Freshwater sponges (Porifera, Demospongiae) in a benthic filter feeding community at the Guanacaste Dry Forest, Costa Rica

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ABSTRACT. The freshwater sponges *Trochospongilla variabilis* Bonetto & Ezcurra de Drago (1973), *Radiospongilla crateriformis* (Potts, 1882), *Spongilla cenota* Penney & Racek (1968) and *Corvoheteromeyenia heterosclera* (Ezcurra de Drago, 1974) compose with the sphaerid bivalve *Eupera cubensis* (Prime, 1865) and several Phylactolaemata bryozoans a benthic filter feeding community living in seasonal lentic and lotic habitats with high Particulate Organic Carbon (POC), low conductivity and acid pH within the Costa Rica Dry Forest biome. The sponge specimens gathered led to the re-description of the four species.

KEYWORDS. Freshwater Sponges, Bryozoans, Bivalves, Central America, Dry Forest.


PALAVRAS-CHAVE. Esponjas continentais, Briozoários, Bivalves, América Central, Floresta Seca.

The first record of the occurrence of freshwater sponges in Central America and the Antilles was made by MEEK (1908), who assigned *Eunapius fragilis* (Leidy, 1851) to Guatemala. JONES & RUTZLER (1975) reported the occurrence of *Eunapius carteri* (Bowerbank, 1863), *Trochospongilla leidii* (Bowerbank, 1863) and *Trochospongilla horrida* (Weltner, 1893), to Panamá. POURRIER (1977) referred to a personal communication by Vincent Resh concerning the occurrence of *Anheteromeyenia ryderi* (Potts, 1882) in Belize. POURRIER & TRABANINO (1989), in turn, registered *Ephydatia fluviatilis* (Linnaeus, 1759) and *Spongilla alba* (Carter, 1849) in El Salvador; and SMITH (1994), in a survey of sponges in the Virgin Islands, detected only *E. fluviatilis*. The latter species was also registered by MURILLO & MORA (1995) in Costa Rica, BASS & VOLKMER-RIBEIRO (1998) assigned and illustrated *Radiospongilla crateriformis* (Potts, 1882) in the islands of Barbados and Nevis. More recently, DEBROT & VAN-TOEVEST (2001) registered *Corvoheteromeyenia heterosclera* (Ezcurra de Drago, 1974) and *S. alba* in the islands of the southern Caribbean, and MANCONI & PRONZATO (2005) described *Anheteromeyenia cheguevarai* in western Cuba and indicated the occurrence of *Ephydatia facunda* Weltner (1895), *R. crateriformis* and *Radiospongilla* sp. on the island.

ROUSH (1999) in announcing the survey of freshwater Bryozoans which he carried out in the Guanacaste Conservation Area, in Costa Rica, remarked the restriction of their occurrences to the Deciduous Forest Area and the occurrence of freshwater sponges in the same habitats. He, preliminarily, identified the sponge genera *Radiospongilla* Penney & Racek, 1968, *Dosilla* Gray, 1867, *Corvomeyenia* Weltner, 1913, *Trochospongilla* Vejdovsky, 1883 and the species *Spongilla cenota* Penney & Racek (1968). ROUSH (2000) published the results of the survey of Bryozoans and sent the sponge material to the senior author for study. The results of that study are now offered and contain the redescriptions, with the first Scanning Electron Microscopy (SEM) illustrations of *S. cenota* and the gemmule structure of *C. heterosclera*. The paper presents the first register of species of sponges that compete with Bryozoans and sessile bivalves in a freshwater environment. The characteristics are reported of the habitats occupied by this community of benthic, sessile and filter-feeding macro-invertebrates in the area. The common functional adaptations presented by the members of this community are also remarked.

