

## FIRST RECORD OF PRESERVED GEMMULES OF A PLEISTOCENE ASSEMBLAGE OF FRESHWATER SPONGES

VANESSA DE SOUZA MACHADO

Programa de Pós-Graduação em Geociências, Instituto de Geociências, UFRGS, Av. Bento Gonçalves, 9500, 91501-970,  
Porto Alegre, RS, Brasil. *biologavsm@gmail.com*

CECILIA VOLKMER-RIBEIRO

Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Cx.P. 1188, 90001-970,  
Porto Alegre, RS, Brasil. *cvolkmer1427@gmail.com*

ROBERTO IANNUZZI

Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, UFRGS, Av. Bento Gonçalves,  
9500, 91501-970, Porto Alegre, RS, Brasil. *roberto.iannuzzi@ufrgs.br*

**ABSTRACT** – Entire structures of freshwater sponges are rare in the paleontological record and no register existed for the Pleistocene. A previous study of the spicules of such sponges composing pleistocenic strata of the Cemitério Paleolake, Brazil, led to the discovery of several *in situ* preserved gemmules. The present research aimed to identify the sponge species which produced these gemmules, their relationship to the already described spicules found in the lake strata and enter a taphonomic enquiry towards the factors which would have led to this remarkable preservation. The materials were mounted for analysis at SEM. The gemmules pertain to the extant species *Corvoheteromeyenia australis*, *Dosilia pydanieli*, *Radiospongilla amazonensis* and *Corvomeyenia thumi*. Young gemmules of *Heterorotula fistula*, a sponge known only from loose spicules in spongillite deposits were also detected and are for the first time figured, confirming the species status. Two factors would have favored this exceptional gemmular preservation. The abundance of young gemmules indicates short immersion periods, which led to the incipient development of pneumatic coats, impairing their buoyancy and accelerating deposition in the lake bottom. Algal blooms, formed next with probable heat and desiccation, would have provided an elastic but consistent crust over the recently deposited gemmules, preventing their dismantling. Radiocarbon dating of the basal-most layer indicated an age of more than 53,780 <sup>14</sup>C years BP.

**Key words:** freshwater sponges, taphonomy, lacustrine deposit, carbonatite complex, Brazil.

**RESUMO** – Estruturas inteiras de esponjas continentais são raras no registro paleontológico e nenhum para o Pleistoceno. Um estudo anterior de espículas dessas esponjas contidas em depósitos pleistocênicos do Paleolago Cemitério, Catalão, Goiás, Brasil, levou à descoberta de diversas gêmulas preservadas *in situ*. Este trabalho visa identificar as esponjas que produziram essas gêmulas e a sua relação com as espículas já descritas para os mesmos estratos do lago, além de abordar os processos tafonômicos que induziram essa excepcional preservação. Os materiais foram montados para análise ao MEV. As gêmulas pertencem às espécies atuais *Corvoheteromeyenia australis*, *Dosilia pydanieli*, *Radiospongilla amazonensis* e *Corvomeyenia thumi*. Gêmulas jovens, inteiras de *Heterorotula fistula*, uma esponja conhecida só por espículas soltas em depósitos de spongilitos, foram também detectadas e pela primeira vez ilustradas, confirmando o *status* da espécie. Dois fatores teriam favorecido essa rara preservação de gêmulas. A abundância de gêmulas jovens aponta para períodos curtos de imersão, responsáveis pelo desenvolvimento precário das camadas pneumáticas, prejudicando a flutuação dessas gêmulas e acelerando seu depósito no fundo do lago. Uma provável cobertura por uma capa de algas, formada em seguida, devido ao calor e a dessecação, forneceu uma crosta elástica, mas consistente, que cobriu as gêmulas recentemente depositadas, impedindo sua desagregação. Datação por carbono radioativo indicou idade de mais de 53.780 anos <sup>14</sup>C AP para a seção mais basal.

**Palavras-chave:** esponjas de água doce, tafonomia, depósito lacustre, complexo carbonatítico, Brasil.

### INTRODUCTION

Preserved structures of freshwater sponges are rare in the geological record. *Eospongilla morrisonensis* Dunagan, 1999 from the Morrison Formation, Late Jurassic in age, Colorado, USA, is the oldest one known. However its fossil remains present only loose spicules and absence of gemmules. Ott &

Volkheimer (1972) described *Palaeospongilla chubutensis* from early Cretaceous rocks of the Chubut Formation, Argentina. Volkmer-Ribeiro & Reitner (1991) demonstrated that the original description of *P. chubutensis* was done upon the epizoic associations of two species of freshwater sponges: *P. chubutensis* and the new species *Spongilla patagonica*. They described the preserved skeletal reticulum,

the oocytes and gemmules of *P. chubutensis*, type species of the monotypic and sole genus placed by them in the new fossil family Palaespongillidae. Also described were the gemmules and gemmoscleres of *S. patagonica*, which was placed by the authors in the actual family Spongillidae.

Müller *et al.* (1982) described and illustrated, upon one single entire gemmule, *Spongilla gutenbergiana* Müller, Zahn & Maidhof, 1982 from middle Eocene rocks of the Darmstadt Formation, early Tertiary in Germany. The species was next improperly transferred to genus *Ephydatia* by Richter & Wuttke (1995) who did not work on the fossil material originally described as *S. gutenbergiana*, but on new materials corresponding to loose gemmoscleres, not declared to belong to the same sediment where *S. gutenbergiana* was found. Also improperly described are the illustrated gemmoscleres, which certainly belong to genus *Ephydatia*, but represent young gemmoscleres, misinterpreted as corroded or malformed gemmoscleres. The empty orifices contained the silicatein soft filaments on the way to form the shaft spines and rotules but not preserved during the fossilization process. This misinterpretation leads to the conclusion that the described gemmoscleres would show larger dimensions when fully developed. Also lost is the interpretation that due to this incipient formation the environment was subjected to a sudden water reduction at the time of the gemmule formation. The conclusion is thus apparent that two species of freshwater sponges may be taken into consideration respecting the Eocene rocks of the Darmstadt Formation, i.e., *S. gutenbergiana* and *Ephydatia* sp.

Only two fossil species with entire structures were described from the Miocene: *Oncosclera kaniensis* Matsuoka & Masuda, 2000 (family Potamolepidae) from the Nakamura Formation, central Japan, and *Ephydatia chiliana* Pisera & Sáez, 2003 (family Spongillidae) from the Quillagua Formation, Atacama region, Chile. Fully preserved gemmiferous specimens of *O. kaniensis* encrusted single as well as articulated valves of the freshwater mollusc *Anadonta* sp. besides compressed and uncompressed wood fragments. *E. chiliana* missed preserved skeleton fibers and was described upon only preserved gemmules.

Harrison & Warner (1986) identified gemmules of genus *Anheteromeyenia* (family Spongillidae) in Holocene sediments dated as 9,400 years BP, from Graham Island, the Queen Charlotte Archipelago, British Columbia, Canada. Pals *et al.* (1980) refer, but do not describe, gemmules in Holocene deposits (750-600 BP) in Noord-Holland, Europe.

The detailed study (Machado *et al.*, 2012) of conspicuous amounts of spicules preserved in Pleistocene sediments of the Cemitério Paleolake, Catalão, Goiás, Central Brazil, took to the finding that seven species of freshwater sponges lived in the lake and contributed to the formed deposits: *Metania spinata* (Carter, 1881), *Dosilia pydanieli* Volkmer, Ribeiro 1992, *Radiospongilla amazonensis* Volkmer-Ribeiro & Maciel, 1983, *Trochospongilla variabilis* Bonetto & Ezcurra de Drago, 1973, *Corvomeyenia thumi* (Traxler, 1895), *Heterorotula fistula* Volkmer-Ribeiro & Motta, 1995 and *Corvoheteromeyenia australis* (Bonetto & Ezcurra de Drago, 1966). These species were seen to compose distinct sponge

assemblages along the 25 spongofacies found in the lake sediments. These past sponge communities partially conform to the actual ones described by Volkmer-Ribeiro (1999) for lakes and bogs within the Cerrado Biome in Brazil.

