

Order Homosclerophorida Dendy, 1905, Family Plakinidae Schulze, 1880

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Homosclerophorida Dendy (Demospongiae, Homoscleromorpha) contains a single family Plakinidae Schulze (including Oscarellidae Lendenfeld and Corticiidae Vosmaer), with seven valid genera and about 60 valid species worldwide. Species live mainly in shallow waters but a few have been recorded from abyssal depths (up to 2460 m). Species are often encrusting, lobate, but massive species are common in some genera (*Plakortis*, *Plakinastrella*); surface is usually smooth or microhispid and consistency varies from soft to cartilaginous. All genera possess flagellated exo- and endopinacocytes, a basement membrane lining both choanoderm and pinacoderm, oval to spherical choanocyte chambers with a sylleibid-like or leuconoid organization, and a unique incubated cinctoblastula-type larvae; spicules, when present, are peculiar tetractines (calthrops) and derivatives. Genera are distinguished mainly by four morphological characters: presence of a siliceous skeleton; presence of a cortex associated with a leuconoid aquiferous system and well-developed mesohyl or a sylleibid aquiferous system with poorly developed mesohyl and ectosome; number of spicule size classes; and presence and type of ramifications in the actines of calthrops (tetractinal spicules), with three distinct general morphologies recognized.

Keywords: Homosclerophorida; Plakinidae; *Corticium*; *Oscarella*; *Placnolopha*; *Plakina*; *Plakinastrella*; *Plakortis*; *Pseudocorticium*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Order: Homosclerophorida Dendy, 1905: 64. Microsclerophora Sollas, 1887: 423 (in part).

Family: Plakinidae Schulze, 1880: 447. Corticiidae Vosmaer, 1887: 324. Oscarellidae Lendenfeld, 1887a: 582. Placnidae Topsent, 1890d: 231.

Definition

Demospongiae with flagellated exo- and endopinacocytes, a basement membrane lining both choanoderm and pinacoderm, oval to spherical choanocyte chambers with a sylleibid-like or leuconoid organization, and a unique incubated cinctoblastula type larvae; spicules, when present, are peculiar tetractines (calthrops) and derivatives through reduction (diodes and triods) or through ramification of one to all four actines (lophose calthrops).

Diagnosis

Thin to massive-encrusting Demospongiae, with few species presenting tubular growth forms (Fig. 1); surface usually smooth to the touch, but sometimes wrinkled or with highly convoluted appearance. Species are usually compressible and very dense, with thinner species tending towards a soft or cartilaginous consistency. A few encrusting species are fixed on the substrate by thin filaments only (some species of *Plakina* and *Corticium*). Skeleton, when present, is usually formed by a combination of small calthrops and/or derivatives through reduction (diodes and triods) (Fig. 2). The rays of calthrops, diodes, or triods may present multiple, sometimes complex branching, in which case the prefix 'lopho-' is used to denominate the branching forms (lophodiodes, lophotriods, and lophocalthrops). Among lophocalthrops the numbers of actines ramifying may involve one ray (monolophose calthrop, Fig. 2D), two rays (dilophose calthrop, Fig. 2E), three rays (trilophose

calthrop, Fig. 2F), or four rays (tetralophose calthrop, Fig. 2G–H). Furthermore, two types of tetralophose calthrops are distinguished, those with all rays presenting a similar branching pattern (homolophose calthrops, typical but not exclusive of *Plakina* spp; Fig. 2G) and those in which one ray's branching pattern is different from the other three (heterolophose calthrops or candelabra,

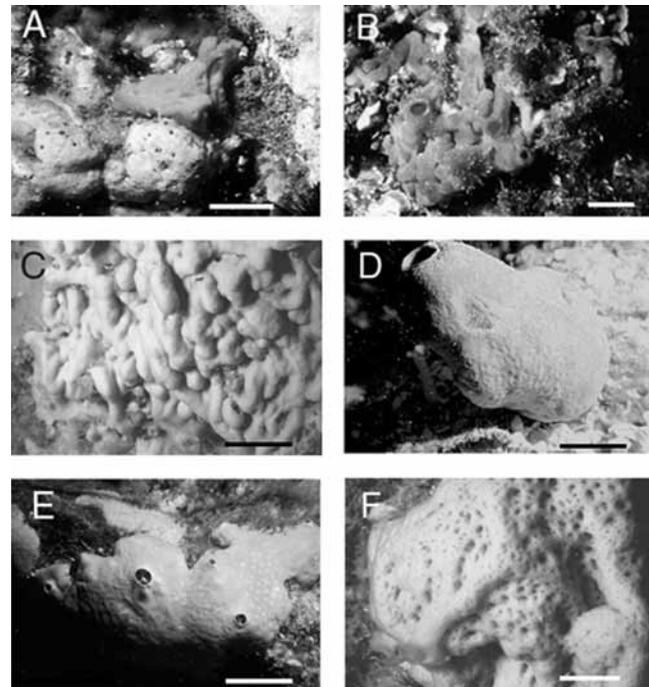


Fig. 1. External morphology of plakinids (underwater close-ups). A, *Corticium candelabrum* Schmidt (Marseille, France), specimen in top center (scale 2 cm). B, *Oscarella lobularis* (Schmidt) (Marseille, France) (scale 2 cm). C, *Plakina jani* Muricy *et al.* (Marseille, France) (scale 5 cm). D, *Plakinastrella onkodes* Uliczka (Carrie Bow Cay, Belize) (scale 5 cm). E, *Plakortis angulospiculatus* (Carter) (Carrie Bow Cay, Belize) (scale 5 cm). F, *Pseudocorticium jarrei* Boury-Esnault *et al.* (Marseille, France) (scale 2 cm).

exclusive of *Corticium* spp; Fig. 2H). The pattern of ramification of the lophose actines in lophocalthrops can be quite distinct among species, and are valuable characters for both generic and specific diagnoses. The patterns of ramification of lophose actines can be described by a simple alpha-numerical code, which takes

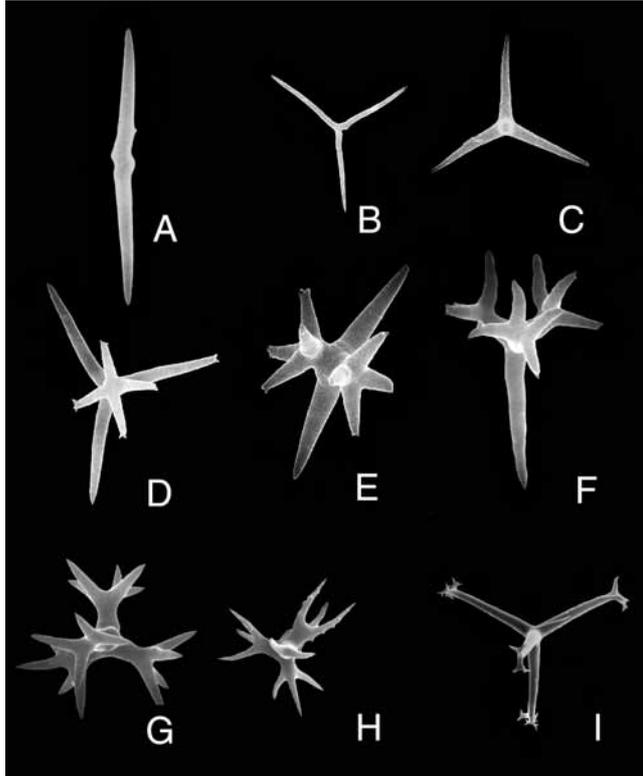


Fig. 2. Spicule types of plakinids. A–C, calthrop and derivatives. A, diod (25–750 μm long). B, triod (actines 8–300 μm long). C, calthrop (actines 8–320 μm long). D–G, homolophose calthrop (actines 7–35 μm long). D, monolophose calthrop. E, dilophose calthrop. F, trilophose calthrop. G, tetralophose calthrop. H, heterolophose calthrop (=candelabrum). I, distally lophate calthrop (*Placinolopha*) (actines 275–300 μm long).

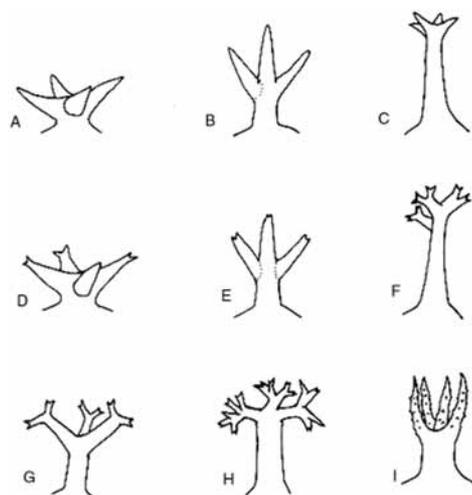


Fig. 3. Ramification patterns of actines in plakinid lophose calthrop. A, '1p' (e.g., basal actines of *Corticium candelabrum*). B, '1m' (e.g., *Plakina monolopha* and *P. trilopha*). C, '1d'. D, '1p, ts' (e.g., *Plakina endoumensis*). E, '1m, ts' (e.g., *Plakina monolopha* and *P. trilopha*). F, '1d, 2d, ts' (e.g., *Plakina crypta*). G, '1m, 2d, ts' (e.g., *Plakina janusi*). H, '1d, 2m, 3m, ts' (e.g., *Placinolopha bedoti*). I, '1p, spined' (e.g., *Corticium candelabrum*).

