

Invertebrates of the Upper Chamber, Gatún Locks, Panama Canal, with Emphasis on *Trochospongilla leidii* (Porifera)

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Abstract

Observations were made on the horizontal distribution of certain invertebrates on the walls and floor of the upper chamber of the Gatún Lock system of the Panama Canal. The hydroid *Cordylophora caspia* (Pallas) and the gastropod *Neritina usnea* Röding extended the full length of the chamber; the oligochaete *Marionina* sp. was confined to the upper half of the chamber (adjacent to Gatún Lake), and the amphipod *Gitanopsis tortugae*? Shoemaker, the isopod *Munna* sp. and the bivalve *Mytilopsis sallei* (Recluz) to the lower half; the sponge *Trochospongilla leidii* (Bowerbank) was distributed from the upper end to near the lower end of the chamber. A peculiar wedge-shaped distribution of *T. leidii* is thought to be a response to the influence of slight increases in salinity. Morphological observations on *T. leidii* are presented.

Introduction

During the past 60 years since the opening of the Panama Canal there has been but one published survey of the fauna and flora of the lock chambers. Hildebrand (1939), although concerned mainly with the fish fauna and the role of the canal in the transisthmian migration of this fauna, observed the distribution of certain invertebrate animals in the various chambers of the lock systems of the canal. Hildebrand's observations were carried out during periods of "dewatering" of the lock chambers for routine maintenance and modification of the chambers.

In March 1974 one of us (M.L.J.) was afforded a similar opportunity to collect biological specimens during the dewatering of all three of the east chambers of the Gatún Locks. For the most part, these collections are still being processed, but observations on the distribution of the sponge *Trochospongilla leidii* (Bowerbank) have proven to be of more than passing interest and have prompted the present paper.

Trochospongilla leidii was described by Bowerbank (1863) as *Spongilla leidii* from the Schuylkill River (Pennsylvania, USA). The synonymy and a redescription, based on the type and on additional material from the type locality, were given by Penney and Racek (1968).

Numerous fragments scraped from four sites of the highest Gatún Lock chamber are deposited in the National Museum of Natural History, Smithsonian Institution, under Catalog No. USNM 24373.

Materials and Methods

As mentioned elsewhere (Jones and Dawson, 1973), chambers in the Panama Canal lock system are about 1000 ft (304.8 m) long, 110 ft (33.5 m) wide, and can accommodate vessels drawing 40 ft (12.4 m), in seawater. The three chambers of the Gatún Locks provide a descent of about 85 ft (25.9 m) from Gatún Lake, directly to the Caribbean Atlantic through Limón Bay. Lockage water for each of the three 28-foot (8.6 m) lowerings of the three chambers comes from Gatún Lake, either directly or from the next higher chamber.

The previous dewatering of the east chambers of the Gatún Locks was carried out in January, 1968; at this time the chambers were dry for about 10 days, and, as is usual, neither the walls nor the floors of the chambers were scraped. Thus, the epifauna of the chambers was recruited some time in the previous 6 years.

An attempt to accompany biological collections with salinity and temperature observations in all of the chambers

of the Gatún Locks, was abortive due to the loss of the sensor cell. However, before this loss, salinity and temperature records were made at 2-m intervals at the two ends of the upper chamber and at two stations outside the lock system in Gatún Lake; these 4 stations represent re-occupations of the sites of Jones and Dawson (1973) shown in their Figs. 2A-D and 4A-D. Surface and bottom salinities in April, 1972 were both 0.1‰ at the upper end of the upper chamber and 0.1 and 0.3‰, respectively, at the lower end; November, 1972 observations were 0.2‰ at both surface and bottom at the upper end, and 0.3‰ at the surface and 0.4‰ at the bottom at the lower end. As before, the present observations were made with a Beckman Model RS5-3 portable salinometer, which also records temperature; all readings were rounded to the nearest

tenth and factory specifications of accuracy were $\pm 0.3\%$ and $\pm 0.5^\circ\text{C}$.

The original intent was to take a series of quantitative samples from both the chamber walls and floors, but the rough texture of these surfaces made this impossible. Thus, qualitative samples of the biota were taken from the walls at a level of about 6 ft (2 m) above the floors and from the floors, at each of 5 sites along the length of each of the three chambers, as well as on the Limón Bay-side of the lower gates of the lowest chamber. In the upper chamber the 5 collection sites, A-E, were at 13, 34, 56, 76, and 93% of the chamber length from the Gatún Lake end of the chamber (Fig. 1).

