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## Studies on Hexactinellid Sponges. III. The Taxonomic Status of Hexactinellida Within the Porifera

H. M. Reiswig and G. O. Mackie

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# STUDIES ON HEXACTINELLID SPONGES. III. THE TAXONOMIC STATUS OF HEXACTINELLIDA WITHIN THE PORIFERA

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Recent findings on the structure and physiology of the enigmatic hexactinellid sponges challenge the conventional definition and classification scheme of the Porifera. The gradual acceptance of the choanocyte element as a diagnostic morphological character of the phylum must be revised in the light of the syncytial (acellular) and enucleate condition of the hexactinellid flagellated chambers.

The contrasts between the hexactinellids and all other sponges are reviewed and considered sufficient to require recognition of a primary subdivision at the subphylum level. The major differences include, respectively, syncytial (or symplastic) as against cellular organization, acellular as against cellular (pinacocytic) epithelia, thin as against abundant mesohyle matrix, absence as against presence of contractility, and presence as against absence of a relatively rapid conduction system. The new findings support Reid's 1958 allocation of classes in his subdivision of the phylum, but the names that he employed, *Nuda* and *Gelatinosa*, are considered inappropriate for present use because of the hypothetical basis of their origin and of the lack of descriptive value of the names in the present context (R. E. H. Reid, *Palaeontogr. Soc. [Monogr.]* **111**, 1–46 (1958)). Two new subphyla are proposed and defined, the *Symplasma* to include the single class Hexactinellida, and the *Cellularia* to include all other extant sponges of the classes Calcarea, Demospongiae and Sclerospongiae.

### 1. INTRODUCTION

The class Hexactinellida, the so-called 'glass sponges' of the deep sea, consists of from 400 to 500 extant species (425 are listed in the most recent catalogue of Ijima (1927), now 55 years old) and an extensive assemblage of extinct members extending from the early Cambrian to

the present. The wide acceptance of a classification reflecting equal status of the three major classes of Porifera, the Hexactinellida, Calcarea and Demospongiae, dating from Minchin's (1900) taxonomic arrangement, can be attributed to the general lack of information on hexactinellid structure, apart from the skeletal system. The early descriptive literature dealing with the syncytial organization of the soft tissues and the development of members of this class is contradictory, unsubstantiated by more recent work, and generally considered not sufficiently well documented to be useful in making taxonomic decisions. Where the early controversial interpretations have been used as a basis for taxonomic changes, these proposals have been conspicuously ignored.

Recent investigations of tissue organization and physiology of the Hexactinellida (Mackie 1979; Reiswig 1979; Lawn *et al.* 1981) have suggested new and startling differences between the hexactinellids and the other members of the phylum Porifera. The detailed confirmation of earlier suggestions and the discovery of new ultrastructural and physiological features described by Mackie & Singla (1983) and Mackie *et al.* (1983) in the preceding papers in this series require a re-evaluation of the relationships between the higher taxa of sponges. At this time we also consider a formal redefinition of Porifera to be both necessary to accommodate the new findings on structure and timely in finally removing the uncertainty of authority for the concept of Porifera that has persisted in the literature dealing with the group for the last 90 years.

## 2. DEFINITION OF PORIFERA: 1825–1978

Full appreciation of the significance of the recent discoveries of hexactinellid structure and physiology requires a clear understanding of the original concept of the Porifera and the changes to that concept with major anatomical discovery. Grant, in his early studies on a variety of sponges, was impressed with the continuous unidirectional water currents that entered the microscopic pores of the tissue surface and exited from the large vents, now called oscula (Grant 1825–26, 1825, 1826*a–d*). As an astute student of comparative anatomy, he reasoned that the currents must have been generated by the action of internal cilia, but he was unable to convince himself that he had observed them. In 1836, Grant proposed his definition of the Porifera, which has been generally accepted as the authority of the concept of the phylum, although it has apparently been rarely read and likewise rarely correctly cited. We feel that the need for awareness of the original definition is particularly acute at this time and here quote Grant's (1836, p. 108) words and figure (figure 1).

'2. *Porifera*, simple, aquatic, soft, animals, without perceptible nervous or muscular filaments or organs of sense, with a fibrous internal skeleton sometimes supported with siliceous and sometimes with calcareous spicula, the body permeated with a soft gelatinous flesh, covered externally with minute absorbent pores, traversed by numerous ramified anastomosing canals, which commence from the pores and terminate in large open vents, as seen in the annexed figure of the *halina papillaris*, Gr. (fig. 29), which represents the animal as alive, under water with the usual currents passing inwards through its pores (aa), traversing its internal canals (b), and escaping by the larger vents (c, d) (see PORIFERA).'

