Chapter 4

Porifera

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I. INTRODUCTION

Sponges in freshwater? Many people react this way when they are told that there might be sponges in a lake or stream. Most people have seen sponges from the ocean but are unaware that they also occur in freshwater. Yet sponges are common and sometimes abundant inhabitants of a wide variety of freshwater habitats. In some situations they comprise a major component of the benthic fauna and may play important roles in ecosystem processes in freshwater.

Sponges are the simplest of the multicellular phyla. They lack organs, and tissues are their highest level of organization. Specialized cells accomplish many basic biological functions in sponges. Despite their simplicity, however, sponges display a variety of elegant adaptations to freshwater habitats including a strong capacity for osmoregulation, complex life cycles, a capability to feed selectively on a broad range of particulate resources, and, in many species, an intimate association with symbiotic algae. This chapter will introduce you to the structure, function, and diversity of freshwater sponges. It will emphasize their taxonomy and their basic ecology. For those whose interests are whetted by this introduction, Berquist[5] and Simpson[115] provide detailed treatments of the biology of the phylum Porifera in general.

II. MORPHOLOGY AND PHYSIOLOGY

The simplicity of a sponge's external features contrasts sharply with the complexity of its internal structure and function. Viewed macroscopically, freshwater sponges exhibit a limited range of nondistinct body forms; however, a microscopic examination reveals a variety of internal features. This contrast derives from the basic organization of sponges in which tissues rather than organs represent the highest level of morphological complexity. In fact, specialized cells operating independently or in association with related cells accomplish such primary functions as food gathering, digestion, and reproduction. An appreciation of the utility of sponge structure, therefore, is possible only by including microscopic examinations. Likewise, it is difficult to discuss the physiological functions of sponges independently of their microscopic structure, and these topics are presented jointly, in a general overview.

There has been substantial debate as to whether sponges should be considered as colonies or individuals[46,114].

[1] Structure, layout and much of the text originated by Thomas Frost, deceased, 2000.

This reflects the continuing difficulties that ecologists, evolutionary biologists, and zoologists in general have with deciding on what an individual is[109]. From an ecological perspective, sponges are much more like colonies, such as corals or bryozoans, in terms of their ecological function than they are like individual arthropods or vertebrates. Overall, however, concepts of colony or individual are not really appropriate for sponges because of their level of biological organization.

A. External Morphology

Freshwater sponges display a variety of morphologies that range from encrusting (Figs. 4.1, 4.2) to rounded (Fig. 4.3) and finger-like (Fig. 4.4) growth forms. Because form can vary substantially within a species[77], external morphology is of very limited use in sponge taxonomy. Variation in growth form is influenced by environmental conditions such as water movement[54,75] and the availability of light[29]. Differences can be particularly dramatic between lentic and lotic habitats[70].

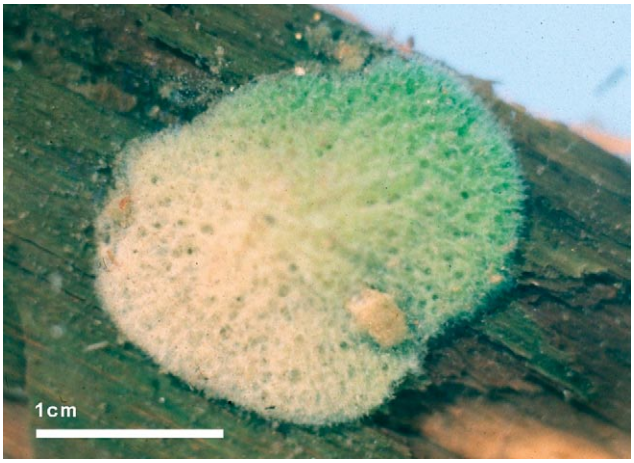

FIGURE 4.1 A small live specimen of *Ephydatia muelleri* with a gradient of associated zoochlorellae (green color).

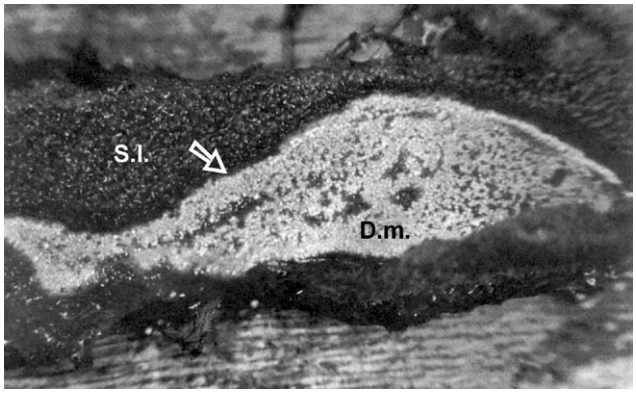

FIGURE 4.2 Gemmulated colonies of *Spongilla lacustris* and *Duosclera mackayi* exhibiting an encrusted growth form. The distinct zone between the two species (arrow) illustrates the typical nonmerging front that occurs when two different freshwater species grow into contact with each other.

The surface structure of sponges varies from flat (Fig. 4.1) to strongly convoluted (Fig. 4.3). Although there are some species-associated differences in surface characteristics, this feature, too, is strongly influenced by habitat conditions. Finer-scale characteristics of external sponge anatomy are related to internal features. Examples, as discussed below, include the incurrent and excurrent portions of the feeding canals and extensions of the skeletal system.

B. Internal Anatomy and Physiology

The basic organization of a sponge consists of a surface epithelium, made up of pinacocytes, surrounding an organic matrix, termed the mesohyl, which contains a broad variety of specialized cells. Cells within the mesohyl interact with the epidermal cells to accomplish basic functions including the processing of water for food uptake and gas exchange, digestion, structural support, and reproduction. Some sponge cells are highly plastic in their behavior and can shift their function with changing environmental conditions. De Vos et al.[14]

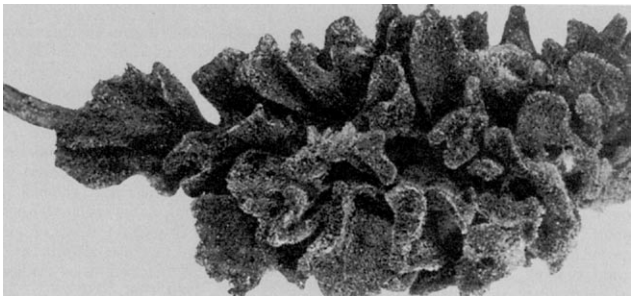

FIGURE 4.3 A colony of *Ephydatia muelleri* exhibiting a rounded and convoluted growth form (from Neidhoefer[70]).

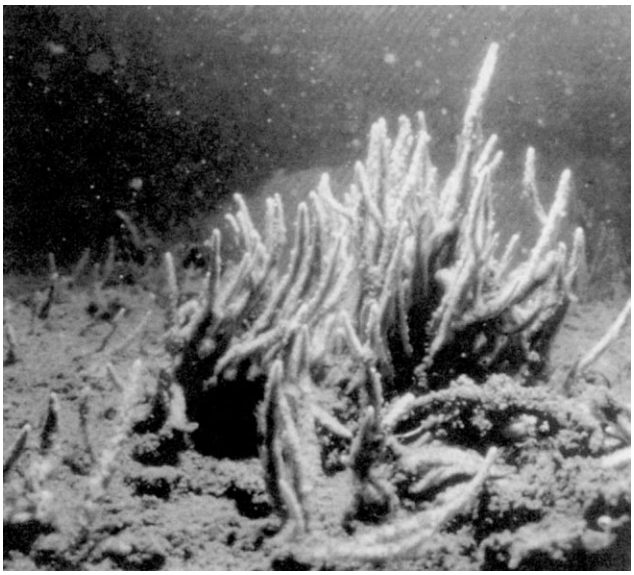

FIGURE 4.4 A colony of the common freshwater sponge *Spongilla lacustris* exhibiting a characteristic, finger-like growth form.

provide a detailed atlas of the overall general morphology of sponges illustrating most cell types with scanning and transmission electron micrographs.

All sponge cells, including those in the epidermis and in the mesohyl, appear to be involved in osmoregulation[137]. This capacity has been critical in allowing invasion of freshwater by sponges from their original marine habitats.

1. Water Processing System

A sponge can be considered, essentially, as a series of progressively finer filters and a mechanism that circulates water through them. The sponge filters can remove particles ranging from large algae to bacterial cells less than 1 μm in diameter and, possibly, to colloidal organic matter[25]. In addition, the movement of water through the canal system, with its extensive surface area, fosters the transport of gases and excreted materials. The main features of the sponge water-processing system (Figs. 4.5, 4.6) have been identified through the efforts of numerous investigators (reviewed in[20,25]) with several papers by Weissenfels and his co-workers [59,137–141,143] providing particularly important details on structure. Although there are some subtle differences among species, the summary below provides a general overview of the structures associated with sponge water processing.

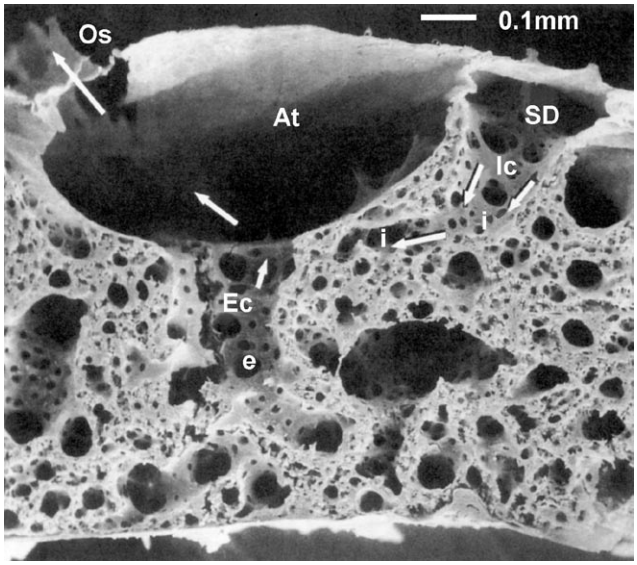

FIGURE 4.6 A scanning electron micrograph of a cross-section of the freshwater sponge *Ephydatia fluviatilis* indicating the form, size, and arrangement of the feeding canal system. Illustrated are a subdermal cavity (SD), an incurrent canal (IC) with lateral branches into the sponge (i), and excurrent canal (EC) and its lateral branches (e), an atrium (At), and an osculum (Os). Arrows indicate the flow path of water and numerous choanocyte chambers are visible throughout the sponge. Magnification, approximately 100× (from Weissenfels[143]).

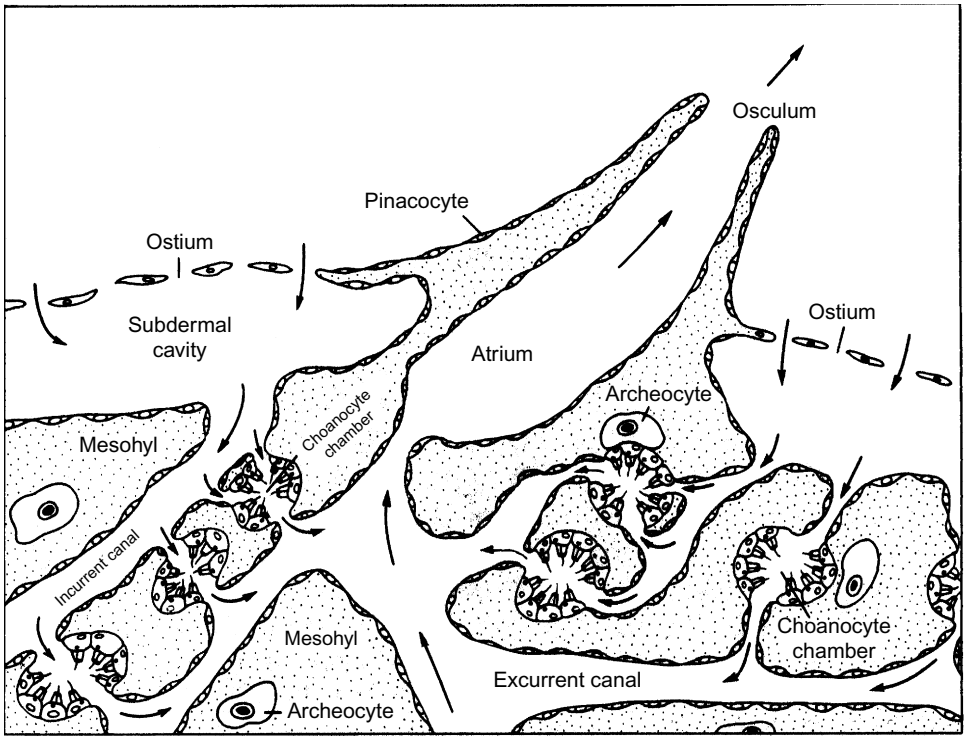

FIGURE 4.5 A schematic diagram indicating the primary components of the sponge-feeding canal system. The diagram is not drawn to scale. Water flow patterns are indicated by arrows.

Water first enters a sponge through a large number of 50-μm diameter openings termed ostia (single: ostium) that are spread across its surface epithelium. Passing through the surface, inflowing water next enters a large subdermal cavity. From there water flows into incurrent canals which branch repeatedly into canals of progressively narrower diameters, until they reach a choanocyte chamber (Fig. 4.5).

Choanocyte chambers are the keystones of the sponge-feeding system. Each chamber consists of numerous choanocytes which are characterized by the presence of a flagellum and a collar of microvilli. Beating by the flagella within these chambers is primarily responsible for establishing water flow through the sponge. Water flow is also facilitated by a sponge's basic hydrodynamic structure. Vogel[131] has demonstrated that water will actually flow passively, albeit at a reduced rate, through the feeding canals of killed sponges because of this structure. Choanocytes also serve as the final filters in the feeding system. The microvilli that make up the collars of the choanocytes are spaced to form openings less than 0.1 μm in diameter.

Once water has passed the choanocyte chambers, it enters the excurrent portion of the water-processing system. Exiting the choanocyte chambers, the canals join together in an anastamosing fashion forming larger and larger diameter vessels, finally entering a broad chamber termed an atrium. From this chamber water exits the sponge body through a specialized structure termed an osculum. Such oscula channel water from large portions of a sponge and each sponge is likely to have several oscula. Water is forced from the oscula with sufficient force so that materials that have passed through the sponge are transported far enough away from the sponge so that they are unlikely to be recaptured by the flow of water entering that sponge.

Although the description above may suggest that the structure of the sponge canals is fixed, the system is actually dynamic. The positions of both the incurrent and excurrent canals, as well as their components, can shift as the sponge grows or as portions of the feeding canals are occluded by ingested materials[68]. Similarly, the mesohyl of freshwater sponges exhibits rhythmic condensation that either assists the choanocyte chamber in pumping water[142] or in clearing the canal systems of clumps of waste[62].

2. Digestion

A second key feature of sponge feeding involves the capacity of the cells within the canal network to engulf particles through phagocytosis. Cell types exhibiting this capacity for phagocytosis include the *porocytes* which form the ostia on the sponge surface, the *pinacocytes* lining the incurrent canals, and the *choanocytes*. Digestion and transport of nutrients within the sponge body also involve phagocytic activities in which materials are exchanged between cells. Detailed studies employing light and electron microscopy[110,127,145] have provided information on activities by cells in sponge digestion.

Phagocytosis can occur when a particle makes contact with a surface within the canal system. Food particles large enough to occlude a sponge's ostia are taken up directly at the epithelium. Smaller particles are taken up after contact with the cells lining the canal walls or with the collars of the choanocytes. Following initial uptake, food particles are transferred to digestive cells, termed archaeocytes, which move freely within the mesohyl. As digestion proceeds, archaeocytes bearing ingested materials move through the sponge interior and transfer nutritional materials to other cells such as those involved with reproduction or skeleton formation.

After the digestion of ingested materials is completed, archaeocytes move to the excurrent portion of the canal network. Nondigested material is released into the water flowing out of the sponge by a reverse phagocytic action. Egested particles are then carried by excurrent flow out through oscula at the sponge surface.

Detailed analyses of cell activities in sponge digestion have revealed a surprising degree of complexity. The time necessary for a particle to traverse the digestive system completely, from initial uptake to release into an excurrent canal, can vary markedly with the nature of the food particle and with environmental conditions. Ordinarily, digestible food particles may be held within archaeocytes for more than 12 h prior to the release into the sponge excurrent. Under certain circumstances, sponges can sense indigestible particles and release them after much shorter time periods[22]. The capacity to speed the processing time for ingested materials is most evident when a sponge is faced with a dense suspension of particles. At such times, food particles may be taken up, cycled, and released almost immediately[110].

The sophistication of the sponge-feeding system is particularly evident in digestive activities because the rapid cycling of ingested particles can be highly selective. While overabundant particles are being quickly cycled through the sponge, other food particles, present in lower concentrations in the feeding suspension, are held within the sponge for periods that are sufficiently long to allow normal digestion[22,24]. Sponges, therefore, are selective feeders, not in their initial uptake of particles as selective feeding is typically defined, but in their ultimate use of these resources[23].

A sponge's capacity to vary particle transit time is linked to the large number of cells that are operating within it. Digestive cells are sufficiently numerous that, under normal feeding conditions, each cell handles only one ingested particle at a time[145]. Each individual archaeocyte then can be considered as a separately functioning digestive unit with the capacity to tune its actions to the characteristics of the food particle that it is processing.

3. Skeleton

The gross structure of freshwater sponges derives from an interplay between two fundamentally different components a mineral skeleton made up of siliceous structures termed spicules and an organic skeleton made up of collagen.

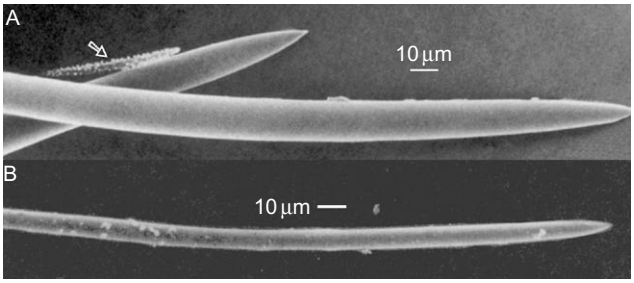

FIGURE 4.7 Scanning electron micrographs of megascleres from *Spongilla lacustris* collected from lakes with a: (a) high concentration of dissolved silica and (b) low concentration of dissolved silica. A spined microsclere is indicated by arrow.

Collagen binds spicules together into rigid structures yielding the sponge's basic framework. All freshwater sponges exhibit skeletal systems comprising siliceous spicules and collagen. Marine sponges exhibit a broader variety of supporting structures[5].

a. Siliceous Spicules

Some major groups of sponges are unique among multicellular organisms in their use of silica as a primary component of their skeleton. Freshwater sponge spicules are made up of opalescent silica that has been laid down along an axial, organic filament by specialized cells termed sclerocytes. Considerable diversity exists in spicule morphology, and, because much of this variability is species-specific, their structure plays a critical role in sponge taxonomy.

