MESOZOIC AND CENOZOIC LITHISTID SPONGES: DICRANOCLADINA, PSEUDORHIZOMORINA, DIDYMMORINA, HELOMORINA, MEGAMORINA, MEGARHIZOMORINA, SPHAEROCLADINA, AND ORDER AND SUBORDER UNCERTAIN

R. E. H. Reid

[formerly of Department of Geology, The Queens University of Belfast]

Suborder DICRANOCLADINA Schrammen, 1924

[*nom. transl.* Reid, 1963d, p. 199, *ex* tribus Dicranocladina Schrammen, 1924a, p. 39]

Desmas monaxial, when axial system is known, and typically strongly tuberculate; most genera with desmas of dipodal to polypodal shapes, which may be dicranoclones *s.s.,* with an erect, crepidal axis in a brachyome-like prominence (the basaltheil of Schrammen, 1910), or similarly shaped forms with axis in line with two of the arms, or no known axial system; other desmas of irregular shapes, with this type sometimes predominant or only type present; zygomes twiglike, rootlike, or clawlike and typically applied to arms, tubercles, or central parts of other desmas; dermalia dichotriaenes, modified dichotriaenes with spines or zygomelike cladi or monaxial, discotriaene-like spicules; supplemental oxeas sometimes present; some with large, rhizoclone-like spicules (megarhizoclonids), small rhizoclonids, or both as supplemental desmas, with either sometimes forming a supplemental, skeletal cortex; microscleres of modern examples amphiasters or spirasters and latter may be varied as metasters or plesiasters. *Upper Jurassic (upper Oxfordian)–Holocene.*

The designation tribus used by Schrammen (1924a) for his Dicranocladina was directly equivalent to suborder, since the taxon formed a primary division of the order Tetraxonia Vosmaer (ascribed to Schulze by Schrammen).

The Dicranocladina have been treated formerly as characterized by the occurrence of dicranoclones, but this is misleading. Dicranoclones *s.s.* (i.e., as described by Schrammen, 1910, p. 65), with the crepidal axis in a basaltheil are in fact known from only one species of *Schrammeniella* Breistroffer (=*Phalangium* Schrammen, *non* Linné; =*Ioued* de Laubenfels), although probably also present in *Procorallistes* Schrammen, whose characteristic desmas have an elongate, basaltheil-like structure. In modern Corallistidae (=Coscinospongiidae von Lendenfeld, 1903, of Schrammen, 1910, p. 28), however, desmas have arms or less regular outgrowths at both ends of an epirhabd (the part enclosing the crepidal axis). Other arms grow out from sides of the epirhabd in three- or four-armed examples. In most fossils, however, the position of the axis is unknown. Schrammen (1924a) and others have assumed that the desmas are dicranoclones *s.s.* if a centrumlike feature or a large, central tubercle is present. Some of these desmas, however, pass gradually into more or less irregular forms (in e.g., *Leiocarenus* Schrammen) like those prevalent in the living *Corallistes* Schmidt or are all irregular types (in *Leiohyphe* Schrammen). Further, modern examples show that a large, central tubercle need not represent a basaltheil. Some fossil desmas with a centrum may grade into variants showing arms at both ends of a distinct, central shaft (in e.g., *Pycnoclonella* Lagneau-Hérenger). Hence this suborder is not defined here in terms of dicranoclones. The two types of desmas comprising dicranoclones *s.l.* are accepted as homologous, however, because forms bearing arms at both ends of an epirhabd are also present in *Schrammeniella,* in addition to dicranoclones *s.s.*

Scope of the taxon is also modified by exclusion of the family Macandrewiidae GRAY, which was included by SCHRAMMEN (1924a). Some of the genera have desmas that are tuberculate on zygomes but central parts that are typically smooth. Desmas of the type genus *Macandrewia* GRAY are smooth rhizoclones. *Macandrewia* also has (a) an anthaspidellid-like structure, not matched in any typical Dicranocladina, and (b) some additional tetraxial desmas that intergrade with the main ones. No tripodal or similar desmas are known. Although desmas in these sponges are comparable with supplemental megarhizoclonids of the Dicranocladina, their homology seems doubtful. This family is therefore removed to a separate suborder, using SCHRAMMEN's old name Pseudorhizomorina (SCHRAMMEN, 1901).

The Dicranocladina appear cryptogenically in the Upper Jurassic, represented by genera (*Kyphonella* KOLB, *Leiocarenus* SCHRAMMEN, *Dicranoclonella* SCHRAMMEN) that already had strongly tuberculate desmas. Some of the desmas have dicranoclone (i.e., dipodal to polypodal) shapes; but none has a typical basaltheil; and others are of more or less irregular shapes as in the living Corallistidae. Some Lower Cretaceous forms (e.g., *Pycnoclonella* LAGNEAU-HÉRENGER) have desmas with a prominent, swollen, central tubercle; but examples with a typical basaltheil or a comparable armlike outgrowth are known only from the Upper Cretaceous. This suggests that dicranoclones *s.s.* are a secondary development, produced from desmas like those of the Jurassic and modern forms by restriction of arms to one end of the epirhabd.

No dicranoclones *s.s.* are known from modern forms. Desmas of *Corallistes* SCHMIDT may be weakly tuberculate with more or less transition into rhizoclones, but those of *Paracorallistes nolitangere* (SCHMIDT) are as stout as in any of the fossils and may be accompanied by typical megarhizoclonids. In various fossils, megarhizoclonids intergrade with the principal desmas, and they seem to be essentially late-formed variants. In *Pseudoverruculina* MORET, there is more or less continuous transition from typical desmas through smaller variants (megarhizoclonids) to small rhizoclonids that form a cortex.

The tuberculate desmas of Dicranocladina are strikingly similar to those of Plinthosellidae and many Theonellidae of the Tetracladina. Dipodal to polypodal forms, especially, are similar to tetracladine triders from these families and two-armed (or dipodal) variants seen in Plinthosellidae. While these resemblances could be simply convergent, they may also mark iterative developments in forms that have shared a common origin. First, some kind of relationship is suggested by occurrence of streptosclere-like microscleres in both *Corallistes* species and the theonellid *Racodiscula* ZITTEL. Second, tubercles and zygomelike spines are interchangeable in corallistids and some modern theonellids. Third, tetraclones of the theonellid *Discodermia* DU BOCAGE are sometimes partly replaced by triodal or diaxial variants, and some of the desmas are triders in the fossil *Pseudojerea* MORET. Plinthosellid desmas are typically triders, and those of *Plinthosella* ZITTEL are in part two-armed variants that are triodal. These forms and the Dicranocladina could then represent three stocks of common origin. The three shared (a) a trend to production of tuberculate desmas, and (b) a trend to reduction of the crepis from tetraxial to triodal, diaxial, or monaxial. The crepis (i) remained incipient only in the typical Theonellidae, and (ii) proceeded to a stage in which desmas became typically triders, to which triodal, two-armed variants may be added in the family Plinthosellidae, first known from the Aptian. Evolution (c) proceeded rapidly to completion in a third stock that became the Dicranocladina before their Upper Jurassic first appearance.

If this is correct, the original root stock may be the family Protetraclisidae SCHRAMMEN of the Tetracladina, although recorded examples of this family are contem-

poraries of early Dicranocladina. Protetraclisidae have branching tetraclones that grade into rhizoclone-like variants; and *Rhizotetraclis* KOLB also has some desmas that resemble a four-armed dicranoclone. *Sontheimia* KOLB of this family has desmas developed as triders, although tetraclones occur also, and has thickening of both zygomes and spines on the arms into incipient tubercles. While this is not conclusive evidence, the occurrence of forms that have features that might be expected in a rootstock (passage of tetraclones into triders and rhizoclone-like spicules; thickening of lateral spines into incipient tubercles) at nearly the right period may not be coincidence.

FINKS (1971b) has suggested derivation of the Dicranocladina from the Paleozoic family Hindiidae RAUFF (suborder Tricranocladina REID, =Eutaxicladina RAUFF *sensu* SCHRAMMEN). The Hindiidae are forms with desmas of triderlike shapes in which the axial system is unknown, but the desmas are markedly tuberculate in the two latest genera (*Scheiia* TSCHERNYCHEV & STEPANOV; *Scheiella* FINKS). Such a derivation is also possible but is open to a number of objections.

(1) No triaenes are known from hindiids, although ectosomal microrhabds are sometimes preserved at the surfaces.

(2) The desmas of the oldest forms (*Hindia* DUNCAN) are constantly tetraxial in shape and were regarded as tetraxons by SCHRAMMEN (1937, p. 77). If this is correct and dicranocladine triaenes are claimed to be derived from monaxons, desmas and dermalia must be pictured as evolving in opposite directions.

(3) If Dicranocladina were hindiid derivatives, one would expect the most constantly tripodal desmas in the oldest forms. In practice, the desmas of Jurassic forms are irregularly variable, and the form in which desmas are most constantly tripodal is Santonian (*Gignouxia* MORET).

(4) No dicranocladine sponge approaches the special radiate structure of hindiids. The oldest Dicranocladina have more or less irregular structures, and the greatest regularity is again seen in *Gignouxia.* In addition, the diagram of its structure shown by DE LAUBENFELS (1955, fig. 46,*5*), is diagrammatic, not factual, and has a structure more like that of hindiids than exists in his material.

(5) Zygomes of hindiid desmas are typically simple terminal expansions, with a single distal facet; but those of dicranocladine desmas are like the zygomes of tetraclones, unless more or less aborted.

(6) Megarhizoclonids of Dicranocladina sometimes clearly intergrade with the principal desmas, with which they are presumably homologous. Supplemental desmas of *Scheiella* do not have this relationship and may be derived from small, supplemental oxeas that sometimes have irregular outgrowths. On these grounds, resemblances between Dicranocladina and Hindiidae are here thought to be convergent, although neither view can currently be verified.

Absence of an obvious axial canal in most fossil dicranocladine desmas is presumed herein to be due to its loss during fossilization. This is not surely always correct; but the crepis is typically minute in the modern Corallistidae where it is sometimes destroyed by internal solution and replacement that reduced central parts of the desmas to a granular marrow.

Family CORALLISTIDAE Sollas, 1888

[Corallistidae SOLLAS, 1888, p. cliv] [=Coscinospongiidae VON LENDENFELD, 1903, p. 135; Pachinionidae SCHRAMMEN, 1924a, p. 39; Gignouxiidae DE LAUBENFELS, 1955, p. 61; Phrissospongiidae LAGNEAU-HÉRENGER, 1962, p. 168]

Desmas more or less strongly tuberculate and of dipodal to polypodal, irregular, or intermediate shapes, that may occur in various combinations and with any type predominant; dicranoclones *s.s.* in one species; tubercles buttonlike or capstanlike, not in regular, transverse rows, and sometimes more or less replaced by conical or branching spinules; dermalia simple dichotriaenes or variants with spinose or polycladose cladi; large, rhizoclone-like desmas (megarhizoclonids) sometimes accompany tuberculate

forms; some with small rhizoclonids that may form a supplemental cortex at surface of skeletal framework; microscleres of modern forms include plesiasters, metasters, spirasters, or amphiasters, and sometimes additional microrhabds. [Desmas of this family are not described generally as dicranoclones: (a) dicranoclones in the strict sense of SCHRAMMEN (1910, p. 65), in which arms are produced from one end of an epirhabd (basaltheil of SCHRAMMEN), are known only from one species, *Schrammeniella scytaliforme* (SCHRAMMEN); (b) outwardly comparable desmas of the living *Corallistes* SCHMIDT, for example, have arms arising from both ends of the epirhabd and sometimes also from its sides; (c) most fossil examples have no axial system and could be of either type; (d) transition from tripodal or tetrapodal desmas, for example, into forms with arms arising from the ends of a short, central shaft (e.g., in *Pycnoclonella* LAGNEAU-HÉRENGER), or into more or less irregular spicules like some *Corallistes* desmas (in e.g., *Dicranoclonella* SCHRAMMEN), suggests that desmas of such genera are not dicranoclones *s.s.*] *Upper Jurassic (upper Oxfordian)–Holocene.*

Subfamily CORALLISTINAE Sollas, 1888

[*nom. transl.* REID, herein, *ex* Corallistidae SOLLAS, 1888, p. cliv]

Desmas mainly or all of more or less irregular shapes, although dipodal to polypodal desmas may also be present, and sometimes grading into rhizoclone-like variants in which spines replace tubercles; dicranoclones *s.s.* unknown; plesiasters, metasters, spirasters, amphiasters, or microrhabds in modern examples. [Includes recent Corallistidae and similar fossils.] *Upper Jurassic (upper Oxfordian)–Holocene.*

Corallistes SCHMIDT, 1870, p. 22 [**C. typus;* OD] [=*Zosterospongia* DE LAUBENFELS, 1953b, p. 109 (type, *Z. thaumasta,* OD)]. Funnel to bowl-like or flabellate, then sometimes irregularly convolute or forming a secondary funnel with exhalant side external; inhalant side of skeletal framework with small ostia or open, skeletal meshes only; exhalant side with larger postica, which sometimes have slightly raised margins; epirhyses and aporhyses vague to distinct, simple or branching; desmas mainly irregular in shape, often weakly tuberculate, but usually including some dipodal and polypodal variants; usually no distinct megarhizoclonids; small, ectosomal rhizoclonids absent; dermalia simple dichotriaenes; microscleres plesiasters, metasters, spirasters, or amphiasters. [Supposed Upper Cretaceous (SOLLAS, 1880c) and Eocene (HINDE & HOLMES, 1892) records are based on isolated dermalia with no diagnostic value, although similar to those of some modern species.] *?Upper Cretaceous, Paleogene (Eocene)–Holocene:* England, *?Upper Cretaceous;* Australia, New Zealand, *Eocene;* cosmopolitan, *Holocene.*——FIG. 158,*4. C.* sp., Eocene, Otago, New Zealand; dichotriaene ascribed to *Corallistes,* ×200 (Hinde & Holmes, 1892).

Dicranoclonella REID, *nom. nov.* herein (SCHRAMMEN, 1937, p. 79, *nom. nud.*) [**D. praecursor* SCHRAMMEN, 1937, p. 79; OD]. Irregularly funnel-like or flabellate; both surfaces of skeletal framework with small, skeletal pores (ostia, postica), from which branching canals (epirhyses, aporhyses) run inwardly; desmas mainly of irregular shapes; dermalia dichotriaenes; small, flattened rhizoclonids may form supplemental cortex; microscleres unknown. [DE LAUBENFELS (1955, p. 62) subsequently designated the type species for *Dicranoclonella,* but according to *Code* Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xxiii, herein).] *Jurassic (upper Oxfordian–Kimmeridgian):* Germany.——FIG. 158,*1a. *D. praecursor,* Weiss Jura, upper Oxfordian, Streitburg; dicranoclone desmas, ×20 (Schrammen, 1937).——FIG. 158,*1b. D. schmidti* SCHRAMMEN, Weiss Jura, Kimmeridgian, Gerstetten; rhizoclonids from supplemental cortex, ×20 (Schrammen, 1937).

Heterophymia POMEL, 1872, p. 143 [**Dactylocalyx heteroformis* BOWERBANK, 1869, p. 86, ="*Conscinospongia heteroformis*" VALENCIENNES ms, *nom. nud., =Heterophymia valenciennesii* POMEL, 1872, p. 144; OD] [=*Coscinospongia* VON LENDENFELD, 1903, p. 135, obj.]. Similar to *Corallistes* SCHMIDT in forms with distinct margins to postica, but with dermal dichotriaenes restricted to inhalant surface; exhalant surface with supplemental cortex formed from flattened rhizoclonids. [Cretaceous to Holocene record in DE LAUBENFELS, 1955, p. 62, as *Coscinospongia* BOWERBANK refers possibly to SCHRAMMEN's record of *Coscinospongia* (Campanian, Germany), based on dermalia of *Paracorallistes* type.] *Holocene:* China.——FIG. 158,*5a–b. *H. heteroformis* (BOWERBANK), Shanghai; *a,* irregular spicule structure of dermal membrane, magnification uncertain; *b,* oval, inhalant pore with projecting spicule tips from dermal layer, apparently for defense against incursions of other animals, magnification uncertain (Bowerbank, 1869).

Kyphoclonella KOLB, 1910 in 1910–1911, p. 212 [**K. multiformis;* OD]. Cylindrical or top shaped, sometimes laterally compressed, with deep, narrow, paragastral cavity; outside with numerous very small ostia from which fine epirhyses run inwardly; paragastral side with larger postica of tubular

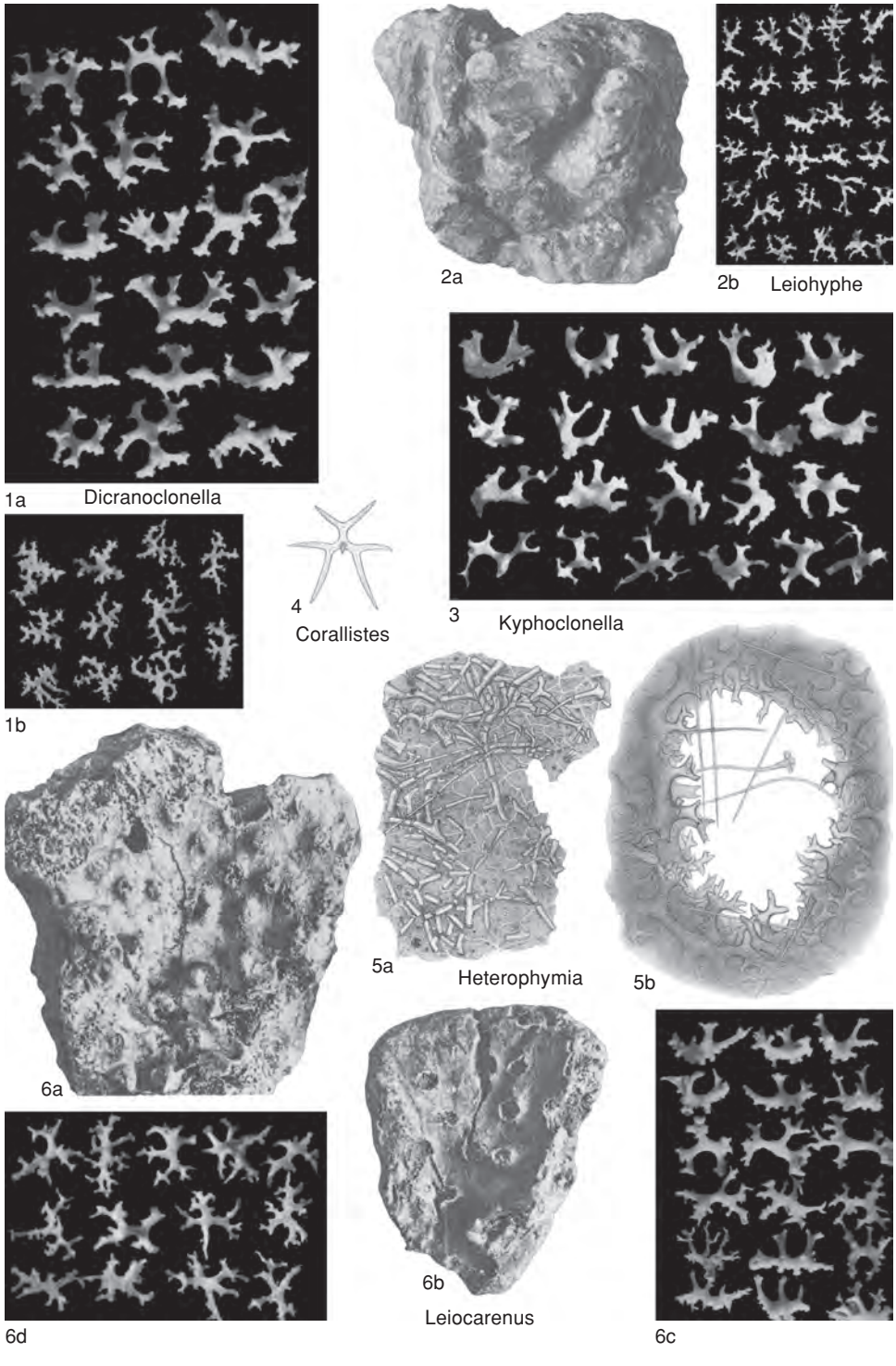


Fig. 158. Corallistidae (p. 242–244).

aporhyses that curve downwardly through wall; desmas partly irregular, partly dipodal to polypodal; dermal triaenes unknown; cortical covering of rhizoclone-like spicules in lower parts of some examples; microscleres unknown. *Jurassic (Kimmeridgian):* Germany.——Fig. 158,*3. *K. multiformis,* Weiss Jura, Sontheim; dicranoclone desmas, ×20 (Schrammen, 1937).

