Freshwater sponges (Porifera, Spongillidae) of eastern Canada: taxonomy, distribution, and ecology

ANTHONY RICCIARDI
Department of Biology, McGill University, Montréal, Que., Canada H3A 1B1

AND

HENRY M. REISWIG
Redpath Museum and Department of Biology, McGill University, Montréal, Que., Canada H3A 2K6

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During a recent survey of the freshwater sponges of eastern Canada (from Ontario to Newfoundland), 15 species were recorded, representing approximately 50% of the total number of species known from North America. *Radiospongilla crateriformis*, *Spongilla aspinosa*, and *Trochospongilla horrida* are reported from Canada for the first time. Two problematic species, *Corvospongilla novaeterrae* and *Spongilla johanseni*, are reviewed and their status is revised. Detailed notes on taxonomy, morphology, distribution, and ecology are given. New limits of tolerance with respect to pH, water temperature, and calcium and magnesium concentrations are established for several species. A taxonomic key to the freshwater sponges of eastern Canada is presented.

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Un inventaire récent des éponges d'eau douce de l'Est canadien, de l'Ontario à Terre-Neuve, indique la présence de 15 espèces, soit environ 50% des espèces connues en Amérique du Nord. *Radiospongilla crateriformis*, *Spongilla aspinosa* et *Trochospongilla horrida* sont signalées au Canada pour la première fois. Deux espèces, qui présentaient des problèmes taxonomiques, *Corvospongilla novaeterrae* et *Spongilla johanseni*, ont fait l'objet d'une révision et leur status a été amendé. On trouvera aussi des notes détaillées sur la taxonomie, la morphologie, la répartition géographique et l'écologie des espèces. De nouvelles limites de tolérance au pH, à la température, au calcium et au magnésium sont notées chez plusieurs espèces. Une clef permet l'identification des espèces de l'Est du Canada.

[Traduit par la rédaction]

Introduction

Freshwater sponges are sessile suspension-feeders found attached to submerged surfaces in most inland water habitats. In some habitats they dominate epibenthic communities (Frost 1978), and their role in nutrient cycling and primary production is of the same magnitude as that of macrophytes (Frost 1978; Frost and Williamson 1980). They are potentially valuable indicators of water quality (Jewell 1935; Harrison 1974; Mysing-Gubala and Poirrier 1981; Francis and Harrison 1988) and are useful tools in quantitative paleolimnological studies (Kratz et al. 1991). Furthermore, they represent an important food source for juvenile ring-necked ducks (McAuley and Longcore 1988) and possibly for other waterfowl. In Canada, however, freshwater sponges have received very little attention and are among the most poorly known faunal groups. Difficulties in species identification and taxonomic confusion are two factors that have probably discouraged attention to this group. Existing Canadian records of freshwater sponges are fragmentary and generally do not provide useful taxonomic and ecological information. The available taxonomic keys for the identification of North American freshwater sponges are based almost entirely on specimens collected in the United States. The majority of these keys are poorly illustrated and lack basic information on environmental variation, i.e., the range of morphological types representing a given species and the environmental factors correlated with these types. Environmental variation has produced a plethora of synonyms, varieties, and misidentifications in the literature, and has therefore contributed to much of the confusion historically associated with freshwater sponge taxonomy (Poirrier 1969, 1974, 1977).

There are fewer than 30 described species of freshwater sponges in North America whose taxonomic status is generally accepted or has not been seriously challenged (Jewell 1959; Penney and Racek 1968; Harrison 1974; Frost 1991). We had expected that a large percentage of these species would be found in eastern Canada, owing to the diversity and abundance of accessible freshwater habitats and the wide range of ecological conditions in the region. To test this hypothesis, we obtained a large number of specimens collected from various parts of Ontario, Quebec, New Brunswick, Nova Scotia, and Newfoundland, and thus representing a general survey of the freshwater sponges of eastern Canada. This paper provides a detailed examination of the morphology, taxonomy, distribution, and ecology of each identified species. Environmental variation is considered in each species description. An illustrated taxonomic key to the eastern Canadian freshwater sponges is presented for the first time.

Materials and methods

We collected freshwater sponges from May to November in 1972–1992 (1972–1992 by H.M.R., 1989–1992 by A.R.) from various regions in Quebec, Ontario, and Nova Scotia. Recently, additional specimens from these and other eastern provinces (New Brunswick and Newfoundland) were obtained from the following collections of museums and universities (referred to subsequently by the abbreviations in parentheses): Academy of Natural Sciences of Philadelphia (ANSP); British Museum (BM); Canadian Museum of Nature (formerly the Canadian Museum of Natural History) (CMN, NMC); New Brunswick Museum (NBM); Nova Scotia Museum (NSM); Redpath Museum, McGill University (RMN); Royal Ontario Museum (ROM); United States National Museum of Natural History (USNM). Speci-

TABLE 1. Freshwater sponges occurring in eastern Canada

Phylum Porifera	
Class Demospongiae	
Order Haplosclerida	
Family Spongillidae	
Anheteromeyenia argyrosperma (Potts, 1880)	1
Anheteromeyenia ryderi (Potts, 1882)	2
Corvomeyenia everetti (Mills, 1884)	3
Corvospongilla novaeterrae (Potts, 1886)	4
Ephydatia fluviatilis (Linnaeus, 1758)	5
Ephydatia muelleri (Lieberkühn, 1856)	6
Eunapius fragilis (Leidy, 1851)	7
Eunapius mackayi (Carter, 1885)	8
Heteromeyenia baileyi (Bowerbank, 1863)	9
Heteromeyenia tubisperma (Potts, 1881)	10
Radiospongilla crateriformis (Potts, 1882)	11
Spongilla aspinosa Potts, 1880	12
Spongilla lacustris (Linnaeus, 1758)	13
Trochospongilla horrida Weltner, 1893	14
Trochospongilla pennsylvanica (Potts, 1882)	15

TABLE 2. Distribution of eastern Canadian freshwater sponges

	Species codes														
Ontario	1	—	—	—	—	6	7	—	—	10	—	—	13	—	15
Quebec	1	2	3	—	5	6	7	8	9	10	11	—	13	14	15
New Brunswick	1	2	—	—	—	6	7	8	9	—	—	—	13	—	15
Nova Scotia	1	2	3	4	5	6	7	8	9	—	—	12	13	—	15
Newfoundland	—	2	3	4	—	6	7	8	—	—	—	—	13	—	15

NOTE: For species codes see Table 1.

mens in our own collections have been given the prefix AR or HMR. In total, over 1500 specimens from eastern Canada were examined.

Water quality data were obtained from most of the collection sites in Quebec and Ontario. Temperature and pH were measured on site, using a Fisher mercury thermometer and a Cole–Parmer digital pH meter (model 05941-20). Hardness due to calcium and magnesium (as $CaCO_3$ and $MgCO_3$, respectively) was determined using a chemical test kit (LaMotte Chemical Products Co., Chestertown, Maryland). Water quality data from New Brunswick were obtained from D. F. McAlpine (New Brunswick Museum), and data from Nova Scotia from J. Kerekes (Canadian Wildlife Service, Atlantic Region) and published studies (Freedman *et al.* 1989; Kerekes *et al.* 1978).

Freshwater sponge taxonomy is based on the morphology and arrangement of spicules (siliceous, needle-like structures which form the mineral skeleton) and gemmules (asexually produced, spherical, resistant resting bodies) (Penny and Racek 1968). Spicules are divided into three general classes: (1) megascleres; large spicules, usually in fibers (fascicles), which form the main skeleton; (2) microscleres; smaller spicules which (when present) are free and abundant in the pinacoderm and, to a lesser extent, in the mesohyl; and (3) gemmoscleres; spicules that surround the gemmule and form either part of its resistant coat or an outer capsule. The presence of gemmoscleres, whose size and morphology are often unique to each species, normally ensures correct species identification (Penney and Racek 1968). In this study, temporary spicule preparations for rapid identification using light microscopy were made by heating a mixture of sponge spicules and bleach ($HClO_4$) on a glass slide. Permanent spicule preparations (for measurement and scanning-electron microscopy) were made using the membrane filter technique described by Reiswig and Browman (1987). A Numonics 2200 digitizing tablet and SigmaScan (version 3.92, Jandel Scientific) software were used to measure spicules and gemmules. Measurements are presented in this paper as minimum–(mean)–maximum. The standard deviations of the mean are given as SD_n, where n is the number of measurements.

A specimen may lack gemmules and gemmoscleres (e.g., sponges collected in early summer may not yet have developed gemmules, or a collector may have ignored gemmules attached to the substrate when removing a specimen); without these structures most taxonomic keys do not allow a correct identification even to the generic level. Therefore, in addition to a species key that requires all structures to be present, we have provided a key that permits freshwater sponges lacking gemmules and gemmoscleres to be identified to as precise a taxonomic level as possible. The user is cautioned that species mixtures (caused, for example, by the overgrowth of two or more specimens; Ricciardi and Reiswig 1992) are common and are easily misidentified. Their identity can be resolved only by careful selection of material for spicule preparation.

Results and discussion

A total of 15 species of freshwater sponges were collected from various regions in eastern Canada (Tables 1 and 2). These species comprise 52% of the total number of species known in North America (Frost 1991; Penney and Racek 1968) and demonstrate that freshwater sponges are more diverse in eastern Canada than previous records have indicated. Further collection would almost certainly add to this list of species, since there are large areas of eastern Canada whose aquatic invertebrate fauna remains poorly known.

Descriptions of each species, including notes on taxonomy, ecology, and distribution in eastern Canada, are presented below. A glossary is provided at the end of the paper. Synonyms given for each species generally follow Penney and Racek (1968) and are limited to those published for eastern Canada. Distribution records for a province, if reported previously, are provided with references; otherwise, the species is reported herein for the first time. Water quality data are provided for active (vegetative) colonies rather than for the more resistant gemmule phase, since active colonies are more sensitive to environmental change (Harrison 1977).

Anheteromeyenia argyrosperma (Potts, 1880) Fig. 1

Heteromeyenia argyrosperma Mackay, 1886*b*, 1889; Gee 1937

Description of eastern Canadian specimens

Sponge generally green (due to presence of symbiotic algae), flat, and encrusting. Megascleres slender amphioxea, sparsely covered with procurved spines (M in Fig. 1); megasclere length 250–(284)–304 μm (SD_{50} = 16), width 10–(12)–15 μm (SD_{50} = 0.5). Microscleres absent.

Gemmules yellow and spherical; diameter 558–(649)–686 μm (SD_{20} = 39.2); foramen a simple pore. Gemmoscleres birotulates of two length groups, somewhat transitional, very similar in shape (*g* in Fig. 1); rotules consist of a few long, strongly recurved rays; shaft bears recurved spines. Shorter birotulates are more abundant, shaft densely spined; length 65–(81)–89 μm (SD_{50} = 4). Larger birotulates are less abundant, shaft sparsely spined; length 114–(130)–160 μm (SD_{50} = 10).

Taxonomy

In many specimens, the gemmoscleres are so intergrading that it is impossible to distinguish the two size classes. However, the large recurved spines and wide length range of the gemmoscleres are reliable features by which this species may be distinguished.

Habitat and general ecology

Anheteromeyenia argyrosperma is found in both lentic and lotic habitats, typically in waters of circumneutral pH, low to moderate alkalinity, and high conductivity (Harrison 1974; Poirrier 1969). The species is generally uncommon in eastern Canada but may be locally abundant in certain habitats, and has been found in the following range of water quality conditions: temperature 9–23°C, pH 6.8–7.4, calcium concentration 20–40 mg/L, magnesium concentration 22–50 mg/L. Small green colonies with gemmules were found epiphytic on *Fontinalis* sp. in water at 9°C in Lac Magnan (approximately 75 km north of Montréal, Quebec); this is the lowest recorded temperature at which *A. argyrosperma* has been collected (cf. Harrison 1974).

