

Wenlock, Arctic Canada; dorsal valve interior, $\times 3.3$ (Zhang, 1989b).

Placotriplesia AMSDEN, 1968, p. 40 [**Triplesia praecipta* ULRICH & COOPER, 1936a, p. 346; OD]. Smooth uniplicate shells resembling *Triplesia* but lacking monticulus and cowl on grooved cardinal process. *Silurian* (Wenlock): USA (Arkansas, Oklahoma, Tennessee), Bohemia, England, Estonia.—FIG. 496, 3a–d. **P. praecipta* (ULRICH & COOPER), Wenlock, Arkansas, Oklahoma; a–c, ventral, anterior, lateral views of complete shell, $\times 4$ (Amsden, 1968); d, posterior view of shell showing ventral interarea, $\times 7$ (Amsden, 1973).

Plectotreta ULRICH & COOPER, 1936a, p. 339 [**P. lindstroemi*; OD]. Outline subcircular, becoming transversely elliptical, lamellose with strong radial plications; monticulate; cardinal process grooved with small cowl. *Silurian* (lower Wenlock–lower Ludlow): northwestern Europe (Gotland, En-

gland).—FIG. 497, 2a–f. **P. lindstroemi*, Wenlock; a–d, dorsal, ventral, anterior, lateral views of complete shell, England, $\times 3.5$ (Bassett, 1972); e, ventral valve, Gotland, $\times 4$; f, damaged dorsal valve, Gotland, $\times 5$ (Wright, 1993b).

Streptis DAVIDSON, 1881, p. 150 [**Terebratula grayii* DAVIDSON, 1848, p. 331; OD]. Small, commonly twisted shells, commissure uniplicate or sinusoidal; strong concentric lamellae, developing into frills; radial ribbing variable; monticulus present; cardinal process with cowl, keeled, becoming grooved by Wenlock. *Upper Ordovician* (Cautleyan)—*Silurian* (Homeric): Europe, Kazakhstan, North America, Greenland.—FIG. 497, 3a–c. **S. grayii* (DAVIDSON), Wenlock, England; a–c, ventral, dorsal, anterior views of complete shell, $\times 3$ (Wright, 1965b).—FIG. 497, 3d. *S. undifera* (SCHMIDT), Ashgill, Estonia; dorsal valve with incomplete fourth frill, $\times 3.3$ (Hints, 1986).

BILLINGSSELLIDA

ALWYN WILLIAMS and DAVID A. T. HARPER

[The University of Glasgow; and University of Copenhagen]

Order BILLINGSSELLIDA Schuchert, 1893

[*nom. transl.* WILLIAMS & HARPER, herein, ex Billingsellidae SCHUCHERT, 1893, p. 152]

Concavoconvex to biconvex strophomenates with a long ventral interarea and a convex pseudodeltidium complementary to a chilidium, foramen apical; teeth transverse to deltidodont, supported by variably disposed dental plates; muscle scars normally well defined but without evidence of adjustor bases; inner socket ridges more or less parallel with the hinge line; notothyrial platform well developed, normally with a ridgelike cardinal process; mantle canal systems saccate to pinnate; secondary layer of shell laminar or fibrous, impunctate, rarely pseudopunctate. *Middle Cambrian–Upper Ordovician* (upper Ashgill).

The grouping of the billingselloids and clitambonitidines into a new order is prompted by the phylogenetic analyses of WILLIAMS and others (1996) but is provisional on further studies of shell structure and the closure

of the delthyrium. The secondary shell of clitambonitidines and billingselloids are respectively fibrous and laminar, which difference is also characteristic of the plectambonitoids and strophomenoids. The laths of billingselloid laminae, however, are not cross bladed but subparallel (WILLIAMS, 1970, p. 312) and may have evolved from flattened fibers. As for the delthyrial covers, WRIGHT and RUBEL (1996) have concluded that those of clitambonitidines are essentially deltidia rather than pseudodeltidia. The cover of the billingselloid delthyrium has always been described as a pseudodeltidium, although this has never been confirmed by an explicit study of young shells.

Notwithstanding these contradictions, the presence of mantle canal imprints along the ventral interareas of clitambonitidines (WRIGHT, 1994b) suggests that this group, at least, had a posterior body wall as postulated for strophomenates as a whole, while the muscle systems of both the billingselloids and clitambonitidines appear not to have included pedicle adjustors.

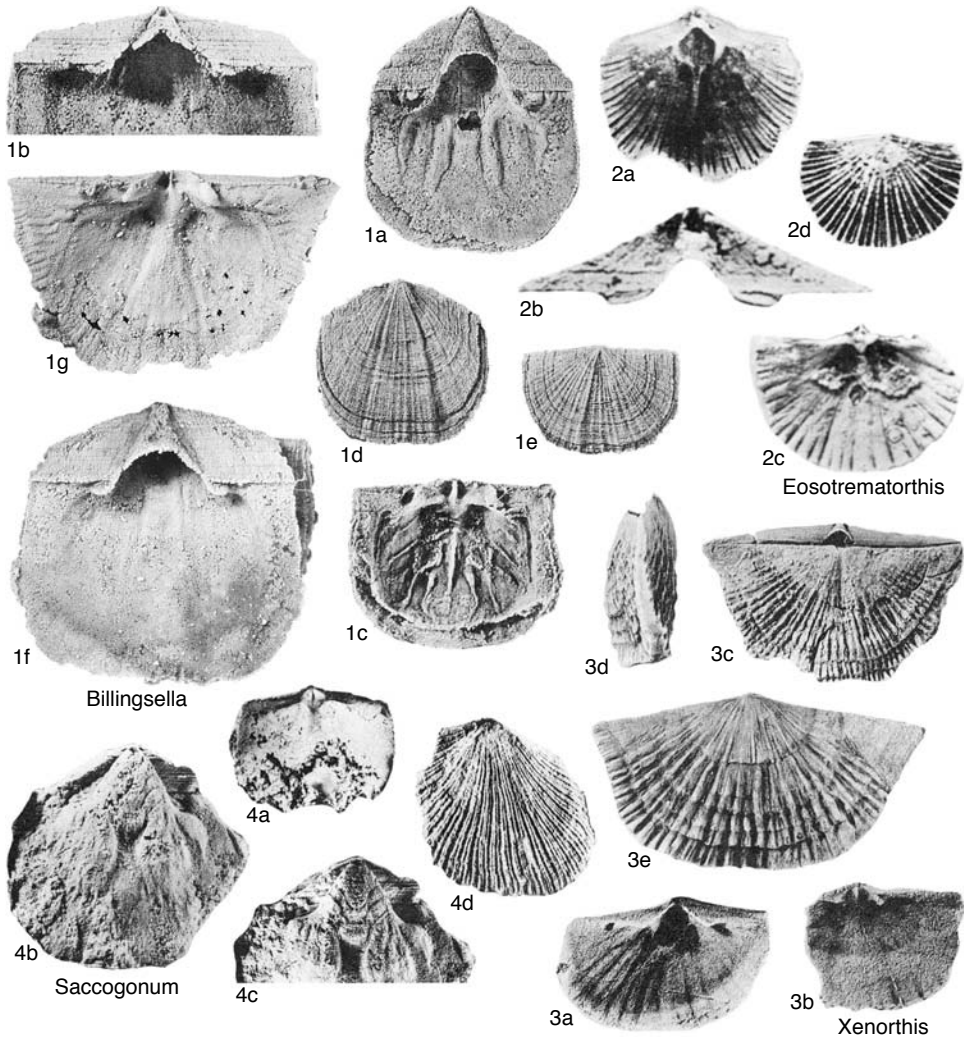


FIG. 498. Billingsellidae (p. 692).

Suborder BILLINGSELLIDINA Schuchert, 1893

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Billingsellidae SCHUCHERT, 1893, p. 152]

Variable size, normally subquadrate, bi-convex, unisulcate, costellate strophomenates with strong pseudodeltidium normally complemented by chilidium, foramen apical or vestigial; ventral interarea flat, very much longer than anacline dorsal interarea; teeth commonly large, transverse, occasionally with shallow crural fossettes, variably sup-

ported by dental plates; ventral muscle scar variable in shape and size, sockets defined by widely splayed rods or plates more or less parallel with hinge line; notothyrial platform well developed, prolonged anteriorly as median ridge and supporting simple cardinal process; dorsal adductor field subequally quadripartite; ventral and dorsal mantle canal systems basically saccate and digitate respectively; secondary layer of shell laminar, impunctate. *Middle Cambrian–Lower Ordovician* (*Arenig*).

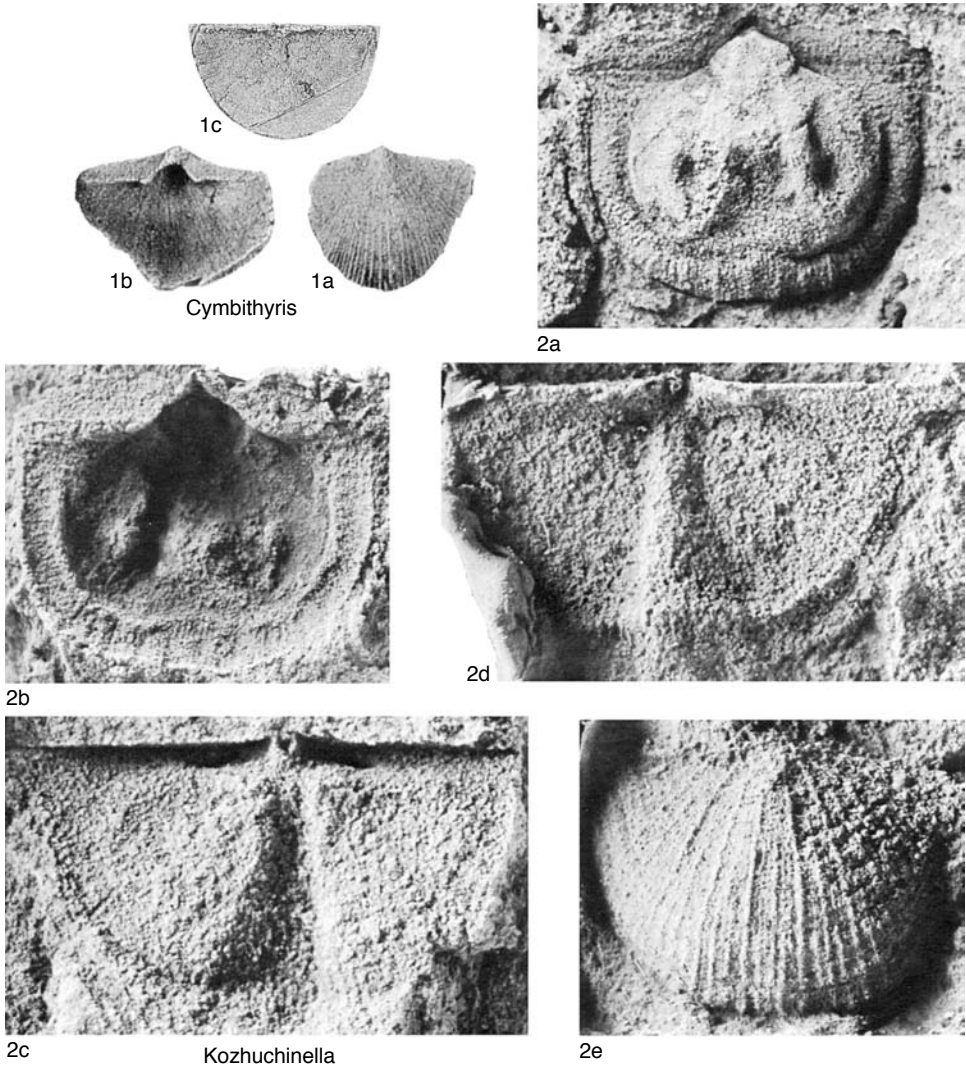


FIG. 499. Billingsellidae (p. 692).

The billingselloids have many features in common with the early Orthida and until recently have been assigned to that order. Yet the presence of a pseudodeltidium and chilidium, the development of transverse teeth and flat-lying socket plates, and especially the discovery that the secondary shell layer of *Billingsella* is composed of cross-bladed laminae in the manner of most strophomenates (WILLIAMS, 1970) recently prompted a reassignment of the superfamily

to the Strophomenida (WILLIAMS & others, 1996) and now to the order Billingsellida (WILLIAMS & HARPER, herein).

**Superfamily
BILLINGSELLOIDEA
Schuchert, 1893**

[*nom. transl.* WILLIAMS, 1965a, p. 305, ex Billingsellidae SCHUCHERT, 1893, p. 152]

Characters as for suborder. *Middle Cambrian–Lower Ordovician (Arenig).*

Family BILLINGSSELLIDAE
Schuchert, 1893

[Billingsellidae SCHUCHERT, 1893, p. 152]

Characters as for superfamily. *Middle Cambrian–Lower Ordovician (Arenig)*.

Billingsella HALL & CLARKE, 1892, p. 230 [**Orthis pepina* HALL, 1863c, p. 134; OD]. Ventribiconvex to planoconvex, multicostellate with variably developed cardinal extremities, apical pedicle foramen, convex chilidium, and orthocline to apsacline ventral interarea; dental plates divergent, ventral muscle field with long, divergent diductor scars usually deeply impressed on tonguelike callus extending anteriorly; subperipheral rim occasionally developed. *Middle Cambrian–Lower Ordovician (Tremadoc)*: cosmopolitan.—FIG. 498, 1a–f. *B. perfecta* ULRICH & COOPER, Upper Cambrian; *a*, ventral interior, Idaho–Wyoming border, ×3; *b*, details of ventral interarea, Idaho–Wyoming border, ×4; *c*, dorsal interior, Idaho–Wyoming border, ×3; *d, e*, ventral exterior, dorsal exterior, Idaho–Wyoming border, ×2 (Ulrich & Cooper, 1938); *f*, ventral interior, Wyoming, ×2.5 (Cocks, new).—FIG. 498, 1g. *B. corrugata* ULRICH & COOPER, Upper Cambrian, Oklahoma; dorsal interior, ×2.5 (Cocks, new).

Cymbithyris COOPER, 1952b, p. 5 [**C. hami*; OD]. Similar to *Billingsella* but concavoconvex with mucronate hinge line and lacking dental plates. *Lower Ordovician (Tremadoc)*: central USA.—FIG. 499, 1a–c. **C. hami*, Tremadoc, Oklahoma; ventral exterior, ventral interior, dorsal interior, ×2 (Cooper, 1952b).

Eosotrematorthis WANG, 1955a, p. 93 [**E. sinensis*; OD]. Similar to *Billingsella* but ramicostellate with apsacline ventral interarea, recessive dental plates, rodlike socket ridges, small, subcordate ventral muscle field with lanceolate adductor track not enclosed by larger subtriangular diductor scars, and low median ridge in ventral valve. *Lower Ordovician (Arenig)*: southern China.—FIG. 498, 2a–d. **E. sinensis*, Arenig, southern China; *a*, ventral interior,

×2; *b*, posterior view of ventral valve showing details of interarea, ×4; *c*, dorsal interior, ×3; *d*, dorsal exterior, ×2 (Wang, 1955a).

Kozhuchinella SEVERINGA, 1967, p. 132 [**K. mariinica*; OD]. Similar to *Billingsella* but more concavoconvex and unequally parvicostellate; ventral muscle field suboval with broad undifferentiated adductor scar; cardinal process relatively strong; subperipheral rims well developed. *Lower Ordovician (Tremadoc)*: Siberia (Kusnetz–Altai).—FIG. 499, 2a–e. **K. mariinica*, Tremadoc, Siberia; *a, b*, internal mold, rubber replica of ventral valve, ×9; *c, d*, internal mold, rubber replica of dorsal valve, ×10; *e*, rubber replica of ventral exterior, ×7 (Cocks & Rong, 1989).

Saccogonum HAVLÍČEK, 1971a, p. 27 [**S. saccatum*; OD]. Similar to *Billingsella* but strongly dorsibiconvex with obtuse cardinal extremities, vestigial pedicle foramen and apsacline ventral interarea; lacking chilidium and dental plates; undifferentiated ventral muscle scar suboval with short postero-medial ridge; ventral gonocoels distended to occupy *vascula media* and *vascula myaria*. *Upper Cambrian*: Morocco.—FIG. 498, 4a–d. **S. saccatum*, Upper Cambrian, Morocco; *a*, internal mold of dorsal valve, ×2; *b*, internal mold of ventral valve, ×2; *c*, posterior part of internal mold of ventral valve, ×2; *d*, rubber replica of ventral exterior, ×2 (Havlíček, 1971a).

Xenorthis ULRICH & COOPER, 1936b, p. 620 [**Strophomena stosei* BASSLER, 1919, p. 250; OD]. Transversely semioval with acute cardinal extremities, subequally biconvex, uniplicate, ramicostellate; foramen vestigial, ventral interarea apsacline; dental plates vestigial, ventral muscle scar subcordate with wide adductor track gently elevated anteriorly; cardinal process simple, ridgelike; dorsal mantle canal digitate. *Upper Cambrian–Lower Ordovician (Tremadoc)*: eastern USA.—FIG. 498, 3a–e. **X. stosei* (BASSLER), Upper Cambrian, Maryland; *a*, ventral interior, ×3; *b*, dorsal interior, ×4; *c, d*, dorsal, lateral views of conjoined valves, ×2; *e*, ventral exterior, ×2 (Ulrich & Cooper, 1938).

CLITAMBONITIDINA

MADIS RUBEL and A. D. WRIGHT

[University of Tartu, Estonia; and Queen's University, Belfast]

Suborder CLITAMBONITIDINA Õpik, 1934

[*nom. correct.* WILLIAMS, 1965c, p. 346, *pro* suborder Clitambonoidea ÕPIK, 1934, p. 75]

Concavoconvex to convexoconcave strophic, deltidodont shells with overwhelmingly costellate ribbing and smooth or filose to imbricate concentric ornament; ventral valve commonly with long procline to

apsacline ventral interarea and arched deltidium enclosing apical pedicle foramen; teeth simple, rarely supplemented by denticles; dental plates commonly uniting to form spondylium simplex or triplex, less commonly extending directly to valve floor, may have pseudospondylium; cardinal process normally simple ridge fused with strong chilidium, set on strong transverse notothyrial platform bearing widely divergent

socket ridges; dorsal adductor field quadripartite to subflabellate; mantle canal system pinnate, more rarely saccate; secondary shell fibrous, impunctate or pseudopunctate. *Lower Ordovician (Tremadoc)–Upper Ordovician (upper Ashgill)*.

The clitambonitidines form a distinctive group of brachiopods that are not known from rocks other than of Ordovician age and, although they attained widespread distribution in the shallow seas of the time, are particularly associated with the Baltic faunas of Estonia and western Russia (Ingria). Like other groups developing in the Early Ordovician, there is considerable intraspecific variation of characters, which later become stable elements both in clitambonitidine genera and in other articulated brachiopods. This variability means that definitive ancestral stocks are still being sought. The PAUP analyses of WILLIAMS and others (1996) suggest an origin from somewhere within the billingselloid plexus, but the clitambonitidine position in the strophomenates is uncertain, and a possible origin from Late Cambrian fibrous orthide stocks with open delthyria and dental plates (WRIGHT, 1996) cannot be ruled out. The oldest known clitambonitidine is the Tremadoc *Protambonites* from Bohemia, while the long-ranging and widespread *Vellamo* is one that persists into the latest Hirnantian age of the Ashgill.

Vellamo (Fig. 500) may be regarded as having a fully developed clitambonitidine morphology with its wide hinge, ventribiconvex profile and costellate exterior; a ventral valve with a long interarea, convex deltidium perforated by a large foramen and strong spondylium; and a dorsal valve with a well-developed chilidium, simple, ridgelike cardinal process, and laterally directed socket ridges. Its fibrous shell substance is standard, but the impunctate nature is not, with that of the gonambonitids being strongly pseudopunctate. Shell such as this is commonly associated with the plectambonitoids, with many features of shell morphology also reflecting divergences away from the standard assemblage of characters toward those

more closely associated with other brachiopod groupings.

Such divergencies in the external form include a resupinate profile (*Antigonambonites*), a radial ornament that may be fine enough (*Raunites*) to mimic a strophomenoid, a concentric ornament of regular or irregular fila, and/or lamellae or imbrications (*Clitambonites*). With strong ribbing, a reticulate pattern may develop (*Lacunarites*), with the possibility of spines (*Gonambonites*) and tubulose ribs (*Estlandia*). Aditicles are the most common form of perforation of the ribs and may pass through to the interior behind the margin (*Kullervo*); arrugiae (WRIGHT, 1981) developing into spines are known from *Acanthotoechia*. Both interareas are always developed although the length varies; the delthyrium may uncommonly be open (*Oslogonites*) or with small deltidial plates (*Apomatella*); the large foramen of the deltidium may develop a distorted, collarlike extension (*Kullervo*), or become sealed as in many stocks (*Clitambonites*, *Clinambon*, *Estlandia*); no pseudodeltidium has yet been confirmed. There is evidence that the shell of high, semicircular chilidia as in *Clitambonites* is laid down beneath the deltidium internally (WRIGHT & RUBEL, 1996). The notothyrium may alternatively have a smaller triangular chilidium (*Estlandia*), a pair of chilidial plates (*Tritoechia*), or remain open (*Oslogonites*).

Internally, the dominating feature of the ventral valve is the spondylium (Fig. 501), which in *Vellamo* is a spondylium simplex but in the gonambonitids is a spondylium triplex that may be free standing (*Estlandia*) or sessile in those forms with closely opposed valves (*Antigonambonites*). The three plates supporting the free-standing spondylium triplex commonly reach the valve floor only close to the umbo; anteriorly they lose contact and are seen simply as longitudinal ridges along the undersurface of the spondylium. The spondylium triplex is mimicked in *Polytoechia* in which the dental plates pass directly to the valve floor rather than uniting above it (WILLIAMS, 1965c). Pseudospondylia are typical of the Polytoechioidea, although

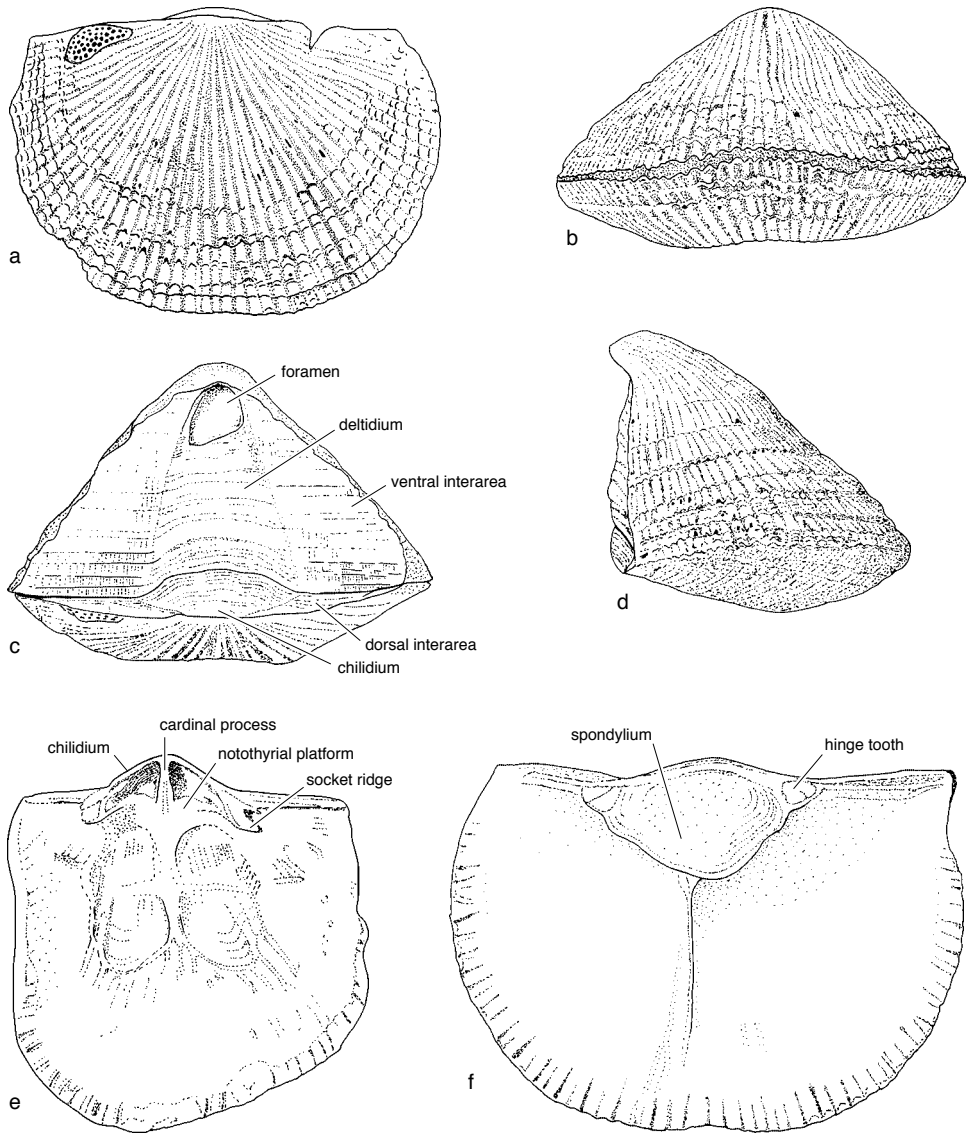


FIG. 500. Basic clitambonitidine morphology, based on specimens of *Vellamo oandoensis* ÖPIK; *a–d*, dorsal, anterior, posterior, lateral views of conjoined valves; *e*, dorsal valve interior with quadripartite adductor scars and some vascular markings preserved; *f*, ventral valve interior (adapted from Wright & Rubel, 1996).

any such structure may be lacking altogether (*Protambonites*, *Platytoechia*). Two important modifications are seen on the surface of the spondylium. That of *Clinambon* has a pair of sharply crested ridges defining the adductor scars laterally, while in *Kullervo* a pair of medianly directed plates almost isolate a lower central chamber (hemisyrinx).

In the dorsal valve, the notothyrial platform may possess ancillary ridges additional to the commonly strong cardinal process, but their variability from strong development to complete absence within species casts considerable doubt on their continued use as generic characters. Variation in the adductor muscle scar pattern is from subquadrate

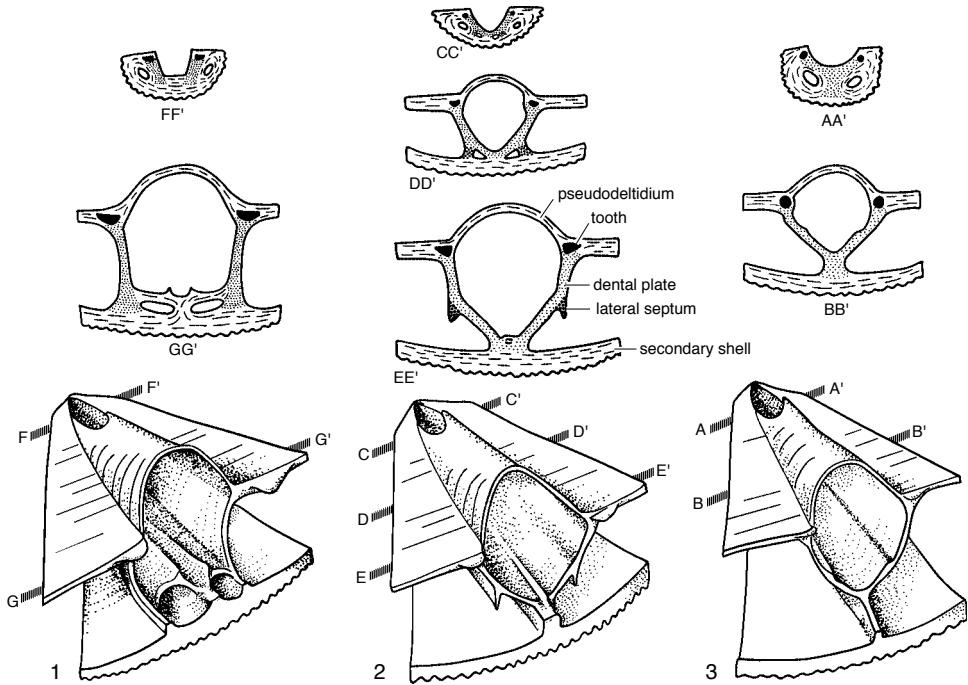


FIG. 501. Parts of three different clitambonitidine ventral valves illustrating spondylia, with sections showing attitudes of dental plates; 1, polytoechiid; 2, gonambonitid; 3, clitambonitid (adapted from Williams & Wright, 1965).

(*Clitambonites*) to radial (*Polytoechia*) or even subpetalloid (*Kullervo*). Relative length of the anterior and posterior pairs may be consistent within a genus or may not (*Vellamo*). Subperipheral rims occur widely in either valve.

The mantle canals of both valves were considered to have a pinnate pattern (WILLIAMS, 1965c) but in *Atelelasma*, *Apomatella*, *Neumania*, and *Hemipronites*, at least the ventral valves differ in displaying a saccate pattern (WRIGHT & RUBEL, 1996). This suggests retention of the ancestral condition in these stocks. Mantle canals are also now known to occur on the ventral interareas (WRIGHT, 1994b).

WILLIAMS (1965c) divided the suborder into two superfamilies, based primarily on the impunctate nature of the shell in the clitambonitaceans and the pseudopunctate shell of the gonambonitaceans. Resulting from a cladistic analysis of 38 morphological characters, along with stratigraphic appearance, in a PAUP program, the 32 accepted

genera are herein recast into the superfamilial groupings of polytoechioids and clitambonitoids. The latter is spondylial bearing and contains the pseudopunctate gonambonitids in addition to the sister family of impunctate clitambonitids.

Superfamily CLITAMBONITOIDEA Winchell & Schuchert, 1893

[*nom. transl.* RUBEL & WRIGHT, herein, ex Clitambonitacea COOPER, 1956, p. 511, *nom. correct. pro* superfamily Clitambonacea SCHUCHERT, 1929, p. 15, *nom. transl. ex* Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377; *emend.*, RUBEL & WRIGHT, herein]

Dental plates form spondylium; shell substance impunctate or pseudopunctate. *Ordovician* (lower *Arenig*–upper *Ashgill*).

Family CLITAMBONITIDAE Winchell & Schuchert, 1893

[Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377]

Well-developed deltidium or rarely deltidial plates; dental plates united to form spondylium simplex; dorsal adductor scars

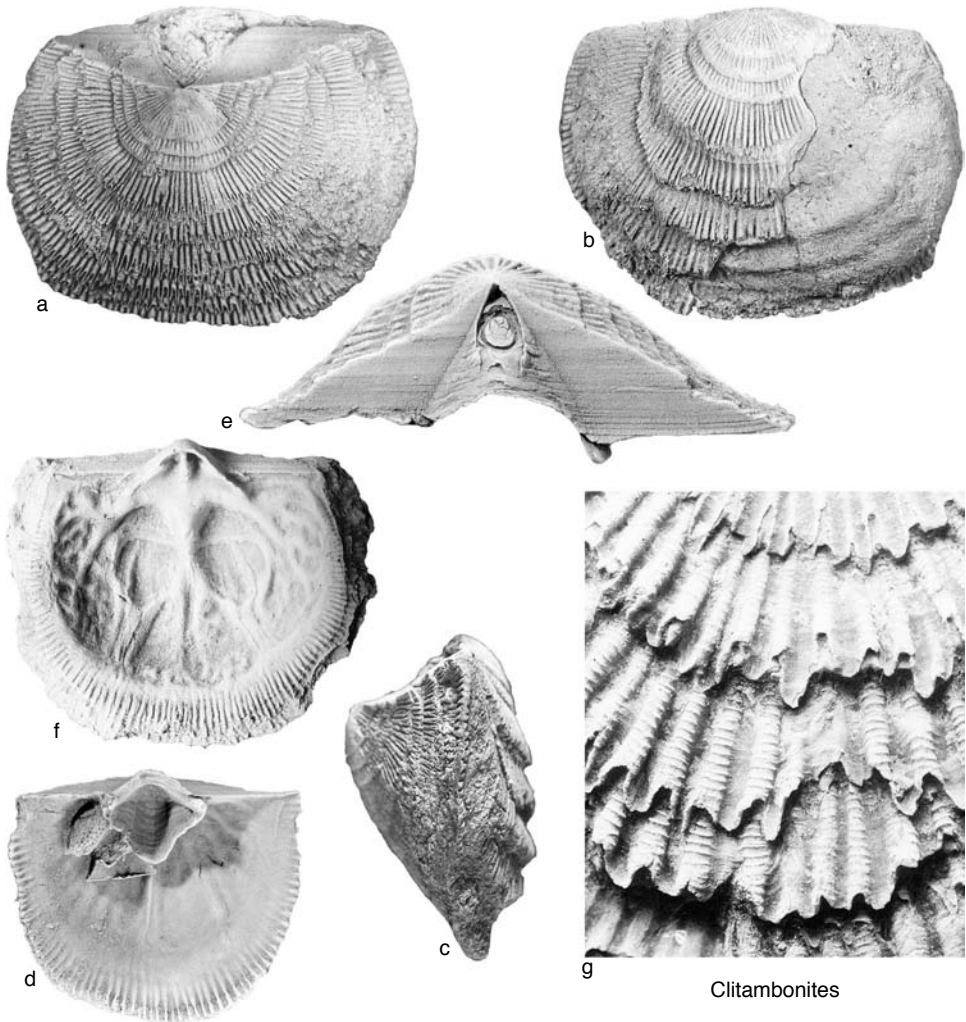


FIG. 502. Clitambonitidae (p. 696).

quadrate; aditricles common. *Ordovician* (*Arenig–upper Ashgill*).

Clitambonites PANDER, 1830, p. 70, *nom. correct.* AGASSIZ, 1846, p. 90 [**Pronites adscendens* PANDER, 1830, p. 71; SD HALL & CLARKE, 1892, p. 234] [= *Klitambonites* PANDER, 1830, p. 70, *nom. neg.*; *Pronites* PANDER, 1830, p. 71, obj.; *Prionites* FISCHER DE WALDHEIM, 1834, p. 288, invalid intentional spelling of previously published name; *Orthisina* D'ORBIGNY, 1847, p. 267, obj.]. Planoconvex to ventribiconvex shells with apsacline to procline ventral interareas, coarse costellae, and strong, concentric imbrications. *Ordovician* (*Arenig–lower Caradoc*): Estonia, Russia, Norway, Sweden, China.—FIG. 502a–c. **C. adscendens* (PANDER),

Llanvirn, Ingria; ventral, dorsal, lateral views of conjoined valves, $\times 2$ (Williams, 1965c).—FIG. 502d,e. *C. squamatus* (PAHLEN), Llandeilo, Estonia; d, ventral valve interior, $\times 2$; e, interarea, $\times 4$ (Wright & Rubel, 1996).—FIG. 502f,g. *C. schmidti* (PAHLEN) *epigonus* ÖPIK, lower Caradoc, Estonia; f, dorsal valve interior, $\times 1.5$; g, ornament, $\times 6$ (Öpik, 1934).

Apomatella SCHUCHERT & COOPER, 1931, p. 245 [**Orthisina ingrca* PAHLEN, 1877, p. 48; OD]. Transverse, subconical ventral valve with procline interarea and small deltidial plates; aditricles lacking; spondylium shorter than in *Neumania*. *Lower Ordovician* (*upper Arenig, ?lower Llanvirn*): Norway, Estonia, western Russia (Ingria).—FIG. 503,1a–e. **A. ingrca* (PAHLEN), Arenig, Ingria; a–c, exterior, interior, lateral views of ventral valve, $\times 4$ (Wright,

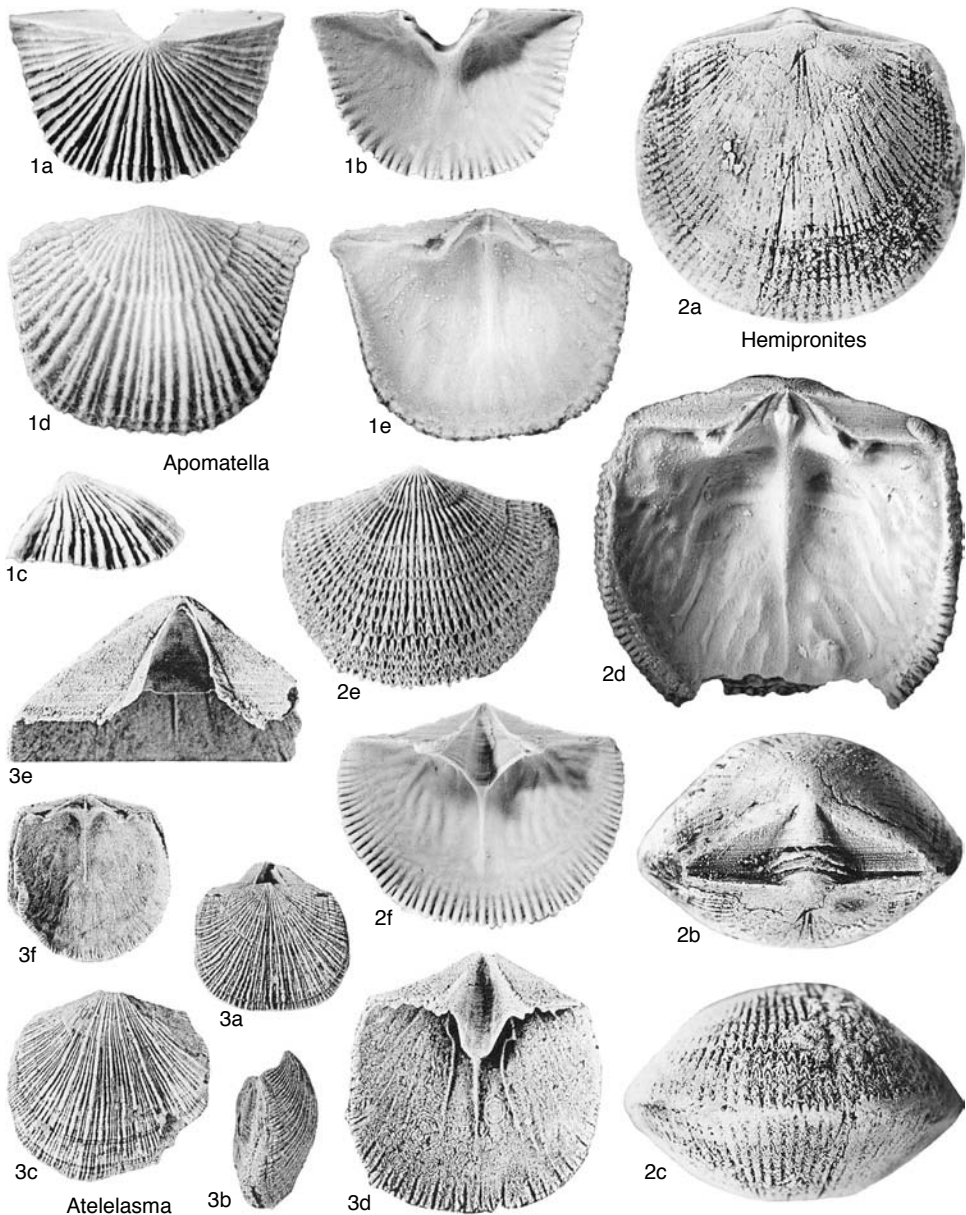


FIG. 503. Clitambonitidae (p. 696–701).

1994b); *d, e*, exterior, interior views of dorsal valve, $\times 4$ (Rubel & Popov, 1994).

Atelelasma COOPER, 1956, p. 517 [*A. perfectum*; OD]. Planoconvex to ventribiconvex subquadrate to subcircular shells; ventral interarea apsacline to procline, laterally disposed deltidial plates only; costellae with aditricles. *Ordovician (Llandeilo-lower Caradoc)*: USA (Virginia, Tennessee, Oklahoma, Alabama, Wisconsin, ?New York, ?Vermont),

Wales, Siberia, Mongolia.—FIG. 503, *3a–f*: **A. perfectum*, Llandeilo, Tennessee; *a, b*, dorsal, lateral views of conjoined valves, $\times 1$; *c*, ventral valve exterior, $\times 1$; *d, e*, ventral valve interior, ventral interarea, $\times 2$; *f*, dorsal valve interior, $\times 1$ (Cooper, 1956).

Clinambon SCHUCHERT & COOPER, 1932, p. 115 [*Anomites anomala* SCHLOTHEIM, 1822, p. 65; OD]. Hemipyramidal ventral valve with strongly procline ventral interarea, dorsal valve with long interarea

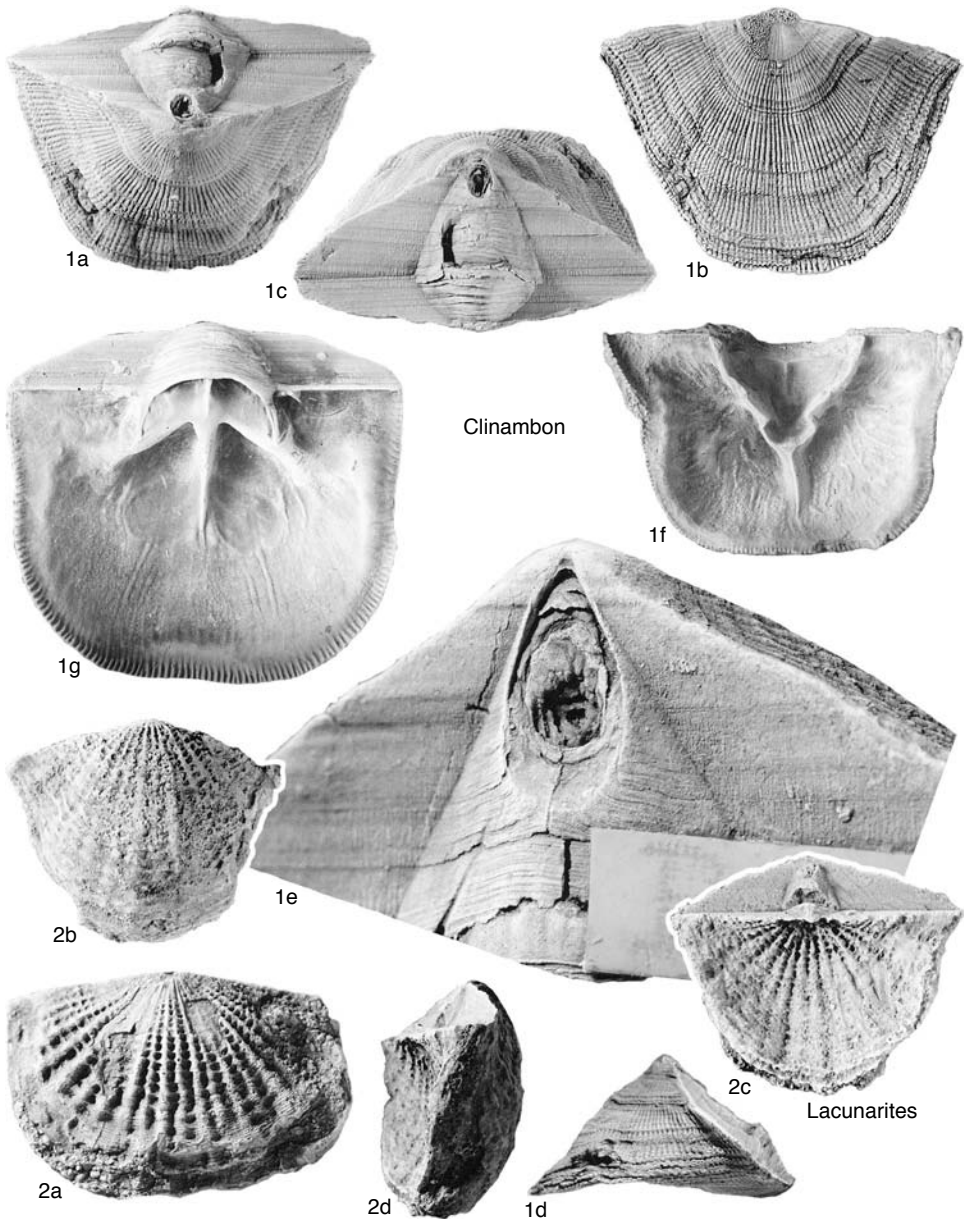


FIG. 504. Clitambonitidae (p. 697–702).

and very strong chilidium; finely costellate, without strong imbrication; ventral adductors on markedly constricted anteromedian portion of spondylium. *Ordovician* (*Caradoc*): Estonia, western Russia (Ingria).—FIG. 504, 1a–f. **C. anomalus anomalus* (SCHLOTHEIM), Caradoc, Estonia; a–d, ventral, dorsal, posterior, lateral views of conjoined valves, $\times 1.3$; e, detail of deltidium with sealed foramen, $\times 6$ (new); f, ventral valve interior, $\times 1$ (Öpik, 1934). —FIG. 504, 1g. **C. anomalus postumus* ÖPIK,

Caradoc, Estonia; dorsal valve interior, $\times 1.5$ (Öpik, 1934).

Fistulogonites NEUMAN, 1971, p. 116 [**F. novaterrensis*; OD]. Ventribiconvex, with pitted, even costellae; notothyrium open; sessile spondylium without median septum; cardinal process absent; pseudo-punctate. *Ordovician* (*Llanvirn*): Newfoundland, China.—FIG. 505, 3a–d. **F. novaterrensis*, Llanvirn, Newfoundland; a, b, holotype, external, internal molds of dorsal valve, $\times 4$; c, d, internal

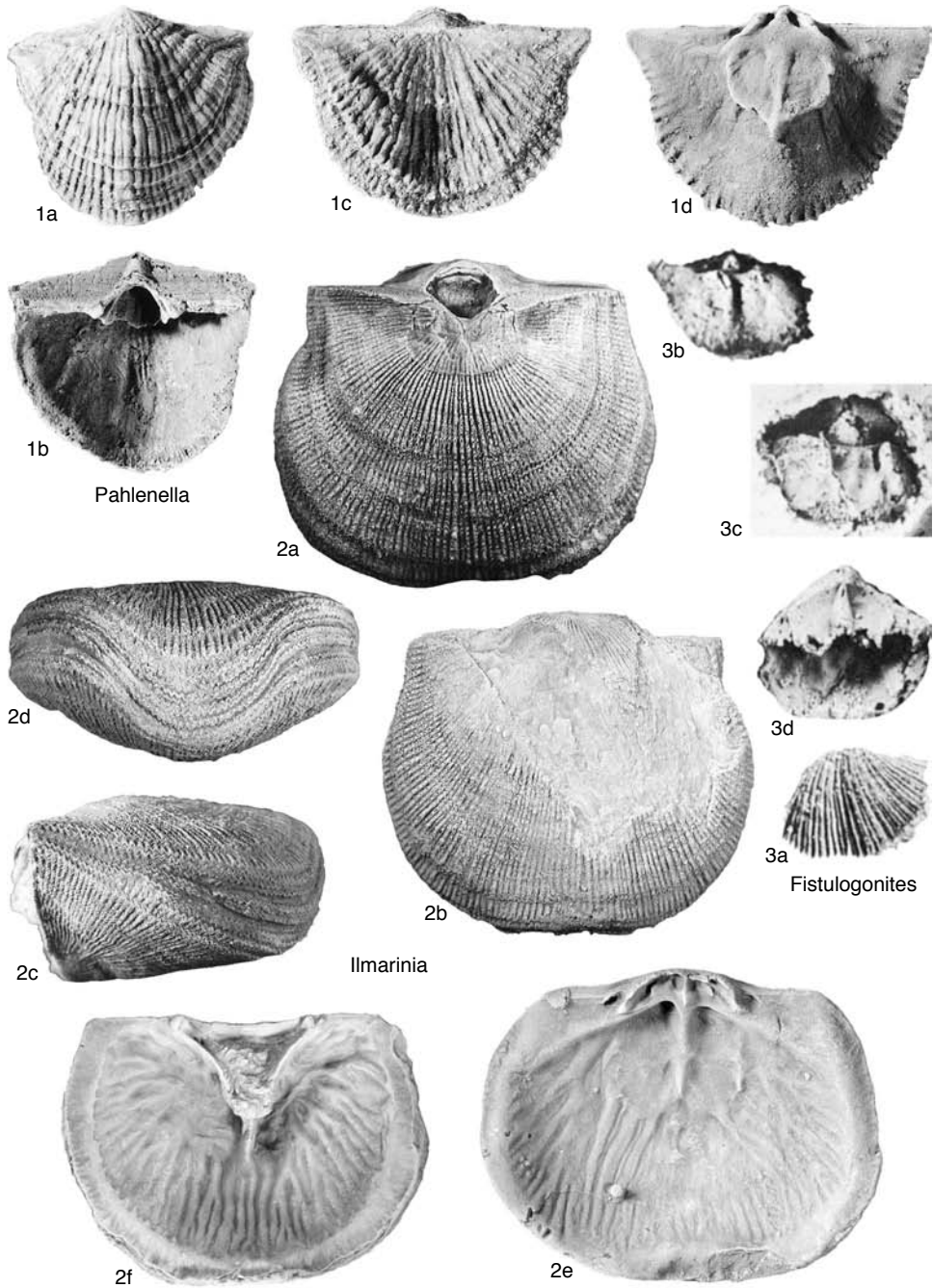


FIG. 505. Clitambonitidae (p. 698–704).

mold, latex cast of ventral valve, $\times 4$ (Neuman, 1971).

Hemipronites PANDER, 1830, p. 74 [*H. tumida*; SD DALL, 1877, p. 31] [= *Ladogiella* ÖPIK, 1934, p. 93 (type, *L. imbricata* ÖPIK, 1934, p. 93)]. Similar to

Clitambonites but strongly biconvex, with apsacline to catacline ventral interareas and finer costellae. Ordovician (upper Arenig–Llanvirn): Estonia, western Russia (Ingria), Norway.—FIG. 503.2a–c. **H. tumida*, Llanvirn, Ingria; a–c, dorsal, posterior,

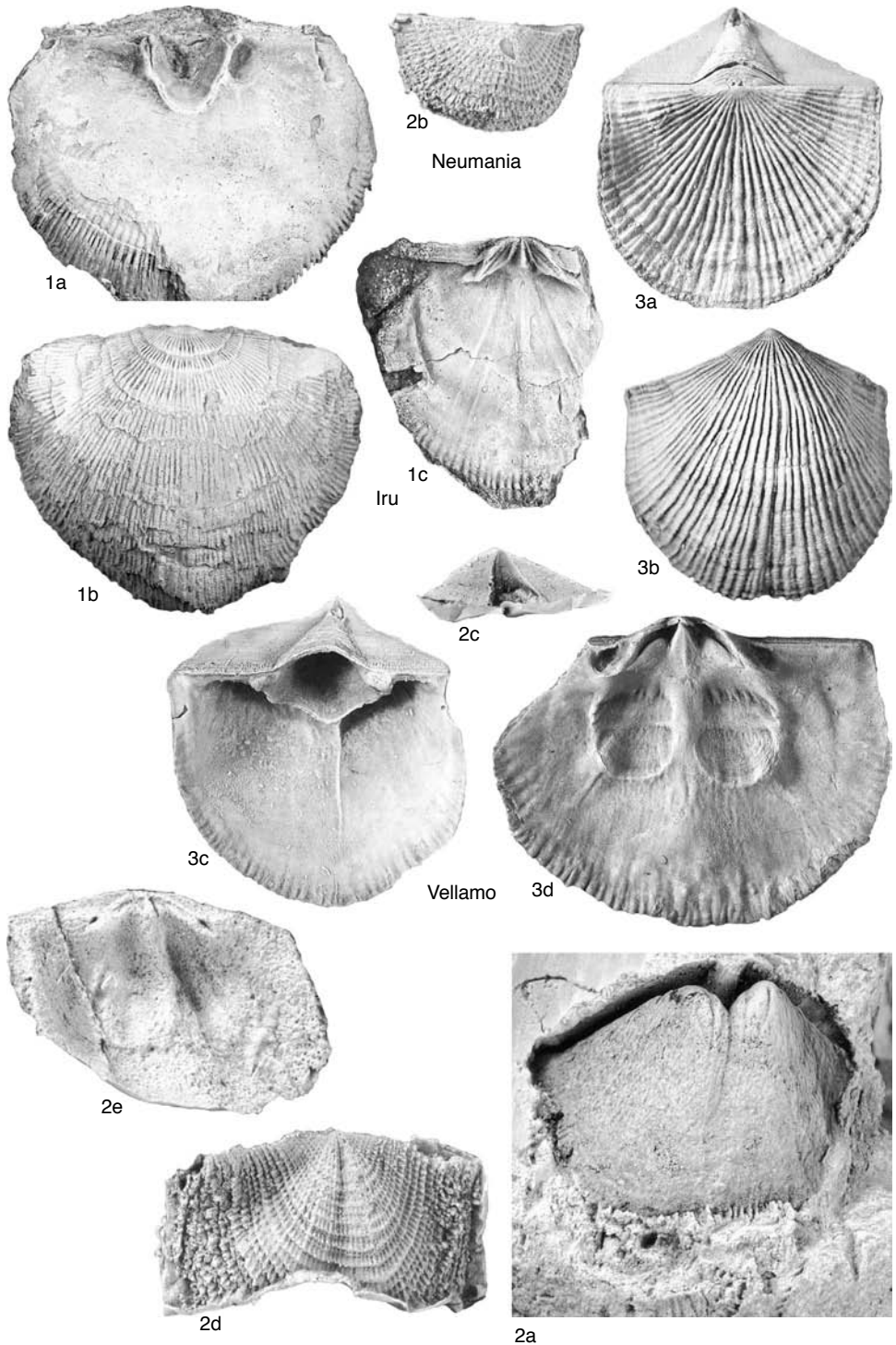


FIG. 506. Clitambonitidae (p. 701–704).