Leiocarenus Reid, *nom. nov.* herein (Schrammen, 1937, p. 78, *nom. nud.*) [**L. papillosus* Schrammen, 1937, p. 78; OD]. Irregularly funnel-like or flabellate; external (inhalant) surface of skeletal framework with very small ostia; paragastral surface with groups of postica in shallow depressions with distinct margins, or at tops of small papillae; desmas mainly irregular, some tuberculate but others developed as smooth rhizoclones; supplemental cortex formed from flattened rhizoclonids on paragastral surface; dermalia dichotriaenes; microscleres unknown. [Very similar to existing *Heterophymia* Pomel (1872, p. 143), possibly identical. de Laubenfels (1955, p. 62) subsequently designated the type species for *Leiocarenus,* but according to *Code* Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xxiii, herein).] *Jurassic (Kimmeridgian):* Germany.——Fig. 158,*6a–d. *L. papillosus,* Weiss Jura, Sirchingen; *a–b,* two specimens have papillae and smooth cortex of paragastral surface, ×1; *c,* tuberculate desmas; *d,* rhizoclones, ×20 (Schrammen, 1937).

Leiohyphe Schrammen, 1924a, p. 67 [**L. solitaria;* M]. Incompletely known; nodular mass with lower parts covered by dense, skeletal cortex; upper parts bare with numerous round, osculelike apertures; desmas irregular, strongly branched in cortical meshwork; supplemental oxeas; no other spicules known. *Cretaceous (Campanian):* Germany.——Fig. 158,*2a–b. *L. solitaria,* Emscher, Sudmerberges; *a,* side view of nodular holotype, ×0.50; *b,* desmas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Subfamily GIGNOUXIINAE de Laubenfels, 1955

[*nom. transl.* Reid, herein, *ex* Gignouxiidae de Laubenfels, 1955, p. 61]

Desmas mainly tripodal to polypodal, although dipodal or irregular forms may occur also and include sometimes true dicranoclones *s.s.* or desmas of similar shape; megarhizoclonids usually more or less distinct from typical desmas; small rhizoclonids sometimes also present; microscleres unknown. *Cretaceous (Aptian)–Neogene (Miocene).*

Gignouxia Moret, 1926b, p. 107 [**G. niciensis;* SD de Laubenfels, 1955, p. 61]. Cup or funnel-like and marginally lobate to flabellate or leaflike; sides sometimes with irregular outgrowths, with osculelike pore at top; exterior of skeletal framework with narrow furrows that contain ostia of epirhyses that run obliquely downward; paragastral side with larger postica having more or less prominent margins, or groups of postica from which shallow furrows radiate; desmas dipodal to polypodal with up to six arms but commonly three; arms of surficial desmas directed inwardly and applied to centra of desmas underlying them; cortical layer of megarhizoclonids; dermalia dichotriaenes with laterally spinulated cladi; microscleres unknown. *Cretaceous (Santonian–Campanian):* France.——Fig. 159,*3a–d. *G. niciensis,* Campanian, Nice, characteristic spicules; *a,* desmas with two, three, and four arms; *b,* dicranoclones; *c,* dermal dichotriaene; *d,* megarhizoclonid; magnification not stated, but about ×50 (Moret, 1926b; courtesy of Société Géologique de France).

Gelasinophorus Schrammen, 1924a, p. 66 [**G. reitemeyeri;* M]. Incompletely known; flabellate to earlike or platelike; surfaces of skeletal framework with small pores, or covered by cortical layer of unknown character (composed of possible rhizoclonids); desmas small; dermalia and microscleres unknown. *Cretaceous (Coniacian):* Germany.——Fig. 159,*2. *G. reitemeyeri,* Emscher, Sudmerberges; dicranoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Gilletia Lagneau-Hérenger, 1962, p. 170 [**G. catalaunica;* OD]. Form not surely known, but apparently flabellate; one surface of skeletal framework with large pores with raised margins, resembling postica of various other genera; desmas stout, tripodal, or tetrapodal, with short arms, very strong, buttonlike tubercles on central part with one in polar position; megarhizoclonids also present; other spicules unknown. *Cretaceous (Aptian):* Spain.——Fig. 159,*4a–c. *G. catalaunica,* Can Casanyas Castellet, Catalogne, characteristic spicules; *a,* isolated desmas; *b,* megarhizoclonids; *c,* fragment of skeletal meshwork showing their relationships, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

Phrissospongia Moret, 1926b, p. 112 [**P. glandiformis;* OD]. Solitary, elongate ovoid with deep, narrow, paragastral cavity, or compound with more than one such sponge arising from common base; exterior of skeletal framework with small ostia; no epirhyses or exhalant features (aporhyses, postica) known; desmas tripodal to polypodal in interior, grading into megarhizoclonids that form cortical layer; dermalia dichotriaenes in which cladi bear sharp, outwardly pointing spines; microscleres unknown. *Cretaceous (Santonian):* France.——Fig. 160,*3a–e. *P. glandiformis,* Saint-Cyr; *a–b,* small, unbranched, normal and twinned individuals, slightly reduced; *c–e,* characteristic spicules including *c,* desmas, *d,* dermal dichotriaenes showing spines, and *e,* megarhizoclonids, magnification not stated, but approximately ×50 (Moret, 1926b; courtesy of Société Géologique de France).

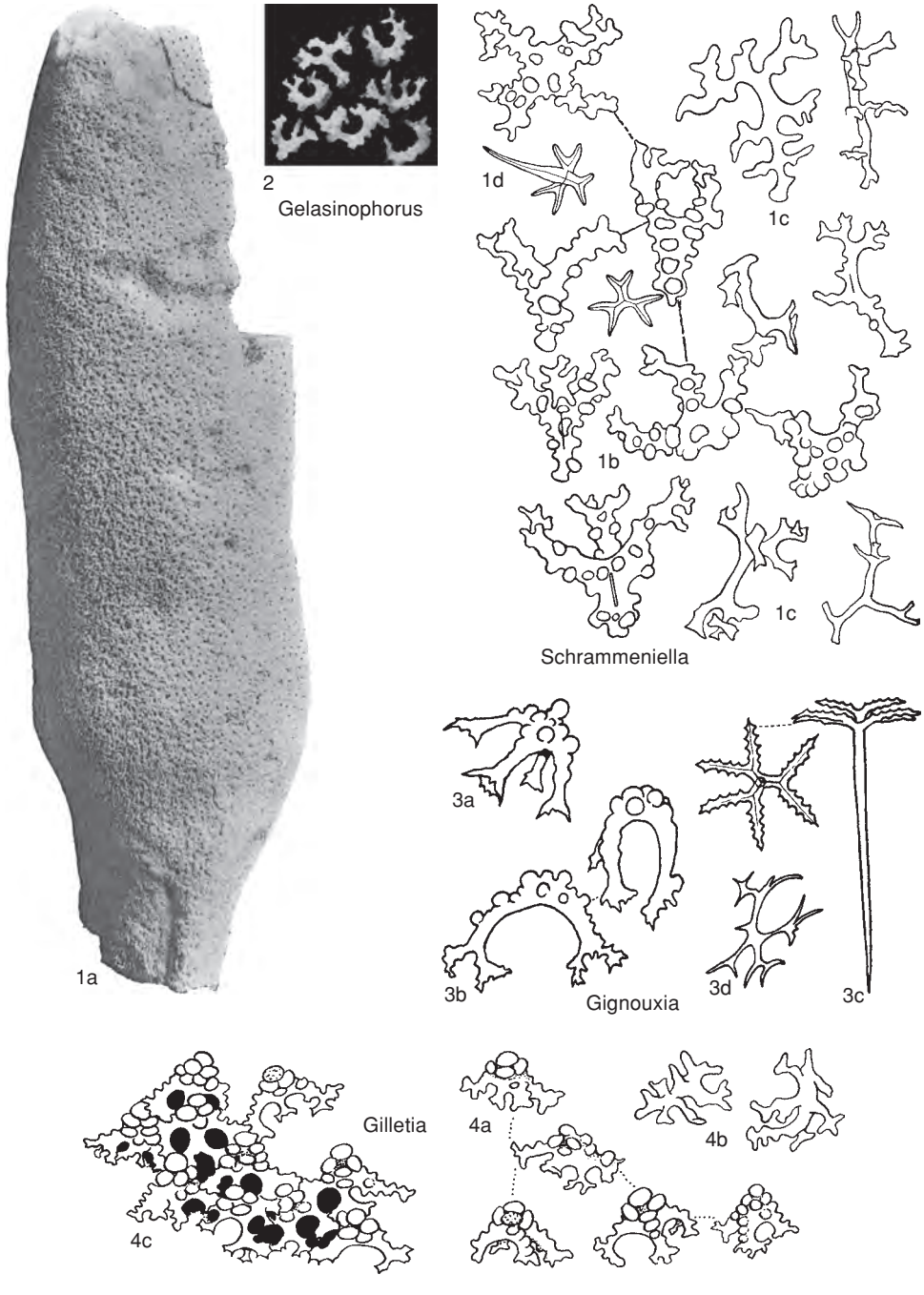


FIG. 159. Corallistidae (p. 244–247).

Procorallistes SCHRAMMEN, 1901, p. 14 [**P. polymorphus;* SD DE LAUBENFELS, 1955, p. 45]. Irregularly funnel-like or flabellate, stalked or not; both sides of skeletal framework with small, skeletal pores (ostia or postica), from which short, radial canals (epirhyses, aporhyses) run inwardly; many desmas dipodal or tripodal and typically with conical or armlike, central outgrowth that bears no

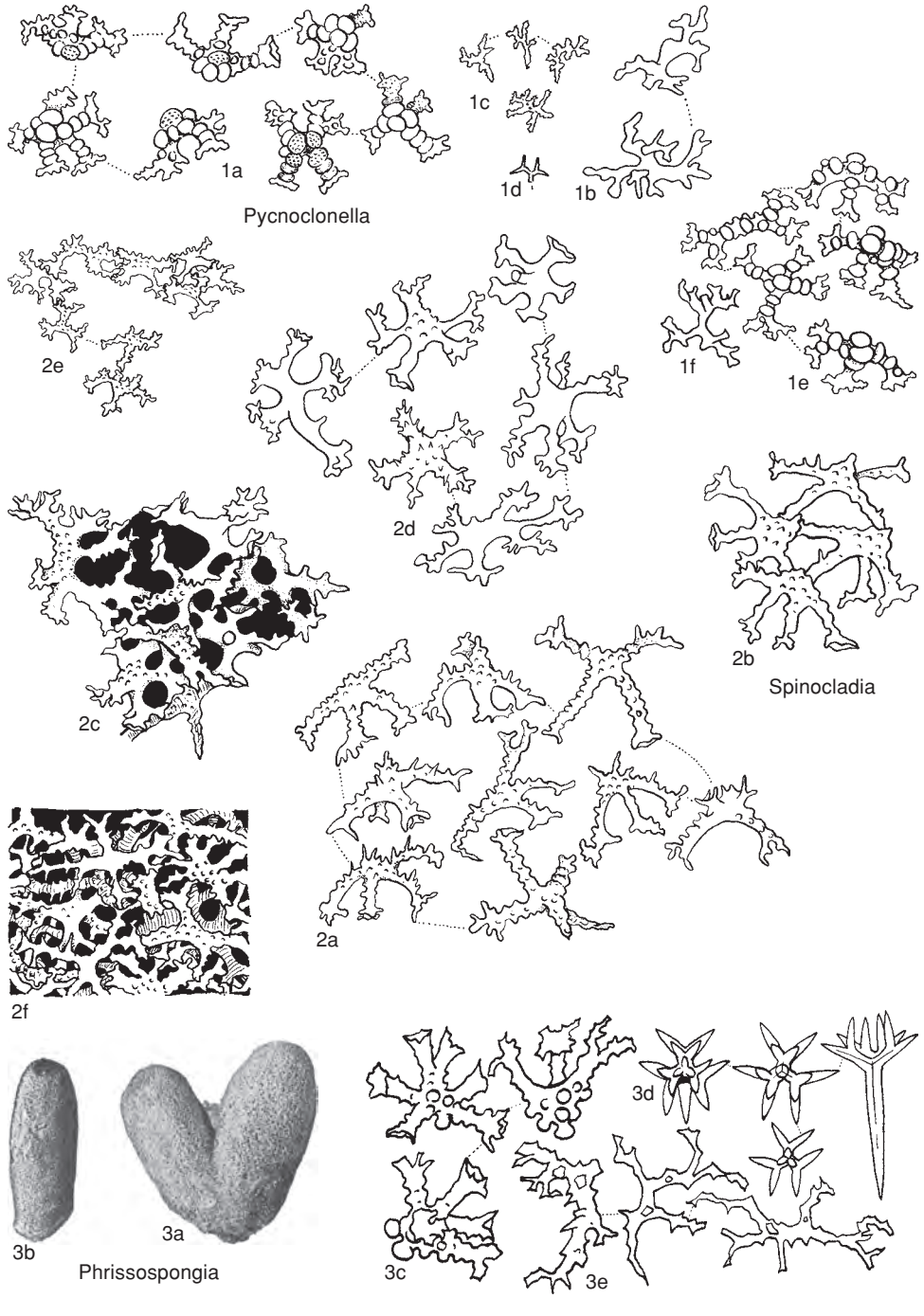


FIG. 160. Corallistidae (p. 244–248).

zygome but may be longer than zygome-bearing arms; these desmas probably dicranoclones *s.s.,* although axial canals are unrecorded; other desmas of irregular shapes and grade into megarhizoclonids; dermalia dichotriaenes; microscleres and small rhizoclonids unknown. *Cretaceous (Albian)–Neogene (Miocene):* Spain, *Albian;* France, *Santonian–Campanian;* Germany, *Turonian–Campanian;* Northern Africa, *Miocene.*——Fig. 161*a–d.* **P. polymorphus,* Mucronatenkreide, Maastrichtian, Misberg, Germany; *a,* side view of irregular, ear-shaped variety of species with long stem, ×1 (Schrammen, 1901); *b,* characteristic spicules, desmas with and without the characteristic long, central growth (or basaltheil), one showing a large, solution cavity that does not represent an axial system; *c,* megarhizoclonids; *d,* dermal dichotriaenes, ×20 (Schrammen, 1910).

Pycnoclonella Lagneau-Hérenger, 1962, p. 168 [**P. dactyliformis;* OD]. Cylindroid with deep, narrow, paragastral cavity and encrusting base, sometimes also with small, hollow outgrowths near base; external surface of skeletal framework with small ostia; no evident epirhyses, aporhyses, or postica; desmas stout, with two to four arms; their central parts bearing large tubercles, one of which may have a polar position; some also grade into forms with two arms at each end of short, central shaft; smooth megarhizoclonids also present; parts of surface with supplemental cortex formed from small rhizoclonids; dermalia not certainly known but apparently dichotriaenes; microscleres unknown. [Dermalia only known from a single, fragmentary dichotriaene, not certainly intrinsic.] *Cretaceous (Aptian):* Spain.——Fig. 160,*1a–d.* **P. dactyliformis,* Can Casanyas Castellet, Catalogne, characteristic spicules; *a,* typical desmas; *b,* megarhizoclonids; *c,* rhizoclonids of cortex; *d,* fragmentary dichotriaene, not certainly intrinsic, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).——Fig. 160,*1e–f.* *P. ramosa* Lagneau-Hérenger, Can Casanyas Castellet, Catalogne; desmas, including one with distinct, central shaft, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

Schrammeniella Breistroffer, 1949, p. 103 [**Phalangium scytaliforme* Schrammen, 1910, p. 70; OD] [=*Iouea* de Laubenfels, 1955, p. 61 (type, *Phalangium cylindratum* Schrammen, 1910, p. 70, OD)]. Cylindrical or branched cylindrical, with deep, narrow, paragastral cavity, or cup-shaped or flabellate; outside of skeletal framework with small ostia or short epirhyses; exhalant features (aporhyses, postica) absent; desmas typically dipodal to tetrapodal and mainly dicranoclones *s.s.,* with axial canal sometimes seen in short, projecting basaltheil; spicules of exterior arranged with arms directed inwardly and applied to central parts of underlying desmas; other irregular desmas and megarhizoclonids also present; small rhizoclonids sometimes forming supplemental cortex; dermalia dichotriaenes; microscleres unknown. [*Schrammeniella* Breistroffer, 1949, and *Iouea* de Laubenfels, 1955, were both proposed as *nom. nov. pro Phalangium* Schrammen, 1910, *non* Linné, 1758, and type species are almost identical ("Allgemeine Form, Oberflache und Kanalsystem wie bei *Phalangium scytaliforme,* wovon sich die Spezies aber durch gracileren Bau gut unterscheidet." Schrammen, 1910, p. 70).] *Cretaceous (Turonian–Campanian):* France, *Santonian;* Germany, Poland, *Turonian–Campanian.*——Fig. 159,*1a–d.* **S. scytaliforme* (Schrammen), Mucronatenkreide, Campanian, Misburg, Germany; *a,* side view of typical cylindrical form with numerous irregular, inhalant ostia, ×1; *b–d,* characteristic spicules including principal desmas, some showing axial canal in basaltheil, megarhizoclonids, one showing axial canal and dermal dichotriaene, ×30 (Schrammen, 1910).

Spinocladia Lagneau-Hérenger, 1962, p. 171 [**S. tubulata;* OD]. Initially cylindrical, with encrusting base and narrow, paragastral cavity, then sometimes laterally branching or expanding upwardly; small

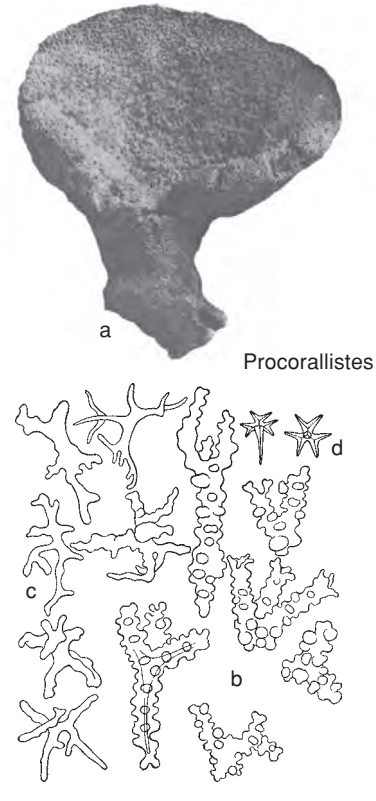


Fig. 161. Corallistidae (p. 245–247).

