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A revision of the supraspecific classification of the subclass Calcinea (Porifera, class Calcarea)

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Abstract. — All existing generic taxa within the subclass Calcinea of the class Calcarea are redefined and discussed. Two orders are recognized within this subclass : Clathrinida and Murrayonida. Seven families and 15 genera are considered within the Clathrinida and three families and three genera within the Murrayonida. In the Clathrinida, several parallel and continuous evolutionary lines may be recognized, starting from simple sponges similar to representatives of the Recent genera *Soleniscus* and *Clathrina.* In contrast, the Murrayonida are represented by only three highly-evolved species. A cladogram of the phylogenetic relationships between members of the Clathrinida is proposed.

Key-words : Porifera, Calcinea, evolution, generic definitions.

Résumé. — Tous les genres récents de la sous-classe Calcinea (classe Calcarea) sont redéfinis et discutés. Deux ordres sont reconnus dans cette sous-classe : Clathrinida Hartman, 1958 emend. avec sept familles généralement polytypiques comprenant quinze genres, et Murrayonida Vacelet, 1981 avec trois familles monotypiques. L'évolution des Clathrinida semble avoir comme point de départ l'olynthus. Cette forme est probablement présente dès les premiers stades de l'ontogenèse de toutes les Clathrinida, et subsiste à l'état adulte chez *Soleniscus.* La croissance à partir de cette forme simple se fait de plusieurs façons : a) un allongement de l'olynthus chez *Soleniscus*, qui aboutit à la formation de diverticules externes (genres *Levinella* et *Burtonulla*) ; b) une augmentation du diamètre de l'olynthus, dans la lignée *Ascandra* ; par formation de plis internes du choanoderme, on atteint l'organisation hétérocoele chez *Leucettusa* et *Leucaltis* ; c) par ramifications et anastomoses d'unités élémentaires olynthus, il se constitue des cormus comme ceux de la lignée *Clathrina, Ascaltis* et *Leucascus* ; l'intégration du cormus chez *Leucetta* et *Pericharax* permet à cette lignée d'atteindre l'organisation leuconoïde typique. La présence dans la faune actuelle de nombreux stades parfois bien diversifiés des étapes de ces trois modalités de croissance et de complication conduit à interpréter l'évolution de cet ordre comme relativement récente. La classification proposée est fondée sur cette interprétation, dans laquelle l'organisation leuconoïde la plus complexe a été atteinte de façon indépendante dans plusieurs lignées et un cladogramme est établi. Au contraire, les Murrayonida, représentées seulement par trois familles, ont toutes une organisation complexe. Ce sont probablement les derniers représentants d'un groupe fossile florissant dont les étapes évolutives ont été perdues. Malgré l'histoire évolutive bien différente des Clathrinida et des Murrayonida, les Calcinea représentent par leur organisation anatomique et cellulaire, leur embryologie et leur squelette un groupe monophylétique homogène.

Mots-clés : Spongiaires, Calcinea, évolution, définitions génériques.

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INTRODUCTION

The class Calcarea represents a well-delimited group among Recent Porifera. It is characterized by the presence of free or fused calcareous spicules to which a rigid calcareous skeleton may be added in rare taxa. The organization of the aquiferous system in Calcarea is highly diversified and this class is the only one among living sponges in which the classic steps

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* Monospecific genus.

of organization — ascon, sycon, leucon — can be found. Since the simplest stage, the ascon, is frequent in the Calcarea, it is often considered to be the most primitive group of the Porifera, and consequently includes the simplest and most primitive metazoans. This is probably the reason why a considerable interest was devoted to their study at the end of the last century and at the beginning of this century. In particular, following the idea that ontogeny repeats phylogeny and that the embryology of the Calcarea is supposed to represent early stages of the passage from the unicellular to the multicellular organization, some of the most prominent zoologists of this period such as HAECKEL, METSCHNIKOFF, MINCHIN and HUXLEY studied this group's biology and embryology.

The first comprehensive system for the Calcarea was proposed by HAECKEL (1869, 1872). In his first study he presented a rather complicated system based exclusively on external form. Subsequently, he recognized the importance of the organization of the aquiferous system and the presence and distribution of spicules. In his great monograph on the Calcarea (1872), he classified all the known calcareous sponges and constructed a system in which genera were characterized by the organization of the aquiferous system and species by the presence of spicule types. This taxonomic hierarchy of anatomical characteristics has proven to be the most satisfactory one and the system proposed by HAECKEL still represents the basis for a consistent classification of the Calcarea.

However, although HAECKEL's system was simple to use and had a great aesthetic value, it was too artificial to correspond to real taxa and to a phylogenetic classification of the Calcarea. It was soon criticized by the British spongologists and by POLÉJAEFF (1883) in his excellent study of the Challenger collections.

Two new systems of classification for calcareous sponges were proposed simultaneously at the end of the last century. MINCHIN (1896) recognized two basic patterns of (1) spicule form, (2) position of the nucleus in the choanocytes and (3) organization of the larvae. Following MINCHIN's observations, BIDDER (1898) proposed that calcarea are diphyletic and he divided them into two groups : the Calcinea and the Calcaronea.

At the same time, DENDY (1891, 1892, 1894 etc.) published his studies of calcareous sponges from Australia. His classification was based on POLÉJAEFF's division of the Calcarea into Homocoela and Heterocoela. In this system, the Homocoela included all calcareous sponges whose central cavity was lined by choanocytes ("ascones") and the Heterocoela, those where choanocytes were restricted to tubular or spherical choanocyte chambers ("sycones" and "leucones"). The evolution from homocoel to heterocoel types of organization was implicit in this system. DENDY characterized most of the genera of calcarea after detailed studies of the organization of the aquiferous system and the precise distribution of different spicule types. After extensive studies of many calcarea, essentially from the Indo-Pacific region, DENDY and ROW (1913) elaborated a revision of all previously described species. This revision is extremely well-documented and discussed in depth. In the present study of the Calcinea, most genera defined by DENDY & ROW (1913) are retained and the reader is referred to this revision for more detailed information on earlier descriptions and classifications. The classification proposed by DENDY & ROW was accepted and followed by all spongologists until the last third of this century.

In 1958, HARTMAN proposed a new classification which combined the systems proposed by BIDDER (1898) and by DENDY & ROW (1913). He divided the Calcarea into two subclasses, the Calcinea and the Calcaronea, and maintained the division between homocoel and heterocoel grades of organization in both groups. This system was thus simultaneously based on the organization of the aquiferous system, the composition of the skeleton, the cytology and the embryology, and it gives quite a satisfactory picture of the group's evolution.

However, the system proposed by HARTMAN (1958) was not immediately accepted. In particular, this system was not followed by BURTON (1963) in his general revision of calcareous sponges. During his study of a large number of calcarea, BURTON was so impressed by their variability that he dismissed characteristics such as the arrangement of the aquiferous system, the position of the nucleus in the choanocyte and the type of larvae as being useless for taxonomy and phylogeny. He thus decided to group a large number of the described calcareous sponges together into " species " based on the understanding of the term " species " as a rather large union of forms with variable morphology and wide geographical distribution. The principal characters used in his classification were the external shape of the sponge and the presence or absence of certain spicule types. Consequently sponges with considerable anatomical, cytological and embryological differences, but with similar external forms and spicules, were united into the same species.

In earlier publications we have had the opportunity to discuss our position on the classification of the Calcarea (BOROJEVIĆ, 1965, 1966, 1968, 1969, 1970, 1979; VACELET, 1970, *in press*). We consider that the system proposed by BIDDER (1898) and revised by HARTMAN (1958) best reflects the phylogeny of these sponges, among which two clearly distinct groups may be distinguished. These groups have many different morphological, cytological and embryological characteristics, and both may be regarded as monophyletic. This division into two evolutionary lines may also be applied to fossil calcarea and, as was first demonstrated by DENDY & ROW (1913), to the few surviving relicts of the " Pharetronids " (ZITTEL, 1878), which display a full set of characteristics of either the Calcinea or the Calcaronea (VACELET, *in press*).

However, it must be emphasized that the fossil record is of little use in the phyletic reconstitution of the Calcarea (ZIEGLER & RIETSCHEL, 1970). This Class would have been represented in the Cambrian if the Heteractinida (middle Cambrian to Permian) are actually calcarea. However, the Heteractinida, which have polyactinal spicules of calcium carbonate, are very different from modern calcarea. Their evolutionary relationship to the Calcaronea and the Calcinea is unknown and probably remote, and they are considered to be a separate class by some authors, such as FINKS (1970). Isolated spicules which may be attributed to the Calcaronea have been described in early Cambrian reefs (JAMES & KLAPPA, 1983), in Ordovician strata (VAN KEMPEN, 1978), and in the lower Carboniferous, but no unequivocal proof of the existence of calcarea has yet been found. The Calcinea have no definitive fossil record (FINKS & HILL, 1967; WENDT, 1980).

We have undertaken a general revision of the classification of calcareous sponges with a redefinition of all the families and genera that are currently recognized. In view of the large number of Recent species of the Calcarea, we shall discuss the Calcinea and Calcaronea separately. In the present work an attempt is made to propose a diagnosis of orders, families and genera of the Calcinea, and to construct a general key for their identification. Photographs of type-species representing the typical organization of most genera are given. Sketches of the organization of the aquiferous system and of the skeletal architecture are included to clarify the anatomical basis for the proposed generic classification. The terminology proposed by BOROJEVIĆ *et al.* (1967) has been followed except for the terminology of spicules (in order to avoid confusion with the nomenclature of the spicules in Demosponges). The material studied for this revision comes from collections of the Muséum national d'Histoire naturelle de Paris, the British Museum of Natural History (London) and those of the authors.

SYSTEMATIC REVIEW

Class CALCAREA Bowerbank, 1864

Diagnosis : Exclusively marine Porifera in which the mineral skeleton is composed entirely of calcium carbonate. Spicules are biradiate, triradiate and quadriradiate. Calcarea are always viviparous.

Subclass CALCINEA Bidder, 1898

Diagnosis : Calcarea with regular (equiangular and equiradiate) or exceptionally parasagittal or sagittal triradiates and a basal system of quadriradiates. In terms of ontogeny, triradiates 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.

Calcinea have a great variability of forms but their general organization 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 (fig. 1). There is no topological relationship between the nucleus and the basal structures of the flagellum. Like the whole class they are viviparous. Their ovocytes are formed in the mesohyl from an as yet undetermined cell-type. The origin of the spermatozoa and fertilization are incompletely known (Hadzi, 1917; Tuzet, 1947). Ovocytes 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" (Borojević, 1969) (fig. 2). Fertilized eggs pass through total and equal divisions, and form coeloblastulae composed of equal blastomeres. Incorporation of maternal cells into the blastocoel is frequent (*Ascandra falcata* Haeckel, 1872, *Leucetta chagosensis* Dendy, 1913), but their destiny in the larva is unknown (Borojević, 1969). In some larvae, a few large non-flagellate cells can be found at the posterior pole; their number may be characteristic of the species. 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, and the internal ones the choanoderm (Borojević, 1969). Early development apparently passes through the olynthus stage of organization. Triradiates are the first spicules secreted. The spicules are essentially regular, equiangular and equiradial (fig. 3). In some species, parasagittal spicules are occasionally present with one ray longer than the others and sometimes one angle different from the paired ones.