Methods used for light and scanning electron microscopy of *Trochospongilla*

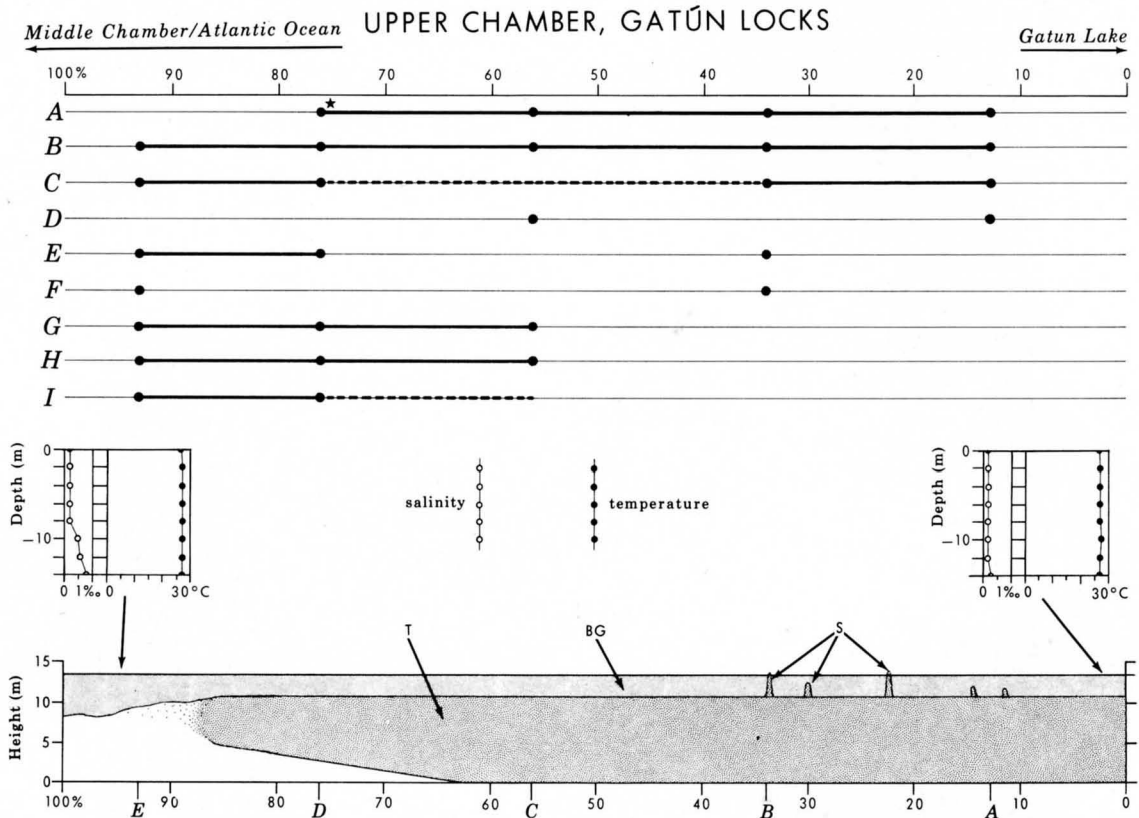


Fig. 1. Distributional patterns of certain invertebrates in east upper chamber, Gatún Locks, Panama Canal. At bottom is a diagram showing distribution of *Trochospongilla leidii* (T) and a presumed blue-green alga (BG) on eastern chamber wall. Also shown are locations of the 5 collection sites (A-E). At top are horizontal distributions of 9 invertebrates along length of the chamber (A: *T. leidii*; B: *Cordylophora caspia*; C: *Neritina usnea*; D: *Marionina* sp.; E: *Paraoroides*? sp.; F: *Tanais stanfordi*; G: *Gitanopsis tortugae*?; H: *Munna* sp.; I: *Mytilopsis sallei*; dashed lines show distribution confirmed by J. Rosewater). Two sets of salinity/temperature profiles are included, based upon observations made just prior to draining of the water from upper chamber; arrows indicate location of these observations. Percentages of chamber length (top and bottom) are based upon usable length of the chamber; these progress from Gatún Lake end (right) to middle chamber end (left). Star: *Trochospongilla leidii* was present in wall samples but not in floor samples at Collecting Site D; S: fresh-water seeps

leidii are those described by Rützler (1974).

Observations

Only two species of invertebrate animals were abundant in the highest chamber of the Gatún Locks. The hydroid *Cordylophora caspia* (Pallas) was found throughout the length of the chamber, both on the chamber walls and on the floor. *Trochospongilla leidii* (Bowerbank) on the other hand, nearly covered the walls and floor of the upper (Gatún Lake) end (Fig. 3d), and extended vertically to near the low operational water level, i.e., the water level of the upper chamber which allows ship-movement between the upper and the middle chambers, about 40 ft (12.2 m) above the chamber floor (Fig. 2: LOWL). The area between the upper distributional boundary of the sponge and the low operational water level (about 2.4 m) was occupied by a dark band, presumably a blue-green alga (Fig. 1 and 2, BG). The density of *T. leidii* on the chamber walls continued unchanged for about 63% of the chamber length, where the lower distributional boundary departed from the chamber floor (Fig. 3c). At approximately

73% of the chamber length, it was some 7 ft (2.1 m) above the floor (Fig. 3b), and by 85% of the length, it was about 14 ft (4.3 m) above the floor (Fig. 3a). The rather complete covering of the wall by colonies of *T. leidii* commenced breaking up at about 82% of the chamber length, and, at 87%, gave way to isolated patches about 25 ft (7.6 m) above the floor. The patches then became even less numerous until, at the lower gate of the upper chamber, only a very few, small, isolated colonies were observed (Figs. 1 and 2). *T. leidii* was not present in the middle or lower chambers of the Gatún Lock system, while *C. caspia* was present throughout the length of the middle chamber, but was absent from the lower chamber.

