# SYSTEMATIC DESCRIPTIONS:
# BRACHIOPODA
# UPDATES TO SYSTEMATIC VOLUMES 2–5

## LINGULIFORMEA

L. E. HOLMER and L. E. POPOV

[University of Uppsala; National Museum of Wales, Cardiff]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

### Subphylum LINGULIFORMEA Williams & others, 1996
### Class LINGULATA Gorjansky & Popov, 1985

The phylogeny and classification of groups within the Lingulata are still most problematic, but the cladistic analyses by HOLMER and POPOV (1996, 2000) indicate that they can be divided into at least two monophyletic orders, the Siphonotretida and Acrotretida, as well as the Lingulida, which cannot be confirmed as a monophyletic group. As defined by HOLMER and POPOV (2000), the Lingulata comprises 22 extinct and only 2 extant families, the Lingulidae and Discinidae.

Recent chemicostructural studies of the shells of living and extinct linguliforms by WILLIAMS and others (1998), CUSACK, WILLIAMS, and BUCKMAN (1999), WILLIAMS and CUSACK (1999), WILLIAMS (2003), and WILLIAMS, HOLMER, and CUSACK (2004), have revealed the extraordinary complexities of organophosphatic skeletal systems. There is no doubt that basic characters of the shell structure are of primary importance for lingulate systematics; however, the significance of homoplasy in the evolution of organophosphatic brachiopod shell lamination, especially in the lingulides, is not yet completely clear. As a result, the published cladograms have so far been inconclusive with highly varying topology depending to a large degree on how characters were coded and which groups were included in the analysis. Thus, a complete phylogenetic revision of linguliform systematics has not been attempted at the present time.

### Order LINGULIDA Waagen, 1885

HOLMER and POPOV (1996, 2000) expanded the concept of the order to include also the Discinoidea and Acrotheloidea, in view of their lingulid-like musculature and shell structure, but the detailed phylogenetic relationships between the Linguloidea and the discinoids and acrotheloids could not be determined. From the detailed structural shell studies and cladistic analyses of WILLIAMS, CUSACK, and BUCKMAN (1998), CUSACK, WILLIAMS, and BUCKMAN (1999), and WILLIAMS and CUSACK (1999), it is clear that the phylogeny and classification of the lingulides need to be revised considerably. These cladistic analyses (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999) of the lingulid superfamilies Linguloidea and Discinoidea indicate that they indeed form a monophyletic group within the Lingulida, defined mainly by the possession of a baculate shell structure (HOLMER, 1989), but excluding some groups that were assigned to the Linguloidea by HOLMER and POPOV (1996, 2000), most importantly the Lingulellotretidae. The latter group includes the earliest known Early Cambrian (Atdabanian) lingulid-like brachiopod with a long fleshy pedicle emerging through an enclosed pedicle foramen (see JIN, HOU, & WANG, 1993; HOLMER & others, 1997), but since it has an acrotretoid-like columnar shell structure (CUSACK, WILLIAMS, & BUCKMAN, 1999)

it cannot be confirmed as a member of the linguloid-discinoid clade. In the same way, CUSACK, WILLIAMS, and BUCKMAN (1999) excluded the Paterulidae and Eoobolidae from the Linguloidea-Discinoidea, based on ultrastructural differences. The phylogenetic relationships and systematic composition of the families Zhanatellidae, Elkaniidae, and Dysoristidae also require revision following the work of CUSACK, WILLIAMS, and BUCKMAN (1999). In particular, the distributions of the various types of superficial pitted imprints need to be looked at in detail, since it is clear that they now can be divided into several distinct types (WILLIAMS, 2003).

In the cladistic analysis of HOLMER and POPOV (1996), the most derived families, the Pseudolingulidae, the Lingulasmatidae, and the Lingulidae, formed a monophyletic group, and this is supported in the cladogram of CUSACK, WILLIAMS, and BUCKMAN (1999). Within this clade, the Lingulidae is also monophyletic, first appearing at around the Late Devonian to Early Carboniferous; the separation between the two modern genera *Glottidia* and *Lingula* can be traced back to the Carboniferous, based on characteristics of their respective shell structure (WILLIAMS & others, 2000).

The new data on soft body anatomy of Early Cambrian lingulides from the Chengjiang Fauna published by ZHANG, HOU, and EMIG (2003) and ZHANG and others (2003) include important anatomical information including preservation of a pedicle, schizolophous lophophore, as well as a recurved, U-shaped digestive tract with a functional anus. This provides the first direct evidence that major features of soft body anatomy characteristic of Recent lingulates were already in place in Early Cambrian members. Considerable variation exists in pedicle morphology among the early lingulides. In particular, the acrotheloid *Diandongia pista* RONG had a long (up to 16 mm) and thin (less than 1 mm in diameter) pedicle lacking any annulations. Its distal part adhered to sand grains or was attached to bioclasts. It could not support the animal, however, to maintain a higher position in the water column or be used in active borrowing, as in Recent lingulides. New findings from the Chengjiang brachiopods also give additional insight into the paleoecology of Early Cambrian lingulids. For example, preservational aspects, the presence of a schizolophous lophophore, as well as pedicle morphology of *Lingulellotreta,* all suggest this lingulide was a high-level suspension feeder and was not adapted to an infaunal mode of life (ZHANG & others, 2004; see also HOLMER & others, 1997).

## Superfamily LINGULOIDEA Menke, 1828

### Family LINGULIDAE Gray, 1840

**Credolingula** SMIRNOVA in SMIRNOVA & USHATINSKAYA, 2001, p. 57 [**C. olferievi*; OD]. Shell slightly biconvex, equivalved, with poorly defined sulcus, bearing low indistinct median fold in both valves; pseudointerareas of both valves vestigial; ventral valve interior with asymmetrical paired umbonal muscle, bisected by pedicle nerve impression; dorsal interior with visceral area occupying about two-thirds of sagittal length; posterolateral muscle fields strongly asymmetrical; mantle canal system of both valves bifurcate. *Lower Cretaceous (Albian):* central European Russia.——FIG. 1669*a–h*. **C. olferievi*, lower Albian, Stoilo quarry near Staryi Oskol, central European Russia; *a*, holotype, ventral valve exterior, PIN4796/1, ×1.8; *b*, dorsal valve exterior, PIN4796/2, ×1.8; *c*, ventral valve exterior, PIN4796/5, ×7; *d*, ventral valve interior, PIN4796/6, ×6.5; *e*, dorsal valve interior, PIN4796/16, ×5; *f*, detail of ventral valve interior showing posterior part of visceral field, PIN4796/3, ×7; *g*, detail of dorsal valve interior showing anterior part of visceral field, PIN4796/17, ×7; *h*, detail of dorsal valve interior showing posterior part of visceral field, PIN4796/4, ×15 (Smirnova & Ushatinskaya, 2001).

### Family PSEUDOLINGULIDAE Holmer, 1991

Meristopacha SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 57 [**Lingula granulata* PHILLIPS in PHILLIPS & SALTER, 1848, p. 370; OD]. Shell weakly biconvex, elongate subrectangular; dorsal valve with hemiperipheral growth; ventral interarea short to obsolescent; ornament of strong regular concentric rugae; ventral interior with low visceral platform raised anteriorly; dorsal interior with strong median ridge crossing visceral area and widely separated central and anterior lateral muscle scars; ventral mantle canals saccate baculate with straight,

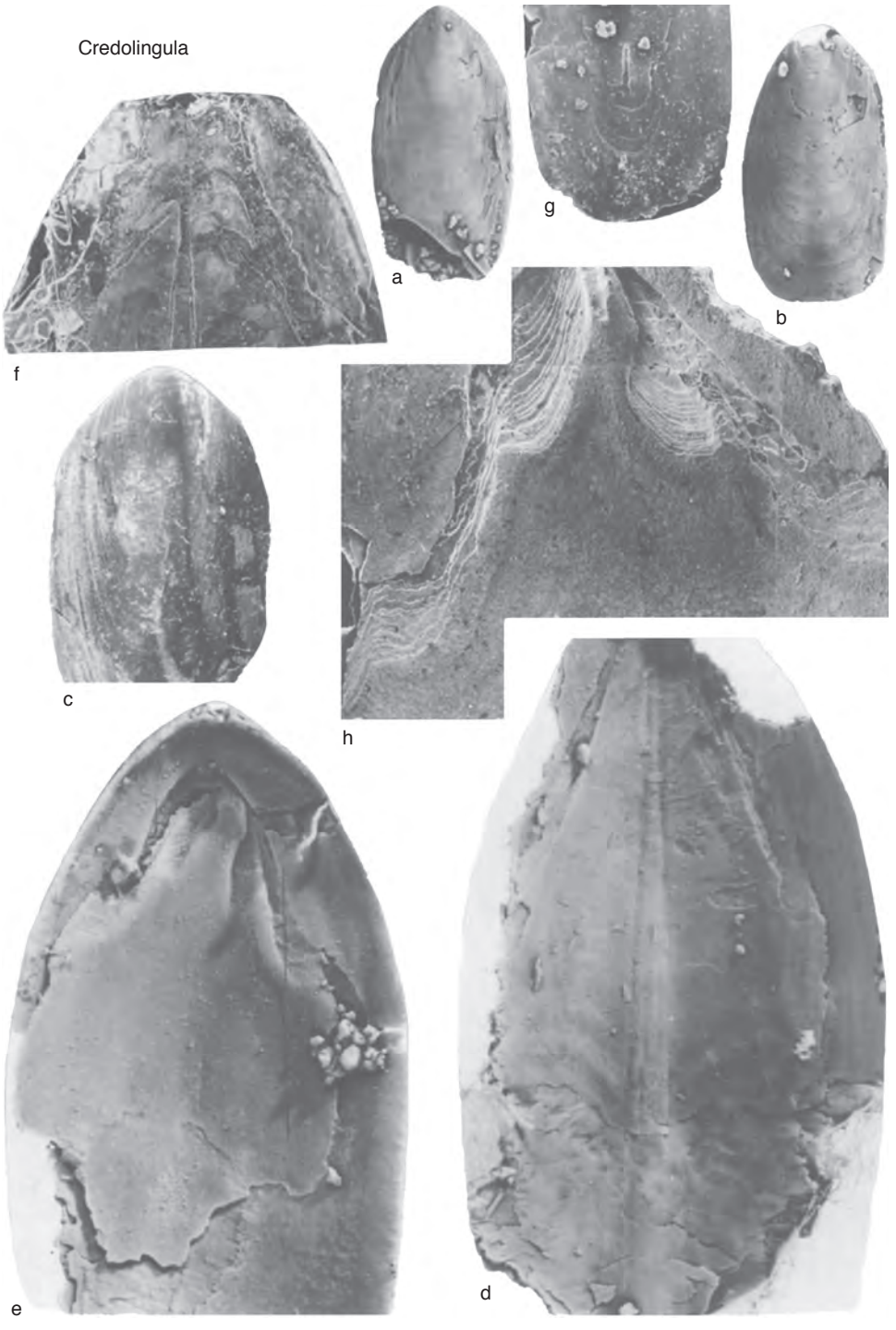



FIG. 1669. Lingulidae (p. 2533).

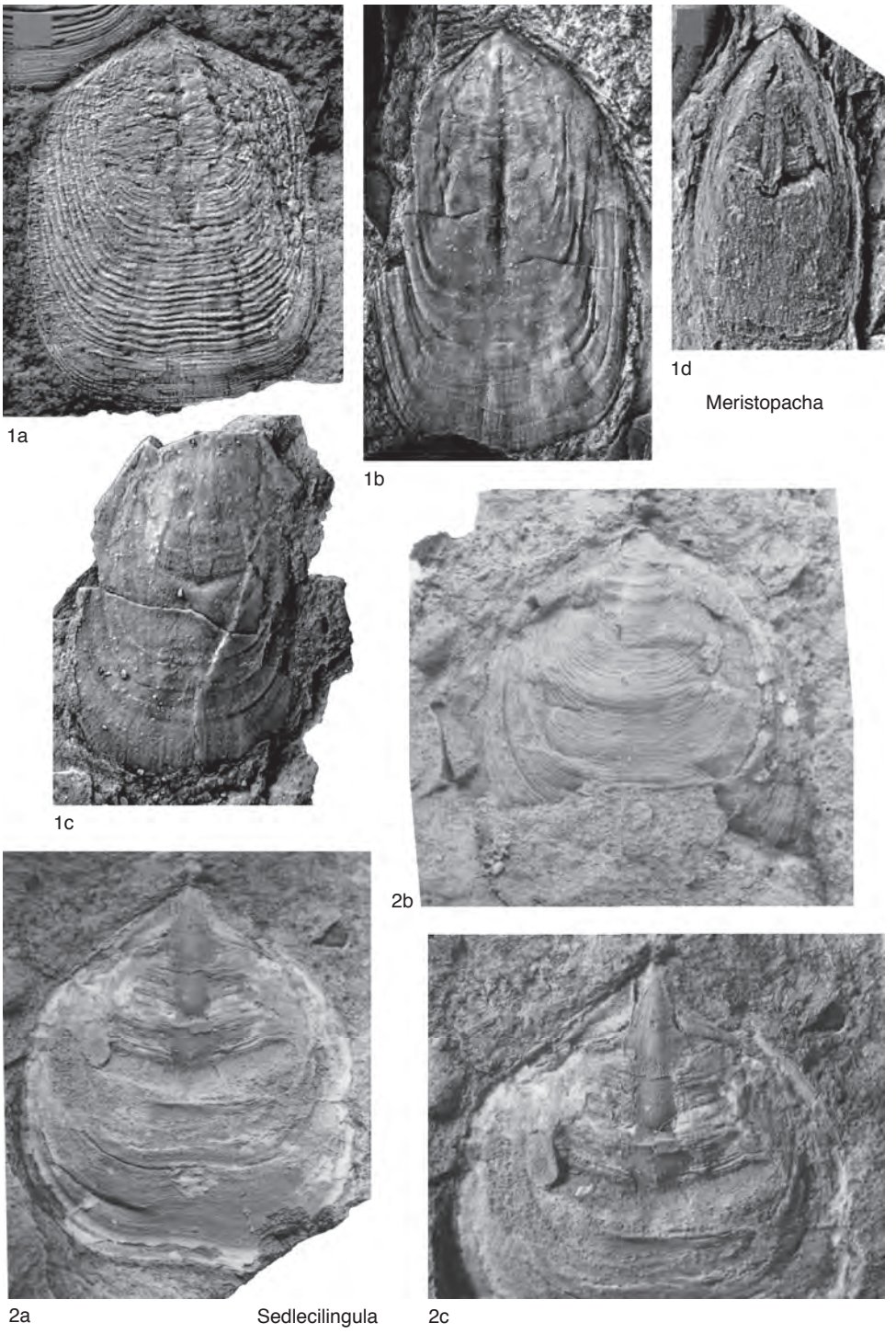



FIG. 1670. Pseudolingulidae (p. 2533–2536).

subparallel *vascula lateralia. Ordovician (Llanvirn–Llandeilo):* Great Britain.——Fig. 1670,*1a–d. *M. granulata* (Phillips), upper Llanvirn–Llandeilo; *a*, ventral valve exterior, SM A45419, ×2.5; *b*, dorsal internal mold, NHM BC51673, ×2.5; *c*, ventral internal mold, NHM BC51797, ×2.5; *d*, ventral internal mold, NMW 27.110G.437a, ×5 (Sutton, Bassett, & Cherns, 1999).

**Sedlecilingula** Mergl, 1997b, p. 98 [**S. sulcata*; OD]. Shell broadly elongate, both valves with sulcus, and weakly emarginated anterior margin; ornamentation with raised concentric fila; sulcus may bear faint radial plications; ventral pseudointerarea large, with well-defined propareas, separated by deep, moderately expanding pedicle groove; ventral interior with large raised muscle platform; posterior part of visceral area finely pitted; dorsal pseudointerarea well developed; dorsal interior lacking median ridge and paired umbonal scars. *Ordovician (Arenig):* Bohemia.——Fig. 1670,*2a–c. *S. sulcata*, Klabava Formation, Sedlec; *a*, holotype, ventral internal mold, ×8; *b*, detail of visceral area and pseudointerarea, ×10; *c*, ventral valve exterior, latex cast, MBHR66837, ×8 (new). [Michal Mergl]

## Family OBOLIDAE King, 1846
## Subfamily OBOLINAE King, 1846

**Atansoria** Popov, 2000a, p. 261 [**A. concava*; OD]. Shell concavoconvex, subcircular; dorsal valve mainly with hemiperipheral growth; dorsal pseudointerarea vestigial but undivided; dorsal interior with limbus; dorsal posterolateral muscle fields large and strongly impressed, outlined by muscle bounding ridges; dorsal central muscle scars strongly impressed, divided by median furrow, and partially enclosing small outside lateral muscle scars; dorsal mantle canal system baculate with arcuate, subperipheral *vascula lateralia* and short, divergent *vascula media*. *Ordovician (upper Caradoc–Ashgill):* Kazakhstan, Australia.——Fig. 1671,*2a–c. *A. concava*, Mayatas Formation, upper Caradoc, northern coast of Atansor lake, Kazakhstan; holotype, dorsal valve interior, oblique lateral, and posterior views, NMW 98.65G.4, ×23 (Popov, 2000a).

**Divobolus** Sutton in Sutton, Bassett, & Cherns, 1999, p. 36 [**Obolus quadratus* Bulman in Stubblefield & Bulman, 1927, p. 121; OD]. Shell weakly biconvex, slightly inequivalved, elongate oval to subcircular; ventral interarea low, apsacline, lacking flexure lines; pedicle groove shallow; dorsal pseudointerarea low, crescent shaped, not raised above valve floor; median groove shallow; visceral areas in both valves weakly impressed; dorsal interior with short median tongue, and closely placed central and outside lateral muscle scars; mantle canal system in both valves baculate; ventral *vascula lateralia* submarginal, widely divergent proximally; dorsal *vascula media* long, divergent. *Ordovician (Tremadoc)*: Great Britain.——Fig. 1672,*2a–d*. **D. quadratus* (Bulman), Shineton Shale Formation, Shropshire, England; *a*, ventral internal mold, NHMBB73823, ×5; *b,* ventral external mold, ×5; *c,* detail of ornament, BGSRU8944A, ×10; *d*, holotype, dorsal internal mold, NHMB47342, ×5 (Sutton, Bassett, & Cherns, 1999).

**Eodicellomus** Holmer & Ushatinskaya in Ushatinskaya & Holmer, 2001, p. 125 [**E. elkaniiformis*; OD]. Shell close to equibiconvex; ornamentation of thin radial costellae; ventral pseudointerarea apsacline; pedicle groove deep, broadly triangular; propareas well developed, elevated; dorsal pseudointerarea anacline, with short median groove and flattened propareas; central and anterior parts of both valves strongly thickened, forming visceral platforms; vascular system of both valves well developed, with deep *vascula lateralia* and dorsal *vascula media. Lower Cambrian (Atdabanian–Botomian):* South Australia, Transantarctic Mountains.——Fig. 1673*a–k*. **E. elkaniiformis*, Parara Limestone, Botomian, Yorke Peninsula and Flinders Ranges; *a*, dorsal valve interior, PIN4664/6246, ×9; *b*, holotype, ventral valve interior, ×10; *c*, detail of visceral area, PIN4664/6172, ×18; *d*, oblique posterior view of dorsal umbo, PIN4664/6167, ×42; *e*, oblique posterolateral view of ventral umbo, ×24; *f*, detail of ornamentation, ×100; *g*, detail of ventral larval shell, PIN4664/6168, ×80; *h*, oblique lateral view of dorsal valve interior, PIN4664/6170, ×16; *i*, dorsal valve interior, ×11; *j*, detail of dorsal pseudointerarea, PIN4664/6173, ×22; *k*, oblique posterolateral view of ventral interior, PIN4664/6164, ×17 (Ushatinskaya & Holmer, 2001).

**Josephobolus** Mergl, 1997a, p. 137 [**J. regificus*; OD]. Shell broadly oval, subacuminate; ornamentation of oblique, parallel terrace lines on flanks; narrow posteromedian and anterolateral sectors with faint terrace lines crossing each other and forming a regular network of asymmetrical pits; ventral pseudointerarea large, with narrow propareas; pedicle groove deep, rapidly expanding anteriorly; dorsal pseudointerarea short; visceral areas of both valves weakly impressed; interior of shell densely covered by large pits. *Ordovician (Arenig):* Bohemia.——Fig. 1672,*1a–c. *J. regificus*, Klabava Formation, Zbiroh; *a*, partial internal mold of ventral valve, MBHR 66781, ×5; *b*, ventral valve exterior, MBHR 66782, ×3.7; *c*, detail of ornamentation of fragmentary valve, MBHR 667893, ×8 (new). [Michal Mergl]

**Kacakiella** Mergl, 2001a, p. 13 [**K. bouceki*; OD]. Shell equibiconvex; ventral pseudointerarea with long pedicle groove; visceral area poorly impressed; exterior of larval shell smooth with several radial ribs, postlarval ornament of shallow pits in divaricate pattern; flanks with oblique terrace lines. *Silurian (Llandovery–Wenlock):* Bohemia.——Fig. 1674,*1a–d. *K. bouceki*, Motol Formation,Wenlock, Loděnice, Svatý Jan pod Skalou; *a*, ventral valve interior, PCZCU503, ×8; *b*, detail of ornamentation, PCZCU466, ×45; *c*, ventral valve exterior

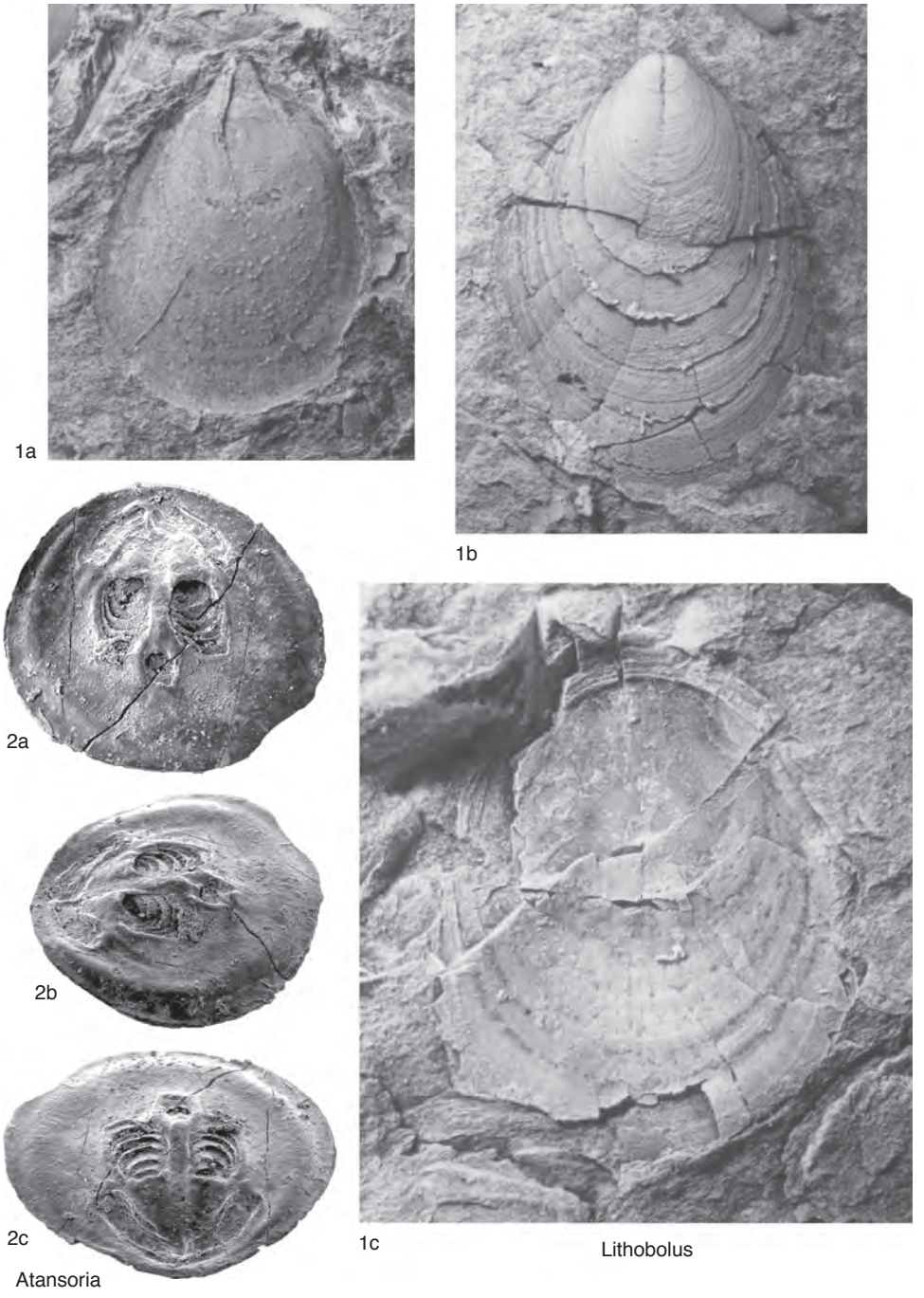



FIG. 1671. Obolidae (p. 2536–2542).

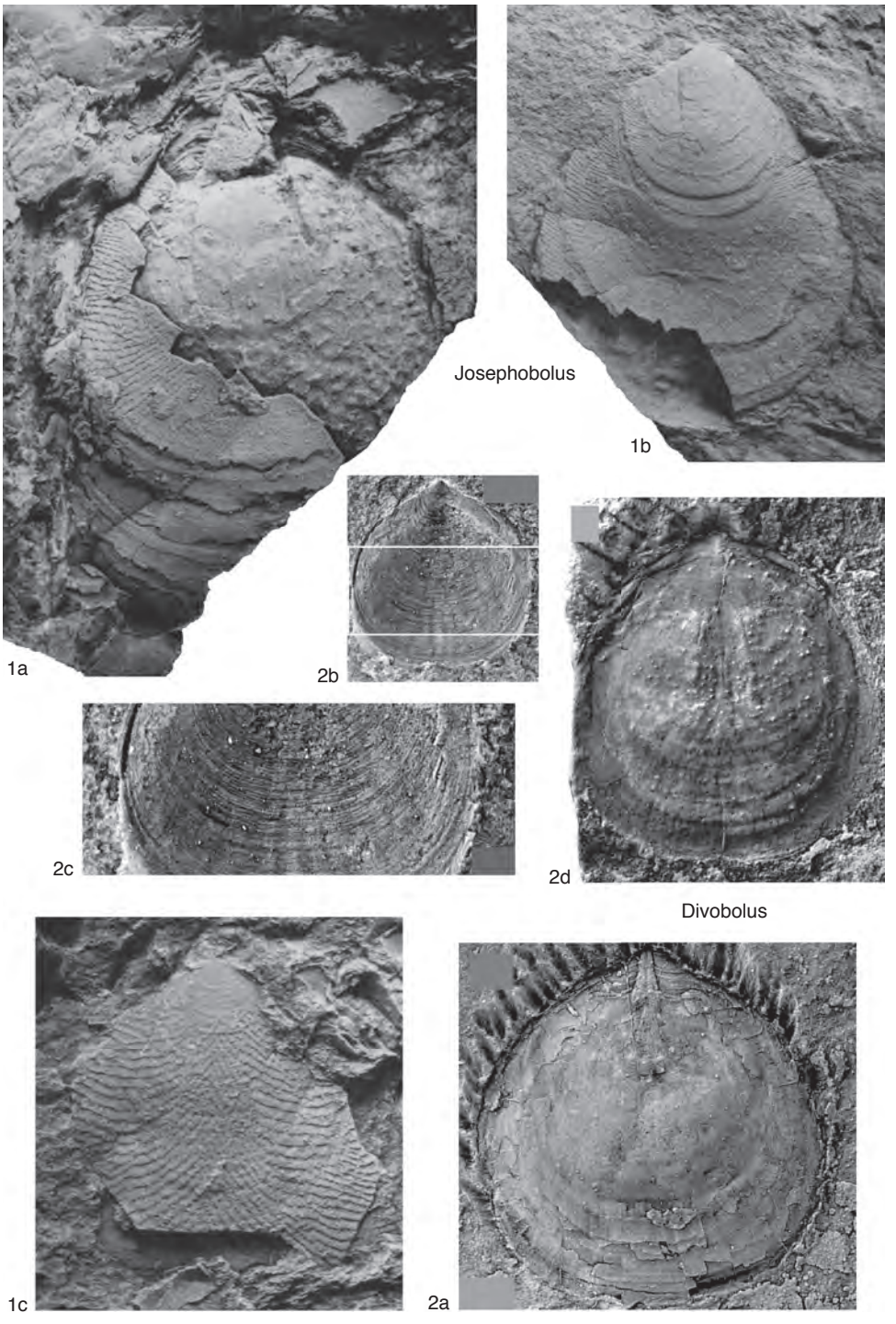



FIG. 1672. Obolidae (p. 2536).

