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SYSTEMA PORIFERA. A GUIDE TO THE CLASSIFICATION OF SPONGES …. THE END OF A BEGINNING

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ABSTRACT

The *Systema Porifera* collaboration (45 authors from 17 countries) produced a two volume treatise revising and defining the supraspecific classification of sponges and spongiomorphs (Kluwer Academic / Plenum Publishers). The *Systema* recognises approximately 680 genera of living sponges and 1000 genera of fossil sponges from many thousands of nominal taxa, and places these taxa in a unified higher systematics scheme (including over forty new higher taxa proposed). Most genera were revised from their type material (where available), reinterpretation of the vast sponge literature, and incorporation of other biological evidence where available. The *Systema*, therefore, has an important theoretical basis, being: the most comprehensive taxonomic revision of sponges at genus level and above; addressing the many long-outstanding nomenclatural problems (and thus stabilising the nomenclature) and providing a sound baseline to focus detailed research questions on sponges in the future. It also has a strong practical focus as a tool for sponge identification: providing concise definitions, diagnoses, keys and illustrations of all the valid (*i.e.*, reinterpreted) genera of extant sponges, and some key fossil sponge genera, unified into a single classification of Porifera; serving as a manual to achieve more accurate faunal inventories that will be of benefit to biodiversity and biogeographic analyses etc., and thus marine conservation and planning. In this paper we critically analyse the strengths (achievements) and weaknesses (remaining challenges) of the *Systema Porifera* project, and highlight some areas where research might be productively directed in the future, including questions of the monophyly of Porifera itself.

INTRODUCTION

The *Systema Porifera* is a unique treatise on the systematics of living and fossil sponges. Aside from the pioneering attempt by DE LAUBENFELS (1936) to make the sponge systematics ‘widely available’ at a practical level of classification (families and genera) no other publication has attempted to achieve what we have achieved here.

The project started life as a small collaboration amongst several authors in an attempt to ‘clear up some of the mess’ in sponge taxonomy, and to make it more widely available to the non-specialist biologist. Seven years later, at its conclusion, the project had expanded to 45 authors from 17 different countries (with a combined experience of over 600 person years). The end product was a large manuscript of 2500 MS pages, 1200 figures, in which approximately 680 genera of living sponges and 1000 genera of fossil sponges were defined, illustrated and placed in a unified higher systematics scheme, including over forty new higher taxa.

The *Systema* revisited and critically reinterpreted the vast sponge literature. It re-examined and redescribed the pertinent type material (where available) of all nominal genera. It revised all existing taxonomic combinations (including the creation of new taxa where necessary), and which for some taxa constituted major systematic revisions. In doing these things it moved closer towards stabilizing the sponge nomenclature. Finally, it provided concise definitions, diagnoses, keys and illustrations of all the valid (*i.e.*, reinterpreted) genera of extant sponges, and some key fossil sponge genera, unified into a single classification of Porifera. Thus, the *Systema* will serve as both a sound theoretical basis to focus detailed research questions in the future, and also as a practical tool for specimen identification. Have we, therefore, now reached the end and achieved a definitive classification for the Phylum Porifera ? Or is the *Systema* just the end of a beginning ?

THE *SYSTEMA* PROJECT

A renewed interest in sponges over the past few decades has accelerated the discovery and documentation of species in all the oceans, with recent estimates from the various museum collections that the extant fauna may be twice as diverse as that currently described ca. 7000 species (*e.g.,* HOOPER & LÉVI, 1994; VAN SOEST, 1994). As a consequence, it was necessary to revisit the existing systematics in order to accommodate these substantial new collections, which was the initial impetus to produce this book, in addition to solving the many outstanding nomenclatural and taxonomic complexities within the existing systematics. Several previous attempts to gather all the described higher taxa together (genus and above) were grossly inadequate and/or incomplete (*e.g.,* DE LAUBENFELS' (1936) monograph on the Dry Tortugas sponges; HOOPER's (1997) 'Sponguide' (http://www.qmuseum.qld.gov.au/organisation/sections/SessileMarineInvertebrates/index.asp); van Soest's unpublished database of species worldwide, etc.). Nevertheless, these sources served as a beginning for this project, which we initially estimated would take between three to four years to complete. The task soon became daunting as more and more genera, long forgotten, misdescribed or misinterpreted, were discovered. Their type species needed to be tracked down (where possible) and redescribed, and the concept of these generic taxa consequently confirmed or revised. Also, other information from the contemporary literature needed to be considered in formulating definitions and in discussing the scope and contents of various higher taxa, such as incorporating additional species into genera (that had the potential to broaden generic definitions), and other biological evidence (such as molecular, reproductive and chemotaxonomic studies) that could confirm or refute morphological hypotheses. Despite causing several years delay in publishing the *Systema*, these reinterpretations of genera were essential prerequisites to serve as objective foundations for defining the higher taxa (families, suborders, orders, and in some cases subclasses).