Grant clearly stressed the simplicity of tissue organization, the variety of skeletal elements, the pores, canals and water currents; he did not refer to the cellular nature of the tissues nor the agent or agents responsible for generation of the water currents, although the 'ciliary' effectors

were both suspected and reported to have been observed in a few species by Grant and several other authors by this time. Through the 1850s and 1860s the cellular nature of the living sponge tissue was widely recognized with various workers reporting the discovery of ciliated, vibratile cells.

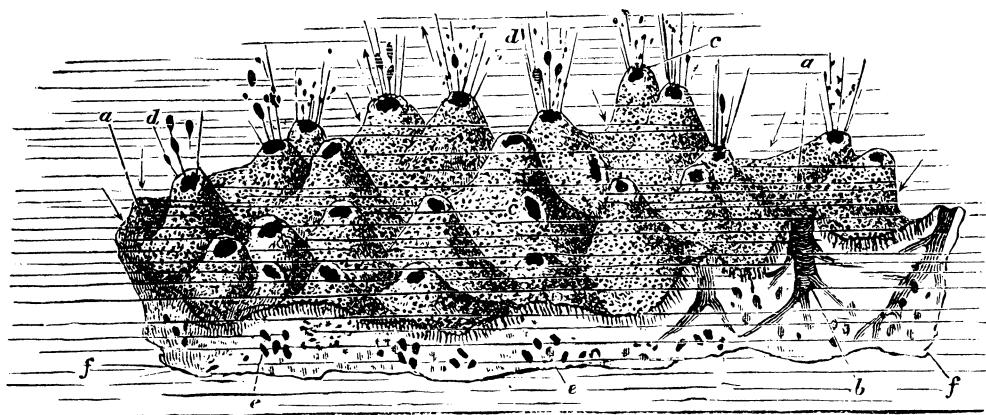


FIGURE 1. R. E. Grant's figure 29 from the original description of 'Porifera', reprinted from Grant (1836, p. 108). See text for explanation of symbols.

It was James-Clark who first reported (1866) and soon after figured (1868) the choanoflagellate-like collar cells as agents responsible for generation of the characteristic through-flowing water currents of sponges. Since that time, the presence of either a continuous or a subdivided layer of choanocytes functioning as water current-generating cells has gradually become one of the most important characters (or even *the* most important single character) of the phylum (Sollas 1887; Minchin 1900; Sollas 1909; Bidder 1929; Hyman 1940; Bergquist 1978). With the presence of a canal system and the lack of recognizable organs, the presence of choanocytes is now routinely used as final proof of the poriferan nature of an unknown organism, and we thus propose addition of this widely recognized character to the formal definition of the phylum Porifera below. The presence of choanocytes or collar-bearing cells alone is not a suitable defining character, owing to the widespread occurrence of this cell type in epidermal and nephridial systems of many invertebrate groups (Salvini-Plawen 1978).

### 3. HEXACTINELLIDA: 1870–1978

The authority for the presently recognized class Hexactinellida is Schmidt (1870). Employing the essential features of Thomson's earlier (1868) order Vitrea for his new group, the Hexactinellidae, Schmidt stressed the triaxonal pattern of the siliceous spicules, and the more fluid and less fibrous nature of the soft tissues relative to those of other sponges. The controversy between Reid (1957, 1963) and de Laubenfels (1955, 1958) over the priority and suitability of Schmidt's name, Hexactinellidae, as against the Hyalospongiae of Claus (1872) or Vosmaer (1885), was effectively resolved by the strength of Reid's arguments. Hexactinellida Schmidt was accepted as the preferred name in the classical taxonomic treatments of Minchin (1900), Sollas (1909), Bidder (1927) and Hyman (1940); more recently the *Zoological Record* has consistently employed Hexactinellida as have virtually all authors of recent papers dealing with this class, with the exception of Koltun (1970). Since no convincing refutation of Reid's (1963) assessment of the

nomenclatural status has been proposed, the names *Hyalospongiae*, *Triaxonia* and *Vitrea* should no longer be considered valid synonyms of *Hexactinellida*.

