MESOZOIC AND CENOZOIC LITHISTID DEMOSPONGES: TETRACLADINA

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Subclass LITHISTIDA Schmidt, 1870

[*nom. transl.* Reid, herein, *ex* order Lithistida Zittel, 1878a, p. 96, *nom. transl. pro* group Lithistida Sollas, 1887, p. 421, *nom. transl. ex* group Lithistina Carter, 1875, p. 185, *nom. correct. pro* group Lithistidae Schmidt, 1870, p. 21]

Demospongea whose principal megascleres are desmas that are normally united by articulation (zygosis) to form coherent, skeletal framework; some also with types of megascleres that may be monaxons (e.g., oxeas), triaenes, or both, or with accessory (supplemental) desmas in addition to main ones; principal desmas tetraxial, triodal, monaxial, or anaxial in those whose character is known; some with tetraxial desmas intergrading with triodal or monaxial forms; articulatory features (zygomes) sometimes simple facets only, but typically twig-, root-, or clawlike, or forming tongue-, cup-, or handlike expansions; few forms with zygosis only weakly developed or absent; skeletal framework uncanalized, or with ostia, postica, or both, or with additional epirhyses, aporhyses, or both, or with skeletal pores or canals of unknown character; triaenes arranged typically at surfaces when present, with shafts running inwardly into meshes of internal framework when long enough, and their cladi in ectosome in living forms; shafts of triaenes never normally incorporated into primary, skeletal meshwork, although sometimes imbedded in secondary meshwork formed by supplemental desmas; supplemental monaxons usually loose in skeletal meshes or lying tangentially at surfaces, but sometimes grasped by zygomes of desmas or incorporated into composite, skeletal fibers; supplemental desmas usually small, rhizoclone-like bodies, found in internal meshes, at surface, or both, and sometimes intergrading with primary desmas; examples found at surface may form a supplemental cortex that coats skeletal framework, and may then cover ostia or postica, or be pierced by intracortical pores or canals; microscleres present or absent in living examples, in which they may be microrhabds, streptoscleres (intergrading plesiasters, metasters, and spirasters), unidentified spirasters or amphiasters, or sigmaspires when present; soft parts as in normal Demospongea, with the ectosome usually a dermis. *Cambrian–Holocene.*

The lithistid sponges were interpreted as monophyletic by Zittel (1878a) and Sollas (1887) but are here considered polyphyletic following Schrammen (1903), Hentschel (1923–1924), Burton (1929), and de Laubenfels (1936). They appear to comprise forms produced by repetitive (or iterative) evolution of lithistid characters in sponges that were sometimes originally choristids but sometimes monaxonids. On this basis, Schrammen, Hentschel, Burton, and de Laubenfels, of the above dates, each attempted to classify lithistids in taxa that also included their nearest supposed nonlithistid relatives and did not use the single group Lithistida. In practice, however, relationships of lithistid and nonlithistid sponges are mainly uncertain, and sometimes probably unknowable. Hence de Laubenfels (1955) reverted to use of order Lithistida in the previous *Treatise, Part E* and his usage is followed here except that the taxon is treated as a subclass. Orders Tetralithistida Lagneau-Hérenger (*sensu nov.*), Megalithistida *nov.,* and Monalithistida Lagneau-Hérenger (*sensu nov.*) are thought to comprise forms that probably have had separate origins. The three orders may also include groups having more than one origin, although this is less certain. In addition to genera that fall in the recognized orders and suborders, there are various isolated modern forms (e.g., *Lophacanthus* HENTSCHEL) for which no attempt is made to classify here.

In further classification, division of orders into suborders is based on methods developed by ZITTEL (1878a), RAUFF (1893, 1894), and SCHRAMMEN (1924b), whose traditional taxa (e.g., Tetracladine ZITTEL, Dicranocladine SCHRAMMEN) are employed at this taxonomic level. Division of suborders into families is based chiefly on the methods of SCHRAMMEN but also on various other sources.

Treatment of genera is based on paleontological methods of ZITTEL (1877a, 1877b, 1878a, 1878b) and later writers, treatments that differ from those of many zoologists. In paleontology, generic diagnoses have been generally based on combinations of details of habitus, internal or external canalization, various characters of the skeletal framework or individual desmas, and such further features as the presence and extent or absence of a supplemental cortex, or presence or absence of intracortical pores when a cortex is present. Reference to loose spicules is almost entirely restricted to the form of dermal triaenes, when these are present. On the other hand, zoological diagnoses given often omit many or all of these characters and may depend entirely on features of the soft parts, on loose megascleres or on microscleres, which are not seen in the fossils.

Some characters used for generic separations in paleontology can certainly be doubted sometimes. For example, the living *Macandrewia azorica* CARTER is irregularly funnel-like or fan shaped with small apopores (or oscules) on the inner surface; but *M. clavatella* (SCHMIDT) is club shaped or toplike, with a few small apopores at the summit. *M. ramosa* TOPSENT is initially similar to *M. azorica* but divides at the top into short branches, which may then divide again into smaller ones. A paleontologist finding such forms as fossils would probably place them into two or three genera on the basis of habitus; yet the habitus of *M. clavatella* is that of the young forms of *M. azorica.* As another instance, otherwise similar sponges would usually be placed in separate genera if they differed in that postica were (a) in groups on an unfurrowed skeletal surface; (b) in groups at the centers of radiating patterns of superficial furrows; or (c) arranged as in (b) but within the furrows roofed over by a skeletal cortex, with separate intracortical postica. On the other hand, a modern form (e.g., *M. azorica,* or species of *Corallistes* SCHMIDT) may have skeletal characters as in (a), but also have radiating, subdermal canals around groups of exhalant canals that emerge through the postica and a dermis with separate, osculelike apopores. This suggests that the skeletal differences cited might depend only on how far development of rigid skeletal meshwork extended outside the choanosome in sponges with identical soft parts. Such differences might represent closely allied species, local subspecies, individual variation, or simply individuals that died at different stages of life.

On the other hand, the paleontologist normally has characters of only the skeletal framework, to which characters of triaenes may be added when these spicules are present, as a basis for generic diagnoses. Distinctions based on presence or absence of microscleres, or on their character or arrangement when present, cannot be used. In addition, greater morphological diversity than is shown by modern forms is often confronted. For example, most modern species of the suborder Tetracladina ZITTEL have been referred to two genera only, *Theonella* Gray and *Discodermia* DU BOCAGE, whose type species are also so similar that their treatment as subgenera could be justified. The same group, however, has the greatest known diversity among Cretaceous Lithistida, with 55 nominal genera, although this total is inflated to some extent by the nontypological practice of proposing new genera for any species with features not mentioned in a previously published, generic diagnosis. The total cannot be substantially reduced without rejection of some major category of observable characters, with results that would differ according to which characters are ignored.

Further, examples exist in which paleontological methods seem clearly the more realistic. For example, *Azorica pfeifferae* CARTER, type species of *Azorica* CARTER of the suborder Rhizomorina ZITTEL, is a typically flabellate or convoluted sponge with the following characteristics: (a) a nonfibrous skeletal framework; (b) well-developed internal epirhyses and aporhyses; (c) strong, superficial furrowing occuring on both surfaces of the skeletal framework, related to subdermal channels of the soft parts, with primary ostia and postica in floors of furrows, and with furrows mainly longitudinal on the inhalant side of the framework, but tending to form radiating patterns on the exhalant (paragastral) side; (d) on the inhalant side, the furrows are roofed over by a thin, dense, skeletal cortex, with numerous closely spaced, small, intracortical ostia; (e) on the other side, a more or less discontinuous, skeletal cortex is developed mainly around apertures of larger, widely spaced, osculelike, intracortical postica. In contrast, "*Seliscothon*" *chonelloides* DOEDERLEIN, described as a supposed living species of the fossil *Seliscothon* ZITTEL, 1878a, has a fibrous skeletal framework, no epirhyses, aporhyses, or primary ostia, and no superficial furrowing, skeletal cortex, or intracortical pores on either surface. Yet this species was referred to *Azorica* by SOLLAS (1888), apparently on the basis of its having a flabellate habitus and no microscleres, as in *Azorica.* These forms seem clearly too different to be placed into one genus; and, if compared with others that have fibrous and nonfibrous structures, it is difficult to justify placing them even into the same family.

Order TETRALITHISTIDA Lagneau-Hérenger, 1962

[*nom. transl.* REID, herein, *ex* suborder Tetralithistida LAGNEAU-HÉRENGER, 1962, p. 35; *emend.,* REID, herein]

Lithistida that typically have triaenes or related types of megascleres as dermalia, and desmas whose zygomes are branching twig-, root-, or clawlike structures; desmas all or mainly tetraxial, triodal, or monaxial, with two of these types sometimes present as intergrading variants but with one subordinate, and smooth, spined, or with zygomes tuberculate, or tuberculate on other parts; tetraxial forms typically tetraclones but sometimes developed as triders; triodal forms triders or two-armed variants; monaxial forms sometimes developed as elongate variants of tetraclones, restricted to stalks or root processes, but found chiefly as principal desmas that may be rhizoclones, dicranoclones *s.l.* or didymoclones; zygosis by zygomes interlocking from desma to desma to form syzygial nodes, or by zygomes grasping arms, central parts, or tubercles of other desmas; one or the other of these two main styles commonly predominant, but with some forms having both styles together; crepides (i.e., initial bodies from which desmas develop), small calthrops, triods, triaenes, or strongyles; dermalia usually dichotriaenes or forms grading from phyllotriaene to discotriaene, but sometimes trichotriaenes, monaxial, discotriaene-like bodies, or anaxial plates; supplemental oxeas in some; many with small, rhizoclone-like bodies (rhizoclonids) as supplemental desmas that may form a dense, supplemental cortex at skeletal surfaces; rhizoclonids often with no obvious axial system but sometimes demonstrably intergrading with principal desmas; microscleres of modern examples microrhabds, amphiasters, plesiasters, metasters, or spirasters. *Upper Triassic (Norian)–Holocene.*

This taxon was proposed by LAGNEAU-HÉRENGER (1962) to comprise all Lithistida with tetraxial megascleres as desmas or dermalia, called lithistid Tetraxonia by SCHRAMMEN (1910, 1912). Although tetraclone desmas of the suborder Tetracladina appear to have been derived from a calthrops from which they develop in ontogeny, the heloclones of the Helomorina and the megaclones of Megamorina are probably monaxon derivatives. The heloclone, especially, develops from an ophirhabd (sinuous oxea) that is almost as large as the fully formed desma and is, in effect, simply a modified ophirhabd in which zygosis is produced in the simplest manner possible (by means of articulatory notches without formation of typical zygomes). The two latter groups are considered here to have arisen independently of the Tetracladina and, as a result, are placed into the new order Megalithistida.

In addition to the Tetracladina, the other forms referred here to the Tetralithistida have desmas that are normally monaxial but have triaenes or related types of megascleres as dermalia and zygomes like those of Tetracladine. Three suborders are distinguished. The Dicranocladina SCHRAMMEN have desmas that are typically tuberculate. Desmas are dicranoclones *s.l.* in the family Corallistidae SOLLAS, and dicranoclone-like forms with the tubercles in transverse rows in the Pseudoverruculinidae DE LAUBENFELS. The Pseudorhizomorina SCHRAMMEN have rhizoclonar desmas, which are sometimes tuberculate on the zygomes but typically not on the central parts, and phyllotriaenes or similar monaxial dermalia in the Macandrewiidae GRAY. With these is grouped *Neopelta* SOLLAS, the only genus of Neopeltidae SOLLAS, whose dermalia are monaxial discs. The Didymmorina RAUFF comprises only the Cylindrophymatidae SCHRAMMEN, in which the desmas are typically didymoclones and the dermalia are dichotriaenes, in the only example in which they are known [in *Cylindrophyma milleporata* (GOLDFUSS)]. The Pseudorhizomorina were included by SCHRAMMEN (1924a) in his Dicranocladina (although the former name is older), but are thought here to be probably of independent origin. He also regarded the Didymmorina as lithistid Monaxonia, i.e., forms without tetraxons and of monaxonid origin; but triaene dermalia, which do not appear to be extrinsic, are now known from a specimen of *C. milleporata* identified by SCHRAMMEN himself.

The relationship of forms with monaxial desmas to the Tetracladina is unproven but is suggested by (a) the similar character of the zygomes; (b) the striking resemblance of desmas of the Corallistidae (Dicranocladina) to those of plinthosellid and many theonellid Tetraclina; (c) the presence of tetraxial desmas, as intergrading subordinates of the main, monaxial ones, in *Macandrewia* GRAY of the Pseudorhizomorina; and (d) the presence of similar special microscleres (plesiasters, metasters, spirasters) in some of the living Tetracladina (e.g., *Racodiscula* ZITTEL), Dicranocladina (*Corallistes* SCHMIDT), and Pseudorhizomorina (*Daedalopelta* SOLLAS). In broader terms, the microscleres cited suggest that these groups are related to the choristid Poecillastrida (families Pachastrellidae SOLLAS and Theneidae GRAY).

The small Upper Jurassic family Protetraclisidae SCHRAMMEN is worth mention as a possible link between the Tetracladina, in which it is included, and other Tetralithistida. The two included genera (*Protetraclis* STEINMANN and *Rhizotetraclis* KOLB) have more or less irregular tetraclones with strongly branching arms that grade into rhizoclone-like desmas. *Rhizotetraclis* has some desmas that resemble tetrapodal dicranoclones and are comparable with desmas of the contemporaneous dicranocladine *Kyphoclonella* KOLB. In *Protetraclis* the dermalia are dichotriaenes. While the known species of this family are contemporaries (not precursors) of the earliest Dicranocladina and the Didymmorina, they have features appropriate to a tetracladine root stock of the groups with monaxial desmas.

If this view of relationships is rejected, alternative comparisons can be made with various Paleozoic lithistids in which triaenes are absent: (a) the Tetracladina and Pseudorhizomorina with the anthaspidellid Orchocladina; (b) the Dicranocladina with the hindiid Tricranocladina (=Eutaxicladina *sensu* SCHRAMMEN); and (c) the Didymmorina with the anomoclonellid Orchocladina, in which some desmas resemble didymoclones. Derivation of the Tetralithistida from these sources, however, presumably involves the *de novo* evolution of triaenes at some point of phylogeny (from monaxons). It is here thought more likely that the triaenes were inherited from choristid ancestors and that resemblances to Paleozoic Lithistida are due to convergence, not relationships.

Suborder TETRACLADINA Zittel, 1878

[*nom transl.* SOLLAS, 1887, p. 423, *ex* family Tetracladina ZITTEL, 1878a, p. 100]

Desmas typically tetraxial and usually developed as tetraclones although sometimes as triders (brachytriders); some also with elongate, diaxial or monaxial desmas in stalks or root processes, or with triodal, diaxial, or monaxial forms as subordinate variants of normal tetraclones; ultimate syzygial processes spinelike or thickened into tubercles, arms of desmas smooth, spined, or tuberculate; smooth and tuberculate forms found mainly in different genera but sometimes together and intergrading; zygosis by zygomes that interlock to form syzygial fibers or nodes, or that clasp arms, centers, or tubercles of other desmas; dermalia usually dichotriaenes, phyllotriaenes, or discotriaenes, but sometimes trichotriaenes, monaxial variants of discotriaenes, or apparently anaxial plates; supplemental oxeas in some; many with small, supplemental rhizoclonids that may form a skeletal cortex when present; modern species mainly with microrhabds as microscleres but some with spirasters that may grade into metasters or plesiasters. *Upper Triassic (Norian)–Holocene.*

The name Tetracladina was originally designated at the family level by ZITTEL (1878a) but cannot be treated as a family name, having no generic basis. It was technically first published as the name of a suborder by SOLLAS (1878) but is here ascribed to ZITTEL in accordance with reality and the practice of all later authors, including SOLLAS.

The suborder Tetracladina is envisaged here as characterized, especially in the fossils, by the combined occurrence of tetraclonar desmas and dermal triaenes and in modern forms additionally by occurrence of the microscleres cited. It is not regarded as including forms without dermal triaenes, unless these spicules are thought to have been lost in phylogeny or before burial and fossilization and does not include forms with desmas of outwardly tetraxial shapes that are either monaxial or anaxial, or are regarded as derived from monaxons. With these restrictions, the suborder seems acceptable as probably a natural assemblage. The oldest known genera with both tetraclones and triaenes are Upper Jurassic, although these forms are sufficiently diverse to imply that the group must be older.

The most important exclusion that results from this concept of the taxon is that of the Paleozoic Anthaspidellidae ULRICH (=Archaeoscyphiidae RAUFF and Aulocopiidae RAUFF in DE LAUBENFELS, 1955), which were formerly included because some of the desmas have the form of tetraclones. Some examples of the characteristic desmas (dendroclones) of this family are similar to tetracladine amphitriders (tetraclones with a large, trifid zygome at the end of the primary arm). On the other hand, the simplest of these desmas are in effect bipolar rhizoclones with unspecialized zygomes at both ends of a smooth, central shaft. Some such spicules are demonstrably monaxial. Intergradations in various genera imply that the tetraclone-like desmas are four-armed chiastoclones homologically and hence probably either monaxial or anaxial (REID, 1963d). In addition, no triaenes are known from any Anthaspidellidae. The resemblance of some anthaspidellids to Tetracladina is, hence, interpreted here as convergent; and the family is referred to the suborder Orchocladina RAUFF (=Orchocladinidae RAUFF, 1895, *nom. correct.* REID, 1963d) of the order Monalithistida LAGNEAU-HÉRENGER.

Jereina FINKS of the Permian is here thought to be an anthaspidellid despite its prevalence of tetraclone-like desmas and resemblance to the tetracladine *Jerea* LAMOUROUX. Both of these genera are cylindriform sponges with a bundle of axial aporhyses and no paragaster; but this resemblance need not have any implication of relationship, because the same type of organization is present for example in *Carterella* ZITTEL of the Helomorina, *Doryderma* ZITTEL of the Megamorina, and *Jereica* ZITTEL of the Rhizomorina.

From the presence of triaenes and of desmas that develop from a calthrops in ontogeny, it seems likely that the Tetracladina are of choristid origin. The occurrence in some species [e.g., *Racodiscula polydiscus* (SCHMIDT)] of spirasters, metasters, and plesiasters points to an origin from the same source as the family Pachastrellidae SOLLAS of the order Poecillastrida (=Streptastrosa SOLLAS or Streptosclerophora DENDY), in which choanosomal megascleres may be calthrops. The occurrence of microrhabds only in many others (mainly species of the two main modern genera, *Theonella* GRAY and *Discodermia* DU BOCAGE) is not opposed to this conclusion because similar bacilliform microrhabds are abundant in some species of *Pachastrella* SCHMIDT and allied genera (e.g., *Yodomia* LEBWOHL).

A possible prototype of the tetraclone is the type of calthrops in which the rays divide terminally into more or less irregular branches as in *Pachastrella abyssi* SCHMIDT. Such a prototype can be pictured as giving rise to a tetraclone with anaxial zygomes by reduction of the terminal branches of the axial filaments. This process is not demonstrable stratigraphically, for the first forms appear cryptogenically; but some modern species have only weak development of zygomes, and one is recorded as having both tetraclones and calthrops together. In addition, a similar development is represented apparently in the isolated genus *Brachiaster* WILSON, which has centrotrider desmas and seems probably to be a lithistid version of the choristid *Triptolemma* DE LAUBENFELS (=*Triptolemus* SOLLAS, 1888, *non* PECKHAM, 1885). As pointed out by SCHRAMMEN (1910, p. 30), the type of spiculation expected in an ancestor of the Tetracladina (choanosomal calthrops, dermal dichotriaenes) occurs in *Propachastrella* SCHRAMMEN, although recorded occurrences of this genus are too late stratigraphically (Late Cretaceous).

After sparse representation in the Upper Jurassic, the Tetracladina have their greatest known development from the Aptian to the Campanian. Tertiary examples are few, and many modern species are referred by zoologists to two genera (*Theonella* and *Discodermia*), although some of these should probably be distinguished generically.

Many Aptian genera fall into two major series, characterized by desmas that are either smooth or strongly tuberculate. Most forms with smooth tetraclones are referred here to the family Siphoniidae D'ORBIGNY, in which dermalia are typically dichotriaenes. Those with tuberculate desmas comprise most of the family Theonellidae VON LENDENFELD (=Discodermiidae SCHRAMMEN), in which dermalia are rarely dichotriaenes but typically phyllotriaenes or discotriaenes, plus the family Plinthosellidae SCHRAMMEN, which differ in that desmas are triders and dermalia sometimes anaxial plates. These two groups presumably mark divergent evolutionary series with the siphoniids, in theory, most similar to the primitive type.

A third distinctive stock, first known from loose desmas in the Upper Jurassic, is the mainly Cretaceous family Phymaraphiniidae SCHRAMMEN, in which dermalia are phyllotriaenes and in which smooth-armed desmas have prominent annulations at the base of each arm. If the phymaraphiniids are regarded as derived from a siphoniid origin, phyllotriaenes of this family presumably evolved independently of those seen in theonellids.

Two *Jerea*-like Cretaceous genera (*Lerouxia* MORET and *Jereomorpha* MORET) have desmas of siphoniid type but phyllotriaene dermalia, which suggests a similar development in siphoniids. If these views are correct, evolution of phyllotriaenes has been iterative in Tetracladina. Some caution is needed, however, because some theonellids have both smooth and tuberculate desmas or smooth desmas only in some species (many species of the modern *Theonella*).

Among theonellids, evolution of phyllotriaenes from dichotrianes appears to have followed two patterns. One pattern resulted by simple broadening of cladi, with the spicule retaining a dichotriaene shape, for example as in *Thamnospongia* HINDE. The other pattern developed through forms that resemble an irregular dichotriaene in which cladi bear spinelike, lateral processes, as in *Cladodermia* SCHRAMMEN. The typical irregularly shaped phyllotriaenes intergrade with discotrianes, which in turn may grade into monaxial variants, with an axis in the rhabdal shaft only, through forms with minute, cladal axes. Since both true discotriaenes and monaxial variants may intergrade in one specimen, they are clearly homologous. Assuming that this sequence has reduction of spicular axes, its end term appears to be development of apparently anaxial scales, seen as probably independent developments in the otherwise dissimilar genera *Placoscytus* SCHRAMMEN (Theonellidae) and *Plinthosella* ZITTEL (Plinthosellidae).