into account the number of rounds of ramification in lophose actines (1–3), their location along the actine ('p' for proximal, 'm' for medial, 'd' for distal), and the presence of terminal spines (ts) (Fig. 3). In this system, the ramification pattern of a spicule with only one round of ramifications close to the base of the lophose actines and bearing tiny terminal spines at their extremities is coded '1p, ts' (Fig. 3D). A spicule with one round of ramification at mid-length of the actine, a second round of ramification close to the extremity of the secondary ray, and bearing terminal spines is coded '1m, 2d, ts', and so on (Fig. 3G; Muricy *et al.*, 1998). Spicules are generally found in one size class; however in *Plakinastrella* and *Placinolopha* the spicules are present in two or more size classes. Spicules are generally arranged uniformly in the sponge body, surrounding the aquiferous system in a regular "alveolar" way or more confusedly dispersed (Fig. 4). Minute diaxial microscleres (*Plakortis*), and small lophocalthrops (*Corticium*, *Plakina*), may be found either dispersed on the sponge body, or concentrated at the surface. The aquiferous system is either sylleibid-like (eurypylous chambers uniformly arranged around large, parallel, descending inhalant and exhalant canals) or leuconoid (mostly diplodal or

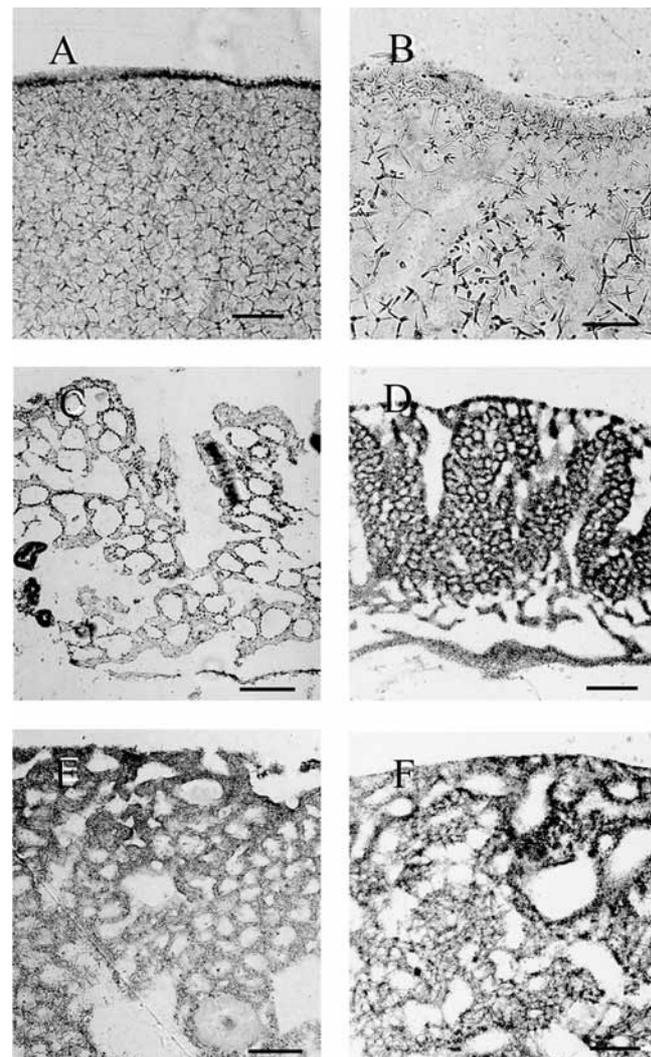


Fig. 4. Spicule arrangement in plakinids (photomicrographs of cross-sections). A–B, *Corticium candelabrum* (scale A, 100 μm , B, 50 μm). C, *Plakina monolopha* (scale 100 μm). D, *P. trilopha* (scale 200 μm). E, *Plakina corticioides* (scale 100 μm). F, *Plakortis angulospiculatus* (scale 200 μm).

aphodal chambers confusedly arranged in a complicated system of small, sinuous inhalant and exhalant canals), often with a large basal exhalant cavity, and sometimes also with ectosomal inhalant cavities (Figs 4, 5). Choanocyte chambers, 30–90 μm diameter, are usually eurypylous in *Plakortis*, *Plakinastrella*, *Plakina*, and *Oscarella*, but are aphodal or diplodal in *Corticium* and *Pseudocorticium*. A basement membrane underlines the choanoderm and pinacoderm in genera that have been studied histologically (*Corticium*, *Oscarella*, *Plakina*, and *Pseudocorticium*). Both exo- and endopinacocytes are flagellated (Fig. 6A). Cytological traits such as apopylar cell morphology and type of cell inclusions may be important generic and specific diagnostic characters of aspiculate plakinids (Fig. 6B–F). Larvae are incubated, of a unique cinctoblastula type, which is a hollow, ovoid larvae, with a single external layer of flagellated cells and an equatorial belt of distinctly pigmented cells (Fig. 7; see also Boury-Esnault & Rützler, 1997).

Remarks

A generic classification of the Plakinidae is centered around four principal diagnostic features: presence/absence of siliceous skeleton; presence/absence of a cortex associated with the architecture of the aquiferous system and type of choanocyte chambers; number of spicule size classes; and presence and type of ramifications in the actines of calthrops, with at least three distinct general morphologies recognized: small homolophose calthrops (*Plakina*, Fig. 2D–G); large lophodioids, lophotrioids and lophocalthrops

(*Placinolopha*, Fig. 2I); and small heterolophose calthrops (*Corticium*, Fig. 2H).

Scope

The order Homosclerophorida (=Microsclerophora Sollas, 1887) was created with three families, Plakinidae, Corticidae, and Thrombidae (Sollas, 1888; Dendy, 1905), of which only Plakinidae still remains. Until recently two families Plakinidae and Oscarellidae were recognized, but they were eventually merged under Plakinidae and the order is currently monofamilial (Solé-Cava *et al.*, 1992; Diaz & Van Soest, 1994; Boury-Esnault *et al.*, 1995; Muricy *et al.*, 1996a; Muricy, 1999). Placinidae Topsent, 1890d is a misspelling of Plakinidae.

Over twelve nominal genera have been included in this family, but only seven are considered to be valid and now included: *Plakortis* Schulze, 1880, *Plakinastrella* Schulze, 1880, *Plakina* Schulze, 1880, *Placinolopha* Topsent, 1897a, *Corticium* Schmidt, 1862, *Oscarella* Vosmaer, 1887 and *Pseudocorticium* Boury-Esnault *et al.*, 1995. The two *incertae sedis* genera, *Corticellopsis* and *Astroplakina*, are excluded based on the clear astrophorid

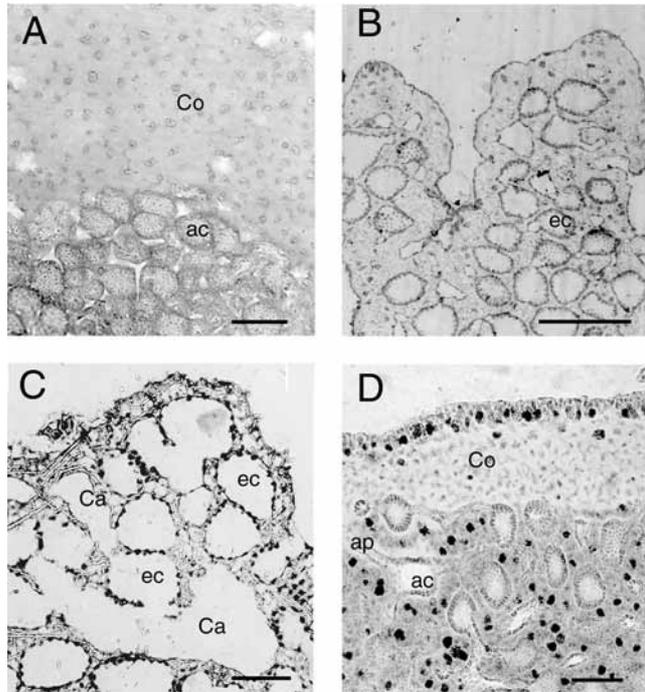


Fig. 5. Aquiferous system of plakinids (photomicrographs of cross-sections). A, *Corticium candelabrum*: micrograph showing the thick cortex (Co) in the upper portion of the photograph, and a leuconoid system with aphodal chambers (ac) towards the lower portion (scale 50 μm). B, *Oscarella lobularis*: micrograph showing a sylleibid aquiferous system with eurypylous chambers (ec) (scale 100 μm). C, *Plakina monolopha*: micrograph showing a sylleibid aquiferous system with eurypylous chambers (ec), and canals (Ca) (scale 100 μm); D, *Pseudocorticium jarrei*: micrograph showing the cortex (Co) in the upper portion of the photograph, and a leuconoid system with aphodal chambers (ac) towards the lower portion; aphodus (ap) can be seen leaving some choanocyte chambers (scale 50 μm).

