Evolutionary study of the freshwater sponge genus *Metania* GRAY, 1867: III. Metaniidae, new family

by

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Abstract

The gondwanic genus *Metania* GRAY, 1867 of freshwater sponges is redefined in this, the third paper of a series concerned with a revision of the Neotropical species of this genus. Newly detected characteristica indicate a relationship between *Metania* and the marine genus *Acanthus* GRAY, 1867 of poecilosclerid sponges. Characteristica similar to those in *Metania* were also detected in the genera *Coromomyenia* WELTNER, 1913, *Acalle* GRAY, 1867 and *Drulia* GRAY, 1867. The genera *Metania*, *Coromomyenia*, *Acalle*, and *Drulia* are transferred from the family *Spongillidae* GRAY, 1867 into the new family Metaniidae, based upon an initial analysis of their shared characteristica.

Keywords: Polyphyletism, Poecilosclerid freshwater sponges, resistant characters, genus *Metania*, Metaniidae, new family.

Resumo

O gênero *Metania* GRAY, 1867, de esponjas de água doce que tem distribuição gondwanica, é refeito após a revisão das quatro espécies que o integram na Região Neotropical. Esta revisão trouxe à luz características que permitem relacionar o gênero *Metania* ao gênero *Acanthus* GRAY, 1867, de esponjas marinhos poeciloscleridas. Características correspondentes ao *Metania* foram percebidas ainda nos gêneros *Coromomyenia* WELTNER, 1913, *Acalle* GRAY, 1867 e *Drulia* GRAY, 1867. Os quatro gêneros são transferidos da família *Spongillidae* para a nova família Metaniidae, após uma primeira análise de suas características comuns.
Introduction

The genus *Metania* GRAY, 1867 shows a typical gondwanic distribution. Two species are registered from the Oriental Region, one from the Ethiopian Region and two from the Neotropical Region (PENNY & RACEK 1968). Quite recently STANISIC (1979) described *Metania ovogemata* from Australia.

An intensive study on a large collection of *Metania* specimens, collected mainly from Amazonian waters, demonstrated that four species are presently registered from the Neotropical Region; *Metania fittkauii* and *Metania subtilis* were described by VOLKMER-RIBEIRO (1979) and two other species, *Metania reticulata* (BOWERBANK, 1863) and *Metania spinata* (CARTER, 1881) were redescribed by VOLKMER-RIBEIRO (1984).

That revision first appeared as a post-doctoral thesis (VOLKMER-RIBEIRO 1976), ending with the suggestion of a Heteromeyenia/Metania relationship in the family Spongillidae. STANISIC (1979) presented another hypothesis explaining the origin of the genus *Metania* from a Radiospongilla stock. In the present paper these two propositions are reviewed in the light of recent work on the systematics of freshwater sponges. A new phyletic position is proposed for *Metania*, within a new family of sponges.

Distribution of the genus *Metania* in the Neotropical Region

Whilst *M. reticulata* has been recorded from the Brazilian and Venezuelan Amazonia, and *M. spinata* may occur as far south as São Paulo State in Brazil (VOLKMER-RIBEIRO 1984), *M. subtilis* and *M. fittkauii* are only known from Amazonian waters (VOLKMER-RIBEIRO 1979). There is a possibility that the genus *Metania* occurs in the Guaxba River, in the extreme south of Brazil (VOLKMER-RIBEIRO et al. 1975), and also in the São Francisco River, Bahia State, Brazil (LUTZ 1915).

The occurrence of *Metania* in the waters of the central part of South America, i.e. the large Parana-Paraguay Rivers basin, has not been recorded.

The Neotropical range of the genus shows a possible discontinuous distribution, with a broad distribution in the Amazon Basin and a presently unconfirmed, restricted distribution in three other areas, south of that basin, at the Brazilian Atlantic border (Fig. 1).

To date, the Neotropical Region supports the largest number (4) of *Metania* species.

The distribution pattern of sponges of the genus *Metania* matches almost perfectly that of the World's Tropical Rain Forests (Fig. 2). All have been collected from bark, branches, twigs or leaves of trees and shrubs which are suspended or subject to prolonged submersion in water.

