



# Phylogenetic relationships of sponges with placochelae or related spicules (Poecilosclerida, Guitarridae) with a systematic revision

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All the currently known sponge species bearing placochelae or placochelae-like spicules (i.e. belonging to the genera *Guitarra*, *Coelodischela*, *Tetrapocillon*, *Euchelipluma*, and *Hoplakithara*) have been reviewed and their relationships delineated by cladistic analysis. A matrix of 18 taxa and 14 characters is included. The species *Isodictya palmata* and *Esperiopsis fucorum* were used as an outgroup, because they shared either monactines or diactines and smooth palmate isochelae with different members of the ingroup. Cladistic analysis using PAUP produced two equally parsimonious trees of 33 steps (CI = 0.758). Strict, Semistrict and Majority Rule consensus trees displayed the same topology. The phylogeny of the trees was not totally resolved. The bootstrap 50% majority-rule consensus tree supported, to a greater or lesser extent, the previously detected monophyletic groups. A common linkage for the ingroup was found in 72% of instances. The genus *Euchelipluma* appeared as monophyletic in 75% of instances while the group which included the genus *Guitarra* did so in 66%. The monophyly of the species with sigmoid microscleres and without spiny isochelae (*G. isabellae/sigmatifera/antarctica/dendyi* and *C. diatomorpha/massa*) received 56% support as did the group of species with spiny isochelae, whereas monophyly of the group *laplani/bipocillifera* received 64% support and the genus *Tetrapocillon* 56%. According to our cladistic analysis, all the species bearing placochelae or derived forms should be allocated to Guitarridae. Within this family, the genus *Euchelipluma* appeared as monophyletic while *Guitarra* was paraphyletic. The single species of the genus *Hoplakithara* clearly belongs to the *Guitarra* (*sigmatifera*) group and thus becomes synonymous with *Guitarra*. *G. solorzanoi* is considered here a synonymy of *G. laplani*. A diagnosis for the 10 valid species of *Guitarra* known to date as well as for the two species of *Coelodischela* and the two of *Euchelipluma* is given.

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ADDITIONAL KEY WORDS: biplacochelae – tetraplacochelae – *Guitarra* – *Coelodischela* – *Tetrapocillon* – *Euchelipluma* – *Hoplakithara* – systematics – cladistic analysis – phylogeny.

## INTRODUCTION

The placochela is a spicule type, which characterizes three genera of Demospongiae (i.e. *Guitarra* Carter, 1874, *Hoplakithara* Kirkpatrick, 1907, and *Euchelipluma* Topsent, 1909). Other spicules closely

related to the placochelae are the biplacochelae, which coexist with the placochelae in some species of *Guitarra* (Lee, 1987), the tetraplacochelae (new name proposed here for the microscleres formerly called tetrapocilla (Boury-Esnault & Rützler, 1997)) typical of the genus *Tetrapocillon* Brønsted, 1924, and the dischelae characteristic of *Coelodischela* Vacelet, Vasseur, and Lévi, 1976. All these related spicules are structurally complex and they have thus been considered of interest

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for phylogenetic purposes (Hadju, 1995). Among them, the dischelae show a particularly complicated structure, with two shafts instead of one and a double central orifice, which is absent from the remaining placocheleoid forms.

The sponges of the above mentioned genera often have, besides placocheleae, complementary microscleres such as isochelae or sigmas. SEM observation of these microscleres in different species of *Guitarra* revealed inter-species differences (Lee, 1987; Boury-Esnault, Pansini & Uriz, 1993; Cristobo, 1998; Carballo & Uriz, 1998), which had been overlooked in previous studies. Some of the genera bearing placocheleae or placocheleoid spicules have successively been allocated to different families: Cladorhizidae (Topsent, 1909), Desmacidonidae Gray (=Desmacididae Smidt, 1870) (e.g. Burton, 1929; Laubenfels, 1936; Bergquist & Fromont, 1988; Boury-Esnault *et al.*, 1993; Pulitzer-Finali, 1993; Hooper & Wiedenmayer, 1994), Esperlopsidae Hentschel, 1923 (e.g. Koltun, 1964; Martínez-Inglés, 1991), Myxillidae? (van Soest, 1988) or Coelosphaeridae Hentschel, 1923 (Vacelet, Vasseur & Lévi, 1976).

We have pursued a two-fold goal. First, we analysed the relationships between species bearing placocheleae or placochele-like spicules by using cladistic analysis. Second, we aimed to clarify the differences among the species of *Guitarra* and those of closely related genera.

## MATERIAL AND METHODS

### CLADISTIC ANALYSIS

All known species of the genera *Guitarra*, *Hoplakithara*, *Tetrapocillon*, *Coelodischela*, and *Euchelipluma* are dealt with in this study (Table 1). A total of 14 characters (39 character states) was used to describe the taxa under consideration (Table 2). The data set (18 species and 14 characters) was analysed using PAUP, version 3.1 (Swofford, 1993). Each character was scored for each species in a taxon/character data matrix (Table 3). Wagner parsimony (Farris, 1970) and Fitch parsimony (Fitch, 1971) methods were used for ordered and unordered characters, respectively. The character-states optimization method used was accelerated transformation (ACCTRAN). The characters spiny isochelae, sigmoid microscleres, placochele-like form, and growth habit were treated as ordered. The remaining characters were bipolar or treated as unordered. All characters were weighted equally. No particular assumption of data polarity was made *a priori*. Characters were polarized by the outgroup comparison, indirect method (Nelson, 1978). We used *Esperiopsis fucorum* Johnston and *Isodictya palmata* Ellis & Solander as a multiple outgroup because they share either monactines or diactines and smooth palmate isochelae with different members of

the ingroup but lack placocheleae. Besides, they had been placed in the old family Desmacididae as some genera of the ingroup had been. The use of a multiple outgroup is considered a stringent test of ingroup monophyly (Bergquist & Kelly-Borges, 1991).

Characters were stated by direct examination of voucher specimens whenever possible (see below for a list of the species examined). Otherwise, the information was extracted from the literature. When the presence of a character was uncertain (e.g. the presence of spiny isochelae in *T. minor* Pulitzer-Finali, 1993) a question mark was used. Character 6 ('megasclere shape') was discarded because it showed a low consistency index (CI=0.267), increased tree length, and decreased consistency index of trees without significantly changing tree topology. Other characters assayed, which did not improve tree resolution, were: placochele shape (with a more or less marked central constriction or with a continuously or discontinuously fringed border), size classes of placocheleae, or a more detailed description of the megasclere shape (i.e. style, tornostongyle, oxea). All these characters may be valuable descriptors at the species level, but they did not help in resolving the phylogeny of the supra-species taxa. The smooth palmate isochelae of the genus *Euchelipluma* were not considered to be homologous to the spiny isochelae of some *Guitarra* and *Tetrapocillon* spp. and they were thus treated separately. Only discrete qualitative characters were considered. Quantitative characters (i.e. spicule size) were not relevant for clustering species, although they may be of interest in distinguishing between close species. The species that do not differ on the basis of the character data-matrix are represented together (i.e. *G. indica/fimbriata*, *G. sigmatifera/antarctica*, and *Coelodischela diatomorpha/massa*). This does not mean that they are considered synonymous.

The maximally parsimonious or minimum length trees were searched using a heuristic method (Kluge & Farris, 1969). The probability of locating the global optimum tree rather than a local optimum was improved by the use of the branch swapping algorithm. The tree bisection-reconnection (TBR) rearrangement was used (Kitching, 1992). The bootstrap method (Felsenstein, 1985) with heuristic search was applied to obtain the degree of support of the phylogeny inferred by random sampling on 1000 bootstrap replicates.

### SPECIES DESCRIPTION

The museum material came from the Muséum National d'Histoire Naturelle, Paris (MNHN); the British Museum of Natural History, London (BMNH), Museo Nacional de Ciencias Naturales, Madrid (MNCN), Museum für Naturkunde der Humboldt Universität, Berlin (ZMB), the Oceanographic Institute of Monaco, and California Academy of Sciences (CASIZ).

**Table 1.** List of the studied species, their geographic distribution, the material examined, and the bibliographic sources consulted

Species studied	Source of information	Distribution
<i>G. fimbriata</i>	Holotype, Carter, 1874	North Atlantic
<i>G. voluta</i>	Holotype, Topsent, 1904	North Atlantic
<i>G. dendyi</i>	Holotype, Kirkpatrick, 1907	Antartic
<i>G. indica</i>	Holotype, Dendy, 1916	Indian Ocean
<i>G. antarctica</i>	Holotype, Hentschel, 1914	Antarctic
<i>G. sigmatifera</i>	Topsent, 1916	Antarctic
<i>G. bipocillifera</i>	Holotype, Brøndsted, 1924; as <i>G. fimbriata</i> Bergquist & Fromont, 1988	Indian Ocean, New Zealand
<i>G. abbotti</i>	Paratype, Lee, 1987	Pacific Ocean
<i>G. isabellae</i>	Lee, 1987	Pacific Ocean
<i>G. laplani</i>	Holotype, as <i>G. solorzanoi</i> Cristobo, 1998	North Atlantic
<i>G. flamenca</i>	Holotype, Type of <i>G. fimbriata</i> var. <i>indica</i> Lévi	South Atlantic
<i>C. diatomorpha</i>	Vacelet <i>et al.</i> , 1976	Indian Ocean
<i>C. massa</i>	Lévi & Lévi, 1983	Pacific Ocean
<i>E. pristina</i>	Topsent, 1909	North Atlantic
<i>E. arbuscula</i>	Topsent, 1928	Japan
<i>T. novaezealandiae</i>	Brøndsted, 1924; Lévi, 1963	Indian Ocean
<i>T. kurushimensis</i>	Tanita, 1961	Japan
<i>T. atlanticus</i>	van Soest, 1988	Central Atlantic
<i>T. minor</i>	Pulitzer-Finali, 1993	Indian Ocean