Three general categories of spicules are recognized: (1) megascleres, which make up the main framework of a sponge; (2) microscleres, which appear to add structural reinforcement for sponge tissues; and (3) gemmoscleres, which form part of the resistant coat of gemmules (see below). Megascleres are needle-shaped structures (Fig. 4.7) that range in length from 150 to 450 µm. Microscleres are similar in form to megascleres but are usually less than one-fifth their length (Fig. 4.7a arrow). Gemmoscleres are similar in size to microscleres and both exhibit a variety of forms ranging from needle-like to dumbbell- or star-shaped. Any of these three spicule forms may be smooth or spined depending upon the species. An elaborate terminology has been developed to describe the varied shapes of spicules. These terms have been summarized in Boury-Esnault and Rützler[8], but their use has been kept to a minimum in this chapter. The fine-scale structure of the spicules, particularly the gemmoscleres, plays a critical role in the taxonomy of sponges, and its importance cannot be overemphasized. The classification of freshwater sponges is based fundamentally on the structure of gemmule spicules[77].

b. Collagen

The predominant form of collagen in sponges is spongin, which serves primarily to bind the spicules of the inorganic skeleton together. A second form of collagen provides small-scale structure within the sponge mesohyl. Finally, collagen, often combined with gemmoscleres, forms the resistant coat of gemmules.

4. Reproduction

Both sexual and asexual processes can play major roles in sponge reproduction. Sexual reproduction involves the activities of numerous isolated reproductive cells functioning throughout the body of an active sponge. Asexual reproduction often involves major changes in all of the cells within a sponge.

a. Sexual Reproduction

Although detailed observations have been made for only a few freshwater species, it appears that the mode of sexual reproduction is usually gonochoristic, with each separate sponge being entirely male or female. In at least some cases, however, the gender of a particular sponge is not fixed but appears to depend upon environmental conditions. In at least one species, *Spongilla lacustris*, sponges have been shown to switch sex from one year to the next[35]. Bisbee[6] reported one hermaphrodite specimen in a population of *S. lacustris* in South Carolina where most sponges exhibited only male or female elements.

Sexual reproduction is accomplished by specialized cells that develop within the mesohyl during limited portions of the year. Reproductive cells are derived from other, more common sponge cells. Spermatogenesis occurs within distinct spermatic cysts which appear to be formed from choanocytes. Egg cells (oocytes) seem to develop either from archaeocytes or from choanocytes. Oocyte growth depends upon a variety of nurse cells that are phagocytized as the egg develops[31]. Because the occurrence of these events does not occur for extensive periods, successful sexual reproduction requires synchronous timing of egg and sperm development across sponge populations in a habitat. This has been documented for some freshwater species[117]. This requirement leads to spectacularly synchronized events of extensive sperm production in some marine species[96].

Fertilization occurs when sperm that have been released into the open water by other sponges are brought into the canal systems of female sponges by their feeding currents. Sperm are then taken up by the sponge, probably by choanocytes, and conveyed to an egg cell where fertilization takes place.

As is the general case within the Porifera, freshwater sponges are viviparous. Larvae undergo extensive development prior to their release from the mother sponge. Material for growth is provided by nurse cells. In the final stages of development, the sponge larva, termed as parenchymula, contains archaeocytes, pinacocytes, sclerocytes, and choanocyte chambers. In addition, its surface is covered by flagellated epithelial cells which allow the larva to swim upon release.

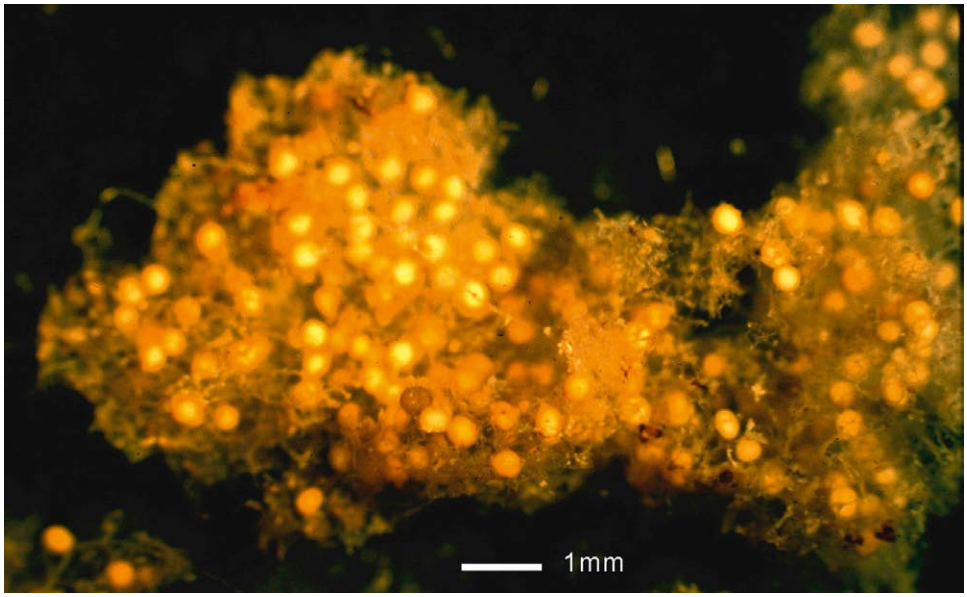

FIGURE 4.8 Numerous gemmules (the small golden spheres) of *Spongilla lacustris* in a formerly active finger-like growth of the sponge.

Once development is completed, larvae are released through the excurrent portion of the feeding canal system. The larvae swim until they settle onto a substratum, where they undergo metamorphosis and quickly develop the structures typical of adult sponges.

b. Asexual Reproduction

Asexual reproduction in sponges may be simple or complex. On one extreme, clonal development of separate, independently functioning sponges can take place through fragmentation. The plastic nature of sponge cells makes it possible for even very small pieces to develop into active, fully functional sponges. Propagation in this fashion occurs commonly in some habitats[26].

On the other extreme, most freshwater sponges typically form gemmules in a complex process of de-differentiation in which the structures of the active sponge regress into a mass of cells surrounded by a resistant coat (Figs. 4.2, 4.8). This process, which often occurs prior to the onset of rigorous environmental conditions, permits sponges to weather periods of stress and to disperse into other habitats.

The coat of a mature gemmule usually consists of three collagen layers. In most species, specialized spicules, gemmoscleres, which are formed only during gemmule formation, are also embedded within the gemmule coat. The coat of each gemmule is continuous with a much thinner layer at a single specialized structure, termed a micropyle or foraminal aperture, through which cells emerge during germination. Within the gemmule are a large numbers of specialized cells, thesocytes, which contain numerous yolk inclusions. Thesocytes can store energy-rich materials which are used for growth following germination. The aggregation of cells to form gemmules takes place within the mesohyl. Gemmules are often present in large numbers within the vestigial skeletons of previously active sponges.

Completely formed gemmules exhibit low metabolic rates until germination is induced, and are extremely resistant to environmental stress. Gemmules of a common freshwater species *Ephydatia muelleri* survived exposure to −80°C for more than nine weeks[3] although cold tolerance has been shown to vary substantially among species[124]. Gemmules can also survive anoxic conditions for several months[100]. Upon germination, the thesocytes increase their metabolic rate, exit from the gemmule coat through the micropyle, and differentiate into the varied cells typical of an active sponge.

At least one freshwater sponge species is also capable of another form of asexual reproduction, budding. Buds exhibit many of the structures of active sponges, but in a smaller form that is capable of dispersal within water[107]. They do not, however, exhibit the same resistance to adverse environmental conditions as gemmules.

5. *Biochemistry*

Sponges exhibit a variety of unusual chemical constituents. Some, particularly those identified as secondary metabolites, have been linked with an ability to deter predation[78]. Particularly unusual among chemical features of sponges has been a major portion of fluorine in the body of a marine species[37]. Most unusual chemicals have been documented in marine species, but some are also likely to occur in freshwater species. It has been suggested that they may provide some defenses against predation and overgrowth by epizooic organisms for freshwater sponges[19].

III. ECOLOGY AND BEHAVIOR

A. Diversity and Distribution

1. Diversity

The diversity of sponges in freshwater is low in comparison with that in the marine habitats from which they have evolved. Although the entire phylum Porifera consists of more than 5000 species[5], there are probably fewer than 300 freshwater species worldwide. The most recent taxonomic revision of freshwater sponges (suborder Spongillina) lists 191 species in 43 genera[64]. While it is certain that there are additional, undescribed species, particularly in tropical regions that have not been thoroughly investigated (e.g., the Amazon Basin[132]), it is clear that freshwater forms represent a small group within the sponge phylum.

In turn, North American freshwater sponges represent only a restricted subset of the world's freshwater species. Overall, within both the Spongillidae and Metaniidae (the latter family of uncertain validity), we have generated a list of 32 species in 12 genera for continental North America, including Mexico and Central America.

2. Distribution

From the broadest perspective, the distribution of sponge species is influenced by biogeographic factors. At smaller scales, species distributions are largely constrained by physical environmental variables; water chemistry (e.g., pH, salinity, silica) appears to play a major role in determining which species will be present in a particular lake or river within a region. Within the lake or river, local conditions such as light, substrata, and wave action will control where species will occur or dominate.

The freshwater sponge species in North America exhibit a variety of distribution patterns[76,77]. Several species have been reported throughout the United States and Canada, while others have been observed in only one or a few habitats. In some cases, a broad distribution in North America represents only a subset of a more extensive range. *Ephydatia fluviatilis* and *Eunapius fragilis* are distributed worldwide, whereas *S. lacustris, E. muelleri,* and *Trochospongilla horrida* occur throughout temperate regions of the Northern Hemisphere. Some species exhibit more restricted intercontinental distributions. *Racekiela ryderi* occurs primarily in eastern North America but has also been reported once in Central America and from several locations in western Europe[73]. Other species are broadly distributed throughout North America, but have not been observed on other continents (e.g., *Duosclera mackayi* and *Trochospongilla pennsylvanica*). Of the remaining North American species, most appear to be restricted to limited regions within Canada and the United States; in the most extreme cases, several rare species have been reported from single locations.

Within Canada and the United States, there have been numerous reports on the occurrence of sponges in provinces and states or regions within them. Some recent examples include reports for Alberta[10], Arizona[122], Connecticut[13], eastern Canada[104], western Montana[4], and southern Lake Michigan[60]. Penney[76] extensively reviewed earlier reports on freshwater sponges. Despite these reports, information available on the occurrence of sponges does not match their overall distribution.

The apparently limited ranges of some species may result from a lack of observations rather than actual restrictions in their distribution. Accepting this limitation, however, there appear to be some general trends in the distribution of sponges across North America. For example, relatively few species of sponges have been reported in western regions, and there appears to be a general east-to-west reduction in sponge species richness. A similar trend occurs between northern and southern regions, with more species reported from the northern United States and southern Canada than more southern regions of the continent. In some situations, the limited distribution of a particular species may involve adaptations to climatic conditions. In many other cases, dispersal limitations are likely to influence regional distribution patterns.

However, there are some notable exceptions to limitations on dispersal, as suggested by the disjunct global distribution of a few species. The spotty northern European occurrences of *R. ryderi*, distributed mainly in eastern North America, are hypothesized to be the result of the long-distance transport of gemmules by birds across the Atlantic Ocean; the occurrence of American species of aquatic plants with similar European distributions lends credence to this argument[63,73]. Furthermore, two freshwater sponges are candidates for recent human-assisted invasions in Central America, both in the Panama Canal: *Eunapius carteri*, previously unrecorded in the Western Hemisphere, and *Trochospongilla leidii,* previously found only in the United States[56,86]. Neither species was mentioned in Hildebrand's[47] survey of invertebrate animals in the canal system, even though *T. leidii* was later found to be abundant and conspicuous on the walls of the Gatún locks[56]. It seems likely that both species were introduced by ship traffic using the canal.

Within regional distribution patterns, the factors that regulate the occurrence of a species in a particular lake or stream are less well understood. There are a few species whose occurrence is determined primarily by a single environmental factor; for example, *Spongilla alba* appears to be restricted to brackish water habitats[83] and *D. mackayi* is restricted to dystrophic waters[104]. However, most other species are influenced by a broad combination of environmental factors. Jewell[54,55] provided the most detailed quantitative information available on this topic. In comparing species across lakes in northern Wisconsin, she found considerable variation in each species' habitat requirements. Some species were restricted to a narrow subset of

environmental conditions, but others occurred throughout a broad range of habitats. Accordingly, chemical factors were correlated with the distributions of some species, but for other species more recent analyses indicate that there is wide tolerance of chemical conditions[11]. In addition, some species were favored by flowing water, while others were more typically associated with standing water. In general, it is difficult to pinpoint any specific factors that control the distribution of sponges. Many species are sufficiently broad in their distribution that most lakes can be expected to contain at least a few species. This is particularly true in certain regions (e.g., northern Wisconsin) where sponges occur in nearly every lake. Aside from cases of geographic isolation, sponges would be excluded only from habitats with frequent physical disturbances, with high pollution levels, or with high loadings of silt or particulates that can clog their feeding systems[39]. Developmental abnormalities and reduced growth rates have been observed in sponges exposed to endocrine disruptors[48]. Not all pollutants affect sponges, however; they appear to be tolerant of high levels of some contaminants, particularly heavy metals[106], although exposure to some metals produces distinct morphological deformities[17].

Within a lake or stream that is suitable for growth, local sponge distribution is controlled by finer scale environmental features. For most sponges, a hard substratum is essential for growth and the absence of such a surface will limit the distribution of sponges even where other conditions are highly favorable. Only a few species, notably *S. lacustris* and, to a lesser extent, *E. muelleri*, can grow in soft sediments. In rivers and streams, sponges are excluded from areas with high flow due to physical disruption. In lakes, sponges can be limited in shallow waters by wave action or ice scour[2]. In deeper waters, sponges can be limited by low oxygen or by colder temperatures. Some species with symbiotic algae may be limited by light availability, particularly where water is darkly stained by dissolved organic materials; however, species with less dependence on symbionts may thrive in such habitats.

B. Reproduction and Life History

The annual life-history pattern for most freshwater sponges involves periods of active growth and dormancy and includes both asexual and sexual reproductive processes. Transitions to and from dormant stages usually involve the asexual processes of gemmule formation and hatching. Asexual reproduction also occurs during active growth periods both in the formation of gemmules and in the generation of separately functioning sponges through fragmentation. Sexual reproduction occurs only for a limited time during periods of active growth. Key features of the freshwater sponge life cycle are summarized in Fig. 4.9 and discussed in detail below. Overall, reproduction in sponges involves responses to two distinct problems,

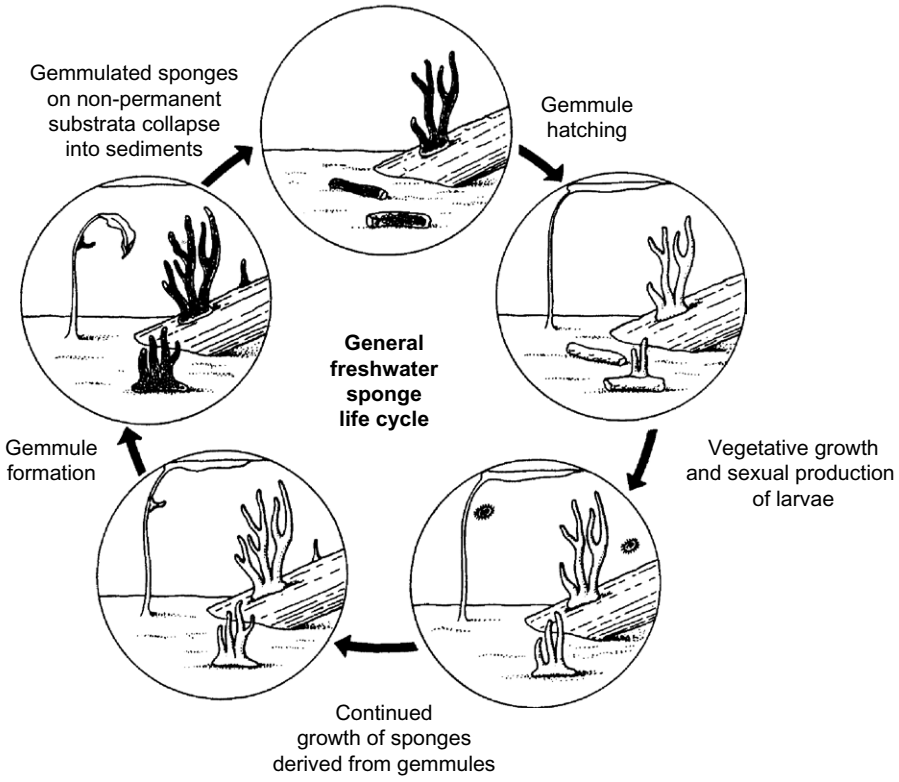

FIGURE 4.9 General features of the annual life history of freshwater sponges (see text for detailed explanations).

propagation within a single habitat and dispersal among habitats. Within-habitat processes are discussed separately below, prior to a consideration of dispersal.

1. Dormancy

In most cases, dormant periods for freshwater sponges are characterized by the complete transformation of all active tissue in a sponge into gemmules[115,116]. More rarely, tissue regression occurs yielding a growth form that functions as a gemmule without its specialized structures[30]. In either situation, sponge-feeding ceases and respiratory activities are greatly reduced. Most studies of dormancy in sponges have focused on transitions involving gemmules.

Despite the common role of gemmules in dormancy, their presence does not in itself signify a transition to a dormant life-cycle period. In many cases, particularly where sponges are large, a few gemmules are produced during most of the active season.

Most freshwater sponges undergo a period of dormancy at some time during the year, typically during periods of environmental stress. In temperate habitats, dormant periods occur most commonly during winter. This is the case for most sponges in North America. However, at lower latitudes, this pattern can be reversed with dormancy occurring during hot, summer periods and active growth taking place during cooler seasons[49,82]. Dormant periods have also been observed in response to drying in ephemeral habitats. While dormancy is a common feature of freshwater sponge life cycles, it does not always occur; some sponges maintain active growth even under winter ice cover.

