costae; beak small, upright, without planareas, foramen hypo- to submesothyrid. Crura short, supported by subparallel crural plates extending to one-third dorsal valve length; dorsal septum absent to vestigial. *Lower Jurassic (?Sinemurian, Pliensbachian)–Upper Jurassic (Kimmeridgian, ?Tithonian):* southern and eastern Europe.——Fig. 827,*3a–m.* **S. sanctaeclarae* (Roemer); *a–e,* dorsal, lateral, anterior, ventral, posterior views, Oxfordian, Jasna Góra, Poland, ×1 (Wisniewska, 1932); *f–m,* transverse serial sections, distances in mm from ventral umbo, 1.4, 2.4, 2.8, 3.3, 3.4, 3.6, 4.5, 5.2, Aiglun, France (Laurin, 1979).

Caucasella Moiseev, 1934, p. 83[187] *non* Hacobjan in Akopyan & others, 1969, Gastropoda, *nec* Longoria, 1974, Foraminiferida [**Rhynchonella trigonella* Rothpletz, 1886, p. 154; OD]. Small, trigonal to securiform, depressed equibiconvex, wide and flat anteriorly; sharply costate, with evenly serrate commissure but no fold or sulcus; beak small, gently incurved, with planareas. Short dental plates, no dorsal median septum, crural plates closely subparallel. *Middle Jurassic (upper Bajocian–Callovian), Upper Jurassic (?Kimmeridgian):* France, Switzerland, Germany, Austria, Italy, Slovakia, Romania, Bulgaria, Ukraine, Yugoslavia, Tisia River (Hungary), Caucasus, Crimea.——Fig. 827,*4a–m.* **C. trigonella* (Rothpletz), Callovian, Greben, Yugoslavia; *a–d,* dorsal, lateral, anterior, ventral views, 4/45, ×1 (Radulovic & Rabrenovic, 1993); *e–m,* transverse serial sections, distances in mm from ventral umbo, 0.5, 1.1, 1.3, 1.8, 2.0, 2.1, 2.6, 4.3, 4.9, Theodosia, Crimea, KHGU 3298/8 (Kamyshan & Babanova, 1973).

Subfamily CALVIRHYNCHIINAE Kamyshan, 1967

[*nom. transl.* Manceñido & Owen, herein, *ex* Calvirhynchiidae Kamyshan, 1967a, p. 56]

Erymnariidae with septiform crura, broadly unisulcate and smooth or only faintly undulate anteriorly. Dental plates reduced, ventrally divergent or concave; median septum ridgelike to absent; crural plates variably fused to socket fulcral plates, remaining joined to dorsal floor; sometimes with cardinal process (or possible callus-infilled septalium); outer hinge plates absent. *Lower Jurassic (?Sinemurian, ?Pliensbachian), Middle Jurassic (Aalenian–Callovian).*

Calvirhynchia Kamyshan, 1967a, p. 56 [**C. kubanensis;* OD]. Small to medium size, smooth, rounded subtrigonal, ventribiconvex; well-defined median dorsal sulcus and ventral fold; beak small, suberect, planareas absent. Pedicle collar absent. *Lower Jurassic (?Sinemurian, ?Pliensbachian), Middle Jurassic (Aalenian–Callovian):* southern Europe, Caucasus, central Asia.——Fig. 827,*2a–k.* **C. kubanensis,* upper Bajocian, Kuban River, Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, KHGU 6/2135, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.1, 1.3, 1.7, 2.1, 2.3, 2.8, 3.3, 4.0, KHGU 6/2140 (Kamyshan, 1967a).

STENOSCISMATOIDEA

S. J. Carlson and R. E. Grant

[University of California, Davis; and deceased]

Superfamily STENOSCISMATOIDEA Oehlert, 1887 (1883)

[*nom. correct.* Carlson, herein, *pro* Stenoscismatacea Muir-Wood, 1955, p. 69, *nom. correct. pro* Stenoscismacea Shrock & Twenhofel, 1953, p. 317, *nom. transl. et correct. ex* Stenoschismatinae Oehlert, 1887a, p. 1304] [=Camerophoriacea Waagen, 1883, p. 435, *nom. transl.* Grabau, 1936, p. 70, *ex* Camerophoriinae Waagen, 1883, p. 435]

Small to medium sized, rarely large; outline commonly subpentagonal, may be triangular, oval, or round; valves moderately to strongly dorsibiconvex; strong uniplication with flat, rarely rounded, fold and sulcus, rarely unisulcate; stolidium present uncommonly in well-preserved individuals of a few species; slit-shaped to oval foramen present; ventral spondylium present, commonly elevated on low duplex septum, less commonly sessile; dorsal camarophorium present, commonly robust, strongly curved, on high median septum; hinge plates undivided, rarely divided in some forms lacking intercamarophorial plate; cardinal process absent, weak, or robust; intercamarophorial plate may be present or absent; crura raduliform. [Regarding the two dates of publication listed for Oehlert, Grant (1965a) states [comments in square brackets by SJC]:

"ICZN (Article 40) requires the retention of family-group names that are based on junior synonyms [as is *Camerophoria* KING, 1846; see for example Parallelelasmatidae, p. 958, herein], unless the synonymy was discovered before 1961, in which case the family-group name is changed, and the change generally accepted. As SCHMIDT (1964, p. 132) has pointed out, the family-group names based on Stenoscismatinae OEHLERT (1887) [as a correction of Stenoschismatinae OEHLERT (1887)] were in general use prior to 1961, and should be retained in the interest of stability. [Stenoscismatinae was placed on the Official List of Family-Group Names in Zoology (Opinion 770, 1966) by the ICZN.] The rules require, however, that the pertinent date in this case is the first recognition of the family group, and this is the date of WAAGEN's (1883) establishment of Camerophoriinae." Thus OEHLERT, 1887 (1883) is recognized as the publication date for Stenoscismatoidea.] *Lower Devonian (Pragian)–Upper Permian (Changhsingian).*

Stenoscismatoids are rhynchonellides distinguished by a dorsal camarophorium and a ventral spondylium and are commonly strongly dorsibiconvex and strongly uniplicate with undivided hinge plates. The classification of the Stenoscismatoidea (GRANT, 1965a, 1965b) has been emended here because of several difficulties, acknowledged by GRANT himself, including the erratic preservation of some characters deemed to be diagnostic, and the unreliable presence of supposedly diagnostic features in named higher taxa because of the frequency of homoplasy. GRANT's classification (1965a) was erected explicitly as a key to the identification of taxa rather than as a statement of phylogenetic relationships, making these difficulties particularly vexing. The revised classification herein is based on a morphologic and stratigraphic analysis of the phylogenetic affinities of the stenoscismatoids (CARLSON, 1998) and is, interestingly, more in agreement with GRANT's informal assessment of relationships (1965a; unpublished notes, 1994) than his classification (1965a, 1965b).

Family STENOSCISMATIDAE Oehlert, 1887 (1883)

[*nom. transl. et correct.* MUIR-WOOD, 1955, p. 91, *ex* Stenoschismatinae OEHLERT, 1887a, p. 1304; *emend.,* CARLSON, herein] [=Camerophoriidae WAAGEN, 1883, p. 435, *nom. transl.* GRABAU, 1936, p. 70, *ex* Camerophoriinae WAAGEN, 1883, p. 435]

Costae commonly strong, sharp, simple, present on anterior half only, may be absent entirely, rarely on entire valve; valve edges commonly overlapping slightly to strongly, rarely not overlapping; beak straight, erect, rarely gently incurved; delthyrium commonly unconstricted by dorsal beak; deltidial plates present, disjunct or conjunct, rarely absent; spondylium elevated on low duplex septum, rarely sessile. *Lower Devonian (Pragian)–Upper Permian (Kazanian, ?Tatarian).*

Subfamily STENOSCISMATINAE Oehlert, 1887 (1883)

[*nom. correct.* MUIR-WOOD, 1955, p. 91, *pro* Stenoschismatinae OEHLERT, 1887a, p. 1304; *emend.,* CARLSON, herein] [=Camerophoriinae WAAGEN, 1883, p. 435]

Geniculation rarely present; beak may be short or elongate; stolidium narrow to broad, present in some species; broad hinge plates; cardinal process robust; intercamarophorial plate strong, thick. *Middle Devonian (Eifelian)–Upper Permian (Kazanian, ?Tatarian).*

Stenoscisma CONRAD, 1839, p. 59, *non Stenocisma* HALL, 1847, p. 142, *nec Stenocisma* CONRAD-HALL in HALL, 1867b, p. 334–335, *nec Stenoschisma* HALL & CLARKE, 1893, p. 187, *nec Stenochisma* SCHUCHERT, 1897, p. 413, *nec Stenochisma* GRABAU & SHIMER, 1907, p. 288 [**Terebratula schlottheimii* VON BUCH, 1834, p. 59–60; OD] [=*Camerophoria* KING, 1844, p. 312, *nom. nud.; Camerophoria* KING, Aug. 1846, p. 89–91, obj.; *Camarophoria* HERRMANNSEN, Dec. 1846, p. 161, obj.; *Stenocisma* DALL, 1877, p. 65, obj.; *Stenoschisma* OEHLERT, 1887a, p. 1309, obj.]. Valves of medium size, may be large; costae rounded or sharp, on fold, flanks, or both, beginning near beaks or far in front of them; broad stolidium around anterior margins of adults; posterolateral edges of ventral valve flattened, strongly overlapped by edges of dorsal valve; beak long, varying from nearly straight to tightly incurved; deltidial plates conjunct or disjunct; foramen oval, open or completely closed; weak muscle marks in spondylium with adductors narrow, medial and diductors large, surrounding adductors; adjustors undifferentiated in apical part of spondylium; *vascula genitalia* deep, transverse, beginning

at anterior edge of median septum; *vascula media* beginning as mesial pair near origin of gonocoels, bifurcating toward margins, extending onto stolidium; large, low, finely striated cardinal process; weak muscle marks in camarophorium with anterior adductors small, paired, medial and posterior adductors larger, lateral; mantle canals as in ventral valve. [Several variations of this generic name exist. Some have been applied to specimens appropriately included within *Stenoscisma schlottheimii,* others not, as indicated above. Several variations of the specific name exist also. VON BUCH (1834) clearly refers to *Terebratula schlottheimii,* the spelling used here. CONRAD (1839), when first referring these specimens to *Stenoscisma,* refers to *Terebratula schlotheimii;* most others afterward refer to *schlotheimi.* It seems that SCHLOTTHEIM allowed his name to appear in print in several different spellings, contributing to the confusion.] *Lower Carboniferous–Upper Permian (Kazanian, ?Tatarian):* cosmopolitan.——FIG. 829,*1a–n. *S. schlottheimii* (VON BUCH), middle Upper Permian, Germany; *a,* dorsal valve exterior; *b,* lateral view, ventral valve on right; *c,* anterior view, ventral valve below; *d,* posterior view, ventral valve below; *e,* lateral interior, ventral valve on right, ×2 (Grant, 1965b); *f–n,* serial transverse sections, ventral valve below, ×2.5 (Weller, 1914).——FIG. 829,*1o–t. S. venustum* (GIRTY), lower Permian, Leonard Formation, Texas, USA; *o,* dorsal valve exterior; *p,* ventral valve exterior; *q,* lateral interior, ventral valve below, ×1.5; *r,* dorsal valve interior, oblique; *s,* dorsal valve interior; *t,* ventral valve interior, ×2 (Grant, 1965a).

Atribonium GRANT, 1965a, p. 37 [**A. simatum;* OD]. Valves small; outline subtrigonal; costae weak, rounded; valve edges overlapping slightly along posterior slopes, geniculate at anterior margin; stolidium absent; small conjunct or nearly conjunct deltidial plates present; spondylium sessile near apex in most species, elevated on low median septum duplex anteriorly; cardinal process low; camarophorium short, relatively flat, braced to underside of hinge plate by short, thick intercamarophorial plate. *Middle Devonian (Eifelian)–Lower Carboniferous (Tournaisian):* USA, Canada, Russia (Urals).——FIG. 830,*1a–k. *A. simatum,* Middle Devonian, Newton Creek Limestone, Michigan, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below; *e,* dorsal valve interior, oblique, ×2; *f–k,* serial transverse sections, ventral valve below, 0.6, 0.8, 1.0, 1.2, 1.5, 1.6 mm from ventral valve beak, ×4 (Grant, 1965b).——FIG. 830,*1l–o. A. ? cooperorum* GRANT, Middle Devonian, Ferron Point Formation, Michigan, USA; *l,* dorsal valve exterior; *m,* ventral valve exterior; *n,* lateral view, ventral valve on left; *o,* anterior view, ventral valve below, ×2 (Grant, 1965b).——FIG. 830,*1p–v. A. cooperorum* GRANT, Middle Devonian, Bell Shale, Michigan, USA; serial transverse sections, ventral valve below, 0.3, 0.5, 0.8, 1.1, 1.4, 2.1, 2.9, ×4 (Grant, 1965b).

Camerisma GRANT, 1965a, p. 63 [**C. prava;* OD] [=*Laevicamera* GRABAU, 1936, p. 87, *nom. nud., non Levicamera* GRABAU, 1934, p. 18; see *Psilocamara,* p. 1224, herein]. Valves of medium size; outline oval or subpentagonal, type species commonly asymmetrical; shell walls commonly thick; costae absent or very weak, confined to anterior fold and sulcus; strong, angular uniplication; valve edges overlapping strongly; stolidium absent; beak thick, blunt, tightly curved against dorsal umbo in some species, constricting delthyrium and foramen. *Lower Carboniferous (Serpukhovian)–Lower Permian (Artinskian):* USA, Europe, Russia, China.——FIG. 829,*2a–h. *C. prava,* Serpukhovian, Alaska, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e–h,* serial transverse sections, ventral valve below, 2.0, 2.6, 2.7, 3.0 mm from ventral valve beak, ×2.7 (Grant, 1965b).

Coledium GRANT, 1965a, p. 95 [**C. erugatum;* OD]. Valves commonly small, only rarely large; costae absent or few, rounded, weak, on anterior half only; stolidium narrow and sporadic or absent; beak short, suberect to incurved; deltidial plates small and disjunct or absent; spondylium on low median septum duplex, rarely sessile posteriorly. *Middle Devonian (Givetian)–Lower Permian (Sakmarian):* USA, Britain, Timor, ?Australia.——FIG. 830,*2a–n. *C. erugatum,* Viséan, Moorefield Formation, Oklahoma, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×2; *e–n,* serial transverse sections, ventral valve below, 1.2, 1.5, 2.1, 2.6, 2.9, 3.0, 3.4, 4.0, 4.2, 4.7 mm from ventral valve beak; *f,* low spondylium duplex; *g,* cardinal process large, distinct; *h,* hinge plates broad, undivided; *i,* camarophorium on high septum with intercamarophorial plate clear, ×4 (Grant, 1965b).——FIG. 830,*2o–q. C. bowsheri* (COOPER), Upper Carboniferous, Magdalena Group, New Mexico, USA; *o,* dorsal valve interior; *p,* anterior view of interior of articulated valves, ventral valve above, ×3; *q,* lateral interior view, ventral valve on right, ×4 (Grant, 1965a).

Sedenticellula COOPER, 1942, p. 231 [**Camarophoria hamburgensis* WELLER, 1910, p. 500; OD]. Valves of medium size, elongate or transverse oval in outline, of moderate dorsibiconvexity; costae low, narrow, rounded, beginning at or very near beaks, simple, bifurcating or intercalating; uniplication weak, rounded; valve edges not overlapping; stolidium absent; beak short, suberect; delthyrium constricted by dorsal beak; deltidial plates absent; spondylium sessile or duplex on low median septum; camarophorium weakly curved, on low median septum; cardinal process not well known. *Lower Carboniferous (Tournaisian):* USA, France.——FIG. 831*a–r. *S. hamburgensis* (WELLER), Hamburg Oolite, Illinois, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* anterior view, ventral valve below, ×2 (Grant, 1965b); *d–l,* dorsal valve, serial transverse sections; *m–r,* ventral valve, serial transverse

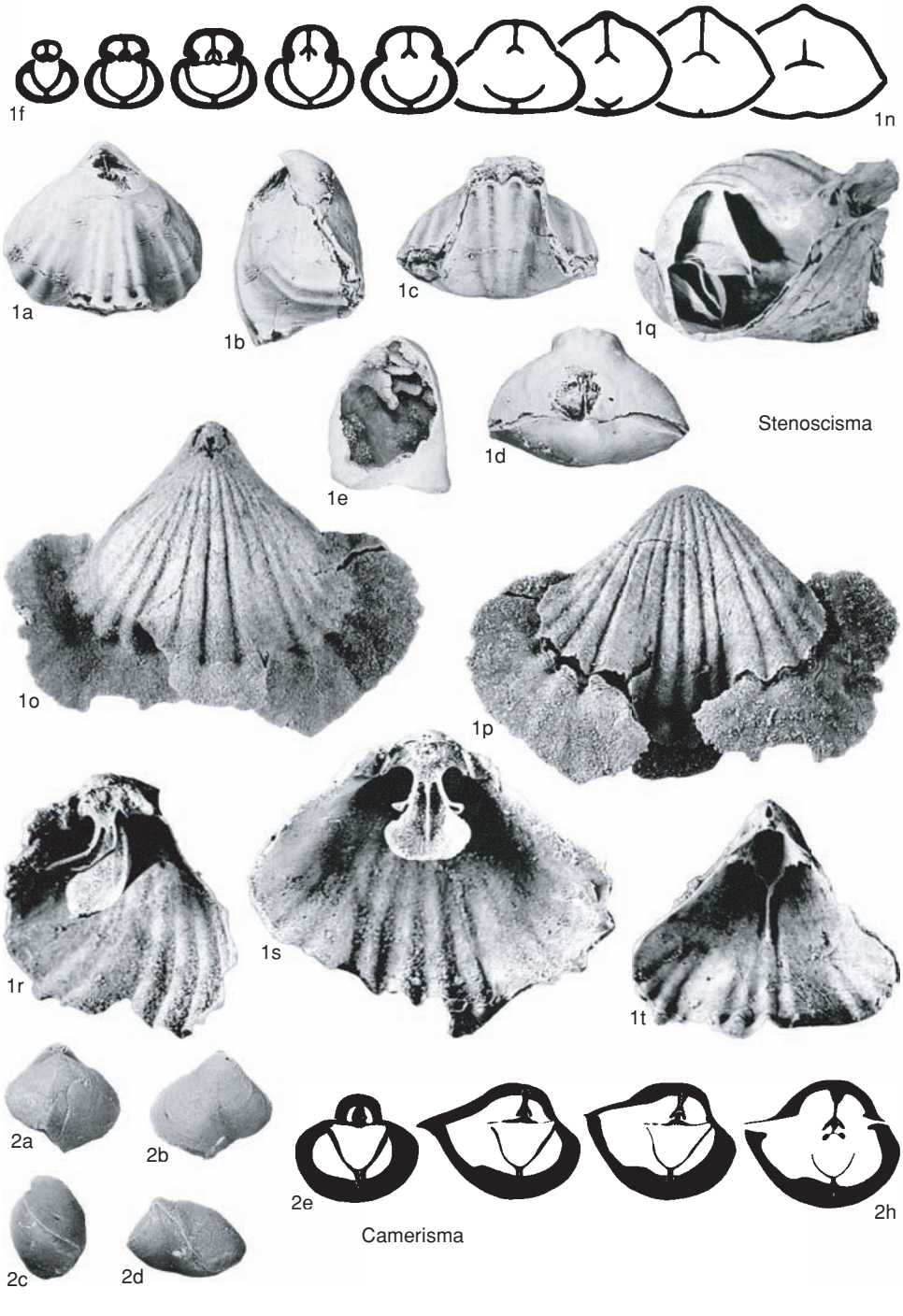

FIG. 829. Stenoscismatidae (p. 1219–1220).

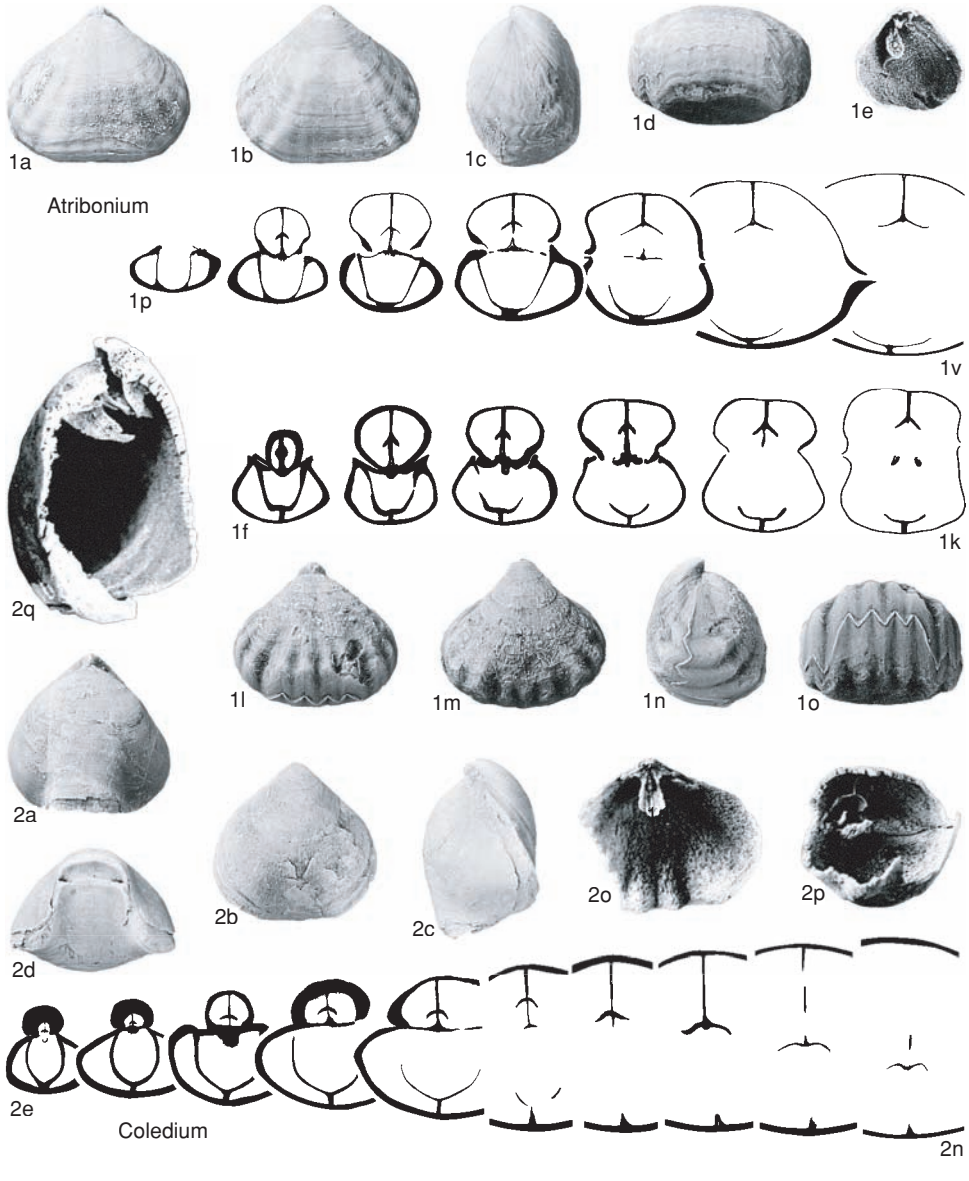

FIG. 830. Stenoscismatidae (p. 1220).

sections, intersection distances unknown, ×2.5 (Weller, 1914).——FIG. 831*s–w. S. sacra* GRANT, Chappel Limestone, Texas, USA; *s,* dorsal valve exterior; *t,* ventral valve exterior; *u,* lateral view, ventral valve on right; *v,* anterior view, ventral valve below; *w,* posterior view, ventral valve below, ×2 (Grant, 1965b).

Torynechus COOPER & GRANT, 1962, p. 1128 [**T. caelatus;* OD]. Valves medium to large, rounded subtrigonal in outline; costae fine, sharp, numerous, beginning at beaks, intercalating and bifurcating; fold and sulcus low, broad; valve edges overlapping slightly, sharply geniculate at anterior margin; stolidium absent or indicated as slight protrusion along anterior margins; beak long; deltidial plates small; foramen small, oval; muscle marks and mantle canals as in *Stenoscisma. Lower Permian (Artinskian):* USA (Texas).——FIG. 832*a–g.* **T. caelatus,* Leonard Formation, Glass Mountains; *a,* dorsal valve exterior; *b,* lateral view, ventral valve on

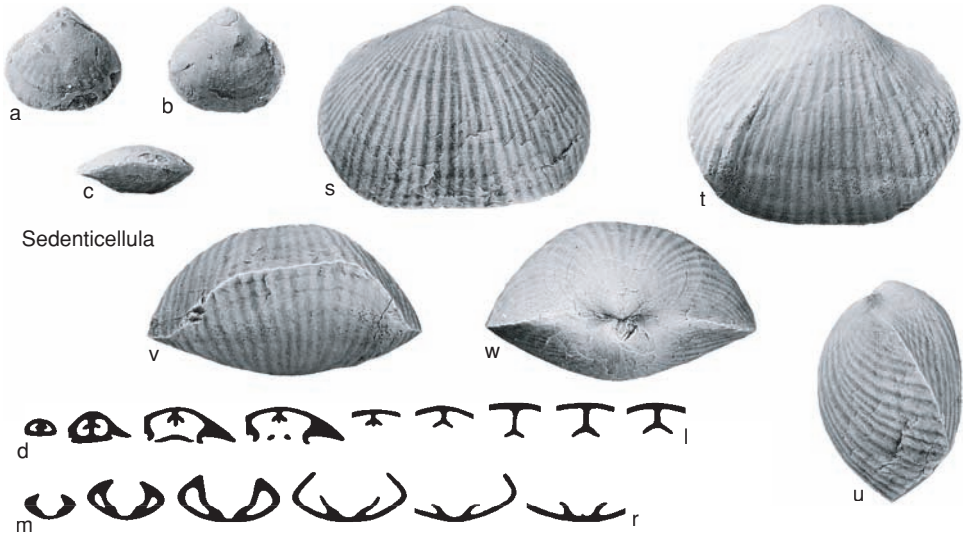

FIG. 831. Stenoscismatidae (p. 1220–1222).

right; *c,* anterior view, ventral valve below; *d,* dorsal valve interior; *e,* ventral valve interior; *f,* lateral interior, ventral valve on right, ×1; *g,* posterior interior, ventral valve below, ×2 (Grant, 1965a).

Subfamily PROATRIBONIINAE Gratsianova, 1967

[Proatriboniinae GRATSIANOVA, 1967, p. 91; *emend.,* CARLSON, herein]

Valves small, rarely of medium size; stolidium absent; beak short; hinge plates narrow, divided, rarely broad, undivided; cardinal process absent; intercamarophorial plate absent. *Lower Devonian (Pragian)–upper Middle Devonian (Givetian).*

Proatribonium GRATSIANOVA, 1967, p. 92 [**P. altaicum;* OD]. Valves subtrigonal in outline; costae weak, on anterior half only; valve edges overlap slightly along sides; hinge plates thick; camarophorium robust, on low median septum. *Lower Devonian (Pragian):* Russia (Altai Range).——FIG. 833,*3a–g. *P. altaicum,* Iakushinskie beds, *kindlei* zone; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve above, ×1.5; *e–g,* serial transverse sections, ventral valve above, 0.9, 1.1, 1.4 mm from ventral valve beak, ×9 (Gratsianova, 1967).

?Beichuanella CHEN in XU, WAN, & CHEN, 1978, p. 338 [**B. uniplicata;* OD]. Valves paucicostate with 1 to 3 strong, sharp costae near anterior margin only; valve edges not overlapping; spondylium sessile, elevated on low median septum anteriorly; hinge plates undivided. [With further study, *Beichuanella* may well be more appropriately assigned to a superfamily other than Stenoscismatoidea within the Rhynchonellida. See also p. 1372 herein.] *upper Middle Devonian (Givetian):* China (Sichuan).——FIG. 833,*1a–h. *B. uniplicata,*Guanwushan Formation, Guangxi; *a,* dorsal valve

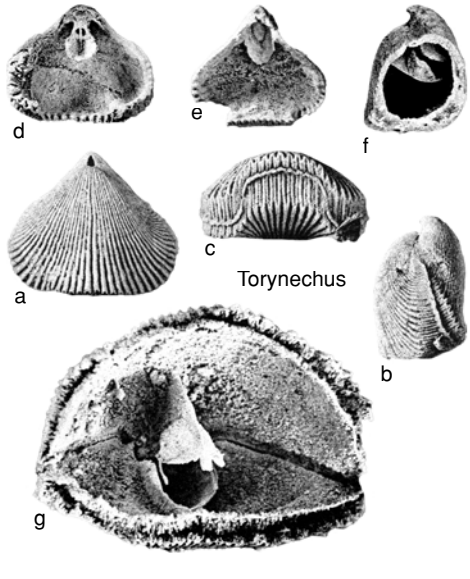

FIG. 832. Stenoscismatidae (p. 1222–1223).

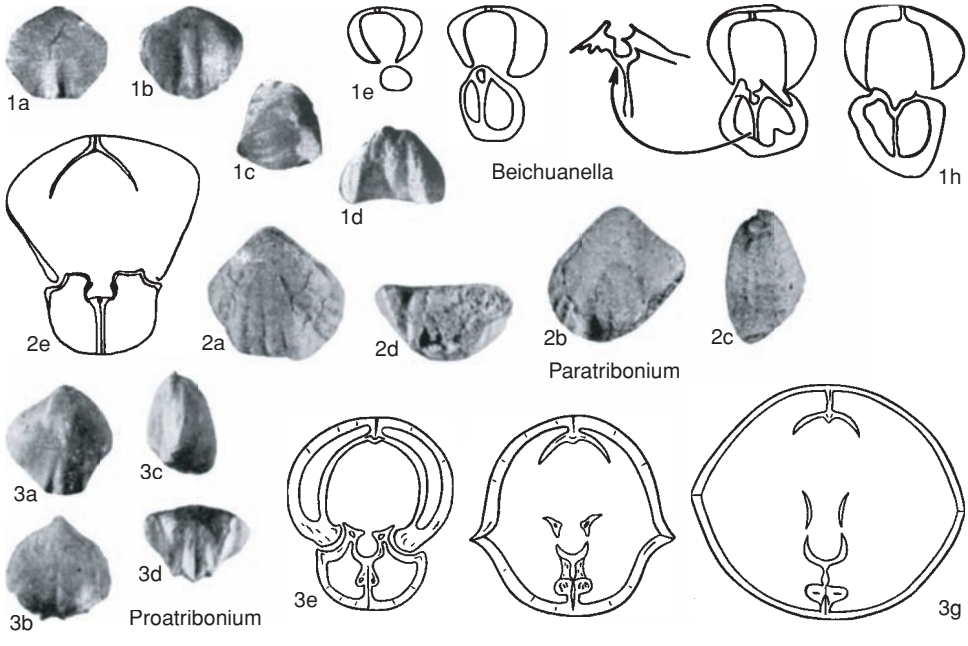

FIG. 833. Stenoscismatidae (p. 1223–1224).

exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral below, ×1; *e–h,* serial transverse sections, ventral valve above, 0.10, 0.45, 0.55, 0.90 mm from ventral valve beak, ×6.6, enlarged drawing of camarophorium, on left, is at ×16 (Xu, Wan, & Chen, 1978).

Paratribonium SAPELNIKOV & MIZENS, 1991, p. 107 [**P. rhomboidalis;* OD]. Valves of medium size, rounded rhombic in outline; nature of deltidium and foramen unknown; camarophorium delicate, gently curved; hinge plates broad, thick. *Lower Devonian (Pragian):* Russia (Urals).——FIG. 833,*2a–e.* **P. rhomboidalis,* Tyutyulen bed, Chelyabinsk Oblast; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve above, ×1; *e,* transverse section, ventral valve above, ×6 (Sapelnikov & Mizens, 1991).

Family PSILOCAMARIDAE Grant, 1965

[*nom. transl.* KOCZYRKEVICZ, 1969, p. 11, *ex* Psilocamarinae GRANT, 1965a, p. 29; *emend.,* CARLSON, herein]

Costae absent entirely, or strong, sharp, simple, and commonly present on entire valve, rarely present on fold and sulcus only; valve edges commonly not overlapping, rarely overlapping slightly or strongly; beak erect, gently, or strongly incurved, short, rarely elongate; deltidial plates absent, rarely present and disjunct; spondylium either sessile or elevated on low duplex septum; hinge plates narrow. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian).*

Subfamily PSILOCAMARINAE Grant, 1965

[Psilocamarinae GRANT, 1965a, p. 29; *emend.,* CARLSON, herein]

Costae present on entire valve, rarely absent or present on fold and sulcus only; valve edges not overlapping; stolidium absent; beak gently incurved, less commonly erect; delthyrium commonly unconstricted; spondylium duplex; cardinal process weak or robust, very rarely absent; intercamarophorial plate absent, rarely present but weak. *middle Upper Carboniferous (Moscovian)–Upper Permian (Changhsingian).*

Psilocamara COOPER, 1956b, p. 523 [**P. renfroarum;* OD] [=*Levicamera* GRABAU, 1934, p. 18, *nom. nud., non Laevicamera* GRABAU, 1936, p. 87; see *Camerisma,* p. 1220, herein]. Valves small, of moderate ventribiconvexity; smooth with strong, angular uniplication; beak gently to strongly incurved; delthyrium constricted by dorsal beak; deltidial plates present, disjunct; delicate, gently curved camarophorium; cardinal process apparently lacking in type species, broad, striated, and comblike in

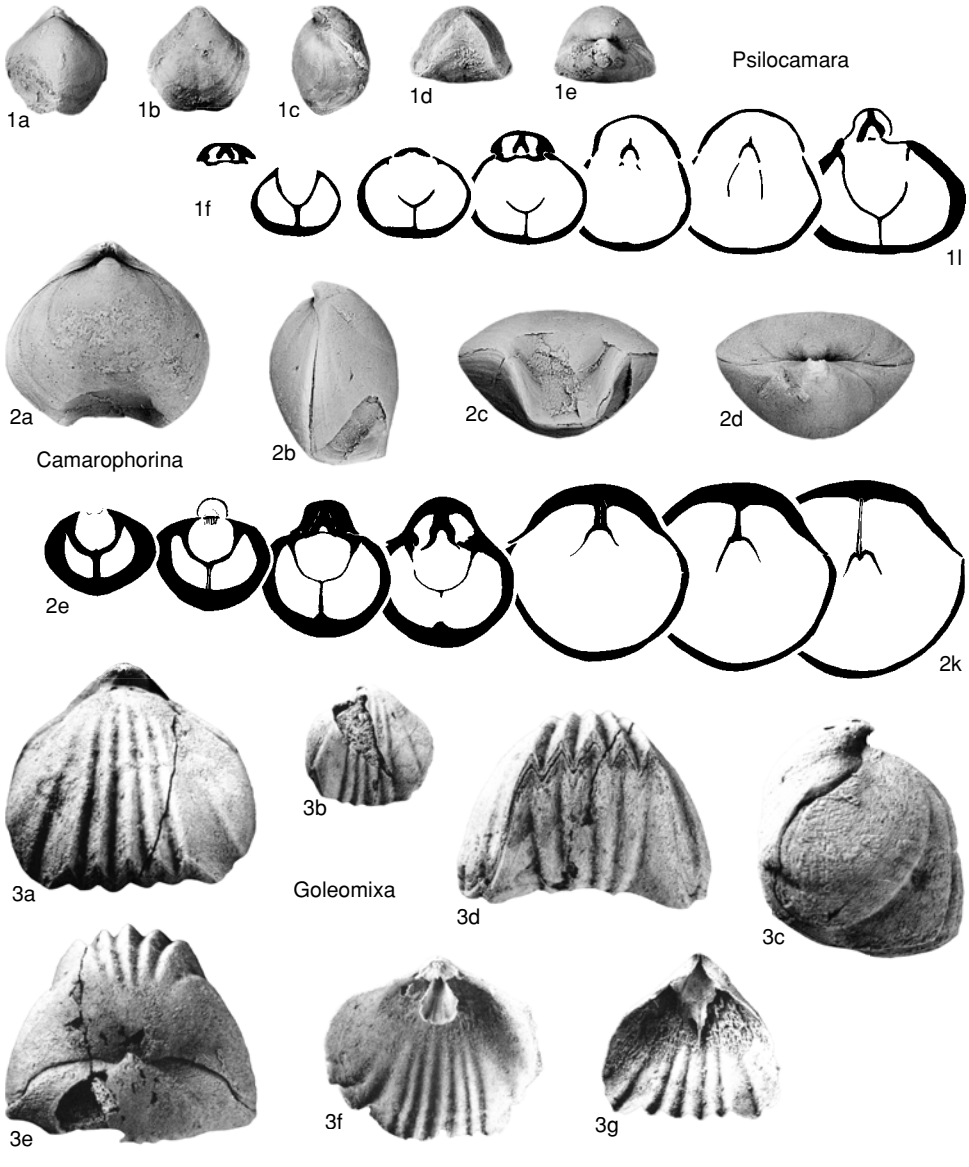

FIG. 834. Stenoscismatidae (p. 1224–1227).

other species. *middle Upper Carboniferous (Moscovian)–Lower Permian (Sakmarian):* USA (Texas, Missouri), China (Nantan, Yunnan), New Zealand.——FIG. 834,*1a–l.* **P. renfroarum,* Moscovian, Mineral Wells Formation, Texas, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, dorsal valve above; *e,* posterior view, dorsal valve above, ×2; *f,* serial transverse section, ventral valve below, ×4.5; *g–k,* ventral valve below, serial transverse sections, 0.3, 0.65, 0.77, 1.0, 1.2 mm from ventral valve beak, ×4 (Cooper, 1956b); *l,* serial transverse section, ventral valve below, 1.0 mm from ventral valve beak, ×5 (Grant, 1965b).

Camarophorina LIKHAREV, 1934, p. 213 [**Camarophoria antisella* BROILI, 1916, p. 58; OD]. Valves small to medium sized, of moderate equibiconvexity, shell walls commonly thick; smooth, or with very weak costae; unisulcation (not uniplication) strong, with flat fold and sulcus; beak suberect; delthyrium constricted by dorsal beak; spondylium on high median septum; cardinal process robust. *Upper Permian (Kazanian–Tatarian):* Timor.——FIG. 834,*2a–k.* **C. antisella* (BROILI), Basleo; *a,*

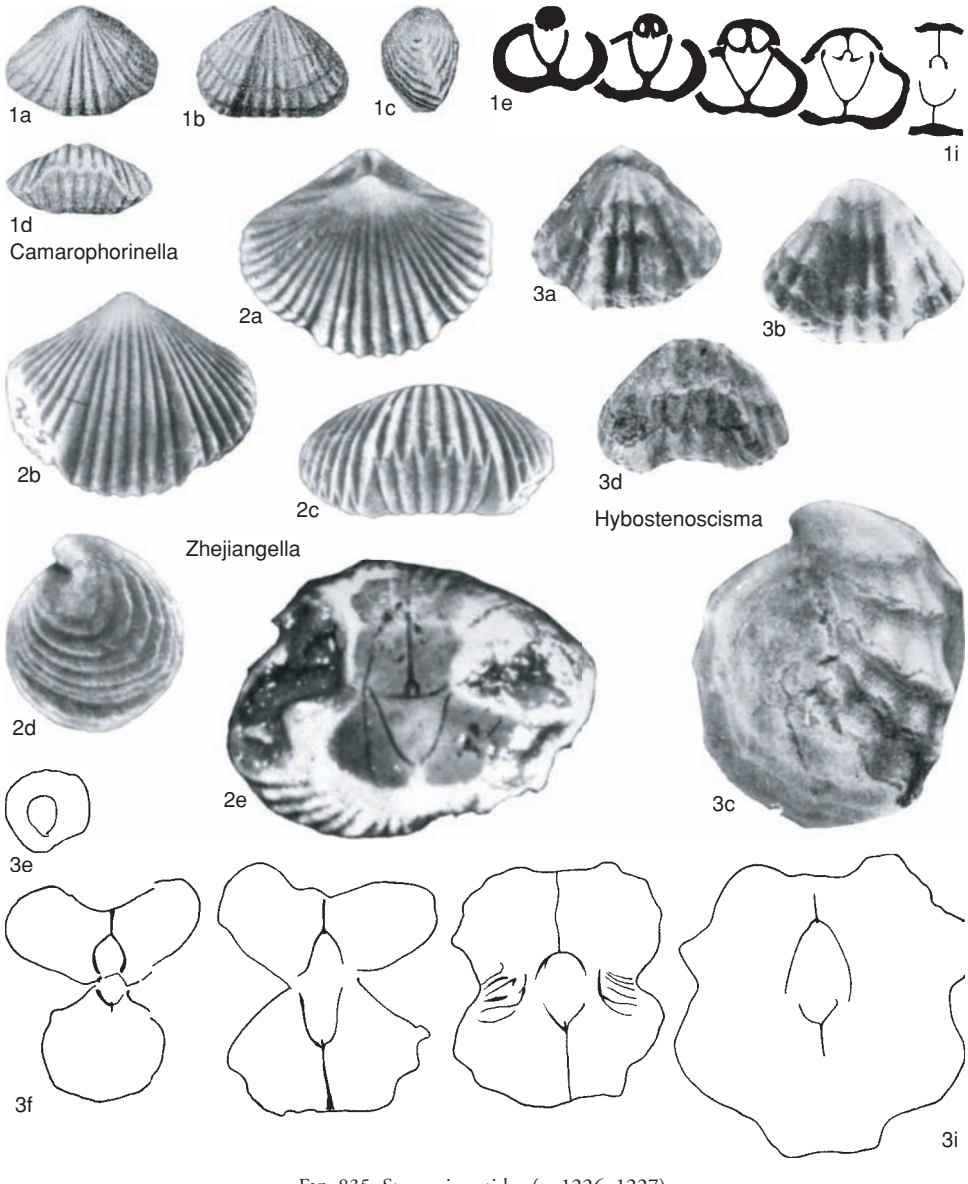

FIG. 835. Stenoscismatidae (p. 1226–1227).

dorsal valve exterior; *b,* lateral view, ventral valve on right; *c,* anterior view, dorsal valve above; *d,* posterior view, dorsal valve above, ×2; *e–k,* serial transverse sections, ventral valve below, 0.8, 1.2, 1.6, 1.8, 2.6, 3.0, 3.4 mm from ventral valve beak, ×3.3 (Grant, 1965b).

Camarophorinella LIKHAREV, 1936, p. 63 [**C. caucasica;* OD]. Valves of medium size, shell walls commonly thick; costae simple, bifurcating, or intercalating; delthyrium, deltidial plates, and foramen unknown; edges of camarophorium attached to sides of hinge plates; hinge plates divided; cardinal process weak. *Upper Permian (Kazanian–Changhsingian):* southern Russia (northern Caucasus), southern China.——FIG. 835,*1a–i. *C. caucasica,* formation unknown, northern Caucasus; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e–i,* serial transverse sections, ventral valve below, intersection distances unknown, ×2 (Grant, 1965b).

Goleomixa GRANT, 1976, p. 180 [**G. acymata;* OD]. Valves small, strongly ventribiconvex; valve flanks smooth, 5 to 7 strong costae present only on ante-

rior half of fold and sulcus; beak erect, elongate; deltidial plates present, disjunct; cardinal process present as small plate or low, minutely serrated knob. *Lower Permian (Kungurian):* southern Thailand.——FIG. 834,*3a–g. *G. acymata,* Rat Buri Limestone, Ko Muk; *a,* dorsal valve exterior, ×2; *b,* ventral valve exterior, ×1; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral below; *e,* posterior view, ventral below; *f,* dorsal valve interior; *g,* ventral valve interior, ×2 (Grant, 1976).

Hybostenoscisma LIAO & MENG, 1986, p. 83 [**H. bambusoides;* OD]. Valves small, subtrigonal in outline; strong, bamboo-jointed costae on entire valve; beak gently incurved; spondylium on high median septum; hinge plates and cardinal process unknown; thin, low intercamarophorial plate present. *Upper Permian (Changhsingian):* China (southern Hunan).——FIG. 835,*3a–i. *H. bambusoides,* Changhsing Formation, Huatang; *a,* dorsal valve exterior; *b,* ventral valve exterior, ×2; *c,* lateral view, ventral valve on right, ×4; *d,* anterior view, ventral valve below, ×2; *e–i,* serial transverse sections, ventral valve above, 0.1, 0.3, 0.4, 0.7, 0.9 mm from ventral valve beak, ×4 (Liao & Meng, 1986).

Zhejiangella LIANG in WANG & others, 1982, p. 236 [**Z. sexplicata;* OD]. Valves large, transversely oval in outline, strongly dorsibiconvex; costae commence slightly anterior to beak; beak suberect; cardinal process robust. *Upper Permian (Capitanian):* eastern China (Zhejiang).——FIG. 835,*2a–e. *Z. sexplicata,* Lengwu Formation, Tonglu; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e,* section through beaks of articulated valves, ventral valve below, ×3 (Liang, 1990).

Zhejiangellina LIANG, 1990, p. 257 [**Z. wangi;* OD]. Valves of medium size, subpentagonal in outline, moderately equibiconvex; costae commence at beak; fold and sulcus and interior of both valves identical to *Zhejiangella.* [*Zhejiangellina* may well be synonymous with *Zhejiangella.*] *Upper Permian (Capitanian):* eastern China (Zhejiang).——FIG. 836*a–e. *Z. wangi,* Lengwu Formation, Tonglu; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve below, ×2; *e,* beaks of articulated valves broken, revealing internal casts, ventral valve below, ×4 (Liang, 1990).

Subfamily CYROLEXINAE new subfamily

[Cyrolexinae CARLSON, herein]

Rounded outline common; costae absent or present on anterior half only; beak strongly incurved; narrow stolidium rarely present; delthyrium constricted by dorsal beak; spondylium sessile; cardinal process robust; intercamarophorial plate present, rarely absent. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian).*

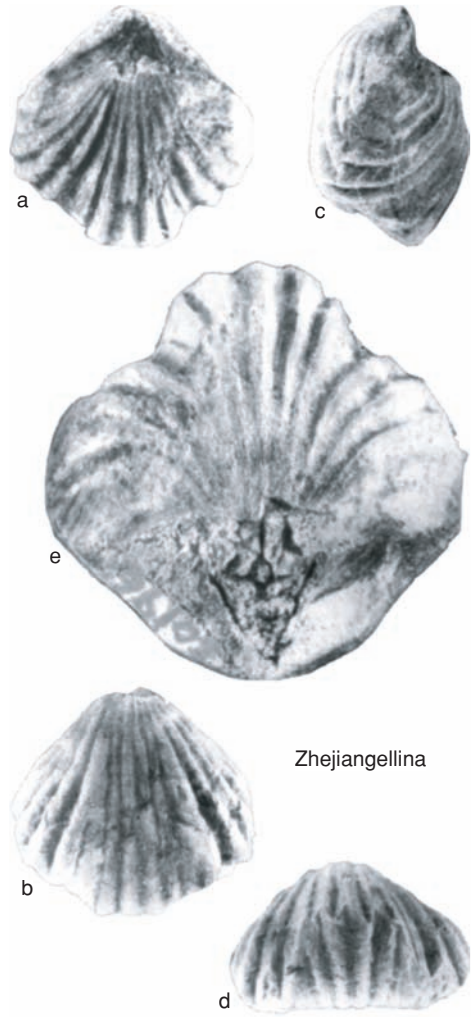

FIG. 836. Stenoscismatidae (p. 1227).

Cyrolexis GRANT, 1965a, p. 88 [**C. haquei;* OD]. Valves of medium size; strong equibiconvexity; weak, rounded costae on anterior half only; valve edges overlapping broadly on posterior slopes; beak short; nature of deltidium and foramen unknown; camarophorium curved strongly ventrally, posterior edges touching underside of hinge plates; intercamarophorial plate weak or absent. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian):* Spain, Russia (Urals, eastern Siberia), Pakistan (Salt Range), southern China, western Japan.——FIG. 837,*2a–m. *C. haquei,* Lower Permian, lower *Productus* Limestone, Rukhla, Pakistan; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, dorsal valve above; *e,* posterior view, dorsal valve above, ×2; *f,* articulated valves in lateral view, ventral valve on left, broken along sagittal plane,

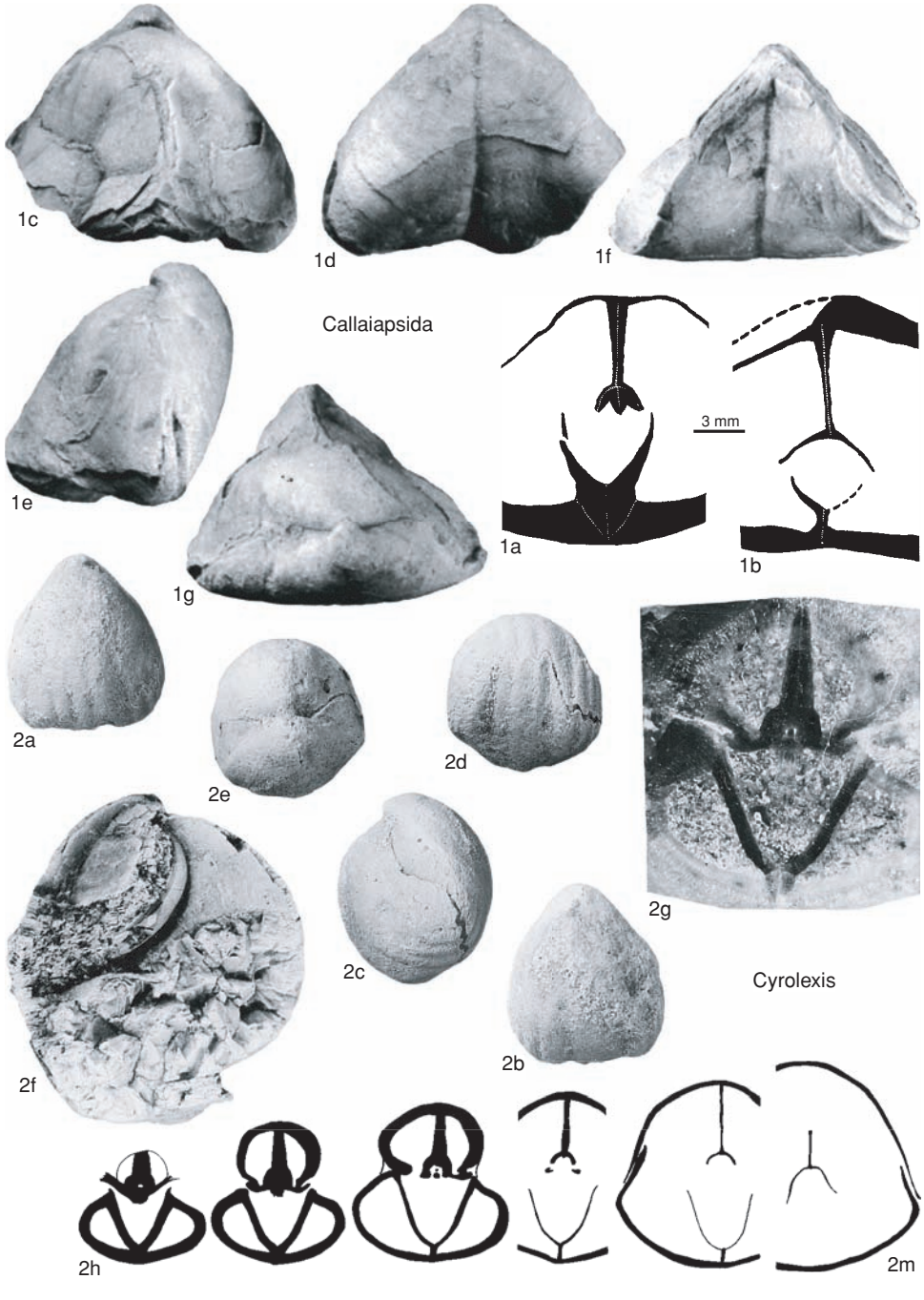

FIG. 837. Stenoscismatidae (p. 1227–1229).

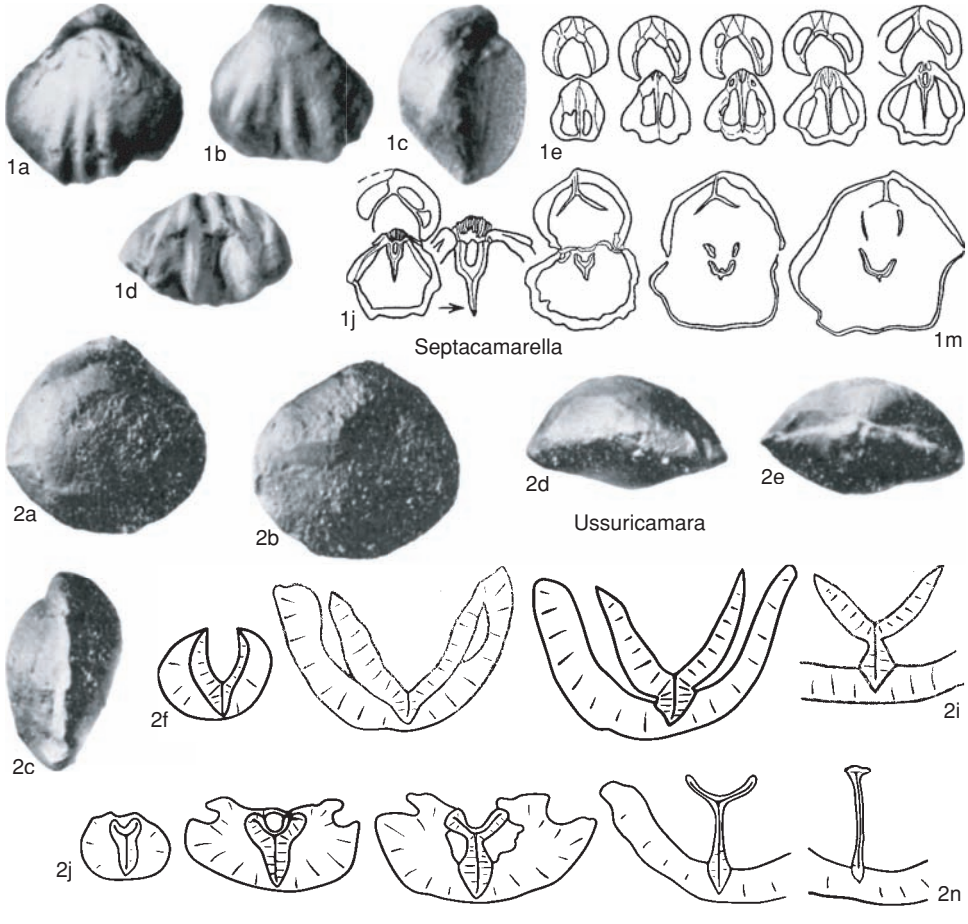

FIG. 838. Stenoscismatidae (p. 1229–1230).

showing profile of camarophorium and spondylium; *g,* cross section of articulated valves, ventral valve below, 0.5 mm from ventral valve beak, ×6; *h–m,* serial transverse sections, ventral valve below, 0.9, 1.1, 1.3, 1.8, 2.4, 3.5 mm from ventral valve beak, ×2.7 (Grant, 1965b).

