Methods in Quaternary Ecology #4. Freshwater Sponges

Frederick W. Harrison
Department of Biology
Western Carolina University
Cullowhee, North Carolina 28723

Summary

In recent years, there has been an increased awareness of the value of fossilized remains of freshwater sponges in Quaternary paleo-ecological reconstructions. Because the taxonomy and ecology of extant forms have been clarified, and because a well-defined fossil record exists that exhibits continuity with extant species, the stage is set for wide-spread utilization of freshwater sponge remains in Quaternary environmental reconstructions. This paper presents an introduction to the freshwater sponges, techniques for their utilization in Quaternary paleo-ecological studies, and summarizes some of the most recent work performed in North America.

Introduction

Despite the astonishment of many individuals, sponges do exist in most freshwater habitats and in fact, have existed for at least 100 million years. We are familiar with marine sponges. Their often brilliant hues attract attention and even if most sponges purchased from the local merchant consist of a non-natural plastic, many of us still remember the day when a "bath sponge" was non-synthetic. But what of these freshwater sponges? What do they look like (Figures 1 and 2), where can one find them, are they *truly* sponges, and how are they important in Quaternary ecology?

Freshwater Sponge Biology: An overview

Freshwater sponges are members of the great poriferan class Demospongiae, a taxonomic grouping that contains most species of marine sponges. The majority of freshwater sponges are members of the family Spongillidae, a widely distributed group characterized by a siliceous spicular skeleton and by asexual reproductive structures, gemmules. Fortunately for the paleo-ecologist, both these diagnostic sponge parts are found as fossils in lacustrine and peat deposits.

As with all sponges, the physiology of freshwater forms is organized around a system of canals that courses through the body of the animal (Figure 3). Water is driven through the canals by clusters of flagellated cells, choanocytes; thus, the animal is in intimate contact with the aquatic environment. Because of this degree of dependency, the sponges are delicate monitors of water quality, degenerating or dying in the presence of adverse conditions. But under favourable circumstances, the sponges utilize their aquatic environment, filtering their bacterial food from it, assimilating dissolved oxygen, and releasing waste products into the excurrent flow of water in their canal systems.

In terms of most criteria, the freshwater sponges are organized and exist upon the same ancient organizational and physiological patterns as most marine sponges. They differ from most marine sponges in their mode of reproduction. While they do reproduce sexually, freshwater sponges also survive the harsh conditions of northern winters or the warm waters of southern summers by entering an asexual phase of resistant gemmules.

The habit of gemmule formation apparently evolved as a response to unstable environmental conditions. This is seen in a few marine species, particularly those found in harsh, fluctuating intertidal environments.