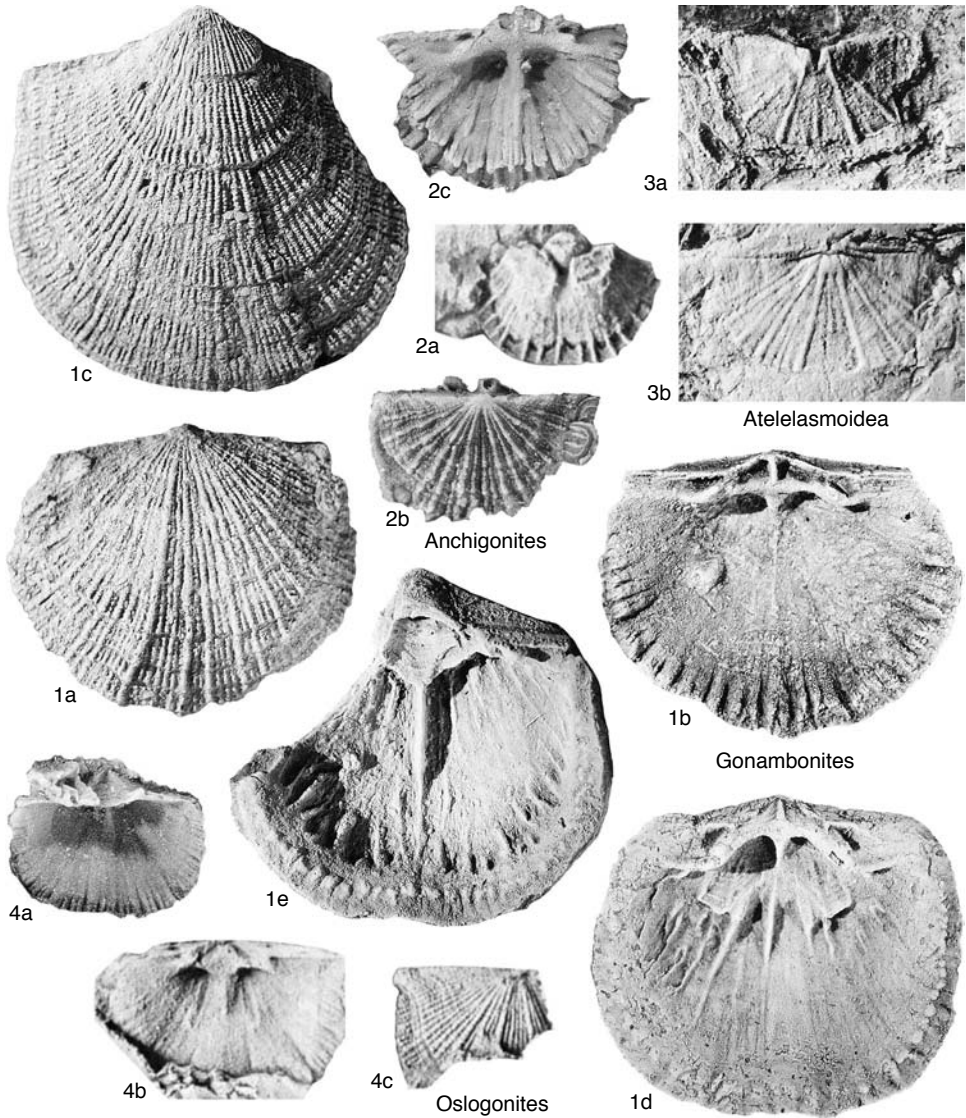


FIG. 507. Gonambonitidae (p. 704).

anterior views of conjoined valves, $\times 4.5$ (Williams, 1965c).—FIG. 503,2*d-f*. *H. imbricata* (ÖPIK), Llanvirn, Ingria; *d*, dorsal valve interior, $\times 3$ (Öpik, 1934); *e, f*, ventral valve exterior, interior, $\times 3$ (Wright, 1994b).

Ilmarinia ÖPIK, 1934, p. 125 [**Orthisina sinuata* PAHLEN, 1877, p. 44; OD]. Similar to *Clinambon* but with ventral sulcus and dorsal fold, larger foramen, reduced dorsal interarea and chilidium, and spondylial constriction only weakly developed. *Upper Ordovician (upper Caradoc–upper Ashgill)*: Estonia, Russia.—FIG. 505,2*a-d*. **I. sinuata* (PAH-

LEN), Ashgill, Estonia; ventral, dorsal, lateral, anterior views of conjoined valves, $\times 1.5$ (Williams, 1965c).—FIG. 505,2*e, f*. *I. dimorpha* ÖPIK, upper Caradoc, Estonia; *e*, dorsal valve interior, $\times 1.5$ (Wright & Rubel, 1996); *f*, ventral valve interior, $\times 1.5$ (Wright, 1994b).

Iru ÖPIK, 1934, p. 89 [**Orthisina concava* PAHLEN, 1877, p. 17; OD]. Convexoconcave, strongly imbricate and filose; weakly developed deltidial cover, and chilidial plates only; spondylium sessile. *Ordovician (Arenig–lower Llanvirn)*: Estonia, western Russia (Ingria).—FIG. 506,1*a-c*. **I. concava* (PAHLEN),

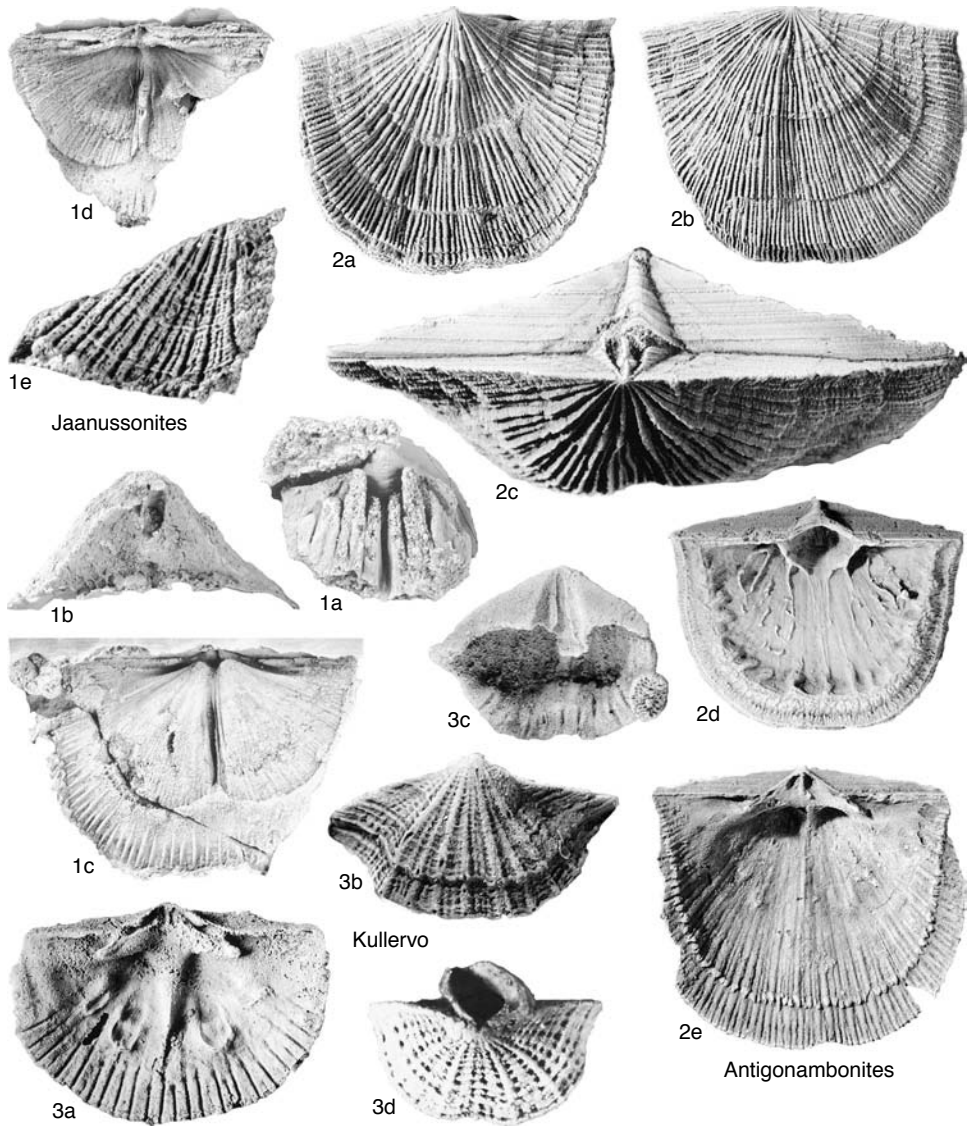


FIG. 508. Gonambonitidae (p. 704).

lower Llanvirn, Estonia; *a, b*, ventral valve interior, dorsal valve exterior, $\times 1.5$; *c*, dorsal valve interior, $\times 2$ (Williams, 1965c).

Lacunarites ÖPIK, 1934, p. 175 [**L. ilmatar*; OD]. Strongly concavoconvex; combined concentric ridges and coarse, spaced costellae producing pits in intercostal spaces; spondylium sessile. *Ordovician (Llanvirn)*: Estonia, western Russia (Ingria).—FIG. 504, 2*a–d*. **L. ilmatar*, lower Llanvirn, Estonia; *a*, ventral valve exterior, $\times 3$; *b–d*, holotype, ventral, dorsal, oblique lateral views, $\times 2$ (new).

Neumania HARPER in BRUTON & HARPER, 1981, p. 162 [*Atelelasma atlanticus* NEUMAN, 1976, p. 24; OD]. Similar to *Apomatella* but with imbricated, transverse shells. *Ordovician (lower Arenig–lower Llanvirn)*: Newfoundland, Wales, Norway, Estonia, western Russia (Ingria).—FIG. 506, 2*a–e*. **N. atlanticus* (NEUMAN), upper Arenig, Newfoundland; *a*, ventral valve internal mold, $\times 3$; *b, c*, ventral, posterior views of latex cast of ventral exterior, $\times 3$; *d*, latex cast of dorsal exterior; *e*, latex cast of dorsal interior, $\times 3$ (Neuman, 1976).

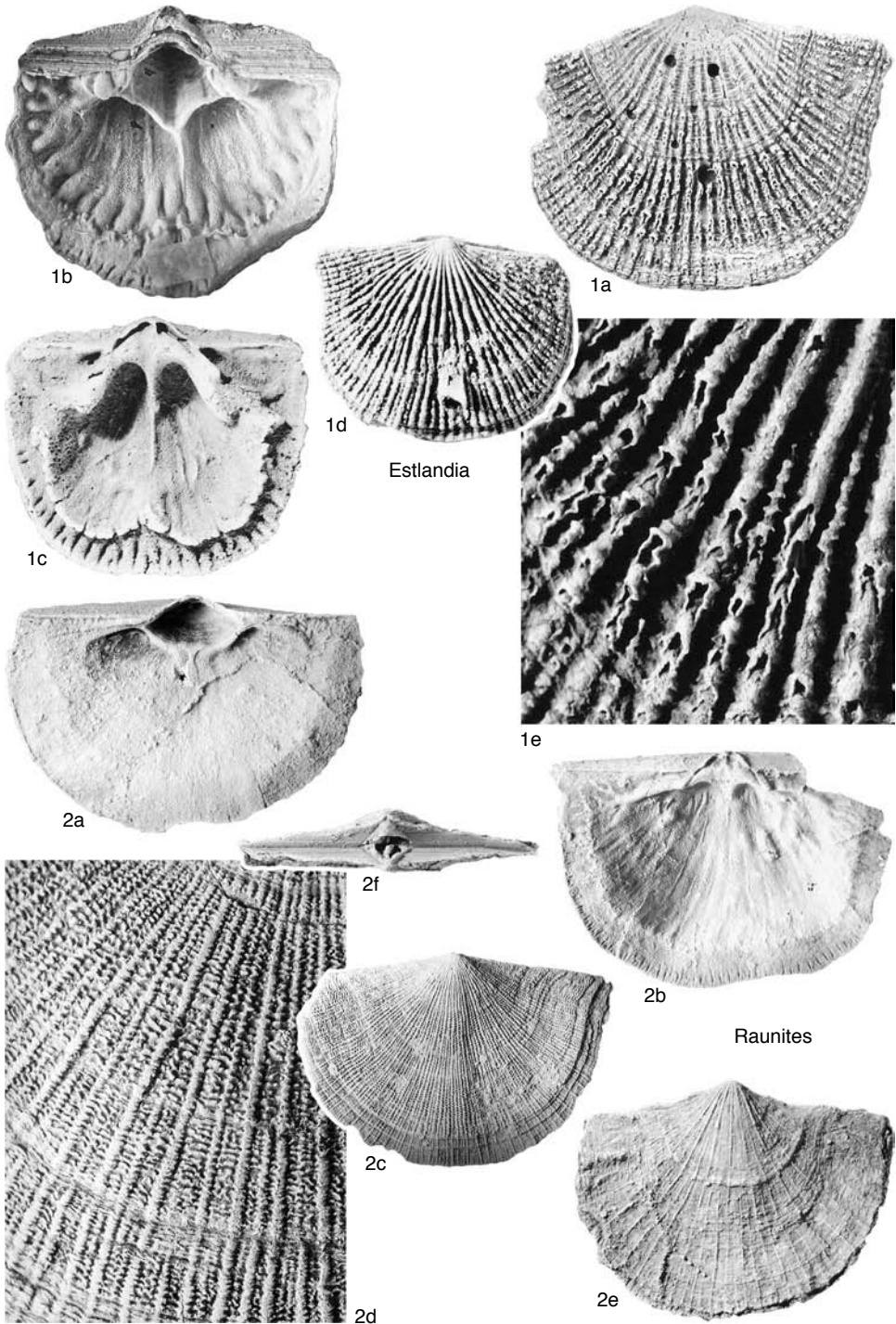


FIG. 509. Gonambonitidae (p. 704–706).

Pahlenella SCHUCHERT & COOPER, 1931, p. 245 [**Orthis trigonula* VON EICHWALD, 1840, p. 148; OD]. Strongly concavoconvex shells with close, branching coarse costellae; dorsal adductor muscles on elevated platform. *Ordovician (lower Llanvirn)*: western Russia (Ingria), Estonia.—FIG. 505, 1a–d. **P. trigonula* (VON EICHWALD), lower Llanvirn, Ingria; a, b, ventral valve exterior, interior, $\times 3$; c, d, lectotype, dorsal valve exterior, interior, $\times 3$ (new).

Vellamo ÕPIK, 1930, p. 212 [**Orthis verneuili* VON EICHWALD, 1842, p. 51]. High subpyramidal ventral and flat to gently convex dorsal valves without strong imbrications, commonly asymmetrical. *Ordovician (Llandeilo–upper Ashgill)*: Eurasia, North America, North Africa, Tasmania.—FIG. 506, 3a–d. **V. verneuili* (VON EICHWALD), Ashgill, Estonia; a, b, dorsal, ventral views of conjoined valves, $\times 1.5$; c, d, interiors of ventral, dorsal valves, $\times 2$ (Williams, 1965c).

Family GONAMBONITIDAE Schuchert & Cooper, 1931

[*nom. transl.* RUBEL, 1963, p. 92, ex Gonambonitinae SCHUCHERT & COOPER, 1931, p. 245] [=Estlandiidae ÕPIK, 1934, p. 76]

Dental plates form spondylium triplex; dorsal adductor scars mostly radiating; shell substance pseudopunctate. *Ordovician (lower Arenig–middle Ashgill)*.

Gonambonites PANDER, 1830, p. 77 [**G. latus*; SD SCHUCHERT & LEVENE, 1929, p. 63] [=Progonambonites ÕPIK, 1934, p. 138 (type, *P. estonus*)]. Unequally biconvex to convexoconcave with medium-sized foramen, commonly sealed; differentiated costellae; dorsal adductor scars strongly impressed. *Ordovician (upper Arenig–lower Llanvirn)*: Estonia, western Russia (Ingria), China.—FIG. 507, 1a, b. **G. latus*, Llanvirn, Ingria; a, b, dorsal valve exterior, interior, $\times 3$ (Rubel, 1963).—FIG. 507, 1c–e. *G. parallelus* PANDER, Llanvirn, Ingria; c, ventral valve exterior, $\times 2$; d, dorsal valve interior, $\times 2.5$ (Rubel, 1963); e, ventral valve interior, $\times 2$ (new).

Anchigonites ÕPIK, 1939, p. 136 [**A. conulus*; OD]. Concavoconvex to planoconvex; chlidial plates present. *Lower Ordovician (Arenig, ?lower Llanvirn)*: Norway, Estonia, western Russia (Ingria), China.—FIG. 507, 2a–c. **A. conulus*, upper Arenig, Norway; a, ventral valve internal mold, $\times 4$ (Õpik, 1939); b, anteriorly tilted view of latex cast of dorsal valve exterior, $\times 4$; c, latex cast of dorsal valve interior, $\times 4$ (new).

Antigonambonites ÕPIK, 1934, p. 147 [**Gonambonites plana* PANDER, 1830, p. 78; OD]. Convexoplane to resupinate, deltidium with minute, sealed foramen; costellae undifferentiated; spondylium triplex sessile. *Lower Ordovician (lower Arenig–lower Llanvirn)*: Norway, Estonia, western Russia (Ingria), Poland, Newfoundland, China.—FIG. 508, 2a–e. **A. planus* (PANDER), Arenig, Ingria; a, b, ventral,

dorsal views of conjoined valves, $\times 1.5$ (new); c, posterior view of conjoined valves, $\times 3$; d, dorsal view of ventral interior, $\times 1.5$ (Wright & Rubel, 1996); e, dorsal valve interior, $\times 2$ (new).

Atelasmaoidea ZENG, 1987, p. 225[531] [**A. typica*; OD]. Micromorphic ventribiconvex shells, ventral interarea apsacline to procline with open delthyrium and notothyrium; cardinal process absent; similar to *Oslogonites*. *Lower Ordovician (Arenig)*: central and southwestern China.—FIG. 507, 3a, b. **A. typica*, Arenig, Hubei; ventral valve, dorsal valve internal molds, $\times 9$ (Zeng, 1987).

Estlandia SCHUCHERT & COOPER, 1931, p. 245 [**Orthisina marginata* PAHLEN, 1877, p. 33; OD]. Dorsibiconvex to convexoplane shells similar to *Gonambonites* but with distinctive tubulose costellae and stronger subperipheral rims. *Ordovician (lower Llanvirn, upper Llanvirn–middle Caradoc)*: Estonia, western Russia (Ingria).—FIG. 509, 1a–e. **E. marginata* (PAHLEN), Llandeilo, Estonia; a, ventral valve exterior, $\times 2$ (Williams, 1965c); b, ventral valve interior, $\times 2$ (Õpik, 1934); c, dorsal valve interior, $\times 3$; d, dorsal valve exterior, $\times 2$; e, detail of ornament, $\times 10$ (Wright & Rubel, 1996).

Jaanussonites NEUMAN, 1976, p. 26 [**J. hornei*; OD]. Concavoconvex to ventribiconvex; intercostal spaces with fine spines, costellae with aditicles; dorsal subperipheral rim bilobed with long median ridge. *Lower Ordovician (upper Arenig)*: eastern North America (Newfoundland, Maine).—FIG. 508, 1a–e. **J. hornei*, upper Arenig, Newfoundland; a, ventral valve internal mold, $\times 2$; b, posterior view of latex cast of ventral valve, $\times 2$; c, d, dorsal valve internal mold, latex cast, $\times 1.5$; e, incomplete dorsal valve external mold, $\times 4$ (Neuman, 1976).

Kullervo ÕPIK, 1932, p. 70 [**Gonambonites panderi* ÕPIK, 1930, p. 234; OD]. Planoconvex with subpyramidal ventral valve; strong radial and concentric ornament producing reticulation; aditicles well developed; foramen commonly large, with high, irregular lip; hemisyrinx present; dorsal adductor scars strongly impressed. *Ordovician (upper Llanvirn–middle Ashgill)*: Eurasia, North America.—FIG. 508, 3a, b. **K. panderi* (ÕPIK), Llandeilo–lower Caradoc, Estonia; a, dorsal valve interior, $\times 3$ (Õpik, 1934); b, ventral valve exterior, $\times 3$ (Wright & Rubel, 1996).—FIG. 508, 3c. **K. lacunata* ÕPIK, lower Caradoc, Estonia; ventral valve interior, $\times 3$ (Wright & Rubel, 1996).—FIG. 508, 3d. **K. complexens* (WIMAN), middle Ashgill, Sweden; ventral valve exterior showing exaggerated lip to foramen, $\times 6$ (Harper, new).

Oslogonites ÕPIK, 1939, p. 133 [**O. costellatus*; OD]. Planoconvex to ventribiconvex; ventral interarea apsacline to catacline, delthyrium and notothyrium open; cardinal process absent. *Ordovician (Arenig–lower Llanvirn)*: Norway, Estonia, ?England.—FIG. 507, 4a–c. **O. costellatus*, upper Arenig, Norway; a, latex cast of ventral valve interior, $\times 4$ (new); b, c, casts of interior, exterior of dorsal valve, $\times 4$ (Õpik, 1939).

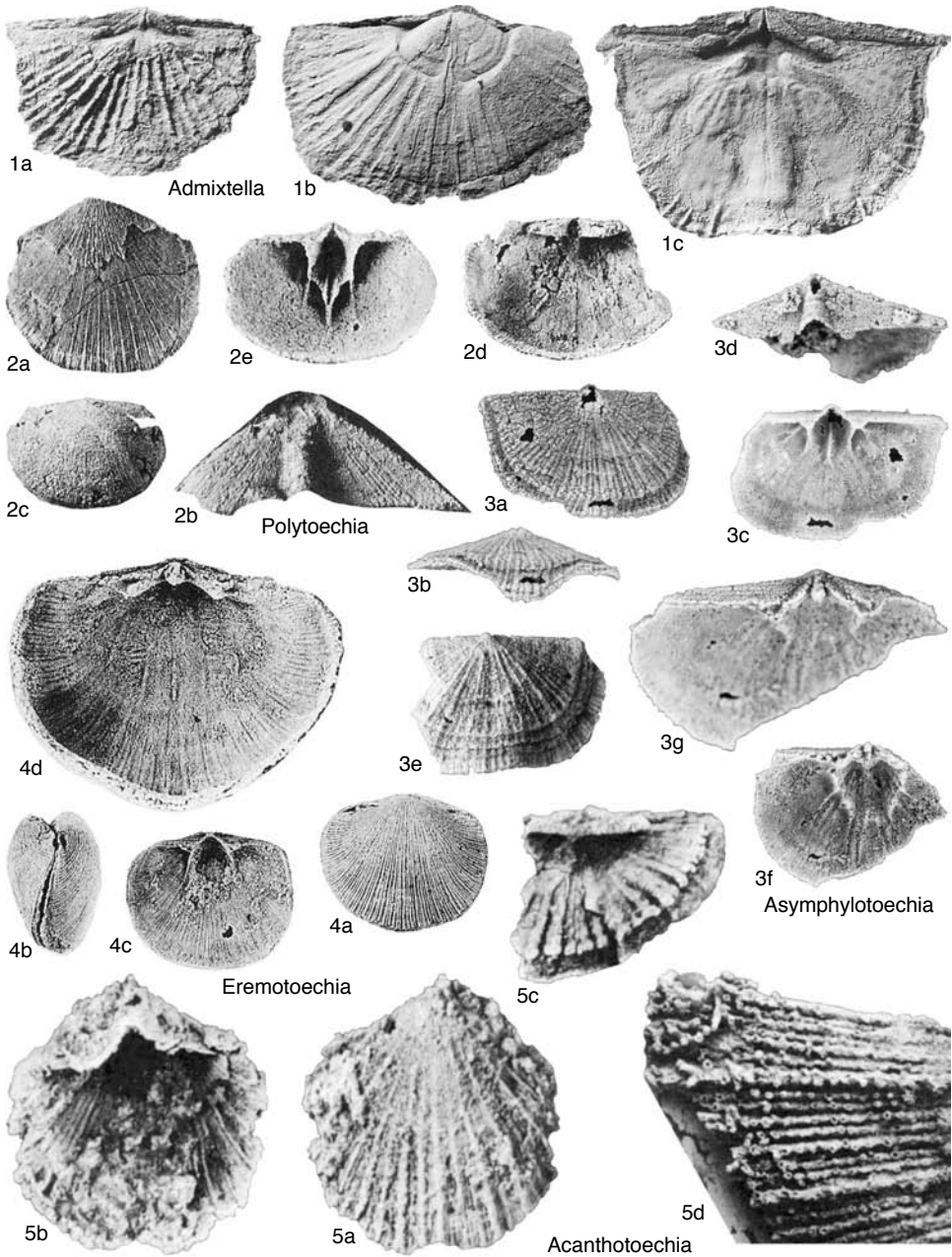


FIG. 510. Polytoechiidae (p. 707–708).

Raunites ÖPIK, 1939, p. 135, *nom. nov. pro Rauna*
 ÖPIK, 1932, p. 70, *non* MÜNSTER, 1839] [**Orthisina*
janischewskyi LESNIKOVA, 1924, p. 153; OD].
 Resupinate shells with unequal costellae and well-

developed concentric fila. Lower Ordovician
 (Arenig—lower Llanvirn): Estonia, western Russia
 (Ingria).—FIG. 509, 2a, b. **R. janischewskyi* (LES-
 NIKOVA), Arenig, Ingria; ventral, dorsal interiors,

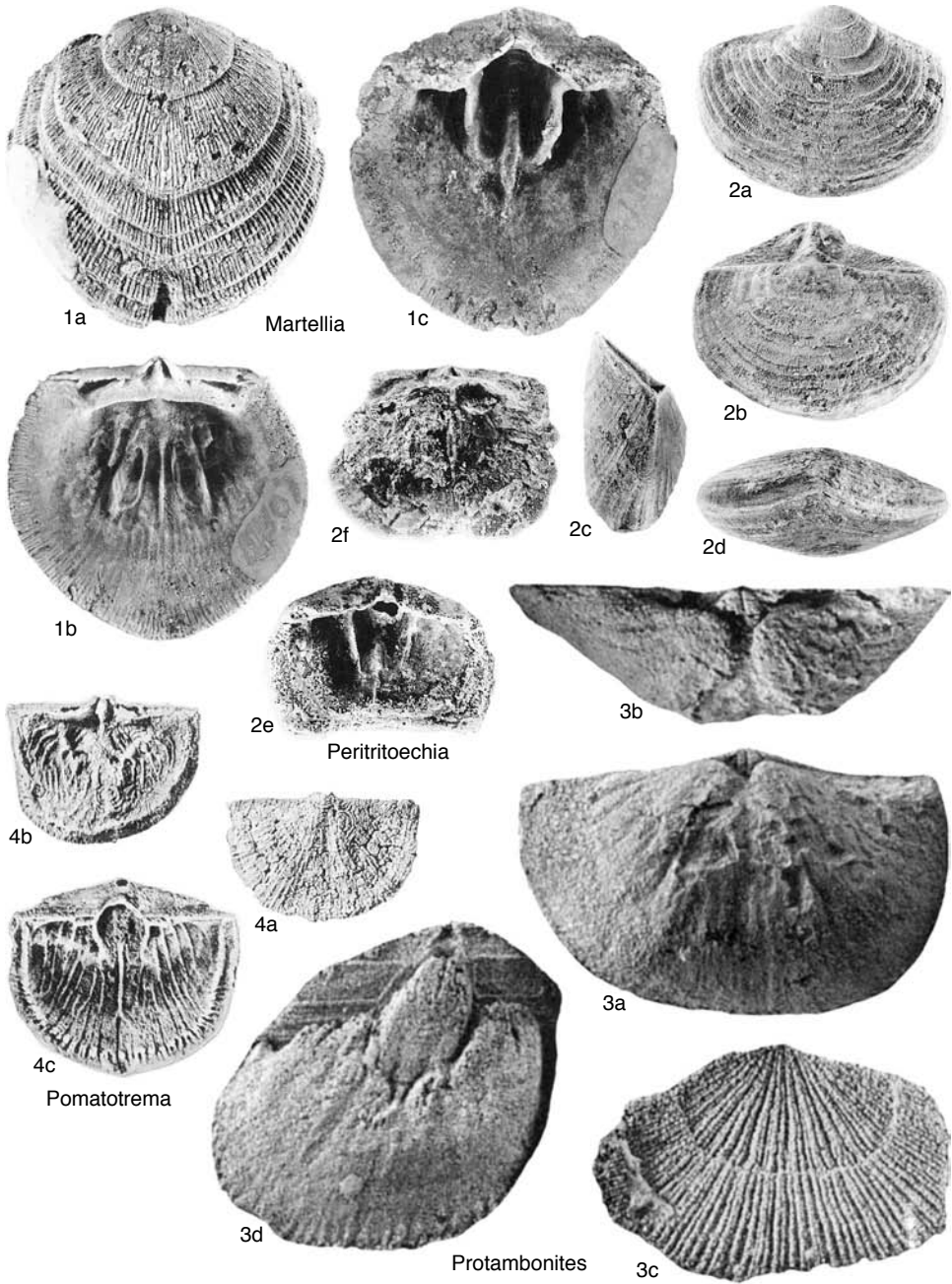


FIG. 511. Polytoechiidae (p. 708).

×1.5 (Öpik, 1934).—FIG. 509,2c. *R. wolchowiana* (Öpik); ventral valve exterior, ×2 (Öpik, 1934).—FIG. 509,2d. *R. venusta* (Öpik), Arenig, Ingria; detail of ornament, ×5 (Öpik, 1934).—

FIG. 509,2e,f. *R. strophomenoides* (Öpik), lower Llanvirn, Estonia; ventral, posterior views of conjoined valves, ×1.5 (new).

Superfamily
POLYTOECHIOIDEA
Öpik, 1934

[*nom. transl.* RUBEL & WRIGHT, herein, ex Polytoechiinae ÖPİK, 1934, p. 76] [=Tritoehiidae ULRICH & COOPER, 1936b, p. 624]

Dental plates reach valve floor to form pseudospondylium; shell substance impunctate. *Ordovician* (*Tremadoc*–*lower Caradoc*).

Family POLYTOECHIIDAE Öpik, 1934

[*nom. transl.* CLOUD, 1948b, p. 461, ex Polytoechiinae ÖPİK, 1934, p. 76] [=Tritoehiidae ULRICH & COOPER, 1936b, p. 624]

Characters as for superfamily. *Ordovician* (*Tremadoc*–*lower Caradoc*).

Polytoechia HALL & CLARKE, 1892, p. 239 [**Hemipronites apicalis* WHITFIELD, 1886, p. 300; OD] [=*Deltatretra* ULRICH in BUTTS, 1926, p. 100 (type, *D. fillistriata* BUTTS, 1926; SD SCHUCHERT & COOPER, 1932, p. 108); *Deltorthis* ULRICH in POULSEN, 1927, p. 297, *nom. nov. pro Waagenia* HALL, 1889, p. 390, *non* VON KRIECHBAUMER, 1874, obj.]. Unequally biconvex; pseudospondylium with differentiated adductor scars, and with forwardly extending dental plates and median septum. *Lower Ordovician* (*Arenig*): USA (Alabama, Arkansas, Oklahoma, Texas, Vermont), Greenland, China (Manchuria).—FIG. 510,2a,b. **P. apicalis* (WHITFIELD), Arenig, Vermont; a, ventral valve exterior, $\times 3$; b, ventral valve interarea, $\times 4$ (Ulrich & Cooper, 1938).—FIG. 510,2c–e. *P. subcircularis* COOPER, Arenig, Oklahoma; c, dorsal valve exterior, $\times 3$; d, dorsal valve interior, $\times 3$; e, anterodorsal view of ventral interior, $\times 3$ (Cooper, 1952b).

Acanthotoechia WILLIAMS & CURRY, 1985, p. 244 [**A. hibernica*; OD]. Concavoconvex; costellae bearing rows of fine spines peripherally; dorsal interior with subperipheral rim. *Lower Ordovician* (*upper Arenig*): Ireland.—FIG. 510,5a–d. **A. hibernica*, Arenig, Ireland; a, b, holotype, exterior, interior of ventral valve, $\times 4$; c, interior of damaged dorsal valve, $\times 8$; d, detail of ornament on fragment, $\times 17$ (Williams & Curry, 1985).

Admixtella ROZMAN, 1978, p. 84 [**A. orientalis*; OD]. Planoconvex, with narrow dorsal fold and ventral sulcus; delthyrium cover unknown; notothyrium open. *Ordovician* (*lower Caradoc*): Tien Shan Mountains, Asia.—FIG. 510,1a–c. **A. orientalis*, lower Caradoc, Tien Shan Mountains; a, ornament on dorsal valve, partly exfoliated umbonally, revealing mold of cardinalia, $\times 3$; b, ventral valve internal mold, $\times 3$; c, dorsal valve internal mold, $\times 3$ (Rozman, 1978).

Asymphylotoechia ROSS, 1970, p. 60 [**A. nolani*; OD]. Biconvex, with dorsal fold and ventral sulcus; chlidium present, cardinal process swollen. *Lower Ordovician* (*upper Llanvirn*): USA (Nevada).—FIG. 510,3a–g. **A. nolani*, upper Llanvirn, Nevada; a–c, exterior, anterior, interior views of ventral valve,

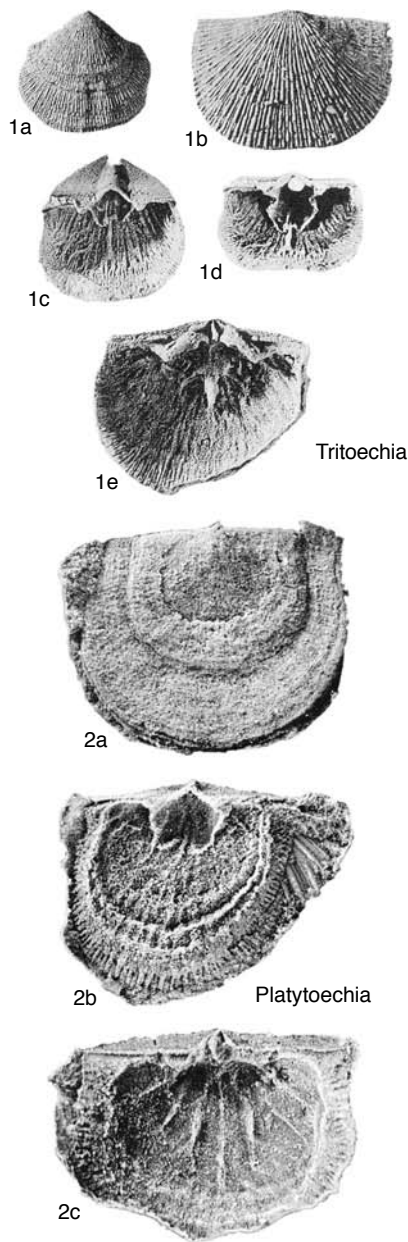


FIG. 512. Polytoechiidae (p. 708).

$\times 3$; d, ventral interarea, $\times 3$; e, dorsal valve exterior, $\times 3$; f, dorsal valve interior, $\times 3$; g, detail of hinge viewed posteroventrally, $\times 5$ (Ross, 1970).

Eremotoechia COOPER, 1956, p. 513 [**E. claudi*; OD]. Dorsibiconvex; chlidial plates, prominent trilobed cardinal process. *Ordovician* (*Llanvirn*–*Llandeilo*):

- USA (Tennessee, Alabama), Scotland, Kazakhstan, Argentina, southwestern China.—FIG. 510,4a–d. **E. claudi*, Llandeilo, Tennessee; *a, b*, dorsal, lateral views of conjoined valves, $\times 1$; *c*, ventral valve interior, $\times 1$; *d*, dorsal valve interior, $\times 2$ (Cooper, 1956).
- Martellia** WIRTH, 1936, p. 300 [**Orthisina giraldii* MARTELLI, 1901, p. 305; OD]. Planoconvex to ventribiconvex; median ridge extending in front of ventral muscle field; chilidium and cardinal process present, strong dorsal median septum. *Ordovician* (upper Arenig–Llanvirn): central and southwestern China, Argentina.—FIG. 511,1a–c. *M. ichangensis* WANG, upper Arenig, Hubei, China; *a, b*, exterior, interior views of dorsal valve, $\times 3$; *c*, ventral valve interior, $\times 3$ (new).
- Peritritoechia** XU, RONG, & LIU, 1974, p. 151 [**P. imbricatia*; OD]. Ventribiconvex shell with imbrications and very fine costellae of equal size; dorsal valve with chilidium and strong, trilobed cardinal process. *Ordovician* (upper Llanvirn–lower Caradoc): southwestern China.—FIG. 511,2a–f. **P. imbricatia*, lower Caradoc, Guizhou, southwestern China; *a–d*, holotype, ventral, dorsal, lateral, anterior views, $\times 1.5$; *e*, ventral valve interior, $\times 1.5$; *f*, dorsal valve interior, $\times 1.5$ (Xu, Rong, & Liu, 1974).
- Platytoechia** NEUMAN, 1964, p. E19 [**P. boucoti*; OD]. Convexoplane to convexoconcave; dorsal interior with strong cardinal process and subperipheral rim. *Lower Ordovician* (upper Arenig): USA (Maine).—FIG. 512,2a–c. **P. boucoti*, upper Arenig, Maine; *a*, holotype, latex cast of ventral valve exterior, $\times 2$; *b, c*, latex casts of ventral, dorsal interiors, $\times 2$ (Neuman, 1964).
- Pomatotrema** ULRICH & COOPER in SCHUCHERT & COOPER, 1932, p. 109 [**P. muralis*; OD]. Planoconvex; chilidial plates and prominent cardinal process; subperipheral rim in each valve. *Ordovician* (Arenig): USA (Oklahoma, Vermont), Canada (Alberta, Quebec), Greenland, Ireland, China, Korea.—FIG. 511,4a–c. **P. murale*, Arenig, Oklahoma; *a*, dorsal valve exterior, $\times 2$; *b*, dorsal valve interior, $\times 2$; *c*, ventral valve interior, $\times 2$ (Ulrich & Cooper, 1938).
- Protambonites** HAVLÍČEK in HAVLÍČEK & JOSOPAIT, 1972, p. 348 [**Tritoechia kolihai* HAVLÍČEK, 1949a, p. 113; OD]. Dorsibiconvex to resupinate; notothyrium open, cardinal process weak. *Lower Ordovician* (Tremadoc–Arenig): Bohemia, Spain, China, Urals.—FIG. 511,3a, b. **P. kolihai* (HAVLÍČEK), Tremadoc, Bohemia; dorsal, posterior views of dorsal valve internal mold, $\times 2$ (Havlíček, 1977a).—FIG. 511,3c, d. *P. soror* (BARRANDE), Tremadoc, Bohemia; external, internal molds of ventral valves, $\times 2.5$ (Havlíček, 1977a).
- Tritoechia** ULRICH & COOPER, 1936b, p. 624 [**Deltatrema typica* SCHUCHERT & COOPER, 1932, p. 206; OD]. Ventribiconvex, with pronounced aditicles; prominent median ridge extending in front of ventral muscle field; chilidial plates present, cardinal process swollen. *Ordovician* (Tremadoc–Arenig): widespread.—FIG. 512,1a–e. **T. typica* (SCHUCHERT & COOPER), Arenig, Oklahoma; *a*, ventral valve exterior, $\times 1$; *b*, dorsal valve exterior, $\times 2$; *c, d*, dorsal, anterodorsal views of ventral interior, $\times 1$; *e*, dorsal valve interior, $\times 2$ (Ulrich & Cooper, 1938).

RHYNCHONELLATA

ALWYN WILLIAMS and SANDRA J. CARLSON

[The University of Glasgow; and The University of California, Davis]

Class RHYNCHONELLATA Williams & others, 1996

[Rhynchonellata WILLIAMS & others, 1996, p. 1193]

Rhynchonelliform brachiopods with fibrous, impunctate, punctate, or endopunctate, biconvex, strophic or astrophic shells, articulated by deltidiodont or cyrtomatodont teeth and sockets buttressed by brachio-phores or supported by parallel socket or hinge plates repeatedly converging to form septalium or cruralium; pedicle opening as delthyrium or rounded foramen; interareas and notothyrium commonly vestigial or absent, well developed in some derived groups; ventral muscle scars with posteromedial adductors flanked or enclosed by diductors and

laterally placed adjustors; dental plates less commonly converging to form spondylium; dorsal adductor scars petaloid or grouped and quadripartite; crura present in later groups and commonly extended as spiralia or loops; mantle canal systems variable as saccate, digitate, pinnate, or lemniscate impressions. *Lower Cambrian–Holocene*.

The Rhynchonellata is the largest class of brachiopods. It is composed of about 3,000 genera assigned to 75 superfamilies and grouped into 10 orders. The diagnostic synapomorphy is a pedicle developed from a rudiment. In such extinct groups as the orthides and syntrophiidines, the presence of such a pedicle is indicated by the imprint of adjustor scars on the shell interior. A pedicle

such as this was variably developed throughout the class, being vestigial in some free-living groups (pentameridines). But in the thecideides and some atrypides the pedicle rudiment developed into an adhesive pad attended by cementation of the ventral valve, a homoplasy that has caused great difficulties in past classifications of the brachiopods.

The rhynchonellides and related spire-bearing and loop-bearing orders are further characterized by the reversal of the mantle rudiment during larval development. This transformation is indicated on the shells by a forward shift of the attachment area of the ventral muscle field to make way for the pedicle capsule. It is, therefore, well documented in extinct groups.

Other synapomorphies evident in the shell and used in classification at the ordinal level are transformations of articulatory devices. In particular, the development of cyrtomato-

dont teeth and the elaboration of cardinalia, giving rise to crura supporting the mouth segment of the lophophore, characterize the rhynchonellides and all derived ordinal groups. Such orders, in turn, are well founded on the nature and disposition of spiralia and loops extending from the crura in support of the variously oriented brachia of the lophophore.

Among other features used in the supra-familial classification of the Rhynchonellata, the strophic shells of spiriferides (*s.l.*), thecideides, and some terebratulides were derived from astrothic stem groups and, therefore, separable taxonomically from those of orthides and protorthides. Punctuation is also homoplastic; but putative homologues of the endopunctae characterizing terebratulides and thecideides occur in Jurassic species of spiriferides (*s.l.*).

PROTORTHIDA

ALWYN WILLIAMS and DAVID A. T. HARPER

[The University of Glasgow; and University of Copenhagen]

Order PROTORTHIDA Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Small, strophic rhynchonelliforms with wide, open delthyrium and notothyrium; apsacline ventral interarea normally long and flat, anacline dorsal interarea short to vestigial; rudimentary or simple, deltiodont teeth with dental ridges, slightly lateral of delthyrial edges, uniting with free spondylium; ventral mantle canal system rarely impressed, saccate; secondary layer of shell presumably fibrous as in skenidioids, impunctate. *Lower Cambrian–Upper Devonian (Frasnian)*.

The taxa herein assigned to the Protorthida are characterized by a free spondylium (apical plate of COOPER, 1976, p. 286), which accommodated the ventral muscle bases. The protorthides are further

characterized by brachiophore plates that converge to form a transverse plate underlying the notothyrial margin. The ontogeny of this plate is not known, but it could have been the same as the early stages in the development of the cardinalia of *Protoskenidioides* prior to the medial fusion of the converging brachiophore plates into a simple cardinal process. For this reason, the Skenidioides is placed within the Protorthida with the Protorthoidea despite the fact that neither superfamily has yet been found in Upper Cambrian rocks.

The assignment of *Leioria* and *Arctohedra* (with *Loperia*) to the Protorthida is less secure taxonomically as the flat brachiophores of the former genus and the notothyrial platform of the latter are more typically orthide. The variability of these structures among early orthides, however, suggests that they, rather than the free spondylium, are more likely to be homoplastic.

Superfamily PROTORTHOIDEA Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, ex Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Protorthides with notothyrium underlain by short, transverse plate without cardinal process; dorsal adductor scars probably linear; ventral mantle canal system saccate with divergent *vascula media*. *Lower Cambrian–Middle Cambrian*.

Family PROTORTHIDAE Schuchert & Cooper, 1931

[Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Generally transversely semioval, uniplicate protorthoids with acute to mucronate cardinal extremities; brachiophores as widely divergent rudimentary brachiophore nubs defining small, shallow sockets. *Lower Cambrian–Middle Cambrian*.

Protorthis HALL & CLARKE, 1892, p. 231 [**Orthis billingsi* HARTT in DAWSON, 1868, p. 644; OD]. Cardinal extremities variable, shells biconvex, rectimarginate, multicostellate; brachiophores subparallel with hinge line; dorsal median ridge absent. *Middle Cambrian*: eastern North America. —FIG. 513,1a–e. **P. billingsi* (HARTT), Middle Cambrian, New Brunswick; a, ventral exterior, $\times 2$; b, ventral interior, $\times 2.7$ (Schuchert & Cooper, 1932); c, dorsal interior, $\times 2$; d, ventral exterior, $\times 2$; e, tilted ventral exterior, $\times 3$ (Hall & Clarke, 1892).

Glyptoria COOPER, 1976, p. 281 [**G. glypta*; OD]. Similar to *Protorthis* but dorsibiconvex, uniplicate, with acute cardinal extremities, coarsely costate and imbricate; small teeth fitting lateral to brachiophore nubs. *Lower Cambrian*: Dead Sea region. —FIG. 513,2a–e. **G. glypta*, Lower Cambrian, Dead Sea region; a, dorsal interior, $\times 2$; b, ventral interior, $\times 2$; c, ventral exterior, $\times 2$; d, e, lateral, anterior view of dorsal exterior, $\times 1$ (Cooper, 1976).

Israelaria COOPER, 1976, p. 281 [**I. parnesi*; OD]. Similar to *Glyptoria* but ventribiconvex and with impersistent, irregularly developed costae. *Lower Cambrian*: Dead Sea region, Morocco. —FIG. 513,4a–d. **I. parnesi*, Lower Cambrian, Dead Sea region; a, ventral interior, $\times 2$; b, view of hinge area of dorsal valve, $\times 2$; c, dorsal interior, $\times 3$; d, ventral exterior, $\times 2$ (Cooper, 1976).

Jamesella WALCOTT, 1905, p. 252 [**Orthis perpasta* POMPECKJ, 1896, p. 515; OD]. Similar to *Israelaria* but subquadrate with slightly mucronate cardinal extremities, uniplicate, coarsely costellate, with concentric lamellae. *Middle Cambrian*: Bohemia, Spain. —FIG. 513,5a–e. **J. perpasta* (POMPECKJ), Middle Cambrian, Bohemia; a, b, normal, tilted

views of rubber replica of ventral interior, $\times 1.7$; c, d, internal mold, rubber replica of dorsal valve, $\times 2.5$; e, rubber replica of dorsal exterior, $\times 1.6$ (Havlíček, 1977a).

Psiloria COOPER, 1976, p. 282 [**P. pauperata*; OD]. Similar to *Glyptoria* but with slightly mucronate cardinal extremities and smooth or faintly costellate exterior. *Lower Cambrian*: Dead Sea region. —FIG. 513,3a–c. **P. pauperata*, Lower Cambrian, Dead Sea region; ventral interior, dorsal interior, ventral exterior, $\times 2$ (Cooper, 1976).

Family ARCTOHEDRIDAE new family

[Arctohedridae WILLIAMS & HARPER, herein]

Costellate, unisulcate protorthoids with subpyramidal ventral valve having curved apsacline to catacline interarea; teeth simple, ventral muscle field with relatively broad, subtriangular adductor track flanked by linear diductor scars, rarely impressed on free spondylium; divergent rodlike brachiophores joined to hinge line by concave fulcral plates defining sockets and subtending narrow notothyrial plate flanking median elevation that extends anteriorly and divides subequally quadripartite adductor scar; ventral mantle canal system probably saccate with divergent *vascula media*. [The Arctohedridae is provisionally assigned to the Protorthoidea on the assumption that the presence of a free spondylium is more likely to be an apomorphy of taxonomic significance than the development of a notothyrial platform. Indeed, the presence of this feature and of the orthidine-like brachiophores of the Leioridae suggests the protorthidine genotype had many features that were later to characterize the orthide shell.] *Middle Cambrian*.

Arctohedra COOPER, 1936, p. 210 [**A. minima*; OD].

Transversely semioval with acute cardinal extremities, ventribiconvex to planoconvex, coarsely costellate to ramicoscostellate. [COOPER (1936, p. 210) described the cardinalia of silicified dorsal valves of the type species of *Arctohedra* as including a well-developed cardinal process and notothyrial platform. ROBERTS and JELL (1990, p. 281), studying their better preserved species *A. alata*, concluded that the notothyrium was occupied by a narrow plate (inappropriately identified as a cardinal plate) ankylosed to a medial plug continuous with the high dorsal median ridge. The latter structure is closer to the protorthoid cardinalia and is assumed to be typical of the arctohedrids as a whole.] *Middle Cambrian*: North America (Alaska), Australia (New South Wales), central Asia (Turkistan, Tyan

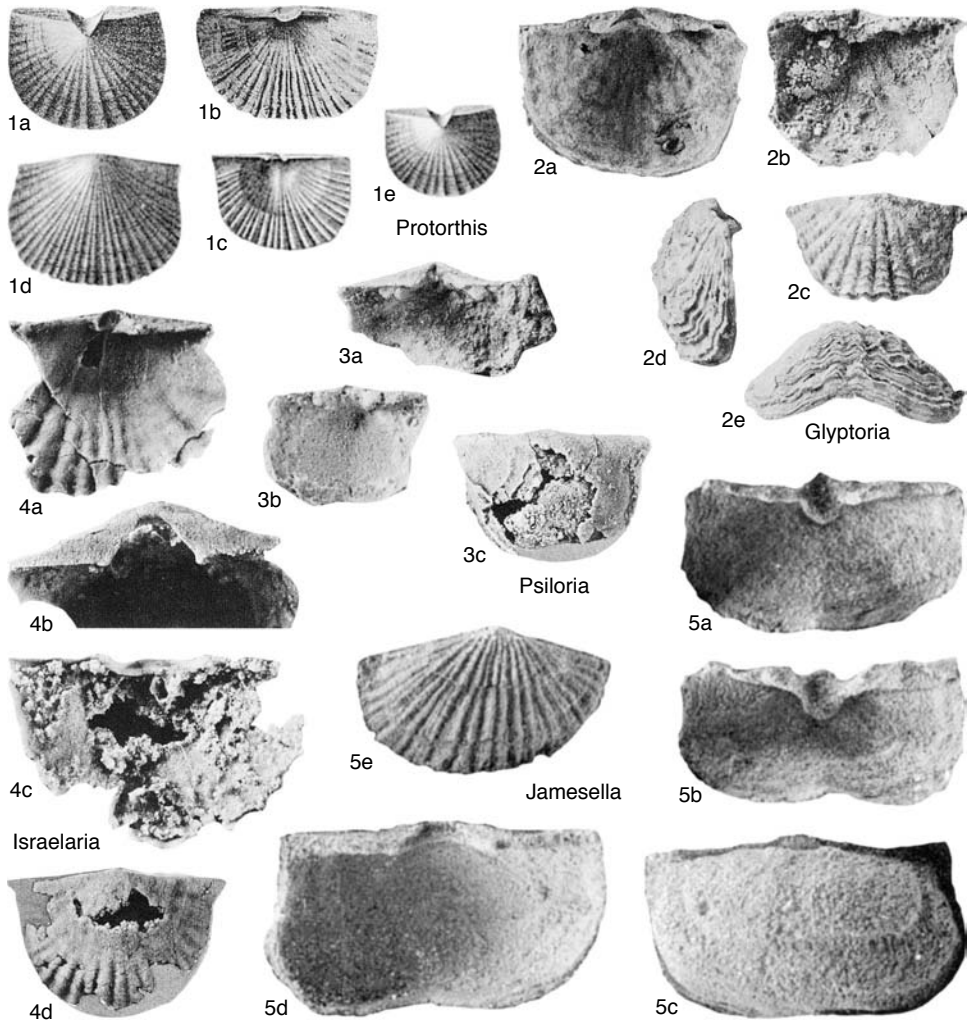


FIG. 513. Protorthidae (p. 710).

Shan).—FIG. 514, 1a–d. **A. minima*, Middle Cambrian, Alaska; *a*, dorsal exterior, $\times 10$; *b*, ventral exterior, $\times 6$; *c*, ventral interior, $\times 6$; *d*, dorsal interior, $\times 10$ (Cooper, 1936).

Loperia WALCOTT, 1905, p. 287 [**Protorthis* (*Loperia*) *dougaldensis*; OD]. Subquadrate with obtuse cardinal extremities, resupinate, multicostellate; delthyrium and notothyrium open, wide; apsacline ventral interarea flat, long; catacline dorsal interarea short; small teeth; socket ridges divergent, bladellike; simple, ridgelike cardinal process supported by small notothyrial platform. [This genus is provisionally included in the Arctohedridae due to its free spondylium and notothyrial platform. In general, however, it differs significantly from arctohedrids in being resupinate and especially in having a well-defined cardinal process.] *Middle Cambrian*: eastern

Canada.—FIG. 514, 2a–c. **L. dougaldensis* (WALCOTT), Middle Cambrian, Cape Breton; *a*, internal mold of dorsal valve, $\times 2$; *b*, internal mold of ventral valve, $\times 2$; *c*, fragment of valve exterior, $\times 2$ (Walcott, 1912).

Family LEIORIIDAE Cooper, 1976

[Leioriidae COOPER, 1976, p. 284]

Ventribiconvex, rectimarginate protorthoids with blunt, bladellike brachiophores erect, narrowly divergent, delineating elongate sockets; dorsal adductor field consisting of 4 elongate, radiating scars separated by low ridges. *Lower Cambrian*.

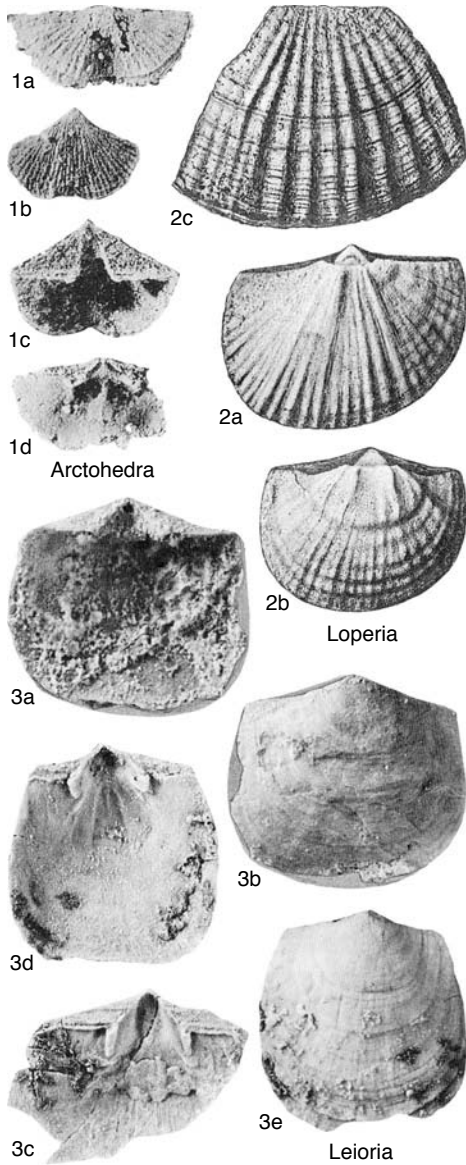


FIG. 514. Arctohedridae and Leioriidae (p. 710–712).

Leioria COOPER, 1976, p. 284 [*L. bentori*; OD]. Small, subquadrate with obtuse cardinal extremities, ornamented only by concentric banding and lines of growth. *Lower Cambrian*: Israel, Jordan.—FIG. 514, 3a–c. **L. bentori*, Lower Cambrian, Dead Sea region; a, b, interior, exterior of ventral valve, $\times 2$; c, dorsal interior, $\times 2$ (Cooper, 1976).—FIG. 514, 3d, e. *L. elongata* COOPER, Lower Cambrian, Dead Sea region; interior, exterior of dorsal valve, $\times 2$ (Cooper, 1976).

Superfamily SKENIDIOIDEA Kozłowski, 1929

[*nom. transl.* WILLIAMS & HARPER, herein, ex Skenidiidae KOZŁOWSKI, 1929, p. 46]

Protorthides with teeth ridges continuous with sides of free spondylium normally supported apically by short ridge; rodlike, divergent brachiophores joined to hinge line by fulcral plates defining elongate sockets and supported by basal plates converging onto high median septum to form septalium; cardinal process normally ridgelike, commonly fused with dorsal median septum; impressions of muscle fields and mantle canals mostly indistinct, ventral mantle canal system probably saccate with convergent *vascula media*, dorsal adductor scar quadripartite. *Lower Ordovician (Arenig)*–*Upper Devonian (Frasnian)*.

Family SKENIDIIDAE Kozłowski, 1929

[*nom. correct.* SCHUCHERT & COOPER, 1931, p. 243, *pro* Skenidiidae KOZŁOWSKI, 1929, p. 46]

Ventribiconvex to planoconvex skenidioids with subpyramidal ventral valve and strongly sulcate dorsal valve normally transversely semioval with acute cardinal extremities. *Lower Ordovician (Arenig)*–*Upper Devonian (Frasnian)*.