Two groups may be distinguished among the Calcinea. The first includes sponges with only free spicules. This is an extremely rich and variable group. All developmental stages, from

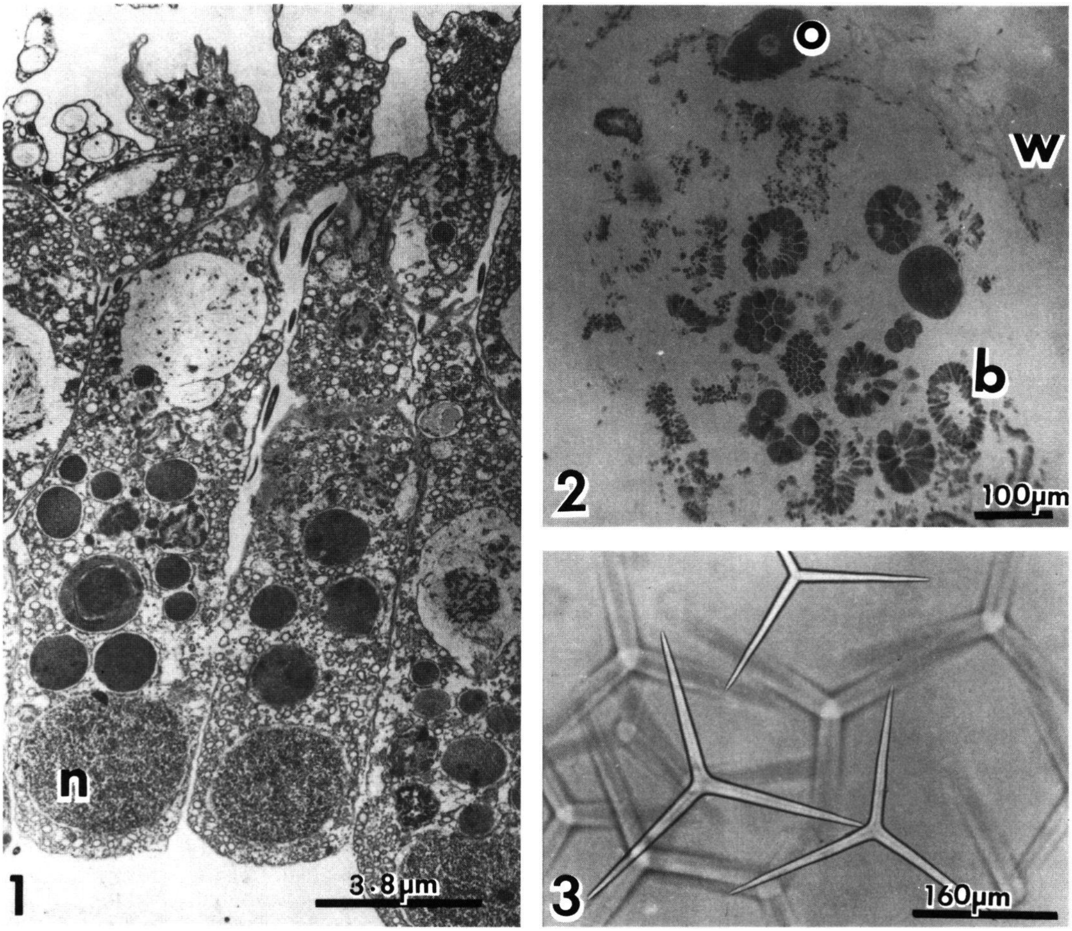

FIG. 1-3. — 1, choanocyte with a basal spherical nucleus (n) from *Clathrina clathrus* (TEM micrograph, courtesy of Dr Klaus RÜTZLER); 2, section through an embryo nest in *Ascandra minchini* (o : ovocyte; b : coeloblastula; w : wall); 3, regular and equiangular triradiates from a species of *Clathrina*.

simple olynthus-like sponges to the complex ones with an elaborate aquiferous system, are present. As will be discussed later, different parallel evolutionary lines may be distinguished, in each of which a complete series from simple asconoid organization to elaborate leuconoid systems can be observed. Although we recognize at least three evolutionary lines among them, they all may originate from sponges organized as the simple olynthus. In all the lines, progressive evolution from a homocoel to a heterocoel grade of organization may be followed. We can thus state that they all represent a monophyletic homogenous group and that they together cannot be divided into two orders, the Clathrinida and the Leucettida by their homocoel or heterocoel grade of organization, as was proposed by HARTMAN (1958). A single order, the Clathrinida, is thus proposed for all of the Calcinea without a hypercalcified skeleton.

The second group, the order 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 of a rigid non-spicular network, as observed in the Murrayonidae, or of spicule tracts with either calcareous plates, as in the Paramurrayonidae or tripods, as in the Lelapiellidae. Unlike the Clathrinida, the order Murrayonida has only a few representatives in Recent fauna and is restricted to three monospecific families. The three known species, which have an elaborate aquiferous system and a complex skeleton, probably represent the end of an old evolutionary line. No sponges with fused spicules are known among the Calcinea, as opposed to calcaronean hypercalcified sponges in which this type of skeleton is frequent (family Minchinellidae).

Order CLATHRINIDA Hartman, 1958 *emend.*

DIAGNOSIS : Calcinea with skeleton composed exclusively of free spicules, without hypercalcified non-spicular reinforcements, spicule tracts, calcareous scales or plates.

Family CLATHRINIDAE Minchin, 1900

DIAGNOSIS : Clathrinida with an essentially tubular organization. A continuous choanoderm lines all the internal cavities. Growth is by longitudinal median divisions and anastomosis of tubes to form large units called the cormus. There is neither a common cortex nor a well-defined inhalant and exhalant aquiferous system.

Clathrinidae are simple calcinean sponges whose organization may be understood as being directly derived from the olynthus. Their constituent tubes are formed by a pinacoderm-

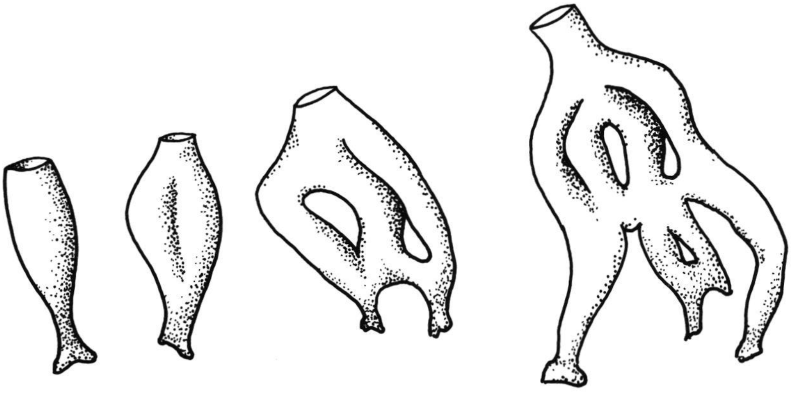

FIG. 4. — Cormogenesis of the family Clathrinidae through longitudinal median divisions of tubes. (After HADZI, 1917.)

covered external layer containing spicules and an internal layer of choanocytes. Both layers are pierced by pores, each surrounded by a porocyte. The organization into a simple tube called the olynthus is found in early development.

Clathrinidae grow from the olynthus grade of organization through division, ramification and anastomosis of tubes to form a larger functional unit called the cormus (Borojević, 1968). A cormus is composed of individual tubes, each of which has an organization corresponding to an olynthus. This cormogenesis is obtained through a longitudinal median division of simple tubes, as described for *Guancha blanca* by Hadzi (1917) (fig. 4).

In the large cormi of the Clathrinidae, certain types of differentiation may be observed in tube size and spiculation. A radial organization of the cormus may be very noticeable, with the central tube taking on the function of a cloaca. This tube becomes larger, but is still covered by a normal choanoderm and has the organization of a typical olynthus [e.g. *Clathrina reticulum* (Schmidt, 1862)]. On the other hand, special spicules, such as tripods in *Clathrina cerebrum* (Haeckel, 1872), or biradiates in *Clathrina contorta* (Bowerbank, 1864), may be found in external tubes of the cormus, which reinforce the external skeleton. However, these spicules are never part of a continuous cortex.

Genus **CLATHRINA** Gray, 1867

Type-species : *Clathrina clathrus* (Schmidt, 1864) (fig. 5).

Diagnosis : Clathrinidae in which the choanoderm is flat or rarely raised up into conuli by the apical rays of the quadriradiates, but never forms true folds, at least when the sponge is in the extended state. The cormus is composed of anastomosed tubes. Regular, equiangular and equiradiate triradiates and/or quadriradiates, to which biradiates or tripods may be added.

The genus *Clathrina* is very large and represented by numerous species in all the world's seas. The classification of *Clathrina* is difficult, especially when the skeleton is composed only of triradiates (Borojević & Boury-Esnault, 1987). Detailed knowledge of their growth, behaviour, ecological distribution and reproductive cycle may give useful information for recognizing the species in a defined habitat (Borojević, 1967; Johnson, 1980). In detailed studies of sponge populations several sympatric species of *Clathrina* are generally distinguished, which occupy distinct microecological spaces. According to the literature many species of *Clathrina* with only a few spicule categories have a cosmopolitan distribution. It is probable, however, that this is frequently due to the lack of recognition of differences between specimens collected by occasional sampling. The use of numerical analysis of shape, size and distribution of the spicules or a biochemical approach by studying isoenzymes may throw new light on the classification of this difficult group of the Calcarea (Solé-Cava *et al.*, in press).

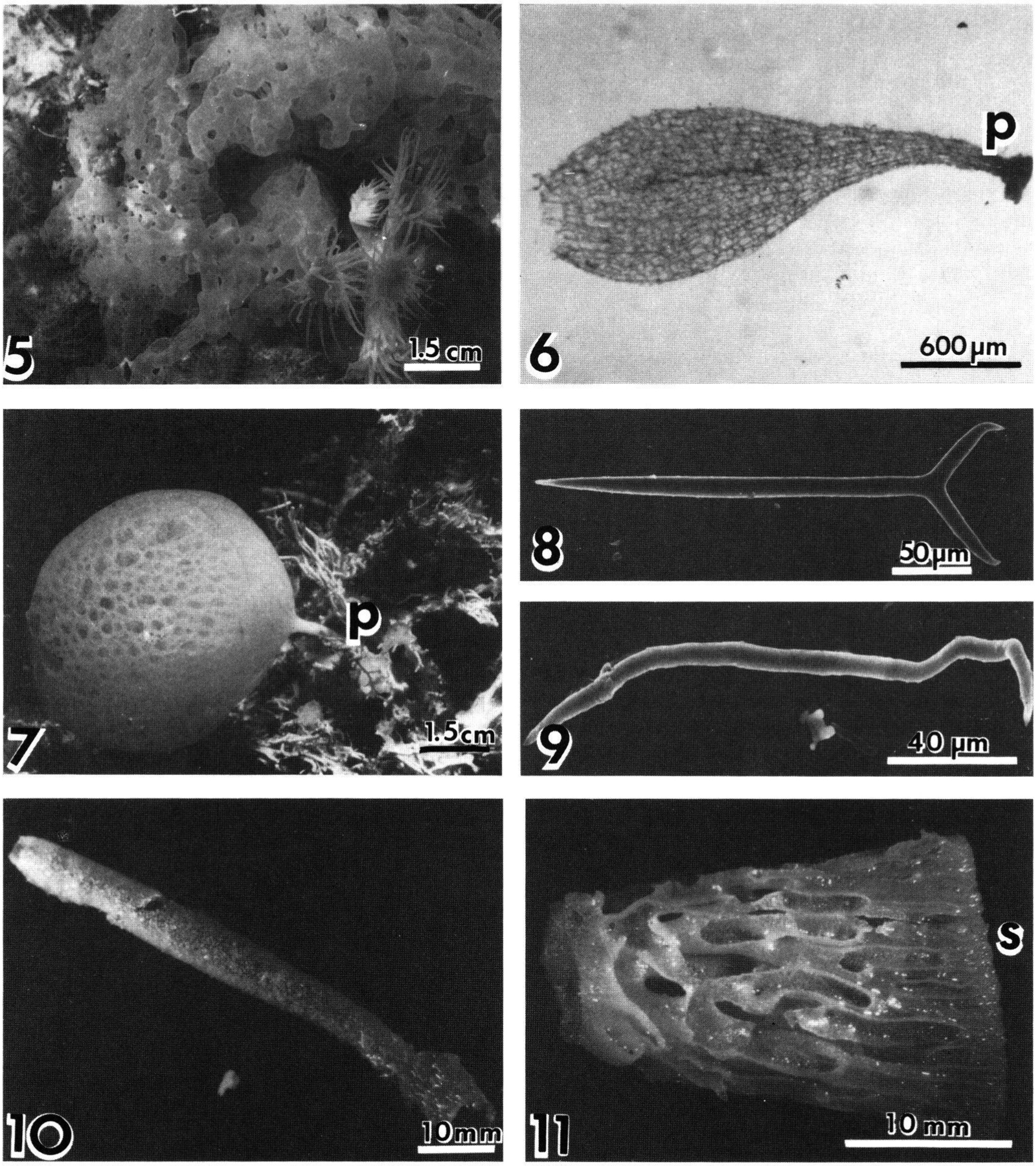

FIG. 5-11. — 5, *Clathrina clathrus* (underwater photograph); 6, *Guancha blanca*, young specimen from the Biscaye Bay (p : peduncle); 7, *Guancha lacunosa* (underwater photograph, p : peduncle); 8, parasagittal triradiate from the peduncular skeleton of *Guancha lacunosa* (SEM micrograph); 9, contorted biradiate from the peduncular skeleton of *Guancha lacunosa* (SEM micrograph); 10, type-specimen of *Soleniscus olynthus* (from BOROJEVIĆ & BOURY-ESNAULT, 1987); 11, type-specimen of *Dendya tripodifera* (from BOROJEVIĆ & BOURY-ESNAULT, 1986).

Genus **GUANCHA** Miklucho Maclay, 1868

TYPE-SPECIES : *Guancha blanca* Miklucho Maclay, 1868 (fig. 6).