Through its long gestation the project took on three primary aims.

The *Systema* was firstly a taxonomic revision. It summarised and revised where necessary the supraspecific classification of the Phylum Porifera (including spongiomorphs such as 'Sphinctozoans', Archaeocyatha and Heteractinida), based firstly on re-evaluation of type material for each genus (when possible), and subsequently incorporating any other recent biological evidence. The *Systema* focuses on the living fauna (at genus level and above), and in most cases provides only a cursory treatment of the fossil fauna and palaeontological literature in an attempt to relate these two classifications more closely. It is anticipated that the forthcoming revision of the *Treatise on Invertebrate Paleontology* will balance this bias (FINKS *et al.,* 2004).

The *Systema* secondly serves as a practical guide, providing accessibility to the supra-specific classification of sponges and spongiomorphs; providing a clear explanation of morphological characters, their importance to the taxonomy and systematics of each higher taxon, and providing keys and illustrating the major characters used to classify each group.

Thirdly, the *Systema* provides a sound baseline for future debate on sponge taxonomy and addresses the many long-outstanding nomenclatural problems that have plagued this phylum for over a century. This is the strength of the project. In revisiting and building on the accumulated knowledge of our forebears we are able to provide (within the rules of the ICZN; ANON., 1999): a stable nomenclature; a sound contemporary classification; a remedy for the nomenclatural mistakes of the past; and incorporating more recent non-morphometric data into a unified contemporary classification of both living and fossil forms. We propose that these efforts will provide a solid platform such that future debates will hopefully now focus more on the phylogenetic controversies and unanswered biological questions than the nomenclatural ones, and which we anticipate will be solved by advances in our biological knowledge and our abilities to better sample the sponge genome.

In a similar way, the *Systema* will also be invaluable to unify our attempts at biodiversity analysis ('biocomplexity') using sponges as models. The uniformly formulated classification and nomenclature presented in the *Systema* will be indispensable for compiling more accurate faunal inventories, biogeographic databases, representative and protected marine areas, and other aspects of marine conservation and planning (*e.g.*, HOOPER *et al.,* 2002).

STRUCTURE OF THE *SYSTEMA*

The structure of the book is aimed primarily at those faced with the daunting task of identifying sponges - providing keys to diagnose classes, subclasses, orders, suborders, families and genera - and within each genus, listing the pertinent literature (where this exists) to potentially identify species. This structure, however, is fundamentally at odds with how most sponge taxonomists operate - which is from the species level upwards (a 'gestalt' approach). Anyone familiar with the appalling difficulties associated with sponge systematics would already know that keys usually work only for few well-known small regional faunas, or for small, well-characterised taxonomic groups (such as some genera and families). Keys to higher taxa comprising large numbers of very different lower taxa and covering large segments of the world oceans show inherent difficulties. These are mostly due to the frequent losses of 'pivotal characters', or the modification of these characters beyond recognition as being 'typical' for a particular taxonomic group, or the difficulty in interpreting whether characters are the same or different between groups of species. This latter problem concerns the interpretation of 'homology', whereby some prominent characters that may appear to be the same across several taxonomic groups actually represent analogous features that do not necessarily reflect phylogeny, or translate into a convenient morphological classification.

Consequently, the secondary structure of this book - and one that is more important to its future as a sound platform to develop the sponge systematics - concerns extensive analyses of sponge characters and their relative importance (homology vs. analogy), to arrive at both a practical classification and a theoretical reconstruction of sponge phylogenies. For those who are mostly interested in simply identifying sponges these phylogenetic analyses and lengthy discussions may appear to be long and confounding. We contend, however, that these data are essential for quality control. Accurate interpretation of characters is essential for the accurate identification of taxa. The *Systema* represents a concerted attempt to both stabilize the sponge nomenclature (through our collective comprehensive re-evaluations of the entire literature), and to revise the Poriferan classification (incorporating recent evidence held by experts in the field). Thus, many of these discussions and analyses are necessary to justify the new taxonomic hypotheses presented here.

SCOPE OF THE PHYLUM PORIFERA

For the purposes of the *Systema* project the Phylum Porifera was treated as a monophyletic taxon, although evidence is accumulating from other non-morphometric sources that this may not be the case, as discussed further below. The Phylum is subdivided into four classes: three (unchallenged) Recent classes (Demospongiae, Calcarea and Hexactinellida), and a fourth, apparently exclusively fossil class (Archaeocyatha) that shows possible affinities to the Demospongiae based on studies of immune responses and peculiar budding types (DEBRENNE & ZHURAVLEV, 1994).

Recent sponges include three classes, seven subclasses, 25 orders, 127 families and 682 valid genera [with over 1600 nominal genera ('available names', but now considered to be junior synonyms), plus approximately 500 other invalid ('unavailable') names]. Treatment of the fossil fauna is far less comprehensive and less critical, with seven major groups or 'class-groups', 30 orders, 245 families and 998 'valid' genera mentioned, although fossil demosponges in particular are not substantially delineated in this work, awaiting a more comprehensive treatment by FINKS *et al.* (2004) (Tab. I). Forty three new taxa are proposed - orders, families, genera and other higher taxa (Tab. II).

