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No longer Demospongiae: Homoscleromorpha formal nomination as a fourth class of Porifera

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Abstract Over the past few years, there has been growing interest among the sponge community in the phylogenetic position of the Homoscleromorpha (i.e. within or outside the class Demospongiae). Recent molecular analyses clearly show that the Homoscleromorpha forms a distinct clade separated from the

Demospongiae and is composed of two families, Oscarellidae and Plakinidae. Within the currently more widely accepted hypothesis of a monophyletic Porifera, we formally propose here to raise Homoscleromorpha to the class rank (the fourth one). We, therefore, provide a definition and a formal diagnosis. In the supplementary materials, we also present an alternative classification of the Homoscleromorpha, following the *PhyloCode*.

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Past and current systematics

For two decades now, phylogenies using genetic and morphological data have provided crucial information toward resolving sponge systematics (Erpenbeck & Wörheide, 2007). While the phylogenetic status of Porifera (monophyly vs. paraphyly) is still debated (Philippe et al., 2009; Sperling et al., 2009), internal phylogenies for the major sponge groups (i.e. the three Recent classes: Demospongiae, Calcarea, and Hexactinellida) are becoming better resolved (Borchiellini et al., 2004; Dohrmann et al., 2006, 2008). However, the affinities and rank of Homoscleromorpha remain unresolved within the Linnaean classification (Muricy, 1999; Muricy & Diaz, 2002).

Traditionally, Homoscleromorpha has been classified as a family or a suborder of the subclass Tetractinellida, within the class Demospongiae, mainly due to the shared presence of siliceous tetractinal-like calthrop spicules (Lévi, 1956). Lévi (1973) later proposed classifying them as a distinct subclass of the Demospongiae. Until 1995, two families were recognized within the Homoscleromorpha, Plakinidae Schulze, 1880 and Oscarellidae Lendenfeld, 1887, distinguished by the presence or absence of the mineral skeleton, respectively. However, in 1990, the discovery of a skeleton-less *Corticium*-like species led Solé Cava et al. (1992) to propose the rejection of the family Oscarellidae. Later, when this species was described as a member of a new genus *Pseudocorticium* (Boury-Esnault et al., 1995), all homoscleromorph genera were merged into a single family, the Plakinidae. *Pseudocorticium* is indeed devoid of a mineral skeleton like the genus *Oscarella*, but is more similar in histological traits (notably the leuconoid aquiferous system and a well-developed ectosome with cortex) to the spiculate genus *Corticium*.

Nowadays, according to the two current synopses of the poriferan classification, *Systema Porifera* (Hooper et al., 2002) and the *World Porifera Database* (<http://www.marinespecies.org/porifera/>; Van Soest, 2011), Homoscleromorpha is a subclass of the class Demospongiae, containing one order Homosclerophorida Dendy, 1905, one family Plakinidae Schulze, 1880, and seven genera: *Oscarella* Vosmaer, 1884; *Plakina* Schulze, 1880; *Plakortis* Schulze, 1880; *Plakinastrella* Schulze, 1880; *Corticium* Schmidt, 1862; *Pseudocorticium* Boury-Esnault et al., 1995; *Placinolopha* Topsent, 1897.

New insights from molecular phylogenies/phylogenomics studies

Since these two synopses were compiled, molecular phylogenies have challenged these traditional classification schemes. Indeed, in 2004, the first molecular phylogeny of an extensive sampling of Demospongiae *sensu lato* (based on 18S and 28S rDNA) suggested that Homoscleromorpha should form a clade on its own, clearly separated from the rest of the Demospongiae (Borchiellini et al., 2004). Subsequent phylogenetic/phylogenomic studies using several nuclear markers corroborated this hypothesis and suggested a sister-

group relationship of Homoscleromorpha and calcareous sponges (Calcarea, also known as Calcispongia) (Dohrmann et al., 2008; Philippe et al., 2009; Pick et al., 2010) (Fig. 1). Alternatively, homoscleromorphs were recovered as the sister group of Eumetazoa, albeit with low statistical support (Sperling et al., 2009). Although analysis of complete mitochondrial genomes seemingly supported the traditional placement within the Demospongiae (Lavrov et al., 2008; Wang & Lavrov, 2008), these studies were hampered by a lack of data from Calcarea, preventing a true test of the phylogenetic position of Homoscleromorpha. In any case, the number of homoscleromorph species included in the above-mentioned studies was very low (one or two).