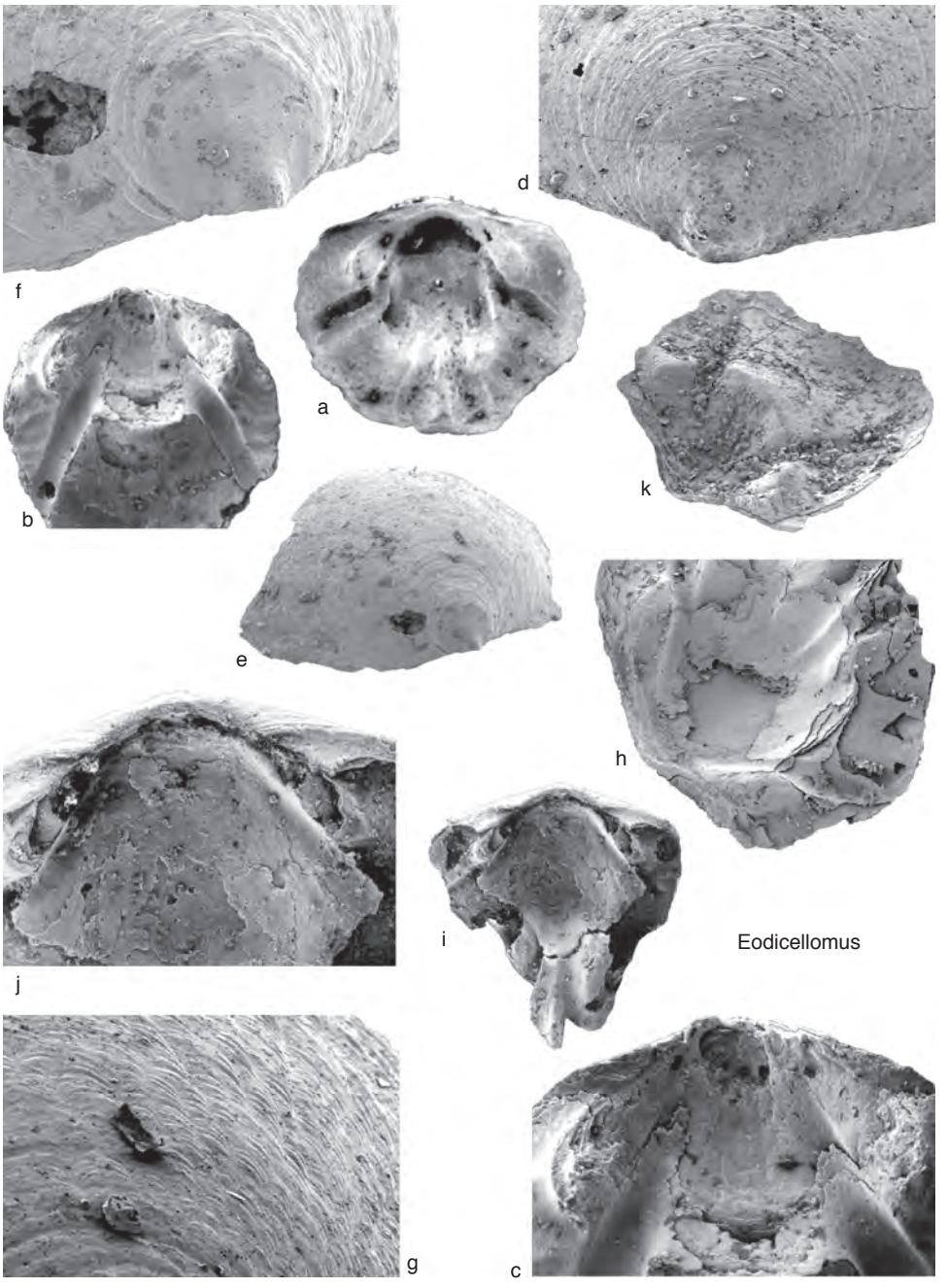



FIG. 1673. Obolidae (p. 2536).

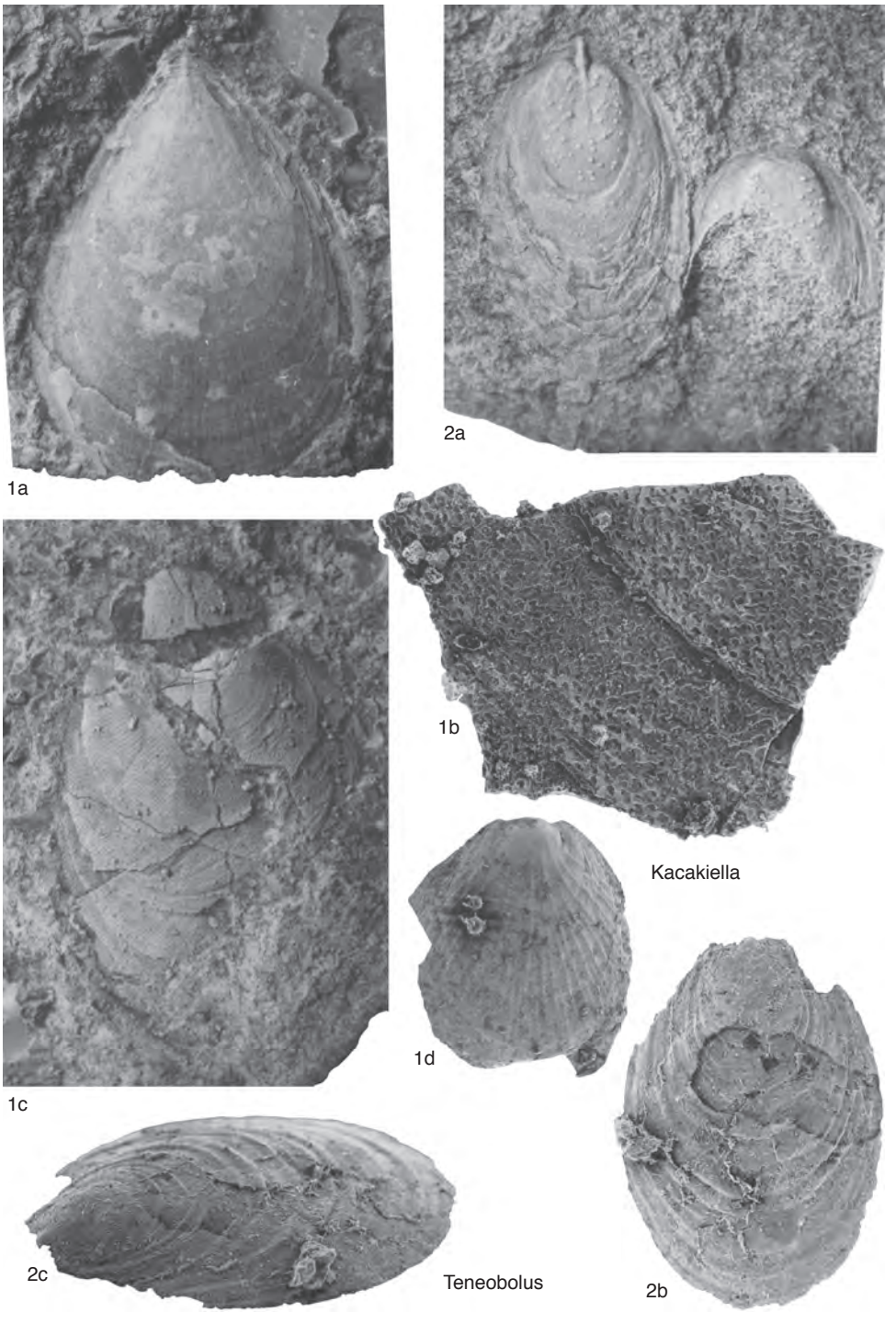



FIG. 1674. Obolidae (p. 2536–2542).

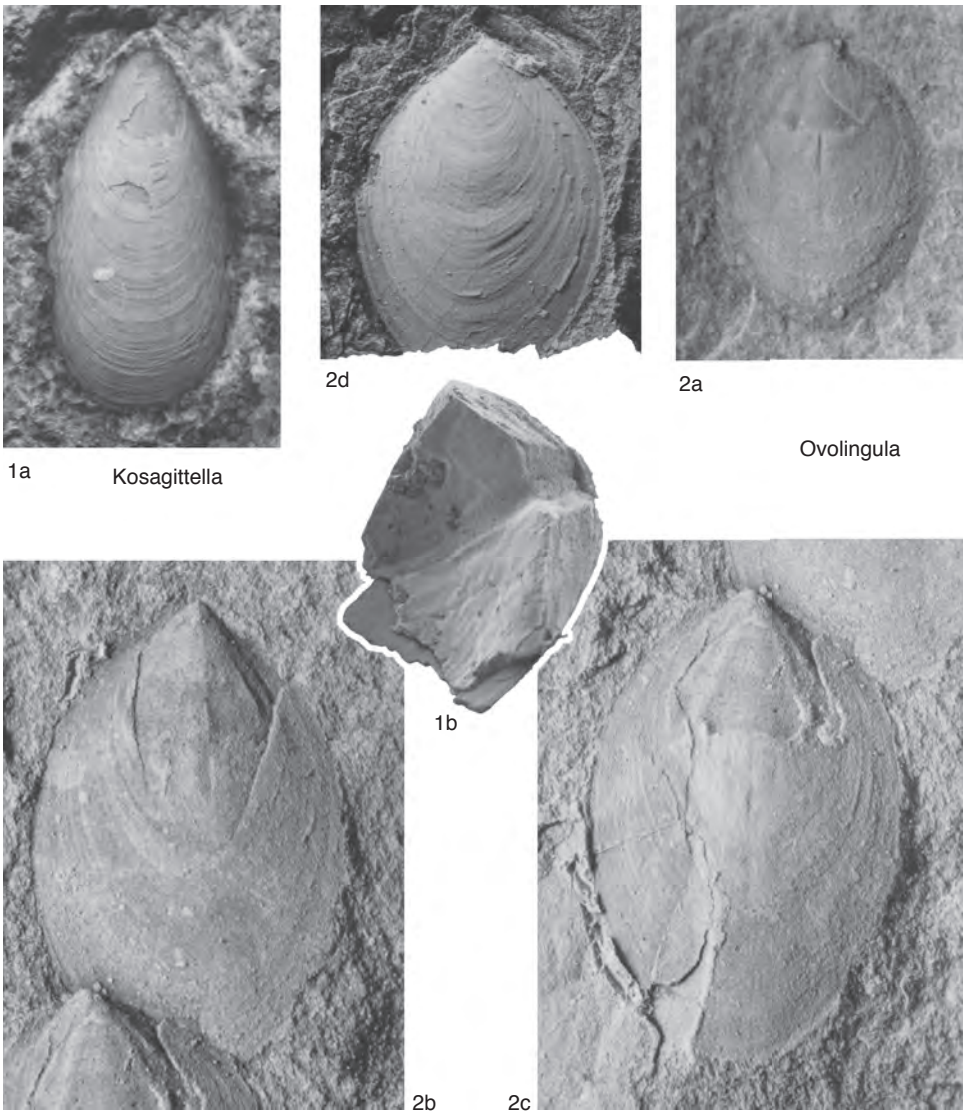



FIG. 1675. Obolidae (p. 2541–2542).

with divaricate ornamentation, PCZCU505, ×8; *d*, juvenile shell with radial ribs, PCZCU, ×40 (new). [Michal Mergl]

**Kosagittella** MERGL, 2001a, p. 11 [**K. clara*; OD]. Shell small, equibiconvex, elongate oval; ventral pseudointerarea small, orthocline; pedicle groove short, shallow; dorsal pseudointerarea short, with wide median groove and small propareas; dorsal *vascula media* subparallel, long, deeply impressed. *Silurian (Ludlow)–Devonian (Eifelian)*: Bohemia. ——FIG. 1675,*1a–b*. **K. clara*, Kopanina Formation, Ludlow, Králův Dvůr, Dlouhá hora; *a*, holotype, ventral valve exterior, NML34253, ×8; *b*, oblique lateral view of ventral pseudointerarea, PCZCU193, ×60 (new). [Michal Mergl]

**Libecoviella** MERGL, 1997a, p. 132 [**Lingula arachne* BARRANDE, 1879, pl. 111; OD]. Shell subacuminate, subtriangular to elongate oval, inequivalved; ornamentation of fine terrace lines, in posteromedian part arranged in divaricate pattern, anterolaterally and anteriorly with zigzag pattern; ventral pseudointerarea small, undercut, flexure lines poorly defined, pedicle groove parallel sided, deep, short; dorsal pseudointerarea short, with

broad median groove; visceral field and muscle scars weakly impressed; ventral *vascula lateralia* broad, submarginal. Dorsal *vascula media* narrow, divergent. *Ordovician (Tremadoc):* Bohemia.——FIG. 1676,*1a–c*. **L. arachne* (BARRANDE), Třenice Formation, Libečov; *a*, dorsal valve exterior, latex cast, SBMNL32018, ×4; *b*, fragmentary ventral valve interior, SBNML32021, ×4; *c*, fragmentary dorsal valve interior, SBNML32020, ×4 (new). [Michal Mergl]

**Lithobolus** MERGL, 1996a, p. 45 [**L. plebeius*; OD]. Shell dorsibiconvex, elongate suboval; ventral pseudointerarea raised, lacking flexure lines; pedicle groove deep, broadly triangular; ventral visceral area poorly defined; dorsal pseudointerarea mainly occupied by median groove; interior of both valves with large pits. *Ordovician (Arenig)*: Bohemia.——FIG. 1671,*1a–c*. **L. plebeius*, Klabava Formation, Prague Basin, Ejpovice, Bukov; *a–b*, holotype, internal mold of ventral valve, latex cast of ventral valve external mold, MBHR66787, ×8; *c*, dorsal valve interior, MBHR66785, ×10 (new). [Michal Mergl]

**Mytoella** MERGL, 2002, p. 28 [**M. krafti*; OD]. Shell strongly biconvex for subfamily, small, thin shelled; ventral pseudointerarea low with distinct flexure lines; pedicle groove narrow and long; dorsal pseudointerarea short, with broad median groove; vascular markings obscure. *Ordovician (Llanvirn):* Bohemia.——FIG. 1677*a–e*. **M. krafti*, Šárka Formation, Osek, Mýto; *a*, holotype, internal mold of ventral valve, ×10; *b,* detail of ventral pseudointerarea, ×13; *c,* external mold of ventral valve, PCZCU557, ×10; *d*, dorsal valve exterior, PCZU556, ×4.8; *e*, internal mold of dorsal valve, PCZCU566, ×7.8 (new). [Michal Mergl]

**Ovolingula** MERGL, 1998, p. 225 [**Lingula ovum* BARRANDE, 1879, pl. 194; OD]. Shell elongate elliptical, biconvex; pseudointerareas of both valves minute; pedicle groove narrow and shallow; ventral visceral area with raised transverse platform; dorsal visceral area with large, triangular, raised platform, anteriorly supported by thin and long median septum. *Ordovician (Ashgill):* Bohemia, Ireland.——FIG. 1675,*2a–d*. **O. ovum* (BARRANDE), Králův Dvůr Formation, Bohemia; *a*, lectotype, internal mold of dorsal valve, SBNML25973, ×9; *b*, internal mold of ventral valve, MBHR1986, ×9; *c*, internal mold of dorsal valve, MBHR1986, ×9; *d*, ventral valve exterior, MBHR1989, ×9 (new). [Michal Mergl]

**Pidiobolus** MERGL, 1995, p. 103 [**P. minimus*; OD]. Shell thickened, strongly biconvex, minute, subcircular; exterior with fine pitting; ventral pseudointerarea undercut with deep and broad pedicle groove; dorsal pseudointerarea with broad median groove and minute propareas; dorsal central muscle scars large, spindle shaped. *Ordovician (Tremadoc–Arenig):* Bohemia.——FIG. 1678*a–g*. **P. minimus*, Klabava Formation, Arenig, Olešná Beds Member, Těně; *a*, ventral valve exterior, ×60; *b*, detail of pitted ornamentation, ×300; *c*, ventral valve interior, PCZCU607, ×60; *d*, detail of ventral pseudointerarea, ×160; *e*, oblique lateral view of ventral valve interior, PCZCU609, ×85; *f*, dorsal valve exterior, PCZCU608, ×60; *g*, oblique posterior view of dorsal valve exterior, PCZCU611, ×60 (new). [Michal Mergl]

**Teneobolus** MERGL, 1995, p. 104 [**T. gracilis*; OD]. Shell equally biconvex, elongate oval, smooth; ventral pseudointerarea with growth lines curved forward along narrow, deep, anteriorly projecting pedicle groove. *Ordovician (Arenig)*: Bohemia.——FIG. 1674,*2a–c*. **T. gracilis*, Klabava Formation, Olešná Beds Member, Těně; *a*, holotype, complete specimen with detached valves, internal mold of ventral (right) and dorsal (left) valves, MM512, ×10; *b*, juvenile dorsal valve exterior, ×55; *c*, oblique posterior view, PCZCU551, ×65 (new). [Michal Mergl]

**Wadiglossella** HAVLÍČEK, 1995, p. 55 [**W. odiosa*; OD; =*Lingula carens* BARRANDE, 1879, pl. 103] [=*Careniellus* MERGL, 2001a, p. 9 (type, *Lingula carens* BARRANDE, 1879, pl. 103; OD)]. Shell weakly equibiconvex, broadly oval; ornament of fine growth lines superposed on coarser fila; ventral pseudointerarea high and very short, with shallow pedicle groove; dorsal pseudointerarea short, undivided. *Silurian (Llandovery)–Devonian (Pragian):* Bohemia.——FIG. 1676,*2a–b*. **W. carens* (BARRANDE), Motol Formation, Wenlock, Loděnice, Černidla; *a*, lectotype, ventral valve interior, SBNML24458, ×8; *b*, dorsal valve exterior, SBNML24457, ×8 (new). [Michal Mergl]

**Wosekella** MERGL, 2002, p. 29 [**Lingula debilis* BARRANDE, 1879, pl. 102; OD]. Shell equibiconvex; ornamentation smooth medianly, with numerous radial plications and oblique wavy fila laterally; ventral pseudointerarea with flexure lines; pedicle groove long and deep; dorsal pseudointerarea with broad median groove; visceral area large but poorly defined. *Ordovician (Arenig–Llanvirn)*: Bohemia.——FIG. 1679*a–e*. **W. debilis* (BARRANDE), Šárka Formation, Llanvirn, Osek, Mýto, Bohemia; *a*, ventral external mold, latex cast, PCZCU573, ×7.8; *b*, external mold, latex cast showing ornamentation, PCZCU577, ×25; *c*, internal mold of ventral valve, PCZCU571, ×7.8; *d*, internal mold of dorsal valve, PCZCU572, ×7.8; *e*, internal mold of dorsal valve, PCZCU570, ×7.8 (new). [Michal Mergl]

## Subfamily GLOSSELLINAE Cooper, 1956

**Barrandeoglossa** MERGL, 2001a, p. 14 [**Lingula fissurata* BARRANDE, 1879, pl. 103; OD]. Shell equibiconvex; ornament of fine, elevated, sometimes wavy concentric fila; ventral pseudointerarea narrow, subtriangular, with deep, short pedicle groove; dorsal pseudointerarea absent; dorsal interior with median ridge. *Silurian (Ludlow)–Devonian*

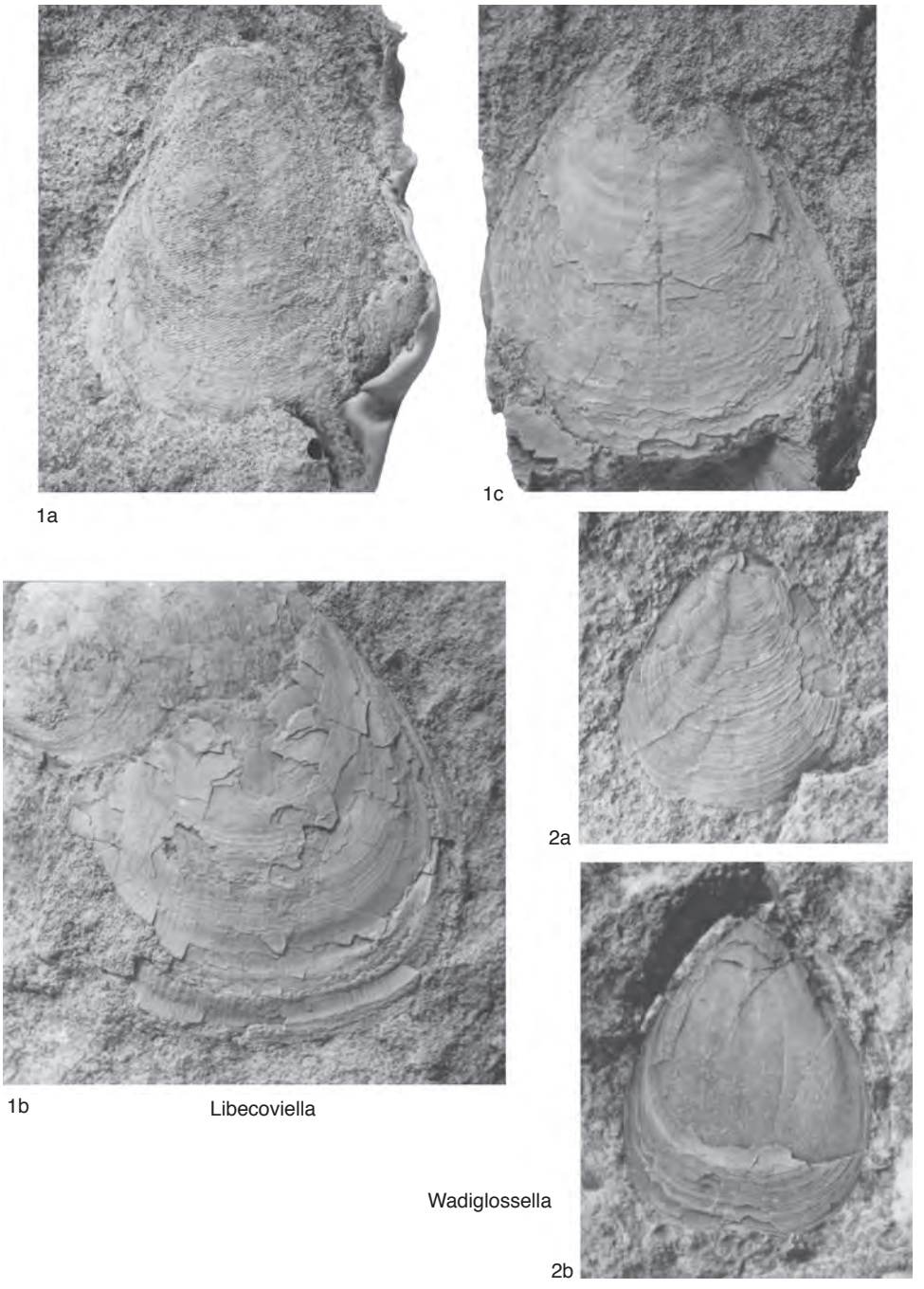



FIG. 1676. Obolidae (p. 2541–2542).

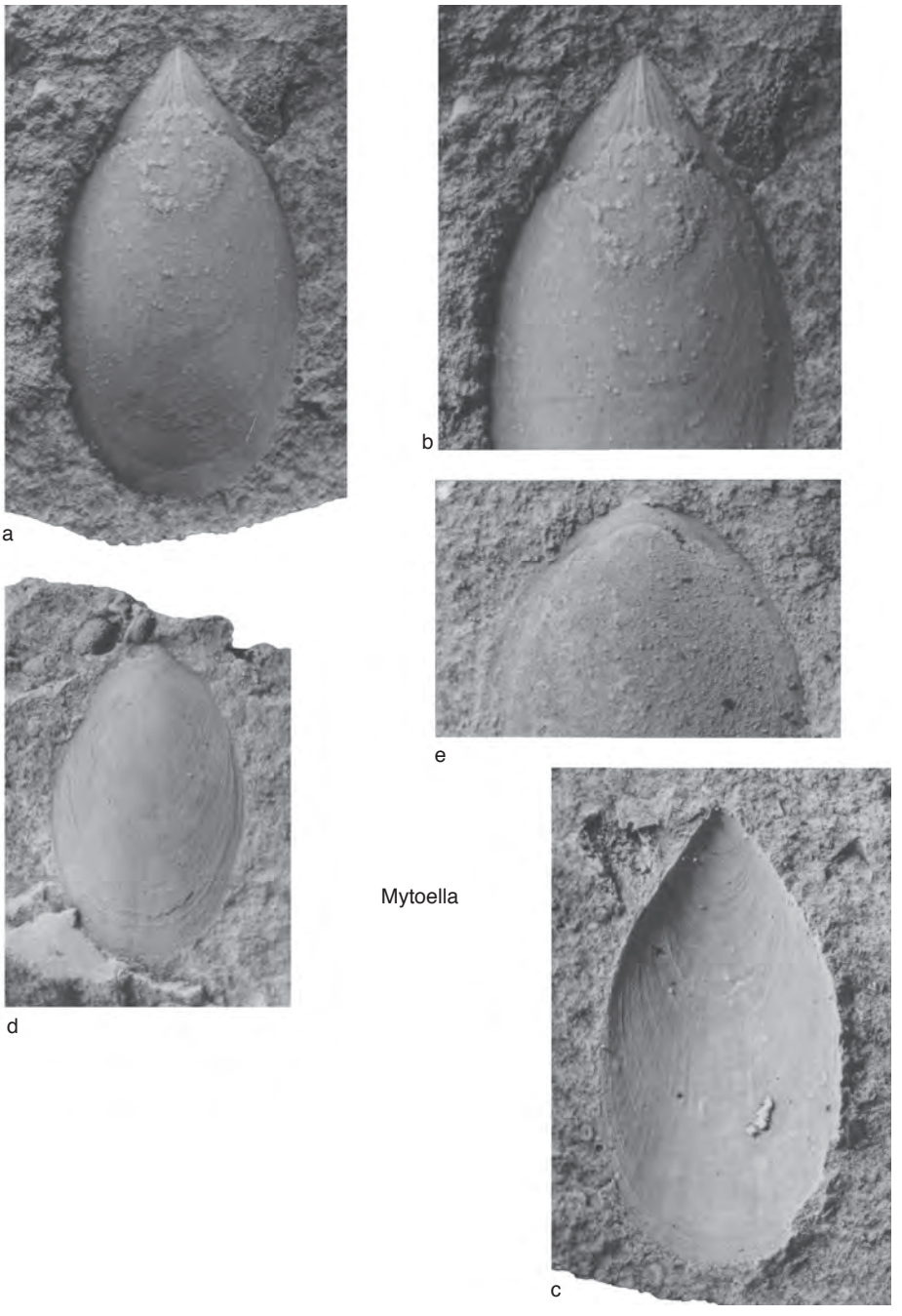



FIG. 1677. Obolidae (p. 2542).

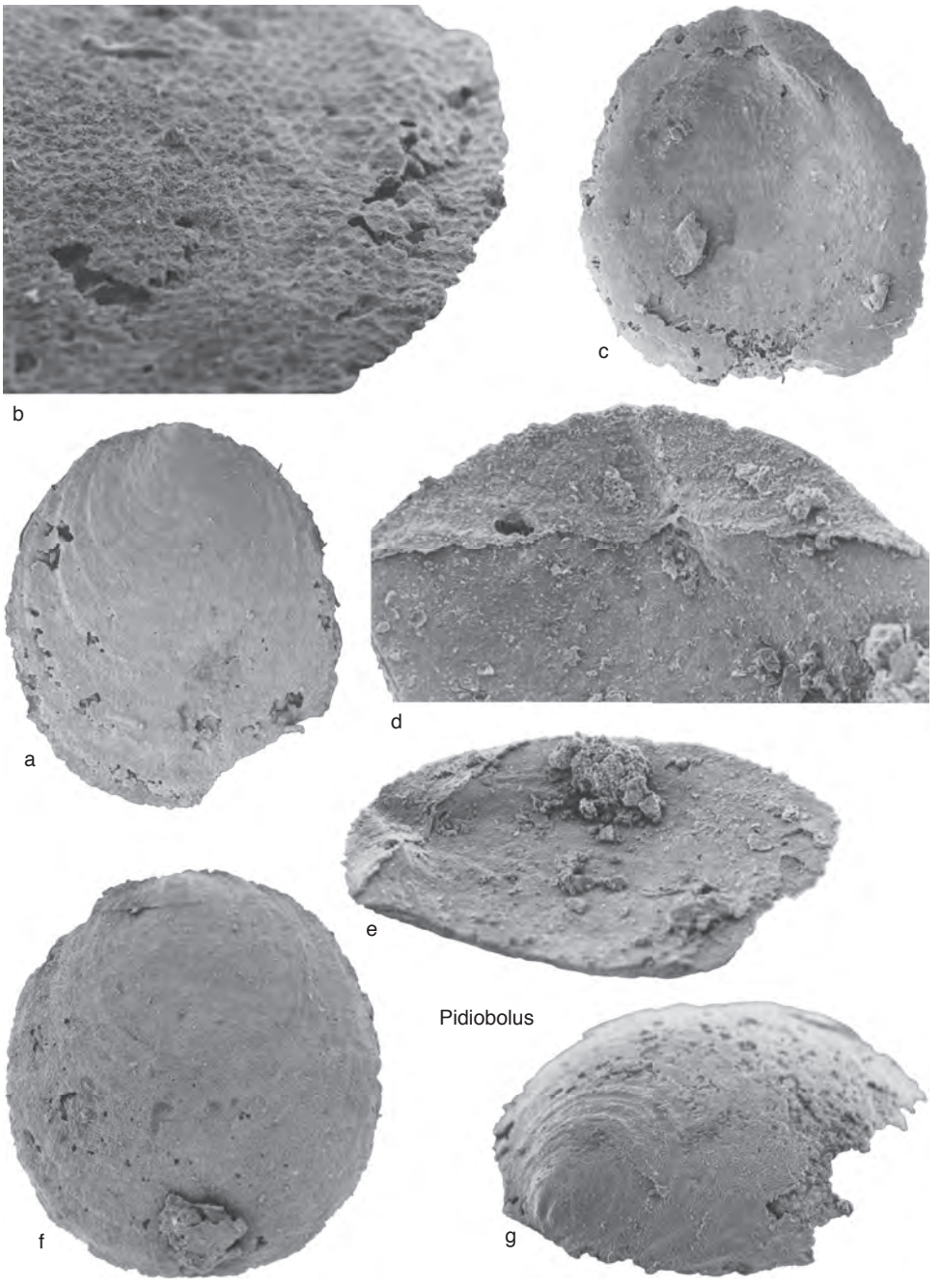



FIG. 1678. Obolidae (p. 2542).