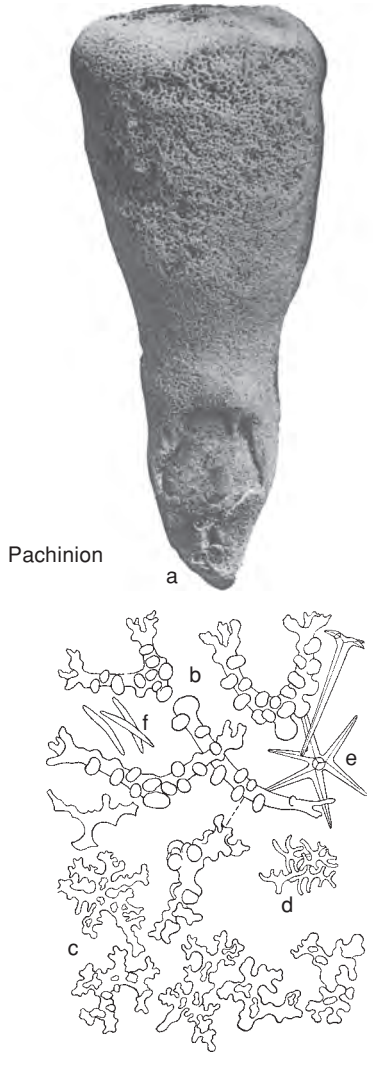


FIG. 162. Corallistidae (p. 248).

ostia at skeletal surface; no epirhyses, aporhyses, or postica; desmas with spines instead of tubercles, mainly tripodal and tetrapodal in interior but less regular and with five or six arms near surface; becoming flattened at surface and passing into megarhizoclonids; some zygomes more or less cupular; supplemental cortex formed by small rhizoclonids; no other spicules known. [Included in the family with some question.] *Cretaceous (Aptian):* Spain.——FIG. 160,*2a–f.* **S. tubulata,* Can Casanyas Castellet, Catalogne, desmas; *a,* dicranoclones of interior; *b,* fragment of interior skeleton; *c,* fragment of outer skeleton; *d–f,* irregular dicranoclones and megarhizoclones from outer part of skeleton, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

Subfamily PACHINIONINAE Schrammen, 1924

[*nom. transl.* REID, herein, *ex* Pachinionidae SCHRAMMEN, 1924a, p. 39; *emend.,* REID, herein]

Desmas mainly dipodal, with one- or three-armed variants subordinate, and arranged to form more or less distinct skeletal fibers; megarhizoclonids and small rhizoclonids present; dermalia dichotriaenes; microscleres unknown. [The group was originally distinguished from Coscinospongiidae LENDENFELD (=Corallistidae SOLLAS) by supposed absence of megarhizoclonids and *deckschicht* (supplemental cortex formed from small rhizoclonids) in the latter; this distinction is here rejected because megarhizoclonids occur in living corallistids; and a cortex formed from small rhizoclonids occurs in living *Heterophymia* POMEL, 1872, p. 143, both of which are herein placed into the subfamily Corallistinae. The subfamily Pachinioninae is here redefined in terms of the skeletal structure of *Pachinion* ZITTEL, 1878a.] *Cretaceous (Aptian–Campanian).*

Pachinion ZITTEL, 1878a, p. 130 [**Jerea scripta* F. A. ROEMER, 1864, p. 34; OD] [=*Pachynion* DE LAUBENFELS, 1955, p. 62, *nom. null.; Neohindia* SCHRAMMEN, 1901, p. 11 (type, *N. cylindrica,* OD)]. Cylindrical to club shaped, with short, basal stalk, or sometimes growing in groups with individuals united at base; paragastral cavity deep, wide, or narrow; no skeletal pores or canals, except at base of paragastral cavity from which a few tubular aporhyses may run down stalk; desmas mainly dipodal but also including tripodal and irregular variants and united to form network of skeletal fibers; no distinct basaltheil in most, although prominent, central tubercle may occur; megarhizoclonids also present; dermalia dichotriaenes, supplemental cortex formed by small, finely branched rhizoclonids in basal parts, or more extensive; small, tangentially arranged oxystrongyles may also occur; microscleres unknown. *Cretaceous (Aptian–Campanian):* Spain, *Aptian–Albian;* France, *Turonian;* England, *Campanian;* Germany, Poland, *Turonian–Campanian.*——FIG. 162*a–f.* **P. scriptum* (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; *a,* small, steeply obconical example, ×1; *b–f,* typical spicules, including characteristic desma, megarhizoclonids, cortical rhizoclonid, dermal dichotriaenes, small, cortical oxeas, ×20 (Schrammen, 1910).

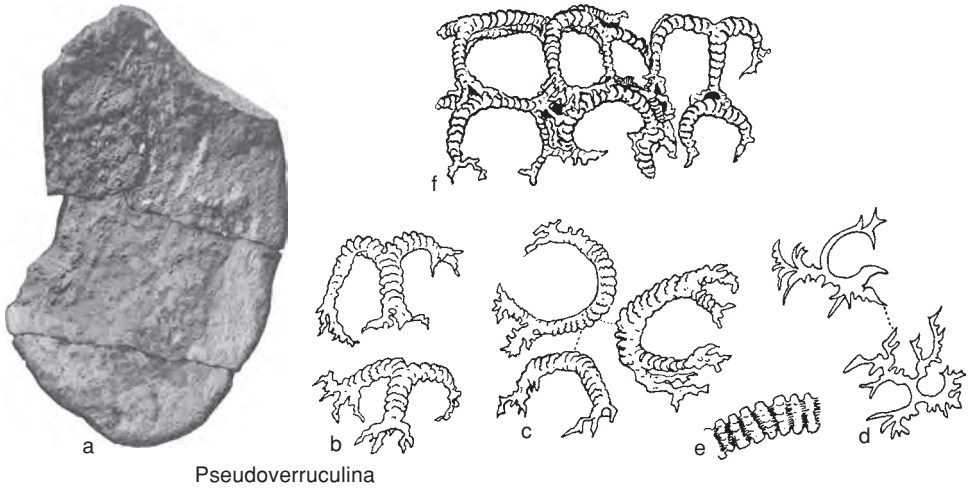


FIG. 163. Pseudoverruculinidae (p. 249).

Family PSEUDOVERRUCULINIDAE de Laubenfels, 1955

[Pseudoverruculinidae DE LAUBENFELS, 1955, p. 63]

Desmas with small tubercles arranged mainly in transverse rows along more or less prominent, semiannular swellings; desmas mainly dipodal, tripodal, or anchor shaped with tuberculated ridges on their convex sides; no brachyome or centrumlike features (i.e., no basaltheil); megarhizoclonids also present; sometimes with small, cortical variants of principal desmas; dermalia and microscleres unknown. [The family is comprised of a single, isolated genus with desmas of distinctive appearance that cannot be dicranoclones *s.s.* because a basaltheil is absent. The family is placed in the suborder Dicranocladina, following MORET (1926b), who included the genus in the family Corallistidae SOLLAS, and LAGNEAU-HÉRENGER, 1962, who placed the genus under the family Pachinionidae SCHRAMMEN. Its desmas could also be compared with the kyphorhabds of *Helminthophyllum* SCHRAMMEN (subclass Choristida; family Helminthophyllidae), and may possibly be of independent origin.] *Cretaceous (Aptian–Santonian).*

Pseudoverruculina MORET, 1926b, p. 105 [**P. niciensis;* OD]. Flabellate lamellar or leaflike; one surface of skeletal framework, presumed inhalant, with small, skeletal pores (ostia); other with larger pores, presumed to be postica, at tops of papillar outgrowths; desmas mainly bow shaped, tripodal, or anchor shaped, and arranged to form skeletal fibers; megarhizoclonids also present; some examples with small, cortical rhizoclonids, and forms intermediate between these and principal desmas; no other spicules known. *Cretaceous (Aptian–Santonian):* Spain, *Aptian;* France, *Santonian.*—— FIG. 163*a–f.* **P. niciensis,* Santonian, Saint-Cyr, France; *a,* upper surface, ×0.5; *b–f,* characteristic spicules include: *b–c,* isolated desmas; *d,* megarhizoclonids; *e,* detail of ornament; *f,* skeletal meshwork, approximately ×20 (Moret, 1926b; courtesy of Société Géologique de France).

Suborder PSEUDORHIZOMORINA Schrammen, 1901

[*nom. transl. et correct.* REID, herein, *ex* tribus Pseudorhizomorinidae SCHRAMMEN, 1901, p. 14; *emend.,* REID, herein]

Desmas typically monaxial and developed as simple rhizoclones, or as more or less tuberculate forms that do not include dicranoclones; some also with subordinate, tetraxial desmas, in which crepis has form of triaene, intergrading with main ones; zygomes spiny, twiglike, or rootlike, forming more or less random zygoses, or united to form radiating, syzygial fibers like those of some Orchocladina; dermalia phyllotriaenes, monaxial, phyllotriaene-like spicules, or monaxial

plates; supplemental rhizoclonids unknown; modern forms with microrhabds, amphiasters, and spirasters that may pass into metasters or plesiasters, or no microscleres. *Cretaceous–Holocene.*

This taxon is revived because of considerable differences between *Macandrewia* GRAY and the typical Dicranocladina, with which it has been included formerly.

SCHRAMMEN's taxon Pseudorhizomorina (as Pseudorhizomorinidae) was proposed originally for the family Corallistidae *sensu* SOLLAS, in which SOLLAS (1888) included *Macandrewia,* plus the fossils *Pachinion* ZITTEL and *Procorallistes* SCHRAMMEN that SCHRAMMEN took to be fossil Corallistidae. These had been treated as Rhizomorinidae by ZITTEL (1878a) and RAUFF (1893, 1894) but were interpreted by SCHRAMMEN (1901) as distinct from true Rhizomorina, in which tetraxial spicules are absent, because these genera have triaene (i.e., tetraxial) dermalia. The name was then dropped in his next classification (1910) and replaced by Dicranocladina in his final one (1937, p. 77).

SCHRAMMEN then distinguished three families of Dicranocladina: (a) Pachinionidae SCHRAMMEN for fossils with dicranoclones *s.l.* and megarhizoclonids; (b) Coscinospongiidae VON LENDENFELD for the modern corallistids, supposed to lack megarhizoclonids; and (c) Macandrewiidae GRAY (ascribed by SCHRAMMEN to himself), for *Macandrewia* and other genera with monaxial, phyllotriaene-like dermalia. Genera that fall in the first and second of these families are essentially similar, except that dicranoclones (or dipodal to polypodal desmas) occur chiefly in the first (Pachinionidae). *Macandrewia* is a sponge in which the desmas are irregular or bipolar rhizoclones that are arranged to form radiating, syzgial fibers similar to those of anthaspidellid Orchocladina. The skeleton is so different from that of any fossil placed by SCHRAMMEN in his Dicranocladina that his familiarity with specimens of the genus may be doubted. *Macandrewia* is also distinguished by occurrence of tetraxial desmas, with the crepidal axes of a triaene, as subordinate variants of the main ones. These are not mentioned in SCHRAMMEN's papers, and he thought that dicranocladine desmas were of monaxon origin. A second genus, *Daedalopelta* SOLLAS, does not have an anthaspidellid-like structure, but its desmas, again, are not like forms called dicranoclones by SCHRAMMEN in the fossils.

In theory, desmas of these sponges might be thought to correspond with megarhizoclonids of typical Dicranocladina, which in turn might represent an unspecialized prototype of typical dicranocladine desmas. In practice, how the desmas are related is entirely unknown; and the group would still need to be pictured as having descended independently since a time before dicranocladine desmas assumed their characteristic aspect. In this light, it seems best to remove them from the Dicranocladina, and the older taxon Pseudorhizomorina is revived to comprise them. This usage seems appropriate because the desmas are of rhizoclonar type, while Dicranocladina is based on the desma name dicranoclone.

Family MACANDREWIIDAE Gray, 1859

[*nom. correct.* SCHRAMMEN, 1924a, p. 39, *pro* Macandrewiadae GRAY, 1859, p. 440]

Desmas large, smooth rhizoclones or tuberculate variants in which the tubercles are typically restricted to zygomes or branches; no tripodal or comparable desmas (i.e., dicranoclones *s.l.*); sometimes with tetraxial variants of normal, rhizoclonar desmas; dermalia phyllotriaenes or discotriaenes, with finely sculptured margins; no rhizoclonids; microscleres microrhabds, amphiasters, or spirasters. [The name was described as new by SCHRAMMEN (1924a) but was first proposed by GRAY in discussion of the type genus, *Macandrewia* GRAY. Dermalia were described as monaxial by SCHRAMMEN (1924a, p. 39), but this is not their character in the two modern genera now included (*Macandrewia* GRAY, *Daedalopelta* SOLLAS) but may refer to *Callipelta* SOLLAS, here excluded because its desmas are of dicrano-

cladine type (strongly tuberculate, sometimes dipodal, and with a strong, central tubercle).] *?Upper Cretaceous, Holocene.*

Macandrewia GRAY, 1859, p. 438 [**M. azorica;* OD]. Irregularly funnel-like, flabellate, club shaped or with short branches arising from clublike stock; usually stalked with encrusting base; lateral surfaces with small pores from which radial epirhyses run inwardly; inside of funnel-like or flabellate examples have small, marginated oscules; beneath these, surface of skeletal framework showing stellate groups of postica from which aporhyses run into skeleton, and shallow furrows radiate on its surface; other forms with aporhyses that open at summit or ends of short branches, with corresponding, exhalant canals opening through small oscules in these positions; desmas mainly smooth, of irregular to bipolar shapes, and mainly arranged so that zygomes unite to form radiating, skeletal fibers that spread out longitudinally and end at skeletal surface; dermalia phyllotriaenes to discotriaenes, with finely sculptured margins and granulated, external surfaces; microscleres microrhabds. *?Upper Cretaceous, Holocene:* Germany, *?Upper Cretaceous;* Northern Atlantic, West Indies, East Indies, *Holocene.*——FIG. 164,*4. *M. azorica,* Holocene, West Indies, Barbados; side view of holotype showing lobed, stalked, obconical form, and scattered, exhalant ostia on gastral surface, ×0.3 (Gray, 1859).

Family NEOPELTIDAE Sollas, 1888

[Neopeltidae SOLLAS, 1888, p. 344] [=Daedalopeltidae DE LAUBENFELS, 1936, p. 184]

Sponges with dermal armor of discotriaenes present and with rhizomorine, principal spicules. *Cretaceous–Holocene.*

Neopelta SCHMIDT, 1880, p. 88 [**N. imperfecta;* OD]. Sponge body irregularly nodose to irregularly obconical; upper end with ostia of open canals; endosomal skeleton of rhizomorine desmas and some smooth oxeas and amphiasters; dermal surface armored with discotriaenes. *Cretaceous–Holocene:* cosmopolitan.——FIG. 164,*6a–b. *N. imperfecta,* Holocene, North Atlantic; *a,* isolated dermal discotriaene, ×50; *b,* spinose amphiaster, ×500 (de Laubenfels, 1955).

Suborder DIDYMMORINA Rauff, 1893

[*nom. transl.* REID, 1963d, p. 200, *ex* tribus Didymmorina SCHRAMMEN, 1937, p. 102, *nom. correct. pro* unter-tribus Didymmorinidae RAUFF, 1893, p. 195]

Desmas monaxial and typically developed as didymoclones, although some may be bipolar or more or less irregular rhizoclones; zygomes twiglike, rootlike, or handlike, and in didymoclones typically applied to swollen pseudocentra of other desmas; dermalia dichotriaenes or apparently absent; small rhizoclonids unknown, but some with skeletal cortex formed by rhizoclones that intergrade with typical didymoclones; no microscleres known. *Middle Jurassic–Upper Jurassic (Kimmeridgian).*

The Didymmorina have formerly been listed as "lithistid Monaxonia" by SCHRAMMEN (1937, p. 102) and as Monalithistida by LAGNEAU-HÉRENGER (1962, p. 40), because tetraxial spicules were unknown. They are placed here in the Tetralithistida because a specimen of *Cylindrophyma milleporata* (GOLDFUSS), identified by SCHRAMMEN himself, shows dichotriaenes that do not appear to be intrusive and because of the character of the zygomes, which are like those of tetraclones and dicranoclones. Relationships are strictly unknown, but the group may be similar to the Dicranocladina because the dermal dichotriaenes of *C. milleporata* are like those of the fossil and modern Corallistidae and some dicranocladine desmas have didymoclone-like shapes, as do some of those of the Jurassic *Leiocarenus* SCHRAMMEN, for example.

In ZITTEL's first classification (1878a, p. 100), the didymmorine genera *Melonella* ZITTEL and *Cylindrophyma* ZITTEL were united with *Lecanella* ZITTEL and *Mastosia* ZITTEL as Anomocladina. The two latter genera have astroclone and sphaeroclone desmas, respectively, and are here placed in the Sphaerocladina SCHRAMMEN. The taxon was defined as though all desmas were sphaeroclones. SOLLAS (1885b) also treated the desmas as sphaeroclones but cited only genera not included by ZITTEL. SOLLAS included the living *Vetulina* SCHMIDT, which SOLLAS had specially investigated, and the Paleozoic Astylospongiidae ZITTEL, which ZITTEL (1877b, p. 44) had mistaken for dictyonine Hexactinellida. RAUFF (1893, p. 159) coined the term didymoclone and proposed a distinction between the Didymmorinidae RAUFF, with didymoclones, and the Anomocladinidae ZITTEL, with desmas termed ennomoclones. The latter spicules

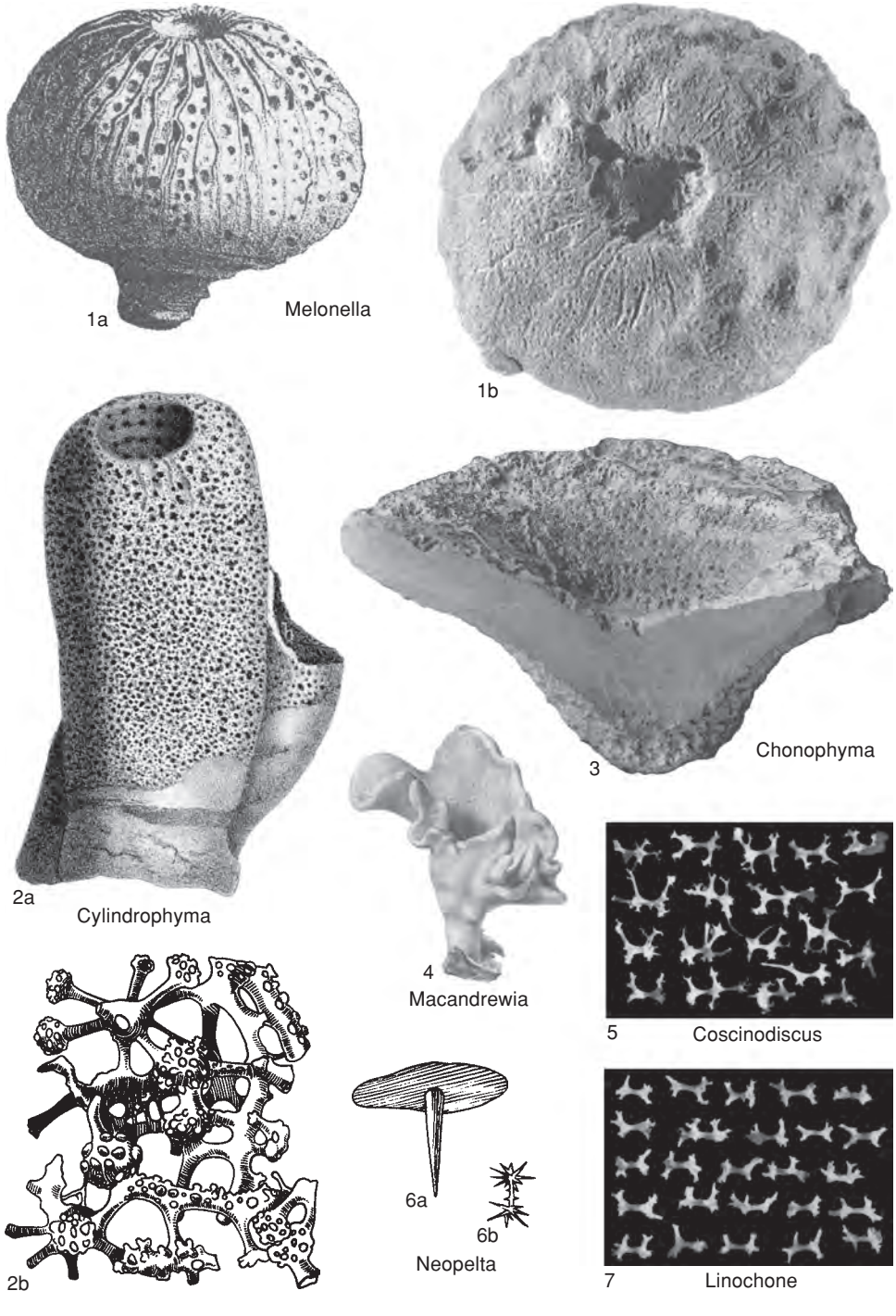


FIG. 164. Macandrewiidae, Neopeltidae, and Cylindrophymatidae (p. 251–252).

include the sphaeroclones of Astylospongiidae and later genera (e.g., *Mastosia, Vetulina*) and the triderlike desmas of the Paleozoic *Hindia* Duncan. *Hindia* had not been established when ZITTEL's first system was published. The *Hindia* desma and the sphaeroclone were supposed to be allied types with simple and branching arms, respectively, which RAUFF termed triders and dichotriders. ZITTEL (1878a), however, preferred to use Anomocladina for RAUFF's Didymmorinidae, despite its being contrary to his first diagnosis, and was followed by RAUFF (1893), who proposed the name Eutaxicladinidae for his former Anomocladinidae.

