REPRODUCTION AND DEVELOPMENT

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REPRODUCTION

The normal method of reproduction by sponges is through shedding of sperm into the exhalant water, fertilization of either shed or retained ova, and dispersal through a planktonic larval stage. Asexual reproduction through budding, fragmentation, or production of **gemmules** also occurs (BERGQUIST, 1978).

Sponges are generally hermaphroditic but with ovarian tissue separated from the testicular tissue either spatially or temporally. In some species sexually ripe individuals seem to be either male or female, but it is not certain whether the sexes are separate or whether there is merely temporal separation of male and female phases (BRIEN, 1973a; GILBERT & SIMPSON, 1976; KAYE, 1990; TANAKA-ICHIHARA & WATANABE, 1990). Ova and spermatozoa are produced from cells having the form of **amoebocytes.** These in turn are produced by the transformation of **choanocytes,** at least in the Calcarea and Demospongea (BRIEN, 1973a; TUZET, 1973a). Among the Hexactinellida the eggs and sperm arise from similar cells (**archaeocytes**), but these have not been seen to arise in turn from choanocytes (TUZET, 1973b).

Among 43 temperate-water species of Demospongea, the breeding season is relatively short, generally in the summer, and averaging two months for viviparous species and one month for oviparous species (LÉVI in BRIEN, 1973a).

Fewer data are available for tropical demosponges, but REISWIG (1973) has observed that in *Mycale* sp. from Jamaica, an r-selected opportunistic species, reproduction is extended through the six warmest months of the year, while in *Verongia gigantea* and *Tethya crypta,* both K-selected specialist species, reproduction is restricted to one and two months, respectively, during the colder season. Continuing to the temperate-water demosponges, the length of the breeding seasons are not correlated with ovoviparity versus viviparity; the species with the longest (*Mycale*) and shortest (*Verongia*) breeding seasons are both viviparous, while a third (*Tethya*) is oviparous. Perhaps among the temperate-water species the viviparous species are largely r-selected types, and this, rather than the habit of larval incubation, determines their longer breeding season (cold-water species among invertebrates in general tend toward both r-selection and larval protection). Among the Calcarea the breeding season seems more extended, and continues throughout the warmer months (VACELET, 1965). Breeding times in the Hexactinellida are not well known, but in *Farrea sollasii* at least sexual reproduction has been observed throughout the year (OKADA, 1928; TUZET, 1973b).

Spermatozoa are discharged through the exhalant orifice of the sponge and are drawn into the inhalant stream of adjacent sponges. The spermatozoon in sponges that incubate their larvae penetrates a choanocyte or amoebocyte that becomes a carrier cell, transporting the spermatozoon to the ovum that is located in the mesoglea, whither it has previously migrated and enlarged itself through the consumption of food-bearing trophocytes. Oviparous or nonincubating sponges have direct penetration of the ovum by the sperm cell (TUZET, 1973a, p. 15).

DEVELOPMENT

LARVAE

Free-swimming sponge larvae are at the blastula stage of embryonic development. The equivalent of gastrulation takes place at the time of fixation and metamorphosis of the larva into a sponge. There are two principal types of larvae in the Demospongea and Calcarea: (1) a **parenchymella** with a

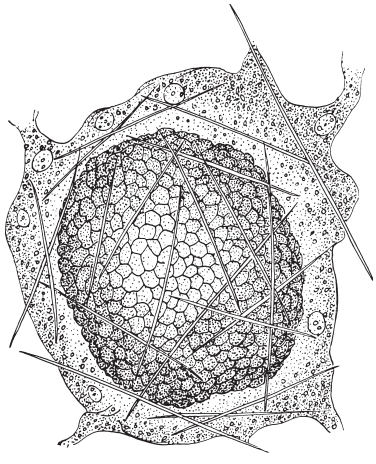

FIG. 64. Larval stage of calcareous *Sycon raphanus* with outer layer of ectoscleroblasts and irregularly oriented, diactine spicules (Tuzet, 1973a).

solid interior and a complete or nearly complete covering of flagellated cells (they may be absent at the posterior end); and (2) an **amphiblastula** with a hollow interior and a clear differentiation between the cells of the anterior half and the cells of the posterior half.

These two types, however, may not be homologous between the Demospongea and the Calcarea. In the Demospongea, both types arise from a solid nonflagellated stereoblastula, while in the Calcarea they both arise from a hollow nonflagellated blastula. The amphiblastula among the demosponges occurs only in the Homosclerophora and develops its hollow by destruction of the interior cells of the stereoblastula (BRIEN, 1973a). It differs also from the amphiblastula of the Calcarea in that cells of the posterior half are ciliated like those of the anterior half (*Octavella* is a partial exception; TUZET & PARIS, 1964). Among the Calcarea these posterior cells are nonflagellated, and there are four specialized cells in the equatorial region arranged in the form of a cross (TUZET, 1973a). It also arises from a hollow stomoblastula with a pore at one end (TUZET, 1973a). The parenchymella of the Calcarea arises from a hollow blastula that is

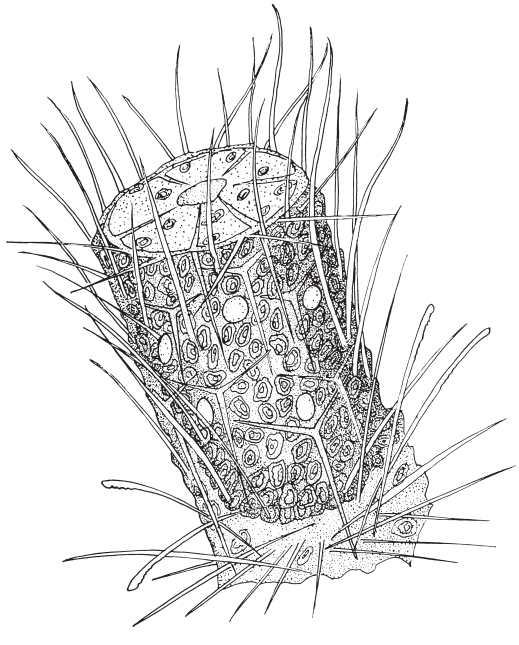

FIG. 65. Young asconoid olynthus stage of calcareous *Sycon raphanus* with regularly arranged triradiates (Tuzet, 1973a).

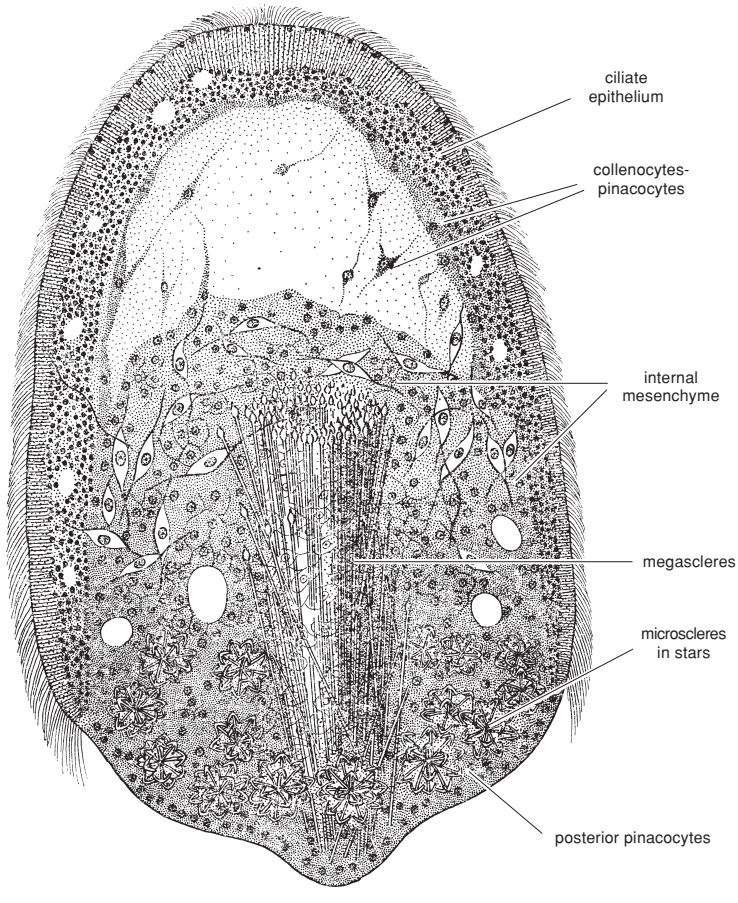

FIG. 66. Section of free-swimming paremchymella of demosponge *Esperia lorenzi* showing posterior concentration of megascleres along medial axis of sponge, and widely developed microscleres in stars; ciliate epithelium; collenocytes-pinacocytes; massive internal mesenchyme condensed in posterior polar area; and posterior pinacocytes (Brien, 1973a).

not a stomoblastula; its solid interior develops by immigration of surface cells.

There thus seems to be a fundamental distinction between the two classes that may be blurred to some extent by the use of common terms for possibly homomorphic larval types. Within the Calcarea, the two types of larvae seem to have considerable taxonomic significance in that they are correlated with the position of the nucleus in the choanocyte and with other characters (BIDDER, 1898; HARTMAN, 1958b).

The larvae of the Hexactinellida are less well known, and information comes chiefly from the study of *Farrea sollasii* by OKADA (1928). Initially the blastula is hollow with an opening to the exterior, resembling thus the stomoblastula of the Calcarea. It soon becomes solid on the interior but at or after fixation develops a choanocyte-lined central cavity with several diverticula and an osculum. At no time is the larva flagellated on the exterior; it is in this respect unlike the larvae of Demospongea and Calcarea (TUZET, 1973b).

LARVAL SPICULATION

In most sponges of all three classes the larva develops a complement of spicules before fixation. It is thus possible that a larva

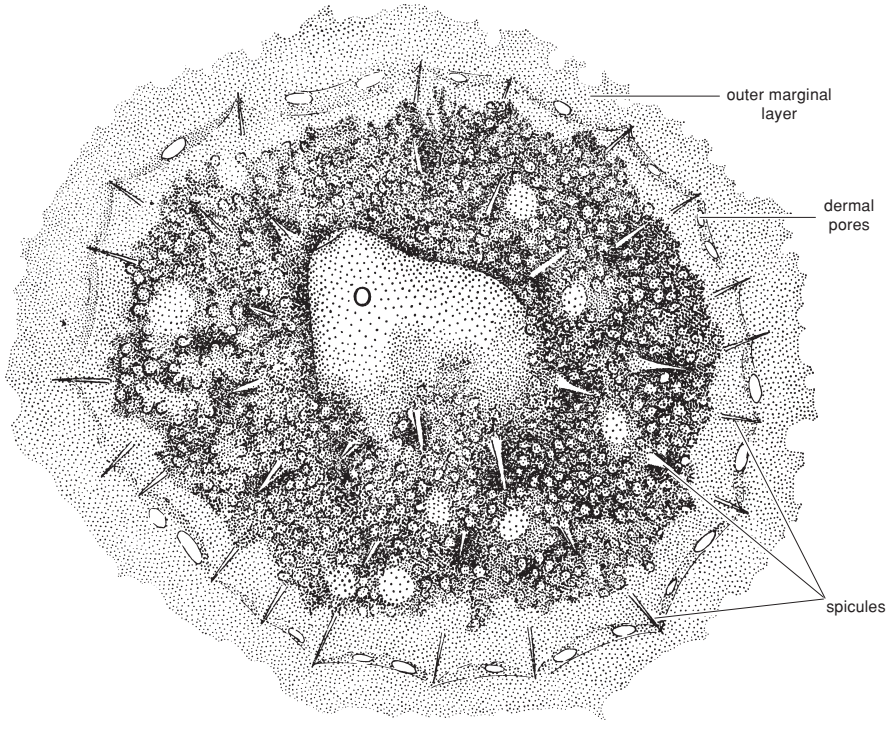

FIG. 67. Demosponge *Esperella* immediately after metamorphosis to small, leuconoid sponge with distinct osculum (*O*); outer marginal layer; dermal pores; numerous clusters of flagellae; and spicules (Brien, 1973a).

could be preserved in the fossil record, albeit under extremely favorable circumstances, inasmuch as it is less than a millimeter in maximum dimension. The spicules are not always the same as those of the adult. If ontogeny recapitulates phylogeny, the larval spiculation may give us some clues as to the evolutionary history of spicules.

Among the Calcarea, *Sycon raphanus,* which in the adult phase possesses diactines, sagittal **triradiates,** and tetraradiates, possesses only irregularly arranged diactines in

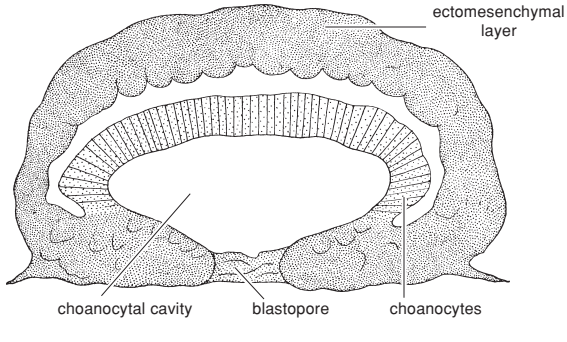

FIG. 68. Asconoid stage of metamorphosis of demosponge *Plakina monolopha* showing large, choanocytal cavity, choanocytes, blastopore, and ectomesenchymal layer (Brien, 1973a).

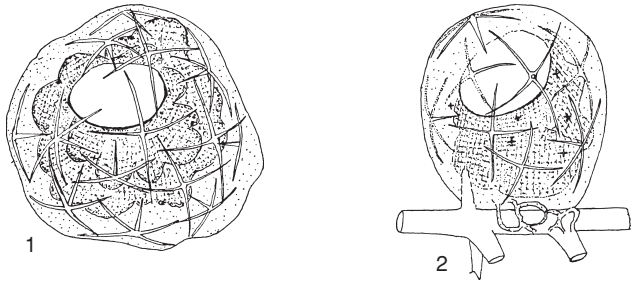

FIG. 69. Examples of young hexactinellid sponge *Farrea sollasii* SCHULZE showing *1,* stauractines of skeleton and choanosome around oscular opening; *2,* a small example (0.68 X 0.57 mm), with skeleton of stauractines and small, discohexaster microscleres, attached to skeletal fragment of larger sponge (Tuzet, 1973b).

the larval stage (Fig. 64), developing them by the time of fixation but before metamorphosis. Following metamorphosis the young sponge (**olynthus**) has the adult complement of spicules with the regular parallel arrangement of triradiates (Fig. 65) although its aquiferous system is asconoid rather than syconoid (TUZET, 1973a). This asconoid stage is characteristic of all young Calcarea.

Among the Demospongea in which the larva is incubated before being released, the free-swimming parenchymella has already

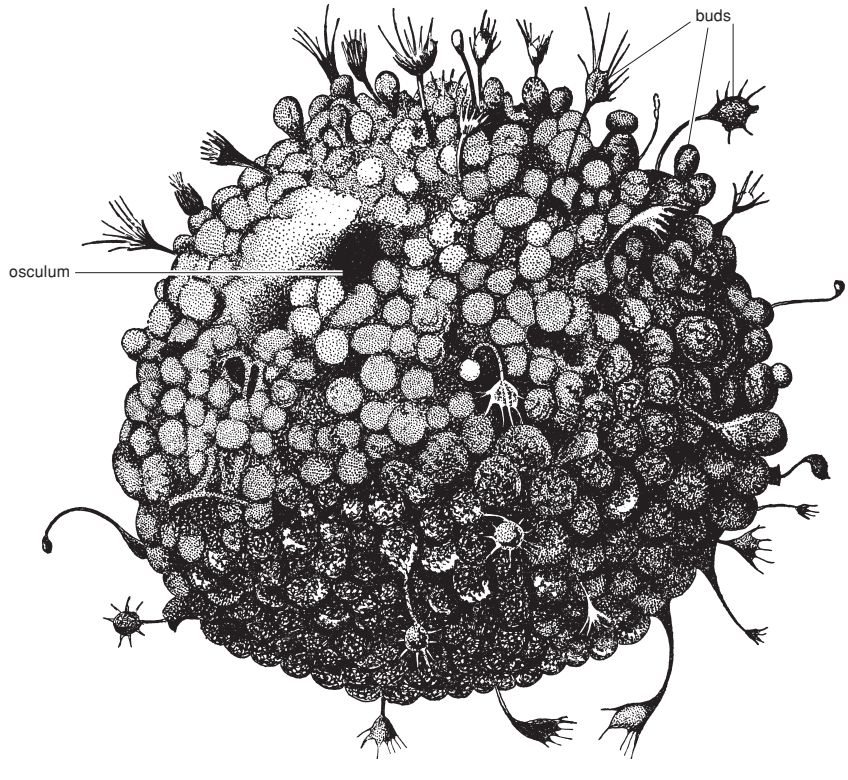

FIG. 70. Demosponge *Tethya maza* with numerous buds in various stages of development, with stalks on those nearly ready to be set free; osculum developed in upper part of parent sponge (Brien, 1973a).

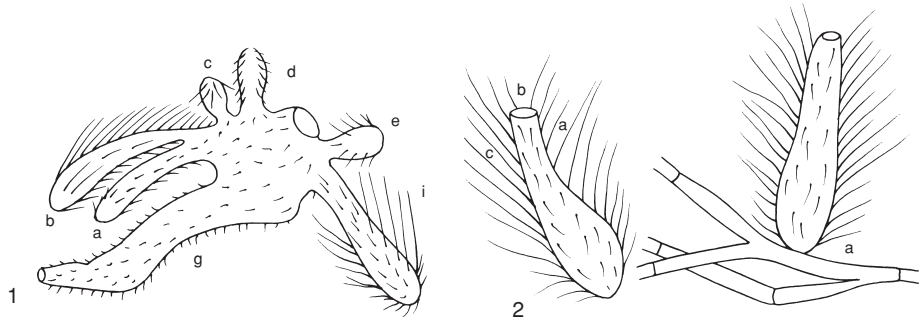

FIG. 71. The calcareous *Leucosolenia botryoides* showing *1,* several buds (*a–e*) in diverse stages of development, grading up to one (*i*), with long spicules, ready to detach from parent (*g*); *2,* free bud, on left, with a terminal osculum (*b*) and characteristic long spicules (*a, c*), and attached example, on right (Tuzet, 1973a).

developed both macroscleres and microscleres (Fig. 66). The spicules are characteristically concentrated in the posterior half of the larva, with the monaxonic megascleres arranged parallel to the anteroposterior axis of the larva (BRIEN, 1973a).

Among oviparous types the larva is less well developed and may even be benthonic rather than planktonic (e.g., *Polymastia busta;* BOROJEVIC, 1968), and the spicules may not appear until after fixation and metamorphosis (BRIEN, 1973a).

FIG. 72. *Lophocalyx (Polypophus) phillippinensis* GRAY, with several buds (Tuzet, 1973b).

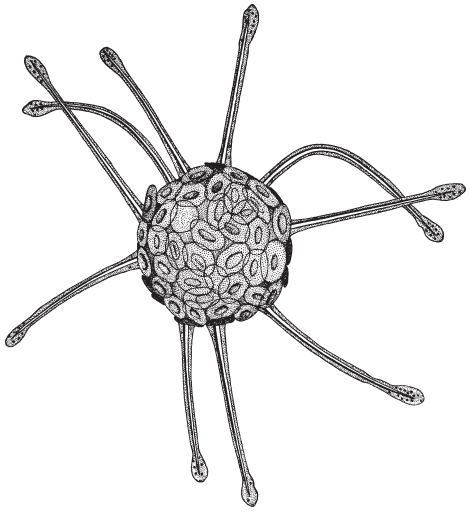

FIG. 73. Young, microscopic, pelagic propagule, approximately ×275 in diameter, coated with coccolith-like spicules and with ten projecting styles, each coated in a thin film of cytoplasm (Brien, 1973a).

Almost all demosponges develop a leuconoid aquiferous system directly at metamorphosis (Fig. 67). A very few, most notably *Halisarca dujardini* and those with amphiblastula larvae, go through brief asconoid and syconoid stages during metamorphosis (Fig. 68) before developing the leuconoid condition (BRIEN, 1973a).

The hexactinellid larva of *Farrea sollasii* develops first six stauractines oriented parallel to the anteroposterior axis; subsequently it develops six microscleres (**discohexasters**). After fixation the young sponge gradually develops the adult complement of spicules (Fig. 69), but stauractines persist for a time in the dermal layer, disappearing before the adult stage. Shortly after fixation the barrel-shaped young sponge has an asconoid structure with diverticula that are to become the pseudosyconoid choanocyte chambers of the adult (TUZET, 1973b). It is of interest that the earliest hexactinellids of the Cambrian have almost exclusively a spiculation of stauractines in a thin-walled sponge body similar to a young *Farrea* in gross shape.

WATANABE (1957), in describing the development of the demosponges *Tetilla serica,* has noted that the tetraxonic **protriaenes** first develop in the young sponge as monaxons, the **cladome** developing subsequently. Whether one sees a phylogeny reflected in this, it demonstrates that there is a developmental process whereby monaxons can become tetraxons; thus the process is not forbidden to phylogeny.