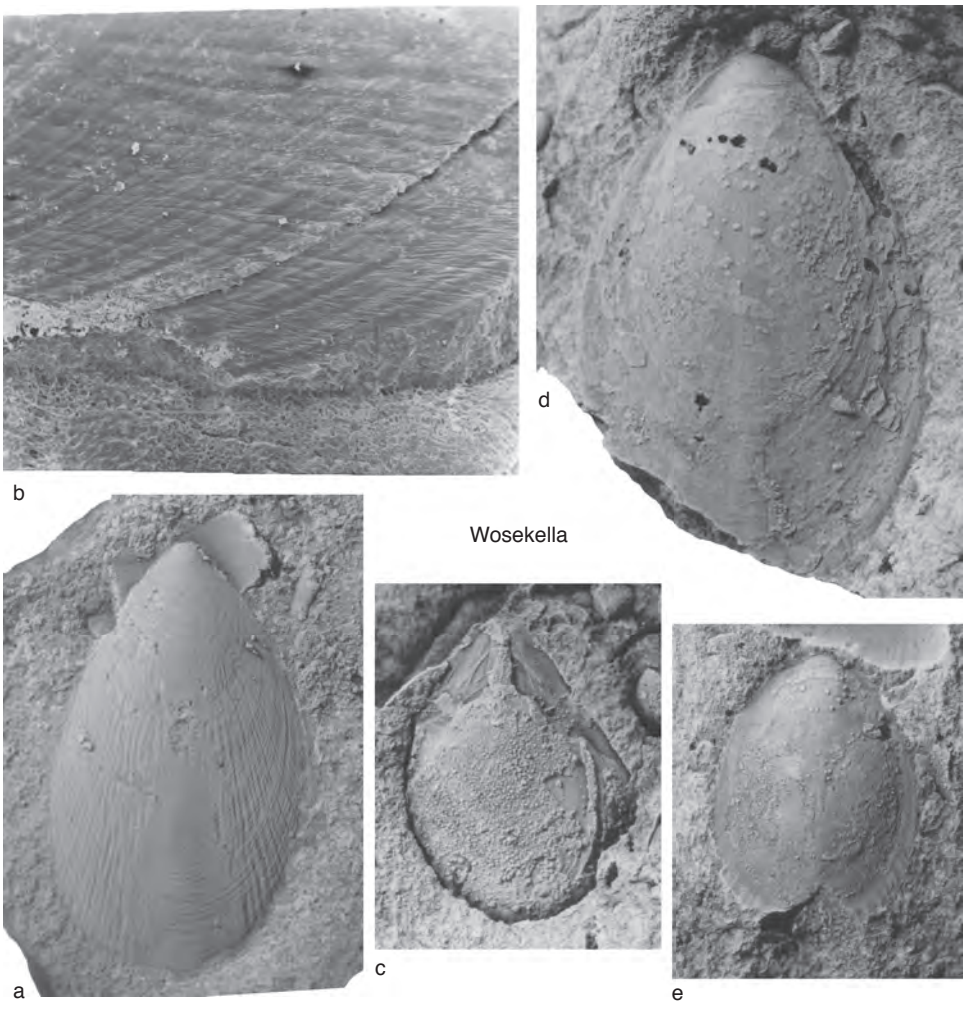



FIG. 1679. Obolidae (p. 2542).

*(Lochkovian)*: Bohemia.——FIG. 1680*a–c*. **B. fissurata* (BARRANDE), Motol Formation, Wenlock, Beroun, Ratinka, and Svatý Jan pod Skalou; *a*, ventral valve interior, SBNML34251, ×5; *b*, dorsal valve interior, SBNML73198, ×5.5; *c*, detail of ornamentation, PCZCU206, ×30 (new). [Michal Mergl]

**Prastavia** MERGL, 2001a, p. 13 [**P. distincta*; OD]. Shell equibiconvex; ornament of discontinuous, elevated concentric fila; ventral pseudointerarea small, low, with shallow pedicle groove; dorsal pseudointerarea absent; visceral area of both valves prominent and thickened; ventral *vascula lateralia* with deeply impressed secondary branches. *Middle Devonian (Eifelian):* Bohemia.——FIG. 1681*a–f*. **P. distincta*, Choteč Formation, Praha–Holyně, Prastav; *a*, ventral valve interior, ×30; *b*, oblique lateral view, PCZCU238, ×38; *c*, holotype, ventral valve interior, ×30; *d*, oblique lateral view, PCZCU237, ×38; *e*, dorsal valve exterior, PCZCU197, ×30; *f*, oblique lateral view of dorsal valve interior, PCZCU235, ×45 (new). [Michal Mergl]

## Subfamily ELLIPTOGLOSSINAE Popov & Holmer, 1994

[incl. Litoperatidae SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 54]

**Litoperata** SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 55 [**L. agolensis*; OD]. Shell weakly biconvex, elongate oval, with hemiperipheral growth; umbo of both valves marginal; ornament of strong, evenly spaced concentric rugellae; muscle

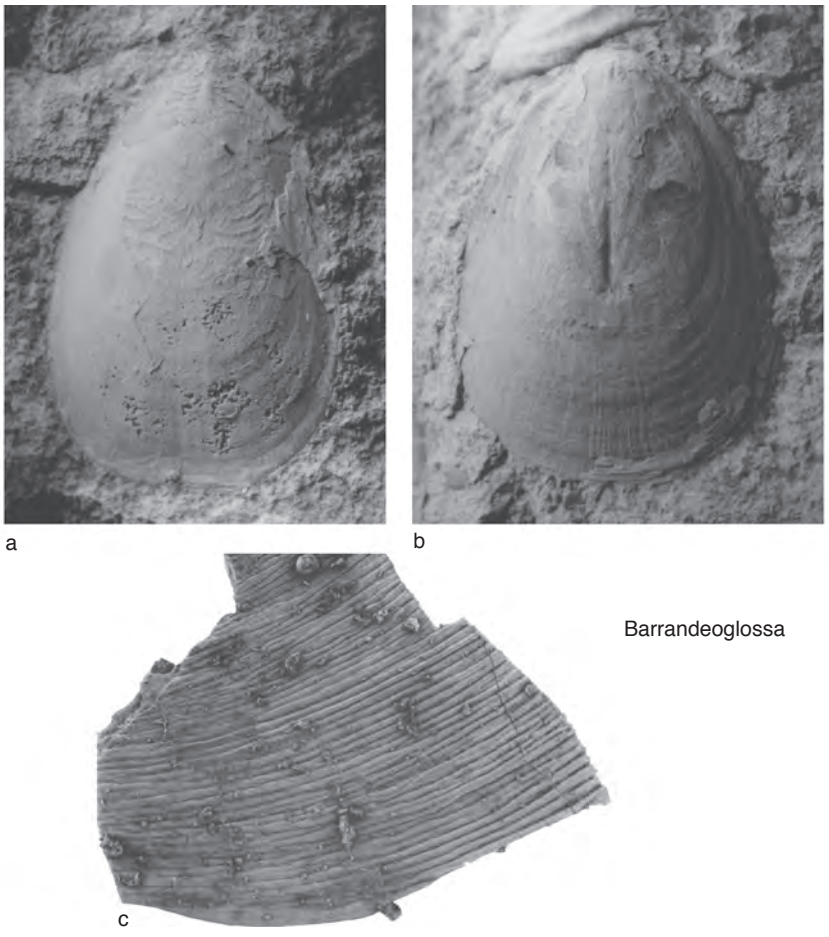



FIG. 1680. Obolidae (p. 2542–2546).

scars and mantle canals not impressed. *Ordovician (Llandeilo–Ashgill): Llandeilo,* Great Britain; *Ashgill,* Sweden.——FIG. 1682*a–d*. **L. agolensis*, Golden Groove Group, Llandeilo, Carmarthenshire, Great Britain; *a*, possible ventral valve exterior, NMW 96.8G.80, ×20; *b*, possible ventral valve interior, NMW 96.8G.803, ×20; *c*, possible dorsal valve exterior, NMW 96.8G.105, ×40; *d*, possible dorsal valve interior, ×40 (Sutton, Bassett, & Cherns, 1999).

## Family ZHANATELLIDAE Koneva, 1986

**Fagusella** MERGL, 1996a, p. 46 [**F. indelibata*; OD]. Shell dorsibiconvex to convexoconcave; rugellose ornamentation; ventral pseudointerarea short, steeply apsacline, with broad and deep pedicle groove terminated posteriorly by large rounded subtriangular emarginature; dorsal pseudointerarea undivided, slightly raised above valve floor; ventral interior with large visceral area, broadly rhomboidal in outline, extended anterior to midvalve; ventral anterolateral muscle fields deeply impressed; dorsal visceral field bordered laterally by low rim, with anterior projection extending anteriorly beyond midvalve; dorsal median ridge long, bisecting visceral area; dorsal anterior lateral muscle scars small, situated close to large central scars. *Ordovician (Arenig):* Bohemia.——FIG. 1683,*1a–b*. **F. indelibata*, Klabava Formation, Prague Basin, Bukov; *a*, oblique lateral view of dorsal valve exterior, MBHR66798, ×35; *b,* holotype, ventral valve interior, MBHR66790a, ×10 (new).

**Koneviella** USHATINSKAYA, 1997, p. 495 [**K. menensis*; OD]. Shell weakly biconvex, subcircular; ornament of slightly irregular concentric rugellae; larval and postlarval shell finely pitted with hemispherical pits of varying sizes; ventral valve with emarginature; propareas raised, flattened and bisected by flexure

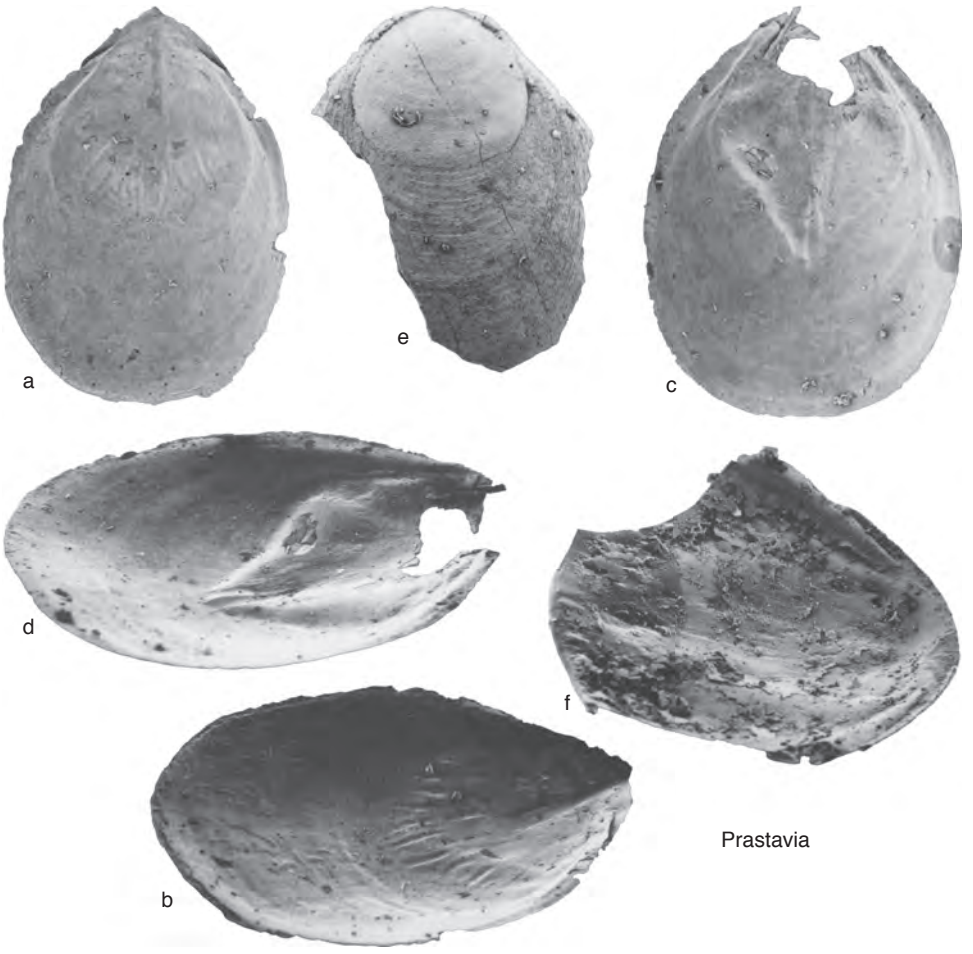



FIG. 1681. Obolidae (p. 2546).

lines, and with pitted ornamentation; pedicle groove deep; dorsal pseudointerarea low, occupied mainly by median groove; visceral areas and muscle scars of both valves weakly impressed; ventral mantle canals baculate with straight, divergent, subcentral *vascula lateralia*. *upper Middle Cambrian:* Russia (Siberia).——FIG. 1683,*2a–d*. **K. menensis*; Eirina Formation, *Glyptagnostus stolidotus* Biozone, Mene river, northcentral Siberia; *a*, holotype, ventral valve exterior, PIN4511/120, ×24; *b*, incomplete ventral valve interior, PIN4290/107, ×21; *c,* dorsal valve interior, ×30; *d,* pitted surface of dorsal propareas, PIN4511/122, ×700 (Ushatinskaya, 1997).

**Wahwahlingula** POPOV, HOLMER, & MILLER, 2002, p. 218 [**Lingula antiquissima* JEREMEJEW, 1856, p. 80; OD]. Shell slightly dorsibiconvex, elongate suboval to subtriangular; larval and postlarval shell with microornament of fine hemispherical pits; ventral pseudointerarea orthocline with narrow and shallow pedicle groove; propareas with flexure lines; dorsal pseudointerarea crescent shaped with rudimentary undivided propareas; ventral interior with weakly impressed visceral area bisected by pedicle nerve impression and baculate, submarginal *vascula lateralia*; dorsal interior with visceral area extending anterior to midvalve and bisected by fine median ridge; *vascular lateralia* marginal, arcuate; *vascular media* short, divergent. *Upper Cambrian–Ordovician (Tremadoc, ?Arenig):* northwestern Russia, western USA, ?Australia (Canning Basin).——FIG. 1683,*3a–e*. **W. antiquissima* (JEREMEJEW), Tosna Formation, Upper Cambrian, (*Cordylodus proavus* Biozone), Lava and Syas rivers, northwestern Russia; *a*, neotype, ventral valve exterior, CNIGR180/12348, ×3; *b*, ventral valve interior, CNIGR182/12348, ×11; *c*, dorsal valve interior, CNIGR12348, ×10; *d*, surface microornament, ×500; *e,* detail of pitted microornament, GLAHM 101691, ×800 (Popov, Holmer, & Miller, 2002).

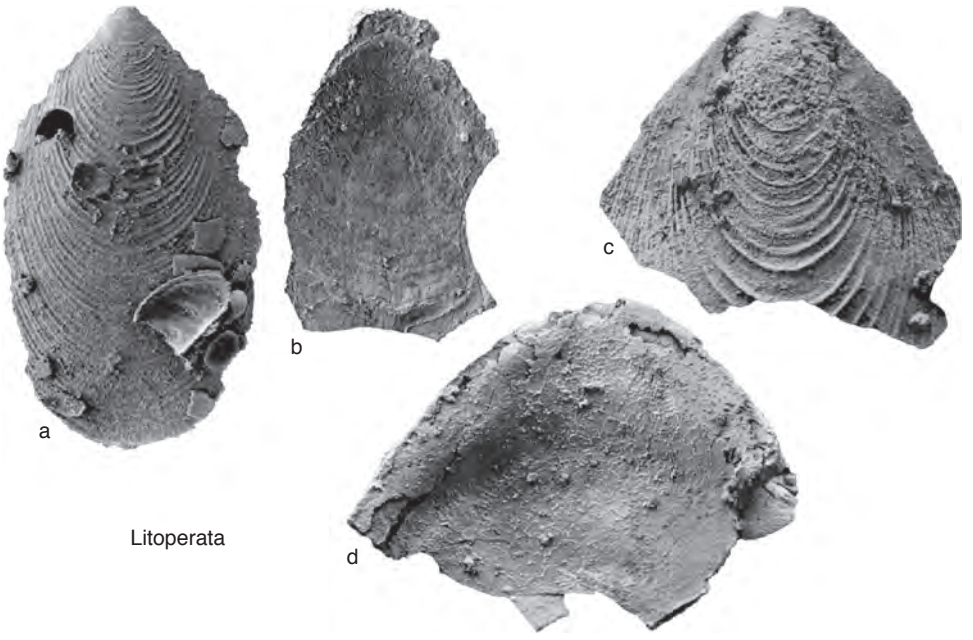



FIG. 1682. Obolidae (p. 2546–2547).

## Family PATERULIDAE Cooper, 1956

**Diencobolus** HOLMER & others, 2001, p. 65 [**D. simplex*; OD]. Shell weakly biconvex, equivalved, elongate oval to subcircular; both valves with holoperipheral growth and eccentric to submarginal umbo; both valves lacking pseudointerareas and pedicle notch; larval and postlarval shell finely pitted with subcircular to subelliptical pits of varying sizes; ventral valve with weakly impressed visceral area, occupying median part of valve posterior to midlength; dorsal interior with a low median ridge widening anteriorly and bearing small, elongate suboval anterior lateral muscle scars at posterior end; central muscle scars large, suboval, at midvalve, lateral to median ridge. *Middle Cambrian–Lower Ordovician (Tremadoc–early Arenig)*: Kazakhstan (Malyi Karatau), Kyrgyzstan, Poland.——FIG. 1684,*2a–h. *D. simplex*, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty, Kazakhstan; *a*, holotype, dorsal valve interior, IGNA427/87, ×13; *b–c*, dorsal valve exterior, oblique lateral view, ×43; *d,* detail of larval shell, ×140; *e,* microornament of larval shell, ×650; *f,* microornament of postlarval shell, NMW98.61G.55, ×1088; *g*, ventral valve interior, IGNA427/729, ×23; *h*, dorsal valve interior, IGNA427/730, ×32 (Holmer & others, 2001).

**Eopaterula** SUTTON in SUTTON, BASSETT, & CHERNS, 2000, p. 73 [**E. curtisi*; OD]. Shell subcircular to elongate suboval; ventral valve acuminate; true pseudointerareas lacking in both valves, but with thickened posterior margins, not differentiated from limbus; ventral thickened posterior margin, with narrow, subtriangular pedicle depression; dorsal thickened margin, with wide subtriangular to semicircular median depression. *Ordovician (Tremadoc):* England.——FIG. 1685*a–f. *E. curtisi*, Micklewood Formation, Tortworth Inlier, Gloucestershire; *a*, holotype, internal mold of ventral valve, latex cast, CMBCc1679, ×15; *b*, internal mold of ventral valve, CMBCc1632a, ×15; *c*, exfoliated ventral valve, CMBCc1631b, ×10; *d*, exfoliated possible ventral valve, CMBCc1678a, ×15; *e*, internal mold of dorsal valve, CMBCc1661a, ×15; *f,* internal mold of dorsal valve, latex cast, CMBCc1654a, ×15 (Sutton, Bassett, & Cherns, 2000).

**Tarphyteina** SUTTON in SUTTON, BASSETT, & CHERNS, 2000, p. 74 [**T. taylorae*; OD]. Shell elongate suboval; true pseudointerareas lacking in both valves, but with thickened posterior margins; ventral thickened posterior margin elongate; dorsal thickened margin short, undivided. *Ordovician (Llandeilo):* Wales.——FIG. 1684,*1a–e. *T. taylorae*, Golden Grove Group, upper Llandeilo, near Llandeilo, Carmarthenshire; *a*, holotype, ventral valve interior, NMW96.8G.109, ×40; *b*, ventral valve exterior, NMW96.8G.160, ×40; *c–d*, dorsal valve exterior, interior, NMW96.8G.108, ×40; *e*, detail of ornamentation, NMW96.8G.461, ×500 (Sutton, Bassett, & Cherns, 2000).

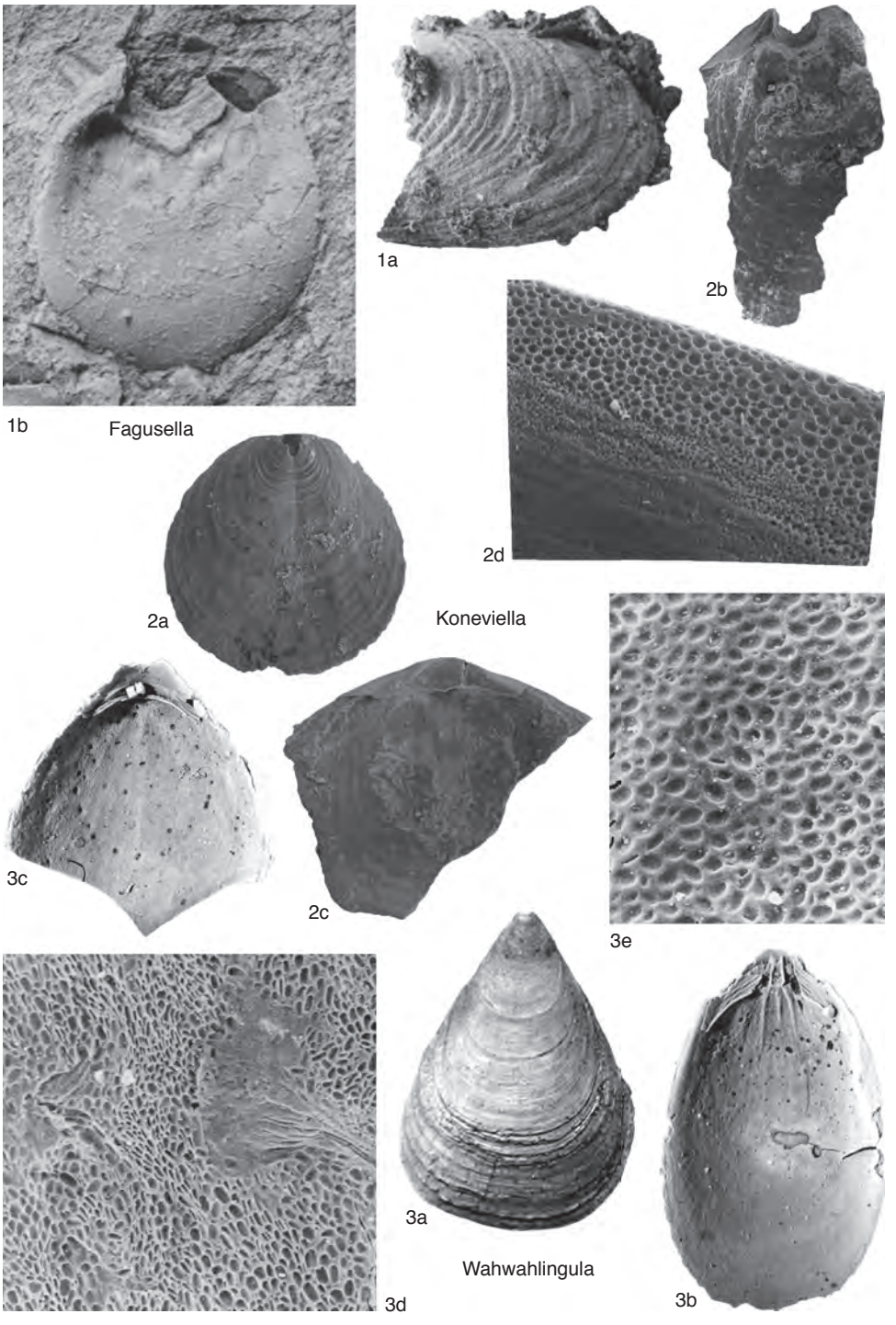



FIG. 1683. Zhanatellidae (p. 2547–2548).

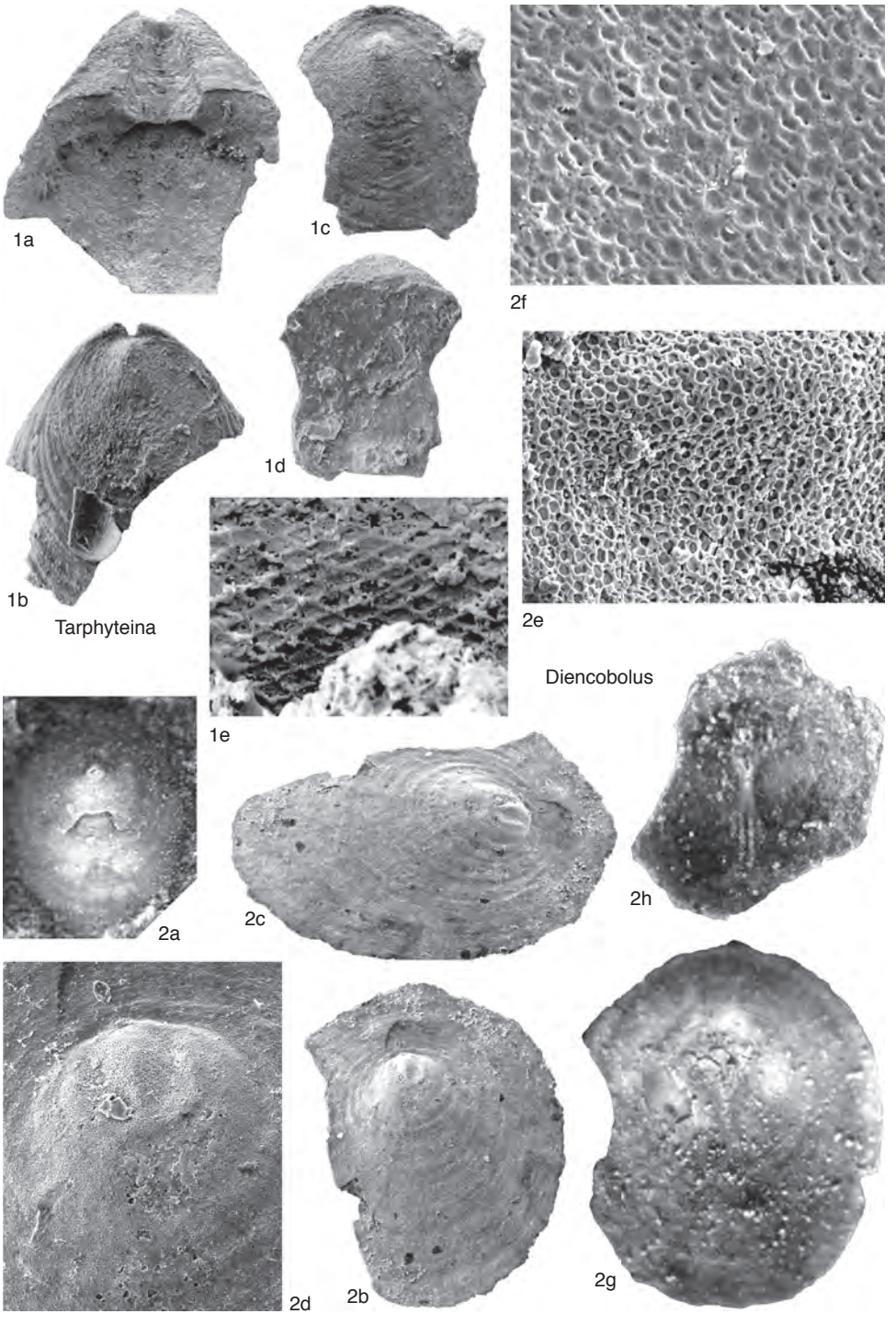



FIG. 1684. Paterulidae (p. 2549).

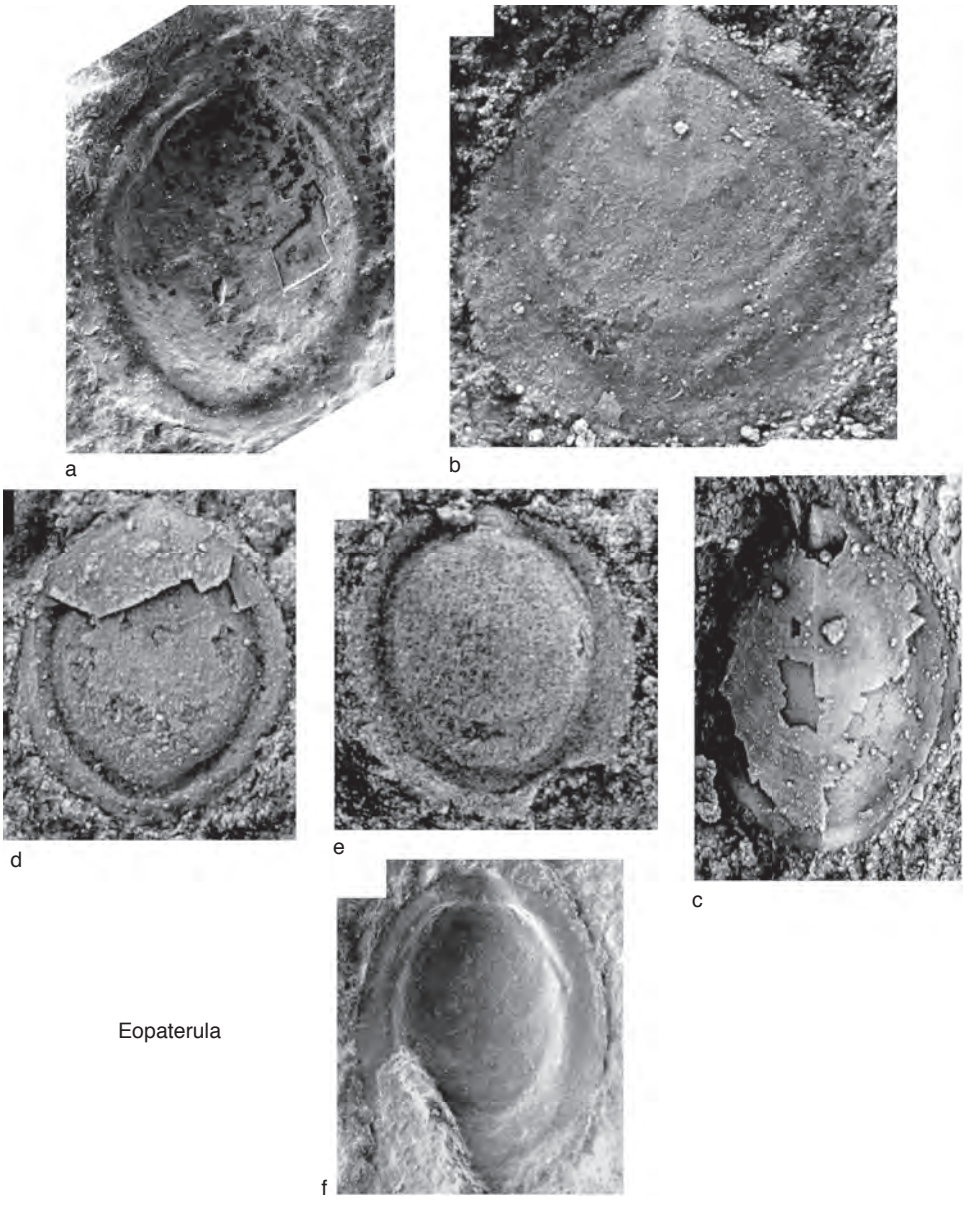



FIG. 1685. Paterulidae (p. 2549).