A further development that seems to be iterative is replacement of tetraclones by triders with one arm reduced to a rudiment and typically bearing no zygome. This is seen in (a) the isolated Jurassic *Sontheimia* KOLB; (b) various Phymaraphiniidae; (c) a few theonellids, for example, *Pseudojerea* MORET, as a minor development; and (d) as a characteristic feature of the family Plinthosellidae. Those of the plinthosellid *Plinthosella* ZITTEL are also typically accompanied by two-armed variants that are triodal or diaxial and strikingly similar to dipodal dicranoclones in appearance. In plinthosellid triders, the axis of the aborted arm (brachyome) is often rudimentary; but in Phymaraphiniidae the corresponding ray of the crepis is typically developed fully and may project as a ray beyond the basal annulation.

In some Siphoniidae (e.g., *Siphonia* GOLDFUSS, *Callopegma* ZITTEL), the zygomes are mainly united to form syzygial fibers or nodes. The latter may have spherical enlargement. In contrast, when desmas are triders the zygomes are typically applied to arms, centers, or tubercles of other desmas, without terminal zygosis. In other forms, a mixture of both styles is usual, and terminal, lateral, and central zygoses may be shown by different arms of one desma. Hence modes of zygosis do not seem to have any major bearing on tetracladine evolution, although two extreme patterns can be recognized (mainly terminal, in some siphoniids; mainly by zygomes applied to central parts, in plinthosellids).

If zygomes were evolved from the terminal branches of a calthrops, the smooth-armed type of tetraclone should be primitive, although sometimes it could be reversional (e.g., in the living *Theonella*). Because the finest branches of siphoniid zygomes may thicken into tubercles and tubercles and zygomelike spines are interchangeable in the living *Theonella* and *Discodermia,* the tuberculate type of desma suggests a secondary spread of zygomelike outgrowths to the rest of the desma. This process seems to be present in the Upper Jurassic *Sontheimia,* in which both zygomes and spines on the arms are more or less thickened into tubercles.

Classification here is based mainly on the character of desmas and dermalia, following SCHRAMMEN (1910) but with some of his families merged or called by senior names (e.g., Siphoniidae D'ORBIGNY for Phymatellidae; Theonellidae VON LENDENFELD for Discodermiidae SCHRAMMEN). Some of the families that include only one or two genera (Sontheimiidae SCHRAMMEN, Astrocladiidae SCHRAMMEN, Chenendoporidae SCHRAMMEN) are essentially for isolated genera whose relationships to others are not evident. This classification differs markedly from that of DE LAUBENFELS (1955).

Family RADIOCELLIIDAE Senowbari-Daryan & Wurm, 1994

[Radiocelliidae SENOWBARI-DARYAN & WURM, 1994, p. 448]

Thalamid demosponges with a skeleton of tetraclones in a chambered sphinctozoan structure but without a rigid, calcareous skeleton. [Treated as sphinctozoan demosponges by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002, p. 1,533).] *Upper Triassic (Norian).*

Radiocella SENOWBARI-DARYAN & WURM, 1994, p. 449 [**R. prima;* OD]. Thalamid sponges with clearly defined, inner segmentation, which is less well defined on exterior; spicular skeleton consisting of tetraclones; basal skeleton not developed; chambers radiating and arranged in whorl or spiral; spongocoel retrosiphonate and extending through entire sponge; interwalls thick. *Upper Triassic (Norian):* Austria.——FIG. 139,*1a–c*. **R. prima,* Dachstein reef limestone, northern Calcareous Alps; *a,* longitudinal section of holotype showing chambers in thick walls, around axial spongocoel, and upwardly divergent, skeletal structure, ×1; *b,* transverse section of holotype with axial spongocoel and radiating chambers in uniform, skeletal structure pierced by small, inhalant canals, ×1; *c,* photomicrograph of tetracladine, spicule arrangement in holotype, BSPGM Senowbari-Daryan 1992, G1-G5, ×30 (Senowbari-Daryan & Wurm, 1994).

Family PROTETRACLISIDAE Schrammen, 1924

[Protetraclisidae SCHRAMMEN, 1924b, p. 148] [=Sontheimiidae SCHRAMMEN, 1924b, p. 148]

Early Tetracladina with tetraclones or triders and irregular, rhizoclone-like desmas, with dichotriaenes when any dermalia are known; arms of desmas sometimes simple but often more or less irregularly branching and smooth, spinose, or finely tuberculate; phyllotriaenes possible in one species; other spicules unknown. [The family comprises early forms difficult to relate to later families and is possibly most similar to Theonellidae. Family name was initially proposed without diagnosis but taken here as validly established because a recognizable type genus (*Protetraclis* KOLB) was cited.] *Jurassic (Kimmeridgian).*

Protetraclis STEINMANN, 1881, p. 154 [**P. linki;* OD]. Cylindrical or top shaped, thick walled, with a deep, tubular, paragastral cavity; paragastral surface with postica of branching aporhyses whose branches also open through small pores in external surface; desmas strongly branching tetraclones that grade into rhizoclone-like variants; dermalia dichotriaenes; other spicules unknown. *Jurassic (Kimmeridgian):* Germany.——FIG. 139,*3*. **P. linki,* Weiss Jura, Heukchstetten; desmas, ×20 (Schrammen, 1937).

Rhizotetraclis KOLB, 1910 in 1910–1911, p. 208 [**R. plana;* OD]. Platelike with rounded margin; both surfaces with small, skeletal pores; no internal canals; desmas strongly branched tetraclones, rhizoclone-like variants, and some that resemble dicranoclones or didymoclones; no other spicules known. *Jurassic (Kimmeridgian):* Germany.——FIG. 139,*2a–d*. **R. plana,* Weiss Jura, Sontheim; *a,* side view with irregular, radiate structure, SSPHG, ×1; *b–d,* branched tetraclone and rhizoclone-like spicules, ×40 (Kolb, 1910–1911).

Sontheimia KOLB, 1910 in 1910–1911, p. 206 [**S. parasitica;* SD DE LAUBENFELS, 1955, p. 56]. Habit variable; sometimes encrusting; globular or forming a group of small, tuberous growths; sometimes cylindrical or toplike with a deep, narrow, paragastral cavity; aporhyses opening through small, stellate groups of postica when a paragastral cavity is absent; extending from postica in paragastral wall to small pores in external surface when a paragastral cavity is present; desmas include some tetraclones but are typically triders with rudimentary brachyome, some more or less irregularly branched and grading into rhizoclone-like bodies; arms of desmas finely spined or tuberculate; dermalia dichotriaenes when known (sometimes possible phyllotriaenes); other spicules unknown. [May include more than one genus if dermalia of *S. parasitica* were phyllotriaenes as thought by SCHRAMMEN, 1937.] *Jurassic (Kimmeridgian):* Germany.——FIG. 139,*4*. **S. parasitica,* Weiss Jura, Gerstetten; characteristic triders and other desmas, ×20 (Schrammen, 1937).

Family SIPHONIIDAE d'Orbigny, 1851

[*nom. correct.* REID, herein, *pro* Siphonidae D'ORBIGNY, 1851, p. 211] [=Phymatellinae SCHRAMMEN, 1910, p. 33; Hallirhoidae DE LAUBENFELS, 1955, p. 56; Aulaxiniidae DE LAUBENFELS, 1955, p. 57; Jereidae DE LAUBENFELS, 1955, p. 57]

Typically with smooth-armed tetraclones as desmas and dichotriaenes as dermalia, but sometimes with more or less strongly tuberculate tetraclones, or with dermal trichotriaenes or phyllotriaenes; some with irregular forms of tetraclones, but triders normally absent; some genera with zygomes united to form regular, syzygial nodes, which may have spherical enlargement, but others with no regular style of zygosis; forms with stalks or root processes may have elongate, monaxial, radical desmas that intergrade with normal tetraclones through irregular intermediates; may have supplemental rhizoclonids that may form a dense supplemental cortex in which dermalia are imbedded; microscleres unknown in most genera, but short spirasters in one modern genus. *Upper Jurassic–Holocene.*

This family is understood in essentially the sense of SCHRAMMEN's (1910) Phymatellinae (=Phymatellidae SCHRAMMEN, 1924a), except for inclusion of two genera

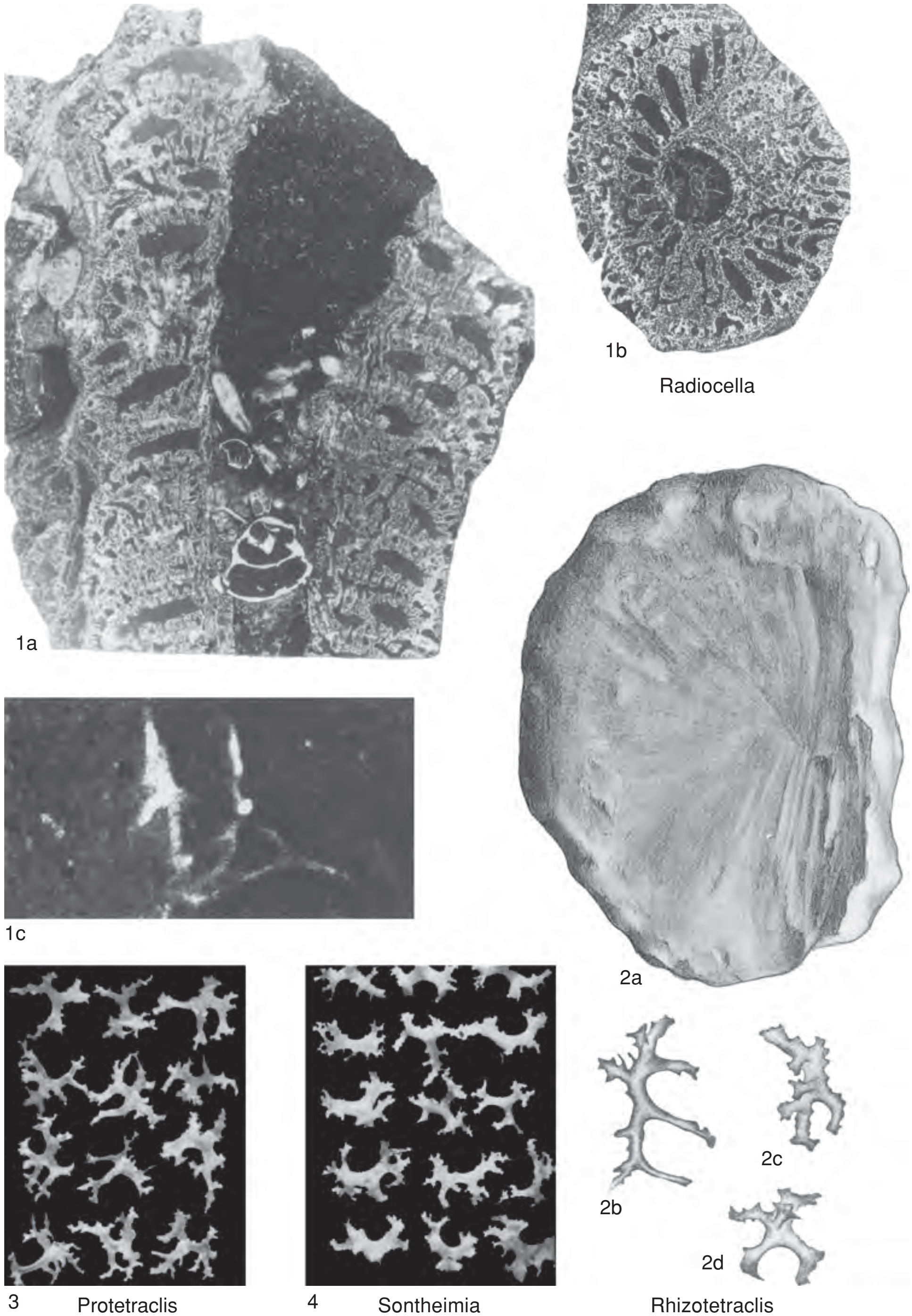

FIG. 139. Radiocelliidae and Protetraclisidae (p. 205–206).

with phyllotriaene dermalia that seem better placed here than in the family Theonellidae. Inclusion of some forms with tuberculate desmas is to allow for *Hallirhoa* LAMOUROUX, 1821, in which desmas are strongly tuberculate in some species not studied by SCHRAMMEN.

DE LAUBENFELS (1955) divided these sponges mainly between three families: Hallirhoidae DE LAUBENFELS, Aulaxiniidae DE LAUBENFELS, and Jereidae DE LAUBENFELS. Of the relevant type genera, *Hallirhoa* is only distinguished from *Siphonia* GOLDFUSS by a lobate outline and has been considered only a subgenus by some authors. *Jerea* LAMOUROUX is difficult to separate from *Siphonia,* generically and is either intergrading or overlapping in characters, according to whether it is distinguished *sensu* ZITTEL (1878a; presence or absence of a paragastral cavity) or *sensu* SCHRAMMEN (1910; size of skeletal meshwork). The types of canal system cited by DE LAUBENFELS are variants of a single type, depending chiefly on different styles of growth, which is mainly terminal in *Jerea* but mainly lateral in the adult *Siphonia. Aulaxinia* ZITTEL, made the type of the family Aulaxiniidae, is a form in which strong, external furrowing is present in adults; but similar furrowing is present in young examples of *Siphonia* and the regular furrowing shown by DE LAUBENFELS (1955, fig. 39,*3a*) is not always present in *Aulaxinia.* It is, therefore, not considered appropriate to base separate families on these genera. Several further genera placed by DE LAUBENFELS as Chenendoporidae also have the desmas and dermalia of Siphoniidae, and one (*Pachycalymma* SCHRAMMEN, 1901) was based on young specimens of *Jerea* (SCHRAMMEN, 1910).

Subfamily SIPHONIINAE d'Orbigny, 1851

[*nom. transl.* REID, herein, *ex* Siphoniidae D'ORBIGNY, 1851, p. 211]

Solitary or compound Siphoniidae with no paragastral cavity, in which aporhyses are longitudinal (vertical) and epirhyses are radial or absent, and similar forms with a paragastral cavity, in which aporhyses run vertically in axial parts but arch outward progressively outside it; dermalia dichotriaenes or rarely trichotriaenes. [A single living genus, *Neosiphonia* SOLLAS (=*Jereopsis* SCHMIDT, 1880, *non Jereopsis* POMEL, 1872; =*Jereica* VON ZITTEL, 1878a), has spiraster microscleres and trichotriaene dermalia.] *Upper Jurassic–Holocene.*

Siphonia GOLDFUSS, 1826, p. 16 [**S. pyriformis;* SD HINDE, 1884a, p. 63; not *Choanites konigii* MANTELL, 1822, p. 178, listed by DE LAUBENFELS, 1955, p. 56 as designated by HINDE, 1887b] [=*Siphoneudea* DE FROMENTEL, 1860a, p. 29 (type, *Siphonia ficus* GOLDFUSS, 1833, pl. 65,*14,* OD)]. Typically stalked-pyriform, tuliplike, or intermediate or other related shapes, with stalk up to several times height of body, and usually divided into lobes or root processes at base; sometimes sessile, stalkless; paragastral cavity usually present, and ranging from shallow depression to deep, narrow, tubular space that extends to near root of stalk but not into it; outer surface with small ostia of radial epirhyses that often slope downwardly in upper parts; paragastral surface with postica of larger aporhyses, often opening in vertical series when paragaster is well developed; aporhyses run vertically downward and into stalk in axial parts, but otherwise arch outwardly and downwardly around it, with those in highest parts following general contour of surface; stalk sometimes with sinuous, longitudinal furrows in which small ostia may open; similar furrows sometimes on other parts; summit sometimes with radiating furrows representing incompletely enclosed aporhyses; desmas typical tetraclones in body, but passing into elongate, fiberlike variants in long stalks; dermalia dichotriaenes; rhizoclonids sometimes present but not usually forming a supplemental cortex; microscleres unknown. [See HINDE, 1883 for discussion of authorship of *Siphonia.*] *Cretaceous (Aptian–Maastrichtian), Neogene (?Miocene):* Britain, Czech Republic, Slovakia, France, Germany, Poland, Russia, Brazil, *Aptian–Maastrichtian;* Italy, *?Miocene*.

S. (**Siphonia**) GOLDFUSS, 1826, p. 16 [**S. pyriformis;* OD]. Skeletal framework typically fine meshed and sometimes especially dense at surface, which then has smooth appearance; no regular development of spherical, syzygial nodes, which are usually absent; stalk normally present, often long. *Cretaceous (Aptian–Maastrichtian):* Britain, Czech Republic, Slovakia, France, Germany, Poland, Russia, Brazil.——FIG. 140,*4a. S. (S.) tulipa* ZITTEL, Upper Greensand, Warminster, Wiltshire, England; skeletal meshwork, ×20 (Hinde, 1884a).——FIG. 140,*4b–c. S. (S.) tuberosa* (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; characteristic spicules including desmas, rhizoclonids, and dichotriaenes, ×30 (Schrammen, 1910).

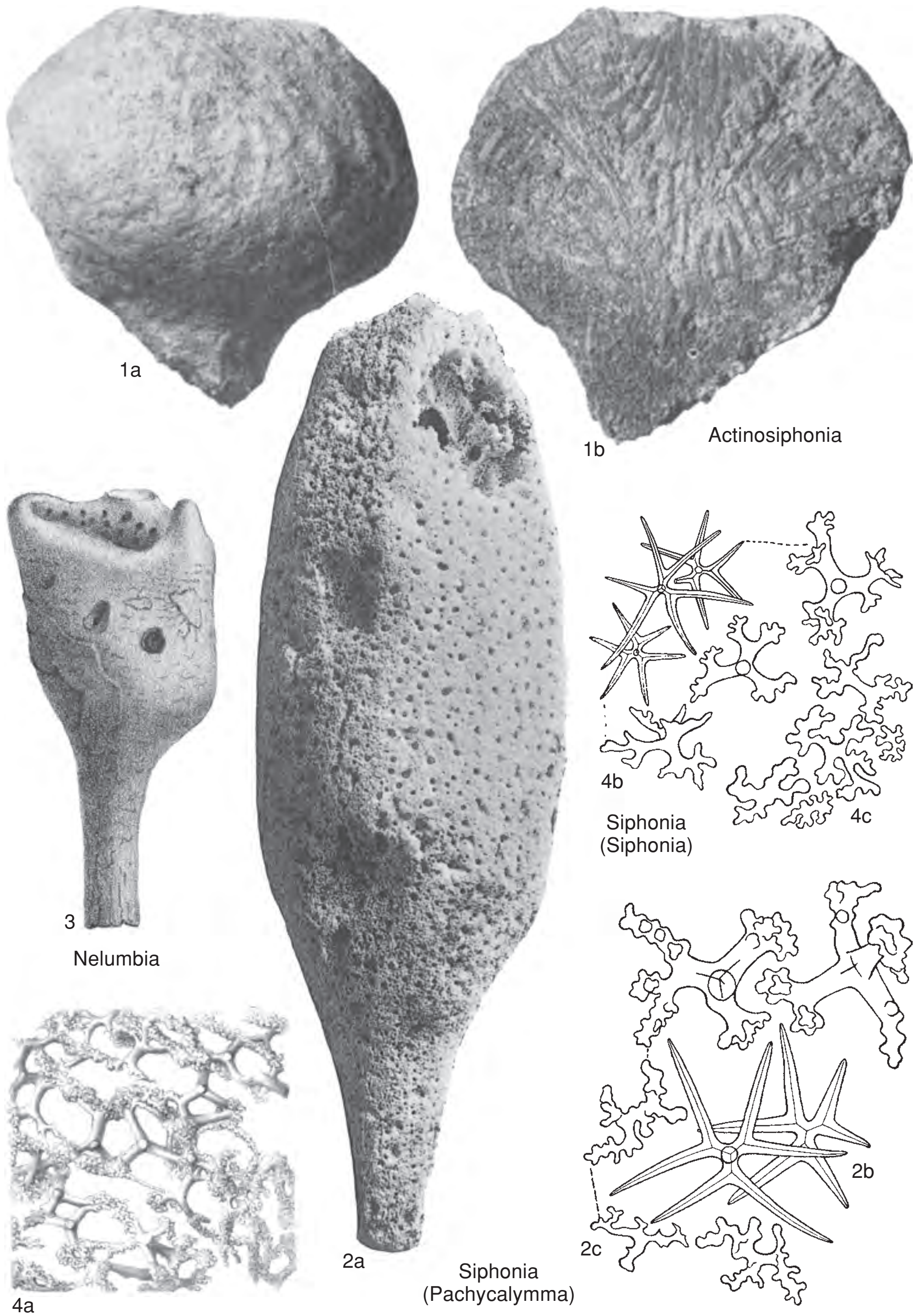

Fig. 140. Siphoniidae (p. 208–212).

S. (Pachycalymma) Schrammen, 1901, p. 9 [**Pachycalymma subglobosa* Schrammen, 1901, p. 10; OD; *not* SD de Laubenfels, 1955, p. 55; =*Jerea quenstedti* Zittel, Schrammen, 1910, p. 89; ?*Jerea quenstedti* Zittel, 1878a, p. 145; ?*Siphonia ficus* Goldfuss, 1831, p. 221]. Skeletal framework wider meshed than in typical *Siphonia s.s.,* due to larger size of desmas, and not being especially dense at surface; regular syzygial nodes may be conspicuous; stalk long, short, or replaced by a number of separate outgrowths, a well-developed, supplemental cortex may coat lowest parts or much of body in small, globular specimens that have died without forming a paragastral cavity. [Type species recognized by Schrammen (1910, p. 89–90) as based on young forms of *J. quenstedti,* as identified by Schrammen, comprised of forms with wide, skeletal meshwork and a deep paragastral cavity, as in *Siphonia, sensu* von Zittel. Schrammen's distinction between *Jerea, sensu* Schrammen, and *Siphonia s.s.,* here transferred to *Pachycalymma* Schrammen as a subgenus of *Siphonia;* diagnosis also based partly on characters of *P. ("Choanites") koenigi* (Mantell) regarded as a further species.] *Cretaceous (Turonian–Campanian):* England, Germany.——Fig. 140,*2a–c.* **S. (P.) globosa* (Schrammen), Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of stalked, subcylindrical form with irregular inhalant ostia, ×1; *b–c,* characteristic spicule assemblage, including desmas, rhizoclonids, and dermalia, ×30 (Schrammen, 1910).

