone sample collected (by C.B.S) from the middle member of the Poleta Formation in Indian Springs Canyon of the northern Montezuma Range, Esmeralda county, Nevada (Fig. 2). The sample (CBS 990918-2) was collected about 5 m above the proposed base of the Dyeran Stage at a proposed boundary stratotype section (Palmer 1999: 38). These new specimens are preserved in a similar manner to our material of *M. cf. occidentis* from Northeast Greenland and appear to have similar ornamentation and shell structure. The shell appears to include acrotretoid-type columns as well as thicker tubes that are open to the exterior surface of the valves (Fig. 2B). The external ornament of fine radiating ridges (Fig. 2A) is identical to that described by Walcott (1912) and Rowell (1977) for *M. occidentis*, but differs from the ornamentation of *M. cf. occidentis* from Northeast Greenland in having more pronounced radiating ridges and in lacking the distinctive pustulose sculpture, with high pustules arranged in offset radiating rows. A full description of *M. occidentis* and the associated fauna are outside the scope of the present paper, as more and better material is in the process of being collected from this and other levels in Nevada (L.E. Babcock personal communication 2000). The Greenland specimens are referred conditionally to the American species awaiting further revision of topotypic material.

Mickwitzia multipunctata described by McMenamin (1992) from the Puerto Blanco Formation of Sonora, Mexico, is very similar to both *M. occidentis* and *M. cf. occidentis*. According to McMenamin (1992: 180), *M. occidentis* differs from *M. multipunctata* only "by being three times as large and by having proportionally larger and less densely spaced punctae". The density of the "punctae" (corresponding to the larger cylinders, here termed *tubes*) varies strongly within *M. cf. occidentis* and depends on preservational factors, and the size-range of the new specimens of *M. occidentis* includes individuals as small as those referred to *M. multipunctata*. The dorsal valves of *M. multipunctata* (McMenamin 1992: fig. 5: 3) and *M. cf. occidentis* are almost identical in all observable characters.

Description

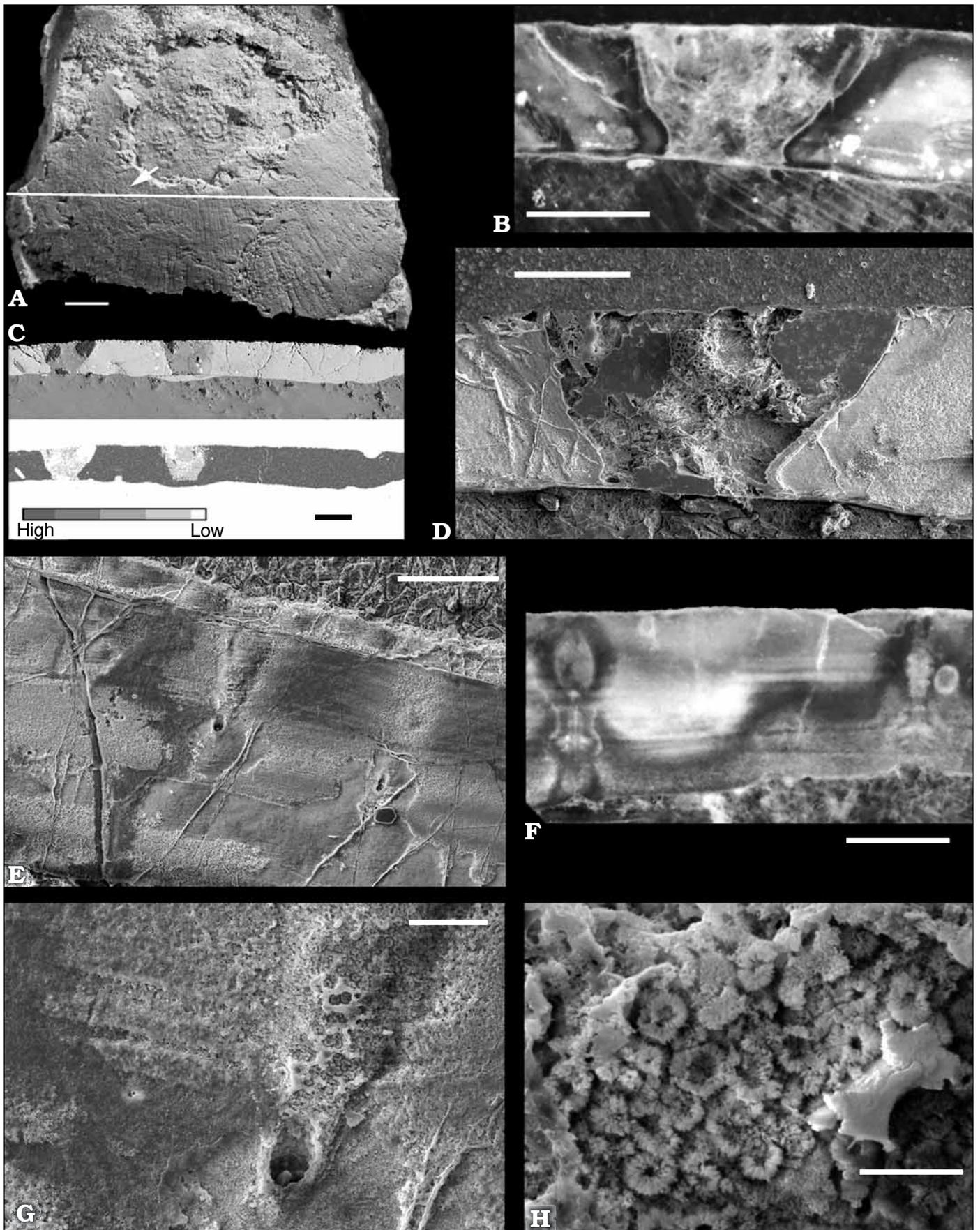
Preservation.—*Mickwitzia cf. occidentis* is very common in the upper Bastion Formation (400 etched valves) and less common in the Ella Island Formation (14 etched valves).

However, no complete outline of either valve is preserved in the available material, and no biometric study could be made on adult valves. The only large macroscopic specimen, still within matrix, comes from the Bastion Formation. It is probably a ventral valve, somewhat more than 8 mm wide (Fig. 3). Analyzed sections through this specimen (described below) indicate that the preserved shell is only partly phosphatic, whereas the remainder of the shell includes zones of calcium carbonate. This would explain why none of the specimens from the etched samples represent complete larger valves. Zones of variable shell mineralogy are also indicated by concentric colour banding and depressions resulting from dissolution of non-phosphatic material during acid preparation (Fig. 4). Most commonly, the apical part of the valves, in particular the ventral, appears to have been phosphatic (Fig. 4). The remaining parts of the valves contain rounded to irregularly shaped patches of phosphate shell that cannot be tied to any particular region of the mature shell when they are isolated by etching (Fig. 4).

The mode of preservation of the shells of *Mickwitzia cf. occidentis* differs in specimens from the two formations. In the Ella Island Formation, the shells are less phosphatized and recrystallized, and preserve finer details of the original shell structure by comparison with the specimens from the Bastion Formation. Consequently, material from the Ella Island Formation forms the main basis for the description of the shell structure (see below).

All material of the phosphatic portions of the shell from both formations preserves spheroidal bodies of phosphate occurring as clusters, partly or entirely filling the shell cavities (Fig. 5A) or as attachments to the inner surfaces of the laminae, tubes, and columns (Fig. 5B). In the specimens from the Ella Island Formation, the bodies adhering to the inner surfaces are commonly almost perfectly spheroidal, ranging between 2.4 and 5.3 μm in diameter (mean diameter = 3.77 μm ; $n = 101$). Their consistent shape and size indicate that they are of biogenic origin, rather than representing some kind of inorganic crystalline growth. Moreover, there is evidence of asexual binary fission (Fig. 5H, I). The bodies also show a variety of deformations, varying in shape from discoidal (Fig. 5E) to domes or ellipsoids (Fig. 5C). The deformation of spheroids into domes attached to tubes, columns, or laminae suggests that they became attached in life (Fig. 5C–E), and it is likely that the spheroids are the phosphatized remains of the capsular coats of cocci. These coats were possibly perforated by apertures (Fig. 5K, L) and seemingly consisted of two layers, an outer platy layer and an inner granular one.

Fig. 3. *Mickwitzia cf. occidentis* Walcott. Ventral (?) valve in small piece of limestone MGUH 26299. The sample comes from an unknown level within the upper Bastion Formation (coll. Christian Poulsen 1929). The orientation in all images is with the shell exterior upward apart from **E, G, H**, where the orientation is not known. **A**. Exterior of exfoliated shell, with approximate direction of analysed section indicated by line. Circular area of apatite indicated by arrow; scale bar 1 mm. **B**. Thin section (under ordinary light microscope) through vase-shaped zone of calcium carbonate surrounding the rounded area of apatite in A; scale bar 200 μm . **C**. Thin section (analysed with electron microprobe) through circular area of apatite in A, showing backscatter image (upper image) and elemental mapping of the distribution of phosphorous (lower image with legend); scale bar 200 μm . **D**. Etched thin section (under SEM) through the vase-shaped structure in B; scale bar 100 μm . **E, G, H**. Etched thin sections (under SEM) through smaller shell fragment (within the piece of limestone), directly below the valve in A. **E**. Detail of two tubes; scale bar 100 μm . **G**. Detail of tube showing flask-shaped zone with cocci around tube and the laminated surrounding shell; scale bar 20 μm . **H**. Detail of flask-shaped zone with cocci; scale bar 5 μm . **F**. Thin section (under ordinary light microscope) through several tubes with flask-shaped zones and laminated surrounding shell; scale bar 100 μm .



In the material from the Bastion Formation, the finer details of the shell structure cannot be readily observed, since the cocci commonly fill the entire shell (Figs. 3, 4), which also appears to have been more strongly recrystallized. With this type of preservation, the thicker tubes are usually visible where dissolution of shell material has affected only parts of the shell. The thinner acrotretoid-type columns are never preserved in any of the available Bastion specimens (Figs. 3, 4). Concentric zones of resistant phosphatic material (usually mostly cocci) around the tubes result in knobs protruding over the surrounding regions. On the internal surface of the shells, the sites of the thicker tubes are often represented by circular depressions, where non-phosphatic material has been dissolved (Fig. 4). Among all the specimens from the upper Bastion Formation, this mode of preservation is unique to *Mickwitzia*. All other taxa with an originally organophosphatic composition (*Discinella micans*, *Mongolitubulus henrikseni*, *Lapworthella* sp., and the lingulate brachiopods *Eoobolus prisca* and *Botsfordia caelata*) have been recrystallized to some degree, but the entire shells still retain their original composition, shell structure and ornamentation, and do not show any obvious phosphatization by cocci comparable with those in *M. cf. occidentis*. The shells of *Botsfordia caelata* essentially preserve a recrystallized original laminar shell with a thin primary layer and a secondary shell with a baculate shell structure (Fig. 6; see also Holmer 1989; Williams et al. 1992, 1994; Cusack et al. 1999). Some laminae in *B. caelata* have a granular to somewhat spherulitic texture, but the individual spheroidal bodies do not show the same complex variation in morphology as the assumed cocci described above; moreover, they are considerably smaller and have a maximum diameter of only around 900 nm (Fig. 6).