MATERIAL AND METHODS

The Guanacaste Conservation Area was established in order to protect the Dry and Deciduous Tropical Forest of Costa Rica. The streams originating in this biome are of low order, shallow and slight inclination, and dry during five or six months of the year. The description and map of the collecting sites, organized for the samples of bryozoans in the area, carried out between 1996 and 1997 are found in ROUSH (2000), together with features of the habitats (temperature, pH, conductivity, current and Particulate Organic Carbon (POC)). The geographical coordinates of the collection sites were furnished by S. A. Roush, in a pers. comm. to the senior author. The species of sponges gathered by S. A. Roush and the object of the present study, were entrusted to the senior author and are thus deposited and catalogued in the Porifera collection of the Museu de Ciências
Radiostrongilla crateriformis (Potts, 1882)
(Figs. 1-3, 8-13)

Meyenia crateriformis Potts (1882):12; Potts (1887):228, pl. V. Fig. VI, pl. X, fig. V.

Material Examined. COSTA RICA, Guanacaste. Guanacaste Conservation Area: Maritza Sector, temporary stream, 19.VIII.1996, S. A. Roush leg. (MCN-POR 6995); Temporary Pond (10º57'06,18''N 85º37'01,64''W), 27.VIII.1996, S. A. Roush leg. (MCN-POR 6998); Fig. 3) environments at the Guanacaste Dry Forest. The fragile specimens conform to the description offered by Rioja (1953) for the ones, obtained from km 286 of the road Mexico-Tuxpan. Also, his drawings of the gemmule structure of R. crateriformis have now been confirmed in every detail with SEM illustration. This is the third record of R. crateriformis for the Caribbean Region, following that of Bass & Volkmer-Ribeiro (1998) for Barbados and that of Manconi & Pronzato (2005) for Cuba. The occurrence of R. crateriformis in Caribbean organically enriched seasonal habitats may now be established as common place (Bass & Volkmer-Ribeiro, 1998; Manconi & Pronzato, 2005) and one not too far away from the the Brazilian savanna (cerrado) seasonal ponds where R. amazonensis Volkmer-Ribeiro & Maciel (1983) is also commonly found Volkmer-Ribeiro et al. (1998).

The sponge MCN-POR 6994, from River Cuajinquil was found associated to several specimens of the sessile sphaerid bivalve E. cubensis (Fig. 35, Tab. I), whilst the sponges MCN-POR 6995 and 6996, from temporary pond, Santa Rosa Sector, were found associated to the bryozoans Plumatella sp.1 and Plumatella sp.3 (Tab. I).

Trophospongilla variabilis Bonetto & Ezcurre de Drago, 1973
(Figs. 4, 14-19)


Material examined. COSTA RICA, Guanacaste: Carretara Cuajinquil (Guanacaste Conservation Area, temporary marsh, 10º57'-06,18''N 85º37'-01,64''W), 27.VIII.1996, S. A. Roush leg. (MCN-POR 6987, 6988).

**Results and Discussion**

The identification of the collection of sponges made by S. A. Roush, revealed the occurrence of *Trophospongilla variabilis* Bonetto & Ezcurre de Drago (1973), *R. crateriformis*, *S. cenota* and *C. heterosclera*. The species were found in lentic and lotic environments (1973), *Meyenia crateriformis* Potts (1882):12; Potts (1887):228, pl. V. (Figs. 1-3, 8-13)

**Description.** Sponges forming yellowish, spherical, fragile crusts 2.5 cm wide and 1cm high with large and conspicuous oscules (MCN-POR 6989; Figs. 1, 2), or shallow, grayish, stouter crusts 3 cm wide and 0.2 cm high (MCN-POR 6995; Fig. 3) on the bark of submerged logs. Skeleton reticulated, anisotropic, from the base to the top, with very slender fibers in the spherical specimens. Megascleres slender, straight to slightly curved, abruptly pointed anfioxea with minute straight spines sparsely distributed along the spicule (Fig. 8). Megascleres length: from 239.02 µm to 446.96 µm (average 344.3 µm); width: 7.02 µm to 17.03 µm (average 12.10 µm). Microscleres absent. Gemmoscleres in one series of slender, straight to slightly curved, strongly spined anfistrongyla, the shorter about half the length of the longer ones (Figs. 8, 9), with larger incurved spines grouped around the extremities of the spicule, thus forming small umbonate rotules (Fig. 10). Gemmoscleres length: from 79.97 µm to 123.10 µm (average 97.71 µm); width: 5.10 µm to 8.23 µm (average 6.83 µm). Gemmules extremely abundant (Figs. 1, 2), distributed from the base to the surface, large, pear shaped (Fig. 11), the older ones grayish and the new ones whitish. Foraminal tube long, contained inside the thick plastic coat, gemmoscleres radially embedded in the pneumatic coat up to the collar which surrounds and surpasses the foraminal tube (Figs. 11, 12). Pneumatic coat consisting of a network of irregular and slender spongin fibers, thus producing also irregular air cameras (Fig. 13). Outer gemmular coat thin, gemmular surface crateriform, each crater containing the starlike rotule of a gemmosclere (Fig. 11).