Seasonal environmental changes trigger the release of endogenous stimuli, perhaps cyclic nucleotides, in the body of the sponge. The ameboid cells of the interior of the sponge migrate and mass in spherical aggregates. As gemmule development proceeds, cells at the aggregate periphery assume a secretory
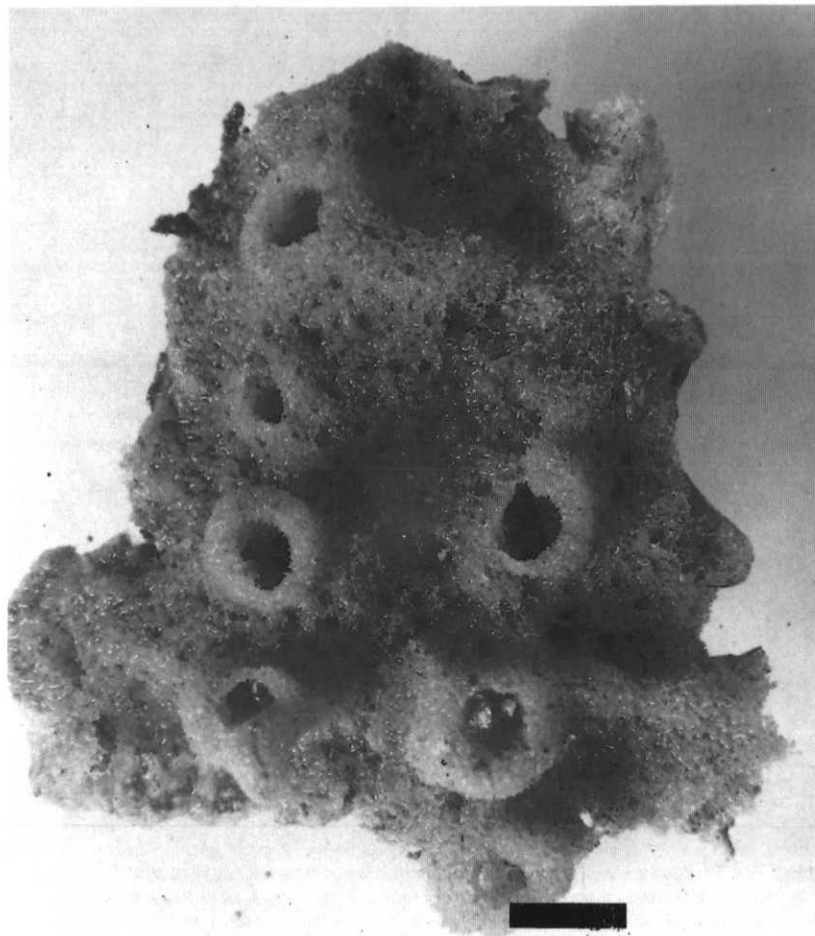

Figure 1 *Modern freshwater sponge,* Eunapius carteri. *The large openings are oscules. Scale bar = 1 cm.*
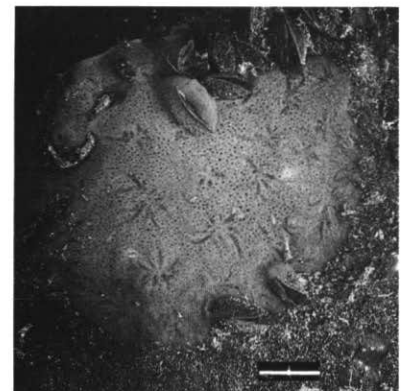
Figure 2 *Modern freshwater sponge,* Eunapius fragilis. *Scale bar equals 1 cm.*

function, depositing a shell of spongin, a form of collagen. Cells in the aggregate interior accumulate yolk in lens-shaped platelets which crowd the cytoplasm of these reproductive cells. However, the gemmules with their protective shells of spongin survive and await the coming of more favourable conditions. With the return of warmer, or cooler, water temperatures, a burst of germinative activity sends the yolk cells of the gemmule migrating out over its surface, spreading upon the substrate, and differentiating into a young sponge. There the sponge grows, forming an encrusting green, tan, or darkly coloured mass on emergent vegetation, upon floating logs, or in the folds and ridges of submerged stones.

The preceding paragraphs offer a brief overview of limited aspects of freshwater sponge biology. The biology of sponges has been reviewed in detail in recent publications. Those seeking further information about these animals should begin with the excellent book by Simpson (1984), *The Cell Biology of Sponges*.

Eventually, siliceous spicules comprising the skeleton of the sponge, and the hard, resistant shells of gemmules become incorporated in the sediment. Although spicules and gemmules which are easily recognizable and diagnostic are preserved in the fossil record, they have not played a significant role in paleoecological reconstructions. Their use has been overlooked by paleoecologists due

to a dearth of knowledge of the ecology of extant freshwater sponge species and long-standing confusion about the taxonomy of the group. Recent advances in both areas of study finally allow the utilization of fossilized sponge remains in paleoecology.

Freshwater sponges in paleoecology: The historical perspective

For freshwater sponges to be useful in paleoecological studies, it is necesary for three factors to exist. First, it is necessary to have a well-defined fossil record that exhibits continuity with extant species. Second, an orderly systematic framework must be available so that the non-specialist on sponges may identify his materials. Finally, the environmental preferences, including physicochemical parameters, of species must be understood. Great effort has been made within the past two decades to meet these three conditions, thus setting the stage for widespread use of this group by paleoecologists.