Fig. 1: Distribution of the genus *Metania* GRAY, 1867 in the Neotropical Region. Dotted outline, areas of reported occurrences; broken line outline, areas of expected occurrence.
Fig. 2: Distribution of the World's Tropical Rain Forests with arrows indicating areas of occurrence of the genus Metania GRAY, 1867. Areas from 1 to 4 after VOLKMER-RIBEIRO 1979, 1984; from 5 to 8 after PENNEY & RACEK 1968 and area 9 after STANISIC 1979. Continuous line, first draft of the overall distribution of the new family Metaniidae.

Characteristics of generic value for Metania

The study of characteristics presented by sponges of the genus Metania allocated to the four Neotropical species, showed that the presence of a so-called "boletiform" gennoscleere (VOLKMER-RIBEIRO 1979, 1984) with a spiny, short shaft, bearing a collar of spines below the lower rotule, is a shared character. Such a characteristic is also recorded in the original descriptions of Metania species from the Oriental, Ethiopian, and Australian regions but is not present in other sponge genera.

Characteristics of specific value for the genus Metania in the Neotropical Region

Changes in shape of alpha and beta megascleres are specifically significant, as are the disposition and number of spines on the beta megascleres, on the microscelere and on the gennoscleere shaft. The shape of the upper knob and of the lower rotule of the gennoscleere also varies in the four species (VOLKMER-RIBEIRO 1979: figs. 1, 2; 1984: figs. 1, 2, 5).

The presence or absence of some kind of sclere may be of specific value, as in M. spinata which has a chela series of microsceleres, or as in M. subtilis where the beta megasclere is missing.

The skeletal structure is based on a reticulate model. Large meshes with primary and secondary net fibres are produced in M. spinata and M. reticulata (VOLKMER-RIBEIRO 1984; figs. 3, 6), there is a more diffuse network in M. fittkau while a reticulum is completely absent in M. subtilis (VOLKMER-RIBEIRO 1979; figs. 4, 5). As can be seen from these figures, the skeletal structure is, on the other hand, linked to the hardness and size of the sponges. M. reticulata, which has the largest spicule fibres and the most conspicuous reticulate structure, produces the largest and hardest specimens. The reticulated skeletal structure decreases in significance from this type, from M. fittkau to M. spinata and to M. subtilis, as do the texture and size of the specimens.

The presence of previously unreported characteristics in Neotropical Metania species rendered it imperative to redefine the genus in view of the redefinition presented by PENNEY & RACEK 1968.

Genus Metania GRAY, 1867, redefined


Acaulis BURTON, 1934, p. 412; ARNDT, 1936, p. 17 (non GRAY, 1867, p. 552).

Protamphioexa BURTON, 1938, p. 461 (non MARSHAL, 1833, p. 568).


Type species: Spongilla reticulata BOWENBANK, 1863.

Diagnosis: Sponges with boletiform gemmoscleres which have a spiny shaft and a collar of spines under the lower rotule.

Redefinition: Megascleres of two distinct classes, the alpha megascleres building the skeletal fibres and the beta megascleres producing gemmular cages or pawed around the gemmules. The second type may be absent. Alpha megascleres smooth, stout amphioexa to amphioexa. Beta megascleres spiny amphioexa to amphioexa usually about half the size of the other series. Both series show large size variation in a single specimen.

Microsceleres of two distinct classes. Spiny minute amphioexa displaying large spines in the middle and a microgranulation at the extremities. The large spines have lanceolate endings. This type is always present and may be abundant or scarce, according to the specimen. Minute chaeta may be present as a second type of microscelere, again with varying degrees of abundance.

Gemmoscleres boletiform and of varying lengths in the same gemmule. Shafts long to short, with a variable number of spines and a collar of spines under the lower rotule. Lower rotule large, stout, polygonal, with curved, undulated margins. Upper rotule knob-like, smooth or with a few recurved, irregularly placed spines or hooks, or approaching a true rotule with marginal incurved spines.
Gemmules abundant to extremely abundant, large, ovoid, cordiform or spherical, contained or not in capsules built of beta megascles and scattered throughout the skeletal meshwork, or devoid of gemmular capsules and forming a basal stratum with a whitish mass of beta megascles in the space between the gemmules. Thin pneumatic coat with large polygonal air spaces, in which the gemmoscleres are radially embedded with their boletiform rotule in the thick inner gemmular coat and the knoblike extremity projecting beyond the pneumatic coat. Two layers of gemmoscleres may be present. Outer gemmular coat ill-defined or absent. Foraminal tube short or long, larger towards the base, covered with slanting gemmoscleres with or without an outcurved collar at the extremity.

