ranean region.——FIG. 399*a,b.* **G. eomesozoica,* Dachstein Reef Limestone, Norian, Austria; *a,* oblique longitudinal section of both valves, ×15; *b,* transverse section of ventral valve and tubular attachment structure, ×15 (Senowbari-Daryan & Flügel, 1996).

Suborder STROPHALOSIIDINA Schuchert, 1913

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *ex* Strophalosiinae SCHUCHERT, 1913a, p. 391, *sensu* LAZAREV, 1989, *non* WATERHOUSE, 1978]

Productides with interareas in ventral valve only or both valves; commonly ventrally attached; profile includes conical shape; spines on ventral or both valves, rarely absent; toothed articulation retained or lost; cardinal process directed ventrally or posteroventrally, never dorsally.

This group of productides is tremendously varied in shape and habit, ranging from chonetid-like in profile to conical or flattened; attachment is by direct cementation of part of the ventral valve or by creeping, irregularly shaped spines. Carboniferous and Permian taxa tend to be adapted to live on hard substrates, commonly reef environments, and the various elaborations of trails appear to have been in response to these habitats. *Lower Devonian (Emsian)–Upper Permian (Changhsingian).*

Superfamily STROPHALOSIOIDEA Schuchert, 1913

[*nom. correct.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *pro* Strophalosiacea MUIR-WOOD & COOPER, 1960, p. 71, *nom. transl. ex* Strophalosiinae SCHUCHERT, 1913a, p. 391]

Cicatrix commonly developed; corpus cavity shallow; teeth retained; brachial ridges commonly extending to disk margins. *Lower Devonian (Emsian)–Upper Permian (Changhsingian).*

Family STROPHALOSIIDAE Schuchert, 1913

[*nom. transl.* STEHLI, 1954, p. 328, *ex* Strophalosiinae SCHUCHERT, 1913a, p. 391]

Outline rounded; strong rhizoid spines over ventral or both valves, may be bidirectional; planoconvex profile, but corpus cavity rather shallow; trails short. *Lower Carboniferous (Hastarian)–Upper Permian (Changhsingian).*

Subfamily STROPHALOSIINAE Schuchert, 1913

[Strophalosiinae SCHUCHERT, 1913a, p. 391] [=Heteralosiinae MUIR-WOOD & COOPER, 1960, p. 80; Truncateninae LIAO, 1982, p. 539; Licharewiellinae ARCHBOLD, 1986, p. 98]

Spines on ventral valve only; plano- to weakly concavoconvex profile. *Lower Carboniferous (Hastarian)–Upper Permian (Changhsingian).*

Strophalosia W. KING, 1844, p. 313 [**S. gerardi* W. KING, 1846, p. 92; SD MUIR-WOOD & COOPER, 1960, p. 74] [=*Leptaenalosia* W. KING, 1850, p. 93, *nom. nud.*]. Medium, slightly transverse subrounded outline with ill-defined small ears; hinge less than maximum width; ventral interarea wide but short; weak concavoconvex profile; concentric ornament weak ventrally, lamellose dorsally; weak capillation may be present on dorsal valve; spines cover ventral valve, suberect, semirecumbent; lateral ridges ventrally, separating ears; medium septum connected to cardinal process, interrupted at adductor scars, reaching two-thirds disk length. *Lower Permian (Sakmarian)–Upper Permian (Kazanian):* Himalayas, Australia ?Arctic Russia, China, Salt Range. ——FIG. 400,*1a–c.* **S. gerardi* W. KING, Ladakh, Himalayas; *a,b,* lectotype, viewed ventrally, dorsally, FC D 267, ×1.5; *c,* incomplete dorsal valve interior, ×1.5 (Brunton, 1966).——FIG. 400,*1d–f. S. irwinensis* COLEMAN, Callytharra Formation, Carnarvon basin, Australia; *d,* ventral valve exterior, ×1.2; *e,* ventral valve internal mold, ×1.6; *f,* dorsal valve interior, ×2 (Archbold, 1986).

Coronalosia WATERHOUSE & GUPTA, 1978, p. 415 [*C. blijniensis;* OD]. Similar to *Strophalosia,* but with fine ventral spines, other than at hinge line; relatively smooth dorsal valve exterior. Published figures inadequate for illustration. *Lower Permian (?Sakmarian):* India.

Craspedalosia MUIR-WOOD & COOPER, 1960, p. 82 [**Orthothrix lamellosa* GEINITZ, 1848, p. 86; OD]. Resembles *Dasyalosia* ventrally, but with dorsal valve strongly lamellose, lacking spines. *upper Lower Permian (Roadian):* Europe.——FIG. 401,*1a–d.* **C. lamellosa* (GEINITZ), lower Zechstein, Gera, Germany; *a–c,* shell viewed ventrally, dorsally, laterally, ×2; *d,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Etherilosia ARCHBOLD, 1993, p. 11 [**Strophalosia etheridgei* PRENDERGAST, 1943, p. 43; OD]. Small, subcircular with hinge less than maximum width; resembling *Heteralosia,* but differing in its relatively larger cicatrix, distinct rhizoid spines, in having only ventral uniform, suberect spines. *Lower Permian*

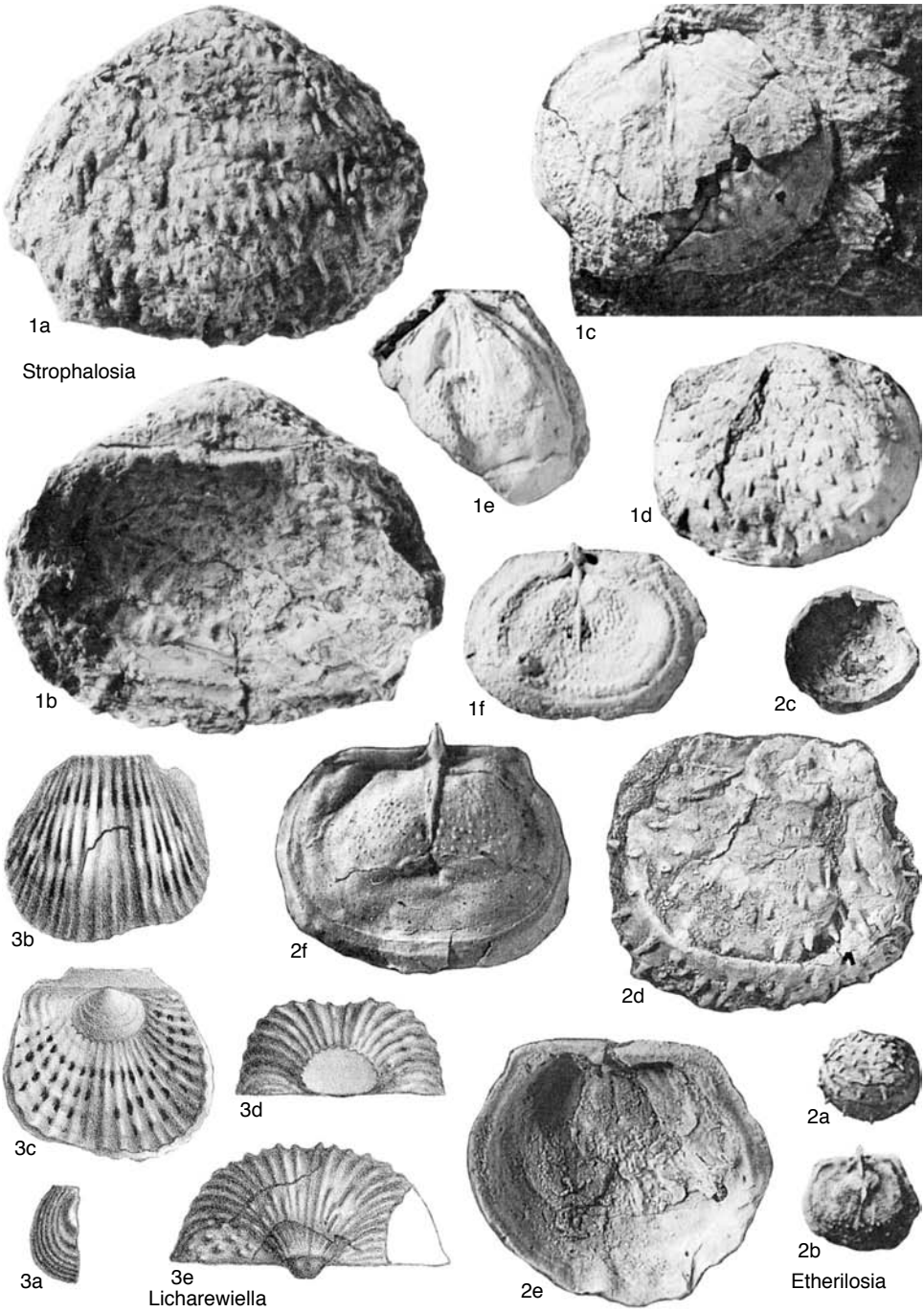

FIG. 400. Strophalosiidae (p. 565–569).

(upper Sakmarian–upper Artinskian): Western Australia.——FIG. 400,*2a–c. *E. etheridgei* (PRENDERGAST), Callytharra Formation; *a,* ventral valve exterior, Carnarvon basin, ×1.5; *b,* dorsal valve interior, Carnarvon basin, ×2; *c,* ventral valve interior, Irwin basin, ×1.5 (Coleman, 1957).——FIG.

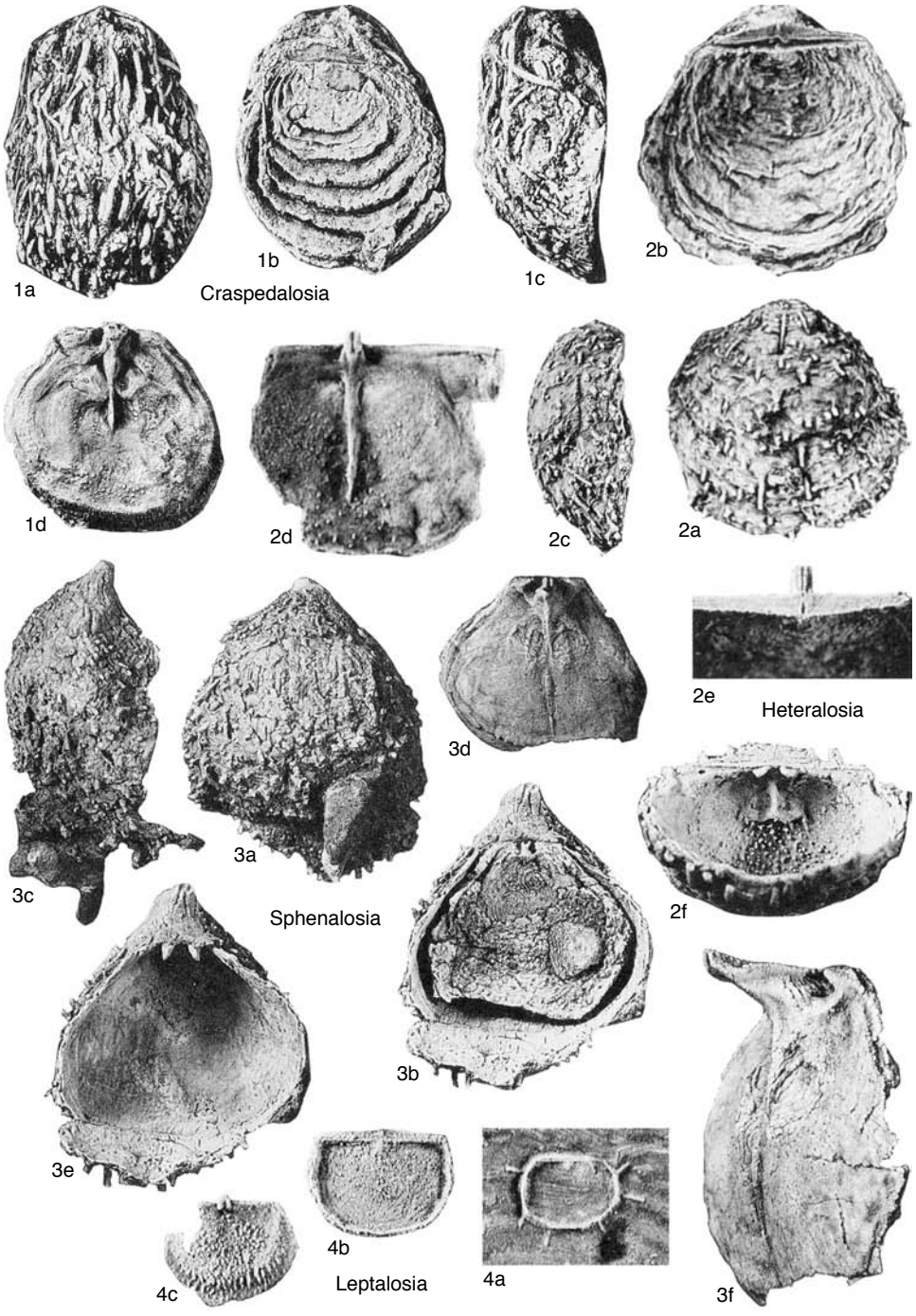

FIG. 401. Strophalosiidae (p. 565–569).

400,*2d–f. E. prendergastae* (COLEMAN), ?Cundlego Formation, Carnarvon basin; *d,* ventral valve exterior, ×3; *e,* ventral valve interior, ×3.2; *f,* dorsal valve interior, ×3.2 (Archbold, 1993).

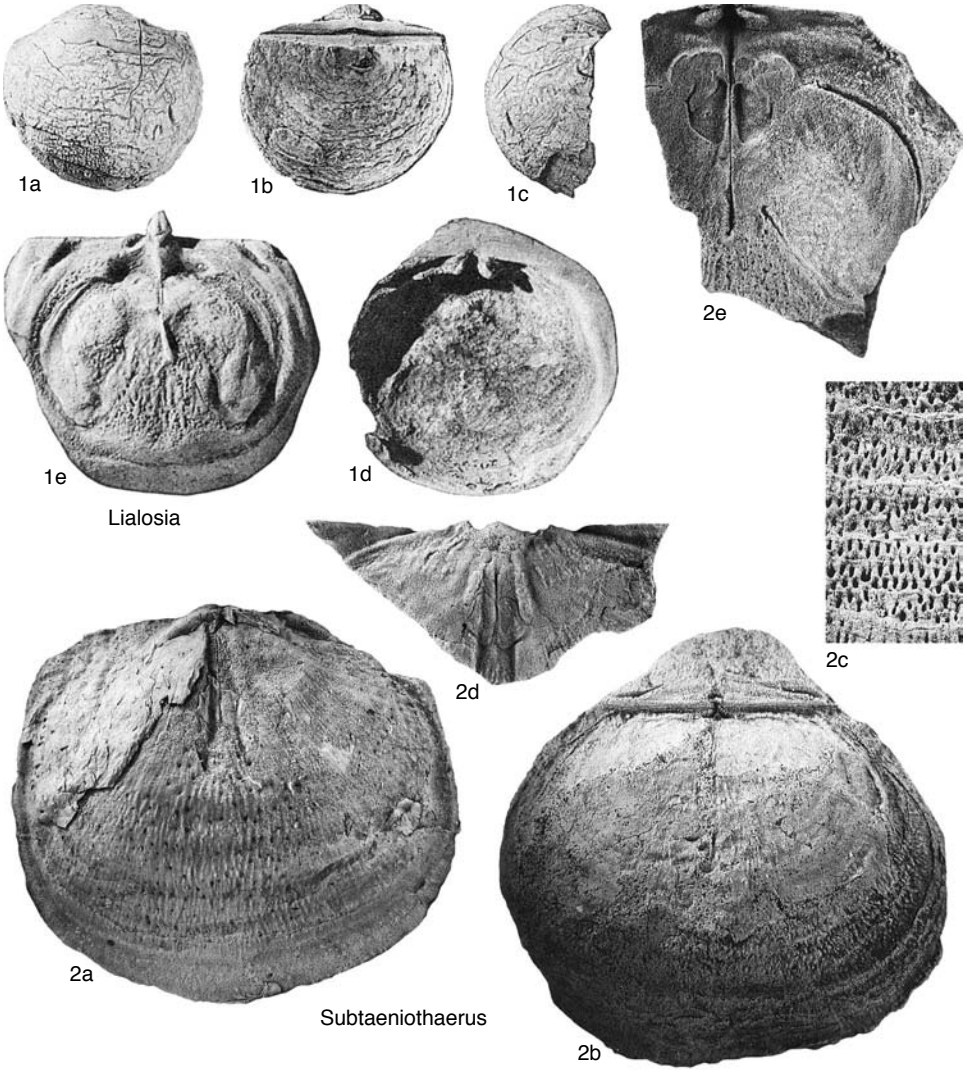

FIG. 402. Strophalosiidae (p. 569).

Heteralosia KING, 1938, p. 278 [**H. slocomi;* OD]. Small; subcircular, gently concavoconvex shells; cicatrix varied, spines bidirectional; both valves lamellose; socket ridges may extend to border adductor scars posteriorly, prominent median septum supports cardinal process. *Lower Carboniferous (Asbian)–lower Upper Permian:* North America, Europe.——FIG. 401,*2a–e*. **H. slocomi,* Gzhelian, Graham Formation, Texas; *a–c,* shell viewed ventrally, dorsally, laterally, ×2; *d,* incomplete dorsal valve interior, ×3; *e,* incomplete dorsal valve, posterior, ×4 (Muir-Wood & Cooper, 1960).——FIG. 401,*2f. H. hystricula* (GIRTY), Wordian, Texas; ventral valve interior showing teeth, muscle field, ×3 (Muir-Wood & Cooper, 1960).

Leptalosia DUNBAR & CONDRA, 1932, p. 260 [**Strophalosia scintilla* BEECHER, 1890b, p. 243; OD]. Minute, around 3 mm wide; interareas short; ventral valve almost fully cemented by cicatrix; few radiating spines from margins, smooth dorsal exterior; cardinal process bilobed anteroventrally, connecting with small socket ridges. [An unsatisfactory genus, possibly representing the young of other strophalosiids]. *Lower Carboniferous (Hastarian)–Upper Carboniferous:* North America, ?Russia.——FIG. 401,*4a–c*. **L. scintilla* (BEECHER), Hastarian, Louisiana Limestone, Missouri; *a,* dorsal view of attached shell, ×4; *b,* dorsal valve exterior, ×8; *c,* dorsal valve interior, ×8 (Muir-Wood & Cooper, 1960).

Lialosia Muir-Wood & Cooper, 1960, p. 86 [**Strophalosia kimberleyensis* Prendergast, 1943, p. 47; OD]. Medium, subcircular outline with hinge less than maximum width; interareas short on both valves, cicatrix present; disks gently concavoconvex with short trails; concentric lamellose ornament more prominent dorsally; capillae faint; spines only in rows at low angle to hinge; dorsal interior thickened around disk, with large brachial areas. *Lower Permian (Artinskian–Kungurian):* Western Australia.——Fig. 402,*1a–e. *L. kimberleyensis* (Prendergast), Wandagee Formation, Carnarvon basin; *a–c,* shell viewed ventrally, dorsally, laterally, ×1; *d,* ventral valve interior, ×1.5; *e,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Licharewiella Ustritsky in Ustritsky, Hu Bin, & Chan, 1960, p. 47, *non* Sokolskaya, 1960, p. 219 (Orthotetidina) [**Strophalosia costata* Waagen, 1884, p. 655; OD] [=*Magniderbyia* Ting, 1965, p. 265; =*Costalosia* Waterhouse & Shah, 1966, p. 230, obj.; *Truncatenia* Liao, 1982, p. 539[542] (type, *T. heshanensis*)]. Small, dorsal corpus transversely subquadrate; ventral profile variable, modified by cicatrix almost perpendicular to short interarea; median sulcus from disk to margin; ribs strong, extending onto trails; rhizoid spines surrounding cicatrix, other spines only ventrally; dorsal interior with prominent marginal ridge; adductor scars probably raised on platforms. *lower Lower Permian–lower Upper Permian:* Pakistan, China, Caucasus.——Fig. 400,*3a–e. *L. costata* (Waagen), lower *Productus* Limestone, Salt Range; *a,* partly exfoliated specimen viewed laterally, ×1; *b–d,* same specimen viewed ventrally, dorsally, posteriorly, ×2; *e,* incomplete specimen viewed posteriorly, ×2 (Waagen, 1884).

Liveringia Archbold, 1987, p. 30 [**L. magnifica;* OD]. Medium size, widest at midlength; interarea wide, short; capillae weak, but more conspicuous dorsally; spines in rows at hinge, ears, ventral spines few, short; dorsal surface with elongate dimples; marginal ridges in both valves, more prominent laterally; cardinal process short, thick, quadrifid; brachial ridges strong. *Upper Permian (upper Capitanian):* Western Australia.——Fig. 403,*1a–f. *L. magnifica,* Hardman Formation, Canning Basin; *a,* holotype, dorsal valve external mold, CPC 26450, ×1.2; *b,* detail of ornament, ×3.2; *c,* ventral valve exterior, ×3.2; *d,* ventral valve internal mold viewed posteriorly, ×1.6; *e,* replica of ventral valve interior, ×1; *f,* dorsal valve interior, ×1 (Archbold, 1987).

Megalosia Waterhouse, 1988, p. 41 [**M. chuluensis;* OD]. Similar to *Marginalosia,* but dorsal spines reportedly absent. *upper Upper Permian (Changhsingian):* Nepal.——Fig. 403,*2a–c. *M. chuluensis,* Nisal Formation, northcentral Nepal; *a,* holotype, viewed dorsally, UQF 76010, ×1; *b,* ventral valve exterior ×1; *c,* replica of dorsal valve interior, ×1 (Waterhouse, 1988).

Sphenalosia Muir-Wood & Cooper, 1960, p. 87 [**S. smedleyi;* OD]. Medium size, rounded trigonal outline without ears, narrow but high ventral interarea; weakly conavoconvex profile; ribbing, rugae absent; spines numerous ventrally, rhizoid posteriorly, semirecumbent elsewhere; teeth, sockets prominent; cardinal process narrow, long, extending ventrally below flat pseudodeltidium; median septum reaching across disk; marginal ridge weak. [This genus may prove to be more suitably assigned to the Gondolininae.] *Upper Permian (Kazanian):* central USA.——Fig. 401,*3a–f. *S. smedleyi,* Phosphoria Formation, Wyoming; *a–c,* holotype, viewed ventrally, dorsally, laterally, ×1; *d,e,* dorsal valve interior, ventral valve interior, USNM 119089, ×1; *f,* oblique view of dorsal valve interior, USNM 119089, ×2 (Muir-Wood & Cooper, 1960).

Subtaeniothaerus Solomina, 1988, p. 40[39] [**S. lungersgauzeni;* OD]. Large, subcircular outline, hinge less than maximum width; ventral interarea short; spine base tubercles small, densely distributed on ventral valve only; no dorsal spines or dimples reported; marginal ridge in ventral valve; dorsal adductor scars with wide posterior, narrow anterior components. *lower Upper Permian:* northern Siberia.——Fig. 402,*2a–e. *S. lungersgauzeni,* Dulgalakh horizon, Verkhoyan; *a,* holotype, incomplete dorsal valve interior, PIN 4218/100, ×1; *b,* dorsal valve external mold, ventral interarea, ×1; *c,* part of ventral valve external mold, ×2; *d,* incomplete ventral valve internal mold, ×1; *e,* incomplete dorsal valve internal mold, ×1 (Solomina, 1988).

Subfamily DASYALOSIINAE Brunton, 1966

[Dasyalosiinae Brunton, 1966, p. 192]

Spines on both valves; dorsal valve commonly flat. *Lower Carboniferous (upper Viséan)–Upper Permian (Capitanian).*

Dasyalosia Muir-Wood & Cooper, 1960, p. 76 [**Spondylus goldfussi* von Münster, 1839, p. 44; OD]. Small to medium size, subcircular outline with variable narrow hinge line; interarea short, pseudodeltidium flat to convex; cicatrix small or absent; spines densely cover both valves, erect, recumbent; teeth prominent, ventral ear baffles; dorsal ear baffles, marginal ridge weak. *upper Lower Carboniferous–lower Upper Permian:* western Europe.——Fig. 404,*1a–c. *D. goldfussi* (von Münster), lower Upper Permian, Zechstein, Gera, Germany; *a,b,* shell viewed ventrally, dorsally, ×1; *c,* ventral valve viewed posteriorly showing interarea, teeth, ×3 (Muir-Wood & Cooper, 1960).——Fig. 404,*1d,e. D. lamnula* Brunton, Asbian, Fermanagh; incomplete dorsal valve exterior, interior, ×5 (Brunton, 1966).

Acanthalosia Waterhouse in Waterhouse & Briggs, 1986, p. 31 [**A. domina;* OD]. Size medium; gently concavoconvex with prominent ventral umbo; interareas, dorsal lophidium; ventral spines bidirectional, thicker than dorsal spines; no ribbing or lamellae; cardinal process large, supported by socket ridges. *Lower Permian (upper Artinskian):* eastern Australia.——Fig. 405,*1a–d. *A. domina,* upper Lower Permian, Dresden Limestone, Bowen basin; *a,* holotype, viewed dorsally, UQF 73978, ×1; *b,* ventral valve external mold, ×1; *c,* dorsal valve

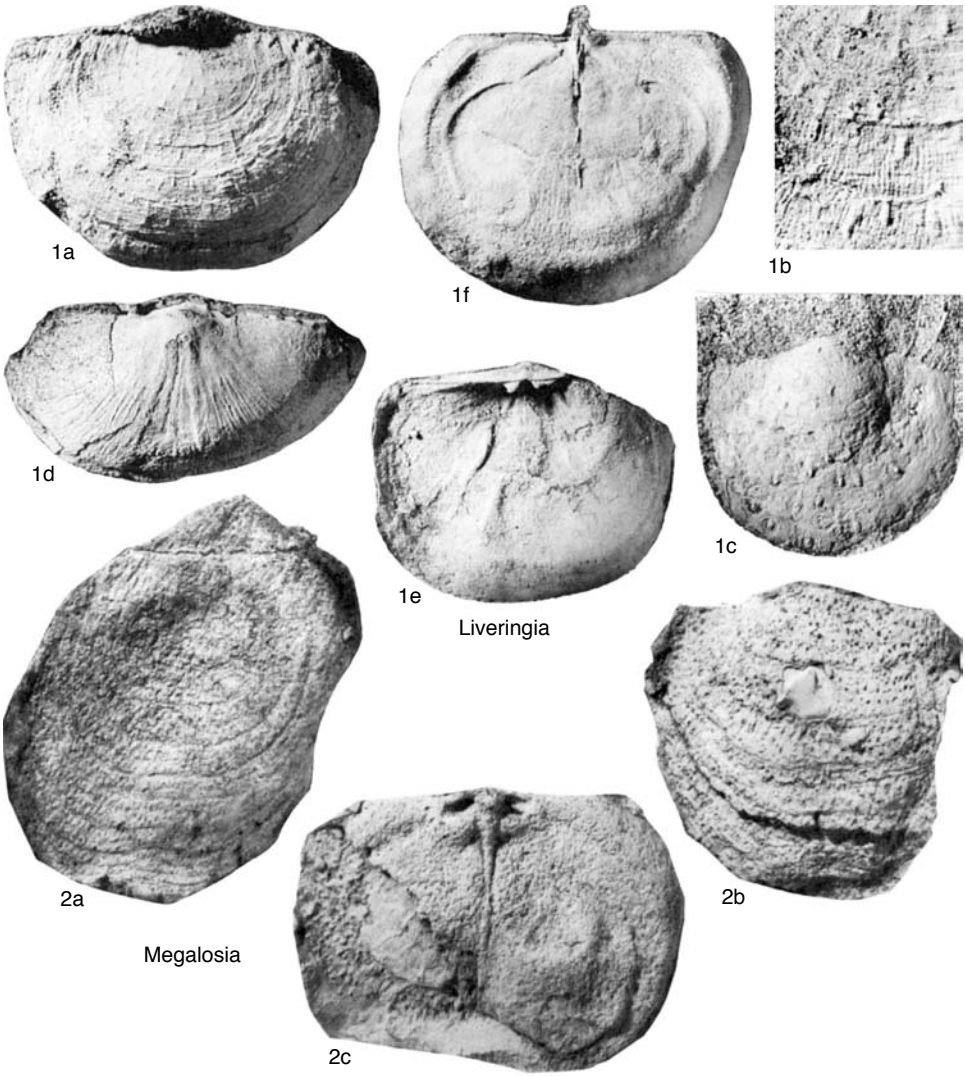

FIG. 403. Strophalosiidae (p. 569).

exterior, ×1; *d,* dorsal valve interior, ×1 (Waterhouse, 1986).

Arcticalosia WATERHOUSE, 1986, p. 2 [**Wyndhamia unispinosa* WATERHOUSE, 1969, p. 34; OD]. Similar to *Marginalosia,* but possibly differing in having more strongly concentrically ornamented dorsal exterior. *upper Lower Permian (lower Wordian)–Upper Permian (Capitanian):* Arctic Canada.——FIG. 404,*3a–c.* **A. unispinosa* (WATERHOUSE), Capitanian, Melville Island; *a,* holotype, ventral valve exterior, GSC 23818, ×1; *b,* dorsal valve exterior, ×1; *c,* dorsal valve interior with broken cardinal process, ×1 (Waterhouse, 1969).

?Costalosiella WATERHOUSE, 1983b, p. 119 [**Costalosia argentea* WATERHOUSE & SHAH, 1966, p. 233; OD]. Poorly known and some key characteristics not recorded; ventral valve inflated with elongate spine bases becoming ribs toward anterior margins; spines on both valves; dorsal disk weakly reticulate. No illustrations suitable for publication. *Lower Permian (?Kungurian), Upper Permian (Kazanian):* Iran (Malukabad).

Crossalosia MUIR-WOOD & COOPER, 1960, p. 75 [**Productus buchianus* DE KONINCK, 1847b, p. 129; OD]. Small, around 9 mm wide; subcircular; high ventral interarea, cicatrix unknown; both valves

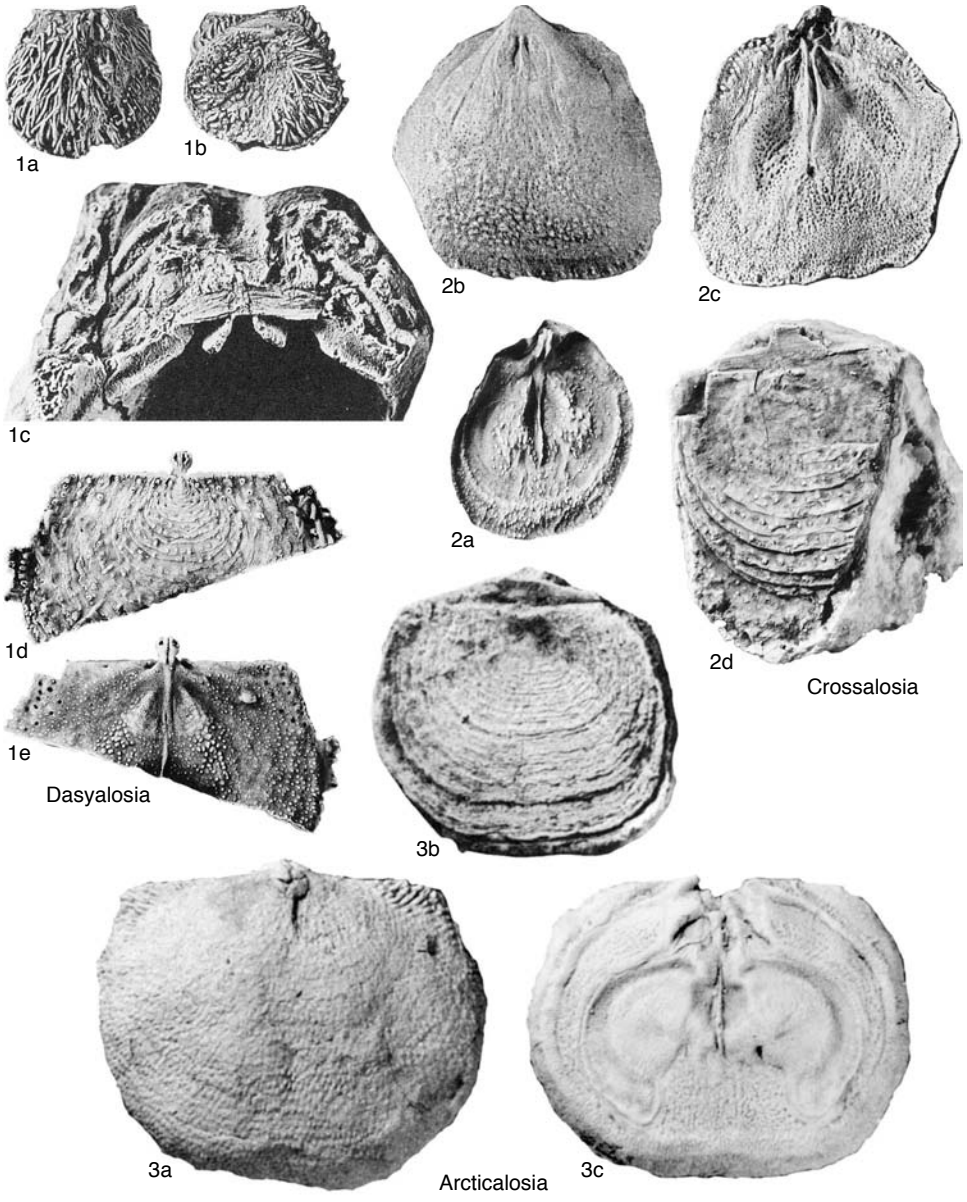

FIG. 404. Strophalosiidae (p. 569–571).

lamellose, with suberect spines; cardinal process narrow, projecting into ventral umbo, median septum over half disk length. *Lower Carboniferous (upper Viséan):* Europe.——FIG. 404,*2a–d. *C. buchiana* (DE KONINCK), Asbian; *a,* lectotype, replica of dorsal valve interior, Visé, BMNH BD 197, ×3 (new); *b,c,* internal mold of shell viewed ventrally, dorsally, Visé, ×2 (Muir-Wood & Cooper, 1960); *d,* incomplete dorsal valve exterior, ventral interarea, North Yorkshire, ×4 (Brunton & Mundy, 1988b).