**Table 2.** Characters and character states used in the cladistic analysis

Characters	Character states
1. Shape of the spiny isochelae	(a) absent; (b) sigmoid; (c) bipocillum-like; (d) palmate; (e) spoon-like.
2. Sigmoid spicules	(a) absent; (b) sigmancistres; (c) sigmancistres/sigmas; (d) sigmas; (e) sigmas in several sizes.
3. Smooth isochelae	(a) absent; (b) present.
4. Exotyles	(a) present; (b) absent.
5. Growth habit	(a) encrusting/massive; (b) erect; (c) pinnate.
6. Megasclere shape	(a) diactines; (b) monactines.
7. Placocheloid spicules	(a) absent; (b) placochela; (c) placochela/biplacochela; (d) dischela; (e) tetraplacochela.
8. Tetraplacochelae categories	(a) absent; (b) one category; (c) two categories.
9. Sketal arrangement	(a) well defined tracts; (b) poorly defined tracts.
10. Ectosomal desmas	(a) absent; (b) present.
11. Tyloles	(a) absent; (b) present.
12. Ectosomal crust	(a) absent; (b) present.
13. Fistulous habit	(a) absent; (b) present.
14. Megasclere types	(a) 1 type; (b) 2 types; (c) 3 types.

The holotypes or syntypes of the species *Guitarra fimbriata* Carter, 1874, *G. indica* Dendy, 1916, *G. antarctica* Hentschel, 1914, *G. abbotti* Lee, 1987, *G. laplani* Boury-Esnault, Pansini & Uriz, 1993, *Guitarra solorzanoi* Cristobo, 1998, *G. flamenca* Carballo & Uriz, 1998, *Euchelipluma congeri* Laubenfels, 1936, and *Hoplakithara dendyi* Kirkpatrick, 1907, and the only extant specimen of *G. bipocillifera* Brøndsted, 1924 were examined and their microscleres were observed

with a Scanning Electron Microscope (SEM). The original descriptions of the species *Guitarra isabellae* Lee 1987, *G. sigmatifera* Topsent 1916, *Euchelipluma pristina* Topsent 1909, *E. arbuscula* (Topsent, 1928), *Coelodischela diatomorpha* Vacelet, Vasseur & Lévi, 1976, *C. massa* Lévi & Lévi, 1983, *Tetrapocillon novaezealandiae* Brøndsted, 1924, *T. kurushimensis* Tanita 1961, *T. atlanticus* van Soest, 1988, and *T. minor* Pulitzer-Finali, 1993 were consulted. Spicules were

**Table 3.** Taxon/character data matrix used to assess the phylogenetic relationships of the species studied. Character codes and their respective states are listed in Table 2. *G. fimbriata* and *G. indica*, *G. sigmatifera* and *G. antarctica*, and *C. diatomorpha* and *C. massa* are represented together because they display the same states for the characters of the data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>G. indica/fimbriata</i>	b	a	a	a	a	a	b	a	a	a	a	a	a	a
<i>G. voluta</i>	a	a	a	a	a	b	b	a	a	a	a	a	a	a
<i>G. dendyi</i>	a	d	a	b	a	a	b	a	a	a	a	a	a	b
<i>G. sigmatifera/antarctica</i>	a	d	a	a	a	a	b	a	a	a	a	a	a	a
<i>G. bipocillifera</i>	e	a	a	a	a	a	b	a	a	a	a	a	a	a
<i>G. isabellae</i>	a	d	a	a	a	a	c	a	a	a	a	a	a	a
<i>G. abbotti</i>	c	a	a	a	a	b	c	a	a	a	a	a	a	a
<i>G. laplani</i>	d	a	a	a	a	b	b	a	a	a	a	a	a	a
<i>G. flamenca</i>	c	a	a	a	a	b	b	a	a	a	a	a	a	a
<i>C. diatomorpha/massa</i>		e	a	a	a	a	d	a	b	a	b	b	b	b
<i>E. pristina</i>	a	b	b	a	c	b	b	a	a	a	a	a	a	c
<i>E. arbuscula</i>	a	c	b	a	c	b	b	a	a	b	a	b	a	c
<i>T. novaezealandiae</i>	c	a	a	a	a	b	e	c	a	a	a	a	a	a
<i>T. kurushimensis</i>	a	a	a	a	a	b	e	b	b	a	a	a	a	a
<i>T. atlanticus</i>	c	a	a	a	a	a	e	c	b	a	a	a	a	a
<i>T. minor</i>	?	a	a	a	a	a	e	b	b	a	a	a	a	a
<i>I. palmata</i>	a	a	b	a	b	a	a	a	a	a	a	a	a	a
<i>E. fucorum</i>	a	a	b	a	b	b	a	a	a	a	a	a	a	a

observed with an SEM (PHILIPS XL-20) at the University of Sevilla; they were cleaned, dehydrated, and gold-coated following Rützler (1978) and Vacelet *et al.* (1989). Spicule measurements in the descriptions came from examination of the holotypes when available. Otherwise, they were obtained from the literature, in which case the sources are mentioned. The numbers between parentheses in the species descriptions correspond to average values of spicule measurements.

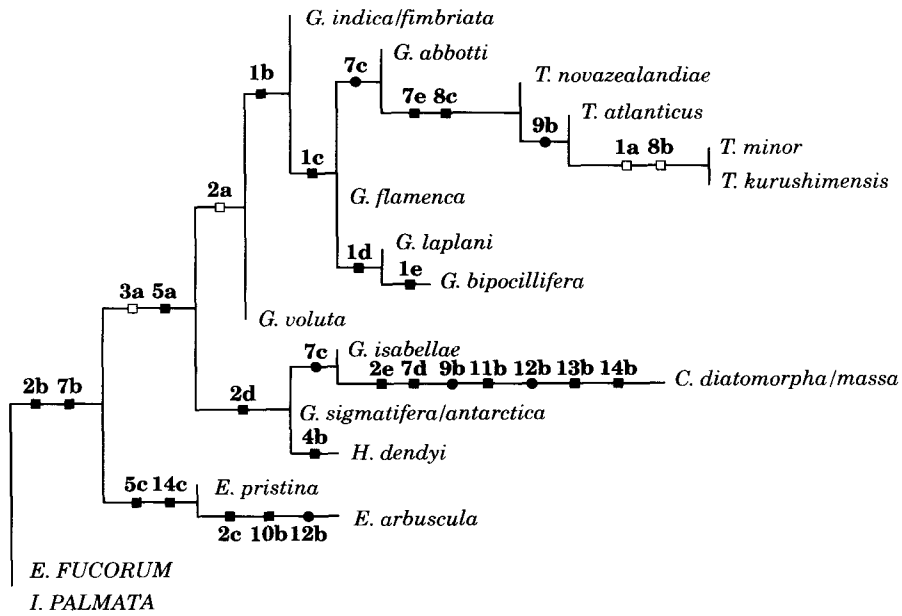
## RESULTS

Cladistic analysis using PAUP produced two equally parsimonious trees of 33 steps (CI=0.758) (Fig. 1). Strict, Semistrict and 50% Majority Rule consensus trees displayed the same topology. Resolution was rather high in these trees (Fig. 2). The ingroup was divided into two monophyletic groups. The first consisted of the two species of the genus *Euchelipluma*, which have the presence of smooth isochelae and the pinnate/branching growth habit as apomorphies. The second group comprised all the species of *Guitarra*, *Hoplakithara*, *Coelodischela*, and *Tetrapocillon*. Within this second group, a trichotomy formed by two subgroups and a monospecific clade (*G. voluta*) was depicted. The first subgroup included the three species of *Guitarra* without spiny isochelae and with sigmas (*isabellae/sigmatifera/indica*), besides the only representative of the genus *Hoplakithara*, and the two