Knowledge of the organization and physiology of the class has remained fragmentary and speculative until the present. In the first series of histological studies, Schulze described the external epithelium as probably being cellular as in other sponges (Schulze 1887), but having basal lateral fusions between adjacent cells (Schulze 1899). Ijima in his 1901 study contradicted Schulze in being unable to substantiate a cellular structure of the dermal membrane. Both authors agreed that the choanocytes were nucleate, although remarkably poor in chromatin and were joined basally by protoplasmic strands. The trabecular net was described as a syncytium with nuclei scattered along the strands and with at least two additional cell types associated with the trabeculae: thesocytes and archaeocytes. The existence of a very thin basal connective tissue plate was a feature claimed by Schulze but denied by Ijima.

The characteristics agreed upon by Schulze and Ijima were accepted with caution by other workers and used conservatively in assessment of relationships with other sponges. Bidder (1927, 1929, 1930) stressed the lack of intercellular matrix and the exposed position of all cellular elements to passing water currents as unique in the hexactinellids. He also argued strongly that a powerful hydraulic pumping system was lacking in this group, in spite of the fact that choanocytes were considered to be present. Hyman (1940) interpreted the trabecular system as pseudopodial fusion of collencytes, archaeocytes, thesocytes and other cells, without having developmental data to support her views. Up to 1978, as Bergquist has clearly pointed out, the level of understanding of the features of the group remained essentially at that of 1901, with the earlier claims of syncytial organization still unsubstantiated by electron microscopy, with no recent re-evaluation of cellular differentiation and with no direct evidence for the presence or absence of flagella-generated water currents, three of the most distinctive features of the phylum Porifera.

#### 4. RELATIONSHIP BETWEEN HEXACTINELLIDA AND OTHER PORIFERA: 1870–1978

While many authors have recognized a great gulf or dissimilarity between the *Hexactinellida* and the non-hexactinellid sponges (universally recognized to be cellular in organization), others have attempted to associate *Hexactinellida* more intimately with other sponge taxa. Before the recognition of the *Hexactinellida* as a major taxon, they were understandably included with what are now considered the silica-secreting members of the *Demospongiae* in the *Silicea* or the *Non-Calcareia* (Gray 1868; Thomson 1868), a view that persisted for a considerable time (Vosmaer 1885; Reid 1957). Other sporadic and unsuccessful attempts to substantiate a close linkage between the *Hexactinellida* and the *Demospongiae* (some or all) include those of W. J. Sollas (1887) and I. B. J. Sollas (1909), based upon the small size of choanocytes in these two groups (*Micromastictora*) relative to the same cells in *Calcareia* (*Megamastictora*), and those of Bidder (1927) and de Laubenfels (1927), based upon the apparent triaxial symmetry of microscleres and some megascleres of poecilosclerid *Demospongiae*. Neither of these suggested classifications has attracted wide support.

The more common and modern treatment of the Porifera has been to recognize the three traditional classes as equidistantly separate, with or without recognition of the *Sclerospongiae* and several of the less well known extinct groups (Minchin 1900; de Laubenfels 1936, 1955;



Hyman 1940; Grassé 1973; Bergquist 1978; *Zoological Record* 1976–1981). Less well known is the attempt by Bidder (1929, 1930) to formalize the distinctions between the Hexactinellidae on the one hand and all other Porifera on the other. Bidder set up two separate phyla, the Nuda for the naked sponges (Hexactinellida) and the Gelatinosa for the true sponges (Calcarea and Demospongiae) as a modification of his abortive 1927 scheme mentioned above. Bidder's intent was to formalize what he considered to be the separate derivation of these from two distinct groups of protozoan collar flagellates; his formal diagnoses are thus completely hypothetical. Bidder did include a series of real characters in adjoining paragraphs and Reid (1958) formally proposed the redefinition of Bidder's taxa as subphyla for separation of the Hexactinellida from the other sponges.

While Reid's formal action has been ignored by sponge workers, the distinctive status of the Hexactinellida among the Porifera has been suspected or acknowledged repeatedly (Thomson 1868; Minchin 1900; Burton 1934; Finks 1970; Bergquist 1978). Reid based his revision of Bidder's Nuda (including only Hexactinellida) upon the following characters: (i) lack of pinacocytes in the external limiting membrane, (ii) lack of a gelatinous mesenchyme in adults, (iii) syncytially connected choanocyte layer situated between regions of syncytial trabeculae, and (iv) unique internal origin of canal systems. At that time (1958), the lack of pinacocytes and the syncytial organization of both trabeculae and choanoderm were not substantiated. The equivocal reception of Reid's scheme can thus be attributed to the lack of acceptable information on Hexactinellida histology.