Echinalosia WATERHOUSE, 1967, p. 167, *nom. nov. pro Multispinula* WATERHOUSE, 1966, p. 11, *non* ROWELL, 1962, p. 147 [**Strophalosia maxwelli* WATERHOUSE, 1964, p. 32; OD]. Similar to *Wyndhamia,* but somewhat smaller, with relatively less wide hinge line, giving more circular outline. *upper Lower Permian–lower Upper Permian:* eastern

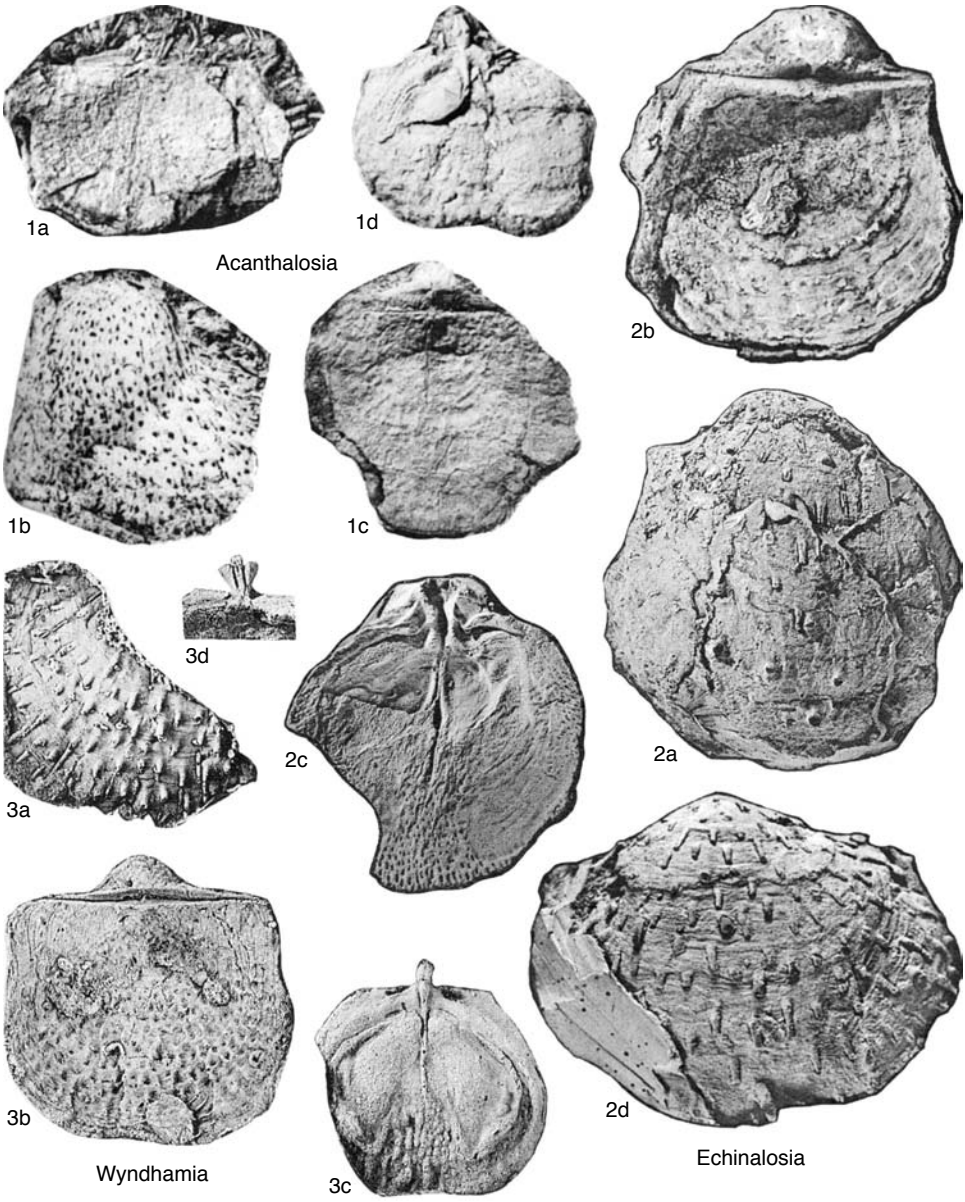

FIG. 405. Strophalosiidae (p. 569–574).

Australia, southern New Zealand, Nepal, Pakistan.——FIG. 405,*2a–d. *E. maxwelli* (WATERHOUSE), *Productus* Creek Group, Southland, New Zealand; *a–c,* holotype, ventral, dorsal exteriors, dorsal valve internal mold, NZGS BR253, ×2; *d,* ventral valve exterior, ×2 (Waterhouse, 1964).

Hontorialosia MARTÍNEZ CHACÓN, 1979, p. 119 [**H. uniplicata;* OD]. Small, up to 10 mm wide; narrow ventral interarea; outline anteriorly emarginate, with ventral sulcus, dorsal fold; rugae weak posteriorly, somewhat lamellose anteriorly; spines relatively fine, bidirectional ventrally. *Upper Carboniferous (upper Moscovian):* southwestern Europe.——FIG. 406,*2a–d. *H. uniplicata,* upper Moscovian, Bolsovian, northern Spain; *a,* holotype, dorsal valve exterior, DPO 8763, ×3.5; *b,* ventral valve viewed ventrally,

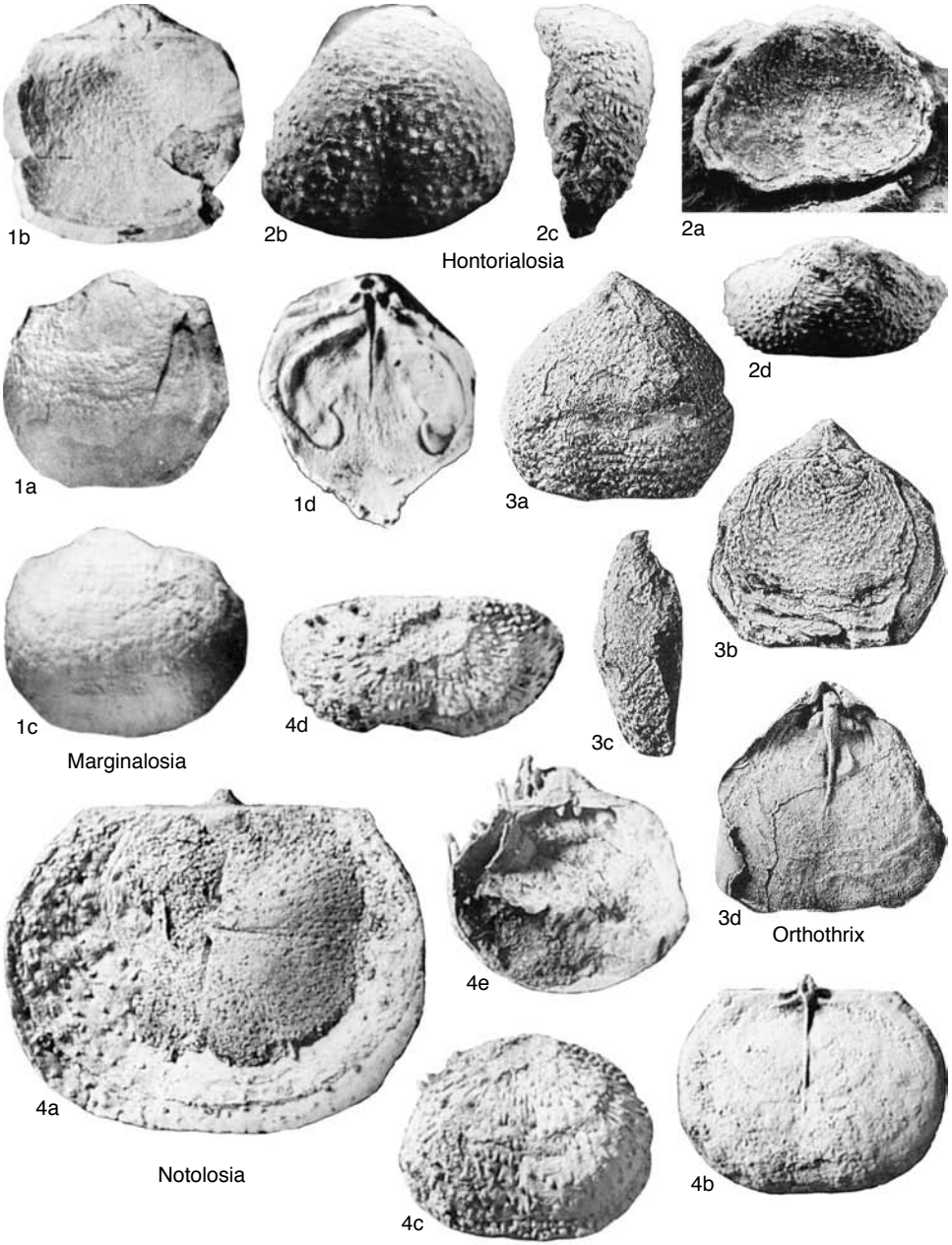

FIG. 406. Strophalosiidae (p. 572–574).

×3.5; *c,d,* ventral valve viewed laterally, posteriorly, ×3 (Martínez Chacón, 1979).

Marginalosia WATERHOUSE, 1978, p. 64 [**?Echinalosia kalikotei* WATERHOUSE, 1975, p. 4; OD]. Resembles *Wyndhamia* internally, but externally differs in having fine densely spaced spines on both valves. *Upper Permian (Capitanian):* northwestern Nepal, ?Russian Arctic, New Zealand.——FIG. 406,*1a–d. *M. kalikotei* (WATERHOUSE), Chhidruan, northwestern Nepal; *a,b,* holotype, viewed ventrally, dorsally,

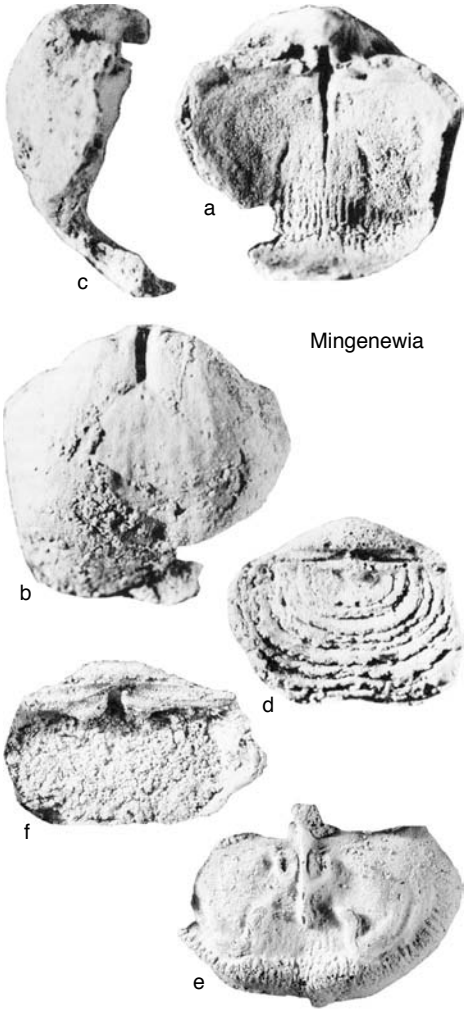

FIG. 407. Strophalosiidae (p. 574).

UQF 68854, ×1 (Waterhouse, 1978); *c,* ventral valve exterior, ×1; *d,* dorsal valve internal mold, ×1 (Waterhouse, 1975).

Notolosia ARCHBOLD, 1986, p. 114 [**Echinalosia (Notolosia) dickinsi;* OD]. Smaller, more rounded outline than *Echinalosia;* cicatrix larger, ventral recumbent spines more closely spaced. *Upper Permian (Capitanian):* Western Australia.——FIG. 406,*4a–e. *N. dickinsi* (ARCHBOLD), Hardman Formation, Canning Basin; *a,b,* holotype, CPC 24451, dorsal valve viewed externally, ×3, internally, ×2; *c,* shell viewed ventrally, ×1.8; *d,* shell viewed posteriorly, ×2; *e,* ventral valve viewed internally, ×2 (Archbold, 1986).

Orthothrix GEINITZ, 1847, p. 84 [**Orthis excavata* GEINITZ, 1842, p. 578; SD DALL, 1877, p. 53]. Small, rounded subtrigonal, maximum width anteriorly, hinge narrow; interarea trigonal, short dorsally; dorsal valve gently convex with relatively deep corpus; dorsal valve lamellose anteriorly; spines fine, recumbent on both valves; cardinal process connected to prominent median septum posteriorly; adductor scars, brachial ridges well developed. *upper Lower Permian (Roadian)–Upper Permian (Kazanian):* Europe.——FIG. 406,*3a–d. *O. excavata* (GEINITZ), mid-Zechstein, Thuringia; *a–c,* partly exfoliated specimen viewed ventrally, dorsally, laterally, ×2; *d,* replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Wyndhamia BOOKER, 1929, p. 24 [**Strophalosia (W.) dalwoodensis;* OD] [=*Branxtonia* BOOKER, 1929, p. 30 (type, *B. typica*); *Pseudostrophalosia* CLARKE, 1970, p. 987 (type, *S. brittoni* MAXWELL, 1954b, *partim*)]. Medium size, dorsal valve outline subquadrate, interareas short; concentric ornament rugose at ears, otherwise weak or rare lamellae; spines semierect but finer spines prostrate from short ridges, fine only on dorsal valve; cardinal process prominent, trifid; socket ridges short, extending as low marginal ridge; dorsal disk with thickened shell anteriorly. *lower Lower Permian–lower Upper Permian:* Australia, New Zealand; Siberia, Arctic Canada, *lower Upper Permian.*——FIG. 405,*3a–c. *W. dalwoodensis* (BOOKER), ?Artinskian, Hobart, Tasmania; *a,* replica of part of ventral valve exterior, ×2; *b,* shell viewed dorsally, ×1; *c,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).——FIG. 405,*3d. W. jukesi* (ETHERIDGE); detail of cardinal process viewed posteriorly, ×1 (Muir-Wood & Cooper, 1960).

Subfamily MINGENEWIINAE Archbold, 1980

[Mingenewiinae ARCHBOLD, 1980a, p. 253]

Spines absent; no cicatrix, dorsal valve lamellose. *Lower Permian (Artinskian).*

Mingenewia ARCHBOLD, 1980a, p. 255 [**M. anomala;* OD]. Small transverse shell; planoconvex, deep corpus with short trails; ventral interarea short, wide; ventral exterior smooth, dorsal exterior almost totally covered by prominent lamellae; brachial ridges prominent anteriorly, close to anterior end of median septum. *Lower Permian (middle Artinskian):* Western Australia.——FIG. 407*a–f. *M. anomala,* Mingenew Formation, Perth Basin; *a–c,* holotype, viewed dorsally, ventrally, laterally, CPC 19145, ×4; *d,* dorsal valve exterior, ×4 (Archbold, 1980b); *e,* replica of dorsal valve interior, ×4.5; *f,* replica of ventral valve posterodorsally, ×5 (new).

Family CHONOPECTIDAE Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *ex* Chonopectinae MUIR-WOOD & COOPER, 1960, p. 157]

Concavoconvex profile, shallow corpus cavity; cicatrix varied; trails short; fine radial

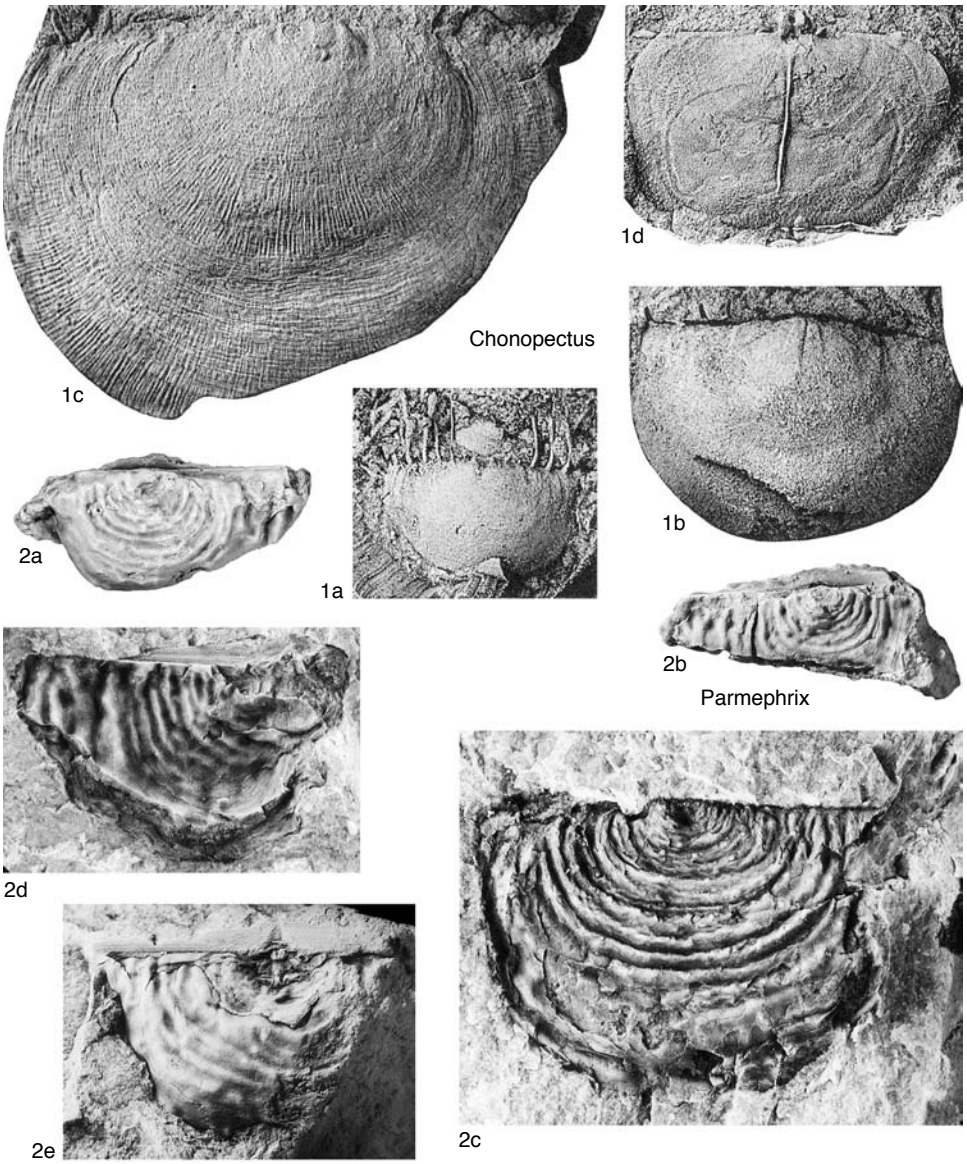

FIG. 408. Chonopectidae (p. 575–576).

ornament, rugae variable; hinge spines plus sparse, fine ventral corpus spines. *Upper Devonian–Lower Carboniferous (Brigantian).*

Chonopectus HALL & CLARKE, 1892, p. 312 [**Chonetes fischeri* NORWOOD & PRATTEN, 1855b, p. 25; OD]. Chonetoid in appearance with hinge spines, short ventral median ridge, but commonly with small cicatrix, additional rare ventral spines; capillae variable, rugae weak, irregular posterolaterally; cardinal process with small flanking sockets, anteromedian pit; long, low median septum. *Upper Devonian–Lower Carboniferous (Hastarian):* North America, western Europe.——FIG. 408,*1a–c.* **C. fischeri* (NORWOOD & PRATTEN), lower Kinderhookian, Iowa; *a,* external replica of ventral valve, ×1; *b,* internal mold of ventral valve, ×2; *c,* ventral valve exterior, ×4 (Muir-Wood & Cooper, 1960).——FIG. 408,*1d. Chonopectus* sp., Upper Devonian, New York; dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Dengalosia MANANKOV & PAVLOVA, 1981, p. 137 [**D. gobica;* OD]. Ventral umbo extending posteriorly of hinge, with prominent interarea; rugae irregular, discontinuous capillae; ventral spines at low angle from hinge, suberect elsewhere; dorsal spines rare, anteriorly; cardinal process narrow, elongate quadrifid, occupying deltidium. *Lower Carboniferous (Viséan):* northern Asia.——FIG. 409,*1a–f.* **D. gobica,* upper Viséan, southern Mongolia; *a,b,* internal mold viewed ventrally, dorsally, ×1.5; *c,* posterior view of shell showing interareas, ×1.5; *d,* detail of ventral exterior with fine capillae, ×3 (new); *e,* exfoliated dorsal valve, ×1; *f,* part of dorsal valve interior, ×3 (Manankov & Pavlova, 1981).

Parmephrix BRUNTON & MUNDY in BRUNTON, RACHEBOEUF, & MUNDY, 1994, p. 58 [**P. eileeni* BRUNTON & MUNDY in BRUNTON, RACHEBOEUF, & MUNDY, 1994, p. 58; OD, *P. eileenarum* BRUNTON, LAZAREV, & GRANT, herein; =*Palmerhytis stebdenensis* BRUNTON & MUNDY, 1986, p. 6, *partim*)]. Resembles *Semenewia,* but flattened irregular disks; small cicatrix, rugae irregular, covering corpus, ventrally bearing scattered spines, no radial ornament; teeth small. *Lower Carboniferous (upper Viséan):* western Europe.——FIG. 408,*2a–e.* **P. eileenarum* BRUNTON, LAZAREV, & GRANT, Asbian, North Yorkshire; *a,b,* ventral, dorsal views of incomplete specimen, ×2; *c,* holotype, partly exfoliated ventral valve exterior showing small cicatrix, BMNH BD 2496, ×2; *d,* incomplete dorsal valve exterior, ×2; *e,* incomplete dorsal valve interior, external mold of ventral interarea, ×2 (Brunton, Racheboeuf, & Mundy, 1994).

Semenewia PAECKELMANN, 1930, p. 217 [**Chonetes concentrica* DE KONINCK, 1847b, p. 186; OD] [=*Palmerhytis* BRUNTON & MUNDY, 1986, p. 6, *partim*]. Cicatrix variable; rugae regular, strongly developed, covering both valves; spines at hinge, smaller on rugae; fine capillae; cardinal process supported by inner socket ridges, short median septum. *Lower Carboniferous (Asbian–Brigantian):* western Europe.——FIG. 409,*2a–e.* **S. concentrica* (DE KONINCK), Asbian–Brigantian, Visé; *a,* lectotype, replica of dorsal valve exterior, ventral interarea, ESNM 20034, ×2; *b,* slightly distorted dorsal valve exterior, ventral hinge spines, ×2; *c,* young ventral valve exterior, ×2; *d,* replica of two ventral valve interiors with hinge spines from lower attached to upper, ×2; *e,* replica of dorsal valve interior, articulated posterior region of ventral valve; note dorsal valve dimples posteriorly indicating ventral spines and fine external capillae, ×3 (Brunton, Racheboeuf, & Mundy, 1994).

Family ARAKSALOSIIDAE Lazarev, 1989

[Araksalosiidae LAZAREV, 1989, p. 34]

Interareas short; concavoconvex, shallow corpus cavity; radial ornamentation commonly absent; cardinal process with pit; cardinal, marginal ridges commonly absent. *Lower Devonian (Emsian)–Lower Carboniferous (Tournaisian), ?Upper Carboniferous (Gzhelian).*

Subfamily ARAKSALOSIINAE Lazarev, 1989

[Araksalosiinae LAZAREV, 1989, p. 35]

Pseudodeltidium, chilidium present; cicatrix reduced; mat of spines on ventral or both valves, commonly with stout rows at ventral hinge; elongate spine bases may form incipient ribs anteriorly; marginal structures absent. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian).*

Araksalosia LAZAREV, 1989, p. 36[32] [**Waagenoconcha maxima* ABRAMJAN, 1957, p. 33; OD]. Resembling *Hamlingella,* about 50 mm wide, but with no dorsal valve spines; spines finer than *Acanthatia. Upper Devonian (upper Famennian):* Transcaucasia, Mongolia.——FIG. 410,*1a–d.* **A. maxima* (ABRAMJAN), uppermost Famennian, Transcaucasia; *a,* deeply exfoliated ventral valve exposing internal mold posteromedianly, ×1 (Lazarev, 1989); *b,* partly exfoliated ventral exterior showing spine bases, ×2 (new); *c,* dorsal valve interior, ×1; *d,* detail of cardinalia, teeth, sockets, ×2 (Lazarev, 1989).

Acanthatia MUIR-WOOD & COOPER, 1960, p. 158 [**Heteralosia nupera* STAINBROOK, 1947, p. 309; OD]. Outline subcircular, cicatrix small; interareas, but reduced in dorsal valve, narrow arched pseudodeltidium; ventral spines strong at hinge, fine prostrate elsewhere, rare dorsally; cardinal process externally quadrifid, supported anteriorly by pair of short weak ridges. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* North America, western Europe, ?northern Africa, ?Asia.——FIG. 411,*1a–e.* **A. nupera* (STAINBROOK), uppermost Famennian, New Mexico, Percha Shale; *a,* ventral valve exterior, ×1.5; *b,* shell viewed laterally, ×1; *c,* shell viewed dorsally, ×1; *d,* shell viewed posteriorly, ×2; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Hamlingella REED, 1943, p. 78 [**Productella goergesi* PAECKELMANN, 1931, p. 56; OD]. Resembling *Whidbornella,* but outline transversely subrounded, hinge line less than maximum width; ventral hinge spines curved with fine recumbent hairlike spines from delicate swollen bases covering valve, more erect spines dorsally; never ribbed; widely divergent ridges support cardinal process, border dorsal adductor scars posterolaterally. *Upper Devonian (upper Famennian):* Germany, England, ?Asia.——FIG. 410,*2a,b.* **H. goergesi* (PAECKELMANN), Famennian, Etroeungt, Rhine; *a,* partly exfoliated ventral valve,

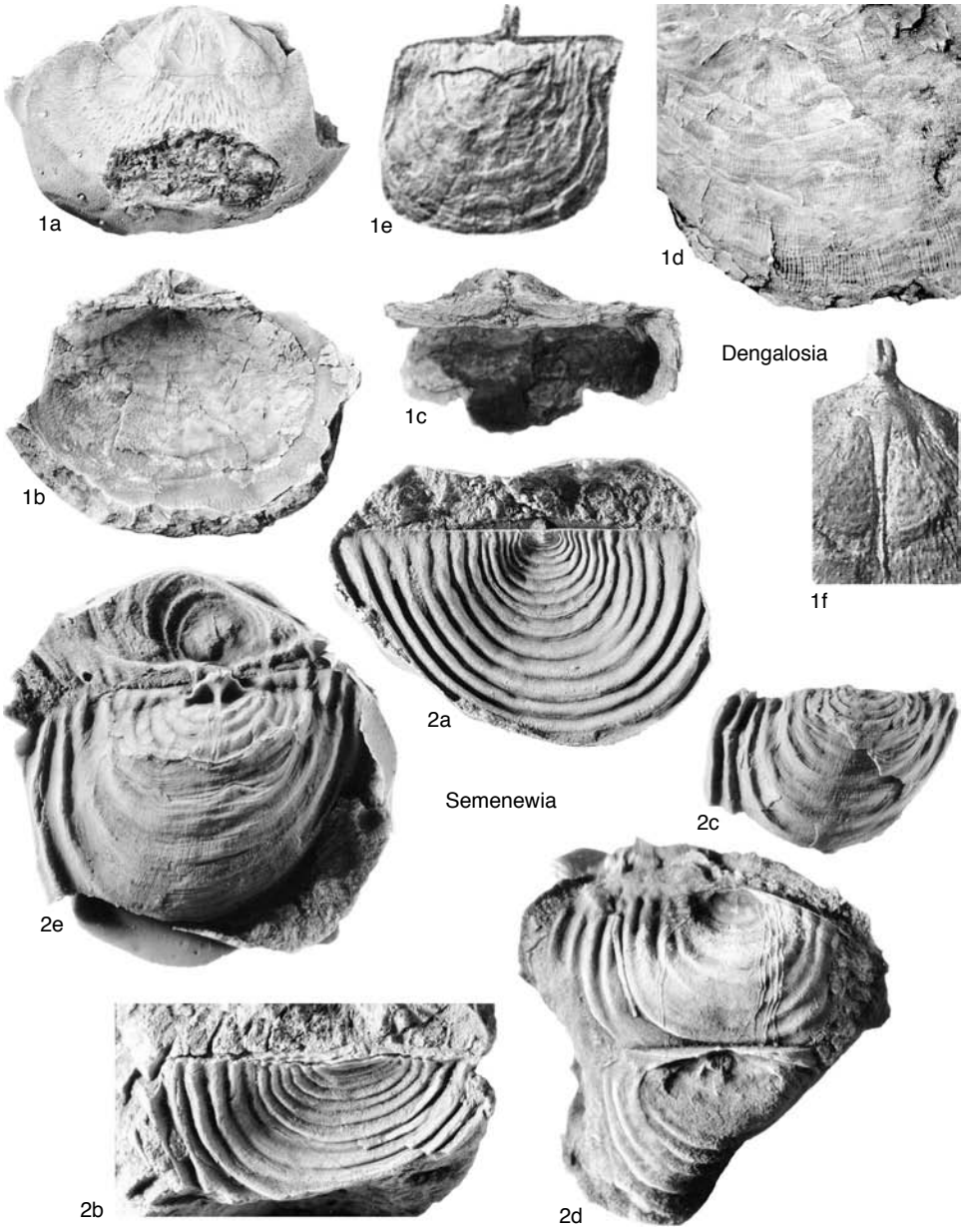

FIG. 409. Chonopectidae (p. 576).

×1; *b,* dorsal valve interior, ×1 (Paeckelmann, 1931).——FIG. 410,*2c,d. H. piltonensis* (REED), Pilton Beds, Devon; *c,* holotype, ventral valve internal mold, SM H 276, ×1; *d,* latex replica, ×1.5 (new).

Kahlella LEGRAND-BLAIN, 1995, p. 430 [**K. meyendorffi;* OD]. Resembles *Whidbornella* with strong row of hinge spines, but with no anterior ribbing or sign of dorsal spines; fine impersistent rugae posterolaterally; cardinalia weak, with pit, not

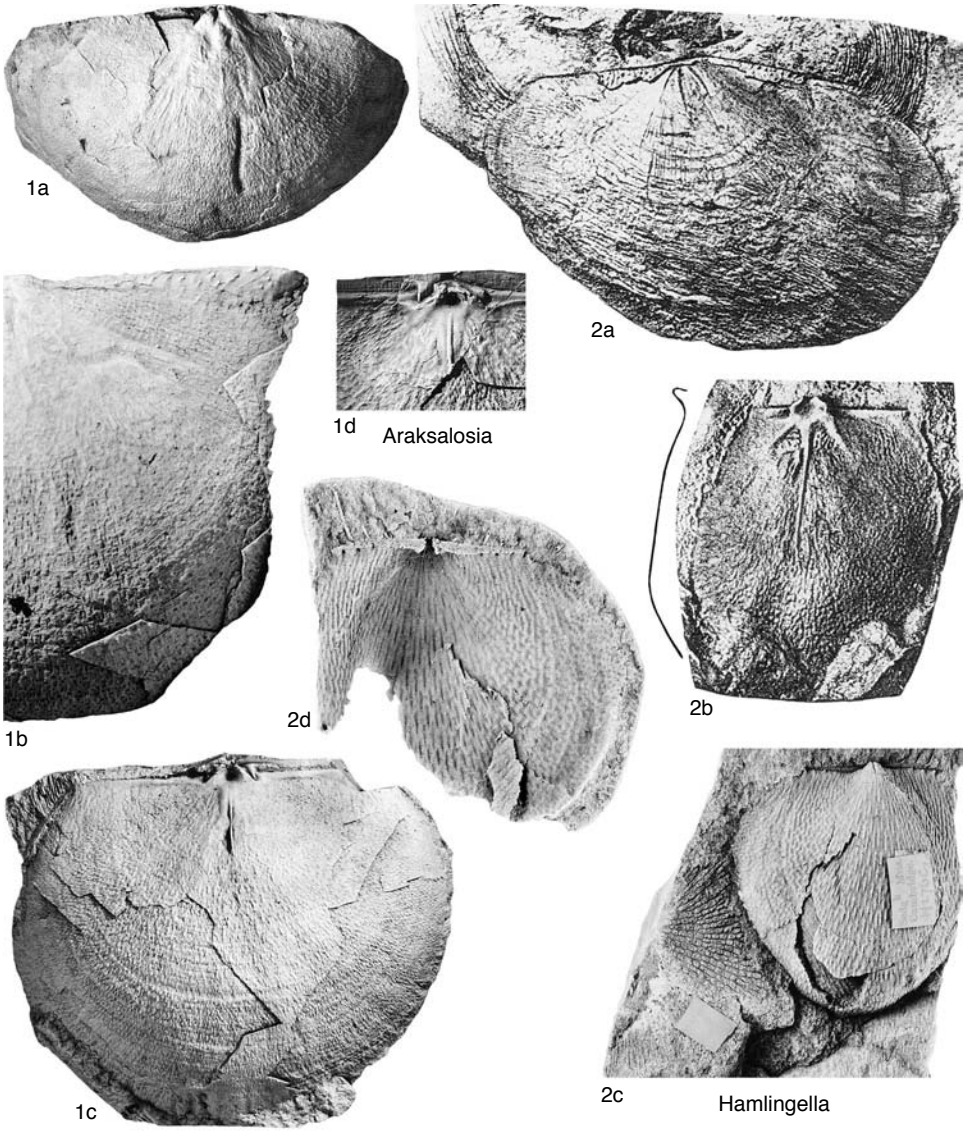

FIG. 410. Araksalosiidae (p. 576–577).

connected to short medium septum. *Upper Devonian (upper Famennian):* Algeria.——FIG. 411,*2a–d. *K. meyendorffi,* upper Famennian, Famennian V–VI, Saharan Algeria; *a,* holotype, dorsal view of shell showing ventral hinge spines, SSL 413602a, ×1.3; *b,* incomplete ventral valve exterior, ×1; *c,* dorsal valve interior, ×1.3; *d,* deeply exfoliated dorsal valve exterior, ×1.3 (Legrand-Blain, 1995).

