

Class Calcarea Bowerbank, 1864

Michaël Manuel¹, Radovan Borojevic², Nicole Boury-Esnault¹ & Jean Vacelet¹

¹Centre d'Océanologie de Marseille, Station Marine d'Endoume, Université de la Méditerranée, UMR-CNRS 6540, rue de la Batterie des Lions, 13007 Marseille, France. (Michael.Manuel@snv.jussieu.fr; esnault@com.univ-mrs.fr; jvacelet@com.univ-mrs.fr)

²Departamento de Histologia e Embriologia, Instituto de Ciências Biomédicas, Universidade Federal do Rio de Janeiro, Caixa Postal 68021, 21941-970 Rio de Janeiro, Brazil. (radovan@iq.ufrj.br)

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, 23 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 biradial or triradial 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, 23 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

work of Haeckel (1870b, 1872), who was the first to propose a comprehensive system for the classification of this group, describing and classifying all calcareous sponge species known at his time. Calcareous sponges also had a significant place in the elaboration of his ideas concerning metazoan origins and evolution. He was also the first to propose direct homologies between the poriferan and cnidarian bodyplans (Haeckel, 1870b), achieved through comparison between a homocoel calcareous sponge and a polyp of coral. Even if such homologies are nowadays highly controversial his work was historically crucial in suggesting the inclusion of sponges within the monophyletic Metazoa. Later, Haeckel (1874) elevated the interest in Calcarea for understanding general metazoan evolution: “the developmental history of the calcareous sponges, the discovery of their gastrula form, as well as the question of their natural affinities and their place in the natural system, necessarily, and of itself, led me on to the general question of the homology of their germ-lamellae with those of the higher animals, and thus further on to that series of ideas whose nucleus, in a word, forms the Gastraea theory”. The Gastraea theory formed the basis of what has remained, until recently, the dominant conception of metazoan phylogeny and evolution.

Haeckel (1872) was also the first to publish a classification of calcareous sponges that attempted to be natural, i.e., devised to reflect their phylogeny. His system comprised three families: Ascones, Sycones and Leucones. Indeed, it is only within the Calcarea that the classical grades of organisation of the aquiferous system – ascon, sycon, leucon – can be found (Fig. 1). Within each of his families the genera were defined on the basis of the presence or absence of particular spicules types. This system was soon criticized and rejected because, ironically, it proved to be very artificial (Poléjaeff, 1883; Dendy, 1891, 1893b; Minchin, 1896). In particular, the separation of Sycones and Leucones resulted in placing a number of species displaying otherwise very similar features remote from each other. Nevertheless, the pioneering role of Haeckel for the systematics of Calcarea in particular, and for our

current understanding of the sponge aquiferous system in general, cannot be ignored despite some virulent and sometimes unjustified and unfair criticism. For example, Burton (1963) qualified Haeckel’s illustrations as “fanciful” while, in our own experience, they are often quite representative of what can be actually observed.

An alternative scheme was later proposed by Poléjaeff (1883) and was very successful for a long time. He divided the group into Homocoela (all body cavity lined with choanocytes, basically the ascons) and Heterocoela (some internal cavities are lined with pinacocytes, basically the sycons and leucons). The Homocoela comprised the unique genus *Leucosolenia* Bowerbank, 1864, while the Heterocoela comprised three distinct families. Some slight modifications were later introduced by Vosmaer (1887), Lendenfeld (1891) and Dendy (1891, 1892, 1893b), who added a few more families to the Heterocoela. The works of Dendy (1891, 1892, 1893b) were important in stressing the importance of characters derived from the architecture of the skeleton, rather than the organisation of the aquiferous system, as justification to recognise distinct families.

Minchin (1896, 1900, 1909) and Bidder (1898) subsequently defended a radically different proposal to subdivide the Calcarea. Minchin (1896) remarked that, among species of the genus *Leucosolenia*, some have the nucleus located basally in the choanocyte whereas others have the nucleus located apically (Fig. 2). For the first group of species he proposed the genus *Clathrina* Gray, 1867a, and for the second group he maintained the name *Leucosolenia*. Bidder (1898) extended Minchin’s observations to the whole Calcarea (and even, tentatively, to all sponges), and proposed to subdivide them between the two subclasses Calcinea (nucleus basal in choanocytes) and Calcaronea (nucleus apical in choanocytes). This proposal was not only based on the position of the nucleus in the choanocyte but also on a combination of other characters. His proposal leads to the following suggested arrangement.

Calcinea. (1) Regular, equiangular triradiate spicules present (Fig. 3A); (2) optic axes of the spicules nearly perpendicular to the walls of the sponge tubes; (3) choanocytes with a spherical nucleus located basally in the cell (Fig. 2A); (4) flagellum of the choanocytes arises independently of the nucleus; (5) coeloblastula larvae (Fig. 4A); (6) triradiates are the first spicules to appear in ontogenesis.