DIAGNOSIS : Clathrinidae with a cormus composed of a peduncle and a clathroid body. The peduncle may be formed by true tubes with a normal choanoderm or may be solid with a special skeleton. The skeleton is composed of regular (equiangular and equiradiate) spicules to which parasagittal spicules are added, at least in the peduncle. In some species, only parasagittal spicules are present, and their unpaired ray is basipetally oriented.

Among the Clathrinidae, massive species composed of anastomosed tubes frequently display a progressive differentiation of particular parts of their cormus. In the *Guancha* evolutionary line, this differentiation involves a progressive distinction between a peduncle and a massive clathroid body. In the simplest species, *G. blanca* (fig. 6), the peduncle is still formed by normal tubes with a complete choanoderm. *Guancha blanca* is only slightly different from a typical *Clathrina*, and only the fact that it represents the starting point for an evolutionary line makes it possible for us to separate it into a distinct genus (BOROJEVIĆ & PEIXINHO, 1976). The peduncle progressively acquires a solid form with a special skeleton. *Guancha pulcherrima* (Dendy, 1891) is a good example of this type of differentiation, but *G. lacunosa* (Johnston, 1842) (fig. 7) is certainly the most typical and differentiated *Guancha* known, and always has a long peduncle supported by a special and elaborate skeleton. In parallel with the differentiation of the pedunculate cormus, *Guancha* species are characterized by parasagittal spicules. In *G. blanca*, these are localized in the peduncle and always arranged in a parallel fashion with their unpaired ray oriented basipetally. This tendency is more noticeable in other *Guancha*. In *G. tetela* Borojević, & Peixinho, 1976, all the spicules are parasagittal and their unpaired angle is larger than the paired ones. In *G. lacunosa*, similar spicules can be observed with vestigial paired rays; these spicules take on the function of large biradiates, in addition to smaller contorted true biradiates that are present in the peduncular skeleton (fig. 8 & 9).

Family SOLENISCIDAE fam. nov.

DIAGNOSIS : Clathrinida with an essentially tubular organization. They grow in the form of an individual olynthus, with several olynthi growing from the basal stolon-like tubes or in the form of distally ramified tubes radially arranged around a central olynthus tube without any special skeletal differentiation. A continuous choanoderm lines all the internal cavities. Spicules are regular triradiates and/or quadriradiates to which tripods or biradiates may be added.

We have decided to separate the genera *Soleniscus* (fig. 10) and *Dendya* (fig. 11) from the typical Clathrinidae to include sponges which correspond in their adult stage to a simple olynthus or to olynthus-like tubes either united at their base or distally ramified. Clathrinidae go through the olynthus grade of organization early after the larvae settle. They grow by longitudinal median division of their tubes directly to form anastomosed clathrate bodies (fig. 12). Contrary to this growth type, Soleniscidae either maintain an olynthus form of organization throughout their life, or their tubes divide terminally, forming cormi composed of distally branched tubes. This form of growth is typical of *Leucosolenia* within the Calcaronea, but it is quite rare among the Calcinea. The family Soleniscidae may be considered to be the Calcinean equivalent of the Calcaronean Leucosoleniidae.

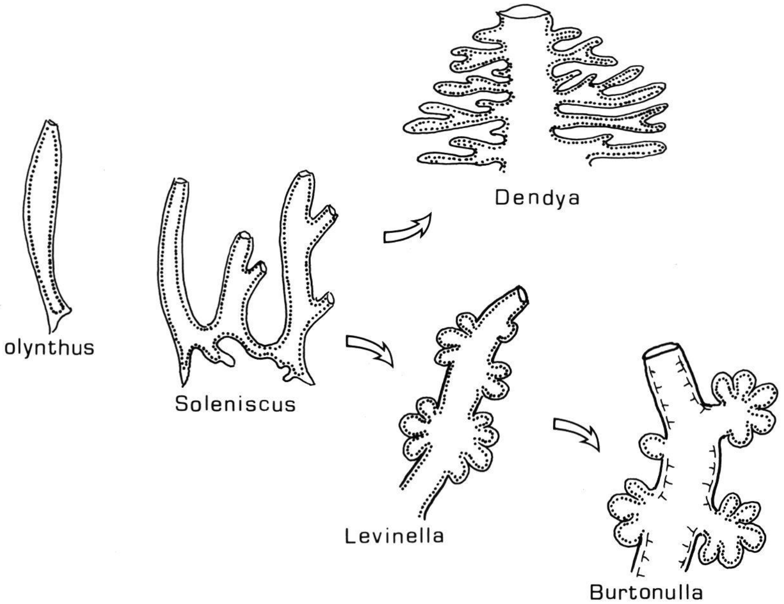

FIG. 12. — Evolution of families Soleniscidae and Levinellidae from the olynthus. Note the formation of the cormus in the Soleniscidae through terminal division and ramification of the olynthus tube and formation of external diverticuli in the family Levinellidae. ... represents choanoderm.

Genus **SOLENISCUS** Haeckel, 1870 *emend.*

TYPE-SPECIES : *Soleniscus stolonifer* (Dendy, 1891).

DIAGNOSIS : Soleniscidae in the form of an individual olynthus, with several olynthi growing from basal stolon-like tubes, or in the form of distally ramified creeping tubes.

The genus *Soleniscus* was described by HAECKEL in his " Prodromus " to include asconoid sponges with individual tubes bearing terminal oscula. It was used in his monograph as a " generic variety " for many species now mainly classified as *Leucosolenia.* This name was never used to designate a genus, but it corresponds to a well-defined organization that we distinguish now from *Clathrina* and we propose to elevate it to the generic level. We will designate *S. stolonifer* (Dendy, 1891) as the type-species, which was the first species described to have this organization. In addition to *Soleniscus stolonifer, S. irregularis* (Jenkin, 1908), *S. hispida* (Brøndsted, 1931), *S. apicalis* (Brøndsted, 1931) and *S. olynthus* (Borojević & Boury-Esnault, 1987) (fig. 10) are also assigned to this genus.

*Genus **DENDYA** Bidder, 1898

TYPE-SPECIES : *Dendya tripodifera* (Carter, 1885) (fig. 11).

DIAGNOSIS : Soleniscidae where the cormus consists of a large central tube from which smaller radially arranged tubes branch off.

The genus *Dendya*, with the single species *D. tripodifera*, is characterized by a rigorously radiate organization (fig. 12). However, the whole cormus is composed of tubes that have the typical organization of the olynthus without a special differentiation of the skeleton and thus represents a typical member of the Soleniscidae.

REMARK

DENDY & ROW (1913) separated the genus *Ascute* from other homocoel sponges on the basis of the presence of a continuous and prominent layer of large external biradiates. *Ascute uteoides* (Dendy, 1892) figures among species with basinucleate choanocytes and this may indicate that the genus *Ascute* should be included in the Soleniscidae. However, according to a reexamination of the *A. asconoides* (Carter, 1885) type-specimen, its spiculation and skeletal organization are typical of the Calcaronea. DENDY's detailed description of *A. uteoides* leaves little doubt that its spiculation is very similar to that of *A. asconoides.* Considering the frequent difficulty in determining the position of nuclei in choanocytes, which may be modified by fixation procedures (VACELET, 1964), it seems that the genus *Ascute* would be more accurately placed closer to *Leucosolenia* among the Calcaronea, until DENDY & ROW's statement (1913) concerning the position of the choanocyte nucleus in this genus can be confirmed.

Family LEVINELLIDAE Borojević & Boury-Esnault, 1986

DIAGNOSIS : Clathrinida with a cormus composed of a central tube, which can be ramified, and of diverticuli isolated or grouped in clusters. The skeleton of the central and radial tubes is composed of regular (equiradiate and equiangular) spicules. The skeleton of the diverticuli is composed of regular and/or parasagittal spicules always clearly distinct from the spicules which compose the skeleton of the central tube. The choanoderm either lines all the central cavity or is restricted to the diverticuli.

The Levinellidae are derived from olynthus-like sponges through the formation of external diverticuli. In young sponges spherical or ovoid diverticuli are individually arranged, while in larger specimens they are clustered. Each cluster may be arranged around a small central cavity which communicates directly with the main cavity (fig. 12). In the simplest genus, *Levinella*, the central tubular cavity is still unique and lined by the choanoderm. In *Burtonulla*, the cormus is ramified and the choanoderm is restricted to external diverticuli. The central tube of *Burtonulla* thus represents an atrium.

Genus **LEVINELLA** Borojević & Boury-Esnault, 1986

TYPE-SPECIES : *Levinella thalassae* Borojević & Boury-Esnault, 1986 (fig. 13).

DIAGNOSIS : Levinellidae with a cormus divided into a central tube and external diverticuli. The central tube is not ramified. A choanoderm lines all the internal cavities.

Young specimens of *Levinella* have a typical olynthus organization. As size increases, diverticuli are formed as new and original structures, as opposed to *Dendya*. They have a specific skeleton clearly different from that supporting the central olynthus. Presumably diverticuli were first formed as occasional extensions of the central body without a skeleton. The diverticuli are consequently secondary formations with a particular skeleton which do not correspond to the original olynthus organization (fig. 14).

*Genus **BURTONULLA** Borojević & Boury-Esnault, 1986

TYPE-SPECIES : *Burtonulla sibogae* Borojević & Boury-Esnault, 1986 (fig. 15).

DIAGNOSIS : Levinellidae whose central tube is ramified. The choanoderm is limited to the external diverticuli.

In *Burtonulla*, the choanoderm is limited to the secondary diverticuli and the primary olynthus lacks choanocytes. This sponge has acquired a heterocoel organization through an entirely original evolutionary pathway.

Family LEUCALTIDAE Dendy & Row, 1913

DIAGNOSIS : Clathrinida with tubular, ramified or even anastomosed cormus either with many oscula, or individualized with a large atrium and a single osculum. The sponge wall is composed of a distinct cortex and choanosome. The skeleton of the choanosome and the atrial wall is absent or composed of small and dispersed triradiates and quadriradiates.

In Leucaltidae, the cortical skeleton largely dominates the choanoskeleton which may be absent (fig. 16). Here the choanoskeleton clearly represents a secondary structure which complements the apical rays of the quadriradiates from the primary external skeletogenous