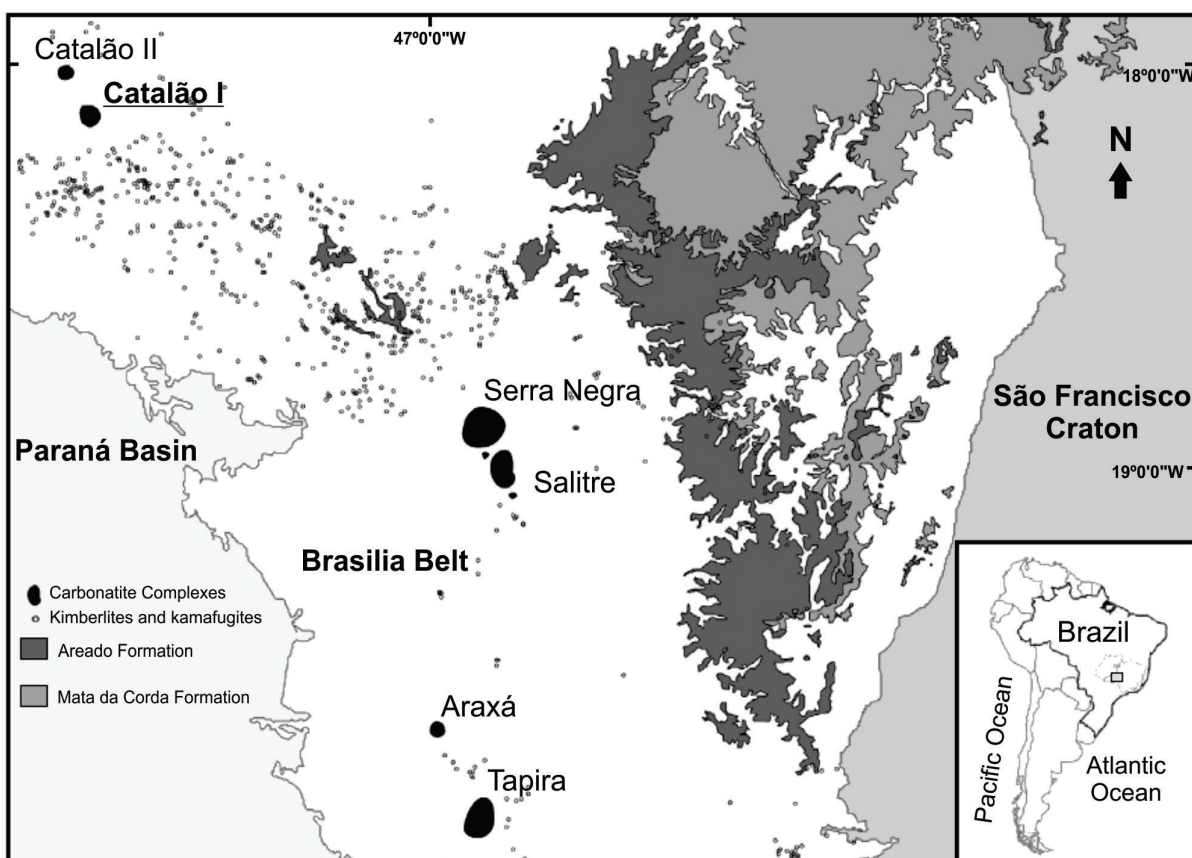
Several entire gemmules were also detected in some of the lake strata but saved for a specific study. These results are here presented altogether with the relationship of the gemmules with the loose spicules previously identified (Machado *et al.*, 2012) in the lake strata. The tafonomic processes involved in this remarkable preservation are focused. The resulting register is the first one for Brazil and for the whole Pleistocene.

## STUDY AREA

The Cemitério Paleolake outcrop, Catalão, Goiás (18°08'S, 47°08'W), conforms a continuously exposed lacustrine deposit, which took place in a depression at the central part of the Catalão I Carbonatite Complex (Figures 1, 2). The sedimentary rocks lie discordantly on a dome of magmatic carbonatite (Ribeiro *et al.*, 2001). The outcropping area composes a sub-circular plateau of 27 km<sup>2</sup>, with the NS and EW axes measuring 6 and 5.5 km, respectively. The average elevation is 900 m, rising 100 m above the surrounding land. The centre of the complex is dominated by a body of carbonatite, while the outer portions consist of ultramafic rock. Apatite, pyrochlore, monazite, anatase and vermiculite are the main mineral resources in the complex (Azzone & Ruberti, 2010), but only the first two are currently subject to mining. There are also noteworthy deposits of phosphate and niobium being mined.

The rocks of the Catalão region are included in the igneous province of the Upper Paranaíba (Figure 1), laying between the Paraná and São Francisco basins (Gibson *et al.*, 1995). In this same region, there is an elongated structure extending NW-SE, the Upper Paranaíba Arch, whose uplift began in the early Cretaceous and intensified during the late Cretaceous. This igneous basin was established as a result of intense alkaline mafic-ultramafic and ultrapotassic magmatism generating intrusive (dikes, pipes, diatremes and plutonic complexes) and extrusive (lava and pyroclastic) bodies. According to Gibson *et al.* (1995), the alkaline rocks of this province include, among others, kamafugites, kimberlite, lamproite and carbonatite complexes. The carbonatite complexes of the Upper Paranaíba include Serra Negra, Salitre I and II, Araxá and Tapira in the state of Minas Gerais, and the Catalão complexes I and II, at the northernmost of the Province, in the state of Goiás (Figure 1).

Ribeiro *et al.* (2001) suggested two hypotheses for the genesis of the "Dry Paleolake," a deposit located in the same Catalão I complex and similar to the Cemitério Paleolake. The first would do with the formation of dolines upon the leaching of the underlying carbonatite and phoscorite, thereby decreasing the volume of the basement rock by up to five times. Also under consideration by the authors were small-scale localised collapses causing subsidences. Both hypotheses point to the appearance of the lakes as a result of erosion occurring in an area of carbonatic basement rocks under the action of karstic processes.



**Figure 1.** Geological map of the Alto Paranaíba Igneous Province, signaling the alkaline-carbonatite plutonic complex of Catalão I (Catalão, Goiás, central Brazil) (adapted from Barbosa *et al.*, 2012).

Sand lenses from the middle interval of the Cemitério Paleolake exposure, Catalão, Goiás (Central Brazil), were previously dated using thermoluminescence to be at least 39,700 years BP (Machado *et al.*, 2012). These sediments are composed of numerous microfossils, such as diatom frustules, continental sponge spicules, spores and pollen grains. The high diatom frustules or sponge spicules contents observed in some specific layers allowed for their classification as diatomites or as spongilite, according to the case (Machado, 2009). Macrofossils consisting of terrestrial plant remains, including fern fronds and abundant dicotyledonous angiosperm leaves are additionally found in some layers (Cardoso & Iannuzzi, 2006).

## MATERIAL AND METHODS

The sampling was performed by R. Iannuzzi and N. Cardoso, by removing blocks of rock either manually or with the aid of machines provided by the Fosfertil Mining Company. Three stratigraphic columns were recorded in distinct sites along the exposure of the Cemitério Paleolake (Figure 2), that corresponds to the margin of this lacustrine deposit. Samples were taken from top to bottom, with 21, 19 and 13 layers collected at respectively Sections 1, 2 and 3 (Figure 2).

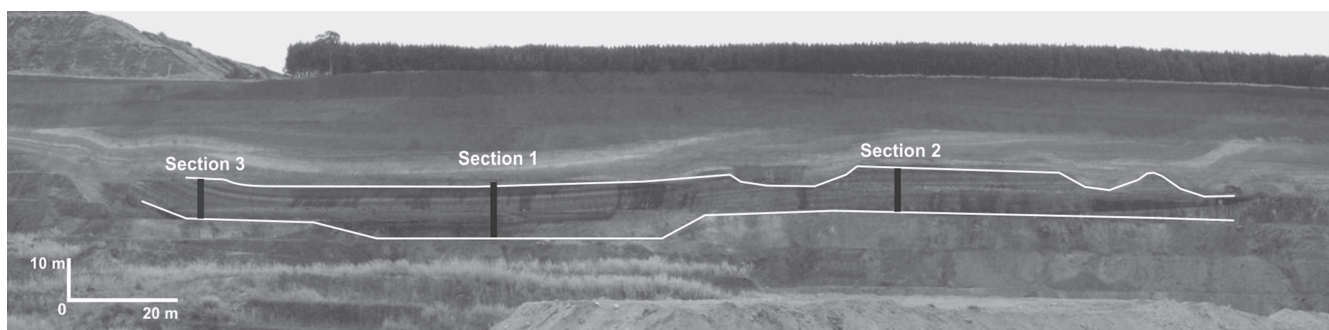
Preserved continental sponge structures previously detected in these samples were now searched for in detail with

the aid of a stereomicroscope. Upon being detected they were detached from the rock matrix, fixed in supports and taken to the SEM for study and photographing which was performed with a Philips Model XL20 at the Microscopy Center of the Lutheran University of Brazil, Canoas Campus, Rio Grande do Sul (ULBRA-RS). All SEM supports containing the studied materials were catalogued and deposited in the Porifera collection of the Museum of Natural Sciences (MCN-POR) of the Fundação Zoobotânica do Rio Grande do Sul (FZB-RS).