Calcaronea. (1) Triradiate spicules predominantly or exclusively sagittal and inequangular (Fig. 3B); (2) optic axes of the spicules vary in orientation according to the distance from the oscular rim; (3) choanocytes with a pear-shaped nucleus apical in position (Fig. 2B); (4) flagellum of the choanocytes arises directly from the nucleus; (5) amphiblastula larvae (Fig. 4B); (6) monaxons are the first spicules to appear in ontogenesis.

As Minchin (1900) underlined, the important cytological character is the relation between the flagellum and the nucleus in the choanocyte; in contrast, the position of the nucleus can vary to some extent (especially if the material is poorly preserved). The new system advocated by these two authors relied mainly on cytological and embryological characters, while previous classifications relied chiefly on the organisation of the aquiferous system. Bidder (1898) strongly criticized Poléjaeff (1883) for his subdivision between Homocoela and Heterocoela as “no more satisfactory than classifying higher animals according to whether they walk, swim or fly”.

The new classification proposed by Minchin and Bidder was not universally accepted. An interesting work, in this respect, is the systematic catalogue published by Dendy & Row (1913). In their

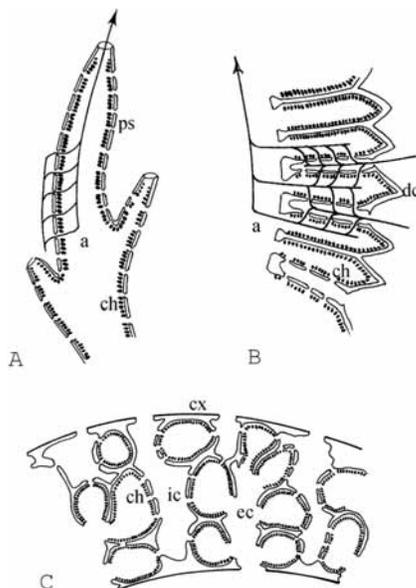


Fig. 1. Different types of aquiferous systems present in the Calcarea. A, asconoid system. B, syconoid system. C, leuconoid system (abbreviations: a, atrium; ch, choanoderm; cx, cortex; dc, distal cones; ec, exhalant cavities; ic, inhalant cavities; ps, pinacoderm and skeletonogenous layer).

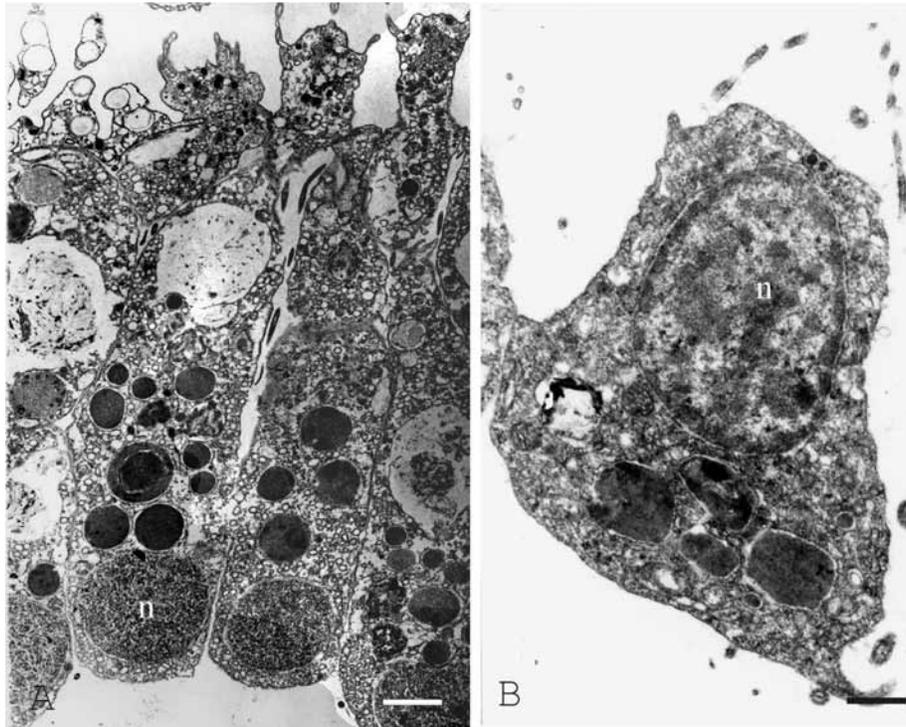


Fig. 2. A, choanocyte showing a typical basal nucleus in *Calcinea* (scale 1.7 μm). B, choanocyte showing a typical apical nucleus in *Calcaronea* (scale 0.8 μm) (abbreviation: n, nucleus).