Skenidium HALL, 1860a, p. 70 [**Orthis insignis* HALL, 1859a, p. 173; SD HALL & CLARKE, 1892, p. 241]. Coarsely costate to dichotomously costellate; ventral interarea usually procline, dorsal interarea vestigial; fulcral plates very wide, flat to concave, defining elongate sockets restricted to concave zones adjacent to hinge line; cardinal process ridgelike, apparently formed of upturned posteromedial edges of brachiophore plates, not continuous with dorsal median septum. *Lower Devonian (Lochkovian)*–*Upper Devonian (Frasnian)*: cosmopolitan.—FIG. 515, 1a–d. **S. insignis* (HALL), Lochkovian, Albany; a, dorsal interior, $\times 6$; b, ventral interior, $\times 6$; c, posterior view of conjoined valves, $\times 6$; d, dorsal exterior, $\times 6$ (Schuchert & Cooper, 1932).

Crossiskenidium WILLIAMS & CURRY, 1985, p. 237 [**C. spinosum*; OD]. Ventribiconvex, multicostellate, lamellose, lamellae fringed with flat spines especially on sides of shell; cardinal process vestigial, dorsal median partition more ridgelike, flanked by elongately oval adductor tracks with raised lateral boundaries. *Lower Ordovician (Arenig)*: Ireland.—FIG. 515, 6a–c. **C. spinosum*, Arenig, western Ireland; a, dorsal interior, $\times 14$; b, ventral interior, $\times 12$; c, dorsal view of conjoined valves, $\times 13$ (Williams & Curry, 1985).

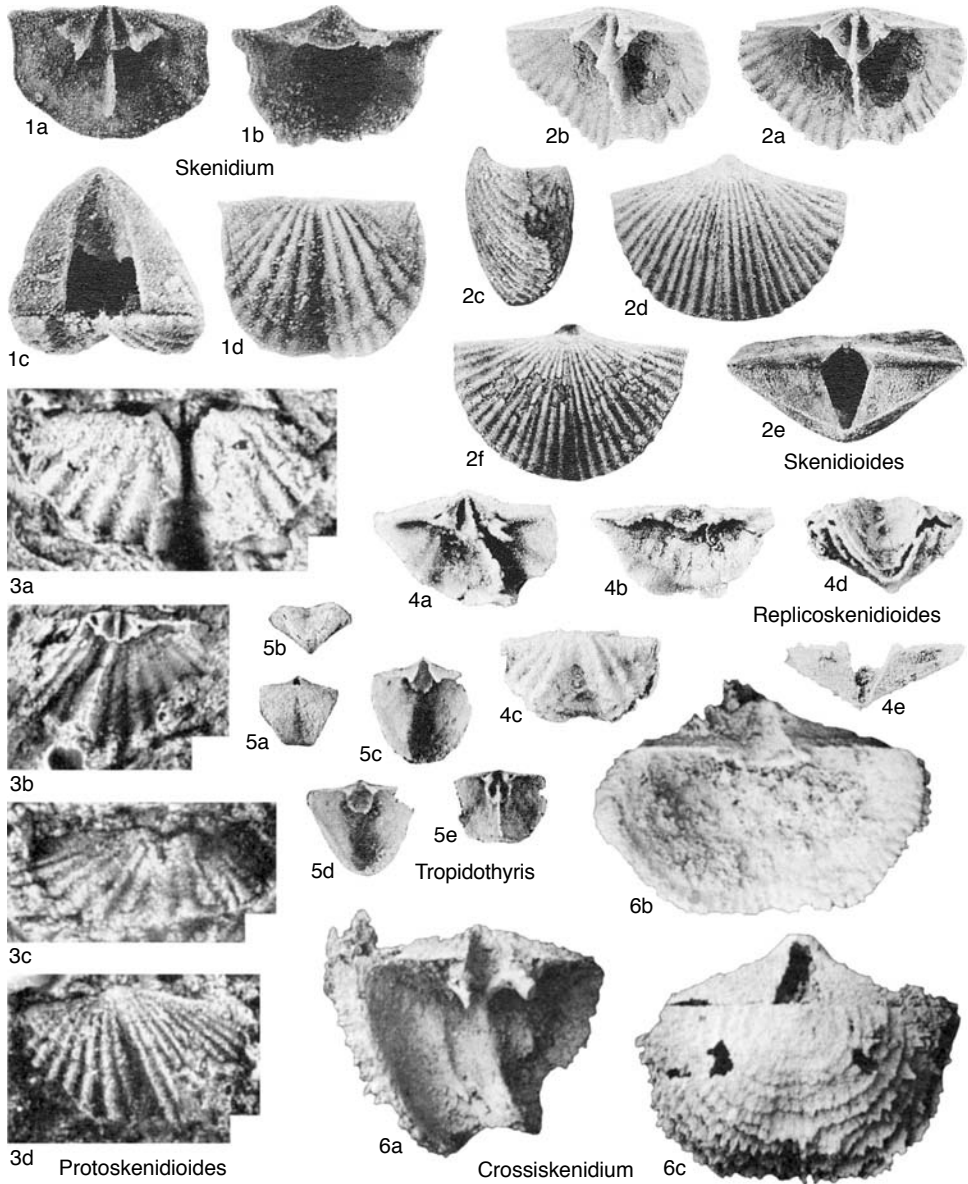


FIG. 515. Skenidiidae (p. 712–714).

Protoskenidioides WILLIAMS, 1974, p. 83 [*P. revelata*; OD]. Usually planoconvex, mucronate, sharply unisulcate, costate; dorsal interarea short, planar; cardinal process ridgelike, formed by coalescence of posteromedial edges of brachiophore plates during early stages of growth; dorsal adductor field bounded laterally by curved ridges, divided by median septum into 2 elongated oval impressions. *Lower Ordovician (Arenig)*: Great Britain, eastern China, Ireland.—FIG. 515, 3a–d. **P. revelata*,

Arenig, Shelve; a, internal mold of dorsal valve, ×12.4; b, rubber replica of dorsal interior, ×9; c, internal mold of ventral interior, ×15; d, rubber replica of dorsal exterior, ×12.5 (Williams, 1974).

Replicoskenidioides POTTER, 1990b, p. 11 [*R. rodneypreggi*; OD]. Similar to *Skenidioides* but ventribiconvex, ramicostellate; brachiophore plates parallel or divergent. *Upper Ordovician (Ashgill)*: western North America.—FIG. 515, 4a–e. **R. rodneypreggi*, Ashgill, western North America; a,

dorsal interior, $\times 7$; *b*, ventral interior, $\times 7$; *c, d*, normal, anterior views of dorsal exterior, $\times 8$; *e*, posterior view of ventral valve, $\times 7$ (Potter, 1990b).

Skenidioides SCHUCHERT & COOPER, 1931, p. 243 [**S. billingsi*; OD]. Usually planoconvex, coarsely costellate; ventral interarea apsacline to catacline; cardinal process commonly differentiated into shaft and compressed myophore and continuous with median septum that bisects sporadically impressed, subequal quadripartite dorsal adductor scars. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian)*: cosmopolitan.—FIG. 515, 2*a–f*. **S. billingsi*, Caradoc, Quebec; *a, b*, normal, oblique views of dorsal interior, $\times 4$; *c, d*, lateral, ventral views of conjoined valves, $\times 4$; *e, f*, posterior, dorsal views of conjoined valves, $\times 4$ (Schuchert & Cooper, 1932).

Tropidothyris COOPER, 1956, p. 507 [**T. pentagona*; OD]. Subpentagonal, ventribiconvex with a tongue-like anterior commissure of deeply sulcate dorsal valve, smooth to variably plicate; dorsal interarea vestigial; cardinal process long, platelike, strongly elevated and continuous with median septum; brachiophore plates subparallel, attaching to floor of valve on either side of median septum that divides elongately oval adductor field, with anterior pair of scars larger than posterior. *Upper Ordovician (Caradoc)*: eastern United States.—FIG. 515, 5*a–e*. **T. pentagona*, Caradoc, Alabama; *a, b*, dorsal, anterior views of conjoined valves, $\times 5$; *c, d*, normal, tilted views of ventral interior, $\times 8$; *e*, dorsal interior, $\times 8$ (Cooper, 1956).

ORTHIDA

ALWYN WILLIAMS and DAVID A. T. HARPER

[The University of Glasgow; and University of Copenhagen]

Order ORTHIDA Schuchert & Cooper, 1932

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, *ex suborder* Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.*, WILLIAMS & HARPER, *herein*]

Strophic, subquadrate, unsulcate, biconvex, radially ornamented rhynchonellates with open delthyria and notothyria, apsacline ventral and anacline dorsal interareas normally short, curved; teeth simple to mainly deltidiodont with crural fossettes and normally supported by dental plates; ventral muscle field variable, impressed on valve floor, pedicle callist well developed in later stocks; elongate sockets may be delineated by fulcral plates, divergent brachiophores, as blades or rods, may be supported by variably disposed plates or accretions of secondary shell, notothyrial platform vestigial to well developed, cardinal process ridgelike becoming differentiated into myophore and shaft; ventral canal system typically saccate with divergent *vascula media*, dorsal canal system saccate, digitate, or lemniscate. *Lower Cambrian–Upper Permian (Tatarian)*.

The Orthida, as here delineated by the 42 sets of character states listed in Table 17 (see p. 720), are an assemblage of extinct Paleozoic stocks that include the oldest known

rhynchonellate brachiopods. They were especially prolific during the Cambrian and Ordovician and became so diversified as to anticipate many of the morphological characteristics of other rhynchonellates. Many of these orthide stocks, however, were short-lived deviations from a small number of persistent lineages that typify the 4 superfamilies of the order. Moreover, the differences between the orthoid *Orthambonites* (Fig. 516) and the dalmanelloid *Howellites* (Fig. 517), which display the most commonly occurring characteristics of their respective superfamilies, involve a minority of features so that a representative orthide can be defined.

The exterior of a typical member of the Orthida is quite distinctive. The shell is biconvex and subquadrate in outline with a maximum width anterior of a well-developed hinge line and a curved apsacline ventral interarea that is longer than the anacline dorsal interarea. A strong, median dorsal sulcus is normally present and the shell surface is usually costellate. Variations include the convexoconcave profile of many plaesiomyids, the bilobed outline of *Dicoelosia*, the reduced or mucronate hinge lines respectively of *Angusticardinia* and *Platystrophia*, the obsolescent interareas of *Productorthis*,

the dorsal median fold of both *Platystrophia* and *Enteleles*, the latter with its additional superimposed radial plications, and the occurrence of hollow ribs (aditicules) among dalmanellidines and plectorthoids. The most important external distinctions, however, are the strophic hinge line and the open delthyrium and notothyrium. Chilidial-like structures are known in some hesperonomiids, productorthids, and plaesiomyids; and deltidial plates were variably developed in a few independent stocks such as *Trematorthis*, *Barbarorthis*, and *Phragmophora*; but the latter structures are not homologous with the strophomenate pseudodeltidium.

Basic similarities are also evident in the impressions of muscle attachment areas and mantle canals. The orthide ventral muscle impressions are normally subtriangular to bilobed in outline and confined to the posterior half of the ventral valve (Fig. 516–517). The umbonal chamber never accommodated the base of the pedicle as in other, later rhynchonellates. It was occupied solely by the muscle system up to a variably developed pedicle callist, by which the cuticle of a flat-based pedicle was evidently attached to the ventral valve. The median adductor scars were normally not enclosed anteriorly and the adjustors and lateral diductor lobes were inserted on the inner surfaces of the dental plates (Fig. 517). There is, however, great variation in the outline of the ventral muscle scars reflecting their differential development, especially the relationship between the adductor and adjacent diductor components. Moreover, outlines can vary with the age as well as the curvature of the valve (WILLIAMS & WRIGHT, 1963, p. 18). Even so, there are several kinds of outlines that are stable and distinctive enough to be used to discriminate genera (Fig. 518).

The adductor impressions on the floors of the orthide dorsal valves are also variable in outline although they are essentially quadripartite and consist of a pair of posterior and anterior scars on either side of a variably developed median ridge. The ridge was built up as a low anterior extension of the notothyrial

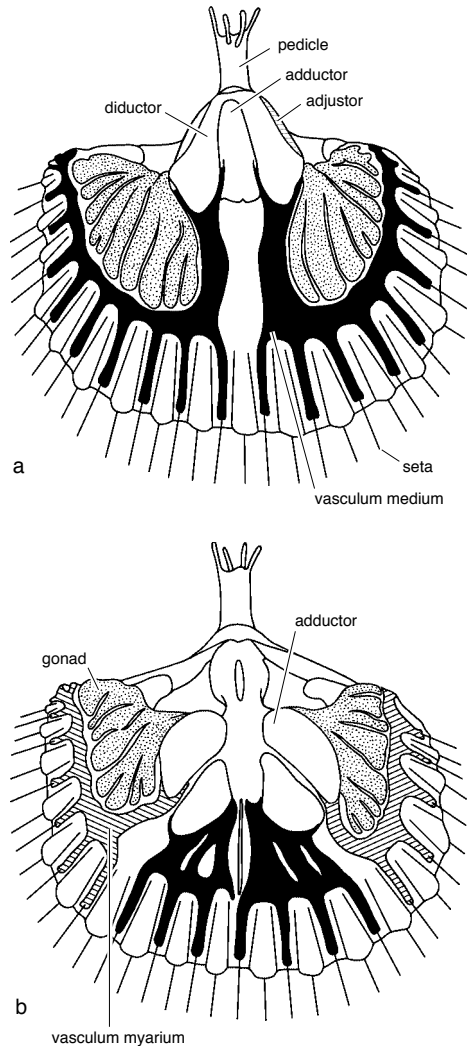


FIG. 516. *Orthambonites*; stylized reconstruction of inferred morphology of soft parts viewed from *a*, ventral and *b*, dorsal exteriors (adapted from Williams & Wright, 1965).

platform or convergent brachiophore plates. Sporadically it culminated in a high median septum, as in the phragmorthids, cremnorthids, and kayserellids. In such stocks as these, the median septum effectively divided the mantle cavity into two compartments, each of which presumably contained a brachium. Irrespective of the nature of the median partition the overall outline of the dorsal

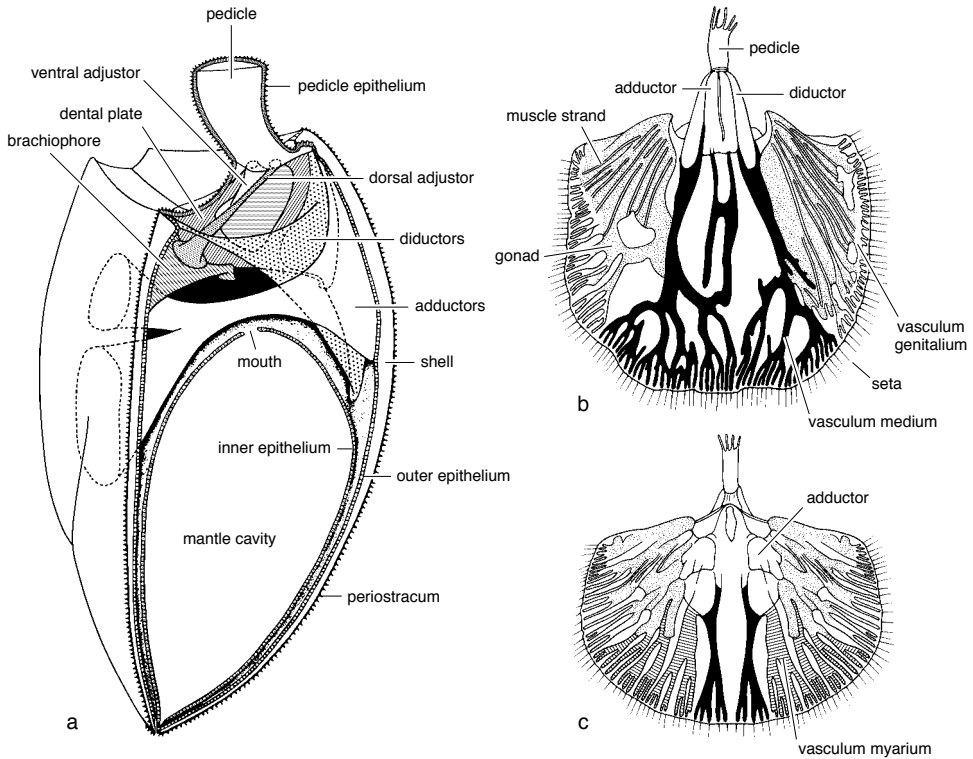


FIG. 517. *Howellites*; *a*, stylized reconstruction of musculature; inferred morphology of soft parts viewed from *b*, ventral and *c*, dorsal exteriors (Williams & Wright, 1963).

adductor field can vary significantly; especially in the relative sizes of individual scars, and the main changes are used to discriminate genera.

Despite the variation that is known to have occurred in the mantle canal systems of the Orthida, one of the least specialized patterns, comprising saccate and digitate distributions in the ventral and dorsal valves respectively, is the most common among early orthoids (Fig. 516). A lemniscate arrangement in both valves, on the other hand, is prevalent among the dalmanelloids and enteletoids (Fig. 517). Yet these differences between superfamilies are not mutually exclusive. The ventral and dorsal patterns of the dalmanelloid paurorthids, for example, are saccate and digitate like most orthoids, while those of the finkelnburgiids (digitate and digitate) and some plectorthids (saccate and digitate but with the gonads pervading the

entire mantles) approach the enteletoid condition.

The most important changes affecting internal morphology were those that led to the diversification of the articulatory devices involving the ventral teeth and dorsal cardinalia. The teeth of Cambrian orthides are typically deltidodont but are grooved by crural fossettes in later stocks. The brachiophores defining the sockets may be rods or blades proximally encased in a notothyrial platform as in most orthoids, or supported by plates reaching to the floor of the dorsal valve as in plectorthoids and most punctate groups. The brachiophore plates together with fulcral plates define sockets that are distally elevated above the floor of the dorsal valve. The disposition of the brachiophore plates can vary greatly even within a series of such closely related genera as those assigned to the Dalmanellidae. Using members of this

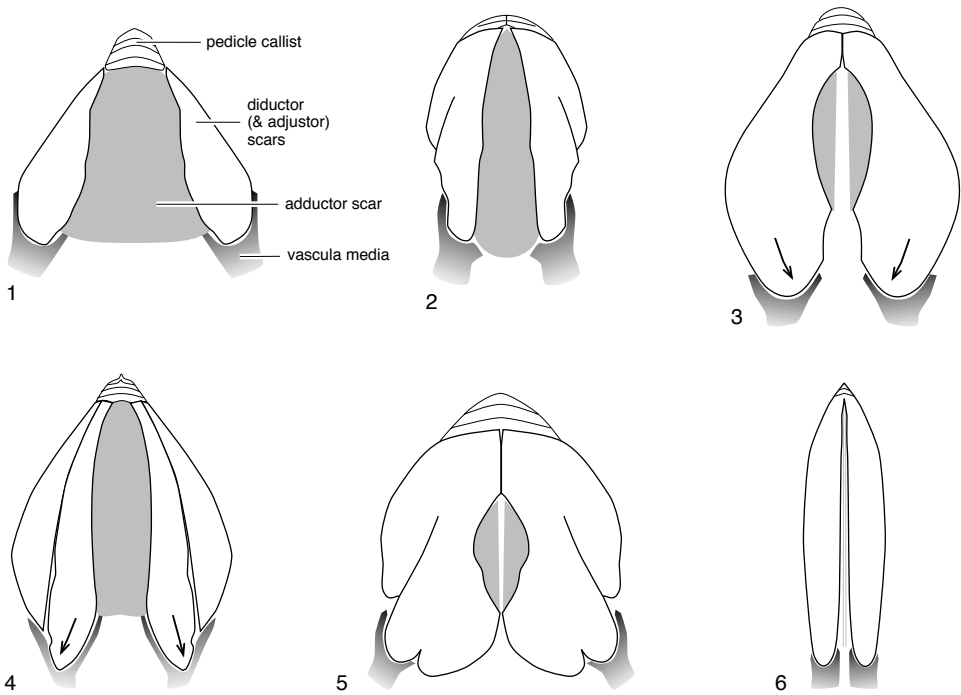


FIG. 518. Outline of orthide ventral muscle scars; 1, subtriangular as in *Cremnorthis*; 2, suboval (*Glyptorthis*); 3, cordate (*Hesperorthis*); 4, bilobed (*Dalmanella*), which may be expanded anteriorly as extended lobes; 5, subquadrate to flabellate (*Plaesiomys*); 6, linear (*Enteletes*) (new).

family, it is possible to demonstrate a continuous gradient of change between arrangements in which the angle subtended by the brachiophore bases is significantly less or greater than that subtended by the tops of the brachiophores. Hence, although *Bancroftina*, *Dalmanella*, and *Howellites* are each characterized by a distinctive attitude, the last two genera together include species showing every conceivable variation in the disposition of the bases relative to the top of the brachiophores (Fig. 519). Generally, however, their attitude tends to be consistent in different stocks, so that they may converge onto a median septum to form a septalium, as in *Linoporella*, or be widely divergent, as in *Enteletes*.

The brachiophores may be prolonged distally as processes in attitudes suggesting their having supported the mouth segment of the lophophore. These elaborations are rare and are well exemplified by the brachiophore ex-

tensions of *Enteletes* and *Phragmorthis*, which evolved independently of one another and of the crura of later rhynchonellates.

There are important differences in the origin and function of the diverse structures, collectively referred to as the cardinal process, that project posteriorly from the notothyrial platform. The lack of such outgrowths is relatively rare and presumably represents the ancestral condition. Yet it is characteristic of species of the Ordovician punctate *Paurorthis*, while well-developed processes are found in such Cambrian stocks as the eoorthid *Jivinella* and the orthoid bohemiellids. In most orthoids, the most common type of cardinal process consists of a median partition that effectively divides the posterior surface of the notothyrial platform into two halves, each of which received the dorsal ends of the diductor muscles. In a few stocks (e.g., *Dolerorthis* and *Hesperonomia*), the notothyrial areas flanking the median partitions

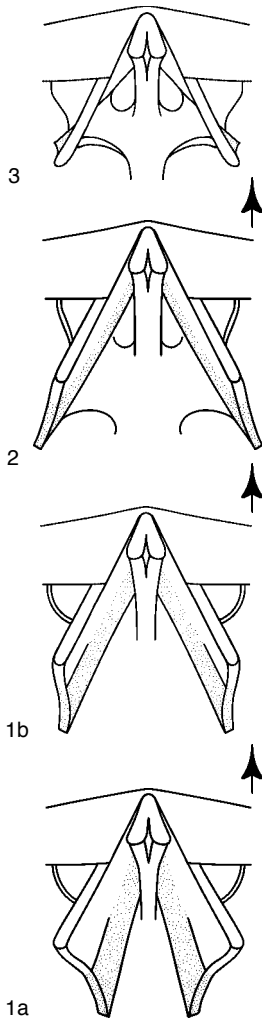


FIG. 519. Evolution of dalmanelloid cardinalia involving lateral migration of brachiophore plates (shaded) from 1a, *Dalmanella*, subtending an angle significantly less than that between tops of brachiophores to 1b, a not significantly smaller angle, to 2, *Howellites*, a not significantly greater angle, and to 3, *Bancroftina*, a significantly greater angle (adapted from Williams & Wright, 1963).

developed into ridges for reception of the diductor bases, and in the orthidiellids these grew high and became fused with the median partition to form a trilobed process. In most plectorthoids, however, further modification involved the migration of the diductor bases onto the posterolateral surfaces of the median partition which, in consequence, is either indented by muscle impressions, as in some plectorthoids, or, more commonly, is differentiated into a bulbous crenulated myophore surmounting a thickened shaft, as in many plasiomyids. This latter arrangement is prevalent among punctate orthides with the myophore mostly fashioned in a bilobed or trilobed manner, thereby separating the diductor bases from each other.

The orthide shell succession appears to have been homologous with that of living rhynchonellides with a banded, calcitic primary layer (normally recrystallized) and a secondary layer composed of orthodoxy stacked fibers ensheathed in glycoproteinaceous membranes. In post-Cambrian times, however, orthides with punctate shells appeared and were the sole representatives of the order in the Late Paleozoic. Orthide punctae with their subconical distal ends are structurally similar to the endopunctae of the later rhynchonellates except that no perforated calcitic canopies to the canals have yet been found. Until the inferred homology of all punctation has been ultrastructurally investigated it still seems better to assume that the punctation of the orthide shell was a single transformation.

Indeed, preliminary study indicates that there is no significant difference in the punctation of the Early Ordovician dalmanelloid *Paurorthis* and the Early Carboniferous dalmanelloid *Rhipidomella* (Fig. 520). The

FIG. 520. 1a–c, Punctae in the fibrous secondary shell, *Paurorthis parva* (PANDER), Lower Ordovician, Volkovian Stage, St. Petersburg, Russia; 1a, b, internal, sectional fracture surfaces showing punctae, $\times 560$, $\times 940$; 1c, fracture section of costa showing calcitic infills of aditicular hollows, $\times 240$; 2a, b, *Rhipidomella* sp., Lower Carboniferous, Lower Limestone Group, near Glasgow, Scotland; internal, sectional fracture surfaces showing punctal infills and punctal hollow in relation to fibers, $\times 700$, $\times 1700$; 3a–c, *Schizophoria resupinata* (MARTIN), Lower Carboniferous, Lower Limestone Group, Ayrshire, Scotland; 3a, external surface showing recrystallized primary layer and infill tops of punctae, $\times 380$; 3b, punctal infill partly covered by fibers, $\times 700$; 3c, punctal hollow bounded by outwardly deflected fibers, $\times 900$ (new).

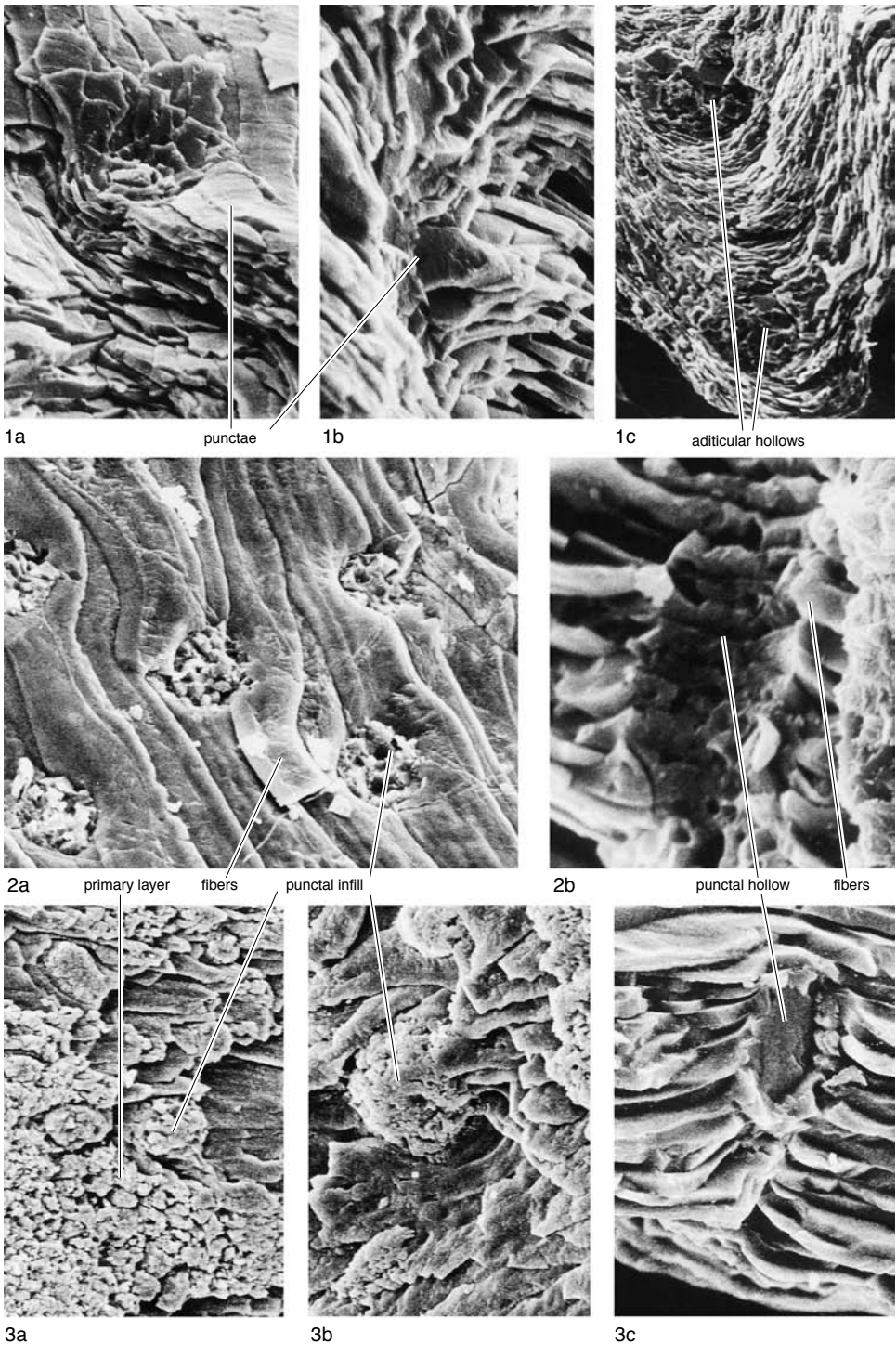


Fig. 520. For explanation, see facing page.

TABLE 17. States of 42 characters used in analyses of order Orthida (new).

SHELL STRUCTURE

1. secondary layer: fibrous (0); cross-bladed laminar (1); foliated (2).
2. punctuation: impunctate (0); endopunctate (1).
3. aditicules: absent (0); present (1).

SHELL SHAPE

4. outline: subcircular (0); subquadrate (1); transversely semioval (2); elongately semioval (3); variable (4); rostrate (5); cordate (6); bilobed (7).
5. cardinal extremities: variable (0); rectangular to obtuse (1); acute (2); mucronate (3).
6. shell size: small (0); variable (1); large (2).
7. profile (long.): biconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); concavoconvex (4); convexiconcave (5); resupinate (6); geniculate (7); variable (8).
8. profile (trans.): rectimarginate (0); unisulcate (1); sharply unisulcate (2); uniplicate (3); sharply uniplicate (4); multiplicate (5); strangulate (6); variable (7).

ORNAMENTATION

9. radial: smooth (0); costate (1); coarsely costellate (2); ramicostellate (3); fascicostellate (4); multicostellate (5); parvicostellate (6).
10. capillae: absent (0); sporadically present (1); present (2).
11. concentric: growth lines (0); imbricate (1); lamellose (2); spiny lamellose (3); nodular lamellose (4); filate (5); cancellate (6).
12. superficial: absent (0); honeycomb (1); pustulose (2); radiating pits (3).

DELTHYRIUM AND NOTOTHYRIUM

13. delthyrial angle: absent (0); vestigial (1); widely divergent (2); subparallel to narrowly divergent (3).
14. delthyrial cover: open (0); apical deltidium (1); deltidial plates (2); deltidium (3); pseudodeltidium (4).
15. foramen: delthyrial (0); apical (1); supra-apical (2); ventral (3); vestigial (4).
16. pedicle callist: absent (0); present, adnate (1); present as apical plate (2).
17. notothyrial angle: absent (0); vestigial (1); widely divergent (2); subparallel to narrowly divergent (3).
18. notothyrial cover: open (0); antigyidium (1); chilidial plates (2); chilidium (3); grooved plates (4).

CARDINAL AREAS

19. ventral: absent (0); vestigial (1); short, curved (2); long, curved (3); short, straight (4); long, straight (5); ginglymus (6); variable (7); subpyramidal (8).
20. inclination (ventral): absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6).
21. dorsal: absent (0); vestigial (1); short, curved (2); long, curved (3); short, straight (4); long, straight (5).
22. inclination (dorsal): absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6).

ARTICULATION

23. teeth: absent or rudimentary (0); deltidiodont (1); deltidiodont with crural fossettes (2); transverse (3); cyrtomatodont (4).
24. dental plates: absent or rudimentary (0); recessive (1); projecting (2); parallel (3); convergent (4); divergent (5); present or absent (6); replaced by free spondylium (7).
25. sockets: absent (0); present (1); rounded (2); elongate (3); parallel to hinge line (4); with hinge plate (5).
26. socket buttresses: absent (0); socket ridges as rods (1); socket ridges as blades (2); brachiophores as nubs (3); brachiophores as rods (4); brachiophores as blades (5); brachiophores with bases (6); brachiophores with fulcral plates (7); brachiophores with bases and fulcral plates (8).
27. brachiophores: absent (0); socket blades or rods (1); parallel or slightly divergent rods (2); widely divergent rods (3); parallel or slightly divergent blades (4); widely divergent blades (5); parallel, long blades (6); hooked to sigmoidal plates (7).
28. brachiophore plates: absent (0); parallel (1); convergent (2); as septalium (3); divergent (4); convergent, recessive (5).
29. fulcral plates: absent (0); present (1).

MUSCULATURE

30. ventral scars: umbonal (0); suboval to subtriangular (1); cordate (2); bilobed (3); extended (4); quadrate to flabellate (5); linear (6); on spondylium (7).
31. ventral muscle supports: unsupported (0); on spondylia, simplex, duplex, or triplex (1); on cella (2); on free spondylium (3).
32. median ridge: absent (0); present (1); grooved (2); double ridge (3); tonguelike (4); forked (5); septum (6).
33. raised ventral scars: impressed on valve floor (0); on callus or pseudospondylium (1); on raised structure (2).

TABLE 17. (Continued).

34. dorsal adductor scars: quadripartite (0); linear as in <i>Nisusia</i> (1); petaloid with anterior pair inserted between posterior pair as in <i>Finkelnburgia</i> (2); dispersed as in the widely separated adductor scars of <i>Wimanella</i> (3).	
35. quadripartite scars: not quadripartite (0); quadripartite subequal (1); posterior pair larger than anterior (2); anterior pair larger than posterior (3); bilobed anterior pair larger than posterior (4).	
36. notothyrial platform: absent or rudimentary (0); transverse plate (1); platform (2); platform with notothyrial ridges (3).	
37. cardinal process: absent or rudimentary (0); median ridge (1); shaft or shaft with myophore (2); bilobed (3); trilobed (4); fused with notothyrial ridges (5); not fused with notothyrial ridges (6); variable (7); composed of convergent brachiophore plates (8).	
38. myophore of cardinal process: undifferentiated (0); differentiated (1); cleft (2); swollen (3); crenulated (4).	
39. median partition: absent or indistinct (0); ridge (1); septum (2); partition (3).	
40. subperipheral rim: absent (0); present (1).	
MANTLE CANALS	
41. ventral systems: saccate with convergent <i>vascula media</i> (0); saccate with divergent <i>vascula media</i> (1); digitate (2); lemniscate (3); pinnate (4).	
42. dorsal systems: saccate (0); digitate (1); lemniscate (2); pinnate (3); apocapate (4).	

fibrous walls of punctae in the secondary shell of *Paurorthis* appear to be more steeply inclined externally than those of *Rhipidomella*. This difference, however, could be related to the more lathlike fibers of the Ordovician genus because the canals of both are more or less equispaced at about 50 μm and range between 9 and 14 μm in diameter. As shown in *Paurorthis* (Fig. 520.1a–c), punctae are immediately distinguishable from the larger, horizontally disposed aditicles.

Punctuation of the enteletoid *Schizophoria* (Fig. 520.3a–c) appears to be homologous with that of the dalmanelloids (Fig. 520.2a,b). The Carboniferous specimens studied were well enough preserved to retain a recrystallized patina on the exterior of the shells underlain by fibrous secondary layer. The patina is assumed to be recrystallized primary layer, through which the distal ends of punctal infills penetrate (Fig. 520.3a). This relationships suggests that, in life, the punctae were not covered by canopies of primary shell, only by an organic plug, possibly little more than the periostracum. In some specimens, the distal ends of fibers partly cover punctal infills (Fig. 520.3b). It is, however, doubtful whether this arrangement is indicative of the closure of some punctae within the fibrous secondary layer. The outward deflection of fibers delineating punctae

(Fig. 520.3c) could simulate partial closure in transverse sections.

The erection of the 300 or so orthide genera currently in circulation has involved the diagnostic use of almost every aspect of shell morphology and structure. In the classification adopted here, 42 character sets have been phylogenetically analyzed to establish an intraordinal hierarchy for all recognized genera (Table 17). This was done in stages. First, each traditional family grouping of genera was analyzed to determine their phylogenetic homogeneity. Excluded genera were then repeatedly analyzed with other families in order to identify the suprageneric taxa, with which they have closest morphological affinities. Finally, all such suprageneric taxa, represented by their internal nodes, were assembled into two cladograms that became the basis of the present infraordinal classification (Fig. 521–522).

All impunctate suprageneric units, including the Protorthidae and Skenidiidae, were analyzed using the nisusiids as the outgroup. Three clades resulted: one representing the Protorthida and the other two a dichotomy of the orthidines (Fig. 521). This is more or less consistent with a division of the orthidines into orthids and plectorthids, in the wide sense, groups that have long been distinguishable especially in the relative

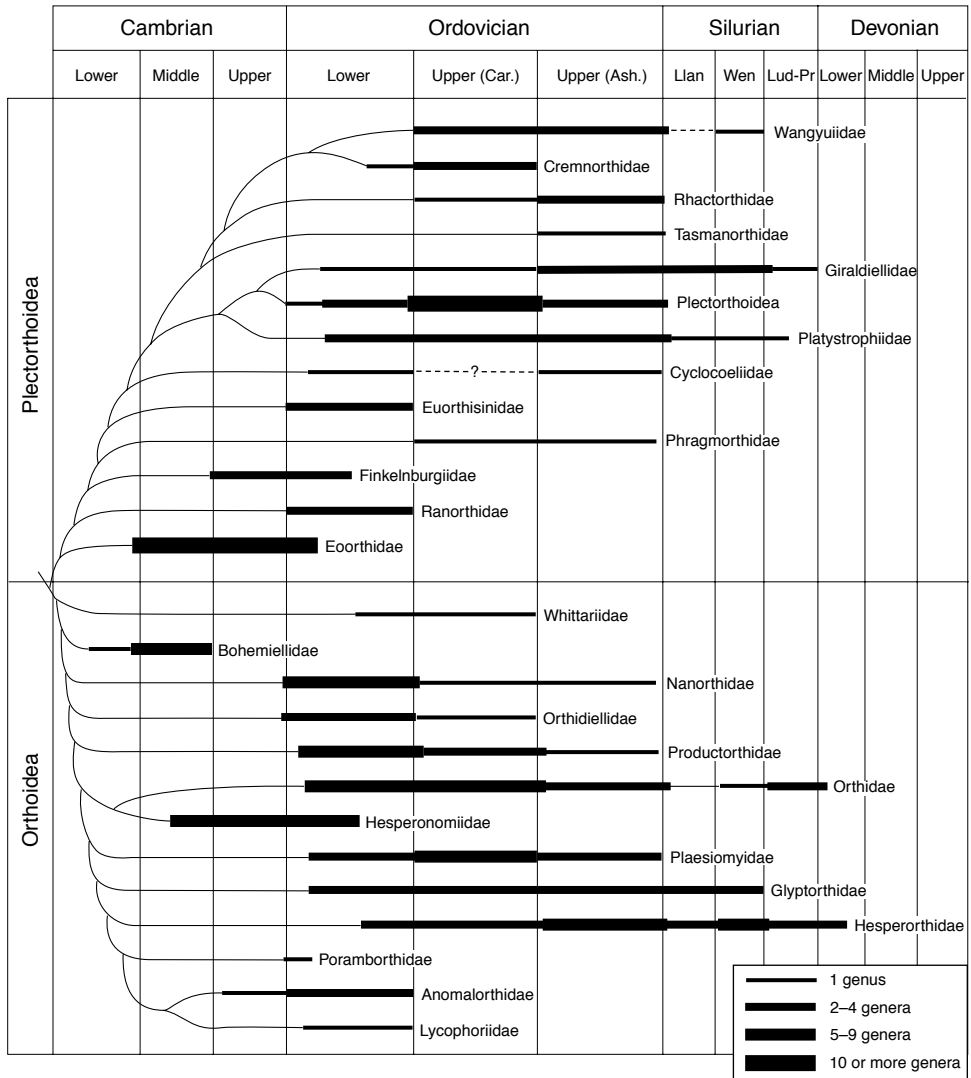


FIG. 521. Cladogram adapted to show chronostratigraphic distribution of constituent orthidine families; the Caradoc (*Car.*) and Ashgill (*Ash.*) series of the Upper Ordovician have been distinguished; the Silurian has been divided into its series: *Llan*, Llandovery; *Wen*, Wenlock; *Lud-Pr*, Ludlow-Přidolí (new).

complexity of the plectorthid cardinalia. Such a grouping can be accommodated within a widely recognized hierarchy consisting of the suborder Orthidina (first proposed by SCHUCHERT & COOPER, 1932, p. 43) and two constituent superfamilies, the Orthoidea (first proposed as Orthacea by WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147) and the Plectorthoidea (first proposed by HAVLIČEK, 1977a, p. 75).

All punctate suprageneric units were analyzed using the plectorthid node as the outgroup (Fig. 522). On morphological grounds, this was an appropriate choice; indeed, HAVLIČEK (1977a, p. 54) identified the nanorthids as ancestral to the dalmanellids. Two well-defined clades emerged, with the paurorthids forming a possible sister group. The clades aggregate around the dalmanellids and the draboviids. The latter are distin-

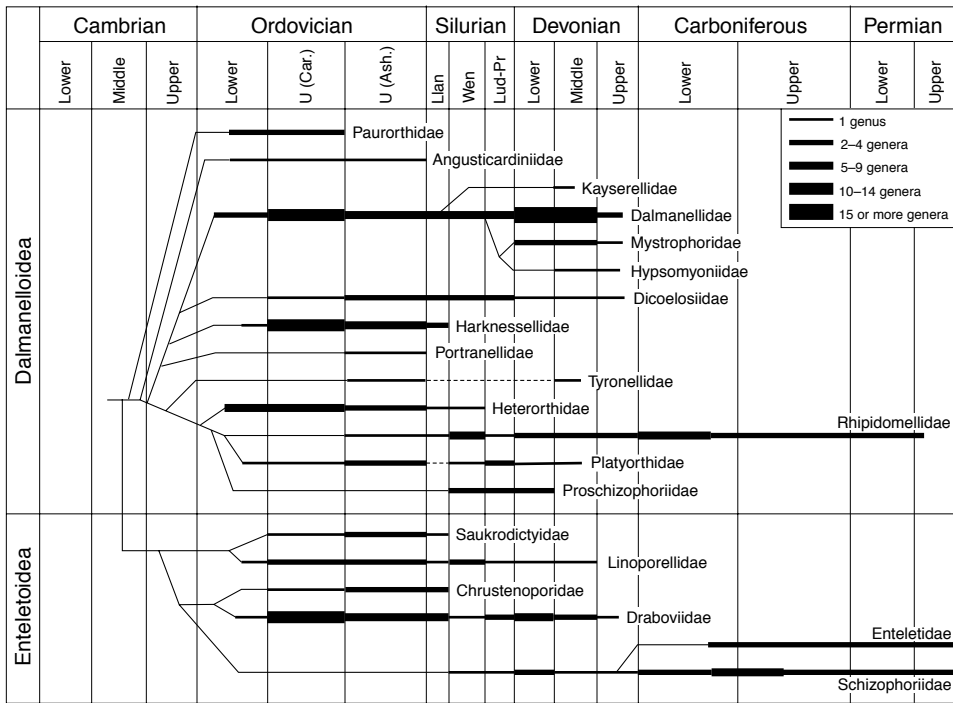


FIG. 522. Cladogram adapted to show chronostratigraphic distribution of constituent dalmanellidine families (new).

guished by their poorly developed notothyrial platform, convergent brachiophore plates, and a relatively simple cardinal process. This grouping is compatible with a hierarchy within the suborder, Dalmanellidina (first proposed by MOORE in MOORE, LALICKER, & FISCHER, 1952), which is composed of the two superfamilies, Dalmanelloidea (first proposed by SCHUCHERT & COOPER, 1931, p. 245) and Enteletoidea (first proposed by ALICHOVA, 1960, p. 193).

The relationship among the orthide superfamilial units was assessed by comparing the nodal codes for the four superfamilies with the nisusiids and protorthides as outgroups. The impunctate and punctate orthides formed two distinct clades, which validated the assignment of these superfamilies to suborders.

This classification is not truly phylogenetic as it has not been possible to identify and allow for all the homoplasy that must have contributed to the evolution of the orthide shell. The repeated lengthening of

the ventral muscle scars is an obvious example of a convergence that cannot easily be categorized for phylogenetic analysis. It is also noteworthy that the sudden appearance of mature stocks in the geological record, as it is presently known, occurred during periods of active plate tectonics. Thus difficulties in assigning, for example, the portranellids and tyronellids within the dalmanelloid clade are more likely to reflect their cryptic appearance in the Late Ordovician than a close common ancestry; while the linoporellids and saukrodictyids were also probably enteletoid latecomers with articular devices and cardinalia that have been modified by the abnormal growth of the cardinal areas in the former and the development of spike-like brachiophores and a septalium in the latter. Notwithstanding the complications such factors impose on attempts to trace orthide phylogeny, familial groupings have been improved by these analyses, which have also eliminated some of the more contrived aspects of previous classifications.

Suborder ORTHIDINA Schuchert & Cooper, 1932

[*nom. correct.* WILLIAMS & WRIGHT, 1965, p. 300, *pro* Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.*, WILLIAMS & HARPER, *herein*]

Essentially same range and variability of characters as for Orthida but having impunctate shell with fibrous secondary layer. *Lower Cambrian—Lower Devonian (Emsian)*.

Superfamily ORTHOIDEA Woodward, 1852

[*nom. correct.* *herein pro* Orthoidea, *nom. transl.* WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147, *ex* Orthidae WOODWARD, 1852, p. 229]

Typically medium-sized, unisulcate, radially ornamented, and filate orthides with wide, open delthyrium and notothyrium and curved apsacline ventral and anacline dorsal interareas; teeth variable but commonly deltidodont with crural fossettes, supported by dental plates, normally recessive; ventral muscle scar variable in outline rarely impressed on pseudospondylium, pedicle callist normally preserved; notothyrial platform commonly strongly developed, supporting typically ridgelike cardinal process and variably disposed rodlike or bladlike brachiophores to form elongate sockets and extending anteriorly as dorsal median ridge bisecting dorsal adductor field that is essentially subequally quadripartite; ventral and dorsal mantle canal systems normally saccate and digitate respectively. *Lower Cambrian—Lower Devonian (Emsian)*.

Family ORTHIDAE Woodward, 1852

[Orthidae WOODWARD, 1852, p. 229]

Variable size, generally subquadrate with obtuse cardinal extremities, ventribiconvex orthoids, apsacline ventral interarea mainly short and curved, anacline dorsal interarea, shorter but more variable; dental plates recessive, ventral muscle field varying from suboval with broad, poorly differentiated adductor track at least as long as flanking diductor scars to subcordate with elongate diductor scars extending anteriorly beyond relatively narrow adductor track impressed on valve floor about low median ridge; car-

dinal process ridgelike; brachiophores normally short, rodlike, moderately divergent; dorsal adductor scar quadripartite, variably impressed on either side of low median ridge and normally with larger anterior pair; ventral mantle canal system saccate, *vascula media* normally divergent; dorsal mantle canal system normally digitate. *Lower Ordovician (Arenig)—Lower Devonian (Lochkovian)*.

Orthis DALMAN, 1828, p. 93 [**O. callactis* DALMAN, 1828, p. 112; SD DAVIDSON, 1853, p. 101]. Large, planoconvex to weakly concavoconvex, rectimarginate, costate, and capillate; ventral muscle scar suboval, brachiophores widely divergent rods; ventral *vascula media* parallel proximally. *Lower Ordovician (Arenig—Llanvirn)*: Baltoscandia.—FIG. 523,3a–g. **O. callactis* DALMAN, Arenig–Llanvirn, Sweden; *a*, dorsal exterior, $\times 2.5$; *b*, dorsal interior, $\times 2$; *c–e*, dorsal, ventral, lateral views of conjoined valves, $\times 2$; *f*, ventral interior, $\times 1$; *g*, details of capillate ornament, $\times 10$ (Jaanusson & Bassett, 1993).

Dioclothofera POTTER, 1990a, p. 58 [**D. conspicua*; OD]. Small, ventribiconvex, strangulate with sulci in both valves, fascicostellate; ventral muscle field suboval, adductor track wide, elevated on medial region of callus extending forward as low ridge; cardinal process commonly bulbous, divergent brachiophores platelike; dorsal adductor field bounded laterally by strong ridges breached by channels for *vascula media* and *myaria*, posterior pair of scars larger, deeply impressed; dorsal median ridge sporadically culminating in low crest; dorsal mantle canal system pinnate. *Upper Ordovician (Ashgill)*: western USA.—FIG. 523,2a–f. **D. conspicua*, Ashgill, western USA; *a, b*, ventral exterior, interior, $\times 4$; *c, d*, dorsal exterior, interior, $\times 5$; *e, f*, dorsal exterior, interior, $\times 4$ (Potter, 1990a).

Orthambonites PANDER, 1830, p. 80 [**Orthis calligramma* DALMAN, 1828, p. 114; SD JAANUSSON & BASSETT, 1993, p. 24–26; =*Orthambonites rotunda* PANDER, 1830, p. 82]. Similar to *Orthis* but subcircular, ventribiconvex, strongly filate, less divergent brachiophores, and lacking ventral median ridge; pedicle callist preserved. *Lower Ordovician (Arenig—Llanvirn)*: Baltoscandia, Russia.—FIG. 524,1a–f. **O. calligramma* (DALMAN), Arenig–Llanvirn; *a–c*, dorsal, ventral, lateral views of conjoined valves, Russia, $\times 2$; *d*, details of capillate ornament, Sweden, $\times 8$; *e*, ventral interior, Sweden, $\times 2$; *f*, dorsal interior, Russia, $\times 2$ (Jaanusson & Bassett, 1993).

Orthokopis BAARLI, 1995, p. 9 [**O. idunnae*; OD]. Small, unisulcate, elongately semioval valves with costellate ornament; ventral muscle scar short, oval to subpentagonal and impressed on callus; dorsal interior with widely divergent bladlike brachiophores. *lower Silurian (Llandovery)*: Norway (Oslo Region).—FIG. 523,1a–f. **O. idunnae*, Llandovery, Oslo Region; *a, b*, internal mold, rubber

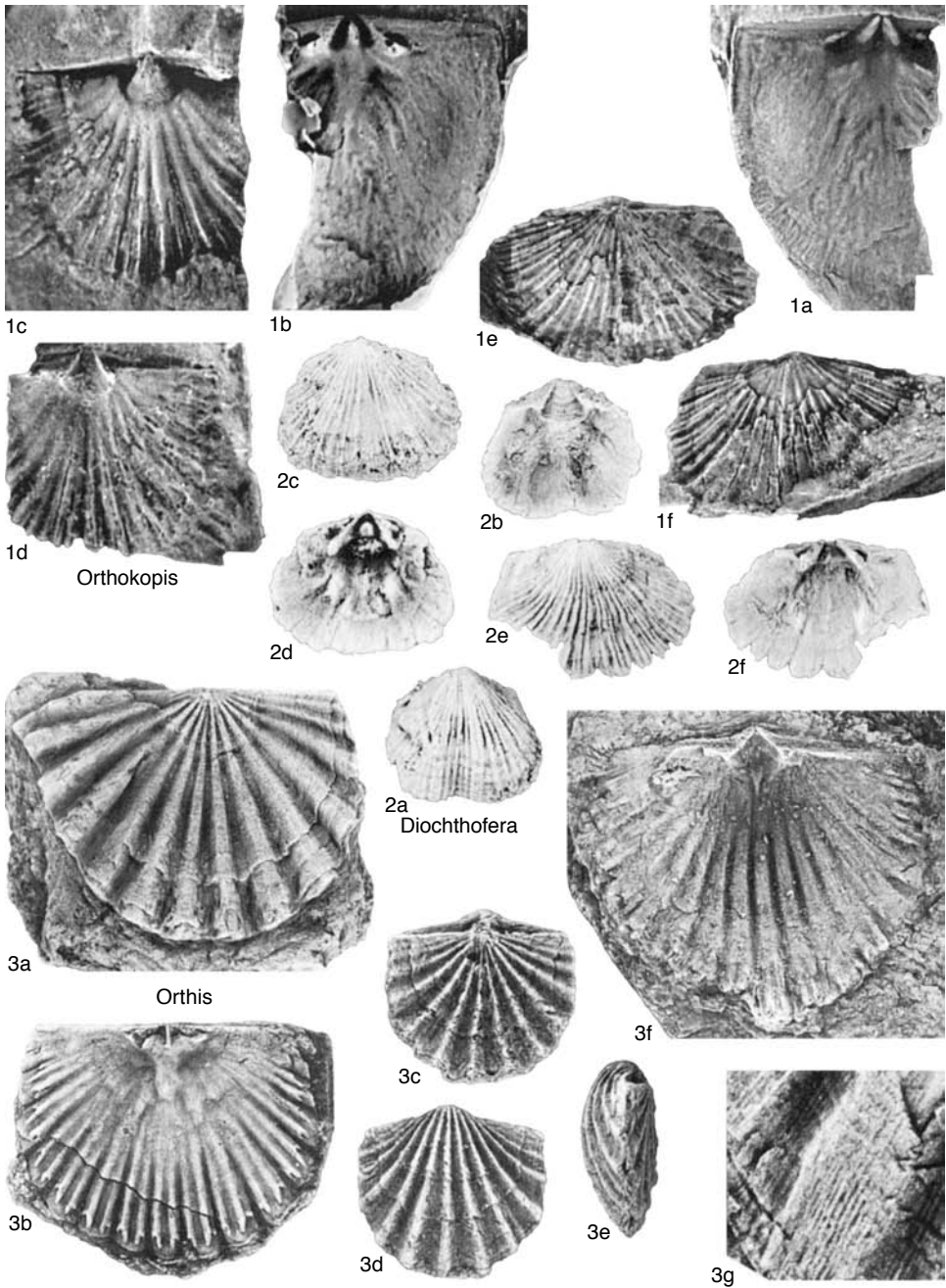


FIG. 523. Orthidae (p. 724–725).

replica of dorsal valve, $\times 3$; *c,d*, internal mold, rubber replica of ventral valve, $\times 4$; *e,f*, dorsal, ventral views of conjoined valves, $\times 3$ (Baarli, 1995).

