SYSTEMA PORIFERA

A Guide to the Classification of Sponges

VOLUME 2

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and

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Preface

Sponges are among the most ancient of multicellular animals alive on the planet today. Ecologically and economically, they are among the most highly successful life forms that have ever existed. First known from the Precambrian, and well established by the Cambrian, they were the major reef builders during the Palaeozoic and Mesozoic Eras. Today they are highly diverse, with an estimated 15,000 species living in all Recent marine and freshwater habitats worldwide, but these undoubtedly represent only a small proportion of those that have ever lived. Sponge body plans do not appear to have changed significantly over the many millennia, such that some species alive today appear to be almost identical to those that once lived in Earth's ancient seas. Consequently, sponges are often regarded as ultra-conservative in their morphology, presumably as successful models of early evolutionary experiments. In contrast, the living fauna is widely diverse in many other biological features, especially in their biochemical constituency that is currently of major interest to the pharmaceutical industry. It is this latter feature, and also the renewed interest in marine biodiversity worldwide, that has attracted a major resurgence of studies on sponges with the consequence that over the past two decades researchers have discovered a living fauna about twice the size of that published in the literature.

Sponge systematics is generally perceived as appallingly difficult. These difficulties stem partly from the sponges themselves, being highly plastic and easily susceptible to environmental modification and frequent character losses. They also stem, perhaps more so, from the inadequacies and inconsistencies of the taxonomic framework. This includes a previously fragmented and uncoordinated research effort, whereby only a few higher groups have had contemporary revisions applied to them, and with the remainder largely unworked since the late 19th century. In turn, this has led to increasing difficulties faced by new workers – among them a growing number from newly developing countries – to access the vast and mostly ancient literature.

The *Systema Porifera* project was devised to revisit the poriferan higher taxa (genus level and above, based on type species data), to accommodate these many new taxa, to correct the many nomenclatural and taxonomic mistakes of the past, and to provide a sound platform for the future development of sponge systematics. For many groups the *Systema* is a major revision, and for all groups it provides a sound framework of sponge systematics based on phylogenetic principles. Perhaps more importantly, this project also provides a practical tool to allocate taxa within this framework, including keys, comprehensive illustrations and descriptions of the major characters used to classify sponges – something that has not previously been attempted.

The *Systema* is published in two volumes. Volume 1 includes a general introduction and the Class Demospongiae. Volume 2 includes Classes Calcarea and Hexactinellida, the fossil Class Archaeocyatha, fossil 'Sphinctozoa', and an annotated list of unrecognisable taxa and unavailable names. We describe approximately 680 genera of sponges in 127 families, 25 orders and three classes of the living fauna. In addition, approximately 1000 fossil genera in 245 families, 30 orders and six 'classes' are also covered. The living fauna is dealt with far more comprehensively than the fossil fauna, with overviews of the fossil classification included mainly in an attempt to relate these two classifications more closely. A far more comprehensive treatment of fossil sponges is currently in preparation for the revised edition of the *Treatise on Invertebrate Palaeontology* (J.K. Rigby *et al.*, editors).

The *Systema* project was only possible to achieve through an intensively collaborative effort amongst 45 researchers from 17 countries, spanning about six years of research effort. We pride ourselves to have among our contributors the major contemporary spongologists, including Patricia R. Bergquist, Nicole Boury-Esnault, Françoise Debrenne, Claude Lévi, Henry Reiswig, Joachim Reitner, Klaus Rützler, Michele Sarà, Maria J. Uriz and Jean Vacelet, as well as several members of the new generation of sponge researchers. The *Systema Porifera* project is not an end – but a sound beginning for this new generation to build on what we propose here.

John N.A. Hooper, Brisbane
Rob W.M. Van Soest, Amsterdam

Key to Symbols, Institutional Acronyms, Abbreviations

†, Denotes an extinct taxon (is used primarily for fossil taxa mentioned in chapters chiefly dealing with Recent sponges).

?, placed in front of taxonomic name denotes that there remains uncertain amongst the contemporary scientific community about the validity or taxonomic placement of a species, genus, family or order.

AM (AMS), Australian Museum, Sydney, Australia (including SUP collection, formerly of Department of Geology and Geophysics, University of Sydney, Australia).

ANSP, Academy Natural Sciences of Philadelphia, USA.

BGU, Buryatan Territorial Geological Survey, Ulan-Ude, Russian Federation.

BMAG, Bristol Museums and Art Gallery, Bristol, United Kingdom.

BMNH, The Natural History Museum, London, United Kingdom [formerly British Museum (Natural History)].