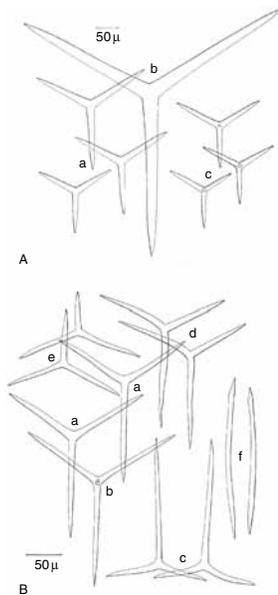


Fig. 3. Different types of spicules present in the Calcarea. A, regular equiangular spicules from a *Calcinea* (*Leucetta chagosensis* Dendy, 1913) (abbreviations: a, small triactines; b, large triactines; c, tetractines) (scale 30 μm). B, sagittal and inequiangular spicules from a *Calcaronea* (*Grantessa syconiformis* Borojevic, 1967) (abbreviations: a, atrial triactines; b, atrial tetractines; c, subatrial triactines; d, distal triactines of the radial tubes; e, triactines of the distal cones; f, diactines) (scale 50 μm).

discussion on the classification of calcareous sponges the authors adopted quite an ambiguous position with respect to the ideas of Minchin and Bidder. On the one hand they judged Bidder's work and proposals as very opportune, and considered that cytological

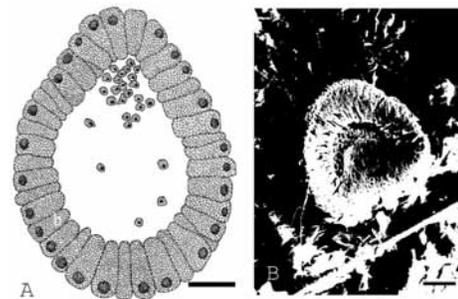


Fig. 4. Two types of larvae from Calcarea. A, calcinean coeloblastula (*Leucetta chagosensis*), with the blastocoel parental cells visible inside the wall (scale 50 μm). B, section through a calcaronean amphiblastula in the parental sponge under scanning electron microscopy (scale 8 μm).

characters of the choanocytes “may ultimately prove ... to afford a means of dividing the whole of the Calcarea into two main branches, one having the nuclei of these cells placed basally, and the other having them apical” (Dendy & Row, 1913: 709). Further, in their discussion about phylogeny (p. 797 *et seq.*), they distinguished two lineages of heterocoel Calcarea based on that same criterion, and implicitly made them derive from two distinct stocks of homocoel Calcarea (i.e., *Leucosolenia* species with basal nuclei, and *Leucosolenia* species with apical nuclei). On the other hand, they considered that “in the present state of our knowledge it is a principle which must not be pushed too far”, and, as a result, they did not formally adopt Bidder's system, and did not even separate asconoid species with basal nuclei from asconoid species with apical nuclei, all of them still being included under the generic name *Leucosolenia*. The main criticism is that data are too partial, and

consequently, that subdividing the whole of Calcarea between Calcinea and Calcaronea “in the present state of knowledge” could be nothing else than an over-generalisation. However, even if Dendy & Row (1913) have been too conservative in regard to the classification of Minchin and Bidder, their revision is a very thoughtful analysis based on the morphology, anatomy and skeletal organization of the Calcarea, and it still forms the basis for the actual definitions of most families and genera of calcareous sponges. They pointed out that the original form of ‘olynthus’ gave rise to two independent evolutionary pathways, one through *Dendya* to Leucascidae and Leucaltidae, and the other through *Sycetta* to all the families actually classified as the heterocoel Calcaronea. They also stated that the living ‘Pharetrones’ represent relicts of several evolutionary pathways independent of the olynthus-derived extant Calcarea. This classification was so successful that even after the revision of Hartman (1958a), unifying the systems proposed by Bidder (1898) and Dendy & Row (1913), only minor modifications were necessary to establish the actual view of the overall classification of Calcarea (Borojevic, 1979; Borojevic *et al.*, 1990, 2000).

Hartman (1958a) re-examined the classification of Minchin and Bidder and the various objections raised in the literature against a subdivision of Calcarea between Calcinea and Calcaronea. He concluded that Bidder’s classification is satisfying and has to be preferred over any of the alternative schemes “if it is indeed the aim of taxonomists to reflect phylogenetic trends in their work”. According to Hartman (1958a), Bidder’s system is more natural because it is “supported by a constellation of both embryological and morphological characteristics”, while the classification of Poléjaeff is based only upon the aquiferous system. He also found that the morphology of triradiates was concordant with other characters, even if there were some isolated exceptions, and states that “the question of assigning a given species to *Clathrina* or *Leucosolenia*, in the absence of cytological and embryological data, is not nearly as difficult as some authors have asserted”.

Following Hartman’s re-examination of Bidder’s classification Burton (1963) published his revision of the classification of the calcareous sponges. Not only did Burton (1963) reject the subdivision Calcinea/Calcaronea but he also denied the taxonomic value of most of the characters that had been used before him – even the usefulness of the organisation of the aquiferous system (e.g., syconoid/sylleibid/leuconoid), or the presence or absence of particular types of spicules (like microxeas), to delimitate genera or species. Pushing forward the intraspecific variability of all such characters, he synonymised dozens of species as hitherto recognized (for example he grouped no less than 122 species from various genera under the specific name *Scypha ciliata*). This revision was rejected immediately, and he was not followed in this minimalist logic by any contemporary workers (see Jones, 1964; Borojevic, 1979; Hartman, 1982; Hooper & Wiedenmayer, 1994; Borojevic *et al.*, 1990, 2000).