Much of our understanding of freshwater sponge systematics dates from the monumental study by A.A. Racek (Penney and Racek, 1968). Racek, in completing the study only just initiated before the death of Professor Penney, brought order out of the chaos of spongillid systematics by recognizing global evolutionary patterns among spongillid species. He demonstrated the artificial nature of the two spongillid sub-

families Spongillinae and Meyeninae, erecting a new genus, *Radiospongilla*, for those sponges showing morphological similarities to the two subfamilies. Although lacking fossil evidence, Racek proposed that the two artificial subfamilies had diverged from a common ancestral stock, a stock that had also given rise to the genus *Radiospongilla*. The fossil spongillid, *Paleospongilla chubutensis*, recovered from Cretaceous strata, exhibits spicular characters combining those found in the two subfamilies, thus suggesting the derivation of both subfamilies and appearing to be the most direct ancestral form of the genus *Radiospongilla* (Racek and Harrison, 1975). With the clarification of spongillid systematics, recent taxonomic treatments and keys (Pennak, 1978) have followed the Penney and Racek (1968) nomenclature. Therefore, as spicules and gemmules (Figures 4 to 8), the same elements that are preserved as fossils, are diagnostic criteria for fossil sponge identification, specialists may identify sponges both extant and fossil with the same level of confidence. Recently, increasing work, particularly on North American species has allowed for a fuller understanding of sponge ecology. The ecology of individual species of North American freshwater sponges is presented in a series of papers by Harrison (1974, 1977, 1979), Harrison et al. (1977), Harrison and Harrison (1977, 1979), Jewell (1935, 1939), Old (1932), and Poirrier (1969, 1974, 1977).

Figure 3 Diagram of the anatomy of a freshwater sponge "Knobbed" arrows indicate incurrent flow of water Arrows without "knobs" indicate excurrent flow. A superior epithelium consisting of a layer of fusiform external pinacocytes and an inner layer of endopinacocytes (black cells) is pierced by pores (p) Environmental water passes through the surface epithelium, into a sub-epithelial space (atrium, at), and into the loosely organized mesohyl (m). Water is both drawn into and expelled from choanocyte chambers (c) by the beating of choanocyte (collar cell) flagella. The excurrent system terminatesin oscular chimneys (o) Water exits the sponge by oscules, openings at the top of the chimney. Ameboid cells (a) migrate through the mesohyl. Skeletal elements, spicules (sp), and the basopinacoderm (b) attachment surface respectively, are bound into fasicles or attach through the matrix material, spongin (s)

Consequently, the three necessary criteria have been met. A fossil record with direct relationships to extant forms dates from Cretaceous time. Freshwater sponge species exist within a well-defined systematic framework and, important for limnologic analysis, the presence of particular species may be useful in characterizing and defining local aquatic environments.

Therefore, building upon earlier European studies (Frey, 1964) and upon pioneering studies by Racek (1966, 1970, 1974) of deposits from Europe, Jordan, and Central America, there has been increasing interest in freshwater deposits particularly in North America (Hall and Hermann, 1980; Harrison et al., 1979; Turner, 1985; Harrison and Warner, 1986).

Field Sampling and Laboratory Extraction Techniques

In the field, lake and peatland cores can be collected with standard coring equipment. For spicule analysis, subsamples are boiled in 1:1 mixture of concentrated nitric and sulphuric acids until a dry white dust remains. Following washing, this residue is retained for microscopic examination. In addition, specific volumes (usually 20 cm³) of fresh sediment are washed on a 250 μm mesh sieve, and the remaining residue is examined for macroscopic gemmules under a dissecting microscope.