BMS, Buffalo Museum of Science, Buffalo, USA.

BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.

CAS, California Academy of Sciences, San Francisco, California, USA.

CE, Departemento de Paleontologia, Universidad Complutense de Madrid, Madrid, Spain.

CEAB, Centro de Estudios Avanzados de Blanes Collection, Blanes, Spain.

CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada (formerly NMC, National Museums of Canada).

CNIGRm, Central Scientific-Researching Geological-Exploration Museum, St Petersburg; Federal Republic of Russia. (new transliteration TsNIGRm).

CNRS, Centre National de la Recherche Scientifique, Paris, France.

CSGM, Central Siberian Geological Museum (see TsSGM= IGiG) (now holding collections of IgiG), Novosibirsk, Russian Federation.

DTRG, Dipartimento per lo studio del Territorio e delle sue Risorse, Università di Genova (Dip. Te. Ris.; ex-IZUG), Italy.

DVGI, Far East Geological Institute, Far East Institute of Mineral Resources, Khabarovsk, Russian Federation.

DVIMS, Far-East Institut of Mineral Resources, Khabarovsk, Russian Federation.

DVTGU, Far-East Territorial Geological Survey, Far-East branch of the Russian Academy of Sciences, Khabarovsk, Russian Federation.

FMNH, Field Museum of Natural History, Chicago, USA.

FZRG, Fundacao Zoobotanica Rio Grande do Sul, Museu de Ciencias Naturais, Porto Alegre, Brazil.

GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russian Federation.

GML, Geiseltalmuseum Martin Luther, University of Halle, Halle, Germany.

GSC, Geological Survey of Canada, Ottawa, Canada.

HBOI/M, Harbor Branch Oceanographic Institution/ Museum, Fort Pierce, Florida, USA.

HMN, Hancock Museum, Newcastle-upon-Tyne, United Kingdom.

IGNS, Institute of Geological and Nuclear Sciences (formerly New Zealand Geological Survey), Lower Hutt, New Zealand.

ICZN, International Code of Zoological Nomenclature (see Anon., 1999).

IgiG, United Institute of Geology, Geophysics and Mineralogy (collections at CSGM), Siberian Branch of the Russian Academy of Sciences; Novosibirsk, Russian Federation.

IM (ZEV), Indian Museum (including, Zoological Survey of India), Calcutta, India.

IMGP, Geowissenschaftliches Zentrum der Universität Göttingen, Section Geobiology [formely Institut und Museum für Geologie und Paläontologie, Göttingen, Germany.

INALI, Instituto Nacional de Limnologia, Santo Tomè, Santa Fe, Argentina.

INM, National Museum of Ireland, Dublin, Ireland.

IORAS, Institute of Oceanology of the Russian Academy of Sciences, Moscow, Russian Federation.

IRS(c)NB, Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium (see also KBIN).

ISM, Imperial Science Museum, Tokyo, Japan (see TIU).

KBIN, Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel, Belgium (see also IRScNB).

KGU, Krasnoyarsk Territorial Geological Survey, Krasnoyarsk State University, Russian Federation.

KMMA, Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (see MRAC).

LFM, Merseyside County Museums, Liverpool, United Kingdom (formerly Liverpool Free Museum).

LMJG, Landesmuseum Joanneum Graz (Abteilung für Zoologie), Graz, Germany.

LSLH, Linnean Society of London Holdings (Linnean Herbarium), United Kingdom.

MABA, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina.

MANSP, Museum of the Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.

MCN, Museo de Ciências Naturais da Fundação Zoobotânica, Porto Alegre, RS, Brasil.

MCNM (MNCN-CSIC), Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas, Madrid, Spain.

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

MCSN, Museo Civico di Storia Naturale, Verona, Italy.

MFSN, Museo Friulano di Storia Naturale, Udine, Italy.

MG, Geological Museum, New Zealand (see VUMG).

MHNG, Muséum d'Histoire naturelle, Genève, Switzerland.

MNHN, Muséum national d'Histoire naturelle, Paris, France.

MNRJ, Museu Nacional, Rio de Janeiro, Brazil.

MOM, Musée Océanographique de Monaco, Monaco.

MRAC, Musée Royal de l'Afrique Centrale de Tervuren, Belgium (see KMMA).

MRCN, Museu Rio-Grandense de Ciências Naturais, Porto Alegre, Rio Grande do Sul, Brasil.

MSNG, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy.

MT Por, Museo e Istituto di Zoología Sistemática dell'Universitá di Torino, Italy (Porifera collection).

MY, Million years.

MYA, Million years ago.