Callaiapsida GRANT, 1971, p. 323 [**Camerisma (Callaiapsida) kekuensis;* OD]. Valves large, strongly ventribiconvex; outline subtrigonal; costae absent; uniplication very strong and angular; median groove present exteriorly along trough of sulcus; valve posterior flanks broadly flanged, with dorsal flange overlapping ventral flange; beak elongate; deltidial plates and foramen unknown; shell commonly thickened at posterior; camarophorium delicate; hinge plates and cardinal process unknown. *Upper Carboniferous (Bashkirian)–Lower Permian (Kungurian):* USA (Alaska), Spain, Svalbard, Russia, Novaya Zemlya, Mongolia.——FIG. 837,*1a–b. *C. kekuensis,* Halleck Formation, Kuiu Island, Alaska, USGS loc. 3683; *a,* section 10 mm anterior to ventral beak, confirming presence of intercamarophorial plate, USNM 163658; *b,* section of fragmentary specimen, about 12 mm anterior to ventral beak, USNM 163659, ×0.75 (Grant, 1971).——FIG. 837,*1c–g. C. arctica,* Lower Permian, unnamed formation, Alaska, USA; *c,* dorsal valve exterior; *d,* ventral valve exterior; *e,* lateral view, ventral valve on right; *f,* anterior view, ventral valve below; *g,* posterior view, ventral valve below, ×1 (Grant, 1971).

Septacamarella GLUSHENKO, 1975, p. 101 [**S. nonnulla;* OD]. Valves small, rotund to subpentagonal, slightly transverse; strong costae present on anterior half of valves; valve edges not overlapping; deltidial plates and foramen unknown; 2 subspondylial (accessory) plates supporting spondylium; long camarophorium on low septum; cardinal process wide, heavy, three-lobed with traces of muscle attachment. *Lower Permian:* Ukraine (Slaviansk Series, northwestern Donets ridge).——FIG. 838,*1a–m. *S. nonnulla,* limestone S_3; *a,* dorsal valve

exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve below, ×3; *e–m,* serial transverse sections, ventral valve above, 0.1, 0.2, 0.25, 0.3, 0.5, 0.6, 0.9, 1.4, 2.25 mm from ventral valve beak, ×4 (Glushenko, 1975).

Ussuricamara Koczyrkevicz, 1969, p. 11 [**U. majchensis;* OD]. Valves small, globular, of moderate dorsibiconvexity; shell walls commonly thick; costae absent; uniplication very weak, rounded; valve edges overlap slightly; narrow stolidium present; foramen absent; camarophorium delicate; hinge plate divided anteriorly; cardinal process poorly known; intercamarophorial plate absent. *Upper Permian:* eastern Russia (southern Primor).——Fig. 838,*2a–n.* **U. majchensis,* Ussuri region; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below; *e,* posterior view, ventral valve below, ×3; *f–i,* serial transverse sections, ventral valve, 0.32, 2.25, 2.65, 3.1 mm from ventral valve beak, *j–n,* serial transverse sections, dorsal valve, 0.35, 1.0, 1.32, 2.1, 3.15 mm from ventral valve beak, ×7 (Koczyrkevicz, 1969).

LAMBDARINOIDEA

Norman M. Savage
[University of Oregon]

Superfamily LAMBDARINOIDEA Brunton & Champion, 1974

[*nom. transl.* Savage, 1996, p. 255, *ex* Lambdarininae Brunton & Champion, 1974, p. 819]

Very small Rhynchonellida with outline bilobed to cordiform; surface smooth; commonly with dorsal and ventral sulci and emarginate anterior; delthyrium with symphytium or conjunct deltidial plates or open; ventral median septum may be present anteriorly; dorsal median septum absent posteriorly but may occur anteriorly; hinge plates short; cardinal process absent. *Upper Devonian (lower Famennian)–Upper Carboniferous (Stephanian).*

Family LAMBDARINIDAE Brunton & Champion, 1974

[*nom. transl.* Savage, 1996, p. 255, *ex* Lambdarininae Brunton & Champion, 1974, p. 819]

Lambdarinoidea with outline bilobed to cordiform; symphytium present or absent; ventral interarea long; foramen circular or delthyrium open; dental plates short or absent; ventral and dorsal median septa absent or present anteriorly. *Upper Devonian (lower Famennian)–Upper Carboniferous (Stephanian).*

Subfamily LAMBDARININAE Brunton & Champion, 1974

[Lambdarininae Brunton & Champion, 1974, p. 819]

Lambdarinidae with symphytium. Ventral interarea long; foramen circular; dental plates short; ventral and dorsal median septa absent. *Lower Carboniferous (upper Tournaisian–upper Viséan).*

Lambdarina Brunton & Champion, 1974, p. 819 [**L. manifoldensis;* OD]. Very small with outline strongly bilobed; each lobe almost as large as rest of shell; lateral profile planoconvex to biconvex, ventral umbone slightly upcurved. Beak straight, elongate; foramen subcircular, apical; symphytium flat, elongate. Bisulcate, dorsal sulcus strong, ventral sulcus weak with median ridge; anterior commissure rectimarginate to sulcate. Surface smooth, impunctate. Dental plates thin, short, developed only in vicinity of teeth; teeth narrow, curved anteromedially. Hinge plates undivided; notothyrial platform thickened; sockets ovoid, weakly excavated into shell wall; inner sockets ridges prominent; cardinal process absent. *Lower Carboniferous (upper Tournaisian–upper Viséan):* Europe, eastern Australia.——Fig. 839,*1a–e.* **L. manifoldensis,* lower Viséan, Carboniferous Limestone, Staffordshire, Wetton, England; *a–b,* holotype, dorsal and ventral views, ×15; *c,* interior of ventral valve posterior, ×22; *d,* interior of dorsal valve posterior, ×42; *e,* drawing of interior of ventral valve showing foramen, symphytium, dental plates, and teeth, ×18 (Brunton & Champion, 1974).

Hampsia Morris, 1994, p. 271 [**H. cooperi;* OD]. Very small with outline bilobed and profile arched. Beak elongate and resupinate, projecting ventrally

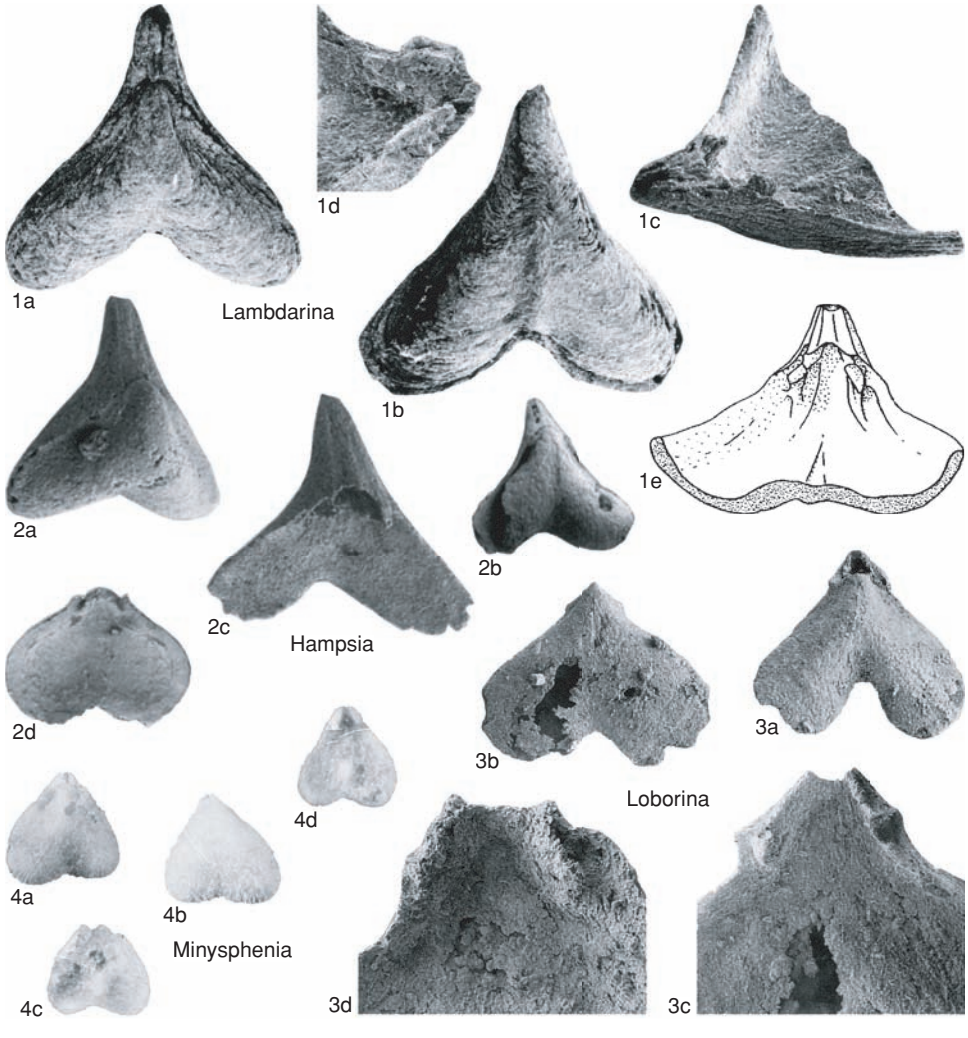

FIG. 839. Lambdarinidae (p. 1230–1232).

away from plane of commissure; foramen minute, rounded, and apical; symphytium long, narrow, closed by single deltidial plate. Dorsal valve markedly convex, ventral valve less so; each valve sulcate anteriorly with anterior shell margin deeply indented; anterior commissure weakly unisulcate. Surface smooth. Dental plates unknown but may be present below symphytium. Teeth project anteriorly from anterior edge of symphytium; ventral muscle field unknown. Hinge plates undivided; notothyrial platform thick; inner and outer socket ridges low; sockets rounded, short; crura unknown; dorsal muscle field short, rounded. *Lower Carboniferous (Viséan):* England.——FIG. 839,*2a–d. *H. cooperi,* Milldale Limestone, Staffordshire, Waterhouses, Brownend Quarry; *a,* holotype, dorsolateral view, ×22; *b,* hypotype, dorsolateral view, ×20; *c,* dorsolateral view of ventral valve interior, ×22; *d,* interior of dorsal valve, ×20 (Morris, 1994).

Subfamily LOBORININAE Savage, 1996

[Loborininae SAVAGE, 1996, p. 255]

Lambdarinidae lacking symphytium. Delthyrium elongate, open; dental plates fused to valve walls; teeth massive; hinge plates poorly developed; ventral and dorsal median septa absent. *Upper Devonian (lower Famennian).*

Loborina BALINSKI, 1982, p. 130 [**L. lobata;* OD]. Very small with outline strongly bilobed; lobes diverging at 45 degrees; profile weakly biconvex.

Bisulcate, with strong dorsal sulcus, weak ventral sulcus; anterior commissure rectimarginate to sulcate. Surface smooth. Beak straight, elongate; foramen ovate, large, apical; delthyrium open. Symphytium absent. Dental plates arising from valve walls, supporting long massive teeth. Hinge plates and notothyrial platform poorly developed; sockets long, bounded by strong inner and outer socket ridges. *Upper Devonian (lower Fammenian):* Poland.——Fig. 839,*3a–d. *L. lobata,* Cracow; *a,* holotype, dorsal view; *b,* hypotype, ventral view, approximately ×15; *c,* interior of ventral valve posterior; *d,* interior of dorsal valve posterior, ×50 (Balinski, 1982).

Subfamily MINYSPHENIINAE Savage, 1996

[*nom. correct.* Savage, herein, *pro* Minispheniinae Savage, 1996, p. 256]

Lambdarinidae lacking symphytium and dental plates, but with dorsal and ventral median septa present anteriorly; teeth directed anteromedially. *Upper Carboniferous (Stephanian).*

Minysphenia Grant, 1988, p. 126 [**M. conopia;* OD]. Very small with outline subtriangular to cordiform and profile biconvex. Beak straight, short; foramen circular, apical; symphytium absent, small conjunct deltidial plates present anterior of foramen. Sulcus weak in both valves; anterior commissure rectimarginate to sulcate. Surface smooth. Dental plates not evident; teeth very small, cyrtomatodont; rounded swelling present at about two-thirds valve length. Incipient cardinal process or swollen notothyrial platform present. *Upper Carboniferous (Stephanian):* USA (New Mexico).——Fig. 839,*4a–d. *M. conopia,* upper Magdalena Formation, Sacramento Mountains, Grapevine Canyon; *a–b,* holotype, dorsal and ventral views; *c–d,* dorsal and ventral interiors, ×8 (Grant, 1988).

RHYNCHOPOROIDEA

Norman M. Savage
[University of Oregon]

Superfamily RHYNCHOPOROIDEA Muir-Wood, 1955

[*nom. transl.* Erlanger, 1993, p. 120, *ex* Rhynchoporidae Muir-Wood, 1955, p. 91]

Rhynchonellida with shell endopunctate; costal interspaces may be developed into marginal spines. *Upper Devonian (lower Famennian)–Upper Permian (Tatarian).*

Family RHYNCHOPORIDAE Muir-Wood, 1955

[Rhynchoporidae Muir-Wood, 1955, p. 91]

Rhynchoporoidea with endopunctae simple or merging. Fold and sulcus variously developed or absent. *Upper Devonian (lower Famennian)–Upper Permian (Tatarian).*

Subfamily RHYNCHOPORINAE Muir-Wood, 1955

[*nom. transl.* Savage, herein, *ex* Rhynchoporidae Muir-Wood, 1955, p. 91]

Rhynchoporidae with simple endopunctae. Dorsal fold and ventral sulcus strong; anterior commissure uniplicate, rectangular. Costae simple, extending from beaks, flattened and grooved anteriorly, extending as sharp spines. *Lower Carboniferous (upper Tournaisian)–Upper Permian (Tatarian).*

Rhynchopora King, 1865, p. 124 [**Terebratula geinitziana* de Verneuil, 1845, p. 83; OD] [=*Rhynchoporina* Oehlert, 1887a, p. 1305, obj.]. Outline transversely subpentagonal and profile dorsibiconvex. Beak straight to suberect; delthyrium oval; deltidial plates disjunct, rarely conjunct. Fold and sulcus becoming prominent anteriorly; tongue distinct, rectangular. Costae numerous, simple, rounded, from beaks; flattened and grooved anteriorly; intertroughs narrow, extending as sharp spines. Shell finely endopunctate. Dental plates short, thin, convergent ventrally; teeth cyrtomatodont. Dorsal median septum short, low; hinge plates united; septalium with cover plate that is often perforated posteriorly; inner socket ridges overhanging sockets; crural bases horizontal; crura ventrally curved, concave dorsomedially in section. Ventral and dorsal muscle fields poorly impressed. Small cardinal process occasionally present. *Lower Carboniferous (upper Tournaisian)–Upper Permian (Tatarian):* cosmopolitan.——Fig. 840,*1a–f. *R. geinitziana* (de Verneuil), lower Kazanian, North Dvina River Basin, Shidrovo, northern European Russia; *a–b,*

holotype, dorsal and lateral views, ×1 (de Verneuil, 1845); *c–e,* ventral, anterior, and lateral views, ×2; *f,* punctae on ground surface 10 mm from beak, ×19 (Erlanger, 1981).——FIG. 840,*1g–n. R. parambula* COOPER & GRANT, lower Guadalupian, Word Formation, Glass Mountains, Hess Canyon, Texas, USA; *g–j,* holotype, dorsal, posterior, lateral, and anterior views, ×1; *k,* holotype, apical view, ×3; *l,* paratype, interior of dorsal valve, ×2; *m,* anterior of another paratype showing spines, ×1.5; *n,* paratype, interior of ventral valve, ×2 (Cooper & Grant, 1976b).——FIG. 840,*1o–s. R. sansabensis* CARTER, upper Kinderhookian–lower Osagian, Chappel Limestone, central Texas, USA; paratype, serial sections 1.0, 1.4, 2.0, 2.4, 3.2 mm from posterior, ×2 (Carter, 1967).

Subfamily GREIRINAE Erlanger, 1993

[*nom. transl.* SAVAGE, herein, *ex* Greiridae ERLANGER, 1993, p. 120]

Rhynchoporidae with two-layered shell and merging endopunctae in fibrous layer. Costae angular, numerous, arising at beaks; anterior commissure uniplicate. Dental plates short. Dorsal median septum well developed. *Upper Devonian (lower Famennian).*

Greira ERLANGER, 1993, p. 120 [**G. transcaucasica;* OD]. Shell small to medium with subrounded to subpentagonal outline and biconvex profile. Beak straight, narrow; delthyrium open. Dorsal fold and ventral sulcus well developed, arising at umbones; anterior commissure uniplicate, rounded. Costae numerous, straight, simple, angular, from beaks. Shell finely punctate with punctae present only in fibrous layer, randomly disposed in umbonal region but arranged in lines parallel to commissure anteriorly; punctae sometimes merging, present on costae and interspaces. Dental plates very short; teeth small and elongate. Dorsal median septum low and thin but extending one-quarter valve length; septalium short, with cover plate bearing medial ridge; sockets small and shallow; inner socket ridges slightly overhanging sockets; crural bases triangular in section; crura long, laterally flattened, slightly oblique, divergent, curved ventrally. Muscle fields poorly impressed. Cardinal process absent. *Upper Devonian (lower Famennian):* Azerbaijan (Nakhichevan Republic).——FIG. 840,*2a-o. *G. transcaucasica, Mesoplica meisteri* Zone, left bank of Arpa River between Geran-Kalasy and Kabakhyal Mountains, Nakhichevan; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* punctae on broken surface of sulcus in ventral valve of topotype, ×100; *g,* transverse section through puncta in dorsal valve of topotype, ×300; *h–o,* serial sections 1.3, 1.4, 1.5, 1.7, 2.1, 2.4, 2.5, 2.75 mm from posterior of topotype, ×3 (Erlanger, 1993).

Subfamily ARARATELLINAE Erlanger, 1986

[*nom. transl.* SAVAGE, herein, *ex* Araratellidae ERLANGER, 1986, p. 54]

Rhynchoporidae with three-layered shell and merging endopunctae in fibrous layer. Costae coarse, rounded, arising at umbones, anterior commissure uniplicate. Dental plates short. Dorsal median septum well developed. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian).*

Araratella ABRAMIAN, PLODOWSKI, & SARTENAER, 1975, p. 5 [**Liorhynchus dichotomians* ABRAMIAN, 1954, p. 66; OD]. Elongate subpentagonal outline and biconvex profile; flanks and anterior not truncated. Beak erect to incurved; foramen small and circular. Fold and sulcus well developed, arising near umbones. Anterior commissure uniplicate; tongue distinct, subrectangular, serrated. Costae coarse, rounded, originating near beaks, strong on fold and in sulcus, weak on flanks. Dental plates short, slightly convergent ventrally; ventral muscle field narrow, well impressed. Dorsal median septum thick, long; septalium long, wide; crural bases closely set; crura short, ventrally curved, V-shaped in section, open dorsally. Fine endopunctae present in fibrous shell layer. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* Armenia, Germany, Spain, Urals, Kazakhstan, Iran, Afghanistan.——FIG. 841,*1a–l. *A. dichotomians* (ABRAMIAN), high in upper Famennian, Nakhichevan, Biralichay River, Armenia; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×1; *e–l,* serial sections 0.5, 0.6, 0.8, 1.0, 1.6, 2.4, 2.55, 2.95 mm from posterior, ×4 (Erlanger, 1986).

Subfamily TRETORHYNCHINAE new subfamily

[Tretorhynchinae SAVAGE, herein]

Rhynchoporidae with subtriangular outline; anterior commissure rectimarginate; endopunctae in fibrous secondary shell layer. *Lower Carboniferous (middle Viséan–upper Viséan).*

Tretorhynchia BRUNTON, 1971, p. 98 [**Terebratula trilatera* DE KONINCK, 1843 in 1841–1844, p. 292; OD]. Outline elongate subtriangular and profile biconvex. Beak straight; delthyrium open; deltidial plates incipient. Both valves sulcate posteriorly but lacking fold or sulcus anteriorly; anterior commissure rectimarginate. Costae numerous, straight, simple, angular, from beaks. Shell finely

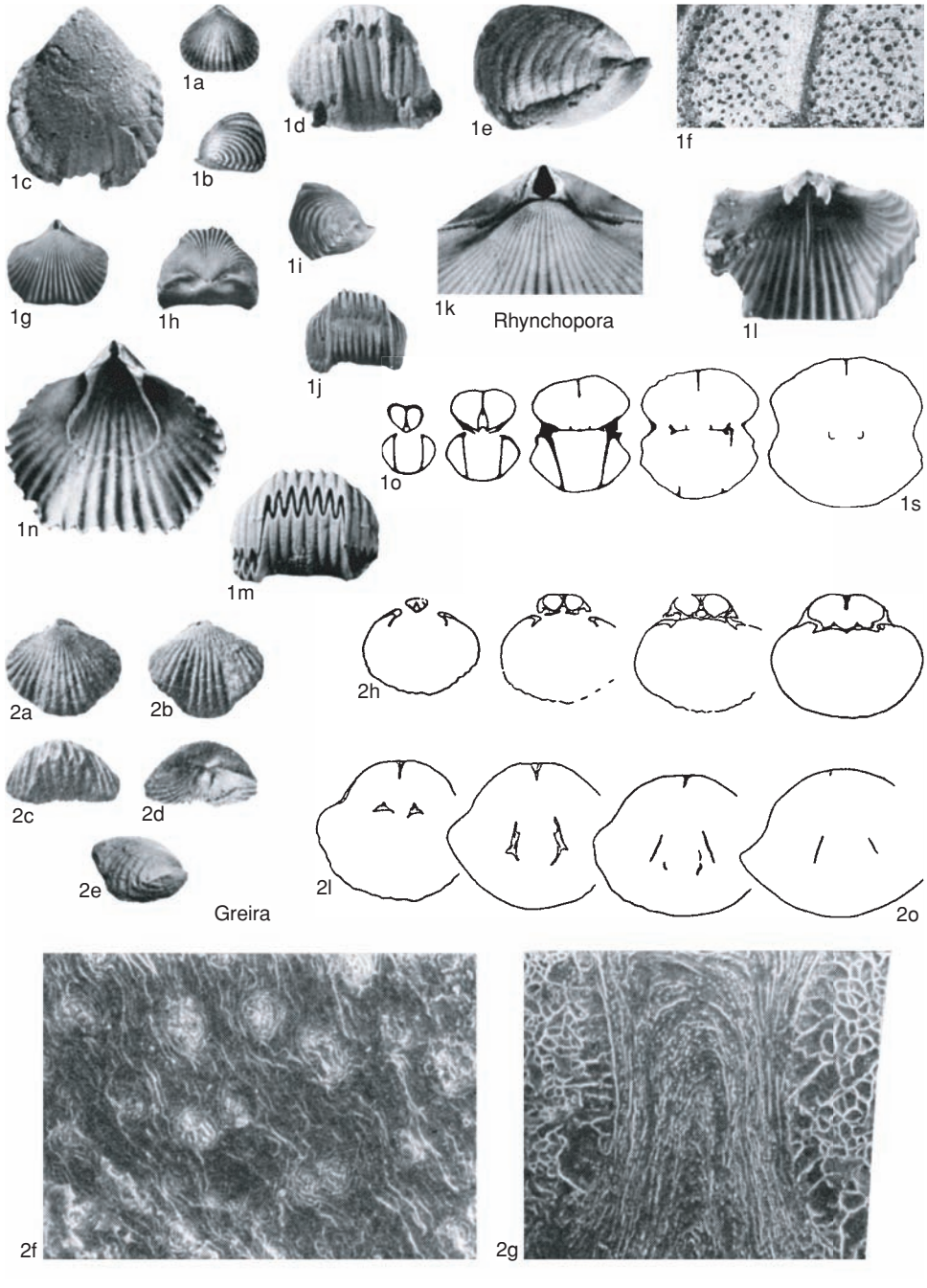

FIG. 840. Rhynchoporidae (p. 1232–1233).

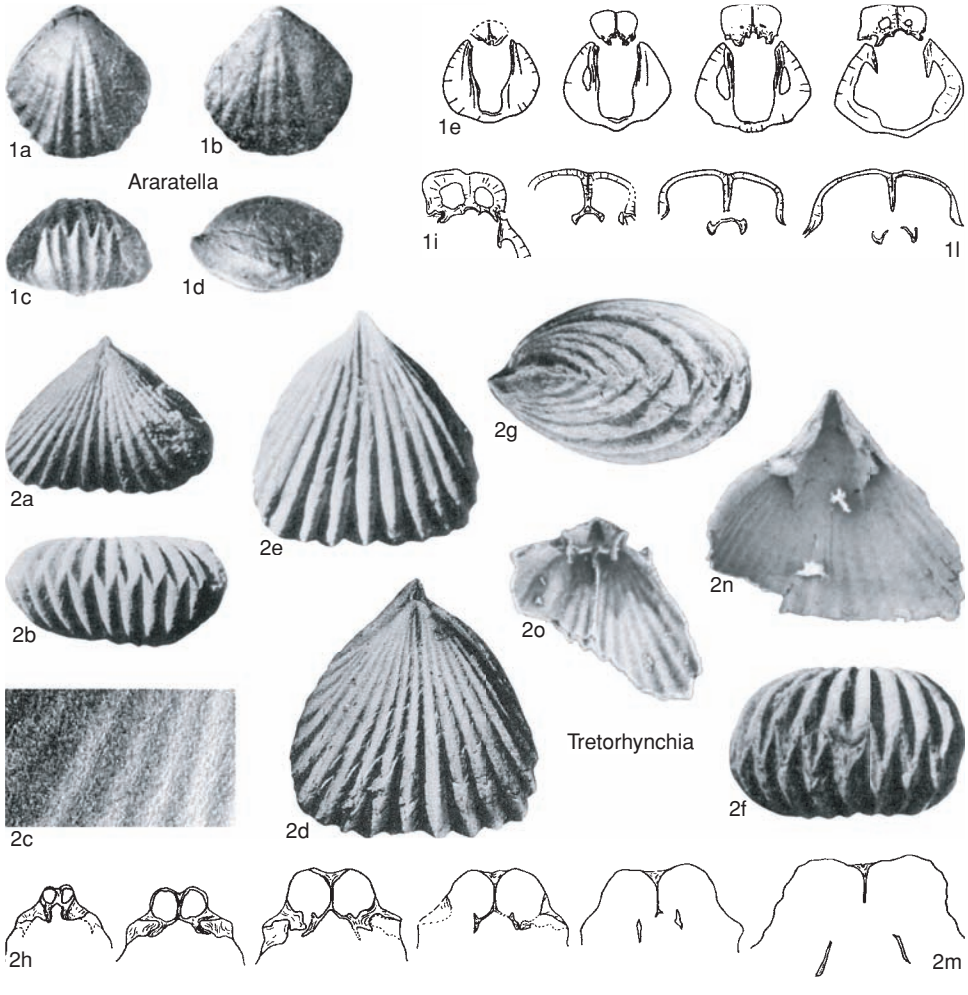

FIG. 841. Rhynchoporidae (p. 1233–1235).

endopunctate. Dental plates short, thin, slightly convergent ventrally; teeth cyrtomatodont. Dorsal median septum short, low; septalium wide; inner socket ridges overhang sockets; crural bases oblique; crura flattened, vertical to slightly oblique, ventrally curved. Ventral and dorsal muscle fields poorly impressed. Cardinal process absent. *Lower Carboniferous (middle Viséan–upper Viséan):* western Europe.——FIG. 841,*2a–o. *T. trilatera* (DE KONINCK); *a–b,* neotype, dorsal and anterior views, Carboniferous Limestone, Visé, Belgium, ×2.6; *c,* enlargement of surface showing punctae, middle Viséan, Llanfair, Anglesey, Wales, ×22; *d,* dorsal view, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×3; *e–f,* ventral and anterior views, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×2.7; *g,* lateral view, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×3; *h–m,* serial sections 0.07, 0.11, 0.39, 0.44, 0.54, 1.04 mm from posterior, middle Viséan, Carboniferous Limestone, Derbyshire, Treak Cliff, England, ×8 (Brunton, 1971); *n,* ventral valve interior, Asbian, Dartry Group, County Fermanagh, Ireland, ×5.6; *o,* dorsal valve interior, Asbian, Dartry Group, County Fermanagh, Ireland, ×6 (Brunton, 1984).

DIMERELLOIDEA

MIGUEL O. MANCEÑIDO,[1] ELLIS F. OWEN,[2] NORMAN M. SAVAGE,[3] and A. S. DAGYS[4]

[[1]La Plata Natural Sciences Museum, Argentina; [2]formerly of The Natural History Museum; [3]University of Oregon; and [4]deceased]

Superfamily DIMERELLOIDEA Buckman, 1918

[*nom. transl.* SAVAGE, 1996, p. 257, *ex* Dimerellidae BUCKMAN, 1918, p. 72]

Rhynchonellida with shells ventribiconvex to equibiconvex, mostly subcircular; tendency to dorsal sulcation; surface smooth or radially ribbed; deltidial plates reduced or absent. Dorsal median septum variable; cardinal process may be present; crura mainly mergiform, submergiform, or ensiform. *Upper Devonian (Famennian)–Holocene.*

Family DIMERELLIDAE Buckman, 1918

[Dimerellidae BUCKMAN, 1918, p. 72]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Usually sulcate dimerelloids, commonly with reduced deltidial plates. Dental plates rudimentary, fused to wall or absent; primarily ensiform bladed crura; dorsal septum may be prominent. *Upper Triassic (Norian)–Upper Jurassic (Tithonian).*

Subfamily DIMERELLINAE Buckman, 1918

[*nom. transl.* AGER, 1959b, p. 330, *ex* Dimerellidae BUCKMAN, 1918, p. 72]

Small dimerellids with dorsal median septum very strong and anteriorly rising; crura precursor of ensiform variant. *Upper Triassic (Norian).*

Dimerella VON ZITTEL, 1870, p. 220 [**D. gümbeli;* M]. Small, depressed, ventribiconvex; transverse oval to heart shaped with wide, straight hinge line and shallow dorsal sulcus; densely costellate throughout; beak high, suberect; delthyrium wide open and beak ridges sharp. Distant teeth stout but dental plates poorly developed; crura long, bladelike, moderately bent ventrally, attaining one-third dorsal valve length; dorsal median septum low posteriorly, rising very high anteriorly, almost up to ventral valve. [Other interior details not well known.] *Upper Triassic (Norian):* Austria, Dinarids.——FIG. 842,*2a–c.* **D. guembeli,* Steiermark, Austria; *a–b,* dorsal, lateral views, ×2; *c,* longitudinal section, ×2 (von Zittel, 1870).

Subfamily RHYNCHONELLININAE Ager, 1959

[Rhynchonellininae AGER, 1959b, p. 330]

Mostly ventribiconvex dimerellids with little or no dorsal median septum and crura extremely long, ensiform (sagittally bladelike or somewhat rodlike); cardinalia strong, crura direct prolongations of narrow hinge plates; muscle fields lanceolate, elongate, about two-thirds to three-quarters shell length. *Upper Triassic (Norian)–Upper Jurassic (Tithonian).*

Rhynchonellina GEMMELLARO, 1871, p. 100[29] [**R. suessi* GEMMELLARO, 1871, p. 102[31]; SD HALL & CLARKE, 1894, p. 1027] [=*Terebratulopsis* DE GREGORIO, 1930b, p. 5, obj., SD AGER, 1960, p. 161; *Rhynconellina* DE GREGORIO, 1930b, p. 12, *nom. null.*]. Medium size, equibiconvex to ventribiconvex, subcircular to ovoid, globose; rectimarginate to sulcate, incipiently ligate, ventral median sulcus possibly indenting front margin; smooth but for feeblest capillation; beak strong suberect to nearly straight, with well-developed palintrope, wide delthyrium, and rudimentary deltidial plates (sometimes conjunct). Dental plates rudimentary; hinge plates divided, cardinal process thick; variable dorsal median septum, often apically confined; crura very long (over one-half valve length), closely parallel, with tips almost touching ventral valve, reportedly with short crural processes proximally. [Alleged Toarcian and younger records unconfirmed.] *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian):* Italy (Sicily), Austria, Switzerland, Dalmatia, Hungary, ?Crimea, Morocco, Algeria.——FIG. 842,*1a–q.* **R. suessi suessi,* Hettangian–Sinemurian, Sicily; *a–e,* dorsal, lateral, anterior, ventral, posterior views, MGUP, ×1; *f–q,* transverse serial sections, distances in mm from ventral umbo, 1.55, 2.5, 2.85, 3.25, 3.4, 3.6, 3.75, 4.2, 4.7, 5.1, 5.75, 7.45, MGUP (Cicardi & Gaetani, 1974).——FIG. 842,*1r–s. R. suessi orobica* CICARDI & GAETANI, upper Hettangian–lower Sinemurian, Lombardia, Italy; *r,* internal mold showing dorsal muscle scars, G507/169; *s,* internal mold showing ventral muscle scars, G507/221, ×1 (Cicardi & Gaetani, 1974).

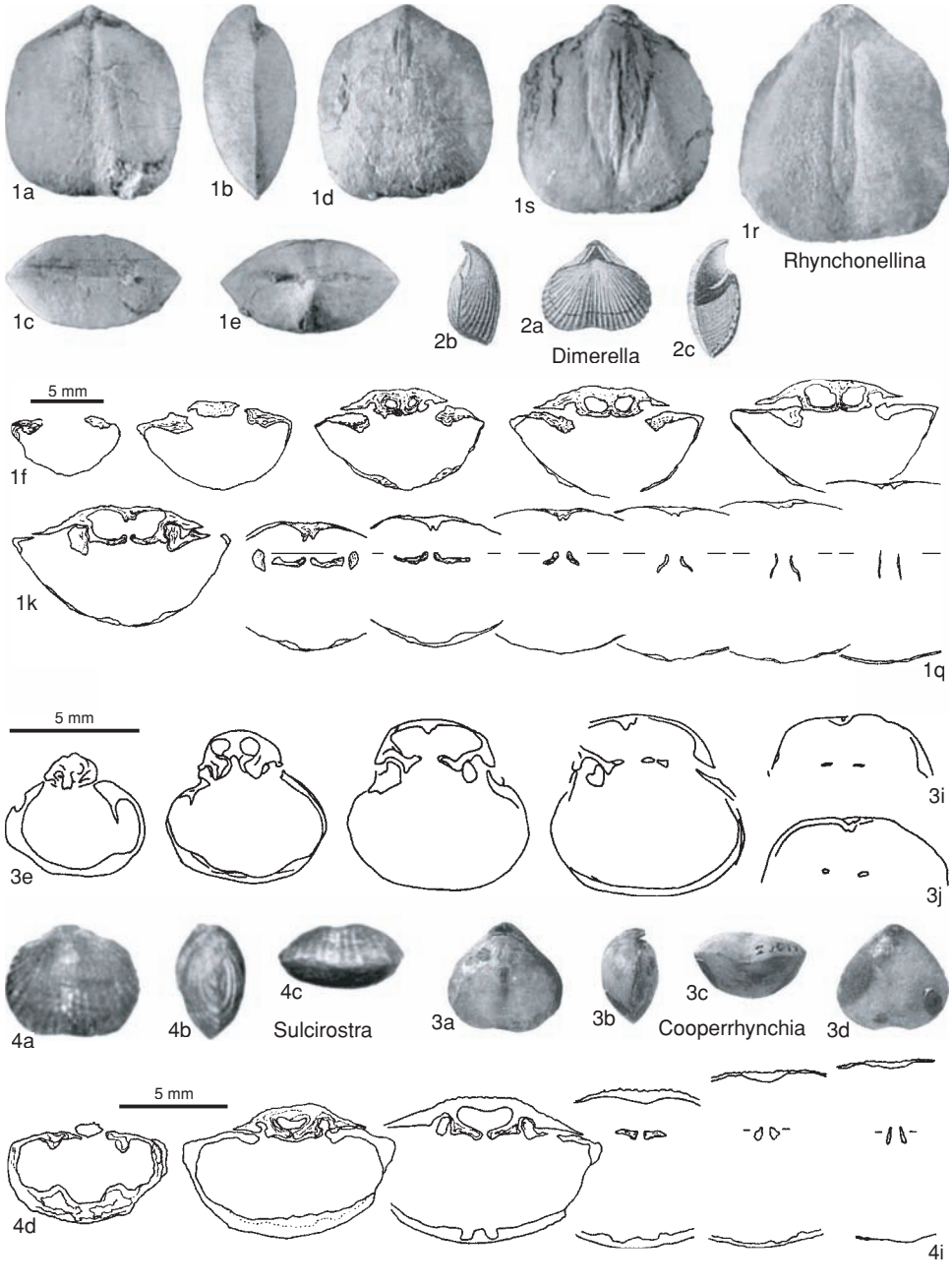

FIG. 842. Dimerellidae (p. 1236–1238).

Cooperrhynchia SANDY & CAMPBELL, 1994, p. 1245 [**Rhynchonella schucherti* STANTON, 1895, p. 31; OD] [=*Bothrorhynchia* COOPER in SANDY & CAMPBELL, 1994, p. 1250, obj.]. Small to medium size, subtriangular, gently ventribiconvex; smooth, sulcate; shallow median sulcus on both valves producing weak anterior margin indentation; beak erect to incurved, deltidial plates conjunct. Dental plates short, weak; long, low dorsal median septum; short septalium; crura closely parallel, less than midvalve

in length. *Upper Jurassic (Tithonian):* USA (California).——Fig. 842,*3a–j. *C. schucherti* (Stanton); *a–d,* lectotype, dorsal, lateral, anterior, ventral views, USNM 23017a, ×1; *e–j,* transverse serial sections, distances in mm from ventral umbo, 1.8, 2.2, 2.7, 3.1, 3.4, 3.7, USNM 23189j (Sandy & Campbell, 1994).

Sulcirostra Cooper & Muir-Wood, 1951, p. 195, *nom. nov. pro Rhynchonellopsis* de Gregorio, 1930b, p. 5, *non* Vincent, 1893, Terebratulida, *nec* Böse, 1894, Rhynchonellida [**Rhynchonellina seguenzae* Gemmellaro, 1871, p. 106[34] (although originally spelled *R. sequenzae,* prevailing usage is preserved under Article 33.3.1 of ICZN, 1999); M]. Small to medium size, equibiconvex to ventribiconvex; dorsal sulcation sometimes indenting front margin; ornament finely and densely costellate, usually also cancellate; delthyrium wide, triangular; deltidial plates rudimentary. Dental plates weak, short; septalium absent; dorsal median septum apically confined or absent; lateral septa, partly fused to fulcral plates, supporting massive hinge plates; crura closely parallel, long, reaching beyond midvalve. [Record from USA (Oregon) requires further research.] *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian), Middle Jurassic (?Aalenian):* Italy (Sicily), Austria, Dalmatia, Slovenia, Hungary, Morocco, Algeria, Turkey.——Fig. 842,*4a–c. *S. seguenzae* (Gemmellaro), Hettangian–Sinemurian, Sicily; dorsal, lateral, anterior views, approximately ×1 (Giovannoni, 1983).——Fig. 842,*4d–i. *S. paronai* (Boese), Pliensbachian, Bergamo, Italy; topotype, transverse serial sections, distances in mm from ventral umbo, 4.3, 5.6, 6.7, 7.95, 9.1, 11.85, G 509/14 (Cicardi & Gaetani, 1974).

Family PEREGRINELLIDAE Ager, 1965

[*nom. transl.* Savage, 1996, p. 257, *ex* Peregrinellinae Ager, 1965, p. 605]

Medium to large, coarsely costate Dimerelloidea with shells ventribiconvex to equibiconvex, discoidal to subglobose; commissure rectimarginate or almost rectimarginate, serrate; dental plates reduced or absent; teeth small. Dorsal median septum present or absent; crura mergiform or submergiform. *Upper Devonian (Famennian)–Lower Cretaceous (Hauterivian).*

Subfamily PEREGRINELLINAE Ager, 1965

[Peregrinellinae Ager, 1965, p. 605]

[Materials prepared by Miguel O. Manceñido & Ellis F. Owen]

Very large, fully costate to capillate Peregrinellidae, mostly ventribiconvex; faint, broad sulcation often perceivable in juveniles, otherwise rectimarginate throughout. Dental plates much reduced and wide apart; hinge plates flat to gently convex, with inner edge strongly deflected inward dorsally and swollen; true mergiform crura arising directly from this point, initially in contact with dorsal median septum, always present. *Upper Triassic (?Norian, Rhaetian)–Lower Cretaceous (Hauterivian).*

Peregrinella Oehlert, 1887a, p. 1305 [**Terebratula peregrina* von Buch, 1834, p. 73; OD; =*Terebratula multicarinata* Lamarck, 1819, p. 253, *non* Schlotheim, 1813]. Large, circular, equibiconvex to ventribiconvex, rectimarginate; costae numerous, deeply incised, sharp; beak massive, incurved. Hinge plates wide, flat; dental plates short, acutely divergent ventrally; teeth small, peglike; crura long, subparallel, laterally concave; septum low, long. *Lower Cretaceous (Berriasian–Hauterivian):* Europe (mainly southern), North America, Asia.

P. (Peregrinella). Costae simple, angular, or sometimes subquadrate. *Lower Cretaceous (Berriasian–Hauterivian):* Crimea, *Berriasian;* France, Alps, Italy, Romania, Carpathians, Caucasus, USA (California, Alaska), ?Mexico, Tibet, northern Siberia, *Valanginian–Hauterivian.*——Fig. 843*a–n. *P. (P.) multicarinata* (Lamarck), Hauterivian, France; *a–c,* dorsal, lateral, anterior views, ×1 (new); *d–n,* transverse serial sections, distances in mm from ventral umbo, 2.5, 3.2, 3.7, 4.1, 4.9, 5.2, 5.6, 5.9, 6.2, 7.4, 12.6, approximately ×2 (Ager, 1968).

P. (Peregrinellina) Hou & Wang, 1984, p. 211 [**P. (P.) xizangensis;* OD]. Similar to *P. (Peregrinella)* but costae dense, subangular, increasing by frequent bifurcation. *Lower Cretaceous (Valanginian–Hauterivian):* northern Tibet, Silesia.——Fig. 844*a–l. *P. (P.) xizangensis,* lower Hauterivian; *a–b,* dorsal, lateral views, GMC IV 83908, ×1; *c,* ventral view, GMC IV 83905, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 5.0, 5.7, 6.1, 6.6, 6.8, 7.6, 8.1, 8.6, 10.7 (Hou & Wang, 1984).

?Carapezzia Tomlin, 1930, p. 24, *nom. nov. pro Geyeria* Carapezza & Schopen, 1897, p. 248, *non* Buchecker, 1876, Insecta, *nec* Buckman, 1899, Cephalopoda, *nec* Fucini, 1901, Cephalopoda, *nec* Wagner, 1914, Gastropoda [**Rhynchonellina (Geyeria) globosa* Carapezza & Schopen, 1897, p. 248; OD]. Large to very large, round to ovoid, strongly globose and massive, ventribiconvex; without median sulcus or fold, rectimarginate or slightly planoplicate; ornament of fine capillae (on well-preserved specimens, otherwise smooth); stout, pointed beak, suberect to strongly incurved when adult; broad palintrope with sharp beak ridges; wide delthyrium and triangular conjunct deltidial plates. Dental plates ventrally divergent and distant

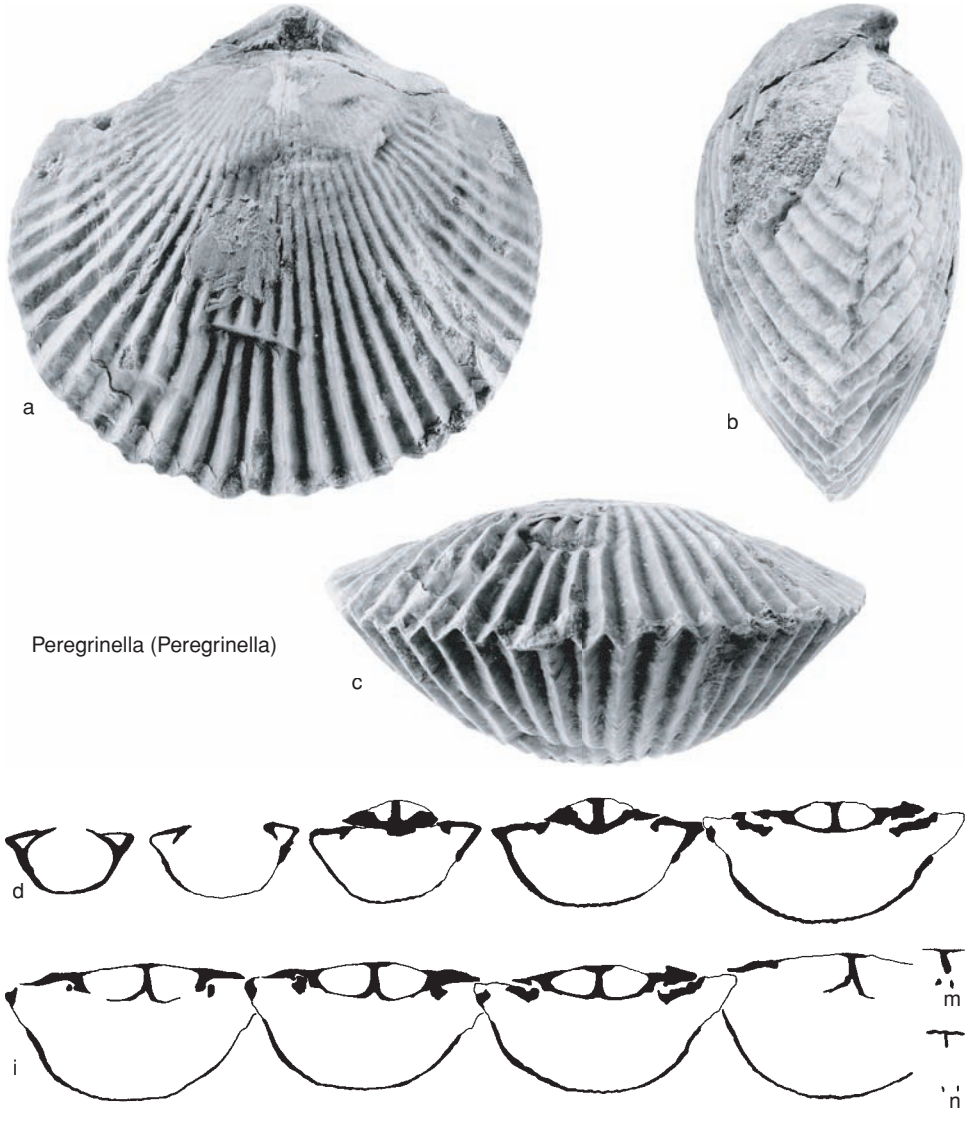

FIG. 843. Peregrinellidae (p. 1238).

or absent; dorsal median septum extending at least one-quarter valve length; crura long, over half shell length, fused apically to divide valve, with short crural processes on ventral side of crura. [Serial sections from type species unknown.] *Upper Triassic (?Norian, Rhaetian)–Lower Jurassic:* Austria, Italy (Sicily), Turkey, Algeria, ?Morocco, ?Crimea.——FIG. 845*a–n. C. geyeri* (BITTNER), Rhaetian, Gailtaler Alps, Austria; *a–c,* lectotype, dorsal, lateral, anterior views, GBA 1898/1, ×1 (Siblík, 1988); *d–n,* transverse serial sections through umbo, approximately ×1.15 (Bittner, 1898).

Subfamily DZIEDUSZYCKIINAE Savage, 1996

[Dzieduszyckiinae SAVAGE, 1996, p. 257]

[Materials prepared by NORMAN M. SAVAGE]

Large, transversely ovate Peregrinellidae with costae strong, simple, full; both valves sulcate; dental plates short, vertical; dorsal median septum short; crura long, thin, closely set. *Upper Devonian (Famennian).*

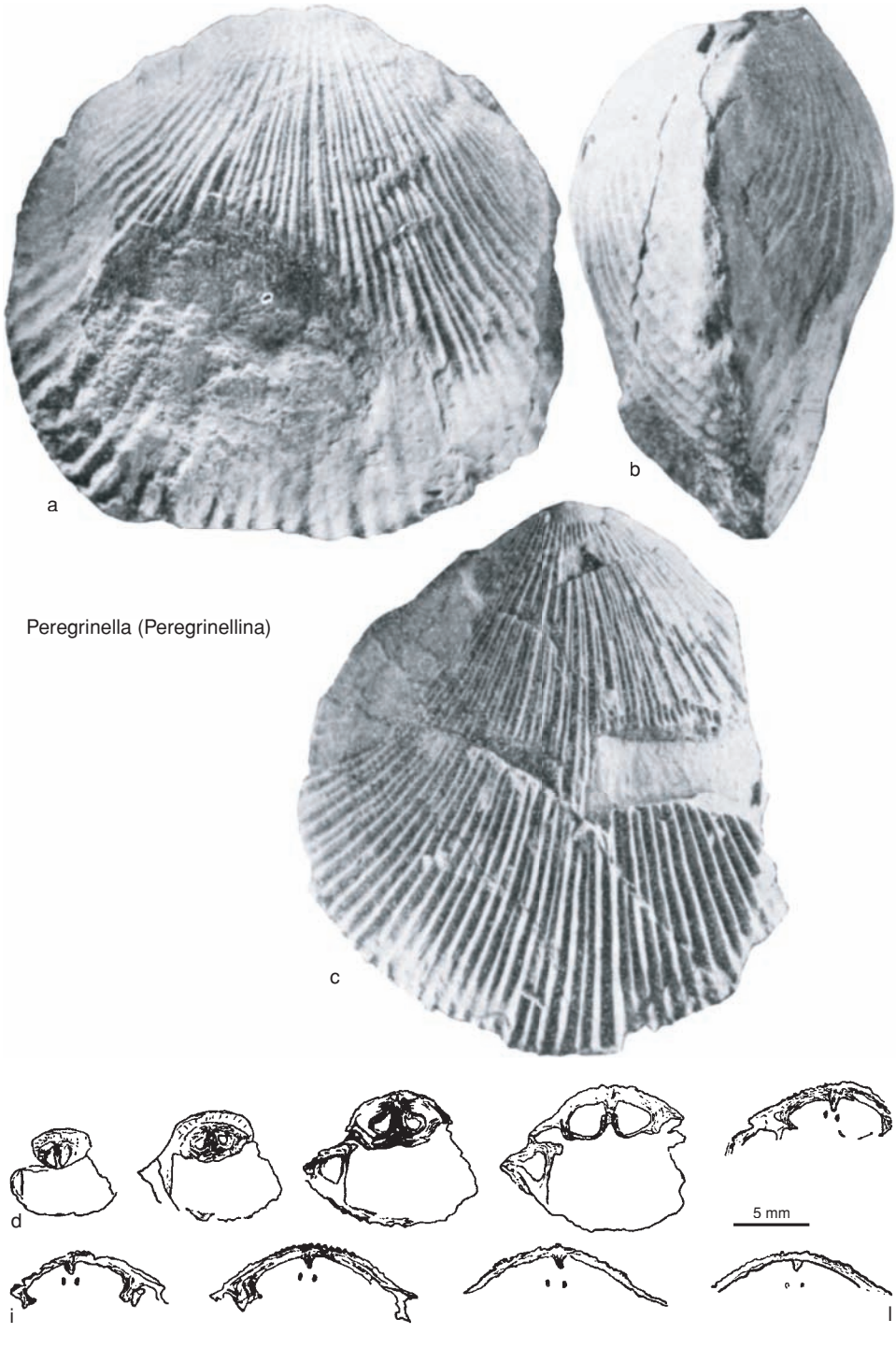

FIG. 844. Peregrinellidae (p. 1238).

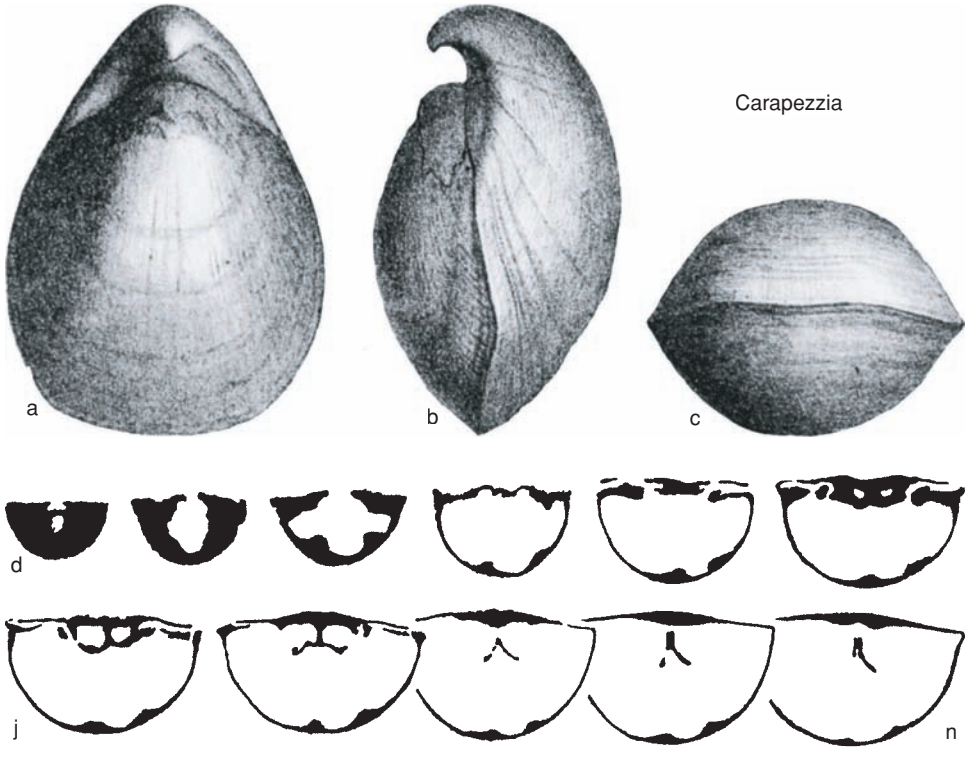

FIG. 845. Peregrinellidae (p. 1238–1239).