The timing of dormancy varies both among species within particular habitats and among habitats for individual species. In Lake Pontchartrain, Louisiana, *S. alba* exhibits a typical pattern of gemmule formation during winter months[83], while a co-occurring population of *E. fluviatilis* exhibits a reciprocal pattern of summer dormancy[45]. At the same time, populations of *E. fluviatilis* in more northern habitats form dormant stages in winter. *S. lacustris* populations in New Hampshire gemmulated during winter and were active during summer[117], whereas population in South Carolina were inactive during summer periods[6]. Sexual reproduction occurred at different times during the seasonal cycle in these areas as well. In Little Rock Lake, Wisconsin, *S. lacustris* undergoes a winter dormancy period, but co-occurring populations of *Corvomeyenia everetti* and *E. muelleri* maintain active growth during the entire winter. Populations of *E. muelleri* in nearby Wisconsin lakes undergo typical winter dormancy.

The transition from an active to a dormant state for sponges usually appears to be cued by environmental factors such as changing temperatures or declining water levels. In some species, this transition may also involve a complex response to previous growth conditions[32]. Within a region, the timing of gemmulation is nearly synchronous across habitats for all populations of a species that exhibit dormancy (Frost, unpublished data). In contrast, different species within a region can vary substantially in the seasonal timing of dormancy and in the rate at which the transition from active tissue to gemmules proceeds. In Mud Pond, New Hampshire, *T. pennsylvanica* begins forming gemmules in mid-August when water temperatures are at their maximum, while *S. lacustris* does not form gemmules until October, when water temperatures fall to 10°C[117].

Sponge species also vary in the factors that induce their release from dormancy[116]. Temperature appears to be the primary environmental cue that induces gemmule hatching in temperate habitats. Gemmules of some sponges hatch while water temperatures are at near-winter levels, suggesting that another cue such as photoperiod or the availability of light is operating.

In some species, gemmules exhibit a form of diapause in which some exposure to cold temperatures is necessary before hatching can occur[116]. Such a delay prevents hatching during short, warming periods prior to the onset of winter. Hatching at such times could lead to major population reductions if time or energy was insufficient for a second formation of gemmules. Not all species form diapausing gemmules and, in these cases, hatching will take place during any period of increasing water temperature. The occurrence of diapause appears to be linked to the timing of gemmule formation; species that form gemmules later in the year are less likely to exhibit diapause. While there are obvious costs to hatching at the wrong time, there may also be advantages to being able to hatch quickly without diapause. Studies of dormancy in freshwater sponges have generally focused on cold-water populations and less is known about the factors that control the transitions to and from dormant stages when they occur in response to hot or dry conditions.

In general, while it is clear that the formation of dormant stages plays a crucial role in the overall life history of most sponges, substantial variability is apparent in: (1) the morphological forms involved in dormant stages; (2) the timing of transitions to and from dormant periods; and (3) the occurrence of diapause. This variability suggests that the overall value of dormancy and the successful strategies by which it can be employed differ markedly among habitats and that sponge responses to such differences involve a diversity of adaptations.

2. Growth, Reproduction, and Dispersal within Habitats

Nondormant periods in the freshwater sponge life cycle appear to be characterized by continuous growth. Although quantitative studies have been limited, sponge growth in some habitats can be extremely prolific. In a pond in New Hampshire, 10 mg dry mass of gemmule tissue of *S. lacustris* that hatched in spring produced an average of 18 g of active sponge tissue just prior to gemmule formation the following

fall[26]. *E. fluviatilis* exhibited comparable prolific growth rates in a European stream[90]. Growth is largely indeterminate for individual sponges, which may reach surprisingly large sizes. In some optimal habitats, for example, a single specimen of *S. lacustris*, consisting of intertwined fingers (as in Fig. 4.4), can occupy more than 1 m^3 of space.

Sexual reproduction for most freshwater sponge populations occurs synchronously throughout a habitat in a one-to-three month period following hatching from dormant conditions[117]. Synchrony across a population is particularly important, because otherwise the sperm released by male sponges would have a low probability of successfully fertilizing an egg[31].

The motile larvae produced by sexual reproduction in freshwater sponges can play an important role in the establishment of new sponges. In particular, the colonization of new substrata will often depend upon such motile forms. While settling on an appropriate substratum is clearly critical for the successful growth of a new sponge, little information is available on substrate choice by settling sponge larvae. Studies of a variety of marine invertebrates suggest, however, that substrate selection by freshwater sponge larvae may be possible.

Fragmentation of intact specimens into separately functioning units may also play an important role in freshwater sponge life cycles. In some cases, such fragmentation occurs during periods of tissue regression and may not lead to growth on new substrata. In other habitats, particularly those with large amounts of aquatic vegetation to which sponges can attach, fragmentation and growth may occur repeatedly during an active season, leading to dispersal throughout a habitat[26].

Although gemmules are frequently associated with dormant periods, they may also be present in freshwater species during periods of growth. Many sponge species routinely contain a few gemmules within otherwise active tissue, particularly in areas of thick growth. In an extreme case, *S. lacustris* develops specialized, summer gemmules which have much thicker coats than the gemmules formed for over-winter periods, which may serve in a "bet-hedging" strategy against some environmental catastrophe occurring prior to more extensive gemmule formation[36]. It seems likely that summer gemmules may also aid dispersal among lakes or streams.

3. Dispersal Among Habitats

As is the case for most freshwater organisms, an ability to disperse among different habitats is critical for the continued success of sponges in freshwater environments. Most lakes and streams are ephemeral from an evolutionary perspective. Nearly all lakes in North America are less than 20,000 years old[18], a brief period compared to the 100 million year history of freshwater sponges[91].

While there has been little documentation of dispersal by freshwater sponges among habitats, it seems likely that gemmules are the primary agent for such movement. Two other life-cycle stages that might function in dispersal among habitats, larvae and sponge fragments, possess neither the structural nor the physiological mechanisms necessary for movement out of water or across significant distances. It is conceivable that these forms, particularly the larvae, could function in short-range dispersal among connected water bodies, but their fragile structure would preclude any out-of-water transport. In contrast, gemmules, with their resistant coats and ability to withstand harsh environmental conditions, appear well suited to dispersal among habitats. For example, Ricciardi and Reiswig[104] observed the rafting of buoyant, gemmule-laden fragments of *S. lacustris* during annual periods of flooding in the Ottawa River.

C. Ecological Interactions

As is the case with all organisms, the size of a freshwater sponge population and its subsequent impact on an ecosystem ultimately result from processes of tissue growth and loss. Growth is regulated by the availability of nutrients and suitable habitat. Losses are influenced by physical environmental conditions and potentially by interactions with other organisms. Although quantitative studies are few, it appears that the dynamics of freshwater sponge populations are mediated largely by the availability of suitable microhabitats within a lake or stream. Where substrata for sponge growth are short-lived or where physical disturbances are frequent, growth and loss rates can be extremely rapid and may operate primarily in a density-independent fashion. Under such circumstances, sponge populations would be regulated by an interplay between the physical environment and their own growth and life-history processes. Concomitantly, interactions with other organisms would exert only minimal influences on sponge population processes. In contrast, where substrata are permanent, sponge populations appear more likely to be regulated by intra- or interspecific biotic interactions[53]. In many sponge habitats where growth on permanent substrata is rare, such biotic interactions could be expected to exert only a secondary role in their population dynamics.

1. Availability of Substrata

The development of freshwater sponge populations usually depends upon the availability of hard substrata. Most species must be attached to a substratum to grow. In addition, all species appear to depend upon solid surfaces for successful settling and growth of their free-swimming larvae. A broad variety of surfaces are suitable; examples range from boulders or exposed bedrock to the branches of fallen trees to the leaves and stems of aquatic macrophytes. Sponge growth is often abundant on human-built structures in water, especially permanent structures providing extensive vertical surfaces, such as bridge foundations, canals, and dams.

Among North American species, only *S. lacustris* has been routinely observed growing out of soft sediments. A quantitative investigation of its population dynamics[26], however, illustrated a crucial role for substrata even where sponges did not depend upon such substrata for their growth. In Mud Pond, New Hampshire, *S. lacustris* grows either directly from soft bottom sediments or attaches to any of the several species of aquatic macrophytes which exhibit large summer populations but which die back completely before winter. Due to the near absence of any permanent substrata in Mud Pond, gemmulated sponges overwinter almost exclusively in sediments on the pond bottom. Successful hatching in spring depends upon the presence of enough gemmulated tissue to grow out of these sediments, and many sponges are not large enough to make this transition. Most sponges are unsuccessful in hatching, and spring populations are sparse. Hatching from sediments, therefore, is the limiting step in the Mud Pond population's dynamics. Despite remarkable growth during summer (1000-fold increase in biomass), the population of *S. lacustris* in Mud Pond was maintained at nearly constant levels throughout five years of observations. Essentially, the population is maintained in a density-independent fashion by a combination of the lack of permanent substrata and the difficulty of gemmule hatching from soft sediments.

Sponge population dynamics appear to be substantially different in habitats where more permanent substrata are available. Populations of *E. fluviatilis* growing on hard substrata in a river in Sardinia, Italy, exhibited growth rates that were still high but were substantially lower than those reported for *S. lacustris*[90]. Populations were persistent on rocks over several years making transitions from active to gemmulated tissue. They were substantially disrupted, however, by a major flooding event, but did recolonize habitats fairly quickly. In general, there appear to be periods of substantial population growth with substantial degeneration during other parts of the year, a process that can be categorized as density-independent[90]. Finally, in Mary Lake, Wisconsin, *S. lacustris* grows attached to trees that have fallen into the lake, and sponges repeatedly make the transition from active tissue to gemmules and back to active tissue within the same skeleton over the course of several years. In contrast with the large fluctuations in sponge density observed in Mud Pond, populations of *S. lacustris* in Mary Lake apparently maintain higher densities throughout the year and lower growth rates during the summer than those seen in Mud Pond (Frost, unpublished data). Under such circumstances, population dynamics can be characterized as primarily density-dependent.

Overall, the availability of substrata exerts a major control over sponge population dynamics. For many species, the lack of substrata limits growth completely. But, even where species are not wholly dependent upon substrata, their nature and availability can exert a major influence over sponge population dynamics. The longevity of an individual sponge, including repeated transitions between active and gemmulated states, would appear to be directly related to the permanence of its substratum. In addition, it seems likely that the importance of both intra- and interspecific biotic interactions in sponge population dynamics will be influenced by the time that a particular substratum has been available for colonization. Only on relatively permanent substrates would sponges be likely to reach sufficient densities to interact with each other.

2. Nutritional Ecology

When suitable habitats are available, sponges are capable of substantial growth. In some cases these high growth rates appear to be linked primarily to a sponge's efficient particle-gathering mechanisms. In other situations, however, sponges have an alternative means of obtaining resources. Many freshwater sponges contain large numbers of intracellular algae. They form symbiotic associations that combine autotrophy and heterotropy. In addition, because sponges require substantial amounts of silica for their spicules, population growth and maintenance have the potential to be influenced by silica availability.

a. Sponge Feeding

Although there have been several detailed studies of the mechanisms by which sponges feed and of the resources they consume[25], much less is known about the influence of food availability on sponge growth under natural conditions. The rates at which sponges filter water can be extremely high. During summer, specimens of *S. lacustris* typically filtered more than 6 mL per hour per mg dry mass of tissue[23]. At this rate, a finger-sized sponge filters more than 125 L in a day. Because a sponge's feeding effectively removes all particles ranging in size from bacteria to large algae from the water it filters, these rates suggest that sponges may exhaust available food under some circumstances. Food limitation would be particularly likely in still water or where particulate resources are sparse. Pile et al.[80] demonstrated that such depletion occurred in Lake Baikal, Russia, where sponges consumed a variety of picoplankton (cells $< 2\,\mu$m diameter) in substantial quantities.

b. Algal Symbionts

In many cases, freshwater sponges are bright green (Fig. 4.10) from large quantities of chlorophyll contained within extensive populations of algal symbionts[33,34]. This situation is so common that freshwater sponges are frequently mistaken for plants. The algal symbiosis in freshwater sponges is representative of a large number of algal–invertebrate associations that are common in marine and freshwater habitats[95]. In these mutualistic associations, the nutritional processes of algae and invertebrates are closely

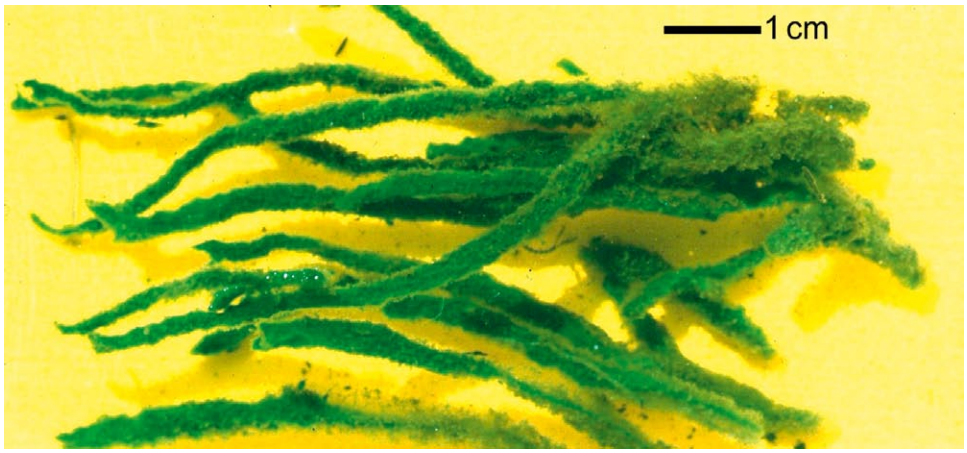

FIGURE 4.10 Live freshly collected *Spongilla lacustris* fragments showing their brilliant green coloration due to associated zoochlorellae.

coupled. In freshwater sponges, and in many other invertebrates, algae are maintained endosymbiotically within the cells of their host.

Algal–invertebrate symbioses combine autotrophic processes with normal animal heterotrophy. In the resulting, mixotrophic nutrition, symbiotic algae provide photosynthetically fixed carbon to the invertebrate host which, in turn, supplies nutrients such as nitrogen or phosphorus or carbon dioxide to the algae. This combination has proved particularly successful in nutrient-poor conditions such as coral reefs[69], but occurs over a broad range of habitats.

Algal symbionts play a major role in the growth of some freshwater sponges. Contributions from symbiotic algae accounted for 50–80% of the growth of *S. lacustris* in Mud Pond, New Hampshire[29]. The contribution of algae was determined by maintaining sponges *in situ* under darkened conditions, which led to the loss of their algae. Comparisons were then made between the growth of such aposysmbiotic sponges and that of normal green sponges maintained under lighted but otherwise identical conditions. In similar experiments in Little Rock Lake, Wisconsin, *S. lacustris* and two other sponge species were incapable of any growth and died after a few weeks under darkened conditions (Frost, personal observation). Symbiotic algae contributed substantially to the growth of *S. lacustris* in a Danish stream[108]. Not all sponges depend upon algal symbionts, however. Some species can live in darkness where their nutrition is based solely on heterotrophic processes.

The factors that control the proportional contribution of autotrophic and heterotrophic processes to overall sponge nutrition are less clear. That sponges failed to grow under darkened conditions in only some habitats indicates that the relationship between a sponge and its algal symbionts can range from facultative to obligate, depending upon environmental conditions. Even for species that sometimes depend to a large extent upon their algae, the amount of algal chlorophyll within a sponge (a rough measure of the potential contribution of its algal symbionts) varies markedly both among habitats for a species, among species within a single habitat, and even between areas within a single specimen (Fig. 4.1). In a survey of northern Wisconsin lakes, the average concentration of algal chlorophyll in *S. lacustris* varied among lakes by more than a factor of three (Frost, unpublished data). Similarly, in Little Rock Lake, Wisconsin, three sponges exhibited consistent species-specific differences in their chlorophyll content which were coupled with significantly different rates of photosynthesis and feeding[27]. These differences occurred even though the three species shared identical environmental conditions.

The symbiotic relationship between sponges and algae differs fundamentally among sponge species. Some species depend to a large extent upon algae for growth, while others exhibit little dependence. These differences among species may involve specializations to particular environmental conditions, in that sponges containing large amounts of algal chlorophyll may grow only where light is readily available. Comparing habitats, it seems likely that sponges would vary the density of their symbionts in response to the relative availability of light and particulate resources. However, this relationship is not simple. Detailed examinations of several sponge species indicate that increasing particulate resources may favor higher rather than lower concentrations of algae[27].

Until recently, it had been thought that all symbiotic associations of algae and invertebrates in freshwater involved the presence of one group of green alga termed zoochlorellae[95]. Invertebrates hosting this alga include protozoans, hydra, flatworms, clams, and sponges. It has now been determined, however, that at least one freshwater sponge species, *C. everetti*, and likely its congener *C. carolinensis*, contain a yellow–green alga as their symbiont[28]. Volkmer-Ribeiro[133] has suggested that the *Corvomeyenia* species have an evolutionary history that is long distinct from sponges with green-algal symbionts. These distinct histories combined with numerous overall similarities between sponges with

green and yellow-green symbionts indicate that two closely convergent symbiotic associations have evolved separately in the freshwater sponges. Morphological affinities between marine algae and the yellow-green symbiont suggest that the symbiotic association in *Corvomeyenia* may have developed in an ancestral marine form and been maintained during a subsequent invasion of freshwater. It is important to note that differences between zoochlorellae and yellow-green algae cannot explain the observed differences in algal contributions to overall sponge nutrition described above. Substantial differences in the contribution of algae have been observed in comparisons of sponge species that contain only green algal symbionts.

The variety of ecological interactions between sponges and algae and the complexity of their evolutionary history indicate that algal symbioses have been important in the diversity and distribution of freshwater sponges.

c. Potential Alternative Nutritional Modes

Additional means of gathering food resources have been documented recently for some marine sponges. Vacelet and Boury-Esnault[125] described a deep-sea sponge that lacks a typical sponge water-processing system and feeds on small animals with a carnivorous-like mechanism. Moreover some carnivorous sponges near deep-sea hydrothermal vents exhibit a symbiotic relationship with methanotrophic bacteria[126]. Neither nutritional mode has been documented in freshwater species, but their existence in marine habitat raises interesting possibilities.

d. Influence of Silica on Skeleton Structure

The availability of silica within a habitat may exert both direct and indirect effects on sponge growth. As discussed previously, some sponges are restricted to high or low silica habitats. However, some species are distributed across habitats exhibiting a broad range of silica conditions where they exhibit major responses to its availability. For example, in populations of *S. lacustris* in different lakes in northern Wisconsin, the total amount of biogenic silica and both the number and morphology of megascleres vary directly with lake silica concentrations (Frost, unpublished data). Total biogenic silica and spicule width (Fig. 4.7) decrease as less silica is available. In contrast, however, the number of megascleres increases as their width decreases. With this combination of changes, the total surface area of megascleres remains constant as silica decreases—a situation that increases the structural support gained per unit of available silica. This suggests a direct and complex response by sponges to different availabilities of silica.