## Superfamily DISCINOIDEA Gray, 1840
### Family DISCINIDAE Gray, 1840

[incl. Ivanothelinae MERGL., 2001a, p. 25]

**Chynithele** HAVLÍČEK in HAVLÍČEK & VANĚK, 1996, pl. 101, case VIII, fig. 1 [**C. ventricona*; OD]. Ventral valve highly conical; dorsal valve flat; ornamentation with prominent rounded rugellae; external pedicle opening close to apex; listrium broad and short; muscle scars and mantle canals weakly impressed. *Lower Devonian (Emsian):* Bohemia.——FIG. 1686,*1a–e.* **C. ventricona*, Zlichov Formation, Chýnice Limestone, Bubovice, Čeřinka, Koněprusy, Zlatý Kůň, Voskop; *a*, ventral valve exterior, MBHR67654, ×10; *b*, internal mold of ventral valve, PCZCU516, ×10; *c*, ventral valve

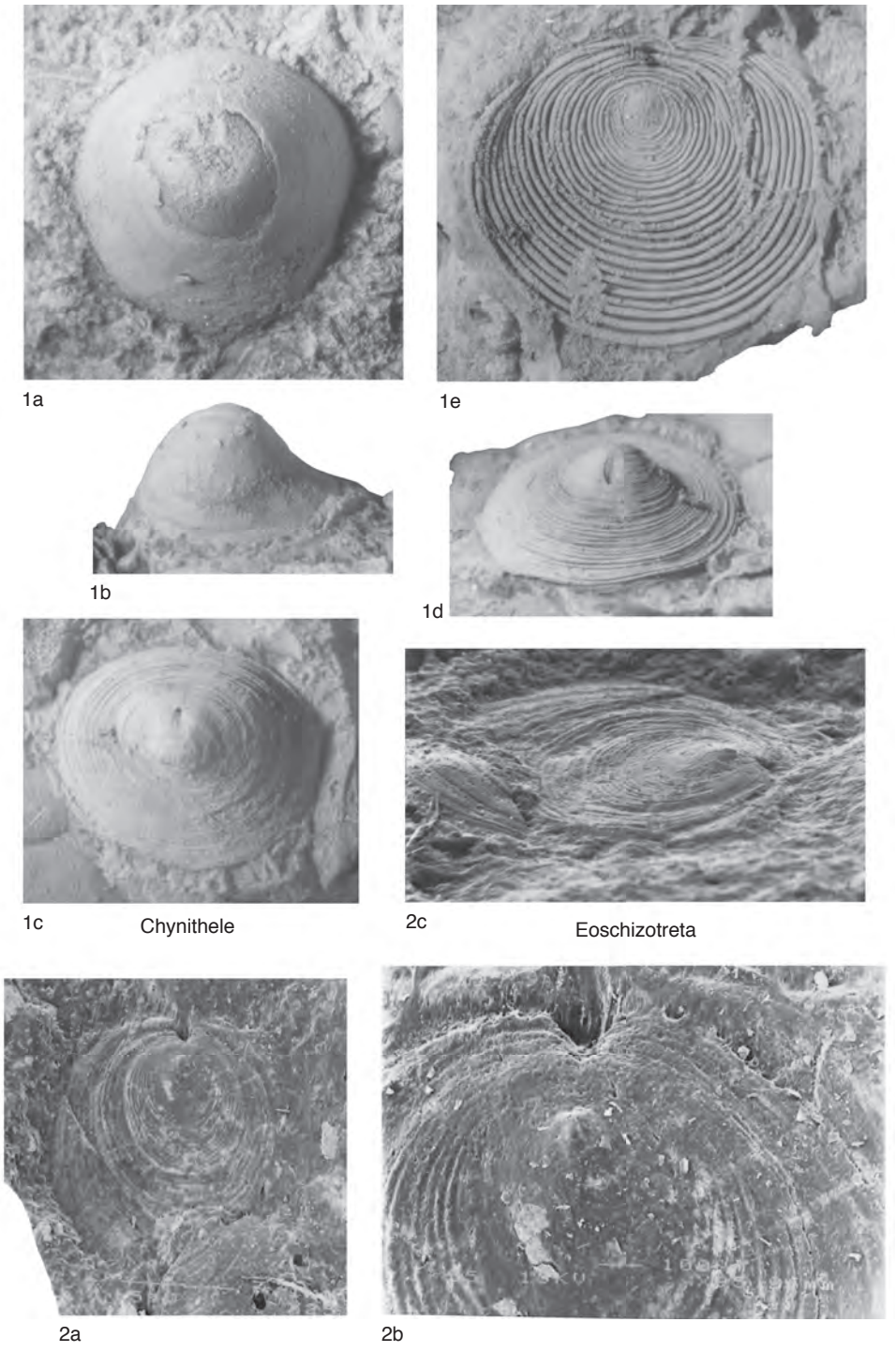



FIG. 1686. Discinidae (p. 2552–2555).

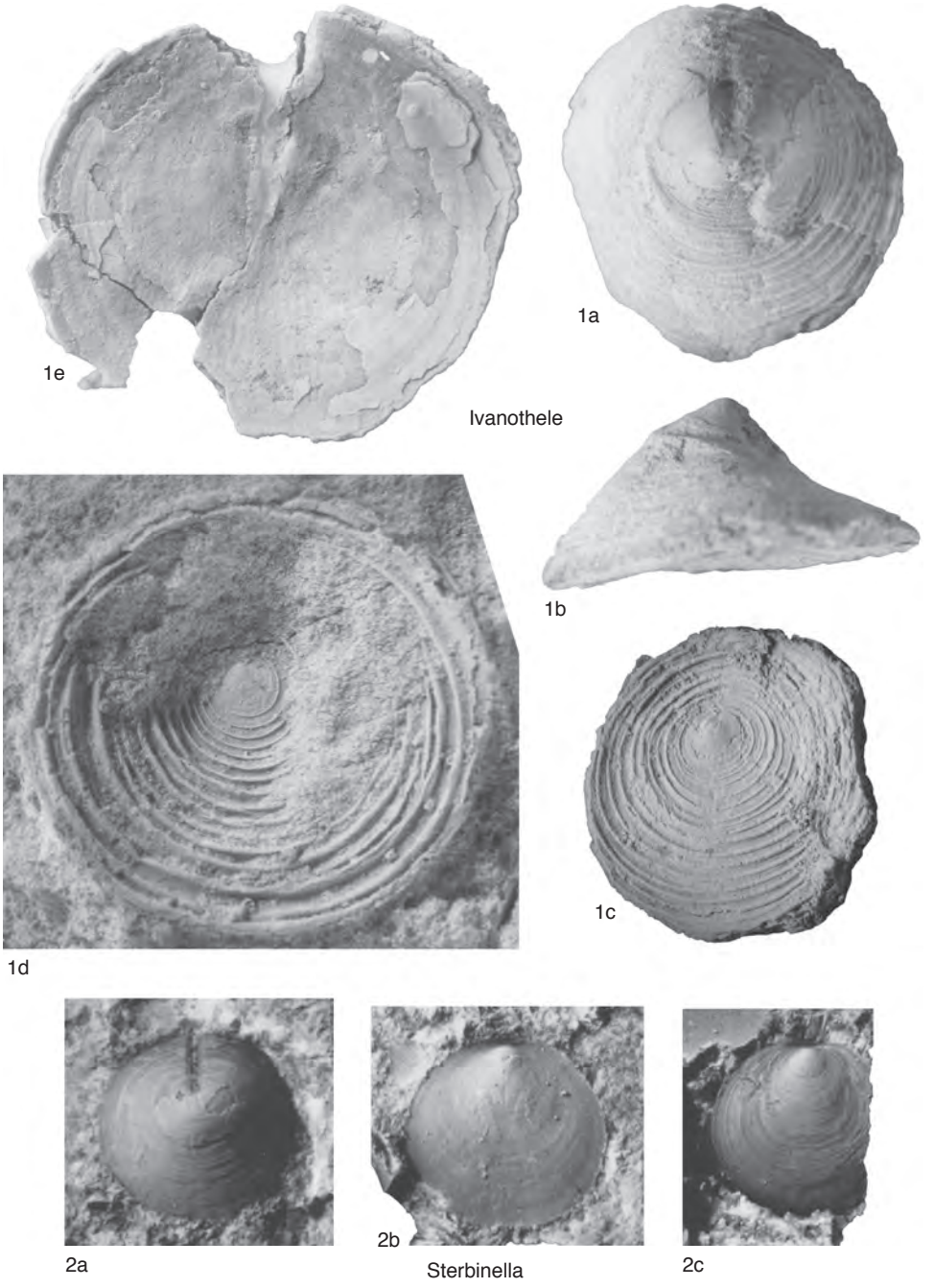



FIG. 1687. Discinidae (p. 2555–2556).

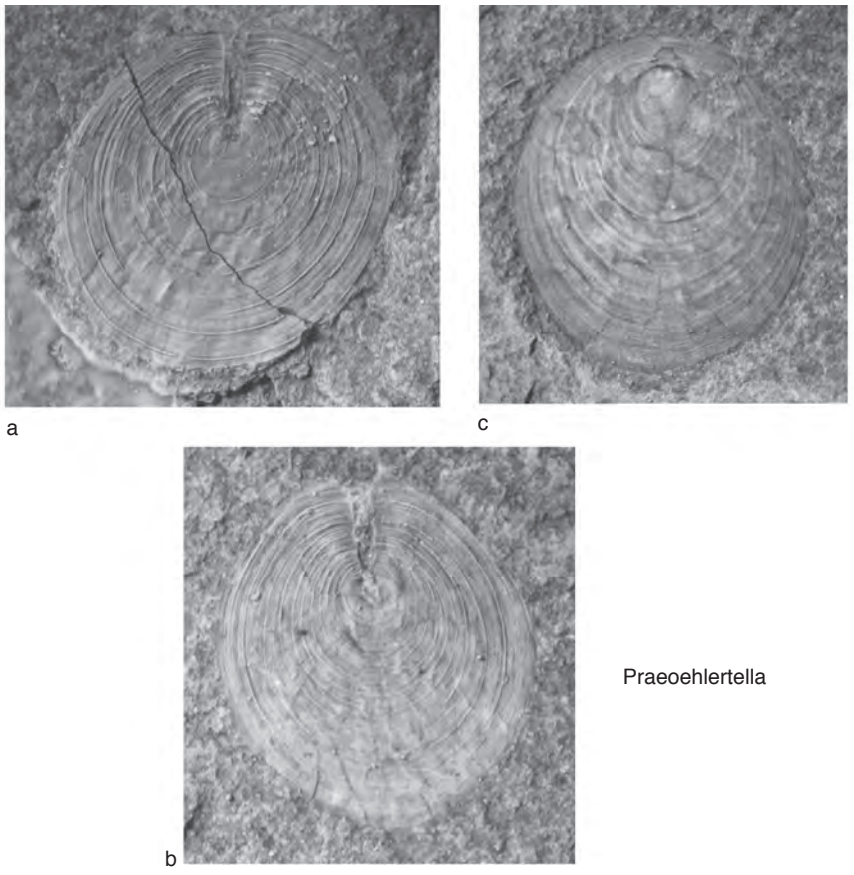



FIG. 1688. Discinidae (p. 2555–2556).

exterior, PCZCU518, ×10; *d*, oblique posterior view of ventral valve exterior, PCZCU518, ×10; *e*, dorsal valve exterior, PCZCU515, ×10 (new). [Michal Mergl]

**Eoschizotreta** MERGL, 2002, p. 46 [**E. veterna*; OD]. Shell with holoperipheral growth, weakly biconvex; pedicle notch short, broad, without distinct listrium; dorsal apex in posterior part of shell; ornament of fine concentric rugellae. *Ordovician (Arenig):* Bohemia.——FIG. 1686,*2a–c*. **E. veterna*, Klabava Formation, Hrádek; *a*, holotype, ventral valve exterior, latex cast, ×17; *b*, detail of umbo and pedicle notch, ×60; *c*, oblique lateral view, PCZCU629, ×23 (new). [Michal Mergl]

**Ivanothele** MERGL, 1996b, p. 123 [**I. mordor*, OD]. Shell planoconvex to concavoconvex, subcircular; exterior with coarse rugellae on both valves; ventral valve high, asymmetrically conical, with curved beak; pedicle track short, wide, mainly closed by listrium; internal tube thick walled, long and irregularly curved; dorsal valve with subcentral beak; dorsal visceral area large, at center of valve, with large anterior adductor muscle scars. *Silurian (Wenlock–Ludlow):* Bohemia.——FIG. 1687,*1a–e*. **I. mordor*, Kopanina Formation, Ludlow; *a–b*, holotype, ventral valve exterior, lateral view, ×5; *c*, dorsal valve exterior, MBHR19627, ×4; *d*, dorsal valve exterior, MM14a, ×5; *e*, dorsal valve interior, MM6a, ×5 (new). [Michal Mergl]

**Praeoehlertella** MERGL, 2001a, p. 28 [**P. umbrosa*; OD]. Shell elongate oval to subcircular, convexo-planar; ornamentation of fine, concentric, regularly spaced fila, passing into coarser, concentric rugellae; ventral valve with narrow pedicle track bordered

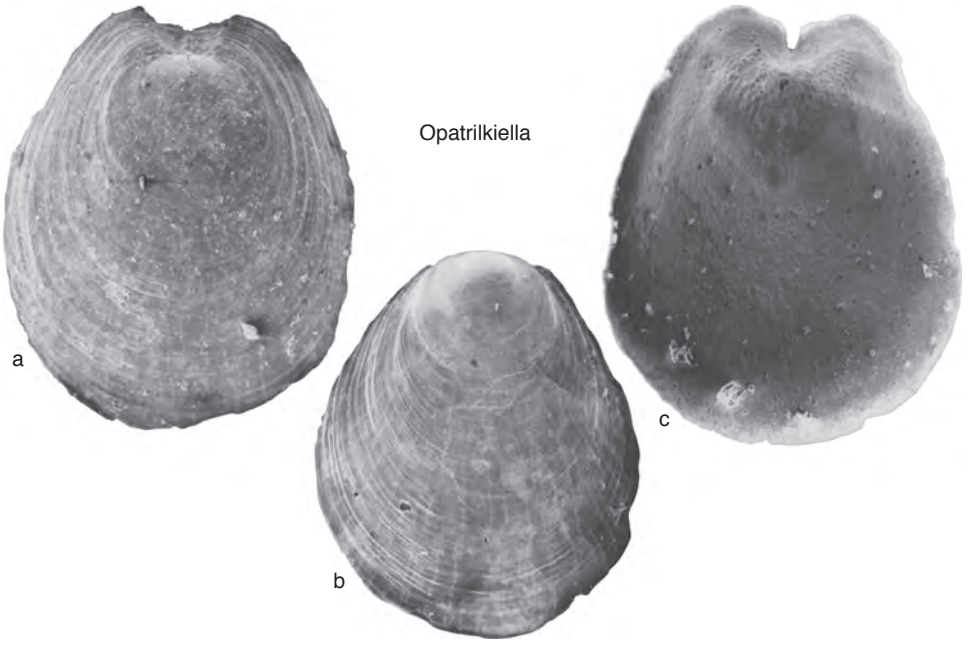



FIG. 1689. Trematidae (p. 2556).

by narrow bands; dorsal valve with submarginal apex. *Silurian (Llandovery)–Devonian (Pragian):* Bohemia.——FIG. 1688*a–c*. **P. umbrosa*, Praha Formation, Dvorce-Prokop Limestone, Pragian, Svatý Jan pod Skalou, Na stydlých vodách Quarry; *a*, holotype, ventral valve exterior, MBHR49779, ×9.5; *b*, ventral valve exterior, MBHR49775, ×9.5; *c*, dorsal valve exterior, MBHR49799, ×9.5 (new). [Michal Mergl]

**Sterbinella** MERGL, 2001a, p. 27 [**S. daphne*; OD]. Shell circular; ornamentation of fine concentric, slightly wavy fila; ventral valve depressed conical; dorsal valve flat with submarginal apex; pedicle track narrow, parallel sided, with narrow parallel slit. *Silurian (Přídoli)–Devonian (Famennian):* Bohemia, Poland.——FIG. 1687,*2a–c*. **S. daphne,* Požáry Formation, Přídoli, Králův Dvůr, Kosov Hill, Bohemia; *a*, ventral valve exterior, PCZCU525, ×13; *b*, dorsal valve exterior, PCZCU519, ×13; *c*, dorsal valve exterior, PCZCU522, ×13 (new). [Michal Mergl]

## Family TREMATIDAE Schuchert, 1893

**Opatrilkiella** MERGL, 2001a, p. 29 [**O. minuta*; OD]. Shell elongate oval, equibiconvex; pitted postlarval microornamentation with wavy radial trails of minute pits superimposed on very finely pitted surface; ventral valve with submarginal apex; ventral pseudointerarea triangular, with narrow pedicle slit and broad propareas; dorsal valve with submarginal apex; dorsal pseudointerarea absent. *Silurian (Přídoli)–Devonian (Famennian):* Bohemia, Poland.——FIG. 1689*a–c*. **O. minuta*, Požáry Formation, Přídoli, Praha-Holyně, Opatřilka Quarry, Bohemia; *a*, ventral valve exterior, PCZCU472, ×55; *b*, holotype, ventral valve interior, PCZCU130, ×50; *c*, dorsal valve exterior, PCZCU124, ×60 (new). [Michal Mergl]

## Family UNCERTAIN

**Pyrodiscus** LITTLE & others, 1999, p. 1056 [**P. lorrainae*; OD]. Genus poorly known; possible discinoid with suboval, uniplicate shell; both valves with mixoperipheral growth; narrow oval pedicle opening extending to posterior margin; listrium present. *?Silurian:* Russia (Orenburg district).

# Superfamily ACROTHELOIDEA Walcott & Schuchert in Walcott, 1908

## Family BOTSFORDIIDAE Schindewolf, 1955

**Curdus** HOLMER & USHATINSKAYA in USHATINSKAYA & HOLMER, 2001, p. 129 [**C. pararaensis*; OD].

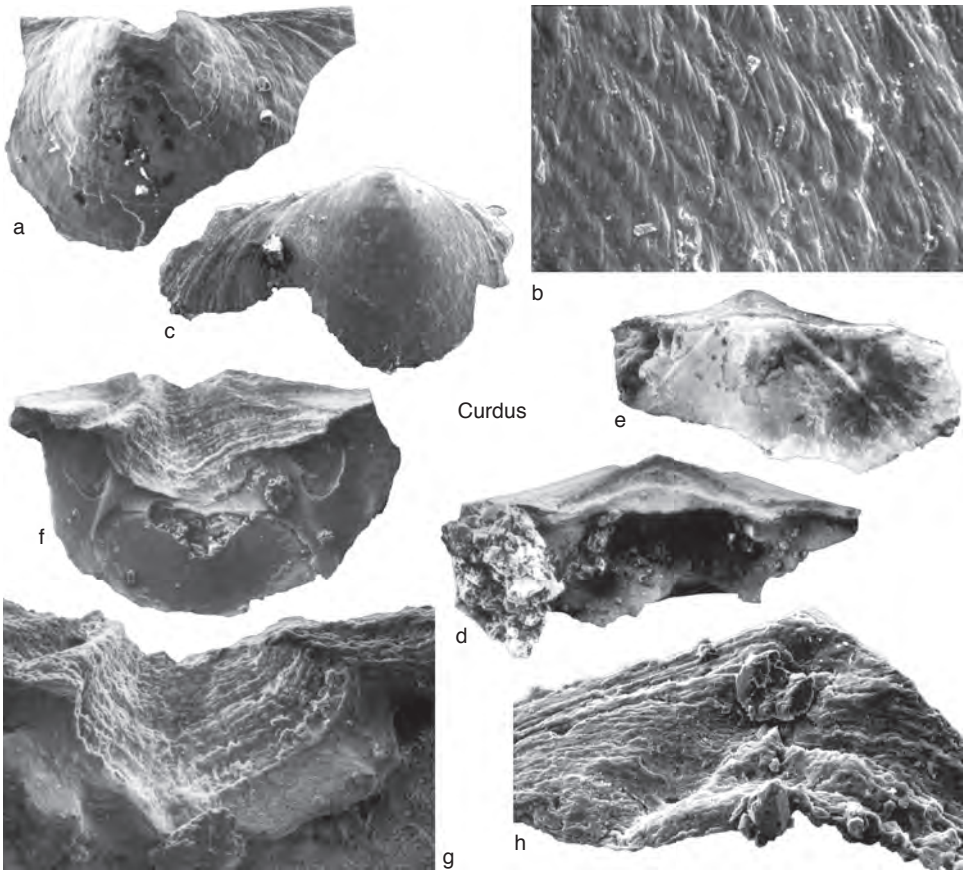



FIG. 1690. Botsfordiidae (p. 2556–2557).

Ventral valve with small umbonal notch; ventral pseudointerarea triangular, apsacline, divided by deep pedicle groove, forming triangular delthyrium; propareas long, with flexure lines; dorsal pseudointerarea anacline, with wide median groove; ornamentation of concentric growth lines, crossed by discontinuous wrinkles; ventral visceral field short, strongly thickened, with elevated posterolateral muscle scars; dorsal visceral field with low median ridge and pair of elongate posterolateral muscle scars; both valves with straight divergent *vascula lateralia*. *Lower Cambrian (Botomian):* South Australia.——FIG. 1690*a–h*. **C. pararaensis*, Koolywurtie Limestone, Yorke Peninsula; *a*, ventral valve exterior, ×24; *b*, detail of ornamentation, PIN4664/6207, ×160; *c*, dorsal valve exterior, PIN4664/6209, ×26; *d*, dorsal valve interior, PIN4664/6212, ×20; *e*, dorsal valve interior, PIN4664/6210, ×16; *f*, holotype, ventral valve interior, PIN4664/6211, ×24; *g*, detail of ventral pseudointerarea, PIN4664/6220, ×48; *h*, detail of dorsal pseudointerarea, PIN4664/6217, ×104 (Ushatinskaya & Holmer, 2001).

**Minlatonia** HOLMER & USHATINSKAYA in USHATINSKAYA & HOLMER, 2001, p. 130 [**M. tuckeri*; OD]. Ventral valve with pointed beak; ventral pseudointerarea apsacline, with triangular pedicle groove and long propareas; dorsal pseudointerarea anacline, flattened, with wide triangular median groove and low propareas; distinctive reticulate ornamentation, produced by intersecting radial and concentric striae; ventral visceral field thickened; dorsal visceral field slightly thickened, with long anterior projection, bisected by median ridge. *Lower*

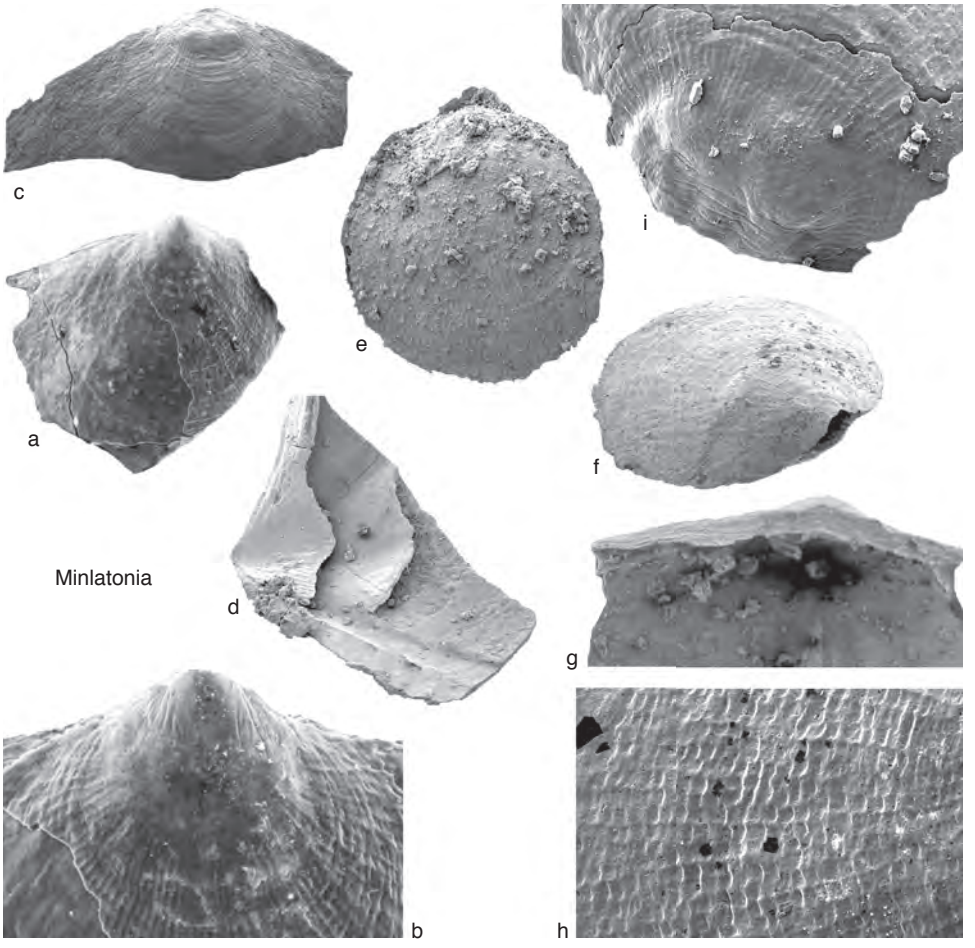
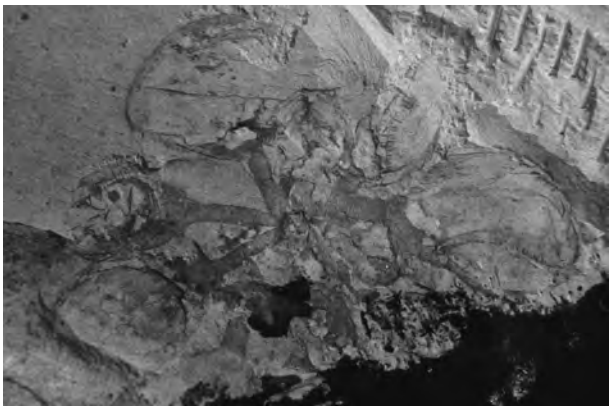



FIG. 1691. Botsfordiidae (p. 2557–2559).



Longtancunella

FIG. 1692. Uncertain (p. 2559).

*Cambrian (Botomian):* South Australia.——FIG. 1691*a–i.* **M. tuckeri*, Parara Limestone, Yorke Peninsula; *a*, ventral valve exterior, ×32; *b*, detail of umbo, PIN4664/6233, ×108; *c*, dorsal valve exterior, PIN4664/6221, ×32; *d*, oblique lateral view of ventral valve interior, PIN4664/6227, ×22; *e*, dorsal view of complete articulated shell, PIN4664/6230, ×30; *f*, oblique posterolateral view of complete articulated shell, PIN4664/6232, ×24; *g*, detail of dorsal pseudointerarea, PIN4664/6226, ×40; *h*, detail of reticulate ornamentation, PIN4664/6228, ×112; *i*, detail of dorsal umbo, PIN4664/6225, ×94 (Ushatinskaya & Holmer, 2001).

## Superfamily and Family UNCERTAIN

**Longtancunella** HOU & others, 1999, p. 80 [**L. chengjiangensis*; OD]. Genus poorly known; thin, lingulid-like shell, slightly convex, subcircular; mostly occurring in clusters, individuals apparently joined by pedicles; internal characters unknown. *Lower Cambrian:* China (Yunnan Province).——FIG. 1692. **L. chengjiangensis*, Yu'anshan Formation, Qiongzhusian Stage; holotype, cluster of specimens with preserved pedicles, part, NIGPA1145a, ×2 (Hou & others, 2004).

# ACROTRETIDA

LARS E. HOLMER and LEONID E. POPOV

[University of Uppsala; and National Museum of Wales]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

## Order ACROTRETIDA Kuhn, 1949

The cladistic analyses by HOLMER and POPOV (1996, 2000) gave support for identifying the Acrotretida, and the Acrotretoidea, as a potential monophyletic group defined by numerous derived characters, including a columnar shell structure, a simplified linguliform muscle system, and development of an apical process; however, the interrelationships within the superfamily could not be resolved completely in any satisfactory way. It seems that the family Acrotretidae is a paraphyletic grouping, from which the other and potentially monophyletic families were derived (HOLMER & POPOV, 2000). This was also indicated in the cladistic analysis by STRENG (1999). The columnar shell structure of the acrotretoids has generally been assumed to be a derived unique feature within this group (HOLMER, 1989; WILLIAMS & HOLMER, 1992); however, as mentioned above (WILLIAMS & CUSACK, p. 2451, herein), this is now known to be a more widely distributed character that may prove to be a plesiomorphy (HOLMER, SKOVSTED, & WILLIAMS, 2002; SKOVSTED & HOLMER, 2003).