Distribution in eastern Canada

Ontario (Gee 1937), Quebec (Gee 1937), New Brunswick, Nova Scotia (Mackay 1886*b*, 1889).

Anheteromeyenia argyrosperma is recorded herein for the first time from New Brunswick from a specimen (NBM, uncatalogued) collected at Beaver Lake, Gloucester County (47°33′N, 66°11′W), on 11 July 1991.

Anheteromeyenia ryderi (Potts, 1882) Fig. 2

Heteromeyenia ryderi Mackay, 1886*b*, 1889; Smith 1930; Gee 1937

Heteromeyenia pictouensis Potts, 1885; Mackay 1886*b*, 1889; Smith 1930

Heteromeyenia macouni Mackay, 1900; Gee 1931

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), brown, or white, forming small hemispherical colonies in running water and massive ramose or papillate colonies in calm, standing water. Megascleres are highly variable among specimens; in the typical *ryderi* form (Fig. 2A), megascleres are slender amphioxea sparsely covered with short procurved spines, except near the tips; in the *pictouensis* form (Fig. 2B), megascleres are short, robust amphistrongyla, densely covered to the tips with recurved spines; in the *macouni* form (Fig. 2C), megascleres are extremely thin amphioxea, sparsely covered with minute, procurved spines. Intergrading types of all of these forms may be found. Overall, megascleres range in length from 141 to 279 μm, and in width from 1 to 21 μm. In the typical *ryderi* form, megasclere length is 194–(220)–253 μm (SD_{30} = 15) and width 7–(11)–14 μm (SD_{30} = 1.7). Microscleres absent.

Gemmules yellow, roughly spherical (diameter 300–400 μm), usually not present in abundance. Gemmoscleres (*g* in Figs. 2A, 2B, and 2C) are birotulates of two distinct classes. Gemmoscleres of one class have umbonate, disk-like rotules with serrated margins; the shaft is either smooth or bears 1–3 spines; gemmosclere length 28–(34)–41 μm (SD_{20} = 2.7), shaft width 3–(4)–5 μm (SD_{20} = 0.5), rotule diameter 20–(23)–28 μm (SD_{30} = 2). Gemmoscleres of the second class have rotules composed of recurved rays, and the shaft bears a variable number of recurved spines; gemmosclere length 46–(56)–64 μm (SD_{20} = 6), shaft width 4–(7)–8.5 μm (SD_{20} = 1.1), rotule diameter 17–(21)–23 μm (SD_{20} = 1.7).

Taxonomy

The *pictouensis* form of this species (Fig. 2B) was originally considered to be a distinct species (*Heteromeyenia pictouensis* Potts), but it differed from the typical form of *ryderi* (Fig. 2A) only in the robustness and dense spination of its megascleres. The variation in *A. ryderi*'s megascleres is apparently ecomorphic, and *pictouensis* is one of many ecological variants of the species (Okland and Okland 1989; Poirrier 1977).

An unusual ecomorph of *A. ryderi*, the *macouni* form (formerly *Heteromeyenia macouni* Mackay) (Fig. 2C), deserves special mention. It is found on Sable Island, a crescentic sandy shoal in the Atlantic Ocean (44°N, 60°W), 160 km southeast of Nova Scotia. The island is 35 km long and less than 2 km wide and holds several brackish and freshwater ponds which regularly receive inputs of salt water carried from the sea by rain (Wright 1989). *Heteromeyenia macouni* was described by Mackay (1990) and was relegated to a synonym of *Anheteromeyenia* (*Heteromeyenia*) *ryderi* by Gee (1931). In the type specimen of *H. macouni* (NSM 899-Z-2-1) the megascleres are long, very thin, and microspined; length 141–(176)–242 μm (SD_{50} = 21.4), width 1–(2)–7 μm (SD_{50} = 1.5). The birotulates are of two intergrading classes. The shorter birotulates have generally smooth, slender shafts, and deeply incised, umbonate rotules composed of 20–25 rays; length 22–(25)–28 μm (SD_{50} = 1.5), shaft width 1–(1.5)–2 μm (SD_{50} = 0.4), rotule diameter 8.5–(14)–18.5 μm (SD_{50} = 2.3); the longer birotulates also have smooth, slender shafts, and umbonate rotules composed of 3–5 distinct rays with recurved tips; length 35–(46)–55 μm (SD_{50} = 3.9), shaft width 1–(2)–4 μm (SD_{50} = 0.6), rotule diameter 9–(12)–15 μm (SD_{50} = 2). Gemmules are large, spherical, and orange or brown, and range from 400 to 800 μm in diameter.

Gee (1931) synonymized *H. macouni* with *A. ryderi* var. *baleni*, a variety characterized by its thin spicules. An examination of the type specimen of *A. ryderi baleni* (ANSP 4766) has shown that its spicules (megasclere width 2–(5)–8 μm, gemmosclere width 2–(3)–6 μm) are generally not as thin as those of *macouni*. The *macouni* and *pictouensis* forms represent the two extremes in a continuous morphological series of forms of *A. ryderi*.

Habitat and general ecology

The *macouni* form of *A. ryderi* is known to occur in 2 of the 13 ponds on Sable Island: Lily Pond (NSM 899-Z-2-1; NSM 953-Z-1-1; NMC 1900-0491) and Pond No. 3 (Wright 1989). Both have the lowest conductivity (124–245 μmho/cm; 1 mho = 1 S) among ponds whose values reach 39 000 μmho/cm (J. Kerekes, unpublished data). The following water quality conditions have been recorded for these two ponds: Lily Pond: temperature 14–17°C, pH 5.5–6.0, conductivity 168–200 μmho/cm, total phosphorus 28.9–35.6 mg P/m^3, chlorophyll *a* 1.6–5.1 mg/m^3; Pond No. 3: temperature 18–19°C, pH 6.0–6.6, conductivity 124–245 μmho/cm, total phosphorus 27.6–33.8 mg P/m^3, chlorophyll *a* 1.3–1.4 mg/m^3.

We have also identified specimens of *A. ryderi macouni* from Yudle Cove Pond, Terra Nova National Park, Newfoundland (CMN slides Nos. 62, 65, and 66). From lakes on the western coast of Norway, Okland and Okland (1989) collected specimens of *A. ryderi* that had slender spicules apparently identical with those of the *macouni* form. Although thin spicules may be associated with low silica levels (Kratz *et al.* 1991), the common feature of all of the habitats in which *A. ryderi macouni* occurs is close proximity to the sea. Therefore, *A. ryderi macouni* may be an ecomorphic form associated with the atmospheric deposition of sea salts on coastal lakes.

To summarize, *A. ryderi* is known to occur in the following range of water quality conditions in eastern Canada: temperature 12–24°C, pH 4.8–8.9, calcium concentration 0.5–9.0 mg/L, magnesium concentration 0.3–2.0 mg/L, conductivity 31–245 μmho/cm.

Distribution in eastern Canada

Quebec (Gee 1937), New Brunswick (Smith 1930), Nova Scotia (Mackay 1886*b*, 1889, 1900), Newfoundland (Smith 1930).

This species is distributed throughout eastern North America (Penney and Racek 1968), and is apparently common in eastern Canada.

Corvomeyenia everetti (Mills, 1884) Fig. 3

Meyenia everetti Mackay, 1885, 1886*a*, 1886*b*, 1889

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae) or brown, with a hispid surface, and often with slender branches (about 2 mm in diameter) projecting from a thin encrusting base. Megascleres slender amphioxea, normally entirely smooth (M in Fig. 3); in rare cases, a variable number of megascleres may be sparsely spined; megasclere length 143–(218)–260 μm (SD_{100} = 21.1), width 3.5–(8)–14 μm (SD_{100} = 3). Microscleres small birotulates, shaft normally smooth, rotules dome-shaped and composed of 3–6 recurved spines (*m* and *r* in Fig. 3); microsclere length 14–(18)–26 μm (SD_{100} = 2.5), shaft width 1–(2)–3.5 μm (SD_{100} = 0.5), rotule diameter 3.5–(5)–7 μm (SD_{100} = 0.5). Gemmules large (diameter 710–(800)–902 μm, SD_{14} = 66) and not very abundant. Gemmoscleres (*g* in Fig. 3) birotulates of a single class (33–(59)–78 μm, SD_{50} = 10), with a smooth, slender shaft (width 3–(4)–6 μm, SD_{50} = 1); rotules slightly umbonate and consist of several short, recurved spines; rotule diameter 10–(20)–26 μm (SD_{50} = 3). Like most birotulates, the gemmoscleres are arranged radially in a single layer in the gemmule crust.

Taxonomy

Volkmer-Ribeiro (1986) erected a new freshwater sponge family, the Metaniidae (order Poecilosclerida), and placed *C. everetti* into this family, based on a hypothesized phylogenetic relationship between the genus *Corvomeyenia* and a marine poeciloscerid genus. This hypothesis deserves rigorous examination, and until more substantial evidence is found to support this relationship we prefer to maintain *C. everetti* in the family Spongillidae.

The spicular components of *Corvomeyenia everetti* (excluding gemmoscleres) are very similar to those of *Corvospongilla novaeterrae*, a problematic eastern Canadian species. While *Corvomeyenia everetti* is found as far inland as Wisconsin (Jewell 1935, 1939), *Corvospongilla novaeterrae* is known only from a few coastal localities in Newfoundland and Nova Scotia and is probably confined to the Marine region. The distinctly birotulate gemmoscleres of *Corvomeyenia everetti*, with their well-defined rotules and smooth, slender shafts, easily differentiate it from *Corvospongilla novaeterrae*. Even in the absence of gemmules, gemmoscleres are sometimes present in the tissues of *Corvomeyenia everetti* and *Corvospongilla novaeterrae*, and specimens may be distinguished in such instances.

Habitat and general ecology

Corvomeyenia everetti occurs in moderately acidic (pH 5.0–6.6) lentic habitats whose water is transparent and low in calcium (0–4 mg/L) and magnesium (0–3 mg/L) (Harrison 1974; Jewell 1935). It is often found associated with two other acidophilic sponges, *Eunapius mackayi* and *Trochospongilla pennsylvanica*. Aquatic plants and woody debris are apparently the preferred substrates.

Distribution in eastern Canada

Quebec, Nova Scotia (Mackay 1885, 1886*a*, 1886*b*, 1889), Newfoundland.

This species, previously unrecorded from Quebec, was collected at Petit Lac Long near Sainte-Agathe-des-Monts (HMR 84-8-5.2), Lac Bourgeois near La Tuque (ROM B-18), and Lac Welly in Parc Mastigouche (AR459S). In Newfoundland, *C. everetti* is known from White Point Pond, Terra Nova National Park (NMC1900-0489).

Corvospongilla novaeterrae (Potts, 1886) Fig. 4

Spongilla novaeterrae Potts, 1886; Mackay 1889; Traxler 1898; Annandale 1911; Ord and Cameron 1950; Penney and Racek 1968

Ephydatia novaeterrae Weltner, 1895

Corvospongilla novaeterrae Jewell, 1952; Volkmer-Ribeiro and Traveset 1987

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), thin, encrusting; slender branches may project from the surface. Megascleres relatively scarce, generally smooth amphioxea (M in Fig. 4), commonly with some canal erosion (hollow axial regions) and a central spicular "bulb"; a few sparsely spined forms, and forms transitional with gemmoscleres, are usually present; megasclere length 112–(154)–170 μm (SD_{130} = 14.5), width 4–(8)–13 μm (SD_{130} = 2.5). Microscleres are abundant, minute birotulates of variable size (*m* in Fig. 4); rotules dome-shaped and composed of 3–6 spines; shafts generally smooth; microsclere length 13–(21)–32 μm (SD_{130} = 5.5), shaft width 1–(2)–3.5 (SD_{70} = 3.5).