**Remarks.** The species occurred with globose, yellowish, fragile, spongin rich specimens in lentic environment (MCN-POR 6995; Figs. 1, 2); and grayish, harder, spongic rich shallow crusts in lotic (MCN-POR 6998; Fig. 3) environments at the Guanacaste Dry Forest. The fragile specimens conform to the description offered by RIOJA (1953) for the ones, obtained from km 286 of the road Mexico-Tuxpan. Also, his drawings of the gemmule structure of *R. crateriformis* have now been confirmed in every detail with SEM illustration. This is the third record of *R. crateriformis* for the Caribbean Region, following that of Bass & Volkmer-Ribeiro (1998) for Barbados and that of Manconi & Pronzato (2005) for Cuba. The occurrence of *R. crateriformis* in Caribbean organically enriched seasonal habitats may now be established as common place (Bass & Volkmer-Ribeiro, 1998; Manconi & Pronzato, 2005) and one not too far away from the the Brazilian savanna (cerrado) seasonal ponds where *R. amazonensis* Volkmer-Ribeiro & Maciel (1983) is also commonly found Volkmer-Ribeiro et al. (1998).

The sponge MCN-POR 6994, from River Cuajinquil was found associated to several specimens of the sessile sphaerid bivalve *E. cubensis* (Fig. 35, Tab. I), whilst the sponges MCN-POR 6995 and 6996, from temporary pond, Santa Rosa Sector, were found associated to the bryozoans *Plumatella* sp.1 and *Plumatella* sp.3 (Tab. I).

Naturais do Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brazil (MCN-POR). The specimens of the bivalve were identified by Dr. M. C. D. Mansur at Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (PUC), Porto Alegre, and catalogued in the Malacological Collection of the Museu de Ciências Naturais of the Fundação Zoobotânica do Rio Grande do Sul (MCN-MOL). Preparations of dissociated spicules of the sponges were obtained according to Volkmer-Ribeiro (1985) and Volkmer-Ribeiro & Turcq (1996), for studies with, respectively, light optical and Scanning Electron Microscopy (SEM). The SEM photographs were obtained at the Electron Microscopy Laboratory of Universidade Luterana do Brasil (ULBRA), in Canoas, Rio Grande do Sul. Fifty measurements were made of each spicule category, considering all the specimens of each one of the species. Digital photographs of representative specimens of each of the four sponge species as well as of the bivalves were also produced.
Description. Sponges forming small, shallow, extremely fragile crusts on the bark of submerged logs (Fig. 4). Pinacoderm bright whitish covering the inner brownish skeleton. Skeleton with parchment structure, the megascleres tangentially criss-crossed on the substrate, skeleton fibers absent, spongin scarce. Megascleres small, slender, slightly curved, spiny anfoxea, with quite variable sizes and gradually tapering very sharp extremities, spines minute and sparsely distributed, the ones at the extremities curved towards the middle of the sclere (Figs. 14, 15). Megascleres length: from 327.45 µm to 538.35 µm (average 454.91 µm); width: 10.73 µm to 23.31 µm (average 16.48 µm). Microscleres absent. Gemmoscleres birrotulates with both rotules turned outwards, the inner one containing the outer one; inner rotule large flat, with thin, smooth border; outer rotule small, cup shaped, border thick, its outer profile circular and smooth and its inner portion undulated, flower like, microspined and containing the rounded projection of the shaft; shaft smooth, slendering towards its central portion (Figs. 14, 16). Gemmoscleres length: from 13.92 µm to 17.93 µm (average 16.44 µm); width: 2.45 µm to 5.75 µm (average 3.93 µm). Gemmules minute, spherical or concave, sparsely distributed along the skeleton (Figs. 17, 18). Foraminal tube short, provided or not with an irregularly shaped collar of spong. Inner gemmular coat in two thin layers; pneumatic coat consisting of a regular network of spongin fibers producing also regular spherical air cells (Fig. 19). Gemmoscleres radially embedded in the pneumatic coat, the outer rotules and the shaft extremity they contain reaching beyond the thick outer coat (Figs. 17, 18, 19).