It is possible that the “micro-environment” within and around the shell of *Mickwitzia* was subject to different taphonomic processes as suggested by comparison with other shells, perhaps due to the intense bacterial activity, but this suggestion needs further confirmation by more detailed study, including *Mickwitzia* from other areas.

Under light microscopy, the shell material of the large macroscopic specimen from the Bastion Formation appears homogeneous with only a faint lamination parallel to the surface of the shell (Fig. 3F). Distinctive canals run through the shell and are surrounded by flask-shaped halos of symmetrical light and dark zones (Fig. 3F). These are interpreted to represent the characteristic larger tubes of the mickwitziid shell described below from the better preserved material in the Ella Island Formation. The surrounding halos probably represent zones of differential phosphatization (mostly by cocci) around tubes,

analogous to the protruding knobs on the etched shells (Fig. 4B). The faint lamination is not disturbed by the flask-shaped

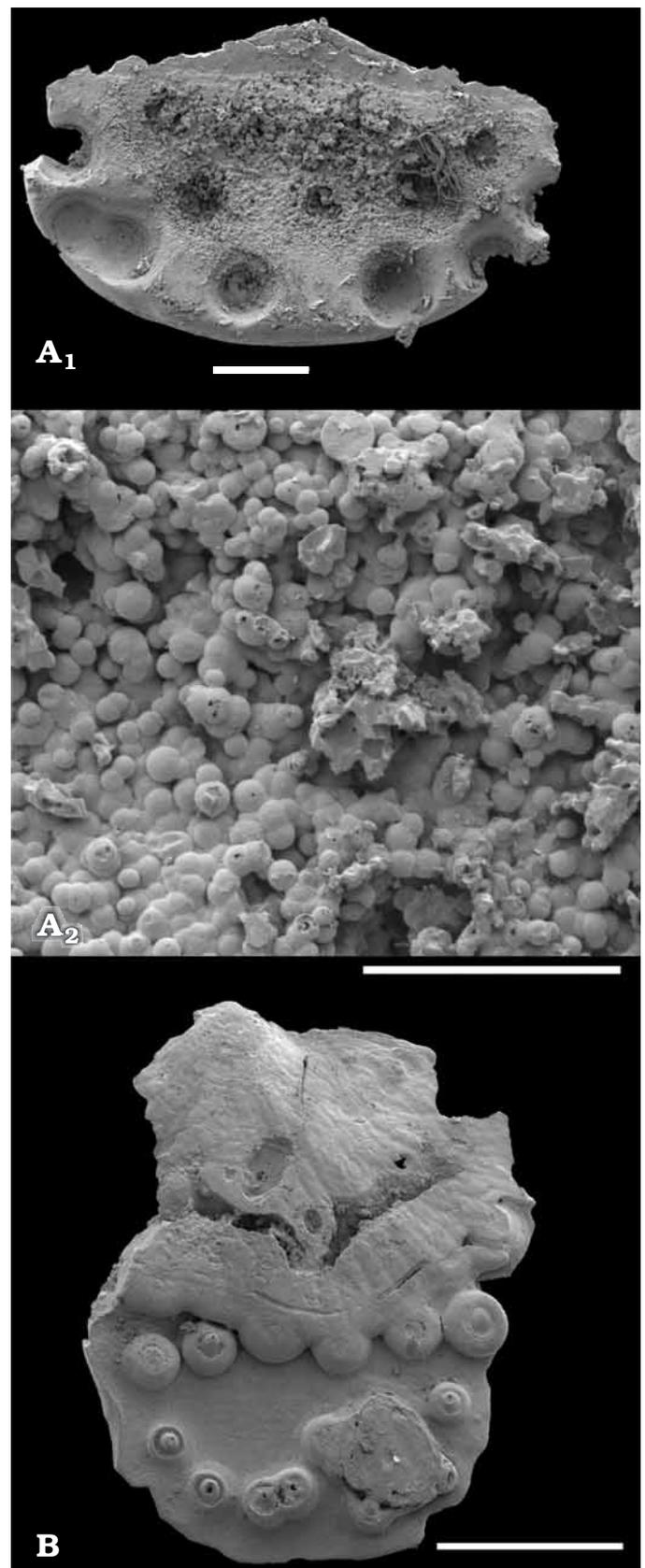


Fig. 4. *Mickwitzia cf. occidentis* Walcott. **A.** Ventral valve MGUH 26296. **A₁**. Interior of juvenile-early mature ventral valve showing tubular openings surrounded by circular depressions, where non-phosphatic material has been dissolved; scale bar 200 μ m. **A₂**. Detail of interior of **A₁**, with recrystallized and secondarily enlarged cocci; scale bar 100 μ m. **B.** Exterior of ventral valve MGUH 26297, showing concentric zones of resistant phosphatic material (cocci) around the tubes result in knobs protruding over the surrounding regions; scale bar 500 μ m. All specimens from the Bastion Formation (sample GGU 314905).

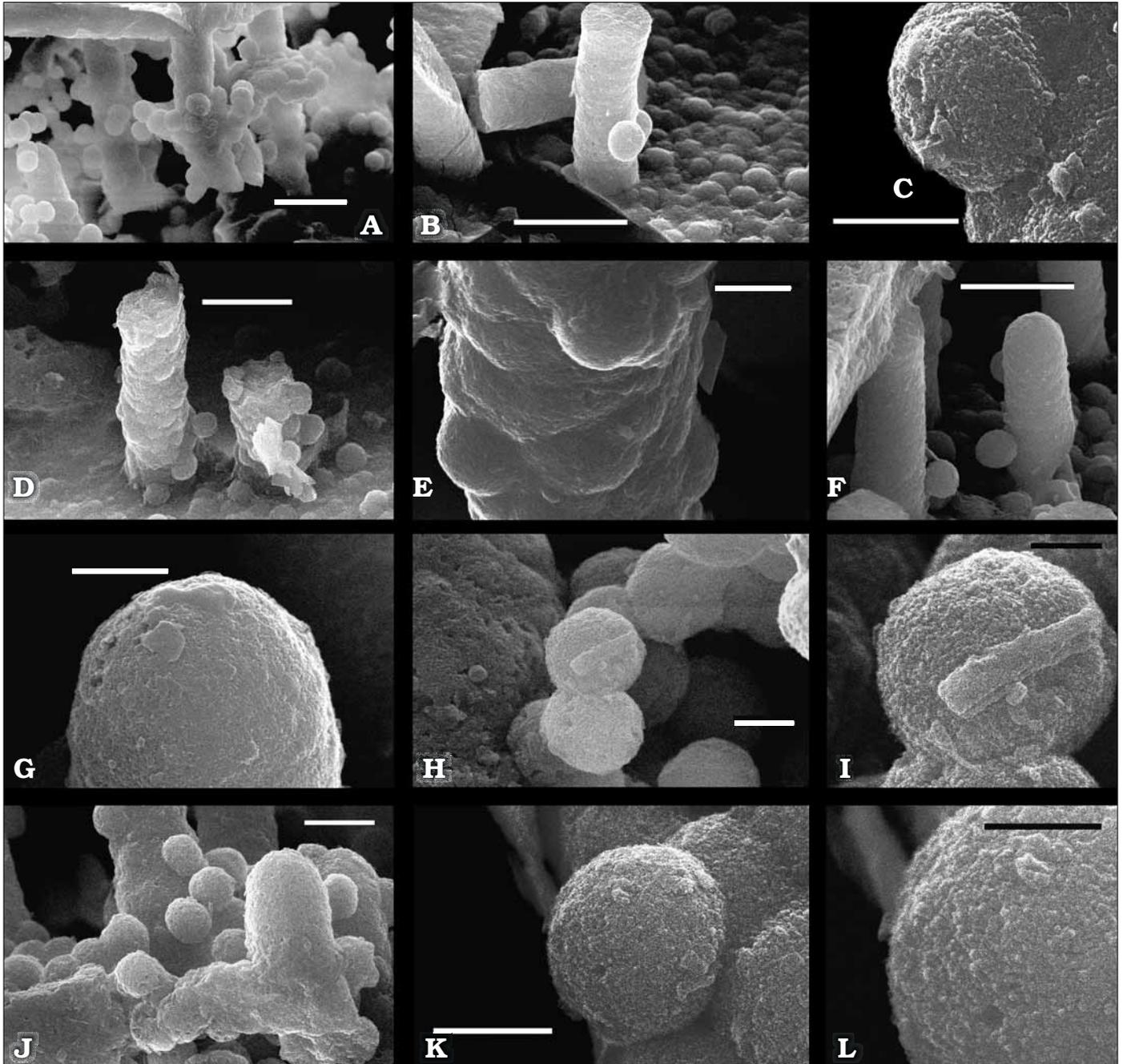
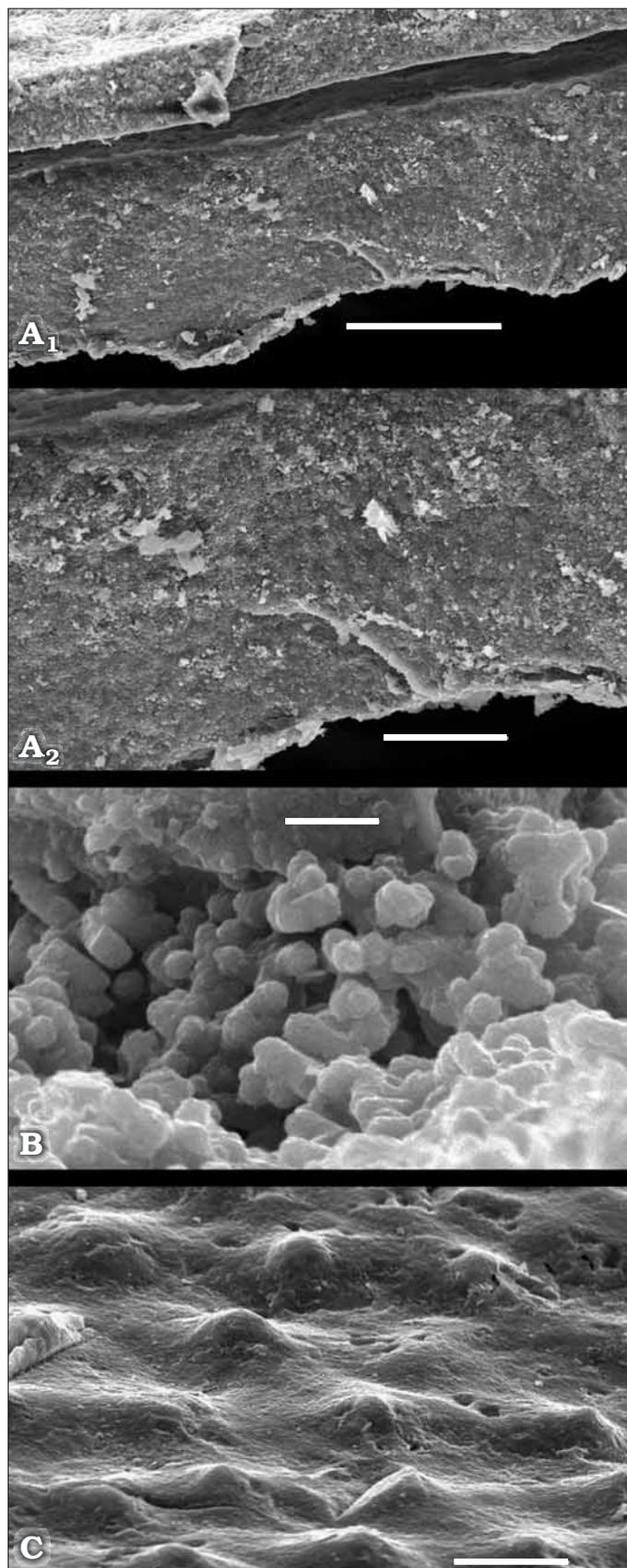