Class DEMOSPONGIAE

Recent Demospongiae contains three subclasses (Homoscleromorpha, Tetractinomorpha, Ceractinomorpha), 15 orders (with 7 suborders), 88 families and 490 'valid' genera (authors Bergquist, Boury-Esnault, Desqueyroux-Faundex, De

Cook, De Weerdt, Diaz, Erpenbeck, Glasby de Alvarez, Hajdu, Hooper, Kelly, Lerner, Lévi, Lobo-Hajdu, Maldonado, Manconi, Muricy, Perez, Pisera, Pronzato, Rützler, Samaai, Sarà, Uriz, Vacelet, Valentine, van Soest).

Of the fossil forms only 7 families and 25 genera of demosponges are dealt with, chosen as representative 'milestones' in the evolution of the group (authors Reitner & Wörheide), and an overview of the enigmatic 'Order Stromatoporoidea' (author Cook). The latter taxon includes 7 orders, 14 families and 109 genera. By comparison, the polyphyletic fossil 'lithistids' are covered in greater detail (authors Pisera & Lévi), with 13 suborders, 34 families and 201 genera comprehensively described and illustrated.

Class CALCAREA

Recent Calcarea is divided into 2 subclasses (Calcinea, Calcaronea), 5 orders, 22 families and 75 'valid' genera (authors Borojevic, Boury-Esnault, Vacelet and Manuel). An overview of fossil forms deals with 2 superorders, 3 orders, 6 families and 74 genera, highlighting only 'key' taxa that were indicative of trends in the evolution of the group (author Pickett). By comparison, one exclusively fossil order, the Heteractinida, is treated in much more detail (author Pickett), containing detailed descriptions and illustrations of 4 families and 20 genera.

Class HEXACTINELLIDA

Recent Hexactinellida contains 2 subclasses (Amphidiscophora, Hexasterophora), 5 orders, 17 families and 118 'valid' genera (authors Menshenina, Reiswig, Tabachnick, Wheeler). Fossil forms are treated in an overview of the group, covering only 2 orders, 2 superfamilies, 18 families and 121 genera, with illustrations and descriptions of only 'key' taxa that are indicative of evolutionary trends in the group (author Krautter).

Class ARCHAEOCYATHA

Fossil Archaeocyathans are classified in 6 orders, 13 suborders, 55 superfamilies, 120 families and 307 genera (authors Debrenne, Zhuravlev and Kruse).

The 'Class Sphinctozoans', or chambered sponges, with most representatives extinct, is treated in a separate section although acknowledging that the taxon is polyphyletic, with representatives now allocated to each of the four established classes (and one alleged living sphinctozoan, *Vaceletia*, included in the Demospongiae). Senowbari-Daryan & García-Bellido recognise 9 orders, 42 families and 141 genera of 'sphinctozoans'.

MONOPHYLY OF PORIFERA

The Phylum Porifera has been suggested to be paraphyletic based on 28S rDNA (*e.g.*, LAFAY *et al.,* 1992) and 18S rDNA (*e.g.*, BORCHIELLINI *et al.,* 2001), with Calcarea allegedly more closely related to other metazoans than to the siliceous sponges (Demospongiae + Hexactinellida), showing deep radiations between these two groups. SIDDALL *et al.* (1995) and CAVALIER-SMITH *et al.* (1996) provided further data to support a closer relationship between calcareans and the ctenophorans than with the siliceous sponges, and ZRZAVÝ *et al.* (1998) listed some possible synapomorphies to define a clade (Calcarea + Ctenophora + Cnidaria), including the possible non-homology of choanocyte flagellae throughout the Porifera (with calcareans having cross-striated flagellar rootlets found in some triploblasts but not in the diploblastic siliceous sponges), and the animal-like mode of sponge embryogenesis in calcareans but not in other poriferans. Although choanocyte characters shared between Calcarea and higher Metazoans may serve as synapomorphies for a Calcarea-Eumetazoa clade, it is not parsimonious to consider choanocytes polyphyletic in view of their occurrence over a large segment of living organisms including Protoctists (Choanoflagellates), all sponges, and many Eumetazoa groups. These authors also suggested that the common possession of calcitic spicules in calcareans and anthozoans is a potential synapomorphy, but this latter hypothesis is here rejected given that these characters are non-homologous, whereby calcarean spicules are secreted extracellularly. ZRZAVÝ *et al.* (1998), supported by BORCHIELLINI *et al.* (2001), proposed to resurrect JOHNSTON's (1842) taxa 'Silicispongiae' (for Demospongiae + Hexactinellida), with a potential apomorphy being the method of secretion of spicules and the ultrastructure of the sclerocytes, and 'Calcispongiae' (for Calcarea) as subphyla, or potential phyla, to reflect the alleged deep molecular divergence between these clades.