Actinosiphonia Sintzova, 1878, p. 34 [**Siphonia radiata* Fischer de Waldheim, 1837 in 1830–1837, p. 179; OD; *non* Quenstedt, 1877]. Type species a typical, stalked, globular *Jerea,* except that dermalia are unknown. Openings of excurrent canals in upper part, less often on lateral surface; principal spicules large and smooth with numerous branches. *Upper Cretaceous:* Russia.——Fig. 140,*1a–b. A. radiata* (Fischer de Waldheim), Santonian, Saratov, Volga region; *a,* side view of exterior; *b,* vertical section showing distribution of major canals in globose sponge, ×1 (Rezvoi, Zhuravleva, & Koltun, 1962).

Aulaxinia Zittel, 1878a, p. 138 [**Siphonocoelia sulcifera* F. A. Roemer, 1864, p. 30; OD]. Apple shaped to elongate ovoid or cylindrical, with stalk at base and sometimes branched in cylindrical examples; paragaster a shallow depression or conical or tubular cavity; external surface with conspicuous, longitudinal furrows that begin at paragastral margin and typically run downwardly as far as start of stalk; intervening surface with ostia of radial epirhyses; similar pores sometimes also present in furrows; furrows sometimes regular and unbranched, with intervening ridges along which are vertical series of ostia; in other examples furrows less regular, narrower and branching, with intervening ostia then showing no regular order; paragaster with postica of large aporhyses, which run downwardly through body, but not usually into stalk; desmas regular tetraclones in body, with zygomes sometimes forming regular syzygial nodes, but irregular in stalk and grade down into fiberlike variants with a single axial canal; supplemental cortex absent; microscleres unknown. *Lower Cretaceous (Aptian)–Upper Cretaceous:* Spain, *Aptian;* Spain, England, *Albian;* England, France, Germany, Poland, *Upper Cretaceous.*——Fig. 141,*2a–c.* **A. sulcifera* (F. A. Roemer), Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of subcylindrical, ovoid form with vertical, dermal furrows; *b,* smaller, branched sponge with parallel, dermal furrows on one branch, ×1 (Schrammen, 1910); *c,* skeletal fragment showing spicule relationships, ×40 (Zittel, 1878a).

Bathotheca Oppliger, 1915, pl. 9–10 [**Batotheca ovata* Oppliger, 1915, p. 60, pl. 9,*4;* SD de Laubenfels, 1955, p. 56] [=*Batotheca* Oppliger, 1915, p. 59, *nom. null.,* obj., *non* Enderlein, 1905, p. 227]. Sponge globose with short, thin, basal stalk, without central spongocoel or osculum; dermal surface with prominent nodes or projections and larger, exhalant ostia and finer, inhalant pores that connect to complicated canal system of large openings throughout; skeleton may be composed of ennomoclones or didymoclones, most with four or five rays that diverge in various directions and range from bent to straight, simple or branched, and thin to thick; knotlike brachyomes are swollen and commonly occur at corners of quadrate openings, but also may be flattened and spread out. [Oppliger (1915) proposed both *Batotheca* (in the text) and *Bathotheca* (in the figure explanations).] *Jurassic:* Switzerland.——Fig. 141,*1a–b.* **B. ovata* (Oppliger), Birmensdorferschichten, Solothurn; *a,* side view of nodular, globose sponge with prominent ostia and pores, ×0.5; *b,* photomicrograph of calcified, skeletal elements, magnification not evident on copy, probably ×40 (Oppliger, 1915; courtesy of Komission der Schweizerischen Paläontologischen Abhandlungen, Basel).

Callopegma Zittel, 1878a, p. 139 [**C. acaule;* SD de Laubenfels, 1955, p. 56]. Pyriform, depressed globular with small, central cone, hemispherical, discoidal, or basin or funnel-like and thick walled; short stalked or sessile; lower surfaces with distinct, skeletal pores (ostia) or with open, skeletal meshes only; center of upper or inner surface with conspicuous group of postica from which large aporhyses run downwardly in central parts but obliquely outward around them; unenclosed branches of outermost aporhyses forming radiating furrows, which may continue to undersurface; desmas regular tetraclones that are mostly united to form regular, syzygial nodes; these nodes often spherically swollen and give external surface a granulated aspect; dermalia dichotriaenes; rhizoclonids not recorded; microscleres unknown. *Cretaceous (Aptian–*

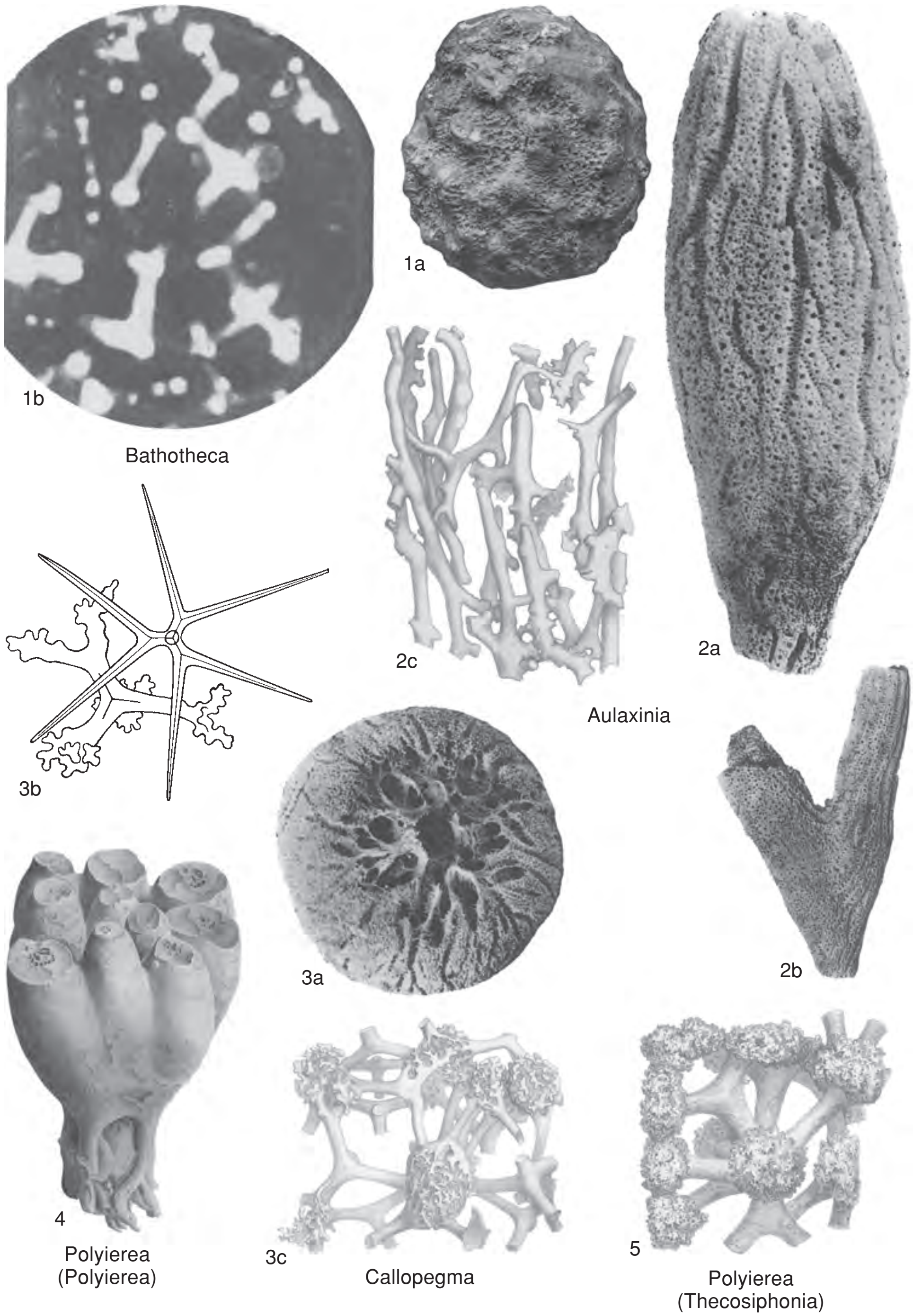

FIG. 141. Siphoniidae (p. 210–214).

Campanian): Spain, *Aptian;* England, Germany, Poland, Puerto Rico, *Campanian.*——FIG. 141,*3a–c.* **C. acaule,* Quadratenkreide, Campanian, Oberg, Germany; *a,* upper surface showing postica and radiating furrows, ×1; *b,* representative spicules including tetraclone and dermal dichotriaene, ×30 (Schrammen, 1910); *c,* skeletal fragment of inner wall with tetraclones united to form syzygial nodes, ×25 (Zittel, 1878a).

Hallirhoa LAMOUROUX, 1821, p. 72 [**H. costata;* OD]. Body apple shaped in profile but radially lobate, with usually four to seven lobes; long stalked, with branching, basal, root processes; paragastral cavity variable, from deep and narrow to almost obsolete; outside of body with small ostia from which radial epirhyses run inwardly; aporhyses larger, vertical in axial parts, but arching outwardly around it; some of axial aporhyses continue down stalk; outermost aporhyses subparallel with external surface and forming radial grooves around paragastral opening or depression in abraded specimens; skeletal framework dense, formed from typical and irregular tetraclones; long, fiberlike desmas in stalk; desmas more or less strongly tuberculate in some species; rhizoclonids not recorded; large oxeas may occur in internal meshes; microscleres unknown. [This genus is similar to *Siphonia* GOLDFUSS and sometimes treated as a subgenus only; but it should be treated as senior synonym if that practice is followed. The definition was extended by HINDE (1884a) to include depressed, lobate forms with phyllotriaene dermalia, here referred to *Phyllodermia* SCHRAMMEN of the Theonellidae.] *Lower Cretaceous (Albian)–Upper Cretaceous:* England, *Albian;* England, France, *Cenomanian;* France, *Santonian–Campanian;* Germany, *Campanian;* Russia, *Upper Cretaceous.*——FIG. 142,*1a–c.* **H. costata,* Upper Greensand, Warminster, Wiltshire, England; *a,* side view of five-lobed example with stem and rootlike terminations; *b,* transverse section from below level of spongocoel showing larger, arched and vertical, exhalant canals, ×0.5; *c,* part of interior skeletal structure of tetraclones that unite at tuberose, ray terminations, ×50 (Hinde, 1884a).

Jerea LAMOUROUX, 1821, p. 79 [**J. pyriformis;* OD]. Stalked-globular or pyriform to cylindrical, with apex truncated or having a shallow depression but no distinct paragastral cavity; stalk long or short and simply expanded, lobate, or dividing into root processes at base; outer surface of body with ostia of small, radial epirhyses; apex or apical depression with postica of larger, tubular aporhyses that run vertically downward, or in part slope somewhat outwardly outside axial parts; desmas simple tetraclones or with one to four arms branching dichotomously before emitting zygomes; when simple, sometimes united to form regular, syzygial nodes that may be spherically swollen; dermalia dichotriaenes; rhizoclonids sometimes present, but not usually forming a cortex. [The genus is here understood *sensu* VON ZITTEL, 1878a. An alternative definition by SCHRAMMEN (1910), based on size of skeletal elements, was not based on comparison of the two relevant type species. On comparison of *J. pyriformis* with a specimen identified by SCHRAMMEN as *Siphonia tubulosa* F. A. ROEMER, MORET (1926b, p. 159) concluded he could not see "la moindre difference appreciable dans la taille des desmes."] *Jurassic (?Oxfordian), Cretaceous (Aptian–Campanian):* Poland, *?Oxfordian;* Spain, *Aptian;* England, *Albian;* England, France, Germany, Czech Republic, Slovakia, Poland, Russia, *Cenomanian–Campanian.*——FIG. 142,*2.* **J. pyriformis,* Holocene, Mediterranean Sea, near Caen, France; type specimen from side showing gobletlike form with truncated apex and numerous exhalant ostia and grooves of canals along margin, ×0.5 (Lamouroux, 1821).

Nelumbia POMEL, 1872, p. 194 [**Polystoma cupula* COURTILLER, 1861, p. 126; SD DE LAUBENFELS, 1955, p. 58]. Elongate, club-shaped with apex truncated or slightly hollowed, and number of small, lateral depressions that are sometimes on nodular prominences; stalk and root processes at base; sides with ostia of small epirhyses; central parts with longitudinal aporhyses that open at summit; further short canals, suggesting accessory aporhyses, may open in lateral depressions; desmas tetraclones; dermalia dichotriaenes; rhizoclonids unknown; microscleres unknown. [Poorly known; in effect a *Jerea* with accessory pseudogastral cavities at the sides, although a "delicate siliceous skin" occurring on some examples by COURTILLER (1861, p. 126) may represent a cortex.] *Upper Cretaceous:* England, France.——FIG. 140,*3.* **N. cupula* (COURTILLER); side view of stalked form with lateral ostia, scale not given, approximately ×1 (Courtiller, 1861).

Polyierea DE FROMENTEL, 1860a, p. 33 [**Jerea gregarea* MICHELIN, 1847 in 1840–1847, p. 134; OD] [=*Polyjerea* POMEL, 1872, p. 173, *nom. null.*]. Sometimes solitary but usually compound, with a group of *Jerea-* or *Siphonia-*like sponges arising from a common base or from branches of a common stalk; apices rounded, truncated, or with distinct, paragastral depressions; base simple or with root processes; exterior of skeletal framework coated more or less extensively by dense, epitheca-like, supplemental cortex, which is usually continuous between sponge individuals and may coat whole surface except where aporhyses open; desmas normal tetraclones; dermalia dichotriaenes when known; additional large oxeas in cortex of one species; microscleres unknown. [Dermalia not recognized by ZITTEL (1878a) or SCHRAMMEN (1910) but recorded by HINDE (1884a, subgenus *P. (Polyierea),* proposed herein) and MORET (1926b, subgenus *P. (Thecosiphonia)* ZITTEL, proposed herein.] *Upper Cretaceous–Neogene:* Spain, *Aptian;* England, France, *Cenomanian;* Germany, *Turonian–Campanian.*

P. (Polyierea) DE FROMENTEL, 1860a, p. 33, *nom. transl.* REID, herein, *ex Polyierea* DE FROMENTEL, 1860a, p. 33. Branched or lobate body of tubules in distinct center typically covered by supplemental cortex, except in terminal parts where aporhyses open. *Cretaceous (Coniacian–*

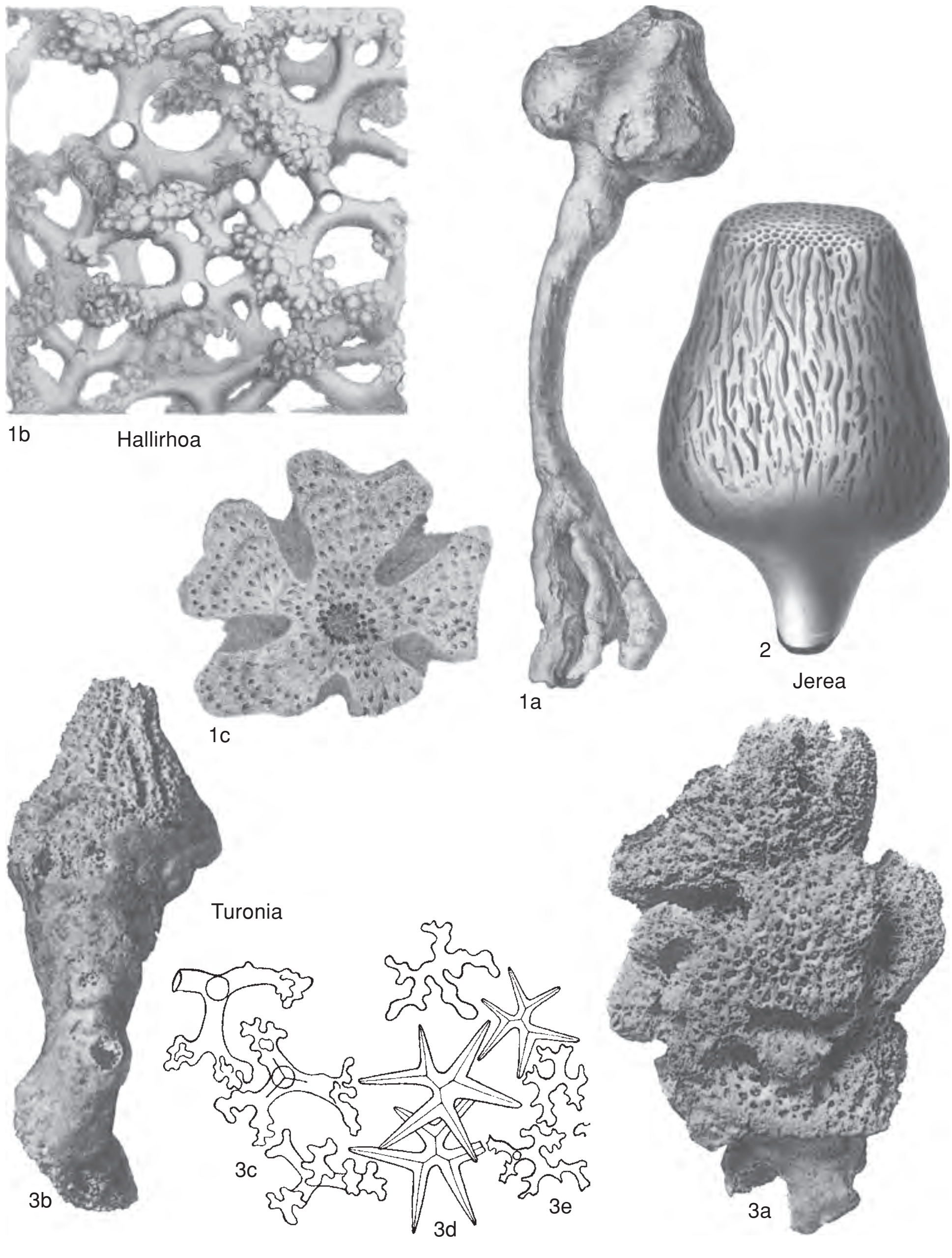

FIG. 142. Siphoniidae (p. 212–214).

Maastrichtian): France.——FIG. 141,*4. *P. (P.) gregarea* (MICHELIN), Chloritic chalk; side view of large sponge showing branched, tubular structure and shallow, terminal depressions that contain large aporhyses, ×0.25 (Michelin, 1840–1847).

P. (Thecosiphonia) ZITTEL, 1878a, p. 148, *nom. transl.* REID, herein, *ex Polyierea* DE FROMENTEL, 1860a, p. 33 [**Lymnorea nobilis* F. A. ROEMER, 1864, p. 37; SD DE LAUBENFELS, 1955, p. 56] [=*Orecyta* DE LAUBENFELS, 1955, p. 49, obj., *nom. nov. pro Cytorea* POMEL, 1872, p. 225, *non*

LAPORTE, 1849]. Cortex usually absent from higher parts of body where skeletal surface has ostia and irregular, superficial furrows; epirhyses sometimes more conspicuous than in *Polyierea s.s.;* one species with large oxeas in cortex. [Proposed as a separate genus by ZITTEL (1878a), but differs from *Polyierea s.s.* only in having cortex less extensively developed.] *Upper Cretaceous–Neogene:* Europe.——FIG. 141,*5. P. (T.) grandis* (ROEMER), Cuvier Pläner, Turonian, Ost Haringen, Germany; drawing of skeletal fragment showing nodes produced by union of ray tips of tetraclones, ×30 (Zittel, 1878a).

Turonia MICHELIN, 1844 in 1840–1847, p. 125 [**T. variabilis;* OD]. Shape very varied, often irregular; lower part of body obconical with small, central stalk and typically coated by dense and transversely corrugated cortex, from which short, accessory root processes may grow downwardly; upper part flattened, conical, subcylindrical, cerebriform, or irregularly lobate or nodular, with central, paragaster-like cavity or none; upper surfaces usually not coated by cortex and have ostia, from which straight epirhyses run inwardly; some forms also with conspicuous, simple or branching furrows that radiate from center of body or from more than one center, at which points there may be either a prominence or a shallow depression; in these forms, vertical canals (aporhyses) open into furrows; in others, network of internal canals or larger spaces originating as ramifications of a paragaster-like cavity and may perforate walls in various places; desmas typical tetraclones, which may unite to form regular, syzygial nodes; cortex formed of rhizoclonids; dermalia dichotriaenes; microscleres unknown. *Lower Cretaceous (Aptian)–Upper Cretaceous:* Spain, *Aptian;* France, *Cenomanian–Campanian;* England, *Upper Cretaceous;* Germany, Poland, *Campanian.*——FIG. 142,*3a–b. *T. variabilis,* Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of example with conical summit, above lumpy base covered with dense dermal layer, ×1; *b,* side view of example with irregularly lobate summit largely lacking dermal layer, ×2 (Schrammen, 1910).——FIG. 142,*3c–e. T. cerebriformis* SCHRAMMEN, Quadratenkreide, Campanian, Oberg, Germany; spicules including tetraclones, dichotriaenes, and rhizoclonids, ×30 (Schrammen, 1910).

Subfamily PHYMATELLINAE Schrammen, 1910

[Phymatellinae SCHRAMMEN, 1910, p. 33]

Mainly solitary Siphoniidae without vertical aporhyses, except sometimes in stalks; epirhyses and aporhyses radial and more or less similar, or developed in various other ways, and sometimes absent; dermalia dichotriaenes. [This subfamily comprises Phymatellinae *sensu* SCHRAMMEN, 1910, minus forms placed here under the subfamily Siphoniinae D'ORBIGNY.] *Upper Jurassic–Cretaceous.*

Phymatella ZITTEL, 1878a, p. 137 [**Eudea intumescens* F. A. ROEMER, 1864, p. 26; SD DE LAUBENFELS, 1955, p. 56] [=*Pseudoplocoscyphia* SCHRAMMEN, 1901, p. 4 (type, *P. maeandrina,* M)]. Stalked or sessile; body roughly globular, pyriform, elongate-ovate, or cylindrical, with lower parts or sides having flattened or bulbous swellings or nipplelike to fingerlike outgrowths; paragastral cavity deep, extending nearly to stalk when a cavity is present; often of irregular width and with diverticula extending into lateral prominences; outside surface with ostia of varying sizes from which radial epirhyses run inwardly; paragastral surface with postica of similar aporhyses; desmas tetraclones in body, pass downwardly into monaxial, fiberlike variants in stalks; rhizoclonids often inconspicuous or absent but sometimes forming a supplemental cortex; microscleres unknown. *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* England, France, Germany, Poland, Czech Republic, Slovakia, *Cenomanian–Campanian.*——FIG. 143,*5a–e. P. bulbosa* ZITTEL, Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of young, globular, pyriform sponge with irregular, coarse, exhalant ostia and fine, inhalant pores, ×1; *b–e,* characteristic spicules including tetraclone, young tetraclone, dichotriaene, and rhizoclonids, ×30 (Schrammen, 1910).