Ruthiphiala CARTER, 1988, p. 30 [**Pustula bushbergensis* BRANSON, 1938, p. 164; OD]. Medium sized; semicircular in outline, ventral valve with hinge spines plus finer prostrate spines from elongate swollen bases producing riblike ornament; inner socket ridges short, median septum extending anteriorly from shallow cardinal process pit. *Lower Carboniferous (Hastarian):* central North America.——FIG. 412,*2a–e. *R. bushbergensis* (BRANSON), lower Kinderhookian, Missouri; *a,* lectotype, viewed posteriorly, UMC 4253, ×2; *b,c,* lectotype, viewed laterally, ventrally, ×1; *d,* dorsal valve interior, ×1; *e,* posteromedian area of dorsal valve interior with external mold of ventral interarea (*arrow*), ×2 (Carter, 1988).

Whidbornella REED, 1943, p. 71 [**Leptaena caperata* J. DE C. SOWERBY, 1840, pl. 53, fig. 4; OD]. Outline subcircular to elongate, wide hinge line; rugae ir-

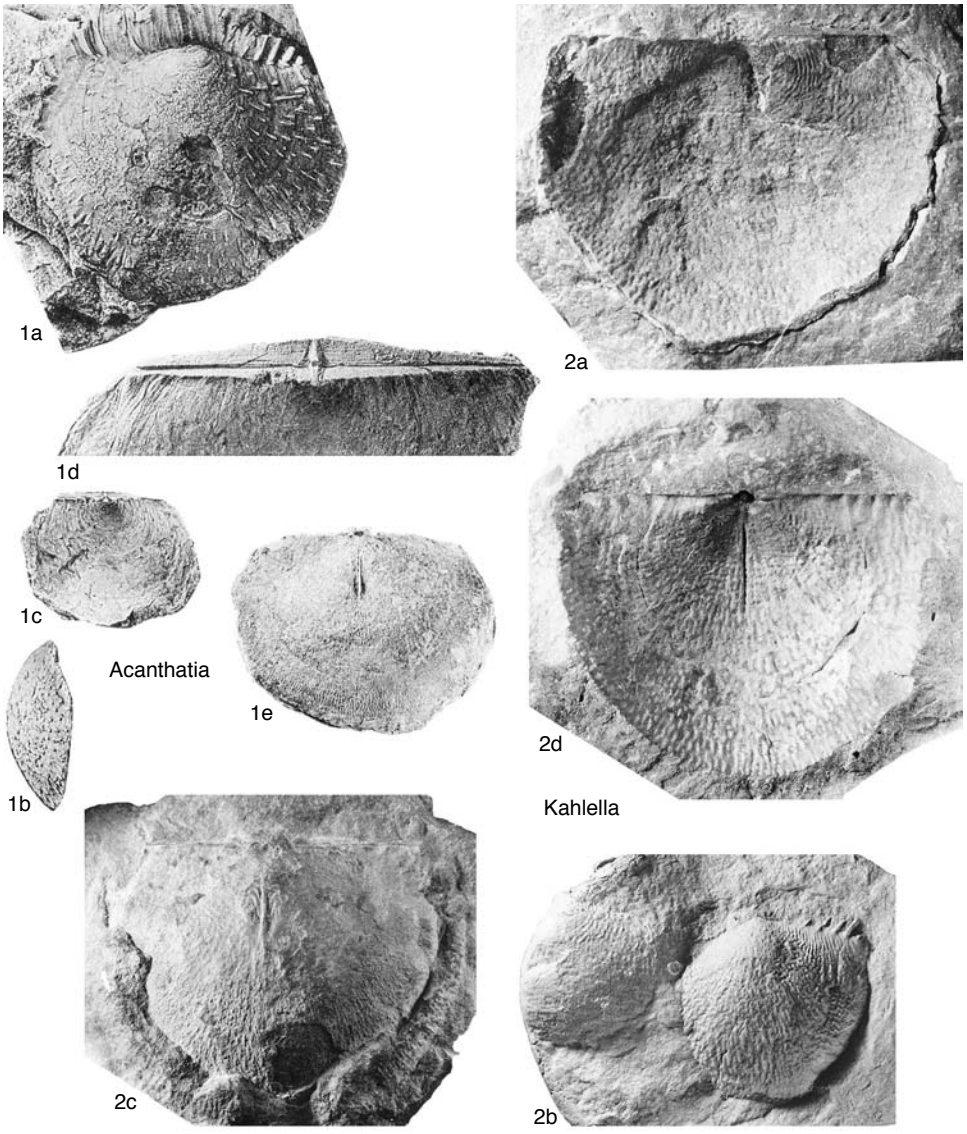

FIG. 411. Araksalosiidae (p. 576–578).

regular, mainly at ears; spines strong at ventral hinge, elongate spine bases tending to form incipient ribs anteromedianly; inner socket ridges at high angle to hinge supporting low cardinal process. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* western Europe, northern Africa, ?North America.——FIG. 412,*1a–d.* **W. caperata* (J. DE C. SOWERBY), uppermost Famennian, Pilton Beds, Devon; *a,* ventral valve external mold, ×1; *b,* replica of ventral valve interior, ×1.5 (new); *c,* dorsal valve external mold, ×1; *d,* replica of incomplete dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Subfamily DONALOSIINAE Lazarev, 1989

[Donalosiinae LAZAREV, 1989, p. 35]

Pseudodeltidium, chilidium present; cicatrix present, may be extensive; spines relatively thick, commonly only on ventral valve; concentric ornament may be lamellose; radial ornament rare on trails. *Lower Devonian (Emsian)–Upper Devonian (Famennian), ?Upper Carboniferous (Gzhelian).*

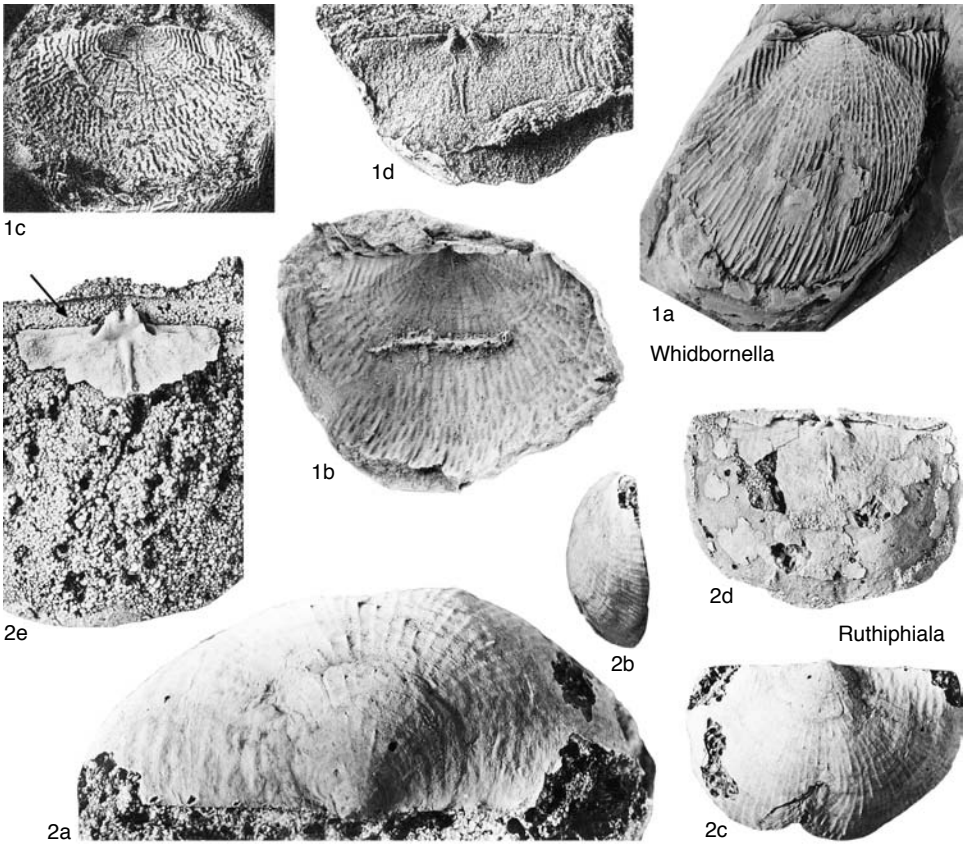

FIG. 412. Araksalosiidae (p. 578–579).

Donalosia LAZAREV, 1989, p. 35[31] [**Productella calva* var. *multispinosa* SOKOLSKAYA, 1948, p. 54; OD]. Convex pseudodeltidium; spines at hinge thicker than elsewhere, absent dorsally; rugae varied, more prominent on dorsal valve posteriorly; brachial ridges spreading widely. *Upper Devonian (Frasnian–Famennian):* eastern Europe, Transcaucasia.——FIG. 413,*1a–d. *D. multispinosa* (SOKOLSKAYA), Famennian, Zadonsk beds, Russian platform; *a,* shell viewed ventrally, ×2; *b,* shell viewed dorsally, ×1; *c,* shell viewed posteriorly, ×2 (new); *d,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).——FIG. 413,*1e. D. caperatiformis* (ABRAMJAN), upper Famennian, Transcaucasia; drawing of ventral internal mold, ×1 (Lazarev, 1989).

?Auchmerella STRUVE, 1964, p. 521 [**A. irmingina;* OD]. Small; abnormal genus, only ventral valves known; strongly cemented by cicatrix, spines spreading radially; ventral interior resembles *Devonalosia,* but with narrow median ridge, weakly elevated diductor scars. *Middle Devonian (Eifelian):* Germany.——FIG. 413,*2. *A. irmingina,* Eifelian, Eifel; replica of holotype, ventral valve interior, SMF 19227, ×3 (new).

Australosia MCKELLAR, 1970, p. 12 [**A. starensis;* OD]. Minute, around 8 mm wide; outline transverse; concavoconvex, commonly with relatively large cicatrix, long trails; ventral interarea with narrow arched pseudodeltidium; rugae weak on disks, costellate anteriorly; spines at hinge line, from ribs anteriorly; socket ridges at low angle to hinge, brachial ridges widely spreading. *Upper Devonian (Famennian):* Australia.——FIG. 413,*3a–c. *A. starensis,* Famennian, Star Beds, Star basin, Queensland; *a,* holotype, replica of dorsal valve exterior, ventral interarea with hinge spines, GSQ F11324, ×3; *b,* ventral valve internal mold, ×4; *c,* replica of dorsal valve interior, ×4 (new).

Devonalosia MUIR-WOOD & COOPER, 1960, p. 83 [**D. wrightorum;* OD]. Small, outline subcircular; flat pseudodeltidium, no chilidium, cicatrix varied; ventral spines only, thick, attaching posteriorly, recumbent anteriorly, arranged concentrically; rugae weak, somewhat lamellose; strong teeth, impressed ventral

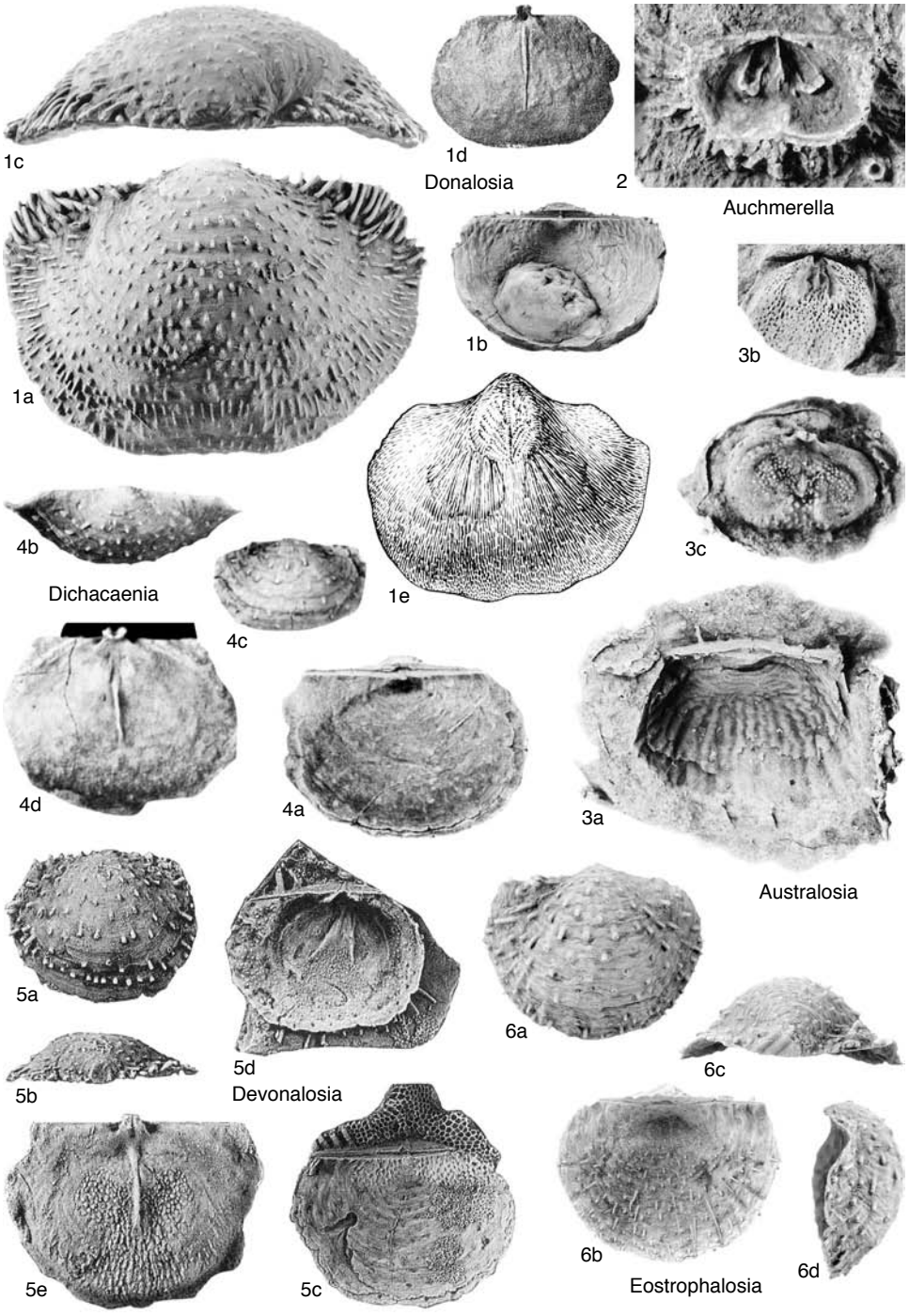

FIG. 413. Araksalosiidae (p. 580–582).

diductor scars; deep sockets, dorsal median septum, tuberculate between brachial impressions. *Middle Devonian (Eifelian–Givetian):* North America.——Fig. 413,*5a–e.* **D. wrightorum,* Givetian, Arkona Shale, Ontario; *a,b,* shell viewed ventrally, posteriorly, ×2; *c,* dorsal view of attached shell, ×3; *d,* ventral valve interior, ×3; *e,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Dichacaenia Cooper & Dutro, 1982, p. 60 [**D. perplexa;* OD]. Small to medium sized; resembling *Devonalosia,* but with impersistent cicatrix, valve surfaces smooth to weakly lamellose; spines only ventrally, evenly and somewhat radially distributed, recumbent with short spine bases; cardinal process internally strongly bilobed, weak ear baffles, tuberculation fine. *Middle Devonian (Givetian):* southern USA, northern Africa, ?France.——Fig. 413,*4a,b.* **D. perplexa,* upper Givetian, Oñata Formation, New Mexico; holotype, viewed dorsally, posteriorly, USNM 200957a, ×1.5 (Cooper & Dutro, 1982).——Fig. 413,*4c,d. D. umbonata* Cooper & Dutro; *c,* ventral valve exterior, ×1; *d,* dorsal valve interior, ×2 (Cooper & Dutro, 1982).

Dotswoodia McKellar, 1970, p. 19 [**Whidbornella (D.) wyatti;* OD]. Outline transversely quadrate, around 30 mm wide; short ventral interarea, no cicatrix, short trails; rugae narrow, irregular on posterior visceral disks; spines on ventral valve only, recumbent from elongate spine bases becoming costate anteriorly, commonly with median spine row; dental sockets small, dorsal median septum prominent, supporting cardinal process. *Upper Devonian (Famennian):* Australia, western Europe.——Fig. 414,*2a–d.* **D. wyatti* (McKellar), Famennian, *Sentosia minuta* Zone, Queensland; *a,* holotype, replica of ventral valve exterior, GSQ F 11477, ×1; *b,* dorsal valve exterior, ×1.5; *c,* replica of part of ventral valve interior, ×2; *d,* replica of incomplete dorsal valve interior, ×1.5 (McKellar, 1970).

?Enigmalosia Czarniecki, 1969, p. 271 [**E. sarytchevae;* OD]. Minute size; extensively cemented ventral valve, somewhat resembling *Australosia,* but with fine costellation, apparently no teeth, thin shell substance. *?Upper Carboniferous (?Gzhelian):* Spitzbergen.——Fig. 414,*1a–d.* **E. sarytchevae,* Gzhelian, western Spitzbergen; *a,b,* anterior, oblique ventral views of ventral valve exterior, ×4; *c,* oblique lateral view of ventral valve exterior, ×4 (new); *d,* drawing of dorsal valve interior, ×4 (Czarniecki, 1969).

Eostrophalosia Stainbrook, 1943, p. 58 [**Strophalosia rockfordensis* Hall & Clarke, 1892, p. 163; OD]. Small with circular outline; ventral interarea prominent medianly, apical arched pseudodeltidium, cicatrix small; spines at ventral hinge, recumbent elsewhere, fine on dorsal valve; rugae weak, lamellose; dorsal valve dimpled. *Upper Devonian (Frasnian):* North America, ?western Europe.——Fig. 413,*6a–d.* **E. rockfordensis* (Hall & Clarke), Frasnian, Hackberry Formation, Rockford, Iowa; specimen viewed ventrally, dorsally, posteriorly, with fragment of shell attached, laterally, ×2 (new).

?Irboskites Bekker, 1924, p. 48 [**I. fixatus;* OD]. Small; profile planoconvex, ventral valve strongly cemented by extensive cicatrix; short ventral interarea; spines apparently lacking, exteriors smooth; ventral interior resembles *Devonalosia* with anteriorly angled teeth; dorsal interior with strong inner plus outer socket ridges, brachial markings extensive. *Upper Devonian (Frasnian):* eastern Europe.——Fig. 415,*3a–c.* **I. fixatus,* lower Frasnian, Irboska Formation, Estonia; *a,* holotype, replica of ventral valve interior, TAGI BR 011, ×2; *b,* exterior of ventral valve with cicatrix to right (note that the pair of objects are possibly the tubes of coiled adherent worms), ×2; *c,* dorsal valve interior, ×2 (new).

Morganella McKellar, 1970, p. 17 [**M. maxwelli;* OD]. Corpus width 30 to 35 mm; shells geniculate with sloping flanks, no median sulcation or folding; ventral interarea short; trail margin slightly flared; thick spines confined to hinge area, fine over ventral corpus; teeth small; cardinal process with pit between small socket ridges. *Upper Devonian (lower Famennian):* Australia.——Fig. 414,*3a–e.* **M. maxwelli,* lower Famennian, Queensland; *a,* lateral oblique view of replica of incomplete ventral valve exterior, ×1.5; *b,* external mold of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×1; *d,* latex replica of dorsal valve interior, ×2 (McKellar, 1970); *e,* latex replica of ventral valve interior showing small teeth, *arrowed,* ×2 (new).

Oligorhachis Imbrie, 1959, p. 403 [**O. oligorhachis;* OD]. Similar to *Devonalosia,* but small, about 8 mm wide; small cicatrix, relatively thick spines. *Middle Devonian:* North America.——Fig. 415,*2a–e.* **O. oligorhachis,* Givetian, Traverse Group, Gravel Point Formation, Michigan; *a–d,* holotype, viewed ventrally, dorsally, laterally, posteriorly, USNM 125574, ×3; *e,* dorsal valve interior, ×3 (Imbrie, 1959).

Ralia Lazarev, 1987, p. 48[44] [**R. primigenia;* OD]. Small; somewhat transverse, concavoconvex shell with moderately inflated ventral umbo; pseudodeltidium convex; spines at ventral hinge, widely scattered; dorsal valve with weak fine ribbing; anderidia present. *Lower Devonian (Emsian):* Mongolia.——Fig. 415,*1a,b.* **R. primigenia,* Emsian, Gobi Altai, Mongolia; *a,* holotype, dorsal exterior of shell with ventral interarea, PIN 4217/2, ×3; *b,* internal mold of ventral valve with shell fragments anterolaterally, ×3 (Lazarev, 1987).

Truncalosia Imbrie, 1959, p. 401 [**T. gibbosa;* OD]. Resembles small *Heteralosia,* but lacking lamellose ornament; spines relatively thin, possibly not bidirectional. *Middle Devonian:* North America.——Fig. 415,*4a–e.* **T. gibbosa,* Givetian, Traverse Group, Gravel Point Formation, Michigan; *a–d,* holotype, viewed dorsally, ventrally, laterally, posteriorly, USNM 125568, ×2; *e,* dorsal valve interior, ×3 (Imbrie, 1959).

Subfamily QUADRATIINAE Lazarev, 1989

[Quadratiinae Lazarev, 1989, p. 38(34)]

Pseudodeltidium, chilidium commonly absent; concentric ornament well developed,

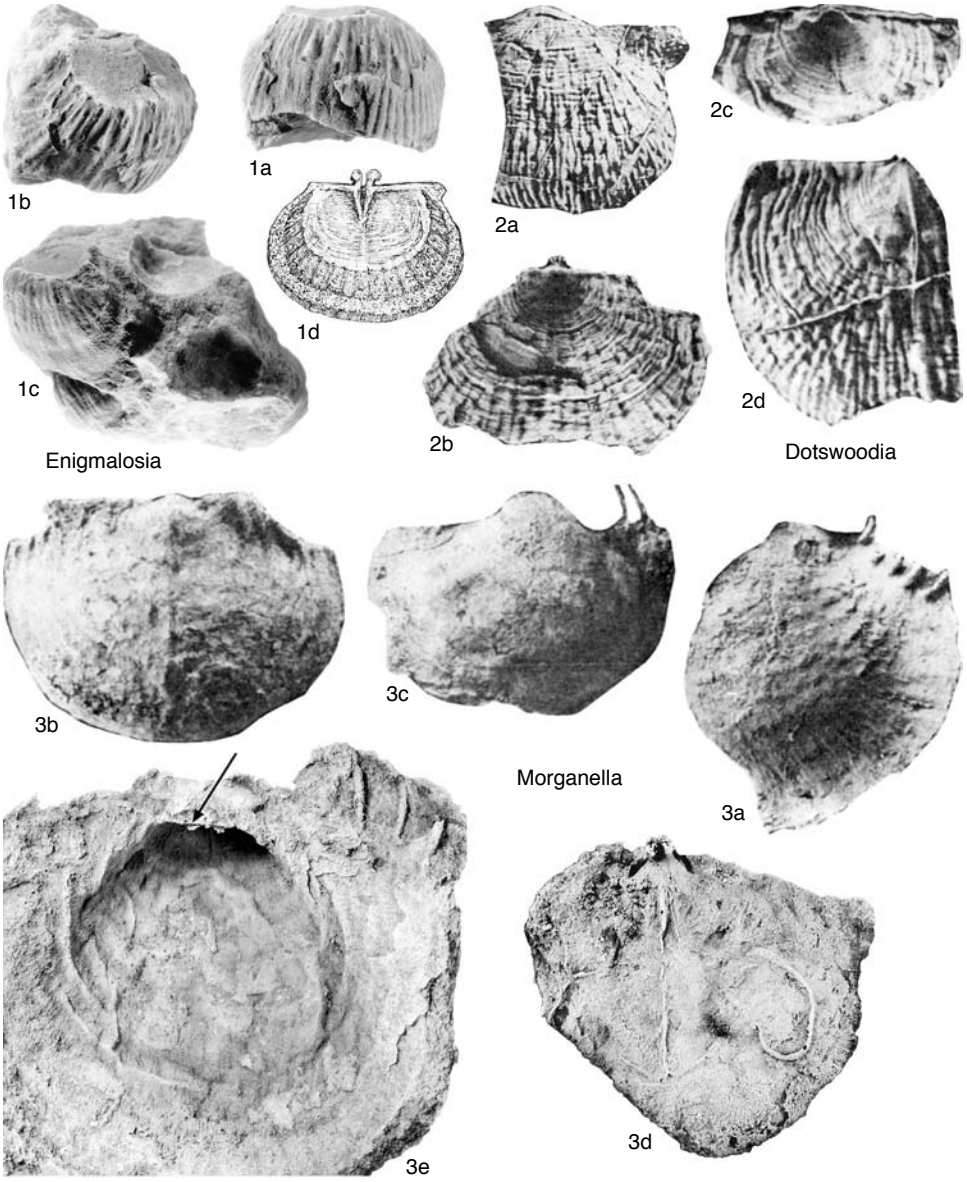

FIG. 414. Araksalosiidae (p. 582).

regular; spines at low angle, rare on dorsal valve; marginal ridges present. *Lower Carboniferous (Hastarian)–Upper Carboniferous (Kasimovian).*

Quadratia MUIR-WOOD & COOPER, 1960, p. 161 [**Productus hirsutiforme* WALCOTT, 1884, p. 133; OD]. Outline transversely subrectangular; interareas wide but short; rugae narrow, entire; ventral spines in row near hinge, elsewhere prostrate, concentric, rare dorsally; well-defined ventral muscle fields, lateral ridges extending across ears; cardinal process occupies delthyrium, small sockets, weak dorsal lateral ridges. *Lower Carboniferous (?Tournaisian, Viséan)–Upper Carboniferous (Serpukhovian):* North America.——FIG. 416,*1a–e.* **Q. hirsutiformis* (WALCOTT), lower Chesterian, Oklahoma; *a–c,* shell viewed ventrally, dorsally, posteriorly, ×1; *d,* posterior view of ventral internal mold, ×1.5; *e,* replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

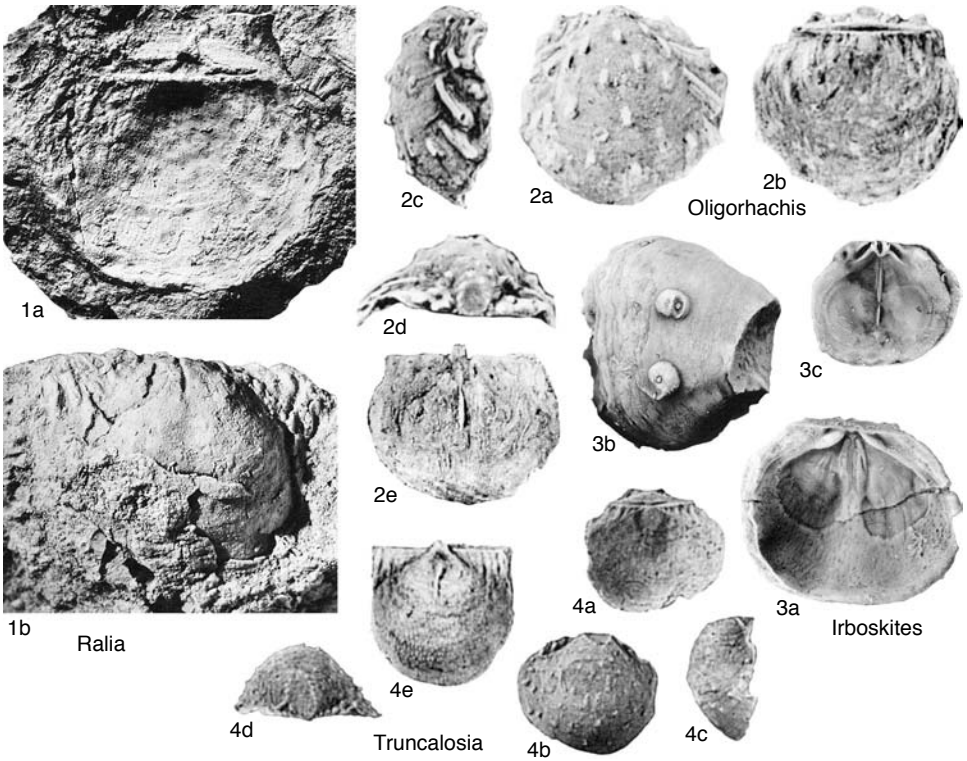

FIG. 415. Araksalosiidae (p. 582).

Chonetipustula PAECKELMANN, 1931, p. 31 [**Productus plicatus* SARRES, 1857, p. 20; OD]. Small, outline semicircular; interareas reduced; both valves rugose; ventral spines long, fine, straight at hinge line, recumbent elsewhere, but rare dorsally; short ventral umbonal myophragm, teeth and sockets small; cardinal process occupies delthyrium, marginal ridges unknown. *Lower Carboniferous (Viséan):* Europe, ?Asia.——FIG. 416,*3a,b.* **C. plicata* (SARRES), upper Viséan, Germany, Rhine; *a,* internal mold of ventral valve, ×1; *b,* ventral valve exterior, ×1 (Muir-Wood & Cooper, 1960).

Cyphotalosia CARTER, 1967, p. 281 [**C. masonensis;* OD]. Small; slightly inflated ventral umbo, differentiated small ears with dorsally flexed extensions; interareas with narrow pseudodeltidium, chilidium, cicatrix small; spines few near ventral hinge, plus scattered and curving on rest of valve, none dorsally; rugae, growth lamellae narrow and somewhat irregular. *Lower Carboniferous (Hastarian):* North America.——FIG. 416,*4a–e.* **C. masonensis,* upper Kinderhookian, Texas; *a,* holotype, viewed ventrally, USNM 154583, ×2; *b,* holotype, viewed dorsoposteriorly, USNM 154583, ×3; *c,d,* ventral valve internal mold viewed ventrally, laterally, ×2; *e,* exfoliated dorsal valve interior, ×2 (Carter, 1967).

Plicaea AISENVERG, 1992, p. 130[168] [**P. insignita;* OD]. Small, 5 mm wide; outline transversely quadrate, geniculate, trails with short flange or gutter; interarea short, cicatrix small; attached also by clasping spines near hinge, other spines rare on rugose corpus, trails smooth; wide sessile cardinal process supported by inner socket ridges subparallel to hinge. *Lower Carboniferous (middle Viséan):* Ukraine.——FIG. 416,*5a–d.* **D. insignita,* Holkerian, Tulsky, Donetz; *a,b,* ventral valve external mold, replica, ×5; *c,d,* dorsal valve internal mold, replica, ×5 (new).