Sponges forming shallow, small, smooth, delicate, non reticulate to crumblor-like reticulate crusts, or harder, hispid, reticulate bulbous growths with projecting tubercles.

**Key to the Neotropical species of Metania (Fig. 3)**

1. Sponges with two series of megascles, one smooth and the other spiny and about half the size of the former ........................................... M. subtilis
2. Spiny megascles with diffusely distributed spines along the whole scere. Spiny megascles with spines localized at the middle of the scere, the extremities smooth ........................................... M. spinata
3. Gemmoscere shaft spiny to strongly spiny; the lower rotule with poorly developed borders ........................................... M. reticulata
   Gemmoscere shaft extremely short, spines rare or absent; lower rotule with strongly developed borders, hiding part of the shaft ........................................... M. fittkaui

Spicule and gemmule sizes of the four Neotropical species are given in Table 1.

**Table 1:** Sizes, in micrometres (minimum and maximum), of spicules and gemmules of the four Neotropical species of *Metania* GRAY, 1867. Corrections were introduced for some of the values presented in VOLKMER-RIBEIRO (1979 and 1984).

<table>
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<tr>
<th>Gemmoscelae</th>
<th>Alpha megascles</th>
<th>Beta megascles</th>
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<td>Width</td>
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<tr>
<td><em>M. reticulata</em></td>
<td>391-588</td>
<td>106-245</td>
</tr>
<tr>
<td><em>M. spinata</em></td>
<td>368-791</td>
<td>250-366</td>
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<tr>
<td><em>M. fittkaui</em></td>
<td>229-690</td>
<td>113-219</td>
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<tr>
<td><em>M. subtilis</em></td>
<td>413-776</td>
<td>216-381</td>
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<tr>
<th>Microsceres</th>
<th>Gonoxe</th>
<th>Chaclae</th>
<th>Gemmoscelae</th>
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<td>Length</td>
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<tr>
<td><em>M. reticulata</em></td>
<td>43-103</td>
<td>3-10</td>
<td>22-38</td>
</tr>
<tr>
<td><em>M. spinata</em></td>
<td>50-116</td>
<td>4-8</td>
<td>27-41</td>
</tr>
<tr>
<td><em>M. fittkaui</em></td>
<td>43-90</td>
<td>3-5</td>
<td>15-25</td>
</tr>
<tr>
<td><em>M. subtilis</em></td>
<td>79-143</td>
<td>9-10</td>
<td>33-56</td>
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Fig. 3: Alpha megascles (am), beta megascles (bm), microsceres (mi = antixoea, an = chaclae) and gemmoscleres (gm) of: A) *Metania spinata* (CARTER, 1881), B) *Metania reticulata* (BOWERBANK, 1863), C) *Metania fittkaui* VOLKMER-RIBEIRO, 1979, D) *Metania subtilis* VOLKMER-RIBEIRO, 1979 (All gemmoscleres at high magnification).
Review of phyletic proposals for the genus Metania

PENNEY & RACEK (1968): 147 redefined the genus Metania on the basis of its "true tubelliform gemmoscleres", which they considered to be atypical birotulate gemmoscleres.

VOLKMER-RIBEIRO (1976) placed Metania phylogenetically between the genus Heteromeyenia POTTS, 1881, "sensu" PENNEY & RACEK, 1968 and Drulia GRAY, 1867 "sensu" PENNEY & RACEK, 1968. This proposition was supported by the author's agreement at that time with the widely accepted view that Metania, together with the other rotula bearing genera, stemmed from a Spongilla-Radiospongilla stock. The characteristics of Heteromeyenia, upon which VOLKMER-RIBEIRO (1976) established a close relationship with Metania, were the differing sizes of the gemmoscleres, the sparsely spinous and fimbriate megascleres with their smooth extremities, the well developed pneumatic coat and the long foraminal tube with its terminal collar. The evolutionary sequence proposed for the Neotropical species of Metania would run from M. subtilis to M. reticulata, through M. spinata and M. fittkaisi. In this way Metania species would have acquired a reticulate skeleton and a second class of megascleres. According to VOLKMER-RIBEIRO (1976) the genus Drulia originated from an ancestral Metania in Neotropical waters by the drastic reduction of shaft length, followed by loss of the upper knob. The genus Drulia, like Metania, is the only other to contain sponges with a very conspicuous reticulate skeleton with net primary and secondary fibres, individual gemmules contained in capsules composed of the second type of short, sparsely spinous megascleres, microscleres amphiheca with larger central spines, megascleres which pass from amphiheca to stout amphiproscler and large, stony hard bulbous sponges.

