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Comprehensive Revision of a Worldwide Collection of Freshwater Sponges (Porifera: Spongillidae)

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FRANK A. TAYLOR
Director, United States National Museum

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Contents

Comprehensive Revision of a Worldwide Collection of Freshwater Sponges (Porifera-Spongillidae)

Introduction

In spite of the fact that serious scientific efforts in the taxonomic study of freshwater sponges were begun in the mid-19th century, and that a great number of subsequent investigators have contributed a massive amount of additional descriptive information, the taxonomy of this group has remained in a most chaotic state. Following Bowerbank's (1863) initial revision of all species of *Spongilla*, Gray (1867) was first to establish useful criteria for their generic differentiation and to erect six new genera in addition to *Spongilla* Lamarck. Unfortunately, this system was criticized and its validity questioned by Carter (1881a), who claimed that Gray established his new genera without having seen Bowerbank's material upon which they were erected. Although fully unjustified in doing so, Carter (1881a) altogether ignored Gray's existing generic names and devised his own system for the inclusion of Bowerbank's species and subsequently collected material. Thus it happened that Gray's well-established genera fell into complete obscurity for many decades, and Carter's system became firmly established, without being seriously challenged by any subsequent taxonomist.

From the turn of this century, several attempts were made to revise comprehensively the status of the ever increasing numbers of species. After the publication of the first bibliography of all freshwater sponges by Weltner (1893), it was chiefly Annandale (1906–1919) who began to build the foundations to an improved and modernized knowledge of spongillid taxonomy. Annandale reestablished some of Gray's generic names, at least at a subgeneric level, and added a number of well-defined new genera to the conglomerate systems of Gray and Carter. Additional revisions were subsequently undertaken by Gee (1926–1937), Schröder (1926–1942), and Arndt (1923–1938), to name just the most important contributors. Generic revisions were attempted by De Laubenfels (1936) and Jewell (1952). However, in spite of the fact that all these investigations have certainly helped to overcome a number of taxonomic difficulties, they seemed to have little effect on the stability of taxonomic nomenclature.

Nathaniel Gist Gee was the first investigator to realize that only a renewed thorough study of all types and syntypes ever deposited and a detailed examination of all genera and species would help in cutting this Gordian knot of taxonomic chaos. Already in possession of a huge collection of freshwater sponges from China and other parts of southeastern Asia, Gee began with systematic collections of data pertaining to almost all spongillids of the world and secured type or syntype material of a great number of species. However, his untimely death brought this promising project to a standstill. His giant collection and comprehensive catalog of species, now in the possession of the Smithsonian Institution, remain mute witnesses of his untiring efforts.

In the mid-fifties another American spongillid investigator, James T. Penney, decided that a thorough revision of all genera and species of freshwater sponges could no longer be delayed. His systematic efforts in securing and studying all the existing type species, his tenacity in requesting and obtaining spongillid material from all major and minor institutions of the world, and finally his discovery of Gee's giant though untapped collection in the Smithsonian Institution, all resulted in the accumulation of data unavailable to any previous investigator. In view of this ever increasing information, Penney faced various difficulties in dealing with all genera simultaneously, and finally decided to approach this problem by a revision of natural groups of genera. His first choice was the Meyeninae, a former subfamily comprising all species with birotulate gemmoscleres, for which he outlined the necessary data for subsequent publication. Unfortunately, Penney's sudden death in 1964 once again halted the progress of spongillid taxonomy, and his comprehensive and untiring efforts seemed to have been made in vain.

Realizing the great importance of Penney's huge collection of material and unpublished data, upon the recommendation of Dr. B. Theodore Cole, the University of South Carolina finally entrusted the writer of this paper with its study and review. Beginning in August 1965, this task consisted of the examination of several thousands of slides, their comparison with existing type or syntype specimens, their correlation with various handwritten notes and photographs by the late author, and finally, to attempt a thoroughly revised taxonomic system. In view of the voluminous material available, the writer considered it imperative to revise all true gemmule-producing species, instead of merely elaborating Penney's outlined account of the Meyeninae. As the result of these additional studies, it was possible to review the status of 18 genera, including 95 fully revised species, and to demonstrate the fallacy of a subdivision of the family Spongillidae by using gem-

mosclere characteristics. This paper, therefore, is the result of two independent studies. J. T. Penney was responsible for the accumulation of a worldwide collection of almost all known genera and species, prepared thousands of slides as well as an elaborate cataloging system, and had begun to outline a thorough revision of the subfamily Meyeninae as the first phase of his planned publication. A. A. Racek reexamined the above collection and extensive additional material from Australasia, Europe, and eastern Asia, reviewed the entire collection of freshwater sponges in the Smithsonian Institution, restored Gray's taxonomic system, established three neotypes, one new species, and three new genera from the material studied, and finally prepared the present report. Whenever the viewpoint of the late author could be established from the notes available or from previous correspondence with the coauthor, reference is made in the text to the "present authors." Personal views or necessary actions of the coauthor alone are denoted by the word "writer" wherever applicable. The entire collection of slides and specimens amassed by the late author and the holotype of one new species have been deposited in the U.S. National Museum, Smithsonian Institution. In addition, some paratypes and part of Gee's collection are now also present in the collection of the Australian Museum, Sydney.

The authors wish to express thanks to all the many persons and institutions throughout the world whose kind cooperation has enabled this study to reach its present form. The international response of a great number of museums, private collectors, and spongillid specialists to the late author's request for comparative material was truly overwhelming. Specimens arrived for this investigation from Denmark, Norway, Sweden, Finland, England, Ireland, the U.S.S.R., Czechoslovakia, Yugoslavia, Hungary, Poland, Switzerland, Austria, Germany, France, Belgium, the Netherlands, India, Indonesia, Malaysia, Thailand, Japan, the Philippines, Australia, South Africa, Argentina, Bolivia, Brazil, Mexico, Canada, and from many parts of the United States.

On his own behalf, the writer is greatly indebted to a number of persons, who in so many ways have contributed to the progress of this huge project: to Dr. B. Theodore Cole, Head, Department of Biology, University of South Carolina, for his constant encouragement, unflagging cooperation, and most generous hospitality; to Dr. F. Harrison, former research assistant to the late author, for his extensive and cheerful assistance in the examination and correlation of the material studied; to Drs. D. F. Squires, W. L. Schmitt, and D. L. Pawson of the Smithsonian Institution for their kind help offered during comparative studies in Washington, D.C.; to Dr. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden, for valuable

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Morphological Features and Definitions

The various morphological criteria of freshwater sponges have never been subjected to detailed comparative studies, even though the nomenclature employed within this superficial group of sponges remained fairly uniform over the past 100 years of systematic research. It is most regrettable that a morphological nomenclature common to both freshwater and marine sponges has not yet been devised, since such a development would greatly assist in the assessment of phylogenetic relationships within all Porifera. However, so long as additional data are unavailable, it is thought advisable to retain in this paper the nomenclature used by the majority of spongillid investigators.

Features of systematic importance in freshwater sponges are the following:

Form and consistency.—Characteristic modes of growth vary with the age of the sponge, and consequently are of importance only in mature specimens; growths may range from thin to thick crusts or cushions, be of bulbous or otherwise massive nature, or display branching, subbranching, or pseudobranching projections. Characteristic consistencies are chiefly determined by the amount of spongin present in the skeletal meshwork, only occasionally by other factors.

Color.—The coloration of spongillids is usually determined by the presence or absence of zoochlorellae within the tissues of the sponge, rarely by the presence of a specific pigment (green or purple) or by adventitious sediments. Apart from a few well-established cases, the coloration seems therefore of little taxonomic significance.

Symplasm and dermal membrane.—Symplasm is herewith suggested as the replacement of the term "parenchyma" of earlier authors; although "dermal membrane" is another outdated and even

ambiguous term, it is retained in this paper for simplicity; the "bubble cells" or "vesicular cells" (Blasenzellen), recorded as a reliable diagnostic feature by many previous authors, were found to lack the taxonomic importance originally accredited to them.

Megascleres.—Under normal conditions, shape and structure of the skeleton spicules remain intraspecifically constant, although ecomorphic alterations can be brought about by adverse environmental conditions; a clear differentiation between amphioxea and amphistrongyla is often difficult in specimens with abruptly pointed amphioxous scleres, and transitional series are frequently produced by the same individual; the relative width of these scleres and the width of their axial canal are subject to great variations and do not represent reliable criteria.

Microscleres.—True free microscleres ("dermals" or "flesh spicules" of earlier authors) represent a very important and intragenerically constant criterion, which often can also be used for specific discrimination. These scleres must not be confused with occasionally abundant immature gemmoscleres (e.g., *Radiospongilla cerebellata* and some of its congeners), since the former are always of quite distinct shape and structure; in form these scleres range from smooth or uniformly spined amphioxea to acerate scleres with large raylike central spines, and finally to stellate spicules which often are inflated to form a "centrum"; minute birotulate microscleres are characteristic of two spongillid genera, irrespective of the presence or absence of birotulate gemmoscleres.

Gemmoscleres.—A new term suggested by the writer and never used before by any other specialist. The gemmoscleres represent the most important taxonomic criterion, in particular in those spongillids which lack true microscleres, and without their presence reliable identification is usually impossible; there is a full transition in shape and structure of these scleres, leading from smooth or spiny amphioxea and amphistrongyla to scleres with unilateral or concentric aggregations of terminal spines, birotulate spicules with various marginal incisions, birotulates possessing rotules with entire margins, and finally to tubelliform and parmuliform scleres; ecomorphic malformations are frequent in adverse environments, resulting in the production of freak scleres; similar malformations can often also be observed as the probable result of hybridization.

Gemmules.—The most useful diagnostic features of these asexual reproductive bodies are structure and width of their pneumatic layer, structure of their micropyle, shape and curvature of their foraminal tubule, presence or absence of foraminal cirri, and the specific arrangement of their gemmoscleres. Their actual size and shape and their relative abundance are features of secondary importance, since

these are subject to conspicuous seasonal variations; however, position, fixation, and aggregation of the gemmules are often useful additional criteria, particularly in those genera and species in which they firmly adhere to the substratum.

Abbreviations Used in the Text

AAR—A. A. Racek
AmstM—Zoologisch Museum, Amsterdam
AusM—Australian Museum, Sydney
BM—British Museum of Natural History
HM—Zoologisches Museum, Hamburg
IM—Indian Museum
JTP—J. T. Penney
LeidM—Rijksmuseum van Natuurlijke Historie, Leiden
MCB—Musée du Congo Belge (Musée Royal de l'Afrique Centrale, Tervuren)
MG—Muséum d'Histoire Naturelle, Genève
MNHP—Muséum d'Histoire Naturelle, Paris
PAS—Philadelphia Academy of Sciences
RMS—Naturhistoriska Riksmuseet, Stockholm
USNM—United States National Museum
ZMB—Zoologisches Museum, Berlin

Family Spongillidae

Spongilladae Gray, 1867, p. 550.
Spongillidae Carter, 1881a, p. 77.—Vejdovsky, 1883b, p. 15.—Potts, 1887, p. 158.—Weltner, 1895, p. 114.—Annandale, 1911c, p. 27.—De Laubenfels, 1936, p. 34.—Jewell, 1952, p. 445.—Penney, 1960, p. 4.

In spite of the latest revising efforts of De Laubenfels (1936) and Jewell (1952), this doubtlessly conglomerate family of Demospongiae must still be considered as extremely ill-defined, if defined at all. De Laubenfels' (1936, p. 34) statement that "This family as here considered is quite frankly defined as consisting of those sponges occurring normally in fresh or occasionally in brackish water," may be taken as a clear indication of the deficiency of our present information on the interrelationship of the many "spongillid" genera to each other, as well as to those of the marine Demospongiae in general. While the relationship of most gemmule-producing freshwater genera is by now fairly well established, the affinities of a great number of normally fresh- or brackish-water Porifera have yet to be demonstrated. It is therefore quite obvious that a subdivision of such a most superficially defined family into a number of subfamilies not only is fully unwarranted, but at present absolutely impossible. The data obtained from the present study have already demonstrated the fallacy of a further retention of the two subfamilies Spongillinae Vejdovsky and Meyeninae Vejdovsky, separated from each other

merely on account of the presence of rodlike or birotulate gemmoscleres, respectively.

Since a redefinition of the family Spongillidae appears to be an impossible task until further detailed comparative investigations involving all freshwater genera of Demospongiae become available, it seems advisable to exclude the following atypical or ill-known genera from the present revision.

Baikalospongia Annandale—removed from the family Spongillidae and placed into a new family, Adociidae, by De Laubenfels (1936).
Baicalolepis Makuschok—gemmules apparently not produced.
Cortispongilla Annandale—gemmules apparently not produced.
Lubomirskia Dybowsky—gemmules apparently not produced.
Nudospongilla Annandale—gemmules, if present, devoid of foramina, pneumatic layer, and spicules.
Ochridaspongia Arndt—gemmules apparently not produced.
Pachydictyum Weltner—gemmules apparently not produced.
Potamolepis Marshall—gemmules apparently not produced.
Swartschewskya Makuschok—gemmules apparently not produced.

The following 18 genera of gemmule-producing freshwater sponges as the typical representatives of the family Spongillidae are fully revised in this paper:

Acalle Gray
Anheteromeyenia Schröder
Corvomeyenia Weltner
Corvospongilla Annandale
Dosilia Gray
Drulia Gray
Ephydatia Lamouroux, redefined
Eunapius Gray, redefined
Heteromeyenia Potts, restricted
Heterorotula, new genus
Metania Gray
Pectispongilla Annandale
Radiospongilla, new genus
Spongilla Lamarck, restricted
Stratospongilla Annandale
Trochospongilla Vejdovsky
Umborotula, new genus
Uruguaya Carter

Genus *Spongilla* Lamarck, 1816, restricted

Spongia Linnaeus, 1758, p. 1348 (part).
Spongilla Lamarck, 1816, p. 98 (part).—Johnston, 1842, p. 110 (part).—Bowerbank, 1863, p. 441 (part).—Gray, 1867, p. 552 (part).—Dybowsky, 1880, p. 5 (part.)—Carter, 1881a, p. 86 (part).—Vejdovsky, 1883, p. 15 (part).—Retzer, 1883, p. 17 (part).—Lendenfeld, 1887, p. 88 (part).—Potts, 1887, p. 182 (part).—Mackay, 1889, p. 87 (part).—Weltner, 1895, p. 116 (part).—Girod, 1899, p. 107 (part).—Annandale, 1909e, p. 559 (part); 1909b, p. 106 (part); 1912d, p. 384 (part); 1918a, p. 210 (part).—Arndt, 1926, p. 341 (part).—Gee, 1931e, p. 49 (part).—De Laubenfels, 1932, p. 110 (part).—Jewell, 1952, p. 445 (part).—Penney, 1960, p. 11 (part).
Euspongilla Vejdovsky, 1883, p. 15; *in* Potts, 1887, p. 172.—Wierzejski, 1885, p. 32.—Annandale, 1911c, p. 69 (part).
(Not *Spongilla* Wierzejski, 1885, p. 17=*Eunapius* Gray, 1867, p. 552).

Type species.—By subsequent selection (Annandale 1911c) *Spongia lacustris* Linnaeus, 1758.

DEFINITION.—Megascleres invariably slender to stout amphioxea, as a rule completely smooth.

Microscleres always present in dermal membrane, usually also in symplasm; they are rather slender amphioxea, conspicuously different from gemmoscleres and, as a rule, entirely spined.

Gemmoscleres, whenever present, stout and strongly spined amphioxea to amphistrongyla with a varying curvature.

Gemmules abundant in maturing sponge, large and spherical, usually scattered throughout sponge; when occasionally grouped at base never form a distinct pavement layer; usually with a moderately strong granular pneumatic layer with very small nonpolygonal air spaces, and with gemmoscleres embedded in this layer more or less tangentially; occasionally without any trace of a pneumatic layer and consequently lacking an armature of gemmoscleres; gemmules then either totally unprotected, or encased in surrounding groups of normal or slightly modified megascleres; foramen or foramina simple to slightly cup-shaped, never distinctly tubular.

Sponges usually massive, or producing long cylindrical branches arising from an irregular base; often of a drab green to bright green color owing to the presence of zoochlorellae; occasionally without such an association and consequently without particular coloration. Consistency moderately firm but often brittle.

Distribution of genus cosmopolitan, although all species possess pronounced zoogeographical boundaries.

DISCUSSION.—The genus *Spongilla* Lamarck, as here restricted, is characterized by the presence of true microscleres in both inner symplasm and dermal membrane, by the structure of the gemmular pneumatic layer which consists of small and nonpolygonal air spaces, and by the tangential or irregular arrangement of the gemmoscleres. It consists of two distinct groups of species, differing from each other in the characteristics of their microscleres as well as in some other morphological features. The first group, often displaying a branching mode of growth and possessing uniformly spined microscleres, is represented by *S. lacustris*, *S. helvetica*, *S. aspinosa*, *S. arctica*, and *S. inarmata*, all in need of additional revision; the second by the closely related species *S. alba*, *S. cenota*, new species, and *S. wagneri*, in which the sponges are more or less cushion-like, and the spines on their microscleres increase in length towards the center of the spicule. The remainder of the species formerly assigned to this genus are now included in *Eunapius* Gray, *Stratospongilla* Annandale, and *Radiospongilla*, new genus, respectively.

Spongilla lacustris (Linnaeus, 1758)

PLATE 1, FIGURES 4, 5

Spongia lacustris Linnaeus, 1758, p. 1348.—De Laubenfels, 1932, p. 110.

Spongilla ramosa Lamarck, 1816, p. 100.—Dutrochet, 1828, p. 205.

Ephydatia lacustris Lamouroux, 1816, p. 7.

Spongilla lacustris Johnston, 1842, p. 110.—Lieberkühn, 1856, p. 510.—Bowerbank, 1863, p. 462; 1874, p. 153.—Gray, 1867, p. 552.—Dybowsky, 1878, p. 53; 1880, p. 6; 1882, p. 6; 1884, p. 507.—Carter, 1881a, p. 87.—Potts, 1884b, p. 216; 1886, p. 228; 1887, p. 186.—MacKay, 1889, p. 90.—Weltner, 1895, p. 114; 1909, p. 181.—Girod, 1899, p. 107.—Annandale, 1908d, p. 245; 1909d, p. 401; 1911c, p. 69; 1918a, p. 207.—Kirsch, 1909, p. 36.—Stephens, 1912, p. 6; 1920, p. 222.—Topsent, 1914, p. 538.—Smith, 1921, p. 13; 1930, p. 183.—Rezvoj, 1926b, p. 64; 1928a, p. 224; 1929a, p. 283; 1930, p. 176.—Arndt, 1926, p. 342; 1928a, p. 62; 1931, p. 37; 1932b, p. 299; 1932a, p. 5.—Gee, 1926c, p. 110; 1927d, p. 258; 1927a, p. 1; 1927b, p. 57; 1928, p. 221; 1929b, p. 13; 1930a, p. 88; 1931d, p. 41; 1931a, p. 501; 1932c, p. 39; 1934, p. 248; 1937, p. 285.—Schröder, 1926, p. 248; 1932b, p. 111; 1938a, p. 295.—Gee and Wu, 1927, p. 258.—Kozhoff, 1930, p. 156.—De Laubenfels, 1932, p. 110.—Old, 1932c, p. 239; 1932b, p. 445; 1932a, p. 131; 1936b, p. 11.—Pesson, 1934, p. 52.—Sasaki, 1934, p. 219; 1940, p. 166.—Jewell, 1952, p. 448.—Zimmer, 1936, p. 126.—Wurtz, 1950, p. 1.—Eshleman, 1950, p. 37.—Suvatti, 1950, p. 3.—Simon, 1952, p. 79; 1953, p. 207.—Pennak, 1953, p. 89.—Penney, 1954, p. 156; 1956, p. 37; 1960, p. 20.

Spongilla paupercula Bowerbank, 1863, p. 470.—Carter, 1881a, p. 86.—Potts, 1882b, p. 70; 1887, p. 187.—Jewell, 1952, p. 448.

Spongilla dawsoni Bowerbank, 1863, p. 467.—Gray, 1867, p. 553.—Potts, 1887, p. 187.—Gee, 1931e, p. 36.—Jewell, 1952, p. 448.

Eunapius paupercula Gray, 1867, p. 552.

Spongilla lieberkühni Noll, 1870, p. 173.—Retzer, 1883, p. 18.—Vejdovsky, *in* Potts, 1887, p. 172.—Schröder, 1926, p. 249.

Spongilla flexispina Dawson, 1878, p. 1.—Potts, 1887, p. 187.

Spongilla abortiva Potts, 1880a, p. 330; 1887, p. 187.—Gee, 1931e, p. 31.

Spongilla jordanensis Vejdovsky, 1877, p. 212; *in* Potts, 1887, p. 172.

Spongilla montana Potts, 1880a, p. 330.

Spongilla multiforis Carter, 1881a, p. 88.—Potts, 1887, p. 187.—Gee, 1931e, p. 44.—Jewell, 1952, p. 448.

Euspongilla lacustris Vejdovsky, 1883, p. 15.—Wierzejski, 1885, p. 1.—Traxler, 1894, p. 363.—Weltner, 1893, p. 12.—Hanitsch, 1895, p. 125.—Levander, 1901, p. 56.—Rousseau, 1906, p. 124.—Lühe, 1908, p. 409.—Arndt, 1923, p. 74.—Gee, 1931e, p. 41.

Spongilla erinaceus Retzer, 1883, p. 24 (part).—Schröder, 1926, p. 249.—Gee, 1931e, p. 37.

Euspongilla jordanensis Vejdovsky, 1883, p. 20.

Euspongilla jordanensis var. *druliaeformis* Vejdovsky, 1883, p. 22.—Gee, 1931e, p. 37.

Spongilla mirabilis Retzer, 1883, p. 25 (part).—Schröder, 1926, p. 249.

Spongilla rhenana Retzer, 1883, p. 21.—Weltner, 1895, p. 114.—Girod, 1899, p. 108.

Euspongilla lacustris var. *macrotheca* Vejdovsky, 1883, p. 18.
Spongilla lacustris var. *dawsoni* MacKay, 1885, p. 233.
Spongilla lacustrioides MacKay, 1885, p. 240.—Potts, 1887, p. 187.
Spongilla lacustris var. *abortiva* Potts, 1887, p. 191.
Spongilla lacustris var. *montana* Potts, 1887, p. 192.
Spongilla lacustris var. *lehighensis* Potts, 1887, p. 193.
Spongilla lacustris var. *multiforis* Potts, 1887, p. 192.
Spongilla lacustris var. *paupercula* Kellicott, 1891, p. 101.—Arndt, 1926, p. 342; 1928a, p. 64.—Gee, 1931e, p. 45.
Euspongilla lacustris var. *lieberkühni* Levander, 1901, p. 56.—Gee, 1931e, p. 41.
Spongilla microgemmata Swartschewsky, 1901, p. 346.—Annandale, 1918a, p. 211.—Gee, 1931e, p. 43.
Spongilla lacustris var. *ineptorum* Annandale, 1919c, p. 86.
Spongilla crustacea Kozhoff, 1925, p. 52; 1930, p. 158.
Spongilla fenestrata Kozhoff, 1925, p. 50; 1930, p. 158.
Spongilla lacustroidcs Kozhoff, 1925, p. 45; 1930, p. 158.—Gee, 1931e, p. 41.
Spongilla lacustris var. *rhenana* Arndt, 1926, p. 342; 1928a, p. 65.—Penney, 1960, p. 23.
Spongilla lacustris var. *jordanensis* Arndt, 1926, p. 342; 1928a, p. 64.—Schröder, 1929, p. 87; 1932b, p. 129; 1938a, p. 295.—Penney, 1960, p. 23.
Spongilla lacustroides corticea Kozhoff, 1930, p. 158.
Spongilla lacustris var. *crustacea* Gee, 1931e, p. 38.—Penney, 1960, p. 22.
Spongilla lacustris var. *fenestrata* Gee, 1931e, p. 38.—Penney, 1960, p. 22.
Spongilla lacustris var. *lacustroides* Gee, 1931e, p. 40.—Penney, 1960, p. 23.

Material.—Extremely numerous specimens and slide material; EUROPE: Sweden, Finland, Netherlands, Belgium, France, Switzerland, Germany, Austria, Hungary, Czechoslovakia, Poland, Yugoslavia, Italy, U.S.S.R.; NORTH AMERICA: U.S.A., Canada; ASIA: U.S.S.R., China, Japan.

Description.—Mature sponge almost invariably producing long cylindrical branches arising from an irregular base; in lotic environment branches often reduced or absent; surface typically hispid, rarely even; oscula rather inconspicuous and small, dermal membrane well developed. Skeleton consisting of polyspicular longitudinal fibers, coated together in thick sheaths of spongin; and of a varying number of secondary transverse fibers. Consistency of live sponge soft but fairly firm, skeleton of dry sponge extremely brittle.

Megascleres slightly curved or straight amphioxea, usually fusiform, invariably entirely smooth; length range 200–350 μ, width range 6–18 μ.

Microscleres in varying abundance in dermal membrane and symplasm, slightly curved amphioxea, entirely covered with small spines or granules of almost equal size and distribution; length range 70–130 μ, width range 2–8 μ.

Gemmoscleres, whenever present, rather stout and slightly to strongly curved amphioxea or amphistrongyla, usually covered with strong, curved spines, only exceptionally smooth; length range 80–130 μ, width range 3–10 μ.

Gemmules abundant in mature sponge, scattered throughout its body, spherical and large; pneumatic layer either well developed, ill defined, or altogether absent. Whenever this layer is present, gemmoscleres embedded in an irregular manner; as a rule absent when this layer is lacking; foramen usually simple, or bearing a shallow peripheral collar; diameter of gemmules ranging 500–800 μ.

Distribution.—Owing to previous taxonomic confusion of this species with others, now belonging to another genus, *S. lacustris* has originally been considered a cosmopolitan species; however, the present studies were able to establish beyond doubt that it is restricted to the Northern Hemisphere, with its greatest expansion in cold-temperate regions.

Color in life.—Usually drab to bright green owing to the presence of a varying number of zoochlorellae.

Discussion.—This species has been adequately described in previous literature, and the present studies have not revealed any additional criteria for discussion. However, it is possible that future studies of the material amassed will indicate a speciation trend in distant populations, and in particular a closer study appears desirable of those specimens (or races) which display a uniform character of their gemmular pneumatic layer. At present no attempt is made to indicate or demonstrate a possible subspecific status for these apparently constantly differing forms, since specimens were examined in which all the three types of gemmules mentioned above were found to be present. Nevertheless, it seems interesting that the majority of cold-temperate and subarctic specimens examined possess gemmules with a rather ill-defined or absent pneumatic layer, a feature apparently shared with those of *S. arctica* Annandale; whereas the gemmules of most central and southern European specimens display gemmules with a rather thick pneumatic coat possessing a great number of gemmoscleres. Should a future revision of this material clearly indicate such a speciation trend, some of the old "varietal" names such as *S. l. paupercula* (Bowerbank) and perhaps also *S. l. jordanensis* Vejdovsky should be revived. The same applies to a number of other species, described as such in previous literature, and in particular to the *S. lacustroides* Kozhoff group of Asian sponges here listed as synonyms of *S. lacustris* pending further detailed work.

Since a type specimen apparently has never been designated, and most certainly does not exist today, a neotype of *Spongia lacustris* Linnaeus therefore had to be selected. This specimen is in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden, Reg. No. 1053, coll. D. v. d. Kuyl, Vlaardingschevaart, Holland, 17. ix. 1941. The mode of growth and spicular components of this neotype

correspond in all details with the descriptions of *Spongilla lacustris* Auct. in previous literature.

Spongilla arctica Annandale, 1915

Spongilla (*Euspongilla*) *arctica* Annandale, 1915d, p. 1; 1918a, p. 211.—Rezvoj, 1928, p. 220; 1929a, p. 284.—Arndt, 1931, p. 35.—Penney, 1960, p. 13.

Material.—Fraction of type, and two slides obtained from the type specimen by N. Gist Gee.

Description.—Sponge, according to Annandale (1915d), consisting of small nodular masses; surface smooth, oscula few and inconspicuous; a delicate brownish membrane present at the base, dermal membrane well developed. Skeleton consisting of slender spicule fibers each encased in spongin, and arising from the basal membrane, running upwards at a slanting angle; these fibers frequently branching in a dichotomous manner with delicate webs of spongin extending across the forks; single spicules or definite transverse fibers occasionally running from one branch to another; in addition to the organized skeleton numerous loose megascleres free in the symplasm of the sponge, and forming an irregular layer at the base; or forming cages around single gemmules or groups of gemmules. Consistency of live sponge soft.

Megascleres of greatly varying size, in the majority small, slender, fusiform amphioxea, entirely smooth; length range 154–280 μ, width range 4–14 μ.

Microscleres present in dermal membrane but apparently absent from symplasm, very small, slender, and fusiform amphioxea, covered with minute straight spines; length range 32–70 μ, width range 2–4 μ.

Gemmoscleres rather robust and slightly curved amphistrongyla, covered with comparatively few but stout spines that are more numerous at the tips of the scleres; length range 80–140 μ, width range 4–6 μ.

Gemmules variable in diameter, ranging 300–700 μ, spherical; pneumatic layer usually extremely thin, often totally absent; gemmoscleres scarce, embedded in this layer tangentially; foramen typical for the genus, simple, or bearing a slightly elevated small collar, not tubular.

Distribution.—Ranging from the Arctic Circle to central U.S.S.R.

Color in life.—Not yet observed.

Discussion.—Annandale's (1915d) original description is in part erroneous, and Rezvoj (1928) as well as Arndt (1931) have corrected some apparent misconceptions. An examination of the type material revealed that the pneumatic layer of the gemmules is invariably ill-defined to completely lacking, quite contrary to Annandale's statement; also the porus, described by Annandale as tubular, is

simple in all gemmules examined, or merely bears a slightly elevated collar. While *S. arctica* displays a most unique arrangement of abundant spongin membranes throughout its skeleton, all other criteria used for its separation from *S. lacustris* could not serve such a purpose. Although future revisions may demonstrate that these two species should be united, it is advisable to retain the separate status of *S. arctica* until more material will be available.

Rezvoj (1928) listed and figured two types of microscleres, one typical amphioxea, the other slender amphistrongyla. Although both these scleres are also present in the type material, the latter must be considered immature gemmoscleres.

Spongilla helvetica Annandale, 1909

PLATE 1, FIGURES 6, 7

Spongilla (*Euspongilla*) *helvetica* Annandale, 1909a, p. 367.
Spongilla helvetica(?) Arndt, 1926, p. 342.—Gee, 1931e, p. 39; 1932c, p. 38.—Penney, 1960, p. 19.

MATERIAL.—Fraction of type and syntype material, and slides from these.

DESCRIPTION.—Sponge, according to Annandale (1909a), forming crusts of varying dimensions, without branches; surface smooth, oscula distinct but small; dermal membrane delicate and adhering the symplasm. Skeleton consisting of slender spicule fibers encased in spongin, and transverse spicule tracts. Consistency of live sponge soft.

Megascleres rather short and fusiform amphioxea, generally smooth, very exceptionally covered with a few scattered conical spines; free megascleres of smaller dimensions also both in dermal membrane and symplasm; length range 148–200 μ, width range 4–9 μ.

Microscleres scarcely present in dermal membrane and symplasm, also sometimes in the vicinity of the gemmules; they are slender and small fusiform amphioxea, covered with minute straight spines or granules; length range 24–55 μ, width range 1–2 μ.

Gemmoscleres rather rare, slender and slightly curved, abruptly pointed amphioxea, covered with numerous small spines which are aggregated at the tips of the scleres; length range 32–68 μ, width range 2–5 μ.

Gemmules variable in diameter, ranging 300–650 μ, spherical; pneumatic layer absent; gemmoscleres occasionally lying tangentially on gemmular membrane, often lacking altogether; foramen or foramina simple, never tubular, occasionally bearing a slightly elevated peripheral collar.

DISTRIBUTION.—At present known only from the type locality, Lake Geneva, Switzerland.

Color in life.—Not yet observed.

Discussion.—The status of this species cannot possibly be fully elucidated until further material will become available. *S. helvetica* shows close affinities to the *S. lacustris* complex, and will probably be found synonymous with the latter. In view of the paucity of material examined, however, it seems advisable to retain the separate status of *S. helvetica* in order not to obscure possible taxonomic evidence.

Annandale (1909a) did not mention the presence of true gemmoscleres, a fact which immediately separates *S. helvetica* from both *S. inarmata* Annandale and *S. aspinosa* Potts. The cages of megascleres around the gemmules in *S. helvetica*, as recorded by Annandale, could not be observed in the material available for this study.

Spongilla aspinosa Potts, 1880

Spongilla aspinosa Potts, 1880b, p. 357; 1887, p. 184.—Kellicott, 1891, p. 102.—Weltner, 1895, p. 114.—Smith, 1921, p. 17.—Gee, 1931e, p. 32; 1932c, p. 36.—Old, 1932a, p. 131; 1932b, p. 468.—Eshleman, 1950, p. 38.—Penney, 1960, p. 13.—(Not *Spongilla aspinosa* Annandale and Kawamura, 1916, p. 6= *Spongilla inarmata* Annandale).

Material.—Sponge fragments and slides: Deep Creek Basin, Virginia; N. Gist Gee, no number, New Jersey.

Description.—Sponge, according to Potts (1880), encrusting, thin, producing long and waving branches from an irregular base; oscula small and inconspicuous. Skeleton consisting of slender spicule fibers encased in spongin, and transverse spicule tracts. Consistency of live sponge soft.

Megascleres slender and fusiform amphioxea, completely smooth; free megascleres of somewhat smaller dimensions often in dermal membrane and symplasm, sometimes also forming loose layer around gemmules; length range 155–215 μ, width range 3–8 μ.

Microscleres not restricted to either dermal membrane or symplasm, but apparently very rare; they are small and slender amphioxea, invariably completely smooth; length range 30–42 μ, width range 1–1.5 μ.

Gemmoscleres not yet recorded.

Gemmules rather large and spherical, ranging 450–700 μ; pneumatic layer extremely thin and granular, but much firmer than in the "unarmed" type of gemmules of *S. lacustris;* smaller megascleres often embedded in this layer, occasionally also freely curving around the gemmules; foramen singular, slightly elevated, bearing a shallow peripheral collar.

Distribution.—At present known only from the United States.

Color in life.—Bright green, due to the presence of zoochlorellae.

Discussion.—The absence of gemmoscleres, and the somewhat mutilated condition of the material examined during the present

study does not permit reliable conclusions as to the relationship of this species to others of the genus, and it is thought advisable to retain its separate specific status until more material will be studied. From all other species of the genus, *S. aspinosa* differs by the presence of smooth microscleres, and from the *S. lacustris* group by the much firmer gemmular membrane, as well as by the participation of a smaller group of megascleres in gemmular protection.

Gee (1928) considered this species to be synonymous with *S. inarmata* Annandale, comparing the arrangements of megascleres around the gemmules, and the absence of gemmoscleres in both species. However, the existing differences between these two species, particularly the grossly different development of the gemmular pneumatic layer, represent a reliable means of their separation. Unless gemmoscleres will yet be found in one or both of these species, indicating the degree of their relationship, it is advisable to consider them closely related though easily separable different species occurring in distant faunal regions.

Spongilla inarmata Annandale, 1913

Spongilla inarmata Annandale, 1918, p. 200.—Gee, 1928, p. 222; 1931e, p. 40; 1932c, p. 39.—Penney, 1960, p. 20.
Spongilla aspinosa Annandale and Kawamura, 1916, p. 6.—(Not Potts, 1880).

Material.—Fraction of type, and two slides of type obtained by N. Gist Gee.

Description.—Sponge, according to Annandale (1918), forming thin crusts, without branches; surface rather hispid, due to projection of megasclere fibers through dermal membrane. Skeleton consisting of a close irregular network of spicule fibers. Consistency of live sponge brittle.

Megascleres of moderate length, relatively slender and fusiform amphioxea, completely smooth; length range 158–290 μ, width range 4–12 μ.

Microscleres apparently confined to dermal membrane; they are somewhat crescentic in outline and sharply pointed, covered with minute spines mostly in their central region, their tips usually smooth; length range 50–79 μ, width range 2–4 μ.

Gemmoscleres not yet recorded.

Gemmules apparently restricted to basal part of sponge, ranging 280–750 μ in diameter; outline subspherical to ovoid; pneumatic layer irregular, but usually very thick and granular; smaller megascleres often embedded in this layer, and usually a cage of smaller megascleres built freely around each gemmule; foramen only slightly raised, bearing a peripheral shallow collar, never tubular.

Distribution.—Apparently restricted to Japan.

Color in life.—Not yet reliably observed.

Discussion.—This species displays some affinities to *S. aspinosa*, and Gee (1928) considered the existing differences unimportant enough to relegate it to a mere synonym of Potts' species. The reason for the retention of both as separate species in this paper were given in the discussion of *S. aspinosa*. It can be added that the different shape and surface of the microscleres in both species are also helpful in their discrimination.

Spongilla alba Carter, 1849

Plate 1, figures 1–3

Spongilla alba Carter, 1849, p. 83; 1881a, p. 88.—Bowerbank, 1863, p. 463.—Gray, 1867, p. 553.—Potts, 1887, p. 193.—Weltner, 1895, p. 114.—Annandale, 1907c, p. 26; 1907b, p. 388; 1912d, p. 384; 1918a, p. 211.—Gee, 1930a, p. 71; 1931e, p. 31; 1932c, p. 36.—Arndt, 1932c, p. 550; 1936, p. 14.—Schröder, 1935, p. 105.—Jewell, 1952, p. 448.—Penney, 1960, p. 12.

Spongilla lacustris var. *bengalensis* Annandale 1906a, p. 56.—Gee, 1931e, p. 33.

Spongilla alba var. *marina* Annandale, 1907b, p. 389.—Gee, 1931e, p. 42.

Spongilla microsclerifera Annandale, 1909i, p. 131; 1911c, p. 53; 1918a, p. 211.—Gee, 1931c, p. 69; 1931e, p. 43; 1932f, p. 507; 1932c, p. 40.—Penney, 1960, p. 25.

Spongilla travancorica Annandale, 1909f, p. 101; 1911c, p. 81; 1912d, p. 384.—Gee, 1931e, p. 50.

Spongilla alba var. *bengalensis* Annandale, 1911c, p. 77.—Gee, 1931e, p. 33.

Spongilla nana Annandale, 1915b, p. 31; 1918a, p. 208.—Gee, 1930f, p. 88; 1931e, p. 44; 1932c, p. 41; 1932g, p. 299.—Suvatti, 1950, p. 3.—Penney, 1960, p. 25.

Spongilla alba var. *rhadinea* Annandale, 1919c, p. 85.—Gee, 1931e, p. 47; 1932c, p. 36.

Material.—Type or syntype material of all species and "varieties" listed above, from the USNM, IM, and N. Gist Gee; material and slides from India, Indonesia, and the Amazon R. (RMS), as well as from Queensland, Australia.

Description.—Sponge forming massive growths, or crusts of considerable dimensions but moderate depths; surface smooth and slightly lobose, with irregular projections; oscula moderately large, usually inconspicuous; dermal membrane closely adherent to symplasm. Skeleton consisting of a comparatively dense network of slender primary and secondary spicule fibers, held together by only little spongin. Consistency of live sponge rather firm but brittle.

Megascleres slender to stout and fusiform amphioxea, completely smooth; length range 256–420 μ, width range 12–22 μ.

Microscleres very numerous in both dermal membrane and symplasm; they are very slender and slightly curved amphioxea, entirely covered with erect spines which are invariably much longer and more prominent in the central parts of the spicule; these spines often with

knoblike inflations at their tips; length range 75–124 μ, width range 2–3 μ.

Gemmoscleres slender and almost cylindrical amphistrongyla, occasionally amphioxea, feebly curved, covered with large and always recurved spines; these often more numerous at the tips of the scleres, where they sometimes form several ringlike aggregations; length range 78–130 μ, width range 5–10 μ.

Gemmules very abundant in sponge, scattered throughout its body, usually large and spherical, ranging 450–600 μ in diameter; pneumatic layer only moderately thick, distinctly granular; gemmoscleres embedded in this layer rather sparsely and at irregular angles, their tips usually projecting beyond outer surface of layer; foramen never tubular, though slightly elevated, and often bearing a shallow peripheral collar.

Distribution.—Formerly known only from India, SE. Asia, and Africa; the present studies were able to extend the known range of this species to Australia and South America.

Color in life.—Pale gray to off white.

Discussion.—*S. alba* possesses, in contrast to *S. lacustris*, a quite pronounced uniformity in the structure of its spicular components, and it is difficult to understand why Annandale (1906, 1907, 1909, 1915, 1919) found it necessary to express some few and immaterial variations in establishing as many as three separate species, as well as three "varieties" of this sponge. With this large number of supposedly differing forms, erected by a known specialist like Annandale, *S. alba* subsequently became a rather obscure species, and further confusion was added in later work, considering even the *S. cerebellata* Bowerbank group of sponges as varietal forms of *S. alba*.

A close examination of all the species and "varieties" listed above as synonyms revealed clearly that their differing structural character of spicules are all well within the usual range of typical scleres found in *S. alba*. Annandale's three "varieties," with respect to their spicular components, display nothing more than ecomorphic alterations caused by a differing chemical and physical environment. *S. nana* and particularly *S. microsclerifera* cannot be mistaken for any species other than *S. alba*, and merely represent a stunted mode of growth due to environmental factors. *S. travancorica* was established by Annandale (1909f) chiefly by one apparently typical criterion, i.e., the grouping of gemmules near the base of the sponge. Apart from the fact that the spicular components of both *S. alba* and *S. travancorica* assessed from the type material examined are almost indistinguishable, the peculiar arrangement of the gemmules in the latter can be fully explained by the flat growth of Annandale's type specimens of *S. travancorica*.

Carter (1881a), by considering the clearly distinct species *S. cerebellata* Bowerbank a "variety" of *S. alba*, has thus founded a taxonomic confusion of these two species which has spread unchallenged to the present day. The *S. cerebellata* group of species apparently has been confused with *S. alba* merely by the superficially similar arrangement of recurved spines on the tips of gemmoscleres in both species and will be dealt with in this paper under a new generic name.

Material collected for a separate study (Racek, MS.) on Australian spongillids revealed the presence of *S. alba* in brackish waters of Queensland. Since part of this material is also present in the collection of this study, *S. alba* is herewith recorded for the first time as occurring in Australia. Material collected for and deposited in the Riksmuseum at Stockholm, also examined during the present studies, has established the first record of occurrence for this species in the Amazon R., South America (RMS no. 94).

Spongilla cenota, new species

Plate 1, figures 8–10, 16

Spongilla lacustris Old, 1936a, p. 29.—Rioja, 1940a, pp. 174, 186.

Material.—Several fragments of dry sponge, collected by M. Goodnight and L. J. Stannard, June 1951 in Cenote Xtoloc, near Chichen Itza, Yucatan, Mexico—Holotype, no. 90328 (Penney); paratypes, several smaller fragments from the same locality, no. 90329 (Penney).

Description.—Sponge apparently forming irregular, and more or less massive cushions of moderate size; surface, not discernible in the dry holotype, described by Old (1936a) as smooth; oscula apparently small and inconspicuous. Skeleton consisting of a dense network of slender primary and secondary fibers, held together by only little spongin, as in *S. alba*. Consistency of live sponge not yet observed, that of the dry holotype firm but rather brittle.

Megascleres comparatively stout and almost cylindrical amphioxea with more or less abruptly pointed tips, completely smooth; length range 310–410 μ, width range 14–22 μ.

Microscleres very numerous in both dermal membrane and symplasm; they are very similar to those of *S. alba*, i.e., very slender and only very slightly curved amphioxea, covered with small granules or spines at their tips and with a group of long and erect spines in their central portion where they often form terminal knoblike inflations, length range 68–123 μ, width range 2–3 μ.

Gemmoscleres very robust and comparatively short amphioxea, feebly curved or straight, entirely covered with stout, sharp, and recurved spines; length range 65–86 μ, width range 9–13 μ.

Gemmules very abundant in sponge, scattered throughout its body, large and spherical, ranging 480–650 μ in diameter; pneumatic layer unusually strong, distinctly granular, very irregular in thickness; outer gemmular membrane thin and produced into a number of radiating lobes of great extent; gemmoscleres comparatively sparse, embedded in the thinner part of the pneumatic layer more or less tangentially to irregularly, displaying a pronounced radial arrangement in the thicker lobes of that layer; their tips do not project beyond the outer gemmular membrane; foramen slightly elevated extending to the surface of pneumatic layer, but not tubular.

Distribution.—As yet known only from the vicinity of the type locality, the cenotes of Yucatan, Mexico.

Color in life.—Recorded by Old (1936a) as light gray to green; the dry holotype of rather whitish color, resembling that of a dry *S. alba*.

Discussion.—This species was first recorded by Old (1936a), who described it as *S. lacustris* Auctorum, and whose views were perpetuated by Rioja (1940a). Thus it happened that *S. lacustris*, a typically cold-temperate species, became mistakenly added to the Mexican spongillid fauna. *S. cenota* differs from *S. lacustris* in many important criteria and cannot possibly be mistaken for it. On the other hand it shares most features with *S. alba*, with which it forms a separate group within the genus. Both *S. alba* and *S. cenota* possess almost identical microscleres, as well as megascleres; in dry condition both species are extremely similar, having a typically white appearance; both have the same close network of the skeleton, making it much firmer than that of the *S. lacustris* group of species. *S. cenota*, however, differs from all other known members of the genus, except *S. wagneri*, by the peculiar, thick, and highly irregular pneumatic layer of the gemmules, which forms distinct lobose projections armed with radially embedded gemmoscleres; and from *S. alba* by the characteristic shape and structure of its gemmoscleres.

Until speciation trends in freshwater sponges will be studied in greater detail, possibly resulting in a trinomial nomenclature for distant populations of apparently similar species, it is thought advisable to elevate *S. cenota* to full specific rank, instead of relegating it to a subspecies of *S. alba*. Its name is derived from the apparently restricted locality, the cenotes of Yucatan.

Spongilla wagneri Potts, 1889

PLATE 1, FIGURES 11–15

Spongilla wagneri Potts, 1889, p. 7.—Smith, 1922, p. 106.—Eshleman, 1950, p. 36.

MATERIAL.—Several slides of sponges collected in eastern South Carolina (Penney).

DESCRIPTION.—Sponge, according to Potts (1889), forming thin crusts without branches; surface greatly roughened, due to an abundant occurrence of peripheral microscleres in dermal membrane. Skeleton texture loose and open. Consistency of live sponge rather brittle.

Megascleres rather long and robust fusiform amphioxea, entirely smooth; length range 144–270 μ, width range 7–12 μ.

Microscleres excessively abundant both in dermal membrane and inner symplasm; they are long and slender amphioxea, slightly curved and delicately pointed, entirely covered with spines; these are erect, somewhat rounded at their extremities, and increase in length towards the center of the spicule; length range 49–62 μ, width range 2–4 μ.

Gemmoscleres long and stout, moderately curved amphioxea, entirely covered with stout, sharp, and recurved spines; these are more numerous towards the extremities of the spicules where they often form distinct "heads"; length range 48–75 μ, width range 6–8 μ.

Gemmules rather abundant in sponge, particularly within the lower layers; according to Potts (1889) often hidden away within the cavity of barnacles or among the coils of *Serpula* upon which the sponge has grown; they are large and spherical, ranging 470–610 μ in diameter; pneumatic layer unusually strong, distinctly granular, very irregular in thickness; outer gemmular membrane thin and produced into a number of radiating thick lobes; gemmoscleres abundant, embedded in this coat in an irregular manner, but displaying a pronounced radial arrangement in the thicker pneumatic lobes; foramen slightly elevated in order to reach the surface of the pneumatic layer, but not tubular.

DISTRIBUTION.—Apparently restricted to the coastline of the southeastern United States, ranging from Florida (Potts, Eshleman) to Louisiana (Smith) and South Carolina; optimal habitat slightly to strongly brackish waters.

COLOR IN LIFE.—Recorded as whitish.

DISCUSSION.—Unfortunately, the present material consists of only a few slides; therefore additional data on the consistency of the skeletal meshwork and mode growth are not available. *S. wagneri* thus remains a rather ill-known species in spite of its correct and sufficient original description by Potts (1889).

The spicular components of this species and the characteristics of the gemmular pneumatic layer make *S. wagneri* a typical member of the *S. alba* group of species that are all known to range into strongly brackish water or to occur in distinctly alkaline habitats. Although it is most likely that *S. wagneri* has been confused with *S. lacustris* on many past occasions, it is distinctly different from the latter in many important criteria. Its closest relative undoubtedly is *S. cenota* from Yucatan with which it shares the typical lobose development of the gemmular pneumatic layer, as well as a similar arrangement of spines on its gemmoscleres. The only character differentiating *S. wagneri* from both *S. alba* and *S. cenota* is its "loose and open" skeletal network, according to Potts' description. However, it is possible that additional collections of this sponge may yet show its skeletal structure comparable with those of the remainder of the group, i.e., rather firm and compact.

Although *S. wagneri* is very closely related to *S. cenota*, the structure and length of its gemmoscleres appear sufficiently different from those of the latter species to warrant their taxonomic separation. After more detailed speciation studies in freshwater sponges, perhaps it will be possible to decide whether the existing differences are of specific or infraspecific importance. It will then also be possible to demonstrate the pathway of expected structural changes from the *S. alba* sensu stricto, now even recorded from South America, via the form displayed by *S. cenota* from Yucatan, to the characteristics of *S. wagneri* from the southeastern United States. Until such studies can be carried out it is better to retain the specific status of both *S. wagneri* and *S. cenota* in order not to obscure possible taxonomic evidence.

Genus *Eunapius* Gray, 1867, redefined

Spongilla Leidy, 1851, p. 278.—Bowerbank, 1863, p. 445 (part).—Carter, 1881a, p. 86 (part).—Mills, 1882, p. 57 (part).—Potts, 1884b, p. 216 (part); 1887, p. 197 (part).—MacKay, 1885, p. 233 (part).—Wierzejski, 1885, p. 1.—Vejdovsky *in* Potts, 1887, p. 167 (part).—Kellicott, 1891, p. 102 (part).—Weltner, 1895, p. 114 (part).—Hanitsch, 1895a, p. 127 (part).—Annandale, 1909b, p. 106 (part); 1909d, p. 402 (part); 1911c, p. 95 (part).—Annandale and Kawamura, 1916, p. 11 (part).—Stephens, 1912, p. 7; 1920, p. 207.—Topsent, 1914, p. 538.—Smith, 1918, p. 239 (part); 1921, p. 17; 1930, p. 184.—Arndt, 1923, p. 74; 1936, p. 14.—Kozhoff, 1925, p. 54 (part).—Rezvoj, 1926b, p. 64; 1930, p. 175.—Schröder, 1926, p. 248; 1932b, p. 111; 1935, p. 99; 1938b, p. 126.—Gee, 1926c, p. 110; 1927a, p. 1; 1927b, p. 63; 1928, p. 225; 1929b, p. 13; 1931c, p. 38; 1932a, p. 132; 1932b, p. 469; 1932c, p. 239.—Sasaki, 1934, p. 226; 1940, p. 166.—Jewell, 1939, p. 16.—Eshleman, 1950, p. 38.—Penney, 1954, p. 156; 1956, p. 37; 1960, p. 11 (part).

Eunapius Gray, 1867, p. 552.

Type species.—By subsequent selection (Annandale, 1911c, for the subgenus *Spongilla* (*Eunapius*)) *Spongilla carteri* Bowerbank, 1863.

Definition.—Megascleres moderately stout to very stout amphioxea or amphistrongyla, usually completely smooth, occasionally strongly spined.

Microscleres absent.

Gemmoscleres slender to robust amphioxea or amphistrongyla, usually strongly spined and only slightly curved.

Gemmules moderately abundant in maturing sponge, comparatively small and often somewhat flattened; either scattered throughout the sponge, single or in coherent groups, or forming distinct pavement layer at the base; typically with a well-developed pneumatic layer consisting of several tiers of large and conspicuously polygonal air spaces resembling plant tissue; this layer often surrounding groups of gemmules or the entire pavement layer; gemmoscleres embedded in this layer strictly tangentially over the gemmules, and in an irregular manner in the interspaces between gemmules; foramen invariably tubular, at least extending to surface of pneumatic coat; tube straight or strongly curved.

Sponges usually forming flat cushions, rarely massive, usually without noticeable projections; associations with zoochlorellae rare and consequently coloration usually a drab gray. Consistency ranging from extremely fragile to almost stony hard.

Widely distributed throughout the world, from the Arctic Circle to cold-temperate regions of the Southern Hemisphere.

Discussion.—The genus *Eunapius* Gray, as here redefined, is characterized by the absence of free microscleres from both inner symplasm and dermal membrane, by the large columnar or polygonal air spaces of the gemmular pneumatic coat, and by the strictly tangential arrangement of the gemmoscleres in this layer. Introduced by Gray (1867) with the view to the separation of those spongillids with "areolated" and "reticulated" pneumatic coats from *Spongilla* Lamarck, its original definition including the presence of "smooth sponge-spicules" must now be considered as ambiguous and insufficient. Obvious shortcomings are Gray's inclusion of *Spongilla paupercula* (synonymous with *S. lacustris*) in *Eunapius*, and his retention of *S. lordii* (synonymous with *E. fragilis*) within Lamarck's only genus. Nevertheless, the generic name *Eunapius* can still be used, and it is to be regretted that by Carter's (1881a) unwarranted rejection of the entire system of Gray, taxonomists once again reverted to the use of the generic name *Spongilla* for all spongillids with acerate gemmoscleres.

Eunapius Gray, first restored as a subgenus of *Spongilla* Lamarck by Annandale (1911c), is herewith elevated to full generic rank. It is

more closely related to *Stratospongilla* Annandale and *Corvospongilla* Annandale than to any other known genus, some species (e.g., *E. sinensis*) displaying features which must be considered transitory to the former genus. At present it seems impossible to distinguish between clear-cut groups of *Eunapius* species, and additional comparative studies are urgently needed. In most species the gemmules adhere to the substratum, although free gemmules, single or in coated groups, are often also present, and in a few species pavement layers of gemmules are still unknown. However, it is possible that gemmular pavements are restricted to species with a very shallow mode of growth (e.g., *E. fragilis*, *E. igloviformis*, and *E. crassissimus*) and absent from such typically lobose species as *E. carteri* and others. Nevertheless, until additional comparative information on gemmular morphology within this genus becomes available, it is better to ignore the gemmular pavement formation as a generic criterion, and instead emphasize the characteristic polygonal or columnar air spaces of the gemmular pneumatic coat.

Eunapius carteri (Bowerbank, 1863)

PLATE 2, FIGURES 1, 2; PLATE 3, FIGURE 2

Spongilla carteri Bowerbank, 1863, p. 469.—Carter, 1881a, p. 86.—Weltner, 1895, p. 117; 1913, p. 475.—Girod, 1899, p. 108.—Annandale, 1906b, p. 187; 1907c, p. 24; 1908b, p. 157; 1911c, p. 87; 1912c, p. 137; 1914, p. 245; 1919c, p. 87.—Kirkpatrick, 1906, p. 218.—Willey, 1907, p. 184.—Cunnington, 1920, p. 507.—Rezvoj, 1926a, p. 108; 1928, p. 219.—Vorstman, 1927, p. 184.—Grimailowskaja, 1928, p. 215.—Gee, 1929d, p. 297; 1930a, p. 70; 1931e, p. 43; 1932g, p. 302; 1932h, p. 185; 1932f, p. 507; 1932d, p. 53; 1932c, p. 36.—Burton, 1929, p. 157.—Arndt, 1932c, p. 552; 1936, p. 14.—Topsent, 1932a, p. 568.—Simm, 1935, p. 194.—De Laubenfels, 1936, p. 36.—Schröder, 1942, p. 247.—Suvatti, 1950, p. 3.—Jewell, 1952, p. 448.—Penney, 1960, p. 14.

Eunapius carteri Gray, 1867, p. 552.

Spongilla carteri var. *cava* Annandale, 1911c, p. 88.—Gee, 1931c, p. 35; 1932h, p. 188.

Spongilla carteri var. *lobosa* Annandale, 1911c, p. 89; 1918a, p. 211.—Gee, 1931e, p. 41; 1932h, p. 188.