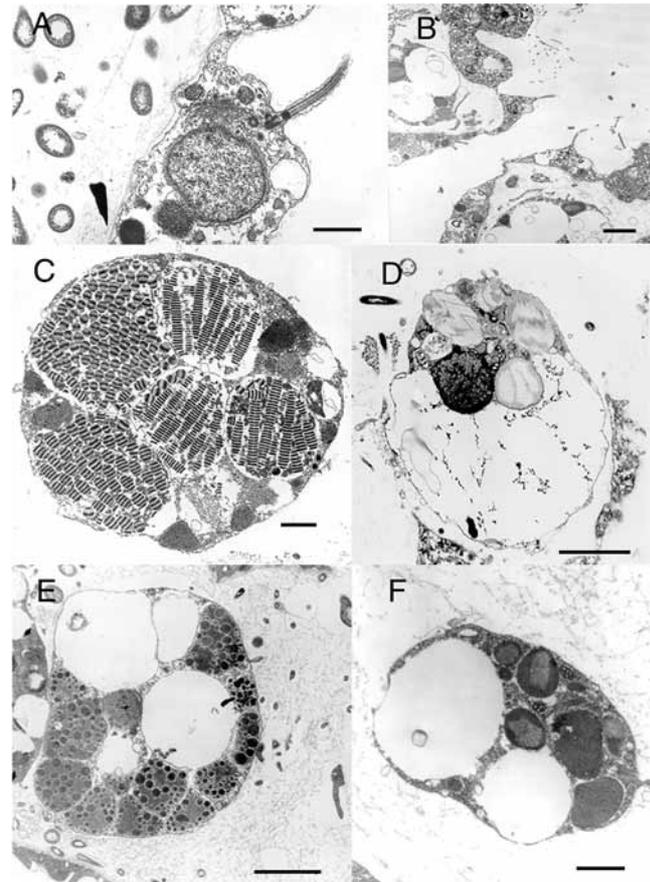


Fig. 6. Some cell types of plakinids. A, flagellated pinacocyte of *Plakina jani* (scale 1 μm). B, apopylar cells of *Oscarella imperialis*, leading towards an excurrent canal (scale 2 μm). C–F, cells with inclusions that characterise genera or species among aspiculate plakinids. C, cells with paracrystalline inclusions, cell type I, of *Pseudocorticium jarrei* (scale 2 μm). D, 'crescent-shaped' cell with inclusions, cell with inclusions type I of *Oscarella viridis* (scale 2 μm). E, spherulous cell with granular inclusions, cell type II of *Oscarella microlobata* (scale 2 μm). F, vacuolar cell with paracrystalline inclusions, cell with inclusions type I of *Oscarella imperialis* (scale 1 μm) (from Boury-Esnault *et al.*, 1995, Muricy *et al.*, 1996a).

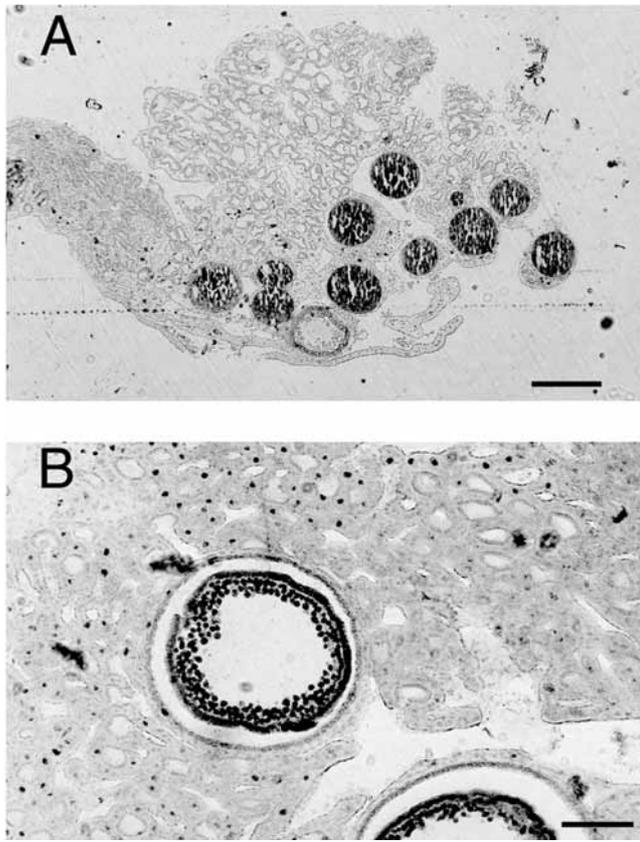


Fig. 7. Embryos and larvae of plakinids. A, *Oscarella lobularis* embryos and larvae in different stages of development (scale 200 μm). B, *Pseudocorticium jarrei* (scale 50 μm).

nature of their spiculation. Until further studies clarify the supra-generic relationships among homosclerophorid genera, we must consider both skeletal and non-skeletal genera as belonging to the former family Plakinidae Schulze (1880). Approximately 70 species of sponges from these genera have been published worldwide but only 60 are considered valid (Table 1). The number of species described in the literature is clearly geographically biased towards areas that have been better studied such as the Mediterranean, the West Pacific and the Caribbean. It is expected that when the least studied biogeographic regions are surveyed for this group the species numbers will increase considerably. Species of various genera such as *Oscarella*, *Plakina*, *Plakortis*, and *Corticium* with relatively simple morphologies are found in distinct biogeographic regions (e.g., *Plakortis* spp. in the Caribbean and in the West Pacific), and several species are considered cosmopolitan (e.g., *Oscarella lobularis*, *Plakortis simplex*, *Plakina monolopha*). Such disjunct populations, although morphologically similar, are expected to be reproductively isolated and to have diverged genetically enough in time to deserve a status of distinct species.

History and Biology

Schulze (1880) erected this family to include three closely related, newly described genera: *Plakina*, *Plakortis*, and *Plakinastrella*. He described the species in the family to include "Tetractinellida with isolated needles (not bound by horny substance), which consist of a series of quadriradiate, triradiate, and

biradiate forms, the triradiate and biradiate forms being derived from the quadriradiate forms by reduction of one or two rays. The biradiates occur in the form of weakly bent oxea, with an irregular, knobby-knotty, curved and in general crooked-looking center". Subsequently, Sollas (1888) grouped the Plakinidae together with Corticiidae Vosmaer and Thrombidae Sollas in the suborder Microsclerophora, order Choristida, next to the suborder Astrophora (which included Pachastrellidae, Ancorinidae, and Geodiidae). The Choristida together with the Lithistida were assigned to the subclass Tetractinellida. Topsent (1895) considered the Microsclerophora as a suborder of the order Carnosa Carter, which was separated from his order Tetractinellida on the basis of lack of large diactinal megascleres and a trend towards reduction in size of tetractinal spicules. Dendy (1905) changed the name Microsclerophora to Homosclerophora based on the common belief that the small plakinid spicules did not represent real microscleres. De Laubenfels (1936a) viewed the Carnosa Carter as composed of the families Halinidae de Laubenfels, Plakinastrellidae de Laubenfels, Chondrillidae Gray, Chondrosiidae Schulze and Dedalopeltidae de Laubenfels. This arrangement was clearly artificial, and subsequent authors abandoned the use of the name Carnosa. The family Plakinidae was maintained in the order Choristida, subclass Tetractinellida, until the introduction of reproductive characteristics into sponge systematics (Lévi, 1957b, 1973). Plakinids were then relocated in a separate subclass Homoscleromorpha, order Homosclerophorida, based on the possession of a distinct morphology combined with a unique amphiblastula-type larva which is non-homologous to the calcarean amphiblastula. The order consisted of two families, the Plakinidae which included the original Schulze's plakinid genera (*Plakina*, *Plakortis*, and *Plakinastrella*) and a few of the Corticiidae genera (*Corticium* Vosmaer, *Rachella* Sollas), and the family Oscarellidae Lendenfeld, which included sponges without any mineral or fibre skeleton (*Oscarella* Vosmaer). Until recently, comprehensive systematic sponge literature (Lévi, 1973; Bergquist, 1978; Hartman, 1982) included twelve genera in the family, which were recently reduced to six valid genera, based mostly on the study of skeletal characters (Diaz & Van Soest, 1994). Another recent modification of this sponge group was the merging of both families (Plakinidae and Oscarellidae) under the former family Plakinidae (Solé-Cava *et al.*, 1992; Boury-Esnault *et al.*, 1992b; Diaz & Van Soest, 1994). The genera recognized were: *Plakortis* Schulze, 1880 (incl. *Roosa* de Laubenfels, 1934), *Plakinastrella* Schulze, 1880 (incl. *Dercitopsis* Dendy, 1905), *Plakina* Schulze, 1880 (incl. *Plakoosa* de Laubenfels, 1936b), *Placinolopha* Topsent, 1897a (incl. *Acanthoplakina* Burton, 1959a; *Diactinolopha* Sarà, 1960b), *Corticium* Schmidt, 1862, and *Oscarella* Vosmaer, 1887 (incl. *Octavella* Tuzet & Paris, 1964). *Astroplakina* Dendy & Burton, 1926, and *Corticellopsis* Sollas, 1888 were excluded from the family, due to their possession of euasters, and placed as *incertae sedis* (Diaz & Van Soest, 1994). A new genus of sponges without skeleton, *Pseudocorticium*, with well-developed cortex, diplodal choanocyte chambers, and a leuconoid *Corticium*-like aquiferous system has been recently described from Mediterranean waters (Boury-Esnault *et al.*, 1995; Figs 1F, 5D, 6C, 7B). This discovery supported the artificiality of homosclerophorid suprageneric classification (Boury-Esnault *et al.*, 1992b; Solé-Cava *et al.*, 1992; Diaz & Van Soest, 1994), which distinguished a separate family for the skeleton-lacking genera (the Oscarellidae). *Pseudocorticium* is an aspiculate genus which presents closer affinity in both biochemical (allozymes) and histological traits with the

Table 1. Plakinid species, with the distribution of the original material described.