At this stage, the name Anomocladina, thus, had been used in four different senses, in terms of the desmas of the forms that were included. There are two more, due to SCHRAMMEN (1937, p. 108) and DE LAUBENFELS (1955). SCHRAMMEN identified the desmas of *Lecanella* as anomoclones and used Anomocladina as a suborder name (tribus, SCHRAMMEN) for his family Lecanellidae SCHRAMMEN, in accordance with his general use of taxa whose names correspond with those of desmas. DE LAUBENFELS (1955, p. 64) used the name Anomocladina but took the desmas as sphaeroclones in his diagnosis. Only one genus included, however, has sphaeroclone desmas (*Mastosia*); the others have didymoclones (e.g., *Cylindrophyma*), dendroclones (e.g., *Anthaspidella* MILLER), anomoclones (*Anomoclonella* RAUFF), do not have desmas of any sort (e.g., *Heliospongia* GIRTY), or have unknown affinities (e.g., *Calathium* BILLINGS). All other genera with sphaeroclones were placed in the Eutaxicladina RAUFF, together with others in which desmas are tricranoclones (*Hindia,* identified with *Microspongia* MILLER), dicranoclones (e.g., *Pachinion* ZITTEL, *Gignouxia* MORET), astroclones (*Regnardia* MORET), dendroclones (e.g., *Phacellopegma* GERTH), or chiastoclones (*Chiastoclonella* RAUFF). RAUFF's (1893, p. 157–158) term ennomoclone was replaced by SCHRAMMEN's dicranoclone, although desmas called dicranoclones by SCHRAMMEN (1910, p. 65) were called rhizoclones by RAUFF (1893, p. 161), not ennomoclones.

Because of this confusion in usage of the name Anomocladina and because the alternative Didymmorina is related to the name of the characteristic desmas, the latter name is here considered preferable. In addition, because first designation of Anomocladina as a suborder was by SOLLAS—not by ZITTEL, who termed his taxon family—the taxon should strictly be treated as equivalent to Sphaerocladina SCHRAMMEN.

The confusion in ZITTEL's original publication was probably due partly to the resemblance of the two pseudocentra of didymoclones to the centra of sphaeroclones and to the similar mode of zygosis (zygomes applied to centra or pseudocentra) of these sponges. SCHRAMMEN at first interpreted didymoclones as monaxial but later suggested (1910, p. 169) that they might be composed of two linked sphaeroclones. This idea was dropped in his final work (1937) and is shown to be mistaken by the gradation of didymoclones into simple rhizoclones and their observable young stages, which are monaxons with incipient outgrowths at the ends.

Family CYLINDROPHYMATIDAE Schrammen, 1936

[*nom. correct.* DE LAUBENFELS, 1955, p. 64, *pro* Cylindrophymidae SCHRAMMEN, 1937, p. 102] [=Coscinodiscidae SCHRAMMEN, 1937, p. 105]

With didymoclones and usually other desmas, having intergradation from didymoclones to rhizoclones; desmas of rhizoclonar type sometimes forming skeletal cortex; dermalia dichotriaenes when present. *Middle Jurassic–Upper Jurassic (Kimmeridgian):*

Cylindrophyma ZITTEL, 1878a, p. 134 [**Scyphia milleporata* GOLDFUSS, 1826, p. 8; SD DE LAUBENFELS, 1955, p. 64] [=*Didymosphaera* LINCK, 1883, p. 59 (type, *D. steinmanni,* OD)]. Cylindrical or pyriform with paragastral cavity extending to base; exterior of skeletal framework with numerous small ostia of fine, radial epirhyses; paragastral surface with larger postica of radial or branching aporhyses; desmas didymoclones and rhizoclonar variants; latter sometimes forming skeletal cortex in

lower parts, then covering ostia of main skeletal framework; dermalia dichotriaenes; other spicules unknown. *Jurassic (Oxfordian–Kimmeridgian):* Germany, Poland, *Oxfordian–Kimmeridgian;* Switzerland, *Kimmeridgian.*——Fig. 164,*2a–b. *C. milleporata* (Goldfuss), Germany; *a,* cylindrical specimen with inhalant ostia in porous dermal surface and coarse exhalant ostia in gastral surface of open paragastral cavity at top; a second attached specimen shows behind, ×0.5 (Quenstedt, 1878–1879); *b,* drawing of part of skeleton, ×30 (de Laubenfels, 1955).

Chonophyma Oppliger, 1921a, p. 204 [**C. perforata;* OD]. Funnel or bowl shaped, thick walled; outside with small, closely spaced ostia of fine, radial epirhyses; paragastral side with rather larger postica of arching aporhyses and other smaller pores that perforate smooth, cortical layer; desmas small didymoclones; other details unknown. [All known material calcified.] *Jurassic (Kimmeridgian):* Switzerland.——Fig. 164,*3. *C. perforata,* Malm, Randen; side view of thick-walled, funnel-shaped type specimen, ×0.5 (Oppliger, 1926).

Coscinodiscus Schrammen, 1937, p. 105 (Schrammen, 1936, p. 186, *nom. nud.*) [**C. suevicus;* OD]. Funnel to bowl shaped to platelike or flabellate, thick walled; exterior of skeletal framework with small ostia of short epirhyses and large, irregular apertures of uncertain character; paragastral surface with large, rounded postica; desmas didymoclones and some irregular variants; other spicules unknown. *Jurassic (Kimmeridgian):* Germany.——Fig. 164,*5. *C. suevicus;* desmas, ×20 (Schrammen, 1937).

Linochone Schrammen, 1937, p. 103 (Schrammen, 1936, p. 186, *nom. nud.*) [**L. rimosa;* OD]. Compressed, funnel shaped, thick walled; outside with closely spaced, rounded to cleftlike ostia; inside with more widely spaced postica; form of internal canals unknown; desmas small didymoclones and variants that are bipolar rhizoclones; other details unknown. *Jurassic (Kimmeridgian):* Germany.——Fig. 164,*7. *L. rimosa,* Weiss Jura, Gerstetten; desmas, didymoclones and rhizoclonar variants, ×20 (Schrammen, 1937).

Melonella Zittel, 1878a, p. 134 [**Siphonia radiata* Quenstedt, 1858, p. 679; OD] [=*Emploca* Sollas, 1883, p. 541 (type, *E. ovata* Sollas, 1883, p. 542, M)]. Globular, apple shaped, pyriform, or hemispherical, with short stalk or none, and narrow, conical, paragastral cavity usually extending to base; outside with small ostia of radial epirhyses and sometimes with furrows that radiate from paragastral margin and represent inceptional aporhyses; paragastral wall with postica of arched aporhyses that curve downwardly in general conformity with external form; desmas didymoclones and rhizoclonar variants, latter may form dense, wrinkled, skeletal cortex on under surface; dermal triaenes and microscleres unknown. *Middle Jurassic (Bajocian)–Upper Jurassic:* England; Germany, Poland, *Oxfordian–Kimmeridgian;* Switzerland, *Kimmeridgian.*——Fig. 164,*1a–b. *M. radiata* (Quenstedt), Kimmeridgian, Germany; *a,* side view of stalked, globose sponge with relatively small osculum at summit of spongocoel, ×1 (Quenstedt, 1858); *b,* oscular view with central osculum and radially arranged, exhalant canals, ZPAL Pf. VIII/119, ×1 (Pisera, 1997; courtesy of *Palaeontologica Polonica*).

Order MEGALITHISTIDA new order

[Megalithistida Reid, herein] [=Megamorina Zittel, 1878a, p. 156, *sensu* Zittel, 1878a, p. 99, *non* Schrammen, 1924a, p. 61]

Lithistids that typically have dermal dichotriaenes and monaxial desmas in form of heloclones or megaclones; dermalia sometimes simple triaenes only or absent, but never phyllotriaenes, discotriaenes, or related types; rarely with additional small rhizoclonids; microscleres of modern examples microrhabds, spirasters, and amphiasters. *Carboniferous (?Mississippian), Upper Jurassic–Holocene.*

This order comprises triaene-bearing lithistids whose desmas appear to be derivatives of ophirhabds, from which they develop in ontogeny in the instance of heloclones. Those of the suborder Helomorina (heloclones) are barely lithistid in character, the zygomes being terminal and lateral notches. A megaclone seems to be simply a more completely lithistid form of the same type of desma, with a much reduced crepis, true anaxial arms, and sometimes prominent, expanded zygomes.

If triaenes are supposed to point to origin from choristids, the occurrence of spirasters in the two living genera (*Costifer* Wilson, *Pleroma* Sollas) suggests a source in the order Pachastrellida; although these spirasters do not pass into plesiasters and, hence, are not surely streptoscleres. The expected spiculation of an ancestral stock (ophirhabds, simple triaenes) is seen in the Cretaceous Cephaloraphiditidae (=Ophiraphiditidae Schrammen), which Moret (1926b) included as Megamorina *s.l.* (i.e., Megalithistida herein); but these forms are too late stratigraphically. A possible true ancestor is *Archaeodoryderma* Reid, in which blunt-ended ophirhabds grade into heloclones and these in turn grade into forms that agree with

the simplest typical megaclones. This genus is, however, only known from loose spicules and is not surely known to have had triaenes, although examples occur with its spicules.

A further problem is occurrence of similar desmas in some probably unrelated sponges and in some sponges of uncertain status. These include (a) small, heloclone-like desmas in the axinellid *Saccospongia* BASSLER (Ordovician; FINKS, 1967a); (b) more or less megaclone-like desmas in the living *Desmatiderma* TOPSENT and *Helophloeina* TOPSENT, which are sublithistid Desmacidontida; and (c) megaclone-like desmas in one species of the fossil *Megarhiza* SCHRAMMEN (*M. colungensis* MORET) that intergrade with typical megarhizoclones. The living *Lyidium* SCHMIDT also has desmas that are megaclones, morphologically but no other megascleres except oxeas. Genera with desmas of these types are not referred here to the order Megalithistida unless the skeleton in general is of megalithistid type. Taxa are certainly not referred to the order if triaenes are absent.

Suborder HELOMORINA Schrammen, 1924

[*nom. transl.* REID, 1963d, p. 199, *ex* tribus Helomorina SCHRAMMEN, 1924a, p. 38]

Desmas typically heloclones but some genera with additional branching variants; dermalia sometimes simple plagiotriaenes but usually dichotriaenes; supplemental oxeas in some; small rhizoclonids in one genus; microscleres of a modern example short spirasters and granulated microrhabds. [The original designation tribus was directly equivalent to suborder as a primary division of an order (Tetraxonia VOSMAER, ascribed to SCHULZE). Includes one living genus, *Costifer* WILSON.] *Upper Jurassic (Kimmeridgian)–Holocene.*

Family CARTERELLIDAE Schrammen, 1901

[Carterellidae SCHRAMMEN, 1901, p. 11] [=Isoraphiniidae SCHRAMMEN, 1924a, p. 38]

Diagnosis as for suborder. [The name Isoraphiniidae used in the previous *Treatise, Part E* (DE LAUBENFELS, 1955, p. 51) is here replaced by Carterellidae on grounds of seniority, but is retained as a subfamily designation in the translated form, Isoraphiniinae SCHRAMMEN, 1924a.] *Upper Jurassic (Kimmeridgian)–Holocene.*

Subfamily CARTERELLINAE Schrammen, 1901

[*nom. transl.* REID, herein, *ex* Carterellidae SCHRAMMEN, 1901, p. 11]

Cylindrical sponges with bundle of vertical, tubular aporhyses in axial parts and their postica at summit of body; some desmas may be branched irregularly or more or less triradiate; dermalia dichotriaenes when known; microscleres unknown. *Cretaceous (Albian–Maastrichtian).*

Carterella ZITTEL, 1878a, p. 132 [**Jerea cylindrica* GÜMBEL, 1868, p. 761; SD DE LAUBENFELS, 1955, p. 50]. Cylindrical, branched cylindrical, or elongate club shaped; exterior of skeletal framework with numerous irregularly shaped ostia of fine, radial epirhyses; summit with postica of bundle of tubular, radial aporhyses that run mainly down axial parts of body but in some instances nearer to surface; lower parts often with irregular, longitudinal furrows; skeletal framework with densely packed heloclones forming longitudinal fibers in parts; some desmas irregularly branched at ends; small rhizoclonids in interspaces locally; dermalia unknown; microscleres unknown. *Cretaceous (Cenomanian–Maastrichtian):* Germany, Poland.——FIG. 165,*4a–c.* **C. cylindrica* (GUMBEL), Greensand, Cenomanian, Regensberg, Germany; *a,* side view of cylindrical sponge, ×0.5; *b,* sketch of part of dermal surface showing irregular ostia between fibers, somewhat enlarged; *c,* transverse section showing radial epirhyses and sectioned aporhyses, ×1 (Zittel, 1878a).

Inodia MORET, 1925, p. 487 [**I. elisabethae;* OD]. Known incompletely from cylindrical fragments only; surface with small ostia; axial parts with bundle of tubular aporhyses; desmas resemble heloclones but have irregular, ramified outgrowths, similar to elongate, basal desmas of some Tetracladina (Siphoniidae); zygosis loose or absent; no other spicules known. *Cretaceous (Cenomanian):* France, Poland.——FIG. 165,*3a–b.* **I. elisabethae,* Sablons, France; characteristic, large desmas, magnification not stated, about ×10 (Moret, 1926b; courtesy of Société Géologique de France).

Nematinion HINDE, 1884a, p. 54 [**N. calyculum;* OD]. Elongate cylindrical, with small, cuplike expansion at top and stalk that ends bluntly or divides into root processes; sides with ostia of radial epirhyses; summit with postica of tubular, vertical aporhyses that traverse axial parts; desmas of interior normal heloclones; those of exterior branching,

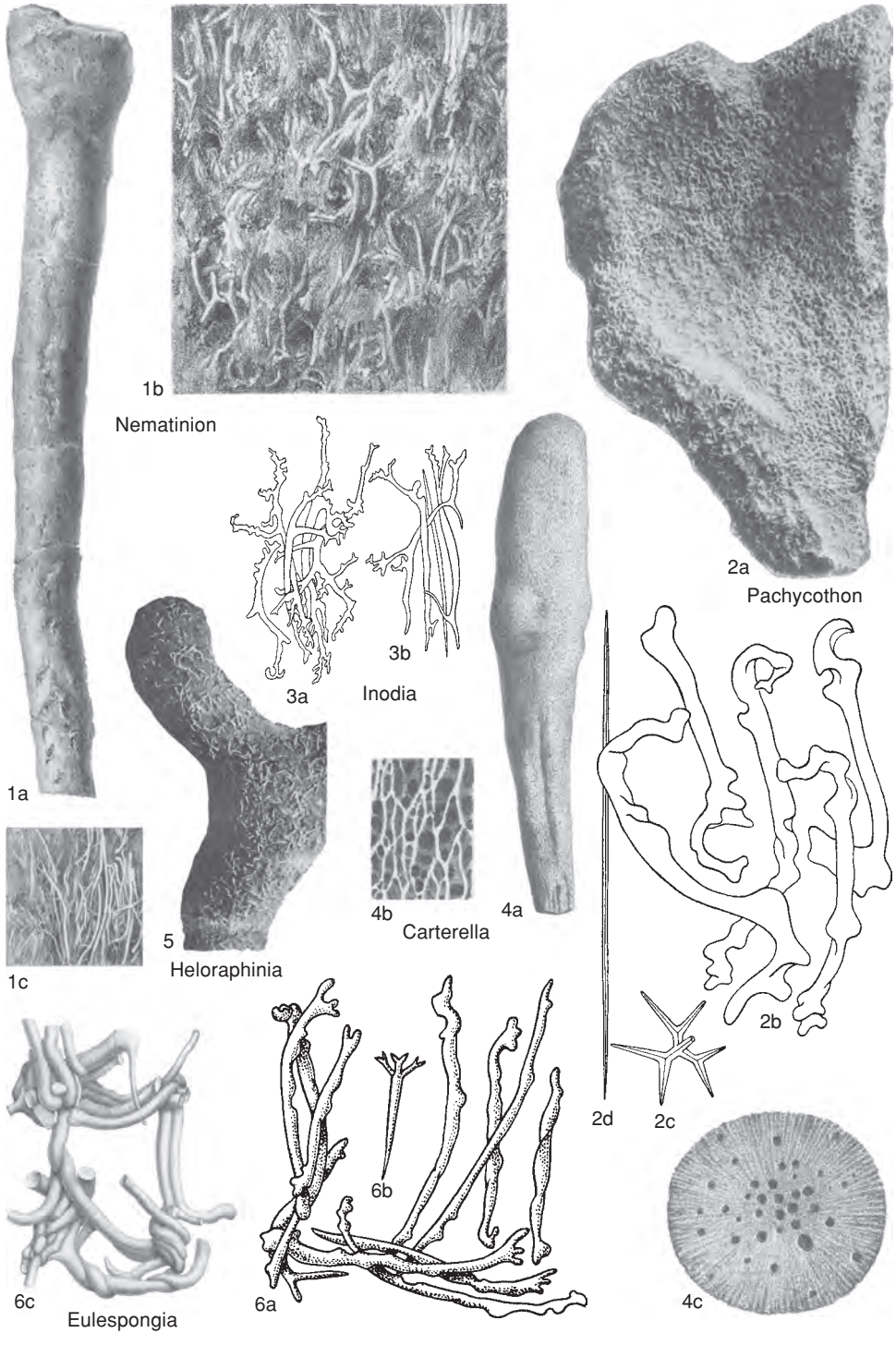


FIG. 165. Carterellidae (p. 255–257).

sometimes triradiate in form; other spicules unknown. *Cretaceous (Albian):* England.——Fig. 165,*1a–c.* **N. calyculum,* Upper Greensand, Warminster, Wiltshire; *a,* side view of cylindrical holotype with cuplike, upper end, ×0.5; *b,* external meshwork with apparently triradiate desmas, ×8; *c,* elongate heloclones of internal meshwork, ×10 (Hinde, 1884a).

Subfamily ISORAPHINIINAE Schrammen, 1924

[*nom. transl.* Reid, herein, *ex* Isoraphiniidae Schrammen, 1924a, p. 38]

Hollow cylindrical, bowl to funnel-like, flabellate, or branched cylindrical sponges that have no canalar features (ostia, postica, epirhyses, aporhyses) in skeletal framework, or with ostia or postica only; desmas all typical heloclones; dermalia plagiotriaenes or dichotriaenes; supplemental oxeas in some, but rhizoclonids unknown; microscleres short spirasters and granulated microrhabds in living example. [The subfamily includes the single living carterellid, *Costifer* Wilson, which is also the only genus with plagiotriaene dermalia.] *Upper Jurassic (Kimmeridgian)–Holocene.*

Eulespongia Quenstedt, 1877 in 1877–1878, p. 105 [**Siphonocoelia texta* F. A. Roemer, 1864, p. 29; SD de Laubenfels, 1955, p. 51; note: listed as OD by de Laubenfels (1955, p. 51), but Zittel (1878a, p. 133) listed *Siphonocoelia hirta* F. A. Roemer, 1864, p. 30, as a possible second species] [=*Isoraphinia* Zittel, 1878a, p. 133, obj.]. Body cylindrical or club shaped, passing downwardly into stalk, with truncated summit and a deep, narrow, paragastral cavity; no skeletal pores or canals; heloclones united in irregular fibers and radiating clusters; dermalia dichotriaenes; no rhizoclonids; some examples with cortical layer of small, tangentially oriented oxeas that underlie heads of dermalia; no microscleres known. *Cretaceous (Cenomanian–Maastrichtian):* England, France, Germany, Czech Republic, Slovakia.——Fig. 165,*6a–c.* **E. texta* (F. A. Roemer), Cenomanian, France; *a,* characteristic, heloclone desmas; *b,* dermal dichotriaene, ×30 (de Laubenfels, 1955); *c,* part of inner wall showing relationships of spicules, ×10 (Zittel, 1878a).

