



HAL
open science

No longer Demospongiae: Homoscleromorph formal nimation as a fourth class of porifera

Eve Gazave, Pascal Lapébie, Alexander Ereskovsky, Jean V Vacelet,
Emmanuelle Renard, Paco Cárdenas, Carole Borchiellini

► **To cite this version:**

Eve Gazave, Pascal Lapébie, Alexander Ereskovsky, Jean V Vacelet, Emmanuelle Renard, et al.. No longer Demospongiae: Homoscleromorph formal nimation as a fourth class of porifera. *Hydrobiologia*, 2012, 687 (1), pp.3 - 10. 10.1007/s10750-011-0842-x . hal-01456632

HAL Id: hal-01456632

<https://hal.science/hal-01456632>

Submitted on 13 Apr 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Eve Gazave · Pascal Lapébie · Alexander V. Ereskovsky ·
Jean Vacelet · Emmanuelle Renard ·
Paco Cárdenas · Carole Borchiellini

Received: 22 February 2011 / Accepted: 30 July 2011 / Published online: 12 August 2011
© Springer Science+Business Media B.V. 2011

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*.

Electronic supplementary material The online version of this article (doi:[10.1007/s10750-011-0842-x](https://doi.org/10.1007/s10750-011-0842-x)) contains supplementary material, which is available to authorized users.

Guest editors: M. Maldonado, X. Turon, M. A. Becerro & M. J. Uriz / Ancient animals, new challenges: developments in sponge research

E. Gazave
Institut Jacques Monod, Université Paris Diderot,
CNRS UMR 7592, Paris, France

E. Gazave · P. Lapébie · A. V. Ereskovsky ·
J. Vacelet · E. Renard · C. Borchiellini (✉)
Centre d'Océanologie de Marseille, Station marine
d'Endoume, Aix-Marseille Université, CNRS UMR
6540-DIMAR, Marseille, France
e-mail: carole.borchiellini@univmed.fr

P. Lapébie
Biologie du Développement, Observatoire
Océanologique, Université Pierre et Marie Curie-Paris 6,
CNRS UMR 7009, Villefranche-sur-Mer, France

P. Cárdenas
Département Milieux et Peuplements Aquatiques,
Muséum National d'Histoire Naturelle,
UMR 7208 "BORéA", Paris, France

Keywords Porifera · New class ·
Homoscleromorpha · Oscarellidae · Plakinidae ·
PhyloCode

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).