Species	Reference	Locality	Species	Reference	Locality
Corticium	Thomas, 1968e	India	<i>P. monolopha</i>	Schulze, 1880	NW Mediterranean
acanthastrum			<i>P. pacifica</i>	Desqueyroux-Faúndez & Van Soest, 1997	Galapagos
<i>C. bargibanti</i>	Lévi & Lévi, 1983b	New Caledonia	<i>P. reducta</i>	(Pulitzer-Finali, 1983)	NW Mediterranean
<i>C. candelabrum</i>	Schmidt, 1862	NW Mediterranean	<i>P. tetralopha</i>	(Hechtel, 1965)	Jamaica
<i>C. niger</i>	Pulitzer-Finali, 1996	New Guinea	<i>P. tetralophoides*</i>	Muricy <i>et al.</i> , 1998	Japan
<i>C. quadripartitum</i>	Topsent, 1923	Caribbean	<i>P. topsenti</i>	(Pouliquen, 1972)	NW Mediterranean
<i>C. simplex</i>	Lendenfeld, 1907	N Australia	<i>P. trilopha</i>	Schulze, 1880	NW Mediterranean
Oscarella	Muricy <i>et al.</i> , 1996a	NW Mediterranean	<i>P. versatile</i>	(Schmidt, 1879)	Gulf of Mexico
imperialis			<i>P. weinbergi</i>	Muricy <i>et al.</i> , 1998	E Mediterranean
<i>O. lobularis</i>	(Schmidt, 1862)	NW Mediterranean	Plakinastrella	(Dendy, 1905)	Sri Lanka
<i>O. microlobata</i>	Muricy <i>et al.</i> , 1996a	NW Mediterranean	ceylonica		
<i>O. tuberculata</i>	(Schmidt, 1868)	NW Mediterranean	<i>P. clathrata</i>	(Kirkpatrick, 1900b)	Funafuti
<i>O. viridis</i>	Muricy <i>et al.</i> , 1996a	NW Mediterranean	<i>P. copiosa</i>	Schulze, 1880	NW Mediterranean
Placinolopha	(Thomas, 1970)	India	<i>P. mammillaris</i>	(Lendenfeld, 1907)	W Australia
acantolopha			<i>P. mixta</i>	Maldonado, 1992	W Mediterranean
<i>P. bedotii</i>	Topsent, 1897a	Indonesia	<i>P. onkodes</i>	Uliczka, 1929	Caribbean
<i>P. europae</i>	Vacelet & Vasseur, 1971	Madagascar	<i>P. oxata</i>	Topsent, 1904b	Azores
<i>P. moncharmonti</i>	(Sarà, 1960b)	NW Mediterranean	<i>P. polysclera</i>	Lévi & Lévi, 1989	Philippines
<i>P. sarai</i>	Lévi & Lévi, 1989	Philippines	<i>P. trunculifera</i>	Topsent, 1927b	Azores
<i>P. spinosa</i>	Kirkpatrick, 1900b	Funafuti	Plakortis	(Carter, 1879b)	Caribbean
Plakina	(Sarà, 1960b)	NW Mediterranean	angulospiculatus		
bowerbanki			<i>P. copiosa</i>	Pulitzer-Finali, 1993	Kenya
<i>P. australis</i>	(Gray, 1867a)	W Australia	<i>P. erythraena</i>	Lévi, 1958	Red Sea
<i>P. brachylopha</i>	Topsent, 1928c	Azores	<i>P. galapagensis</i>	Desqueyroux-Faúndez & Van Soest, 1997	Galapagos
<i>P. corticioides</i>	Vacelet <i>et al.</i> , 1976	Madagascar	<i>P. halichondroides</i>	(Wilson, 1902)	Caribbean
<i>P. corticolopha</i>	Lévi & Lévi, 1983b	New Caledonia	<i>P. kenyensis</i>	Pulitzer-Finali, 1993	Kenya
<i>P. crypta</i>	Muricy <i>et al.</i> , 1998	NW Mediterranean	<i>P. lita</i>	de Laubenfels, 1954	Caroline Isl.
<i>P. dilopha</i>	Schulze, 1880	NW Mediterranean	<i>P. nigra</i>	Lévi, 1953b	Red Sea
<i>P. elisa</i>	(de Laubenfels, 1936b)	Caribbean	<i>P. quasiamphiaster</i>	Diaz & Van Soest, 1994	Vanuatu
<i>P. endoumensis</i>	Muricy <i>et al.</i> , 1998	NW Mediterranean	<i>P. simplex</i>	Schulze, 1880	NW Mediterranean
<i>P. fragilis</i>	Desqueyroux-Faúndez & Van Soest, 1997	Galapagos	<i>P. zygompha</i>	(de Laubenfels, 1934)	Caribbean
<i>P. jamaicensis</i>	Lehnert & Van Soest, 1998	Jamaica	Pseudocorticium	Boury-Esnault <i>et al.</i> , 1995	NW Mediterranean
<i>P. jani</i>	Muricy <i>et al.</i> , 1998	NW Mediterranean	jarrei		
<i>P. microlobata</i>	Desqueyroux-Faúndez & Van Soest, 1997	Galapagos			

* *Plakina tetralophoides* Muricy *et al.*, 1998 was first described as *P. tetralopha* by Tanita & Hoshino (1989).

Further Notes. *Plakinastrella schulzei* and *P. intermedia* are not included as they belong to the astrophorid genus *Penares*. *Dercitopsis ceylonica* and *D. minor* were assigned to *Plakinastrella* (the latter considered a junior synonym of *P. clathrata*; Diaz & Van Soest, 1994). *Placinolopha europae* was described as *P. spinosa europae* Vacelet & Vasseur, 1971; *P. mirabilis* de Laubenfels, 1954 probably belongs to *Theonella* (Theonellidae, 'Lithistida'); *Oscarella cruenta* (Carter, 1881b) *sensu* Keller (1889) is probably a *Chondrosia* (Chondrosida: Chondrillidae). *Oscarella membranacea* Hentschel, 1909 and *O. tenuis* Hentschel, 1909 are considered insufficiently described (Muricy *et al.*, 1996a). Hooper & Wiedenmayer (1994) suggested that *Achinoe australis* Gray, 1867a might belong to *Corticium*, whereas it more probably belongs to *Plakina* (see text). Species *incertae sedis* are *Astroplakina stelligera* Dendy & Burton, 1926, *Corticellopsis stelligera* Schmidt, 1862, and *Corticellopsis novaezealandiae* Bergquist, 1968 – these are not included as they are probably astrophorids.

skeletal genus, *Corticium*, than with the non-skeletal genus *Oscarella* (Solé-Cava *et al.*, 1992; Boury-Esnault *et al.*, 1995). However, *Pseudocorticium* seems closer to *Oscarella* than to *Corticium* or *Plakina* in cell composition, and the possibility remains that the aspiculate plakinids are indeed monophyletic (Muricy *et al.*, 1996a; Muricy, 1999). Histological, cytological and biochemical studies were conducted on *Oscarella*, *Corticium*, *Plakina*, and *Pseudocorticium* (Solé-Cava *et al.*, 1992; Boury-Esnault *et al.*, 1992b, 1995; Muricy, 1999; Muricy *et al.*, 1996a,b, 1998, 1999). These studies demonstrated the importance of these traits to the characterization of genera and species, and to the understanding of the phylogenetic relationships among plakinid genera. Similar studies on the poorly known genera *Plakortis*, *Plakinastrella*, and *Placinolopha* would be of particular interest to achieve a more detailed picture of the phylogeny of the Plakinidae. Also, a complete characterization of the plakinid fauna in regions other than the

Mediterranean is essential to understand the true diversity of the family and the relationships among its members.

Biochemical characteristics of species from three genera (*Oscarella*, *Plakina*, and *Plakortis*) have been described by several authors (Bergquist & Hartman, 1969; Cimino *et al.*, 1975; Higgs & Faulkner, 1978; Ravi *et al.*, 1979; Faulkner *et al.*, 1979; Stierle & Faulkner, 1980; Faulkner & Ravi, 1980; Rosser & Faulkner, 1984; Bergquist *et al.*, 1984; Sakemi *et al.*, 1987; Aiello *et al.*, 1990; Inman *et al.*, 1990; West *et al.*, 1990; Davidson, 1991). Among the most interesting chemical components of plakinid species are rare, cytotoxic epoxy-sterols in *Oscarella* (Aiello *et al.*, 1990), and antimicrobial steroidal alkaloids in *Plakina* (Rosser & Faulkner, 1984). Species of *Plakortis* are known to produce both monoterpene derivatives unknown from other sponges (Faulkner & Ravi, 1980), cytotoxic alkaloid pigments (West *et al.*, 1990), cytotoxic peroxydes (Sakemi *et al.*, 1987; Davidson, 1991), and pentacyclic

aromatic alkaloids with anti-helminthic and anti-reverse transcriptase activities (Inman *et al.*, 1990).

Plakinid species comprise mostly small, thinly to massively encrusting species, widely distributed geographically and bathymetrically, from tidal depths up to at least 2460 m (*Plakina brachylopha*; Topsent, 1928c). They grow only on hard substrates. Softer and thinner forms predominate in sheltered habitats (caves, crevices, etc.), whereas in exposed areas (rock outcrops, coral colonies, etc.) the species tend to be more massive and rigid (Fig. 1). Species descriptions and surveys are found dispersed in a series of sponge monographs from all the world's oceans (Table 1). Definitions of the constituent taxa and important taxonomic characters are given by Diaz & Van Soest (1994), Boury-Esnault *et al.* (1984, 1992b, 1995), Muricy *et al.* (1996a, 1998, 1999).