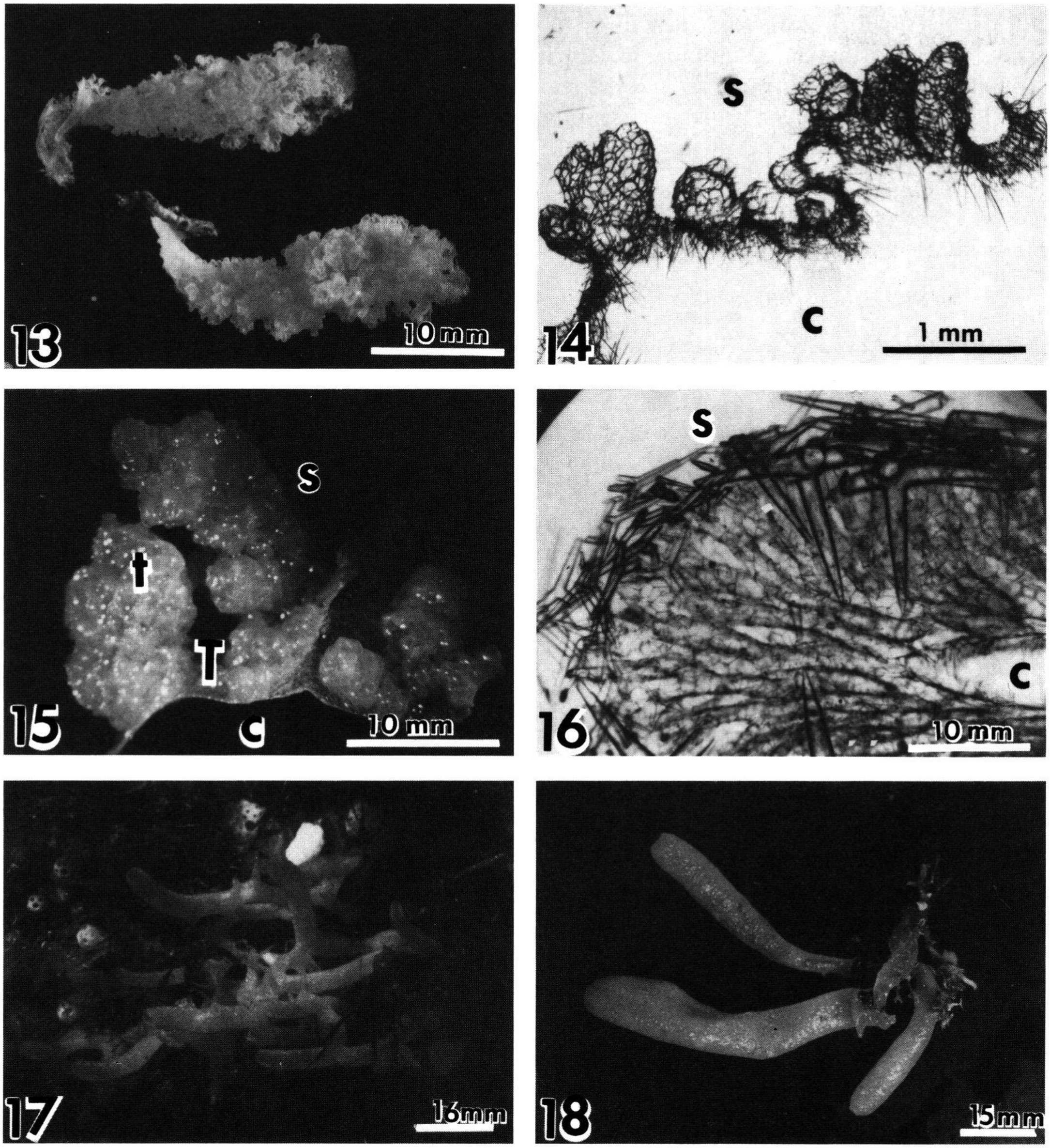

FIG. 13-18. — 13, type-specimen of *Levinella thalassae* (from BOROJEVIĆ & BOURY-ESNAULT, 1986); 14, sections through the wall of *Levinella thalassae* (S : external surface; C : central cavity; from BOROJEVIĆ & BOURY-ESNAULT, 1986); 15, portion of the type-specimen of *Burtonulla sibogae* (S : external surface; C : central cavity; t. : lateral tubes; T : central tube; from BOROJEVIĆ & BOURY-ESNAULT, 1986); 16, section through *Leucaltis clathria* (S : external surface; C : central cavity); 17, *Ascandra falcata* (underwater photograph); 18, type-specimen of *Ascandra minchini*.

layer. In the genus *Ascandra*, the most primitive species, *A. falcata* (fig. 17), has an organization similar to that of *Clathrina*, with a basal region composed of anastomosed tubes, and larger solitary vertical tubes, which display the typical organization of Leucaltidae with internal folds of the choanoderm. In *A. minchini* Borojević, 1966 (fig. 18) and in other Leucaltidae, the choanosome is formed by extensive folding of the choanoderm. Large apical rays of external quadriradiates support the whole choanosome, and in *A. minchini* and *Leucettusa simplissima* Burton, 1932, no other spicules are present in the choanoskeleton. In species where additional spicules are present in the choanosome, the choanoskeleton is composed of small and scattered spicules having no distinct relationship with the arrangement of the choanocyte tubes. Simultaneously, the development of a distinct atrial cavity is followed by the formation of a secondary skeleton for the atrial wall (fig. 19).

Genus **ASCANDRA** Haeckel, 1872

TYPE-SPECIES : *Ascandra falcata* Haeckel, 1872 (fig. 17).

DIAGNOSIS : Leucaltidae in which the choanoderm forms folds inside the choanocoel which isolate radially arranged shallow cavities or true radial tubes. The choanosomal folds are supported by apical rays of external quadriradiates only.

The genus *Ascandra* represents an independant evolutionary line among Clathrinida in which the increase in the choanodermal surface is obtained by the formation of folds inside the choanocoel. These folds delimit new spaces which are shallow cavities in *A. falcata* (fig. 19), but which represent deep radial tubes in *A. minchini* (fig. 19, 20). Consequently *A. minchini* (fig. 18) could take on the form of large individual tubes of which the external surface is covered by a continuous pinacoderm and supported by a specific skeleton corresponding to a cortex. The distance between the external surface and the internal parts of the choanoderm makes the constitution of a complex system of inhalant aquiferous cavities necessary. However, the central choanocoel opens directly into the osculum. Functionally, the

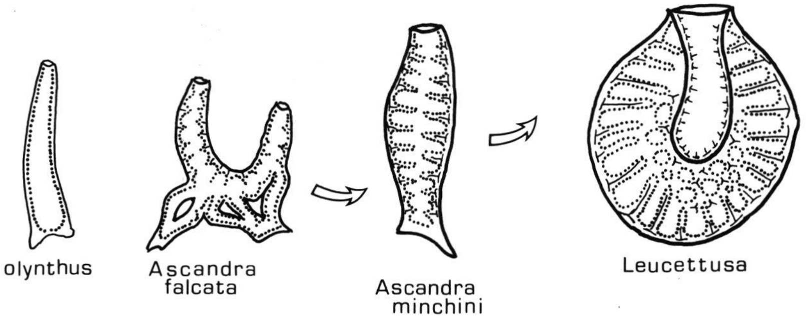

FIG. 19. — Evolution of the family Leucaltidae from olynthus through formation of internal choanodermal folds. ... represents choanoderm.

organization of *Ascandra* is analogous to that of *Grantia* Fleming, 1828 of the subclass Calcaronea. However, the evolution of these genera is totally different and indicates that the sycon-like organization could occur through two parallel and distinct evolutionary lines.

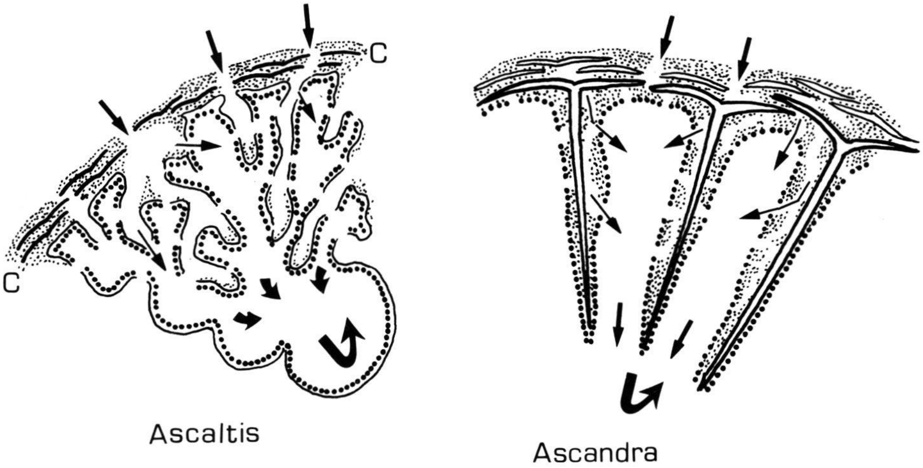

FIG. 20. — Formation of inhalant systems in genera *Ascandra* and *Ascaltis*. In *Ascandra* inhalant lacunae interconnect the external surface of the original olynthus tube with internal folds of choanoderm. In *Ascaltis* an inhalant system interconnects ostia of the cortex with openings on the wall of the choanocyte tube. c : cortex. → indicates the water current flow; ... represents choanoderm.

*Genus **LEUCALTIS** Haeckel, 1872

TYPE-SPECIES : *Leucaltis clathria* Haeckel, 1872.

DIAGNOSIS : Leucaltidae with a body composed of large, ramified and anastomosed tubes. Each tube has a distinct cortex, a choanoderm composed of elongated and ramified choanocyte chambers and a central atrium. The choanoderm and the atrial wall have a secondary skeleton composed of small triradiates and quadriradiates.

The body of the unique species, *Leucaltis clathria*, is composed of large anastomosed tubes, reminiscent of *Ascandra falcata*. The large atrium is an original structure developed after the formation of radial tubes (fig. 16).

Genus **LEUCETTUSA** Haeckel, 1872

TYPE-SPECIES : *Leucettusa corticata* Haeckel, 1872.

DIAGNOSIS : Leucaltidae with a simple tubular body, a large atrium and choanocyte chambers which are either elongated, spherical or both.

The genus *Leucettusa* bears a clear resemblance to *Ascandra minchini*. The simplest representative of the genus, *L. simplicissima* (fig. 21), differs from *A. minchini* only in the formation of an atrium with delicate periatrial spicules. The whole choanosome is composed of radially arranged elongated chambers, supported exclusively by the large apical rays of cortical quadriradiates (fig. 22). Its organization is thus typically syconoid. In *L. vera* (Poléjaeff, 1883), spherical chambers are added to the elongated ones and a choanoskeleton is progressively developed. In *L. corticata*, the whole aquiferous system is leuconoid.

Incertae sedis

*Genus **LEUCLATHRINA** Borojević & Boury-Esnault, 1987

TYPE-SPECIES : *Leuclathrina asconoides* Borojević & Boury-Esnault, 1987.

DIAGNOSIS : Leucaltidae (?) with leuconoid organization. The skeleton is restricted to the cortex and the choanosome completely lacks spicules.

Leuclathrina may be derived from an olynthus through progressive folding of the choanoderm inside the primary olynthus tube. In *Ascandra*, in which the radially arranged apical rays of quadriradiates support the choanodermal folds, the radial organization of the choanoderm is preserved. In the spherical choanocyte chambers of *Leucettusa*, the leuconoid organization is obtained through progressive rounding of elongated choanocyte chambers, and in *Leucettusa vera* for example both forms of choanocyte chambers still coexist in the same sponge. In *Leuclathrina*, in which no elements of the external skeleton of primary olynthus support the choanoderm folds, the radial organization is lost and a lacunar, leuconoid type of organization has been acquired directly without a passage through the syconoid organization.

The choanosome of *L. asconoides* is located only in the central part of the sponge, and the oscula are situated at the end of chimneys with no choanoderm.

Family LEUCASCIDAE Dendy, 1892

DIAGNOSIS : Clathrinida with a body differentiated into a cortex and a choanosome whose organization is reminiscent of a clathroid body composed of anastomosed tubes. The cortex contains a specific skeleton and is composed of large triradiates and/or quadriradiates. Choanocyte chambers are tubular, often highly ramified and anastomosed. The choanoskeleton is restricted to the walls of the choanocyte chambers, maintaining a distinctly tubular organization.

The Leucascidae are clearly derived from species similar to massive *Clathrina* with a cormus composed of densely anastomosed tubes. As pointed out by DENDY & ROW (1913) and BOROJEVIĆ (1968), the acquisition of a common cortex is a new grade of integration for the sponge body and this makes it necessary clearly to separate these species from the Clathrinidae. It should be emphasized that this cortex is not derived from the outermost tubes

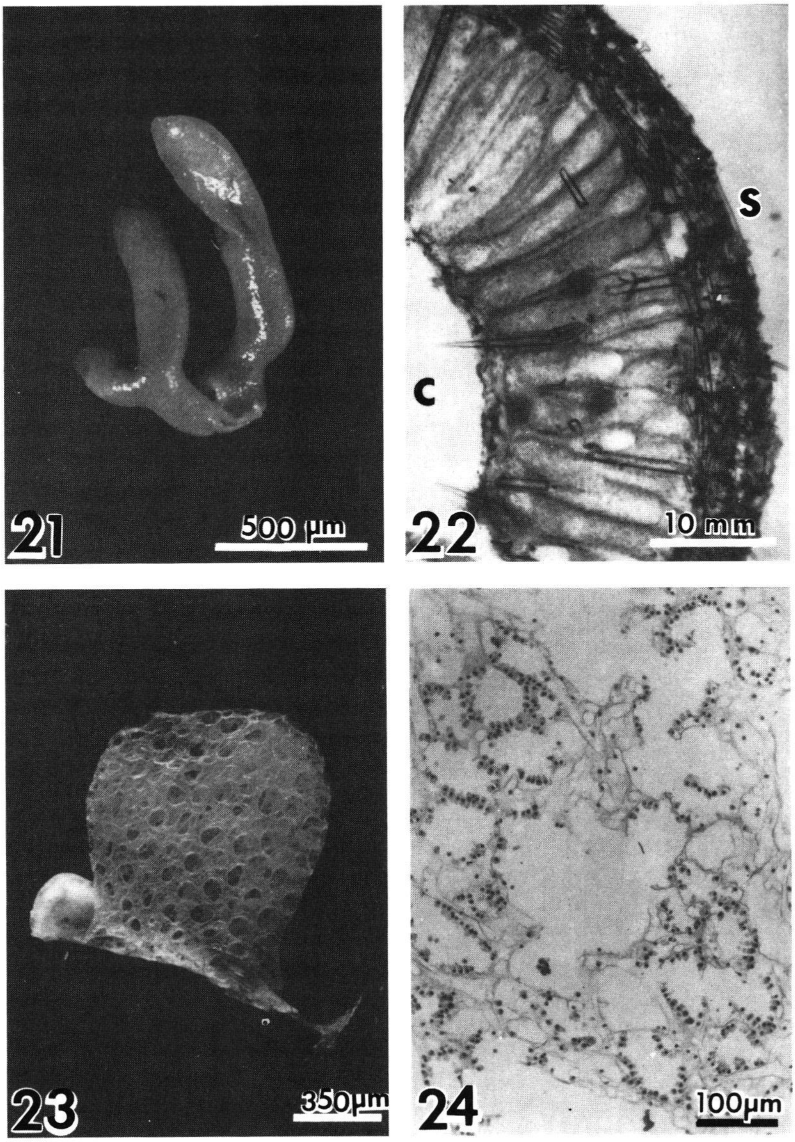

FIG. 21-24. — 21, type-specimen of *Leucettusa simplicissima*; 22, section through a specimen of *Leucettusa simplicissima* (S : external surface; C : central cavity); 23, *Ascaltis lamarcki*, specimen from the Bay of Biscay; 24, section through *Leucetta chagosensis* showing the leuconoid organization.

of the clathroid cormus, but is a new structure composed only of the pinacoderm and the skeletogenous layer. In *Ascaltis* only the inhalant aquiferous system evolved to lead the water current from the cortex to the innermost choanocyte tubes (fig. 20). In *Leucascus*, a central exhalant atrium is also differentiated and surrounded by a wall with no choanoderm. The evolution from *Leucascus* to Leucettidae simply goes through the reorganization of the choanosome and formation of a true leuconoid aquiferous system.