Orthostrophella AMSDEN, 1968, p. 23 [**Orthostrophia dartae* SCHUCHERT & COOPER, 1932, p. 71; OD]. Similar to *Orthostrophia* but uniplicate with

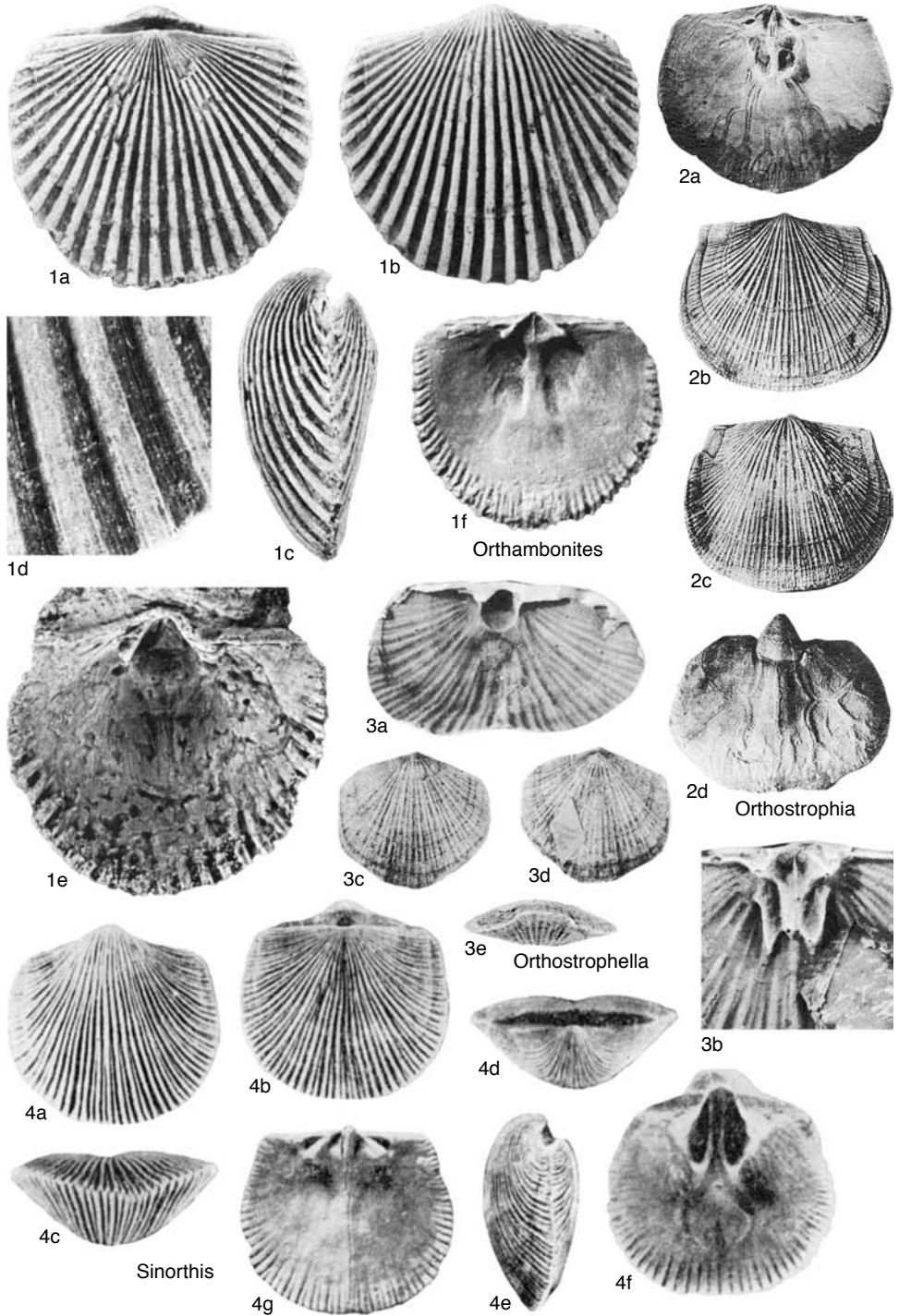


FIG. 524. Orthidae (p. 724–727).

- anteriorly sulcate adult ventral valve. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*: North America (USA, eastern Canada), Bohemia, Great Britain.—FIG. 524,3a–e. **O. dartae* (SCHUCHERT & COOPER), Wenlock, Quebec; *a*, rubber replica of ventral interior, $\times 3$; *b*, rubber replica of dorsal interior, $\times 3$; *c–e*, ventral, dorsal, anterior views of conjoined valves, $\times 1$ (Amsden, 1968).
- Orthostrophia** HALL, 1883, pl. 36, fig. 32–34 [**Orthis strophomenoides* HALL, 1857, p. 46; OD]. Medium sized to large, dorsibiconvex to resupinate, unisulcate, ramicostellate; ventral muscle scar subtriangular with broadly triangular, undifferentiated adductor track; cardinal process ridgelike, occasionally flanked by pair of low notothyrial ridges; mantle canal systems of both valves normally impressed, saccate with ventral *vascula media* curving posterolaterally toward posterior part of valve and branching repeatedly toward anterior margin. [A plectorthid subfamily, the Orthostrophinae, was erected by SCHUCHERT & COOPER (1932, p. 70) because, although the ventral musculature and cardinalia are like those of *Orthis* and *Hesperorthis*, the mantle canal systems resemble those of *Mimella*. Mantle canal systems, however, are less reliable than cardinalia in establishing stock affinities. Consequently, the subfamily was later discarded and *Orthostrophia* was assigned to the Orthinae (WILLIAMS, 1965b, p. 313). The subfamily was then resuscitated by HAVLÍČEK (1977a, p. 76) on the grounds that the cardinalia are plectorthid. That is not so for *Orthostrophia*; its relatively restricted notothyrial platform is an expression of the strong convexity of the dorsal valve.] *upper Silurian (Přídolí)–Lower Devonian (Lochkovian)*: North America, Bohemia, Australia, South America (Argentina), northern China.—FIG. 524,2a–c. **O. strophomenoides* (HALL) Lochkovian; *a*, rubber replica of dorsal interior, New York, $\times 2$; *b, c*, ventral, dorsal exteriors, Tennessee, $\times 1$ (Schuchert & Cooper, 1932).—FIG. 524,2d. *O. sp. aff. O. strophomenoides*, Přídolí, Oklahoma; internal mold of ventral valve, $\times 1.5$ (Schuchert & Cooper, 1932).
- Paralenorthis** HAVLÍČEK & BRANISA, 1980, p. 15 [**P. immitatrix*; OD]. Costate, capillate without filia; suboval ventral muscle scar lacking median ridge; brachiophores short, blunt, divergent. *Lower Ordovician (Arenig–Llanvirn)*: cosmopolitan.—FIG. 525,3a–e. **P. immitatrix*, Arenig–Llanvirn, Bolivia; *a*, internal mold of ventral valve, $\times 2.3$; *b*, internal mold of dorsal valve, $\times 4.5$; *c*, internal mold of dorsal valve, $\times 2.3$; *d*, rubber replica of dorsal exterior, $\times 2.3$; *e*, rubber replica of ventral exterior, $\times 2.3$ (Havlíček & Branisa, 1980).
- Sinorthis** WANG, 1955b, p. 327 [**S. typica*; OD] [= *Yichangorthis* ZENG, 1987, p. 214 (type, *Y. elegans*)]. Ramicostellate; dental plates narrowly divergent, flanking elongate bilobed ventral muscle scar; brachiophores widely divergent. [*Yichangorthis* ZENG, from the same stratigraphic horizon and locality as *Sinorthis*, differs only in having less well-
- developed brachiophores and cardinal process.] *Lower Ordovician (Arenig)*: southern China, France.—FIG. 524,4a–g. **S. typica*, Arenig, southern China; *a–e*, ventral, dorsal, anterior, posterior, lateral views of conjoined valves, $\times 3$; *f*, ventral interior, $\times 3$; *g*, dorsal interior, $\times 3$ (Wang, 1955b).
- Sivorthis** JAANUSSON & BASSETT, 1993, p. 45 [**S. filistera*; OD]. Costellate and capillate with strong filia, long ventral interarea; ventral muscle scar subcordate with shallow median groove; brachiophores short; quadripartite adductor scar with larger posterior pair; ventral *vascula media* parallel proximally. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*: North America, Europe.—FIG. 525,1a–g. **S. filistera*, Caradoc, Sweden; *a–c*, dorsal, ventral, lateral views of conjoined valves, $\times 3$; *d*, details of ornament, $\times 8$; *e*, ventral interior, $\times 3$; *f, g*, dorsal interior, exterior, $\times 3$ (Jaanusson & Bassett, 1993).
- Sulcatorthis** ZENG, 1987, p. 216 [**S. sulcata*; OD]. Small, subcircular, sharply unisulcate, coarsely costellate; dental plates not developed; muscle scars in both valves obscure. [This genus is based on young individuals from the Arenig. On balance the specimens have the strongest affinities with immature orthid shells rather than those of others within the orthidines.] *Lower Ordovician (Arenig)*: southern China.—FIG. 525,2a, b. **S. sulcata*, Arenig, southern China; internal mold of ventral valve, internal mold of dorsal valve, $\times 10$ (Zeng, 1987).
- Sulevorthis** JAANUSSON & BASSETT, 1993, p. 37 [**Orthis lyckholmiensis* WYSOGÓRSKI, 1900, p. 231; OD]. Small, transversely semioval with variable cardinal extremities, costate with strong filia; short, flat interareas; cardinal process differentiated into shaft and crenulated crest, divergent brachiophores blade-like, sockets deep and rounded, delineated anterolaterally by raised ridges simulating fulcral plates; ventral *vascula media* divergent, dorsal mantle canal system apocapate; radially arranged exopunctae along sides of costae. *Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill)*: North America, Europe.—FIG. 526,1a–e. **S. lyckholmiensis* (WYSOGÓRSKI), Ashgill, Estonia; *a–c*, dorsal, ventral, lateral views of conjoined valves, $\times 3$; *d*, details of ornament, $\times 12$; *e*, ventral interior, $\times 3$ (Jaanusson & Bassett, 1993).—FIG. 526,1f. *S. sp. cf. S. lyckholmiensis*, Ashgill, Sweden; dorsal interior, $\times 5$ (Jaanusson & Bassett, 1993).
- Taphrorthis** COOPER, 1956, p. 326 [**T. emarginata*; OD]. Ramicostellate with strong filia; ventral muscle scar subcordate with low median ridge; brachiophores short, rodlike, widely divergent; quadripartite adductor muscle scars with larger anterior pair; ventral *vascula media* apparently subparallel proximally. *Upper Ordovician (Caradoc)*: North America, Scotland, Ireland, Estonia, China.—FIG. 526,2a–b. **T. emarginata*, Caradoc; *a, b*, dorsal interior, ventral interior, Tennessee, $\times 2$; *c–g*, posterior, anterior, lateral, ventral, dorsal views of conjoined valves, Alabama, $\times 1$; *h*, enlarged dorsal view of conjoined valves, $\times 2$ (Cooper, 1956).

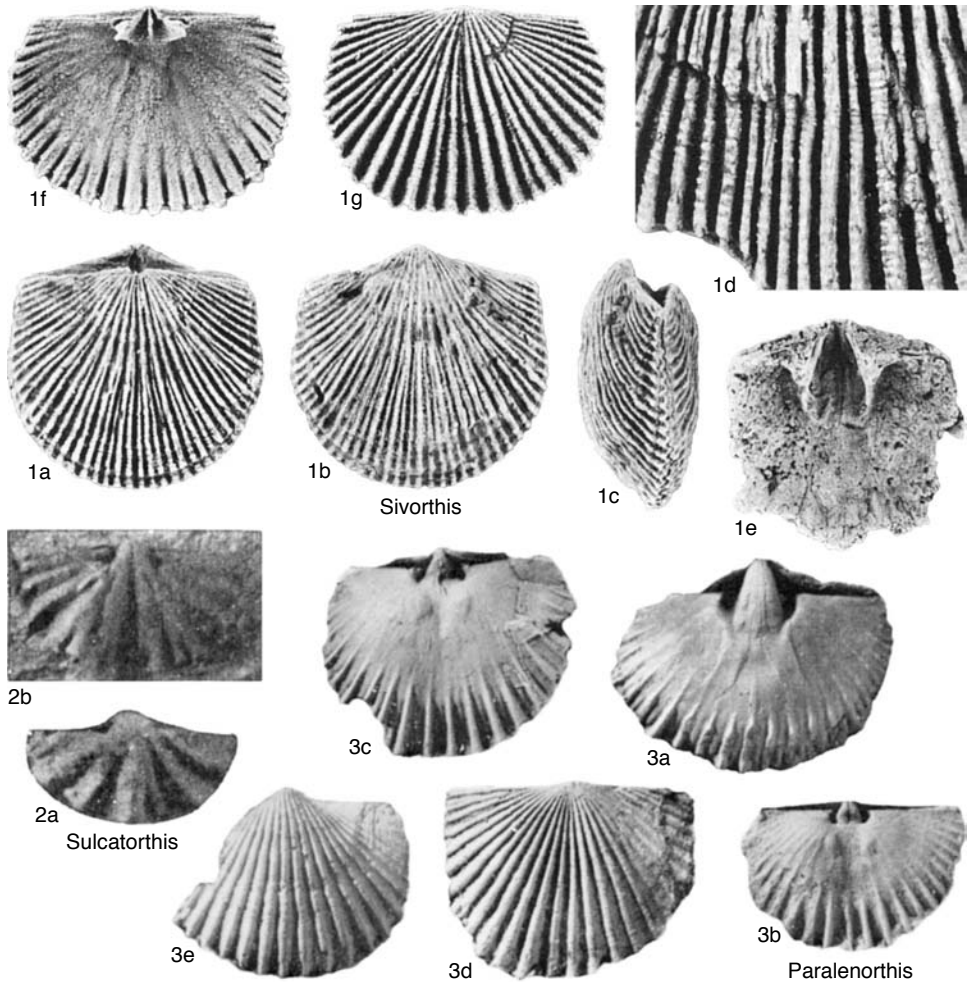


FIG. 525. Orthidae (p. 727).

Trondorthis NEUMAN in NEUMAN & BRUTON, 1974, p. 77 [*Orthambonites bifurcatus* COOPER, 1956, p. 297; OD] [= *Ocorthis* MÉLOU, 1982, p. 25 (type, *O. occitanensis*)]. Similar to *Taphrorthis* but elongately oval and without fila; ventral muscle scar suboval, without ventral median ridge. [According to the diagnoses at hand, *Ocorthis*, based on specimens from the Lower Ordovician of France (Montagne Noire), differs from *Trondorthis* only in its more subquadrate outline.] Lower Ordovician (*Arenig-Llanvirn*): North America, Baltoscandia, France, central Asia.—FIG. 526, 3a–f. **T. bifurcatus* (COOPER), Arenig-Llanvirn, Toquima Range; a–d, ventral, dorsal, anterior, posterior views of conjoined valves, $\times 1.5$; e, dorsal interior, $\times 1.5$; f, ventral interior, $\times 1.5$ (Neuman & Bruton, 1974).

Family ANOMALORTHIDAE

Ulrich & Cooper, 1936

[Anomalorthidae ULRICH & COOPER, 1936b, p. 622] [= Alimbellidae ANDREEVA, 1960, p. 291]

Dorsibiconvex, strongly uniplicate, subquadrate orthoids with obtuse cardinal extremities; simple teeth normally without dental plates, ventral muscle scar suboval, impressed on pseudospondylium with fine median ridge, pedicle callist not developed; bladlike cardinal process and strong, outwardly curving brachiophores supported by thick notothyrial platform; quadripartite

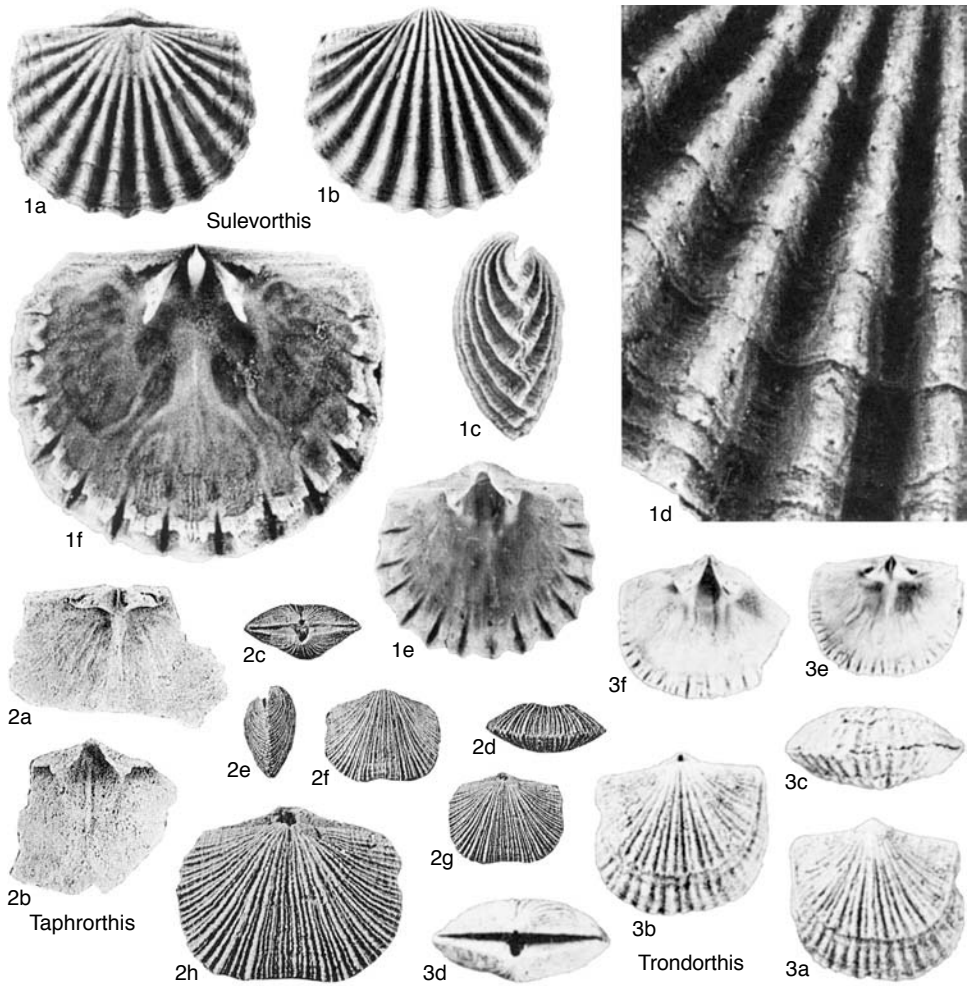


FIG. 526. Orthidae (p. 727–728).

dorsal adductor scar large, deeply impressed, commonly on elevated callus; ventral mantle canal system less commonly impressed, digitate. *Upper Cambrian–Lower Ordovician (Llanvirn)*.

Anomalorthis ULRICH & COOPER, 1936b, p. 622 [*A. utabensis*; OD]. Unequally biconvex to convexoconcave, weakly uniplicate, multicostellate valves with long ventral interarea; delthyrium open with small apical plate; ventral interior with muscle scars impressed on raised callus; dorsal interior with simple ridgelike cardinal process. *Lower Ordovician (Arenig–Llanvirn)*: USA (Utah, Nevada, Oklahoma, Vermont).—FIG. 527, 1a–e. *A. utabensis*, Arenig–Llanvirn, Utah; a–c, exterior together with normal

and tilted views of ventral interior, $\times 2$; d, dorsal interior, $\times 2$; e, internal mold of dorsal valve, $\times 2$ (Ulrich & Cooper, 1938).

Alimbella ANDREEVA, 1960, p. 292 [*A. armata*; OD]. Large, smooth with some impersistent radial markings; teeth large, small rhomboidal depression anteromedianly of ventral muscle field with narrow adductor scars; brachiophores massive, encased in secondary shell defining rounded sockets; posterior pair of dorsal adductor scars larger than anterior pair. *Lower Ordovician (Tremadoc)*: Russia (Urals).—FIG. 527, 2a–c. *A. armata*, Tremadoc, Urals; a, ventral exterior, $\times 1$; b, internal mold of ventral valve, $\times 1$; c, dorsal interior, $\times 3$ (Andreeva, 1960).

Astraborthis WILLIAMS, 1974, p. 68 [*A. uniplicata*; OD]. Medium size, subcircular with coarse, angular

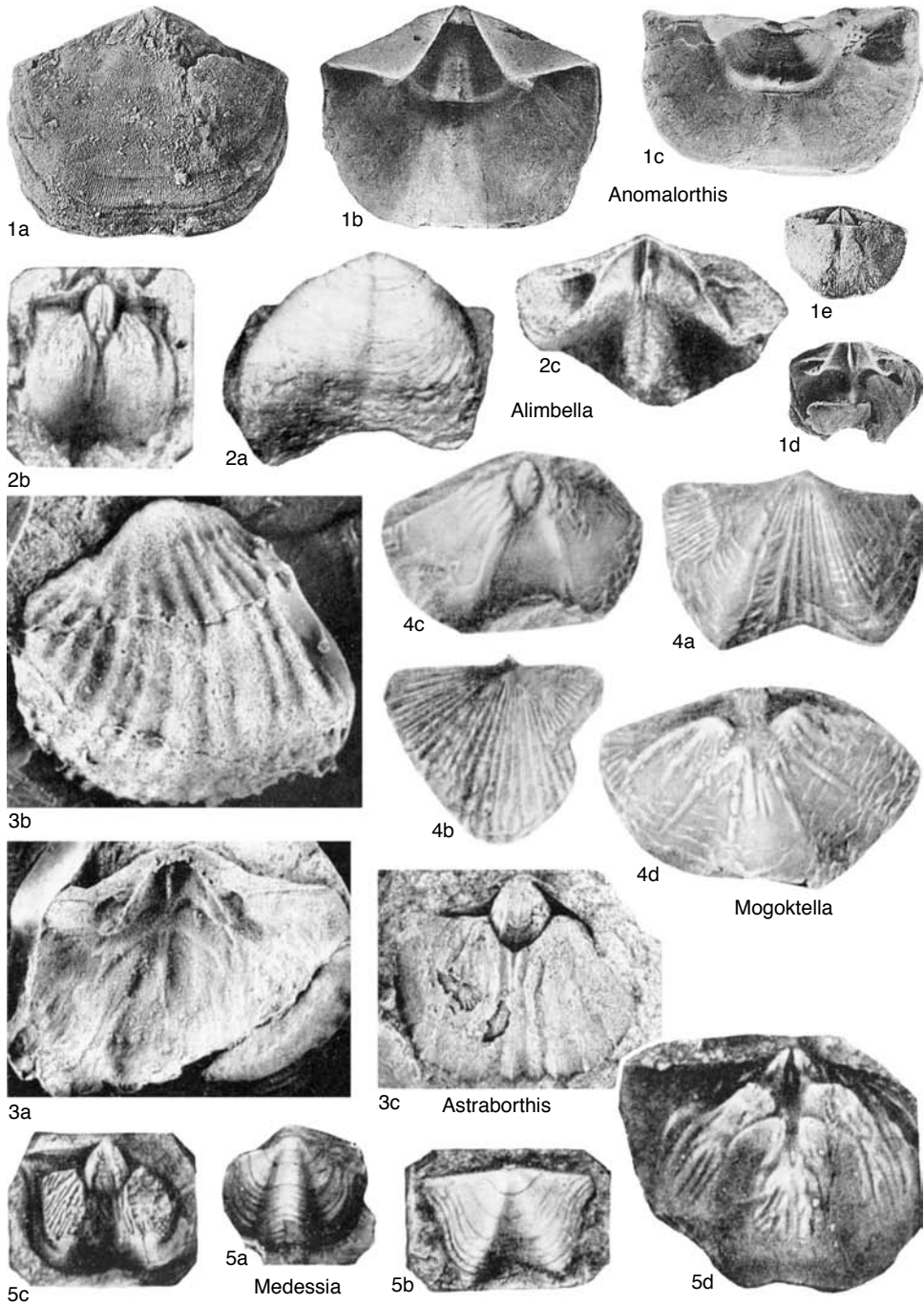


FIG. 527. Anomalorthidae (p. 729–731).

costellae; ventral muscle field with relatively broad, medially divided adductor scars; bilobed anterior pair of dorsal adductor scars larger than posterior

pair. Lower Ordovician (Arenig): Great Britain.—FIG. 527, 3a–c. **A. uniplicata*, Arenig, Shelve; a, rubber replica of dorsal interior, $\times 4$; b, rubber rep-

lica of dorsal exterior, $\times 4.7$; *c*, internal mold of ventral valve, $\times 2.8$ (Williams, 1974).

- Medessia** ANDREEVA, 1960, p. 295 [**M. uralica*; OD]. Similar to *Alimbella* but medium size, capillate, and with subequal dorsal adductor scars. *Lower Ordovician (Tremadoc)*: Russia (Urals).—FIG. 527,5a–d. **M. uralica*, Tremadoc, Urals; *a*, dorsal exterior, $\times 1$; *b*, ventral exterior, $\times 1$; *c*, internal mold of ventral valve, $\times 1.5$; *d*, internal mold of dorsal valve, $\times 3$ (Andreeva, 1960).
- Mogoktella** ANDREEVA, 1968, p. 82 [**M. islandica*; OD]. Medium size, ramicostellate with variable interspacing of costellae, ventral interarea relatively short; recessive dental plates present; cardinal process ridgelike, dorsal adductor scar quadripartite and splayed with smaller anterior pair inserted submedianly between posterior pair and separated by low median ridge; dorsal mantle canal system digitate (equidistributate). *Upper Cambrian*: northwestern central Siberia.—FIG. 527,4a–d. **M. islandica*, Upper Cambrian, northwestern central Siberia; *a*, replica of ventral exterior, $\times 3$; *b*, replica of dorsal exterior, $\times 3$; *c*, internal mold of ventral valve, $\times 3$; *d*, internal mold of dorsal valve, $\times 3$ (Andreeva, 1968).

Family BOHEMIELLIDAE Havlíček, 1977

[Bohemiellidae HAVLÍČEK, 1977a, p. 28; *emend.*, WILLIAMS & HARPER, herein]

Mainly biconvex, subquadrate orthoids with obtuse cardinal extremities; apsacline ventral interarea usually long and curved, anacline dorsal interarea short and flat; teeth transverse and ridgelike, dental plates very rarely developed; ventral muscle scar subtriangular, mainly restricted to delthyrial cavity, notothyrial platform flat, normally with simple cardinal process; brachiophores short, ridgelike, widely divergent, quadripartite adductor scar relatively widely dispersed about low, broad median ridge; ventral mantle canal system saccate with divergent *vascula media*, dorsal system saccate to digitate. *Lower Cambrian–Middle Cambrian*.

- Bohemiella** SCHUCHERT & COOPER, 1931, p. 242 [**Orthis romingeri* BARRANDE, 1879, p. 203; OD] [= *Shiragia* KOBAYASHI, 1935b, p. 70 (type, *S. bilobata*)]. Planoconvex with variable cardinal extremities and multicostellate ornamentation; ventral adductor scar separated from flanking diductor scars by low, slightly divergent ridges, transverse teeth ridges with fine denticles; rounded sockets subtended by short, ridgelike brachiophores and passing laterally into denticulate ridges immediately below hinge line; larger anterior dorsal adductor scars separated from posterior pair by fine oblique ridges. *Middle Cambrian*: Bohemia, New

Zealand.—FIG. 528,3a–c. **B. romingeri* (BARRANDE), Middle Cambrian, Bohemia; *a*, internal mold of ventral valve, $\times 3.9$; *b*, internal mold of dorsal valve, $\times 5$; *c*, rubber replica of dorsal exterior, $\times 2.8$ (Havlíček, 1977a).

- Chilidorthis** HAVLÍČEK & JOSOPAIT, 1972, p. 342 [**C. tecta*; OD]. Medium sized, planoconvex with weakly developed multicostellae; teeth unknown; lacking dental plates, ventral muscle scar obscure but associated with divergent *vascula media*; ridgelike cardinal process and wide, low, dorsal muscle field; mantle canal system unknown. [This genus is doubtfully assigned to the Bohemiellidae. It is based on poorly preserved molds, scarcely distinguishable below familial rank; but it has been identified as a bohemiellid by its authors notwithstanding the presence of a chilidium (or chilidial plates).] *Middle Cambrian*: Spain.—FIG. 529,2a–c. **C. tecta*, Middle Cambrian, northern Spain; *a*, internal mold of ventral valve, $\times 2.4$; *b*, internal mold of dorsal valve, $\times 2.7$; *c*, external mold of dorsal valve, $\times 3$ (Havlíček & Josopait, 1972).
- Cymbricia** ROBERTS & JELL, 1990, p. 272 [**C. spinicostata*; OD]. Ventribiconvex, rectimarginate with variable cardinal extremities, multicostellate, cancellate; ventral interarea planar, dorsal one curved; ventral muscle field subcordate with adductor track inserted anteromedianly in heart-shaped pit and not enclosed by elongate diductor scars; cardinal process ridgelike, not always developed. *Middle Cambrian*: Australia (New South Wales).—FIG. 528,2a–f. **C. spinicostata*, Middle Cambrian, New South Wales; *a*, ventral exterior, $\times 1.5$; *b, c*, interior, posterior views of ventral valve, $\times 3$; *d*, ventral interior, $\times 3$; *e*, dorsal interior, $\times 6$; *f*, details of ornament, $\times 3$ (Roberts & Jell, 1990).
- Diraphora** BELL, 1941, p. 243 [**Eoorthis bellicostata* WALCOTT, 1924, p. 505; OD]. Similar to *Wimanella* but unisulcate with subdued multicostellae and filae. *Middle Cambrian*: North America, Iran, Siberia, Australia.—FIG. 528,1a. **D. bellicostata* (WALCOTT), Middle Cambrian, British Columbia; dorsal interior, $\times 3$ (Walcott, 1924).—FIG. 528,1b–d. *D. striata* (WALCOTT), Middle Cambrian, Montana; *b*, dorsal exterior, $\times 3$; *c*, ventral exterior, $\times 3$; *d*, mold of ventral interior, $\times 2$ (Bell, 1941).
- Murrinyinella** KRUSE, 1990, p. 39 [**M. garradin*; OD]. Similar to *Wimanella* but transversely to elongately semioval, unisulcate in young growth stages; teeth apices placed more or less medially in transverse teeth ridges, ventral muscle scar unknown; cardinal process simple. *Middle Cambrian*: northern Western Australia.—FIG. 529,1a–e. **M. garradin*, Middle Cambrian, Northern Territory; *a–c*, ventral, dorsal, lateral views of conjoined valves, $\times 5$; *d*, dorsal interior, $\times 5$; *e*, broken ventral interior, $\times 5$ (Kruse, 1990).
- Oligomys** SCHUCHERT & COOPER, 1931, p. 243 [**Orthis exporrrecta* LINNARSSON, 1876, p. 12; OD]. Transversely semioval, variably planoconvex, costellate, capillate; small wide teeth with rudimentary dental plates, ventral adductor track linear, expanding anteriorly and extending beyond flanking diductor scars; simple cardinal process, short, widely

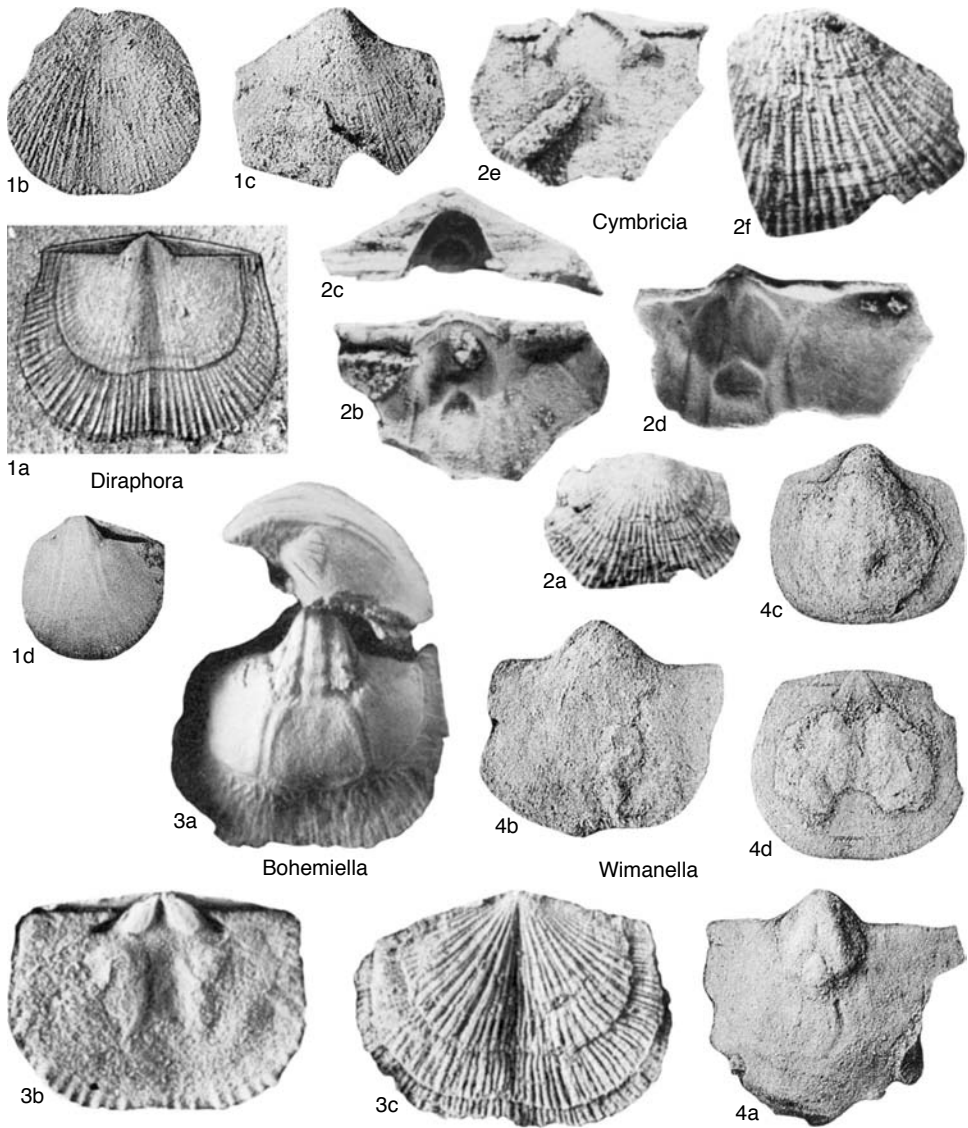


FIG. 528. Bohemiellidae (p. 731–732).

divergent brachiophores. *Middle Cambrian*: Europe.—FIG. 529,3a,b. **O. exporrectus* (LINNARSSON), Middle Cambrian, Sweden; *a*, internal mold of ventral valve, $\times 2.5$; *b*, dorsal interior, $\times 2.5$ (Schuchert & Cooper, 1932).

Wimanella WALCOTT, 1908, p. 98 [**W. simplex*; OD]. Subquadrate with variable cardinal extremities, biconvex, unisulcate to rectimarginate, smooth except for concentric growth lines and sporadic, low radial ridges but finely striate on internal margins; teeth apices near delthyrial boundary of transverse teeth

ridges; ventral diductor scars elongate, separated posteriorly by low median ridge that bifurcates anteriorly to contain medial adductor scar; cardinal process absent or rudimentary. *Lower Cambrian–Middle Cambrian*: North America, Australia, Siberian Platform, eastern China.—FIG. 528,4a–d. **W. simplex*, Middle Cambrian, Montana; *a*, internal mold of ventral valve, $\times 2$; *b*, ventral exterior, $\times 3$; *c*, internal mold of ventral valve, $\times 3$; *d*, internal mold of dorsal valve, $\times 2$ (Bell, 1941).

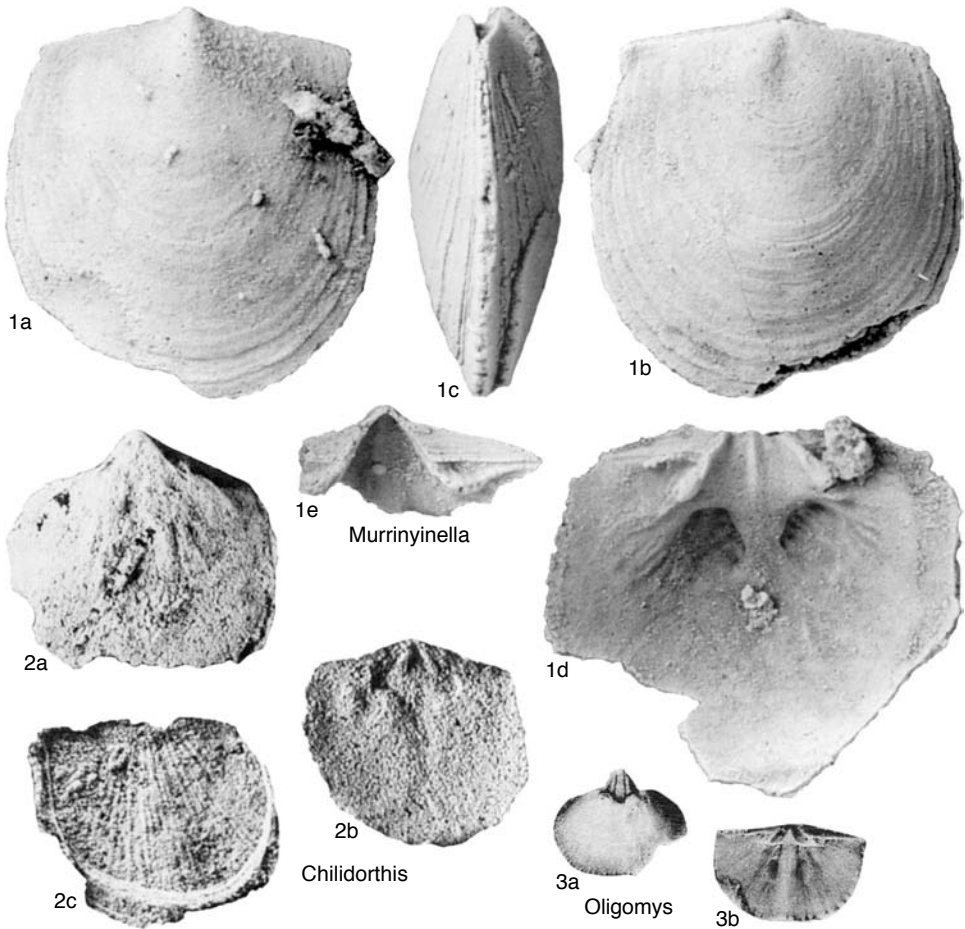


FIG. 529. Bohemiellidae (p. 731–732).

Family GLYPTORTHIDAE
Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, ex Glyptorthinae SCHUCHERT & COOPER, 1931, p. 243]

Medium to large, subquadrate usually with obtuse cardinal extremities, costate to costellate with strong concentric ornamentation developed as lamellose frills or even drawn out as spines; delthyrium and notothyrium varying in width, exceptionally covered, short dorsal interarea variably orientated; dental plates normally present, recessive, ventral muscle scar variable, with relatively broad adductor track rarely shorter than diductor scars, pedicle callist usually

well developed; brachiophores variably structured and disposed, well-developed notothyrial platform normally supporting simple cardinal process and invariably prolonged anteriorly as median ridge; quadripartite dorsal scars commonly with anterior pair larger than posterior pair; sporadically impressed mantle canals with saccate ventral and digitate dorsal systems. *Lower Ordovician (Arenig)–middle Silurian (Wenlock).*

Glyptorthis FOERSTE, 1914, p. 257 [*Orthis insculpta* HALL, 1847, p. 125; OD]. Variable in size and in cardinal extremities, subequally biconvex, rami-costellate, strongly lamellose, ventral interarea of varying length, dorsal interarea short, curved; ventral muscle scars subcordate with adductors

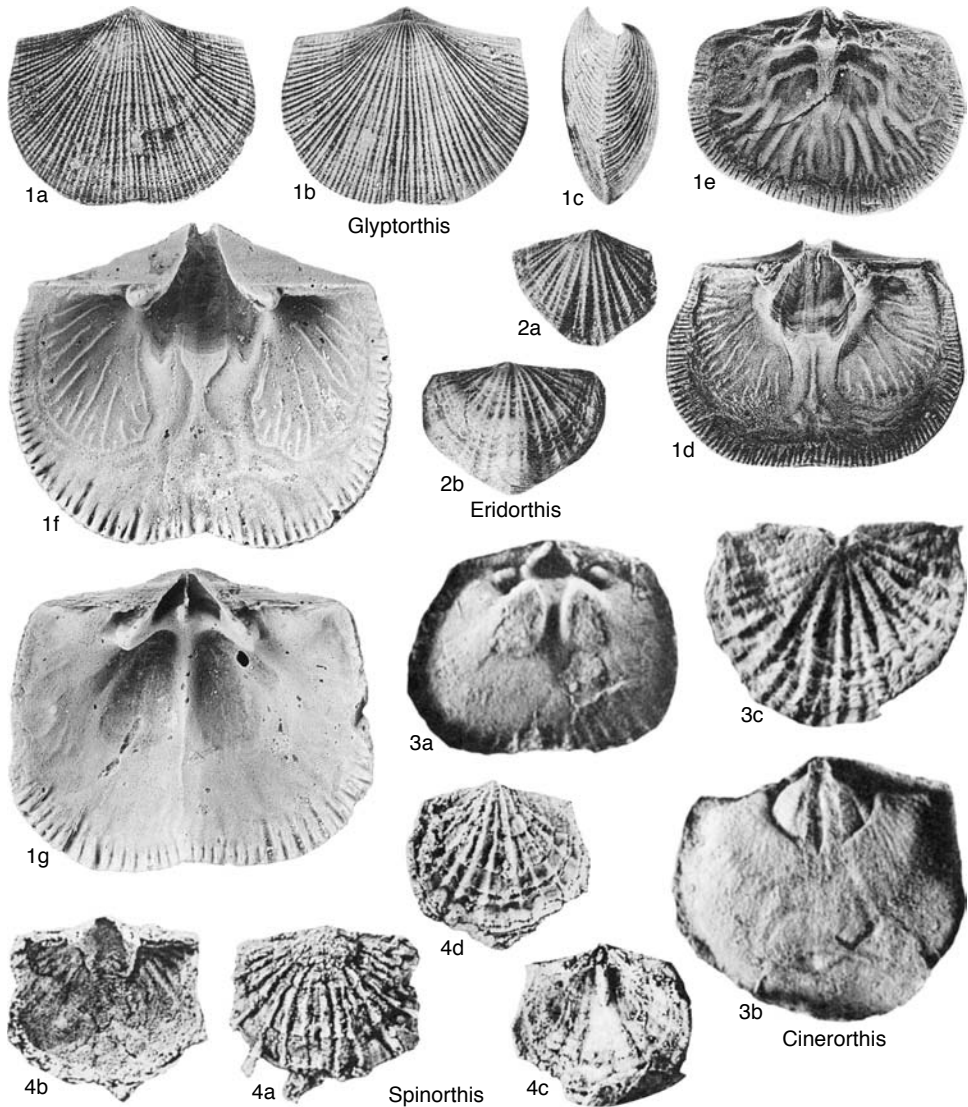


FIG. 530. Glyptorthidae (p. 733–736).

commonly raised on median callist extending forward as tongue of secondary shell; brachiophores divergent, rodlike. *Lower Ordovician (Llanvirn)–middle Silurian (Wenlock)*: Northern Hemisphere.

—FIG. 530, 1a–e. **G. insculpta* (HALL), Ashgill, Ohio; a–c, ventral, dorsal, lateral views of conjoined valves, $\times 1.5$; d, ventral interior, $\times 1.5$; e, dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 530, 1f, g. *G. pulchra*, Ashgill, Iowa; ventral interior, dorsal interior, $\times 2$ (Cocks, new).

Cinerorthis HAVLIČEK, 1974, p. 167 [**C. cineraria*; OD]. Dorsibiconvex to resupinate, uniplicate, coarsely costellate, delthyrium with convex deltid-

ium commonly perforate apically; interareas short, flat; ventral muscle scar subpentagonal, impressed on callus, adductor track divided by median ridge; undifferentiated cardinal process thick, occupying much of notothyrial platform, divergent brachiophores bladlike. *middle Silurian (Wenlock)*: Bohemia.—FIG. 530, 3a–c. **C. cineraria*, Wenlock, Bohemia; a, internal mold of dorsal valve, $\times 2.8$; b, internal mold of ventral valve, $\times 1.7$; c, rubber replica of ventral exterior, $\times 3$ (Havliček, 1977a).

Eridorthis FOERSTE, 1909b, p. 223 [**Plectorthis (Eridorthis) nicklesi*; OD]. Similar to *Glyptorthis* but uniplicate with dorsal median sulcus replaced by

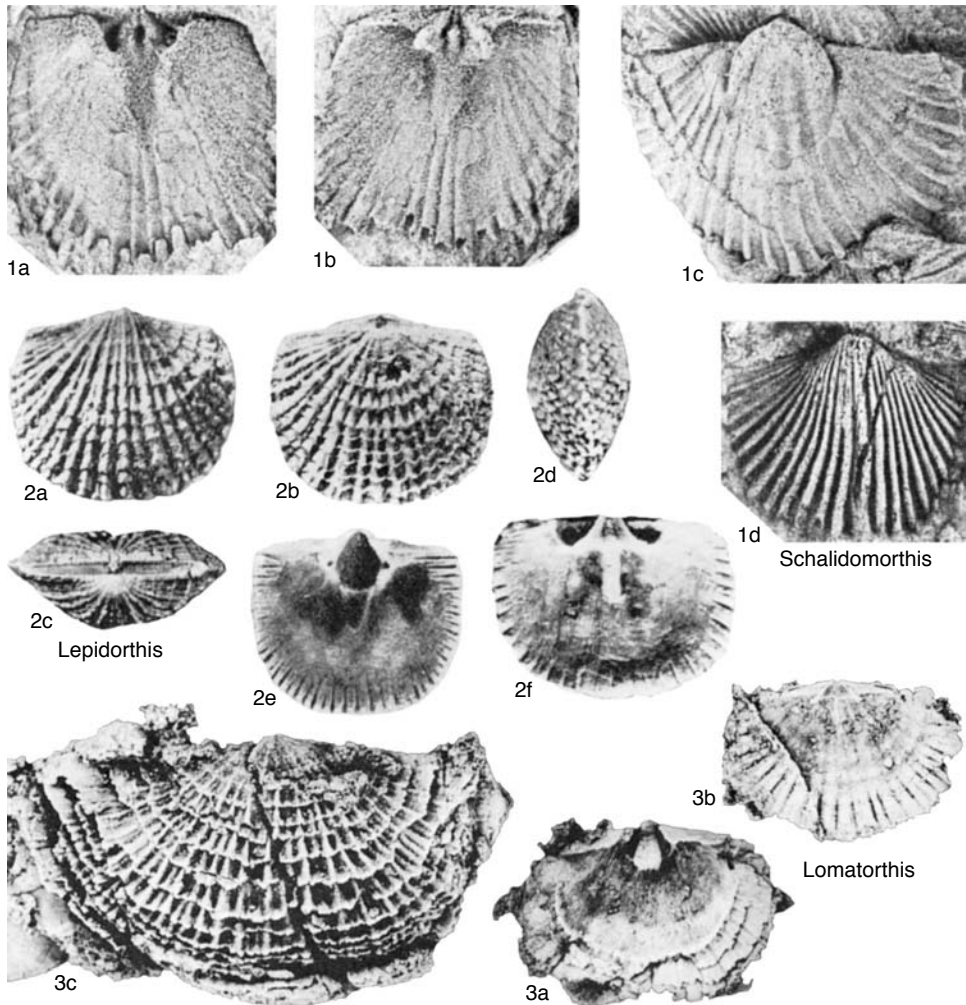


FIG. 531. Glyptorthidae (p. 735–736).

fold in adult shells, obtuse cardinal extremities, long curved ventral interarea and apsacline dorsal interarea, ventral muscle scar supported by callus, adductor track relatively narrow, expanding anteriorly. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock)*: North America, Europe, Siberia, central Asia, North Africa, Australia, China.—FIG. 530,2a. **E. nicklesi* (FOERSTE), Caradoc, Kentucky; ventral exterior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 530,2b. *E. rogerensis* FOERSTE, Caradoc, Kentucky; dorsal exterior, $\times 1.5$ (Schuchert & Cooper, 1932).

Lepidorthis WANG, 1955b, p. 330 [**L. typicalis*; OD]. Ventribiconvex with relatively narrow delthyrium and notothyrium, curved ventral interarea moderately long; ventral muscle scar suboval with median ridge; cardinal process absent, sockets defined later-

ally by fulcral plates. *Lower Ordovician (Arenig)*: southern China.—FIG. 531,2a–f. **L. typicalis*, Arenig, southern China; a–d, ventral, dorsal, posterior, lateral views of conjoined valves, $\times 3.5$; e, ventral interior, $\times 3.5$; f, dorsal interior, $\times 3.5$ (Wang, 1955b).

Lomatorthis WILLIAMS & CURRY, 1985, p. 230 [**L. mimula*; OD]. Subequally biconvex with flattened or gently resupinate margins, rectimarginate, ramicostellate, interareas short, curved; teeth simple, deltidiodont; ventral muscle field elongate with broad adductor components impressed on elevated tonguelike platform, no apical callist seen; cardinal process absent, divergent brachiophores short, bladeliike; quadripartite dorsal adductor scar with subequal parts; subperipheral rim developed in adult ventral valves. *Lower Ordovician (Arenig)*:

Ireland.—FIG. 531,3a–c. **L. mimula*, Arenig, western Ireland; *a*, ventral interior, $\times 2$; *b*, dorsal interior, $\times 3$; *c*, dorsal exterior, $\times 3$ (Williams & Curry, 1985).

Schalidomorthis BASSETT, 1981, p. 650 [**S. stubblefieldi*; OD]. Similar to *Lepidorthis* but costate and lacking concentric lamellae, interareas plane with wide delthyrium and notothyrium. *Lower Ordovician (Llanvirn)*: southwestern England.—FIG. 531,1a–d. **S. stubblefieldi*, Llanvirn, southwestern England; *a, b*, internal mold, rubber replica of dorsal valve, $\times 2.5$; *c*, internal mold of ventral valve, $\times 2.5$; *d*, rubber replica of ventral exterior, $\times 2.5$ (Bassett, 1981).

Spinorthis WRIGHT, 1964, p. 184 [**S. geniculata*; OD]. Similar to *Glyptorthis* but with adult shell geniculate dorsally and lamellae prolonged into suberect spines along coarser costellae, cardinal extremities obtuse, dorsal interarea vestigial; ventral muscle scar without elevations of secondary shell; brachiophores widely divergent. *Upper Ordovician (Ashgill)*: Ireland, Belgium, Wales.—FIG. 530,4a–d. **S. geniculata*, Ashgill, eastern Ireland; *a, b*, exterior, interior of ventral valve, $\times 2.1$; *c, d*, interior, exterior of dorsal valve, $\times 2.1$ (Wright, 1964).

Family HESPERONOMIIDAE Ulrich & Cooper, 1936

[Hesperonomiidae ULRICH & COOPER, 1936b, p. 621]

Unequally parvicostellate orthoids with variable outline, cardinal extremities normally acute; variably oriented ventral interarea normally short, flat, anacline; dorsal interarea very short, flat; teeth normally simple with variably developed dental plates; ventral muscle field variable, impressed directly on valve floor; notothyrial platform supporting variably developed cardinal process, normally extending forward as median ridge, quadripartite dorsal adductor scars rarely impressed; mantle canal systems rarely impressed, ventral saccate with divergent *vascula media*, dorsal digitate. *Middle Cambrian–Lower Ordovician (Llanvirn)*.

Hesperonomia ULRICH & COOPER, 1936b, p. 621 [**H. planidorsalis*; OD]. Elongately semioval with acute cardinal extremities, concavoconvex; apsacline ventral interarea short, flat; deltidodont teeth with recessive dental plates; ventral muscle field subcordate with undifferentiated adductor muscle track not enclosed by diductor scars; notothyrial platform bearing notothyrial ridges fused with simple cardinal process and extending anteriorly as median ridge, divergent brachiophores rodlike; dorsal adductor muscle scar vaguely impressed. *Lower Ordovician (Tremadoc–Arenig)*: North America, Siberia, Great Britain, South America (Argentina),

France, central Asia, China.—FIG. 532,1a–d. **H. planidorsalis*, Tremadoc, Alberta; *a*, ventral interior, $\times 2$; *b*, dorsal interior, $\times 2$; *c*, details of cardinalia, $\times 4$; *d*, dorsal exterior, $\times 2$ (Ulrich & Cooper, 1938).

Hesperonomiella ULRICH & COOPER, 1936b, p. 622 [**Protorthis porcia* WALCOTT, 1924, p. 504; OD] [= *Engenella* ANDREEVA, 1987, p. 36 (type, *E. sibirica*)]. Subquadrate with obtuse cardinal extremities, narrowly biconvex; teeth with crural fossettes supported by recessive dental plates; ventral muscle field suboval with a broad adductor track as long as diductor scars; notothyrial platform with simple cardinal process, divergent brachiophores rodlike; quadripartite dorsal adductor scar impressed on either side of low median ridge with posterior pair larger than anterior pair; mantle canal systems impressed, ventral saccate with divergent *vascula media*, dorsal digitate. [According to the brief descriptions and illustrations of the specimens from the *Middle Cambrian* of the Siberian Platform, on which *Engenella* was established, the stock differs from *Hesperonomiella* only in being more strongly biconvex.] *Middle Cambrian–Lower Ordovician (Arenig)*: North America, Wales, Ireland, Bohemia, Afghanistan, central Asia, Australia (Tasmania), China, Russia.—FIG. 532,2a–d. **H. porcia* (WALCOTT), Tremadoc, Alberta; *a*, internal mold of ventral valve, $\times 1.5$; *b, c*, internal mold, replica of dorsal valve, $\times 2$; *d*, replica of ventral exterior, $\times 2$ (Ulrich & Cooper, 1938).

Monorthis BATES, 1968, p. 144 [**M. typis*; OD]. Subquadrate with acute cardinal extremities, narrowly biconvex, catacline ventral interarea, short, curved; teeth unknown, dental plates recessive, ventral muscle scar unknown; notothyrial platform with simple cardinal process and extending anteriorly as low median ridge; divergent brachiophores bladlike, defining elongate sockets; dorsal adductor muscle scar unknown. *Lower Ordovician (Arenig–Llanvirn)*: Wales, Argentina.—FIG. 532,3a–d. **M. typis*, Llanvirn, northern Wales; *a, b*, internal mold, rubber replica of dorsal valve, $\times 3.4$; *c*, internal mold of ventral valve, $\times 3.2$; *d*, rubber replica of ventral exterior, $\times 3.2$ (Bates, 1968).

Murjukiana SEVERGINA, 1967, p. 134 [**M. ilovata*; OD]. Similar to *Hesperonomia* but with suboval ventral muscle field having broadly triangular adductor track together with simple, bulbous cardinal process and well-developed dorsal subperipheral rim. *Lower Ordovician (Llanvirn)*: Siberia (Kuznetz Altai, Altai-Sayan).—FIG. 533,2a–d. **M. ilovata*, Llanvirn, Kuznetz Altai; *a*, internal mold of ventral valve, $\times 3$; *b, c*, internal mold, rubber replica of dorsal valve, $\times 2.25$; *d*, rubber replica of dorsal exterior, $\times 2.25$ (Cocks & Rong, 1989).