Responses to low-silica conditions are related to changes in the stiffness and growth form of sponges. Specimens of *S. lacustris* from high-silica habitats are much stronger and more resistant to breakage than those growing where silica is low. Sponges in low-silica habitats, therefore, may be limited to growing closely attached to substrata or in waters with little wave action. Also, because spicules may play a role in the resistance of sponges to predation (see below), populations in low-silica habitats may be more vulnerable to consumption.

3. Biotic Interactions

a. Competition for Space

The availability of suitable surfaces on which to grow plays a crucial role in the population dynamics of freshwater sponges. As such, competition for space may be important to sponge distribution and abundance. A sponge has the potential to compete for space whenever its growth leads to contact with another sponge or any other organisms. There are reports of significant interactions within and between sponge species, as well as between sponges and other organisms. Such interactions do not appear to occur commonly, however, and the role of competition for space in the regulation of freshwater sponge populations remains largely unexplored. In part, this is due to the minimal attention that has been given to such competitive interactions among freshwater organisms in general. In addition, because freshwater sponge populations are often limited by density-independent processes, the abundance of sponges within a habitat is usually sparse, with little potential for competitive interactions.

When specimens of same sponge species grow into contact with each other on a substratum, two distinctly different results have been observed[128]. In some cases, the separate sponges will form a single, functionally integrated unit. In other instances, a distinct structural barrier is erected in areas of contact and the two sponges continue to function as completely separate units. The genetic relationship between sponges appears to control whether they will merge or develop a barrier. Separate sponges grown from fragments or gemmules taken from the same original sponge will always merge with each other. In contrast, experimental manipulations have indicated the existence of distinct strains within a sponge species which will not merge with each other[130]. Studies of marine sponges originally suggested that only sponges that are genetically identical would merge with each other[72]. However, subsequent analyses have indicated that, while the probability of merging appears to be a function of the genetic similarity of sponges, specimens need not be genetically identical in order to join into a single unit[123]. Such fusion interactions in sponges operate at a cellular level[129] and have attracted the attention of researchers interested in the basic process of cell–cell recognition. These studies have direct implications for the understanding of immune-response systems in more complex invertebrates and in vertebrates[121].

Competition among different sponge species for space has been thoroughly documented in marine systems. Marine studies have demonstrated a complex hierarchy in which

certain sponge species can completely overgrow and kill other species[53]. These interactions have a major influence on the structure of benthic communities[52]. Observations of competitive interactions in freshwater sponges have been limited to instances where sponges have been shown to develop a nonmerging front similar to that described above for intraspecies interactions (Fig. 4.2). In temperate regions, *E. fragilis* has a life-history strategy that involves the formation of an attached pavement layer of gemmules for overwintering. The simultaneous hatching of these gemmules and the subsequent rapid growth of a confluent sponge colony early in the spring effectively conserves much of the substrate occupied by the previous colony, resulting in a competitive advantage where space is limited[104]. On relatively permanent substrates, some sponge species may completely overgrow other sponges, but the significance of such interactions in freshwater habitats remains to be demonstrated.

Competition for space between sponges and other organisms had likewise received little attention in freshwater habitats. However, sponges have been shown to overgrow and kill invasive dreissenid mussels (zebra mussel *Dreissena polymorpha* and quagga mussel *D. bugensis*) in Europe and North America[58,61,105]. Unfortunately, while sponge overgrowth can have lethal and sublethal effects, it is unlikely to control invasive mussel populations because of the high rate of mussel recruitment and environmental constraints on sponge growth[105].

Sponges often overgrow and sometimes kill colonies of plumatellid bryozoans (Ricciardi and Frost, personal observations). Some species (e.g., *E. fragilis*) commonly grow massively on the exposed shells of unionid mussels, possibly benefiting from suspended food particles drawn toward it by the siphonal current generated by the mussel[104]. Sponges often encrust fronds and stems of aquatic macrophytes, but do not seem to harm the plants.

b. Predation and Infaunal Organisms

Conspicuous predation upon sponges, in which major portions are consumed by a larger organism, is rare. Various smaller organisms consume portions of sponges, but they appear to act as grazers or parasites, leaving the sponge that they consume largely intact. Such species that feed on sponge tissue represent a subset of the diverse infaunal community that typically occurs within freshwater sponges. Other infaunal organisms appear only to make use of the structure provided by a sponge in a commensal relationship.

Resistance to predation by larger organisms appears to be characteristic of the Porifera in general[92,101]. Mechanical and chemical defenses combine to make sponges resistant to predation. Spicules provide mechanical deterrence to predators; these sharp spines are thought to act as an irritant to its mouth and digestive system. The effectiveness of spicules in deterring predation was evident in experimental tests in which snails would not consume *S. lacustris* from habitats were it contained robust spicules but would consume specimens from habitats in which low silica availability limited the size of spicules (Frost and A. Covich, personal observation). Chemical deterrence to predation has been attributed to a variety of toxic and pharmacologically active compounds that are well documented in marine sponges[9] and that are also likely to occur in freshwater species.

Despite the general effectiveness of sponge defense mechanisms, a few organisms prey effectively upon sponges. In some cases, sponge predators have developed a nearly complete dependence upon sponges. The few large predators on freshwater sponges include fishes, crayfishes, ring-necked ducks, and possibly snails. Extensive predation by fish on sponges has been documented in Africa[15] and South America[135] but is not common in North America. Crayfish were implicated as causing major reductions in a sponge population in a Massachusetts stream[146], although widespread consumption of sponges by crayfish has not been reported. Juvenile ring-necked ducks sometimes depend upon sponges as a food source[66]. Snails will consume and can subsist on freshwater sponges under laboratory conditions (Frost and Covich, personal observation), but here too, their significance as predators under natural conditions remains unknown.

Numerous small invertebrates reside within, or attached to, freshwater sponges. Examples include protozoans, oligochaetes, nematodes, rotifers, bivalves, water mites, and aquatic insects[12,101,134]. Various relationships exist between these infaunal organisms and their sponge hosts. Some infaunal species feed upon sponges while others use the sponge body as a habitat. In some cases the relationships are obligate, at least for certain life-cycle stages, and such species may show a striking degree of specialization to the sponge host. A recently reported freshwater shrimp–sponge association was reported in an ancient African lake[136]; such associations are common in marine systems, but previously unknown for freshwater sponges.

Several groups of aquatic insects typify organisms with obligate, specialized feeding on freshwater sponges. Numerous species within three insect orders, the Diptera, Neuroptera, and Trichoptera, depend upon freshwater sponges during major portions of their life cycle[101]. One neuropteran family, the Sisyridae, is so commonly associated with sponges that its members are referred to as spongilla flies. Not all relationships between insects and sponges are obligate. Some insect genera that contain obligate sponge-feeding species also contain species that are only occasionally or never associated with sponges[102]. The variety of interactions evident between sponges and related insect species indicates that the evolutionary history of insect–sponge relationships is diverse and complex[12].

Obligate relationships with freshwater sponges have also been documented for water mites[89] that apparently depend upon the sponge primarily for structure. The water mites live

and lay their eggs within the sponge's feeding canal system. These and other organisms that live within sponges (e.g., clams, insects, and protozoans) may be taking advantage of the lack of predation on sponges. Spicules and chemical defenses may provide a general refuge against predators on infauna as well as sponges.

The community ecology of the infaunal organisms themselves is also complex. The presence and abundance of a particular infaunal species results from an interplay of its own life cycle, the life cycle of the host sponge, and potentially the abundance of other infaunal organisms. For example, data from northern Wisconsin sponge populations indicate that most other infaunal species are rare or absent during periods when water mites are abundant within sponges (J. Elias and Frost, unpublished data). Again, this is an area that has received little attention.

4. Functional Role in Ecosystems

In most lakes and streams, populations of freshwater sponges are sufficiently sparse that they are unlikely to play a major role in ecosystem function. However, there are marked exceptions to this general pattern. In some habitats, sponges are the dominant component of the benthic community and exert a substantial influence on total nutrient cycling and primary production. Quantitative analyses of freshwater sponge populations are rare, but a detailed study of one population illustrates the potentially major impact of sponges on ecosystems[21,26]. At the peak of its population size in early October, *S. lacustris*, in Mud Pond, New Hampshire, reached an average biomass of greater than 3.5 g dry mass per m^2. At this density, the total sponge population in the pond would filter more than 10^7 L of pond water per day, a rate that would cycle a volume equivalent to that of the entire pond every seven days. Since the sponges can remove most phytoplankton and bacteria from the water they filter, their potential impact on Mud Pond is substantial. Because of their algal symbionts, sponges can also account for a substantial portion of the primary production in Mud Pond. During late summer and fall, the chlorophyll within the sponges can approximately equal the entire phytoplankton community[21,29].

Sponges also play a major role in flowing water ecosystems. A detailed study of the River Thames in England, found that sponges accounted for nearly 40% of the total production by benthic animals[65].

Clearly, sponges can be a major component of the biota of some ecosystems. While detailed quantitative studies are rare, observations indicate that the populations in Mud Pond and River Thames are representative of sponges in many other lakes and streams. Sponge populations in some northern Wisconsin lakes, for example, appear to be substantially larger than those in Mud Pond (Frost, personal observation). At the same time, sponges in many ecosystems represent only a minor component when compared with other organisms.

Even when sponges account for substantial portions of an ecosystem's primary and secondary production, they may not interact directly with higher trophic levels. The lack of predation on sponges can lead to an accumulation of material in sponge biomass that is not passed directly up the food chain. A sponge's interactions with other ecosystem components may be indirect, operating primarily to limit the availability of materials to other organisms within the food web.

5. Paleolimnology

The siliceous nature of sponge spicules makes them resistant to decomposition under most circumstances. As such they are usually well preserved in lake sediments and may serve as a useful tool in indicating historic lake conditions. In situations where specific habitat requirements can be defined for a species[54], the presence of its spicules in the sediments of a lake from which it is currently absent can indicate changes over time in that lake's environmental conditions. Likewise, even when a sponge species is present throughout an extended period within a lake, quantitative changes in spicule morphology can indicate shifts in the availability of silica within that lake over time. For example, silica in lakes throughout northern Wisconsin appear to have declined by more than 50% over the last 12,000 years[57]. Paleolimnological investigations employing sponge spicules are a potentially fruitful area for study[41]. Studies in 28 Connecticut water bodies revealed that most lakes had maintained the same sponge populations over the past century, while a few lakes had exhibited changes in sponge populations that might indicate a decline in water quality[74]. Spicule presence and distribution has been used to infer the history of selected Florida soils[112]. Further studies have the potential to reveal other important features of lake history.

IV. EVOLUTION AND PHYLOGENETICS

All freshwater sponges belong to the class Demospongiae, the most diverse and morphologically complex of the four major groups in the sponge phylum. Within the demosponge order Haplosclerida, the freshwater sponges are grouped together as a distinct suborder, the Spongillina[64]. The evolutionary history of the freshwater sponges is long and almost certainly polyphyletic. Fossil freshwater sponges are reported from at least 100 MYA[91] and, although there is still debate in this area, there may have been at least three, and possibly six, separate, successful invasions of freshwater from marine habitats, some as far back as the Jurassic Period (210–140 MYA). The separate invasions are presently classified into distinct families among the freshwater sponges[64,133,134].

The phylogenetic diversity of freshwater sponges is not well represented in North America where species are confined primarily to the most cosmopolitan family, the Spongillidae[77]. Volkmer-Ribeiro[133] proposed that species in the genus *Corvomeyenia* should be grouped, along with several South American species, in the family Metaniidae with an evolutionary history in freshwater that is distinct from the spongillids. Only two North American species, *C. everetti* and *C. carolinensis*, occur in this proposed family which has a worldwide, primarily tropical, distribution[133]. Not all sponge biologists, however, have recognized the Metaniidae as a separate family[104,118].

The four other recent freshwater sponge families are absent from North America. Species in the Lumbomerskiidae appear to be confined to a few large and ancient lakes in Europe and Asia (e.g., Lakes Baikal and Ochrid) and the family is characterized by a large degree of endemism. Species in the Potamolepidae are widely distributed throughout Africa and South America[134]. The Metchnikowiidae consists of a single species endemic to the Caspian Sea[64]. The Malawaspongiidae includes six species endemic to ancient lakes ranging from Africa to Celebes[64].

Freshwater sponges have been used in molecular sequence analyses either as a small subset in exploration of the large-scale phylogeny of demosponges[7,71,94], of the relationship between freshwater sponges and marine sponges[50], or have focused explicitly on phylogeny within the smaller group of freshwater sponges[1,51,67,79,111]. Only small subsets of the six recent families have been used so far. The results cannot yet be considered to be very useful for making significant phylogenetic conclusions, but they support the contention that the freshwater sponges are a monophyletic group among Demospongiae. These studies do not support separate lineages for the families Lubomirskiidae and Spongillidae, the two groups most widely examined. Little can be concluded yet concerning the other families for which no or few species have been included. Status of Metaniidae remains inconclusive relative to Spongillidae, although the metaniid genus *Corvomeyenia* is consistently found to be the most deeply branching component of the Spongillina clade. Meixner et al.[67] suggest that the present distinct endemic species in remote lakes has had frequent and independent origin from a few cosmopolitan founder freshwater species, arguing against multiple independent marine intrusions as origins of the different families presently recognized.

V. COLLECTING, REARING, AND PREPARATION FOR IDENTIFICATION

Collecting sponges is usually straightforward. In many cases, sponges grow in shallow water and can be obtained simply by hand or with a long-handled rake. Where sponges are rare, it may be easiest to collect them while snorkeling. This may be the case particularly when collecting in areas with numerous hard substrata where small stones must be overturned and the undersides of fallen trees and large boulders must be examined. Where sponges grow in deeper waters, scuba techniques afford the most efficient means of collection. Dredges or nets dragged across substrata in deeper waters are likely to miss most sponges and, at the same time, are likely to disrupt substantial bottom areas. In very deep waters, however, these may be the only practical means of collecting.

When searching a lake or stream for sponges, it is best to examine as broad a variety of substrata as possible. Aquatic macrophytes, rocks, and fallen logs are common sites for sponge growth. In bog habitats, the roots of vegetation growing at the edges of bog mats or on the undersides of the mats themselves are likely sites for sponges. Where sponges are rare, it may be necessary to examine a large number of different substrata before finding any specimens. In other habitats, however, sponges will be conspicuous.

Growing or maintaining sponges under controlled environmental conditions is much more difficult than collecting them. Some investigators have grown small sponges from gemmules in the laboratory for cytological investigations[16,93]. Such specimens can also be particularly useful in examining small-scale structural details of sponges. Poirrier et al.[87] developed an effective, continuous-flow system for sponges using bacteria as a food source. Laboratory investigations of this sort can provide important insights into sponge ecology[45], particularly when controlled conditions are essential. Sponges appear to be highly sensitive to environmental conditions, however, and the responses of sponges obtained in laboratory studies must be compared carefully with their behavior under field situations. As such, to evaluate sponge behavior under natural conditions, it is often best to work with freshly collected sponges and to conduct experiments *in situ* whenever possible.

The identification of freshwater sponges depends primarily on characteristics of spicules and on features of intact gemmules. Successful species identifications require obtaining all the spicules (megascleres, gemmoscleres, and, if present in a species, microscleres) occurring in a species. Thus, it is absolutely essential to obtain samples of sponges that include all spicule types. Gemmoscleres are particularly important, and this can present a problem because gemmules (Figs. 4.2 and 4.8) may only occur during certain times of the year. Some gemmoscleres may remain in active sponge tissue after gemmules have hatched, so there is some chance of identifying sponges without gemmules visible in them. Gemmules should be sought carefully in any survey, however.

As the primary step in species identification, samples of all types of spicules that occur in a species should be prepared for microscopic examination. To obtain spicule preparations, organic portions of a sponge should be digested with acid and the remaining spicules mounted on a glass

microscope slide. Sponge tissue can be digested with nitric acid in a centrifuge tube immersed in boiling water for one hour. The spicules can then be concentrated by graviational settling or gentle centrifugation, after which the acid is poured off and the spicules are then washed with ethanol or methanol. Washing and settling or centrifugation should be repeated at least three times, after which the spicules are mounted on a microscope slide using a cover slip and a permanent medium (e.g., Permount®). Reiswig and Browman[97] described a more rapid and precise method of bypassing gravitational settling or centrifugation by collection of spicules on filters and mounting the filter with spicules on microscope slides.

Intact gemmules can be removed from sponge tissue and mounted directly on microscope slides after either drying or clearing. Specimens of entire sponges are necessary for museum collections. Whole sponges can be dried or preserved in alcohol. Formalin is fine for fixation, but specimens eventually disintegrate if stored in formalin solutions; transfer them to ethanol for storage. Simpson[113] described methods that can be used for preparing freshwater sponges for cytological observations, such as are necessary for examining reproductive cycles.

VI. IDENTIFICATION OF FRESHWATER SPONGES

A. Classification

A stable classification scheme for freshwater sponges has not yet been developed, hence the species descriptions are listed here alphabetically. The most recent definition of genera and their arrangement has been assembled in the monumental revision of the suborder by Manconi and Pronzato[64], but their species lists were not completely authoritative and several generic arrangements have changed since that publication. It serves as the primary source of descriptions of generic-type species. The scheme used by Penney and Racek[77], the most complete species-level taxonomic revision of the family Spongillidae, remains the most important source of detailed descriptions of most of the species reported here and should be consulted for rigorous taxonomic investigations. Information for several species in this chapter is based upon reports other than that by Penney and Racek, most of which have been published since 1968. In cases where substantial information about a species has been obtained from a source other than, or in addition to, Penney and Racek, these sources have been cited along with the species description in the list of species below. In addition, there are a number of cases where species reported for Canada and the United States by Penney and Racek[77] have been subsequently judged as invalid[40,42,44,82,84], and these species have not been included here. Ricciardi and Reiswig[104] provided another valuable source of information on 15 sponge species that occur in eastern Canada and this report should be consulted for more detailed information on these species. All North American species names that remain taxonomically valid as of this revision, are included, despite their absence in earlier versions of this chapter and in spite of the very high likelihood that some of them are junior synonyms of the more common species.