Gemmules spherical, large, free in the skeleton or attached to the substrate; gemmule diameter 820–(1083)–1418 μm (SD_{66} = 129); pneumatic layer very thin, almost completely absent; foramen simple; 3–8 foraminal pores are found on each gemmule (6 per gemmule, on average). Gemmoscleres highly variable, abundant, short, robust amphistrongyla or amphioxea, bearing a variable number of large, recurved spines which tend to concentrate near the ends of the shaft, occasionally giving the spicule a birotulate appearance (*g* in Fig. 4); gemmosclere length 21–(39)–63 μm (SD_{130} = 8.0), shaft width (excluding spines) 3–(6)–9 μm (SD_{120} = 4.2); gemmoscleres are generally arranged tangentially in the gemmule crust, although several of the more birotulate forms are found projecting radially from the surface.

Taxonomy

Corvospongilla novaeterrae is remarkably similar to *Corvomeyenia everetti* in that the two species have nearly identical growth forms and similar megascleres (smooth or microspined amphioxea), birotulate microscleres, and gemmules. However, they differ in the following ways: (*i*) the gemmoscleres of *Corvospongilla novaeterrae* are generally short, robust, rod-shaped spicules (*g* in Fig. 4), often heavily spined, while those of *Corvomeyenia everetti* are elongate birotulates with smooth, slender shafts (*g* in Fig. 3); (*ii*) the pneumatic layer is generally well-developed in the *C. everetti* gemmule but is extremely reduced in the *C. novaeterrae* gemmule; (*iii*) *Corvospongilla novaeterrae* is apparently restricted to the Maritime coast, while *Corvomeyenia everetti* is widely distributed in northeastern North America.

On the basis of its birotulate microscleres, tangentially arranged rod-shaped gemmoscleres, and large gemmules with a reduced pneumatic layer, *Spongilla novaeterrae* Potts is assignable to the genus *Corvospongilla* Annandale, a taxonomic interpretation made by Jewell (1959) and supported by Volkmer-Ribeiro and Traveset (1987). However, both Annandale (1911) and Weltner (1895) maintained that the highly variable gemmoscleres of *C. novaeterrae* are simply malformed birotulates. The distal aggregation of spines on the gemmosclere and the tendency for the more birotulate-like spicules to assume radial positions in the gemmule crust indicates that they are intermediate between rod-shaped and birotulate forms. There is a similarity between the gemmoscleres of *C. novaeterrae* and malformed birotulates of *Ephydatia muelleri* or *Anheteromeyenia ryderi*, which leads to the possibility that *C. novaeterrae* may simply be an aberrant form of *Corvomeyenia everetti*. Traxler (1898) and Penney and Racek (1968) considered *Corvospongilla novaeterrae* to be a sexual hybrid of *Corvomeyenia everetti* and some other genus, based on their interpretation of Potts' type material: a presumably syntypic group of specimens on 7 stones (ANSP 4521, 4522, 4545-4549) and 2 accompanying slides. On examination, we found this material to be mixed with specimens clearly identifiable as *Eunapius mackayi*. Specimens ANSP 4545, 4546, 4547, and 4549, all part of Potts' collection from the type locality in Newfoundland and considered paralectotypes (Volkmer-Ribeiro and Traveset 1987), comprise almost exclusively *E. mackayi* spicules and a few gemmules. Valid specimens of *C. novaeterrae* (ANSP 4521, 4522, and 4528) were mixed with *E. mackayi*; specimens of both species were often encrusting the same stone. The lectotype (ANSP 4521) designated by Volkmer-Ribeiro and Traveset (1987) is the specimen that is least contaminated with *E. mackayi* spicules. Potts (1886) apparently recognized these foreign spicules in his type material and therefore did not include them in his description and illustration of *C. novaeterrae*. We have recently identified a pure specimen of *C. novaeterrae* from Warren Lake, Nova Scotia (NSM 1976-Z-324-1), which has no spicules resembling those of *E. mackayi*, and closely fits Potts' (1886) original description.

The assumption of sexual hybridization is based on an erroneous interpretation of the spicule mixture and *C. novaeterrae*'s unusual gemmoscleres. Such a hybrid would presumably have intermediate characteristics of both parent species, but the characteristics of the Warren Lake specimen cannot be confidently assigned to any other North American species. Furthermore, hybridization should be equally likely to occur throughout the overlapping range of both parent species. While *C. everetti, E. mackayi*, and most other species have relatively extensive ranges in eastern North America, *Corvospongilla novaeterrae* is known only from coastal regions of Nova Scotia and Newfoundland. Therefore, there remain only two plausible hypotheses concerning the status of *C. novaeterrae*: (1) it is a valid species of *Corvospongilla*; (2) it is an ecomorphic form of *Corvomeyenia everetti*.

The large gemmules with simple foramina and a weakly developed pneumatic layer, the size and shape of the birotulate microscleres, and the predominantly rod-shaped gemmoscleres are characteristics shared by most *Corvospongilla* species. Highly variable gemmoscleres, including some obviously tending toward a birotulate form, are found in two South American species whose taxonomic status has not been challenged: *Corvospongilla seckti* (Bonetto and Ezcurra de Drago 1966) and *C. volkmeri* (Rosa-Barbosa 1988). Both of these species differ from *C. novaeterrae* primarily by their densely spined amphistrongyle megascleres. If the taxonomic validity of *Corvospongilla novaeterrae* depends solely on the interpretation of its highly variable gemmoscleres, then the acceptance of *Corvospongilla seckti* and *C. volkmeri* supports the validity of *C. novaeterrae* and its inclusion in the genus *Corvospongilla*. In each of these species (as in certain other genera, such as *Radiospongilla*; *Pectispongilla*) the gemmoscleres may be natural evolutionary intermediates between amphioxea and birotulates.

Conversely, the irregular gemmoscleres of *C. novaeterrae* may simply be ecomorphic. The loss of birotulate form may be associated with the reduction of the gemmule pneumatic layer, which in turn may be an ecophenotypic response to a particular environmental factor. Since all the sites at which *C. novaeterrae* has been collected are located very close to the ocean (Warren Lake, for example, is less than 3 km from the coast), this factor might be salinity. The aerosol influence that is the likely cause of the *macouni* ecomorph of *A. ryderi* could conceivably result in a highly aberrant form of *C. everetti*.

The status of *Corvospongilla novaeterrae* can only be fully resolved by rearing living sponges under different water quality conditions to determine the effect on spicule morphology. Until such a conclusive examination is made, we believe that *C. novaeterrae* should be maintained as a distinct species to avoid obscuring taxonomic information.

Habitat and general ecology

Spicular malformations such as canal erosion and bulbous structures are found in many species and are generally interpreted as ecomorphic responses to adverse water quality (e.g., Poirrier and Trabanino 1989). *Corvospongilla novaeterrae* and certain other species (e.g., *Corvomeyenia everetti, Ephydatia muelleri*) are apparently more predisposed to such malformations.

All known specimens of *C. novaeterrae* were collected from clear shallow areas of lakes located in coastal regions. The species was found in the following water quality conditions at Warren Lake (Kerekes *et al.* 1978): pH 5.2−6.3, conductivity 26−37 μmho/cm, color 30−70 Hazen units, turbidity 0.1−0.2 Jackson turbidity units (JTU), phosphorus concentration 3.5−9.6 mg/m^3, chlorophyll *a* 0.3−2.1 mg/m^3.

Distribution in eastern Canada

Nova Scotia, Newfoundland.

In Nova Scotia, *C. novaeterrae* is known from Bluff and Eagle lakes in Halifax County (Ord and Cameron 1950) and Warren Lake in Cape Breton Highlands National Park. In Newfoundland, the species was collected at Heart's Content, Trinity Bay (approximately 48°N) (Potts 1886). It may occur in lakes in the coastal areas of Prince Edward Island and New Brunswick.

Ephydatia fluviatilis (Linnaeus, 1758) Fig. 5

Ephydatia fluviatilis Smith, 1921; Gee 1937

Description of eastern Canadian specimens

Megascleres amphioxea (M in Fig. 5), generally smooth; a few microspined forms usually present; megasclere length 253–(343)–439 μm (SD_{100} = 38.6), width 9–(13)–17 μm (SD_{100} = 2.0). Microscleres absent.

Gemmules abundant, spherical, normally 400–600 μm in diameter. Gemmoscleres birotulates of one type (*g* in Fig. 5); rotules disk-like, not deeply incised, margins serrated, with numerous (often more than 20) teeth (*r* in Fig. 5); shaft smooth, or bearing 1–4 large spines; gemmosclere length always greater than rotule diameter; gemmosclere length 20–(23)–26 μm (SD_{50} = 1.5), width (at center) 2–(3)–4 μm (SD_{50} = 0.5); rotule diameter 13–(18)–24 μm (SD_{50} = 3.0).

Taxonomy

This species has historically been confused with its congener *Ephydatia muelleri* (Lieberkühn), since the original descriptions treated both forms as the same species. However, they may be consistently separated by their gemmosclere morphology (Old 1932; Jewell 1959; and others). The gemmosclere length is always greater than the rotule diameter in *E. fluviatilis* (*g* in Fig. 5) and always less than or equal to the rotule diameter in *E. muelleri* (*g* in Fig. 6). The rotules of *E. muelleri* are more deeply incised and composed of far fewer teeth (normally 12 or fewer) than those of *E. fluviatilis*. Although most North American keys have employed these characteristics to separate *E. fluviatilis* and *E. muelleri* since the early part of this century, the taxonomic confusion surrounding the two species has persisted for some time; this is particularly true in Canada, where most species records were established before 1940. Gee (1937) could not find a single valid specimen of *E. fluviatilis* from collections of previous workers, despite numerous reports of its occurrence. Judging from the available specimens, *Ephydatia muelleri* is more common than *E. fluviatilis* in eastern Canada; consequently, the majority of records referring to *E. fluviatilis* in this region likely belong to *E. muelleri*.

Habitat and general ecology

Ephydatia fluviatilis is found in alkaline waters rich in calcium (Francis *et al.* 1982; Harrison 1974; Poirrier 1974). The two specimens (AR486S and RMM-I-3614) that we have collected were found as thin, brown encrustations on the underside of rocks in shallow, sluggish streams (temperature 15–17°C, pH 8.4, calcium concentration 68 mg/L, magnesium concentration 28 mg/L).

Ephydatia fluviatilis has been shown to be sensitive to low concentrations of heavy metals. Exposure to 0.001 mg/L of cadmium or mercury causes distinct gemmosclere malformations and may inhibit gemmule formation (Mysing-Gubala and Poirrier 1981). Copper and zinc are toxic to sponge cells at micromolar concentrations (Francis and Harrison 1988).

Distribution in eastern Canada

Quebec, Nova Scotia.

This species is apparently rare in eastern Canada, although it is common in western regions of Canada. Valid museum specimens of *E. fluviatilis* have been collected from Wabamum Lake, Alberta (NMC1900-0587B), and from a small pond near Minnedosa, Manitoba (ROM, uncatalogued). The only valid specimens known from eastern Canada were collected from a tributary of the Chateauguay River near Huntington, Quebec (AR486S), and from Brierly Brook at Antigonish, Nova Scotia (RMM-I-3614).

Ephydatia muelleri (Lieberkühn, 1856) Fig. 6

Spongilla stagnalis Dawson, 1878
Spongilla asperrima Dawson, 1878
Meyenia fluviatilis Mackay, 1889
Ephydatia muelleri Smith, 1921, 1930; Gee 1937; Benfey and Reiswig 1982; Barbeau *et al.* 1989; Ricciardi and Lewis 1991

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), brown, or grey; surface irregular and papillate. Megascleres stout or slender amphioxea, usually densely covered with short conical spines, except near the tips (M in Fig. 6); in rare cases, megascleres are entirely smooth; both smooth and variably spined forms are often present in the same specimen; megasclere length 171–(245)–311 μm (SD_{259} = 26.4), width 5–(11)–23 μm (SD_{220} = 3.7). Microscleres absent.