Protohesperonomia WILLIAMS & CURRY, 1985, p. 218 [**P. resupinata*; OD]. Transversely semioval with acute cardinal extremities, concavoconvex to weakly resupinate, rectimarginate, ventral interarea catacline; simple deltidodont teeth with divergent dental plates; ventral muscle field strongly bilobed presumably with short adductor field limited to median, tapering ridge; notothyrial platform poorly

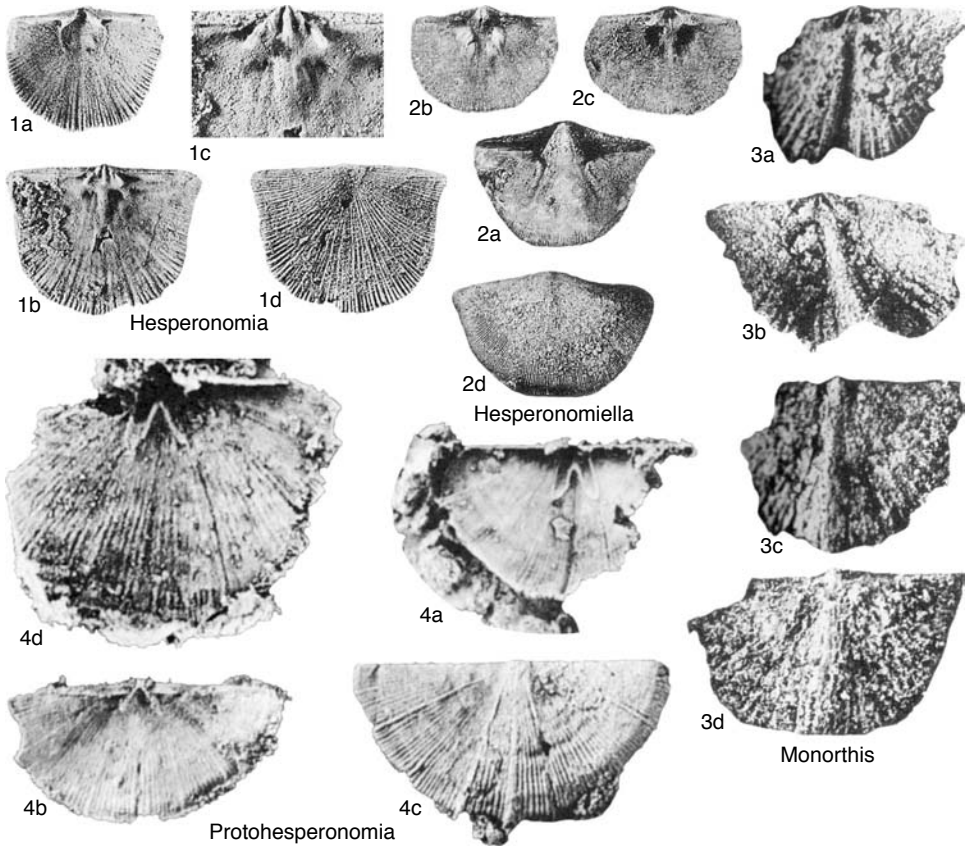


FIG. 532. Hesperonomiidae (p. 736–737).

developed but extending anteriorly as low median ridge; cardinal process absent, divergent brachio-phores bladlike, defining elongate sockets. *Lower Ordovician (Arenig)*: Ireland, Bohemia.—FIG. 532, 4a–d. **P. resupinata*, Arenig, western Ireland; a, ventral interior, X6; b, dorsal interior, X5; c, ventral exterior, X5; d, ventral interior, X6 (Williams & Curry, 1985).

Treioria NEUMAN & BATES, 1978, p. 584 [**T. chaulioda*; OD]. Transversely semioval with acute cardinal extremities, narrowly concavoconvex becoming gently resupinate rectimarginate, ventral interarea catacline; large teeth with short, divergent dental plates; ventral muscle field widely subtriangular with slightly elevated, broad, triangular adductor track; notothyrial platform wide with simple cardinal process, not extending anteromedianly, widely divergent, short brachio-phores bladlike. *Lower Ordovician (Arenig–Llanvirn)*: Wales, Ireland.—FIG. 533, 1a–d. **T. chaulioda*, Llanvirn, northern Wales; a, b, internal mold, rubber replica of ventral valve, X2; c, rubber replica of dorsal interior, X2; d,

external mold of ventral valve, X2 (Neuman & Bates, 1978).

Family HESPERORTHIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, *hercini*, *ex Hesperorthinae* SCHUCHERT & COOPER, 1931, p. 243]

More elongately than transversely semi-oval, costate to fascicostellate, variably capillate orthoids almost invariably lacking lamellae; delthyrium and notothyrium commonly narrow with variably developed covers; ventral interarea normally long and flat, dorsal interarea almost invariably ancline, of variable length and curvature; dental plates recessive, cordate ventral muscle scar impressed on valve floor; adductor track typically differentiated, narrow, parallel-sided to lanceolate,

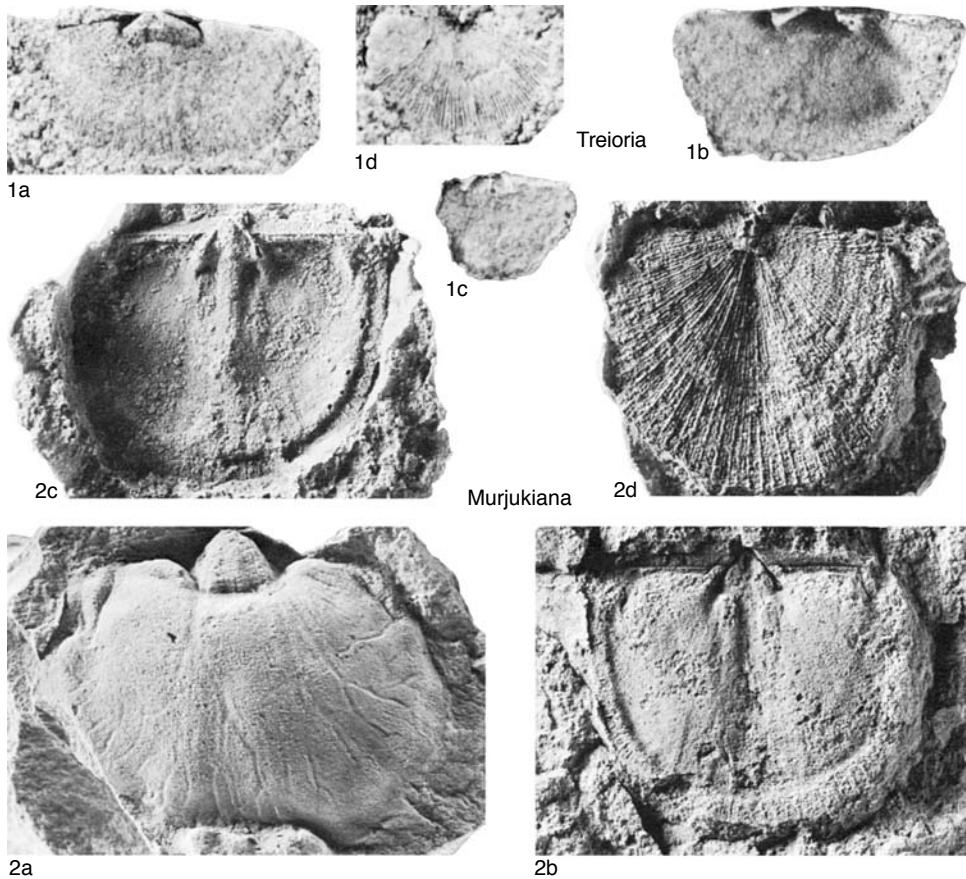


FIG. 533. Hesperonomiidae (p. 736–737).

normally shorter than flanking diductor scars and generally lacking median ridge; notothyrial platform weak to rudimentary but with broad median ridge extending anteriorly, cardinal process almost invariably simple, ridgelike, brachiophores divergent, bladellike; quadripartite dorsal adductor scars generally lightly impressed, variable; ventral mantle canal system saccate with subparallel *vascula media*, dorsal system less well preserved, mainly digitate. *Lower Ordovician (Arenig)–Lower Devonian (Emsian)*.

Hesperorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis tricenaria* CONRAD, 1843, p. 333; OD]. Medium to large, elongately semioval with variable cardinal extremities, planoconvex, rectimarginate, costate, capillate; delthyrium with apical plate, notothyrium with antigyidium; interareas relatively

long and flat; posterior pair of dorsal adductor scars larger than anterior. *Lower Ordovician (Llanvirn)–middle Silurian (Wenlock)*: cosmopolitan.—FIG. 534, 1a–f. **H. tricenaria* (CONRAD), Caradoc, eastern USA; a, ventral interior, $\times 2$; b, dorsal interior, $\times 2$; c–e, ventral, dorsal, posterior views of conjoined valves, $\times 1.5$; f, detail of ventral interarea, $\times 1.5$ (Schuchert & Cooper, 1932).

Barbarorthis ÖPIK, 1934, p. 183 [**B. foraminifera*; OD]. Similar to *Hesperorthis* but coarsely costellate, without surface capillae; delthyrium partly closed by delthyrial plates. *Upper Ordovician (Ashgill)*: Baltoscandia.—FIG. 534, 2a–d. **B. foraminifera*, Ashgill, Estonia; a, dorsal interior, $\times 4.5$; b–d, dorsal, ventral, posterior views of conjoined valves, $\times 5$ (Öpik, 1934).

Boreadorthis ÖPIK, 1934, p. 184 [**B. crassa*; OD]. Similar to *Hesperorthis* but with a strongly and uniformly convex brachial valve. *Upper Ordovician (Ashgill)*: Baltoscandia, central Asia, Siberia, Ukraine, Belgium.—FIG. 534, 3a–d. **B. crassa*, Ashgill, Estonia; a, dorsal interior, $\times 2$; b, ventral

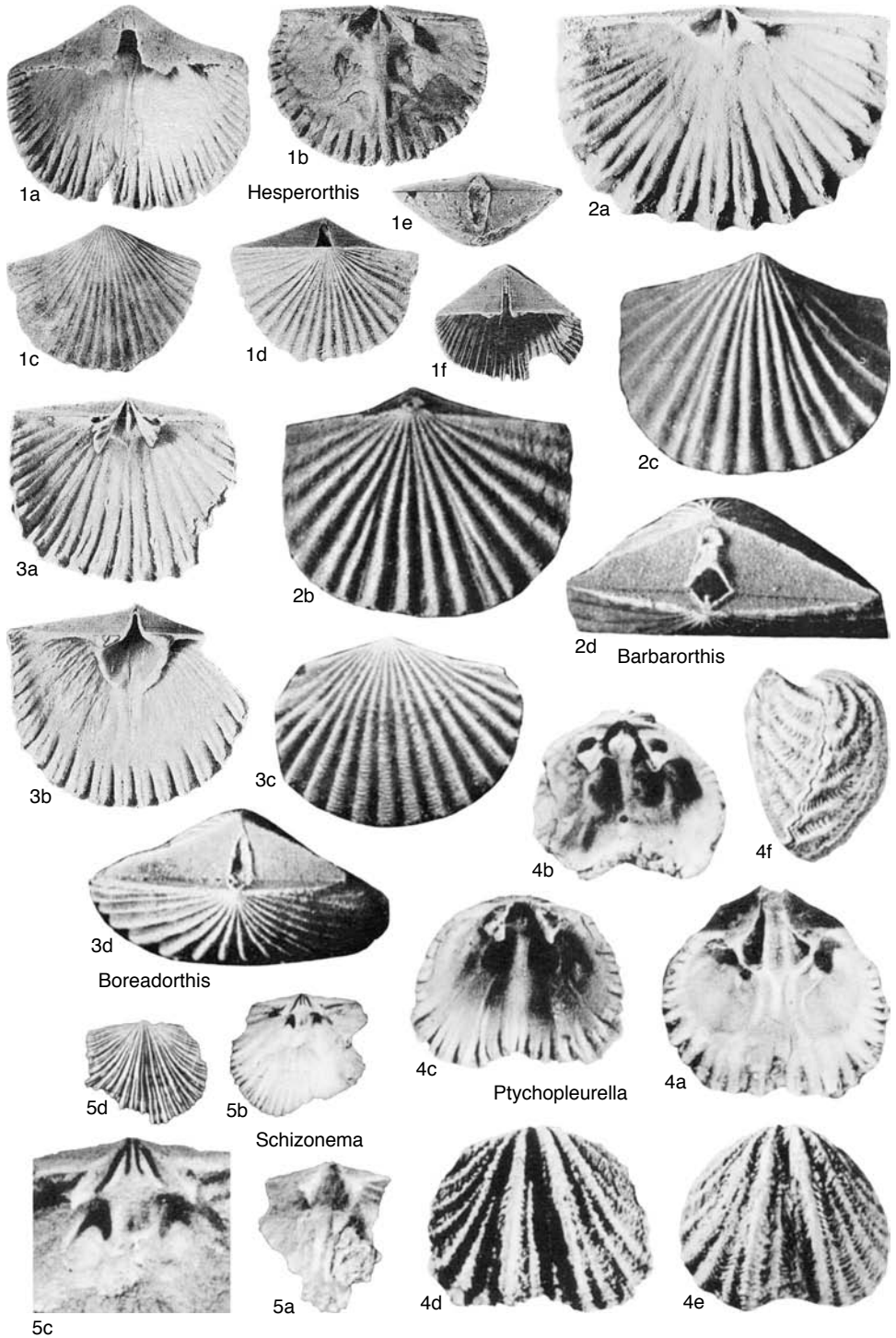


FIG. 534. Hesperorthidae (p. 738–740).

interior, $\times 2$; *c, d*, dorsal, posterior views of conjoined valves, $\times 5$ (Öpik, 1934).

Dolerorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis interplicata*; OD] [= *Altaeorthis* SEVERGINA, 1967, p. 124 (type, *A. uskutchevi*); *Munhella* NEUMAN, 1971, p. 117 (type, *M. cummingsi*)]. Transversely semioval, cardinal extremities variable, biconvex to convexoconcave, uniplicate, coarsely costellate without capillae; delthyrium and notothyrium wide; interarea relatively long, curved; ventral muscle scar with median ridge, pedicle callist not developed; posterior pair of dorsal adductor scars lying posterolaterally of anterior pair and separated by strong, divergent *vascula myaria*; dorsal mantle canal system apocapate. [*Altaeorthis* was proposed for specimens from the Middle Ordovician of Siberia (Altai Mountains) that are similar to *Dolerorthis* except for the greater convexity of the ventral valve. The relative convexity of European *Dolerorthis*, however, is also variable; and, since ventribiconvexity is likely to have developed independently in several stocks, it is phylogenetically undesirable to found a genus exclusively on this feature. *Munhella* was erected for deformed brachiopod molds from the Arenig of Newfoundland on the assumption that it was close to the orthid *Glossorthis* except for the dorsibiconvexity of the valves and the lack of a raised callus of secondary shell for the ventral muscle field. These features, like others described and illustrated, are characteristic of *Dolerorthis*.] *Upper Ordovician (Arenig)–Lower Devonian (Emsian)*: cosmopolitan.—FIG. 535, 1a. **D. interplicata* (SCHUCHERT & COOPER), Wenlock, Indiana; dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 535, 1b, c. *D. flabellites* (FOERSTE), Wenlock, Indiana; *b*, ventral interior, $\times 1.5$; *c*, dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 535, 1d–g. *D. rustica* (J. DE C. SOWERBY); *d–f*, ventral, dorsal, lateral views of conjoined valves, Wenlock, Sweden, $\times 1.5$; *g*, dorsal interior, Wenlock, England, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 535, 1h–k. *D. rigida* (DAVIDSON), Wenlock, Shropshire; *h*, dorsal interior, $\times 1.5$; *i–k*, dorsal, ventral, lateral views of conjoined valves, $\times 1$ (Bassett, 1970).

Flabellitesia ZHANG, 1989a, p. 56 [**Hesperorthis kessei* BOUCOT, JOHNSON, & ZHANG, 1988, p. 107; OD]. Similar to *Hesperorthis* but dorsibiconvex to resupinate, shallowly unisulcate, sporadically developed capillae; delthyrium open; dorsal interarea narrow. *middle Silurian (Wenlock)*: North America, Europe.—FIG. 535, 4a–d. **F. kessei* (BOUCOT, JOHNSON, & ZHANG), Wenlock, Baillie Hamilton Island; *a, b*, interior, exterior of ventral valve, $\times 2$; *c, d*, interior, exterior of dorsal valve, $\times 2$ (Zhang, 1989a).

Lordorthis ROSS, 1959, p. 446 [**L. variabilis*; OD]. Similar to *Hesperorthis* but resupinate and coarsely costellate (capillae not reported). *Upper Ordovician (Ashgill)*: western North America.—FIG. 535, 2a–f. **L. variabilis*, Ashgill, Lemhi Range; *a–d*, ventral, dorsal, posterior, lateral views of conjoined valves,

$\times 1$; *e*, ventral interior, $\times 1$; *f*, dorsal interior, $\times 1$ (Ross, 1959).

Paradolerorthis ZENG, 1987, p. 218 [**D. (P.) calla*; OD]. Similar to *Dolerorthis* but more subquadrate with obtuse cardinal extremities, biconvex, rami-costellate; delthyrial opening relatively narrow in shorter ventral interarea; notothyrial platform better developed. *Lower Ordovician (Llanvirn)*: southern China.—FIG. 535, 3a–c. **P. calla*, Llanvirn, southern China; ventral interior, ventral exterior, internal mold of dorsal valve, $\times 3$ (Zeng, 1987).

Ptychopleurella SCHUCHERT & COOPER, 1931, p. 244 [**Orthis bouchardi* DAVIDSON, 1847, p. 64; OD]. Small, transversely semioval with obtuse cardinal extremities, biconvex with subpyramidal ventral valve, strangulate, rectimarginate to gently unisulcate, coarsely costellate without capillae, lamellose; delthyrium and notothyrium narrowly divergent, open; dorsal interarea short, curved, orthocline; ventral muscle scar suboval to subpentagonal with adductor component usually impressed on flat ridge, pedicle callist unknown; rudimentary notothyrial platform with cardinal process, rarely absent, usually thick in maturity; anterior pair of quadripartite dorsal adductor scars larger than posterior. [This genus has long been regarded as a close relative of *Glyptorthis* mainly because of its ornamentation. Other morphological features, however, including the nature of the delthyrium and notothyrium and the longitudinal profile of the ventral valve, are more suggestive of the hesperorthisids, with which family it is presently associated cladistically.] *Lower Ordovician (Llanvirn)–Lower Devonian (Emsian)*: cosmopolitan.—FIG. 534, 4a–f. **P. bouchardi* (DAVIDSON), Wenlock, Welsh Borderlands; *a*, ventral interior, $\times 3$; *b*, dorsal interior, $\times 3$; *c, d*, dorsal interior, exterior, $\times 3$; *e, f*, ventral, lateral views of conjoined valves, $\times 3$ (Bassett, 1972).

Schizonema FOERSTE, 1909a, p. 76 [**Hebertella (Schizonema) fissistriata*; OD] [= *Schizoramma* FOERSTE, 1912, p. 139 (type *H. (Schizonema) fissistriata*)]. Similar to *Dolerorthis* but with obtuse cardinal extremities, subequally biconvex to slightly dorsibiconvex with shallow, impersistent dorsal sulcus, fascicostellate, well-developed pedicle callist and low notothyrial ridges flanking simple cardinal process. *lower Silurian (Llandoverly)–middle Silurian (Wenlock)*: cosmopolitan.—FIG. 534, 5a–d. **S. fissistriata* (FOERSTE), Wenlock, Indiana; *a*, ventral interior, $\times 1$; *b*, dorsal interior, $\times 1$; *c*, details of cardinalia, $\times 3$; *d*, dorsal exterior, $\times 1$ (Bassett, 1972).

Family LYCOPHORIIDAE Schuchert & Cooper, 1931

[Lycophoriidae SCHUCHERT & COOPER, 1931, p. 245]

Globular with obtuse cardinal extremities, dorsibiconvex, multicostellate; delthyrium and notothyrium open, narrow, apsacline

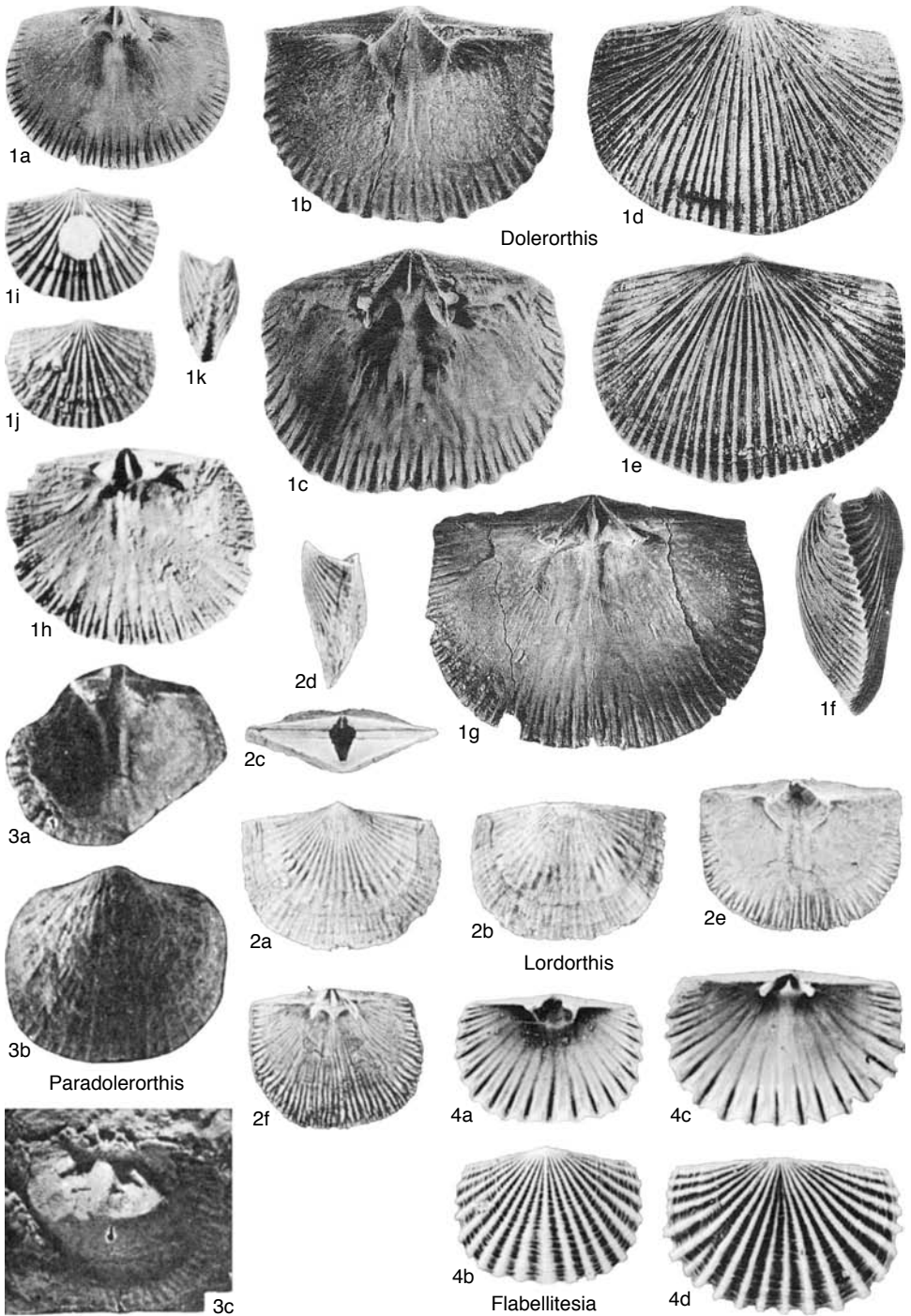


FIG. 535. Hesperorthidae (p. 740).

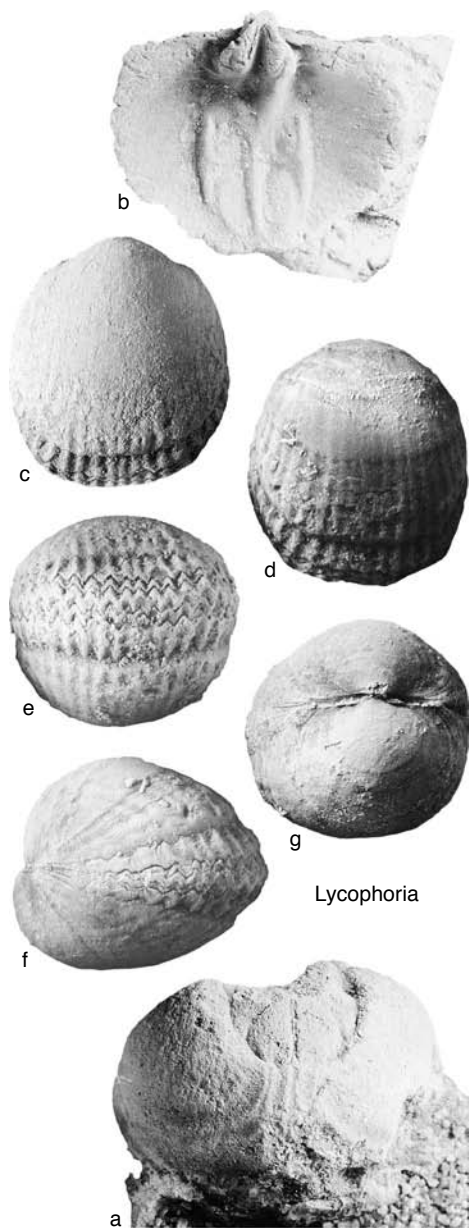


FIG. 536. Lycophoridiidae (p. 742).

ventral interarea short, curved, dorsal interarea obsolete; teeth with crural fossettes supported by subparallel dental plates, ventral muscle scar long, bilobed with subcircular adductor track enclosed by elongate diductor scars that are separated anteriorly by median ridge, pedicle callist developed; cardinal pro-

cess long, curved, bifurcating distally with chilidial plate (hood) on its dorsal surface; brachiophores small, rodlike, emerging from thick notothyrial platform excavated laterally as deep sockets; elongate dorsal adductor field with thickened margins, quadripartite with bilobed anterior pair larger than posterior pair; ventral mantle canal system probably saccate. *Lower Ordovician (Arenig–Llanvirn)*.

Lycophoria LAHUSEN, 1886, p. 221 [**Atrypa nucella* DALMAN, 1828, p. 130; OD]. Medium to large in size, variably uniplicate at anterior margin. *Lower Ordovician (Arenig–Llanvirn)*: Baltoscandia, Poland.—FIG. 536a–g. **L. nucella* (DALMAN), Arenig, Estonia; a, internal mold of ventral valve, $\times 3$; b, dorsal interior, $\times 2.5$; c–g, ventral, dorsal, anterior, lateral, posterior views of conjoined valves, $\times 2.5$ (Rubel, 1961a).

Family NANORTHIDAE Havlíček, 1977

[Nanorthidae HAVLÍČEK, 1977a, p. 59]

Generally small, ventribiconvex costellate orthoids with very short, curved interareas; teeth usually supported by short, recessive dental plates, suboval ventral muscle scar normally impressed on valve floor without median ridge; adductor track undifferentiated and relatively wide, not shorter than flanking diductor scars; pedicle callist well developed in some species; notothyrial platform normally present with usually simple cardinal process; variably disposed brachiophores typically short, bladlike, dorsal adductor scars quadripartite, variably impressed on either side of median ridge with postero-medial parts of anterior scars inserted between posterior pair; ventral mantle canal system saccate with divergent *vascula media*, dorsal system more rarely impressed, digitate to pinnate. *Lower Ordovician (Tremadoc)–Upper Ordovician (Ashgill)*.

Nanorthis ULRICH & COOPER, 1936b, p. 621 [**Orthis hamburgensis* WALCOTT, 1884, p. 73; OD] [= *Evenkinorthis* YADRENKINA, 1977, p. 27 (type, *E. dualis*)]. Subcircular with obtuse cardinal extremities, ramicostellate; short, bladlike brachiophores, notothyrial platform rudimentary, lacking cardinal process. [*Evenkinorthis* has been erected for inadequately described and illustrated specimens from the Ordovician of Siberia. With regard to such features as are unambiguously determinable, the genus is indistinguishable from *Nanorthis*.] *Lower Ordovi-*

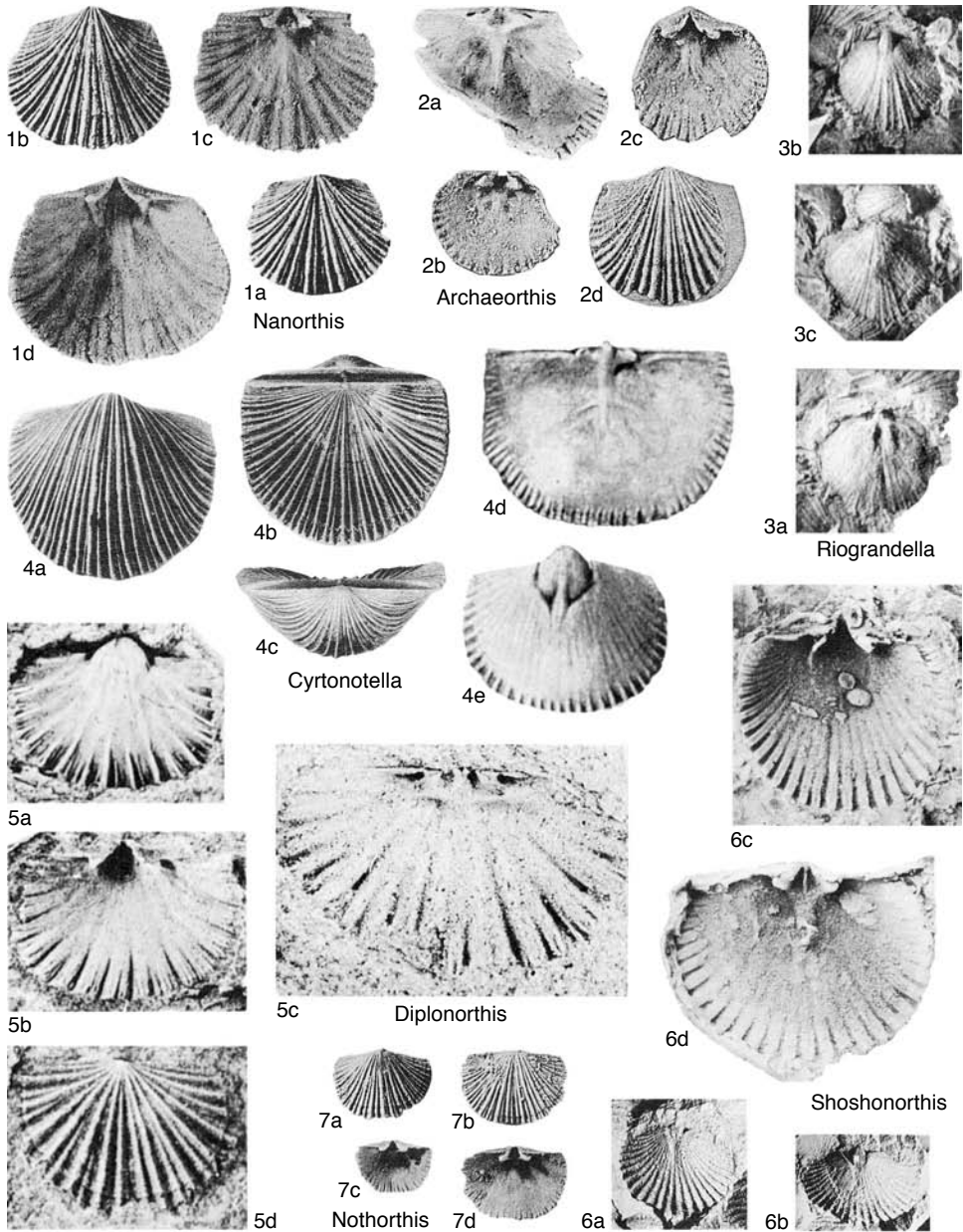


FIG. 537. Nanorthidae (p. 742-745).

cian (Tremadoc): cosmopolitan.—FIG. 537, 1a-d.

**N. hamburgensis* (WALCOTT), Tremadoc, western USA; a, dorsal exterior, ×3; b, ventral exterior, ×3; c, dorsal interior, ×4; d, ventral interior, ×4 (Ulrich & Cooper, 1938).

Archaeorthis SCHUCHERT & COOPER, 1931, p. 243 [**Orthis electra* BILLINGS, 1865 in 1861-1865, p. 79; OD]. Medium size, subcircular with obtuse cardinal extremities, multicostellate; elongately oval ventral

muscle scar impressed on callosity prolonged forward of scar as wide, median ridge; cardinal process absent. **Lower Ordovician (Tremadoc-Arenig)**: North America, Europe, South America, Asia.—FIG. 537, 2a. **A. electra* (BILLINGS), Tremadoc, Quebec; dorsal interior, ×4 (Schuchert & Cooper, 1932). —FIG. 537, 2b-d. *A. biconvexa*, Tremadoc, Oklahoma; b, dorsal interior, ×3; c, ventral interior, ×3; d, ventral interior, ×3 (Cooper, 1956).

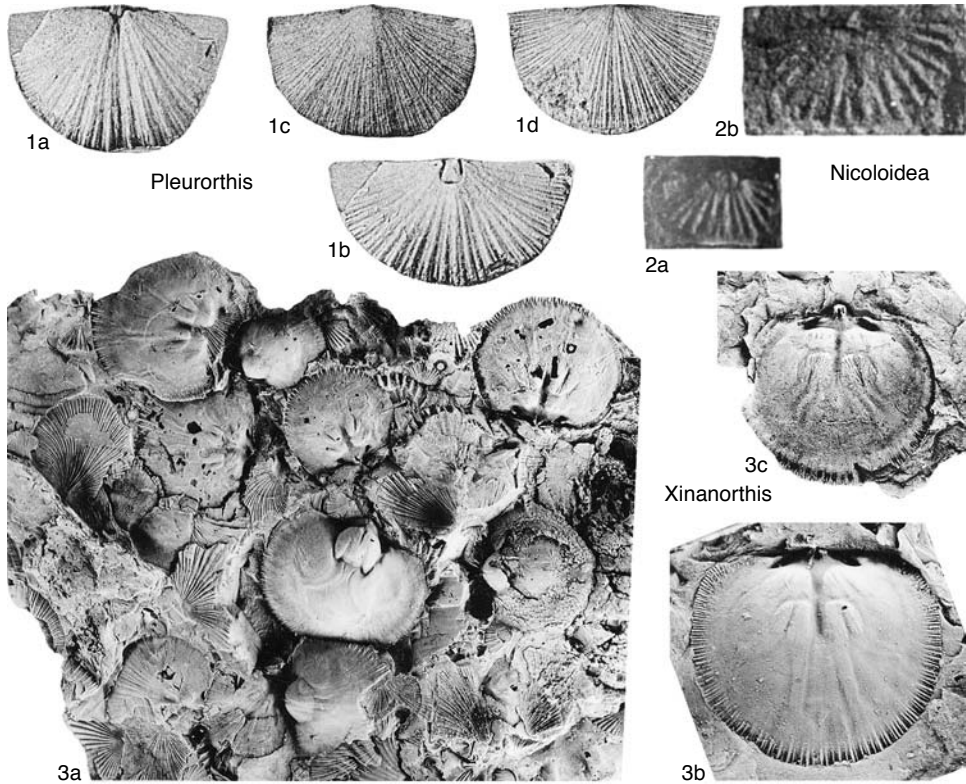


FIG. 538. Nanorthidae (p. 744–745).

Cyrtotonella SCHUCHERT & COOPER, 1931, p. 243 [**Orthis semicircularis* VON EICHWALD, 1829, p. 276; OD]. Medium size, transversely semioval with acute cardinal extremities, plano- to concavoconvex, rectimarginate, coarsely costellate and filate, ventral interarea anacline; divergent dental plates; short, divergent, bladelike brachiophores. *Lower Ordovician (Llanvirn)*–*Upper Ordovician (Caradoc)*: Northern Hemisphere.—FIG. 537, 4a–c. **C. semicircularis* (VON EICHWALD), middle Ordovician, Russia; ventral, dorsal, posterior views of conjoined valves, $\times 5$ (Schuchert & Cooper, 1932).—FIG. 537, 4d, e. *C. kukersiana* (WYSOGÓRSKI), middle Ordovician, Russia; d, dorsal interior, $\times 2.25$; e, internal mold of ventral valve, $\times 1$ (Sarytcheva, 1960).

Diplonorthis MITCHELL, 1977, p. 30 [**D. portlocki*; OD]. Subquadrate with obtuse cardinal extremities, coarsely costellate; ventral muscle field short, subtriangular with broad adductor tract, well-developed pedicle callist; widely divergent brachiophores, cardinal process consisting of shaft and bilobed crest. *Upper Ordovician (Ashgill)*: Ireland, Wales.—FIG. 537, 5a–d. **D. portlocki*, Ashgill, northern Ireland; a, b, internal mold, rubber replica of ventral valve, $\times 3.6$; c, rubber replica of dorsal interior, $\times 6$; d, rubber replica of dorsal exterior, $\times 9$ (Mitchell, 1977).

Nicoloidea ZENG, 1987, p. 215 [**N. mina*; OD]. Similar to *Cyrtotonella* but small with recessive dental plates and lacking cardinal process and dorsal median ridge. *Lower Ordovician (Tremadoc)*: southern China.—FIG. 538, 2a, b. **N. mina*, Tremadoc, southern China; a, internal mold of ventral valve, $\times 9$; b, internal mold of dorsal valve, $\times 9$ (Zeng, 1987).

Nothorthis ULRICH & COOPER, 1938, p. 106 [**N. delicatula*; OD]. Subquadrate with obtuse cardinal extremities, ramicostellate; teeth deltidodont (crural fossettes not recorded); suboval ventral muscle scar impressed on callosity; short, divergent brachiophores. *Lower Ordovician (Tremadoc)*: eastern North America, eastern North America; a, ventral exterior, $\times 3$; b, dorsal exterior, $\times 3$; c, ventral interior, $\times 3$; d, dorsal interior, $\times 3$ (Ulrich & Cooper, 1938). [Note added in proof: wrong family, see p. 777.]

Pleurorthis COOPER, 1956, p. 329 [**P. fascicostellata*; OD] [= *Ambardella* ANDREEVA, 1987, p. 37 (type, *A. anabarensis*)]. Medium size, subquadrate with variable cardinal extremities, dorsibiconvex with dorsal posteromedian sulcus passing into fold in adult shell, fascicostellate; weakly developed, platelike, notothyrial platform and cardinal process with short

median ridge, divergent, short, bladlike brachiophores. [*Ambardella* was proposed for *Upper Cambrian* brachiopods from Siberia (central Techenie), which were typified as flattened costellate shells without capillae. The description and illustrations of other features, however, confirm only that the specimens are orthoid and, provisionally, better assigned to *Pleurorthis*.] *Lower Ordovician* (*Tremadoc–Arenig*): eastern North America, Siberia, South America (Argentina).—FIG. 538, 1a–d. **P. fascicostellata*, Tremadoc, Quebec; *a*, internal mold of dorsal valve, $\times 2$; *b*, internal mold of ventral valve, $\times 2$; *c*, replica of ventral exterior, $\times 1$; *d*, dorsal exterior, $\times 1$ (Cooper, 1956).

Riograndella KOBAYASHI, 1937, p. 422 [**R. subcircus*; OD]. A typical nanorthis but multicostellate and with shallow, weakly developed notothyrial platform. *Lower Ordovician* (*Tremadoc*): Bolivia.—FIG. 537, 3a–c. **R. subcircus*, Tremadoc, Bolivia; *a*, internal mold of dorsal valve, $\times 1.5$; *b*, internal mold of ventral valve, $\times 1.5$; *c*, ventral exterior, $\times 1.5$ (Kobayashi, 1937).

Shoshonorthis JAANUSSON & BASSETT, 1993, p. 51 [**Orthis michaelis* CLARK, 1935, p. 242; OD]. Medium size, subquadrate with obtuse cardinal extremities, rectimarginate, costate and capillate; relatively long, subparallel dental plates flanking elongate, bilobed ventral muscle scar; brachiophores divergent, rodlike; dorsal adductor scars with posterior pair larger than anterior pair. *Lower Ordovician* (*Arenig–Llanvirn*): North America, China, northern Africa.—FIG. 537, 6a–d. **S. michaelis* (CLARK), Llanvirn, Utah; *a*, dorsal interior, $\times 1$; *b*, dorsal interior, $\times 1$ (Clark, 1935); *c*, rubber replica of ventral interior, $\times 2$; *d*, rubber replica of dorsal interior, $\times 2$ (Ross, 1967).

Xinanorthis XU, RONG, & LIU, 1974, p. 145 [**X. striata*; OD]. Similar to *Archaeorthis* but lacking wide median ridge extending anteriorly of ventral muscle scar and with low, ridgelike cardinal process on relatively well-developed notothyrial platform; bilobed anterior pair of quadripartite dorsal adductor scar larger than posterior pair; fila not reported. *Lower Ordovician* (*Arenig*): China.—FIG. 538, 3a–c. **X. striata*, Arenig, China; *a*, internal molds of ventral valve (center) together with internal molds of dorsal valves (top), $\times 1$; *b*, internal mold of dorsal valve, $\times 3$; *c*, internal mold of dorsal valve, $\times 1$ (Rong, new).

Family ORTHIDIELLIDAE

Ulrich & Cooper, 1936

[Orthidiellidae ULRICH & COOPER, 1936b, p. 621]

Medium size, variably unisulcate, costellate, normally ventribiconvex orthoids with delthyrium and notothyrium rarely constricted by covers, interareas normally short and curved; dental plates recessive, ventral muscle scar variably developed but with broad adductor track not encircled by nar-

rower diductor scars; notothyrial platform supporting high, ridgelike cardinal process ankylosed to pair of notothyrial ridges to simulate trilobed myophore and joined to rodlike brachiophores; variably impressed dorsal adductor scars with posterior pair lying posterolaterally to anterior pair on either side of variably developed dorsal median ridge; saccate ventral mantle canal system sporadically impressed, dorsal mantle canal system poorly impressed, probably digitate. *Lower Ordovician* (*Tremadoc*)–*Upper Ordovician* (*Caradoc*).

Orthidiella ULRICH & COOPER, 1936b, p. 621 [**O. longwelli*; OD]. Subquadrate with obtuse cardinal extremities, sharply unisulcate, ramicostellate with delthyrial apical plate; ventral muscle scar bilobed with elongate diductor and wide adductor impressions; brachiophore rods divergent. *Lower Ordovician* (*Arenig–Llanvirn*): North America, Estonia, Siberia, South America (Argentina).—FIG. 539, 1a–e. **O. longwelli*, Llanvirn, Nevada; *a*, ventral interior, $\times 2$; *b*, dorsal interior, $\times 4$; *c*, details of cardinalia, $\times 12$; *d, e*, ventral, dorsal views of conjoined valves, $\times 4$ (Ulrich & Cooper, 1938).

Eostrophomena WALCOTT, 1905, p. 256 [**Strophomena* (*Eostrophomena*) *elegantula*; OD]. Transversely semioval with acute cardinal extremities, concavoconvex, parvicostellate and imbricate; delthyrium open, notothyrium partly closed by chilidium, ventral muscle scar subcordate; brachiophore rods widely divergent; subperipheral rims present in both valves. [The assignment of this genus to the Orthidiellidae rests mainly on cardinal process ankylosed to high notothyrial ridges, open delthyrium, and allegedly impunctate shell. Other features are plectambonitoid and even the cardinal process could be interpreted as being trilobed by association with chilidial plates dependent on whether they arise lateral to the posteromedian ends of the brachiophores.] *Lower Ordovician* (*Tremadoc*): Sweden, eastern Baltic.—FIG. 539, 2a–c. **E. elegantula* (WALCOTT), Tremadoc, Västergötland; *a*, dorsal interior, $\times 2$; *b*, ventral interior, $\times 2$; *c*, partly exfoliated ventral exterior, $\times 2$ (Williams, 1965b).

Orthidium HALL & CLARKE, 1892, p. 244 [**Orthis gemmicula* BILLINGS, 1862 in 1861–1865, p. 75; OD]. Similar to *Orthidiella* but more strongly ventribiconvex with variable cardinal extremities and long, curved ventral interarea, strongly imbricate. *Lower Ordovician* (*Tremadoc–Llanvirn*): North America, western Ireland, Scotland, northwestern China, South America (Argentina).—FIG. 539, 5a–d. **O. gemmicula* (BILLINGS), Tremadoc, Quebec; *a*, ventral interior, $\times 6$; *b*, dorsal interior, $\times 6$; *c*, dorsal exterior, $\times 4$; *d*, ventral exterior, $\times 4$ (Ulrich & Cooper, 1938).—FIG. 539, 5e–g. *O. bellullum*, Llanvirn, Nevada; dorsal, ventral, anterior views, $\times 4$ (Cooper, 1956).

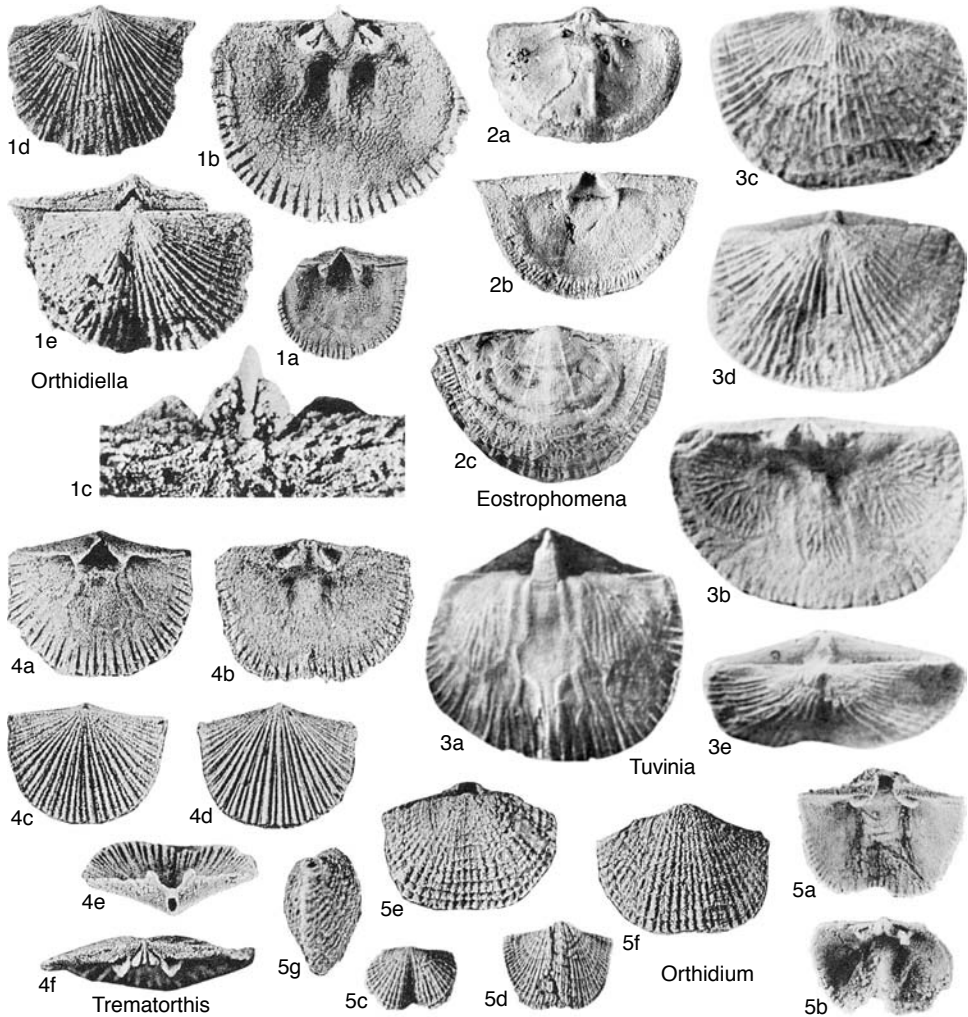


FIG. 539. Orthidiellidae (p. 745–746).

Trematorthis ULRICH & COOPER, 1938, p. 112 [**T. masoni*; OD]. Subquadrate with variable cardinal extremities, ramicostellate, delthyrium partly covered by deltidium with apical foramen, notothyrium open, ventral interarea relatively long, curved; ventral muscle scar suboval. *Lower Ordovician (Arenig-Llanvirn)*: North America, South America (Argentina).—FIG. 539, 4a–f. **T. masoni*, Llanvirn, Nevada; a, ventral interior, $\times 3$; b, dorsal interior, $\times 3$; c, d, dorsal, ventral views of conjoined valves, $\times 3$; e, posterior views of ventral valve, $\times 3$; f, posterior view of dorsal valve, $\times 4$ (Cooper, 1956).

Tuvinia ANDREEVA, 1982, p. 53 [**T. radiata*; OD]. Subquadrate with variably angled cardinal extremities, unisulcate, ramicostellate; well-developed deltidium with apical foramen; ventral muscle scar subtriangular; cardinal process consisting of median

plate flanked by pair of notothyrial ridges, quadripartite adductor scars subequal; ventral mantle canal system saccate with widely parallel *vascula media* dividing toward anterior margin, dorsal system saccate with gonadal pouches developed between widely spaced *vascula media*. [The illustrations of this genus suggest that the cardinal process is not solely a simple plate, as indicated in the diagnosis, but a trifid structure involving lateral notothyrial ridges. There is also an interesting similarity between the mantle canal systems of *Tuvinia* and *Orthostrophina*.] *Upper Ordovician (Caradoc)*: central Asia.—FIG. 539, 3a–e. *T. radiata*, Upper Ordovician, central Asia; a, internal mold of ventral valve, $\times 4$; b, rubber replica of dorsal interior, $\times 4$; c–e, ventral, dorsal, posterior views of conjoined valves, $\times 4$ (Andreeva, 1982).

Family PLAESIOMYIDAE Schuchert, 1913

[*nom. transl. et correct.* WILLIAMS, 1965b, p. 319, *ex* Plaesiomiinae SCHUCHERT, 1913b, p. 382] [=Dinorthisidae SCHUCHERT & COOPER, 1931, p. 244]

Costellate orthoids with receding or subparallel dental plates, ventral muscle scar subquadrate to bilobate, with variable enclosure by elongate diductor scars of lanceolate to oval adductor track; notothyrial platform supporting large cardinal process and divergent brachiophores; saccate ventral mantle canal system with divergent *vascula media*, dorsal system sporadically preserved, variable. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill)*.

Subfamily PLAESIOMYINAE Schuchert, 1913

[*nom. correct.* WILLIAMS, 1965b, p. 319, *pro* Plaesiomiinae SCHUCHERT, 1913b, p. 382]

Large, usually transversely semioval with variable cardinal extremities, subequally biconvex to convexoconcave, normally rectimarginate; costellae exceptionally with aditicles; apsacline ventral interarea varying in length and curvature, dorsal interarea extremely variable; ventral muscle scar normally with median ridge, pedicle callist reported in some genera; notothyrial platform strong with low, discrete ridges flanking cardinal process differentiated into myophore and shaft, divergent brachiophores rodlike, sockets obliquely elongate, quadripartite dorsal muscle scar poorly impressed; dorsal system not well known, normally lemniscate. *Ordovician (Llanvirn–Ashgill)*.

Plaesiomys HALL & CLARKE, 1892, p. 196 [**Orthis subquadrata* HALL, 1847, p. 126; OD]. Cardinal extremities obtuse, convexoconcave, broadly unisulcate, multicostellate, sporadically lamellose; ventral interarea short, curved, anacline dorsal interarea vestigial; ventral muscle scar without median ridge; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Caradoc–Ashgill)*: Northern Hemisphere.—FIG. 540, 1a–d. **P. subquadrata* (HALL), Ashgill, Indiana; a, b, ventral, dorsal exteriors of conjoined pair, $\times 1$; c, ventral interior, $\times 1.5$; d, dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).

Austinella FOERSTE, 1909b, p. 224 [**Orthis kankakensis* MCCHESENEY, 1861, p. 77; SD BASSLER, 1915, p. 1002]. Subequally biconvex, unisulcate, ramicostel-

late with sporadic aditicles, strongly filate; ventral interarea long, curved, anacline dorsal interarea short, plane; ventral muscle scar with thickened margin; dorsal adductor scar subequally quadripartite. *Upper Ordovician (Ashgill)*: North America, Europe, Siberia, Kazakhstan, northeastern and northwestern China.—FIG. 540, 3a–d. *A. whitfieldi* (WINCHELL), Ashgill, Minnesota; a, internal mold of ventral valve, $\times 1.5$; b, dorsal interior, $\times 1.5$; c, d, ventral, dorsal exteriors, $\times 1.5$ (Schuchert & Cooper, 1932).

Campylorthis ULRICH & COOPER, 1942, p. 621 [**Strophomena deflecta* CONRAD, 1843, p. 332; OD]. Dorsibiconvex to convexoconcave, rectimarginate to uniplicate, multicostellate, apically perforated deltidium and well-developed chilidium; ventral interarea long, plane, dorsal interarea orthocline to anacline. *Upper Ordovician (Caradoc)*: United States, Scotland, Ireland.—FIG. 540, 2a–d. **C. deflecta* (CONRAD), Caradoc, Wisconsin; ventral, dorsal, lateral, posterior views of conjoined valves, $\times 1$ (Cooper, 1956).

Chaulistomella COOPER, 1956, p. 432 [**C. inequistriata*; OD]. Subquadrate with acute cardinal extremities, convexoconcave to convexoplane, generally rectimarginate but varying from slightly uniplicate to unisulcate, multicostellate, strongly filate; ventral interarea long, curved, dorsal interarea relatively long, orthocline to apsacline; pedicle callist well developed; posterior pair of quadripartite dorsal adductor scars larger than anterior; dorsal mantle canal system lemniscate. *Upper Ordovician (Caradoc)*: eastern North America, Scotland, Siberia, Kirghizia.—FIG. 541, 4a–e. **C. inequistriata*, Caradoc, Virginia; a–c, ventral, dorsal, posterior views of conjoined valves, $\times 1$; d, ventral interior, $\times 1$; e, dorsal interior, $\times 2$ (Cooper, 1956).

Dinorthis HALL & CLARKE, 1892, p. 195 [**Orthis pectinella* EMMONS, 1842, p. 394; OD] [=Diorthis KOBAYASHI, 1937, p. 12, *nom. nud.*]. Cardinal extremities obtuse, convexoconcave, costate; ventral interarea short, curved, apsacline; dorsal interarea short, curved; dental plates projecting anteriorly, subparallel. *Upper Ordovician (Caradoc)*: Northern Hemisphere.—FIG. 541, 1a, b. **D. pectinella* (EMMONS), Caradoc, eastern United States; a, ventral exterior, $\times 0.75$; b, ventral interior, $\times 1$ (Schuchert & Cooper, 1932).—FIG. 541, 1c–f. *D. boldeni* (WILLARD), Caradoc, eastern United States; c, dorsal interior, $\times 2$; d, details of cardinalia, $\times 3$; e, ventral interior, $\times 2$; f, ventral exterior, $\times 2$ (Cooper, 1956).