Fig. 5. *Mickwitzia cf. occidentis* Walcott, fragment of mature shell MGUH 26298. **A.** Acrotretoid-type column with clusters of adhering cocci; scale bar 10 μm . **B.** Acrotretoid-type column entirely filled by centripetal lamination. Note the two single adhering cocci; scale bar 10 μm . **C.** Detail of single dome-shaped coccus attached to column; scale bar 2 μm . **D.** Acrotretoid-type column (left) entirely covered by attached and overlapping discoidal bodies (= deformed cocci) and some individual spheroidal cocci; scale bar 10 μm . **E.** Detail of surface of left column with overlapping discoidal structures; scale bar 2 μm . **F.** Aborted, dome-shaped acrotretoid-type column, with indications of annulations; scale bar 10 μm . **G.** Detail of top of aborted column in F, showing a finely platy cover; scale bar 2 μm . **H.** Cluster of cocci, with indication of asexual binary fission; scale bar 2 μm . **I.** Detail of central cocci in H, showing platy cover; scale bar 1 μm . **J.** Detail of cocci-covered lamina and columns; scale bar 5 μm . **K.** Detail of single spheroidal cocci attached to column; scale bar 2 μm . **L.** Detail of K, showing possible aperture. Note the platy appearance of the outer surface; scale bar 1 μm . The specimen is from the Ella Island Formation (sample GGU 314816).

halos. The tubes and associated halos appear not to be substantially different from surrounding shell material in elemental composition, and are not delineated by elemental microprobe mapping (Fig. 3C). The shell material shows a uniformly high content of phosphorus, and low amounts of iron and silica.

However, after etching in dilute hydrochloric acid the tubes and halos are faintly delineated (Fig. 3E, G), implying a somewhat higher resistance to the acid compared with the surrounding shell material. After etching, the tubes themselves are represented by hollow canals (Fig. 3E, G).

The thin section through the macroscopic specimen cuts through one of the circular structures, which is seen on the

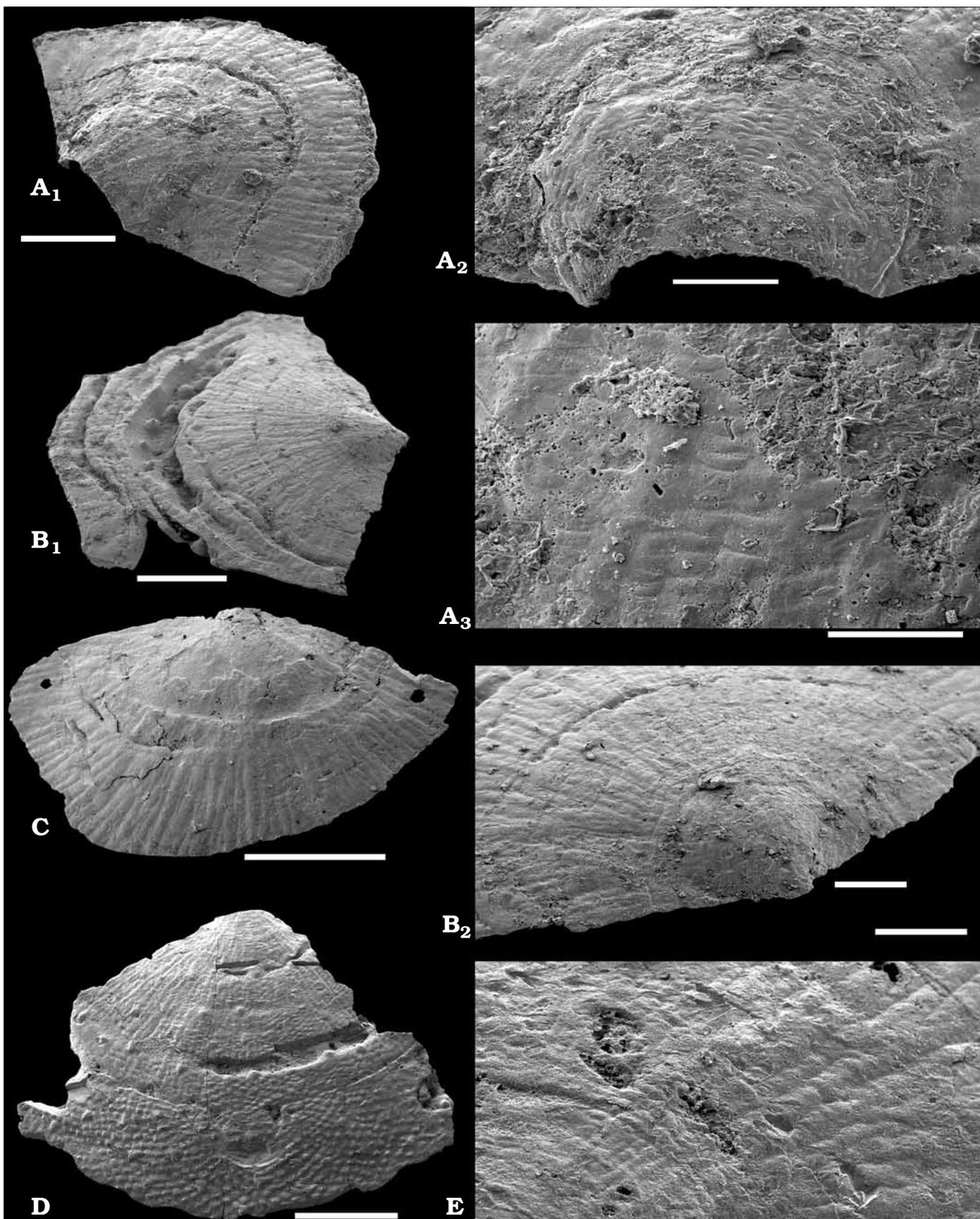


surface of the specimen (marked by arrow on Fig. 3A). In the section, the central part of the circular structure consists of phosphate, surrounded by a circular zone with a vase-shaped cross-section. This zone is also seen clearly in the thin section, where it is defined by differences in colour and structure. The two cross-sections through the circular zone have a width comparable with the thickness of the shell at the internal surface and broaden to approximately twice the shell thickness at the external surface. There are some indications of the shell lamination continuing into the vase-shaped structures, but this pattern is not entirely clear. Elemental mapping reveals a striking difference between the zones and the surrounding shell. The broad vase-shaped structures have only a moderate to low phosphorous content and variable amounts of iron and silica (Fig. 3C). Faint horseshoe-shaped zones in both structures contain medium to high levels of iron and silica, while the remainder of the structures proved low in all three elements mapped for. It is clear that these vase-shaped structures are composed mainly of calcium carbonate, which is confirmed by the fact that these areas are more susceptible to etching with acid by comparison with the rest of the shell (Fig. 3D). As noted above, the zones with calcium carbonate in the macroscopic valve may explain why no more complete valve has been obtained by etching, and also explain the rounded shape of many isolated shell fragments. The huge disparity between the number of ventral versus dorsal valves might possibly be due to sorting.

Ventral valve exterior.—The isolated apical regions of the ventral valve are the most common in the samples and comprise more than 99% of the 414 etched and identifiable valves. They are generally transversely triangular in outline with a rounded anterior margin, and are on average about 58% as long as wide (Figs. 7, 8). In lateral view the valve is very gently and evenly conical (Figs. 7B₁, 8B₃). The size-range of the apical regions of the valves is rather restricted, varying in

Fig. 6. *Botsfordia caelata* (Hall). A. Dorsal valve MGUH 26318. A₁. Detail of laminar shell, with section through two exterior pustules, fragment of mature shell; scale bar 50 µm. A₂. Detail of A₁, showing traces of a recrystallized baculate secondary layer, and thin primary layer; scale bar 20 µm. B. Dorsal valve MGUH 26319, detail of exfoliated laminae in secondary layer with spheroidal structures; scale bar 2 µm. C. Dorsal valve MGUH 26320, detail of surface of mature primary layer with pustules; scale bar 10 µm. All specimens from the Bastion Formation. A, sample GGU 314835; B, C, coll. Christian Poulsen 1929.