#### 5. RECENT INFORMATION: 1979–1982

Recent investigations of the hexactinellid populations on the northwest Pacific Coast water of British Columbia, Canada, and Washington, U.S.A., have caused the older claims and controversies on microscopic organization to be reviewed (Reiswig 1979) and have provided new information on physiology and behaviour of Hexactinellida (Mackie 1979; Lawn *et al.* 1981). The long-awaited successful application of transmission electron microscopy (Mackie & Singla 1983) has permitted verification of some earlier hypotheses based upon light microscopy as well as demonstrating certain totally new features of organization in these organisms. Unless otherwise noted, the features discussed below are considered to be general to all known members of the class Hexactinellida. Our personal information stems from the analysis of fine structure of one species, *Rhabdocalyptus dawsoni*, previously reported low power electron microscopy and light microscopy of thick (1–2  $\mu\text{m}$ ) epoxy sections of *Aphrocallistes vastus* and *Chonelasma calyx*. In addition, one of us (H.M.R.) has recently collected, processed and surveyed by light microscopy thick epoxy sections of *Aulocystus grayi* and *Dactylocalyx pumiceus*. These five species are distributed in four families of the order Hexasterophora. The general details noted below are fully compatible with the descriptions of both Schulze and Ijima in their extensive surveys of hexactinellid tissues, after allowances are made for the technical limitations of their methods and misinterpretations made by them near the limits of optical resolution, e.g. on nuclei of choanocytes.

The syncytial organization of the general trabeculum and the dermal membrane, a pattern suggested by almost all previous workers, is substantiated, with no major distinguishing differences between these elements. The pathways of continuity within these syncytia are broad and cannot be considered as pseudopodial derivatives as proposed by Hyman (1940). Cellular

linings equivalent to the endo- or ecto-pinacocytes of other sponges are apparently non-existent in Hexactinellida from information to date, and there is no evidence for myocytes or comparably specialized syncytial structures.

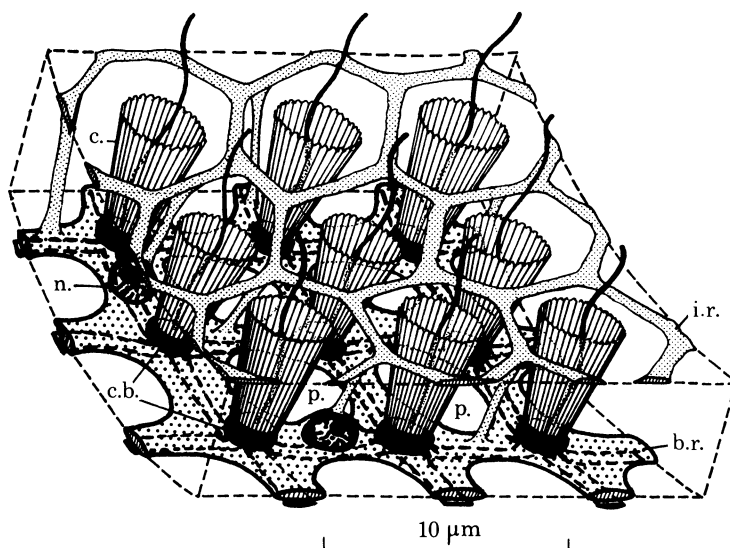


FIGURE 2. A diagrammatic representation of a small portion of the flagellated chamber wall of a hexactinellid. The two-tiered reticulum of the wall is demonstrated in this composite from light microscopy of several species and electron microscopy of *Rhabdocalyptus dawsoni*. The cytoplasmic bridges (stolons) joining collar bodies (forming the choanosyncytium) underlie the basal reticulum (b.r.) and are indicated by dashed lines. Abbreviations: c, collar; c.b., collar body; p., prosopyle; n., nucleus of trabecular syncytium; b.r., basal reticulum of trabecular syncytium; i.r., inner or secondary reticulum of trabecular syncytium.

The long-supposed syncytial nature of the choanoderm (choanosyncytium) is verified, but the demonstration of the enucleate condition of the active differentiated portion of this tissue element is a totally new character for the class, as well as for the phylum. The term 'choanocyte' as recently considered a major defining character of the Porifera is technically inappropriate for this class. Associated with the syncytial choanoderm is the distinctive secondary or inner reticululum of the flagellated chamber wall (figure 2), a structural organization presumably related to the relatively wide spacing between collar units of hexactinellids and totally unknown in other Porifera.