Spongilla carteri var. *mollis* Annandale, 1911c, p. 88; 1918a, p. 211.—Gee, 1931e, p. 43; 1932h, p. 187.

Spongilla carteri var. *balatonensis* Arndt, 1923, p. 79; 1926, p. 342.—Gee, 1931e, p. 33; 1932h, p. 189.

Spongilla carteri var. *melli* Arndt, 1923, p. 80.—Gee, 1926c, p. 110; 1927a, p. 1; 1927c, p. 184; 1928, p. 221; 1930e, p. 27; 1931e, p. 42; 1932h, p. 189.

?Spongilla aetheriae Annandale, 1913b, p. 237.

?Spongilla rotundacuta Rezvoj, 1925, p. 567.—Arndt, 1926, p. 342.

?Spongilla carteri var. *rotundacuta* Gee, 1931e, p. 48; 1932h, p. 193.

Spongilla friabilis Carter, 1849, p. 83 (not Lamarck, 1816, p. 100).

MATERIAL.—Material and slides of type and syntypes of *S. carteri* and its "varieties"; type slide of *S. aetheriae* (IM no. ZEV 6034/7),

extensive material from India, Indonesia, China, Philippines, Burma, Malaysia, Ceylon, and Hungary.

DESCRIPTION.—Sponge forming irregular masses of varying dimensions, ranging from rather flattish crusts to bulbous growths, with or without rounded or lobelike projections; surface rarely smooth, as a rule hispid; oscula large, often opening in distal parts of rounded projections; dermal membrane well developed. Skeleton consisting of definite vertical spicule fibers, interconnected by a varying number of irregular transverse fibers, and held together by a moderate amount of spongin. Consistency of live sponge ranging from fragile to moderately soft.

Megascleres rather stout, fusiform, and slightly curved amphioxea, completely smooth; length range 265–370 μ, width range 14–24 μ.

Microscleres absent.

Gemmoscleres in shape and structure very similar to megascleres, but considerably smaller, more curved, and sharply pointed; length range 145–210 μ, width range 5–8 μ.

Gemmules very abundant in mature sponge, scattered singly throughout the skeletal meshes; they are spherical and comparatively large, ranging 440–610 μ in diameter; pneumatic layer very thick, consisting of several tiers of regularly arranged polygonal air spaces; gemmoscleres embedded in this coat tangentially or in an irregular manner; foramen distinctly tubular, porus tube proximally often slightly constricted and straight, distally ending into a funnel-shaped depression of the pneumatic layer.

DISTRIBUTION.—Ranging from the type locality in India east through Malaysia, Indonesia, Burma, and China to the Philippines, and west through Turkestan, Iran, and southern U.S.S.R. to Lake Balaton, Hungary. Apparently also represented in Africa.

COLOR IN LIFE.—Yellowish brown to tan.

DISCUSSION.—Gee (1932h) demonstrated his reason for considering this species as being first mentioned by Carter (1849), but the fact remains that Bowerbank (1863) was first in fully describing *E. carteri* under this specific name. The present authors, therefore, follow the taxonomic procedure of the majority of previous writers in introducing this species under Bowerbank's name.

The reasons for considering the "varieties" *S. c. cava, S. c. lobosa, S. c. mollis, S. c. balatonensis,* and *S. c. melli* synonymous with *E. carteri* were well documented by Gee (1932h). The present investigations support Gee's views that, in spite of an apparent diversity in the mode of growth, all the spicular components of these forms remain fully identical. A reexamination of the type slide of *Spongilla aetheriae* Annandale (IM no. ZEV 6034/7) revealed that its scleres are morphometrically fully comparable with those of an immature *E. carteri,* and

it is possible that future research may relegate the former to a synonym of the latter. The presence of *E. carteri* in Africa is not surprising, since this species was recorded from that continent by Kirkpatrick (1906), even though that author's views were queried by Annandale (1914). Until detailed studies of all African species can be made, it appears advisable to list *S. aetheriae* as a possible synonym of *E. carteri*, which it resembles most closely.

The status of *S. rotundacuta* Rezvoj has yet to be resolved, since material of this species was not available for the present study. Although it certainly is closely related to *E. carteri*, and probably represents a distinct geographic race, it seems to possess criteria of specific importance (pavement layer of gemmules, structure of megascleres).

The distributional path of *E. carteri* into eastern Europe is highly interesting and would deserve detailed ecological and zoogeographic studies. In spite of a thorough search for this species in Australian waters (Racek, MS.), it has not yet been found there, although it is quite common in surrounding countries of the Indo-West Pacific region.

Eunapius fragilis (Leidy 1851)

PLATE 3, FIGURE 1

Spongilla fragilis Leidy, 1851, p. 278.—Mills, 1882, p. 57.—Potts, 1884b, p. 216; 1886, p. 228; 1887, p. 197.—MacKay, 1885, p. 233.—Wierzejski, 1884, p. 239.—Vejdovsky *in* Potts, 1887, p. 167.—Kellicott, 1891, p. 102; 1897, p. 50.—Weltner, 1895, p. 114; 1909, p. 183; 1910, p. 137.—Hanitsch, 1895a, p. 127.—Girod, 1897, p. 51; 1899, p. 108.—Levander, 1901, p. 56.—Rousseau, 1906, p. 124.—Lühe, 1908, p. 312.—Kirsch, 1909, p. 36.—Annandale, 1909b, p. 106; 1909d, p. 402; 1910c, p. 31; 1911, p. 95.—Annandale and Kawamura, 1916, p. 11.—Stephens, 1912, p. 7; 1920, p. 207.—Topsent, 1914, p. 538.—Smith, 1918, p. 239; 1921, p. 17; 1930, p. 184.—Arndt, 1923, p. 74; 1926, p. 342; 1928b, p. 165; 1931, p. 33; 1933c, p. 305; 1936, p. 14.—Kozhoff, 1925, p. 54; 1930, p. 160.—Rezvoj, 1926b, p. 64; 1930, p. 175.—Gee, 1926c, p. 110; 1927b, p. 63; 1927a, p. 1; 1928, p. 225; 1929b, p. 13; 1931e, p. 38; 1931d, p. 28; 1932c, p. 37; 1932d, p. 53; 1933b, p. 73; 1934, p. 284; 1937, p. 285.—Schröder, 1926, p. 248; 1932b, p. 111; 1935, p. 99; 1938b, p. 126.—Old, 1932c, p. 239; 1932b, p. 469; 1932a, p. 132; 1936b, p. 11.—Pesson, 1934, p. 52.—Sasaki, 1934, p. 226; 1940, p. 166.—Jewell, 1935, p. 462; 1939, p. 16.—Simm, 1939, p. 1.—Rioja, 1940a, p. 175.—Eshleman, 1950, p. 38.—Simon, 1952, p. 79.—Penney, 1954, p. 156; 1956, p. 37; 1960, p. 16.

Spongilla lordii Bowerbank, 1863, p. 466.—Carter, 1881a, p. 89.—Potts, 1887, p. 197.

Spongilla contecta Noll, 1870, p. 173.—Retzer, 1883, p. 20.

Spongilla ottawaensis Dawson, 1878, p. 5.—Mills, 1882, p. 57.—Potts, 1887, p. 197.

Spongilla sibirica Dybowsky, 1878, p. 53; 1882, p. 10; 1885, p. 137.

Spongilla morgiana Potts, 1880a, p. 330.—Potts, 1887, p. 197.

Spongilla glomerata Noll, 1886, p. 682.

Spongilla fragilis var. *minutissima* Potts, 1880b, p. 357.
Spongilla fragilis var. *minuta* Potts, 1880b, p. 357.
Spongilla fragilis var. *irregularis* Potts, 1880, p. 357.
Spongilla recticuba Kozhoff, 1925, p. 58.
Spongilla fragilis var. *kendelana* Schröder, 1938a, p. 302.
Spongilla fragilis var. *zempoalensis* Rioja, 1940b, p. 555.
Spongilla decipiens Weber, 1890, p. 40.—Weltner, 1895, p. 114.—Annandale, 1907c, p. 15; 1911c, p. 97; 1918a, p. 212.—Gee, 1929d, p. 297.
Spongilla fragilis var. *decipiens* Gee, 1930a, p. 74; 1931e, p. 37.
Spongilla ambigua Annandale, 1909e, p. 559; 1914, p. 246.—Weltner, 1913, p. 475.—Gee, 1932c, p. 36.—Arndt, 1933c, p. 308.

Material.—Extremely numerous specimens and slide material; EUROPE: Germany, Austria, Czechoslovakia, Hungary, Switzerland, Netherlands, Poland, U.S.S.R.; NORTH AMERICA: U.S.A., Alaska, Canada; ASIA: Malaysia, Indonesia, China, Japan; AFRICA: Congo, Rhodesia, Natal; AUSTRALIA: New South Wales.

Description.—Mature sponge invariably forming flat crusts of varying dimensions; surface typically smooth and usually even; oscula small but conspicuous, often producing radial canals in lotic environment; dermal membrane well developed. Skeleton consisting of radial and transverse spicule fibers, joined together by only small amounts of spongin. Consistency of live sponge extremely fragile and soft.

Megascleres almost straight or only slightly curved, fusiform amphioxea, invariably entirely smooth; length range 180–270 μ, width range 5–12 μ.

Microscleres absent.

Gemmoscleres slender to rather stout and inconspicuously curved or almost straight amphioxea or amphistrongyla, typically covered with a varying number of conspicuous spines that often are aggregated at the tips of the scleres; length range 75–140 μ, width range 2–7 μ.

Gemmules moderately abundant in mature sponge; either forming a distinct pavement layer, fastened to the substratum, when sponge is a flat crust; or also present in groups of 2–5 scattered throughout the body of the sponge, when this displays a more massive mode of growth; diameter of inner gemmular membrane 180–290 μ; pneumatic layer extremely well developed, consisting of large polygonal air spaces, and forming a continuous coat over all gemmules; gemmoscleres embedded in this layer strictly tangentially over the gemmular membrane, and in an irregular manner in the interstices; often arranged in two separate tiers above the gemmules, separated from each other by the thick pneumatic coat; foramen invariably tubular, porus tube of varying length and curvature at least reaching to surface of pneumatic layer, opening outward.

Distribution.—This species has a truly cosmopolitan distribution,

having been found in all continents and climates, as well as in caves and at high altitudes.

Color in life.—Usually light gray to whitish, occasionally green.

Discussion.—The fact that the original description of *E. fragilis* by Leidy (1851) has been overlooked by many authors of the 19th century accounts for the extensive number of synonyms listed above. In view of its successful adaptation to waters of drastically different chemical and physical properties, this species shows a large range of morphological variations of its spicular components as well as gemmules that at first glance seem to justify at least racial discrimination. However, the extensive study of all specimens from almost to the Arctic Circle down to New Zealand reveals clearly that all "forms" listed above as synonyms do not even represent geographic races but must be considered as belonging to the one species, regardless of a possible later introduction of trinomial nomenclature for the taxonomy of spongillids. The many names given to this species during the previous century have already been corrected by previous authors. *Spongilla recticuba* Kozhoff (1925), as well as the "varieties" *S. f. kendelana* Schröder (1938a) and *S. f. zempoalensis* Rioja (1940b), cannot be considered more than malformed or modified specimens of *E. fragilis*, the full morphological range of which has been observed in Australian waters by Racek (MS.). Even the slight morphological differences of *S. decipiens* Weber (1890), particularly the shorter porus tube of its gemmules and the double arrangement of its gemmoscleres, cannot possibly separate this species from *E. fragilis* with which it is fully synonymous. Finally, *S. ambigua* Annandale (1909e) has been shown by Arndt (1933c), who corrected a number of misconceptions by Annandale, as synonymous with the species discussed; the present investigations fully support Arndt's view that the megascleres are not microspined but invariably smooth, and that the few observed microscleres are immature gemmoscleres.

It is the opinion of the authors that *E. fragilis* should be studied in detail before final conclusions as to possible speciation trends in distant populations can be made and subspecies be erected. Apart from the clear synonyms, a number of species and "varieties" in the literature are not present in the material studied. Most of them occur in the Asian part of the U.S.S.R. and some in Lake Baikal, a typically ancient lake. Until material from this part of the world becomes available for a comprehensive study, it appears impossible to draw any conclusions as to the relationship of these "forms" to *E. fragilis*, and they are here disregarded.

In order not to obscure taxonomic evidence, some "variations" such as *S. f. calcuttana* Annandale (1911c) are here treated as separate species, since they display morphological differences of importance.

Ennapius calcuttanus (Annandale, 1911)

PLATE 2, FIGURES 7–9

Spongilla fragilis var. *calcuttana* Annandale, 1911c, p. 96; 1918a, p. 212.—Gee, 1931e, p. 34; 1932c, p. 38.—Arndt, 1933c, p. 307.—Penney, 1960, p. 18.

MATERIAL.—Type slide (IM no. P 43/1) and two syntype slides (N. Gist Gee).

DESCRIPTION.—Sponge, according to Annandale (1911, 1918), apparently very similar in structure and consistency to *E. fragilis*.

Megascleres slender, fusiform, and smooth amphioxea with rather abruptly pointed and peculiar tips that almost invariably form somewhat lanceolate apical projections; length range 170–230 μ, width range 6–11 μ.

Microscleres absent.

Gemmoscleres very slender and cylindrical amphistrongyla, covered with small and regular spines throughout their length; spines on tips of scleres recurved; length range 85–120 μ, width range 2–4 μ.

Gemmules spherical and small, diameter of inner gemmular membrane 190–230 μ; pneumatic layer well developed and thick, consisting of large polygonal air spaces, and forming a continuous coat over the gemmules; gemmoscleres embedded in this layer tangentially over the gemmular membrane, and in an irregular manner in the interstices; foramen invariably tubular, porus tube conspicuously bent and long, well projecting beyond surface of pneumatic layer.

DISTRIBUTION.—Apparently restricted to India.

COLOR IN LIFE.—Light gray to light brown.

DISCUSSION.—An examination of the type slide from the IM revealed the presence of two species, *E. calcuttanus* and *E. crassissimus*, which accounts for some discrepancies in Annandale's (1911c) description. The syntype slides examined contain only spicular components of *E. calcuttanus* and display the characteristic shape of the gemmoscleres, as well as the long and curved foraminal tube of the gemmules. Annandale (1911c) described the latter as "usually long and bent, but sometimes very short and quite straight," thus indicating that he observed this condition in two quite different species on the same slide.

Until additional material will be collected for a detailed study of *E. calcuttanus*, it is thought advisable to raise it to full specific status. While the morphology of this species and that of its gemmules show close affinities to *E. fragilis*, the megascleres and to some extent even the gemmoscleres are different enough to establish a ready discrimination of these two sponges.

Eunapius michaelseni (Annandale, 1914)

PLATE 2, FIGURES 5, 6

Spongilla michaelseni Annandale, 1914, p. 239.—Gee, 1931e, p. 43; 1932c, p. 40.—Topsent, 1932b, p. 1002.—Arndt, 1933c, p. 308; 1936, p. 15.—Penney, 1960, p. 24.

MATERIAL.—Three slides from the type (HM no. 1854), Zambesi R., Africa.

DESCRIPTION.—Sponge, according to Annandale (1914), forming thin flat crusts of moderate dimensions; oscula small and inconspicuous, dermal membrane moderately developed, subdermal space relatively small. Skeleton consisting of noncoherent radial spicule fibers, joined together by an irregular network of spicules and only small amounts of spongin. Consistency of live sponge moderately hard but brittle.

Megascleres feebly curved, fusiform smooth amphioxea; length range 290–360 μ, width range 10–18 μ.

Microscleres absent; a number of immature gemmoscleres occasionally present in the slides examined.

Gemmoscleres moderately stout, straight or feebly curved amphistrongyla, covered with characteristic spines aggregated near the tips of the scleres, where they are conspicuously recurved; sometimes an apical spine present on one or both tips; length range 75–145 μ, width range 5–15 μ.

Gemmules subspherical, somewhat depressed, and small; diameter of inner gemmular membrane 220–340 μ; not forming distinct pavement layer, but loosely occurring together in small groups near the base of the sponge; pneumatic layer moderately thick, consisting of large polygonal air spaces, not forming a continuous coat over the gemmules; gemmoscleres embedded in this layer more or less tangentially; foramen distinctly tubular, porus tube rather stout and straight.

DISTRIBUTION.—Hitherto only known from central Africa.

COLOR IN LIFE.—Light gray.

DISCUSSION.—Unless more material of this species will become available, its correct relationship to other species of this genus will be difficult to assess. *E. michaelseni* differs from *E. fragilis* by the presence of free gemmules, as well as by quite characteristic gemmoscleres; an additional criterion, the presence of free microscleres, as described by Annandale (1914) and quoted by Arndt (1933c), must be dismissed since these scleres represent immature gemmoscleres. The species discussed also differs from *E. nitens*, another African

species with noncoherent gemmules, sufficiently not to be confused with it and certainly cannot be mistaken for any other species. Although additional studies of African spongillids are very desirable, *E. michaelseni* can reliably be considered a good species.

Eunapius crassissimus (Annandale, 1907)

PLATE 2, FIGURES 10, 11

Spongilla crassissima Annandale, 1907c, p. 17; 1911c, p. 98; 1918a, p. 212.—Gee, 1931e, p. 36; 1932c, p. 37.—Penney, 1960, p. 16.
Spongilla crassissima var. *bigemmulata* Annandale, 1907c, p. 18.
Spongilla crassior Annandale, 1907b, p. 389.
Spongilla crassissima var. *crassior* Annandale, 1911c, p. 98; 1918a, p. 212.—Stephens, 1919, p. 97.—Gee, 1931e, p. 36; 1932c, p. 37.—Penney, 1960, p. 16.

MATERIAL.—Material and slides of types of species and "varieties" listed; material and slides from India (N. Gist Gee and HM).

DESCRIPTION.—Sponge, according to Annandale (1907), forming massive encrusting growths; surface without noticeable projections, but hispid due to projecting spicule fibers; oscula grouped in star-shaped areas, conspicuous; dermal membrane well developed. Skeleton formed of very firm spicule fibers and extensive webs of spongin. Consistency of live sponge very hard.

Megascleres, in mature form, invariably stout, cylindrical, and completely smooth amphistrongyla, often bearing a minute terminal projection; immature megascleres often slender amphioxea; length range 250–310 μ, width range 6–15 μ.

Microscleres absent.

Gemmoscleres rather short and cylindrical amphistrongyla, or abruptly pointed amphioxea, entirely covered with small and irregular spines; length range 80–120 μ, width range 3–9 μ.

Gemmules moderately abundant in mature sponge, spherical, diameter of inner gemmular membrane 280–310 μ; usually confined to base of sponge, but not forming distinct pavement layer, occasionally in free groups of 4 to 8; pneumatic layer well developed and thick, consisting of large polygonal air spaces, and forming a continuous coat over the gemmules; gemmoscleres embedded in this layer strictly tangentially over the gemmular membrane, and in an irregular manner in the interstices; often arranged in two separate tiers above the gemmules, separated from each other by the thick pneumatic coat; foramen invariably tubular, porus tube moderately long, rarely projecting beyond surface of pneumatic layer.

DISTRIBUTION.—Apparently restricted to India and tropical SE. Asia, possibly occurring in Australia (Racek, MS.).

COLOR IN LIFE.—Dark leaden gray to dull green.

Discussion.—The general morphology of the gemmules of *Eunapius crassissimus* displays close affinities to that of *E. fragilis*, and the gemmoscleres are similar in both species. However, the porus tube of the former is conspicuously shorter and approaches in form that of *S. ambigua* and *S. decipiens*, and all the other criteria are in sharp contrast to *E. fragilis*. When fully mature the megascleres are distinct amphistrongyla; the extensive amount of spongin used for the binding of megascleres gives the skeleton an extremely rigid, almost stony consistency; although often restricted to the base of the sponge, the gemmules rarely form a distinct pavement layer. All these characters are sufficient to separate this species clearly from *E. fragilis*. Recent studies (Racek, MS.) indicate that *E. crassissimus* may also occur in New South Wales, Australia. However, further taxonomic studies are necessary before this Asian species can be reliably recorded from Australia.

Eunapius igloviformis (Potts, 1334)

Spongilla igloviformis Potts, 1884b, p. 216; 1887, p. 202.—Weltner, 1895, p. 114.—Smith, 1921, p. 17.—Gee, 1931e, p. 40; 1932c, p. 38; 1937, p. 285.—Old, 1932b, pp. 447, 469; 1932a, p. 131.—Jewell, 1939, p. 20.—Eshleman, 1950, p. 38.—Wurtz, 1950, p. 4.—Penney, 1960, p. 20.

Material.—Very numerous specimens and slides from the United States and Canada (Gee, USNM, Jewell).

Description.—Maturing sponge forming flat crusts or irregular growths; surface typically smooth and usually even; oscula small but conspicuous, dermal membrane well developed. Skeleton consisting of radial and transverse spicule fibers joined together by only small amounts of spongin. Consistency of live sponge moderately firm to fragile.

Megascleres almost straight or only slightly curved and fusiform amphioxea, entirely covered with coarse spines; length range 190–265 μ, width range 6–13 μ.

Microscleres absent.

Gemmoscleres rather stout and feebly curved amphioxea or amphistrongyla, covered with strong and irregular spines; length range 68–120 μ, width range 4–7 μ.

Gemmules in compact hemispherical groups of 7–20, diameter of inner gemmular membrane 180–260 μ; pneumatic layer extremely well developed, consisting of large polygonal air spaces, and forming a continuous coat over all gemmules; gemmoscleres embedded in this layer strictly tangentially over the gemmules, and in an irregular manner in the interstices; foramen invariably tubular, porus tube long and curved, opening inward.

Distribution.—Known only from the United States and Canada

Color in life.—Light gray to brown.

Discussion.—*E. igloviformis* is a well described and equally well-known species, which can be easily separated from its closest congener, *E. fragilis*, by the structure of the megascleres, the dome-shaped arrangement of gemmule groups, and by the inward opening foraminal tubules.

Jewell, *in* Ward and Whipple (1959), relegated this species to a synonym of *S. mackayi* Carter without giving any reasons for her decision. The latter species is poorly represented in the material for this study and cannot be fully compared with the material of *E. igloviformis*. Even though the spicular components of *S. mackayi* show certain affinities to those of the species discussed, it could well be possible that the differences discernible are caused by an ecomorphic malformation of the former, resulting in freak scleres. Until more material of *S. mackayi* becomes available, it is thought advisable to retain the specific status of *E. igloviformis*.

Eunapius geminus (Annandale, 1911)

Plate 2, figures 12, 13

Spongilla gemina Annandale, 1911c, p. 97; 1918a, p. 211.—Gee, 1931e, p. 39; 1932c, p. 38.—Penney, 1960, p. 19.

Material.—Slides of syntype (N. Gist Gee).

Description.—Sponge, according to Annandale (1911c), forming small and shallow cushions of circular outline; surface minutely hispid, oscula numerous but minute and inconspicuous; dermal membrane closely adhering to symplasm. Skeleton consisting of a close and regular network at the base, becoming more diffuse in upper parts. Consistency of live sponge moderately hard but friable.

Megascleres slender, fusiform amphioxea, entirely smooth; length range 175–240 μ, width range 6–11 μ.

Microscleres absent.

Gemmoscleres slender and cylindrical amphistrongyles or amphioxea, irregularly covered with minute straight spines; length range 75–105 μ, width range 2–4 μ.

Gemmules characteristically bound together in pairs, irrespective of their location, diameter of inner gemmular membrane 180–220 μ; pneumatic layer only moderately well developed, consisting of a thin coat of large polygonal air spaces; gemmoscleres embedded in this coat tangentially; foramen produced into a long curved tube, opening outward.

Distribution.—Known only from the type locality in India.

Color in life.—Gray to brown (Annandale).

Discussion.—The fact that *E. geminus* has been found only once renders its comparison with other allied species highly unreliable. Furthermore, the paucity of material for this study does not permit any assessment of its intrageneric relationships. The species discussed, however, seems to possess features similar to those displayed by *E. fragilis*, and it is not unlikely that when additional specimens are available it will have to be relegated to a mere synonym of that truly cosmopolitan species. On the other hand, future material may also prove its identity with some of the lesser known congeners, and it is thought advisable to retain provisionally its separate specific status.

Eunapius coniferus (Annandale, 1916)

Spongilla conifera Annandale, 1916, p. 51; 1918a, p. 203.—Gee and Wu, 1927, p. 258.—Gee, 1931c, p. 36; 1932c, p. 37; 1932d, p. 54.—Penney, 1960, p. 15.

Material.—Fraction of syntype, and several slides of syntype obtained by N. Gist Gee; material and slides from China (N. Gist Gee).

Description.—Sponge forming thin crust of moderate dimensions; surface smooth, oscula small and inconspicuous. Skeleton consisting of a close and regular network of slender spicule fibers, running obliquely through the sponge, and held together by very little spongin. Consistency of dry sponge very brittle.

Megascleres small and slender fusiform amphioxea, entirely smooth, straight or only slightly curved; length range 157–210 μ, width range 4–9 μ.

Microscleres absent.

Gemmoscleres extremely minute, feebly curved amphioxea, covered with microspines in an irregular manner; length range 19–32 μ, width range 2–3 μ.

Gemmules not very abundant in mature sponge, scattered freely throughout skeletal meshwork; they have a conical outline and a flattened base, and rarely measure more than 155 μ at their greatest diameter; pneumatic layer well but unevenly developed; base and sides of gemmule covered with a single layer of large polygonal air spaces, the upper surface with several to many tiers of such air spaces; the few gemmoscleres embedded in this layer only in the thicker upper part, more or less tangentially; foramen distinctly tubular, porus tube long and slender, traversing the thick polygonal pneumatic layer.

Distribution.—Apparently restricted to China.

Color in life.—Light brown (Annandale).

Discussion.—The unique structure, form, and armature of the gemmules of *E. coniferus*, as well as its considerably smaller spicular components, make this species readily distinguishable from any other

of this genus. Although it is represented by many specimens in the material available for this study, its distribution appears to be restricted to the Chinese mainland.

Eunapius geei (Annandale, 1913)

Plate 2, figure 16; Plate 3, figures 5, 6

Spongilla geei Annandale, 1918a, p. 202.—Gee, 1926c, p. 110; 1927b, p. 60; 1927a, p. 4; 1928, p. 225; 1930c, p. 27; 1931c, p. 39; 1932c, p. 38; 1932d, p. 54.—Penney, 1960, p. 19.

Material.—Fraction of syntype, obtained by N. Gist Gee, and several slides.

Description.—Sponge, according to Annandale (1918) and Gee (1926), apparently massive and nodulose, with a smooth surface. Skeleton consisting of a regular network, with the radiating spicule fibers better developed than the transverse ones; spongin moderately abundant. Consistency of preserved sponge firm and compact.

Megascleres comparatively short and stout amphioxea, entirely smooth, abruptly pointed at their tips; length range 170–230 μ, width range 13–17 μ.

Microscleres absent.

Gemmoscleres slender and feebly curved amphioxea, covered with a varying number of small and irregular spines; length range 70–95 μ, width range 4–7 μ.

Gemmules somewhat flattened, subspherical, numerous and freely scattered throughout the sponge, each closely surrounded by skeletal network; diameter 430–460 μ; pneumatic layer uniform and thick, consisting of large polygonal air spaces; gemmoscleres, few in number, embedded in this layer more or less tangentially; foramen provided with a long and curved tubule, lying in a crater-like depression of the pneumatic coat.

Distribution.—Apparently restricted to the Chinese mainland.

Color in life.—Light brown (Gee).

Discussion.—This species shows close affinities to *E. nitens* (Carter) from the African continent; it seems to differ from that species merely by its obtusely pointed megascleres and by its less massive skeleton. It is very likely that future comparative studies may relegate *E. geei* to a synonym of *E. nitens*, but the material available for this study is not large enough to permit such a decision. *E. geei* is therefore provisionally retained as a separate species in this paper.

Eunapius tinei (Gee, 1932)

Spongilla tinei Gee, 1932f, p. 526; 1932e, p. 42.—Penney, 1960, p. 31.

Material.—Slides of syntype (USNM no. 22180).

Description.—Sponge, according to Gee (1932f), forming a thin

crust on various supports; surface hispid due to projection of vertical spicule fibers through dermal membrane. Skeleton consisting of large irregular meshes at the base, and of strong vertical fibers in the upper portion; spongin moderately abundant. Consistency of dry sponge moderately firm but brittle.

Megascleres very slender and slightly curved amphioxea, entirely smooth, ranging from fusiform to cylindrical in outline; length range 200–260 μ, width range 4–9 μ.

Microscleres absent.

Gemmoscleres irregular in outline, usually slightly curved amphioxea with lanceolate or rounded tips, covered with microspines that often are more numerous at the tips of the scleres; length range 110–145 μ, width range 1.5–4 μ.

Gemmules somewhat flattened, subspherical, numerous and freely scattered in groups of two or three throughout the upper portions of the sponge, or forming a continuous layer on the support, held in position by the skeletal meshwork; diameter 400–470 μ; pneumatic layer consisting of a thick layer of large polygonal air spaces showing a columnar effect; gemmoscleres, few in number, embedded in this layer in an irregular manner but usually tangentially; foramen producing a moderately long, curved, and blackish tube.

Distribution.—Known only from the type locality in the Philippines.

Color in life.—Almost colorless when free of sediment.

Discussion.—The relationship of *E. tinei* to other species of this genus has yet to be resolved. It shares certain characteristics with some species of the *E. fragilis* group, but in others appears to link up with the group represented by *E. nitens*. Until additional material will be available and comparative studies made, it is best to retain its separate specific status, which at present seems well documented.

Eunapius nitens (Carter, 1881)

Plate 2, figures 17, 18

Spongilla nitens Carter, 1881a, p. 89.—Hilgendorf, 1883, p. 87.—Potts, 1887, p. 158.—Weltner, 1895, p. 114; 1913, p. 475.—Annandale, 1914a, p. 245.—Cunnington, 1920, p. 507.—Gee, 1931c, p. 45; 1932c, p. 41.—Topsent, 1932a, p. 570.—Arndt, 1933c, p. 302; 1936, p. 9.—Burton, 1938, p. 458.—Jewell, 1952, p. 448.

Spongilla nitens var. Gee, 1932c, p. 41.

Material.—Fraction of sponge and two slides, from the Ugalla R., Africa, obtained by N. Gist Gee.

Description.—Sponge, according to previous descriptions, invariably massive and nodulose, surface from irregular to smooth. Skeleton consisting of a regular network of radiating and transverse

spicule fibers; spongin moderately abundant. Consistency of preserved sponge firm and compact.

Megascleres stout and comparatively large amphistrongyla, ranging to abruptly pointed cylindrical amphioxea, entirely smooth; length range 300–460 μ, width range 18–30 μ.

Microscleres absent.

Gemmoscleres feebly curved to straight amphioxea, entirely covered with minute spines; tips of scleres often rounded to appear as amphistrongyla; length range 76–122 μ, width range 4–6 μ.

Gemmules not very abundant, scattered freely in skeletal meshes, spherical; diameter ranging 440–590 μ; pneumatic layer thick and consisting of large polygonal air spaces; gemmoscleres, few in number, embedded in this layer tangentially; foramen provided with a moderately long, and slightly curved porus tube.

Distribution.—Known under this specific name only from Africa.

Color in life.—Not yet reliably recorded; preserved specimens are yellowish brown (Arndt).

Discussion.—*E. nitens* has been considered a species restricted to the African Continent. However, in view of the close similarity of *E. geei* to this species, it is possible that it ranges into Asia, probably displaying some morphological variations and modifications in distant populations. The criteria separating *E. nitens* from *E. geei* are few and chiefly restricted to the slightly differing shape of the megascleres, as well as the differing consistency of the skeleton, in both species. Although it is very likely that these two species will have to be united, following a future detailed comparison, they are here listed separately in order not to obscure possible taxonomic evidence. The original description of Carter (1881a) refers to amphistrongyles as the megascleres typical for *E. nitens*. However, Arndt's (1933c) work and the present studies found true amphistrongyles to be rare in this species, and the majority of its scleres must be considered as very abruptly pointed amphioxea, just as those found in *E. geei*. Further detailed comparative studies involving both these as well as other closely related species are therefore extremely desirable.

Eunapius sinensis (Annandale, 1910)

Plate 3, figures 3, 4

Spongilla (*Stratospongilla*) *sinensis* Annandale, 1910a, p. 183; 1911c, p. 53; 1918a, p. 201.—Stephens, 1919, p. 99.—Gee and Wu, 1925b, p. 567.—Gee, 1926c, p. 110; 1927b, p. 57; 1927a, p. 1; 1928, p. 225; 1930e, p. 27; 1931e, p. 49; 1932d, p. 53; 1932c, p. 41.

Spongilla sinensis Penney, 1960, p. 29.

Spongilla (*Stratospongilla*) *stanleyi* Annandale, 1916, p. 50; 1918a, p. 201.—Gee and Wu, 1925b, p. 609.—Gee, 1926c, p. 110; 1927c, p. 184; 1928, p. 225; 1930e, p. 27; 1931e, p. 49; 1932d, p. 54; 1932c, p. 41.—Rezvoj, 1930, p. 175.

Spongilla stanleyi Penney, 1960, p. 29.

MATERIAL.—Syntype slides of *S. sinensis* (N. Gist Gee), and specimens from Soochow, China; specimens and slides of *S. stanleyi* (N. Gist Gee) from China and Northern Manchuria.

DESCRIPTION.—Sponge usually forming nodulose crusts on shells of living bivalves; surface rather smooth, but hispid due to the projection of vertical spicule fibers through dermal membrane; oscula small and inconspicuous, sometimes surrounded by radial canals; dermal membrane closely adhering to symplasm, subdermal cavity very small. Skeleton consisting of a dense but irregular network of spicule fibers, forming polygonal meshes at the base and singular fibers toward the surface of the sponge; spongin moderately abundant. Consistency of live sponge firm and compact.

Megascleres feebly curved to straight, stout amphioxea with abruptly pointed tips, entirely smooth; length range 200–295 μ, width range 12–19 μ.

Microscleres absent.

Gemmoscleres rather robust, usually slightly curved amphioxea, rarely amphistrongyla, ranging from almost smooth to covered with few to many large and irregular spines; length range 65–125 μ, width range 8–13 μ; malformations of gemmoscleres quite frequent, irregular spiny spherasters often also present.

Gemmules somewhat depressed, subspherical, forming pavement layer at base of sponge, firmly adhering to support; diameter of inner gemmular membrane 280–350 μ; pneumatic layer more or less well developed, of varying thickness, consisting of large polygonal air spaces and forming a continuous coat over gemmules; gemmoscleres embedded in this layer in great numbers, forming several tangential layers over the gemmules; foramen distinctly tubular, porus tube curved and at least reaching surface of pneumatic layer.

DISTRIBUTION.—Apparently restricted to Asia, ranging from mainland China north to Manchuria and the U.S.S.R.

COLOR IN LIFE.—Light green, gray, or blackish brown (Rezvoj).

DISCUSSION.—Annandale (1910a, 1916, 1918a) reluctantly placed both his *S. sinensis* and *S. stanleyi* into his newly erected subgenus *Stratospongilla*, stating that both these species form a distinct group in that subgenus and that they differed in many regards from all its other species. Gee (1926–1932) used Annandale's grouping without any further comment, but Rezvoj (1930), while retaining the taxonomic position of *S. stanleyi* within the subgenus *Stratospongilla*, made very useful comments on the insufficiency of the original definition of that subgenus. As will be shown below, the species to be referred to that genus as here restricted possess gemmules with an ill-developed or entirely absent granular pneumatic layer without discernible air spaces, and instead a cover of a dense chitinoid mem-

brane or membranes. In both *S. sinensis* and *S. stanleyi* the pneumatic layer always consists of clearly discernible polygonal air spaces, and the gemmoscleres are amphioxea, in contrast to the *Stratospongilla* spp., as restricted in this paper, whose gemmoscleres are typically sausage-shaped amphistrongyla. Even if Rezvoj's (1930) view that *S. stanleyi* and *S. sinensis* represent intermediate forms between *Eunapius* and *Stratospongilla* is taken into consideration, the general characteristics of both these species seem to fit much better into the definition of the former genus.

The only criterion differentiating *S. stanleyi* from *S. sinensis*, as described by Annandale, is the shape of the gemmoscleres in both species, being rather irregularly spiny in the former and almost entirely smooth in the latter. The structure, consistency, and skeletal components of both species are fully identical, and so are form, pneumatic coat, and armature of the gemmules. It is obvious that the slightly different gemmoscleres in both species are the result of ecomorphic adaptations, and that the retention of *S. stanleyi* as a separate species is unwarranted. Future detailed workers will have to decide whether it should be differentiated on a subspecific level.

Eunapius potamolepis (Annandale, 1918)

PLATE 2, FIGURES 14, 15

Spongilla (*Eunapius*) *potamolepis* Annandale, 1918a, p. 208.
Spongilla potamolepis Gee, 1932g, p. 303.

MATERIAL.—Slides of type (IM, Reg. no. ZEV 7164/7).

DESCRIPTION.—Sponge, according to Annandale (1918), forming thin crusts on sticks and bamboos; surface smooth and without noticeable projections; oscula small and scattered, each approached by a ramifying horizontal subdermal channel. Skeleton consisting of a close network of single spicules and bundles that are arranged in a polygonal manner. Consistency of live sponge extremely hard and not at all brittle.

Megascleres, in inner symplasm, rather stout, cylindrical, and entirely smooth amphistrongyla, sometimes inflated at their tips; those in peripheral areas of younger sponges often smooth amphioxea; length range 240–330 μ, width range 7–17 μ.

Microscleres absent.

Gemmoscleres comparatively short and stout, cylindrical, and abruptly pointed amphioxea, entirely covered with minute spines; length range 80–105 μ, width range 4–9 μ.

Gemmules moderately abundant to very rare in mature sponge, subspherical, diameter of inner gemmular membrane about 300 μ; confined to base of sponge, usually forming distinct pavement layer, and tightly adhering to support; pneumatic layer well developed and

thick; consisting of rather small polygonal air spaces; gemmoscleres embedded in this layer strictly tangentially in peripheral region; foramen tubular, porus tube moderately long, rarely projecting beyond surface of pneumatic layer.

Distribution.—Known only from the type locality, Lampam, Thailand.

Color in life.—Recorded as brownish or clay colored.

Discussion.—Annandale (1918a) and Gee (1932g) drew attention to the similarity in skeletal characteristics of this sponge to the genus *Potamolepis* Marshall, from which it derives its specific name. Annandale furthermore recorded the apparent futility of retaining *Potamolepis* as a distinct genus, which at present merely represents a somewhat artificial grouping of extremely to moderately hard spongillids with stout amphistrongylous megascleres, the gemmules of which have not yet been recorded.

In order not to obscure possible taxonomic evidence, *E. potamolepis* is here retained as a distinct species until a comprehensive revision of all spongillids without recorded gemmules will become possible. Following such a future detailed study it appears very likely that most, if not all, species of the presently recognized genera *Potamolepis*, *Nudospongilla*, *Cortispongilla*, and *Pachydictyum* will eventually be distributed among those genera dealt with in this paper. The absence of gemmules in the collections of species of the above four genera does not necessarily mean that these asexual reproductive bodies have not been produced. As in many spongillid species, but particularly in the genera *Eunapius*, *Stratospongilla*, and *Corvospongilla*, gemmules are known to adhere to the substratum to such an extent that they can easily be left behind after the sponge has been dislodged. Future more careful collecting efforts might yet succeed in locating such "evasive" gemmules and in revising some problematic genera.

Eunapius potamolepis is most closely related to a number of its congeners, in particular to *E. nitens* and *E. crassissimus*. From the first it differs chiefly in the morphology of its gemmoscleres, from the second in its much more compact skeletal structure. At present the relationship of this "group" cannot be fully elucidated. The amphistrongylous shape of the megascleres is perhaps of only little significance, since in *E. potamolepis* amphioxea are often also present in peripheral parts of the sponge skeleton, and in *E. crassissimus* the majority of megascleres are at the most abruptly pointed amphioxea. It is possible that future detailed ecological and morphometric studies, apart from revealing speciation trends in distant populations of "similar" species, will establish a number of distinct "modes of growth" within one species. Until such additional evidence and data become available, all efforts to clarify interspecific relationships

must remain highly speculative. A spongillid closely resembling *E. potamolepis* has recently been found in Australia (Racek, MS.) and will be subjected to a detailed morphological study.

Genus *Stratospongilla* Annandale, 1909, redefined

Spongilla (*Stratospongilla*) Annandale, 1909c, p. 561; 1911c, p. 122; 1912d, p. 385; 1914, p. 245; 1918a, p. 212; 1919a, p. 160.—Annandale and Kawamura, 1916, p. 1.—Weltner, 1913, p. 481.—Stephens, 1919, p. 99.—Gee, 1931c, p. 34; 1932c, p. 36.—Arndt, 1936, p. 14.

Type species.—*Spongilla bombayensis* Carter, 1882.

Definition.—Megascleres usually stout amphioxea or amphistrongyla, smooth or roughened by minute and irregular projections.

Microscleres, comparable with the "flesh spicules" of other genera, usually present in dermal membrane and vicinity of the gemmules; if present, they invariably are short and slender amphioxea, almost straight, covered with relatively long and irregular spines.

Gemmoscleres more or less strongly bent amphistrongyles, covered with minute spines of unequal size, or slightly curved spined amphioxea, or a combination of both.

Gemmules large and spherical, as a rule with a flattened base, aggregated in the basal membrane of the sponge, usually firmly adherent to the substratum; occasionally free in inner symplasm of sponge; pneumatic layer without noticeable air spaces, often poorly developed or altogether absent, situated entirely outside the layer of gemmoscleres; the latter embedded tangentially in the outer gemmular membrane, in one or more compact layers; foramen or foramina always tubular, tube either short and straight, or long and recurved.

Sponge usually forming shallow cushions of moderate size; coloration often a bright green. Consistency ranging from hard to almost stony hard.

Apparently restricted to the tropics, with greatest abundance in Asia and Africa; not yet recorded from tropical Australia.

Discussion.—*Stratospongilla*, originally introduced by Annandale (1909e) as a subgenus of *Spongilla* and retained as such until the present, is herewith elevated to full generic rank. It is most closely related to the genus *Corvospongilla*, with which it shares the peculiar characteristics of the gemmules, as well as features of general morphology and distribution, but from which it differs by the absence of microbirotulates as free microscleres.

Apart from the species complexes discussed in dealing with *S. bombayensis*, *S. sumatrana*, *S. indica*, *S. gravelyi*, *S. rousseletii*, *S. schubotzi*, and *S. gilsoni*, material of which was available for the present study, two species of somewhat doubtful generic relationships are also often referred to the genus *Stratospongilla*, *S. clementis*

Annandale and *S. navicella* Carter. The former, although present in our material, did not reveal any additional criteria for discussion, and its retention within this genus remains problematic. Material of the latter could not yet be secured, and even the recent accounts of *S. navicella* by Boretto and Ezcurra (1962) fail to substantiate the assumption of a number of previous authors that this species too should be placed into the genus discussed.

Stratospongilla bombayensis (Carter, 1882)

Spongilla bombayensis Carter, 1882, p. 369.—Potts, 1887, p. 196.—Weltner, 1895, p. 114; 1913, p. 475.—Annandale, 1907c, p. 26; 1909e, p. 561; 1911c, p. 102; 1912d, p. 384; 1918a, p. 212.—Stephens, 1919, p. 99.—Arndt, 1936, p. 14.—Penney, 1960, p. 13,

Spongilla (*Stratospongilla*) *bombayensis* Annandale, 1911b, p. 225; 1912c, p. 138; 1914, p. 246.—Gee, 1931e, p. 34; 1932c, p. 36.

Spongilla bombayensis var. *pneumatica* Annandale, 1911c, p. 241; 1918a, p. 212.—Gee, 1931e, p. 46; 1932c, p. 36.—Penney, 1960, p. 14.

Material.—Slides of types (IM, BM) and syntypes (AmstM).

Description.—Sponge forming comparatively thin layers on solid objects; surface irregular, oscula inconspicuous, dermal membrane closely adhering to symplasm. Skeleton, owing to the large number of spicules, compact but incoherent and almost amorphous (Annandale, 1909e); vertical spicule fibers present in places, but almost devoid of joining spongin. Consistency of live sponge moderately hard but brittle.

Megascleres straight or feebly curved, slender and comparatively short amphioxea, rarely entirely smooth, usually covered with an irregular arrangement of small spines, occasionally roughened; length range 220–300 μ, width range 12–17 μ.

Microscleres slender and short, sharply pointed amphioxea, feebly curved or straight, entirely microspined; rare in inner symplasm, almost entirely restricted to dermal membrane and the vicinity of gemmules; length range 45–60 μ, width range 3–4 μ.

Gemmoscleres rather stout and short amphistrongyla to abruptly pointed amphioxea, usually only slightly curved, and entirely granulated; length range 35–67 μ, width range 6–8 μ, very variable in proportions.

Gemmules variable in size, spherical or ovoid, usually distinctly flattened at base; pneumatic layer ill-defined but often thick in places, air spaces not discernible; outer gemmular membrane in close contact with the support causes the gemmules to adhere firmly; gemmoscleres embedded in this coat usually in two layers, separated by an empty space, the lower in contact with the inner gemmular membrane; the outer, often several spicules thick, fastened together in the outer membrane in which dark granules are usually also present;

foramen or foramina distinctly tubular, tube ranging from short and straight to long and curved, situated laterally.

Distribution.—Ranging from India to central Africa.

Color in life.—Insufficiently known.

Discussion.—*Stratospongilla bombayensis* differs from its closest congeners by the apparently characteristic arrangement of the gemmoscleres, which form two distinct layers separated by an empty space. Excepting this criterion, the spicular components of this species are very similar to those of *S. sumatrana*, and additional data may yet demonstrate that these two species should be united or, at the most, differentiated on an infraspecific level. At the present, such a decision cannot be contemplated. Annandale's (1911c) variety *S. b. pneumatica* is difficult to distinguish from the typical species, and its separation is most likely unwarranted.

Stratospongilla sumatrana (Weber, 1890)

Plate 3, figures 7–10

Spongilla sumatrana Weber, 1890, p. 38.—Weltner, 1895, p. 114; 1898b, p. 128.—Stephens, 1919, p. 99.—Penney, 1960, p. 29.

Spongilla (*Stratospongilla*) *sumatrana* Annandale, 1911c, p. 53; 1918a, p. 212; 1919a, p. 160.—Gee, 1929e, p. 297; 1930a, p. 81; 1931e, p. 50; 1932c, p. 41.—Arndt, 1932c, p. 566; 1938a, p. 22.

Spongilla sumatrana var. α Weltner, 1898b, p. 129; 1913, p. 475.—Annandale, 1914, p. 245.—Stephens, 1919, p. 95.—Gee, 1931e, p. 50; 1932c, p. 41.—Arndt, 1936, p. 15.—Penney, 1960, p. 30.

Spongilla sumatrana var. β Weltner, 1898b, p. 130; 1913, p. 475.—Annandale, 1914a, p. 245.—Stephens, 1919, p. 95.—Gee, 1932e, p. 41.—Arndt, 1936, p. 15.—Penney, 1960, p. 30.

Spongilla sumatrana var. *rivularis* Annandale, 1919a, p. 161.—Gee, 1931e, p. 48; 1932e, p. 42. Penney, 1960, p. 31.

Material.—Type and syntype material of the species proper and of *S. s. rivularis* (USNM, IM, AmstM, N. Gist Gee).

Description.—Sponge, according to Weber (1890) and Gee (1930a), forming thin layers of circular or irregular shape on solid supports; surface described as smooth. Skeleton consisting of large, loosely organized and thin spicule fibers, though compact. Consistency recorded as moderately hard.

Megascleres are almost straight, fusiform, and sharply pointed amphioxea; thinly covered, except at their tips, with very short spines arising from rather broad bases; length range 210–290 μ, width range 9–14 μ.

Microscleres occasionally found in inner symplasm, but mostly restricted to the vicinity of gemmules; they are feebly curved, sharply pointed amphioxea, entirely covered with minute spinules; length range 47–65 μ, width range 3–4 μ; a larger type of microscleres,

recorded as such by Weber (1890), are most likely deformed gemmoscleres.

Gemmoscleres are stout and short amphistrongyla, straight to feebly curved, covered with rather uniform minute spines; length range 32–43 μ, width range 11–13 μ.

Gemmules apparently not abundant in mature sponge, recorded as free, never grouped together; diameter of gemmule 450–600 μ; pneumatic layer irregularly developed, without noticeable air spaces; outer gemmular membrane in continuity with a short and straight porus tube; gemmoscleres closely crowded in this coat, embedded strictly tangentially, and forming a mosaic layer.

Distribution.—Ranging from Indonesia via India to Africa.

Color in life.—Recorded as light gray.

Discussion.—The great variability of scleres in the specimens assigned to this species by a number of previous workers appears to have marred earlier attempts to solve the true relationship of *S. sumatrana* to other species of the genus. The species discussed has never before been suspected of being extremely closely related to or even identical with *S. bombayensis*, yet other and much more differing specimens, such as *S. indica* and *S. gravelyi*, have been relegated to mere "varieties" of *S. sumatrana* by Annandale after having been considered separate species by him. As already stressed in the discussion of the foregoing species, *S. sumatrana* and *S. bombayensis* form a clearly defined group and are possibly even identical. On the other hand, *S. gravelyi* differs from this group by the characteristics of its microscleres, as well as by its apparently nonadhering gemmules; *S. indica* with all its "varieties" differs by the amphistrongylous shape of its megascleres. Should it be possible to consider these last two species, including their races, conspecific with *S. sumatrana* it would be just as possible to consider the entire range of characters from *S. bombayensis* to *S. indica* a manifestation of ecomorphic changes in distant populations, and all these forms would have to become at the most subspecies of *S. bombayensis*. Apart from the fact that such an arrangement would certainly obscure possible taxonomic evidence, the material hitherto collected does not allow such a decision. In this paper, therefore, *S. sumatrana* with the varieties listed above is treated as a separate species, and at the same time the specific status of *S. gravelyi* and *S. indica* is restored. This appears to be a justified preliminary arrangement before future studies, and particularly additional material, will make a comprehensive revision of the entire genus possible.

Such a rearrangement, however, would make it necessary to review the features displayed by the megascleres of the numerous "varieties" in order to find reasonable means of allocating them between the two

species now to be restored, i.e., *S. sumatrana* and *S. indica*. Unfortunately, such a distribution can only be contemplated for such "varieties" of both species that are represented in the material for our present study, and a future detailed comparative study of all forms involved appears highly desirable. The synonymies, as listed under *S. sumatrana* and *S. indica*, respectively, are therefore not to be considered a final solution of this challenging taxonomic problem.

Of the "varieties" present in our material or well documented in the literature available, only *S. sumatrana rivularis* can reasonably be placed within the closer complex of *S. sumatrana*, since in that variety the majority of megascleres are distinct though somewhat abruptly pointed amphioxea. The "varieties" *S. s. centralis*, *S. s. siamensis*, and *S. s. baniensis* certainly appear much closer related to *S. indica* and should therefore be transferred to the complex of the latter species, since all these forms possess amphistrongylous megascleres.

Stratospongilla indica (Annandale, 1908)

Plate 3, figures 11–14

Spongilla indica Annandale, 1908a, p. 25; 1911c, p. 100; 1912d, p. 384.

Spongilla sumatrana var. *indica* Annandale, 1918a, p. 212; 1919a, p. 161.—Stephens, 1919, p. 99.—Gee, 1931e, p. 40; 1932c, p. 42.—Penney, 1960, p. 31.

Spongilla sumatrana var. *centralis* Annandale, 1919a, p. 161.—Gee, 1931e, p. 35; 1932c, p. 41.—Penney, 1960, p. 30.

Spongilla sumatrana var. *baniensis* Topsent, 1932a, p. 578.—Arndt, 1936, p. 16.—Penney, 1960, p. 30.

Spongilla sumatrana var. *siamensis* Gee, 1932g, p. 305.—Suvatti, 1950, p. 3.

Material.—Slides of type and syntype material of nominal species and of all varieties except *S. s. baniensis* (IM, AmstM, N. Gist Gee).

Description.—Sponge forming small and shallow cushions on solid supports; external surface smooth, oscula minute. Skeleton rather loosely defined, consisting of slender spicule fibers. Consistency of live sponge apparently hard but brittle.

Megascleres moderately long, almost straight, cylindrical amphistrongyla, covered with a number of short and minute spines, arising from a rather broad base; tips of scleres often surrounded by several "rings" of smaller spines; length range 210–270 μ, width range 12–17 μ.

Microscleres almost straight, more or less sharply pointed amphioxea, covered with relatively long and irregular spines inserted at right angles to the axis of the sclere; length range 37–59 μ, width range 3–4 μ.

Gemmoscleres feebly curved to straight, stout amphistrongyla, densely covered with minute granules or blunt spines; length range 35–48 μ, width range 7–8 μ.

Gemmules ranging 420–500 μ in diameter, subspherical, with flattened base, usually firmly adhering to the support of the sponge; pneumatic coat feebly and irregularly developed, without discernible air spaces, usually forming a basal membrane by which the gemmule is fastened; gemmoscleres forming a dense, tangentially arranged mosaic layer over inner gemmular membrane; foramen provided with a short and straight porus tube.

Distribution.—Apparently ranging from Thailand via India to Africa.

Color in life.—Recorded as green to gray.

Discussion.—The spicular components of *S. indica* are sufficiently different from those of *S. sumatrana*, as here restored, to enable an easy separation of these two species. The megascleres of this complex are always distinct amphistrongyla, and the gemmules are as a rule fixed in groups at the base of the sponge, although free gemmules are occasionally also produced. The reasons for placing some of the "varieties," previously considered races of *S. sumatrana*, into *S. indica* have been given in the discussion of the foregoing species.

Stratospongilla gravelyi (Annandale, 1912)

Plate 3, figures 15–18

Spongilla (*Stratospongilla*) *gravelyi* Annandale, 1912d, p. 384.
Spongilla sumatrana var. *gravelyi* Annandale, 1918a, p. 212; 1919a, p. 161.—Stephens, 1919, p. 99.—Gee, 1931e, p. 39; 1932c, p. 42.—Penney, 1960, p. 30.

Material.—Slides of syntype (N. Gist Gee).

Description.—Sponge, according to Annandale (1912), forming small and shallow cushions on solid supports; external surface smooth, oscula minute, surrounded by shallow radiating channels beneath the dermal membrane. Skeleton consisting of a regular network of single spicules and slender, ill-defined spicule fibers, the vertical ones more distinct than the transverse. Consistency of live sponge very hard but easily broken.

Megascleres almost straight, fusiform, and sharply pointed amphioxea; their surface neither smooth, nor spiny, but covered with minute irregular blunt projections; sometimes a ring of terminal short spicules present around the tips of the scleres; length range 230–310 μ, width range 11–17 μ.

Microscleres not abundant, and chiefly restricted to dermal membrane and vicinity of gemmules; they are sharply pointed and almost straight amphioxea, covered with relatively long and very irregular spines, inserted at right angles to the axis of the sclere; length range 42–56 μ, width range 3–4 μ.

Gemmoscleres strongly curved amphistrongyla, often forming a wide arc, and usually with inflated tips, entirely covered with minute blunt spines or granules; length range 35–63 μ, width range 7–8 μ.

Gemmules ranging in diameter 440–580 μ, spherical, and situated in small loculi near the base of the sponge, apparently not adherent to the support; pneumatic coat feebly developed, without discernible air spaces, not forming a basal membrane as in the majority of other species of this genus; gemmoscleres forming a dense, tangentially arranged mosaic layer over inner gemmular membrane; foramen provided with a short and straight porus tube.

Distribution.—Found only in type locality in India.

Color in life.—Recorded as bright green.