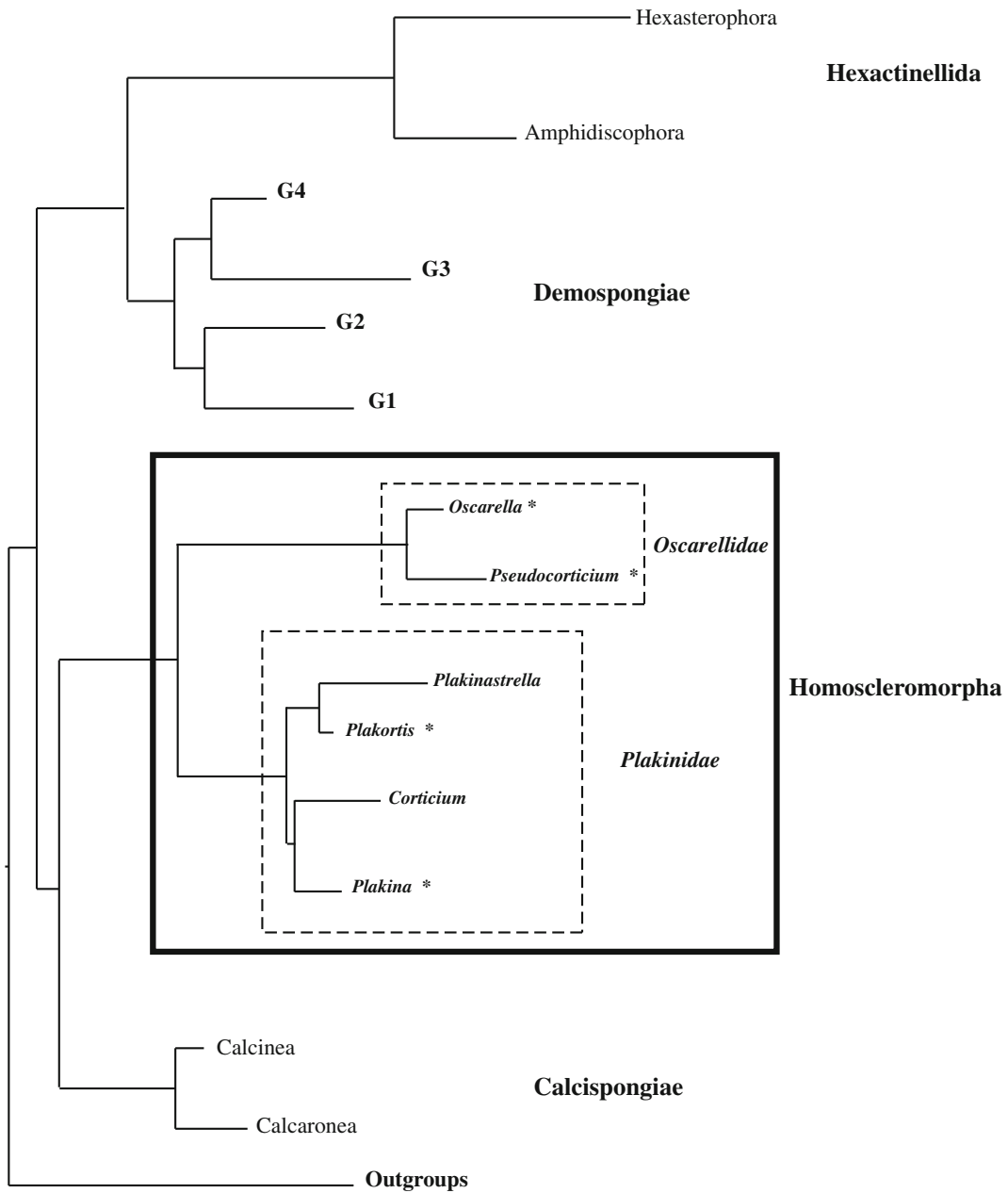


Fig. 1 Porifera simplified tree, following the monophyly hypothesis, mentioning the Linnaean names of the Homoscleromorpha families and genera. Homoscleromorpha genera that

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 & Pearce, 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 cinctoblastula 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).

Acknowledgments We thank the organizers of the conference in Girona for this excellent meeting and for giving us the opportunity to contribute to the special volume of *Hydrobiologia* dedicated to sponges. We are also very grateful to Dr. Nicole Boury-Esnault for stimulating discussions on the *PhyloCode*. We thank three anonymous reviewers for helpful comments. This work was partly supported by bilateral program RFBR-PICS No. 5581. The English language has been revised by Michael Paul.