Maximum area coverage by individual colonies of *Trochospongilla leidii* is difficult to establish, but might have approached 300 to 400 cm². The total population covered an area of more than 2400 m² rather densely on the west chamber wall (Fig. 2, T). Thickness of the incrustations varied from 0.5 to 2.0 mm.

A number of other invertebrates were also noted in the upper chamber (Fig. 1). *Neritina usnea* Röding, a gastropod, was present throughout the length of the chamber (J. Rosewater, personal com-

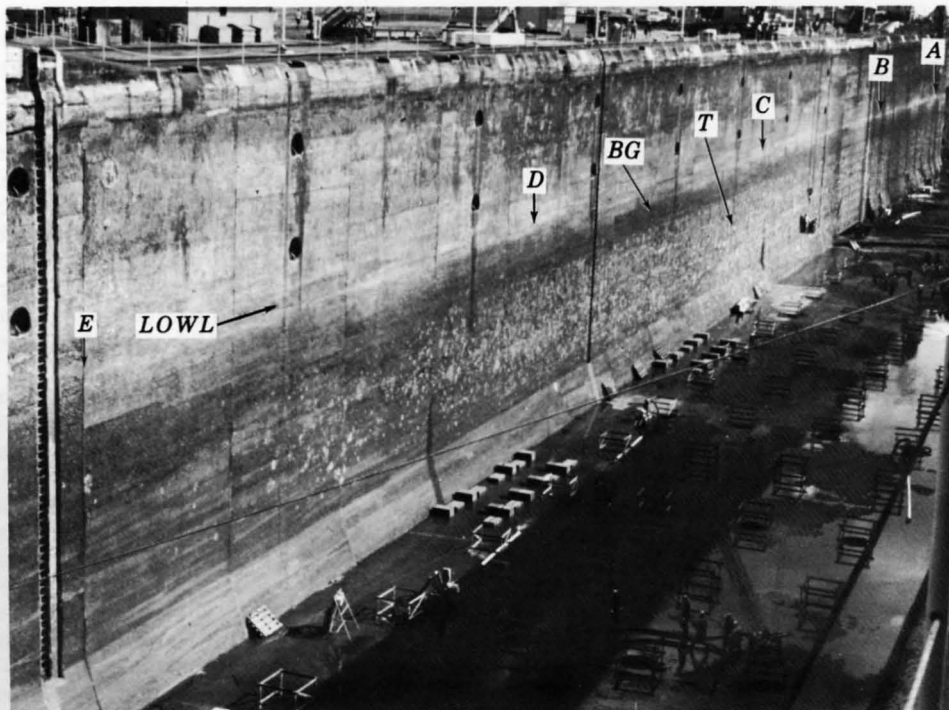


Fig. 2. View of eastern wall of east upper chamber, Gatún Locks. from lower end, toward Gatún Lake end. Letters A-E indicate locations of collecting sites; LOWL: low operational water level; BG: band of presumed blue-green alga; T: dried, white colonies of *Trochospongilla leidii*. Rungs of ladder at left are 0.3 m apart