Discussion.—The reasons for the restoration of *S. gravelyi* as a separate species were given in the discussion of *S. sumatrana*. *Stratospongilla gravelyi* displays a characteristic mode of gemmular attachment, and its free microscleres are distinctly different from those of other species, so that it cannot possibly be retained as a mere "variety" of the *S. sumatrana* complex. Annandale (1912d, p. 386) made the most interesting observation that, in regard to megascleres and general structure, *S. gravelyi* resembles most closely the "mountain form" of *Spongilla cinerea* Carter, although the structure of the skeleton and that of the gemmules were different in these two sponges. In the few slides of *S. cinerea* available for study, this resemblance was again discovered, and some of the gemmules of material labeled *S. cinerea* clearly possess a very few stratospongillid amphistrongylous gemmoscleres in addition to the rather radially arranged typical amphioxea. Since *S. cinerea* is a poorly represented and ill-known species, the true generic relationship of which remains somewhat vague, its paucity in material collected could well be explained by its representing a mere growth form of a *Stratospongilla* sp. Even though this view is still little more than speculation, the similarity of the gemmoscleres of *S. cinerea* to the free microscleres of *S. gravelyi* is indeed striking, and the stratospongillid microscleres, restricted to the vicinity of gemmules in this genus, could possibly be gemmoscleres of a different growth form. Should this assumption be documented by further detailed studies, *S. cinerea*, which still defies a generic definition, could finally be put into its proper taxonomic place.

Stratospongilla rousseletii (Kirkpatrick, 1906)

Spongilla rousseletii Kirkpatrick, 1906, p. 223.—Weltner, 1913, p. 476.—Annandale, 1914, p. 245.—Stephens, 1919, p. 99.—Gee, 1931e, p. 48; 1932c, p. 41.—Arndt, 1933c, p. 309; 1936, p. 15.—Penney, 1960, p. 27.

Material.—Slides of type (BM and N. Gist Gee).

Description.—Sponge, according to Kirkpatrick (1906), forming

shallow encrustations of considerable dimensions; surface smooth, oscula inconspicuous. Skeleton rather loosely defined, consisting of slender spicule fibers, about six scleres thick, with little amounts of spongin. Consistency of live sponge apparently not yet recorded.

Megascleres usually slightly curved and entirely smooth amphioxea, often with subtornote tips; length range 210–260 μ, width range 12–19 μ.

Microscleres such as known in other congeners apparently absent.

Gemmoscleres variable in size and shape; as a rule stout and slightly curved amphistrongyla, covered with short and blunt spines that are more numerous at the extremities of the scleres than in their center; length range 63–71 μ, width range 12–16 μ.

Gemmules spherical, ranging 380–420 μ in diameter; pneumatic coat comparatively thick but irregular and apparently without air spaces; gemmoscleres embedded in this coat tangentially in one or more layers; when only one layer is produced, the mosaic-like arrangement of the gemmoscleres can be readily observed; foramen or foramina provided with a porus tube of varying shape and thickness, rising up to 18 μ above the outer gemmular membrane.

Distribution.—Apparently restricted to tropical Africa.

Color in life.—Recorded as dirty white.

Discussion.—This species differs clearly from all other congeners mentioned earlier by its rather stout and entirely smooth amphioxous megascleres, and by the absence of free microscleres in the symplasm. Its specific separation from other members of the genus is therefore justified. The material studied by the present authors did not reveal any additional criteria for discussion.

Stratospongilla schubotzi Weltner, 1913

Spongilla (*Stratospongilla*) *schubotzi* Weltner, 1913, p. 481.—Annandale, 1914, p. 245.—Stephens, 1919, p. 95.—Gee, 1931e, p. 48; 1932c, p. 41.—Arndt, 1936, p. 15.—Penney, 1960, p. 28.

Material.—Slides of type obtained from ZMB by N. Gist Gee.

Description.—Sponge, according to Weltner (1913), forming shallow encrustations on shells of *Aetheria elliptica;* additional data on external features lacking. Skeleton apparently well defined and moderately firm, consisting of slender spicule fibers, 1–6 scleres thick, with little amounts of spongin. Consistency of live sponge recorded as hard.

Megascleres extremely variable in shape and length; the majority are stout and cylindrical amphioxea with more or less abruptly pointed tips, occasionally with a few true amphistrongyla intermixed; however, all possible types of scleres are present, ranging from oxea over styles or tornotes to strongyla; the surface of all these skeletal components is entirely smooth; length range of typical amphioxea 120–170 μ,

their width 11–14 μ; the few amphistrongyla measure 110–120 μ in length and 12–13 μ in width.

Microscleres have not yet been recorded.

Gemmoscleres of similar variability as found in megascleres; the majority are short and stout, abruptly pointed and cylindrical amphioxea, often assuming an amphistrongylous character, entirely smooth; a large number of deformed scleres, ranging from spheres to irregularly shaped bodies, also present; length range of larger amphioxea 68–88 μ, width range 10–12 μ; strongyla and styles of the gemmule armature attain a length of 64 μ and a width of 10 μ.

Gemmules apparently not yet observed in natural condition; those treated with boiling hydrochloric acid (fide Weltner, 1913) are almost spherical, range 500–800 μ in diameter, and appear to lack a micropyle; they are surrounded by tangentially arranged layers of gemmoscleres.

Distribution.—Found only in the type locality, the Aruwimi R., near Banalia in Central Africa.

Color in life.—Recorded as white.

Discussion.—*Stratospongilla schubotzi* obviously is most closely related to *S. rousseletii*, the only usable separating criterion being the absolutely smooth surface of the gemmoscleres in the former. However, additional collections may yet substantiate the assumption of the present authors that Weltner's species merely represents a malformed specimen of *S. rousseletii*, and that eventually it will have to become a synonym of that species. The great irregularity of spicular components in *S. schubotzi* appears to be a reliable indication of an adverse environment and the lack of granules or spinules on its gemmoscleres could well be an ecomorphic phenomenon. In spite of the almost complete agreement of other criteria in both *S. rousseletii* and *S. schubotzi*, it is thought advisable to retain their separate specific status until additional evidence becomes available.

Stratospongilla gilsoni (Topsent, 1912)

Spongilla (*Stratospongilla*) *gilsoni* Topsent, 1912, p. 187.—Stephens, 1919, p. 99.—Gee, 1931e, p. 39; 1932c, p. 38.
Spongilla gilsoni Penney, 1960, p. 19.

Material.—Slides of syntype (N. Gist Gee).

Description.—Sponge, according to Topsent (1912), forming flat cushions on rocks of volcanic origin, present in the vicinity of rapids; surface slightly lobose and irregular, oscula inconspicuous but numerous. Skeleton apparently of somewhat loose construction. Consistency comparatively soft.

Megascleres feebly curved rather cylindrical amphioxea with abruptly pointed tips, covered with short straight spines except at the extremities; length range 135–230 μ, width range 11–15 μ.

Microscleres apparently absent.

Gemmoscleres short and wide amphistrongyla, ranging in appearance from subspherical or ovoid bodies to almost straight rods, covered with fine spines or granules; length range 8–21 μ, width range 8–11 μ.

Gemmules abundant in the lower part of the sponge, subspherical to ovoid, ranging in diameter 110–180 μ; pneumatic layer ill-developed, and without discernible air spaces; gemmoscleres embedded in this layer tangentially, or slightly irregularly, usually present in two tiers; foramen not distinctly tubular, but elevated in the form of a broad cone.

Distribution.—Found only in the type locality, the Waidina R. on Viti Levu, Fiji Islands.

Color in life.—Recorded as dark green.

Discussion.—The reexamination of type material of this species has not revealed any additional criteria for discussion. However, *S. gilsoni* differs from most of its congeners by its rather fragile and comparatively soft consistency, its abundant and nonadherent gemmules, and its gemmular micropyles that are not produced into a typical tubule but merely represent a conical elevation. In most other features, *S. gilsoni* seems most closely related to the African congeners *S. rousseletti* and *S. schubotzi* from which, however, it is readily separable. The retention of the separate specific status of *S. gilsoni* is therefore fully justified.

A future study of additional material of all *Stratospongilla* spp. may yet demonstrate the possibility, or necessity, of a generic or subgeneric separation of the group of species possessing free microscleres from those apparently lacking these spicular components. At the present such a separation appears ill-documented and therefore unwarranted, and additional data are highly desirable.

Stratospongilla clementis (Annandale, 1909)

Plate 3, figures 19, 20

Spongilla clementis Annandale, 1909h, p. 631; 1911c, p. 53; 1918a, p. 201.—Stephens, 1919, p. 99.—Gee, 1926c, p. 110; 1927b, p. 58; 1927a, p. 1; 1918, p. 225; 1930e, p. 27; 1931c, p. 69; 1931e, p. 36; 1932f, p. 507; 1932c, p. 37.—Arndt, 1936, p. 14.—Penney, 1960, p. 15.

Spongilla yunnanensis Annandale, 1910d, p. 197; 1911c, p. 53.—Gee, 1931e, p. 52.

Material.—Piece of syntype of *S. clementis*, donated by Annandale to the AusM, Reg. no. Z 860; also slide of type (USNM).

Description.—Sponge, according to Annandale (1909), forming small cushions on solid supports; external surface usually smooth, oscula large, numerous, and elevated. Skeleton consisting of a rather regular network of spicule fibers of moderate thickness. Consistency

of live sponge ranging from soft to very hard, dried skeleton usually rigid.

Megascleres as a rule smooth, stout, and very abruptly pointed amphioxea, ranging to amphistrongyla, sometimes bearing irregular and small spines in their central portion; length range 230–275 μ, width range 19–21 μ.

Microscleres have not yet been recorded.

Gemmoscleres very slender, cylindrical, and nearly straight amphistrongyla, their extremities often armed with a terminal spine, finely covered with very small spinules which seem to increase slightly in size towards the tips of the scleres; average length 52–56 μ, width 3–4 μ.

Gemmules apparently very rare in mature sponge, occurring singly in the basal membrane of the sponge and firmly adhering to the substratum; they are spherical, about 350 μ in diameter, with a feebly developed granular pneumatic coat apparently without air spaces, but with a strong outer sheath of spongin in continuity with the basal membrane of the sponge; gemmoscleres embedded in the pneumatic coat more or less strictly tangentially, not forming a mosaic layer but crossing each other at all angles; foramen produced into a straight porus tube.

Distribution.—Ranging from the Philippines, the type locality, to China, Japan, and the tropical west coast of Africa, the latter record most probably based on an erroneous identification.

Color in life.—Recorded as gray to green.

Discussion.—Annandale (1909h), in the original description of this species, expressed some doubt as to its generic position, a view that was perpetuated by Stephens (1919) and all subsequent writers. Indeed, *Stratospongilla clementis* displays a number of features quite atypical for the genus into which it has been provisionally placed: its megascleres are very like those of the genus *Eunapius;* its gemmoscleres display close affinities to those of the *E. nitens* group of species, and their arrangement on the gemmules is vastly different from that usually found in the genus *Stratospongilla;* free microscleres, as found in the majority of members of this latter genus, are absent. On the other hand, however, the gemmules lack the large polygonal air spaces of all *Eunapius* sp. and certainly possess criteria typical for the genus *Stratospongilla.*

Annandale and Kawamura (1916), after studying a considerable number of specimens from Japan, found that *S. clementis* seems to form three different types of growth, each vastly different from the other. The first phase are flat crusts of lichenoid outline; the second more massive than the first, often bright green, sometimes producing branches, and with large and conspicuous oscula; and the third

represented by compact, ovoid, or pedunculate masses of a grayish or whitish color, either fixed to solid supports, or lying free on the bottom. According to these authors, phase two corresponds with the specimens on which the description of *S. clementis* was based, while phase three is very similar to the sponge originally described as *S. yunnanensis*. From these most interesting observations it is obvious that the present generic position of *S. clementis* is far more obscure and uncertain than originally anticipated by Annandale. This problem is unlikely to be solved by the mere revision of those clear-cut genera dealt with in this study, but will have to be approached through a detailed study of all genera, such as *Nudospongilla*, *Cortispongilla*, *Potamolepis*, and *Pachydictyum*, the gemmules of which are not yet known or perhaps not produced at all. Until such comprehensive comparative studies can be carried out, it is best to leave *S. clementis* within the genus originally assigned by Annandale.

The present authors were unable to confirm or contradict the record of this species for Africa by Arndt (1936), since material from these localities was unavailable for this study. However, since the African specimens could possibly belong to the *E. nitens* group of species, the Cameroons record of *S. clementis* needs yet to be confirmed.

Genus *Corvospongilla* Annandale, 1911

Corvospongilla Annandale, 1911c, p. 122; 1912d, p. 387; 1913a, p. 78; 1918a, p. 213.—Gee, 1931e, p. 36; 1932c, p. 27.—De Laubenfels, 1936, p. 36.—Jewell, 1952, p. 445.—Penney, 1960, p. 35.

Type species.—*Spongilla loricata* Weltner, 1895.

Definition.—Megascleres usually robust amphistrongyles, often inflated at their extremities, smooth to granulated, only slightly curved, occasionally amphioxea, exceptionally present in two distinct series.

Microscleres representing almost straight to slightly curved microbirotulates with smooth or spined shafts, and a small number of terminal recurved spines of varying length; only exceptionally also spined amphioxea, which could well be adventitious.

Gemmoscleres invariably spined and distinctly curved amphistrongyla of rather unequal size.

Gemmules moderately to very large, spherical, with flattened base, or oval in outline; usually found in groups at the base of the sponge and fastened to the support by an outer casing of megascleres or without such a cage; pneumatic coat ill-defined or absent; gemmoscleres embedded in inner gemmular membrane, lying close together as to form a mosaic cover; foramen as a rule tubular and often lateral; occasionally free gemmules also present, usually different in form and structure of pneumatic coat.

Sponges encrusting, flat; coloration black to dark gray. Consistency extremely hard and firm, ranging to delicate in some species.

Apparently restricted to tropical regions of Africa and Asia.

Discussion.—The genus *Corvospongilla* was one of the first taxonomic subdivisions introduced in the formerly recognized subfamily Spongillinae, in which the conglomerate genus *Spongilla* seemed to have survived to present days apparently without much challenge. The presence of typical birotulates as free microscleres in the symplasm of sponges, the gemmoscleres of which are amphioxea or amphistrongyla, certainly fully justified the introduction of the new genus *Corvospongilla* by Annandale (1911c). However, that author's choice of *S. loricata* Weltner as its type species must be regretted, since this African species was insufficiently described and a type specimen apparently was not preserved. Thus it happened that Annandale himself considered a number of specimens from India and East Asia as distinct species, a view which has not been challenged by any of the numerous subsequent authors.

This genus comprises three quite distinct groups of species, differing from each other by a number of decisive criteria. The spicular components of *C. loricata* are more or less shared by *C. burmanica* and *C. lapidosa*, and apparently by *C. zambesiana* of which little information was available for this study; the megascleres in this group are stout amphistrongyla, often inflated at their extremities, and usually entirely smooth. The second group is represented by *C. böhmii*, *C. micramphidiscoides*, and *C. scabrispiculis*, in which the megascleres are slightly smaller and entirely covered with rounded tubercles or blunt spines. The third group is somewhat aberrant and can easily be distinguished by the possession of amphioxea as megascleres; it is represented by *C. ultima* and *C. caunteri*.

In the *C. loricata* group the intrageneric relationship of all species recorded is difficult to review, and future additional collections together with detailed morphometric and ecological comparisons are highly desirable. All show strikingly similar skeletal and other spicular components, and the justification for their specific separation can already be doubted.

In the *C. böhmii* group only the nominal species can be readily distinguished from the remaining two by its characteristic microbirotulates, whereas *C. micramphidiscoides* and *C. scabrispiculis* display close affinities to each other, though their separation is still possible.

The group represented by *C. ultima* and *C. caunteri* is most characteristic not only by their amphioxous megascleres and more or less delicate skeletal structure, but also by the frequent presence of free gemmules, which in *C. caunteri* possess a pneumatic coat displaying minute but clearly defined air spaces.

C. zambesiana (Kirkpatrick) and *C. victoriae* Annandale are poorly represented in the material for this study, the latter to such an extent that comparative work was impossible. It is hoped that future studies will be able to assess and demonstrate the relationship of these two species to others of the genus discussed.

Sponges of this genus are most closely related to all *Stratospongilla* spp., as elevated in this paper to specific status, the main distinguishing criterion being the presence or absence of free microbirotulates in the symplasm. It is therefore possible that future discoveries of such typical microscleres in species hitherto included in *Stratospongilla* may result in the transfer of such species to *Corvospongilla.*

Corvospongilla loricata (Weltner, 1895)

Spongilla loricata Weltner, 1895, p. 138.
Corvospongilla loricata Weltner, 1913, p. 476.—Annandale, 1913b, p. 237; 1914, p. 245.—Stephens, 1919, p. 94.—Gee, 1931e, p. 42; 1932c, p. 27.—Arndt, 1936, p. 16.—Jewell, 1952, p. 453.—Penney, 1960, p. 37.

Material.—One defective slide of type, obtained from ZMB by N. Gist Gee.

Description.—Sponge apparently not yet reliably known, relevant data absent from literature available.

Megascleres of two distinct series: (1) large, feebly curved, and entirely smooth amphistrongyla, ranging 220–226 μ in length and about 20 μ in width; and (2) somewhat more slender amphistrongyla with distinctly inflated extremities, usually finely granulated, rarely entirely smooth, ranging 125–130 μ in length, and about 7 μ in width.

Microscleres represented by microbirotulates with a smooth shaft and terminally with a smaller number of recurved hooks of medium size; average length 20–40 μ, diameter of the rotules 4–12 μ.

Gemmoscleres slightly curved stout amphistrongyla, sparsely covered with stout spines, and of greatly varying dimensions; length range 34–75 μ, width range 8–14 μ.

Gemmules spherical and large, ranging 500–950 μ in diameter; pneumatic coat practically absent, without discernible air spaces; gemmoscleres forming a tangential mosaic layer on gemmular membrane; foramen produced into a short porus tube.

Distribution.—Hitherto known only from one locality in Africa (no particular type locality given), growing on shells of *Aetheria* sp.

Color in life.—Not yet observed.

Discussion.—It is to be regretted that this rather ill-known species has been chosen as type species of the genus, for its relationship to its many congeners has yet to be demonstrated. Until additional data become available, *C. loricata* must remain a doubtful species and the assessment of probable synonymy cannot be contemplated.

Corvospongilla burmanica (Kirkpatrick, 1908)

Spongilla loricata var. *burmanica* Kirkpatrick, 1908, p. 97.
Corvospongilla burmanica Annandale, 1911c, p. 123; 1918a, p. 213.—Stephens, 1919, p. 98.—Gee, 1931e, p. 34; 1932c, p. 27.—Penney, 1960, p. 36.
Corvospongilla burmanica var. *bombayensis* Annandale, 1911b, p. 225; 1912d, p. 384; 1918a, p. 213.—Gee, 1931e, p. 34; 1932c, p. 27.—Penney, 1960, p. 36.

Material.—Slide of type of var. *bombayensis* (IM).

Description.—Sponge, according to original descriptions, forming flat crusts of often considerable dimensions on solid supports; surface coarsely hispid due to projection of skeletal fibers; oscula usually elevated on turret-like eminences, or similar projections of irregular shape. Skeleton consisting of well-defined spicule fibers, reticulate, but with only little spongin. Consistency of live sponge hard but brittle.

Megascleres large, feebly curved, and entirely smooth amphistrongyla, often inflated at their extremities; length range 220–235 μ, width almost constantly 20 μ.

Microscleres represented by microbirotulates with only slightly curved smooth shafts, and terminally with a smaller number of recurved hooks of medium size; average length 30 μ, diameter of rotule 6–12 μ.

Gemmoscleres slightly to strongly curved amphistrongyla, relatively short and stout, covered with minute spinules or tubercles, and of greatly varying dimensions; length range 38–56 μ, width range 7–8 μ.

Gemmules not very abundant, rather large (800 μ) and subspherical; as a rule singly adhering to support, but sometimes also free in inner symplasm; pneumatic layer in adhering gemmules feebly developed, the gemmules surrounded by loculi of megascleres; in free gemmules a well-developed pneumatic coat; gemmoscleres forming a concentric layer or layers on inner gemmular membrane; foramen produced into a short cylindrical porus tube.

Distribution.—Ranging from Burma (type locality) to India.

Color in life.—Not yet reliably recorded; dry sponge pale brown.

Discussion.—Since Kirkpatrick (1908) considered this form of sponge a mere variety of *C. loricata*, its elevation to separate specific status by Annandale (1911c) and all subsequent authors seems difficult to understand. Although *C. loricata* must still be considered an ill-known species, most of the characteristics of *C. burmanica* appear very similar to, if not identical with, those of the genotype. However, a direct comparison of *C. burmanica* with *C. loricata* during the present study was impossible since the former is represented in our material only by the varietal form *C. burmanica bombayensis*, and the latter by a few spicules. Even though future research will likely demon-

strate that these two species are identical, such views must remain highly speculative and *C. burmanica* is therefore provisionally retained as a separate species.

The retention of the varietal form *C. b. bombayensis*, merely based on the absence of turret-like oscular elevations, does not, however, appear to be of any taxonomic significance.

Corvospongilla lapidosa (Annandale, 1908)

PLATE 4, FIGURES 1–3

Spongilla lapidosa Annandale, 1908a, p. 26.
Corvospongilla lapidosa Annandale, 1911c, p. 124; 1912d, p. 384.—Stephens, 1919, p. 98.—Gee, 1931c, p. 41; 1932c, p. 27.—Penney, 1960, p. 36.

MATERIAL.—Slides of type (IM).

DESCRIPTION.—Sponge, according to Annandale (1908), forming flat crusts on solid supports, external surface without spicular projections, smooth. Skeleton consisting of well-defined spicule fibers joined together by a considerable amount of spongin. Consistency of live sponge almost stony hard.

Megascleres stout and slightly curved amphistrongyla, ranging from microspined to entirely smooth; length range 190–230 μ, width range 17–19 μ.

Microscleres represented by microbirotulates with a smooth shaft and terminally with a smaller number of recurved hooks of medium size; average length 22–35 μ, diameter of rotules 5–11 μ.

Gemmoscleres slightly curved stout amphistrongyla, covered with blunt spines or tubercles except at their extremities, of greatly varying dimensions; length range 33–68 μ, width range 8–14 μ.

Gemmules firmly adhering to substratum, always subspherical to considerably flattened, ranging 600–700 μ in diameter; pneumatic coat feebly developed, without discernible air spaces; gemmoscleres present in one or two layers, arranged in a mosaic-like covering of inner gemmular membrane; foramen produced into small and straight tubule, usually situated laterally.

DISTRIBUTION.—India.

COLOR IN LIFE.—Recorded as black to gray.

DISCUSSION.—*Corvospongilla lapidosa* is another species of the *C. loricata* group that seems separated from its closest congeners on somewhat flimsy evidence, based mainly on its stony consistency. Until additional collections and data become available it is thought advisable to retain its separate specific status in order not to obscure possible taxonomic evidence. The slides of the type available for this study are most certainly insufficient to contemplate a worthwhile revision, and future collections of this and related species are highly desirable.

Corvospongilla böhmii (Hilgendorf, 1883)

PLATE 4, FIGURES 4–6

Spongilla böhmii Hilgendorf, 1883, p. 87.—Potts, 1887, p. 205.—Weltner, 1895, p. 114; 1898b, p. 119.

Corvospongilla böhmii Weltner, 1913, p. 475.—Annandale, 1914, p. 245.—Cunnington, 1920, p. 587.—Gee, 1931e, p. 34; 1932c, p. 27.—Arndt, 1936, p. 16.—Penney, 1960, p. 35.

Corvospongilla böhmii var. *elegans* Topsent, 1932a, p. 580.—Arndt, 1936, p. 16.—Penney, 1960, p. 36.

MATERIAL.—Slides of type material from ZMB in N. Gist Gee's collection.

DESCRIPTION.—Sponge, according to Hilgendorf (1883), forming thin crusts overgrowing *Eunapius nitens;* according to Weltner (1898b) forming encrustations on *Aetheria* species; little information available as to outer morphology. Skeleton apparently loosely defined. Consistency recorded as fragile.

Megascleres rather short, and not very thick, slightly curved or almost straight amphistrongyla, often with inflated extremities, and covered with a dense coat of tubercles or blunt spines arising from a broad base; length range 120–150 μ, width range 11–14 μ; occasionally a number of amphioxea also present, covered with very minute spines and ranging 80–100 μ in length, 3.5–5 μ in width.

Microscleres relatively abundant in outer symplasm of the sponge, represented by microbirotulates with a smooth to sparsely spiny shaft which is slightly curved, and terminally with 4 to rarely 5 strongly recurved hooks of somewhat greater length than in other species of this genus; length of shaft varying from 24–39 μ, diameter of rotules 10–12 μ.

Gemmoscleres not present in material for this revision; recorded as bluntly pointed amphioxea ranging to amphistrongyla, more or less distinctly curved, and covered with short acute spines; length range 40–55 μ, width range 14–15 μ.

Gemmules not studied by the present authors; recorded as subspherical, of medium diameter, and adhering to the substratum.

DISTRIBUTION.—Found only in three localities of equatorial Africa.

COLOR IN LIFE.—Apparently not yet observed.

DISCUSSION.—Even though this species remains insufficiently known, it can be distinguished at a glance from all congeners by the longer and more deeply cleft prongs of the microscleres. The infraspecific separation of *C. b. elegans* by Topsent (1932a) from *C. böhmii* of Hilgendorf (1883) and Weltner (1898b) appears unwarranted, and the smaller and somewhat more slender spicular components of the "variety" can be explained by its limited growth area on shells of *Aetheria* sp. Topsent (1932a) furthermore considered *C. scabri-*

spiculis Annandale (1913b) as fully comparable with the typical form of *C. böhmii,* an opinion which cannot be shared by the present authors. Although the shape and average measurements of the megascleres seem similar in the two species just mentioned and also in *C. micramphidiscoides,* the microscleres of *C. böhmii* cannot be confused with those of any other species of the genus. Until additional collections and data become available it is better to consider these three sponges closely related but separate species.

Corvospongilla micramphidiscoides Weltner, 1913

Corvospongilla micramphidiscoides Weltner, 1913, p. 477.—Annandale, 1914, p. 246.—Stephens, 1919, p. 95.—Gee, 1931c, p. 43; 1932c, p. 27.—Arndt, 1936, p. 16.—Penney, 1960, p. 37.

Material.—Slides of type material (N. Gist Gee no. 54994).

Description.—Sponge, according to original description, forming shallow encrustations on shells of *Aetheria elliptica;* surface of live sponge not yet recorded. Skeleton consisting of slender, spicule fibers, formed by 2–4 scleres, somewhat loosely defined and irregularly reticulate. Consistency of live sponge not recorded.

Megascleres slightly curved and cylindrical amphistrongyla, sparsely covered with minute spines, and of greatly varying dimensions; length range 115–150 μ, width range 18–20 μ; occasionally slightly spiny amphioxea of somewhat smaller dimensions also present.

Microscleres of two distinct series: (1) slightly curved to almost straight, sharply pointed amphioxea, covered with long perpendicular spines that are longest in the center of the scleres; length range 52–70 μ, width range 7–8 μ; and (2) microbirotulates with a slightly curved, smooth shaft and terminally with a smaller number of strongly recurved hooks; average length 19–21 μ, diameter of rotule 10–12 μ.

Gemmoscleres rarely straight, usually strongly curved and stout amphistrongyla, finely granulated, and of greatly varying dimensions; length range 32–55 μ, width range 8–12 μ.

Gemmules separate, not forming aggregations, chiefly fastened to the support but occasionally also free in inner symplasm of sponge; they are spherical to subspherical, ranging 250–450 μ in diameter, apparently lack a pneumatic coat as well as a micropyle (fide Weltner, 1913); gemmoscleres arranged in 2–5 concentric layers, the lowest one in contact with the inner gemmular membrane.

Distribution.—Known only from the Congo R. system, Africa.

Color in life.—Not recorded; dry sponge gray.

Discussion.—The affinities of this species to other closely allied forms have already been commented on in the discussions of *C. böhmii* and *C. scabrispiculis,* respectively. Annandale (1913b), after

comparing the latter species with Weltner's (1913) species here discussed, found the distinguishing criteria important enough to retain his *C. scabrispiculis* as a distinct species. The present authors, therefore, follow Annandale's views, at least until additional collections become available and comparative studies can be made. Should future research establish the identity of *C. micramphidiscoides* with *C. scabrispiculis*, the latter will have to be relegated to a synonym since Weltner's paper, although published in the same year as Annandale's, has priority of several weeks.

Corvospongilla scabrispiculis Annandale, 1913

Plate 4, figures 14–18

Corvospongilla scabrispiculis Annandale, 1913b, p. 238; 1914, p. 245.—Stephens, 1919, p. 95.—Gee, 1931c, p. 48; 1932c, p. 27.—Arndt, 1936, p. 16.—Penney, 1960, p. 37.

Material.—Slide of type specimen (IM no. ZEV 5504/7).

Description.—External form of sponge unknown, apparently hard but brittle; a stout basal membrane present; found growing on shells of *Aetheria* sp. Skeleton of the basis of sponge a stout network, formed of spicules enclosed in a membrane of spongin continuous with the basal membrane, which also contains spicules in considerable numbers. Consistency of live sponge unknown.

Megascleres small and moderately slender, feebly curved to straight amphistrongyla, often with inflated extremities, covered with minute tubercles throughout their length; length range 120–150 μ, width almost constantly 16–17 μ.

Microscleres represented by microbirotulates with only slightly curved smooth shafts, and terminally with a smaller number of hooks, which are less recurved than in most other congeners; average length 25 μ, diameter of rotule 8–11 μ.

Gemmoscleres in shape and armature similar to megascleres, but smaller and relatively stouter, greatly variable in length and form; length range 58–85 μ, width range 10–13 μ.

Gemmules numerous, enclosed in spicular cages formed by megascleres, restricted to base of sponge, and arranged in a distinct pavement layer; pneumatic coat apparently absent; gemmoscleres forming a somewhat sparse cover on inner gemmular membrane; loculi of gemmules consisting of a roof of megascleres and a floor represented by the stout basal membrane; gemmules proper are spherical, averaging 270 μ in diameter; foramen produced into cylindrical porus tube of moderate dimensions.

Distribution.—Tropical Africa, probably the Nile Basin.

Color in life.—Not yet reliably observed; dry sponge recorded as "dark."

Discussion.—*Corvospongilla scabrispiculis* is certainly closely

related to *C. böhmii* and *C. micramphidiscoides*, which together form a rather defined group of this genus, so far as the skeletal components are concerned. However, *C. böhmii* differs from the species discussed in possessing characteristic microscleres, and *C. micramphidiscoides* is recorded as possessing two distinct series of microscleres, one of them sharply pointed amphioxea. Even though it is possible that future research may demonstrate that such acerate microscleres are adventitious and belong to the spicular components of another genus, it is best to retain the separate specific status of *C. scabrispiculis* until additional data become available. A future revision cannot rest with the study of this apparently well-defined group alone, but will have to deal with the entire genus, all species of which are in urgent need of a comprehensive review.

Corvospongilla ultima (Annandale, 1910)

Plate 4, FIGURES 12, 13

Spongilla ultima Annandale, 1910c, p. 31; 1911c, p. 104; 1912b, p. 99.
Corvospongilla ultima Annandale, 1912d, p. 384; 1918a, p. 213.—Gee, 1931e, p. 51; 1932c, p. 27.—Penney, 1960, p. 38.
Corvospongilla ultima var. *spinosa* Annandale, 1912d, p. 390.—Gee, 1931e, p. 49; 1932c, p. 27.—Penney, 1960, p. 38.

MATERIAL.—Syntype of *S. ultima* (AusM. Reg. no. Z 851), slides of type of *C. ultima* var. *spinosa* (IM and N. Gist Gee no. 54606).

DESCRIPTION.—Sponge forming thin crusts on solid supports; surface slightly rough to distinctly spiny, oscula small but conspicuous. Skeleton forming a compact but somewhat irregular reticulation, amount of joining spongin considerable. Consistency of live sponge hard.

Megascleres almost straight to feebly curved stout amphioxea, entirely smooth; length range 200–255 μ, width range 16–20 μ.

Microscleres apparently rare in symplasm; represented by microbirotulates with a smooth, only feebly curved shaft, terminal spines relatively short but distinctly incurved; length range 24–40 μ, diameter of rotules 4–9 μ.

Gemmoscleres usually slightly to moderately curved and stout amphistrongyla, irregularly spiny, and of greatly varying lengths; length range 33–70 μ, width range 8–15 μ.

Gemmules usually adhering to substratum, but often a number of free gemmules also present in inner symplasm; they are spherical, large, ranging from 400 μ (free) to almost 900 μ (adhering) in diameter; pneumatic coat feebly developed and without discernible air spaces; gemmoscleres present in two distinct layers, not separated from each other by an empty space; inner layer resting on inner gemmular membrane, outer enclosed in the strong basal membrane of the sponge;

gemmular aperture always tubular, tube short and cylindrical, in free gemmules usually 2 micropyles present.

Distribution.—Apparently restricted to India, ranging from Bombay to the southernmost tip of the subcontinent.

Color in life.—Not yet reliably recorded; dried sponge pale green.

Discussion.—*Corvospongilla ultima* is a slightly aberrant member of the genus, closely related only to *C. caunteri* with which it forms a distinct group. Its megascleres are invariably smooth amphioxea, and gemmules are found adhering to the substratum, as well as free in the inner symplasm. The extreme paucity of free microscleres in all specimens recorded caused initial difficulties in the assessment of its generic position.

Annandale (1912d) erected an additional "variety" of this species, *C. u. spinosa*, chiefly on the differing surface of the two forms of sponges. After comparing the type slides of both, their spicular components are considered by the present authors fully identical and their separation, even on an infraspecific level, as unwarranted.

Corvospongilla caunteri Annandale, 1911

Plate 4, figures 7–10

Corvospongilla caunteri Annandale, 1911c, p. 243; 1912d, p. 384; 1918a, p. 213.—Gee, 1931e, p. 35; 1932c, p. 27.—Penney, 1960, p. 36.

Material.—Slides of syntype (N. Gist Gee).

Description.—Sponge, according to Annandale (1911c), forming thin crusts of considerable dimensions; surface smooth. Skeleton rather loosely defined, reticulate, but almost devoid of spongin; basal membrane well developed and stout. Consistency of live sponge moderately hard but brittle.

Megascleres variable in size and shape, as a rule almost straight, bluntly or abruptly pointed amphioxea, entirely smooth; occasionally granulated or spiny at their extremities, often sharply pointed; length range 190–220 μ, width range 15–20 μ.

Microscleres represented by microbirotulates with a smooth shaft, which is never strongly curved, terminal spines relatively short, not strongly incurved; length range 22–38 μ, diameter of rotules 4–9 μ.

Gemmoscleres usually slightly curved amphistrongyla, rarely blunt amphioxea, irregularly spiny, and of greatly varying lengths; length range 30–68 μ, width range 7–14 μ.

Gemmules not adhering to substratum but free in lower parts of inner symplasm, spherical to somewhat depressed, variable in size; average diameter 600 μ; pneumatic coat rather thick, apparently consisting of very minute air spaces; below this layer gemmoscleres ar-

ranged in a tangential mosaic-like manner on inner gemmular membrane; foramen recorded as depressed (Annandale).

Distribution.—India.

Color in life.—Recorded as bright green.

Discussion.—*Corvospongilla caunteri* displays close affinities to *C. ultima*, and the spicular components are very similar in both these species. However, *C. caunteri* appears to lack fixed gemmules altogether, and the pneumatic coat of these bodies consists of hardly discernible but nevertheless present minute air spaces. Further collections may yet demonstrate that this species, when fully mature and large, also produces adhering gemmules. Until such additional evidence becomes available, it is advisable to consider *C. caunteri* a distinct species, since at least at present it can be easily differentiated from its closest relative, *C. ultima*, by several criteria.

Corvospongilla zambesiana (Kirkpatrick, 1906)

Spongilla? zambesiana Kirkpatrick, 1906, p. 225.
Corvospongilla? zambesiana Weltner, 1913, p. 475.
Corvospongilla zambesiana Annandale, 1914, p. 245.—Gee, 1931e, p. 52; 1932c, p. 27.—Arndt, 1933c, p. 309; 1936, p. 16.—Penney, 1960, p. 38.

Material.—Slide of type specimen (BM).

Description.—Sponge, according to Kirkpatrick (1906), forming a thick crust; surface irregular. Skeleton a dense network of very thick spicule fibers. Consistency recorded as hard.

Megascleres apparently of two different series: (1) stout and slightly curved amphistrongyla, inflated at their extremities and entirely smooth, forming the mass of the skeleton, and (2) a few slender, curved and smooth amphioxea; length range of (1) 170–200 μ, of (2) 156–175 μ; width range of (1) 20–24 μ, of (2) 7–9 μ.

Microscleres represented by microbirotulates with feebly curved and smooth shafts, and terminally with a smaller number of sharply recurved hooks; average length 35 μ, diameter of rotule 6–11 μ.

Gemmoscleres and gemmules not observed by the authors.

Distribution.—Zambesi River system, Africa.

Color in life.—Not yet observed.

Discussion.—*Corvospongilla zambesiana* is insufficiently represented in the material available for this study, and its revision and comparison with its congeners therefore is impossible. At present, its separation from the *C. loricata* group of species appears highly difficult.

Radiospongilla, new genus

Spongilla Bowerbank, 1863, p. 465 (part).—Gray, 1867, p. 553 (part).—Carter, 1881a, p. 88.—Haswell, 1882, p. 209.—Potts, 1887, p. 194 (part).—Lendenfeld, 1887, p. 89 (part).—Whitelegge, 1889, p. 306.—Weltner, 1895, p.

114 (part); 1910, p. 137.—Traxler, 1896b, p. 97.—Kirkpatrick, 1907, p. 523.—Annandale, 1907b, p. 387; 1911c, p. 76 (part); 1914, p. 245 (part); 1918a, p. 210 (part).—Rezvoj, 1926a, p. 108; 1929, p. 158.—Gee, 1931e, p. 37; 1932c, p. 41; 1933d, p. 456.—Arndt, 1932c, p. 556.—Schröder, 1935, p. 98 (part).—Sasaki, 1936, p. 4.—Penney, 1960, p. 11 (part).

Meyenia Potts, 1882a, p. 12; 1887, p. 228 (part).—Penney, 1954, p. 156; 1956, p. 38; 1960, p. 46 (part).

Ephydatia Weltner, 1895, p. 114 (part).—Annandale, 1909d, p. 402.—Gee, 1928, p. 225; 1930e, p. 27; 1930b, p. 170; 1930a, p. 87; 1935, p. 263.—Sasaki, 1936, p. 12.—Jewell, 1939, p. 11.—Rioja, 1940a, p. 187.—Carvalho, 1942, p. 267.

Pectispongilla Annandale, 1915a, p. 245 (part).—Gee, 1931e, p. 48 (part); 1932c, p. 35 (part).—Arndt, 1936, p. 16 (part).—Penney, 1960, p. 8 (part).

Type species.—By present selection *Spongilla sceptroides* Haswell, 1882.

Definition.—Megascleres moderately stout to slender amphioxea, rarely amphistrongyla; as a rule covered with a variable number of minute to conspicuous spines, only in one species entirely smooth.

True microscleres absent; in the growing phases of some species immature gemmoscleres of only slightly aberrant shape often abundantly present in dermal membrane and inner symplasm, hitherto recorded as microscleres.

Gemmoscleres rather slender amphioxea or amphistrongyla, invariably strongly spined, ranging from moderately long to very long, and from straight to distinctly curved; their spines often conspicuously aggregated and larger in the vicinity of the tips of the scleres, forming club- or scepter-like terminal structures, or pseudorotules of a varying degree of perfection.

Gemmules often abundant in maturing sponges, in perennial forms usually rare or absent; they are large and spherical, usually scattered throughout the sponge; when occasionally grouped together at the base they never form a distinct pavement layer; typically with a strong and thick pneumatic layer consisting of air spaces of small size and slightly irregular outline, and with gemmoscleres embedded in this layer more or less radially; foramen invariably tubular, tube delicate, straight or slightly curved, rarely projecting beyond outer gemmular membrane, surrounded by a conical depression created by the displacement of gemmoscleres around the micropyle.

Sponges ranging from minute cushions to large flat crusts, with or without occasional delicate and cylindrical branches, rarely massive; often an emerald green color owing to the presence of a specific pigment, rarely associated with zoochlorellae. Consistency moderately firm and usually elastic.

Widely distributed in tropical and subtropical regions of all continents, rarely ranging into cold-temperate climates of both hemispheres.

Discussion.—With the restoration of Gray's (1867) system, the restriction of the genus *Spongilla* Lamarck, and the elevation of *Stratospongilla* Annandale to full generic rank, it became necessary to define a new genus, *Radiospongilla*, for the inclusion of those members of the formerly recognized subfamily Spongillinae, which possess gemmules with a thick pneumatic coat and a conspicuous porus tube, more or less radially arranged gemmoscleres with a characteristic arrangement of terminal spines, and lack true microscleres in their dermal membrane and inner symplasm. All these species display a number of constant intrageneric characters and form a distinct group of intermediate position between the "Spongillinae" and "Meyeninae" of previous authors, so that a further retention of these subfamilies has become meaningless and futile.

Radiospongilla consists of two clearly separable groups of species. One is represented by *R. cerebellata* (Bowerbank), with which *S. biseriata* Weltner, *S. reticulata* Annandale, *S. proliferens* Annandale, *S. semispongilla* Annandale, *S. micron* Annandale, and *S. sectospina* Rezvoj are synonymous, and is characterized by the possession of generally smooth megascleres and a double layer of gemmoscleres. The other consists of a large number of closely related species, displaying spiny megascleres and a singular arrangement of gemmoscleres, typically represented by *R. sceptroides* (Haswell) and *R. crateriformis* (Potts). *R. cantonensis* (Gee), elevated to full specific rank in this paper, represents an extreme of this latter group, almost linking up to spicular conditions found in *Umborotula*, but is still a clearly defined species of the present genus.

A number of species, which certainly also belong to this latter group of *Radiospongilla* spp., must still be considered as insufficiently known. Since most of them are not represented in the material available for the present study, the assessment of their intrageneric relationships is impossible. They are *S. luzonensis* Gee (1932) from the Philippines, with which *S. hozawai* Sasaki (1936) from Japan most probably is synonymous, and two additional Japanese species recorded by Sasaki (1936), *S. sendai* and *E. crateriformis*, the latter appears closely related to *R. indica* (Annandale).

Four additional species recently found in Australian waters will be described in a forthcoming paper (Racek, MS.), one of these already recorded under the erroneous name *S. botryoides* Haswell by Gee (1931d). In spite of the extensive search for this highly dubious species of Haswell (1882) in the Australian region, and the great number of specimens and species collected, no spongillid has ever been found to correspond, even vaguely, with the short description of the original author. Since a type specimen of *S. botryoides* apparently has never

been deposited, and certainly does not exist today, the true identity of Haswell's species most likely will never be established.

The generic position of *S. cinerea* Carter (1849), doubtfully referred in this paper to *Radiospongilla*, has yet to be demonstrated. The extent of the taxonomic difficulties involving this species has been discussed in dealing with *Stratospongilla gravelyi* (p. 46).

***Radiospongilla sceptroides* (Haswell, 1882)**

PLATE 5, FIGURES 4–6, 11, 12

Spongilla sceptroides Haswell, 1882, p. 209.—Lendenfeld, 1887, p. 89.—Potts, 1887, p. 197.—Whitelegge, 1889, p. 306.—Weltner, 1895, p. 114; 1910, p. 137.—Traxler, 1896b, p. 97.—Gee, 1931e, p. 48 (part); 1931d, p. 25; 1932e, p. 41.—Penney, 1960, p. 25. (Not Annandale 1909h, p. 627.)

?Spongilla philippinensis Annandale, 1909h, p. 627; 1911c, p. 53; 1918a, p. 211.—Gee, 1931e, p. 46; 1931c, p. 62; 1932e, p. 526; 1932f, p. 507.—Penney, 1960, p. 26.

Spongilla multispinifera Gee, 1933d, p. 456.—Penney, 1960, p. 25.

Spongilla rotoitiensis Schröder, 1935, p. 98.—Penney, 1960, p. 27.

Ephydatia crateriformis Gee, 1935, p. 263.

MATERIAL.—Numerous specimens of *R. sceptroides* from eastern Australia (collection AAR and AusM); fragments and slides of type of *S. multispinifera* (N. Gist Gee); slide material of *S. sceptroides* Annandale, 1909h (USNM); slide material of *S. rotoitiensis* (N. Gist Gee).

DESCRIPTION.—Sponge forming flat encrustations on submerged timber or aquatic plants, mature specimens often of considerable spread; surface ranging from smooth to distinctly papillose, sometimes producing long and thin finger-like projections; oscula numerous, in specimens from lotic habitats often surrounded by a system of radiating furrows; dermal membrane well developed. Skeleton consisting of a rather regular arrangement of slender horizontal, and irregular transverse fibers, both joined together by a comparatively small amount of spongin. Consistency of live sponge rather firm and elastic.

Megascleres slender and fusiform, slightly curved amphioxea with sharply pointed tips, covered with minute and inconspicuous spines except in the vicinity of their extremities; in acid environment these spines often more numerous and readily visible, their tips occasionally subdivided or otherwise malformed; length range 240–310 μ, width range 8–11 μ.

Microscleres absent, though immature gemmoscleres occasionally present in inner symplasm.

Gemmoscleres moderately long and slender amphistrongyla, armed with numerous acute spines that form distinct aggregations in the vicinity of the extremities of the scleres, which represent scepter-like distal arrangements of recurved teeth; in acid environment gem-

moscleres often shorter and more robust, their spines often malformed or subdivided; length range of typical gemmoscleres 72–105 μ, width range 3.5–5 μ.

Gemmules abundant in mature sponge, more or less restricted to basal parts of the skeletal meshes without forming a pavement layer; in perennial specimens often extremely rare or altogether absent; they are spherical, ranging in diameter 420–500 μ, and possess a well developed and thick pneumatic coat consisting of minute irregular air spaces; gemmoscleres embedded in this coat more or less radially, frequently slightly crossing each other, arranged in a single layer, their tips slightly penetrating outer gemmular membrane that thus attains a hispid appearance; foramen distinctly tubular, porus tube invariably short and relatively wide, in length not reaching to level of outer gemmular membrane; surrounded by a conical depression caused by slanting gemmoscleres in its vicinity.

Distribution.—Widely distributed in eastern Australia, ranging from Victoria to central Queensland; also recorded from New Zealand, and most probably also present in New Guinea and New Caledonia (Racek, MS.).

Color in life.—Emerald green, regardless of position to light.

Discussion.—Because of the insufficient original description by Haswell (1882) and the regrettable fact that its type apparently has never been deposited, *R. sceptroides* remained a most dubious species for many decades. Unfortunately, the material of *S. sceptroides* deposited in the USNM and redescribed under this name by Annandale (1909h) is not a specimen of Haswell's species; it represents a new species of this genus that will be described by the writer in a forthcoming paper. Gee (1931d, p. 37) used Annandale's descriptions and illustrations in his revision of *S. sceptroides*, and he consequently noted inexplicable differences between the material from the USNM and the previous descriptions of Haswell's species by Lendenfeld (1887), Whitelegge (1889), and Traxler (1896b).

Gee (1931d) drew attention to the fact that a jar marked "Type, *S. sceptroides* Haswell, Lillesmere Lagoon, Lower Burdekin R., Queensland" in the collection of the AusM could hardly represent the true type material. Under reexamination, this jar turned out to contain still another spongillid without gemmules, which most probably represents *Ephydatia fluviatilis*. Apart from the fact that this sponge certainly belongs to another genus, it cannot possibly be Haswell's type specimen which came from the vicinity of Brisbane, several hundred miles to the south. Since the true type of *S. sceptroides* could not be located in the two institutions, i.e., the Macleay Museum and the AusM, where most of Haswell's type specimens are deposited, it must now be considered as lost. The writer, therefore, has selected as the neotype of

S. sceptroides Haswell a typical specimen in the collection of the AusM, Reg. no. Z 2837; Merrika R., near Womboyne, N.S.W.; coll. F. Hersey, 6. iii. 1958; growing on upper side of rock in about 2 feet of water, originally forming a large cushion, 460 x 200 mm., and about 11 mm. in thickness.

The reexamination of *S. multispinifera* Gee has demonstrated beyond doubt that the supposedly characteristic structure and arrangement of spines on its megascleres and gemmoscleres represent ecomorphic malformations, which can often be observed within the morphometric range of *R. sceptroides*. Gee would certainly have come to the same conclusion had he been able to compare his "new species" with the true *S. sceptroides*, then unknown to him.

The specific identity of *S. philippinensis* still poses some problems, since its spicular components, while readily comparable with those of the specimen in the collection of the USNM described by Annandale (1909h) as *S. sceptroides*, differ in many regards from the scleres of Haswell's species. The megascleres of *S. philippinensis* are much stouter, altogether smooth or differently spined, and the gemmoscleres are considerably longer and produce burlike aggregations of terminal spines, and more numerous spines along their shafts. In all these features it closely resembles another abundant Australian species of this genus, which will be described in a forthcoming paper. It is therefore advisable to retain *S. philippinensis* as a dubious synonym of *R. sceptroides*, until further comparative studies are possible.

The erection of *S. rotoitiensis* from New Zealand by Schröder (1935) also appears to have been aided by the previous misconceptions of *S. sceptroides*. The examination of Schröder's species proved clearly that the sponge from New Zealand is identical with the true *S. sceptroides* in all respects, and that its separate status, even on a subspecific level, is fully unwarranted.

Radiospongilla crateriformis (Potts, 1882)

Plate 5, figures 1–3; Plate 6, figures 1, 2

Meyenia crateriformis Potts, 1882a, p. 12; 1887, p. 228.—Kellicott, 1897, p. 50.—Eshleman, 1950, p. 40.—Wurtz, 1950, p. 5.—Moore, 1951, p. 63.—Penney, 1954, p. 156; 1956, p. 38; 1960, p. 47.

Ephydatia crateriformis Weltner, 1895, p. 114.—Girod, 1899, p. 111.—Annandale, 1909d, p. 402.—Smith, 1921, p. 17.—Gee, 1928, p. 225; 1930e, p. 27; 1930b, p. 170; 1930f, p. 87; 1931e, p. 36; 1932d, p. 53; 1932f, p. 507.—Arndt, 1932c, p. 556; 1933a, p. 24.—Old, 1932c, p. 239; 1932a, p. 131; 1932b, p. 470; 1936a, p. 29; 1936b, p. 11.—Sasaki, 1936, p. 12.—Jewell, 1939, p. 11.—Rioja, 1940a, p. 187.

Spongilla crateriformis Annandale, 1911c, p. 85; 1912d, p. 384; 1918a, p. 211.—Vorstman, 1927, p. 183.—Gee, 1929d, p. 297.

?Spongilla crateriformis var. *insularis* Annandale, 1911c, p. 85 (footnote).

?Ephydatia crateriformis var. *arndti* Carvalho, 1942, p. 267.

Material.—Numerous slides of specimens from various localities in the United States (Jewell, N. Gist Gee), India (IM) and Indonesia (AusM); slide of type of *S. c.* var. *insularis* (IM).

Description.—Sponge, according to previous descriptions, forming thin and small cushions of a rather even surface; oscula numerous but inconspicuous, dermal membrane well developed. Skeleton consisting of irregular spicule fibers, joined together by a small amount of spongin. Consistency of live sponge soft.

Megascleres slender, fusiform and sharply pointed amphioxea, sparsely microspined except at their tips; length range 240–300 μ, width range 9–11 μ.

Microscleres absent.

Gemmoscleres typically slender amphistrongyla, their slightly curved shafts armed with a variable number of small conical spines, and terminally with one to several rows of radiating slightly recurved spines, arranged in such a way that pseudorotules are produced; length range 60–75 μ, width range 3–5 μ.

Gemmules moderately abundant to abundant in mature sponge, spherical, ranging in diameter 370–450 μ; pneumatic layer well developed and thick, consisting of minute irregular air spaces; gemmoscleres embedded in this coat more or less radially, but often crossing each other at various angles, arranged in one layer only, their distal pseudorotules not penetrating the outer gemmular membrane; foramen distinctly tubular, porus tube short and straight, in length not reaching to level of outer gemmular membrane; gemmoscleres in the vicinity of this tube displaced and slanting, forming a crater-like depression around the micropyle.

Distribution.—Discontinuous, recorded from various localities in the United States, ranging to Mexico; also recorded from China, Japan, and parts of southeast Asia; record from Australia (Gee, 1935) a result of wrong identification.

Color in life.—Ranging from flesh colored to light green.

Discussion.—The great variability of the gemmoscleres in this species makes it difficult to decide how many different species of this and other genera have been described under the name of *Meyenia crateriformis* Potts. Similar difficulties were encountered by a number of authors who were unable to interpret the greatly inconsistent shape of the pseudorotules and repeatedly shifted the species discussed from one subfamily to the other. Since pseudorotules are often produced in a number of other *Radiospongilla* species, this criterion alone cannot possibly be used for their reliable specific separation. Gee's (1935) identification of a sponge from Australia under the name of *Ephydatia crateriformis* (reexamined as a slightly atypical specimen of *R. sceptroides*) and Arndt's (1930a) comparison

of his *Spongilla hemephydatia* from New Guinea with *R. crateriformis* are only two examples of obvious taxonomic difficulties.

Furthermore, the discontinuous distribution of *R. crateriformis* is bound to increase speciation trends in distant populations, a phenomenon which has not been given full attention. Although the general characteristics of North American specimens are in full accordance with those from Asian localities and all these specimens display considerable variations of their spicular components, it is possible that future more detailed studies will be able to establish clear-cut races of subspecific importance. Until such additional data become available, it is advisable to consider the various ecomorphic forms of *R. crateriformis* within the morphometric range of this species as known today.

However, the former variety of *Ephydatia crateriformis cantonensis* has been elevated to full specific rank, since it possesses a number of sufficiently distinctive criteria for its clear separation from the nominal species.

Radiospongilla indica (Annandale, 1907)

Plate 6, figures 4–10

Ephydatia indica Annandale, 1907c, p. 20; 1907, p. 272; 1909d, p. 402.—Gee, 1931e, p. 40.
Spongilla crateriformis Annandale, 1911c, p. 83.
Ephydatia crateriformis Gee, 1932e, p. 533.
?Ephydatia fluviatilis var. *ramsayi* Annandale, 1909c, p. 421.

Material.—Specimens on 26 slides from India (IM), Indonesia (AmstM), and New Guinea (AAR).

Description.—Sponge, according to previous descriptions, forming flat cushions of moderate size; surface smooth and even, oscula inconspicuous; dermal membrane apparently well developed. Skeleton consisting of irregular spicule fibers, joined together by a small amount of spongin. Consistency of live sponge soft, texture loose.

Megascleres subcylindrical and comparatively long amphistrongyla, rarely amphioxea; usually with bulbous terminal swelling, rarely with lanceolate tips; scleres armed with acute though scattered spines in their central portion, and with a more dense arrangement of rather blunt spines on the terminal expansions; length range 230–360 μ, width range in center 9–13 μ.

Microscleres absent.

Gemmoscleres slender amphistrongyla with slightly curved or almost straight shafts which bear a variable number of small conical spines, and terminally with several rows of larger straight spines, the distal of which form comparatively flat pseudorotules; length range 60–72 μ, width of shaft 3–4 μ, diameter of pseudorotule about 8 μ.

Gemmules relatively small, ranging in diameter 230–350 μ, spherical, scattered through the skeletal meshes; pneumatic layer well developed and thick, consisting of minute irregular air spaces; gemmoscleres embedded in this layer radially, rarely crossing each other at various angles, arranged in a single layer, their distal pseudorotules not projecting beyond outer gemmular membrane; foramen distinctly tubular, porus tube short and straight, surrounded by a conical depression caused by slanting gemmoscleres in its vicinity.

Distribution.—Ranging from India (type locality) to Indonesia and the Philippines, probably also present in New Guinea.

Color in life.—Recorded as "colorless" even when exposed to light.

Discussion.—The possession of amphistrongylous megascleres, which display most typical bulbous aggregations of terminal blunt spines, as well as the structure of the pseudorotules on the gemmoscleres, make this species clearly distinguishable from *R. crateriformis*. The question whether the existing spicular differences of *R. indica* are to be considered of specific or subspecific importance can only be answered by future studies of a large range of additional material of both these spongillids. For the present, it seems advisable not to obscure perceptible taxonomic evidence by relegating the species discussed to a synonym of *R. crateriformis*, therefore the separate specific status of *R. indica* is herewith restored.

The megascleres of *R. indica* from all localities on the Indo-Pakistani subcontinent are amphistrongyla with distinct terminal bulbous swellings, while those from Indonesia merely bear terminal aggregations of spines or attain lanceolate spiny tips. The gemmoscleres of both these morphometric forms, however, are fully comparable.