OVIPARITY VS. VIVIPARITY

Some demosponges, notably the Clavulina or Hadromerida, Epipolasida, Spirosclerida, and Axinellida, shed their eggs into the water after fertilization in the mother sponge. An even larger number of sponges, however, incubate the fertilized eggs to the larval stage before they are released into the

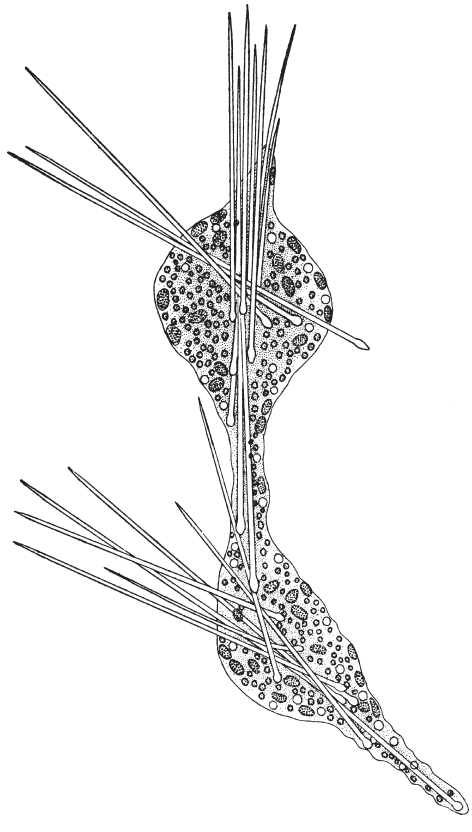

FIG. 74. Small pelagic propagule composed of two parts, each with numerous tylostyle spicules along axes of lobes and in peduncle; microscleres not present in this stage of development (Brien, 1973a).

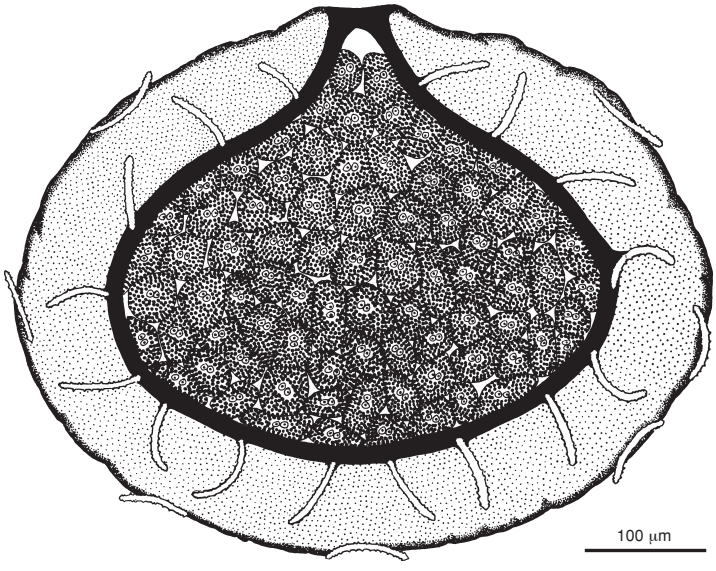

FIG. 75. Schematic drawing of vertical section through gemmule of *Spongilla lacustris* showing its general shape, with upper, micropyle opening and development of strongyles in outer, alveolar shell (Brien, 1973a).

water; these viviparous sponges include the Sigmatosclerophora, Keratosa, and Homosclerophora among the demosponges and apparently all the Calcarea and Hexactinellida that have been studied. In such sponges the developing larva is surrounded by choanocytes (in some instances an entire choanocyte chamber) that serve as food for the developing embryo. In some instances these cells penetrate the internal cavity of the embryo as well as surrounding it. The carrier cells of the sperm (a peculiar feature of vi-

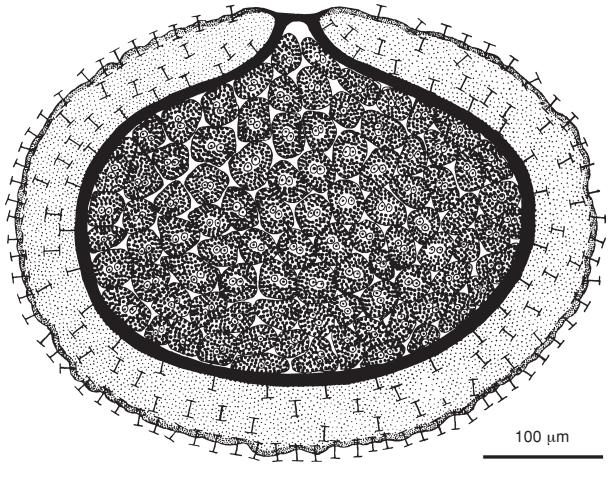

FIG. 76. Schematic drawing of vertical section through gemmule of *Ephidatia mülleri,* which has amphidiscs as spicules in outer capsule (Brien, 1973a).

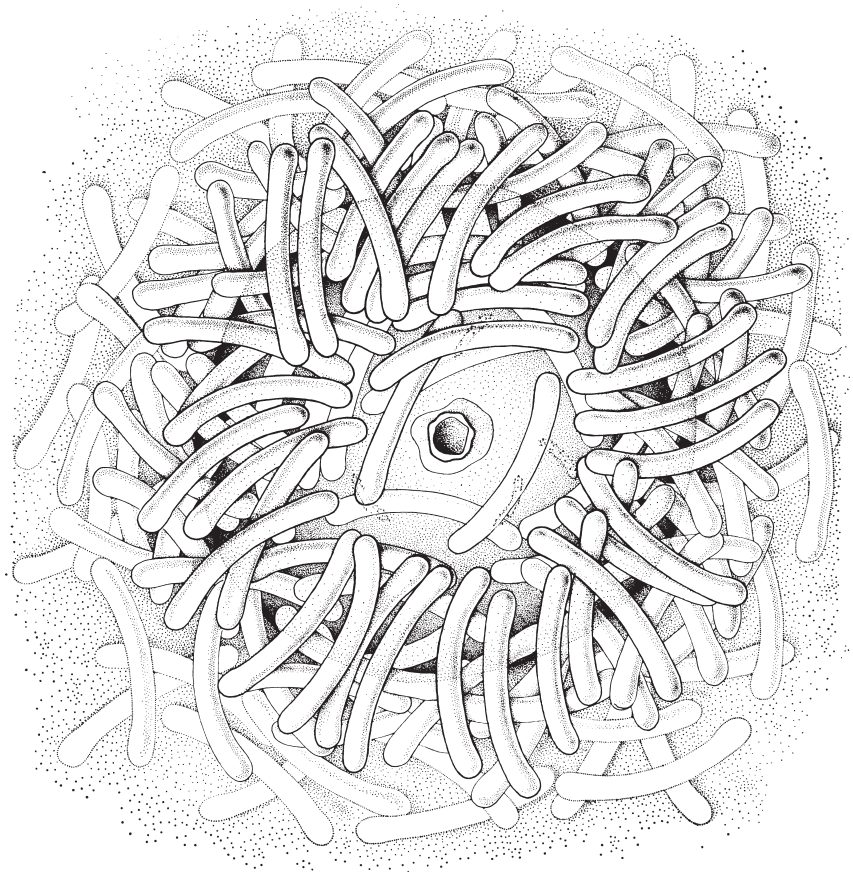

FIG. 77. Gemmule of *Corvospongylla thysi* with prominent amphistrongyles forming cuticular layer around small, central micropyle (Brien, 1973a).

viparous sponges) also serve as nourishing cells for the embryo (BRIEN, 1973a; LÉVI, 1973; TUZET, 1973a, 1973b).

Presence or absence of viviparity appears to be of fundamental taxonomic significance inasmuch as entire groups at the subordinal, ordinal, or even class level appear to be characterized by one or the other mode of reproduction. Among animals in general, incubation of larvae appears to be a more advanced character.

ASEXUAL REPRODUCTION

Reproduction by asexual means among sponges may take place through external buds, planktonic propagules, and internal statoblasts or gemmules. Such methods seem to occur most often in freshwater and shallow-marine forms in which winter conditions may kill the adults or in deep-sea forms in which, perhaps, a sparse population makes fertilization risky.

External buds, which grow from the surface of the parent and ultimately drop off to begin life as separate individuals, are known in the demosponges *Tethya maza* (Fig. 70) and *Mycale contrarenii* (BRIEN, 1973a), the calcareous sponge *Leucosolenia botryoides* (Fig. 71) (TUZET, 1973a), and the hexactinellids *Lophocalyx philippinensis* (Fig. 72), *Scyphidium longispina,* and *Aulocalyx ijimai* (TUZET, 1973b).

Propagules are microscopic bodies found in the plankton that are apparently produced

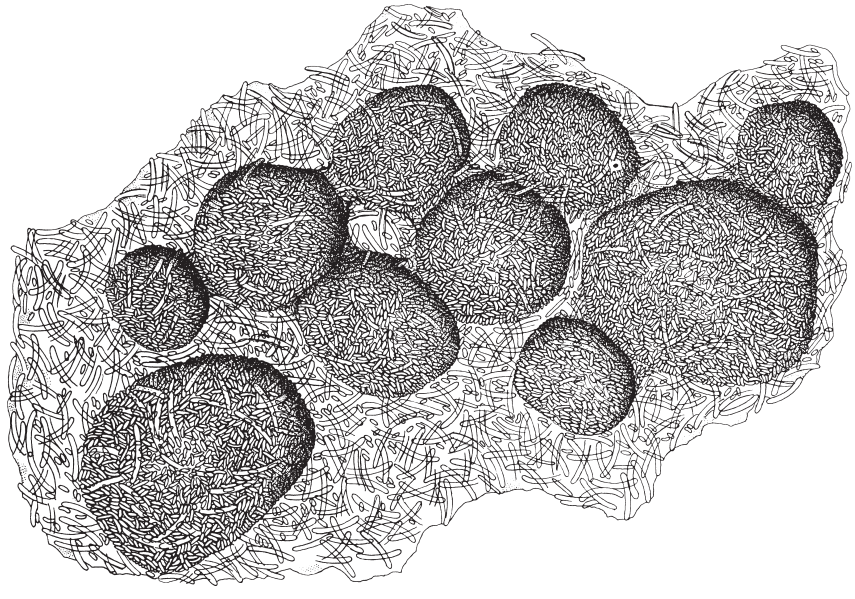

FIG. 78. Cluster of statoblasts of *Potamophloios gilberti,* up to 1 mm in diameter, that are attached to base of parent sponge; they lack a micropyle, such as is developed in gemmules, but are armored by layer of tangential strongyles (Brien, 1973a).

asexually by some demosponges. Those of *Alectona milleri* and *Thoosa armata* (both deep-water Hadromerida) have a special armor of coccolith-like spicules not found in the adult sponge, together with projecting styles (Fig. 73). The propagules have been found both in the adult sponge and free in the plankton. A different type with tylostyles and various astrose microscleres correspond with the spiculation of *Tethya aurantium,* its presumed source, although others may lack microscleres (Fig. 74) (TRÉBOUGOFF, 1942; BRIEN, 1973a).

Statoblasts, sorites, and gemmules are bodies covered with a special protective coating; they are formed within the parent sponge, generally near its base, and are capable of withstanding unfavorable conditions after being released by the death of the parent. They develop into new sponges with the return of favorable conditions.

They are best developed in the freshwater spongillids, where the body, called a gemmule, is provided with a special alveolar shell armed with spicules and bearing an opening (micropyle). The spiculation is characteristic (amphidiscs in some genera, spinose strongyles in others (Fig. 75–76). These objects are quite capable of fossilization, as are the spiculated capsules formed by the parent of *Corvospongilla thysi* around its gemmules (Fig. 77) (BRIEN, 1973a). In another freshwater family, the Potamolepidae, the genus *Potamophloios* bears statoblasts up to l mm in diameter that lack a micropyle as in true gemmules but are armored with tangential strongyles (Fig. 78) and are equally capable of fossilization (BRIEN, 1973a).

Several common genera of shallow-water marine demosponges (*Cliona, Chalina, Craniella, Suberites*) produce similar statoblasts, although not all are armed with spicules (BRIEN, 1973a). These statoblasts are larger than the gemmules of spongillids, reaching 1 or 2 mm in diameter and as much as 2.5 mm in the boring sponge *Cliona vastifica* (BRIEN, 1973a, p. 388).

In the spongillids the gemmule is part of the regular life cycle, the adult dying each year with the onset of the winter season or the dry season. Among the marine sponges, formation of statoblasts seems to be more sporadic (BRIEN, 1973a) and is apparently a preparation for more accidental conditions.

PHYSIOLOGY

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FEEDING MECHANISM

Sponges are filter feeders with intracellular digestion. Energy for moving water through the sponge is supplied by flagella of the choanocytes. The direction water takes seems to be determined by size of openings into and out of **flagellated chambers** (**prosopyles** and **apopyles,** respectively). The apopyle, usually single, has a larger diameter than the prosopyles. In *Ephydatia fluviatilis* the apopyle is 25 to 30 μm in diameter, as compared to 4 μm for the prosopyles (KILIAN, 1952, p. 416–417). When the water within the flagellated chamber is stirred by the flagella, it tends to move through the apopyle into the exhalant canals, drawing water into the chamber through the prosopyles.

Careful observations made by KILIAN (1952) on preparations of the freshwater sponge *Ephydatia fluviatilis* grown on microscope slides have confirmed this process. KILIAN (1952, p. 419) further observed that collars of individual choanocytes tend to direct the water down their longitudinal axes, which are oriented toward the apopyle of the chamber. The motion of each flagellum draws water through the porous surrounding collar (see below), which acts as the ultimate filtering mechanism in the feeding system, although not the only one.

Directional or coordinated movement of the choanocyte flagella is not necessary, nor does it occur. In the asconoid calcisponge *Leucosolenia* the entire cloaca is lined with choanocytes. That opening is a space much larger than the usual flagellated chamber and has as its exit the osculum of the sponge. Even in such coarse structures the directional flow of water is maintained solely by differences in diameters between osculum and inhalant canals. Flagella of adjacent choanocytes of *Leucosolenia* beat in different planes, always, however, perpendicular to the wall, and at different frequencies (JONES, 1964).

In the small calcareous species *Leucandra aspera* studied by BIDDER (1923), a 9 cm-long sponge circulated nearly a liter (936 cc) of water per hour. Sponges of this species (at 18° C) project exhalant streams up to 45 cm from the osculum at a calculated velocity of some 8.5 cm per second. BIDDER (1923, p. 313) pointed out that in colder waters the combined effect of lowered metabolic rate and increased water viscosity (important at the size-level of single flagella) may reduce energy of the oscular current. This may have a bearing on distribution of sponges in cold and deep waters.

Filtration rates of marine sponges fall within the same range as those of bivalves and ascidians (JØRGENSEN, 1955, 1966). Expressed in terms of body weight (grams of nitrogen) for purpose of comparison, they are: sponges, 45 to 170 ml/hr/mg N; bivalves, 5 to 160 ml/hr/mg N; ascidians, 110 to 150 ml/hr/mg N.

All cells of the sponge except **scleroblasts** (KILIAN, 1952) are capable of engulfing suspended particles that come into contact with the cell surface (POURBAIX, 1931, 1933; VAN WEEL, 1949; KILIAN, 1952; SIMPSON, 1963). The indispensable function of the choanocytes is that of maintaining a current. In sponges with small flagellated chambers, such as the spongillids, the prosopyles are no larger than 4 μm. Many suspended particles that sponges take into their cells are larger than this (POURBAIX, 1931, cited bacteria 11 μm long), and such particles are captured from the water stream by cells lining the canals or stretching netlike across them and even by cells on the sponge surface (KILIAN, 1952; SIMPSON, 1963).

Most observers concur, however, that the choanocytes ingest the major part of

suspended particulate matter carried into the sponge and that particles are subsequently transferred to the amoebocytes of the **mesenchyme** (see KILIAN, 1952, for extensive observations on *Ephydatia* with illustrations). This has been strikingly confirmed by study of the absorption by *Sycon* of dissolved glycine tagged with C^{14} (EFREMOVA, 1965). Although the epithelial **pinacocytes** also absorbed some of the glycine, the greatest concentration of labeled carbon immediately after feeding was found in the choanocytes. Within 24 hours the concentration of C^{14} decreased in the choanocytes but increased in the adjacent mesenchyme, indicating transfer of absorbed material to mesenchymal amoebocytes.

The choanocytes are in themselves filtering mechanisms, as shown by electron-microscope investigations of the fine structure of the collar (RASMONT, 1959; FJERDINGSTAD, 1961). The collar is not solid, as once believed, but is constructed of a single layer of longitudinal fibrils (about 0.2 μm apart in Spongillidae) connected by finer transverse fibrils. Motion of the flagellum draws water through the interfibrillar spaces and filters out suspended particles that are larger than the 0.2 μm interfibrillar spaces. Uptake of food particles by choanocytes may be aided because water velocities are lowest in the flagellated chambers, as noted by BIDDER (1923).

The osculum is an essential part of the hydraulic system of many sponges. Its diameter is narrower than that of the cloaca so that the velocity of effluent water is increased and projected as a jet away from the sponge. BIDDER (1923) has shown that for the calcisponge *Leucandra,* the oscular diameter is close to the theoretical optimum, that is, the diameter that will project the longest jet for a given flagellar pressure and a given energy loss from internal friction. The longer this efferent jet the greater the separation of exhaust from intake. In all but the most highly agitated water, this increases the effective radius of unfiltered water available to the sponge.

Functioning of such a hydraulic system depends upon fluid pressure developed within the choanocyte-lined chambers. This in turn depends upon tension and elasticity of the chamber wall. Flagellated chambers are more cohesive than the rest of the sponge (KILIAN, 1952) and apparently are elastic (JONES, 1962, p. 28). Given the same properties of the chamber wall (and, of course, of the canal system and choanocytes), the smaller the chamber the larger the pressure. [Observed pressures cited by BIDDER (1923) include 0.8 mm of water in the large-chambered *Leucandra* and 4 mm of water in the small-chambered *Stylotella.*] Such a relationship provides an adaptive basis for evolution of the small flagellated chambers of the leuconoid canal system that is possessed by most sponges.

That such a canal system developed very early among demosponges is indicated by the thick-walled, three-dimensional, fine-meshed skeletal net found in some of the earliest lithistid sponges, the Lower Ordovician *Archaeoscyphia* (or probably the even earlier Upper Cambrian *Gallatinospongia* and *Wilbernicyathus*). Earlier demosponges are principally the Middle Cambrian monaxonid sponges *Hazelia, Wapkia,* and others from the Burgess Shale of British Columbia and Middle Cambrian units of Utah. These sponges appear to be relatively thin walled and could have had a less advanced form of canal system.

Among the hexactinellids there is distinct fossil evidence of increasing complexity during the Cambrian. The earliest spicules assignable to this class are stauractines of Early Cambrian age that must have supported thin-walled sponges of asconoid or near-asconoid architecture. Whole sponges (*Protospongia*) consisting of a single layer of stauractines and pentactines are well known from Middle Cambrian beds. The interpretation of an asconoid structure is supported

by the ontogeny of living hexactinellids, whose embryos are asconoid sponges with a skeleton of stauractines. The first common hexactines, indicating the development of a thicker body wall, occur in upper Middle Cambrian *Bolaspis* zone. Whole sponges of a semi-encrusting habit with thick walls supported by two or three layers of hexactines (*Multivasculatus* HOWELL & VAN HOUTEN) are known from Upper Cambrian rocks. It seems probable that the semi-syconoid structure characteristic of living hexactinellids developed during the Cambrian.

Although BIDDER (1923) emphasized the adaptive value of separating influent and effluent water (partly confirmed experimentally by WARBURTON, 1960) this is by no means an absolute requirement, and other adaptive considerations must surely come into play. JØRGENSEN (1955) pointed out that a higher filtration rate can be obtained for the same expenditure of energy if internal fluid pressure is lower. Thus, if concentration of food in the ambient is low, passage of larger quantities of water per given energy expenditure may take precedence over efficient separation of water currents. Indeed, recirculation of water may insure effective removal of all available food material.

BIDDER (1923, p. 312) ascribed the open canal system of hexactinellids and their presumed lack of hydraulic evolution to constant currents in the deep-sea environment, currents that sweep through their open framework and carry away waste water, thereby obviating any need for hydraulic efficiency. Hexactinellids, however, have not always lived predominantly in deep water. It is possible that the hexactinellids have specialized in the metabolically efficient passage of large volumes of water at low pressure to extract food at low concentration. VON BRAND (1939) has shown that particulate matter rich in organic nitrogen is very rare in the deep sea as compared with surface waters. This may account for present hexactinellid abundance in the deep sea (freedom from competition of other filter feeders that may require higher food concentrations) and possibly for their earlier flourishing in shallow water at a time when ambient suspended food may have been less abundant.