Remarks. This is the first time T. variabilis is reported for the Caribbean Area. The species was sampled only from the temporary marsh at the Guanacaste Dry forest, which conforms to its known occurrence in temporary peat bog ponds in the Brazilian savanna and savanna remnants inside the Amazonian Forest (Volkmer-Ribeiro et al., 1998). The studied specimens also conform the characteristics presented by the brazilian materials (Volkmer-Ribeiro, 1992).

The T. variabilis specimens (MCN-POR 6987 and 6988) were found associated to the bryozoans Plumatella sp.5 and Plumatella sp.6 (Tab. I).

### Spongilla cenota Penney & Racek, 1968
(Figs. 5, 6, 20-26)

**Spongilla cenota** Penney & Racek (1968):18, pl. I, figs. 8-10, 16 (and synonymy); Porrer (1976):207, fig. 3; (1982):59; Frost (1991):120, fig. 4.23.


Description. Sponge forming thin, stout, whitish crusts, up to 3 cm in diameter, on rock fragments (Figs. 5, 6). Skeleton reticulated, isodictyal, grayish, capped by a conspicuous, whitish pinacoderm charged with a dense incrustation of microscleres. Oscular appendages abundant and conspicuous. Megascleres are stout, straight to curved, microspined oxeas, with abruptly pointed extremities (Figs. 20, 21). Megascleres length: from 390.12 µm to 677.10 µm (average 552.72 µm); width: 13.49 µm to 31.03 µm (average 20.58 µm). Microscleres extremely abundant, slender, slightly curved, spiny oxeas, all spines capped by a rosette of microscleres (Figs. 20, 22). Microscleres length: from 78.60 µm to 137.63 µm (average 106.80 µm); width: 1.90 µm to 4.70 µm (average 3.08 µm). Gemmules are short, stout, spiny oxeas, about 1/2 to 2/3 the length of the microscleres, straight to slightly curved, covered by large spines curved towards the middle part of the sclere, their extremities split into a few smaller spines (Figs. 20, 23). Gemmules length: from 60.33 µm to 86.20 µm (average 73.76 µm); width: 8.39 µm to 18.62 µm (average 12.23 µm). Gemmules extremely abundant, distributed throughout the skeleton, but in a closer arrangement towards the basal part of the sponge; large, withish, tuberculated due to irregular projections of the thick, pneumatic and outer coat layers; gemmular surface hispid due to the projection of gemmoscleres extremities or incrusted slanting megascleres (Figs. 24, 25). Gemmoscleres sparsely and irregularly embedded in the pneumatic and outer coat layers (Fig. 26). Inner gemmular coat in two

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<td>4- Temporary Pond, Santa Rosa Sector</td>
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<td>6996</td>
<td>4- Temporary Pond, Santa Rosa Sector</td>
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<td>6997</td>
<td>4- Temporary Pond, Santa Rosa Sector</td>
<td><em>R. crateriformis</em></td>
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layers. Pneumatic coat consisting of a quite close regular network of thin spongin fibers producing regular, minute, corklike spherical air cameras. Foramen lacking a foraminal tube and placed in a large irregular depression of the pneumatic coat (Figs. 24, 25).