Recently, molecular phylogenetic taxon sampling of Homoscleromorpha was substantially improved to include 18S, 28S rDNA sequences and mitochondrial genomes of six of the seven presently described genera (Gazave et al., 2010a). This study greatly contributed to resolve internal relationships of the group, restored the supra-generic classification of Homoscleromorpha abandoned in 1995 (Boury-Esnault et al., 1995), and reinstated the families Oscarellidae and Plakinidae on the basis of molecular and morphological evidence (Fig. 1). Uncertainties remain concerning the monophyly of *Oscarella* but it clearly appears that *Corticium* and *Plakinastrella* are monophyletic genera. The *Plakina* issue is more challenging and calls for further detailed molecular investigations (Fig. 1).

Linnaean classification of Homoscleromorpha

Taking into account the recent molecular studies, we consider that it is now well-established that Homoscleromorpha is not closely related to other demosponges. We feel that these new insights should be reflected in the Linnaean classification. In this classification system, the rank of both Homoscleromorpha and Calcarea is directly dependent on the phylogenetic status of Porifera. The most complete and robust molecular study of Porifera to date clearly supports the hypothesis of its monophyly, a hypothesis that is also consistent with morphological characters (Philippe et al., 2009; Pick et al., 2010). We thus formally propose, in the present paper, to raise Homoscleromorpha from subclass within Demospongiae to a fourth Recent class of Porifera (there is also a fifth extinct class of Porifera, the Archaeocyatha e.g. Debrenne et al., 2002).

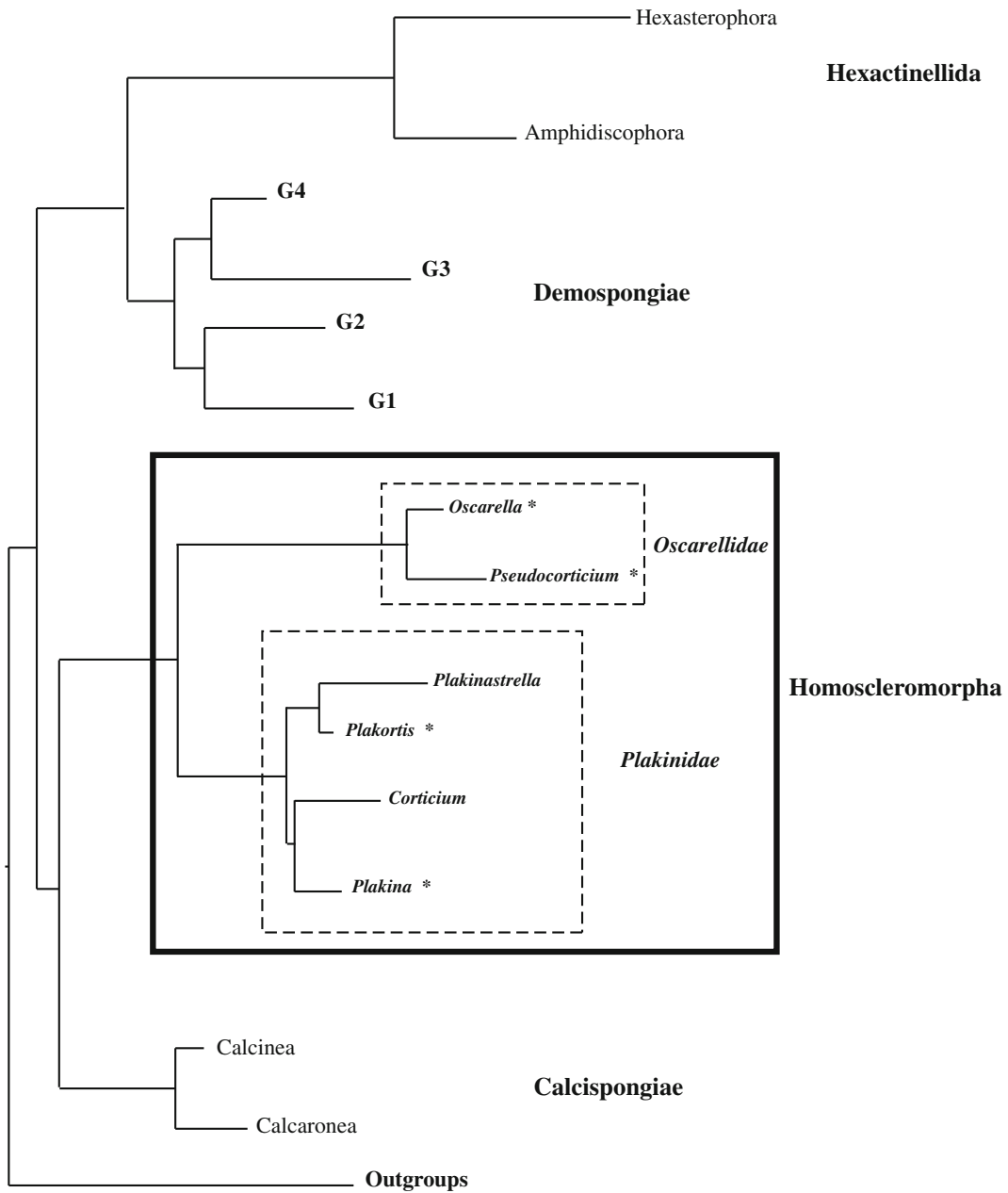


Fig. 1 Porifera simplified tree, following the monophyly hypothesis, mentioning the Linnaean names of the Homoscleromorpha families and genera. Homoscleromorpha genera that

are not monophyletic or from which uncertainties subsist are identified with an *asterisk*