Dzieduszyckia SIEMIRADZKI, 1909, p. 768 [**Terebratula (?) kielcensis* ROEMER, 1866, p. 671; OD] [=*Eoperegrinella* AGER, 1968, p. 61 (type, *Halorella crassicostata* TERMIER & TERMIER, 1948, p. 51, fig. 4–5)]. Large with outline transversely ovate and profile biconvex. Beak prominent. Bisulcate with ventral sulcus usually more marked; anterior commissure weakly uniplicate to rectimarginate; serrate. Shells commonly asymmetrical, possibly resulting from crowding in monospecific groups. Costae numerous, rounded, arising at beaks, simple or sometimes dichotomous. Dental plates distinct, vertical to slightly convergent ventrally, well separated from valve walls, leaving large lateral umbonal cavities; teeth small; ventral muscle field only weakly impressed. Dorsal median septum long, low; septalium distinct, small; crura long, thin, closely set. *Upper Devonian (Famennian):* Poland, Morocco, Urals, Kazakhstan, USA.——FIG. 846,*1a–h.* **D. kielcensis* (ROEMER), upper Famennian, Holy Cross Mountains, Kielce, Kadzielnia Quarry, Poland; *a–d,* neotype, dorsal, ventral, anterior, and posterior views, ×1; *e–h,* serial sections 23.3, 22.8, 22.5, 21.5 mm from anterior, ×6 (Biernat, 1967).

Subfamily PEREGRINELLOIDEINAE Dagys, 1968

[*nom. transl.* MANCEÑIDO & OWEN, herein, *ex* Peregrinelloideidae DAGYS, 1968, p. 42]

[Materials prepared by MIGUEL O. MANCEÑIDO, ELLIS F. OWEN, & A. S. DAGYS]

Medium to large, fully costate Peregrinellidae, mostly equibiconvex, discoidal, and rectimarginate. Dental plates and dorsal median septum absent; flat, wide, subhorizontal hinge plates with inner edge deflected inward ventrally, giving rise to submergiform crura. *Lower Jurassic, ?Middle Jurassic.*

Peregrinelloidea DAGYS, 1968, p. 43 [**P. malkovi;* OD]. Large, laterally oval, thin, equibiconvex, shallow sulcus in posterior of dorsal valve, anterior commissure rectimarginate; surface with distinct, branching costae; beak suberect, ridges distinct,

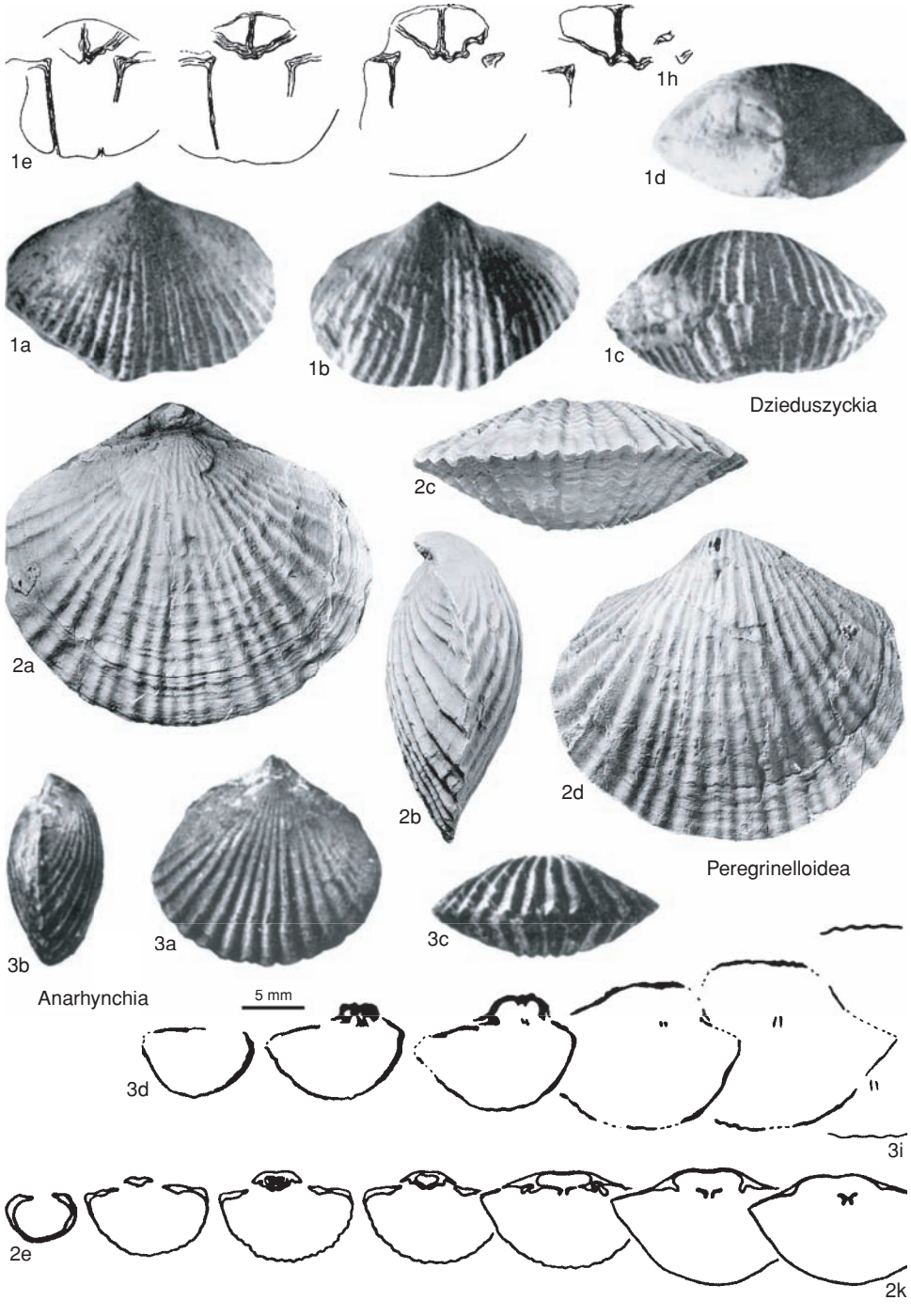

FIG. 846. Peregrinellidae (p. 1241–1243).

foramen hypothyrid, deltidial plates disjunct. Dental plates, pedicle collar, and median septum absent; outer hinge plates broad, incipiently concave in section, crural bases directed only ventrally; crura long, parallel, situated along commissural plane. *Lower Jurassic (Pliensbachian):* northeastern Siberia, ?Argentina.——Fig. 846,*2a–k. *P. malkovi,* northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 215/78, ×1; *e–k,* transverse serial sections, distances in mm from first section, 0.7, 2.6, 3.2, 3.6, 4.3, 5.1, 5.7 (Dagys, 1968).

Anarhynchia Ager, 1968, p. 63 [**A. gabbi;* OD]. Large, subcircular to transverse elliptical; dorsal valve almost equibiconvex, somewhat flattened posteriorly; both valves fully costate; costae numerous, strong, blunt, attenuated on either side; rectimarginate, serrate; beak prominent, upright to suberect, with large, mesothyrid foramen. No dental plates, teeth small, arising from valve wall; hinge plates fused, no septalium; crura long, closely set, bladelike, extended along commissural plane, distally gently curved. *Lower Jurassic, ?Middle Jurassic:* western USA (California, ?Oregon), ?Argentina.——Fig. 846,*3a–i. *A. gabbi,* ?Callovian, California; *a–c,* dorsal, lateral, anterior views, personal collection, Derek Ager, J.1223, ×1; *d–i,* transverse serial sections, distances in mm from ventral umbo, 3.4, 4.2, 4.8, 6.6, 8.6, 17.5, USNM M899 (Ager, 1968).

?Family HALORELLIDAE Ager, 1965

[*nom. transl.* Dagys, 1974, p. 85, *ex* Halorellinae Ager, 1965, p. 605]

[Materials prepared by Miguel O. Manceñido, Ellis F. Owen, & A. S. Dagys]

Large rhynchonellide shells, with wide, straight hinge line, rectimarginate or nearly so, commonly with opposite sulci, may be asymmetrical; beak high, hypothyrid. Dental plates widely spaced, septum very small or absent; crura direct prolongations of hinge plates, flattened in plane of commissure (ciliform type). [A distinctive group tentatively retained within this superfamily following Ager, Childs, and Pearson (1972), although Dagys (1974) placed it within the basiliolids.] *Upper Triassic (?upper Carnian, Norian).*

Halorella Bittner, 1884, p. 107 [**Rhynchonella amphitoma* Bronn, 1832, p. 162; SD Hall & Clarke, 1894, p. 832] [=*Harorella* Ching, Sun, & Ye in Ching & others, 1979, p. 166, *nom. null.; Halorelella* Gupta, 1984, p. 105–106, *nom. null.*]. Medium size to large, transverse oval to subpentagonal with sharp costae beginning from umbo; sulci on both valves or uniplicate; beak suberect, ridges sharp, foramen oval, hypothyrid, deltidial plates conjunct. Dental plates distinct, ventrally divergent, pedicle collar present; septum weak or absent, long ciliform crura. *Upper Triassic (?upper Carnian, Norian):* Alps, Carpathians, Turkey, Pamirs, northeastern Siberia, China, Indonesia, western USA, New Zealand.——Fig. 847,*1a–r. *H. amphitoma* (Bronn), Norian, Pamirs; *a–c,* dorsal, ventral, anterior views, IGiG 200/6, ×1; *d–r,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.6, 1.2, 1.8, 2.4, 2.7, 3.1, 3.3, 3.6, 4.1, 4.6, 5.3, 5.9, 6.7 (Dagys, 1963).

Halorelloidea Ager, 1960, p. 159 [**Halorella rectifrons* Bittner, 1884, p. 107; OD]. Similar to *Halorella* but smooth or with low, rounded costae. Dental plates subparallel, pedicle collar present; septum and septalium absent; crura long, curved ventrally, ciliform. *Upper Triassic (Norian):* eastern Alps, Carpathians, Italy (Sicily), Pamirs, Himalayas, Indonesia (Seran), Primorye.——Fig. 847,*2a–p. *H. rectifrons* (Bittner), Pamirs; *a–b,* dorsal, anterior views, IGiG 200/32, ×1; *c–p,* transverse serial sections, distances in mm, 0.3, 0.8, 1.3, 1.6, 2.0, 2.3, 2.5, 2.9, 3.2, 3.5, 3.9, 4.3, 4.6, 4.9 (Dagys, 1963).

?Family CRYPTOPORIDAE Muir-Wood, 1955

[Cryptoporidae Muir-Wood, 1955, p. 76]

[Materials prepared by Miguel O. Manceñido & Ellis F. Owen]

Small, smooth rhynchonellide shells, with large deltoid foramen slightly restricted by elongate, triangular, auriculate deltidial plates, distant from each other; beak ridges sharp. Dental plates variably developed to absent; crura moderately long, maniculiform, continuous with socket ridges; dorsal median septum usually elevated anteriorly; cardinal process a bilobate thickening between socket ridges; single pair of metanephridia, 2 pairs of adductor muscles and circinate spirolophe. [A seemingly primitive and controversial group that is tentatively included in this superfamily in spite of a considerable Cretaceous gap; alternatively, possible relationships with norelloids may not be totally ruled out.] *Upper Cretaceous (upper Campanian)–Holocene.*

Cryptopora Jeffreys, 1869, p. 136 [**C. gnomon;* M; =*Atretia gnomon* Jeffreys, 1876, p. 251] [=*Atretia* Jeffreys in Carpenter, Jeffreys, & Thomson, 1870, p. 421 (type, *A. gnomon* Jeffreys, 1876, p. 251); *Neatretia* Fischer & Oehlert, 1891, p. 122, obj.; *Crytopora* Cooper, 1959, p. 22, *nom. null.; Mannia* Davidson, 1874a, p. 156 (type, *M. nysti,*

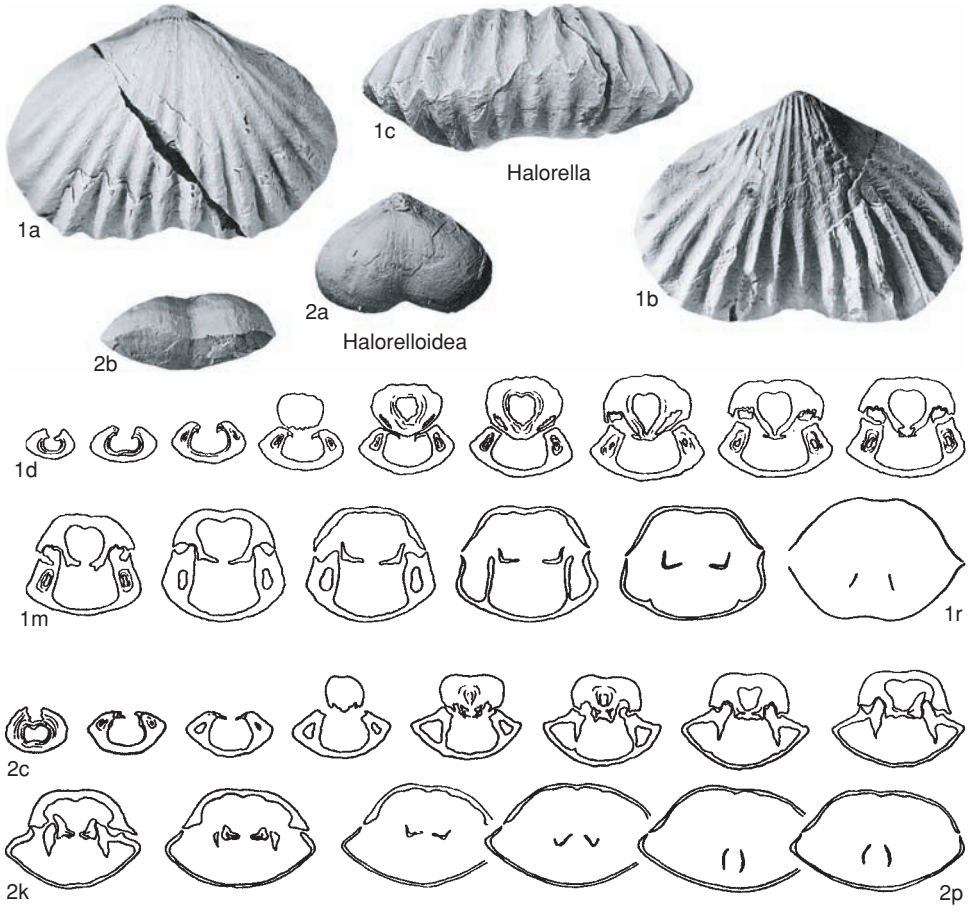

FIG. 847. Halorellidae (p. 1243).

M); *Mannia* DEWALQUE, 1868, p. 432, *nom. nud.*]. Small, translucent, subtrigonal to ovoid-lenticular, almost equibiconvex; rectimarginate to broadly sulcate, smooth; beak moderately long, pointed, nearly straight; foramen large, incomplete; deltidial plates auriculate, rudimentary, disjunct. Dental plates distinct, subvertical; cardinal process small and transverse; dorsal median septum high; crura digitate distally. [Living species range from abyssal to sublittoral.] *Paleogene (lower Danian)–Neogene (Pliocene), Holocene:* Denmark, Belgium, Spain, Austria, Italy, Sardinia, Poland, Hungary, Ukraine, USA (Alabama), Cuba, Venezuela, Fiji, Antarctica, *lower Danian–Pliocene;* North Atlantic (Massachusetts), South Atlantic, Africa, Indopacific, *Holocene.*——FIG. 848,*1a–d. *C. gnomon* (JEFFREYS), Holocene, Massachusetts, off eastern USA; *a–b,* ventral, lateral views, USNM 44911a, ×6; *c,* anterior view, USNM 44911c, ×6; *d,* interior of dorsal valve with maniculiform crura, USNM 44911d, ×8 (Cooper, 1959).——FIG. 848,*1e. C. nysti* (DAVIDSON), dorsal view showing auriculate deltidial plates and incomplete foramen, upper Miocene, Antwerp, Belgium, USNM 549422a, ×20 (Cooper, 1959).

Aulites RICHARDSON, 1987, p. 45 [**Atretia brazieri* CRANE, 1886, p. 183; OD]. Similar to *Cryptopora* but without dental plates, rectimarginate to gently uniplicate; foramen large with narrow marginal deltidial plates bordering delthyrium. Crura nondigitate maniculiform and inwardly curving; hinge plates well developed; cardinal process as paired semicircular thickenings. *Paleogene (upper Oligocene)–Holocene:* Australia (neritic to bathyal).——FIG. 848,*2a–h. *A. brazieri* (CRANE), Holocene, southeastern Australia; *a–f,* dorsal view, ventral view, ventral valve interior, dorsal valve interior, lateral view, anterior view, ×10; *g,* interior of dorsal umbo showing cardinalia, ×30; *h,* interior of dorsal valve showing maniculiform crura, ×30 (Richardson, 1987).

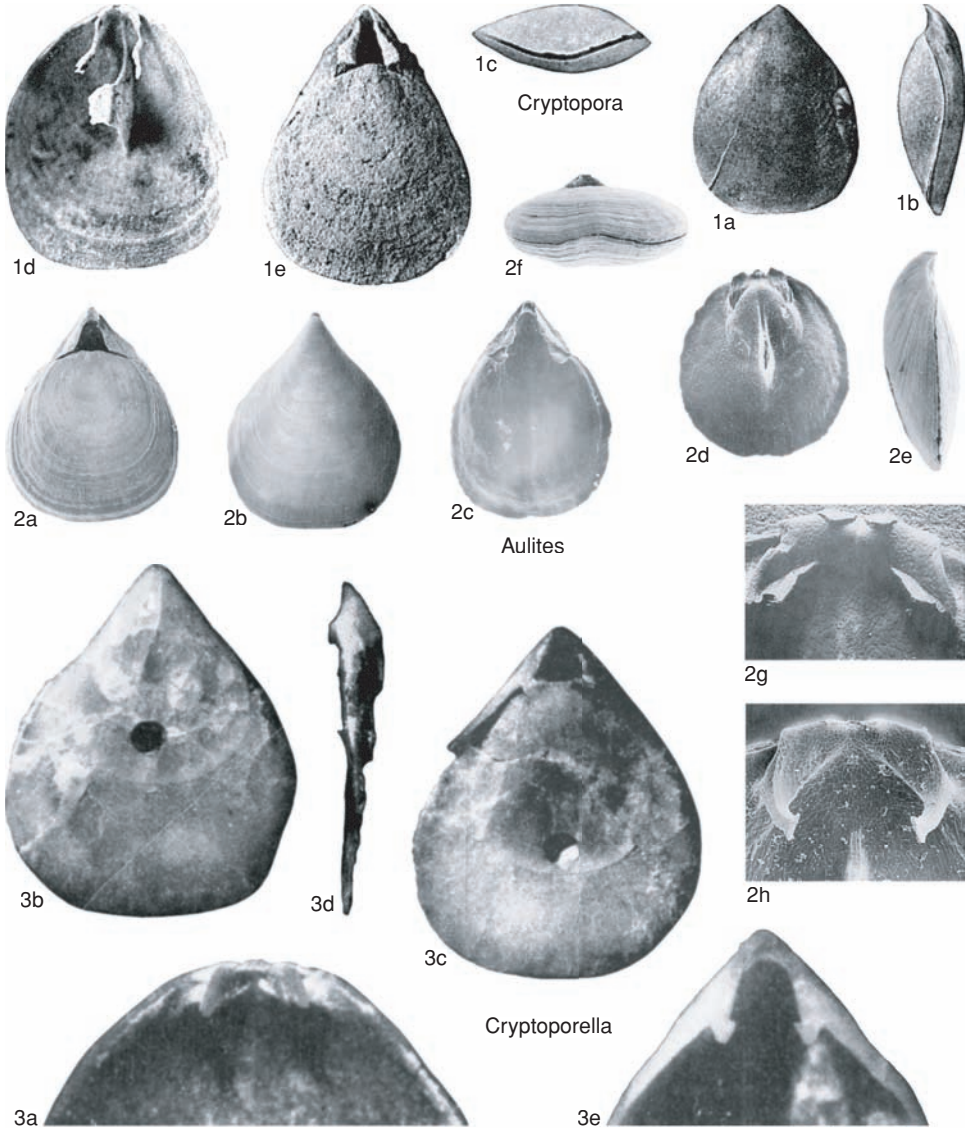

FIG. 848. Cryptoporidae (p. 1243–1245).

?**Cryptoporella** BITNER & PISERA, 1979, p. 71 [**C. antiqua;* OD]. Small, smooth, subtrigonal; externally similar to *Cryptopora,* rectimarginate, greatest width anterior to midvalve; moderately biconvex; beak sharp, fairly long, foramen large, triangular. Hinge teeth long, inwardly curved, and deeply inserted, supported by parallel dental plates; crura very short and wide; median septum absent. [Lack of dorsal septum unusual; family allocation requires revision.] *Upper Cretaceous (upper Campanian–lower Maastrichtian):* eastern Poland. ——FIG. 848,*3a–e. *C. antiqua,* lower Maastrichtian, Mielnik; *a,* dorsal valve interior, ×20; *b–d,* ventral valve, dorsal valve, lateral view of ventral valve, ×15; *e,* pedicle valve, inner view, ×20 (Bitner & Pisera, 1979).

RHYNCHOTETRADOIDEA

NORMAN M. SAVAGE,[1] MIGUEL O. MANCEÑIDO,[2] ELLIS F. OWEN,[3] and A. S. DAGYS[4]

[[1]University of Oregon; [2]La Plata Natural Sciences Museum, Argentina; [3]formerly of The Natural History Museum; and [4]deceased]

Superfamily RHYNCHOTETRADOIDEA Licharew, 1956

[*nom. transl.* SAVAGE, 1996, p. 254, *ex* Rhynchotetradidae MCLAREN, 1965, p. 589, *nom. correct. pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

Rhynchonellida with elongate oval outline; apical angle acute; dorsal fold and ventral sulcus weak; planareas distinct, often concave; costae coarse to very coarse, often with superimposed striae anteriorly; foramen with conjunct deltidial plates. Dental plates converge ventrally to form sessile spondylium or spondylium duplex; spondylium with or without lateral buttresses, atrophied and lost in all Mesozoic genera. Dorsal median septum strong; septalium present without cover plate; cardinal process absent; crural bases usually triangular in cross section. *Upper Devonian (Famennian)–Middle Jurassic (Callovian).*

Family RHYNCHOTETRADIDAE Licharew, 1956

[*nom. correct.* MCLAREN, 1965, p. 589, *pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

[Materials prepared by NORMAN M. SAVAGE]

Rhynchotetradoidea without lateral buttresses in ventral valve; shell surface with radial striae. *Upper Devonian (Famennian)–Upper Carboniferous (lower Bashkirian).*

Subfamily RHYNCHOTETRADINAE Licharew, 1956

[*nom. transl.* SAVAGE, 1996, p. 255, *ex* Rhynchotetradidae MCLAREN, 1965, p. 589, *nom. correct. pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

Rhynchotetradidae with sessile spondylium or spondylium duplex in ventral valve. *Lower Carboniferous (Tournaisian)–Upper Carboniferous (lower Bashkirian).*

Rhynchotetra WELLER, 1910, p. 506 [**Rhynchonella caput testudinis* WHITE, 1865, p. 23; OD]. Subtriangular to elongate outline and biconvex profile; anterior and lateral margins subvertical; posterolateral margins concave. Beak erect. Fold and sulcus weak; anterior commissure uniplicate; tongue distinct, serrate. Costae rounded, some bifurcation and intercalation; shell surface with fine radial striae. Dental plates meet as sessile or supported spondylium. Dorsal median septum strong, extending to midlength; septalium narrow, deep, long, open but with medially projecting edges; crural bases triangular in section. *Lower Carboniferous (Tournaisian):* North America, Russia.——FIG. 849,*1a–c. *R. caputtestudinis* (WHITE), Kinderhookian, Burlington Limestone, Burlington, Iowa, USA; dorsal, lateral, and anterior views, ×1 (Weller, 1914).——FIG. 849,*1d–k. R. missouriensis,* Kinderhookian, Burlington Limestone, Missouri; *d–g,* dorsal, ventral, anterior, and lateral views, ×1; *h–k,* serial sections, ×2.5 (Weller, 1914).

Goniophoria JANISCHEWSKY, 1910, p. 80 [**G. monstrosa;* SD SCHUCHERT & LEVENE, 1929a, p. 63]. Large with elongate subpentagonal outline and biconvex profile; anterior and lateral margins truncated. Beak erect. Dorsal fold and ventral sulcus obscured by plicae; anterior commissure sulciplicate. Plicae strong, arising at umbones, typically 4 on dorsal valve with 2 on fold, and 5 on ventral valve with 1 in sulcus. Spondylium in ventral valve supported by strong median septum. Dorsal median septum protruding into large U-shaped septalium. *Carboniferous (Tournaisian–Namurian):* Urals, Donetz basin, Siberia, China.——FIG. 849,*2a–c. *G. monstrosa,* Lower Carboniferous, Khabar, southern Urals; holotype, dorsal, lateral, and anterior views, ×1 (Licharew, 1957).——FIG. 849,*2d. G. carinata* JANISCHEWSKY, Lower Carboniferous, southern Urals; transverse section near posterior, ×2 (Licharew, 1957).

Nepasitoechia HAVLÍČEK, 1979, p. 91 [**N. sartenaeri;* OD]. Elongate triangular outline and thin, biconvex profile. Beak straight; foramen not recorded. Fold and sulcus very weak to absent; anterior commissure rectimarginate. Costae numerous, some bifurcation and intercalation; fine striae occasionally preserved. Dental plates strong, slightly convergent ventrally. Dorsal median septum short, low, thick; septalium deep, U-shaped, partly restricted by projecting inner edges of hinge plates; hinge plates divided anterior of septalium. *Lower Carboniferous (lower Tournaisian):* Bohemia.——FIG. 850*a–j. *N. sartenaeri,* 4 m above *Clymenia* Zone, Nepasice borehole, Hradec Kralove; *a,* holotype, dorsal view; *b–d,* topotype, dorsal, ventral, and lateral views; *e,* anterior view of another topotype, ×2.8; *f–j,* serial sections 0.1, 0.2, 0.4, 0.7, 1.3 mm from posterior, approximately ×5 (Havlíček, 1979).

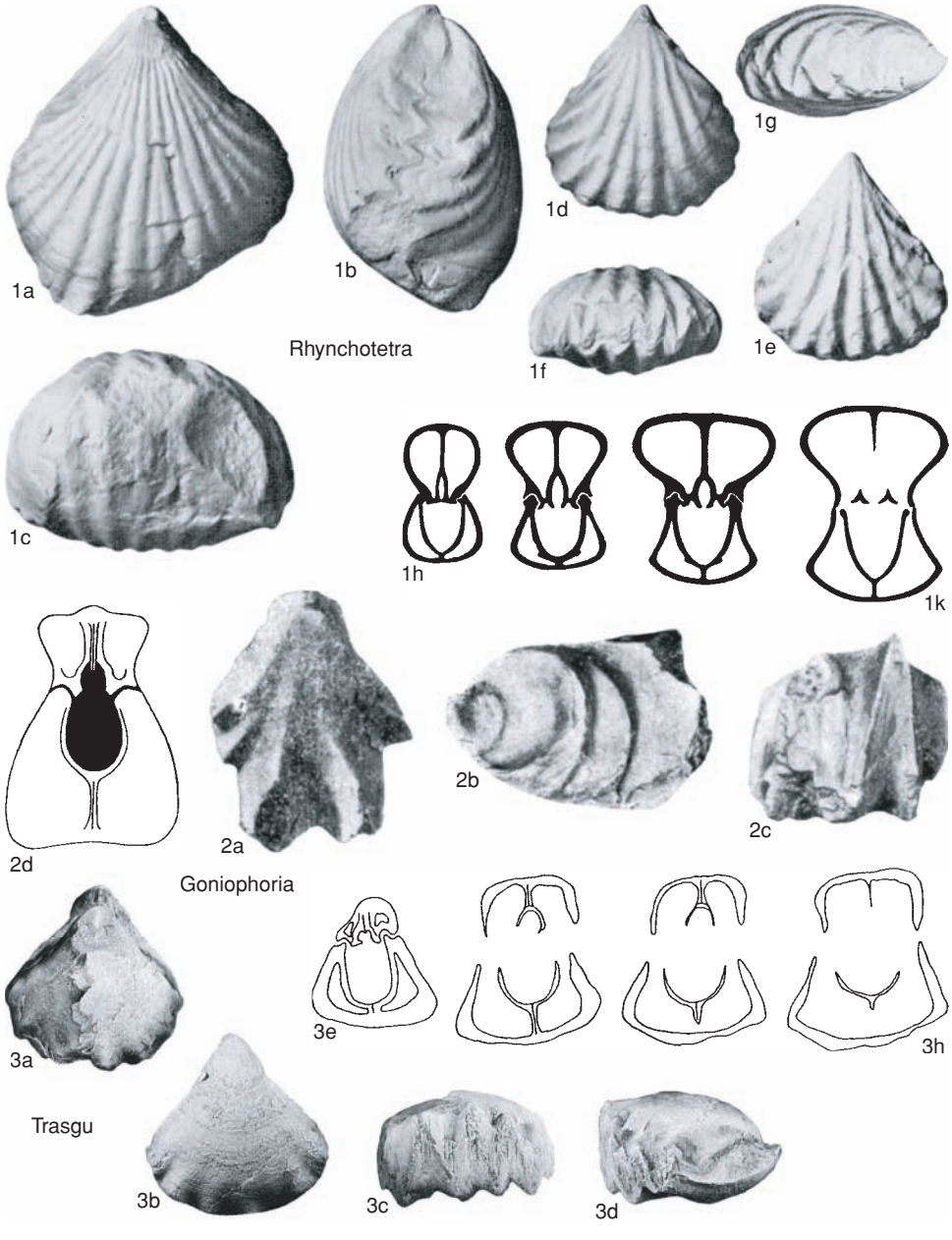

FIG. 849. Rhynchotetradidae (p. 1246–1248).

Trasgu MARTÍNEZ-CHACÓN, 1979, p. 251 [**T. minor;* OD]. Small with subtriangular outline and dorsibiconvex, anteriorly inflated profile; anterior margin subvertical; posterolateral margins concave. Beak erect. Fold and sulcus very weak to absent; anterior commissure uniplicate; tongue low, coarsely denticulate. Costae very coarse, mostly restricted to anterior margin. Dental plates and ventral median septum forming large U-shaped spondylium. Dorsal median septum wide, low, supporting septalium; septalium long, U-shaped, with median septum projecting slightly into septalium; crura laterally flattened. *Upper Carboniferous (lower Bashkirian):* Spain (Cantabrian Mountains).——FIG. 849,*3a–h.*

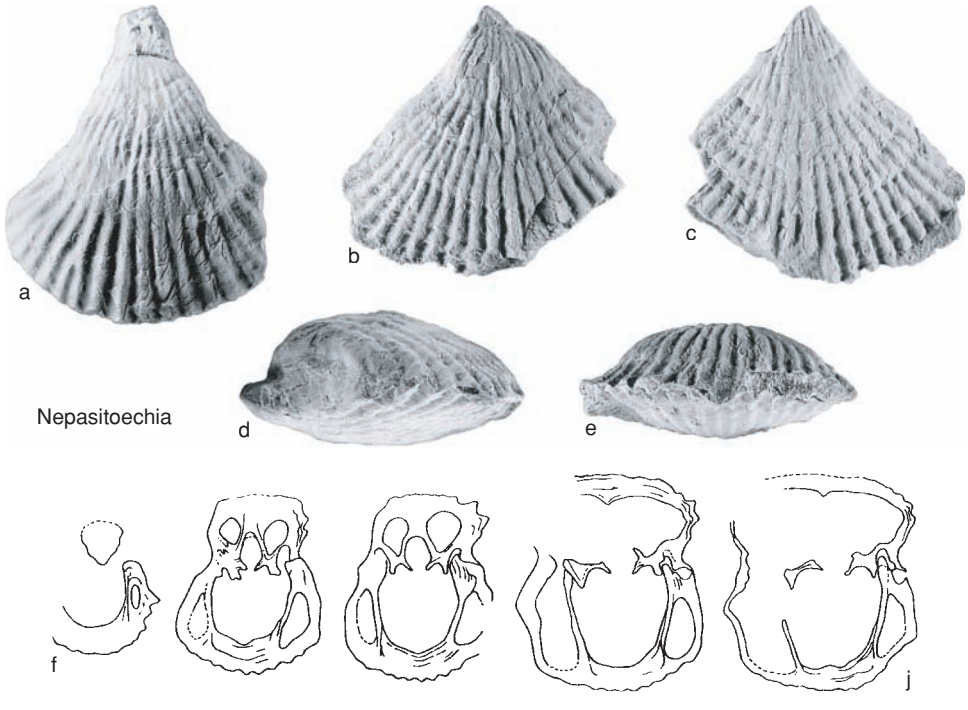

FIG. 850. Rhynchotetradidae (p. 1246).

**T. minor,* upper Valdeteja Formation, Oviedo; *a–d,* holotype, dorsal, ventral, anterior, lateral views, ×2.5; *e–h,* serial sections 1.2, 2.2, 2.3, 2.6 mm from posterior, ×4.5 (Martínez-Chacón, 1979).

Subfamily AXIODEANEIINAE Savage, 1996

[Axiodeaneiinae SAVAGE, 1996, p. 255]

Rhynchotetradidae with sessile spondylium; elongate outline; costae very coarse. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian).*

Axiodeaneia CLARK, 1917, p. 374 [**A. platypleura;* OD]. Narrowly elongate outline and biconvex profile; anterior and lateral margins subvertical. Beak erect; foramen present apically. Fold and sulcus weak; anterior commissure uniplicate; tongue low, typically tridentate. Costae very coarse, angular; shell surface with fine radial striae. Dental plates converging ventrally but not meeting, extending one-quarter valve length. Dorsal median septum strong, long, reaching one-third valve length; septalium wide, V-shaped; hinge plates ending with septalium; crural bases large, ventrally concave; crura with triangular cross section. *Lower Carboniferous (Tournaisian):* North America.——FIG. 851,*1a–f.* **A. platypleura,* Lodgepole Formation, Bridger Mountains, Montana, USA; *a–d,* dorsal, ventral, anterior, and lateral views, ×1.25; *e–f,* interiors of dorsal and ventral valves, ×3 (new).——FIG. 851,*1g–o. A. usheri* (BROWN), Banff Formation, Jasper Park, western Alberta, Canada; serial sections 2.0, 2.6, 3.0, 3.2, 3.6, 4.2, 5.2, 5.4, 6.2 mm from posterior, ×2 (Carter, 1987).

Paraphorhynchus WELLER, 1905, p. 260 [**P. elongatum;* OD]. Elongate oval to subtriangular outline and biconvex profile; subvertical anterior and lateral margins. Beak erect; foramen elongate. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue high, broad, serrate. Costae rounded, arising at umbones, weak on flanks; shell surface with fine radial striae. Dental plates long, almost meeting ventrally; narrow ventral muscle field between dental plates. Dorsal median septum strong, short; septalium large, open; hinge plates divided anterior of septalium. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America, Europe, Urals, Novaya Zemlya, Kazakhstan.——FIG. 851,*2a–j.* **P. elongatum,* lower Mississippian, Kinderhookian, Knox County, Missouri, USA; *a–e,* dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–j,* serial sections, ×2 (Weller, 1914).

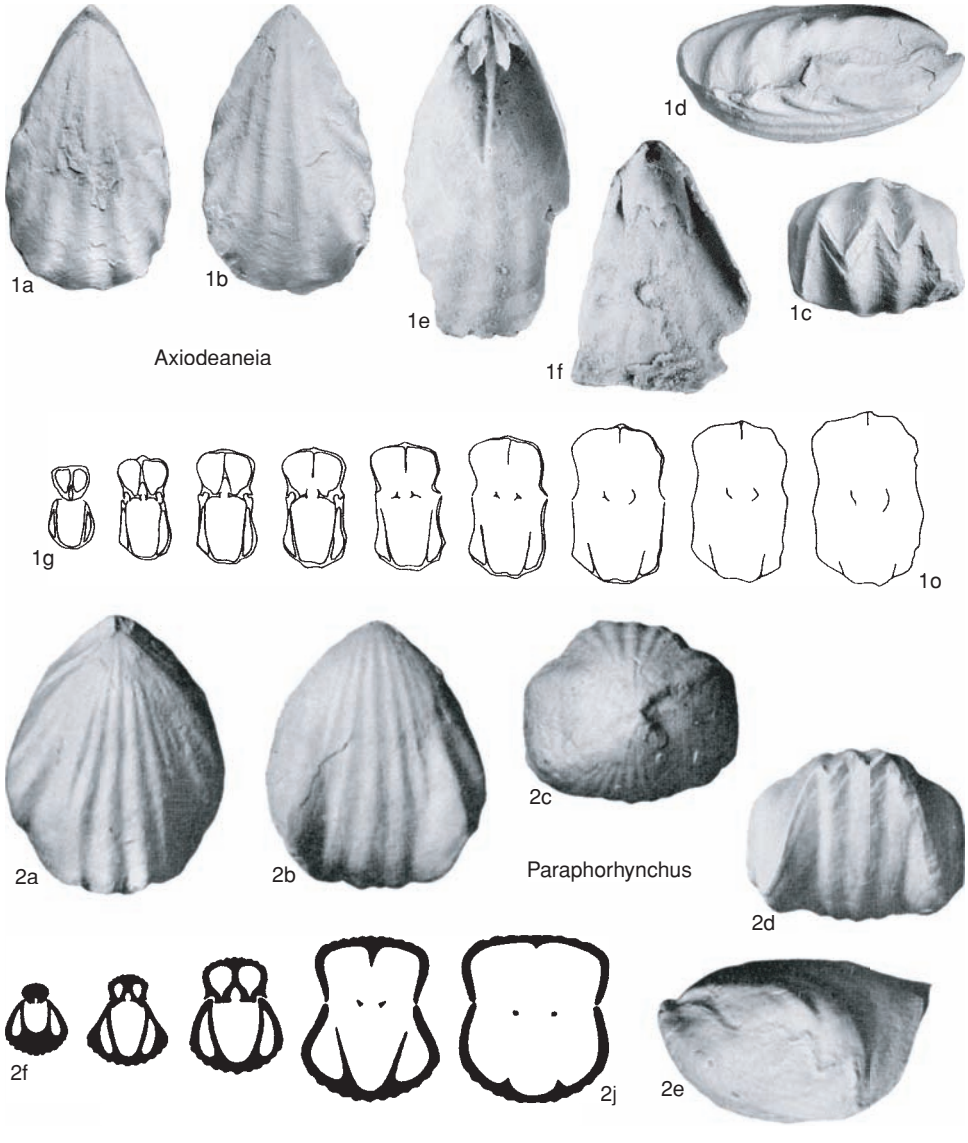

FIG. 851. Rhynchotetradidae (p. 1248).

Family TETRACAMERIDAE Licharew, 1956

[*nom. transl.* RZHONSNITSKAIA, 1958, p. 115, *ex* Tetracamerinae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

[Materials prepared by NORMAN M. SAVAGE]

Rhynchotetradoidea with lateral buttresses in ventral valve; shell surface without radial striae. *Lower Carboniferous (lower Tournaisian–upper Tournaisian).*

Tetracamera WELLER, 1910, p. 503 [**Rhynchonella subcuneata* HALL, 1858b, p. 11; OD]. Outline subtriangular and biconvex, profile subrectangular; anterior and lateral margins vertical. Beak small, erect; delthyrium with small foramen apically. Fold and sulcus very low; anterior commissure weakly uniplicate to rectimarginate; dentate. Costae angular, simple, from beaks. Shell surface with fine radial striae. Dental plates converging as sessile spondylium with a lateral buttress plate across each umbonal cavity. Dorsal median septum strong, extending almost to midlength; septalium narrow,

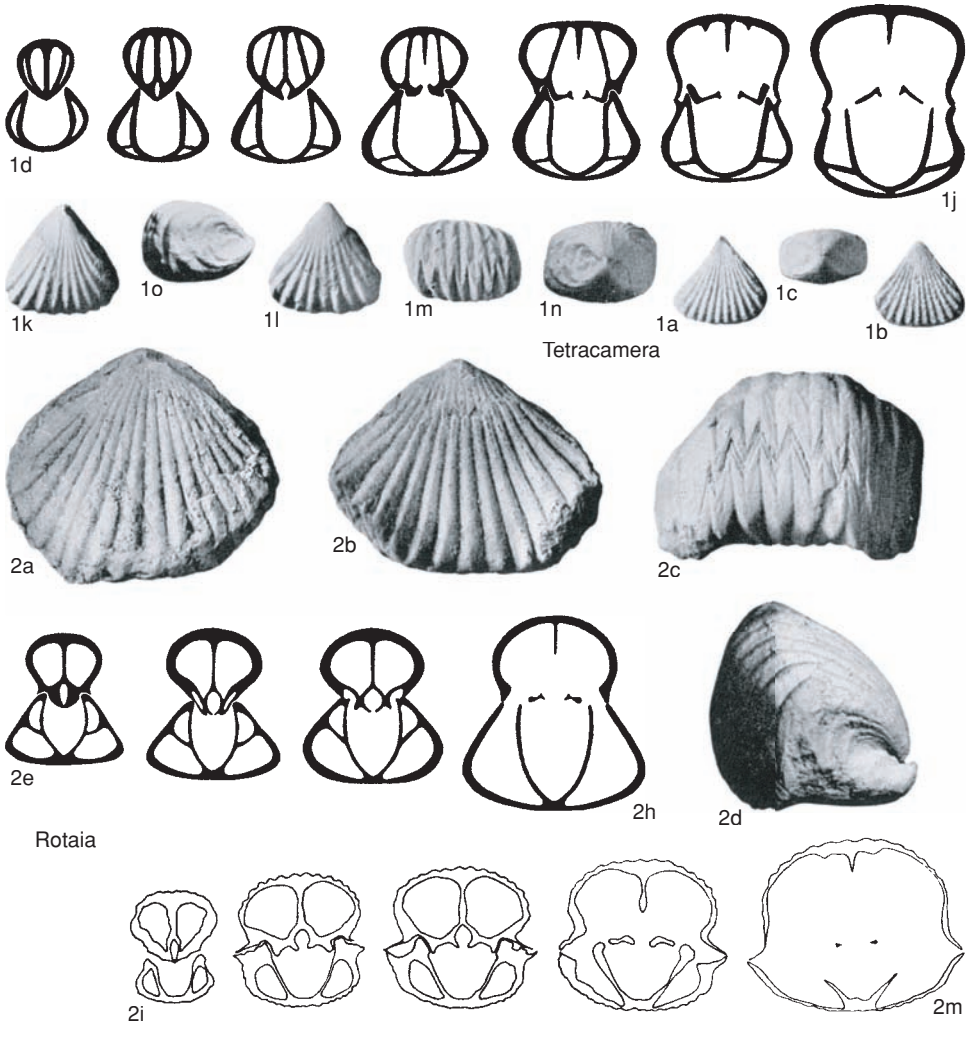

FIG. 852. Tetracameridae (p. 1249–1251).

short, open; hinge plates dividing immediately anterior of septalium, supported by subvertical plates extending to valve floor; crural bases inclined ventrolaterally. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* North America, Kazakhstan, Urals, Australia.——FIG. 852,*1a–j. *T. subcuneata* (HALL), Mississippian, Osagean, Salem Limestone, Salem, Indiana, USA; *a–c,* dorsal, ventral, and posterior views, ×1; *d–j,* serial sections, ×2.5 (Weller, 1914).——FIG. 852,*1k–o. T. arctirostrata* (SWALLOW), Mississippian, Osagean, Salem Limestone, Alton, Illinois, USA; dorsal, ventral, anterior, posterior, and lateral views, ×1 (Weller, 1914).

Rotaia RZHONSNITSKAIA, 1959, p. 30, *nom. nov. pro Welleria* ROTAI, 1941, p. 107, *non* ULRICH & BASSLER, 1923 [**Rhynchonella subtrigona* MEEK & WORTHEN, 1860, p. 451; OD]. Large with subpentagonal to transversely subtrigonal outline and biconvex profile; vertical anterior and lateral margins truncated. Beak erect. Fold and sulcus broad, from umbones; anterior commissure uniplicate, low, dentate. Dental plates meeting as sessile spondylium, with high buttress plates. Septalium long, deep, wide, partly covered by inner hinge plates; hinge plates divided, without lateral supporting plates; dorsal median septum strong, to midlength, crural bases transversely ovate; crura short, straight, delicate, triangular in section. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* North America, European Russia, Altai, Siberia, China. ——FIG. 852,*2a–h. *R. subtrigona* (MEEK & WORTHEN), Mississippian, Osagean, Keokuk Lime-

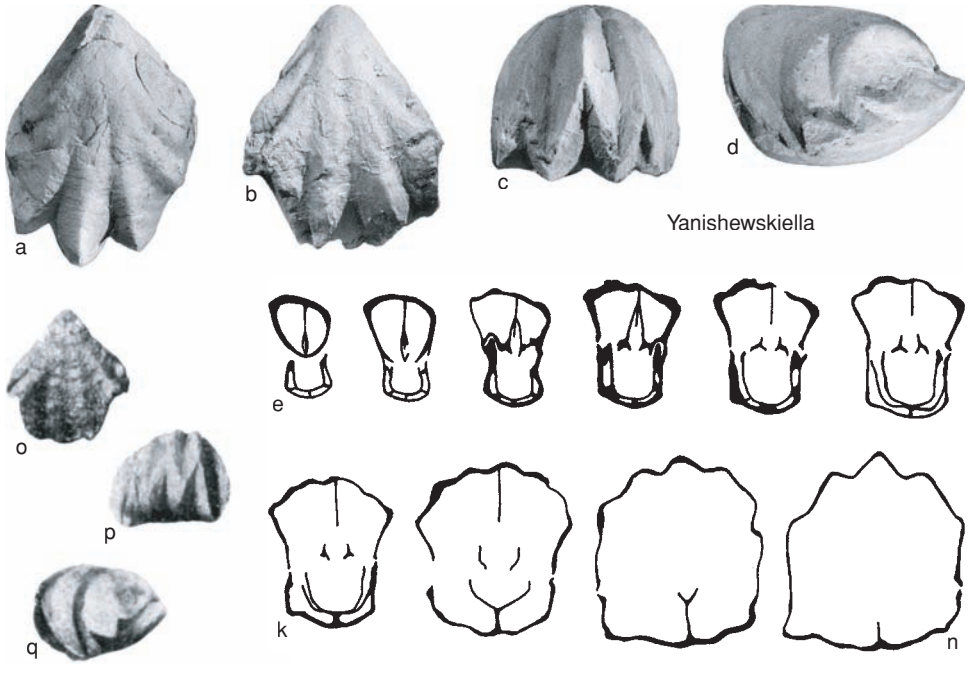

FIG. 853. Tetracameridae (p. 1251).

stone, Warsaw, Illinois, USA; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h,* serial sections, ×1.25 (Weller, 1914).——FIG. 852,*2i–m. Rotaia* sp., Mississippian, Chappel Limestone, Texas, USA; serial sections 1.8, 2.8, 3.0, 3.4, 4.6 mm from posterior, ×1.5 (Carter, 1967).

Yanishewskiella LICHAREW, 1957, p. 139 [**Anomia angulata* LINNAEUS, 1758, p. 703; OD]. Subpentagonal outline and dorsibiconvex profile; vertical anterior and lateral margins; concave posterolateral margins. Beak suberect; delthyrium with foramen apically. Fold and sulcus weak; anterior commissure gently uniplicate but strongly dentate. Plicae angular, simple, from umbones. Shell surface with fine radial striae. Dental plates converge as spondylium supported by low median septum and short lateral buttresses; septalium extending to one-third valve length, ventral median septum to half valve length. Dorsal median septum strong, long; septalium narrow, deep; median septum projecting ventrally well into septalium; hinge plates divided immediately anterior of septalium; crural bases triangular in section, long; crura laterally flattened, slightly sigmoidal. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* Uzbekistan, Urals, Europe, Japan. ——FIG. 853*a–q*. **Y. angulata* (LINNAEUS); *a–d,* dorsal, ventral, anterior, and lateral views, Lancashire, England, ×1.5 (new); *e–n,* serial sections 1.6, 2.0, 2.2, 2.6, 3.0, 3.4, 4.2, 6.0, 7.8, 9.4 mm from anterior, Lancashire, England, ×1.8 (new); *o–q,* lectotype, ventral, anterior, and lateral views, Fergana, Uzbekistan, ×1 (Licharew, 1957).

?Family AUSTRIRHYNCHIIDAE Ager, 1959

[Austrirhynchiidae AGER, 1959b, p. 331]

[Materials prepared by MIGUEL O. MANCEÑIDO, ELLIS F. OWEN, & A. S. DAGYS]

Rhynchonellida with shells triangular to extremely expanded laterally; planareas flat to concave. Dental plates subparallel to ventrally divergent, close to wall; dorsal median septum short and weak; crura distally compressed or concave; alleged cardinal process spurious; spondylium undeveloped. [Formerly thought to be related to cyclothyridines (AGER, CHILDS, & PEARSON, 1972) and even regarded as a subfamily only (DAGYS, 1974, p. 109; PEARSON, 1977, p. 53), this peculiar group is here tentatively retained as a family and reallocated among dominantly cuneiform rhynchotetradoids.] *Middle Triassic–Upper Triassic.*

Austrirhynchia AGER, 1959b, p. 325 [**Terebratula cornigera* SCHAFHÄUTL, 1851, p. 407; OD]. Small, triangular, with anterolateral wings, moderately equibiconvex, both valves flattened, multicostate, except for smooth lateral sides, which are curved at right angles to plane of commissure; anterior commissure rectimarginate or weakly uniplicate; beak short, incurved, ridges distinct, foramen large, elliptical, deltidial plates conjunct. Dental plates subparallel, pedicle collar long, fused to dental plates; septum weak, outer hinge plates narrow, indistinct, fused to socket ridges, crura raduliform. *Upper Triassic (Rhaetian):* northern Alps, Carpathians, northwestern Caucasus, Turkey, Iran.——FIG. 854,*4a–u.* **A. cornigera* (SCHAFHÄUTL), northern Alps; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/231, ×1; *e–u,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.5, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.7, 1.9, 2.1, 2.3, 2.6, 2.8, 3.0, 3.2, IGiG 394/232, approximately ×2 (Dagys, 1974).

Decurtella GAETANI, 1966, p. 344 [**Terebratula decurtata* GIRARD, 1843, p. 474; OD]. Small, triangular, moderately and equally biconvex, weakly uniplicate; both valves flattened, distinctly costate, lateral sides smooth, curved at right angle to commissural plane, forming structures similar to planareas, which never continue into wings; beak suberect, ridges distinct, foramen oval, hypothyrid, deltidial plates disjunct. Dental plates subparallel, diverging anteriorly; umbonal chambers small, partly filled by callus, no pedicle collar; septalium shallow, supported by short septum only in posterior part, crura raduliform. *Middle Triassic (Anisian–Ladinian):* Alps, Balkans, Carpathians, Transdanubian range, northwestern Caucasus.——FIG. 854,*2a–n.* **D. decurtata* (GIRARD), Anisian; *a–e,* dorsal, lateral, anterior, ventral, posterior views, Lombardia, northern Italy, ×2; *f,* detail of apical region, Lombardia, northern Italy, G 4/1, ×15 (Gaetani, 1966); *g–n,* transverse serial sections, distances in mm from ventral umbo, 0.6, 0.9, 1.05, 1.15, 1.3, 1.4, 1.75, 2.1, Balaton area, Hungary (Pálfy, 1988).

Excavatorhynchia CHING & FENG, 1977, p. 44 [**Rhynchonella raxana* BITTNER, 1892, p. 31; OD]. Small, cuneiform, nearly equibiconvex; umbo flattened; lateral and anterior margin abruptly geniculated; large, concave planareas posterolaterally; commissure slightly uniplicate or nearly rectimarginate; dorsal fold low, flat, developed only at anterior half; shallow ventral sulcus bent dorsally into low, truncate linguiform extension; costation variable, usually attenuated or evanescent posteriorly; beak incurved; foramen mesothyrid. Dental plates short, thin, close to lateral wall; low, thick septum supporting very small septalium; crura possibly raduliform, distally subvertical, bladelike. *Middle Triassic–Upper Triassic:* Alps, China.——FIG. 854,*3a–m.* **E. raxana* (BITTNER), Carnian, Yunnan, China; *a–e,* dorsal, lateral, anterior, ventral, posterior views, NIGP 26829, ×1.5 (new); *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.6, 0.7, 1.0, 1.2, 1.5, 1.9, 2.5, NIGP 26829 (Ching & Feng, 1977).

?Trigonirhynchella DAGYS, 1963, p. 41, *nom. nov. pro Trigonirhynchia* DAGYS, 1961, p. 94, *non* COOPER, 1942, Rhynchonellida [**Trigonirhynchia trigona* DAGYS, 1961, p. 95; OD]. Small, trigonal, medially flattened, moderately biconvex, smooth posteriorly, with few rounded costae anteriorly; sulci possibly present on both valves; commissure unisulcate to uniplicate; beak small, suberect, ridges rounded. No pedicle collar, dental plates short, divergent, almost fused to lateral walls; weak dorsal median septum confined apically, supporting septalium; crura distally subvertical, bladelike. [Alternatively may be related to *Prelissorhynchia,* according to XU, 1990, p. 77.] *Upper Triassic (Norian):* ?Alps, Carpathians, Hungary, northwestern Caucasus, Pamirs, Vietnam.——FIG. 854,*1a–k.* **T. trigona* (DAGYS), Norian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, IGiG 179/20, ×1; *d–k,* transverse serial sections, distances in mm from first section, 1.0, 1.4, 1.6, 1.9, 2.2, 2.3, 2.8, 3.6 (Dagys, 1961).