These data conflict with earlier phylogenetic hypotheses that support the monophyly of Porifera (*e.g.*, REITNER & MEHL, 1996). Furthermore, a recent investigation of new full-length 28S and 18S rDNA sequences (MEDINA *et al.,* 2001), including re-examination of some previously published sequences by these authors, found very strong support for the clade (Demospongiae + Hexactinellida), for which they used the later name of Silicea Gray, 1867. They did not, however, find conclusive or statistically significant support for Poriferan paraphyly, or resolve the position of the Calcarea within the phylum, suggesting that earlier conclusions about 'Phylum Calcispongiae' must be interpreted cautiously for the time being, including any inferred relationships of the Calcarea with the Eumetazoa. These findings also suggest that these genetic markers (18S and 28S rDNA) might not be the most appropriate to resolve this specific question of Calcarean relationships. Although presently unresolved it is predictable that escalating molecular evidence based on multiple gene sequences may soon approach a satisfactory resolution to answer the question whether 'sponges' are monophyletic or paraphyletic.

PHYLOGENETIC 'CLADES' VERSUS 'GRADES' OF CONSTRUCTION

HARTMAN (1969, 1979) proposed a fourth class of Porifera, 'Sclerospongiae', based on recognition of the sponge nature of the so-called coralline sponges (sponges with solid limestone 'hypercalcified' basal skeletons). However, subsequent investigations (*e.g.*, VACELET, 1985) clearly showed that solid limestone skeletons have been developed independently in several unrelated lines of demosponges. 'Sclerosponges', or coralline sponges, or hypercalcified sponges, are now included in various orders of which the majority of families do not possess the solid limestone skeleton. Similarly, possession of basal skeletons composed of desmas ('lithistids', previously assigned to order Lithistida), or different grades of skeletal construction (*e.g.*, 'sphinctozoans' in class Sphinctozoa, 'stromatoporoids' in class Stromatoporoidea) also remain contentious (*e.g.*, WOOD, 1991), with present indications suggesting that these features are homeoplastic and their indicated taxa are polyphyletic - with the similar consequence that, where possible from other corroboratory evidence (*e.g.*, geometry of free spicules), these taxa are distributed amongst the established classes and orders of Porifera. Achieving this task completely, however, remains elusive and hence the systematics of Porifera is still largely unresolved at higher levels of classification. For this reason the *Systema Porifera* project has deliberately focussed on the intermediate taxa (families, genera), and includes the higher taxa (suborders, orders, and above) only to provide an 'indicative context' to these more practical units of classification. Resolving the higher systematics of sponges is clearly beyond the scope of this book, but at the same time we provide the basis from which research into this field can be directed. To illustrate this we provide an overview of current classification controversies needing a fresh approach using new scientific tools.

CLASSIFICATION ISSUES UNDER DISCUSSION

Having obtained a comprehensive high quality inventory of extant sponge taxa considered valid, along with their synonyms, the *Systema Porifera* is not only a state-of-the-art database and key to all higher taxa, but, as argued above, at the same time also a platform from which to address and focus critical research questions. In the *Systema* taxa of the genus level have been arranged in a classification of families and orders, which in the perception of the editors comprises the currently accepted or majority view of the taxonomic community. We have chosen to leave behind the classification paradigms based on 'reproductive modes' (*e.g.*, LÉVI, 1973) and 'grades of construction' (*e.g.*, HARTMAN, 1982), in favour of a more balanced multi-character approach (*e.g.*, HOOPER, 1991; VAN SOEST, 1991), in which spicules, skeletal structure, soft parts and life history characteristics are all considered at their appropriate level, resulting in an internally consistent higher taxa classification.

Nevertheless, we cannot and will not ignore that there are many controversial issues, raised by colleagues and ourselves in previous scientific studies, which have been 'solved' arbitrarily by the editors or the chapter authors. In Tab. III, we provide a - probably non-exhaustive - list of controversial issues that have been raised and which may need to be addressed in the near future to correct flaws in the *Systema Porifera* system and strengthen the robustness of the higher taxonomic classification. Such future research addressing these various controversial issues is strongly encouraged (see also below), but at the same time it is emphasized, that if a particular part of the classification presented in our volume is perceived as based on an arbitrary use of morphological characters, it is not helping us forward to propose a rivalling classification based on equally arbitrary use of such characters. We suggest here that we need ***new*** characters or improved analyses for such proposed changes.

Some of the urgent issues are discussed below and more extensively listed in Tab. III. The lists are biased towards Recent Demospongiae, for many reasons, the most important being that the editors are most familiar with that class.