In previous publications dealing with the taxonomy of Calcarea, Borojevic (1979), Vacelet (1981, 1985), Borojevic *et al.* (1990, 2000) followed Hartman (1958a) in adopting the subdivision between Calcinea and Calcaronea. One consequence of this was to split the former ‘pharetronids’, which are viewed as polyphyletic, between Calcinea (order Murrayonida) and Calcaronea (order Lithonida) (Vacelet, 1985; Borojevic *et al.*, 1990, 2000). More recently a new character – differences in δO^{18} ratio of spicules – was introduced into calcarean systematics that supported the dichotomy between Calcinea and Calcaronea (Wörheide &

Hooper, 1999). The only contemporary authors to question the validity of taxon Calcinea are Reitner & Mehl (1996).

The calcarean phylogeny is still not entirely resolved, however, especially when considered from the point of view of modern phylogenetic systematics, or cladistics. The lack of data for many genera and species, as underlined by Dendy & Row (1913), still remains somewhat puzzling. Furthermore, even if the congruence and consistency of many characters are evidence of their importance at high taxonomic level, the Calcinea/Calcaronea subdivision has always been argued on pre-Hennigian grounds, and has never been inferred as the result of an explicit and reproducible analysis of characters (i.e., objective criteria). Particularly problematic is the fact that morphological characters used in support of such a ‘deep dichotomy’ are not polarised: the basal or apical nucleus – is one derived with respect to the other, or are the two states derived from an unknown ancestral state? The same question can be asked for larval types, spicule morphology and other characters. Unfortunately there is currently no obvious answer. If one set of character states (either those of the calcineans or the calcaroneans) turned out to be derived with respect to the other, then the first subgroup would be monophyletic while the other would be paraphyletic. It has often happened with traditional ‘dichotomies’ where one group is paraphyletic with respect to the other (e.g., Apterygota with respect to Pterygota among the Hexapoda; Brusca & Brusca, 1990). Morphology alone is of little use to resolve the question of monophyly of Calcinea and Calcaronea because of the low number of characters that can be defined and the impossibility of polarising them. In contrast, we have obtained recently good support for the monophyly of both Calcinea and Calcaronea from molecular phylogeny (Borchiellini *et al.*, 2001, Manuel, 2001), and for that reason we are quite confident that both taxa will remain in future (phylogenetic) classifications.

Remarks

Within each of the two subclasses Borojevic *et al.* (1990, 2000) introduced substantial changes from previous schemes at the ordinal level (in particular as compared with that of Hartman, 1958a). Within subclass Calcinea two orders are now recognised (following Borojevic *et al.*, 1990). Clathrinida Hartman, 1958a was emended to now include all families previously allocated to Leucettida Hartman, 1958a. This undoubtedly is progress towards a phylogenetic classification, since the Clathrinida in Hartman’s sense were nothing more than a grade of simpler organisation with respect to his Leucettida. The second order of Calcinea, Murrayonida Vacelet, 1981, contains those calcareous sponges with a reinforced skeleton and calcinean features. Within subclass Calcaronea three orders were recognised (following Borojevic *et al.*, 2000). Leucosolenida Hartman, 1958a was emended to include all families previously allocated to Sycettida by Hartman (1958a). A new proposal was to create the order Baerida Borojevic *et al.*, 2000 for several genera united by unique characters such as the abundance of microdiactines, or the presence of dagger-shape tetractines (pugioles) as constituent of the skeleton of the exhalant aquiferous system. A third order, Lithonida Vacelet, 1981, contains genera displaying a reinforced skeleton and calcaronean features.

Despite the major recent revisions of the two subclasses the diagnoses of families and genera remain generally similar to those proposed by Dendy & Row (1913). This result highlights the importance of a detailed consideration of skeletal architecture in calcarean systematics. This is also true for the species-level taxon

where it is imperative for a description of a new species to be accompanied by a precise description of the organisation of the sponge, based upon good quality transverse and longitudinal sections. Conversely, in our collective experience many other characters that have been classically used in calcareous sponge taxonomy (such as external form or spicule measurements) are highly variable – although the extent of this intra-specific variability remains to be appreciated with respect to differentiating phenotypic versus genotypic differences at the population level. However, recent biochemical studies indicate that very small morphological differences may correspond to extensive genetic differences, and a full genetic separation of both sympatric and allopatric populations of Calcarea is often associated with very faint or even undetectable separation as judged by the traditional morphological criteria (Solé-Cava *et al.*, 1991; Klautau *et al.*, 1994). The classical taxonomy based solely on morphological criteria is thus clearly over-conservative. The consequence of these data is that many specimens previously classified as simple variations of existing taxa, many of which are often allegedly cosmopolitan species, probably represent genetically distinct taxa.