Genus **ASCALTIS** Haeckel, 1872

TYPE-SPECIES : *Ascaltis lamarcki* Haeckel, 1872 (fig. 23).

DIAGNOSIS : Leucascidae with a massive cormus composed of ramified and anastomosed tubes covered by a common cortex. The inhalant aquiferous system is represented by spaces delimited by the cortex and the walls of choanosomal tubes. The exhalant aquiferous system is reduced to the osculum or to a secondary atrial cavity formed by the calyciform growth of the cormus.

The simplest species of the genus *Ascaltis* are very similar to *Clathrina* with the cormus organized around a large central tube. The only distinction between, for example, *Clathrina reticulum* and *A. lamarcki* is the presence in the latter of a thin continuous cortex surrounding all the cormus and delimiting the inhalant spaces (fig. 25). In more differentiated *Ascaltis*, such

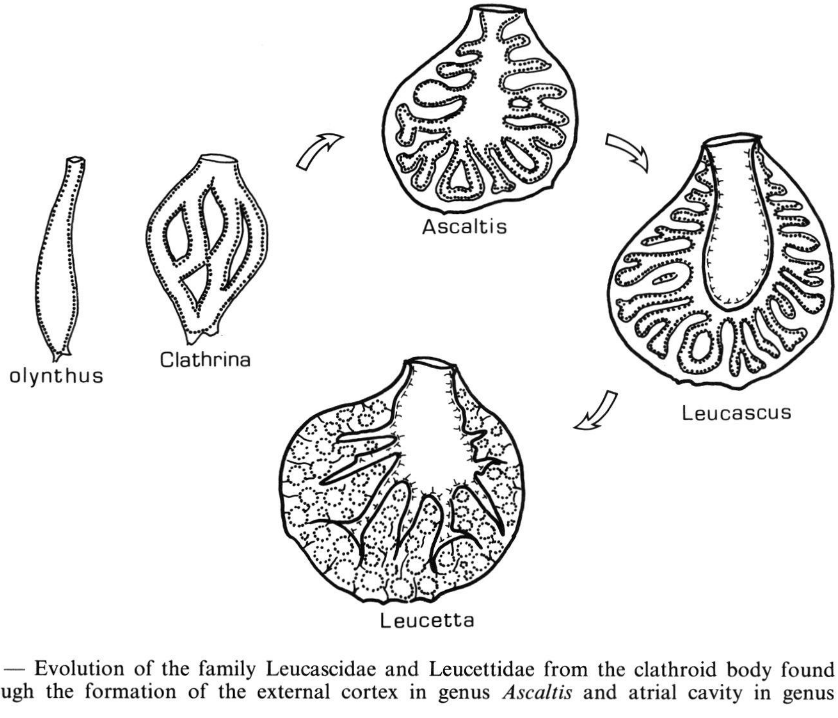

FIG. 25. — Evolution of the family Leucascidae and Leucettidae from the clathroid body found in genus *Clathrina* through the formation of the external cortex in genus *Ascaltis* and atrial cavity in genus *Leucascus*.

as *A. compressa* (Dendy & Frederick, 1924), the cortex becomes well-structured and the sponge body acquires a solid and well-defined form.

Genus **LEUCASCUS** Dendy, 1892

TYPE-SPECIES : *Leucascus simplex* Dendy, 1892.

DIAGNOSIS : Leucascidae with copiously branched and anastomosed choanocyte tubes. The exhalant aquiferous system is represented by a well-developed atrium delimited by a specific wall with no choanoderm.

The genus *Leucascus* is similar to *Ascaltis* and clearly reminiscent of the tubular organization of the clathroid cormus. However, the constitution of a common atrium, distinct from both the inhalant and exhalant aquiferous systems, is a new evolutionary advance and merits a generic distinction from *Ascaltis* (fig. 25).

Family LEUCETTIDAE Borojević, 1968

DIAGNOSIS : Clathrinida with a solid body. The aquiferous system is always leuconoid. The choanoskeleton is well-developed and in the form of a regular network composed of triradiates and/or quadriradiates. The cortex is thin and composed of spicules similar to those in the choanoskeleton.

The Leucettidae are apparently Clathrinida that have reached the highest degree of differentiation. They are probably derived from Leucascidae. Spherical choanocyte chambers are diffusely distributed throughout the choanosome supported by a regular network of the choanoskeleton. The choanosome of Leucettidae no longer recalls the tubular organization of the clathroid cormus. While in Leucascidae the choanoskeleton is still a two-dimensional structure formed by the curved walls of the choanocyte tubes, in Leucettidae the choanoskeleton is a true three-dimensional structure (fig. 25).

Genus **LEUCETTA** Haeckel, 1872

TYPE-SPECIES : *Leucetta primigenia* Haeckel, 1872.

DIAGNOSIS : Leucettidae with a homogenous organization of the wall and a typical leuconoid aquiferous system. There is neither a clear distinction between the cortex and the choanoskeleton, nor the presence of a distinct layer of subcortical inhalant cavities. The atrium is frequently reduced to a system of exhalant channels that open directly into the osculum.

We use DENDY and ROW's (1913) definition of the genus *Leucetta*. These sponges have attained a high degree of functional organization, similar to that of most Porifera, particularly the demosponges, which are typically leuconoid (fig. 24). They are well-adapted to shallow water habitats and are the most frequent Calcinea of tropical regions, where they can reach a considerable size and distribution density.

Genus **PERICHARAX** Poléjaeff, 1883

TYPE-SPECIES : *Pericharax heteroraphis* Poléjaeff, 1883.

DIAGNOSIS : Leucettidae with a large central atrium surrounded by a thick wall. The wall is divided into a choanoderm and a thin subcortical layer of inhalant cavities supported by a peculiar skeleton partially composed of the centripetal rays of the special cortical triradiates.

The genus *Pericharax* has an organization similar to that of *Leucetta*. However, the presence of a particular differentiation of the subcortical inhalant cavities with a specific skeleton clearly demonstrates the difference between these genera (fig. 25).

Incertae sedis

*Genus **LEUCOMALTHE** Haeckel, 1872

TYPE-SPECIES : *Leucomalthe bomba* Haeckel, 1872.

DIAGNOSIS : Clathrinida (?) with a solid body and a large central cavity. Choanocyte chambers greatly elongated, tubular and copiously branched. Skeleton consists of regular triradiates and microbiradiates in the cortical skeleton, regular triradiates in the choanoskeleton and sagittal quadriradiates both in the atrial skeleton and in the exhalant channels. Large longitudinal biradiates present throughout the body.

This sponge, which was described by HAECKEL from a unique specimen, has never been found again. The special organization of its aquiferous system is reminiscent of *Dendya* and one may speculate that it originated from a *Dendya*-like sponge through progressive corticalization and formation of an atrium. However, as pointed out by DENDY & ROW (1913), this sponge was placed in the Calcinea on somewhat dubious grounds. In particular, sagittal spicules in the atrial skeleton are not normally found in Calcinea, and it will be necessary to examine new material to identify the exact taxonomic position of this species.

Order MURRAYONIDA Vacelet, 1981

DIAGNOSIS : Calcinea with a reinforcement of the skeleton composed of either spicule tracts, calcareous plates or a rigid monospicular skeleton. The canal system is leuconoid in the three known species. Diapasons (tuning-fork shaped triradiates) or modified biradiates are present, and are generally fasciculated.

This diagnosis is modified from VACELET (1981) to include Lelapiellidae.

Family MURRAYONIDAE Dendy & Row, 1913

DIAGNOSIS : Murrayonida in which the choanosomal skeleton is composed of a rigid calcareous, aspicular network. The cortex is composed chiefly of overlapping calcareous scales.

*Genus **MURRAYONA** Kirkpatrick, 1910

TYPE-SPECIES : *Murrayona phanolepis* Kirkpatrick, 1910 (fig. 26-29 & 31).

DIAGNOSIS : Murrayonidae with a definite pore-zone whose cortical skeleton consists of small triradiates. Diapasons (tuning-fork shaped spicules) present beneath the dermal scales.

The only species, *Murrayona phanolepis*, is a stony sponge which may be globular, pyriform or lamellate (fig. 26). The lamellate specimens have a distinct inhalant and exhalant surface; the globular ones have special generally-equatorial inhalant areas. The cortical skeleton of the inhalant areas is made up of a tangential reticulation of triradiates, while the exhalant surfaces are covered by scales (fig. 28) originating from regular triradiates. The diapasons (fig. 29) are isolated under the scales and do not build tracts (fig. 31). A circlet of special triradiates with long lateral rays surrounds the osculum. The mains skeleton is reticulate and made up of fused, irregularly-shaped calcitic elements (sclerodermites) without entrapped spicules. The aquiferous system is leuconoid with basinucleated choanocytes. Embryos are of the blastula type.

Family PARAMURRAYONIDAE Vacelet, 1967

DIAGNOSIS : Murrayonida with choanosomal skeleton made up of fascicles of diapasons (tuning-fork triradiates) without any rigid structure. Cortical skeleton composed chiefly of a superficial layer of overlapping calcareous scales and of an internal layer of free calcareous plates.

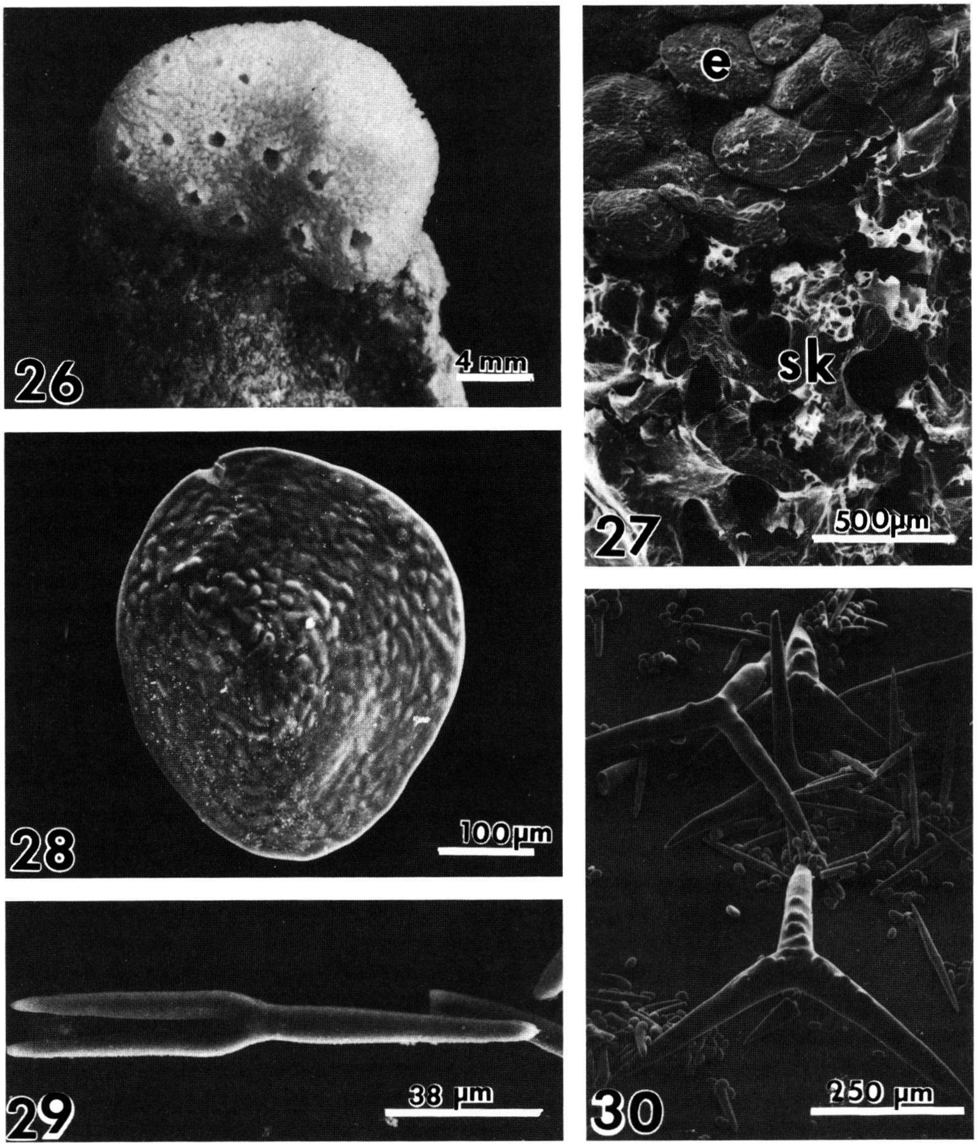

FIG. 26-30. — 26, *Murrayona phanolepis*, exhalant side of a lamellate specimen from Moorea (from VACELET, 1977); 27, *Murrayona phanolepsi*, specimen from Moorea (e : exhalant surface; sk : aspicular skeleton; SEM micrograph); 28, *Murrayona phanolepsis*, calcareous scale (SEM micrograph); 29, *Murrayona phanolepis*, tuning-fork triradiate (SEM micrograph); 30, *Lelapiella incrustans*, spicules of a specimen from Hawaii (SEM micrograph).