Demosponge issues

The subclasses in Demospongiae were launched by LÉVI (*e.g.* 1955) to accommodate his 'reproductive mode' findings. Since then these reproductive modes were found to be non-exclusive, but the use of subclasses persisted until today. The subclass Homoscleromorpha is monotypic and its affinities remain undecided, due to unique non-overlapping morphological features. The subclasses Tetractinomorpha and Ceractinomorpha underwent some erosion and the current border between them is fuzzy, due to controversial proposals for the affinities and classification of Axinellidae, Halichondriidae, Hemiasterellidae, Suberitidae and Polymastiidae. Other assemblages of orders combined into higher taxa units are apparent, but are not currently in use, *e.g.*, Haplosclerida and Poecilosclerida, Agelasida and Halichondrida, Dictyoceratida and Dendroceratida. Some of the urgent ordinal issues are highlighted here:

Order Spirophorida: what if any are its relationhips with the 'Lithistida' family Scleritodermidae; is Samidae a member of this order, or is it more closely related to the clionaid or alectonid sponges; is Spirasigmidae a valid higher taxon ?

Order Astrophorida: are the aster morphologies and distributions within the skeleton consistent with the current family classification (issue raised by the molecular studies of CHOMBARD *et al.,* 1997); is Calthropellidae a valid higher taxon; what is the true affinity of *Thrombus* and *Lamellomorpha* ?

Order Hadromerida: is there a fundamental divergence in astrose and non-astrose groups (issue raised by the molecular studies of CHOMBARD *et al.,* 1997); is Hemiasterellidae indeed closely related to other astrose families; is Alectonidae really Hadromerida; what are the affinities of *Sollasella*; is Trachycladidae not merely a rather specialized form of *Spirastrella*?

'Order' Lithistida: is it possible to discover the affinities of families lacking microscleres; can fossil and recent Lithistida linked by shared desma characters ?

Order Poecilosclerida: are Latrunculina a monophyletic group excluding Podospongiidae; are these groups which lack chelae, sigmas, toxas, acanthostyles, trichodragmas, and microxeas indeed Poecilosclerida?

Order Halichondrida: is the order monophyletic; are Dictyonellidae a monophyletic assemblage; are Suberitidae and Polymastiidae closely related to Halichondriidae (issue raised by CHOMBARD & BOURY-ESNAULT, 1999)?

Order Agelasida: is the order valid (alternatively is it a member of Halichondrida)?

Order Haplosclerida: is it a monophyletic group (issue raised by *e.g.*, BERGQUIST, 1980); are freshwater sponges member of this order; are the currently recognized families of Haplosclerina and Petrosina monophyletic groups (issue raised by MCCORMACK *et al.,* 2002).

Order Dictyoceratida: is Dysideidae a member of this order (issue raised by *e.g.*, VACELET *et al.,* 1989)?

Order Dendroceratida: are they a valid group separate from Dictyoceratida (issue raised by VAN SOEST & BRAEKMAN, 1999)?

Order Halisarcida: what are its affinities?

Calcarea issues

Due to the small effort made in Calcarean systematics over the last century, the group had many larger and smaller taxonomic problems. In their gallant revision most of these problems were solved by BOROJEVIC *et al.* (*Systema Porifera*). Some problems at lower taxon levels remain, such as the apparent large number of monotypical taxa, which is possibly due to the lack of adequate numbers of students this group has suffered from. Still remaining are a large number of Haeckelian genus names, not used since their inception, the status of which is controversial. Checking all these names was clearly beyond the possibilities of the small group of experts (and many were placed in a section *incertae sedis* unrecognisable taxa in the *Systema* volume).

The subclass level in Calcarea is not currently under challenge, but at first glance, several of the characters upon which the subclasses are based appear non-exclusive, *i.e.* they refer to majorities of taxa sharing apomorphic characters rather than all taxa. In their *Systema Porifera* chapter, BOROJEVIC *et al.* indicate that the dichotomy of Calcarean subclasses may need to be further supported, possibly with non-morphological features such as stable isotope properties, which appear to show a consistent difference between Calcarea and Calcaronea (WÖERHEIDE & HOOPER, 1999). It would certainly be helpful if we would understand the physiological significance of major subclass characters such as the position of the nucleus in the choanocytes and the positive vs. negative ∂^{18}O values of the calcite skeleton. There are also proposals (*e.g.*, ZRZAVÝ *et al.,* 1998; BORCHIELLINI *et al.,* 2001) to elevate the calcarean subclasses, and other taxa, to higher categories (as noted above), but these remain contentious hypotheses in terms of relating molecular and morphological datasets.

To emphasize that the Calcarea classification is the product of a small group of experts (*i.e.*, with few others presently capable of critical comment), the editors of the *Systema Porifera* allowed the Calcarea chapters to deviate from the rigid family-based structure found elsewhere in the volume.

Hexactinellida issues

Like in Calcarea systematics, the number of practicing Hexactinellida systematists is very small, and this inevitably has led to many larger and smaller classification problems, such as several *incertae sedis* taxa. The recent erection of a new order of Hexasterophora (Aulocalycoida; TABACHNICK & REISWIG, 2000) may be the starting point for further rearrangements of higher taxa in the Hexactinellida.