Fig. 7. *Mickwitzia cf. occidentis* Walcott. Ventral valves; MGUH 26300 (A), MGUH 26301 (B), MGUH 26302 (C), MGUH 26303 (D), MGUH 26304 (E). A₁. Oblique lateral view of early mature valve; scale bar 200 µm. A₂. Detail of juvenile shell of A₁; scale bar 100 µm. A₃. Detail of filar ornamentation with nick-points of A₂; scale bar 50 µm. B₁. Oblique lateral view of mature valve; scale bar 500 µm. B₂. Detail of apex with juvenile shell of B₁; scale bar 200 µm. C. Mature valve with exfoliated apex and radiating trails of nick-points; scale bar 500 µm. D. Mature valve showing transition to pustulose mature ornamentation; scale bar 500 µm. E. Detail of ornamentation with radiating trails of nick-points on early mature shell; scale bar 100 µm. All specimens from the Bastion Formation. A, sample GGU 314835; B, sample GGU 314807; C, E, sample GGU 314910; D, sample GGU 314804.



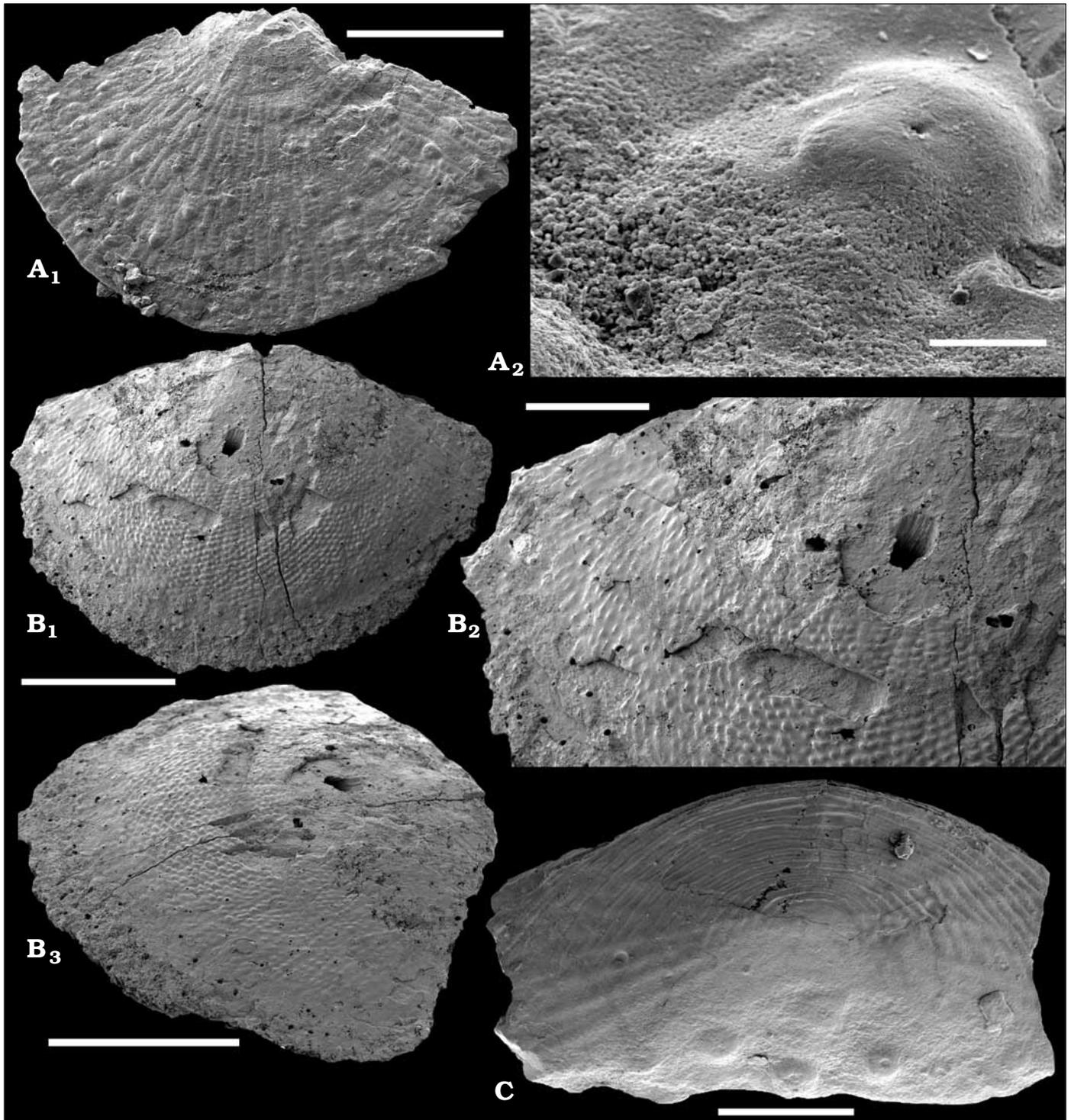


Fig. 8. *Mickwitzia cf. occidentis* Walcott. **A, B.** Ventral valves; MGUH 26305 (**A**), MGUH 26306 (**B**). **A₁**. Early mature valve showing beginning pustulose ornamentation; scale bar 500 µm. **A₂**. Detail of pustule of **A₁**; scale bar 20 µm. **B₁**. Mature valve with exfoliated apex showing pustulose ornamentation with offset radiating rows; scale bar 500 µm. **B₂**. Detail of pustulose ornamentation **B₁**; scale bar 200 µm. **B₃**. Oblique lateral view of **B₁**; scale bar 500 µm. **C.** Dorsal valve MGUH 26307; scale bar 200 µm. All specimens from the Bastion Formation. **A**, sample GGU 314804; **B**, sample GGU 314814; **C**, sample GGU 314905.

width between 0.93–1.82 mm. In four of the ventral valves a band of growth disturbance delineates an earlier growth stage, which is here termed the juvenile (brepheic?) shell (see Williams 2003). In most other ventral valves, the juvenile shell is not clearly visible due to exfoliation, recrystallisation or ad-

hering phosphatic material. The juvenile shell is transversely suboval and varies somewhat in size (width ca. 0.4–0.5 mm, length ca. 0.3–0.4 mm). The entire surface of the juvenile shell is covered by concentric fila (fine anticlinal ridges), with a wavelength of 6–9 µm (Fig. 7A₂, A₃). The fila are invariably

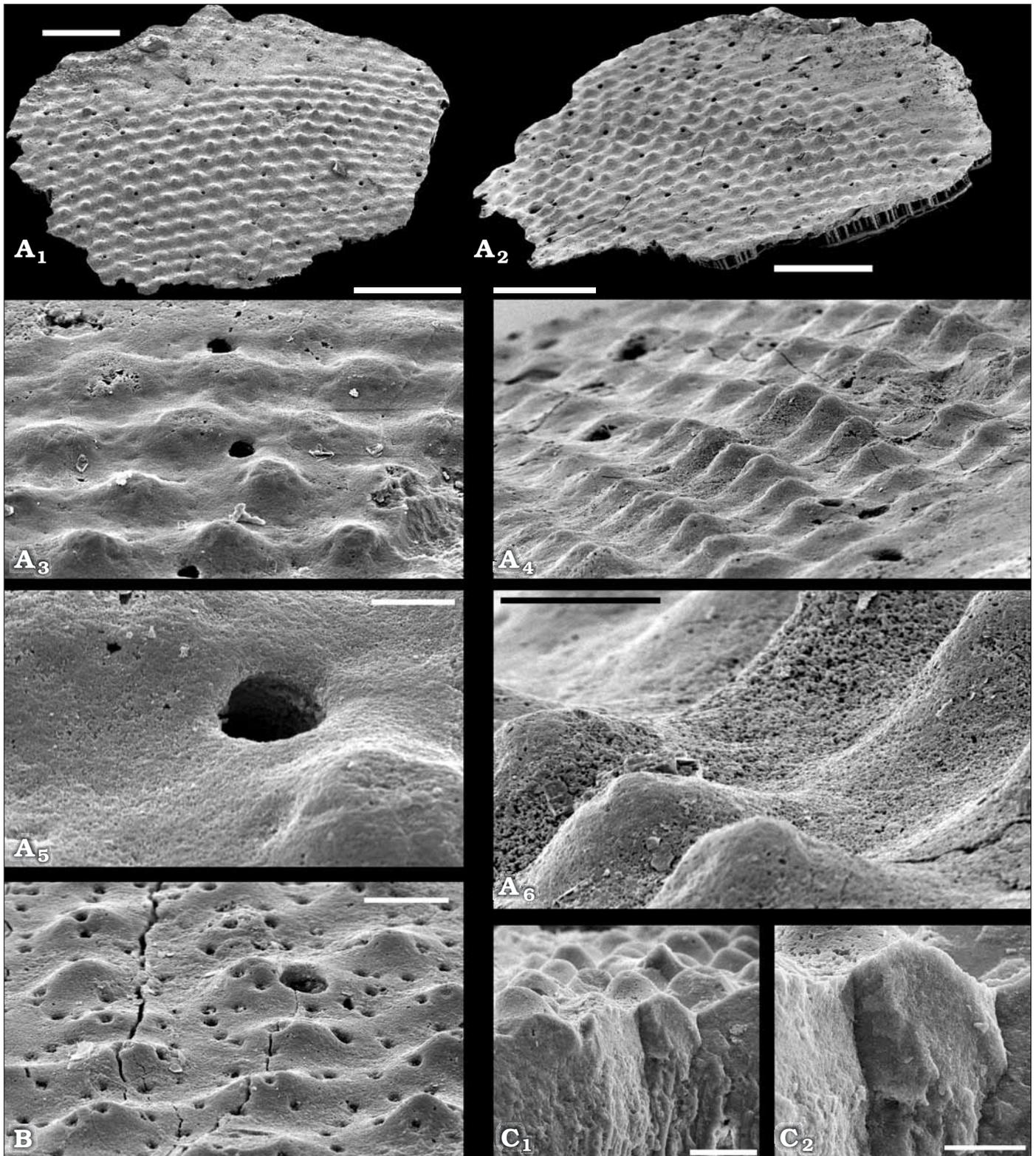


Fig. 9. *Mickwitzia* cf. *occidentis* Walcott. Fragmentary mature valves (indeterminate) MGUH 26311 (A), MGUH 26312 (B), MGUH 26313 (C). A₁, A₂. Pustulose mature ornamentation with low cone-shaped pustules, perforated by the radiating rows of large tubular openings; scale bar 200 μ m. A₃. Detail of cone-shaped pustules of A, also showing three large tubular openings; scale bar 50 μ m. A₄. Detail of pyramidal pustules of A₁, showing also scattered large tubular openings; scale bar 50 μ m. A₅. Detail of large tubular opening of A₁. Note lack of depressions around the aperture; scale bar 10 μ m. A₆. Detail of granular surface structure of A₁ and pyramidal pustules; scale bar 50 μ m. B. Detail of exfoliated surface of mature valve showing numerous openings to acrotreoid-type columns and single large tubular opening; scale bar 20 μ m. C₁. Section through re-crystallized primary layer with pyramidal pustules; scale bar 20 μ m. C₂. Detail of primary layer of C₁; scale bar 10 μ m. All specimens from the Ella Island Formation, sample GGU 314816.

indented by so-called nick-points (see Williams and Holmer 1992: 662) into outwardly convex drapes with somewhat varying widths; close to the median anterior margin of the juvenile shell, the drapes are up to 24 μm wide, whereas drapes toward the lateral edges of the juvenile shell can be around 14 μm wide (Fig. 7A₂, A₃). One juvenile shell has a total of ca. 29 nick-points at the edge of the shell (Fig. 7A₂).