Radiospongilla hemephydatia (Annandale, 1909)

Plate 5, figures 7–10

Spongilla hemephydatia Annandale, 1909g, p. 275; 1911c, p. 82; 1918a, p. 211.—?Arndt, 1930a, p. 5.—Gee, 1931e, p. 39; 1932c, p. 38.—Penney, 1960, p. 19.

Material.—Slides of syntype (N. Gist Gee and AusM); specimen from New South Wales, Australia.

Description.—Sponge, according to previous descriptions, forming flat cushions of small size on aquatic plants; surface smooth and even, oscula inconspicuous. Skeleton consisting of irregular spicule fibers, joined together by a very small amount of spongin. Consistency of live sponge very soft and fragile.

Megascleres slender and distinctly fusiform, sharply pointed amphioxea, either entirely smooth or covered with a small number of inconspicuous spinules in their central portion; length range 290–330 μ, width range 9–12 μ.

True microscleres absent; however, immature gemmoscleres often abundant in dermal membrane, also present in dense isolated batches in inner symplasm.

Gemmoscleres almost straight, club-shaped amphistrongyla, covered with short and straight spines throughout their length, these spines forming distinct aggregations at the extremities of the sclere, without increasing in length; length range 60–68 μ, width of shaft 3–4 μ.

Gemmules numerous in maturing sponge, spherical, scattered throughout skeletal meshes, and easily dislodged; diameter ranging 310–370 μ; pneumatic layer well developed and thick, consisting of minute irregular air spaces; gemmoscleres embedded in this coat more or less radially, arranged in a single layer, their extremities occasionally slightly protruding through outer gemmular membrane; foramen distinctly tubular, porus tube flask-shaped, slender, and relatively long, surrounded by 3–4 mammiform aspiculous enlargements of the pneumatic coat.

Distribution.—India (type locality), and possibly New Guinea (Arndt, 1930a); recently also recorded from eastern Australia (Racek, MS.).

Color in life.—Ranging from dirty yellow (Annandale) to bright green (Australian specimen).

Discussion.—This species is closely related to *R. sansibarica*, but differs from the latter by its smaller and sparsely spined megascleres, by some differences in shape and length of its gemmoscleres, and by the presence of mammiform aspiculous elevations of the pneumatic coat surrounding the gemmular micropyle.

Arndt's (1930a) record of *R. hemephydatia* from New Guinea, material of which was unavailable for the present study, needs confirmation. The megascleres of the New Guinea sponge are entirely smooth and almost cylindrical and the gemmoscleres are illustrated as resembling those of *R. crateriformis* or *R. cantonensis*. Additional material is highly desirable in order to establish the true identity of this particular spongillid.

Radiospongilla sansibarica (Weltner, 1895)

Plate 6, figures 12–14

Spongilla sansibarica Weltner, 1895, p. 140; 1898b, p. 127; 1913, p. 475.—Arndt, 1938a, p. 21.

Pectispongilla sansibarica Annandale, 1914, p. 245.—Gee, 1931e, p. 48; 1932c, p. 35.—Arndt, 1936, p. 16.—Penney, 1960, p. 9.

Material.—Slides of type (N. Gist Gee).

Description.—Sponge, according to Weltner (1895), forming encrustations on aquatic plants; surface hispid due to projection of radiating spicule fibers; dermal membrane well developed. Skeleton

not yet described in detail. Consistency of live sponge recorded as soft but elastic.

Megascleres slightly curved and distinctly fusiform amphioxea, armed with rather conspicuous spines except at their tips; spines short and arising from a broad base; length range 250–350 μ, width range 8–13 μ.

Microscleres absent.

Gemmoscleres slightly curved or almost straight amphistrongyla, their central portion ranging from smooth to feebly spined, their extremities displaying an aggregation of dense spines, so that terminally the scleres attain a clublike shape; length range 65–75 μ, width of central stem 4 μ, of extremities 10 μ.

Gemmules abundant in mature sponge, spherical, ranging in diameter 350–400 μ; pneumatic layer well developed and thick, consisting of minute spherical air spaces; gemmoscleres embedded in this coat more or less radially, often crossing each other at various angles, and arranged in a singular layer; foramen distinctly tubular, porus tube comparatively long, slightly exceeding level of outer gemmular membrane, surrounded by a conical depression caused by slanting gemmoscleres in its vicinity.

Distribution.—Apparently restricted to Africa, hitherto found only in Sansibar, the Belgian Congo, and Northern Rhodesia.

Color in life.—Has yet to be confirmed.

Discussion.—This species is most closely related to *R. hemephydatia* in many features but can be distinguished from the latter by its distinctly larger and conspicuously spined megascleres, by slight though perceptible differences in the shape and length of its gemmoscleres, and by the absence of mammiform aspiculous elevations of the pneumatic coat in the vicinity of the gemmular micropyle. Its separate specific status, at least at the present, is therefore fully justified.

The fact that the terminal aggregations of spines on the gemmoscleres of *R. sansibarica* are often slightly asymmetrical has caused Annandale (1914) to place this species tentatively in the genus *Pectispongilla*, an arrangement which was followed by most subsequent authors. However, the reexamination of the type during the present studies proved clearly that *R. sansibarica* cannot possibly represent a *Pectispongilla* species for a number of reasons. Its gemmules are moderately large to large, possess relatively long gemmoscleres, and consequently a thick pneumatic coat; the spines on its gemmoscleres, although occasionally irregular in length, do not form unilateral arrangements of comb rows, but distinct club-shaped terminal aggregations; microscleres of any kind are absent from

dermal membrane and symplasm; and the gemmular porus tube is of considerable length.

Radiospongilla cantonensis (Gee, 1929)

PLATE 5, FIGURES 19–22

Ephydatia crateriformis var. *cantonensis* Gee, 1929c, p. 1; 1930b, p. 170; 1930e, p. 27; 1931e, p. 35; 1932d, p. 53; 1932c, p. 28.
Meyenia crateriformis var. *cantonensis* Penney, 1960, p. 48.

MATERIAL.—Slides of type (USNM, N. Gist Gee).

DESCRIPTION.—Sponge, according to Gee (1929c), forming a thin layer over the surface of small clods of clay; surface of live sponge apparently not yet recorded. Skeleton consisting of slender vertical spicule fibers, made up from 3–5 spicules, and of irregular transverse bundles of scleres, joined together by a small amount of spongin. Consistency of live sponge apparently fragile, texture loose.

Megascleres fusiform and sharply pointed, almost straight amphioxea, armed with a great number of conspicuous acute spines, except at their very tips, length range 180–230 μ, width range 8–11 μ.

Microscleres absent.

Gemmoscleres invariably straight amphistrongyla, their shaft abundantly armed with long acute spines arising from a wide base, and terminally with a singular arrangement of a number of slightly recurved spines, so that almost perfect rotules of umbonate shape are produced; length range 65–72 μ, width of shaft about 5 μ, diameter of rotules 8–9 μ.

Gemmules numerous in mature sponge, spherical, scattered throughout the skeletal meshes, and easily dislodged; diameter ranging 365–410 μ; pneumatic layer well developed and thick, consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, arranged in a single layer, not protruding through outer gemmular membrane; foramen distinctly tubular, porus tube short and inconspicuously curved, surrounded by a conical depression caused by slanting gemmoscleres in its vicinity.

DISTRIBUTION.—Known only from mainland China.

COLOR IN LIFE.—Not yet reliably recorded.

DISCUSSION.—The gemmoscleres of this species, with their straight shafts and almost perfect terminal rotules of umbonate spines, resemble in many regards birotulates of other genera, in particular those of *Umborotula*. However, the rotules of *R. cantonensis* are extremely small and lack a central disk and can thus be rather compared with the terminal arrangement of radiating spines on the gemmoscleres often present in a number of *Radiospongilla* species. Although Gee (1929c) considered the species discussed a mere race of

R. crateriformis, the present studies indicate that its elevation to full specific rank is fully justified.

Radiospongilla cantonensis is perhaps the best example of the futility for further retention of the subfamilies Spongillinae and Meyeninae. While the closely related *R. crateriformis* possesses gemmoscleres of an intermediate form, leading towards true birotulates, those of the species discussed have all the features of birotulates with the exception of their feebly developed rotules.

Radiospongilla cerebellata (Bowerbank, 1863)

Plate 5, figures 13–18

Spongilla cerebellata Bowerbank, 1863, p. 465.—Gray, 1867, p. 553.—Carter, 1881a, p. 88.—Potts, 1887, p. 194.—Weltner, 1895, p. 114.—Kirkpatrick, 1907, p. 523.—Arndt, 1936, p. 14.—Jewell, 1952, p. 448.

Spongilla cinerea Weber, 1890, p. 35 (not *S. cinerea* of other authors).

Spongilla biseriata Weltner, 1895, p. 138; 1898b, p. 119; 1913, p. 475.—Kirkpatrick, 1906, p. 218.—Annandale, 1914, p. 245.—Cunnington, 1920, p. 587.—Gee, 1931e, p. 34; 1932c, p. 36.—Schröder, 1933, p. 113; ?1942, p. 247.—Arndt, 1936, p. 14.—Penney, 1960, p. 13.

Spongilla reticulata Annandale, 1907b, p. 387.

Spongilla proliferens Annandale, 1907c, p. 15; 1907a, p. 267; 1908b, p. 157; 1910d, p. 197; 1911a, p. 63; 1911c, p. 72; 1912d, p. 384; 1918a, p. 210.—Vorstman, 1927, p. 183; 1928, p. 116.—Rezvoj, 1929, p. 158.—Gee, 1929d, p. 297; 1930a, p. 77; 1932f, p. 506; 1933b, p. 73.—Arndt, 1932c, p. 556.—Penney, 1960, p. 27.

Ephydatia semispongilla Annandale, 1909b, p. 107.

Spongilla semispongilla Annandale and Kawamura, 1916, p. 5.—Annandale, 1918a, p. 200.—Gee, 1926c, p. 110; 1927a, p. 1; 1927b, p. 60; 1928b, p. 225; 1930e, p. 27; 1931e, p. 48; 1932c, p. 41.—Sasaki, 1936, p. 4.

Spongilla alba var. *cerebellata* Annandale, 1911c, p. 76; 1914, p. 245.

Spongilla lacustris var. *reticulata* Annandale, 1911c, p. 71; 1912c, p. 137; 1912d, p. 384; 1918a, p. 210.—Penney, 1960, p. 23.

Spongilla lacustris var. *cerebellata* Weltner, 1913, p. 475.

Spongilla micron Annandale, 1916a, p. 49.—Gee, 1926d, p. 87.

Spongilla sectospina Rezvoj, 1926a, p. 108; 1928, p. 223; 1929b, p. 158.—Penney, 1960, p. 28.

Spongilla lacustris var. *proliferens* Gee, 1931e, p. 47; 1932c, p. 40.

Material.—Sponge fragments and slides of syntypes of *S. proliferens* and *S. reticulata* (AusM), *S. semispongilla*, *S. micron*, and *S. sectospina* (N. Gist Gee); several specimens of all morphometric forms from India, Indonesia, China, and central Africa.

Description.—General shape of sponge ranging from small and shallow cushions to bulbous masses of the size of a fist; surface rather uneven in larger specimens, distinctly corrugated, brainlike; oscula conspicuous, dermal membrane well developed. Skeleton irregular in small and flat specimens, forming distinct transverse and radiating spicule fibers of variable thickness in those of massive growth; amount

of spongin always insignificant. Consistency of live sponge soft, texture loose.

Megascleres feebly curved to almost straight fusiform amphioxea, sharply pointed at their tips, and entirely smooth; length range 240–330 μ, width range 10–12 μ.

True microscleres absent; however, immature and slender gemmoscleres often abundant in dermal membrane, also occurring in isolated batches in inner symplasm.

Gemmoscleres typically often distinctly curved, rarely straight, cylindrical amphistrongyla, sometimes bearing a single terminal spine in the prolongation of their axis, thus resembling amphioxea; their shaft abundantly spined, spines erect and often subdivided in the central portion of the scleres, progressively recurving towards their extremities; length range 72–110 μ, width range 2–4 μ.

Gemmules numerous in mature sponge, abundantly produced even in small specimens, spherical, ranging in diameter 420–590 μ; pneumatic coat well developed and unusually thick, consisting of minute spherical air spaces; gemmoscleres embedded in this coat in two distinct layers, i.e., (1) more or less radially arranged, arising from inner gemmular membrane, often crossing each other at various angles, and not reaching to outer gemmular membrane; and (2) lying on top of the first, more or less tangentially arranged, embedded with their proximal portions in the pneumatic coat, their distal ends protruding through outer gemmular membrane; foramen distinctly tubular, porus tube slender and straight, always at least reaching to level of pneumatic coat.

Distribution.—Apparently widely distributed in tropical and subtropical regions of Africa, the Indo-Pakistani subcontinent, and Indonesia, ranging to the Philippines and New Guinea, as well as through China to the U.S.S.R., and perhaps also to parts of southeastern Europe (Schröder, 1942).

Color in life.—Ranging from yellowish gray to dark green.

Discussion.—In view of the clear and sufficient description of *S. cerebellata* by Bowerbank (1863) and a number of subsequent authors, it is difficult to understand why this species became relegated to a most dubious position by the revising efforts of later workers. Weltner (1895) recorded it from Africa under the name of *S. biseriata*, not realizing its identity with *S. cerebellata*, and Annandale (1907b, c, 1909b, 1916) described another four species without being aware of the obvious affinities to each other as well as to Bowerbank's species. However, more serious taxonomic confusions were yet to come. The often abundant presence of immature gemmoscleres in the dermal membrane and inner symplasm of some of these additional "species" has led to the description of true microscleres in these

sponges, which consequently were considered mere "varieties" of *S. lacustris* or *S. alba*, often by the same author. This resulted in an ever widening separation of *S. cerebellata* from the other "species" described, and their true generic and specific relationship became thus permanently obscured. Although Schröder (1933) correctly relegated *S. proliferens* to a synonym of *S. biseriata*, he too failed to realize that Annandale's three additional species, together with Weltner's species, are morphometrically fully identical with *S. cerebellata* Bowerbank. This latter species finally became so obscure that it is not even mentioned in the latest and comprehensive revision of Penney (1960).

The results of the present studies, during which numerous specimens and slides of all recorded "species" of this complex were examined, demonstrate beyond doubt that *S. biseriata*, *S. reticulata*, *S. proliferens*, *S. semispongilla*, *S. micron*, and even *S. sectospina* are morphometrically fully comparable with *S. cerebellata*, and that they must be considered synonymous with Bowerbank's species. While *S. reticulata* and *S. proliferens* are fully indistinguishable, and *S. sectospina* merely displays abnormal spines on its gemmoscleres often also found in *S. proliferens*, *S. biseriata*, and *S. semispongilla* merely differ in the apparent absence of "microscleres," as recorded in the remaining species of Annandale and Rezvoj. Since these immature gemmoscleres are by no means a constant criterion, and all the remaining features, i.e., megascleres, gemmoscleres, and characteristics of the gemmules, are fully identical in all the sponges of this complex, the separate status of all these "species" even on a subspecific level appears unjustified.

R. cerebellata differs from all other *Radiospongilla* spp. in possessing smooth megascleres and in the peculiar double arrangement of gemmoscleres on its gemmules, which thus usually attain a rather large diameter. The occasionally occurring single layer of gemmoscleres, such as described by Annandale (1909b) in *S. semispongilla*, most certainly is the result of seasonal variations or refers to immature gemmules of developing specimens.

?Radiospongilla cinerea (Carter, 1849)

Spongilla cinerea Carter, 1849, p. 82; 1881b, p. 263.—Bowerbank, 1863, p. 468.—Gray, 1867, p. 553.—Potts, 1887, p. 197.—Weltner, 1895, p. 114.—Annandale, 1907c, p. 26; 1911b, p. 225; 1911c, p. 79; 1912c, p. 137; 1912d, p. 384; 1918a, p. 211; 1919a, p. 158.—Gee, 1929d, p. 297; 1931e, p. 35; 1932c, p. 36.—Jewell, 1952, p. 448.—Penney, 1960, p. 15 (not Weber, 1890, p. 35).

?Spongilla (*Euspongilla*) *perviridis* Annandale, 1919a, p. 159.—Gee, 1931e, p. 46; 1932c, p. 41.

?Spongilla perviridis Penney, 1960, p. 26.

MATERIAL.—Slides of syntype (N. Gist Gee) of *S. cinerea*.

Description.—Sponge, according to previous descriptions, forming flat crusts of small dimensions; surface and skeletal structure insufficiently known. Consistency recorded as fragile.

Megascleres distinctly fusiform, sharply pointed, and slightly curved amphioxea, covered with minute and inconspicuous spines except at their extremities; length range 230–275 μ, width range 8–10 μ.

Microscleres absent.

Gemmoscleres slightly curved, somewhat abruptly pointed amphioxea, armed with rather coarse spines throughout their length, spines in terminal region of sclere somewhat aggregated, without much increasing in length; length range 47–62 μ, width range 3–4 μ.

Gemmules spherical, ranging in diameter 310–330 μ; pneumatic layer well developed, consisting of clearly visible subspherical air spaces, or granular without discernible air spaces; gemmoscleres embedded in this coat strictly radially, forming a single layer, their extremities penetrating outer gemmular membrane, so that surface of gemmules appears distinctly hispid; foramen distinctly tubular, porus tube slender and straight, slightly surpassing in length outer gemmular membrane, and without a surrounding conical depression.

Distribution.—Known only from the vicinity of Bombay (*S. cinerea*) and the Himalayas (*S. perviridis*). Weber's (1890) record from Indonesia based on wrong identification.

Color in life.—Ash gray to bright green.

Discussion.—The generic position of this insufficiently known species must still be considered as highly dubious. As mentioned in the discussion of *Stratospongilla gravelyi*, the slides of the syntype of *Spongilla cinerea* contain some gemmules which, in addition to the radially arranged gemmoscleres of this species, also possess a very few stratospongillid tangential amphistrongyla. While in these few cases the pneumatic coat, although of the same thickness, does not display any discernible air spaces, those of the remaining more numerous gemmules are small and subspherical, a typical feature in all *Radiospongilla* species. In spite of the striking similarity of the acerate radially arranged gemmoscleres in both types of gemmules, it is possible that gemmules of two different spongillids are present in the type material examined. However, it is equally possible that the sponge known as *S. cinerea* represents a distinct growth form of a *Stratospongilla* species, as suggested by Annandale (1912d, p. 386). This would also account for the most apparent paucity of material of *S. cinerea* collected. Its inclusion in the genus *Radiospongilla* must therefore be considered a tentative solution of this unsolved taxonomic problem, and additional studies are highly desirable.

The equally insufficiently known *S. perviridis* Annandale, unavailable for the present studies, has provisionally been relegated in this paper to a doubtful synonym of *S. cinerea* until additional data become available. It seems most likely that these two spongillids are closely related, even though they differ from each other in some less important criteria, such as color in life and the density of spines on their megascleres.

Genus *Pectispongilla* Annandale, 1909

Pectispongilla Annandale, 1909f, p. 103; 1911c, p. 106; 1912d, p. 384; 1915a, p. 171; 1918a, p. 212.—Gee, 1931e, p. 46; 1932c, p. 35.—De Laubenfels, 1936, p. 35.—Penney, 1960, p. 8.

Type species.—*Pectispongilla aurea* Annandale, 1909.

Definition.—Megascleres fusiform amphioxea, ranging from microspined to entirely smooth.

Microscleres slender, microspined, fusiform, straight amphioxea; often of two different size groups; occasionally spherasters also present.

Gemmoscleres very minute, cylindrical, and relatively stout, possessing a feebly curved smooth shaft, and terminally a unilateral arrangement of spines in the shape of a hairbrush.

Gemmules minute, spherical and scattered through the skeletal meshes; pneumatic layer distinctly granular, well developed; gemmoscleres embedded in this layer more or less radially, but often at a slanting angle; foramen produced into a short porus tube.

Sponges forming small cushions on solid support, coloration bright yellow to golden. Consistency soft and fragile.

Apparently restricted to SE. Asia and Australia (Racek, MS.).

Discussion.—This genus comprises three species, *P. aurea*, *P. stellifera*, and *P. subspinosa*, the latter of which was elevated to specific rank by Annandale (1915a). Another species, to be described in a forthcoming paper (Racek, MS.), has since been found in Australia. *Spongilla sansibarica* Weltner (1895) from Africa was considered by Annandale (1914) as belonging to this genus, a view retained in subsequent works (Gee, 1931e, 1932c; Arndt, 1936; Penney, 1960). However, *S. sansibarica* does not display any affinities to *Pectispongilla* species and is dealt with in the present paper under the generic name of *Radiospongilla*.

Pectispongilla aurea Annandale, 1909

Plate 6, figures 11, 15, 17, 18

Pectispongilla aurea Annandale, 1909f, p. 103; 1911c, p. 106; 1912d, p. 384; 1915a, p. 171; 1918a, p. 212.—Gee, 1931e, p. 32; 1932c, p. 35.—Penney, 1960, p. 9.

Material.—Slides of syntype (N. Gist Gee no. 54316).

Description.—Sponge, according to Annandale (1909f), forming small cushions on solid support; oscula few and comparatively large, dermal membrane closely adhering to symplasm; surface minutely hispid. Skeleton consisting of feebly coherent spicule fibers. Consistency of live sponge soft.

Megascleres fusiform and sharply pointed amphioxea, feebly curved or nearly straight, entirely smooth; length range 270–320 μ, width range 13–16 μ.

Microscleres of two different groups: (1) small, slender, straight, fusiform and microspined amphioxea; and (2) minute, rhomboidal, relatively thick, and smooth amphioxea; length range of (1) 45–52 μ, of (2) 22–24 μ; width range of (1) 1.5–2.5 μ, of (2) 3–3.5 μ.

Gemmoscleres typical for this genus, minute, with smooth cylindrical slightly curved shafts, and a bipolar but unilateral arrangement of rows of spines which arise from a broad base and appear joined to each other by silicious webs under high magnification; length range 31–37 μ, width range of shaft 2.5–4 μ; length of comb-rows 17 μ.

Gemmules very minute, ranging in diameter 190–220 μ, spherical, scattered in the skeletal meshes; pneumatic coat well developed and distinctly granular; gemmoscleres embedded in this coat radially, but crossing each other at slanting angles, with their comb-rows pointing in all directions; foramen tubular, porus tube rather short.

Distribution.—Hitherto known only from India.

Color in life.—Recorded as deep golden (Annandale).

Discussion.—*P. aurea* is closely allied to *P. stellifera* and *P. subspinosa*, all erected by Annandale, and to another species recently found in Australia (Racek, MS.). The few distinguishing criteria chiefly refer to the surface of the megascleres and to the slightly varying structure of the microscleres which seem to occur in two series in all species known. Until it will be possible to identify the Australian species, and additional material from India will become available, it is better to consider all species as distinct in order not to obscure possible taxonomic evidence. The descriptions of *P. stellifera* and *P. subspinosa*, however, will here be shortened to demonstrate only their most characteristic differences from *P. aurea*.

Pectispongilla stellifera Annandale, 1915

Plate 6, figure 20

Pectispongilla stellifera Annandale, 1915a, p. 175; 1918a, p. 212.—Gee, 1931e, p. 50; 1932c, p. 35.—Penney, 1960, p. 9.

Material.—Slide of type (IM no. ZEV 3790/7).

Description.—Sponge, according to Annandale (1915a), similar in shape and structure to *P. aurea*.

Megascleres slender amphioxea, covered with minute rounded spines or tubercles except at their tips. Length and width ranges comparable with those of *P. aurea.*

Microscleres of two distinct kinds: (1) slender, fusiform, spiny, and straight amphioxea; and (2) subspherical tuberculate spherasters; length range of (1) 52–56 μ, width range 2.5–4 μ; diameter of (2) 8–13 μ.

Gemmoscleres resembling those of *P. aurea* but a little stouter.

Gemmules indistinguishable from those of the previous species.

Distribution.—Hitherto known only from India.

Color in life.—Not yet observed.

Discussion.—It is possible that future research and a larger range of specimens may demonstrate that even *P. aurea* possesses a certain percentage of microspined megascleres, which at present cannot be found in the type slide of that species. The microscleres of series (1) in *P. stellifera* are slightly longer, but otherwise fully comparable with the same series of the previous species; the spherasters, however, have not yet been found in any other species of the genus, although they possibly represent ecomorphic malformations.

Pectispongilla subspinosa Annandale, 1911

Plate 6, figures 16, 19

Pectispongilla aurea var. *subspinosa* Annandale, 1911c, p. 107; 1912d, p. 384.
Pectispongilla subspinosa Annandale, 1915a, p. 177; 1918a, p. 212.—Gee, 1931e, p. 50; 1932c, p. 35.—Penney, 1960, p. 9.

Material.—Two slides from syntype (N. Gist Gee).

Description.—Sponge, according to Annandale (1911c, 1915a), similar in shape and structure to *P. aurea.*

Megascleres similar in shape and structure to those of *P. stellifera,* but their spines are somewhat more conspicuous.

Microscleres apparently of only one series, comparable to those of series (1) in *P. aurea* in all characteristics.

Gemmoscleres and gemmules are indistinguishable from those of *P. stellifera.*

Distribution.—Hitherto known only from India.

Color in life.—Not yet reliably recorded.

Discussion.—*P. subspinosa* does not display any criteria of importance that can be used for its separation from *P. stellifera,* apart from the absence of the spherasters found in the latter species. The series (2) of microscleres, recorded by Annandale (1915a, p. 177) as being truncate at their ends and bearing rudimentary rotules, must be dismissed as belonging to the genus, since they represent typical gemmoscleres of *Radiospongilla indica* present on the same slide.

Genus *Ephydatia* Lamouroux, 1816, redefined

Spongia Linnaeus, 1758, p. 1348 (part).

Ephydatia Lamouroux, 1816, p. 2 (part).—Gray, 1867, p. 550 (part).—Vejdovsky, 1883b, p. 23; *in* Potts, 1887, p. 177.—Wierzejski, 1886, p. 205.—Weltner, 1895, p. 114.—Hanitsch, 1895a, p. 127.—Girod, 1899, p. 110.—Rousseau, 1906, p. 126.—Annandale, 1909b, p. 107; 1909e, p. 567; 1911c, p. 108; 1912d, p. 384; 1918a, p. 212.—Annandale and Kawamura, 1916, p. 12.—Gee and Wu, 1925c, p. 9; 1928, p. 3.—Gee, 1927c, p. 179; 1930b, p. 170; 1931c, p. 37; 1932c, p. 28.—Arndt, 1926, p. 342; 1928a, p. 66.—De Laubenfels, 1932, p. 111; 1936, p. 37.—Jewell, 1952, p. 445.

Halichondria Fleming, 1828, p. 524 (part).

Spongilla Lamarck, 1816, p. 98 (part).—Johnston, 1842, p. 5.—Lieberkühn, 1856, p. 510 (part).—Bowerbank, 1863, p. 445 (part).—Carter, 1868, p. 247 (part).—Vejdovsky, 1877, p. 213 (part).—Dawson, 1878, p. 1 (part).—Potts, 1880a, p. 357 (part).

Trachyspongilla Dybowsky, 1878, p. 53.—De Laubenfels, 1936, p. 37.

Pleiomeyenia Mills, 1884, p. 147.

Meyenia Carter, 1881a, p. 90 (part).—Potts, 1887, p. 210 (part).—Haswell, 1882, p. 210.—Lendenfeld, 1887, p. 91.—MacKay, 1889, p. 92 (part).—Kirsch, 1909, p. 37.—De Laubenfels, 1936, p. 36.—Eshleman, 1950, p. 38.—Wurtz, 1952, p. 4.—Jewell, 1952, p. 445.—Penney, 1960, p. 46 (part).

Type species.—By present selection *Spongia fluviatilis* Linnaeus, 1758.

Definition.—Megascleres slender and fusiform to rather robust and cylindrical amphioxea, entirely smooth or covered with a variable number of spines, except at their tips.

Microscleres absent.

Gemmoscleres typically birotulates of one length group in all species with smooth megascleres; in those possessing spiny megascleres often of varying lengths, but not representing two distinct length groups; rotules of identical or only slightly differing outline, always flat in lateral view; shafts either slender, smooth or incipiently spined, or rather robust and covered with erect acute spines.

Gemmules moderately large to large, subspherical to spherical, scattered throughout skeletal meshwork, usually very abundant; pneumatic layer well developed but of irregular thickness, consisting of minute spherical to subspherical air spaces; gemmoscleres embedded in this coat strictly radially, in one or more layers, their distal rotules often clearly visible through outer gemmular membrane; foramen a simple elevation, without a porus tube, usually surrounded by a narrow peripheral collar.

Sponges forming flat to massive encrustations, surface as a rule distinctly corrugated; associations with zoochlorellae recorded for some species. Consistency ranging from soft to moderately firm.

Distribution of one species cosmopolitan, with preference to cold- and warm-temperate climates; several species widely scattered throughout the Northern Hemisphere, and absent from the tropics

and Southern Hemisphere; some others ranging from southern temperate climates to and beyond the tropics.

Discussion.—The status of the generic name *Ephydatia* Lamouroux, particularly since its restoration by Gray (1867), has been an ever recurring problem to the many spongillid systematists of the past. Carter's (1881a) fully unjustified rejection of Gray's system, and in particular the former author's replacement of *Ephydatia* by *Meyenia*, has had its most regrettable consequences right to the present day. Although the great majority of subsequent authors followed Carter's system in all other respects, the genus *Ephydatia* remained in common use by all European, South American, and Asian workers, whereas *Meyenia* was used by almost all systematists of North America.

De Laubenfels (1936), in his attempt to solve this problem in a legalistic way, pointed to the fact that the spongillid genus *Tupha* Oken had priority of one year over *Ephydatia* Lamouroux, so that the latter must fall into synonymy with Oken's genus. De Laubenfels therefore restored Carter's genus *Meyenia*, with *M. fluviatilis* Carter as the type species, an arrangement which was followed by Jewell (1952). However, according to Opinion 417, the International Commission on Zoological Nomenclature (1956, Opin. Decl. Int. Comm. Zool. Nomencl., vol. 14, pp. 1–42) rejected for nomenclatorial purposes Oken's 1815–1816 Lehrbuch der Naturgeschichte, vol. 3, and placed it on the Official Index. This opinion states that "no name published in the foregoing volume (vol. 3) of the above work (Oken, 1815–1816) acquired the status of availability by reason of having been so published." Since the genus *Tupha* Oken can therefore be conveniently ignored as being without a status in nomenclature, *Ephydatia* Lamouroux must now be considered the next available generic name, and *Meyenia* Carter relegated to its synonymy, an arrangement in common use by the great majority of spongillid taxonomists.

Apparently a type species of *Ephydatia* has never been designated, although Annandale (1911c) mentioned *Spongilla fluviatilis* Auct. as the type of this genus. De Laubenfels (1936) and Jewell (1952), who rightfully claim that no such species had been described in 1816 when Lamouroux established his genus, suggest that Annandale probably meant *Spongia fluviatilis* Linnaeus, which they both consider unrecognizable. However, if their criticism were strictly applied even *Meyenia fluviatilis* Carter would also have to be considered as unrecognizable, since Carter made no distinction between the two species *E. fluviatilis* Auct. and *E. mülleri* (Lieberkühn) in his material.

The recognition of most species nominated by early workers certainly remains highly problematic, particularly in the case of such

lower invertebrates as sponges. The fact that *Spongia lacustris* Linnaeus, in those days still considered a plant-like organism, appears vaguely recognizable today is not derived from its precise description, but from it being mentioned as producing branches. The second Linnean species, *Spongia fluviatilis*, appears to have been amorphous, and therefore no direct information on its specific identity is now available, even though the possibility that it could be identical with *S. lacustris* can be ruled out.

Since most spongillid taxonomists, particularly in Europe and Asia, have used Linnaeus' specific name *S. fluviatilis* for a well-defined, clearly recognizable, and very common species, the retention of its designation as *Ephydatia fluviatilis* Auct. must now be considered as improper taxonomic procedure. *Spongia fluviatilis* Linnaeus, for which a neotype is now recorded in the description of *Ephydatia fluviatilis* below, is therefore herewith selected as the type species of *Ephydatia* Lamouroux.

Ephydatia fluviatilis (Linneaus, 1758)

PLATE 7, FIGURES 4, 5

Spongia fluviatilis Linnaeus, 1758, p. 1348.

Ephydatia fluviatilis Lamouroux, 1816, p. 6.—Gray, 1867, p. 550.—Parfitt, 1868, p. 443.—Dybowsky, 1878, p. 53.—Vejdovsky, 1883, p. 24.—Wierzejski, 1887, p. 122.—Traxler, 1889, p. 14.—Weber, 1890, p. 32.—Topsent, 1893, p. 326; 1914, p. 538.—Garbini, 1894, p. 1.—Weltner, 1895, p. 114; 1909, p. 185; 1911, p. 60.—Hanitsch, 1895a, p. 127.—Girod, 1899, p. 110.—Rousseau, 1906, p. 124.—Lühe, 1908, p. 309.—Annandale, 1909e, p. 567; 1911c, p. 242; 1918a, p. 216; 1919c, p. 87.—Müller, 1911, p. 495.—Stephens, 1912, p. 8; 1920, p. 227.—Smith, 1921, p. 17.—Arndt, 1923, p. 77; 1926, p. 343; 1928b, p. 164; 1928a, p. 66; 1932c, p. 556; 1933a, p. 23; 1936, p. 16; 1938a, p. 14.—Poisson, 1923, p. 61.—Rezvoj, 1926a, p. 107; 1926b, p. 64.—Schröder, 1926, p. 249; 1932b, p. 111; 1938b, p. 126.—Gee, 1926c, p. 110; 1927a, p. 1; 1928, p. 225; 1929d, p. 297; 1929b, p. 13; 1930e, p. 27; 1930b, p. 170; 1931e, p. 38; 1931a, p. 502; 1931d, p. 42; 1932c, p. 28; 1932d, p. 54; 1933b, p. 73.—Grimailowskaja, 1928, p. 215.—Gee and Wu, 1928, p. 40.—Kozhoff, 1930, p. 165.—Old, 1932b, p. 470; 1932a, p. 131.—Sasaki, 1934, p. 232; 1940, p. 182.—Jewell, 1939, p. 11.—Rioja, 1940a, p. 173.—Simon, 1952, p. 80; 1953, p. 207.

Spongilla fluviatilis Johnston, 1842, p. 5.—Bowerbank, 1863, p. 445 (part); 1874, p. 151 (part).—Retzer, 1883, p. 21.

Spongilla sceptrifera Bowerbank, 1874, p. 206.—Gee, 1931e, p. 48.

Spongilla stagnalis Dawson, 1878, p. 1.—Gee, 1931e, p. 49.

Meyenia fluviatilis Carter, 1881, p. 92 (part).—Potts, 1887, p. 219 (part).—Dybowsky, 1884, p. 507.—Lendenfeld, 1887, p. 92.—Kellicott, 1897, p. 50 (part).—Kirsch, 1909, p. 37.—De Laubenfels, 1936, p. 35 (part).—Wurtz, 1950, p. 5.—Pennak, 1953, p. 93.—Penney, 1960, p. 48.

Meyenia fluviatilis var. *gracilis* Carter, 1885, p. 180.—Potts, 1887, p. 224.

Meyenia fluviatilis var. *angustibirotulata* Carter, 1885, p. 454.—Potts, 1887, p. 219.

Meyenia mexicana Potts, 1885, p. 810.

Meyenia fluviatilis var. *mexicana* Potts, 1887, p. 219.
Ephydatia goriaevii Swartschewsky, 1901, p. 344.—Gee, 1931e, p. 39.
Ephydatia fluviatilis var. *capensis* Kirkpatrick, 1907, p. 524.—Weltner, 1913, p. 475.—Annandale, 1914, p. 246.—Gee, 1931e, p. 35.
Ephydatia fluviatilis var. *syriaca* Topsent, 1910, p. 47.—Annandale, 1913a, p. 59; 1915c, p. 473; 1918a, p. 212.
Ephydatia fluviatilis var. *himalayensis* Annandale, 1910d, p. 198; 1918a, p. 212.—Gee, 1932c, p. 30.
Ephydatia fluviatilis var. *intha* Annandale, 1918b, p. 76; 1918a, p. 212.
Ephydatia fluviatilis var. *chui* Gee, 1926c, p. 110; 1926a, p. 184; 1927a, p. 7; 1927b, p. 63; 1928, p. 225; 1930d, p. 369; 1930b, p. 170; 1931e, p. 35; 1932c, p. 30.—Rezvoj, 1930, p. 175.
Ephydatia fluviatilis var. *teberdana* Rezvoj, 1928, p. 228.
Ephydatia fluviatilis var. *hastifera* Rezvoj, 1930, p. 185.
Ephydatia fluviatilis var. *mexicana* Gee, 1931e, p. 43; 1932c, p. 30.—Rioja, 1940a, p. 178.—Martinez, 1940, p. 191.

Material.—Extremely numerous specimens and slide material; EUROPE: Sweden, Finland, Netherlands, Belgium, France, Switzerland, Germany, Austria, Hungary, Czechoslovakia, Poland, Yugoslavia, Italy, U.S.S.R.; NORTH AMERICA: U.S.A., Mexico; ASIA: U.S.S.R., China, India, Japan; AUSTRALIA: New South Wales, Queensland; AFRICA: slides of syntype of *E. f. capensis.*

Description.—Mature sponge often forming bulbous and corrugated growths on timber and aquatic plants, rarely flat crusts; surface typically uneven and lobose, oscula numerous and relatively large, dermal membrane well developed. Skeleton consisting of polyspicular longitudinal fibers, coated together in well defined sheaths of spongin; and of a variable number of secondary transverse fibers. Consistency of live sponge firm but nevertheless fragile, skeleton of dry sponge extremely brittle.

Megascleres slightly curved, rarely straight amphioxea, ranging from fusiform to almost cylindrical, typically entirely smooth; length range 210–400 μ, width range 6–19 μ.

Microscleres absent.

Gemmoscleres typically birotulates of one class, with a slender and smooth shaft, and terminally with rotules of equal diameter and distinctly flat shape, irregularly and not too deeply incised; malformations frequent in adverse environments, resulting in the projection of the axis through the rotules, or a number of irregular spines on the shafts; length of shaft typically 26–30 μ, diameter of rotules ranging 18–21 μ; marginal teeth on rotules usually not less than 20.

Gemmules rather abundant, scattered throughout skeletal meshwork, spherical, ranging in diameter 350–450 μ; pneumatic layer well developed but comparatively shallow, consisting of minute spherical air spaces; gemmoscleres embedded in this coat in one layer and strictly radially, resting with one rotule on inner gemmular

membrane, with the other just reaching to outer membrane; foramen only very slightly elevated, surrounded by a minute collar, never tubular.

Distribution.—Apparently cosmopolitan, widely dispersed in both hemispheres, with preference to cold- to warm-temperate regions, occasionally also occurring in subtropical climates.

Color in life.—Usually drab yellow to brown, occasionally green due to presence of zoochlorellae.

Discussion.—As evident in all species with a truly cosmopolitan distribution, *E. fluviatilis* displays great variability in skeletal and spicular structure and is subject to numerous ecomorphic malformations in adverse habitats. Our reexamination revealed that most of the former "varieties" of this species certainly are nothing more than malformed specimens of the nominal species. However, there are some others, like *E. f. syriaca* and *E. f. himalayensis*, of which the spicules seem to be transitory in shape and structure to those of the *E. ramsayi* group of species, that are here temporarily listed as synonymy of *E. fluviatilis* until a future study of this complex will be possible.

This species has been adequately described in previous literature and the present studies have not revealed any additional criteria of importance. Since a type specimen apparently has never been designated, and most certainly does not exist today, a neotype of *Spongia fluviatilis* Linnaeus therefore had to be selected. This is a specimen in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden, reg. no. 1166, coll. A. W. Lacourt, 12. ix. 1942, Angstel R., Abcoude, Holland. The mode of growth and spicular components of this neotype correspond in all details with the majority of descriptions of *Ephydatia fluviatilis* Auct. available in previous literature.

Ephydatia meyeni (Carter, 1849)

Plate 7, figure 20

Spongilla meyeni Carter, 1849, p. 84; 1881a, p. 93.—Bowerbank, 1863, p. 448.
Ephydatia meyeni Gray, 1867, p. 550.—Annandale, 1907a, p. 272; 1911c, p. 108; 1912d, p. 384; 1918a, p. 204.—Gee, 1926c, p. 110; 1927a, p. 7; 1928, p. 225; 1929d, p. 297; 1930b, p. 170.
Meyenia fluviatilis var. *meyeni* Potts, 1887, p. 221.—Penney, 1960, p. 50.
Ephydatia mülleri Weltner, 1895, p. 125 (part).
Ephydatia mülleri var. *meyeni* Annandale, 1908c, p. 306.
Ephydatia fluviatilis var. *meyeni* Gee, 1932c, p. 30; 1932e, p. 535; 1932f, p. 507.

Material.—Slides of type (IM) and syntype (N. Gist Gee).

Description.—Mature sponge forming massive growths of irregular outline; surface uneven and distinctly corrugated; oscula rather inconspicuous, dermal membrane well developed. Skeleton consisting

of polyspicular radiating fibers, coated together in well defined sheaths of spongin; and of a variable number of secondary transverse fibers. Consistency of live sponge firm and moderately hard, skeleton of dry sponge very brittle. Bubble cells abundant in inner symplasm.

Megascleres very slightly curved, almost cylindrical amphioxea, entirely smooth; length range 275–310 μ, width range 11–15 μ.

Microscleres absent.

Gemmoscleres birotulates of one class, with moderately stout shafts, occasionally armed with 1–3 sharp spines, usually entirely smooth; and terminally with rotules of equal diameter and more or less flat shape, irregularly and deeply incised; malformations frequent in adverse environments; length of shaft 28–33 μ, diameter of rotules ranging 25–29 μ; marginal teeth on rotules 19–22.

Gemmules abundant in mature sponge, scattered throughout skeletal meshwork, spherical, ranging in diameter 480–610 μ; pneumatic layer well developed but irregular, consisting of minute spherical air spaces; gemmoscleres embedded in this coat in one or two layers, the inner always strictly radially arranged, the outer layer often irregularly inserted; while the inner layer is always fully contained within the pneumatic coat, the distal rotules of the outer invariably penetrate the outer gemmular membrane; foramen distinctly elevated but simple, never attaining the shape of a tube.

Distribution.—Known only from a few localities in India and China.

Color in life.—Light to dark brown.

Discussion.—*Ephydatia meyeni*, although very closely related to *E. fluviatilis*, displays a number of constant criteria that certainly are not obvious within the normal morphometric range of the latter. Unless a thorough study of the entire *E. fluviatilis* complex finally can be contemplated that would result in a better understanding of the various ecomorphic fluctuations in shape and measurements of the spicular components, it seems advisable to retain the separate specific status of the species discussed. Only the results of such detailed future studies will be able to demonstrate whether *E. meyeni* differs from *E. fluviatilis* by criteria of specific or subspecific importance.

Ephydatia mülleri (Lieberkühn, 1855)

Plate 7, figures 6, 7

Spongilla mülleri Lieberkühn, 1856, p. 510.—Vejdovsky, 1877, p. 213.
Spongilla fluviatilis var. *parfitti* Carter, 1868, p. 247; 1881, p. 93.
Spongilla parfitti Bowerbank, 1874, p. 295.
Spongilla asperrima Dawson, 1878, p. 1.—Mills, 1882, p. 57.—Potts, 1887, p. 219.
Trachyspongilla mülleri Dybowsky, 1878, p. 53.—Vejdovsky, 1883, p. 26.
Spongilla astrosperma Potts, 1880b, p. 357.

Spongilla polymorpha Potts, 1880b, p. 357.
Meyenia fluviatilis Carter, 1881a, p. 92 (part).—Potts, 1886, p. 228 (part); 1887, p. 219 (part).—MacKay, 1885, p. 233; 1889, p. 92.
Meyenia acuminata Potts, 1882, p. 70.
Ephydatia amphizona Vejdovsky, 1883a, p. 331.
Ephydatia mülleri Vejdovsky, 1883b, p. 26.—Petr, 1886, p. 107.—Traxler, 1889, p. 14.—Hanitsch, 1895a, p. 125.—Weltner, 1895, p. 114; 1909, p. 186.—Levander, 1901, p. 56.—Rousseau, 1906, p. 124.—Lühe, 1908, p. 311.—Stephens, 1912, p. 8; 1920, p. 235.—Topsent, 1914, p. 538.—Smith, 1921, p. 17; 1930, p. 184.—Arndt, 1923, p. 75; 1926, p. 342; 1928a, p. 68; 1931, p. 37; 1932b, p. 304; 1933a, p. 19; 1938b, p. 76.—Poisson, 1923, p. 62; 1925, p. 94.—Rezvoj, 1926b, p. 64; 1928a, p. 231; 1930, p. 183.—Gee, 1929b, p. 13; 1930d, p. 369; 1930b, p. 170; 1930e, p. 27; 1931d, p. 44; 1931b, p. 269; 1931a, p. 502; 1932c, p. 30; 1932d, p. 54; 1937, p. 285.—Shröder, 1938a, p. 295.—Jewell, 1935, p. 461; 1939, p. 16.—Karaman, 1935, p. 46.—Old, 1936b, p. 11.—Zimmer, 1936, p. 126.—Sasaki, 1940, p. 183.—Simon, 1952, p. 80; 1953, p. 207.
Spongilla mirabilis Retzer, 1883, p. 25 (part).—Schröder, 1926, p. 249.
Ephydatia mülleri var. *astrodiscus* Vejdovsky, 1883b, p. 29.—Arndt, 1926, p. 343.
Pleiomeyenia calumeticus Mills, 1884, p. 147.—Smith, 1921, p. 12.—Gee, 1931e, p. 35.
Pleiomeyenia walkeri Mills, 1884, p. 147.
Pleiomeyenia spinifera Mills, 1884, p. 149.
Meyenia astrosperma Potts, 1887, p. 219.
Meyenia polymorpha Potts, 1887, p. 219.
Meyenia fluviatilis var. *acuminata* Potts, 1887, p. 219.
Ephydatia olchonensis Swartschewsky, 1901, p. 9.—Annandale, 1918a, p. 213.—Gee, 1931e, p. 45.
Ephydatia mülleri var. *behningi* Kirkpatrick, 1915, p. 104.—Arndt, 1926, p. 343.—Gee, 1931e, p. 33.
Ephydatia obtusosclera Kozhoff, 1925, p. 38.—Gee, 1931e, p. 45.
Ephydatia sibirica Kozhoff, 1925, p. 29.—Gee, 1931e, p. 49.
Ephydatia solida Kozhoff, 1925, p. 36.—Gee, 1931e, p. 49.
Ephydatia mülleri var. *acuminata* Arndt, 1926, p. 343.—Rezvoj, 1928a, p. 231; 1929, p. 291.—Smith, 1930, p. 184.
Ephydatia mülleri var. *obtusosclera* Kozhoff, 1930, p. 164.
Ephydatia mülleri var. *sibirica* Kozhoff, 1930, p. 162.
Ephydatia mülleri var. *solida* Gee, 1932c, p. 30.
Meyenia mülleri Old, 1932a, p. 132.—Wurtz, 1950, p. 4.—Pennak, 1953, p. 93.—Penney, 1960, p. 51 (part).

Material.—Extremely numerous specimens and slide material; EUROPE: Sweden, Finland, Netherlands, Belgium, Switzerland, Germany, Austria, Hungary, Czechoslovakia, Poland, U.S.S.R.; NORTH AMERICA: U.S.A., Canada; ASIA: U.S.S.R., China, Japan.

Description.—Mature sponge variable in shape, ranging from very thin films to moderately thick crusts; surface even in flat specimens, forming rounded elevations in more massive growths, always slightly hispid; oscula inconspicuous, dermal membrane well developed. Skeleton forming an irregular network of distinct vertical

and rather ill-defined horizontal spicule fibers, joined together by a considerable amount of spongin. Consistency of live sponge firm and moderately hard, skeleton of dry sponge compact. Bubble cells abundant in inner symplasm.

Megascleres straight to slightly curved and stout amphioxea, distinctly fusiform, typically armed with small but acute spines except at their tips, very rarely incipiently spined or altogether smooth; length range 200–350 μ, width range 9–20 μ.

Microscleres absent.

Gemmoscleres birotulates of one class, with a moderately thick and short shaft, as a rule smooth, and terminally with rotules of equal diameter and distinctly flat shape, irregularly and deeply incised into a smaller number of long rays, usually not more than 12; malformations frequent in adverse habitats; length of shaft typically 12–20 μ, diameter of rotules ranging 20–25 μ, width of shaft 4–6 μ.

Gemmules moderately abundant in mature sponge, either scattered in the skeletal meshwork, or aggregated in the basal region without forming a pavement layer; they are spherical to subspherical in shape, ranging in diameter 350–450 μ; pneumatic layer well developed but shallow, consisting of minute subspherical air spaces; gemmoscleres embedded in this coat typically in one layer, occasionally forming an additional distal layer on top of the first; outer gemmular membrane usually feebly developed or altogether lacking, distal rotules of gemmoscleres clearly perceptible; foramen only very slightly elevated, never tubular.

Distribution.—Apparently restricted to the Northern Hemisphere, with preference to cold- to warm-temperate regions, widely distributed.

Color in life.—Usually drab yellow to brown, occasionally green due to presence of zoochlorellae.

Discussion.—This species has been adequately described in previous literature and the present studies have not revealed any additional criteria for discussion. As can be expected in sponges with a widely scattered distribution, *E. mülleri* displays some slight variations in distant populations which, however, are not significant enough to permit a clear discrimination of races. The multiple arrangement of gemmoscleres, as sometimes present, as well as the occasional malformation of megascleres certainly cannot be used for such a purpose. However, the condition displayed by *E. japonica*, in spite of the various arguments involved in this problem, is here considered to represent at least a racial variant of importance. In order not to obscure perceptible taxonomic evidence, *E. japonica* in this paper is dealt with as a separate species until evidence to the contrary can be obtained by future detailed studies.

***Ephydatia japonica* (Hilgendorf, 1882)**

Spongilla fluviatilis var. *japonica* Hilgendorf, 1882, p. 26.
Ephydatia fluviatilis var. *japonica* Weltner, 1895, p. 123.
Ephydatia japonica Annandale, 1909b, p. 112; 1910b, p. 649.—Smith, 1921, p. 17.
Ephydatia mülleri var. *japonica* Annandale and Kawamura, 1916, p. 13.—Annandale, 1918a, p. 200.—Gee, 1928, p. 222.—Sasaki, 1934, p. 238.
Ephydatia mülleri Gee, 1930b, p. 175 (part); 1931b, p. 269 (part).
Meyenia mülleri Penney, 1960, p. 51 (part).

Material.—Slides of syntype (N. Gist Gee) and of a specimen from Japan.

Description.—Mature sponge forming flat cushions on aquatic plants, occasionally more massive growths; surface often uneven and rough; oscula relatively large and deep in massive forms, inconspicuous in flat crusts; dermal membrane well developed. Skeleton consisting of an irregular network of multispicular vertical and slender horizontal fibers, joined together by a small amount of spongin. Consistency of live sponge rather soft and fragile.

Megascleres distinctly fusiform and slender amphioxea, straight to feebly curved, as a rule entirely smooth; length range 220–360 μ, width range 12–16 μ.

Microscleres absent.

Gemmoscleres birotulates of one class, with a moderately stout and short shaft, as a rule smooth, and terminally with rotules of equal diameter and distinctly flat shape, irregularly and deeply incised into a small number of long rays, usually less than 12; length of shaft 12–15 μ, diameter of rotules 16–22 μ, width of shaft 4–6 μ.

Gemmules abundant in mature sponge, particularly in basal regions, spherical, ranging in diameter 350–520 μ; pneumatic coat well developed but shallow, consisting of minute spherical air spaces; gemmoscleres embedded in this coat in one, only rarely in two layers; outer gemmular membrane feebly developed, distal rotules of gemmoscleres often slightly protruding; foramen slightly elevated, surrounded by a narrow collar, never tubular.

Distribution.—Hitherto considered discontinuous; recorded from the United States, Manchuria, and Japan.

Color in life.—Ranging from light yellow to gray, occasionally green.

Discussion.—This species was originally described by Hilgendorf (1882) as a "variety" of *E. fluviatilis* an error resulting from the failure of Carter (1881a) and a number of subsequent authors to distinguish *E. fluviatilis* and *E. mülleri* specifically. Annandale (1909b) at first raised it to full specific rank, but later (1916, 1918a) relegated it to a varietal form of *E. mülleri*, thus aiding its inclusion within the morphometric range of this latter species by Gee (1930b, 1931b) and Penney (1960).

The reexamination of the syntype available for the present study revealed clearly that a number of criteria displayed by *E. japonica* are at distinct variance with those of *E. mülleri*. Until additional material will be available and the true range of Hilgendorf's sponge established, it therefore seems advisable to restore its separate specific status in order not to obscure possible taxonomic evidence.

Ephydatia ramsayi (Haswell, 1882)

PLATE 7, FIGURES 13–15, 21

Meyenia ramsayi Haswell, 1882, p. 210.—Potts, 1887, p. 228.—Penney, 1960, p. 53.
Spongilla fluviatilis var. *ramsayi* Lendenfeld, 1887, p. 92.
?Ephydatia ramsayi Annandale, 1909c, p. 421.
Ephydatia ramsayi Weltner, 1895, p. 114; 1910, p. 137.—Annandale, 1918a, p. 213.—Gee, 1931e, p. 47; 1931d, p. 59; 1932c, p. 32.—Schröder, 1935, p. 102.
Ephydatia fluviatilis var. *ramsayi* Vorstman, 1927, p. 181.—Gee, 1929d, p. 297; 1931d, p. 26.

MATERIAL.—Type material and slides (AusM); several specimens from New South Wales and Queensland.

DESCRIPTION.—Mature sponge massive and tubercular; surface of large specimens always distinctly corrugated and hispid, that of thinner modes of growth ranging from smooth to irregularly lobose; oscula few in number and conspicuous, dermal membrane well developed. Skeleton composed of distinct polyspicular vertical, and rather ill-defined horizontal fibers, both joined together by a considerable amount of spongin. Consistency of live sponge moderately hard and firm, skeleton of dry sponge often very hard.

Megascleres slightly curved and moderately stout amphioxea, usually rather cylindrical, rarely distinctly fusiform, their great majority armed with inconspicuous spines, except at their tips, only exceptionally entirely smooth; length range 230–350 μ, width range 11–17 μ.

Microscleres absent.

Gemmoscleres typically birotulates of one class, with stout cylindrical shafts, invariably bearing 1–10 acute and prominent spines, and terminally with rotules of equal diameter and distinctly flat shape, irregularly incised in a number of lobes and rays; malformations quite frequent, resulting in freak scleres, the deposition of granules of silica on the outer face of the rotules, and a heterogeneous growth of the birotulates which then differ from each other in length to a varying degree; length of shaft typically 32–42 μ, diameter of rotules ranging 20–23 μ, width of shaft about 6–7 μ; abnormal spicules, while fully comparable in diameter of rotules and width of shaft, often ranging 28–45 μ in length on the same gemmule.

Gemmules more abundant in basal regions of the sponge than in other parts, spherical in shape, ranging in diameter 350–460 μ; pneumatic layer well developed and comparatively thick, consisting of

minute spherical air spaces; gemmoscleres embedded in this coat in a single layer, their distal rotules never penetrating outer gemmular membrane, which is well defined and distinctly uneven; foramen slightly elevated, surrounded by a minute collar, never tubular.

Distribution.—Hitherto known only from eastern Australia and New Zealand; record from New Guinea (Annandale, 1909) needs confirmation.

Color in life.—Flesh colored to light brown.