Similar to Calcarea, the subclass level in Hexactinellida is not currently disputed, although some disturbing microsclere morphologies were recently detected (TABACHNICK & LÉVI, 1997) combining the characters of both subclasses (genus *Amphidiscella*). For the time being, convergent evolution is a parsimonious assumption, but there is room for questioning the dichotomy of Hexactinellida subclasses.

Fossil issues

Although the *Systema Porifera* only provides an outline of fossil sponges and spongiomorphs (with only a few groups covered in more detail), it is apparent that there are grave - or possibly unsolvable - problems, preventing an 'integrated' fossil-Recent classification of natural groups. As outlined above, recognition of phylogenetic relationships always relies heavily on characters of the soft parts and on microsclere morphology, both of which are virtually absent in fossils. Accepting Archaeocyatha as sponges is a pragmatic decision, based on numerous pieces of circumstantial evidence, but the sponge synapomorphies cannot and presumably never will be demonstrated. Claims that some Paleozoic fossil taxa may still be extant in Recent faunas appear to be misguided, because these persistent taxa almost inevitably are characterized by adaptive characters such as limestone basal skeletons or rigid lithistid or calcareous spicule skeletons, which appear to have evolved several times in the course of sponge evolution.

The earliest (Proterozoic) fossils are Hexactinellida, and most of the subclass and ordinal groups are recognizable from the Paleozoic onwards. From the occurrence of isolated fossil spicules (WIEDENMAYER, 1994; KRAUTTER, *Systema Porifera*), and occasional megascleres fossilized *in situ* (REITNER & WÖERHEIDE, *Systema Porifera*), a fragmentary picture of fossil sponge evolution may be built from the late Paleozoic onwards. However, only in Mesozoic periods some of the isolated spicules appear to have an unequivocal morphology also present in Recent sponges. This allows a reliable delimitation of the fossil record of taxa of the family and genus level. Unfortunately, only few such taxa are recorded up until now.

Genus level problems

Enumerating particular genus classification problems is beyond the scope of the present review, considering there are thousands of genus names treated in the *Systema Porifera*. However, one general problem has come forward: a limited number of genera in various groups appear to have become unmanageably large. This is partially due to the 'lumping' process, which resulted from the critical 'cladistic' evaluation of many paraphyletic or polyphyletic genera in the 1980's. For the most part, however, these genera appear to have genuinely undergone excessive morphological and presumably genetic radiation. Examples are *Callyspongia*, *Clathria, Clathrina, Cliona, Dysidea, Geodia, Haliclona, Ircinia, Hymedesmia*, *Mycale, Sycon* and *Tethya.* In order to be able to 'handle' the taxonomy and ecology of such speciose groups, we need to employ other levels of nomenclature than the customary Linnaean binomen. Some of the genera have already been subdivided into subgenera, many of which are pragmatic rather than phylogenetic units (*e.g.*, as done by HOOPER, 1996, for the large family Microcionidae), but that might not be enough. Other levels are recognized - though not encouraged - by the ICZN, such as superspecies and prospecies. Future usage of these taxon levels may prove to be helpful.

Loose-end taxa issues

Several monotypical families, or left-over genera were assigned arbitrarily - or at least insufficiently underbuilt - to a higher taxon by the editors. Examples are Spirasigmidae, Latrunculiidae, Calcifibrospongiidae, Verticillitidae, genus *Vosmaeria*. In some cases, it was not even possible to make an arbitrary decision, and taxa were left *incertae sedis*: *e.g.*, *Lamellomorpha,* Spongillina *incertae sedis*, Demospongiae *incertae sedis*, Hexactinosida *incertae sedis*, Lyssacinosida *incertae sedis*. From a scientific point of view such *incertae sedis* taxa are intolerable, as they testify our inability to classify extant organisms, and potentially threaten the stability of the current classification. We urgently need to have these solved.

SOLVING THE CONTROVERSIAL ISSUES

The classification employed in the *Systema Porifera* is essentially a morphology-based system, in which the taxa are characterized by suites of morphological synapomorphies including cell biological features, arrangement and organization of the aquiferous system, mineralogy and geometry of the spicules, and structure of the skeleton. Higher resolution techniques, increased data accumulation, and improved methodology for data analysis of the past decades have shown that morphological characters are by no means exhausted. Soft part characters such as cell morphology and cell composition appear under-explored. Nevertheless, new techniques less susceptible to subjective interpretation, especially molecular systematics, are necessary to (1) confirm morphology-based hypotheses, and (2) solve remaining controversies and unclear relationships.