Multicostella SCHUCHERT & COOPER, 1931, p. 244 [**Orthis saffordi* HALL & CLARKE, 1892, p. 217; OD]. Subquadrate with acute or obtuse cardinal extremities, subequally biconvex, rectimarginate to unisulcate, multicostellate, strongly filate; ventral interarea long, curved, orthocline dorsal interarea relatively short, curved; ventral muscle scar without median ridge, pedicle callist well developed; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Caradoc)*:

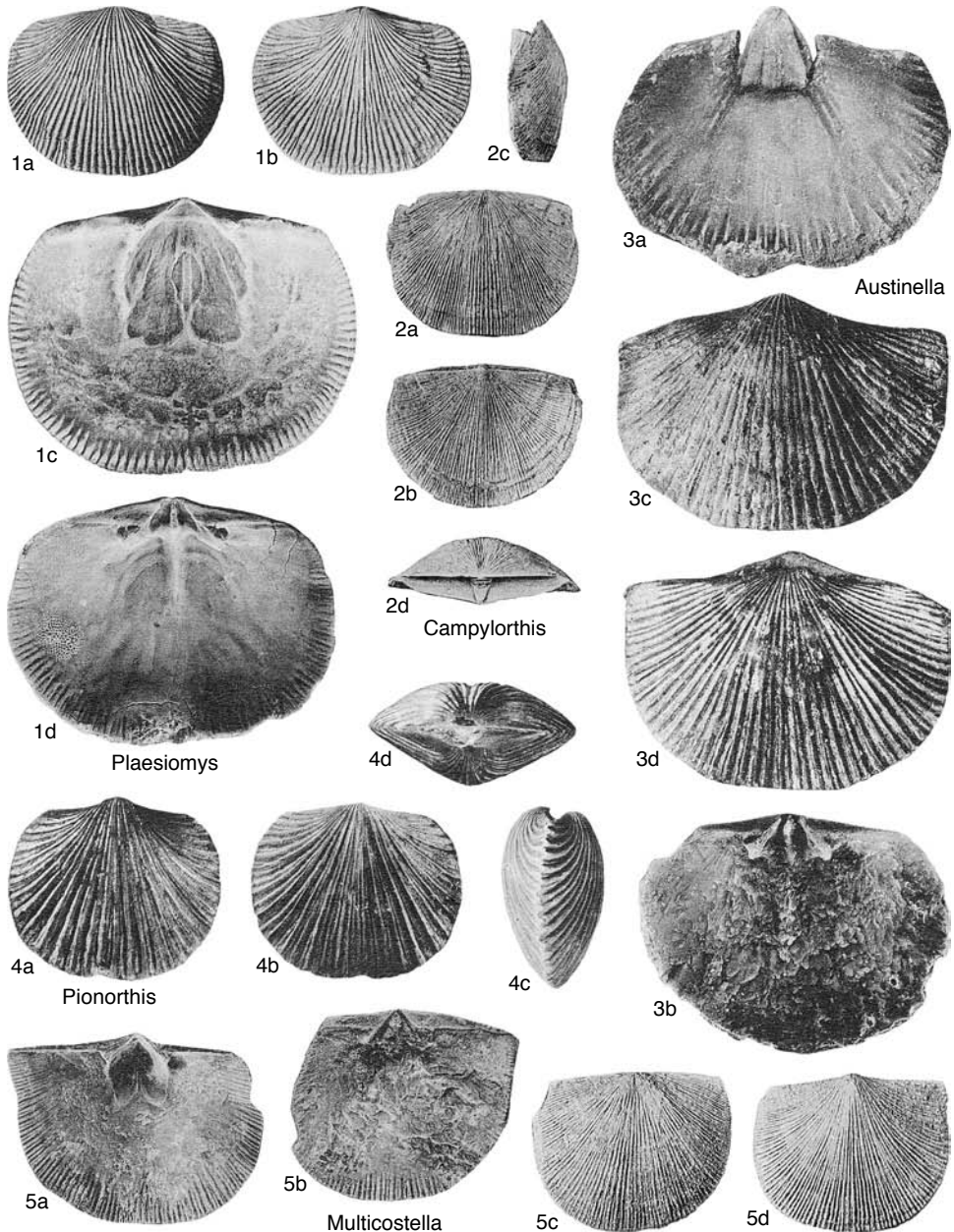


FIG. 540. Plaesiomysidae (p. 747-749).

Northern Hemisphere.—FIG. 540, 5a, b. **M. saffordi* (HALL & CLARKE), Caradoc, Tennessee; a, ventral interior, $\times 1.5$; b, dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 540, 5c, d. *M. gerontica* (COOPER), Caradoc, Tennessee; c, dorsal exterior, $\times 1$; d, ventral exterior, $\times 1$ (Cooper, 1956).

Pionorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis sola* BILLINGS, 1866, p. 12; OD]. Similar to *Plaesiomys* but subequally biconvex and coarsely costellate; apsacline dorsal interarea short curved; ventral muscle scar with low median ridge. *Upper Ordovician (Ashgill)*: North America, northwestern

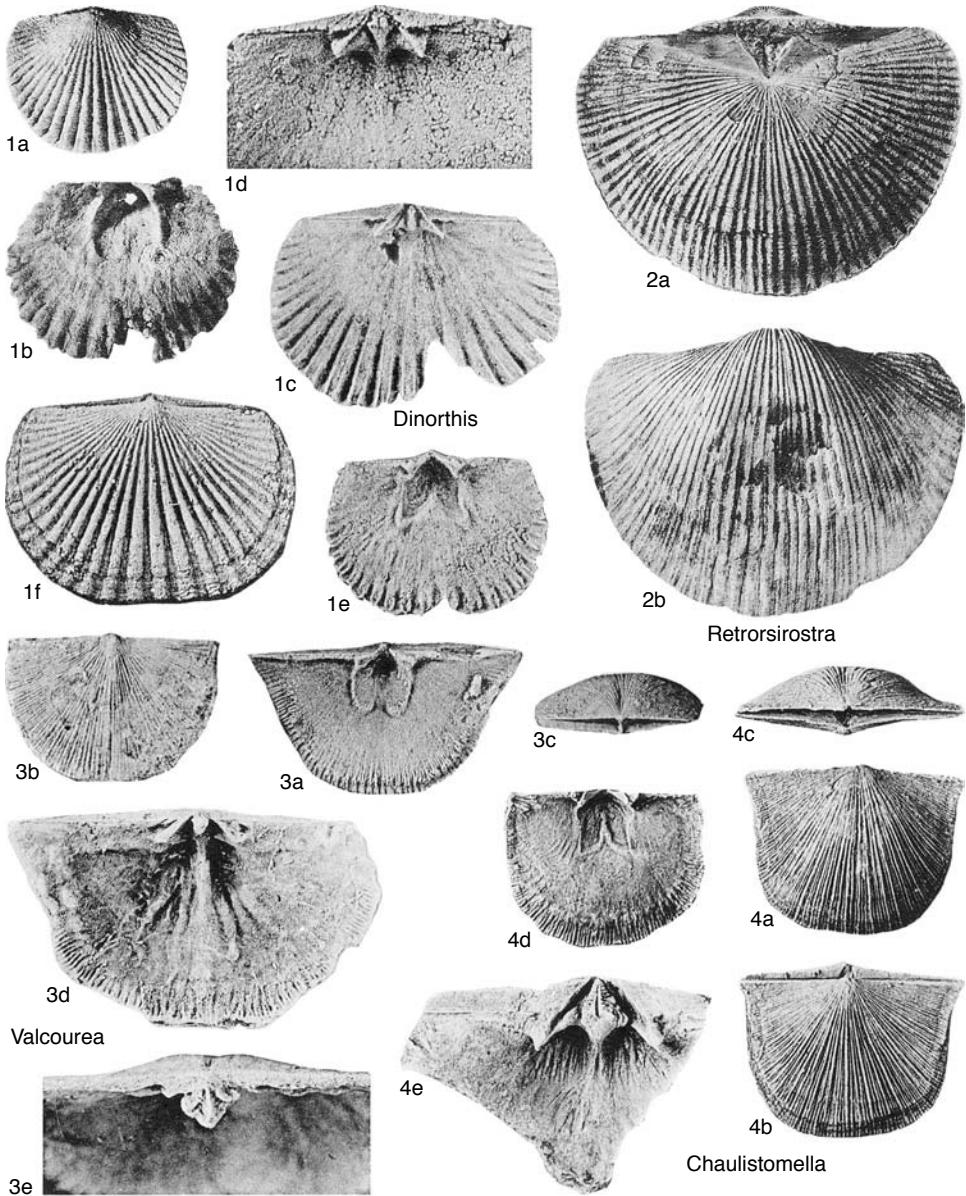


FIG. 541. Plaeiomyiidae (p. 747-750).

China. — FIG. 540, 4a-d. **P. sola* (BILLINGS), Ashgill, Anticosti; ventral, dorsal, lateral, posterior views of conjoined valves, $\times 1.5$ (Schuchert & Cooper, 1932).

Retrorsirostra SCHUCHERT & COOPER, 1931, p. 244 [*Orthis carleyi* HALL, 1847, p. 120; OD]. Similar to *Plaeiomys* but rectimarginate, coarsely costellate, and filate; procline ventral interarea long, planar, orthocline dorsal interarea short, curved; dental

plates projecting subparallel, ventral muscle scar impressed on low callus with median ridge. *Upper Ordovician* (Ashgill): Northern Hemisphere. —

FIG. 541, 2a, b. **R. carleyi* (HALL), Ashgill, Indiana; ventral, dorsal exteriors, $\times 1.5$ (Schuchert & Cooper, 1932).

Valcourea RAYMOND, 1911, p. 239 [*Plaeiomys strophomenoides* RAYMOND, 1905, p. 370; OD]. Cardinal extremities acute, convexoconcave, sharply

unisulcate umbonally with sulcus becoming fainter toward margin of adult valves, multicostellate to unequally parvicostellate, strongly filate with aditicles; imperforate deltidium and strong chilidium; ventral interarea relatively long planar, dorsal interarea shorter, orthocline to apsacline; dental plates projecting subparallel, ventral muscle scar quadrate, tending to become bilobed anteriorly with diductor enclosing adductor impressions, pedicle callist well developed; subperipheral rim in ventral valve; dorsal mantle canal system pinnate. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*: North America, Scotland, Norway, northeastern China, central Asia, South America (Argentina).—FIG. 541,3a–c. **V. strophomenoides* (RAYMOND), Caradoc, New York; *a*, ventral interior, $\times 3$; *b*, ventral exterior, $\times 2$; *c*, posterior view of dorsal valve, $\times 2$ (Cooper, 1956).—FIG. 541,3d,e. *V. deckeri* (COOPER), Caradoc, Oklahoma; *d*, dorsal interior, $\times 2$; *e*, details of cardinalia, $\times 3$ (Cooper, 1956).

Subfamily EVENKININAE Williams, 1965

[Evenkininae WILLIAMS, 1965b, p. 321]

Planoconvex or rarely dorsibiconvex, strongly unisulcate; interareas short, curved; ventral muscle scar subquadrate with diductor scars enclosing median ridge probably bearing adductor track; brachiophores platelike, ankylosed to valve floor, cardinal process undifferentiated or with traces of posterior bilobation. *Upper Ordovician (Caradoc)*.

Evenkina ANDREEVA in NIKIFOROVA & ANDREEVA, 1961, p. 96 [**E. anarbensis*; OD]. Small, subquadrate with variable cardinal extremities, ramicostellate; quadripartite dorsal adductor scars subequal. *Upper Ordovician (Caradoc)*: Siberia.—FIG. 542,1a–d. **E. anarbensis*, Caradoc, Siberia; *a*, dorsal exterior, $\times 3$; *b*, ventral interior, $\times 4$; *c*, dorsal interior, $\times 2$; *d*, posterior view of dorsal interior, $\times 4$ (Nikiforova & Andreeva, 1961).

Subfamily METORTHINAE Williams, 1965

[Metorthinae WILLIAMS, 1965b, p. 322]

Planoconvex, unisulcate; notothyrial edges elevated; interareas relatively short, planar; ventral muscle scar elongately bilobed not entirely surrounding lanceolate adductor track; brachiophores rodlike, pointed and embedded in strong notothyrial platform with excavated elongate sockets, cardinal process undifferentiated, dorsal

mantle canal system digitate. *Lower Ordovician (Arenig)*.

Metorthis WANG, 1955b, p. 333 [**M. alata*; OD]. Subquadrate with variable cardinal extremities, ramicostellate; quadripartite dorsal adductor scars subequal. *Lower Ordovician (Arenig)*: China.—FIG. 542,2a–d. **M. alata*, Arenig, southern China; *a, b*, dorsal, posterior views of conjoined valves, $\times 2.5$; *c*, ventral interior, $\times 2.5$; *d*, dorsal interior, $\times 2.5$ (Wang, 1955b).

Family PORAMBORTHIDAE Havlíček, 1950

[Poramborthidae HAVLÍČEK, 1950, p. 58]

Subcircular, biconvex, rectimarginate orthoids with dichotomizing capillae cancelled by imbricariae; interareas relatively short, curved; dental plates subparallel to narrowly divergent, flanking suboval ventral muscle scar with short ridge posteromedian of elongate adductor track; notothyrial platform rudimentary to low, bearing linear diductor scars on either side of ridgelike cardinal process, divergent brachiophores bladelike, dorsal median ridge absent; adductor scars narrow with posterior pair larger than anterior pair; ventral mantle canal system pinnate with divergent *vascula media*, dorsal system probably pinnate. *Lower Ordovician (Tremadoc)*.

Poramborthis HAVLÍČEK, 1949a, p. 107 [**P. klouceki*; OD]. Medium to large size, cardinal extremities obtuse, ventral muscle scar commonly elongate in adult shells. *Lower Ordovician (Tremadoc)*: Bohemia, Bavaria, Spain.—FIG. 542,3a–d. **P. klouceki*, Tremadoc, Bohemia; *a*, internal mold of ventral valve, $\times 4.3$; *b*, internal mold of ventral valve, $\times 4.4$; *c*, internal mold of dorsal valve, $\times 4.7$; *d*, external mold, $\times 6.6$ (Havlíček, 1977a).

Family PRODUCTORTHIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, ex Productorthinae SCHUCHERT & COOPER, 1931, p. 241]

Subquadrate, costellate orthoids lacking capillae; teeth normally supported by divergent dental plates, ventral muscle field suboval to subcordate with broad, subtriangular or parallel-sided adductor track commonly undifferentiated and rarely shorter than flanking diductor scars, usually associated with well-developed pedicle callist, less com-

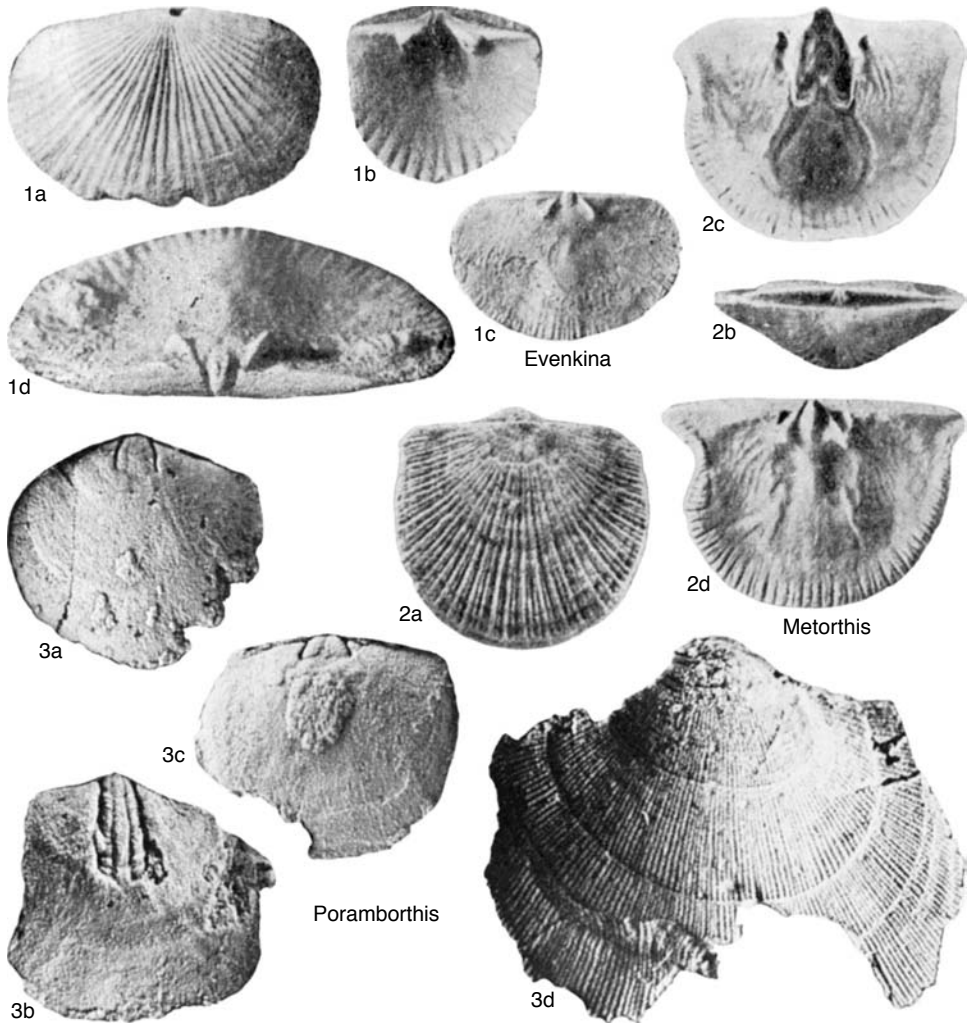


FIG. 542. Plaesiomysidae and Poramborthisidae (p. 750).

monly impressed on pseudospondylium; notothyrial platform with cardinal process, typically simple ridge of variable strength; dorsal adductor scars quadripartite with each of larger anterior pair divided into larger inner and smaller outer lobe. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill)*.

Subfamily PRODUCTORTHINAE
Schuchert & Cooper, 1931

[Productorthinae SCHUCHERT & COOPER, 1931, p. 243]

Generally medium-size, planoconvex, gently unisulcate, coarsely costellate product-

orthids commonly with acute cardinal extremities, short to vestigial interareas; pseudospondylium or callist commonly developed but rarely prolonged anteromedianly as ridge; notothyrial platform extending anteriorly as median ridge, cardinal process of variable complexity; divergent brachiophores rodlike; saccate ventral mantle canal system normally with divergent *vascula media*, dorsal system digitate or less commonly lemniscate. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill)*.

Productorthis KOZŁOWSKI, 1927, p. 9 [**Productus obtusus* PANDER, 1830, p. 87; OD]. Rectimarginate to broadly unisulcate, lamellose, ventral beak curved, usually resorbed presumably as pedicle passage, dorsal beak vestigial; interareas vestigial with ventral posterior margin grooved (ginglymoid joint) to accommodate linear, dorsal posterior margin; apical pedicle foramen; ventral muscle scar elongately suboval impressed on thick callist; cardinal process differentiated into thick shaft and carinate myophore, commonly bearing small circular supposed chilidium; saccate ventral mental canal system with subparallel *vascula media* greatly divided anteriorly, dorsal mantle canal system poorly known. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc)*: cosmopolitan.—FIG. 543, 1a–e. *P. parallela* (PANDER), Arenig, Russia; a, dorsal interior, $\times 3$; b, ventral interior, $\times 3$; c, d, ventral, dorsal exteriors of conjoined valves, $\times 3$; e, dorsal exterior, $\times 3$ (Schuchert & Cooper, 1932).

Ferrax HAVLIČEK, 1975, p. 231 [**Prantlina oolitica* HAVLIČEK, 1949b, p. 251; OD]. Ventribiconvex with nearly flat dorsal valve, cardinal extremities variable, rectimarginate, sporadically lamellose, apsacline ventral and shorter anacline dorsal interareas flat; ventral muscle scar subtriangular, impressed on low callist bounded by anterior, transverse ridge; cardinal process thick, trilobed; ventral mantle canal system saccate with divergent *vascula media*, dorsal system digitate. *Lower Ordovician (Arenig)*: Bohemia.—FIG. 543, 2a–c. **F. oolitica*, Arenig, Bohemia; a, internal mold of ventral valve, $\times 3.8$; b, internal mold of dorsal valve, $\times 4$; c, external mold of dorsal valve, $\times 3.3$ (Havliček, 1977a).

Nicolella REED, 1917, p. 860 [**Orthis actoniae* J. DE C. SOWERBY, 1839, p. 639; OD]. Rectimarginate, lamellose, notothyrium closed by chilidial plates flanking simple, erect cardinal process; orthocline ventral interarea short, curved, anacline dorsal interarea very short; dental plates widely divergent, ventral muscle field subcordate, impressed on weak callist, diductor scars not enclosing adductor track; anterior dorsal adductor scars probably quadripartite, obscured by impressions of digitate to lemniscate mantle canal system; ventral mantle canal system saccate, slightly divergent *vascula media* divided anteriorly. *Upper Ordovician (Caradoc–Ashgill)*: Europe, North America, northern Africa, Asia.—FIG. 544, 1a–d. **N. actoniae* (SOWERBY), Caradoc, Shropshire, England; a, b, internal mold, rubber replica of dorsal valve, $\times 1.5$; c, internal mold of ventral valve, $\times 1.5$; d, rubber replica of dorsal exterior, $\times 1.5$ (Cocks, new).

Panderina SCHUCHERT & COOPER, 1931, p. 243 [**Productus abscessus* PANDER, 1830, p. 86; OD]. Ramicostellate, filate, vestigial interareas, ventral beak usually resorbed; ventral muscle scar suboval, impressed on pseudospondylium extending anteriorly as low median ridge; cardinal process simple, thick. *Lower Ordovician (Arenig)*: Baltic Region, China.—FIG. 544, 3a, b. **P. abscessus* (PANDER), Arenig, Russia; dorsal, ventral views of conjoined valves, $\times 2.25$ (Schuchert & Cooper, 1932).—

FIG. 544, 3c, d. *P. tetragonum* (PANDER), Arenig, Russia; c, dorsal interior, $\times 1.5$; d, ventral interior, $\times 1.5$ (Schuchert & Cooper, 1932).

Saucrorthis XU, RONG, & LIU, 1974, p. 150 [**S. minor*; OD]. Similar to *Nicolella* but small, costate, finely pustulose, and lacking chilidial plates. *Lower Ordovician (Llanvirn)*: southern China.—FIG. 544, 2a–c. **S. minor*, Llanvirn, southwestern China; a, internal mold of ventral valve, $\times 8$; b, internal mold of ventral valve, $\times 8$; c, internal mold of dorsal valve, $\times 8$ (Rong, new).

Styxorthis MERGL, 1991, p. 7 [**S. tuffogena*; OD]. Ramicostellate, apsacline ventral interarea short, curved, dorsal interarea vestigial; ventral muscle scar suboval, impressed on valve floor; trilobed cardinal process with high median ridge; ventral mantle canal system saccate, dorsal mantle canal system digitate. *Lower Ordovician (Arenig)*: Bohemia.—FIG. 543, 3a–e. **S. tuffogena*, Arenig, Bohemia; a, internal mold of ventral valve, $\times 3$; b, c, internal mold, rubber replica of dorsal valve, $\times 3$; d, e, normal, anterior view of ventral exterior, $\times 3$ (Mergl, 1991).

Subfamily GLOSSORTHINAE new subfamily

[Glossorthinae WILLIAMS & HARPER, herein]

Large productorthids normally ramicostellate with variable cardinal extremities, rectimarginate; ventral interarea normally apsacline, short, and curved, dorsal interarea very short, curved or flat; brachiophores normally bladelike, subparallel to divergent; suboval ventral muscle scar normally impressed on pseudospondylium, prolonged anteriorly as median ridge, cardinal process normally simple, notothyrial platform usually extending anteriorly as median ridge; mantle canal systems rarely impressed, ventral digitate, dorsal saccate. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc)*.

Glossorthis ÖPIK, 1930, p. 82 [**G. tacens*; OD]. Ventribiconvex, coarsely costellate, orthocline ventral interarea short, curved, anacline dorsal interarea, very short, flat; dental plates subparallel, pseudospondylium well developed and prolonged anteromedianly as tongue-like projection, pedicle callist not recorded; brachiophores moderately divergent, bladelike. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc)*: Europe, northern Africa.—FIG. 545, 1a–d. **G. tacens*, Caradoc, Estonia; a, b, ventral interior, exterior, $\times 1.5$; c, d, dorsal interior, exterior, $\times 1.5$ (Schuchert & Cooper, 1932).

Krattorthis JAANUSSON & BASSETT, 1993, p. 56 [**Glossorthis verneuili* RUBEL, 1961a, p. 184]. Similar to *Glossorthis* but ramicostellate with more convex dorsal valve, very short curved dorsal interarea and vestigial dorsal median ridge. *Lower Ordovician*

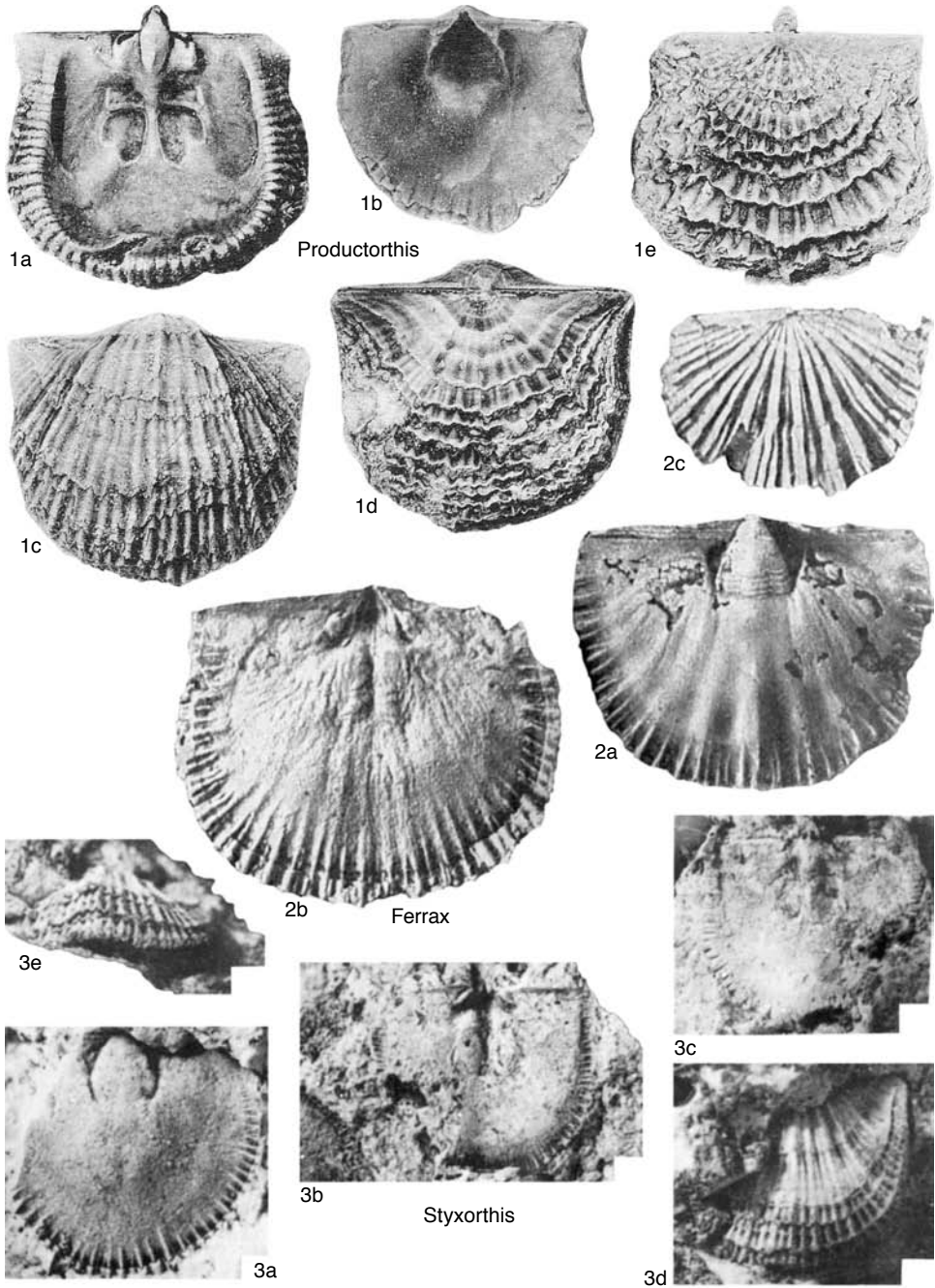


FIG. 543. Productorthidae (p. 752).

(Llanvirn): Baltic Region.—FIG. 545, 3a–e. **K. verneuli* (RUBEL), Llanvirn, eastern Baltic; a, b, ventral, lateral views of conjoined valves, $\times 2$; c, details of ornament, $\times 5$; d, e, internal molds of ventral,

dorsal valves of conjoined pair, $\times 2$ (Jaanusson & Bassett, 1993).
Nicolorthis HAVLIČEK, 1981, p. 7 [**N. instantia*; OD].
 Medium size, planoconvex to gently ventribiconvex,

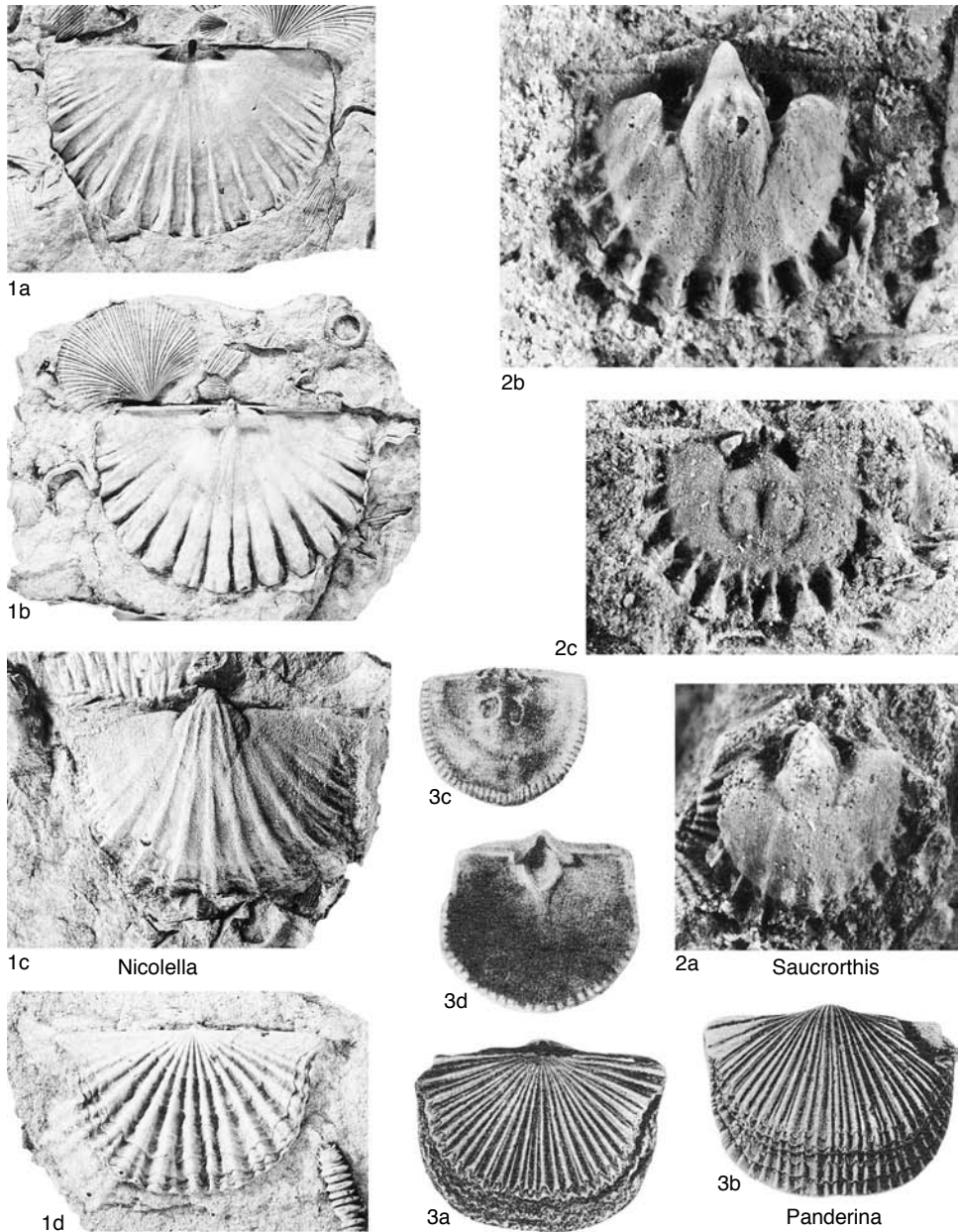


FIG. 544. Productorthidae (p. 752).

unisulcate, ramicostellate and lacking fila, orthocline ventral interarea short, curved, anacline dorsal interarea vestigial; ventral interior unknown; brachiophores narrowly divergent, bladelike, cardinal process thick with trilobed posterior face. *Upper Ordovician (Caradoc):* France (Montagne Noire). —FIG. 546a–d. **N. instantia*, Caradoc, Montagne

Noire; *a, b*, dorsal, ventral views of conjoined valves, $\times 1.3$; *c*, dorsal interior, $\times 1.5$; *d*, internal mold of dorsal valve, $\times 1.6$ (Havlíček, 1981).

Prantlina HAVLÍČEK, 1949b, p. 250 [*Orthis desiderata* BARRANDE, 1848, pl. 18, fig. 6; OD]. Gently ventribiconvex, unisulcate, ramicostellate, flate, apsacline ventral interarea short, flat; anacline dor-

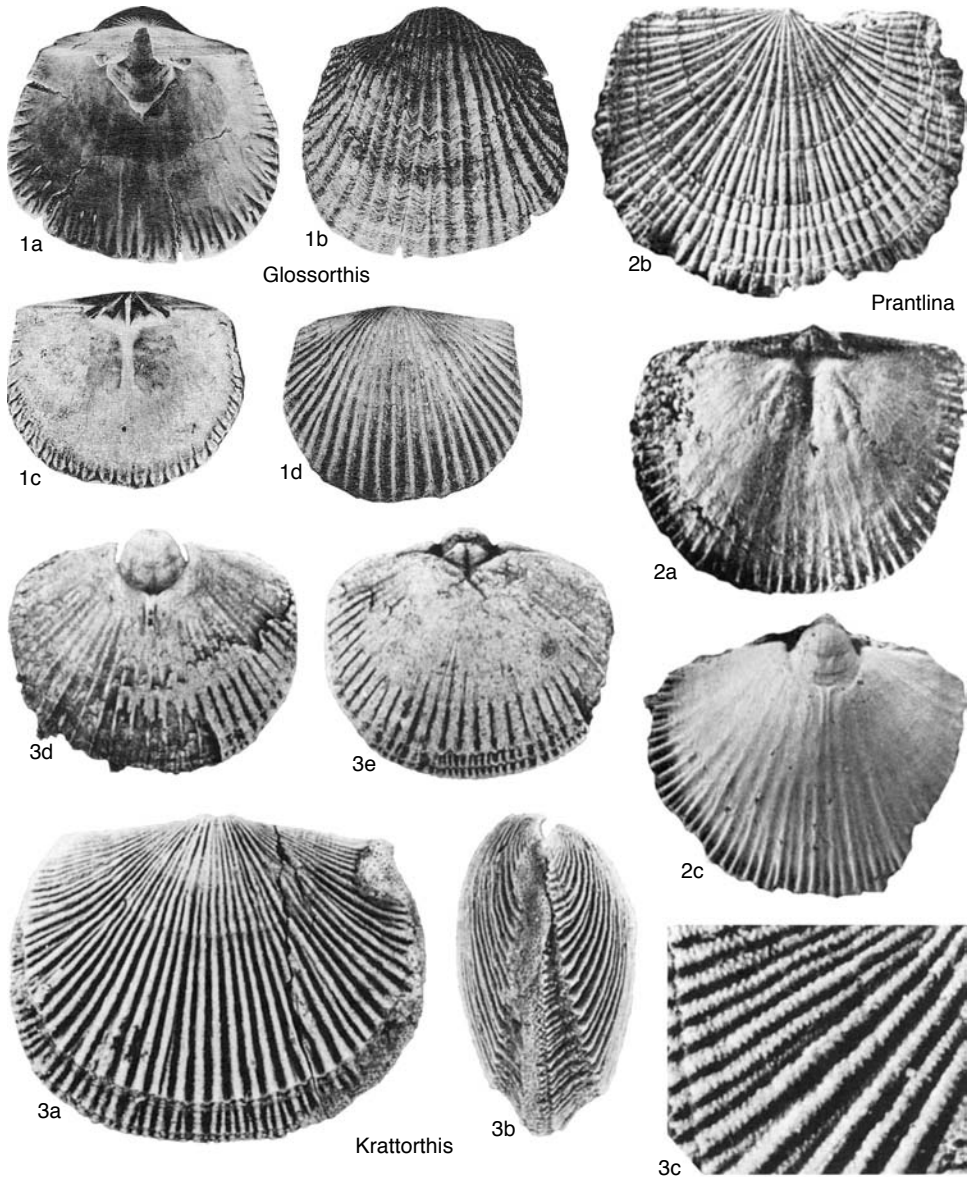


FIG. 545. Productorthidae (p. 752–755).

sal interarea very short, flat; dental plates widely divergent, pseudospondylium absent, pedicle callist well developed; widely divergent brachiophores rod-like; ventral mantle canal system digitate. *Lower Ordovician (Arenig–Llanvirn)*: Bohemia, Estonia, France (Montagne Noire).—FIG. 545, 2a–c. **P. desiderata* (BARRANDE), Arenig, Bohemia; a, internal mold of dorsal valve, $\times 2$; b, external mold of dorsal valve, $\times 2$; c, internal mold of ventral valve, $\times 1.7$ (Havlíček, 1977a).

Family WHITTARDIIDAE
Williams, 1974

[*nom. transl.* WILLIAMS & HARPER, herein, ex Whittardiinae WILLIAMS, 1974, p. 60]

Subquadrate, plano- to concavoconvex, disharmonically costellate orthoids; simple oblique teeth, dental plates recessive and subparallel, ventral muscle field short,

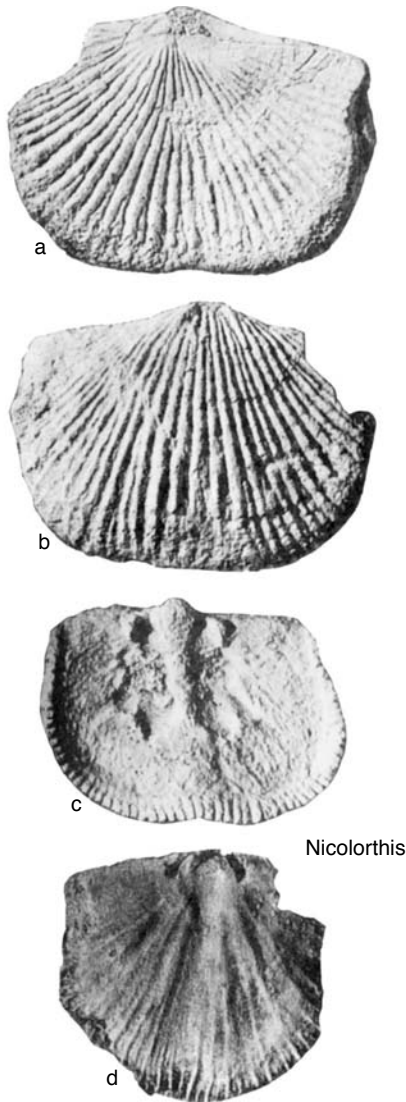


FIG. 546. Productorthidae (p. 753–754).

bilobed with undifferentiated adductor muscle track; notothyrial platform shallow, extending forward as short median ridge, cardinal process ridgelike, widely divergent; short brachiophores ridgelike; narrow, quadripartite dorsal adductor field with smaller posterior pair deeply inserted, dorsal subperipheral rim variably developed with dorsally directed geniculation; ventral mantle canal system probably saccate with *vascula media* branching early, dorsal system lemniscate or

pinnate. *Lower Ordovician (Llanvirn)*–*Upper Ordovician (Caradoc)*.

Whittardia WILLIAMS, 1974, p. 62 [**W. paradoxica*; OD]. Medium size with multicostellate and filate ornamentation on both valves but with dorsal umbonal region bearing only 6, strong, symmetrically disposed costae becoming subdued anteriorly; ventral interarea curved catacline to procline with mesothyridid foramen, dorsal interarea anacline, very short; ventral interior with 3 or 4 pairs of low ridges radiating from muscle field and fading away peripherally. *Upper Ordovician (Caradoc)*: Great Britain.—FIG. 547, 1a–e. **W. paradoxica*, Caradoc, England; a, internal mold of dorsal valve, $\times 3.6$; b, internal mold of ventral valve, $\times 5$; c, rubber replica of ventral exterior, $\times 5$; d, detail of ornament, $\times 12.5$; e, rubber replica of dorsal exterior, $\times 4.8$ (Williams, 1974).

Marginorthis LIU, ZHU, & XUE, 1985, p. 40 [**M. crassocostata*; OD]. Small, multicostellate to fascicostellate; ventral interarea apsacline. [The disharmony of the ribbing and the subperipheral rims with a dorsal deflection of the dorsal margin suggest at least a morphological comparison with *Whittardia*; *Marginorthis* is included provisionally in this family.] *Lower Ordovician (Llanvirn)*: northeastern China.—FIG. 547, 2a–e. **M. crassocostata*, Llanvirn, northeastern China; a, internal mold of dorsal valve, $\times 3$; b, internal mold of ventral valve, $\times 3$ (Liu, Zhu, & Xue, 1985); c, internal mold of dorsal valve, $\times 8$; d, internal mold of dorsal valve, $\times 4$; e, external mold of dorsal valve, $\times 4$ (Rong, new).

Nicolorthis

Superfamily PLECTORTHOIDEA Schuchert & LeVene, 1929

[*nom. transl.* HAVLIČEK, 1977a, p. 75, ex Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14]

Costate to costellate orthides with delthyrium and notothyrium open, normally wide; apsacline ventral and almost invariably anacline dorsal interareas variable in length and curvature; teeth normally with crural fossettes, usually supported by divergent dental plates; ventral muscle field variable, impressed on floor of valve; pedicle callist normally well developed; divergent brachiophores usually bladelike, normally joined to hinge line by concave fulcral plates defining elongate sockets and supported by basal plates converging to form notothyrial septalium containing variably developed cardinal process; notothyrial platform variably developed, usually with short subdued dorsal median ridge more rarely culminating in high,

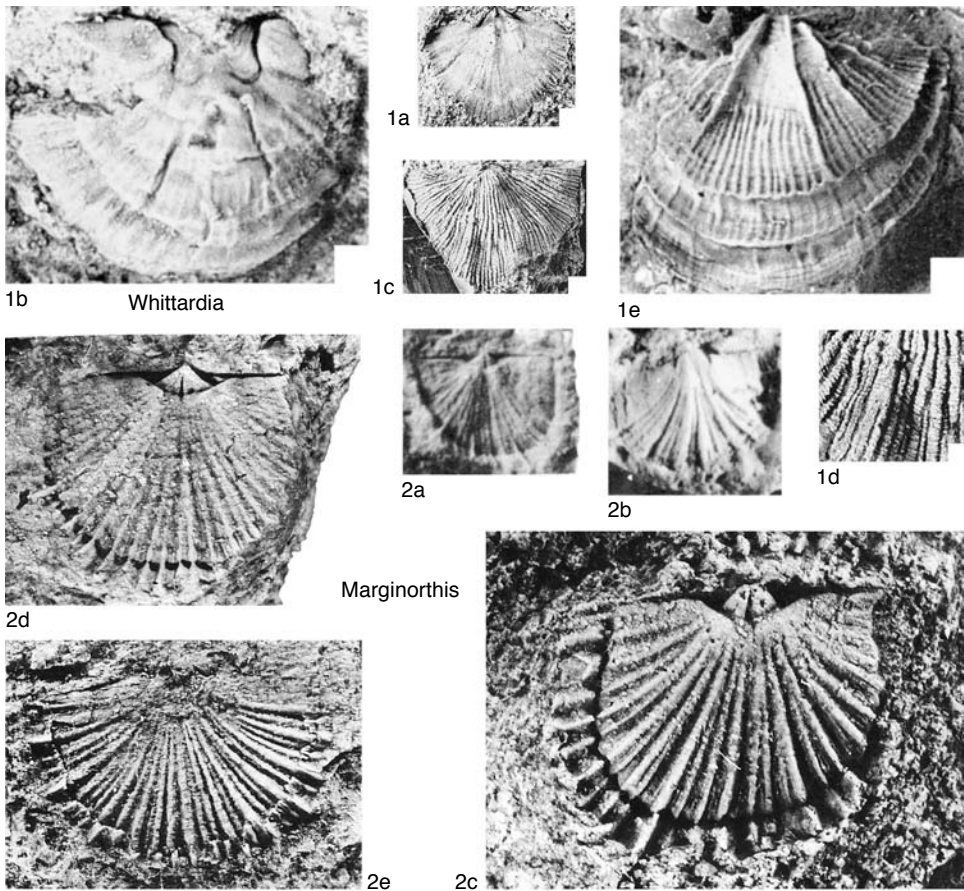


FIG. 547. Whittardiidae (p. 756).

bladellike septum; dorsal adductor field quadripartite; ventral mantle canal system saccate normally with parallel *vascula media*; dorsal system saccate to lemniscate. *Middle Cambrian–upper Silurian (Ludlow)*.

Family PLECTORTHIDAE
Schuchert & LeVene, 1929

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 243, *ex* Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14]

Subcircular to transversely semioval plectorthoids commonly with obtuse cardinal extremities, apical plate rarely developed in delthyrium; ventral interarea curved, dorsal interarea variable in length and disposition; teeth with crural fossettes supported by variably disposed plates, ventral muscle field

variably cordate but without diductor scars enclosing adductor tracks; brachiophores divergent, bladellike, joined to hinge line by concave fulcral plates and supported by plates convergent on to valve floor, extending forward as variably developed median ridge and containing cardinal process of variable complexity with negligible notothyrial platform; dorsal adductor scars quadripartite, normally with posterior pair larger than anterior. *Lower Ordovician (Tremadoc)–Upper Ordovician (Ashgill)*.

Plectorthis HALL & CLARKE, 1892, p. 194 [**Orthis plicatella* HALL, 1847, p. 122; OD]. Transversely semioval, subequally gently biconvex with faintly sulcate to uniplicate anterior commissure, costate to coarsely costellate, filate; ventral interarea short, shorter dorsal interarea orthocline to faintly

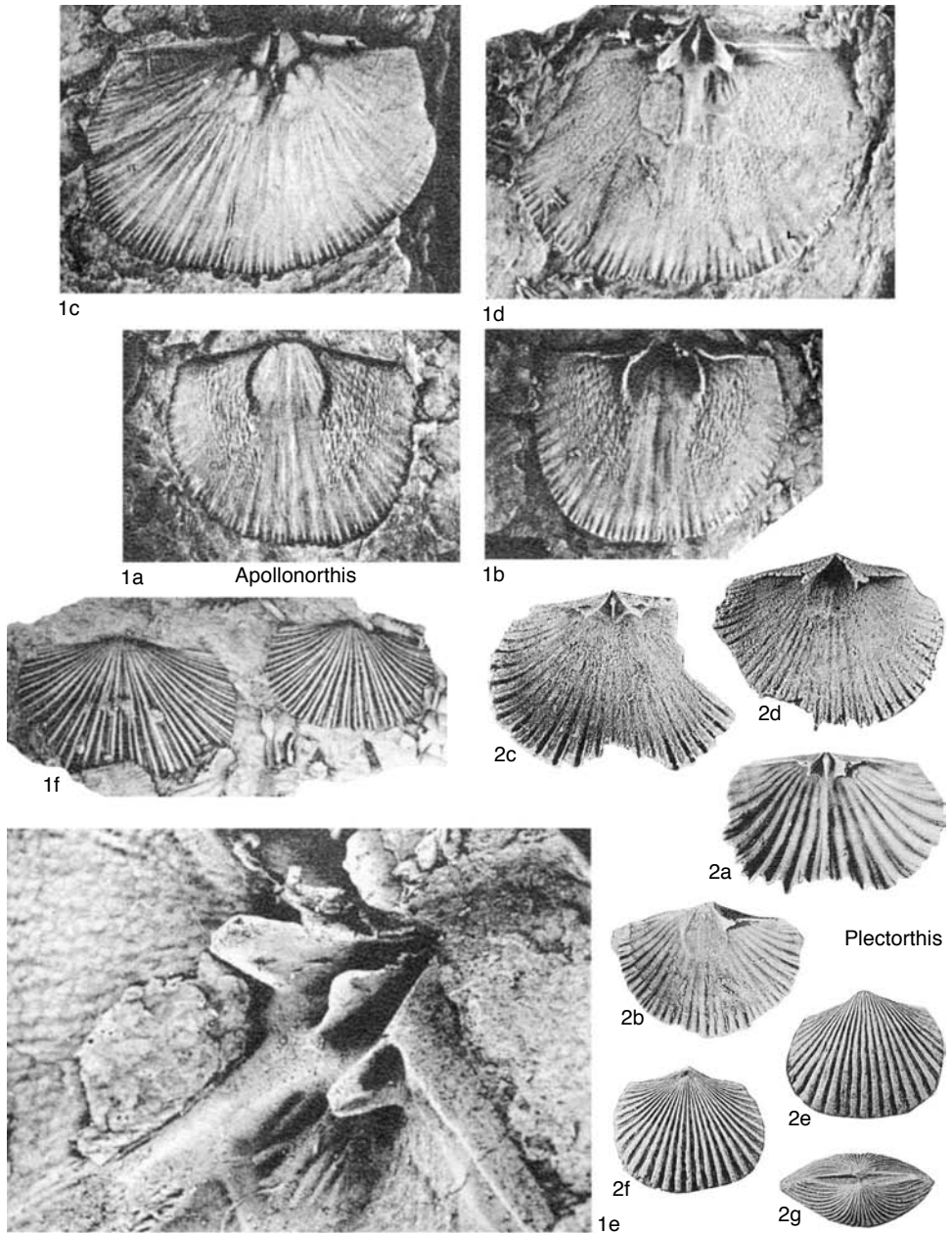


FIG. 548. Plectorthidae (p. 757–759).

anacline; dental plates divergent, ventral muscle field subcordate with linear adductor track contained by subcrescentic diductor scars separated anteriorly by low median ridge; pedicle callist not reported; cardinal process a thick, rounded ridge and crenulated myophore; exopunctate with radially

distributed aditules in some species. *Upper Ordovician (Caradoc–Ashgill)*: cosmopolitan.—FIG. 548, 2a, b. **P. plicatella* (HALL), Ashgill, Ohio; a, dorsal interior, $\times 1.5$; b, ventral interior, $\times 1.5$ (Schuchert & Cooper, 1932).—FIG. 548, 2c, d. *P. compacta*, Caradoc, Tennessee; c, dorsal interior, $\times 2$;

- d*, ventral interior, $\times 2$ (Cooper, 1956).—FIG. 548,2e–g. *P. ponderosa*, Caradoc, Virginia; ventral, dorsal, posterior views of conjoined valves, $\times 1$ (Cooper, 1956).
- Apollonorthis** MITCHELL, 1974, p. 392 [**A. lusitanica*; OD; = *Orthis bussacensis* SHARPE in RIBEIRO, 1853, p. 152]. Subquadrate, ventribiconvex, gently unisulcate, ramicostellate with aditicles, filate; interareas planar; dental plates divergent, ventral muscle field subcordate, bounded by thickened ridges, with broad adductor track not enclosed anteriorly by diductor scars; undifferentiated cardinal process platelike; posterior pair of quadripartite dorsal adductor scars larger than anterior pair. [This genus has also been assigned to the Hesperorthidae (MÉLOU, 1976, p. 694) because of its undifferentiated cardinal process. In fact, differentiation of the cardinal process took place among plectorthoids after the development of their highly distinctive cardinalia.] *Lower Ordovician (Llanvirn)*: western Europe (Portugal, France).—FIG. 548,1a–f. **A. bussacensis* (SHARPE), Llanvirn, northwestern France; *a, b*, internal mold, rubber replica of ventral valve, $\times 2$; *c, d*, internal mold, rubber replica of dorsal valve, $\times 2$; *e*, details of cardinalia, $\times 6$; *f*, rubber replica of dorsal exterior, $\times 2$ (Mélou, 1976).
- Atlantida** HAVLIČEK, 1971a, p. 37 [**A. atlantis*; OD]. Large, transversely subquadrate, strongly biconvex to resupinate, ramicostellate (aditicles not reported); subcordate tending to flabellate ventral muscle field with diductor scars enclosing suboval adductor tracks; simple cardinal process. *Lower Ordovician (Llanvirn)*: northern Africa.—FIG. 549,3a–c. **A. atlantis*, Llanvirn, northern Africa; *a*, internal mold of ventral valve, $\times 1.5$; *b*, internal mold of dorsal valve, $\times 1.5$; *c*, external mold of dorsal valve, $\times 1.7$ (Havliček, 1971a).
- Corineorthis** STUBBLEFIELD, 1939, p. 67 [**C. decipiens*; OD]. Subcircular, convexoconcave to resupinate, rectimarginate but with impersistent dorsal sulcus, multicostellate, with aditicles and strong fila simulating exopunctae in intercostellate grooves; open delthyrium and notothyrium relatively narrow; ventral interarea short, shorter dorsal interarea planar, anacline; dental plates short, parallel or narrowly divergent, ventral muscle field cordate with diductor scars not enclosing median adductor tracks that are divided by shallow groove; cardinal process with thick shaft and bulbous myophore, low median ridge bisecting subequally quadripartite adductor muscle scars. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*: Great Britain, France, southwestern China.—FIG. 549,2a–f. *C. cornubensis*, Llanvirn, southwestern England; *a, b*, internal mold, rubber replica of dorsal valve, $\times 2$; *c, d*, internal mold, rubber replica of ventral valve, $\times 2$; *e, f*, external mold, rubber replica of ventral valve, $\times 2$ (Basset, 1981).
- Desmorthis** ULRICH & COOPER, 1936b, p. 624 [**D. nevadensis*; OD]. Similar to *Plectorthis* but more subcircular with rectangular to obtuse cardinal extremities, ventribiconvex; delthyrium with apical plate, dorsal interarea anacline; dental plates narrowly divergent, ventral muscle field quadrate with adductor ridge extending forward; cardinal process simple, platelike. *Lower Ordovician (Llanvirn)*: North America, England, Bolivia, southwestern China.—FIG. 549,1a–d. **D. nevadensis*, Llanvirn, Nevada; *a*, ventral exterior, $\times 2$; *b*, details of ornament, $\times 4$; *c*, ventral interior, $\times 3$; *d*, dorsal interior, $\times 3$ (Ulrich & Cooper, 1938).
- Doleroides** COOPER, 1930, p. 375 [**Orthis gibbosa* BILLINGS, 1857, p. 296; OD]. Transversely subelliptical to subquadrate, subequally biconvex, sharply uniplicate, multicostellate with aditicles; both interareas relatively long and curved, dorsal anacline; ventral muscle field quadrate with elliptical adductor track divided by median ridge and not enclosed by diductor scars; cardinal process varying from thin plate to shaft with expanded myophore; ventral mantle canal system lemniscate. *Upper Ordovician (Caradoc–Ashgill)*: North America, Scotland, northern Ireland, Kazakhstan, Australia, western China (including Tibet).—FIG. 549,5a–d. **D. gibbosa* (BILLINGS), Caradoc, Minnesota; *a–c*, ventral, dorsal, anterior views of conjoined valves, $\times 1$; *d*, ventral interior, $\times 2$ (Cooper, 1956).—FIG. 549,5e, f. *D. tennesseensis* (COOPER), Caradoc, Tennessee; dorsal interior, normal and tilted views, $\times 1$ (Cooper, 1956).
- Hebertella** HALL & CLARKE, 1892, p. 198 [**Orthis sinuata* HALL, 1847, p. 128; OD]. Mainly large, subquadrate with variable angled cardinal extremities, convexoconcave, uniplicate, multicostellate with aditicles, filate; both interareas relatively long, dorsal apsacline; dental plates divergent, ventral muscle scar subcordate, bounded by ridge, with elongately oval adductor scars impressed on double ridge, not enclosed by diductor tracks; adult cardinal process thick ridge with compressed myophore, brachiophore plates convergent, recessive; posterior pair of quadripartite adductor muscle scars larger than anterior pair. *Upper Ordovician (Caradoc–Ashgill)*: North America, Ireland, Kazakhstan, Estonia, Australia.—FIG. 550,1a–f. **H. sinuata* (HALL), Ashgill, Ohio; *a–d*, dorsal, ventral, lateral, posterior views of conjoined valves, $\times 1.5$; *e*, ventral interior, $\times 2$; *f*, dorsal interior, $\times 2$ (Schuchert & Cooper, 1932).
- Irhirea** HAVLIČEK, 1971a, p. 44 [**Corineorthis gigantea* TERMIER & TERMIER, 1950, p. 41; OD]. Large, subcircular, variably convexoplane, rectimarginate, multicostellate (aditicles not reported); ventral interarea relatively short, not much longer than apsacline dorsal interarea; elongately bilobed ventral muscle field bounded by ridge with ovoid adductor tracks divided by median ridge, not completely enclosed by diductor scars; cardinal process simple plate, convergent brachiophore plates forming small septalium. *Upper Ordovician (Caradoc)*: north Africa.—FIG. 551,1a–d. **I. gigantea* (TERMIER & TERMIER), Caradoc, northern Africa; *a*, internal mold of ventral valve, $\times 1.5$; *b*, internal mold of ventral valve, $\times 1.4$; *c*, internal mold of dorsal valve, $\times 1.5$; *d*, anterior view of conjoined valves, $\times 1.5$ (Havliček, 1971a).