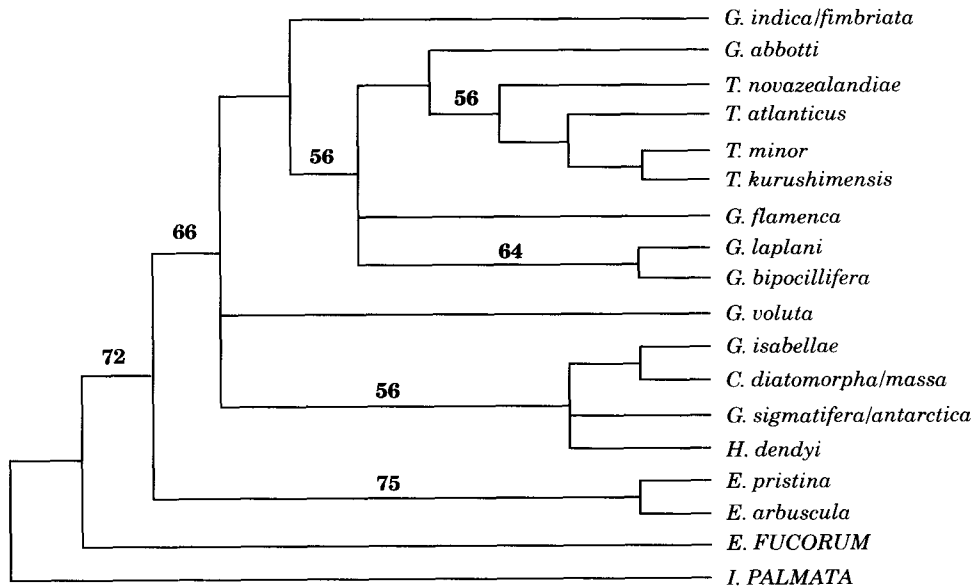
species of *Coelodischela*. The second subgroup comprised all the species with spiny isochelae, which included some representatives of *Guitarra* and the three species of the genus *Tetrapocillon* (characterized by the presence of tetraplacochelae and spiny isochelae with a bipocillum-like shape). Among the second subgroup, the species with spiny isochelae of the sigmoid type (*G. indica* and *G. fimbriata*) appeared separated from those with other types of spiny isochelae. This last clade was divided into two subgroups plus a monospecific clade, that of the species with the spines of the isochelae arranged in a row along the spicule border (*G. laplani/bipocillifera*), that comprising the three known species of the genus *Tetrapocillon* plus *G. abbotti* (all of them with bipocillum-like isochelae), and the clade formed by *G. flamenca*. The position of this last species appeared unresolved in the trees although it seems to be related to some extent to the genus *Tetrapocillon* and to *G. abbotti* due to the presence of the bipocillum-like spiny isochelae.

The phylogram representing solution 2 has been chosen to illustrate homologous (apomorphic and synapomorphic) and homoplastic (reversal or parallelism) characters (Fig. 1). The disappearance of characters is also shown. Apomorphies are more abundant at the base of the branches than on the branches leading directly to species. Homoplastic characters are more frequent in these upper branches.

The bootstrap 50% majority-rule consensus tree



**Figure 1.** Most parsimonious solution of the cladistic analysis depicting the relationships of the studied taxa. Character changes are indicated on tree number 2. Open boxes indicate definitive disappearance of characters, black boxes indicate synapomorphies and apomorphies, black circles indicate homoplasies (assumed parallel developments and/or reversals). Numbers and letters refer to characters and character states listed in Table 2.



**Figure 2.** Strict consensus tree (Semistrict consensus and Majority Rule trees display the same topology). Percentages of 1000 bootstrap replicates supporting a branching pattern are given above the corresponding branches.

(1000 replicates) supported the groups previously detected monophyletic (Fig. 2), although no group was supported at the 95% level (Felsenstein, 1985). A common linkage for the ingroup was found in 72% of instances. The genus *Euchelipluma* appeared as monophyletic in 75% of instances while the group containing

the genus *Guitarra* did so in 66%. The monophyly of the species with sigmoid microscleres and without spiny isochelae (*G. isabellae*/*sigmatifera/antarctica/dendyi* and *Coelodischela* spp.) received 56% support, similar to that of the group of species with spiny isochelae. Within the latter, the group *laplani*/

*bipocillifera* was monophyletic in 64% of instances while the genus *Tetrapocillon* was in 56%.

Characters 3, 4, 8, 10, 13 and 14, proved to be the most consistent (CI=1), with characters 1, 2 and 7 rather less consistent (CI=0.7); characters 5 and 9 had a CI=0.5. Characters 4 (presence of exotytes), 10 (ectosomal desmas), 11 (presence of tylotes), 12 (ectosomal crust), and 13 (fistulous habit) characterized terminal taxa and thus do not contain phylogenetic information.

### SPECIES DESCRIPTIONS

According to the results of our cladistic analysis, all the species bearing placochelae or derived forms should be allocated to Guitarridae. Within this family, the genera *Euchelipluma*, *Coelodischela*, *Tetrapocillon* and *Guitarra* are provisionally maintained, although the genus *Guitarra* appears to be paraphyletic. The single species of the genus *Hoplakithara* clearly belongs to the *Guitarra* (*sigmatifera*) group and, thus, *Hoplakithara* becomes synonymous of *Guitarra*.

#### ORDER POECILOSCLERIDA

##### FAMILY GUITARRIDAE DENDY, 1924 AS GUITARREAE

*New diagnosis* (no diagnosis of this family was provided by Dendy, 1924).

Poecilosclerid with placochelae or placochelae-derived microscleres (biplacochelae or tetraplacochelae) often together with smooth or spiny isochelae or sigmoid microscleres. Megascleres are monactine or diactine spicules with all the possible intermediate forms (oxeas, strongyloxeas, tornostromyloxeas, styles, strongyles, and subtylostyles). In some cases, exotytes are present.

Five nominal genera are included in this family: *Guitarra* Carter, 1874, *Tetrapocillon* Brøndsted, 1924, *Coelodischela* Vacelet, Vasseur & Lévi, 1976, *Hoplakithara* Kirkpatrick, 1907, and *Euchelipluma* Topsent, 1909.

#### GENUS GUITARRA CARTER, 1874

*Diagnosis.* Guitarridae in which the choanosomal skeleton consists of a reticulation of oxeas, tornostromyloxeas or styles of one size category forming more or less well-defined tracts. Brushes of megascleres are present at the sponge surface. The characteristic microscleres are placochelae, sometimes together with biplacochelae, which may be accompanied by spiny isochelae and sigmas. Exotytes may also be present. Aquiferous orifices clustered in papillae-like areas (slightly modified from Carballo & Uriz, 1998).

Type species: *G. fimbriata* Carter, 1874 by monotypy.

#### GUITARRA FIMBRIATA CARTER, 1874

*Material examined.* Holotype: BMNH 1882.2.7.28.109 (consisting of some slides, and four SEM preparations).

*Diagnosis.* *Guitarra* with oxeas as megascleres. Placochelae progressively narrower from the end towards the waist, with a broad central diamond-shaped pelucid area and a continuously fringed border. Spiny isochelae of a sigmoid type.

*Spicules* (Figs 4, 7, 8). Oxeas, sometimes fusiform, finely pointed, nearly straight, 250–(369.6)–450 µm × 1.3–(3.9)–5 µm. Placochelae in one size-class, although with a wide range of sizes, 41–98 × 4.5–10 µm. Spiny isochelae of a sigmoid type, 10–12 µm in length, with very reduced alae and stout spines clustered in clumps.

*Distribution.* Atlantic Ocean (off the NW coast of the British Isles), deep sea (Carter, 1874).

*Remarks.* Only one size-category of placochelae has been detected in the size-frequency distribution of the 38 spicules measured on the slides of the holotype. Burton (1929), after re-examination of the holotype, described two size-categories of 40–100 µm and 10–23 µm, respectively. The low number of spicules

#### Key to genera

- |    |  |   |
|----|--|---|
| 1. | With typical placochelae .....                                       | 3   |
|    | With placochela-like spicules (dischelae and tetraplacochelae) ..... | 2   |
| 2. | With tetraplacochelae .....  | <i>Tetrapocillon</i>                        |
|    | With dischelae .....   | <i>Coelodischela</i>                        |
| 3. | With smooth palmate isochelae .....                                  | <i>Euchelipluma</i>                         |
|    | – Without smooth palmate isochelae .....                             | 3   |
| 3. | – Without spiny isochelae .....                                      | 4   |
|    | – With spiny isochelae, without sigmas .....                         | <i>Guitarra</i> (typus <i>fimbriata</i> )   |
| 4. | – With sigmas .....  | <i>Guitarra</i> (typus <i>sigmatifera</i> ) |
|    | – Without sigmas .....   | <i>Guitarra</i> (typus <i>voluta</i> )      |

present on the slides of the holotype prevented confirmation of the presence of either one or two placochelae categories.

*GUITARRA INDICA* DENDY, 1916

*Material examined.* Syntypes (8 specimens). BMNH 1920.12.9.35.

*Diagnosis.* *Guitarra* with tornostrongyles as megascleres. Placochelae in two size classes, the larger ones with a marked central constriction. Pellucid area hexagonal in shape, and with a discontinuously fringed border (as in *G. flamenca*). Sigmoid spiny isochelae.

*Spicules* (Figs 3, 7, 8). Tornostrongyles nearly straight, sometimes transformed into strongyloxeas or with a slightly lanceolate end,  $232.8\text{--}(261.3)\text{--}300 \times 3.6\text{--}(6)\text{--}7.8 \mu\text{m}$  ( $266 \times 7 \mu\text{m}$  in Dendy, 1916). Placochelae in two size classes of similar morphology. The central constriction is abrupt in the larger placochelae while it is smooth in the smaller placochelae. Measurements:  $37.1\text{--}45.8 \times 4.9\text{--}7.8 \mu\text{m}$ , and  $28.3\text{--}34.5 \times 4\text{--}5.1 \mu\text{m}$  for the two size-categories. Spiny isochelae of the sigmoid-type (as in *G. fimbriata*) but thinner and with the alae more reduced and much more separated from each other. All these characteristics, even visible through light microscope, confer a sigmoid appearance to the isochelae.

*Distribution.* India. Beyt Island, Kattiawar, infralittoral (Dendy, 1916).

*GUITARRA ABBOTTI* LEE, 1987

*Material examined.* Paratype CASIZ 057852.

*Diagnosis.* *Guitarra* with styles. The placochelae show a slightly defined waist, a central pellucid area in a broad rhomboid-shaped and a continuously fringed border. With biplacochelae and spiny isochelae of the bipocillum-like type.