What may we expect in the short term from the available new techniques, such as sampling nucleic acid sequences from various genes? Certainly not a ‘panacea’ for all the problems, as it is already amply clear that these approaches have their own methodological problems. To name a few: failure to obtain a PCR product, failure to obtain a conservative alignment, low information content, and especially limitation of sample size. For proper and exhaustive analysis of the data matrices only several dozens of taxa can be processed in a single run at the present moment. In practice this means that most of the studies suffer from incomplete taxonomic sampling. Relatively random sampling of lower taxa from among the higher taxa may easily result in both misrepresentation and in samples of taxa that are inadequate to test the hypothesis, due to long-branch phenomena, for example. A further problem is the practice of studying only a small part of a single gene, due to financial and technical constraints. The choice of the gene and its aptness to solve a given problem remains largely a matter of trial and error. Ideally, a strategy of sequencing various genes and long strands, would improve confidence in the results, especially when strongly controversial issues are the subjects of investigation. Analysing multi-gene sequences faces problems of computer power and bias related to 'total evidence' problems. No doubt, molecular methodologies will improve and be automated further, computer memory and speed will increase, and the molecular techniques will become more accessible.

In Tab. IV, the techniques appearing in the sponge literature and their advantages and shortcomings for the study of poriferan relationships are summarized.

If we succeed to obtain robust and convincing molecular results, and if these would fail to confirm classification schemes based on morphology, only one feasible course remains open to us: 'mapping' individual morphological characters considered synapomorphies on the gene tree and try to develop alternative hypotheses of character evolution. We should be aware of the possibility that most of the sponge characters we employ in the *Systema Porifera* classification are subject to higher or lower levels of parallel development.

Secondary metabolites and presence of co-evolved symbionts are indirect non-morphological characters that may in some isolated cases be employed to confirm or elucidate problematic phylogenetic relationships of sponges. However, the biological and biogenetic aspects of these character-types are largely unexplored, and this makes them susceptible to misinterpretation.

Tab. I. List of major higher taxa defined for living and fossil sponges.

TAXON	SUB-CLASSES	ORDERS	SUB-ORDERS	FAMILIES	GENERA
Extant Porifera (3 Classes)	7	25	-	127	682
Demospongiae	3	15	7	88	490
Calcarea	2	5	-	22	75
Hexactinellida	2	5	-	17	118
Fossil Porifera (6 'Classes')	-	30	-	245	998 (>1500 nominal genera)
Demospongiae	-	-	-	7	25
Lithistida	-	-	13	34	201
Sphinctozoa	-	9	-	42	141
Stromatoporoidea	-	7	-	14	109
Heteractinida	-	-	-	4	20
Calcarea	-	3	-	6	74
Hexactinellida	-	2	2	18	121
Archaeocyatha	-	6	13	120	307

Tab. II. List of numbers of new higher taxa proposed for living and fossil sponges.

TAXON	SUB-CLASS	ORDER	SUB-ORDER	SUPER-FAMILY	FAMILY	SUB-FAMILY	GENERA	SUB-GENERA
New	0	1	2	1	10	6	17	6

Tab. III. Suprageneric classification issues to be solved by future research.

Taxon	Problem
Phylum & Class relationships	are sponges paraphyletic?
Homoscleromorida	affinities unclear
Samidae	may be Alectonidae
Spirasigmidae	monotypical, ill-known
Calthropellidae	?artificial
Thrombidae	monotypical, affinities unclear
Astrophorida *incertae sedis*	genus of uncertain affinity
Hadromerida (general)	monophyly of order (microsclere divergence)
Hemiasterellidae	Hadromerid affinity contested
Alectonidae	Hadromerid affinity contested
Sollasellidae	monotypical, affinity unclear
Stylocordylidae	monotypical
Suberitidae + Polymastiidae	possible affinity with Halichondriidae
Timeidae	monotypical
Trachycladidae	relationship with Spirastrellidae unclear
Lithistida (general)	polyphyletic, numerous fossil relatives
Scleritodermidae	spirophorid affinity claimed
Corallistidae	possible affinity with Astrophorida
Pleromidae	possible affinity with Astrophorida
Theonellidae	possible affinity with Astrophorida
Desmanthidae	affinity with Bubaridae suggested
Vetulinidae	affinity with Crambeidae suggested
Poecilosclerida (general)	microsclere types shared with Haplosclerida
Raspailiidae	classical affinity with Axinellidae
Rhabderemiidae	monotypical
Myxillina (general)	monophyly contested
Coelosphaeridae	monophyly contested
Hymedesmiidae	monophyly contested
Esperiopsidae	affinity with Mycalidae
Podospongiidae	affinity with Latrunculina
Isodictyidae	Poecilosclerida membership contested
Latrunculina / Latrunculiidae	poecilosclerid nature contested
Halichondrida (general)	monophyly contested
Axinellidae	membership of Halichondrida contested
Bubaridae	independence from Axinellidae contested
Dictyonellidae	artificial ? (dustbin family)
Halichondriidae	postulated affinity with Suberitidae + Polymastiidae
Agelasida	affinity with Axinellidae/Halichondrida
Haplosclerida	monophyly contested
Spongillina *incertae sedis*	affinity unclear
Dictyoceratida/Dendroceratida	relationship under discussion
Dysideidae	affinities under discussion
Halisarcida	monotypical, affinities unclear
Verticillitida/Verticillitidae	Recent/fossil relationships, affinities unclear
Demospongiae *incertae sedis* (Myceliospongia)	monotypical, affinities unclear
Calcarea – Heteractinida	monophyly of Recent and fossil higher taxa uncertain
Calcaronea	classification juveniles difficult
Calcinea	large complement (approx. 50%) monotypical genera
Leucettidae *incertae sedis*	affinity unclear
Murrayonida/Lithonida	parallel developments and overlap of spicule types
Amphidiscophora/Hexasterophora	overlap of synapomorphies
'Rossellimorpha'	paraphyletic group of similar fossil and Recent taxa