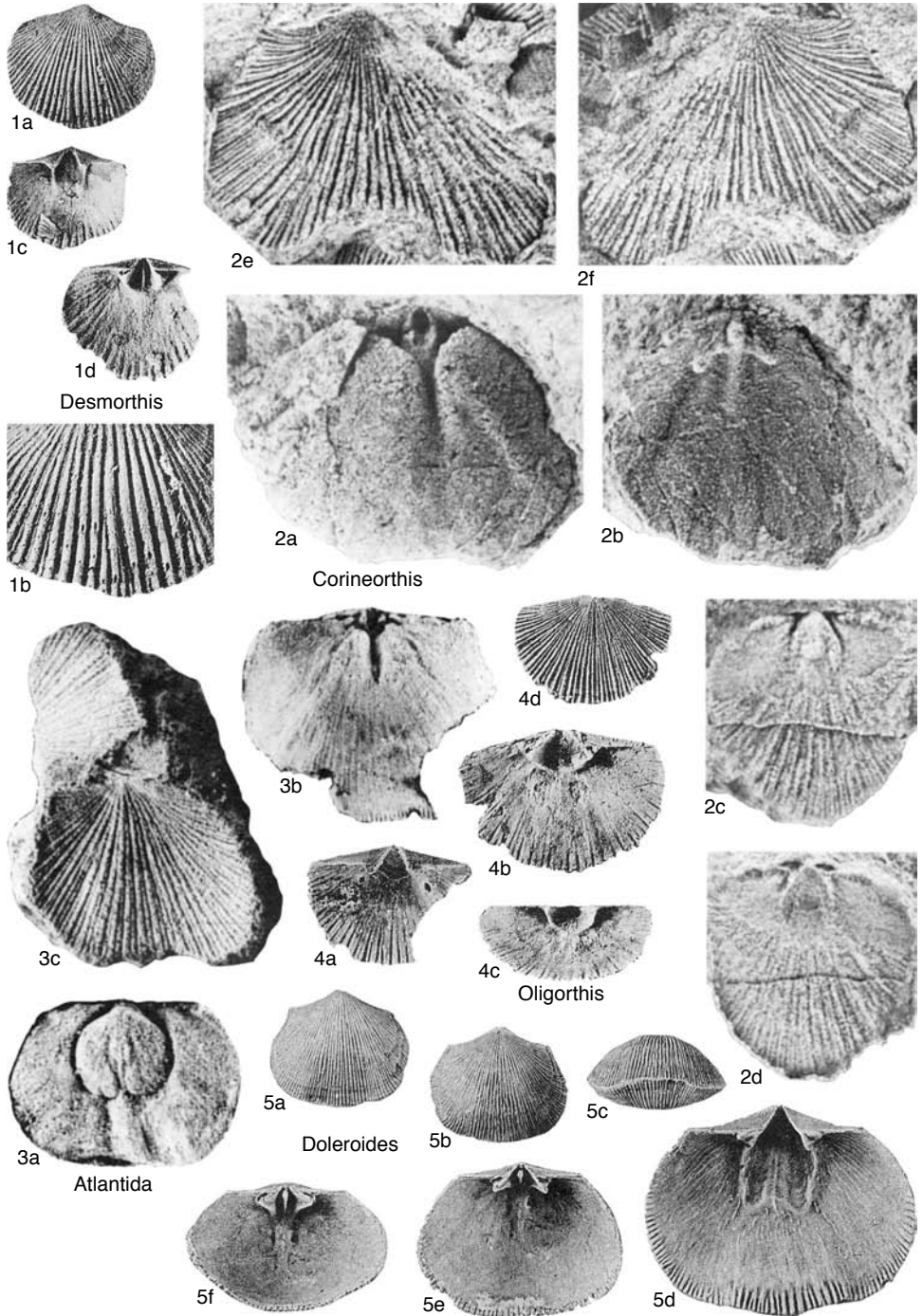


FIG. 549. Plectorthidae (p. 759–762).

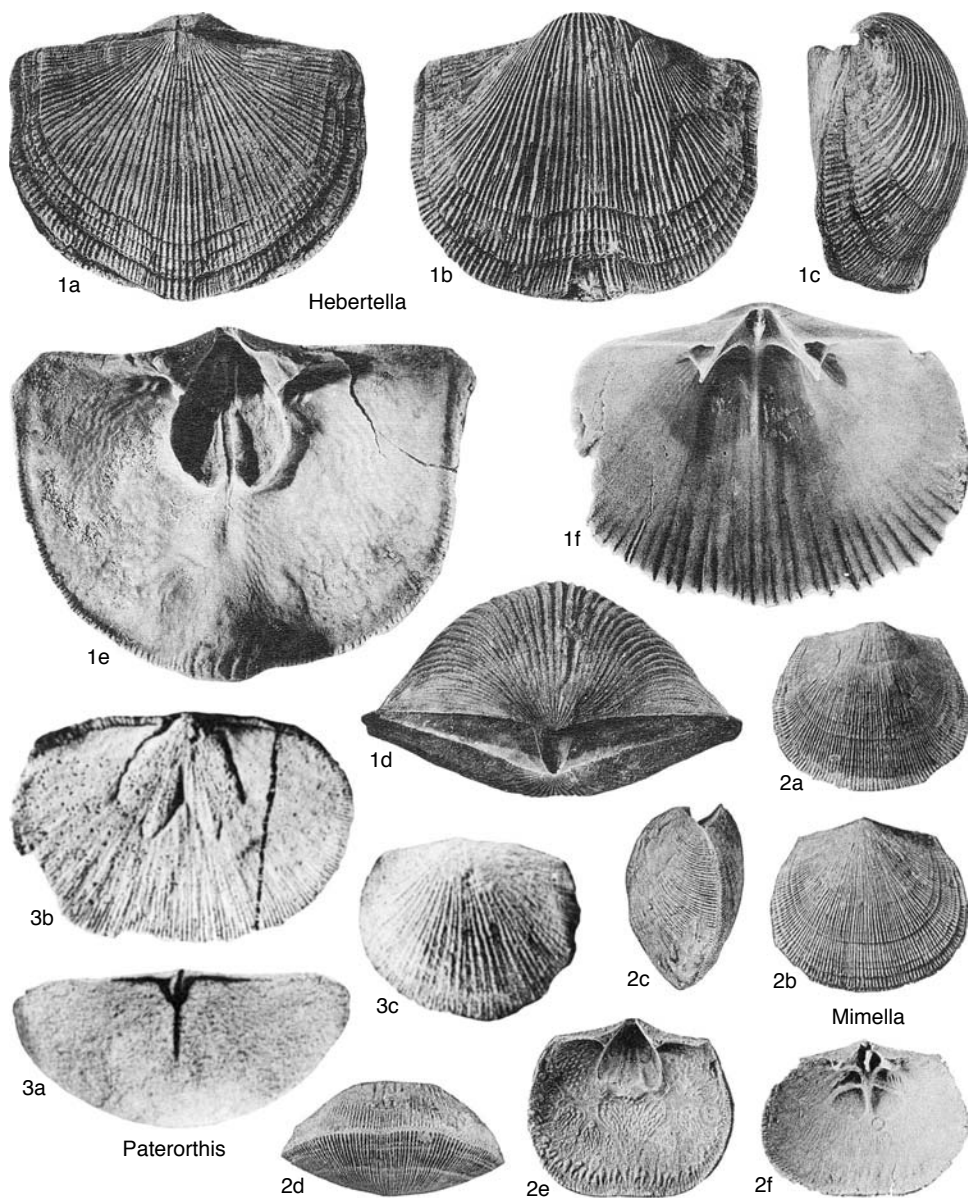


FIG. 550. Plectorthidae (p. 759-762).

Mimella COOPER, 1930, p. 375 [*Pionodema globosa* WILLARD, 1928, p. 274; OD] [=*Sonculina* MISIUS, 1986, p. 111 (type, *S. prima*)]. Similar to *Hebertella* but dorsibiconvex with obtuse cardinal extremities and without fila; dental plates recessive, bilobed ventral muscle scar consisting of long, subparallel impressed diductor scars not enclosing long, anteri-

orly expanding, elevated adductor track; cardinal process simple, platelike, brachioophore plates convergent to form small septalium; quadripartite dorsal adductor scars with subequal tracks; mantle canal systems well preserved, ventral saccate, dorsal variably digitate. [*Sonculina*, based on shells from the middle Ordovician of Khirgiz, has been

distinguished by its author (MISIUS, 1986, p. 113) from *Mimella* in having a fibrous shell and a saccate mantle canal system. These features are, in fact, typical of *Mimella* as are such other characters as were described and illustrated (MISIUS, 1986).] *Upper Ordovician (Caradoc)*: Northern Hemisphere.—FIG. 550, 2a–f. **M. globosa* (WILLARD), Caradoc; a–d, dorsal, ventral, lateral, anterior views of conjoined valves, Tennessee, $\times 1$; e, ventral interior, Tennessee, $\times 1$; f, dorsal interior, Virginia, $\times 1$ (Cooper, 1956).

Oligorthis ULRICH & COOPER, 1936b, p. 624 [**O. arbucklensis*; OD]. Similar to *Desmorthis* but more transversely semioval with variably angled cardinal extremities, unisulcate, more finely costellate and without apical plate in delthyrium, cardinal process also lacking. *Lower Ordovician (Tremadoc–Arenig)*: North America, southwestern China, Scotland.—FIG. 549, 4a–d. **O. arbucklensis*, Tremadoc, Oklahoma; a, ventral interior, $\times 3$; b, c, normal, tilted views of dorsal interior, $\times 4$; d, dorsal exterior, $\times 3$ (Ulrich & Cooper, 1938).

Paterorthis HAVLIČEK, 1971a, p. 45 [**P. paterina*; OD]. Large, subcircular, convexoconcave with hemispherical dorsal valve, gently uniplicate, multicostellate (aditicles not reported); ventral interarea catacline, dorsal interarea vestigial; ventral muscle field large, bilobed to flabellate with lanceolate adductor track, pedicle callist well developed; cardinal process simple, bladelikey; brachiophore plates converging to form small posteromedian septalium. *Lower Ordovician (Llanvirn)*: northern Africa.—FIG. 550, 3a–c. **P. paterina*, Llanvirn, northern Africa; a, posterior view of internal mold of dorsal valve, $\times 1.6$; b, internal mold of ventral valve, $\times 1.5$; c, rubber replica of exterior, $\times 1.5$ (Havlíček, 1971a).

Pseudomimella XU & LIU, 1984, p. 179 [**Mimella formosa* WANG, 1955c, p. 125; OD]. Large, subquadrate, dorsibiconvex, rectimarginate, multicostellate; interareas relatively short; dental plates recessive, ventral muscle field suboval with wide undifferentiated adductor track as long as lateral diductor scars; cardinal process platelike; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system saccate with long, subparallel *vascula media*, dorsal system probably saccate. *Lower Ordovician (Arenig)*: southwestern China.—FIG. 551, 2a–f. **P. formosa* (WANG), Arenig, southwestern China; a, internal mold of dorsal valve, $\times 1$; b, rubber replica of dorsal interior, $\times 1$; c, internal mold of ventral valve, $\times 1$; d–f, ventral, lateral, anterior views of conjoined valves, $\times 1.5$ (Xu & Lui, 1984).

Schizophorella REED, 1917, p. 858 [**Orthis fallax* SALTER, 1846, p. 72; OD]. Transversely semioval to subquadrate, dorsibiconvex with strong median fold in dorsal valve, uniplicate, multicostellate (no aditicles reported); interareas short, dorsal anacline; dental plates subparallel continuous with ridges flanking elongately bilobed ventral muscle field with diductor scars enclosing lanceolate adductor track divided by low median ridge extending

anteriorly beyond muscle field; cardinal process ridgelike with crenulated myophore; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Ashgill)*: Great Britain, Ireland, Kazakhstan, northwestern China, Spain, central Asia, Norway.—FIG. 552a–f. *S. fallax alta* HARPER, Ashgill, southwestern Scotland; a, ventral view of conjoined internal molds, $\times 4$; b, dorsal view of conjoined internal molds, $\times 3$; c, d, internal mold, rubber replica of dorsal valve, $\times 5$; e, external mold of ventral exterior, $\times 3$; f, rubber replica of ventral exterior, $\times 4$ (Harper, 1984).

Severginella ROZMAN, 1981, p. 122 [**Pionodema(?) altaica* SEVERGINA, 1960, p. 405; OD]. Similar to *Pseudomimella* but uniplicate, ventral adductor track variable in width, cardinal process wide, differentiated into myophore and shaft; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Upper Ordovician (Caradoc–Ashgill)*: central Asia (Altai Mountains, Mongolia, Tuva).—FIG. 551, 3a, b. **S. altaica* (SEVERGINA), Caradoc, Altai Mountains; a, internal mold of dorsal valve, $\times 2$; b, internal mold of ventral valve, $\times 2$ (Rozman, 1981).

Family CREMNORTHIDAE Williams, 1963

[*Cremnorthidae* WILLIAMS, 1963, p. 377]

Elongately oval unisulcate mainly fascicostellate plectorthoids; delthyrium and notothyrium normally narrow; apsacline ventral interarea curved, anacline dorsal interarea short, curved teeth with crural fossettes, usually without dental plates; ventral muscle scar short, subtriangular with wide undifferentiated adductor scar; cardinal process massive with well-differentiated myophore; brachiophores widely divergent, supporting plates curving laterally and defining sockets; quadripartite dorsal adductor scars with anterior pair larger than posterior, normally divided by high, bladelikey median septum; ventral mantle canal system saccate, dorsal system usually indistinct. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*.

Cremnorthis WILLIAMS, 1963, p. 378 [**C. parva*; OD]. Sharply unisulcate with acute cardinal extremities; massive cardinal process having trilobate myophore with high median crest. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*: Wales, Estonia, Ireland.—FIG. 553, 1a–f. **C. parva*, Caradoc, Wales; a, b, internal mold, rubber replica of ventral valve, $\times 6.5$; c, internal mold of dorsal valve, $\times 8.5$; d, rubber replica of dorsal valve, $\times 9.5$; e, internal mold of dorsal valve, $\times 7$; f, rubber replica of dorsal exterior of conjoined valves, $\times 6$ (Williams, 1963).

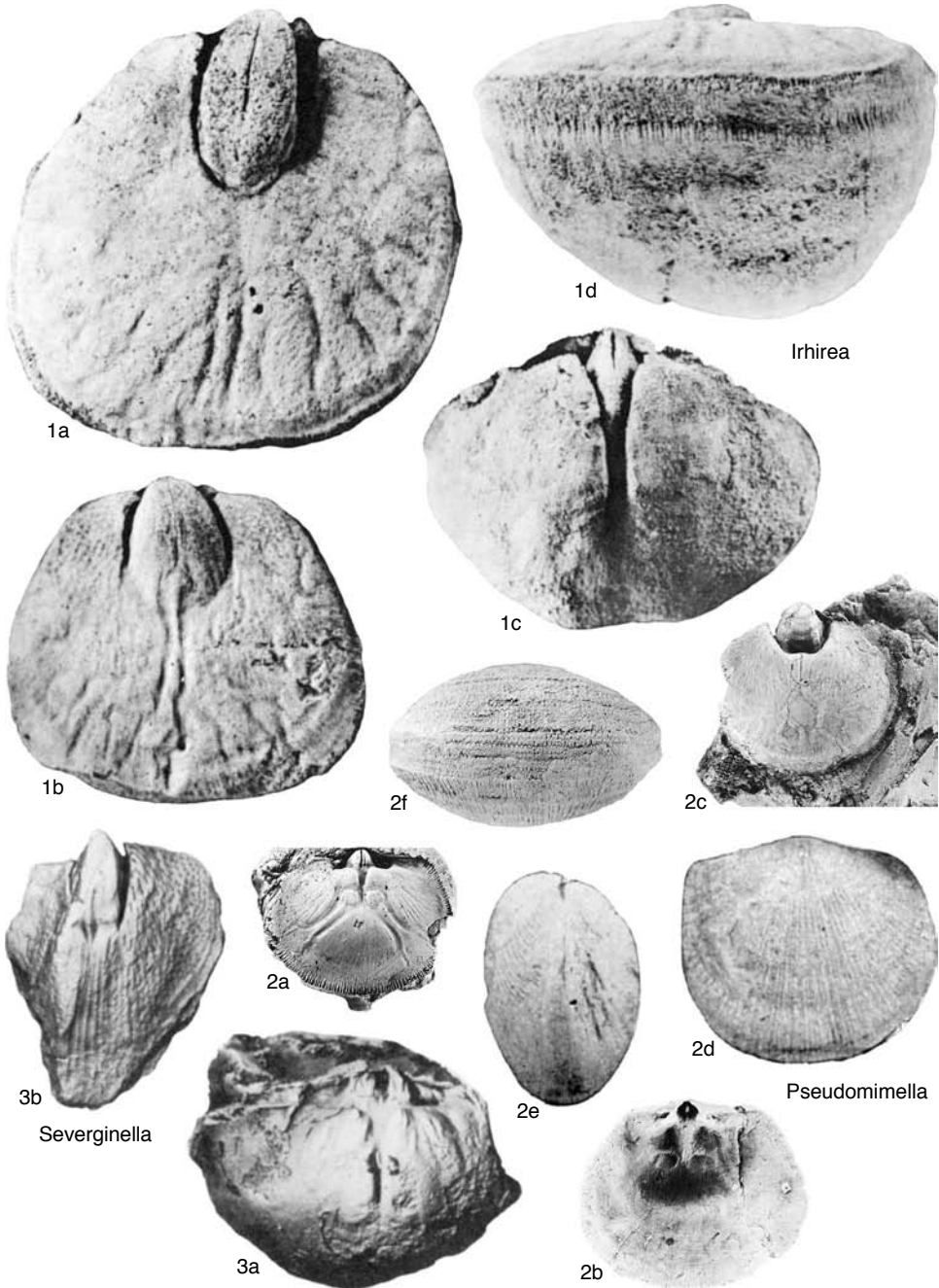
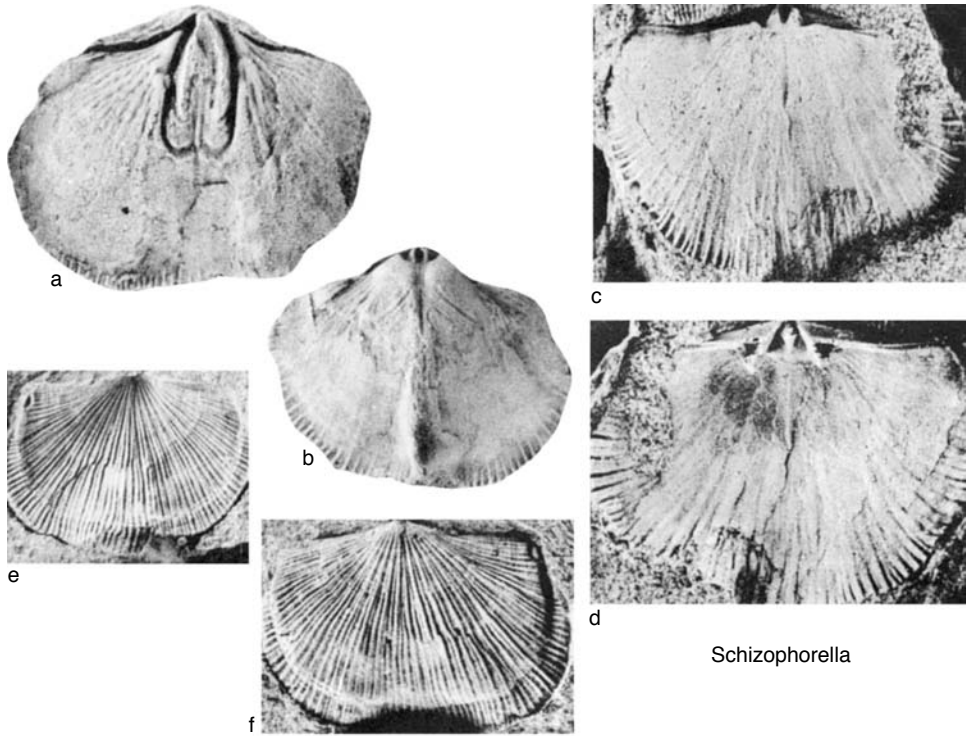


FIG. 551. Plectorthidae (p. 759–762).

Brandysia HAVLIČEK, 1975, p. 231 [**B. benigna*; OD].
Subquadrate with obtuse cardinal extremities;
delthyrium and notothyrium wide; dorsal interarea
vestigial; teeth supported by short, recessive dental

plates; cardinal process with bilobate myophore.
Lower Ordovician (Llanvirn): Bohemia, northeastern
China.—FIG. 553, 2a–d. **B. benigna*, Llanvirn,
Bohemia; a, internal mold of ventral valve, ×11.2;



Schizophorella

FIG. 552. Plectorthidae (p. 762).

b, internal mold of dorsal valve, $\times 10$; *c*, internal mold of dorsal valve, $\times 10.5$; *d*, rubber replica of ventral exterior, $\times 10$ (Havlíček, 1977a).

Septorthis HINTS, 1973, p. 251 [*S. engurensis*; OD]. Ramicostellate, with obtuse cardinal extremities; cardinal process undifferentiated or with bilobate myophore; quadripartite dorsal adductor field bisected by median septum, consisting of broad, posterior scars with inner lobes impressed on raised platforms, separated from anterior scars by curved, transverse ridges. *Upper Ordovician (Caradoc)*: Latvia, Sweden.—FIG. 553,3a-f. *S. engurensis*, Caradoc, Latvia; *a-c*, ventral, dorsal, anterior views of conjoined valves, $\times 7.6$; *d, e*, normal, tilted views of dorsal interior, $\times 7.6$; *f*, ventral interior, $\times 7.7$ (Hints, 1973).

Family CYCLOCOELIIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, ex Cyclocoeliidae SCHUCHERT & COOPER, 1931, p. 243]

Rostrate, biconvex, costate plectorthoids with very narrow hinge lines. *Lower Ordovician (Arenig)*–*Upper Ordovician (Ashgill)*.

Cyclocoelia FOERSTE, 1909b, p. 227 [*Atrypa sordida* HALL, 1847, p. 148; OD] [= *Encyclodema* FOERSTE,

1912, p. 139, obj.]. Small, rhynchonelliform to subcircular, rectimarginate to gently uniplicate; apsacline ventral interarea short curved, apsacline dorsal interarea very short; strong teeth supported by divergent dental plates; brachiophores supported by convergent plates, cardinal process faint, median ridge long; muscle and mantle canal impressions unknown. *Upper Ordovician (Ashgill)*: USA (Ohio), central Asia, eastern Canada, northwestern China.—FIG. 554,1a-d. **C. sordida* (HALL), Ashgill, Ohio; *a, b*, ventral, dorsal exteriors, $\times 2$; *c*, internal mold of ventral valve, $\times 2$; *d*, internal mold of dorsal valve, $\times 2$ (Schuchert & Cooper, 1932).

Rhynchorthis BATES, 1968, p. 160 [**R. rotundus*; OD]. Medium size, dorsibiconvex, uniplicate, filate, strongly apsacline interareas relatively short, curved; strong teeth supported by recessive dental plates; ventral muscle scar, impressed on callus, elongately oval with wide adductor track; pedicle callist well defined; bladelike brachiophores with fulcral plates and recessive convergent supporting plates, bladelike cardinal process flanked by low, notothyrial ridges; bilobed anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral mantle canal system saccate, dorsal lemniscate. *Lower Ordovician (Arenig–Llanvirn)*: Wales, south-eastern Ireland.—FIG. 554,2a-f. **R. rotundus*, Arenig, northern Wales; *a, b*, internal mold, rubber replica of ventral valve, $\times 2$; *c, d*, internal mold, rub-

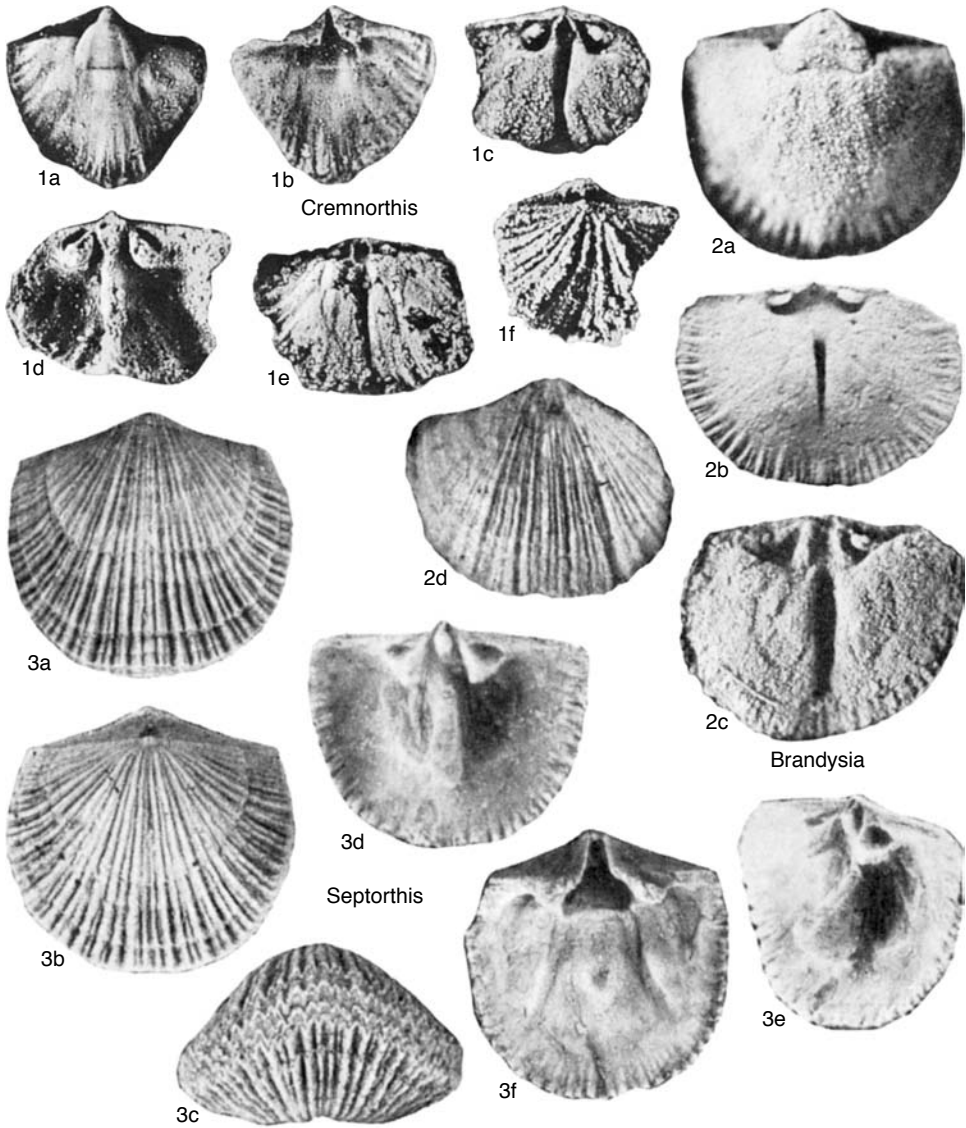


FIG. 553. Cremnorthidae (p. 762–764).

ber replica of dorsal interior, $\times 2$; *e, f*, external mold, rubber replica of dorsal valve, $\times 2$ (Neuman & Bates, 1978).

Family EOORTHIDAE Walcott, 1908

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 242, *ex Eoorthinae* WALCOTT, 1908, p. 148]

Normally subquadrate, biconvex, unisulcate, and variably costellate with curved ventral apsacline and dorsal anacline interareas; delthyrium and notothyrium open; deltidio-

dont teeth variably supported; ventral muscle field impressed on callus, suboval to subtriangular, commonly with broad, elongate undifferentiated adductor track not enclosed by diductor scars; notothyrial platform and cardinal process variably developed; divergent brachiophores short, bladeliike, defining elongate sockets; adductor scars quadripartite with subtriangular anterior pair inserted posteromedianly

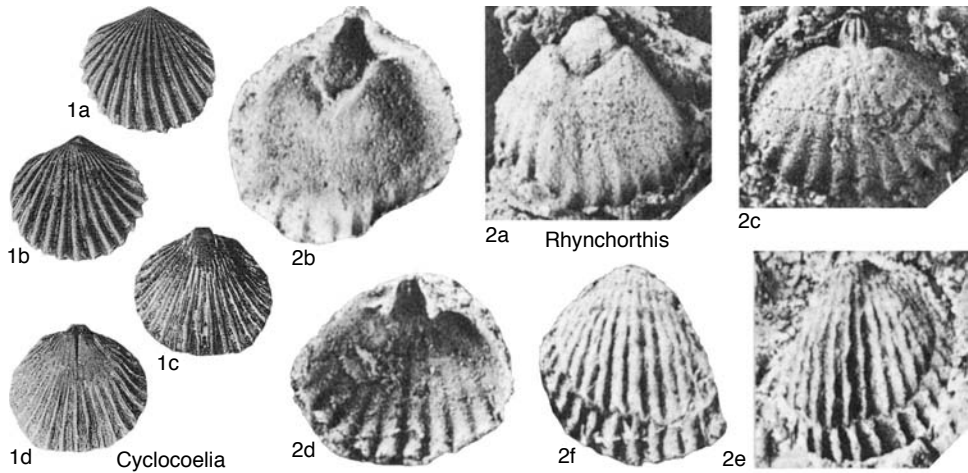


FIG. 554. Cyclocoeliidae (p. 764–765).

between subtriangular posterior pair; ventral mantle canal system saccate, dorsal system obscure but with divergent *vascula media*. [This family clusters with the plectorthoids as the Lower Cambrian stem group with a morphology that differs significantly from that of other, older plectorthoids, finkelnburgiids, and ranorthids only in the lack of development of brachiophore supporting plates or fulcral plates. The eorthids, however, also have strong affinities with early orthoids and are presently best accepted as representing the link group(s) between the plectorthoids and orthoids.] *Middle Cambrian–Lower Ordovician (Tremadoc)*.

Eoorthis WALCOTT, 1908, p. 102 [**Orthis remnicha* WINCHELL, 1885, p. 317; OD]. Radial ornamentation of coarse costellae with superimposed capillae, dental plates receding, ventral muscle scar enclosed by a low ridge; cardinal process simple, dorsal median ridge wide. *Upper Cambrian–Lower Ordovician (Tremadoc)*: cosmopolitan.—FIG. 555, 1a–e. **E. remnicha* (WINCHELL), Upper Cambrian, Montana; a, b, interior, exterior of dorsal valve, $\times 2$; c, d, internal mold, rubber replica of ventral valve, $\times 3$ (Bell, 1941); e, dorsal interior, $\times 2$ (Schuchert & Cooper, 1932).

Apheoorthina HAVLIČEK, 1949a, p. 99 [**A. ferrigena*; OD]. Similar to *Apheoorthis* but filate with elongately cordate ventral muscle field with diductor scars enclosing lanceolate adductor track and stronger notothyrial platform with ridgelike cardinal process. *Lower Ordovician (Tremadoc)*: Bohemia, Baltic.—FIG. 555, 5a–c. **A. ferrigena*, Tremadoc, Bohemia; a, internal mold of dorsal valve, $\times 3.3$; b, internal mold

of ventral valve, $\times 2.9$; c, dorsal exterior, $\times 3.6$ (Havlíček, 1977a).

Apheoorthis ULRICH & COOPER, 1936b, p. 620 [**Eoorthis lineocosta* WALCOTT, 1924, p. 508; OD]. Fascicostellate, dorsal valve strongly sulcate, dental plates well developed on either side of pseudospondylium; notothyrial platform and ridgelike cardinal process rudimentary. *Upper Cambrian–Ordovician (Tremadoc)*: North America, Kazakhstan, Siberian Platform, Colombia, Sweden, Baltic, Ireland, eastern, northern, and northeastern China, Australia (Tasmania), Afghanistan.—FIG. 555, 3a–e. **A. lineocosta* (WALCOTT), Upper Cambrian, Colorado; a, b, interior, exterior of ventral valve, $\times 2$; c, details of posteromedian part of ventral interior, $\times 4$; d, e, interior, exterior of dorsal valve, $\times 2$ (Ulrich & Cooper, 1938).

Austrohedra ROBERTS & JELL, 1990, p. 276 [**A. mimica*; OD]. Ventribiconvex, with long, flat, catacline to slightly apsacline ventral interarea, ramicostellate; dental plates well developed; cardinal process rudimentary. *Middle Cambrian*: Australia (New South Wales).—FIG. 555, 2a–d. **A. mimica*, Middle Cambrian, New South Wales; a, b, interior, exterior of dorsal valve, $\times 6$; c, d, interior, posterior views of ventral valve, $\times 4$ (Roberts & Jell, 1990).

Brahimorthis HAVLIČEK, 1971a, p. 29 [**B. antiqua*; OD]. Ramicostellate and filate, lacking dental plates and cardinal process; small bilobed adductor muscle scars impressed on transverse ridge enclosing delthyrial cavity of ventral valve, with anterior tips of diductor scars possibly enclosing oval adductor track. *Middle Cambrian*: Europe, northern Africa.—FIG. 555, 4a–c. **B. antiqua*, Middle Cambrian, northern Africa; a, dorsal interior, $\times 1.7$; b, internal mold of ventral valve, $\times 2$; c, dorsal exterior, $\times 1.5$ (Havlíček, 1971a).

Glaphyrorthis ROBERTS & JELL, 1990, p. 278 [**G. fastigiata*; OD]. Small, mucronate, transversely semioval, sharply unisulcate, smooth shells with

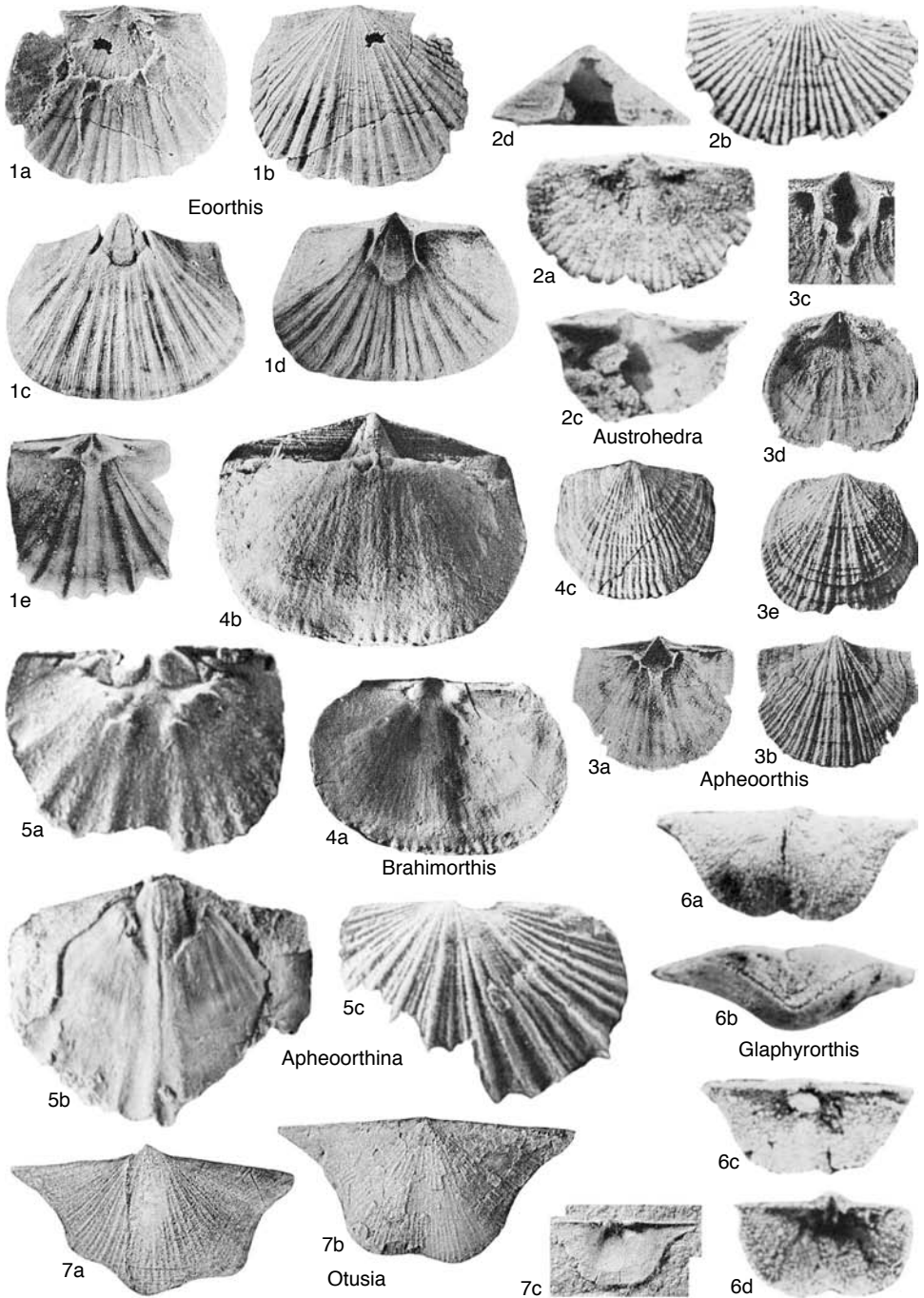


FIG. 555. Eoorthidae (p. 766–769).

well-developed dental plates and a pseudodeltidium; cardinal process not seen. [The inclusion of this genus within the Eoorthidae is provisional based on

further information about the cardinalia and the external surfaces of the type species that are presently known only in the silicified state.] *Middle*

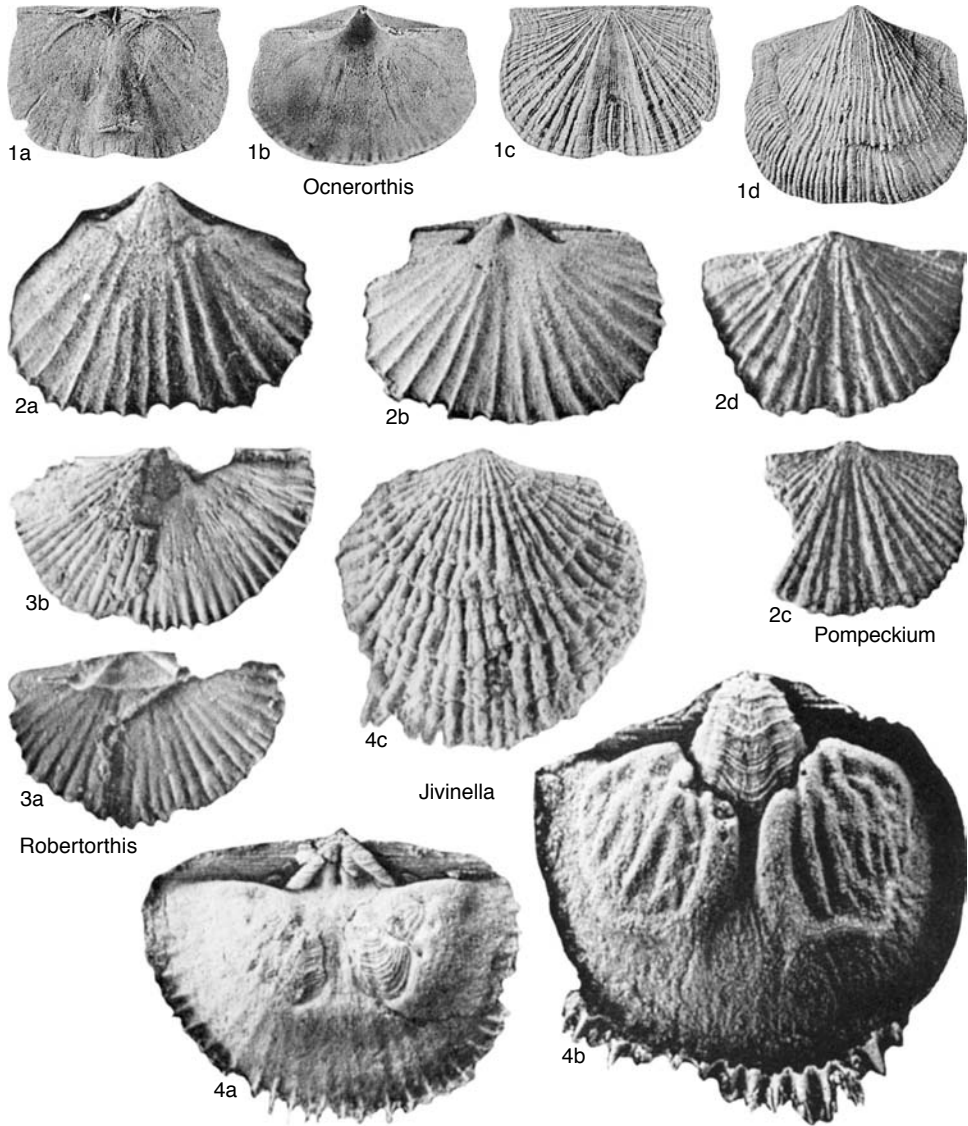


FIG. 556. Eoorthidae (p. 768–769).

Cambrian: Australia (New South Wales).—FIG. 555, 6a–d. **G. fastigiata*, Middle Cambrian, New South Wales; a, b, dorsal, anterior views of conjoined valves, $\times 8$; c, dorsal interior, $\times 8$; d, ventral interior, $\times 8$ (Roberts & Jell, 1990).

Jivinella HAVLIČEK, 1949a, p. 94 [**Orthis incola* BARRANDE, 1879, pl. 126, fig. IV; OD] [= *Jevinellina* LIU in LIU, XU, & LIANG, 1983, p. 262 (type, *J. involuta*)]. Ventribiconvex, rectimarginate, interareas strongly developed, fascicostellate and finely capillate in interspaces, imbricate; dental plates recessive, pedicle collar obtusely triangular, transverse

ventral muscle scar impressed on pseudospondylium with anterior median ridge; simple cardinal process flanked by discrete notothyrial ridges, and rodlike brachiophores widely divergent. [According to LIU (in LIU, XU, & LIANG, 1983, p. 262), the type species of *Jevinellina* from the Lower Ordovician of southern China differs from European species of *Jivinella* only in being dorsibiconvex and in the development of a short median ridge in the dorsal valve. LIU doubted whether these variably developed features were sufficient to erect a new genus and we agree.] *Lower Ordovician (Tremadoc)*: Bohemia,

Spain, southern China, Germany.—FIG. 556,4a–c. *J. involuta*, Tremadoc, Bohemia; *a*, internal mold of dorsal valve, $\times 3.5$; *b*, internal mold of ventral valve, $\times 5.2$; *c*, rubber replica of ventral exterior, $\times 3.5$ (Havlíček, 1977a).

Ocnorthis BELL, 1941, p. 251 [**O. cooperi*; OD].

Unequally biconvex to planoconvex, fascicostellate, strongly apsacline to nearly orthocline ventral interarea; dental plates variably present, ventral muscle scar suboval with anteromedian callosity; brachiophores widely divergent, sockets associated with laterally curving ridges; ventral mantle canal system possibly digitate with narrowly divergent *vascula media*. *Upper Cambrian–Lower Ordovician (Tremadoc)*: North America, Bohemia, Novaya Zemlya.—FIG. 556,1a–d. **O. cooperi*, Upper Cambrian, Wyoming; *a*, dorsal interior, $\times 3$; *b*, ventral interior, $\times 3$; *c*, dorsal exterior, $\times 3$; *d*, ventral exterior, $\times 3$ (Bell, 1941).

Otusia WALCOTT, 1905, p. 246 [**Orthis sandbergi* WINCHELL, 1885, p. 318; OD].

Small, mucronate, transversely semioval, ventribiconvex, strongly unisulcate, multicostellate; dental plates divergent with suboval ventral muscle scar impressed on valve floor; cardinal process rudimentary, brachiophores short, divergent. *Upper Cambrian*: North America, Argentina.—FIG. 555,7a–c. **O. sandbergi* (WINCHELL), Upper Cambrian, Montana; *a*, ventral exterior, $\times 4$; *b*, dorsal exterior, $\times 3$ (Bell, 1941); *c*, dorsal interior, $\times 2.5$ (Grant, 1965).

Pompeckium HAVLÍČEK, 1970b, p. 290 [**Orthis kuthani* POMPECKJ, 1896, p. 514].

Gently unisulcate, coarsely costellate, filate, ventral interarea long and curved; dental plates absent, suboval ventral muscle field with broad, triangular adductor track impressed directly on valve floor; simple cardinal process, short, divergent rodlike brachiophores; ventral mantle canal system digitate. *Middle Cambrian*: Bohemia, central USA.—FIG. 556,2a–d. **P. kuthani* (POMPECKJ), Middle Cambrian, Bohemia; *a*, internal mold of ventral interior, $\times 3$; *b*, internal mold of dorsal interior, $\times 3$; *c, d*, rubber replicas of dorsal exteriors, $\times 3.3$ (Havlíček, 1977a).

Robertorthis HAVLÍČEK, 1977a, p. 51 [**R. holoubkovensis*; OD].

Similar to *Eoorthis* but coarsely costellate without fila and with transverse, well-developed notothyrial platform. *Lower Ordovician (Tremadoc)*: Bohemia.—FIG. 556,3a, b. **R. holoubkovensis*, Tremadoc, Bohemia; *a*, dorsal interior, $\times 4.9$; *b*, broken ventral interior, $\times 3.1$ (Havlíček, 1977a).

Family EUORTHISINIDAE Havlíček, 1977

[Euorthisinidae HAVLÍČEK, 1977a, p. 293]

Medium size, transversely suboval with variable cardinal extremities, rectimarginate, coarsely costellate, filate plectrothoids; wide delthyrium and notothyrium; strongly apsacline to orthocline ventral and anacline dor-

sal interareas short, curved; simple teeth supported by projecting subparallel to divergent dental plates; platelike bases of rodlike brachiophores converging to form small, posteromedian septalium, cardinal process not developed, muscle and mantle impressions unknown. [*Euorthisina* was first assigned by its author (HAVLÍČEK, 1950, p. 16) to the syntrophiidines. This attribution was rejected by BIERNAT in the first edition of the *Treatise on Invertebrate Paleontology* on the Brachiopoda (1965, p. 523–536) because of the development of wide interareas in *Euorthisina* that also lacked a dorsal fold and ventral sulcus. In 1977, HAVLÍČEK (1977a, p. 293) created a family based on *Euorthisina*, which he assigned to the plectrothoids. The family does, in fact, share features with both the plectrothoids and the syntrophiidines but on balance is best retained within the plectrothoids. *Lower Ordovician (Tremadoc–Llanvirn)*.

Euorthisina HAVLÍČEK, 1950, p. 16 [**Orthisina moesta* BARRANDE, 1879, pl. 57, case I].

Dental plates subparallel; septalium resting on thin dorsal median septum. *Ordovician (Arenig–Llanvirn)*: Europe, northern Africa, Bolivia, southwestern, northwestern, and eastern China.—FIG. 557,1a–c. **E. moesta* (BARRANDE), Llanvirn, Bohemia; *a*, internal mold of ventral valve, $\times 2.4$; *b*, internal mold of dorsal valve, $\times 2.5$; *c*, dorsal view of internal mold of conjoined valves, $\times 1.8$ (Williams, 1974).

Notorthisina HAVLÍČEK & BRANISA, 1980, p. 28 [**N. notoconcha*; OD].

Dental plates divergent; septalium resting on floor of dorsal valve. *Ordovician (Tremadoc)*: Bolivia.—FIG. 557,2a–c. **N. notoconcha*, Tremadoc, Bolivia; *a*, internal mold of dorsal valve, $\times 8.4$; *b*, internal mold of ventral valve, $\times 9.3$; *c*, rubber replicas of exteriors, $\times 7.6$ (Havlíček & Branisa, 1980).

Family FINKELNBURGIIDAE Schuchert & Cooper, 1931

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 54, ex Finkelburgiinae SCHUCHERT & COOPER, 1931, p. 243]

Generally medium size, biconvex, rectimarginate, costellate plectrothoids with an apsacline, short, curved ventral interarea and an anacline, very short dorsal interarea; teeth supported by variably developed dental plates, ventral muscle field subtriangular to suboval impressed on pseudospondylium, adductor track normally wide and elevated

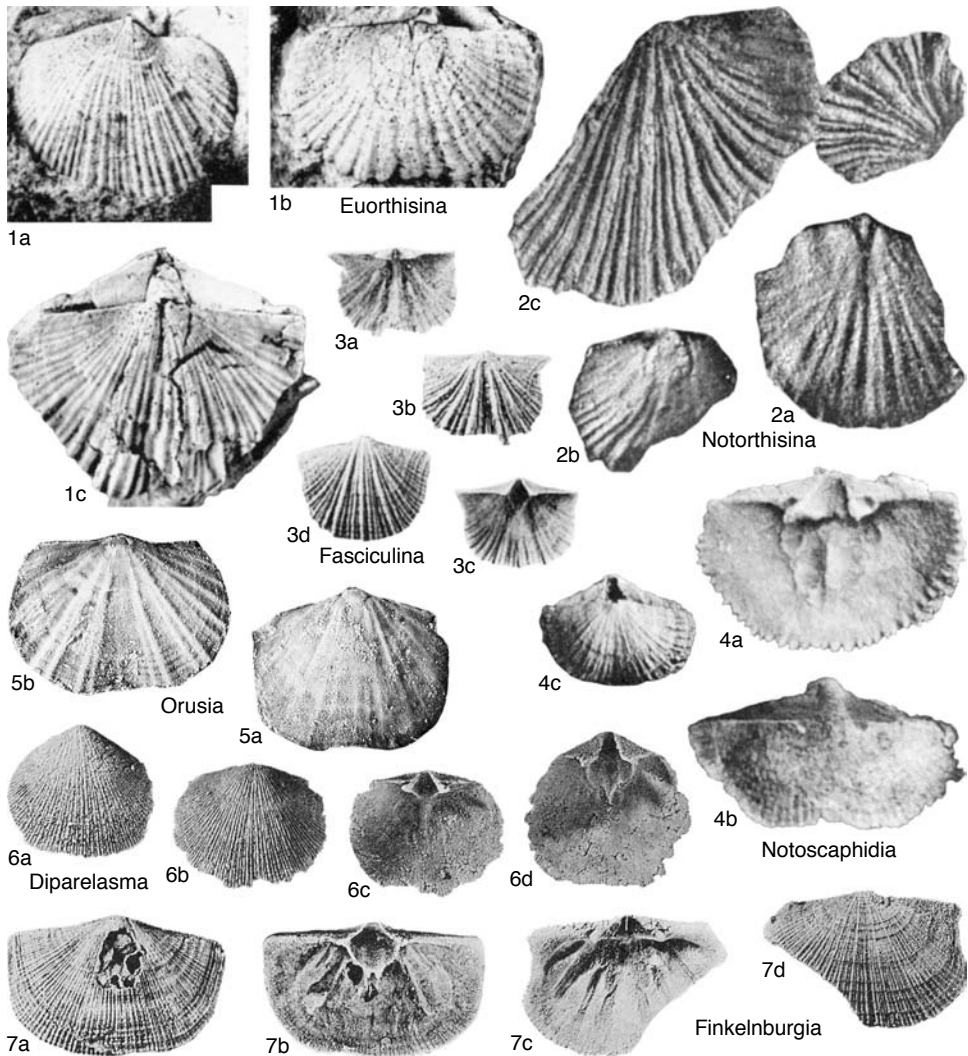


FIG. 557. Euorthisinidae and Finkelnburgiidae (p. 769–771).

and at least as long as flanking diductor scars; notothyrial platform and cardinal process absent or rudimentary; brachiophores variably developed; supported by convergent platelike bases; sockets delineated by small fulcral plates; dorsal median ridge normally developed; quadripartite dorsal adductor scars impressed on low callosities with anterior pair inserted posteromedianly between the posterior pair; mantle canal systems of both valves digitate, variably preserved.

Middle Cambrian–Lower Ordovician (Arenig).

Finkelnburgia WALCOTT, 1905, p. 277 [*F. finkelnburgi*; OD] [= *Marcharella* ANDREEVA, 1968, p. 75 (type, *M. marchensis*)]. Transversely semioval with variably shaped cardinal extremities, multicostellate; dental plates recessive, pseudospondylium prolonged forward as median ridge; brachiophores blunt, divergent, rudimentary cardinal process rarely developed. [*Marcharella* ANDREEVA from the upper Cambrian of the northeastern Siberian Platform differs from *Finkelnburgia* only in its subquadrate outline.] *Upper Cambrian–Lower Or-*

dovician (Tremadoc): Northern Hemisphere.—FIG. 557,7a–d. *F. buttsi*, Upper Cambrian, Virginia; *a, b*, exterior, interior of ventral valve, $\times 2$; *c, d*, interior, exterior of dorsal valve, $\times 2$ (Ulrich & Cooper, 1938).

Diparelasma ULRICH & COOPER, 1936b, p. 623 [*D. typicum*; OD]. Subcircular with obtuse cardinal extremities, finely multicostellate; pedicle callist present; dental plates parallel; cardinal process not developed. *Lower Ordovician (Tremadoc–Arenig)*: North America, Great Britain, eastern and north-eastern China.—FIG. 557,6a–d. **D. typicum*, Arenig, Oklahoma; *a, b*, ventral, dorsal exteriors of conjoined valves, $\times 2$; *c*, dorsal interior, $\times 2$; *d*, ventral interior, $\times 2$ (Ulrich & Cooper, 1938).

Fasciculina COOPER, 1952b, p. 7 [**Orthis desmopleura* MEEK, 1871b, p. 295; OD]. Transversely semioval with mucronate cardinal extremities, unisulcate, fascicostellate; ventral median ridge accentuating pseudospondylium; dorsal median ridge formed by internal crest of sulcus. *Lower Ordovician (Tremadoc–Arenig)*: North America, Scotland.—FIG. 557,3a–d. *F. fasciculata*, Tremadoc, Oklahoma; *a, b*, interior, exterior of dorsal valve, $\times 2$; *c*, ventral interior, $\times 2$; *d*, ventral exterior, $\times 2$ (Cooper, 1952b).