Heloraphinia Schrammen, 1937, p. 76 (Schrammen, 1936, p. 184, *nom. nud.*) [**H. arborescens;* OD]. Only known from branched, cylindrical fragments; skeletal framework wide meshed with no paragastral cavity or canalar features; no other spicules known. *Jurassic* (*Kimmeridgian), Cretaceous (?Aptian, Cenomanian):* Germany, *Kimmeridgian;* Spain, *?Aptian;* Poland, *Cenomanian.*——Fig. 165,*5.* **H. arborescens,* Weiss Jura, Kimmeridgian, Schwabtal, Germany; side view of branched holotype with heloclones in dermal layer, ×2 (Schrammen, 1937).

Pachycothon Schrammen, 1901, p. 11 [**P. giganteum;* OD; =*Cupulospongia gigantea* F. A. Roemer, 1864, p. 51, according to Schrammen, 1910, p. 130]. Funnel- to platelike or flabellate, stalked or not, fairly thick walled; skeletal surfaces with open, skeletal meshes only, or with distinct ostia and postica; no epirhyses or aporhyses; skeletal framework a network of large, terminally connected heloclones; dermalia dichotriaenes; supplemental oxeas may occur; no other spicules known. *Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian):* Germany, *Kimmeridgian;* France, *Santonian;* Germany, Poland, *Turonian–Campanian.*——Fig. 165,*2a–d.* **P. giganteum,* Campanian, Germany; *a,* fragment of flabellate example, ×1 (Schrammen, 1901); *b–d,* characteristic spicules including heloclones, dermal dichotriaene, and supplemental oxea, ×5 (Schrammen, 1910).

Suborder MEGAMORINA Zittel, 1878

[*nom. transl.* Schrammen, 1924a, p. 38, *ex* family Megamorina Zittel, 1878a, p. 99; *emend.,* Reid, 1968a, p. 23] [tribus Megamorina Zittel; here accepted as equivalent to suborder, as a primary division of order Tetraxonida Vosmaer (ascribed to Schulze by Schrammen), emended by Reid, 1968a, p. 23]

Desmas megaclones; dermalia dichotriaenes except for occasional variants with some cladi unbranched; large or small rhizoclonids sometimes present; supplemental oxeas may occur; microscleres spirasters and microrhabds in a living example. *Carboniferous (?Mississippian), Upper Jurassic (Kimmeridgian)–Holocene.*

One certain living genus, *Pleroma* Sollas, is included in the suborder. A possible second genus, *Lyidium* Schmidt, has megaclone desmas but is not known to have either triaenes or spirasters.

Members of this group have been placed into four nominal families (Pleromatidae Sollas, 1888; Dorydermatidae Schrammen, 1901; Heterostiniidae Schrammen, 1924a; Megalithistidae Schrammen, 1924a), but the differences relied on for separation are tenuous. The characteristic desmas of *Pleroma* Sollas have unusually elongate shafts, with arms along one side but are otherwise like those of other forms. There are also unusual branched variants of this type, but other variants resemble some forms of *Doryderma* Zittel. Passage of typical megaclones into

branched, sometimes rhizoclone-like variants occurs also in the Jurassic *Megalithista* ZITTEL and the allied *Anomorphites* KOLB. *Doryderma* has desmas in which the zygomes are mainly longitudinal facets, instead of cup- or hand-shaped or tonguelike expansions as in most other forms; but *Pachypoterion* HINDE may have desmas of *Doryderma* type in the lower parts and desmas with expanded zygomes in upper ones. *Heterostinia* ZITTEL has accessory rhizoclonids, which were emphasized by LAGNEAU-HÉRENGER (1962); and MORET (1926b) found that small rhizoclonids may occur in *Doryderma.* Desmas of *Megalithista* are mainly forms with branching zygomes at ends of an arched or straight shaft; and similar forms also occur in *Heterostinia.* Thus, none of the types of these nominal families has a specially distinctive spiculation.

An alternative grouping can be based on the pattern of canalization: (a) the names Pleromatidae and Dorydermatidae are based on sponges with tubular, axial aporhyses traversing a top-shaped to cylindrical, branched cylindrical or fan-shaped body; (b) the names Heterostiniidae and Megalithistidae are based on sponges that typically have distinct, paragastral and external surfaces, in which canals are usually radial, when present, and in which vertical aporhyses are seen only in stalks, if at all. This distinction is taken here as distinguishing subfamilies Pleromatinae SOLLAS and Heterostiniinae SCHRAMMEN.

Division of these sponges between Pleromatidae and Dorydermatidae by DE LAUBENFELS (1955, p. 50), based on occurrence of branching in the latter, is rejected because this places forms with and without axial aporhyses in both groups and places species of *Doryderma* ZITTEL in both groups (e.g., *D. benetti* HINDE, unbranched; *D. roemeri* HINDE, branching). The additional family Helobrachiidae SCHRAMMEN, described as having megaclones by DE LAUBENFELS (1955, p. 51), comprises a single choristid genus (*Helobrachium* SCHRAMMEN) with no spicules other than large, hooked tripods (helotriaenes, SCHRAMMEN).

Family PLEROMATIDAE Sollas, 1888

[*nom. correct.* VON LENDENFELD, 1903, p. 140, *pro* Pleromidae SOLLAS, 1888, p. 312] [=Dorydermatidae SCHRAMMEN, 1901, p. 12, *nom. correct.* DE LAUBENFELS, 1955, p. 50, *pro* Dorydermidae SCHRAMMEN, 1901, p. 12 (ascribed to MORET, 1926b); Heterostiniidae SCHRAMMEN, 1924a, p. 39; Megalithistidae SCHRAMMEN, 1924a, p. 148]

Diagnosis as for suborder. *Carboniferous (?Mississippian), Upper Jurassic (Kimmeridgian)–Holocene.*

Subfamily PLEROMATINAE Sollas, 1888

[*nom. transl. et correct.* REID, herein, *ex* Pleromidae SOLLAS, 1888, p. 312]

Top- to club-shaped, cylindrical, branched cylindrical, or leaf- or fan-shaped sponges with long, tubular, longitudinal aporhyses and normally no paragastral cavity; epirhyses radial when present; dermalia dichotriaenes; rhizoclonids occasionally present; microscleres microrhabds and spirasters in single living example. [The microscleres are known in the living type genus, *Pleroma* SOLLAS, 1888.] *Carboniferous (?Mississippian), Cretaceous (Albian)–Holocene.*

Pleroma SOLLAS, 1888, p. 312, *non* SMITH, 1891, p. 113 [**P. turbinatum;* OD] [?=*Propleroma* MORET, 1925, p. 486 (type, *P. regnardi,* OD)]. Small, top-shaped sponge with shallow depression at top; base encrusting; no ostia or epirhyses; summit with postica of vertical aporhyses that form axial bundle; desmas with more or less elongate axis in typical examples but grading into short forms and spicules approaching megarhizoclones; normal forms typically arranged so that zygomes grasp outer surfaces of shafts of desmas below them in skeleton; dermalia dichotriaenes, supplemental oxeas present; microscleres microxeas and elongate spirasters that may pass into amphiasters. [Fossil examples cited as the new genus *Propleroma* by MORET, 1925, p. 486, may represent *Pleroma* in the Cretaceous record.] *?Upper Cretaceous, Paleogene (Eocene)–Holocene:* France, *?Upper Cretaceous;* Western Australia, *Eocene;* Spain, *Miocene;* East Indies, *Holocene.*——FIG. 166,*1a–f.* **P. turbinatum,* Holocene, East Indies; *a–b,* side view of characteristic rhabdocrepid desmas; *c–d,* short and elongate desmas, from below; *e,* megarhizoclone-like desma; *f,* two desmas showing mode of zygosis, ×50 (Sollas, 1888).

Doryderma ZITTEL, 1878a, p. 131 [**Polyjerea dichotoma* F. A. ROEMER, 1864, p. 36; SD DE LAUBENFELS, 1955, p. 50; =*Doryderma roemeri* HINDE, 1884a, p. 49, obj.] [=*Dichojerea* POMEL, 1872, p. 176, obj.; *Brochodora* SCHRAMMEN, 1910, p. 58, obj.]. Typically branched cylindrical but sometimes simply cylindrical or pyriform; no paragastral cavity; external surface of skeletal

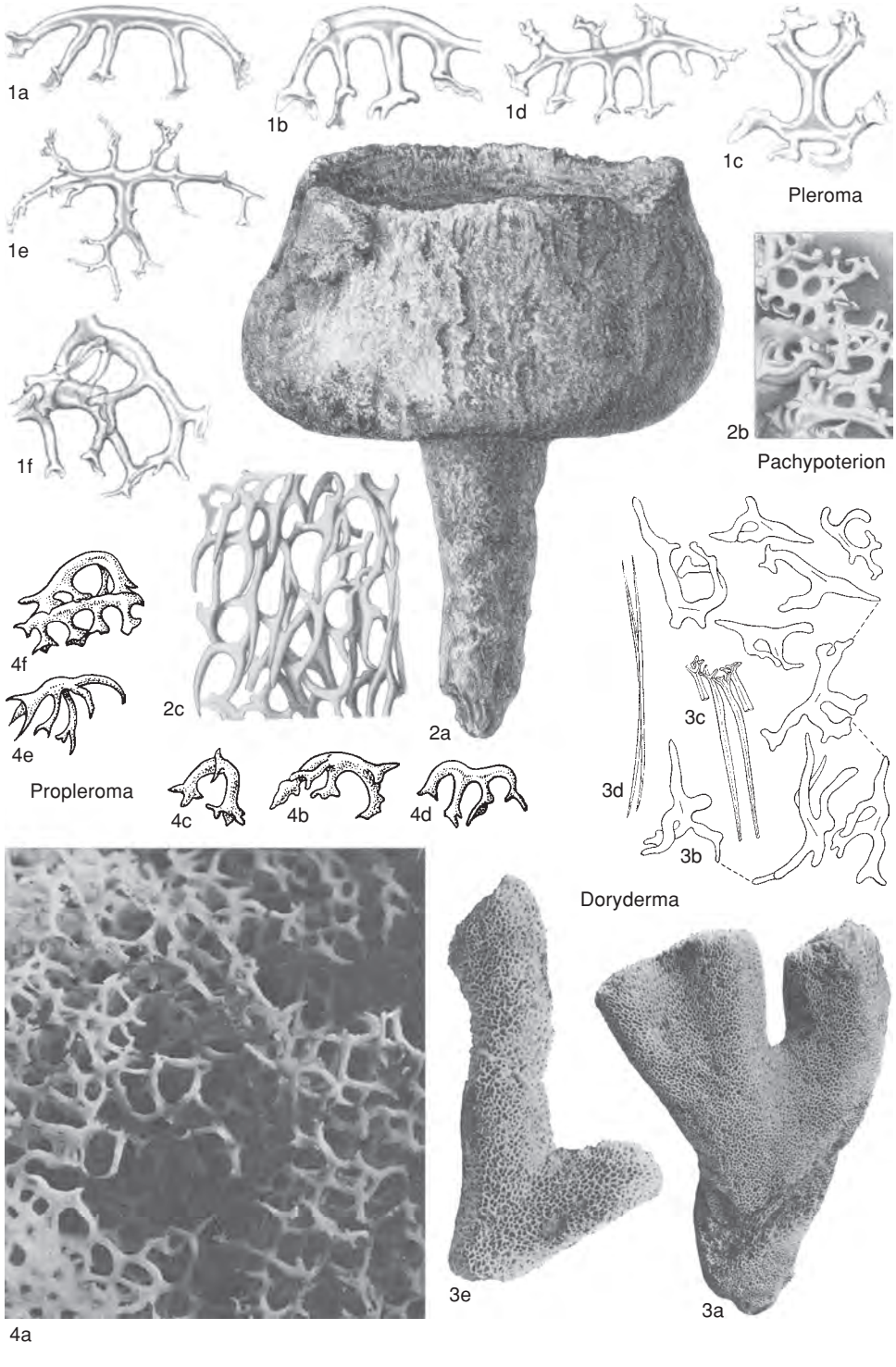


FIG. 166. Pleromatidae (p. 258–262).

framework with large, open meshes only (i.e., no distinct ostia); a short, radial canal (epirhysis) usually runs inwardly from each external meshwork opening; axial parts with bundle of tubular, longitudinal aporhyses, with postica at ends of branches or at summit in unbranched examples; desmas large, irregular megaclones, with zygomes typically as oblique, longitudinal facets at ends of arms or absent on some arms; in outer parts of skeleton, desmas mostly branched irregularly at ends of epirhabd and arranged so that epirhabds lie in partitions between epirhyses, with ends interlocked between groups of epirhyses; in axial parts, desmas more elongate and aligned longitudinally; dermalia dichotriaenes; supplemental oxeas common, often arranged radially when present; rhizoclonids typically absent, but rarely present at skeletal surface; microscleres unknown. [*Dichojerea* is an objective synonym of *Doryderma* Zittel, 1878a, due to subsequent designation of *Polyjerea dichotoma* F. A. Roemer, 1864, as type species of both nominal genera by de Laubenfels (1955): of *Doryderma* Zittel as *Doryderma roemeri* Hinde, 1884a, *pro Polyjerea dichotoma* Roemer, "1861" [*sic.,* 1864 is correct date]; de Laubenfels, 1955, p. 50); and of *Dichojerea* Pomel (1872, p. 176), as *Polyjerea dichotoma* Roemer, 1864 (de Laubenfels, 1955, p. 57). These nominal genera were not treated as synonyms by de Laubenfels. He referred *Doryderma* Zittel to the family Dorydermatidae Schrammen, 1901 (Moret, 1926b; de Laubenfels, 1955, p. 50) of the suborder Megamorina Zittel and referred *Dichojerea* Pomel to the family Jereidae de Laubenfels (1955, p. 57) of the suborder Tetracladina Zittel. *Dichojerea* is here suppressed under *Code* Art. 23.2 (ICZN, 1999) as not used as a senior synonym within the required period.

Brochodora Schrammen (1910, p. 58) was proposed as a subgenus of *Doryderma* Zittel, 1878a, with the species *B. roemeri* (Hinde) [=*Doryderma roemeri* Hinde, 1884a, p. 49, *nom. nov. pro Polyjerea dichotoma* F. A. Roemer, 1864, *non Doryderma dichotoma* (Benett) Hinde, 1884a, p. 47, =*Polypothecia dichotoma* Benett, 1831, pl. 13] and *B. ramusculus* Schrammen, 1910. The type species is distinguished from *D. dichotoma* (F. A. Roemer) only by dimensions ("Korperform, Kanalsystem und Skelett wie bie *Brochodora roemeri,* von der sich *Brachodora ramusculus* aber durch gracileren Bau und viel geringere Dimensionen unterscheidet," Schrammen, 1910, p. 59). In this writer's opinion, the species was based simply on small forms of *D. dichotoma*.] *Carboniferous (?Mississippian), Cretaceous (Albian–Campanian):* Russia, *?Mississippian;* England, France, Germany, Spain, Czech Republic, Slovakia, Poland, Russia, *Albian–Campanian.*——Fig. 166,*3a–d.* **D. dichotoma* (F. A. Roemer) (=*D. roemeri* Hinde), Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of branched sponge with widely spaced, inhalant ostia and coarse, skeletal pores, ×0.5; *b–d,* characteristic spicules including desmas, dermal dichotriaenes, and oxeas, ×10 (Schrammen, 1910).——Fig. 166,*3e. B. ramusculus* Schrammen, Quadratenkreide, Campanian, Oberg, Germany; side view of small, branched fragment, ×1 (Schrammen, 1910).

Homalodoriana Reid, herein, *nom. nov. pro Homolodora* Schrammen, 1910, p. 59, *non* Motschoulsky, 1860 [**Spongia ramosa* Mantell, 1822, p. 162; OD] [=*Trachycinclis* Pomel, 1872, p. 110, obj., *nom. oblit.*]. Branched cylindrical, stalked pyriform, globular, and related shapes, sometimes strongly compressed; lateral surfaces of skeletal framework fine meshed between widely spaced, rounded ostia of short epirhyses, which run in radially or curve obliquely downward; other mesh spaces not canaliform (as in *Doryderma* Zittel); outer skeletal meshwork correspondingly not showing *Doryderma* structure; longitudinal aporhyses in central parts open terminally in branching examples, and in corresponding positions in others; desmas similar to those of *Doryderma;* dermalia dichotriaenes where known; no other spicules known. *Cretaceous (Albian–Campanian):* England, France, Germany, Poland.——Fig. 167,*1a.* **H. ramosa* (Mantell), Quadratenkreide, Campanian, Oberg, Germany; side view of multibranched sponge with terminal osculum in each branch and inhalant ostia in dermal mesh, ×0.5 (Schrammen, 1910).——Fig. 167,*1b. H. plana* Schrammen, Quadratenkreide, Campanian, Oberg, Germany; side view of compressed, leaf-shaped example, ×0.5 (Schrammen, 1910).——Fig. 167,*1c. H. dichotoma* (Benett), Upper Greensand, Albian, Wiltshire, England; part of external surface showing ostia and small, skeletal meshes, ×8 (Hinde, 1884a).

Pachypoterion Hinde, 1884a, p. 51 [**P. robustum;* SD de Laubenfels, 1955, p. 50]. Stalked, cup or gobletlike sponges with upper part mainly solid, but with shallow depression or paragastral cavity at top, and similar forms in which upper part forms thick-walled, open funnel; exterior with vague ostia, from which radial epirhyses extend inwardly; axial parts with bundle of vertical, tubular aporhyses and other aporhyses around them sloping obliquely outward; postica of aporhyses occur in floor of summit depression or in walls of paragastral cavity, if present; desmas irregularly branching with short epirhabd and well-developed zygomes in main part of body, but elongate and articulated by longitudinal facets in stalk; supplemental oxeas may occur; dermalia, rhizoclonids, and microscleres unknown. [Dichotriaenes were incorrectly cited as dermalia of the genus by Schrammen (1910, p. 63) but this record was based on spicules of *P. auritum* Schrammen, 1910, p. 64, which was later designated as the type species of *Gigantodesma* Schrammen, 1924a and removed from *Pachypoterion.* See p. 263 herein.] *Cretaceous (Albian–Cenomanian):* England, Spain, *Albian;*

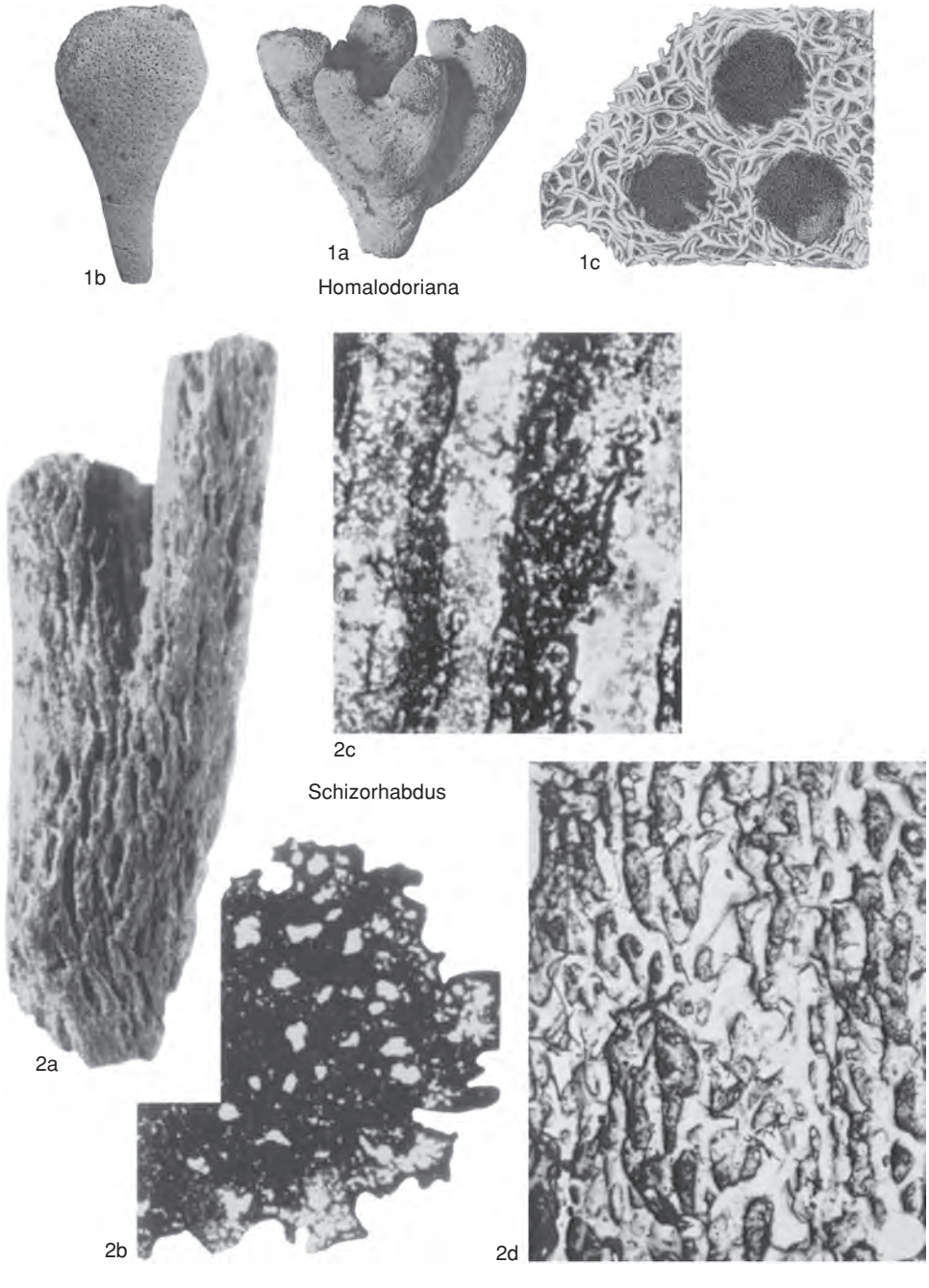


FIG. 167. Pleromatidae (p. 260–262).