MZUS, Musée de Zoologie de l'Université de Strasbourg, France.

NHRM, Naturhistoriska Riksmuseet, Stockholm, Sweden.

NIGP, Nanjing Institute of Geology and Paleontology of the Chinese Academy of Sciences, Nanjing, China.

NMB, Naturhistorisches Museum zu Basel, Basel, Switzerland.

NMNZ, Te Papa, Museum of New Zealand, Wellington, New Zealand (formerly National Museum of New Zealand, and formerly Dominion Musuem).

NMS, National Museum of Scotland, Edinburgh, Scotland.

NMV, Museums of Victoria, Melbourne, Australia (formerly National Museum of Victoria).

NSM, National Science Museum, Tokyo, Japan.

NTM, Northern Territory Museum of Arts and Sciences, Museums and Art Galleries of the Northern Territory, Darwin, Australia.

NYSM, New York State Museum, Albany, New York State, USA.

NZGS, New Zealand Geological Survey, Wellington, New Zealand.

NZMW, National Zoological Museum Warsaw, Poland.

PGO, Zabsibgeologiya, Novokuznetsk, Russian Federation.

PGU, Primor'ye Territorial Geological Survey; Khabarovsk, Russian Federation.

PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russian Federation.

PMJ, Phyletisches Museum, Jena, Germany.

PU, Princeton University Bedfords' Collections (now housed in USNM Washington).

QM, Queensland Museum, Brisbane and Townsville (including MTQ, Museum of Tropical Queensland).

RASMAS, Rosenstiel School of Marine and Atmospheric Sciences (see UMML).

RIB, (see IRScNB).

RMM, Redpath Museum, McGill University, Montreal, Quebec, Canada.

RMNH, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (formerly Rijksmuseum van Natuurlijke Historie).

ROM, Royal Ontario Museum, Toronto, Canada.

RSME, Royal Scottish Museum Edinburgh, Scotland.

SAMP, South African Museum, Pretoria, Republic of South Africa.

SAM, South Australian Museum, Adelaide, Australia (including collections of UA – The University of Adelaide).

SAMC, South African Museum, Capetown, Republic of South Africa.

SBR, Station Biologique de Roscoff, France.

SDCC, Private collections of Steve de C. Cook (destined for the NMNZ).

SEM, Scanning electron microscopy.

SME, Station Marine d'Endoume, Marseille, France.

SMF, Natur-Museum und Forschunginstitut Senckenberg, Frankfurt-am-Main, Germany.

SNIIGGIMS, Siberian Scientific Research Institute of Geology, Geophysics and Mineral Resources, Novosibirsk, Federal Republic of Russia.

SUP, Department of Geology and Geophysics, The University of Sydney, Australia (now housed in The Australian Museum; see AM).

TEM, Transmission electron microscopy.

TIU, Imperial University Museum, Tokyo, Japan.

TsNIGRm, new transliteration for CNIGRm.

TsSGM, new transliteration for CSGM.

UA, Department of Geology, University of Alberta, Edmonton, Alberta, Canada.

UA, University of Adelaide (see SAM).

UAM, University of Alaska Museum, Alaska, USA.

UBC, University of British Columbia, Vancouver, Canada.

UCLZ, University College of London, Zoology.

UCPM, University of California Paleontology Museum, Berkeley, California, USA.

UFRJPOR, Universidade Federal do Rio de Janeiro, Brazil.

UKL, University of Kansas, Lawrence, USA.

UMML, Marine Invertebrate Museum, University of Miami, Rosenstiel School of Marine and Atmospheric Sciences.

USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (formerly United States National Museum).

UTBEG, Texas Memorial Museum, Bureau of Economic Geology, Austin, Texas, USA.

UWIJ, University of West Indies, Mona, Jamaica, West Indies (Zoology Department) [MSUJ].

VSEGEI, All-Russian Geological Institute, St Petersburg, Russian Federation (transfer of collections to TsNIGRm in progress).

VUMG, Victoria University of Wellington, Museum of Geology, Wellington; New Zealand.

WAM, Western Australian Museum, Perth, Australia.

YPM, Yale University, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

ZEV, (see IM).

ZIL, Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russian Federation.

ZMA, Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, The Netherlands.

ZMB, Zoologisches Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany.

ZMH, Zoologisches Museum für Hamburg, Hamburg, Germany.

ZMUB, Zoological Museum, University of Bergen, Norway.

ZMUC, Zoologisk Museum Universitet Copenhagen, Copenhagen, Denmark.

ZMUZ, Zoologisches Museum der Universität, Zürich, Switzerland.

ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

ZRS, Zoologiska Rijkmuseum, Stockolm, Sweden.

ZSGGU, West Siberian State Geological Trust (=WSSGE; =WSSGT, =ZSTGU) Novokuznetsk, Russian Federation.

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Class Calcarea Bowerbank, 1864

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Calcarea Bowerbank (Porifera) includes sponges having a mineral skeleton composed entirely of calcium carbonate, consisting of free, rarely linked or cemented, di-, tri-, tetra- and/or polyactinal spicules, sometimes with a solid basal calcitic skeleton, and with blastula larvae and viviparous mode of reproduction. Two Recent subclasses are recognised, Calcinea and Calcaronea, containing five orders, 22 families and 75 valid genera, with species exclusively marine and distributed worldwide.
Keywords: Porifera; Calcarea; Calcinea; Calcaronea.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Calcispongia Johnston, 1842. Calcarea Bowerbank, 1864.

Previous reviews

Haeckel, 1872; Poléjaeff, 1883; Lendenfeld, 1891; Minchin, 1896; Bidder, 1898; Minchin, 1900; Dendy & Row, 1913; de Laubenfels, 1936a; Hartman, 1958a; Burton, 1963; Borojevic, 1979; Borojevic *et al.*, 1990; Vacelet, 1991; Hooper & Wiedenmayer, 1994; Borojevic *et al.*, 2000.

Diagnosis

Marine Porifera in which the mineral skeleton is composed entirely of calcium carbonate. The skeleton is composed of free diactine, triactine, tetractine and/or polyactine spicules, to which can be added a solid basal calcitic skeleton with basal spicules either cemented together or completely embedded in an enveloping calcareous cement. The aquiferous system can be asconoid, syconoid, sylleibid or leuconoid. Members of the Calcarea are viviparous and their larvae are blastulae.

Biology and scope

Calcarea are sponges with a reputation for being obscure and taxonomically difficult. The total number of described species (ca. 500) represents less than 5% of all described sponges, partially due to a bias in taxonomic effort. Most species are relatively inconspicuous, being generally quite small and colourless, with many living in cryptic habitats such as marine caves, overhangs and in the interstices of hard substrata. However, the aesthetic qualities of their organisation have long been recognised, especially towards the end of the 19th century with many authors "delighted in the beauty and fragrance of the calcareous sponges" (Burton, 1963). Not only did they provide an aesthetic interest but also served as important models for understanding poriferan and metazoan evolution.

Fleming (1828) was the first to create a special taxon (the genus *Grantia*) to group all sponges having a skeleton made of calcium carbonate. The name *Calcispongia* (Blainville, 1830; originally proposed as a genus), was elevated to class level by Johnston (1842) and followed by Nardo (1845), Schmidt (1862) and Haeckel (1872) to contain all calcitic sponges. Bowerbank (1864) subsequently proposed the name Calcarea to define this group which was adopted by virtually all subsequent authors and has been in general use throughout the 20th century.

The possession of a skeleton made of calcareous spicules makes the Calcarea unique with respect to all other sponges. Some demosponges (referred to as 'sclerosponges', a polyphyletic assemblage; see Vacelet, 1985; Chombard *et al.*, 1997) possess a calcareous skeleton consisting of a solid mass of calcium carbonate, but this structure is very distinct from the calcareous spicules forming the skeleton of Calcarea. The question of whether or not Calcarea are monophyletic has never been resolved satisfactorily by traditional morphological studies. Even if the combination of calcareous spicules and basically biradiate or triradiate spicule morphologies seems to offer reasonable support for monophyly, both the capacity to precipitate calcium carbonate and the morphology and symmetry of these spicules could be potentially convergent. However, recent molecular work (Borchiellini *et al.*, 2001) strongly supports the monophyly of this class.

More recently, the taxon Calcispongia has returned to the literature as a potential phylum, based on evidence from molecular phylogenies that infers Porifera may be paraphyletic, with calcareous sponges being more closely related to Eumetazoa than to other sponges (Zrzavy *et al.*, 1998; Borchiellini *et al.*, 2001). Zrzavy *et al.* (1998) formally proposed to elevate calcareous sponges to the rank of phylum and proposed to resurrect the name Calcispongia for this purpose. However, for the purposes of this present volume we retain the current usage of Calcarea as a class within Porifera.

The present work recognises two subclasses, five orders, 22 families and 75 valid genera, although there are many hundreds of nominal genera that are currently considered to be junior synonyms, and many unavailable names (particularly those of Haeckel).

History

The taxonomic history of calcareous sponges is both complicated and very instructive. Particular emphasis must be given to the