*Spicules* (Figs 5, 7, 8). Styles, most often straight (Fig. 6),  $259\text{--}(341)\text{--}379 \times 5\text{--}(7)\text{--}19$  ( $249\text{--}396 \times 5\text{--}10 \mu\text{m}$  in Lee, 1987). Placochelae two size classes of similar morphology,  $64.2\text{--}(83.3)\text{--}100.1 \mu\text{m}$  and  $26.7\text{--}(37.5)\text{--}49.7 \mu\text{m}$ , respectively. Biplacochelae  $22.8\text{--}(35.2)\text{--}45.7 \mu\text{m}$  in length. Spiny isochelae of the bipocillum-like shape with a very short stem, sometimes absent. The alae are wholly fused in the form of a hemisphere (from a lateral view). The isochelae are clearly different from those of *G. flamenca* because of the long, thin stem that separates the two cup-like ends in the latter. Length:  $2.8\text{--}(7.5)\text{--}14 \mu\text{m}$ .

*Distribution.* Pacific coast of North America (Cordell Bank, Marin County, California), and Galapagos Islands. Depth: 31–60 m, over rocks, frequently associated with *Mycale* spp.

*GUITARRA FLAMENCA* CARBALLO & URIZ, 1998

*Syn. Guitarra fimbriata* var. *indica* Lévi, 1963.

*Material examined.* Holotype MCNM (Madrid) 1.01/177; Paratype MNHN, L.B.I.M. no. CL440, as *Guitarra fimbriata* var. *indica*.

*Diagnosis.* *Guitarra* with tornostrongyles as megascleres, placochelae with a discontinuous fringed border, in two size-classes, the larger ones with a marked central constriction. The pellucid area is hexagonal. Spiny isochelae of the bipocillum-like type (from Carballo & Uriz, 1998).

*Spicules* (Figs 7, 8). Tornostrongyles frequently undulating, with one acerate end, sometimes, lanceolate extremity. Occasionally, they present a central swelling. Measurements:  $252\text{--}(312)\text{--}380 \times 6\text{--}(12)\text{--}18 \mu\text{m}$ . Placochelae in two size-classes slightly different in form. The larger ones measure  $74.4\text{--}95 \mu\text{m}$  in length, and  $16.8\text{--}22.5 \mu\text{m}$  in width at the waist; the smaller ones  $31\text{--}50 \mu\text{m}$  and  $4.2\text{--}8.75 \mu\text{m}$ . Spiny isochelae of the bipocillum-like form, with a relatively long and thin shaft and the alae fused in the form of a hemispheric cup. Spines,  $11\text{--}18.5 \mu\text{m}$  in length, clustered in clumps covering both the alae and shaft.

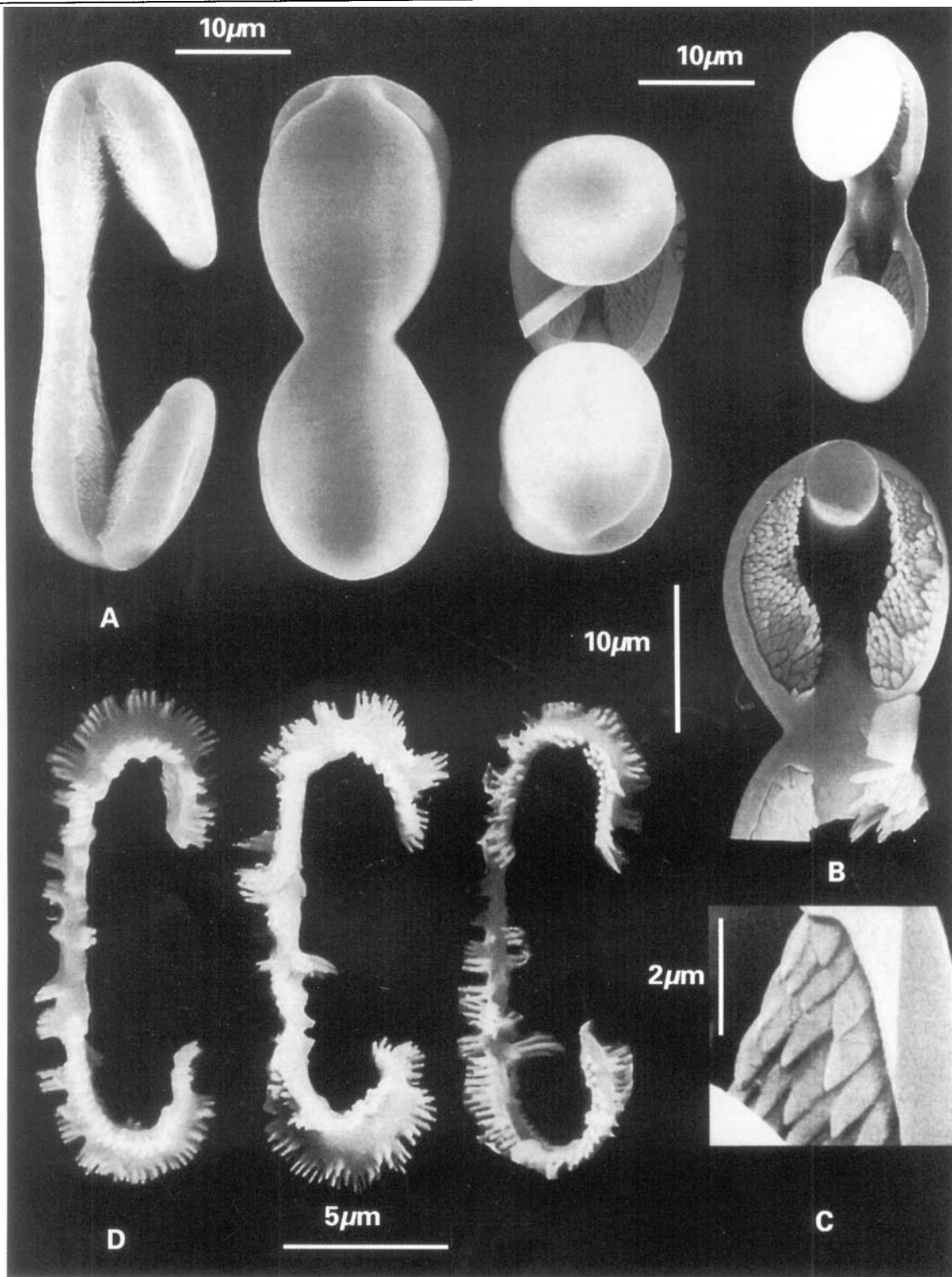
*Distribution.* South-East Atlantic Ocean, South Africa, Namibia (Shark Island, Lüderitz). In sandy and rocky bottoms, on rocks, stones, shells, and in the *Laminaria* sp. assemblage, at a depth of 5–14 m (Carballo & Uriz, 1998).

*GUITARRA LAPLANI* BOURY-ESNAULT,  
PANSINI & URIZ, 1993

*Syn. Guitarra solorzanoi* Cristobo, 1998.

*Material examined.* Holotype MNHN Paris. LBIM-NBE.MP.MU-13. *Guitarra solorzanoi* MNCN 1.01/169, holotype and paratypes.

*Diagnosis.* *Guitarra* with asymmetrical styles, and placochelae in only one size class with a slightly defined