Identification of freshwater sponge remains relies upon analysis of spicules and gemmules. There are three spicule types in freshwater sponges: megascleres, gemmoscleres, and microscleres. The largest, megascleres, are skeletal spicules which form a supportive framework for the delicate sponge tissues. Megascleres are of limited taxonomic value although they are the predominant spicule type in the sponge. Gemmoscleres which are components of the gemmule coat form the armature of gemmules. Their morphology and placement in the gemmule coat are of considerable diagnostic value in taxonomy. Microscleres, the small "dermal" spicules, are not found in all species. However, their presence or absence and their morphology are of considerable value in taxonomic determinations. A taxonomic key to North American fresh water sponges is presented in Pennak (1978). The original Penney and Racek (1968) monograph is valuable because of the clarity of illustrations. The scanning electron microscope promises to be of exceptional value in taxonomic analysis, but at present, has been rarely used (Harrison, 1981).

### Quaternary Environmental Reconstructions

Although there have been few studies utilizing freshwater sponge remains, the most recent studies involve examination of lake sediments from Canada and from Kentucky, USA. Analyses of fossil spicules and whole gemmules of freshwater sponges were performed on early Holocene sediments collected from Serendipity Bog, a bog lake on eastern Graham Island, Queen Charlotte Islands, British Columbia (Harrison and Warner, 1986). Their study established the essential criterion of corroboration of data obtained from analyses of freshwater sponge remains with data derived independently from other fossilized components, e.g., pollen and plant macrofossils.

Examination of the spicular components in limnic sediments from the Serendipity Bog site revealed a flourishing freshwater sponge population between about 9400 and 8500 years B.P., composed of Spongilla lacustris and a member of the genus Anheteromeyenia. Of the two species, apparently, Anheteromeyenia was the community dominant throughout this period. Two peaks of fossil spicules, one at 3.15-3.10 m and another at 2.95-2.90 m depth, indicate that there were two major periods exceptionally favourable to the growth of sponges. Of the species represented in the Serendipity core, members of the genus Anheteromeyenia generally are more specific in their environmental requirements than is the cosmopolitan S. lacustris.

Sponges of the genus Anheteromeyenia prefer waters of moderate to low alkalinities (known range, 2-80 mg $CaCO_3 \cdot L^{-1}$; Harrison, 1974, 1977) that have high specific conductances (known range, 37-750 μmhos; Old, 1932; Jewell, 1939; Poirrier, 1969; Harrison, 1974, 1977). They prefer waters that are slightly acidic, but will grow well in circum-neutral to slightly basic habitats (known range, pH 4.2-8.5; Harrison, 1974, 1977).