Although most of the living tissue of hexactinellids consists of the dermal-trabecular syncytium and the choanosyncytium, a suite of more-or-less discrete cell types is also present in all species studied. These include archaeocytes and thesocytes which are easily identified by light microscopy; choanoblasts, spherulous cells, granulated cells, scleroblasts and spermatids may be distinguished in electron microscope studies of *Rhabdocalyptus* and eventually perhaps in all other species. Present information suggests that these cells are either intermittently or continuously attached by membrane-bound cytoplasmic bridges to the major syncytial trabeculum. The lack of phagosomes and pseudopodia suggests that the archaeocytes of hexactinellids are relatively sedentary compared with those of the demosponges. Further electron microscopy surveys are required before distribution of cell types can be discussed.

The controversy concerning the presence or absence of a connective tissue matrix has been settled in favour of Schulze's claim (1899, 1904) of a basal membrane. This structure, described as the mesolamella (Mackie & Singla 1983), consists of thin sheets of fibrils which show

characteristics similar to those of collagen. The mesolamella is apparently continuous throughout entire sponges, forming a suspensory network for attachment and support of trabecular tissues. Although it appears that both silica deposition and spicule symmetry differ between hexactinellids and demosponges (Reiswig 1971), these subjects need to be reinvestigated by modern techniques before their taxonomic significance can be meaningfully assessed.

The mesohyle of sponges is generally defined as the portions of the body lying subepithelial in position and thus not directly bathed by the water conducted through the aquiferous system. In hexactinellids, the mesohyle can be considered to include the mesolamella network, the invested siliceous elements, the archaeocyte 'congeries' on flagellated chamber walls, the cysts of differentiating reproductive cells in the trabecular syncytium, and, in species where they occur, the cord syncytia (Reiswig 1979).

The final, and perhaps the most important, finding in the recent electron microscope work is the distinctive perforate septal partition or plug found between differentiated regions of the syncytial complex of *R. dawsoni*. Since these structures are known only from this single species, they cannot at present be considered general features of the class Hexactinellida. The similarity of organizational pattern of all other known hexactinellids to that of *R. dawsoni* suggests that the plug is probably widespread through the class and may eventually constitute an additional major character difference between the Hexactinellida and all other groups of Porifera.

In conjunction with these organizational studies, the series of physiological studies reported by Mackie (1979), Lawn *et al.* (1981) and Mackie *et al.* (1983) necessitates further changes in the recent concept of the Hexactinellida. *R. dawsoni* does maintain a vigorous through-flow water current which can be assumed to be generated by the flagellated chambers, contrary to Bidder's (1927) long-held and widely quoted assumption of dependence upon passive ventilatory flow by this group of sponges. In addition, these workers have shown a relatively rapid conduction system and a coordinated effector response, probably consisting of total flagellar arrest, in *R. dawsoni*. This pair of features contrasts with the repeated failure to demonstrate such systems and responses in the other (cellular) sponges.

The large body of new information on both structural organization and physiology of hexactinellids warrants a redefinition of the class, as well as a formal redefinition of the phylum Porifera, based upon Grant's original diagnosis. The need for re-evaluation of the status of the Porifera is reinforced by the fact that the terminology suggested by Borojevic *et al.* (1968) cannot be applied to hexactinellids. Indeed some of the terms that these authors reject must be retained in the present case.

In view of the verification of major differences between the hexactinellids and other sponges, we support Reid's (1958) division of the phylum into two subphyla with modifications of his concepts as required by recent research, but we reject the use of Bidder's (1929) names, Nuda and Gelatinosa, for these groups. Bidder's names were based on totally hypothetical concepts, as noted above, and their descriptive alternatives, 'naked' as against 'gelatinous' nature of the mesohyle, are far less appropriate than the more important morphological alternatives, 'syncytial' as against 'cellular' organization. We hope that the documentation of previously suspected characters and the description of new morphological and physiological features of the hexactinellids in this series of reports will encourage wide acceptance of the division of the Porifera at the subphylum level and encourage further study of phylogenetic relationships between the major groups of sponges.



## 6. PROPOSAL

The following taxonomic proposal includes a new definition of the phylum Porifera, and definition and description of two new subphyla, the Symplasma and Cellularia. In keeping with our feelings for the terms 'sponges' and Porifera, and our perceptions of the feelings of other workers involved with these organisms, we support the maintenance of the Hexactinellida within the Porifera, thereby agreeing with Reid in rejection of Bidder's (1929) proposal to put them in a separate phylum. In this action we do not intend to imply that the syncytial and cellular sponges are necessarily co-descendants from a common protistan ancestor. We are likewise not considering the status of Parazoa and Enantozoa which have recently been reviewed by Tuzet (1973) and Bergquist (1978), both of whom rejected the terms and concepts that they represent.