Discussion.—In view of Haswell's (1882) brief and slightly incorrect original description of *E. ramsayi*, this species remained in obscurity till the time of Gee's (1931d) revision. After reexamining the type in the AusM, Gee pointed out that the megascleres in this species are not "perfectly smooth," as stated by Haswell, but invariably covered with a number of inconspicuous spines except at their tips. The reexamination of the type during the present studies confirmed Gee's statement, and the great majority of megascleres range from incipiently spiny to covered with small but conspicuous spines, although there and then a smooth sclere could be found. Had this information been available in earlier literature, a number of closely related species, particularly *E. facunda* and the *E. fortis* complex, would not likely have been given separate specific status. In fact, *E. ramsayi*, in its typical mode of growth, is quite difficult to distinguish from these congeners; all might yet be relegated to subspecies of the nominal species from Australia, when more detailed studies will result in the erection of a trinomial nomenclature for most spongillids. Even though the interrelationship of all these "species" cannot be fully demonstrated, and their merging into one species could well obscure existing taxonomic evidence, this group of closely related spongillids have a great number of features in common. They usually form massive to bulbous growths of irregularly ripply surface and are moderately to distinctly firm in skeletal construction; megascleres are incipiently to conspicuously spiny and moderately stout to stout; gemmules possess a well-developed and thick pneumatic layer and usually possess a well-defined outer membrane; gemmoscleres are robust birotulates with typically spiny cylindrical shafts of distinctly unequal length, without forming perceptible length classes and terminally with flat rotules, irregularly incised in lobes and teeth, often granulated; with some minor exceptions, distribution seems to be restricted to warmer climates; and all are subject to extreme malformations of spicules, often resulting in the superficial resemblance of gemmoscleres to the condition displayed in the genus *Heteromeyenia*.

However, the morphometric differences between all species of this group are sufficient enough to retain their separate status. While *E. ramsayi* and *E. facunda*, from which latter *E. ramsayi talaensis*

has been found morphometrically indistinguishable, form one extreme of the group; the species of the *E. fortis* group, with their pronounced tendencies to ecomorphic malformations, represent the other. Since little is known about the North American species *E. robusta* and *E. subdivisa*, which take up a central position on this grade, it seems advisable not to merge all these species with *E. ramsayi* until additional data will be available.

In Australia, *E. ramsayi* is a widely distributed species, and its occurrence in New Zealand has been recorded by Schröder (1935). Annandale's (1909c) record from New Guinea is still dubious, since it possibly refers to a species of *Radiospongilla*, perhaps *R. indica* or *R. crateriformis*. Material of this sponge was not available for study.

Ephydatia robusta (Potts, 1887)

PLATE 7, FIGURES 11, 12

Meyenia robusta Potts, 1887, p. 225.—Kirsch, 1909, p. 37.—Pennak, 1953, p. 93.—Penney, 1960, p. 53.

Ephydatia robusta Weltner, 1895, p. 114.—?Garbini, 1897, p. 477.—?Annandale, 1907c, p. 24.—Smith, 1921, p. 17.—Arndt, 1926, p. 343.—De Laubenfels, 1932, p. 111.—Old, 1936b, p. 11.

Meyenia subdivisa Potts, 1887, p. 226 (no name but description in Mills, 1884, p. 147).—Kirsch, 1909, p. 37.—Eshleman, 1950, p. 40.—Moore, 1951, p. 63.—Pennak, 1953, p. 91.—Penney, 1960, p. 54.

Ephydatia subdivisa Weltner, 1895, p. 114.—Smith, 1921, p. 17.—Gee, 1931e, p. 50; 1932c, p. 32.

MATERIAL.—Several slides of Pott's collection (USNM), also a number of slides from specimens fitting both the descriptions of *M. robusta* and *M. subdivisa* (N. Gist Gee and JTP).

DESCRIPTION.—Sponge, according to previous descriptions, forming encrustations to massive growths; additional data on surface, oscula, and consistency not reliably recorded.

Megascleres slightly curved and moderately stout amphioxea, ranging from cylindrical to subfusiform, armed with inconspicuous spines except at their tips, exceptionally entirely smooth; length range 230–330 μ, width range 12–17 μ.

Microscleres absent.

Gemmoscleres birotulates of one class, with stout cylindrical shafts, typically with a number of acute and prominent spines, rarely smooth; and terminally with rotules of equal diameter and distinctly flat shape, irregularly incised in a number of lobes and rays; malformations frequent, outer surface of rotules often granulated, spines on shaft forked or subdivided, rotules abnormally developed; length of shaft typically 45–50 μ, diameter of rotules 20–22 μ, width of shaft 6–7 μ.

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Gemmules recorded as being scarce in mature sponge; they are spherical, ranging in diameter 360–450 μ, and possess a well-developed granular pneumatic layer, consisting of minute irregular air spaces; gemmoscleres embedded in this coat in a single layer, their distal rotules not penetrating the well-defined outer gemmular membrane; foramen slightly elevated, surrounded by a minute collar, never tubular.

Distribution.—Hitherto reliably known only from the eastern U.S.A., Mexico, and from California.

Color in life.—Not yet reliably recorded.

Discussion.—In spite of being well-described species, both *E. robusta* and *E. subdivisa* must still be considered insufficiently known. Morphometrically both these "species" are fully comparable, and the peculiar structure of the spines on the gemmoscleres of the latter certainly represent mere ecomorphic malformations, as displayed in a great number of other spongillids from adverse habitats. Although their specific separation is thus fully unwarranted, future research may demonstrate speciation trends of these two "forms" from the eastern and western U.S.A., respectively, and relegate *E. subdivisa* to subspecific rank.

Ephydatia facunda Weltner, 1895

Plate 7, figures 16–19

Ephydatia facunda Weltner, 1895, p. 140.—Gee, 1930a, p. 98; 1931e, p. 38; 1932c, p. 28.
Meyenia facunda Penney, 1960, p. 48.
Ephydatia ramsayi var. *talaensis* Weltner, 1898a, p. 331.—Gee, 1931e, p. 50; 1932c, p. 32.
Meyenia ramsayi var. *talaensis* Penney, 1960, p. 53.

Material.—Slides of syntypes of *E. facunda* and *E. r. talaensis* (N. Gist Gee).

Description.—Sponge, according to previous descriptions, forming cone-shaped masses on submerged timber; additional data on surface, oscula, and consistency not reliably recorded. Skeleton consisting of an irregular meshwork of transverse and radiating spicule fibers, joined together by a small amount of spongin.

Megascleres rather slender, slightly curved and fusiform amphioxea, armed with inconspicuous spines except at their tips; length range 250–370 μ, width range 9–12 μ.

Microscleres absent.

Gemmoscleres typically birotulates of one class, but of greatly varying length; their shafts are moderately stout and cylindrical, usually armed with acute and prominent spines; their rotules are of equal diameter and distinctly flat shape, irregularly incised in a

number of lobes and rays, their outer surface slightly but distinctly granulated; length of shaft 36–52 μ, usually 45 μ, diameter of rotules 23–27 μ, width of shaft 4–5 μ.

Gemmules moderately abundant in mature sponge, spherical, ranging in diameter 410–480 μ; pneumatic coat well developed and granular, consisting of minute subspherical air spaces; gemmoscleres embedded in this coat in a single layer, their distal rotules not protruding through the well-defined outer gemmular membrane; foramen slightly elevated, but in height not reaching to level of outer gemmular membrane, thus appearing slightly sunken.

Distribution.—Known only from central and southern parts of South America.

Color in life.—Apparently not recorded.

Discussion.—This is another spongillid of the *E. ramsayi* group of species which displays somewhat slender and incipiently spined megascleres and gemmoscleres of moderately stout shafts and greatly different lengths. While the erection of *E. facunda* was undoubtedly aided by the incorrect description of *E. ramsayi* by Haswell (1882), the description of yet another sponge from South America by Weltner (1898a) as a "variety" of *E. ramsayi* demonstrates the taxonomic difficulties experienced by the describing author. The morphometric reexamination of both *E. facunda* and *E. ramsayi talaensis* has shown that these two sponges are identical in all major criteria, while the affinities of the latter to *E. ramsayi* from Australia are remote. Pending a further revision of this group, and particularly the collection of additional material from South America, the specific status of *E. facunda* is here retained, and at the same time *E. ramsayi talaensis* relegated to its synonymy.

Ephydatia fortis Weltner, 1895

Plate 7, figures 8–10

Ephydatia fortis Weltner, 1895, p. 141.—Annandale, 1911c, p. 53.—Gee, 1931e, p. 38; 1931c, p. 71; 1932c, p. 30; 1932f, p. 507; 1932e, p. 526.—Arndt, 1932c, p. 560.
Ephydatia fortis var. *hebridensis* Gee, 1929a, p. 131; 1930a, p. 98; 1932c, p. 30.
Ephydatia fortis var. *vorstmani* Gee, 1930a, p. 94; 1932c, p. 30; 1932f, p. 524.—Arndt, 1932c, p. 562.
Ephydatia fluviatilis var. *etorohuensis* Sasaki, 1940, p. 176.
Meyenia fluviatilis var. *etorohuensis* Penney, 1960, p. 49.
Meyenia fortis Penney, 1960, p. 50 (and varieties).

Material.—Slides of syntypes of the nominal species, *E. f. hebridensis*, and *E. f. vorstmani* (N. Gist Gee, USNM, AmstM).

Description.—Sponge ranging from thin flat crusts to moderately massive growths; surface even but hispid in flat specimens, possessing irregular ridges in thicker forms, oscula few and inconspicuous;

dermal membrane well developed. Skeleton consisting of polyspicular vertical and much slimmer and irregular horizontal fibers, joined together by a small amount of spongin. Consistency of live sponge moderately hard and firm, skeleton of dry sponge very coherent.

Megascleres feebly curved to straight, stout, and distinctly fusiform amphioxea, thickly covered with small spines except at their tips; length range 290–370 μ, width range 15–28 μ.

Microscleres absent.

Gemmoscleres typically birotulates of one class, but of distinctly varying length; their shafts are very stout and cylindrical, invariably armed with at least 2–3, and up to 12–16 rather large spines that are often subdivided or otherwise malformed; their rotules are of more or less equal diameter, of irregular outline in lateral view, irregularly incised in a number of lobes and rays, their outer surface often distinctly granulated; length of shaft 38–65 μ, occasionally even longer, diameter of rotules 23–28 μ, width of shaft 6–8 μ.

Gemmules moderately abundant in mature sponge, spherical, ranging in diameter 410–500 μ; pneumatic coat well developed and distinctly granular, consisting of minute spherical air spaces; gemmoscleres embedded in this coat in a single layer, their distal rotules as a rule not protruding through the well-defined outer gemmular membrane, which has a ripply appearance; foramen distinctly elevated, in height almost reaching to level of outer gemmular membrane, never tubular.

Distribution.—Known from various areas in the Indo-West Pacific region, ranging from Indonesia to the Philippines, Japan, and the New Hebrides.

Color in life.—Yellowish brown (straw color).

Discussion.—Gee (1930a) tabulated the differences between *E. fortis* and its two "varieties" *E. f. hebridensis* and *E. f. vorstmani* and compared all three sponges with other closely related species of the *E. ramsayi* group. Although Gee found that the two varieties closely resemble *E. fortis*, he considered them sufficiently distinct to be separated at a subspecific level. The reexamination of all these spongillids demonstrated beyond doubt that their racial distinction cannot be contemplated, since the various criteria are by no means constant in the same specimen. It is obvious that *E. fortis* displays certain features that can be interpreted as ecomorphic malformations in a particular habitat, such as is also perceptible in any range of *E. ramsayi*. The "variety" *E. f. hebridensis* represents an extreme of such an abnormal development, while most of the scleres of *E. f. vorstmani* seem outright "freaks."

Considering all criteria, the entire *E. fortis* group seems to differ from *E. ramsayi* merely by its possession of much stouter spicular

components, as well as by the much more conspicuous armature of spines on its megascleres. Both *E. ramsayi* and the *E. fortis* group occur in neighboring regions of the Indo-West Pacific, therefore it is possible to consider them the result of speciation trends in distant populations of one species. Additional material from New Caledonia seems to substantiate this assumption. Although it is most likely that future studies, leading to the introduction of a trinomial nomenclature for spongillids, will ultimately relegate all species of the *E. fortis* group to mere subspecies of *E. ramsayi*, the paucity of material and data available makes such a decision at the present impossible. The separate specific status of *E. fortis* is therefore here retained, and the "varieties" *E. f. hebridensis* and *E. f. vorstmani* relegated to its synonymy.

Ephydatia fluviatilis var. *etorohuensis* Sasaki, judging from its description and illustrations, is tentatively considered synonymous, although its gemmoscleres are slightly smaller and less crowded than usually found in this complex.

Ephydatia millsii (Potts, 1887)

PLATE 7, FIGURES 1–3

Meyenia millsii Potts, 1887, p. 225.—Kellicott, 1891, p. 103.—Kirsch, 1909, p. 37.—Eshleman, 1950, p. 40.—Pennak, 1953, p. 91.—Penney, 1960, p. 51.
Ephydatia millsii Weltner, 1895, p. 114.—Smith, 1921, p. 17.—Gee, 1931e, p. 43; 1932c, p. 30.

MATERIAL.—Slides of a specimen from Florida (N. Gist Gee).

DESCRIPTION.—Sponge, according to previous descriptions, forming flat crusts of moderate thickness; surface slightly hispid but generally even, oscula apparently inconspicuous. Skeleton forming an irregular network of spicule fibers, loosely joined together by a small amount of spongin. Consistency of live sponge recorded as soft, texture loose.

Megascleres feebly curved to almost straight amphioxea, almost cylindrical, armed with numerous small spines except at their tips; in distal parts of the scleres these spines often inserted at an angle, pointing to spicular tips length range 180–270 μ, width range 9–12 μ.

Microscleres absent.

Gemmoscleres birotulates of almost constant lengths and distinctly of one class; their shafts are concave, widening towards the rotules, and invariably entirely smooth; their rotules are of equal diameter and distinct flat shape, representing circular disks with incipient crenulations or extremely small incisions at their margins, outer surface often granulated; length of shaft 36–48 μ, diameter of rotules 23–28 μ.

Gemmules moderately abundant, subspherical to spherical, ranging in diameter 300–360 μ; pneumatic layer regularly but somewhat

feebly developed, consisting of moderately large irregular air spaces; gemmoscleres closely crowded together in this coat in a single layer; foramen slightly elevated but simple.

Distribution.—Known only from Florida, U.S.A.

Color in life.—Apparently not yet recorded.

Discussion.—This species is a slightly aberrant member of the genus *Ephydatia* and can be easily separated from all its congeners by the typical shape and serrations of its gemmosclere rotules. In view of the regrettable fact that *E. millsii* must still be considered as rather insufficiently known, detailed intrageneric comparisons cannot be contemplated, and additional material and data are extremely desirable.

Heterorotula, new genus

Ephydatia Gray, 1867, p. 550 (part).—Weltner, 1895, p. 122 (part); 1910, p. 138.—Traxler, 1896b, p. 97.—Gee, 1931d, p. 25 (part); 1931e, p. 37 (part); 1932c, p. 28 (part).—Schröder, 1935, p. 100.

Meyenia Carter, 1881a, p. 93 (part).—Haswell, 1882, p. 208 (part).—Penney, 1960, p. 47 (part).

Tubella Lendenfeld, 1887, p. 91.—Weltner, 1895, pp. 128 (part), 142 (not *Tubella* Carter 1881).

Type species.—By present selection *Spongilla capewelli* Bowerbank, 1863.

Definition.—Megascleres slender to stout amphioxea, occasionally entirely smooth, but as a rule covered with a varying number of minute scattered spines, except at their tips.

Microscleres absent.

Gemmoscleres birotulates of conspicuously unequal length, with rather slender, usually granulated shafts, and terminally with comparatively wide and flat rotules of moderately to greatly varying diameter, the inner invariably larger than the outer.

Gemmules large and spherical, scattered throughout skeletal network in large and bulbous specimens, confined to the base in encrusting forms; pneumatic layer very thick, granular, consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, their inner larger rotules often interlocked with each other to form a close covering of the inner gemmular membrane; outer gemmular membrane corrugated by covering gemmoscleres of varying length; foramen always simple, but slightly elevated.

Young sponges often forming shallow encrustations of varying size; mature sponges of massive or bulbous appearance, with uneven surface or producing rounded lobes separated by deep clefts. Coloration never green, sponges usually dark yellow to light tan. Consistency varying from soft and fragile to rather hard but brittle.

Apparently restricted to the Australasian region, well dispersed throughout Australia, and insufficiently known from New Zealand.

Discussion.—The peculiar structure and often greatly varying length of the gemmoscleres, so typical for this genus, created initial difficulties in the assessment of its generic status by all previous workers. These were furthermore increased by the absence of sufficient data on all Australian sponges prior to a recent comprehensive revision (Racek, MS.). The unequal development of gemmosclere rotules, discernible at a varying degree in all Australian species, caused Lendenfeld (1887) and Weltner (1895) to place some species within the genus *Tubella* Carter, whereas others were recorded under *Ephydatia* and *Meyenia*, respectively.

The erection of a new genus became necessary to demonstrate the conspicuous differences of this typically Australasian group of species from other spongillid genera. Although the writer intended to introduce this new genus in his forthcoming revision of all Australian Spongillidae, the scope of the present work made it imperative to incorporate the genus *Heterorotula* into this attempt of a worldwide revision. However, since a number of recently found Australian species are not represented in Penney's original collections for this study, only the well-established species of this genus can here be considered.

Heterorotula is more closely related to *Ephydatia* than to any other genus, but it occurs in Australia side by side with the latter without displaying any signs of hybridization. *H. capewelli*, *H. multidentata*, and *H. multiformis* are by now well-known representatives of this genus. *H. kakahuensis* from New Zealand is insufficiently described, and gemmules are absent from our material available. Its generic status, therefore, cannot as yet be reliably resolved. Until further material can be studied, it seems advisable to leave the New Zealand species provisionally within this genus.

Heterorotula capewelli (Bowerbank, 1863)

Plate 8, figures 1, 5, 8

Spongilla capewelli Bowerbank, 1863, p. 447.
Ephydatia capewelli Gray, 1867, p. 550.—Weltner, 1895, p. 122; 1910, p. 137.—Gee, 1931d, p. 25; 1931e, p. 35.
Meyenia capewelli Carter, 1881a, p. 93.—Potts, 1887, p. 158.—Penney, 1960, p. 47.

Material.—Slides of type (BM) and syntype (N. Gist Gee and ZMB); material and slides from western New South Wales, Australia (Racek).

Description.—Sponge rather massive and bulbous; surface distinctly lobular, with high and rounded irregular ridges separated from each other by comparatively deep clefts; oscula few in number but

conspicuous; dermal membrane well developed, often separated from the underlying symplasm. Skeleton consisting of rather thick vertical spicule fibers, coated together by a fair amount of spongin, and of a somewhat slimmer arrangement of transverse and radiating spicule fibers. Consistency of live sponge moderately hard, firm but brittle.

Megascleres stout, often cylindrical, but usually typically fusiform amphioxea, entirely smooth or rarely inconspicuously microspined; length range 195–330 μ, width range 13–18 μ.

Microscleres absent.

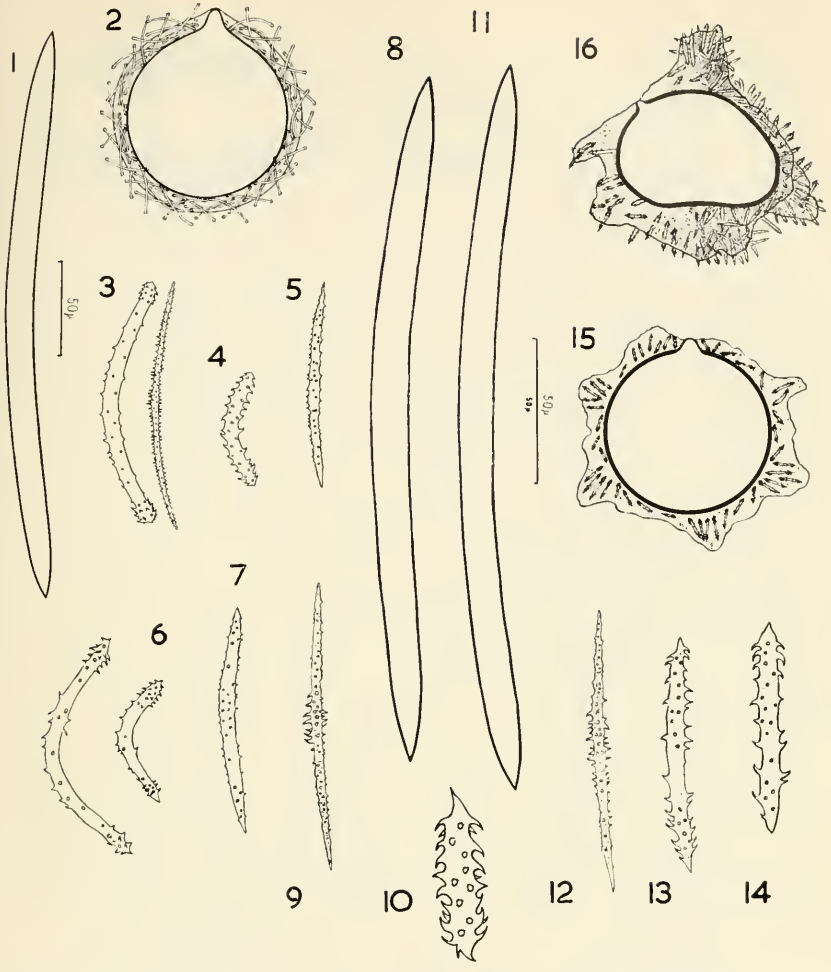
Gemmoscleres birotulates with a very slender finely granulated shaft, and terminally with flat rotules of slightly unequal diameter; faces of rotules distinctly granulated, arrangement of granules almost radial; margin of rotules irregularly crenulated, rarely bearing discernible teeth; length differences of birotulates moderate: length range of larger series 38–52 μ, of smaller 34–45 μ; width range of lower rotule 24–28 μ, of upper 20–23 μ; thickness of shaft 3–4 μ.

Gemmules spherical and large, scattered through skeletal meshwork, more abundant in basal parts, diameter ranging 510–600 μ; pneumatic layer very thick and irregular, in places much higher than the longest gemmoscleres, consisting of minute air spaces; gemmoscleres embedded in this coat strictly radially, with their larger rotules firmly inserted in the inner gemmular membrane; outer parts of pneumatic layer devoid of gemmoscleres, but strongly reinforced by a varying number of normal megascleres; outer gemmular membrane distinctly corrugated, and of pale yellow color; foramen simple or bearing a shallow peripheral collar.

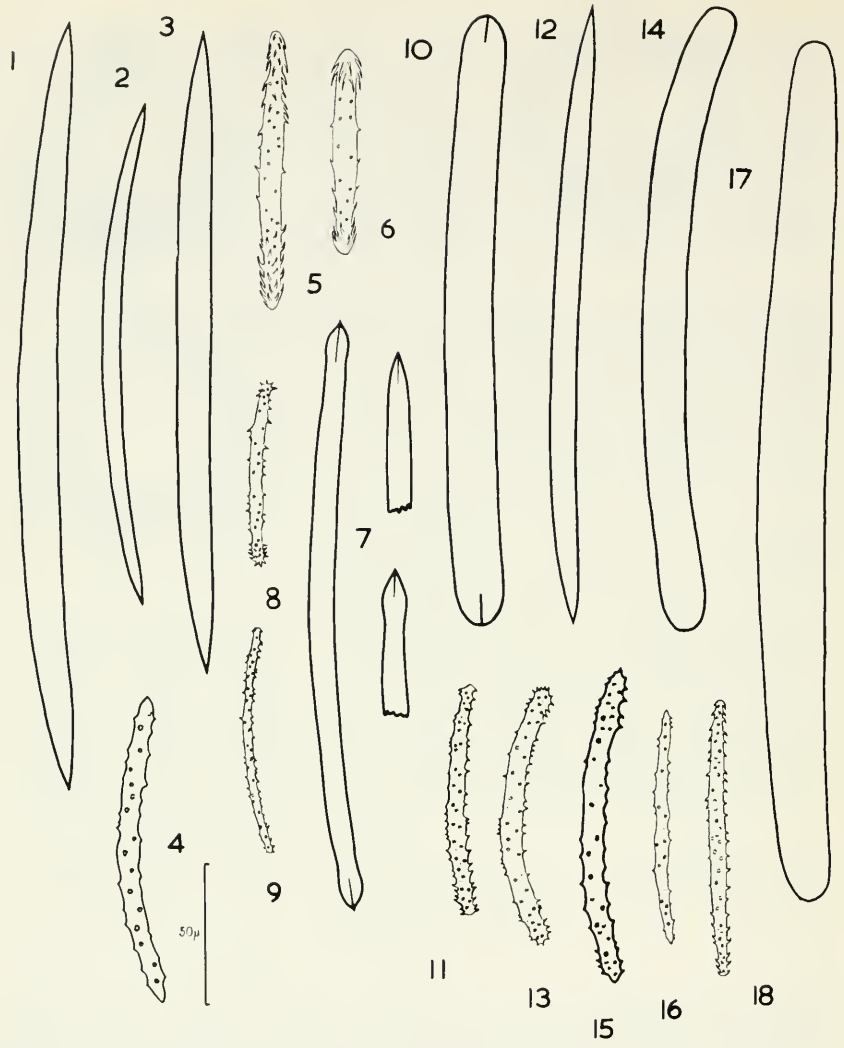
Distribution.—Apparently restricted to an area reaching from Central Australia east to the Dividing Range and north to Queensland, preferring inland waters of slight salinities.

Color in life.—Light tan to brown.

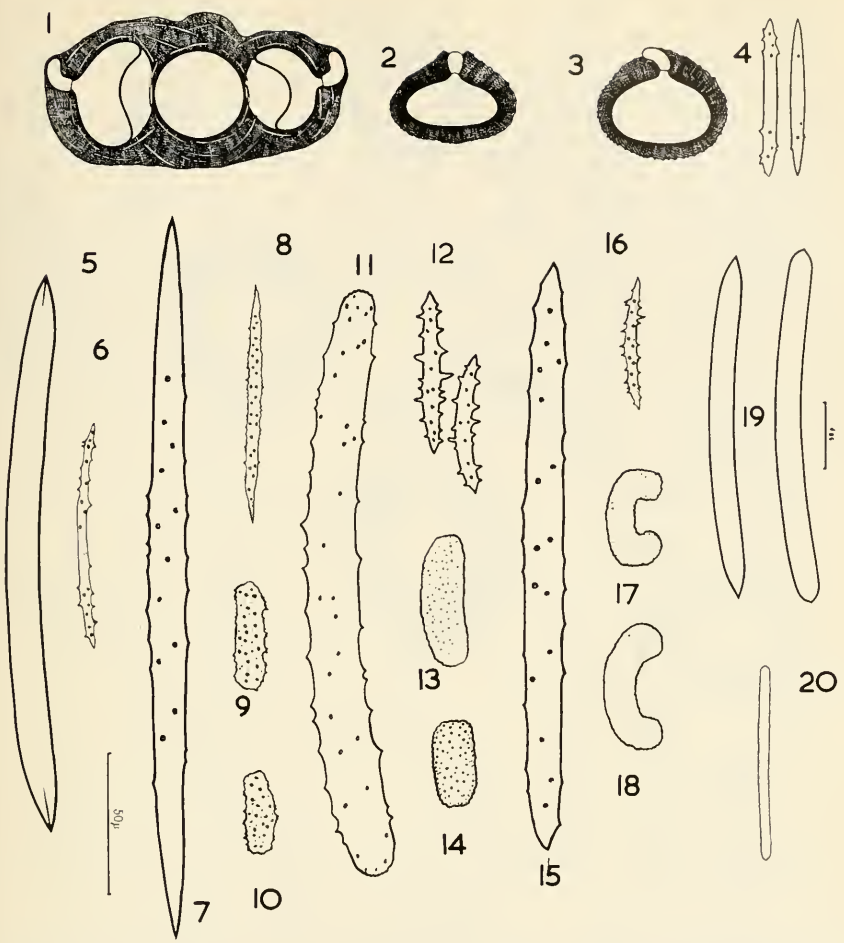
Discussion.—This species represents one extreme in the intergrading series of gemmosclere characters, and the length differences between the longer and shorter sets of its birotulates are not greatly pronounced. Other unusual criteria, as the participation of normal megascleres in the outer protection of the gemmules and the small size differences between the upper and lower rotule, makes *H. capewelli*, the type species of this genus, a rather atypical member of *Heterorotula*. Extensive studies in Australian waters (Racek, MS.) revealed that even its optimal habitat is quite unusual, since it seems to be restricted to slightly brackish waters of the arid parts of Australia. The intrageneric relationship will be dealt with in detail in a forthcoming paper by the writer.



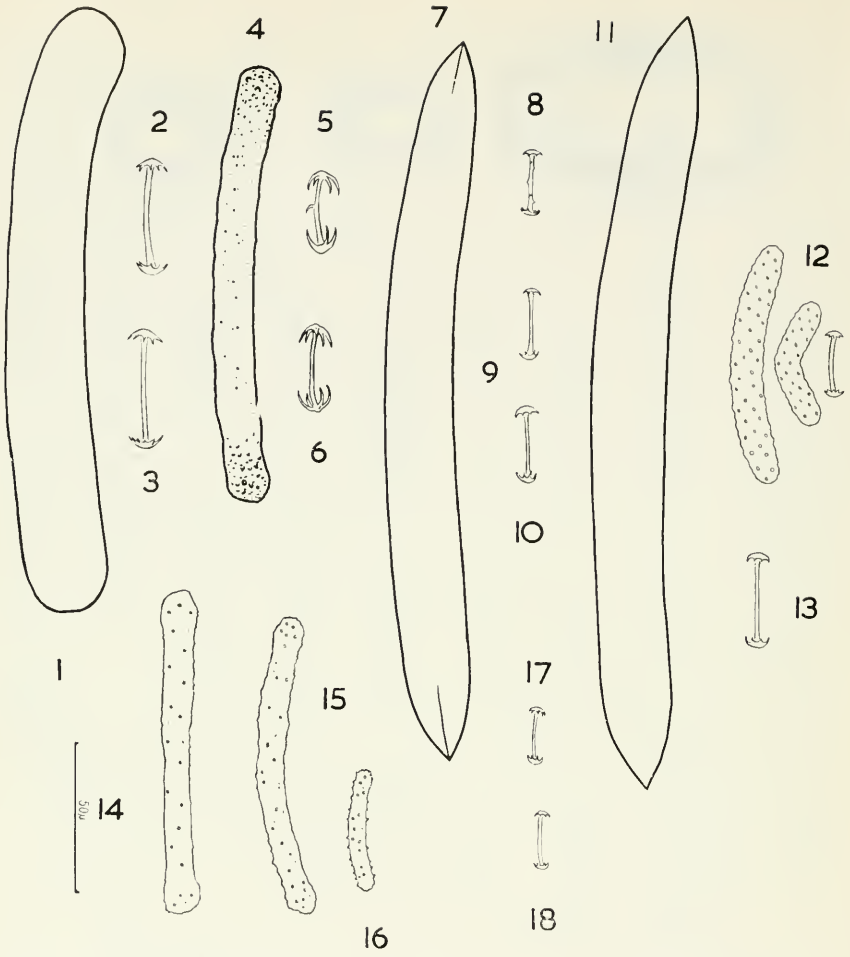
FIGURES 1–16.—1, Megasclere, *Spongilla alba;* 2, gemmule, *S. alba,* optical sect.; 3, gemmosclere and microsclere, *S. alba;* 4, gemmosclere, *S. lacustris;* 5, microsclere, *S. lacustris;* 6, gemmoscleres, *S. helvetica;* 7, microsclere, *S. helvetica;* 8, megasclere, *S. cenota;* 9, microsclere, *S. cenota;* 10, gemmosclere, *S. cenota;* 11, megasclere, *S. wagneri;* 12, microsclere, *S. wagneri;* 13, 14, gemmoscleres, *S. wagneri;* 15, gemmule, *S. wagneri,* optical sect.; 16, gemmule, *S. cenota,* optical sect.



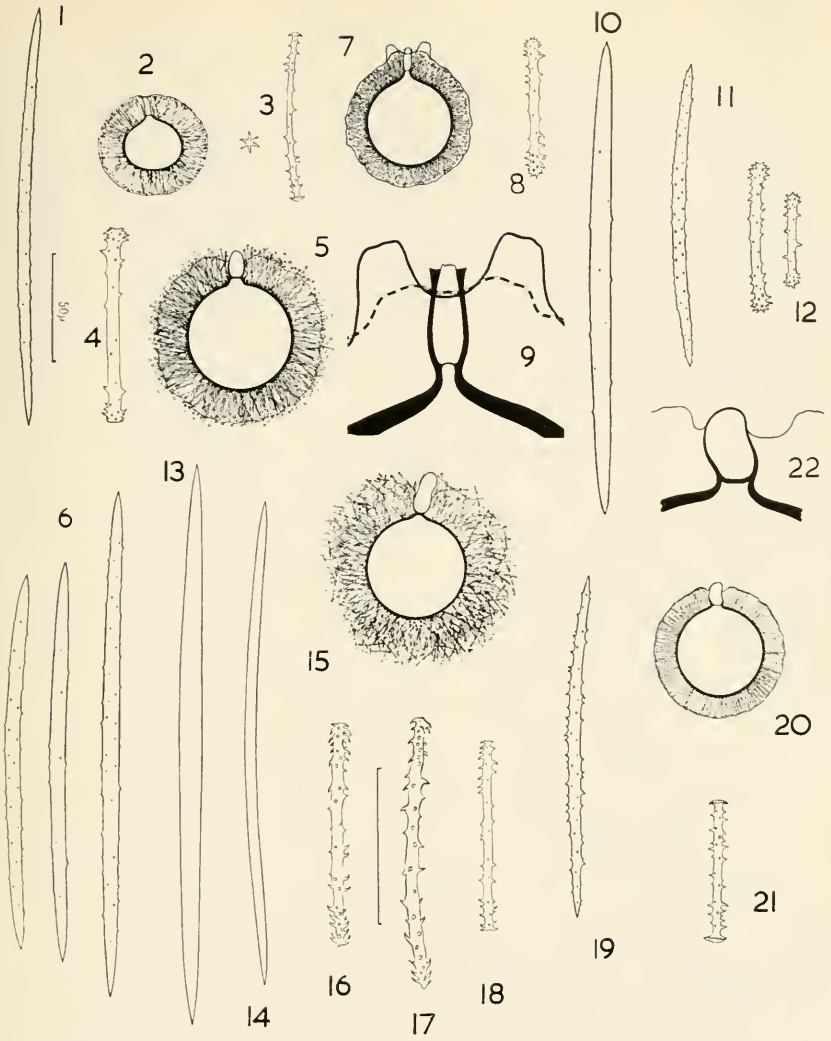
FIGURES 1–18.—1, Megasclere, *Eunapius carteri;* 2, gemmosclere, *E. carteri;* 3, megasclere, *E. decipiens;* 4, gemmosclere, *E. decipiens;* 5, 6, gemmoscleres, *E. michaelseni;* 7, megascleres, *E. calcuttanus;* 8, 9, gemmoscleres, *E. calcuttanus;* 10, megasclere, *E. crassissimus;* 11, gemmosclere, *E. crassissimus;* 12, megasclere, *E. geminus;* 13, gemmosclere, *E. geminus;* 14, megasclere, *E. potamolepis;* 15, gemmosclere, *E. potamolepis;* 16, gemmosclere, *E. geei;* 17, megasclere, *E. nitens;* 18, gemmosclere, *E. nitens.*



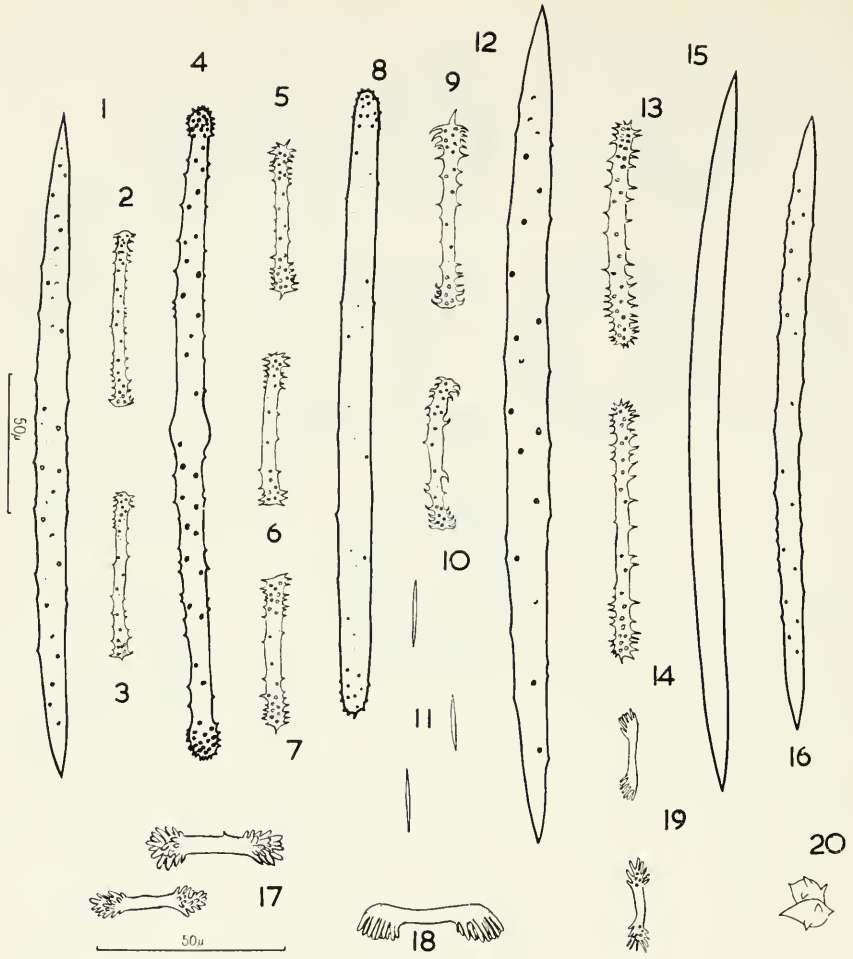
FIGURES 1–20.—1, Gemmules, *Eunapius fragilis*, optical sect.; 2, gemmule, *E. carteri*, optical sect.; 3, gemmule, *E. sinensis*, optical sect.; 4, gemmoscleres, *E. sinensis;* 5, megasclere, *E. geei;* 6, gemmosclere, *E. geei;* 7, megasclere, *Stratospongilla sumatrana;* 8, microsclere, *S. sumatrana;* 9, 10 gemmoscleres, *S. sumatrana;* 11, megasclere, *S. indica;* 12 microscleres, *S. indica;* 13, 14, gemmoscleres, *S. indica;* 15, megasclere, *S. gravelyi;* 16, microsclere, *S. gravelyi;* 17, 18, gemmoscleres, *S. gravelyi;* 19, megascleres, *S. clementis;* 20, gemmosclere, *S. clementis*.



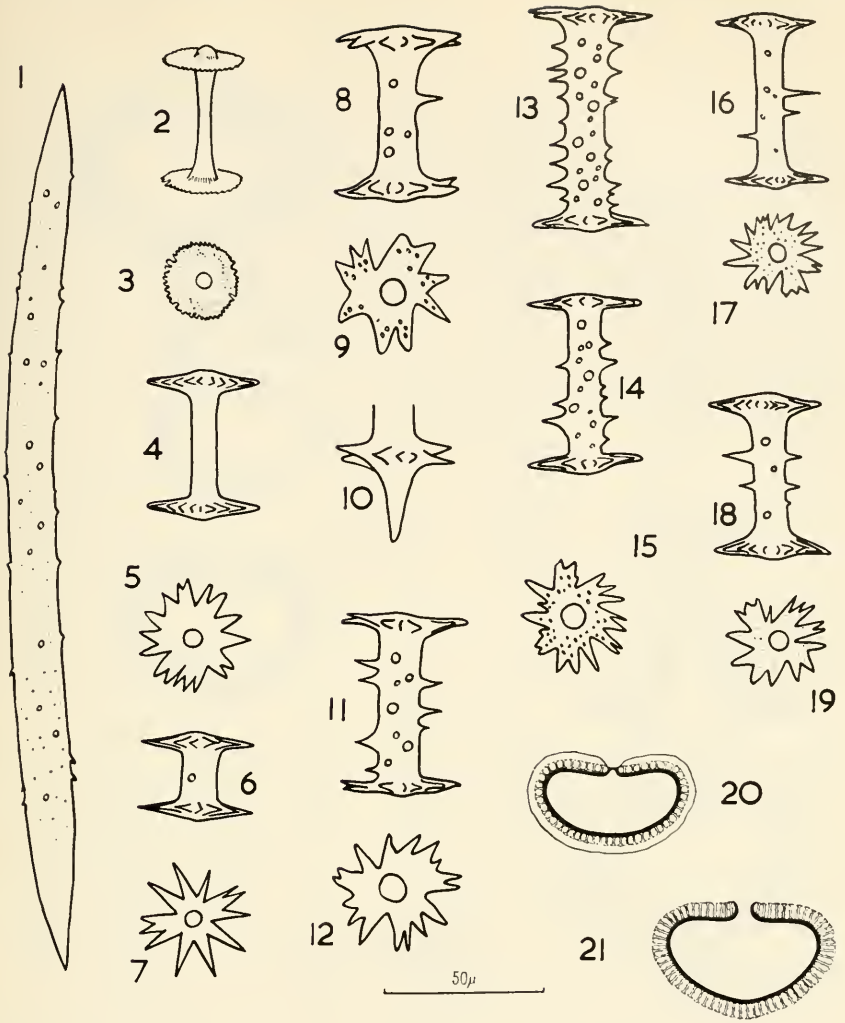
FIGURES 1–18.—1, Megasclere, *Corvospongilla lapiaosa;* 2, 3, microscleres, *C. lapidosa;* 4, megasclere, *C. böhmii;* 5, 6, microscleres, *C. böhmii;* 7, megasclere, *C. caunteri;* 8–10, microscleres, *C. caunteri;* 11, megasclere, *C. ultima;* 12, gemmoscleres and microsclere, *C. ultima;* 13, microsclere, *C. ultima;* 14, 15, megascleres, *C. scabrispiculis;* 16, gemmosclere, *C. scabrispiculis;* 17, 18, microscleres, *C. scabrispiculis.*



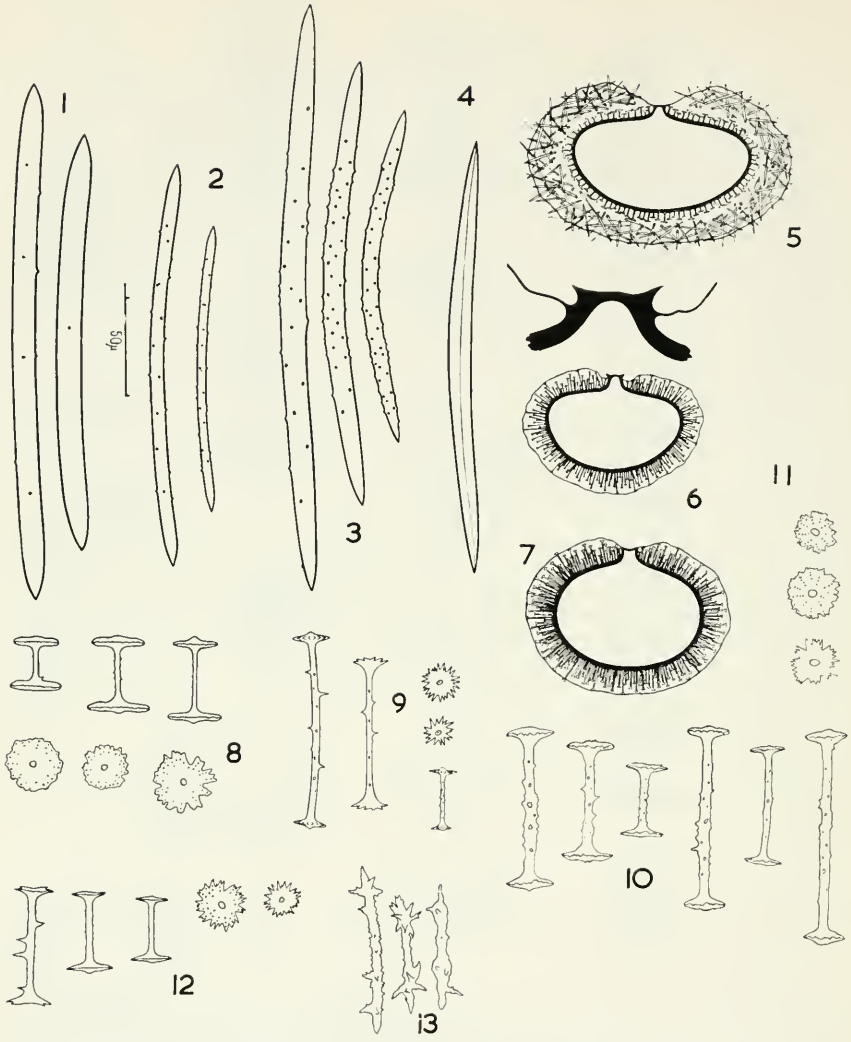
FIGURES 1–22.—1, Megasclere, *Radiospongilla crateriformis*, India; 2, gemmule, *R. crateriformis*, India; 3, gemmosclere, *R. crateriformis*, India; 4, gemmosclere, *R. sceptroides;* 5, gemmule, *R. sceptroides*, optical sect.; 6, megascleres, *R. sceptroides;* 7, gemmule, *R. hemephydatia*, optical sect.; 8, gemmosclere, *R. hemephydatia;* 9, enlarged gemmule porus tube, *R. hemephydatia;* 10, megasclere, *R. hemephydatia;* 11, megasclere, *Spongilla multispinifera;* 12, microscleres, *S. multispinifera;* 13, megasclere, *S. reticulata;* 14, megasclere, *S. proliferens;* 15, gemmule, *S. proliferens*, optical sect.; 16, gemmosclere, *S. reticulata;* 17, gemmosclere, *S. cerebellata;* 18, gemmosclere, *S. proliferens;* 19, megasclere, *Radiospongilla cantonensis;* 20, gemmule, *R. cantonensis*, optical sect.; 21, gemmosclere, *R. cantonensis;* 22, enlarged gemmule porus tube, *R. cantonensis.*



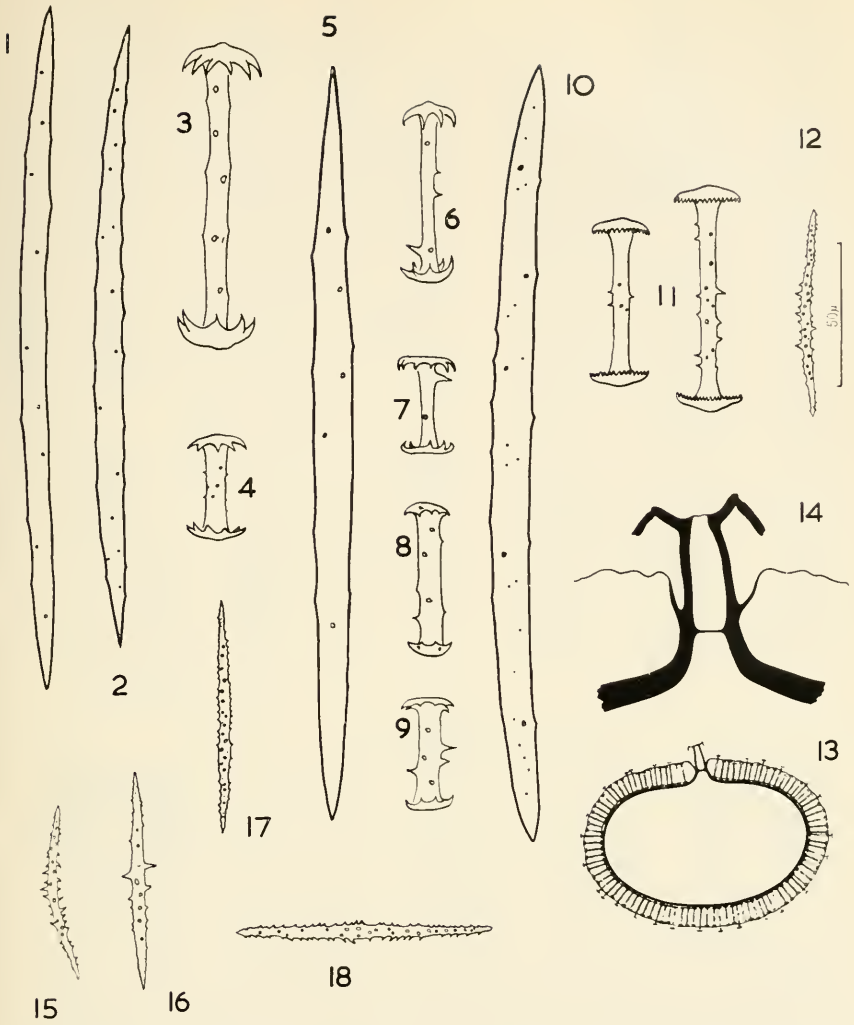
FIGURES 1–20.—1, Megasclere, *Radiospongilla crateriformis*, Indonesia; 2, 3, microscleres, *R. crateriformis*, Indonesia; 4, megasclere, *R. indica*, India; 5–7, gemmoscleres, *R. indica*, India; 8, megasclere, *R. indica*, Indonesia; 9, 10, gemmoscleres, *R. indica*, Indonesia; 11, microscleres, *Pectispongilla aurea;* 12, megasclere, *Radiospongilla sansibarica;* 13, 14, gemmoscleres, *R. sansibarica;* 15, megasclere, *Pectispongilla aurea;* 16, megasclere, *P. subspinosa;* 17, 18, gemmoscleres, *P. aurea;* 19, gemmoscleres, *P. subspinosa;* 20, spheraster, *P. stellifera.*



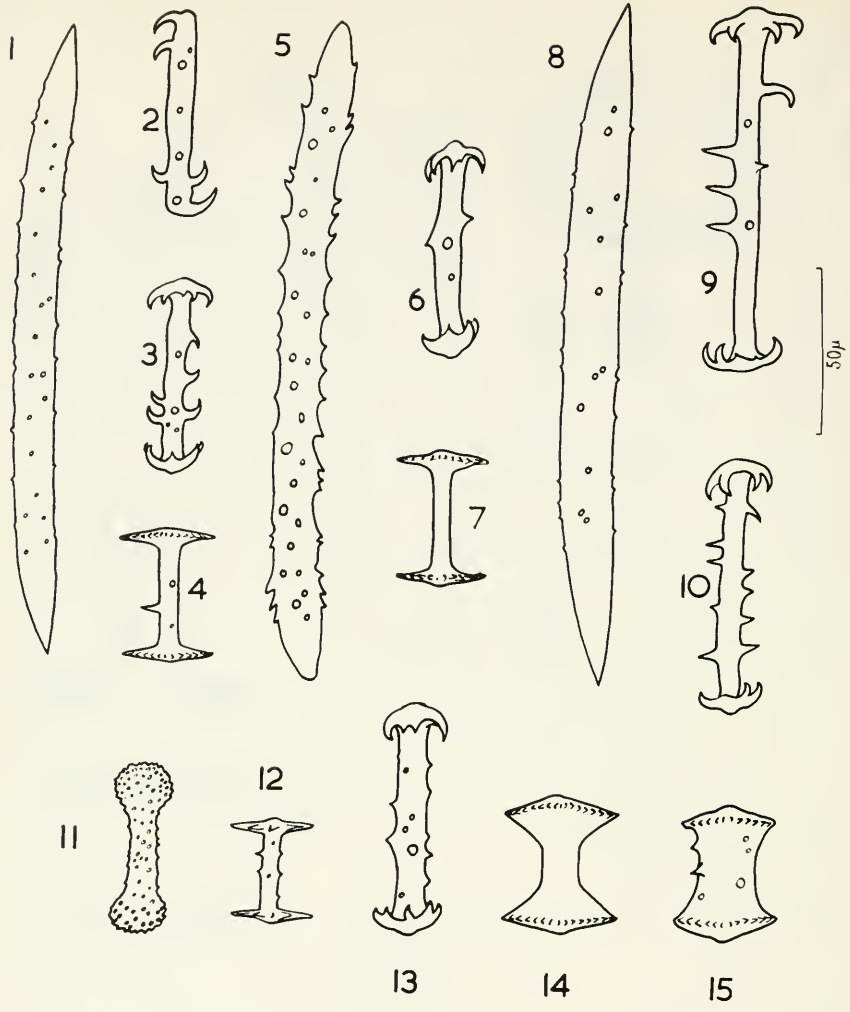
FIGURES 1–21.—1, Megasclere, *Ephydatia millsi;* 2, 3, gemmosclere, *E. millsi;* 4, 5, gemmosclere, *E. fluviatilis;* 6, 7, gemmosclere, *E. mülleri;* 8, 9, gemmosclere, *E. fortis;* 10, gemmosclere, *E. fortis* with freak rotule; 11, 12, gemmosclere. *E. robusta;* 13, longer gemmosclere, *E. ramsayi;* 14, shorter gemmosclere, *E. ramsayi;* 15, rotule of gemmosclere, *E. ramsayi;* 16, 17, gemmosclere, *E. facunda;* 18, 19, gemmosclere, *E. talaensis;* 20, gemmule, *E. meyeni*, optical sect.; 21, gemmule, *E. ramsayi*, optical sect.



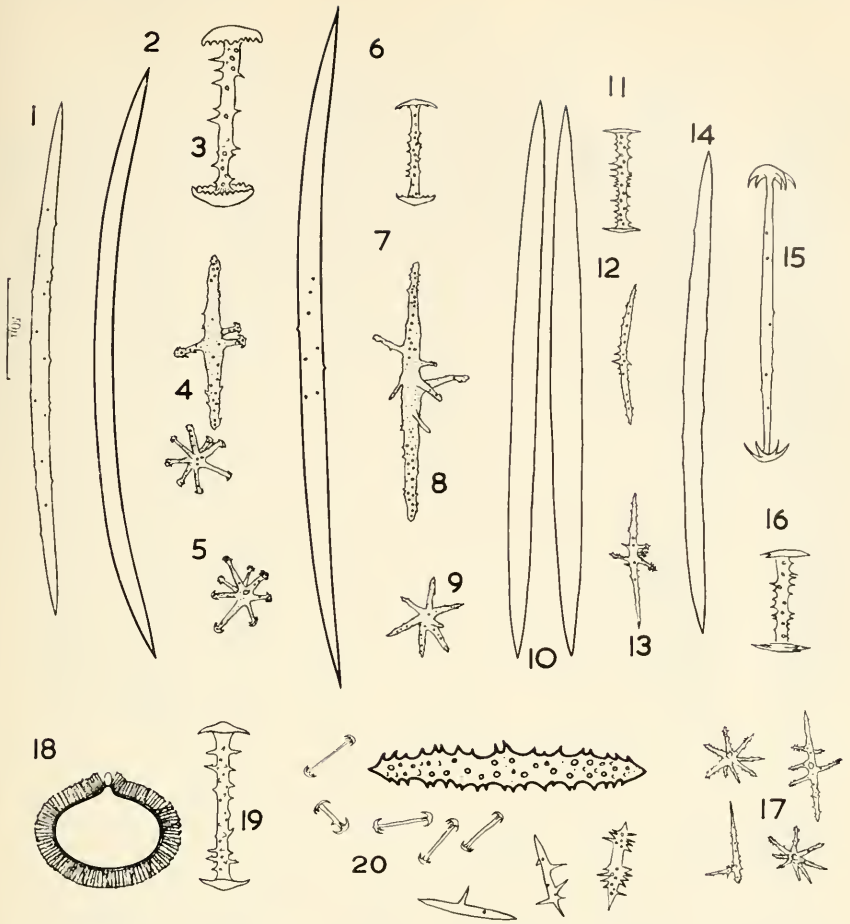
FIGURES 1–13.—1, Megascleres, *Heterorotula capewelli;* 2, megascleres, *H. nigra;* 3, megascleres, *H. multidentata;* 4, megasclere, *H. multiformis;* 5, gemmule, *H. capewelli,* optical sect.; 6, gemmule, *H. nigra,* optical sect. and enlarged porus tube; 7, gemmule, *H. multidentata,* optical sect.; 8, range of gemmoscleres, *H. capewelli;* 9, range of gemmoscleres, *H. nigra;* 10, range of gemmoscleres, *H. multidentata;* 11, rotules of gemmoscleres, *H. multidentata;* 12, range of gemmoscleres, *H. multiformis;* 13, malformed gemmoscleres, *H. multidentata,* probably a result of hybridization.