The gemmoscleres, *i.e.*, the spicules that cover the gemmules, are the most important morphological character in the characterisation of families, genera and species of freshwater sponges (Volkmer-Ribeiro & Pauls, 2000). As these spicules were preserved *in situ* in the detected gemmules their study at the SEM allowed for a precise identification of the sponge species which lived in the lake and formed such gemmules. The taxonomic identification followed Volkmer-Ribeiro (1992), Volkmer-Ribeiro & Motta (1995) and Machado *et al.* (2012).

The degree of formation and fragmentation of the gemmoscleres was also registered having in mind to elucidate the taphonomic processes involved in this remarkable preservation. Twenty measurements were taken of the gemmoscleres in the fossil gemmules. Table I presents the measures of the gemmoscleres ( $\mu\text{m}$ ) taken from the gemmules





**Figure 2.** Photograph of the Cemitério Paleolake exposure, Catalão, Goiás, central Brazil. The white outline traces the limit of the deposit. The black bars indicate the positions of the three sampled sections (modified from Machado *et al.*, 2012).

preserved at Cemitério Paleolake, compared to those taken from living specimens presented in Ezcurra de Drago (1979), Volkmer-Ribeiro & Maciel (1983), Volkmer-Ribeiro (1992), Volkmer-Ribeiro & Costa (1992) and Volkmer-Ribeiro & Machado (2009).

The basal interval of the Cemitério Paleolake deposit was dated herein using  $^{14}\text{C}$  isotopes obtained from plant macrofossils, which consisted of fragments of a fern frond (*Pteridium* sp.) and of carbonised wood, Layers # 4 and 5 of Section 1, respectively, and of a dicotyledonous angiosperm leaf, Layer # 2 of Section 2. The radiocarbon analysis was carried out by Accelerator Mass Spectrometry (AMS) at the Center for Applied Isotope Studies (CAIS), University of Georgia, USA.

The sediments were classified according to both the particle size and organic matter content at the Centro de Estudos Costeiros e Oceanográficos da Universidade Federal do Rio Grande do Sul (CECO-UFRGS). For the particle size, the coarse sediments were separated using a set of 1 mm Ø sieves (Wentworth, 1922; Krumbein, 1934); for fine sediments, the small particle sedimentation method in a liquid medium was used, according to Krumbein & Pettijohn (1938). The combustion-based organic matter elimination method was used (Wetzel, 1975) for determination of the organic matter (OM) content in the fine sediments (silt and clay).

## RESULTS

### Age

The radiocarbon dating of the basal-most layer (Layers # 4 and 5, Section 1) indicated an age of more than 53,780 years  $^{14}\text{C}$  BP (UGAMS 9289) for the fragment of fossil wood and  $51,780 \pm 400$  years  $^{14}\text{C}$  BP (UGAMS 9287) for the fern frond. The angiosperm leaf from Layer # 2, Section 2, was shown to be from  $48,333 \pm 400$  years  $^{14}\text{C}$  BP (UGAMS 9288) (Figure 3). Thus, this deposit was initially generated in the Late Pleistocene.

The unprecedented dates made available herein enabled the correlation of sections 1 and 2, confirming that the base of Section 2 ( $48,333 \pm 400$  years  $^{14}\text{C}$  BP) most likely correlates with the rocks overlying the Layers # 4 and 5 of Section 1 (Figure 3). The radiocarbon dating of a fossil wood fragment taken from Layers # 4 / 5 of Section 1 yielded an age of more

than 53,780 years  $^{14}\text{C}$  BP for the origin of the Cemitério Paleolake basin.

Considering this correlation, the structures of sponges studied herein can be dated as follows: the sponge materials from Layers # 12 and 15, at Section 2, have respectively an estimated age between  $48,333 \pm 400$  and 29,700 years BP, according to the thermoluminescence (Machado *et al.*, 2012) and radiocarbon dating of Layers # 2 and 16 in the same section (Figure 3). However, Layer # 14, at Section 1, could be considered slightly younger than 29,700 years BP, based on the correlation with the Section 2, where the youngest age was estimated at 4 meters underlying Layer # 16 (Figure 3).

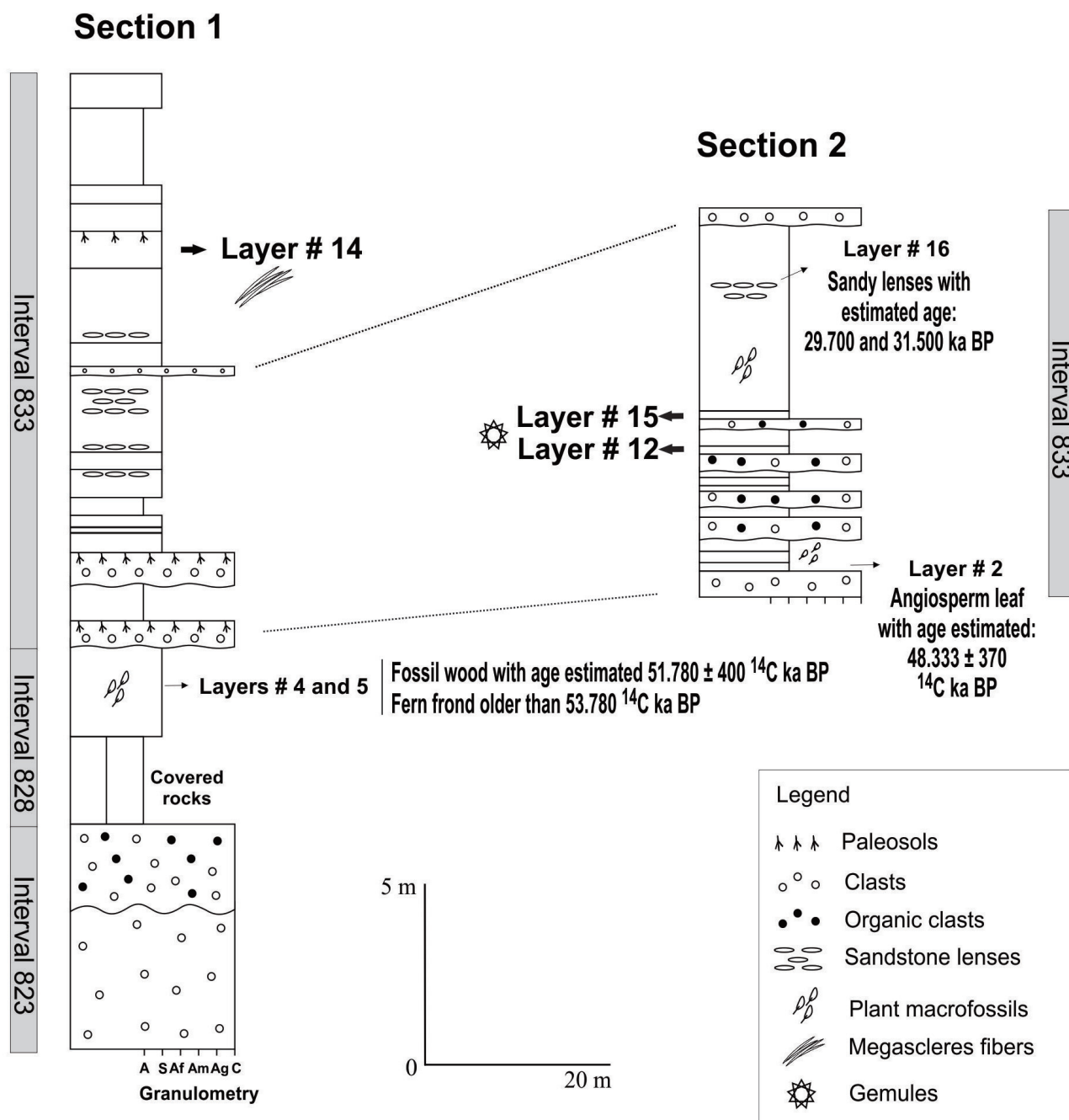
### Granulometry and organic matter

Layer # 14 has a thickness of 0.90 cm and is composed of 26.2% clay, 73.3% silt and 0.5% sand. The organic matter (OM) content was 15.30%. Layer # 12 has a thickness of 0.10 cm and contains 11% clay, 88% silt and 1% sand, while Layer # 15 is 0.05 cm thick and consists of 24.2% clay, 75.7% silt and 0.1% sand (Figure 3). The OM reading in Layers # 12 and 15 was 29.70% and 34.05%, respectively. Due to this predominant composition of fine sized particles, these sediments are considered as pelitic.