Remarks

Most plakinid genera are clearly associated by the common nature of their skeleton, aquiferous system, cytological features and larval morphology. However two major problems still haunt our understanding of this group. Firstly, important biological aspects of approximately half of plakinid genera remain poorly studied (*Plakortis* Schulze, 1880, *Plakinastrella* Schulze, 1880, *Placinolopha* Topsent, 1897a). This prevents us from drawing a

more definitive phylogenetic picture of the family. Further biological characterization of all plakinid genera (cytological, histological, and genetic) such as in previous studies with species of *Oscarella*, *Corticium*, *Pseudocorticium*, and *Plakina* will aid in understanding intergeneric affinities. Secondly, until the present, these sponges, with their unique cinctoblastula larvae, a basement membrane lining both choanoderm and pinacoderm, flagellated pinacocytes, and the distinctive morphology of their spicules, aquiferous system and larvae, remain isolated from other extant Demosponges and its outgroup relationships are still unclear (e.g., see Van Soest, 1984a; Grothe, 1989; Muricy, 1999). The answer to this problem seems to depend on molecular studies (e.g., sequencing of 18S ribosomal genes) to discern the relationships of this family with other sponge groups (e.g., Astrophorida, Calcaronea). A first approach to the phylogeny of the Plakinidae, including species of four genera (*Corticium*, *Oscarella*, *Plakina*, and *Pseudocorticium*) was attempted by Muricy (1999), using morphological and cytological characters and *Discodermia* (Lithistida) as the outgroup. Muricy (1999) found little support for a monophyletic family Oscarellidae clustering *Oscarella* and *Pseudocorticium*, and both aspiculate genera were kept in the family Plakinidae. These analyses must however be complemented by inclusion of other genera (*Plakortis*, *Plakinastrella*, and *Placinolopha*) and study of other characters (e.g., DNA sequences).

KEY TO GENERA

- | | |
|--|------------------------|
| (1) With inorganic (spicular) skeletal complement | 2 |
| Without inorganic (spicular) skeletal complement | 6 |
| (2) Skeleton mainly composed of diods, triods, and/or calthrops in one size class | 3 |
| Skeleton mainly composed of diods, triods and/or calthrops with a large size variation | 5 |
| (3) Lophose diods, triods, or calthrops complement the main skeleton of non-lophose spicules | 4 |
| Lophose spicules absent, diactinal "microscleres" (microrhabs) present in some species..... | <i>Plakortis</i> |
| (4) Heterolophose calthrops (candelabra) complement the main skeleton of non-lophose spicules, which might be absent or rare; choanocyte chambers usually aphodal | <i>Corticium</i> |
| Lophocalthrops with one to four homogeneously ramified actines complement the main skeleton of non-lophose spicules; candelabra absent; choanocyte chambers usually eurypylous | <i>Plakina</i> |
| (5) Skeleton composed of non-lophose diods, triods and/or calthrops in three size classes | <i>Plakinastrella</i> |
| Skeleton formed by diods, triods, and/or calthrops with large size variation; the larger spicular category presents terminally-branching rays | <i>Placinolopha</i> |
| (6) With syllebid-like aquiferous system and eurypylous choanocyte chambers; ectosome thin, proportion of mesohyl to chambers <1:1 | <i>Oscarella</i> |
| With leuconoid aquiferous system and diplodal choanocyte chambers; ectosome thick, proportion of mesohyl to chambers >2:1 | <i>Pseudocorticium</i> |

CORTICIUM SCHMIDT, 1862

Synonymy

Corticium Schmidt, 1862: 42.

Type species

Corticium candelabrum Schmidt, 1862: 42 (by monotypy).

Definition

Thin to thick encrusting plakinid, with a skeleton dominated by non-lophose calthrops and heterolophose calthrops; homolophose calthrops can be found in certain species.

Diagnosis

Thinly encrusting to cushion-shaped Plakinidae with a spiculation consisting almost exclusively of non-lophose calthrops in one size class and heterolophose calthrops ('candelabra'; Fig. 2H). Homolophose calthrops may also be present (Fig. 2D), and non-lophose calthrops are absent in some species. Aquiferous system leuconoid, with aphodal choanocyte chambers, and about 300 choanocytes per chamber (Boury-Esnault *et al.*, 1984). The species of this genus present variable but usually thick cortex (100–300 µm), and a proportion of mesohyl to chambers of about 1:1 (Boury-Esnault *et al.*, 1995).

Description of type species

Corticium candelabrum Schmidt, 1862 (Figs 1A, 2H, 3A, I, 4A–B, 5A).

Synonymy. *Corticium candelabrum* Schmidt, 1862: 42.

Material examined. Lectotype: LMJG 15353/0 – Sibenik, Croatia (here designated). Other material. LMJG 15508 – no designated locality. USNM 23889 – Adriatic. USNM 39217 – Marseille, France. ZMA Por. 52 – Banyuls, France.

Description. Thinly encrusting to cushion-shaped, lobate, up to 3 cm long and 1.5 cm thick, which contracts when taken out of the water to such an extent that its surface takes a highly convoluted appearance. Body fixed on the substratum by thin filaments. Surface uneven, slightly rough to touch. Round oscula, 1–5 mm in diameter, contractile. Colour alive light brown to tan, preserved in spirit. Consistency firm, cartilaginous. Ectosome with a well defined cortex 100–300 µm thick, with abundant amoeboid cells. Subectosomal cavities absent, basal cavity well developed. Aquiferous system leuconoid, with ovoid, aphodal choanocyte chambers, 50–70 µm in diameter. Skeleton confused, with spicules scattered between choanocyte chambers. Although also present in the choanosome, candelabra are concentrated at the surface and bordering canals. Spicules are irregular, non-lophose calthrops in one size class (actines 23–35 µm); monolophose calthrops (actines 25–32 µm) with a ramification pattern in which lophose actines have only one, proximal ramification point which gives rise to 3–5 conical, smooth rays (a pattern coded '1p, conical'), and candelabra 23–35 µm long. The 3 'basal' (equally ramified) actines of candelabra have a ramification pattern similar to that of monolophose calthrops (1p, conical); the fourth actine ramifies basally in 4–10 longer and thinner microspined rays (Figs 2H, 3A, I).

Remarks. The best apomorphy of the genus *Corticium* is the presence of heterolophose calthrops (candelabra), which are a special kind of tetralophose calthrops in which three actines are ramified in a simple pattern (one medial ramification point, 3–4 conical rays, smooth), and the fourth actine has a unique pattern of ramification: seven to ten thin, micro-spined rays diverge from a proximal ramification point. Several species described in the genus *Corticium* lack candelabra, having instead homogeneously ramified trilophose and/or tetralophose calthrops typical of *Plakina* (*Corticium versatile* Schmidt, 1879; *C. bowerbankii* Sarà, 1960b; *C. tetralophum* Hechtel, 1965; *C. topsenti* Pouliquen, 1972; and *C. reductum* Pulitzer-Finali, 1983). These species were accordingly transferred to *Plakina* (Muricy *et al.*, 1998). The genus *Corticium* shares with *Plakina* the presence of simple, monolophose calthrops and non-lophose calthrops, as well as large apopylar cells with osmiophilic inclusions (Muricy *et al.*, 1999). Schmidt (1862) did not designate a holotype for the type species. We found two specimens from the type locality (Sibenik, Croatia), which apparently belong to the original series. Specimen LMJG 15353/0 is here designated as the lectotype, in accordance with the ICZN (Art. 74) (Anon., 1999). Specimen LMJG 15508 (no designated locality) is here designated as a paralectotype. *Corticium candelabrum* seems to be a well defined, easily identifiable species, and it would seem inappropriate to consider *a priori* that non-Mediterranean records were misidentifications. However, in the closely related genus *Plakina* it was shown that allozyme patterns and very subtle differences in the ramification pattern of lophocalthrops were diagnostic at the species level and may reveal cryptic speciation (Muricy *et al.*, 1996b, 1998). *Corticium candelabrum* awaits similar studies to prove or disprove its cosmopolitan nature.

Distribution

Six species are known from the Mediterranean (Schmidt, 1862; Topsent, 1895; Uriz & Bibiloni, 1984), Eastern Atlantic

(Cruz & Bacallado, 1981), Caribbean (Topsent, 1923), Indian Ocean (Thomas, 1968e, 1970), Australia (Gray, 1867a; Lendenfeld, 1907; Burton, 1934a; Wiedenmayer, 1989; Hooper & Wiedenmayer, 1994), New Guinea (Pulitzer-Finali, 1996), and New Caledonia (Lévi & Lévi, 1983b) (Table 1).

OSCARELLA VOSMAER, 1884

Synonymy

[*Oscaria*] Vosmaer, 1881: 163 (preocc. by *Oscaria* Gray, 1873 (Reptilia)). *Oscarella* Vosmaer, 1884: pl. 8 (explanation); 1887: 326 (*nom. nov.* for [*Oscaria*] Vosmaer). *Oscarella* Vosmaer, 1887: 326. *Octavella* Tuzet & Paris, 1964: 88 (no type specimens designated). Taxonomic decision after Vosmaer (1887: 326); Boury-Esnault *et al.* (1984: 13, 1992b: 282); Diaz & Van Soest (1994: 102).

Type species

Halisarca lobularis Schmidt, 1862 (by monotypy).

Definition

Plakinidae without spicules, with an aquiferous system made up of spherical, eurypylous choanocyte chambers uniformly arranged around large, regular exhalant canals.

Diagnosis

Plakinidae without skeleton, with thinly encrusting to lobate shape. Thin ectosome (<100 µm), often nearly limited to the pinacoderm, true cortex absent. Mesohyl ill-developed, with a proportion of mesohyl to chambers varying from 0.5:1 to 1.2:1. The aquiferous system has a syllebid-like organization, with spherical, eurypylous choanocyte chambers uniformly arranged around large, regular exhalant canals, and a large basal exhalant cavity (Fig. 5B) (after Boury-Esnault *et al.*, 1995).

Description of type species

Oscarella lobularis (Schmidt, 1862) (Figs 1B, 5B, 7A).