France, Poland, *Cenomanian.*——Fig. 166,*2a–c. *P. robustum,* Upper Greensand, Albian, Pewsey, England; *a,* side view of goblet-shaped, figured syntype, herein designated lectotype, ×0.5; *b,* skeletal meshwork with desmas of main body, as shown in thin section; *c,* desmas at surface of stalk with absence of expanded zygomes, ×10 (Hinde, 1884a).

?Propleroma Moret, 1925, p. 486 [**P. regnardi;* OD]. Cylindrical with small, lateral outgrowths; a few surface meshes rounded to form ostia, from which radial epirhyses run inwardly; axial part with group of longitudinal aporhyses; characteristic desmas have arched to elongate shaft with short, zygome-bearing arms on one side, which is convex in arched examples; arms arranged facing inwardly and applied to shafts of other desmas, as in *Pleroma* Sollas; some also of tripodal or irregular shapes; supplemental oxeas present; no other spicules known. [Fossil examples from the Cretaceous of France with skeletal structure and spicules similar to those of *Pleroma* were placed in the new genus *Propleroma* by Moret (1925), but they might be included in the Holocene genus.] *Cretaceous (Cenomanian–Maastrichtian):* France, Poland.——Fig. 166,*4a–f. *P. regnardi,* Cenomanian, Coulonges-les-Sablons, France; *a,* skeletal meshwork, ×20 (Moret, 1926b); *b–f,* desmas, ×40 (Hill, 1972).

Schizorhabdus Zittel, 1877b, p. 51 [**S. libycus;* OD]. Cylindrical to steeply obconical sponges, occasionally branched, exterior somewhat grooved or longitudinally fluted with bifurcated and braided elements; commonly with vertical, axial cluster of exhalant canals, but may have limited, central spongocoel and additional isolated, coarse, vertical, exhalant canals; radially convergent, inhalant canals much smaller and more difficult to trace; skeleton of irregularly branched, megaclone desmas that interlock to form a rigid framework. *Cretaceous (Maastrichtian)–Paleogene (Paleocene):* Libya, Egypt.——Fig. 167,*2a–d. *S. libycus,* Sudr Formation, Maastrichtian, Wadi Natila, Sinai Peninsula, Egypt; *a,* side view of branched sponge showing characteristic exterior, GIK 1007, ×1; *b,* transverse section with dark skeleton and light canals, GIK 1012, ×5; *c,* longitudinal section with light, vertical, exhalant canals and darker, skeletal tracts between, GIK 1913, ×10; *d,* electron photomicrograph of vertical section showing variously sized, intergrown megaclones, ×15 (Jux, 1994; courtesy of *Senckenberg Naturforschende Gesellschaft*).

Trachycinclis Pomel, 1872, p. 110 [**Spongia ramosa* Mantell, 1822, p. 162; OD]. Listed with same type species as *Homalodora* Schrammen, 1910, by de Laubenfels, 1955, p. 66; but not recognized as synonym of *Homalodora,* and placed into suborder Uncertain, herein treated as *nomen oblitum* under *Code* Article 23.2 (ICZN, 1999). *Upper Cretaceous:* England.

Subfamily HETEROSTINIINAE Schrammen, 1924

[*nom. transl.* Reid, herein, *ex* Heterostiniidae Schrammen, 1924a, p. 39]

Hollow, cylindrical to cup-shaped or platelike sponges in which epirhyses and aporhyses are typically similar when any are developed; without vertical, tubular aporhyses, except sometimes in stalks; dermalia dichotriaenes; rhizoclonids present; microscleres unknown. [A possible living genus, *Lyidium* Schmidt, has desmas of megaclone type but apparently lacks both triaenes and spirasters and cannot be referred certainly to this suborder.] *Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian).*

Heterostinia Zittel, 1878a, p. 133 [**H. cyathiformis;* OD] [=*Valhalla* de Laubenfels, 1955, p. 50 (type, *Asteroderma expansa* Schrammen, 1901, p. 14, OD), *nom. nov. pro Asteroderma* Schrammen, 1901, p. 13, *non* Perrier, 1888]. Body cup shaped or funnel-like, flabellate, or forming a convoluted plate, sometimes stalked; both surfaces of skeletal framework with more or less distinct, skeletal pores (ostia, postica), from which simple canals (epirhyses, aporhyses) may extend inwardly; a few vertical aporhyses may traverse stalk if one is present; megaclones usually stout with short epirhabds, in part branched irregularly and in part simply arched or tripodal examples; rhizoclonids usually present, sometimes forming supplemental cortex at surfaces, but may be only sparsely represented in other specimens; supplemental oxeas may occur; dermalia dichotriaenes; microscleres unknown. *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* France, England, *Cenomanian–Santonian;* Germany, Poland, *Campanian.*——Fig. 168,*2a–c. H. obliqua* (Benett), Mucronatenkreide, Campanian, Misburg, Germany; *a,* fan-shaped example showing paragastral surface, ×0.5; *b–c,* characteristic spicules including arched and tripodal desmas with granular ornament on convex sides and dermal dichotriaenes, ×16 (Schrammen, 1910).

Amphiplectella Schrammen, 1901, p. 13 [**A. piriformis;* OD]. Stalked pyriform and variant shapes with deep, narrow, paragastral cavity; outside with ostia of epirhyses that run into wall obliquely downward; interior with postica of aporhyses, which cross with epirhyses within wall; desmas mainly arched forms with fairly simple ends; dermalia dichotriaenes; no other spicules known. *Cretaceous (Campanian):* Germany.——Fig. 169,*1a–c. *A. piriformis,* Quadratenkreide, Oberg; *a,* side view of stalked, pyriform sponge with irregularly distributed, inhalant ostia in moderately coarse, dermal mesh, ×0.5; *b–c,* characteristic spicules includeing desmas and dichotriaenes, ×10 (Schrammen, 1910).

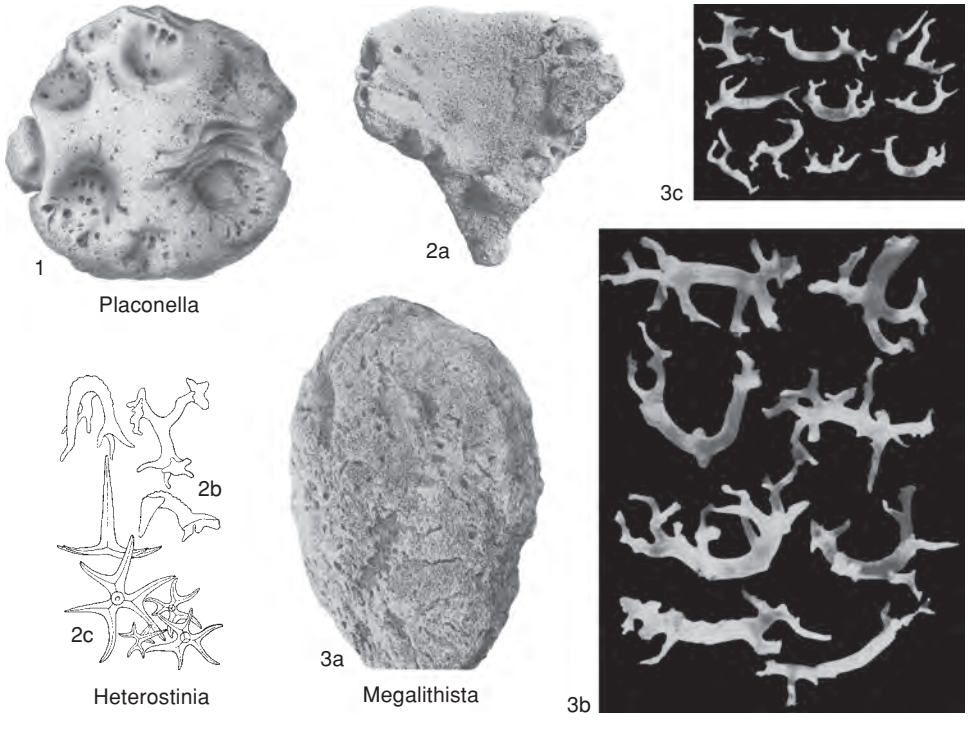


FIG. 168. Pleromatidae (p. 262–265).

Anomorphites KOLB, 1910 in 1910–1911, p. 249 [**A. plicatus;* SD DE LAUBENFELS, 1955, p. 50]. Convoluted cup or plate, fairly thick walled, small; no apparent canalization; desmas like those of *Megalithista* ZITTEL; no other spicules known. [Character uncertain due to poor material.] *Jurassic (Kimmeridgian):* Germany, Switzerland.——FIG. 169,*2a–d.* **A. plicatus,* Weiss Jura, Kimmeridgian, Sontheim; *a,* side view of cup-shaped sponge, SSPHG, ×1; *b–d,* representative spicules, ×40 (Kolb, 1910–1911).

Gigantodesma SCHRAMMEN, 1924a, p. 62 [**Pachypoterion auritum* SCHRAMMEN, 1910, p. 64; OD]. Cup- or earlike, sometimes marginally lobate, thick walled; exterior with ostia in openings of skeletal mesh, as in *Doryderma* ZITTEL; other canals and postica not developed; desmas with well-developed zygomes; dermalia dichotriaenes; no other spicules known. [See also *Pachypoterion,* p. 260 herein.] *Cretaceous (Campanian):* Germany.——FIG. 169,*3a–c.* **G. auritum* (SCHRAMMEN), Mucronatenkreide, Misburg; *a,* cup-shaped example with lobate margins showing ostia in form of open meshes, ×0.5; *b,* views of a dermal dichotriaene, ×10 (Schrammen, 1910); *c,* megaclone desmas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Holodictyon HINDE, 1884a, p. 50 [**H. capitatum;* OD]. Body inverted conical or nodular, with short, massive stalk and root processes; top rounded or flattened with central depression or cavity; no skeletal pores or canals; desmas similar to those of *Doryderma* ZITTEL, with articulation mainly by oblique, longitudinal facets; no other spicules known. *Cretaceous (Albian):* England.——FIG. 169,*4a–c.* **H. capitatum,* Upper Greensand, Warminster, Yorkshire; *a,* side view of obconical holotype with massive stalk, ×0.5; *b,* upper part of sponge in vertical section, ×1; *c,* desmas of surface, ×25 (Hinde, 1884a).

Megalithista ZITTEL, 1878a, p. 130 [**M. foraminosa;* OD] [?=*Placonella* HINDE, 1884a, p. 47 (type, *P. perforata,* M)]. Pyriform, cylindrical, or top-shaped with deep, narrow, paragastral cavity, or cuplike and thick walled; exterior sometimes transversely wrinkled or with irregular swellings; exterior with ostia of short epirhyses; sometimes locally also with short, irregular furrows in which some ostia are located; interior with postica of similar or larger postica or aporhyses that are vertical in central part of body and arch outwardly around central cavity; desmas typically with arched, central shaft and simple or branching ends, sometimes passing into forms that resemble megarhizoclones; dermalia

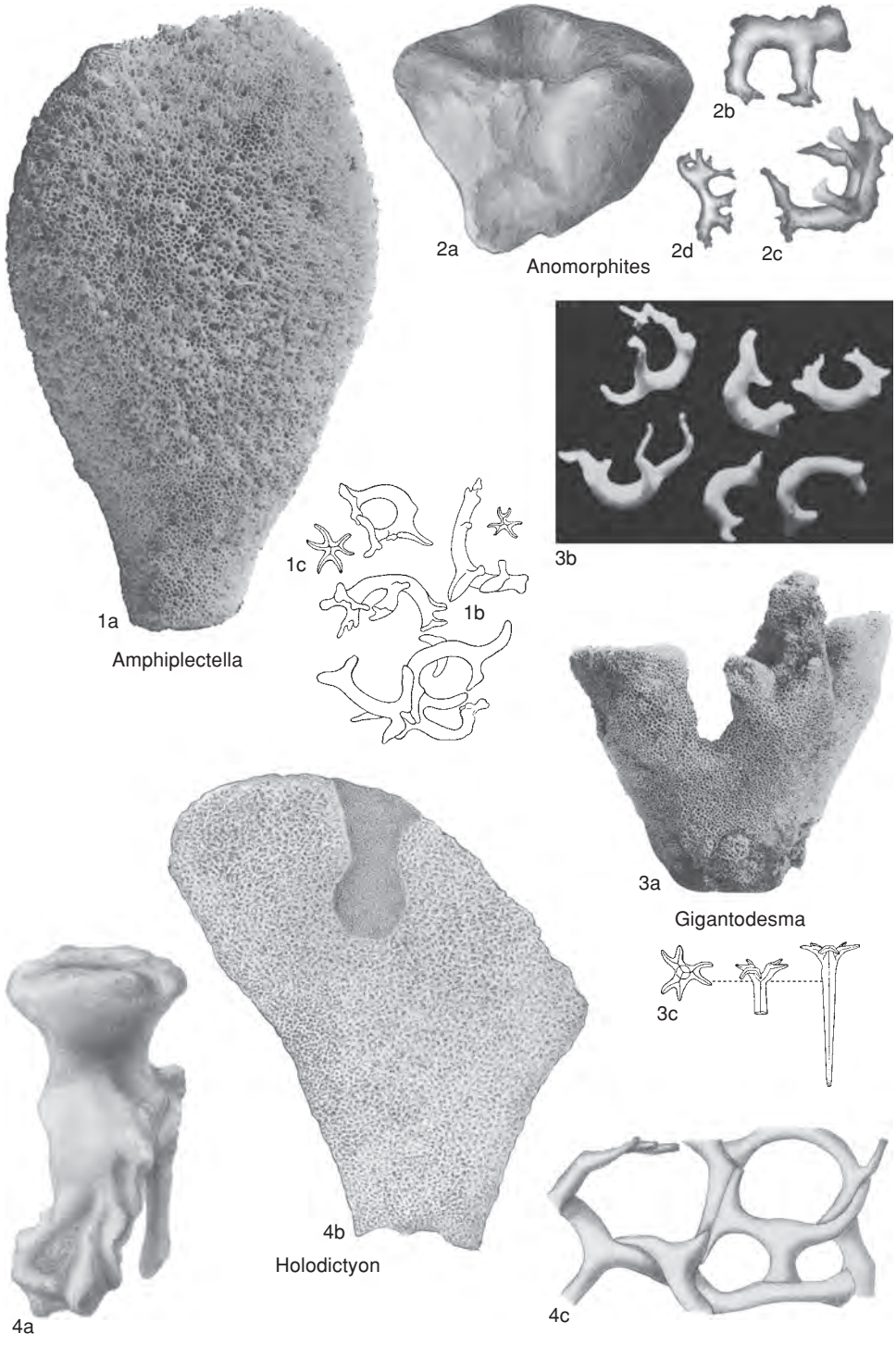


Fig. 169. Pleromatidae (p. 262–263).

possible dichotriaenes; other spicules unknown. [Dermalia unknown according to SCHRAMMEN, 1937, but recorded by ZITTEL, 1878a.] *Jurassic (Kimmeridgian):* Germany, Switzerland.——FIG. 168,*3a–c.* **M. foraminosa,* Weiss Jura, Gerstetten, Germany; *a,* side view of medium-sized, top-shaped sponge with irregular, short furrows and scattered, inhalant ostia, ×0.5; *b,* desmas, mainly branching examples, ×5; *c,* desmas, but mainly simpler examples, ×5 (Schrammen, 1937).

?Placonella HINDE, 1884a, p. 47 [**P. perforata;* OD]. Flattened, cake-shaped mass with several shallow depressions in convex, upper surface; apertures of skeletal canals (possible aporhyses) in depressions, and of smaller ones (possible epirhyses) scattered on surface between them; desmas like those of *Megalithista* ZITTEL; dermalia unknown. [Based on a single specimen, regarded by SCHRAMMEN (1937, p. 75) as part of a specimen of *Megalithista foraminosa* ZITTEL.] *Jurassic (Kimmeridgian):* Germany.——FIG. 168,*1.* **P. perforata,* upper Jura, Würtemberg; upper surface of holotype, possibly base of specimen of *M. foraminosa* ZITTEL, ×0.5 (Hinde, 1884a).

Order MONALITHISTIDA Lagneau-Hérenger, 1955

[Monalithistida LAGNEAU-HÉRENGER, 1955, p. 1,564]

Lithistida in which desmas are monaxial or anaxial and developed as rhizoclones, megarhizoclones, sphaeroclones, or variants of these types, but without tetraxial megascleres as either desmas or dermalia; some forms with supplemental monaxons (oxeas etc.) in addition to desmas; a few with supplemental rhizoclonids when desmas are anaxial; modern examples with or without microscleres that may be microrhabds or sigmaspires when present.

[The original Monalithistida of LAGNEAU-HÉRENGER, proposed as a suborder of the order Tetraxonia VOSMAER (ascribed to SCHULZE), comprised the lithistid Monaxonia of SCHRAMMEN that here fall into the suborders Didymmorina, Rhizomorina ZITTEL, and Megarhizomorina SCHRAMMEN. The Didymmorina are here removed to the order Tetralithistida because of discovery of tetraxial dermalia in *Cylindrophyma* ZITTEL of that suborder. The suborder Orchocladina RAUFF, included formerly with the Tetracladina, is added herein because the desmas are thought to be monaxial, not tetraxial, and the Sphaerocladina are regarded as probably derived from the Orchocladina. The order is regarded as probably polyphyletic, and this seems likely also to be true of the Rhizomorina.