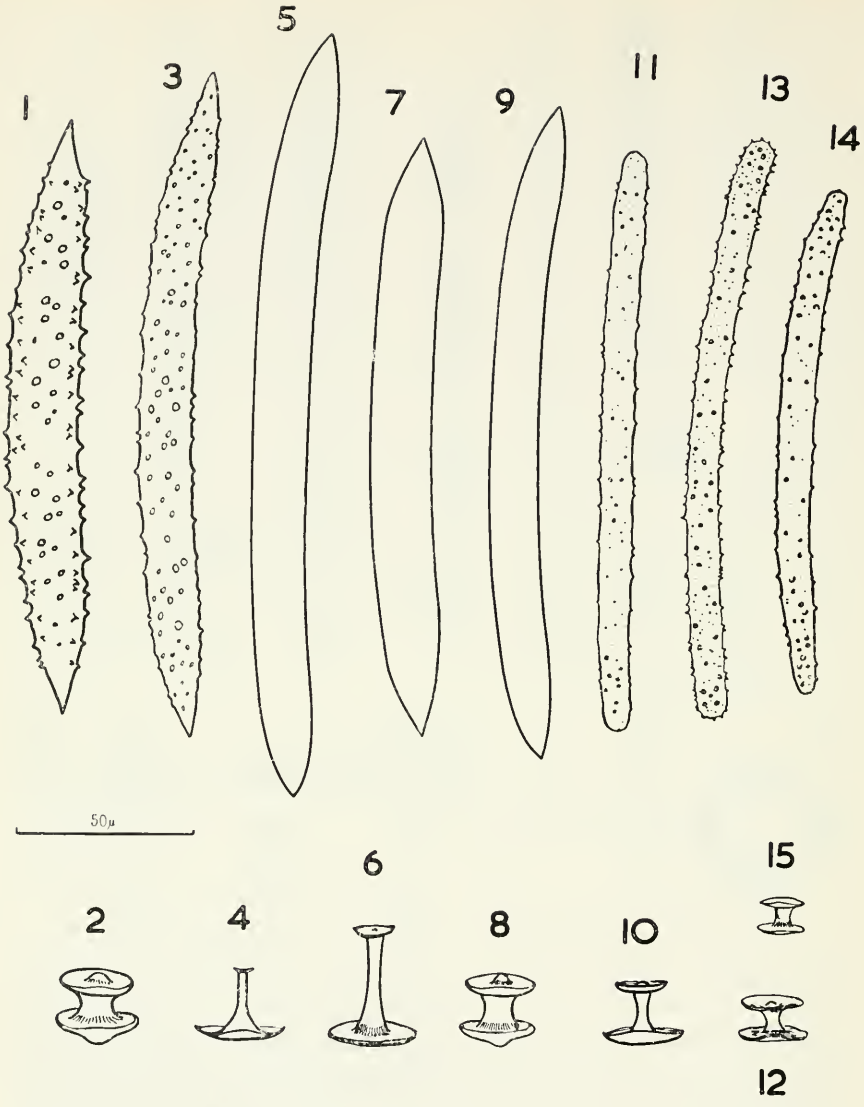
FIGURES 1–18.—1, Megasclere, *Heteromeyenia baileyi*, type; 2, megasclere, *H. repens;* 3, longer gemmosclere, *H. repens;* 4, shorter gemmosclere, *H. repens;* 5, megasclere, *H. tubisperma;* 6, longer gemmosclere, *H. tubisperma;* 7, shorter gemmosclere, *H. tubisperma;* 8, longer gemmosclere, *H. tentasperma;* 9, shorter gemmosclere, *H. tentasperma;* 10, megasclere, *H. stepanowii;* 11, gemmoscleres, *H. stepanowii;* 12, microsclere, *H. stepanowii;* 13, gemmule, *H. stepanowii*, optical sect.; 14, enlarged gemmule porus tube, *H. stepanowii;* 15, microsclere, *H. baileyi*, type; 16, microsclere, *H. repens;* 17, microsclere, *H. tubisperma;* 18, microsclere, *H. tentasperma.*



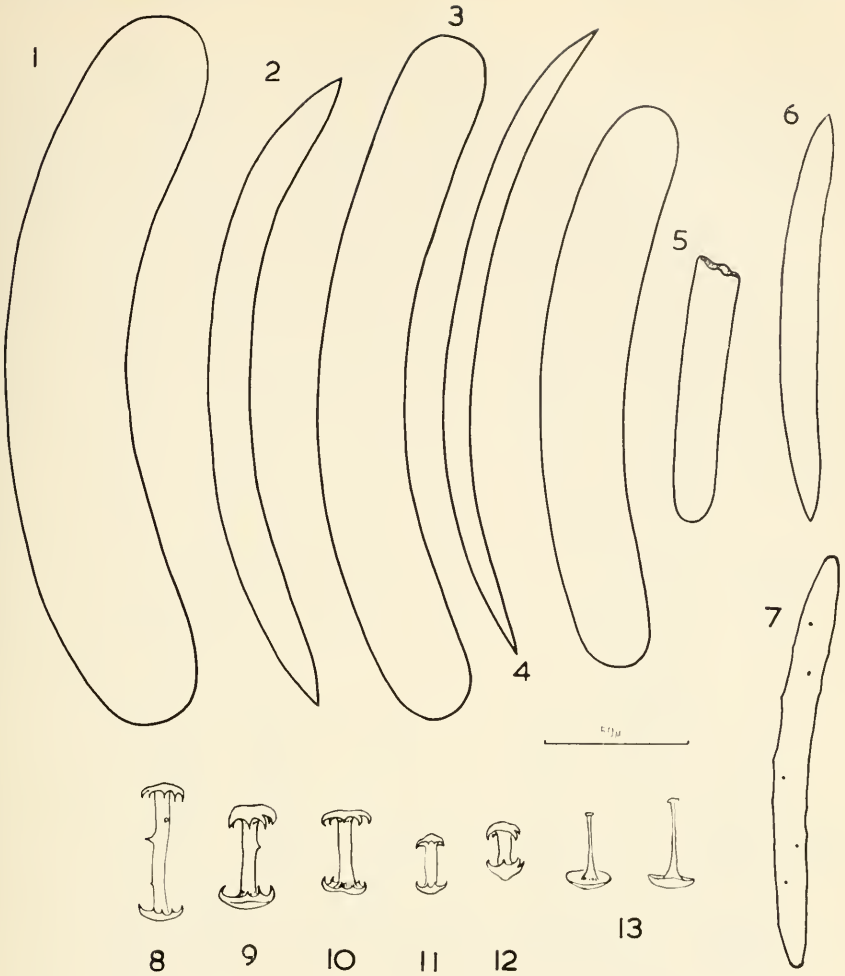
FIGURES 1–15.—1, Megasclere, *Anheteromeyenia ryderi;* 2, malformed longer gemmosclere, *A. ryderi;* 3, longer gemmosclere, *A. ryderi;* 4, shorter gemmosclere, *A. ryderi;* 5, megasclere, *A. pictovensis;* 6, longer gemmosclere, *A. pictovensis;* 7, shorter gemmosclere, *A. pictovensis;* 8, megasclere, *A. argyrosperma;* 9, longer gemmosclere, *A. argyrosperma;* 10, shorter gemmosclere, *A. argyrosperma;* 11, longer gemmosclere, *A. biceps;* 12, shorter gemmosclere, *A. biceps;* 13, longer gemmosclere, *Heteromeyenia conigera;* 14, shorter gemmosclere, *H. conigera;* 15, malformed shorter gemmosclere, *H. conigera.*



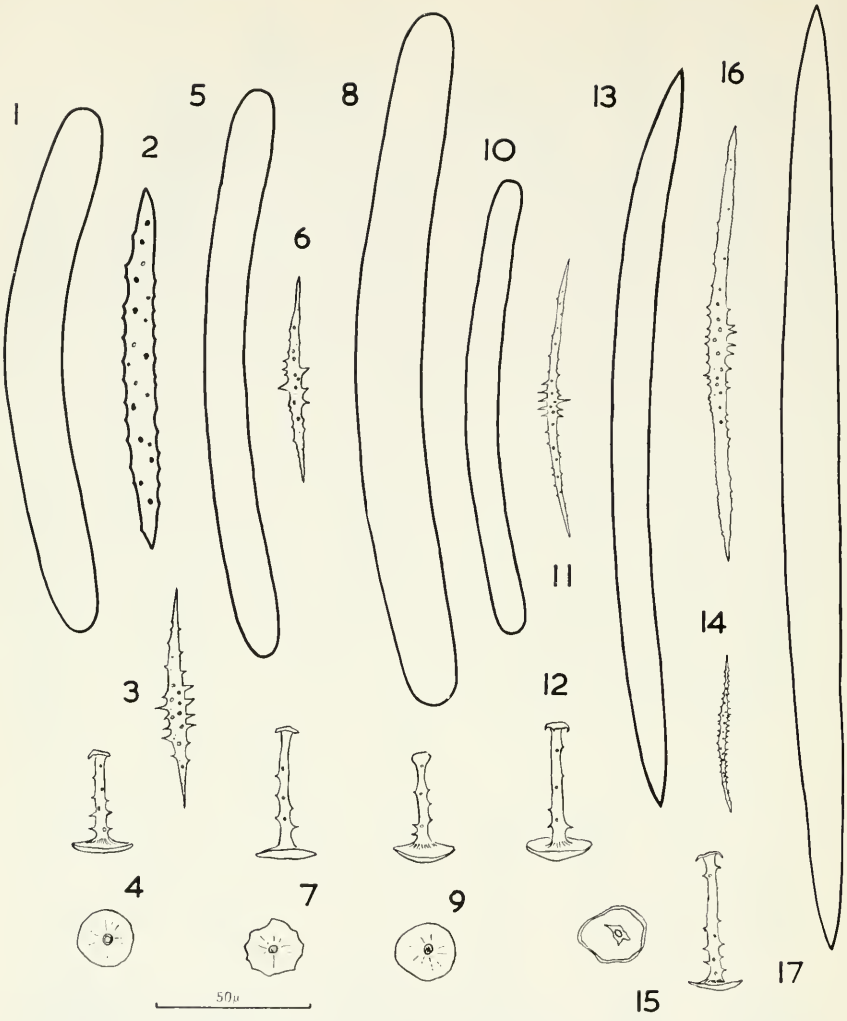
FIGURES 1–20.—1, Megasclere, *Umborotula bogorensis;* 2, megasclere, *Dosilia plumosa;* 3, gemmosclere, *D. plumosa;* 4, acerate microsclere, *D. plumosa;* 5, stellate microscleres, *D. plumosa;* 6, megasclere, *D. palmeri;* 7, gemmosclere, *D. palmeri;* 8, acerate microsclere, *D. palmeri;* 9, stellate microsclere, *D. palmeri;* 10, megascleres, *D. brouni;* 11, gemmosclere, *D. brouni;* 12, 13, microscleres, *D. brouni;* 14, megasclere, *D. radiospiculata;* 15, longer gemmosclere, *D. radiospiculata;* 16, shorter gemmosclere, *D. radiospiculata;* 17, range of microscleres, *D. radiospiculata;* 18, gemmule, *Umborotula bogorensis,* optical sect.; 19, gemmosclere, *U. bogorensis;* 20, range of spicular components, *Spongilla novae-terrae.*



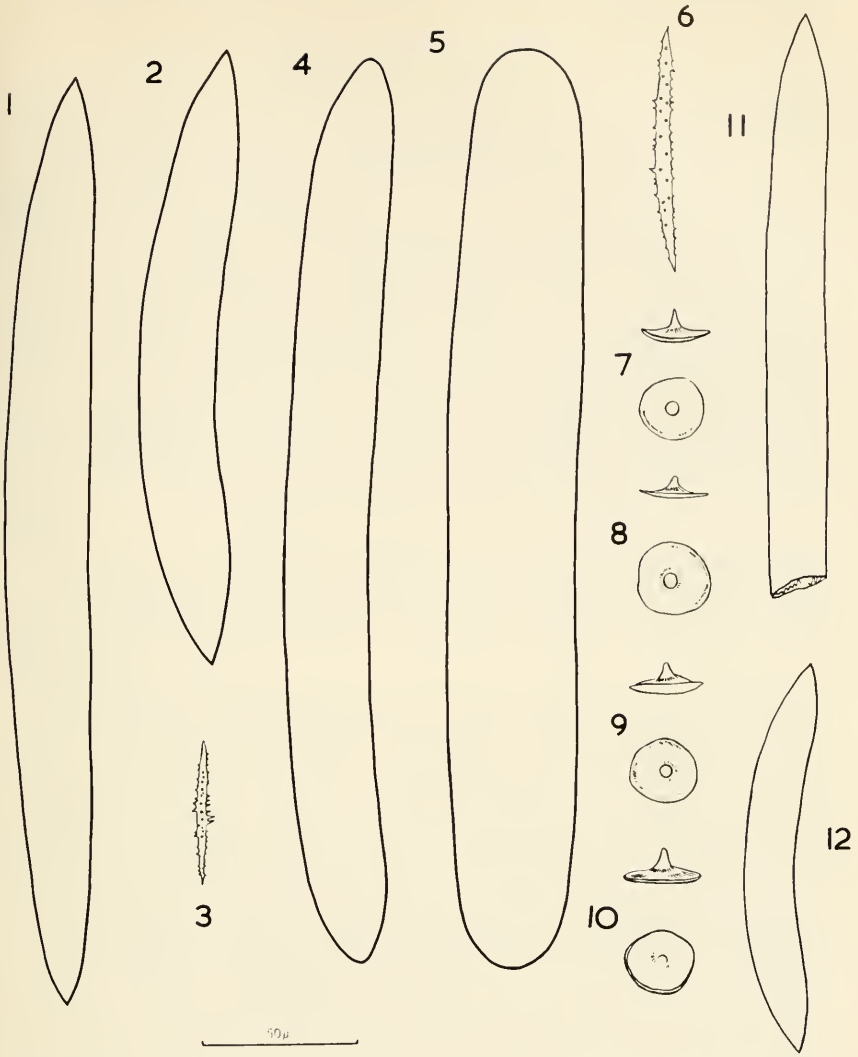
FIGURES 1–15.—1, Megasclere, *Trochospongilla horrida;* 2, gemmosclere, *T. horrida;* 3, megasclere, *T. pennsylvanica;* 4, gemmosclere, *T. pennsylvanica;* 5, megasclere, *T. paulula;* 6, gemmosclere, *T. paulula;* 7, megasclere, *T. leidyi;* 8, gemmosclere, *T. leidyi;* 9, megasclere, *T. latouchiana;* 10, gemmosclere, *T. latouchiana;* 11, megasclere, *T. philottiana;* 12, gemmosclere, *T. philottiana;* 13, megasclere, *T. philottiana* var. *javanensis;* 14, megasclere, *T. philottiana* var. *tunghuensis;* 15, gemmosclere, *T. philottiana* var. *tunghuensis.*



FIGURES 1–13.—1, Stouter megasclere, *Uruguaya corallioides;* 2, slender megasclere, *U. corallioides;* 3, stouter megasclere, *U. macandrewi;* 4, slender megasclere, *U. macandrewi;* 5, megascleres, *U. repens;* 6, 7, megascleres, *Acalle recurvata;* 8–12, birotulate gemmoscleres found in slide of type, *A. recurvata;* 13, tubelliform gemmoscleres of inner series, *A. recurvata.*



FIGURES 1–17.—1, Normal megasclere, *Metania reticulata;* 2, unusual megasclere, *M. reticulata;* 3, microsclere, *M. reticulata;* 4, gemmosclere, *M. reticulata;* 5, megasclere, *M. vesparia;* 6, microsclere, *M. vesparia;* 7, gemmosclere, *M. vesparia;* 8, megasclere, *M. pottsi;* 9, gemmosclere, *M. pottsi;* 10, megasclere, *M. lissostrongyla;* 11, microsclere, *M. lissostrongyla;* 12, gemmosclere, *M. lissostrongyla;* 13, megasclere, *M. vesparioides;* 14, microsclere, *M. vesparioides;* 15, gemmosclere, *M. vesparioides;* 16, microsclere, *M. rhodesiana;* 17, megasclere, *M. rhodesiana.*



FIGURES 1–12.—1, Longer megasclere, *Drulia brownii*, type; 2, shorter megascleres, *D. brownii*, type; 3, microsclere, *D. brownii*, type; 4, megasclere, *D. geayi;* 5, megasclere, *D. cristata;* 6 microsclere, *D. cristata;* 7, gemmosclere, *D. brownii;* 8, gemmosclere, *D. geayi;* 9, gemmosclere, *D. cristata;* 10, gemmosclere, *D. batesii;* 11, longer megasclere, *D. batesii;* 12, shorter megasclere, *D. batesii.*

Heterorotula nigra (Lendenfeld, 1887)

PLATE 8, FIGURES 2, 6, 9

Tubella nigra Lendenfeld, 1887, p. 91.—Whitelegge, 1889, p. 306.—Weltner, 1895, p. 128; 1910, p. 137.—Gee, 1931d, p. 28.
Ephydatia nigra Gee, 1931c, p. 44; 1931d, p. 56; 1932c, p. 32.
Meyenia nigra Penney, 1960, p. 53.

MATERIAL.—Slides of type (AusM) and syntype (N. Gist Gee); material and slides from Australia (Racek).

DESCRIPTION.—Sponge usually forming flat encrustations on aquatic plants, when occurring on reeds or timber often massive; surface comparatively even and smooth, rarely slightly lobose; oscula few and inconspicuous; dermal membrane well developed, closely adhering to symplasm. Skeleton consisting of ill-defined and very slender spicule fibers, coated together by only small amounts of spongin. Consistency of live sponge moderately soft and very fragile.

Megascleres slender and fusiform amphioxea, in the majority entirely smooth, occasionally covered with a small number of inconspicuous spines except at their tips; length range 224–360 μ, width range 7–13 μ.

Microscleres absent.

Gemmoscleres birotulates with a very slender, finely granulated shaft, and terminally with flat rotules of unequal diameter; faces of rotules smooth; margin of rotules regularly or irregularly incised to form distinct teeth; length differences of birotulates very pronounced; length range of larger series 56–73 μ, of smaller 35–48 μ; width range of lower rotule 13–16 μ, of upper 10–14 μ; thickness of shaft 2–4 μ.

Gemmules spherical and moderately large, scattered in basal parts of sponge, almost at its base in small encrusting forms, diameter ranging 230–360 μ; pneumatic layer well developed and irregular, but never higher than the longest gemmoscleres; consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, with their large rotules firmly inserted in the inner gemmular membrane; reinforcement of pneumatic coat by megascleres absent; outer gemmular membrane distinctly corrugated, and almost white; foramen simple or bearing a very shallow peripheral collar.

DISTRIBUTION.—Apparently restricted to swampy areas of eastern Australia.

COLOR IN LIFE.—Light to dark brown, rarely dark gray to black due to presence of mud particles in the symplasm.

DISCUSSION.—This species represents the other extreme in the intergrading series of gemmosclere characters. Although more than

two classes of birotulates are present in all *Heterorotula* species (cf. *Heteromeyenia, Anheteromeyenia, Dosilia,* and *Corvomeyenia*) the length differences between the longest and shortest gemmoscleres are most conspicuous.

Lendenfeld (1887) described the megascleres of this species as being entirely smooth. A wide range of specimens examined (Racek, MS.), however, revealed that the surface of megascleres of *H. nigra* is frequently covered with minute spines, which can be seen only under very high power. Lendenfeld's specific name, referring to a black color in life, is quite insignificant, since most of the specimens of *H. nigra* examined were of flesh color or of somewhat darker brownish shades. The presence of mud particles within any live sponge often changes the original color of specimens from swampy regions into darker hues, irrespective of species or genera.

Heterorotula multidentata (Weltner, 1895)

PLATE 8, FIGURES 3, 7, 10, 11, 13

Tubella multidentata Weltner, 1895, p. 142.
Ephydatia multidentata Weltner, 1900, p. 519.—Gee, 1931d, p. 51; 1931e, p. 44; 1935, p. 264.
Meyenia multidentata Penney, 1960, p. 53.
Ephydatia lendenfeldi Traxler, 1896b, p. 97.—Gee, 1931d, p. 28.
Spongilla lacustris var. *sphaerica* Lendenfeld, 1887, p. 90.—Weltner, 1895, p. 119.—Gee, 1931d, p. 28.

MATERIAL.—Slides of syntype (AusM, MG, and N. Gist Gee); numerous specimens from eastern and northern Australia (Racek).

DESCRIPTION.—Young sponge forming shallow encrustations of varying dimensions; mature sponge rather massive and often spherical; surface distinctly lobose, with high and rounded ridges of irregular shape separated from each other by deep clefts; oscula inconspicuous, dermal membrane well developed and slightly separated from the underlying symplasm. Skeleton consisting of rather thick vertical spicule fibers, coated together by only little amounts of spongin, and of ill-defined transverse fibers. Consistency of live sponge moderately soft and very fragile.

Megascleres feebly curved and slender amphioxea, distinctly fusiform, ranging from entirely smooth to distinctly microspined; spines small and inconspicuous, never present on tips of scleres; length range 280–320 μ, width range 10–18 μ.

Microscleres absent. Some slender amphioxea of 120–140 μ length occasionally present in symplasm, covered with fine granulations throughout, their tips bearing several rows of small and sharp spines; their identity has not yet been resolved.

Gemmoscleres birotulates with a moderately slender, finely granulated shaft which often bears stout but blunt conical teeth, and

terminally with flat rotules of unequal diameter; faces of rotules invariably strongly granular, arrangement of granules more or less radial; margin of rotules irregularly crenulated or incised, often bearing a number of discernible teeth separated by varying distances; length differences of birotulates very pronounced: length range of larger series 64–84 μ, of smaller 32–48 μ; width range of lower rotule 19–22 μ, of upper 17–20 μ; thickness of shaft 4–6 μ.

Gemmules extremely abundant in mature sponge, scattered throughout skeletal meshwork; in younger sponges necessarily confined to basal parts; they are large and spherical, ranging in diameter 490–585 μ; pneumatic layer very thick and irregular but rarely higher than the longest gemmoscleres, consisting of minute air spaces; gemmoscleres embedded in this coat with their larger rotules firmly inserted in the inner gemmular membrane; outer parts of pneumatic layer occasionally reinforced by a small number of apparently adventitious megascleres; outer gemmular membrane distinctly corrugated, and almost white; foramen simple or bearing a very shallow peripheral collar.

Distribution.—Widely distributed in eastern Australia, rarely penetrating the Dividing Range westward.

Color in life.—Light tan to brown, typically of flesh color.

Discussion.—Weltner's (1895) original description and his further notes on additional material (1900) were based on incompletely developed specimens. When fully mature, specimens of *H. multidentata* always form large bulbous growths, and its gemmules are extremely abundant and freely scattered through the skeletal meshwork. With respect to its spicular components this species displays discernible variations. The form of gemmoscleres used by Traxler (1896b) for the erection of his *Ephydatia lendenfeldi* can be found in any range of specimens of *H. multidentata* from distant localities, and Traxler's specific name therefore must now be considered synonymous.

The spicular components of *Spongilla lacustris* var. *sphaerica*, the true identity of which remained doubtful until the present, were found during our studies to be identical with those of *H. multidentata* in all respects, and the relegation of Lendenfeld's variety to a synonym of Weltner's species is now possible. This procedure finally eliminates *S. lacustris*, erroneously recorded for the Southern Hemisphere, from the list of Australian species.

The distribution of *H. multidentata* seems to be confined to the eastern watershed of the Australian Great Divide, its place on the western slopes and in the interior of the eastern states taken by a closely related but distinctly separable species, which will be described in a forthcoming paper (Racek, MS.).

Heterorotula multiformis (Weltner, 1910)

PLATE 8, FIGURES 4, 12

Ephydatia multiformis Weltner, 1910, p. 138.—Gee, 1931e, p. 44; 1931d, p. 53; 1932c, p. 30.
Meyenia multiformis Penney, 1960, p. 53.

MATERIAL.—Slides of syntype (HM); two specimens from Western Australia (Racek).

DESCRIPTION.—Sponge forming encrustations of various dimensions, mature specimens slightly bulbous; surface comparatively even and smooth; oscula few in number and very inconspicuous, dermal membrane well developed and adhering to the underlying symplasm. Skeleton consisting of an irregular meshwork of spicule fibers joined together by only small amounts of spongin. Consistency of live sponge soft and very fragile.

Megascleres comparatively long and moderately stout amphioxea, slightly curved, and as a rule entirely smooth; length range 330–420 μ, width range 13–20 μ.

Microscleres absent.

Gemmoscleres birotulates with slender and smooth shaft, only occasionally bearing 1 or 2 conical teeth, and terminally with flat rotules of distinctly unequal diameter; faces of rotules slightly granulated; margin of rotules irregularly incised, bearing a varying number of distinct teeth; length differences of birotulates moderately pronounced: length range of larger series 35–52 μ, of smaller 24–44 μ; width range of lower rotule 14–24 μ, of upper 14–18 μ; thickness of shaft 2–4 μ.

Gemmules abundant in mature sponge, scattered throughout skeletal meshwork; they are large and spherical, ranging in diameter 480–680 μ; pneumatic layer very thick and irregular but rarely higher than the longest gemmoscleres, consisting of minute air spaces; gemmoscleres embedded in this coat with their larger rotules firmly inserted in the inner gemmular membrane; outer gemmular membrane distinctly corrugated; foramen simple or bearing a shallow peripheral collar.

DISTRIBUTION.—Known only from Western Australia.

COLOR IN LIFE.—Light brown.

DISCUSSION.—This species differs from *H. multidentata* in skeletal details, in the shape of its peculiar and small gemmoscleres, and in the possession of entirely smooth megascleres. From *H. capewelli*, with which it shares smooth megascleres, *H. multiformis* can be distinguished by its very soft consistency, smooth body surface, conspicuously different gemmoscleres and megascleres, and the absence of the latter spicules on its gemmules. The species here discussed is therefore clearly separable from all its congeners, even though a better

understanding of the range of criteria in *Heterorotula* may yet result in the erection of a trinomial nomenclature, separating the various species on a subspecific level. Until this will be possible, it is advisable not to obscure possible taxonomic evidence and to retain the different members of this genus, at least provisionally, as distinct species.

Heterorotula kakahuensis (Traxler, 1896)

Ephydatia kakahuensis Traxler, 1896*a*, p. 30.—Gee, 1931e, p. 41; 1931d, p. 46; 1932c, p. 30.—Schröder, 1935, p. 101.
Meyenia kakahuensis Penney, 1960, p. 51.

Material.—Slides of syntype (LeidM); slides of material from New Zealand (N. Gist Gee).

Description.—Sponge, according to Traxler (1896a) and Schröder (1935), forming encrustations of various dimensions and of soft consistency; other criteria still insufficiently known.

Megascleres slender amphioxea, as a rule covered with a varying number of inconspicuous spines except at their tips, only exceptionally entirely smooth; length range 185–260 μ, width range 9–12 μ.

Microscleres absent.

Gemmoscleres not present in the material available for the present study; those described by Traxler (1896a) and Schröder (1935) are birotulates of comparatively small size differences, possessing smooth shafts and nongranulated flat discs of slightly unequal size; length range of gemmoscleres 30–42 μ (Schröder), diameter of rotules ranging 17–22 μ.

Gemmules were not seen by the authors; they were described by Schröder to be spherical, ranging in diameter 380–540 μ, and devoid of an outer gemmular membrane; foramen apparently simple, surrounded by an elevated collar.

Distribution.—Known only from New Zealand.

Color in life.—Not yet observed.

Discussion.—No gemmules or even a single gemmosclere were contained in the slides examined during the present study or in the syntype specimen from LeidM examined by the writer on an earlier occasion. The systematic position of this species must therefore remain uncertain until additional material from New Zealand can be obtained. From the accounts of previous authors it is very likely that *E. kakahuensis* Traxler is a member of this genus, since most of its known criteria clearly fit its definition. Instead of listing this species as a dubious one, the authors consider it advisable to include it provisionally in the genus *Heterorotula* until evidence as to the contrary can be demonstrated.

Genus *Heteromeyenia* Potts, 1831, restricted

Heteromeyenia Potts, 1881, p. 150 (part); 1887, p. 236 (part).—MacKay, 1889, p. 93 (part).—Hanitsch, 1895, p. 128.—Weltner, 1895, p. 114 (part).—Girod, 1899, p. 106 (part).—Kirsch, 1909, p. 37 (part).—Annandale, 1909d, p. 404 (part); 1918a, p. 213 (part).—Arndt, 1926, p. 344.—Schröder, 1927b, p. 107 (part).—Gee and Wu, 1928, p. 11.—Gee, 1931e, p. 39.—De Laubenfels, 1936, p. 36 (part).—Eshleman, 1950, p. 41 (part).—Wurtz, 1950, p. 5 (part).—Jewell, 1952, p. 451 (part, not type species).—Simon, 1952, p. 80.—Penney, 1960, p. 40 (part).

Dosilia Gray, 1867, p. 550 (part).—Dybowsky, 1884, p. 507.

Carterella Potts, 1881, p. 150.

Carterius Petr, 1886, p. 92.—Mills, 1887, p. 167.—Vejdovsky, 1886, p. 175; *in* Potts, 1887, p. 179.—Weltner, 1895, p. 114.—Girod, 1899, p. 113.—Lauterborn, 1902, p. 519.—Kirsch, 1909, p. 37.—Arndt, 1926, p. 344.—Schröder, 1926, p. 240.—Gee, 1931e, p. 35; 1932c, p. 26.—De Laubenfels, 1932, p. 111; 1936, p. 36.—Eshleman, 1950, p. 44.—Wurtz, 1950, p. 6.—Jewell, 1952, p. 452.—Penney, 1960, p. 33.

Heteromeyenia (*Oxheteromeyenia*) Schröder, 1927b, p. 107.

TYPE SPECIES.—By subsequent selection (De Laubenfels, 1936) *Heteromeyenia repens* Potts, 1881, now a synonym of *Heteromeyenia baileyi* (Bowerbank, 1863).

DEFINITION.—Megascleres usually slender and distinctly fusiform amphioxea, covered with minute and irregular spines except at their tips.

Microscleres long and thin, sharply pointed and fusiform amphioxea, entirely spined, spines as a rule increasing in length towards the center of the scleres, and often ending there in rounded knobs.

Gemmoscleres birotulates of two more or less distinct length groups, only slightly differing from each other, or identical, in their rotules and general outline; the shafts of both series often stout and cylindrical and covered with erect conical spines.

Gemmules moderately large to large, subspherical to spherical, scattered throughout skeletal meshwork, usually abundant; pneumatic layer well developed but typically not very thick, consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, the outer rotules of the shorter series either concealed in the pneumatic coat or slightly surpassing it, those of the fewer longer series always considerably reaching beyond the outer gemmular membrane; foramen distinctly tubular, porus tube ranging from moderately long to very long in the various species; distolateral margins of tube often expanded and rimlike, with or without cirrous appendages of varying length and arrangement.

Sponges forming flat to massive encrustations, with surfaces ranging from smooth to irregularly papillose; associations with zoochlorellae frequent, and consequently coloration a varying shade of green. Consistency ranging from soft to moderately firm.

Scattered but apparently widespread distribution in eastern parts of the North American Continent, one species also recorded from Ireland and eastern Europe, another ranging from central Europe through the U.S.S.R. to China, Japan, and Australia, but absent in America.

Discussion.—The genus *Heteromeyenia*, as here restricted, now includes only such species of the formerly conglomerate genus of that name which possess free microscleres in the form of acanthoxea, while those lacking microscleres altogether had to be transferred to *Anheteromeyenia* Schröder, raised to full generic rank by de Laubenfels (1936). That author, correctly avoiding Schröder's (1927b) redundant subgeneric name *Oxheteromeyenia* for all species with acerate microscleres, also redefined the available generic name *Heteromeyenia* Potts and, in the absence of a designated genotype, proposed as its type species *H. repens* Potts, now a synonym of *H. baileyi* (Bowerbank).

In spite of Schröder's (1927b) convincing demonstration of the close interrelationship of all species formerly grouped in Potts' unrestricted genus *Heteromeyenia*, his interspecific comparative studies of the gemmular porus tube have only added to the already existing taxonomic confusion. Having established for the first time the heterogeneous character of the gemmoscleres in the type of *Spongilla baileyi*, he had no hesitation in considering, in addition to the clearly synonymous *H. repens*, even some species of the former genus *Carterius* as mere races of Bowerbank's nominal species, an arrangement which cannot possibly be retained. While in the *H. baileyi* complex the gemmoscleres are heterogeneous both in regard to length and shape of rotules, the birotulates of the *Carterius stepanowii* complex differ only in length, and possess almost to fully identical rotules. Although, as shown by Schröder (1927b), the separate status of the genus *Carterius* is fully unjustified, all its previous species moreover share an additional criterion, i.e., the foraminal cirrous appendages or their visible rudiments, which in the *H. baileyi* complex are lacking altogether. The revised genus *Heteromeyenia* Potts therefore must be considered to consist of two morphologically distinct groups, both having acerate microscleres in their symplasm and dermal membrane. The first, with two distinct classes of heterogeneous gemmoscleres and without foraminal projections, is represented by the *H. baileyi* complex, by the insufficiently known *H. longistylis* Mills, and perhaps also by the still dubious *H. insignis* Weltner; the latter two could not be examined during the present study. The second, displaying more or less only two length groups in their gemmoscleres and conspicuous foraminal tendrils on their gemmules, comprises *H. stepanowii* (Dybowsky) with its "varieties" *arndti*, *bohemica*, *palatina*, and *petri*, *H. latitenta* (Potts), *H. tentasperma* (Potts), and *H. tubisperma*

(Potts). *Carterius primitivus* Swartschewsky from Lake Baikal, U.S.S.R., although absent in the material available for this study, most certainly also belongs here.

In view of the restoration of Gray's (1867) system, and following Schröder's (1927b) excellent revision, the remaining species of Potts' original genus *Heteromeyenia* are now allocated to the genera *Dosilia* Gray and *Anheteromeyenia*, respectively, depending on their possession of stellate microscleres or complete absence of "dermal" spicules. Consequently, the genera *Carterius* Petr, *Asteromeyenia* Annandale, as well as Schröder's subgenera *Oxheteromeyenia* and *Astroheteromeyenia*, although widely used in previous literature, have thus become useless in taxonomic procedure.

Heteromeyenia baileyi (Bowerbank, 1863)

PLATE 9, FIGURES 1–4, 15

Spongilla baileyi Bowerbank, 1863, p. 451.—Dawson, 1878, p. 1.
Dosilia baileyi Gray, 1867, p. 551.
Meyenia baileyi Carter, 1881, p. 95.—Potts, 1887, p. 227.—Kirsch, 1909, p. 37.—Wurtz, 1950, p. 4.
Ephydatia baileyi Weltner, 1895, p. 114.—Smith, 1921, p. 17.
Heteromeyenia baileyi Schröder, 1927b, p. 108; 1932b, p. 111.—Gee, 1931e, p. 33; 1932c, p. 32.—Penney, 1960, p. 41.
Spongilla repens Potts, 1880b, p. 357.
Heteromeyenia repens Potts, 1887, p. 237.—Kellicott, 1891, p. 103.—Wierzejski, 1892, p. 142.—Girod, 1899, p. 113.—Weltner, 1895, p. 114.—Smith, 1921, p. 17; 1930, p. 184.—Kirsch, 1909, p. 37.—Arndt, 1926, p. 344; 1928a, p. 72—Schröder, 1927b, p. 75.—Old, 1931, p. 298; 1932b, p. 449.—De Laubenfels, 1936, p. 36.—Jewell, 1939, p. 17.—Eshleman, 1950, p. 41.—Wurtz, 1950, p. 5.—Moore, 1951, p. 63.—Jewell, 1952, p. 451.
Heteromeyenia baileyi var. *repens* Gee, 1931e, p. 47; 1932c, p. 33; 1937, p. 285.—Zimmer, 1936, p. 126.—Schröder, 1927b, p. 107; 1938b, p. 127.
?Heteromeyenia repens var. *spinulosa* Rioja, 1940a, p. 182.—Martinez, 1940, p. 191.—Penney, 1960, p. 44.

MATERIAL.—Slides of type of *H. baileyi* (BM through N. Gist Gee), numerous specimens of *H. repens* from the United States.

DESCRIPTION.—Sponge, according to previous descriptions, forming thin encrustation; surface slightly uneven and distinctly hispid due to projection of skeleton fibers through dermal membrane, oscula inconspicuous. Skeleton forming a rather irregular network, joined together by a small amount of spongin. Consistency of live sponge soft, texture loose.

Megascleres slender, distinctly fusiform and sharply pointed amphioxea, sparsely microspined except in the vicinity of their tips; length range 255–315 μ, width range 11–10 μ.

Microscleres delicate, fusiform, and sharply pointed amphioxea, slightly curved to almost straight, spined throughout their length;

spines increasing in length towards the central portion of the scleres, where they are perpendicular and large and often end in rounded knobs; length range 75–85 μ, width range 2–3 μ without spines.

Gemmoscleres birotulates of two distinct length groups, in shape only slightly differing from each other; the longer class few in number, with irregularly cylindrical shafts, as a rule entirely straight, bearing conspicuous conical spines in a variable arrangement, and terminally with strongly umbonate rotules, bearing at their margins a number of deeply incised recurved teeth; the smaller class considerably shorter and more abundant, their cylindrical shafts often spined, their rotules similar in shape to those of the longer class; length range of longer class 80–85 μ, of shorter 50–60 μ; diameter of rotules in both about 22 μ.

Gemmules not very abundant in mature sponge, ranging in diameter 450–480 μ, slightly subspherical; pneumatic layer well developed and granular, consisting of minute spherical air spaces; shorter gemmoscleres contained within this layer, longer considerably surpassing it; foramen distinctly tubular, porus tube slender and straight, without terminal cirri.

Distribution.—Widely scattered distribution in eastern parts of the North American Continent, ranging from Louisiana to Canada, also some solitary records from Germany and Poland; the "variety" *H. repens spinulosa* described from Mexico.

Color in life.—Recorded as bright green.

Discussion.—The failure of Bowerbank (1863) to observe the certainly elusive longer class of birotulate gemmoscleres in his *Spongilla baileyi* caused a great number of subsequent authors to ignore this species as a possible member of the genus *Heteromeyenia*, and to place it within the genera *Meyenia* or *Ephydatia*. Potts (1887), in transferring his *Spongilla repens* to *Heteromeyenia*, expressed the opinion that his species could well be found identical with *S. baileyi*. However, subsequent authors did not find it necessary to revise the type of the latter in the British Museum, and thus *H. repens* became a rather well-known species, while the status of *S. baileyi* remained uncertain for more than 60 years.

In his desire to find a better taxonomic arrangement for the rather conglomerate group of spongillids with heterogeneous birotulate gemmoscleres, Schröder (1927b) carried out the first revision of the type material of *S. baileyi* and corrected and augmented Bowerbank's (1863) original description of this species. After establishing the presence of two classes of gemmoscleres in the type, Schröder demonstrated the necessity of considering *S. baileyi* congeneric with *H. repens*, as well as with a number of formerly known separate species, and suggested that all these represent mere races of the nominal

species *H. baileyi*. Even though some of Schröder's "varieties," in particular the *Carterius stepanowii* complex, can no longer be retained as races of *H. baileyi*, *H. repens* most certainly does not possess distinct morphological criteria to justify its specific separation.

Although Old (1932b, p. 449) considered *H. repens* "sufficiently distinct from *H. baileyi* to stand alone," he failed to demonstrate any particular reasons for his opinion. Morphometric comparisons of a wide range of material of *H. repens* with the type slides of *H. baileyi* during the present studies did not reveal any marked differences between the spicular components; the megascleres and the microscleres were indistinguishable. Some slight differences occur in the spininess of both classes of gemmoscleres, which in *H. repens* usually is somewhat subdued, whereas in *H. baileyi* these spines are rather more abundant and larger. However, in a wide range of *H. repens* such apparent characteristics are by no means constant, and gemmoscleres intermediate between those described as typical can be found in both these species discussed.

The futility of retaining *H. repens* as a distinct species has thus become obvious, and the present authors have no hesitation in relegating it to a synonym of *H. baileyi*, which has precedence of many years. Only future detailed studies will be able to decide whether some obvious though immaterial morphometric differences are constant enough to justify a separation of *H. repens* at a subspecific level. A similar arrangement will possibly be found necessary for the classification of *H. repens* var. *spinulosa*, which has not been available for the present study. Although displaying some unusual features, this Mexican spongillid is therefore listed in this paper as a dubious synonym until additional material becomes available.

Heteromeyenia stepanowii (Dybowsky, 1884)

Plate 9, figures 10–14

Dosilia(?) stepanowii Dybowsky, 1884a, p. 507; 1884b, p. 476.

Carterius stepanowii Petr, 1886, p. 93.—Vejdovsky, *in* Potts, 1887, p. 179.—Potts, 1887, p. 262.—Lauterborn, 1902, p. 519.—Weltner, 1895, p. 114; 1909, p. 187.—Wierzejski, 1892, p. 142.—Girod, 1899, p. 113.—Arndt, 1923, p. 77; 1926, p. 344.—Schröder, 1926, p. 240; 1927b, p. 101.

Ephydatia bohemica Petr, 1886, p. 102.—Vejdovsky, *in* Potts, 1887, p. 179.—Weltner, 1895, p. 114.

Carterius bohemicus Girod, 1899, p. 54.

Carterius stepanowii forma *petri* Lauterborn, 1902, p. 519.—Schröder, 1926, p. 243.—Arndt, 1926, p. 344.

Carterius stepanowii forma *palatinus* Lauterborn, 1902, p. 519.—Schröder, 1926, p. 244.—Arndt, 1926, p. 344.

Carterius stepanowii var. *bohemicus* Weltner, 1909, p. 189.—Arndt, 1926, p. 344.

Heteromeyenia kawamurae Annandale and Kawamura, 1916, p. 14.—Annandale, 1918a, p. 200.—Gee and Wu, 1928, p. 40.—Gee, 1931c, p. 41.

Heteromeyenia baileyi var. *arndti* Schröder, 1927a, p. 75; 1927 b, p. 107.—Zimmer, 1936, p. 126.
Heteromeyenia baileyi var. *bohemica* Schröder, 1927b, p. 107.—Arndt, 1928a, p. 78.
Heteromeyenia baileyi var. *palatina* Schröder, 1927b, p. 107.
Heteromeyenia baileyi var. *petri* Schröder, 1927b, p. 107.—Arndt, 1928a, p. 74.—Gee, 1928, p. 225; 1929b, p. 13; 1930e, p. 27; 1931e, p. 46.—Sasaki, 1934, p. 241.—Zimmer, 1936, p. 126.
Heteromeyenia baileyi var. *stepanowi* Schröder, 1927b, p. 107; 1938b, p. 127.—Grimailowskaja, 1928, p. 215.
Meyenia hungarica Traxler, 1888, p. 2.

Material.—Numerous specimens and slides; EUROPE: Czechoslovakia, Germany, Poland, U.S.S.R.; ASIA: China, Japan; AUSTRALIA: New South Wales.

Description.—Sponge forming delicate and shallow cushions on aquatic plants or dead branches; surface usually even but always distinctly hispid due to projection of spicule fibers through dermal membrane. Skeleton forming a rather regular network of long spicule fibers, joined together by a considerable amount of spongin. Consistency of live sponge moderately firm.

Megascleres fusiform and slender, sharply pointed amphioxea, slightly curved to almost straight, sparsely covered with inconspicuous spines except at their extremities; length range 180–310 μ, width range 8–11 μ.

Microscleres delicate, fusiform, and sharply pointed amphioxea, slightly curved, spined throughout their length; spines increasing in length towards the central portion of the scleres, where they are perpendicular and often end in knoblike expansions; length range 78–86 μ, width range 2–3 μ without spines.

Gemmoscleres birotulates of two distinct length groups, usually possessing identical rotules, rarely displaying marked differences in the shape of the rotules in the two groups; shafts of both covered with rather long and conical spines, perpendicular to their axes; rotules of equal diameter, slightly but distinctly umbonate, bearing at their lateral margins a greater number of regular, comparatively small, and strongly recurved teeth; birotulates of both classes occasionally malformed, resulting in a projection of the axis through the rotules, or in an irregular incision of their margin; length range of longer class 75–88 μ, of shorter 58–65 μ; diameter of rotules in both about 18 μ.

Gemmules moderately abundant in mature sponge, ranging in diameter 430–520 μ, spherical; pneumatic layer well developed and granular, consisting of minute spherical air spaces; width of this layer ranging 28–42 μ, so that both classes of gemmoscleres project beyond the outer gemmular membrane; foramen distinctly tubular, tube moderately long and slender, terminally bearing a crownlike rim,

lobelike projections, or an irregular number of filaments of variable length.

Distribution.—Ranging from the type locality in the European U.S.S.R. west to Czechoslovakia and Germany, southeast to China and Japan, recently also recorded from Australia (Racek, MS.); as subfossil remains recorded from Hungary (Traxler) and from sediments in Lago di Monterosi, Italy (Racek, MS.).

Color in life.—Association with zoochlorellae quite frequent, and color usually dark green, ranging to greenish yellow.

Discussion.—The apparent absence of this species in western countries, its rather obscure original description, and the great variability of the terminal foraminal projections of its gemmules have all contributed to the regrettable fact that *H. stepanowii* remained an ill-known species. The many descriptions by subsequent writers of a range of "varieties," all based solely on the structure and shape of the foraminal cirri, have only added to the already existing confusion. Schröder (1927b) has to be commended for his pioneering attempt to find a solution of this problem by comparative studies of the gemmular porus tube in all spongillids with heterogeneous birotulate gemmoscleres. However, in spite of his convincing demonstration of the close relationship of all *Heteromeyenia* species with acanthoxea as free microscleres and his justified abolition of the ill-conceived genus *Carterius* Petr, he too added to the confusion by relegating *H. stepanowii* to mere "varieties" of his rediscovered *H. baileyi*. Although, as shown in the discussion of *H. baileyi*, the morphometric differences between the spicular components of *H. baileyi* and *H. repens* are extremely insignificant, the *H. stepanowii* complex displays a great number of such differences which justify its clear separation from *H. baileyi*.

Schröder's (1927b) revision furthermore failed to do away with the highly unstable additional criterion used by all previous authors for the differentiation of the various species of *Carterius* Petr, i.e., the extent and shape of the distolateral foraminal projections of the gemmules. Petr (1886), in describing variations of this tube in *E. bohemica*, expressed his views as to the possibility of this species being identical with *H. stepanowii*, and the shape and number of the foraminal projections in *Carterius stepanowii* formae *arndti*, *palatinus*, and *petri* are so similar that this criterion cannot possibly be retained for their separation, even on a subspecific level. Recent studies of *H. stepanowii*, found isolated in Australia (Racek, MS.), revealed the great variability of foraminal projections under different growth conditions and made it obvious that this criterion alone is fully unsuitable for racial discrimination within that species.

Heteromeyenia latitenta (Potts, 1881)

Carterella latitenta Potts, 1881b, p. 176; 1882a, p. 12.—Carter, 1882, p. 370.
Carterius latitentus Petr, 1886, p. 92.—Wurtz, 1950, p. 7.—Penney, 1960, p. 33.
Carterius latitenta Mills, 1887, p. 162.—Potts, 1887, p. 246.—Kellicott, 1891, p. 104.—Weltner, 1895, p. 114.—Kirsch, 1909, p. 38.—Smith, 1921, p. 17.—Schröder, 1927b, p. 101.
Heteromeyenia latitenta Schröder, 1927b, p. 107.—Gee, 1931e, p. 41; 1932c, p. 33.

Material.—Slides of specimen from Pennsylvania (N. Gist Gee).

Description.—Sponge, according to original descriptions, forming shallow cushions on rocks in rapidly running water; surface even but distinctly hispid, oscula inconspicuous. Skeleton forming an irregular network of spicule fibers, joined together by a small amount of spongin. Consistency of live sponge, soft, texture loose.

Megascleres smooth to sparsely microspined fusifrom amphioxea, slender and sharply pointed; length range 265–285 μ, width range 8–11 μ.

Microscleres slender amphioxea, entirely spined, spines only slightly larger in central portion of sclere; length range 85–100 μ, width range 2–3 μ.

Gemmoscleres birotulates of two length groups, usually possessing identical rotules, rarely displaying marked differences in the shape of the rotules in the two groups; shafts of both stout, armed with numerous long and pointed spines; rotules of equal diameter, slightly but distinctly umbonate, at their lateral margins deeply cleft into a number of recurved teeth; length range of longer class 60–78 μ, of shorter 50–55 μ; diameter of rotules in both about 16–18 μ.

Gemmules numerous in mature sponge, ranging in diameter 410–480 μ, spherical; pneumatic layer well developed and granular, consisting of minute subspherical air spaces; shorter gemmoscleres contained within this layer, the few longer projecting beyond outer gemmular membrane; foramen distinctly tubular, porus tube slender and long, bearing one to two very long cirrous projections, arising from a flat disk, flat and ribbon-like at their base and cylindrical in distal parts.

Distribution.—Found only in northeastern parts of the United States.

Color in life.—Recorded as green.

Discussion.—In view of the only slightly differing lengths of the two classes of birotulate gemmoscleres, Annandale (1909d) suggested the inclusion of this species in the genus *Ephydatia*, together with *H. tentasperma*. However, subsequent studies have clearly revealed the heterogenous character of the gemmoscleres in both these species, which together with the presence of typical microscleres make their retention within the genus *Heteromeyenia* necessary. Even omitting the

typical structure of the cirrous foraminal appendages on the gemmules of *H. latitenta*, the gemmoscleres too are sufficiently different from those of any of its congeners to warrant the separate specific status of this species.

Heteromeyenia tentasperma (Potts, 1880)

PLATE 9, FIGURES 8, 9, 18

Spongilla tentasperma Potts, 1880a, p. 331.
Spongilla tenosperma Potts, 1880b, p. 356.
Carterella tenosperma Potts, 1881a, p. 149.
Carterius tenosperma Potts, 1887, p. 245.—Kellicott, 1891, p. 104.—Weltner, 1895, p. 114.—Kirsch, 1909, p. 38.—Smith, 1921, p. 17.—Old, 1936b, p. 11.—Jewell, 1939, p. 11.
Heteromeyenia tenosperma Schröder, 1927b, p. 108.—Gee, 1931e, p. 51; 1932c, p. 34.
Carterius tentaspermus Wurtz, 1950, p. 6.—Penney, 1960, p. 34.
Carterius tentasperma Jewell, 1952, p. 452.

MATERIAL.—Slides of specimen from Wisconsin (N. Gist Gee).

DESCRIPTION.—Sponge, according to original descriptions, forming irregular masses on aquatic plants or shallow cushions on rocks; surface comparatively even but hispid, oscula inconspicuous. Skeleton forming an irregular network of spicule fibers, joined together by a small amount of spongin. Consistency of live sponge not reliably recorded.

Megascleres sparsely microspined fusiform amphioxea, very slender and sharply pointed; length range 260–280 μ, width range 7–10 μ.

Microscleres more or less uniformly spined slender amphioxea; length range 75–80 μ width range 2–3 μ.

Gemmoscleres of two length groups, usually possessing identical rotules; shafts of both stout and cylindrical, armed with a smaller number of acute spines; rotules represented by a burlike arrangement of lateral spines, often penetrated by a prolongation of the shaft; length range of longer class 65–72 μ of shorter 50–55 μ; diameter of rotules 15–18 μ.

Gemmules numerous in mature sponge, ranging in diameter 420–450 μ, spherical; pneumatic layer well developed, consisting of minute subspherical air spaces; shorter gemmoscleres entirely contained within this layer, the few longer often projecting slightly beyond outer gemmular membrane; foramen distinctly tubular, porus tube comparatively short and conical, bearing three to six irregular and long cirrous projections.

DISTRIBUTION.—Found only in northeastern parts of the United States.

COLOR IN LIFE.—Recorded as yellowish green.

DISCUSSION.—This species, although listed by the majority of authors as *Carterius tenospermus* or *Heteromeyenia tenosperma*, was

originally described by Potts (1880a) under the name of *Spongilla tentasperma*. Although a few pages later Potts redescribed the same species under the name of *S. tenosperma* and thus aided the retention of this specific name by most subsequent authors, *S. tentasperma* certainly has page priority and therefore represents the correct specific name of the spongillid discussed.

The spicules of *H. tentasperma* closely resemble those of *H. latitenta* in general structure, but the peculiar burlike "rotules" together with the entirely different shape, length, and armature of the gemmular porous tube in the former species are sufficient criteria to separate it readily from the latter. However, additional material and data are desirable in order to assess possible evironmental factors leading to the often freak condition of the gemmoscleres in *H. tentasperma*, which could well point to a greater relationship to *H. latitenta* than hitherto demonstrated.

Heteromeyenia tubisperma (Potts, 1881)

PLATE 9, FIGURES 5–7, 17

Carterella tubisperma Potts, 1881a, p. 150.—Mills, 1882, p. 57.
Carterius tubisperma Mills, 1887, p. 162.—Potts, 1887, p. 263.—Kellicott, 1891, p. 103.—Weltner, 1895, p. 114.—Kirsch, 1909, p. 37.—Smith, 1921, p. 17.—Old, 1932b, p. 471; 1936b, p. 11.—Arndt, 1926, p. 344.—De Laubenfels, 1932, p. 111.—Eshleman, 1950, p. 44.
Heteromeyenia tubisperma Schröder, 1927b, p. 108.—Gee, 1931e, p. 51; 1932c, p. 25; 1937, p. 285.
Carterius tubispermus Wurtz, 1950, p. 7.—Penney, 1960, p. 34.

MATERIAL.—Slides of specimen from Canada (N. Gist Gee).

DESCRIPTION.—Sponge, according to previous descriptions, forming irregularly massive encrustations on solid objects; surface uneven to slightly papillose, oscula inconspicuous. Skeleton forming an irregular network of spicule fibers, amount of spongin apparently not yet recorded. Consistency of live sponge soft, texture loose.

Megascleres sparsely microspined fusiform amphioxea, slender and sharply pointed; length range 190–230 μ, width range 7–10 μ.

Microscleres slender and rather long amphioxea, entirely spined, spines in central portion of sclere distinctly larger; length range 85–90 μ, width range 2–3 μ.

Gemmoscleres birotulates of two length groups, usually possessing identical rotules in both classes; shafts of both cylindrical and stout, armed with few acute spines, occasionally entirely smooth; rotules of equal diameter, markedly umbonate, at their lateral margins with numerous deeply cleft and distinctly recurved teeth; length range of longer class 60–70 μ, of shorter 40–48 μ; diameter of rotules 18–19 μ.

Gemmules numerous in mature sponge, ranging in diameter 500–550 μ, spherical; pneumatic layer well developed, consisting of minute

subspherical air spaces; shorter gemmoscleres entirely contained in this layer, longer set protruding through outer gemmular membrane; foramen distinctly tubular, porus tube slender and very long, ranging from 0.5 to 0.9 diameter of gemmule, slightly enlarged at its distal margin, and bearing five to six long cylindrical cirrous appendages.

Distribution.—Apparently restricted to the eastern half of the North American Continent, ranging from Louisiana to Canada; record from Italy (Garbini, 1897) based on the presence of one spicule, probably a result of wrong identification.

Color in life.—Recorded as ranging from brown to green.

Discussion.—This species can be distinguished from other congeners at a glance by the unusually long porus tube, as well as by the characteristics of the gemmoscleres. Furthermore, its comparatively massive mode of growth, an unusual feature of the genus *Heteromeyenia* as here restricted, should represent a most valuable factor in its identification in the field.

Although Mills (1880) was first to give a detailed description of this spongillid, he failed to give it a name; consequently Potts (1881a) redescribed it under the name of *Carterella tubisperma*. In spite of the fact that Mills was thus considered the original author of this specific name, *H. tubisperma* must be correctly associated with Potts and not with Mills.

Genus *Anheteromeyenia* Schröder, 1927

Heteromeyenia (*Anheteromeyenia*) Schröder, 1927b, p. 108.—Gee, 1931e, p. 32.
Anheteromeyenia de Laubenfels, 1936, p. 36.
Heteromeyenia Potts, 1881a, p. 150 (part); 1887, p. 236 (part.)—Eshleman, 1950, p. 41 (part).—Jewell, 1952, p. 455 (part).—Penney, 1960, p. 40 (part).