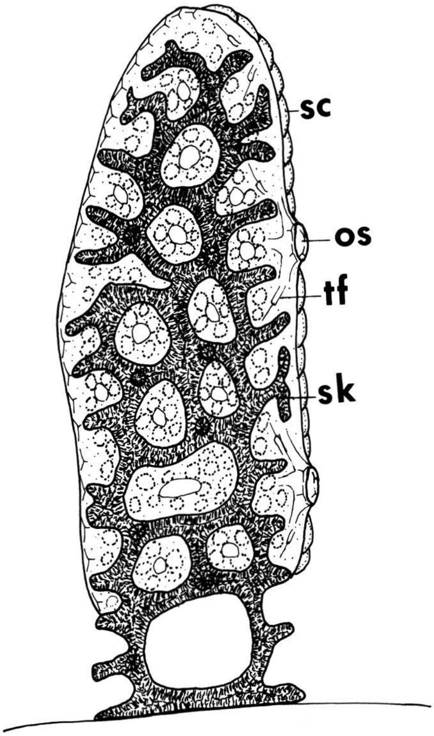

FIG. 31. — *Murrayona phanolepis* (original). Section through a lamellar specimen, supported by a dead basal part. The inhalant side is on the left, the exhalant one on the right (os : osculum; sc : calcareous scales of the exhalant side; sk : aspicular calcareous skeleton; tf : tuning-fork triradiate).

*Genus **PARAMURRAYONA** Vacelet, 1967

TYPE-SPECIES : *Paramurrayona corticata* Vacelet, 1967 (fig. 32).

DIAGNOSIS : Same as the family.

The only species, *P. corticata*, may be derived from the Murrayonidae through loss of the rigid calcareous network. The calcareous plates of the cortical skeleton are not fused, but are loosely joined by organic material. They probably originate from the external scales which are modified triradiates. Oscula are surrounded by a circlet of special quadriradiates. The choanosomal skeleton is composed exclusively of tuning-fork triradiates which are generally disposed in fascicles. Some spicules, including free tuning-fork triradiates, triradiates and quadriradiates, can be observed at the periphery of the sponge where the inhalant areas are presumably located. The aquiferous system is leuconoid with basinucleated choanocytes. Embryos are of the blastula type.

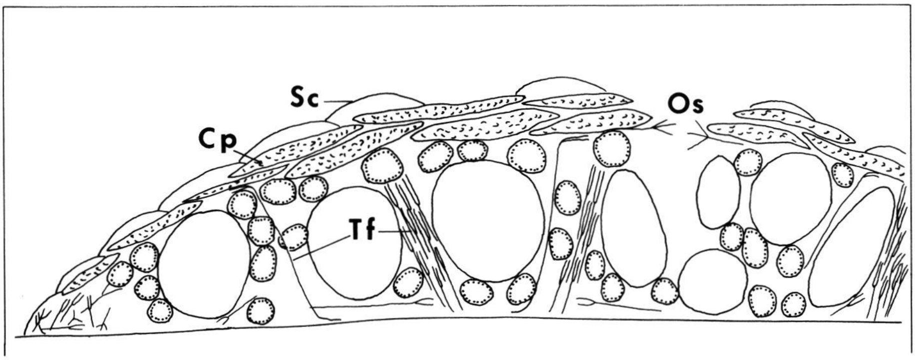

FIG. 32. — Section through *Paramurrayona corticata* (cp : calcareous plates ; os : osculum ; sc : calcareous scales ; tf : tuning-fork triradiates ; from VACELET, 1967).

Family LELAPIELLIDAE fam. nov.

DIAGNOSIS : Murrayonida with choanosomal skeleton made up of fascicles of biradiates without any rigid structure. Cortical skeleton composed chiefly of a layer of tripods and curved biradiates.

*Genus **LELAPIELLA** Vacelet, 1977

TYPE-SPECIES : *Lelapiella incrustans* Vacelet, 1977 (fig. 30, 33).

DIAGNOSIS : Same as the family.

The reinforcement of the skeleton of this incrusting sponge is weak compared to that of the two recent representatives of Murrayonida. It consists of a dense cortical layer of large tripods and curved biradiates, a dense basal layer of intermingled curved biradiates, and of fascicles of biradiates running obliquely through the choanosome and binding together the two layers. The osculum is surrounded by several rows of sagittal triradiates. The aquiferous system is leuconoid with basinucleate choanocytes. Embryos are unknown.

Lelapiella incrustans was first classified in the family Lelapiidae of the Calcaronea based on the presence of fascicles of special, elongated spicules, which here are modified biradiates. However, the choanocyte nucleus was later found to be basal in position (VACELET, 1981), and this is confirmed again here on new well-preserved material from New Caledonia. Furthermore, the tripods (fig. 30) of the cortical skeleton are derived from equiangular triradiates. Based on these two calcinean characters and on the general organizational similarities with *Paramurrayona*, we suggest classifying this sponge in the Calcinea, order Murrayonida.

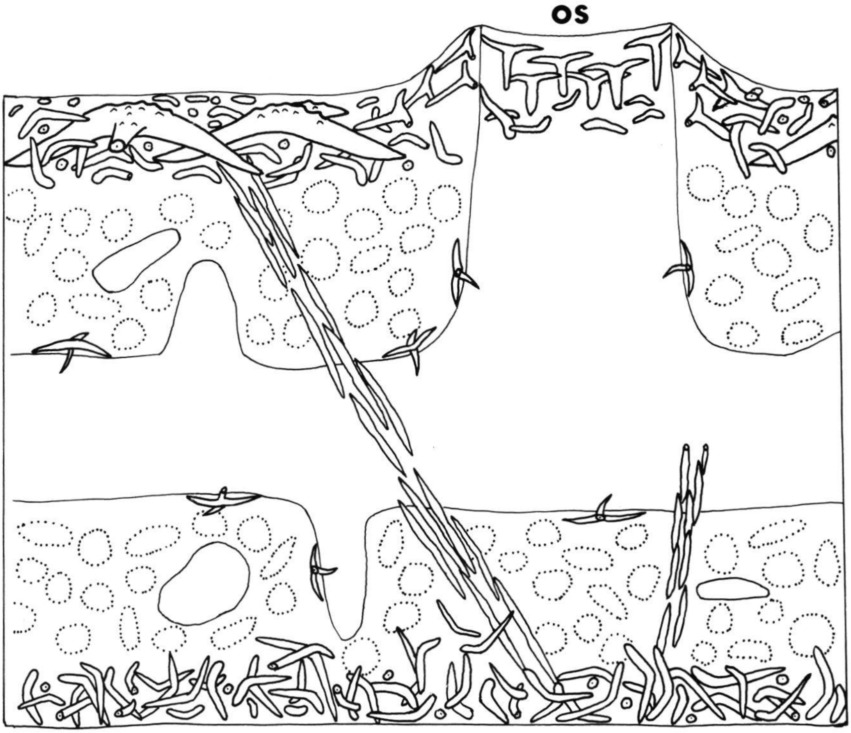

FIG. 33. — Section through *Lelapiella incrustans* (os : osculum; from VACELET, 1977).

DISCUSSION

The evolution of the Clathrinida seems to have its starting point in the olynthus grade of organization. This form is probably found in the early developmental stages of all of the Clathrinida and is rarely present in adult sponges. The increase in the size of an individual olynthus is limited. The increase in its diameter consequently involves a modification in the ratio between the volume of the internal water column and the surface of the choanoderm, which is responsible for maintaining the water current in the olynthus tube. An increase in diameter must be followed by an increase in the choanodermal surface.

Growth from this simple form may follow four pathways :

1) One of the possible lines of evolution is the increase of the choanoderm inside the olynthus itself through the formation of internal folds (fig. 19). This mode of growth is exemplified by the genus *Ascandra*, where internal folds may delimit shallow cavities, as in *A. falcata*, or true radial tubes, as in *A. minchini*. The next evolutionary step may be the

division of the choanosome into radial or spherical spaces, i.e. true choanocyte chambers, where the ratio between water volume and choanodermal surface is favourable. Inhalant and exhalant aquiferous systems must be developed to conduct the water current in and out of the sponge. Genera with a heterocoel grade of organization are thus progressively formed from sponges with an asconoid organization. We have found this evolutionary line among Leucaltidae.

2) Another possibility for the increase of choanodermal surface is the formation of external diverticuli on the olynthus (fig. 12). This evolutionary pathway has been extensively followed by the Calcaronea, in which most genera originate from the *Sycetta* type of organization, corresponding to a large central tube with radially arranged diverticuli. Among the Calcinea this evolutionary line was only followed by the family Levinellidae. Young specimens of *Levinella thalassae* have a typical olynthus organization, but during their growth, diverticuli are formed as new external structures with their own skeleton. At first solitary, they become progressively grouped in bunches around a small central cavity. In *Levinella*, the central tube is still covered by a choanoderm, while in *Burtonulla* the choanoderm has apparently become restricted to diverticuli. The organization of small *Burtonulla* corresponds exactly to that of *Sycetta*. One may wonder why this form gave rise to a very flourishing evolutionary line in the Calcaronea, but not in the Calcinea. This may be explained by the fact that cormus growth in Levinellidae is obtained by the multiplication of spherical diverticuli. This implies the multiplication of tubes that carry the diverticuli, followed by their ramification and the formation of large, fragile structures. Among the Calcaronea growth is obtained by the elongation of diverticuli in the genus *Sycetta*. They become progressively coalescent and form compact solid structures found in the genus *Sycon* Risso, 1826. The corticalization represents the subsequent step which yields the grantioid type of organization in the families Grantiidae, Heteropiidae, Amphoriscidae, etc.

3) The increase in olynthus length is limited by the fragility of the long linear structures (fig. 12). In the genus *Soleniscus*, which is representative of this grade of organization, only a few species form longer creeping tubes with short offshoots. Two solutions were found for this problem. In the genus *Dendya*, regular subdivision of tubes and a rigorous radial organization has formed a compact body that can reach a considerable size without any reinforcement of the whole body by a common external structure, such as a cortex. However, if *Leucomalthe* is actually a calcinean sponge formed through the corticalization of a *Dendya*-like structure, this evolutionary line is remarkably similar to that linking *Sycon* to Grantiidae.

4) In the evolutionary line followed by the Clathrinidae, Leucascidae and Leucettidae growth of the olynthus is followed by the formation of anastomosed, interconnected tube systems, constituting mechanically resistant units described as cormi (fig. 4). Inside the cormus, the olynthus-like tubes become integrated with a progressive specialization. The central tube takes over the function of expelling water from the cormus, as is the case of *Clathrina reticulum*. External tubes may develop a special skeleton, as can be observed in *Clathrina cerebrum*. In the genus *Guancha*, a peduncle is progressively formed, which acquires a specific and elaborate skeleton. A continuous cortex may be progressively formed giving structural unity to the whole cormus, as can be observed in *Ascaltis lamarcki* (fig. 20). This solution was followed by numerous sponges as seen by the progressive corticalization and differentiation of inhalant and exhalant systems, which are fully exemplified by the

evolutionary lines extending from the Clathrinidae through the Leucascidae to the Leucettidae (fig. 25).