Gemmules yellow, spherical, abundant, and scattered throughout the sponge, ranging from 300 to 400 μm in diameter. Gemmoscleres birotulates of one class (*g* in Fig. 6); rotules flat, umbonate, deeply and irregularly incised, forming no more than 12 long rays; shaft normally smooth, rarely with 1 or 2 spines; gemmosclere length never greater than rotule diameter; malformations are common, often resulting in a loss of birotulate form; gemmosclere length 8–(17)–28 μm (SD_{250} = 3.8), shaft width 1–(4)–9 μm (SD_{137} = 1.3), rotule diameter 8–(15)–27 μm (SD_{270} = 3.5).

Taxonomy

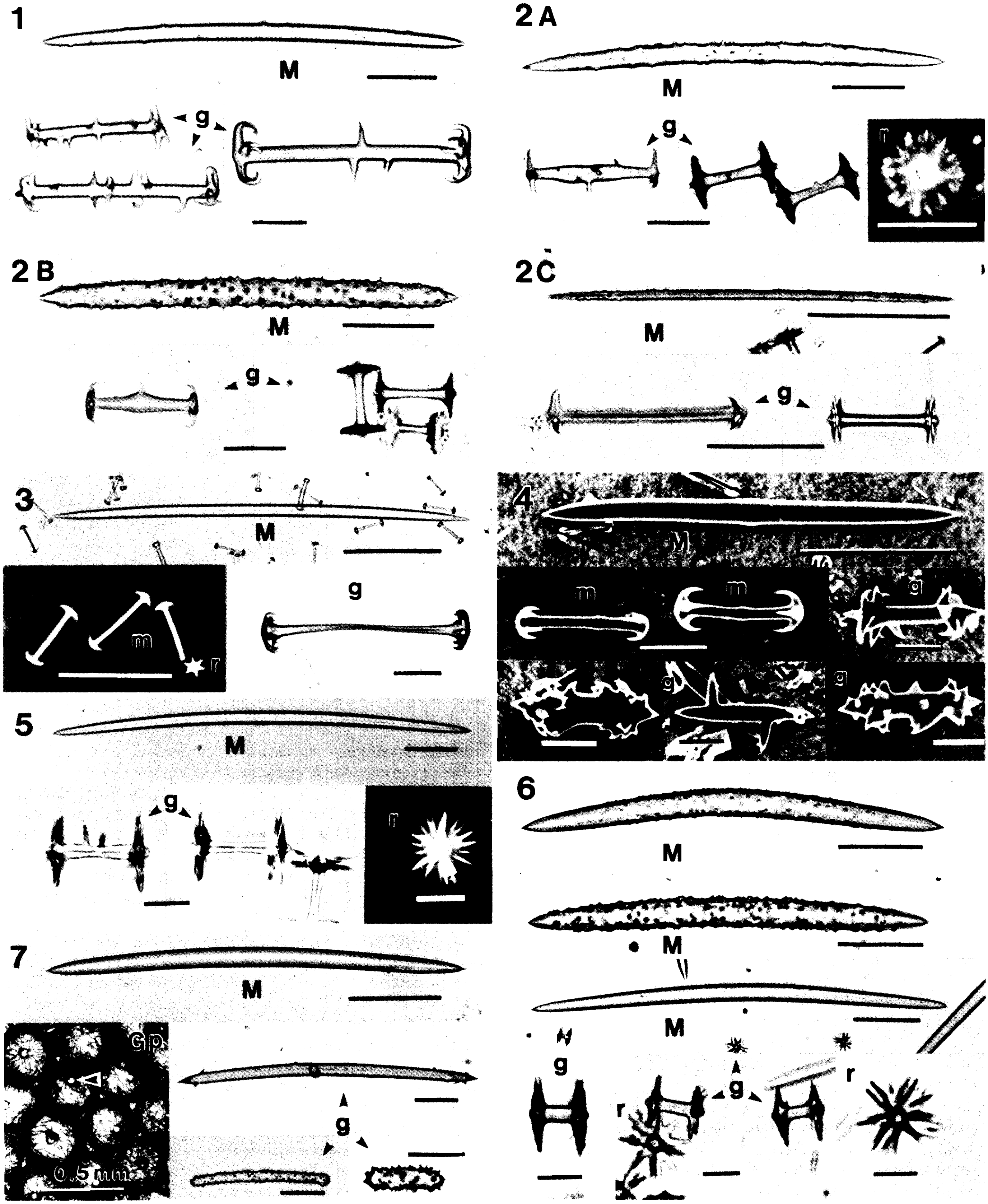
As mentioned previously, *E. muelleri* is consistently separated from its congener *E. fluviatilis* by gemmosclere morphology. In *E. muelleri*, the length of the gemmosclere is never greater than the diameter of the rotules, and the margins of the rotules are deeply incised to form no more than 12 long rays; in *E. fluviatilis*, the length of the gemmosclere is always greater than the diameter of the rotules (*g* in Fig. 5) and the rotule margin is weakly or deeply incised to form 13–20 (or more) short teeth. Most eastern Canadian records of *Ephydatia fluviatilis* dated prior to 1930 probably refer to *E. muelleri*.

Habitat and general ecology

Specimens of *E. muelleri* were collected from areas in eastern Canada with the following water quality conditions: temperature 9–24°C, pH 5.9–9.1, calcium concentration 18–78 mg/L, magnesium concentration 12–70 mg/L. Colonies were most often associated with the sponges *Spongilla lacustris* and *Eunapius fragilis* and the bryozoans *Cristatella mucedo* and *Pectinatella magnifica*. Active green colonies were collected in 9°C at Lac Magnan (near Lachute, Quebec); this temperature represents a new tolerance limit for the vegetative phase of the species. Benfey and Reiswig (1982) found that the gemmules of *E. muelleri* were sensitive to decreases in pH, and that exposure to relatively low pH (5.8–6.5) resulted in reduced gemmule hatchability. Gemmules of this species may withstand long-term exposure to temperatures as low as −80°C without loss of hatchability (Barbeau *et al.* 1989).

Distribution in eastern Canada

Ontario (Dawson 1878; Gee 1937), Quebec (Dawson 1878; Gee 1937; Benfey and Reiswig 1982; Barbeau *et al.* 1989; Ricciardi and Lewis 1991), New Brunswick, Nova Scotia (Mackay 1889), Newfoundland (Mackay 1889).



FIGS. 1–7. Spicules and gemmules of eastern Canadian freshwater sponges. Fig. 1. *Anheteromeyenia argyrosperma*. Fig. 2. *Anheteromeyenia ryderi*, showing typical form (A), *pictouensis* form (B), and *mackayi* form (C). Fig. 3. *Corvomeyenia everetti*. Fig. 4. *Corvospongilla novaeterrae*, showing various microsclere and gemmosclere forms. Fig. 5. *Ephydatia fluviatilis*, showing spined and smooth gemmosclere forms. Fig. 6. *Ephydatia muelleri*, showing smooth and spined megasclere forms. Fig. 7. *Eunapius fragilis*, showing gemmule pavement and range of gemmosclere forms. The large arrowhead points to a foraminal pore (micropyle) on dorsal surface of the gemmule pavement (Gp). M, megasclere (scale bars = 50 μm for all complete megascleres); *m*, microsclere (scale bar = 25 μm for all figures); *g*, gemmosclere (scale bars = 10 μm for Figs. 4–6 and 25 μm for remaining figures).

Ephydatia muelleri is one of the most widely distributed and frequently encountered sponges in eastern Canada. It is common in subarctic lakes (approximately 55°N) near Schefferville, Quebec. Although *E. muelleri* was previously unreported for New Brunswick, specimens were collected from the Hammond and Miramichi rivers (NBM, uncatalogued).

Eunapius fragilis (Leidy, 1851) Fig. 7

Spongilla ottawaensis Dawson, 1878
Spongilla fragilis Mackay, 1886*b*, 1889; Huntsman 1913; Smith 1930; Gee 1937
Eunapius fragilis Ricciardi and Lewis, 1991

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), grey, or brown, normally forming thick hemispherical masses with conspicuously large oscula. Megascleres smooth amphioxea (M in Fig. 7), length = 165−(189)−261 μm (SD_{150} = 19.8), width 4−(10)−14 μm (SD_{150} = 1.7). Microscleres absent.

Mature gemmules are enclosed in a common brown coat, forming a pavement layer cemented to the substrate (Gp in Fig. 7), or individual clusters of 2−4 gemmules; foramina extend through the coat as short tubes, always directed upward from the pavement layer or outward from the cluster. Gemmoscleres are of one class (*g* in Fig. 7), amphistrongyla, and densely covered with spines; length 32−(57)−121 μm (SD_{100} = 12.6), width 3−(5)−8 μm (SD_{100} = 1.1); a small number of spicules transitional in form between gemmoscleres and megascleres (amphioxea or amphistrongyla, bearing a few spines at the tips; *g* in Fig. 7, top) are usually present in the gemmule coat.

Taxonomy

This species is easily distinguished from its congener, *Eunapius mackayi* (Fig. 8), which has spiny megascleres and hemispherical gemmule clusters in which the foramina are always oriented inward or toward the substrate.

Habitat and general ecology

Eunapius fragilis occurs in both lentic and lotic habitats, occasionally in great abundance; it is one of the sponges most commonly found in alkaline, calcium-rich habitats in eastern Canada. Vegetative (active) colonies were collected from the following range of water quality conditions: temperature 9−26°C, pH 6.8−9.4, calcium concentration 8−130 mg/L, magnesium concentration 0.5−150 mg/L.

Eunapius fragilis often occurs with other sponges (*Spongilla lacustris* and *Ephydatia muelleri*) and bryozoans (*Paludicella articulata* and *Pectinatella magnifica*). It is associated with recently established populations of the zebra mussel, *Dreissena polymorpha* (Bivalvia: Dreissenidae), in the St. Lawrence River and is one of the most common epizoic organisms on unionid mussels in both the St. Lawrence and lower Ottawa rivers. The shells of over 30% of living mussels (*Elliptio complanata*, *E. dilatata*, and *Lampsilis radiata*) collected along the north shore of Île Perrot during the summer of 1991 were encrusted with tissue or gemmule pavement of *E. fragilis*. The sponge grows predominantly on the siphonal end of the mussel, where it presumably benefits from the suspended food particles drawn toward it by the siphonal current. The growth may become so luxuriant that it visibly interferes with the functioning of the siphon or the opening of the valves. In muddy or sandy areas, the exposed siphonal end of a mussel shell may offer the only firm substrate available for sponge colonization. Since a single unionid mussel may live for several years (Pennak 1989), it could provide a substrate for several successive generations of a sponge that produces a gemmule pavement. It is not known whether sponge larvae preferentially colonize living mussels.

The life-history strategy of *E. fragilis* in eastern Canada is based on the simultaneous hatching of the entire gemmule pavement at low temperature (4−5°C in Fell 1990) and subsequent rapid growth. This results in a large, confluent colony early in the year, and appears to be a successful strategy in the competition with other organisms for substrate. The gemmules exist solely for overwintering, conserving the substrate, and recruiting a new colony early in the spring. Dispersal appears to be accomplished primarily through the production of motile larvae.

Distribution in eastern Canada

Ontario (Huntsman 1913; Gee 1937), Quebec (Dawson 1878; Gee 1937; Ricciardi and Lewis 1991), New Brunswick, Nova Scotia (Mackay 1886*b*, 1889, Smith 1930), Newfoundland (Mackay 1889).

Eunapius fragilis is one of the most common and widely distributed sponges in eastern Canada. Its occurrence in New Brunswick is recorded here for the first time from specimens collected from the Hammond River and various lakes in Saint John, Gloucester, and Restigouche counties (NBM, uncatalogued specimens).