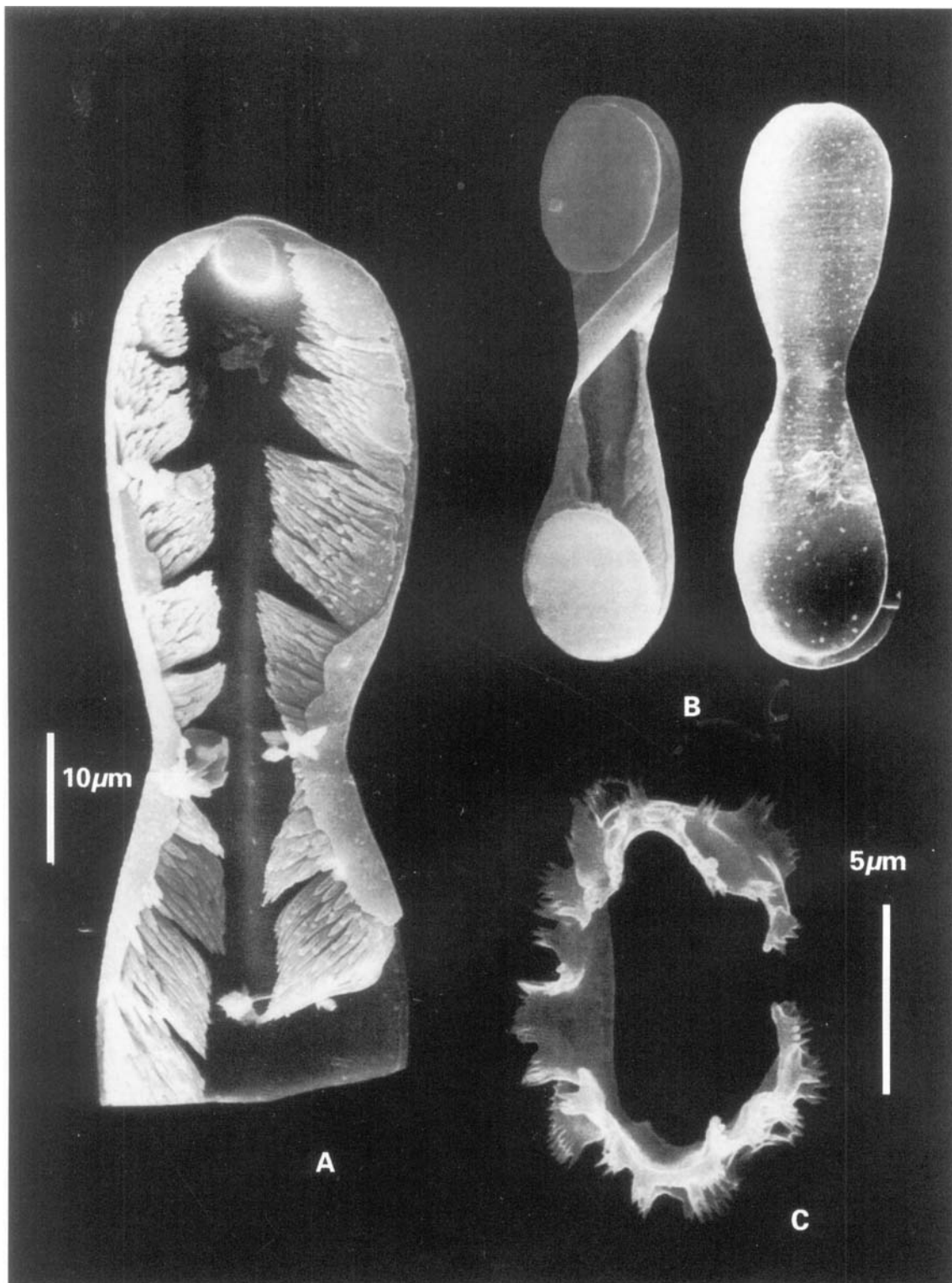


**Figure 3.** *Guitarra indica*. (A) placochelae with a marked central constriction; (B,C) details of the fringed border (discontinuous), and end plate falx of a placochelae; (D) spiny sigmoid isochelae.

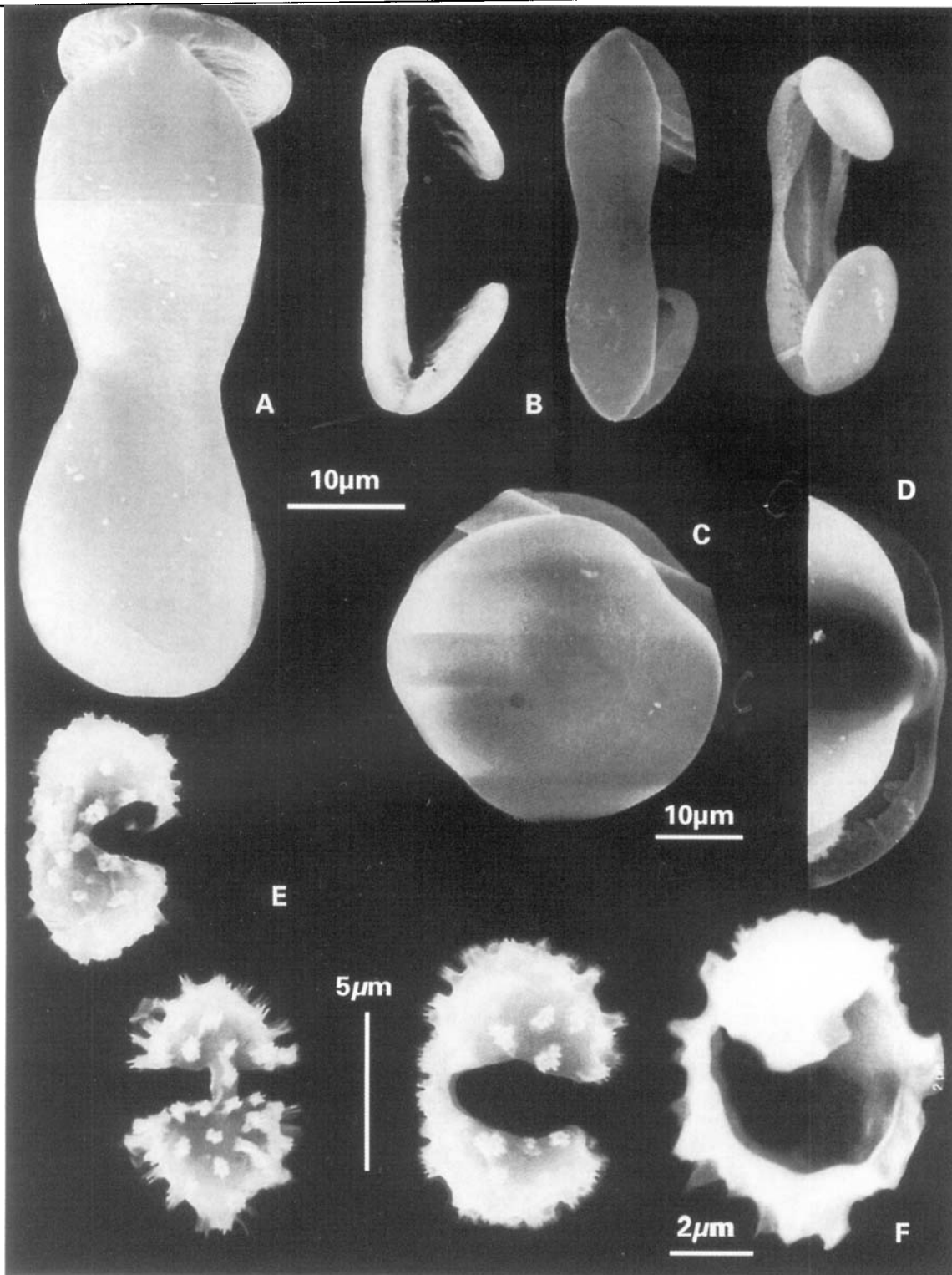
waist, the central pellucid area in a broad rhomboid shape and a continuously fringed border. Palmate spiny isochelae with the spines forming a fringe along

the spicule border, which has more or less prominent lobules, depending on the individuals. (Modified from Boury-Esnault *et al.*, 1993).