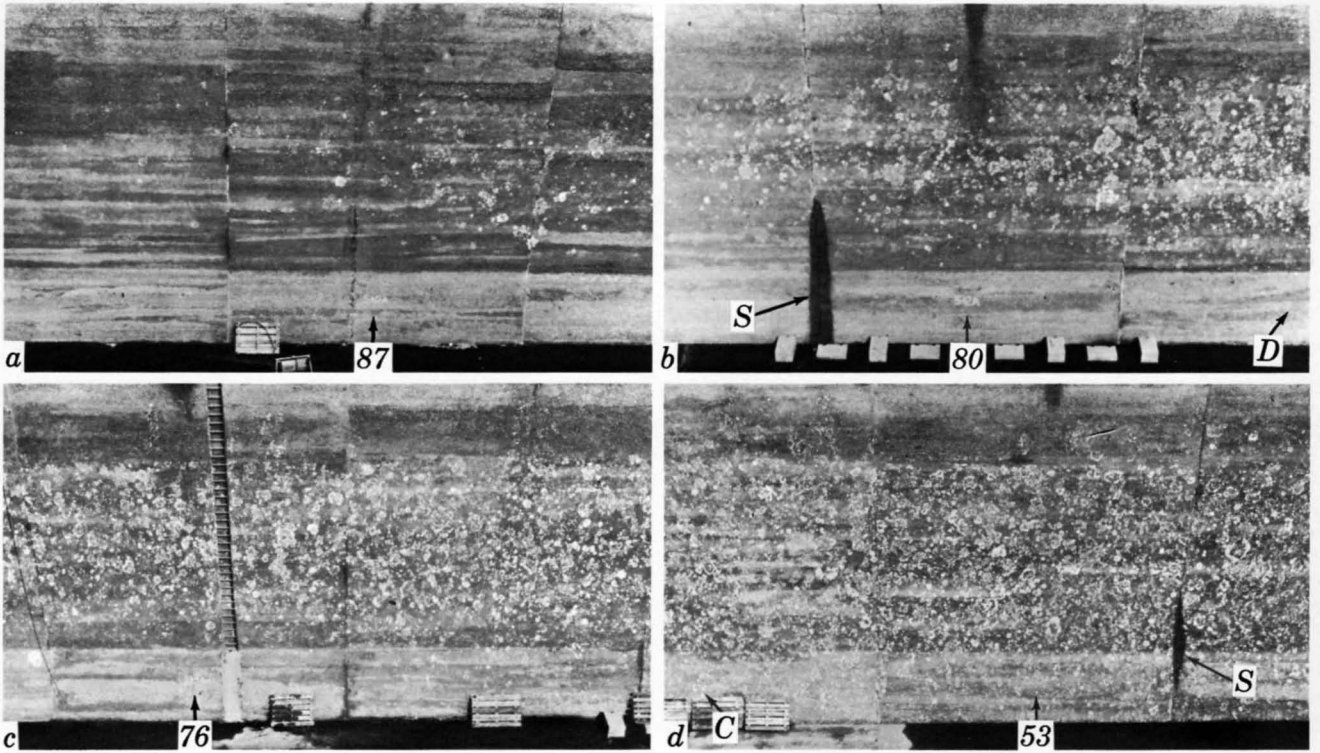


Fig. 3. Direct views of eastern wall of east upper chamber, Gatún Locks, showing changes of density and distribution of dried, white colonies of *Trochospongilla leidii* (a) at about 87% of chamber length from lake end; (b) at about 80%; (c) at about 76%; (d) at about 53%. Low operational water level is at upper margin of all 4 photographs; C and D: Collection Sites C and D (see Fig. 2). Photographs taken from top of western wall. Rungs of ladder in Fig. (c) are 0.3 m apart, and this scale applies to (a) - (d). S: Fresh-water seeps

munication) although it was present in only 4 of our collections. *Marionina* sp., an enchytraeid oligochaete, was confined to the upper half of the chamber, while *Gitanopsis tortugae*? Shoemaker, an amphilo-chid amphipod, and *Munna* sp., an asellote isopod, were confined to the lower half. A distribution similar to those of the latter 2 species was also exhibited by *Mytilopsis sallei* (Recluz), a bivalve, according to Rosewater (personal communication), although it was present only in the lowest two of our collections. Finally, so few specimens of *Tanais stanfordi* Richardson, a tanaid, and *Paraoroides*? sp., an aorid amphipod, were obtained that little can be said of their distribution in the chamber. No living large crustaceans were collected, although the carapace of a decapod (*Callinectes* sp.) was observed; in addition, some dead shells of the bivalve *Brachidontes exustus* Linné were also seen.

Observed temperatures (Fig. 1) varied from 26.9°C at the surface to 27.0°C at the bottom at the upper end of the chamber, and from 26.7°C at the surface to 27.0°C at the bottom at the lower end. Salinities varied from 0.02‰ at the sur-

face to 0.3‰ at the bottom at the upper end of the chamber, and from 0.2‰ at the surface to 0.8‰ at the bottom at the lower end. These readings were taken when the water in the chamber was at the low operational level. The observations in Gatún Lake, just outside the upper chamber, indicated homogeneous salinities in the water columns (0.2‰ from surface to bottom) and rather uniform temperatures (from 27.2°C at the surface to 27.0°C at the bottom).

It was mentioned above that in the upper part of the upper chamber *Trochospongilla leidii* extended from the chamber floor to near the low operational water level. A number of exceptions to this general upper boundary were noted coinciding with fresh-water seeps in the upper wall face from the culverts which carry water from Gatún Lake along the sides of the three lock chambers (Fig. 1, S).

In August, 1974, several cursory attempts were made to determine the extent of intrusion of *Trochospongilla leidii* into Gatún Lake. Scrapings from the walls of the approach to the Gatún Locks failed to yield *T. leidii*, due, no doubt, to an

inadequate sampler. Shore collecting from submerged rocks and pieces of wood near Gamboa (approximately 35 km from the Gatún Locks or about 73% of the channel length of Gatún Lake toward the Pedro Miguel Locks, near the Pacific end of the canal) failed to show the presence of the sponge, but did provide numerous specimens of *Tanais stanfordi*, a single colony of *Cordylophora caspia*, and a colony of the fresh-water bryozoan, *Plumatella emarginata* Allman. Finally, scrapings from the walls of the approach to the Pedro Miguel Locks also failed to yield *Trochospongilla leidii*.

In February, 1975, the east chamber of the Pedro Miguel Locks was drained for routine maintenance. At this time a series of 5 pairs of samples were made (by M.L.J.) along the length of the chamber, similar to those made in the Gatún Locks. *Trochospongilla leidii* was present in the same abundance as in the upper part of the upper chamber of the Gatún Locks; however, in contrast to the observations recorded above, there was no vertical diminution of the sponge anywhere along the whole length of the Pedro Miguel chamber. Further, the wall area between a caisson which acted as a temporary dam between Mirflores Lake, at the seaward end of the Pedro Miguel Lock chamber, and the gates at the lower end of the chamber, was likewise covered with *T. leidii*. This, then, extends the distribution of the sponge into Miraflores Lake, with no indication of a wedge-shaped termination of distribution similar to that observed within and at the lower end of the upper chamber of the Gatún Locks.