How far are we from a phylogenetic classification of Calcarea? Clearly, much work remains to be done in this respect. Interfamilial phylogenetic relationships within Calcinea or Calcaronea remain virtually unknown. Even widely accepted ideas, such as the primitiveness of the asconoid (olythus-like) aquiferous system within each of the two lineages, have yet to be tested. One pressing question concerns the monophyly and phylogenetic position of Murrayonida within Calcinea, and Lithonida within Calcaronea: are these taxa deep-branching ‘relict’ groups (as postulated by Vacelet, 1985), or alternatively, more recently evolved and morphologically specialised groups? Several taxa within Calcaronea could well turn out to be paraphyletic, such as the Leucosolenida with respect to Baerida, or the Sycettidae (or maybe even the genus *Sycon*) with respect to both Grantiidae and Heteropiidae (if assumptions found in the literature, that the two latter “arose from” the former are verified, see Dendy & Row 1913). All these questions and others should be resolved in the future through explicit, cladistic analyses of characters. Unfortunately, Calcarea offer very few morphological characters for reliable (informative) phylogenetic analysis – perhaps even less than the Demospongiae given their relative uniformities amongst spicule types. Further, calcarean morphological characters appear to be highly susceptible to convergence. Molecular data appear to be essential to provide corroboratory evidence for phylogeny based on morphological hypotheses.

It is clear that our knowledge of the world fauna of Calcarea is very fragmentary. Many of the species described by Haeckel and Dendy have never been found since they were originally described. Even in relatively well-explored regions where the study of local marine faunas has received considerable effort (such as in the Mediterranean, both sides of the Channel in the Atlantic Ocean, or the coasts of Japan in the Pacific Ocean), many new forms are being discovered by comprehensive surveys of the local marine biota. Consequently, the present revision is far from complete, and further faunistic studies will undoubtedly turn up many species new to science, and their detailed analyses (morphometrics + molecular analysis) will clarify the position of many taxa which have, at present, only a putative position in the system. Thus, the classification offered here should be considered as a starting point for future investigations.

Calcareous sponges have been largely neglected by contemporary sponge biologists, although more recent phylogenetic

hypotheses that these taxa may constitute a potential phylum (Calcispongia) and a sister-group of the Eumetazoa (Zrzavy *et al.*, 1998; Borchiellini *et al.*, 2001), will probably stimulate new research using calcareous sponges as models to understand the early origin and evolution of Metazoa (Manuel & Le Parco, 2000).

REMARKS ON HAECKEL'S ‘PRODROMUS’

Haeckel's (1872) ‘Monograph on Calcareous Sponges’ was the first comprehensive classification proposed for this group. Unfortunately, several nomenclatorial problems were introduced by this study, which require further discussion.

The first problem stems from the fact that Haeckel (1870b) proposed in his ‘Prodromus eines Systems der Kalkschwämme’ a preliminary classification of Calcarea, based on the external organisation, number and quality of oscules, and organisation of the aquiferous system. Haeckel proposed 39 genera with new names, including 289 species. Each genus was subdivided into subgenera with proper names. Descriptions of genera and species were extremely succinct such that they cannot now be used to differentiate sponge species. This system was subsequently qualified by Haeckel himself as ‘artificial’, and in his ‘Monograph’ (Haeckel, 1872) it was completely abandoned, together with all the generic and subgeneric names proposed earlier. Conversely, most of the 289 specific names proposed in the ‘Prodromus’ (Haeckel, 1870b) were used in the ‘Monograph’, where they were more completely described and associated with new generic names. Although Haeckel (1872) referred to his earlier genus and species combinations proposed in the ‘Prodromus’ (in some places in the text and in the list appended at the end of the text), these species are recognisable as such only from their published descriptions in the ‘Monograph’. Virtually all scientists studying Calcarea since Haeckel's publications agree that the plethora of generic and subgeneric names proposed in the ‘Prodromus’ are not valid. As they have not been used since, for well over 50 years, they fall into the category of *nomina oblita* as defined by the International Code of Zoological Nomenclature (Anon., 1999). We follow this position here and do not cite the ‘Prodromus’ names in our lists of the generic synonyms (see ‘Annotated list of unrecognisable sponge taxa and unavailable names’, this volume).

The second problem stems from the fact that in his ‘Monograph’ Haeckel (1872) devised an aesthetic and an entirely ‘closed classification’ for all proposed generic names. He followed the rule that the prefix of the generic name indicated the aquiferous system organisation (hence generic names prefixed by ‘Asc-’, ‘Syc-’ or ‘Leuc-’ corresponded to the asconoid, syconoid or leuconoid organisation, respectively). The suffix corresponded to the spicule types present (hence ‘-etta’, ‘-illa’, ‘-yssa’, ‘-altis’, ‘-ortis’, ‘-ulmis’ and ‘-andra’ corresponded to different combinations of the three major spicule types (diactines, triactines and tetractines). In promoting this system, as logical as it appeared at the time, Haeckel (1872) ignored the priority of the valid generic names proposed by previous authors. Subsequent studies had to revisit the original descriptions and reinstate the earlier generic names. Simultaneously, Haeckel's (1872) scope of genera was not followed subsequently in all cases. On the one hand, it was necessary to use earlier generic names for groups of species associated with the type species of the genus described before Haeckel (1872) (e.g., *Sycortis lingua* and *Sycandra raphanus* now belong to the genus *Sycon*, with the type species *Sycon humboldtii* Risso). On

the other hand, species described by Haeckel (1872), which were not associated with an earlier generic name, had to be used subsequently as valid genus/species combinations (e.g., *Sycetta primitiva* Haeckel). In the former case Haeckel's (1872) generic name is a junior synonym when combined with the species previously described in a valid genus, but in the latter case it is valid when associated with species described by Haeckel himself.