Asterocalyx MORET, 1926b, p. 150 [**A. beaussetense;* OD]. Cup or funnel shaped, stalked; outside with ostia of radial epirhyses that run inwardly; inside with postica of smaller aporhyses, arranged in groups at centers of clusters of short, radiating furrows; desmas tetraclones; dermalia dichotriaenes; rhizoclonids forming supplemental cortex in lower parts; microscleres unknown. *Cretaceous (Santonian):* France.——FIG. 143,*1a–d. *A. beaussetense,* Saint-Cyr; *a,* side view of obconical type specimen with ostia of radial epirhyses, slightly reduced; *b–d,* tetraclones and dichotriaene, magnification not stated (Moret, 1926b; courtesy of Société Géologique de France).

Astrolemma SCHRAMMEN, 1924a, p. 59 [**A. semiglobosa;* OD]. Hemispherical with undersurface concentrically wrinkled; upper surface with scattered apertures presumed to be postica and numerous smaller, skeletal pores (possibly ostia); internal canals apparently absent; undersurface covered by dense, epitheca-like, supplemental cortex of small rhizoclonids; dermalia dichotriaenes; microscleres unknown. [Cited illustrations are poor; no other suitable illustrations are known.] *Cretaceous (Campanian):* Germany.——FIG. 143,*3. *A. semiglobosa,* Emscher, Sudmerberges; side view of hemispheroidal type with scattered oscula or postica, ×0.5 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Bolojerea RAUFF, 1933, p. 63 [**B. glebuta*; OD]. Irregularly globular with no paragastral cavity;

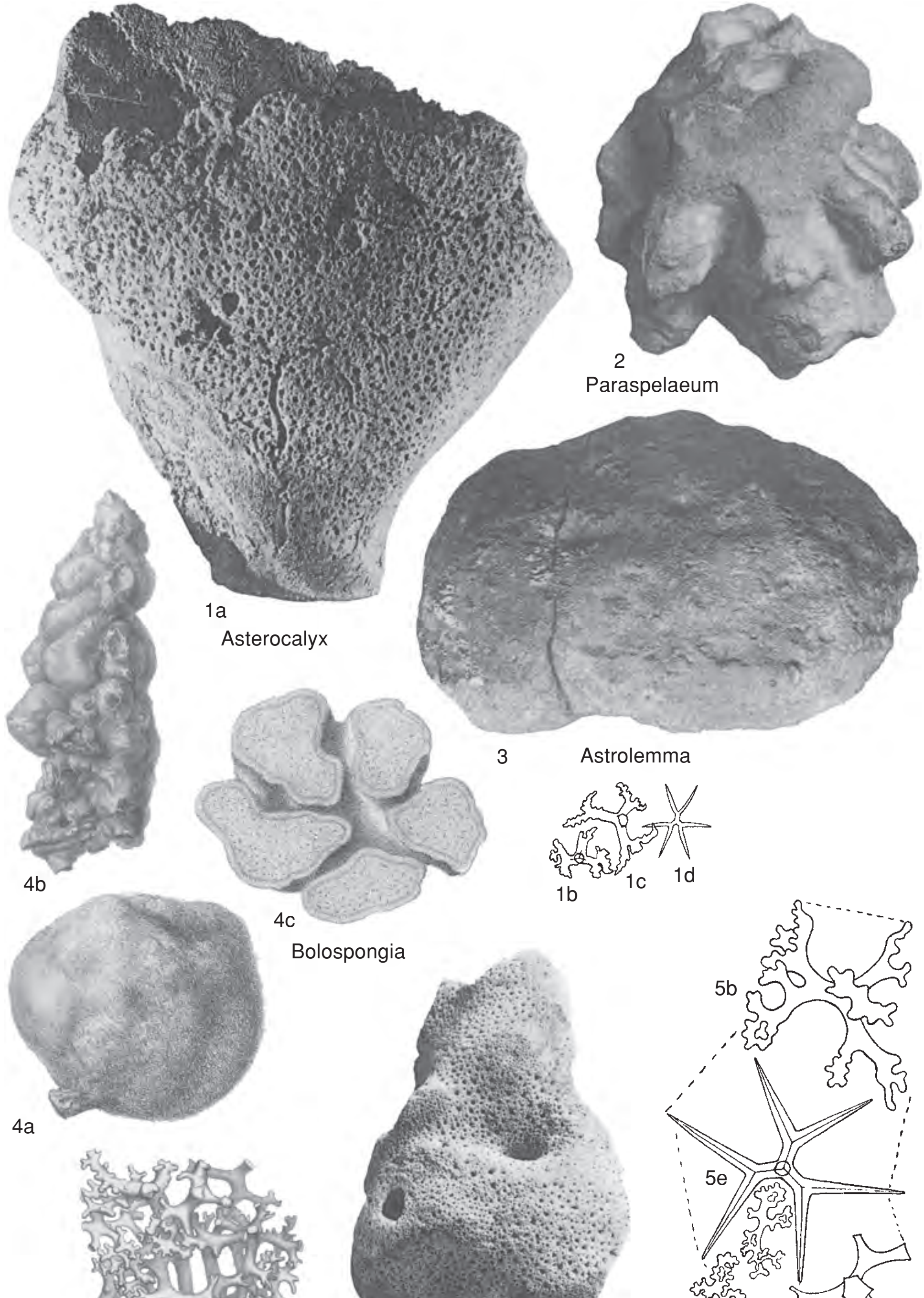

FIG. 143. Siphoniidae (p. 214–218).

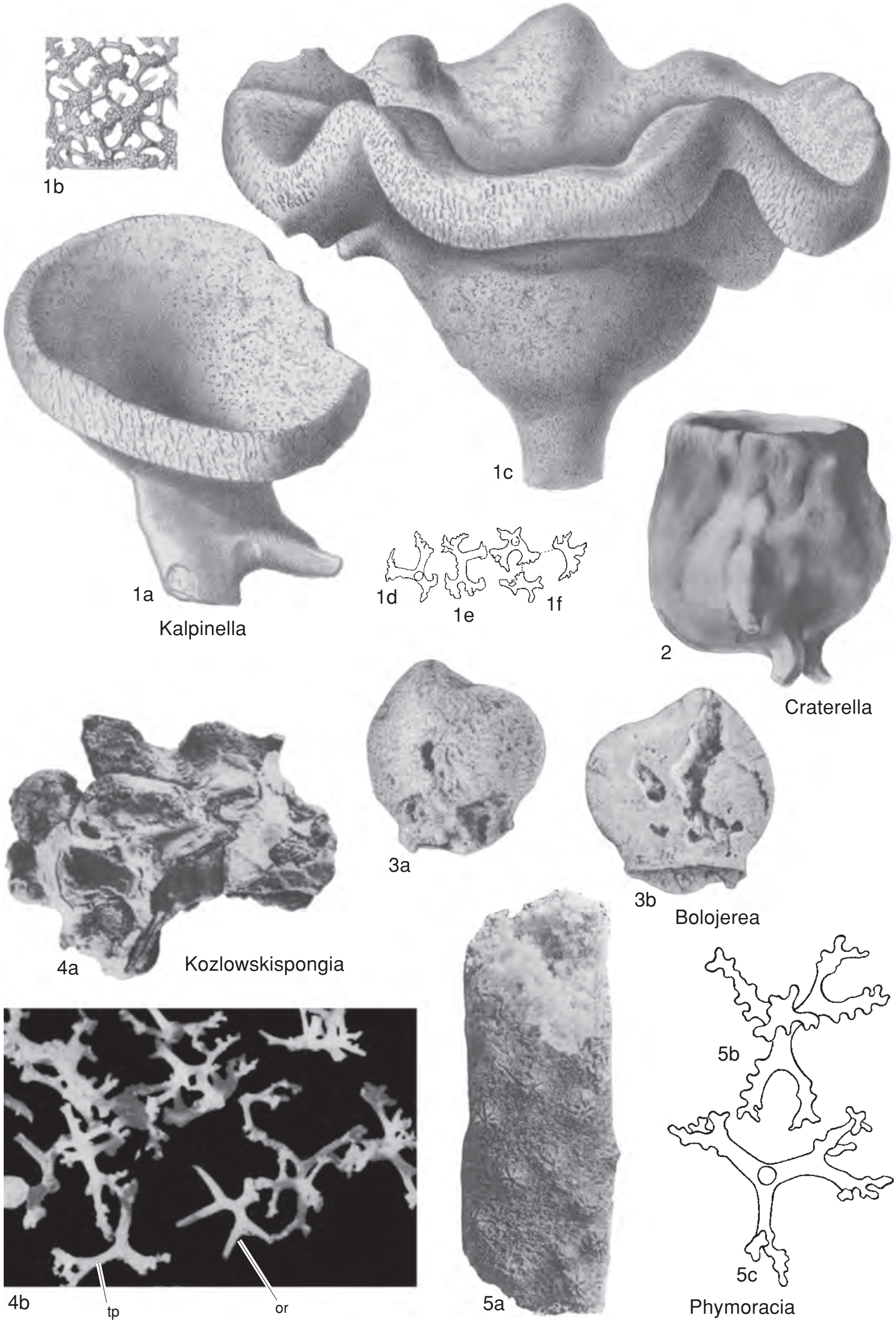

FIG. 144. Siphoniidae (p. 214–218).

exterior with scattered ostia; interior with fine, radial canals, epirhyses and aporhyses not distinguishable; desmas tetraclones, united mainly to form swollen, syzygial nodes; oxeas and microstrongyles recorded; dermalia and rhizoclonids unknown. [Possibly identical with *Bolospongia* HINDE.] *Cretaceous (Turonian):* Germany.——FIG. 144,*3a–b*. **B. glebuta,* Greensand, upper Turonian, Ruhr Valley; *a,* side view of small, globular sponge; *b,* vertical, median section showing small, inhalant, radial canals, larger openings are secondary borings, ×1 (Rauff, 1933).

?Bolospongia HINDE, 1884a, p. 73 [**B. globata;* SD DE LAUBENFELS, 1955, p. 56]. Stalked, globular and small or columnar and irregularly lobate; irregularly hollowed internally with internal spaces opening through osculum-like apertures or between adjacent lobes; no skeletal pores or canals apparent although fine, external furrows may radiate from apertures of internal cavities; desmas smooth tetraclones; dense, cortical layer of unknown composition present; dermal triaenes and microscleres unknown. [Position uncertain but clearly a tetracladine and possibly allied to *Phymatella* ZITTEL.] *Upper Cretaceous (?Campanian):* England.——FIG. 143,*4a*. **B. globata,* Upper Chalk; side view of globose sponge, ×1 (Hinde, 1884b).——FIG. 143,*4b–c*. *B. constricta* HINDE, Upper Chalk, Campanian, Flamborough, Yorkshire; *b,* side view showing nodular exterior, ×0.5; *c,* transverse section showing internal cavities and cortex, ×1 (Hinde, 1884b).

Calymmatina ZITTEL, 1878a, p. 149 [**C. rimosa;* SD DE LAUBENFELS, 1955, p. 54; =*Scyphia dichotoma* MICHELIN, 1847 in 1840–1847, p. 5, *non* BENETT, 1831, *teste* ZITTEL, 1878a, p. 129]. Compound or solitary, in former example with individual sponges united at base or side by side; individuals nodular, top, club shaped, or cylindrical, with deep, narrow, paragastral cavities; base massive or stalked; external surface of skeletal framework with short, irregular, longitudinal, and transverse furrows, in which are ostia of short, radial epirhyses; paragastral wall with postica of similar aporhyses; most of external surface typically covered by smooth or transversely wrinkled, supplemental cortex that covers furrows and ostia; dermalia dichotriaenes; microscleres unknown. *Cretaceous (Coniacian–Maastrichtian):* England, France, Germany.——FIG. 145,*2a–d*. **C. rimosa,* Mucronatenkreide, Campanian, Misburg, Germany; characteristic spicules including desmas, rhizoclonids, dermal dichotriaene, and calthrops-like, young tetraclone, ×30 (Schrammen, 1910).

Craterella SCHRAMMEN, 1901, p. 4 [**C. tuberosa;* OD] [=*Carterella* DE LAUBENFELS, 1955, p. 56, *nom. null., non* ZITTEL, 1878a]. Cup, funnel, or ear shaped, thick walled; sessile or with a few short, root processes; exterior with small ostia of short, radial epirhyses; paragastral surface with similar postica or with additional, larger apertures of canals that anastomose internally; desmas large tetraclones; dermalia dichotriaenes; rhizoclonids and microscleres unknown. [*Carterella* DE LAUBENFELS, 1955 appears to be a misprint, since the cited type species *C. tuberosa* can only be the type of the present genus. Forms identified by MORET (1926b) and LAGNEAU-HÉRENGER (1962) as *Craterella* SCHRAMMEN should probably be described as a new genus.] *Upper Cretaceous (Campanian):* Germany.——FIG. 144,*2*. **C. tuberosa,* Quadratenkreide, Misburg; side view of type specimen, ×0.5 (Schrammen, 1901).

Kalpinella HINDE, 1884a, p. 76 [**K. pateraeformis;* SD DE LAUBENFELS, 1955, p. 55]. Cup or bowl shaped, thick walled, with margin folded up and down in some examples; stalk and root processes at base; external surface with numerous small ostia; paragastral surface with similar postica; epirhyses and aporhyses in wall similar and radial, oblique, or sinuous; skeletal margin rounded or truncated, with open furrows representing incompletely enclosed canals; a few long, vertical aporhyses in stalk; desmas tetraclones or variants with some arms aborted and tending to be tuberculate on zygomes; dermalia, rhizoclonids, and microscleres unknown. *Cretaceous (Aptian–Cenomanian):* Spain, *Aptian;* England, *Albian–Cenomanian;* France, *Santonian.*——FIG. 144,*1a–b*. **K. pateraeformis,* Albian, Upper Greensand, Warminster, England; *a,* side view of stalked, open, funnel-shaped form, ×0.5; *b,* skeletal meshwork showing nodular zygomes, ×25 (Hinde, 1884b).——FIG. 144,*1c*. *K. rugosa* HINDE, Upper Greensand, Albian, Warminster, Yorkshire, England; side view of funnel-shaped form with crenulate margin, ×0.5 (Hinde, 1884b).——FIG. 144,*1d–f*. *K. pateraeformis,* Santonian, Saint-Cyr, France; desmas, approximately ×25 (Moret, 1926b; courtesy of Société Géologique de France).

Kozlowskispongia HURCEWICZ, 1966, p. 44 [**K. bulbosa* HURCEWICZ, 1966, p. 45; OD]. Sponges with hollow, irregularly bulbous, hemispherical protuberances on platelike form; canal system poorly defined but apparently piercing plate; exhalant postica well defined and uniformly developed over entire dermal surface; inhalant ostia smaller and indistinctly outlined; dermal skeleton continuous with fairly large orthodichotriaenes; parenchymal tetraclones somewhat variable in size but smooth with branched zygomes. *Upper Cretaceous (Campanian):* Poland.——FIG. 144,*4a–b*. **K. bulbosa,* Miechów; *a,* lateral view of holotype with bulbous, dermal protuberances, ×0.5; *b,* isolated megascleres from holotype; *or,* dermal orthodichotriaenes; *tp,* parenchymal tetraclones, ×30; Z. Pal. UL Sp. II/93 (Hurcewicz, 1966).

Marginospongia D'ORBIGNY, 1849, p. 549 [**Alcyonium infundibulum* DE FRANCE, 1816, p. 107; OD] [=*Marginoierea* FROMENTEL, 1860a, p. 33, obj.]. Similar to *Kalpinella* but pores minute. [LAMOUROUX (1822, p. 131) was cited as the author of the type species by DE LAUBENFELS (1955, p. 55), but SHERBORN (1922 in 1922–1932, p. 3,887) indicated that DE FRANCE (1816) was probably author of the species.] *Cretaceous*: Europe.

Paraspelaeum SCHRAMMEN, 1924a, p. 60 [**P. obductum;* OD]. Nodular sponge with deep, narrow, paragastral cavity and radially lobate walls;

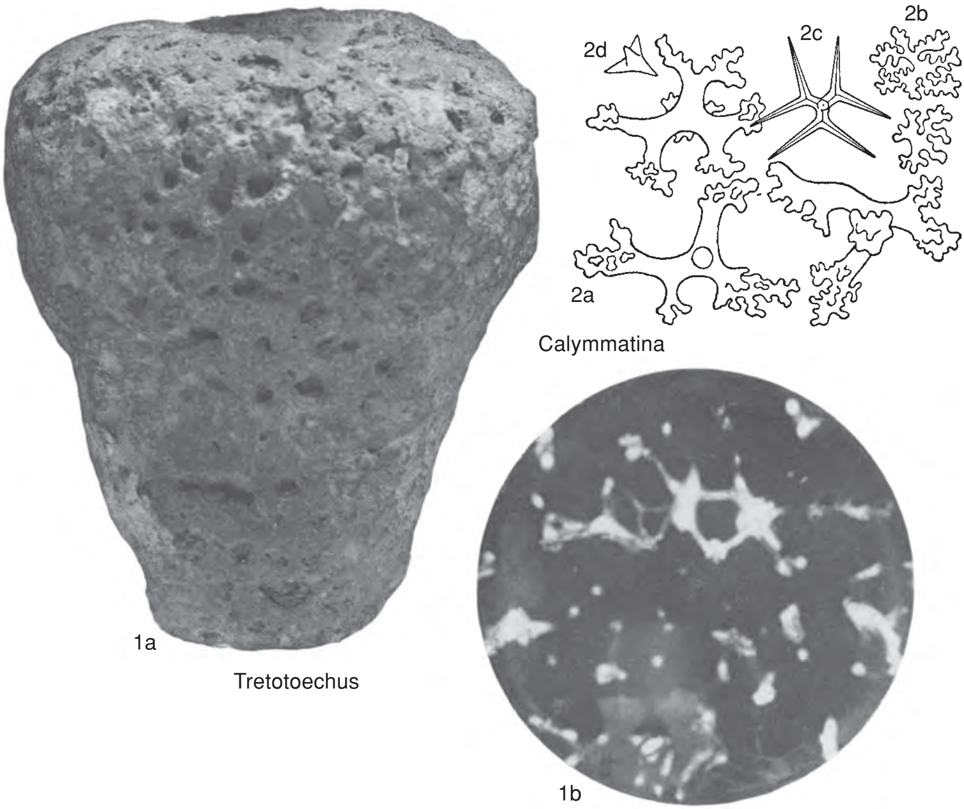

FIG. 145. Siphoniidae (p. 217–219).

ostia and postica very small; skeletal canals apparently absent; desmas tetraclones; dermalia dichotriaenes; rhizoclonids form supplemental cortex; microscleres unknown. [This genus shows little difference from *Phymatella* ZITTEL, except for weaker canalization.] *Cretaceous (Campanian):* Germany. ——FIG. 143,*2*. **P. obductum,* Mukronatenkreide, Misburg; side view of nodular sponge with small ostia in dermal layer, ×0.75 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Phymoracia POMEL, 1872, p. 227 [**Stellispongia verrucosa* F. A. ROEMER, 1864, p. 50; OD] [=*Myrmeciophytum* SCHRAMMEN, 1910, p. 80, obj.]. Cylindrical (possibly branched cylindrical) with no paragastral cavity; sides with groups of postica surrounded by radiating furrows, postica groups on short, conical prominences in some examples; desmas large, smooth tetraclones; dermalia, rhizoclonids, and microscleres unknown. [The type species was regarded as a form of *Astrocladia* ZITTEL by ZITTEL, 1878a, but was distinguished by the character of the desmas by SCHRAMMEN, 1910. It is here regarded as probably allied to *Trachysycon* ZITTEL, with the paragastral cavity suppressed and replaced functionally by lateral aporhyses and oscula.] *Cretaceous (Campanian):* Germany, Poland. ——FIG. 144,*5a–c*. **P. verrucosa* (F. A. ROEMER), Quadratenkreide, Oberg, Germany; *a,* cylindrical fragment with clusters of exhalant ostia and radial canals on low nodes, ×1; *b–c,* characteristic tetraclones, ×30 (Schrammen, 1910).

Trachysycon ZITTEL, 1878a, p. 140 [**Plocoscyphia muricata* F. A. ROEMER, 1864, p. 28; OD]. Stalked-pyriform to elongate ovoid, with exterior showing conical prominences with fine furrows radiating from their tops; intervening surface with small ostia; paragastral cavity deep, with postica of radial aporhyses; desmas normal tetraclones; rhizoclonids may form a supplemental cortex on stalk or lower parts of body; dermalia and microscleres unknown. [Lateral features suggest presence of secondary, lateral oscula, with radiating, exhalant canals in the subdermal region.] *Cretaceous (Cenomanian–Campanian):* England (Upper Chalk), *Cenomanian;* Germany, *Campanian.*——FIG. 143,*6*. **T. muricatum* (ROEMER), Quadratenkreide, Campanian, Sutmerberg, Germany; camera lucida drawing of skeletal structure of tetraclone desmas, with minor rhizoclones, ×30 (Zittel, 1878a).