Extant S. lacustris exhibits broader habitat tolerances, although Poirrier (1969) notes that the species is common in acidic water low in bicarbonate; that it exists through a
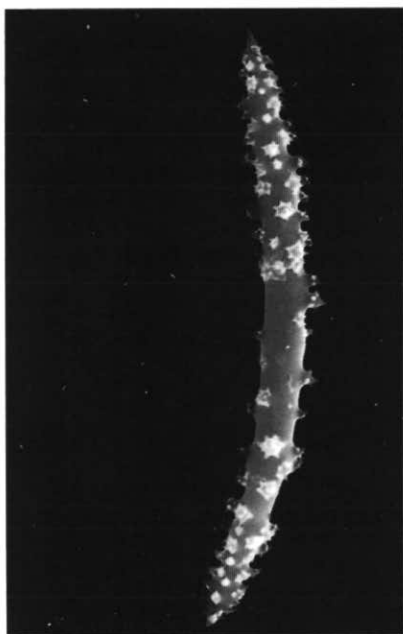
Figure 4 Scanning electron micrograph of a microsclere of Spongilla lacustris. Although this spicule type is not found in all freshwater sponge species, when present, the microscleres are of considerable diagnostic value. Magnification 2400×.
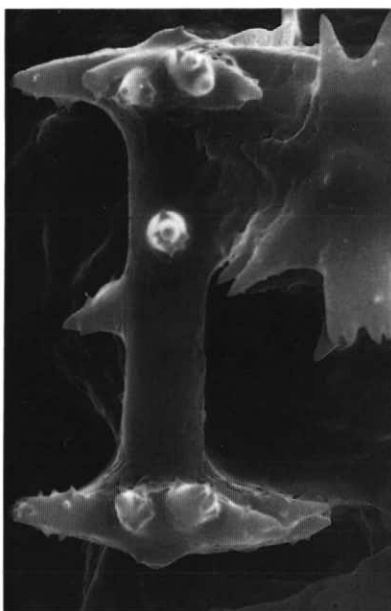
Figure 5 Scanning electron micrograph of a birotulate gemmosclere of Ephydatia fluviatilis. The rotule of another spicule is seen in the upper right of the figure. Magnification 2000×.
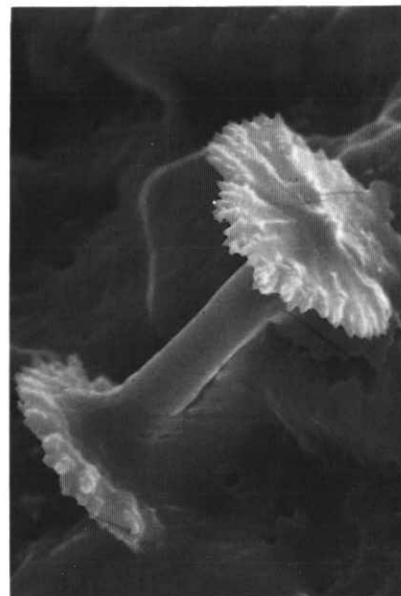
Figure 6 Scanning electron micrograph of a gemmosclere of Anheteromeyenia ryderi. Compare rotule morphology with that of the E. fluviatilis gemmosclere seen in Figure 5. This spicule is partly embedded in the spongin coat of the gemmule. Magnification 1800×.

wide range of pH; and that it shows a slight tolerance to basic waters of higher specific conductances, silicon concentrations, and colour (i.e., dissolved organics) (known ranges, total hardness as $CaCO_3$, 28.8-250.0 mg·L^{-1}; pH 5.3-9.0; specific conductance, 9.4-470 μmhos; silicon 0-20.5 ppm; colour 0-202; Harrison, 1974). Neither of these species is capable of withstanding high levels of turbidity, since suspended silt and clay particles tend to clog the canal system of the sponge's body.

Spicule development in S. lacustris and in other freshwater sponges is related directly to silicon levels (Jewell, 1939). Conspicuously abnormal (i.e., underdeveloped) skeletal elements from S. lacustris were not observed in the fossil sequence, which suggested moderate to high levels of silicon in the water, an interpretation proffered in consideration of the quartzo-feldspathic sand deposits that lie beneath the Serendipity basin.

Available ecological information confirms that S. lacustris prefers habitats with high light intensity. Modern colonies of S. lacustris which were attached to small crystalline rocks, associated with Isoetes echinospora on the shore of Hippa Lake, west of Graham Island were observed in water about 15 cm deep. Spicules of S. lacustris appeared to be more abundant near the base of the Serendipity core, and progressively declined upward. Paleobotanical data indicated the presence of submerged and floating-leaved aquatic macrophytes (Warner, 1984), which

may suggest higher light intensities during earlier phases of development of the Serendipity basin. Subsequent macrophytic growth and progression to a fen community might have increased shading, and hence may have contributed to a reduction in the population of S. lacustris.

Members of the Anheteromeyenia group express variable responses to light. Perhaps the fossil remains of Anheteromeyenia were in fact those of A. ryderi, a species known to prefer shaded habitats. This factor may explain its better representation in the fossil sequence, inasmuch as it would be able to survive the shading effect of associated prolific macrophytic growth.

The presence of fossil materials from the submerged macrophyte Potamogeton filiformis corroborated limnological tolerances indicated by the freshwater sponge fauna. Like S. lacustris and Anheteromeyenia sp., P. filiformis occurs in circum-neutral to basic waters with pH usually above 5.9, and is indifferent to alkalinity of the water and specific conductance. However, P. filiformis almost always is confined to mineral substrates and to water from between 0.5 and 2.0 m deep (Warner, 1984).