Notoscaphidia WILLIAMS & CURRY, 1985, p. 233 [*N. revelata*; OD]. Small, transversely semioval, variable cardinal extremities, ventribiconvex, unisulcate, coarsely costellate; ventral interarea long, curved. *Lower Ordovician (Arenig)*: Ireland.—FIG. 557,4a–c. **N. revelata*, Arenig, western Ireland; *a*, dorsal interior, $\times 8$; *b*, ventral interior, $\times 8$; *c*, dorsal view of conjoined valves, $\times 4$ (Williams & Curry, 1985).

Orusia WALCOTT, 1905, p. 273 [**Anomites lenticularis* WAHLENBERG, 1821, p. 66; OD]. Small, subcircular with obtuse cardinal extremities, subequally biconvex, gently unisulcate to rectimarginate, coarsely costellate and filate; pseudospondylium weakly developed; dental plates divergent; brachiophores long, sharp, dorsal median ridge rudimentary. *Middle Cambrian–Lower Ordovician (Tremadoc)*: North eastern North America, Baltoscandia, Wales, Argentina, northeastern China.—FIG. 557,5a, b. **O. lenticularis* (WAHLENBERG), Middle Cambrian, Sweden; *a*, partly exfoliated ventral valve, $\times 5$; *b*, partly exfoliated dorsal valve, $\times 5$ (Williams, 1965b).

Family GIRALDIELLIDAE new family

[Giraldiellidae WILLIAMS & HARPER, herein]

Costellate plectorthoids, commonly medium size, unisulcate and subcircular to subquadrate with obtuse cardinal extremities; ventral muscle field normally small, triangular to subpentagonal, with wide, triangular, poorly differentiated adductor track flanked by short diductor scars, pedicle

callist not always deeply impressed; cardinalia small, commonly delicate with concave fulcral plates, narrowly divergent brachiophores supported by converging plates to form notothyrial chamber or septalium, cardinal process normally simple and bladelikey, notothyrial platform not developed; mantle canal systems rarely impressed, ventral probably saccate, dorsal tending to be lemniscate; aditicles not reported. *Lower Ordovician (Arenig)–upper Silurian (Ludlow)*.

Giraldiella BANCROFT, 1949, p. 5 [**Orthis protensa* J. DE C. SOWERBY, 1839, p. 638; OD]. Transversely semioval with variable cardinal extremities, dorsibiconvex, multicostellate, filate; short, planar interareas; dental plates parallel to narrowly divergent. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery)*: Wales, Sweden, central Asia (Altai Mountains, Altai Syan, Tyan Shan).—FIG. 558,3a–c. **G. protensa* (SOWERBY), Llandovery, Wales; *a*, internal mold of ventral valve, $\times 2$; *b*, rubber replica of dorsal interior, $\times 2$; *c*, rubber replica of dorsal exterior, $\times 2$ (Williams, 1965b).

Comatopoma HAVLÍČEK, 1950, p. 54 [**C. barrandei*; OD]. Large, subcircular, ventribiconvex, multicostellate; ventral interarea short, curved; dorsal vestigial; ventral muscle scar umbonal with broadly triangular adductor track; brachiophore plates subparallel, dorsal median septum not developed. *Upper Ordovician (Ashgill)*: Bohemia, northern Africa.—FIG. 558,2a–e. **C. barrandei*, Ashgill, Bohemia; *a–c*, ventral, dorsal, anterior views of conjoined valves, $\times 2$; *d*, internal mold of ventral valve, $\times 3.4$; *e*, internal mold of dorsal valve, $\times 3$ (Havlíček, 1977a).

Famatinothia LEVY & NULLO, 1973, p. 146 [**F. turneri*; OD]. Large, subcircular, dorsibiconvex to convexoplane, multicostellate, ventral interarea relatively long and curved; dental plates divergent, ventral muscle scar suboval, impressed on callist with widely triangular adductor track; simple, bladelikey cardinal process. *Lower Ordovician (Arenig)*: Argentina, northeastern China, eastern North America.—FIG. 558,1a–d. **F. turneri*, Arenig, Argentina; *a*, internal mold of ventral valve, $\times 1.5$; *b*, internal mold of dorsal valve, $\times 2$; *c*, rubber replica of dorsal interior, $\times 3.5$; *d*, rubber replica of dorsal exterior, $\times 1.5$ (Benedetto, 1994).

Gelidorthina HAVLÍČEK, 1974, p. 168 [**O. sanctoivanensis* BARRANDE, 1879, pl. 66, case I; OD]. Medium size, subcircular, strongly biconvex, rectimarginate, multicostellate, interareas relatively short, planar; ventral muscle field small, limited to delthyrial cavity with broadly triangular adductor track impressed on low callosity; simple, bladelikey cardinal process; ventral mantle canal system probably saccate with subparallel *vascula media*. *lower Silurian (Llandovery)–upper Silurian (Ludlow)*: Bohemia.—FIG. 558,4a–c. **G. sanctoivanensis* (BARRANDE),

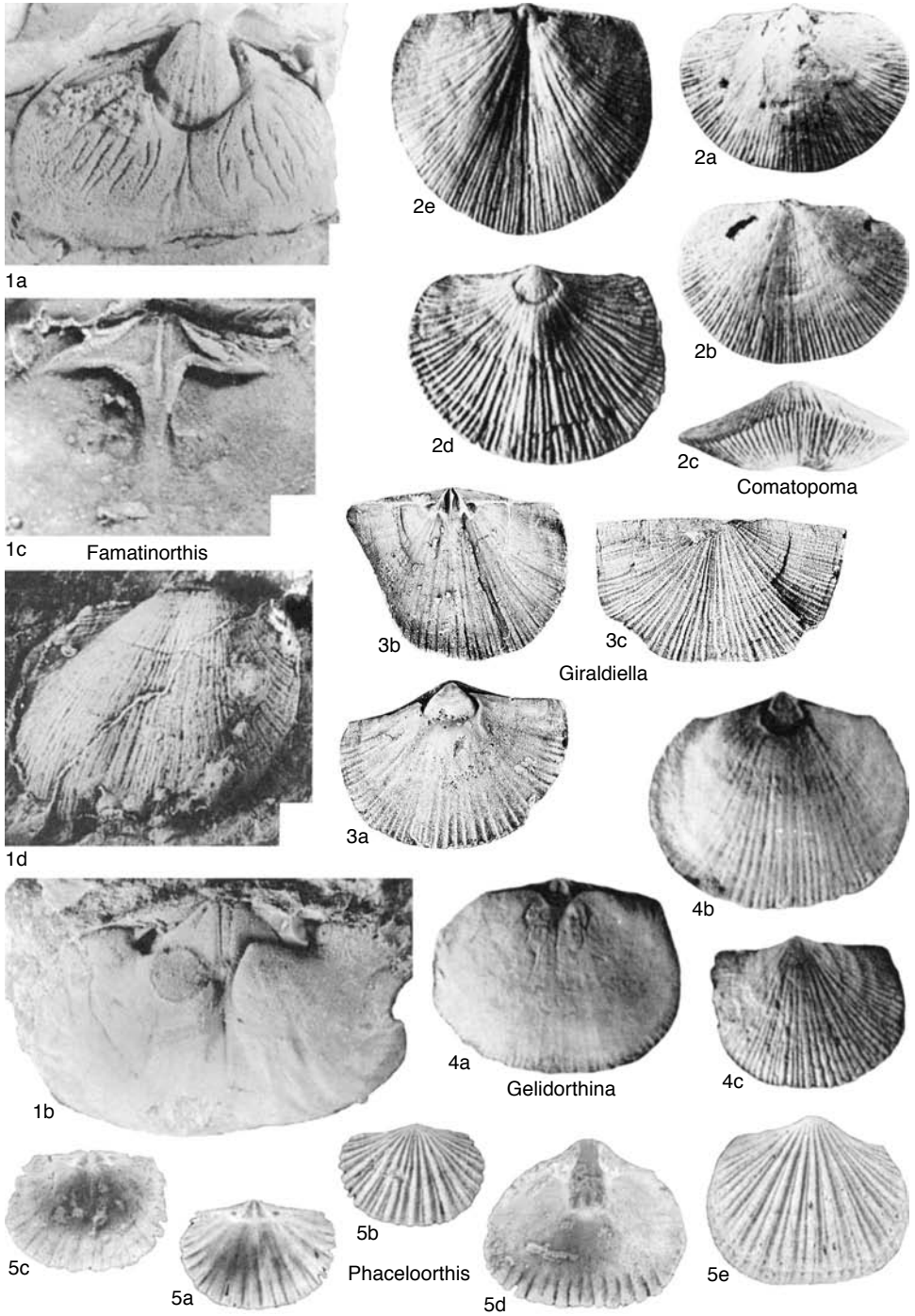


FIG. 558. Giraldiellidae (p. 771–774).

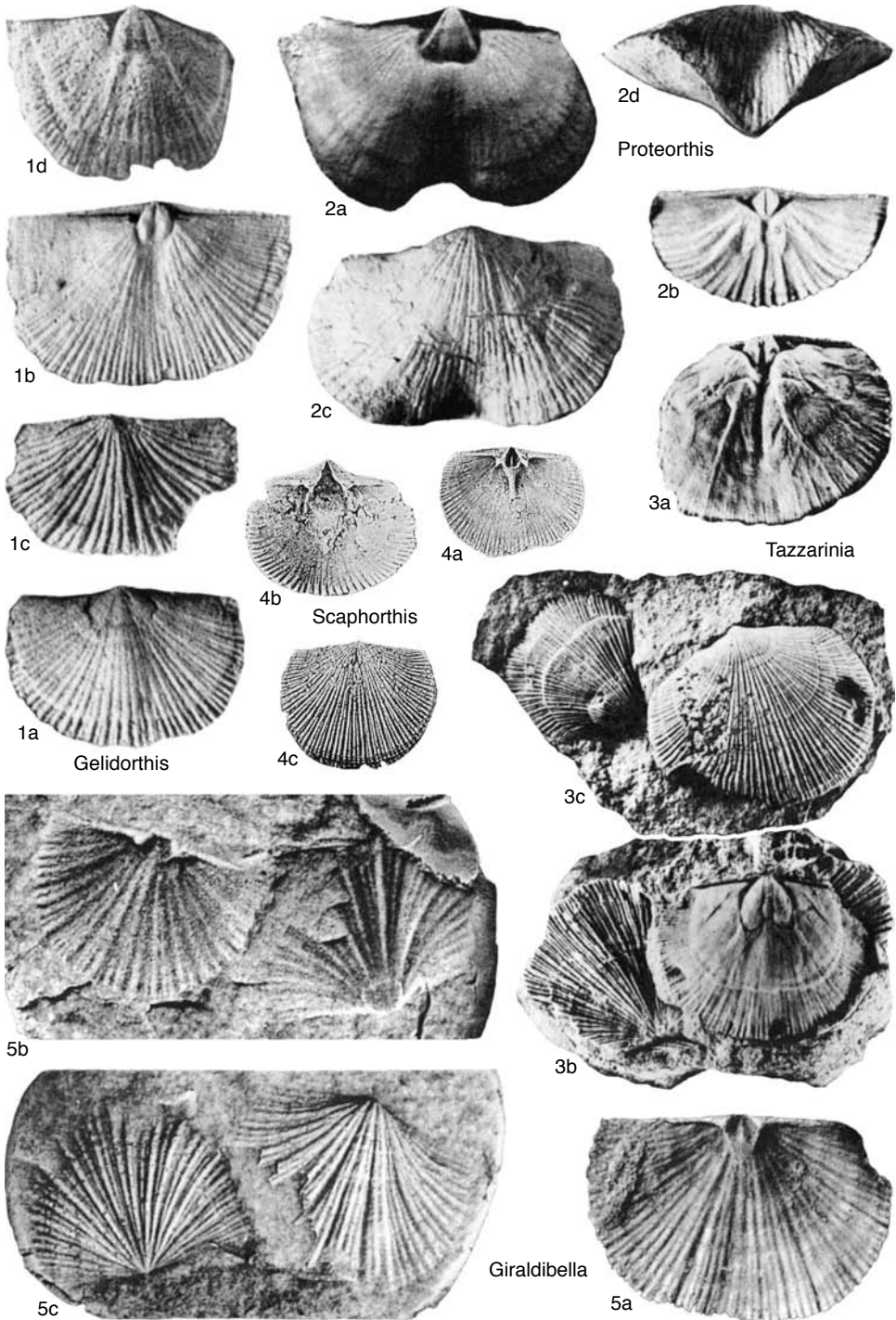


FIG. 559. Giraldiellidae (p. 774).

Wenlock, Bohemia; *a*, internal mold of dorsal valve, $\times 3$; *b*, internal mold of ventral valve, $\times 3$; *c*, ventral exterior, $\times 3$ (Havlíček, 1974).

Gelidorthis HAVLÍČEK, 1968, p. 125 [**Orthis partita* BARRANDE, 1879, pl. 63, case II; OD]. Medium size, subquadrate with acute cardinal extremities, unisulcate, ventribiconvex, ramicostellate; ventral interarea short, planar, dorsal interarea vestigial; ventral muscle scar subpentagonal with broadly triangular adductor track and pair of low median ridges, pedicle callist well developed; adult cardinal process ridgelike with raised bilobate myophore; ventral mantle canal system probably saccate with divergent *vascula media*. *Upper Ordovician (Caradoc)*: Europe, northern Africa.—FIG. 559, 1*a–d*. **G. partita* (BARRANDE), Caradoc, Bohemia; *a*, internal mold of ventral valve, $\times 2.9$; *b*, internal mold of dorsal valve, $\times 3.1$; *c*, rubber replica of ventral exterior, $\times 4.2$ (Havlíček, 1977a); *d*, internal mold of ventral valve, $\times 3.3$ (Havlíček, 1968).

Giraldibella HAVLÍČEK, 1977a, p. 87 [**Giraldiella bella* BERGSTRÖM, 1968, p. 8; OD]. Similar to *Gelidorthis* but fascicostellate with obtuse cardinal extremities, short planar dorsal interarea, proportionately smaller ventral muscle scar, and simple, bladelike cardinal process. *Upper Ordovician (Ashgill)—middle Silurian (Wenlock)*: Europe, Kazakhstan, Siberia, northeastern China, central Asia (Altai Mountains).—FIG. 559, 5*a–c*. **G. bella* (BERGSTRÖM), Ashgill, Sweden; *a*, rubber replica of dorsal interior, $\times 3$; *b, c*, rubber replicas of two ventral interiors and exteriors, $\times 3$ (Bergström, 1968).

Phaceloorthis PERCIVAL, 1991, p. 129 [**P. decoris*; OD] [= *Boonderella* PERCIVAL, 1991, p. 130 (type, *B. fasciculata*)]. Transversely subquadrate, ventribiconvex, unisulcate, fascicostellate, filate; ventral interarea short, curved dorsal interarea very short, planar, orthocline; ventral muscle scar quadrate suboval with broad adductor track slightly elevated anteriorly; cardinal process differentiated into thickened shaft and crenulated myophore, sockets rounded; mantle canal systems in both valves probably saccate with subparallel *vascula media*. [*Boonderella* is based on three silicified valves, each from a different locality, which have been distinguished from penecontemporaneous *Phaceloorthis* shells only in having a ridgelike cardinal process and a more elevated ventral muscle field. Immature *Phaceloorthis*, however, have ridgelike cardinal processes, and the shell thickening is variable, judging from illustration. *Phaceloorthis* is only provisionally assigned to the Giraldiellidae as it is cladistically more closely related to the stem group of both the Giraldiellidae and Plectorthidae.] *Upper Ordovician (Caradoc)*: Australia (New South Wales).—FIG. 558, 5*a–e*. **P. decoris*, Caradoc, New South Wales; *a, b*, interior, exterior of dorsal valve, $\times 2$; *c*, dorsal interior, $\times 2$; *d*, ventral interior, $\times 2$; *e*, ventral exterior, $\times 2$ (Percival, 1991).

Proteorthis HAVLÍČEK, 1974, p. 168 [**Orthis tardissima* BARRANDE, 1879, pl. 108, case VI; OD]. Large, transversely subquadrate, dorsibiconvex, strongly

uniplicate, coarsely costellate, filate; apsacline ventral and orthocline dorsal interareas short, curved; ventral muscle field impressed on callus; cardinal process simple, bladelike; anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral mantle canal system pinnate. *middle Silurian (Wenlock)*: Bohemia.—FIG. 559, 2*a–d*. **P. tardissima* (BARRANDE), Wenlock, Bohemia; *a*, internal mold of ventral valve, $\times 3.4$; *b*, posterodorsal view of internal mold of dorsal valve, $\times 1.7$; *c, d*, ventral, anterior views of conjoined pair, $\times 1.7$ (Havlíček, 1977a).

Scaphorthis COOPER, 1956, p. 502 [**S. virginiensis*; OD]. Subcircular, ventribiconvex, rectimarginate to unisulcate, multicostellate; interareas relatively short, curved; ventral muscle scar subcordate with wide, triangular adductor track impressed on low callosity anteriorly; cardinal process with narrow shaft and thin, bladelike myophore; anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral and dorsal muscle canal systems saccate with parallel *vascula media* and lemniscate respectively. *Upper Ordovician (Caradoc–Ashgill)*: North America, Scotland, Ireland, Australia (New South Wales), central Asia, Kazakhstan.—FIG. 559, 4*a–c*. **S. virginiensis*, Caradoc, Virginia; *a*, dorsal interior, $\times 2$; *b*, ventral interior, $\times 2$; *c*, ventral exterior, $\times 2$ (Cooper, 1956).

Tazzarinia HAVLÍČEK, 1971a, p. 39 [**T. drotae*; OD]. Subquadrate, ventribiconvex, unisulcate, multicostellate, filate; ventral interarea short, planar, dorsal vestigial; ventral muscle scar short, bilobed with wide adductor track, pedicle callist well developed; cardinal process differentiated into thick shaft and bilobed myophore; quadripartite adductor muscle scars subequal; ventral and dorsal mantle canal systems saccate (with divergent *vascula media*) and lemniscate respectively. *Upper Ordovician (Caradoc)*: northern Africa, England, Bohemia.—FIG. 559, 3*a–c*. **T. drotae*, Caradoc, Morocco; *a*, internal mold of dorsal valve, $\times 2$; *b*, internal mold of ventral valve, $\times 1.9$; *c*, rubber replicas of two ventral exteriors, $\times 1.9$ (Havlíček, 1971a).

Family PHRAGMORTHIDAE Williams, 1965

[*nom. transl.* WILLIAMS & HARPER, herein, ex Phragmorthinae WILLIAMS, 1965b, p. 327]

Multicostellate, delthyrial and notothyrial openings narrow: apsacline ventral interarea long, curved, anacline dorsal interarea, short, curved; simple teeth supported by recessive dental plates uniting with thickened anterior boundary to short suboval ventral muscle field; pedicle callist not reported; brachio-phores long with supporting plates converging posteromedianly onto median septum to form septalium containing low, ridgelike car-

dinal process; socket plates normally encased in secondary shell and defining deep sockets; dorsal muscle field quadripartite with anterior pair of scars larger than posterior; ventral mantle canal system saccate with convergent *vascula media*. *Upper Ordovician (Caradoc–Ashgill)*.

Phragmorthis COOPER, 1956, p. 508 [**P. buttsi*; OD]. Subquadrate, unisulcate, costellae sporadically swollen. *Upper Ordovician (Caradoc–Ashgill)*: North America, Scotland, Kazakhstan, Ireland, Argentina, southwestern China. —FIG. 560*a–f*. **P. buttsi*, Caradoc, Virginia; *a–c*, ventral, dorsal, posterior views of conjoined valves, $\times 2$; *d, e*, normal, tilted views of dorsal interior, $\times 4$; *f*, ventral interior, $\times 4$ (Cooper, 1956).

Family PLATYSTROPHIIDAE Schuchert & LeVene, 1929

[*nom. transl.* WILLIAMS & HARPER, herein, ex Platystrophiinae SCHUCHERT & LEVENE, 1929, p. 14]

Transversely subquadrate to semioval, dorsibiconvex, normally strongly uniplicate, medium-sized plectorthooids; interareas proportionately long and curved; teeth normally with crural fossettes supported by subparallel dental plates flanking poorly differentiated, elongately oval ventral muscle scar with broad adductor track impressed on thick callist, pedicle callist rarely preserved; divergent, bladelike brachiophores joined to hinge line by concave fulcral plates and supported by plates converging posteromedianly to form small septalium, cardinal process bladelike; scars of quadripartite dorsal adductor field variable in size, bisected by median ridge, mantle canal systems rarely impressed. *Lower Ordovician (Arenig)–middle Silurian (Wenlock)*.

Platystrophia KING, 1850, p. 106 [**Terebratulites biforatus* VON SCHLOTHEIM, 1820, p. 265; OD]. Normally large, spiriferoid in outline with acute to mucronate cardinal extremities, strongly biconvex, costate and finely granulose, variably lamellose, ventral beak commonly resorbed with apical foramen; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system digitate. *Lower Ordovician (Arenig)–middle Silurian (Wenlock)*: cosmopolitan. —FIG. 561, *1a*. **P. biforata*, Caradoc, Cincinnati; dorsal exterior, $\times 2$ (Cocks, new). —FIG. 561, *1b–e*. *P. ponderosa* FOERSTE, Ashgill, eastern North America; ventral, dorsal, posterior, anterior views of conjoined valves,

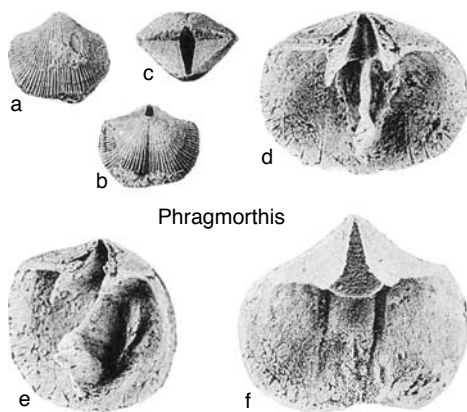


FIG. 560. Phragmorthidae (p. 775).

$\times 1$ (Shimer & Shrock, 1944). —FIG. 561, *1f, g*. *P. laticosta* (MEEK), Ashgill, Ohio; *f*, ventral interior, $\times 1.5$; *g*, dorsal interior, $\times 1.5$ (Schuchert & Cooper, 1932).

Acanthorthis NEUMAN, 1976, p. 22 [**A. terreneuvensis*; OD]. Subquadrate with obtuse cardinal extremities, multicostellate with spinose lamellae; simple teeth supported by divergent dental plates; brachiophores rodlike; widely divergent; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Lower Ordovician (Arenig)*: eastern Canada. —FIG. 561, *3a–c*. **A. terreneuvensis*, Arenig, central Newfoundland; *a*, internal mold of dorsal valve, $\times 1.5$; *b*, internal mold of ventral valve, $\times 1.5$; *c*, external mold of ventral valve, $\times 1.5$ (Neuman, 1976).

Ffynnionia NEUMAN & BATES, 1978, p. 592 [**Pleurorthis costatus* BATES, 1968, p. 149; OD]. Subquadrate with acute cardinal extremities, coarsely costellate; curved interareas relatively short; dental plates recessive; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Lower Ordovician (Arenig–Llanvirn)*: Wales, Ireland. —FIG. 562, *1a–e*. **F. costatus* (BATES), Llanvirn, Anglesey; *a, b*, internal mold, rubber replica of dorsal valve, $\times 2$; *c, d*, internal mold, rubber replica of ventral valve, $\times 2$; *e*, rubber replica of ventral exterior, $\times 2$ (Neuman & Bates, 1978).

McEwanella FOERSTE, 1920, p. 197 [**Platystrophia fernvalensis* MCEWAN, 1919, p. 428; OD; =*Hebertella lineolata* SAVAGE, 1917, p. 267]. Similar to *Platystrophia* but with a fine costellate ornamentation commonly superimposed on coarsely costate arrangement of *Platystrophia*. *Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill)*: USA, Great Britain, Ireland, Norway, central Asia (Altai, Kunlun, and Altai Mountains), Spain, France, northwestern China. —FIG. 561, *2a, b*. **M. lineolata* (SAVAGE), Ashgill, Missouri; *a*, ventral interior, $\times 1$; *b*, ventral exterior, $\times 1$ (McEwan, 1919). —FIG. 561, *2c–f*. *M. raymondi* FOERSTE, Ashgill, Missouri; *c*, ventral exterior, $\times 1$; *d*, dorsal view of con-

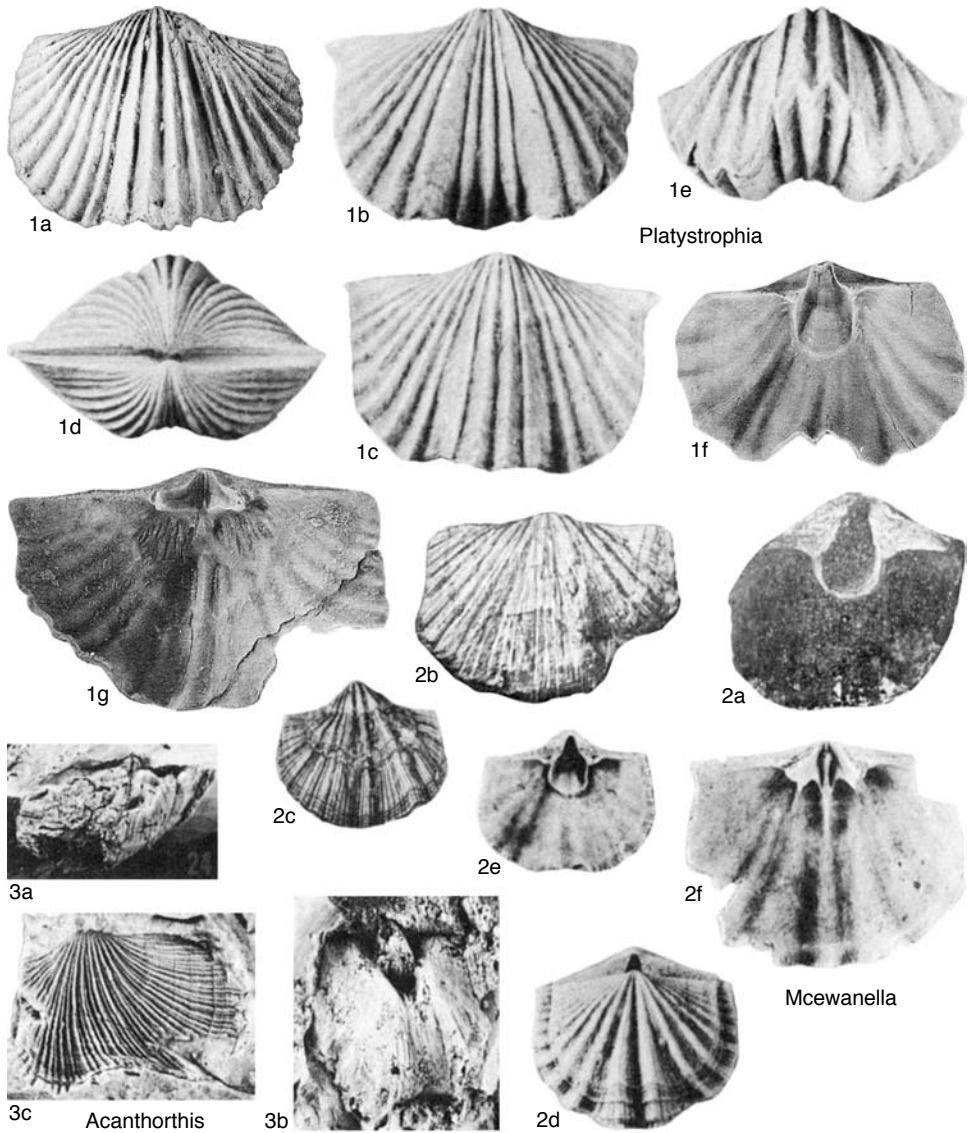


FIG. 561. Platystrophiidae (p. 775-776).

joined valves, $\times 2$; *e*, ventral interior, $\times 1$; *f*, dorsal interior, $\times 2$ (Shimer & Shrock, 1944).

Salacorthis WILLIAMS, 1974, p. 79 [*S. costellata*; OD].

Subquadrate with obtuse cardinal extremities, costate to sporadically costellate with densely distributed, coarse exopunctae quincuncially arranged; ventral muscle scar impressed directly on valve floor, pedicle callist well developed; dorsal adductor scars subequal. *Upper Ordovician (Caradoc–Ashgill)*: England, Wales.—FIG. 562, 2a–e. **S. costellata*, Caradoc, Shelve; *a*, internal mold of dorsal valve, $\times 7.6$; *b*, rubber replica of dorsal valve, $\times 4.9$; *c*, external mold of dorsal valve, $\times 7.6$; *d*, internal mold

of ventral valve, $\times 3.1$; *e*, rubber replica of partial dorsal exterior (Williams, 1974).

Family RANORTHIDAE Havlíček, 1949

[Ranorthidae HAVLÍČEK, 1949b, p. 252]

Unisulcate, ramicostellate plectrothoids with apsacline ventral interarea short, curved, shorter anacline dorsal interarea more variable; deltidiodont teeth supported by recessive dental plates, ventral muscle field suboval with broad, subtriangular adductor

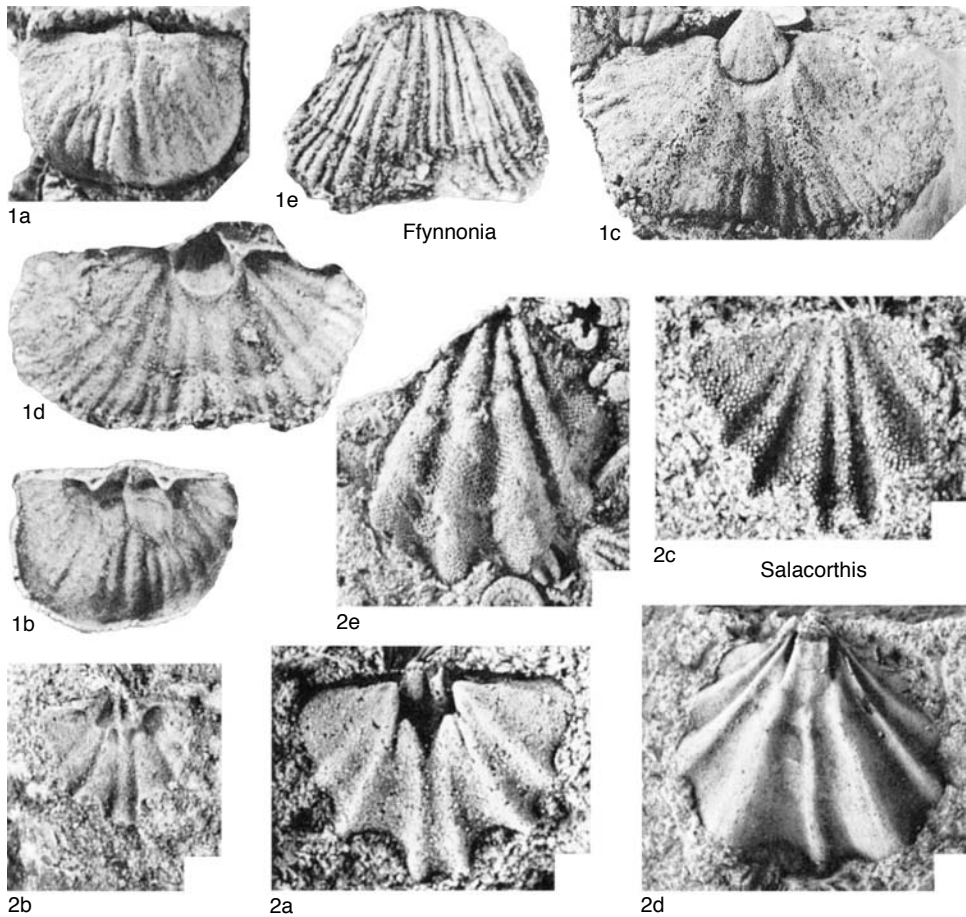


FIG. 562. Platystrophiidae (p. 775–776).

track as long as flanking diductor scars; notothyrial platform usually well developed, prolonged anteriorly as median ridge; cardinal process variable, divergent brachiophores bladelike, lacking supporting plates but joined to hinge line by fulcral plates; narrowly diverging *vascula myaria* forming oblique boundaries separating posterior pair of quadripartite dorsal adductor field from larger anterior pair; ventral mantle canal system saccate with divergent *vascula media*, sporadically impressed dorsal system digitate. *Lower Ordovician (Tremadoc–Arenig)*.

Ranorthis ÖPIK, 1939, p. 119 [**R. norvegica*; OD]. Small, subcarinate, elongately semioval with rectangular to obtuse cardinal extremities, dorsal interarea curved, cardinal process rudimentary to ridgelike.

Lower Ordovician (Tremadoc–Arenig): Europe, northern Africa.—FIG. 563, 1a–d. **R. norvegica*, Arenig, Oslo Region; a, internal mold of dorsal valve, $\times 3.8$; b, internal mold of ventral valve, $\times 8.2$; c, ventral exterior, $\times 3.8$; d, external mold of dorsal valve, $\times 3.8$ (Öpik, 1939).

Eodalmanella HAVLÍČEK, 1950, p. 24 [**Orthis socialis* BARRANDE, 1879, p. 63]. Medium sized, elongately subquadrate with variable cardinal extremities, dorsal interarea planar, cardinal process differentiated into shaft and bilobed myophore. *Lower Ordovician (Llanvirn)*: Bohemia, eastern North America, Kazakhstan, central Asia (Altai Mountains).—FIG. 563, 2a–e. **E. socialis* (BARRANDE), Llanvirn, Bohemia; a, internal mold of ventral valve, $\times 4.9$; b, c, internal molds of dorsal valves, $\times 3$; d, rubber replica of ventral exterior, $\times 5.2$; e, rubber replica of dorsal exterior, $\times 4.1$ (Havlíček, 1977a).

Nothorthis ULRICH & COOPER, 1938, p. 106 [**N. delicatula*; OD] [= *Althorthis* ANDREEVA, 1960, p. 288 (type, *A. kindertensis*)]. Transversely semioval with

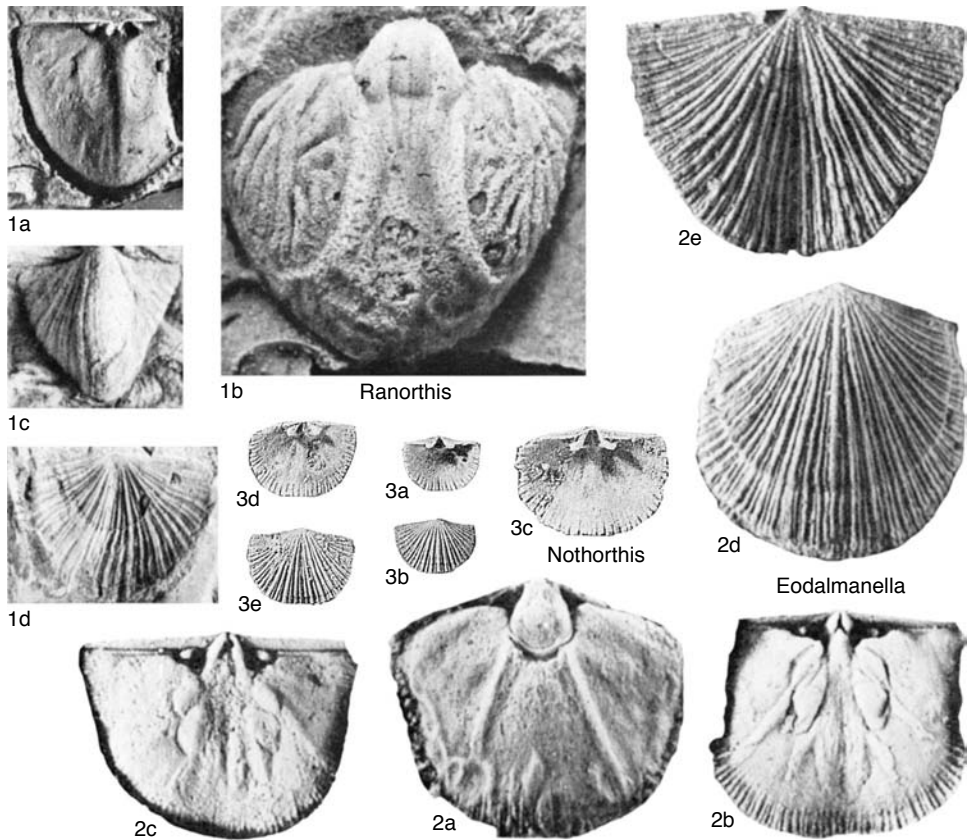


FIG. 563. Ranorthidae (p. 777–778).

obtuse cardinal extremities, ramicostellate; suboval ventral muscle scar impressed on callosity; short, rodlike, divergent brachiophores, notothyrial platform rudimentary, cardinal process absent or rudimentary. *Lower Ordovician (Tremadoc–Llanvirn)*: eastern North America, Baltic, Siberia, Scotland, Bohemia, eastern China, central Asia (Altai Mountains).—FIG. 563, 3a–e. **N. delicatula*, Tremadoc, Quebec; a, b, interior, exterior of ventral valve, $\times 3$; c, dorsal interior, $\times 4.5$; d, e, interior, exterior of dorsal valve, $\times 3$ (Cooper, 1956). [Note added in proof: with fulcral plates; see Fig. 563, 3c.]

Family RHACTORTHIDAE Williams, 1963

[*nom. transl.* WILLIAMS & HARPER, herein, ex Rhactorthinae WILLIAMS, 1963, p. 371]

Medium size, ventribiconvex plectorthoids normally subquadrate with obtuse cardinal extremities, costellate with aditicules; interareas normally planar; ventral muscle field subtriangular to weakly bilobed with wide, triangular, poorly differentiated adduc-

tor track normally impressed on elevated median callus; brachiophores widely divergent without basal plates, supported by concave fulcral plates joined to hinge line and defining elongate sockets; cardinal process well differentiated into shaft and myophore; quadripartite dorsal adductor scars indistinct. *Upper Ordovician (Caradoc–Ashgill)*.

Rhactorthis WILLIAMS, 1963, p. 371 [**R. crassa*; OD].

Sharply unisulcate, multicostellate, interareas proportionately long; dental plates recessive, ventral adductor track not much elevated, pedicle callist well developed; brachiophores rodlike, cardinal process thickened with crenulated myophore, continuous with median ridge; ventral mantle canal system possibly saccate with subparallel *vascula media*, dorsal system also possibly saccate but with divergent *vascula media*. *Upper Ordovician (Caradoc–Ashgill)*: Great Britain, Ireland, Estonia, Norway, Bohemia.—FIG. 564, 2a–d. **R. crassa*, Caradoc, Wales; a, internal mold of dorsal valve, $\times 6.6$; b, internal mold of ventral valve, $\times 3.5$; c, rubber replica

of ventral exterior, $\times 3.1$; *d*, rubber replica of dorsal exterior, $\times 3.2$ (Williams, 1963).

Aberia MÉLOU, 1990, p. 549 [**A. havliceki*; OD].

Subcircular, rectimarginate, ramicostellate, interareas planar, relatively long; ventral muscle scar weakly bilobed; cardinal process thickened with bilobed myophore; dorsal median ridge vestigial. *Upper Ordovician (Ashgill)*: France.—FIG. 564, 1a–d. **A. havliceki*, Ashgill, Brittany; *a*, rubber replica of dorsal interior, $\times 2$; *b*, rubber replica of ventral interior, $\times 2$; *c*, internal mold of ventral valve, $\times 2$; *d*, rubber replica of dorsal exterior, $\times 2$ (Mélou, 1990).

Eripanifera POTTER, 1990a, p. 108 [**E. praecipitis*; OD].

Strongly unisulcate, fascicostellate (aditicles not observed), interareas proportionately long, curved; ventral muscle scar subtriangular with anteromedian elevated callus; brachiophores bladellike, supported by fulcral plates and subparallel ancillary struts that are not typical brachiophore plates; cardinal process rodlike, continuous with the median ridge and with bulbous myophore, flanked by low notothyrial thickenings in some valves; quadripartite dorsal adductor field petaloid, bounded by ridge and divided into posterior and anterior components by narrowly divergent *vascula myaria*; mantle canal systems in both valves digitate. *Upper Ordovician (Ashgill)*: USA (California, Alaska).—FIG. 564, 3a–e. **E. praecipitis*, Ashgill, California; *a, b*, interior, exterior of ventral valve, $\times 2$; *c, d*, interior, exterior of dorsal valve, $\times 3.5$; *e*, dorsal interior, $\times 4$ (Potter, 1990a).

Family TASMANORTHIDAE Laurie, 1991

[*nom. transl.* WILLIAMS & HARPER, herein, ex Tasmanorthinae LAURIE, 1991, p. 41]

Subequally biconvex, rectimarginate, costate to coarsely costellate, capillate, pustulose plectorthooids; interareas relatively long, curved; simple teeth supported by divergent dental plates, ventral muscle scar elongately quadrate, adductor track broad, triangular, divided by low median ridge; cardinal process differentiated into short shaft and bilobed myophore; brachiophores bladellike with divergent bases, fulcral plates variably developed, defining elongate sockets; notothyrial platform vestigial, dorsal median ridge low; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system probably saccate with divergent *vascula media*, dorsal system unknown. *Upper Ordovician (Caradoc)*.

Tasmanorthis LAURIE, 1991, p. 41 [**T. costata*; OD].

Medium size, subquadrate with obtuse cardinal extremities. *Upper Ordovician (Caradoc)*: Australia (Tasmania).—FIG. 565, 1a–f. **T. costata*, Caradoc,

Tasmania; *a–c*, interior, exterior, posterior view of ventral valve, $\times 2$; *d, e*, interior, exterior of dorsal valve, $\times 2$; *f*, details of ornament, $\times 8$ (Laurie, 1991).

Family WANGYUIDAE Zhang, 1989

[Wangyuidae ZHANG, 1989a, p. 58] [=Sigmelasmidae POTTER, 1990b, p. 23]

Subquadrate to transversely semioval with variable cardinal extremities, ventribiconvex with ventral valve commonly subpyramidal, unisulcate, costellate plectorthooids; delthyrium and notothyrium open, narrow; apsacline ventral interarea long, curved, anacline dorsal interarea short, curved; teeth with recessive dental plates, ventral muscle field subtriangular to bilobate with elongate adductor scars commonly elevated on median ridge; brachiophores long, narrowly divergent with plates S-shaped in section, free of valve floor except posteromedianly, fulcral plates variably developed; cardinal process simple ridge, rarely with bilobed myophore; dorsal median partition ridgelike or absent, dorsal muscle field and mantle canal systems indistinctly impressed. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock)*.

Wangyuia ZHANG, 1989a, p. 58 [**W. thorsteinssoni*; OD].

Transversely semioval with variable cardinal extremities, coarsely costellate, weakly lamellose; subpyramidal ventral interarea steeply apsacline to procline; ventral muscle field bilobed, cardinal process rodlike, occasionally capped with bilobed myophore; dorsal adductor field elongately quadripartite with anterior pair of scars larger than posterior pair, dorsal median ridge low. *middle Silurian (Wenlock)*: Arctic Canada.—FIG. 565, 4a–e. **W. thorsteinssoni*, Wenlock, Arctic Canada; *a, b*, interior, exterior of ventral valve, $\times 8$; *c, d*, interior, exterior of dorsal valve, $\times 8$; *e*, interior of dorsal valve, $\times 8$ (Zhang, 1989a).

Bowanorthis PERCIVAL, 1991, p. 123 [**B. fragilis*; OD].

Subquadrate, delthyrium with apical plate; catacline ventral interarea long, curved, anacline to catacline dorsal interarea shorter, planar; vestigial notothyrial platform continuous with long dorsal median ridge; dorsal adductor field sills equally quadripartite; ventral mantle canal system probably saccate with subparallel *vascula media*. *Upper Ordovician (Caradoc)*: Australia (New South Wales).—FIG. 565, 5a–f. **B. fragilis*, Caradoc, New South Wales; *a–c*, dorsal, posterior, anterior views of conjoined valves, $\times 5$; *d, e*, interior, exterior of dorsal valve, $\times 5$; *f*, ventral interior, $\times 5$ (Percival, 1991).

Sigmelasma POTTER, 1990b, p. 23 [**S. pantherae*; OD].

Subquadrate, strongly apsacline ventral interarea planar, of variable length, anacline dorsal interarea shorter; notothyrial platform and dorsal median

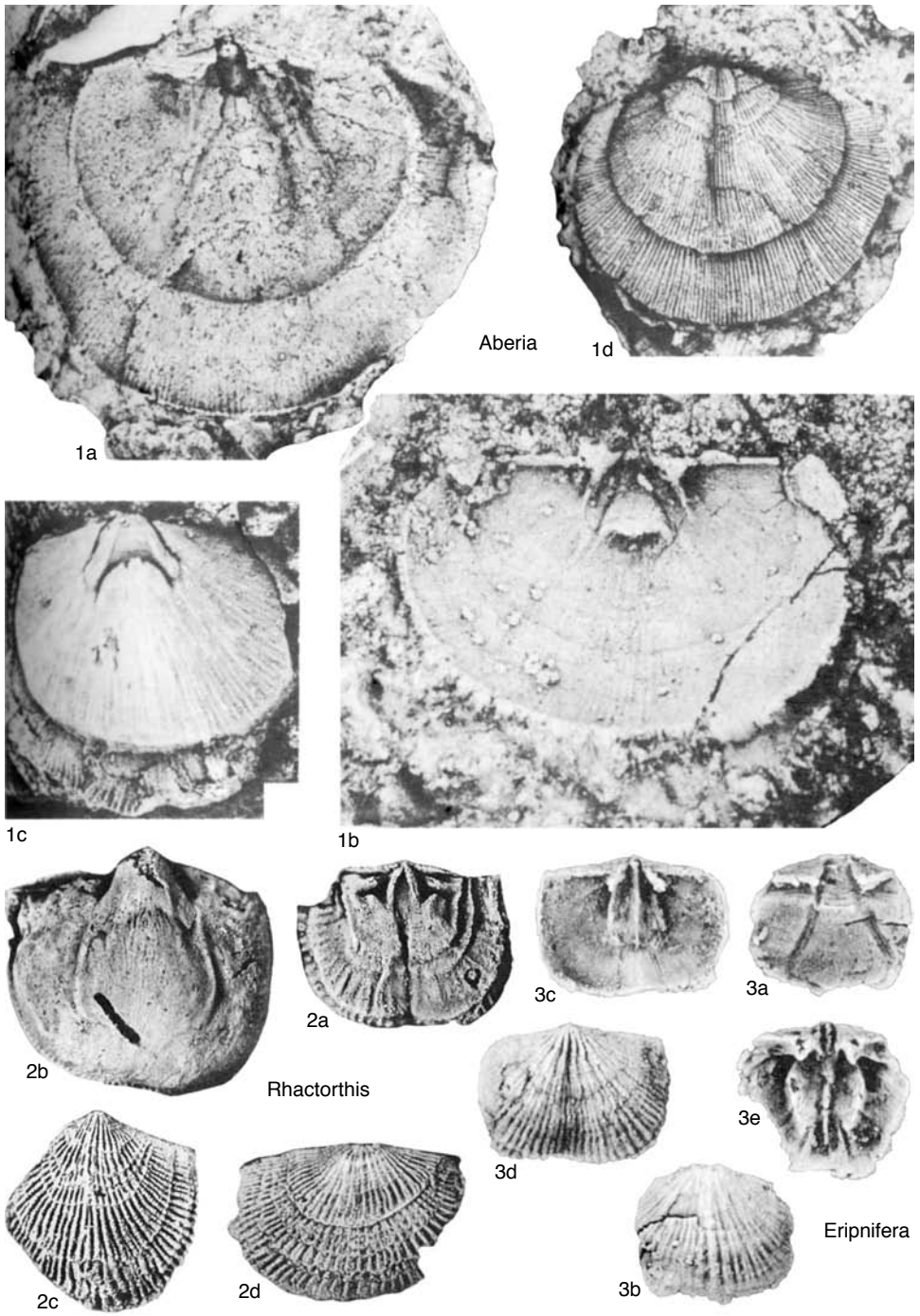


FIG. 564. Rhactorthidae (p. 778–779).

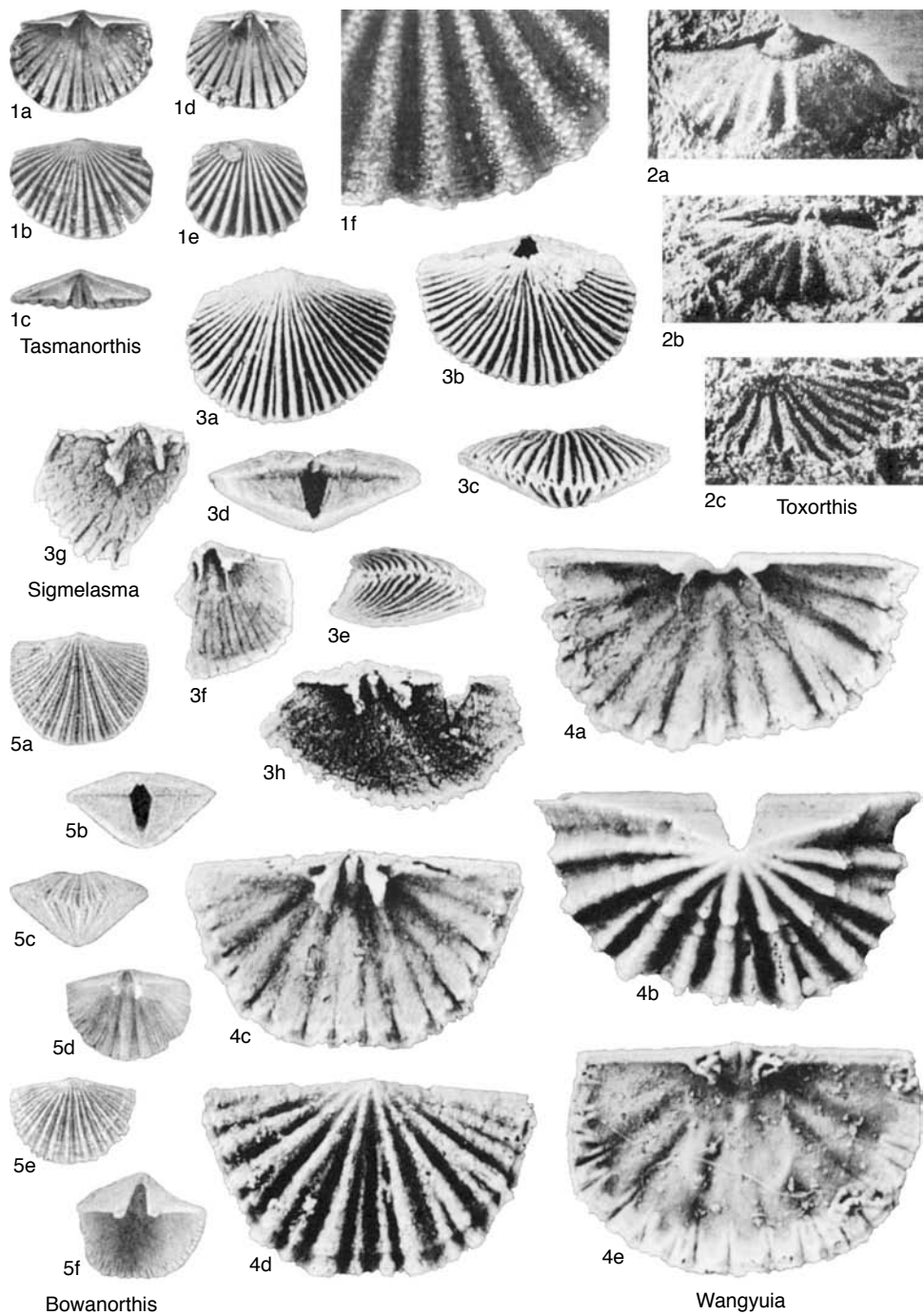


FIG. 565. Tasmanorthidae and Wangyuiidae (p. 779–782).

septum absent. *Upper Ordovician (Caradoc)*: western United States.—FIG. 565,3a–b. **S. pantherae*, Caradoc, California; a–e, ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×6; f, broken ventral interior, ×6; g, broken dorsal interior, ×6; h, dorsal interior, ×6 (Potter, 1990b).

Toxorthis TEMPLE, 1968, p. 20 [**T. proteus*; OD]. Transversely semioval with acute cardinal extremities, strongly unisulcate, coarsely costellate; interareas relatively short; teeth usually as elongate ridges, ventral muscle field subtriangular, undifferentiated; cardinal process absent, simple or as a low, bilobed myophore; platelike brachiophores supported at ends of elongate fulcral plates. [The family Toxorthidae RONG, 1984 has already been erected for this genus and, in fact, predates the

Wangyuiidae. There is some doubt, however, regarding the relationship between *Toxorthis* and *Wangyuiia*. The most distinctive familial feature of the latter (and *Bowanorthis*) are the large S-curved brachiophores. Only the proximal parts of the brachiophores of *Toxorthis* are known as all species assigned to the genus are based exclusively on molds. If further study confirms brachiophore similarity, then the Wangyuiidae will become a junior synonym of Toxorthidae.] *Upper Ordovician (Ashgill)*: Great Britain, central China (western Hubei).—FIG. 565,2a–c. **T. proteus*, Ashgill, northwestern England; a, internal mold of ventral valve, ×10; b, internal mold of dorsal valve, ×10; c, external mold of dorsal valve, ×10 (Temple, 1968).

DALMANELLIDINA

DAVID A. T. HARPER

[University of Copenhagen]

Suborder DALMANELLIDINA Moore, 1952

[*nom. correct.* HARPER, herein, *pro* Dalmanelloidea MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220; *emend.*, HARPER, herein]

Delthyrium and notothyrium normally open; deltiodont teeth commonly with dental fossettes, supported by variably developed and disposed dental plates; ventral muscle scar normally suboval to cordate and impressed on valve floor, rarely associated with raised structures; cardinalia usually with bilobed, trilobed, or lobate cardinal process and shaft, occasionally modified, rarely simple, ridgelike, or absent, situated on variably developed notothyrial platform; brachiophores as blades, rods, or spikes with convergent or divergent plates onto valve floor, together with fulcral plates, where present, define variably developed sockets; dorsal septa, partitions, and platforms rarely developed, mainly in later taxa; ventral mantle canal system normally lemniscate, rarely saccate; dorsal mantle canal system lemniscate to digitate and pinnate; shell with fibrous secondary layer, punctate (possibly endopunctate). *Lower Ordovician (Arenig)*–*Upper Permian (Tatarian)*.

The punctate orthides were first accorded superfamilial status as the Dalmanellacea by SCHUCHERT and COOPER (1931, p. 245) on the basis of their endopunctate shell structure. The majority of subsequent authors have accepted variants on this term to describe the group. MOORE (in MOORE, LALICKER, & FISCHER, 1952) first raised the taxon to subordinal status. Alternatively, WRIGHT (1965a, p. 328) argued for a single superfamily to contain the punctate orthide genera, to be named the Enteleteacea on grounds of priority (*ex* Enteletinæ WAAGEN, 1884, p. 548; *contra* Dalmanellinae SCHUCHERT, 1913b, p. 382). He recognized, however, that a term associated with the widespread, more generalized, earlier, and probably better-known *Dalmanella* would be more appropriate for the group than one based on the later, aberrant *Enteletes*.

Two superfamilies are recognized cladistically, mainly on the features of the cardinalia. The Dalmanelloidea has a well-developed notothyrial platform, reduced in later taxa, with a cardinal process evolving complex and modified, bilobed, trilobed, and generally lobate morphologies; brachiophores are gen-