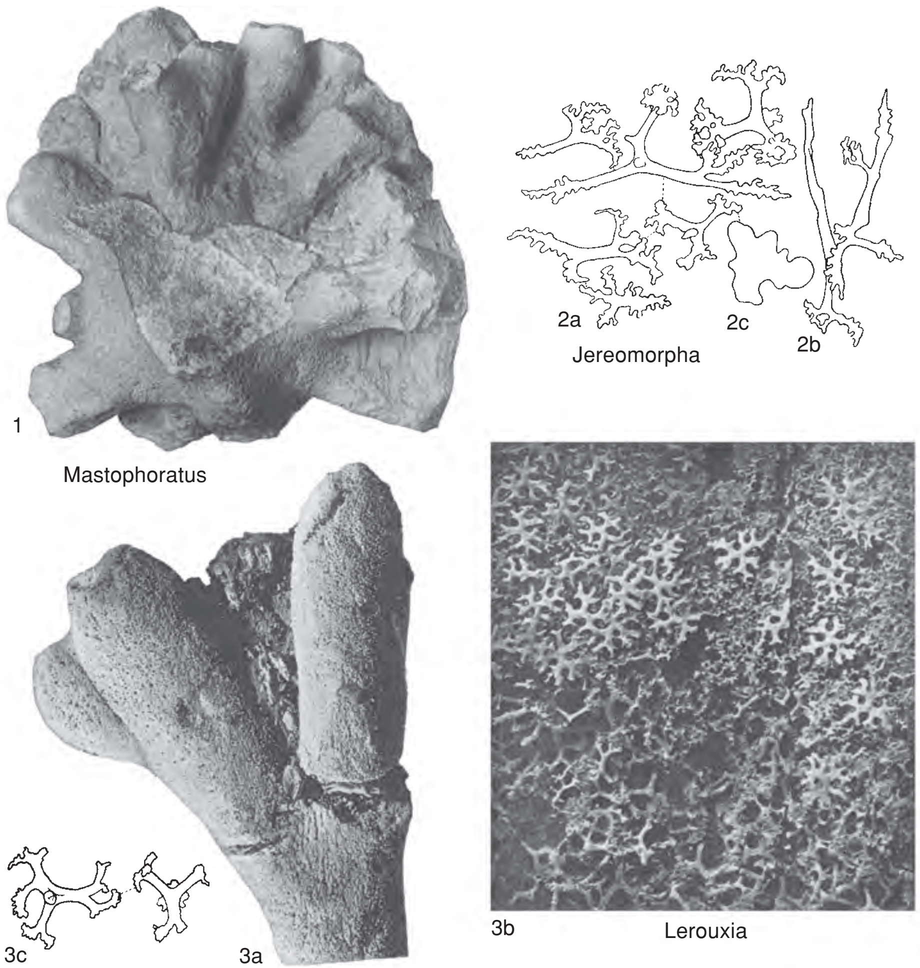

FIG. 146. Siphoniidae (p. 220).

?Tretotoechus OPPLIGER, 1915, p. 56 [**T. coniformis;* OD]. Narrow, top-shaped sponge with tubular, paragastral cavity; outside with large apertures, apparently of radial canals (epirhyses); aporhyses and postica not known, but summit with radiating furrows that may be incipient aporhyses; desmas smooth-armed tetraclones; no other spicules known. [Known only from poor material but apparently an early siphoniid with unusually large epirhyses, unless the lateral features are pseudogasters.] *Upper Jurassic:* Switzerland.——FIG. 145,*1a–b.* **T. coniformis,* Weiss Jura, Kimmeridgian, Aarau; *a,* side view of top-shaped holotype with distinct oscula on summit and ostia probably of large, radial canals on sides, ×1; *b,* photomicrograph of skeletal structure with tetraclones, ×50 (Oppliger, 1915).

Subfamily LEROUXIINAE Moret, 1926

[*nom. transl. et correct.* REID, herein, *ex* Le Rouxides MORET, 1926b, p. 172]

Jerea-like sponges with phyllotriaene dermalia; distinct epirhyses present or absent; long, tubular aporhyses in axial bundle; desmas smooth, regular tetraclones, or partly irregular and grading into elongate, monaxial variants; rhizoclonids present or absent; microscleres unknown. [This subfamily could be placed into the family Theonellidae VON LENDENFELD from the form of the dermalia, as they were by PISERA

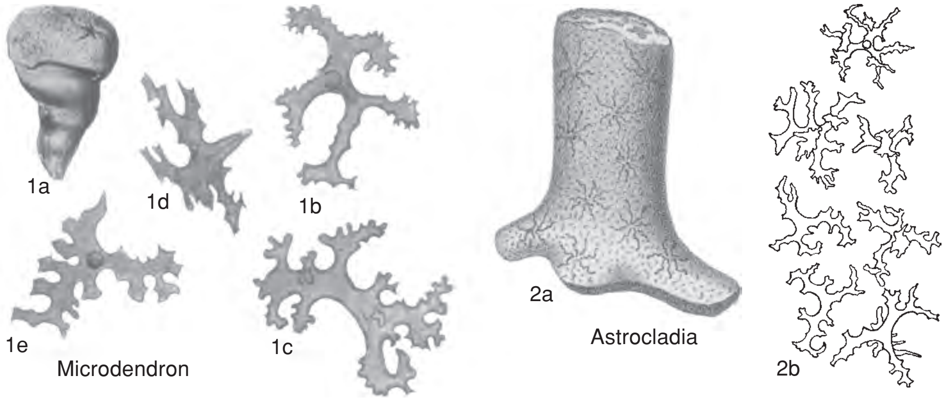

FIG. 147. Astrocladiidae (p. 221).

(2002, p. 402), but are here regarded as siphoniids from the character of the desmas.] *Upper Cretaceous (Cenomanian–Campanian).*

Lerouxia MORET, 1926b, p. 173 [**L. galloprovincalis;* OD]. Branched cylindrical with no paragastral cavity; sides with small, scattered ostia and locally with intersecting furrows in which additional ostia may occur at points of intersection; ends of branches with postica of long, tubular aporhyses that traverse axial parts in bundles; desmas mainly tetraclones, to which monaxial variants are added, and usually smooth armed but sometimes tuberculate; dermalia phyllotriaenes; rhizoclonids forming supplemental cortex; microscleres unknown. [In 1955 DE LAUBENFELS (p. 58) corrected the name from *Le Rouxia* MORET, 1926b.] *Cretaceous (Santonian):* France.——FIG. 146,*3a–c.* **L. galloprovincalis,* Saint-Cyr; *a,* side view of branched fragment showing ends of branches, ×1; *b,* surface showing phyllotriaenes, supplemental cortex, and some desmas of underlying framework, ×15; *c,* spicules including tetraclone and variant, phyllotriaenes, and rhizoclonid, magnification not stated, approximately ×45 (Moret, 1926b; courtesy of Société Géologique de France).

Jereomorpha MORET, 1926b, p. 174 [**J. cenomanense;* OD]. Club shaped or pyriform, stalked; summit rather flattened and with no paragastral depression; sides with numerous small ostia of radial epirhyses that curve downwardly toward interior; summit with postica of axial bundle of tubular aporhyses; some desmas regular tetraclones but others with arms of varying lengths, grading into elongate forms similar to those found in stalks of various other siphoniids; dermalia broadly trilobed phyllotriaenes; some rather large rhizoclonids present but not forming a cortex; microscleres unknown. *Cretaceous (Cenomanian):* France.——FIG. 146,*2a–c.* **J. cenomanense,* Sablons; characteristic spicules including tetraclones, irregular variants, and phyllotriaene, magnification not stated, approximately ×45 (Moret, 1926b; courtesy of Société Géologique de France).

?Mastophoratus REID, herein, *nom. nov. pro Mastophorus* SCHRAMMEN, 1924a, p. 54, *non* DIESING, 1853 [**Mastophorus arborescens* SCHRAMMEN, 1924a, p. 54; OD]. Radiating mass of more or less fused cylindrical branches; no paragaster, epirhyses, or ostia; each branch traversed by bundle of tubular aporhyses; desmas large, smooth tetraclones; dermalia unknown, but thought by SCHRAMMEN to be probably phyllotriaenes. [The genus is questionably included in the subfamily because the nature of dermalia is uncertain.] *Cretaceous (Campanian):* Germany.——FIG. 146,*1.* **M. arborescens* (SCHRAMMEN), Mukronatenkreide, Misburg; diagonal view of radiating, branched sponge, ×0.5 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Family ASTROCLADIIDAE Schrammen, 1901

[*nom. correct.* SCHRAMMEN, 1924a, p. 38, *pro* Astrocladidae SCHRAMMEN, 1901, p. 10]

Sponges with small, smooth-armed tetraclones as desmas and phyllotriaenes as dermal triaenes, when any are present; paragastral cavity absent; postica in stellate groups from which radiate short furrows; branched cylindrical in habit, with postica in lateral positions, or pyriform to cylindrical, simple or compound, with postica terminal; zygomes of desmas strongly branched, spiny; rhizoclonids forming supplemental cortex; microscleres unknown. [This is a small group of uncertain relationship, perhaps derived from a genus closely related to *Trachysycon* ZITTEL and

Myrmeciophytum SCHRAMMEN of the Siphoniidae (Phymatellinae). They were placed in the Theonellidae LENDENFELD, 1903, by PISERA (2002, p. 401).] *Upper Cretaceous (Cenomanian–Maastrichtian).*

Astrocladia ZITTEL, 1878a, p. 147 [**Asterospongia laevis* F. A. ROEMER, 1864, p. 54; SD DE LAUBENFELS, 1955, p. 57]. Narrow, cylindrical growths with no paragastral cavity, often branched dichotomously; exterior of skeletal framework with conspicuous, stellate features formed by small groups of skeletal pores presumed to be postica, and short, radiating furrows; intervening surface with ostia of short epirhyses; a few longitudinal aporhyses may be present in axial parts; desmas small tetraclones with very short, smooth, primary arms and strongly branched, spiny zygomes, passing into irregular, rhizoclone-like variants; rhizoclonids forming supplemental cortex, which may cover ostia and other lateral features when well developed; no dermal triaenes or microscleres known. [*Asterospongia* ROEMER, 1864, was listed by DE LAUBENFELS (1955, p. 65) as a separate genus, with the same type species. It is recommended that *Asterospongia sensu* DE LAUBENFELS not be used.] *Cretaceous (Cenomanian–Maastrichtian):* England, Germany, Poland, *Cenomanian–Turonian;* France, Germany, *Coniacian–Maastrichtian.*——FIG. 147,*2a.* **A. laevis* (F. A. ROEMER), Coniacian, Germany; side view of holotype, basal parts with stellate features and ostia, but without cortex, ×1 (Roemer, 1864).——FIG. 147,*2b. A. subramosa* (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; tetraclones and irregular, rhizoclone-like variants, ×30 (Schrammen, 1910).

Microdendron SCHRAMMEN, 1901, p. 10 [**M. ramulosum;* OD]. Solitary or compound; individuals pyriform to cylindrical, joined basally in compound examples; sides of skeletal framework with small ostia; stellate groups of postica and furrows on terminal parts, which may be rounded or flattened; desmas small tetraclones and rhizoclone-like variants, similar to those of *Astrocladia* ZITTEL; dermalia small phyllotriaenes with irregularly sculptured cladi; basal parts and sides covered by dense, supplemental cortex formed from small rhizoclonids that conceal ostia; microscleres unknown. *Upper Cretaceous (Campanian):* Germany.——FIG. 147,*1a–e.* **M. ramulosum,* Mucronatenkreide, Misburg; *a,* side view of club-shaped sponge, ×1; *b–e,* characteristic spicules including desmas and phyllotriaenes, ×50 (Schrammen, 1901).

Family PHYMARAPHINIIDAE Schrammen, 1910

[*nom. transl. et correct.* SCHRAMMEN, 1924a, p. 38, *ex* Phymaraphininae SCHRAMMEN, 1910, p. 34] [=Kaliapsidae DE LAUBENFELS, 1936, p. 175, *partim*]

Sponges with desmas in which base of each arm typically surrounded by annular swelling, and with dermal phyllotriaenes or discotriaenes; principal desmas tetraclones, triders, or both; arms of desmas typically smooth beyond basal annulation but sometimes tuberculate or with further annulations; reduced arms (brachyomes) of triders retain annular swelling and may either form buttonlike feature or have crepidal ray protruding through it; some forms with variant desmas in which two or three arms are aborted in this manner, or with elongate, radical desmas with diactinal or monaxial crepides; rhizoclonids frequent, sometimes forming supplemental cortex in which shafts of dermalia are imbedded; microscleres unknown. [This is a small, compact group presumably divergent from the same source as the Siphoniidae but distinguished by the annulated desmas and modified dermalia. The Upper Jurassic record is based on isolated desmas that have the characteristic annulation. The family is regarded here as not including the living *Calliopsis* BURBANK, in which annulation of arms is restricted to special basal triders.] *Lower Cretaceous (Aptian)–Upper Cretaceous.*

Phymaraphinia SCHRAMMEN, 1901, p. 8 [**P. infundibuliformis;* OD]. Funnel-like or flabellate with short stalk sometimes present at base; both surfaces of skeletal framework strongly sculptured by narrow, closely spaced furrows in which ostia or postica are located; furrows short, sinuous, and irregularly reticulating to elongate and subparallel, then typically radiating from base, but sometimes also changing direction abruptly in upper parts; desmas mainly tetraclones, in which arms are smooth beyond annulations, but including variant forms in which one to three arms are represented by buttonlike rudiments; dermalia phyllotriaenes; rhizoclonids present at both surfaces, sometimes forming dense, supplemental cortex that covers superficial furrows; microscleres unknown. *Cretaceous (Aptian–Maastrichtian):* Spain, *Aptian–Albian;* England, Germany, *Coniacian–Maastrichtian.*——FIG. 148,*2a–b.* **P. infundibuliformis,* Mucronatenkreide, Campanian, Misburg, Germany; *a,* side view of medium-sized, obconical type specimen, ×1; *b,* large fragment showing variation in form of superficial furrows, ×0.5 (Schrammen, 1910).

Compsapsis SOLLAS, 1880d, p. 387 [**C. cretacea;* OD]. Name based on isolated tetraclones with characteristic phymeraphiniid annulations. *Upper Cretaceous (Maastrichtian):* England.——FIG. 148,*3a–b.* **C. cretacea,* Trimmingham Chalk, Norfolk; type tetraclone spicules, scale uncertain (Sollas, 1880d).

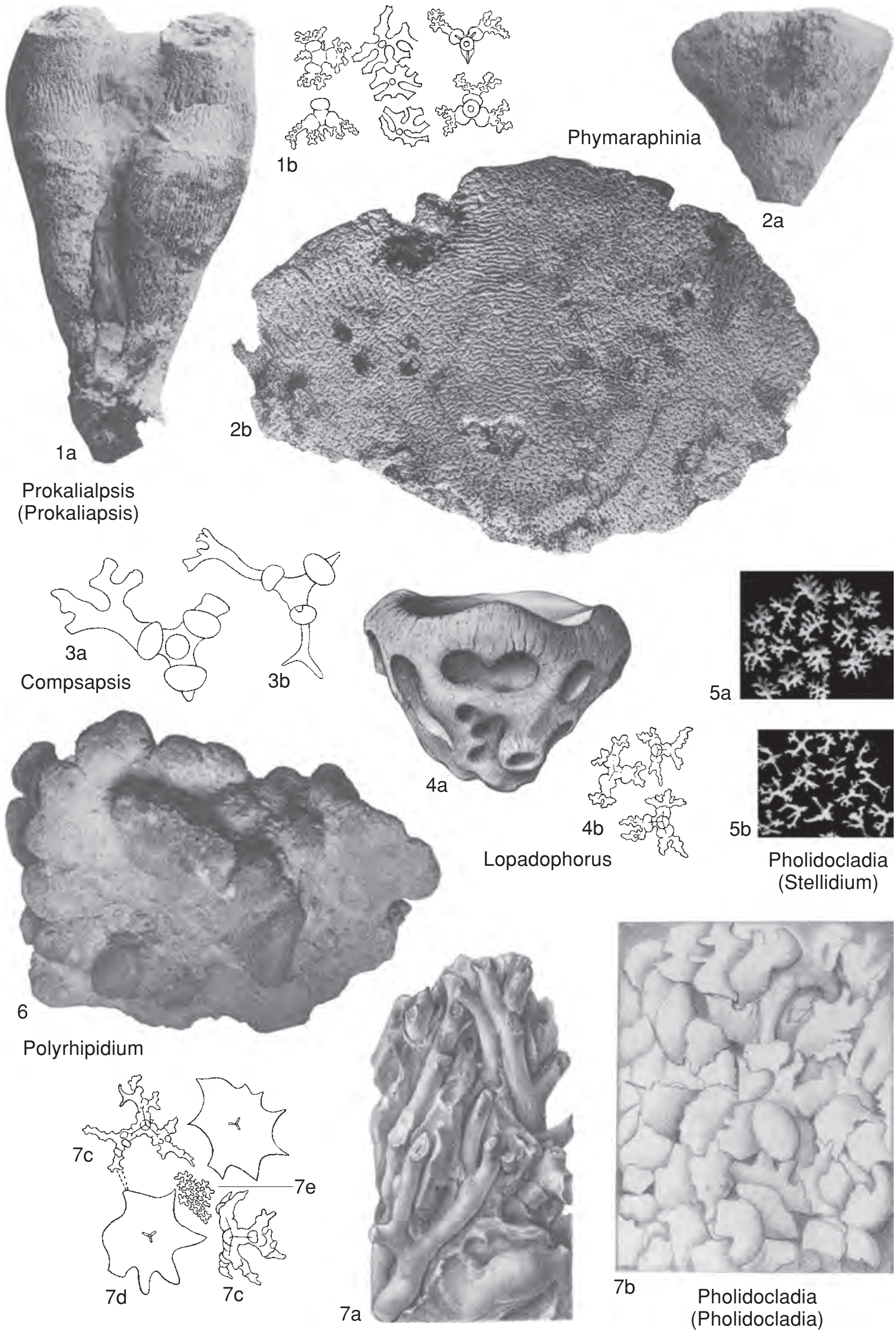

Fig. 148. Phymaraphiniidae (p. 221–224).

Cycloclema Schrammen, 1910, p. 105 [**Rhagadinia compressa* Hinde, 1884a, p. 82; OD]. Funnel-like, wide or narrow, sometimes laterally compressed, with short, basal stalk; expanded, encrusting base sometimes present; skeletal surfaces with apertures (ostia, postica) of tubular epirhyses and aporhyses that enter wall obliquely upward, often at upper ends of short, longitudinal furrows; desmas tetraclones with arms smooth beyond basal annulations and variants with one to three arms aborted; latter with suppressed arms represented by buttonlike rudiments; those near surface may be mainly triders, with buttonlike, short arm (brachyome) facing outwardly; rhizoclonids not recorded; dermalia phyllotriaenes; microscleres unknown. *Cretaceous (Campanian):* England, France, Germany, Poland.——Fig. 149*a–d. C. compressa* (Hinde), Quadratenkreide, Oberg, Germany; *a,* outside or lower surface with elongate ostia of canals that enter wall obliquely upward; *b,* inside or upper surface with circular, exhalant ostia in shallow grooves, ×0.5; *c–d,* characteristic spicules including desmas (tetraclone and trider) and dermal phyllotriaene, ×20 (Schrammen, 1910).

Lopadophorus Schrammen, 1910, p. 109 [**Oculispongia janus* F. A. Roemer, 1864, p. 48; SD de Laubenfels, 1955, p. 59]. Shape variable, for example, irregularly nodular, roughly globular, hemispherical, or top shaped with summit flat or concave, cup shaped, or related shapes; sides have more or less numerous large, hemispherical depressions, sometimes on prominences; base encrusting; fine, radiating furrows around some or all of lateral depressions and on paragastral margin when body is cuplike; summit or central cavity with pores presumed to be postica, from which short canals (aporhyses) run inwardly; sides with similar or smaller ostia; desmas tetraclones and triders, rather small; dermalia phyllotriaenes; rhizoclonids and cortex not recorded; microscleres unknown. *Cretaceous (Aptian–Maastrichtian):* Spain, *Aptian;* England, Germany, *Coniacian–Maastrichtian.*——Fig. 148,*4a.* **L. janus* (F. A. Roemer), Santonian, Sudmerberges near Goslar, Germany; side view with broad, upper osculum and irregular depressions on sides, ×0.5 (Schrammen, 1910).——Fig. 148,*4b. L. lacunosus* Schrammen, Quadratenkreide, Campanian, Oberg, Germany; representative triders, ×20 (Schrammen, 1910).

Pholidocladia Hinde, 1884a, p. 80 [**P. dichotoma;* SD de Laubenfels, 1955, p. 59]. Small, repeatedly branching growths with cylindrical or vermiform branches; no distinct epirhyses or ostia; ends of branches with one to several postica of tubular aporhyses that traverse branches, or without these features; desmas mainly triders with a buttonlike brachyome or with a crepidal ray projecting through basal annulation; skeletal meshwork usually very dense; dermalia phyllotriaenes or discotriaenes; rhizoclonids that may or may not form supplemental cortex; microscleres unknown. *Upper Cretaceous (Turonian–Campanian):* Europe.

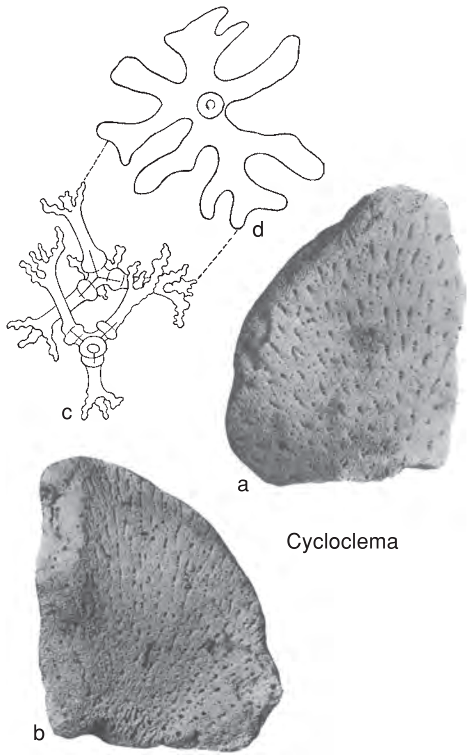

Fig. 149. Phymaraphiniidae (p. 223).

P. (**Pholidocladia**). Desmas tuberculate beyond their basal annulations; dermalia discotriaenes that range from marginally scalloped discs to irregularly ovate plates; rhizoclonids sometimes present. *Cretaceous (Turonian–Campanian):* Germany, England; France, *Santonian–Campanian.*——Fig. 148,*7a–e.* **P. (P.) dichotoma; a,* repeatedly branched specimen preserved in flint, Upper Chalk, Wiltshire, England, ×0.5; *b,* dermal skeleton showing overlapping discotriaenes, Upper Chalk, Wiltshire, England, ×50 (Hinde, 1884b); *c–e,* typical spicules including desmas, discotriaenes, and rhizoclonids, Quadratenkreide, Campanian, Oberg, Germany, ×20 (Schrammen, 1910).