The ring of growth disturbance marking the edge of the juvenile shell is usually most distinct towards the lateral side, whereas in the median part, the transition to the early mature section of the valve is more gradual (Fig. 7A₂). The transition to the early mature shell is also marked commonly by a change in the direction of shell growth; the juvenile shell usually has a somewhat more acute apical angle than the angle subtended by the posterolateral margins of the remainder of the valve (Figs. 7B₁, 8A₁). The concentric fila on the early mature shell are much less distinct than those on the juvenile shell, and close to the margin of the valve they are commonly not clearly discernible at all (Fig. 7E). However, the nick-points invariably form well-developed radiating trails, 14–34 μm apart, defining raised areas that are sometimes almost rib-like in appearance. One well preserved early mature shell (0.93 mm wide, 0.60 mm long) has a total of around 50 nick-points at the margin (Fig. 7C). The transition to the mature shell is also marked by the gradual appearance of the pustulose ornamentation that is developed on the rest of the mature shell. Most early mature valves larger than about 1 mm wide only have scattered pustules of somewhat varying size and shape. One such valve (width 1.63 mm, length 1.05 mm) has some 40 pustules arranged loosely in concentric rows (about 100–130 μm apart), which are defined by the radiating system of nick-points (Fig. 8A₁). Most commonly the pustules on early mature shells form low, somewhat asymmetrical domes with a rounded anterior margin, about 20–40 μm in diameter and generally less than 5 μm high (Fig. 8A₂).

In somewhat larger mature shells (above 1.5 mm wide), the pustulose ornamentation changes gradually; the pustules become higher, more densely spaced and entirely cover the surface of the shell, in particular in the median sector of the valve (Fig. 7D). These pustules are generally arranged in a fairly symmetrical pattern, apparently with offset radiating rows (Figs. 8B, 9; see also Wright 1981), but because of the small number of more completely preserved shells, this pattern could not be confirmed in more than three specimens. In one shell, the geometrical pattern of pustules is clearly interrupted by several trails of nick-points (Fig. 8B₂), whereas in other valves the nick-points are entirely absent from the ma-

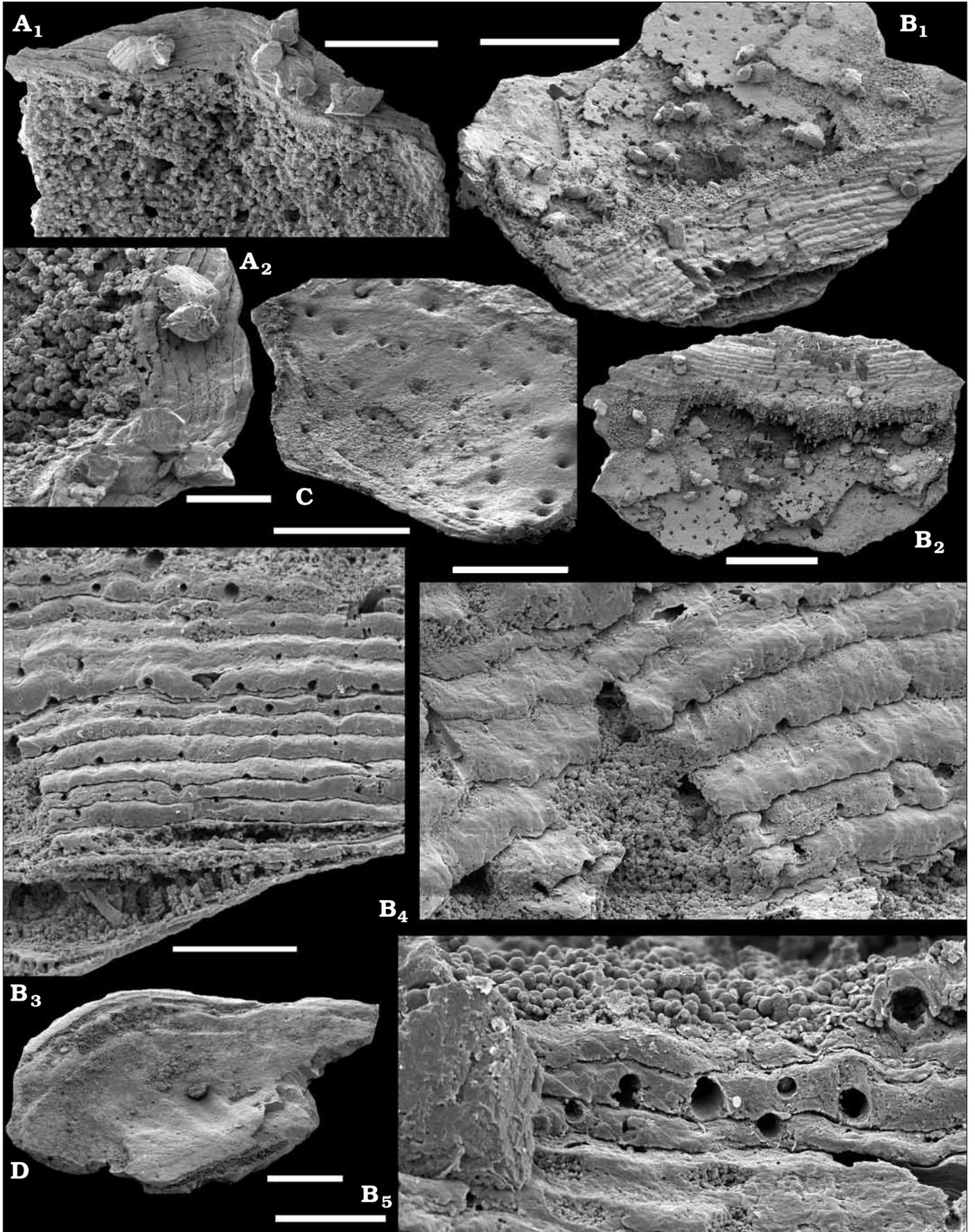
ture shell (Fig. 9A). In cross-section, the pustules in the larger mature shells vary in shape from approximately even-sided and rounded cones to almost pyramidal, about 20–40 μm wide at the base; they are generally less than 10 μm high. The pustules are mostly made up of primary shell, but exfoliated surfaces show that they are also composed partly of secondary shell (Fig. 9B).

The ventral pseudointerarea is most commonly preserved only partly, or not at all, in juvenile to early mature valves. Some shells show a partly preserved pseudointerarea of very varying morphology and size (Fig. 10A–C). In all available specimens the ventral pseudointerarea is formed by simple internal shell accretion, with individual laminae between 10 to 20 μm thick (measured along the plane of the pseudointerarea), and perforated by open tubes (described below). It is most commonly anacline to almost orthocline, but can also be weakly procline in early growth stages. In one fragmentary valve (less than 1 mm long) the pseudointerarea forms a narrow anacline rim (0.8 mm wide) along the posterior margin of the valve and has a distinctly lingulid-like morphology with a pedicle groove (up to 136 μm wide and 127 μm long) and propareas (Fig. 10A). However, the pedicle groove in most other specimens is less well developed; in several early mature valves the outline of a narrow pseudointerarea with a possible pedicle groove can only be inferred, but is not clearly developed (Fig. 10C). In one of the larger shell fragments (about 2 mm wide), the pseudointerarea is close to orthocline and triangular in outline, occupying the entire width of the fragment and around 0.5 mm long; the pedicle groove is poorly differentiated from the propareas, and the posterior section of the pseudointerarea is not preserved (Fig. 10B).

Dorsal valve exterior.—The apical region of the dorsal valve could only be observed on a single isolated specimen, approximately 1 mm wide (Fig. 8C). The valve is very low conical with a submarginal apex, and the posterior margin is gently rounded. The apex is worn and a juvenile shell is not clearly seen. Details of the ornamentation are poorly preserved, because the valve is covered by adhering phosphatic material. However, the concentric sculpture appears to be somewhat different with more strongly pronounced fila than on most ventral valves. The mature shell has radiating rib-like trails of nick-points comparable with those described from the better preserved ventral valves. The dorsal pseudointerarea is not differentiated from the rest of the shell.

Internal morphology.—Details of the morphology of both valve interiors of *M. cf. occidentens* are invariably largely ob-

Fig. 10. *Mickwitzia cf. occidentens* Walcott. A–C. Ventral valves MGUH 26308 (A), MGUH 26279 (B), MGUH 26309 (C). A₁. Interior of early mature valve showing pseudointerarea with pedicle groove; scale bar 200 μm . B₁. Oblique posterior view of mature valve with pseudointerarea; scale bar 500 μm . A₂. Detail of pedicle groove of A₁; scale bar 100 μm . C. Oblique posterior view of mature valve with poorly preserved pseudointerarea; scale bar 500 μm . B₂. Interior view of B₁; scale bar 500 μm . B₃. Detail of pseudointerarea of B₁ showing numerous open setigerous tubes; scale bar 100 μm . B₄. Detail of pseudointerarea of B₁ showing opening of setigerous tubes with associated with depressions in the surrounding laminae; scale bar 50 μm . D. Oblique anterior view of interior of dorsal valve with indications of ridges MGUH 26310; scale bar 500 μm . B₅. Detail of pseudointerarea of B₁ showing openings of setigerous tubes; scale bar 50 μm . Specimens from the Bastion Formation (C, sample GGU 314910; D, sample GGU 314806) and the Ella Island Formation (A, B, sample GGU 314814).