For further comments, see suborder descriptions.] *Lower Jurassic (Pliensbachian)–Holocene.*

Suborder MEGARHIZOMORINA Schrammen, 1924

[*nom. transl.* REID, herein, *ex* tribus Megarhizomorina SCHRAMMEN, 1924a, p. 69]

Principal megascleres are large, monaxial, rhizoclone-like spicules (megarhizoclones) with firm or loose zygosis or are partly or all unconnected; zygomes more or less like those of megaclones when distinctly developed; supplemental oxeas or other monaxons sometimes present; some with smaller, flattened, rhizoclone-like bodies as ectosomal spicules; no microscleres known. [The original designation tribus is here regarded as equivalent to suborder, as applied to a primary division of the order Monaxonia SCHULZE. The single family, Megarhizidae SCHRAMMEN, was created for fossil genera, *Megarhiza* SCHRAMMEN and *Chalaropegma* SCHRAMMEN, but the living *Monanthus* KIRKPATRICK and *Petromica* TOPSENT have comparable desmas. Although these modern genera are of uncertain affinities, some features suggest evolution from an ancestor in the order Axinellida.] *Upper Cretaceous (Cenomanian–Campanian).*

Family MEGARHIZIDAE Schrammen, 1901

[Megarhizidae SCHRAMMEN, 1901, p. 15]

Diagnosis as for suborder. *Upper Cretaceous (Cenomanian–Campanian).*

Megarhiza SCHRAMMEN, 1901, p. 15 [**M. dubia;* OD; *not* SD DE LAUBENFELS, 1955, p. 52]. Body nodular, truncated conical or cylindrical, built in succession of thin, superimposed layers; outside covered by skeletal cortex, below which are ostia of fine epirhyses that run inward horizontally; axial parts with bundle of vertical, tubular aporhyses that open through postica at summit; desmas large megarhizoclones, to which megaclone-like variants sometimes added; cortex formed from smaller, flattened, rhizoclone-like desmas; oxeas and strongyles

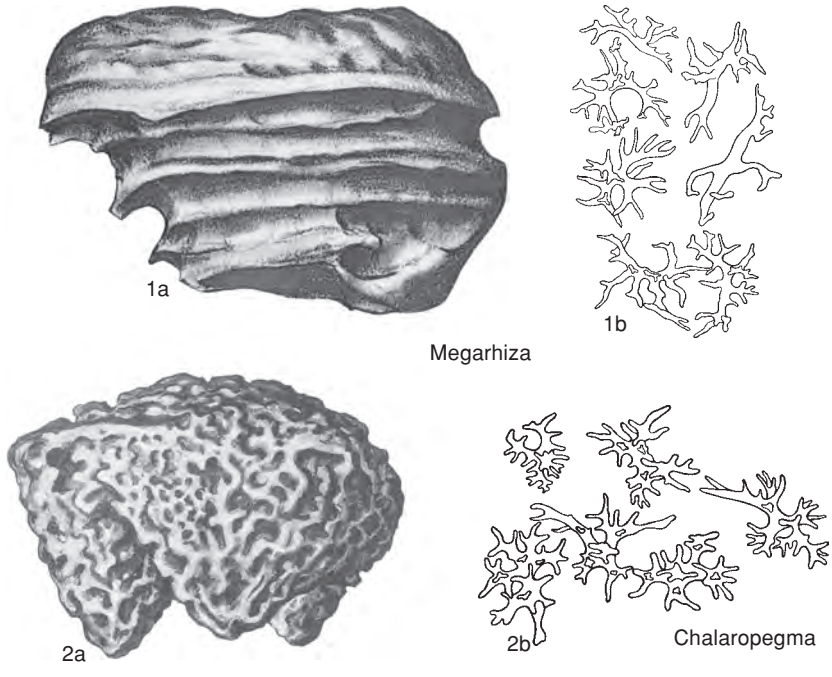


FIG. 170. Megarhizidae (p. 265–266).

also present in interior; microscleres unknown. *Cretaceous (Cenomanian–Campanian):* France, *Cenomanian;* Germany, *Campanian.*——FIG. 170,*1a–b. *M. dubia,* Campanian, Germany; side view showing superimposed layers of body, ×1; *b,* characteristic megarhizoclones, ×10 (Schrammen, 1910).

Chalaropegma SCHRAMMEN, 1910, p. 168 [**C. cerebriformis;* OD]. Body nodular mass with surface covered with sinuous, anastomosing ridges similar to surface convolutions of brain; no apparent canalar features; desmas typical megarhizoclones, loosely coherent, smaller than in *Megarhiza* SCHRAMMEN; no other spicules known. [Placed into suborder Tetracladina, family Uncertain, by DE LAUBENFELS (1955, p. 59) but contains no tetraclones or triaenes, and was placed into family Megarhizidae by SCHRAMMEN when first proposed.] *Cretaceous (Campanian):* Germany.——FIG. 170,*2a–b. *C. cerebriformis,* Mucronatenkreide, Misburg; *a,* nodular holotype with coarse, anastomosing ridges, ×0.5; *b,* characteristic megarhizoclones, ×16 (Schrammen, 1910).

Suborder SPHAEROCLADINA Schrammen, 1924

[*nom. transl.* REID, 1968a, p. 23, *ex* tribus Sphaerocladina (=primary subdivision of order Cryptaxonia SCHRAMMEN) SCHRAMMEN, 1924a, p. 130; *sensu* REID, 1968a, p. 23]

Desmas anaxial where their character is known, and developed as sphaeroclones, astroclones, or intermediates, to which irregular variants may be added; centrum of sphaeroclone desmas may contain a granular nucleus that develops by enclosure of a hilumlike depression in ontogeny, or a sinuous canal of unknown origin, which does not represent a crepidal body or axis; some with anaxial, phyllotriaene-like spicules as dermalia; supplemental monaxons may occur; no microscleres in *Vetulina,* the single living genus. [SCHRAMMEN named the new tribus Sphaerocladina in 1924a, p. 78 in a list to include the family he had named the Sphaerocladinidae in 1910, p. 37. REID in 1968 raised the Sphaerocladina (*sensu* SCHRAMMEN, 1924a) to suborder rank within the order Cryptaxonia as that name was used by SCHRAMMEN, 1924a, p. 130. The Sphaerocladina are now included in the order Monalithistida LAGNEAU-HERENGER, 1955.] *Lower Jurassic (Pliensbachian)–Holocene.*

Post-Paleozoic Sphaerocladina comprise two contrasting groups of sponges with comparable desmas but possibly of different origins. These are (a) forms grouped here as

Vetulinidae VON LENDENFELD, in which typical desmas are small sphaeroclones that may have a nucleus or a sinuous canal in the centrum and a centrum that is often finely spined; and (b) forms grouped as Lecanellidae SCHRAMMEN, which have large, smooth desmas that are sphaeroclones, astroclones, or intermediates.

In the first group, desma size compares with that of Paleozoic Astylospongiidae, and some genera (*Macrobrochus* SCHRAMMEN, *Ozotrachelus* DE LAUBENFELS) resemble astylospongiids in their general morphology. In the second group, size of desmas is more like that of megaclones; and their shapes and zygomes suggest comparison with desmas of the sublithistids *Desmatiderma* TOPSENT and *Crambe* VOSMAER, although those of the former are monaxial, not anaxial. Hence these families could have different origins and relationships, although this is not demonstrable. The relationship of forms with small desmas (Vetulinidae) to the Astylospongiidae is also not demonstrable, because of the gap between the latest Paleozoic astylospongiids and the later forms. Grouping is, hence, based here on morphological resemblance of the desmas, without certainty that all forms included are related, although they may be.

Family VETULINIDAE von Lendenfeld, 1904

[Vetulinidae VON LENDENFELD, 1904c, p. 149] [=Anomocladina SOLLAS, 1885b, p. 492, *partim;* Anomocladidae *sensu* SOLLAS, 1888, p. 354, *partim;* Mastosiidae SCHRAMMEN, 1924a, p. 154]

Desmas small; typically sphaeroclones to which subordinate astroclones may be added, but sometimes with astroclones predominant; centra of sphaeroclones sometimes with granular nucleus, or with sinuous, internal canal, and often with simple or branching spines; zygomes root-, hand-, or cuplike; supplemental monaxons in some; phyllotriaene-like dermalia may occur; no microscleres in single living genus. [The family comprises forms that could be grouped with the middle Paleozoic Astylospongiidae based on the size of their desmas, but these Jurassic to Holocene sponges are mainly of different habits and occur much later in time. There is a living genus, *Vetulina* SCHMIDT, 1880.] *Middle Jurassic (Bathonian)–Holocene.*

Subfamily VETULININAE von Lendenfeld, 1904

[Vetulininae VON LENDENFELD, 1904c, p. 149]

Vetulinidae of varying habits, not resembling Astylospongiidae except in character of desmas. *Middle Jurassic (Bathonian)–Holocene.*

Vetulina SCHMIDT, 1879, p. 19 [**V. stalactites;* OD]. Irregular, convoluted plates attached by encrusting structures and with more or less marked, concentric growth lines on one surface; both skeletal surfaces with small pores (ostia, postica) from which canals (epirhyses, aporhyses) run radially inward; desmas mainly sphaeroclones whose centra bear branching, rootlike spines that may take part in zygosis when zygomes of other desmas are applied to them; sphaeroclones also grading into astroclones or irregular variants, which may locally be more abundant; supplemental strongyles present; no dermalia; no microscleres in life. *?Upper Cretaceous, Holocene:* France, *?Upper Cretaceous;* West Indies, *Holocene.* ——FIG. 171,*1a–e. *V. stalactites,* Holocene, West Indies; *a–d,* characteristic desmas including astroclone, sphaeroclone, irregular desma, and inceptional body, showing nucleus, ×30 (de Laubenfels, 1955); *e,* side view of type sponge composed of convoluted plates, ×0.5 (Schmidt, 1879).

Cladodia MORET, 1926b, p. 137 [**C. kiliani;* OD]. Incompletely known from cylindrical fragments; surface with small, skeletal pores; other canalar features unknown; desmas typical sphaeroclones internally, passing outwardly into astroclones; phyllotriaene-like dermalia present; no other spicules known. [Skeleton much like that of *Multipocula* DE LAUBENFELS; possibly based on a stalk of that genus.] *Cretaceous (Santonian):* France.——FIG. 171,*2a–c. *C. kiliani,* Nice, characteristic spicules; *a,* fragment of meshwork; *b,* sphaeroclone; *c,* astroclones of outer parts, ×50 (Moret, 1926b; courtesy of Société Géologique de France).

Cryptodesma SCHRAMMEN, 1924a, p. 132 [**Asterospongia globosa* F. A. ROEMER, 1864, p. 54; OD] [=*Asteropagia* POMEL, 1872, p. 245, *nom. oblit.* (type, *Asterospongia globosa* F. A. ROEMER, 1864, p. 54, SD DE LAUBENFELS, 1955, p. 104), use of name not traceable since first proposed]. Hemispherical, base encrusting; surface with small ostia and stellate groups of larger postica from which short furrows radiate; desmas sphaeroclones; no other spicules known. *Cretaceous (Coniacian–Maastrichtian):* Germany.——FIG. 171,*3a–b. *C. globosa* (F. A. ROEMER); side view showing radiating patterns of furrows that presumably mark positions of subdermal, exhalant canals, Campanian, ×1 (Roemer, 1864); *b,* sphaeroclone desmas, Emscher,

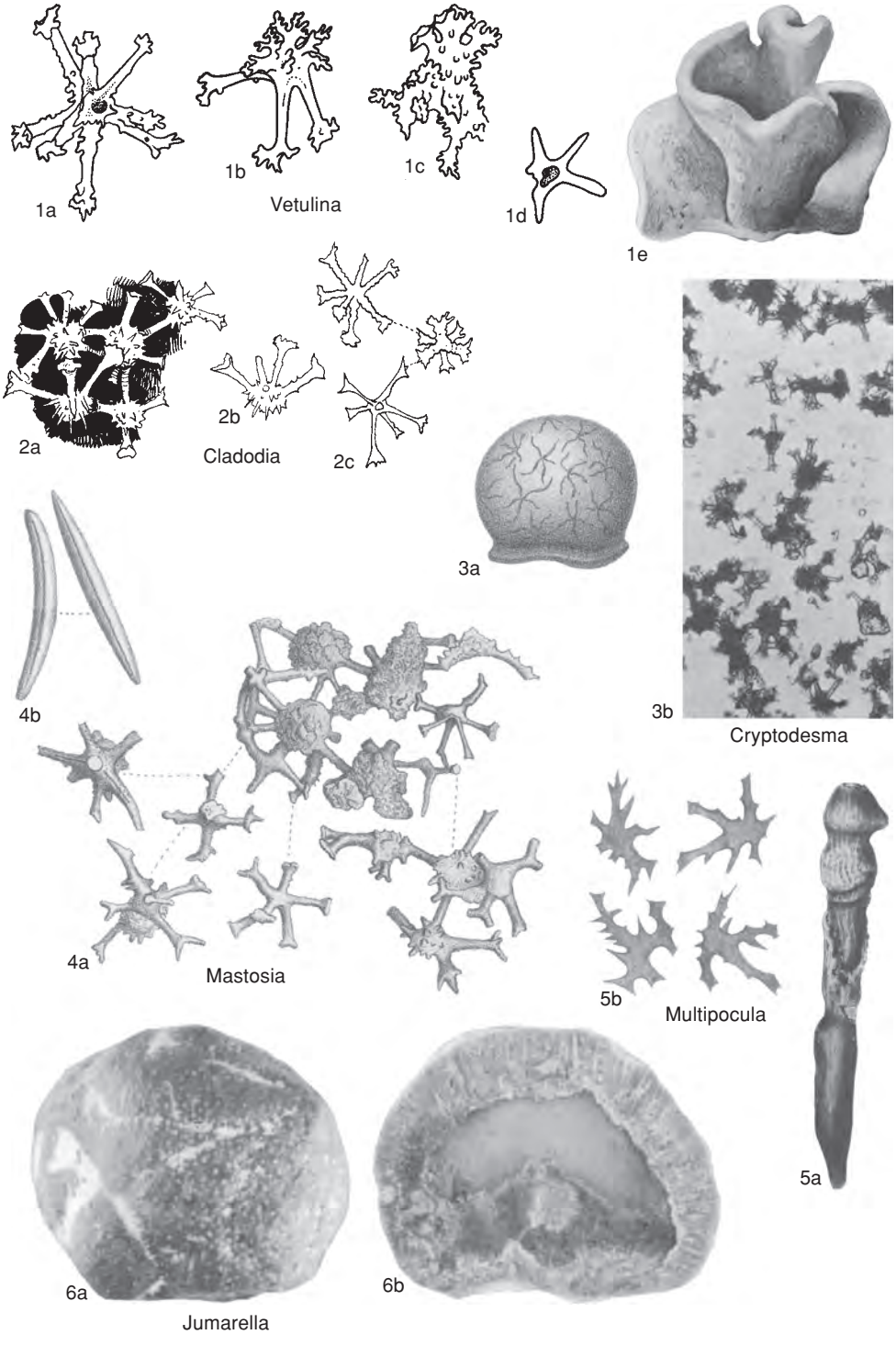


FIG. 171. Vetulinidae (p. 267–269).

Coniacian, Sudmerberges, Germany, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Exodictydia MORET, 1926b, p. 138 [**E. canalifera;* SD DE LAUBENFELS, 1955, p. 63]. Club or cup shaped; surface of club-shaped forms and both surfaces of cup-shaped ones with numerous small, skeletal pores, supposedly ostia, between which there is network of very fine, superficial furrows; small canals, supposedly epirhyses, run inwardly from these pores; aporhyses in axial bundle open through postica at summit in clublike examples, or open in groups into irregular or roughly stellate clefts in internal surface of cuplike sponges; desmas sphaeroclones, in which a sinuous canal may be present; other spicules unknown. *Cretaceous (Santonian):* France.——FIG. 172,*1a–b. *E. canalifera,* Saint-Cyr; *a,* club-shaped example with numerous inhalant ostia, ×0.5; *b,* isolated and associated sphaeroclones, about ×50 (Moret, 1926b; courtesy of Société Géologique de France).——FIG. 172,*1c–d. E. cyathiformis* MORET, Saint-Cyr; *c,* incomplete, cuplike example from above showing interior and wall section, ×0.5; *d,* external surface showing skeleton, ×35 (Moret, 1926b; courtesy of Société Géologique de France).

Jumarella MEHL & FÜRSICH, 1997, p. 26 [**J. astrorhiza;* OD]. Hemispherical sponge with broad, flat base, without spongocoel but with deep astrorhizae that radiate from several elevated centers distributed over entire upper surface; prominent, radial, narrow canals correspond with small, circular pores; spicules are small sphaeroclones. *Jurassic (Bathonian):* India.——FIG. 171,*6a–b. *J. astrorhiza,* Patcham Formation, Jumara Dome, Kachchh, western India; *a,* side view of exterior of holotype with astrorhizae, ×1; *b,* polished, vertical section showing prominent, radial canals in outer part of geodelike preservation, PIW1997I 77, ×1 (Mehl & Fürsich, 1997).

Mastosia ZITTEL, 1878a, p. 136 [**M. wetzleri;* OD]. Nodular or crustose, some forms hollowed below with nipplelike or fingerlike outgrowths above; upper surface with numerous small, skeletal pores, all of similar size; no skeletal canals, paragastral cavity, or oscula; desma sphaeroclones and some astroclones; centra of sphaeroclones with conical spines in some examples; no other spicules known. [Other spicules noted by ZITTEL, here regarded as extrinsic; cf. ZITTEL, 1878a, p. 136 and SCHRAMMEN, 1937, p. 106.] *Jurassic (Kimmeridgian):* Germany.——FIG. 171,*4a–b. *M. wetzleri,* Weiss Jura, Günzburg; *a,* isolated, characteristic desmas and fragments of skeletal meshwork, ×64; *b,* monaxons from surface, here regarded as extrinsic, because similar spicules have a general distribution in sediment (cf. SCHRAMMEN, 1937, p. 106), ×64 (Zittel, 1878a).

Multipocula DE LAUBENFELS, 1955, p. 49, *nom. nov. pro Polypora* SCHRAMMEN, 1901, p. 16, *non* M'COY, 1842 [**Polypora reticulata* SCHRAMMEN, 1901, p. 16; OD]. Elongate, irregularly cylindrical, with narrow, tubular, paragastral cavity; exterior with ostia, some of which are in narrow, longitudinal furrows; desmas small, spiny sphaeroclones and rhizoclone-like variants; further details and other spicules unknown. [Poorly known from one specimen with skeleton preserved as limonite only; possibly a form of *Ozotrachelus* DE LAUBENFELS, to which this name would be senior, since the type species was referred to *Pachytrachelus* SCHRAMMEN (=*Ozotrachelus*) by SCHRAMMEN, 1910, p. 171.] *Cretaceous (Campanian):* Germany.——FIG. 171,*5a–b. *M. reticulata* (SCHRAMMEN), Quadratenkreide, Misburg; *a,* side view of only known example, ×0.5; *b,* desmas, ×50 (Schrammen, 1901).

Rhytidoderma SCHRAMMEN, 1937, p. 107 (SCHRAMMEN, 1924b, p. 154, *nom. nud.*) [**R. berckhemeri;* OD]. Nodular; surface irregularly sculptured, with skeletal pores in interspaces of network of narrow, anastomosing ridges; tubular skeletal canals run inwardly from these pores; desmas small sphaeroclones, similar to those of *Mastosia* ZITTEL; no other spicules known. [Canals epirhyses *teste* SCHRAMMEN, 1937, p. 107, but function unknown. Original publication was without diagnosis. First formal diagnosis was by SCHRAMMEN, 1937, p. 107.] *Jurassic (Kimmeridgian):* Germany.——FIG. 172,*3a–b. *R. berckhemeri,* Weiss Jura, Gerstetten; *a,* irregular surface with anastomosing ridges and circular pores, ×0.5; *b,* typical sphaeroclones, ×20 (Schrammen, 1937).

Tetraspongia TERMIER & TERMIER in MASSA, TERMIER, & TERMIER, 1989, p. 828 [**T. balmensis;* OD]. Fig-shaped sponges with isolated dichotriaenes with long, bifurcated rays as dermalia, over principalia of alternating layers of sphaeroclones, locally bordered by spongin frameworks in outer part, and frameworks of dicranoclones with aligned, small spines; subcircular pores occurring in latter layers. *Cretaceous (Albian):* France.——FIG. 172,*2a–b. *T. balmensis,* Cretaceous beds, Sainte-Baume, Provence; *a,* sketch showing disposition of various types of spicules and skeletal elements in layers; *1,* framework of spongin; *2,* dermal layer of dichotriaenes; *3,* layer of sphaeroclones; *4,* internal framework of dicranoclones, not to scale; *b,* drawing of quadrangular distribution of spongin (*black*) around subjacent, circular, spinose nodes of sphaeroclones, approximately ×40 (Massa, Termier, & Termier, 1989; courtesy of *Geobios*).