Family PRIONORHYNCHIIDAE new family

[Prionorhynchiidae MANCEÑIDO & OWEN, herein]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Medium to large Rhynchotetradoidea, subtriangular to subpentagonal, cuneiform, or securiform; planareas mostly concave, or flat; beak narrow, suberect to scarcely incurved, with small hypothyrid foramen. Ventrally convergent to subparallel dental plates; dorsal median septum and septalium present, though variably developed; crura raduliform to distally flattened and somewhat flared or crescentic; triangular crural bases; spondylium undeveloped. *?Middle Triassic, Upper Triassic–Middle Jurassic (Callovian).*

Prionorhynchia BUCKMAN, 1918, p. 62 [**Terebratula serrata* J. de C. SOWERBY, 1825 in 1823–1825, p. 168; OD] [=*Prionorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, subtrigonal to subpentagonal, depressed equibiconvex to globose dorsibiconvex; without interarea but planareas well developed; rectimarginate or uniplicate; costae strong, sharp; beak very small, somewhat incurved; deltidial plates narrow, thick. Dental plates thin, ventrally convergent to subparallel, often with low apical ventral median ridge in between; dorsal median septum very short; septalium small, pitlike;

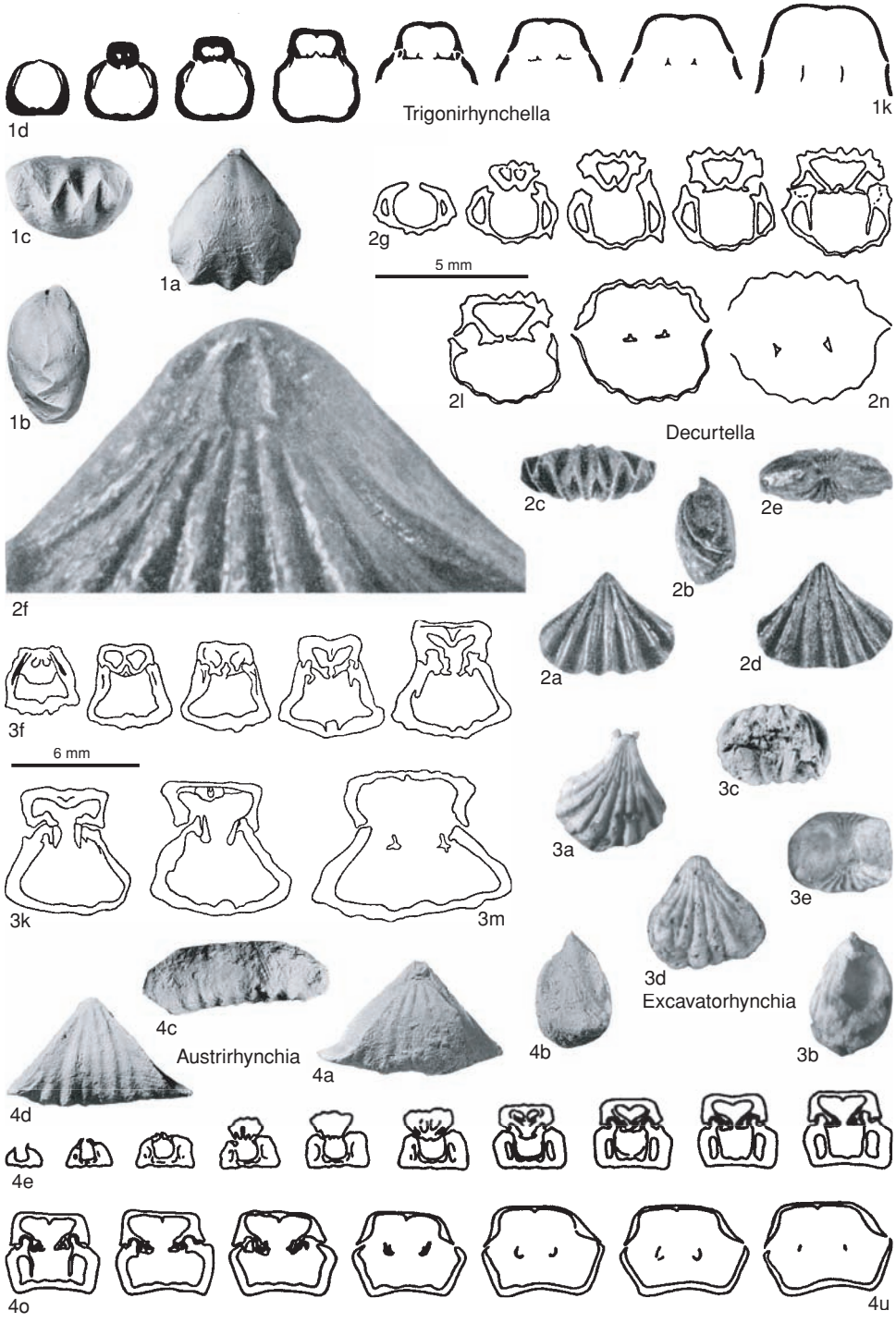

FIG. 854. Austrirhynchiidae (p. 1252).

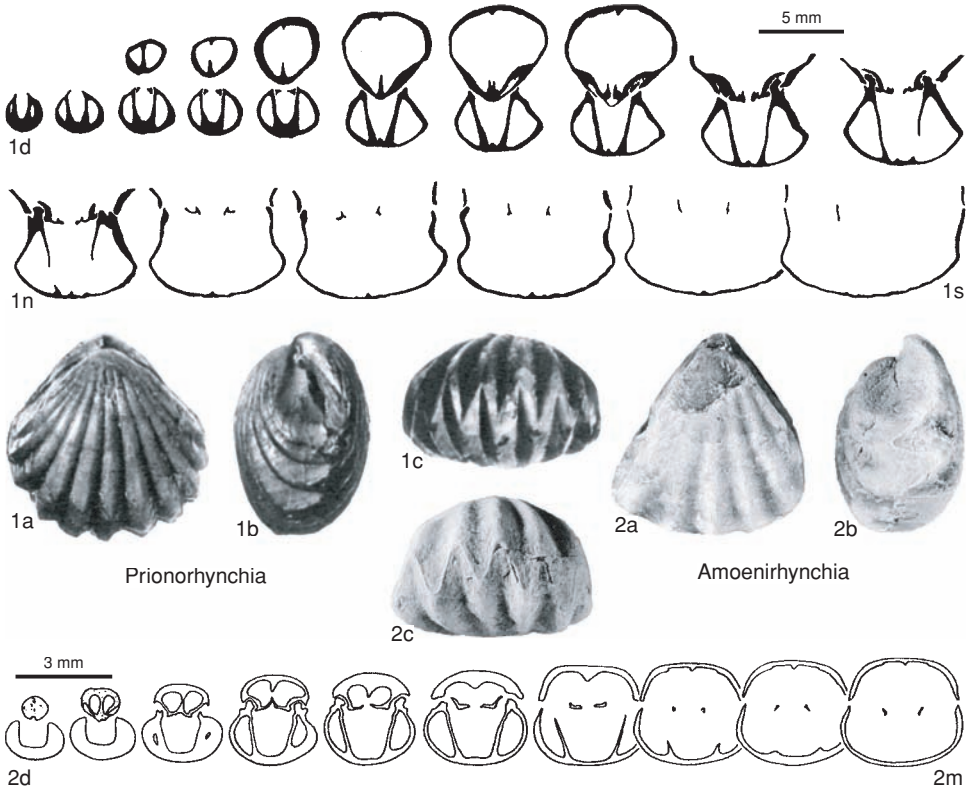

FIG. 855. Prionorhynchiidae (p. 1252–1253).

hinge teeth may be crenulated; crura raduliform to possibly incipiently canaliform. *Lower Jurassic (?Hettangian, Sinemurian)–Middle Jurassic (Aalenian):* England, France, Germany, Austria, Italy, Spain, Switzerland, Slovakia, Hungary, Yugoslavia, Greece, Bulgaria, Morocco, Algeria, Anatolia, Caucasus, Thailand, Indonesia (Seran, ?Timor), Argentina, ?New Zealand.——FIG. 855,*1a–s.* **P. serrata* (J. de C. SOWERBY), upper Pliensbachian, Dorset, England; *a–c,* holotype, dorsal, lateral, anterior views, BMNH B.61517, ×1; *d–s,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.9, 1.0, 1.1, 1.6, 1.8, 2.0, 2.3, 2.6, 2.9, 3.5, 4.1, 4.3, 4.7, 5.3, BMNH B.33333 (Ager, 1956).

Amoenirhynchia SIBLÍK, 1986, p. 23 [**Rhynchonella seydelii* BITTNER, 1891, p. 56; OD]. Small, triangular, moderately equibiconvex, costae low, rounded, developed only anteriorly, no distinct sulcus and fold, anterior commissure rectimarginate or incipiently uniplicate; beak suberect, ridges distinct, planareas well developed. Dental plates long, subparallel to ventrally convergent, pedicle collar absent; septum low, septalium short, present only posteriorly; hinge teeth without crenulation; crura raduliform to incipiently flared. *?Middle Triassic, Upper Triassic:* Alps, Carpathians.——FIG. 855,*2a–m.* **A. seydelii* (BITTNER), Carnian, Slovakia; *a–c,* dorsal, lateral, anterior views, SNM Z 19428, ×3; *d–m,* transverse serial sections, distances in mm from ventral umbo, 0.15, 0.45, 0.95, 1.55, 2.3, 3.8, 4.85, 6.0, 7.3, 8.7 (Siblík, 1986).

Lokutella VÖRÖS, 1983, p. 6 [**Rhynchonella palmaeformis* HAAS, 1912, p. 232; OD]. Small to medium size, trigonal to securiform; nearly equibiconvex; fold and sulcus absent; anterior commissure straight but forming wide sinus; planareas well developed, generally concave; costae few, usually strong, after variable posterior smooth stage; beak small, erect to slightly incurved. Strong subparallel dental plates and crenulated teeth; dorsal median septum long but low; hinge plates fused, forming septalium; crura distally crescentic and outwardly convex. *Lower Jurassic (upper Sinemurian–Pliensbachian):* Sicily, Apennines, southern Alps, Hungary, ?Greece.——FIG. 856,*1a–l.* **L. palmaeformis* (HAAS), Pliensbachian, Kericser, Hungary; *a–e,* dorsal, lateral, anterior, ventral, posterior views, HNHMB M.98.3, ×1.5 (new); *f–l,* transverse serial sections, distances in mm from ventral umbo, 0.3, 1.0, 1.3, 1.8, 2.4, 2.8, 3.1, HGI J.9185 (Vörös, 1983).

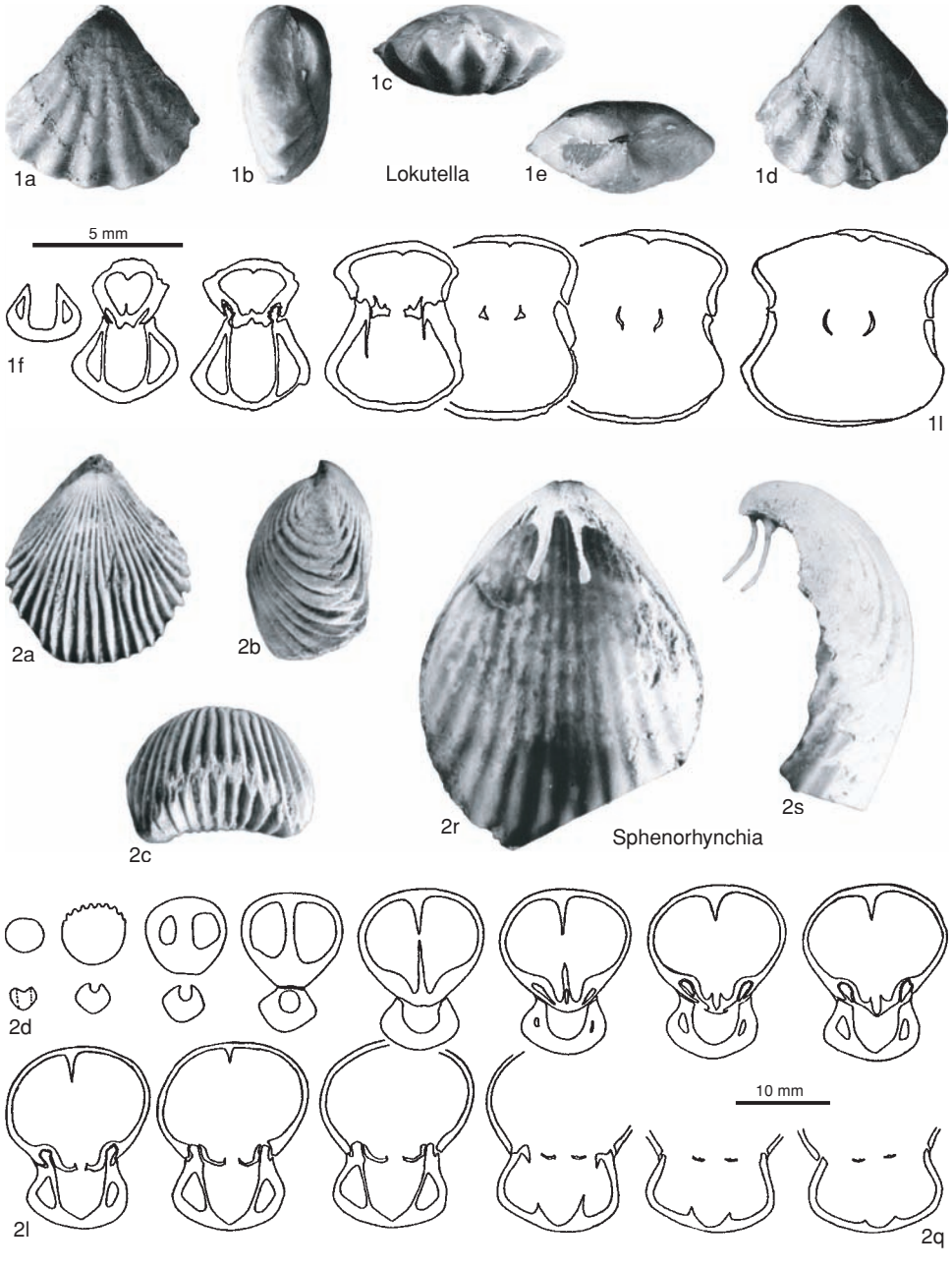

FIG. 856. Prionorhynchiidae (p. 1254–1256).

?Sphenorhynchia BUCKMAN, 1918, p. 30 [**Terebratula plicatella* J. de C. SOWERBY, 1825 in 1823–1825, p. 167; OD] [=*Sphenorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, globose, equibiconvex to dorsibiconvex; elongate oval to subtrigonal; wedge shaped due to well-developed, concave planareas; squama and glotta junction dorsoconvex; uniplication arcuate, but dorsal fold rarely or not at all raised; flattish ventral valve may bear ill-defined, shallow, wide sulcus anteriorly; costae numerous, prominent, narrow, sharp, and

sometimes dichotomous; beak small, massive, suberect to erect, rarely incurved; conjunct deltidial plates. Dental plates ventrally convergent to subparallel, teeth massive, crenulated; oblique hinge plates; dorsal median septum strong, septalium narrow; raduliform crura, becoming dorsally concave distally. *Middle Jurassic (Bajocian–Callovian):* England, France, Germany, Switzerland, Austria, Poland, Romania, Bulgaria, Crimea, Caucasus, ?Arabia, ?Afghanistan, China, Morocco, Algeria, ?Madagascar.——Fig. 856,*2a–q.* **S. plicatella* (J. de C. Sowerby), upper Bajocian; *a–c,* dorsal, lateral, anterior, Dorset, England, USNM 88733a, ×1 (Shi & Grant, 1993); *d–q,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.9, 1.3, 1.9, 2.8, 3.1, 3.5, 3.7, 3.9, 4.3, 4.5, 5.0, 5.2, 5.5, Calvados, France, FSL 49413 (Alméras, 1980). ——Fig. 856,*2r–s. S. matisconensis* (Lissajous), upper Bajocian, Monsard, France; *r,* dorsal interior showing variant of raduliform crura; *s,* same, oblique lateral view, USNM 429399, ×1.8 (Shi & Grant, 1993).

WELLERELLOIDEA

Norman M. Savage,[1] Miguel O. Manceñido,[2] Ellis F. Owen,[3] A. S. Dagys,[4] and Sun Dong-Li[5]

[[1]University of Oregon; [2]La Plata Natural Sciences Museum, Argentina; [3]formerly of The Natural History Museum; [4]deceased; and [5]Nanjing Institute of Geology and Palaeontology]

Superfamily WELLERELLOIDEA Licharew, 1956

[*nom. correct.* Savage, 1996, p. 255, *pro* Wellerellacea Xu & Liu, 1983, p. 73, *nom. transl. ex* Wellerellidae Licharew in Rzhonsnitskaia, 1956a, p. 125]

Rhynchonellida with subcircular to subpentagonal outline; dorsal fold and ventral sulcus strong to weak; costae usually simple; umbones commonly smooth; delthyrium with or without deltidial plates. Dental plates and dorsal median septum variously developed; hinge plates undivided, notched, or totally divided; septalium occasionally present in Mesozoic genera; cardinal process absent; crura falciform in Paleozoic genera, may be hamiform in Mesozoic genera. *Lower Carboniferous (Tournaisian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Family WELLERELLIDAE Licharew, 1956

[Wellerellidae Licharew in Rzhonsnitskaia, 1956a, p. 125]

[Materials prepared by Norman M. Savage & Miguel O. Manceñido]

Wellerelloidea with mostly subpentagonal outline; costae usually coarse. Dental plates often short and vertical, occasionally convergent ventrally, rarely absent. *Upper Carboniferous (Westphalian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Subfamily WELLERELLINAE Licharew, 1956

[Wellerellinae Licharew in Rzhonsnitskaia, 1956a, p. 125]

[Materials prepared by Norman M. Savage]

Wellerellidae with short dental plates and costae arising anterior of beaks. Delthyrium with conjunct deltidial plates; dorsal median septum present; hinge plates usually undivided. *Upper Carboniferous (Westphalian)–Upper Permian (Kazanian).*

Wellerella Dunbar & Condra, 1932, p. 286 [**W. tetrahedra;* OD] [=*Changyangrhynchus* Yang, 1984, p. 229 (type, *C. nantanelloides,* OD)]. Small; subcircular to subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak straight to suberect; deltidial plates conjunct anteriorly, leaving small oval submesothyrid foramen. Fold and sulcus strong; commissure uniplicate anteriorly; tongue high, wide, usually triserrate. Costae coarse, from midlength; umbones smooth. Dental plates short, vertical; ventral muscle field elongate oval, extending to one-third valve length. Hinge plates undivided; dorsal median septum short, low; dorsal muscle field small, subcircular, with median myophragm; crura laterally flattened, twisted, dorsally carinate. *Upper Carboniferous (Stephanian)–Upper Permian (Kazanian):* cosmopolitan.——Fig. 857,*1a–e.* **W. tetrahedra,* middle Pennsylvanian, Marmaton Group, Missouri, USA; *a–b,* anterior and posterior views of different paratypes, ×2; *c–e,* paratype, serial sections of posterior (Dunbar & Condra, 1932).——Fig. 857,*1f–i. W. girtyi girtyi* Cooper & Grant, Guadalupian, Word Formation, Glass Mountains, Texas, USA; *f–*

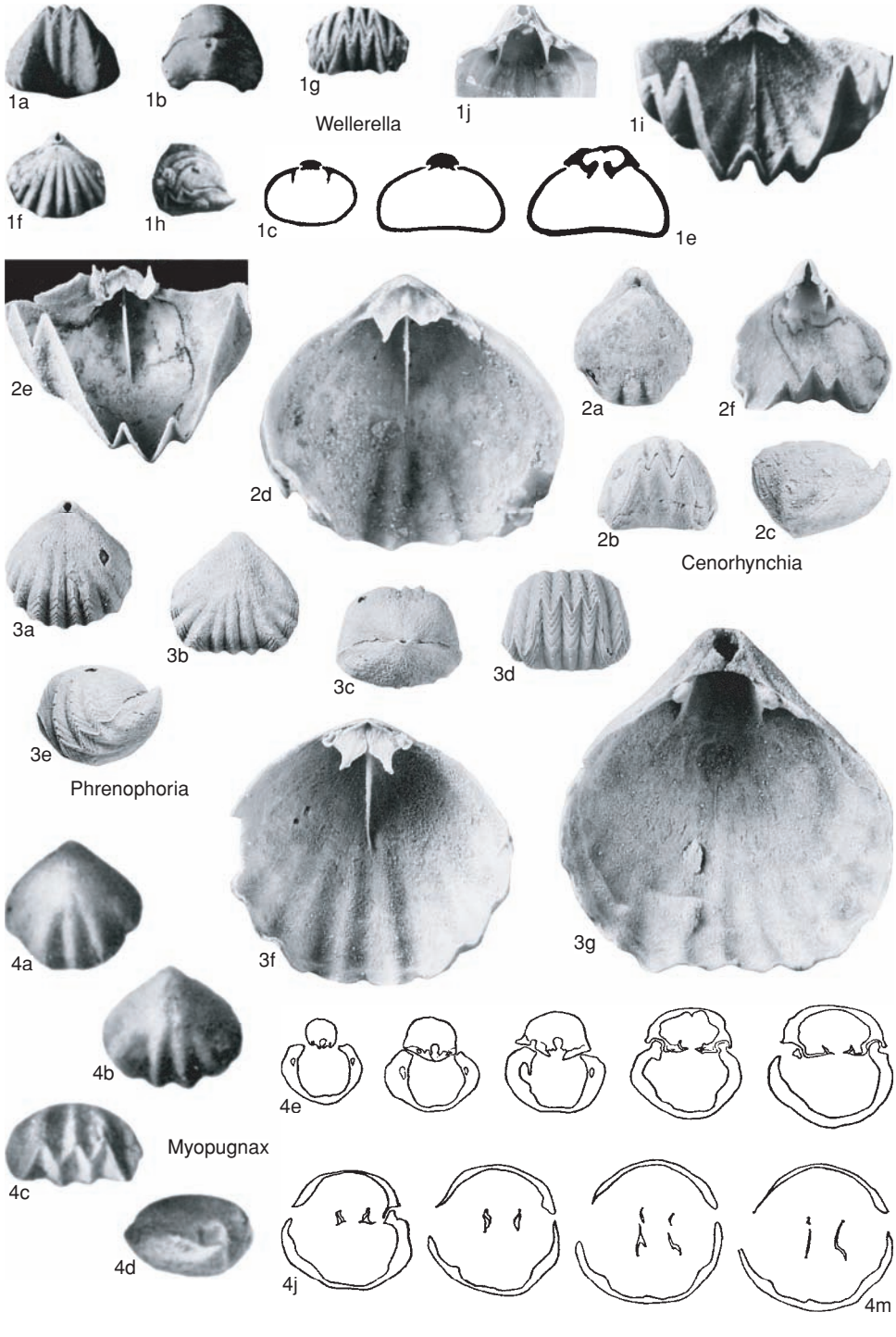

FIG. 857. Wellerellidae (p. 1256–1258).

h, paratype, dorsal, anterior, and lateral views, ×1; *i,* paratype, interior view of tilted dorsal valve, ×3 (Cooper & Grant, 1976a).——Fig. 857,*1j. W. girtyi seorsa* Cooper & Grant, Guadalupian, Cherry Canyon Formation, Guadalupe Mountains, Texas, USA; interior of ventral valve posterior, ×3 (Cooper & Grant, 1976a).

Cenorhynchia Cooper & Grant, 1976a, p. 1986 [**C. fracida;* OD]. Small; elongate subpentagonal outline and dorsibiconvex profile. Beak erect; delthyrium ovate; deltidial plates incipient. Fold and sulcus weak to moderate, from midlength; anterior commissure uniplicate; tongue high, biserrate to triserrate. Costae coarse, restricted to anterior margin and fold and sulcus. Dental plates short, vertical. Dorsal median septum high, long, extending to one-third valve length and supporting undivided hinge plates posteriorly; dorsal muscle field suboval, divided by myophragm; crura laterally flattened, concave medially, dorsally carinate. *Lower Permian (Sakmarian–Kungurian):* USA.——Fig. 857,*2a–f.* **C. fracida,* lower Guadalupian, Wordian, Word Formation, Glass Mountains, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* paratype, ventral view of dorsal valve interior; *e,* paratype, anterior view of dorsal valve interior, ×4; *f,* paratype, dorsal view of ventral valve interior, ×1.5 (Cooper & Grant, 1976a).

Lissella Campbell, 1961, p. 452 [**L. booralensis;* OD]. Small; subcircular to elongate oval outline; biconvex profile. Foramen large, circular; deltidial plates narrow, short. Fold and sulcus weak, from midlength; anterior commissure uniplicate. Plicae rounded, from one-third valve length, 2 to 4 on fold, 1 to 3 in sulcus, weakly developed on flanks. Dental plates thin, concave medially. Dorsal median septum long, thick, high; appearing not to support hinge plates. Hinge plates undivided, with low median ridge on upper surface; dorsal muscle field elongate oval; crural bases triangular in section. *Upper Carboniferous (Westphalian):* Australia (New South Wales).——Fig. 858,*3a–g.* **L. booralensis,* middle Westphalian, Booral Formation, Newcastle, Booral; *a,* holotype, dorsal internal mold, ×2; *b,* posterior view of steinkern, ×2; *c–g,* serial transverse sections, ×3 (Campbell, 1961).

Myopugnax Glushenko, 1975, p. 96 [**M. priva;* OD]. Small; subcircular to subpentagonal outline; biconvex profile. Beak suberect to erect; foramen small. Fold and sulcus low, wide, from midlength; anterior commissure uniplicate, typically triserrate. Dental plates short, buried in callus; ventral muscle field well impressed. Dorsal median septum and septalium absent; hinge plates divided; crural bases triangular in section; crura laterally flattened, strongly curved ventrally, tips bearing V-shaped grooves. *Lower Permian (Sakmarian–Artinskian):* Russia (Donetz basin).——Fig. 857,*4a–m.* **M. priva,* Slaviansk Series, Iziumsk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–m,* serial sections 0.45, 0.55, 0.70, 1.00, 1.15, 1.4, 1.7, 2.0, 2.05 mm from posterior, ×6 (Glushenko, 1975).

Phrenophoria Cooper & Grant, 1969, p. 12 [**P. subcarinata;* OD]. Subcircular to subpentagonal outline and dorsibiconvex, anteriorly inflated profile; anterior and lateral margins steep. Beak straight to erect; deltidial plates conjunct anteriorly, foramen small, oval, submesothyrid to mesothyrid. Fold and sulcus poorly defined; anterior commissure uniplicate; tongue wide, trapezoid, serrate. Costae angular, from midlength, umbones smooth. Dental plates short, vertical; ventral muscle field cordate. Dorsal median septum high posteriorly, low anteriorly, supporting undivided hinge plates; dorsal muscle field elongate oval, divided by septum; crura ventrally curved, anteriorly divergent, with dorsal carina. *Lower Permian (Sakmarian–Kungurian):* USA.——Fig. 857,*3a–g.* **P. subcarinata,* lower Guadalupian, Wordian, Word Formation, Glass Mountains, Texas; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–g,* paratype, ventral view of dorsal valve interior, dorsal view of ventral valve interior, ×3 (Cooper & Grant, 1976a).

Plekonella Campbell, 1953, p. 17 [**P. acuta;* OD]. Subpentagonal to transversely oval outline and biconvex profile. Beak suberect. Fold and sulcus moderately strong, from umbones; anterior commissure uniplicate; tongue low, rounded, serrate. Costae coarse, simple, from beaks, on fold, sulcus, flanks. Dental plates short, vertical. Hinge plates undivided, bearing low median ridge; dorsal median septum low, stout, extending to midlength. *Upper Carboniferous (Stephanian)–Lower Permian (Kungurian):* eastern Australia, New Zealand.——Fig. 858,*2a–i.* **P. acuta,* Artinskian–Kungurian, Ingelara Formation, Queensland, eastern Australia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i,* serial sections from several specimens (Campbell, 1953).

Tautosia Cooper & Grant, 1969, p. 14 [**T. fastigiata;* OD]. Transversely triangular outline and dorsibiconvex profile; apical angle acute; lateral slopes gentle. Beak straight; deltidial plates conjunct; foramen elongate, mesothyrid. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue wide, low, trapezoid, dentate. Costae strong, from one-third valve length, simple; umbones smooth. Dental plates short, vertical; ventral muscle field elongate oval. Hinge plates undivided; dorsal median septum high, supporting hinge plates; dorsal muscle field subcircular, extending to midlength; crura twisted, dorsally carinate, curved ventrally. *Permian (Sakmarian–Kungurian):* USA.——Fig. 858,*1a–h.* **T. fastigiata,* Leonardian, Cathedral Mountain Formation, Glass Mountains, Cathedral Mountain, Texas; *a–d,* holotype, dorsal, ventral, anterior, and posterior views; *e,* paratype, lateral view, ×1; *f,* anterior view of interior, ×2; *g,* interior of ventral valve, ×1.5; *h,* view of foramen, ×3 (Cooper & Grant, 1976a).

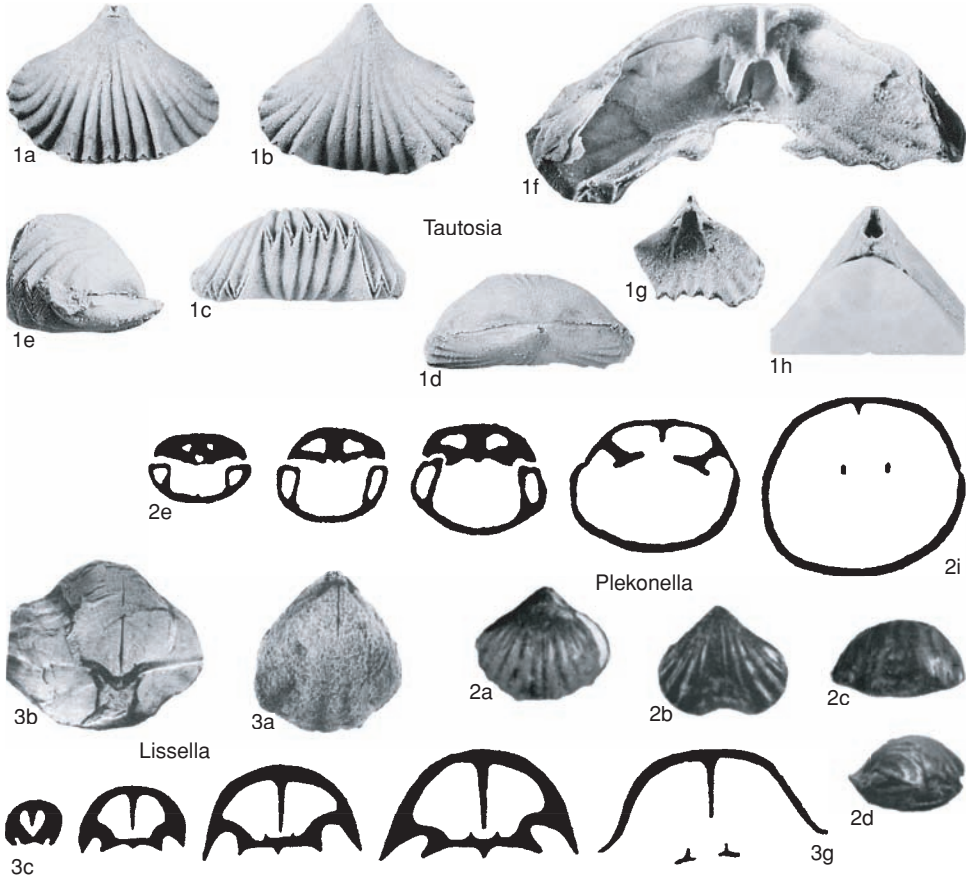

FIG. 858. Wellerellidae (p. 1258).

Subfamily TRICORIINAE Cooper & Grant, 1976

[Tricoriinae COOPER & GRANT, 1976a, p. 2077]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with completely costate shells, rectimarginate anterior commissure, obsolete dental plates, and high dorsal median septum. *Lower Permian (Asselian).*

Tricoria COOPER & GRANT, 1976a, p. 1945 [**T. hirpex;* OD]. Small; outline transverse and subpentagonal; profile subequally biconvex. Beak erect to incurved; delthyrium open, without deltidial plates. Fold and sulcus weak to absent; anterior commissure rectimarginate. Costae fine, simple, arising at beaks. Dental plates weak to obsolete; ventral muscle field triangular. Dorsal median septum high; septalium short; crura laterally compressed; sharply curved ventrally. *Lower Permian (Asselian):* USA (Texas). ——FIG. 859,*1a–f.* **T. hirpex,* Skinner Ranch Formation, Glass Mountains; *a–d,* holotype, dorsal, anterior, posterior, and lateral views, ×1; *e,* ventral interior; *f,* dorsal interior, ×4 (Cooper & Grant, 1976a).

Subfamily NIPPONIRHYNCHIINAE Savage, 1996

[Nipponirhynchiinae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with costae flattened anteriorly; marginal spines developed from intertroughs. Dorsal median septum high; septalium well developed. *Lower Permian (Sakmarian).*

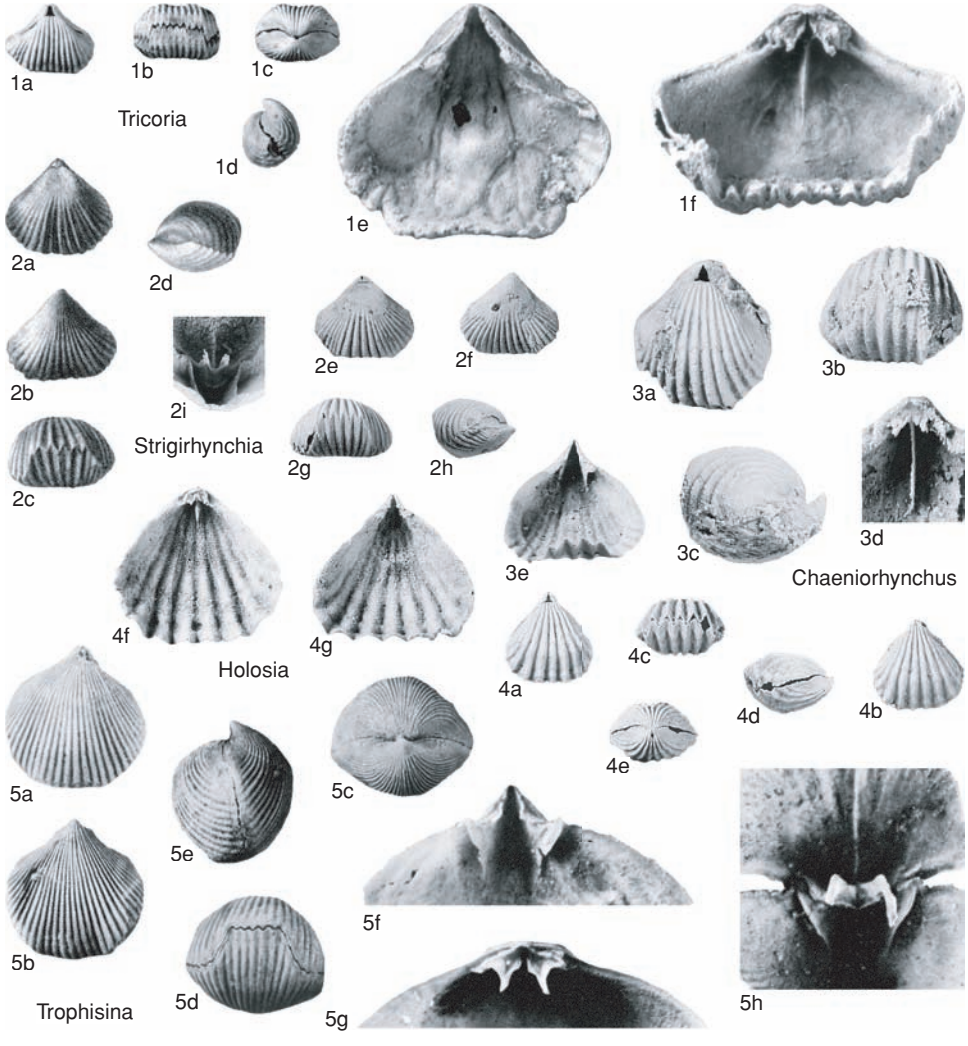

FIG. 859. Wellerellidae (p. 1259–1263).

Nipponirhynchia YANAGIDA & NISHIKAWA, 1984, p. 163 [**N. shutoi;* OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak suberect. Fold and sulcus wide, rounded, from umbones; tongue broad, rounded. Costae numerous, simple, subangular, arising at beaks, with deep intertroughs; costal crests flattened and grooved on *paries geniculatus;* intertroughs extended into marginal spines. Dental plates prominent, ventrally convergent. Dorsal median septum thick, long; septalium deep, wide; hinge plates divided anterior of septalium; crural bases triangular in section. *Lower Permian (Sakmarian):* Japan.——FIG. 860,*1a–h.* **N. shutoi,* holotype, Yaikian, Kawai Limestone, Hiroshima, Kawai, Joge; *a–d,* dorsal, ventral, anterior, and lateral views, ×1.5; *e–k,* serial sections, ×2.3 (Yanagida & Nishikawa, 1984).

Subfamily UNCINUNELLININAE Savage, 1996

[Uncinunellininae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with costae flattened anteriorly and marginal spines developed from intertroughs. Median septum low to absent; septalium absent. *Permian (Sakmarian–Tatarian).*

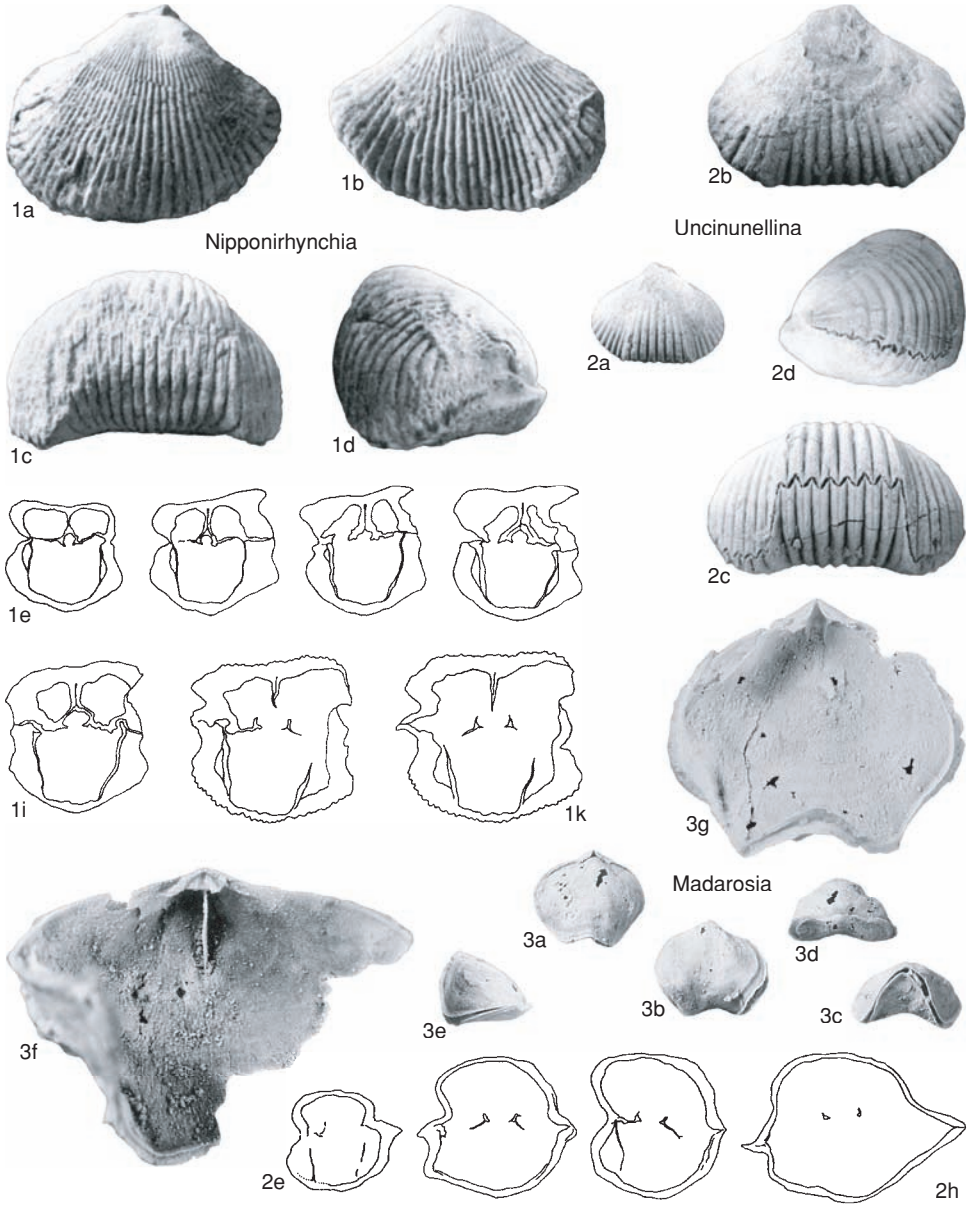

FIG. 860. Wellerellidae (p. 1260–1263).

Uncinunellina GRABAU, 1932a, p. 100 [**Uncinulus theobaldi* WAAGEN, 1883, p. 425; OD]. Transversely ovate outline and dorsibiconvex profile. Beak sharp, straight to suberect; foramen small; deltidial plates small, disjunct. Fold and sulcus low, wide, flat, arising at midlength; tongue wide, trapezoid. Umbones generally smooth. Costae low, simple, rounded, with narrow intertroughs, crests flattened and grooved on *paries geniculatus;* intertroughs extended at anterior and lateral margins to form spines that insert into holes near margin of opposite valve. Dental plates short, vertical to ventrally convergent; ventral muscle field weakly impressed. Dorsal median ridge low to absent; hinge plates thin, divided; crura ventrally curved. *Permian (Sakmarian–Tatarian):* Pakistan, India, Thailand, China,

Mongolia, Japan, Iran, Fergana, Pamir, Urals, Ukraine, Mexico.——Fig. 860,*2a–d. *U. theobaldi* (Waagen), Kungurian, Wargal Limestone, Kalabagh Member, Salt Range, Pakistan; *a,* topotype, dorsal view, ×1; *b–d,* topotype, ventral, anterior, and lateral views, ×1.8 (Grant, 1976). ——Fig. 860,*2e–h. U. hayasakai* Yanagida & Nishikawa, Sakmarian, Yaikian, Kawai Limestone, Hiroshima, Kawai, Joge, Japan; paratype, serial sections, ×3 (Yanagida & Nishikawa, 1984).

Subfamily TROPHISININAE Cooper & Grant, 1976

[Trophisininae Cooper & Grant, 1976a, p. 2077]

[Materials prepared by Norman M. Savage]

Wellerellidae with finely costate shells and strongly convergent dental plates. *Lower Permian (Artinskian).*

Trophisina Cooper & Grant, 1976a, p. 2078 [**T. fenaria;* OD]. Subcircular outline and strongly biconvex to globose profile. Beak suberect; foramen large, ovate; delthyrium with disjunct deltidial plates. Fold and sulcus weak; anterior commissure low, trapezoid. Costae numerous, simple, arising at beaks. Dental plates short, ventrally convergent. Hinge plates undivided; dorsal septum short; septalium wide; crura slender, ventrally curved, concave medially. *Lower Permian (Artinskian):* USA (Texas).——Fig. 859,*5a–h. *T. fenaria,* lower Cathedral Mountain Formation, Glass Mountains, Split Tank; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×2; *f,* paratype, interior of ventral valve posterior, ×5; *g–h,* paratype, interior of dorsal valve posterior, interior of conjoined valves, ×6 (Cooper & Grant, 1976a).

Subfamily STRIGIRHYNCHIINAE Cooper & Grant, 1976

[Strigirhynchiinae Cooper & Grant, 1976a, p. 1996]

[Materials prepared by Norman M. Savage]

Wellerellidae with costae arising at beaks; dental plates short; dorsal median septum high; hinge plates usually undivided. *Permian (Artinskian–Kazanian).*

Strigirhynchia Cooper & Grant, 1969, p. 14 [**Rhynchonella? indentata* Shumard, 1860b, p. 393; OD]. Outline subtriangular to subpentagonal and profile equibiconvex. Beak straight to suberect; deltidial plates conjunct anteriorly, foramen small, oval. Fold and sulcus weak, dorsal umbone flattened or concave; anterior commissure uniplicate; tongue low, trapezoid. Costae simple, extending from beaks. Dental plates short, vertical; ventral muscle field elongate-oval. Dorsal median septum high, bisecting posterior half of muscle field and supporting undivided hinge plates; dorsal muscle field elongate-oval; crura diverging anteriorly and curving ventrally, each with dorsal carina. *Upper Permian (Kungurian–Kazanian):* USA.——Fig. 859,*2a–i. *S. indentata* (Shumard), Capitan Group, Guadalupe Mountains, Texas; *a–d,* dorsal, ventral, anterior, and lateral views, ×1 (Girty, 1909); *e–h,* dorsal, ventral, anterior, and lateral views, ×1; *i,* interior of conjunct specimen showing cardinalia and dental plates, ×3 (Cooper & Grant, 1976a).

Chaeniorhynchus Cooper & Grant, 1976a, p. 1999 [**C. inauris;* OD]. Small; outline subtriangular to subpentagonal; profile dorsibiconvex; greatest thickness at midlength. Beak suberect to erect; delthyrium open, no deltidial plates. Fold and sulcus weak to moderate; anterior commissure uniplicate; tongue moderate, trapezoid, serrate. Costae fine to medium, extending from beaks. Dental plates strong, vertical to slightly convergent ventrally; ventral muscle field elongate oval. Dorsal median septum high, supporting undivided hinge plates; dorsal muscle field small, oval, expanding anteriorly; crura divergent anteriorly and ventrally, dorsally carinate. *Lower Permian (Artinskian):* USA.——Fig. 859,*3a–d. *C. inauris,* Cathedral Mountain Formation, Glass Mountains, Split Tank, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* interior of posterior of dorsal valve, ×4 (Cooper & Grant, 1976a).——Fig. 859,*3e. C. salutare* Cooper & Grant, upper Leonardian, Road Canyon Formation, Glass Mountains, Texas; interior of ventral valve, ×2 (Cooper & Grant, 1976a).

Holosia Cooper & Grant, 1976a, p. 1971 [**H. regularis;* OD]. Small; subtriangular outline and equibiconvex profile; anterior and lateral margins subvertical. Beak straight; deltidial plates conjunct anteriorly, foramen oval mesothyrid to submesothyrid. Fold and sulcus weak; anterior commissure weakly uniplicate; tongue low, wide, serrate. Costae medium to fine, simple, rounded, arising at beaks. Dental plates short, vertical, close to walls; ventral muscle field small, ovate. Hinge plates small, undivided; dorsal median septum high posteriorly where it supports hinge plate. *Upper Permian (Kungurian–Kazanian):* USA.——Fig. 859,*4a–g. *H. regularis,* holotype, upper Guadalupian, Bell Canyon Formation, Guadalupe Mountains, Texas; *a–e,* dorsal, ventral, anterior, lateral, and posterior views, ×1; *f,* interior of dorsal valve; *g,* interior of ventral valve, ×2 (Cooper & Grant, 1976a).

Subfamily MADAROSIINAE Savage, 1996

[Madarosiinae Savage, 1996, p. 255]

[Materials prepared by Norman M. Savage]

Wellerellidae with surface smooth, anterior emarginate, dorsal median septum high, and delthyrium open. *Upper Permian (Kungurian–Kazanian).*

Madarosia Cooper & Grant, 1976a, p. 2002 [**M. anterolamellata;* OD]. Transversely ovate to subpentagonal outline with emarginate anterior and anterolateral borders; convexiplane to convexiconcave form, inflated anteriorly. Beak suberect; delthyrium open, deltidial plates absent or incipient. Fold and sulcus weak posteriorly, strong anteriorly; anterior commissure strongly uniplicate, rounded. Surface smooth apart from concentric lamellae. Dental plates short, confining narrow delthyrial chamber; ventral muscle field elongate oval. Dorsal median septum high, supporting small undivided hinge plates; crura laterally compressed, diverging anteriorly and ventrally, dorsally carinate. *Upper Permian (Kungurian–Kazanian):* USA.——Fig. 860,*3a–g.* **M. anterolamellata,* upper Guadalupian, Bell Canyon Formation, Guadalupe Mountains, Texas; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* paratype, interior of dorsal valve, ×4; *g,* paratype, interior of ventral valve, ×3 (Cooper & Grant, 1976a).

Subfamily CIRPINAE Ager, 1965

[Cirpinae Ager, 1965, p. 605] [=Cipridae Ovcharenko, 1983, p. 50, *nom. nud.*]

[Materials prepared by Miguel O. Manceñido, Ellis F. Owen, & A. S. Dagys]

Multicostate Wellerellidae, hinge plates fused; dorsal median septum usually very much reduced; beak generally small and incurved, with well-developed planareas and small foramen. Double deltidial plates thick and distinctive; crura hamiform where known; septalium usually absent. *Middle Triassic (?Anisian), Upper Triassic (Carnian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Cirpa de Gregorio, 1930a, p. 40 [**Rhynchonella (C.) primitiva;* OD; =*R. briseis* Gemmellaro, 1874, p. 97, subj.] [=*Cipra* Makridin in Sarycheva, 1960, p. 255, *nom. null.*]. Medium size, subtriangular to subpentagonal, depressed dorsibiconvex, rectangular and flattened anteriorly; with low fold, flattopped uniplication, and a few strong, sharp costae; beak small, flattened planareas with diffuse boundaries. Hinge plates flat, fused; dorsal median septum very short; crenulated teeth; crura hamiform. *Lower Jurassic (Sinemurian–Pliensbachian, ?Toarcian):* England, France, Germany, Austria, Italy, Greece, Switzerland, Slovakia, Dinarids, Hungary, Algeria, Turkey (Anatolia), ?Himalayas, Indonesia (Seram), ?New Zealand, Argentina.——Fig. 861,*1a–m.* **C. briseis* (Gemmellaro), middle Lias, Sicily, Italy; *a–e,* dorsal, lateral, anterior, ventral, posterior views, ×1.5 (Benigni, 1978); *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.2, 1.4, 1.8, 2.0, 2.4, 3.0, 3.4, BMNH B.167748 (Ager, 1959a).

Apertirhynchella Siblík, 1986, p. 26 [**A. triplex;* OD]. Small to medium size, subpentagonal, sulcus and fold distinct although low, anterior commissure uniplicate, blunt costae only in fold and sinus, lateral parts of valves smooth; beak short, suberect, ridges well developed. Dental plates very short, fused to lateral walls, pedicle collar absent; no septum, outer hinge plates broad, horizontal in section, inner hinge plate very short; crura hamiform. *Middle Triassic (?Anisian), Upper Triassic:* Dinarids, Transdanubian ranges (Carnian), Alps, Carpathians, Germany.——Fig. 861,*3a–k.* **A. triplex,* Carnian, southeastern Slovakia; *a–c,* holotype, dorsal, lateral, anterior views, SNM Z19430, ×2; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.3, 0.75, 1.2, 1.4, 1.7, 2.4, 2.8 (Siblík, 1986).

Calcirhynchia Buckman, 1918, p. 30 [**C. calcaria;* OD] [=*Calcirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, subtrigonal to subpentagonal or pyriform, globose to depressed subequibiconvex; with wide, flattopped uniplication, low fold and many sharp costae (2 to 7 on fold), no posterior smooth stage; beak small, incurved. Dental plates thin and subparallel, small crenulated teeth; dorsal median septum very short; crura hamiform. *Upper Triassic (Norian)–Lower Jurassic (Sinemurian, ?Pliensbachian):* Germany, Austria, Slovakia, Hungary, Romania, *Norian–Rhaetian;* England, France, Luxemburg, Spain, Germany, Switzerland, Austria, Italy, Sicily, Dinarids, Hungary, Greece, ?Algeria, Turkey, ?Iran, *Hettangian–Sinemurian, ?Pliensbachian.*——Fig. 862,*3a–k.* **C. calcaria,* Hettangian–Sinemurian, England; *a–c,* holotype, dorsal, lateral, anterior, GSM 31947, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.8, 0.9, 1.2, 1.35, 1.7, 2.3, personal collection, Derek Ager, J.107/1 (Ager, 1962).