Plicatiferina KALASHNIKOV, 1980, p. 45 [**Productus pseudoplicatilis* STEPANOV, 1948, p. 33; OD]. Resembles *Quadratia* in size, outline, but with prominent, narrow rugae on both valves; ventral median sulcus in some; spines fine on ventral valve; interiors almost unknown. *Upper Carboniferous (Kasimovian):* eastern Europe.——FIG. 416,*2a.* **P. pseudoplicatilis* (STEPANOV), Kasimovian, Bashkiria; ventral valve exterior, ×1 (Stepanov, 1948).——FIG. 416,*2b–d. P. neoplicatilis* (STEPANOV), northern Urals; *b,* ventral valve exterior, ×1; *c,* ventral valve

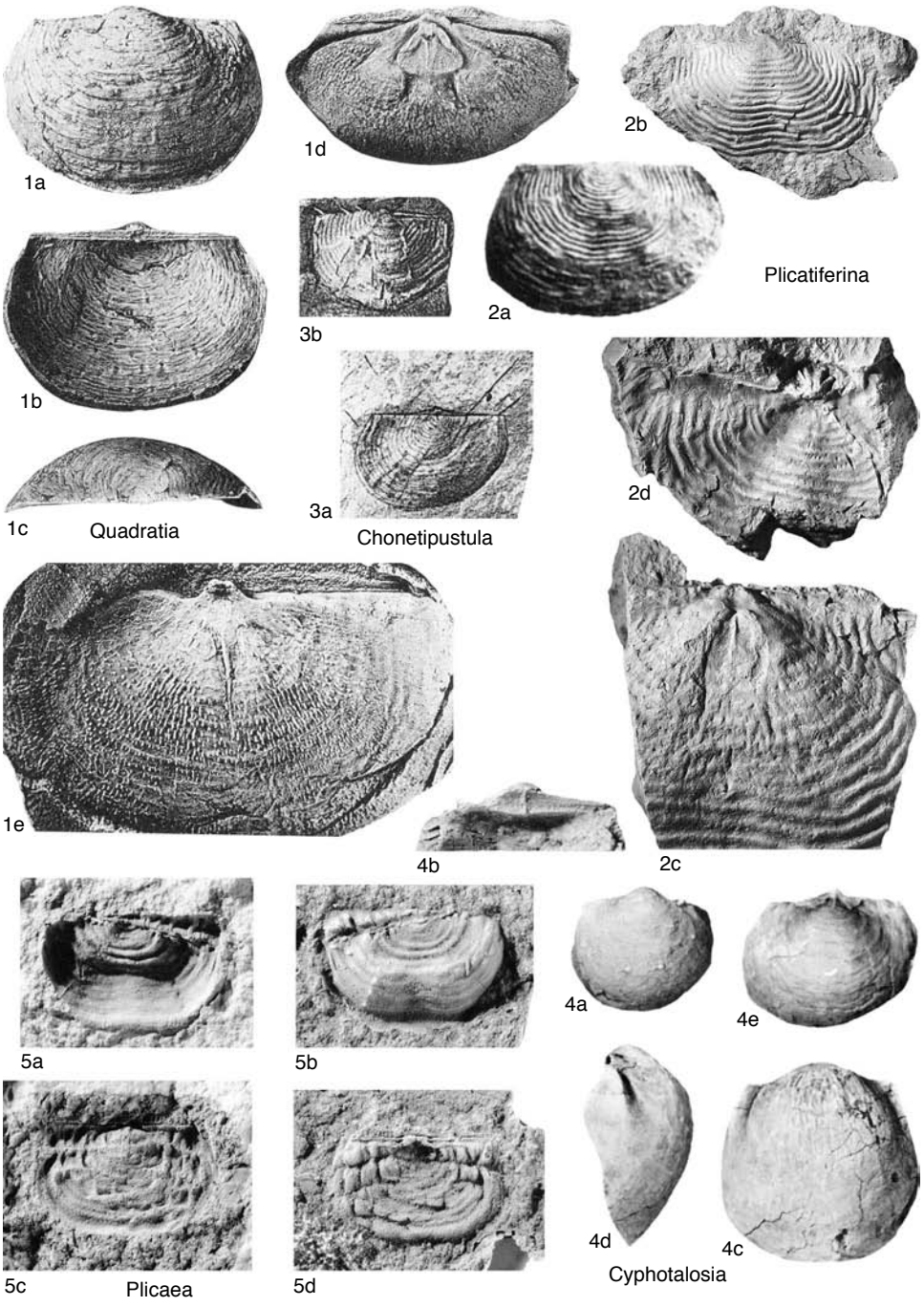

FIG. 416. Araksalosiidae (p. 583–586).

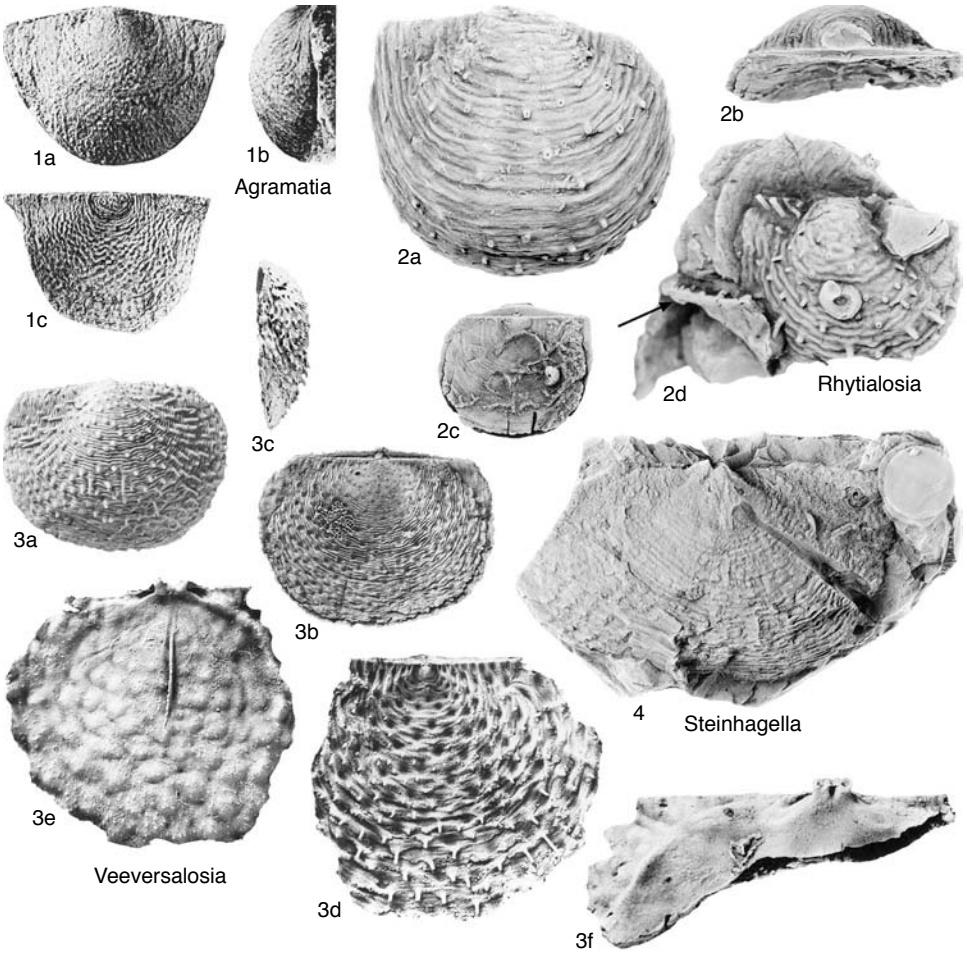

FIG. 417. Araksalosiidae (p. 586–587).

internal mold, ×1.5; *d,* incomplete dorsal valve exterior, ×2 (new).

Subfamily RHYTIALOSIINAE Lazarev, 1989

[Rhytialosiinae LAZAREV, 1989, p. 38(35)]

Cicatrix present; undulose rugae prominent but discontinuous; spines dense on ventral valve, fewer on dorsal valve. *Upper Devonian (middle Frasnian–Famennian).*

Rhytialosia LAZAREV, 1989, p. 38[35] [**Productus petini* NALIVKIN, 1930, p. 71; OD]. Maximum width at hinge, cicatrix present; ventral spines only, relatively thick, especially close to hinge; rugae more prominent ventrally, entire, undulose; dorsal median septum full length of disk. *Upper Devonian (middle Frasnian):* Europe.——FIG. 417,*2a–d.* **R. petini* (NALIVKIN), middle Frasnian, Russian Platform; *a,b,* shell viewed ventrally, posteriorly, ×2; *c,* shell viewed dorsally, ×1; *d,* two ventral valves, one externally, one incomplete dorsolaterally showing tooth, *arrowed,* ×2 (new).

Agramatia SOKOLSKAYA, 1948, p. 39 [**Productus agramati* NALIVKIN in MARKOWSKII & NALIVKIN, 1934, p. 21; OD]. Small; outline subsemicircular with adult hinge at maximum width; interareas reduced, cicatrix small; spines fine ventrally, unknown dorsally; rugae impersistent medianly, nodose, absent anteriorly where spine bases tend to be elongate. *Upper Devonian (lower Famennian):* Russia, ?North America.——FIG. 417,*1a–c.* **A. agramati* (NALIVKIN), lower Famennian, central Russia; *a,b,* ventral valve exterior viewed ventrally, laterally, ×2; *c,* dorsal valve exterior, ×2 (Muir-Wood & Cooper, 1960).

Steinhagella GOLDRING, 1957, p. 223 [**Leptaena membranacea* PHILLIPS, 1841, p. 60; OD]. Outline

subsemicircular, resembles *Agramatia,* but undulose rugae more persistent medianly, lacking swollen spine bases; dorsal valve with fewer, erect spines. *Upper Devonian (Famennian):* Eurasia, northern Africa.——Fig. 417,*4. *S. membranacea* (Phillips), Famennian V–VI, Cornwall; lectotype, internal mold of ventral valve, GSM 95430, ×2 (new).

Veeversalosia Lazarev, 1989, p. 39[35] [**Steinhagella numida* Veevers, 1959, p. 77; OD]. Cicatrix minute, short interareas, small apical pseudodeltidium; spines on both valves, lacking strong hinge spines; rugae fine; differs from *Steinhagella* by having inner socket ridges extended as lateral ridges, ear baffles; median septum short. *Upper Devonian (middle Frasnian):* Western Australia.——Fig. 417,*3a–f. *V. numida* (Veevers), middle Frasnian, Fitzroy Basin; *a–c,* holotype, viewed ventrally, dorsally, laterally, CPC 2954, ×1; *d,e,* young dorsal valve exterior, interior, ×3.5; *f,* incomplete dorsal valve interior, ×2 (Veevers, 1959).

Superfamily AULOSTEGOIDEA Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 932, *ex* Aulostegidae Muir-Wood & Cooper, 1960, p. 94]

Probably attached permanently by spines or direct cementation; ventral interarea present, dorsal interarea small or absent, no chilidium; trails commonly elaborated or conical in Permian, when corpus cavity became deep; teeth absent; brachial ridges may be restricted. *Lower Carboniferous (Ivorian)–Upper Permian (Changhsingian).*

Family AULOSTEGIDAE Muir-Wood & Cooper, 1960

[Aulostegidae Muir-Wood & Cooper, 1960, p. 94]

Plano- to weakly concavoconvex profile, corpus moderate depth; commonly with ventral rhizoid spines; cardinal process trifid or quadrifid, adductor scars dendritic. *Lower Carboniferous (Ivorian)–Upper Permian (Changhsingian).*

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

[Aulosteginae Muir-Wood & Cooper, 1960, p. 95]

Elaborated trails; spines numerous on both valves; ribbing absent; shell material thick. *Lower Permian (Sakmarian)–Upper Permian (Capitanian).*

Aulosteges von Helmersen, 1847, p. 330–331 [**A. wangenheimi* de Verneuil, 1845, p. 194; OD; =*A. variabilis* von Helmersen, 1847, p. 330]. Medium size, variable to long, may be asymmetric; ventral interarea with elongate to subtrigonal outline; total profile weakly concavoconvex with variably developed cicatrix; concentric ornament weak or absent; spines densely distributed on both valves, of two sizes ventrally; dorsal interior with rhomboidal pit separating cardinal process from median septum. *Upper Permian (Kazanian):* northern Eurasia, ?Australia.——Fig. 418,*1a–d. *A. wangenheimi* de Verneuil, Kazanian, Orenburg, Russia; *a–c,* shell viewed ventrally, dorsally, laterally, ×1; *d,* incomplete dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Lipanteris Briggs in Waterhouse & Briggs, 1986, p. 36 [**Aulosteges (Taeniothaerus) subquadratus* var. *cracowensis* Hill, 1950, p. 8; OD]. Resembles *Taeniothaerus,* but with somewhat narrower hinge line, lamellae only on dorsal trail, spines larger and more widely spaced on venter, commonly on radial ridges anteriorly. *Lower Permian (Artinskian–Kungurian):* eastern Australia.——Fig. 418,*2a,b. *L. cracowensis* (Hill), Fairyland Formation, Bowen basin; *a,* ventral valve viewed laterally, ×1; *b,* ventral valve internal mold, ×1 (Waterhouse & Briggs, 1986).——Fig. 418,*2c–e. L. sparsispinosus* Briggs; *c,d,* holotype, ventral valve internal mold viewed laterally, its replica viewed anteroventrally, UQF 72797, ×1; *e,* replica of incomplete dorsal valve interior, ×1 (Waterhouse & Briggs, 1986).

Megasteges Waterhouse, 1975, p. 6 [**M. nepalensis;* OD]. Similar to *Wyatkina,* but reportedly with only one size of ventral spines; said to differ from *Taeniothaerus* by having longer interarea, thicker ventral spines, and ventral diductor scars that enclose adductor scars more closely anteriorly. *Upper Permian (Capitanian):* Himalayas (northwestern Nepal), ?eastern Australia.——Fig. 419,*2a,b. *M. nepalensis,* Punjabian, Dolpo Region, Nepal; *a,* holotype, internal mold viewed dorsally, 314, repository unknown, ×1; *b,* internal mold viewed ventrally, ×1 (Waterhouse, 1975).

Reedoconcha G. Kotlyar, 1964, p. 124 [**Productus (Taeniotherus) permixtus* Reed, 1932b, p. 12; OD]. Medium size with elongate outline, maximum width anteriorly; interarea short, occupying about half hinge width; median sulcus weak, variable; beak acute; elongate spine bases simulate ribbing on ventral valve; spines cover both valves, ventrally strong, semirecumbent, dorsally fine; no anterior spine bands; cardinal process with paired ridges on shaft; median septum long; adductor scars well developed. *Lower Permian:* Oman, Afghanistan, Himalayas.——Fig. 419,*1a–f. *R. permixta* (Reed), Sakmarian; *a,* ventral valve exterior, Agglomeritic Slate, Kashmir, ×0.75; *b,* ventral valve internal mold, Agglomeritic Slate, Kashmir, ×1; *c,* dorsal valve internal mold, Agglomeritic Slate, Kashmir, ×1 (Reed, 1932b); *d,* ventral valve viewed posteroventrally, Saiwan Formation, southern Oman, ×1; *e,* complete specimen viewed dorsally, Saiwan Formation, southern Oman, ×1; *f,* dorsal cardinalia viewed internally, Saiwan Formation, southern Oman, ×1 (new).

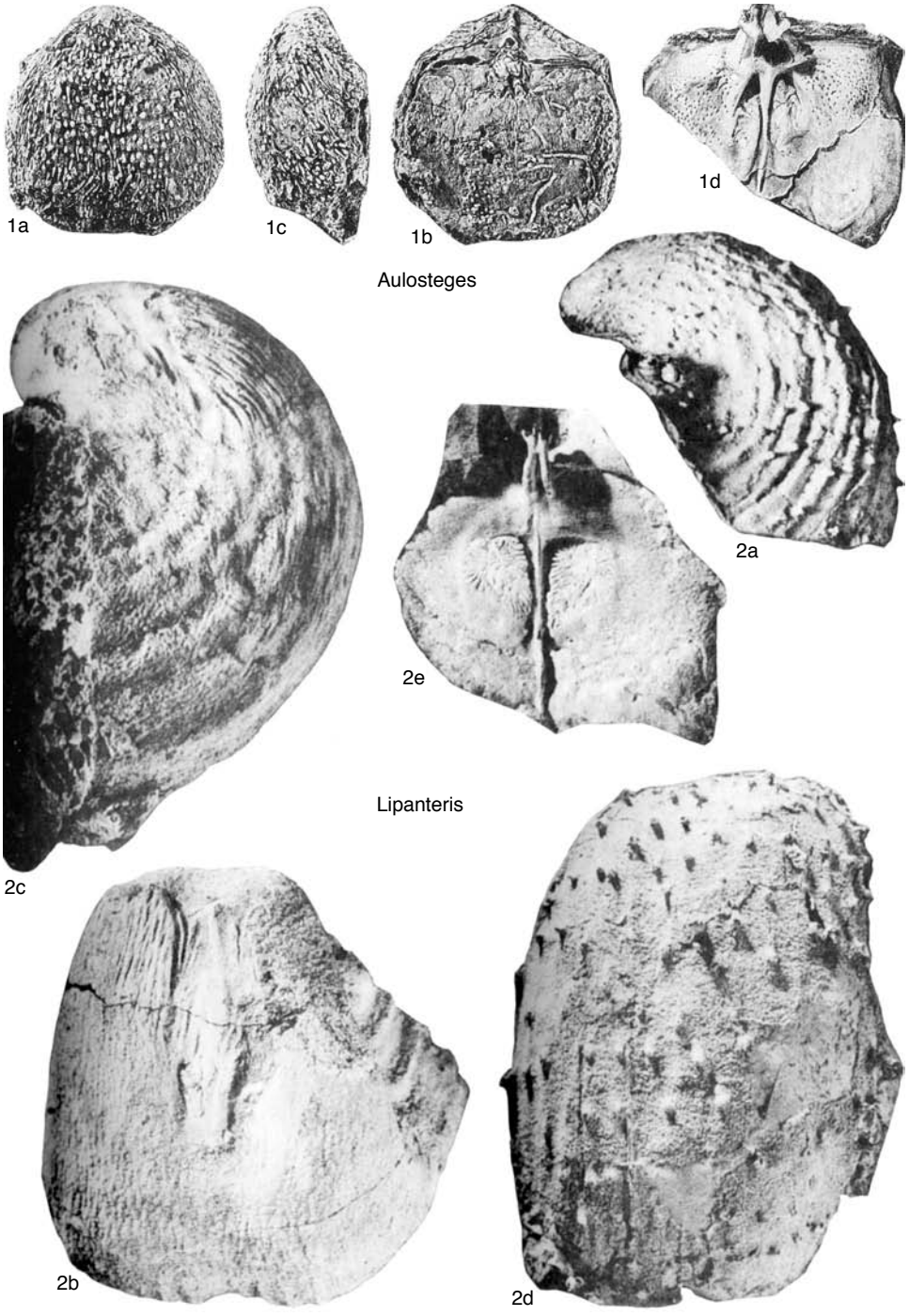

FIG. 418. Aulostegidae (p. 587).

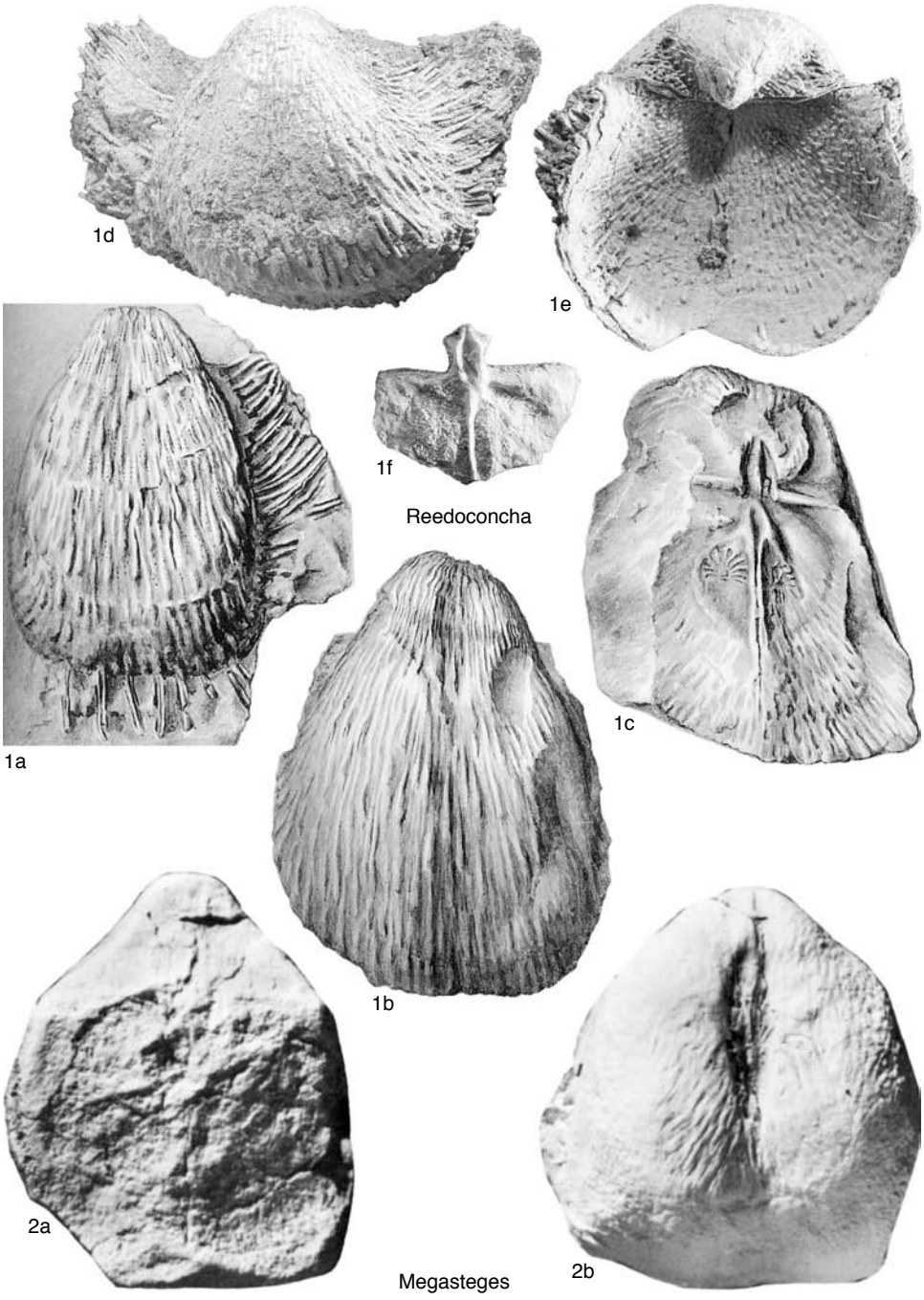

FIG. 419. Aulostegidae (p. 587).

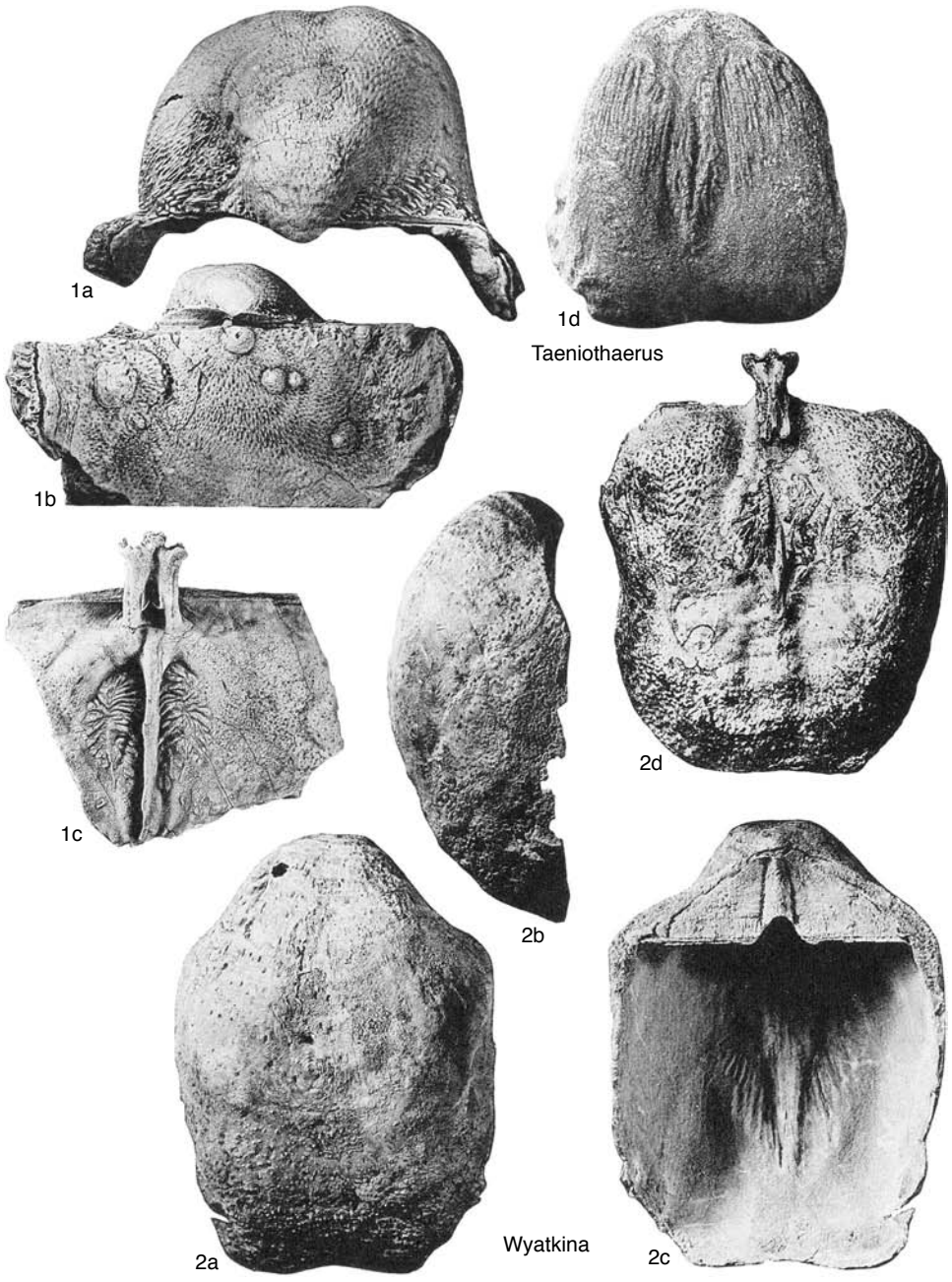

FIG. 420. Aulostegidae (p. 590–591).

Taeniothaerus WHITEHOUSE, 1928, p. 281 [**P. subquadratus* MORRIS in DE STREZELECKI, 1845, p. 248; OD]. Large with thick-shelled valves; transverse profile highly arched with steep flanks; interareas short, but wide; spines relatively fine, densely distributed on both valves with clusters of thicker spines on posterior flanks; ventral adductor scars positioned anteriorly; cardinal process shaft

medianly sulcate, myophores large, trifid to quadrifid. *Lower Permian (Sakmarian–Artinskian):* Australia, ?Asia.——Fig. 420,*1a–d. *T. subquadratus* (Morris); *a,b,* ventral valve viewed posteriorly, dorsally, Wandagee Series, Western Australia, ×0.75; *c,* incomplete dorsal valve interior, Wandagee Series, Western Australia, ×0.75; *d,* ventral valve internal mold, Gympie Beds, Queensland, ×0.75 (Muir-Wood & Cooper, 1960).

Wyatkina Fredericks, 1931, p. 211 [**Aulosteges gigas* Nechaev, 1894, p. 155; OD]. Resembles *Aulosteges,* but larger, with wider, less variable ventral interarea almost equal to maximum width of shell; ventral profile more strongly and evenly convex; spines less thick, possibly absent from dorsal valves. *Upper Permian (Kazanian):* Eurasia.——Fig. 420,*2a–d. *W. gigas* (Nechaev), Wyatka River; *a–c,* ventral valve viewed ventrally, laterally, internally, ×1; *d,* dorsal valve interior, ×0.75 (Muir-Wood & Cooper, 1960).

Subfamily AGELESIINAE Cooper & Grant, 1975

[*nom. transl.* Brunton, Grant, & Lazarev, 1995, p. 932, Agelesiidae Cooper & Grant, 1975, p. 890]

Corpus outline triangular; ventral interarea reduced; no dorsal spines but having strong concentric ornament; ear baffles strong; dorsal adductor platforms commonly raised. *Lower Carboniferous (upper Viséan)–Lower Permian (Artinskian).*

Agelesia Cooper & Grant, 1969, p. 6 [**A. triagonalis* R. E. King, 1931, p. 94; OD]. Small, commonly distorted; cluster of rhizoid spines confined to posterior half of ventral valve, creating dimples on dorsal valve; both valves finely rugose; cardinal process variable, commonly strongly bilobed; dorsal adductor scars raised, endospines anteriorly. *Lower Permian (Artinskian):* USA.——Fig. 421,*1a–d. *A. triagonalis* R. E. King, Cathedral Mountain Formation, Texas; *a–c,* complete specimen viewed ventrally, laterally, dorsally, ×2; *d,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

?Rhytibulbus Li Li in Ding Yunjie & others, 1991, p. 157[185] [**R. zhen'anensis;* OD]. Poorly known; small to medium, elongate outline with wide hinge line, well-defined ears; interarea short; ventral profile semicircular; costellae extending to trail between rugae on disks; spines on ventral valve only, with wide bases; interiors unknown. *Lower Permian:* China.——Fig. 421,*2a–c. *R. zhenanensis,* Quinling Range; *a,b,* ventral valve viewed posteroventrally, laterally, ×1; *c,* dorsal valve exterior, ×1 (Ding & others, 1991).

Stipulina Muir-Wood & Cooper, 1960, p. 200 [**Productus deshayesianus* de Koninck, 1842, p. 193; OD]. Outline of corpus plus trails elongate, with well-differentiated ears; ventral interarea small, restricted medianly; long spines from swollen bases on ventral corpus; ear baffles strong; brachial markings elongate, commonly raised anteriorly. *Lower Carboniferous (upper Viséan):* western Europe.——Fig. 421,*3a–g. *S. deshayesianus* (de Koninck); *a,* ventral valve internal mold viewed laterally, Visé, ×6; *b,c,* ventral valve internal mold viewed posteriorly, replica showing strong ear baffles, Visé, ×5 (Muir-Wood & Cooper, 1960); *d,* replica of dorsal valve interior, Visé, ×5; *e,f,* ventral valve exterior viewed ventrally, laterally, Asbian, Northern Yorkshire, ×4; *g,* part of dorsal valve exterior showing large ears, Asbian, Northern Yorkshire, ×4 (Brunton & Mundy, 1988b).

Subfamily CHONOSTEGINAE Muir-Wood & Cooper, 1960

[Chonosteginae Muir-Wood & Cooper, 1960, p. 113]

Small, with complex, valvelike, spinose corpus margin, strong geniculation, short trails; strong ribbing anteriorly. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Chonosteges Muir-Wood & Cooper, 1960, p. 113 [**Aulosteges magnicostatus* Girty, 1909, p. 278; OD]. Small, subcircular to subpentagonal outline; ventral interarea, umbo variable, depending on attachment; lophidium, zygidium present in some; planoconvex corpus profile with strong geniculation; ribbing strong anterior to geniculation; spines rhizoid on ventral disk, ribs; both trails reflexed ventrally, at corpus margin complex series of interdigitating spines and funnel-like processes. *Lower Permian (Artinskian):* southern USA, Russia, ?Malaysia.——Fig. 422,*4a. *C. magnicostatus* (Girty), Delaware Mountain Formation, Texas; holotype, viewed dorsally, USNM 118548, ×3 (Cooper & Grant, 1975).——Fig. 422,*4b–e. C. variabilis* Cooper & Grant, Cathedral Mountain Formation, Texas; *b,* detail of shell commissure anteriorly with ventral attachment spines below, ×3; *c,* dorsal valve exterior, ×1; *d,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960); *e,* ventral valve exterior, ×2 (Cooper & Grant, 1975).

Chonostegoides Sarytcheva in Sarytcheva & Sokolskaya, 1965, p. 212 [**C. ogbinensis;* OD]. Medium size, subquadrate outline with small ears; interarea short; corpus planoconvex, deep; trails reflexed, ribbed; spine bases slightly swollen, elongate on ventral corpus, dorsal spines larger anteriorly; marginal structures similar to *Chonosteges;* dorsal interior with complete marginal ridge. *upper Lower Permian (Roadian):* Transcaucasus.——Fig. 422,*1a–c. *C. ogbinensis,* Ufimian, Gnishiksky Horizon, Ogbin; *a,b,* holotype, ventral exterior, largely exfoliated dorsal valve interior, PIN 2071/76, ×1; *c,* dorsal valve exterior, ×1 (Sarytcheva & Sokolskaya, 1965).——Fig. 422,*1d. C. armenicus* Sarytcheva; detail of external mold of dorsal valve flange, ×6 (Sarytcheva & Sokolskaya, 1965).