Trochospongilla leidii

The color of the fresh sponge (observed after several hours exposure to air) was grayish to drab, and has not changed in alcohol. The type material was described as yellow, with a tint of green (Bowerbank, 1863). It should be noted, however, that the cellular material of our specimens is reduced, most likely due to being exposed to air after dewatering of the lock chamber. For this reason no data on ectosomal structures can be given. The consistency of the sponge is firm but brittle.

The skeleton consists of plurispicular strands of oxea oriented perpendicularly to the surface; these are interconnected by single or fasciculated spicules to form a firm three-dimensional network. The ends of the spicules are held together by small amounts of spongin. There are no somal microscleres.

The gemmules (Fig. 4) are confined to a single layer at the base of the sponge.

They are encased in a capsule of densely packed oxea and connected to a solid sheet of oxea. These capsular oxea are slightly more stout and blunt than those of the main skeleton, but are otherwise identical. They also are cemented by spongin. The foramina (Fig. 4a, b), are directed toward the sponge surface and are elevated on a conical mound about 30 to 40 μm high. The diameter of the gemmules ranges from 380 to 520 μm . Their walls (Fig. 4c, d) are about 16 μm thick, and consist of an inner solid, striated layer of spongin (6 μm) and an outer pneumatic layer (10 μm). The perpendicularly oriented gemmoscleres are embedded with their lower halves in the pneumatic layer. The upper portions of the birotules are freely protruding. The disks of the birotules usually overlap those of the adjacent spicules, thus greatly improving mechanical resistance. There is only a single layer of gemmoscleres. In sponge fragments with a lesser degree of tissue degradation many developing stages of gemmulae were found.

The spicules of the main skeleton are moderately curved, stout, more or less fusiform oxea (Figs. 5a, 6a), with rather abruptly tapered points. Their surface appears smooth under the light microscope (Fig. 5a); however, the scanning electron microscope (SEM) reveals that the oxea are densely covered by minute spines, about 0.1 μm tall (Fig. 6a). The oxea of the gemmular capsule (Figs. 5b, 6b, c) are very similar, but tend to be shorter, stouter and blunter. They also tend to malformations, i.e., two or more sharp bends, T-shapes, central annular swellings and mammiform tips; they are provided with a slightly coarser spination (0.2 to 0.3 μm) than those of the main skeleton. The gemmoscleres (Figs. 5c, d, 6d) are birotules with a short, thick, smooth shaft which generally protrudes beyond the outer surfaces of the rotules and forms low mounds or spikes. Both rotules have entire margins which are exflected in the same direction, i.e., away from the surface of the gemmula. The lower rotule, embedded in the pneumatic layer is slightly (about 4%) larger than the upper rotule.

The following sizes of spicules were computed from 25 random measurements of each dimension. Ranges are given with means \pm 1 standard deviation in parentheses. Oxea of the main skeleton (length \times width): 125.0 to 175.0 (149.6 \pm 10.8) \times 10.0 to 13.8 (12.6 \pm 0.8) μm . Oxea of the gemmular capsule (length \times width): 105.0 to 155.0 (141.9 \pm 14.2) \times 11.3 to 16.3 (13.4 \pm 1.3) μm . Birotules, total length: 11.5 to 13.2 (12.6 \pm 0.6) μm ; width of shaft: 4.2 to 6.9 (5.8 \pm 0.8) μm ;