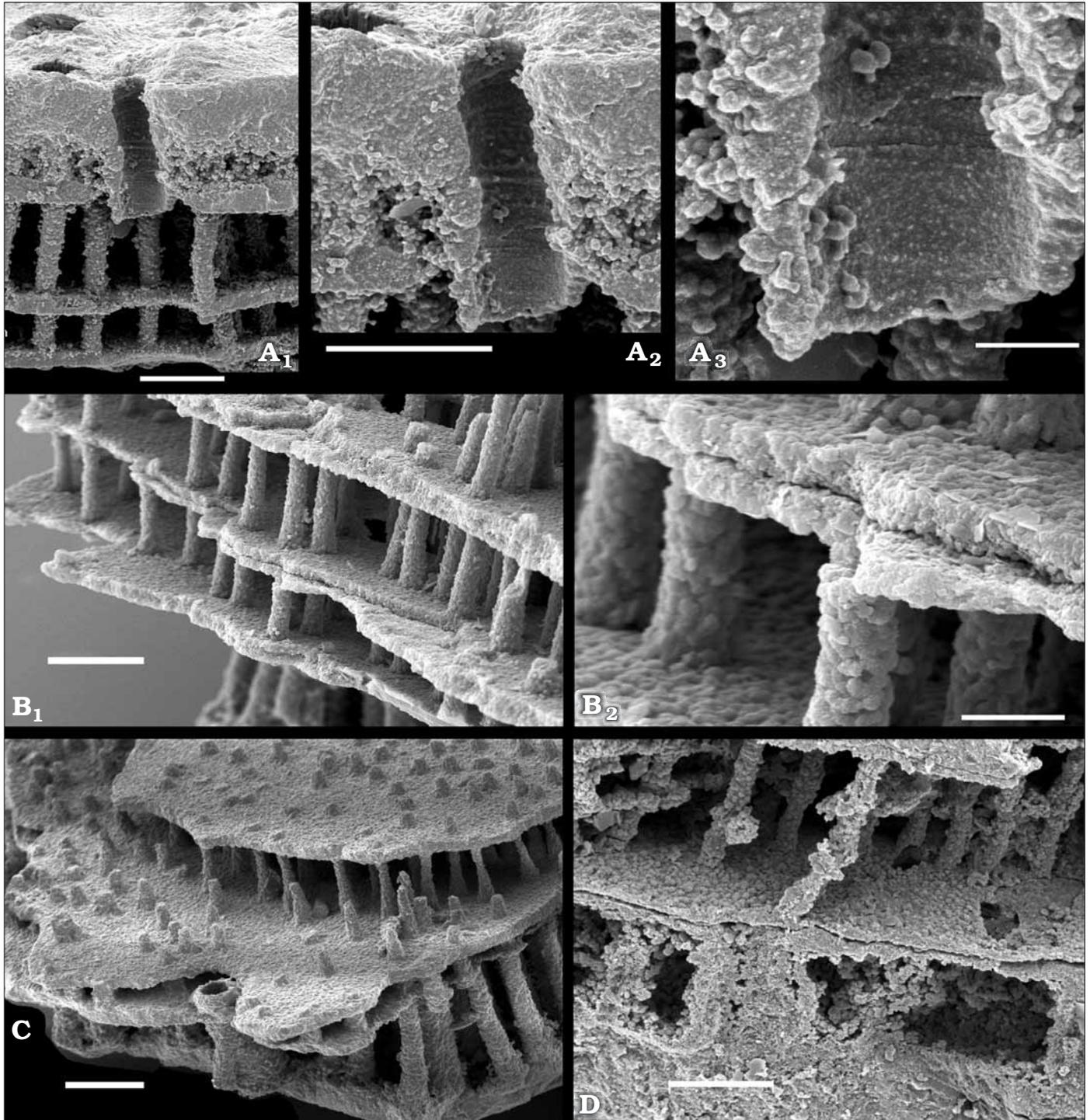


Fig. 11. *Mickwitzia* cf. *occidentens* Walcott. Fragmentary mature valves (indeterminate) MGUH 26280 (A), MGUH 26314 (B), MGUH 26315 (C), MGUH 26316 (D). **A₁**. Section through primary and secondary layer with large tube and smaller acrotretoid-type columns; scale bar 20 μ m. **A₂**. Detail of large tube perforating primary layer of A₁; scale bar 20 μ m. **A₃**. Detail of tubular wall of A₁ showing adhering cocci and possibly annulations; scale bar 5 μ m. **B₁**. Detail of secondary layer with acrotretoid-type columns and laminar shell; scale bar 20 μ m. **B₂**. Detail of B₁ showing median slit between laminae and cover of adhering discoidal structures; scale bar 5 μ m. **C**. Detail of secondary layer with numerous acrotretoid-type columns and single large tube; scale bar 20 μ m. **D**. Detail of secondary layer with thin laminae with median slit and acrotretoid-type columns and single cross-section through large tube; scale bar 20 μ m. All specimens from the Ella Island Formation, sample GGU 314816.

scured by recrystallization and adhering phosphatic material (see section on preservation; e.g., Fig. 10A). Commonly only the internal openings to the thick tubes are preserved (Fig.

4A₁; described below). The interior of a single poorly preserved dorsal valve appears to have three median ridges (Fig. 10D).

Shell structure.—Description of the shell structure is restricted to the phosphatic sections of the well-preserved specimens from the Ella Island Formation.

The outermost first-formed layer cannot be differentiated clearly from the underlying secondary shell as it is invariably recrystallized, and its detailed structure could not be determined. Judging from somewhat less recrystallized fractures through the pustulose early mature parts of the shell (Fig. 9C), and exfoliated surfaces (Fig. 9B), it may generally have been around 5 μm thick. In high magnification, the re-crystallized primary layer appears to have a finely granular appearance, but the size and structure of individual grains could not be determined (Fig. 9A₆). The primary shell is not penetrated by any open cylindroids over most of the early mature pustulose shell, where open apertures to the thick tubes are visible only on some exfoliated surfaces.

The underlying secondary shell is identical with the so-called columnar structure of acrotretoids (Holmer 1989; Williams and Holmer 1992). It consists essentially of a laminar succession with stacks of phosphatic laminae pierced by vertical cylindrical structures (Fig. 11). The stratiform laminae are each about 15 to 30 μm thick, but their thickness is influenced strongly by the cover of spheroidal to flattened discoidal bodies of the assumed cocci (see section on preservation above), which most commonly also obscures the inner structure of the laminae (Fig. 11B₂). Most of the primary structures of the laminae have also been strongly altered by recrystallization, but some of the less re-crystallized and covered laminae appear to be compact without obvious signs of internal stratification and have a very fine granular microstructure (Fig. 11D). As in linguliform brachiopods, the paired laminae are separated by a narrow median slit, around 1–2 μm wide (Fig. 11B₂, D).

The cylindrical structures that penetrate most of the laminar succession range between 4–11 μm in diameter, measured over a single exposed (exfoliated) lamina (Fig. 12A). There is a clear bimodal cluster at 5.5 and 8.4 μm ($n = 311$), and the two types are also clearly differentiated by their detailed structure. However, the measurements obtained are obviously influenced by the adhering phosphatic material (mostly cocci).

The relatively thinner cylindroids are identical in their basic structure to the columns of acrotretoid brachiopods (Holmer 1989; Williams and Holmer 1992). In *Mickwitzia cf. occidens*, the acrotretoid-type columns are the most common type of cylindroid. From one shell, a density of close to 6000 acrotretoid columns/ mm^2 was recorded (Fig. 12A). The thinner cylindroids are almost solid columns of apatite (Fig. 12A₂, A₃), but as in other parts of the shell the detailed structure of the columns is most commonly obscured by recrystallization and adhering cocci. As in the acrotretoids, some columns are aborted and form so-called domes (cf. Williams and Holmer 1992: text-fig. 7), which commonly have a platy coat of discoids (Fig. 5F, G). Other columns appear to be annulated and composed of stacked platy discoids of the same type as in the domes, and most frequently the centripetally added laminae do not fill the entire core, but have an empty central canal, most commonly 1–3 μm in diameter, as in the acrotretoids (Fig. 12A₂, A₃). The acrotretoid-type columns never penetrate the

primary layer, and they are visible only on the surface of the valve, when the primary layer has been exfoliated (Fig. 9B).

The second type of relatively thicker cylindroids is developed as regular tubes, which have widely different morphologies in different parts of the valve. Most commonly they penetrate vertically through the lamination, like the acrotretoid-type columns, but on the ventral pseudointerarea they are more or less parallel to the laminae. The recorded densities of the thicker tubes are invariably much lower by comparison with the columns, with 134 tubes/ mm^2 recorded from one shell (Fig. 12A). The preservation of the tubes is also much more variable compared with the acrotretoid-type columns. In sections through the mature shell, the tubes are sometimes preserved as solid-walled cylindroids, up to 13 μm in diameter, with a porous recrystallized wall (4 μm thick) and a central canal (6 μm in diameter) which is either filled with a phosphatic material, or empty (Fig. 12B₂). More commonly the tubes are preserved as hollow perforations, having a cover of cocci that must have adhered to the outer wall surface of the tube (Fig. 12A₂); thus the tubular wall itself is not preserved. In other sections of the mature shell, the tube lacks an external cover of cocci, and the cocci are adhering only to the inside of the central canal, which is surrounded by an empty perforation through the laminae (Fig. 12A₄). In larger mature shells, the primary layer is clearly penetrated by the thick tubes (Fig. 11A), and on the surface, the tubular openings are distributed roughly concentrically in arcs (around 0.1–0.2 mm apart). The distribution of apertures is evidently not tied to the development of pustules, and there are no clear signs of any depressions or indentations around the tubular aperture (Fig. 9A, B). The tubes open to the shell surface as smooth-rimmed apertures, 8–10 μm in diameter, and the tube is commonly continued internally as an empty perforation, lacking walls (Fig. 11A). On the ventral pseudointerarea, the thicker tubes lie parallel to the lamination and are invariably open to the external surface through an aperture between 7 to 13 μm in diameter (Fig. 10B₃–B₅). The surface of the pseudointerarea, immediately outside the tubular aperture, is most commonly indented by cylindrical depressions (Fig. 10B₄). Some tubes on the pseudointerarea preserve internal striations with alternating grooves and ridges, up to 600 nm wide and parallel to the long axis of the tube (Fig. 12B₃, B₄). The majority of the tubes appear to be made up entirely of cocci adhering to the tubular wall, which is mostly not preserved (Fig. 12B₃).