P. (**Stelidium**) Schrammen, 1924a, p. 55 [**S. vermiculare;* OD]. Arms of desmas smooth beyond basal annulations; dermalia phyllotriaenes, rhizoclonids unknown. *Cretaceous (Campanian):* Germany.——Fig. 148,*5a–b.* **P. (S.) vermiculare,* Mukronatenkreide, Misburg; *a,* phyllotriaenes; *b,* desmas, triders, and irregular variants, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Polyrhipidium Schrammen, 1924a, p. 54 [**P. cristagalli;* OD]. Clump of intergrown, subcylindrical stems or lateral branches; crest of cluster with numerous round postica; ostia on margins are scarce; supporting skeleton made of small tetraclones, each with a ring or bulge near center of ray divergence; dermalia unknown. *Cretaceous (Santonian):* Germany.——FIG. 148,*6.* **P. cristagalli,* Emscher beds, Sudmerberges; side view of clumped sponge, ×1 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Prokaliapsis SCHRAMMEN, 1901, p. 7 [**P. cylindrica;* SD DE LAUBENFELS, 1955, p. 59; =*Rhagadinia clavata* HINDE, 1884a, p. 84, subj.] [=*Procaliapsis* SCHRAMMEN, 1910, p. 108, *nom. null.*]. Globular, club shaped, cylindrical, or branched cylindrical, with unbranched forms sometimes in groups; no paragastral cavity; sides finely furrowed, with furrows of various directions but often subparallel locally and with widely scattered ostia from which short epirhyses run inwardly; summit(s) with postica of bundle of longitudinal aporhyses that traverse axial parts; desmas tetraclones and variants without one or more arms in interior, but as triders near surface, with buttonlike rudiment facing outwardly; dermalia phyllotriaenes; supplemental cortex over parts of surface; microscleres unknown. *Lower Cretaceous (Aptian)–Upper Cretaceous:* Europe.

P. (**Prokaliapsis**). Comprises species that are typically solitary, although individuals sometimes grow in groups. *Lower Cretaceous (Aptian)–Upper Cretaceous:* Spain, *Aptian;* France, *Santonian–Campanian;* Germany, *Campanian;* England, *Upper Cretaceous.*——FIG. 148,*1a–b.* **P. (P.) clavata* (HINDE), Quadratenkreide, Campanian, Oberg, Germany; *a,* example of two steeply obconical individuals that have arisen from common base, ×1; *b,* characteristic spicules including triders and phyllotriaenes, ×20 (Schrammen, 1910).

Family THEONELLIDAE von Lendenfeld, 1904

[Theonellidae VON LENDENFELD, 1904c, p. 126] [=Discodermiidae SCHRAMMEN, 1924a, p. 37, *nom. correct. pro* Discoderminae SCHRAMMEN, 1910, p. 97]

Sponges typically with desmas that are strongly tuberculate tetraclones and with dermal phyllotriaenes or discotriaenes; but including apparently related forms showing different conditions in which desmas are mainly or all smooth or spinose, or are partly forms with less than four arms, or the normal dermalia are replaced by dichotriaenes or siliceous discs; desmas never exclusively triders; rhizoclonids present or absent, where present sometimes comprising a supplemental cortex; microscleres of modern forms all microrhabds, or including plesiasters, metasters, spirasters, or amphiasters; spirasters in one fossil genus. [The modern family type *Theonella* GRAY comprises species in which the desmas are typically nontuberculate; but the holotype of the type species, *T. swinhoei* GRAY, has strongly tuberculate desmas in the lower parts. The type species of *Discodermia* DU BOCAGE, *D. polydiscus* DU BOCAGE, is also not a sponge of the type called *Discodermia* by SCHRAMMEN (1910) and MORET (1926b) but a form here thought similar to *Theonella* and separable perhaps only subgenerically. The Acrochordoniidae, as proposed by *Schrammen* (1924a), is included in the Theonellidae as a subfamily.] *Lower Cretaceous–Holocene.*

Subfamily THEONELLINAE von Lendenfeld, 1904

[*nom. transl.* REID, herein, *pro* Theonellinae VON LENDENFELD, 1904c, p. 126]

Modern Theonellidae in which rhizoclonids are absent, and similar fossils in which they appear to be absent; microscleres of modern forms microrhabds only, or including plesiasters, metasters, spirasters, or amphiasters. [The subfamily should possibly include forms placed here in the family Protetraclisidae SCHRAMMEN (Upper Jurassic).] *Lower Cretaceous–Holocene.*

Theonella GRAY, 1868b, p. 565 [**T. swinhoei* GRAY, 1868b, p. 566; OD]. Cup- or funnel-like, thick walled, or clublike, with a tubular, central cavity that extends to base; outside smooth or with irregular, nodular or shelflike projections; external surface of skeletal framework with scattered ostia, from which tubular epirhyses run in radially or obliquely; paragastral surface with similar or larger postica of aporhyses that usually branch within wall; desmas typically long-armed tetraclones, with zygomes sometimes slightly developed and usually smooth, but sometimes more or less strongly tuberculate in basal parts; dermalia typically slender phyllotriaenes with distinct protocladi and curving branches, arranged to enclose rounded, porelike interspaces; some also with zygomelike articulations on cladi but not on rhabdal shafts; rhizoclonids absent; microscleres microrhabds only. [Doubtful Eocene record based on isolated phyllotriaenes (HINDE & HOLMES, 1892).] *Paleogene (?Eocene), Holocene:* New Zealand, *?Eocene;* cosmopolitan, *Holocene.* ——FIG. 150,*1.* isolated phyllotriaene ascribed to *Theonella* GRAY, ×40 (Hinde & Holmes, 1892).

Colossolacis SCHRAMMEN, 1910, p. 103 [**C. plicata;* OD]. Basically funnel shaped but with wall irregularly plicated, and with folds anastomosing, base with rootlike processes; outside with numerous small ostia; gastral surfaces with similar postica and larger apertures of pitlike cavities; desmas mainly smooth-armed tetraclones, to which amphitrider-like variants may be added; rhizoclonids apparently absent; microscleres unknown. *Cretaceous (Campanian):* Germany.——FIG. 151,*1a–d*. **C. plicata,* Quadratenkreide, Oberg; *a,* lower surface of plicated to digitate sponge; *b,* upper surface of same, ×0.25; *c,* fragment in spicular preservation with postica and other apertures of paragastral surface, ×0.5; *d,* typical tetraclone desmas, ×20 (Schrammen, 1910).

Discodermia DU BOCAGE, 1869, p. 160 [**D. polydiscus;* OD] [?=*Rhoptrum* SCHRAMMEN, 1910, p. 104 (type, *R. scytaliforme,* OD); *?Leiophyllum* SCHRAMMEN, 1924a, p. 52 (type, *L. panniculosum,* OD); *?Nedlandsia* DE LAUBENFELS, 1953b, p. 113 (type, *N. clarkei,* OD)]. Typically cuplike or funnel-like, sometimes in groups, but may be flabellate or pass into other shapes; outside with small ostia, from which simple or branching epirhyses run into skeletal framework; paragastral surface with larger postica of similar aporhyses with more or less prominent rims in some species; desmas mainly or all tetraclones, to which irregular variants may be added, and typically tuberculate but sometimes smooth armed or more or less spinose; irregular tetraclone variants sometimes triodal or diaxial; dermalia phyllotrianes, discotriaenes, or both, and intermediates; discotriaenes typically arranged to form overlapping pavement, overlapped spicules may have marginally notched discs grown around shafts of other spicules; no rhizoclonids; microscleres microrhabds only. [Other supposed records based on form are referred here to other genera.] *?Upper Cretaceous, Paleogene (?Eocene), Neogene (Miocene)–Holocene:* Germany, *?Upper Cretaceous;* Australia, New Zealand, *?Eocene;* Spain, ?Northern Africa, *Miocene;* cosmopolitan, *Holocene.*——FIG. 150,*3a–b*. **D. polydiscus,* Holocene, Atlantic Ocean, Portugal; *a,* side view of small sponge with irregular nodes, ×1; *b,* dermal spicules, ×100 (du Bocage, 1869).——FIG. 150,*3c*. *D.* sp., Eocene, Otago, New Zealand; discotriaene ascribed to *Discodermia* sp., ×100 (Hinde & Holmes, 1892).——FIG. 150,*3d*. *D. sinuosa* CARTER, Eocene, Otago, New Zealand; phyllotriaene ascribed to modern species, ×100 (Hinde & Holmes, 1892).

Leiophyllum SCHRAMMEN, 1924a, p. 52 [**L. panniculosum;* OD]. Flabellate, forming irregularly lobate plate; surfaces with anastomosing furrows and irregular, skeletal pores; desmas tuberculate tetraclones; dermalia phyllotriaenes; rhizoclonids apparently absent; microscleres unknown. [Acceptable as a true *Discodermia* if rhizoclonids were absent and microscleres were microrhabds.] *Cretaceous (Campanian):* Germany.——FIG. 150,*2*. **L. panniculosum,* Quadratenkreide, Höver; irregularly lobate sponge, ×0.50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

?Placoscytus SCHRAMMEN, 1910, p. 101, *nom. nov. pro Sollasella* SCHRAMMEN, 1901, p. 6, *non* VON LENDENFELD, 1887 [**Sollasella jereaeformis* SCHRAMMEN, 1901, p. 6; OD]. Simple or compound, stalked; individuals top shaped to cylindrical, with summit rounded, truncated, or slightly hollowed; sides with shallow, sinuous, anastomosing furrows and small ostia, which occur both within furrows and between them; summit(s) with postica of tubular aporhyses, which run downwardly through body; desmas smooth and slightly tuberculate tetraclones; dermalia siliceous plates with denticulated margins; rhizoclonids apparently absent; microscleres unknown. [Dermalia interpreted as discotriaenes by SCHRAMMEN, 1910, but axial canals not certainly present.] *Cretaceous (Campanian):* Germany.——FIG. 151,*5a–d*. **P. jereaeformis* (SCHRAMMEN), Quadratenkreide, Misburg; *a,* stalked, compound example with

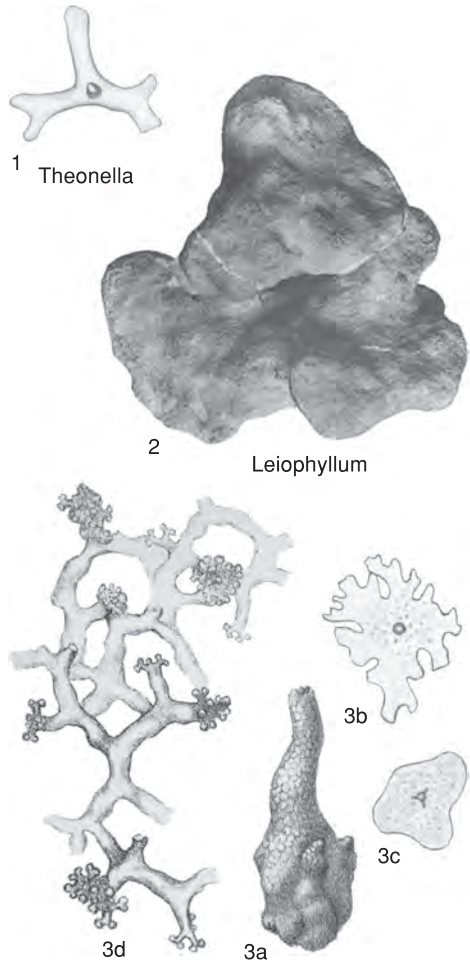

FIG. 150. Theonellidae (p. 224–225).

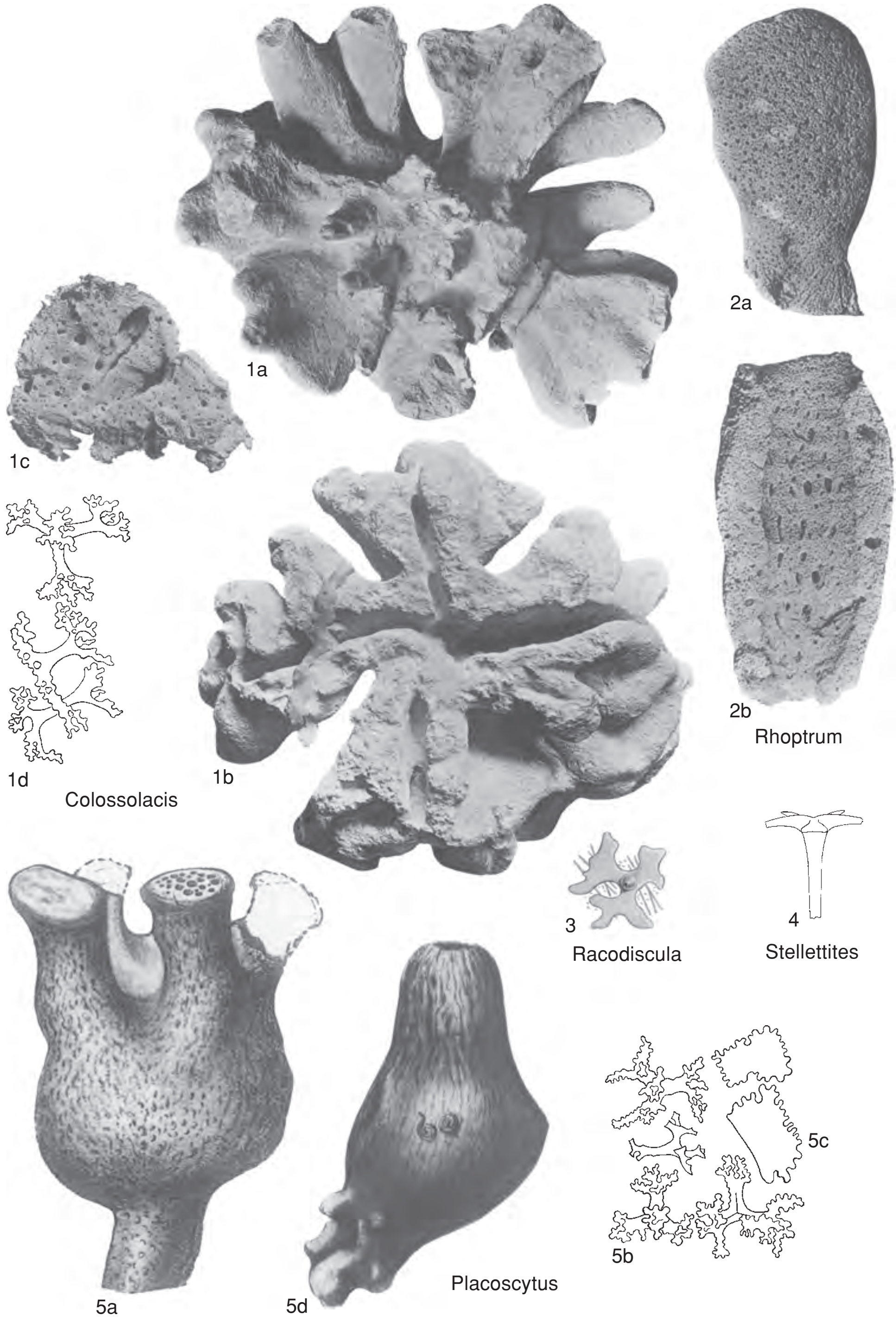

FIG. 151. Theonellidae (p. 224–227).

cylindrical, upper branches, ×1; *b–c,* characteristic spicules including tetraclones and dermal plates ×20 (Schrammen, 1910); *d,* solitary example, ×1 (Schrammen, 1901).

Racodiscula ZITTEL, 1878a, p. 151 [**Corallistes polydiscus* SCHMIDT, 1870, p. 24; =*R. asteroides* ZITTEL, 1878a, p. 151 (ascribed to CARTER, 1873, p. 441); SD DE LAUBENFELS, 1955, p. 58, as *C. asteroides* CARTER]. Nodular, club shaped or cylindrical, with no paragastral cavity; summit with postica of vertical, tubular aporhyses; ostia apparently absent; dermalia discotriaenes with simple, lobate, or denticulated margins; desmas irregular tetraclones, not markedly tuberculate; rhizoclonids absent; microscleres microrhabds, plesiasters, metasters, spirasters, or amphiasters. [Supposed *Cretaceous* record by ZITTEL, 1878a, based on isolated dermalia, also claimed by SOLLAS (1880d) to represent dicranocladine *Macandrewia* GRAY. The name *asteroides* ascribed to CARTER by ZITTEL and DE LAUBENFELS was not proposed as the name of a species but mentioned as an alternative MS name on a slide of *C. polydiscus* supplied by SCHMIDT (see CARTER, 1873, p. 442).] *?Cretaceous; Holocene:* cosmopolitan.——FIG. 151,*3. R.* sp., Holocene, Philippine Islands; isolated, lobate, dermal discotriaene, ×30 (Zittel, 1878a).

Rhoptrum SCHRAMMEN, 1910, p. 104 [**R. scytaliforme;* OD]. Pyriform, club shaped or cylindrical, with paragastral cavity extending to base; exterior with small, rounded ostia; no epirhyses; paragastral surface with larger postica of short aporhyses, which enter wall obliquely upward; desmas more or less irregular tetraclones, smooth or tuberculate; dermalia phyllotriaenes; rhizoclonids unknown; microscleres unknown. [Acceptable as *Discodermia sensu* DU BOCAGE if rhizoclonids were absent and microscleres were microrhabds.] *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* Germany, *Campanian.*——FIG. 151,*2a–b.* **R. scytaliforme,* Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of club-shaped specimen; *b,* longitudinal section of subcylindrical specimen showing relatively thin walls and coarse, exhalant ostia in gastral surface of broad spongocoel, ×1 (Schrammen, 1910).

Stellettites CARTER, 1871, p. 129 [**S. haldonensis;* OD]. Spicules resembling those of *Dactylocalycites* but with rays spread horizontally or laterally and branches somewhat recurved. *Lower Cretaceous:* Europe.——FIG. 151,*4.* **S. haldonensis,* Upper Greensand, Exeter; isolated spicule, ×25 (Carter, 1871).

Subfamily ACROCHORDONIINAE Schrammen, 1910

[*nom. correct.* REID, herein, *pro* Acrochordoninae SCHRAMMEN, 1910, p. 33; *emend.,* REID, herein] [=Acrochordoniidae SCHRAMMEN, 1924a, p. 38]

Theonellidae with rhizoclonids that often form a supplemental cortex and with dermalia that are sometimes dichotriaenes, but typically phyllotriaenes or discotriaenes; canal systems commonly like those of *Siphonia* or *Jerea* of family Siphoniidae, but sometimes of other types; microscleres unknown. [The subfamily was proposed by SCHRAMMEN, 1910 for *Acrochordonia* only, in which dermalia are dichotriaenes. This genus is here regarded as similar to *Phyllodermia* SCHRAMMEN, in which dermalia are slightly modified dichotriaenes in the subgenus *Cladodermia* SCHRAMMEN. The type genus was placed into the suborder Dicranocladina by LAGNEAU-HÉRENGER (1962) but is a true tetracladine.] *Lower Cretaceous (Aptian)–Neogene (Miocene).*

Acrochordonia SCHRAMMEN, 1901, p. 6 [**A. ramosa;* OD]. Branched cylindrical, irregularly nodular, funnel-like, or flabellate with lobate margins, or in intermediate shapes; postica open in a number of shallow depressions, usually on upper surface when one is apparent; ostia scattered over other parts of surface; tubular aporhyses radiating from groups of postica, with outermost imperfectly enclosed and forming radiating furrows; desmas strongly tuberculate tetraclones; rhizoclonids sometimes possibly present; dermalia dichotriaenes; microscleres unknown. [Rhizoclonids claimed by MORET (1926b, p. 175) in generic diagnosis, but not described in any species.] *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* France, *Santonian;* Germany, Poland, *Campanian.*——FIG. 152,*4a–c.* **A. ramosa,* Quadratenkreide, Campanian, Oberg, Germany; *a,* example with three nodular lobes radiating from common stalk, ×0.5; *b–c,* representative spicules including desmas and dichotriaenes, ×20 (Schrammen, 1910).

Achrochordiella RIGBY, 1981, p. 129 [**A. vokesi* RIGBY, 1981, p. 130; OD]. Massive, lobate to anastomosing or branched, fingerlike sponges; principal skeleton of small to medium-sized, warty tetraclones; dermalia characteristic dichotriaenes or modifications of dichotriaenes that may have lost one or two primary or secondary branches; phyllotriaenes rare; surfaces marked by moderately indented, strong, somewhat anastomosing but generally nearly vertical canals; individual branches without spongocoel and relatively dense. *Paleogene (Eocene):* USA (North Carolina).——FIG. 152,*3a–l.* **A. vokesi,* Castle Hayne Limestone, Wayne County; *a,* side view of branched holotype, USNM 252489, ×0.5; *b,* photomicrograph of principle, skeletal net with nodes formed by junctions of tetraclone, ray tips, ×10; *c,* dichotriaenes of dermal net, ×20; *d–l,* characteristic spicules including *d–f,* dichotriaenes of dermal net, *g–h,* simple orthotriaenes, *i–j,* knobby tetraclones, and *k–l,* bladed phyllotriaenes,

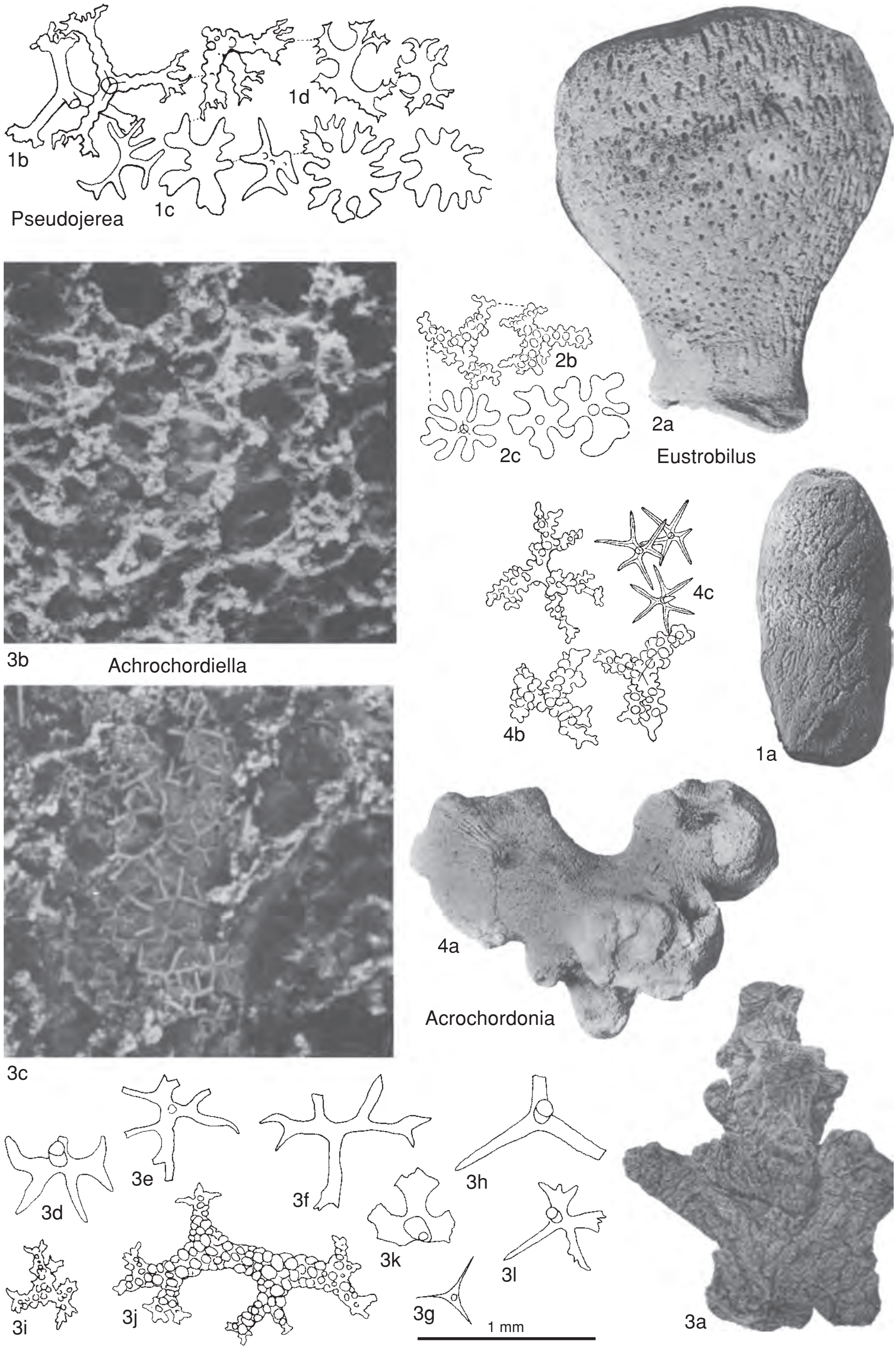

FIG. 152. Theonellidae (p. 227–230).