Definition (modified from Hooper & Van Soest, 2002)

Definition

Class Homoscleromorpha Bergquist, 1978
 Other names. Microsclerophora Sollas, 1885.
 Carnosa Carter, 1875.

Porifera with cinctoblastula larvae and embryonic incubation; flagellated exo- and endopinacocytes; a basement membrane lining both choanoderm and pinacoderm; skeleton, if present, composed of

tetraxonic siliceous spicules–calthrops- and its derivatives with equal rays (diodes, triods, and lophate spicules), arranged around oval to spherical choanocyte chambers reflecting the canal structure (sylleibid-like or leuconoid organization); no differentiation between megascleres and microscleres although size differences do occur between types of spicules; spicules usually small (100 μm or less), not localized in any particular region; choanocyte chambers with large choanocytes.

Remark

Order Homosclerophorida Dendy, 1905 has the same definition as the class Homoscleromorpha (except for the fact that it concerns the Demospongiae instead of the Porifera).

Formal diagnosis (in complement to Muricy & Diaz, 2002)

Diversity and area distribution

Homoscleromorphs are a small group of exclusively marine sponges. Among the 84 presently described species, they are 16 species of *Oscarella*, one of *Pseudocortidium*, 6 of *Corticium*, 6 of *Placinolopha*, 25 of *Plakina*, 11 of *Plakinastrella*, and 19 of *Plakortis*. They are encrusting or lumpy with a smooth surface, usually occurring at shallow depths. Recently, several new species have been described from various areas (from Brazil to Alaska, Africa and Indo-Australian coasts). They mainly pertain to the *Oscarella* and *Plakortis* genera (Moraes & Muricy, 2003; Muricy & Pearse, 2004; Ereskovsky, 2006; Ereskovsky et al., 2009a; Muricy, 2011; Pérez et al., 2011).

Skeleton

If present, it consists of small calthrops (peculiar type of tetractines spicules) and/or their derivatives (lophose calthrops, diodes and triodes). These spicules are evenly distributed in the sponge body and do not form a well-organized skeleton. Spicules are secreted by sclerocytes, pinacocytes of the external epithelium and also, to a lesser degree, by pinacocytes of the internal epithelia (Maldonado & Riesgo, 2007). In contrast to the axial filament of siliceous spicules in Demospongiae and Hexactinellida, the organic core

of the spicules of Homoscleromorpha is amorphous, indicating a possible lack of a tertiary structure of the protein contained (Uriz, 2006).

Ultrastructure

The aquiferous system is sylleibid or leuconoid, with large choanocyte chambers (eurypilous, aphodal, or diploid). The homoscleromorphs are the only Porifera that have a true basement membrane with type IV collagen, tenascin and laminin, underlying the choanoderm and the pinacoderm (Boute et al., 1996) and larval ciliated epithelium (Boury-Esnault et al., 2003). Homoscleromorpha possess flagellated exopinacocytes and endopinacocytes, peculiar flagellated apopylar cells, and *zonula adhaerens* cell junctions in adults and larval epithelia (Ereskovsky et al., 2009a).

Development

Homoscleromorpha are sponges with embryos incubation (Ereskovsky, 2010). Spermatogenesis is asynchronous inside one spermatid cyst and a gradient in cell differentiation occurs along the spermatid cysts, with spermatocytes at one side and spermatozooids on the opposite side (Gaino et al., 1986; Ereskovsky, 2005). The spermatozooids have an acrosome (Baccetti et al., 1986; Riesgo et al., 2007). The hollow blastula is formed by means of multipolar egression (centrifugal migration of cells from the center to the periphery of the morula) and presents a central cavity (Ereskovsky & Boury-Esnault, 2002). The cincto-blastula larva possesses a belt of postero-lateral cells with an intranuclear crystalloid and ciliated cells with cross-striated rootlet (Boury-Esnault et al., 2003), which derives from the secondary centriole (Maldonado & Riesgo, 2008). All morphogenesis processes follow the epithelial type (Ereskovsky et al., 2009b).