Synonymy. *Halisarca lobularis* Schmidt, 1862: 80. *Octavella galangau* Tuzet & Paris, 1964: 88.

Material examined. Neotype: MNHN LBIM DNBE 1991-1 – Marseille, France. Other material. UFRJPOR 4378, 4379, 4380 – Marseille, France.

Description. Shape thinly to massively encrusting, lobate. Size up to 20 cm wide and 3 cm high, lobes 1 cm wide and high. Colour variable (purple, violet, or blue, often with cream tinges at the base). Surface smooth, with scattered inhalant ostia and circular oscula (5–10 mm in diameter) at the top of the lobes. Consistency soft. Aquiferous system syllebid-like (with a radial arrangement of chambers around exhalant canals), with eurypylous choanocyte chambers 35–90 µm in diameter. Ectosome thin (5–80 µm), unspecialized, without ectosomal cavities. A large exhalant basal cavity extends through the center of the lobes to the oscula. Proportion of mesohyl to chambers approximately 0.5:1. Spicule and fibre skeleton absent.

Remarks. *Oscarella* species are homogeneous in morphological, anatomical and reproductive characters: all are thinly to thickly encrusting, lobate, with reduced mesohyl and thin ectosome (usually less than 100 μm thick). The aquiferous system superficially resembles the syllebid organization of some Calcarea: spherical, eurypylous choanocyte chambers are arranged around inhalant and exhalant canals, which run perpendicularly from the surface down to a basal exhalant cavity, ramifying and anastomosing in the choanosome (Fig. 5B). *Oscarella* species are hard to characterize morphologically except in a few cases by the use of field characters. Examination of cytological characters (at least in semithin sections of properly fixed specimens) is essential for species discrimination in *Oscarella*, especially when taken in connection with molecular methods such as allozyme electrophoresis (Muricy *et al.*, 1996a), or DNA analysis. *Oscarella* shares with *Pseudocortidium* the absence of skeleton and cytological traits such as thin, triangular apopylar cells and two peculiar types of cells with inclusions (Boury-Esnault *et al.*, 1995; Muricy *et al.*, 1996a; Fig. 6B, D–E). They are distinguished by the presence in *Pseudocortidium* of well-developed mesohyl, a relatively thick cortex, leuconoid aquiferous system and diploidal choanocyte chambers (Fig. 5D). *Oscarella lobularis* is very simple morphologically (Fig. 1B), and it has often been confounded with its sibling species *O. tuberculata* (Schmidt, 1868), which is abundant in the NW Mediterranean (Boury-Esnault *et al.*, 1992b). These two species can only be confidently distinguished by molecular or cytological methods, and all records of *O. lobularis* published before this distinction was made must have their specific status re-evaluated (especially those from outside the Mediterranean). The synonymy of *Octavella* and *Oscarella* is justified since the only difference between the type species of both genera is the alleged absence of flagella in endopinacocytes of *O. galangau*, which is probably due to poor preservation conditions (Boury-Esnault *et al.*, 1984).

Distribution

Cosmopolitan: Mediterranean (Schmidt, 1862; Topsent, 1895; Uriz & Bibiloni, 1984; Lévi, 1957b), E Atlantic (Lévi, 1952; Cruz & Bacallado, 1981; Boury-Esnault & Lopes, 1985), N Atlantic (Van Soest & Weinberg, 1980; Burton, 1959a; Koltun, 1964b), S Atlantic (Burton, 1930e), Caribbean (G. Muricy, unpublished data), Red Sea (Lévi, 1958), Indian Ocean (Vacelet *et al.*, 1976), NW Pacific (Koltun, 1962b) and Antarctic (Topsent, 1917). However, only five species of *Oscarella* are currently recognized, all from the Mediterranean: the type species *O. lobularis* (Schmidt, 1862), *O. tuberculata* (Schmidt, 1868), *O. viridis* Muricy *et al.*, 1996a, *O. microlobata* Muricy *et al.*, 1996a, and *O. imperialis* Muricy *et al.*, 1996a. The correct specific assignment of the several records of *O. lobularis* worldwide awaits a detailed anatomical and cytological revision, but it is already clear that most of these might consist of cryptic sibling species representing new taxa.

PLACINOLOPHA TOPSENT, 1897

Synonymy

Placinolopha Topsent, 1897a: 429. *Plakinolopha* de Laubenfels, 1954: 249. [*Acanthoplakina*] Burton, 1959a: 156 [unavailable name, see remarks]. *Diactinolopha* Sarà, 1960b: 2 (after Lévi & Lévi, 1989: 45; Diaz & Van Soest, 1994: 102).

Type species

Placinolopha bedoti Topsent, 1897a: 429 (by original designation).

Definition

Plakinidae with a spiculation of large lophodioids, sometimes supplemented by lophotriods and/or lophocalthrops, and a complement of non-lophose diods, triods, and/or calthrops.

Diagnosis

Thinly to massively encrusting Plakinidae with a spiculation of large lophodioids, sometimes supplemented by lophotriods and/or lophocalthrops, and a complement of non-lophose diods, triods, and/or calthrops. Tetralophose calthrops are found in one species (*P. acantholopha*).

Description of type species

Placinolopha bedoti Topsent, 1897a (Figs 2I, 3H).

Synonymy. *Placinolopha bedoti* Topsent, 1897a: 429.

Material examined. Holotype: MHNG C-12/6 (slide MNHN LBIM DT1814) – Amboine, Indonesia (Desqueyroux-Faúndez, 1981: 756).

Description. Topsent (1897a) described *Placinolopha bedoti* as a thinly encrusting sponge, 30 \times 23 mm wide and 1–3 mm thick. Colour white in spirit. Surface smooth, without visible openings. Consistency firm, brittle. Spiculation dense, composed of calthrops and derivatives in three size classes: smaller spicules are abundant diods (100–160 \times 3–7 μm), sinuous, acerate, centrotylote and variable in shape, less common triods (actines 60–70 \times 5 μm), and rare calthrops (actines 50 μm long); medium-size spicules are diods (350–550 \times 11–25 μm), triods and calthrops (both with actines 110–190 \times 20 μm); larger spicules are abundant lophodioids (750 \times 50 μm), rare lophotriods and abundant lophocalthrops (both with actines 275–300 \times 35–50 μm), and sometimes also lophopentactines. Lophocalthrops predominate at the surface, and lophodioids are more common in the choanosome. Lophose spicules ramify dichotomously several times, forming straight or curved conical rays arranged in a tree-like fashion. Our analysis of the type species material conforms overall to Topsent's (1897a) description, to which a few observations could be added. The choanosomal skeleton has spicules of all types randomly dispersed. The ramification pattern of lophose spicules is peculiar, with one distal ramification point from which depart 2–3 conical, curved secondary rays which often bear a second and a third medial points of ramification (with give rise to 2–4 secondary rays each) before ending in acerate or less often terminally spined extremities (a general pattern coded '1d, 2m, 3m'; Figs 2I, 3H). The number of ramifications varies among actines of the same spicule or rays of the same actine, but they always show the typical conical, curved shape. Spicules of MNHN LBIM DT1814 are similar in both general shape and ramification pattern to MHNG C-12/6, although slightly larger: abundant diods (60–550 \times 2–8 μm); rare triods (actines 20–40 \times 2–6 μm); rare calthrops (actines 40–210 μm); common lophodioids (430–720 \times 15–50 μm); lophotriods absent; common lophocalthrops (actines 190–250 \times 25–52 μm).

Remarks. *Placinolopha* was synonymized with *Plakina* by Lendenfeld (1903) but reinstated by Topsent (1928c) and de

Laubenfels (1936a) without apparent justification (Sarà, 1960b). These two genera are consistently different in the possession of spicule size classes and the much greater upper range in the size of spicules in *Placinolopha* (which are shared with *Plakinastrella*), and in the ramification pattern of their lophose spicules. *Plakinolopha* de Laubenfels, 1954 is a misspelling of *Placinolopha* Topsent. In *Placinolopha bedoti* the actines of long lophodiods, lophotriods and lophocalthrops bear a terminal ramification point giving rise to secondary rays which in turn ramify medially in conical rays; a few actines of some spicules may also show a third, medial ramification round (a pattern coded '1d, 2m, 3m, conical') (Fig. 3H). In *Plakina*, small lophocalthrops have several different branching patterns which are diagnostic at the species level (Fig. 2D–G; Muricy *et al.*, 1998). *Diactinolopha* Sarà (1960b) was synonymized with *Placinolopha* based on the similarity of the spiculation of its type species, *D. moncharmonti* Sarà, 1960b, to that of *P. bedoti*. [*Acanthoplakina*] Burton, 1959a is here considered an unavailable name since it was erected without a description or definition, or a valid type species designation (ICZN Art. 13). The genus *Placinolopha* has been very poorly studied and there is no information on the choanocyte chambers type or organization. Species distinction is based on the size and number of spicule types and size categories, together with external morphological characteristics.

Distribution

Six species have been described from the Mediterranean (Sarà, 1960b), Indo-West Pacific (Topsent, 1897a; Kirkpatrick, 1900b; Lévi & Lévi, 1989), and Indian Ocean (Thomas, 1970; Vacelet & Vasseur, 1971) (Table 1).

PLAKINA SCHULZE, 1880

Synonymy

[*Achinoe*] Gray, 1867a: 546 (unavailable name, see Remarks). *Plakina* Schulze, 1880: 448. *Placina* Topsent, 1890d: 231. *Plakoosa* de Laubenfels, 1936b: 462 (after Topsent, 1937: 7).

Type species

Plakina monolopha Schulze, 1880: 407 (by original designation).