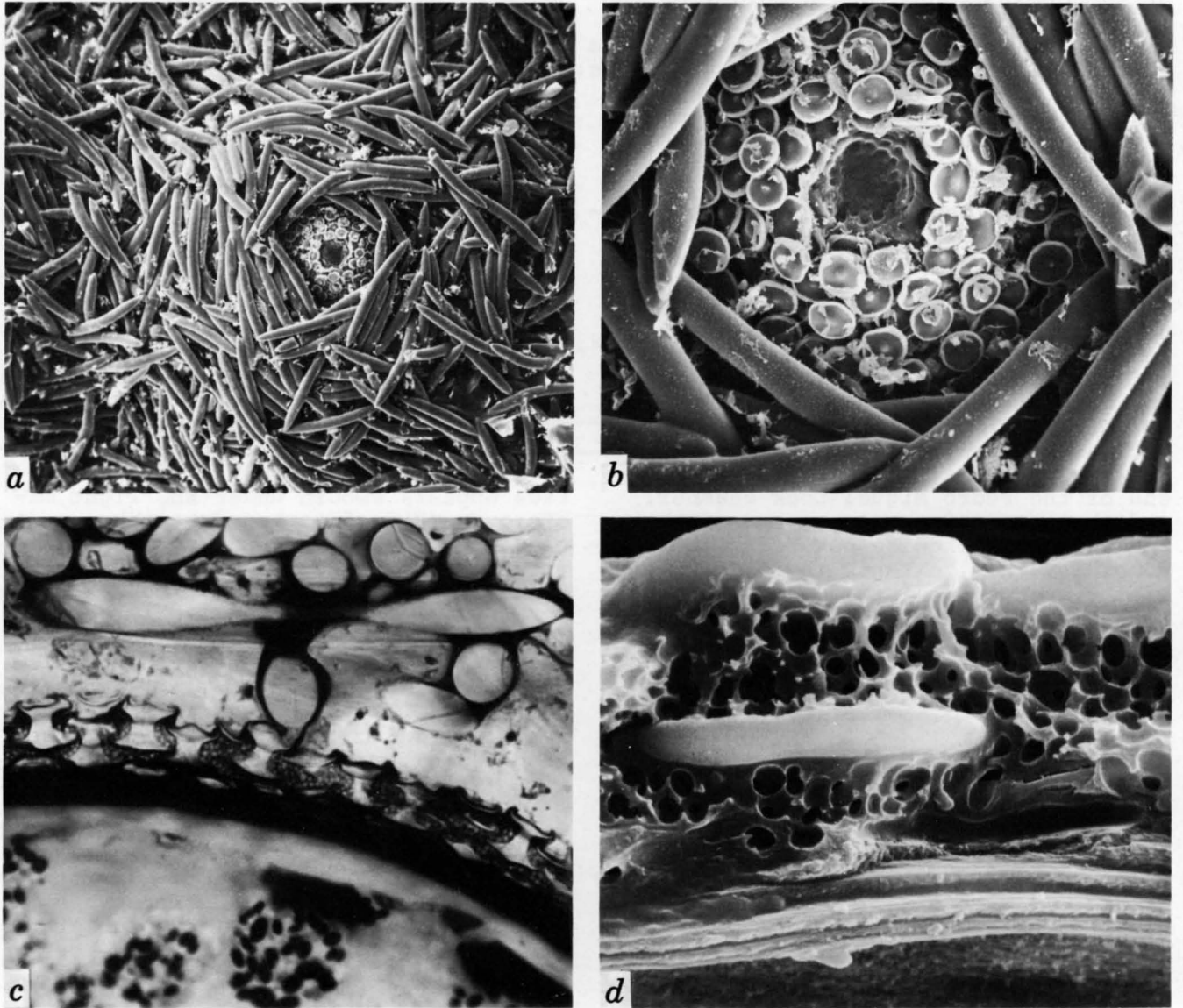


Fig. 4. *Trochospongilla leidii*. Gemmules. (a) Capsule of oxea (scanning electron microscope; 120 x); (b) foramen and arrangement of birotules (SEM; 500 x); (c) light microscope section through gemmular wall showing embedded birotules and oxea of capsule (toluidine-blue stain; 500 x); (d) fractured gemmular wall showing striated spongin and pneumatic layer with embedded birotules (SEM; 3000 x)

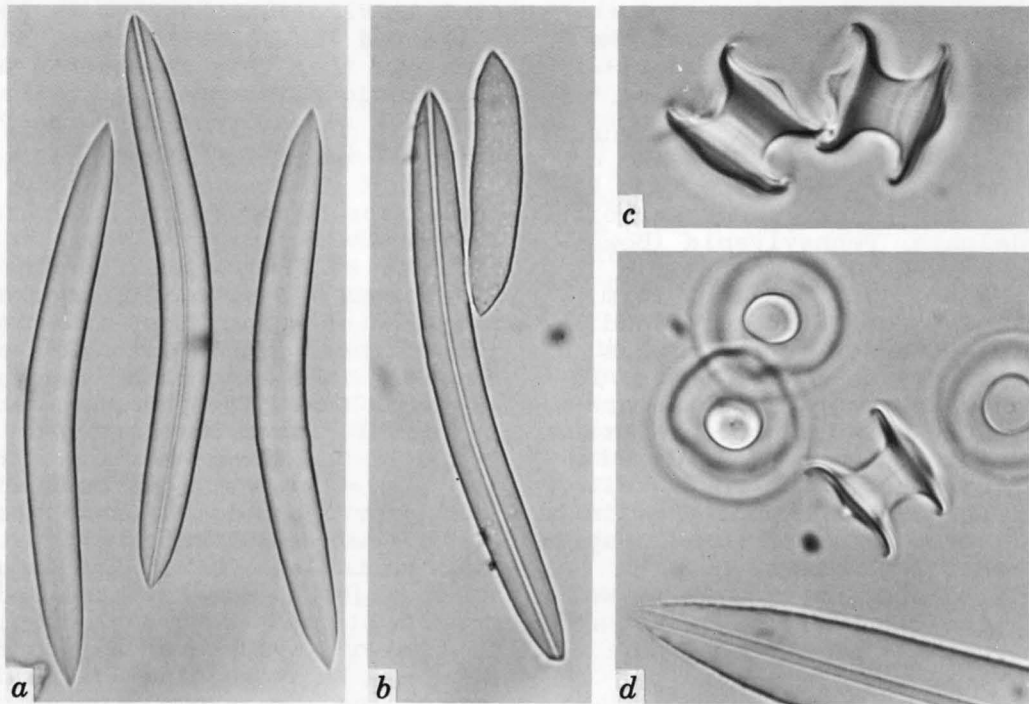


Fig. 5. *Trochospongilla leidii*. Spicules; light microscope. (a) Oxea of main skeleton (600 x); (b) oxea of gemmular capsule (600 x); (c) (d) birotules (1300 x)