Remarks. This is the third and most southerly record of *S. cenota* in the Caribbean area. The species was originally registered for the Xtoloc Cenote, Yucatan (Mexico) and next for the Everglades (Florida), in a collection carried out by POIRRÉ (1976), who reports the collecting site, The Tamiami Canal, off U.S. Hwy 41, to be related to limestone rocks. So are the Yucatan Cenotes, thus suggesting a preference of *S. cenota* for clear, alkaline, slow running waters. Again in the Guanacaste Protected Area the sponge was found only in the Cuajiniquil River, however in a quite low pH (ROUSH, 2000). The present studied specimens conform in all details to the original description. POIRRÉ (1976) after a comparative study of materials of *S. alba* (*containing S. wagneri* in its synonymy) as a species apart of *S. cenota*, on account of the gemmular structure, gemmoscleres and habitat characteristics presented by the two species. The hypothesis put forth by PENNEY & RACEK (1968) that the materials from Cenote Xtoloc they described as *S. cenota* (and which OLD, 1936 had previously identified as *Spongilla lacustris*) might represent a distant population of *S. alba* was thus refuted by POIRRÉ (1976).

The specimen MCN-POR 6993, from River Cuajiniquil, was found associated to specimens of the bryozoan *Plumatella* sp.1 (Tab. 1).

*Corvoheteromeyenia heterosclera* (Ezcurra de Drago, 1974)

(Figs. 7, 27-34)


Figures 1-7. 1-3, *Radiospongilla crateriformes* (Potts, 1882): 1, upper surface of yellowish specimen (MCN-POR 6989); 2, lower surface of yellowish specimen (MCN-POR 6989); 3, grayish specimen on the substrate (MCN-POR 6995); 4, *Trochospongilla variabilis* Bonetto & Ezcurra de Drago, 1973 (MCN-POR 6988); 5,6, *Spongilla cenota* Penney & Racek, 1968 (MCN-POR 6990); 5, lower surface of specimen; 6, upper surface of specimen; 7, *Corvoheteromeyenia heterosclera* (Ezcurra de Drago, 1974) (skeleton with gemmules; MCN-POR 6991); Scales: 1cm.


Description. The material MCN-POR 6991 corresponds to numerous gemmules and small fragments of an extremely gemmuliferous open reticulum (Fig. 7), previously encrusted on small pieces of charcoal. Skeleton with rarely discernible primary fibers which project at the sponge surface, secondary fibers ill defined. Megascleres are smooth, slender, straight to slightly curved anfoxeas with gradually sharpened extremities (Fig. 27). Megascleres length: from 279.35 µm to 442.15 µm (average 366.93 µm); width: 10.36 µm to 22.94 µm (average 17.23 µm). Microscleres in two classes: one of small spiny oxieas (Fig. 27) with larger spines at the middle portion, some of these oxieas may present the micro-rotules described for the species; length: from 62.13 µm to 137.60 µm (average 99.27 µm); width: 3.53 µm to 6.86 µm (average 5.10 µm); the other, of tiny, slender anfidiscs with straight, spiny shafts and small umbonate rotules deeply cut in a small and irregular number of minute hooks, curved towards the shaft (Fig. 28); length: from 10.64 µm to 24.92 µm (average 17.13 µm); width: 1.90 µm to 2.73 µm (average 2.12 µm); this second class of microscleres may be absent. Gemmoscleres in one class of birotulates with little variation in lenght, rotules almost flat, smooth, with

Figures 8-13. Radiospongilla crateriformes (Potts, 1882), SEM illustration of spicules and gemmules: 8, megascleere and gemmoscleres; 9, gemmosclere; 10, detail of the gemmosclere extremity; 11, gemmule showing the crateriform gemmular surface and the collar around the foraminal tube; 12, cross section of the gemmule with the long foraminal tube; 13, detail of the pneumatic layer of the gemmule. (meg, megascleeres; gem, gemmoscleres).
borders regularly cut in small teeth, shaft with abundant, large, regular, straight, acute spines (Figs. 27, 29, 30, 31). Gemmoscleres length: from 83.01 µm to 102.41 µm (average 93.73 µm); width: 4.90 µm to 7.55 µm (average 6.23 µm). Gemmules abundant, large, spherical, or concave (Fig. 32), whitish, distributed along the whole skeletal network. Foraminal tube short, with an expanded flower-like collar sustained by slanting gemmoscleres (Figs. 32, 33). Gemmoscleres radially embedded in the thick pneumatic coat, the longer ones projecting beyond the gemmule surface (Fig. 34). Pneumatic coat consisting of a quite dense network of thin spongin fibers producing regular, minute, cork-like spherical air cameras. Outer gemmular coat absent. Inner gemmular coat in two layers (Fig. 34).