### Sponge structures and taphonomy

Only Layer # 14 from Section 1 (MCN-POR 8161) and Layers # 12 (MCN-POR 8181 and 8182) and 15 (MCN-POR 8185 and 8186) from Section 2 (Figure 3) from the Cemitério Paleolake deposit were found to contain, on the bedding planes, preserved parts of the sponges.

Fibers of the skeletal reticulum of *Corvoheteromeyenia australis* (Bonetto & Ezcurra de Drago, 1966) (Figure 4A), consisting of aligned megascleres (Figure 4B) and the longer microscleres (beta series) (Figure 4C) were found in Layer # 14, from Section 1 (Figure 3). Gemmules were detected only in Layers # 12 and 15 from Section 2 (Figure 3). Layer 12 contained gemmules of *Heterorotula fistula* Volkmer-Ribeiro & Motta (1995) (Figures 5A, B), *C. australis* (Figures 5C-E), *Dosilia pydanieli* Volkmer-Ribeiro (1992) (Figures 5F-I) and *Radiospongilla amazonensis* Volkmer-Ribeiro & Maciel (1983) (Figures 6A-C). Layer # 15 preserved gemmules of *H. fistula*, *C. australis*, *Corvomeyenia thumi* (Traxler, 1895) (Figure 7) and, of particular note, an exceptional cluster of



**Figure 3.** Profiles of Sections 1 and 2 from the Cemitério Paleolake, Catalão, Goiás, central Brazil, showing the proposed <sup>14</sup>C correlated depositional sequences (Layers # 4 and 5, Section 1, and Layer # 2, Section 2) containing the presently studied fossils of freshwater sponges (modified from Machado *et al.*, 2012). **Abbreviations:** A, argillite; S, siltstone; Af, fine sandstone; Am, medium sandstone; Ag, coarse sandstone; C, conglomerate.

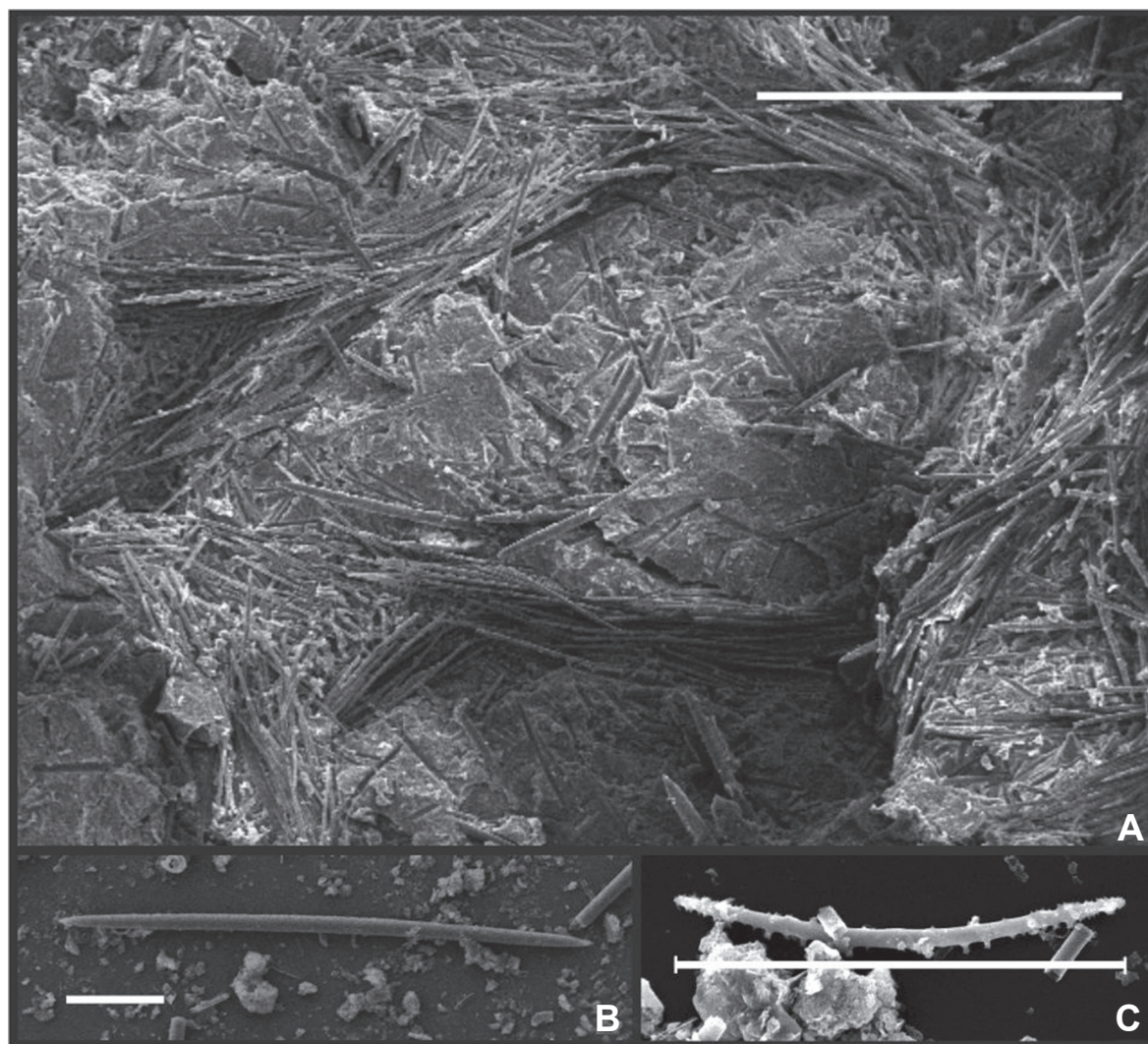
more than fifty gemmules of *R. amazonensis* (Figure 6C). This gemmular cluster was coated by a film which followed the bedding plane (Figure 6D).

Upon splitting the sedimentary shales, one hemisphere of a gemmule was observed to be retained in one face, while the other hemisphere was retained in the opposite face, leading to the hypothesis that some gemmules had been buried and wholly preserved (Figures 5B; 6B). The organic structure of the pneumatic layer in which the

gemmoscleres are inserted was not preserved, though certainly this structural support was present in its initial stage of formation, as it enabled the maintenance of the radial disposition of the gemmoscleres around the gemmules (Figures 5A, C, F; 6A). However, this did not occur in the gemmules of *Corvomeyenya thumi*, thus the original disposition of the gemmoscleres was lost (Figure 7), added to which is the fact that the long and thin axes of the gemmoscleres most likely led to immediate

**Table 1.** Measures of the gemmoscleres ( $\mu\text{m}$ ) taken from the gemmules preserved at Cemitério Paleolake, compared to those taken from living specimens presented in Ezcurra de Drago (1979), Volkmer-Ribeiro & Maciel (1983), Volkmer-Ribeiro (1992), Volkmer-Ribeiro & Costa (1992) and Volkmer-Ribeiro & Machado (2009).

Species	Gemmoscleres from fossilized specimens (average)		Gemmoscleres from modern/current specimens (minimum - maximum)	
	length	width	length	width
<i>H. fistula</i>				
long-type gemmoscleres	120	4.1	-	-
<i>C. australis</i>				
shorter gemmoscleres	52	2.4	47 - 77.5	3.7 - 5
longer gemmoscleres	86	4.1	62.5 - 90	3.7 - 6.2
<i>D. pydanieli</i>				
gemmoscleres	96	2.6	69 - 100	1 - 5
<i>R. amazonensis</i>				
gemmoscleres	52.6	4.6	75 - 94	3 - 8
<i>M. spinata</i>				
gemmoscleres	-	-	43 - 86	2 - 5
<i>T. variabilis</i>				
gemmoscleres	-	-	13.93 - 17.93	2.45 - 5.75



**Figure 4.** SEM images of the spicular tracts of *Corvoheteromeyenia australis* (Bonetto & Ezcurra de Drago, 1966), Layer # 14, Section 1 (MCN-POR nº 8161). **A**, megascleres composing the fibres; **B**, megasclere; **C**, microscle. Scale bars: A = 500  $\mu\text{m}$ ; B = 100  $\mu\text{m}$ ; C = 91  $\mu\text{m}$ .