Euxinella Moiseev, 1936, p. 41, *non* Drensky, 1938, Arachnida, *nec* Nordsieck, 1973, Gastropoda [**E. iatirgvantaensis, error pro E. iatirgvartaensis;* OD]. Small, rounded or rounded-pentagonal, globose, multicostate, strong uniplication, distinct fold absent; beak short, incurved, ridges rounded, foramen hypothyrid; deltidial plates double, conjunct. Dental plates subparallel, pedicle collar feeble; septum low, short, outer hinge plates broad, equal to inner hinge plate, horizontal in section, crura hamiform. [The species was originally described and illustrated (Moiseev, 1936, p. 42–43) as *iatirgvartaensis,* but on page 41, which fixing the species, the name was recorded as "genotip *Euxinella iatirgvantaensis* nov. sp." Subsequent usage is *iatirgvartaensis,* as in the Caucasian locality Iatirgvarta.] *Upper Triassic (Norian–Rhaetian):* Alps, Carpathians, Balkans, Romania, Crimea, northwestern Caucasus, Anatolia, Pamirs, Tibet.——Fig. 862,*4a–r.* **E. iatirgvartaensis,* Rhaetian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, TsGM 1/4801, ×1; *d–r,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.4, 0.6, 0.9,

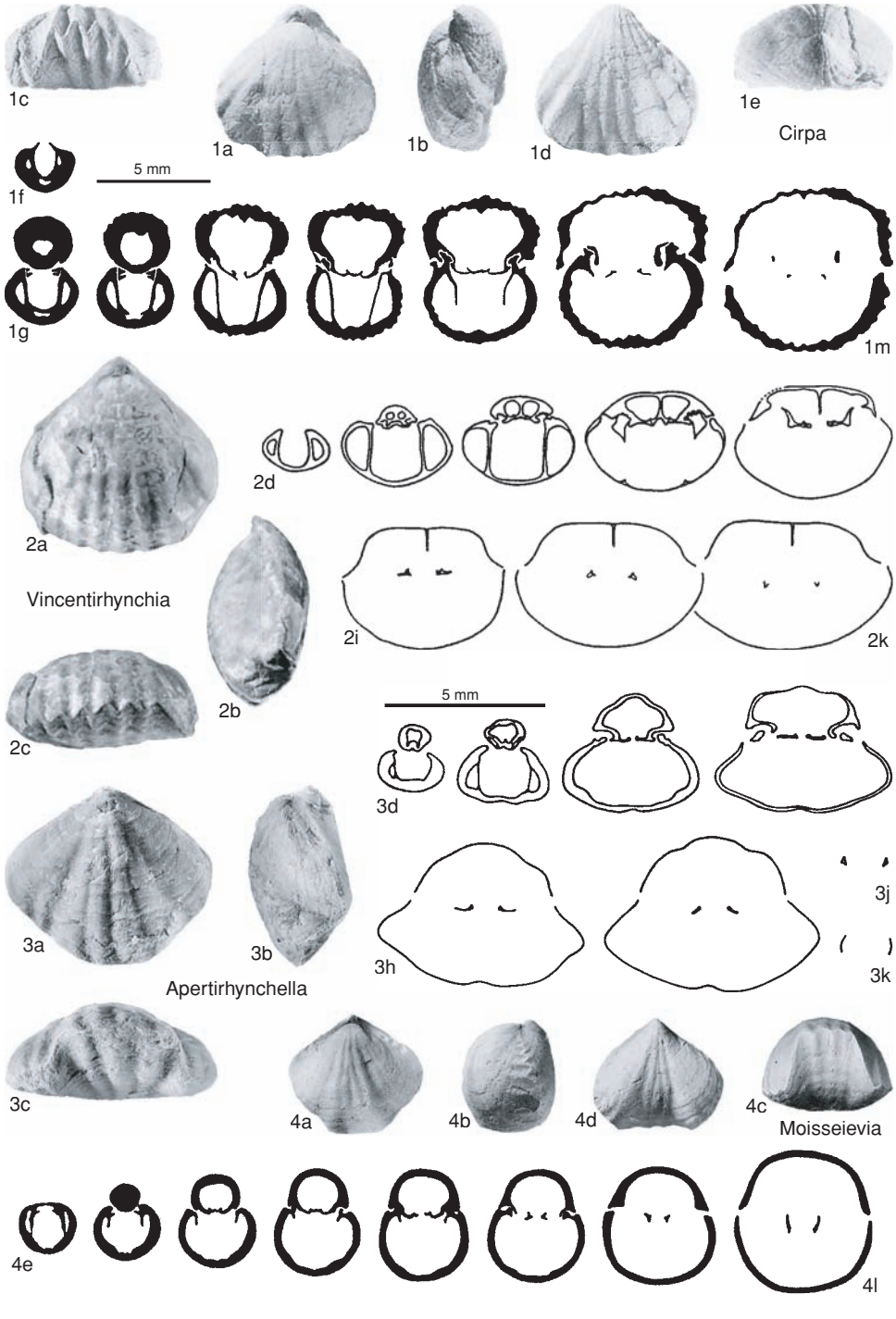

FIG. 861. Wellerellidae (p. 1263–1266).

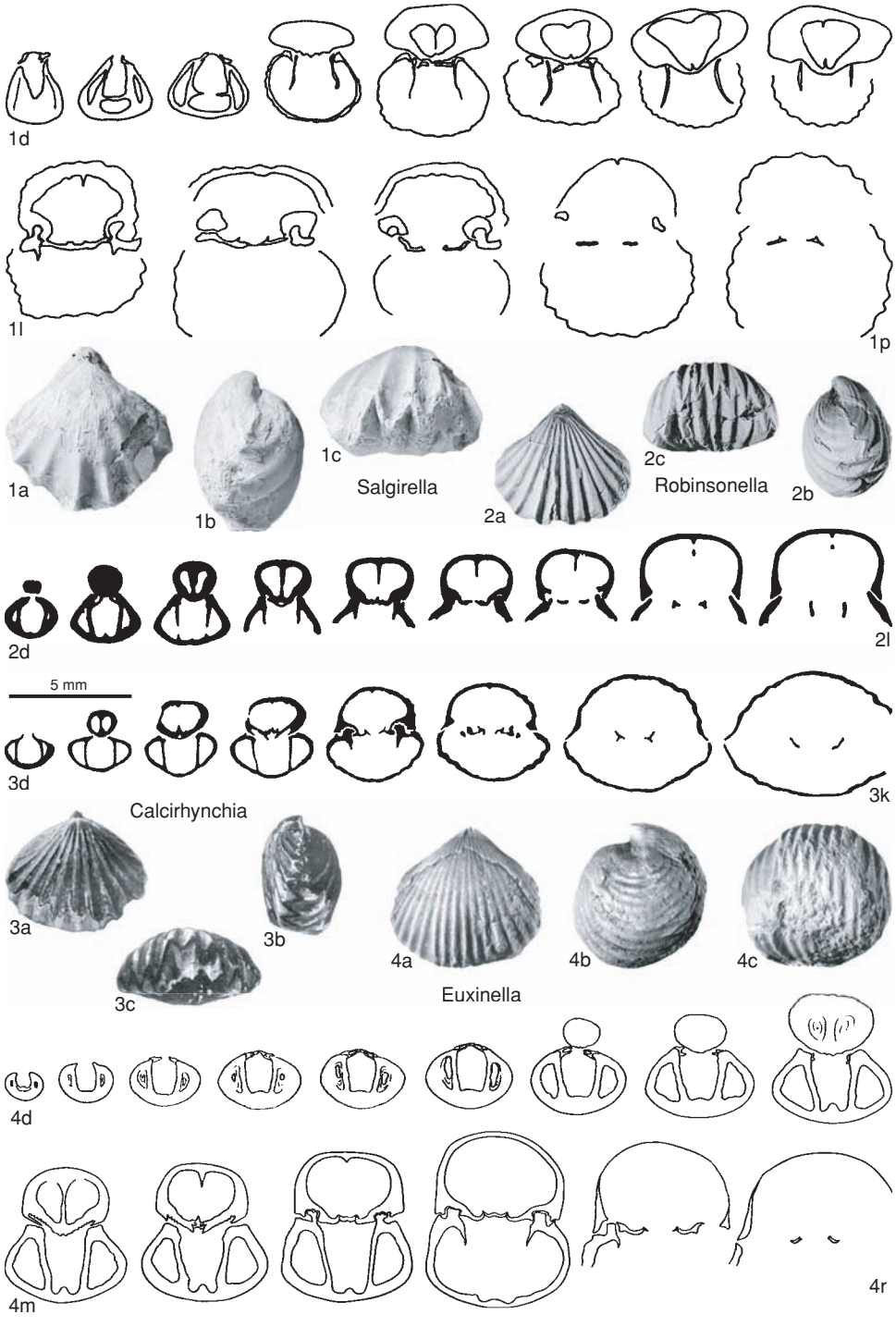

FIG. 862. Wellerellidae (p. 1263–1266).

1.1, 1.5, 1.7, 2.1, 2.5, 2.8, 3.2, 3.5, 3.9, 4.2 (Dagys, 1963).

Moisseievia Dagys, 1963, p. 46 [**M. moisseievi;* OD]. Small, subpentagonal, with distinct fold and sulcus; low, rounded costae in sulcus and on fold; indistinct costae only in anterior part on lateral sides; beak short, ridges rounded, foramen hypothyrid, deltidial plates double, conjunct. Dental plates short, parallel, pedicle collar fused to dental plates; median septum absent, hinge plate thin, horizontal in section, crura hamiform. *Upper Triassic (Norian):* Balkans, Carpathians, Crimea, northwestern Caucasus, Pamirs, China.——Fig. 861,*4a–l.* **M. moisseievi,* northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 91/640, ×1; *e–l,* transverse serial sections, distances in mm from first section, 0.6, 0.8, 1.2, 1.6, 1.7, 1.9, 2.3, 2.9 (Dagys, 1963).

?Robinsonella Moiseev, 1936, p. 45 [**R. mastakanensis;* OD]. Small, subpentagonal, moderately biconvex, strongly costate, with distinct sinus and feeble corresponding fold; beak short, incurved, ridges rounded, foramen hypothyrid, deltidial plates double, conjunct. Dental plates subparallel, no pedicle collar; septum distinct, about one-third valve length, hinge plate horizontal in section, crura allegedly hamiform. [Alternatively, may be related to ivanoviellines (hinted by development of ribbing, dorsal septum, and pitlike septalium); further studies of crura needed.] *Upper Triassic (Norian–Rhaetian):* northwestern Caucasus, India, China, Vietnam, Japan, ?New Guinea.——Fig. 862,*2a–l.* **R. mastakanensis,* Rhaetian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, TsGM 55/4801, ×1; *d–l,* transverse serial sections, distances in mm from first section, 0.6, 1.0, 1.5, 1.8, 2.1, 2.5, 3.0, 3.8, 4.3 (Dagys, 1963).

?Salgirella Moiseev, 1936, p. 48 [**Rhynchonella albertii* Oppel, 1861, p. 546; OD]. Rounded-pentagonal, beak thick, curved, no pseudointerarea; costae acute, coarse, simple, no radial striae, dorsal valve with fold. Dental plates ventrally divergent to subparallel, detached from valve floor anteriorly; pedicle collar present; deltidial plates wavy; dorsal median septum weakly developed, hinge plate flat, entire near beak, distinct anteriorly; septalium not supported by septum; crura slender, ventrally curved. [Very closely related, if not synonymous with *Cirpa* de Gregorio, 1930a, p. 40.] *Lower Jurassic (Hettangian–Pliensbachian):* Crimea, Caucasus, Austria, Hungary, Romania.——Fig. 862,*1a–p.* **S. alberti* (Oppel), Pliensbachian, Salgir river, Crimea; *a–c,* dorsal, lateral, anterior views, CNIGR 512/3808, ×1 (new); *d–p,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.1, 1.6, 2.1, 2.9, 3.3, 3.6, 4.0, 5.0, 5.4, 5.7, 6.15, 6.3, CNIGR N.509/3808 (new; courtesy of S. V. Lobacheva).

?Vincentirhynchia MacFarlan, 1992, p. 145 [**Rhynchonella pomeyroli* Drot, 1953, p. 99; OD]. Moderate size, subtriangular to subpentagonal; equibiconvex, moderately inflated; both valves with broad, flat, central parts and narrow lateral slopes; uniplication broad, shallow, flattopped; costae low, rounded, almost extending back to umbo; beak small, erect, with relatively large submesothyrid foramen. Dental plates subparallel and widely apart; dorsal valve with narrow hinge plates, and septalium supported by thin median septum. [Best restricted to type species, as other assigned species may be referable to *Cirpa* and *Prionorhynchia.*] *Upper Triassic (Rhaetian)–Lower Jurassic (Hettangian, ?Sinemurian):* New Zealand, New Caledonia, ?Siberia.——Fig. 861,*2a–k.* **V. pomeyroli* (Drot); *a–c,* holotype, dorsal, lateral, anterior views, Otapirian, Rhaetian, New Caledonia, MNHN B8395, ×1.5 (MacFarlan, 1992); *d–k,* transverse serial sections, distances in mm from first section, 0.0, 1.0, 1.3, 1.7, 2.3, 2.6, 2.9, 3.3, Hettangian, Siberia (Dagys, 1968).

Family ALLORHYNCHIDAE Cooper & Grant, 1976

[Allorhynchidae Cooper & Grant, 1976a, p. 2003] [=Septaliphorioididae Xu & Liu, 1983, p. 73]

[Materials prepared by Norman M. Savage & Miguel O. Manceñido]

Wellerelloidea with subcircular to subpentagonal outline; narrow costae extending all or most of shell length, bifurcated or intercalated in all Mesozoic and several Permian genera; dorsal fold and ventral sulcus weak to absent; delthyrium with or without deltidial plates. Thin dental plates, often almost fused to wall or absent; dorsal median septum low to absent; hinge plates divided; crura generally falciform, subfalciform, or hamifom. *Lower Carboniferous (Tournaisian)–Upper Triassic (Norian, ?Rhaetian).*

Allorhynchus Weller, 1910, p. 509 [**Rhynchonella heteropis* Winchell, 1865, p. 121; OD]. Subtriangular to subpentagonal outline and dorsibiconvex profile. Beak straight to suberect; delthyrium open, triangular, deltidial plates marginal, narrow. Fold and sulcus weak to moderate; anterior commissure uniplicate; tongue low, trapezoid. Costae of medium size, simple, subangular, extending from beaks, covering entire shell. Dental plates short, vertical; ventral muscle field elongate oval, expanding anteriorly. Hinge plates divided; dorsal median septum absent; dorsal muscle field elongate, posterior adductors elongate, narrow, partly flanking larger anterior adductors; crura diverge anteriorly, curved ventrally, dorsal edges carinate. *Lower Carboniferous (Tournaisian)–Upper Permian (Tatarian):* North America, Donetz Basin, Kazakhstan, China, Japan.——Fig. 863,*1a–i.* **A. heteropis* (Winchell), lower Mississippian, Kinderhookian, Burlington, Iowa, USA; *a–d,* dorsal, ventral, anterior, and lateral views, ×1; *e–i,*

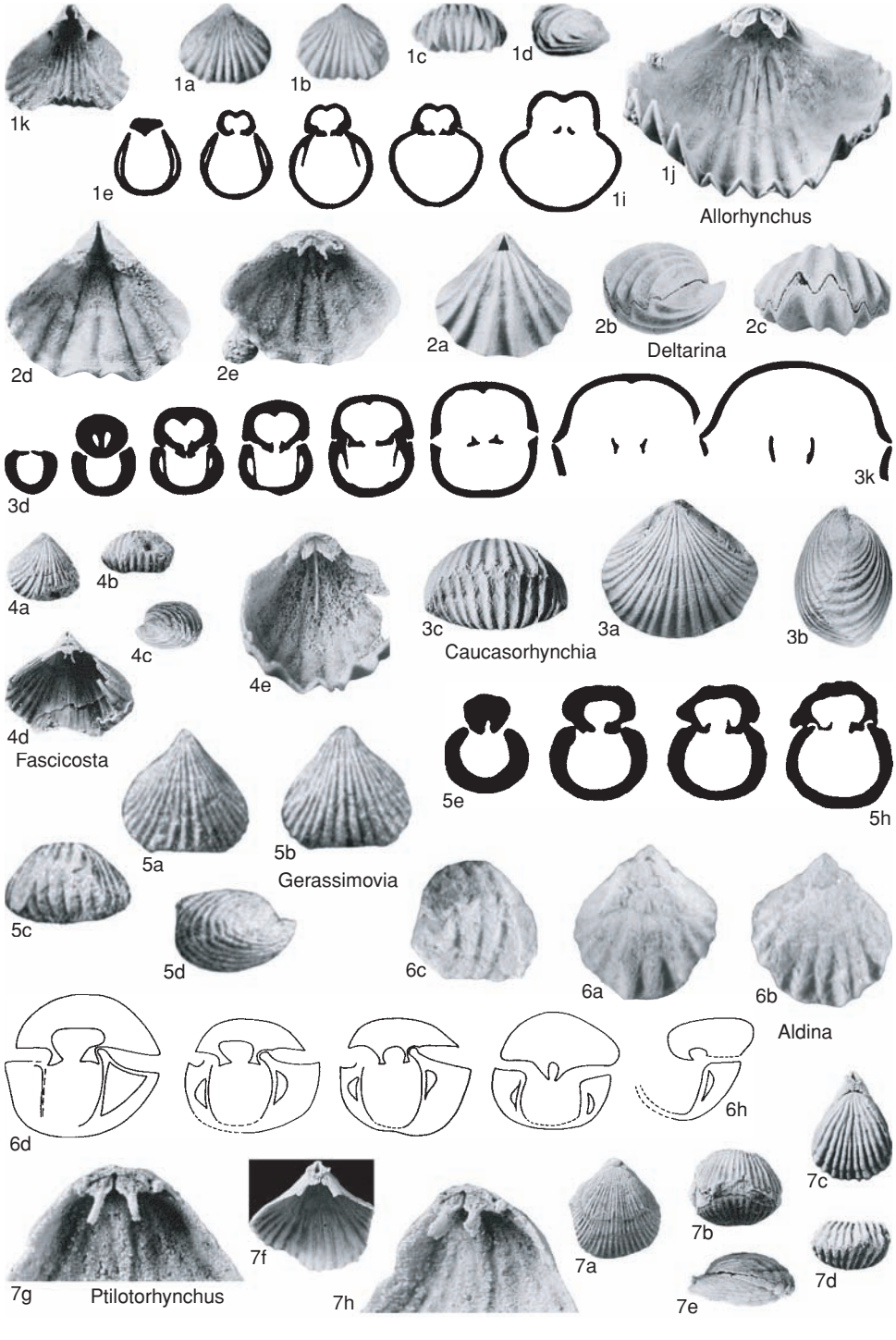

FIG. 863. Allorhynchidae (p. 1266–1270).

serial sections, ×3.8 (Weller, 1914).——Fig. 863,*1j–k. A. permianum permianum* Stehli; *j,* interior of tilted dorsal valve, ×3; *k,* interior of tilted ventral valve, ×1.5 (Cooper & Grant, 1976a).

Aldina Angiolini, 1995, p. 209 [**A. exilis;* OD]. Small; subtriangular to subpentagonal outline and dorsibiconvex profile, strongly inflated anteriorly. Ventral beak suberect; foramen small, deltidial plates conjunct. Fold and sulcus starting at midlength; anterior commissure uniplicate; tongue high, wide, typically tridentate. Costae strong, simple, angular, arising at midlength. Dental plates short, vertical. Hinge plates divided; dorsal median septum absent. *Lower Permian (Kungurian):* Pakistan.——Fig. 863,*6a–h. *A. exilis,* Bolorian, Lashkargaz Formation, Karakoram Mountains; *a–b,* holotype, dorsal and ventral views, ×3 (Angiolini, 1995); *c,* topotype, anterior view, ×3 (new); *d–h,* serial sections of topotype, 0.9, 1.1, 1.3, 1.6, 1.8 mm from posterior, no scale given (Angiolini, 1995).

Caucasorhynchia Dagys, 1963, p. 66 [**C. kunensis;* OD]. Small to medium size, rounded-pentagonal, sulcus shallow and fold low or absent, multicostate, costae with intensive branching; beak short, ridges rounded, foramen hypothyrid, deltidial plates conjunct. Dental plates short, weakly diverging, umbonal chambers, pedicle collar absent; dorsal median septum apically confined, ridgelike to absent; septalium absent; outer hinge plates incipiently ventrally convex in section; crura hamiform. *Middle Triassic (?Anisian), Upper Triassic (Carnian–Norian, ?Rhaetian):* Alps, Carpathians, northwestern Caucasus, Pamirs, Turkey, China (Himalayas, Tibet).——Fig. 863,*3a–k. *C. kunensis,* Norian, northwestern Caucasus; *a–c,* dorsal, lateral, anterior views, IGiG 49/5, ×1; *d–k,* transverse serial sections, distances in mm from first section, 0.3, 0.9, 1.2, 1.4, 1.8, 2.2, 2.9, 3.8 (Dagys, 1963).

Deltarina Cooper & Grant, 1976a, p. 2012 [**D. magnicostata;* OD]. Small; subtriangular outline and equibiconvex profile. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow. Fold and sulcus weak to moderate, anterior commissure sulciplicate. Costae moderate to coarse but usually with 1 large plication in sulcus and 2 on fold. Dental plates short, ventrally convergent; ventral muscle field elongate oval, expanding anteriorly. Hinge plates divided; dorsal median septum absent to low; crura strongly divergent anteriorly, laterally compressed, short. *Upper Permian (Kazanian):* USA.——Fig. 863,*2a–e. *D. magnicostata,* Bell Canyon Formation, Guadalupe Mountains, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d–e,* paratype, ventral valve interior, dorsal valve interior, ×3 (Cooper & Grant, 1976a).

Fascicosta Stehli, 1955, p. 71 [**Rhynchonella? longaeva* Girty, 1909, p. 322; OD]. Small; outline subtriangular to subpentagonal; profile equibiconvex; maximum thickness near midlength. Beak straight to suberect; delthyrium open, triangular, deltidial plates absent. Fold and sulcus very weak; anterior commissure uniplicate, low. Costae fine to moderate, extending from beaks, fasciculate, some bifurcation. Dental plates short, convergent ventrally; ventral muscle field elongate oval, expanded anteriorly. Hinge plates divided; dorsal median septum low, thin, supporting hinge plates posteriorly; dorsal muscle field quadripartite, expanded anteriorly; crura divergent anteriorly, ventrally curved, dorsal surface carinate. *Upper Permian (Kazanian):* USA.——Fig. 863,*4a–e. *F. longaeva* (Girty), Guadalupe Mountains, Texas; *a–c,* lectotype, dorsal, anterior, and lateral views, Capitan Limestone, El Capitan Mountain; *d,* ventral valve interior and foramen, Bell Canyon Formation, McKittrick Canyon Draw, ×1; *e,* dorsal valve interior, Bell Canyon Formation, Hegler Ranch, ×3 (Cooper & Grant, 1976a).

Gerassimovia Licharew, 1956, p. 59 [**G. gefoensis;* OD]. Small with outline subtriangular to subpentagonal and profile equibiconvex. Beak suberect to erect. Fold and sulcus low. Numerous strong costae extending from beaks, fasciculate, increasing by bifurcation and intercalation. Dental plates absent. Hinge plates divided; dorsal median septum absent. *Permian (Kungurian–Tatarian):* northern Caucasus, Pamir.——Fig. 863,*5a–h. *G. gefoensis,* northern Caucasus; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–h,* serial sections, ×6 (Licharew, 1956).

Grammorhynchus Roberts, 1971, p. 144 [**Camarotoechia eganensis* Veevers, 1959a, p. 9; OD]. Outline subcircular to longitudinally ovate; profile strongly biconvex to globular. Beak incurved, truncated by circular, mesothyrid foramen. Fold and sulcus weak, broad; anterior commissure uniplicate; tongue low, serrate. Costae strong, subangular, simple, arising at beaks, present on entire shell. Dental plates long, vertical, may be obscured by callus; ventral muscle field narrow, impressed. Hinge plates divided; dorsal median septum long, low; septalium short, deep; dorsal muscle field narrow, deeply impressed, expanded anteriorly; crural bases with triangular section; crura long, gently curved ventrally. *Lower Carboniferous (Tournaisian):* northwestern Australia.——Fig. 864,*1a–m. *G. eganensis* (Veevers), Laurel Formation, Fitzroy basin; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2 (Veevers, 1959a); *e–m,* serial sections 2.2, 3.0, 3.4, 3.6, 3.8, 4.0, 4.2, 4.4, 4.8 mm from posterior, ×2.6 (Roberts, 1971).

Hagabirhynchia Jefferies, 1961, p. 5 [**H. arabica;* OD] [=*Magabirhynchia* Xu & Liu, 1983, p. 71, *nom. null.*]. Small, rounded-pentagonal, with sulcus shallow and fold low, costae strong and extending from umbo and often forking; beak thick, suberect, deltidial plates conjunct. Dental plates diverging, pedicle collar absent; dorsal median septum low, septalium rudimentary, outer hinge plates narrow, divided; crura hamiform. *Upper Triassic (Norian):* Oman, China, India, ?New Guinea.——Fig. 864,*3a–l. *H. arabica,* Oman; *a–c,* holotype, dorsal, lateral, anterior views, ×2; *d,* holotype, ventral view,

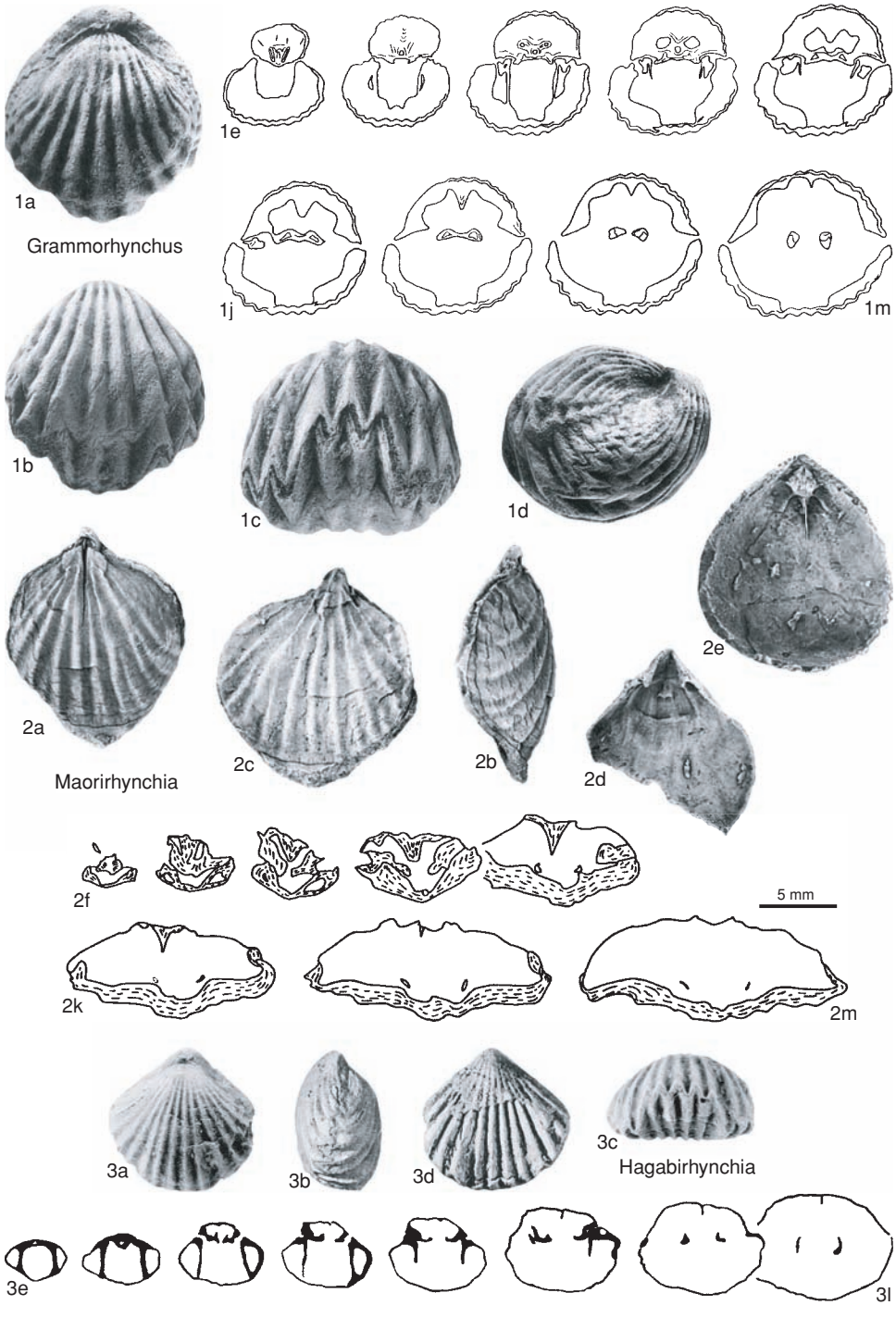

FIG. 864. Allorhynchidae (p. 1268–1270).

BMNH BB.20248, ×2 (new); *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.0, 1.2, 1.3, 1.5, 2.0, 2.3, 2.7, BMNH BB.20249, approximately ×3.2 (Jefferies, 1961).

Hemileurus Cooper & Grant, 1976a, p. 2017 [**H. runcinatus;* OD]. Small; outline subtriangular; profile equibiconvex; maximum thickness just anterior of midlength. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow. Fold and sulcus very weak; anterior commissure uniplicate, low, serrate. Costae moderate, simple, rounded, arising anterior of umbones. Dental plates short, vertical; ventral muscle field forming elongate triangle, expanded anteriorly. Hinge plates divided by deep notch; dorsal median septum absent; dorsal muscle field oval, quadripartite, slightly expanded anteriorly; crura divergent anteriorly, curved ventrally, twisted, dorsal edges carinate. *Lower Permian (Asselian–Sakmarian):* USA.——Fig. 865,*1a–d.* **H. runcinatus,* Neal Ranch Formation, Glass Mountains, Wolf Camp Hills, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×1; *d,* view of broken shell showing cardinalia, ×4 (Cooper & Grant, 1976a).

?Maorirhynchia MacFarlan, 1992, p. 71 [**Rhynchonella nuggetensis* Wilckens, 1927, p. 22; OD]. Moderate to large size, rounded-subtriangular to subcircular or elliptical; equibiconvex, slightly to moderately inflated; costae low, rounded or obsolescent, typically extending back to beak and bifurcating, occasionally dying out near anterior margin; rectimarginate to uniplicate, fold and sulcus usually broad and arcuate; beak small with minute foramen. Dorsal valve with broad horizontal hinge plates and shallow septalium; posterior part of both valves may be greatly thickened internally, dental plates almost fused to wall. *?Lower Triassic, Middle Triassic (Anisian)–Upper Triassic (lower Norian):* New Zealand, New Caledonia.——Fig. 864,*2a–m.* **M. nuggetensis* (Wilckens), Ladinian, Kaihikuan, Southland, New Zealand; *a–c,* dorsal, lateral, ventral views, OU NZ C2455; *d,* latex mold of pedicle valve interior, OU NZ C2969, ×1; *e,* latex mold of brachial valve interior, OU NZ C2952, ×1; *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.7, 1.3, 1.5, 2.1, 3.1, 4.1, 5.1, 5.9, OU NZ 16309 (MacFarlan, 1992).

Neofascicosta Xu, 1978, p. 277 [**N. pulchra;* OD]. Small to medium, roundly trigonal, moderately biconvex to nearly flat; fold and sulcus weakly developed; anterior commissure slightly uniplicate, commonly somewhat ligate; covered with clustered subangular costae increasing anteriorly by bifurcation or intercalation; ornamented with dense, fine concentric growth lines and concentric lamellae marginally; beak small and nearly straight; foramen hypothyrid to mesothyrid; beak ridges angular, planareas narrow. Dental plates well developed; teeth stout; dorsal beak projecting into delthyrial cavity; hinge plates divided and fused with inner socket ridges; septalium shallow and short; septum low and thick, ridgelike anteriorly; crural bases trigonal; crura hamiform to subfalciform. *Upper Triassic:* southwestern and southeastern China (Sichuan, Qinghai).——Fig. 865,*4a–i.* **N. pulchra,* Sichuan; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CIGMR SCSb 6020, ×1; *e–i,* transverse serial sections, distances in mm from first section, 0.0, 0.55, 0.7, 0.8, 1.5 (Xu, 1978).

Pseudowellerella Licharew, 1956, p. 58 [**P. nikchitchi;* OD] [=*Denticuliphoria* Licharew, 1956, p. 57 (type, *D. rara,* OD); *Wairakiella* Waterhouse, 1967, p. 87 (type, *W. rostrata,* OD)]. Small; subtriangular to subpentagonal outline; equibiconvex profile. Beak suberect to erect; foramen small. Fold and sulcus weak, wide; anterior commissure uniplicate, serrate. Costae medium size, numerous, extending from beak. Dental plates poorly developed or absent. Hinge plates united; dorsal median ridge short, low. *Permian (Kungurian–Tatarian):* northern Caucasus, New Zealand.——Fig. 865,*3a–f.* **P. nikchitchi; a–d,* dorsal, ventral, anterior, and lateral views, ×2; *e–f,* transverse sections, ×5.3 (Licharew, 1956).

Ptilotorhynchus Cooper & Grant, 1976a, p. 2010 [**P. delicatum;* OD]. Outline elongate subtriangular with greatest width near anterior; profile weakly dorsibiconvex. Beak straight; delthyrium with large conjunct alate deltidial plates, foramen oval, close to beak. Fold and sulcus weak; anterior commissure uniplicate, low. Costae fine, increasing by bifurcation and intercalation. Dental plates short to absent; ventral muscle field large, rounded. Hinge plates short, divided; dorsal median septum very short, supporting posterior of hinge plates; dorsal muscle field elongate, divided by low myophragm; crura curved ventrally, laterally flattened. *Permian (Kungurian–Kazanian):* USA.——Fig. 863,*7a–h.* **P. delicatum,* Guadalupe Mountains, Texas; *a–b,* holotype, dorsal and anterior views, ×1; *c–e,* paratype, dorsal, anterior, and lateral views of young specimen, ×3; *f,* paratype, posterior of ventral valve showing alate deltidial plates, ×2; *g–h,* interiors of dorsal valve showing cardinalia, ×6 (Cooper & Grant, 1976a).

Septaliphorioidea Yang & Xu, 1966, p. 29[101] [**S. paucicostata;* OD] [=*Septaliphoroidea* Ching, Sun, & Ye in Ching & others, 1979, p. 131–132, *nom. null.*]. Small, roundly triangular to subpentagonal, depressed subequibiconvex, uniplicate; ventral sulcus and dorsal fold well developed, fold flattopped and truncated at front; covered with plicae, bifurcating on dorsal but intercalating on ventral valve; rounded costae, extending from umbo, 2 to 4 on fold, 3 to 4 on lateral slopes; beak straight to slightly incurved; narrow deltidial plates. Dental plates short; hinge plates divided; median ridge weak and low, septalium absent. *Middle Triassic (Anisian):* western China.——Fig. 865,*5a–l.* **S. paucicostata,* paratype, Gheizhou; *a–d,* dorsal, lateral, anterior, ventral views, MCMB DDR3C3, ×2; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.7, 0.9, 1.1, 1.25, 1.4, 1.7, 2.0, MCMB DDR III D3-2 (Yang & Xu, 1966).

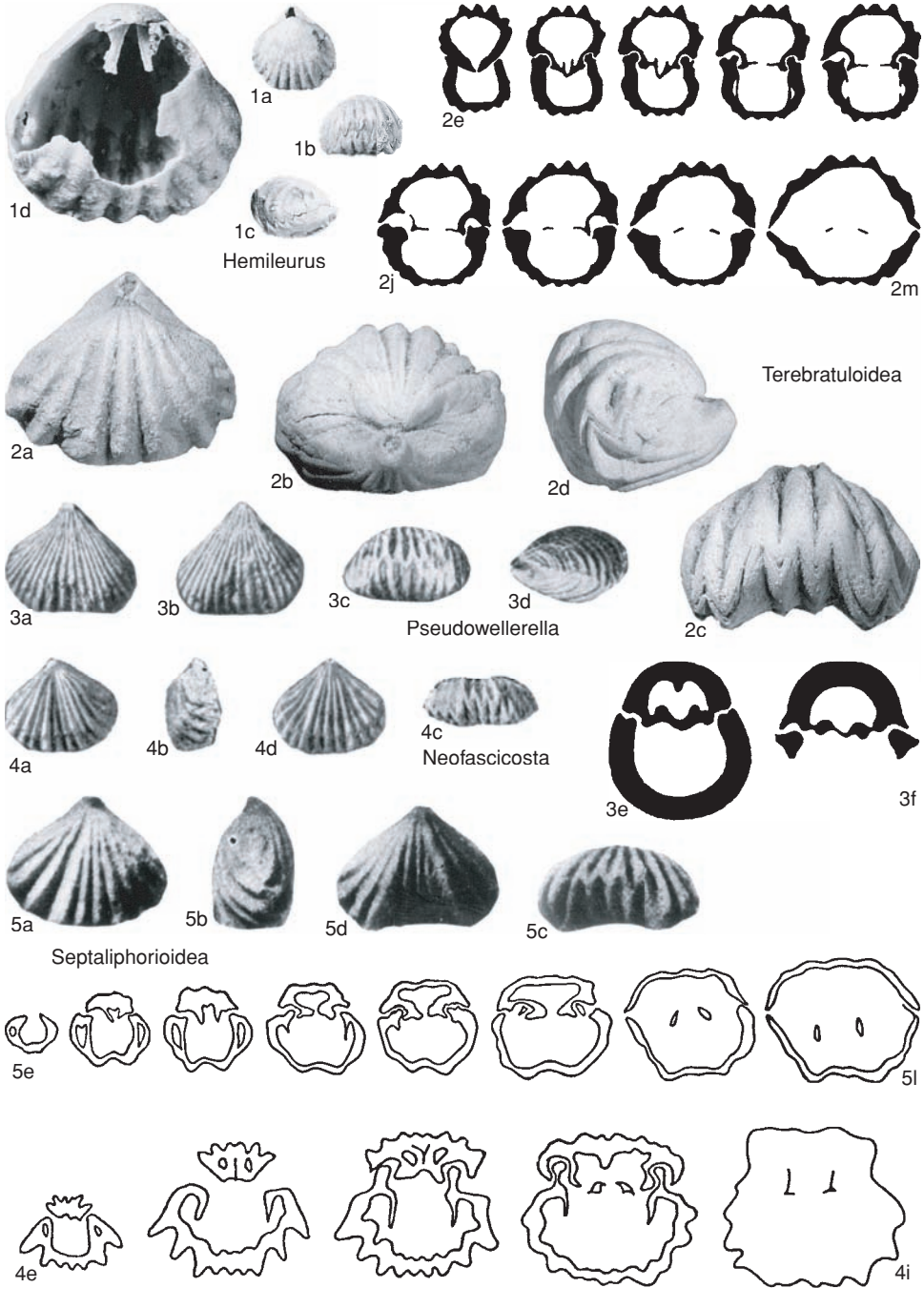

FIG. 865. Allorhynchidae (p. 1270–1272).

Terebratuloidea Waagen, 1883, p. 410 [**T. davidsoni;* OD]. Outline transversely subpentagonal and profile dorsibiconvex. Beak suberect and truncated by large circular mesothyrid foramen; delthyrium with conjunct deltidial plates. Fold and sulcus moderately strong, arising at umbones; anterior commissure uniplicate, serrate. Costae coarse, arising at beaks, rounded in profile. Dental plates close to valve walls, may be obscured by callus but distinct in specimen sectioned; teeth large, rounded. Dorsal median septum absent; hinge plates joined posteriorly by convex plate, divided for most of length; crural bases and crura horizontal to slightly oblique. *Lower Carboniferous (Viséan)–Upper Permian (Kazanian):* Pakistan, India, central and southeastern Asia, China, Europe, Urals.——Fig. 865,*2a–m.* **T. davidsoni,* Wordian, Salt Range, Pakistan; *a–d,* dorsal, posterior, anterior, and lateral views, Buri Khel, ×1.3 (new); *e–m,* serial sections 3.6, 3.9, 4.2, 4.4, 4.6, 5.0, 5.2, 5.6, 6.4 mm from posterior, middle *Productus* Limestone, Seminodular band, Dhak Pass Nala, ×1.4 (new).

Family PONTISIIDAE Cooper & Grant, 1976

[Pontisiidae Cooper & Grant, 1976a, p. 2019] [=Lissorhynchiidae Xu, 1990, p. 77]

[Materials prepared by Norman M. Savage & Miguel O. Manceñido]

Wellerellidae with dorsal median septum weak to absent. Costae usually coarse. Dental plates commonly distinct; hinge plates undivided but notched anteriorly; dorsal median septum absent. *Upper Carboniferous (Bolsovian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Subfamily PONTISIINAE Cooper & Grant, 1976

[*nom. transl.* Savage, 1996, p. 255, *ex* Pontisiidae Cooper & Grant, 1976a, p. 2019] [=Lissorhynchiinae Xu & Liu, 1983, p. 73]

[Materials prepared by Norman M. Savage & Miguel O. Manceñido]

Pontisiidae with coarse costae. *Upper Carboniferous (Bolsovian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Pontisia Cooper & Grant, 1969, p. 13 [**P. stehlii;* OD]. Outline subtriangular to subpentagonal and profile dorsibiconvex, strongly inflated anteriorly. Beak suberect; delthyrium triangular, foramen elongate oval, deltidial plates conjunct. Fold and sulcus strong, wide, from umbones; anterior commissure uniplicate; tongue high, wide, typically tridentate. Costae strong, simple, angular, arising at umbones. Dental plates strong, vertical; ventral muscle field transversely subtriangular, expanded anteriorly. Hinge plates undivided; inner socket ridges large, inclined over crenulate sockets; dorsal median septum absent, median ridge low; dorsal muscle field elongate quadripartite, expanded anteriorly; crura with horizontal bases, strongly twisted to become laterally flattened, dorsally carinate, curved ventrally. *Upper Carboniferous (Bolsovian)–Upper Permian (Kazanian):* USA, Guatemala, Venezuela, Thailand, Spain, Kazakhstan.——Fig. 866,*1a–g.* **P. stehlii,* upper Leonardian, Road Canyon Formation, Glass Mountains, Hess Canyon, Texas, USA; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* interior of dorsal valve, ×4.5; *g,* interior of posterior of ventral valve, ×4 (Cooper & Grant, 1976a).

Anteridocus Cooper & Grant, 1976a, p. 2054 [**A. gongylus;* OD]. Small; subpentagonal outline; dorsibiconvex profile, inflated anteriorly. Beak suberect; delthyrium triangular, deltidial plates disjunct, foramen oval. Fold and sulcus moderate, extending from one-third shell length; anterior commissure uniplicate; tongue moderate to low, typically triserrate. Costae coarse, simple, from one-third shell length. Dental plates strong, ventrally convergent; ventral muscle field cordate, expanded anteriorly. Hinge plates undivided but with deep notch; inner socket ridges narrow; dorsal median septum low, very short; crura laterally compressed, long, dorsally carinate. *Permian (Sakmarian–Kazanian):* USA.——Fig. 866,*3a–e.* **A. gongylus,* Leonardian, Cathedral Mountain Formation, Glass Mountains, Split Tank, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d,* interior of conjoined posterior, showing dental plates and cardinalia, ×4; *e,* interior of dorsal valve, ×6 (Cooper & Grant, 1976a).

Antronaria Cooper & Grant, 1976a, p. 2036 [**A. speciosa;* OD]. Transversely subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak suberect; delthyrium triangular, deltidial plates just conjunct, foramen oval. Fold and sulcus strong, wide, from umbones; anterior commissure uniplicate; tongue high, wide, typically triserrate. Costae strong, simple, arising at umbones. Dental plates strong, vertical to medially convex; ventral muscle field large, cordate, expanded anteriorly. Hinge plates undivided; dorsal median septum absent, median ridge low, thick; dorsal muscle field elongate oval; crura long, twisted, dorsally carinate, curved ventrally. *Lower Permian (Sakmarian–Artinskian):* USA.——Fig. 866,*5a–g.* **A. speciosa,* upper Wolfcampian, Hess Formation, Glass Mountains, Taylor Ranch, Texas; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views; *f,* paratype, interior of ventral valve, ×1; *g,* paratype, tilted view of dorsal valve interior, ×3 (Cooper & Grant, 1976a).

?Bodrakella Moiseev, 1936, p. 47 [**Rhynchonella bodrakensis* Moiseev, 1934, p. 56; OD]. Shell small, oval, beak slightly incurved, thin, sharp, without pseudointerarea, sulcus shallow, fold weakly developed; costae coarse, simple, only near shell margin, growth lines well developed, no radial striae. Pedicle

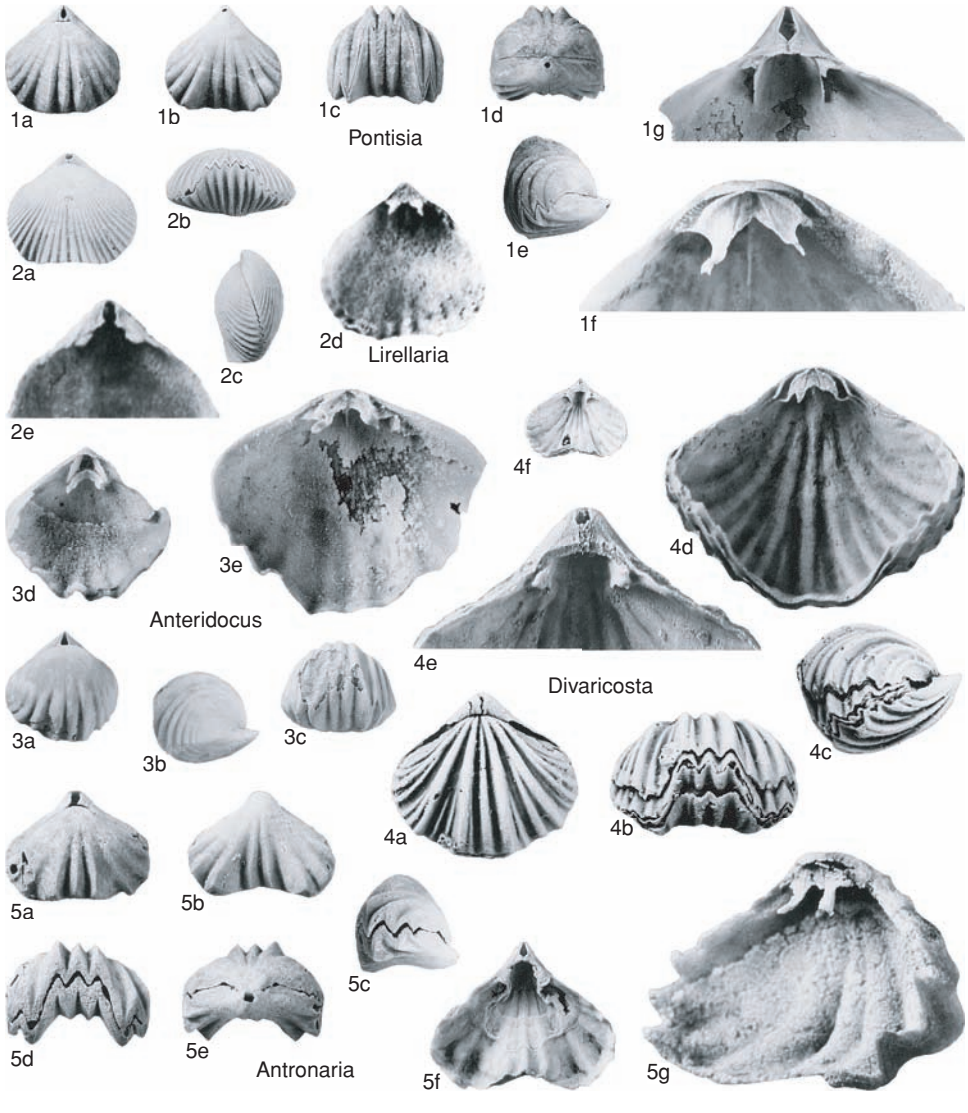

FIG. 866. Pontisiidae (p. 1272–1275).

collar present, dental plates vertical, joined to shell not the whole distance; teeth massive, teeth and sockets crenulated, denticula absent; dorsal median septum weakly developed; hinge plate entire, at level of socket ridges; crura slender, ventrally incurved. *Lower Jurassic (?Sinemurian, Pliensbachian, ?Toarcian):* Crimea, Bulgaria, ?Caucasus. ——FIG. 867,*1a–l. *B. bodrakensis* (MOISEEV), Pliensbachian, Crimea; *a–d,* dorsal, lateral, anterior, ventral, ×1.5 (new); *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.55, 0.9, 1.35, 1.6, 2.0, 2.2, 2.8, 3.2, CNIGR 601/3808 (new; courtesy of S. V. Lobacheva).

Divaricosta COOPER & GRANT, 1969, p. 11 [**D. squarrosa;* OD]. Small; outline subtriangular to subpentagonal; profile dorsibiconvex, not inflated anteriorly. Beak straight to suberect; delthyrium wide, almost closed by large deltidial plates. Dorsal fold and sulcus low, from midlength; anterior commissure uniplicate; tongue low to moderate, serrate. Costae varied in size, markedly fasciculate, increasing by bifurcation and intercalation. Dental plates strong, vertical, close to walls; ventral muscle field narrowly triangular, expanding anteriorly. Hinge plates large, undivided; inner socket ridges slightly overhanging sockets; dorsal median septum absent,

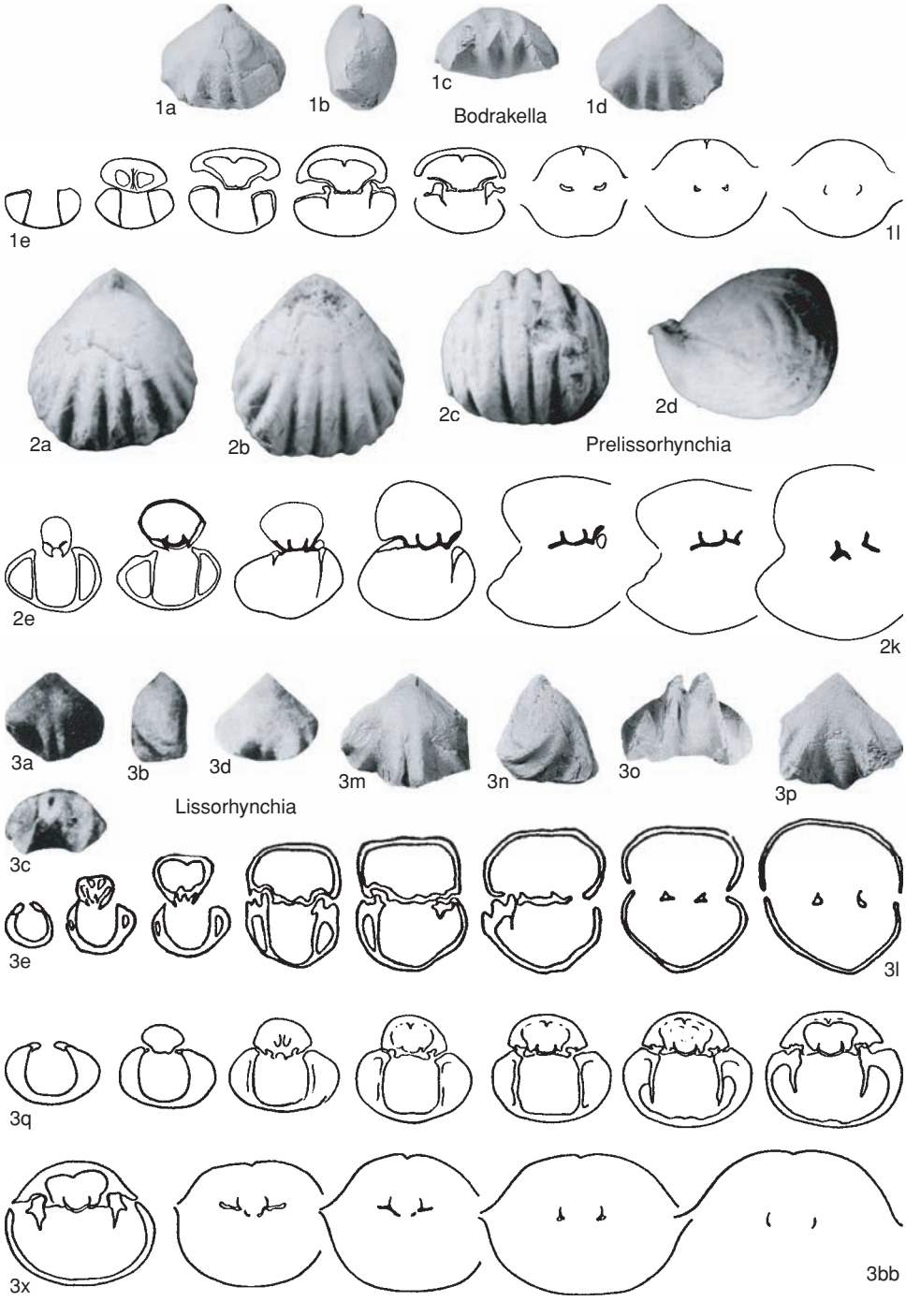

FIG. 867. Pontisiidae (p. 1272–1275).

median ridge moderately low, thick, short; dorsal muscle field elongate, quadripartite, expanded anteriorly; crura laterally compressed, not twisted, curved ventrally. *Lower Permian (Kungurian):* USA.——Fig. 866,*4a–f. *D. squarrosa,* lower Guadalupian, Cherry Canyon Formation, Getaway Member, Guadalupe Mountains, Guadalupe Pass, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* interior of dorsal valve posterior, ×4; *e,* interior of ventral valve; *f,* interior of tilted ventral valve, ×1 (Cooper & Grant, 1976a).

Lirellaria Cooper & Grant, 1976a, p. 2031 [**L. costellata;* OD]. Outline subpentagonal to subcircular and profile equibiconvex. Beak suberect to erect; delthyrium triangular, deltidial plates conjunct, foramen oval, submesothyrid. Fold and sulcus weak, arising at about midlength; anterior commissure uniplicate, low, rounded. Costae fine, simple, extending from umbones. Dental plates short, strong. Hinge plates undivided, outer hinge plates small, inner hinge plates coalesced; inner socket ridges strong; dorsal median septum absent; crura ventrally curved, concave medially, laterally compressed. *Permian (Artinskian–Kazanian):* USA.——Fig. 866,*2a–e. *L. costellata,* upper Guadalupian, Bell Canyon Formation, Lamar Member, Guadalupe Mountains, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* dorsal valve interior, ×3; *e,* interior of ventral valve posterior, ×4 (Cooper & Grant, 1976a).

Lissorhynchia Yang & Xu, 1966, p. 14[94] [**L. pygmaea;* OD] [=*Neowellerella* Dagys, 1974, p. 116 (type, *N. vesca,* OD)]. Small, subtrigonal to subpentagonal, dorsibiconvex, with flattened ventral valve; smooth posteriorly, with ventral sulcus and dorsal fold developed anteriorly; commissure uniplicate bidentate; each lateral slope bearing pair of marginal plicae; beak small, slightly incurved; disjunct deltidial plates narrow, foramen small, submesothyrid to hypothyrid. Muscle scars elongate oval, indistinctly differentiated into several pairs; septalium very small, median ridge exceedingly short and crura short and slightly incurved. *Lower Triassic (Scythian)–Middle Triassic:* Caucasus, Russia, *Lower Triassic;* Alps, Himalayas, southwestern China (southern Qilian), *Middle Triassic*.——Fig. 867,*3a–l. *L. pygmaea,* Anisian, Gheizhou, China; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MCMB DDR VI 1, ×2; *e–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 0.9, 1.1, 1.2, 1.35, 1.4, 1.8, MCMB DDR VI 1-2 (Yang & Xu, 1966).——Fig. 867,*3m–bb. L. vesca* (Dagys), Induan, Scythian, northwestern Caucasus; *m–p,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/71, ×2; *q–bb,* transverse serial sections, distances in mm from first section, 0.1, 0.2, 0.4, 0.6, 0.66, 0.76, 0.96, 1.16, 1.31, 1.41, 1.51, 1.76, IGiG 394/72 (Dagys, 1974).