*Phylum Porifera Grant, 1836*

Aquatic, usually sessile, multicellular or multinucleate syncytial metazoans lacking columnar tissue layers supported on basement membranes; organs usually absent, but simple superficial effectors (cribiform sieve systems) do occur; without a nervous system or sensory structures in adults; with an internal supporting skeleton of varying complexity, composed of a dispersed organic collagen fibril matrix, with or without compact organic (spongin) fibres, with or without siliceous or calcareous deposits in the form of spicules or basal deposits or pillars; body surface penetrated by orifices of two sizes; smaller pores serving for inhalation of water and larger apertures for exhalation of water; orifices joined by a canal system of varying complexity but lined in part by a monolayer of choanocytes or an enucleate choanosyncytium effective in generation of the unidirectional water current for filter feeding; captured particulate food may be supplemented by products of symbionts (bacteria or algae) and by uptake of dissolved organic matter; sexual reproduction involving typical male and female gametes resulting in production of free, flagellated larvae in most forms; asexual reproduction by active bud formation or passive (accidental) subdivision of tissue mass.

*Subphylum 1. Symplasma nov.*

Porifera of primary symplastic or syncytial organizations; lacking pinacocytes in the surface membrane of adults; with reduced mesohyle consisting of a thin collagenous mesolamella, skeletal elements and disjunct groups of more or less discrete cellular elements; collar elements not occurring as cellular units but as nodal structures in an enucleate, reticulate syncytium which is joined to nucleate choanoblast cells by cytoplasmic bridges. (Symplasma: greek συν (syn), together with πλάσμα (plasma), anything formed or moulded.)

*Class 1. Hexactinellida Schmidt, 1870.* Syncytial sponges with skeletons composed of siliceous megasclere and microsclere spicules of triaxial form, with three axes intersecting at right angles; spicules typically hexactine, but reduction of ray number is common; large saccate flagellated chambers with unique two-tiered reticulate walls; contractile cells (myocytes) and general body wall contractility absent.

*Subphylum 2. Cellularia nov.*

Porifera of primary cellular organization; with dermal surfaces composed of pinacocytes; mesohyle typically includes abundant collagen matrix, skeletal elements and amoeboid cells of

several types; collar units borne singly on nucleated choanocytes; the pattern of internal cavities lined by choanocyte monolayer varies from branching or unbranching axial canals to numerous, separate, small spherical chambers; without a secondary inner reticulum on choanoderm; composition of the skeletal system highly variable, but not based upon triaxon siliceous spicules; myocytes and limited contractability common. (Latin *cellula*, small cell or compartment.)

*Class 2.* Calcarea Bowerbank, 1864. Including Heteractinida Hinde, 1888 (Laubenfels 1955), following Finks (1960) and Rigby & Nitecki (1975).

*Class 3.* Demospongiae Sollas, 1885. Including Sphinctozoa Steinmann, 1882 (*partim*), following Vacelet (1981).

*Class 4.* Sclerospongiae† Hartman and Goreau, 1970

#### *Uncertain affinity*

Archaeocyatha Vologdin, 1937 (Vologdin 1937).