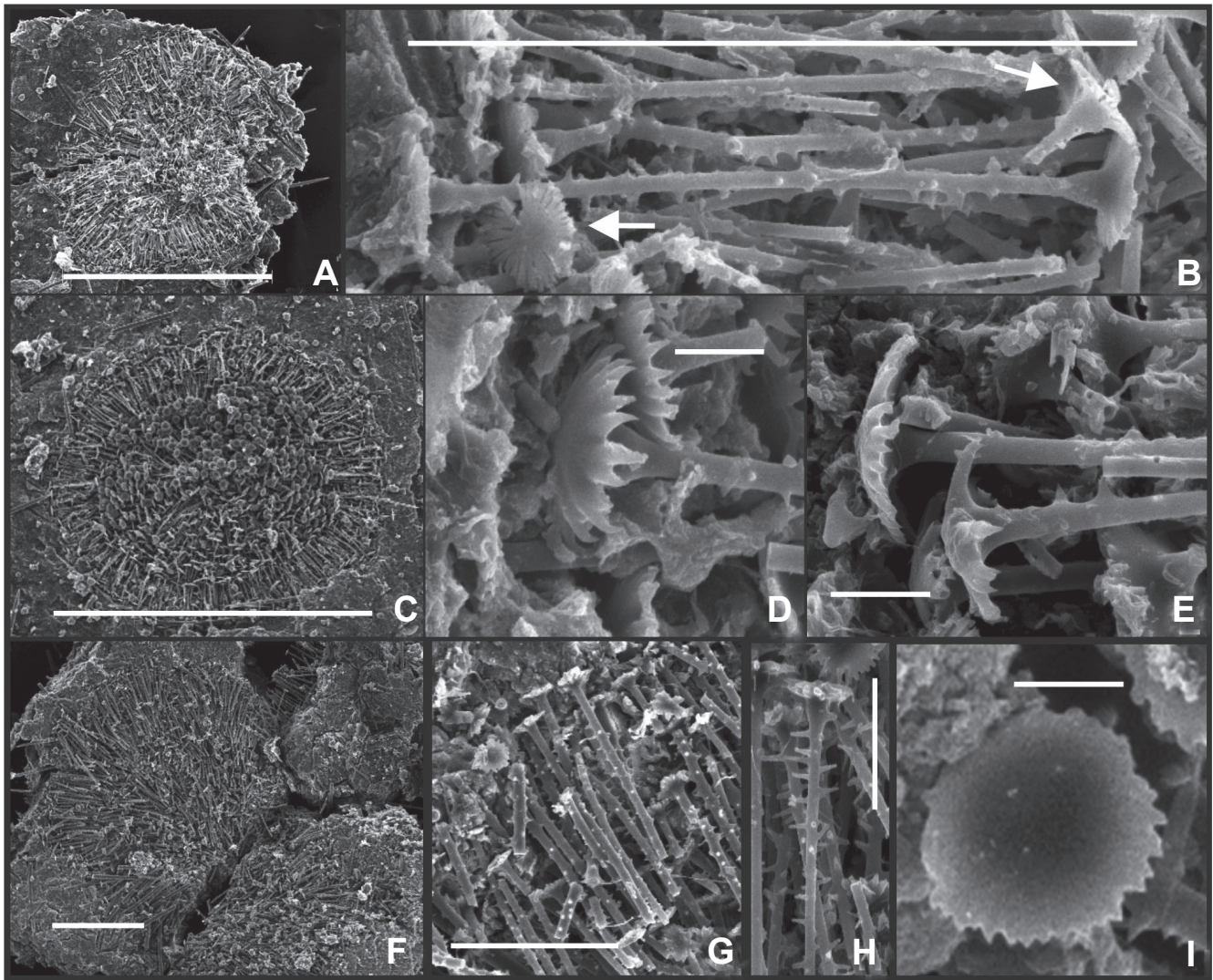


fragmentation upon burial, while the rotules were preserved due to their higher concentration of silica.

All the observed gemmoscleres were seen to be incompletely formed, with their edges still open (Figure 5B), as was the case with the spines on the shaft of *Heterorotula fistula*, *Corvoheteromeyenia australis* and *Dosilia pydanieli* (Figures 5B, H), which explains their sizes being smaller than those found in the current specimens. In the specific case of *H. fistula*, the second category of gemmoscleres, which, supposedly, would cover the outer part of the gemmules, was not formed. However, the megascleres typical of the spicule set described for *H. fistula* are present in these layers (Machado *et al.*, 2012). The figures point to gemmules still in the process of formation and so missing the outer sealing layer with its smaller category of gemmoscleres. This

hypothesis finds support in the comparison of sizes between the gemmoscleres found in the preserved gemmules and those from gemmoscleres in living specimens of four of the involved species (Table 1). *H. fistula* is missing in Table 1 because no living specimens of this species have been found to the present to allow for an appreciation of what the sizes of its gemmoscleres would be in fully developed gemmules. *Corvomeyenia thumi* is also missing in Table 1, due to the fragmentation of the long and thin shafts of its incipiently formed gemmoscleres.

The gemmoscleres of *Radiospongilla amazonensis* were found to be intact, which is attributed to the fact that they are short and relatively thick (Figure 6B). In contrast, in *Corvoheteromeyenia australis*, *Heterorotula fistula* and *Dosilia pydanieli*, because the gemmoscleres are birotulated



**Figure 5.** SEM images of the freshwater sponge fossil gemmules from Cemitério Paleolake, Catalão, Goiás, central Brazil, Layers # 12 and 15, Section 2 (MCN-POR n° 8181 and 8182). **A, B,** *Heterorotula fistula* Volkmer-Ribeiro & Motta (1995): **A**, gemmule; **B**, detail of the long gemmoscleres. The arrows point to the characteristic serrated border of the rotules. **C, D, E,** *Corvoheteromeyenia australis* (Bonetto & Ezcurra de Drago, 1966): **C**, gemmule; **D**, detail of the rotules of the short gemmoscleres; **E**, detail of the rotules of long gemmoscleres. **F-I,** *Dosilia pydanieli* Volkmer-Ribeiro (1992): **F**, gemmule; **G, H**, gemmoscleres with straight long shafts provided with abundant spines; **I**, detail of the indented border of rotules. Several gemmoscleres show incipient formation of the rotules indicating the reduced time available for gemmule completion before the burial event. Scale bars: **A** = 618 µm; **B** = 91 µm; **C** = 700 µm; **D-E** = 10 µm; **F** = 200 µm; **G** = 50 µm; **H** = 20 µm; **I** = 5 µm.



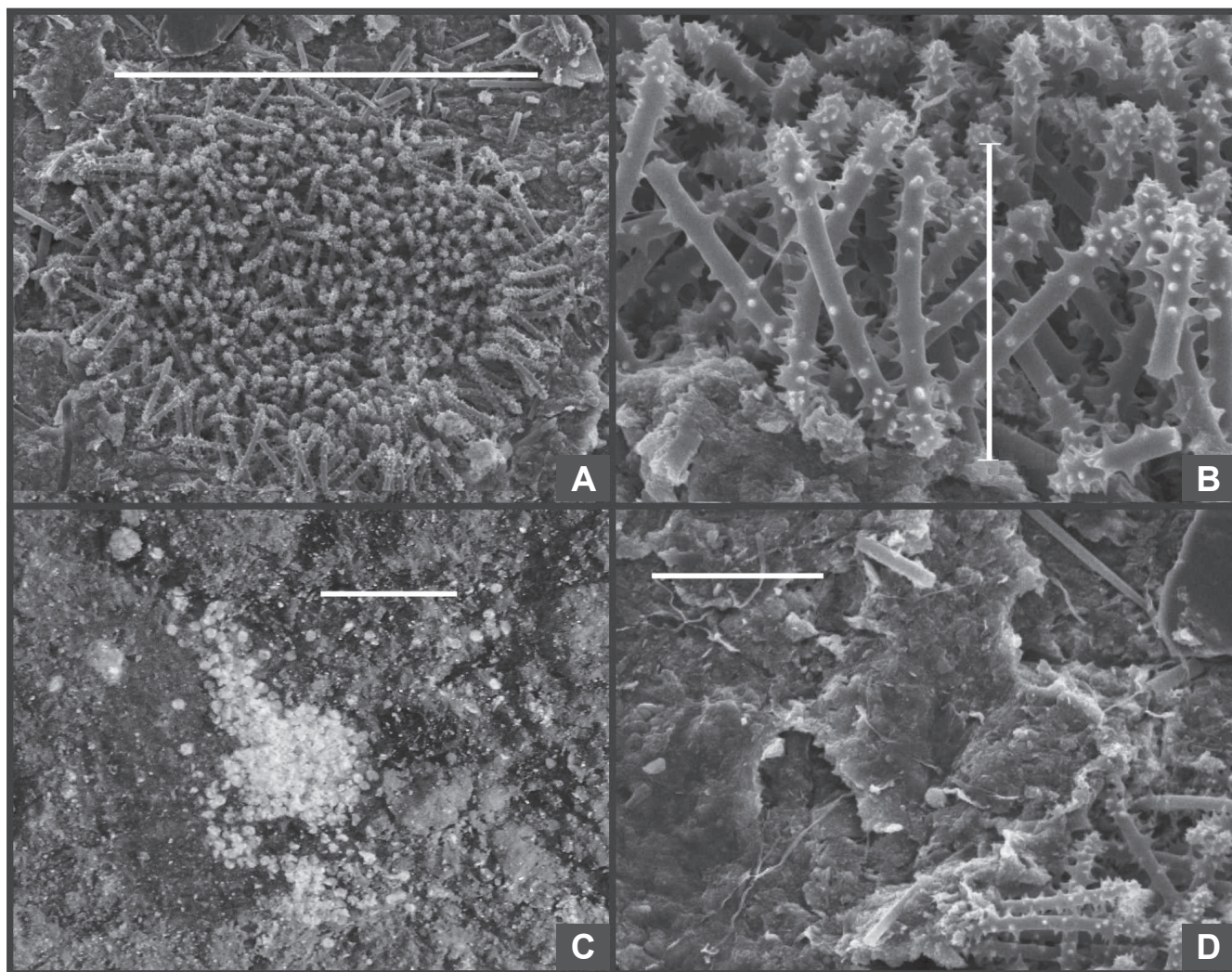
and have slender shafts, differentiated ruptures always occurred close to one of the rotules (Figures 5B, D, E, G), as also occurred in *Corvomeyenia thumi*. However, in the first three species, most likely due to the maintenance of the pneumatic layer during burial, the crown of gemmoscleres was preserved *in situ* (Figures 5A, C, F). The subsequent disintegration of the pneumatic layer and compression led to the fragmentation observed in these gemmoscleres.