B. Identification

In general, the freshwater sponge species in Canada and the United States can be distinguished by characteristics of their spicules. Taxa are separated primarily by the presence, shape, and spination of microscleres and/or gemmoscleres, although the presence or absence of spines on megascleres can be a useful characteristic in some cases in distinguishing species within a genus. Spicules are usually either needle- to rod-like (Fig. 4.7) or dumbell-shaped (Fig. 4.11). The latter are termed birotulate, and their ends, originating as disks, are called rotules. Some difficulty occurs when

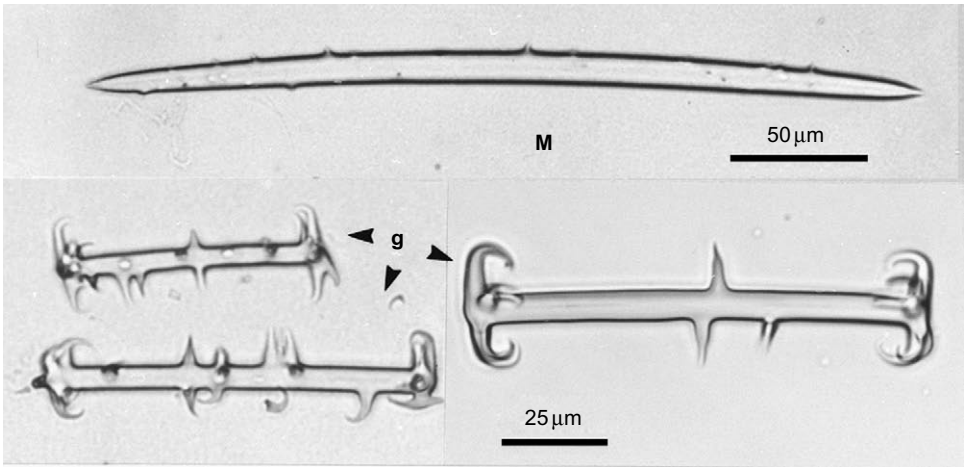

FIGURE 4.11 *Anheteromeyenia argyrosperma* spicules; megasclere (M) and gemmoscleres (g) (from Ricciardi and Reiswig[104]).

similar spicules are derived from true birotulates and rod-form spicules. True rotules are often marginally incised to form rays, and some nonrotular spicules have spines aggregated at the tips to form rotule-like structures; the latter are called pseudobirotulates. In the descriptions here, a spicule should be assumed to be needle- to rod-like unless it is described as otherwise. Also, the descriptions reported here are based upon examinations with light microscopes. More detailed examinations with a scanning electron microscope (SEM) can reveal fine structures, primarily spines, that are not apparent in light microscope observations. Such finer scale observations should be interpreted with caution when employing the descriptions and key provided here.

Gemmoscleres are critical in the classification of freshwater sponges, and it is important to include gemmules when preparing sponge specimens for identification. Obtaining gemmoscleres may be a problem, particularly in young sponges derived from larvae, where gemmules and their spicules may not be present during certain times of the year. Examine a collected specimen closely to insure that gemmules are present (Figs. 4.2 and 4.8). It is possible, particularly in larger specimens, that some gemmoscleres may have been left in a sponge body from a previous year's gemmules. However, it is also possible that a few stray gemmoscleres or even entire gemmules from another sponge species may have been incorporated into a sponge specimen. The growth of the tissue of one sponge species over the gemmules of another species has lead to some erroneous species identifications[103]. Thus, identifications based upon only a few gemmoscleres should be made with caution.

In some species with microscleres, it may be difficult to distinguish between microscleres and gemmoscleres on the basis of structure alone. By separating gemmules from intact sponges and making separate spicule preparations of them, it is possible to obtain samples in which gemmoscleres predominate. Alternatively, by carefully sampling tissue from the surface of a sponge in areas of new growth, it may be possible to obtain material in which gemmoscleres are rare and in which microscleres and megascleres predominate. Because of the important role that microscleres play in separating species, identifications based on only a few microscleres should also be made with caution.

It is important to consider that ecomorphic variation can be substantial for some sponge species, particularly *R. ryderi, E. fluviatilis,* and *S. lacustris*. Cautions about particularly troublesome situations are raised in the species descriptions below.

In using the key presented here, there are only two cases in which characteristics other than the structure of spicules are required to distinguish among taxa. In contrasting the genera *Ephydatia* and *Radiospongilla*, it is necessary to obtain a cross-section of intact gemmules to view the arrangement of gemmoscleres within the gemmule coat. Similarly, within the genus *Heteromeyenia*, one must employ the size, shape, and structures of the foraminal aperture of entire gemmules to distinguish among species. Particularly important for *Heteromeyenia* are the forms of structures on the end of the foraminal tubule termed cirrous projections.

Ricciardi and Reiswig[104] reported an extensive survey of sponges in eastern Canada in which they reported 15 species. The report is extremely useful and should be consulted for detailed information on the species that it reports. It even includes a key for distinguishing, to a certain extent, among sponges for which gemmoscleres are not available, a critical requirement of the key here and for using that by Penney and Racek[77].

C. List of Freshwater Sponge Species of North America

Summarized below are the spicular characteristics and distribution patterns of freshwater sponges reported from North America, Alaska to Panama, but excluding the Caribbean Islands. Dimensions presented for spicules are the ranges that have been reported for them; average values to be expected are very approximately the mean of the numbers listed below. In some cases, mean dimension values are reported as "upper range-(mean)-lower range." It is important to note that these mean values are from Ricciardi and Reiswig[104]. They may be specific to sponges from eastern Canada and may not be representative of sponges growing in other regions. Values for ranges are the widest values that have been published in the papers reported here. Some sponge spicule features may vary from habitat to habitat. For a few species, information is also provided on features of gemmules, such as the distribution of gemmoscleres within them, their opening structures (foraminal apertures), and their overall distribution within a sponge body. Geographic distribution patterns not only emphasize the occurrence of sponges in North America but also describe the overall distributions reported for each species.

1. Anheteromeyenia argyrosperma *(Potts) (Fig. 4.11)*

Spicules: megascleres slender oxeas, 240-(284)-304 μm in length, and sparsely covered with small, sharply pointed spines; microscleres absent; gemmoscleres birotulates of two distinct length groups, 65-(81)-89 and 110-(130)-160 μm, with both size classes similar in form, exhibiting spines on their entire shaft and with conspicuous recurved, claw-like hooks on their ends.

Distribution: reported from the eastern half of North America from Florida to Canada but confined to this region.

2. Anheteromeyenia biceps *(Lindenschmidt)*

Spicules: megascleres slender oxeas, 255–325 μm in length, smooth to completely covered with microspines except

at ends; microscleres absent; gemmosclere birotulates of two kinds, the shorter and more numerous is 17–22 μm in length, slender with flat, deeply serrate rotules; the longer is 24–30 μm in length, stout, and tylote or dumbell-shaped, with knob-like rotules. This geographically, very restricted species is likely a variant of one of the more common species. Harrison and Harrison[42] suggested that it is an ecomorph of *E. muelleri*, but their supporting evidence was unconvincing. The more likely possibility that this is an aberrant form of *E. fluviatilis* has not yet been explored.

Distribution: reported only from creeks near Douglas Lake, Cheboygan Co., Michigan.

3. Corvomeyenia carolinensis *(Harrison)*

Spicules: megascleres slender, straight to slightly curved oxeas, entirely smooth, ranging in length from 194 to 280 μm; microscleres small birotulates with straight to strongly curved (>80%), smooth shafts, 15–25 μm in length terminating in rotules 4–7 μm in diameter with 4–6 recurved hooks; gemmoscleres large birotulates with straight to slightly curved, smooth shafts ranging in length from 60 to 158 μm and terminating in rotules of 13–22 μm diameter with 5–8 recurved hooks[38]. Distinction between *C. carolinensis* and *C. everetti* is questionable; both were reported from a single Connecticut lake[1] and differ mainly in the proportion of curved microscleres.

Distribution: reported from one pond in South Carolina and one lake in Connecticut.

4. Corvomeyenia everetti *(Mills) (Fig. 4.12)*

Spicules: megascleres slender, slightly curved, and entirely smooth oxeas, 143-(218)-285 μm in length (in rare cases, a variable number of megascleres may be sparsely spined); microscleres small birotulates, mostly straight or slightly curved, 14-(18)-26 μm in length terminating in rotules 3-(5)-7 μm in diameter with three to six small, distinctly recurved spines; gemmoscleres large birotulates with straight to slightly curved, smooth shafts, ranging in length as 33-(59)-78 μm and terminating in rotules 10-(20)-26 μm in diameter bearing five to seven recurved hooks. See notes above on *C. carolinensis* and below on *Corvospongilla novaeterrae* and information in Ricciardi and Reiswig[104].

Distribution: reported only from the eastern half of Canada and northeastern United States.

5. Corvospongilla becki *(Poirrier)*

Spicules: megascleres stout oxeas to strongyles, 130–218 μm in length, usually curved, covered with spines, the spines being larger near the ends of a spicule; microscleres birotulate, 25–44 μm in length, rotules 9–17 μm in diameter usually with four recurved hooks; gemmoscleres strongyles of two distinct length classes, the smaller 28–56 μm in length, is slightly to strongly curved and spined except in the inner curved region, the larger 71–139 μm in length, is straight to slightly curved and completely spined (somewhat similar in form to the gemmoscleres of *S. lacustris* in Fig. 4.25)[85]. See information on *C. novaeterrae* below.

Distribution: reported only from one lake in Louisiana.

6. Corvospongilla novaeterrae *(Potts) (Fig. 4.13)*

Spicules: megascleres stout, smooth oxeas, 112-(154)-170 μm in length and relatively scarce, a few short sparsely-spined forms typically also occur; microscleres are abundant small birotulates, 13-(21)-32 μm in length with smooth shafts, rotules are dome-shaped with 3–6 spines; gemmoscleres are highly variable, from smooth oxeas to forms bearing numerous large, recurved spines near the ends of the shaft, sometimes approaching birotulate shape, lengths 21-(39)-63 μm and widths, excluding spines, 3-(6)-9 μm. This species is remarkably similar to *C. everetti* in its basic growth form except that *C. novaeterrae* gemmoscleres are not thin, elongate birotulates and *C. novaeterrae* gemmules have a very poorly developed outer layer. See detailed information on *C. novaeterrae* in Reiswig and Ricciardi[98] and Ricciardi and Reiswig[104].

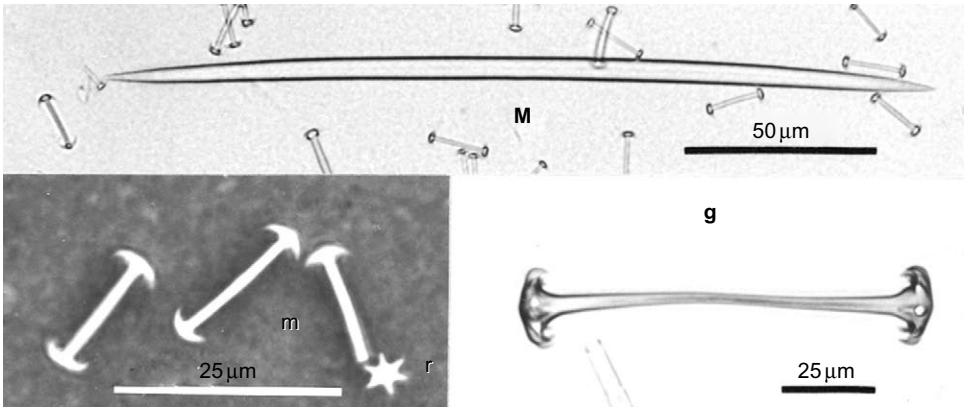

FIGURE 4.12 *Corvomeyenia everetti* spicules; megasclere (M), microscleres (m), and gemmosclere (g) (from Ricciardi and Reiswig[104]).

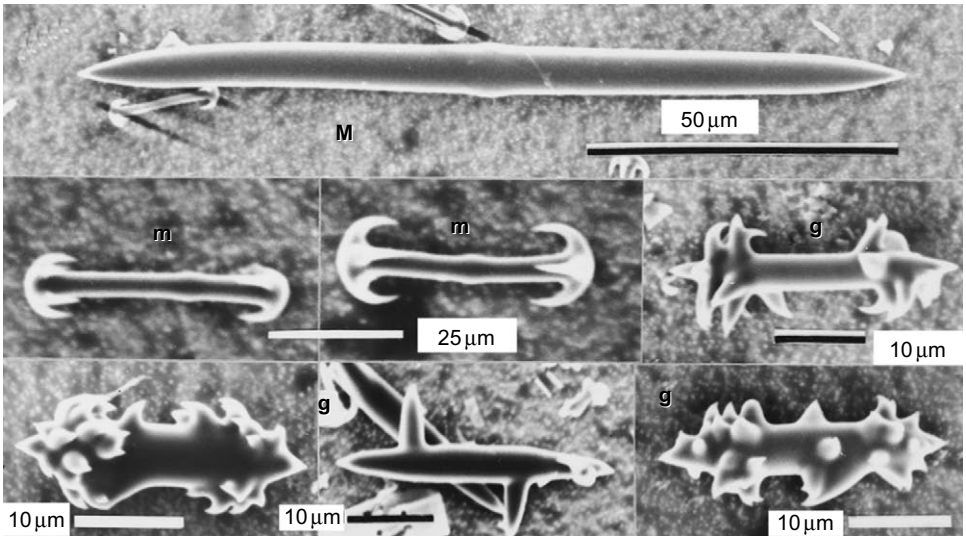

FIGURE 4.13 *Corvospongilla novaeterrae* spicules; megasclere (M), microscleres (m) and gemmoscleres (g) (from Ricciardi and Reiswig[104]).

Distribution: reported from a few lakes in the maritime provinces of Canada and one lake in Connecticut[13].

7. Dosilia palmeri *(Potts)*

Spicules: megascleres slender oxeas, 370–450 µm in length, slightly curved to nearly straight, covered with sparse spines in their central portion; microscleres stellate with 8–12 usually smooth rays arising from a central nodule, length is extremely variable; gemmoscleres birotulates, 55–85 µm in length, occurring in two subtly distinct size classes, with strong spines on their central shaft and with equal sized rotules, 23–25 µm in diameter, bearing numerous blunt recurved teeth[76].

Distribution: reported from Florida, Texas, and Arizona; and possibly other locations in Central America.

8. Dosilia radiospiculata *(Mills)*

Spicules: megascleres slender oxeas, 290–400 µm in length, entirely smooth or covered with minute spines; microscleres stellate with 6–8 microspined rays projecting from their center, length is extremely variable; gemmoscleres birotulates of two distinctly different size classes, longer forms exhibiting short-spined or nonspined shafts and ranging in length from 120–230 µm, shorter forms exhibiting strongly spined shafts and ranging in length from 45–82 µm. There is some question as to whether the two species of *Dosilia* in North America are distinct or simply ecomorphic variants of a single species.

Distribution: reported from the Canadian border south into Mexico but only from this region.

9. Duosclera mackayi *(Carter) (Fig. 4.14)*

Spicules: megascleres in two distinct classes of oxeas, the first is relatively scarce, straight or slightly curved, 177-(200)-302 µm in length, 7-(12)-18 µm in width (excluding spines), covered with coarse procurved spines; and the second is somewhat shorter, 79-(156)-267 µm in length, 2-(8)-20 µm in width (excluding spines), and densely covered with spines that are long, pointed, strongly recurved near the tips of the spicule, and perpendicular near its center; microscleres absent; gemmoscleres are oxeas of the same size and shape as the second class of megascleres, which are always present in a specimen even when gemmules are absent. When intact gemmules are present, gemmoscleres are arrayed tangential to the surface of the gemmule except near the foraminal aperture. The overall orientation of gemmules can help distinguish *D. mackayi* from a similar species, *E. fragilis*. In *D. Mackayi* the foraminal apertures of gemmules in groups are always oriented inward or towards a substrate while those in *E. fragilis* gemmules groups are always directed outward or, in layers on pavements, away from the substrate. This species has recently been classified as type species of a new genus[99]. It has previously been reported as *Eunapius igloviformis* in Penney and Racek[77] and as *Eunapius mackayi* in Ricciardi and Reiswig[104].

Distribution: throughout the United States and Canada but confined to these regions.

10. Ephydatia cooperensis *(Peterson and Addis)*

Spicules: megascleres straight to slightly curved, moderately thick oxeas, 210-(343)-439 µm in length, with slight centrotylote bulb and usually covered with minute conical spines except at tips; spination is variable among spicules from entirely smooth to very coarse; microscleres absent; gemmoscleres absent since gemmules are apparently never formed. The species, originally described as the only member of a new genus, *Clypeatula*, now considered a synonym of *Ephydatia*, may be an ecomorph of *E. muelleri*. A more recent molecular sequence study[1] suggested that it is a sister species of *E. fluviatilis*, with which it may yet prove to be synonymous.

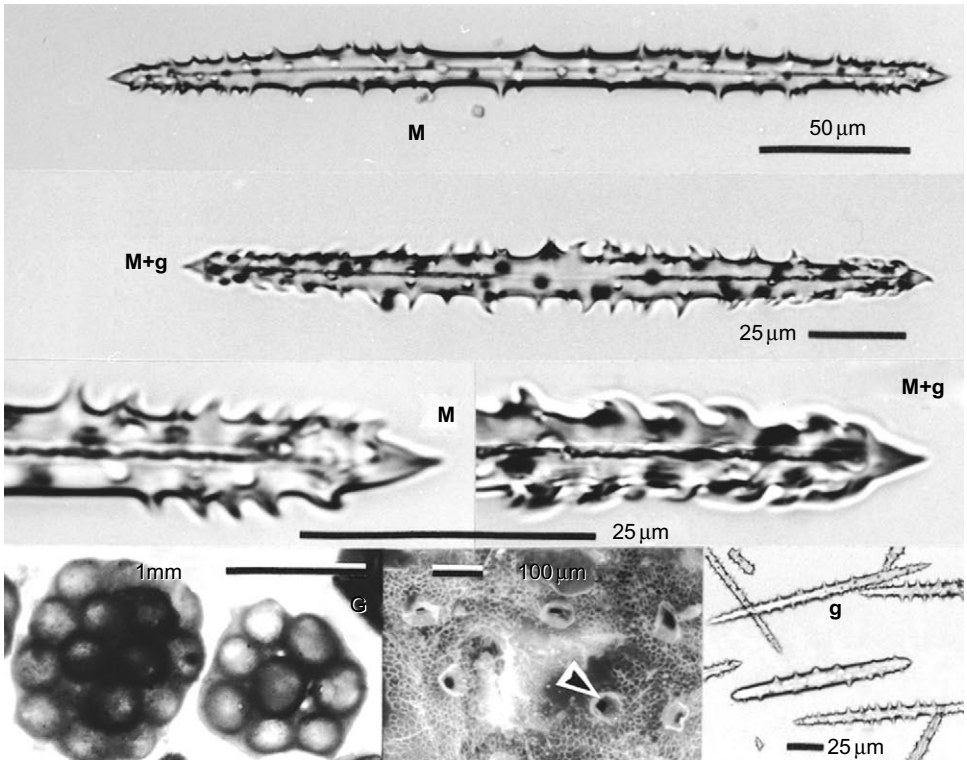

FIGURE 4.14 *Duosclerea mackayi* spicules and gemmules; main megascleres (M), secondary megascleres and gemmoscleres (M + g), gemmoscleres (g), and gemmules (G) with foramin indicated by arrowhead (from Ricciardi and Reiswig[104]).