References

- Baccetti, B., E. Gaino & M. Sara, 1986. A sponge with acrosome: *Oscarella lobularis*. *Journal of Ultrastructure and molecular structure research* 94: 195–198.
- Bergquist, P. R., 1978. Sponges. Hutchinson & Co, London.
- Borchiellini, C., C. Chombard, M. Manuel, E. Alivon, J. Vacelet & N. Boury-Esnault, 2004. Molecular phylogeny of Demospongiae: implications for classification and scenarios of character evolution. *Molecular phylogenetics and evolution* 32: 823–837.
- Boury-Esnault, N., G. Muricy, M. F. Gallissian & J. Vacelet, 1995. Sponges without skeleton: a new Mediterranean genus of Homoscleromorpha (Porifera, Demospongiae). *Ophelia* 43: 25–43.
- Boury-Esnault, N., A. V. Ereskovsky, C. Bezac & D. B. Tokina, 2003. Larval development in Homoscleromorpha (Porifera, Demospongiae). *Invertebrate Biology* 122: 187–202.
- Boute, N., J. Y. Exposito, N. Boury-Esnault, J. Vacelet, N. Noro, K. Miyazaki, K. Yoshizato & R. Garrone, 1996. Type IV collagen in sponges, the missing link in basement membrane ubiquity. *Biology of the Cell* 88: 37–44.
- Cárdenas, P., H. T. Rapp, C. Schander & O. S. Tender, 2010. Molecular taxonomy and phylogeny of the Geodiidae (Porifera, Demospongiae, Astrophorida)—combining phylogenetic and Linnaean classification. *Zoologica scripta* 39: 89–106.
- Cárdenas, P., J. R. Xavier, J. Reveillaud, C. Schander & H. T. Rapp, 2011. Molecular phylogeny of the astrophorida (Porifera, Demospongiae^P) reveals an unexpected high level of spicule homoplasy. *PLoS ONE* 6(4): e18318. doi:10.1371/journal.pone.0018318.
- Carter, H. J., 1875. Notes introductory to the study and classification of the Spongida. *The Annals and Magazine of Natural History* 4: 1–40 (126–145, 177–200).
- Debrenne, F., A. Y. Zhuravlev & P. D. Kruse, 2002. Class Archaeocyatha Bornemann, 1884. In Hooper, J. N. A. & R. W. M. Van Soest (eds), *Systema Porifera: A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York: 1539–1699.
- Dendy, A., 1905. Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. Royal Society, London.
- Dohrmann, M., O. Voigt, D. Erpenbeck & G. Wörheide, 2006. Non-monophyly of most supraspecific taxa of calcareous sponges (Porifera, Calcarea) revealed by increased taxon sampling and partitioned Bayesian analysis of ribosomal DNA. *Molecular Phylogenetics and Evolution* 40: 830–843.
- Dohrmann, M., D. Janussen, J. Reitner, A. G. Collins & G. Wörheide, 2008. Phylogeny and evolution of glass sponges (Porifera, Hexactinellida). *Systematic Biology* 57: 388–405.
- Ereskovsky, A. V., 2005. *Comparative Embryology of Sponges (Porifera)*. Saint-Petersburg University Press, Saint-Petersburg.
- Ereskovsky, A. V., 2006. A new species of *Oscarella* (Demospongiae: Plakinidae) from the Western Sea of Japan. *Zootaxa* 1376: 37–51.
- Ereskovsky, A. V., 2010. *The Comparative Embryology of Sponges*. Springer-Verlag, Dordrecht, Heidelberg, London, New York.
- Ereskovsky, A. V. & N. Boury-Esnault, 2002. Cleavage pattern in *Oscarella* species (Porifera, Demospongiae, Homoscleromorpha): transmission of maternal cells and symbiotic bacteria. *Journal of Natural History* 36: 1761–1775.
- Ereskovsky, A. V. & D. B. Tokina, 2007. Asexual reproduction in homoscleromorph sponges (Porifera; Homoscleromorpha). *Marine Biology* 151: 425–434.
- Ereskovsky, A. V. & P. Willenz, 2008. Larval development in *Guancha arnesenae* (Porifera, Calcispongiae, Calcinea). *Zoomorphology* 127: 175–187.
- Ereskovsky, A. V., D. B. Tokina, C. Bezac & N. Boury-Esnault, 2007. Metamorphosis of Cinctoblastula Larvae (Homoscleromorpha, Porifera). *Journal of Morphology* 268: 518–528.
- Ereskovsky, A. V., K. Sanamyan & A. E. Vishnyakov, 2009a. *Oscarella kamchatkensis* sp. nov. from the North-West of Pacific. *Cahiers de Biologie marine* 50: 369–381.
- Ereskovsky, A. V., C. Borchiellini, E. Gazave, J. Ivanisevic, P. Lapebie, T. Perez, E. Renard & J. Vacelet, 2009b. The Homoscleromorph sponge *Oscarella lobularis*, a promising sponge model in evolutionary and developmental biology. *Bioessays* 31: 89–97.
- Erpenbeck, D. & G. Wörheide, 2007. On the molecular phylogeny of sponges. *Zootaxa* 1668: 107–126.
- Gaino, E., B. Burlando, P. Buffa & M. Sara, 1986. Ultrastructural study of spermatogenesis in *Oscarella lobularis* (Porifera, Demospongiae). *International Journal of Invertebrates Reproduction and Development* 10: 297–305.
- Gallissian, M. F. & J. Vacelet, 1992. Ultrastructure of the oocyte and embryo of the calcified sponge, *Petrobiona massiliana* (Porifera, Calcarea). *Zoomorphology* 112: 133–141.
- Gazave, E., P. Lapebie, E. Renard, J. Vacelet, C. Rocher, A. V. Ereskovsky, D. V. Lavrov & C. Borchiellini, 2010a.

