Taxonomy of Calcareous Sponges

This iconoclastic work, **A Revision of the Classification of the Calcareous Sponges** [British Museum (Natural History), London, 1963. 693 pp. Illus. $42], by Maurice Burton, comprises a synopsis of the more than 500 species of sponges of the Class Calcarea, described up to the early 1950's. Diagnoses and discussions of the 54 genera hitherto recognized are given, and each named species is provided with a description including spicule measurements, a list of synonymy, and the geographic range. Figures, redrawn after the original author in each case, are reproduced for most of the species. As such, Burton's monograph is a highly useful compendium and will serve as a point of departure for future work on the systematics of calcareous sponges.

The conclusions that Burton has reached from his revisionary studies are, however, highly questionable in my opinion. Briefly stated, Burton has become so impressed with variability in the Calcarea that he dismisses such characters as the arrangement of the canal system and the position of the nucleus in the choanocyte as useless to the taxonomist in species definition and phylogeny. He believes that spicules provide the only valid characters, and even with regard to these Burton sees a remarkably wide degree of intraspecific variability in shape and size and in the presence or absence of spicule categories. On the basis of his interpretation of variability within the Calcarea, Burton reduces the number of genera from 54 to 22 and the number of species from more than 500 to 47. Such a simplification of a classification system is a remarkable achievement, but we must examine the premises on which it is based.

Burton first records his impressions of the variability in spicule size and shape, in the size and shape of adult individuals, in the presence or absence of spicule categories, and in the degree of development of the dermal cortex in a series of species of common European calcareous sponges. On the basis of his observations of the variability of these characters in large numbers of individuals of each species collected or studied in the field in restricted geographic areas of the British Isles, he generalizes to the point of including numerous previously described species from all parts of the world in each of his species. For example, having established the broad limits of variability within the species *Sycon ciliatum* as he has observed it in England, Burton finds it possible to include 102 species previously described from all parts of the world (except Antarctica) within his concept of *S. ciliatum*.

Burton synonymizes 43 species in his concept of *Leucosolenia botryoides* and cites in support of this procedure the work of Sarà [*Ann. Ist. Mus. Zool. Univ. Napoli* **5** (7), 1 (1953)] in which an analysis of spicule variability in three species of *Leucosolenia* found in the Bay of Naples led Sarà to regard these species as forms of *L. botryoides*. However, Burton has overlooked Sarà's later study of the genus *Leucosolenia* at Roscoff [*Boll. Zool.* **23** (2), 1 (1956)], in which Sarà concluded that *L. botryoides, L. complicata*, and *L. variabilis* (the latter two were considered "forms" of the first in Sarà's earlier paper) are valid species readily distinguishable on the basis of external form, spiculation, and ecological niche differentiation. Sarà has also reported that where populations of *L. variabilis* and *L. complicata* coexist in intermediate habitats, hybridization takes place between the species. In view of these studies one may ask whether critical analyses of other groups of species within the genus *Leucosolenia* will not lead to comparable conclusions and present further evidence against Burton's extensive synonymizing.

Second, Burton questions the significance of the structure of the canal system of calcareous sponges as a taxonomic character and as an aid in interpreting phylogenetic trends. His point is well made that it is difficult or impossible to determine whether the simplicity of the asconoid grade of construction of calcareous sponges is primary or derived. He states further that the more complex types of canal systems (syconoid, sylleibid, and leuconoid) may occur as variations within the same species, as in *Leuconia fistulosa*. This may well be so in some species, but again it is questionable whether Burton is warranted in generalizing from his observations on a single population of sponges in England to all calcareous sponges. Undoubtedly it is the results of his studies at Plymouth on the variability of the canal system of *Leuconia fistulosa* (which he regards as a synonym of *Sycon ciliatum*) that have enabled him to include so many typically leuconoid species in his all-embracing concept of *S. ciliatum*. The species *L. heathi* Urban, for example, occurs on the California coast. In external form, adult individuals are consistently subspherical to top-shaped; young specimens are cylindrical. The canal system is always leuconoid, and the spicule complement is reasonably constant, according to the literature reports available. It seems incredible that this species should be synonymized by Burton with *S. ciliatum* because the variable characters of the latter species, as he has observed it in England, happen to overlap many of the characters of *L. heathi*. The external form of adults, the consistently leuconoid canal system, and the absence of endosomal quadriradiates in the California sponge differentiate it quite clearly from *S. ciliatum*.

Third, Burton doubts the value of the position of the nucleus in the choanocyte in taxonomic and phylogenetic studies of calcareous sponges. Burton thereby rejects Bidder's system of classification [*Proc. Roy. Soc. London* **64**, 61 (1898), but he does so without recognizing its full significance —namely, that it is based on a constellation of characters and not on a single character as Burton implies [see further discussion in W. D. Hartman, *Syst. Zool.* **7**, 97 (1958)]. In his simplified system Burton cites two examples of species in which choanocyte nucleus position is inconsistent with Bidder's scheme. These are *Leucosolenia asconoides* (Carter) and *Leuconia barbata* (Duch. and Mich.). The former species is admittedly difficult to place in Bidder's system. As an asconoid sponge with basal choanocyte nuclei, it would fall into the family Clathrinidae; yet in external form it is like a *Leucosolenia*. Regrettably larval characters, which form another important part of Bidder's system, are unknown for *L. asconoides*. Burton's second example is a problem only if we accept his synonymy. He states that in *L. barbata* some specimens have basal and others apical choanocyte nuclei. It should be noted that choanocyte nuclear position has not been recorded in the literature for *Leuconia barbata* [*sensu stricto*]; only two records of this West Indian sponge exist—those of Duchassaing and Michelotti and of de Laubenfels. In Burton's broad view of the species, he has included species of genera with apical nuclei, such as

Vosmaeropsis and *Leucandra*, as well as species of genera with basal nuclei, such as *Leucascus* and *Leucetta*. Burton's synonymy of these species is based on "external appearance [which in reality varies considerably from species to species] and the general form of the skeleton"; he has rejected the opinions of previous authors, which are based on character complexes, including position of choanocyte nucleus and consistent differences in spicule types and canal system structure. In setting limits to his species, he also seems unconcerned about geographical disjunction.