Discussion and interpretation

Development.—The earliest growth stage recorded in *Mickwitzia* from Greenland is comparable in size and shape with the juvenile shell of Recent and fossil linguliform brachiopods. There is no trace of a first-formed shell (in the sense of Williams 2003). In Recent lingulids and discinids, the juveniles are essentially miniature adults, around 0.4–0.75 mm wide, at the time of settlement. The trauma associated with settlement and the transition from a planktotrophic to a sedentary mode of life can be seen most commonly as a ring of major

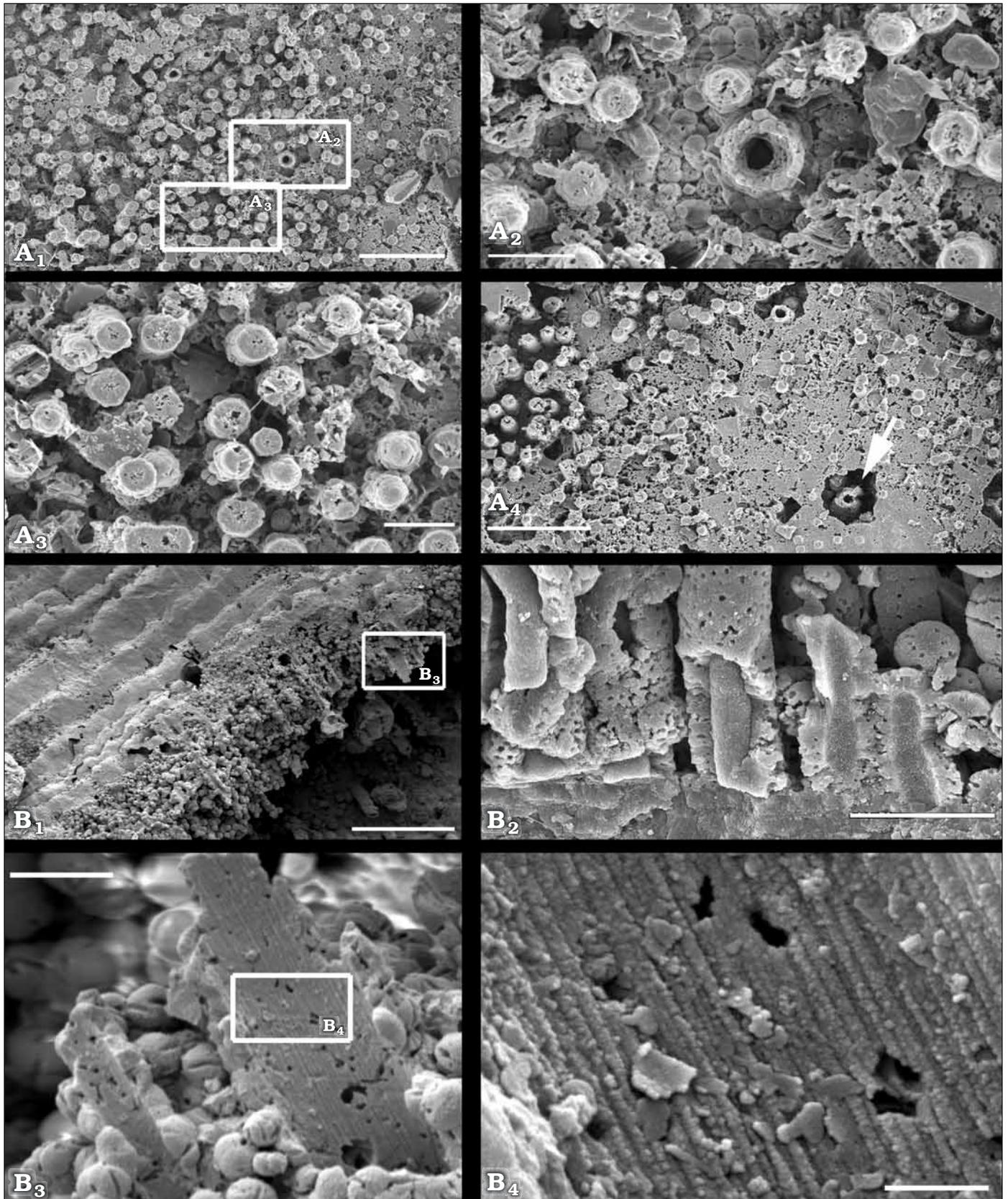


Fig. 12. *Mickwitzia* cf. *occidens* Walcott. A. Fragmentary mature valve (indeterminate) MGUH 26317. **A₁**. Exfoliated interior surface showing numerous acrotretoid-type columns and scattered large tubes, position of **A₂** and **A₃** indicated; scale bar 50 μ m. **A₂**. Detail of **A₁** showing single large tube with adhering cocci and numerous acrotretoid-type columns; scale bar 10 μ m. **A₃**. Detail of **A₁** showing numerous acrotretoid-type columns, some of which have a central canal of varying diameter or are completely filled; scale bar 10 μ m. **A₄**. Detail of **A₁** showing lamina perforated by empty large tube (marked by arrow) →

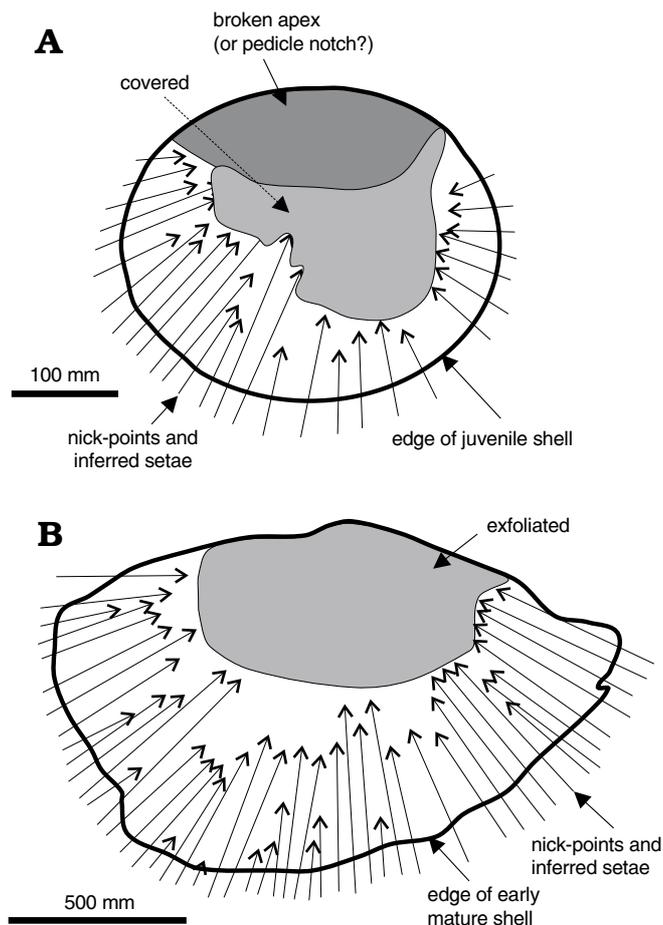


Fig. 13. Inferred distribution of setae (as indicated by nick-points) in juvenile (A) and early mature ventral valves of *Mickwitzia cf. occidentens* Walcott.

growth disturbance around the juvenile shell (Chuang 1961, 1962, 1977). Similar sized growth disturbances around the juvenile shell have also been identified from many fossil lingulids and discinids (e.g., Holmer 1989). The juvenile shell of *M. cf. occidentens* is covered by well-developed fila and trails of nick-points that are most likely formed by stresses within the outer mantle lobe induced by the brachiopod setal muscles (Williams and Holmer 1992). Unlike *M. cf. occidentens*, most previously described fossil juvenile shells have rather faint concentric filar ornamentation, mostly lacking nick-points (e.g., Holmer 1989: fig. 48N), and the same is true for Recent linguliforms, where the nick-points are best seen on the mature shell (Williams and Holmer 1992; but see also Baliński 1997, 2001). The nick-points indicate that the juvenile *M. cf. occidentens* had close to 30 mantle setae at around the time of settlement (Fig. 13A), which is close to the number recorded from, e.g., juvenile Recent *Lingula* (Yatsu 1902).

The pustulose mature ornamentation is a distinctive feature of all described species of *Mickwitzia* (referred to as

“papillose ornamentation” by Walcott 1912 and McMenamin 1992). According to Walcott (1912: 330) and McMenamin (1992: 180) each pustule is perforated by one of the larger tubes. This pattern could not be confirmed in *M. cf. occidentens*, and the distribution of the open tubular apertures over the mature shell is seemingly independent of the pustulose ornamentation. The distribution and general structure of the mickwitziid pustules are quite similar to the pustulose ornamentation found on the mature shells of the Botsfordiidae (Fig. 6C) and Eoobolidae. More detailed comparative studies of the distribution and detailed nature of this type of ornamentation are needed in order to check the possible phylogenetic importance and relationships.

It is clear that *M. cf. occidentens* had a functional pedicle (Fig. 14) by the early mature growth stage as indicated by a ventral pseudointerarea with a pedicle groove. The fact that some ventral pseudointerareas seemingly lack a well differentiated groove probably indicates that the pedicle was rather small and not always extending along a groove in the pseudointerarea. The pedicle may have atrophied in larger mature forms, but this cannot be determined on the material at hand. However, it is likely that most large *Mickwitzia* were essentially free lying as adults, and there is no recorded clear evidence for an adult pedicle in any of the known species (Walcott 1912; McMenamin 1992).

Musculature.—There are virtually no preserved interior characters. The dorsal median ridges developed in a single valve are somewhat similar to the ridges described from the type species *M. monilifera*, and these have been interpreted as the traces of muscles (e.g., Walcott 1912: 331, pl. 6: 1d, f).

Skeletal succession.—There is no doubt that the shell of *Mickwitzia* originally included primary secretion of apatite, but much of the patterns have been obscured by secondary phosphatization and recrystallization. As noted by Skovsted and Holmer (2001) and Holmer et al. (2002), the structures described from the preserved apatitic laminar shell are clearly homologous with those described from living and fossil organophosphatic linguliform brachiopods (e.g., Iwata 1981; Watabe and Pan 1984; Holmer 1989; Williams et al. 1992, 1994; Cusack et al. 1999), as well as from the organophosphatic sclerites of the problematic *Micrina* (Williams and Holmer 2002). The work by Holmer (1989), Williams and Holmer (1992), Williams et al. (1998), Cusack et al. (1999), and Williams and Cusack (1999), demonstrated clearly that finer details of the shell structure in extant linguliforms can be preserved and interpreted even in strongly recrystallized fossil linguliforms.