Remarks. All the studied materials indicate that the sponge is investing its short seasonal life time in the production of gemmules instead of fully developed specimens. MCN-POR 7784 is a small, initial, brownish crust of the sponge, devoid of gemmules, but with conspicuous slender primary fibers. The specimen shares the substrate with *T. variabilis* (MCN-POR 6987). The preparation of a little part of the material revealed the presence of megascleres, a few young gemmoscleres, identical to those of MCN-POR 6991 and a large amount of the tiny anfidisc microscleres which tipify the species, but the spiny oxeas microscleres are missing. The specimen MCN-POR 7785 consists of a slide with the microscopical preparation of a single gemmule found close to the above quoted specimen of *T. variabilis*. The specimen MCN-POR 6992 which comprises only sparse megascleres and microscleres sticking to rocky substrate was identified by ROUSH (1999) as *Dosilia* sp. The author probably did not know at the time of the existence of genus *Corvoheteromeyenia* Ezcurra de Drago, 1979, reason why he took the small spiny oxeas microscleres with larger spines at the middle portion present in MCN-POR 6992 for microscleres of genus *Dosilia*. The same reason must have underlined his identification of the *Corvoheteromeyenia* materials as *Corvomeyenia*.

Several specimens of the native, small, sessil, Sphaerid bivalve *E. cubensis* (Fig. 35) and specimens of the bryozoans *Plumatella* sp.2 and *F. browni* (Tab. I) were found mingled with the crusts of respectively the specimens *C. heterosclera* (MCN-POR 6991 and 6992), at River Cuajiniquil.

Figures 14-19. *Trochospongilla variabilis* Bonetto & Ezcurra de Drago, 1973, SEM illustration of spicules and gemmules: 14, megasclere and gemmoscleres; 15, detail of the megasclere; 16, gemmosclere seen in profile and upper rotule of gemmosclere; 17, gemmular surface; 18, upper surface of the gemmule with foraminal collar; 19, section of the gemmular wall showing the inner, the pneumatic and the outer gemmular coats. (meg, megascleres; gem, gemmoscleres).
The taxonomic composition of the community of sponges discovered is distinct from those registered to date for Central America and the Caribbean islands (Manconi & Pronzato, 2005) due to the present reporting of *S. cenota* and *T. variabilis*. The present extension of the distribution of *S. cenota* in the Caribbean Region, allied to the confirmation of its specific status grants this species and *A. cheguevari* the condition of the two only endemic continental sponges in the Caribbean Region. In what respects the surveyed sponges there is a strong similarity with the sponge community subjected to drastic seasonality in the northeast of Brazil, as seen in the Lençóis Maranhenses National Park, in Maranhão State (Volkmer-Ribeiro et al., 1999), where sponge assemblies typical of the temporary savannah lakes (in which occur *T. variabilis* and *R. amazonensis*) compete with those typical of the coastal dune region (with *C. heterosclera*).

The detected sponge species point to a relatively diverse fauna, adapted to both lentic and lotic environments, but with the common characteristic of the seasonality imposed by the region of the Pacific Dry Forest in the Guanacaste Conservation Area (GCA). Comparison of the results obtained show that *R. crateriformis* and *C. heterosclera* were able to colonize both lentic and lotic habitats, while *T. variabilis* was restricted to the lentic environment, and *S. cenota* to the lotic environment. For this reason, the former two species are recorded as having the widest distribution within the Guanacaste protection area.