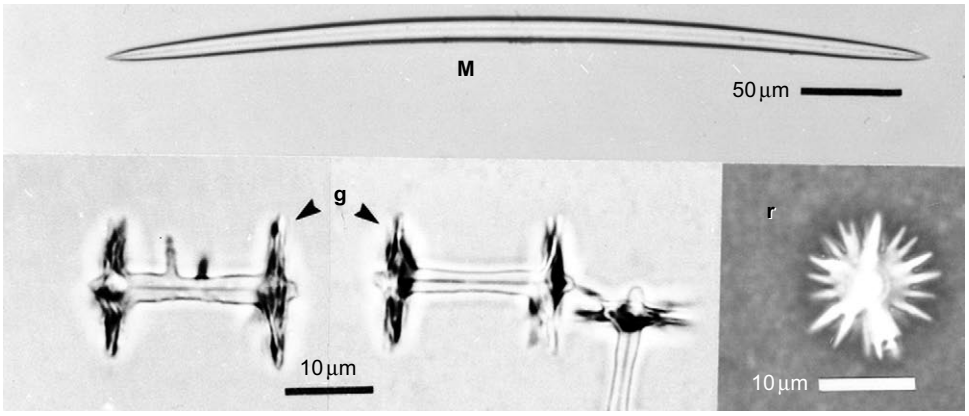

FIGURE 4.15 *Ephydatia fluviatilis* spicules; megasclere (M), gemmoscleres (g), and end view of gemmosclere rotule (r) (from Ricciardi and Reiswig[104]).

Distribution: known only from three lakes in the northern rocky mountains of western Montana.

11. Ephydatia fluviatilis *(Linneaus) (Fig. 4.15)*

Spicules: megascleres usually slightly curved oxeas, 210-(343)-439 µm in length, and usually entirely smooth, although in some cases sparsely spined megascleres co-occur with smooth forms; microscleres absent; gemmoscleres birotulates of one class, 20-(23)-30 µm in length with a slender, smooth shaft, which sometimes has 1–4 large spines, with flat irregularly shaped rotules of equal, 13-(18)-24 µm diameters and more than 20 teeth that are not deeply incised. *E. fluviatilis* can sometimes be confused with *E. muelleri*. These species can be most surely distinguished by comparing gemmosclere length to rotule diameter. Gemmosclere length is always greater than rotule diameter in *E. fluviatilis* while gemmosclere length is less than or equal to rotule diameter in *E. muelleri*[104].

Distribution: truly cosmopolitan with more frequent occurrence in temperate than in tropical zones.

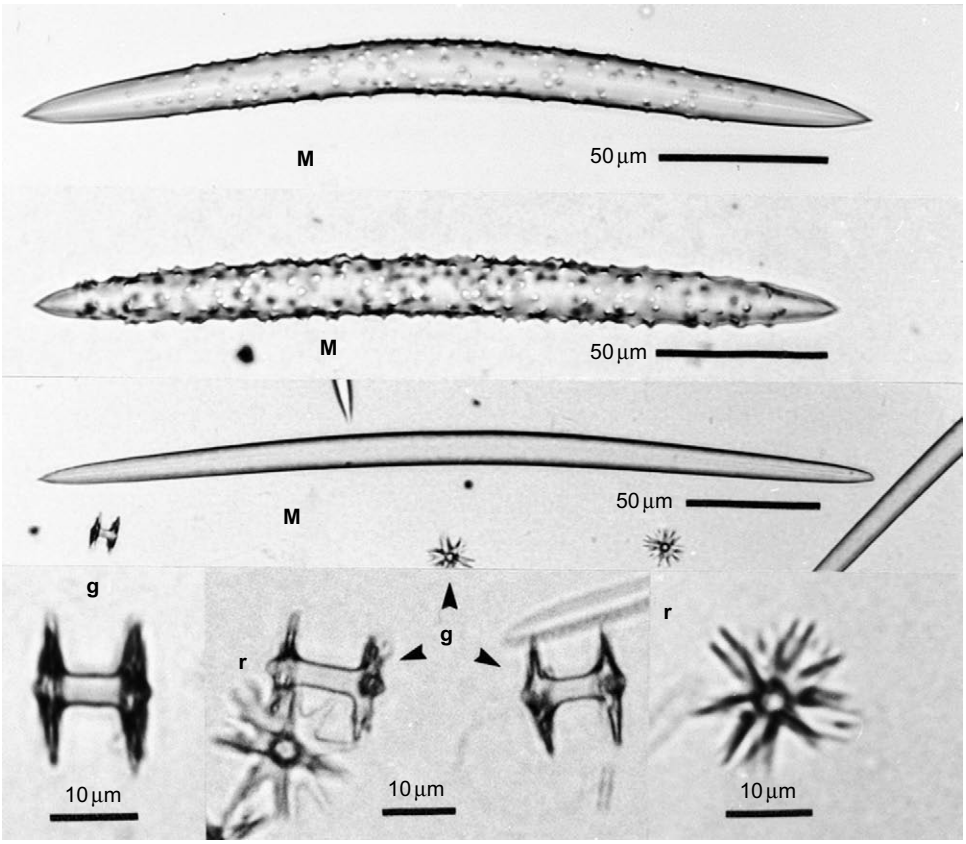

FIGURE 4.16 *Ephydatia muelleri* spicules; megascleres (M), gemmoscleres (g), and end view of gemmosclere rotule (r) (from Ricciardi and Reiswig[104]).

12. Ephydatia millsii *(Potts)*

Spicules: megascleres slightly curved to nearly straight oxeas, 180–270 µm in length, with numerous small spines except at the tips; microscleres absent; gemmoscleres birotulates of one size class, 36–48 µm in length, with smooth shafts that are clearly broader near the rotules and with distinctly flat, circular, disk-shaped rotules of equal, 22–28 µm diameters, and only very small incisions at their margins. This may eventually prove to be an ecomorph of one of the more widely distributed *Ephydatia* species.

Distribution: reported only from Florida.

13. Ephydatia muelleri *(Lieberkühn) (Fig. 4.16)*

Spicules: megascleres straight to slightly curved oxeas, 171-(245)-350 µm in length, usually covered with small spines except at the tips, but entirely smooth in rare cases; microscleres absent; gemmoscleres birotulates of one class, 8-(17)-28 µm in length, with thick smooth shafts and with flat, irregularly shaped rotules of equal, 8-(15)-27 µm diameters and usually with fewer than 12 teeth deeply incised into long rays. *E. muelleri* can sometimes be confused with *E. fluviatilis*. These species can be most surely distinguished by comparing gemmosclere length to rotule diameter. Gemmosclere length is always greater than rotule diameter in *E. fluviatilis* while gemmosclere length is less than or equal to rotule diameter in *E. muelleri*[104].

Distribution: widely distributed throughout the Northern Hemisphere with a preference for temperate regions.

14. Ephydatia subtilis *(Weltner)*

Spicules: megascleres strikingly slender oxeas, 158 µm in length by 2.6 µm in width, with sparse short spines; microscleres absent; gemmoscleres as delicate, slender birotulates of various lengths, average 23 µm long with rotules 9.5 µm in diameter, rotules deeply incised with 10–20 blunt rays. This often ignored species is known only from Weltner's (1895) text description; the spicule descriptions are very similar to some forms of *E. fluviatilis*, but rotules of the gemmoscleres are much smaller than those of that species. The spicules of this geographically restricted species have never been figured. Attempts to obtain new specimens from the type location failed[40], hence resolution of the status of this species will probably depend upon restudy of the type specimen in the Humbolt Museum, Berlin.

Distribution: known only from the type locality, Lake Kissimmee, Florida.

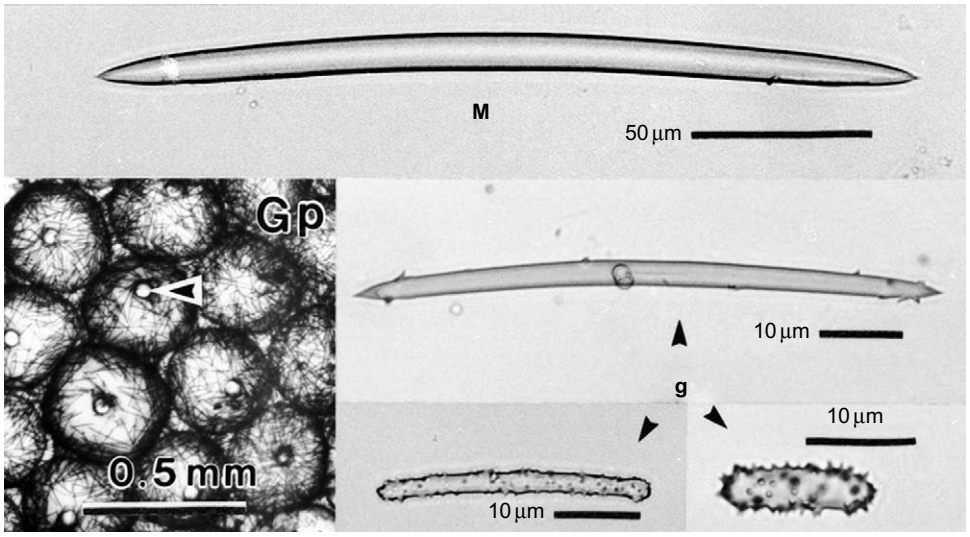

FIGURE 4.17 *Eunapius fragilis* spicules and gemmules; megasclere (M), gemmoscleres (g), gemmule pavement (Gp) with foramin indicated by arrowhead (from Ricciardi and Reiswig[104]).

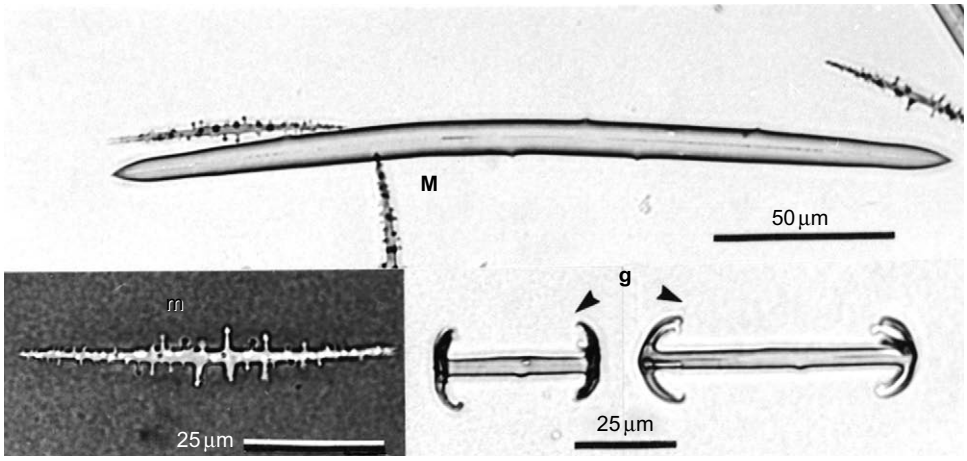

FIGURE 4.18 *Heteromeyenia baileyi* spicules; megasclere (M), microsclere (m), and gemmoscleres (g) (from Ricciardi and Reiswig[104]).

15. Eunapius carteri *(Bowerbank)*

Spicules: megascleres rather stout, fusiform, slightly curved, completely smooth oxeas, 265–370 µm in length; microscleres absent; gemmoscleres are oxeas similar to megascleres but smaller and more curved, 145–210 µm in length, arrayed tangentially within gemmule coat. Gemmules are spherical and occur singly, scattered throughout the skeletal meshes. This is a new addition to the list of North American freshwater sponges.

Distribution: known only from a single report in the Western Hemisphere as a likely recent introduction to Panama[86] but distributed throughout southern Asia to southeast Europe in the Eastern Hemisphere.

16. Eunapius fragilis *(Leidy) (Fig. 4.17)*

Spicules: megascleres entirely smooth oxeas, 165-(189)-271 µm in length; microscleres absent; gemmoscleres straight to slightly curved strongyles covered with conspicuous spines which are often more dense near the tips, a few oxeas with sparse spines are often also pressent, 32-(57)-140 µm. Mature gemmules are enclosed in a common brown coat either forming a pavement layer cemented to the substrate (Gp in Fig. 4.17) or in individual clusters of 2–4 gemmules. The overall orientation of gemmules can help distinguish *E. fragilis* from a similar species, *D. mackayi*. In *E. fragilis*, the foraminal apertures are always directed outward from a cluster or upward from a pavement layer while those in *D. mackayi* are always oriented inward or towards a substrate[104].

Distribution: truly cosmopolitan.

17. Heteromeyenia baileyi *(Bowerbank) (Fig. 4.18)*

Spicules: megascleres as slender oxeas, 216-(247)-320 µm in length, smooth or with sparse microspines except near

the tips; microscleres oxeas 53-(67)-85 μm in length, delicate, slightly curved to almost straight with spines that occur throughout their length but which increase in length towards the central region where they are often knobbed and distinctly perpendicular to the main axis; gemmoscleres birotulates in two types: type A with two morphologically distinct forms of overlapping lengths, shorter birotules with flat, serrate rotules 13-(18)-22 μm in diameter, 38-(51)-60 μm in length and long birotules 49-(70)-85 μm in length with rotules 18-(22)-28 μm in diameter, with of long recurved hooks giving an umbrella-like appearance, hooks often have knobbed tips; type B with all birotulates of form similar to the longer ones of type A, but with a wider size range, 67–160 μm in length. Foraminal apertures of gemmules do not have terminal cirrous projections like those for *H. latitenta* (Fig. 4.19), *H. tentasperma* (Fig. 4.20), and *H. tubisperma* (Fig. 4.21). The long middle spines on the microscleres of *H. baileyi* are also useful in distinguishing it from other species in the genus. Their maximum length is on average greater than the width of the microsclere. The presence of two types of gemmosclere spiculation suggests that two distinct populations may be presently be included under this species name; they may require separation at the species level when detailed studies are carried out[120].

Distribution: widely distributed throughout eastern United States and Canada with a few reports from Europe and South America.

18. Heteromeyenia latitenta *(Potts) (Fig. 4.19)*

Spicules: megascleres as straight oxeas, 265–285 μm in length, smooth to sparsely microspined; microscleres as slender oxeas, entirely spined with spines in the central region only slightly larger than those on the ends, 85–100 μm in length; gemmoscleres birotulates of one widely overlapping length group or two distinct length groups, 50–55 or 60–78 μm with shafts bearing numerous stout and pointed spines, both rotules of equal, 16–18 μm diameters, margins forming numerous conspicuous, recurved teeth. Foraminal apertures of gemmules with one or two very long, cirrous projections originating from a flat disk. Detailed length analysis of gemmoscleres is needed to ensure correct genus allocation of this species.

Distribution: reported only from northeastern United States.

19. Heteromeyenia longistylis *(Mills)*

Spicules: megascleres as slender, very sparsely spined, oxeas, 259–330 μm in length; microscleres as small, fusiform, entirely spined oxeas with spines longer in middle, 58–68 μm in length; gemmoscleres as birotulates in two classes, the shorter birotules, 73–76 μm in length, have straight, spined shafts and slightly umbonate rotules 20 μm in diameter, the longer birotules, 125–129 μm in length, have curved , smooth shafts and more hemispheric rotules 23 μm in diameter, with marginal claws strongly curved in towards shaft. This rarely mentioned species is extremely poorly known; nothing is known of its gemmule foraminal structure and its megascleres have never been figured. Data given here does not represent spicule ranges but rather individual measurements given by various authorities. It is almost certainly a junior synonym of *H. baileyi* as the two species cannot be separated by available characters in the following key. Since, however, the taxonomic status of *H. longistylis* has not been formally resolved, it is included here in the valid species list.

Distribution: known only from the Lehigh River near Bethlehem, Pennsylvania.

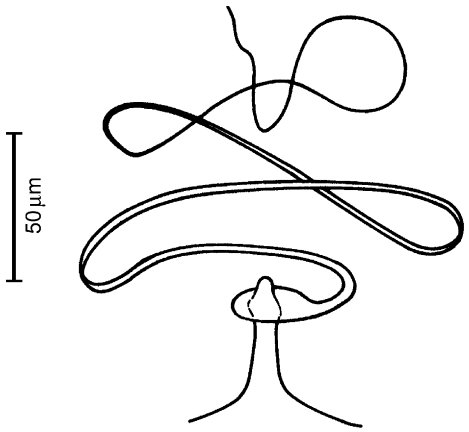

FIGURE 4.19 *Heteromeyenia latitenta* foraminal aperture with a single long cirrous projection (after Neidhoefer[70]).

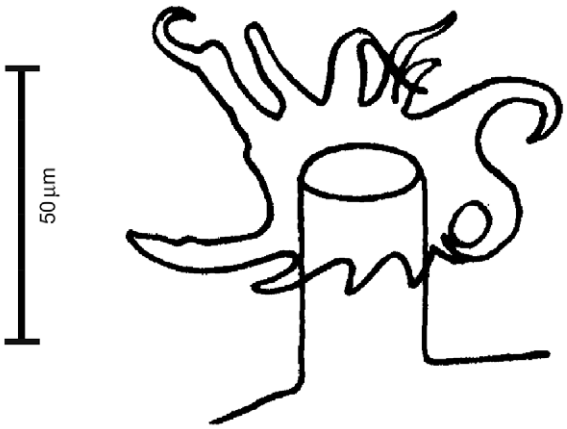

FIGURE 4.20 *Heteromeyenia tentasperma* foraminal aperture with several short, irregular cirrous projections (after Neidhoefer[70]).

20. Heteromeyenia tentasperma *(Potts) (Fig. 4.20)*

Spicules: megascleres as very slender oxeas, 260–280 μm in length, with sparse microspines; microscleres slender

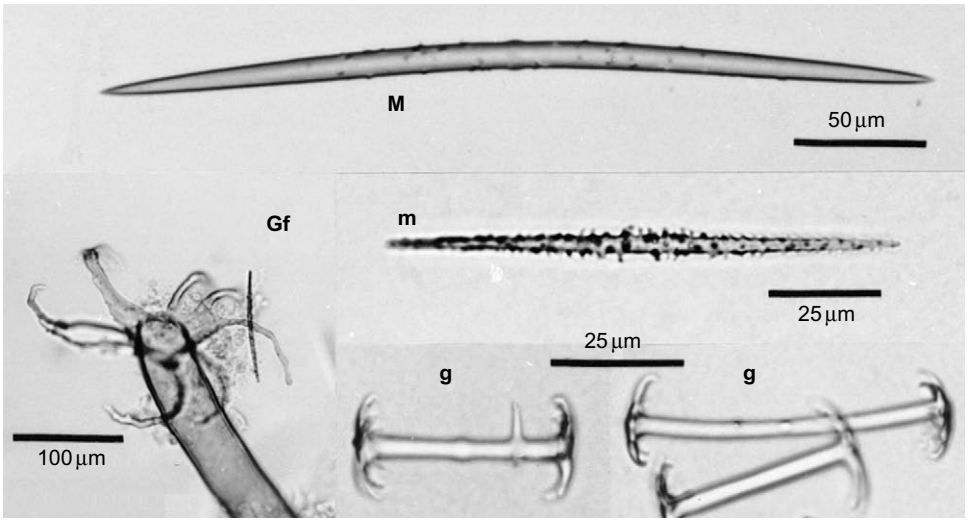

FIGURE 4.21 *Heteromeyenia tubisperma* spicules and foraminal aperture; megasclere (M), microsclere (m), gemmoscleres (g), and gemmule foraminal tubule (Gp) with eight cirrous projections (from Ricciardi and Reiswig[104]).

oxeas with sparse microspines, 75–80 µm in length; gemmoscleres pseudobirotulates or strongyles of two length groups, 50–55 and 65–72 µm with stout shafts bearing a small number of acute spines and with both burr-like pseudorotules of equal, 15–18 µm diameters and consisting of an arrangement of lateral spines. Foraminal apertures of gemmules distinctly tubular and relatively short with 3–6 long and irregular cirrous projections.