The third problem stems from the fact that in the 'Monograph' Haeckel (1872) attributed to each described species the 'Generische Varietäten', which referred to some particularities in the external organisation, number and quality of oscula, etc. He had already used these external characters to define genera in the 'Prodromus' (Haeckel, 1870b). In order to underline these characteristics already described in his earlier studies Haeckel (1872) used the generic names proposed in the 'Prodromus'. It is clear from Haeckel's (1872) text that he no longer considered them as valid genera but as simple 'variations' on the standard pattern of growth of the described sponges, and he used these names subsequently (1872) simply as descriptors. Consequently, beyond each genus-species combination he proposed, several other combinations are listed as 'varieties' using earlier 'Prodromus' generic names. For the reasons cited above we consider that the 'Prodromus' names are *nomina oblita*, and we do not consider the 'generic varieties/species' combinations of the 'Monograph' valid or worth listing here. In addition to these 'Generische Varietäten', each of Haeckel's (1872) species also often had a list of named 'Specifische Varietäten'. These correspond to the 'subspecies' as defined in modern systematic studies, and each of them is a combination of only one generic and subspecific name. Many of them have been elevated subsequently to the species level in the contemporary literature, and they potentially represent valid genus/species nominal combinations.

The fourth problem arises from the fact that the larger of Haeckel's (1872) genera were subdivided into subgenera, with proper names given which are not the names used in the 'Prodromus'. A number of species is clearly attributed to each subgenus, and a fairly good definition is given for each subgenus taxon. When subsequent studies have shown that one or several of the species associated with one particular subgenus should be separated into a valid genus, the combination of the Haeckel's (1872) subgenus/species name is valid, and it has been used since

(e.g., *Leucettusa corticata* Haeckel). It is important to clearly define in these studies that elevate Haeckel's (1872) subgenera to the generic level the combination which is to be considered as a type species of the proposed genus.

The fifth problem stems from the fact that Haeckel (1872) provided a list of earlier synonymies and citations for each species, referring to both published and manuscript names of other spongiologists, as well as to the synonymies from the 'Prodromus' which are *nomina oblita* described by himself in the previous study (1870b). Although many of these are helpful to establish previous descriptions and potentially valid senior synonymies, Haeckel had access to many manuscript documents and to sponges sent to him by other biologists, including the previously described specimens, as well as many 'manuscript' names and descriptions. These synonymies are entirely Haeckel's (1872) responsibility, and subsequent studies must decide upon their validity on a case-by-case basis. On the other hand, the 'manuscript' names cited by Haeckel (1872), such as *Djeddea* and *Mlea* Miklucho Maclay, have not been published in the meaning of Article 8 of ICZN (Anon., 1999), and obviously they are not available names.

In view of the availability of many names coined by Haeckel (1870b, 1872), subsequent studies have occasionally used these names in an entirely different context, referring to a particular character recognised and originally pointed out by Haeckel, and avoiding the creation of a new name (e.g., the use of *Soleniscus* by Borojevic *et al.*, 1990). These studies, and similar ones in the future, need to indicate clearly that the scope of the species or genus is emended, and to define the new scope and the new type specimen or type species for the respective taxa.

While the question of generic synonymies for Calcarea appear to be confused and convoluted, Dendy & Row (1913) provided a thorough analysis of all these previously proposed names and their synonymies. They also provided, at the end of their study, a list of rejected generic names, explaining the reasons why they should be rejected, and indicated their prior use in combination with species names in order to facilitate determining the true generic names and the corresponding type species (should any of these names be revived for use). We fully agree with a large majority of the positions taken by Dendy & Row (1913), and the reader is referred to this study for any further details (see 'Annotated list of unrecognisable sponge taxa and unavailable names', this volume).

KEY TO ORDERS OF CALCINEA AND CALCARONEA

- (1) Regular (equiangular and equiradiate) triactines and tetractines, choanocytes basinucleate with spherical nuclei (**Calcinea**) 2
Sagittal triactines & tetractines, choanocytes apinucleate (**Calcaronea**) 3
- (2) Skeleton composed exclusively of free spicules **Clathrinida**
Reinforcement of the skeleton composed of either spicule tracts, calcareous plates or a rigid nonspicular skeleton. Diapasons or modified diactines present and generally fasciculated **Murrayonida**
- (3) Skeleton composed exclusively of free spicules 4
Reinforcement of the skeleton consisting either of linked or cemented basal actines of tetractines, or of a rigid basal mass of calcite. Diapason spicules generally present. Aquiferous system leuconoid **Lithonida**
- (4) Skeleton either composed exclusively of microdiactines or in which microdiactines constitute exclusively or predominantly a specific sector of the skeleton. Large or giant spicules frequently present in the cortical skeleton. Dagger-shaped small tetractines (pugioles) frequently the sole skeleton of the exhalant aquiferous system. Aquiferous system leuconoid **Baerida**
Free spicules diactines, sagittal triactines/tetractines. Aquiferous system asconoid, syconoid, sylleibid or leuconoid **Leucosolenida**

SUBCLASS CALCINEA BIDDER, 1898**Synonymy**

Calcinea Bidder, 1898: 73.