One of the most important findings of the survey carried out by Roush (2000) was the absence of bryozoans in permanent rivers, originating from cloud and rain forest, with clear acidic water and low levels of Particulate Organic Carbon (POC). The bryozoans in the GCA were found...
exclusively in the Dry Forest in small, shallow rivers and lakes subjected to periods of 5 to 6 months of drought. The rivers are characterised by turbidity, acidity, little current and high levels of POC. Obviously, these characteristics fulfil the habitat requirements of the three elements of this community of filter feeders, including the sponges and bivalves surveyed.

The detected association of sponges, bryozoans and bivalves at the River Cuajiniquil collecting site (Tab. 1), suggests the presence of a filter feeding community consisting of three phyla of benthic macroinvertebrates in the Atlantic Dry Forest of Costa Rica. These results are the first record of a community of freshwater filter-feeding, benthic, sessile and seasonal macroinvertebrates, composed of sponges, bryozoans and bivalves. Frost (1991), when referring to the competition for substrate between continental sponges and other organisms, highlights his personal notes regarding sponges covering and killing colonies of bryozoans. The occurrence of sponges and bryozoans on the submerged parts of macrophytes, particularly the stalks of the water hyacinths Eichhornia azurea and E. crassipes (Pontederiaceae) Solms-Laubach is a common place in areas of preserved floating meadows like the Pacaya-Samiria National Reserve (Loreto, Peru) and the Jacuí Delta Park (Rio Grande do Sul State, Brazil; Volkmer-Ribeiro, pers. obs.). Nevertheless, in the Guanacaste Deciduous Forest, the environments and substrate appear to be very different from those of floating meadows, as the sponges, bryozoans and bivalves encrust preferably woody or leafy material fallen from the shoreline vegetation within the environments of marshes or small rivers existing in the area. Volkmer-Ribeiro & De Rosa-Barbosa (1974) had already registered
sphærid bivalves of genus *Eupera* Bourguignat, 1854 living inside sponges of genera *Trochospongilla*, *Drulia* Gray, 1867 and *Metania* Gray, 1867 encrusted on the bark of trees affected by the Amazonian seasonal floods. In the present study, no superimposition of the sponges over the bryozoans or vice-versa was found, though the samples and surfaces occupied were small, suggesting the absence of competition for substrate among the three faunal groups considered.

Hence, the association of these three distinct groups of benthic, sessile and filter-feeding animals, in a markedly seasonal environment with high levels of POC, is justified by two basic factors. The first consists in the asexual production of anatomical resistance mechanisms, particularly to drought, such as the statoblasts and sessoblasts of Bryozoans, and the gemmules of sponges. In the particular case of the genus *Eupera* the possibility had already been considered that these minute bivalves, attached to substrate by byssus, resist dry periods (*Volkmer-Ribeiro & De Rosa-Barbosa*, 1974). Remembering that *Herrington* (1962) reported remarkable adaptations of freshwater Sphaeridae of North America to habitats subjected to droughts which last several months each year, *Irmler* (1978, 1989), when studying the fauna of the flood-prone forest of the Central Amazon area distinguished adaptations to the changes in water level experienced by the communities of land and aquatic animals. Of particular note within this latter group is *Eupera simoni* (Jousseaume, 1889), found permanently within the flood zone, but that makes use of the differentiated seasonal rhythms, entering in diapause prior to the dry period and into accelerated reproduction as soon as the flood period starts, which results in a large number of young present in the population during the season of floods. This clear difference in size can be seen in the specimens illustrated in Fig. 35.

*Ussiglio-Polatera et al.* (2000), on their assay of grouping benthic freshwater macroinvertebrates following common biological/ecological traits had Porifera and Bryozoa clustered together on account of they being filter feeders, sessile and producers of asexual resistant bodies. On the other hand *Stuart & Klumpp* (1984), upon a study of particle-size selection and food-resource partitioning among marine benthic filter feeders which commonly depend on the suspended particulate organic material in the media (an ascidia, 3 bivalves and a sponge) demonstrated that: “a mixed assemblage of sponges and bivalves may be able to utilize the suspended material more efficiently than a single-species population, due to recycling of some of the particles”.

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