Prelissorhynchia Xu & Grant, 1994, p. 36 [**Pugnax pseudoutah* Huang, 1933, p. 64; OD] [=*Prelissorhynchia* Xu, 1990, p. 68, *nom. nud.;* ?*Wellerellina* Shen, He, & Zhu, 1992, p. 183 (type, *W. chongqingensis,* OD)]. Small; outline subcircular to ovate; profile inflated dorsibiconvex. Beak straight to suberect; delthyrium open or with small deltidial plates. Fold and sulcus prominent anteriorly; tongue high, trapezoid, typically tridentate. Costae coarse, rounded, simple, from umbones. Dental plates short, vertical. Hinge plates undivided, inner hinge plates arched; crural bases arising from dorsal edges of hinge plates; crura twisted, dorsally carinate. [*Wellerellina* may eventually be shown to be the senior synonym, but present knowledge of interior is insufficient to indicate this.] *Upper Permian (Tatarian)–Lower Triassic (Scythian):* China.——Fig. 867,*2a–k. *P. pseudoutah* (Huang), Tatarian, Changxing Formation, Sichuan Province; *a–d,* dorsal, ventral, anterior, and lateral views, ×3; *e–k,* serial sections (Xu & Grant, 1994).

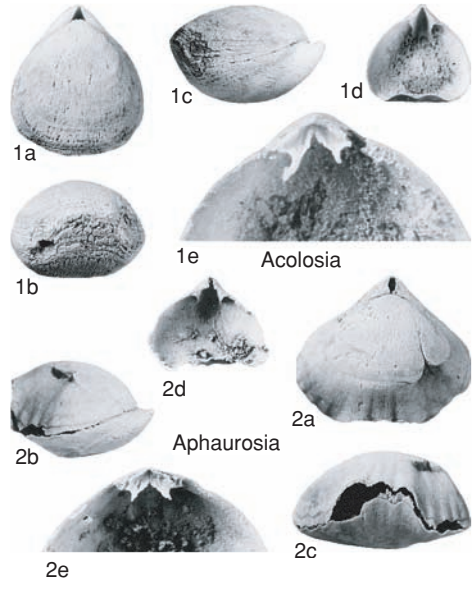

Fig. 868. Pontisiidae (p. 1275–1276).

Subfamily ACOLOSIINAE Savage, 1996

[Acolosiinae Savage, 1996, p. 255]

[Materials prepared by Norman M. Savage]

Pontisiidae with surface smooth except for very weak costae anteriorly. *Permian (Sakmarian–Kazanian).*

Acolosia Cooper & Grant, 1976a, p. 2050 [**A. glabra;* OD]. Small; outline elongate oval; profile equibiconvex. Beak suberect to erect; delthyrium open, triangular; deltidial plates absent. Dorsal fold and ventral sulcus weak, limited to anterior third of

shell; anterior commissure weakly uniplicate, rounded. Surface smooth except for 3 very weak costae at anterior of fold and sulcus and 1 very weak costa on each flank. Dental plates strong, vertical. Hinge plates undivided; inner socket ridges stout; dorsal median septum absent, median ridge low; crura short, laterally compressed. *Permian (Sakmarian–Kungurian):* USA.——Fig. 868,*1a–e. *A. glabra,* lower Guadalupian, Wordian, Word Formation, China Tank Member, Glass Mountains, Hess Canyon, Texas; *a–c,* holotype, dorsal, anterior, and lateral views; *d,* interior of ventral valve, ×2; *e,* interior of dorsal valve posterior, ×6 (Cooper & Grant, 1976a).

Aphaurosia Cooper & Grant, 1976a, p. 2048 [**A. scutata;* OD]. Outline transversely subpentagonal and profile dorsibiconvex. Beak suberect; delthyrium triangular, deltidial plates disjunct, foramen oval. Fold and sulcus low, wide, developed in anterior third of shell; anterior commissure uniplicate, low to moderate, serrate. Costae weak, low, rounded, developed only anteriorly. Hinge plates triangular, undivided; dorsal median septum absent, median ridge thick, short, low; dorsal muscle field elongate quadripartite, expanded anteriorly; crura long, concave medially. *Upper Permian (Kazanian):* USA.——Fig. 868,*2a–e. *A. scutata,* upper Guadalupian, Bell Canyon Formation, Lamar Member, Guadalupe Mountains, Pratt Place, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d,* paratype, interior of ventral valve, ×1; *e,* paratype, interior of dorsal valve, ×3 (Cooper & Grant, 1976a).

Family PETASMATHERIDAE Cooper & Grant, 1976

[Petasmatheridae Cooper & Grant, 1976a, p. 1928]

[Materials prepared by Norman M. Savage]

Small Wellerelloidea with dorsal fold weak to absent; anterior commissure rectimarginate; costae strong, simple, arising at beaks; interarea well developed; delthyrium open, without deltidial plates. Dental plates short; hinge plates divided. *Lower Permian (Sakmarian–Kungurian).*

Petasmatherus Cooper & Grant, 1969, p. 12 [**P. opulus;* OD]. Small; outline subpentagonal; profile equibiconvex. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow, disjunct. Dorsal fold and ventral sulcus weak; anterior commissure uniplicate to rectimarginate; serrate. Costae coarse relative to shell size, simple, from beaks. Dental plates short, vertical or slightly convergent ventrally, close to or fused to walls; ventral muscle field elongate oval, expanded anteriorly. Hinge plates divided; dorsal median septum absent but low median ridge may be present; dorsal muscle field quadripartite, expanded anteriorly; crura short, widely divergent, laterally compressed, slightly curved ventrally. *Lower Permian (Sakmarian–Kungurian):* USA (Texas).——Fig. 869,*1a–h. *P. opulus,* lower Guadalupian, Word Formation, Glass Mountains, Hess Canyon; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f,* hypotype, interior of conjoined valves showing dental plates and cardinalia; *g,* paratype, interior of dorsal valve, ×6; *h,* hypotype, interior of ventral valve, ×3 (Cooper & Grant, 1976a).

Elassonia Cooper & Grant, 1976a, p. 1935 [**E. micraria;* OD]. Very small; outline subcircular to subpentagonal; profile equibiconvex. Beak straight; delthyrium open, triangular, deltidial plates absent. Weak ventral fold and dorsal sulcus; anterior commissure weakly sulcate. Costae moderately strong for size of shell, fasciculate, multiplying by bifurcation and intercalation. Dental plates short, vertical, close to valve walls; ventral muscle field elongate oval. Hingle plates deeply divided; dorsal median septum absent, median ridge low; dorsal muscle field elongate, quadripartite, expanded anteriorly; crura long, laterally compressed. *Lower Permian (Sakmarian–upper Artinskian):* USA (Texas).——Fig. 869,*2a–h. *E. micraria,* upper Leonardian, Road Canyon Formation, Glass Mountains, Old Word Ranch; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×3; *f,* paratype, ventral valve interior; *g,* paratype, dorsal valve interior; *h,* interior of inclined ventral valve, ×12 (Cooper & Grant, 1976a).

Iotina Cooper & Grant, 1976a, p. 1944 [**I. minuta;* OD]. Small; outline subpentagonal; profile biconvex. Beak straight; delthyrium long, open, triangular, deltidial plates absent. Fold and sulcus strong, narrow, from beaks; anterior commissure sulciplicate, narrow. Costae coarse for size, simple, arising near beaks, typically 2 on fold. Dental plates absent. Hinge plates deeply divided; dorsal median septum absent; crura short, laterally compressed, concave medially. *Lower Permian (Sakmarian):* USA (Texas).——Fig. 869,*3a–e. *I. minuta,* lower Bone Spring Formation, Sierra Diablo, Black John Canyon; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d–e,* paratype, dorsal valve interior, ventral valve interior, ×4 (Cooper & Grant, 1976a).

Ptygmactrum Cooper & Grant, 1976a, p. 1939 [**P. extensum;* OD]. Small; outline transversely semicircular; profile equibiconvex; cardinal margin very wide, alate. Beak straight; delthyrium narrow, triangular, open, deltidial plates absent. Dorsal fold and ventral sulcus very weak; anterior commissure rectimarginate to weakly uniplicate; serrate. Costae coarse for size, simple, from cardinal margin. Dental plates short, vertical. Hinge plates deeply divided; dorsal median septum absent, median ridge

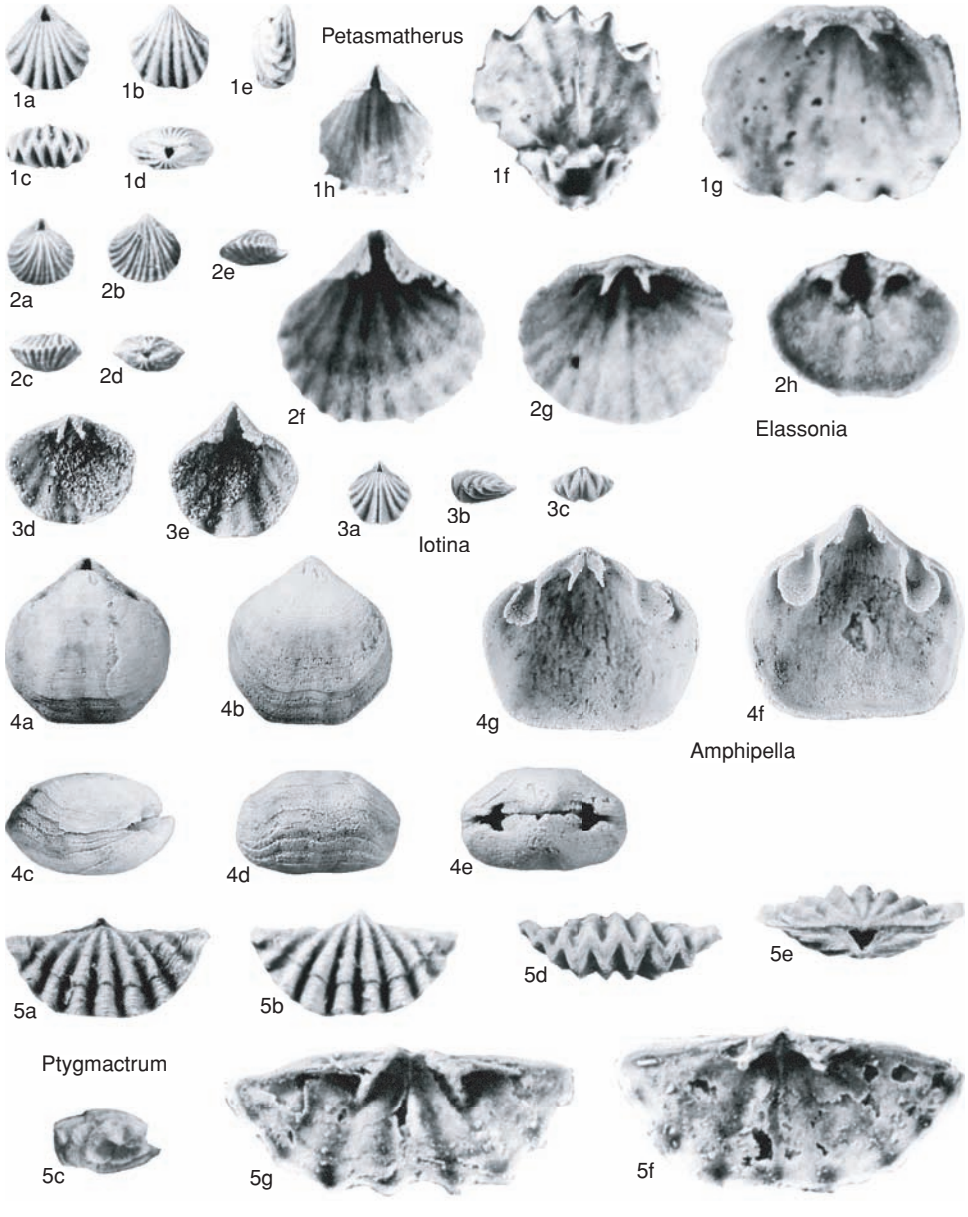

FIG. 869. Petasmatheridae and Amphipellidae (p. 1276–1278).

low; crura short, laterally compressed. *Lower Permian (lower Artinskian–Kungurian):* USA (Texas).——FIG. 869,*5a–g. *P. extensum,* upper Leonardian, lower Road Canyon Formation, Glass Mountains, Old Word Ranch; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×4; *f–g,* paratype, dorsal valve interior, ventral valve interior, ×9 (Cooper & Grant, 1976a).

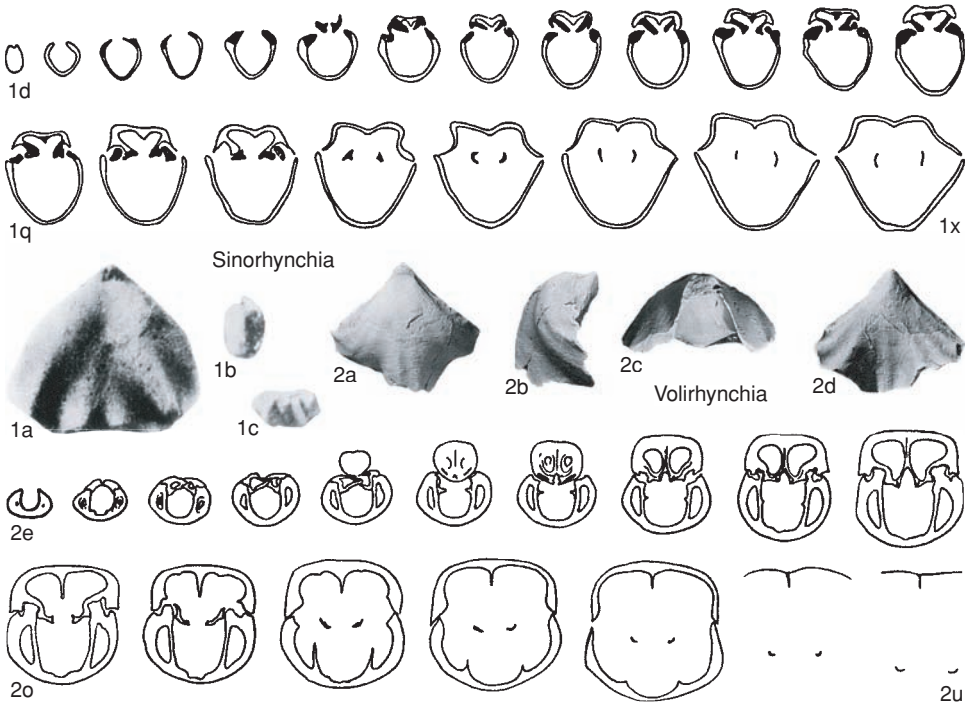

FIG. 870. Sinorhynchiidae (p. 1278–1279).

Family AMPHIPELLIDAE Cooper & Grant, 1976

[Amphipellidae COOPER & GRANT, 1976a, p. 1947]

[Materials prepared by NORMAN M. SAVAGE]

Small Wellerelloidea with outline subcircular, posterolateral pouches (apricatria) in both valves, and dental plates very short. *Lower Permian (Artinskian).*

Amphipella COOPER & GRANT, 1969, p. 11 [**A. arcaria;* OD]. Very small with outline subcircular to subpentagonal and profile equibiconvex. Posterolateral pouches (apricatria of COOPER & GRANT, 1976a, p. 1948) in both dorsal and ventral valves, visible as invaginations along posterolateral margins. Beak suberect to erect; delthyrium open, triangular, deltidial plates absent. Very weak dorsal fold and ventral sulcus; anterior commissure rectimarginate to weakly uniplicate. Surface smooth, growth lines pronounced anteriorly. Dental plates short, slightly convergent ventrally, may be fused to walls; large, narrow-necked apricatrial pouches present each side of delthyrium; ventral muscle field small, heart shaped. Hinge plate divided; dorsal median septum absent, median ridge low; apricatria present flanking cardinalia, similar to apricatria in ventral valve and closing onto them to form globose pouches; dorsal muscle field weakly impressed, wide, multilobed; crura falciform, short, slightly curved ventrally. *Lower Permian (Artinskian):* USA (Texas).——FIG. 869,*4a–g. *A. arcaria,* lower Leonardian, lower Cathedral Mountain Formation, Glass Mountains, Split Tank; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views; *f,* ventral valve interior; *g,* dorsal valve interior, ×6 (Cooper & Grant, 1976a).

Family SINORHYNCHIIDAE Xu & Liu, 1983

[*nom. correct.* XU, 1990, p. 77, *pro* Sinorhynchidae XU & LIU, 1983, p. 73]

[Materials prepared by MIGUEL O. MANCEÑIDO & SUN DONG-LI]

Subtriangular Wellerelloidea with long smooth stage, few coarse marginal plicae; conspicuous dorsal sulcus starting early and split anteriorly by rising dorsal fold. Hinge plates typically divided; dental plates absent or thin and parallel. *Middle Triassic (Anisian–Ladinian).*

Sinorhynchia YANG & XU, 1966, p. 32[102] [**S. bifaceta;* OD]. Small, roundly triangular,

ventribiconvex, thickest slightly posterior to midlength; completely smooth posteriorly, with 5 to 6 rounded, marginal plicae; dorsal sulcus developing from posterior and widening forward, becoming divided by 2 short plications at about midlength; commissure bidentate, flanked by round sulci; beak small, pointed, and strongly incurved; delthyrium small, open, possibly without deltidial plates. Hinge teeth small; dental plates, septalium, and median septum absent, with short median ridge only; hinge plates narrow, divided; crura short, hamiform, concavity facing medially. *Middle Triassic (Anisian):* China (Guizhou), ?Alps.——Fig. 870,*1a–x.* **S. bifaceta,* Guizhou; *a,* holotype, dorsal view, ×3; *b–c,* lateral, anterior views, MCMB DDRc65, ×1; *d–x,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.6, 0.7, 0.8, 0.95, 1.0, 1.07, 1.15, 1.2, 1.25, 1.3, 1.4, 1.5, 1.58, 1.65, 1.8, 1.9, 2.0, 2.1, 2.25, MCMB DDKc65 1-3 (Yang & Xu, 1966).

?Volirhynchia Dagys, 1974, p. 104 [**Rhynchonella volitans* Bittner, 1890, p. 47; OD] [=*Uolirhynchia* Xu & Liu, 1983, p. 72, *nom. null.*]. Small, subpentagonal, unequally biconvex, ventral valve feebly convex posteriorly and flattened on lateral sides, strongly uniplicate; few, blunt costae only in anterior part, smooth posteriorly; beak suberect, ridges rounded, foramen submesothyrid, deltidial plates double, conjunct. Dental plates long, subparallel, pedicle collar absent; septalium deep, supported by high septum about one-half valve length, crura thin, intermediate between raduliform and hamiform, concavity facing dorsally. [Genus in need of revision; affinities with Rhynchonellinae cannot be discounted.] *Middle Triassic (Anisian–Ladinian):* Alps, Dinarids, Carpathians, northwestern Caucasus, ?India, ?China.——Fig. 870,*2a–u.* **V. volitans* (Bittner), Anisian, northwestern Caucasus; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/226, ×1; *e–u,* transverse serial sections, distances in mm from first section, 0.0, 0.4, 0.6, 0.8, 0.9, 1.0, 1.1, 1.4, 1.6, 1.9, 2.1, 2.2, 2.4, 2.5, 2.8, 3.2, 3.7, IGiG 394/228 (Dagys, 1974).

RHYNCHONELLOIDEA

Ellis F. Owen and Miguel O. Manceñido
[formerly of The Natural History Museum; and La Plata Natural Sciences Museum, Argentina]

Superfamily RHYNCHONELLOIDEA d'Orbigny, 1847

[*nom. transl.* Schuchert, 1896, p. 323, *ex* Rhynchonellidae Gray, 1848, p. 438, *recte* d'Orbigny, 1847, p. 268 (see Manceñido, Owen, & Morris, 1993, p. 197)]

Rhynchonellida with shells subtriangular to subpentagonal, partly or fully costate; central uniplication well developed; surface may be also smooth, capillate, or covered with spines. Crura raduliform, calcariform, or variation thereof; dorsal median septum and uncovered septalium present; ventral septum, squama, and glotta absent. *Lower Triassic–Upper Cretaceous (Maastrichtian).*

Family RHYNCHONELLIDAE d'Orbigny, 1847

[Rhynchonellidae d'Orbigny, 1847, p. 268] [=Rhinchonellidae [Bronn], 1848, p. 246; Rhynconellidae Carpenter, 1853 in Davidson, 1853b, p. 35 (see Manceñido, Owen, & Morris, 1993, p. 197)]

Rhynchonelloidea with anterior commissure rectimarginate or uniplicate, most often with costation superimposed; surface covered with nonlamellose growth lines, spines not developed; dorsal median septum and septalium variably developed; crura comparatively short and bent ventrally, cardinal process absent. *Lower Triassic–Upper Cretaceous (Maastrichtian).*

Subfamily RHYNCHONELLINAE d'Orbigny, 1847

[*nom. transl.* Gill, 1871, p. 25, *ex* Rhynchonellidae Davidson, 1853b, p. 93, *recte* d'Orbigny, 1847, p. 268 (see Manceñido, Owen, & Morris, 1993, p. 197)]

Dorsibiconvex Rhynchonellidae with strong, sharp dorsal fold and paucidentate uniplication, typically cynocephalous; with usually long smooth stage posteriorly and paucicostate anteriorly, seldom fully costate. Crura raduliform, triangular in cross section, somewhat expanded distally; dorsal median septum and septalium well developed; lateral umbonal chambers small, triangular, wide apart. *Lower Triassic–Lower Cretaceous (upper Hauterivian, ?Barremian).*

Rhynchonella Fischer de Waldheim, 1809, p. 35 [**R. loxiae;* OD] [=*Eurhynchonella* Leidhold, 1921, p. 352, obj.; *Rhynchonellis* Keferstein, 1829, p. 50, *nom. null.; Rhyngonella* Fischer de Waldheim, 1843, p. 117, *nom. null.; Rhinchonella* d'Orbigny, 1851 in 1848–1851, p. 343, *nom. null.; Rhynconella* Carpenter in Davidson, 1853b, p. 35, *nom. null.*]. Small to medium, subtriangular, gibbous, nearly convexiplane and cynocephalous; dorsal fold high, ventral sulcus somewhat flattened; smooth stage long, costae few and sharp anteriorly; commissure uniplicate, acuminate to paucidentate; beak small, slightly incurved. Dental plates strong, septalium shallow, dorsal median septum short; crura short, raduliform. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Valanginian, ?Barremian):* Britain, France, Germany, Poland, Russia, Slovakia, Bulgaria, Mexico.——Fig. 871,*1a–v. *R. loxiae,* upper Volgian, Khoroschevo, near Moscow, Russia; *a–e,* dorsal, lateral, anterior, ventral, posterior, BMNH B.39132, ×1 (new); *f–v,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.6, 1.0, 1.3, 1.5, 1.6, 1.7, 1.8, 1.9, 2.0, 2.3, 2.5, 2.7, 3.1, 3.2, 3.4, 3.6, BMNH B.1325 (Ager, 1957).

?Curtirhynchia Buckman, 1918, p. 36 [**Rhynchonella oolitica* Davidson, 1852b, p. 81; OD] [=*Curtirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, subpentagonal, depressed dorsibiconvex; fold low, dorsal, uniplication tridentate to tetradentate; costae few, blunt anteriorly, smooth posteriorly; beak sharp, suberect, foramen hypothyrid. Dorsal median septum high, septalium small, pitlike, pedicle collar may be present; crura raduliform, distally expanded. *Middle Jurassic (Aalenian):* England, ?France, Morocco.——Fig. 871,*3a–j. *C. oolitica* (Davidson), Aalenian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, BMNH B.31753, ×1; *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.0, 1.4, 1.6, 1.8, 2.0, 2.6, 3.5, CDP 23, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

?Fusirhynchia Dagys, 1968, p. 68 [**Rhynchonella microptery*x d'Eichwald, 1865–1868, p. 344; OD]. Medium, subquadrate, acutely dorsibiconvex; coarsely costate with few, deep, angular costae; median dorsal fold well defined, flattopped, bi- to tetradentate; dorsal umbo inflated, posteriorly smooth; ventral sulcus broadly trapezoidal with fairly extensive linguiform extension; umbo short, beak sharp, suberect to almost erect. Dental plates strong, ventrally divergent to subparallel; pedicle collar short, fused to dental plates; hinge plates subhorizontal, inner and outer socket ridges well developed; high median septum supporting deep septalium; crural bases triangular. *Upper Jurassic (lower Volgian)–Lower Cretaceous (Valanginian):* northern Urals, northern Siberia, ?England (Dorset).——Fig. 872,*2a–k. *F. microptery*x (d'Eichwald), lower Volgian, northern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, ×1; *e–k,* transverse serial sections, distances in mm from first section, 2.1, 2.6, 3.1, 3.5, 3.7, 4.4, 4.9 (Dagys, 1968).

?Herangirhynchia MacFarlan, 1992, p. 155 [**H. herangiensis;* OD]. Small, subcircular to subpentagonal; equibiconvex to dorsibiconvex, moderately inflated, almost subcynocephalous; dorsal valve possibly bearing faint posterior sulcation; generally with strong narrow sulcus and fold; uniplication fairly high, usually bidentate or acuminate; beak small, broad with small foramen and sharp beak ridges. Dental plates short, thick, slightly ventrally divergent; median septum long, massive; hinge plates dorsally inclined with shallow septalium; crura raduliform; transversely crenulated hinge teeth. *Upper Triassic (Rhaetian)–Lower Jurassic (Toarcian), ?Middle Jurassic (?Aalenian):* New Zealand, New Caledonia.——Fig. 871,*2a–j. *H. herangiensis,* Toarcian, upper Ururoan, Awakino, New Zealand; *a–d,* dorsal, lateral, anterior, ventral views, OU NZ 16719, ×2; *e–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.4, 1.6, 1.7, 1.9, 2.4, 2.8, OU NZ 17307 (MacFarlan, 1992).

Homoeorhynchia Buckman, 1918, p. 36 [**Terebratula acuta* J. Sowerby, 1816 in 1815–1818, p. 115; OD; *non* J. de C. Sowerby, 1825] [=*Homoeorhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Blochmannella* Leidhold, 1921, p. 356 (type, *Rhynchonella Friereni* Branco, 1879, p. 128, OD, *error pro R. Frireni*), =*Blochmanella* Schuchert & LeVene, 1929a, p. 132, unjustified emend.; *Slovenirhynchia* Siblík, 1967, p. 159 (type, *S. maninensis,* OD)]. Small to medium (seldom large), subtrigonal to subpentagonal, cynocephalous; dorsibiconvex to almost convexoplane, strongly inequivalve and everted with uniplication acuminate to multidentate; dorsal fold high, sharp, and costae few and sharp anteriorly, starting after onset of fold; beak small, incurved. Dorsal median septum short and high; deep septalium; crura fairly long, raduliform. *Upper Triassic (Carnian, Rhaetian), Lower Jurassic (?Sinemurian, Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Alps, *Carnian, Rhaetian;* Europe (mainly southern), Morocco, Algeria, Turkey, southwestern China, Canada, Peru, *?Sinemurian, Pliensbachian–Aalenian, ?Bajocian.*——Fig. 872, *3a–k. *H. acuta* (J. de C. Sowerby), upper Pliensbachian; *a–c,* dorsal, lateral, anterior views, England, BMNH BM.67719, ×1.6 (new); *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.7, 1.3, 1.7, 1.8, 2.2, 2.6, 3.0, 4.5, Ardeche, France, FSL 49276 (Alméras, 1979).——Fig. 872,*3l–o. H. frireni* (Branco), Aalenian, Lorraine, France; dorsal, lateral, anterior, ventral views, ×1 (Branco, 1879).——Fig. 872,*3p–z. H. maninensis* (Siblík), upper Pliensbachian, Kostelec, Slovakia; *p–r,* holotype, dorsal, lateral, anterior views, CGS MS 167, ×1; *s–z,* transverse serial

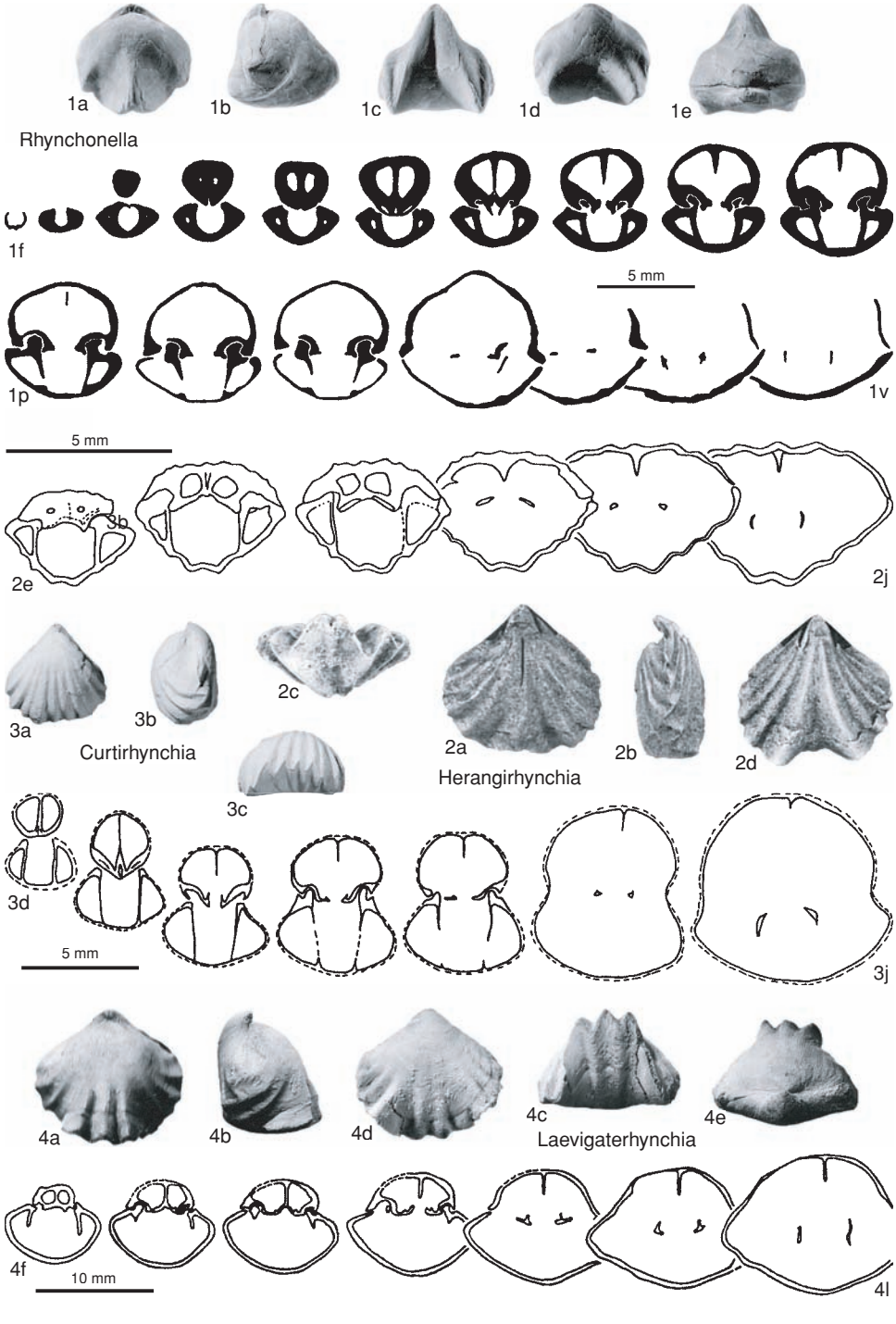

FIG. 871. Rhynchonellidae (p. 1280–1283).

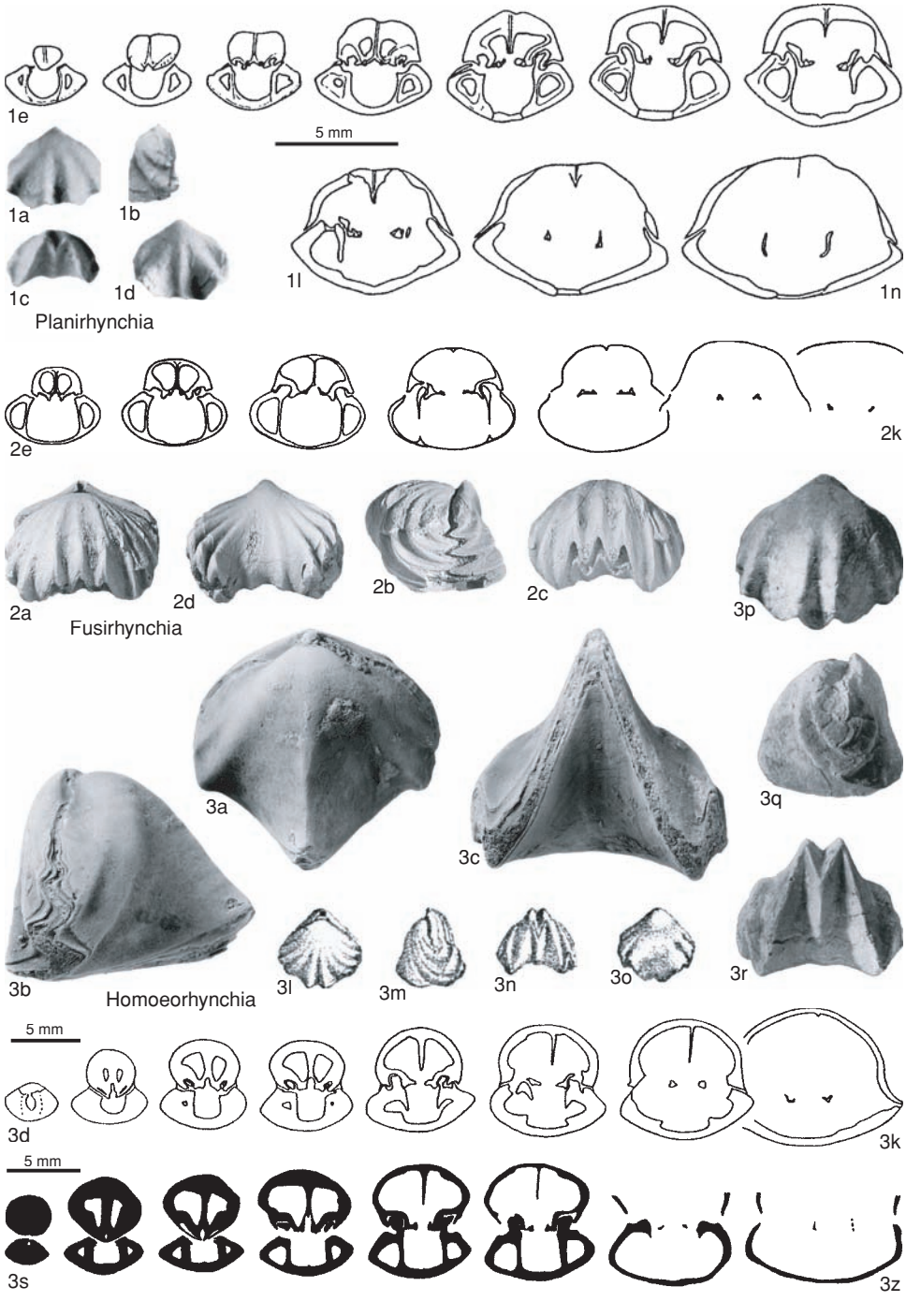

FIG. 872. Rhynchonellidae (p. 1280–1283).

sections, distances in mm from ventral umbo, 0.7, 1.8, 2.1, 2.7, 3.2, 3.8, 4.9, 6.5 (Siblík, 1967).

Kabanoviella Smirnova, 1973, p. 43 [**Rhynchonella obliterata* Lahusen, 1874, p. 54; OD]. Small, dorsibiconvex; costae simple, coarse, originating some distance from umbo; broadly uniplicate, sulcus and fold clearly defined; beak short, erect, pointed; foramen auriculate. Dental plates short, teeth crenulated; dorsal median septum long, reaching midlength, supporting short septalium; hinge plates broad, dorsally concave, indistinctly separated from inner socket ridges; crura ventrally deflected. [Hardly distinguishable from *Rhynchonella s.s.*] *Lower Cretaceous (upper Hauterivian):* Russian Platform.——Fig. 873,*1a–d. *K. obliterata* (Lahusen), Ulianovsk area; dorsal, ventral, lateral, anterior views, MGU 139/342, ×1 (Smirnova, 1990a).——Fig. 873,*1e–k. K. lahuseni;* transverse serial sections, distances in mm from first section, 0.3, 0.7, 1.0, 1.2, 1.8, 2.5, 3.2, approximately ×2 (Smirnova, 1978).

Laevigaterhynchia Wisniewska-Zelichowska, 1978, p. 112[150] [**Terebratula triplicosa* Quenstedt, 1851–1852, p. 454; OD] [=*Laevigatorhynchia* Wisniewska-Zelichowska, 1978, p. 65 (alternative original spelling)]. Small to medium, dorsibiconvex, usually somewhat longer than wide; fold on dorsal valve and ventral sulcus, both distinct, deflected dorsally in wide, trapeziform, linguiform extension; beak erect or suberect; foramen slightly oval; 8 to 10 subangular costae, beginning closer to anterior part of shell, central fold bidentate to multidentate; surfaces smooth, without capillae. Dorsal median septum high and septalium small; crura allegedly falciform, in fact raduliform, distally expanded. *Middle Jurassic (Callovian):* Germany, Poland, Switzerland, Carpatho-Balkanids, ?Greenland.——Fig. 871,*4a–l. *L. triplicosa* (Quenstedt), Czestochowa area, Poland; *a–e,* dorsal, lateral, anterior, ventral, posterior views, Muz IG 1352.2.162, ×1 (new); *f–l,* transverse serial sections, distances in mm from first section, 1.5, 2.0, 2.2, 2.4, 2.7, 2.9, 3.6 (Wisniewska-Zelichowska, 1978).

?Lunarhynchia Jin, Manceñido, & Sun, 1997, p. 392, *nom. nov. pro Lunaria* Ching, Sun, & Ye in Ching & others, 1979, p. 155–156, *non* Fabricius, 1823, Mollusca [**Lunaria dorsata* Ching, Sun, & Ye in Ching & others, 1979, p. 155; OD]. Medium to large, pyriform to pentagonal, almost convexoplane; dorsal fold and ventral sulcus well defined, developed anteriorly; linguiform extension subquadrate; lateral slopes smooth or with few, short, coarse plicae; plicae on sulcus and fold usually extending from umbo; ventral beak short and straight; beak ridges angular; foramen submesothyrid; delthyrium covered with symphytium. Dental plates vertical, subparallel, not extending beyond articulation zone; dorsal median septum reaching midvalve; septalium wide and shallow; hinge plates flat, fused with inner socket ridges; raduliform crura projecting horizontally to end ventrally incurved. [Shell shape of type species is unusual; evidence from other assigned species tends to support this subfamily allocation.] *Upper Triassic:* China (Tibet, Qinghai, Sichuan, Yunnan).——Fig. 873,*5a–n. *L. dorsata* (Ching, Sun, & Ye), Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42838, ×1; *e–n,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 0.9, 1.2, 1.55, 2.1, 2.4, 2.55, 2.95, 4.0, NIGP 42837 (Ching & others, 1979).

?Nudirostralina Yang & Xu, 1966, p. 21[97] [**N. subtrinodosi;* OD] [=*Nudirostrolina* Sun, 1981, p. 196, *nom. null.; Nudirostrlina* Xu & Liu, 1983, p. 72, *nom. null.*]. Medium size, subtrigonal to subpentagonal, dorsibiconvex to gently everted; ventral sulcus and dorsal fold well marked anteriorly; commissure uniplicate, bidentate to multidentate; shell completely smooth posteriorly and with only few short plicae anteriorly and laterally, 2 to 5 on fold, usually 2 on each lateral slope; beak small, slightly incurved; deltidial plates small, covering delthyrium, hypothyrid to submesothyrid. Dental plates ventrally divergent; dorsal median septum short, supporting septalium; crura short, ventrally curved. *Lower Triassic–Upper Triassic:* China (Guizhou, Qinghai, Tibet), ?India.——Fig. 873,*4a–l. *N. subtrinodosi,* Anisian, Guizhou; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MCMB DDR IA4-2, ×1; *e–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.2, 0.9, 1.3, 1.5, 1.8, 2.05, 2.2, 2.4, MCMB DDR Ia4-4 (Yang & Xu, 1966).

?Planirhynchia Sucic-Protic, 1969, p. 19 [**P. tantilla;* OD]. Medium to small, depressed subpentagonal; smooth in posterior half and covered with few, low, blunt costae in anterior half; commissure uniplicate, bidentate, or tridentate; linguiform extension flattopped, wide, and shallow; beak straight to fairly curved, with round submesothyrid foramen. Septalium wide, dorsal median septum low, long, and massive; crura raduliform, fairly curved. [Tchoumatchenko (1989, p. 18) regarded the type species as a subjective junior synonym of *Homoeorhynchia almaensis* (Moiseev).] *Upper Triassic (Carnian)–Lower Jurassic (Pliensbachian):* Siberia, ?southern Europe, *Carnian–Rhaetian;* Yugoslavia (Carpatho-Balkanids), *Pliensbachian.*——Fig. 872,*1a–n. *P. tantilla,* middle Lias, Carpatho-Balkanids, Yugoslavia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MFMGB 3/1669, ×1; *e–n,* transverse serial sections, distances in mm from first section, 0.8, 0.9, 1.0, 1.3, 1.4, 1.6, 1.9, 2.2, 2.5, 3.1 (Sucic-Protic, 1969).

Rhynchonelloidea Buckman, 1918, p. 38 [**Rhynchonella ruthenensis* Reynès, 1868, p. 107; OD] [=*Rhynchonelloidea* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small to medium, strongly dorsibiconvex, rounded subpentagonal, more or less everted, dorsal fold pronounced and uniplication bidentate to multidentate; costae few and fairly

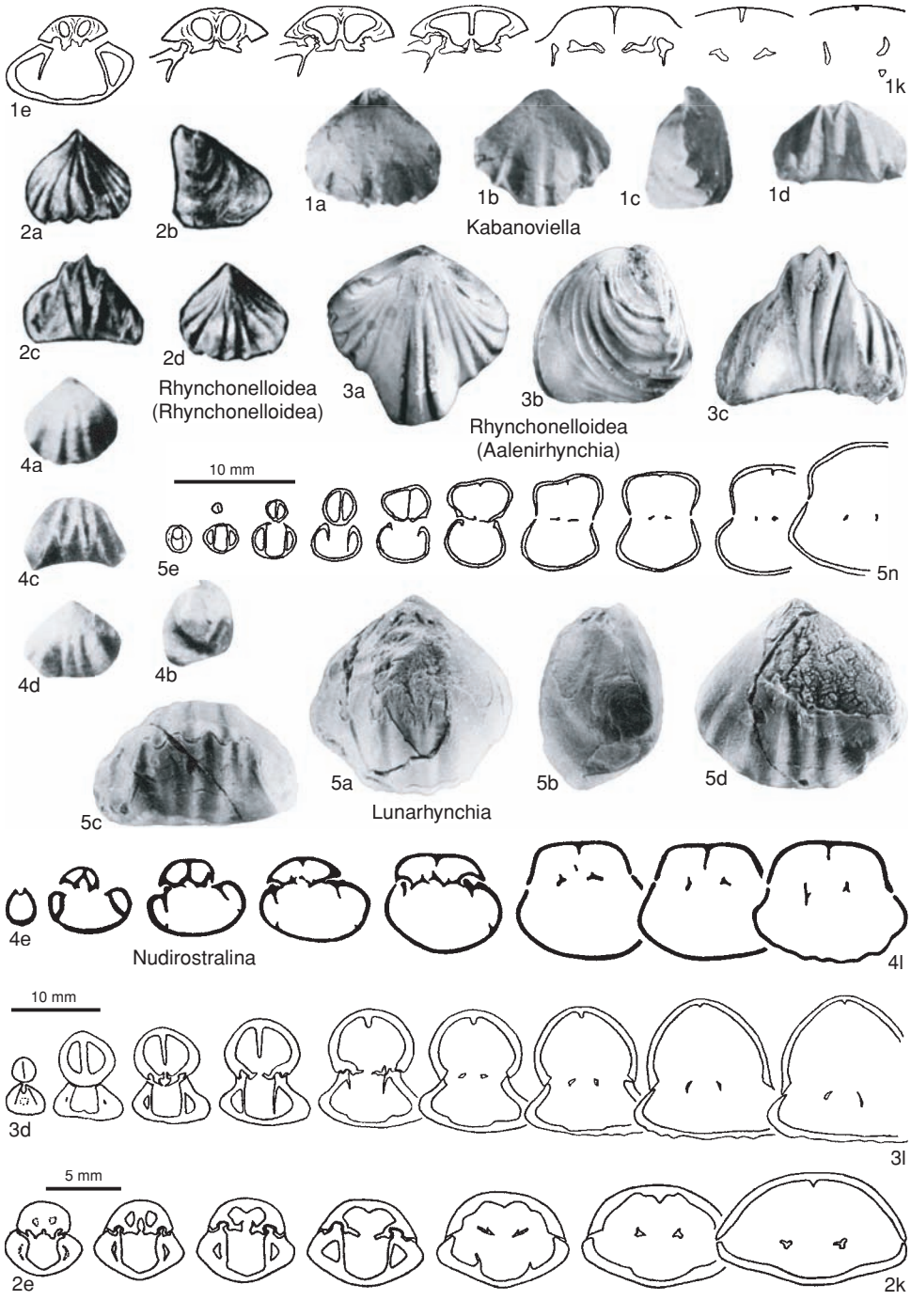

FIG. 873. Rhynchonellidae (p. 1283–1285).

sharp, starting before onset of fold, smooth stage negligible to absent. Dorsal septum strong, short; septalium narrow, pitlike; crura raduliform, may be distally concave. *Upper Triassic (?Rhaetian), Lower Jurassic (Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Europe, northern Africa, Asia, South America.

R. (Rhynchonelloidea). Subcynocephalous, costae coarse, simple, flanks of fold and sulcus smooth; beak small, acute and erect; deltidial plates disjunct. *Upper Triassic (?Rhaetian), Lower Jurassic (Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Great Britain, France, Spain, Switzerland, Austria, Yugoslavia, Romania, Bulgaria, ?Germany, Caucasus, Argentina, Algeria, southwestern China.——Fig. 873,*2a–k. *R. (R.) ruthenensis* (Reynès), lower Aalenian, Aveyron, France; *a–d,* dorsal, lateral, anterior, ventral views, FSL 49254, ×1; *e–k,* transverse serial sections, distances in mm from ventral umbo, 1.5, 1.8, 2.0, 2.4, 2.9, 3.4, 4.4, FSL 49254 (Alméras, 1979).

R. (Aalenirhynchia) Shi & Grant, 1993, p. 57 [**Rhynchonella subdecorata* Davidson, 1855, p. 21; OD]. Cynocephalous, may attain larger size; costae may be finer, denser, with 1 or 2 dying out along flanks of median fold before reaching front; incurved beak may conceal foramen and deltidial plates. *Lower Jurassic (Toarcian)–Middle Jurassic (Aalenian):* England, Spain, Argentina.——Fig. 873,*3a–l. *R. (A.) subdecorata* (Davidson), Aalenian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.9, 2.3, 2.8, 3.3, 3.5, 4.0, 4.9, 5.5, USNM 123721b (Shi & Grant, 1993).

Subfamily PIARORHYNCHIINAE Shi & Grant, 1993

[Piarorhynchiinae Shi & Grant, 1993, p. 21]

Small to medium Rhynchonellidae, moderately equibiconvex to subglobose; beak and foramen small; smooth areas well developed posteriorly, with costae few, strong, and rounded anteriorly; rectangular uniplication not well detached from lateral slopes. Crura raduliform; dorsal median septum and septalium conspicuous; dental plates present; lateral umbonal chambers often filled up. *Lower Triassic–Lower Cretaceous (Albian).*

Piarorhynchia Buckman, 1918, p. 34 [**Rhynchonella lineata* var. *radstockiensis* Davidson, 1878, p. 210; OD] [=*Piarorhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Tropiorhynchia* Buckman, 1918, p. 33 (type, *Rhynchonella thalia* d'Orbigny, 1850 in 1849–1852, p. 239, OD); *Tropiorhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, globose to depressed, nearly equibiconvex, uniplicate, dorsal fold low, flattopped; pronounced smooth stage posteriorly, costae rounded anteriorly; beak small, incurved. Dorsal septum massive; crura raduliform; thick horizontal hinge plates. *Upper Triassic (Carnian)–Lower Jurassic (Toarcian):* Alps, Siberia, Japan, western Canada and USA, *Carnian–Rhaetian;* England, France, Portugal, Spain, Sweden, Germany, Switzerland, Austria, Yugoslavia, Hungary, Ukraine, Morocco, Turkey (Anatolia, Taurids), Argentina, ?Chile, western Canada, *Hettangian–Toarcian.*——Fig. 874,*1a–v. *P. radstockiensis* (Davidson), lower Pliensbachian, Somerset, England; *a–e,* dorsal, lateral, anterior, ventral, posterior views, BMNH BB.33750, ×1.5 (new); *f–v,* transverse serial sections, distances in mm from ventral umbo, 0.4, 1.4, 1.5, 1.7, 2.0, 2.1, 2.2, 2.3, 2.5, 2.7, 2.8, 3.0, 3.2, 3.6, 4.0, 4.5, 4.8, J.197, Derek Ager, personal collection (Ager, 1962).——Fig. 874,*1w–y. P. thalia* (d'Orbigny), Pliensbachian, Calvados, France; dorsal, lateral, anterior views, MNHN, ×1.5 (Ager, 1962).

Abrekia Dagys, 1974, p. 98 [**A. sulcata;* OD]. Small, subpentagonal, moderately depressed, equibiconvex; sulcus on posterior half of dorsal valve and shallow ventral sulcus and low dorsal fold on anterior half; few rounded costae anteriorly, smooth posteriorly; beak suberect, ridges rounded, foramen submesothyrid. Dental plates short, ventrally convergent; septum and septalium distinct; hinge plates subhorizontal; crura raduliform; pedicle collar absent. *Lower Triassic–Middle Triassic:* far eastern Russia, Tibet, Himalayas, Caucasus.——Fig. 875,*3a–k. *A. sulcata,* Lower Triassic, Induan, Scythian, Primorye, Russia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/40, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.4, 0.6, 0.8, 0.9, 1.35, 1.55, 1.65, IGiG 394/45 (Dagys, 1974).

Aorhynchia MacFarlan, 1992, p. 173 [**A. ohaiensis;* OD]. Small to moderate size, rounded outline; dorsibiconvex, moderate to great inflation; uniplication narrow, rounded, but fold and sulcus poorly developed; costae low, rounded, usually after a posterior smooth stage; beak large, blunt, erect, with large, round, mesothyrid foramen and long pedicle collar. Hinge plates small, septalium poorly defined, troughlike or pitlike; dorsal median septum short; raduliform crura short, distally bladelike and concave. *Middle Triassic (Anisian):* New Zealand.——Fig. 875,*2a–k. *A. ohaiensis,* lower Anisian, Malakovian, South Island; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, OU NZ 14667, ×2; *f–k,* transverse serial sections, distances in mm from ventral umbo, 0.7, 0.8, 1.2, 1.5, 1.9, 2.3, OU NZ 177418 (MacFarlan, 1992).

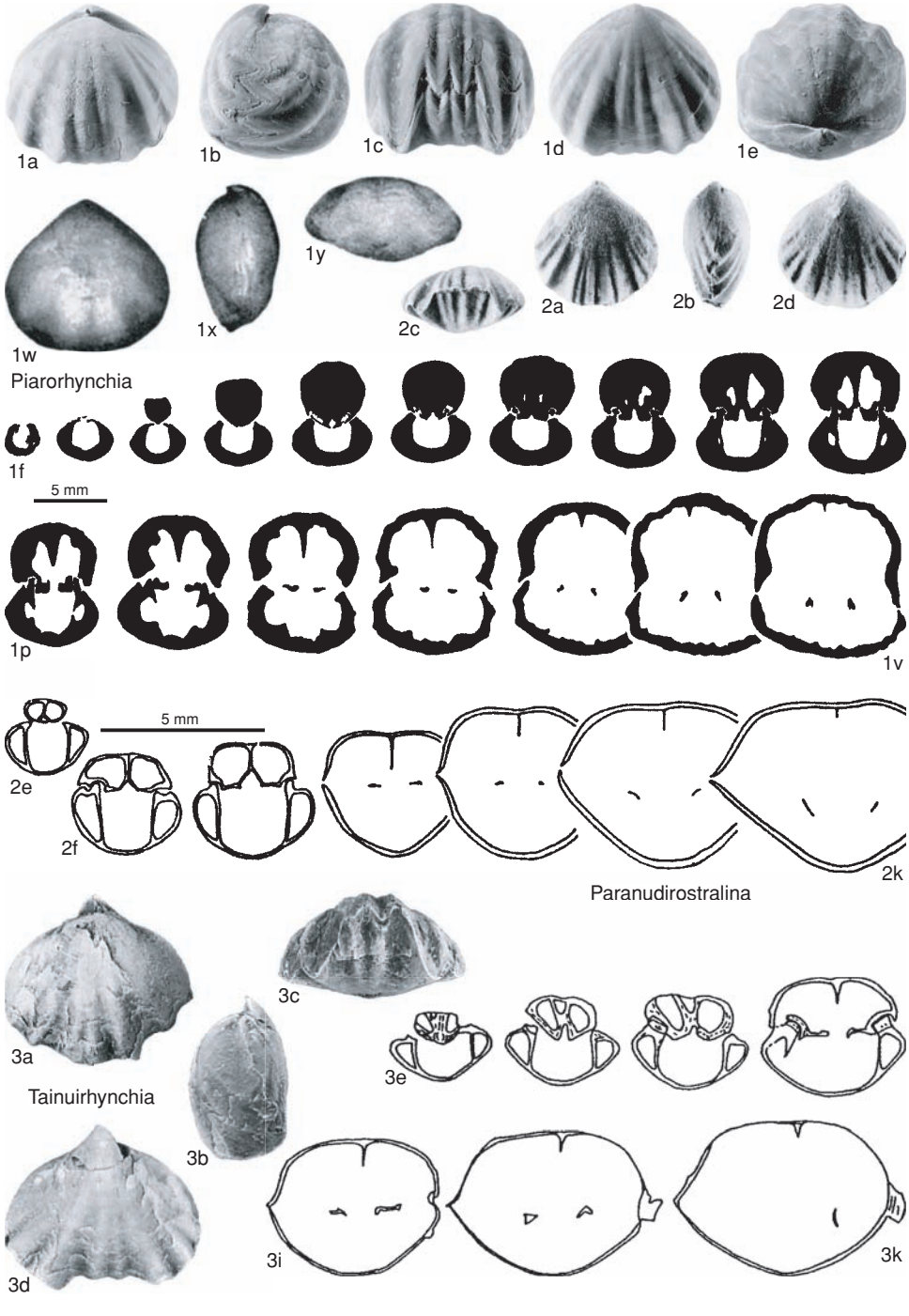

FIG. 874. Rhynchonellidae (p. 1285–1290).