Scope of the taxon (in complement of Muricy & Diaz, 2002)

Families Oscarellidae and Plakinidae, composed, respectively, of *Oscarella* and *Pseudocortidium* genera and *Plakortis*, *Plakinastrella*, *Corticium*, *Placinolopha*, and *Plakina* genera (Gazave et al., 2010a; Ivanisevic et al., 2010).

Discussion

Although molecular phylogenetic/phylogenomic studies have profoundly increased our understanding of this peculiar group of sponge, one main point is still uncertain: the evolutionary history of the basement membrane (Leys et al., 2009; Philippe et al., 2009). The appearance of a basement membrane as a histological barrier may have important implications concerning cell type specification systems and cell movement mechanisms. This baso-epithelial basement membrane present in both larvae and adult of homoscleromorphs but also in eumetazoans (1) may have been inherited from Urmetazoa (the last common ancestor of animals) and then subsequently lost in the three other sponge classes or (2) may have appeared independently twice in the course of evolution, in Homoscleromorpha sponges and in Eumetazoa. It may be noted that, alternatively, according to the sponge paraphyly hypothesis, this basement membrane may equally represent a synapomorphy of a clade containing Homoscleromorpha and Eumetazoa (named by some authors Epitheliozoa (Sperling et al., 2009)). To date, this issue has not yet been resolved but comparison of basement membrane molecular components between all Porifera classes and Eumetazoa may provide new evidence in the future.

In addition to molecular data, several morphological and developmental differences may be noticed between Homoscleromorpha and Demospongiae that support the molecular topology discussed above. The most remarkable morphological difference is the presence of a true epithelium (basement membrane and apical cell junctions) in Homoscleromorpha and its absence in Demospongiae (as well as in other sponge groups) (Ereskovsky, 2010). Another important cytological character is the flagellated exopinacoderm, which is absent in demosponges, calcareans and hexactinellids. An alveolar choanosomal skeleton, typical of many Plakinidae species, as well as diodes and triodes is also absent in demosponges (Muricy & Diaz, 2002). Concerning the developmental features that are different between those sponge classes, one can note: (1) asynchronous spermatogenesis, whereas it is synchronous in the Demospongiae (Gaino et al., 1986); (2) a multipolar egression during embryonic development (Ereskovsky & Boury-Esnault, 2002); (3) an epithelial invagination

during metamorphosis (Ereskovsky et al., 2007); (4) a budding process by morphallactic morphogenesis (Ereskovsky & Tokina, 2007).

Morphological characters supporting the proposed sister-group relationship between Homoscleromorpha and Calcarea are more scarce. A remarkable resemblance is the presence of cross-striated rootlet in larval ciliated cells of both cinctoblastula (Homoscleromorpha) (Boury-Esnault et al., 2003) and amphiblastula (Calcaronea) and calciblastula (Calcinea) (Gallissian & Vacelet, 1992; Ereskovsky & Willenz, 2008). This type of rootlet is absent in other sponge groups and may represent a synapomorphy of a clade (Homoscleromorpha + Calcarea).

Relationships among Homoscleromorpha species also provide a basis for a new hypothesis regarding the evolution of morphological characters. Due to the restoration of the two Homoscleromorpha families (Oscarellidae and Plakinidae), the cortex, aquiferous system organization, and outer morphological similarities encountered between *Corticium* and *Pseudocorticium* (and previously proposed as synapomorphies) would appear to represent homoplastic characters.

Concerning the nonmonophyly of the genus *Plakina*, this may explain the wide variability in morphological characters previously observed in this genus (Muricy et al., 1998). Thus, the genus *Plakina* should be redefined in the future and, potentially subdivided into several genera on the basis of a comprehensive molecular and morphological analysis of extant species.

Conclusion

In this paper, we chose to follow the strongly supported sponge monophyly hypothesis and formally raised the Homoscleromorpha as a fourth poriferan class. Should the alternative hypothesis that Porifera is paraphyletic (Sperling et al., 2009) gain significant support in the future and the sponge monophyly hypothesis be convincingly refuted, Homoscleromorpha and Calcarea would need to change ranks and be reconsidered as potential distinct phyla. This example illustrates the constraints of a rank-based (hierarchical) nomenclatural system whereby molecular data may support a clade but without necessarily the support of morphological synapomorphies. We consider that the information obtained

from molecular (and other) datasets that do not necessarily fit into a hierarchical classification should not be lost (Manuel et al., 2003; Borchiellini et al., 2004; Cárdenas et al., 2010, 2011; Gazave et al., 2010b), and therefore, we provide here an alternative classification of Homoscleromorpha, using the draft recommendations and processes defined by the *PhyloCode* (<http://www.ohio.edu/phylocode>) (online resources 1 and 2).

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