×25 (Rigby, 1981; courtesy of *Tulane Studies in Geology and Paleontology*).

Eustrobilus Schrammen, 1910, p. 102 [**E. callosus;* OD]. Top shaped or cylindrical with the summit truncated, short stalked; base encrusting or dividing into processes; paragastral cavity deep, narrow; outside with numerous rounded ostia from which short furrows commonly run downwardly; paragastral wall with simple postica; epirhyses and aporhyses deep and overlapping within wall; inceptional examples of both form radiating furrows around paragastral margin; desmas tuberculate tetraclones; dermalia phyllotriaenes; rhizoclonids apparently absent. [Absence of rhizoclonids is queried because a cortex appears to be present in Schrammen's (1910) figured material.] *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* France, *Santonian;* Germany, Poland, *Campanian.*——Fig. 152,*2a–c.* **E. callosus,* Quadratenkreide, Campanian, Oberg, Germany; *a,* side view of club-shaped example with circular ostia above grooves, ×1; *b–c,* characteristic spicules including desmas and phyllotriaenes, ×20 (Schrammen, 1910).

Phyllodermia Schrammen, 1924a, p. 48 [**Discodermia antiqua* Schrammen, 1901, p. 5; OD; not *Phyllodermia spinosa* Schrammen, 1924a, p. 50, SD de Laubenfels, 1955, p. 58]. Solitary in normal individuals but sometimes in groups; individuals pyriform to cylindrical, top shaped, discoidal, or other related shapes; paragaster varies from shallow depression to deep, central cavity; encrusting base, multiple root processes, or no evident attachment; external surfaces of skeletal framework with small ostia or open meshes only and sometimes furrowed in varying directions; paragastral surface with postica of aporhyses, unless these veiled by superficial accretion of desmas; aporhyses vertical in axial parts but arch outwardly away from them with highest ones sometimes horizontal or sloping upwardly according to body form; incompletely enclosed aporhyses may form conspicuous furrows around paragastral margin; desmas tetraclones, all tuberculate or including smooth examples; usually with supplemental cortex formed from flattened rhizoclonids; microscleres unknown. [For Schrammen's original designation of the type species, see the paragraph before his (1924a) formal diagnosis. Diagnosis combines characters of *Phyllodermia sensu* Schrammen and *Cladodermia* Schrammen, here regarded as subgenera.] *Cretaceous (Aptian–Santonian), Paleogene (?Eocene):*

P. (Phyllodermia). Dermalia normal phyllotriaenes; paragastral cavity typically shallow, sometimes obsolete; with encrusting base, multiple root processes, or no evident attachment. *Cretaceous (Aptian–Campanian):* Spain, *Aptian;* France, *Santonian;* Germany, *Campanian.*——Fig. 153,*1a–d.* **P. (P.) antiqua* (Schrammen), Quadratenkreide, Campanian, Oberg, Germany; *a,* vertically sectioned example showing spongocoel with aporhyses and postica veiled by accretion of desmas of gastral layer, ×1; *b–d,* spicules including *b,* smooth-armed tetraclones and a triodal variant, *c,* tuberculate tetraclone, and *d,* a dermal phyllotriaene, ×20 (Schrammen, 1910).——Fig. 153,*1e. P. (P.) stellata* (Moret), Santonian, Saint-Cyr, France; obconical sponge with shallow, paragastral cavity and prominent, radial structure and canals, ×1 (Moret, 1926b; courtesy of Société Géologique de France).

P. (Cladodermia) Schrammen, 1924a, p. 51 [**Discodermia colossea* Schrammen, 1910, p. 98; OD]. Dermalia finely branched phyllotriaenes in which cladi are not markedly flattened and terminal branches are pointed; paragastral cavity deep, tubular; base encrusting. *Cretaceous (Aptian–Campanian), Paleogene (?Eocene):* Spain, *Aptian;* England, *?Albian;* Germany, *Campanian;* New Zealand, *?Eocene.*——Fig. 153,*4a.* **P. (C.) colossea* (Schrammen), Mukronatenkreide, Campanian, Misburg, Germany; dermal phyllotriaene, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).——Fig. 153,*4b–c. P. (C.)* type, ?Eocene, Otago, New Zealand; phyllotriaenes, ×40 (Hinde & Holmes, 1892).

Pliegatella Brimaud & Vachard, 1986, p. 305 [**P. genovefae;* OD]. Sponges with branched, stalked, or asymmetric and irregular growth; both short and long ranches have rounded or flattened ends, never depressed or ending in apochetes; exhalant system is often indistinct; inhalant canals have little bifurcation; surface is rough on a small scale because of warty swellings of exposed desmas that are large tetraclones, which may be locally smooth, and some very typical dicranoclones; cortical skeleton not observed. [*Pliegatella* differs from *Achrochordiella* in growth form, rarity of radial canals, and the large size of its tetraclones and their close packing.] *Neogene (Miocene):* Spain.——Fig. 153,*3a–b.* **P. genovefae,* Tortonian strata, upper Miocene, Pliego, southern Spain; *a,* side view of irregularly branched sponge with large tetraclones in upper right, IPM R6941, ×0.5; *b,* photomicrograph of typical tetraclones with nodular sculpture, IPM R6948, ×50 (Brimaud & Vachard, 1986; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Pseudojerea Moret, 1926b, p. 181 [**P. massiliensis;* SD de Laubenfels, 1955, p. 58]. Pyriform to club shaped, or cylindrical with irregular, radial lobes; paragastral cavity deep to shallow or absent; sides with ostia and sometimes reticulating furrows; some with vertical aporhyses only, which open at conical apex or in shallow depression; others with additional lateral aporhyses that open in vertical series in walls of distinct paragaster; size of ostia and postica similar; desmas smooth and tuberculated tetraclones and tuberculate triders; dermalia phyllotriaenes and forming gradational to discotriaenes; lower parts covered by supplemental cortex, formed from large rhizoclonids; microscleres unknown. *Cretaceous (Santonian):* France.——Fig. 152,*1a–d.* **P. massiliensis,* Saint-Cyr; *a,* pyriform sponge with shallow, apical (paragastral) depression and reticulated furrows on flanks with scattered ostia in upper

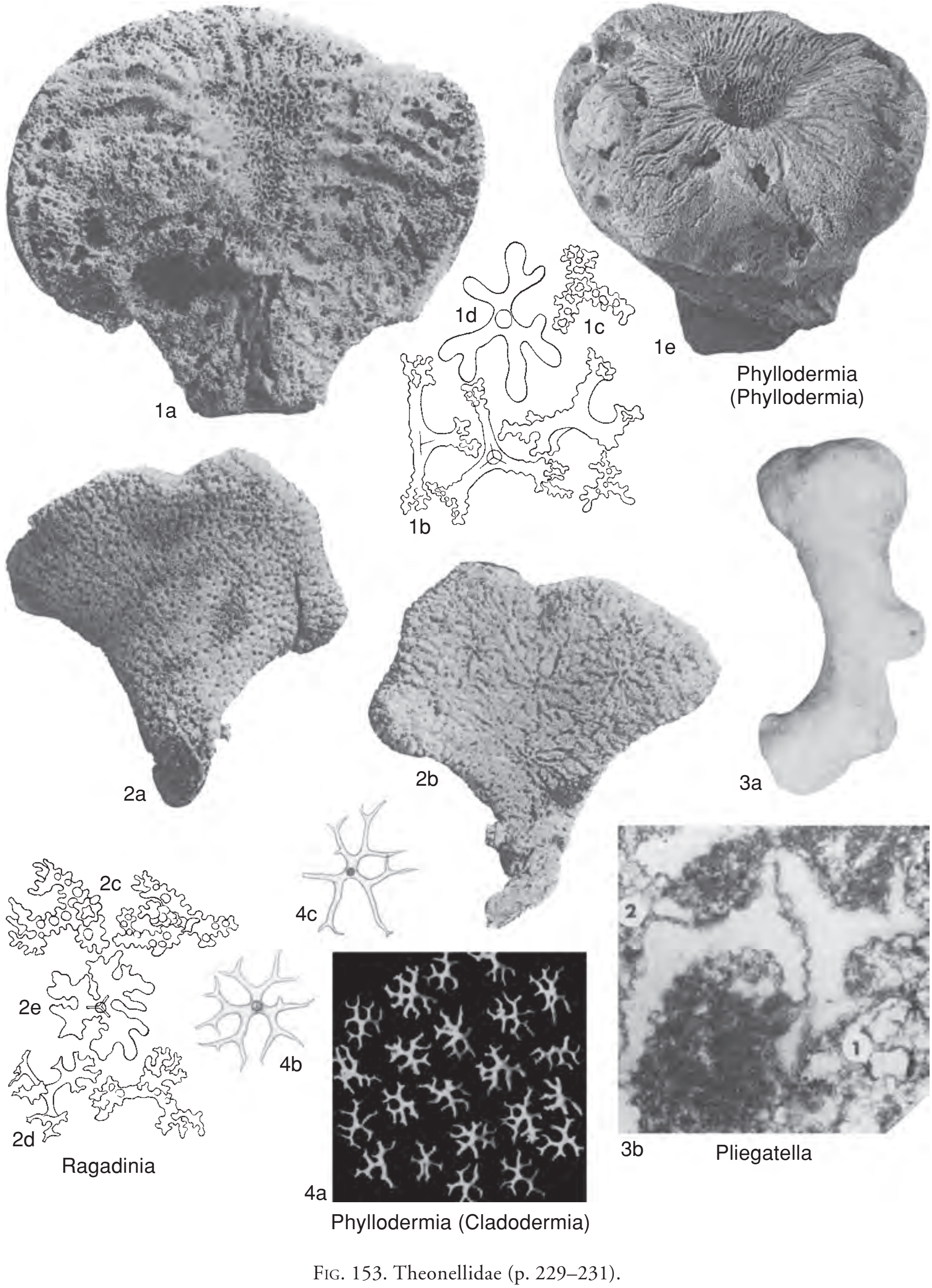

FIG. 153. Theonellidae (p. 229–231).

parts, slightly reduced; *b–d,* characteristic spicules including tetraclones, trider, and cortical rhizoclonids, magnification not stated but approximately ×40 (Moret, 1926b; courtesy of Société Géologique de France).

Ragadinia ZITTEL, 1878a, p. 152 [**Cupulospongia rimosa* F. A. ROEMER, 1864, p. 51; OD] [=*Rhagadinia* SCHRAMMEN, 1910, p. 100, obj., *nom. null.*]. Funnel or bowl-like, or in flabellate shapes; stalked or sessile; exterior of skeletal framework with radiating network of fine, irregular furrows in which ostia are located, or with closely spaced and irregularly interconnected ostia; paragastral surface sometimes similar, but typically with postica in groups

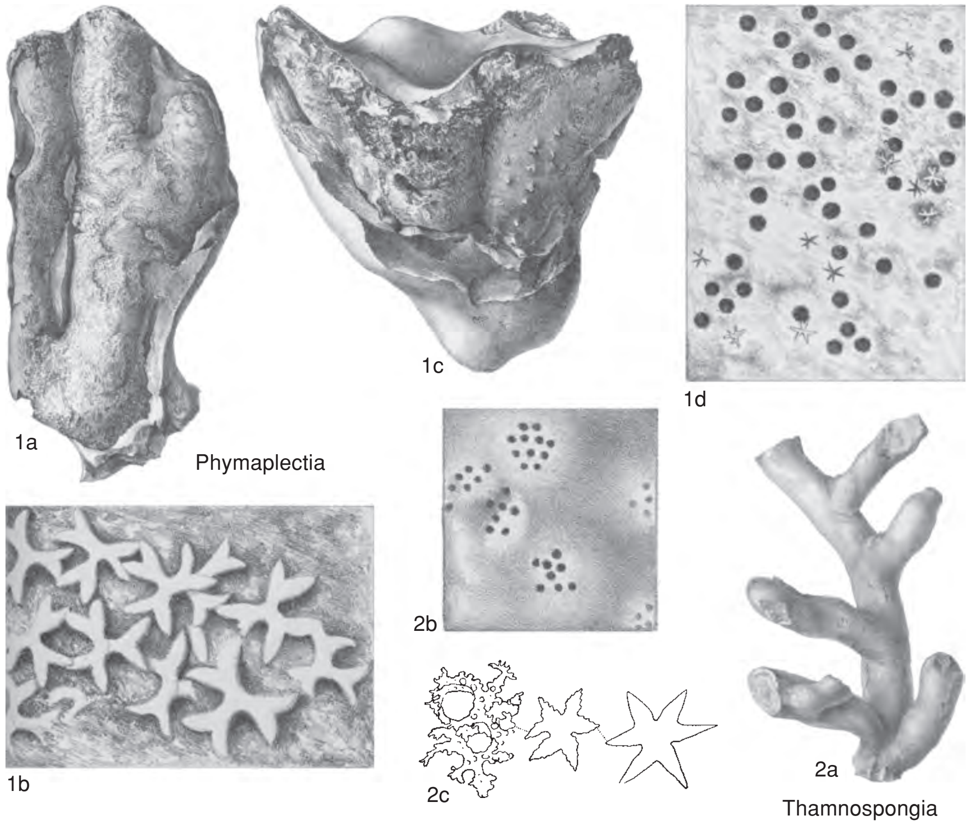

FIG. 154. Theonellidae (p. 231–232).

from which some furrows radiate; epirhyses and aporhyses short; postica groups sometimes in shallow depressions; without postica and external furrows in some variants, although paragastral furrows still present; desmas tuberculate tetraclones and smooth or partly smooth variants; dermalia phyllotriaenes; rhizoclonids forming supplemental cortex on both sides of skeletal framework, whose surfaces are concealed unless cortex is lost; supplemental cortex of gastral side sometimes forming small, conical elevations over groups of postica; microscleres unknown. [*Ragadinia* spp. of HINDE (1884a, Upper Chalk, England) are Phymaraphiniidae: *cf.* SCHRAMMEN, 1910.] *Cretaceous (Cenomanian–Campanian):* Czech Republic, Slovakia, *Cenomanian;* France, *Santonian;* Germany, Poland, *Campanian.*——FIG. 153,*2a–e.* **R. rimosa* (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; *a,* inhalant surface of flabellate example with evenly distributed, inhalant ostia, ×1; *b,* exhalant surface of same specimen with grooves radiating from several centers, ×1; *c–e,* characteristic spicules including tuberculate desmas, smooth and partly smooth variants, one of which is probably a young form, and phyllotriaene, ×20 (Schrammen, 1910).

Subfamily PHYMAPLECTIINAE new subfamily

[Phymaplectiinae REID, herein] [type genus, *Phymaplectia* HINDE, 1884a, p. 87]

Dermalia dichotriaenes with slightly flattened cladi or dichotriaene-like phyllotriaenes; rhizoclonids present, sometimes forming a supplemental cortex that may be pierced by conspicuous, intracortical pores; spiraster microscleres in one fossil (Eocene) species. [This is a small group distinguished chiefly by distinctive dermalia.] *Upper Cretaceous–Paleogene (Eocene).*

Phymaplectia HINDE, 1884a, p. 87 [**P. irregularis;* SD DE LAUBENFELS, 1955, p. 56]. Flabellate and leaf shaped to digitate, or irregularly convoluted, or assuming secondary funnel shape through union of infolded margins; thin walled; skeletal pores and canals absent or sparsely developed; surfaces sometimes with irregular furrows that may radiate from small, conical prominences on one surface; desmas more or less irregular, tuberculate tetraclones and triders; dermalia sometimes simple dichotriaenes, but typically phyllodichotriaenes with flattened cladi; supplemental cortex formed by small rhizoclonids; cortex sometimes pierced by intracortical pores; microscleres unknown. *Upper Cretaceous, Paleogene (?Eocene):* England; France, *Santonian;* Western Australia, *?Eocene.*——FIG. 154,*1a–b.* **P. irregularis,* Upper Chalk, Santonian, Wiltshire, England; *a,* side view of specimen in flint, ×0.5; *b,* dermal surface showing phyllodichotriaenes, ×25 (Hinde, 1884a).——FIG. 154,*1c. P. spinosa* HINDE, Upper Chalk, Santonian, Wiltshire, England; surface of skeletal framework, ×25 (Hinde, 1884a).——FIG. 154,*1d. P. cribrata* HINDE, Upper Chalk, Santonian, Wiltshire, England; surface showing cortex, intracortical ostia, and small dichotriaenes, ×25 (Hinde, 1884a).

Thamnospongia HINDE, 1884a, p. 78 [**T. glabra;* SD DE LAUBENFELS, 1955, p. 59]. Branched cylindrical, with single, upright stem and lateral branches, or forming bushlike group of cylindrical branches, some of which may more or less coalesce; lateral branches sometimes rudimentary or represented only by conical prominences; ends of branches with one or more postica of tubular, longitudinal aporhyses that traverse axial parts; no other skeletal pores; desmas small tetraclones and irregular variants, strongly tuberculate; dermalia dichotriaenes with slightly flattened cladi, or well-developed dichophyllotriaenes; sometimes with supplemental cortex formed from small rhizoclonids and pierced by intracortical pores, which may be in groups; spiraster microscleres in one Eocene species. *Upper Cretaceous–Paleogene (Eocene):* England, *Upper Cretaceous;* France, *Santonian;* Germany, *Campanian;* Western Australia, *Eocene.*——FIG. 154,*2a–c.* **T. glabra,* Santonian; *a,* branched holotype, Upper Chalk, Berkhampton, England, ×0.5; *b,* enlarged surface of specimen showing groups of intracortical pores, Upper Chalk, Berkhampton, England, ×32 (Hinde, 1884b); *c,* characteristic spicules including tetraclones and dermal phyllodichotriaenes, Saint-Cyr, France, magnification not stated but about ×25 (Moret, 1926b; courtesy of Société Géologique de France).

Subfamily UNCERTAIN

Genera whose only known spicules are tuberculate desmas of theonellid type, unless oxeas are also present.

Pachycorynea POČTA, 1907, p. 171 [**P. erecta;* OD]. Cylindrical initially with ovoid, terminal swelling and lateral, paragastral opening; shallow furrows around this opening but no other canalar features; desmas large, regular tetraclones with spined to tuberculate arms; supplemental oxeas at surface; no other spicules known. [One specimen known.] *Cretaceous (Santonian):* France.——FIG. 155,*3a–b.* **P. erecta,* Nice; characteristic spicules include various tetraclones, magnification not stated (Moret, 1926b; courtesy of Société Géologique de France).

Rhopalospongia HINDE, 1884a, p. 89 [**Polypothecia gregaria* BENETT, 1831, p. 9; SD DE LAUBENFELS, 1955, p. 57]. Elongate, club-shaped, stalked sponges, growing singly, in groups united side by side, or with two or more individuals on one stalk; root processes at base; no paragastral cavity; external surface smooth or with small, pustular elevations, and with ostia of skeletal canals (possible epirhyses) that curve downwardly toward axis of body; no apparent aporhyses if these canals are regarded as epirhyses; stalk sometimes with vertical furrows; desmas strongly tuberculate and regular tetraclones in interior, but more or less irregular at surface; no other spicules known. *Cretaceous (Albian):* England.——FIG. 155,*1a–b.* **R. gregaria* (BENETT), Upper Greensand, Warminster; *a,* group of individuals, ×0.5; *b,* spicular meshwork of tubercular desmas of interior, ×50 (Hinde, 1884a).

Verrucodesma REID, *nom. nov.* herein (LAGNEAU-HÉRENGER, 1962, p. 141, *nom. nud.*) [**V. subconica* LAGNEAU-HÉRENGER, 1962, p. 141; OD]. Cylindroconical or cylindrical with tubular, paragastral cavity; outside of skeletal framework with numerous small ostia; fine furrows around paragastral opening; no other canalar features; desmas smooth and tuberculate tetraclones in which arms may be tuberculate and unbranched, or smooth and branched more or less strongly; no other spicules known. *Cretaceous (Aptian):* Spain.——FIG. 155,*2a–b.* **V. subconica,* Can Casanyas Castellet, Catalogne; *a,* side view of conicocylindrical sponge with osculum at top and minor canals around its margin, with numerous inhalant ostia in dermal surface, ×1; *b,* tuberculate tetraclones from main skeleton, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

Zitteleus DE LAUBENFELS, 1955, p. 56, *nom. nov. pro Spongodiscus* ZITTEL, 1878a, p. 153, *non* EHRENBURG, 1854 [**Turonia radiata* COURTILLER, 1861, p. 142; OD]. Discoidal, lenticular, or hemispherical; one surface, presumed to be upper, with radial ridges and furrows; other side, presumed lower, ribbed radially nodular, or concentrically corrugated, and sometimes with a few central outgrowths that appear to be root processes; no skeletal pores or canals; main part of skeletal framework formed from regular, tuberculate tetraclones with weakly developed zygomes, but supposed lower surface with skeletal cortex in which desmas are irregular and more or less elongate; large supplemental strongyles sometimes present; no other spicules known. *Cretaceous (Santonian):* France.——FIG. 155,*4a–b.* **Z. radiata* (COURTILLER); *a,* view of discoidal form from above with radial ridges or furrows, approximately ×1; *b,* vertical section showing distribution of canals in interior, ×1 (Courtiller, 1861).