## Superfamily ACROTRETOIDEA Schuchert, 1893

### Family ACROTRETIDAE Schuchert, 1893

[incl. Neotretinae ROBSON, NOWLAN, & PRATT, 2003, p. 206]

**Eohadrotreta** LI & HOLMER, 2004, p. 204 [**E. zhenbaensis*; OD]. Shell subcircular to transversely oval, with rounded to straight posterior margin; ventral valve low conical to gently convex; ventral pseudointerarea gently procline, with shallow to vestigial intertrough; pedicle foramen not enclosed within larval shell, remaining as open notch through much of ontogeny; apical process and apical pits vestigial to absent; dorsal valve gently convex; dorsal pseudointerarea narrowly triangular, orthocline, with median groove; dorsal median buttress well developed; dorsal median septum well developed, extending anterior to midvalve. *Lower Cambrian:* China (Shaanxi Province).—FIG. 1693*a–h*. **E. zhenbaensis*, lower Shuijingtuo Formation, Qiongzhusian Stage, Xiaoyang section, Zhenba, South Shaanxi; *a*, dorsal valve exterior, NIGP135167, ×47; *b*, dorsal valve interior, ×50; *c,* oblique lateral view, NIGP135170, ×80; *d–e*, holotype, ventral valve exterior, oblique posterior view, NIGP135165, ×40; *f*, oblique posterior view of dorsal valve exterior, NIGP135176, ×93; *g*, posterior view of complete articulated juvenile shell, NIGP135175, ×100; *h*, oblique anterior view of ventral valve interior, ×80 (new).—FIG. 1694*a–c*. **E. zhenbaensis*, lower Shuijingtuo Formation, Qiongzhusian Stage, Xiaoyang section, Zhenba, South Shaanxi; *a,* oblique posterior view of unrestricted delthyrium, NIGP135174, ×400; *b*, ventral valve interior, NIGP135173, ×60; *c*, detail of larval shell and pedicle foramen, NIGP135166, ×200 (new).

**Kostjubella** POPOV, HOLMER, & GORJANSKY, 1996, p. 306 [**K. relaxata*, OD]. Shell ventribiconvex; ventral valve strongly convex in lateral profile with maximum height anterior to umbo; ventral pseudointerarea narrow, divided by deep intertrough; pedicle foramen small, elongate suboval, not enclosed within larval shell; dorsal valve gently convex with shallow sulcus; dorsal pseudointerarea low, with lenslike median groove; ventral interior with bosslike apical process, anterior to short internal pedicle tube; ventral mantle canals baculate; dorsal median ridge strong, subtriangular, buttressed posteriorly. *Middle Cambrian (Mayaian):* Kazakhstan (Tarbagatay Range).—FIG. 1695,*1a–f*. **K. relaxata*, Kostyube Mountain; *a*, ventral valve exterior, PMKz63, ×26; *b,* oblique lateral view, ×34; *c,* oblique posterior view, ×40; *d*, holotype, dorsal valve, interior, PMKz61, ×46.5; *e,* oblique lateral view, ×52.2; *f*, ventral valve interior, PMKz64, ×45 (Popov, Holmer, & Gorjansky, 1996).

**Mixotreta** USHATINSKAYA, 1998, p. 39 [**M. quasidentata*; OD]. Shell ventribiconvex; subcircular; ventral valve subconical; pseudointerarea procline to catacline, divided by narrow and shallow intertrough;

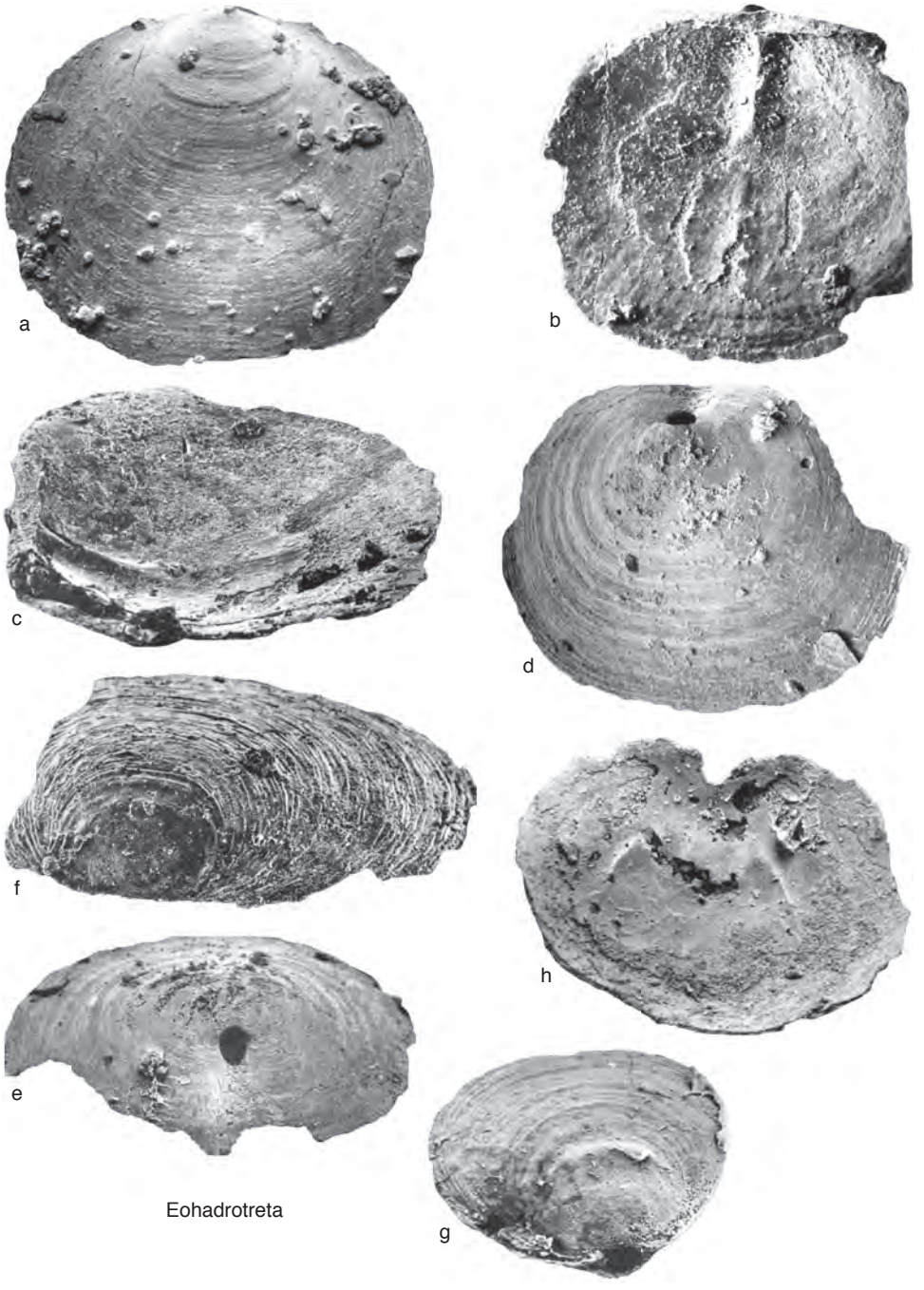



FIG. 1693. Acrotretidae (p. 2560).

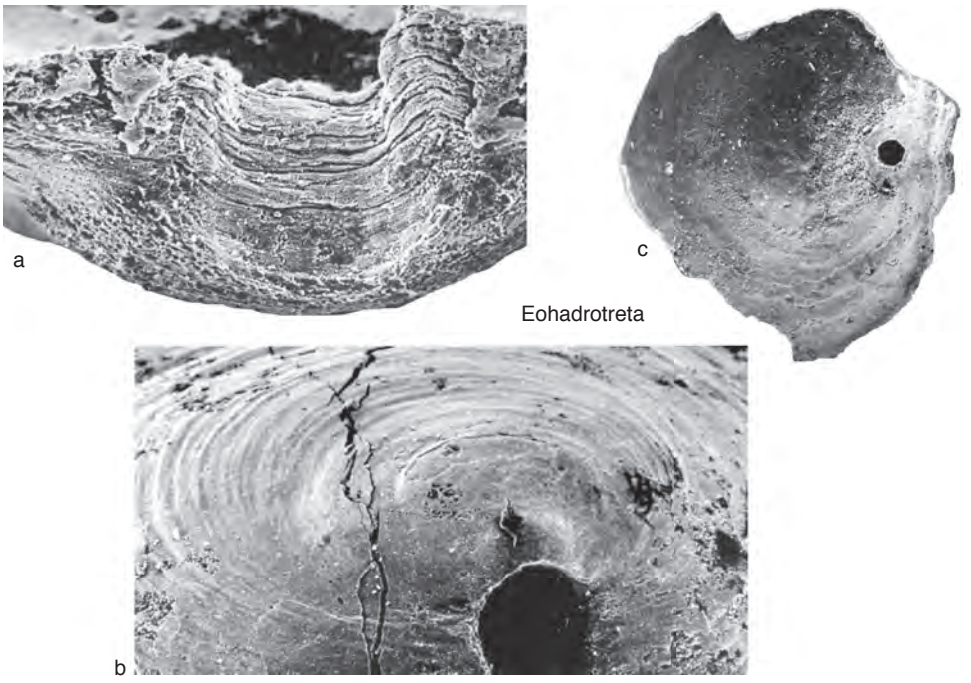



FIG. 1694. Acrotretidae (p. 2560).

pedicle foramen small, circular, within larval shell, at end of short recurved external tube; dorsal valve gently convex; pseudointerarea orthocline; median groove bisected by low ridge and bounded anteriorly by pair of toothlike projections; dorsal larval shell with median depression; apical process occluding umbonal part of valve and projecting anteriorly; internal pedicle tube perforating apical process, flanked by pair of apical pits; dorsal interior with large cardinal muscle fields separated by median buttress; central muscle scars well developed near midvalve; dorsal median ridge weakly developed or absent. *Middle Cambrian (Mayaian):* Russia (Siberia).——FIG. 1696,*1a–d*. **M. quasidentata*, *Corynexochus perforatus–Anopolenus henrici* biozones, Olenek river near mouth of Khorbusonka river, north-central Siberia; *a*, holotype, posterior view of conjoined valves, PIN 4290/301, ×50; *b*, ventral valve interior, PIN 4290/309, ×50; *c*, dorsal valve interior, ×30; *d,* pseudointerarea, PIN 4290/305, ×220 (Ushatinskaya, 1998).

**Odontotreta** USHATINSKAYA, 1998, p. 40 [**O. mirabilis*; OD; =*Stilpnotreta galinae* POPOV, HOLMER, & GORJANSKY, 1996, p. 310]. Shell ventribiconvex; ventral valve strongly convex to subconical; pseudointerarea apsacline, divided by intertrough, terminating with pair of toothlike projections; pedicle foramen within larval shell; dorsal valve convex; pseudointerarea subtriangular, orthocline, mainly occupied by median grove, which is divided medianly by strong ridge; ventral interior with elongate subtriangular apical process anterior to internal foramen; ventral mantle canals baculate; dorsal cardinal muscle large, fields extending anteriorly to midlength; median ridge low. *Middle Cambrian (Mayaian)*: Kazakhstan, Sweden, Denmark (Bornholm).——FIG. 1697,*1a–d*. **O. galinae* (POPOV, HOLMER, & GORJANSKY), Chingiz Formation, Chingiz Range, Central Kazakhstan; *a*, holotype, oblique posterior view of complete shell, PIN4672/1, ×65; *b*, oblique posterolateral view of ventral valve exterior, ×40; *c*, detail of ventral pseudointerarea with toothlike projections, PIN4672/2, ×130; *d*, dorsal valve interior, PIN4672/7, ×50 (Ushatinskaya, 1998).

**Ombergia** HOLMER, POPOV, & BASSETT, 2000, p. 374 [**O. mirabilis*; OD]. Shell subcircular; ventral valve highly conical with extremely long external pedicle tube; ventral pseudointerarea catacline to slightly procline, divided by weak intertrough; dorsal valve weakly convex, with subtriangular pseudointerarea, occupying about half of valve width, divided by broad median groove; ventral interior with thick apical process occluding umbo, buttressed dorsoanteriorly by septum; dorsal interior with thick, low, subtriangular median septum slightly buttressed posteriorly; dorsal cardinal muscle scars large, raised, extending anteriorly about half valve length. *Ordovician (upper Tremadoc–lower Arenig):* Baltoscandia, South Kyrgyzstan.——FIG. 1698*a–g*. **O. mirabilis*, Latorp Limestone, Hunneberg Regional Stage, Sweden; *a*, dorsal valve exterior,

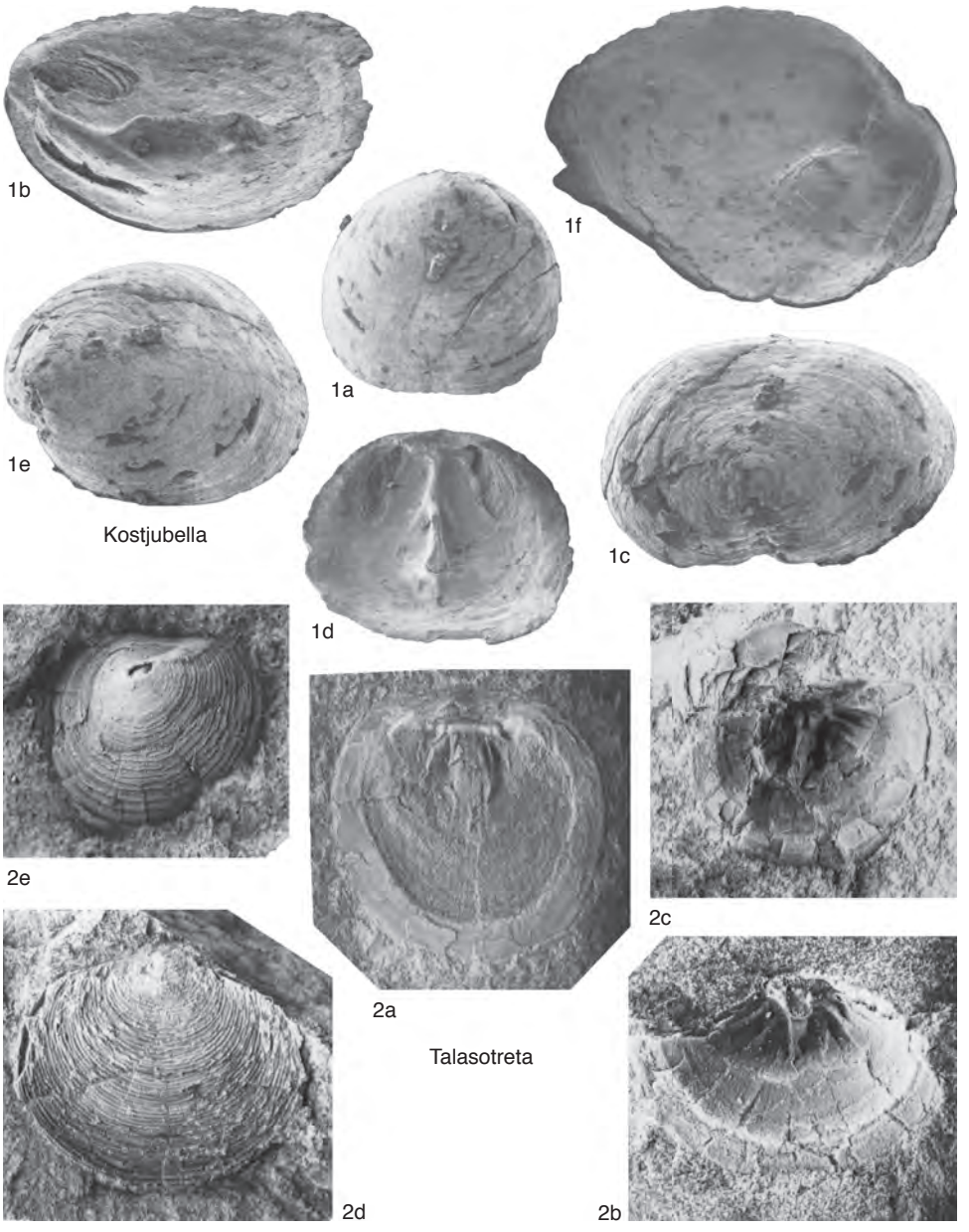



FIG. 1695. Acrotretidae (p. 2560–2566).

×32; *b*, detail of larval shell, ×110; *c*, detail of postlarval ornamentation, SGUType8511, ×235; *d*, dorsal valve interior, SGUType8512, ×40; *e*, holotype, ventral valve exterior, SGUType8508, ×25; *f*, oblique lateral view of ventral valve exterior, showing apical process buttressed by septum, SGUType8509, ×65; *g*, ventral valve interior, SGUType8510, ×75 (Holmer, Popov, & Bassett, 2000).

**Talasotreta** HOLMER, KONEVA, & POPOV in HOLMER & others, 1996, p. 484 [**T. apollonovi*; OD]. Shell ventribiconvex, ornamented by regularly spaced concentric rugellae, ventral valve broadly conical with procline to catacline pseudointerarea divided by intertrough; pedicle foramen enclosed within larval shell; dorsal valve gently convex with moderately high pseudointerarea divided by shallow broad subtriangular median grove;

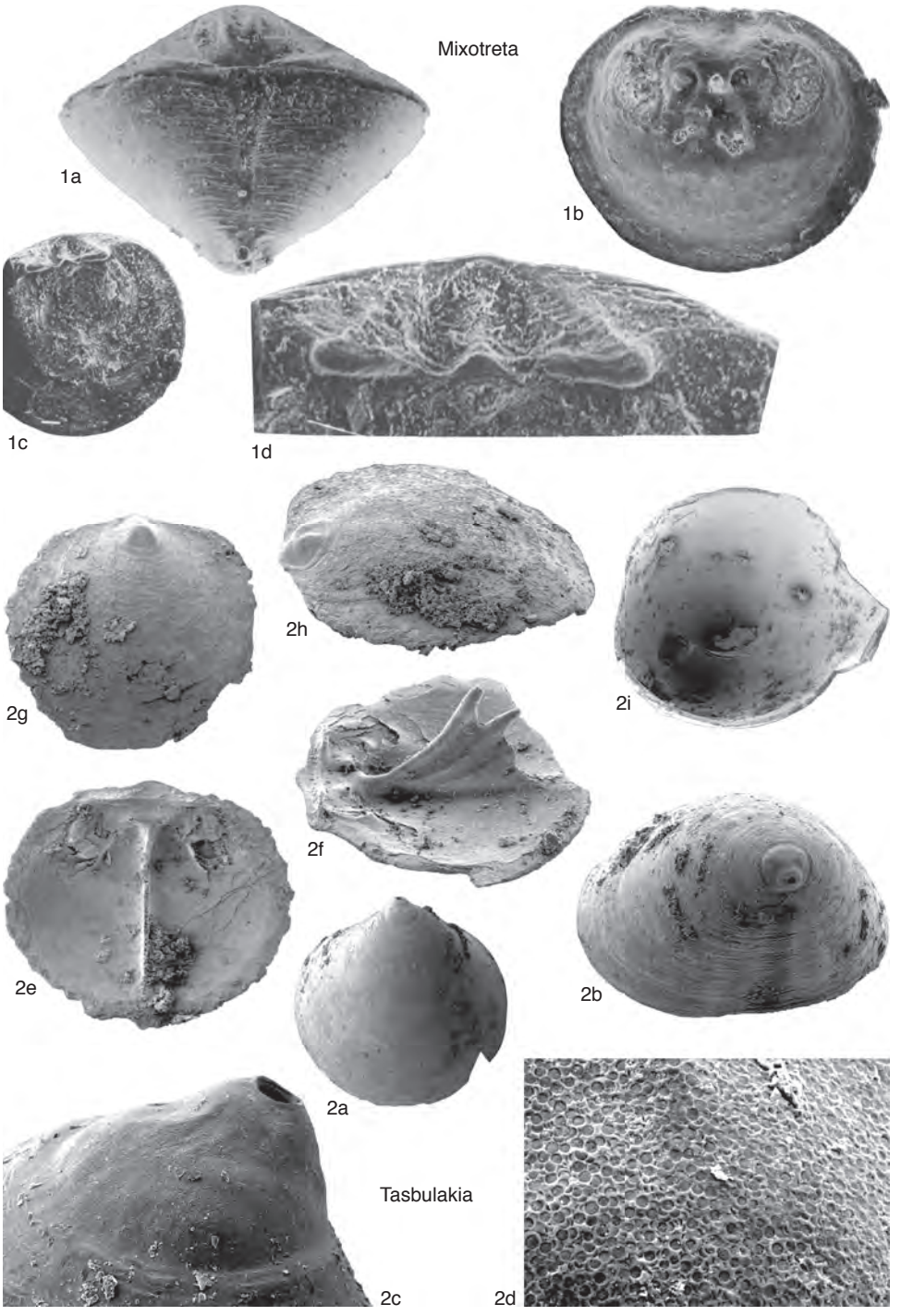



FIG. 1696. Acrotretidae (p. 2560–2566).

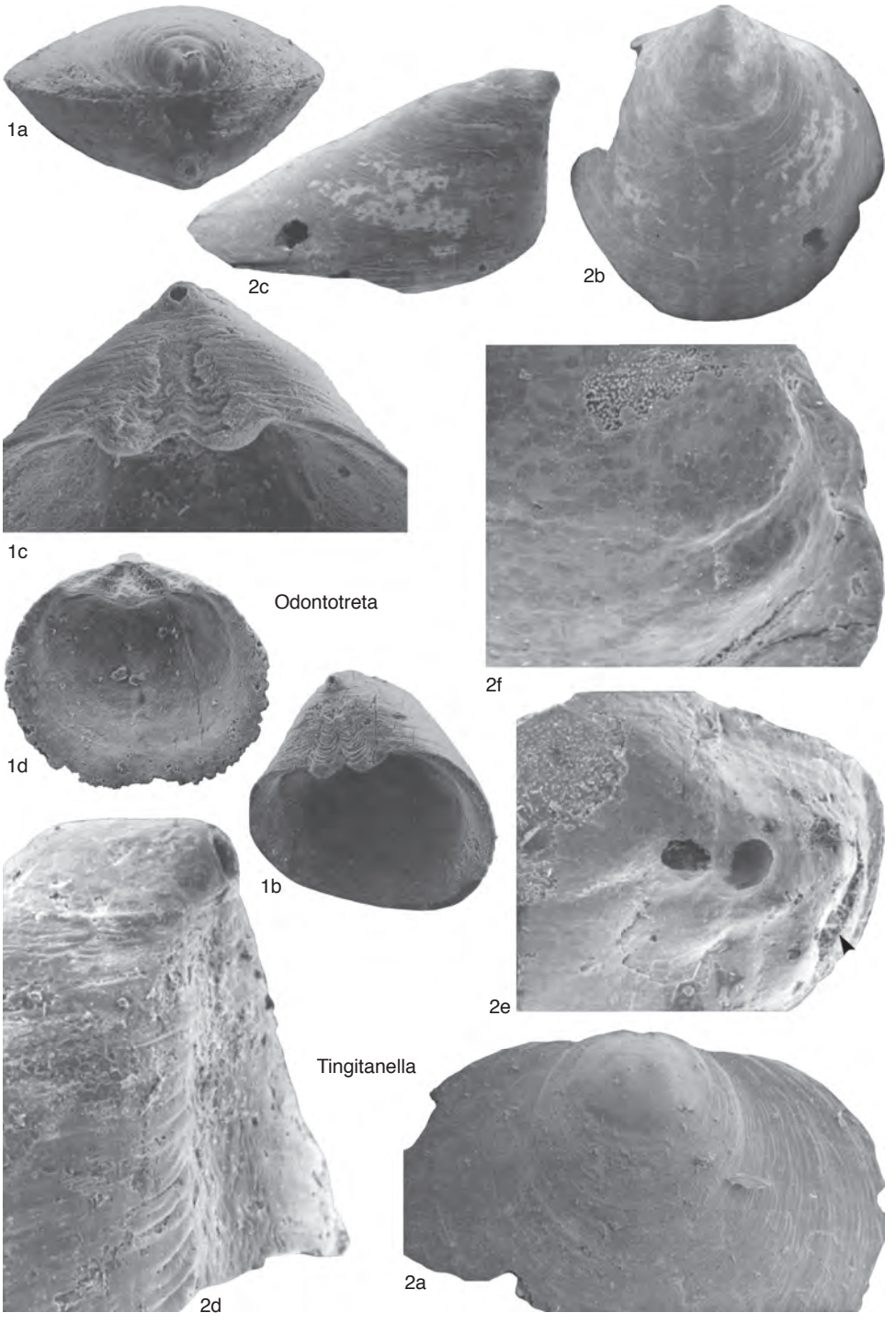



FIG. 1697. Acrotretidae (p. 2562–2566).

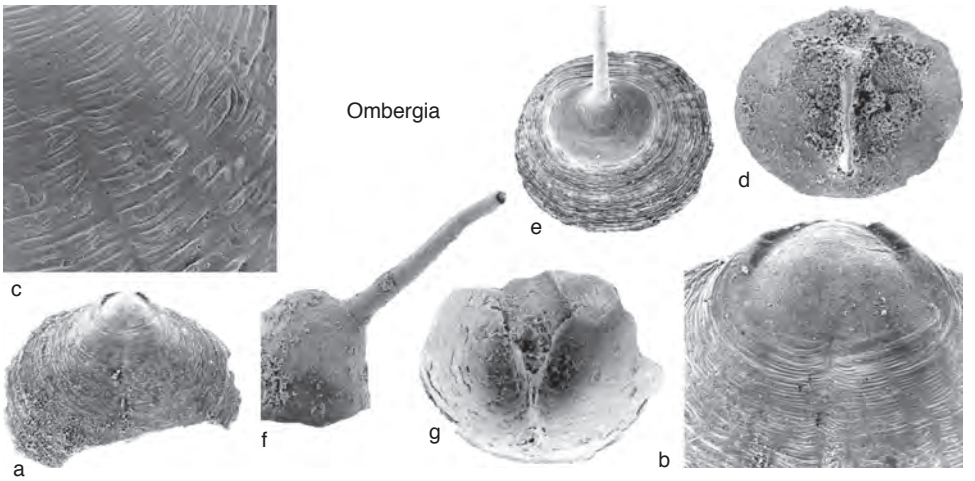



FIG. 1698. Acrotretidae (p. 2562–2563).

ventral interior with ridgelike apical process anterior to internal foramen, or occluding umbonal area in some species, ventral mantle canals pinnate; dorsal interior with low median ridge buttressed posteriorly. *Ordovician (upper Arenig–Llanvirn): Llanvirn,* Sweden, USA; *upper Arenig–Llanvirn,* Kazakhstan.——FIG. 1695,*2a–e. *T. apollonovi*, Zyrykauz Formation, Llanvirn, Malyi Karatau Range; *a*, dorsal valve interior, IGCA 2943/28, ×4.5; *b*, ventral valve interior, IGCA 2943/31, ×5; *c*, ventral valve interior, IGCA 2943/32, ×5; *d*, dorsal valve exterior, IGCA 2943/33, ×5; *e*, ventral valve exterior, latex cast, IGCA, 2943/36, ×5 (Holmer & others, 1996).

**Tasbulakia** POPOV, 2000b, p. 425 [**T. tenuis*; OD]. Shell subcircular; ventral valve high, slightly apsaconical; ventral pseudointerarea poorly defined, divided by weak intertrough; pedicle foramen circular, facing posteriorly, within larval shell; dorsal pseudointerarea narrow, divided by deep median grove; internal pedicle tube supported anteriorly by ridgelike apical process; dorsal median septum high, triangular, bearing up to five septal rods, projecting anteriorly as long spines; dorsal cardinal muscle fields small, situated on raised platforms. *Upper Ordovician (lower Ashgill):* Kazakhstan.——FIG. 1696,*2a–i. *T. tenuis*, Zharyk Beds, Zharyk; *a*, holotype, ventral valve exterior, ×20; *b,* oblique posterolateral view, ×29; *c,* detail of larval shell, ×174; *d,* detail of larval pitting, NMW98.65G.82, ×940; *e*, dorsal valve interior, NMW98.65G.89, ×25; *f*, oblique lateral view of ventral valve interior, NMW98.65G.86, ×46; *g*, dorsal valve exterior, ×26; *h,* oblique lateral view, NMW98.65G.93, ×35; *i*, ventral valve interior, NMW98.65G.91, ×38 (Popov, 2000b).

**Tingitanella** STRENG, 1999, p. 48 [**T. calamisca*; OD]. Shell subcircular to pentagonal in outline; posterior margin straight to gently convex; ventral valve apsaconical to cataconical; ventral pseudointerarea well defined, bisected by poorly defined intertrough; pedicle foramen circular, enclosed within larval shell, forming short external tube; dorsal valve gently convex; dorsal pseudointerarea with orthocline median groove and anacline propareas; apical process poorly developed, low, triangular; median buttress present; median septum or ridge absent. *lower Middle Cambrian:* Morocco.——FIG. 1697,*2a–f. *T. calamisca*, Jbel Wawrmast Formation, *Hupeolenus*?, *Cephalopyge notabilis–Ornamentaspis frequens* biozones, Anti-Atlas; *a*, dorsal valve exterior, PIW96X134.2, ×70; *b*, holotype, ventral valve exterior, ×40; *c,* holotype, oblique lateral view, ×50; *d,* holotype, detail of pseudointerarea, PIW96X30.12, ×160; *e*, oblique anterolateral view of ventral valve interior, PIW96X30.11, ×100; *f*, oblique lateral view of dorsal valve interior, PIW96X30.14, ×160 (Streng, 1999).