It should be pointed out that Vacelet [*Syst. Zool.* **10**, 45 (1961)] and Sarà [*Monit. Zool. Ital.* **71**, 229 (1963)] have shown that the complex of characters used by Bidder to separate the Calcarea into two subclasses are not distributed consistently among the species of pharetronid calcareous sponges. The work of these authors therefore bears out Burton's doubt about the usefulness of choanocyte nucleus position in systematic studies of calcareous sponges and leads me to recognize my error in placing the Pharetronida as an order in the subclass Calcinea [*Syst. Zool.* **7**, 97 (1958)]. It does not necessarily follow, however, that Bidder's classification should now be abandoned. The character complexes used by Bidder still provide a valid basis for subdividing the bulk of the Calcarea into two subclasses, according to data available so far. The pharetronids, a group of calcareous sponges with fused skeletons, may be interpreted in one of two ways. On the one hand, they may represent a polyphyletic group in which the pharetronid type of skeleton has arisen independently from several families of Calcarea. The pharetronids would then be comparable in their origin to the lithistids among the Demospongiae, according to the views put forth by de Laubenfels [*Paps. Tortugas Lab.* **30**, 1 (1936) and *Treatise on Invertebrate Paleontology* (Univ. of Kansas Press, Lawrence, 1955), pt. E, p. 21]. On the other hand, they may represent an early offshoot of the Calcarea, which has diverged in its own right since its origin in late Paleozoic times (the earliest fossil pharetronids date from the Permian). The characters that consistently occur together in the Calcinea and Calcaronea and thus provide a basis for separating these subclasses may have changed in a random fashion among the Pharetronida. It can only be hoped that additional discoveries of pharetronids comparable to those of Vacelet and Sarà will provide further material for evaluating the alternatives presented here.

Burton's monograph is important, therefore, not only as a catalog of the described species of Calcarea but also in pointing out a number of problems about the structure of these animals which need further study. How general is the occurrence of syconoid and leuconoid canal systems within a single individual, an observation which Burton uses to help justify his synonymy of *Sycon ciliatum* and *Leuconia fistulosa*? Will the significance of Bidder's complex of characters break down completely when more species of nonpharetronid Calcarea have been studied in detail? Is extrusion of spicules a sufficiently wide occurrence among species of Calcarea to cast doubt on the importance of the presence or absence of spicule types in species definitions? Answers to these questions are essential to an evaluation of Burton's simplified classification. Burton has concluded that, in the light of the confusing variability which he has observed in characters among the Calcarea, the best solution for the practical museum taxonomist is to become an extreme lumper. On the contrary, it is my feeling that it is best to err on the side of splitting until individual species complexes have been analyzed in a critical manner. Calling attention to differences rather than submerging them seems to me to be of greater value to future revisers of animal groups.

There is little doubt that many tangled synonymies will be uncovered among the 500 known species of calcareous sponges when thorough revisionary studies have been made. Burton has laid the groundwork for such studies by bringing together information on all species described so far. In my opinion, however, his extensive synonymies must be viewed with extreme skepticism at this time.

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Numerical Taxonomy and Biological Classification

Numbers and numerical concepts have of course always been used in biological classification. Toward the end of the 19th century, these procedures and concepts began to be affected, usually for the better, by increasing sophistication of methods. One development, which is not discussed by Robert Sokal and Peter Sneath in their book **Principles of Numerical Taxonomy** (Freeman, San Francisco, Calif., 1963. 375 pp. $8.50), involved the treatment of numerical characteristics of organisms not as measurements of individual types but as parameters of variation in populations. Associated with that biometric approach were methods of inference from sample to population and methods of establishing confidence intervals for populational parameters. Other important developments had to do with similarities and differences among populations and with the recognition of associations, which permitted taxonomic formalization of groups, sets, or clusters of populations. Obviously these had always been leading concepts of taxonomy, even in creationist-typological days, and they are still more so in our modern evolutionary-populational taxonomy. What was new was the invention and application of concretely quantitative measurements to these taxonomic procedures.

That quantitative approach has made considerable progress since the 1890's, but the most sophisticated procedures met opposition and still are used only by a minute fraction of practicing taxonomists. Apart from sheer inertia, there were many reasons for the opposition and lack of use. One reason was, and is, that a single measure of similarity involves an enormous loss of information, mainly on the character, direction, and origin of differences, essential for really meaningful classification. Divorced from their *biological* significance, the results as pure numbers can too readily lead to banal or false conclusions. Another reason for limited acceptance was and is that the selection, measurement, and coding of multiple characters and their combination into a measurement of similarity is a highly subjective and arbitrary matter. It can be repeated or understood by a second worker only if he knows and adopts the same data, methods, and conventions. Moreover, in most fields the most thoroughly numerical