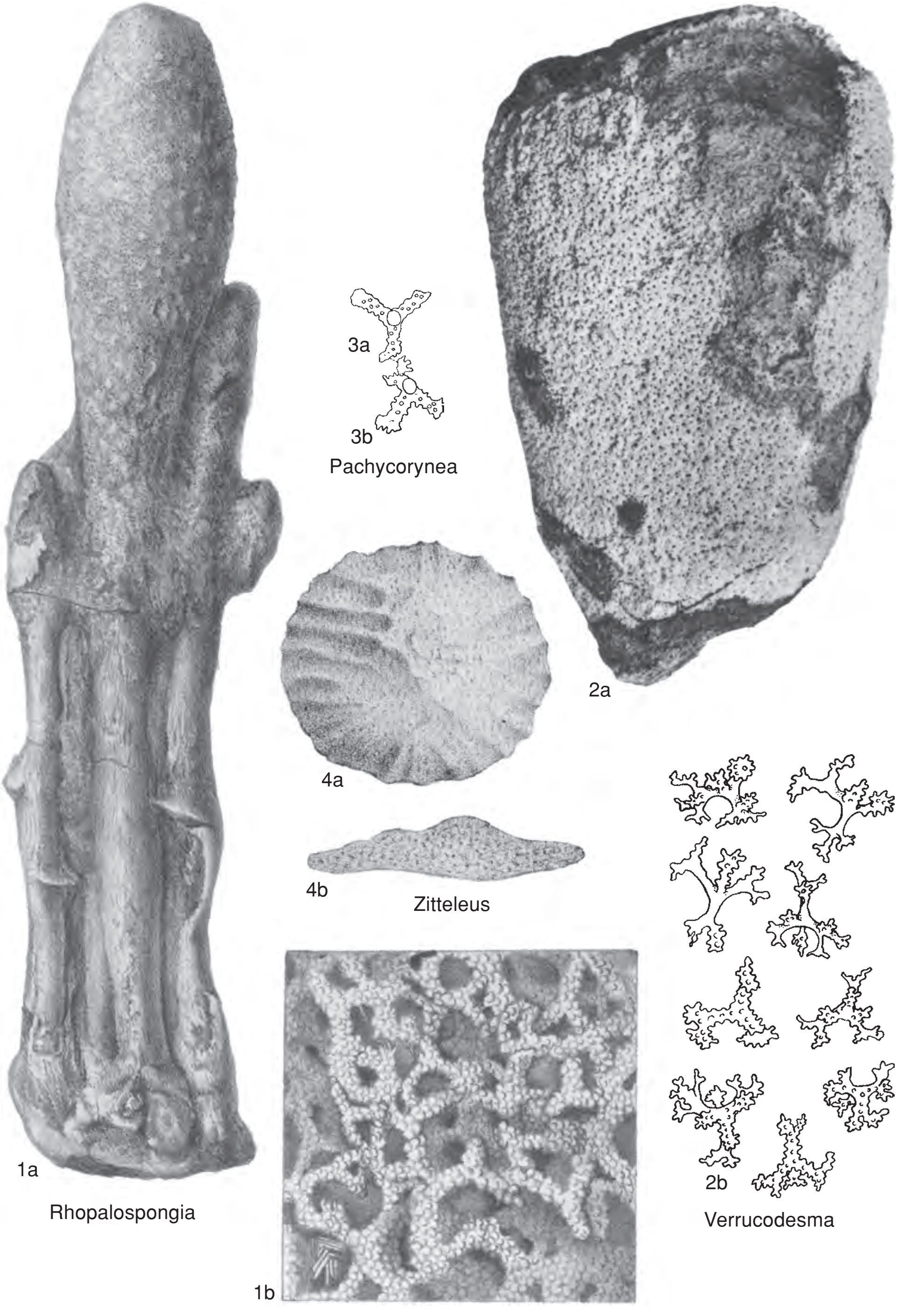

FIG. 155. Theonellidae (p. 232).

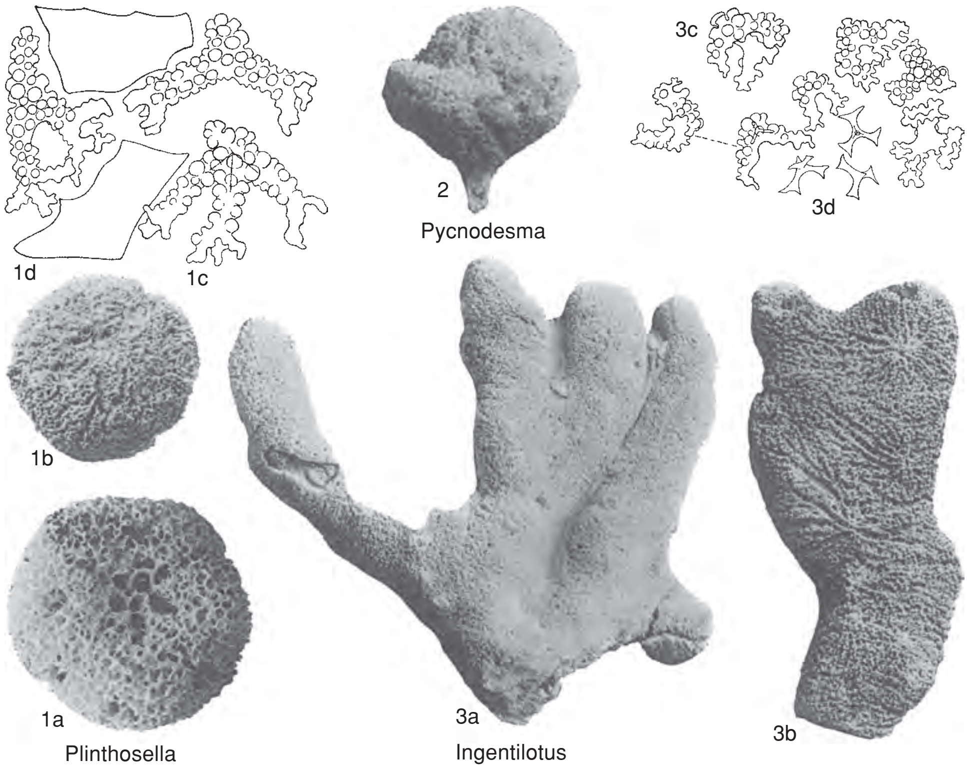

FIG. 156. Plinthosellidae (p. 234–235).

Family PLINTHOSELLIDAE Schrammen, 1910

[*nom. transl. et correct.* SCHRAMMEN, 1924a, p. 38, *ex* Plinthosellinae SCHRAMMEN, 1910, p. 34]

Sponges with strongly tuberculate desmas that are typically triders, to which variants with only two arms may be added, and with phyllotriaenes, discotriaenes, or irregular siliceous plates as dermalia; four-armed tetraclones absent; axial systems of desmas sometimes tetraxial, sometimes triodal or diaxial; supplemental rhizoclonids sometimes present; microscleres unknown. [The family is here used *sensu* SCHRAMMEN, 1910 (not *sensu* SCHRAMMEN, 1924a) because passage from phyllotriaenes like those of *Ingentilotus* DE LAUBENFELS (=*Dactylotus* SCHRAMMEN, 1910, *non* SCHOENHERR, 1844) to irregular plates like those of *Plinthosella* ZITTEL occurs in *Plinthosellopsis.* The family is probably from the same stock as the Theonellidae but distinguished by desmas being triders or two-armed variants, perhaps representing descendants of Jurassic *Sontheimia* KOLB (see family Protetraclisidae), in which desmas are triders.] *Lower Cretaceous (Albian)–Upper Cretaceous.*

Plinthosella ZITTEL, 1878a, p. 153 [**P. squamosa;* OD]. Typically small, globular, with basal stalk or none; top rounded, flattened, or with shallow depression or distinct, cuplike, paragastral cavity; lateral surfaces of skeletal framework with small ostia, irregular furrows, or both or neither; top or central cavity with group of postica, from which aporhyses run downwardly; desmas large, tuberculate triders and two-armed variants, with distinct, short brachyome or none, that sometimes have adventitious zygomes on outwardly facing sides; triders tetraxial or triodal, with axis corresponding with brachyome that may be rudimentary or absent; two-armed forms correspondingly triodal or diaxial; dermalia scalelike, anaxial plates of irregularly variable shapes; some examples with small rhizoclonids that form supplemental cortex in lower parts; microscleres unknown. *Cretaceous (Albian–Maastrichtian):* England; France, *Cenomanian–*

Campanian; Czech Republic, Slovakia, *Turonian;* Germany, Poland, *Campanian.*——FIG. 156,*1a–d.* **P. squamosa,* Quadratenkreide, Campanian, Oberg, Germany; *a,* spheroidal sponge seen from above showing postica, ×2; *b,* view of same specimen from below showing inhalant ostia and limited surficial grooves, ×1; *c–d,* characteristic spicules including trider and two-armed variants and dermal plates, ×20 (Schrammen, 1910).

Ingentilotus DE LAUBENFELS, 1955, p. 57, *nom. nov. pro Dactylotus* SCHRAMMEN, 1910, p. 115, *non* SCHOENHERR, 1884 [**Dactylotus micropelta* SCHRAMMEN, 1910, p. 115; OD]. Flattened branching to handlike or leaflike growths; both surfaces with small, skeletal pores, one side (supposedly gastral) may be furrowed with locally radiating arrangement; no distinct internal canals; desmas mainly tuberculate triders with brachyome strongly tuberculate, centrumlike swelling, but including two-armed variants in some examples; triders usually tetraxial but two-armed forms triodal; rhizoclonids and microscleres unknown. *Upper Cretaceous:* Europe.——FIG. 156,*3a–d.* **I. micropelta* (SCHRAMMEN), Mucronatenkreide, Campanian, Misburg, Germany; *a,* handlike example, from presumed dermal side, ×1; *b,* branch fragment, from furrowed (possibly gastral) side, ×2; *c–d,* characteristic desmas including triders and two-armed variants and young desmas, ×20 (Schrammen, 1910).

Pycnodesma SCHRAMMEN, 1910, p. 115 [**P. globosa;* OD]. Small, globular or nodular, with or without rootlike stalk; no paragastral depression; exterior with small ostia a little larger than normal skeletal meshes and a few irregular furrows; no distinct postica; desmas small, tuberculate triders; meshwork, hence, denser in appearance than *Plinthosella* species; no other spicules known. [This genus is included here on the basis of the form of the desmas; it is similar to *Plinthosella* ZITTEL, but the genus lacks the central group of aporhyses that the denser meshwork should have outlined if corresponding canals were present.] *Cretaceous (Santonian–Campanian):* France, *Santonian;* Germany, *Campanian.*——FIG. 156,*2.* **P. globosa,* Quadratenkreide, Oberg; side view of small, globular, stalked sponge, ×1 (Schrammen, 1910).

Family CHENENDOPORIDAE F. A. Roemer, 1864

[*nom. correct.* SCHRAMMEN, 1924a, p. 38, *pro* Chenendoporinae SCHRAMMEN, 1910, p. 34, *nom. transl. ex* Chenendoporidea F. A. ROEMER, 1864, p. 2]

Sponges with small, smooth-armed or tuberculate tetraclones that grade into rhizoclone-like variants toward skeletal surfaces; no other spicules known (dermalia possible dichotriaenes). [The name was described as new by SCHRAMMEN (1910) and ascribed to him by other authors, but in fact it was proposed first by ROEMER (1864). The type genus, *Chenendopora* LAMOUROUX, was placed in the Rhizomorina by ZITTEL (1878a), but the tetraxial character of the desmas was detected by SCHRAMMEN (1910). Dermalia are unknown in material from England, France, Germany, Czech Republic, and Slovakia but were said to be dichotriaenes in REZVOI, ZHURAVLEVA, and KOLTUN (1962, p. 55). The family is listed here because *Chenendopora* must be placed into ROEMER's family, but relationship to other Tetracladina is uncertain.] *Cretaceous (Aptian–Maastrichtian), Paleogene (?Eocene).*

Chenendopora LAMOUROUX, 1821, p. 77 [**C. fungiformis;* OD] [=*Bicupula* COURTILLER, 1861, pl. 35–37 (type, *B. gratiosa* COURTILLER, 1861, pl. 35,*1,* SD DE LAUBENFELS, 1955, p. 104); *?Dimorphina* REID, *nom. nov.* herein, p. 235 (type, *Dimorpha cornuta* COURTILLER, 1861, p. 124, OD); *?Tragalimus* POMEL, 1872, p. 202 (type, *Dimorpha balanus* COURTILLER, 1861, p. 123, SD DE LAUBENFELS, 1955, p. 49)]. Sometimes earlike or cuplike but typically funnel shaped, more or less long stalked, with simple, basal expansion or rootlike processes; wall thick; margin rounded or abruptly truncated; exterior sometimes with small ostia and short, irregular furrows, but usually with these features obliterated by skeletal accretion; surface then smooth or irregularly corrugated; no epirhyses; inner surface with postica of more or less sinuous aporhyses that enter wall obliquely downward, with inclination of these canals increasing toward stalk, and lowermost ones continuing down it; margin often with furrows that represent incompletely enclosed aporhyses; desmas tetraclones in interior, but grade outwardly into flattened and rhizoclone-like variants that form secondary, cortical meshwork of exterior; stalk sometimes furrowed longitudinally and with more or less elongate desmas; supplemental strongyles sometimes present; no dermalia or microscleres known. [Dichotriaenes are reported as dermalia according to REZVOI, ZHURAVLEVA, and KOLTUN, 1962, but these spicules are not known from other material.] *Lower Cretaceous (Albian)–Upper Cretaceous:* England, Spain, *Albian;* Czech Republic, Slovakia, *Cenomanian;* France, *Cenomanian, Campanian;* Germany, *Campanian;* Russia, *Upper Cretaceous.*——FIG. 157,*1a.* **C. fungiformis,* Mucronatenkreide, Campanian, Misburg, Germany; characteristic tetraclones, ×20 (Schrammen, 1910).——FIG. 157,*1b. C. gratiosa* COURTILLER, Senonian, Touraine, France; longitudinally sectioned example showing internal surface, shallow spongocoel, and aporhyses, ×0.5 (Moret, 1926b; courtesy of Société Géologique de France).

?Dimorphina REID, herein, *nom. nov. pro Dimorpha* COURTILLER, 1861, p. 123, *non* JURINE, 1807, *nec* HUEBNER, 1822, *nec* GRAY, 1840, *nec* HODGSON,

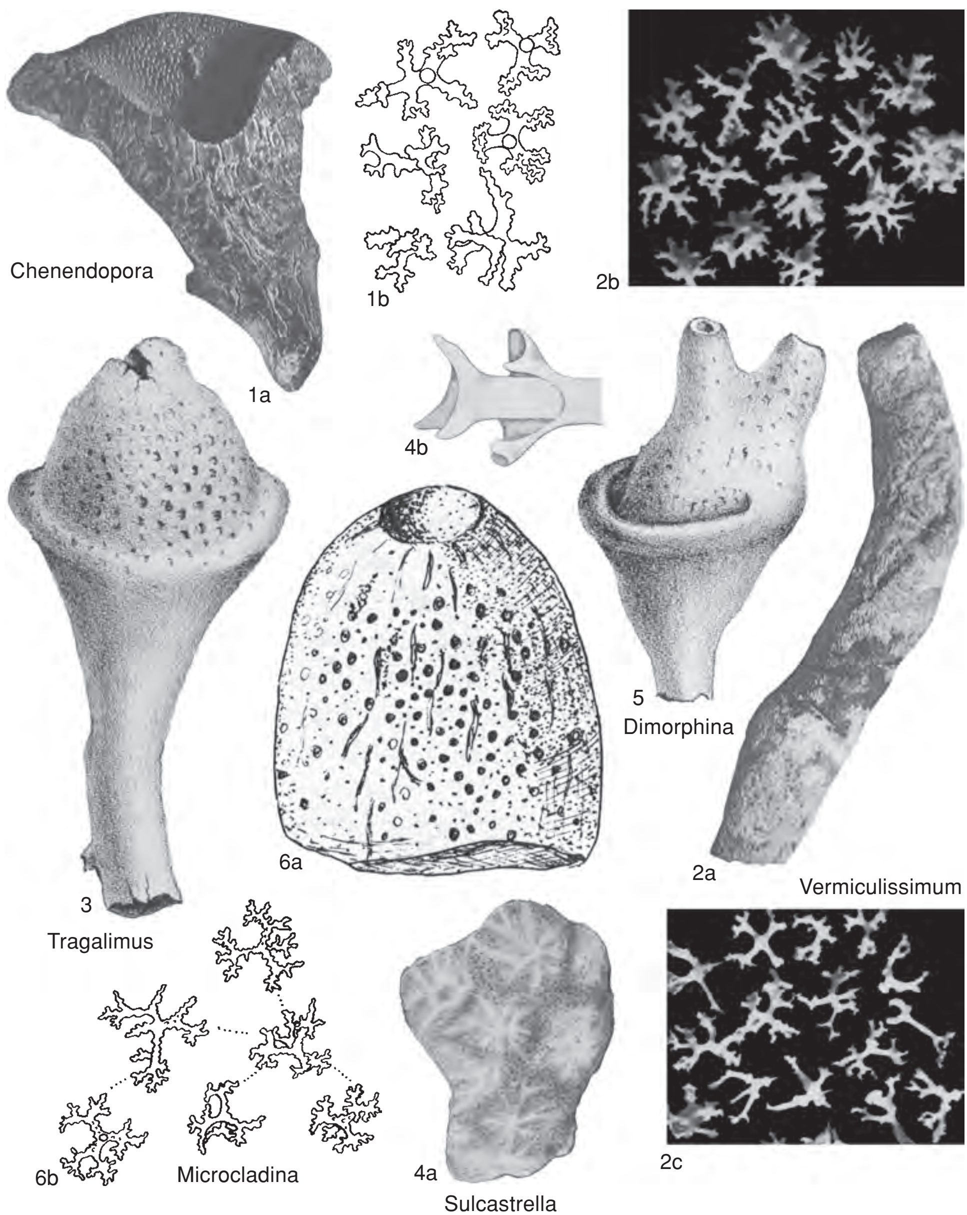

FIG. 157. Chenendoporidae and Uncertain (p. 235–237).

1841 [**Dimorpha cornuta* COURTILLER, 1861, p. 124; OD]. Character uncertain, but possibly based on gerontic *Chenendopora* in which secondary growths have arisen from paragastral surface; skeletal structure unknown. *Cretaceous (Coniacian–Maastrichtian):* France.——FIG. 157,*5*. **D. cornuta* (COURTILLER); side view of obconical form with secondary branched growth in upper part, ×0.5 (Courtiller, 1861).

Microcladina LAGNEAU-HÉRENGER, 1962, p. 146 [**M. aptiensis;* OD]. Cylindrical with rounded summit, sometimes growing in groups, and with deep, narrow, paragastral cavity that extends to base; exterior with pores of two sizes, larger are ostia of radial epirhyses, and with irregular, longitudinal furrows that radiate from paragastral margin; aporhyses longitudinal, some beginning as furrows around paragastral margin or opening into other furrows; character of paragastral surface not stated; desmas small, regular tetraclones with granular ornament in interior, becoming small and passing into rhizoclone-like bodies toward outside; no other spicules known. [Placed in Discodermiidae (=Theonellidae) by LAGNEAU-HÉRENGER (1962) but here thought probably similar to *Chenendopora.*] *Cretaceous (Aptian):* Spain.——FIG. 157,*6a–b.* **M. aptiensis,* Mas de Artis, Catalogne; *a,* side view of terminal part of sponge with many inhalant ostia and minor, surficial grooves, ×1; *b,* small, regular tetraclones with fine granulations, ×25 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

?Tragalimus POMEL, 1872, p. 202 [**Dimorpha balanus* COURTILLER, 1861, p. 123; SD DE LAUBENFELS, 1955, p. 49]. Character uncertain but possibly a gerontic *Chenendopora* with a hollow, ovate, secondary growth arising from paragastral surface; skeletal characters unknown. *Cretaceous (Coniacian–Maastrichtian), Paleogene (?Eocene):* France, *Coniacian–Maastrichtian;* Western Australia, *?Eocene.*——FIG. 157,*3.* **T. balanus* (COURTILLER), Senonian, France; side view of obconical sponge with hollow, secondary mound and osculum above, ×0.5 (Courtiller, 1861).

Family UNCERTAIN

Sulcastrella SCHMIDT, 1879, p. 27 [**S. clausa;* OD]. Has the outward appearance of *Astrobolia* ZITTEL, but its stellate grooves lead into large oscula. *Cretaceous–Holocene:* Europe, Gulf of Mexico.——FIG. 157,*4a–b.* **S. clausa,* Holocene, Gulf of Mexico; *a,* side view of small sponge with stellate grooves and fine pores, ×1; *b,* tips of isolated spicules showing three-rayed tips to coarse axes, magnification unknown (Schmidt, 1879).

Vermiculissimum DE LAUBENFELS, 1955, p. 59, *nom. nov. pro Stelidium* SCHRAMMEN, 1924a, p. 55, *non* ROBERTSON, 1903 [**Stelidium vermiculare* SCHRAMMEN, 1924a, p. 55; OD]. Small finger- to wormlike, with very small pores; upper end more or less covered with dermal layer with short-rayed and branched phyllotriaenes; principal skeleton fine meshed and composed of small tetraclones. *Cretaceous (Cenomanian):* Germany.——FIG. 157,*2a–c.* **V. vermiculare* (SCHRAMMEN), Mukronatenkreide, Misburg; *a,* side view of cylindrical sponge with small pores, ×1; *b,* photomicrograph of dermal phyllotriaenes; *c,* tetraclones of interior skeleton, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).