Eunapius mackayi (Carter, 1885) Fig. 8

Spongilla mackayi Carter, 1885; Mackay 1885, 1886*b*, 1886*c*, 1889
Spongilla johanseni Smith, 1930
Spongilla igloviformis Gee, 1937

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae) or brown, thin, with a slightly hispid surface. Megascleres relatively scarce, long, straight or slightly curved, spined amphioxea or amphistrongyla (M in Fig. 8); spines procurved, more abundant and prominent near the tips of the spicule; megasclere length 177−(200)−302 μm (SD_{204} = 23), width (excluding spines) 7−(12)−18 μm (SD_{204} = 3), maximum spine length 1−(3.5)−7 μm (SD_{41} = 1.2).

Gemmules occur near the substratum in compact hemispherical clusters of 7−20 or more, with the concavity and foramina oriented toward the substratum (G in Fig. 8). The gemmule cluster is enclosed by a common pneumatic coat and a dense, nestlike arrangement of gemmoscleres. Individual gemmules are green or yellow, subspherical, somewhat flattened around the foramen; foramen consists of a short, sometimes flaring, collar; gemmule diameter 263−(421)−841 μm (SD_{76} = 73). Gemmoscleres (*g* in Fig. 8) are straight amphioxea or amphistrongyla, densely spined; spines are long, pointed, strongly recurved near the tips of the spicule, perpendicular near the center of the spicule; gemmosclere length 79−(156)−267 μm (SD_{287} = 30), width (excluding spines) 2−(8)−20 μm (SD_{287} = 1.2), maximum spine length 1−(4)−9 μm (SD_{287} = 1.5); gemmoscleres are radially embedded in the pneumatic layer and tangentially enclose the gemmule cluster, but are absent near the foramina.

Spicules identical with gemmoscleres are found in abundance in the sponge tissue, regardless of whether gemmules are present. They differ morphologically from the megascleres by their shorter length and dense covering of prominent recurved spines, but these distinctions are often complicated by the presence of intergrading forms. They differ functionally from the megascleres by their position and arrangement in the sponge tissue. Megascleres line the sponge canals and form weak fascicles but are otherwise scarce. Spicules morphologically identical with gemmoscleres are abundantly distributed throughout the sponge tissue, except locally around the canals; they generally do not form fascicles and are not more abundant in any particular region of the tissue except in the vicinity of gemmules. Therefore, they appear to have the functions of both microscleres and gemmoscleres.

Taxonomy

The multiple function of the tissue and gemmule spicules in *Eunapius mackayi* is not unique. The same situation occurs in the sponge *Radiospongilla cerebellata* (Bowerbank), in which regular microscleres are apparently used in the construction of the gemmule coat (Saller 1990*c*). *Trochospongilla horrida* has two classes of megascleres differing in size and function: the longer spicules compose the sponge skeleton, while the smaller spicules support the pinacoderm and are also embedded in the coat that binds the gemmules together in a pavement layer (Saller 1990*a*, 1990*b*); however, the individual gemmule coats have their own birotulate gemmoscleres.

Poirrier (1969) asserted that *Spongilla igloviformis* (Potts 1887) and *Spongilla mackayi* (Carter 1885) are synonymous, based on their published descriptions. We have examined the type specimens of *S. igloviformis* (ANSP 4523) and *S. mackayi* (BM 1890-1-9-279) and have found them to be almost identical in spicule morphology and in the form and arrangement of their gemmules; they are undoubtedly the same species. Since the earliest description of the species was provided by Carter (1885), the name *Spongilla mackayi* Carter is given priority. Penney and Racek (1968) assigned the species to the genus *Eunapius*, based on the rod-shaped gemmoscleres, the tendency for gemmules to form coherent groups, and the assumed absence of microscleres. The presence of tissue spicules of two size classes necessitates a reexamination of the systematic position of *E. mackayi*.

The spicule morphology of *E. mackayi* appears to be highly ecomorphic. While the typical procurved and recurved spination of the megascleres and gemmoscleres occurs in specimens collected from slighty acidic habitats, it is often indistinct in specimens from strongly acidic habitats (pH <5.0), which are probably deficient in silica. These specimens have thin, poorly developed spicules covered with minute perpendicular spines that tend to be concentrated near the tips of the spicule. Nevertheless, although characteristic differences in spination may be lost, spicules of two size classes are usually discernible. The most reliable feature is the formation of hemispherical gemmule clusters with substrate-directed foramina.

Spongilla johanseni, a species described by Smith (1930) from a bog lake near Shippigan, New Brunswick, has the characteristics of *E. mackayi* collected from highly acidic habitats. The holotype of *S. johanseni* (USNM 30782) has very thin, straight spicules with minute perpendicular spines. On some spicules, the spines are distinctly concentrated near the tips. The gemmules are in hemispherical clusters with their foramina directed inward. The gemmoscleres are almost indistinguishable from the spicules that are found in the tissue; gemmosclere length 79–(114)–162 μm (SD_{80} = 20). The tissue spicules have a similar size range but, on average, are longer; length 96–(141)–180 μm (SD_{80} = 21). Clearly, on the basis of the above characters, *Spongilla johanseni* should be considered a junior synonym of *Eunapius mackayi*.

Habitat and general ecology

Eunapius mackayi is restricted to dystrophic, lentic waters with a pH range of 4.7–6.2. It is commonly associated with two other acidophilic sponges, *Corvomeyenia everetti* and *Trochospongilla pennsylvanica*. We collected green colonies of *E. mackayi* from water of pH 4.7 and a temperature of 4°C at Lac Stevens (Parc Mastigouche, Quebec; 46°26′N, 73°09′W) in November 1991. The spicule morphology of these specimens (AR492S) closely resembles that of *S. johanseni*. One other species collected from the lake, *T. pennsylvanica*, was found only as gemmule pavement and clearly was not as abundant as *E. mackayi*. We have obtained green colonies of *E. mackayi* from other acidic lakes in Parc Mastigouche and in the Adirondack Mountains (New York), although previous accounts of this species (e.g., Eshleman 1950; Moore 1953; Neidhoefer 1940; Old 1932; Poirrier 1969) fail to mention the presence of symbiotic algae in the tissue or gemmules.

The formation of hemispherical gemmule clusters with inwardly directed foramina likely has adaptive significance. The inward orientation of the foramina may be designed to avoid fouling or siltation. With synchronous hatching, this orientation may also aid in the rapid fusion of germinal material from each gemmule, resulting in a larger, more viable regenerant. The concave gemmule cluster may conserve substrate for the regenerant (by preventing colonization by periphyton), and may shield it from harmful ultraviolet light during early stages of development.

Distribution in eastern Canada

Quebec (Gee 1937), New Brunswick (Smith 1930), Nova Scotia (Carter 1885; Mackay 1885, 1886*b*, 1886*c*, 1889), Newfoundland (Mackay 1886*c*, 1889).

This species is known from New Brunswick from specimens collected at Shippigan ("*S. johanseni*," USNM 30782) and Williams Lake, Kings County (NBM, uncatalogued). It has been reported from Alger County, Michigan, near Lake Superior (Old 1932), and therefore likely occurs in southern Ontario.

Heteromeyenia baileyi (Bowerbank, 1863) Fig. 9

Heteromeyenia repens Smith, 1930
Heteromeyenia baileyi var. *repens* Gee, 1937

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae) or pale yellow, thin, encrusting, with a hispid surface. Megascleres amphioxea, smooth or sparsely spined (M in Fig. 9); spines minute, blunt, and rosettelike; megasclere length 216–(247)–320 μm (SD_{30} = 18.9), width 5–(8)–13 μm (SD_{30} = 1.7). Microscleres amphioxea, extensively covered with spines; spines increasing in length toward the center of the spicule, where they are perpendicular and have knobbed tips (*m* in Fig. 9); maximum spine length greater than maximum spicule width; microsclere length 53–(67)–83 μm (SD_{30} = 6.5), width (excluding spines) 1–(2.5)–4 μm (SD_{30} = 0.5).

Gemmules yellow, spherical, generally less than 500 μm in diameter; foramen slightly raised, without terminal cirri. Gemmoscleres (*g* in Fig. 9) are of two intergrading classes: (1) short birotulates with flat, serrated rotules; spicule length 38–(44)–51 μm (SD_{30} = 2.7), shaft width 3–(5)–7 μm (SD_{30} =

1.1), rotule diameter 13−(18)−22 μm (SD_{30} = 2.3); (2) long birotulates with rotules composed of long recurved hooks, giving the rotule an umbrella-like appearance; hooks often have knobbed tips; spicule length 49−(70)−86 μm (SD_{30} = 9.8), shaft width 3−(5)−7 μm (SD_{30} = 1.0), rotule diameter 18−(22)−28 μm (SD_{30} = 2.0).

Taxonomy

Heteromeyenia baileyi is readily separated from its congener *H. tubisperma* by the foraminal structure of its gemmule: the foramen of *H. tubisperma* is an extended tube (Gf in Fig. 10), whose length is at least half of the diameter of the gemmule and which bears several terminal cirri or tendrils; *H. baileyi* lacks an extended foraminal tube. The umbrella-like rotules on the longer gemmosclere class are a fairly distinctive feature. Megascleres of both species are quite similar. In the absence of gemmules or gemmoscleres, the morphology of the microscleres is often useful in distinguishing the two species. Microscleres of *H. baileyi* are generally shorter (53−(67)−83 μm) than those of *H. tubisperma* (73−(100)−118 μm). Microscleres of *H. tubisperma* (*m* in Fig. 10) are more densely spined; the spines near the ends of the spicule are distinctly recurved but become perpendicular and larger toward the center of the spicule. Spines on the *H. baileyi* microsclere are more or less perpendicular throughout; they are disproportionately long near the center of the spicule and their maximum length is, on average, greater than the width of the spicule. Spines on the *H. tubisperma* microsclere are never longer than the width of the spicule.

The morphology of eastern Canadian specimens of *H. baileyi* corresponds to that originally described for *Heteromeyenia repens* (Potts 1887), a form considered to be a junior synonym of *H. baileyi* (Penney and Racek 1968).

Habitat and general ecology

Heteromeyenia baileyi encrusts stones and vegetation in lakes and sluggish streams. It is commonly associated with the sponges *Anheteromeyenia argyrosperma* and *Eunapius fragilis*. In eastern Canada, specimens are known from the following range of water quality conditions: pH 5.9−8.2, water temperature 15−26°C, calcium concentration 20−130 mg/L, magnesium concentration 20−150 mg/L. The concentrations of 130 and 150 mg/L were recorded from a creek on Île Perrot (Ottawa River, Quebec) and represent new tolerance limits for calcium (as $CaCO_3$) and magnesium (as $MgCO_3$), respectively, for *H. baileyi*.

Distribution in eastern Canada

Quebec (Gee 1937), New Brunswick, Nova Scotia (Smith 1930).

Heteromeyenia baileyi is locally abundant in some lake outflows in the Laurentian region, north of Montréal (Quebec), but is generally uncommon. In New Brunswick, the species occurs in Oak Bay, Charlotte county (45°14′N, 67°12′W) (NBM, uncatalogued).

Heteromeyenia tubisperma (Potts, 1881) Fig. 10

Carterius tubisperma Huntsman, 1913; Gee 1937

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), brown, or white, papillose, and encrusting. Megascleres smooth or sparsely microspined (in many specimens from eastern Canada, the spines are barely visible) (M in Fig. 10); length 238−(290)−337 μm (SD_{80} = 20), width 9−(12)−15 μm (SD_{80} = 1.5). Microscleres (*m* in Fig. 10) long, slender amphioxea, densely spined; spines small and recurved near the spicule tips but larger near the center of the spicule, straight, with terminal knobs; spine length not greater than the width of the spicule; microsclere length 73−(100)−118 μm (SD_{80} = 9.5), width (excluding spines) 2−(3)−4.5 μm (SD_{80} = 0.6).