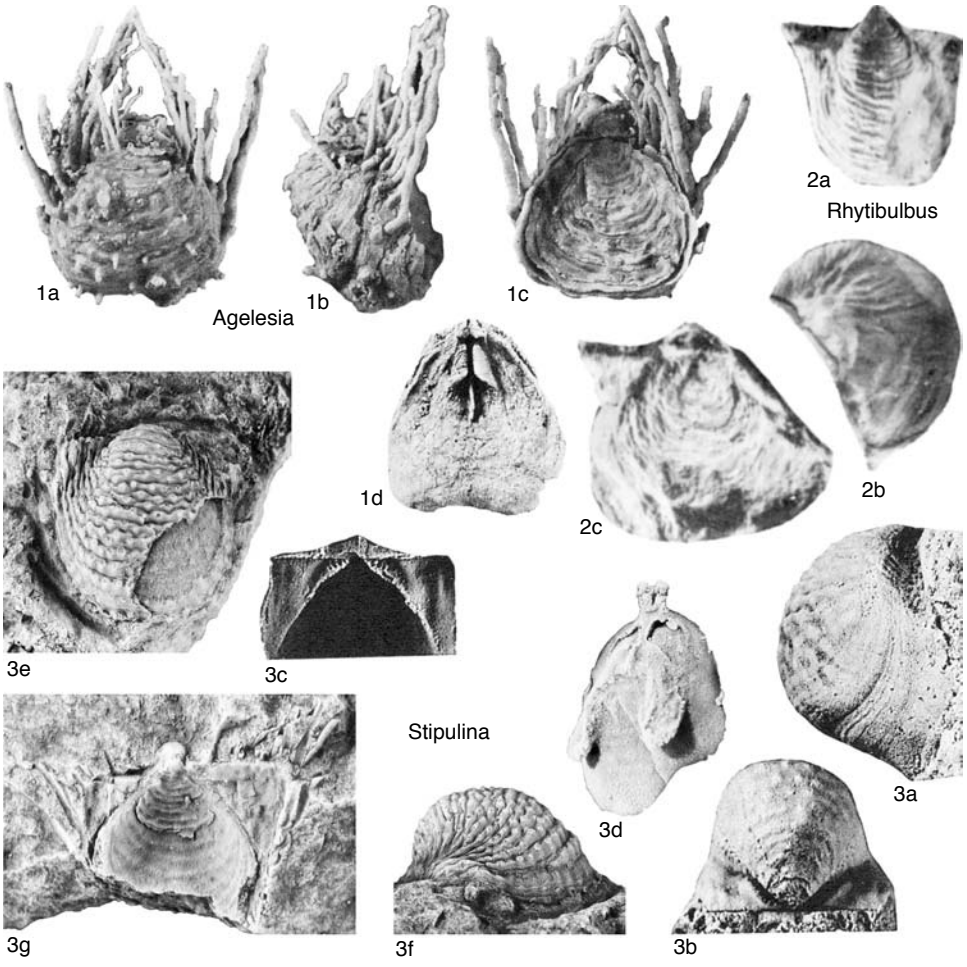

FIG. 421. Aulostegidae (p. 591).

Costisteges LIAO, 1982, p. 540[543] [**C. dongluoensis;* OD]. Resembles *Chonosteges,* but lacks the complex spine, funnel arrangement bordering the corpus cavity. Published figures inadequate for illustration. *Upper Permian (Changhsingian):* China.

Urushtenia LICHAREW, 1935, p. 370 [**Productus pseudomedusa* CHERNYSCHEV, 1902, p. 293; OD]. Small, transverse with planoconvex flattened corpus, geniculate with trails; ventral interarea short, cicatrix small; ribbing starts on disks, prominent on trails; rugae narrow on disks; spines distributed on both disks, fine dorsally; spinose marginal ridges, gutters of trails resembling *Chonesteges. Lower Permian (Asselian–Sakmarian):* Russia, China.——FIG. 422,*3a–e.* **U. pseudomedusa* (TSCHERNYSCHEW); *a,* specimen viewed ventrally, Sakmarian, Schwagerina Limestone, Ural Mountains, ×2; *b,* specimen viewed dorsally, Sakmarian, Schwagerina Limestone, Ural Mountains, ×1; *c,d,* specimen viewed posteriorly, laterally, Kasarmensky Kamen, Russia, ×2 (Muir-Wood & Cooper, 1960); *e,* dorsal valve interior, Kasarmensky Kamen, Russia, ×2.5 (Sarytcheva & Grunt, 1969).

Urushtenoidea JING YU-GAN & HU SHI-ZHONG, 1978, p. 116 [**Urushtenia chaoi* CHING YU-GAN, 1963; OD] [=*Uncisteges* JING YU-GAN & HU SHI-ZHONG, 1978, p. 117 (type, *Eomarginifera crenulatea* TING PEI-CHEN in YANG TSUN-YI & others, 1962, p. 85; OD)]. Small, planoconvex corpus, geniculated to trails; ribbing originates on disks, prominent on trails; rugae impersistent, more prominent on ventral disk; spines erect on ribs; trail margins extending as interlocking spines similar to *Chonosteges;* cardinal process with basal pit; adductor field may be elevated; marginal ridge with row of spines. *upper Lower Permian:* southern China.——FIG. 422,*2a–c.* **U. chaoi* (CHING), ?Roadian, Hsiaojiangbian Formation, Jiangxi; *a,b,* specimen viewed anteriorly, laterally, ×1; *c,* specimen viewed anteriorly showing commissural spines, ×1 (new).——FIG.

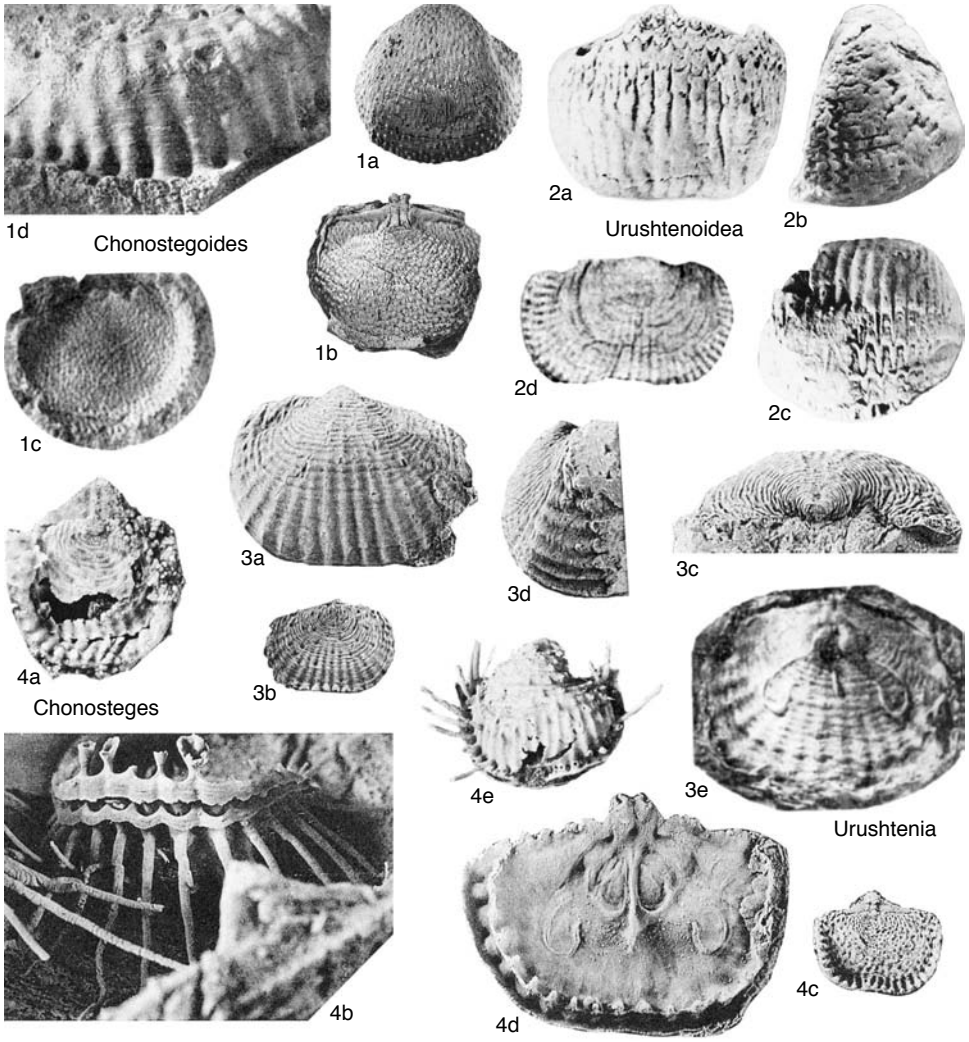

FIG. 422. Aulostegidae (p. 591–593).

422,*2d. U. chenanensis* (CHAN), Kuhfeng Formation, Shangxi; ventral valve exterior, ×1.5 (Jing & Hu, 1978).

Subfamily CTENALOSIINAE Muir-Wood & Cooper, 1960

[Ctenalosiinae MUIR-WOOD & COOPER, 1960, p. 91]

Interarea short; ribbing varied, no dorsal spines; hinge lines denticulate. *Lower Permian (Roadian)–Upper Permian (Kazanian).*

Ctenalosia COOPER & STEHLI, 1955, p. 470 *[*C. fixata;* OD]. Small, subcircular, with hinge of variable width; corpus planoconvex with anterior series of short dorsal trails; interarea short, with internal single row of denticles fitting dorsal hinge pits; ribbing variably developed on trails; both disks anteriorly rugose or lamellose; spines rhizoid on ventral corpus, posterior trail; cardinal process relatively strong; adductor platforms closely spaced with short median septum anteriorly. *Upper Permian (lower Kazanian):* USA.——FIG. 423,*1a–e. *C. fixata,* Word Formation, Texas; *a,b,* holotype, viewed posteriorly, dorsally, USNM 124123a, ×3; *c,d,* attached ventral valve viewed anteriorly, internally, ×3; *e,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Mongolosia MANANKOV & PAVLOVA, 1976, p. 354 [*M. morenkovi;* OD]. Medium size, transverse outline; concavoconvex corpus, profile geniculate; no sulcus; cicatrix present; interarea short; concentric lamellae on dorsal valve, ribbing fine; spines in row at hinge,

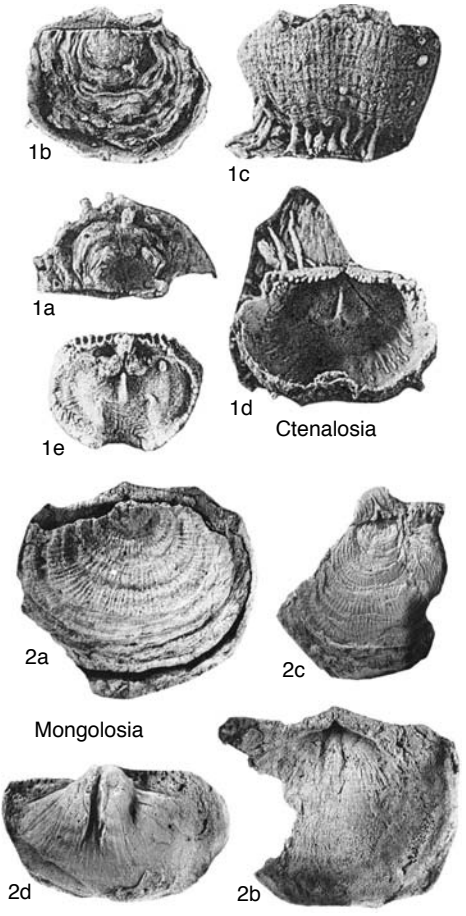

FIG. 423. Aulostegidae (p. 593–594).

scattered on ears, venter; up to 30 conical denticles at ventral hinge fitting pits on dorsal interior; cardinal process trifid with large median ridge, supported anteriorly by two ridges. *upper Lower Permian (Roadian)–lower Upper Permian:* central Mongolia.——FIG. 423,*2a–d. *M. morenkovi; a,b,* holotype, viewed dorsally, showing dorsal valve exterior, ventral valve interior, PIN 3158/1, ×1; *c,* external mold of dorsal valve, ×1; *d,* internal mold of ventral valve, ×1 (Manankov & Pavlova, 1976).

Subfamily ECHINOSTEGINAE Muir-Wood & Cooper, 1960

[Echinosteginae MUIR-WOOD & COOPER, 1960, p. 101]

Ventral interarea distinct, but variable; dorsal spines commonly absent; dorsal, ventral adductor scars prominent. *Lower Carboniferous (Tournaisian)–Upper Permian (Capitanian).*

Echinosteges MUIR-WOOD & COOPER, 1960, p. 101 [**Aulosteges tuberculatus* R. E. KING, 1931, p. 95; OD]. Medium size, subquadrate to elongate with strong but variable ventral interarea; corpus planoconvex, gently geniculate with anteriorly flanged trail; ventral disk with swollen spine bases, coarse ribbing on trail; spines rhizoid in clusters on ears and flanks, small, semirecumbent, evenly distributed over ventral valve; dorsal disk dimpled, spines rare; cardinal ridge parallel to hinge, forming sharp angle with complete marginal ridge. *lower Upper Permian:* USA.——FIG. 424,*1a–e. *E. tuberculatus* (R. E. KING), Word Limestone, Texas; *a,* ventral valve exterior, ×1; *b,c,* ventral valve exterior, interior, ×1; *d,* shell viewed dorsally, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Archaiosteges CARTER, 1991, p. 360 [**A. harperi;* OD]. Small; hinge less than maximum corpus width; ?without cicatrix; weakly concavoconvex, shallow with short trails; almost completely rugose; ventral swollen spine bases regularly distributed, spines fine; no ribbing; cardinal and marginal ridges; cardinal process thick, strongly supported by nonfunctional ridges resembling inner socket ridges. *Lower Carboniferous (Ivorian, ?Chadian):* USA.——FIG. 424,*2a–g. *A. harperi,* lower Osagean, Iowa; *a–c,* holotype, viewed ventrally, anteriorly, laterally, CMNH 34953, ×2; *d,e,* ventral, posterodorsal views, ×3; *f,* young dorsal valve exterior, ×3; *g,* dorsal valve interior, ×2 (Carter, 1991).

Baissalosteges G. KOTLYAR, 1989, p. 119 [**B. gracilis;* OD]. Medium size, subquadrate outline, maximum width anteriorly; ventral interarea prominent; dorsal disk weakly concave, geniculate with short trail; corpus cavity shallow; capillation fine, indistinct on both valves; spines fine, recumbent, covering valve, rhizoid near hinge, cluster on ears; cardinal ridges, medium septum reach half dorsal disk length; shell material thin. *Upper Permian (Capitanian):* Transcaucasus, ?China.——FIG. 425,*3a–e. *B. gracilis,* Khachikek Horizon, Transcaucasus; *a,b,* holotype, incomplete shell viewed ventrally, dorsally, TsNIGRA 36/12540, ×1; *c,* ventral valve exterior, ×1; *d,* shell viewed dorsally, ×1; *e,* detail of ventral valve exterior, ×3 (Kotlyar, 1989).

Edriosteges MUIR-WOOD & COOPER, 1960, p. 103 [**E. multispinosus;* OD] [=*Neoedriosteges* LIANG, 1990, p. 150[460] (type, *N. transversa;* OD)]. Medium, circular to subquadrate outline with short but wide ventral interarea; corpus gently concavoconvex with trails commonly having gutter; concentric ornament variably lamellose, especially dorsally; fine radial capillae commonly preserved on trails; ventral spines as in *Echinosteges,* but anteriorly tend to be distributed concentrically; no dorsal spines; interiors resemble *Echinosteges. Lower Permian:* USA, China, Tibet, Salt Range.——FIG. 425,*2a–e. *E. multispinosus,* upper Leonard Formation, Texas; *a,b,* holotype, viewed ventrally, laterally, USNM 123906a, ×1; *c,* ventral valve interior, ×1; *d,* shell viewed dorsally, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

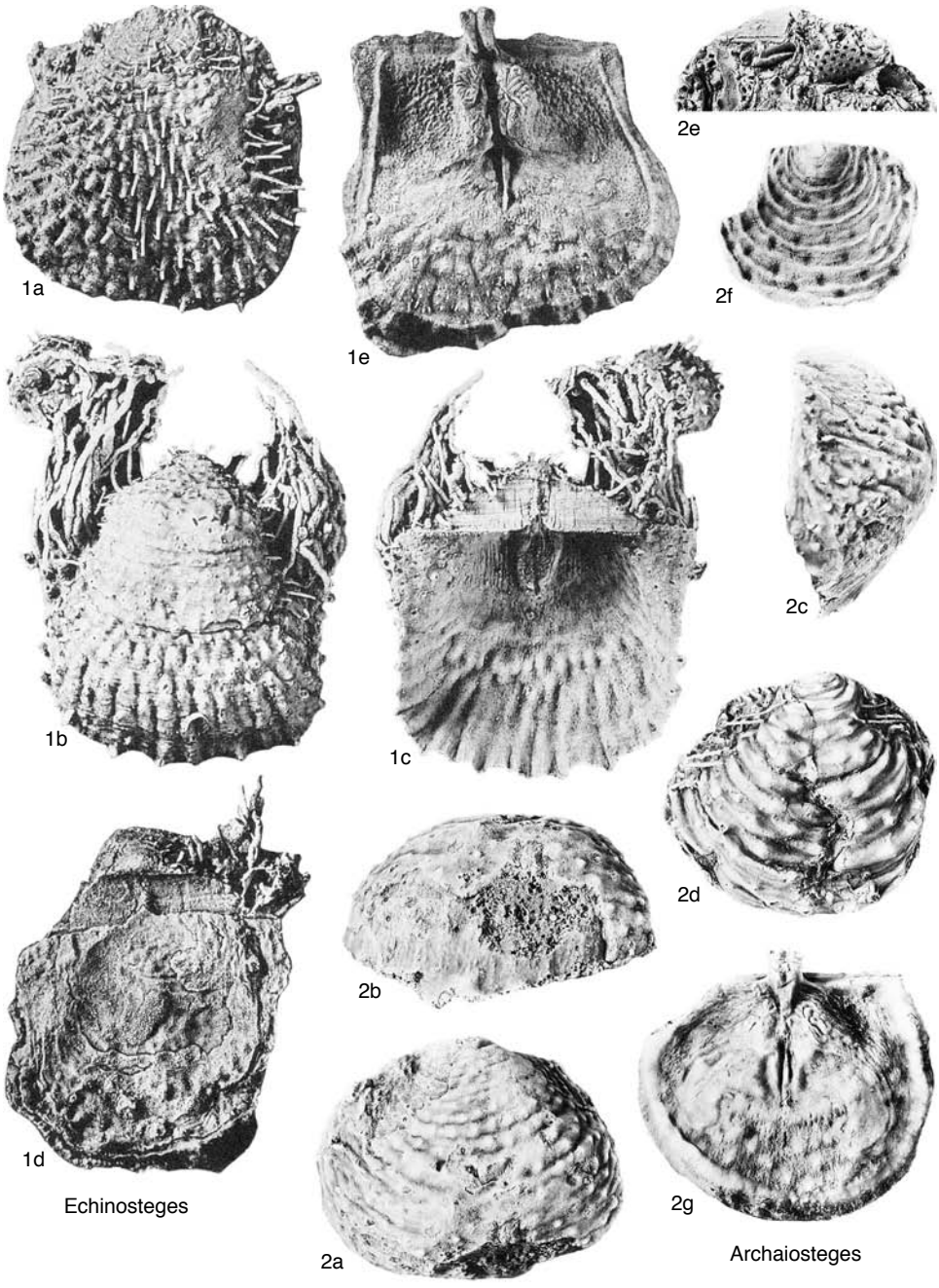

FIG. 424. Aulostegidae (p. 594).

Girlasia DE GREGORIO, 1930, p. 21 [**Strophalosia (Girlasia) superelegans;* OD]. Small, elongate outline, narrow hinge with short interarea; corpus weakly concavoconvex; exteriors smooth; spines evenly distributed on ventral valve, with slight rounded basal swellings, dorsal spines suberect, fine, rare; internal hinge lines denticulate. *Permian (Wordian):* Sicily. ——FIG. 426,*3a–c.* **G. superelegans* DE GREGORIO,

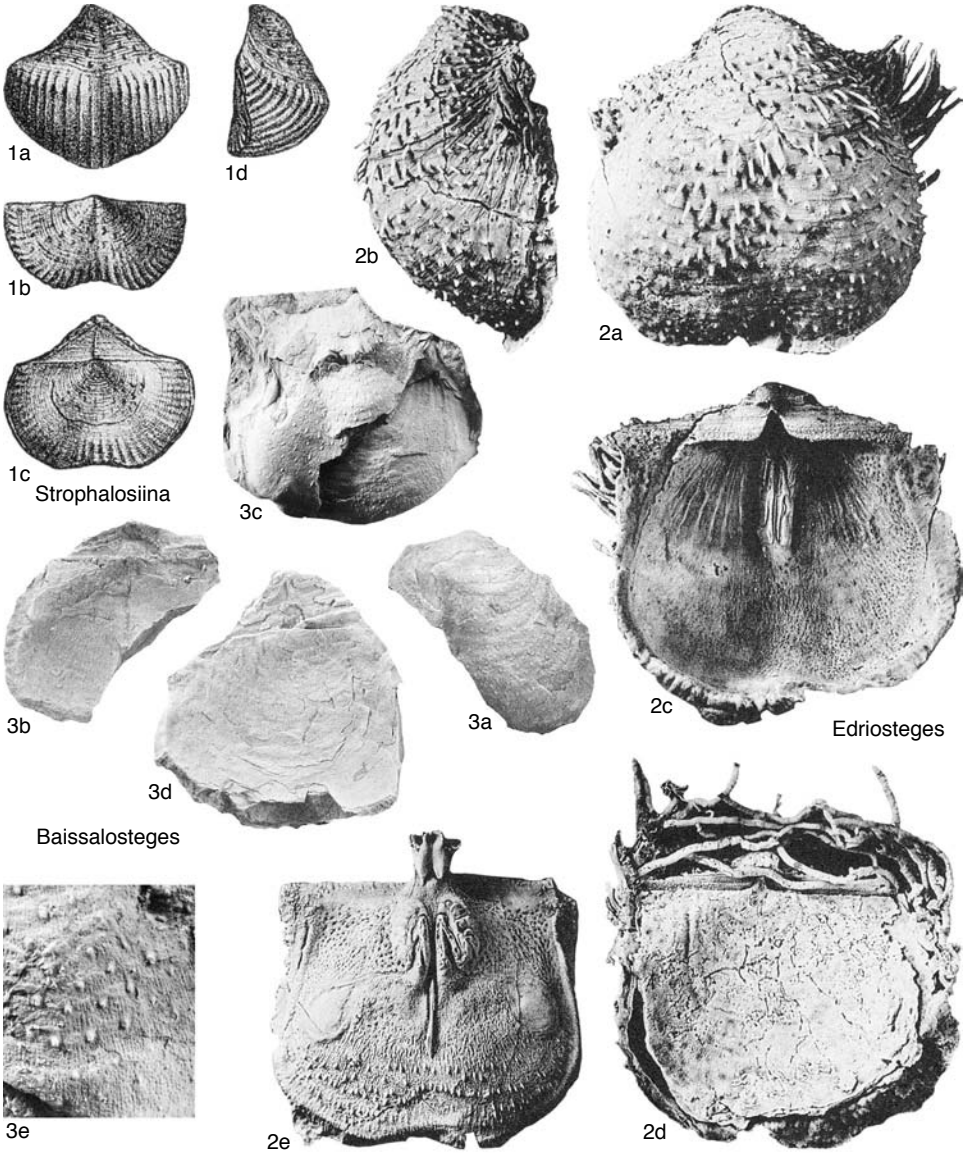

FIG. 425. Aulostegidae (p. 594–599).

Sosio Limestone, Palermo; *a,b,* shell viewed ventrally, dorsally, ×3; *c,* shell viewed laterally, ×2 (Muir-Wood & Cooper, 1960).

Howseia LOGAN, 1963, p. 756 [**Productus latirostratus* HOWSE, 1848, p. 256; OD]. Medium size, weakly sulcate shell; hinge narrower than width of midlength; ribbing absent, growth lines strong; spines in row on ventral flanks, few on venter; ventral adductor scars dendritic; dorsal scars striated; cardinal process bilobed, quadrifid, extending ventrally. *lower Upper Permian (lower Kazanian):* England.——FIG. 426,*1a–f.* **H. latirostrata* (HOWSE), middle Magnesian Limestone, County Durham; *a–c,* lectotype, viewed ventrally, dorsally, laterally, GSM 59737, ×1.5; *d,* posteriorly exfoliated ventral valve exterior, ×1.25; *e,* ventral valve internal mold plus shell on right ear, ×1.5; *f,* dorsal valve interior, cardinalia, ×3 (Logan, 1963).

Limbella STEHLI, 1954, p. 329 [**Aulosteges wolfcampensis* R. E. KING, 1931, p. 95; OD]. Me-

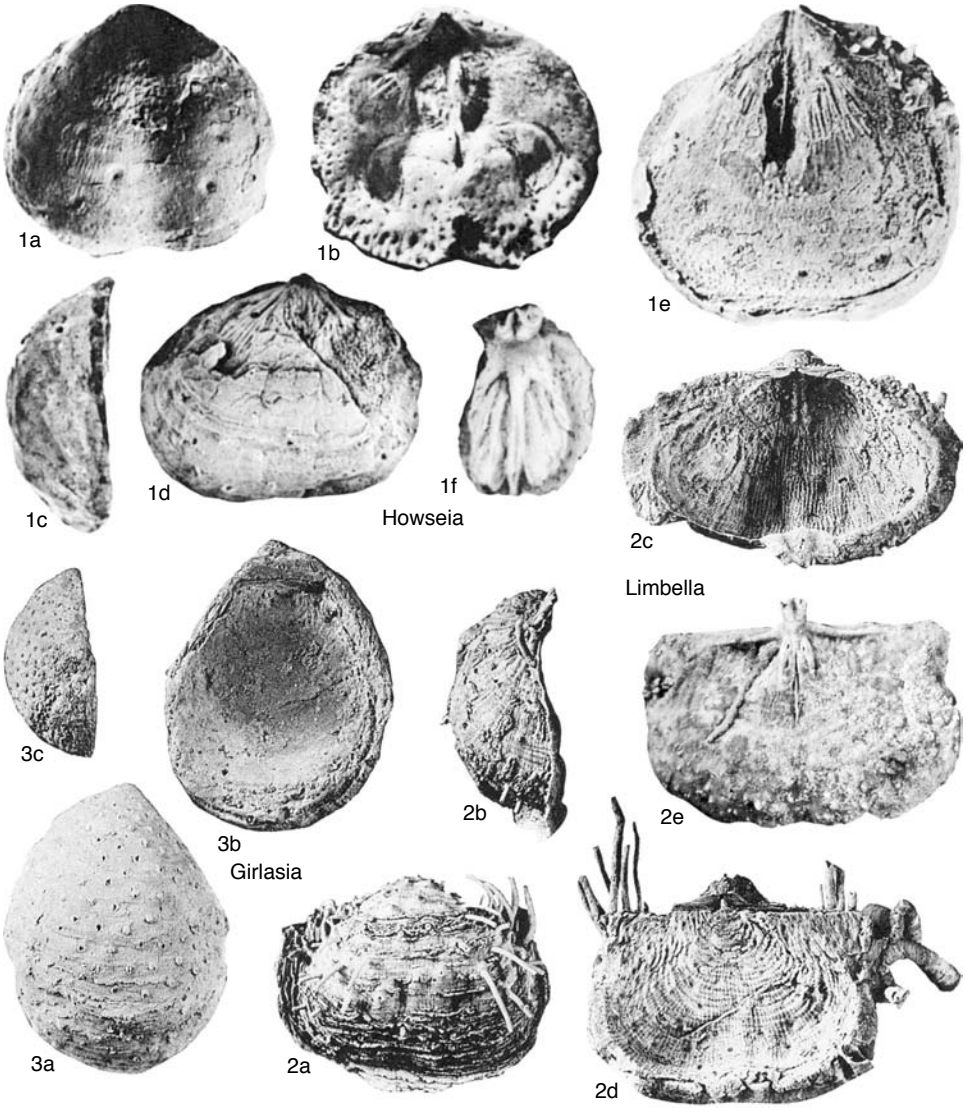

FIG. 426. Aulostegidae (p. 595–597).

dium size, resembling *Edriosteges,* but differing in its distictive fine ribbing, tendency to be lamellose, fewer ventral corpus spines; interareas, relationships of cardinal process to delthyrium vary in both genera; internally has short, well-developed cardinal ridges, lacking marginal ridges and with relatively weak, narrow dorsal adductor scars. *Upper Carboniferous–Lower Permian:* USA.——FIG. 426,*2a–e.* **L. wolfcampensis* (R. E. KING), Asselian, Neal Ranch Formation, Texas; *a,* ventral valve exterior, ×1; *b,* ventral valve viewed laterally, ×1; *c,* ventral valve interior, ×1; *d,* shell viewed dorsally, ×1 (Muir-Wood & Cooper, 1960); *e,* dorsal valve interior, ×1 (Cooper & Grant, 1975).

Sphenosteges MUIR-WOOD & COOPER, 1960, p. 108 [**Aulosteges hispidus* GIRTY, 1920, p. 644; OD]. Externally somewhat resembling *Sphenalosia,* but differs in having fine ribbing, narrow convex pseudodeltidium; no teeth; cardinal process less narrow, shorter. *Upper Permian (Kazanian):* central USA.——FIG. 427,*4a–f.* **S. hispidus* (GIRTY), Phosphoria Formation, Wyoming; *a,b,* holotype, viewed ventrally, laterally, USNM 119088, ×1; *c,* detail of ventral valve exterior, ×2; *d,* incomplete

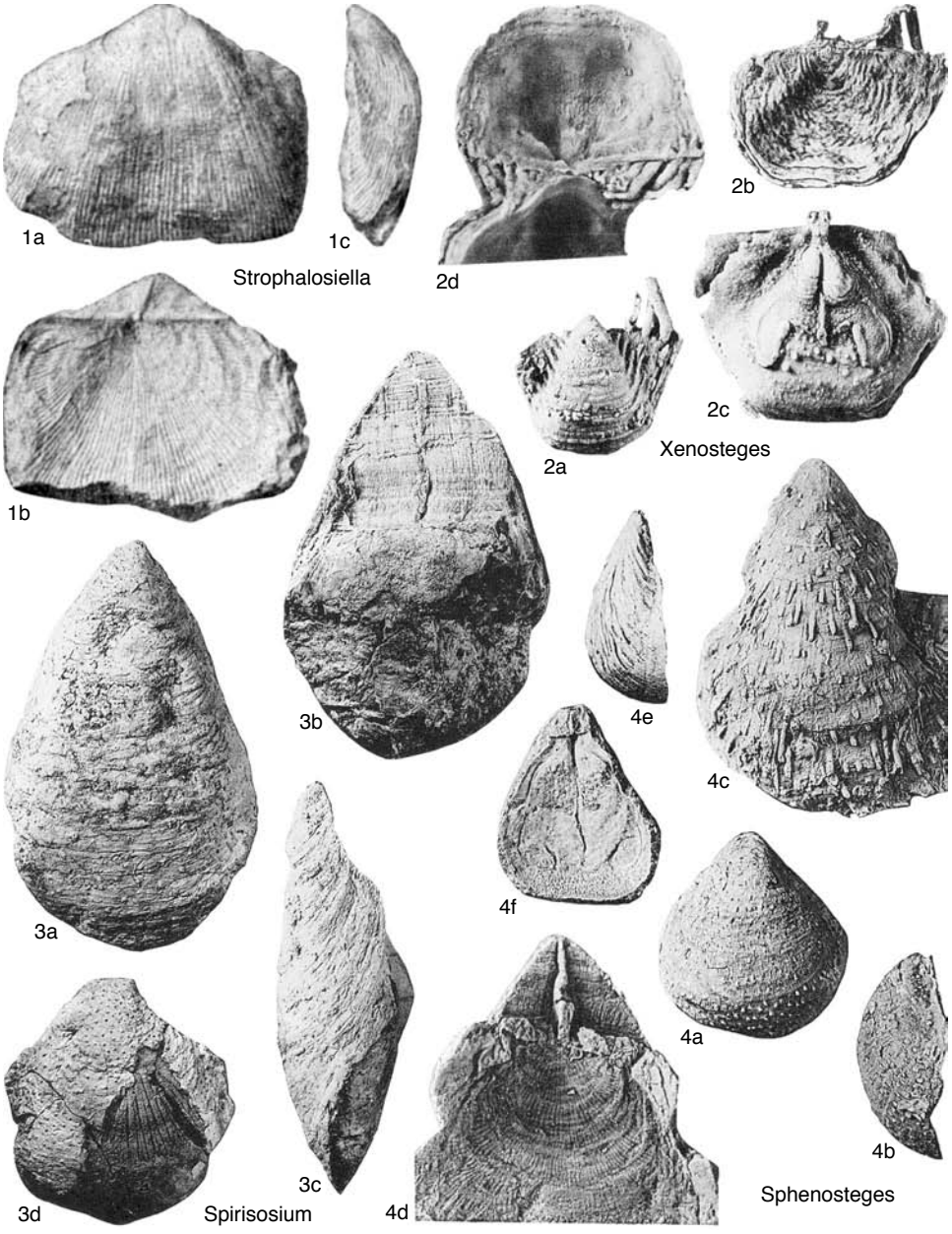

FIG. 427. Aulostegidae (p. 597–599).

dorsal view of shell, ×3; *e,* lateral view of ventral valve internal mold, ×1; *f,* internal mold of dorsal valve, ×1 (Muir-Wood & Cooper, 1960).

?Spirisosium DE GREGORIO, 1930, p. 23 [**S. primarium;* OD; =*Aulosteges karpinskyi* GEMMELLARO, 1892, p. 26]. Poorly known, medium size; elongate trigonal outline, no sulcus; interarea long, trigonal, narrow pseudodeltidium; concentric lamellose ornament weak; spines at edges of interarea, on flanks and small, distributed over ventral valve; reportedly rare on dorsal valve; interiors unknown. [This genus may prove to be more suitably

assigned to the Gondolininae.] *?Permian (?Wordian):* Sicily.——Fig. 427,*3a–d. *S. karpinskyi* (Gemmellaro), Sosio Limestone, Sicily; *a–c,* shell viewed ventrally, dorsally, laterally, ×0.75; *d,* partly exfoliated ventral valve showing part of diductor scar, ×0.75 (Muir-Wood & Cooper, 1960).