Therefore, both the sponge fauna and the submerged aquatic flora as reconstructed from fossil evidence reflect that the early Serendipity basin was shallow. This basin contained standing or slow-moving waters that exhibited circum-neutral to slightly basic pH with moderate to low carbonate alkalinity and high specific conductance, silicon, and dissolved organic content.

The site of a second study utilizing fossil remains of freshwater sponges is Jackson Pond, a sink-hole lake located in the north-central region of Kentucky. The pond lies in

the northern portion of the Interior Low Plateaus and within 190 km of the full-glacial ice margin (Wilkins, 1985; Delcourt et al., 1986). Jackson Pond sediments have been radiocarbon-dated from 20,000 years B.P. to the present (Wilkins, 1985).

Pollen records from Jackson Pond (Wilkins, 1985) indicate that the full-glacial (20,000 to 17,000 years B.P.) and late-glacial (17,000 to 11,500 years B.P.) intervals in central Kentucky were periods of cool, wet climate with high sedimentation rates in the pond, indicative of sheetwash erosion from the nearby uplands. These high sedimentation rates were associated with conditions of high levels of soil moisture (Delcourt, 1985; Wilkins, 1985). During the full-glacial interval, the region was occupied by closed boreal forest dominated by spruce with jack pine as a sub-dominant. After 17,000 years B.P., a period of open boreal woodlands characterized by both tree populations, but with an increase in herbaceous plants, persisted until the Holocene transition.

This transition may mark a shift to a more moderate, warm, wet environment. The open boreal woodland was replaced by an open deciduous woodland dominated by Quercus and Ostrya/Carpinus.

The mid-Holocene interval (7500 to 3500 years B.P.) was a warmer, drier period with low soil moisture. The pollen record indicates an upland mosaic of vegetation with open woodland and prairie patches. The upland deciduous forest was characterized by tree populations of oak, hickory, and chestnut. On mesic slopes surrounding Jackson Pond, forests contained black ash, willow, sweetgum and blackgum.

During late Holocene time (3500 years B.P. to the present), the climate was warm

Figure 7 Scanning electron micrography of a gemmule of Anheteromeyenia ryderi. Close examination of the figure will reveal the two gemmosclere forms characteristic of the species. The shorter, "flat-head" rotule form is also seen in Figure 6. Magnification 440×.
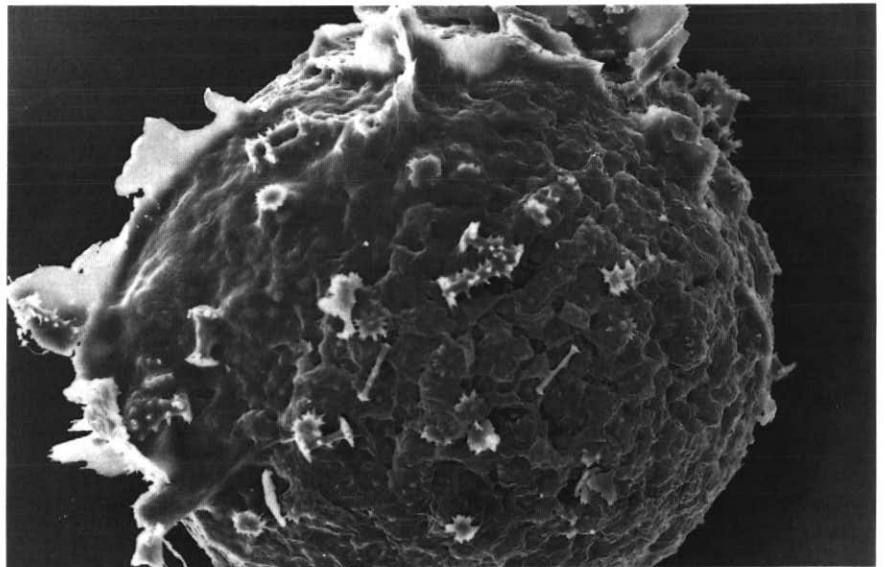
Figure 8 Scanning electron micrograph of a gemmule of Ephydatia fluviatilis. Gemmules of this species exhibit only one class of gemmosclere (Figure 5) as opposed to A. ryderi (Figures 6 and 7). Magnification 180×.