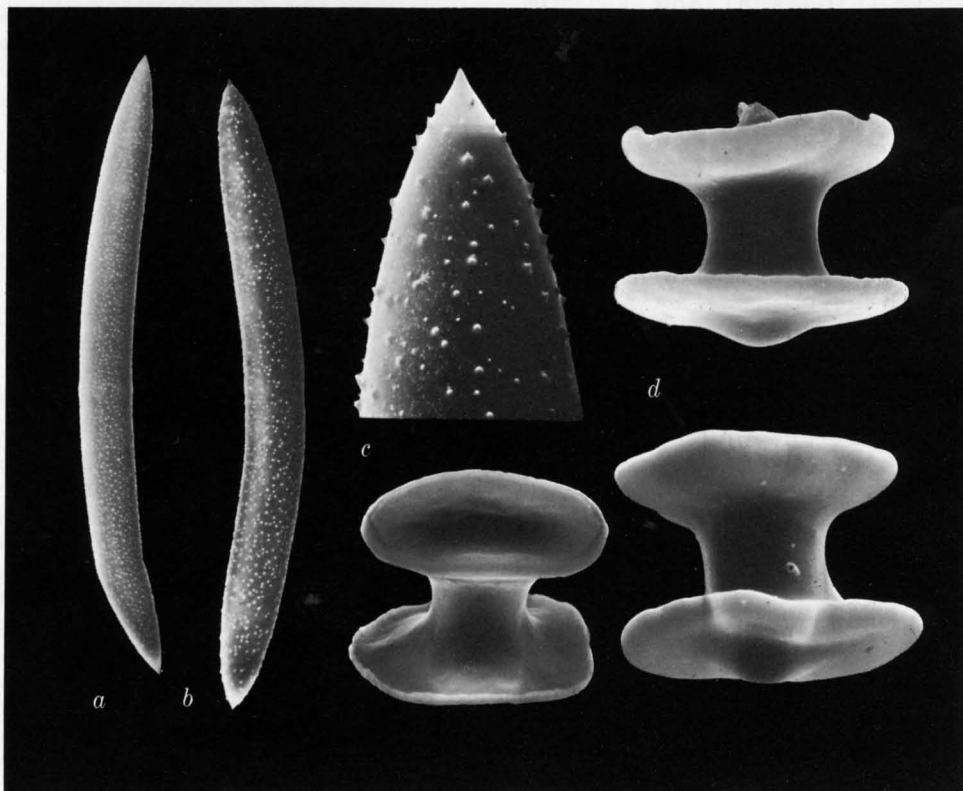


Fig. 6. *Trochospongilla leidii*. Spicules; scanning electron microscope. (a) Oxeon of main skeleton (800 x); (b) oxeon of gemmular capsule (800 x); (c) oxeon of gemmular capsule, tip and spination (3300 x); (d) birotules (3300 x)

diameter of the lower rotule: 13.0 to 16.6 (15.4 \pm 1.0) μ m; diameter of the upper rotule: 12.0 to 16.2 (14.8 \pm 1.2) μ m.

All previous detailed descriptions of *Trochospongilla leidii* have been based on material from or very near the type locality, Schuylkill River and reservoirs near Philadelphia, Pennsylvania (Bowerbank, 1863; Potts, 1887; Gee, 1931; Penney and Racek, 1968). Growth form, consistency, internal structure, and spicular dimensions of our specimens agree surprisingly well with these, in spite of the wide geographical separation. The minute spination of the oxea in our material cannot be considered a significant difference and could well have been present, but beyond the limits of light microscope resolution, in specimens from other localities. A very closely related species, *T. horrida* Weltner, is distinct in having a very constant, heavy spination of the oxea.

Although *Trochospongilla leidii* is a fairly abundant species in eastern North America, very little is known about its biology or ecology. Potts (1887) observed that it thinly coated timbers, pipes, and the stone work of dam, reservoir, and lock structures, covering "yards of surface". It was commonly associated with *Spongilla lacustris* (Linnaeus) and *Eunapius* [= *Spongilla*] *fragilis* (Leidy) but, in contrast to these and most other fresh-water sponges, it grew to a depth of 3 m or more, and was found even in the complete darkness inside long iron pipes. Potts also noted that *T. leidii*, more than any other species, had been found in association with iron structures. Specimens from heavily rusted pipes showed pronounced erosion of the spicules. Potts (1887) finally observed that this sponge, although commonly encountered as a thin incrustation, can develop thick sheets (of about 2 cm) after "many years undisturbed growth". In this case, however, a series of thin laminae, each formed on top of the other, can be distinguished in cross-section, each representing a successive season.

The geographical distribution of *Trochospongilla leidii* to date has been restricted to the eastern United States. Apart from the type locality in Pennsylvania, the species has been reported from New Jersey, Ohio, Illinois, West Virginia, Kentucky, Arkansas, Florida, Louisiana and Texas (Penney, 1960).