Gemmoscleres birotulates of two roughly defined size classes and of similar shape (*g* in Fig. 10); rotules flat, with numerous recurved hooks; shafts sparsely spined; gemmosclere length (of combined classes) 33−(44)−62 μm (SD_{80} = 7), width 2−(4)−6 μm (SD_{80} = 0.7), rotule diameter 12−(19)−25 μm (SD_{80} = 2.3).

Gemmules yellow, spherical, free, abundant in the basal portion of mature sponge; diameter 534−(585)−661 μm (SD_{10} = 47); foramen an extended tube (Gf in Fig. 10), length at least half of gemmule diameter; foraminal length 216−(291)−355 μm (SD_{10} = 58), width 48−(57)−65 μm (SD_{10} = 7); normally bearing 4−8 terminal tendrils (90−200 μm in length, 4−14 μm in width). Foramina of developing gemmules often lack terminal tendrils.

Taxonomy

This species is distinguished by the long foraminal tube and tendrils on its gemmule, which can be observed with a hand lens. In the absence of gemmules, microsclere morphology may help distinguish this species from its congener *Heteromeyenia baileyi*, which has shorter microscleres with longer spines.

Habitat and general ecology

Heteromeyenia tubisperma is found in alkaline waters ranging from clear to green and very turbid, in both lentic and lotic habitats. Eastern Canadian specimens were collected in the following water quality conditions: temperature 11−26°C, pH 7.1−9.0, calcium concentration 12−130 mg/L, magnesium concentration 22−150 mg/L. The upper limits for pH, calcium, and magnesium represent new tolerance limits for *H. tubisperma*. Species commonly found in association with *H. tubisperma* include the sponges *Spongilla lacustris*, *Eunapius fragilis*, and *Ephydatia muelleri* and the bryozoans *Paludicella articulata* and *Plumatella emarginata*.

The long foraminal tendrils on the gemmule are likely adapted for dispersal (e.g., by waterfowl).

Distribution in eastern Canada

Ontario (Huntsman 1913; Gee 1937), Quebec.

This species was previously reported from southern Ontario in the vicinity of Lake St. Clair (Gee 1937) and Toronto (Huntsman 1913); it is probably widespread throughout the Great Lakes region. Although previously unreported in Quebec, it is fairly common in Lac Saint-Louis (St. Lawrence River) and in alkaline lakes and streams throughout the southern part of the province.

Radiospongilla crateriformis (Potts, 1882) Fig. 11

Description of eastern Canadian specimens

Sponge brown or white, small, thin, flat, encrusting. Megascleres slender amphioxea, sparsely microspined (M in Fig. 11); spines procurved, generally absent from the tips of the spicule; megasclere length 254−(278)−298 μm (SD_{35} = 11.7), width 9−(11)−14 μm (SD_{35} = 1.1).

Gemmules white, small, spherical, free, clearly visible within the thin sponge; gemmule diameter 261−(383)−520 μm (SD_{10} = 93.2). Foramen raised, conelike. Gemmoscleres arranged radially around the gemmule except in the immediate vicinity of the foramen, where they lean away to form a crater-like depression around the micropyle (G in Fig. 11). Gemmoscleres with distal aggregations of recurved spines, which often given the spicule a birotulate form (*g* in Fig. 11); gemmosclere length 60–(71)–80 μm (SD_{60} = 4.5), shaft width 2.5–(4)–6 μm (SD_{60} = 0.7), rotule diameter 8–(11)–13.5 μm (SD_{60} = 1.2). Free gemmoscleres are always present in sponge tissue, even in the absence of gemmules.

Taxonomy

In most species of *Radiospongilla*, spicules identical with gemmoscleres are commonly found free in the sponge tissue regardless of whether gemmules are present. Penney and Racek (1968) referred to these as "immature gemmoscleres," but for at least one species, *R. cerebellata* (Saller 1990*c*), they appear to be regular microscleres that are used in constructing the gemmule coat. This may also be true for *R. crateriformis*.

The distal recurved spines on the gemmosclere are highly variable in length; short spines give the gemmosclere an amphistrongyle, scepterlike appearance, longer spines give it a birotulate appearance. Unlike most birotulates, the gemmosclere is several times longer overall than the rotule diameter; like most birotulates, however, the gemmoscleres are arranged radially on the gemmule.

Habitat and general ecology

Radiospongilla crateriformis prefers stagnant, turbid, alkaline waters (Harrison 1974; Poirrier 1969). In Canada the species is known only from Île Perrot (Ottawa River, Quebec): specimens were collected in late July and early August 1991 from a shallow canal (<50 cm depth) on this island fed by the Ottawa River in the spring and subject to annual drying in the summer. Water quality conditions were as follows: temperature 23–26°C, pH 7.9–8.2, calcium concentration 130 mg/L, magnesium concentration 150 mg/L. Other sponges collected on these occasions were *Heteromeyenia tubisperma* and *H. baileyi*.

Distribution in eastern Canada

Île Perrot, Quebec (AR422S, AR432S).

Mackay (1886*a*) collected a few "large hooked birotulates" which he assumed to be "*Meyenia crateriforma*" (= *R. crateriformis*) from lake sediments in Nova Scotia, but no slides or specimens exist; it is very unlikely that a confident identification could be made from such limited material, therefore we consider this record to be doubtful.

Spongilla aspinosa Potts, 1880 Fig. 12

Description of eastern Canadian specimens

Sponge green (due to presence of algal symbionts), thin, with long slender branches. Megascleres smooth, straight amphioxea (M in Fig. 12), length 222–(274)–338 μm (SD_{110} = 28), width 5–(10)–15 μm (SD_{110} = 2). Microscleres (*m* in Fig. 12) abundant, smooth or very sparsely microspined, thin, needle-like, and predominantly straight; length 21–(50)–78 μm (SD_{120} = 15), width 0.4–(1.5)–3.2 μm (SD_{110} = 0.5).

Gemmules scarce, occurring in clusters of various sizes, with foramina oriented toward the substrate; gemmoscleres abundant and enclose each gemmule in a nestlike capsule, but are not embedded in the gemmule pneumatic layer; individual gemmules large, thick-coated, diameter 603–(660)–809 μm (SD_{16} = 63); foramen simple. Gemmoscleres smooth amphioxea (*g* in Fig. 12), resembling small megascleres; length 129–(247)–306 μm (SD_{50} = 34), width 6–(9)–15 μm (SD_{50} = 2.5).

Taxonomy

Historically, this species has been distinguished from its congener *Spongilla lacustris* by its smooth microscleres. However, as shown by Volkmer-Ribeiro and Traveset (1987) through scanning-electron microscopy, the microscleres of *S. aspinosa* are sparsely covered with minute spines, except near the tips. The spines are often discernible under regular light microscopy. Conversely, the microscleres of *S. lacustris* (*m* in Fig. 13) are more densely and conspicuously spined, particularly near the tips; however, microscleres from silica-poor habitats may be so thin that the spines are invisible (Jewell 1935; A. Ricciardi and H. M. Reiswig, personal observation). The most consistent differences between both species are in the arrangement of the gemmules and their gemmoscleres. The thick-coated gemmules of *S. aspinosa* are organized into small clusters with their foramina oriented toward the substrate. Gemmules of *S. lacustris* may be either thin- or thick-coated, are far more abundant than those of *S. aspinosa*, and are never organized into distinct clusters. The gemmule spicules of *S. aspinosa* are smooth amphioxea, are always present in abundance, but are not embedded in the pneumatic layer of the gemmule; gemmoscleres of *S. lacustris* are spined amphioxea, not always present, rarely abundant, and embedded in the gemmule pneumatic layer.

There is some debate (e.g., Smith 1991) concerning whether the spicules surrounding *S. aspinosa*'s gemmule represent true gemmoscleres or are simply megacleres used to line the gemmule. In descriptions of this species, some authors (e.g., Penney and Racek 1968; Frost 1991) state that gemmoscleres are unknown for this species, implying that the gemmules do not bear any spicules. Since there are spicules that form an outer capsule around each gemmule, *S. aspinosa* clearly has functional gemmoscleres. They are almost identical with the megascleres in shape, but are significantly shorter (*t*-test, $p < 0.01$). For the purposes of identification, therefore, we treat them as gemmoscleres in this paper.

Habitat and general ecology

Ecological data for *S. aspinosa* are scarce. Previous reports (Eshleman 1950; Jewell and Brown 1929; Potts 1887) indicate that the species occurs in clear, acidic lakes. In Nova Scotia it has been found in the following water quality conditions: temperature 24°C, pH 4.8–5.4, conductivity 87 μmho/cm, turbidity 0.14 JTU, color 50–90 Hazen units, calcium concentration 0.4 mg/L, magnesium concentration 0.4 mg/L.

Potts (1887) attributed the scarcity of gemmules in *S. aspinosa* to a perennial existence that places minimal importance on the production of overwintering structures; the gemmules likely serve only as insurance against adverse environmental conditions. The substrate-directed orientation of the foramina has not been previously described. As in *Eunapius mackayi*, this orientation may be adapted to protect the foraminal openings from siltation or fouling.

Distribution in eastern Canada

Nova Scotia.

This species has not been previously reported from Canada. We have identified specimens of *S. aspinosa* collected from Jigging Cove Lake, Cape Breton Highlands National Park (NSM 1976-Z-321-1; NSM 1976-Z-319-7), and Little Peskowesk Lake, Kejimkujik National Park (NSM 1972-Z-591-4), in Nova Scotia.

Spongilla lacustris (Linnaeus, 1758) Fig. 13

Spongilla dawsoni Dawson, 1878
Spongilla flexispina Dawson, 1878
Spongilla lacustroides Mackay, 1886*a*
Spongilla lacustris var. *dawsoni* Mackay, 1885, 1886*b*
Spongilla lacustris Mackay, 1889; Huntsman 1913; Smith 1921, 1930; Gee 1937; Ricciardi and Lewis 1991

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae), brown, or white; mature colonies with long, cylindrical branches (up to 8 mm diameter) projecting from an encrusting base. Megascleres smooth amphioxea (M in Fig. 13), length 158−(254)−362 μm (SD_{200} = 28.9), width 4−(10)−17 μm (SD_{200} = 2.9). Microscleres spined amphioxea (*m* in Fig. 13), slightly to strongly curved, and densely covered with small spines, especially near the tips; microsclere length 32−(61)−94 μm (SD_{200} = 12.5), width 1.0−(3.5)−7.5 μm (SD_{200} = 1.4).

Gemmules green or brown, abundant in base and branches of mature sponge; pneumatic coat thin, thick, or absent; foramen simple or with a short peripheral collar; 1−4 foramina may be present; gemmule diameter 290−(425)−842 μm (SD_{50} = 71.3). Gemmoscleres present or absent, usually scarce, slightly to strongly curved amphioxea or amphistrongyla (*g* in Fig. 13); covered with a variable number of recurved spines that tend to be concentrated near the tips; gemmosclere length 18−(32)−58 μm (SD_{50} = 9.2), width 3−(5)−7 μm (SD_{50} = 1.0).

Taxonomy

This highly variable species is usually easily distinguished from its congener *S. aspinosa*, which has smooth or sparsely spined microscleres lacking spines near the tips, thick-coated gemmules occurring in clusters, and smooth gemmoscleres. Green branching forms of *S. lacustris* are often mistaken for aquatic weeds, especially when viewed from above the water surface.

Habitat and general ecology

Spongilla lacustris is a light-positive species found in a wide range of water quality conditions and a wide range of lentic and lotic habitats. Colonies grow more luxuriantly in clear, permanent, standing waters. Eastern Canadian specimens were found in the following range of water quality conditions: temperature 4−25°C, pH 4.8−9.0, calcium concentration 0.4−60 mg/L, magnesium concentration 0.4−64 mg/L. Specimens were collected from Little Peskowesk Lake, Kijimkujik National Park, Nova Scotia (NSM 1972-Z-591-2), which has a pH of 4.8, the highest acidity level recorded for the species. *Spongilla lacustris* is most commonly associated with the sponges *Eunapius fragilis* and *Ephydatia muelleri* and the bryozoan *Paludicella articulata*. Like *Eunapius fragilis*, *S. lacustris* commonly grows on the shells of living unionid clams.