STANISIC (1979) put forth another hypothesis to explain the occurrence of a single Metania species in Australia. He followed the reasoning of PENNEY & RACEK (1968) and RACEK & HARRISON (1975) that birotulate gemmoscleres would have evolved from a Radiospongilla PENNEY & RACEK (op. cit.) stock in which the circle of spines at the gemmosclere extremities attained a rotular condition, considering the Metania gemmoscleres birotulate. STANISIC (1979) however resisted the idea that a monophyletic origin would explain the conspicuous morphological diversity of the birotulate genera. He also rejected the gemmosclere as a diagnostic character on which intergeneric relationships could be established, reporting work by POIRIER (1974, 1975) and STANISIC (1977) where gemmesclere ecomorphies in Ephydatia fluviatilid (LINNAEUS, 1758) and Radiospongilla sceptorides (HASWELL, 1882) were considered so important as to mask ancestral characters and evolutionary gains.

STANISIC (1979) then turned to the variation in megasclere length in the genus Radiospongilla and proposed that two evolutionary lines diverged, at different times, from the same stock, represented by the Radiospongilla cerebellaon (BOWERBANK, 1863) group. Such diverging lines could account for a polyphyletic origin of the birotulate freshwater sponges, the genus Metania having arisen from one of them in Australia.

A new phyletic position for the genus Metania

The gemmoscleres in Metania present such outstanding diversity compared to gemmoscleres in other genera of the family Spongillidae, that their use in the recognition of a group of the genus rank was largely accepted. However the gemmosclere was completely disregarded by STANISIC (1979) proposal on generic relationships of Metania, or was under-valued because of assumptions that it represented an atypical birotulate (PENNEY & RACEK 1968) or a modification of a Heteromeyenia birotulate (VOLKMER-RIBEIRO 1976).

A slow process of evolution has long been recognized within the Portiera. LEVI (1973) and BERGUIST (1978), with supporting bibliography, comment that sponges are very conservative organisms. FINKS (1971) suggested a mosaic pattern of evolution for the Spongillidae, in which one structure changes while the rest of the organization remains stable. This evolutionary process would take place with widely separated saltation events and intervening long periods of stability, and would, in the whole, be very slow.

The recently proposed evidence from VOLKMER-RIBEIRO & DE ROSA-BARBOSA (1979) and VOLKMER-RIBEIRO & WATANABE (1983) confirm MARSHALL'S (1883) and BRIAN'S (1970) assumptions of a polyphyletic origin for freshwater sponges, and indicate that the polyphyley may be greater than previously thought. Demonstration by the former authors that some spicular components of marine sponges may occur, with little or no modification, in the freshwater branches of that stock offers the first evidence for the exclusion of convergent evolution from phylogenetic considerations on some freshwater sponges.

Such marine spicules, which have passed unchanged into the freshwater habitat, did so as gemmonscleres and, curiously enough, are given high value as diagnostic elements in the taxonomy of marine sponges. In Sieracteae thalassiae A. VOLKMER-RIBEIRO & DE ROSA-BARBOSA (1979) the gemmosclere is a sterrator, and other characteristics of the sponge also indicate an origin from a Hadromerid stock. In Sanistractae yokotensoi A. VOLKMER-RIBEIRO & WATANABE (1983) the gemmosclere reveals the transformation of a spinated sandaster into a peculiar new gemmosclere, while again, other characteristics indicate its evolution from Hadromerid stock.

The gemmosclere character is thus the morphological structure which twice carried a "marine" character into freshwater habitat, in two largely independent geographical areas, Brazil and Japan, probably also in separate geological periods. The gemmosclere therefore emerges as a reliable character for phylogenetic studies and should, in any case, be carefully studied for its similarities to marine sponge spicules. A second step would be the search for other characteristics which strengthens overall similarity with the marine group, and allow the definite exclusion of convergent evolution.