FOOD SUBSTANCES

Sponge cells appear to engulf particles without regard to nutritive value. Nonnutritive substances, such as carmine or graphite particles, are subsequently excreted in normal fashion but more rapidly than such organic materials as egg-white droplets, which appear to be digested (KILIAN, 1952; JØRGENSEN, 1955). The natural food of sponges is still not known with certainty. Because digestion is exclusively intracellular, the maximum size of food particles is determined by what can be ingested by a single sponge cell. The largest cells are some 10 to 20 μm in diameter. Such a size rules out feeding on such organisms as protozoans and rotifers (KILIAN, 1952, p. 431) as well as many that are still larger. The smallest particles observed to be completely filtered out of water by sponges are 0.5 to 1.0 μm (VAN TRIGT, 1919; JØRGENSEN, 1955). Bacteria are frequently cited as a principal food of sponges. MADRI and others (1967) reported that when bacteria (*Escherichia coli*) are added to the water surrounding *Microciona prolifera* they are apparently removed from the water and concentrated in the sponge. POURBAIX (1931, 1932, 1933) has observed ingestion and apparent digestion of bacteria by archaeocytes of marine demosponges. To what extent they are a source of food is unknown. Studies of SOROKIN (1964) show that the abundance of living bacteria in ocean waters decreases sharply below 200 meters and that they are practically absent below 600 meters. The many sponges that occur below these depths must therefore feed on something else. Absence of bacteria is not a limiting factor in sponge distribution. Phytoplankton may be a food source. KILIAN (1952, p. 443)

reported algae being digested apparently in cells of *Ephydatia fluviatilis,* although SIMON (1953, p. 231) was unable to maintain the same species by feeding it algae and concluded that algae could not be used as food. Suspended but nonliving, organic particles may provide a considerable source of food for most sponges. Recently it has been shown unequivocally that sponges can absorb dissolved amino acids directly (C^{14}-tagged glycine; EFREMOVA, 1965), but the extent to which this operates in nature remains undetermined, although many authors have postulated such a food source (see KILIAN, 1952, p. 430).

JØRGENSEN (1955, p. 445) estimated that sponges, bivalves, and ascidians, all of which filter about 15 liters of water for each milliliter of O_2 consumed in metabolism, can meet their food requirements for maintenance and optimal growth when 0.15 to 0.20 mg of useable organic matter is available per liter of water. JØRGENSEN gave the quantity of dissolved organic matter in seawater as 2.2 to 4.6 mg/liter and the protein fraction as one-third to one-half of this (*vis.,* 0.7 to 2.3 mg/liter). If EFREMOVA's observations are generally valid, Holocene sponges could meet all their food requirements from direct absorption of dissolved matter. Because sponges do effectively filter out particulate matter from their feeding currents down to sizes of 0.5 μm, however, it seems likely that this must provide nutrients and is not a mere exercise.

Symbiotic algae are present in many shallow-water sponges, including most freshwater species. VAN WEEL (1949) noted that starch was not present in such algae when in the amoebocytes of *Spongilla proliferans,* although starch was present when the same algae were isolated from the sponge. Upon being returned to an algae-free sponge, the starch disappeared from the algae after a week. VAN WEEL suggested that such symbionts normally supply the sponge with carbohydrates, probably directly absorbed as soluble sugars. Symbiotic algae may, thus, supply soluble foodstuffs to those sponges that possess them (KILIAN, 1952, p. 443).

DIGESTION AND EXCRETION

Such particles as have been fed to sponges under experimental conditions appear to be digested in food vacuoles over a period of 12 to 24 hours (KILIAN, 1952) or more (POURBAIX, 1931, 1933). Small, condensed masses of indigestible matter remain in the food vacuoles of amoebocytes. These cells wander to exhalant canals, where the vacuole breaks through the cell wall and releases its contents into the efferent current. The empty vacuole is shed from the cell shortly thereafter and is carried off in the excurrent stream as a bladderlike object (KILIAN, 1952, p. 439). VAN WEEL (1949) observed that if an amoebocyte protrudes a feces-laden vacuole into an inhalant canal, by mistake as it were, it is withdrawn and the cell wanders off until it encounters an exhalant canal. KILIAN (1952, p. 438) suggested that possible chemical differences between afferent and efferent water may guide the amoebocytes in this respect, and that the greater surface area of the exhalant passages reduces the probability of mistakes, even with random movement. Solid wastes from digestion by cells other than amoebocytes may be transferred to the latter for excretion (VAN WEEL, 1949), but KILIAN (1952) noted that much excretion is carried out by pinacocytes lining the exhalant canals, presumably obtained in part from amoebocytes.

The mechanism by which soluble metabolic wastes are eliminated appears to be poorly known. VAN WEEL (1949) observed that *Spongilla,* vitally stained with pyrrhol blue, eliminated this soluble dye by concentrating it in liquid droplets that were subsequently voided as food vacuoles from the amoebocytes. Excretory products are complex nitrogen bases, such as agmatine and guanidine derivatives, according to JAKOWSKA and NIGRELLI (1960).

Presence of contractile vacuoles in amoebocytes (*sensu lato,* including scleroblasts) and choanocytes of freshwater sponges (*Spongilla* and *Ephydatia*) have been demonstrated by JEPPS (1947) and GATENBY and TAHMISIAN (1959). These latter authors were

unable to find such contractile vacuoles in ten genera of marine Calcarea and Demospongea, although noncontractile vacuoles were found in a similar position in the marine calcareous sponge *Grantia compressa.* Presumably contractile vacuoles of freshwater sponges eliminate excess water that enters the cells osmotically.

TRANSPORT OF METABOLITES

No circulatory system exists in a sponge. Motile amoebocytes appear to carry phagocytosed and partly digested food to other cells and to carry away solid wastes. The mechanism is either by momentary fusion of the cells involved in the transfer (Van Weel, 1949) or more likely by transfer of food vacuoles or solid particles through the apposed membranes of adjacent cells (Kilian, 1952). Soluble metabolites may be transferred by diffusion across cell membranes. Scleroblasts apparently do not carry out phagocytosis (Kilian, 1952) and presumably receive all metabolites in dissolved (i.e., molecular) form.

Specialized cells called thesocytes, possibly derived from choanocytes, have been interpreted as loci of storage of reserve metabolites. In the peculiar pharetronid calcareous sponge *Petrobiona massiliana* Vacelet & Lévi, 1958 thesocytes are concentrated in specialized areas and gradually disperse during the winter, suggesting their function as a reserve food supply for unfavorable times (Vacelet, 1962). The reserves are interpreted from staining reactions as being DNA or a similar glycoprotein. Stored glycogen is present in the posterior cells of the larva of this species (Vacelet, 1965). Liaci (1963) reported lipofuchsins, melanins, and sterols in thesocytes of the marine demosponge *Aaptos aaptos* that seem to lose their stored contents at the time the sponges reach the breeding season, presumably transferring the stored products to the gametes.

In the freshwater *Spongilla proliferans,* glycogen is stored in ovocytes and a concentration of protein occurs in cells making up the gemmules (Van Weel, 1949). Lutfy (1960) similarly found glycogen in amoebocytes and archaeocytes of *Ephydatia fluviatilis.* Lévi (1966) noted the presence of glycogen in some cells in the cortex of the marine demosponges *Ophlitaspongia seriata, Microciona prolifera, Pachymatisma johnstoni,* and *Mycale contarenii;* their abundance shows no seasonal connection with sexual maturity, and Lévi noted that it is not clear whether the glycogen is stockpiled for metabolism of the cells involved or is a reserve for the whole sponge. The latter would imply a greater degree of metabolic integration (Table 2).

IRRITABILITY AND BEHAVIOR

Sponges respond defensively to unfavorable stimuli by limited movements that minimize surface area and volume and close off access to interior spaces. Such responses include generalized or local contraction of the body and closure of oscules and of inhalant pores. Stimuli that evoke such responses include exposure to air, light, heat, reduced O_2, increased CO_2, stillness of ambient water, dissolved toxic substances in ambient water (e.g., alkaloids), and direct mechanical or electrical stimulation.

Few data are available for Hexactinellida. Most Calcarea respond only locally (Jones, 1957). The sponges most ready for overall contractions are Demospongea with a cortex, such as *Tethya.* Bullock and Horridge (1965) suggested that the layer of elongate cells just beneath the surface may be responsible.

Closure of oscules is brought about by contraction of a ring of specialized amoebocytes that surrounds the orifice like a sphincter. Inhalant pores located within porocytes are closed by contraction of the latter. Generalized contraction is apparently brought about partly by contraction of the individual cells (pinacocytes, **collencytes,** and **myocytes**) and partly by collapse of internal canal spaces following cessation of choanocyte flagellar action and closure of dermal pores. The contractile cells contain

TABLE 2. Storage products in cytoplasm of sponge cells (new).

SUBSTANCE	LOCATION	SPECIES	SOURCE
glycoprotein (DNA)	thesocytes of trabecular cords	*Petrobiona massiliana*	Vacelet & Lévi, 1958
	ovocytes	*Hippospongia communis*	Tuzet & Pavans de Ceccatty, 1959
glycogen	posterior cells of larva	*Petrobiona massiliana*	Vacelet, 1965
	ovocytes	*Spongilla proliferans*	Van Weel, 1949
		Ephydatia fluviatilis	Lutfy, 1960
	archaeocytes	*Ephydatia fluviatilis*	Lutfy, 1960
		Pachymatisma johnstoni	Lévi, 1966
	pinacocytes	*Ephydatia fluviatilis*	Lutfy, 1960
	"gray cells"	*Microciona prolifera*	Simpson, 1963
		Ophlitaspongia seriata	Borojevic & Lévi, 1964
	collencytes	*Mycale contrarenii*	Lévi, 1966
melanin	thesocytes	*Aaptos aaptos*	Liaci, 1963
	archaeocytes	*Pachymatisma johnstoni*	Lévi, 1966
lipofuchsin	thesocytes	*Aaptos aaptos*	Liaci, 1963
protein	gemmules	*Spongilla proliferans*	Van Weel, 1949
sterols	thesocytes	*Aaptos aaptos*	Liaci, 1963
fats	?	?	

filaments similar to those of muscle cells of higher animals, although their chemistry is somewhat different (BAGBY, 1965).

A stimulus affects initially only the immediate area exposed to it, but the response may spread slowly from the stimulated area for a limited distance. Summation of stimuli, both temporal and spatial, has also been observed (PROSSER, 1960; PAVANS DE CECCATTY, 1960).

The means whereby excitation is spread is not clear. TUZET and PAVANS DE CECCATTY (1959) and coworkers considered some cells to be primitive nerve cells and sensory cells, but their interpretation was not accepted by reviewers of the problem (JONES, 1962; BULLOCK & HORRIDGE, 1965). Cell-to-cell conduction would seem most likely, but WINTERMANN (1951) has suggested released chemical substances carried in the water currents. This has not been tested.

LENTZ (1966) reported the presence of neurohumors (acetylcholinesterase, monoamine oxidase, epinephrine, norepinephrine, 5-hydroxytryptamine) in spindle-shaped, bipolar or multipolar cells in the mesenchyme of the calcareous sponge *Sycon.* This appears to favor the ideas of TUZET and her coworkers. REISWIG (1971) concluded that myocyte type cells occur in a network and have a pacemaker-like activity so that contractions pass quickly from cell to cell and coordinated rhythmic activity occurs.

Movements of sponges with rigid skeletons, of the sort most frequently preserved as fossils, must be extremely limited. BURTON (1948) and ARNDT (1941) have reported limited locomotion among fixed adult sponges, presumably by migration of cells over the substrate.

RESPIRATION

Gas exchange is effected by each cell, either directly with the internally circulating water of the feeding currents, by diffusion through the mesoglea for short distances, or directly with the external ambient water. Consumption of O_2 appears to be relatively low, although few measurements have been published. BERGQUIST (1978) noted that there is little consistency in rates of sponge respiration reported in the literature. She observed that the only observations to that time on respiration rates in Demospongea that need no qualification were those reported by REISWIG (1974).

POURBAIX (1939) found that in fresh slices of the marine demosponge *Tethya lyncurium,* the choanosome consumed an average of 0.237 mm^3 of O_2 per hour per mg of dry weight (less spicules). The corresponding figure for the ectosome was 0.081 mm^3/mg/hr. Choanocytes seem, therefore, to have a higher metabolic rate than other cells, a conclusion not unexpected in view of their flagellar activity and their role as principal sites of ingestion and digestion. These rates are low with respect to tissues of other invertebrates, however, which average 0.5 to 1.0 mm^3/mg (dry)/hr (POURBAIX, 1939).

HYMAN (1925) found that the O_2 consumption rate varied inversely with the size of the individual in the calcareous sponge *Sycon* and is greater in the upper half of the sponge than in the lower half.

The O_2 consumption also varies with the state of activity, as measured by the rate of water currents in the sponge. Table 3 shows several measurements of various sponges. They are not strictly comparable, as some are based on weight of dry organic matter, whereas others are fresh weights, including the nonmetabolizing spicules that may account for a significant proportion of the total weight.

Symbiotic, intracellular algae are probably a source of O_2 for many shallow-water sponges that possess them, both freshwater and marine. DE LAUBENFELS (1932) found that three species of marine demosponges have decreased O_2 consumption in sunlight as opposed to shade, and in one instance the amount of O_2 actually increased (see Table 3).

CHEMICAL COMPOSITION

Living sponges have a number of chemical characteristics that tend to emphasize their separateness from other branches of the animal kingdom. BERGMANN and his coworkers (BERGMANN & FEENEY, 1949, 1950; BERGMANN & MCTIGUE, 1949; BERGMANN & others, 1950; BERGMANN & MCALEER, 1951) have isolated a number of sterols from various sponges that either do not occur or occur but rarely in other animals. Neospongosterol and aaptostanol occur only in demosponges of the family Suberitidae (BERGMANN & others, 1950). Chondrillasterol and haliclonasterol occur elsewhere only in green algae (ALTMAN & DITTMER, 1964). Clionasterol and poriferasterol occur elsewhere only in molluscs (ALTMAN & DITTMER, 1964).

24-Methylenecholesterol occurs elsewhere only in molluscs and in the honeybee. All have 28 or 29 carbon atoms rather than the 27 found in most of the common sterols of animals. Most of the other known 28- or 29-carbon atom sterols have been recovered from plants.

Another peculiar feature of sponges is the high concentration of protein-bound halogens (iodine and bromine) present in spongin (in the form of 3, 5-diiodotyrosine and dibromotyrosine). Iodine may constitute as much as 10 percent or more of spongin (VINOGRADOV, 1953).

Sponge pigments are likewise unusual among animals in that carotenes tend to dominate over xanthophylls (NICOL, 1967). Individual sponges have revealed peculiarities of composition that may be of more general distribution in the phylum. The demosponge *Cryptotethya crypta* has yielded three unique nucleic acids: spongothymidine (2-D-arabofuranoside of thymine), spongouridine (2-d-arabofuranoside of uracil) and spongosine (2-D-ribofuranoside of 2-methoxyadenine) (STEMPIEN, 1960). The demosponge *Microciona prolifera* yields a substance or substances extractable with organic solvents and as yet undetermined chemically (but named *ectyonin*) that has antibiotic properties against *Escherichia coli,* tuberculosis bacilli, *Pseudomonas pyocyanea, Staphylococcus aureus,* and *Candida albicans* (JAKOWSKA & NIGRELLI, 1960).

The sterols studied by BERGMANN are of interest in revealing a pattern of distribution within the class Demospongea that is somewhat tied to taxonomic subdivisions erected on morphologic grounds. Clionasterol and poriferasterol have been obtained only from

TABLE 3. Respiratory rates of sponges (new).

SPECIES	RATE	SOURCE
Tethya lyncurium		Pourbaix, 1939
choanosome	0.237mm^3 O_2/hr/mg dry wt. (less spicules)	
ectosome	0.081 mm^3/hr/mg dry wt. (less spicules)	
Iotrochota birotulata		de Laubenfels, 1932b
in shade	0.154 cm^3 O_2/hr/cm^3 sponge (wet incl. spicules)	
in sun	0.067 units as above	
Haliclona rubens		de Laubenfels, 1932b
in shade	0.150 units as above	
in sun	0.055 units as above	
Haliclona longleyi		de Laubenfels, 1932b
in shade	0.053 units as above	
in sun	0.002 units as above (produced by the sponge)	
Grantia compressa	0.05 ml O_2/hr/gm (wet wt.) incl. spicules) at 21°–23° C in an individual weighing about 0.15 gm	Hyman, 1925
Sycon sp.	0.04–0.16 cm^3 O_2/hr/gm (wet wt. incl. spicules) varying inversely with size of sponge	Hyman, 1925
Suberites sp. *Aplysina* sp.	0.0117 ml O_2/hr/gm (wet wt. incl. spicules) at 20°–22° C in 20–25 gm individuals	van Budden-Brock, 1939
Suberites massa	0.34 ml O_2/hr/gm (dry wt. less spicules) at 22° C	Putter, 1914
Mycale sp.	0.126 ml O_2/hr/gm (wet wt.)	Reiswig, 1974
Verongia gigantea	0.1004 ml O_2/hr/gm (wet wt.)	Reiswig, 1974
Tethya crypta	0.0329 ml O_2/hr/gm (wet wt.)	Reiswig, 1974

species belonging to the Sigmatosclerophora, Clavulina, and Epipolasida (*vis., Spongilla,* 1 sp.; *Haliclona,* 3 spp.; *Callyspongia,* 1 sp.; *Tedania,* 1 sp.; *Spheciospongia,* 2 spp.; *Anthosigmella,* 1 sp.; *Cliona,* 2 spp.; and *Cryptotethya,* 1 sp.). Cholesterol is confined to the Sigmatosclerophora (*Haliclona,* 2 spp.; *Microciona,* 1 sp.; and *Halichondria,* 2 spp.), as is haliclonasterol (*Haliclona longleyi*) (BERGMANN & MCTIGUE, 1949; BERGMANN & others, 1950; BERGMANN & FEENEY, 1950).

The Suberitidae are the only sponges to have yielded neospongosterol (*Suberites,* 3 spp.) and aaptostanol (*Aaptos* sp., *Radiella sol, Weberella bursa, Polymastia infrapilosa*) and share cholestanol with the Sigmatosclerophora (suberitids: *Suberites,* 3 spp.; *Terpios,* 2 spp.; *Aaptos,* 1 sp.; *Weberella,* 1 sp.; *Polymastia,* 1 sp.; Sigmatosclerophora: *Microciona,* 1 sp.; *Halichondria,* 2 spp.; *Hymeniacidon,* 1 sp.) (BERGMANN & FEENEY, 1949; BERGMANN & others, 1950).

The homosclerophoran *Chondrilla nucula* is the only sponge to yield chondrillasterol. The sigmatosclerophoran *Haliclona oculata* and the spirosclerophoran *Craniella crania*

are the only sponges to have yielded 24-methylenecholesterol (chalinasterol or ostreasterol) (Bergmann & Feeney, 1949; Altman & Dittmer, 1964).

All the Keratosa (8 spp.), Axinellida (2 spp.), Euasterophora (1 sp.), Hexactinellida (1 sp.), and Calcarea (1 sp). studied by Bergmann, as well as five species of Sigmatosclerophora and two of Epipolasida, have yielded as yet only poorly defined sterols that are not clearly any of the foregoing.

It is probably too early to draw phylogenetic conclusions from the promising study of the distribution of sterols, but in a preliminary way a relationship of the monaxonid groups Sigmatosclerophora, Clavulina, and Epipolasida is suggested through the common occurrence of clionasterol-poriferasterol, as well as their separation from the monaxonid family Suberitidae, which uniquely possesses aaptostanol-neospongosterol and lacks clionasterol-poriferasterol. Since the remaining groups of demosponges are set off from the foregoing only by the fact that their sterols have not been clearly determined, however, some sterols may turn out to have a wider distribution. Also, needless to say, we do not yet know to what extent sterol chemistry is a conservative character.

Other noteworthy substances that occur in sponges include unusually large amounts of histamine (100 mg/kg) in the tissues of the demosponge *Geodia gigas* (Duner & Pernow, 1963), and true chitin in the walls of gemmules of freshwater spongillids (Jeuniaux, 1963).

The skeletal material of the sponges varies somewhat compositionally from taxon to taxon. Few analyses of scleroprotein spongin, which is confined to the class Demospongea are available. One analysis (Saper & White, 1958) of the keratose sponge *Hippospongia equina* revealed the following amino acids: alanine, Y-aminobutyric acid, arginine, aspartic acid, cystine, glutamic acid, glycine, histidine, hydroxyproline, leucin-isoleucine, lysine, ornithine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, 3,5-diiodotyrosine (plus 3-monoiodotyrosine considered an artifact of breakdown), and valine. Low (1951) found in *Spongia officinalis obliqua* the additional amino acids: Y-aminobutyric acid, dibromotyrosine, and methionine. Elemental analyses of spongin of Keratosa must be interpreted with caution, for foreign particles are frequently incorporated into the spongin fibers.

Silica of siliceous spicules of the classes Demosponges and Hexactinellida is hydrated. The proportion of water is variable from one species to another; demosponge silica is less hydrated than that of the hexactinellids (5.97 to 7.34% and 7.16 to 13.18% respectively) (Vinogradov, 1953). Variability within a single spicule was reported by Vosmaer and Wijsman (1904) in the demosponge *Tethya aurantia.* They observed that the axial portion was more soluble in HF than the peripheral part, probably because of a greater degree of hydration of the axial part (this may account for the enlarged axial canal in many fossil spicules). A possible instance of an actual gel phase of silicic acid may obtain in the peculiar saclike bodies of gel in the aberrant demosponge *Collosclerophora arenacea* Dendy, 1917. At the other extreme, Vernadsky (1934) reported birefringence, and therefore a crystalline state, in some hexactinellid spicules, although this has not been confirmed by later investigators. Small amounts of alkali and alkaline earth elements may be present in siliceous spicules, greater in demosponges than in hexactinellids (Vinogradov, 1953).