Type species.—By present selection *Spongilla argyrosperma* Potts, 1880.

Definition.—Megascleres usually stout amphioxea, only occasionally amphistrongyla, as a rule conspicuously to coarsely spined.

Microscleres absent.

Gemmoscleres birotulates of two distinct series, each differing from the other in length, as well as often also in shape; the shafts of both series usually bearing a number of strong conical spines; rotules of the longer class relatively small, consisting of a number of strongly recurved hooks, or irregularly shaped; rotules of shorter class flat to slightly dome-shaped, typically with a larger number of marginal teeth.

Gemmules moderately large to large, subspherical to spherical, scattered throughout skeletal meshwork; pneumatic layer well developed and typically thick, granular, consisting of minute subspherical air spaces; gemmoscleres embedded in this layer strictly

radially, the outer rotules of the smaller series not quite extending to the outer gemmular membrane, those of the longer series often considerably surpassing it; foramen slightly elevated or distinctly tubular; if porus tube present, its distolateral margins always without cirri.

Sponges forming flat to massive encrustations, with surfaces ranging from smooth to irregularly lobose; association with zoochlorellae frequent, and consequently coloration often a light green. Consistency ranging from soft to moderately firm.

Scattered but apparently widespread distribution in eastern parts of the North American Continent, some species also recorded from Ireland.

Discussion.—The subgenus *Anheteromeyenia,* erected by Schröder (1927b) for the inclusion of those species of *Heteromeyenia* which lack free microscleres, was elevated by de Laubenfels (1936) to full generic rank. The failure of both these authors to designate a generic type species has led to the consideration of *S. argyrosperma* Potts as the type species of *Heteromeyenia* sensu lato by Jewell (1952). However, Jewell did not actually designate the type species mentioned but merely stated in dealing with the genus *Heteromeyenia:* "No type species was designated, but as *H. argyrosperma* was first to be mentioned and first described it has usually been regarded as the genotype" (p. 451). Since *S. argyrosperma* Potts lacks free microscleres, and therefore cannot possibly be considered as the type species of *Heteromeyenia* as here restricted, it is herewith designated as the type species of *Anheteromeyenia,* while *H. repens* Potts (now a synonym of *H. bayleyi* (Bowerbank)) must be considered to represent the type species of *Heteromeyenia* sensu stricto.

The very few species comprising the genus *Anheteromeyenia* can be separated into two morphologically distinct groups. In one, represented by *A. argyrosperma,* the gemmules possess a distinct porus tube and their two length series of gemmoscleres are quite similar in shape. The other is represented by the extremely variable *A. ryderi* with some of its "varieties," by *A. pictovensis,* and by the still somewhat dubious and probably malformed species *A. conigera* and *A. biceps.* In this group the gemmoscleres are distinctly heterogeneous in length as well as in shape, and the micropyle of the gemmules is devoid of a distinct porus tube and only slightly elevated. While the present studies revealed no significant morphometric differences between the nominal species of *A. ryderi* and those of its former "varieties" *A. r. baleni* and *A. r. walshii,* the different structure of the spicular components of *A. pictovensis* makes it plausible to consider this spongillid a distinct species. The apparently characteristic gemmoscleres of *A. conigera* agree morphometrically with those usually found in *A. ryderi,* excepting those conical "swellings" around the rotules of the shorter

class; and *A. biceps*, although at present not readily comparable with any congener, is better to be considered a dubious species until additional material becomes available.

Anheteromeyenia argyrosperma (Potts, 1880)

PLATE 10, FIGURES 8–10

Spongilla argyrosperma Potts, 1880b, p. 357.

Heteromeyenia argyrosperma Potts, 1881a, p. 150; 1884b, p. 216; 1887, p. 239.—MacKay, 1885, p. 233; 1889, p. 93.—Weltner, 1895, p. 114.—Smith, 1921, p. 17.—Gee, 1931e, p. 32; 1937, p. 285.—Old, 1932c, p. 239; 1936b, p. 11.—Jewell, 1939, p. 20; 1952, p. 452.—Eshleman, 1950, p. 42.—Penney, 1956, p. 43; 1960, p. 40.

Heteromeyenia (*Anheteromeyenia*) *argyrosperma* Schröder, 1927b, p. 108.

Heteromeyenia argyrosperma var. *tenuis* Potts, 1887, p. 240.—Gee, 1931e, p. 51; 1932c, p. 32.—Penney, 1960, p. 41.

Heteromeyenia (*Anheteromeyenia*) *argyrosperma* var. *tenuis* Schröder, 1927b, p. 108.

MATERIAL.—Numerous specimens from the United States and Canada.

DESCRIPTION.—Sponge, according to previous descriptions, forming small to minute cushions on solid objects; surface slightly hispid but otherwise even, oscula inconspicuous. Skeleton forming an irregular network, joined together by a small amount of spongin. Consistency of live sponge soft, texture loose.

Megascleres slender, subfusiform to cylindrical, abruptly pointed amphioxea, sparsely covered with small but sharply pointed spines; length range 240–280 μ, width range 13–17 μ.

Microscleres absent.

Gemmoscleres birotulates of two distinct length groups, in shape only slightly differing from each other; the longer class with rather robust and irregularly cylindrical shafts, often bent, and bearing occasional recurved spines, and terminally with a smaller number of strongly recurved, clawlike hooks; the smaller class considerably shorter, their cylindrical shafts abundantly spined, their terminal rotules, consisting of strongly recurved hooks, somewhat flatter than in the longer series; length range of longer class 110–125 μ, width range 7–10 μ; length range of smaller class 65–80 μ, width range 6–8 μ.

Gemmules abundant in mature sponge, ranging in diameter 400–450 μ; pneumatic layer well developed and granular, consisting of minute subspherical air spaces; gemmoscleres embedded in this layer strictly radially, the shorter series not reaching to outer gemmular membrane, the longer considerably surpassing it; foramen distinctly tubular, porus tube slender and decreasing in width towards its apex; marginal cirri absent.

DISTRIBUTION.—Apparently restricted to the eastern half of the North American Continent, ranging from Florida to Canada.

COLOR IN LIFE.—Recorded as gray.

DISCUSSION.—*A. argyrosperma* can be easily separated from other congeners by its only slightly pronounced difference in the shape of both classes of gemmoscleres. However, as in all other species of this genus, the spicular components are often malformed due to varying chemical properties of the environment, and the retention of a separate status for Potts' "variety" *A. a. tenuis* seems fully unwarranted.

Anheteromeyenia ryderi (Potts, 1882)

PLATE 10, FIGURES 1–4

Heteromeyenia ryderi Potts, 1882a, p. 13; 1884b, p. 216; 1887, p. 242.—Mills, 1884, p. 146.—MacKay, 1885, p. 233; 1889, p. 87.—Kellicott, 1891, p. 103.—Hanitsch, 1895b, p. 511.—Weltner, 1895, p. 114.—Stephens, 1912, p. 9; 1920, p. 237.—Smith, 1921, p. 17.—Arndt, 1926, p. 344; 1928b, p. 156.—Gee, 1931e, p. 48; 1932c, p. 34; 1937, p. 285.—Old, 1932b, p. 450; 1936b, p. 11.—Jewell, 1939, p. 20.—Eshleman, 1950, p. 41.—Penney, 1954, p. 156; 1956, p. 38; 1960, p. 44.

Heteromeyenia (*Anheteromeyenia*) *ryderi* Schröder, 1927b, p. 108.

Heteromeyenia ryderi var. *baleni* Potts, 1887, p. 247.—Stephens, 1920, p. 242.—Smith, 1921, p. 17.—Arndt, 1926, p. 344; 1928b, p. 164.—Gee, 1931e, p. 33; 1931c, p. 34.—Penney, 1931, p. 242; 1956, p. 36; 1960, p. 44.

Heteromeyenia ryderi var. *walshii* Potts, 1887, p. 246.—Schröder, 1927b, p. 108.—Gee, 1931e, p. 52; 1932c, p. 34.—Penney, 1960, p. 45.

Heteromeyenia macouni MacKay, 1900, p. 319.—Gee, 1931e, p. 42.

?Heteromeyenia conigera Old, 1931, p. 298.—Gee, 1932c, p. 33.—Penney, 1960, p. 43.

MATERIAL.—Numerous specimens from the United States (Louisiana to Maine) and Canada.

DESCRIPTION.—Sponge, according to original descriptions, forming massive, often hemispherical cushions on solid objects; surface irregular to lobose, oscula conspicuous and numerous. Skeleton forming an irregular network joined together by a small amount of spongin. Consistency of live sponge comparatively soft, texture loose.

Megascleres variable in shape and armature, as a rule somewhat short and fusiform amphioxea, covered with broadly conical spines except at the extremities; length range 190–220 μ, width range 13–19 μ.

Microscleres absent.

Gemmoscleres birotulates of two distinct classes, both in regard to length and shape; the longer class with rather robust and irregularly cylindrical shafts, bearing a number of recurved spines, and terminally with a smaller number of rather short and strongly recurved hooks; the smaller class considerably shorter, their cylindrical shafts with one or few spines, and terminally with flat to slightly umbonate rotules

of equal size, with a large number of small crenulate teeth on their slightly recurved margin; length range of longer class 50–75 μ, width range 6–8 μ; length range of smaller class 30–40 μ, width range of shaft 3–4 μ, of rotule 25–27 μ.

Gemmules abundant in mature sponge, ranging in diameter 320–350 μ; pneumatic layer well developed and granular, consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, their longer class protruding from the outer gemmular membrane; foramen more or less simple without a discernible porus tube, but present on a conical elevation.

Distribution.—Apparently restricted to the eastern half of the North American Continent, ranging from Louisiana to Canada.

Color in life.—Recorded as light green.

Discussion.—The great variability of spicular components of the gemmular armature, a well-known phenomenon in most spongillids with heterospecific gemmoscleres, is perhaps more pronounced in *A. ryderi* than in other species of this complex. The gemmoscleres of *A. ryderi* are hardly identical in any two specimens of the same locality and tend to be greatly different in distant populations. Malformations of gemmoscleres are quite frequent (see pl. 10, fig. 2) and the longer as well as the shorter class are thus affected. The "varieties" *baleni* and *walshii* of this species certainly fall into the usual morphometric range of the nominal species, and the retention of these two slightly aberrant sponges as distinct races seems unjustified. The species *H. macouni* MacKay (1900), not present in the material available for this study, was relegated by Gee (1931e) to a synonym of *H. baleni*, so that it too must now be considered to fall clearly within the morphometric range of *A. ryderi*, as here revised.

As mentioned in the generic discussion, *H. conigera* Old (1931) most probably is nothing more than a malformed specimen of *A. ryderi*. An examination of the holotype of the former clearly demonstrated that the megascleres are fully comparable with those of any range of the latter species, and that the longer gemmoscleres are almost inseparable from those of *A. ryderi* in shape as well as in measurements (see pl. 10, figs. 13–15). Omitting the characteristic cone like swellings under the rotules of the smaller class of gemmoscleres, even the general shape of their rotules is similar in both species. Considering the frequence of malformed birotulate gemmoscleres in nearly all genera displaying them, it appears very likely that these particular "swellings" in *H. conigera* are the result of a freak deposit of silica due to some adverse environmental factors. This assumption appears strengthened by the great variability displayed by the shorter class of gemmoscleres in *H. conigera*, and that this species apparently has been found only once.

Anheteromeyenia pictovensis (Potts, 1885)

PLATE 10, FIGURES 5–7

Heteromeyenia pictovensis Potts, 1885a, p. 28; 1886, p. 228.—MacKay, 1885, p. 233; 1886, p. 21; 1889, p. 87.
Heteromeyenia ryderi var. *pictovensis* Potts, 1887, p. 244.—Arndt, 1928b, p. 164.—Gee, 1931e, p. 46; 1932c, p. 34.
Heteromeyenia ryderi forma *pictovensis* Stephens, 1920, p. 241.—Arndt, 1926, p. 344.
Heteromeyenia pictouensis Smith, 1921, p. 17.
Heteromeyenia ryderi pictovensis Smith, 1930, p. 184.
Anheteromeyenia ryderi var. *pictovensis* Schröder, 1927b, p. 108.
Heteromeyenia ryderi var. *pictouensis* Penney, 1960, p. 45.

MATERIAL.—A small number of specimens from Canada (N. Gist Gee) and the New England States (Penney).

DESCRIPTION.—Sponge, according to previous descriptions, forming massive crusts on solid objects; surface smooth to slightly irregular, oscula conspicuous and numerous. Skeleton forming an irregular network joined together by a considerable amount of spongin. Consistency of live sponge recorded as comparatively firm, texture compact.

Megascleres cylindrical, comparatively short and robust amphistrongyla, sometimes amphioxea with rounded or abruptly pointed tips, superficially resembling amphistrongyla; they are covered with strong spines throughout their length, which are straight and conical in the central portion of the sclere, and gradually curving towards its tips near the extremities; length range 165–210 μ, width range 17–23 μ.

Microscleres absent.

Gemmoscleres birotulates of similar differences in length and shape as in *A. ryderi*, but with either smooth or only sparsely spined shafts; length range of longer class 52–75 μ, width of shaft 6–8 μ; length range of smaller class 30–40 μ, width range of shaft 3–4 μ, of rotule 25–28 μ.

Gemmules not very abundant in mature sponge, ranging in diameter 350–380 μ, spherical; pneumatic layer well developed and granular, consisting of minute spherical air spaces; gemmoscleres embedded in this layer strictly radially, their longer class conspicuously protruding from the outer gemmular membrane; foramen more or less simple, not forming a distinct porus tube, only slightly elevated.

DISTRIBUTION.—Apparently restricted to eastern Canada, ranging south to about New York.

COLOR IN LIFE.—Recorded as light green.

DISCUSSION.—Although the shape of the gemmular spicular components demonstrates a close affinity to *A. ryderi*, the existing morphological differences, particularly the entirely different structure of

the megascleres, seem important enough to consider *A. pictovensis* a distinct and separable "form." Its specific status, erected by Potts (1885a, 1886) and MacKay (1885, 1886, 1889), is herewith restored.

***Anheteromeyenia biceps* (Lindenschmidt, 1950)**

PLATE 10, FIGURES 11, 12

Heteromeyenia biceps Lindenschmidt, 1950, p. 214.—Penney, 1960, p. 43.

MATERIAL.—Type specimen (USNM).

DESCRIPTION.—Sponge, according to Lindenschmidt (1950), forming shallow cushions of small dimensions; surface comparatively even, oscula small. Skeleton forming an irregular network, joined together by small amounts of spongin. Consistency of live sponge recorded as rather firm, texture compact.

Megascleres subfusiform to cylindrical amphioxea, ranging from smooth to microspined, their tips always entirely smooth; length range 260–310 μ, width range 15–17 μ.

Microscleres absent.

Gemmoscleres birotulates of two distinct classes, both in regard to length and shape; the longer class with stout cylindrical shafts, usually microspined, and terminally with a bulbous swelling bearing a dense arrangement of coarse and rather blunt spines; the smaller class with extremely slender shafts slightly longer than the diameter of the rotules, and occasionally protrude beyond them; and terminally with flat rotules consisting of a smaller number of long rays, the latter often subdivided; length range of longer class 30–42 μ, width of shaft 4–5 μ; length range of shorter class 23–26 μ, width of shaft 2 μ, of rotule 20–22 μ.

Gemmules abundant in basal parts of mature sponge, spherical, ranging in diameter 350–380 μ; pneumatic layer well developed but not very high, consisting of minute subspherical air spaces; gemmoscleres embedded in this layer radially, the longer class often inserted at a slanting angle; foramen more or less simple, without discernible tube, only slightly elevated.

DISTRIBUTION.—Found only in the type locality, the inlet and outlet of Douglas Lake, Michigan, U.S.A.

COLOR IN LIFE.—Recorded as ranging from yellow to green.

DISCUSSION.—The intrageneric relationship of this spongillid, known from only one locality, is at present difficult to assess. Because of the heterogeneous structure of its gemmoscleres and the absence of microscleres, the authors have little hesitation in placing this species in the genus *Anheteromeyenia;* its affinities to the other known congeners have yet to be demonstrated.

The extremely fragile shafts and irregularly incised rotules of the shorter set of gemmoscleres, the unusual form of the longer set, and

the complete absence of their terminal rotules point to malformations of the spicular components of the gemmular armature due to unknown factors. Whether these malformations are the result of hybridization or caused by adverse chemical properties of the environment is a problem which can be solved only by future detailed studies of additional material. Until then it appears advisable to retain the separate specific status of *A. biceps* so that possible taxonomic evidence will not be obscured.

Umborotula, new genus

Ephydatia Weber, 1890, p. 33 (part).—Weltner, 1895, p. 114 (part).—Evans, 1901, p. 71.—Annandale, 1911, p. 54 (part); 1918a, p. 201 (part).—Gee and Wu, 1925b, p. 393 (part).—Vorstman, 1927, p. 184 (part).—Gee, 1926c, p. 110 (part); 1927a, p. 1 (part); 1927b, p. 61 (part); 1928, p. 225 (part); 1929d, p. 297 (part); 1930a, p. 84 (part); 1930b, p. 170 (part); 1931e, p. 34; 1932a, p. 449 (part).—Arndt, 1932c, p. 564 (part).—Suvatti, 1950, p. 3 (part).

Meyenia Penney, 1960, p. 46 (part).

Type species.—By monotypy *Ephydatia bogorensis* Weber, 1890.

Definition.—Megascleres long and slender amphioxea, usually covered with a small number of minute and inconspicuous conical spines, rarely entirely smooth.

Microscleres absent.

Gemmoscleres birotulates of equal length, with rather long shafts covered with large conical spines, and at either end with conspicuously umbonate rotules of equal size and shape; margin of rotules slightly recurved, bearing a large number of small and regular indentations.

Gemmules rather scarce, large and spherical; pneumatic coat well developed, granular, consisting of minute and regular air spaces; gemmoscleres embedded in this layer strictly radially, their basal rotules almost touching each other; foramen distinctly tubular, tube delicate and in length only slightly surpassing width of pneumatic layer.

Sponges forming delicate cushions of small size on aquatic plants; coloration usually vivid green, owing to the presence of zoochlorellae. Consistency soft and fragile.

Apparently restricted to Southeast Asia.

Discussion.—As a result of Pott's (1887) erection of *Heteromeyenia*, a certainly meaningless genus formerly including all spongillid species with heterogeneous birotulate gemmoscleres, the only species of *Umborotula* was left by all previous authors in the genus *Ephydatia* (=*Meyenia*) for the simple reason that its gemmoscleres are homogeneous. It is quite obvious that such an arrangement cannot be retained in modern spongillid taxonomy, since *E. bogorensis* Weber differs

from all species of *Ephydatia*, as here redefined, to such an extent that it cannot possibly be considered congeneric. On the other hand, although displaying close affinities to most species of *Heteromeyenia*, and particularly to *Dosilia*, the presence of homogeneous gemmoscleres and the absence of asters from the latter genus would eliminate it from belonging to the former. In order to demonstrate the conspicuous differences of this SE Asian and Australian species from all other spongillid genera, the erection of a new genus became inevitable. Although the writer intended to use this genus in his forthcoming revision of all Australian Spongillidae, the scope of the present work made it imperative to introduce it at this stage.

***Umborotula bogorensis* (Weber, 1890)**

PLATE 11, FIGURES 1, 18, 19

Ephydatia bogorensis Weber, 1890, p. 33.—Weltner, 1895, p. 114.—Annandale 1911c, p. 54; 1918a, p. 201.—Gee and Wu, 1925b, p. 393.—Vorstman, 1927, p. 184.—Gee, 1926c, p. 110; 1927a, p. 1; 1927b, p. 61; 1928, p. 225; 1929d, p. 297; 1930a, p. 84; 1930b, p. 170; 1930e, p. 27; 1931e, p. 34; 1932a, p. 449; 1932c, p. 28.—Arndt, 1932c, p. 564.

Ephydatia blembingia Evans, 1901, p. 71.—Annandale, 1907a, p. 269; 1911c, p. 54; 1918a, p. 207.—Gee, 1930a, p. 90.

Ephydatia bogorensis var. *blembingia* Gee, 1931e, p. 34; 1932a, p. 449; 1932g, p. 308; 1932c, p. 28.—Suvatti, 1950, p. 3.

Meyenia bogorensis Penney, 1960, p. 46.

Meyenia bogorensis var. *blembingia* Penney, 1960, p. 46.

MATERIAL.—Slides of types of *E. bogorensis* (AmstM) and *E. blembingia* (BM), and specimens of *U. bogorensis* from Soochow, China, and Java.

DESCRIPTION.—Sponge forming circular or irregular crusts or nodules of minute size on aquatic plants; surface slightly hispid due to projection of spicule fibers through dermal membrane; oscula small and inconspicuous. Skeleton consisting of an open meshwork formed of spicule fibers bound together by only small amounts of spongin. Consistency of live sponge very soft and fragile.

Megascleres feebly curved and slender amphioxea, which are fusiform and covered, with the exception of their tips, with very minute conical spines; length range 240–370 μ, width range 13–16 μ.

Microscleres absent.

Gemmoscleres, when fully developed, birotulates with comparatively long and spiny shafts, and with equal umbonate rotules whose margins are distinctly recurved and regularly incised; length range 60–78 μ, width range of shafts 3–4 μ, diameter of rotules 22–27 μ.

Gemmules very scarce and scattered throughout meshwork of sponge, spherical, ranging in diameter 450–600 μ; pneumatic coat well developed, consisting of very minute air spaces, and granular;

gemmoscleres embedded in this coat radially, their basal rotules almost touching each other, and their distal rotules projecting beyond outer surface of pneumatic layer; foramen produced into a short, somewhat conical porus tube.

Distribution.—Formerly known only from Malaysia, Indonesia, Thailand, and China; also occurring in Australia (Racek, MS.).

Color in life.—Light brown (Gee) to dark green.

Discussion.—After a detailed comparative study of *E. bogorensis* and *E. blembingia*, Gee (1930a) found the existing differences between these two formerly separated species so small that he encountered difficulties in expressing them; he had no hesitation in relegating the latter to a varietal form of the former. The reexamination of the type material of both species during the present study revealed clearly that their separation, even on a subspecific level, is fully unwarranted. It is obvious that Evans (1901) was unaware of the description of *E. bogorensis* by Weber (1890), or he would have compared his newly erected species with Weber's sponge as well as with *Dosilia plumosa*.

U. bogorensis is closely related to a number of species belonging to other genera, and in particular to *Heteromeyenia* species (megascleres, gemmoscleres, structure of gemmules, coloration, and minute form of sponge) and *Dosilia* (megascleres and gemmoscleres). However, it differs from species of both these genera in the complete absence of free microscleres, and from *Anheteromeyenia* species in a number of decisive criteria.

Genus *Corvomeyenia* Weltner, 1913

Meyenia Mills, 1884, p. 146 (part).—Potts, 1884b, p. 216 (part); 1887, p. 230 (part).—MacKay, 1889, p. 92.—Kellicott, 1891, p. 103 (part).—Kirsch 1909, p. 37 (part).—Jewell, 1952, p. 453 (part).—Weltner, 1895, p. 122 (part); 1913, p. 480.

Ephydatia Smith, 1921, p. 17 (part).—Gee, 1931e, p. 37 (part); 1932c, p. 27 (part).—Jewell, 1939, p. 16 (part).

Corvomeyenia Weltner, 1913, p. 480.—Gee, 1931e, p. 36; 1932c, p. 27.—De Laubenfels, 1936, p. 36.—Jewell, 1952, p. 453.—Penney, 1960, p. 35.

Parameyenia Jewell, 1952, p. 455.

Type species.—*Meyenia everetti* Mills, 1884.

Definition.—Megascleres slender and fusiform amphioxea, entirely smooth.

Microscleres always present in dermal membrane and symplasm; they are microbirotulates with straight to strongly curved slender shafts, and terminally with a small number of recurved hooks of moderate length.

Gemmoscleres birotulates of two length groups, both with slender and smooth shafts and terminally with a smaller number of recurved

teeth, representing distinctly umbonate rotules; size differences of the two classes either negligible or very distinct.

Gemmules rather scarce, large and spherical; pneumatic coat well developed, consisting of minute air spaces, often somewhat granular; gemmoscleres embedded within this layer radially, the longer class protruding from the outer gemmular membrane.

Sponges forming extremely delicate and small encrustations on aquatic plants. Coloration always vivid green, owing to the presence of zoochlorellae. Consistency very soft and fragile.

Discussion.—The genus *Corvomeyenia* was loosely introduced by Weltner (1913) to include those freshwater sponges which, in addition to their birotulate gemmoscleres, possess minute birotulate microscleres in both their symplasm and dermal membrane. Apart from the species *Meyenia everetti* Mills, designated by Jewell (1952), two additional sponges of highly dubious identity, *Spongilla novae-terrae* Potts and *Spongilla discoides* Penney, were also included in this genus. However, the present investigations revealed beyond doubt that their retention in this genus is fully unwarranted.

The dubious identity of *S. novae-terrae* is best demonstrated by the difficulty of authors to document its generic position, since this "species" has alternatively been listed as belonging to *Spongilla* and *Ephydatia* (=*Meyenia*), as well as to *Corvomeyenia* and *Corvospongilla*. The reexamination of its type slides made it quite clear that it cannot be considered a distinct species, but that it represents a hybrid of *C. everetti* and a species of another not clearly recognizable genus, possibly *Eunapius* or *Spongilla*. The presence of unmistakably typical microbirotulates of *C. everetti* in the spicular mixture of *S. novae-terrae* and the grossly malformed gemmoscleres are proof of a sexual hybridization between the former species and that of some other genus, rather than a mere ecomorphic variation of the latter.

The inclusion of *S. discoides* Penney in the present genus has been aided by the incorrectness of its original description and by the presence of distinct microbirotulates. Jewell (1952), using Penney's original description, found the apparent presence of two classes of "flesh spicules" important enough to erect a new genus, *Parameyenia*. Penney (1957), while correcting his earlier mistake in recording abnormal disklike gemmules of this species, placed it into *Corvomeyenia* in spite of the absence of gemmules in the only specimen found. The reexamination of the type of *S. discoides* (USNM no. 22194) during the present studies made it clear that this species contains some, probably adventitious, microbirotulates of *C. everetti* or a closely allied species, but that the remainder of its spicular components are those of *Anheteromeyenia ryderi*, claimed by Penney (1933) to occur in the type locality of *S. discoides*. The two types of "flesh spicules"

described and figured by Penney (1933) and used by Jewell (1952) for the erection of *Parameyenia* are the two types of typical gemmoscleres in any range of *A. ryderi*, and the megascleres obviously also belong to that species. Consequently, the genus *Parameyenia* must now be considered a nomen nudum and *S. discoides* relegated to a synonym of *A. ryderi*.

While the identity of *S. novae-terrae* and *S. discoides* can now be considered as resolved, some additional taxonomic problems have yet to be cleared up. In the material available for this study, specimens are represented which certainly belong to this genus, but which seem specifically or at least subspecifically distinct from *C. everetti*. These specimens are here disregarded, since they will be dealt with in a forthcoming paper by F. Harrison (pers. comm.).

***Corvomeyenia everetti* (Mills, 1884)**

Meyenia everetti Mills, 1884, p. 146.—Potts, 1884b, p. 216; 1887, p. 230.—MacKay, 1889, p. 92.—Kellicott, 1891, p. 103.—Kirsch, 1909, p. 37.—Jewell, 1952, p. 453.

Ephydatia everetti Weltner, 1895, p. 122; 1913, p. 480.—Smith, 1921, p. 17.—Jewell, 1939, p. 163.

Corvomeyenia everetti Weltner, 1913, p. 480.—Gee, 1931e, p. 37; 1932c, p. 27.—Jewell, 1952, p. 453.—Penney, 1960, p. 35.

Materials.—Specimens and slides from various localities in the eastern U.S.A. (Jewell, N. Gist Gee).

Description.—Sponge always extremely delicate, forming very small encrustations on aquatic plants; surface with noticeable projections, but distinctly hispid; oscula extremely inconspicuous, dermal membrane well developed and closely adhering to symplasm. Skeleton consisting of ill-defined and irregular spicule fibers without organized arrangement, joined together by negligible amounts of spongin. Consistency very soft and fragile.

Megascleres slender, feebly curved, distinctly fusiform amphioxea, entirely smooth; length range 195–285 μ, width range 609 μ.

Microscleres microbirotulates with a slender, smooth, feebly curved or straight shaft, and terminally with a circular arrangement of 5–8 distinctly recurved spines, representing an umbonate rotule; length range 16–19 μ, average thickness of shaft 2 μ, diameter of rotules 3–5 μ.

Gemmoscleres birotulates of two not very distinct length groups, but more or less of one class; consisting of a straight, slender, and smooth shaft, and terminally of equal umbonate rotules, represented by a circular arrangement of 5–7 distinctly recurved stout spines; length range of longer series 60–72 μ, of smaller 42–57 μ; thickness of shaft 3–5 μ, diameter of rotules 16–19 μ.

Gemmules apparently scarce, scattered through skeletal meshwork, spherical, ranging in diameter 480–530 μ; pneumatic layer well developed, consisting of very minute and regular air spaces; gemmoscleres embedded in this coat in a single, rather dense layer, the longer class protruding through outer surface of pneumatic layer; shape of foramen not reliably observed.

Distribution.—Apparently restricted to the northern half of the eastern U.S.A. and southern Canada.

Color in life.—Emerald green.

Discussion.—The insufficient original description of *C. everetti* and the comparative paucity of material of this species collected caused most previous authors to believe that the gemmoscleres in this species are homogeneous in length. Even though the length differences between the longer and shorter gemmoscleres of *C. everetti* are not very pronounced, two distinct length groups could be observed on all slides examined. The intimate relationship of this species to those of *Heteromeyenia* and *Anheteromeyenia* is thus quite obvious.

Extensive material collected in southeastern United States, particularly in South Carolina, seems to possess spicular criteria distinctly different from those displayed by the typical species. A forthcoming comparative study of this material by Harrison (pers. comm.) will decide whether these clearly discernible differences are to be considered of specific or subspecific significance. At present it is advisable to consider *Corvomeyenia* a monotypic genus, even though provisions have been made in the generic definition to include certain criteria displayed by the southern specimens mentioned above.

Genus *Dosilia* Gray, 1867, redefined

Dosilia Gray, 1867, p. 550 (part).—Annandale, 1911c, p. 110; 1912d, p. 384; 1918a, p. 213.—Gee, 1931e, p. 37; 1932c, p. 28.—De Laubenfels, 1936, p. 37.—Jewell, 1952, p. 450.—Penney, 1960, p. 38. (Not *Dosilia* Dybowsky, 1884b.)

Spongilla Carter, 1849, p. 85 (part).—Bowerbank, 1863, p. 449 (part).

Meyenia Carter, 1881a, p. 94 (part).—Potts, 1887, p. 233 (part).

Heteromeyenia Mills, 1888, p. 313 (part).—Weltner, 1895, p. 127 (part).

Ephydatia Weltner, 1895, p. 126 (part).—Kirkpatrick, 1906, p. 226.

Asteromeyenia Annandale, 1912a, p. 593.—De Laubenfels, 1936, p. 36.—Gee, 1931e, p. 32.—Wurtz, 1950, p. 5.—Eshleman, 1950, p. 42.—Jewell, 1952, p. 453.—Penney, 1960, p. 33.

Astromeyenia Schröder, 1927b, p. 101.

Type species.—By subsequent designation (De Laubenfels, 1936) *Spongilla plumosa* Carter, 1849.

Definition.—Megascleres slender and distinctly fusiform amphioxea, either entirely smooth, or covered with minute and scattered spines except at their tips.

Microscleres present in varying abundance in dermal membrane

and symplasm, either distinct asters, usually with rays arising from a central spherical nodule, or rough amphioxea which in their central portion bear a number of long perpendicular radiating rays, or a combination of both of these types.

Gemmoscleres of either slightly or markedly differing length groups, in the latter case of two distinct classes, never of equal length; they are stout birotulates with strongly spined shafts and terminally with distinctly umbonate rotules of equal diameter, their margins incised into a number of recurved teeth.

Gemmules usually very abundant, scattered in the skeletal meshwork, large and always subspherical, often distinctly ovoid; pneumatic layer consisting of minute spherical air spaces; gemmoscleres with their upper rotules often protruding through outer surface of this layer; foramen produced into a short and straight tubule.

Sponges often large and spherical with a rather uneven and lobose surface, giving them a feathery appearance; oscula small but conspicuous, dermal membrane well developed. Skeleton consisting of defined radial spicule fibers, and an irregular arrangement of slightly coherent transverse fibers. Consistency moderately soft but very fragile. Coloration varying from green to brown.

Distribution distinctly discontinuous, most species apparently preferring tropical and subtropical climates.

Discussion.—As mentioned in other sections of this paper, the erectionof Pott's (1887) genus *Heteromeyenia*, a heterogeneous assemblage of not always related spongillid species, had its most regrettable taxonomic consequences right to the present day. The system of Potts failed to provide for microscleral criteria as distinguishing features, characters of utmost importance for the reliable assessment of the intergeneric relationship, regardless of an apparently similar shape or arrangement of the gemmoscleres. This failure, together with the ensuing division of the "Meyeninae" into species with homogeneous and heterogeneous birotulates by later authors, led to an artificial generic split of many closely related species. While *D. plumosa*, *D. palmeri*, and *D. brouni* were thought to possess one length group of birotulates and retained in *Ephydatia* (=*Meyenia*), *H. radiospiculata* Mills and *H. plumosa* Weltner with their conspicuously differing two length groups of birotulates were relegated to species of *Heteromeyenia*.

In his justified desire to separate *H. radiospiculata* and *H. palmeri* on account of their stellate microscleres from *Heteromeyenia*, Annandale (1912a) added to the confusion by his erection of a new genus, *Asteromeyenia*, for their inclusion. Schröder (1927b), realizing the intrageneric relationships within *Heteromeyenia*, made the first attempt to subdivide Pott's genus into a number of more natural

groups. However, he too failed to see the intimate relationship of those "heterogeneous" species with stellate microscleres, which he grouped into the new subgenus *Astroheteromeyenia*, to the "homogeneous" group represented by *Dosilia*.

Since the definition of *Dosilia* Gray, as here amended, makes it possible to include all known species with stellate microscleres into this genus, no apparent purpose can be served by severing their obvious natural relationships with their relegation to two different genera. Moreover, the transfer of the two heterogeneous species of *Dosilia* to *Heteromeyenia* is now impossible, since the latter genus has been restricted in this paper for the inclusion of those species with heterogeneous gemmoscleres which possess diactine microscleres. Both *H. radiospiculata* Mills and *H. plumosa* Weltner are therefore herewith included in *Dosilia*, an arrangement that will make it necessary to rename Weltner's species, should this eventually not be found identical with *H. radiospiculata* as assumed by the present authors.

***Dosilia plumosa* (Carter, 1849)**

PLATE 11, FIGURES 2–5

Spongilla plumosa Carter, 1849, p. 85.—Bowerbank, 1863, p. 449.
Dosilia plumosa Gray, 1867, p. 551.—Annandale, 1911c, p. 111; 1912d, p. 384; 1918a, p. 213.—Gee, 1932c, p. 28; 1932f, p. 529.—De Laubenfels, 1936, p. 37.—Jewell, 1952, p. 450.—Penney, 1960, p. 39.
Meyenia plumosa Carter, 1881a, p. 94.—Potts, 1887, p. 233.
Ephydatia plumosa Weltner, 1895, p. 126.
(Not *Heteromeyenia plumosa* Weltner, 1895.)

MATERIAL.—Slides of type (BM and IM); specimens and slides from India (N. Gist Gee).

DESCRIPTION.—Sponge, according to previous authors, massive and bulbous; surface uneven, lobose, oscula small but conspicuous, dermal membrane well developed. Skeleton consisting of well-defined radial spicule fibers, coated together by a varying amount of spongin, and much slimmer transverse fibers. Consistency moderately soft but very fragile.

Megascleres slightly curved, distinctly fusiform, and smooth amphioxea; length range 400–520 μ, width range 15–21 μ.

Microscleres present in great abundance in the symplasm and the vicinity of gemmules; they are stellate spicules consisting of 8–12 rays projecting from a distinct central globular nodule; the rays usually smooth, terminating in a small number of minute recurved distal spines; occasionally the microscleres are represented by granulated amphioxea which bear in their central portion a number of radiating and perpendicular rays; length range of microscleres extremely variable, radius of rays not exceeding 15–18 μ.

Gemmoscleres birotulates with a strongly spined cylindrical shaft which abruptly increases in width just below the rotules; rotules distinctly umbonate and of equal size and shape, their margins incised into numerous blunt and recurved teeth; length range 55–85 μ, thickness of shaft 3–4 μ, diameter of rotules 23–25 μ.

Gemmules usually very abundant, scattered throughout skeletal meshwork, and strongly subspherical to ovoid averaging 500–680 μ in diameter; pneumatic layer well developed and granular, consisting of minute spherical air spaces; gemmoscleres regularly embedded in this coat, their upper rotules rarely protruding through its outer surface; foramen produced into a short and straight tubule.

Distribution.—Known from India (type locality) and the Philippines, probably also occurring in other parts of SE. Asia.

Color in life.—Recorded as green and pale brown.

Discussion.—This species has been adequately described by previous authors, and the present studies did not reveal additional criteria for discussion. In all slides examined, however, its gemmoscleres are slightly but distinctly unequal in length, more or less forming two length series. This observation is in contrast to the statements of all previous authors, who described the gemmoscleres of this species as homogeneous, thus aiding its separation from other species of this genus with more conspicuous length differences of their gemmoscleres.

Kirkpatrick (1906, p. 226), in comparing this species with his "variety" *brouni* of *E. plumosa*, found the shafts of the gemmoscleres in the Indian sponges uniformly cylindrical. However, in our material studied the great majority of gemmosclere shafts distinctly increase in thickness just below the rotules, just as in other related species. It is obvious, therefore, that this criterion cannot be considered of specific importance.

Dosilia palmeri (Potts, 1885)

Plate 11, figures 6–9

Meyenia plumosa var. *palmeri* Potts, 1885, p. 587; 1887, p. 234.—Kellicott, 1891, p. 103.

Dosilia palmeri Annandale, 1911c, p. 111.—Smith, 1921, p. 17.—Gee, 1932c, p. 28.—Arndt, 1933a, p. 18.—Rioja, 1940a, p. 187.—Eshleman, 1950, p. 40.—Penney, 1960, p. 39.

Material.—Slides of type (USNM no. 5419) and of a specimen in Gee's collection (no. 54286).

Description.—Sponge, according to Potts (1887), forming large spherical masses on branches of trees; surface not reliably observed, appearance of sponge rather feathery. Skeleton apparently of a similar construction of that of the foregoing species. Consistency soft and very fragile.

Megascleres feebly curved to almost straight and fusiform amphioxea, sparsely microspined in their central portion; length range 370–450 μ, width range 14–20 μ.

Microscleres not very abundant in dermal membrane or symplasm; in form and size fully comparable with those of *D. plumosa*, but terminal pseudorotules on rays absent, or represented by an irregular arrangement of distal spines.

Gemmoscleres very similar to those of the preceding species but somewhat larger and stouter; length range 75–95 μ, thickness of shaft 5–6 μ, diameter of rotules 26–28 μ.

Gemmules numerous in the lower part of the sponge, subspherical to ovoid, ranging in diameter 450–690 μ; pneumatic layer well developed and granular, consisting of minute spherical air spaces; gemmoscleres with their upper rotules often projecting through outer surface of pneumatic coat; foramen produced into a short and straight tubule.

Distribution.—Apparently restricted to central America.

Color in life.—Not yet reliably observed; dry sponge recorded as dark brown (Potts).

Discussion.—This species is very closely allied to *D. plumosa* from SE Asia, but differs in the possession of distinctly microspined megascleres, in the absence of pseudorotules on the rays of its microscleres, and by its stouter and longer gemmoscleres. Annandale (1911c) was first to elevate Pott's "variety" to full specific rank, an arrangement followed by all subsequent authors. As in *D. plumosa*, even the gemmoscleres of *D. palmeri* are slightly but distinctly of two length series, although this condition has not been recorded in previous literature.

Kirkpatrick (1906) gave a brief but valuable comparison of this and the preceding species with *D. brouni* from the Nile R. Our examinations of the various slides of all these sponges mentioned were able to demonstrate beyond doubt that they represent distinct species.

Dosilia brouni (Kirkpatrick, 1906)

Plate 11, figures 10–13

Ephydatia plumosa var. *brouni* Kirkpatrick, 1906, p. 226.—Weltner, 1913, p. 475.
Dosilia brounii Annandale, 1914, p. 245.—Penney, 1960, p. 39.
Dosilia plumosa var. *brownii* Gee, 1931e, p. 34.
Dosilia brownii Gee, 1932c, p. 28.
Dosilia brouni Arndt, 1936, p. 17.

Material.—Slides of syntype (N. Gist Gee).

Description.—No data available on the form, skeletal criteria, and consistency of this species; original description referred to its resemblance to *D. plumosa* from India.

Megascleres almost straight, distinctly fusiform and entirely smooth amphioxea; length range 380–550 μ, width range 17–21 μ.

Microscleres very abundant in dermal membrane and symplasm; true stellate forms (asters) comparatively rare, the majority being slender and microspined amphioxea which bear in their central portion a number of long and perpendicular rays; length range 65–75 μ, length of rays 22–40 μ.

Gemmoscleres birotulates of slightly but distinctly unequal length, with a strongly spined cylindrical shaft which occasionally is slightly bent and abruptly increases in width towards the rotules; the latter less distinctly umbonate as in the foregoing two species, their margins incised into a number of rather sharp and recurved teeth; length range 52–75 μ, thickness of shaft 3–4 μ, diameter of rotules 23–24 μ.

Gemmules slightly subspherical, ranging in diameter 490–600 μ; pneumatic layer well developed and granular, consisting of minute spherical air spaces; gemmoscleres with their upper rotules rarely projecting through its outer surface; shape of foramen could not be resolved in the material available for this study.

Distribution.—Only known from the type locality, the Nile R.

Color in life.—Not yet recorded.

Discussion.—In his original description of this species, Kirkpatrick (1906) listed a number of valuable spicular differences from the preceding two species. Disregarding one of them, the supposedly different form of the gemmosclere shafts, as incorrectly observed, the remainder of criteria are in much sharper contrast to both *D. plumosa* and *D. palmeri* than those separating these latter two species. The almost complete absence of true asters, and their replacement by a transitional amphioxous sclere with perpendicularly arranged central rays, as well as the rather flattish shape of the umbonate rotules are perhaps the most outstanding distinguishing criteria which clearly separate *D. brouni* from all its congeners. However, it is to be regretted that no data are available on the general characteristics of this species, and future collections are highly desirable.

Dosilia radiospiculata (Mills, 1888)

Plate 11, figures 14–17

Heteromeyenia radiospiculata Mills, 1888, p. 313.—Weltner, 1895, p. 128.—Kellicott, 1897, p. 50.—Gee, 1932c, p. 34.

Asteromeyenia radiospiculata Annandale, 1912a, p. 593.—Smith, 1921, p. 17.—Old, 1936b, p. 11.—Wurtz, 1950, p. 5.—Jewell, 1952, p. 453.—Penney, 1960, p. 33.

Astromeyenia radiospiculata Schröder, 1927b, p. 101.

?Heteromeyenia plumosa Weltner, 1895, p. 127.—Gee, 1931e, p. 46; 1932c, p. 25.

?Asteromeyenia plumosa Smith, 1921, p. 17.—Old, 1936b, p. 11.—Eshleman, 1950, p. 42.—Penney, 1960, p. 33.

?Astromeyenia plumosa Schröder, 1927b, p. 101.

Material.—Specimens and slides from Granite City, Ill. (USNM no. 8438), Fish Hatchery at Marion, Ala., Virdigris R., Okla., Ohio R., Loyola University, La., Illinois; also from New Orleans (Gee no. 53037), Everglades, Fla. (USNM no. 6183), Rio Grande, Tex., and Arkansas (USNM no. 8459); syntype of *H. plumosa* Weltner (slide of type in ZMB, now at USNM).

Description.—Sponge usually forming bulbous masses; surface of live specimens not yet reliably recorded. Skeleton consisting of well defined radial and irregularly arranged slimmer transverse spicule fibers. Consistency moderately soft but very brittle.

Megascleres slightly curved, slender, and distinctly fusiform amphioxea, ranging from entirely smooth to distinctly microspined; length range 290–400 μ, width range 14–23 μ.

Microscleres moderately abundant in the symplasm and the vicinity of gemmules; they are stellate spicules consisting of 6–8 rays projecting from a distinct central nodule; the rays usually microspined, terminating in a small number of minute recurved distal spines arranged in the shape of a small rotule; occasionally transitional amphioxous microscleres, distinctly granulated, and bearing in their central portion a number of perpendicular long rays; length range of microscleres extremely variable.

Gemmoscleres of two conspicuously distinct classes: (1) Birotulates of slightly but distinctly unequal length, with a strongly spined cylindrical shaft, and terminally with umbonate rotules of equal diameter whose margins bear an irregular arrangement of triangular teeth; and (2) extremely long birotulates of greatly varying length, their shafts often bent and smooth, occasionally bearing a few spines, their rotules represented by a small number of strongly recurved hooks; shaft cylindrical, as a rule distinctly fusiform, resembling the shape of megascleres; length range of (1) 45–82 μ, thickness of shaft 8–19 μ, diameter of rotules 22–26 μ; length range of (2) 120–230 μ, thickness of shaft in central portion 16–20 μ.

Gemmules spherical, ranging in diameter 540–610 μ; pneumatic coat well developed, consisting of minute spherical air spaces; smaller class of gemmules within this coat, larger class invariably projecting through its outer surface, often for a great distance; foramen produced into a short and straight tube, projecting through pneumatic coat but not surpassing its outer surface.

Distribution.—Ranging from the Canadian border south to Mexico.

Color in life.—Apparently not yet recorded.

Discussion.—*Dosilia radiospiculata* agrees with the three preceding species in all structural and spicular details, but in addition it possesses an extremely large and distinctly heterogeneous class of longer

gemmoscleres. These unusual spicules, however, cannot be considered a constant feature either in size, form, or abundance. Their shafts are quite frequently distinctly fusiform, fully resembling the shape of megascleres, and their "rotules" represented by a small number of long hooks of varying curvature.

During the present studies it became obvious that a clear differentiation of characters displayed by this species and *H. plumosa* Weltner is extremely difficult, if not altogether impossible. Although the former species is recorded as possessing microspined megascleres and strongly recurved hooks on their longer class of gemmoscleres, this condition was often also found in specimens labeled *H. plumosa*, and many transitory spicules were present in specimens of both these "species" recorded. Since *H. plumosa* could not be located, it is impossible to decide whether or not these two species are identical and additional studies are highly desirable.

Should later research indicate that Weltner's species is entitled to specific or subspecific rank, it will be necessary to change its present specific name, since it represents a junior homonym of *D. plumosa* (Carter). The nomen novum *Dosilia heterogena* is herewith proposed.

Genus *Trochospongilla* Vejdovsky, 1883

Trochospongilla Vejdovsky, 1883b, p. 31; 1883a, p. 332; *in* Potts, 1887, p. 176.—Weltner, 1893, p. 7; 1895, p. 120.—Girod, 1899, p. 109.—Annandale, 1911c, p. 113; 1912d, p. 384; 1918a, p. 213.—Gee and Wu, 1925c, p. 11.—Gee, 1926a, p. 180; 1927c, p. 185; 1931e, p. 51; 1932b, p. 1; 1932c, p. 42.—Arndt, 1926, p. 344; 1928a, p. 78.—De Laubenfels, 1936, p. 37.—Eshleman, 1950, p. 42.—Jewell, 1952, p. 452.—Simon, 1952, p. 80.—Penney, 1960, p. 55.

Tubella Potts, 1882, p. 14; 1884, p. 216; 1886, p. 228; 1887, p. 210 (part).—MacKay, 1885, p. 233; 1889, p. 87.—Kellicott, 1891, p. 104.—Weltner, 1895, p. 128 (part).—Girod, 1899, p. 112 (part).—Annandale, 1908d, p. 248 (part); 1909f, p. 102 (part).—Smith, 1921, p. 17; 1930, p. 184.—Penney, 1931, p. 240; 1960, p. 58 (part).—Jewell, 1939, p. 20.

TYPE SPECIES.—By original designation *Spongilla erinaceus* Lieberkühn (1856), declared an invalid name by Weltner (1893), and replaced by that author with *Trochospongilla horrida*.

DEFINITION.—Megascleres usually short and stout amphioxea or amphistrongyla, either completely smooth or covered with a varying number of small to very strong spines.

Microscleres absent.

Gemmoscleres minute birotulates with rather stout, smooth, and comparatively short shafts, and at either end with circular rotules of entire margins, which frequently are recurved in the same direction; in some species both rotules of equal size and shape; more often outer rotule conspicuously smaller than inner; exceptionally outer rotule reduced to a small disc of regular or irregular shape.

Gemmules often very abundant, extremely small and subspherical to spherical; pneumatic coat well developed but usually very thin, consisting of small rounded air spaces; both gemmular membranes well developed; gemmoscleres embedded in the pneumatic coat radially, usually forming one layer only, their inner rotules often overlapping each other; gemmules sometimes encased in a capsule of normal megascleres; foramen simple to slightly tubular, always somewhat elevated.

Sponges forming shallow but often extensive encrustations on various substrata; surface hispid and uneven, with a number of short and erect tubular projections; most species apparently shunning light. Coloration a dark brown. Consistency moderately soft to very hard.

Widely distributed throughout the world as a genus, though most species possess more or less sharply defined zoogeographical boundaries.

Discussion.—The genus *Trochospongilla* was among the first newly erected genera designed for a clearer subdivision of the Meyeninae Carter, considered by most previous authors as a separable subfamily. At the time of its erection, only four of the six then known species seemed to fit the generic definition by Vejdovsky (1883b), and the two remaining obvious congeners *T. paulula* and *T. pennsylvanica* were retained in the superficially applicable genus *Tubella* Carter by even some most recent authors. Although the gemmosclere rotules of some *Trochospongilla* species are equal in size and shape, the upper rotule of the majority of species is invariably smaller, and it is not surprising to find some extremes in which the upper rotule is very small, or even rudimentary. All the species of *Trochospongilla*, as here redefined, form a distinct group of spongillids and none of them can be considered to belong to another genus. Annandale (1911c), while describing additional species from Asia, was first to demonstrate the proper generic position of *T. pennsylvanica*, and Gee (1926–1932) correctly used the generic name of *Trochospongilla* also for *T. paulula*, the type species of *Tubella* Carter, now a synonym of *Metania* Gray.

Some nomenclatural problems will still have to be solved in the clearly distinct genera *Trochospongilla* and *Metania*, as here redefined. The genus *Uruguaya*, designed by Carter (1881a) for the inclusion of only one species with the gemmules still unknown, now contains a number of closely related species displaying features of great similarity to those of *Trochospongilla*. Annandale (1911c) suggested the relegation of *Uruguaya* to a subgenus of *Trochospongilla*, a taxonomic procedure which would be impossible to follow, since the first genus has a priority of two years over the second. At present these two genera are still separable by their greatly differing structure of their skeletons, which in *Uruguaya* is of almost stony consistency, as well as by a number of minor criteria. However, future research may demonstrate

transitional skeletal constructions leading from the mode found in *Trochospongilla* to that of *Uruguaya*. Species of the former genus are now also known to possess firm, though never stony, skeletal arrangements and it could well be possible that intermediate links will be found. Should this happen, the relegation of the well-known and well-defined cosmopolitan genus of Vejdovsky to a synonym of the localized name of Carter's genus will be inevitable, or legalistic steps will have to be taken to declare *Uruguaya* an inappropriate genus. It certainly would be a choice of evils.

Six of the eight presently known species of *Trochospongilla* are dealt with below in detail. The remaining two, *T. gregaria* (Bowerbank) and *T. minuta* (Potts), are not represented in the material available for this study and have to be disregarded.

Trochospongilla horrida Weltner, 1893

PLATE 12, FIGURES 1, 2

Spongilla erinaceus Lieberkühn, 1856, p. 496.

Trochospongilla erinaceus Vejdovsky, 1883b, p. 31; 1883a, p. 332; *in* Potts, 1887, p. 176.—Dybowsky, 1882, p. 3; 1886, p. 295.—Wierzejski, 1885, p. 1.

Trochospongilla horrida Weltner, 1893, p. 12; 1895, p. 120.—Girod, 1899, p. 109.—Topsent, 1914, p. 538.—Smith, 1921, p. 17.—Arndt, 1923, p. 75; 1926, p. 344; 1928a, p. 78.—Rezvoj, 1926b, p. 64; 1928, p. 226.—Gee, 1926a, p. 182; 1931a, p. 501; 1931e, p. 40; 1932b, p. 4; 1932c, p. 42.—Schröder, 1926, p. 249; 1938a, p. 295; 1938b, p. 126.—Grimailowskaja, 1928, p. 215.—Old, 1932c, p. 239; 1936b, p. 11.—Eshleman, 1950, p. 44.—Wurtz, 1950, p. 6.—Simon, 1951, p. 133; 1952, p. 80; 1953, p. 207.—Penney, 1954, p. 156; 1960, p. 55.

Meyenia erinaceus Carter, 1881a, p. 90.—Potts, 1887, p. 210.

Trochospongilla horrida var. *ningpoensis* Gee, 1926a, p. 182; 1926c, p. 110; 1927a, p. 1; 1927b, p. 63; 1928b, p. 225; 1930e, p. 27; 1930d, p. 369; 1931e, p. 44; 1932b, p. 6; 1932c, p. 42; 1932d, p. 54.

Trochospongilla sol Annandale, 1918a, p. 205.—Gee and Wu, 1925b, p. 342.—Gee, 1926a, p. 183; 1926c, p. 110; 1926b, p. 237; 1927b, p. 61; 1927a, p. 1; 1928b, p. 225.

Trochospongilla horrida var. *sol* Gee, 1931e, p. 49; 1932b, p. 9; 1932d, p. 53; 1932c, p. 42.—Penney, 1960, p. 56.

Trochospongilla polysclera Rezvoj, 1926a, p. 109.

MATERIAL.—Very numerous specimens and slides; EUROPE: Germany, Poland, Czechoslovakia, U.S.S.R.; NORTH AMERICA: Illinois, Ohio, South Carolina; ASIA: U.S.S.R., China; two slides of type of *T. polysclera* (N. Gist Gee).

DESCRIPTION.—Mature sponge forming flat crusts of moderate dimensions; surface slightly uneven and hispid, oscula conspicuous but small. Skeleton consisting of an irregular network of spicule fibers, joined together by a varying amount of spongin. Consistency ranging from fragile to moderately hard.

Megascleres straight to feebly curved, broadly fusiform, sharply pointed amphioxea, covered with stout and sharp spines in varying patterns; length range 170–235 μ, width range 11–15 μ.

Microscleres absent.

Gemmoscleres minute birotulates with a stout, smooth, and short shaft, and terminally with rotules of more or less recurved circular margins and of equal size and shape; length of shaft about 11 μ, its thickness about 4–5 μ; diameter of rotules ranging 9–12 μ.

Gemmules rather abundant, confined to lower parts of sponge, spherical and moderately small; usually encased in capsules of normal megascleres; diameter ranging 475–540 μ; pneumatic layer well developed, but never thicker than the length of gemmoscleres, consisting of rather large air spaces; gemmoscleres embedded in this coat in a single layer; foramen produced into a conical and short porus tube.

Distribution.—Apparently discontinuous but wide dispersal in all continents of the Northern Hemisphere, with preference to cold-temperate regions.

Color in life.—Ranging from light yellow to dark brown.

Discussion.—Although not very abundant, *T. horrida* is a well-described species, and the present studies did not reveal any additional criteria for discussion. As can be expected in sponges with a widely scattered distribution, this species displays some slight variations in distant populations which are not significant enough to permit a clear discrimination of races. *T. horrida ningpoensis* Gee (1926a) differs from *T. horrida* only in the smaller size of its spicular components and must therefore be considered an unimportant ecomorphic variation. *T. sol* Annandale, relegated by Gee (1931e) to varietal rank, merely displays pronounced radial reinforcements on both rotules of its gemmoscleres, a condition often also found in a number of slides of the typical *T. horrida* examined.