## DISCUSSION AND CONCLUSIONS

A comparison with the habitat of *Corvoheteromeyenia australis* in modern environments explains the preservation of the fibers of its skeletal reticulum (Figure 4A), seen in Layer # 14 from Section 1 (Figure 3). Live specimens of *C. australis* have shown a preference for encrusting the roots of the macrophyte *Eichornia azurea* (Sw.) Kunth, both in the State Park of the Jacuí Delta, Rio Grande do Sul, Brazil (Tavares *et al.*, 2003), and in two lakes in Santa Fe, Argentina

(Bonetto & Ezcurra de Drago, 1966; Ezcurra de Drago, 1979). The presence of fossil root marks (= palaeosols) in life position in the analyzed layer (Layer # 14, Section 1, Figure 3) supports this hypothesis. A following new episode of sedimentation would have covered *in situ* the bank-side deposit, preserving both the roots and the skeletal reticulum of the adhering sponge. This *in situ* preservation points to a habitat with shallow and very calm waters allowing the skeletal reticulum to be slowly filled with fine sediments (silt and clay).

The preservational history of the gemmules is significantly more complex. It is difficult to assess the length of time that the gemmules were exposed prior to burial because they are structures specialized in the dispersion of species. Moreover, largely due to the pneumatic wrapping that provides buoyancy, they can easily be displaced by the movement of water and also by the wind (Volkmer-Ribeiro & Pauls, 2000). Two factors may have favored this particular preservation in the Cemitério Paleolake deposit, the first being the possible



**Figure 6.** SEM images of the gemmules of *Radiospongilla amazonensis* Volkmer-Ribeiro & Maciel (1983), Layer # 15, Section 2 (MCN-POR n° 8185 and 8186). **A**, one fossil gemmule; **B**, gemmoscleres; **C**, patch of fossilised gemmules evidencing a calm depositional environment; **D**, fossilised thin (probable algal origin) coat deposited on the gemmules of *R. amazonensis*. Scale bars: A = 240 µm; B = 49 µm; C = 50 mm; D = 50 µm.



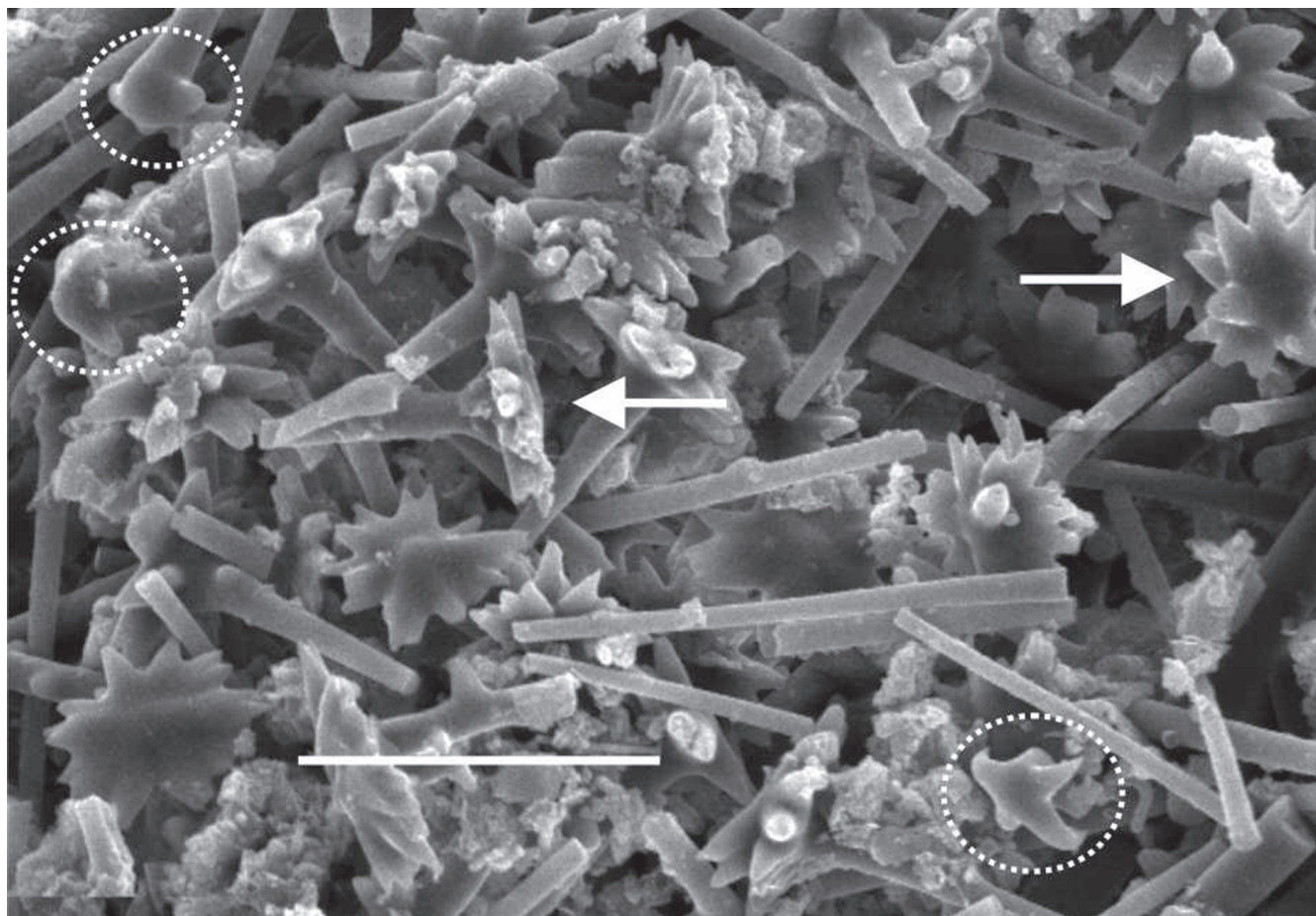
incomplete formation of these gemmules/gemmoscleres when incorporated into the sediment. They were devoid of completed pneumatic layers, thus impairing their buoyancy and accelerating their deposition on the lake bottom. The gemmules of the genus *Anheteromeyenia* recorded by Harrison & Warner (1986), on the west coast of Canada, were also preserved with its gemmoscleres *in situ* however incompletely formed, missing the pneumatic layer.

The second factor relates to the filmy coating that covers the gemmules of *Radiospongilla amazonensis* following the bedding plane of Layer # 15 from Section 2 (Figure 6D). Algal blooms are frequent in tropical ponds subjected to seasonal droughts. The bacteria and algae are intertwined in the process of flowering, caused by heat and the reduction of the water level, initially forming a gelatinous crust that later becomes dry and hardens (Figure 8). Thus, the film seen over the gemmules of *R. amazonensis* (Figure 6D) stands for a vestige of such a crust that, after burial, was pressed and replaced by the surrounding sediments.