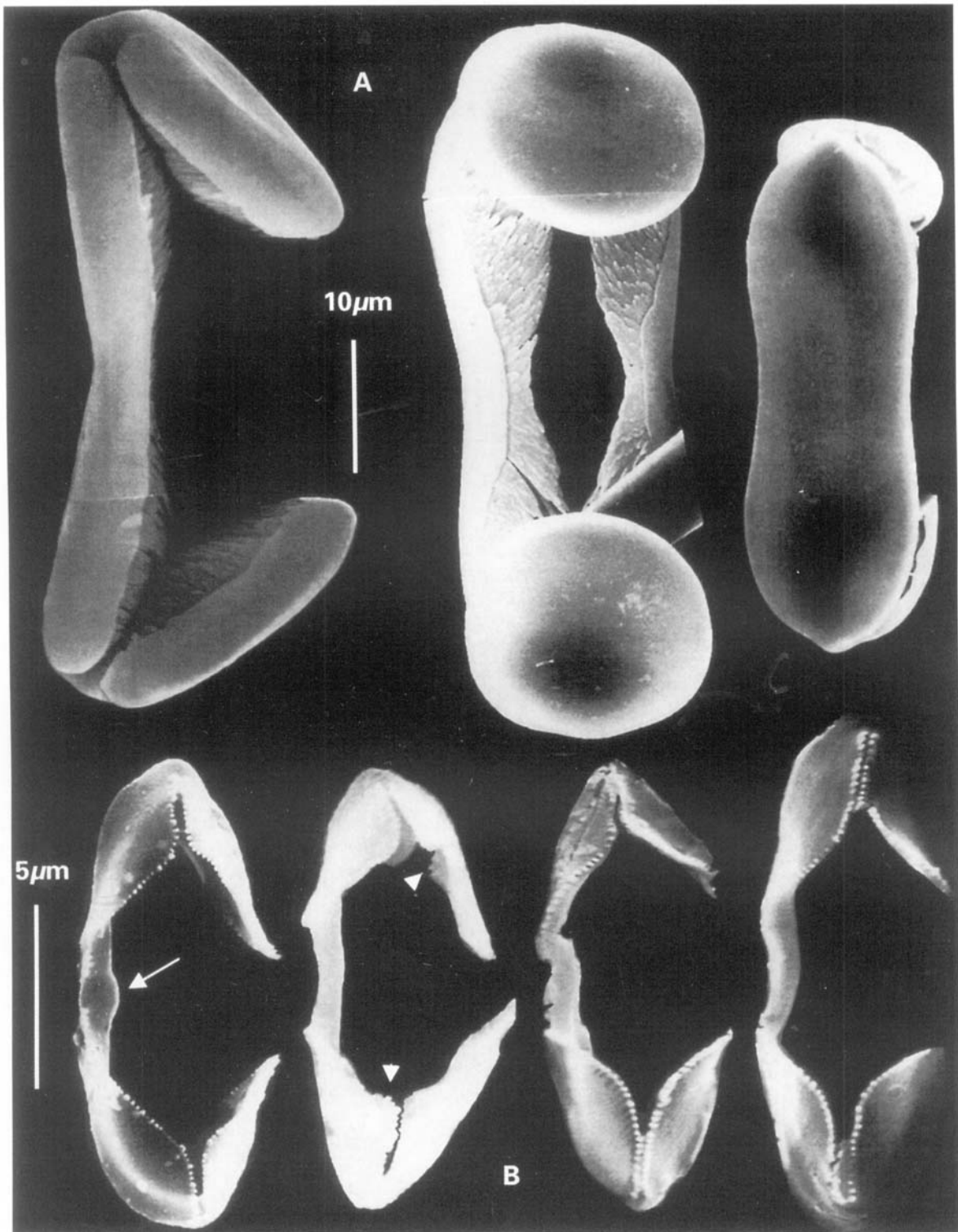




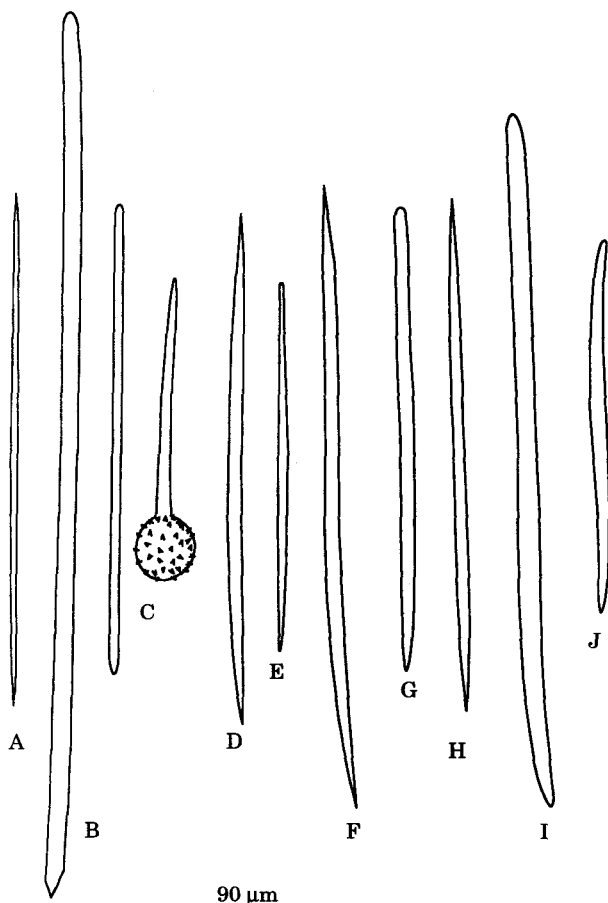
**Figure 4.** *Guitarra fimbriata*. (A,B) placochelae with a progressive narrowing from the ends towards the waist and a continuous fringed border (A,B same scale); C) spiny sigmoid isochelae.



**Figure 5.** *Guitarra abbotti*. (A) placochelae I and (B) placochelae II, both with a conspicuous waist; (C,D) biplacochelae; (E) bipocilla-type isochelae; (F) aberrant bipocilla.



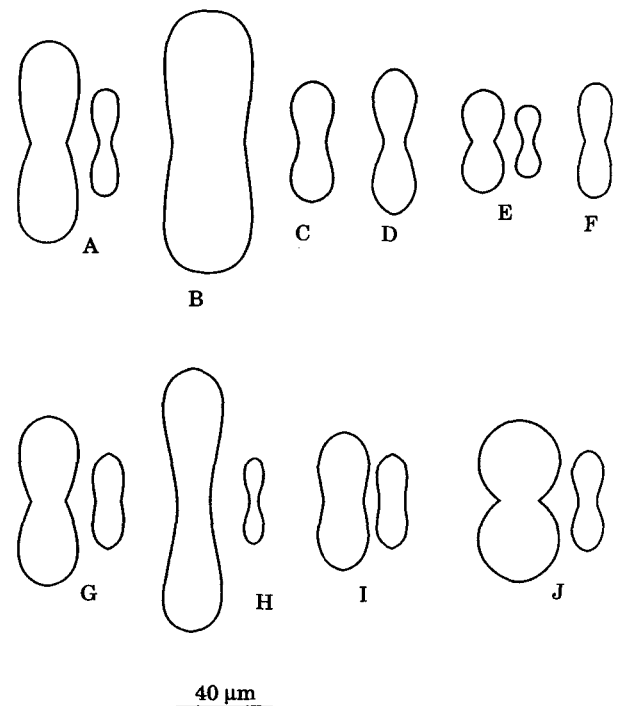
**Figure 6.** *Guitarra laplani*. (A) placocheles with a conspicuous waist and a continuous fringed border; (B) spiny palmate isochelae with an incipient central swelling (arrow) and slight lobules on the teeth (arrowheads).



**Figure 7.** Megascleres in *Guitarra* species. (A) *G. fimbriata*; (B) *G. voluta*; (C) *G. dendyi*; (D) *G. antarctica*; (E) *G. indica*; (F) *G. bipocillifera*; (G.) *G. abbotti*; (H) *G. isabellae*; (I) *G. laplani*; (J) *G. flamenca*.

**Spicules** (Figs 6–8). Styles straight or slightly flexuous, occasionally with a sub-proximal tyle, and a pointed distal end. Measurements: 400–(457)–525 × 5–(7)–11 µm. (360–515 × 2–11 µm, in Boury-Esnault *et al.*, 1993), 271–(296)–479 µm × 4.2(7.2)10.7 µm in Cristobo (1998) as *G. solorzano*. Placochelae in one size class, 40–(53.6)–65 × 13–(14)18 µm (Boury-Esnault *et al.*, 1993), 39.7–50.1 µm × 11.1–19.8 µm (Cristobo, 1998, as *G. solorzano*). Spiny isochelae palmate, with the spines in a row along the spicule border and the alae without fusing completely. They sometimes show an incipient central swelling in the shaft, and several more or less developed lobules at the alae. Measurements: 11–15 µm in length; 13.2–17.4 × 6.2–8 µm in Cristobo (1998) as *G. solorzano*.

**Distribution.** North Atlantic, Straits of Gibraltar (Ibero-Moroccan Gulf), detritic bottom with Foraminifera and Pteropoda. 478–1108 m (Boury-Esnault *et al.*,



**Figure 8.** Placochelae outlines in *Guitarra* species. (A) *G. fimbriata*; (B) *G. voluta*; (C) *G. dendyi*; (D) *G. antarctica*; (E) *G. indica*; (F) *G. bipocillifera*; (G) *G. abbotti*; (H) *G. isabellae*; (I) *G. laplani*; (J) *G. flamenca*.

1993); As Merloeiras, Galicia, NW Spain, rocky bottom, at a depth of 35–50 m (Cristobo, 1998, as *G. solorzano*).

**Remarks.** After re-examination of the respective holotypes, we did not find consistent differences between the spicules of *G. solorzano* and *G. laplani*. Shape and size of megascleres and placochelae are similar in both species. Moreover, in both species, the spiny isochelae are palmate with spines arranged in a row along the spicule border. Some isochelae of *G. solorzano* have marked lobules while other spicules (probably the young ones) only show incipient lobes like those of *G. laplani*. On the other hand, both species display similar growth habit: massive with the inhalant orifices clustered in papillae-like structures, and a close geographical distribution. These similarities indicate that both species are synonymous.

#### *GUITARRA BIPOCILLIFERA* BRØNDSTED, 1924

**Syn.** *Guitarra fimbriata sensu* Bergquist & Fromont, 1988.

**Type material.** Whereabouts unknown (not found in ZMUC).

**Diagnosis.** *Guitarra* with oxeas as megascleres, placochelae on one single size-class and spoon-shaped

spiny isochelae. The placochelae show a progressive reduction in diameter from the ends towards the waist, a continuously-fringed border, and a rhomboid central pellucid area.

*Spicules* (Figs 7, 8). Long and slender oxeas, straight or nearly so, often a little irregularly undulated, with the apices rather abruptly set off. Measurements: 350–425 × 6–10 µm according to Bergquist & Fromont (1988), who re-measured the holotype, up to 450 µm *sensu* Brøndsted (1924). Placochelae measure 40–100 µm (Brøndsted, 1924; Bergquist & Fromont, 1988). Spiny isochelae with a characteristic spoon-like shape. The spines, 10–14 µm, are arranged in a row around the alae border and are absent from the shaft (Brøndsted, 1924, Bergquist & Fromont, 1988).

*Distribution*. New Zealand, Colville Channel, sandy mud, 68 m (Brøndsted, 1924). Three Kings Is, 55–110 m and Cuvier Island 55 m (Bergquist & Fromont, 1988).

#### GUIARRA VOLUTA TOPSENT, 1904

*Material examined*. Syntypes MNHN Paris.

*Diagnosis*. *Guitarra* with styles as megascleres, and only with placochelae as microscleres. The placochelae have a poorly-defined waist, the central pellucid area in the shape of a broad rhombus and a continuously fringed border.

*Spicules* (Figs 7, 8): Styles (called 'tornostromyles' by Topsent, 1904) straight and sometimes slightly flexuous with one end rounded and the other acerate. Measurements: 690–735 × 13–15 µm (Topsent, 1904). Placochelae into two size categories. The larger ones measure 120–140 × 30 µm at the centre and 40 µm at the plates; the smaller ones measure 67–70 × 13–23 µm (Topsent, 1904).

*Distribution*. Atlantic Ocean (Azores), at a depth between 599–1165 m (Topsent, 1904).

#### GUIARRA ISABELLAE LEE, 1987

*Type material*. Holotype: BMNH 1986:5:7:1; 1986:5:7:1a. Paratypes: USNM 34060, CASIZ 061407, CASIZ 061408, CASIZ 061409.

*Diagnosis*. *Guitarra* with oxeas as megascleres, placochelae with a slightly defined waist, the central pellucid area in the shape of a broad rhombus and a continuously fringed border. With biplacochelae, and sigmas.