?Strophalosiella Licharew, 1935, p. 372 [**S. coraeformis;* OD]. Medium size, broadly subcircular with hinge slightly less than maximum width, high trigonal interarea with narrow pseudodeltidium; ribbing fine, entire other than at beak; rugae posterolaterally on dorsal valve; spines reported from edges of interarea, flanks, and possibly scattered on ventral valve only; interiors unknown. *Lower Permian:* northern Europe, Russia.——Fig. 427,*1a–c. *S. coraeformis,* Vymm basin, Russia; incomplete specimen viewed ventrally, dorsally, laterally, ×1 (Sarytcheva, Licharew, & Sokolskaja, 1960).

Strophalosiina Licharew, 1935, p. 369 [**Aulosteges tibeticus* Diener, 1897, p. 35; OD]. Smaller medium size, pentagonal outline with high triangular interarea; median sulcus full length of valve; profile strongly geniculate; ribbing on trails only; rugae on disks, narrow; spines scattered on ventral disk; interiors unknown. *upper Lower Permian (Artinskian)–Upper Permian (Kazanian*): Himalayas, Caucasus.——Fig. 425,*1a–d. *S. tibeticus* (Diener), Chitichum Limestone, Tibet, Diener specimen; viewed anteroventrally, ventrally, dorsally, laterally, ×1 (Muir-Wood & Cooper, 1960).

Xenosteges Muir-Wood & Cooper, 1960, p. 111 [**X. adherens;* OD]. Small, subquadrate outline with prominent wide ears; interarea short; delthyrium open; lamellose concentric ornament, especially on dorsal valve; spines large, rhizoid on hinge, ears, and at umbo, lacking elsewhere; lateral ridges in both valves, dorsally variably connected to marginal ridge. *upper Lower Permian (Artinskian)–lower Upper Permian (lower Kazanian):* southern USA.——Fig. 427,*2a–d. *X. adherens,* Cathedral Mountain Formation, Texas; *a,* ventral valve exterior, ×2; *b,* dorsal valve exterior, ×2; *c,* dorsal valve interior, ×4 (Muir-Wood & Cooper, 1960); *d,* attached ventral valve viewed internally, ×2 (Cooper & Grant, 1975).

Subfamily INSTITELLINAE Muir-Wood & Cooper, 1960

[Institellinae Muir-Wood & Cooper, 1960, p. 117] [=Costellariinae Muir-Wood & Cooper, 1960, p. 123; Sinuatellidae Muir-Wood & Cooper, 1960, p. 124]

Corpus rugose to reticulate; trails commonly ribbed with bordering structures of flanges or gutters; dorsal spines commonly absent. *Lower Carboniferous (Viséan)–lower Upper Permian (Capitanian).*

Institina Muir-Wood & Cooper, 1960, p. 164 [**Productus marginalis* de Koninck, 1847a, p. 238; OD]. Rugae on visceral disks, ribbing on trail from geniculated cincture; cardinal process narrow, cardinal ridges reach ears. *Lower Carboniferous (upper Viséan):* Europe.——Fig. 428,*1a–f. *I. marginalis* (de Koninck), Asbian, Visé; *a–d,* partially exfoliated shell viewed ventrally, dorsally, posteriorly, laterally, ×2; *e,* oblique lateral view of ventral valve exterior with trail, ×2 (new); *f,* replica of dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Costellarina Cooper & Muir-Wood, 1967, p. 808, *nom. nov. pro Costellaria* Muir-Wood & Cooper, 1960, p. 123, *non* Swainson, 1840 [**C. costellata* Muir-Wood & Cooper, 1960, p. 124; OD]. Small, around 10 mm wide, subquadrate outline, gently concavoconvex profile; interarea wide, short; cicatrix; ribbing starting anteriorly on reticulate disks; spines semirecumbent, scattered over ventral valve plus clusters on ears; cardinal process sessile, broadly bilobed. [The described specimens may not be adult.] *Lower Permian:* USA.——Fig. 428,*2a–g. *C. costellata* Muir-Wood & Cooper, Talpa Formation, Texas; *a,* holotype, viewed dorsally, USNM 124110a, ×2; *b–d,* shell viewed ventrally, posteriorly, laterally, ×2; *e,* ventral valve exterior, ×3; *f,* dorsal valve interior, ×4; *g,* detail of cardinal process externally, ×6 (Muir-Wood & Cooper, 1960).

Craspedona Cooper & Grant, 1975, p. 881 [**C. newelli;* OD]. Small circular corpus with wide hinge, tubiform anterior trails forming part of flanges; ventral interarea short; cicatrix minute; both disks weakly reticulate, ribbing becoming stronger anteriorly; spines rhizoid at posterior margins and ears, fine spines scattered on ventral corpus; lateral plus marginal ventral ridges; cardinal process small, sessile, partly overhung dorsally by zygidium extending as lateral ridges, ear baffles; near hinge irregular tubercles fit corresponding pits in ventral hinge region. *upper Lower Permian (Kungurian)–Upper Permian (Capitanian):* USA.——Fig. 429,*1a–e. *C. newelli,* Bell Canyon Formation, Texas; *a,b,* holotype, viewed ventrally, dorsally, USNM 154172a, ×1; *c,* ventral valve exterior, ×1.5; *d,* ventral valve interior, ×1.5; *e,* dorsal valve interior, ×1.5 (Cooper & Grant, 1975).

Glyptosteges Cooper & Grant, 1975, p. 876 [**G. intricatus;* OD]. Small, with small cicatrix; spines rhizoid posteriorly, recumbent on venter; both valves strongly, fully costate; ventral adductor scars elevated, surrounded by flabellate diductor scars; cardinal process small; lateral ridges extending straight across ears. *Lower Permian (Sakmarian–Artinskian):* USA.——Fig. 429,*3a–e. *G. intricatus,* Skinner Ranch Formation, Texas; *a,b,* ventral valve viewed ventrally, laterally, ×1; *c,* attached ventral valve exterior, ×2; *d,e,* dorsal valve exterior, interior, ×1.5 (Cooper & Grant, 1975).

Institella Cooper, 1942, p. 230 [**Productus leonardensis* R. E. King, 1931, p. 70; OD]. Medium size; ventral profile with disk weakly convex, geniculate with trail margin reflexed; median sulcus prominent, forming V-shaped fold in gutter; interarea short; cicatrix small; ribbing disappearing on gutter; spines thick, rhizoid at hinge, ears, smaller and scattered on venter; dorsal lateral ridges variable, may extend

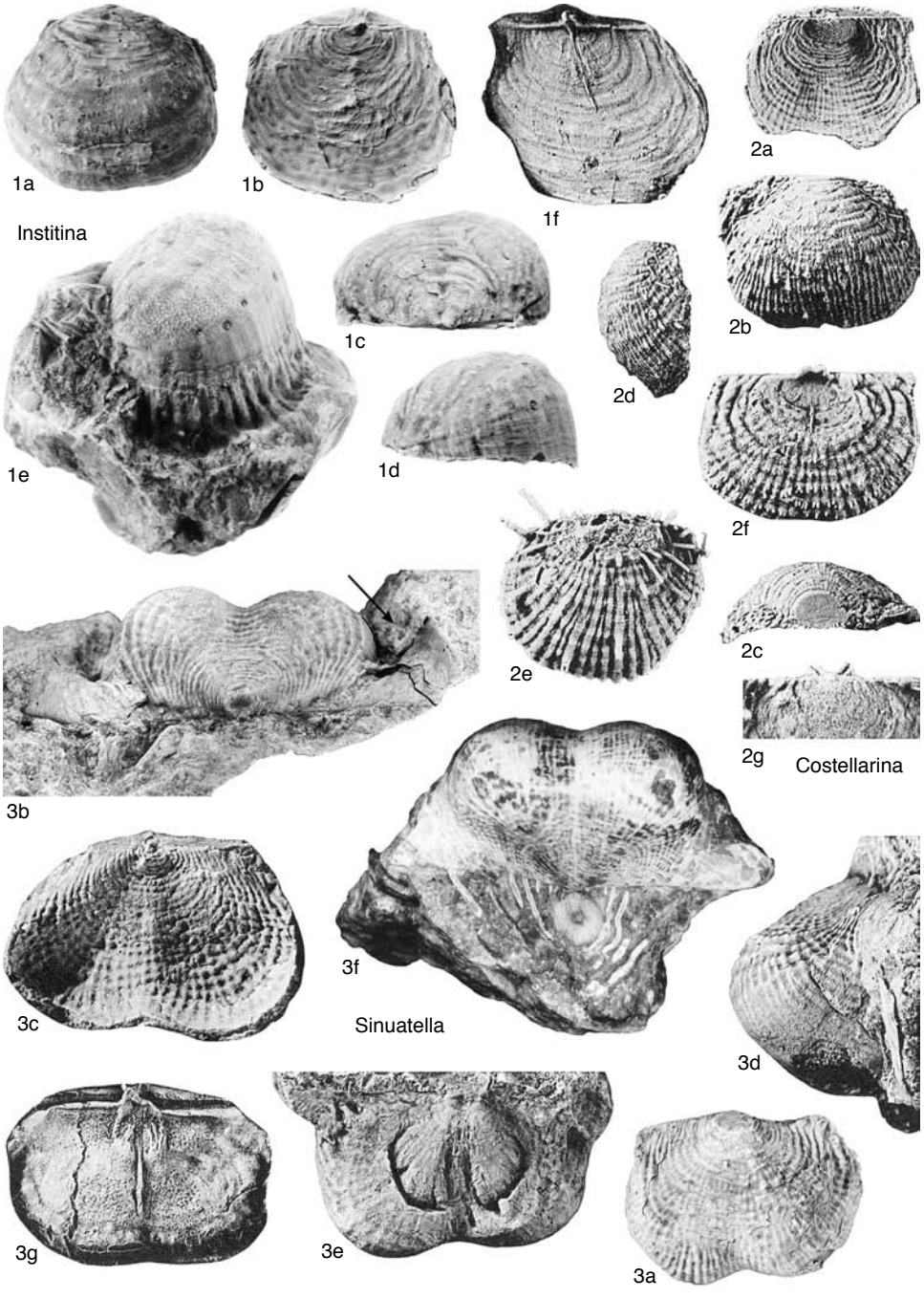

FIG. 428. Aulostegidae (p. 599–604).

to lateral margins. *upper Lower Permian–lower Upper Permian:* USA.——FIG. 429,*4a–e. *I. leonardensis* (R. E. KING), Cathedral Mountain Formation, Texas; *a,* ventral valve exterior, ×1.5; *b,* lateral view of ventral valve, ×1; *c,* shell viewed dorsally, ×1; *d,* dorsal valve interior, ×1 (Muir-Wood & Cooper,

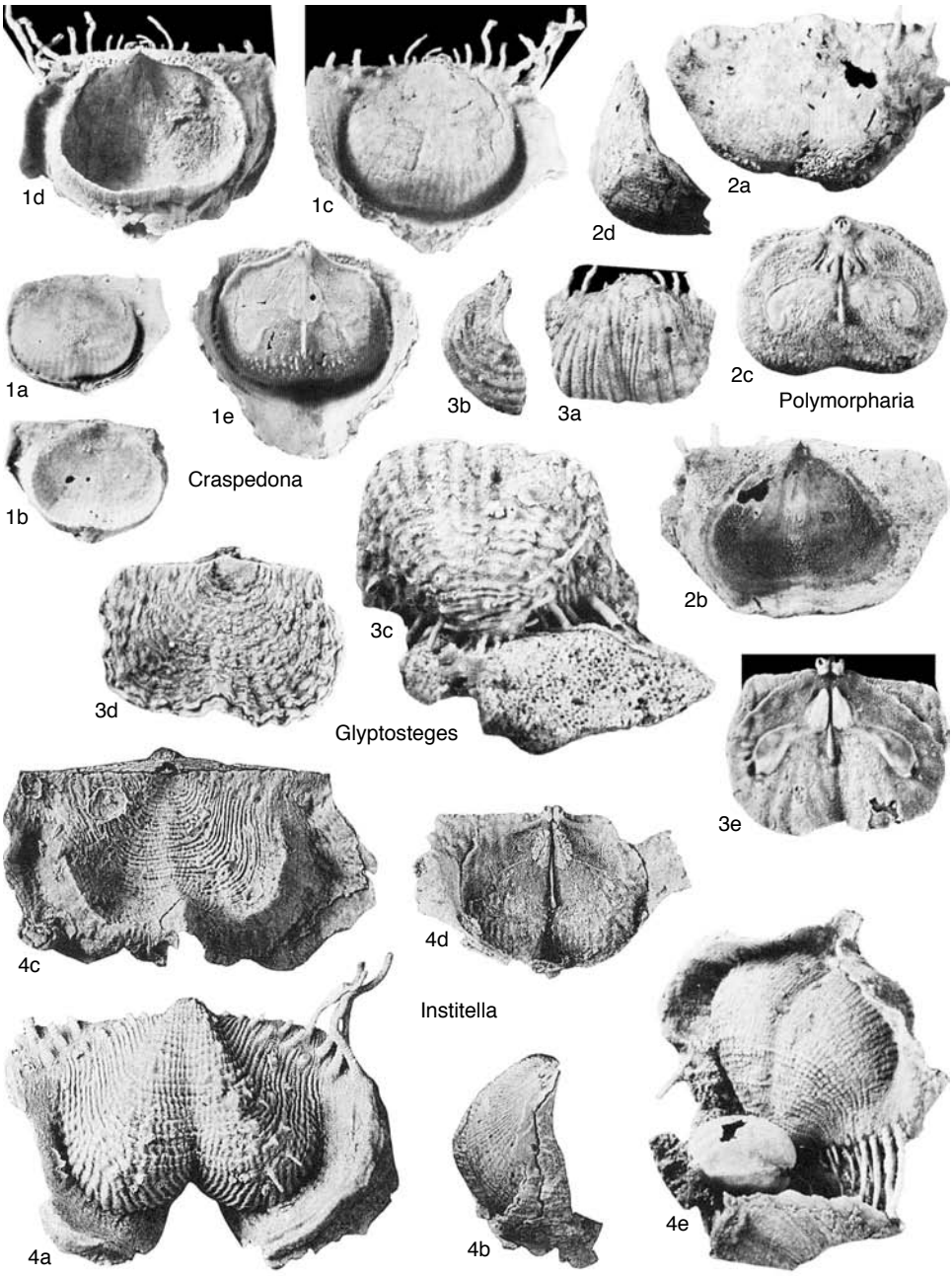

FIG. 429. Aulostegidae (p. 599–601).

1960); *e,* oblique view of attached shell, ×1 (Cooper & Grant, 1975).

Polymorpharia COOPER & GRANT, 1975, p. 1143 [**P. polymorpha;* OD]. Resembles *Crespedona,* but without strong median flanged trail; lacking rugae on disks; dorsal adductor scars shorter, strongly marked. *upper Lower Permian (Roadian)–lower Upper Permian (Wordian):* USA.——FIG. 429,*2a–d.* **P. polymorpha,* Cherry Canyon Formation, Texas; *a,b,* ventral valve exterior, interior, ×1; *c,* dorsal valve interior, ×1; *d,* dorsal valve viewed laterally, ×1 (Cooper & Grant, 1975).

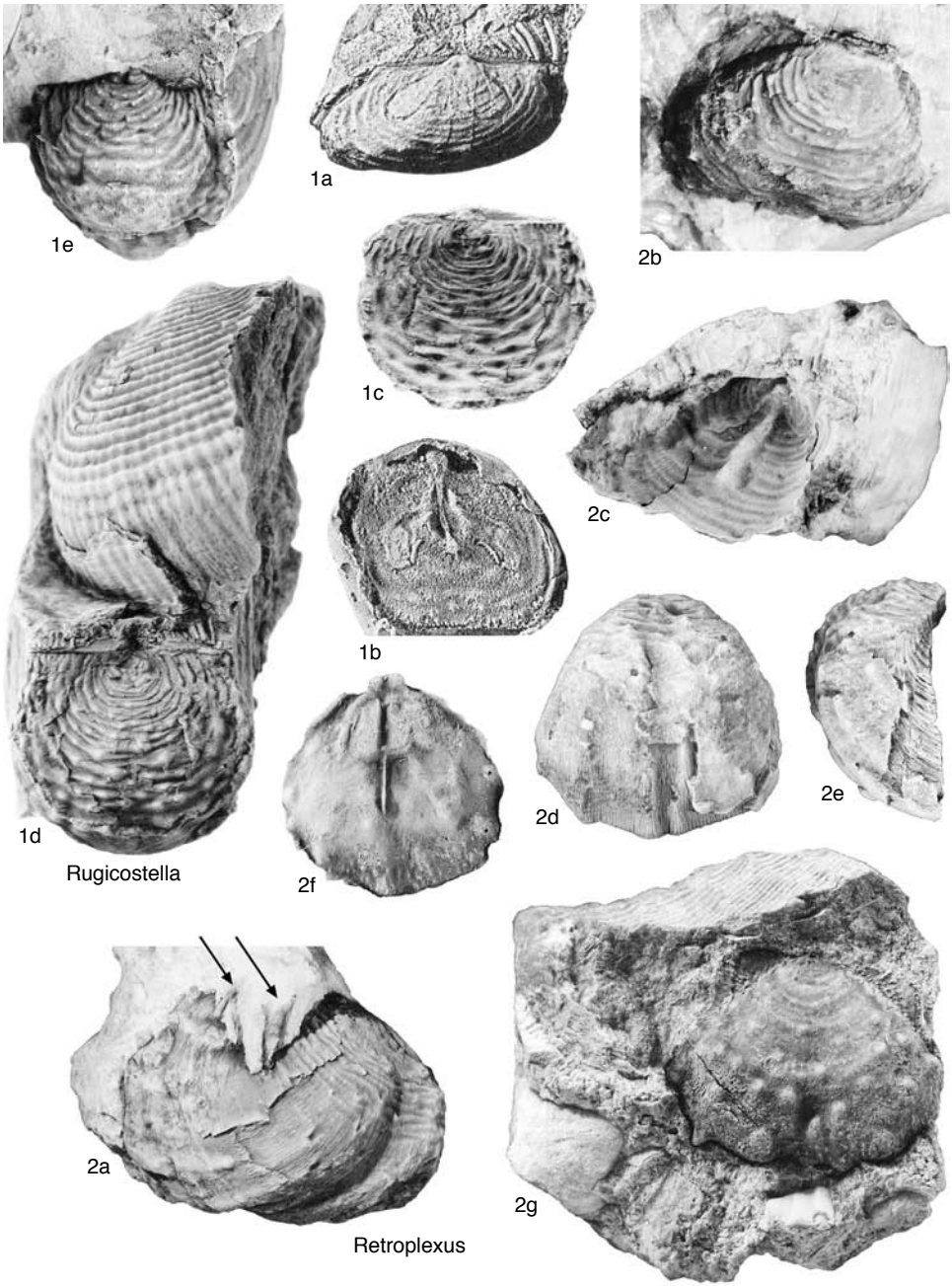

FIG. 430. Aulostegidae (p. 602–604).

Retroplexus BRUNTON & MUNDY, 1988b, p. 74 [**R. parkhousensis;* OD]. Cicatrix small, variable; visceral disks strongly differentiated from ears, rugose; trails smooth with distal spine ridges, rhizoid spines long from hinge and flanks, other spines on ventral corpus and trail; dorsal adductor scars slightly elevated; ear baffles. *Lower Carboniferous (upper Viséan):* British Isles, ?western Europe.——FIG. 430,*2a–g.* **R. parkhousensis,* Asbian; *a,* holotype, viewed anterolaterally showing spines extending into matrix (*ar-*

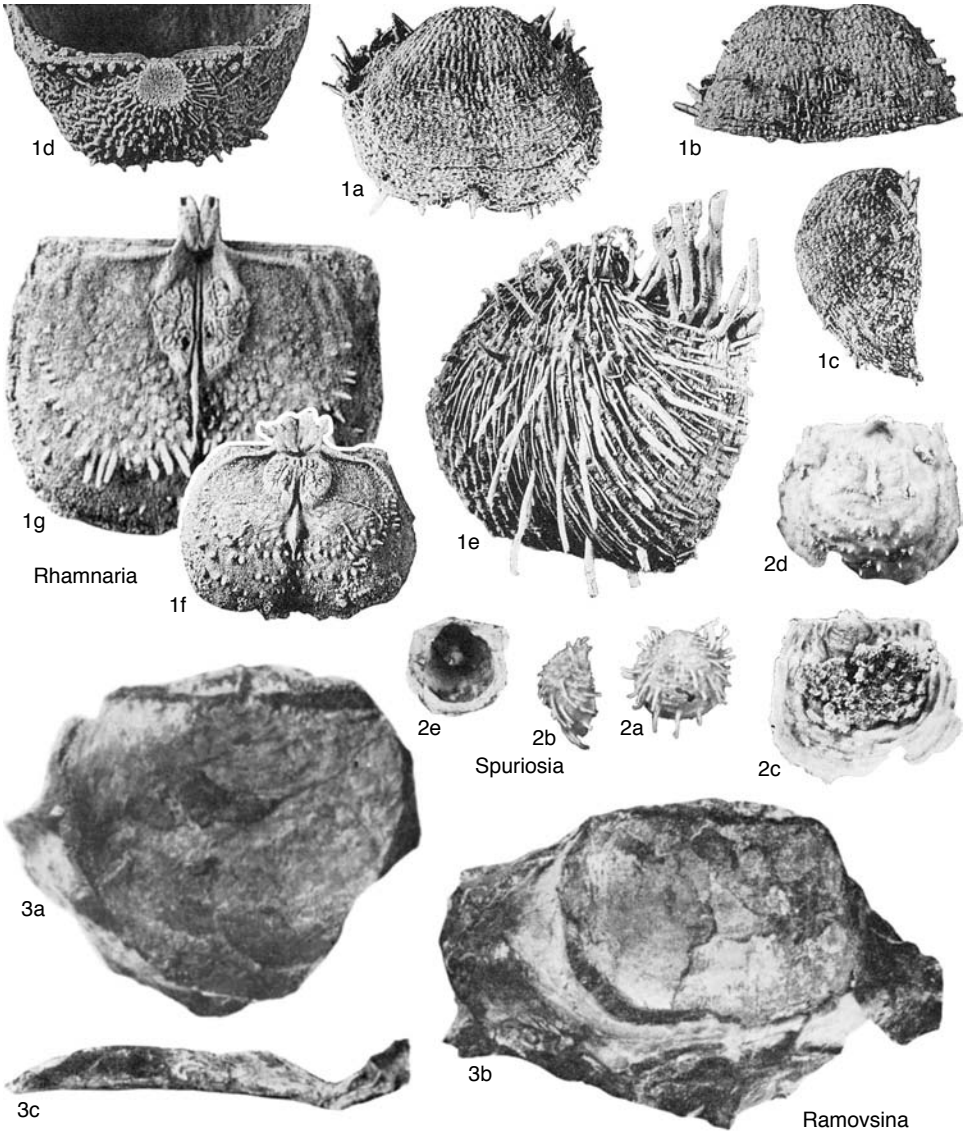

FIG. 431. Aulostegidae (p. 604–605).

rows), Derbyshire, BMNH BB58751, ×2; *b,* juvenile ventral valve with cicatrix adhering to *Tabulipora,* Derbyshire, ×3; *c,* incomplete ventral interior, Derbyshire, ×3; *d–f,* internal mold viewed anteriorly, laterally, and replica of dorsal valve corpus interior, Staffordshire, ×2; *g,* deeply exfoliated dorsal valve interior with pustules indicating ventral spine positions, Staffordshire, ×2 (Brunton & Mundy, 1988b).

Rugicostella MUIR-WOOD & COOPER, 1960, p. 166 [**Productus nystianus* DE KONINCK, 1842, p. 202; OD]. Small; strongly geniculate with short ventral interarea; ventral corpus with irregular rugae, swollen spine bases, attachment spines at ventral hinge; cincture, trail smooth to coarsely ribbed; cardinal process supported by short median ridge; cardinal ridges extend as ear baffles, subperipheral rim. *Lower Carboniferous (upper Viséan):* Europe, ?Far East.——FIG. 430,*1a–e.* **R. nystiana* (DE KONINCK); *a,* internal mold of ventral valve with hinge spines, upper Viséan, Visé, ×3; *b,* replica of dorsal valve interior, upper Viséan, Visé, ×4 (Muir-Wood & Cooper, 1960); *c,* dorsal view of complete corpus with *d,* showing its counterpart attached to

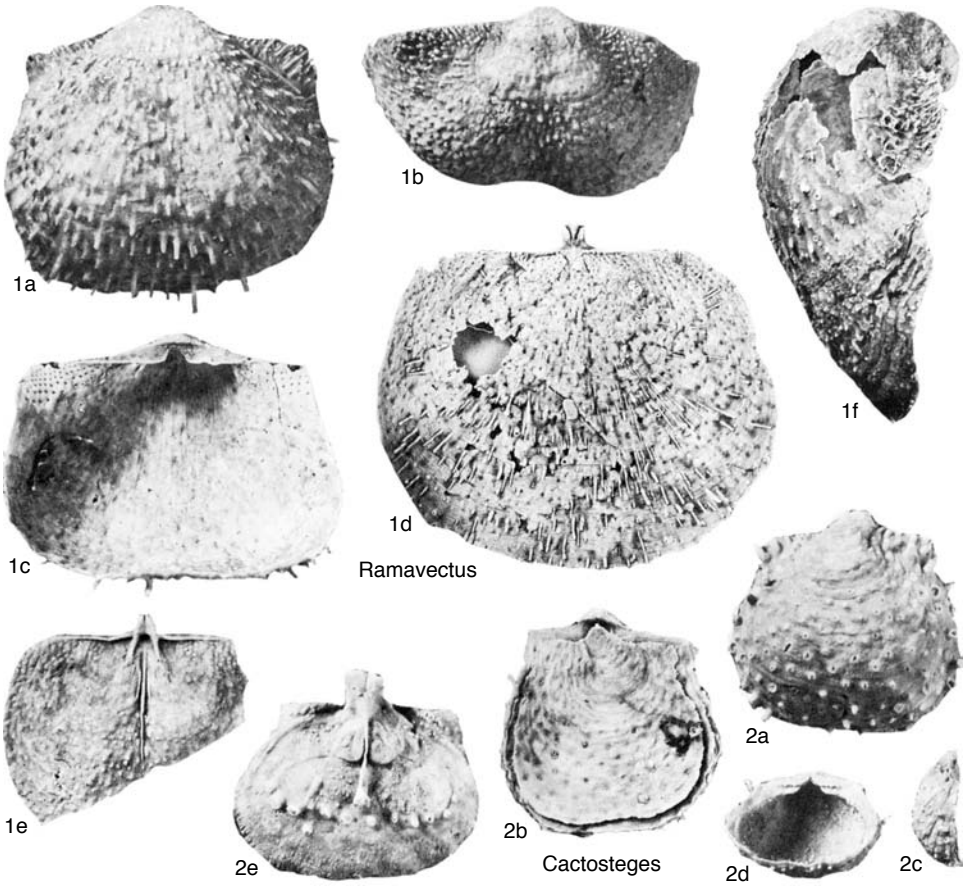

FIG. 432. Aulostegidae (p. 605).

Limbifera, Asbian, northern Yorkshire, ×3; *e,* ventral view of corpus and part of long trail, Asbian, northern Yorkshire, ×3 (new).

Sinuatella MUIR-WOOD, 1928, p. 37 [**Leptaena sinuata* DE KONINCK, 1851, p. 654; OD]. Ventral outline transverse, anteriorly sulcate; visceral disks reticulate, trails weakly ribbed with flange or gutters; cicatrix; attachment spines posteriorly and finer, rare corpus spines; ventral muscle field bordered anterolaterally by ridges. *Lower Carboniferous (Viséan–lower Namurian):* Eurasia. ——FIG. 428,*3a–g.* **S. sinuata* (DE KONINCK); *a,* ventral valve exterior with cicatrix, Asbian, North Yorkshire, ×1.5; *b,* posterior view of specimen with cicatrix, lateral gutter (*arrow*), Asbian, North Yorkshire, ×2 (new); *c,* dorsal valve exterior, Asbian, North Yorkshire, ×2; *d,* lateral view showing geniculate ventral valve, upper Viséan, Staffordshire, ×2; *e,* partial internal mold of ventral valve, upper Viséan, Staffordshire, ×2 (Muir-Wood & Cooper, 1960); *f,* ventral view of shell with spines clasping section of crinoid stem, Asbian, Derbyshire, ×1.5 (new); *g,* replica of young dorsal valve interior, Visé, ×2 (Muir-Wood & Cooper, 1960).

Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

[Rhamnariinae MUIR-WOOD & COOPER, 1960, p. 119] [=Ramovsiinidae SREMAC, 1986, p. 14]

Interarea reduced or rudimentary; spines on both valves; cardinal process commonly wide; dorsal adductor scars raised or on platforms. *Lower Permian (Asselian)–Upper Permian (Kazanian).*

Rhamnaria MUIR-WOOD & COOPER, 1960, p. 119 [**R. kingorum;* OD]. Medium, subcircular outline with weakly developed ears; commonly with cicatrix; sulcation weak; disks plano- to slightly concavo-convex with short dorsal trail; dorsal valve strongly

dimpled; spine bases swollen on ventral disk, elongate anteriorly, spines thick in clusters at hinge and flanks, semierect and mixed with thin recumbent spines on rest of valve; cardinal process variable, wide; endospines strong anteriorly on disk. *lower Upper Permian:* southern USA.——Fig. 431,*1a–g.* **R. kingorum,* Word Limestone, Texas; *a–c,* holotype, ventral valve viewed ventrally, anteriorly, laterally, USNM 124072b, ×1; *d,* ventral valve viewed posteriorly, ×1; *e,* ventral valve viewed obliquely, ×1; *f,* dorsal valve interior, ×1; *g,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Cactosteges Cooper & Grant, 1975, p. 850 [**C. anomalus;* OD]. Small, subcircular shells with reduced ventral interarea; concentric ornament weak; dorsal spines more fine than ventral spines; ventral adductor scars elevated on low platforms; cardinal process thick set, weakly bilobed; medium septum low, thin, extending almost to disk margin; endospines prominent anteriorly. *lower Upper Permian:* USA.——Fig. 432,*2a–e.* **C. anomalus,* Word Formation, Texas; *a,b,* holotype viewed ventrally, dorsally, USNM 151297a, ×2; *c,* holotype viewed laterally, USNM 151297a, ×1; *d,* ventral valve interior, ×1; *e,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

Ramavectus Stehli, 1954, p. 327 [**R. diabloensis;* OD]. Somewhat resembles *Reedoconcha* in size and shape, with concentric lamellae becoming marked toward ventral margin; ventral spine bases elongate posteriorly with semirecumbent spines, more erect spines at hinge and ears, dorsal spines fine and semirecumbent; cardinal process short, trifid, supported by pair of divergent ridges enclosing posterior edges of weak adductor scars; cardinal ridges barely reaching ears. *Lower Permian (Artinskian):* southern USA.——Fig. 432,*1a–f.* **R. diabloensis,* Bone Spring Formation, Texas; *a–c,* ventral valve viewed ventrally, posteriorly, internally, ×1; *d,* dorsal valve exterior, ×1; *e,* dorsal valve interior, ×1; *f,* lateral view of large ventral valve, ×0.75 (Cooper & Grant, 1975).

Ramovsina Sremac, 1986, p. 14 [**R. likana;* OD]. Medium-sized corpus with laterally and anteriorly extended trails; ventral interarea short, approximately equal to corpus width; spines both coarse, fine on both valves, coarse on hinge, ears; cardinal process large, quadrifid. *lower Upper Permian (Kazanian):* Croatia.——Fig. 431,*3a–c.* **R. likana,* Murghabinian, Velebit Mountains; *a,* holotype, viewed dorsally, GPZ 1223, ×1; *b,c,* dorsal, lateral views of specimen with wide flange on right, ×0.75 (Sremac, 1986).

Spuriosia Cooper & Grant, 1975, p. 898 [**S. circularis;* OD]. Small, around 5 mm wide, with minute cicatrix; ventral interarea very short, dorsal valve with irregular fine rugae, sparse spines. *Lower Permian (Asselian–Sakmarian):* USA.——Fig. 431,*2a–e.* **S. circularis,* Neal Ranch Formation, Texas; *a,b,* holotype, viewed ventrally, laterally, USNM 153490a, ×2; *c,d,* dorsal valve exterior, interior, ×4; *e,* ventral valve interior, ×2 (Cooper & Grant, 1975).

Subfamily GONDOLININAE Jin Yu-gan, Brunton, & Lazarev, 1998

[Gondolininae Jin Yu-gan, Brunton, & Lazarev, 1998, p. 8]

Elongate trigonal, homeomorph of *Striatifera,* but with long, narrow ventral interarea; spines rhizoid on ventral umbonal margins. *Lower Carboniferous (upper Viséan–lower Serpukhovian).*

Gondolina Ching Yu-gan & Liao Zhao-ting in Wang Yu, Ching Yu-gan, & Fang Da-wei, 1966, p. 412 [**G. weiningensis;* OD]. Resembles *Striatifera* in outline, but with extended ventral umbo, long triangular interarea; rugae irregular, interrupting ribbing; spines thin, rhizoid, in clusters on umbonal flanks and unknown elsewhere. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* China.——Fig. 433*a–c.* **G. weiningensis,* lower Serpukhovian, Guizhou; holotype, viewed ventrally, dorsally, laterally, NIGP 22444, ×0.75 (Wang, Ching, & Fang, 1966).