Our reexamination of the type slides of *T. polysclera* supports Gee's (1931e) view that this species is fully synonymous with *T. horrida*. These slides clearly contain spicular components of two spongillid species, one of them, containing the peculiar microscleres described by Rezvoj (1926a) as well as smooth megascleres, probably belonging to the *Spongilla lacustris* group. The rapid growth of all *Trochospongilla* species, studied in detail in Australian waters (Racek, MS.), often results in their fastening to already developed sponges of other species, so that frequently a spicular mixture can be observed. This phenomenon has also been recorded by previous authors and accounts for the confusion of a number of previous species of this and other genera (e.g., *Spongilla tanganyikae* Evans, *Metania lissostrongyla* Burton, and others).

Trochospongilla pennsylvanica (Potts, 1882)

PLATE 12, FIGURES 3, 4

Tubella pennsylvanica Potts, 1882a, p. 14; 1884b, p. 216; 1886, p. 228; 1887, p. 251.—MacKay, 1885, p. 233; 1889, p. 87.—Kellicott, 1891, p. 104.—Weltner, 1895, p. 114.—Girod, 1899, p. 112.—Annandale, 1908d, p. 248; 1909f, p. 102.—Smith, 1921, p. 17; 1930, p. 184.—Penney, 1931, p. 240; 1960, p. 58.—Jewell, 1939, p. 20.—Wurtz, 1950, p. 6.

Trochospongilla pennsylvanica Annandale, 1911c, p. 118; 1912d, p. 384; 1918a, p. 213.—Gee, 1926a, p. 184; 1931e, p. 46; 1931a, p. 502; 1932b, p. 22; 1937, p. 285.—Arndt, 1928b, p. 164.—Old, 1932a, p. 132; 1932c, p. 239; 1932b, p. 442; 1936b, p. 11.—Eshleman, 1950, p. 42.—Moore, 1951, p. 63; 1953, p. 25.

Tubella pennsylvanica var. *minima* Potts, 1887, p. 252.

Trochospongilla pennsylvanica var. *minima* Gee, 1931e, p. 43; 1932b, p. 25; 1932c, p. 43.

Tubella fanshawi Potts, 1887, p. 252.

Tubella intermedia Potts, 1887, p. 252.

Trochospongilla pennsylvanica var. *mackayi* Gee, 1931e, p. 42.

MATERIAL.—Numerous specimens and slides from the United States and Canada.

DESCRIPTION.—Sponge forming flat crusts of moderate dimensions; surface slightly hispid and irregular, with a number of sloping eminences surrounded by radiating furrows; oscula conspicuous but small and few in number. Skeleton consisting of an irregular network, joined together by very little spongin. Consistency of life sponge moderately soft to fragile.

Megascleres somewhat slender, feebly curved, sharply pointed amphioxea, rarely amphistrongyla, entirely covered with small, conical, and sharp spines; length range 140–210 μ, width range 8–11 μ.

Microscleres absent.

Gemmoscleres minute birotulates with slender shafts, and terminally with rotules of more or less recurved circular margins, usually of similar shape but invariably of greatly differing diameter; lower rotule always normally developed, upper rotule frequently rudimentary, sometimes irregular; length of shaft 9–11 μ, its thickness about 2 μ; diameter of lower rotule 16–20 μ, of upper 3.5–8.5 μ.

Gemmules rather abundant, confined to lower parts of sponge, spherical, and minute; apparently not encased in cages of megascleres; diameter ranging 190–390 μ; pneumatic layer granular and comparatively thin, rarely covering the upper rotule of gemmoscleres; gemmoscleres crowded in this layer so that their lower rotules distinctly overlap each other; foramen produced into a conical and short porus tube.

DISTRIBUTION.—Apparently restricted to the North American Continent, its recorded occurrence in Ireland and Scotland needs confirmation.

Color in life.—Light gray to light brown.

Discussion.—The inclusion of this species in the genus *Tubella* Carter by earlier authors was aided by the rudimentary development of the upper rotule of the great majority of its gemmoscleres. However, Annandale (1911c) realized that this ecomorphic condition represents a convergence of characters comparable to but not identical with that found in *Tubella* species and relegated *T. pennsylvanica* to its proper position within the genus *Trochospongilla*. The species discussed merely represents one extreme of an intergrading series of species, almost all of which display some degree of size differences between their upper and lower gemmosclere rotules. It cannot possibly be left in *Tubella*, relegated to a synonym of *Metania* in this paper, since all true members of this genus possess free microscleres, a vastly different construction of their skeleton and gemmules, and gemmoscleres with clearly distinct rotules, in size as well as in structure.

All the specific and varietal names listed above must be considered fully synonymous with *T. pennsylvanica* for reasons mentioned in the discussion of *T. horrida*. Only when comparing a full range of specimens from distant localities, as was possible during the present studies, the futility of establishing clear-cut races within *T. pennsylvanica* becomes obvious.

Trochospongilla leidii (Bowerbank, 1863)

Plate 12, figures 7, 8

Spongilla leidii Bowerbank, 1863, p. 445.
Ephydatia leidyi Gray, 1867, p. 550.
Meyenia leidii Carter, 1881a, p. 91.
Meyenia leidyi Potts, 1884a, p. 184; 1887, p. 212.—Kellicott, 1891, p. 103; 1897, p. 50.—Kirsch, 1909, p. 37.
Trochospongilla leidyi Weltner, 1895, p. 114.—Annandale, 1909d, p. 404.—Smith, 1921, p. 17.—Gee, 1926a, p. 181; 1931e, p. 41; 1932b, p. 16; 1932c, p. 43.—Old, 1936b, p. 11.—Eshleman, 1950, p. 44.
Trochospongilla leidii Penney, 1960, p. 56.

Material.—Slides of type (BM) and of Pott's material (USNM no. 8639).

Description.—Sponge, according to the original descriptions by Bowerbank (1863) and Potts (1887), forming thin encrusting layers of considerable dimensions; surface even, sometimes rising into round eminences. Skeleton a rather firm network of more or less regular spicule fibers, forming polyhedral meshes. Consistency of live sponge very hard and firm.

Megascleres straight to feebly curved stout amphioxea, broadly fusiform and entirely smooth; length range 150–170 μ, width range 8–13 μ.

Microscleres absent.

Gemmoscleres minute birotulates with a stout, smooth and short shaft, and terminally with rotules of more or less circular and recurved margins, the upper only very slightly smaller than the lower; length of shaft about 11 μ, its thickness about 4–5 μ, diameter of rotules ranging 12–14 μ.

Gemmules rather abundant, confined to lower parts of sponge, subspherical, ranging in diameter 370–410 μ; usually encased in capsule of normal megascleres; pneumatic layer apparently granular, never thicker than the length of gemmoscleres; these embedded in a single layer in this coat; foramen produced into a short conical porus tube.

Distribution.—Known only from a restricted region in the eastern United States.

Color in life.—Light gray to drab.

Discussion.—The examination of the few slides available for this study did not reveal any additional criteria for discussion, and future observations and particularly the collection of new material are highly desirable.

***Trochospongilla paulula* (Bowerbank, 1863)**

Plate 12, figures 5, 6

Spongilla paulula Bowerbank, 1863, p. 453.—Jewell, 1952, p. 448.
Metania paulata Gray, 1867, p. 551.
Tubella paulula Carter, 1881a, p. 96.—Potts, 1887, p. 248.—Weltner, 1895, p. 114.
Trochospongilla paulula Gee, 1931e, p. 45; 1932b, p. 20.—Schröder, 1932a, p. 165.
Spongilla paulata de Laubenfels, 1936, p. 37.

Material.—Slides of type (BM); material and slides from the Amazon R. (Gee no. 54826).

Description.—Sponge, according to previous descriptions, forming small cushions of aquatic vegetation; surface rather uneven, with conical eminences. Skeleton apparently irregular but stout. Consistency rigid.

Megascleres feebly curved, slender, and distinctly fusiform amphioxea, as a rule entirely smooth, rarely bearing a varying number of minute spines or granules; length range 230–260 μ, width range 14–16 μ.

Microscleres absent.

Gemmoscleres moderately large birotulates with a slender and comparatively long shaft, and terminally with rotules of more or less circular and slightly recurved margins, the upper one considerably smaller than the lower; length of shaft 24–29 μ, its thickness about 4–5 μ, diameter of lower rotule 22–26 μ, of upper 9–14 μ.

Gemmules spherical, ranging in diameter 390–430 μ; pneumatic layer well developed and distinctly granular; gemmoscleres embedded

in this coat in one layer; foramen produced into a short and conical porus tube.

Distribution.—Apparently known only from the type locality, the Amazon R.

Color in life.—Not yet observed; dry sponge recorded as light brown.

Discussion.—Gee (1932b) drew attention to the fact that, contrary to Carter's (1881) observations, the type material of this species contains only one type of gemmoscleres. Our reexamination of the type and syntype slides equally failed to find the smaller type described by Carter, although a few gemmoscleres are slightly frailer than the majority examined.

Gee (1932b), while comparing the differing length range of gemmoscleres present in *T. latouchiana* and *T. latouchiana sinensis*, respectively, suggested a possible future relegation of that group of sponges to synonyms of *T. paulula*. However, the present studies revealed that the length of gemmoscleres in the *T. latouchiana* group cannot be considered a constant criterion, since many intergrading conditions can be found, and that their mean length of gemmoscleres is considerably below that found in *T. paulula*. A further distinguishing character is the upper rotule, which in the *T. latouchiana* group is only slightly smaller than the lower, whereas in the South American species it is drastically reduced to a rudimentary disk. The separation of *T. paulula* from its Chinese and Indian congeners is therefore fully justified, even though future collections of the insufficiently known South American species may yet demonstrate the possibility of their subspecific discrimination.

Trochospongilla latouchiana Annandale, 1907

Plate 12, figures 9, 10

Trochospongilla latouchiana Annandale, 1907c, p. 21; 1908b, p. 157; 1911c, p. 115; 1918a, p. 201.—Gee, 1926c, p. 110; 1926a, p. 181; 1927a, p. 1; 1927b, p. 60; 1928, p. 225; 1929d, p. 297; 1930a, p. 98; 1930e, p. 27; 1931e, p. 41; 1932b, p. 10; 1932f, p. 507; 1932c, p. 44.—Vorstman, 1927, p. 184; 1928, p. 116.—Rao, 1929, p. 269.—Arndt, 1932c, p. 566; 1936, p. 10.—Schröder, 1935, p. 104.—Penney, 1960, p. 56.

Trochospongilla latouchiana subsp. *sinensis* Annandale, 1919b, p. 457.—Gee and Wu, 1925a, p. 226.—Gee, 1926a, p. 181; 1931e, p. 49; 1932b, p. 13.

Trochospongilla latouchiana var. *pasigensis* Gee, 1932b, p. 14; 1932f, p. 526; 1932c, p. 42.—Penney, 1960, p. 56.

Material.—Slides of types or syntypes of all forms listed (IM, USNM, N. Gist Gee); numerous specimens of *T. latouchiana* and *T. l. sinensis* from India and China respectively (N. Gist Gee and AusM).

Description.—Sponge forming comparatively shallow cushions, ranging from insignificant sizes to extensive encrustations; surface

rarely smooth, more often with a number of irregular tubular projections; oscula comparatively few but conspicuous, often present on conical eminences. Skeleton consisting of distinct vertical spicule fibers, tightly bound together by spongin, and an irregular arrangement of transverse fibers. Consistency of live sponge very rigid but often brittle.

Megascleres almost straight or only feebly curved cylindrical amphioxea, as a rule entirely smooth; length range 220–310 μ, width range 11–16 μ.

Microscleres absent.

Gemmoscleres minute birotulates with a slender shaft, and terminally with circular rotules of unequal diameter; upper rotule often considerably recurved to form a bowllike structure; length of shaft 13–17 μ, its thickness 3–4 μ, diameter of lower rotule 16–19 μ, of upper 13–16 μ.

Gemmules rather abundant, scattered through and loosely held in position by skeletal meshwork, not encased in capsules of megascleres; diameter ranging 175–235 μ; pneumatic layer relatively thin and granular; gemmoscleres embedded in this coat in one layer, foramen produced into a conical and short porus tube.

Distribution.—Ranging from India through SE. Asia north to China, and south to eastern Australia (Racek, MS.).

Color in life.—Varying shades of brown, usually dark tan.

Discussion.—The justification for Annandale's (1919b) separation of *T. latouchiana sinensis* as a distinct and geographically isolated subspecies has been doubted by Gee (1932b), who found the gemmoscleres in that subspecies, as well as in the Indian species, to vary to such a degree that they did not seem to represent a reliable distinguishing criterion. Observations on the extensive material available for the present study fully support Gee's views, and many intergrading series of gemmoscleres were found in the same individual of this complex. The retention of *T. l. sinensis* as a geographic race of *T. latouchiana* is therefore impossible.

Gee's (1932b) "variety" *T. l. pasigensis* from the Philippines is obviously a freak. Its spicules display a large number of striking irregularities most common in sponges living in an adverse environment: Its megascleres are thinner and shorter and bear bulblike central enlargements; its gemmoscleres have thinner and often spiny shafts, usually protruding through both rotules; both rotules are frequently at various angles to the shaft, which itself is not always straight. While *T. paulula*, as mentioned above, is clearly separable from the *T. latouchiana* group, no purpose can be served by dividing the latter into subspecies or "varieties," the characters of which are highly variable and cannot be demonstrated.

Trochospongilla philottiana Annandale, 1907

PLATE 12, FIGURES 11–15

Trochospongilla philottiana Annandale, 1907c, p. 22; 1907a, p. 269; 1908b, p. 157; 1909f, p. 103; 1911c, p. 117; 1918a, p. 213.—Gee, 1926a, p. 181; 1929d, p. 297; 1930c, p. 491; 1931e, p. 46; 1932b, p. 26; 1932c, p. 43.—Arndt, 1938a, p. 23.—Penney, 1960, p. 57.

Trochospongilla tunghuensis Gee, 1926a, p. 181; 1926c, p. 110; 1927a, p. 1; 1927b, p. 63; 1928, p. 225.

Trochospongilla philottiana var. *tunghuensis* Gee, 1930d, p. 369; 1930c, p. 491; 1931e, p. 51; 1932b, p. 29; 1932c, p. 43; 1932d, p. 53; 1932f, p. 507.—Penney, 1960, p. 58.

Trochospongilla tunghuensis var. *javanensis* Gee, 1930a, p. 102.

Trochospongilla philottiana var. *javancnsis* Gee, 1931e, p. 40; 1932b, p. 31; 1932c, p. 43.—Penney, 1960, p. 57.

Trochospongilla philottiana var. *minima* Gee, 1930c, p. 491; 1932b, p. 28.—Penney, 1960, p. 57.

?Spongilla tanganyikae Evans, 1899, p. 481.—Kirkpatrick, 1906, p. 221.

Trochospongilla tanganyikae Burton, 1938, p. 460.

MATERIAL.—Slides of types or syntypes of all forms listed, except *S. tanganyikae* and *T. tanganyikae* (IM, USNM, N. Gist Gee); numerous specimens of *T. philottiana* from India, SE. Asia, and Africa (N. Gist Gee and MCB).

DESCRIPTION.—Sponge forming flat crusts of moderate dimensions; surface rather even but distinctly hispid; oscula few in number and inconspicuous. Skeleton consisting of relatively slender spicule fibers, forming triangular meshes. Consistency of live sponge rigid but relatively brittle.

Megascleres somewhat slender, feebly curved amphistrongyla, only rarely abruptly pointed amphioxea or tornota, almost uniformly covered with small conical spines; length range of typical scleres 165–190 μ, width range 9–12 μ.

Microscleres absent.

Gemmoscleres minute birotulates with slender shafts, and terminally with circular rotules of unequal diameter; both rotules often considerably recurved, the upper usually forming a bowllike structure; length of shaft typically 14–16 μ, its thickness 3–4 μ, diameter of lower rotule 18–22 μ, of upper 14–18 μ.

Gemmules rather abundant, confined to base of sponge, spherical and minute, usually surrounded by a capsule of normal megascleres; diameter ranging 340–390 μ; pneumatic layer distinctly granular and very thin; gemmoscleres embedded in this coat in a single layer, their lower rotules alternatively overlapping; foramen produced into a short and conical porus tube.

DISTRIBUTION.—Restricted to tropical regions of Asia, occurring from India through southern China and SE. Asia to the Philippines, apparently also occurring in Africa.

Color in life.—Pale yellow to light brown.

Discussion.—The difficulties in distinguishing the many "varieties" from the typical *T. philottiana* were commented on by Gee (1932b). The reexamination of type material of all "varieties" during the present study made it clear that the minor differences of criteria in the various forms do not afford means of racial discrimination. Apart from size differences of spicular components, such as can be observed in *T. ph. minima* and which certainly are the result of an adverse environment, there are only minor differences in the shape and structure of megascleres within the entire group. *T. ph. tunghuensis* and to a certain degree also *T. ph. javanensis* occasionally possess megascleres of almost amphioxous shape, but such scleres can also be observed in a range of specimens of the typical species. Since it appears impossible to find constant criteria to distinguish the many formerly established "varieties," all varietal forms must be relegated to synonyms of *T. philottiana*.

However, the nomenclatural problems of the entire *T. philottiana* group do not rest with this decision. Arndt (1938a) recorded this species for the first time for Africa, after comparing his specimens with the description of *Spongilla tanganyikae* by Evans (1899) and Kirkpatrick (1906). From Burton's (1938) account of *Trochospongilla tanganyikae*, as well as from our examinations of *M. vesparia* from Africa, with which the former is associated, it is obvious that Burton's *T. tanganyikae* certainly is a typical *T. philottiana*. While the latter can now be recorded for the second time from African waters, the identity of *S. tanganyikae* has still to be resolved, since material of it was not available for the present study. Should later research demonstrate the correctness of our presently ill-documented view that Evans' insufficiently described *S. tanganyikae* is identical with *T. philottiana*, the latter name will have to be relegated to a synonym, and the sponge here discussed to be referred to as *T. tanganyikae*.

Genus *Uruguaya* Carter, 1881

Uruguaya Carter, 1881a, p. 100.—Potts, 1887, p. 268.—Kirsch, 1909, p. 36.—Annandale, 1911c, p. 27.—Cordero, 1925, p. 117.—Gee, 1931e, p. 51; 1932c, p. 44.—De Laubenfels, 1936, p. 37.—Penney, 1960, p. 60.
Drulia Gray, 1867, p. 552 (part).

Type species.—By original designation *Spongilla corallioides* Bowerbank (1863).

Definition.—Megascleres stout to very stout amphistrongyla, either entirely smooth or delicately granulated; often more than one class present, occasionally also slender amphioxea.

Microscleres absent.

Gemmoscleres minute birotulates with stout, smooth, and short

shafts, and at either end with distally deflected circular rotules of entire margins; rotules always of equal size and shape.

Gemmules subspherical, very small, usually restricted to the base of the sponge and fastened to the substratum by a surrounding capsule of a smaller series of megascleres; often arranged in groups of 2–5; pneumatic layer consisting of a solid mass of spongin without any trace of air spaces; gemmoscleres embedded in this layer radially, their inner rotules often overlapping each other; foramen simple, but slightly elevated.

Sponges forming flat encrustations or conspicuously branching masses on various substrata; surface smooth to strongly hispid. Coloration usually light to dark brown. Consistency hard to stony hard.

Known only from tropical South America.

Discussion.—The genus *Uruguaya* consists of a small number of insufficiently known and apparently very closely related species, all restricted to tropical South America. It displays intimate affinities to the genus *Trochospongilla* in most regards; the gemmoscleres in both are almost indistinguishable. However, the megascleres of *Uruguaya* and the structure and consistency of its skeleton are distinctly different so that both genera still can be satisfactorily separated. Some future nomenclatural problems were commented on in the discussion of *Trochospongilla* (p. 134).

Members of the genus *Uruguaya* are poorly represented in the material available for this study; *U. amazonica* Weltner and *U. pygmaea* are altogether absent. If additional material cannot be studied in detail and gemmules of *U. corallioides* remain unknown, the status of the few species dealt with is difficult to assess.

Uruguaya corallioides (Bowerbank, 1863)

Plate 13, figures 1, 2

Spongilla corallioides Bowerbank, 1863, p. 460.—Jewell, 1952, p. 448.
Uruguaya corallioides Carter, 1881a, p. 100.—Potts, 1887, p. 268.—Hinde, 1888, p. 6.—Weltner, 1895, p. 114.—Cordero, 1923, p. 134; 1925, p. 113; 1928, p. 259.—Gee, 1931c, p. 36; 1932c, p. 44.—Penney, 1960, p. 60.
Drulia corallioides Gray, 1867, p. 552.

Material.—Slides of syntype (BM); specimens and slides from Uruguay (N. Gist Gee no. 54396) and the Amazon R. (RMS).

Description.—Sponge usually forming anastomosing cylindrical branches, arising from a flat base, immature specimens often flat crusts; surface comparatively even but distinctly hispid; oscula of moderate size but very conspicuous, usually situated on slightly raised elevations. Skeleton consisting of thick and regular spicule fibers, forming triangular meshes, firmly united by a considerable amount of

spongin. Consistency of live sponge stony hard, dry sponge resembling coral growths.

Megascleres apparently of only one class, i.e., stout, distinctly curved, and entirely smooth amphistrongyla; a great number of megascleres of smaller dimensions often typically amphioxous, probably representing immature scleres; length range typically 270–310 μ, width range 45–50 μ.

Microscleres absent.

Gemmoscleres have not yet been reliably recorded, since gemmules of this species apparently are still unknown.

Distribution.—Known only from the Uruguay R. (type locality) and the Amazon R.

Color in life.—Apparently gray to light brown.

Discussion.—In view of the paucity of specimens collected and the absence of gemmules in the material available for this study, additional criteria cannot be demonstrated. From the account of this and related species of *Uruguaya* by Cordero (1925) and the key to species of this genus given by that author, it appears that gemmule-bearing specimens of *U. corallioides* have not yet been found. This fact impairs our present knowledge of this sponge, and future extensive studies by workers in South America would appear imperative before any reliable conclusions as to its intrageneric relationship can be made.

Uruguaya macandrewi Hinde, 1888

Plate 13, figures 3, 4

Uruguaya macandrewi Hinde, 1888, p. 4.—Weltner, 1895, p. 114.—Gee, 1931e, p. 42; 1932c, p. 44.—Cordero, 1925, p. 117 (key).
Uruguaya macandrewsi Penney, 1960, p. 60.

Material.—Slide of type (BM).

Description.—Sponge, according to Hinde (1888), forming anastomosing branches, arising from a flat base; surface smooth and even; oscula conspicuous, distributed rather irregularly over the surface of the branches. Skeleton apparently of similar construction as that of the foregoing species. Consistency rigid and very hard.

Megascleres used for the skeleton of only one class, i.e., moderately stout, distinctly curved amphistrongyla, entirely covered with extremely minute granulations; length range 250–320 μ, width range 30–40 μ; smaller megascleres found only in the vicinity of gemmules.

Microscleres absent.

Gemmoscleres minute birotulates with a stout, smooth, and short shaft, and terminally with equal rotules of strongly recurved circular margins; length of shaft 13–14 μ; its thickness about 5–6 μ; diameter of rotules 16–17 μ.

Gemmules comparatively few in number, subspherical, diameter ranging 480–600 μ; restricted to base of sponge, firmly adhering substratum, occurring in groups of 2–5, surrounded by a strong capsule of typical but smaller megascleres; pneumatic coat apparently a solid mass of spongin; gemmoscleres embedded in this coat in one layer, their inner rotules overlapping; foramen not reliably determinable.

Distribution.—Apparently known only from the type locality, "Paraguay."

Color in life.—Not yet observed; dry sponge almost black in upper parts, lighter in its interior.

Discussion.—With our present insufficient knowledge of members of this genus, the relationship of the species discussed cannot be reliably ascertained. From *U. corallioides* it seems only to differ by its microgranulated and somewhat slimmer megascleres, the other known criteria of both are almost identical. Additional studies, and in particular collections in South American waters, are of utmost importance.

Uruguaya repens Hinde, 1888

Plate 13, figure 5

Uruguaya repens Hinde, 1888, p. 2.—Weltner, 1895, p. 114.—Gee, 1931e, p. 47; 1932c, p. 44.—Cordero, 1925, p. 117 (key).—Penney, 1960, p. 61.

Material.—Slide of syntype (N. Gist Gee no. 54827).

Description.—Sponge, according to Hinde (1888), forming flat encrustations without branches; surface smooth and even. Skeleton rigid and hard.

Megascleres used for the skeleton of only one class, i.e., stout, moderately curved, cylindrical, and entirely smooth amphistrongyla; microgranulations often present at their tips; length range 165–250 μ, width range 24–35 μ; smaller megascleres found only in the vicinity of gemmules.

Microscleres absent.

Gemmoscleres minute birotulates with a stout, smooth, and short shaft, and terminally with equal rotules of strongly recurved circular margins; length of shaft 14–15 μ, its thickness about 6 μ; diameter of rotules 15–16 μ.

Gemmules invariably attached to the substratum, subspherical, diameter ranging 240–480 μ, occurring in groups from 3–5, surrounded by a strong capsule of typical but smaller megascleres; pneumatic coat apparently a solid mass of spongin; gemmoscleres embedded in this coat in one layer, the outer rotules slightly exceeding surface of pneumatic coat; foramen not reliably determinable.

Distribution.—Apparently known only from the type locality, the Uruguay R.

COLOR IN LIFE.—Not yet observed; dry sponge recorded as light lead-brown.

DISCUSSION.—This species seems to differ from *U. corallioides* only by its possession of gemmules and by its branchless encrusting growth. Future studies may yet establish its identity with the former, but the present material does not permit any reliable conclusions in this regard.

Genus *Metania* Gray, 1867, redefined

Metania Gray, 1867, p. 551.—De Laubenfels, 1936, p. 36.—Burton, 1938, p. 463 (part synonymy only).—Jewell, 1952, p. 450.—Penney, 1960, p. 45.
Tubella Carter, 1881a, p. 96 (part).—Potts, 1887, p. 248 (part).—Annandale, 1909f, p. 102; 1911c, p. 120; 1918a, p. 213.—Gee, 1933c, p. 237 (part).
Acalle Burton, 1934, p. 412 (non Gray, 1867, p. 552).
(Not *Tubella* Lendenfeld, 1887, p. 90)

TYPE SPECIES.—*Spongilla reticulata* Bowerbank (1863).

DEFINITION.—Megascleres stout amphistrongyla or amphioxea, smooth or microspined, often differing in length in the same individual, occasionally of two distinct classes.

Microscleres present in all species, but of varying abundance; they are slender, fusiform, and spined amphioxea, with their central spines large and erect.

Gemmoscleres tubelliform, with more or less spiny shafts; lower rotule circular or irregularly polygonal, with or without marginal indentations, often with radial striations; upper rotule invariably knoblike, either represented by a rounded boss, or bearing a number of recurved marginal spines.

Gemmules abundant in mature sponge, large and spherical, usually scattered through skeletal meshes, rarely restricted to base; pneumatic layer feebly developed, often thin, consisting of rather large polygonal air spaces; gemmoscleres embedded in this strictly radially, resting with fully developed rotule on inner gemmular membrane, and projecting with terminal knob beyond surface of pneumatic coat; outer gemmular membrane ill-defined or absent; foramen tubular, porus tube straight and comparatively short, surrounded by a circle of slanting gemmoscleres.

Sponges invariably bulbous and massive, in growth often resembling the structure of a wasp nest, surface rather reticulate and hispid; color in life dark gray to dark brown; consistency rigid but quite brittle.

Apparently restricted to the tropics, possessing a discontinuous distribution; not yet found in tropical Australia.

DISCUSSION.—The genus *Metania* Gray, as here redefined, includes all those species with true tubelliform gemmoscleres which possess

free microscleres in the form of spined amphioxea, and whose gemmules lack an external arrangement of typically birotulate gemmoscleres. Following the present studies, the genus *Tubella* Carter cannot be retained in spongillid taxonomy since it represents a heterogeneous grouping of species now known to belong to *Metania* Gray, *Trochospongilla* Vejdovsky, and even *Heterorotula*, new genus.

The presence of free microscleres, although previously not recorded for *M. vesparia* (von Martens) and *M. vesparoides* (Annandale), has now been established for all *Metania* species alike. The present studies furthermore revealed that the two species formerly known as *Tubella pottsi* Weltner and *Metania lissostrongyla* Burton are identical, and that both display no criteria of importance to justify even racial differences between them and *M. vesparia*.

Of other species, unfortunately not available in the material studied, *M. spinata* (Carter) certainly belongs here and possibly also *M. thumii* (Traxler), known only from subfossil deposits. *Tubella anonyma* (Carter) is insufficiently described and most probably belongs to a different genus (Gee, 1933c).

The identity of *M. rhodesiana* Burton and *M. innominata* Burton has yet to be resolved. Although present in the material for this study, the slides of these two species appear to be a mixture of spicular components of several species. *M. rhodesiana* is generically indeterminable, since gemmules and gemmoscleres are absent, and the growth of the sponge as well as the structure of its megascleres are quite atypical for *Metania*. *M. innominata* on the other hand possesses typical gemmules and gemmoscleres of this genus, which Burton admits to be practically identical with those of *M. lissostrongyla*, but its megascleres are fusiform amphioxea. Since the free microscleres in both *M. innominata* and *M. rhodesiana* are described by Burton as almost identical with those of the insufficiently known *Spongilla brieni* Burton, it is impossible to deal with this complex until additional material will be available.

Metania reticulata (Bowerbank, 1863)

Plate 14, figures 1–4

Spongilla reticulata Bowerbank, 1863, p. 455.
Metania reticulata Gray, 1867, p. 551.—Penney, 1960, p. 46.
Tubella reticulata Carter, 1881a, p. 97.—Potts, 1887, p. 249.—Weltner, 1895, p. 114.—Gee, 1931c, p. 47; 1932c, p. 43; 1933c, p. 243.

Material.—Slides of the type (BM).

Description.—Sponge, according to Bowerbank (1863), forming a nodulose growth on a submerged branch; surface irregularly tubercular, oscula inconspicuous. Skeleton a coarse but rigid spicular net-

work, penetrating the dermal membrane in a great number of places to form spiny elevations. Consistency rigid but brittle.

Megascleres short, stout, and cylindrical amphioxea with abruptly pointed tips, occasionally true amphistrongyla, smooth to feebly microspined; length range 115–175 μ, width range 14–25 μ. A smaller type of megascleres occasionally present; these are strongly spined, bluntly pointed amphioxea, of an average length of 95 μ.

Microscleres feebly curved, fusiform, and sharply pointed amphioxea, covered with small granules at their tips and bearing large and erect spines in their central portion; length range 65–75 μ, width range 2–3 μ.

Gemmoscleres tubelliform, lower rotule almost invariably circular with an entire, slightly recurved margin; shaft ranging from smooth to bearing a few spines; terminal knob bearing a small number of minute recurved teeth; length range 20–37 μ, diameter of rotule 18–21 μ, of knob 7 μ, width of shaft 2–4 μ.

Gemmules subspherical, ranging in diameter 400–650 μ; pneumatic coat feebly developed, almost granular; gemmoscleres embedded in a manner typical for the genus; foramen produced into a very short porus tube.

Distribution.—Known only from the type locality in the Amazon R.

Color in life.—Not yet recorded.

Discussion.—While the presence or absence of free microscleres was not mentioned in the original descriptions of this species, Gee (1933c) failed to recognize them in the type material reexamined by him. Such microscleres, however, are present in the type, although they seem to be very rare.

The only gemmule examined during the present studies is much too mutilated to allow reliable comparisons with those of other species of this genus. The pneumatic layer appears granular, whereas in the majority of other species it is composed of rather large air spaces. It is hoped that *M. reticulata* can soon be relocated in South American waters so that additional taxonomic evidence can be demonstrated.

Metania vesparia (von Martens, 1868)

Plate 14, figures 5–12

Spongilla vesparium von Martens, 1868, p. 61.

Tubella vesparium Weltner, 1895, p. 114.—Annandale, 1911c, p. 54; 1918a, p. 213.—Gee, 1929d, p. 297; 1930a, p. 105; 1933c, p. 248.—Penney, 1960, p. 59.

Tubella pottsi Weltner, 1895, p. 143; 1913, p. 475.—Annandale, 1914, p. 245.—Gee, 1931e, p. 46; 1933c, p. 240.—De Laubenfels, 1936, p. 37.—Penney, 1960, p. 59.

Acalle pottsi Burton, 1934, p. 412.—Arndt, 1936, p. 17.

Metania lissostrongyla Burton, 1938, p. 463.—Penney, 1960, p. 45.

Material.—*S. vesparium:* Slide of syntype (N. Gist Gee); material and slides from Kalimantan (Borneo); *T. pottsi:* Slides of syntype (MCB); *M. lissostrongyla:* Fraction and slides of type (MCB); numerous specimens from various African localities (MCB).

Description.—Sponge forming large bulbous growths, resembling the structure of a wasp nest; surface strongly reticulate and hispid; oscula moderately large but inconspicuous; dermal membrane closely adhering to symplasm. Skeleton consisting of thick and strong radial spicule fibers, arising perpendicularly from the base, and of somewhat slimmer transverse fibers; both forming a very firm and compact network of wide meshes. Consistency of dry sponge very rigid but brittle.

Megascleres cylindrical, slightly curved, and entirely smooth amphistrongyla of greatly varying lengths, ranging 150–220 μ, width range 11–16 μ.

Microscleres almost straight, fusiform, and sharply pointed amphioxea, covered with small granules at their tips and bearing a group of larger spines in their central portion; length range 54–67 μ, width range 2–3 μ.

Gemmoscleres tubelliform, lower rotule almost invariably circular with an entire, slightly recurved margin; shaft usually irregularly covered with large tubercles or blunt spines; terminal knob either smoothly rounded, or bearing a small number of recurved minute spines; length range 35–55 μ, diameter or rotule 18–20 μ, of knob 6–8 μ, width of shaft 3 μ.

Gemmules scattered through the skeletal meshwork, spherical, ranging in diameter 400–500 μ; pneumatic layer feebly developed and comparatively thin, consisting of larger air spaces; gemmoscleres embedded in this layer in a manner typical for the genus; foramen produced into a short and straight tubule.

Distribution.—Known from Borneo (Kalimantan), Indonesia, and central Africa, distribution apparently discontinuous.

Color in life.—Not yet reliably recorded; dry sponge usually dark brown to almost black.

Discussion.—The curious fact that von Martens' (1868) paper had been overlooked by all his contemporary workers and by many subsequent authors led to the erection of *Tubella pottsi* by Weltner (1895), which now must be considered identical with *M. vesparia*. Further confusion resulted from the failure of revising authors (Annandale, Gee) to recognize free microscleres in the type slides reexamined where they are very rare but nevertheless present. This contributed to the retention of Carter's (1881a) heterogeneous generic name *Tubella* for those species apparently without microscleres and the introduction of

the revived genus *Metania* (de Laubenfels, 1936; Burton, 1938, Penney, 1960) for the rest.

The erection of *M. lissostrongyla* from Africa by Burton (1938) was the result of a wrong translation of Weltner's (1895) German description of *T. pottsi*, which clearly states that the megascleres of the latter species are stout, smooth, and feebly curved amphistrongyla, and not "spined, instead of smooth strongyla" as quoted by Burton. The specific name *lissostrongyla*, designed to differentiate Burton's species from that of Weltner, is therefore meaningless.

Morphometric comparisons of *M. vesparia* with both *M. pottsi* and *M. lissostrongyla* revealed that these three species must be considered identical, since they display uniform characters in most regards. Some slight and certainly unimportant differences, like the length range of megascleres and the rate of abundance of free microscleres, represent nothing more than ecomorphic variations in distant populations and cannot even be used for racial discrimination. It will be most interesting to find possible distributional bridges between the populations of *M. vesparia* in Southeast Asia and those in Africa. However, since the Indian spongillids have been studied in great detail, and *M. vesparia* does not seem to occur on that subcontinent, the distribution of this species must still be considered to be discontinuous.

Metania vesparioides (Annandale, 1908)

PLATE 14, FIGURES 13–15

Tubella vesparioides Annandale, 1908b, p. 157; 1911c, p. 120; 1918a, p. 213.—Gee, 1931e, p. 52; 1932c, p. 42; 1933c, p. 249.—Penney, 1960, p. 59.

MATERIAL.—Slide of type (IM); slides of syntype (N. Gist Gee, and AmstM); material and slides of syntype (AusM).

DESCRIPTION.—Sponge massive and bulbous; surface strongly reticulate and hispid, due to projection of radiating spicule fibers through dermal membrane; dermal membrane closely adhering to symplasm. Skeleton consisting of strong radial spicule fibers, and slightly slimmer transverse fibers; both forming a rigid and compact network of open meshes. Consistency of dry sponge firm but brittle.

Megascleres stout, fusiform, slightly curved, and smooth amphioxea of rather uniform length; length range 300–325 μ, width range 12–15 μ.

Microscleres almost straight, fusiform, and sharply pointed amphioxea, covered with small granules at their tips, and bearing numerous larger spines in their central portion; length range 68–75 μ, width range 2–3 μ.

Gemmoscleres tubelliform, lower rotule often irregular or polygonal and with slightly recurved margin, which as a rule is entire; radial

striations of this rotule often well developed, creating the superficial impression of an indented margin; shaft irregularly covered with large tubercles or blunt spines; terminal knob either smoothly rounded or bearing a small number of recurved minute spines; length range 42–58 μ, diameter of rotule 16–20 μ, of knob 6–8 μ, width of shaft 3 μ.

Gemmules scattered through the skeletal meshwork, spherical, ranging in diameter 400–500 μ; pneumatic layer only partially developed and comparatively thin, consisting of rather large air spaces; gemmoscleres embedded in this layer in a manner typical for the genus; foramen produced into a straight and short porus tube, surrounded by a circle of slanting gemmoscleres.

Distribution.—Apparently restricted to Burma.

Color in life.—Not yet recorded; dry sponge almost black.

Discussion.—*M. vesparioides* can be distinguished at a glance from the group represented by *M. vesparia* by its amphioxous megascleres, which never possess abruptly pointed tips as those occasionally found in the latter species. The microscleres, described by previous authors as lacking, are rare in all slides examined, but are present in the type slides revised by Gee (1933c). The marginal indentations of the lower rotule of gemmoscleres, as recorded by Annandale (1908b), were found to be an optical deception. The strong radial reinforcements of this rotule in mature gemmoscleres meet the margin in such a way that a siliceous web of polygonal outline is formed between them. While this web remains very thin the margin of the rotule, although entire, makes the impression of being irregularly incised.

M. vesparioides is thus very closely allied to *M. vesparia*, and future research may yet relegate it to subspecific rank. However, until additional material can be studied it is better to retain its separate specific status, so that possible taxonomic evidence will not be obscured.

Genus *Acalle* Gray, 1867

Acalle Gray, 1867, p. 551.—Gee, 1931c, p. 31.—De Laubenfels, 1936, p. 36.—Jewell, 1952, p. 445.—Penney, 1960, p. 32.

Tubella Carter, 1881a, p. 98 (part).—Potts, 1887, p. 250 (part).—Gee, 1931c, p. 47 (part); 1932c, p. 43 (part); 1933c, p. 241 (part).

(Not *Acalle* Burton, 1934.)

Type species.—*Spongilla recurvata* Bowerbank, 1863.

Definition.—Megascleres rather stout and cylindrical amphioxea with abruptly pointed or rounded tips, closely approaching amphistrongyla in appearance; an aggregation of terminal spines often present.

Microscleres not yet recorded.

Gemmoscleres of two different types and series: an inner layer of typically tubelliform scleres with a delicate smooth shaft, their lower rotule well developed, circular, and slightly curved inward, their upper rotule represented by a knoblike structure; and an outer layer of short and thick birotulates of unequal length, consisting of a straight smooth shaft and terminally of umbonate heads of equal size, their circular margins regularly divided into a small number of strongly recurved and stout conical teeth.

Gemmules moderately large and spherical; pneumatic layer well developed and granular; gemmoscleres embedded in this layer radially in two series: (1) Tubelliform spicules resting with their large rotule on the inner gemmular membrane, and reaching with their knobs to outer membrane; (2) birotulates with their lower rotule embedded in outer gemmular membrane, with their upper projecting beyond it; foramen tubular, porus tube short and straight.

Sponges forming thin film on solid support; surface recorded as even; color in life not yet observed; consistency fragile, crumbling.

Known only from South America.

Discussion.—The rejection of the entire system of Gray (1867) by Carter (1881a) caused the sufficiently defined but forgotten genus *Acalle* to remain in obscurity for almost 70 years. Burton (1934) was first to reintroduce this genus in spongillid taxonomy but erroneously applied it to a *Metania* species, namely *Tubella pottsi* Weltner. In a later paper, Burton (1938) listed *Acalle* as a synonym of *Metania*, correctly referring to *Spongilla reticulata* as the type species of the latter genus. Thus for the second time *Acalle* fell into obscurity until Jewell (1952) reestablished it, naming *Spongilla recurvata* Bowerbank as its type species by monotypy.

De Laubenfels (1936) loosely compared *Acalle* with *Asteromeyenia*, now a synonym of *Dosilia*, and drew attention to the fact that both possess "two types of microscleres." However, this criterion cannot be used for an assessment of an intergeneric relationship since the two series in *Acalle* are gemmoscleres, whereas in *Asteromeyenia* they are free microscleres.

Acalle is most closely related to *Metania*, from which it differs chiefly in the possession of an outer series of birotulates resembling those of *Heteromeyenia* species, and in the absence of free microscleres. The chance that the outer birotulates could be adventitious is unlikely though not impossible. Only future studies of the only representative of *Acalle*, apparently found on only two occasions, will decide whether the genus can be retained or whether it finally should be relegated to a synonym of *Metania*.

Acalle recurvata (Bowerbank, 1863)

PLATE 13, FIGURES 6–13

Spongilla recurvata Bowerbank, 1863, p. 456.
Acalle recurvata Gray, 1867, p. 552.—Penney, 1960, p. 32.
Tubella recurvata Carter, 1881a, p. 98.—Potts, 1887, p. 250.—Gee, 1931e, p. 47; 1932c, p. 43; 1933c, p. 241.

MATERIAL.—Slides of the type (BM); slides of material from the Beni R. (Bolivia) (PAS).

DESCRIPTION.—Sponge according to Bowerbank (1863) and Carter (1881), forming crusts of an even surface; oscula numerous, inconspicuous, and scattered. Consistency of dry sponge fragile and crumbling.

Megascleres cylindrical, as a rule smooth and feebly curved amphioxea with rather abruptly pointed or rounded tips, closely approaching amphistrongyla in appearance; sometimes these scleres are sparsely microspined, or bear an aggregation of minute spines on their tips, length range 120–148 μ, width range 14–16 μ.

Microscleres have not yet been recorded.

Gemmoscleres typically as discussed in the generic definition; length range of tubelliform scleres 30–33 μ, width of shaft 1.1–5 μ, diameter of lower rotule 15–16 μ.

Gemmules with an irregularly pitted surface, spherical, ranging in diameter 350–420 μ; pneumatic coat well developed, distinctly granular; gemmoscleres embedded in two series, as discussed in generic definition; foramen produced into a short straight tubule.

DISTRIBUTION.—Known only from the type locality, the Amazon R. and the Beni R., Bolivia.

COLOR IN LIFE.—Not yet reliably recorded.

DISCUSSION.—The reasons for the present retention of *Spongilla recurvata* Bowerbank in the genus *Acalle*, erected especially for this species by Gray (1867), were dealt with in the discussion of this genus. Until additional material from South America will be collected and thoroughly studied, it is better to consider this species distinct from all *Metania* species, to which it doubtlessly is closely related.

Genus *Drulia* Gray, 1867, redefined

Drulia Gray, 1867, p. 552 (part).—Gee, 1931e, p. 31 (part).—De Laubenfels, 1936, p. 36.—Jewell, 1952, p. 450.—Penney, 1960, p. 39.
Parmula Carter, 1881a, p. 99.—Potts, 1887, p. 256.—Weltner, 1895, p. 114.—Gravier, 1899, p. 128.—Cordero, 1923, p. 134; 1925, p. 113; 1928, p. 259.—Gee, 1931e, p. 33; 1932c, p. 35.—Penney, 1960, p. 54.

TYPE SPECIES.—*Spongilla brownii* Bowerbank, 1863.

DEFINITION.—Megascleres stout, curved, and almost cylindrical amphioxea, occasionally amphistrongyla, entirely smooth; often of

two distinct length groups, the smaller series then forming spicular cages around the gemmules; occasionally the smaller set only covered with irregular granulations.

Microscleres of varying abundance, always slender, fusiform and spiny amphioxea; present in symplasm and often participating in the protection of the gemmular pneumatic layer.

Gemmoscleres parmuliform, consisting of a large rotule with an internal conical depression and of more or less circular outline, and a short tapering stem without distal reinforcements.

Gemmules very large and spherical, scattered through skeletal meshwork, held in position by surrounding capsules of smaller megascleres, or without such cages; pneumatic layer either very thin, containing one to more immediately adjoining parmuliform gemmoscleres, or thick and distinctly corrugated, holding an outer and an inner gemmosclere layer separated by a wide granular space; microscleres used in varying abundance for an additional protection of the gemmules, only rarely absent; foramen produced into a wide and short tubule, bearing a distinct peripheral collar.

Sponges forming nodulose to spherical growths on submerged twigs; surface coarsely reticulate and strongly hispid. Coloration usually a dark brown. Consistency very rigid to hard, but often brittle.

Apparently restricted to tropical South America, but local dispersal still insufficiently known.

Discussion.—Carter (1881a), by rejecting the entire system of Gray (1867), introduced the generic name *Parmula* for two of Gray's three species of *Drulia, Spongilla batesii* Bowerbank and *S. brownii* Bowerbank. Although it defied the obvious priority of the well defined genus *Drulia,* this arrangement remained unchallenged for more than 50 years. De Laubenfels (1936), in giving a somewhat loose comment on all spongillid genera, correctly referred to *S. brownii* as the type species of *Drulia,* but he erroneously claimed it to be characterized "by the great difference between the size of the discs on its birotulates." That author, apparently unaware of the similarity of gemmoscleres within the genus *Drulia,* as here redefined, also retained Carter's genus *Parmula* and established *S. batesii* Bowerbank as its type species. Thus it happened that Jewell (1952) and Penney (1960) listed both *Drulia* and *Parmula* and distributed the various species between these two genera.

It will be shown in the discussion of *S. batesii* and *S. brownii* that both are certainly distinct species, but the use of their distinguishing criteria for a generic separation is fully unwarranted. In spite of its wide use by spongillid systematists, *Parmula* Carter cannot be retained and must now be relegated to a synonym of *Drulia* Gray,

the type species of which was established by de Laubenfels (1936) as *S. brownii* Bowerbank.

Drulia brownii (Bowerbank), *D. geayi* (Gravier), *D. cristata* (Weltner), and *D. batesii* (Bowerbank), even though poorly represented in the material for this study, will be dealt with below. However, no attempt can be made at the present to document their intrageneric relationship which cannot be resolved without access to additional data. *D. rusbyi* (Potts), relegated to varietal rank by Gee (1931e), and *D. brownii tuberculata* (Potts) have not yet been examined by the present authors.

***Drulia brownii* (Bowerbank, 1863)**

PLATE 15, FIGURES 1–3, 7

Spongilla brownii Bowerbank, 1863, p. 457.
Drulia brownii Gray, 1867, p. 552.—Penney, 1960, p. 39.
Parmula brownii Carter, 1881a, p. 99.—Potts, 1887, p. 257.—Weltner, 1895, p. 114.—Arndt, 1930b, p. 48.—Schröder, 1932a, p. 161.—Gee, 1932c, p. 35.

MATERIAL.—Slides of type (BM) and syntype (ZMB); material and slides from Brazil (N. Gist Gee no. 54687).

DESCRIPTION.—Sponge forming nodulose, subspherical to spherical growths, usually embracing submerged branches of trees; surface coarsely reticulate and hispid, due to projection of thornlike spicule fibers through dermal membrane. Skeleton consisting of thick and strong radial spicule fibers, arising almost perpendicularly from base, and of somewhat slimmer transverse fibers; both forming an open but very firm and compact network of wide meshes. Consistency of dry sponge very rigid to extremely hard.

Megascleres rather stout and cylindrical to broadly fusiform amphioxea with abruptly pointed tips, of two distinct lengths, entirely smooth; length range of longer series 300–400 μ, of shorter 210–290 μ; width range of longer series 28–32 μ, of shorter 22–28 μ.

Microscleres not very abundant in symplasm, or in the vicinity of gemmules; they are thin and sharply pointed amphioxea, almost straight or only feebly curved, covered with smaller spines at their tips and with larger erect spines in their central portion; length range 45–70 μ, width range 3–5 μ.

Gemmoscleres typically parmuliform, rotule with internal conical depression and with slightly recurved margins, in lateral view distinctly umbonate; margins ranging in shape from almost circular to irregular, diameter of rotule 25–28 μ.

Gemmules enclosed in cages of the smaller series of megascleres, spherical, and very large; ranging in diameter 580–700 μ; pneumatic coat comparatively thin and granular; parmuliform gemmoscleres embedded in this layer strictly radially, with their rotules resting on

the inner gemmular membrane and with their tips projecting through the outer; quite frequently present in two, rarely more, adjoining layers, one on top of the other, not separated by a space of the pneumatic coat; microscleres often completely absent, or only sparsely used in the outer protection of gemmules; outer gemmular membrane thin and slightly corrugated; foramen produced into a very wide and short porus tube, bearing a peripheral collar, with a group of slanting gemmoscleres surrounding it.

Distribution.—Known only from South America.

Color in life.—Not yet reliably observed; recorded as light green (Carter) and gray to brown (Cordero).

Discussion.—Carter (1881a) stresses the absence of a spicular cage around the gemmules, but such cages are present around two of the six gemmules examined. That author, as well as Cordero (1925), furthermore mention only a single layer of gemmoscleres to occur on the gemmules. Although this has been found correct for most of the gemmules, one gemmule of the type (BM) has distinctly two immediately adjoining layers, and thus forms transition of characters to the gemmules of *Parmula geayi* Gravier.

Drulia geayi (Gravier, 1899)

Plate 15, figures 4, 8

Parmula geayi Gravier, 1899, p. 126.—Gee, 1931e, p. 39; 1932c, p. 35.—Penney, 1960, p. 55.

Material.—Slides of type (MNHP) and of syntype (N. Gist Gee).

Description.—Sponge forming nodulose to spherical growths; surface coarsely reticulate and hispid. Skeleton consisting of a similar arrangement of spicules like in the foregoing species. Consistency of dry sponge rigid and hard.

Megascleres, microscleres, and gemmoscleres indistinguishable in structure and size from those of *D. brownii;* microscleres are similarly rare in both symplasm and pneumatic gemmular layer.

Gemmules enclosed in cages of the smaller series of megascleres, and range in diameter 570–720 μ; pneumatic layer comparatively thin and distinctly granular; parmuliform gemmoscleres embedded in this layer strictly radially, and arranged in more than two, usually four or five adjoining layers, one on top of the other; porus tube very wide, bearing a peripheral collar, with a group of slanting gemmoscleres around it.

Distribution.—Known only from Venezuela.

Color in life.—Not yet reliably observed; dry sponge recorded as dark brown to blackish (Gravier).

Discussion.—*Drulia geayi* displays characters of such great similarity to those of *D. brownii* that its separation is difficult. The

multiple arrangement of the parmuliform gemmoscleres could well be an ecomorphic phenomenon, since even in *D. brownii* a duplication of the gemmular armature has been observed. In view of the paucity of observations on South American spongillids, however, *D. geayi* is here retained as a distinct species until more material of all *Drulia* species can be studied in detail. One of Gee's slides (no. 54981) examined during the present study, and marked "*Parmula geayi* var.," even seems to share gemmular characters with those of *D. batesii*, stressing the utmost importance of a future more detailed revision of this genus.

Drulia cristata (Weltner, 1895)

PLATE 15, FIGURES 5, 6, 9

Parmula cristata Weltner, 1895, p. 143.—Gee, 1931c, p. 36; 1932c, p. 35.—Penney, 1960, p. 55.

MATERIAL.—Slide of syntype (N. Gist Gee no. 54987).

DESCRIPTION.—Sponge hemispherical; surface uneven, strongly reticulated, hispid. Skeleton of similar arrangement to that of the foregoing species. Consistency of dry sponge hard and brittle.

Megascleres stout and entirely smooth amphistrongyla, occasional abruptly and bluntly pointed amphioxea also present, apparently of only one series; length range 390–430 μ, width range 28–37 μ.

Microscleres thin and sharply pointed amphioxea, almost straight or only feebly curved, covered with small spines at their tips and with larger erect spines in their central portion; length range 55–65 μ, width range 2–3 μ.

Gemmoscleres typically parmuliform and similar to those of all species previously discussed; their margin as a rule circular, rarely irregular.

Gemmules apparently not enclosed in a cage of megascleres; pneumatic layer thin, gemmoscleres apparently forming a singular layer only; diameter ranging 340–370 μ; no data available on structure of foramen.

DISTRIBUTION.—Known only from the type locality, the Tapajos R., Brazil.

COLOR IN LIFE.—Not yet observed; dry sponge dark brown.

DISCUSSION.—This is another insufficiently known species closely allied to the *D. brownii* group but easily distinguishable from the latter by the presence of distinct amphistrongyla as megascleres. *D. cristata* is poorly represented in the material available for this study; future collections and subsequent studies are extremely desirable.

Drulia batesii (Bowerbank, 1863)

PLATE 15, FIGURES 10–12

Spongilla batesii Bowerbank, 1863, p. 459.
Drulia batesii Gray, 1867, p. 552.
Parmula batesii Carter, 1881a, p. 99.—Potts, 1887, p. 256.—Weltner, 1895, p. 114.—Cordero, 1923, p. 134; 1925, p. 113; 1928, p. 259.—Gee, 1931c, p. 33; 1932c, p. 35.—De Laubenfels, 1936, p. 37.—Jewell, 1952, p. 450.—Penney, 1960, p. 54.

MATERIAL.—Slides of type (BM) and syntype (N. Gist Gee).

DESCRIPTION.—Sponge forming subspherical to spherical growths on submerged twigs; surface coarsely reticulate and hispid due to the projection of thornlike spicule fibers through dermal membrane. Skeleton consisting of strong radial and somewhat slimmer transverse spicule fibers; both forming an open but very firm and compact network of wide meshes. Consistency of live sponge hard but brittle.

Megascleres stout and almost cylindrical, exceptionally broadly fusiform, smooth amphioxea with abruptly pointed tips; the latter occasionally rounded, resembling amphistrongyla; all scleres distinctly of two lengths, length range of longer series 320–410 μ, of shorter 220–300 μ; width range of longer series 27–30 μ, of shorter 22–28 μ.

Microscleres extremely abundant in symplasm and particularly in the vicinity of gemmules; they are thin and pointed amphioxea, almost straight, covered with smaller spines at their extremities, and with larger erect spines in their central portion; length range 54–72 μ, width range 3–4 μ.

Gemmoscleres typically parmuliform, rotule with a pronounced internal conical depression, and with more or less circular and recurved margin; diameter of rotule 26–28 μ.

Gemmules enclosed in rigid capsules formed by the smaller class of megascleres, scattered throughout the skeletal meshwork, spherical and very large; diameter ranging 590–720 μ; pneumatic layer well developed and thick, distinctly granular; parmuliform gemmoscleres embedded in two layers, one surrounding the inner gemmular membrane, the other just below the outer gemmular membrane, with their tips projecting through it; outer membrane well developed, distinctly corrugated and containing, apart from the gemmoscleres mentioned, a great number of reinforcing microscleres; foramen produced into a moderately wide and short porus tube, bearing a peripheral collar, with a group of slanting gemmoscleres surrounding it.

DISTRIBUTION.—Known only from South America.

COLOR IN LIFE.—Not yet reliably recorded.

Discussion.—*Drulia batesii* is clearly distinct from *D. browni* by its gemmular characteristics and by its prolific abundance of free and gemmular microscleres. Although these criteria permit an easy separation of both on a specific level, their use for generic differentiation, i.e., *Drulia* Gray and *Parmula* Carter, is fully unjustified. Both species seem to be the extremes of an intergrading series of species, all in urgent need of detailed revision. It is hoped that the extremely neglected spongillid fauna of Latin America will be studied more comprehensively, resulting in a better understanding of the species involved.

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