Calcareous spicules of the Calcarea are composed of magnesian calcite. The proportion of magnesium varies from about 4 percent to 14 percent (Vinogradov, 1953). Strontium and traces of lithium (0.005%) have been reported (Fox & Ramage, 1931) from *Clathrina.* The very peculiar sponges *Astrosclera willeyana* and the probably closely related *Ceratoporella nicholsonii* have massive exoskeletons of aragonite in the form of closely packed spheroids. The soft parts contain siliceous acanthostyles and are

TABLE 4. Life span of sponges (new).

SPECIES	LIFE SPAN	REFERENCE
Demospongea		
Hippospongia sp.	50 years	Altman & Dittmer, 1962
Dysidea spinifera	2–3 years (aquarium)	Arndt, 1941
Adocia "alba"	1.5 years (aquarium)	Arndt, 1941
Gellius angulatus	2 years (aquarium)	Arndt, 1941
Suberites carnosus	1.83 years (aquarium)	Arndt, 1941
Axinella sp.	4 years	Altman & Dittmer, 1962
Hymeniacidon perlevis	1.5 years, at least	Burton, 1948
Halichondria panicea	1.5 years, at least	Burton, 1948
Pachymatisma johnstoni	1.5 years, at least	Burton, 1948
Calcarea		
Grantia capillosa	3 months	Altman & Dittmer, 1962

anatomically demosponge-like. The calcareous skeleton in its gross morphology is like that of the calcitic pharetrone Calcarea (VACELET, 1965), as well as like that of the extinct Stromatoporoidea (HARTMAN & GOREAU, 1966).

Despite the wide variety of substances produced by sponges, the quantity of DNA in sponge nuclei is considerably less than that in more complex animals. Sponges give values of about 0.1 picograms per cell, bacteria (*E. coli*) about 0.01, coelenterates about 0.3, and mammals about 3.0 (RENDEL, 1965).

LIFE SPAN

The natural life span of a sponge varies from less than a year for forms that live in freshwater that freezes over during the winter and for small marine forms to more than 50 years for a large, marine, keratose sponge. Some observed life spans are given in the table above (Table 4).

An attempt has been made (FINKS, 1955) to determine the longevity of a Permian sphinctozoan calcisponge (*Guadalupia*). Two generations of empty brachiopod valves grew on the sponge, one valve overgrowing the other after its death, and the sponge overgrew both. Thus the sponge was older than two successive brachiopod lifetimes. This was estimated as a minimum of two years if the brachiopods had a limited annual breeding season, although that assumption is open to question.

FUNCTIONAL MORPHOLOGY AND ADAPTATION

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INTRODUCTION

To the extent that fossilizable structures of sponges can be linked to specific modes of functioning of the organism, they can be used to identify the paleoenvironment and to interpret sponge evolution in terms of the natural selection of particular functions. The principal functional requirements of sponges include 1. hydraulic efficiency of the water system; 2. maximization of surface area in contact with the ambient water to permit gas exchange; 3. mechanical support of the tissues; 4. stabilization of the organism against displacement; and 5. protection against predation.

These requirements must be reconciled with each other as well as with environmental conditions. Moreover, these needs must be reconciled with the growth (i.e., volume increase) of the individual in the course of its lifetime. Many of these adaptations are reflected, directly or indirectly, in the preservable skeletal structure of the sponge.

HYDRAULIC SYSTEM

The central activity of the sponge is related to production of its water current, which brings food and oxygen to the sponge and removes metabolic wastes. Thus hydraulic efficiency of the water system is of prime importance. Fundamental needs of the system have been discussed in the chapter on Physiology (see p. 201).

The external form of a sponge, a readily observable feature of fossils, is related to aspects of the hydraulic function. BIDDER (1923) has analyzed this. The dispersion of metabolic wastes and depleted water from the immediate vicinity of the sponge in all but the most agitated water requires the separation of effluent water from intake and maximization of the distance traveled by effluent before any of it can be recirculated into the sponge. Diameter of the returning eddy was termed the diameter of supply by BIDDER. Length of the effluent jet is increased by concentrating its flow through one or a few large oscules, which reduces the energy loss due to friction with surrounding water for a given volume of effluent. The maximum angle between the effluent stream and the inflowing streams of water was termed the angle of supply by BIDDER. For a sponge resting on the sea floor with an oscule located on the upper surface, the angle of supply is 90°. It may be increased beyond 90° by elevating the sponge on a stalk so that water may be drawn from below the sponge. In such cases the efficiency of separation of inflow from exhaust may be enough to reduce the need for an osculum, and the sponge may open out into a cup, the interior of the cup being homologous with the cloaca.

Another method of separation is development of a **flabellate** form in which one side, homologous with the cloacal lining, contains all the exhalant pores and the opposite side all the inhalant pores. For such a structure the angle of supply would be 180°. These examples of BIDDER do not exhaust the possibilities of sponge shape. Massive and encrusting forms with multiple oscules may be regarded as a series of closely spaced hydraulic systems with a common 90° angle of supply. The more spread out such a sponge is or the more individual sponges are crowded together, the more important is it for the effluent jet to be projected for a greater distance under given wave-energy conditions. One expects such sponges to have greater development of oscular chimneys, for example, in quiet water. The common cylindrical sponge shape may be regarded as approaching the advantages of a stalked form in having a wide angle of supply.

Some forms of sponges seem to depart radically from the ideal system analyzed by BIDDER. Sponges that lack large oscules

entirely seem to be incapable of projecting the effluent water very far above the sponge surface and have a diameter of supply close to zero. Spheroidal sponges, on the other hand, in which the oscules are indifferently scattered over the surface and facing in all directions, seem to dispense entirely with any concern over angle of supply. The spherical Paleozoic hindiids, indeed, have no signs of attachment and may have rolled about freely on the sea floor. Some of these forms live or may have lived in agitated water that quickly dispersed the wastes.

It would be rash, therefore, to interpret paleoenergetics of ambient water from the form of fossil sponges. The crowded conditions in which sponges sometimes live, even in the deep sea below the photic zone where antipollutant ministrations of symbiotic algae cannot be invoked, suggest a certain tolerance to recirculation of used water.

In addition to separation of inflow and exhaust outside the sponge, functional efficiency of the hydraulic system requires maintenance of pressure relationships within the sponge. The inhalant canal system has lower water pressure than the exhalant system, owing to activity of the choanocytes and the directional effect imposed by the larger diameter of the apopyles. Existence of this pressure differential can be demonstrated by distension of the oscular tube under exhalant pressure and by collapse of the dermal membrane onto the subdermal spaces of the inhalant system if its support is removed (Ankel, Wintermann-Kilian, & Kilian, 1955). Complete separation of inhalant and exhalant canal systems except through the flagellated chambers is required. Likewise, resistance to expansion on the part of the flagellated chamber walls, and to a lesser extent of the exhalant canal walls, is necessary to maintain pressure in the system, as is resistance to collapse on the part of inhalant canals.

Smaller flagellated chambers resist expansion better than larger ones (see chapter on Physiology, p. 201), which provides one of the adaptive reasons for evolution of the leuconoid canal system (for another see below). The skeleton appears to play a principal role in keeping the inhalant canals open, at least in the case of large subdermal spaces (Ankel, Wintermann-Kilian, & Kilian, 1955). The **mesoglea** may play a role in holding smaller inhalant canals open. Pressure relations have not been studied in Hexactinellida in the laboratory, but from the relative openness of the entire canal system they are assumed to have a lower pressure differential than other classes and consequently to filter at a lower rate. Absence of mesoglea with its possible supportive function for the canal walls may be related to the presumed lower pressures.

A third aspect of hydraulic efficiency that may have affected evolution of the canal systems is reduction of internal friction through centralization. Development of relatively few large oscules and a leuconoid canal system, as pointed out by Bidder (1923), by increasing the volume of an individual **efferent** jet reduces friction per unit volume with the external water. Even when a cloaca with a single osculum is not developed, efferent channels tend to be collected into a few exhalant openings. Development of **chones** or large subdermal spaces in the inhalant system may also be related to reduction of friction and in some sponges, at least, appears to be functionally connected with development of a centralized exhalant system. In *Ephydatia fluviatilis* Linné, 1759, grown on microscope slides, a single osculum normally serves the entire set of flagellated chambers of the small sponge, and a single subdermal space communicates almost directly with prosopyles of the flagellated chambers. If the sponge is grown in silica-free water, spicules that normally support the dermal layer above the subdermal space do not develop. The subdermal space collapses, and each flagellated chamber draws its water only through the dermal pores immediately adjacent to it. The single large osculum does not develop under such circumstances, but instead many small oscules grow, each serving only a few flagellated chambers (Ankel, Wintermann-

KILIAN, & KILIAN, 1955). The apparent restriction on free inflow leads to a corresponding reduction in outflow. Incidentally, this illustrates the fact that the number of oscules is determined by purely functional considerations. Therefore, the concept that each oscule represents a so-called sponge individual, as suggested by HYMAN (1940) and followed by many authors, seems to be misleading.

SURFACE AREA

An important functional consideration in sponges and one that affects gross morphology and external shape is the lack of a circulatory system for internal transport of metabolites. The ability of most individual cells to ingest and digest food renders such a system less necessary than in higher animals, and the wandering amoebocytes serve as a primitive internal transport system. Nevertheless, gaseous metabolites involved in respiration and probably soluble metabolic wastes as well must be exchanged directly with the ambient medium by each cell.

It is the canal system, primarily, that brings the ambient water within reach of diffusion of each cell. Nevertheless, as narrow canals are increased in length, energy loss due to friction with the walls is increased and inefficiency of circulation results. These relationships set a size limit on sponges with a spheroidal or massive shape unless some means can be found to bring ambient water into the interior in the form of broad spaces. The **cavaedia** of demosponges and the various **rhyses** of hexactinellids represent such tunnels through the sponge body. A possible effect of the absence of such large spaces leading to the interior of a massive sponge occurs in the Paleozoic spherical hindiids. A central hollow space filled with loose spicules may develop in larger individuals, although not in small ones, and possibly represents a moribund area due to lack of oxygen.

Another way of solving this problem lies in development of shapes that inherently have a greater surface area per unit volume. Such forms include **clathrate** cylinders, open cups, plicate cups, expanded sheets, either stalked or encrusted forms, and various branching straplike forms. All these forms represent various ways of bending or subdividing a thin sheet, in which one side of the sheet bears the inhalant openings and the other side the exhalant ones.

The form taken by a particular sponge results from reconciliation of many functional needs and is also determined by growth possibilities of its skeletal system. A very broad expanded sheet held above the sea bottom on a stalk fulfills the requirement for maximum contact of each cell with the seawater. Such a form, however, is impossible to support without a relatively rigid spicular skeleton. Given such a skeleton it would be still more disadvantageous if the species lived in rough water. Growth would be limited in even the most quiet water by the weight that the stalk could support.

Deep-sea sponges often have elaborate lateral outgrowths of the body, particularly in stalked forms. This growth form is permitted not only by the quietness of the water but also has probably a functional advantage in enabling the sponge to draw food from as large a volume of water as possible.

Some sponges have a very limited repertory of shapes. Others have a great range of potentialities. It is the latter that may be useful in interpreting paleoenvironment, for the shape represents a response to the environment rather than reflecting genetic limitations. An example of a very plastic genus, the Permian sphinctozoan calcisponge *Guadalupia,* is shown in Figure 79.

A possible example of the inherent limitations imposed on shape by growth possibilities of its skeletal system is the group of hindiids referred to earlier. Their tripodal spicules are of such form that they can be put together most efficiently as concentric shells or layers of hexagonally packed spicules. The whole sponge, thus, is commonly limited to spherical or hemispherical shapes, although other shapes have developed in some members of the family (RIGBY & WEBBY, 1988).

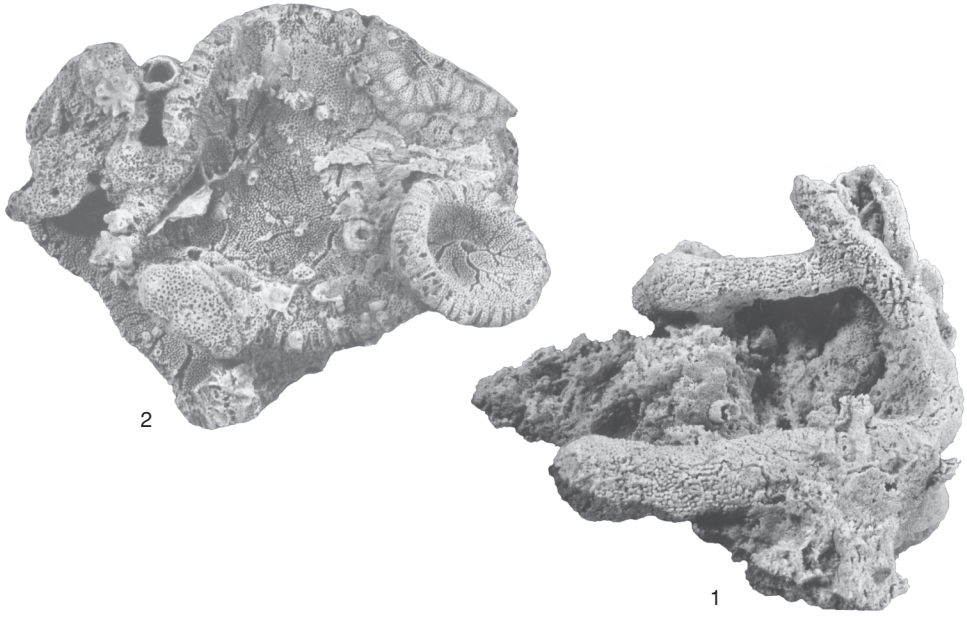

FIG. 79. *Guadalupia zitteliana* GIRTY, 1908; *1,* aberrant, irregularly branched form of species, AMNH 44652, ×1; *2,* characteristic, irregular to regular, bowl-shaped specimens demonstrating plasticity in form of species, USNM 133160, Cherry Canyon Formation, Guadalupe Mountains, Texas, USA, ×1 (new).

MECHANICAL SUPPORT

The supportive function of sponge structures is carried out by the following materials, either alone or in combination: 1. mesoglea; 2. collagen fibers; 3. spongin fibers; 4. foreign particles (sand grains, etc.); 5. spicules; 6. massive mineral deposits; and 7. chitin. Fixed structures thus maintained include the canal system, other internal spaces (parietal gaps, cavaedia, rhyses), the dermal membrane with its **porocytes,** specialized protective cortexes, stalks, branches and other lateral expansions, various forms of attachment and stabilization structures, and reproductive bodies (gemmules).

Smaller canals and flagellated chambers are supported in part by mesoglea in the Demospongea and Calcarea. In the Hexactinellida, where no mesoglea is present, the viscosity of the protoplasm apparently maintains the syncytial network of cells in position. Larger canals of the hydraulic system, as well as other spaces within the sponge, such as parietal gaps, cavaedia, and the cloaca are outlined by the spicular network or the network of spongin.

The dermal membrane may be supported above a subdermal space by spicules arranged at high angles to the membrane in the manner of tent poles. If the subdermal space is part of the inhalant system, the dermal membrane may collapse if the spicular supports are removed (ANKEL, WINTERMANN-KILIAN, & KILIAN, 1955). The dermal membrane is frequently stiffened by spicules, with some or all of their rays in the plane of the membrane. In sponges with a rigid principal skeleton, spicules of the dermal membrane are frequently not attached to the main skeleton.

External **cortexes** are often stiffened by dense concentrations of spicules and sometimes microscleres. *Geodia* has a cortex packed with sterrasters; *Cladorhiza* and *Asbestopluma* have a surface layer of chelae;

and *Desmatiderma* has one of monocrepid desmoids. In each of these cases, maintenance of characteristic form of the sponge body as a whole is due largely to the stiff outer layer, which has a supportive function as well as, probably, a protective one.

In most sponges, however, the skeleton may be regarded as performing two separate and to some extent contrasting functions: one, the provision of an open, three-dimensional scaffolding for the hydraulic system and the other, support of an outer protective and regulatory surface membrane. Because mechanical requirements are somewhat different, the two functions are often performed by different and physically separate skeletal systems, differences reflected in the forms of spicules. Those of the dermal layer have often most of their rays in one plane and are less commonly fused together. Spicules of the interior mesh tend to have several rays equally developed in different planes and are more likely to be fused together or interconnected with spongin. Monaxonic spicules may function in either situation, in the dermal layer being oriented in the plane of the membrane as stiffeners or perpendicular to it as supports and in the interior mesh being organized into strands, either singly or in bundles.

The two functions tend to converge in thin-walled asconoid sponges, such as small Calcarea, embryonic Hexactinellida, and probably some adult Paleozoic hexactinellids and heteractinids (*Eiffelia*). In such sponges a three-dimensional mesh is unnecessary to support the hydraulic system, and the spicules are planar types (triradiates, stauractines, sexiradiates).

In general, when the main interior supporting skeleton develops rigidity through interlocking or fusion of spicules, the organization is uniform throughout. In some late Paleozoic hexactinellids (*Stioderma, Docoderma*), however, the major burden of mechanical support through spicular fusion is assumed by the large, outermost spicules, probably homologous with the hypodermal spicules of the Lyssacinosa. Remaining spicules of the principal skeleton are unfused.

Gemmules of freshwater spongillids are strengthened and protected by an outer layer of specialized spicules along with chitin, apparently the only occurrence of this substance in the phylum.

PROTECTION

Protection against predation and mechanical injury due to external agents is difficult to separate from adaptations for general mechanical support, so far as morphological manifestations go. Cortical specializations mentioned above, as well as the general development of specialized dermal and hypodermal spicule types, not only support the outer layer of the sponge but also offer mechanical protection to the sponge as a whole. Nevertheless, we recognize spicule arrangements involving protrusion of sharp-pointed rays from the sponge surface, a possible specific adaptation for discouragement of predation or of settling of larvae of sessile organisms. Such arrangements may involve simple monaxons or more elaborate dermal spicules, such as pinules and scopules of some hexactinellids. Such defensive adaptations, if that is what they are, can be traced back into the early Paleozoic: pinulelike spicules occur in Mississippian dictyosponges, protruding rhabdodiactines in the Ordovician lyssacine *Cyathophycus,* hispid tufts of sharp-ended styles in the Ordovician demosponge *Saccospongia,* and oxeas in the Middle Cambrian *Hazelia.*

Some living sponges are irritating to the human skin (e.g., *Fibulia uolitaupere, Tedania ignis*), although the chemical substance responsible has not been identified. It is possible that the prevailing bright colors of many sponges (including *Tedania*) are warning colors to potential predators. Paleobiochemical methods may permit the recognition of pigment substances associated with sponge fossils, such as carotenes and malignance, although so far no such studies have been reported.

The boring habit of the clavuline demosponge *Cliona* and its relatives may be considered an adaptation for protection. Borings resembling those of *Cliona* occur in the geologic record back to the Cambrian.

An antibacterial and antifungal substance produced by *Microciona* (JAKOWSKA & NIGRELLI, 1960) may protect the sponge from infection.

ADAPTATIONS TO ROUGH OR QUIET WATER

Unfortunately, little can be said with any certainty on this subject, which is potentially very useful for environmental reconstruction. By analogy with experiments on scleractinian corals (see VAUGHAN & WELLS, 1943) one might expect encrusting forms to be characteristic of very rough water and more delicately branching forms of quiet water. To be sure, sponges growing in the surf zone are frequently encrusting forms, but the encrusting habit is found in waters below 366 m (200 fathoms), and one would be rash to use such forms as indicators of rough-water environments.

Nevertheless BURTON (1928) pointed out that in the species *Halichondria panicea,* forms from the surf zone are encrusting or irregular in shape, while those from deeper and quieter water are more symmetrical, being either cylindrical or spherical. He also noted that deep-water sponges tend toward greater symmetry as a general rule.

Another way in which a sponge may become modified in rough water is to allow for freer movement of the water through and around it. For example, BURTON (1928) cited WHITELEGGE's observations (1901) on Australian *Pachychalina communis,* which in quiet but shallow water has a flabellate or lamellose form, whereas in rougher water it assumes a digitate form.

In general, one is struck by the prevalence of forms with long, delicate branches (*Asbestopluma, Cladorhiza, Chondrocladia, Desmatiderma*) or long stalks (*Hyalonema, Stylocordyla*) among sponges from bathyal or abyssal depths. It is tempting to see in such shapes, when occurring among fossils, an indication of quiet, although not necessarily deep water. *A priori* one might expect that forms with slender bases and top-heavy shapes, such as the mushroomlike *Coeloptychium,* would indicate quiet water, as would such delicate, thin-walled, nonrigid sponges as many Paleozoic reticulosids.