Family COOPERINIDAE Pajaud, 1968

[*nom. transl.* Cooper & Grant, 1975, p. 822, *ex* Cooperininae Pajaud, 1968, p. 158]

Small elongate to bilobate outline, cemented by large cicatrix, spines, or both; fine spines commonly also on dorsal valves; hinge teeth, pseudodeltidium absent; dorsal interior with adductor platform, prominent brachial ridges. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Subfamily COOPERININAE Pajaud, 1968

[Cooperininae Pajaud, 1968, p. 158]

Size small for family; ventral interarea, cicatrix surrounded by rhizoid spines; dorsal muscle platforms short. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Cooperina Termier, Termier, & Pajaud, 1966, p. 332 [**C. inexpectata;* OD]. Minute, subquadrate; ventral exterior slightly lamellose, spinose; dorsal valve flat to slightly concave, some spinose; anterior commissure emarginate; ventral interior with long, low, median ridge; dorsal disk almost surrounded by brachial ridges; cardinal process weakly bilobed; adductor scars on platforms elevated anteriorly. *Permian (Wordian):* USA, Thailand.——Fig. 434,*1a–d.* **C. inexpectata,* Wordian, Texas; *a,b,* shell with large cicatrix viewed ventrally, dorsally, ×6; *c,* ventral valve interior, ×6; *d,* dorsal valve interior, ×6 (Cooper & Grant, 1975).

Ansehia Termier & Termier, 1970, p. 456 [**A. thecideiformis;* OD]. Small, around 5 mm wide,

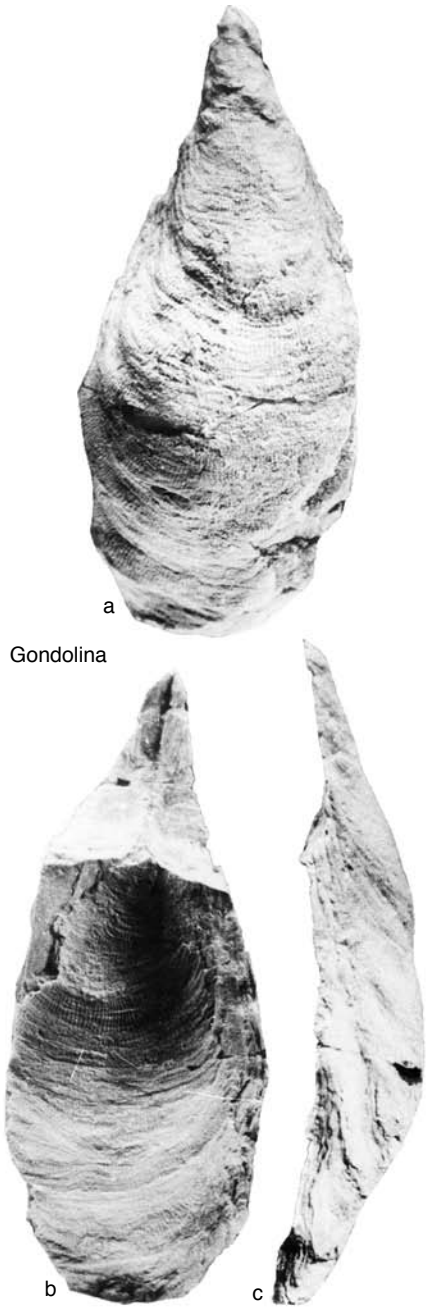

FIG. 433. Aulostegidae (p. 605).

elongate, but with small ears at wide hinge; ventral interarea prominent, flat; shell attached ventrally; strongly uniplicate with narrow, deep ventral sulcus, high dorsal fold; spines on ventral valve only, curved forward, semirecumbent; interiors unknown. *Upper Permian (Capitanian):* Cambodia.——FIG. 434,*4a,b. *A. thecideiformis,* Dzhulfian, Pnom Ansch; holotype, viewed ventrally, dorsally, number and repository unknown, ×6 (Termier & Termier, 1970).

Atelestegastus COOPER & GRANT, 1975, p. 828 [**A. marginatus;* OD]. Minute, attached by cicatrix, rhizoid spines; outline subcircular, rectimarginate; ventral interarea variable, commonly narrow; dorsal disk flat with short geniculate trail; cardinal process bilobed, quadrifid with short shaft; lateral ridges separate ears; dorsal muscle scars slightly raised; brachial ridges large, bounded anteriorly by row of endospines. *Lower Permian (Asselian–Sakmarian):* USA.——FIG. 434,*2a–e. *A. marginatus,* Neal Ranch Formation, Texas; *a–c,* holotype, viewed ventrally, laterally, dorsally, USNM 154135a, ×6; *d,* ventral valve exterior, ×6; *e,* dorsal valve interior, ×6 (Cooper & Grant, 1975).

Falafer GRANT, 1972, p. 216 [**F. epidelus;* OD]. Small with sporadic ventral sulcus; ventral interarea short, flat to concave; spines few, on ventral valve only; ventral interior with broad muscle platform having median notch; dorsal interior with paired crenulated ptycholophous brachidia arching posteriorly; cardinal process slender, quadrifid. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 434,*3a–f. *F. epidelus,* Episkope Limestone, Idhra; *a,* holotype, slightly gaping, viewed anteriorly, USNM 169763, ×6; *b,* ventral valve interior, ×6; *c,* shell exterior viewed dorsally, ×6; *d,* dorsal valve interior viewed ventrally, ×6; *e,f,* anteroventral, lateral views of dorsal valve interior, brachidium, ×6 (Grant, 1972).

Subfamily EPICELIINAE Grant, 1972

[Epiceliinae GRANT, 1972, p. 223]

Large for family; hinge narrow with small interarea; ventral spines restricted around cicatrix; brachial ridges multilobed. *Upper Permian (?Capitanian, Changhsingian).*

Epicelia GRANT, 1972, p. 223 [**E. episcopiensis;* OD]. Small, outline bilobate; ventral valve deeply sulcate with large cicatrix; spines fused together around cicatrix; dorsal valve thick, strongly emarginate, exterior with short spines and paired pits reflecting internal brachiophore platforms; cardinal process small, trifid, extending ventrally. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 435,*1a–f. *E. episcopiensis,* Episkopi Limestone, Idhra; *a–d,* holotype, viewed ventrally, dorsally, anteriorly, laterally, USNM 169751, ×6; *e,* ventral valve interior, ×6; *f,* dorsal valve interior, ×6 (Grant, 1972).

Ceocypea GRANT, 1972, p. 225 [**C. dischides;* OD]. Ventral valve bilobate with deep sulcus; cicatrix surrounded by fine flattened spines; cardinal process small, knoblike; brachial ridges strong, indicative of ptycholophe. *Upper Permian (?Capitanian, Changhsingian):* Thailand, Pakistan, Greece.——FIG. 435,*2a–c. *C. dischides,* Episkopi Limestone,

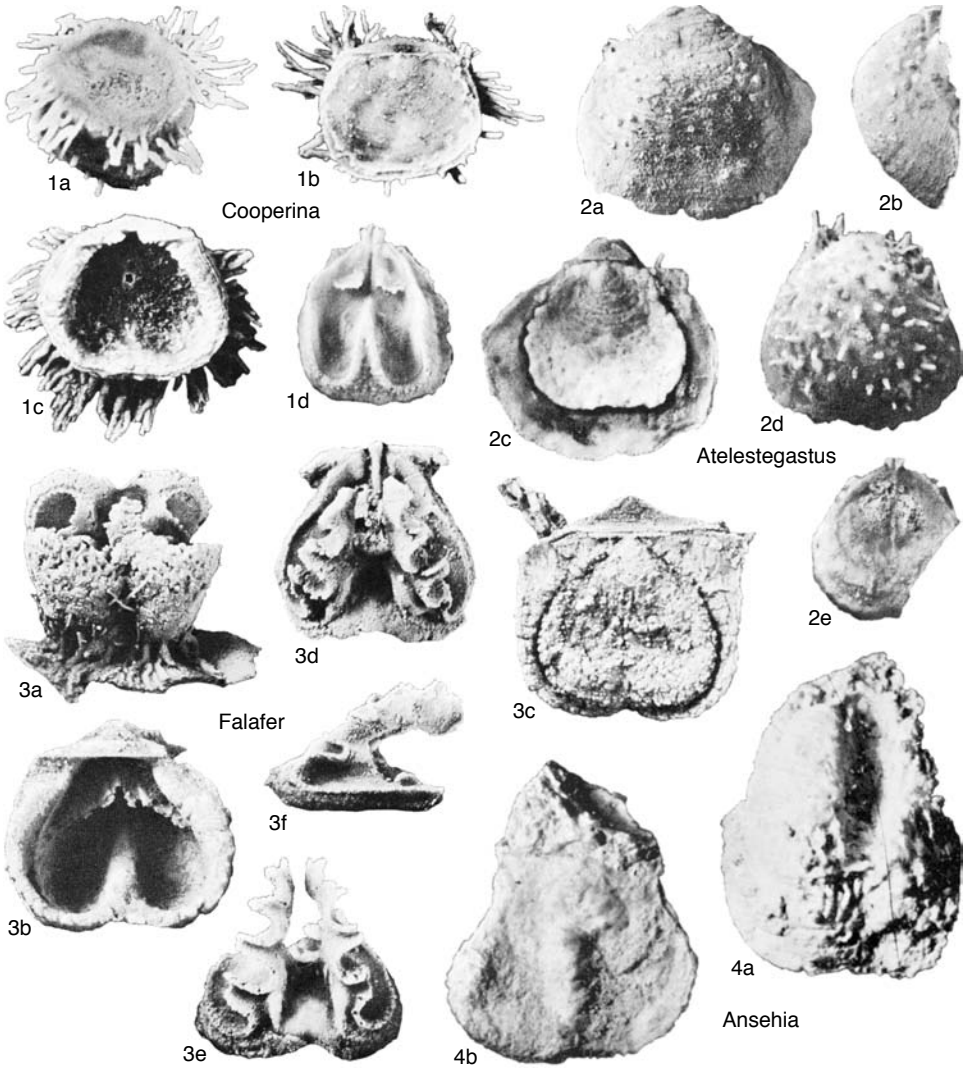

FIG. 434. Cooperinidae (p. 605–606).

Idhra; holotype, viewed ventrally, dorsally, laterally, USNM 169762, ×4 (Grant, 1972).——FIG. 435,*2d,e. C. chytrina* GRANT, Changhsingian, Kalabagh to Wargal Limestones, Khisor Range; *d,* internal mold of ventral valve, ×4; *e,* incomplete dorsal valve interior, ×4 (Grant, 1972).

Family SCACCHINELLIDAE Licharew, 1928

[*nom. transl.* WILLIAMS, 1953b, p. 12, *ex* Scacchinellinae LICHAREW, 1928, p. 265]

Prominent ventral median septum, widely bilobed cardinal process. *Lower Permian–Upper Permian (Capitanian).*

Subfamily SCACCHINELLINAE Licharew, 1928

[Scacchinellinae LICHAREW, 1928, p. 265]

Ventral valve conical with transverse partitions apically; dorsal valve lidlike; deep corpus cavity. *Lower Permian–Upper Permian (Wordian).*

Scacchinella GEMMELLARO, 1891, p. 22 (1897, p. 114) [**S. variabilis* GEMMELLARO, 1897, p. 114; SD SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 110]. Commonly deeply conical with weakly convex dorsal valve, prominent and wide ventral interarea occupying one side; spines rhizoid

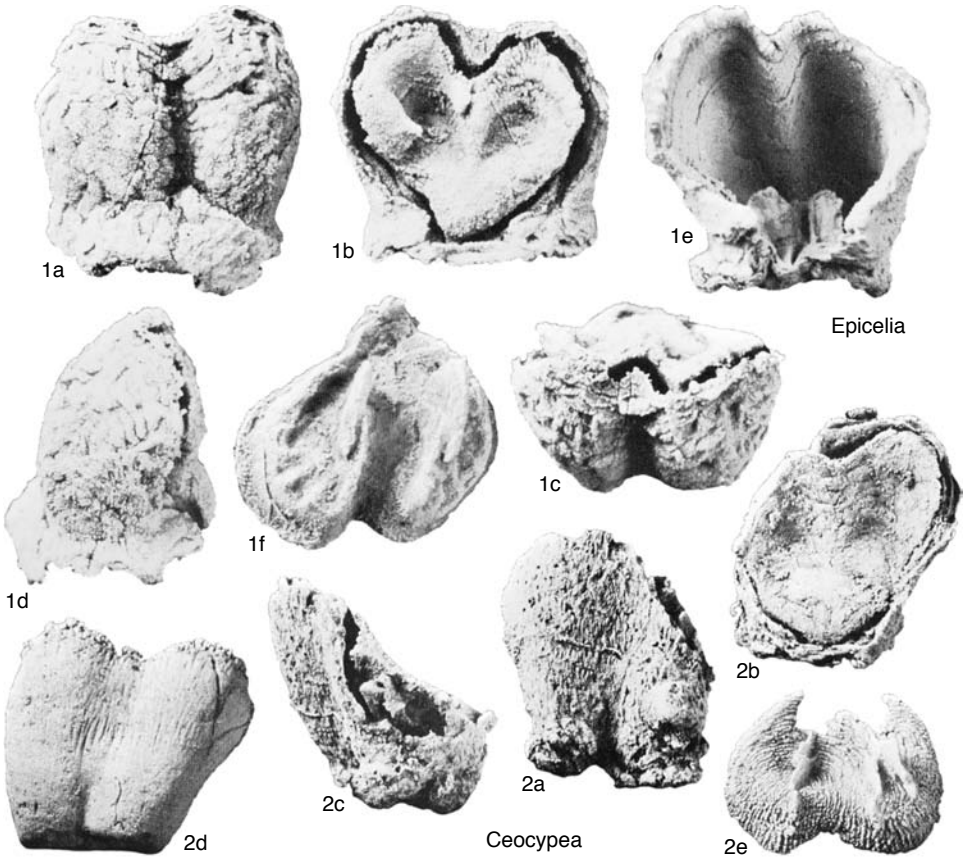

FIG. 435. Cooperinidae (p. 606–607).

ventrally, fine dorsally; dorsal adductor platforms overhang laterally. *Permian (Wordian):* North America, southern Europe, Russia.——FIG. 436,*1a.* **S. variabilis* GEMMELLARO, Sosio Limestone, Sicily; shell viewed posteriorly, ×3 (Rudwick & Cowen, 1968).——FIG. 436,*1b–d. S. americana* STEHLI, Hess Formation, Texas; *b,* attached specimen viewed anteriorly, ×1; *c,* posterior internal region of articulated valves showing cardinal process, ventral septum, ×1; *d,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Derbyella GRABAU, 1931, p. 269 [**D. bureri;* OD]. Poorly known, small to medium subconical outline with long, triangular ventral interarea; ribbing apparently interrupted by concentric ornament; ventral interior with median septum, myocoelidium. *Lower Permian:* Mongolia.——FIG. 436,*4a,b.* **D. bureri,* Jisu Honguer Limestone, Jisu Honguer; *a,* holotype viewed ventrally, GSC 1416, ×1; *b,* holotype viewed dorsally, GSC 1416, ×2 (Grabau, 1931).

Subfamily TSCHERNYSCHEWIINAE Muir-Wood & Cooper, 1960

[Tschernyschewiinae MUIR-WOOD & COOPER, 1960, p. 126]

Concavoconvex profile; cicatrix common, plus support spines. *Upper Permian (Capitanian).*

Tschernyschewia STOYANOW, 1910, p. 853 [**T. typica;* OD]. Smaller medium size with subcircular corpus outline, short trails; cicatrix small, variable; hinge narrow with short interareas; external ornament somewhat resembling *Waagenoconcha,* but internally with high ventral median septum fitting between lobes of cardinal process. [*Septoproductus* FRECH, 1911, p. 132 (type, *Productus abichi* WAAGEN, 1884, p. 697 was misidentified by FRECH (1911) and suppression of his genus is sought; BRUNTON, 1997, ICZN Case 3034.] *Upper Permian (Capitanian):* southern Europe, China.——FIG. 436,*3a–e.* **T.*

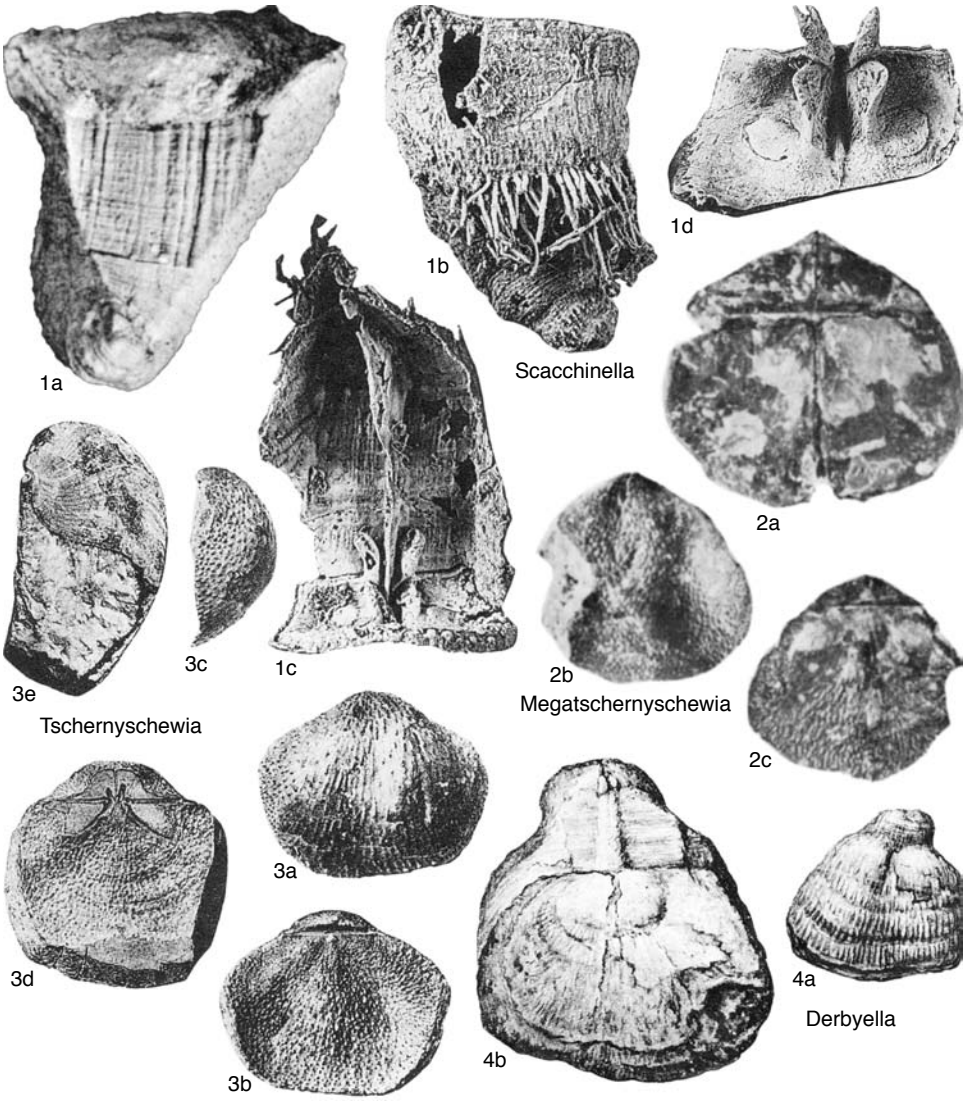

FIG. 436. Scacchinellidae (p. 607–609).

typica, Dzhulfian, Armenia; *a–c,* specimen viewed ventrally, dorsally, laterally, ×1; *d,* dorsal view of specimen cut at beak showing cardinal process, median septum, ×1; *e,* longitudinal section of specimen showing large ventral median septum, ×1 (Muir-Wood & Cooper, 1960).

Megatschernyschewia SREMAC, 1986, p. 19 [**M. longiseptata;* OD]. Similar to *Tschernyschewia,* but larger, around 40 mm wide, with longer, triangular ventral interarea. *Upper Permian (Kazanian):* Croatia.——FIG. 436,*2a–c.* **M. longiseptata,* Murghabian, Velebit Mountains; *a,* holotype, internal mold of specimen retaining pieces of shell, viewed dorsally, GPZ 1237, ×1; *b,c,* specimen viewed ventrally, dorsally, ×1 (Sremac, 1986).

RICHTHOFENIOIDEA

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Superfamily RICHTHOFENIOIDEA Waagen, 1885

[*nom. correct.* BRUNTON, LAZAREV, & GRANT, 1995, p. 933, *pro* Richthofeniacea MUIR-WOOD, 1955, p. 69, *nom. transl. ex* Richthofeniidae WAAGEN, 1885, p. 729]

Ventral valve conical or sphenoid, dorsal valve caplike or recessed below ventral margin; ventral valve attached to substrate directly or by rhizoid spines, or by both; interarea absent. *Upper Carboniferous–Upper Permian.*

Richthofenioids, with their coral-like appearance, are among the more unusual brachiopods but can be derived morphologically from more conventional productides. Among the Strophalosiidina there is a tendency toward long or elaborate ventral trails. Any initially attached form that continued to grow its ventral trail so as to curve up and posteriorly toward the umbo would, if rotated anteriorly and with the lateral margins of the trails fused posteriorly, display the basic shape of a richthofenioid. Just such an early richthofenioid was described as *Ardmosteges* by SUTHERLAND (1996) from the early Upper Carboniferous Morrowan Series in Oklahoma, USA. This is the earliest known richthofenioid, and SUTHERLAND (1996) described how a juvenile aulostegid stage with a ventral interarea grew into the adult-richthofenid conelike form with virtually no interarea showing. The juvenile shell provides good evidence for derivation from the Aulostegidae (Fig. 437).

The greatest diversification of the Richthofenioidea took place in the Permian, with steady expansion into the middle part of the period followed by decline toward the end of that period. COOPER and GRANT (1975, p. 927) followed the classification by MUIR-WOOD and COOPER (1960) in excluding *Teguliferina* from the Richthofenioidea and placing it in the Strophalosioidea. Here it is reunited with the richthofenioids on the basis of its lack of an interarea in adults and the judgment that the cardinal process is neither sufficiently different from that of most Richthofenioidea nor sufficiently similar to that of most strophalosiidines to justify the earlier placement. As remarked by COOPER and GRANT (1975), the position of *Teguliferina* in the Upper Carboniferous (Pennsylvanian) and Early Permian suggests that it may have been an ancestor of the richthofenioids. We unite *Ardmosteges* with *Teguliferina* and other teguliferines to form the stem group for the superfamily.

All richthofenioids lived attached, initially by the beak, and generally developed stabilizing spines early in their ontogeny. The rare *Collumatus* of the Texas Permian is stabilized by successive sheets of shell material rather than spines, but this is regarded as simply an aberration, not a deeply significant taxonomic character (COOPER & GRANT, 1975, p. 961). *Zalvera,* after the first few mm of growth when it too resembled an aulostegid, is aspinose and appears to have been an early aberrant form.

The four families of the Richthofenioidea are separated by differing external shapes and in their ventral valve muscle attachment structures. The Gemmellaroiidae are less securely classified, having been placed at times with the orthotetidines (e.g., WILLIAMS, 1953b; GRANT, 1993a) or with productides (e.g., MUIR-WOOD & COOPER, 1960; MUIR-WOOD in MOORE, 1965). Discussion has centered mainly on the presence or absence of external spines; GRANT (1993a) also stressed the importance of koskinoid umbonal perforations in ventral valves of *Tectarea* and *Cyndalia* in this group as well as in some orthotetidines. WILLIAMS and BRUNTON (1993) questioned the validity of koskinoid structures in taxonomy, and studies of *Gemmellaroia* from Italy have revealed

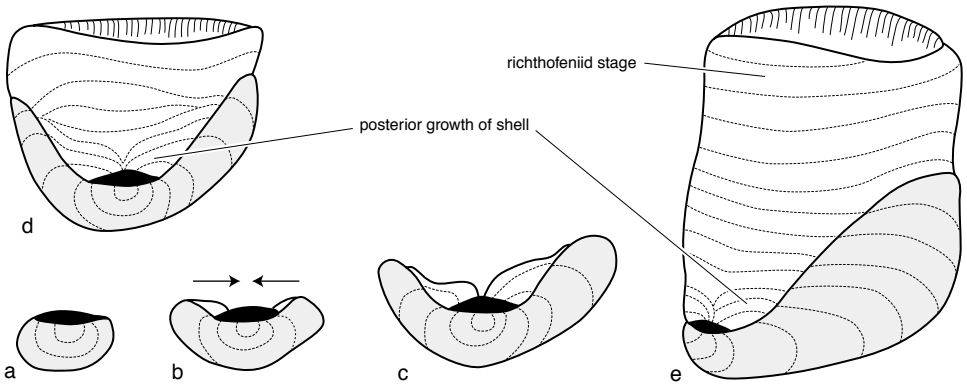

FIG. 437. *Ardmosteges orchamus* SUTHERLAND showing growth of ventral valve, viewed *a–d,* posteriorly and *e,* obliquely; early aulostegid stage *shaded;* interarea *black;* posterior growth of shell shows in early growth lines, indicated in *b* (*arrows*) and *c,* lead to posteromedian fusion dorsal to the interarea and continued annular growth formed the adult conical richthofeniid stage (*a–c,* new; *d,e,* adapted from Sutherland, 1996).

the bases of external spines. Therefore, we here include two of the four genera discussed by GRANT (1993a) as belonging to the Gemmellaroiidae; *Cyndalia* is included with less certainty; and *Loczyella* is assigned to the lyttoniidine superfamily Permianelloidea.

The rare and poorly illustrated forms *Striirichthofenia, Neorichthofenia,* and *Strophorichthofenia* are difficult to place. Both *Neorichthofenia* and *Strophorichthofenia* appear to have a ventral median septum that would place them in the Hercosiidae. The internal features of *Striirichthofenia* are not known, so it is placed with uncertainty in the Richthofeniidae, the common Asian richthofenioids.

The genus *Prorichthofenia* (KING, 1931, p. 97) based on *Crania permiana* SCHUMARD (1859, p. 395) is abandoned. SCHUMARD's specimens, lost in a fire, were never illustrated. KING (1931) placed specimens belonging to several currently recognized genera from western Texas in this genus, so it cannot be synonymized with any of them. The most abundant forms in the Glass Mountains of Texas are species of *Hercosia, Hercosestria,* and *Cyclacantharia*. KING (1931, pl. 28–30) illustrated specimens of all of them under the name *Prorichthofenia.* Details were explained by COOPER and GRANT (1975, p. 939, 963).

Family RICHTHOFENIIDAE Waagen, 1885

[Richthofeniidae WAAGEN, 1885, p. 729]

Conical, spines rhizoid, ventral myocoelidium. *Lower Permian–Upper Permian.*

Richthofenia KAYSER, 1881, p. 352 [**Anomia lawrenciana* DE KONINCK, 1863, p. 18; OD]. Aperture spines possibly similar to those of *Prorichthofenia, Hercosia, Hercosestria,* and *Cyclacantharia;* myocoelidium with three septa. *Lower Permian–Upper Permian:* Sicily, Russia, China, Japan, Pakistan, Timor.——FIG. 438,*3a–c.* **R. lawrenciana* (DE KONINCK), Pakistan; *a,* ventral valve interior with myocoelidium, ×0.85; *b,* dorsal valve exterior, ×0.85; *c,* ventral valve longitudinal section showing cystose shell structure, ×0.85 (Waagen, 1885).

Coscinarina MUIR-WOOD & COOPER, 1960, p. 138 [**Richthofenia communis* GEMMELLARO, 1894, p. 7; OD; described and illustrated by DI-STEFANO, 1914, p. 16]. Large, with cone much elongated, aperture covered by arched, reticulated meshwork of spines; myocoelidium with single septum, extending length of cup. *middle Permian:* Europe.——FIG. 438,*1a–c.* **C. communis* (GEMMELLARO), Sosio Limestone, Wordian, Sicily; *a,* dorsolateral view of large specimen, reticulate covering, ×0.85; *b,* specimen showing dorsal valve and myocoelidium, ×0.85 (Di-Stefano, 1914); *c,* dorsal valve interior, ×0.85 (Muir-Wood & Cooper, 1960).

Globosobucina WATERHOUSE & PIYASIN, 1970, p. 123 [**G. scopae;* OD]. Squat cone attached by beak and stout rhizoid spines; dorsal valve lidlike, convex, not recessed into ventral vestibule; ventral myocoelidium capacious, visible eternally, internally bilobate and containing median septum as in *Richthofenia;* dorsal interior with prominent cardinal process;

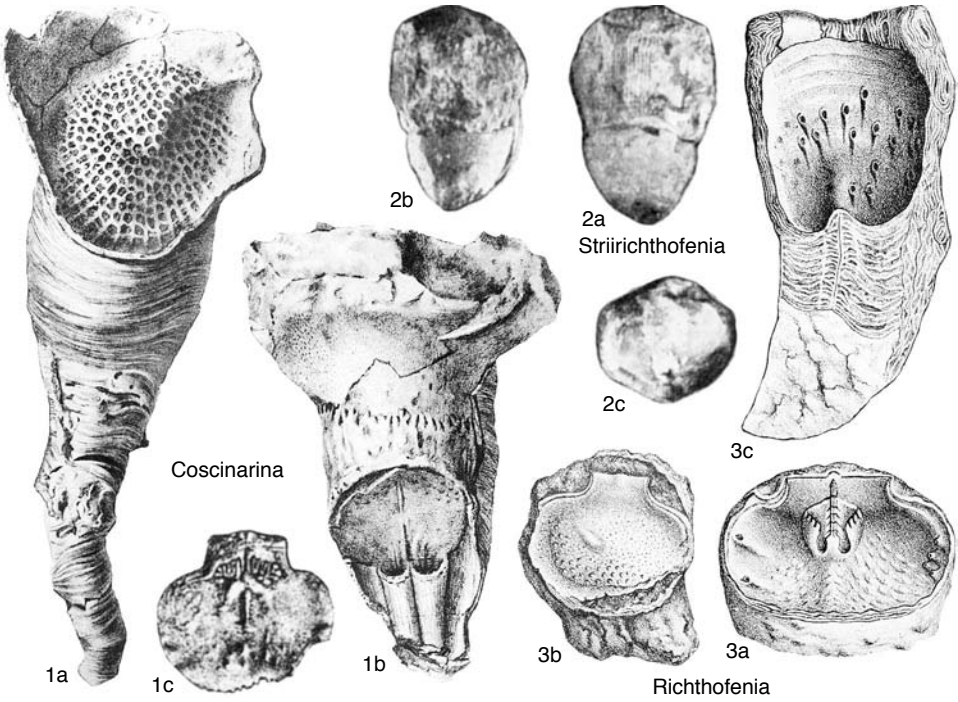

FIG. 438. Richthofeniidae (p. 611–612).

stout endospines, denticulate margin. *Lower Permian (Roadian)–Upper Permian (Wordian):* Thailand (Rat Buri).——FIG. 439,*2a–f.* **G. scopae,* holotype, UTC B538, Rat Buri Limestone; *a,* lateral view showing anterior face of ventral valve with large tubular spines, and inner surface of dorsal valve (above) bearing submarginal spines, ×1; *b,* view of internal ventral spines on anterior face of valve (below), looking through gap between two valves, ×1; *c,* posterior view of ventral valve, showing myocoelidium, growth lamellae, and tubular spines, ×1; *d,* lateral view, with dorsal valve above and ventral valve covered by tubular spines and growth lamellae, ×1; *e,f,* anterior view looking through gap between dorsal (above) and ventral valves; same view, tilted to show internal face of myocoelidium, ×1 (Waterhouse & Piyasin, 1970).

Seseloidia GRANT, 1993b, p. 10 [**S. phelbodes;* OD]. Conical, ventral valve walls thick, vesicular, with rough exterior; supporting spines few, scattered randomly; apertural spines absent; dorsal valve pustulose, resting on prominent shelf recessed within ventral aperture; hinge narrowed by proximal swellings of ventral shelf; ventral interior containing low, front-to-back swelling on floor; myocoelidium long, reaching from floor to just below hinge, containing high median septum arising from floor of myocoelidium and not reaching valve wall except at valve floor; muscle marks visible within myocoelidium; apical parts of high shells filled by cystose tissue. *Lower Permian: Verbeekina* Zone, Greece (Khios Island).——FIG. 439,*1a–d.* **S. phelbodes,* Kungurian, Khios; *a,* ventral interior showing myocoelidium and internal bases of spines, ×1.5; *b,* lateral view of juvenile with both valves, ×2; *c,d,* holotype, exterior views, side and posterior, USNM 402133, ×1 (Grant, 1993b).

Striirichthofenia LU TONG-CHEN, 1982, p. 609[611] [**S. mianchuensis;* OD]. Small, irregularly conical, base rounded, aperture widely flaring; dorsal valve lidlike, not recessed; pseudodeltidium internal, covered by outer shell layer; outer shell capillate. *Lower Permian:* China (Sichuan Province).——FIG. 438,*2a–c.* **S. mianchuensis;* Artinskian, Mianchu, Sichuan; *a,b,* anterior view, posterior view, ×1; *c,* holotype, upper view, ×1 (Lu, 1982).