*Spicules* (Figs 7, 8). Oxeas (Fig. 6) measuring 224 (354, 45) 406 × 7.62 µm (Lee, 1987). Placochelae in

two size-classes of similar form to those of *G. voluta*. Measurements: (I) 72.3–(106)–122.9 µm, (II) 26.5–(45.49)–62.7 µm (Lee, 1987). Biplacochelae: 22.2–(27.33)–33.3 µm (Lee, 1987). Sigmas: 14.4–(28.47)–36.2 µm (Lee, 1987).

*Distribution*. Eastern Pacific (Tagus Cove, Albemarle Islands, Galapagos Islands), rocky bottoms, 82.3 m in depth (Lee, 1987).

#### GUIARRA SIGMATIFERA TOPSENT, 1916

*Type material*. Whereabouts unknown (not found in MNHN Paris).

*Diagnosis*. *Guitarra* with tornostromyles as megascleres, placochelae and sigmas as microscleres. The placochelae show a slightly defined waist, a broad rhomboid-shaped central pellucid area and a continuously fringed border.

*Spicules*. Tornostromyles sometimes with an enlarged mucronate tip and a subterminal swelling. Measurements: 570–680 × 15–17 µm (Topsent, 1916). Placochelae, 87–95(length) × 13–15 (waist) µm (Topsent, 1916). Sigmas of 10–11 µm in chord (Topsent, 1916).

*Distribution*. Antarctic Peninsula. Marguerite Bay, 200 m in depth (Topsent, 1916).

*Remarks*. Topsent (1916) does not draw the spicules of *G. sigmatifera*, and no later descriptions are known. The author states, however, that the placochelae stem was wide at its central part 'à tige large au centre' which is in concordance with a slightly marked central constriction. This species is only distinguishable from *G. antarctica* (Hentschel, 1914) because it possesses tornostromyles instead of oxeas and because its sigmas are smaller (10–11 µm versus 23–36 µm in *G. antarctica*). The placochelae belong in a sole size category while there are two categories in *G. antarctica*. All these slight differences allow us to maintain both species separate. However, confirmation of the validity of these two species must await the finding of new specimens.

#### GUIARRA ANTARCTICA HENTSCHEL, 1914

*Syn. Guitarra antarctica* var. *novaezealandiae* Dendy, 1924.

*Material examined*. Holotype ZMB 4788 Nr.314-14IV1902 (one fragment); Nr.1064-17XII1902 (two fragments and three slides).

*Diagnosis*. *Guitarra* with oxeas as megascleres and placochelae and sigmas as microscleres. The placochelae show a slightly defined waist, a central pellucid area in the shape of a broad rhombus and a continuously fringed border.

*Spicules* (Figs 7, 8). Oxeas straight and sometimes slightly flexuous (Fig. 5). Measurements: 408–496 × 7–11 µm. Placochelae in two size classes of 89–(100)–114 × 14–19 µm, and 41–(48)–58 × 7–10 µm. They have a slightly defined waist as in *G. laplani*. Sigmas C-shaped, 23–36 µm in length.

*Distribution*. Australian Antarctic Territories off Wilhelm II Coast, depth 380–385 m (Hentschel, 1914); New Zealand (Cape Maria van Diemen), depth 33–72 m (Dendy, 1924).

#### GUITARRA DENDYI (KIRKPATRICK, 1907)

*Syn. Hoplakithara dendyi* Kirkpatrick 1907.

*Material examined*. Holotype BMNH 1908:2:5:187 (three slides).

*Diagnosis*. Massive *Guitarra* with strongyles and exotyles ('sphaerotypes') as megascleres, and placochelae and sigmas as microscleres. Placochelae with slightly defined waist, with a central diamond-shaped pellucid area and a continuously fringed border.

*Spicules* (Figs 7, 8). Strongyles straight or, sometimes, slightly curved (Fig. 5), 400–490 × 8–12 µm. Exotyles with a microspined head, 360–392 × 5–7 µm. Placochelae in one size-class, 52–78 × 18–24 µm. Sigmas C-shaped, 8–16 µm in length.

*Distribution*. Antarctic (Kirkpatrick, 1908; Hentschel, 1914; Koltun, 1976).

*Remark*. This species is the type of the genus *Hoplakithara* Kirkpatrick. The latter based the new genus on the presence of its characteristic 'sphaerotypes'. However, the remaining spicules are typical of the genus *Guitarra*. In the cladistic analysis, this species was placed within the group of the *Guitarra* species bearing sigmas and lacking spiny isochelae.

#### GENUS EUCHELIPLUMA TOPSENT, 1909

*Syn. Desmatiderma* Topsent, 1928.

*Diagnosis*. Erect, pinnate or branched Guitarridae, with monaxon spicules as megascleres, which may present modifications at their tips in different zones of the sponge (styles, subtylostyles-tylostyles, and strongyles). Smooth palmate isochelae, sigmoid spicules and placochelae as microscleres. Monocrepidial desmas, when present, form an ectosomal crust (modified from Topsent, 1909).

*Type species*. *E. pristina* Topsent 1909 by monotypy.

*Remarks*. Three nominal species of this genus are known at present: *E. pristina* Topsent, 1909, from

the North Atlantic, *E. arbuscula* (Topsent 1928) from Japan, and *E. congeri* Laubenfels, 1936 from the Central Atlantic. After examination of the holotype of *E. congeri* (BMNH 1936:7:8:32) consisting of a sole slide, we can conclude that this species has no placochelae. Laubenfels (1936) in the description of the holotype expresses concern about the presence of true isochelae and mentions the abundance of placochelae, 13–15 µm in length, in which the fimbriations were seen "only dimly". This size corresponds to that of the abundant isochelae found in the holotype, which Laubenfels may have misinterpreted as placochelae. Furthermore, the spicules interpreted by Laubenfels as sigmancistras are true sigmas. The sponge shape is globular, instead of pinnate or branched as in the two remaining species of *Euchelipluma*. All these characters indicate that this species does not belong to the genus *Euchelipluma* but is probably an *Esperiopsis* with sigmas (as already indicated by Van Soest, 1984).

#### E. PRISTINA TOPSENT, 1909

*Type material*. Musée Océanographique de Monaco?

*Diagnosis*. *Euchelipluma* with a basal swelling from which a stalk covered with two or three series of lateral spines arises. Styles in the shaft, flexuous strongyles at the sponge base, and subtylostyles in the spines as megascleres. Palmate isochelae, placochelae, and sigmancistras in two-size categories as microscleres. The spicules of gemmules are styles, isochelae and large sigmancistras.

*Spicules* (Fig. 9G–L, from Topsent, 1909): Styles 1000 × 30 µm, straight, slightly fusiform with an short obtuse point. They are abundant at the sponge shaft and become shorter (600 × 20 µm) and bent towards the sponge base. Strongyles flexuous, 240–370 × 10–14 µm, at the sponge base. Subtylostyles straight, sometimes polytylote, 400–600 × 11 µm, with a short point, and a slightly marked terminal swelling. Smooth isochelae palmate, 80–100 µm long, with a bent, 6 µm wide shaft. Placochelae 60–73 µm long with a slightly marked waist; alae twice as long as wide. Sigmancistras in two size-categories: 12 µm and 22–24 µm long. The smaller ones are very abundant.

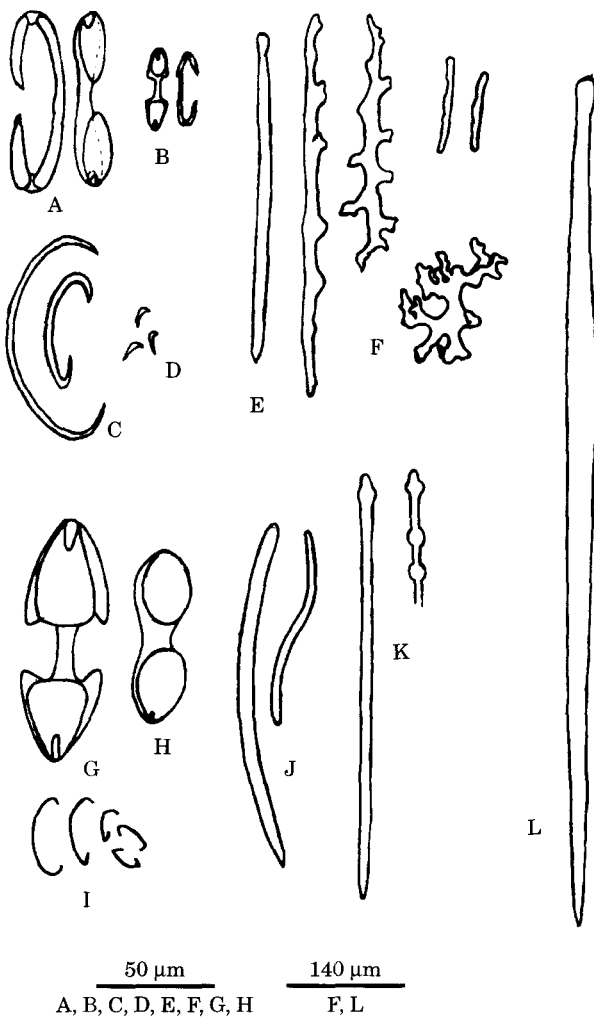
*Distribution*. North Atlantic (Cape Verde Archipelago).

#### EUCHELIPLUMA ARBUSCULA (TOPSENT, 1928)

*Syn. Desmatiderma arbuscula* Topsent, 1928.