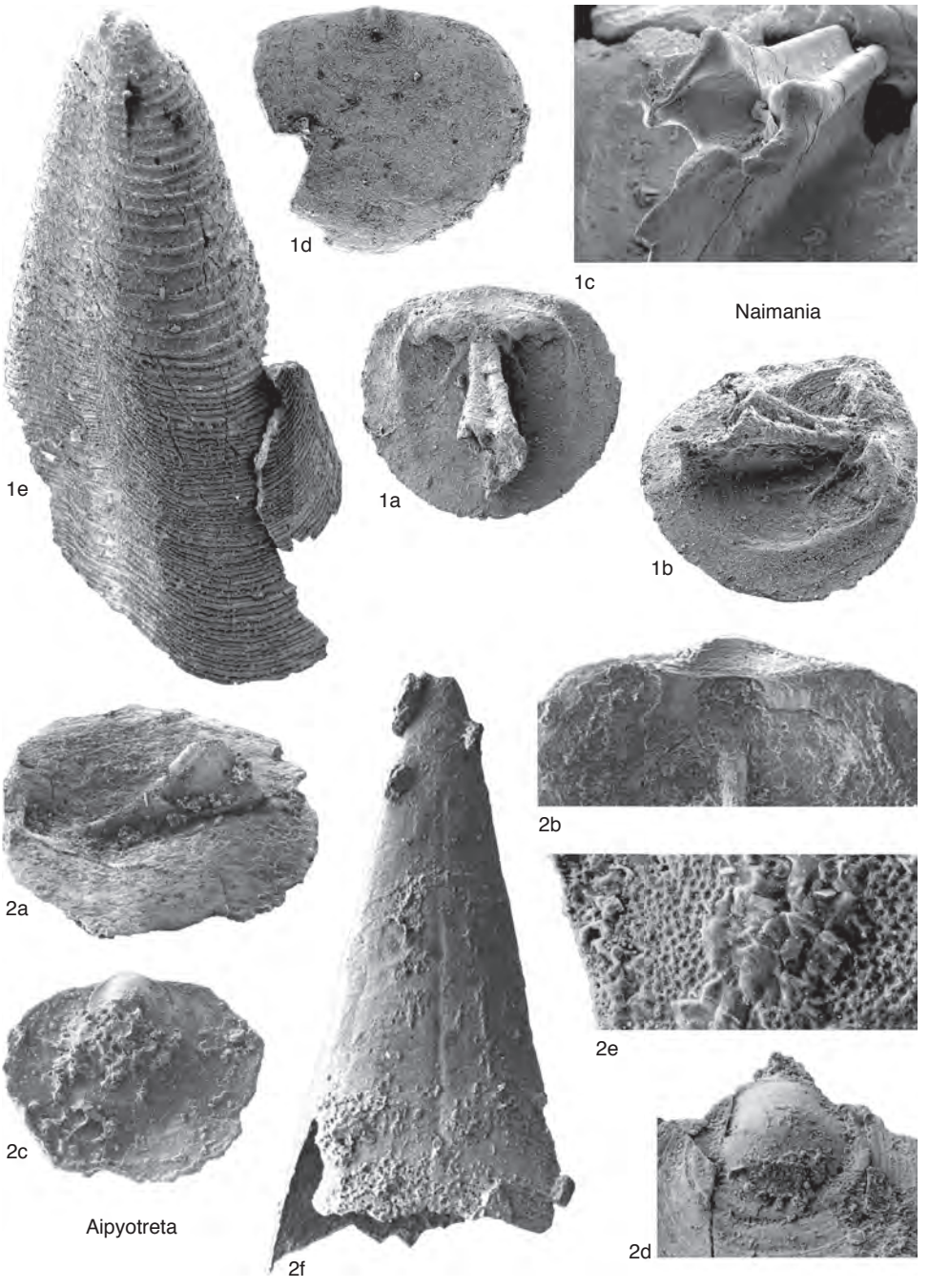



FIG. 1699. Torynelasmatidae and Ephippelasmatidae (p. 2568).

## Family TORYNELASMATIDAE Cooper, 1956

**Naimania** Popov, 2000a, p. 271 [**Issedonia procera* Popov in Nazarov & Popov, 1980, p. 105; OD]. Shell subcircular in dorsal outline; ventral valve high, conical, nearly tubular; ventral pseudointerarea flat, catacline, with narrow intertrough; dorsal valve gently concave; dorsal pseudointerarea straight, anacline, divided by weak median groove; internal pedicle tube supported anteriorly by rudimentary ridgelike apical process; dorsal cardinal muscle scars large, strongly impressed; dorsal median septum high, triangular, with single rod and concave surmounting plate, bearing hemispherical cavity flanked by pair of rodlike processes. [No satisfactory illustrations of the holotype are available.] *Ordovician (upper Caradoc):* Kazakhstan.——Fig. 1699,*1a–e. A. concava*, Mayatas Formation, northern coast of Atansor lake; *a*, dorsal valve interior, ×28; *b,* oblique lateral view, NMW98.65.G.47, ×39; *c*, dorsal valve median septum and surmounting plate, NMW 98.65G.44, ×55; *d*, dorsal valve exterior, NMW98.65G.45, ×34; *e*, oblique posterolateral view of ventral valve exterior, NMW98.65G.43, ×67 (Popov, 2000a).

## Family EPHIPPELASMATIDAE Rowell, 1965

**Aipyotreta** Sutton in Sutton, Bassett, & Cherns, 2000, p. 98 [**A. lockleyi*; OD]. Ventral valve highly conical; ventral pseudointerarea catacline to procline; ventral larval shell as conical as rest of valve; dorsal valve transversely oval; dorsal median septum consisting of simple vertical plate with surmounting rod. *Ordovician (Llandeilo):* Wales.——Fig. 1699,*2a–f. *A. lockleyi*, Golden Grove Group, upper Llandeilo, Pen-yr-Allt, Carmarthenshire; *a*, holotype, oblique lateral view of dorsal interior, ×75; *b,* holotype, detail of dorsal pseudointerarea, ×100; *c,* holotype, dorsal valve exterior, NMW96.8G.775, ×50; *d*, detail of larval shell, NMW96.8G.770, ×100; *e*, detail of larval pitting, NMW96.8G.781, ×750; *f*, posterior view of ventral valve, NMW96.8G.766, ×50 (Sutton, Bassett, & Cherns, 2000).

## Family BIERNATIDAE Holmer, 1989

**Bathmoleca** Sutton in Sutton, Bassett, & Cherns, 2000, p. 103 [**B. addisoni*; OD]. Ventral valve extremely conical, strongly apsacline; ventral larval shell less conical and apsacline; dorsal cardinal muscle scars on raised platform, undercut anteriorly; dorsal median septum with hollow surmounting rod on posterior slope of septum. *Ordovician (Llandeilo):* Wales.——Fig. 1700,*2a–f. *B. addisoni*, Golden Grove Group, lower Llandeilo, near Llandeilo, Carmarthenshire; *a–b*, holotype, dorsal valve interior, oblique lateral view, NMW96.8G.181, ×60; *c–d*, dorsal valve exterior, interior, NMW96.8G.742, ×60; *e–f,* ventral valve lateral and top down views, NMW96.8G.203, ×60 (Sutton, Bassett, & Cherns, 2000).

**Concaviseptum** Brock, Engelbretsen, & Dean-Jones, 1995, p. 114 [**C. laurei*; OD]. Ventral interior with two parallel ridges extending along anterior internal surface; dorsal median septum high, deeply anteriorly excavated, with surmounting plate draping over to fuse dorsally with inner surface of valve; dorsal central muscle scars pyriform. *Lower Devonian (Pragian):* Australia (Victoria).——Fig. 1700,*1a–e. *C. laurei*, Cooper Creek Limestone; *a,* dorsal valve exterior, AMF92867, ×44; *b*, dorsal valve interior, ×47; *c–d,* anterior and lateral view, AMF92865, ×60; *e*, ventral valve, oblique view of interior, AMF92869, ×83 (Brock, Engelbretsen, & Dean-Jones, 1995).

**Havlicekion** Mergl, 2001a, p. 35 [**H. splendidus*; OD]. Ventral valve highly conical; dorsal valve weakly sulcate, with deeply impressed muscle scars; dorsal median septum low, with robust, narrowly triangular to rodlike surmounting plate; postlarval shell with prominent, regular concentric rugellae. *Silurian (Wenlock)–Devonian (Pragian):* Bohemia, Australia.——Fig. 1701*a–d. *H. splendidus*, Praha Formation, Dvorce-Prokop Limestone, Svatý Jan pod Skalou, Na Stydlých vodách Quarry, Bohemia; *a*, holotype, dorsal valve interior, ×60; *b*, oblique lateral view, PCZCU40, ×60; *c*, oblique lateral view of ventral valve exterior, ×60; *d*, oblique anterior view of ventral valve exterior, PCZCU36, ×60 (new). [Michal Mergl]

## Family CERATRETIDAE Rowell, 1965

**Acanthatreta** Streng, 1999, p. 38 [**A. meiwirthae*; OD]. Shell ventribiconvex, transversely oval; ventral pseudointerarea poorly defined, steeply procline to catacline, bisected by intertrough; pedicle foramen circular to elongate oval, not enclosed within larval shell; dorsal pseudointerarea with deep, triangular median groove, with small propareas; apical process forming ridge connecting posterior and anterior valve slopes, and placed anterior to internal foramen, with filigree spine. *lower Middle Cambrian:* Morocco.——Fig. 1702*a–i. *A. meiwirthae*, Jbel Wawrmast Formation, *Cephalopyge notabilis* Biozone, Tachguelt, High Atlas; *a*, dorsal valve exterior, PIW96X125.8, ×55; *b*, ventral valve exterior, PIW96X125.7, ×30; *c*, dorsal valve interior, PIW96X126.1, ×40; *d*, holotype, oblique anterolateral view of ventral valve interior, PIW96X25.15, ×35; *e*, detail of ventral pseudointerarea, PIW96X125.3, ×65; *f*, lateral view of ventral valve exterior, PIW96X25.9, ×50; *g*, oblique anterolateral view of dorsal valve interior, PIW96X25.14, ×50; *h*, detail of apical process, PIW96X30.1, ×95; *i*, detail of apical process, PIW96X25.11, ×150 (Streng, 1999).

**Almohadella** Streng, 1999, p. 43 [**A. braunae*; OD]. Shell ventribiconvex, transversely oval; ventral pseudointerarea steeply procline, bisected by broad intertrough, widening dorsally; pedicle foramen slitlike, not enclosed within larval shell; dorsal pseudointerarea with broad, triangular median

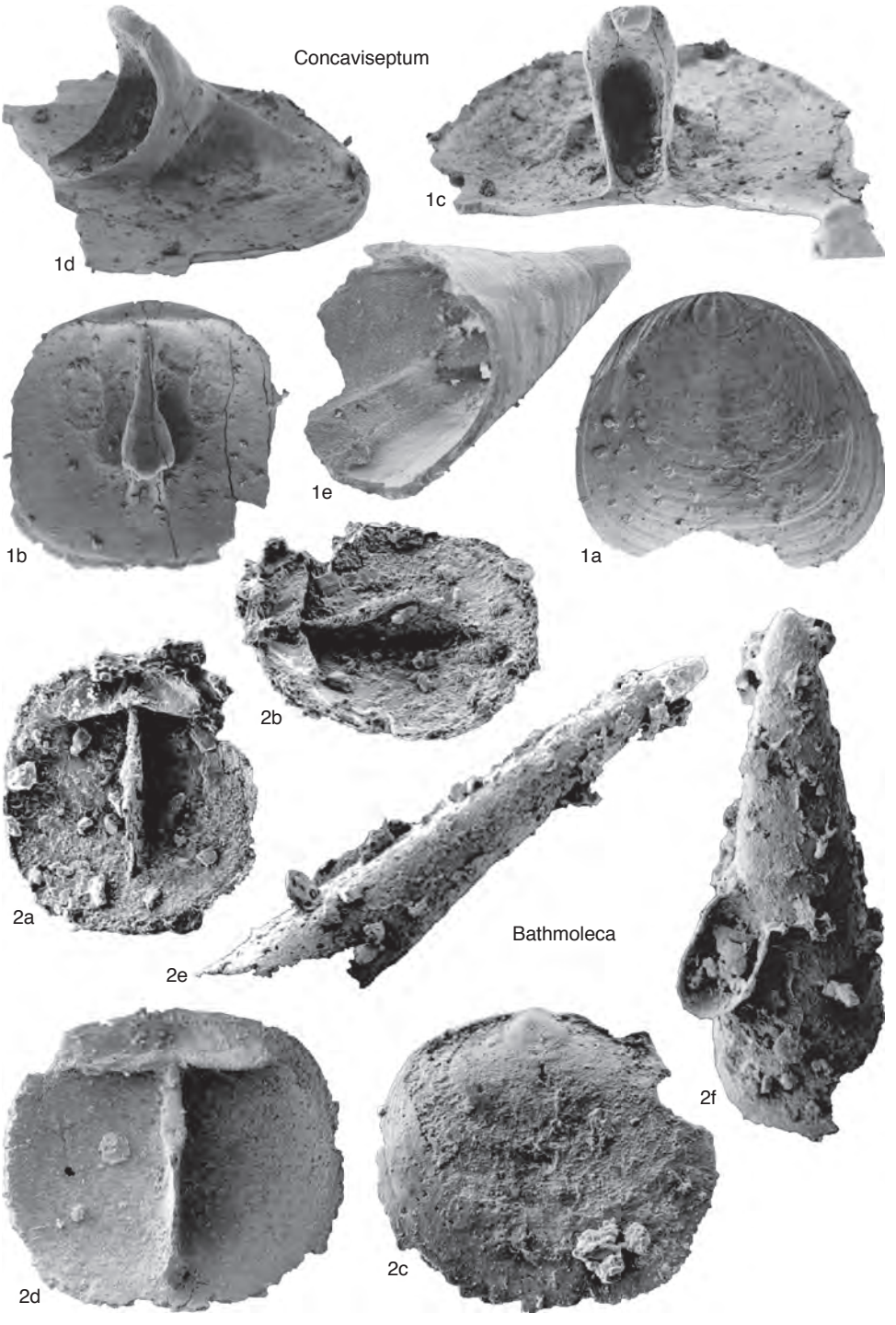



FIG. 1700. Biernatidae (p. 2568).

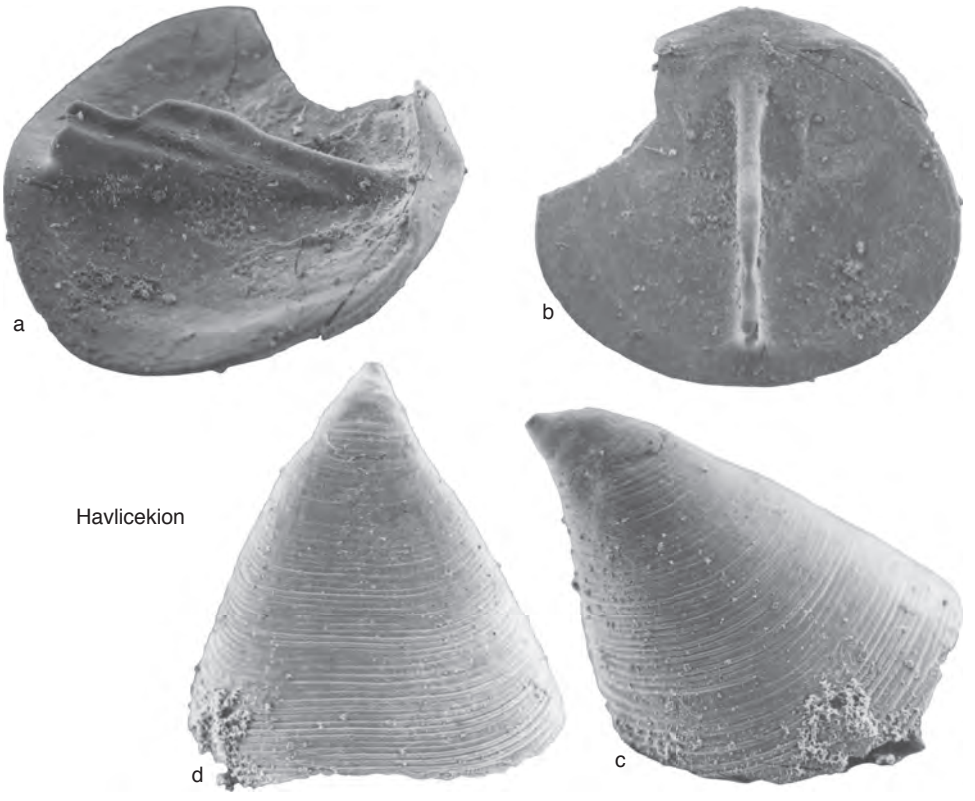



FIG. 1701. Biernatidae (p. 2568).

groove; propareas small; apical process forming robust ridge connecting posterior and anterior valve slopes; median buttress broad. *lower Middle Cambrian:* Morocco.——FIG. 1703*a–f.* **A. braunae*, Jbel Wawrmast Formation, *Cephalopyge notabilis–Ornamentaspis frequens* biozones, Lemdad Syncline, High Atlas; *a*, dorsal valve exterior, PIW96X21.3, ×35; *b*, dorsal valve interior, PIW96X22.6, ×40; *c*, detail of pedicle foramen, PIW96X18.6, ×160; *d*, oblique anterolateral view of dorsal valve interior, PIW96X22.9, ×40; *e*, holotype, ventral valve interior, ×25; *f*, holotype, detail of apical process, PIW96X3.14, ×85 (Streng, 1999).

**Monophthalma** STRENG, 1999, p. 32 [**Acrotreta eggegrundensis* WIMAN, 1903, p. 55; OD]. Ventral valve convex to low subconical; ventral pseudointerarea procline to slightly apsacline; pedicle foramen not enclosed within larval shell; dorsal pseudointerarea wide, with broad, subtriangular median groove; propareas small; ventral interior with collarlike thickening around apical process, with low ridge extending along anterior valve

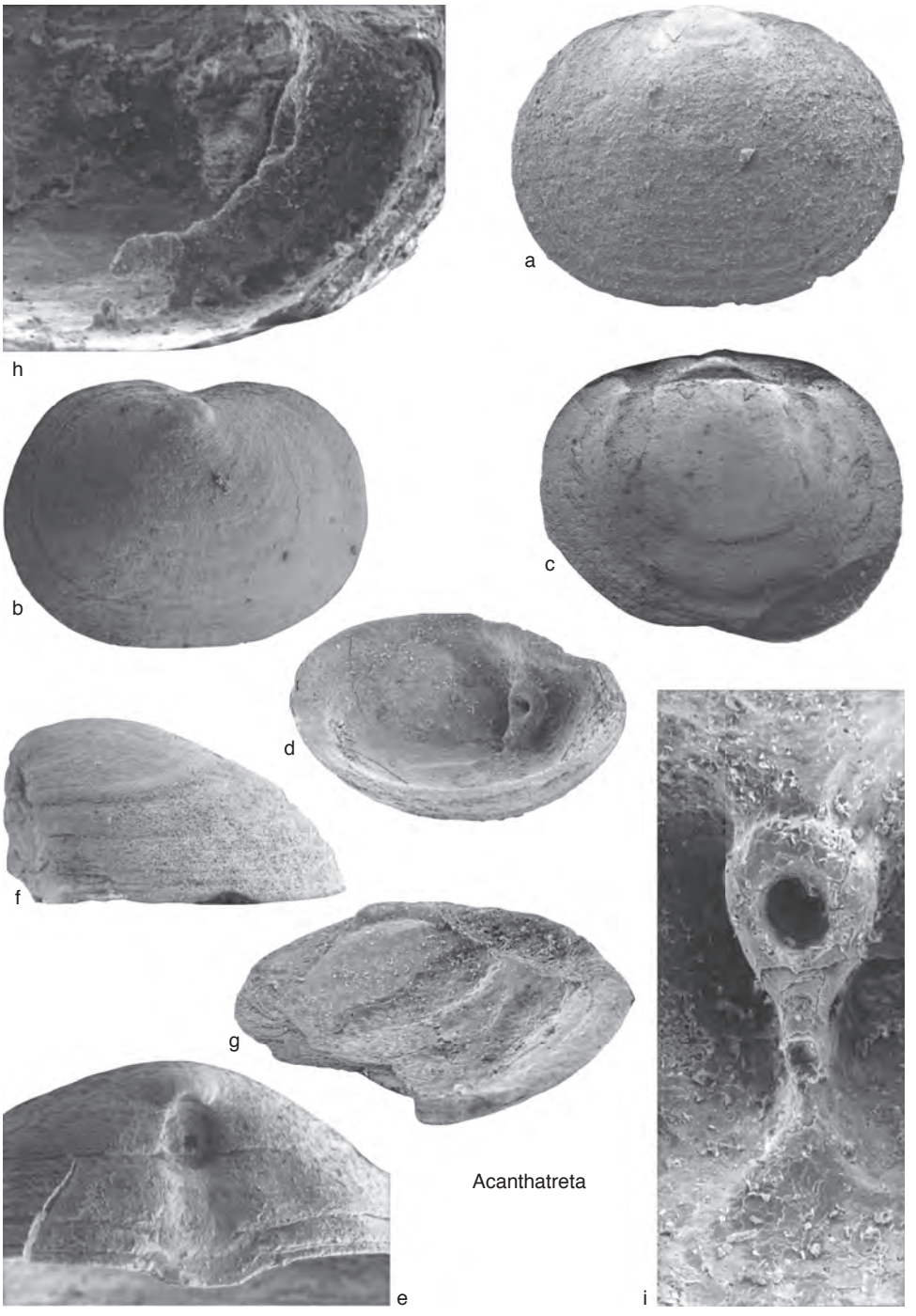



FIG. 1702. Ceratretidae (p. 2568).

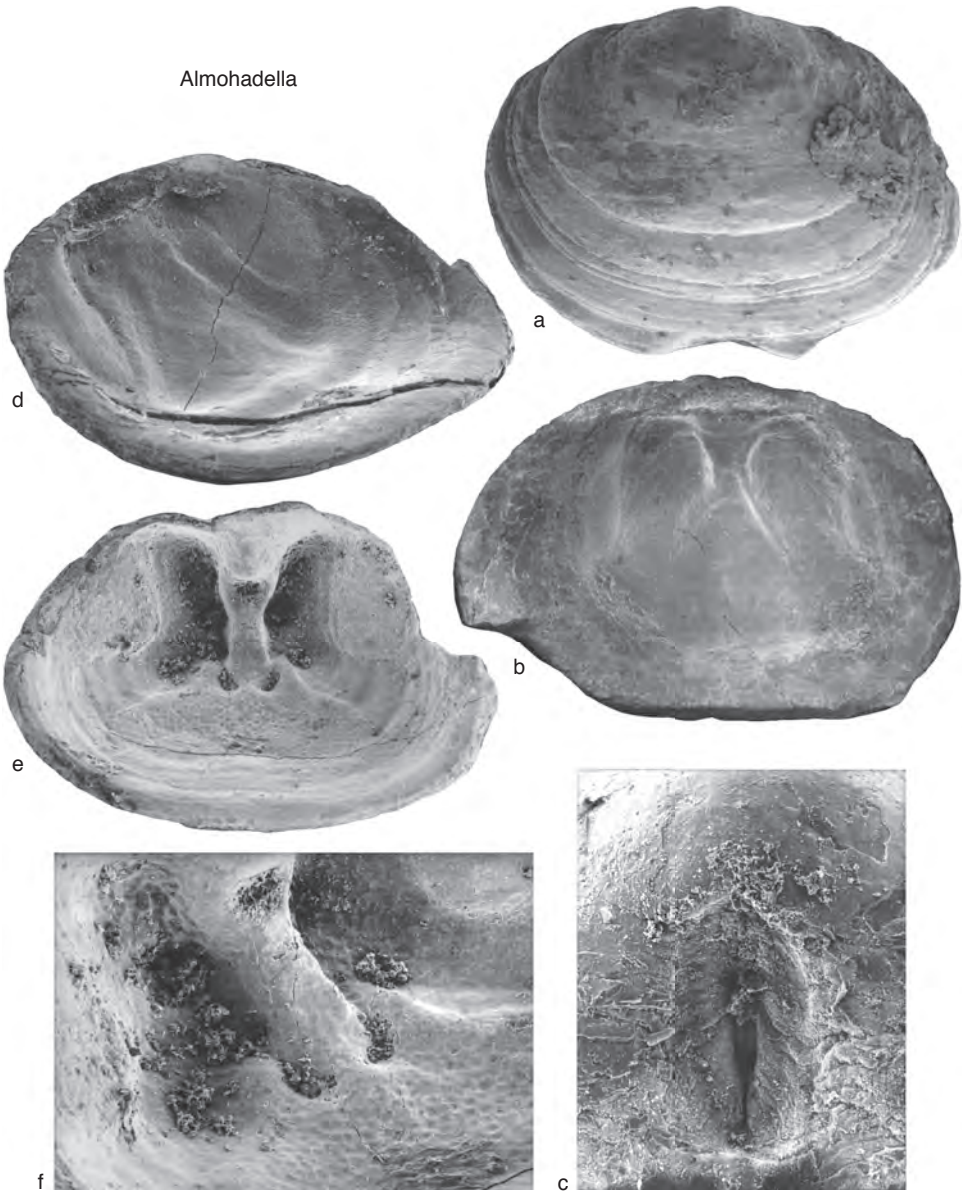



FIG. 1703. Ceratretidae (p. 2568–2570).

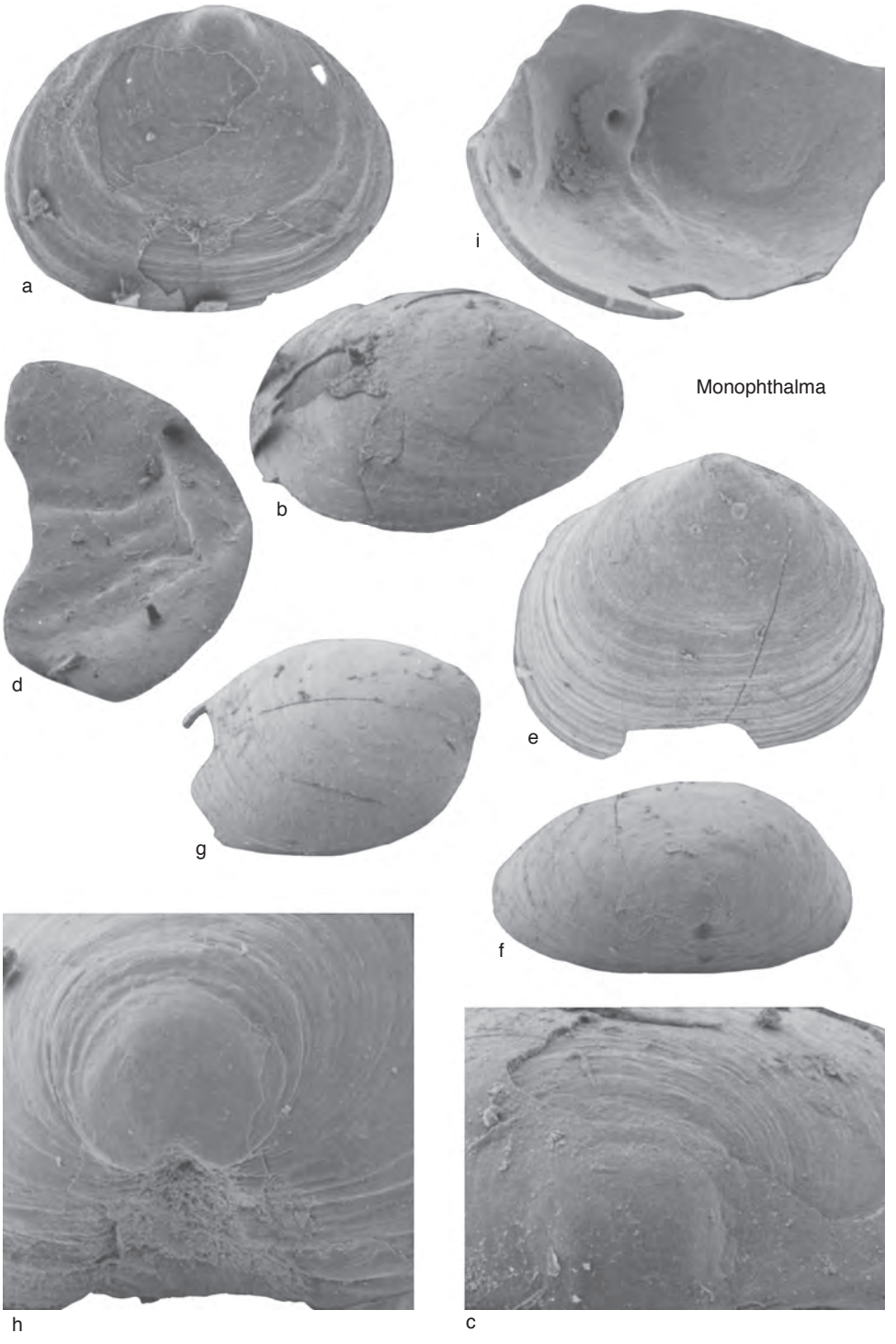
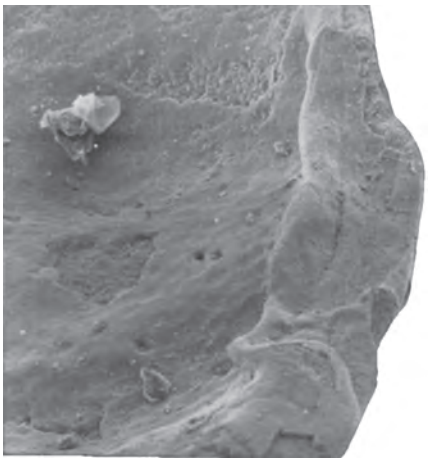



FIG. 1704. Ceratretidae (p. 2570–2574).