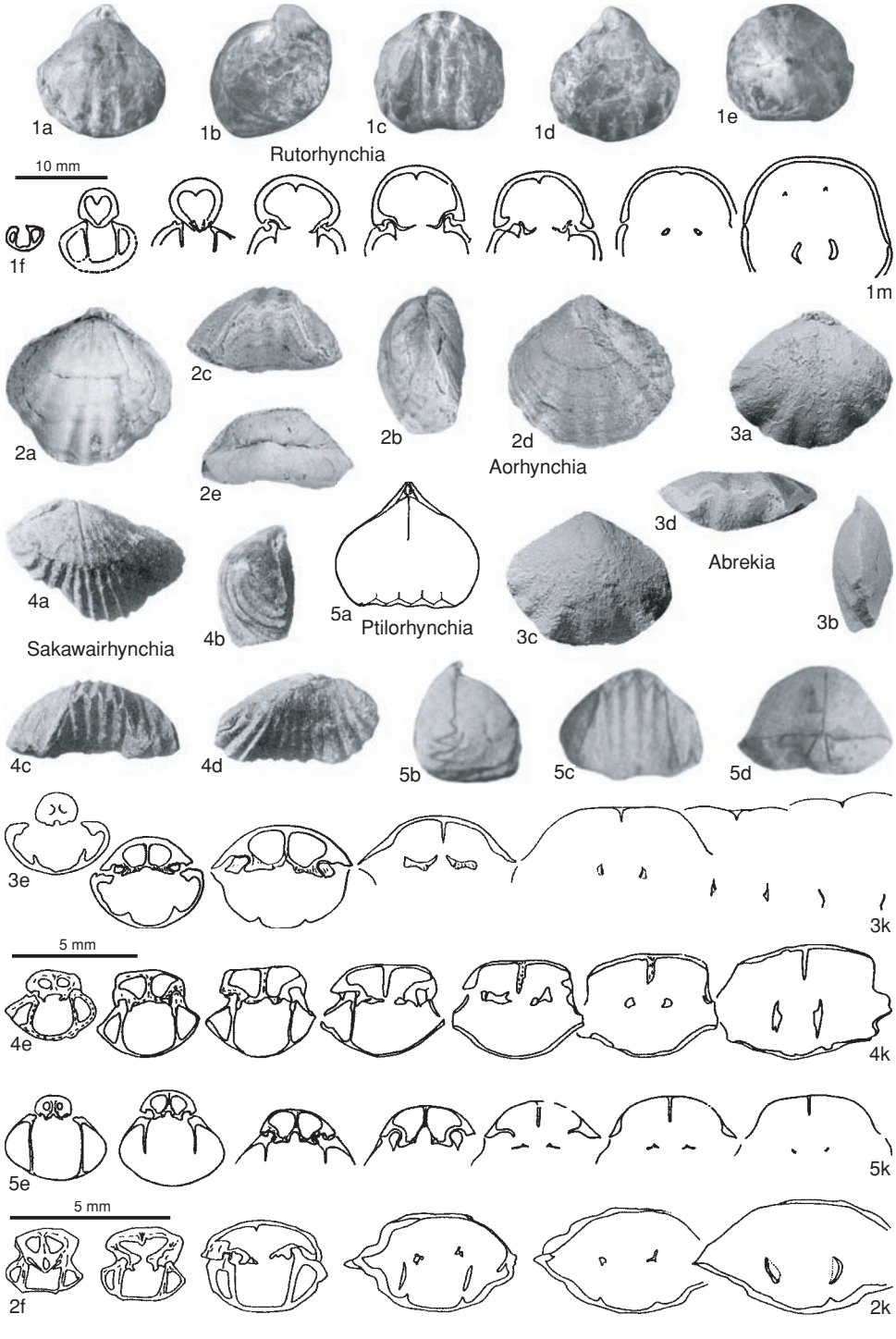

FIG. 875. Rhynchonellidae (p. 1285–1290).

Caledorhynchia MacFarlan, 1992, p. 209 [**C. caledonica;* OD]. Medium size, rounded triangular to subpentagonal; dorsibiconvex, strongly inflated to globose; fold and sulcus well defined, uniplication shallow, flattopped, anterior margin may be geniculate; costae few, strong, rounded or angular, after posterior smooth stage; beak prominent, erect, with hypothyrid foramen and pedicle collar. Massive hinge plates with narrow, deep septalium; dorsal median septum long and high; shell thick, muscle scar may be deeply incised. *Lower Jurassic (Sinemurian)–Middle Jurassic (Callovian):* New Zealand, New Caledonia.——Fig. 876,*2a–n. *C. caledonica,* middle Temaikan, New Caledonia; *a–e,* dorsal, lateral, anterior, ventral, posterior views of bivalved steinkern, OU NZ 17202, ×1.5; *f–n,* topotype, transverse serial sections, distances in mm from ventral umbo, 2.2, 2.4, 2.6, 2.8, 3.0, 3.2, 3.6, 3.9, 4.7, OU NZ 17491 (MacFarlan, 1992).

Cuneirhynchia Buckman, 1918, p. 35 [**Rhynchonella dalmasi* Dumortier, 1869, p. 331; OD] [=*Cuneirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, depressed subtriangular, convexiplane or convexiconcave; pronounced smooth stage with costae few, blunt anteriorly; uniplicate, but fold slightly developed, if at all; beak small, upright to erect. Dental plates gently convergent ventrally; hinge plates massive; dorsal median septum long and low; crura raduliform. *Lower Jurassic (?Hettangian, Sinemurian–Pliensbachian, ?Toarcian):* England, France, Germany, Switzerland, Austria, Italy, Slovakia, Hungary, Romania, Yugoslavia, Greece, ?Crimea, ?Algeria, Turkey (Anatolia, Taurids), Siberia.——Fig. 876,*1a–i. *C. dalmasi* (Dumortier), lower Pliensbachian, Somerset, England; *a–c,* dorsal, lateral, anterior views, HM L.2464, ×2; *d–i,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.2, 1.7, 2.0, 2.4, 2.8, J.1202, Derek Ager, personal collection (Ager, 1962).

Paranudirostralina Sun & Ye, 1982, p. 156[169] [**P. bifurcata;* OD]. Small to medium; subtriangular to subpentagonal, equibiconvex, with greatest convexity posteriorly; uniplicate, with ventral sulcus and dorsal fold well defined anteriorly; shell surface smooth posteriorly, but with few subangular plicae anteriorly, increasing by bifurcation or intercalation; beak small, slightly incurved to suberect; foramen small, mesothyrid or permesothyrid; delthyrium open. Dental plates long, subparallel; hinge plates flat, merged with socket ridges; median septum high and stout, septalium deep; crural bases triangular; crura raduliform, strongly curved ventrally. [May be a subgenus of *Abrekia.*] *Middle Triassic (Anisian):* China (Qinghai).——Fig. 874,*2a–k. *P. bifurcata; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67016, ×1.5; *e–k,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.34, 0.6, 0.78, 0.86, 1.04, 1.34, 1.54, NIGP 67018 (Sun & Ye, 1982).

Ptilorhynchia Crickmay, 1933, p. 877 [**P. plumasensis;* OD] [=*Ptylorhynchia* Smirnova, 1984, p. 77, *nom. null.*]. Medium size, triangular to subpentagonal, subglobose, dorsibiconvex; uniplication marked with strong, short, marginal plicae; anterior commissure rarely asymmetrical; dorsal fold almost imperceptible, ventral sulcus broad, shallow, linguiform extension trapezoidal. Dental plates long, subparallel; hinge plates horizontal to dorsally deflected; dorsal septum high with well-marked septalium. [Inconclusive evidence hints of a possible persistence in Antarctica well into the Upper Cretaceous (Sandy, 1991).] *Middle Jurassic (?Bajocian, Bathonian)–Lower Cretaceous (Aptian):* USA (California), western Canada (British Columbia), northern Siberia, Urals, *?Bajocian, Callovian–Volgian;* northern Siberia, ?Slovakia, Antarctica, Argentina (mainly circum-Pacific), *Berriasian–Aptian.*——Fig. 875,*5a–d. *P. plumasensis,* Callovian, California; holotype, dorsal, lateral, anterior, posterior views, ×1 (Crickmay, 1933).——Fig. 875,*5e–k. P. anadyrensis* Dagys, Bathonian–Callovian, northeastern Siberia, Anadyr basin; transverse serial sections, distances in mm from first section, 1.7, 2.0, 2.3, 2.7, 3.0, 3.3, 3.8 (Dagys, 1968).

Rutorhynchia Sun, 1981, p. 201 [**R. jieshanensis;* OD] [=*Roturhynchia* Shi & Grant, 1993, p. 18, *nom. null.*]. Medium size; oval to trigonal; globose, equibiconvex; dorsal fold and ventral sinus low and flat with subquadrate linguiform extension; posterior smooth stage variable; few, stout plicae developed marginally; uniplication bidentate to tetradentate; beak sharp, pointed, and incurved; beak ridges angular; foramen small and mesothyrid to hypothyrid, delthyrium covered with symphytium. Dental plates subparallel; outer hinge plates narrow, dorsal septum reduced to low ridge and short; septalium undeveloped, only rudimentary pendant septalial plates; crura strongly bent; pedicle collar absent. *Upper Jurassic:* Tibet.——Fig. 875,*1a–m. *R. jieshanensis; a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, NIGP 48427, ×1 (new); *f–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.7, 3.3, 3.6, 4.3, 4.7, 5.0, 5.6, 6.4, NIGP 48429 (Sun, 1981).

Sakawairhynchia Tokuyama, 1957, p. 126 [**S. tokomboensis* Kobayashi & Tokuyama in Tokuyama, 1957, p. 127; OD; *Rhynchonella tokomboensis* Kobayashi, 1931, p. 231, *nom. nud.*]. Moderate size, subpentagonal or elliptical; dorsibiconvex, moderately to greatly inflated; strongly uniplicate, with fold flattopped and sulcus moderately deep; variable smooth stage posteriorly, few, blunt costae anteriorly, exceptionally noncostate; beak small erect, with poorly developed beak ridges. Hinge plates broad, subhorizontal, with shallow septalium; dorsal median septum long and high; dental plates well developed; raduliform crura long, sharply bent. *Middle Triassic (Ladinian)–Lower Jurassic (lower Toarcian):* New Zealand, New Caledonia,

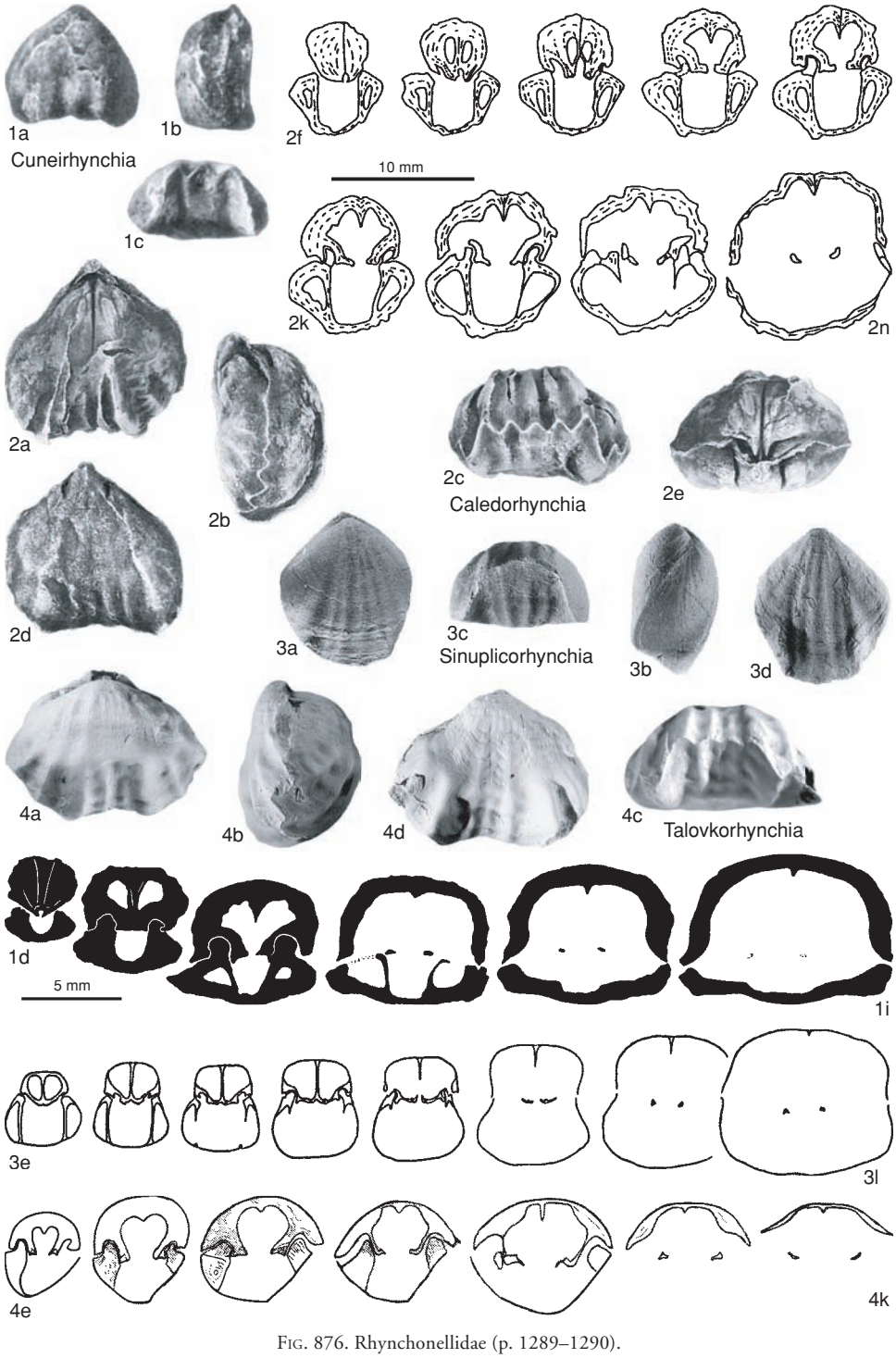

FIG. 876. Rhynchonellidae (p. 1289–1290).

Ladinian–lower Toarcian; Japan, Canada, Siberia, Primorye, Thailand, Hungary, *Carnian.*——FIG. 875,*4a–d. *S. tokomboensis* KOBAYASHI & TOKUYAMA, Carnian, Kochi, Japan; syntype, dorsal, lateral, anterior, ventral views, ×1.5 (Tokuyama, 1957).——FIG. 875,*4e–k. S. zealandica* (TRECHMANN), Ladinian, Kaihikuan, Hokonui, New Zealand; transverse serial sections, distances in mm from ventral umbo, 1.3, 1.9, 2.2, 2.4, 2.6, 3.0, 3.7, OU NZ 15789 (MacFarlan, 1992).

Sinuplicorhynchia DAGYS, 1965, p. 56 [**S. kegalensis;* OD]. Small to medium size, rounded-pentagonal, distinctly uniplicate but with low fold. Sulcus and fold with low, rounded costae, lateral surfaces smooth; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates conjunct. Dental plates thin, subparallel, pedicle collar absent; dorsal septum long, more than one-half valve length, septalium narrow, distinct, outer hinge plates broad, incipiently ventrally convex, crura raduliform. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* northeastern Siberia, ?China, USA (Alaska).——FIG. 876,*3a–l. *S. kegalensis,* Ladinian, northeastern Siberia; *a–d,* dorsal, lateral, anterior, ventral views, ×1 (new); *e–l,* transverse serial sections, distances in mm from first section, 0.7, 1.3, 1.7, 2.2, 2.7, 3.2, 3.7, 4.5 (Dagys, 1965).

?Tainuirhynchia MACFARLAN, 1992, p. 233 [**T. tainuii;* OD]. Medium size, subtriangular to subpentagonal; dorsibiconvex; uniplication flattopped, bidentate to pentadentate; fold and sulcus broad and low; posterior part smooth or with faint capillae, anterior with few, strong, round or angular costae; beak prominent, sharp, erect, with small foramen and short pedicle collar. Hinge plates short, thick, with deep, narrow septalium; dorsal median septum long, high; crural bases triangular. *Middle Jurassic (?Bathonian, Callovian)–Upper Jurassic (Tithonian):* New Zealand, ?New Caledonia. ——FIG. 874,*3a–k. *T. tainuii,* Oxfordian, middle Heterian, Kawhia, New Zealand; *a–d,* holotype, dorsal, lateral, anterior, ventral views, AU B254, ×1.5; *e–k,* transverse serial sections, distances in mm from ventral umbo, 2.0, 2.2, 2.6, 3.0, 3.6, 4.2, 4.6, NZGS BR1791, ×2.8 (MacFarlan, 1992).

Talovkorhynchia SMIRNOVA, 1994, p. 31 [**T. pochialajneni;* OD]. Medium, moderately biconvex with prominent dorsal sulcus, deep ventral sulcus, and extensive trapezoidal linguiform extension; ornamentation of few strong costae with 4 on fold and 3 to 4 in ventral sulcus. Dental plates fused; hinge teeth massive, subquadrate, and slightly inwardly directed; hinge plates short, slender, dorsally concave; dorsal septum reduced to median ridge; crural bases with concave distal ends. *Lower Cretaceous (Albian):* northeastern Russia (Kamchatka). ——FIG. 876,*4a–k. *T. pochialajneni; a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 138/405, ×1.5; *e–k* transverse serial sections, distances in mm from ventral umbo, 1.4, 2.1, 2.8, 3.4, 3.6, 4.5, 5.3, MGU 138/407, ×1.3 (Smirnova, 1994).

Subfamily URALORHYNCHIINAE new subfamily

[Uralorhynchiinae MANCEÑIDO & OWEN, herein]

Small to medium-sized Rhynchonellidae, moderately dorsibiconvex to subglobose; beak and foramen small; few coarse, rounded costae anteriorly and extensive posterior smooth areas, which may be finely capillate; arcuate uniplication not well detached from lateral slopes. Crura raduliform proximally, very close to strong dorsal median septum; septalium shallow; dental plates almost fused to wall; lateral umbonal chambers mostly filled up. *Middle Triassic (Ladinian)–Upper Triassic (Norian), Upper Jurassic (lower Volgian)–Lower Cretaceous (Berriasian).*

Uralorhynchia DAGYS, 1968, p. 54 [**Terebratula striatissima* D'EICHWALD, 1865–1868, p. 313; OD]. Large to medium size, smooth, strongly dorsibiconvex, oval; with dorsal median fold high, ill defined; ventral valve with broad, shallow extensive sulcus and linguiform extension; uniplicate anterior commissure showing faint marginal plicae. Short hinge plates with inner and outer socket ridges well developed; thickened septalium supported by short median septum; umbonal chambers callus filled. *Upper Jurassic (lower Volgian)–Lower Cretaceous (Berriasian):* northern Urals, Siberia.——FIG. 877,*1a–t. *U. striatissima* (D'EICHWALD), upper Volgian, northern Siberia; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 256/78, ×1; *e–t,* transverse serial sections, distances in mm from first section, 0.4, 1.1, 1.5, 1.8, 2.0, 2.2, 2.7, 3.0, 3.2, 3.5, 3.8, 4.3, 4.8, 5.2, 5.5, 5.9, approximately ×1.5 (Dagys, 1968).

Omolonella MOISEEV, 1936, p. 39 [**O. omolonensis;* OD]. Medium size, oval, unequally biconvex, ventral valve essentially flattened with wide sulcus, fold low or absent, anterior commissure distinctly uniplicate, smooth, with costae few and faint anteriorly; beak short, incurved, ridges rounded, foramen submesothyrid, deltidial plates conjunct. Dental plates, septum, and septalium distinct in young specimens, in adults umbonal chambers filled with callus, crura thick, raduliform; pedicle collar absent. *Upper Triassic (Norian):* northeastern Siberia, southwestern China.——FIG. 877,*3a–v. *O. omolonensis,* northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, TsGM 30/4803, ×1 (Moiseev, 1936); *e–v,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.6, 0.9, 1.1, 1.3, 1.6, 1.8, 2.1, 2.5, 2.7, 3.1, 3.3, 3.6, 4.0, 4.2, 4.5, 4.7 (Dagys, 1965).

Sulcorhynchia DAGYS, 1974, p. 103 [**Holcorhynchia borealis* DAGYS, 1965, p. 75; OD]. Small, rounded-pentagonal to oval, moderately equibiconvex;

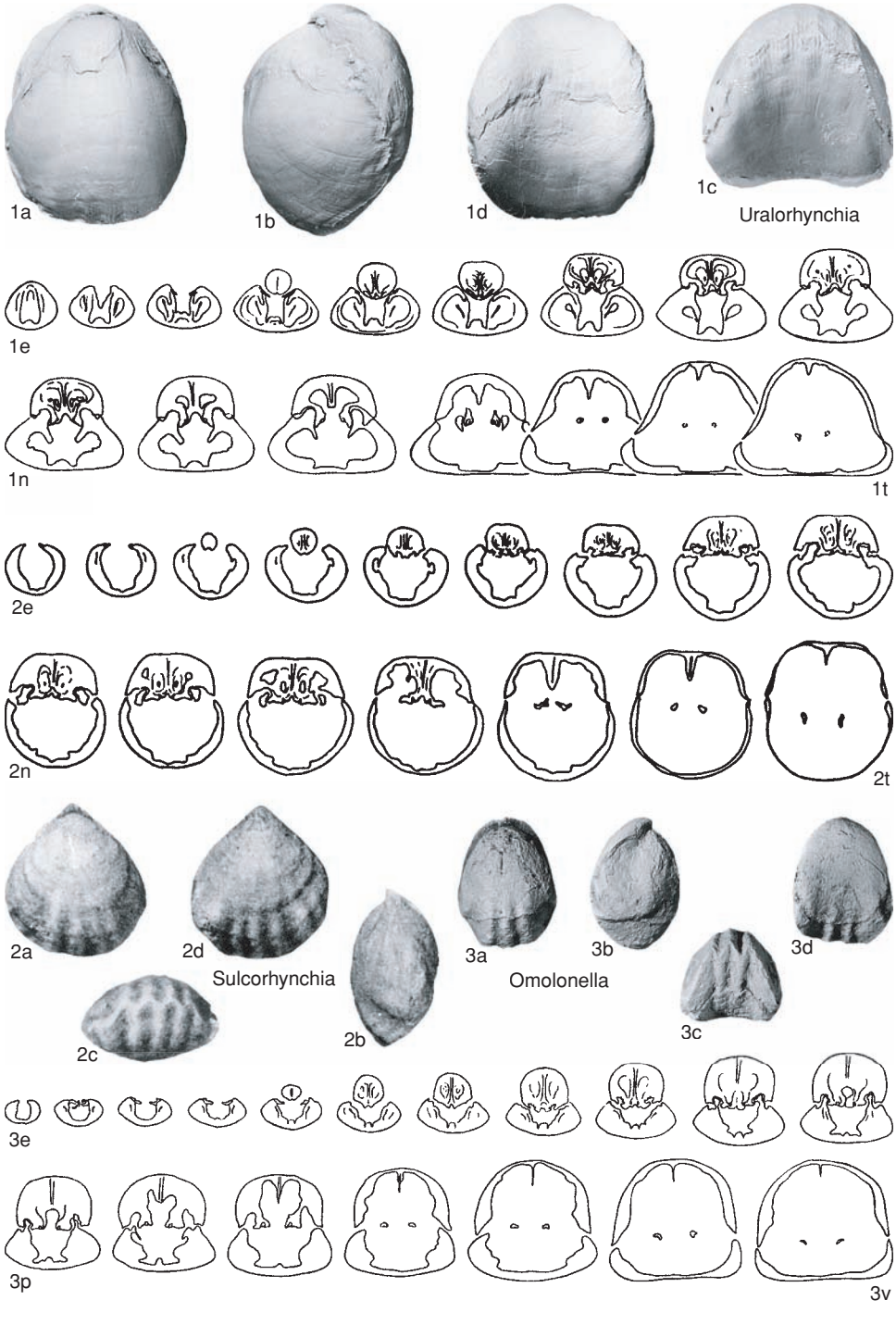

FIG. 877. Rhynchonellidae (p. 1290–1292).

posterior with dorsal sulcus, anterior with low, indistinct dorsal fold and matching shallow ventral sulcus; costae few and rounded in anterior part, posteriorly smooth; beak short, incurved, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Young specimens with distinct diverging dental plates, high septum, supporting deep septalium; adults with massive cardinalia, umbonal chambers filled with callus, crura thin, raduliform. *Middle Triassic (Ladinian)–Upper Triassic (Norian):* northeastern Siberia, Himalayas, Japan.——Fig. 877,*2a–t.* **S. borealis* (Dagys), Norian, northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 146/118, ×1.5; *e–t,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.7, 0.8, 0.9, 1.0, 1.2, 1.4, 1.5, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 3.1 (Dagys, 1965).

Subfamily IVANOVIELLINAE Makridin, 1964

[Ivanoviellinae Makridin, 1964, p. 129] [=Ivanoviellinae Kats, 1962, p. 132, *nom. nud.*]

Small- to medium-sized Rhynchonellidae, with costae strong and subangular to rounded, and posterior smooth area variably developed; uniplication well marked and linguiform extension often well developed; subcynocephalous to cynocephalous. Septalium reduced, sometimes sessile or absent, dorsal median septum variably developed, crura calcariform. *Upper Triassic (Norian)–Upper Cretaceous (Maastrichtian).*

Ivanoviella Makridin, 1955, p. 83, *non* Ivanova in Abushik & others, 1960, Ostracoda [**Rhynchonella alemanica sensu* Makridin, 1955*;* OD; *non* Rollier, 1917; =*Ivanoviella gaetanii* Alméras, Benigni, & Tintori, 1991, p. 431] [=*Jvanoviella* Makridin, 1955, p. 83 (alternative original spelling, first reviser Ager, 1965, p. 611); *Ivanoviella* Makridin, 1954, p. 103, *nom. nud.; Ivanowiella* Wisniewska-Zelichowska, 1978, p. 65, *nom. null.*]. Small, sulcus and fold pronounced in maturity, radial costae numerous, narrow, simple, covering shell, beginning near beak after variable smooth stage; beak slender, short, usually weakly incurved, foramen elliptical, sometimes almost circular, submesothyrid; deltidial plates conjunct. Dental plates thin, wide apart, becoming detached around articulation zone; crura short, bladelike, extending ventrally; dorsal septum thin, united with hinge plate margins; ventral muscle scars rounded-rectangular, dorsal anterior adductors pear shaped, dorsal posterior adductors oval. *Middle Jurassic (Bajocian–Callovian), Upper Jurassic (?Oxfordian):* France, Germany, Switzerland, Russian Platform, Poland, Crimea, Caucasus, central Asia, western Himalayas (India, Nepal), China.——Fig. 878,*3a–l.* **I. gaetanii* Alméras, Benigni, & Tintori, Middle Callovian, Ryazan region, Russia; *a–c,* dorsal, lateral, anterior views, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.7, 2.05, 2.6, 2.75, 3.0, 3.1, 3.5, 3.7 (Makridin, 1964).

Bihendulirhynchia Muir-Wood, 1935, p. 104 [**B. afra;* OD] [=*Bihenidulirhynchia* Shi, 1987a, p. 20, *nom. null.*]. Small, dorsibiconvex, smooth and sulcate posteriorly, uniplicate anteriorly with low fold and about 10 subangular costae (3 to 4 on fold; beak erect, foramen hypothyrid, disjunct deltidial plates. Pedicle collar present; dorsal median septum short and low; septalium shallow, confined to apex; calcariform crura shaped as curved blades. *Middle Jurassic (Bathonian–Callovian), Upper Jurassic (?lower Kimmeridgian):* Somaliland, ?Kenya, ?Iran, ?India, ?China.——Fig. 878,*2a–j.* **B. afra,* ?lower Kimmeridgian, Daghani, Somaliland; *a–c,* holotype, dorsal, lateral, anterior views, BMNH B.85633, ×1; *d–j,* transverse serial sections, BMNH B.89276 (Muir-Wood, 1935).

?Bradfordirhynchia Shi & Grant, 1993, p. 26 [**Cryptorhynchia bradfordensis* Buckman, 1918, p. 228; OD]. Similar to *Sharpirhynchia,* but dental plates gently ventrally divergent, septalium short, pitlike, or pendant (though allegedly absent), and crura with slightly more extended subvertical blades. [Distinction between these two closely similar genera requires better substantiation.] *Middle Jurassic (upper Bathonian):* England, France.——Fig. 878,*5a–k.* **B. bradfordensis* (Buckman), Bradford-on-Avon, England; *a–c,* topotype, dorsal, lateral, anterior views, USNM 104765b, ×1; *d–k,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.9, 2.2, 2.8, 3.3, 3.7, 3.9, 4.2, 4.6, USNM 104765d (Shi & Grant, 1993).

Grasirhynchia Owen, 1968, p. 19 [**Rhynchonella grasiana* d'Orbigny, 1849 in 1848–1851, p. 38; OD]. Small to medium, transversely oval to subcircular; almost planoconvex, dorsal valve markedly convex with imperceptible median fold; ventral valve less convex with wide shallow sulcus; anterior commissure broadly arcuate; linguiform extension extensive; umbo short, beak suberect with small foramen and auriculate deltidial plates; interarea triangular, poorly exposed; beak ridges hypothyrid. Crura long. *Cretaceous (upper Albian–Cenomanian):* England, France, Germany, Denmark, Belgium, ?Poland, Crimea.——Fig. 879,*1a–k.* **G. grasiana* (d'Orbigny), Cenomanian; *a–c,* lectotype, dorsal, lateral, anterior views, MNHN 6497, Le Havre, France, ×2; *d,* detail of apical region showing auriculate deltidial plates, Le Havre, France, BMNH BB.84908, ×6; *e–k,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.1, 1.3, 1.5, 2.1, 2.6, 3.0, BMNH BB.43909, Sussex, England, ×3.5 (Owen, 1968).

?Himalairhynchia Ching & Sun in Ching, Sun, & Rong, 1976, p. 292 [**H. media;* OD]. Small to medium size, roundly pentagonal, equibiconvex, truncated front and sides steeply sloping, fold and sulcus developed only in anterior half and

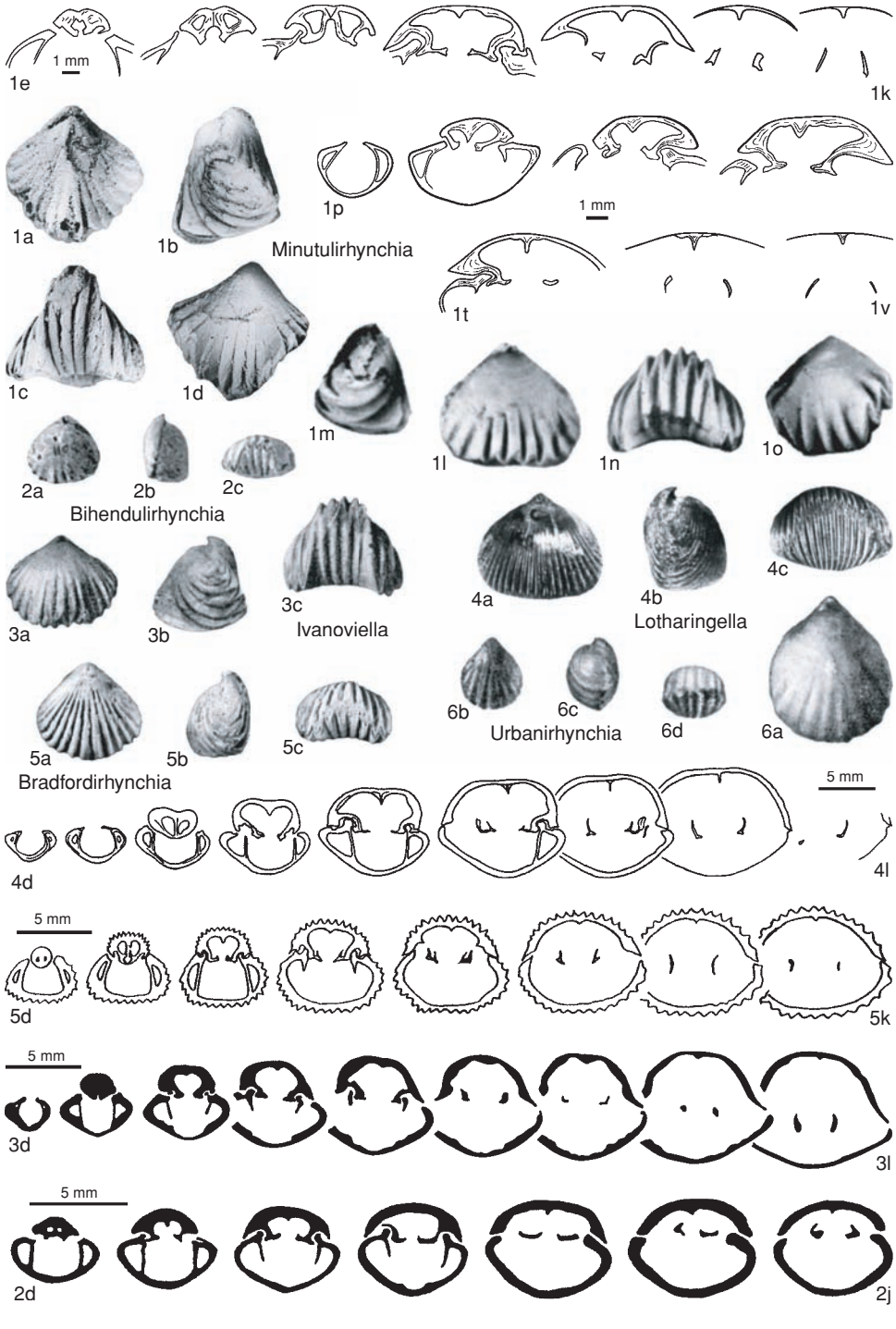

FIG. 878. Rhynchonellidae (p. 1292–1297).

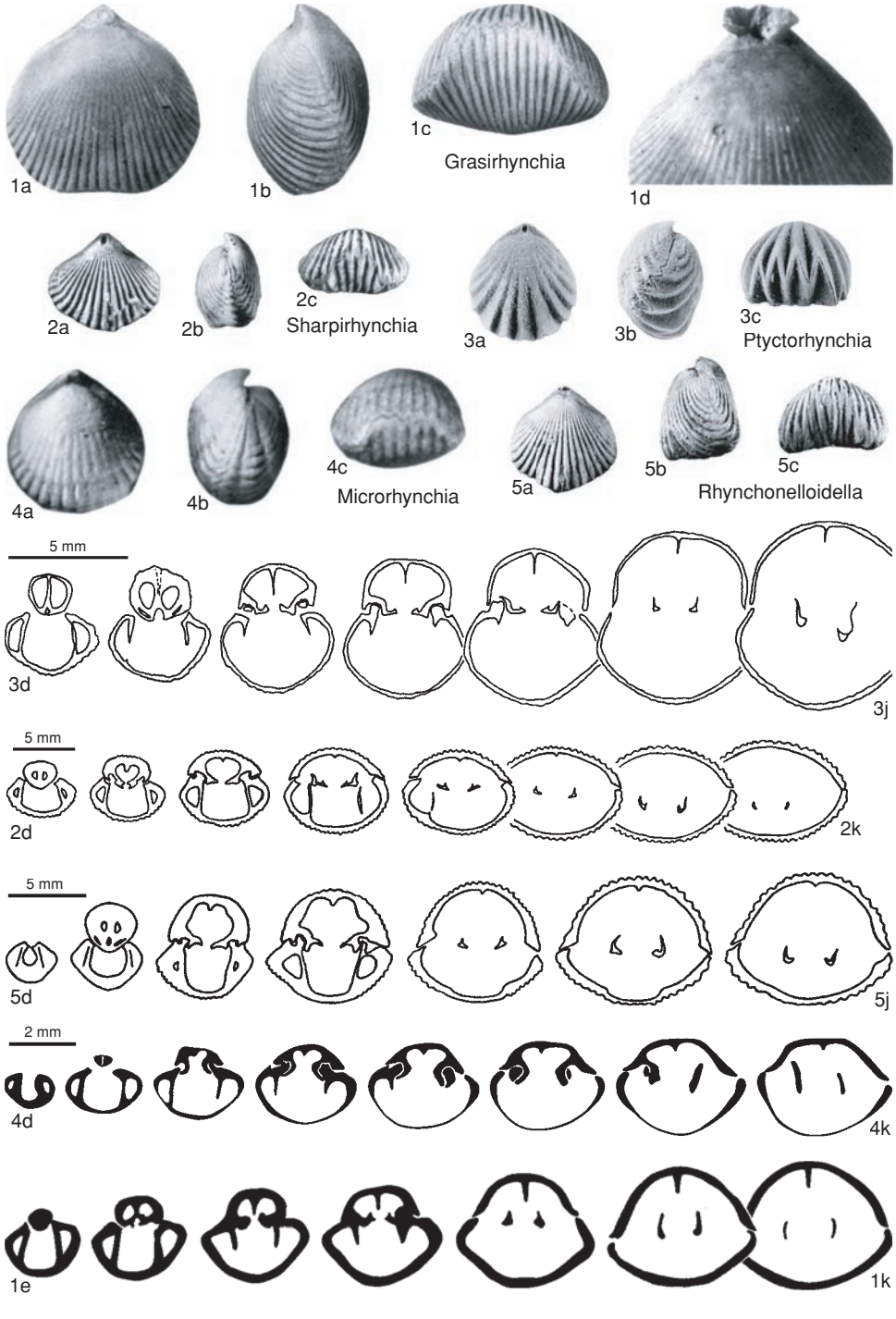

FIG. 879. Rhynchonellidae (p. 1292–1297).

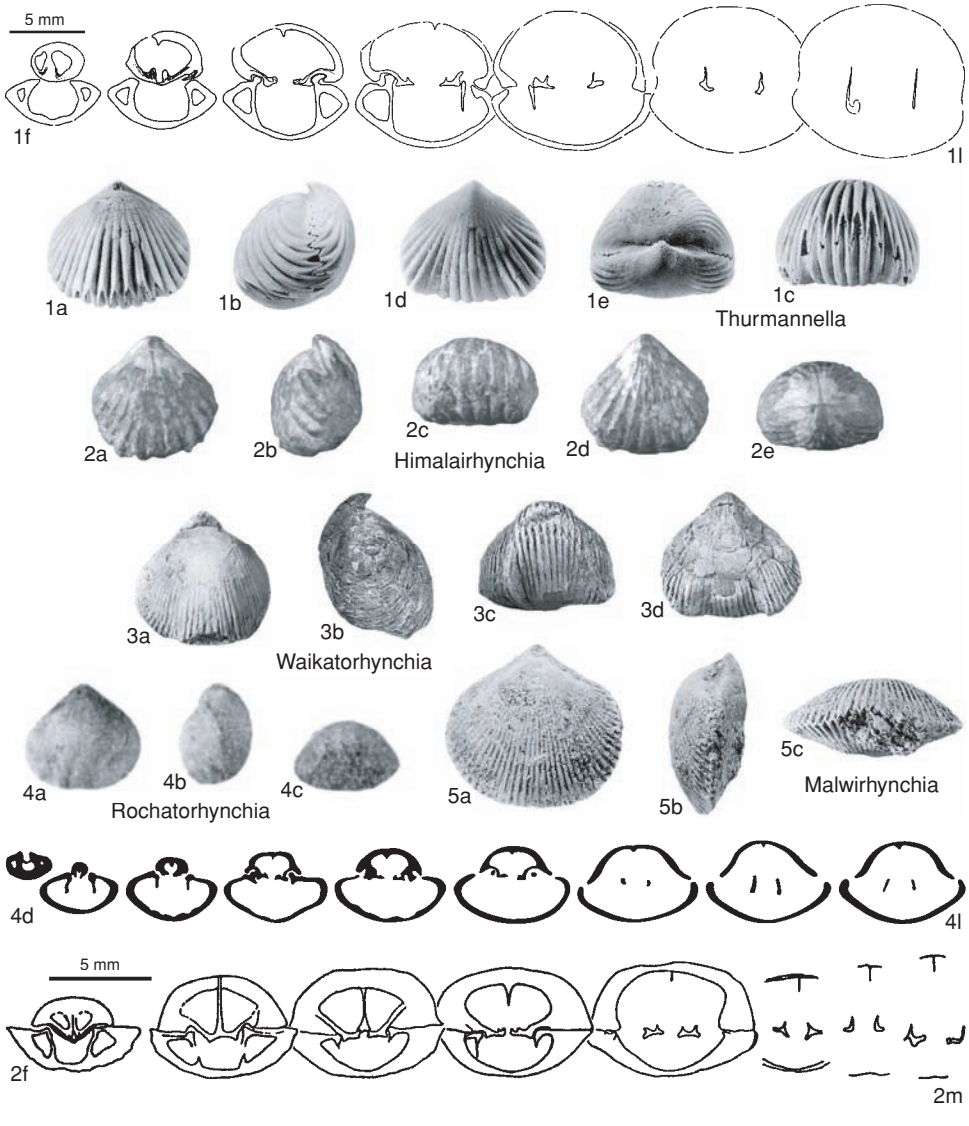

FIG. 880. Rhynchonellidae (p. 1292–1297).

demarcated clearly from sides; linguiform extension subquadrate; subangular costae starting from beak; furrows between costae projecting beyond margin of valves as slender spines and extending under costae of opposite valve; beak short and slightly incurved; beak ridges obtuse, delthyrium covered by symphytium; foramen circular, permesothyrid. Dental plates short, thin and ventrally convergent; hinge plates flat, subhorizontal, median septum supporting septalium; crura calcariform, distally modified. *Upper Triassic (Norian):* China (Qinghai, Tibet), Austria.——FIG. 880,*2a–m. *H. media,* Tibet; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, NIGP 28746, ×1.5 (new); *f–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.9, 2.3, 2.5, 2.7, 3.0, 3.4, 3.8, 4.3, NIGP 28749 (Ching, Sun, & Rong, 1976).

Lotharingella LAURIN, 1984, p. 368 [**L. woevrica;* OD]. Small to medium size, globose equibiconvex to dorsibiconvex; with arcuate uniplication relatively narrow but without raised fold on dorsal valve; fine costae developing after a rather well-marked sulcate stage (6 to 9 on uniplication); beak small, incurved, with rather sharp beak ridges.

Septalium apparently absent; crura varying its shape during ontogeny, from calcariform to nearly raduliform. *Middle Jurassic (lower Bathonian–lower Callovian):* France, England, China (Qinghai, Tibet).——Fig. 878,*4a–c. *L. woevrica woevrica,* Bathonian, Lorraine, France; holotype, dorsal, lateral, anterior views, ×1 (Laurin, 1984).——Fig. 878,*4d–l. L. woevrica minor* Laurin, Bathonian, France; transverse serial sections, distances in mm from ventral umbo, 1.9, 2.2, 2.7, 3.1, 3.6, 4.0, 4.3, 4.7 (Laurin, 1984).

Malwirhynchia Chiplonker, 1938, p. 306 [**M. transversalis;* OD]. Small, transversely oval, uniplication low, broadly arcuate, and dorsal fold ill defined; costellae numerous and fine, bifurcating anteriorly; umbo short, beak suberect with relatively large foramen; deltidial plates conjunct, auriculate; dorsal umbo planate. Median septum low, up to one-half the length of dorsal valve; crural bases extended dorsally; crura ventrally deflected. *Cretaceous (Albian–Cenomanian):* India, ?Don basin.——Fig. 880,*5a–c. *M. transversalis,* India; dorsal, lateral, anterior views, BMNH unregistered, ×1.5 (new).

?Microrhynchia Muir-Wood, 1952, p. 124 [**M. barnackensis;* OD]. Small, rarely sulcoconvex in early stage, becoming biconvex, everted, median fold and sinus often ill defined; shell smooth to finely costate; beak suberect to slightly incurved, deltidial plates conjunct in adult; hypothyrid to just mesothyrid. Dental plates thin, subparallel; median septum extending almost up to midvalve; crura calcariform; hinge plates almost indistinguishable from inner socket ridges and obliquely inclined relative to low median septum. *Middle Jurassic (?Aalenian, Bajocian):* England, ?France, ?Russia.——Fig. 879,*4a–k. *M. barnackensis,* Bajocian, Northamptonshire, England; *a–c,* holotype, dorsal, lateral, anterior views, BMNH BB.9718, ×4; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.6, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3, BMNH B.15856 (Muir-Wood, 1952).

Minutulirhynchia Smirnova, 1992, p. 27 [**M. triangularis;* OD] [=*Sulciphoria* Smirnova, 1992, p. 23 (type, *S. acutimarginata* Smirnova, 1992, p. 24, OD)]. Small, acutely biconvex to cynocephalous, with ventral sulcus deep, and linguiform extension greatly extended; 1 to 2 costae on lateral flanks of sulcus. Dental plates parallel to ventrally divergent; dorsal septum low, ridgelike; septalium almost sessile; crura strongly curved, distally shaped as flat, inclined blades. [Differences between each type species insufficient for generic separation, and clear distinction of both from *Rhynchonelloidella* Muir-Wood, 1936b, p. 49 and *Ivanoviella* Makridin, 1955, p. 83 requires substantiation.] *Middle Jurassic (Callovian)–Upper Jurassic (Oxfordian):* Kazakhstan (Aktyubinsk region).——Fig. 878,*1a–k. *M. triangularis,* Callovian; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 139/1311, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.7, 1.6, 1.9, 2.2, 2.32, 2.41, 2.53 (Smirnova, 1992).——Fig. 878,*1l–v. M. acutimarginata* (Smirnova), Callovian; *l–o,* holotype, dorsal, lateral, anterior, ventral views, MGU 139/1673, ×2; *p–v,* transverse serial sections, distances in mm from first section, 0.2, 1.0, 1.5, 1.73, 2.46, 2.96, 3.56, MGU 139/1701 (Smirnova, 1992).

Ptyctorhynchia Buckman, 1918, p. 47 [**Rhynchonella pentaptycta* Buckman, 1910, p. 103; OD] [=*Ptyctorhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Ptychtorhynchia* Ager, Childs, & Pearson, 1972, p. 163, *nom. null.*]. Small, subcircular, globose, subequibiconvex; uniplication low and wide and fold indistinct; smooth stage posteriorly and relatively strong, round, costae developed anteriorly (5 to 7 on fold); beak small, suberect, with hypothyrid, slightly rimmed, foramen. Dorsal median septum well developed; septalium variable; crura deflected ventrally as curved blades. *Lower Jurassic (?upper Toarcian), Middle Jurassic (Aalenian, ?lower Bajocian):* England, ?France, ?Spain, ?Morocco, Tibet.——Fig. 879,*3a–j. *P. pentaptycta* (Buckman), ?uppermost Toarcian, Aalenian, Dorset, England; *a–c,* dorsal, lateral, anterior views, BMNH B.68376, ×1.5 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.3, 1.5, 1.8, 2.0, 2.2, 2.7, 3.1, CDP 7, C. D. Prosser, personal collection (new; courtesy of C. Prosser).

Rhynchonelloidella Muir-Wood, 1936b, p. 49 [**Rhynchonella varians* var. *smithii* Davidson, 1878, p. 213; OD] [=*Phynchonelloidella* Shi, 1987a, p. 20, *nom. null.*]. Medium size, subtrigonal to subpentagonal, dorsibiconvex to cynocephalous; ventral valve often almost flat, dorsal valve everted; strongly uniplicate, dorsal fold variably raised; costae numerous, fine, subangular (3 to 10 on fold); beak small, suberect to incurved. Dental plates long, umbonal chambers small; dorsal median septum low, supporting septalium; crura calcariform or slight variant thereof. *Lower Jurassic (Toarcian), Middle Jurassic (Aalenian–Callovian), Upper Jurassic (?Oxfordian):* England, France, Germany, Switzerland, Poland, Russia, Crimea, Caucasus, ?Armenia, China, Argentina, *Bajocian–Callovian, ?Oxfordian;* Spain, *Aalenian;* Morocco, *Toarcian.*——Fig. 879,*5a–j. *R. smithii* (Davidson), Bathonian, Bath, Somerset, England; *a–c,* topotype, dorsal, lateral, anterior views, USNM 75628a, ×1; *d–j,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.6, 2.3, 3.1, 3.4, 4.0, 4.3, USNM 75628d (Shi & Grant, 1993).

Rochatorhynchia Kats, 1962, p. 132 [**R. rochatensis;* OD]. Small, smooth, equibiconvex, rounded-pentagonal to broadly oval; maximum breadth and thickness at midvalve; sulcus and fold poorly defined; anterior commissure polyplicate with linguiform extension moderately long; beak short, suberect, beak ridges distinct, foramen small, circular, mesothyrid to permesothyrid. Pedicle collar present; dental plates thin, subparallel; dorsal septum low, short with septalium in early stages; hinge plates divided; crural bases often V-shaped. *Upper Cretaceous (Maastrichtian):* Tadzhikistan.——Fig. 880,*4a–l. *R. rochatensis,* lower Maastrichtian; *a–c,* dorsal, lateral, anterior views, KHGU 4-787, ×1;

d–l, transverse serial sections, distances in mm from ventral umbo, 0.5, 1.6, 2.2, 3.1, 3.4, 3.7, 4.2, 4.3, 4.5, ×1 (Kats, 1962).

Sharpirhynchia Shi & Grant, 1993, p. 49 [**Kallirhynchia sharpi* Muir-Wood, 1938, p. 74; OD]. Small, depressed to moderately dorsibiconvex, subtrigonal to transverse-oval; uniplicate, with low dorsal fold; fully costate, with numerous fine costae and conspicuous, dense growth lines; beak suberect, with rimmed hypothyrid foramen. Dorsal median septum reduced; septalium absent (but if present, tiny, pitlike); relatively narrow calcariform crura. *Middle Jurassic (?upper Bajocian, lower Bathonian):* England, France.——Fig. 879,*2a–k.* **S. sharpi* (Muir-Wood), lower Bathonian, Kettering, England; *a–c,* dorsal, lateral, anterior views, USNM 429195, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.8, 2.1, 2.8, 3.2, 3.4, 4.0, 4.6, 4.8, USNM 429196 (Shi & Grant, 1993).

Thurmannella Leidhold, 1921, p. 357 [**Terebratula obtrita* Defrance, 1828, p. 161–162; SD Schuchert & LeVene, 1929a, p. 124] [=*Thurmanella* Wisniewska, 1932, p. 3, unjustified emendation]. Small to medium size, subpentagonal, dorsibiconvex to almost convexiplane; with uniplication strong and fold slight; linguiform extension high, trapeziform; posterior smooth area variably developed, with numerous simple, subangular costae (4 to 9 on fold); beak small, sharp, suberect. Dorsal median septum short and thick, septalium poorly developed; crura calcariform, strongly curved and expanded ventrally, with distal points directed toward each other. *Middle Jurassic (middle Callovian)–Upper Jurassic (lower Oxfordian, ?lower Tithonian):* England, France, Switzerland, Russian platform, Crimea, Caucasus, China (?Qinghai), Argentina, ?Indonesia, ?Algeria.——Fig. 880,*1a–l.* **T. obtrita* (Defrance), lower Oxfordian, Lorraine, France; *a–e,* dorsal, lateral, anterior, ventral, posterior views, BMNH BB.44154, ×1 (new); *f–l,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.4, 1.6, 2.0, 2.4, 2.8, 3.2, 3.6 (Childs, 1969).

?Urbanirhynchia Kats, 1974, p. 252 [**U. urbani;* OD]. Small, subcircular, subequibiconvex; paucicostate with some intercalations toward the anterior margin; uniplication broad, arcuate. Septalium narrow and buttressed by euseptum; crura well developed, reported as calcariform. *Upper Cretaceous (Cenomanian–Turonian):* Don basin, Crimea, Caucasus, Russia.——Fig. 878,*6a–d.* **U. urbani,* upper Turonian, Don basin; *a,* dorsal view, ×2; *b–d,* holotype, ventral, lateral, anterior views, ×1 (Kats, 1974).

?Waikatorhynchia MacFarlan, 1992, p. 243 [**W. waikatoensis;* OD]. Medium size, elongate-oval to subcircular outline; equibiconvex to dorsibiconvex, inflation moderate to great; dorsal valve with flat central part posteriorly and strongly convex lateral slopes; rectimarginate or with arcuate uniplication; fold and sulcus poorly developed; costae even and dense throughout; beak sharp, erect to slightly incurved, with sharp beak ridges and short pedicle collar. Hinge plates short, with small septalium; dorsal median septum high, narrow; dental plates wide apart, umbonal chambers narrow; crura unknown. *Upper Jurassic (Kimmeridgian–Tithonian):* New Zealand (North Island).——Fig. 880,*3a–d.* **W. waikatoensis,* Tithonian, Puaroan; holotype, dorsal, lateral, anterior, ventral views, AU B273, ×1 (MacFarlan, 1992).