Strong forms on the other hand, although capable of surviving in rough water, need not be confined to it. The Permian *Stioderma,* which has a rather rigid and heavy skeleton, is almost the only Permian lyssacine to occur in shell-bank deposits, yet it is also found in adjacent deep-basin deposits (FINKS, 1960). Those, however, may be transported occurrences.

As a preliminary test of the relationship between sponge form and water agitation, FINKS plotted the bathymetric frequency distribution of sponges by shape (Fig. 80), as reported in a broad faunal study (BURTON, 1956). One may assume that mechanical considerations would be largely operative in matters of sponge shape and that, therefore, of all the parameters that vary with depth, that of water agitation will be the only one to affect sponge shape strongly since, in a general way water agitation decreases with increasing depth.

It is apparent that there is some difference in the distribution of the different shapes. Two types, *cylindrical* and *spheroidal,* appear to be distinctly deeper-water forms than the others, not occurring shallower than 55 m (30 fathoms). The spheroidal forms have a distinct peak of abundance around 91 m (50 fathoms). The spheroidal forms have a distinct peak of abundance around 91 m (50 fathoms), and cylindrical forms are less clearly concentrated at a particular depth, but share the same overall range of 55 to 165 m (30–90 fathoms). Massive forms, on the other hand, appear to be limited to shallower water, do not occur below 91 m (50 fathoms), have a distinct peak at 55 m (30 fathoms) and range up into depths of only 27 m (15 fathoms), the shallowest depth collected. Other form categories occurring at shallow

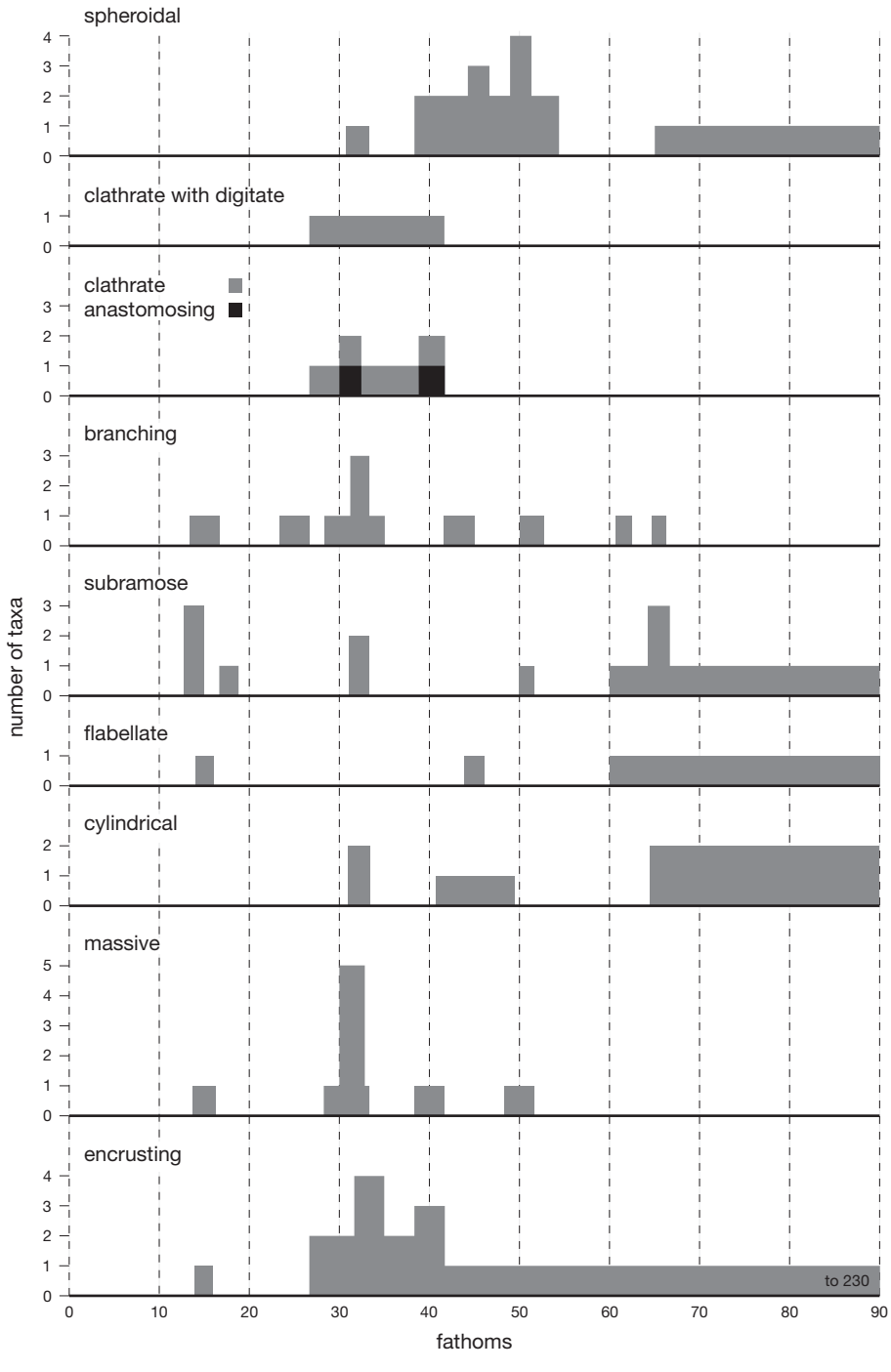

FIG. 80. Bathymetric distribution of sponges by shape, as reported in broad faunal study of sponges of West Africa by Burton (1956) (new).

depths have a wider range: branching forms and flabellate forms both range down to 165 m (90 fathoms), the former with a distinct peak at 55 m (30 fathoms). Encrusting forms have the widest range of all, extending from shallow water down to the deepest sample, from 428 m (234 fathoms). Clathrate-anastomosing forms have the most restricted range, occurring between about 55 to 73 m (30–40 fathoms).

The results tend to confirm the hypothesis that symmetrical shapes are characteristic of quiet water and do not develop in agitated water. The results also indicate that both branching and encrusting forms are indifferent to the degree of water agitation.

ADAPTATIONS TO SUSPENDED SEDIMENT

Another potentially useful indicator of paleoenvironmental conditions is morphological adaptations of sponges to excessive suspended mineral matter in the water. That such suspended matter is likely to be harmful to sponges by way of clogging their pores seems to be a safe assumption, yet observations by DE LAUBENFELS (1953a) and WIEDENMAYER (1977a) that some sponges appear to survive while growing partially buried in the mud, make even this somewhat doubtful. Nevertheless, a heavy accumulation of sediment on the upper surface of a sponge seems to be harmful, and sponges with broad horizontal expansions, such as open cups or mushroom-shaped forms, probably did not live in turbid waters.

Long stalks of deep-sea forms may represent an adaptation to elevating the sponge above an oozy bottom, from which quantities of fine, suspended matter are likely to be raised by passing vagrant benthos. Very long-stalked fossil forms may have lived under similar conditions, although one must be careful to discriminate between a root tuft buried in mud and a stalk raised above it.

STABILIZATION

One of the most obvious morphologic adaptations of most sponges is the provision for maintenance of position on the substrate. This includes keeping the sponge from becoming buried in the substrate, if the substrate happens to be soft sediment, as well as maintaining exhalant openings in a constant position, generally facing away from the substrate.

Stabilization of position may be achieved in a variety of ways. One of the simplest is development of a broad base, without other means of attachment. Such a shape not only resists overturning but also reduces the possibility of sinking into the sediment by distributing the weight over a wide area. Examples include the Permian hexactinellid *Pileolites,* which grew in flat-bottomed, cake-shaped forms, and the Ordovician hexactinellid *Brachiospongia,* whose flat base is expanded radially in lobate extensions. The lobes of *Brachiospongia* extend downward as well as outward (Fig. 81), apparently raising the main body of the sponge above the sea floor. In both these forms oscules are located opposite the base.

Encrusting forms may be considered the ultimate development of this type of stabilization, in which lateral extension is many times greater than vertical. The Cambrian hexactinellid *Multivasculatus* seems to be a form with more or less indefinite and irregular lateral extension over the sediment, with evenly spaced, low cups developed on the upper surface. More typical encrusting forms, such as many living monaxonid demosponges, are extremely thin sheets that grow on solid objects.

Boring sponges that excavate galleries in shells, corals, and limestone undoubtedly have the most intimate and fixed contact with the substrate. Many, perhaps all, species of *Cliona* and other boring sponges grow ultimately above the riddled substrate, the embedded parts of the sponge serving as a means of attachment.

Physical adherence of sponge skeletal material to the substrate is a means of stabilization in many forms. Encrusting shapes are often so attached, but so are more narrowly based forms, such as those with stalked or

FIG. 81. Two associated specimens of *Brachiospongia digitata* (OWEN) showing lobate margins of sponge that apparently raised sponge above sea floor; *1,* from the side, and *2,* from above, FMNH 10851, Trenton, Frankfort, Kentucky, USA, ×0.5 (new).

obconical shapes. This type of attachment is common in pharetronid calcisponges, where massive deposits of calcium carbonate form an important part of the skeleton (*Stellispongia*). It is also present in many siliceous sponges, in which secondary deposits of silica in the outermost layer of the skeleton make direct contact with the substrate. Such attachment requires a solid substrate, most often the shells of other organisms.

In narrowly based, stalked, obconical, or cylindrical sponges that have direct contact with the substrate, a basal encrusting expansion (the hexactinellid *Myliusia,* the heteractinid *Wewokella,* or the pharetrone *Eusiphonella*) or branching, rootlike extensions of the sponge body (the lithistid *Siphonia,* or the hexactinellids, *Coscinopora, Camerospongia,* and *Verruculina*) may be developed. Such bases both resist overturning and distribute the weight so as to minimize sinking into the bottom. In this way stability may be achieved while enjoying the advantages of a wider angle of supply or a greater elevation above a muddy bottom than is possible with a broad-based body

resting directly on the substrate. A related adaptation is seen in the hexactinellid *Becksia,* in which many slender, stiltlike processes raise the main body of the sponge above the substrate.

Many siliceous sponges have developed a root tuft of long spicules. These tufts commonly both anchor the sponge in a soft bottom and raise it above the sediment. The tufts take many forms. In the spheroidal demosponge *Radiella sol* an equatorial fringe prevents overturning. In the related *Radiella tissieri* tuft spicules are distributed over the entire lower hemisphere and fix the sponge to the bottom (VACELET, 1961). In *Tetilla grandis* the root spicules form a cushionlike mat beneath the sponge and appear to function both as a fixing device and as ballast to prevent overturning because it is probably more dense than the main body of the sponge. In *Thenea wyvilli* a similar cushionlike mat is surmounted by several stalklike tufts that hold the sponge body well above the sea floor (BURTON, 1928); here fixing, ballasting, and supporting functions seem to be combined. In the long, single root tufts of the hexactinellid *Hyalonema,* the sponge is elevated well above the sea floor, as demonstrated both by bottom photographs and by the occurrence of symbiotic anemones covering much of its length. Here the uplifting function is emphasized at some expense to stability, a situation probably permitted by quietness of the deep sea environment where these sponges live.

In Paleozoic demosponges of the order Orchocladina, the upper hemispherical body of the sponge often overhangs a conical basal portion that is covered with a dense and nearly imperforate surface layer. That this basal portion may have been embedded in sediment and to some extent served as a stabilizing device is suggested by its reduction or absence where the sponge has grown upon and surrounded a shell or crinoid stem that presumably supported it above the bottom (FINKS, 1960).

Some sponges appear actually to grow within sediment to some extent. WIEDENMAYER (1977a) cited forms that are partly buried in mud, with circulation carried on in those parts that protrude above the sediment. A possible example from the Permian is presented by a species of the pharetronid *Virgola* recovered through acid-etching of a block of sediment (Fig. 82). The very irregular sponge has incorporated quantities of shells in its lower half, whose size and spacing are identical to shells in the immediately adjacent sediment. Such relationships indicate that the sponge ramified through the loose shell hash on the sea floor, at least partly below the sediment-water interface. A possible ballasting function performed by incorporation of a mass of mud in the base of the demosponge *Radiella tissieri* has been described by VACELET (1961).

Last we must call attention to those sponges that seem to dispense entirely with the maintenance of stability. BURTON (1932) has described several demosponges (species of *Tedania, Thenea, Cinachyra, Polymastia, Monosyringa, Disyringa*) that have no signs of attachment and which he believed may have hovered above the sea floor by virtue of a density close to that of sea water, being gently wafted about by currents. He noted that specimens of *Polymastia invaginata* incorporate a small pebble or shell in the base opposite the osculum and suggested that this pebble functioned as ballast, sufficient to keep the osculum directed upward but not heavy enough to anchor the sponge in one place. BURTON mentioned that pores on the subspherical *Cinachyra antarctica* are uniformly developed over the entire sponge surface, which one would not expect if part of it continually rested on the sea floor. He suggested that it rolled about freely. The same arguments surely apply to the spherical Paleozoic lithistids such as *Hindia, Scheiia, Caryospongia,* and *Carpospongia,* which also have pores equally developed on all sides and have no sign of attachment. These were certainly too dense to have floated, with their closely packed net of siliceous spicules, but they could well have rolled on the bottom. The similarly spheroidal *Astylospongia* raises

FIG. 82. Side view of *Cooperaria getawayensis* FINKS and associated, skeletal debris exposed by etching, that suggests sponge may have lived partly buried in substrate and ramified through adjacent debris during growth, AMNH 44654, Getaway Limestone Member, Cherry Canyon Formation, Guadalupe Mountains, Texas, USA, ×1 (new).

an unsolved problem. It has no sign of attachment but it has a well-differentiated area of exhalant pores at one end, such that it could not have been a matter of functional indifference if the sponge was turned upside down. One cannot easily invoke differences in ambient wave energy, for *Astylospongia* appears to occur together with *Caryospongia* and *Carpospongia.*

MODES OF GROWTH

Sponges must reconcile the needs for a supportive and protective skeletal system with the needs of growth. Where spicules are not attached to one another they can and do change their relative positions and thereby permit internal expansion and rearrangement in connection with growth. In many hexactinellids, especially Paleozoic forms, spicules appear to pull apart from one another and increase in size as the sponge body expands. New spicules of smaller size are intercalated between them. In this manner, size may increase proportionally in all parts, including interspicular spaces, parietal gaps, and canals.

Where spicules are held together by spongin, as in most demosponges, the resulting net has a fibrous structure, with only limited capabilities for internal expansion. Enlargement of the sponge body requires lengthening of preexisting fibers, or the laying down of new fibers more or less parallel to the old. Such a mode of growth may lead to a radial structure: either symmetrical about a central point and producing a spherical or discoidal shape or radiating asymmetrically from an eccentric point or points and producing flabellate, cylindrical, or branching cylindrical shapes, with or without a central cloaca.

One of the persistent trends in all groups of sponges has been development of rigidly fused spicular skeletons. For obvious reasons, most fossil sponges are in this group. In some forms the state of rigidity is attained only after the sponge reaches advanced size, as in the Paleozoic hexactinellids *Docoderma* and *Stioderma,* in which only the dermal spicules

fused (FINKS, 1960). These forms appear to have grown by expansion of the entire body and intercalation of new spicules that were continually enlarged. Fusion of the dermal layer stopped the growth process.

Among hexactinosan and lychniscosan hexactinellids the skeleton is rigid from the beginning. Growth, thus, must proceed peripherally without expansion of the already formed parts. This may explain the frequent occurrence of tubular and sheetlike structures in these groups, often forming a body of considerable internal complexity.

Lithistid demosponges, likewise, are rigid from the outset. They seem to have grown in three ways. Some have tended to grow by adding shells parallel to the surface to produce a massive sponge (Hindiidae, Astylospongiidae, Chiastoclonellidae, Anthracosyconidae). Others have tended to produce radial rows of spicules that were added to at the upper or outer end to form more or less expanded cups (Anthaspidellidae). A third group produced fiber tracts of more or less irregularity and anastomosis and grew peripherally in a variety of directions, permitting greater freedom of shape (Dystactospongiidae, Rhizomorina, most other Mesozoic and Cenozoic lithistids).

The pharetronid Calcarea developed more massive mineral deposits that sometimes exceed the spicules in volume if they do not completely substitute for them. Some forms (*Petrobiona*) have such a massive skeleton that the flesh is limited to a thin surface layer (VACELET, 1965). Most of the pharetronids have an irregular, fibrous skeleton that grows peripherally to form rather massive sponges.

VARIABILITY AND VARIATION

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INTRODUCTION

The phenomenon of variability is a central problem to be dealt with in practical recognition of species. In sponges, both living and fossil, limits of individual variation within a species are not well known. It is apparent from studies of both living and fossil collections, however, that sponges have a wider variability in external form among members of a local population of a species than more complex animals. In this they resemble plants; and, like plants, the repertory of shapes shown by a species, although relatively broad, is not unlimited and can be very useful for species recognition (BURTON, 1932, p. 376).

Sponges are peculiar in that most morphological features other than external form relate to small repetitive parts, such as spicules, pores, and canals. This introduces another aspect of variability, namely, variation within an individual organism. As with leaves of a tree, this variability is not unlimited and may characterize species [analogy courtesy of Dr. J. W. Wells of Cornell University, who introduced it during a discussion of coloniality in corals]. In sponges, however, this sort of variability has not been extensively investigated.

Study of variation is useful in another context in addition to discrimination of species. It can be used in reconstruction of ecological and environmental conditions, when the environmental factors that cause particular variations are known. Not only gross form but also the shape and dimensions of pores, pore clusters, and canals may be determined by local environmental conditions. Such local factors may operate not only between individuals but also within a single individual. Indeed, knowledge of intra-individual effects may be easier to come by and may aid us in interpreting variation between individuals. There are some kinds of variability, however, particularly the size and form of spicules, that cannot be related always to external conditions or functional needs.

Temporal variations within individuals may reflect seasonal changes in the environment; or cyclic changes in physiology, such as breeding periods; or unidirectional ontogenetic change. Among sponges with rigid skeletons, such as are most frequently found as fossils, these temporal changes may be preserved in the skeleton as intra-individual variation, but the same temporal changes will result in interindividual variation among individuals that die young, or for sponges that can reorganize their skeletons through resorption, discarding, and regrowth of skeletal elements.

SKELETAL TREATMENT

Statistical analysis has two important uses in taxonomic studies; one is descriptive

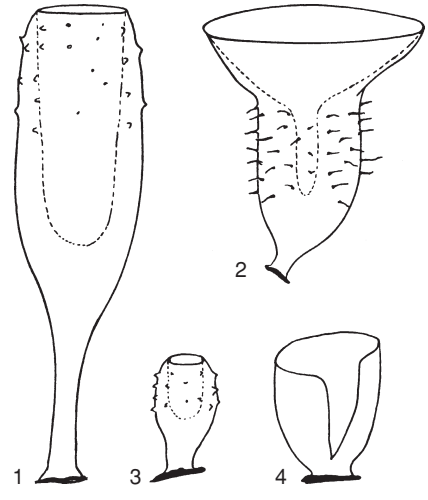

FIG. 83. Series showing external form in smaller specimens of *Haliclona bilamellata* BURTON; *1–4,* diagram; *dotted lines* indicate shape and position of cloaca (Burton, 1932; courtesy of Cambridge University Press).