Distribution: reported only from northeastern to midwestern United States.

21. Heteromeyenia tubisperma *(Potts) (Fig. 4.21)*

Spicules: megascleres as slender oxeas, 190-(290)-337 µm in length, smooth to sparsely microspined; microscleres as oxeas, 73-(100)-118 µm in length, slender and entirely spined with spines near the tips small and recurved and those near the central portion distinctly larger, straight, and with knobs; gemmoscleres birotulates of one size class 33-(44)-70 µm in length with stout shafts bearing a small number of acute spines and with both rotules of equal, 12-(19)-25 µm diameters, consisting of an arrangement of lateral spines. Foraminal apertures of gemmules distinctly tubular, slender and very long (0.5–0.9 times the gemmule diameter) with 5–10 cylindrical cirrous projections. It is important to note that developing gemmules may have stunted foraminal development such that they resemble *H. latitenta* and *H. tentasperma*. Specimens should be thoroughly inspected for fully developed gemmules. *H. tentasperma* can be distinguished from *H. baileyi* which has shorter microscleres with longer spines. This species has previously been described as having two size classes of gemmoscleres; suggestion that there is probably only one continuous size class should incite detailed study which may cause change of genus allocation of this species.

Distribution: reported only from the eastern half of North America.

22. Racekiela ryderi *(Potts) (Fig. 4.22)*

Spicules: megascleres as oxeas which are extremely variable from habitat to habitat with lengths ranging from 141-(220)-279 µm, with broadly conical spines; microscleres absent; gemmoscleres birotulates of two distinct length groups, 28-(34)-41and 45-(64)-75 µm, with clear differences in their shapes, shorter forms have shafts with only one or a few spines and flattened rotules with a large number of small teeth; larger forms are robust with numerous recurved spines on their shaft and with strongly recurved hooks on their ends. This species was previously assigned to the genus *Anheteromeyenia*.

Distribution: reported from the eastern half of North America, from Louisiana to Canada but confined to this region.

23. Radiospongilla cerebellata *(Bowerbank)*

Spicules: megascleres straight to slightly curved, smooth oxeas, 240–330 µm in length; microscleres absent although immature gemmoscleres may be abundant in some portions of the dermal membrane; gemmoscleres strongyles usually distinctly curved, rarely straight, 72–110 µm in length, covered with abundant spines that are pronouncedly recurved toward the terminal ends. In intact gemmules, gemmoscleres are arrayed in two distinct layers with those in the inner layer arranged radially and with those in the outer layer arranged tangentially[81].

Distribution: reported only from Texas in the United States but widely distributed in tropical and subtropical Asia and Africa.

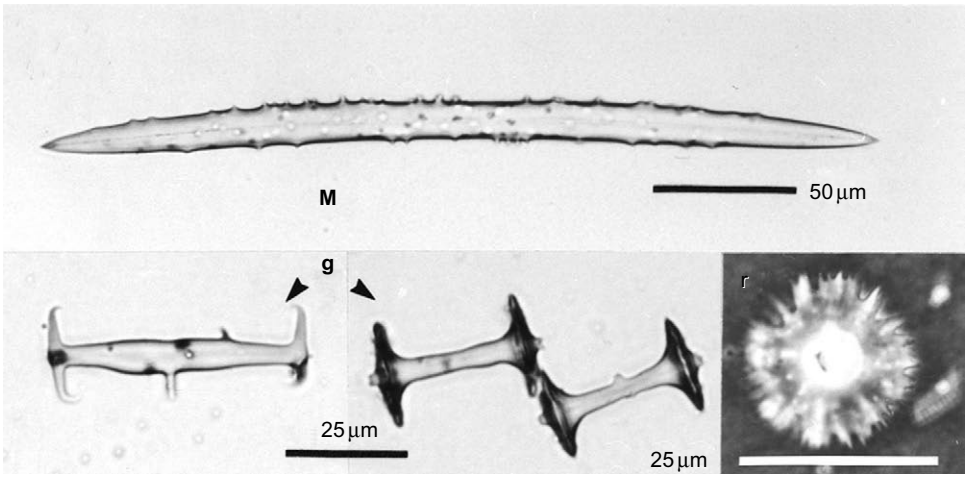

FIGURE 4.22 *Racekiela ryderi* spicules; megasclere (M), gemmoscleres (g), and end view of gemmosclere rotule (r) (from Ricciardi and Reiswig[104]).

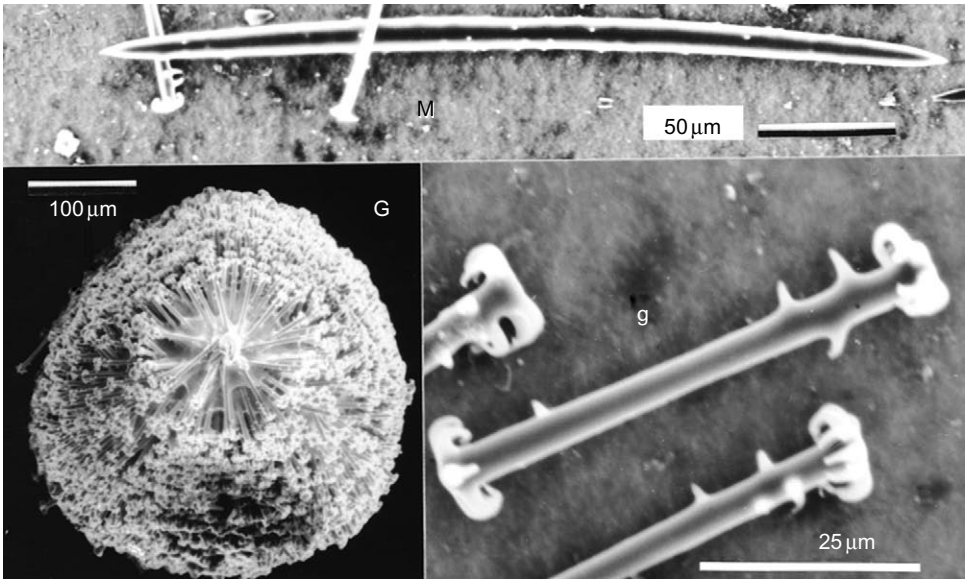

FIGURE 4.23 *Radiospongilla crateriformis* spicules and gemmule; megasclere (M), gemmoscleres (g), and gemmule (G) with view of foramen and surrounding crater (from Ricciardi and Reiswig[104]).

24. Radiospongilla crateriformis *(Potts) (Fig. 4.23)*

Spicules: megascleres slender and slightly curved oxeas, 240-(278)-300 µm in length, sparsely covered by very small spines except at their tips; microscleres absent; gemmoscleres pseudobirotulates, slender, shaft with small conical spines only at ends or all over but always more abundant at ends where larger, slightly recurved spines are sufficiently dense to form pseudorotules, 60-(71)-80 µm in length. Gemmoscleres in intact gemmules are arranged radially except in the immediate vicinity of the foraminal aperture where they form a crater-like depression leaning away from the aperture.

Distribution: reported primarily from the eastern half of the United States but as far west as Wisconsin and Texas, also occurring in southern Canada[104], as well as China, Japan, southeast Asia, and Australia.

25. Spongilla alba *(Carter)*

Spicules: megascleres entirely smooth oxeas, 144–420 µm in length; microscleres slender and slightly curved oxeas with erect spines that are longer in the central region, 49–124 µm; gemmoscleres slightly to moderately curved strongyles with stout, sharp, recurved spines that are more dense at the ends, forming distinct heads but not pseudorotules, 48–130 µm[83].

Distribution: occurs in warmer regions worldwide with a strong preference for brackish water, reported from the southeastern coastal regions of the United States.

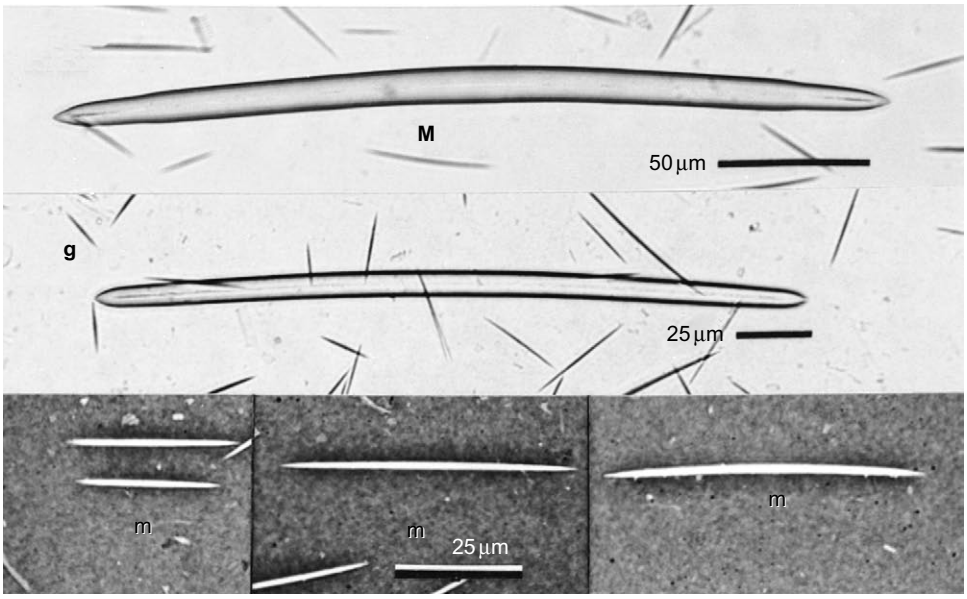

FIGURE 4.24 *Spongilla aspinosa* spicules; megasclere (M), microscleres (m), and gemmosclere (g) (from Ricciardi and Reiswig[104]).

26. Spongilla aspinosa *(Potts) (Fig. 4.24)*

Spicules: megascleres slender, entirely smooth oxeas, 155-(274)-338 μm in length; microscleres as microxeas, from rare to abundant, smooth or very sparsely microspined, 21-(50)-78 μm in length; gemmoscleres smooth oxeas resembling small megascleres with very abruptly pointed or blunt tips, 129-(274)-306 μm in length.

Distribution: reported from Florida to Michigan in the United States, and from eastern Canada.

27. Spongilla cenota *(Penney and Racek)*

Spicules: megascleres as stout and completely smooth oxeas, 310–410 μm in length; microscleres numerous and slender oxeas, covered with small spines at their tip and with a group of clearly larger spines in their center, 68–123 μm; gemmoscleres extremely stout oxeas, entirely covered with stout, sharp, recurved spines 65–86 μm[83].

Distribution: reported only from Florida and Yucatan, Mexico.

28. Spongilla lacustris *(Linneaus) (Fig. 4.25)*

Spicules: megascleres as entirely smooth oxeas, 158-(254)-362 μm in length; microscleres small oxeas densely covered with small spines, 30-(61)-130 μm in length; gemmoscleres present or absent, thick-walled summer gemmules have slightly to strongly curved oxeas to strongyles, usually covered with strong, curved spines that tend to be concentrated near the tips, 18-(32)-130 μm long; thin-walled winter gemmules generally lack gemmoscleres[88].

Distribution: throughout the Northern Hemisphere; one of the most common species throughout the United States and Canada.

29. Stratospongilla penneyi *(Harrison)*

Spicules: megascleres as slightly curved oxeas, 215–296 μm in length, smooth to very delicately microspined; microscleres slender oxeas, 38–75 μm in length, covered with very small spines; gemmoscleres curved to distinctly bent oxeas, 48–123 μm in length, smooth to delicately microspined with sharply pointed tips. The genus *Stratospongilla*, to which this species was previously assigned, was recently redefined[64], excluding *S. penneyi* and thus leaving it without a generic assignment. The type series of *S. penneyi* will need restudy to determine its proper placement.

Distribution: reported from only one location, a canal in southern Florida[40].

30. Trochospongilla horrida *(Weltner) (Fig. 4.26)*

Spicules: megascleres straight to slightly curved oxeas, 155-(187)-250 μm in length, covered with stout, blunt, truncated spines; microscleres absent; gemmoscleres as small birotulates, 8–10 μm in length, with stout smooth shafts and rotules of nearly equal size, the smaller 9–13 μm

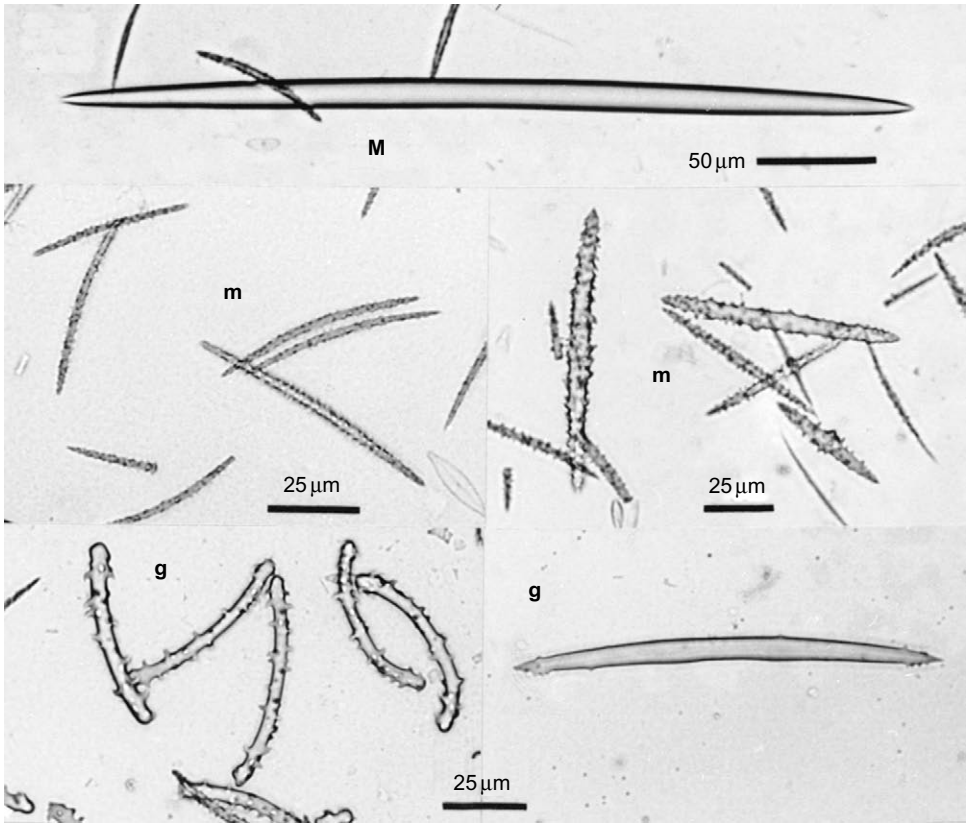

FIGURE 4.25 *Spongilla lacustris* spicules; megasclere (M), microscleres (m), and gemmoscleres (g) (from Ricciardi and Reiswig[104]).

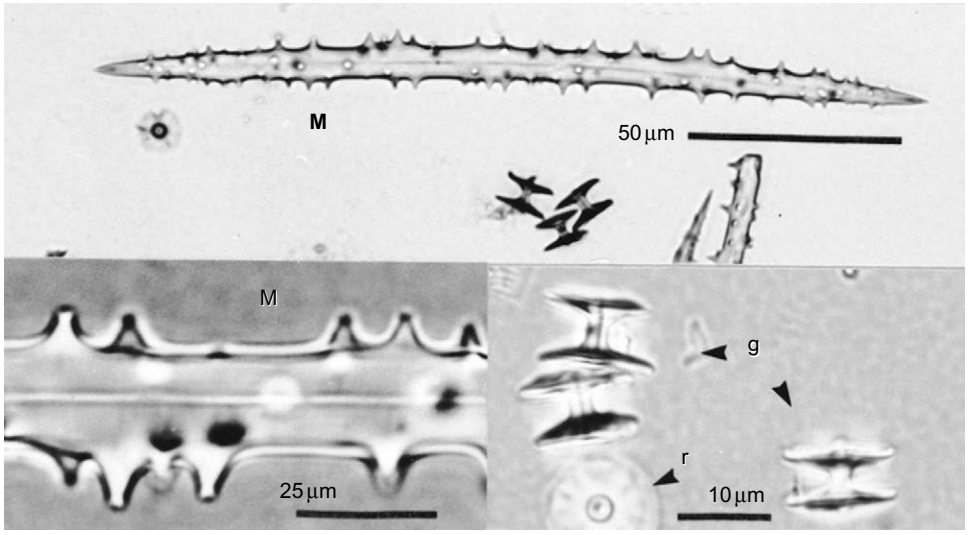

FIGURE 4.26 *Trochospongilla horrida* spicules; whole megasclere and magnified view of spines (M), and gemmoscleres (g) with end view of rotule (r) (from Ricciardi and Reiswig[104]).

and the larger 13–16 µm in diameter with circular margins (overall length of gemmoscleres is never greater than the diameter of the smaller rotule). A distinct class of oxeas similar to megascleres serves both as a special dermal spicule and as an outer capsule of gemmules in European specimens[107] but this has not yet been verified for North American specimens. Compare with information for *T. pennsylvanica* to confirm an identification.