Previous reviews

Bidder, 1898: 73; Hartman, 1958a; Borojevic *et al.*, 1999: 247.

Diagnosis

Calcarea with a regular (equiangular and equiradial) or exceptionally parasagittal or sagittal triactines and/or a basal system of tetractines. In addition to the free spicules, there may be a non-spicular basal calcareous skeleton. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinucleate with spherical nuclei. The basal body of the flagellum is not adjacent to the nucleus. Calcinea incubate coeloblastula larvae.

Biology

Calcinea have a great variability of forms, but their general organisation and the basic characteristics of their cytology and embryology show that they represent a homogeneous group. All Calcinea have large choanocytes with basal spherical nuclei. There is no topological relationship between the nucleus and the basal structures of the flagellum. Like the whole class they are viviparous. Their oocytes are formed in the mesohyl from a yet undetermined cell-type. The origin of the spermatozoa and fertilization are incompletely known (Hadzi, 1917; Tuzet, 1947). Oocytes grow by incorporation of nurse-cells, most of which are degenerated choanocytes. Embryogenesis proceeds diffusely in the sponge body, or in special structures described as "nests" (Borojevic, 1969). Fertilised eggs pass through total and equal divisions, and form a coeloblastula composed of equal blastomeres. Incorporation of maternal cells into the blastocoel is frequent, but their destiny in the larva is unknown (Borojevic, 1969) (Fig. 4A). In some larvae a few large non-flagellate cells can be found at the posterior pole. Their number may be characteristic of the species (Johnson, 1978). Larvae are free-swimming flagellated blastulae. The internal cell mass is progressively formed by immigration of flagellated external cells. When metamorphosis occurs, a pupa is formed which is composed of apparently totipotent cells that differentiate according to their position: the external ones yield the future pinacoderm and the skeletogenous tissue, while the internal ones differentiate into the choanoderm (Borojevic, 1969). Early post-larval development apparently passes through the olynthus stage of organisation. Triactines are the first spicules secreted. The spicules are essentially regular, equiangular and equiradial. In some species, parasagittal spicules are also present, with one actine longer than the others, and sometimes the unpaired angle different from the paired ones.

Scope

Two groups may be distinguished among the Calcinea. Clathrinida includes sponges with only free spicules. This is an extremely rich and variable group. All developmental stages are present, from simple olynthus-like sponges to complex ones with an elaborate aquiferous system. Parallel lines of increasing

complexity, which often correspond to the calcinean families may be distinguished. In each line a complete series from the simple asconoid to the elaborate leuconoid aquiferous systems can be observed. Murrayonida Vacelet, 1981, includes only a few Recent sponges in which the skeleton is composed of spicule tracts, and/or a supplementary non-spicular calcareous skeleton along with free calcareous spicules. This skeleton may be composed either of a rigid non-spicular network, such as observed in the Murrayonidae, or of spicule tracts with either calcareous plates, such as observed in the Paramurrayonidae, or tripods, such as found in the Lelapiellidae. Unlike the Clathrinida the order Murrayonida has only a few representatives in Recent faunas and is restricted to three monospecific families. No sponges with fused spicules are known among the Calcinea, as opposed to calcaronean hypercalcified sponges in which this type of skeleton is frequent.

SUBCLASS CALCARONEA BIDDER, 1898**Synonymy**

Calcaronea Bidder, 1898: 73.

Previous reviews

Bidder, 1898: 73; Hartman, 1958a; Borojevic *et al.*, 2000: 207.

Diagnosis

Calcarea with diactines and/or sagittal triactines and tetractines, rarely also with regular spicules. In addition to free spicules there may be a non-spicular basal calcareous skeleton in which basal spicules are cemented together or completely embedded in an enveloping calcareous cement. In their ontogeny the first spicules to be produced are diactines in the settled larva. Choanocytes are apinucleate, and the basal system of the flagellum is adjacent to the apical region of the nucleus. Calcaronea incubate amphiblastula larvae.

Biology

Like Calcinea, Calcaronea are extremely variable in size, form, organization of the aquiferous system, and skeleton. Most representatives are known only from Recent seas. Isolated spicules, which may belong to calcaronean sponges, have been reported from Early Cambrian reefs (James & Klappa, 1983) and in Ordovician strata (Kempen, 1978).