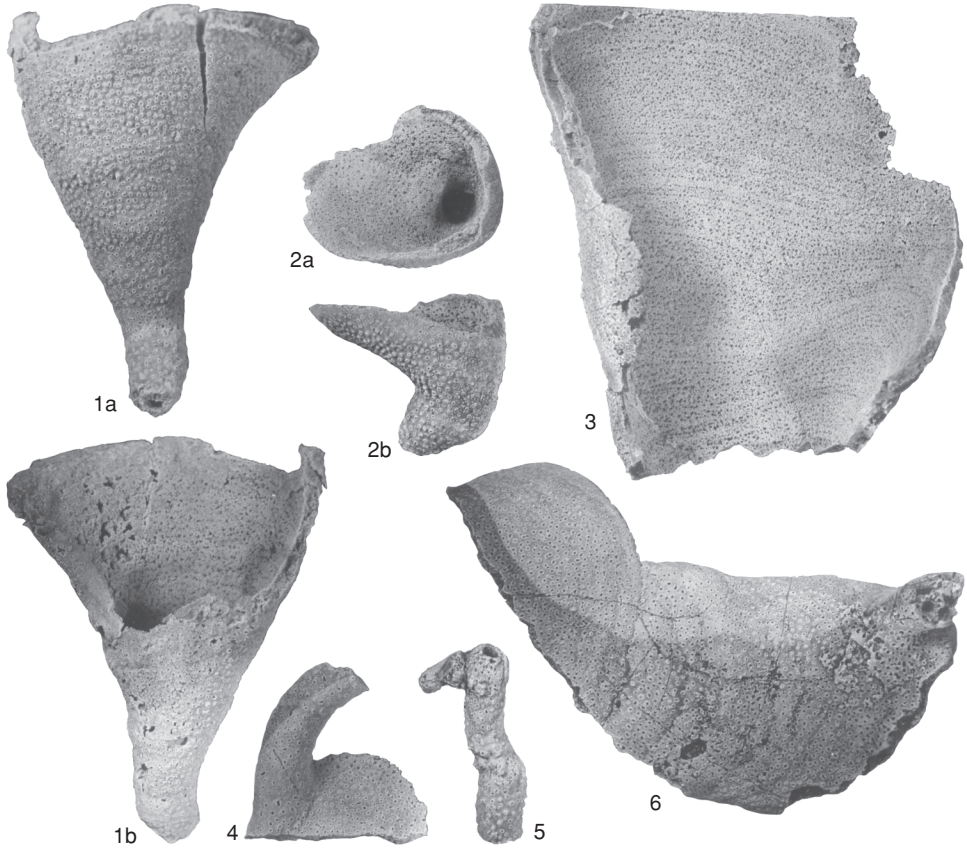

FIG. 84. Individual variation in external form in *Coelocladia spinosa* GIRTY among specimens from a single locality, Pennsylvanian Rock Hill Limestone, Bridgeport, Texas, USA; *1–2,* two views of single, funnel-shaped specimens with basal stalks and upper, thin walls; *3,* inner or gastral view of large, funnel-shaped fragment showing aligned pores; *4,* tubular branch growing from relatively flat, outer surface of wall; *5,* cylindrical specimen with osculum at top, with attached fragment of another individual, both of which are near basal parts of species; *6,* part of large frond with unbroken, upper surface, but broken left and right ends, sponge grew from left to right, ×0.7 (Finks, 1960).

characterization of a given population; the other is assessment of the probability that observed differences arise from sampling two different populations rather than a single one. The usual parametric methods of characterization of populations by the mean, the standard deviation, and so forth and the usual tests of significance of difference, such as chi-square of Student's *t,* involve the assumption that the frequencies in the population follow the normal or Gaussian distribution. FRY (1970) pointed out that characters most often measured on sponges, such as spicule sizes, are not normally distributed. Thus, nonparametric methods are to be preferred. FRY recommended the use of simple histograms for descriptions of size-frequency distributions and the comparison of these through nonparametric tests. He demonstrated the use of one such method, the Kolmogorov-Smirnov test, by analysis of the generated probability values to determine the degree of similarity between sponges from four different localities.

EXTERNAL FORM

It will suffice to point out some examples of the range of external shape to be found within a single species. The living

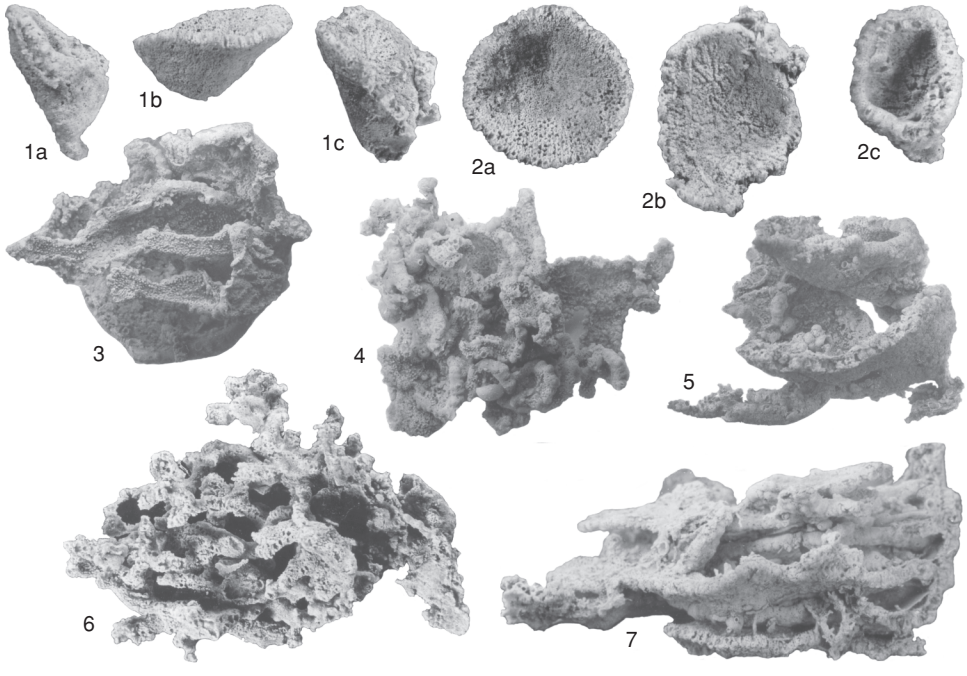

FIG. 85. Individual variation in external form in species of *Guadalupia* GIRTY from single locality, basal bioherms of Permian Road Canyon Formation, near Old Word Ranch House, Glass Mountains, Texas, USNM 703a; *1,* approximately ×0.67; *2–5,* ×1; *6,* ×0.77; *7,* approximately ×0.67 (new).

demosponge *Haliclona bilamellata* BURTON, 1932, is a stalked cylindrical form with a deep cloaca and external protuberances. Besides variation in proportionate length of the stalk, the upper end may be expanded to form a broad funnel or the sponge opened on one side in a nearly flabellate shape; likewise, the external protuberances may be reduced or absent (BURTON, 1932, p. 268, fig. 6; Fig. 83 herein).

Similar variability was reported by FINKS (1960) for the Pennsylvanian *Coelocladia*

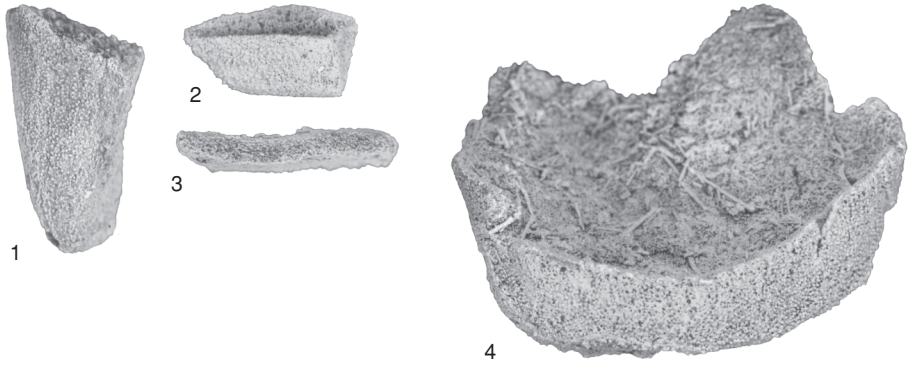

FIG. 86. Profile views of four individuals of *Pileolites baccatus* FINKS, 1960, from single block of limestone, showing individual variation; Permian Skinner Ranch Formation, Glass Mountains, Texas, USNM 707ha, ×2 (Finks, 1960).

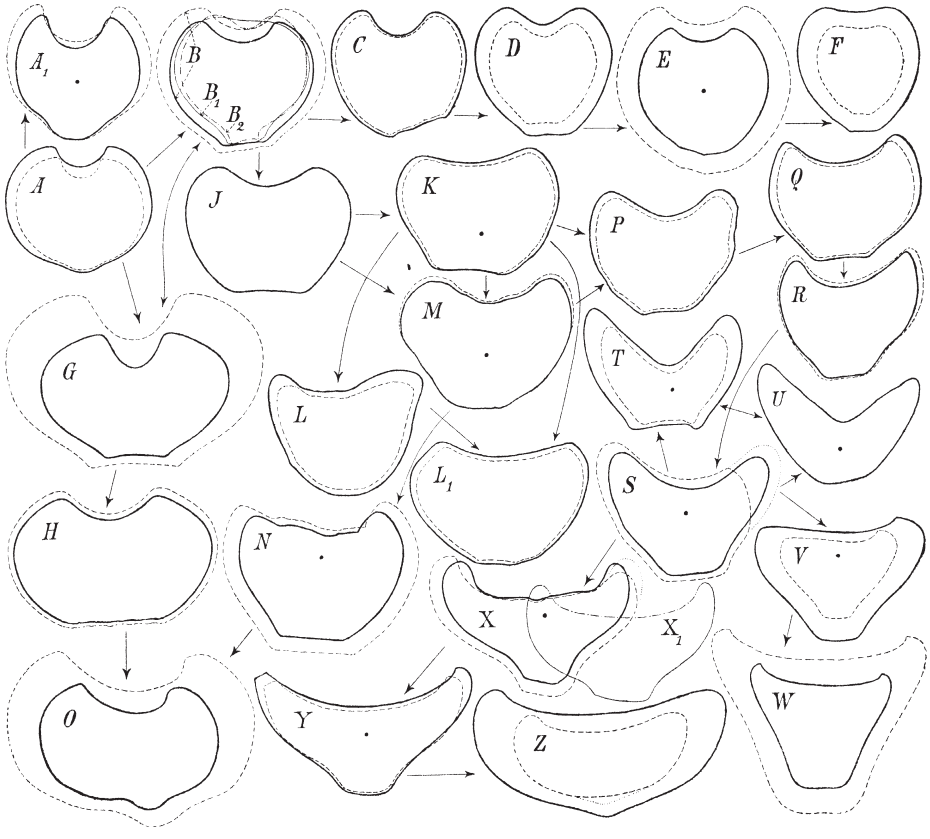

FIG. 87. Profiles of various growth forms of *Palaeomanon cratera* (ROEMER, 1848), middle Silurian (Niagaran), western Tennessee; *letters* indicate different subspecies; *arrows* indicate direction of change in morphology; *solid lines* indicate reduced size for comparison purposes; *dotted lines* indicate actual size (Rauff, 1893).

spinosa GIRTY, 1908, which varied at a single locality from simple small cylinders, through tall, narrow funnels, to broad, highly asymmetrical funnels that may be nearly laminar or tongue shaped (FINKS, 1960, pl. 5–6; Fig. 84 herein). A species of the Permian calcisponge *Guadalupia* GIRTY also varies at a single locality from circular open cups, through multitiered asymmetric cups, to similar forms with long, subparallel, tongue-like extensions on one side (Fig. 85). The Permian hexactinellid *Pileolites baccatus* FINKS, 1960, among specimens from a single block of limestone, varied from thimble-shaped, through wedge-shaped, to pancake-shaped forms (FINKS, 1960, pl. 50; Fig. 86 herein). RAUFF (1894, fig. 64, pl. 13,*1–5;* Fig. 87–88 herein) has recorded the range of form of the lithistid *Palaeomanon cratera* (ROEMER, 1848) from the middle Silurian of western Tennessee. This species has a limited range of shapes, but there is considerable variation in proportion and in depths of the bowl-like exhalant surface. It will be apparent from these examples, which from their continuous intergradation at a single locality appear to be members of a single species, that many separate species and even genera reported in the literature may be merely individual variants. Nevertheless, each of the cited species has a limited repertory of form, and it should be noted that some genera, such as the toadstool-like Cretaceous hexactinellid *Coeloptychium,* are nearly invariant in external form.

The ecologic significance of external form is briefly discussed in the chapter on Ecology and Paleoecology (p. 243) but the

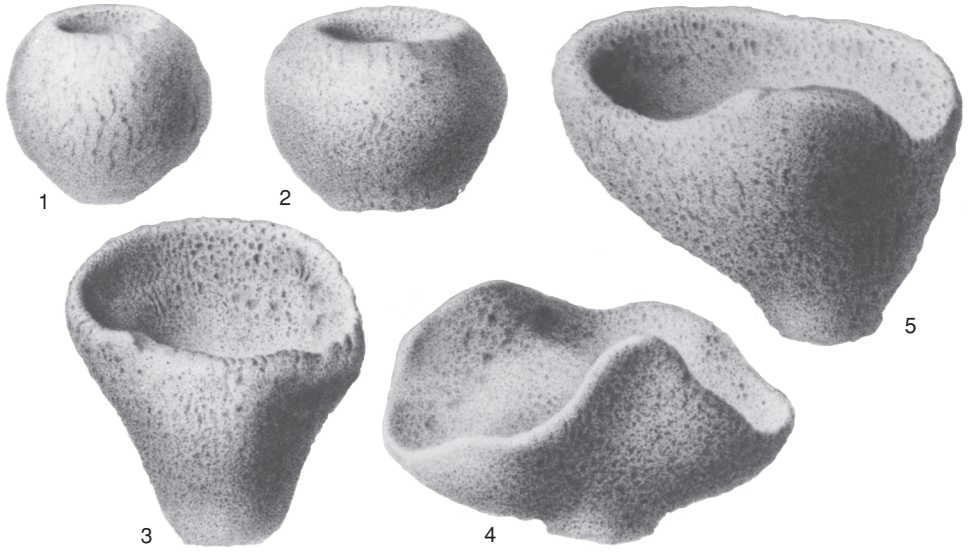

FIG. 88. *Palaeomanon cratera* (ROEMER, 1848) showing variant growth forms, Niagaran, Silurian, Decatur County, Tennessee, USA, ×1 (Rauff, 1893).

ecologic significance of the above-mentioned examples can be conjectured only. It seems reasonable to suppose, however, that at least some and perhaps all are responses to environmental circumstances rather than being reflections of genetic differences. Next to nothing is known of the genetics of living sponges and to what extent individual

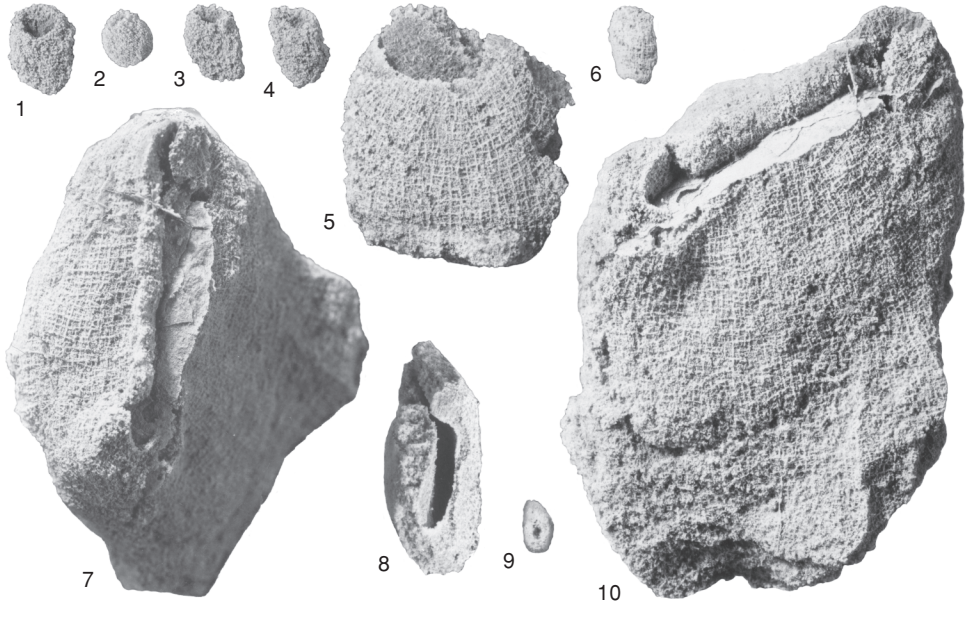

FIG. 89. Shape variation (ontogenetic) with size in *Microstaura doliolum* FINKS, 1960, from single locality in Permian Road Canyon Formation, Glass Mountains, Texas, USNM 703c, ×2 (Finks, 1960).

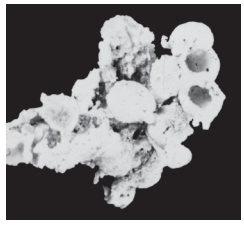

FIG. 90. *Girtyocoelia beedei* (GIRTY, 1908) showing absence of cloaca in juvenile stages (sectioned chambers at right); sponge grew on front of *Guadalupia* GIRTY, Permian Cathedral Mountain Formation, Glass Mountains, Texas, AMNH 504, ×2 (new).

variation is determined by it. One can assert on *a priori* grounds that major differences between species are genetically determined.

FRY (1970) questioned the taxonomic value of external form on the grounds that form and functioning of the whole sponge are determined by interactions at the cellular level and that the sponge should be treated as a population of cells and cell products analogous to a mixed population of whole organisms. This seems to be an extreme view. To reject one whole class of information on the grounds of presumed incompatibility with another class of information is to abandon the principle of multiple working hypotheses. *A priori* considerations aside, most paleontological classifications will have to rely heavily on external form and intermediate-level structures, such as pores, canals, and skeletal organization, because statistically useful populations of spicules are not always available, and of cells not at all. Furthermore, inasmuch as a natural classification is a statement about phylogeny, the more lines of evidence that converge to establish it, the more securely founded it is.

FIG. 91. *Stylopegma* sp. showing absence of cloaca in early stage in separated lower end of specimen (*1a*), as viewed in cross section (*1b*), Permian, Getaway Limestone, Guadalupe Mountains, Texas, AMNH 512, ×2 (new).

TEMPORAL VARIATION

Many individual sponges undergo considerable changes in shape during their lifetimes. Some of these changes may be ontogenetic, that is, a regular sequence characteristic of the life history of the species. Other sponges, however, particularly encrusting forms, appear to undergo constant and often drastic changes in shape of an irregular and unpredictable sort.

Ontogenetic variability may involve changes in proportion. The Permian hexactinellid *Microstaura doliolum* FINKS, 1960, occurs in a range of sizes at a single locality. The very small ones are nearly spherical, while the larger and presumably older are barrel shaped and subprismatic, and the larger ones are more elongate (FINKS, 1960, pl. 34; Fig. 89 herein). Some Permian cateniform Sphinctozoa, such as *Girtyocoelia beedei* (GIRTY, 1908) and a species of *Stylopegma* KING, 1943, lack in the earliest stages the central cloaca characteristic of the genus (Fig. 90–91).

A more irregular type of temporal change has been described by BURTON (1949, fig. 12–13) and SARÀ (1970, fig. 3–4; Fig. 92–93 herein), based on observations of the same sponges over periods of a year or more. Outlines of these encrusting sponges changed, partly by growth, partly by coalescence of neighboring individuals, partly by

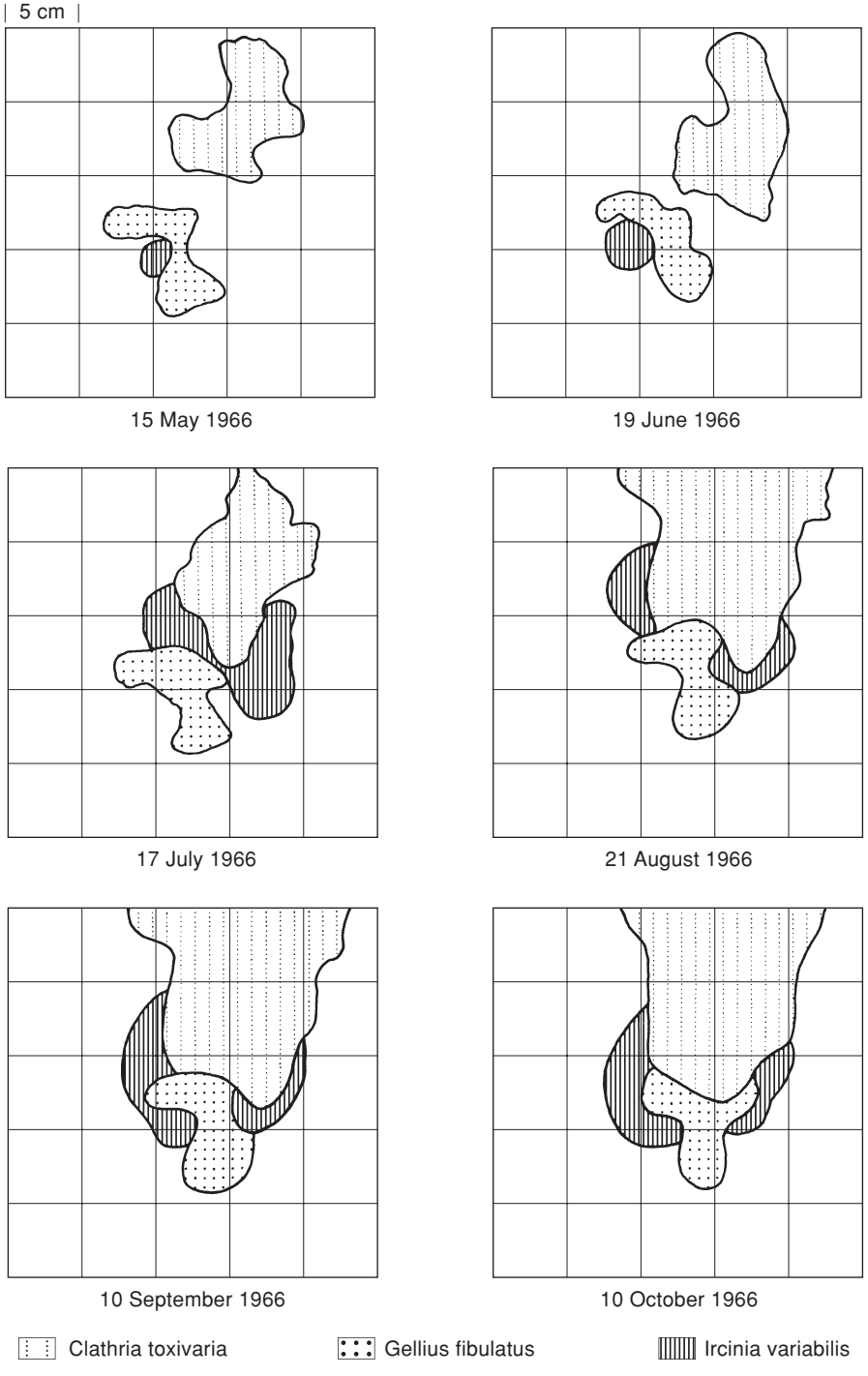

FIG. 92. Variations with time in part of sponge population in Grotta della Regina, near Monopoli, in southern Italy (May–October, 1966) (Sarà, 1970; courtesy of Zoological Society of London).