- Molecular phylogeny restores the supra-generic subdivision of Homoscleromorph sponges (Porifera, Homoscleromorpha). PLoS ONE. doi:10.1371/journal.pone.0014290.
- Gazave, E., S. Carteron, E. Richelle-Maurer, N. Boury-Esnault & C. Borchellini, 2010b. Polyphyly of the genus *Axinella* and of the family Axinellidae (Porifera: Demospongiae). *Molecular Phylogenetics and Evolution* 57: 35–47.
- Hooper JNA, van Soest RWM (2002) *Systema Porifera: A Guide to the Classification of Sponges*. New York: Kluwer Academic/Plenum Publishers.
- Hooper, J. N., R. W. M. Van Soest & F. Debrenne (eds), 2002. *Phylum Porifera Grant, 1836; Systema Porifera: A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York.
- Ivanisevic, J., O. P. Thomas, C. Lejeune, P. Chevaldonné & T. Pérez, 2010. Metabolic fingerprinting as an indicator of biodiversity: towards understanding inter-specific relationships among Homoscleromorpha sponges. *Metabolics*. doi:10.1007/s11306-010-0239-2.
- Lavrov, D. V., X. Wang & M. Kelly, 2008. Reconstructing ordinal relationships in the Demospongiae using mitochondrial genomic data. *Molecular Phylogenetics and Evolution* 49: 111–124.
- Lendenfeld, R. V., 1887. On the systematic position and classification of sponges. *Proceedings of the Zoological Society of London* 1887: 558–662.
- Lévi, C., 1956. Etude des Halisarca de Roscoff. *Embryologie et systématique des démosponges*. *Archives de Zoology Experimentale et Generale* 93: 1–184.
- Lévi, C., 1973. *Systématique de la classe des Demospongiaria (Demosponges)*. In Grassé, P. P. (ed.), *Spongiaires*. Masson & Compagnie, Paris: 577–632.
- Leys, S. P., S. A. Nichols & E. D. M. Adams, 2009. Epithelia and integration in sponges. *Integrative and Comparative Biology* 49: 167–177.
- Maldonado, M. & A. Riesgo, 2007. Intraepithelial spicules in a homosclerophorid sponge. *Cell and Tissue Research* 328: 639–650.
- Maldonado, M. & A. Riesgo, 2008. Reproductive output in a Mediterranean population of the homosclerophorid *Corticium candelabrum* (Porifera, Demospongiae), with notes on the ultrastructure and behavior of the larva. *Marine Ecology* 29: 298–316.
- Manuel, M., C. Borchellini, E. Alivon, Y. Le Parco, J. Vacelet & N. Boury-Esnault, 2003. Phylogeny and evolution of calcareous sponges: monophyly of Calcinea and Calcaronea, high level of morphological homoplasy, and the primitive nature of axial symmetry. *Systematic Biology* 52: 311–333.
- Moraes, F. C. & G. Muricy, 2003. Taxonomy of Plakortis and Plakinastrella (Demospongiae: Plakinidae) from oceanic islands off north-eastern Brazil, with description of three new species. *Journal of the Marine Biological Association of the United Kingdom* 83: 385–397.
- Muricy, G., 1999. An evaluation of morphological and cytological data sets for the phylogeny of Homosclerophorida (Porifera: Demospongiae). *Memoirs of the Queensland Museum* 44: 399–409.
- Muricy, G., 2011. Diversity of Indo-Australian *Plakortis* (Demospongiae: Plakinidae), with description of four new species. *Journal of the Marine Biological Association of the United Kingdom* 91: 303–319.
- Muricy, G. & M. C. Diaz, 2002. Order Homosclerophorida Dendy, 1905, Family Plakinidae Schulze, 1880. In *Systema Porifera*. In Hooper, J. N. A. & R. W. M. Van Soest (eds), *A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York: 71–82.