Monophthalma

FIG. 1705. Ceratretidae (p. 2570–2574).

slope; dorsal median buttress and median ridge vestigial to absent; cardinal scars of both valves oval, widely separated. *Lower Cambrian (?Botomian), lower Middle Cambrian:* Sweden (South Bothnian Sea), Morocco.——FIG. 1704*a–i. *M. eggegrundensis* (WIMAN), Cambrian glacial erratic boulder, ?Botomian, Eggegrund island, South Bothnian Sea, outside Gävle, Sweden; *a*, dorsal valve exterior, ×57; *b,* oblique lateral view, ×67; *c,* detail of larval shell, PMUB593, ×165; *d,* oblique lateral view of dorsal interior, PMUB594, ×49; *e*, ventral valve exterior, ×35; *f,* oblique posterior view, ×38; *g,* oblique lateral view, PMUB596, ×35; *h*, detail of ventral larval shell, PMUB598, ×135; *i*, ventral valve interior, PMUB597, ×45 (Holmer & Ushatinskaya, 1994).——FIG. 1705. **M. eggegrundensis* (WIMAN), Cambrian glacial erratic boulder, ?Botomian, Eggegrund island, South Bothnian Sea, outside Gävle, Sweden; oblique lateral view of dorsal pseudointerarea, PMUB595, ×180 (Holmer & Ushatinskaya, 1994).

# SIPHONOTRETIDA

LARS E. HOLMER,[1] LEONID E. POPOV,[2] and MICHAEL G. BASSETT[2]

[[1]University of Uppsala; and [2]National Museum of Wales]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

## Order SIPHONOTRETIDA Kuhn, 1949

Adult shell with hollow spines, in all but three genera, or completely lacking spines (*Schizambon* only) but with elongated pustules; adult shell of two genera (*Gorchakovia* and *Helmersenia*) perforated by canals with external depressions that probably contained chitinous tubercles in life; immature shell of most genera (except *Schizambon*) perforated by canals; shell usually ventribiconvex, inequivalved; shell structure with prismatic laminae with sporadically distributed cavities containing apatitic residues; larval and postlarval shell lacking pitted microornament; growth of ventral valve mixoperipheral or holoperipheral; pedicle foramen apical, circular, or extending anteriorly through resorption, producing elongate pedicle track; posterior part of pedicle track may be closed by plate, which may continue as internal pedicle tube; pseudointerareas of both valves poorly divided, lacking flexure lines; musculature not well known but apparently similar to that of lingulides; mantle canal system baculate with dorsal and ventral *vascula lateralia*; *vascula media* may be present. *upper Middle Cambrian (Mayaian)–Lower Devonian (Pragian, Emsian).*

The presence of hollow spines was regarded previously as the most important potential synapomorphic character of the order Siphonotretida (HOLMER & POPOV, 2000), but a recent study of the oldest siphonotretide, *Schizambon*, reveals that its shell is imperforated (WILLIAMS, HOLMER, & CUSACK, 2004). The surface ornamentation of *S. typicalis*, the type species of the genus, is covered by regular lamellae with upturned edges superimposed on sharp parvicostellae. The nodes formed at their intersection acquire the shape of elongate spinelike pustules (5–50 µm long), which were previously mistaken for bases of broken hollow spines (e.g., POPOV, HOLMER, & MILLER, 2002). These spines, however, are solid, superficial structures, more likely to be homologous with the pustules of *Gorchakovia,* but not with the hollow spines of other siphonotretides (WILLIAMS, HOLMER, & CUSACK, 2004).

The shells of *Helmersenia* and *Gorchakovia* also lack spines, but they are perforated by canals with external depressions (antechambers) that possibly contained chitinous tubercles in life. Similar perforations can be observed also in the umbonal areas of both valves of *Siphonotreta* and most other siphonotretids. The mature part of their shells, however, bears recumbent, rheomorphic, hollow spines that grew forward out of pits (WILLIAMS, HOLMER, & CUSACK, 2004). It is possible that the canals with external depressions and their inferred external chitinous structures are homologous with the setigerous tubes found within the stem group of the Brachiopoda (see Organophosphatic Bivalved Stem-Group Brachiopods, p. 2580 herein), and represent a retained plesiomorphic character for the Siphonotretida. If this interpretation is correct, it would indicate that *Schizambon* is a derived member of the order that has

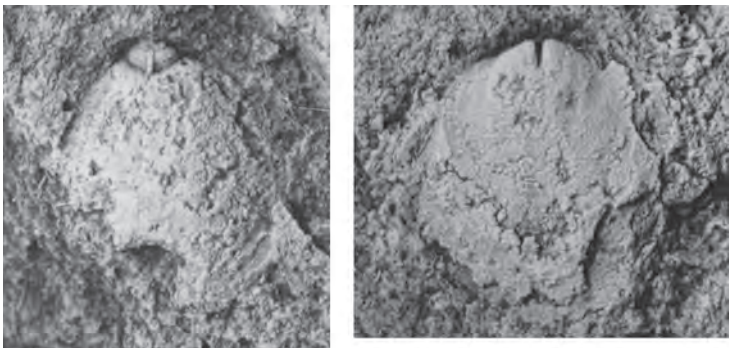



FIG. 1706. Siphonotretidae (p. 2576).

lost both the hollow spines and canals with external depressions.

The siphontretide pedicle foramen invariably is situated within and confined to the ventral valve. It is commonly enlarged anteriorly by shell resorption. This suggests that the pedicle of siphonotretides originated from within the epithelial tissue secreting the ventral valve. Thus, the siphonotretide foramen is here regarded provisionally as not being homologous with pedicle openings within the ventral valves of acrotretides or lingulides, such as the acrothelids and dysoristids, which represent postlarval enclosures of pedicles by the precocious differentiation of the posteromedial mantle lobe seen in immature *Discinisca*. The location of the siphonotretide pedicle wholly within the ventral valve may have been unique among linguliforms (WILLIAMS & CARLSON, p. 2843, herein).

Siphonotretides were long regarded as almost extinct by the end of the Ordovician. The recent discovery of *Orbaspina* by VALENTINE and BROCK (2003) expands the stratigraphic range of the group into the late Llandovery, however, and MERGL (2001a, 2001b) reported on the occurrence of the siphonotretide shell fragments in the lower Silurian to Lower Devonian of Bohemia. Unpublished occurrences from the Silurian of Canada, Great Britain, and the Island of Gotland also exist.

## Order SIPHONOTRETIDA Kuhn, 1949
## Superfamily SIPHONOTRETOIDEA Kutorga, 1848
### Family SIPHONOTRETIDAE Kutorga, 1848

**Collarotretella** MERGL, 1997b, p. 102 [**C. septata*; OD]. Shell biconvex, broadly oval; exterior sparsely spinose, nearly smooth; foramen large, circular, directed posteroventrally, internally with thickened collar; ventral pseudointerarea low, small, undivided; dorsal pseudointerarea obscure; dorsal interior with short, distinct median septum. *Ordovician (Arenig):* Bohemia.——FIG. 1706*a–b*. **C. septata*, Klabava Formation, Hrádek; *a*, holotype, ventral valve internal mold, MBHR 66845, ×15; *b,* dorsal valve internal mold, MBHR 66847, ×15 (new). [Michal Mergl]

**Orbaspina** VALENTINE & BROCK, 2003, p. 237 [**O. gelasinus*; OD]. Pedicle foramen large, keyhole shaped, extending forward through resorption to form elongate, broadly triangular, pedicle track; pedicle track covered posteriorly by concave plate and anteriorly by short listrium-like plate; tubular hollow spines of uniform size; postlarval shell with numerous subcircular dimples, loosely arranged in concentric rows. *Silurian (Llandovery–Wenlock):* Australia (New South Wales).——FIG. 1707*a–g*. **O. gelasinus*, Boree Creek Formation, uppermost Llandovery, *amorphognathoides* Zone, to earliest Wenlock, *ranuliformis* Zone, central-western New South Wales; *a–b*, holotype, dorsal valve exterior, interior, ×17; *c,* detail of pseudointerarea, AMF120610, ×50; *d*, detail of postlarval dimpling, AMF122212, ×50; *e–f*, ventral valve exterior, interior, ×30; *g,* detail of spines, AMF120612, ×300 (new).

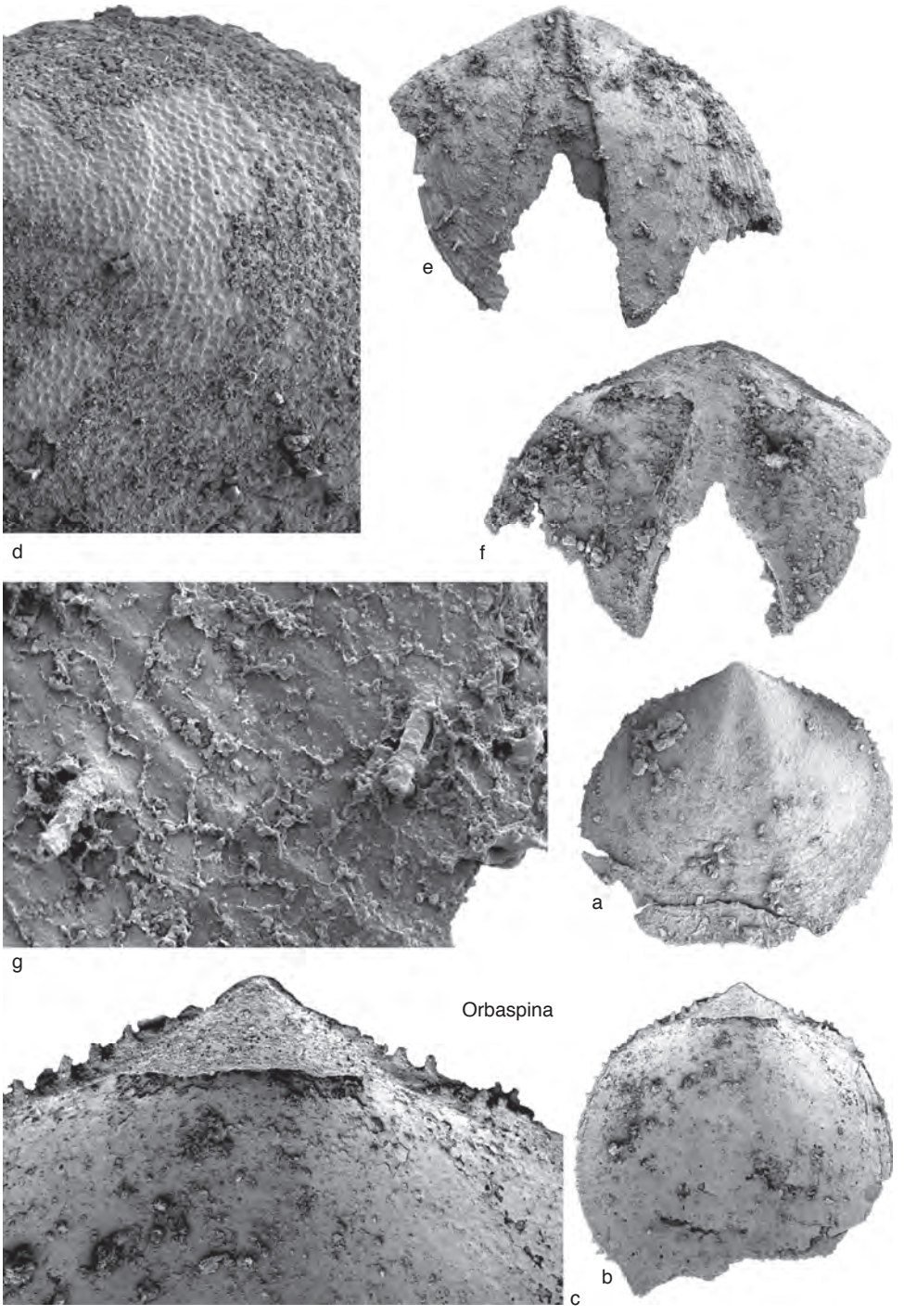



FIG. 1707. Siphonotretidae (p. 2576).

# PATERINATA

LARS E. HOLMER and LEONID E. POPOV

[University of Uppsala; and National Museum of Wales]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

## Class PATERINATA Williams & others, 1996

The inclusion of the extinct class Paterinata within the Linguliformea is problematic, but is mainly due to the presence of an organophosphatic shell. [This small clade includes just 12 genera, divided into 2 families, the Cryptotretidae and Paterinidae (LAURIE, 2000). The paterinates have been difficult to classify since they were first discovered (WILLIAMS, POPOV, & others, 1998). The work by WILLIAMS, POPOV, and others (1998) indicates that they had fused mantle lobes in combination with an attachment to the substrate by means of a cuticular pad from the ventral mantle. The paterinates also differ from all other linguliforms in that they have true interareas with delthyria and notothyria and a musculature with diductor muscles, as well as rhynchonelliform mantle canal systems that may have contained gonads (LAURIE, 1987, 2000; WILLIAMS, POPOV, & others, 1998, fig. 3). WILLIAMS, POPOV, and others (1998) proposed that some of these features possibly represent plesiomorphic characters retained from the stem group. The paterinates also differ in shell structure from the linguliforms in that a canal system is lacking (e.g., WILLIAMS & CUSACK, 1999; WILLIAMS, POPOV, & others, 1998).]

## Order PATERINIDA Rowell, 1965

## Superfamily PATERINOIDEA Schuchert, 1893

### Family PATERINIDAE Schuchert, 1893

**Olenekina** USHATINSKAYA, 1997, p. 55 [**O. olenekensis*; OD]. Shell ventribiconvex, transversely suboval; postlarval shell covered with slightly irregular concentric rugellae; larval shell finely granulated; ventral valve with open delthyrium and apsacline interarea; dorsal valve with open notothyrium underlined by median plate inside valve; interior characters weakly impressed with a pair of ridges parallel to hinge line in both valves. *upper Middle Cambrian:* north-central Siberia, Russia.——FIG. 1708,*2a–c*. **O. olenekensis*, Eirina Formation, *Glyptagnostus stolidotus* Biozone, Kotui river; *a*, holotype, dorsal valve exterior, PIN4510/141, ×25; *b*, ventral valve exterior, PIN4290/206, ×45; *c,* dorsal valve interior showing ridges along hinge line, PIN4510/146, ×70 (Ushatinskaya, 1997).

**?Wynnia** WALCOTT, 1908, p. 142 [**Orthis warthi* WAAGEN, 1891, p. 102; OD]. Genus inadequately known (previously questionably assigned to Orthida, but with organophosphatic shell); shell ventribiconvex, subcircular; ventral valve with open delthyrium and apsacline interarea; dorsal valve sulcate, with open notothyrium; ventral valve with elongate triangular muscle field, divided

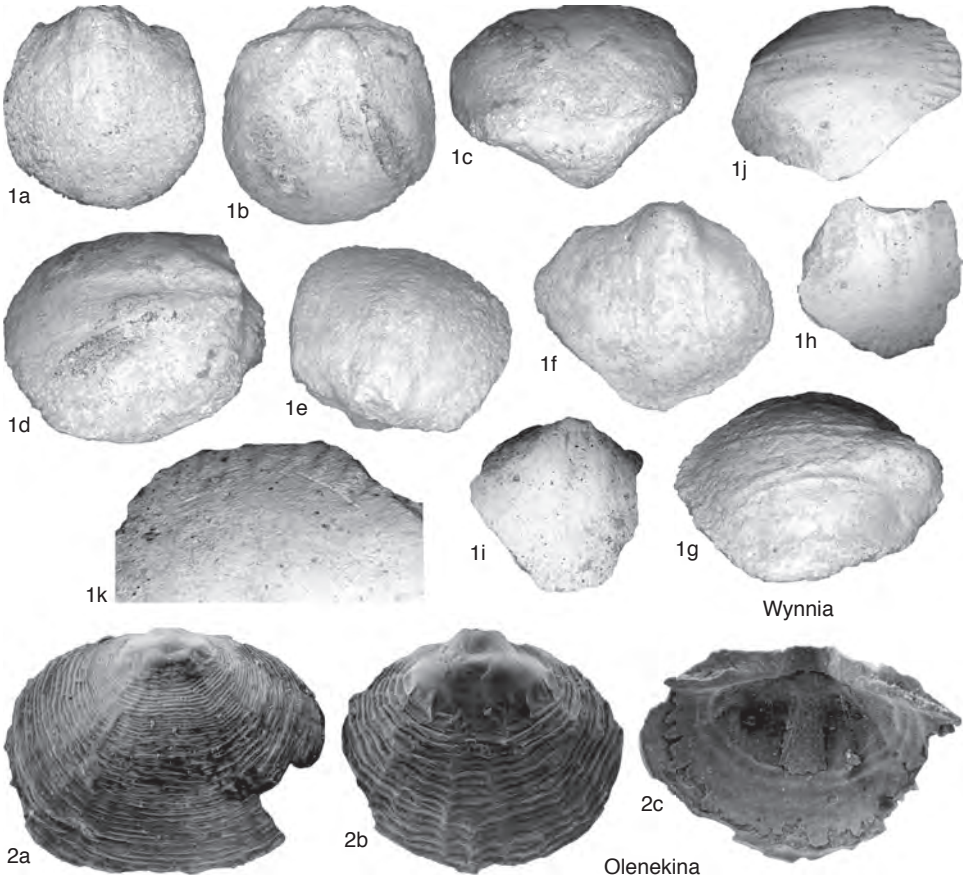



FIG. 1708. Paterinidae (p. 2578–2579).

by two subparallel *vascula media*; dorsal interior with poorly defined muscle fields separated by median ridge. *Lower Cambrian:* Pakistan.——FIG. 1708,*1a–k*. **W. warthi* (WAAGEN), *Neobolus* Beds, Tsanglangpuian, Kussak Fort Hill, Salt Range; *a–e*, internal mold of complete articulated shell, ventral view, dorsal view, oblique posterior dorsal view, oblique lateral dorsal view, oblique posterior ventral view, TUBr1080/110, ×4; *f–g*, internal mold of ventral valve, oblique lateral view, TUBr1080/109, ×4; *h–j*, exfoliated ventral valve (organophosphatic), oblique anterior view, oblique lateral view, ×6; *k*, detail of terminal vascular trunks, TUBr1080/111, ×15 (new).

# INCERTAE SEDIS
# ORGANOPHOSPHATIC BIVALVED STEM-GROUP BRACHIOPODS

LARS E. HOLMER and LEONID E. POPOV

[University of Uppsala; and National Museum of Wales]

## INTRODUCTION

With few exceptions, the stem and crown group concept (e.g., BUDD & JENSEN, 2000) has not been used generally for analyzing phylogenetic relationships within the Brachiopoda (CONWAY MORRIS, 1993, 1998; CONWAY MORRIS & PEEL, 1995; HOLMER, 2001). This situation is now changing rapidly, however, as a surprisingly rich record of Early Cambrian organophosphatic-shelled potential stem-group brachiopods is beginning to emerge (HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; SKOVSTED & HOLMER, 2003; BALTHASAR, 2004a; WILLIAMS & CARLSON, p. 2829, herein). These stem-group taxa fall outside any of the formal taxonomic units within the two currently recognized classes of the subphylum Linguliformea, the Lingulata and the Paterinata, discussed below; however, their organophosphatic shell, evidence of setae, and, in some exceptionally preserved forms, the presence of a lophophore (ZHANG, HOU, & EMIG, 2003), indicate clearly that they are linked phylogenetically with the linguliforms.

Proposed Early Cambrian stem-group brachiopods include the vermiform, organophosphatic, sclerite-bearing tannuolinids (WILLIAMS & HOLMER, 2002; LI & XIAO, 2004) and the more brachiopod-like *Mickwitzia* and *Heliomedusa* (HOLMER, SKOVSTED, & WILLIAMS, 2002; SKOVSTED & HOLMER, 2003; BALTHASAR, 2004a). But because the tannuolinids fall outside the clade defined by the presence of a bivalved body plan with lophophore (Fig. 1709), they are excluded here from further consideration.

The enigmatic bivalved organophosphatic-shelled *Mickwitzia* SCHMIDT is one of the largest known bivalved organisms from the Early Cambrian; the width of the shell can reach 60–72 mm. Although it has been referred commonly to the paterinid brachiopods (subphylum Linguliformea, class Paterinata; ROWELL, 1965), others questioned its brachiopod affinity. It was tentatively excluded from the Brachiopoda by LAURIE (2000, p. 156), in view of its enigmatic "punctate, three-layered phosphatic shell," as well as the lack of any unequivocal brachiopod characters apart from the simple bivalved shell as apparent in all available material of the type species, *M. monilifera* (LINNARSSON), from the Early Cambrian of Baltoscandia. Better preserved material of *Mickwitzia* (referred to *M.* sp. cf. *occidens* WALCOTT, but probably a new species; see Fig. 1711–1712) described by SKOVSTED and HOLMER (2003) from the Early Cambrian of Greenland, demonstrates that the shell structure of *Mickwitzia*, on the contrary, is closely similar to the columnar shell of linguliform acrotretoid brachiopods as well as to the linguloid *Lingulellotreta,* in that it has slender columns in the laminar succession (CUSACK, WILLIAMS, & BUCKMAN, 1999). A columnar fabric is known also from the tannuolinid *Micrina*, thus indicating that this type of shell structure may be a plesiomorphic character (Fig. 1898, herein; WILLIAMS & HOLMER, 1992; CUSACK, WILLIAMS, & BUCKMAN, 1999; HOLMER, SKOVSTED, & WILLIAMS, 2002). The shell of *M.* sp. cf. *occidens* also has a very different kind of thicker cylindrical tubes, however, which were clearly open to the exterior surface and have a fine internal striation; this striation most probably represents imprints of microvilli, and the tubes can be inferred to have contained setal structures penetrating the shell (and causing external cylindrical imprints in the surrounding laminae; see

Fig. 1712c, 1713a; see also Balthasar, 2004a). This type of setae is not present in any known member of the crown group Brachiopoda, but identical structures have been described from tannuolinids (Conway Morris & Chen, 1990; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Li & Xiao, 2004). *M.* sp. cf. *occidens* also has evidence of a brachiopod-like soft anatomy, including a well-defined larval shell with preserved traces (so-called nick points) of setal follicles (Fig. 1712b), comparable with those described from other linguliform brachiopods by Williams and Holmer (1992), as well as a ventral pseudointerarea with a pedicle groove (Fig. 1712a).

*M. occidens* Walcott, from a new Lower Cambrian Lagerstätte in Nevada, confirms the setigerous nature of the thicker canals, since it has pyritized setae preserved extending from them (Fig. 1711d–f), and the interior surface of the parallel canals has striations that are identical with those from the other mickwitziids (Fig. 1711g–i).

The enigmatic *Heliomedusa* Sun and Hou, from the Early Cambrian Chengjiang Lagerstätte (Yu'anshan Formation), Yunnan, was most recently assigned provisionally to the craniopsid group of brachiopods (subphylum Craniiformea, class Craniata, order Craniopsida; Popov & Holmer, 2000a; Zhang, Hou, & Emig, 2003). New material demonstrates that the shell structure of *Heliomedusa* is identical with that of *Mickwitzia*, however, and has a punctate shell that was perforated by tubes, some of which contain chitinous setae at the surface (Fig. 1714–1716). The presence of these characters indicates instead that *Heliomedusa* belongs within the stem-group brachiopods together with *Mickwitzia* (but see Williams & Carlson, p. 2889 herein, and Chen, Huang, & Chuang, 2007, for an alternative point of view).

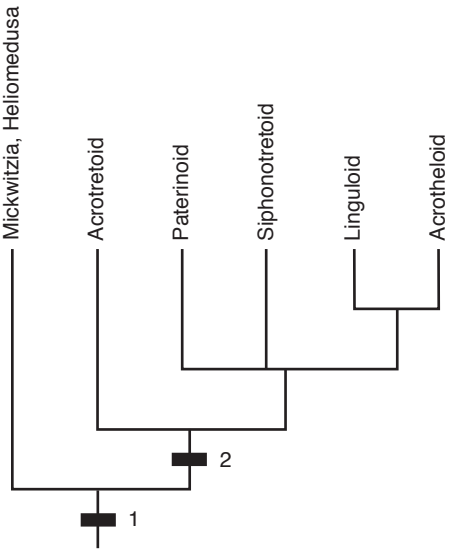



Fig. 1709. Cladogram of stem-group (*Heliomedusa* and *Mickwitzia*) and crown-group brachiopods (Acrotretoidea, Paterinoidea, Siphonotretoidea, Linguloidea, Acrotheloidea). The numbered transformations are *1,* bivalved body plan with lophophore, organophosphatic shell perforated by setigerous tubes, follicular mantle setae; *2,* loss of setigerous tubes (although highly modified tubes may be present in Siphonotretoidea), adult setae all follicular (topology adapted from Holmer, Skovsted, & Williams, 2002, fig. 4).

## MICKWITZIIDS

[incl. Mickwitziidae Gorjansky, 1969, p. 104]

The family Mickwitziidae as used by Laurie (2000) and others (Skovsted & Holmer, 2003) is probably not a monophyletic group but seemingly represents a paraphyletic stem group, which now includes only two genera, *Mickwitzia* and *Heliomedusa*. At present it is preferred to include these taxa only within an informal grouping of mickwitziid-like stem-group brachiopods, pending further study. As noted by Balthasar (2004a), the great morphological variation between species presently placed within *Mickwitzia* (*sensu lato*) needs to be further investigated pending restudy of the type species. *Lower Cambrian (Atdabanian–Toyonian), ?Middle Cambrian*.

**Mickwitzia** Schmidt, 1888, p. 24 [*?*Lingula monilifera* Linnarsson, 1869, p. 344; OD] [=*Causea* Wiman, 1902, p. 53 (type, *C. formosa;* OD); ?*Microschedia* Geyer, 1994, p. 710 (type, *M. amphitrite,* OD)]. Shell ventribiconvex to planoconvex, inequivalved, ovate to subcircular; apex of both valves commonly submarginal and erect; ventral apex may be curved over posterior margin; lingulid-like larval shell may

be present; mature shell pustulose, commonly with pustules arranged in radiating rows; pseudointerareas of both valves usually poorly defined in adults; ventral pseudointerarea rarely anacline (in early growth stages), more commonly apsacline to procline (in adults), and sometimes with narrow pedicle groove in juveniles; ventral pseudointerarea of some forms with minute arch-shaped posterior ridge (homeodeltidium) flanked by small procline to apsacline interareas in juveniles; interior of both valves inadequately known; shell organophosphatic, but may generally have been poorly mineralized; punctate shell structure; finely stratiform; may include slender acrotretoid-type columns (but not yet observed from type species) and thicker canals (=punctae) that are usually orthogonal, but also may be close to parallel with shell laminae; thicker canals open to external surface, internal striations (imprints of microvilli) may be present; shell layers most commonly bend inward at insertion of canals and form distinct inward-pointing cones with canals, forming a central tube; canals open to interior and exterior through shallow funnels that may be associated with cylindrical depressions; some forms also with internally striated thicker canals on ventral pseudointerarea; mantle canals poorly known. *Lower Cambrian (Atdabanian–Toyonian), ?Middle Cambrian*: USA (California, Nevada), Canada (Alberta, British Columbia, Nova Scotia), Greenland, Mexico, Sweden, Finland, Estonia, Lithuania, ?Morocco.——Fig. 1710*a–k*. **M. monilifera* (Linnarsson), File Haidar Formation (Mickwitzia beds), Atdabanian, Västergötland, Uppland (glacial erratics), Sweden; *a–c,* ventral valve exterior, oblique posterior, lateral view, PMB28, holotype of *C. formosa* Wiman, ×0.6; *d–f,* ventral valve exterior, exfoliated, posterior view, ×1, lateral view, SGUAa172, ×2; *g,* detail of lateral margin, showing more irregularly distributed parallel canals, ×24; *h*, juvenile ventral valve exterior, with pustulose ornamentation, RMBr1609, ×7; *i*, detail of pustulose ornamentation of juvenile dorsal valve, slightly exfoliated, RMBr1567, ×46; *j*, detail of margin of dorsal valve interior, exfoliated, showing possible terminal trunks of mantle canals, RMBr1593, ×3; *k*, detail of sectioned and polished section, etched with 3% HCl, showing thick, orthogonal canals, with shell layers bending inward to form distinct inward-pointing cones, with canals forming a central tube, RMBr133552, ×75 (new).——Fig. 1711*a–c*. **M. monilifera* (Linnarsson), File Haidar Formation (Mickwitzia beds), Atdabanian, Västergötland, Uppland (glacial erratics), Sweden; *a*, dorsal valve interior, exfoliated, ×2.5; *b,* detail of central median section, showing section through 13 regularly spaced thicker canals that are parallel with shell laminae, and numerous orthogonal canals, ×12; *c,* detail of parallel canal, RMBr1567, ×110 (new).——Fig. 1711*d–i*. *M. occidens* Walcott, Poleta Formation, upper Montezuman–lower Dyeran, Indian Springs Canyon, Esmeralda County, Nevada, USA; *d*, ventral valve exterior, exfoliated, with soft-bodied preservation of setae, ×3; *e,* detail of setae, backscatter image, ×40; *f,* detail of framboidal pyrite preservation of setae, USNM, ×160; *g*, detail of apex of ventral valve, smooth larval shell, and postlarval pustulose ornamentation, perforated by openings of thicker orthogonal canals, USNM, ×65; *h*, shell fragment with orthogonal and parallel canals, ×26; *i,* detail of striated interior of parallel canal, USNM, ×600 (new).——Fig. 1712*a–c*. *M.* sp. cf. *occidens* Walcott, Bastion and Ella Island Formations, Botomian, northeastern Greenland; *a*, ventral pseudointerarea of early mature valve with pedicle groove, MGUH26308, ×105; *b*, oblique posterior view of broken ventral apex, showing larval shell with nick points (disturbance by muscles of marginal setae), MGUH26300, ×95; *c*, ventral pseudointerarea, showing openings of setigerous thicker canals, causing cylindrical indentations in surrounding laminae, ×400 (new).——Fig. 1713*a–c*. *M.* sp. cf. *occidens* Walcott, Bastion and Ella Island Formations, Botomian, northeastern Greenland; *a,* detail of striated interior of two canals, MGUH26279, ×1900; *b*, fragmentary mature valve with pustulose ornamentation in radiating rows and openings of canals, MGUH26311, ×70; *c*, section through primary and secondary layer of mature shell, showing larger canals and columnar shell structure, MGUH26280, ×700 (new).