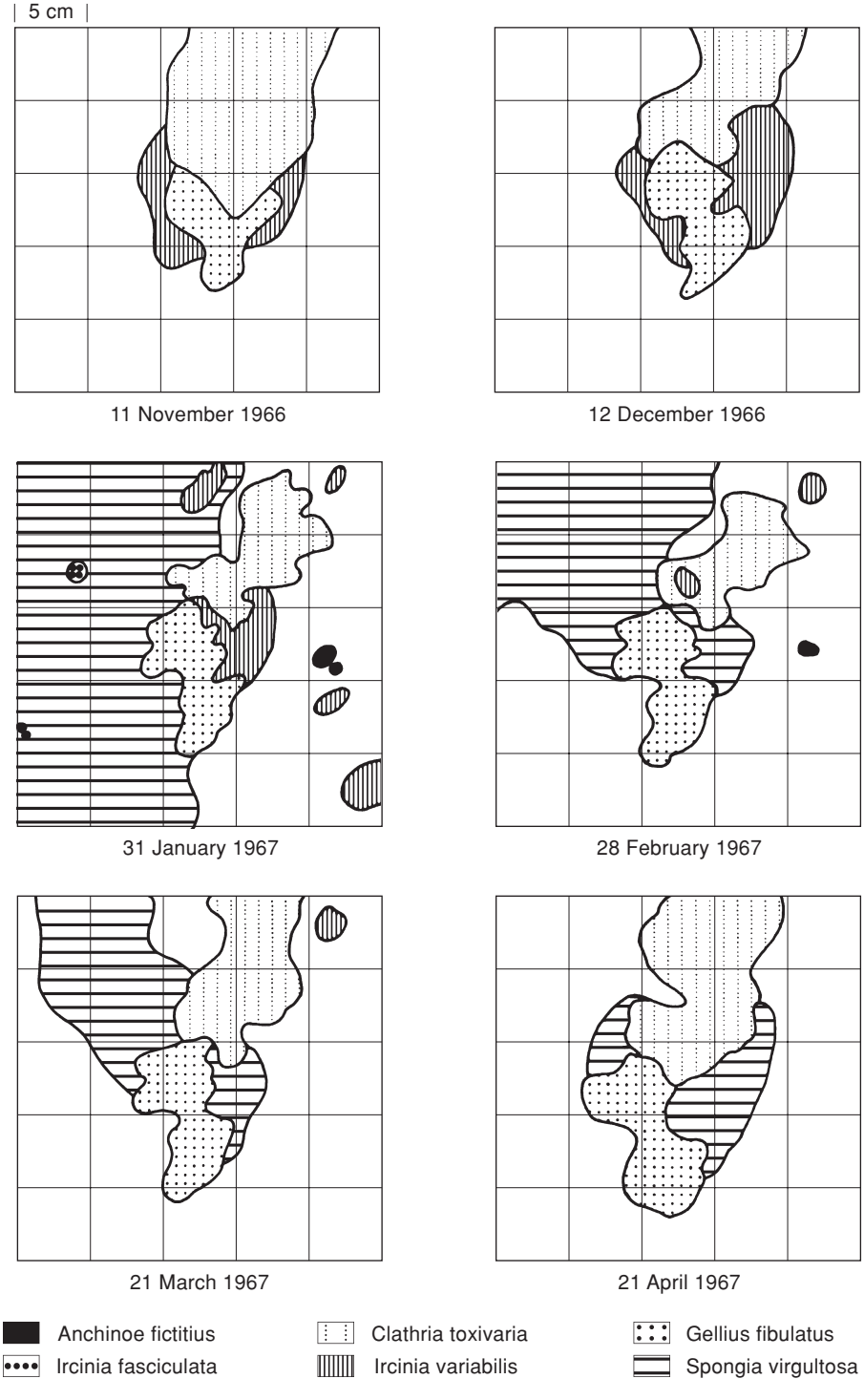

FIG. 93. Variations with time in part of sponge population in Grotta della Regina, near Monopoli in southern Italy (November, 1966–April, 1967) (Sarà, 1970; courtesy of Zoological Society of London).

the presumed dying or disintegration of tissues, or, as BURTON suggested (1949, p. 909), by slow movement of the tissues. BOROJEVIC (oral commununication, 1968) has observed in the laboratory that small, starved sponges will abandon their skeletons and migrate slowly over the substrate; consequently, such motion seems to be possible.

BURTON (1949) made an effort to avoid sites where sponges were altered in form by predation. Predation and mechanical injury will affect obviously the form of a sponge, and in species with a characteristic shape, such teratological changes can be recognized, as in a specimen of the Permian *Stylopegma* KING, 1943 (Fig. 94), which has been injured and healed.

Seasonal changes have been reported by SIRIBELLI (1961) in species of the demosponge *Axinella.* In *A. verrucosa* (ESPER, 1794) specimens collected in the fall and winter are thinly branched with a slightly hispid surface, while those collected in the summer have progressively thicker branches with a rugose surface and have **anastomoses** between neighboring branches. *A. damicornis* (ESPER, 1794) is flabellate and anastomosing all year round, but the branches become very thin in the fall and winter and thicken in the spring and summer. Internal arrangements of spicules differs between the two species and is apparently constant.

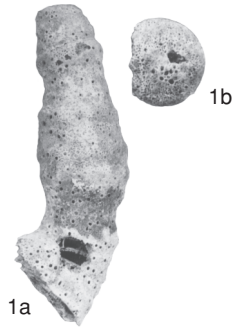

FIG. 94. Healed injuries in *Stylopegma* sp.; *1a,* hole at base of left specimen is an injury that apparently led to constriction of part of specimen above it; *1b,* viewed from above, showing flattening of normally circular outline, at left, where part of side was removed, perhaps the bite of a predator, and then healed over; Permian Getaway Limestone, Guadalupe Mountains, Texas, AMNH 512, ×1 (new).

SPICULES

The form and dimensions of spicules and the relative frequency of various types have long been used in sponge taxonomy, apparently not always with proper appreciation of their variability. In a detailed study of the demosponge *Ophlitaspongia seriata* (GRANT, 1826) from four localities, two in Wales and two in northern France (Brittany), FRY (1970) demonstrated differences between the populations and also between oscular and interoscular parts of the sponge, both in relative frequencies of spicules types (tylostyles, subtylostyles, and toxas) and in the size-frequency distribution within each type (FRY, 1970, p. 156, fig. 12 and table IX; Fig. 95, Table 5). Differences between the two Welsh localities, on the one hand, and the two French localities, on the other hand, are readily apparent in both figures. With the relative frequencies of tylostyles, however, this distinction is more marked in interoscular than in oscular samples and among subtylostyles more marked in oscular than in interoscular ones. When oscular and interoscular frequencies are combined (Table 5), discrepancies are compensated largely. Size-frequencies (Fig. 95) (oscular) of toxas are different between the two Welsh populations as well as between the French ones. It is also apparent from the histograms (Fig. 95) that the size-frequency distributions are highly skewed and in some instances bimodal or polymodal.

Polymodality in size-frequency distribution was demonstrated for amphidisc microscleres in several species of the hexactinellid *Hyalonema* by LENDENFELD (1915). In most of his species there were two sizes of amphidiscs, each often separable into two subgroups (LENDENFELD, 1915, fig. 9, 13; Fig. 96–97 herein). Where spicules from more than one individual were plotted separately, position of the modes is more or less the same (LENDENFELD, 1915, fig. 19;

TABLE 5. Mean percentage frequencies of spicules; *O,* oscular sample; *IO,* interoscular sample; *E,* edge sample (Fry, 1970; courtesy of Zoological Society of London).

	O	IO	O+IO	E
subtylostyles				
Church Island	65.88%	69.63%	67.75%	77.33%
Bodorgan	72.80	62.01	67.40	65.76
Menenett	55.47	63.36	59.41	63.48
Le Loup	58.85	61.00	59.92	57.04
tylostyles				
Church Island	6.73%	7.22%	6.98%	4.40%
Bodorgan	3.95	8.39	6.18	9.62
Menenett	4.22	3.20	3.72	3.73
Le Loup	2.37	2.91	2.65	2.26
toxa				
Church Island	27.39%	23.15%	2.27%	18.27%
Bodorgan	23.25	29.60	26.42	24.61
Menenett	40.31	33.44	36.87	32.79
Le Loup	38.78	36.09	37.43	40.70

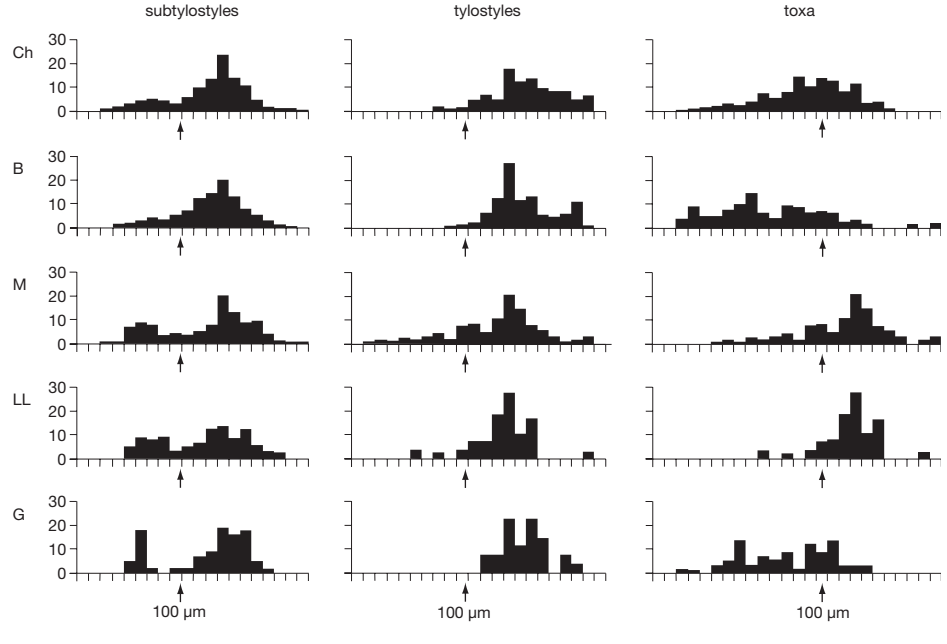

FIG. 95. Percentage size frequency distributions of three spicule types in oscular samples from four populations of *Ophlitaspongia seriata; Ch,* Church Island; *B,* Bodorgan; *M,* Menenett; *LL,* Le Loup; *G,* data for slide preparation that is probably from holotype of *Ophlitaspongia papilla* BOWERBANK, 1866, collected from Guernsey; with exception of G data, histograms based on data from two oscular samples from five specimens from each population; size represents greatest chord length and is shown in class intervals of 6.75 µm (Fry, 1970).

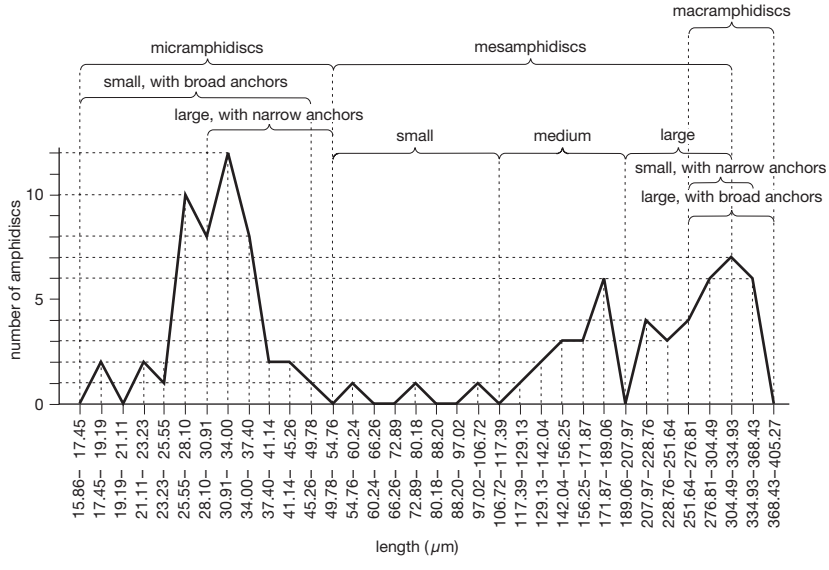

FIG. 96. Length-frequency curve of amphidiscs in *Hyalonema (Hyalonema) placuna* Form B (Lendenfeld, 1915).

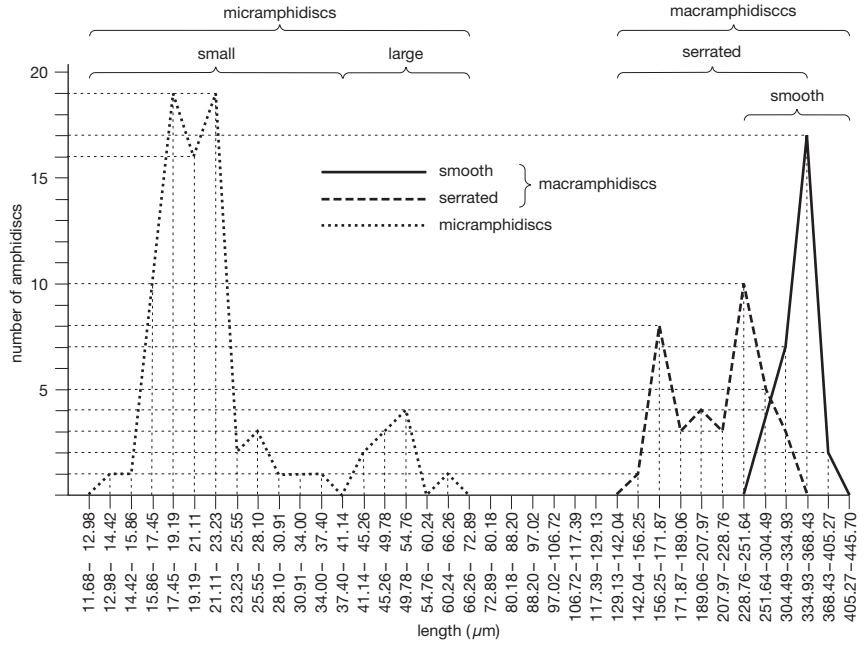

FIG. 97. Length-frequency curve of amphidiscs in *Hyalonema (Prionema) crassum* (Lendenfeld, 1915).

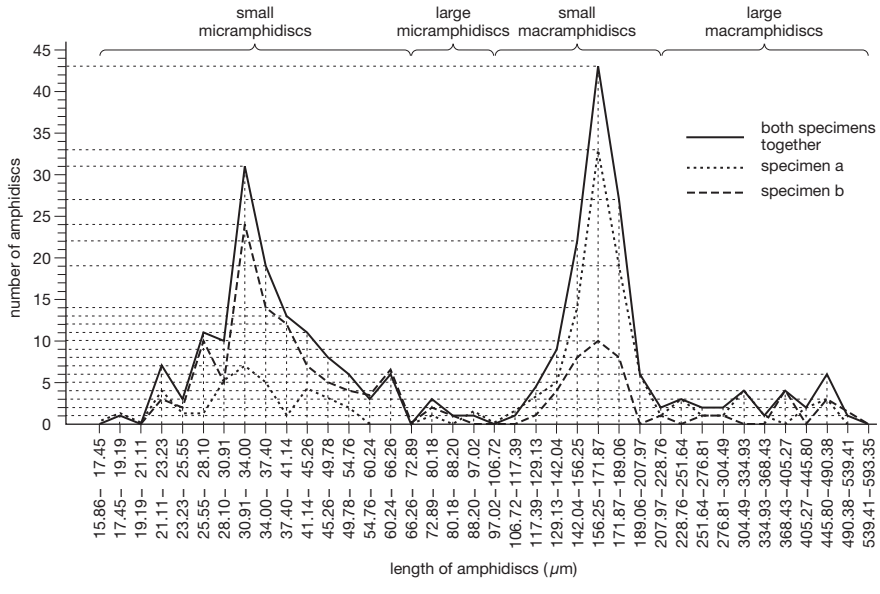

FIG. 98. Length-frequency curve of amphidiscs in *Hyalonema (Oonema) bianchoratum pinulina* (Lendenfeld, 1915).

Fig. 98 herein). Measurements given by SIMON (1953, fig. 12–15) for spicules of the freshwater demosponge *Spongilla lacustris* (LINNÉ, 1759) have a more nearly symmetrical distribution, but they vary between individuals at a given locality (SIMON, 1953, fig. 13; Fig. 99 herein) as well as between distributions of average values from different lakes (SIMON, 1953, fig. 15; Fig. 100 herein).

Causes of size variation of spicules are not known. To the extent that size reflects stages in growth of individual spicules, polymodality may represent cyclicity in spicules production. In many instances size distinction is apparently functional, for spicules of the same sort but of different size occupy special areas of the sponge, such as the dermal membrane. FRY (1970, p. 157) suggested that postlarval stages of different genotypes may fuse to form a single sponge; the spicules produced by descendant cells of each larva differ. This is not known with certainty to occur, but fusion of separate conspecific sponges has been observed. In any case the observed skewness and polymodality in the size-frequency distribution of spicules supports FRY's (1970, p. 145 ff.) assertion that information is lost if only the mean and extreme sizes are given. It is also important to note from what part of the sponge the spicules were obtained.

Variability in frequency of different spicule types between individuals of the same species may occur to the extent that one of the spicule types, sometimes a diagnostic one, may be absent or so reduced in numbers that it is difficult to find on the specimen. Several apparent instances of this sort have been reported by DE LAUBENFELS (1936) and BURTON (1932), among others.

Spicules of a given type may also vary in shape or ornamentation. The example given by BURTON (1932, fig. 23–24; Fig. 101–102 herein) from the demosponge *Iophon proximum* (RIDLEY) may be representative of a number of similar instances. The variability affects both the principal acanthostyles and the chelalike microscleres. Some variability of this sort may be clearly teratological. Such instances have been reported by SIMON (1953) and by TUZET and CONNES (1962) for the freshwater demosponges *Spongilla lacustris* (LINNÉ, 1759) and

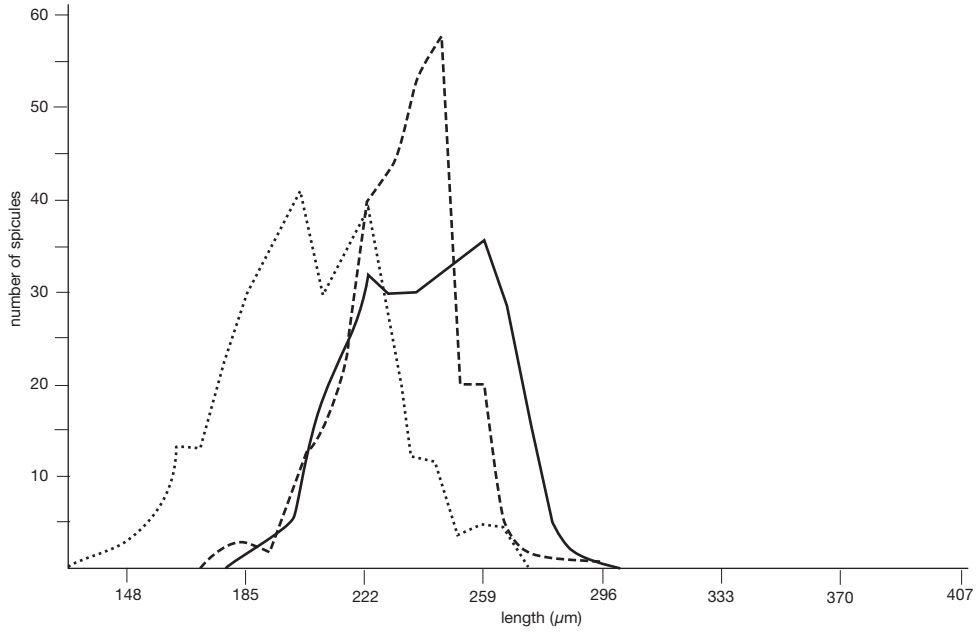

FIG. 99. Spicule length-frequency curves of three different colonies of *Spongillia lacustris* (300 spicules from each colony) from Schleinsee (Simon, 1953).