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#### REFERENCES

- Bergquist, P. R. 1978 *Sponges*. Berkeley: University of California Press.
- Bidder, G. P. 1927 The ancient history of sponges and animals. *Rep. Br. Ass. Advmt Sci.* **95**, 58–74.
- Bidder, G. P. 1929 Sponges. In *Encyclopaedia Britannica* (14th edn), vol. 21, pp. 254–261. London: The Encyclopaedia Britannica Company.
- Bidder, G. P. 1930 On the classification of sponges. *Proc. Linn. Soc. Lond.* **141**, 44–47.
- Borojevic, R., Fry, W. G., Jones, W. C., Lévi, C., Rasmont, R., Sarà, M. & Vacelet, J. 1968 Mise au point actuelle de la terminologie des éponges. *Bull. Mus. natn. Hist. nat.* (2) **39**, 1224–1235.
- Burton, M. 1934 *Further zoological results of the Swedish Antarctic Expedition of 1901–1903; sponges*, pp. 1–58. Stockholm.
- Claus, C. 1872 *Grundzuge der Zoologie* (2nd edn). Marburg and Leipzig: N. G. Elwert.
- Finks, R. M. 1960 Late Paleozoic sponge faunas of the Texas region. *Bull. Am. Mus. nat. Hist.* **120**, 1–160.
- Finks, R. M. 1970 The evolution and ecologic history of sponges during Paleozoic time. *Symp. zool. Soc. Lond.* **25**, 3–22.
- Grant, R. E. 1825–26 Observations and experiments on the structure and function of the sponge. *Edinb. Phil. J.* **13**, 94–105 and 333–346; **14**, 113–124 and 336–341.
- Grant, R. E. 1825 On the ova of the sponge. *Edinb. Phil. J.* **13**, 381–383.
- Grant, R. E. 1826*a* On the structure and nature of the *Spongilla friabilis*. *Edinb. Phil. J.* **14**, 270–284.
- Grant, R. E. 1826*b* Notice of a new zoophyte (*Cliona celata*, Gr.) from the Firth of Forth. *Edinb. new Phil. J.* **1**, 78–81.
- Grant, R. E. 1826*c* Remarks on the structure of some calcareous sponges. *Edinb. new Phil. J.* **1**, 166–171.
- Grant, R. E. 1826*d* Observations on the structure and function of the sponge. *Edinb. new Phil. J.* **2**, 121–141.
- Grant, R. E. 1836 Animal kingdom. In *The cyclopaedia of anatomy and physiology*, vol. 1 (ed. R. B. Todd), pp. 107–118. London: Sherwood, Gilbert and Piper.
- Grassé, P.-P. (ed.) 1973 Spongiaires. *Traité de zoologie*, vol. 4. Paris: Masson.
- Gray, J. E. 1868 Observations on sponges and on their arrangement and nomenclature. *Ann. Mag. nat. Hist.* (4) **1**, 161–173.
- Hyman, L. H. 1940 Porifera. In *The invertebrates*, vol. 1 (Protozoa through Ctenophora), pp. 284–264. New York: McGraw-Hill.

† Vacelet (1981) has proposed inclusion of the living Sclerospongiae among several orders within the class Demospongiae, leaving several fossil groups often included in the Sclerospongiae (Stromatoporida, Chaetetida, Favositida) uncertain in position.

The status of the Stromatoporoidea remains unclear. Stearn's (1975) proposal of subphylum status for Stromatoporida has not found general acceptance. Recently Stearn (1980) has proposed the class Stromatoporoidea Nicholson and Murie, 1879, to encompass the Palaeozoic stromatoporoids. It is unclear if this group is to be considered totally distinct from the Mesozoic forms and if the class as constituted includes any of the recent calcifying sponges as members.