**Heliomedusa** Sun & Hou, 1987, p. 261[269] [**H. orienta;* OD]. Shell biconvex, inequivalved, subcircular; mixoperipheral growth in ventral valve, with beak marginal, and apsacline pseudointerarea; holoperipheral growth in dorsal valve, apex placed posterior to center; visceral area of both valves thickened slightly anteriorly, extending anterior to center; shell originally organophosphatic, but may generally have been poorly mineralized (invariably replaced by framboidal pyrite and clay minerals); punctate shell structure includes thick canals that are usually orthogonal, but also may be close to parallel with shell laminae; canals of both types can contain pyritized spinelike setae at surface; surface of both valves commonly also covered with impressions of numerous thinner, shorter spinelike possible setal structures; ontogeny includes differentiated juvenile shell, delineated by growth disturbance; both juvenile and mature shells with pustulose ornamentation, with pustules arranged in radiating rows. *Lower Cambrian (Atdabanian):* China (Yunnan).——Fig. 1714*a–f*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a*, ventral valve exterior, partly exfoliated, ×2; *b,* detail of posterior margin with preserved spinelike setae, ×15; *c,* exfoliated compressed ventral valve exterior covered by pyritized short spinelike structures, which may represent setal structures, ×15; *d,* detail of pyritized spinelike structures, NIGP12, ×100; *e*, thick spinelike pyritized setae at valve margin, NIGP34, ×15; *f,* exfoliated compressed ventral valve exterior covered by impressions of short spinelike structures, which may represent setal structures, NIGP14, ×30 (new).——Fig.

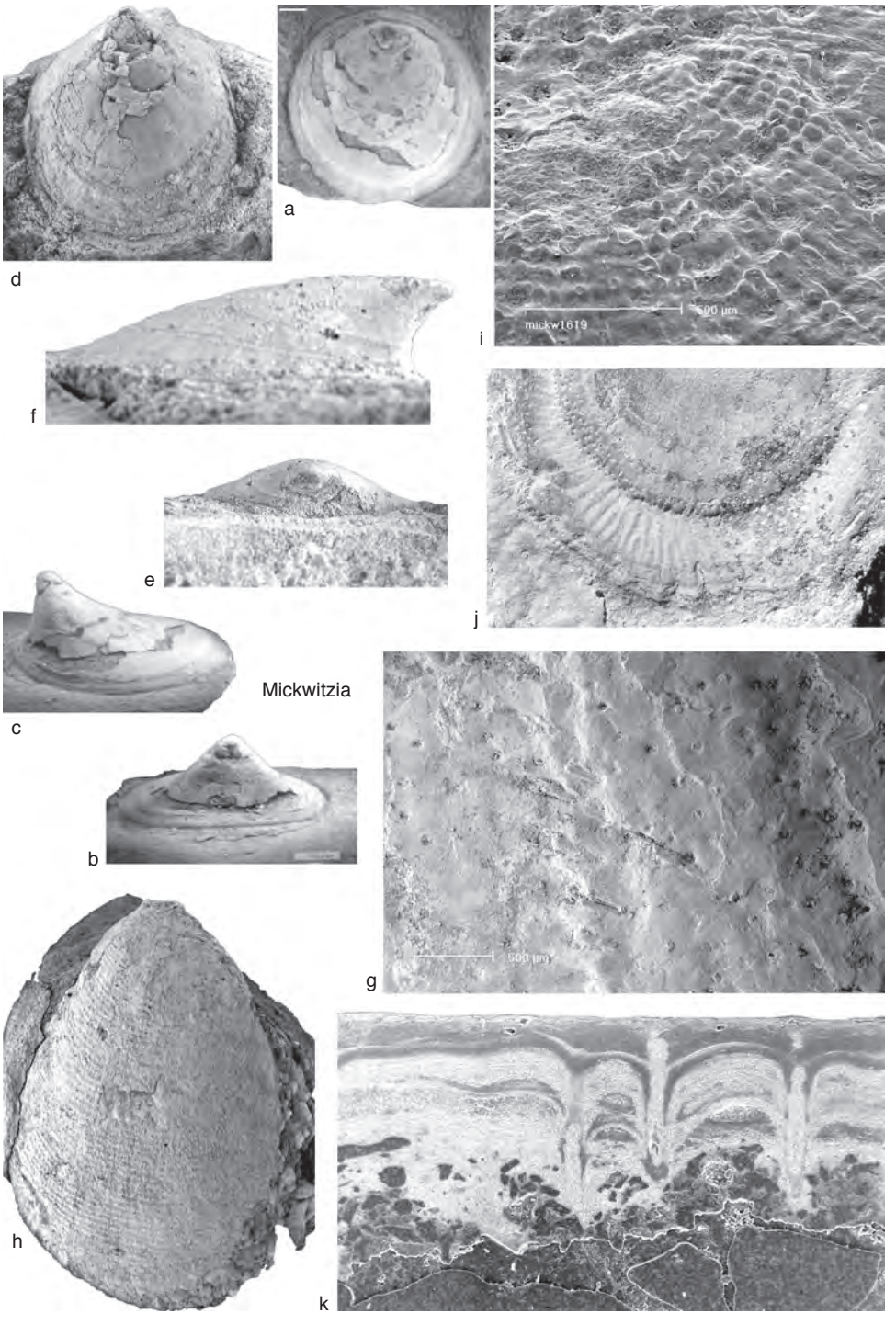



FIG. 1710. Mickwitziids (p. 2581–2582).

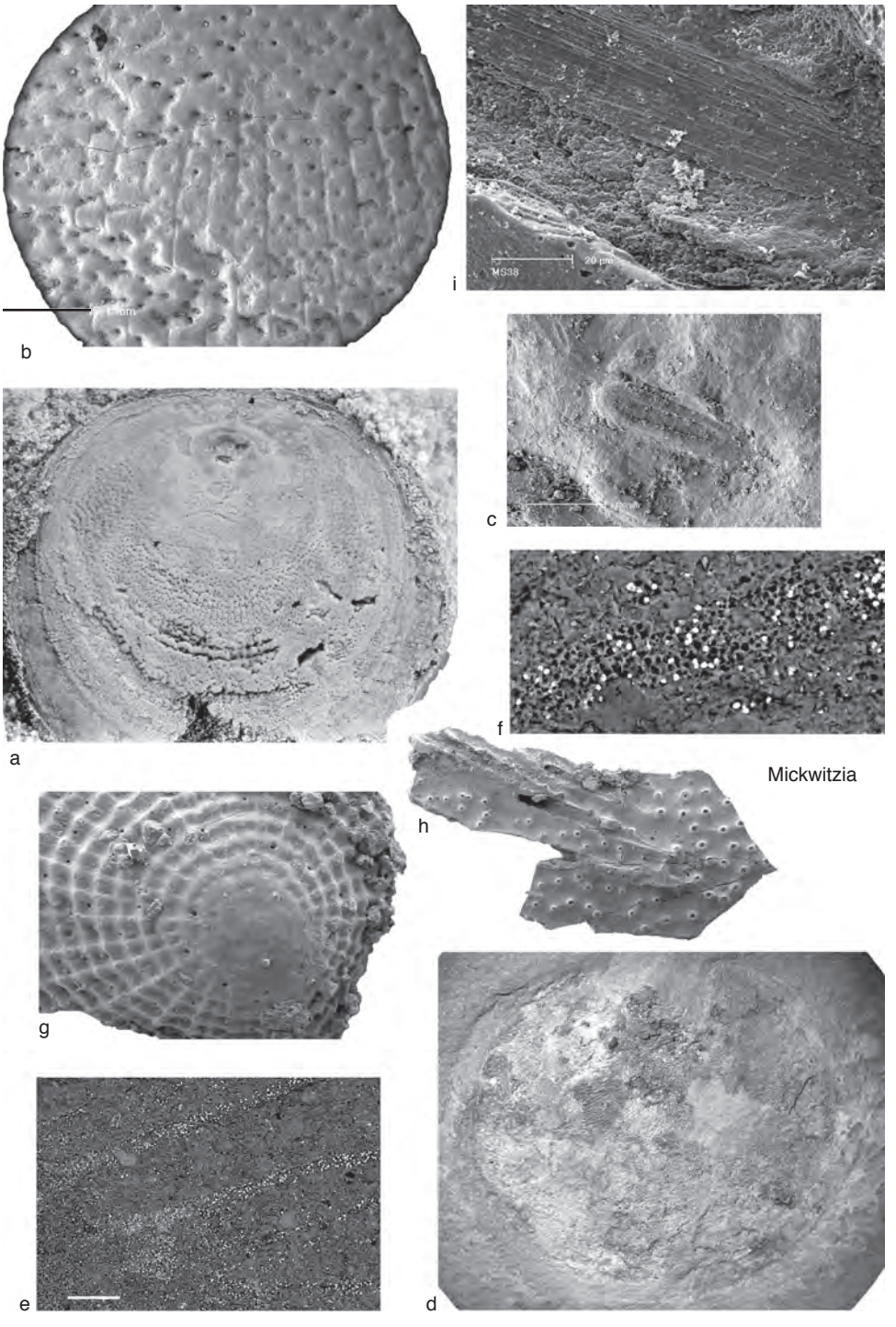



FIG. 1711. Mickwitziids (p. 2581–2582).

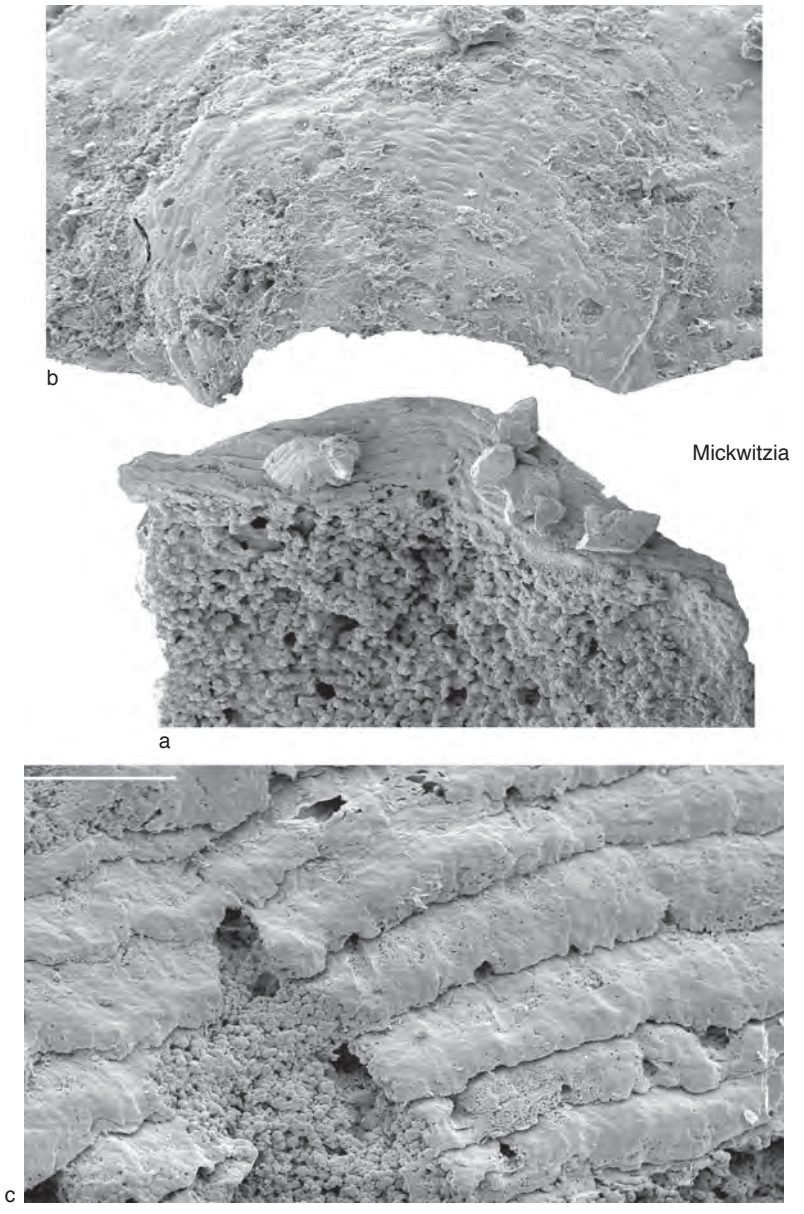



FIG. 1712. Mickwitziids (p. 2581–2582).

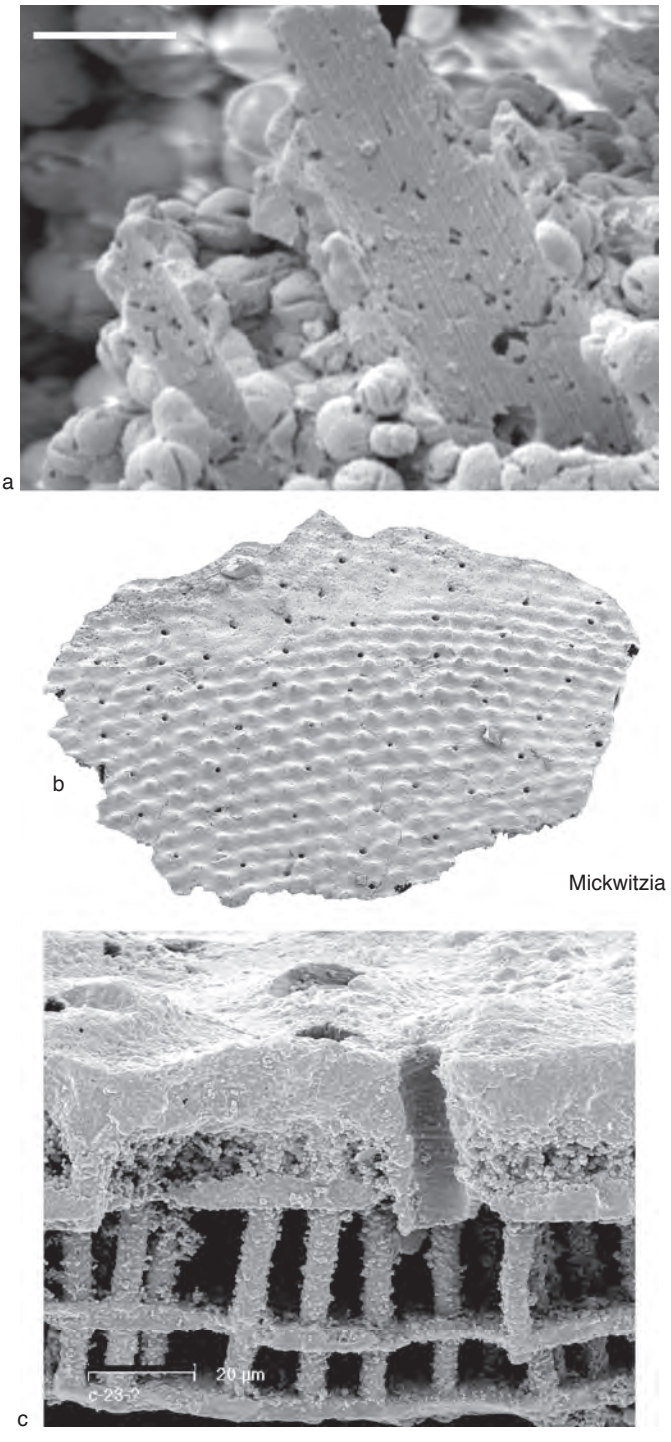



FIG. 1713. Mickwitziids (p. 2581–2582).

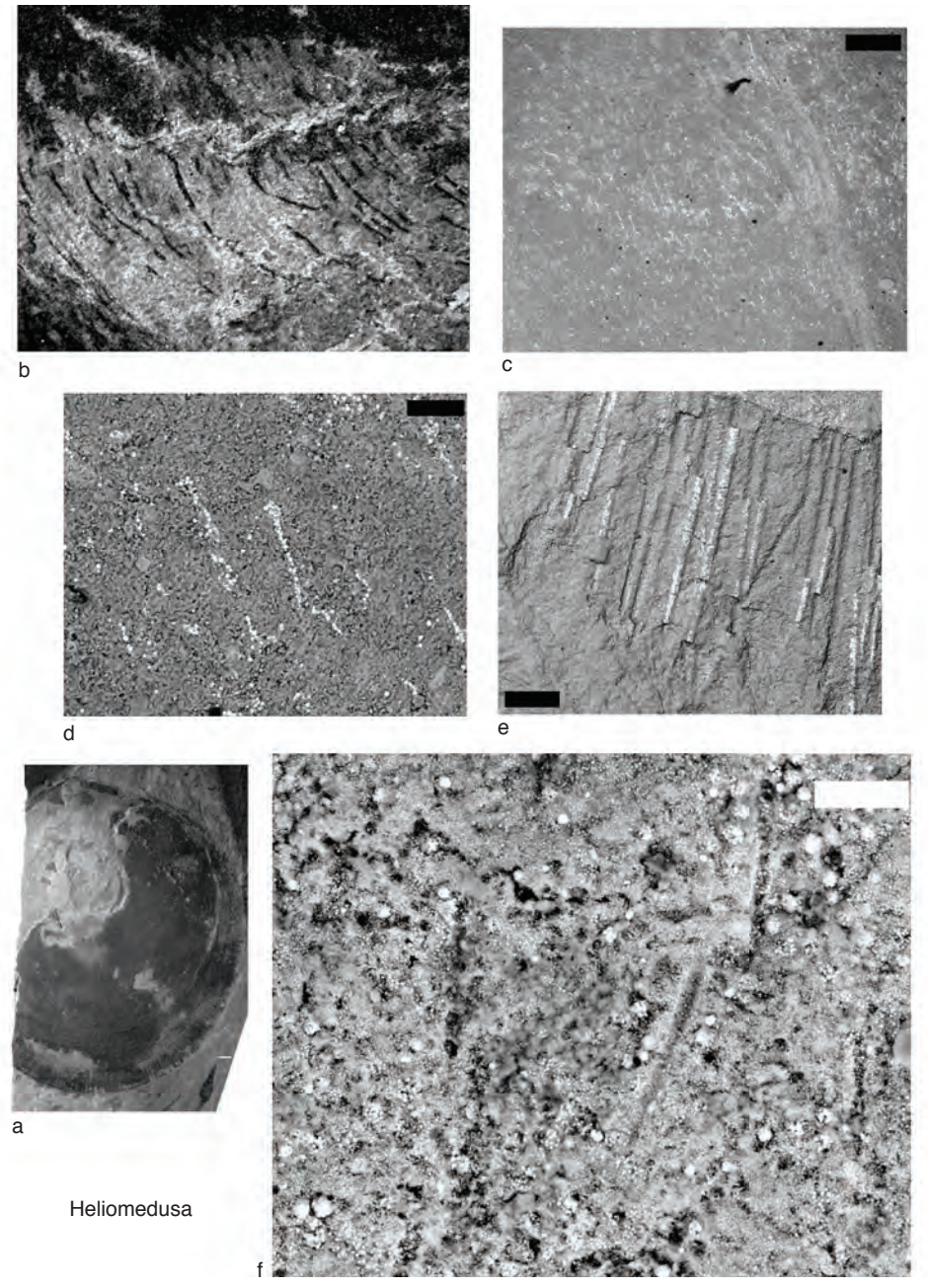



FIG. 1714. Mickwitziids (p. 2582–2590).

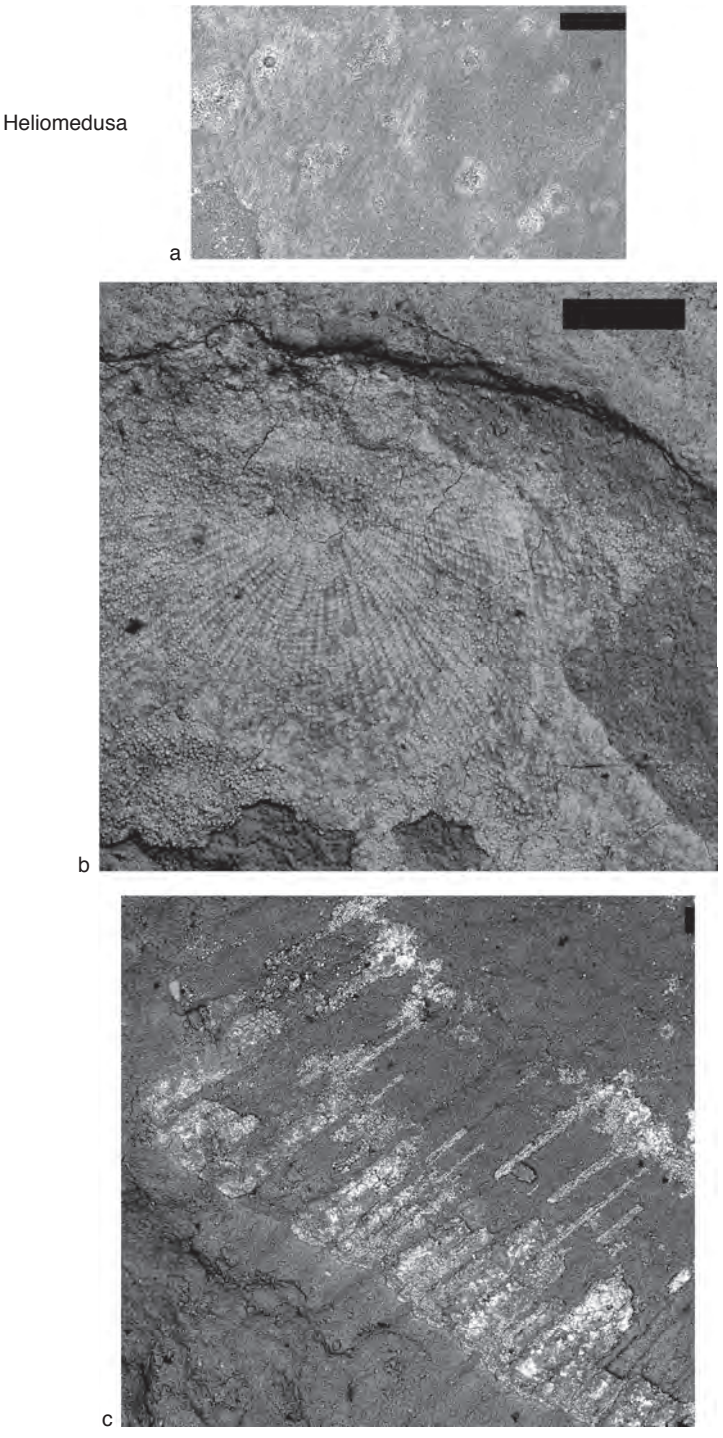



FIG. 1715. Mickwitziids (p. 2582–2590).

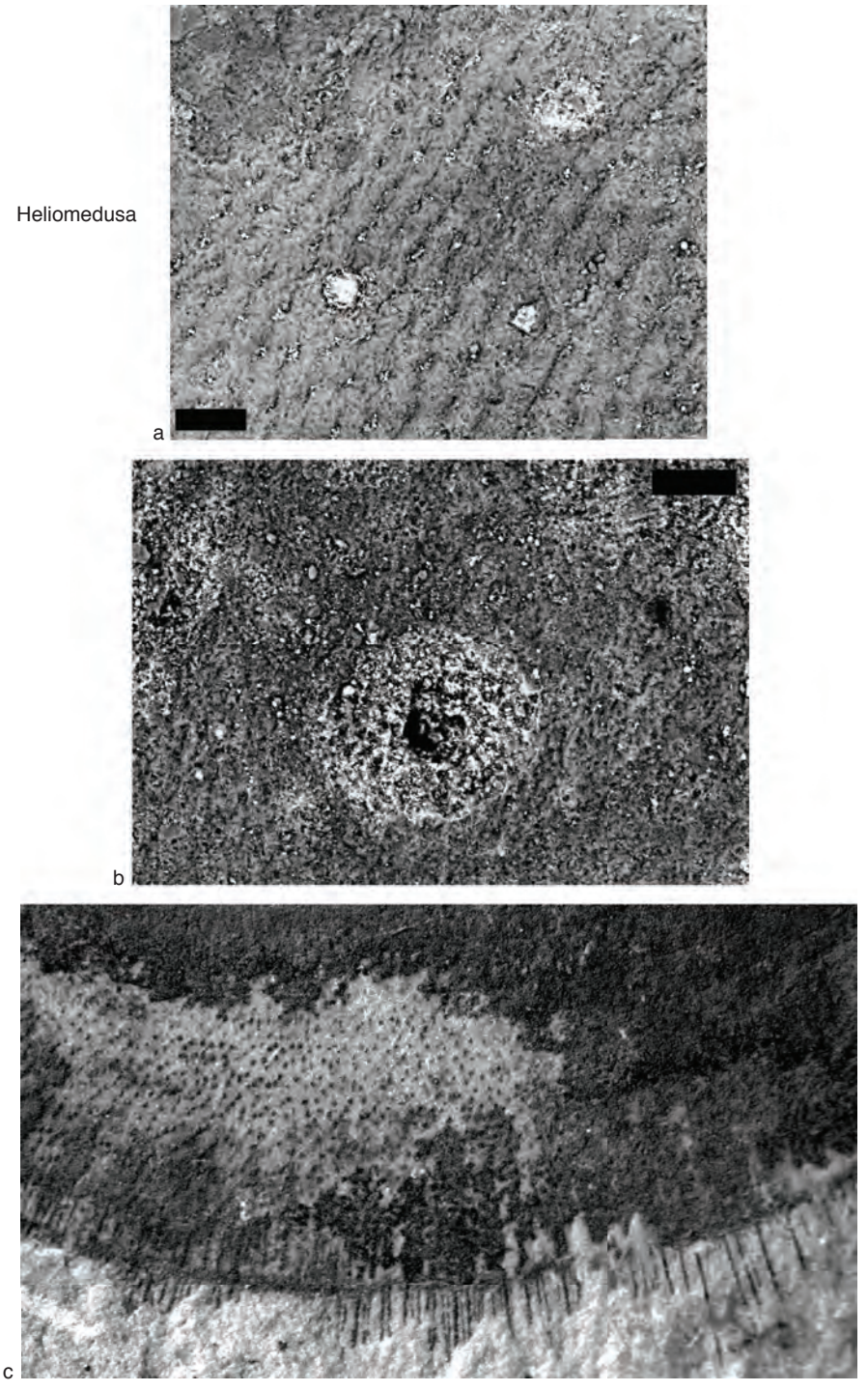



FIG. 1716. Mickwitziids (p. 2582–2590).

1715*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* apex of dorsal valve exterior, showing delineated juvenile shell, with rows of pustules, ×40; *b,* detail of anterolateral margin, showing parallel thick tubes, with pyritized spinelike setae, NIGP11, ×30; *c,* detail of punctate shell structure with thick orthogonal canals exposed on exfoliated surface of ventral valve exterior, ×40 (new).——FIG. 1716*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* detail of anterior margin showing punctate shell structure with openings of thick canals and preserved thick spinelike setae, as well as thinner (=possible marginal) setae, NIGP33, ×7; *b,* detail of one canal showing wall and central canal, width may have been enlarged during taphonomy, ×150; *c,* detail of pustulose ornamentation, with openings (and pyritized matter inside, which may represent setae) of orthogonal canals close to umbo, NIGP9, ×200 (new).

# CRANIATA

LEONID E. POPOV,[1] MICHAEL G. BASSETT,[1] and LARS E. HOLMER[2]

[[1]National Museum of Wales; and [2]University of Uppsala]

## Subphylum CRANIIFORMEA Popov & others, 1993 Class CRANIATA Williams & others, 1996

POPOV, BASSETT, and HOLMER (2000) reviewed the problems surrounding the classification of the groups included currently within the Craniata. In most previous phylogenetic models it was assumed that the three main groups of craniates, the Craniidae, Craniopsidae, and Trimerellidae, had originated from separate organophosphatic-shelled ancestors around the Ordovician, approximately (e.g., WILLIAMS & ROWELL, 1965c, fig. 141). The craniates form a monophyletic group in the analyses by HOLMER and others (1995), POPOV, HOLMER, and BASSETT (1996), and POPOV, HOLMER, and BASSETT (2000, fig. 1), whereas several cladograms in the studies by WILLIAMS and others (1996) and WILLIAMS, CARLSON, and BRUNTON (2000) were inconclusive, in particular regarding the phylogenetic position of the craniates relative to the class Chileata. This problem clearly needs further study, and the phylogenetic relationships between the three orders of craniates are still unresolved. The enigmatic *Heliomedusa* SUN & HOU from the Early Cambrian Chengjiang Lagerstätte (Yu'anshan Formation), Yunnan, was most recently assigned provisionally to the order Craniopsida within the Craniata (POPOV & HOLMER, 2000a; ZHANG, HOU, & EMIG, 2003). It can now be shown (reference to section above) to belong within the stem-group brachiopods, however, together with *Mickwitzia*. Thus, there is no longer any member of the class Craniata recorded from the Lower Cambrian, with only a potential Middle Cambrian representative (POPOV & HOLMER, 2000a), and the Cambrian origin of the craniiforms remains a problem.

Potential synapomorphies of the Craniata include possession of a nonfibrous carbonate shell and the lack of a pedicle. The mode of attachment of modern craniids may be important for understanding the origin and evolution of the brachiopod holdfast, however; WILLIAMS, BRUNTON, and MACKINNON (1997, p. 353) proposed that the attachment of modern *Novocrania* (NIELSEN, 1991), which consists of a thin patch of epithelium that is central to a shell secreted holoperipherally during postlarval growth, probably had as its plesiomorphy an atrophied holdfast acting as a pedicle. It is possible that this type of attachment may possibly be close to the primitive type of craniiform-rhynchonelliform pedicle. No craniate preserves any clear trace of a larval shell (CHUANG, 1977; but see FREEMAN & LUNDELIUS, 1999 for a contrasting view), indicating that their ontogeny was like that of Recent *Novocrania* (NIELSEN, 1991), where the first shell is secreted only after