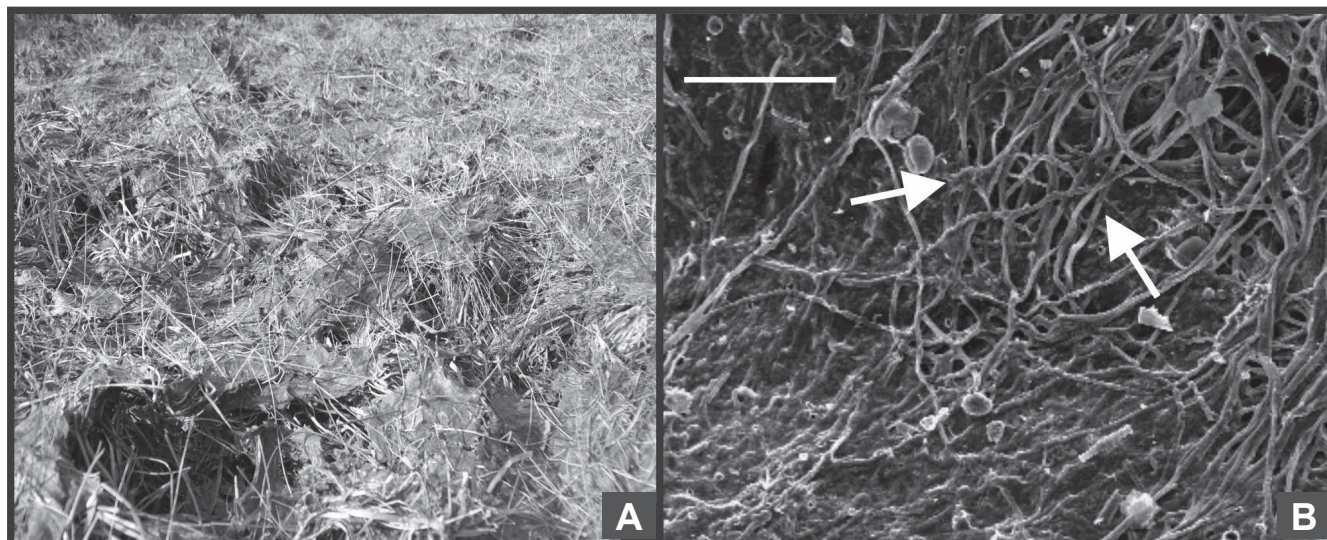
The oldest preserved fossil of the body structure of a continental sponge, that of *Eospongilla morrisonensis*, from the Upper Jurassic (Morrison Formation, USA), was also associated with Charophyta algae (stems and gyrogonites)

(Dunagan, 1999). Moreover, the fossils of the skeletal reticulum with oocytes and gemmules of *Palaeospongilla chubutensis* and gemmules of *Spongilla patagonica*, dating from the Early Cretaceous (Chubut Formation, Argentina) (Volkmer-Ribeiro & Reitner, 1991), were also covered by a crust of blue-green algae, to which Ott & Volkheimer (1972) attributed their remarkable preservation.

Matsuoka & Masuda (2000), provided an accurate description of the taphonomic process involved in the preservation of the skeletal reticulum with gemmules of *Oncosclera kaniensis* (from Miocene rocks of the Nakamura Formation, central Japan), which was still attached to the substrate, what enabled the authors to enter the species to the current genus *Oncosclera*, of the family Potamolepididae. This family is characterised by a skeletal reticulum that is rich in silica, guaranteeing a harder and more resistant structure, typical of environments with greater water flow (Volkmer-Ribeiro & Pauls, 2000). Therefore, that register differs from the one here presented for the Cemitério Paleolake, where all the identified sponges integrate the family Spongillidae, composed by genera and species from lentic habitats and with fragile skeletons rich in spongin (Volkmer-Ribeiro & Pauls, 2000).



**Figure 7.** SEM images of fragmented gemmoscleres of one gemmule of *Corvomeyenia thumi* (Traxler, 1895), Layer # 15, Section 2 (MCN-POR nº 8185 and 8186). The arrows indicate the flat, expanded inner rotules and the circular, umbonate small outer rotules characteristic of the *C. thumi* gemmoscleres. Scale bar = 50 µm.



**Figure 8.** A, Crust of intertwined cyanobacteria and algae sampled by Volkmer Ribeiro in Verde Lake, Minas Gerais, Brazil, at the dry season of 2011. Such crusts resulted from the drying of the algal bloom which covered the decaying aquatic vegetation as well as encrusted specimens of *Metania spinata* (Carter, 1881) as the water receded from the lake margins. B, SEM images of the crust underside, revealing (arrows) the filamentous algae. Scale bar = 200  $\mu$ m.

Loose spicules of all the species which appeared with preserved structures in Layers # 12 and 15 from Section 2 (gemmules of *Dosilia pydanieli*, *Radiospongilla amazonensis*, *Corvomeyenia thumi*, *Heterorotula fistula* and *Corvoheteromeyenia australis*) and Layer # 14 from Section 1 (skeletal reticulum of *C. australis*) of the Cemit rio Paleolake, occurred in these same layers (Machado *et al.*, 2012). Two other species, *Metania spinata* (Carter, 1881) and *Trochospongilla variabilis* Bonetto & Ezcurra de Drago (1973), had their spicules, but not their gemmules, detected by the just referred authors in these same layers.

The Cemit rio Paleolake outcrop (Figure 2) corresponds to the margin of a past lentic system, which was, therefore, more or less susceptible to fluctuations in water level. Thus, the large number of gemmules found in Layers # 12 and 15, from Section 2 (Figure 3), indicates the occurrence of an environment prone to desiccation, such that there were at least two successive periods of considerable decrease in the water column, which are well-defined in Layers # 12 and 15, at Section 2 (Figure 3). However, this waterless event seems to have been more intense during the deposition of Layer # 15, as it preserved gemmules of *Corvomeyenia thumi* (Figure 9) and clustered gemmules of *Radiospongilla amazonensis* (Figure 7). The palaeoenvironment at that time was most likely shallower, with the probable establishment of acidic water, resulting from a natural process of eutrophication caused by the production of macrophyte vegetation in the basin. The high organic matter content in both layers from Section 2 supports this hypothesis. Sponges are not adverse to low pH environments (Harrison, 1974; Frost, 1991). According to Volkmer-Ribeiro & Motta (1995), the species *R. amazonensis*, *Trochospongilla variabilis* and *C. thumi* co-occur associated precisely with periods of peat formation and, consequently, the greater shallowing phases of existing lakes consist with low

pH settings. The absence of entire gemmules of *T. variabilis* in the Cemit rio Paleolake deposit may be due to the small size of the gemmoscleres and the thin gemmular coating once the species occurs with its loose spicules in Layers # 12 and 15 (Machado *et al.*, 2012). The same applies to *Metania spinata* which appeared with spicules but no preserved gemmules in the referred sections. The hypothesis is the same presented for *T. variabilis*, *i.e.*, the short length of the gemmosclere shaft when compared to that of the species with preserved gemmules. Yet, in the particular case of gemmoscleres *M. spinata* the outer rotule is drastically reduced thus lowering the resistance of the gemmular wall to the pressure exercised by the water column and the sediment piling.

The species in this community are current because they were detected as live specimens in a lake environment within the Cerrado Biome region (Volkmer-Ribeiro, 1999). There remains some reservation regarding the extant condition of *Heterorotula fistula*, which was described only by its loose spicules in lake sediments (Volkmer-Ribeiro & Motta, 1995) and for which there is no record of live specimens. Anyhow the present identification of its gemmules comes to confirm the taxonomic status of the species. The question remains as to how the structure of its living specimens and wholly formed gemmules will look whenever found.

There is a noteworthy similarity between the Miocene Quillagua Formation and the Pleistocene Cemit rio Paleolake deposit, regarding the occurrence of diatomite and the influence of volcanic rocks, respectively, from the Andes Mountains and the Upper Parana ba carbonatite complex. Pisera & S ez (2003) attributed the high silica content in the lake environment to the volcanic origin of the sediments, thus encouraging the development of diatom algae and freshwater sponges. The same explanation could be applied in the present deposit.



## ACKNOWLEDGMENTS

The senior author acknowledges the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the Ph.D. scholarship under accomplishment in the Geoscience Graduate Program of the Universidade Federal do Rio Grande do Sul (PPGGeo-UFRGS). C. Volkmer-Ribeiro acknowledges CNPq for granting of the Universal Project (process 481555/2009), essential for the development of this research. The second and third authors acknowledge CNPq for the granted research fellowships (process PQ305687/2010-7 to RI). The authors are in debt to the Fosfertil Mining Company and Anglo-America Mining Company for sampling permission as well as for logistic support during the field work. Last but not least, they acknowledge the valuable suggestions offered by the two anonymous referees.