*Type material*. Musée Océanographique, Monaco.

*Diagnosis*. *Euchelipluma* of a branching habit. Styles, strongyles and monocrepidial desmas as megascleres,



**Figure 9.** Spicules of *Euchelipluma arbuscula* (redrawn from Topsent, 1928). (A) placochelae; (B) palmate isochelae; (C) sigmas; (D) sigmancistra; (E) style to strongyle; (F) monocrepidal desmas which form a crust of variable thickness. Spicules of *Euchelipluma pristina* (redrawn from Topsent, 1909); (G) smooth palmate isochelae; (H) placochelae; (I) sigmancistra; (J–L) styles, strongyles and subtylostyles.

the latter forming an ectosomal crust. Sigmancistra and sigmas, besides smooth palmate isochelae and placochelae, as microscleres (from Topsent, 1928).

*Spicules* (Fig. 9A–F, from Topsent, 1928). Styles, variable in shape according to the sponge zone. Those from the axis are slightly bent with an almost indistinguishable swelling and an obtuse sharp point,  $413\text{--}455\ \mu\text{m} \times 15\text{--}17\ \mu\text{m}$ . Those from the terminal swellings of the branches are only  $180\ \mu\text{m}$  in length. Strongyles bent or flexuous, more or less polytylote, somewhat asymmetrical with an inflated end,

$85\text{--}140\ \mu\text{m} \times 5.5\text{--}12.5\ \mu\text{m}$ . They proliferate in the terminal swellings of branches, and rarely in the sponge axis. Desmas monocrepidal,  $480\text{--}560\ \mu\text{m}$  in length and up to  $20\ \mu\text{m}$  in thickness, with simple tubercles ( $10\text{--}40\ \mu\text{m}$  in length). They are modified styles, which form a crust of variable thickness at the sponge base and along the main branches. Palmate isochelae,  $24\text{--}28\ \mu\text{m}$  in length. Placochelae  $52\text{--}58\ \mu\text{m}$  in length,  $9\ \mu\text{m}$  wide at the plates, and  $5\ \mu\text{m}$  wide in the waist, with continuously fringed border. Sigmas  $50\text{--}65\ \mu\text{m} \times 1\text{--}1.8\ \mu\text{m}$  in chord. Sigmancistra  $7\text{--}7.5\ \mu\text{m}$  in length.

*Distribution.* Japan (Bay of Sagami).

GENUS *COELODISCHELAE* VACELET,  
VASSEUR & LÉVI, 1976

*Diagnosis.* Encrusting to massive sponges provided with open fistules. Strongyles and tylotes placed tangentially at the ectosome and forming strong reticulate tracks in the choanosome, as megascleres. Dischelae and sigmas as microscleres (modified from Vacelet *et al.*, 1976).

*Type species.* *Coelodischela diatomorpha* Vacelet, Vasseur & Lévi, by monotypy.

Two species of this genus have been recorded to date: *C. diatomorpha* from Madagascar and *C. massa* Lévi & Lévi 1983 from New Caledonia, which only differ in their growth habit and spicule dimensions.

GENUS *TETRAPOCILLON* BRØNDSTED, 1924

*Diagnosis.* Encrusting to massive Guitarridae with diactines (strongyles) or monactines (styles) as megascleres and tetrapocilla (tetraplacochelae) as microscleres. Spiny isochelae (of the bipocillum-like type) are often present (modified from van Soest, 1988).

*Type species.* *T. novaezealandiae* by monotypy.

Four species of this genus have been recorded to date: (1) *T. novaezealandiae* Brøndsted with styles/subtylostyles and without an ectosomal skeleton, from New Zealand (Brøndsted, 1924) and South Africa (Lévi, 1963). (2) *T. kurushimensis* Tanita with styles and tetraplacochelae, from Japan (Tanita, 1961). (3) *T. atlanticus* van Soest, with strongyles and clusters of tangential megascleres, from the Cape Verde Islands (van Soest, 1988). (4) *T. minor* Pulitzer-Finali, with asymmetrical oxeads, and tetraplacochelae (spiny isochelae were not mentioned in the original description) from East Africa (Pulitzer-Finali, 1993).

## OUTGROUP

*ESPERIOPSIS* CARTER, 1882

*Diagnosis.* Mycalidae with choanosomal skeleton consisting of plumose or plumo-reticulate tracts of styles or subtylostyles. Styles may be also scattered interstitially, and spongin fibre development may occur in some species. The ectosomal skeleton, if present, consists of the same spicules that constitute the choanosomal skeleton. Microscleres are palmate isochelae, which may be accompanied by sigmas, toxas, and raphides (*sensu* Bergquist & Fromont, 1988).

*Type species.* *Esperia villosa* Carter, 1874.

*ESPERIOPSIS FUCORUM* (ESPER, 1794)

*Diagnosis.* Encrusting Esperipsidae, which project narrow, long digitations that can divide and anastomose. Surface irregularly hispid. The ectosome is conspicuous. The megascleres, consisting of smooth styles slightly bent, form irregularly reticulate tracts. Microscleres: palmate isochelae (from Uriz, 1983).

*Distribution.* Atlantic, Indian, Pacific, and Antarctic Oceans; Mediterranean Sea.

*ISODICTYA* BOWERBANK, 1864

*Diagnosis.* Sponges with a reticulate or plumo-reticulate skeleton. The diactinal megascleres are uniform in size and the microscleres are palmate isochelae (from Bergquist & Fromont, 1988).

*Type species.* *Isodictya palmata* (Lamarck 1814) by subsequent designation.

This genus had been placed in Desmacididae together with *Desmacidon* and *Esperiopsis* (e.g. Lévi, 1973). However, *Esperiopsis* has been later moved to Mycalidae (e.g. Bergquist & Fromont, 1988) and the family allocation of *Isodictya* remains uncertain.

*ISODICTYA PALMATA* (LAMARCK, 1814)

*Diagnosis.* Sessile or slightly pedicelled, flabellate or digitate, compressed sponges. Surface even. Megascleres stout and rather short oxeas. Ectosome with oxeas irregularly dispersed. Choanosomal skeleton consisting of multispiculate reticulate tracts. Microscleres: palmate isochelae (modified from Bowerbank, 1866).

*Distribution.* North Atlantic.

## DISCUSSION

The genera *Guitarra*, *Tetrapocillon*, *Euchelipluma*, and *Hoplakithara* have been traditionally placed within

Family Desmaceriidae (e.g. Bergquist & Fromont, 1988; Boury-Esnault *et al.*, 1993) on the basis of a common spicule arrangement in irregularly reticulate tracts. This skeleton arrangement, however, is not present in the genus *Euchelipluma* (with ascending spicule bundles) or in *Tetrapocillon atlanticus* (with an hymedesmioid skeleton). Our cladistic analysis supports the views of van Soest (1988) and Hadju (1995) that all the genera bearing placochela or placochela-like spicules should be allocated to a family different from Desmaceriidae. The placochelae, biplacochelae, dischelae, and tetraplacochelae (hitherto called 'tetrapocilli'), absent from Desmaceriidae, are the typical spicules characterizing this family. Dendy (1924), followed by Burton (1929) placed the genus *Guitarra* within a section of Desmaceriidae called Guitarraeae. However, no diagnosis of this section was supplied by either of these two authors. Later, Hadju (1995) indicated that the family name Guitarridae was available to include the genera with placochelae but, again, he did not supply a family diagnosis.

The genus *Euchelipluma* is well characterized by the presence of smooth isochelae and its particular growth habit. Conversely, the only known species of *Hoplakithara* appeared in the phylogenetic trees among the species of *Guitarra* with sigmas, from which it only differed in the presence of exotyles. The genus *Tetrapocillon*, although characterized by its tetraplacochelae spicules, is close to *Guitarra* since it appeared as a sister group of *G. abotti* in the phylogenetic trees. The cladistic analysis also showed five clades within the genus *Guitarra*. The morphology of the spiny isochelae, besides the presence of sigmancistras or sigmas, appeared to be the main characters separating these groups. The genus *Coelodischela* appeared in the trees among the group of *Guitarra* spp with sigmas and without spiny isochelae. However, it was clearly differentiated from their sister species by several autapomorphic characters, which justifies maintaining it as a separate genus. However, the allocation of this genus to Guitarridae, although supported by the cladistic analysis, should be made with some caution. When we performed the same analysis without including *Coelodischela*, the tree topology was maintained but we obtained only one most parsimonious solution of 21 steps (instead of 33) with a higher consistency index (CI = 0.857 (Fig. 9)).

The bootstrap 50% majority-rule consensus tree supports the previously detected monophyletic groups to a certain extent. The bootstrap techniques, used to establish how much 'confidence' can be ascribed to a particular branching diagram, provide the percentage of occurrences of a particular component that appears in the trees. Although Felsenstein (1985) advocates the use of a 95% threshold, the percentages obtained can be considered as a relative ranking of the degree



of support for different groups within the same tree, not true confidence limits in the statistical sense (Siebert, 1992; Hillis & Bull, 1993). Therefore, even values below 95% may correspond to true monophyletic clades.

Skeletal elements and external shape are the only characters available to describe the species studied. The advantage of this type of character is that they can be assessed for all the species considered, including preserved holotypes. However, although useful, these characters are relatively few in this group of species. Biochemical, genetic, and molecular characters can be added to those skeletal and morphological traits in the near future to produce a more robust phylogeny.

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