The increasing evidence for a polyphyletic origin for freshwater sponges, allied to the peculiarity of the gemmosclere in Metania and its complex spicular set, necessitated comparison between this genus and genera of Pocilloclerida.

The comparative study revealed striking similarity in the spicular components and skeletal structure in Metania GRAY, 1867 and Acaruns GRAY, 1867. The genus Acaruns is the only other with an "unequal birotulate", i.e. a smooth or acanthose cladostyle.
two or three kinds of “megascleres” and two kinds of microscleres, including a chaelate series. Sponges of the genus *Acarus* have a characteristic reticulate skeleton with conspicuous ascending fibres and usually a hispid surface which may be ridged or furrowed. Quite hard sponges are also produced in *Acarus*. Because this comparative study was carried out after the description of *Metania* subtilis and *Metania* fitkani but before submission of the redescriptions of M. reticulata and M. spinata for publication the four species were again revised, in view of the spicular set of *Acarus*, to search for possibly unnoted spicular components. The chaelate series of microscleres in *M. spinata* was at that stage detected and included in the redescriptions of the species (Volkmer-Ribeiro 1984).

*Metania* spinata appears to be the most primitive species of the genus in the Neotropical Region, being the only one which has retained the chaelate series of microscleres and the basal localization of the ancanthose megascleres. The primary ascending fibres of the reticulate skeleton are also conspicuous. *M. spinata* also has quite long gemmoscleres (Table 1), in which the upper knob is very similar to that seen in *Acarus* cladotylotes, while the lower rotule is not as developed as in the other three species.

The assumption that *Metania* diverged from the marine stock which also gave rise to the genus *Acarus* allows the recognition of a group of freshwater sponges which show affinities with either *Metania* or *Acarus*. Such sponges belong in the genera *Corvomeyenia* Weltner, 1913 “sensu” Harrison, 1971, *Acalle* Gray, 1867 “sensu” Volkmer-Ribeiro & de rosa-barbosa, 1972 and *Druliu* Gray, 1867 “sensu” Mothes de Moraes, 1983. *Corvomeyenia*, *Acallle* and *Metania* seem to be closer to *Acarus* while *Druliu* is phylogenetically closer to *Metania*.

In *Corvomeyenia* the whole gemmosclere was remained very similar to the smooth cladotylote in *Acarus*. An extensive study of the gemmoscleres in *C. everetti* (Mills, 1884) produced a series which grades from slightly transformed smooth cladotylotes to the “birotulate” gemmoscleres described for this genus (Fig. 4). The birotular condition of the gemmosclere in *Corvomeyenia* was attained by convergent evolution, when double (birotulata) silicious sealing of the gemmular coat was selected for, rather than a single one. The ancanthose cladotylotes can be recognized as one microsclere series and are present in the three species of the genus, i.e. *C. everetti* (Mills, 1884), *C. australis* Bonetto & Ezcurra de drago, 1966 and *C. carolinensis* Harrison, 1971. The chaelate, second series of megascleres, is missing in *C. everetti* only. The spinny series of megascleres, which corresponds to the ancanthostyles in *Acarus*, or to the beta megascleres in *Metania*, is missing in *Corvomeyenia*.

*Acallle* is the only genus mentioned which is monotypic and has two series of gemmoscleres. In *A. recurvata* (Bowerbank, 1863) the inner series must have been driven from a smooth cladotylote: the cladiform extremity evolved into a rotule when a silicious web extended among the rays, as in *Metania*. The outer gemmoscleres series quite probably originated from a ancanthocladothylote. Two kinds of megascleres are also present in *Acallle* and both have small spines at the extremities, the ancanthose megascleres line the excurrent canals in the basal portion of *A. recurvata*, the two series of microscleres are lacking but the skeletal structure retains the main ascending fibres (Volkmer-Ribeiro & de rosa-barbosa 1972).

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Fig. 4:
Spicular components of *Corvomeyenia everetti* (Mills, 1884). N. Gist Goo no. 54 055, USA. Above gemmoscleres and microscleres at high magnification. Below the entire spicular set of *C. everetti* at lower magnification.
The frequently advanced hypothesis of a hybrid origin for some freshwater sponge species which have an "abnormal" second series of gemmoscleres (Penney & Racek 1968; Volkmer-Ribeiro 1976a), including A. recurvata, now requires careful revision, in the search for an ancestral with a complex spicular set. What emerges from the present study is that Metania inherited a larger part of an ancestral spicular set like that of Acanthus, whilst Corvomeyenia, Acalle and Drulia inherited smaller parts.