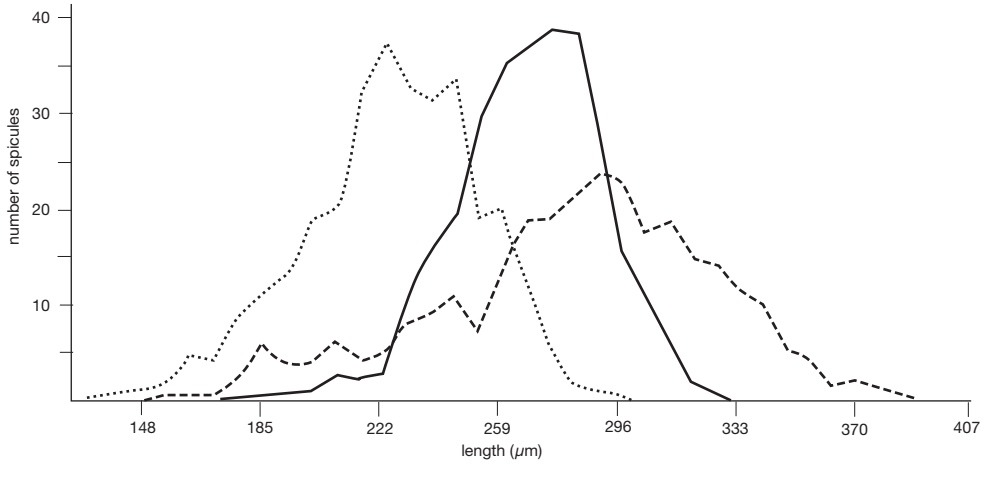

FIG. 100. Average frequencies of spicules of given length in *Spongilla lacustris* from each of three German lakes: Schleinsee (3 colonies: 900 spicules) represented by *dotted line;* Meisinger See (4 colonies: 1200 spicules), *solid line;* Klosterweiher (3 colonies: 900 spicules), *dashed line* (Simon, 1953).

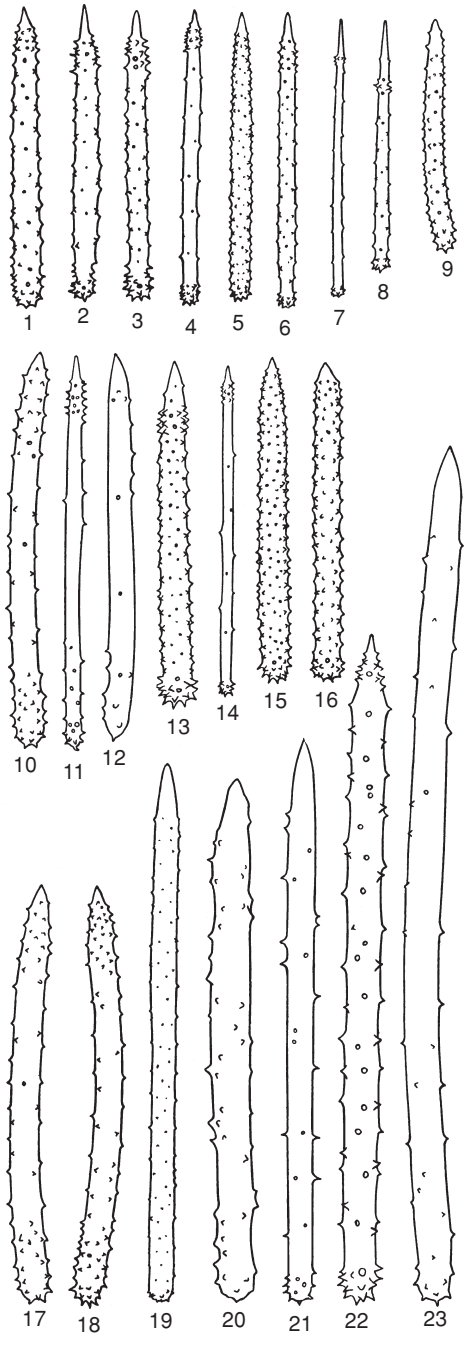

FIG. 101. Variation in size and shape of acanthostyles in *Iophon proximum* (RIDLEY), ×200 (Burton, 1932; courtesy of Cambridge University Press).

Ephydatia fluviatilis (LINNÉ, 1759), respectively. SIMON (1953, p. 220) noted that particular malformations characterized each lake from which the sponges were obtained (*ibid.,* fig. 16; Fig. 103 herein), thus pointing to ecological causes. TUZET and CONNES ascribed the malformations of their sponges to conditions of strong currents (the sponges occur in water passages of a pumping station). Strong currents were previously noted by SIMON (*fide* TUZET & CONNES, 1962) as inducing malformations.

Variability may occur regularly within an individual sponge. Differences in size within a given spicule type, such as oxeas and hexactines, may be related to their position within the sponge. The dermal membrane in particular may contain smaller sizes of such spicules than occur in the principal skeleton (*vis.,* oxeas in the Permian lithistid *Scheiia tuberosa* TSCHERNYCHEV & STEPANOV, 1916 (FINKS, 1971b) or triactines in the Permian hexactinellid *Carphites plectus* FINKS, 1960 (FINKS, 1960, pl. 43,*5–6;* Fig. 104 herein). Other variability may be ontogenetic. In the earliest formed layers of spicules in the Permian lithistids *Anthracosycon* GIRTY, 1908, and *Haplistion* YOUNG & YOUNG, 1877, the monaxonic desmas occur singly in an isodictyal net and bear only terminal zygoses (dendroclones) (Fig. 105). Very soon the spicules were grouped in parallel bundles and bore lateral zygoses for mutual articulation; in *Haplistion* the terminal zygoses are absent in these later spicules, and they have the form of typical rhizoclones (FINKS, 1960, p. 78, 89, pl. 20,*4–5,* pl. 26,*10,12*). Here the variant forms seem to be homologous and their differences related to changing functional needs within the organism. This indicates that spicule form is determined not only by the genotype but also by the internal milieu.

Seeming variability in spicules could result from incorporation of foreign spicules from the sediment by the sponge. This does not seem to be a common occurrence,

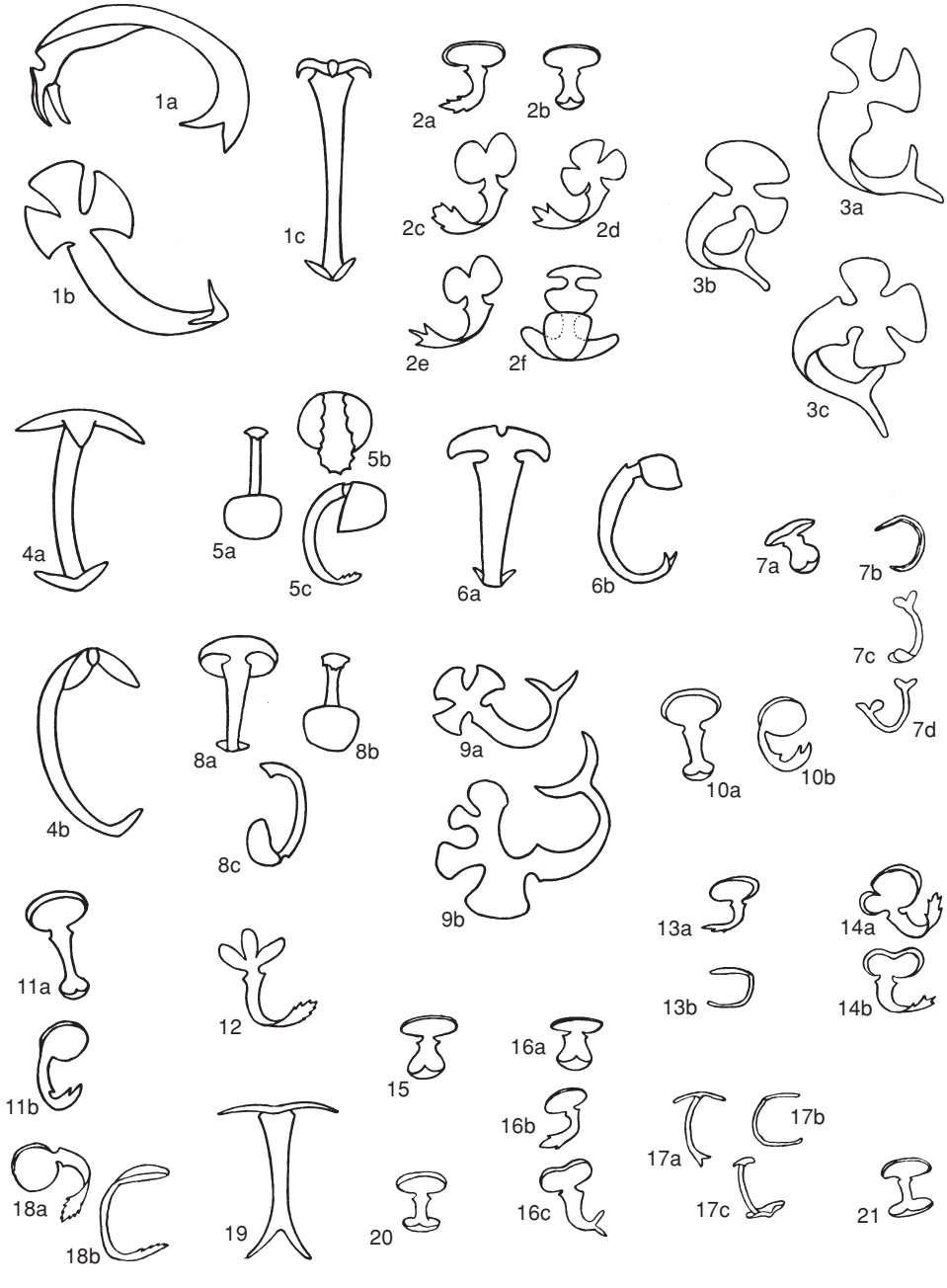

FIG. 102. Variation in size and shape of chelate microscleres in *?Iophon proximum* (RIDLEY), ×1 (Burton, 1932; courtesy of Cambridge University Press).

FIG. 103. Spicule malformations in *Spongilla lacustris; 1–5,* Meisinger See; *6–10,* Schleinsee; *11–13,* Klosterweiher, approximately ×133 (Simon, 1953).

however. Keratose sponges, which do not secrete any spicules of their own, frequently incorporate sand grains and sometimes spicules of other sponges in their spongin fibers (DE LAUBENFELS, 1936). Sponges that secrete their own spicules, however, seem to be discriminatory toward foreign spicules. SIMON (1953) studied this experimentally with the freshwater sponges *Spongilla, Ephydatia,* and *Trochospongilla.* He found that *Spongilla lacustris* (LINNÉ, 1759) accepted spicules of *Ephydatia fluviatilis* (LINNÉ, 1759) only af-

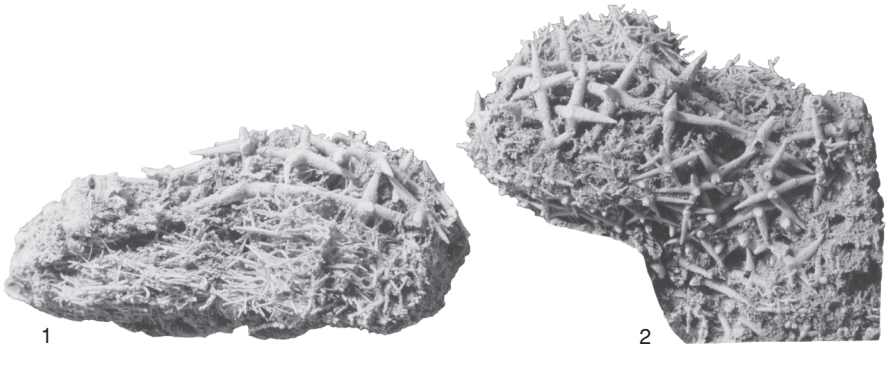

FIG. 104. Views of *Carphites plectus* FINKS, 1960, showing small triactines in dermal layer, above large hexactines, and large triactines in interior beneath large hexactines, Permian Road Canyon Formation, Glass Mountains, Texas; *1,* section and *2,* top, ×1.3 (Finks, 1960).

ter their organic coatings had been removed through treatment with H_2SO_4 and H_2O_2. *Trochospongilla horrida* WELTNER accepted both *Spongilla* and *Ephydatia* spicules to only a limited extent even after such treatment and to a very slight extent when treated with HCl only. *Ephydatia* did not accept foreign spicules at all, even when treated. Such evidence of positive rejection of foreign spicules explains the rarity of such incorporation. Among fossils, of course, there is the possibility that loose foreign spicules were swept into the skeleton after death of the sponge.

SKELETAL NET

Spatial organization of spicules and other skeletal elements is an important familial, generic, and specific character. Although it is relatively constant within a species, usually more so than the external form, individual variation does occur. This is restricted usually to variation in thickness of skeletal fibers or in numbers of spicules lying side-by-side in them (see, for example, BURTON, 1932, p. 268) rather than involving major differences in the geometry of the net. Nevertheless, even this much can be quite constant in some groups. In the Permian lithistid *Anthracosycon* the skeletal fibers are composed of several spicules side-by-side in some populations and of single spicules in others (FINKS, 1960, p. 77 ff.; see also Fig. 105 herein), but each population from a single locality (named as species) is either of one composition or the other. SIRIBELLI (1961, fig. 5–6; Fig. 105 herein) illustrated two types of skeletal net in *Axinella,* characterizing each of two species, which remain constant despite considerable individual variation in external form.

AQUIFEROUS SYSTEM

Form of the canal system and size, spacing, and grouping of pores are also useful taxonomic characters, especially at generic and specific levels. Size and grouping of homologous pores, however, may indicate

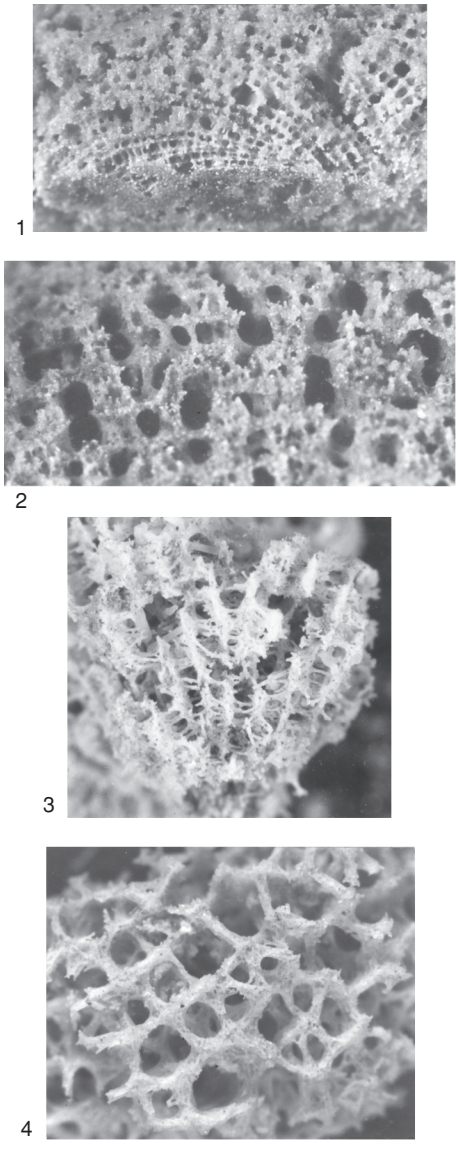

FIG. 105. Ontogenetic change in spicule form and skeletal net. In initial part of skeleton, spicules are dendroclone-like and occur singly, whereas in upper, later-formed part, spicules are rhizoclone-like and grouped in bundles (Finks, 1960); *1–2, Anthracosycon ficus* GIRTY, 1909, holotype, Permian Bone Spring Formation, Guadalupe Mountains, Texas; *1,* earlier and *2,* later parts, ×15; *3–4, Haplistion aeluroglossa* FINKS, 1960, holotype, Permian Road Canyon Formation, Glass Mountains, Texas; *3,* earlier and *4,* later parts, ×15 (Finks, 1960).

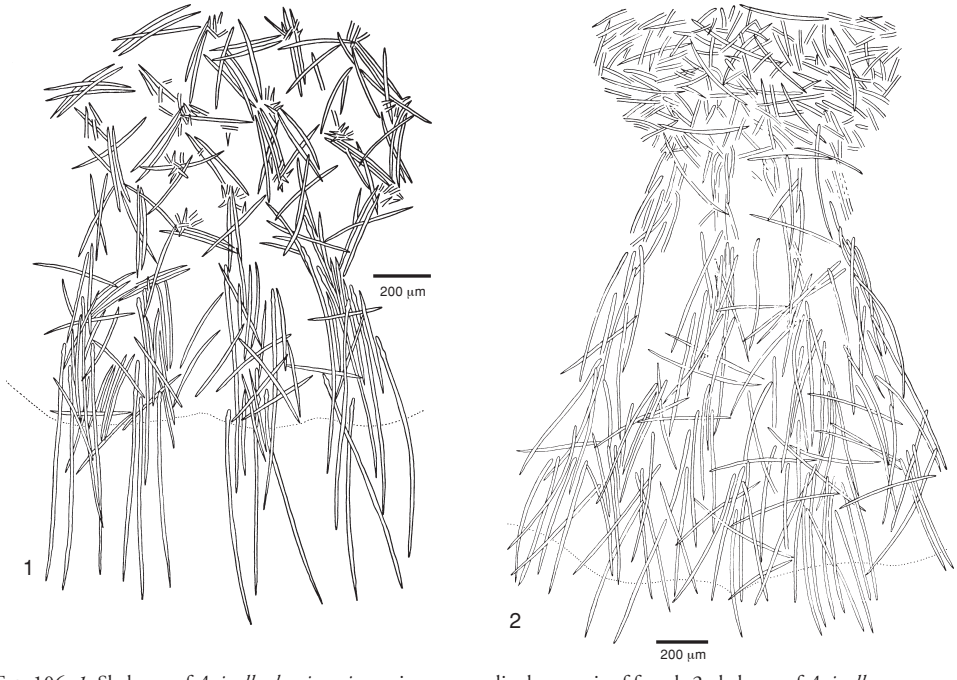

FIG. 106. *1,* Skeleton of *Axinella damicornis,* section perpendicular to axis of frond; *2,* skeleton of *Axinella verrucosa* section perpendicular to axis of branch (Siribelli, 1961).

individual variation within species and also on parts of the same specimen. For example, in the Permian lithistid *Multistella porosa* FINKS, 1960, the number of pores in the exhalant clusters and the spacing of these clusters is variable in the same specimen (FINKS, 1960, pl. 9,*3;* Fig. 107 herein). The number of pores in a cluster varies within narrow limits and is determined probably by functional factors, namely the volume served by each exhalant cluster. Their spacing on the sponge surface, however, is more irregular, and presumably fortuitous or unique events during development were the cause of the irregularities in their dispersion.

FIG. 107. Variability in dispersion of exhalant pore clusters on *Multistella porosa* FINKS, 1960, Permian Getaway Limestone, Guadalupe Mountains, Texas, ×2 (Finks, 1960).

In the Permian lithistid *Collatipora? pyriformis* FINKS, exhalant pores low on the side of the sponge are more widely spaced and have collarlike rims about them (FINKS, 1960, p. 84, pl. 23,*1,3;* Fig. 108 herein). This may be a compensatory adaptation for increasing the velocity of outflow from them under conditions of less agitated ambient water than prevails on the upper part of the sponge, thus carrying the waste water away from the sponge. The oscular collar as an adaptation for quiet water is predicted by

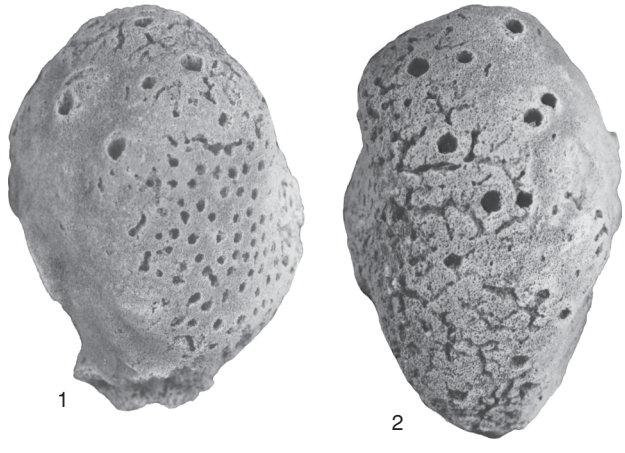

FIG. 108. Views of *Collatipora? pyriformia* FINKS, 1960, showing how oscules in sheltered location on side of sponge (*1,* those at left, and *2,* at right) developed raised lips to direct exhalant currents upwardly, while oscules on exposed top of sponge are flush with surface; smaller pores to right in view *1* presumed to be inhalant; Permian, Road Canyon Formation, Glass Mountains, Texas, *1,* side and *2,* top, ×1.6 (Finks, 1960).

BIDDER's theoretical analysis (BIDDER, 1923). This instance of intra-individual variation may thus be related to functional needs; consequently another specimen of the same species that bore collared exhalant pores over the entire surface might be interpreted as having lived in quieter water.

CONCLUSION

Almost every character used to describe and characterize sponges is subject to considerable intraspecific variation. Consequently it is necessary to indicate the extent of variation when describing any character, whether quantitatively or qualitatively, so that the species definition will conform to or parallel the reality of a natural population. Likewise, it is important to record, when possible, the correlation of variation with environmental and sedimentologic conditions, so that an ecologic interpretation of variation may become possible in conjuction with theoretical models of functional morphology.