- Ijima, I. 1901 Studies on the Hexactinellida. Contribution I (Euplectellidae). *J. Coll. Sci. imp. Univ. Tokyo* **15**, 1–299.
- Ijima, I. 1927 The Hexactinellida of the Siboga Expedition. *Siboga Expedition Report*, vol. 6.
- James-Clark, H. 1866 Conclusive proofs of the animality of the ciliate sponges, and of their affinities with the Infusoria flagellata. *Am. J. Sci.* (2) **42**, 320–324.
- James-Clark, H. 1868 On the *Spongiae ciliatae* as *Infusoria flagellata*; or observations on the structure, animality, and relationships of *Leucosolenia botryoides* Bowerbank. *Ann. Mag. nat. Hist.* (4) **1**, 133–142, 188–215 and 250–264.
- Koltun, V. M. 1970 Sponges of the Arctic and Antarctic; a faunistic review. *Symp. zool. Soc. Lond.* **25**, 285–297.
- Laubenfels, M. W. de 1927 The red sponges of the Monterey Peninsula, California. *Ann. Mag. nat. Hist.* (9) **19**, 258–266.
- Laubenfels, M. W. de 1936 A discussion of the sponge fauna of the Dry Tortugas, in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Instn Wash. Publ.* no. 467.
- Laubenfels, M. W. de 1955 Porifera. *Treatise on invertebrate paleontology*, pt E (Archeocyatha and Porifera; ed. R. C. Moore), pp. E21–E112. Lawrence, Kansas: Geological Society of America and University of Kansas Press.
- Laubenfels, M. W. de 1958 Nomenclature of Porifera, especially concerning the so-called ‘glass sponges’ or Hyalospongea. *J. Paleont.* **32**, 611–616.
- Lawn, I. D., Mackie, G. O. & Silver, G. 1981 Conduction system in a sponge. *Science, N.Y.* **211**, 1169–1171
- Mackie, G. O. 1979 Is there a conduction system in sponges? *Colloques int. Cent. natn. Rech. scient.*, no. 291 (Biologie des spongiaires), pp. 145–151.
- Mackie, G. O. & Singla, C. L. 1983 Studies on hexactinellid sponges I. Histology of *Rhabdocalyptus dawsoni* (Lambe, 1873). *Phil. Trans. R. Soc. Lond.* **B 301**, 365–400.
- Mackie, G. O., Lawn, I. D. & Pavans de Ceccatty, M. 1983 Studies on hexactinellid sponges II. Excitability, conduction and coordination of responses in *Rhabdocalyptus dawsoni* (Lambe, 1873). *Phil. Trans. R. Soc. Lond.* **B 301**, 401–418.
- Minchin, E. A. 1900 Porifera. *A treatise on zoology*, pt 2 (The Porifera and Coelentera; ed. E. R. Lankester), ch. 3, pp. 1–178. London: A. C. Black.
- Reid, R. E. H. 1955 On the Gelatinosa and Nuda of Bidder. *Ann. Mag. nat. Hist.* (12) **8**, 721–723.
- Reid, R. E. H. 1957 On Hexactinellida, ‘Hyalospongea’, and the classification of siliceous sponges. *J. Paleont.* **31**, 282–286.
- Reid, R. E. H. 1958 A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part I. *Palaeontogr. Soc. [Monogr.]* **111**, 1–46.
- Reid, R. E. H. 1963 Hexactinellida or Hyalospongea. *J. Paleont.* **37**, 232–243.
- Reiswig, H. M. 1971 Axial symmetry of sponge spicules and its phylogenetic significance. *Cah. Biol. mar.* **12**, 505–514.
- Reiswig, H. M. 1979 Histology of Hexactinellida (Porifera). *Colloques int. Cent. natn. Res. scient.*, no. 291 (Biologie des spongiaires), pp. 173–180.
- Rigby, J. K. & Nitecki, M. H. 1975 An unusually well preserved heteractinid sponge from the Pennsylvanian of Illinois and a possible classification and evolutionary scheme for the Heteractinida. *J. Paleont.* **49**, 329–339.
- Salvini-Plawen, L. 1978 On the origin and evolution of the lower Metazoa. *Z. Zool. syst. Evolutionforsch.* **16**, 40–88.
- Schmidt, O. 1870 *Grundzüge einer Spongien-fauna des Atlantischen Gebietes*. Leipzig: Engelmann.
- Schulze, F. E. 1887 Report on the Hexactinellida collected by H.M.S. *Challenger* during the years 1873–1876. *Rep. Sci. Res. Challenger, Zool.* **21**.
- Schulze, F. E. 1899 Zur Histologie der Hexactinelliden. *Sber. dt. Wiss. Berlin* **14**, 198–209.
- Schulze, F. E. 1904 Hexactinellida. *Wiss. Ergebn. dt. Tiefsee-Exped. ‘Valdivia’* **4**.
- Sollas, I. B. J. 1909 Porifera (sponges). In *The Cambridge natural history*, vol. 1 (ed. S. F. Harmer & A. E. Shipley), ch. 7–9, pp. 163–242. London: MacMillan.
- Sollas, W. J. 1887 Sponges: In *Encyclopaedia Britannica* (9th edn), vol. 22, pp. 412–429. Edinburgh: Adam & Charles Black.
- Stearn, C. W. 1975 The stromatoporoid animal. *Lethaia* **8**, 89–100.
- Stearn, C. W. 1980 Classification of the Paleozoic stromatoporoids. *J. Paleont.* **54**, 881–902.
- Thomson, C. W. 1868 On the ‘vitreous’ sponges. *Ann. Mag. nat. Hist.* (4) **1**, 114–132.
- Tuzet, O. 1973 Introduction et place des spongiaires dans la classification. In *Traité de zoologies*, vol. 3 (Spongiaires; ed. P.-P. Grassé), pp. 1–26. Paris: Masson.
- Vacelet, J. 1981 Éponges hypercalcifiées (Pharetronides, Sclerosponges) des cavités de récifs coralliens de Nouvelle-Calédonie. *Bull. Mus. natn. Hist. Nat.* **3**, 313–351.
- Vosmaer, G. C. J. 1885 Spongien (Porifera). *Die Klassen und Ordnungen des Tierreichs*, vol. 2 (4) (ed. H. G. Bronn), pp. 177–369, and pl. 19–25. Leipzig: C. F. Winter. (Bound with parts 1–5 with title page dated 1887.)
- Zoological Record, The* 1976–1981 Porifera together with Archaeocyatha. *Zool. Rec.* **110–115** (covering years 1973–1978), §§3.