Frost *et al.* (1982) observed that *S. lacustris* rapidly colonizes substrate that it contacts, and suggested that the branching growth form aids its local dispersal. In shallow waters we have observed individual colonies interconnected by one or two stoloniferous branches; this mode of propagation is similar to that of macrophytes and apparently serves for both recruitment and dispersal. Simpson (1980) noted the lack of evidence that gemmules serve as dispersal agents. Luxuriant branching colonies of *S. lacustris* in the lower Ottawa River (Quebec) have an annual mode of dispersal involving gemmules. *Spongilla lacustris* overwinters in this region as a mass of gemmules enclosed in its original sponge skeleton. The onset of spring flooding in the Ottawa River valley causes fragmentation of the buoyant, gemmule-laden branches, which are then carried downstream by the current. For three successive seasons of spring flooding (1990−1992) we have collected fragments of these branches either directly from the current or in bays where they had become entrained along the river.

In addition to aiding dispersal, the branching growth form of *S. lacustris* may alleviate the effects of siltation and substrate competition (Manconi and Pronzato 1991), allow the colony to escape anoxic bottom sediments (Frost *et al.* 1982), and increase feeding efficiency by providing a higher surface to volume ratio (Frost and Williamson 1980).

Through the activity of its algal symbionts, *S. lacustris* may contribute significantly to the primary production of small lentic habitats (Frost 1978, 1991). In clear, soft-water lakes (where macrophytes are scarce or lacking), the green branching form of *S. lacustris* appears to assume the primary producer function of a macrophyte.

Distribution in eastern Canada

Ontario (Dawson 1878; Mackay 1889; Huntsman 1913; Gee 1937), Quebec (Dawson 1878; Gee 1937; Ricciardi and Lewis 1991), New Brunswick (Smith 1930; Gee 1937), Nova Scotia (Mackay 1885, 1886*a*, 1886*b*, 1889; Smith 1930; Gee 1937), Newfoundland (Mackay 1889; Smith 1930).

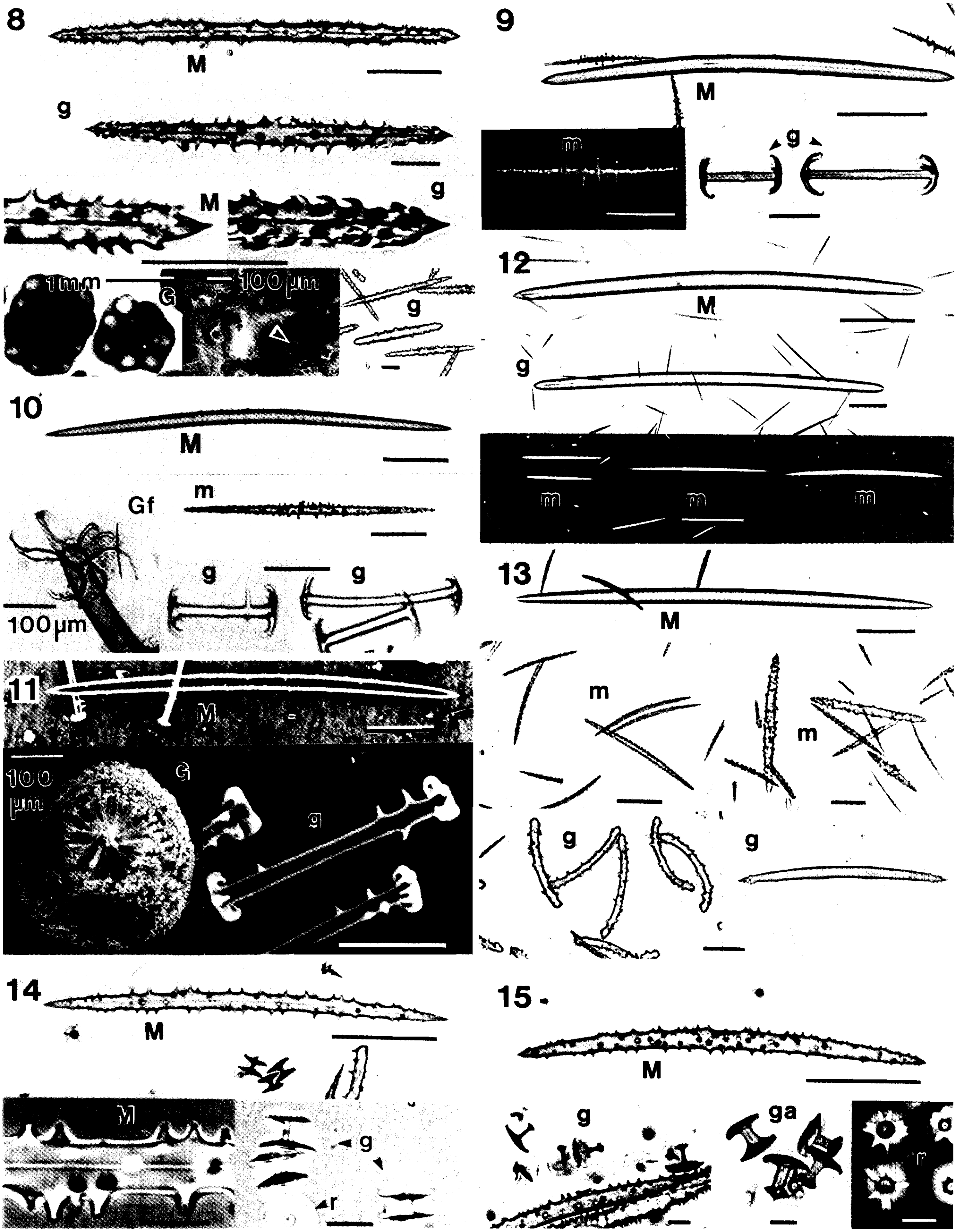
Spongilla lacustris is the most common and widely distributed freshwater sponge in eastern Canada.

Trochospongilla horrida Weltner, 1893 Fig. 14

Description of eastern Canadian specimens

Sponge green (due to presence of symbiotic algae) or brown, flat, encrusting. Megascleres amphioxea (rarely amphistrongyla) densely covered with blunt, truncated spines typical of the genus (M in Fig. 14); megasclere tips usually sparsely spined, rarely densely spined; megasclere length 155−(187)−250 μm (SD_{30} = 10). Microscleres absent.

FIGS. 8−15. Spicules and gemmules of eastern Canadian freshwater sponges. Fig. 8. *Eunapius mackayi*. The arrowhead indicates the micropyle on the underside of a gemmule cluster (G). Fig. 9. *Heteromeyenia baileyi*. Fig. 10. *Heteromeyenia tubisperma*. Fig. 11. *Radiospongilla crateriformis*, dorsal view of gemmule (G), showing craterlike depression around the foramen. Fig. 12. *Spongilla aspinosa* (with a range of microsclere forms). Fig. 13. *Spongilla lacustris* (microscleres and gemmosclere forms). Centre right: a mixture of normal and aberrant microscleres (or possibly gemmoscleres). Fig. 14. *Trochospongilla horrida*, enlargement of megasclere (lower left) showing the truncated spines typical of the genus. Fig. 15. *Trochospongilla pennsylvanica*. M, megasclere (scale bars = 50 μm for all complete megascleres); scale bars = 25 μm for magnified megasclere portions (Figs. 8 and 14); *m*, microsclere (scale bar = 25 μm for all figures); G, gemmule; Gf, gemmule foraminal region; Gp, gemmule pavement; *g*, gemmosclere; *ga*, abnormal form (scale bar = 10 μm for Figs. 14 and 15; scale bar = 25 μm for all other figures); *r*, rotule (axial view of gemmosclere or microslere) (scale bars are the same as for the microsclere or gemmosclere to which the rotule belongs).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Gemmules yellow or brown, spherical, normally cemented to the substrate in a pavement layer, with foramina directed upward; gemmule diameter 324–(380)–537 μm (SD_{15} = 54). Gemmoscleres small birotulates (*g* in Fig. 14); rotules disk-like, with smooth margins, and nearly equal in diameter; overall length of gemmosclere never greater than diameter of smaller rotule; gemmosclere length 8–(9)–10 μm (SD_{30} = 0.5); diameter of smaller rotule 10–(12)–13 μm (SD_{30} = 1.2); diameter of larger rotule 13–(14)–16 μm (SD_{30} = 1.0).

Taxonomy

A recent redescription of this species is provided by Saller (1990*a*). Most taxonomic keys separate *T. horrida* from its congener *T. pennsylvanica* by the relative sizes of the gemmosclere rotules; in *T. horrida* the rotules are nearly equal in diameter, whereas in typical specimens of *T. pennsylvanica* (*g* in Fig. 15) one rotule is disproportionately larger than the other. In some aberrant forms of *T. pennsylvanica* the rotules are equal (or nearly equal) in diameter (*ga* in Fig. 15). Because of this apparent morphological overlap, Poirrier (1969) considered *T. horrida* to be an ecomorphic variant of *T. pennsylvanica*. However, the two species can consistently be separated by comparing the length of the gemmosclere with the diameter of its smaller rotule (similar to the criterion used to separate *Ephydatia muelleri* and *E. fluviatilis*): for *T. horrida*, the length of the gemmosclere is, on average, less than the diameter of the smaller rotule; for *T. pennsylvanica*, the length of the gemmosclere is greater than (or, in rare cases, equal to) the diameter of the smaller rotule. Similar observations by Smith (1991) support this distinction.

Habitat and general ecology

In Quebec, *Trochospongilla horrida* is rare and occurs only in alkaline, lotic habitats. Our specimens were collected from the underside of rocks in shallow, slow-flowing water (temperature 20–22°C, pH 7.4–8.1, calcium concentration 10–60 mg/L, magnesium concentration 30–50 mg/L).

Distribution in eastern Canada

Quebec (AR1S; HMR 90-9-8.7; HMR 90-9-8.17).

Trochospongilla horrida has not been previously recorded in Canada. It is known only from the lower Ottawa and St. Lawrence rivers near the Island of Montréal.

Trochospongilla pennsylvanica (Potts, 1882) Fig. 15

Tubella pennsylvanica Mackay, 1886*b*, 1889; Smith 1930
Trochospongilla pennsylvanica Gee, 1937

Description of eastern Canadian specimens

Sponge small, flat, encrusting; brown, grey, or green (due to presence of symbiotic algae). Megascleres amphistrongyla or (rarely) amphioxea (M in Fig. 15), densely covered to the tips with spines; spines straight and generally blunt or truncated; megasclere length 100–(253)–432 μm (SD_{144} = 88.5), width 6–(13)–25 μm (SD_{144} = 4.0). Microscleres absent.

Gemmules yellow, spherical; normally in a pavement layer, with foramina oriented upward; gemmule diameter 310–(350)–396 μm (SD_{26} = 27.0). Gemmoscleres birotulates; rotules disk-like, normally with smooth margins and strongly unequal in diameter (*g* in Fig. 15); lower rotule (which lies next to the gemmule) typically disporportionately larger than the often rudimentary upper rotule; in rare cases, rotules almost equal in diameter (*ga* in Fig. 15); length of the gemmosclere, on average, greater than or equal to diameter of smaller (upper) rotule; gemmosclere length 11–(17)–41 μm (SD_{134} = 4.9); diameter of upper rotule 3.5–(9)–23 μm (SD_{134} = 4); diameter of lower rotule 13–(24)–41 μm (SD_{134} = 8.1).