It is not known how *Trochospongilla leidii* came to be in the freshwaters adjacent to Gatún Lake. It is possible that the species is distributed throughout Cen-

tral America, but has not as yet been collected and reported upon. It is also possible that this represents a localized, unique introduction by ballast water of ships transiting the Panama Canal or by local aquarists.

Discussion

Hildebrand (1939, p. 22) recorded the presence of a number of invertebrates in the chambers of the Gatún Locks, but is explicit in noting that "...the collections of these lower forms must be considered far from complete" (p. 21). He observed that *Cordylophora lacustris* Allman [= *C. caspia* (Pallas)] was most abundant in the upper chamber, as was a gastropod, *Neritina meleagris* Lamarck [= *N. usnea* Röding]; two crustaceans, *Callinectes sapidus acutidens* Rathbun [= *C. sapidus* Rathbun] and *Macrobrachium olfersii* (Wiegmann) completed the listing of invertebrates from the upper chamber. In spite of Hildebrand's comment concerning the incompleteness of his invertebrate collections, the present distribution of *Trochospongilla leidii* is such that there seems little doubt that it was not present in the chambers of the Gatún Locks some 40 years ago. In fact, Potts' (1887) observations on multilaminar growth of this species, if undisturbed for several successive seasons, would suggest that the presumed population explosion has taken place quite recently. A similar event has been reported by Bretschko¹ from Volta Lake, Ghana. Investigation of the lake in April, 1971 had not revealed sponges of any kind. In April, 1972 mass development of *Corvospongilla boehmii* (Hilgendorf) had been observed in the study area. The sponge, obviously introduced during 1971-1972, encrusted wide areas of submerged trees in the south of the lake (particularly dense in Amankwatonu). Its occurrence was correlated with high phytoplankton production in the area.

It would seem also that yet another invertebrate has undergone a latter-day introduction into the Gatún Locks. In his observations on the fauna of the Miraflores Locks, at the Pacific end of the canal, Hildebrand makes a special point of noting the presence of *Congerina* (*Mytilopsis*) *sallei* Recluz [= *Mytilopsis sallei* (Recluz)], but does not mention its presence in the Gatún Locks. During our

¹G. Bretschko: unpublished Progress Report 1972, Volta Lake Research Project, Akosombo, Ghana.

collections we found *M. sallei* to be abundant in the middle chamber and present in the upper chamber.

Several explanations might be offered to explain the curious distribution of *Trochospongilla leidii* at the lower end of the upper chamber of the Gatún Locks. Since diminution occurs in an area adjacent to the gates between two consecutive chambers, it might well be that the turbulence attendant upon the opening and closing of the gates might be implicated. However, the wedge-shaped distributional pattern is not found near the gates at the upper end of the chamber where it connects with Gatún Lake; further, such a distribution is not found at either end of the chamber of the Pedro Miguel Locks, the Pacific counterpart of the upper chamber of the Gatún Locks.

It is difficult to conceive the pattern being a function of light, turbidity, or temperature, for the distribution of *Trochospongilla leidii* on the floors and walls of the upper part of the chamber shows no such restriction.

Jones and Dawson (1973, p. 90) have noted that, although there is a general vertical homogeneity of salinity and temperature readings in the chambers of all the locks, there may not be a horizontal homogeneity within a given chamber. While their examples of horizontal heterogeneity were more striking, such might also be the case in the upper chamber of the Gatún Locks (Fig. 1). Although the differences in bottom salinities between the upper and lower ends of the upper chamber are not great enough to fall outside the limits of accuracy of our equipment (0.3 and $0.8 \pm 0.3\%$ S), the suggestion that there is a real salinity difference at the ends of the chamber is strengthened by the distribution of several of the invertebrates encountered here. *T. leidii* and, perhaps, *Marionina* sp., are excluded from the lower portion of the chamber; *Mytilopsis sallei*, *Gitanopsis tortugae?* and *Munna* sp., on the other hand, are restricted to the lower portion of the chamber. The most obvious conclusion to be drawn would involve a chemical difference between the lower and upper ends of the chamber, most probably the subtle and apparently minor salinity differences. Indeed, the distributional pattern of *T. leidii* at the lower end of the upper chamber strongly suggests the intrusion of some kind of chemical "wedge". It is difficult to accept this in light of the comments of Jones and Dawson (1973, p. 89) concerning vertical homogeneity and the turbulence attendant upon the filling and draining

of lock chambers and the passing of ships, but perhaps it is related, in some way, to the density currents set up by the opening of the gates between successive chambers just before ships move from one to the next (p. 90). Since all filling and draining of the lock chambers is by gravity-flow from Gatún Lake or a higher chamber, these density currents are the only mechanism for moving more saline water from a lower chamber to a higher one.

It is also of more than passing interest that, while for the most part the upper distributional boundary of *Trochospongilla leidii* is the low operational water level, upward extensions of the sponge occur coincidentally with freshwater seeps. These apparently allow *T. leidii* to survive the inevitable drying of the upper chamber wall during the passage of each ship.

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