Subfamily NUCLEUSORHYNCHIINAE Xu, 1990

[*nom. transl.* Owen & Manceñido, herein, *ex* Nucleusorhynchiidae Xu, 1990, p. 77]

Rhynchonellidae with smooth shell and typically rectimarginate commissure; ventral sulcus absent and dorsal fold inconspicuous, broad, and flat if present. Dental plates developed; dorsal median septum and septalium present; crura raduliform. *Middle Triassic (Anisian)–Lower Jurassic (Hettangian, ?Sinemurian).*

Nucleusorhynchia Sun & Ye, 1982, p. 159[170] [**N. typica;* OD]. Small, gently biconvex, lenticular, smooth, rectimarginate; beak short and small; foramen permesothyrid; deltidial plates discrete; beak ridges rounded. Dental plates subparallel; septalium wide and shallow; median septum thick and low; crura rodlike proximally, narrow, bladelike, inclined inward distally, and slightly curved ventrally. *Middle Triassic (Anisian):* China (Qinghai).——Fig. 881,*1a–j.* **N. typica; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67026, ×2; *e–j,* holotype, transverse serial sections, distances in mm from ventral umbo, 0.68, 0.94, 1.12, 1.4, 1.58, 2.22, NIGP 67026 (Sun & Ye, 1982).

?Murihikurhynchia MacFarlan, 1992, p. 131 [**M. malingi;* OD]. Small subtriangular to subpentagonal; equibiconvex, slightly to moderately inflated; lateral slopes of both valves more strongly convex than central part; dorsal valve flat or sulcate posteriorly, with uniplication broad, shallow anteriorly; fold and sulcus low; costae few, low, blunt, after long posterior smooth stage (exceptionally non-costate); beak small, sharp, erect, with rounded beak ridges; deltidial plates disjunct. Hinge plates thick, flat, often with medially ridged shallow septalium; dorsal median septum long, thin, moderately high. *Upper Triassic (upper Carnian)–Lower Jurassic (Hettangian, ?Sinemurian):* New Zealand, New Caledonia.——Fig. 881,*2a–b.* **M. malingi,* lower Norian, Otamitan, Southland syncline, New Zealand; holotype, dorsal, ventral views, OU NZ 16428, ×2 (MacFarlan, 1992).——Fig. 881,*2c–e. M. braxtonensis* MacFarlan, upper Carnian–Norian, Oretian, Southland syncline, New Zealand; holotype, dorsal, lateral, anterior views, OU NZ 16641, ×1 (MacFarlan, 1992).

Uniplicatorhynchia Sun & Ye, 1982, p. 158[169] [**U. trigona;* OD]. Medium size, subtriangular to round pentagonal, equibiconvex, smooth; broad, low ventral sulcus and dorsal fold; commissure uniplicate,

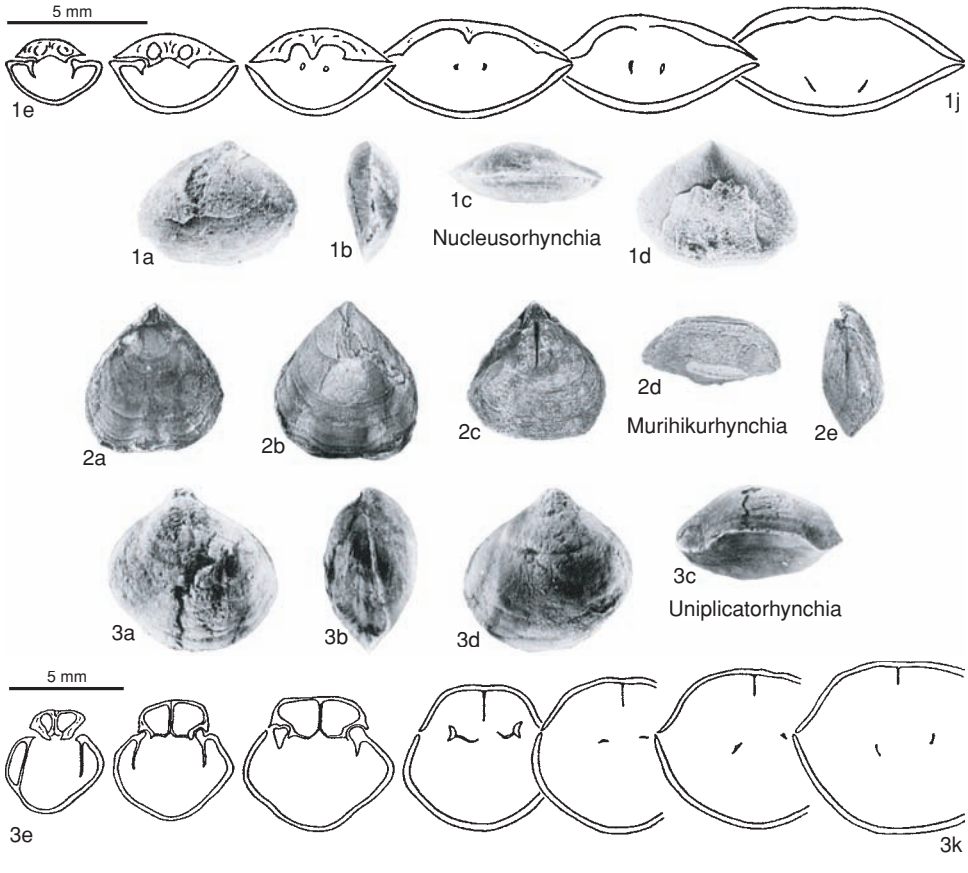

FIG. 881. Rhynchonellidae (p. 1297–1298).

flattopped; ventral beak small, incurved; foramen small, permesothyrid; delthyrium open. Dental plates long and parallel; hinge plates flat, subhorizontal; shallow, V-shaped septalium; median septum thin, high, long; crura raduliform, with trigonal crural bases and narrow bladelike distal ends. *Middle Triassic (Anisian)–Upper Triassic (Carnian):* China (Qinghai), Nepal.——FIG. 881,*3a–k.* **U. trigona,* Anisian, Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67025, ×1.5; *e–k,* holotype, transverse serial sections, distances in mm from ventral umbo, 1.1, 1.5, 1.75, 2.1, 2.35, 2.7, 3.05, NIGP 67025 (Sun & Ye, 1982).

Subfamily BILAMINELLINAE Babanova, 1964

[*nom. transl.* OWEN & MANCEÑIDO, herein, *ex* Bilaminellini BABANOVA, 1964, p. 66; *emend.,* OWEN & MANCEÑIDO, herein]

Small- to medium-sized Rhynchonellidae, transversely elliptical, almost fully costate, with uniplication wide, flattopped, bearing a fairly dense, delicate, blunt costation superimposed. Ventral valve with pair of ovoid posterolateral hinge pouches that, in cross section, give impression of bifurcate dental plates (alluded to in original diagnosis of tribe); dental plates subparallel, umbonal chambers ample; crura raduliform or variation thereof; septalium present, at least in early ontogeny. *Upper Triassic (Norian)–Middle Jurassic (Callovian), Upper Jurassic (?Oxfordian).*

Bilaminella BABANOVA, 1964, p. 66 [**B. inaequicostata;* OD]. Medium size, subpentagonal, depressed dorsibiconvex, broadly uniplicate; radial costae narrow, simple, rounded. Hinge teeth and denticula well developed; alleged radially bifurcated dental plates due to convergence of pouch structure walls with subparallel dental plates; septalium observed only in early stages of shell; crura calcariform. *Middle Jurassic (Callovian), Upper Jurassic*

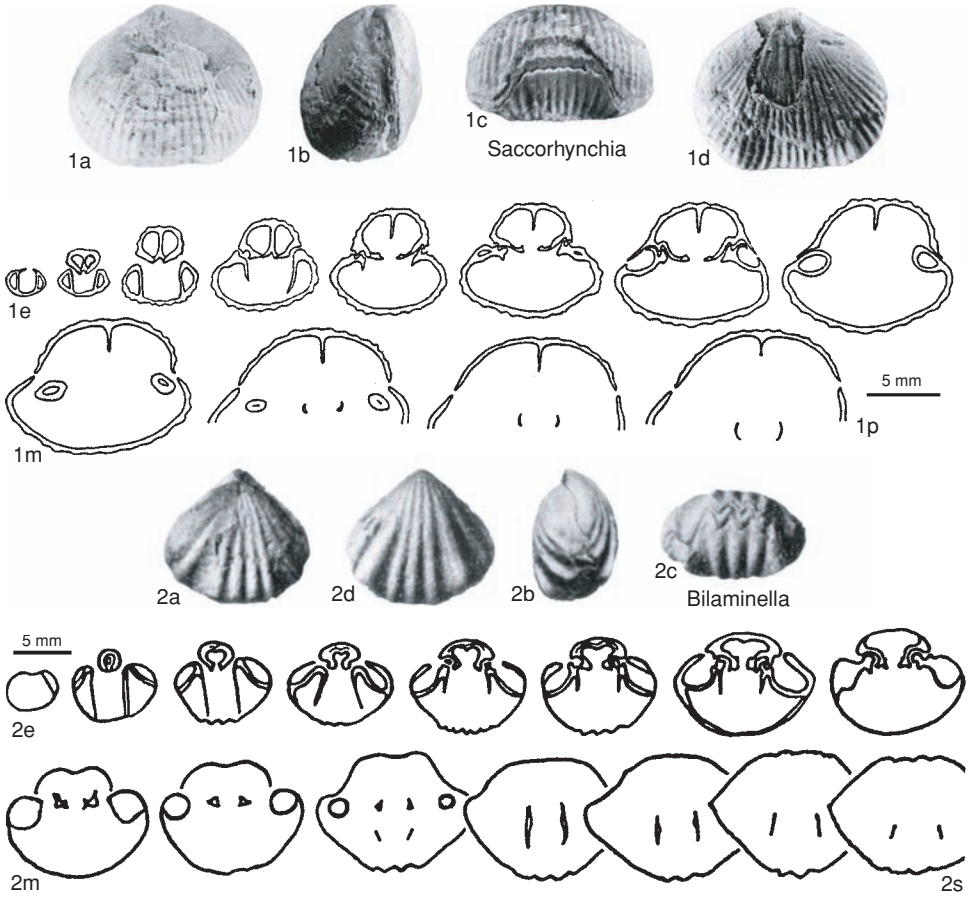

FIG. 882. Rhynchonellidae (p. 1298–1299).

(?Oxfordian): Ukraine (Crimea), central Asia.——FIG. 882,*2a–s.* **B. inaequicostata,* upper Callovian, Crimea; *a–d,* holotype, dorsal, lateral, anterior, ventral views, KHGU 4031/8, ×2 (Babanova, 1964); *e–s,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.4, 0.5, 0.6, 0.9, 1.1, 1.2, 1.3, 1.4, 1.6, 1.8, 1.9, 2.4, 2.8, 3.1, KHGU 2007/8 (Kamyshan & Babanova, 1973).

Saccorhynchia CHING, SUN, & YE in CHING & others, 1979, p. 154 [**S. xiangdaica;* OD]. Large size; roundly pentagonal, dorsibiconvex; fold and sulcus low, developed only anteriorly; linguiform extension roundly arched; costae thin, round, beginning from beak and increasing by intercalation or bifurcation; beak short and nearly straight; foramen submesothyrid; delthyrium covered by raised symphytium. Teeth angular; dental plates short, subparallel; pouch structure present anterolaterally of dental plate; dorsal septum high; septalium short and shallow; crura raduliform. *Upper Triassic (Norian):* China (Qinghai, Xizang).——FIG. 882,*1a–p.* **S. xiangdaica,* Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42830, ×1; *e–p,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.65, 1.0, 1.2, 1.3, 1.9, 2.3, 3.25, 3.55, 3.75, 4.3, 4.8, NIGP 42830 (Ching & others, 1979).

Subfamily DAVANIRHYNCHIINAE Ovcharenko, 1983

[Davanirhynchiinae OVCHARENKO, 1983, p. 41]

Small- to medium-sized Rhynchonellidae with complex, antidichotomous costae; thin, ventrally divergent to subparallel dental plates; subhorizontal hinge plates; dorsal median septum and septalium variously developed, and raduliform to calcariform crura. [These are reminiscent of Paleozoic yunnannellids.] *Upper Triassic (Norian)–Lower Cretaceous (Valanginian).*

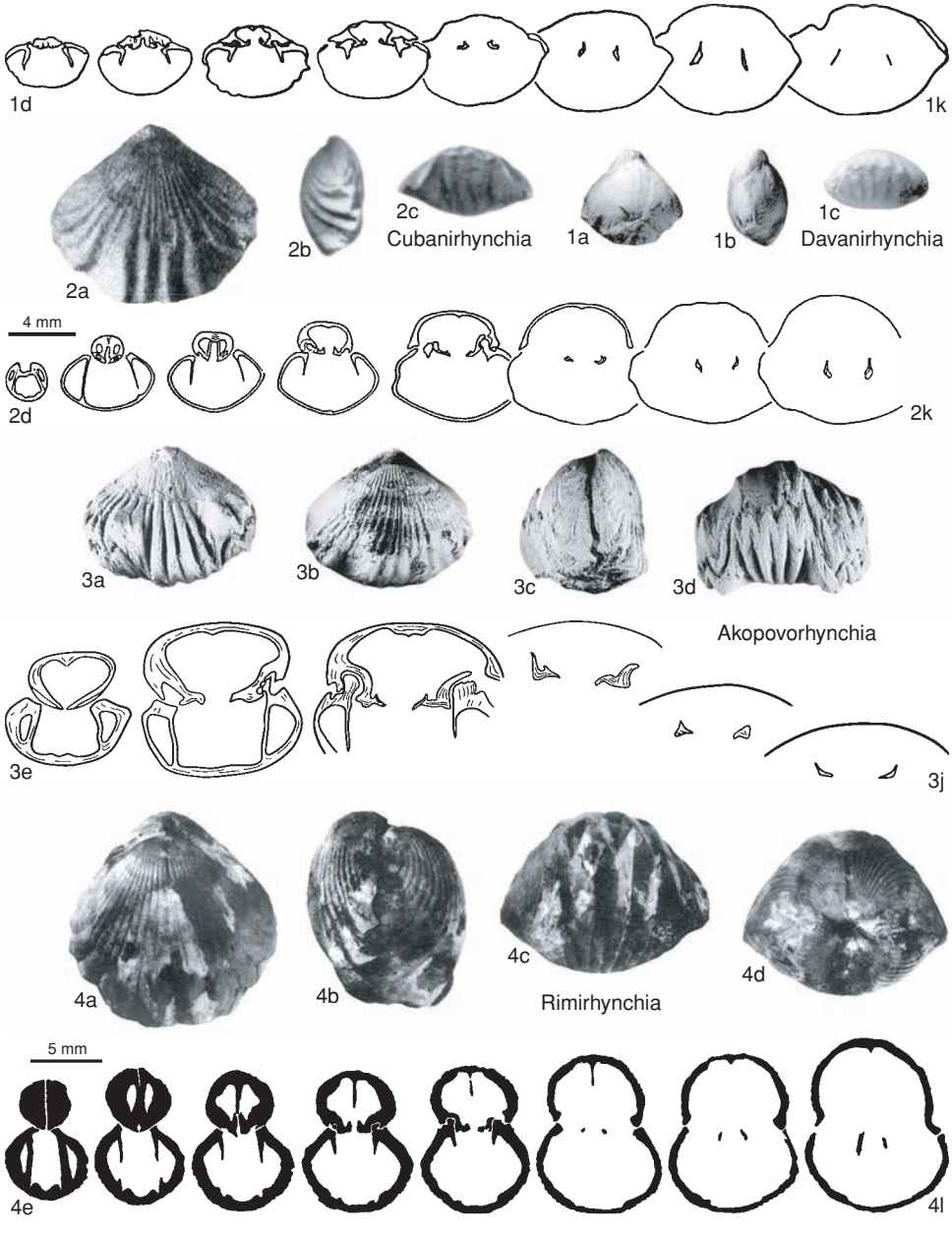

FIG. 883. Rhynchonellidae (p. 1300–1301).

Davanirhynchia OVCHARENKO, 1983, p. 42 [**D. davanensis;* OD]. Small shells, rounded-trigonal, costellae numerous and thin posteriorly, passing into fewer rounded plicae anteriorly. Dental plates short, diverging ventrally, hinge plates broad, convex ventrally, inclined dorsally; dorsal median septum reduced to ridge, barely buttressing a nearly sessile, narrow septalium; crura raduliform approaching to spinuliform. *Middle Jurassic (Bathonian):* southeastern Pamirs.——FIG. 883, *1a–k. *D. davanensis; a–c,* holotype, dorsal, lateral, anterior views, MUGT 92/1266, ×1; *d–k,*

transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.65, 0.9, 1.2, 1.5, 1.8, 2.0, MUGT 91/1266 (Ovcharenko, 1983).

Akopovorhynchia Smirnova, 1990b, p. 47 [**A. akopovi;* OD] [=*Acopovorhynchia* Smirnova, 1994, p. 31, *nom. null.*]. Medium, moderately to strongly dorsibiconvex, with numerous sharp, angular, deeply incised costae; dorsal fold well developed; commissure with fairly extensive trapezoidal linguiform extension; beak massive, incurved. Hinge teeth massive, deeply inserted with lateral secondary denticles; pedicle collar present; dental plates long, subparallel; crura with gently concave distal ends. *Lower Cretaceous (Valanginian):* northwestern Kazakhstan.——Fig. 883,*3a–j. *A. akopovi; a–d,* dorsal, ventral, lateral, anterior views, ×1; *e–j,* transverse serial sections, distances in mm from first section, 2.2, 3.0, 3.6, 3.95, 5.12, 5.73, approximately ×2.5 (Smirnova, 1990b).

Cubanirhynchia Kamyshan, 1968, p. 57 [**C. rostovzevi;* OD]. Marginal plicae formed by fusion of 2 thin radial costellae or by further growth of one of them whereas its companion vanishes. Pedicle collar present, dental plates diverging ventrally; septalial plates distinct, parallel to each other or converging dorsally sometimes, sessile in early stages, hanging free in other species, or joining to weakly developed dorsal median septum in later stages; crura calcariform or similar. [Usage in Kamyshan, 1967b, p. 7, of doubtful availability.] *Lower Jurassic (?Toarcian), Middle Jurassic (Aalenian–Bajocian):* Caucasus, Armenia, Alps, Transcarpathia.——Fig. 883,*2a–k. *C. rostovzevi,* lower Bajocian, northwestern Caucasus; *a,* holotype, dorsal view, ×1.5 (Kamyshan, 1968); *b–c,* holotype, lateral, anterior views, KHGU 6/1485, ×1 (Kamyshan & Babanova, 1973); *d–k,* transverse serial sections, 0.4, 1.7, 1.9, 2.2, 3.0, 3.5, 3.8, 4.0, KHGU 6/1488 (Kamyshan, 1968, text-fig. 3, not 4).

Furcirhynchia Buckman, 1918, p. 59 [**F. furcata;* OD] [=*Furcirhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Lineirhynchia* Buckman, 1918, p. 59 (type, *L. cotteswoldiae* Upton, 1899, p. 129, OD); *Lineirhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Small to medium size, transverse-oval to subtrigonal, equibiconvex to dorsibiconvex, depressed to subcynocephalous; sharp uniplication and fold; capillate posteriorly, with few strong, sharp costae anteriorly; beak strong, upright, with large, oval foramen. Dorsal median septum long; hinge plates horizontal, with shallow septalium; crura raduliform. *Lower Jurassic (Hettangian–Toarcian):* England, France, Germany, Slovakia, Italy, Austria, ?Switzerland, western Canada, Siberia, Japan, Indonesia (Seran), New Zealand, New Caledonia, Argentina, ?Chile.——Fig. 884,*2a–k. *F. furcata,* lower Pliensbachian, Dorset, England; *a–c,* holotype, dorsal, lateral, anterior views, GSM 31871, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.9, 2.3, 2.9, 3.1, 3.4, 4.0, 4.6, 4.9, J.1068/2, Derek Ager, personal collection (Ager, 1959a).——Fig. 884,*2l–v. F. cotteswoldiae* (Upton), Toarcian, Gloucestershire, England; *l–n,* syntype, dorsal, lateral, anterior views, Gloucester Museum, ×1.5; *o–v,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.0, 1.2, 1.3, 1.5, 1.7, 2.1, 2.3, J.1157, personal collection, Derek Ager (Ager, 1962).

Rimirhynchia Buckman, 1918, p. 60 [**R. rimosiformis;* OD; =*Rhynchonella anglica* Rollier, 1917, p. 92] [=*Rimirhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium to large, globose dorsibiconvex, subcircular; strong obtuse uniplication and fold; both valves bearing many fine capillae posteriorly giving way to few strong costae anteriorly; beak massive, strongly incurved with submesothyrid foramen. Hinge plates horizontal with deep septalium; crura raduliform, distally transitional to calcariform. *Lower Jurassic (upper Sinemurian–Pliensbachian):* England, Scotland, Germany, France, ?Switzerland, ?Crimea, Siberia, northwestern Canada (mainly boreal).——Fig. 883,*4a–l. *R. anglica* (Rollier), lower Pliensbachian, Somerset, England; *a–d,* holotype, dorsal, lateral, anterior, posterior views, BMNH B.12282, ×1.5; *e–l,* transverse serial sections, distances in mm from ventral umbo, 1.9, 2.4, 2.5, 2.8, 3.2, 3.8, 4.1, 4.7, personal collection, Derek Ager (Ager, 1959a).

Rimirhynchopsis Dagys, 1963, p. 71 [**R. triadicus;* OD]. Medium size, laterally ovate or subpentagonal, with distinct sulcus and low fold, fine capillae posteriorly, rare, strong, rounded costae anteriorly; beak low, suberect, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Dental plates short, almost fused to wall; no pedicle collar; septum and septalium stout, umbonal chambers small, partly filled with callus, gently curved raduliform crura. *Upper Triassic (Norian–Rhaetian):* Alps, northwestern Caucasus, China (Qinghai).——Fig. 884,*1a–k. *R. triadica,* Norian, northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 179/160, ×1; *e–k,* transverse serial sections, distances in mm from first section, 1.6, 2.2, 2.4, 2.7, 3.3, 3.7, 4.4 (Dagys, 1963).

Subfamily STRIIRHYNCHIINAE Kamyshan, 1968

[Striirhynchiinae Kamyshan, 1968, p. 55]

Rhynchonellidae covered with numerous thin radial costae that may be dichotomous or intercalated, appearing at various distances from beak; small folds (plicae) in anterior part of shell; small, incurved beak; deltidial plates narrow, disjunct. Outer hinge plates well developed; septalial plates variously oriented, sessile in early stages; dorsal

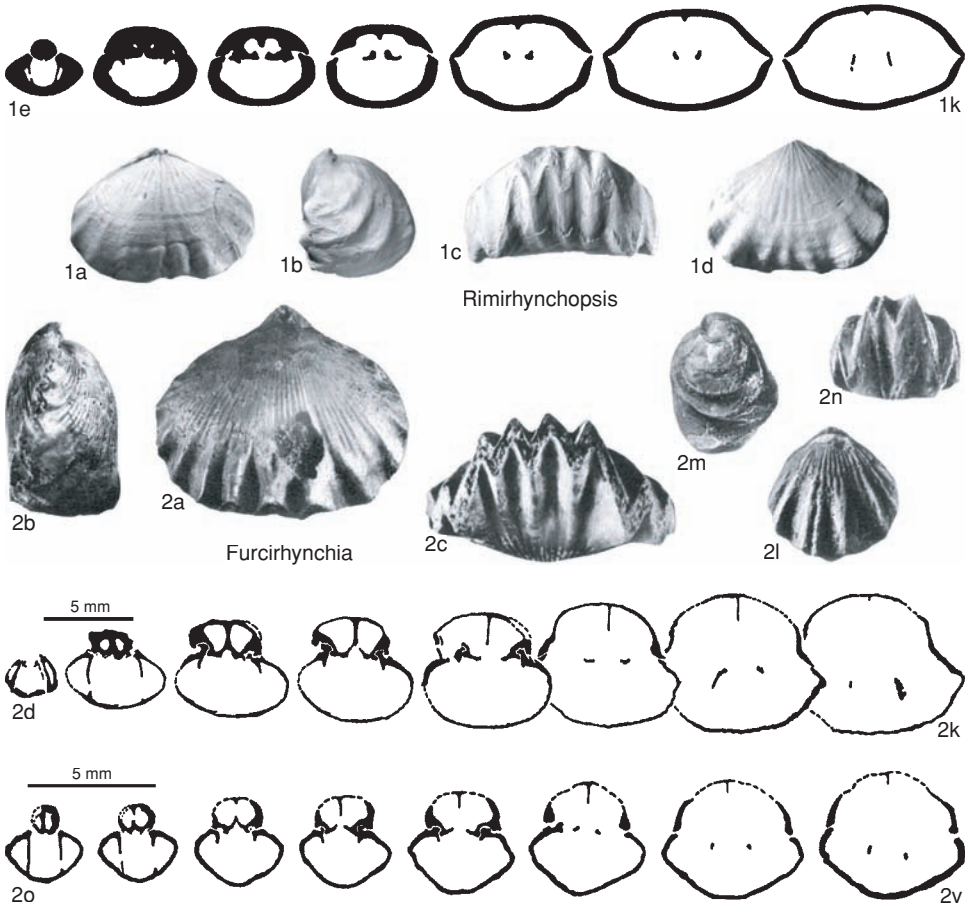

FIG. 884. Rhynchonellidae (p. 1301).

median septum weakly developed; crura calcariform or gently curved raduliform. *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Callovian).*

Striirhynchia BUCKMAN, 1918, p. 68 [**S. dorsetensis;* OD; =*Rhynchonella dorsetiensis* DAVIDSON, 1884, p. 277] [=*Striirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Stiirhynchia* AGER, 1965, p. 619, unjustified emendation]. Small to medium size, depressed, uniplicate, with many fine dichotomizing capillae, costae absent; beak small, sharp. Dental plates short; dorsal septum feeble. *Middle Jurassic (Aalenian–Bathonian):* England, Austria, Hungary, Poland, Slovakia, Sicily, Caspian Basin, Transcarpathia, Caucasus, Armenia, Nakhichevan, Algeria.——FIG. 885,*2a–o. *S. dorsetiensis* (DAVIDSON), lower Bajocian, Dorset, England; *a–b,* dorsal, anterior views, GSM 3758, ×2; *c–o,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 1.1, 1.3, 1.4, 1.5, 1.6, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, BMNH B.70673 (new; courtesy of C. D. Prosser).

Capillirhynchia BUCKMAN, 1918, p. 58 [**Rhynchonella wrightii* DAVIDSON, 1852b, p. 69; OD] [=*Capillirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Large, globose, dorsibiconvex, rounded to subpentagonal, broadly uniplicate, with low fold; capillae all over shell, strong, sharp costae anteriorly (3 to 10 on fold); beak strong, suberect. *Middle Jurassic (Aalenian–Callovian):* England, France, Poland, Bulgaria, Yugoslavia, ?Hungary, ?Russian platform, Crimea, Caucasus, western North America.——FIG. 885,*3a–t. *C. wrightii* (DAVIDSON), Aalenian, Cotswolds, England; *a–c,* topotype, dorsal, lateral, anterior views, GSM 31942, ×1; *d–t,* topotype, transverse serial sections, distances in

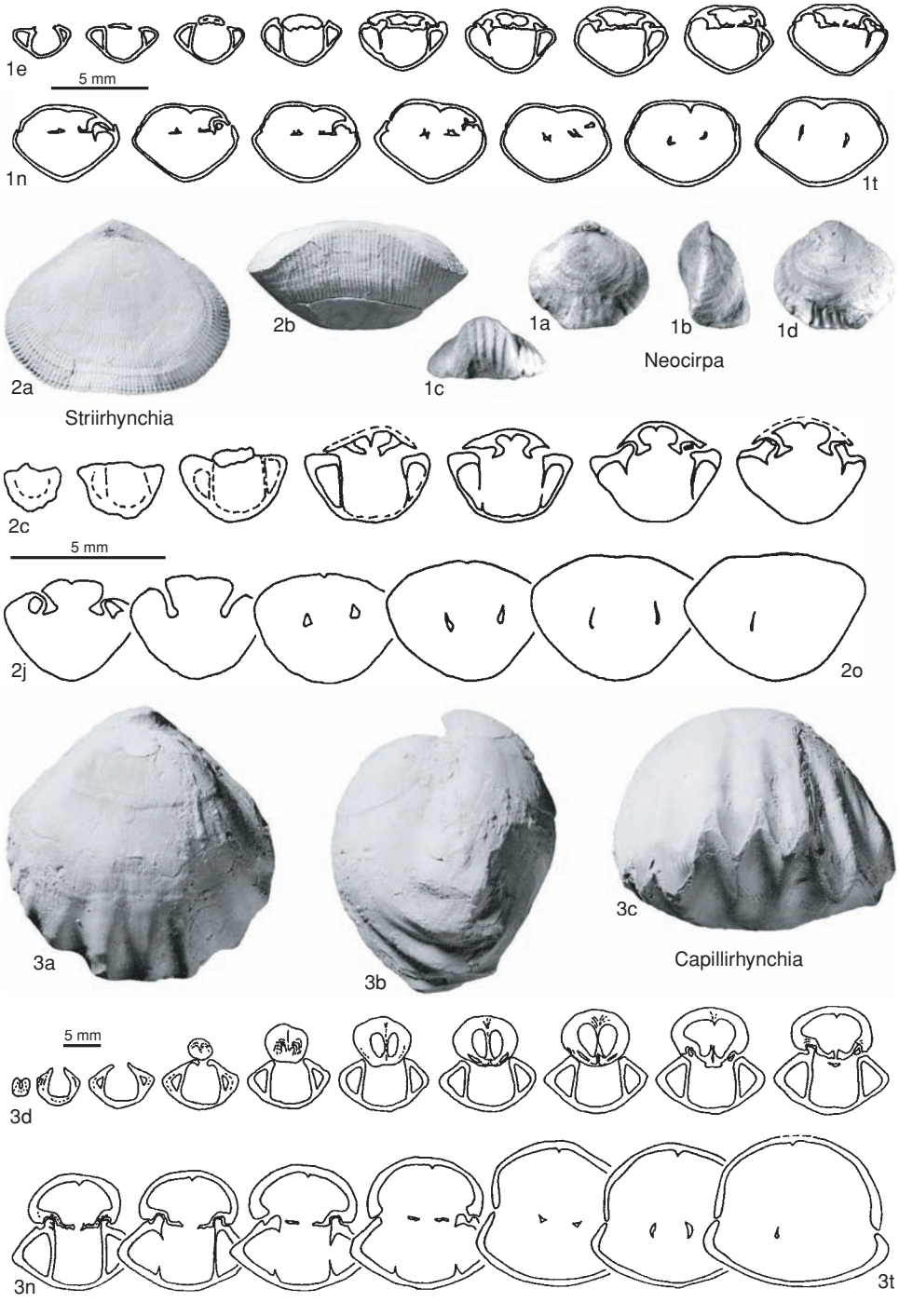

FIG. 885. Rhynchonellidae (p. 1302–1304).

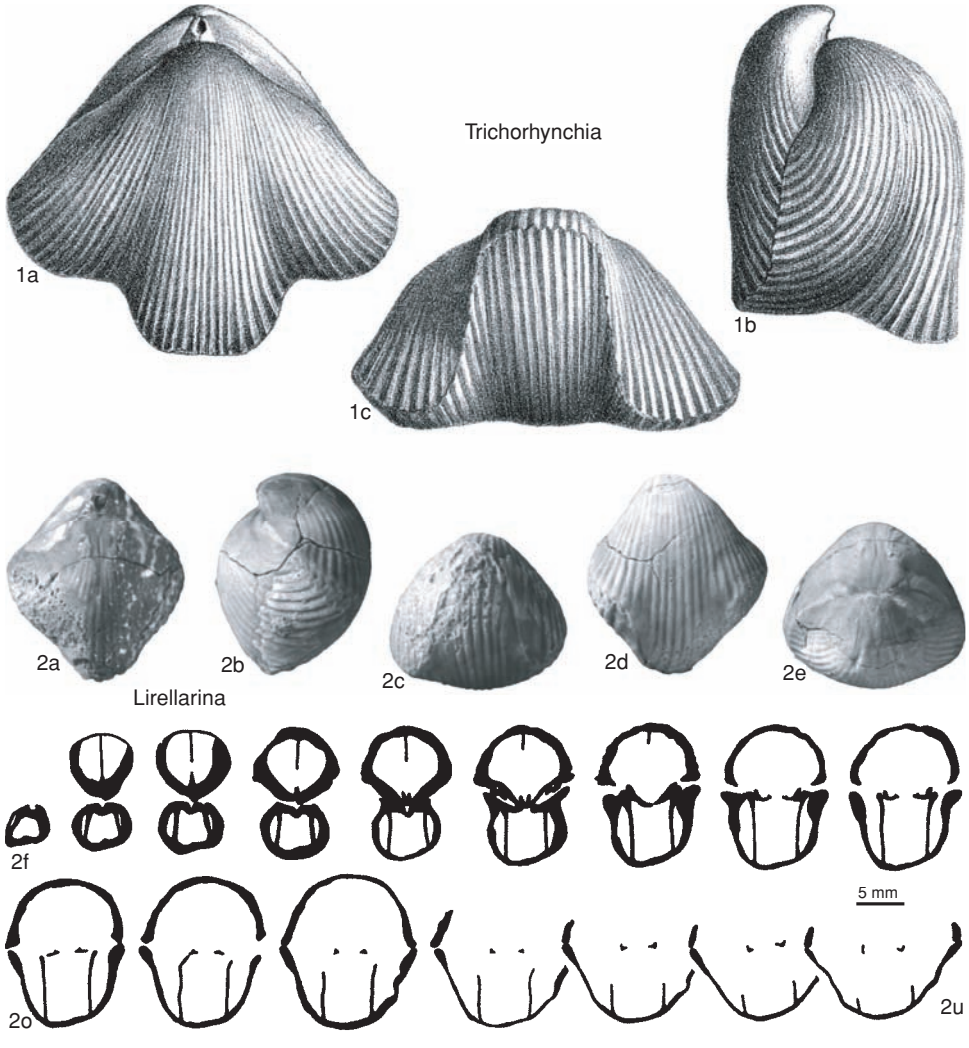

FIG. 886. Rhynchonellidae (p. 1304–1305).

mm from ventral umbo, 0.5, 1.8, 2.7, 3.2, 3.7, 3.9, 4.5, 4.7, 5.0, 5.2, 5.6, 6.0, 6.2, 6.8, 8.4, 8.7, 9.3, CDP 27, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

?Lirellarina COOPER, 1989, p. 49 [**L. costellata;* OD]. Medium size, dorsibiconvex; subpentagonal; strongly uniplicate, narrow, rounded, dorsal fold, strongly raised in anterior third; costellate, with costellae bifurcating on umbones and flanks; beak low, suberect; deltidial plates conjunct; foramen oval, rimmed. Dental plates long, thin, parallel; dorsal median septum long; septalium small; raduliform crura. *Middle Jurassic (Bajocian):* Arabia.——FIG. 886,*2a–u. *L. costellata,* upper Bajocian, Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380241c, ×1.5; *f–u,* transverse serial sections, distances in mm from ventral umbo, 0.6, 0.9, 1.2, 1.4, 1.7, 2.1, 2.4, 2.6, 2.8, 3.1, 3.4, 3.6, 3.8, 4.3, 4.6, 4.9, USNM 380690 (Cooper, 1989).

?Neocirpa PROZOROVSKAIA, 1985, p. 110 [**N. armenica;* OD]. Small, subpentagonal, very small beak, uniplicate with fold low, arcuate, smooth or striate posteriorly, costate anteriorly. Entire hinge plates rather thin, septum ridgelike; septalium absent; crura raduliform. *Middle Jurassic (Bajocian):* Armenia, Nakhichevan.——FIG. 885,*1a–t. *N. armenica,* upper Bajocian, Armenia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CNIGR 1166a/12282, ×1; *e–t,* transverse serial sections, distances

in mm from ventral umbo, 2.1, 2.4, 2.8, 3.1, 3.7, 3.8, 4.0, 4.2, 4.3, 4.5, 4.7, 4.8, 4.9, 5.0, 5.2, 5.5 (Prozorovskaia, 1985).

?Trichorhynchia Buckman, 1918, p. 58 [**Rhynchonella deslongchampsii* Davidson, 1852a, p. 253; OD] [=*Trichorhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium to large, trilobate, dorsibiconvex; sometimes nasute, with wide uniplication, strong, flattened, high, narrow, dorsal fold; many fine costellae throughout, sometimes dichotomous or intercalated; beak massive. *?Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Bajocian):* England, France, northwestern Caucasus.——Fig. 886,*1a–c.* **T. deslongchampsii* (Davidson), Liassic, ?Pliensbachian, Normandy, France; dorsal, lateral, anterior views, ×1 (Davidson, 1852a).

Family ACANTHOTHIRIDIDAE Schuchert, 1913

[*nom. correct.* Owen & Manceñido, herein, *pro* Acanthothyrididae Shi & Grant, 1993, p. 23, *nom. transl. ex* Acanthothyridinae Ager, 1965, p. 611, *nom. correct. pro* Acanthothyrinae Schuchert, 1913, p. 400]

Spinose, subequibiconvex to dorsibiconvex Rhynchonelloidea, crura variable, usually raduliform or its varieties; cardinal process rarely present or absent. [Name based on unjustified emendation of *Acanthothiris,* herein corrected in accordance with ICZN, 1999, Art. 35.4.1.] *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian)–Lower Cretaceous (lower Aptian).*

Subfamily ACANTHOTHIRIDINAE Schuchert, 1913

[*nom. correct.* Owen & Manceñido, herein, *pro* Acanthothyridinae Ager, 1965, p. 611, *nom. correct. pro* Acanthothyrinae Schuchert, 1913, p. 400]

Acanthothiriddidae with shell ornamented, costae coarse and spines relatively few but strong; beak strongly incurved. Dental plates and dorsal median septum present; septalium generally present; cardinal process absent; crura raduliform or modification thereof; deltidial plates and pedicle collar usually well developed. [Name based on unjustified emendation of *Acanthothiris,* herein corrected in accordance with ICZN, 1999, Art. 35.4.1.] *Middle Jurassic (Aalenian)–Upper Jurassic (Tithonian).*

Acanthothiris d'Orbigny, 1850, p. 323 [**Hemithiris spinosa* d'Orbigny, 1850 in 1849–1852, p. 268; SD Buckman & Walker, 1889, p. 43; =*Anomia spinosa* von Linné, 1767, p. 1154] [=*Acanthothyris* Bronn, 1862, p. 303, obj.]. Medium size, globose, dorsibiconvex to equibiconvex; uniplicate with dorsal fold low, ill defined; fully costate, no smooth stage; with many costae, intercalating, bi- or trifurcating, coarsely spinose throughout; beak small, incurved, pedicle collar may be tubelike. Dorsal median septum low and short; crura raduliform, sometimes with modified distal ends; septalial plates narrow, poorly developed, usually on early growth stages. *Middle Jurassic (Aalenian–Callovian):* England, France, Germany, Switzerland, Poland, Romania, Bulgaria, Slovakia, Crimea, Caucasus, Morocco, Afghanistan, Pamirs.——Fig. 887,*1a–n.* **A. spinosa* (von Linné), Bajocian, England; *a–e,* neotype, dorsal, lateral, anterior, ventral, posterior views, BMNH BB.45400, ×1; *f,* enlargement of dorsal view with spines, BMNH B.10617, ×1.5 (new); *g–n,* transverse serial sections through umbo, ×4 (Ager, 1965).

Kawhiarhynchia MacFarlan, 1992, p. 255 [**Rhynchonella (Cryptorhynchia) kawhiana* Trechmann, 1923, p. 283; OD]. Medium size, rounded to transverse-elliptical outline; equibiconvex to dorsibiconvex, moderately to well inflated; usually with uniplication broad, arcuate but no definite fold; shell covered with rounded or angular costae, foliaceous growth lamellae, and crescentic or tubular spines; beak broad, suberect to erect with large foramen and pedicle collar thick. Ventral median ridge low, possibly occurring posteriorly; dorsal valve with broad hinge plate, long, low median septum; crura short, with vertical terminations. *Middle Jurassic (?Bathonian, Callovian)–Upper Jurassic (Tithonian):* New Zealand.——Fig. 887,*3a–m.* **K. kawhiana* (Trechmann), Oxfordian, middle Heterian, North Island; *a–d,* dorsal, anterior, ventral, posterior views, NZGS BR2296, ×1.5; *e,* latex mold of dorsal exterior showing spine bases, OU NZ 17239, ×1.5; *f,* lateral view, OU NZ 17235, ×1.5; *g–m,* transverse serial sections, distances in mm from ventral umbo, 2.4, 2.8, 3.0, 3.6, 4.2, 4.6, 4.9, OU NZ 17230 (MacFarlan, 1992).

?Paraacanthothyris Kamyshan in Kamyshan & Babanova, 1973, p. 67–68 [**P. paucicostata;* OD] [=*Paraacanthothyris* Kamyshan, 1967b, p. 7, unavailable name; *Paracanthothyris* Kamyshan in Ager, Childs, & Pearson, 1972, p. 163, *nom. nud.*]. Medium size, dorsibiconvex, uniplicate, with coarse, sparsely spinose costae, subdued on perumbonal region (3 to 7 of them on low dorsal fold). Dental plates ventrally divergent or parallel; dorsal median septum long, well developed; septalial plates wide, almost sessile in early stages, joining the median septum later, more rarely arising from it to form a V- or U-shaped septalium; crura calcariform. *Middle Jurassic (Aalenian–Bajocian):* ?France, northwestern Caucasus.——Fig. 887,*2a–j.* **P. paucicostata,* Bajocian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, KHGU 6/1925, ×1.5; *d–j,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.4, 1.7, 1.9, 2.1, 2.4, 3.0 (Kamyshan & Babanova, 1973).

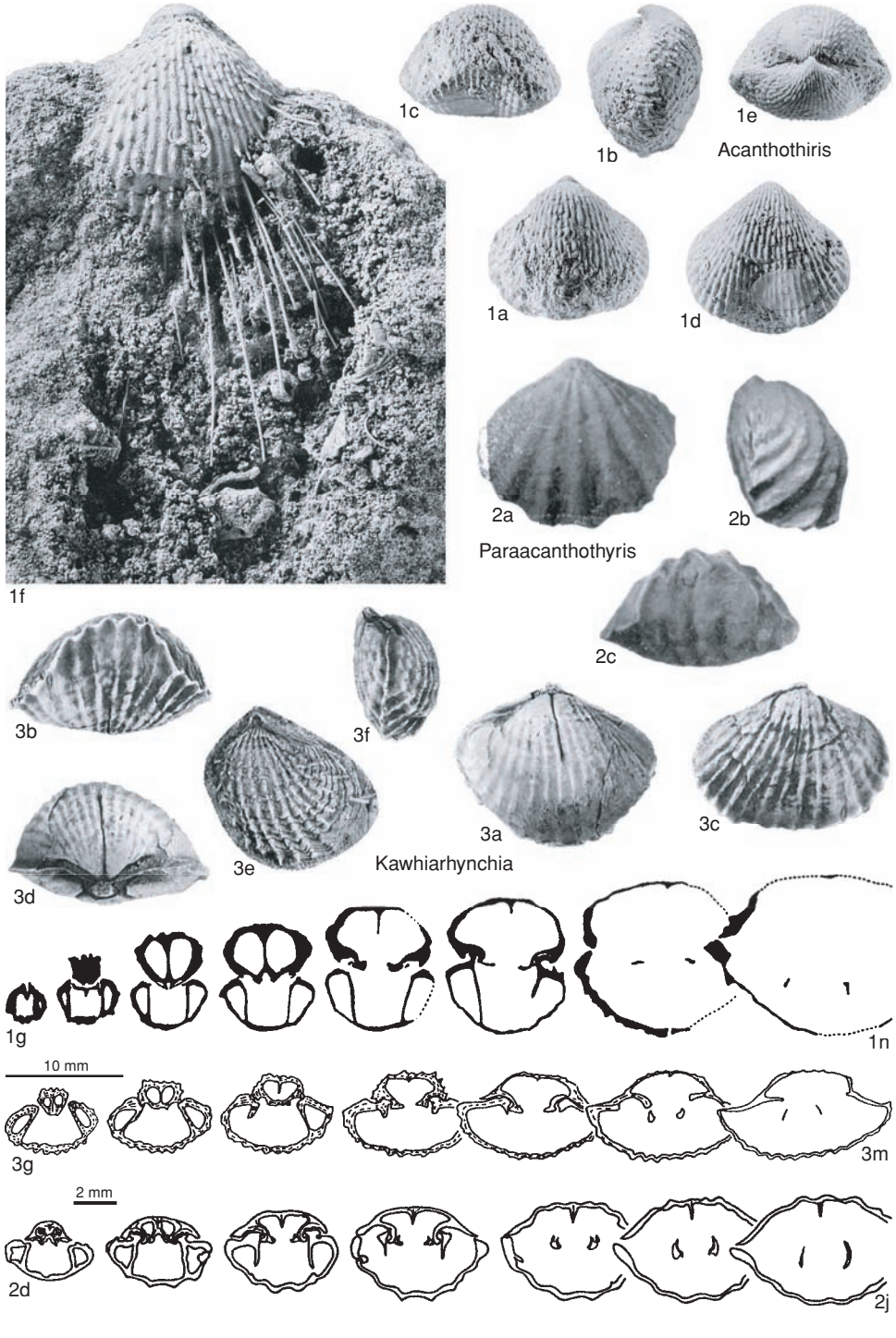

FIG. 887. Acanthothiriididae (p. 1305).

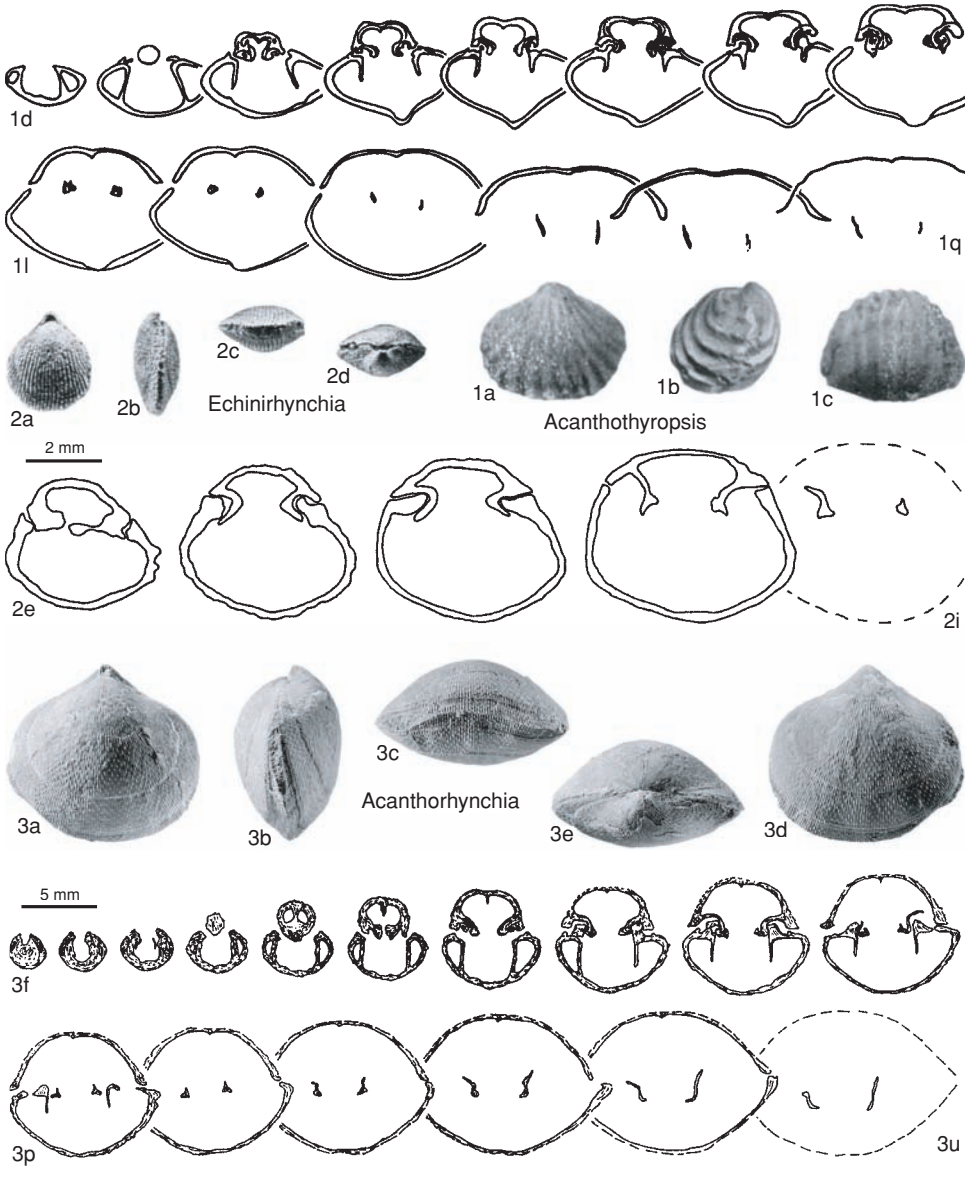

FIG. 888. Acanthothirididae (p. 1307–1308).

Subfamily ACANTHORHYNCHIINAE Shi & Grant, 1993

[Acanthorhynchiinae SHI & GRANT, 1993, p. 24]

Acanthothirididae with shell typically covered with numerous costellae and delicate, fine spines. Dental plates and hinge plates variable, often reduced or absent; septalium and dorsal median septum usually reduced or absent; crura calcariform to possibly subfalciform; cardinal process alleged to occur in some species. *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian)–Lower Cretaceous (lower Aptian).*

Acanthorhynchia BUCKMAN, 1918, p. 69 [**Acanthothyris panacanthina* BUCKMAN & WALKER, 1889, p. 53; OD] [=*Acanthorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971,

Opinion 957)]. Medium to large size, equibiconvex to dorsibiconvex; transversely oval; very slightly uniplicate, but no proper fold; thin test, very densely and finely costellate, often dichotomously, delicately spinose throughout; beak strong, sharp, suberect to incurved; disjunct deltidial plates. Dorsal median septum feeble, apically confined; crura calcariform or raduliform; cardinal process or small septalium sometimes present; dental plates weak, wide apart. *Middle Jurassic (upper Bajocian)–Lower Cretaceous (Berriasian):* western and eastern Europe, Africa, India.——Fig. 888,*3a–u. *A. panacanthina* (Buckman & Walker), upper Bajocian, Dorset, England; *a–e,* lectotype, dorsal, lateral, anterior, ventral, posterior views, BMNH B.12082, ×1 (new); *f–u,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.4, 1.0, 1.2, 1.4, 1.7, 1.9, 2.3, 2.6, 2.9, 3.2, 3.4, 3.6, 4.0, 4.3, 4.6, 5.0 (Childs, 1969).

?Acanthothyropsis Kamyshan, 1967b, p. 7 [**Rhynchonella crossi* Walker, 1869, p. 215; OD; virtual monotypy] [=*Acanthotnyropsis* Kamyshan in Kamyshan & Babanova, 1973, p. 64, obj.]. Small, equibiconvex to dorsibiconvex; uniplicate, dorsal fold gentle to well marked, bearing 2 to 8 costae; costae simple, effaced posteriorly to smooth stage and bearing few rows of weak, mostly peripheral, spines; beak suberect to incurved; deltidial plates disjunct. Sessile septalial plates parallel or dorsally divergent, separated from myophragm; hinge plates absent; crura thickly based and sharply bent (allegedly calcariform or spinuliform). *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Bajocian):* England, ?Switzerland, ?France, Caucasus, *?Pliensbachian, Aalenian–Bajocian;* ?Argentina, *?Pliensbachian.*——Fig. 888,*1a–q. *A. crossi* (Walker), Bajocian, northwestern Caucasus; *a–c,* dorsal, lateral, anterior views, ×1.5; *d–q,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.7, 0.8, 0.9, 0.95, 1.05, 1.15, 1.35, 1.45, 1.65, 1.75, 1.85, 1.95, 2.05 (Kamyshan & Babanova, 1973).

Echinirhynchia Childs, 1969, p. 73 [**Terebratulites senticosus* von Schlotheim, 1820 in 1820–1823, p. 268; OD] [=*Spinulirhynchia* Smirnova, 1972, p. 52, *nom. nud.*]. Similar to *Acanthorhynchia,* but smaller, equibiconvex to ventribiconvex; usually subtriangular, rectimarginate or sulcate. Dental plates and septalium absent. *Upper Jurassic (Oxfordian)–Lower Cretaceous (lower Aptian):* western and eastern Europe, Crimea, Caucasus, Antarctica.——Fig. 888,*2a–i. *E. senticosa* (von Schlotheim), Kimmeridgian, Franconia, near Erlangen, Germany; *a–d,* dorsal, lateral, anterior, posterior views, ×1; *e–i,* transverse serial sections, distances in mm from ventral umbo, 1.7, 2.0, 2.4, 2.8, 3.1 (Childs, 1969).

NORELLOIDEA

Miguel O. Manceñido,[1] Ellis F. Owen,[2] A. S. Dagys,[3] and Sun Dong-Li[4]

[[1]La Plata Natural Sciences Museum, Argentina; [2]formerly of The Natural History Museum; [3]deceased; and [4]Nanjing Institute of Geology and Palaeontology]

Superfamily NORELLOIDEA Ager, 1959

[*nom. transl.* Manceñido, Owen, Dagys, & Sun, herein, *ex* Norellinae Ager, 1959b, p. 330]

Rhynchonellida with shells smooth to capillate or gently fluted, ovoid to subtriangular, with generally sulcate dorsal valves, minute beak and foramen; squama and glotta absent. Crura arcuiform or a derivation thereof; dorsal median septum variable to absent. *Lower Triassic–Holocene.*

Family NORELLIDAE Ager, 1959

[*nom. transl.* Ager, Childs, & Pearson, 1972, p. 175, *ex* Norellinae Ager, 1959b, p. 330]

Small- to medium-sized Norelloidea, smooth or with plicae blunt, radial, commonly with sulcate dorsal valves (at least in juvenile, often also in adult stage), and often with ventral valves subcarinate. Dorsal median septum absent or present. *Lower Triassic–Upper Cretaceous (Turonian).*

Subfamily NORELLINAE Ager, 1959

[Norellinae Ager, 1959b, p. 330]

Small, mostly smooth Norellidae with small delthyria; dorsally sulcate to rectimarginate, or dorsal fold broad and flat, if present. Crura arcuiform where known; dorsal septum and septalium absent. *Middle Triassic (Anisian)–Middle Jurassic (Bathonian).*

Norella Bittner, 1890, p. 315 [**Rhynchonella refractifrons* Bittner, 1890, p. 39; SD ICZN, 1962, Opinion 633, p. 148]. Small, smooth, unequally biconvex, with dorsal valve flattened, anterior