Definition

Plakinidae with a spiculation of diods, triods, and calthrops in a single size class, and with homolophose calthrops with one, two, three, or four lophate rays.

Diagnosis

Thinly to massively encrusting Plakinidae with a spiculation of diods, triods, and calthrops, and with homogeneously ramified lophocalthrops with one, two, three, or four lophate rays. Candelabra (heterolophose calthrops) absent. Lophocalthrops usually concentrated at the sponge surface and bordering canals. Development of the ectosome is variable, and subectosomal cavities may be present (e.g., *P. trilopha* Schulze, 1880). A large basal cavity is present in most species. Proportion of mesohyl to chambers varies from 0.7 to 1.8:1. Choanocyte chambers are euryplous

or aphodal, usually with a radial arrangement around incurrent and excurrent canals (called sylleibid-like arrangement, such as in *P. monolopha*, *P. elisa*).

Description of type species

Plakina monolopha Schulze, 1880 (Figs 2D, 3B, E, 4C, 5C).

Synonymy. *Plakina monolopha* Schulze, 1880: 407.

Material examined. Lectotype: BMNH 1883.12.4.29 – Naples (Muricy *et al.*, 1998). Other material. ZMA POR 4391, 4424 – Ireland. ZMA POR 5123 – Brittany, France. ZMA POR 1821 – Curaçao. ZMA POR 7978, 8064, 8398 – Indonesia. UFRJ-POR 4350, 4351, 4352 – Grand Congloue Island, Rioux Archipelago, Marseille, France.

Description. Sponges small, thinly encrusting, up to 2 × 2 cm wide and 1–5 mm thick. Shape discoidal or irregular, with smooth, elevated borders forming a 'ring canal' around the sponge body. Body attached to the substratum by thin filaments. Surface microlobate, with rugose, irregular lobes 0.5–2.0 mm in diameter and height, which may fuse together. Colour alive and in spirit white or cream. Consistency soft, fragile. Ectosome poorly developed, 15–30 µm thick, without subectosomal cavities. Spaces between lobes form open inter-digitations 50–100 µm wide; inhalant canals are absent, and ostia lead water almost directly to the chambers. Aquiferous system sylleibid-like, with spherical, euryplous choanocyte chambers. Exhalant canals lead to a system of basal cavities and then to the oscula, located at the borders of the sponge. Proportion of mesohyl to choanocyte chambers varies from 0.5:1 to 1.2:1 (mean 0.8:1). Skeleton dense, confused reticulation of diods, triods and calthrops in a single size class around the aquiferous system. Monolophose calthrops concentrated at the surface of the sponge, most with their lophose actines pointing outward, with a few dispersed in the choanosome or lining canals and basal cavities. Lophose and non-ramified spicules may form a dense palisade at the surface, 25–50 µm thick. Diods slender, irregular, sinuous, with actines gradually pointing to sharp ends (52–93 µm). Actines often irregularly spined, with variable number and size of spines. The central swelling may be knotty-crooked, centrotylote or almost smooth. Triods often with one or two ill-developed or malformed actines. The central swelling, actine size and angle between actines vary widely (actines 11–34 µm). Calthrops show the same general shape and variations, and one actine is usually reduced to a small button (actines 15–31 µm). Monolophose calthrops, 8–31 µm long, are irregular, and each lophose actine have two to six rays. Lophose actines ramify once at the middle of their length in two to five slender, cylindrical rays, which usually show two or three tiny terminal spines (a pattern of ramification coded '1m, ts') (Fig. 3E).

Remarks. [*Achinoe*] Gray, 1867a, with type species *Achinoe australis* Gray, 1867a (by monotypy) was erected for two spicule drawings of an unknown sponge from Western Australia (Freemantle) by Bowerbank (1864: Figs 235–236), showing typical spined calthrops of Homosclerophorida. De Laubenfels (1936: 80) associated it with *Trikentrion* and *Cyamon* (Raspailiidae); Hooper & Wiedenmayer (1994) suggested the type species may belong to *Corticium*; conversely, it is far more likely that it belongs to *Plakina* in which there are species with profusely spined lophocalthrops. [*Achinoe*] Gray, 1867a has seniority over *Plakina* Schulze, 1880, but the name can be suppressed as a *nomen oblitum* since it has not been used since. '(ICZN Art. 23.9.1)'

Plakoosa de Laubenfels (type species *Plakoosa elisa* de Laubenfels, 1936b: 463, by monotypy; holotype USNM 22237), is a clear synonym of *Plakina*, since the spicules called “microme-soorthotrichotriaenes” by de Laubenfels (1936b) are in fact dilophose calthrops similar to those of *Plakina dilopha* Schulze, 1880 (Topsent, 1937). *Placina* Topsent (1890d) is a misspelling of *Plakina* Schulze. *Plakina* shares with *Corticium* the possession of spicules with true lophose rays (rays which subdivide close to the base in two to several branches which then might ramify again). Moreover, the type species of both genera share the presence of monolophose calthrops (although with slightly different ramification patterns). Therefore, the genus *Plakina* does not have any good synapomorphy of its own, and it is likely to be a paraphyletic group (see also Muricy, 1999; Muricy *et al.*, 1998). However, lophocalthrops of *Plakina* are always homogeneously ramified, whereas *Corticium* also has heterolophose calthrops (autapomorphic for that genus). Thus, we prefer to consider *Plakina* as a valid genus until further phylogenetic studies demonstrate more clearly its paraphyly and how to divide it in monophyletic subgroups. Species distinction is based on the number of lophose actines in lophocalthrops (1–4) and on details of their patterns of ramification, as well as on external morphological features and the architecture of the aquiferous system. *Plakina tetralophoides* Muricy *et al.*, 1998 is a *nomen novum* for *P. tetralopha* Tanita & Hoshino, 1989, required because it became a junior homonym of *Corticium tetralophum* Hechtel, 1965 after the transfer of the latter to *Plakina* (with the consequent change of its specific epithet from *tetralophum* to *tetralopha* (Muricy *et al.*, 1998).

The possible conspecificity of the disjunct, morphologically similar populations of the type species, *P. monolopha*, seems unlikely and awaits genetic, reproductive, and/or cytological studies to be corroborated. Studies on the shape and pattern of ramification of lophocalthrops suggest that most records from outside the Mediterranean basin have been incorrectly identified, with the possible exception of Northeastern Atlantic specimens (Muricy *et al.*, 1998).

Distribution

Twenty-two species of *Plakina* are known worldwide, from the Mediterranean (Schulze, 1880; Sarà, 1960b; Pulitzer-Finali, 1983; Muricy *et al.* 1998), Atlantic (Topsent, 1928c), Caribbean (Schmidt, 1879; de Laubenfels, 1936b; Lehnert & Van Soest, 1998), Indian Ocean (Vacelet *et al.*, 1976), Pacific (Lévi & Lévi, 1983b; Tanita & Hoshino, 1989; Desqueyroux-Faúndez & Van Soest, 1997) and Antarctic (Topsent, 1901a, 1917; Lendenfeld, 1907) (Table 1).

PLAKINASTRELLA SCHULZE, 1880

Synonymy

Plakinastrella Schulze, 1880: 449. *Placinastrella* Sollas, 1888: 103. *Dercitopsis* Dendy, 1905: 65 (after Topsent, 1928c: 33).

Type species

Plakinastrella copiosa Schulze, 1880: 433 (by monotypy).

Definition

Plakinidae with a skeleton composed of non-lophose diods, triods, and/or calthrops with wide size variation, usually in three size classes.

Diagnosis

Thinly to massively encrusting, sometimes lobate or tubular Plakinidae, usually tough in consistency and with surface smooth to the eye but rough to the touch. Subectosomal inhalant cavities present in some species; choanocyte chambers eurypylous or dipodal. Skeleton composed of non-lophose diods, triods, and/or calthrops with wide size variation, usually in three size classes. The small diactines are accumulated on the surface, either forming a palisade or disposed tangentially to the surface.

Description of type species

Plakinastrella copiosa Schulze, 1880: 433.

Synonymy. *Plakinastrella copiosa* Schulze, 1880: 433.

Material examined. Holotype: Not available. Slide UFRJPOR 4856 (made by Topsent) from an unregistered specimen collected from Banyuls, France.

Description. Schulze (1880) described *P. copiosa* as cushion-shaped, 2 cm wide, 5 mm high, light yellow in alcohol, with a low oscular tube at the top of the sponge. Ectosome well developed, with regular subdermal cavities. Basal cavities absent. Canal system richly developed, ramifying like a tree. Skeleton confused, made up of spicules in three size classes, with transitions: larger spicules diods, triods and calthrops, of which the first two may appear in the cortex; medium-size spicules diactines and triactines only; small spicules diods, triods and calthrops restricted to the cortex, with some malformations. Candelabra absent. Topsent's (1895) description of the species conforms to that of Schulze (1880), adding certain aspects to the species description: “A smooth surface, even or marked by small ridges, covered by microscopic ostia. Choanosome well developed, with a rich canal system and eurypylous choanocyte chambers. Endopinacocytes flagellated. Spherulous cells abundant in the ectosome but also present in the choanosome. Viviparous. Skeleton confused, dense, composed by calthrops and derivatives in three size classes: larger spicules are diods (600–700 × 30–35 μm), triods, and calthrops (both with actines 320 × 30–35 μm); medium-sized spicules are diods and triods, but not calthrops; smaller spicules are diods (25–40 × 1–2 μm), triods and calthrops (both with actines 8–12 μm long). Larger spicules are concentrated at the choanosome, and smaller spicules concentrated at the ectosome and around subdermal cavities.” In the specimen from Banyuls spicules are diods and triods in three size classes, supplemented by calthrops in the largest size class only. Diods I: 310–520 μm; diods II: 73–130 μm; diods III: 11–45 μm; triods I: actines 120–325 μm; triods II: actines 24–39 μm; triods III: actines 12–18 μm; calthrops: actines 80–250 μm.