and moist. Willow populations decreased near Jackson Pond. Open grasslands succeeded at the expense of upland woodlands; grasses increased to comprise up to 20% of the upland pollen assemblage. Fossil pollen of *Petalostemon* occurred throughout this interval, indicating the areal expansion of prairie (Wilkins, 1985).

Freshwater sponge spicule analysis was performed on the complete sediment profile from 20,000 years B.P. to the present. The analyses were performed at about 1000-year intervals. During the full-glacial and late-glacial intervals (20,000 to 11,500 years B.P.), the dominant freshwater sponge species in Jackson Pond was *Heteromeyenia latitenta*. Populations of this sponge co-existed with cool-temperate populations of aquatic plants such as naiads and pond-weeds (such as *Najas gracillima, N. flexilis*, and *Potamogeton spirillus* found together today in the Great Lakes and New England regions). Populations of this cold-water sponge declined in Jackson Pond in the early Holocene and disappeared during the warm, dry mid-Holocene interval. No *H. latitenta* spicules were found after 6000 years B.P. The known distributional range of extant populations of this sponge is limited to the northeastern United States. This is consistent with the relict boreal populations of spruce, persisting until about 6000 years ago in the cool microclimate around Jackson Pond.

A population of the sponge, *Ephydatia fluviatilis* co-existed with *H. latitenta* and has persisted to the present. This species is favoured by water conditions of high conductivity, $CaCO_3$ hardness, and alkalinity. It can withstand silt-laden, turbid waters. Macrophyte abundance of oospores of marl-forming charophytes confirm conditions of $CaCO_3$ hardness and alkalinity, particularly between 20,000 and 7000 years B.P. Between 8000 and 7000 years B.P., a third sponge species, *Anheteromeyenia ryderi*, colonized Jackson Pond. This coincided in time with the fossil evidence for the establishment of upland populations of warm-temperate trees such as chestnut and the colonization of lower slopes and wetlands at the margin of Jackson Pond by warm-temperate species of sweetgum, willow, black gum, buttonbush, Virginia willow, and alder. By 7000 years B.P., the bottomland species of willow, buttonbush, Virginia willow and alder formed extensive thickets in the shallow water of the peripheral littoral zone. This complex of swamp forest and shrub thicket probably served as a vegetative screen to filter out mineral sediment eroding from the uplands, thus reducing turbidity levels of water in Jackson Pond. In the middle Holocene, the marginal thicket may have provided an organic substrate for the direct colonization by *A. ryderi*, a sponge species inhibited by high turbidity. Between 7500 and 3500 years ago, the climate was warmer and drier, water tables were lower, and siltation

levels probably decreased. Correspondingly, the turbidity-inhibited populations of *A. ryderi* flourished as the turbidity-tolerant populations of *E. fluviatilis* decreased significantly. Around 3500 years B.P., with a return to the warm and moist climate of the late Holocene, the water level rose in the basin, substantially reducing the area occupied by swamp forest, and reducing the effectiveness of swamp/thicket barrier in filtering out mineral sediment carried from the uplands. *Ephydatia fluviatilis* once again became the dominant species in Jackson Pond. At present, two sponge species inhabit the pond as co-dominants with the introduction of the cosmopolitan species, *Spongilla lacustris*, within the past 500 years, the historic period of European settlement.

The Serendipity and Jackson Pond studies and current studies involving analysis of sediments from northern Ontario indicate that fossilized remains of freshwater sponge spicules and gemmules are well-preserved in most Quaternary wetland and aquatic deposits. Because spicule and gemmule morphologies are species-specific, the most commonly utilized criteria of neosystematics are available to the paleoecologist.

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