- Muricy, G. & J. S. Pearce, 2004. A new species of *Oscarella* (Demospongiae: Plakinidae) from California. *Proceedings of the California Academy of Sciences* 55: 598–612.
- Muricy, G., N. Boury-Esnault, C. Bézac & J. Vacelet, 1998. Taxonomic revision of the Mediterranean *Plakina* Schulze (Porifera, Demospongiae, Homoscleromorpha). *Zoological Journal of the Linnean Society* 124: 169–203.
- Pérez, T., J. Ivanisevic, M. Dubois, L. Pedel, O. P. Thomas, D. Tokina & A. V. Ereskovsky, 2011. *Oscarella balibaloï*, a new sponge species (Homoscleromorpha: Plakinidae) from the Western Mediterranean Sea: cytological description, reproductive cycle and ecology. *Marine Ecology* 32: 174–187.
- Philippe, H., R. Derelle, P. Lopez, K. Pick, C. Borchellini, N. Boury-Esnault, J. Vacelet, E. Renard, E. Houliston, E. Queinac, C. Da Silva, P. Wincker, H. Le Guyader, S. Leys, D. J. Jackson, F. Schreiber, D. Erpenbeck, B. Morgenstern, G. Wörheide & M. Manuel, 2009. Phylogenomics revives traditional views on deep animal relationships. *Current Biology* 19: 706–712.
- Pick, K. S., H. Philippe, F. Schreiber, D. Erpenbeck, D. J. Jackson, P. Wrede, M. Wiens, A. Alié, B. Morgenstern, M. Manuel & G. Wörheide, 2010. Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. *Molecular Biology and Evolution* 27: 1983–1987. doi:10.1093/molbev/msq089.
- Riesgo, A., M. Maldonado & M. Durfort, 2007. Dynamics of gametogenesis, embryogenesis, and larval release in a Mediterranean homosclerophorid demersal sponge. *Marine and Freshwater Research* 58: 398–417.
- Schmidt, O., 1862. *Die Spongien des Adriatischen Meeres*. Verlag Von Wilhelm Engelmann, Leipzig: 88.
- Schulze, F. E., 1880. Untersuchungen über den Bau und die Entwicklung der Spongien. Neunte Mittheilung. Die Plakiniden. *Zeitschrift für Wissenschaftliche Zoologie Abt A* 34: 407–451.
- Solé Cava, A. M., N. Boury-Esnault, J. Vacelet & J. P. Thorpe, 1992. Biochemical genetic divergence and systematics in sponges of the genera *Corticium* and *Oscarella* (Demospongiae: Homoscleromorpha) in the Mediterranean Sea. *Marine Biology* 113: 299–304.
- Sollas, W. J., 1885. A classification of the sponges. *Annals and Magazine of Natural History* 5: 395.
- Sperling, E. A., K. J. Peterson & D. Pisani, 2009. Phylogenetic signal dissection of nuclear housekeeping genes supports the paraphyly of sponges and the monophyly of Eumetazoa. *Molecular Biology and Evolution* 26: 2261–2274.
- Topsent, E., 1897. Spongiaires de la Baie d'Amboine. (Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais). *Revue Suisse de Zoologie* 4: 421–487.
- Uriz, M. J., 2006. Mineral skeletogenesis in sponges. *Canadian Journal of Zoology* 84: 322–356.

- Van Soest, R., 2011. Homoscleromorpha. In: Van Soest, R. W. M., N. Boury-Esnault, J. N. A. Hooper, K. Rützler, N. J. de Voogd, B. Alvarez de Glasby, E. Hajdu, A. B. Pisera, R. Manconi, C. Schoenberg, D. Janussen, K. R. Tabachnick, M. Klautau, B. Picton, M. Kelly (eds), World Porifera database. <http://www.marinespecies.org/porifera/porifera.php?p=taxdetails&id=131587>, on April 26, 2011.
- Vosmaer, G. C. J., 1884. Studies on sponges: II–IV. Mitteilungen aus der Zoologischen Station zu Neapel 5: 483–493.
- Wang, X. & D. V. Lavrov, 2008. Seventeen new complete mtDNA sequences reveal extensive mitochondrial genome evolution within the Demospongiae. PLoS ONE 3: e2723.