The genus Drulia seems to be at the end of an evolutionary series in which the length of the shaft, and the knobbed extremity of the Acanthus cladotylote were gradually reduced (Fig. 5). This reduction started with Corvomeyenia, followed by Metania and Acalle, to reach Drulia where the shaft is reduced to a spine, which may bear a vestigial knobbed extremity, as in Drulia cristata (Weltner, 1895). Spiny megascleres occur in Drulia and Metania and are used to build up the gemmular cages. The microscleres are reduced to the spiny exoete series, which, in D. browni (Bowerbank, 1863), shows characteristics of an ancestral short acanthocladotylote (Mothes de Moraes 1983, fig. 3 and 8).

Overall comparison of the four genera shows that Drulia is closer to Metania on account of its reticulate skeleton with very conspicuous primary and secondary fibres, beta megascleres and gemmular cages, its amphiplocote series of microscleres and the production of large, hard, bulbous growths.

An entirely new evolutionary sequence is now envisaged for the genus Metania in the Neotropical Region.

The study of the specific characteristics within Neotropical Metania species indicates that evolution from an ancestral stock, in common with Acanthus, would have operated by reduction of the spicular classes as well as modification of the spicular shape and size. The evolutionary sequence in the Neotropical Region would thus start with M. spinata and end with M. subtilis, which shows the most drastic reduction of the generic characteristics.

The evidence that a group of marine sponges has further evolved in freshwater as well as in marine habitats permits, for the first time, comparative study of sponge evolution in freshwater and marine environments. It further recommends that the genus Metania, Corvomeyenia, Acalle and Drulia be removed from the family Spongillidae and placed in a new family of freshwater sponges.

The genus Metania is selected as the type genus of the new family because of its wide distribution (Fig. 2). Corvomeyenia has a Nearctic and Neotropical distribution whilst Acalle and Drulia are exclusively Neotropical. The new family is defined as follows:

**Definition:**

Pocilloclerida freshwater sponges with modified cladotylotes as gemmoscleres.

**Type Genus:**

Metania Gray, 1867, as presently redefined.

In addition to Metania the new family includes the genera Corvomeyenia Weltner, 1913 "sensu" Harison, 1971, Acalle Gray, 1867 "sensu" Volkmer-Ribeiro & de Rosa-Barbosa, 1972 and Drulia Gray, 1867 "sensu" Mothes de Moraes, 1983.

In view of the short definition proposed by Topsent (1928) for the family Acanthidae, it is apparent that this family requires revision beginning with a fresh study of the several species recently described in Acanthus and Acanthacarthus Levill, 1962 (Levill erected the genus Acanthacarthus to include those species of Acanthus with acanthostyles). It seems quite probable that the family Acanthidae will be monotypic, containing only the genus Acanthus, but even if that is be, the family must be retained within the marine sponges, an opinion apparently shared, among other authors, by Boury-Esnault (1973). The pattern of evolution within the new family Mataniidae may suggest the evolutionary spectrum which could be expected within the Acanthidae.
and gemmoscleres lower megascleres, A upper SEM photos Fig. 6: and view of megascleres and gemmoscleres of two species of the Metaniidae, after a first analysis of their shared characteristics.

References


Summary

The gondwanic freshwater sponge genus Metania GRAY, 1867 is redefined after a through revision of its four Neotropical species. New characteristics were detected which suggested the retention or slow modification of characteristics of a marine stock, related to the genus Acarnus GRAY, 1867 of Pocilloporid sponge. Those "persistent" characteristics could be also perceived in the freshwater genera Corvovemysia WELTNER, 1913, Acalle GRAY, 1867, and Drulia GRAY, 1867. Metania, Corvovemysia, Acalle, and Drulia are transferred from the family Spongillidae GRAY, 1867 into a new family, the Metaniidae, after a first analysis of their shared characteristics.

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N. AERNUS) (Porifera: Spongillidae) with comments upon its systematics and ecology. - Hydrobiologia 44: 337 - 347.