We must emphasize that, among the Clathrinida, all these growth possibilities have been used with success, and complex heterocoel structures have been formed in all evolutionary lines, most of which are represented by solid, resistant and highly functional calcareous sponges.

A cladogram representing a hypothetical phylogenetic relationship between the Clathrinida genera is proposed (fig. 34). All four evolutionary lines are developed from a simple

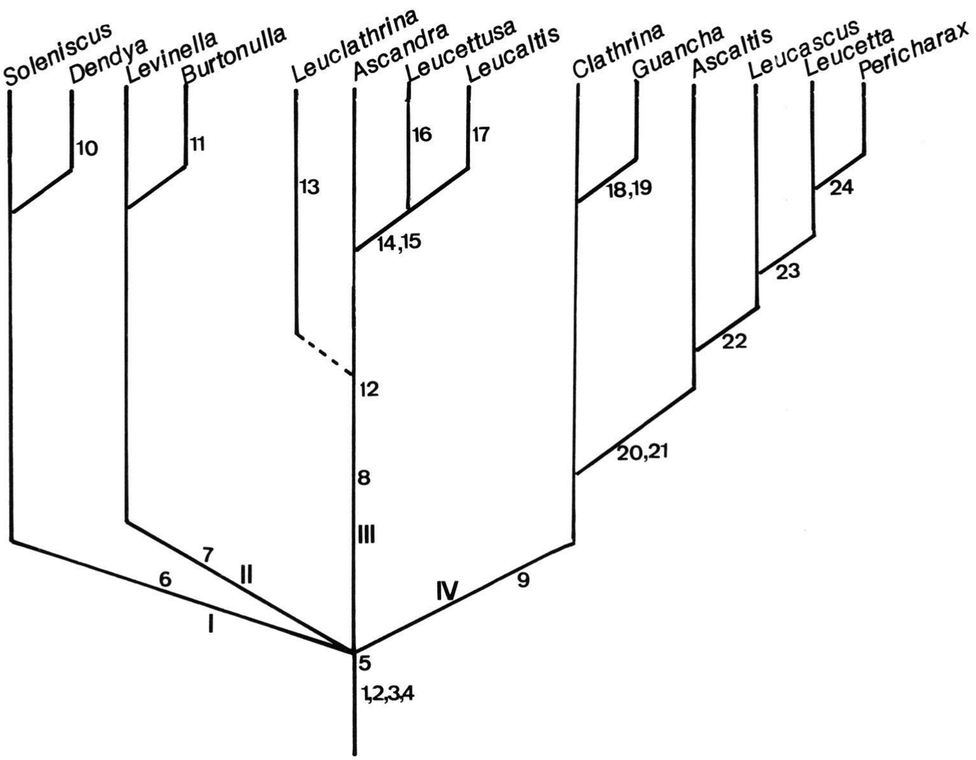

FIG. 34. — Cladogram of a proposed phylogeny of Clathrinida through four evolutionary lines I, II, III, IV. **1** : Basinucleate choanocyte (fig. 1). **2** : Coeloblastula larvae (fig. 2). **3** : Regular, equiradiate and equiangular spicules (fig. 3). **4** : Triradiates are the first spicules in ontogeny. **5** : Olynthus grade of organization. **6** : Increase in length of the olynthus (fig. 12). **7** : Formation of external diverticuli on the olynthus with development of a secondary skeleton (fig. 12). **8** : Increase in the olynthus diameter with formation of internal folds of choanoderm (fig. 19). **9** : Growth of the olynthus through longitudinal division and anastomosis, with formation of complex cormi (fig. 4). **10** : Rigorous radial organization of cormi with terminal division of tubes (fig. 12). **11** : Choanoderm limited to external diverticuli (fig. 12). **12** : Inhalant system interconnecting external surface and internal folds of choanoderm (fig. 20). **13** : Lacunar leuconoid organization. **14** : Formation of central atrium and secondary atrial wall (fig. 19). **15** : Secondary choanoskeleton. **16** : Solitary body. **17** : Body formed of large anastomosed tubes. **18** : Formation of distinct peduncle. **19** : Presence of parasagittal spicules. **20** : Formation of a common cortex covering all the cormus (fig. 25). **21** : Inhalant system interconnecting ostia of the cortex and choanocyte tubes (fig. 20). **22** : Formation of common exhalant system replacing central choanocyte tube (fig. 25). **23** : Typical leuconoid organization (fig. 25). **24** : Formation of subcortical inhalant cavities with specific skeleton.

olynthus. In evolutionary line I, this grade of organization may be present in adult sponges, and, if we exclude a possible evolution of *Leucomalthe* from this line, it may be considered to be the least evolved one. Lines II, III, and IV correspond to the three proposed solutions to the increase and progressive constitution of complex forms from the olynthus. They all have independently reached the heterocoel grade of organization.

CONCLUSION

Calcinea have characteristics that may lead us to consider them as an ancient and primitive group of sponges with a direct evolution from simple to complex forms. The simplest grade of sponge organization, the olynthus, is found among the Soleniscidae, which includes rare species in which the olynthus corresponds to the adult organization. One may thus be tempted to suppose that there is a direct evolution from simple to complex forms in the Calcinea, i.e. from the Soleniscidae and Clathrinidae to the Murrayonidae. Indeed, when discussing the Murrayonidae DENDY & ROW (1913) pointed out that "this family seems to mark the culminating point of the Leucascid-Leucettid line of evolution, and there is no other known calcareous sponge with a skeleton so highly specialized as *Murrayona*". However, two different modes of evolution must be distinguished in the subclass Calcinea.

In the Clathrinida, it seems that a progressive step by step evolution from simple to complex forms has occurred. All the possibilities of the progressive elaboration of complex structures, from the elementary functional form, the olynthus, are known and all intermediate stages are still present. Evolution apparently occurred along parallel lines from homocoel (ascon) to heterocoel (sycon and leucon) grades of organization. A true leuconoid organization has only been obtained in all the members of the family Leucettidae.

Clathrinida live primarily in shallow waters. They are exposed to variable ecological conditions and subjected to frequent and rapid modifications. The presence of a complete evolutive series living under these conditions is not consistent with the group's supposed age. The whole pattern of the relationship between the Clathrinida and their ecological distribution leads the consideration that they are a young group which underwent a relatively recent surge in evolution and is now in full expansion. Rapid and rich evolution has created numerous species where few intermediate forms have been lost. No calcareous sponges similar to the Clathrinida are known as fossils. However, it must be considered that fossilization of Clathrinida may be difficult.

Opposed to this, the Murrayonida are represented by only a few species with a particular and elaborate organization and without any apparent relationship to the Clathrinida. Similar to other "Pharetronids", the Murrayonida live in extreme ecological conditions where competition is low. Simultaneously, their geographical distribution is quite large. It is known that hypercalcified fossil sponges had a very large distribution and actively participated in the formation of fossil reefs. The Recent Murrayonida, as well as other Recent hypercalcified sponges, are the rare relicts of a large ancient group and thus represent living fossils which have been conserved only in specific and extreme ecological conditions (VACELET, 1985; VACELET, in press).

Despite this discrepancy, due to their anatomical and cellular organization, their embryology and their skeleton, all of the Calcinea represent a unique and homogeneous group. The group of apparently "young" Clathrinida cannot have originated directly from complex Murrayonida. It is also difficult to accept the idea of a direct and linear evolution of Murrayonida from the Clathrinidae along the Leucascid-Leucettid line, as proposed by Dendy & Row (1913), and more recently, as the "Theorie I", by Reitner (1987).

An alternative hypothesis would be the evolution of non-hypercalcified Calcinea (Clathrinida) from the hypercalcified ones (Murrayonida) through the progressive reduction and loss of the rigid basal or reinforced cortical skeleton, as proposed by Hartman (1980) and by Reitner (1987) in his "Theorie II". This implies the regressive evolution of all Recent Clathrinida, from the most complex to the simplest forms. Such an extensive regressive evolution in such a large zoological group would be highly unusual, although this has possibly occurred in some parasitic animals. However, Murrayonida probably pass through the olynthus grade of organization in their ontogenesis during the post-larval period. If these morphologically immature stages could have reached sexual maturity, in a phenomenon corresponding to neoteny, a simple olynthus-like species could have recently evolved from ancient sponges with complex structures. This form may have initiated a new evolutionary surge, adapted to Recent ecological conditions.

It seems likely that the Calcinea have undergone successive and independent surges from a common ancestral form during their evolution. Fossil "pharetronids" have developed large populations in earlier geological periods and Recent Murrayonida are relicts of this early surge whose non-hypercalcified stages are lost. Clathrinida represents a relatively recent surge starting from a simple type of organization similar to the Recent *Soleniscus* or *Clathrina*.

In conclution, independent of their mutual relationship, the Clathrinida are a relatively recent group which display a continuous evolution from simple to complex forms, while the Murrayonida are simultaneously the most complex and the most ancient group of the Calcinea, whose evolutionary history has apparently been lost.

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GENERAL KEY FOR THE GENERA OF CALCINEA

1 — Calcinea with skeleton composed of free triradiates and/or quadriradiates, to which biradiates may be added; no hypercalcified skeleton .... CLATHRINIDA 2
— Calcinea with skeleton including non-spicular elements or spicule tracts. MURRAYONIDA 16

2 — Sponge body composed of individual, anastomosed or ramified tubes, choanocytes line all the internal cavities of the sponge 3
— Choanocytes do not line all the internal cavities of the sponge 9

3 — No differentiated diverticuli on the external part of the tubes; when a large cormus is formed there is no common cortex covering the whole body 4
— Differentiated diverticuli on the external part of the tubes with particular skeleton. *Levinella*

4 — Choanoderm flat or exceptionally elevated in the form of cones around apical rays of quadriradiates, but never forming true folds 5
— Choanoderm forming folds inside the choanocoel delimiting shallow or deep radial spaces or tubes, supported by apical rays or quadriradiates from the external skeletogenous layer.... .... *Ascandra*

5 — Sponge body in the form of solitary, sometimes distally ramified tubes, or composed of anastomosed tubes forming a large cormus 6
— Sponge in the form of a large central tube and radially arranged radiate tubes, amply ramified in their distal part and occasionally anastomosed in their proximal part .... *Dendya*

6 — Sponge in the form of solitary tubes, sometimes terminally ramified, or erected tubes growing from creeping stolon-like tubes .... *Soleniscus*
— Sponge in the form of anastomosed tubes 7

7 — Sponge cormus with distinct peduncle, solid or formed of normally organized, partially or fully coalescent tubes. Skeleton composed of parasagittal spicules, or of regular spicules to which parasagittal spicules are added, at least in the peduncle .... *Guancha*
— Sponge cormus without a distinct peduncle 8

8 — Sponge body formed of anastomosed tubes, without a common cortex surrounding the whole cormus .... *Clathrina*
— Sponge body composed of amply anastomosed tubes covered by a distinct cortex surrounding the whole body. No exhalant aquiferous system; a pseudoatrium may exceptionally be formed through the calyciform growth of the sponge .... *Ascaltis*

9 — Sponge composed of central, occasionally ramified tubes ornated with distinct external diverticuli having their own skeleton, different from that of the central tube .... *Burtonulla*
— Sponge with a solid body without external diverticuli 10

10 — Sponge body composed of a network of anastomosed and ramified tubes with a proper skeleton and covered by a thin cortex. Central atrial cavity surrounded by a thin wall. *Leucascus*
— Sponge body solid; when the choanocyte chambers are elongated, they do not have a proper skeleton, but are embedded in the choanosomal skeleton 11

11 — Sponge with a clear distinction between a solid cortex and the choanosome. Choanoskeleton and/or atrial skeleton absent, or, when present, composed of diffuse triradiates and/or quadriradiates much smaller than spicules of the cortical skeleton 12
— Sponge without a clear distinction between the solid cortex and the choanosome supported by a reduced choanoskeleton 15

12 — Sponge with copiously ramified but not anastomosed tubular choanocyte chambers arranged radially around a central atrium; skeleton containing large longitudinal biradiates distributed throughout the body wall .... *Leucomalthe*
— Sponge with tubular, elongated or spherical choanocyte chambers without large biradiates in the body wall 13

13 — Sponge composed of external wall sustained by large radiate spicules; aquiferous system leuconoid, choanosome devoid of skeleton .... *Leuclathrina*
— Sponge with elongate and/or spherical choanocyte chambers; in addition to the strong cortical skeleton, smaller spicules present in atrial and/or choanosomal skeleton 14

14 — Sponge body composed of large anastomosed tubes; the wall of each tube consists of a distinct cortex, a choanosome containing elongated choanocyte chambers and a large central atrium. .... *Leucaltis*

— Sponge body solid, occasionally ramified, but not in the form of anastomosed tubes; aquiferous system containing elongated and/or spherical chambers. Large central atrium always present. .... *Leucettusa*

15 — Sponge body solid; atrium often reduced to exhalant channels opening directly into osculum. Leuconoid organization with choanosome supported by a regular network of triradiates to which quadriradiates may be added; no distinct subcortical layer of inhalant chambers.... .... *Leucetta*

— Sponge body solid with large atrium. Leuconoid organization with subcortical system of inhalant cavities supported by a skeleton in part composed of centripetal rays of cortical triradiates. .... *Pericharax*

16 — Sponge skeleton contains rigid internal calcareous aspicular network .... *Murrayona*

— Sponge without a rigid calcareous network and with spicular tracts 17

17 — Sponge with tuning-fork spicules in tracts and cortical calcareous plates. *Paramurrayona*

— Sponge with biradiates in tracts and cortical tripods .... *Lelapiella*

REFERENCES

BIDDER, G., 1898. — The skeleton and the classification of calcareous sponges. *Proc. R. Soc.*, London, **64** : 61-76.