Subfamily MACROBROCHINAE new subfamily

[Macrobrochinae REID, herein] [type genus, *Macrobrochus* SCHRAMMEN, 1910, p. 174]

Vetulinidae with canal systems like those of typical Astylospongiidae, but much later in time. *Upper Cretaceous (Santonian–Campanian).*

Macrobrochus SCHRAMMEN, 1910, p. 174 [**M. emscherensis;* SD DE LAUBENFELS, 1955, p. 50]. Hemispherical to conical, with small, paragastral depression at summit, or none; sides with

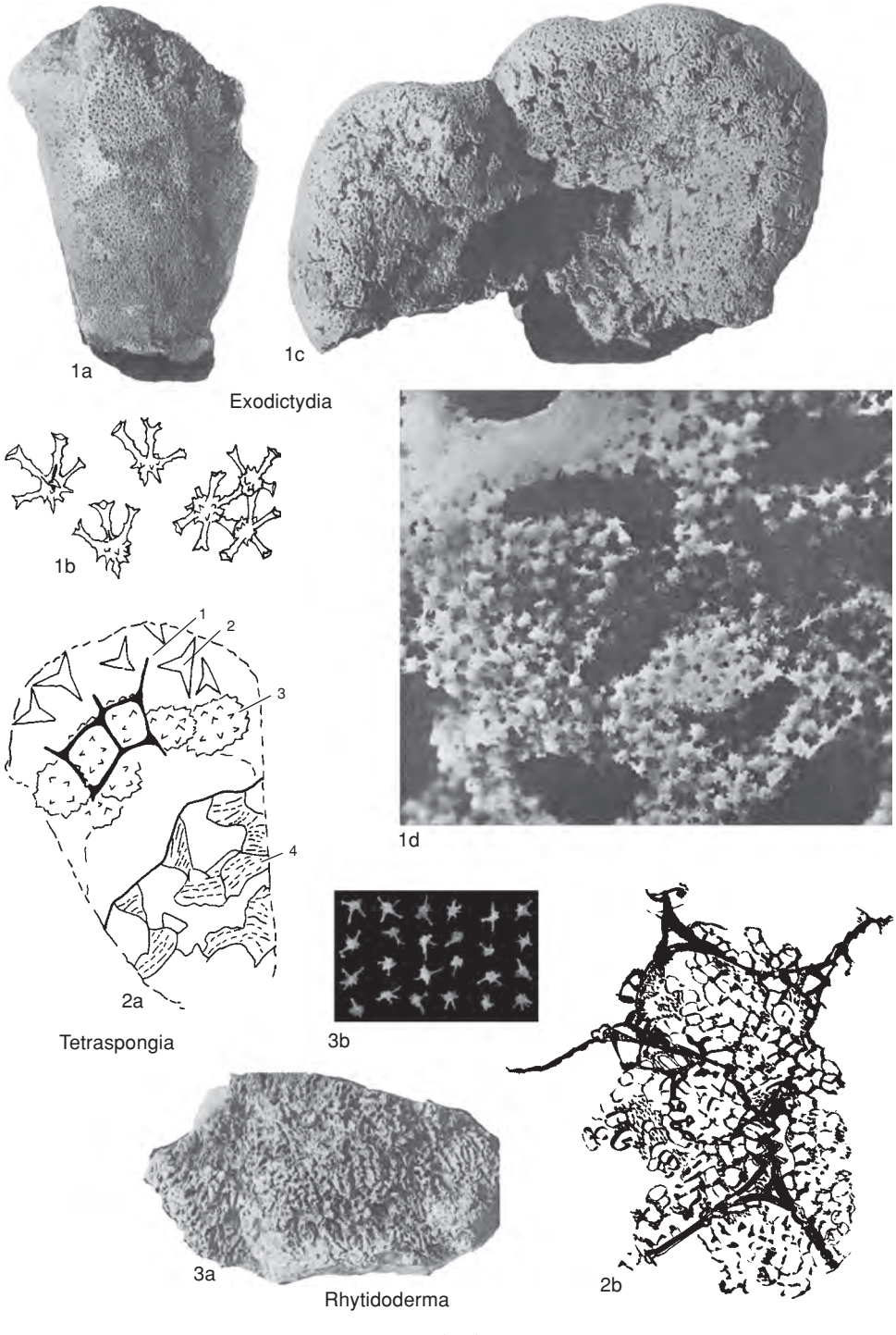


FIG. 172. Vetulinidae (p. 269).

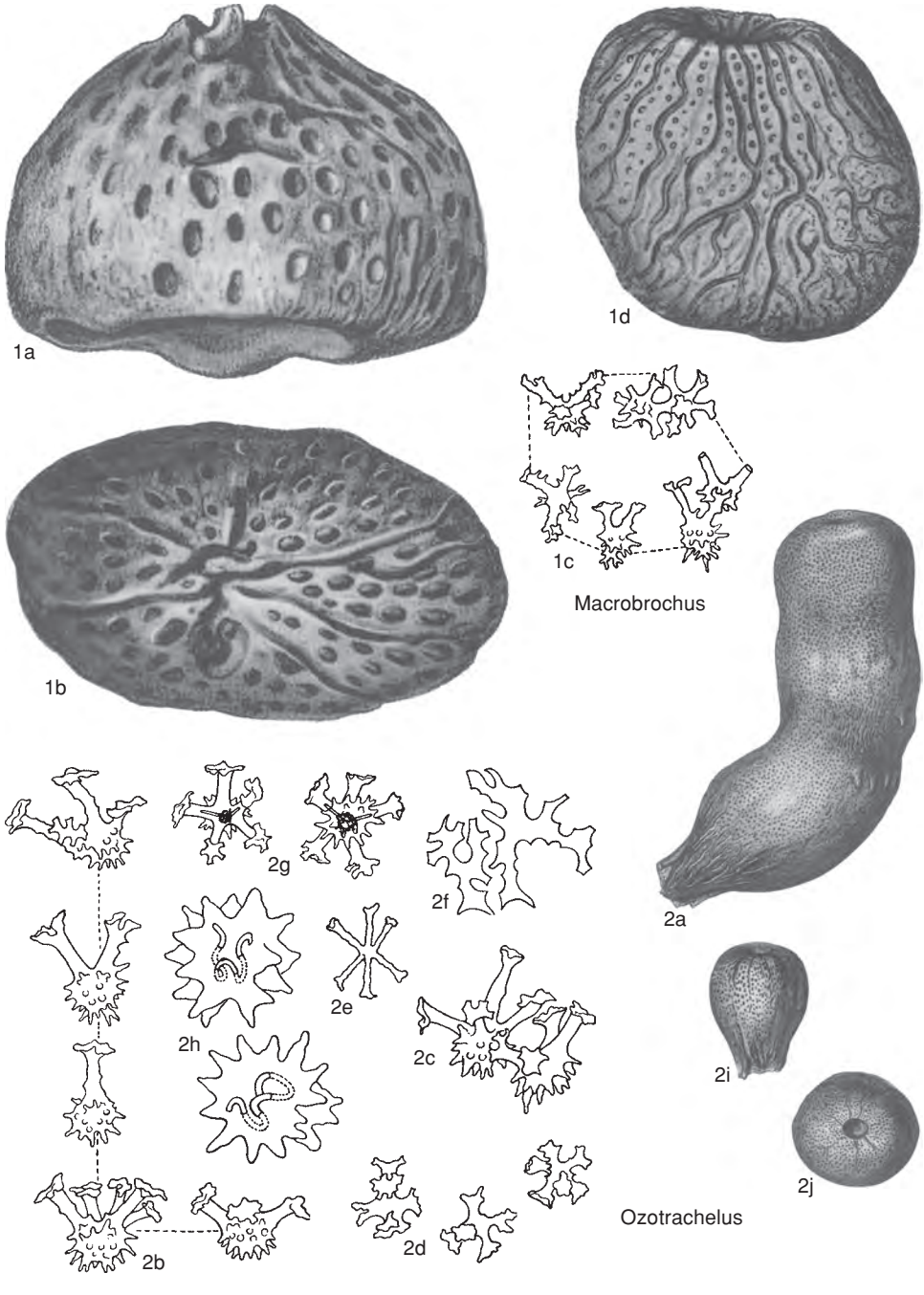


FIG. 173. Vetulinidae (p. 269–272).

conspicuous furrows that radiate from summit and may branch and anastomose downwardly, here regarded as subdermal, aporhytic channels; between these are ostia of radial epirhyses; internal aporhyses not known; desmas small sphaeroclones with spiny centra; other spicules unknown. *Cretaceous (Santonian–Campanian):* Germany.——Fig. 173,*1a–c. *M. emscherensis,* Westphalicuskreide, Santonian, Ilsede; *a,* side view showing large ostia on flanks of coarse, hemispherical sponge; *b,* view of same from above showing ostia and radiating furrows, but no paragastral cavity, ×1; *c,* characteristic desmas, ×50 (Schrammen, 1910).——Fig. 173,*1d. M. rimosus* Schrammen, Mucronatenkreide, Campanian, Misburg; side view showing ostia, external furrows, and osculum to shallow, paragastral cavity, ×1 (Schrammen, 1910).

Ozotrachelus de Laubenfels, 1955, p. 61, *nom. nov. pro Pachytrachelus* Schrammen, 1910, p. 170, *non* Chaudoir, 1852 [**Pachytrachelus exspectatus* Schrammen, 1910, p. 174; OD as *P. expectatus* de Laubenfels, 1955, p. 61, *nom. null.,* here accepted as intended to designate *P. exspectatus*]. Pyriform to cylindrical with rounded top; stalked or with short, root processes; paragastral cavity narrow, deep or shallow; external surface with numerous small, closely spaced ostia, from which simple epirhyses run horizontally or obliquely downward; paragastral surface with postica of aporhyses that curve down toward external surface; incipient aporhyses at summit may form narrow, radiating furrows around paragastral margin; desmas mainly sphaeroclones with spiny centra but including some astroclones; a sinuous canal may occur in centra of sphaeroclones; phyllotriaene-like siliceous plates may occur as dermalia; no other spicules known. *Cretaceous (Campanian):* Germany.——Fig. 173,*2a–h. *O. exspectatus* (Schrammen), Mucronatenkreide, Misburg; *a,* side view of subcylindrical sponge with rounded top and distinct osculum, ×0.5; *b–h,* characteristic spicules including: *b,* sphaeroclones with 1 to 5 arms, ×50; *c,* two connected sphaeroclones, ×50; *d–e,* six-armed astroclones, ×50; *f,* phyllotriaene-like dermalia, ×60; *g,* sphaeroclone with an internal canal, from above and below, ×50; *h,* centra showing sinuous canals, ×100 (Schrammen, 1910).——Fig. 173,*2i–j. O. conica* (F. A. Roemer), Sudmerberges; *i,* summit showing ostia, paragastral opening, and radiating furrows; *j,* side view of top-shaped sponge, ×1 (Schrammen, 1910).

Family LECANELLIDAE Schrammen, 1924

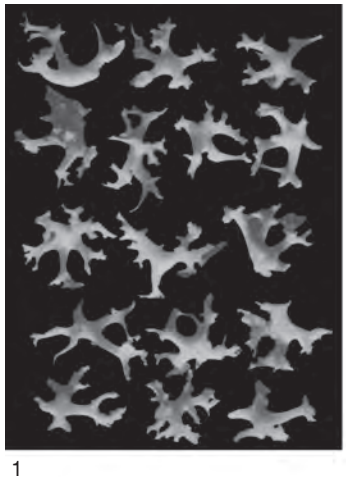
[Lecanellidae Schrammen, 1924b, p. 154]

Desmas large, developed as astroclones (=anomoclones *sensu* Schrammen, 1937, *non* Rauff, 1895), as forms between this type and sphaeroclones, or partly as modified (e.g., elongate, flattened, irregular) variants of astroclones or sphaeroclones; zygomes sometimes scarcely developed; internal canals unknown, although a granular nucleus or marrow is present in some forms; no other spicules known. [Desmas of this family were called anomoclones by Schrammen (1937) but do not correspond with the anomoclones of the Anomoclonellidae (suborder Orchocladina). Schrammen's usage seems to have depended on Rauff's (1895) description of anomoclones as irregular ennomoclones (i.e., sphaeroclones); but anomoclones are here thought to be related to chiastoclones and dendroclones. The large size of the desmas suggests that this group may have had a different origin from the Vetulinidae, although this is not demonstrable. Original publication was without diagnosis but in new combination with type genus. First formal diagnosis was by Schrammen, 1937, p. 108.] *Upper Jurassic (Oxfordian)–Upper Cretaceous.*

Lecanella Zittel, 1878a, p. 135 [**L. pateraeformis;* OD]. Funnel- to basinlike or ear shaped, thin or thick walled; both surfaces with small, skeletal pores when well preserved; skeletal canals (epirhyses, aporhyses) simple and radial or absent; desmas typical astroclones and flattened variants, latter with discoidal or arcuate centers in some examples, and then sometimes with a nucleus; zygosis often more or less loose; no other spicules known. *Jurassic (Oxfordian–Kimmeridgian):* Poland, *Oxfordian;* Germany, Switzerland, *Kimmeridgian.*——Fig. 174,*3a–b. *L. pateraeformis,* Weiss Jura, Kimmeridgian, Sontheim, Germany; *a,* camera lucida drawing of part of inner wall showing relationships of spicules, ×50 (Zittel, 1878a); *b,* astroclone desmas, ×20 (Schrammen, 1937).

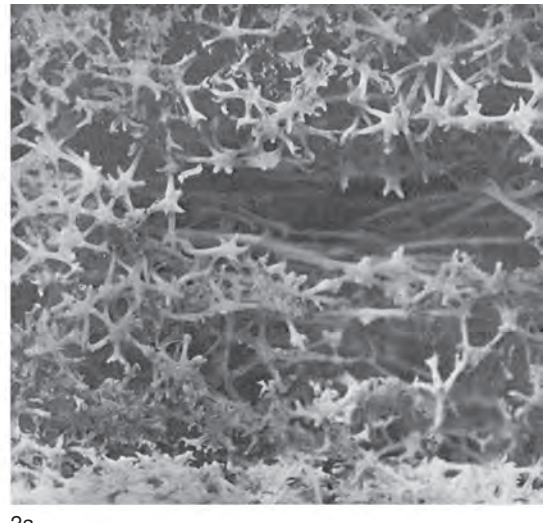
Poterionella Počta, 1903a, p. 8 [**P. trunciformis;* OD]. Sponge, similar to *Lecanella* in exterior form and skeletal structure, thin walled and globose with short-necked osculum and large stalk or stem; walls without distinct ostia so water must have flowed through irregular, interstitial openings; spicules without regular arrangement are large and approach tetraclones in appearance but individual elements difficult to distinguish. *Upper Cretaceous:* Czech Republic, Slovakia.——Fig. 174,*5a–b. *P. trunciformis,* Beds of Korycany, upper Cenomanian, Kutná Hora; *a,* side view of upper part of globose sponge with a necked osculum, ×0.5; *b,* skeletal fragment of coarse, fused elements, ×40 (Počta, 1903a).

Regnardia Moret, 1925, p. 487 [**R. lapparenti;* OD]. Known incompletely from cylindrical fragments, which are traversed by longitudinal, skeletal canals (presumed to be aporhyses) in axial parts; principal

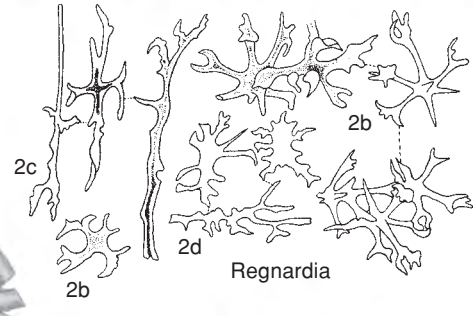


1

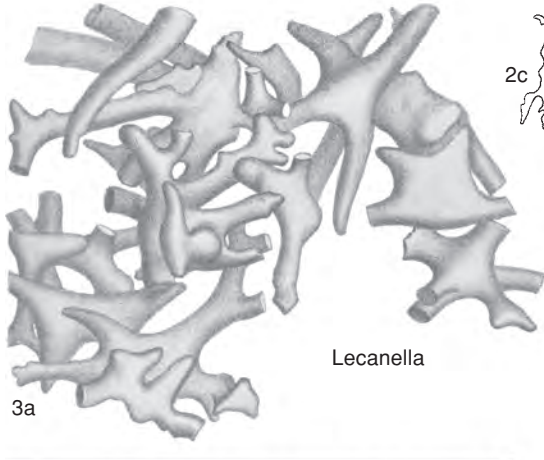
Sphaeropegma



2a

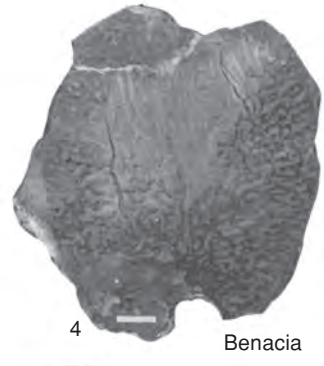


Regnardia



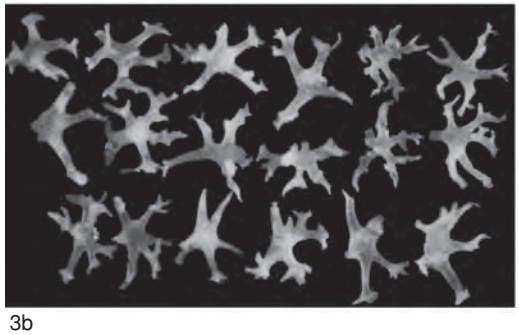
Lecanella

3a



4

Benacia



3b

Poterionella

FIG. 174. Lecanellidae and Uncertain (p. 272–274).

FIG. 175. Uncertain (p. 274).

desmas between typical astroclones and sphaeroclones, with arms well developed and ending in zygomes on one side of center; these forms grade into flattened and irregular variants and into elongate desmas suggesting irregular megaclones in axial parts; some desmas with granular marrow; no other spicules known. *Cretaceous (Cenomanian):* France.——FIG. 174,*2a–d.* **R. lapparenti,* Sablons; *a,* skeleton showing normal desmas and elongate variants, ×20; *b–d,* characteristic spicules including normal desmas, elongate desma variants, and irregular variants, magnification not given but approximately ×25 (Moret, 1926b; courtesy of Société Géologique de France).

Sphaeropegma SCHRAMMEN, 1937, p. 109 (SCHRAMMEN, 1924b, p. 154, *nom. nud.;* SCHRAMMEN, 1936, p. 186, *nom. nud.*) [**S. nuda;* OD]. Globular with central cavity, thick walled; outside with small, skeletal pores (ostia); paragastral surface with postica of tubular aporhyses that are vertical in axial parts but arch outwardly following form of growth layers around them; desmas like those of *Lecanella* ZITTEL; no other spicules known. [Original publication was without diagnosis. First formal diagnosis was by SCHRAMMEN, 1937, p. 109.] *Jurassic (Kimmeridgian):* Germany.——FIG. 174,*1.* **S. nuda,* Weiss Jura, Streitberg; astroclone desmas, ×20 (Schrammen, 1937).

Family UNCERTAIN

Benacia KRAUTTER, 1996, p. 308 [**B. princeps;* OD]. Nodular sponge, without spongocoel, irregularly radial, inhalant canals in walls converging to axial cluster of vertical, exhalant canals; skeleton of very small, four-rayed anomoclones. *Lower Jurassic (Pliensbachian):* Italy.——174,*4.* **B. princeps,* Misonekalk, southern Alps; vertical section of holotype showing axial cluster of exhalant canals and surrounding irregularly convergent, inhalant canals in outer part of skeleton, S 758, ×0.5 (Krautter, 1996).

Order and Suborder UNCERTAIN

Hippalimus LAMOUROUX, 1821, p. 77 [**H. fungoides;* OD]. Mushroom-shaped sponge with dense, dermal layer on flat base around stalk; summit with broad, deep spongocoel and numerous moderately distinct, inhalant ostia in surrounding upper dermal layer; spicule structure unknown. *Upper Cretaceous:* Europe.——FIG. 175. **H. fungoides,* Upper Cretaceous blue marl or clay, Calvados, Normandy, France; side view of sponge with stalked base and conical, upper part with distinct spongocoel, ×0.5 (Lamouroux, 1822).