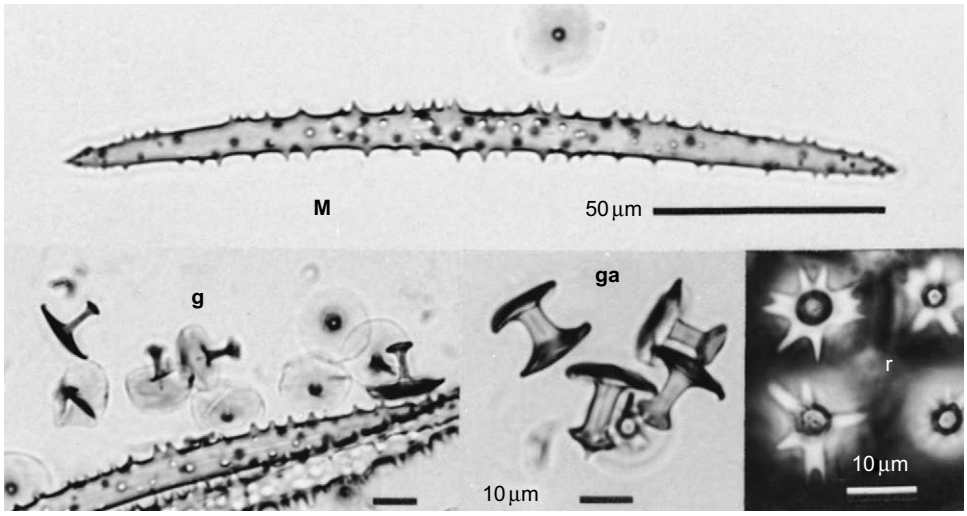

FIGURE 4.27 *Trochospongilla pensylvannica* spicules; megasclere (M), normal gemmoscleres (g), abnormal gemmoscleres (ga), and end view of smaller rotules (r) (from Ricciardi and Reiswig[104]).

Distribution: widely dispersed throughout the Northern Hemisphere with few reports from eastern Canada.

31. Trochospongilla leidii *(Bowerbank)*

Spicules: megascleres straight to slightly curved and entirely smooth oxeas, 150–170 µm in length; microscleres absent; gemmoscleres small birotulates, 11 µm in length, terminating in rotules with circular margins and equal, 12–14 µm, diameters.

Distribution: reported from limited regions of the eastern United States, with one report of a population from the Panama Canal[56].

32. Trochospongilla pennsylvanica *(Potts) (Fig. 4.27)*

Spicules: megascleres slender and slightly curved oxeas, 100-(253)-432 µm in length, entirely covered with blunt, truncated spines; microscleres absent; gemmoscleres as small birotulates with slender shafts, 11-(17)-41 µm in length, terminating in rotules with circular margins and usually with two distinctly different diameters, 3-(9)-23 µm and 13-(24)-41 µm. In some cases both rotules of the gemmoscleres appear to have the same diameters leading them to be identified incorrectly as *T. horrida* using this chapter's key. In such cases, the two species can be distinguished by the length of the gemmosclere shaft relative to the rotule diameter. The shaft length is longer than, or in rare cases equal to, the diameter of the smaller rotule in *T. pennsylvanica* and shorter than the diameter of the rotules in *T. horrida*[104].

Distribution: reported throughout, but apparently restricted to, the North American continent (Fig. 4.28).

VII. KEY TO THE FRESHWATER SPONGES OF NORTH AMERICA

Please note that the successful use of this key depends upon obtaining a fully representative sample of all the types of spicules occurring within a sponge species (megascleres, gemmoscleres, and, if they occur in a species, microscleres). If a species ordinarily exhibits gemmoscleres or microscleres and they are not contained within a specimen, it will not be possible to even identify its genus. The one exception to this rule occurs for *S. lacustris* which is unique among the species in this key in its lack of gemmoscleres in its winter gemmules. If gemmules are clearly present in a specimen but gemmoscleres are absent, it is most likely *S. lacustris*. Caution is necessary here in that some foreign bodies in sponges may resemble gemmules superficially, for example, the eggs of water mites. Gemmules can be distinguished by their highly resistant coats. It is important to note that *S. lacustris* may also have gemmoscleres; they occur when summer gemmules are or have been present. (Table 4.1)

Also note that this key is intended only for use with the species from North America listed above. The key's couplets have been designed only for this particular subset of the world's freshwater sponges. Those examining specimens from other regions will need to consult Penney and Racek[77] and more recent taxonomic work[64,133], as well as the references cited in the species list above. The

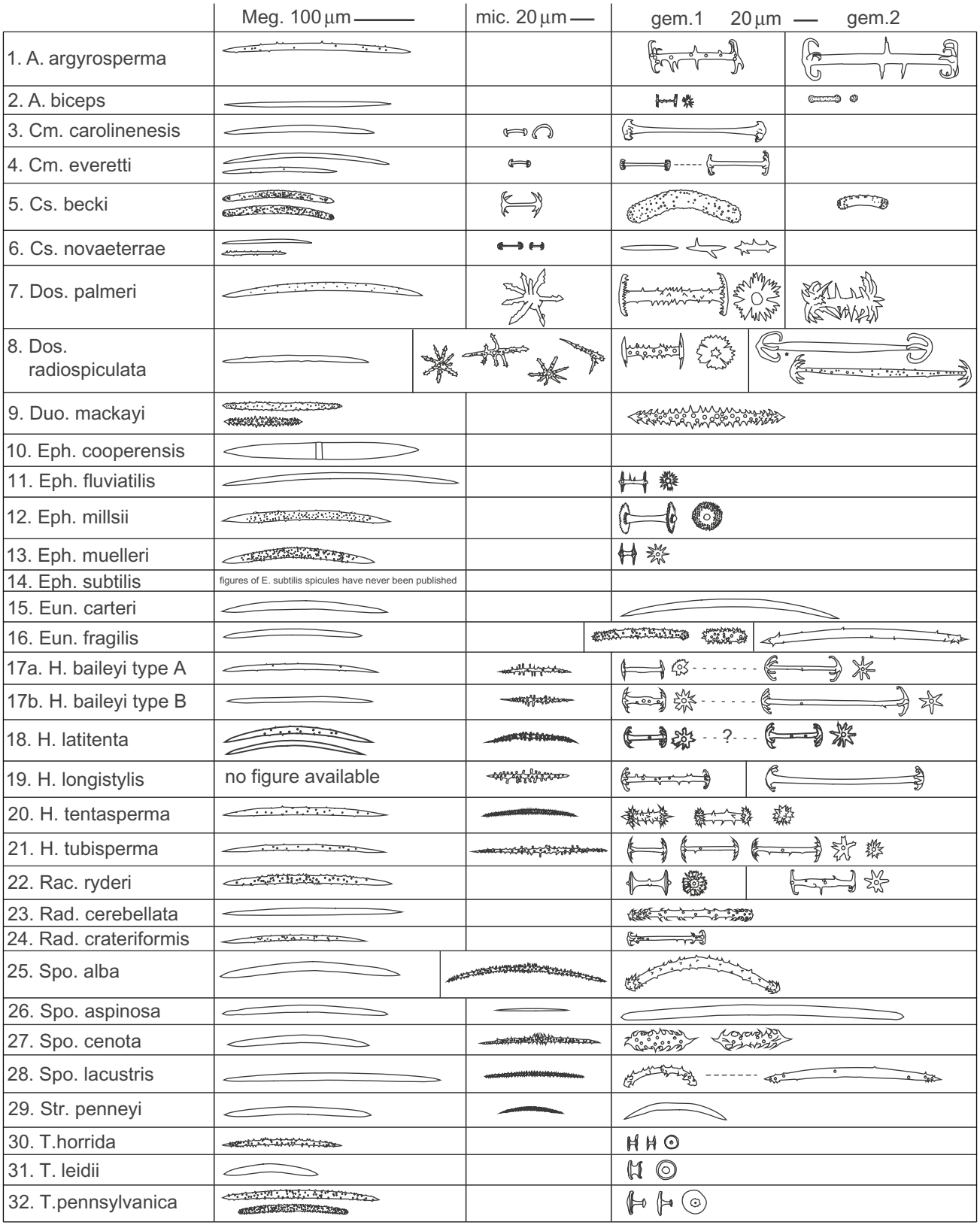

FIGURE 4.28 Comparison spicule diagram of all known North American freshwater sponges; megascleres (Meg.), microscleres (mic.), gemmoscleres (gem.). Note that scales of microscleres and gemmoscleres are uniform but differ from that for megascleres. Drawings were made from the most authoritative sources available, but some contained obvious scale errors which are unfortunately still retained.

TABLE 4.1 List of junior synonyms of freshwater sponges of North America.

abortiva, Spongilla lacustris var. Potts > Spongilla lacustris	*minuta, Spongilla fragilis var. Potts > Eunapius fragilis*
acuminata, Meyenia Potts > Ephdatia muelleri	*montana, Spongilla lacustris var. Potts > Spongilla lacustris*
asperrima, Spongilla Dawson > Ephydatia muelleri	*morgiana, Spongilla Potts > Eunapius fragilis*
astrosperma, Spongilla Potts > Ephydatia muelleri	*multiforis, Spongilla Carter > Spongilla lacustris*
baleni, Heteromeyenia ryderi var. Potts > Racekiela ryderi	*mutica, Spongilla Potts > Spongilla lacustris*
calumeti, Spongilla Thomas > Eunapius fragilis	*ottawaensis, Spongilla Dawson > Eunapius fragilis*
calumetica, Meyenia Thomas > Ephydatia muelleri	*paupercula, Spongilla Bowerbank > Spongilla lacustris*
calumeticus, Pleiomeyenia Mills > Ephydatia muelleri	*pictouensis, Heteromeyenia Potts > Racekiela ryderi*
conigera, Heteromeyenia Old > Racekiela ryderi	*plumosa, Heteromeyenia Weltneri > Dosilia radiospiculata*
dawsoni, Spongilla Bowerbank > Spongilla lacustris	*polymorpha, Meyenia Potts > Ephydatia muelleri*
discoides, Spongilla Penney > mixture of Racekiela ryderi, Corvomeyenia everetti and statoblasts of ectoproct	*polymorpha, Meyenia Potts > Ephydatia muelleri*
fanshawei, Tubella Potts > Trochospongilla pennsylvanica	*polymorpha, Meyenia Potts > Ephydatia muelleri*
flexispina, Spongilla Dawson > Spongilla lacustris	*repens, Spongilla Potts > Heteromeyenia baileyi*
heterosclerifera, Spongilla Smith > mixture of Eunapius fragilis and Ephydatia muelleri	*robusta, Meyenia Potts > Ephydatia fluviatilis*
igloviformis, Spongilla Potts > Duosclera mackayi	*spinifera, Pleiomeyenia Mills > Ephydatia muelleri*
intermedia, Tubella Potts > Trochospongilla pennsylvanica	*sponginosa, Spongilla Penney > Racekiela ryderi*
japonica, Spongilla fluviatilis var. Hilgendorf > Ephydatia muelleri	*stagnalis, Spongilla Dawson > Ephydatia muelleri*
johanseni, Spongilla Smith > Duosclera mackayi	*subdivisa, Meyenia Mills > Ephydatia fluviatilis*
lacustrioides, Spongilla Potts > Spongilla lacustris	*tenosperma, Spongilla Potts > Heteromeyenia tentasperma*
lacustroides, Spongilla MacKay > Spongilla lacustris	*viridis, Ephydatia Zorilla > Ephydatia fluviatilis*
lehighensis, Spongilla lacustris var. Potts > Spongilla lacustris	*wagneri, Spongilla Potts > Spongilla alba*
macouni, Heteromeyenia MacKay > Racekiela ryderi	*walkeri, Pleiomeyenia Mills > Ephydatia muelleri*
mexicana, Meyenia Potts > Ephydatia fluviatilis	*walshi, Heteromeyenia ryderi var. Potts > Racekiela ryderi*
minima, Tubella pennsylvanica var. Potts > Trochospongilla pennsylvanica	

key is arranged systematically so that genera are usually separated prior to species within a genus. In most cases, therefore, a valid identification to genus may be possible even if a species has not previously been reported in North America. Even to separate genera, however, it is necessary to have included all of the possible spicule types from a specimen.

1a. Microscleres present 2

1b. Microscleres absent 16

2a (1a). Microscleres star-shaped (Fig. 4.28 #7) or birotulate (Figs. 4.11, 4.22) 3

2b. Microscleres rod-shaped to needle-like in structure (Figs. 4.18, 4.21) 8

3a (2a). Microscleres star-shaped with several rays extending from central region of the spicules (Fig. 4.28 #7) ..... *Dosilia* *4*

3b. Microscleres birotulate (Fig. 4.12) 5

4a (3a). Gemmoscleres birotulate in two distinctly different size categories (45–82 μm in length and 120–230 μm in length) ..... *Dosilia radiospiculata*

4b. Gemmoscleres birotulate in two size categories that are nearly equal in length (55–85 μm) ..... *Dosilia palmeri*

5a (3b). Gemmoscleres birotulate (Fig. 4.12) ..... *Corvomeyenia* 6

5b. Gemmoscleres rod- or needle-shaped (Fig. 4.13) ..... *Corvospongilla* 7

6a (5a). Microscleres predominantely straight birotulates (Fig. 4.12) ..... *Corvomeyenia everetti*

6b. Microscleres predominantly curved birotulates (Fig. 4.28 #3) ..... *Corvomeyenia carolinensis*

7a (5b). Megascleres covered with spines ..... *Corvospongilla becki*

7b. Megascleres mostly smooth, a few may be sparsely spined ..... *Corvospongilla novaeterrae*

8a (2b). Gemmoscleres birotulate (Fig. 4.18) ..... *Heteromeyenia* 9

8b. Gemmoscleres needle-like (Fig. 4.25) or absent 12

9a (8a). Foraminal aperture of gemmules without terminal cirrous projections (contrast with Figs. 4.19–4.21) ..... *Heteromeyenia baileyi* and *H. longistylis*

9b. Foraminal aperture of gemmules with distinct, terminal cirrous projections (Figs. 4.19–4.21) 10

10a (9b). Foraminal aperture of gemmules with one or two very long cirrous projections starting from a flat disk (Fig. 4.19) ..... *Heteromeyenia latitenta*

10b. Foraminal aperture of gemmules with three to six cirrous projections that are short when compared with those of *H. latitenta* 11

11a (10b). Foraminal aperture of gemmules distinctly tubular and very long ranging from 0.5–0.9 times the diameter of the gemmule (Fig. 4.21) ..... *Heteromeyenia tubisperma*

11b. Foraminal aperture of gemmules distinctly tubular but short, less than 0.4 times the diameter of the gemmule (Fig. 4.21) ..... *Heteromeyenia tentasperma*

12a (8b). Gemmoscleres smooth or covered with very fine spines 13

12b. Gemmoscleres absent or covered with robust, conspicuous spines (Figs. 4.25, 4.28 #27) 14

13a (12a). Microscleres smooth or very sparsely microspined (Fig. 4.24) ..... *Spongilla aspinosa*

13b. Microscleres covered with very small spines ..... *[Stratospongilla] penneyi*

14a (12a). Gemmoscleres club-like with spines conspicuously more dense on the ends than in the center (Fig. 4.28 #25) ..... *Spongilla alba*

14b. Gemmoscleres absent or with spines distributed evenly across the length of the spicule (Figs. 4.25, 4.28 #27) 15

15a (14b). Microscleres with conspicuously denser and longer spines in the central region (Fig. 4.28 #27) ..... *Spongilla cenota*

15b. Microscleres with spines distributed evenly across the length of the spicule (Fig. 4.25) ..... *Spongilla lacustris*

16a (1b). Megascleres of a single size category 17

16b. Megascleres in two distinctly different size categories (Fig. 4.14) with the smaller category serving also as gemmoscleres although both sizes of megascleres are always present even when gemmules are absent ..... *Duosclera mackayi*

17a (16a). Gemmules and gemmoscleres absent at all stages of life cycle ..... *Ephydatia cooperensis*

17b. Gemmules and gemmoscleres present at some stage of life cycle 18

18a (17b) Gemmules clearly birotulate (Fig. 4.26) 19

18b. Gemmoscleres oxeote (Fig. 4.28 #15), strongylote (Fig. 4.17), or pseudobirotulate (Fig. 4.28 #24) 28

19a(18a) Margins of rotules completely smooth (Figs. 4.26, 4.28 #31) ..... *Trochospongilla* 20

19b. Margins of rotules distinctly spined or serrated (Figs. 4.15–4.16) 22

20a (19a). Megascleres conspicuously spined (Fig. 4.26) 21

20b. Megascleres smooth or with very fine spines (Fig. 4.28 #31) ..... *Trochospongilla leidii*

21a (20a). Gemmoscleres with rotules of two distinctly different diameters (Fig. 4.27) ..... *Trochospongilla pennsylvanica*

21b. Gemmoscleres with rotules of nearly equal diameters. (Fig. 4.26) ..... *Trochospongilla horrida*

22a (19b). Gemmoscleres occurring in two distinct size classes (Fig. 4.11) 23

22b. Gemmoscleres occurring in only one size class (Fig. 4.15) ..... *Ephydatia* (gemmulating members) 25

23a (22a). Gemmoscleres of two classes that are similar in shape but clearly different in length (Fig. 4.11) ..... *Anheteromeyenia argyrosperma*

23b. Gemmoscleres of two classes that are distinct in both shape and size (Fig. 4.22) 24

24a (23b). Megascleres coarsly spined (Fig. 4.22) ..... *Racekelia ryderi*

24b. Megascleres generally smooth (Fig. 4.28 #2) ..... *Anheteromeyenia biceps*

25a (23b). Rotules of gemmoscleres with margins that are nearly smooth bearing numerous, very small incisions (Fig. 4.28 #12) .. *Ephydatia millsii*

25b. Rotules of gemmoscleres with clearly indented margins (Fig. 4.15) 26

26a (25b). Mean gemmosclere length less than 20 μm with rotules bearing fewer than 12 teeth deeply incised into long rays, gemmosclere length less than or equal to rotule diameter (Fig. 4.16) ..... *Ephydatia muelleri*

26b. Mean gemmosclere length greater than 20 μm with rotules bearing more than 20 teeth that are not deeply incised (Fig. 4.15) 27

27a (26b). Mean diameter of gemmosclere rotules less than 11 μm ..... *Ephydatia subtilis*

27b. Mean diameter of gemmosclere rotules over 11 μm (Fig. 4.15) ..... *Ephydatia fluviatilis*

28a (18b). Most gemmoscleres in intact gemmules arrayed in a distinctly radial fashion within the gemmule coat (Fig. 4.23) ..... *Radiospongilla* 30

28b. Gemmoscleres in intact gemmules arrayed tangentially ..... *Eunapius* 29

29a (28b). Gemmoscleres as smooth oxeas similar to megascleres (Fig. 4.28 #15) ..... *Eunapius carteri*

29b. Gemmoscleres as spiny strongyles (Fig. 4.17) ..... *Eunapius fragilis*

30a (28a). Megascleres sparsely covered with small spines (Fig. 4.23) ..... *Radiospongilla crateriformis*

30b. Megascleres entirely smooth (Fig. 4.28 #23) ..... *Radiospongilla cerebellata*

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