The aquiferous system in the Calcaronea can be asconoid, syconoid, sylleibid, or leuconoid. Asconoid, syconoid, and sylleibid systems are found only in the Leucosolenida. The leuconoid aquiferous system, such as that seen in the Leucosolenida, can be easily derived from a syconoid-type of organization as these sponges retain traces of the radial organization of the skeleton and the usually clearly defined central atrium. However, the leuconoid systems in the Baerida and the Lithonida bear no trace of an original tubular or radial organization, but are instead quite similar to the leuconoid aquiferous systems of the Demospongiae.

Calcaronean sponges have choanocytes with an apical, ovoid or pyriform nucleus. The basal flagellar roots are always in contact with the nuclear envelope at the apical pole of the nucleus. In many

species, a glycocalyx layer is present between the microvilli which form the collar. The interpretation of the localization of the nucleus within the choanocytes is often hampered by artifacts caused by handling of sponge after collection and their fixation. Since this is one of the most distinctive characters distinguishing the Calcarea from the Calcaronea, sections of preserved material must be interpreted with caution (Vacelet, 1964).

Despite the great diversity of organisation, our present knowledge of calcaronean biology, in particular their cell and skeletal morphology, indicates that there are a number of homologies among currently known species, and strongly supports the hypothesis of their common origin as well as a rather close relationship among all the sponges belonging to this subclass. Most notably, Calcaronea have a fertilization process and a very particular pattern of embryogenesis and larval morphogenesis that can be construed as 'typical' for the subclass.

During fertilization, the spermatozoa are captured by choanocytes, which transform into a particular spermatozoan carrier cell containing the spermiocyst (Duboscq & Tuzet, 1937; 1942; Vacelet, 1964; Gallissian, 1989; Gallissian & Vacelet, 1990). These cells migrate into the subchoanodermal space where they fertilize large mature oocytes. The entrance point of the carrier cell into the oocyte determines the symmetry of the future larva in the Leucosolenida, but apparently not in a sponge that we currently classify in the Baerida (Duboscq & Tuzet, 1937, 1942). Only small differences in the fertilization process have been observed between calcaronean species studied so far. There is also one report of a similar fertilization process in the rest of the Calcarea (Tuzet, 1947), as well as three reports in the Demospongiae (Boury-Esnault & Jamieson, 1999).

The amphiblastula larva has large aflagellated cells at one end and small flagellated cells at the other (Fig. 4B). There are four 'cellules en croix' which have the presumed function of photoreceptors (Duboscq & Tuzet, 1941; Borojevic, 1970; Amano & Hori, 1992). At the early blastula stage the flagella are directed inwards into the primary blastocoel. Subsequently, in the stage called the stomoblastula, the aflagellated cells form an opening through which the flagellated blastula wall evaginates, inverting the larval wall and turning the flagella outwards. The larva closes again, delimiting a secondary blastocoel. At this stage the larva is a typical amphiblastula with clearly marked poles. The flagellated pole

corresponds to the anterior pole of the free-swimming larva, while the large aflagellated cells are restricted to the posterior pole. After settlement, the large aflagellated cells give rise to pinacocytes, sclerocytes and to other amoeboid cells, while the flagellated cells differentiate into choanocytes (Amano & Hori, 1993). The inversion of the early larva is unique and specific to the subclass Calcaronea, and is reminiscent of the morphogenesis of *Volvox* (Ivanov, 1971). Amphiblastula larvae of the Calcaronea differ from all other sponge larvae. Their resemblances to the cinctoblastula larvae of the Homoscleromorpha, which have been called amphiblastula for a long time, are only superficial (Boury-Esnault *et al.*, 1995). In the order Leucosolenida, after the settlement of the larva, an asconoid tubular sponge is formed, which can remain at this stage of organization (e.g., *Leucosolenia*) or form radial outgrowths which give rise to the radial tubes of the syconoid grade of organization (Schulze, 1875). The postlarval development of the two other orders of the Calcaronea is not known.

Scope

Borojevic *et al.* (2000) proposed a tentative scheme to identify the taxonomic units that potentially represent monophyletic groups of species within the Calcaronea. The conventional view is adopted here: that the simple 'ascon' type of sponge organization is 'primitive', and the more complex types of skeletal and tissue organization are derived from the more simpler ones. This does not mean that the progressive increase in complexity is necessarily the true evolutionary pathway, which cannot be reconstructed from morphological data alone. Using this approach, the separation of sponges that are now grouped in the order Leucosolenida, from those belonging to the Lithonida, has been confirmed (Borojevic, 1979; Vacelet, 1991; Borojevic *et al.*, 2000). This has also led to a separation of a group of sponges considered as 'aberrant' by Dendy & Row (1913) from the Leucosolenida, described as Baerida, a new order of Calcaronea (Borojevic *et al.*, 2000).

The scope of most of the genera is that proposed by Dendy & Row (1913), who provided very detailed descriptions of the genera, and provided extensive discussions, synonymies and comparisons with previously described taxa. These detailed discussion on earlier synonymies are not repeated here, and should be referred to in Dendy & Row (1913).