Tab. IV. Advantages and disadvantages of available methodologies to address controversial classification issues.

Technique	Advantage	Taxonomic sample	Disadvantage
MORPHOLOGICAL	old samples usable (holotypes) fossil data little chance of contamination	comprehensive	only phenotypic characters character set usually small subjective interpretation of characters (micro-) habitat modifications
Light microscopy			
- thick sections, classical	easy, cheap	comprehensive	subjective interpretation sectioning artefacts dehydrated preparations
- thick sections, 3-D photomicroscopy	3-D insight	small because of elaborate procedures	expensive equipment
- spicule mounts	easy, cheap (precise) metric data	comprehensive	restricted to spicule-bearing taxa possible contamination biased against small spicules
- histology/thin sections	soft body characters	mostly taxa without spicules	skeleton and spicules misrepresented dehydrated preparations special fixations
Electron microscopy			
TEM	cells, symbionts, high resolution	small, because of elaborate procedures	skeleton and spicules misrepresented low accessibility, expensive equipment
SEM	3-D, high resolution, both hard and soft	large, but restricted due to elaborate procedures	dehydrated preparations, expensive equipment

Technique	Advantage	Taxonomic sample	Disadvantage
MOLECULAR	genotypic changes objective, numerical / statistical	often small taxonset	only fresh samples optimal
DNA-, RNA-, protein sequences	large character set	same	expensive, incomplete taxonset, possible contamination not all PCR's succeed
	small samples sufficient "morphological" characters possible (*e.g.* loops, inserts) models for character evolution in DNA and amino acids	same	long-branch problems, danger of paralogy on most genes, cloning necessary (WHY?)
RDNA	often high variability	same	occasionally alignment problems
18S	only classes or higher levels	same	conserved (not applicable to lower levels)
28S	informative for families / genera? "established" (primers) large data set	same	(genus levels only[1]) (to be tested[2]) [1]Not true. See MEDINA *et al.,* 2001 [2]See MALLATT, 2002, MBE 19
5,8S + 5S	higher tax. levels only	same	fragment too short (too conservative)
ITS	(infra-) species levels only[1] hybridisation studies [1]No. also infra-family as demonstrated for Leucettidae	same	(to be further tested)
ETS	(infra-) species levels only	same	(to be tested)
Proteins	unambiguous alignment, better detection of paralogy/pseudogenes, various phylogenetic levels due to 3 codon positions and amino acid translation	same	often more conserved that rDNA

Technique	Advantage	Taxonomic sample	Disadvantage
COI	Same clonal / no recombination (theoretically)	same	family/genus levels only small data set so far
COII	same	same	appears conserved (to be further tested)
Other Proteins (Hsp70, RTK, integrin, lectins, EF, Bcl2, etc.)	higher taxa phylogenies some could be monocopy genes	same	mostly very conserved, small database yet
Allozyme electrophoresis	objective limited char. Set cheaper than DNA seq. population level detection of sibling species hybridisation studies	larger taxon sets	search for appropriate locus, low phylogenetic levels only not comparable between laboratories contamination problems needs fresh or deep frozen material most loci not selectively neutral
Mini / microsatellites	population studies	larger taxon sets	to be tested for sponges, low phylogenetic levels only primers for variable loci have to be developed *de novo* (and found first)
RFLP	population studies, easy, relatively cheap	large taxon sets	to be tested for sponges, lower taxa levels only, limited interpretation contamination (bacteria)
AFLP	population studies	large taxon sets	sometimes ambiguous results, to be tested for sponges, lower taxa levels only contamination (bacteria)
Secondary metabolites	objective variety of character states (due to isomers)	small taxon set	bioactive tests, possible contamination from symbiont source, time consuming, uncertain records (no record ≠ absent) homology of biosynthesis pathway uncertain, little phylogenetic impact, interpretation of isomers difficult, influenced by temporary ecological factors

Technique	Advantage	Taxonomic sample	Disadvantage
OTHER			
Symbiont occurrence	objective co-speciation studies	small taxon set	identification problems, horizontal transfer, influenced by temporary ecological factors, misinterpretation due to food bacteria
Lipid biomarkers	higher taxa only	comprehensive	expensive equipment special laboratory preparation specialist interpretation

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