Remarks. The synonymy of *Dercitopsis* and *Plakinastrella* is justified because the type species of *Dercitopsis*, *D. ceylonica* Dendy, 1905, is very similar to *Plakinastrella copiosa* in spiculation and skeletal arrangement (Topsent, 1928c). *Placinastrella* Sollas (1888: 103) is a misspelling of *Plakinastrella* Schulze. *Pachamphilla* Lendenfeld, 1906 was considered a junior synonym of *Dercitopsis* by de Laubenfels (1936a: 180), but reexamination of the holotype of the type species *P. allata* Lendenfeld, 1907 (M. Maldonado, pers. comm.) indicates instead a relationship to *Penares* Gray (Astrophorida). Species of *Plakinastrella* possess large calthrops similar to those of astrophorids such as *Calthropella*, *Pachastrella*, *Penares*, and *Erylus*. Species described by Dendy (1905) in *Plakinastrella* (*P. schulzei* and *P. intermedia*) have been found to belong to the *Penares* (Topsent, 1928c; Diaz & Van Soest, 1994). *Plakinastrella* shares the presence of spicules in three size classes

with *Placinolopha*, and the possession of small smooth calthrops and derivatives with *Plakortis*, *Plakina*, *Corticium*, and *Placinolopha*. We have not studied the nature of the aquiferous system of this genus, however, Schulze (1880) described the canal system of *P. copiosa* as well-developed, ramifying as a tree, with subdermal inhalant lacunae but without basal exhalant cavities. Subdermal cavities are also found in *P. clathrata* Kirkpatrick and *P. mammilaris* Lendenfeld. Dendy (1905) described eurypylous choanocyte chambers in *P. ceylonica*, and diplodal chambers in *P. mammilaris*. Comparisons of aquiferous systems should be made among the different species of *Plakinastrella* and other plakinid genera to clarify their relationships.

Distribution

Nine species are known from the Mediterranean (Schulze, 1880; Maldonado, 1992), Indian Ocean (Dendy, 1905), W Pacific (Kirkpatrick, 1900b; Lendenfeld, 1907; Lévi & Lévi, 1989), Atlantic (Topsent, 1904b, 1927b), and Caribbean (Uliczka, 1929) (Table 1).

PLAKORTIS SCHULZE, 1880

Synonymy

Plakortis Schulze, 1880: 449. *Placortis* Topsent, 1895: 557. *Roosa* de Laubenfels, 1934: 2 (after Topsent, 1937: 7).

Type species

Plakortis simplex Schulze, 1880: 430 (by original designation).

Definition

Plakinidae with a skeleton formed by small diods with triods in varying abundance. Diactine-derived 'microscleres' (microrhabds) may be present in some species.

Diagnosis

Thinly to massively encrusting plakinids with a skeleton mainly formed by small (50–200 μm) diods with triods in varying abundance. Deformed calthrops can be found in some specimens. Some species have microrhabds (5–20 μm) distributed regularly in the sponge body. Aquiferous system intermediate between syllebid-like and leuconoid, with eurypylous choanocyte chambers regularly distributed around exhalant canals. Both ectosomal inhalant cavities and basal exhalant cavities are usually present. Skeleton confused, dense, without ectosomal specialization or differential location of spicules.

Description of type species

Plakortis simplex Schulze, 1880.

Synonymy. *Plakortis simplex* Schulze, 1880: 449.

Material examined. Holotype: Not available. Other material. USNM 8433, 9433 – Ireland. ZMA POR 7054, 7143, 7149 – Cape Verde Islands, 1–15 m depth. SME 59 – Marseille, France.

Description. Thinly-encrusting sponges, generally 2–5 mm thick, usually light in color: brown, white, yellow, or tan. Surface smooth and regularly pierced by ostia; oscules <1 mm diameter

and low in frequency. Compressible in life. Aquiferous system intermediate between syllebid-like and leuconoid, with eurypylous choanocyte chambers regularly distributed around exhalant canals. Both ectosomal inhalant cavities and basal exhalant cavities are present, the latter also being bordered by choanocyte chambers. Skeleton confused, dense, without ectosomal specialization or differential location of spicules. Spicules mostly diods centrotylote or with knobby-knotty centers, somewhat sinuous, 60–150 \times 3–6 μm , and less common, sometimes absent smaller triods 25–50 \times 3–6 μm . Spicules are regularly distributed and densely packed throughout the body.

Remarks. *Roosa* de Laubenfels, 1934 (type species *R. zygompha* de Laubenfels, 1934: 2; by original designation; holotype USNM 22277), was synonymized with *Plakortis* because the spiculation of its type species, with diods 50–140 μm long and triods 25–50 μm long, is typical of *Plakortis* species (Topsent, 1937). *Placortis* Topsent, 1895 is a misspelling of *Plakortis* Schulze. The original definition of the genus was modified (Diaz & Van Soest, 1994) to include the possibility of finding calthrops and diactinal 'microscleres', as complement to diods and triods. Due to the simplicity of the spiculation of this genus, the species diagnosis is quite difficult without the observation of anatomical characters (e.g., architecture of the aquiferous system) and external characteristics.

Distribution

Eleven species of *Plakortis* are known from the Mediterranean (Schulze, 1880), Atlantic (Pulitzer-Finali, 1993), Caribbean (Carter, 1879b; Wilson, 1902; de Laubenfels, 1934; Zea, 1987), Red Sea and E Africa (Lévi, 1953b, 1958; Diaz & Van Soest, 1994), E Pacific (Desqueyroux-Faúndez & Van Soest, 1997), and W Pacific (de Laubenfels, 1954; Diaz & Van Soest, 1994) (Table 1). From the literature, it would seem that some *Plakortis* species have an apparent cosmopolitan distribution (i.e., *Plakortis simplex*, *P. angulospiculatus*). However biogeographical considerations (isolation of the Pacific and Atlantic basins for 3–5 MY; low dispersal potential of sponges) are at odds with such an hypothesis. The apparent conspecificity of these specimens might be just a consequence of the simple and non-diagnostic nature of their skeleton and external morphology (see also Lévi, 1953b). The conspecificity of such morphologically similar but geographically disjunct populations awaits more detailed anatomical, reproductive and genetic studies.

PSEUDOCORTICIUM BOURY-ESNAULT ET AL., 1995

Synonymy

Pseudocorticiium Boury-Esnault et al., 1995: 28.

Type species

Pseudocorticiium jarrei Boury-Esnault et al., 1995 (by original designation).

Definition

Plakinidae without mineral skeleton, with a well-developed ectosome, a leuconoid organization of the aquiferous system, and diplodal choanocyte chambers.

Diagnosis

Plakinidae without skeleton, with a well-developed ectosome, a leuconoid organization of the aquiferous system, and diplodal choanocyte chambers. Proportion of mesohyl to chambers greater than 2:1.

Description of type species

Pseudocorticium jarrei Boury-Esnault *et al.*, 1995.

Synonymy. *Pseudocorticium jarrei* Boury-Esnault *et al.*, 1995: 28.

Material examined. Holotype: MNHN DNBE-94.1 – Jarre Island, Marseille, in a cave. Other material. UFRJPOR T-5 and T-6 – Jarre Island, Marseille, in a cave.

Description. Thickly encrusting to lobate sponge, with lobes up to 12 cm long by 2 cm wide, hanging down from the sponge in ceilings of caves. Base irregular, 3–10 cm wide and 5–30 mm thick. Colour alive cream; in spirit it varies from yellowish white to brownish gray. Surface smooth and slippery but corrugated, folded with irregular depressions. Superficial exhalant canals (2–5 mm in diameter) lead to circular oscula (5–10 mm in diameter). Oscula located at the top or on the sides of the lobes, 5 mm high, surrounded by a slightly transparent oscular rim. Consistency firm, cartilaginous. Within the lobes there is usually a central exhalant canal 1–3 mm in diameter. Ectosome with a dense cortex, 50–350 μm thick. Aquiferous system leuconoid, with diplodal choanocyte chambers (25–60 μm diameter). Mesohyl granular, with abundant bacteria, collencytes, archaeocytes and cells with inclusions. Choanocyte chambers and canals surrounded by a clear, relatively bacteria-free layer of mesohyl (1–6 μm thick). A thin basement membrane underlines both choanoderm and pinacoderm. Proportion of mesohyl to choanocyte chambers in the choanosome varies from 2.2:1 to 2.8:1. Both spicule and fibre skeleton

absent. NW Mediterranean (Marseilles; Boury-Esnault *et al.*, 1995) (Table 1).

Remarks. *Pseudocorticium* shares the absence of skeleton, thin, triangular apopylar cells, and two types of cells of inclusions with species of *Oscarella*, from which it differs by its well developed cortex, leuconoid aquiferous system and diplodal choanocyte chambers. The recent proposal to synonymise the families Plakinidae and Oscarellidae (Solé-Cava *et al.*, 1992; Diaz & Van Soest, 1994; Boury-Esnault *et al.*, 1995) was based on its greater similarity to *Corticium* than to *Oscarella* in anatomical and external morphological characters, supported by allozyme data.

Distribution

This monotypic genus is so far known only from two semi-obscure caves at Marseilles, France (NW Mediterranean) (Table 1; Solé-Cava *et al.*, 1992; Boury-Esnault *et al.*, 1995; J. Vacelet, pers. comm.).

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