## REFERENCES

- Azzone, R.G. & Ruberti, E. 2010. The compositional evolution of the phyllosilicates in the lateritic profile of the Catalão I Ultramafic Alkaline-carbonatitic Complex (GO). *Revista do Instituto de Geociências*, **10**:23-43.
- Barbosa, E.S.R.; Brod, J.A.; Junqueira-Brod, T.C.; Dantas, E.L.; Cordeiro, P.F.O. & Gomide, C.S. 2012. Bebedourite from its type area (Salitre I complex): a key petrogenetic series in the Late-Cretaceous Alto Paranaíba kamafugite-carbonatite-phoscorite association, Central Brazil. *Lithos*, **144/145**:56-72. doi:10.1016/j.lithos.2012.04.013
- Bonetto, A.A. & Ezcurra de Drago, I. 1966. Nuevos aportes al conocimiento de las esponjas argentinas. *Physis*, **26**:129-140.
- Bonetto, A.A. & Ezcurra de Drago, I. 1973. Las esponjas del género *Trochospongilla* Vejdovsky en aguas argentinas. *Physis*, **32**:13-18.
- Cardoso, N. & Iannuzzi, R. 2006. *Pteridium catalensis* sp. nov., uma nova pteridófito fóssil do Complexo Carbonatítico Catalão I, Goiás. *Revista Brasileira de Paleontologia*, **9**:303-310.
- Carter, H.J. 1881. History and classification of the known species of *Spongilla*. *Annals and Magazine of Natural History*, **5**:77-107.
- Dunagan, S.P. 1999. A North American freshwater sponge (*Eospongilla morrisonensis* new genus and species) from the Morrison Formation (Upper Jurassic), Colorado. *Journal of Paleontology*, **73**:389-393. doi:0022-3360/99/0073-389
- Ezcurra de Drago, I. 1979. Un nuevo genero sudamericano de esponjas: *Corvoheteromeyenia* gen. nov. (Porifera Spongillidae). *Neotropica*, **25**:109-118.
- Frost, T.M. 1991. Porifera. In: J.H. Thorpy & A.P. Covich (eds.) *Ecology and Classification of North American Freshwater Invertebrates*, Academic Press, p. 95-124.
- Gibson, S.A.; Thompson, R.N.; Leonardos, O.H.; Dickinson, A.P. & Mitchell, J.G. 1995. The Late Cretaceous impact of the Trindade mantle plume: evidence from large volume, mafic, potassic magmatism in SE Brazil. *Journal of Petrology*, **36**:189-229. doi: 10.1093/petrology/36.1.189
- Harrison, F.W. 1974. Porifera. In: C.W. Hart & S.L.H. Fuller (eds.) *Pollution ecology of fresh-water invertebrates*, Academic Press, p. 29-66.
- Harrison, F.W. & Warner, B.G. 1986. Fossil freshwater sponges (Porifera: Spongillidae) from Western Canada: an overlooked group of Quaternary paleoecological indicators. *Transactions of the American Microscopical Society*, **105**:110-120.
- Krumbein, W.C. 1934. Size frequency distribution of sediments. *Journal of Sedimentary Petrology*, **4**:65-77.
- Krumbein, W.C. & Pettijohn, F.J. 1938. *Manual of sedimentary petrography*. New York, Appleton Century Crofts, 549 p.
- Machado, V.S. 2009. *Espongofauna do Paleolago Cemitério, Catalão, Goiás*. Programa de Pós-graduação em Geociências, Universidade Federal do Rio Grande do Sul, Dissertação de Mestrado, 108 p.
- Machado, V.S.; Volkmer-Ribeiro, C. & Iannuzzi, R. 2012. Inventory of the sponge fauna of the Cemitério Paleolake, Catalão, Goiás, Brazil. *Anais da Academia Brasileira de Ciências*, **84**:17-34. doi:10.1590/S0001-37652012000100004
- Matsuoka, K. & Masuda, Y. 2000. A new potamolepid freshwater sponge (Demospongiae) from the Miocene Nakamura Formation, central Japan. *Paleontological Research*, **4**:131-137.
- Müller, W.E.G.; Zahn, R.K. & Maidhof, A. 1982. *Spongilla gutenbergiana* n. sp., ein Süßwasserschwamm aus dem Mittel-Eozän von Messel. *Senckenbergiana Lethaea*, **63**:465-472.
- Ott, E. & Volkheimer, W. 1972. *Palaeospongilla chubutensis* n. g. et n. sp. - ein süßwasserschwamm aus der Kreide Patagoniens. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **140**:49-63.
- Pals, J.P.; Van Geel, B. & Delfos, A. 1980. Paleocological studies in the Klokkeel Bog near Hoogkarspel (Prov. of Noord-Holland). *Review of Paleobotany and Palynology*, **30**:371-418. doi: 10.1016/0034-6667(80)90020-2
- Pisera, A. & Sáez, A. 2003. Paleoenvironmental significance of a new species of freshwater sponge from the Late Miocene Quillagua Formation (N Chile). *Journal of South American Earth Sciences*, **15**:847-852. doi: 10.1016/S0895-9811(03)00012-9
- Ribeiro, C.C.; Brod, J.A.; Junqueira-Abrod, T.C.; Gaspar, J.C. & Petrinovic, I.A. 2001. Pipes de brecha e atividade magmática explosiva no Complexo Alcalino-carbonatítico de Catalão I, Goiás. *Revista Brasileira de Geociências*, **31**:417-426.
- Richter, G. & Wuttke, M. 1995. Der Messel Süßwasser-Kieselschwamm *Spongilla gutenbergiana*, eine *Ephydatia*. *Natur und Museum*, **125**:134-135.
- Tavares, M.C.M.; Volkmer-Ribeiro, C. & Da Rosa-Barbosa, R. 2003. Primeiro registro de *Corvoheteromeyenia australis* (Bonetto & Ezcurra de Drago) para o Brasil com chave taxonômica para os poríferos do Parque Estadual Delta do Jacu, Rio Grande do Sul, Brasil. *Revista Brasileira de Zoologia*, **20**:169-182. doi: 10.1590/S0101-81752003000200001
- Traxler, L. 1895. Spikule von Süßwasserschwämmen aus Brasilien. *Földtani Kozlony Colonia*, **25**:62-64.
- Volkmer-Ribeiro, C. 1992. The freshwater sponges in some peat-bog ponds in Brazil. *Amazoniana*, **12**:317-335.
- Volkmer-Ribeiro, C. 1999. Esponjas. In: C.A. Joly & C.E.M. Bicudo (eds.) *Biodiversidade do Estado de São Paulo, Brasil: síntese do conhecimento ao final do século XX, 4: invertebrados de água doce*, FAPESP, p.1-9.
- Volkmer-Ribeiro, C. & Costa, P.R.C. 1992. On *Metania spinata* (Carter, 1881) and *Metania kiliani* n.sp.: Porifera, Metaniidae. *Amazoniana*, **12**:7-16.
- Volkmer-Ribeiro, C. & Machado, V.S. 2009. Freshwater sponges (Porifera, Demospongiae) in a benthic filter feeding community at the Guanacaste Dry Forest, Costa Rica. *Iheringia, Série Zoologia*, **99**:335-344. doi:10.1590/S0073-47212009000400001
- Volkmer-Ribeiro, C. & Maciel, S.B. 1983. New freshwater sponges from Amazonian waters. *Amazoniana*, **8**:255-264.
- Volkmer-Ribeiro, C. & Motta, J.F.M. 1995. Esponjas formadoras de espongilitos em lagoas no Triângulo Mineiro e adjacências, com indicação de preservação de habitat. *Biociências*, **3**:145-169.

- Volkmer-Ribeiro, C. & Pauls, S.M. 2000. Esponjas de agua dulce (Porifera: Demospongiae) de Venezuela. *Acta Biologica Venezuelica*, **20**:1-28.
- Volkmer-Ribeiro, C. & Reitner, J. 1991. Renewed study of the type material of *Palaespongilla chubutensis* Ott and Volkheimer (1972). In: J. Reitner & H. Keupp (eds.) *Fossil and Recent Sponges*, Springer-Verlag, p. 121-133.
- Wentworth, C.K. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology*, **30**:377-92.
- Wetzel, R.G. 1975. *Limnology*. Philadelphia, W. B. Saunders Company, 743 p.

*Received in December, 2012; accepted in May, 2013.*