BOROJEVIĆ, R., 1965. — Éponges calcaires des côtes de France. I. — *Amphiute paulini* Hanitsch ; les genres *Amphiute* Hanitsch et *Paraheteropia* n. gen. *Archs Zool. exp. gén.*, **106** : 665-670.

— 1966. — Éponges calcaires des côtes de France. II. — Le genre *Ascandra* Haeckel emend. *Archs Zool. exp. gén.*, **107** (2) : 357-368.

— 1967. — Importance de l'étude de la répartition écologique pour la taxonomie des éponges calcaires. *Helgoländer wiss. Meeresunters,* **15** : 116-119.

— 1968. — Éponges calcaires des côtes de France. IV. — Le genre *Ascaltis* Haeckel emend. *Archs Zool. exp. gén.*, **109** (2) : 193-210.

— 1969. — Étude du développement et de la différenciation cellulaire d'Éponges Calcaires Calcinéennes (Genres *Clathrina* et *Ascandra*). *Annls Emb. Morphogen.*, **2** (1) : 15-36.

— 1970. — Différenciation cellulaire dans l'embryogénèse et la morphogénèse chez les Spongiaires. *In* : Biology of the Porifera, ed. W. G. FRY. *Symp. Zool. Soc.*, London, **25** : 467-490.

— 1971. — Éponges calcaires des côtes du sud-est du Brésil, épibiontes sur *Laminaria brasiliensis* et *Sargassum cymorum*. *Revta bras. Biol.*, **31** (4) : 525-530.

— 1979. — Évolution des Spongiaires Calcarea. *In* : Biologie des Spongiaires, eds C. LÉVI & N. BOURY-ESNAULT. Colloques internationaux CNRS, **291** : 527-530.

BOROJEVIĆ, R., & N. BOURY-ESNAULT, 1986. — Une nouvelle voie d'évolution chez les éponges calcaires Calcinea : description des genres *Burtonulla* n. g. et *Levinella* n. g. *Bull. Mus. natn Hist. nat., Paris*, 4ᵉ sér., **8**, A (3) : 443-455.

BOROJEVIĆ, R., & N. BOURY-ESNAULT, 1987. — Calcareous sponges collected by N. O. Thalassa on the continental margin of the Bay of Biscaye : I. — Calcinea. *In* : Taxonomy of Porifera from the NE Atlantic and Mediterranean Sea, J. VACELET & N. BOURY-ESNAULT (eds), NATO Asi Series, G13, 1-27

BOROJEVIĆ, R., W. G. FRY, W. C. JONES, C. LÉVI, R. RASMONT, M. SARÀ & J. VACELET, 1967. — Mise au point actuelle de la terminologie des éponges. *Bull. Mus. natn. Hist. nat., Paris*, 2ᵉ sér., **39** (6) : 1224-1235.

BOROJEVIĆ, R., & S. PEIXINHO, 1976. — Éponges calcaires du nord-nord-est du Brésil. *Bull. Mus. natn. Hist. nat., Paris*, 3ᵉ sér., nº 402, Zool. 279 : 987-1036.

BOWERBANK, J. S., 1864. — A monograph of the British Spongiadae. Ray Society, 290 p.

BRØNDSTED, H. V., 1931. — Die Kalkschwämme. *Dt. Südpol.-Exped.*, 1901-03, **20** : 1-47.

BURTON, M., 1932. — Sponges. *'Discovery' Rep.*, **7** : 237-392.

— 1963. — A revision of the classification of the Calcareous sponges. British Museum (National History), London, 693 p.

CARTER, H. J., 1885-1886. — Descriptions of Sponges from the neighbourhood of Port Philip Heads, South Australia, *Ann. Mag. nat. Hist.*, **15-18** (5) : 431-441.

DENDY, A., 1891. — A monograph of the Victorian sponges. I. — The organization and classification of the Calcarea Homocoela, with description of the Victorian species. *Trans R. Soc. Vict.*, **3** (1) : 1-81.

— 1892. — Synopsis of the Australian *Calcarea heterocoela*, with a proposed classification of the group and descriptions of some new genera and species. *Proc. R. Soc. Vict.*, **5** : 69-116.

— 1894. — Studies on the comparative anatomy of sponges. VI. — On the anatomy and relationships of *Lelapia australis*, a living representative of the fossil pharetrones. *Q. J. microsc. Sci.*, **36** : 127-142.

— 1913. — Report on the Calcareous sponges collected by the Sealark Expedition in the Indian ocean. *Trans. Linn. Soc. London*, Zool., **16** : 1-29.

DENDY, A., & L. M. FREDERICK, 1924. — On a collection of sponges from the Abrolhos Islands, Western Australia. *Trans. Linn. Soc. Lond.*, Zool., **35** : 477-519.

DENDY, A., & H. ROW, 1913. — The classification and phylogeny of the calcareous sponges, with a reference list of all the described species, systematically arranged. *Proc. zool. Soc. Lond.*, 704-813.

FLEMING, J., 1828. — A History of British Animals. Edinburgh.

FINKS, R. M., & D. HILL, 1967. — Porifera and Archaeocyatha. *In* : The Fossil Record. A symposium with documentation. Geological Society of London : 333-345.

FINKS, R. W., 1970. — The evolution and ecologic history of sponges during Palaeozoic times. *In* : Biology of the Porifera, ed. W. G. FRY. *Symp. zool. Soc. Lond.*, **25** : 3-22.

GRAY, J., 1867. — Notes on the arrangement of sponges with the description of some new genera. *Proc. zool. Soc. Lond.*, 492-558.

HADZI, J., 1917. — Rezultai bioloskih istrazivanja Jadranskoga mora. Porifera. Calcarea I. *Clathrina blanca* (Miklucho-Maclay); grada i razvoj s osobitim obzirom na opès pitanja o spuzvama. *Prirodosl. Istraz. hrv. slov. Potak.*, **9-10** : 1-168.

HAECKEL, E., 1969. — Prodromus eines Systems der Kalkschwämme. *Jena. Z. Naturw.*, **5** : 176-191.

— 1872. — Die Kalkschwämme, eine monographie. Berlin.

HARTMAN, W., 1958. — A re-examination of Bidder's classification of the Calcarea. *Syst. Zool.*, **7** : 97-110.

— 1980. — Calcareous Sponges in Living and fossil sponges. Notes fort a short course. *Sedimenta*, **8** : 169-214.

JAMES, N. P., & C. F. KLAPPA, 1983. — Petrogenesis of early Cambrian reef limestones, Labrador, Canada. *J. sedim. Petrol.*, **53** (4) : 1051-1096.

JENKIN, C. F., 1908. — Porifera. III. Calcarea. *In* : National Antarctic Expedition (Nat. Hist.). London, **4** : 49 p.

JOHNSON, M. F., 1980. — Habitats and habitat preferences of the calcareous sponges *Clathrina coriacea* (Montagu) and *Clathrina blanca* (Miklucho-Maclay) from Santa Carolina Island, California. *Wasmann J. Biol.*, **38** (1-2) : 1-9.

JOHNSTON, G., 1842. — A History of British Sponges and Lithophytes. Edinburgh, London, Dublin, **8** : 264 p.

KEMPEN, T. M. G. VAN, 1978. — Anthaspidellid sponges from the early Paleozoic of Europe and Australia. *Neues Jb. Geol. Paläont. Abh.*, **156** (3) : 305-337.

KIRKPATRICK, R., 1910. — On a remarkable Pharetronid sponge from Christmas Island. *Proc. r. Soc.*, London, **83** : 124-133.

MIKLUCHO-MACLAY, N. DE, 1868. — Beiträge zur Kenntniss der Spongien. I. Über *Guancha blanca*, einen neven Kalschwämm. *Jenaische Z.*, **4** : 221-240.

MINCHIN, E. A., 1896. — Note on the larval and post larval development of *Leucosolenia variabilis*, n. sp., with remarks on the development of other Asconidae. *Proc. r. Soc.*, London, **40** : 42-52.

— 1900. — Porifera. *In* : Treatise on Zoology. II. 1-188. Lankester R. (ed.), London : A. et C. Black.

POLÉJAEFF, N., 1883. — Report on the Calcarea dredged by H.M.S. Challenger during the years 1873-76. *Zool. Chall. Exp.*, **24** : 1-76.

REITNER, J., 1987. — Phylogenie und konvergenzen bei Rezenten und Fossilen Calcarea (Porifera) mit einen Kalkigen Basalskelett ("Inozoa", "Pharetronida"). *Berl. geowiss. Abh.*, **86** : 87-125.

RISSO, A., 1826. — Histoire naturelle des principales Productions de l'Europe Méridionale et particulièrement de celles des environs de Nice. **5**, Paris.

SCHMIDT, O., 1862. — Die Spongien des adriatischen Meeres. Leipzig, 88 p.

— 1864. — Supplement des Spongien des Adriatischen Meeres, enthaltend die Histologie und systematische Ergänzungen. Leipzig.

SOLÉ-CAVA, A., M. KLAUTAU, N. BOURY-ESNAULT, R. BOROJEVIĆ & J. P. THORPE. — Genetic evidence for cryptic speciation in allopatric populations od two cosmopolitan species of the calcareous sponge *Clathrina*. *Mar. Biol.* (in press).

TUZET, O., 1947. — L'ovogénèse et la fécondation de l'éponge calcaire *Leucosolenia (Clathrina) coriacea* Montagu et de l'éponge siliceuse *Reniera elegans* Bow. *Archs Zool. exp. gén.*, **85** : 127-148.

VACELET, J., 1964. — Étude monographique de l'éponge calcaire pharétronide de Méditerranée, *Petrobiona massiliana* Vacelet & Lévi. Les Pharétronides actuelles et fossiles. *Recl Trav. Stn. mar. Endoume*, **34** (50) : 1-125.

— 1967. — Descriptions d'éponges Pharétonides actuelles des tunnels obscurs sous-récifaux de Tuléar (Madagascar). *Recl Trav. Stn. mar. Endoume*, suppl. **6** : 37-62.

— 1970. — Les éponges Pharétronides actuelles. *In* : Biology of the Porifera, ed. W. G. FRY. *Symp. zool. Soc. Lond.*, **25** : 189-204.

— 1977. — Éponges Pharétronides actuelles et Sclérosponges de Polynésie française, de Madagascar et de La Réunion. *Bull. Mus. natn. Hist. nat., Paris*, 3ᵉ sér., nº 444, Zool. 307 : 345-368.

— 1981. — Éponges hypercalcifiées (« Pharétronides », « Sclérosponges ») des cavités des récifs coralliens de Nouvelle-Calédonie. *Bull. Mus. natn. Hist. nat., Paris*, 4ᵉ série, **3** A, (2) : 313-351.

— 1985. — Coralline sponges and the evolution of Porifera. *In* : The origins and relationships of lower invertebrates, eds S. CONWAY MORRIS, J. D. GEORGE, R. GIBSON & H. M. PLATT. The systematics Association, special volume **28** : 1-13.

— In press. — Recent Calcarea with a reinforced skeleton ("Pharetronids"). *Proc. int. Symp. fossil & recent Sponges*, Berlin, September, 1988.

WENDT, J., 1980. — Calcareous Sponges. The non-spicular skeleton. *Sedimenta,* **8** : 196-214.

ZIEGLER, B., & S. RIETSCHEL, 1970. — Phylogenetic relationships of fossil calcisponges. *In* : Biology of the Porifera, ed. W. G. FRY. *Symp. zool. Soc. Lond.*, **25** : 23-40.

ZITTEL, K., 1878. — Studien über fossile Spongien. 3. — Monactinellidae, Tetractinellidae und Calcispongiae. *Abh. K. bayer. Akad.*, **13** : 91-138.