Taxonomy

As mentioned previously, *T. pennsylvanica* gemmoscleres having nearly equal rotules are distinguished from those of *T. horrida* by comparing the length of the gemmosclere with the diameter of the smaller rotule; if the gemmosclere length is, on average, greater than or equal to the diameter of the smaller rotule, then the specimen is likely to be *T. pennsylvanica*.

Some *T. pennsylvanica* specimens from highly acidic lakes (pH <5.0) have malformed gemmoscleres in which both rotules are deeply incised into 4–6 distinct rays (*r* in Fig. 15); this may be the result of silica deficiency associated with the acidic conditions.

Habitat and general ecology

Trochospongilla pennsylvanica is found as small, thin patches on the underside of submerged objects in acidic to weakly alkaline waters in both lentic and lotic habitats. In acidic lakes (pH <6.0) it is found associated with *Eunapius mackayi* and *Corvomeyenia everetti*. Specimens have been collected in the following water quality conditions: temperature 9–24°C, pH 5.0–7.2, calcium concentration 0–20 mg/L, magnesium concentration 0–10 mg/L. Specimens found at 9°C, a new tolerance limit for *T. pennsylvanica* (cf. Harrison 1974), were brown and showed little sign of deterioration.

Distribution in eastern Canada

Ontario (Gee 1937), Quebec (Gee 1937), New Brunswick, Nova Scotia (Mackay 1886*b*, 1889), Newfoundland (Mackay 1889; Smith 1930).

We have identified a specimen of *T. pennsylvanica* from Lucky Lake, Restigouche County, New Brunswick (47°34′N, 66°13′W) (NBM, uncatalogued), which represents a new record for the province.

Key to the freshwater sponges (Porifera: Spongillidae) of eastern Canada

1*a*. Miscroscleres present[1] 2
1*b*. Microscleres absent 9

2*a*. Microscleres birotulate (*m* in Figs. 3 and 4) 3
2*b*. Microscleres rod-shaped (e.g., *m* in Figs. 10, 12, and 13) 4

3*a*. Gemmoscleres birotulate, with a smooth, slender shaft (*g* in Fig. 3) .... *Corvomeyenia everetti*
3*b*. Gemmoscleres highly variable, but generally rod-shaped with coarse spines (*g* in Fig. 4) .... *Corvospongilla novaeterrae*

4*a*. Gemmoscleres birotulate; central spines on microsclere with terminal knobs (*m* in Figs. 9 and 10) .... *Heteromeyenia*, 5
4*b*. Gemmoscleres rod-shaped or absent; microsclere spines without terminal knobs 7

5*a*. Foramen of mature gemmule an extended tube; central spines on microsclere not disproportionately long, maximum spine length less than maximum spicule width; spines recurved near the tips of the spicule; microsclere length ranging from 73 to 118 μm 6

5*b*. Foramen of mature gemmule not as above; central spines on microsclere disproportionately long, maximum spine length greater than maximum spicule width (*m* in Fig. 9); microsclere length ranging from 53 to 83 μm .... *Heteromeyenia baileyi*

6*a*. Foraminal tube long, greater than one-half the diameter of the gemmule, and bearing several short terminal tendrils (Gf in Fig. 10) .... *Heteromeyenia tubisperma*

6*b*. Foraminal tube short, less than one-half the diameter of the gemmule, and bearing one or two very long, threadlike tendrils (several times longer than the diameter of the gemmule); a rare species, suspected to be present but unrecorded in eastern Canada .... *Heteromeyenia latitenta*[2]

7*a*. Megascleres spined (M in Fig. 8); mature gemmules normally in hemispherical clusters, with foramina directed inward or toward the substrate (G in Fig. 8); colony thin and unbranched .... *Eunapius mackayi*[1]

7*b*. Megascleres smooth (M in Fig. 13); gemmules not in hemispherical clusters; colony often with long, fingerlike branches .... *Spongilla*, 8

8*a*. Microscleres smooth or sparsely spined (*m* in Fig. 12); gemmules thick-coated, occurring in clusters with foramina directed toward the substrate; gemmoscleres smooth (*g* in Fig. 12), shape identical with that of megascleres .... *Spongilla aspinosa*

8*b*. Microscleres densely spined, especially at the tips (*m* in Fig. 13); gemmules not in clusters; gemmoscleres spined (*g* in Fig. 13) .... *Spongilla lacustris*

9*a*. Gemmoscleres rod-shaped; mature gemmules fixed in groups enclosed in a common coat (Gp in Fig. 7, G in Fig. 8) .... *Eunapius*, 10

9*b*. Gemmoscleres birotulate, or with blunt ends, somewhat resembling rotules; gemmules not as above 11

10*a*. Foraminal pores of gemmules directed outward or away from the substrate (Gp in Fig. 7); megascleres smooth (M in Fig. 7) .... *Eunapius fragilis*

10*b*. Foraminal pores of gemmules directed inward or toward the substrate (G in Fig. 8); megascleres spined (M in Fig. 8) .... *Eunapius mackayi*[1]

11*a*. Megascleres densely covered with blunt or truncated spines (M in Fig. 14); mature gemmules in a pavement layer cemented to the substrate; gemmosclere rotules normally with smooth margins (*g* in Figs. 14 and 15) .... *Trochospongilla*, 12

11*b*. Megascleres with pointed spines, or completely smooth; mature gemmules not as above; gemmosclere rotules with incised or serrated margins (*r* in Fig. 5) or recurved hooks (*g* in Fig. 1) 13

12*a*. Gemmosclere rotules normally strongly unequal in diameter (*g* in Fig. 15); on average, gemmosclere length greater than or equal to diameter of smaller rotule .... *Trochospongilla pennsylvanica*

12*b*. Gemmosclere rotules almost equal in diameter (*g* in Fig. 14); gemmosclere length less than diameter of smaller rotule .... *Trochospongilla horrida*

13*a*. Gemmoscleres of two distinct shapes (*g* in Figs. 2A, 2B, and 2C), or similar shapes of highly variable length (*g* in Fig. 1) .... *Anheteromeyenia*, 14

13*b*. Gemmoscleres of one distinct size and shape 15

14*a*. Gemmoscleres of one class with flat, disk-like rotules with incised margins (*r* in Fig. 2A); gemmosclere length ranging from 22 to 64 μm .... *Anheteromeyenia ryderi*

14*b*. Gemmoscleres having rotules composed of a few large, recurved hooks (*g* in Fig. 1); gemmosclere length ranging from 65 to 160 μm .... *Anheteromeyenia argyrosperma*

15*a*. Gemmosclere larger than 60 μm, rotule diameter several times smaller than spicule length, rotules with recurved hooks (*g* in Fig. 11); megascleres (M in Fig. 11) covered with distinctly procurved spines; foramen of gemmule centered in a craterlike depression (*G* in Fig. 11) formed by slanting gemmoscleres .... *Radiospongilla crateriformis*

15*b*. Gemmosclere length less than 30 μm, rotule diameter almost as large as spicule length, rotules without recurved hooks (*g* in Figs. 5 and 6); megascleres smooth or spined, spines not distinctly procurved; gemmule not as above .... *Ephydatia*, 16

16*a*. Gemmosclere length less than or equal to rotule diameter (*g* in Fig. 6); rotules deeply incised to form no more than 12 long rays (*r* in Fig. 6) .... *Ephydatia muelleri*

16*b*. Gemmosclere length greater than rotule diameter (*g* in Fig. 5); rotules weakly or deeply incised, forming 13 or more serrations (*r* in Fig. 5) .... *Ephydatia fluvatilis*

Key to eastern Canadian freshwater sponges lacking gemmules and gemmoscleres

1*a*. Megascleres entirely smooth 2

1*b*. Megascleres spined, or a mixture of spined and smooth forms is present 5

2*a*. Microscleres present 3

2*b*. Microscleres absent .... *Eunapius fragilis* and *Ephydatia* spp.

3*a*. Microscleres rod-shaped (*m* in Figs. 12 and 13) .... *Spongilla*, 4

3*b*. Microscleres birotulate (*m* in Figs. 3 and 4) .... *Corvomeyenia everetti* and *Corvospongilla novaeterrae*

4*a*. Microscleres smooth or sparsely spined, thin and needle-like; predominantly straight (*m* in Fig. 12) .... *Spongilla aspinosa*

4*b*. Microscleres densely spined, especially near the tips; straight or curved (*m* in Fig. 13) .... *Spongilla lacustris*

5*a*. Microscleres present[a] 6
5*b*. Microscleres absent 9

6*a*. Microscleres rod-shaped (*g* in Fig. 8, *m* in Figs. 9 and 10) 7
6*b*. Microscleres birotulate (*m* in Figs. 3 and 4) .... *Corvomeyenia everetti* and *Corvospongilla novaeterrae*

7*a*. Microscleres and megascleres differing greatly in size and form; microscleres ranging from 53 to 118 μm in length and having spines with terminal knobs (*m* in Fig. 9) .... *Heteromeyenia*, 8
7*b*. Microscleres (*g* in Fig. 8) similar in size and form to megascleres (M in Fig. 8), but differing in the orientation of their spines; microsclere length ranging from 114 to 270 μm, spines with pointed tips .... *Eunapius mackayi*[1]

8*a*. Microsclere spines disproportionately long at the center of the spicule (M in Fig. 9), maximum spine length greater than or equal to maximum spicule width; microsclere length ranging from 53 to 83 μm .... *Heteromeyenia baileyi*
8*b*. Microsclere spines not disproportionately long (*m* in Fig. 10), maximum spine length less than maximum spicule width; spines recurved near the tips of the spicule; microsclere length ranging from 73 to 118 μm .... *Heteromeyenia tubisperma* and *H. latitenta*[2] (rare)

9*a*. Spines pointed and curved, usually sparse or absent near the tips of the spicule 10
9*b*. Spines blunt or truncated, generally straight (M in Fig. 14); often densely cover the tips of the spicule .... *Trochospongilla* spp.

10*a*. Spines procurved (M in Figs. 1, 2B, and 11) .... *Radiospongilla crateriformis* and *Anheteromeyenia* spp.
10*b*. Spines generally not procurved; both smooth and variably spined megascleres often present in the same specimen (M in Fig. 6) .... *Ephydatia* spp.

[1]Eunapius mackayi has spicules of two classes differing in the length and orientation of the spines (M and *g* in Fig. 8). The shorter spicules (*g* in Fig. 8) are indistinguishable from those surrounding the gemmule, but are present even in the absence of gemmules and are distributed throughout the sponge tissue; therefore, they may be interpreted as regular microscleres that are also used in the construction of the gemmule.

[2]Heteromeyenia latitenta is a rare species known from scattered locations in northeastern North America (Penney 1960); although presently unrecorded, it likely occurs in eastern Canada.

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Glossary

Amphioxea	Spicules with gradually tapered, sharp-pointed tips (e.g., M in Fig. 1)
Amphistrongyla	Spicules with blunt or abruptly terminated tips (e.g., M in Figs. 2B and 8, *g* in Fig. 8)
Birotulate	Spicule (gemmosclere or microsclere) with a disk-like structure (rotule) at both ends (e.g., *g* in Figs. 1 and 2A)
Foramen	Structure surrounding an aperture (micropyle) in the gemmule coat through which cells are released during germination; foraminal structure differs among species, ranging from a simple pore (e.g., *Spongilla lacustris*) to an extended tube (*Heteromeyenia tubisperma*)
Mesohyl	Material lying beneath the pinacoderm of a sponge
Oscula	Large external pores in the pinacoderm through which water leaves the sponge
Ostia	Small external pores in the pinacoderm through which water enters the sponge
Pinacoderm	Epidermal membrane of a sponge
Procurved	Directed toward the tips of a spicule (referring to the orientation of spines) (e.g., M in Fig. 8)
Recurved	Directed away from the tips of a spicule (referring to the orientation of spines) (e.g., *g* in Fig. 8)
Umbonate	Describes a birotulate spicule whose shaft extends slightly beyond the rotules (e.g., *g* in Fig. 5)