As noted above, the shells of *M. cf. occidentens* from both localities invariably have numerous spheroidal phosphatic bodies that are here interpreted as phosphatized cocci. All observed variations in their morphology suggest that the cocci

interior canal replicated by adhering cocci; scale bar 50 μ m. **B.** Ventral valve MGUH 26279. **B₁.** Detail of pseudointerarea with location of B₃ indicated; scale bar 100 μ m. **B₂.** Detail of secondary shell in B₁ showing large tubes with mineralized porous wall and filled or empty central canal; scale bar 20 μ m. **B₃.** Detail of B₁, showing striated large setigerous tubes replicated by adhering cocci, location of B₄ indicated; scale bar 10 μ m. **B₄.** Detail of B₃ showing striated (impressions of microvilli) tube; scale bar 2 μ m. All specimens from the Ella Island Formation. **A.** sample GGU 314924; **B.** sample GGU 314816.

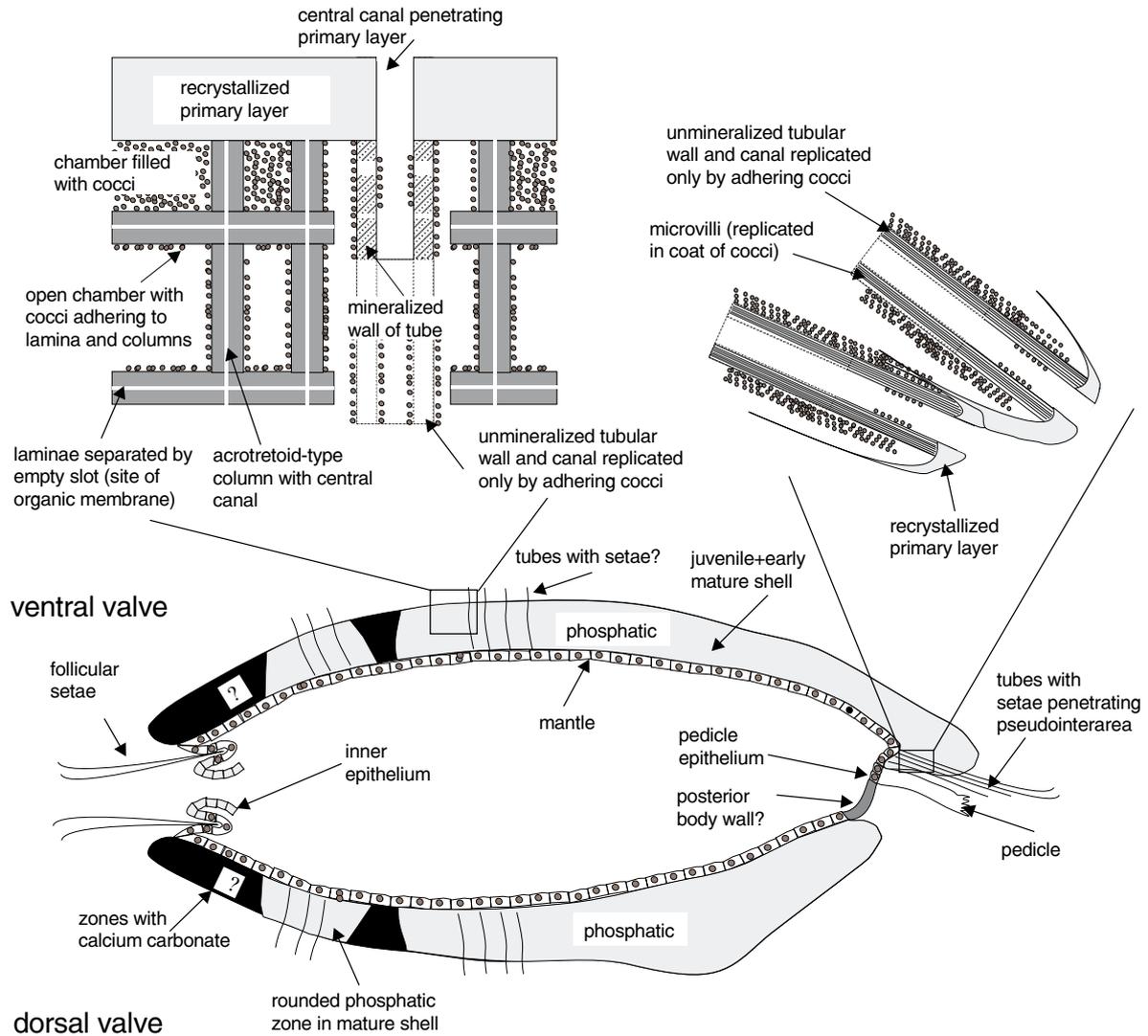


Fig. 14. Schematic reconstruction of inferred relationships between mantle, shell, pedicle, and the various types of setae in a reconstructed cross-section of a living *Mickwitzia cf. occidentis* Walcott, with enlarged crosssections showing the interpretation of the various types of cylindroid structures penetrating the shell.

became attached in life to the mineralized walls and organic membranes, but it is not possible to determine if they invaded the shell after the death of the animal or actually represent symbionts of some kind. However, the fact that no other shells from the same samples have preserved cocci of the same type may indicate that they somehow are specific to *Mickwitzia*. Moreover, it is clear that they were in place before diagenesis had affected the shell to any great extent. Similar cocci are apparently present also in the valves of *M. occidentis* from Nevada (Fig. 2B), as well as in most of the *Mickwitzia* described by McMenamin (1992: figs. 1: 1, 5: 1).

The smallest mineralized constituent in the phosphatic shell of *M. cf. occidentis* cannot be identified with confidence due to recrystallization and phosphatization. Some surfaces have a granular appearance, whereas others are clearly coated by platy discoids (which may also represent cocci). The stacked laminal succession is identical to that found in Recent linguliforms, and in life would have consisted of minute phosphatic grains that were protein-coated and secreted

onto organic substrates. The narrow empty slit between successive closely stacked laminae would have been the site of an organic membrane (see e.g., Williams and Cusack 1999: fig. 7; Fig. 14).

Earlier descriptions of mickwitziid shell structure (Walcott 1912; McMenamin 1992) indicated that the shell could be differentiated into three layers. The following description by McMenamin (1992: 180) summarized the prevalent view.

“Inner layer coarsely punctate to smooth; each puncta bears an axial hollow phosphatic tube. Middle layer may be marked by numerous radiating and concentric ridges and small punctae that may become very numerous toward the anterior margin (nearest apex) of shell; this middle layer may consist of two or more layers. Punctae and axial tubes continue into this layer. Outer layer, exfoliated in many specimens, may be papillose; each papilla represents the termination of a puncta. Pores open to shell surface through a papilla or short hollow spine on outer wall surface”.

It is now clear that the so-called mickwitziid “punctae” are the thicker setigerous tubes described here, whereas the relatively thinner acrotretoid type of columns were not known previously from *Mickwitzia*. However, Walcott (1912: 329) briefly referred to “fine and large punctae”, but these were not illustrated clearly. The preservation of the thick tubes in the material described by McMenamin (1992: figs. 1: 1, 5: 1) indicates that they are mostly preserved simply as the cocci-coated external and internal surface, whereas the tubular wall itself is missing (Fig. 14). This type of preservation is also prevalent in the new material of *M. occidentis* from Nevada (Fig. 2B). McMenamin (1992: 175) first discussed the general similarity between the tubes of *Mickwitzia* and those described by Conway Morris and Chen (1990) from sclerites of the problematic *Tannuolina*. However, he noted that the inner surfaces on the cylindroids of *Tannuolina* are striated and he did not consider them to be homologous with the orthogonally disposed cylindroids penetrating the mature shell of *Mickwitzia*.

Holmer et al. (2002) interpreted both the acrotretoid-type columns and thicker tubes of *M. cf. occidentis* as primary structures of apatite secreted on cylindroid membranes by papillae of mantle epithelium. The laminar wall of the thicker tubes indicates that laminae were added by centripetal growth, and this was most likely secreted by mantle papillae. On the ventral pseudointerarea, the internally striated thicker tubes are oriented parallel to, and clearly both penetrate as well as cause exterior indentation in the laminar succession. As noted by Holmer et al. (2002), these tubes can be homologized with the striated setigerous tubes of *Micrina* (Williams and Holmer 2002: text-fig. 2); in life, the tubes would have been secreted by setoblasts and contained setae that extended from the open apertures and indentations in the shell exterior on the ventral pseudointerarea (Fig. 14; see also Holmer et al. 2002: text-fig. 1).

Outside the ventral pseudointerarea, the larger tubes are invariably disposed orthogonally to the laminar succession. Although it is clear that these tubes sometimes penetrate the primary layer and are open to the exterior through an aperture, there is no clear evidence of internal striation like that found in the tubes on the ventral pseudointerarea. However, all other aspects of their morphology are identical to the setigerous tubes that penetrate the pseudointerarea, and some kind of setal structures may have also filled these tubes. Yet we have not observed any clear signs of setae extending through the aperture and causing indentations in the shell. Moreover, the apertures in *Mickwitzia* are quite different and have a much more simple morphology compared with the more complex structures in the setigerous openings in *Micrina* (see Williams and Holmer 2002: text-fig. 6). This may indicate that the tubular setae of *M. cf. occidentis* were essentially some kind of evolutionary relicts that had lost their original function. In any event they were lost in all crown group Brachiopoda. The development of the filar nick-points in the ornamentation indicates that *Mickwitzia* also had the normal crown group brachiopod-type of follicular setae within mantle grooves (Fig. 14; see also Holmer et al. 2002: text-fig. 1).

As noted by Holmer et al. (2002) the acrotretoid-type columns were evidently secreted in a similar fashion to that of

the setigerous tubes on the pseudointerarea, and the infilling of both cylindroids suggests that they were all secreted centripetally by mantle papillae that retreated as the shell thickened. Holmer et al. (2002) proposed that degenerate setoblasts may have been involved in the secretion of the acrotretoid-type columns in *Mickwitzia*. Regardless of whether the orthogonal larger tubes contained setae or not, it is likely that they also were secreted by setoblasts. There is no evidence to suggest that they secreted some kind of “chemical deterrence” as proposed by McMenamin (1986, 1992).

The mature shell of *M. cf. occidentis* includes zones that entirely lack phosphatic mineralization and are composed mainly of calcium carbonate. Unfortunately, only the single specimen still in matrix was available for analysis of these calcareous zones, and their interpretation is very uncertain. The presence of both phosphate and calcium carbonate zones may indicate that both biominerals were secreted or that the calcareous zones were originally composed entirely of organic material (Fig. 14).

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