Family HERCOSIIDAE Cooper & Grant, 1975

[Hercosiidae COOPER & GRANT, 1975, p. 928]

Conical, spines rhizoid, ventral median septum. *Lower Permian–Upper Permian.*

Hercosia COOPER & GRANT, 1969, p. 7 [**Richthofenia uddeni* BÖSE, 1916; OD]. High cones, tend to cluster, mostly anchored by rhizoid spines, rarely by beak; aperture protected by spines on ventral anterior rim and complimentary long dorsal endospines,

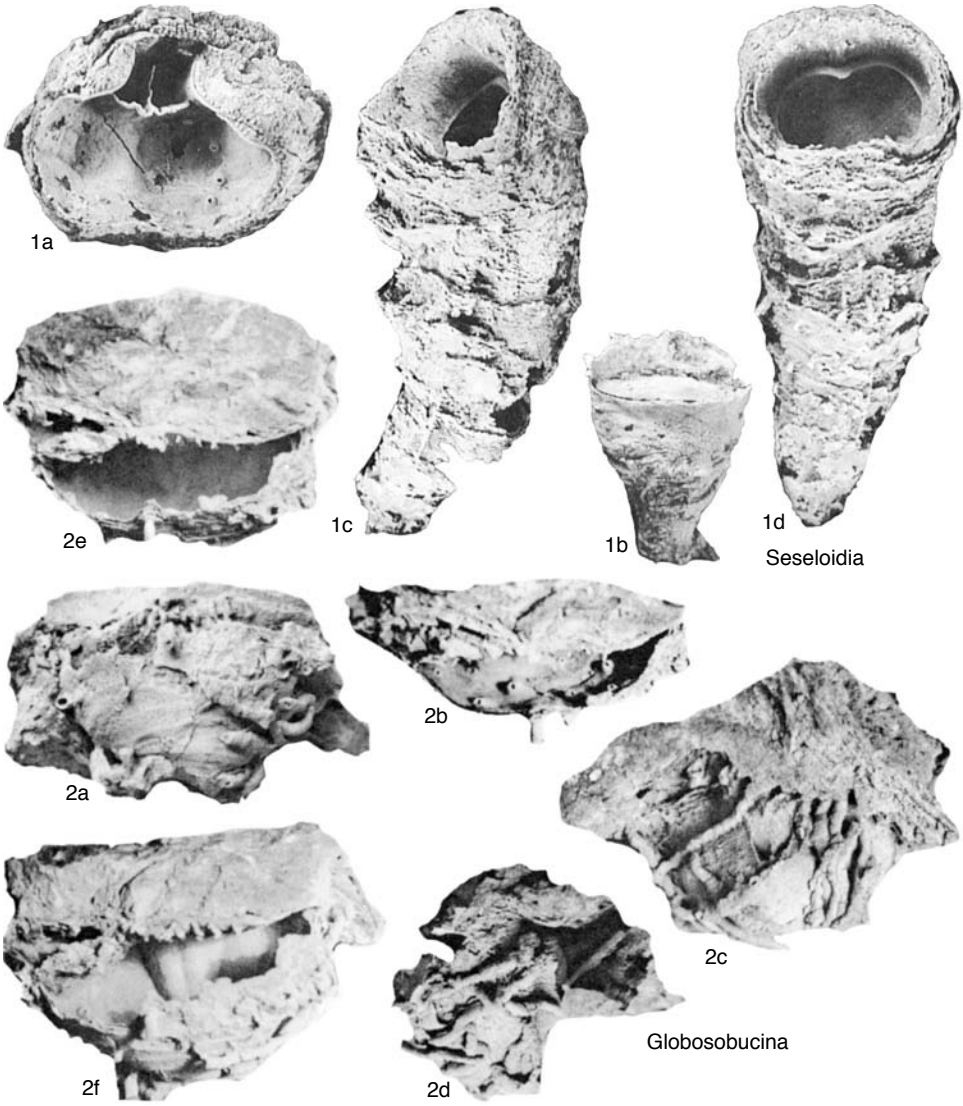

FIG. 439. Richthofeniidae (p. 611–612).

both crossing gape during feeding; ventral interior with high bladelike septum for muscle attachment in adults (juveniles have a myocoelidium as in *Richthofenia*); dorsal interior with bilobed cardinal process, visible adductor muscle marks, and aforesaid endospines. *Lower Permian (Artinskian–Kungurian):* USA (western Texas).——FIG. 440,*2a–d. *H. uddeni* (BÖSE), Leonardian, western Texas; *a,b,* anterior, dorsal views of young adult, ×1; *c,* broken ventral valve showing median septum and growth track of hinge, ×1; *d,* interior of dorsal valve showing endospines and cardinal process, ×2 (Cooper & Grant, 1975).

Hercosestria COOPER & GRANT, 1969, p. 7 [**H. cribrosa;* OD]. Small cone tending to form clusters, hence typically distorted; attached by beak or numerous rhizoid spines; dorsal valve deeply recessed below low meshwork (coscinidium) protecting aperture (not highly domed as in *Sestropoma*); ventral interior with high, bladelike median septum; dorsal interior with all features reduced: endospines short and few, cardinal process low, short, bilobed. *Lower Permian (Artinskian–Roadian):* USA (western Texas).——FIG. 440,*3a–c. *H. cribrosa,* Roadian, western Texas, *a,b,* side, dorsal view showing coscinidium over aperture, ×1; *c,* interior of dorsal

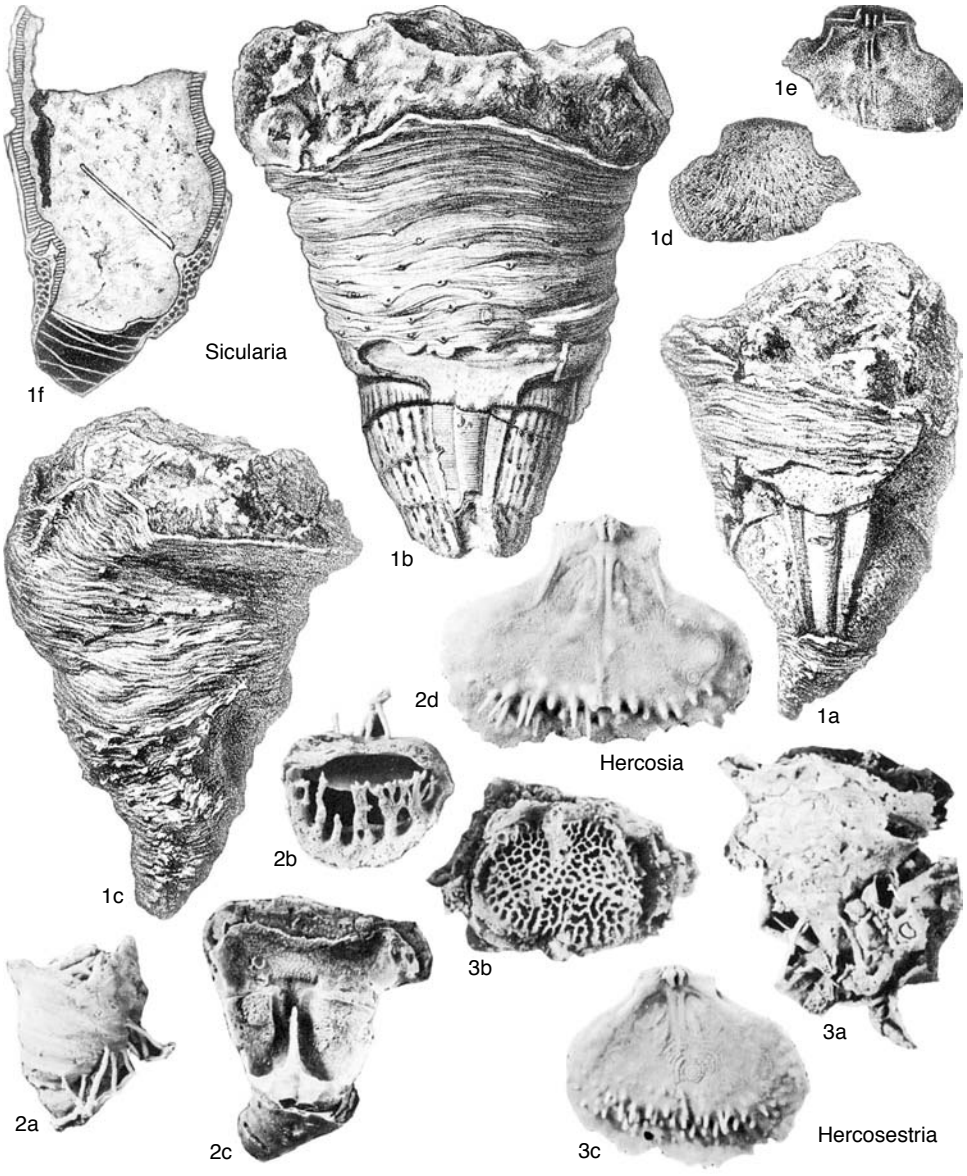

FIG. 440. Hercosiidae (p. 612–615).

valve showing lobate cardinal process and stunted endospines, ×1 (Cooper & Grant, 1969).

Neorichthofenia SHEN, HE, & ZHU, 1992, p. 180[193] [**Richthofenia mabutii* TAZAWA & ARAKI, 1984, p. 3; OD]. Ventral valve external features unknown, but anteriorly sulcate; interior has low anterior median ridge, numerous fine and irregular radial ribs on anterior sides of valves; dorsal interior with bilobed cardinal process, slender and long shafted, row of endospines two-thirds distance from posterior end. *Upper Permian (Changhsingian):* China, Japan.——FIG. 441,*2a–d.* **N. mabutii* (TAZAWA & ARAKI), Kanokura Formation, Kitakami Mountains, Japan, internal mold of conjoined valves; *a,* dorsal valve interior, ×2; *b–d,* ventral valve interior viewed anteriorly, posteriorly, ventrally, ×2 (Tazawa & Araki, 1984).

Sicularia GRANT, 1993b, p. 11 [**Richthofenia sicula* GEMMELLARO, 1894, p. 7; described and illustrated by DI-STEFANO, 1914, p. 22]. Conventionally conical richthofenioid lacking either coscinidium or, in adults, myocoelidium, but having long, low, thin

median septum along inside of posterior wall of ventral valve. *Lower Permian–Upper Permian:* Sicily.——Fig. 440,*1a–f.* **S. sicula* (Gemmellaro), Wordian, Sosio Limestone, Sicily; *a,* posterior view with exfoliated valve revealing internal trace of muscle field, ×1; *b,* posterior view, ×1; *c,* anterior view, ×1; *d,e,* external, internal view of dorsal valve, ×1; *f,* longitudinal section showing low median septum and dorsal valve, ×1 (Di-Stefano, 1914).

Strophorichthofenia Termier & others, 1974, p. 123 [**S. afghana;* OD]. Small, conical ventral valve with flat dorsal valve resting just below ventral margin (opercular); both valves with low median septa; ventral valve with scattered rhizoid spine bases, large cicatrix of attachment, growth lines, and rugae. *Upper Permian (Kazanian):* Afghanistan.——Fig. 441,*1.* **S. afghana,* lower Murghabian, Wardak, central Afghanistan; holotype, posterior view of complete specimen, ×2 (Termier & others, 1974).

Family CYCLACANTHARIIDAE Cooper & Grant, 1975

[Cyclacanthariidae Cooper & Grant, 1975, p. 938]

Conical, spines rhizoid or absent, ventral muscle callosity. *Upper Carboniferous (Bashkirian)–Upper Permian (Capitanian).*

Subfamily CYCLACANTHARIINAE Cooper & Grant, 1975

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 933, *ex* Cyclacanthariidae Cooper & Grant, 1975, p. 938]

Conical, with coscinidium or rim of protective spines; no rhizoid spines in *Collumatus. upper Lower Permian (Roadian)–Upper Permian (Capitanian).*

Cyclacantharia Cooper & Grant, 1969, p. 7 [**C. kingorum;* OD]. High cone, commonly distorted by clustering; variably flared rim entirely surrounded by medianly directed protective spines; ventral valve attached by beak and many anchoring spines; ventral interior with thickened muscle area but no septa; dorsal interior with small bilobed cardinal process and few long stout endospines that cross ventral spines to protect during feeding. *Permian (Wordian):* USA (western Texas).——Fig. 442,*1a–d.* **C. kingorum,* Word Formation, western Texas; *a,* dorsal valve exterior, ×1; *b,* dorsal valve interior showing endospines, ×1; *c,d,* holotype, side and dorsal (apertural) views, USNM 153831, ×1 (Cooper & Grant, 1969).

Collumatus Cooper & Grant, 1969, p. 6 [**C. solitarius;* OD]. Small squat cone of solitary habit, attached by base and concentric sheets of shelly tissue, lacking supporting spines; coscinidium of coarse meshwork of flattened anastomosing spines; ventral interior with low adductor thickening and flabellate diductor scars; dorsal interior with short bilobed cardinal process and dendritic adductor scars. *upper Lower Permian (Roadian):* USA (western Texas).——Fig. 442,*2a–f.* **C. solitarius,* Roadian, western Texas; *a–e,* holotype, side, posterodorsal, ventral, anterior, posterior views, USNM 153548a, ×2; *f,* dorsal oblique view into open shell showing dorsal valve interior with small cardinal process, ×1 (Cooper & Grant, 1974).

Sestropoma Cooper & Grant, 1969, p. 8 [**S. cribriferum;* OD]. Variably conical, ventral valve long and tapering to short and squat; marginal rim narrow or flared; coscinidium highly arched with

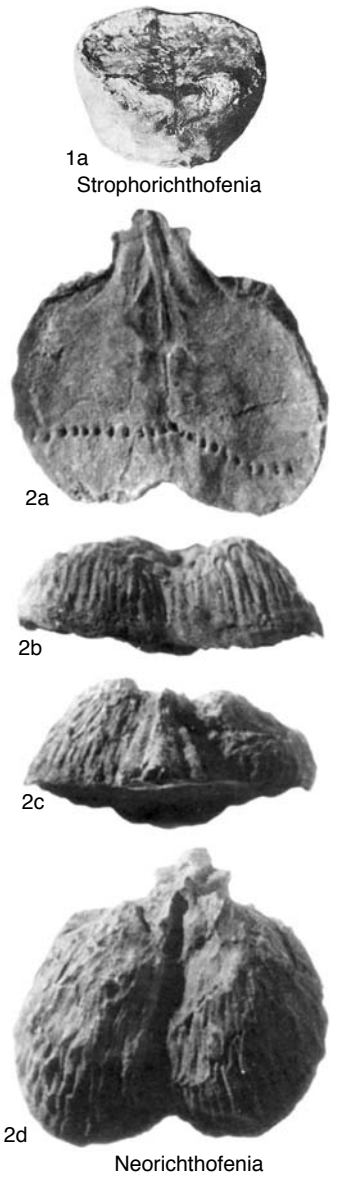

Fig. 441. Hercosiidae (p. 614–615).

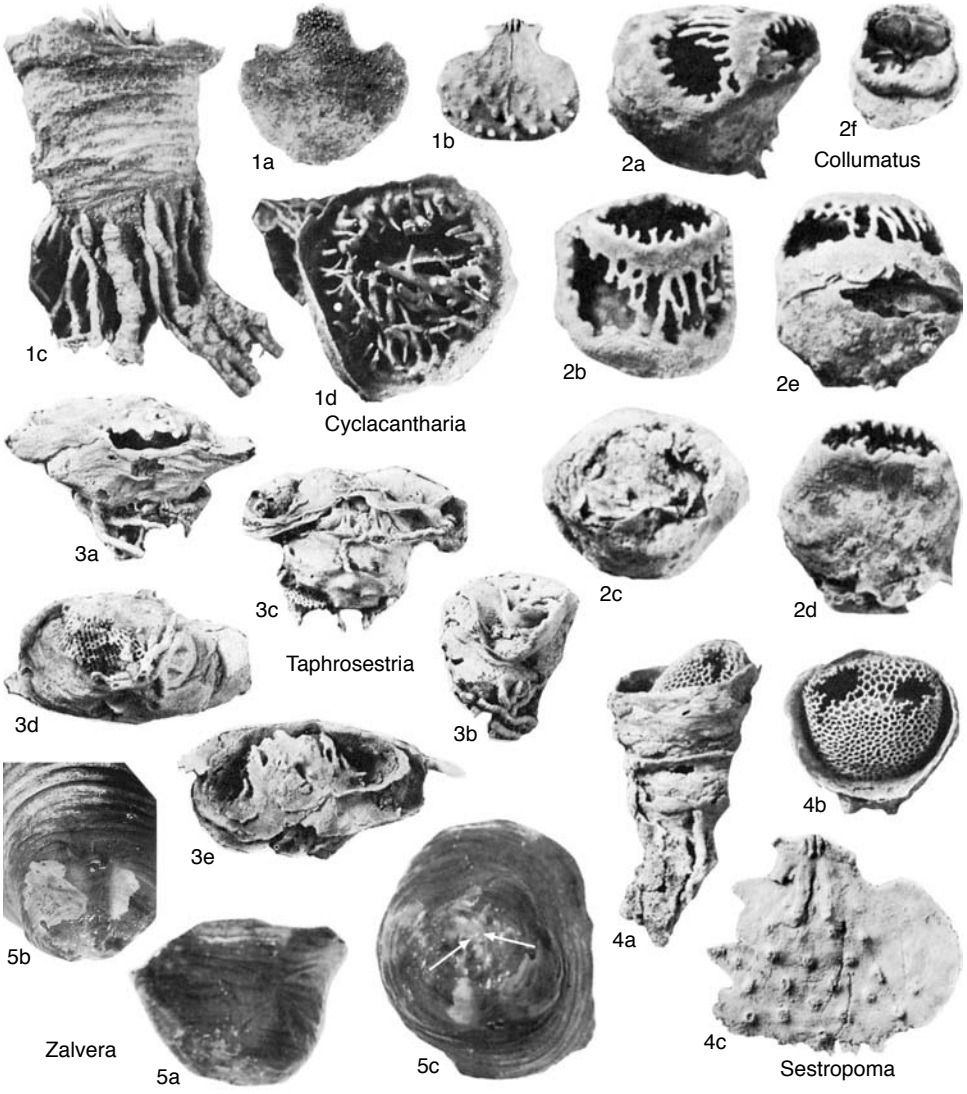

FIG. 442. Cyclacanthariidae (p. 615–617).

profile reflecting exactly the sweep of dorsal valve opening and remaining at full gape; general aspect like *Hercosestria* but with more regular and higher coscinidium, and lacking internal median septum. *Upper Permian (upper Wordian–Capitanian):* USA (western Texas), Mexico.——FIG. 442,*4a–c.* **S. cribriferum,* upper Wordian–Capitanian, western Texas; *a,b,* side, dorsal (apertural) views showing thick rhizoid spines and strongly elevated and rounded coscinidium over aperture, ×1; *c,* interior of dorsal valve, ×3 (Cooper & Grant, 1969).

Taphrosestria COOPER & GRANT, 1975, p. 954 [**T. peculiaris;* OD]. Squat cone with flaring marginal rim; external surface strongly rugose and squamose; attached at base and stabilized by strong spines of circular cross section; dorsal valve deeply recessed, protected by coscinidium of flattened anastomosing spines; ventral interior without septa but thickened muscle field showing attachment scars; dorsal interior nearly smooth, without endospines, brachial ridges rarely visible; cardinal process short, bilobed; muscle field thickened slightly. *upper Lower Permian (Roadian):* USA (western Texas).——FIG. 442,*3a–e.* **T. peculiaris,* Road Canyon Formation, western Texas; anterior, lateral, posterior, ventral, dorsal views, ×1 (Cooper & Grant, 1975).

Subfamily TEGULIFERININAE Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 933, *ex* Teguliferinidae Muir-Wood & Cooper, 1960, p. 92]

Sphenoid (obliquely conical), spines rhizoid; no coscinidium. *Upper Carboniferous (Bashkirian)–Lower Permian, ?Upper Permian.*

Teguliferina Schuchert & LeVene, 1929, p. 121, *nom. nov. pro Tegulifera* Schellwien, 1898, p. 362, *non* Saalmüller, 1880 [**Tegulifera deformis* Schellwien, 1898, p. 362; OD]. Low oblique cone (sphenoid); ventral surface wrinkled and irregular; attached by ventral beak, anchored by strong circular or flattened spines reinforced by connecting shelly tissue; anterior edge of ventral cup bearing inwardly pointing protective spines; ventral interior with slightly thickened muscle field but no septa; dorsal interior with short bilobate cardinal process, each lobe with pit for diductor attachment; hinge narrow, with short articulating knob on each side; brachial ridges visible on some specimens. *Upper Carboniferous (Bashkirian)–Lower Permian, ?Upper Permian:* Yugoslavia, Japan, China, Russia, Ferghana, USA (Kansas, western Texas).——Fig. 443,*1a,b.* **T. deformis* (Schellwien), Lower Permian, Yugoslavia; *a,* dorsal valve exterior, elongate ventral valve above, ×1; *b,* dorsal valve internal mold, ×2 (Schellwien, 1898).

Acritosia Cooper & Grant, 1969, p. 5 [**A. magna;* OD]. Low conical, oblique in youth, becoming more symmetrical with growth; ventral cup margin flared, bearing inwardly directed protective spines only anteriorly; valve attached by rhizoid spines of circular cross section; ventral interior without septum but with low median myophragm; dorsal muscle area slightly thickened; cardinal process short, erect; hinge apical; endospines few, stout. *Lower Permian:* USA (Texas).——Fig. 443,*2a,b.* **A. magna,* Lower Permian, western Texas; holotype, lateral view, dorsal view showing open dorsal valve in attached position (*arrow*), USNM 151739a, ×1 (Cooper & Grant, 1969).

Ardmosteges Sutherland, 1996, p. 8 [**A. orchamus;* OD]. Sphenoid ventral valve having an early aulostegid growth stage with interarea closed by elytridium and lophidium, followed by a richthofeniid growth stage of progressive fusion of ventral valve posteriorly and dorsal to interarea, developing into a richthofeniid-like cone anchored by rhizoid spines. *Upper Carboniferous (Bashkirian):* USA (Oklahoma).——Fig. 443,*3a–c.* **A. orchamus,* holotype, OU 10260, upper Morrowan, Oklahoma; *a,* posterior view showing growth lines indicating infilling of shell above interarea (*arrow,* ventral valve broken laterally), ×2; *b,* dorsal view showing tilted dorsal valve in partly open position and protective endospines most frequently on anterior side, ×2; *c,* lateral view with juvenile spinose aulostegid stage below, ×2 (Sutherland, 1996).

Planispina Stehli, 1954, p. 331 [**P. conida;* OD]. Similar to *Teguliferina,* but attachment spines fused together and to sides of cup by flat shelly tissue; anterior margin of cup with long protective spines. *Upper Carboniferous–Lower Permian:* North America.——Fig. 443,*8a–c.* **P. conida,* Lower Permian, western Texas; *a,* holotype, lateral view showing nested cones and flattened spines, AMNH 27313/1:1, ×1; *b,* ventral valve interior showing a few large protective spines, ×1; *c,* dorsal valve interior showing cardinal process, median ridge, and marginal endospines, ×1 (Stehli, 1954).

Proteguliferina Licharew in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 236 [**Tegulifera rossica* Ivanov, 1925, p. 111; OD]. Similar to *Teguliferina* but spines along periphery of both valves, rudimentary ventral interarea covered by hoodlike later shell tissue; dorsal valve less deeply inserted. *Upper Carboniferous–Lower Permian:* Russia (Moscow basin, Donetz Basin), ?North America.——Fig. 443,*7a,b.* **P. rossica* (Ivanov), Upper Carboniferous, Moscow basin; *a,* dorsal view of complete shell with hood concealing ventral interarea, ×1; *b,* interarea exposed by removal of hood, ×1 (Ivanov, 1925).

Subfamily ZALVERINAE Brunton, 1996

[*nom. transl.* Wardlaw, Grant, & Brunton, herein, *ex* Zalveridae Brunton, 1996, p. 53]

Conical, no external or apertural spines, and weakly attached. *Upper Carboniferous (Bashkirian–Moscovian).*

Zalvera Brunton, 1996, p. 53 [**Z. sibaica;* OD]. No external body spines or ventral marginal protective structures; broad rugae irregular; dorsal valve deep within ventral cone, corpus cavity shallow; short, subparallel, internal ventral ridges (*arrows*) associated with chamber near apical area involved in articulation of valves. *Upper Carboniferous (Bashkirian–Moscovian):* Russia (Urals), ?northern Spain.——Fig. 442,*5a–c.* **Z. sibaica,* Upper Bashkirian–lower Moscovian, Ural River; holotype, anterior, apical oblique, apical views, BMNH BD9653, ×1.5 (Brunton, 1996).

Family GEMMELLAROIIDAE Williams, 1953

[Gemmellaroiidae Williams, 1953b, p. 10]

Conical, with long ventral interarea; spines few, on ventral valve only or absent; dorsal valve caplike; ventral myocoelidium present. *Lower Permian–Upper Permian.*

Gemmellaroia Cossmann, 1898, p. 77, *nom. nov. pro Megarhynchus* Gemmellaro, 1894, p. 7, *non* de Laporte, 1832 [**Megarhynchus marii* Gemmellaro, 1894, p. 7; SD Mabuti, 1937, p. 16] [=*Megalorhynchus* de Gregorio, 1930, p. 23 (*errore pro Megarhynchus); Gemmellaroiella* Mabuti, 1937, p. 16 (type, *G. ozawai*)]. Exterior rugose and finely

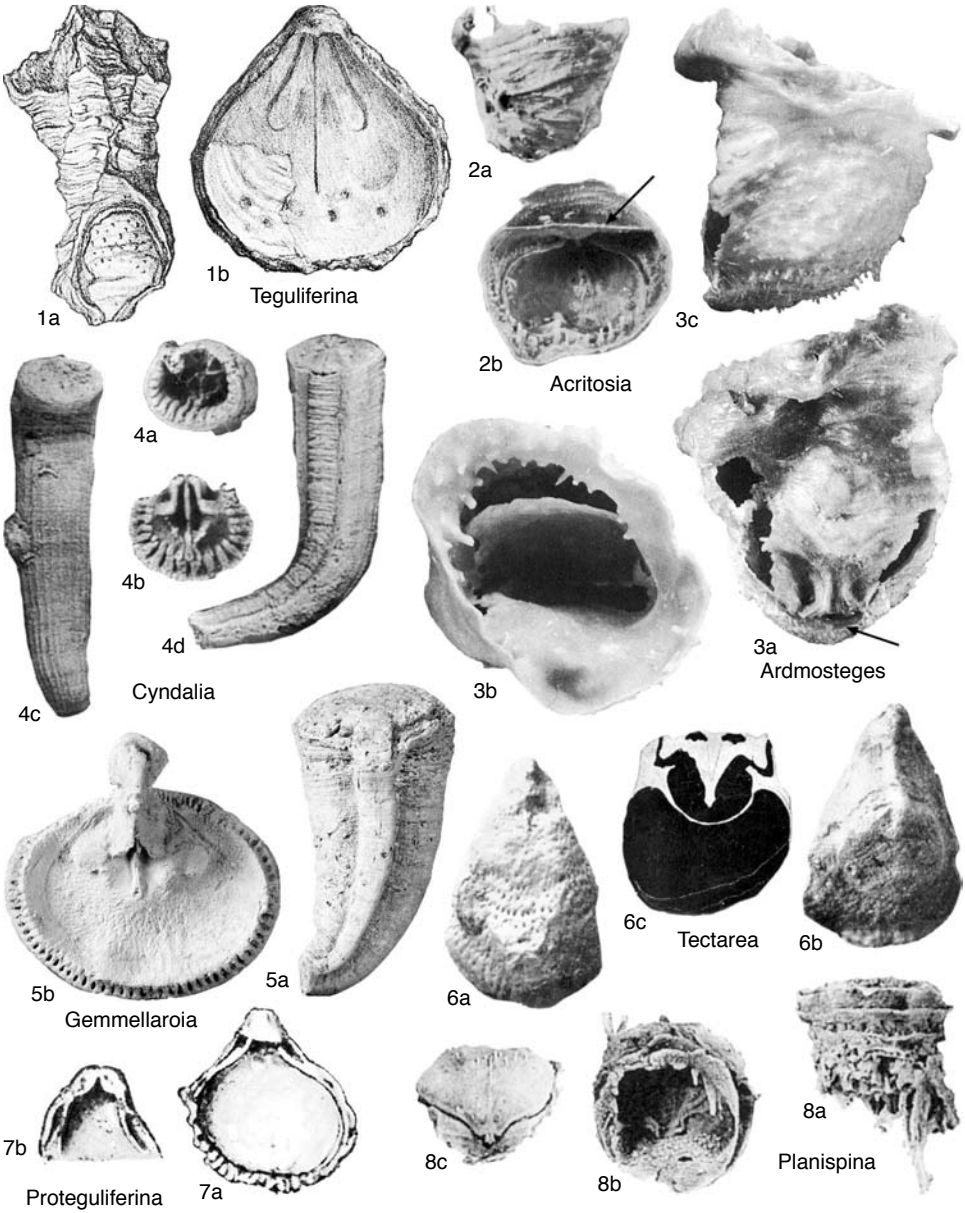

FIG. 443. Cyclacanthariidae and Gemmellaroiidae (p. 617–619).

spinose; myocoelidium long, anteriorly grooved and having internal median septum; internal margins of both valves denticulate. *Lower Permian–Upper Permian:* Europe, Asia.——FIG. 443,*5a,b.* **G. marii* (GEMMELLARO), Sosio Limestone, ?Kazanian, Sicily; *a,* posterior view showing conical ventral valve with pseudodeltidium and lidlike dorsal valve, ×1; *b,* dorsal valve interior with cardinal process and denticulate margin, ×2 (Gemmellaro, 1897).

Cyndalia GRANT, 1993a, p. 55 [**C. rudistiformis;* OD]. Minute, high conical shells with interarea and prominent convex pseudodeltidium extending from umbo to commissure; subcircular dorsal valve with weak radial costae; ventral costae weak; cicatrix api-

cal, small, no spines recorded; teeth peglike and with myocoelidium; cardinal process lobes separated medianly, but continuous with sockets, prominent median septum and strong marginal crenulations; valve walls thick. *Upper Permian (?Capitanian, Changhsingian):* Greece.——Fig. 443,*4a–d.* **C. rudistiformis,* Capitanian, Episcopi Limestone, Hydra; *a,* ventral interior showing teeth, ×4; *b,* dorsal valve interior, ×6; *c,* holotype, anterior view of complete shell, USNM 460380, ×4; *d,* posterior view of complete shell, ×4 (Grant, 1993a).

Tectarea Licharew, 1928, p. 268 [**T. robinsoni;* OD]. Probably attached by umbo; exterior usually decorticated, probably capillate with intervening radially arranged pits; myocoelidium long, without septum or anterior groove, may be filled with secondary deposit; each valve with toothlike process and socket articulating with similar structures on other valve. *Lower Permian:* Europe (Caucasus).——Fig. 443,*6a–c.* **T. robinsoni; a,b,* ventral, dorsal views of specimen, ×3; *c,* transverse section showing cardinal process and myocoelidium, ×3 (Licharew, 1928).

LYTTONIIDINA

Alwyn Williams,[1] David A. T. Harper,[2] and R. E. Grant[3]
[[1]The University of Glasgow; [2]University of Copenhagen; and [3]deceased]

Suborder LYTTONIIDINA new suborder

[Lyttoniidina Williams, Harper, & Grant, herein] [=Oldhaminidina Williams, 1965f, p. 510, *nom. nov. pro* suborder Oldhaminoidea Williams, 1953c, p. 286]

Grossly inequivalve productide brachiopods with the smaller dorsal valve consisting mainly of lobate brachidial plate; lacking rhizoid spines but rarely with spinose projections at ventral margin; ventral valve lacking interarea but with variably developed and disposed posterior flap of shell; hinge line normally covered by ventral shell, articulatory structures ill defined; secondary shell layer pseudopunctate. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

The morphology and classification of the lyttonioid brachiopods warrant a full discussion. Although vaguely suggestive of a strophalosiidine ancestry, the morphology is so bizarre as to continue to defy any confident interpretation of its details. This is true not only of certain morphological features of both valves but also of the shell structure and growth of the valves themselves. Consequently, the interpretation of shell morphology and the classification presented here, although benefitting from much new data since publication of the last *Treatise* account of the group (Williams, 1965f, p. 511–521), may yet undergo fundamental revision.

The shells are functionally bivalved, with the inner surface of the ventral valve everywhere extending well beyond the edge of the dorsal valve so that some of the ventral mantle margin, despite evidence for retractability, must have been permanently exposed during life. Moreover, the significantly smaller dorsal valve generally has a highly lobate outline resembling that of a ptycholophous lophophore, which led Termier and Termier (1949b) to postulate that the exposed part of the valve is a brachidium.

There is another line of evidence that supports this interpretation. The shell structure of the ventral valve is pseudopunctate, with a thin primary layer orthodoxly forming the entire outer surface of the valve (Fig. 444), which is characteristically ornamented by growth banding, growth disturbances, and evidence of shell repair.