HEXACTINELLIDA AFTER 132 YEARS OF STUDY -- WHAT'S NEW?

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ABSTRACT

The presently used taxonomic arrangement of Hexactinellida has been reached through a series of modifications introduced at 10-year intervals. The place of Hexactinellida within the Porifera remains controversial in spite of advances in knowledge of soft-tissue structure and several molecular sequence studies. New observations on development of *Oopsacas minuta* confirm classic work on *Farrea sollasi*, and conclude that early cleavage is complete, suggesting hexactinellids are primary cellular organisms. Analysis of postlarval and juvenile skeletal formation is expected to be useful for unraveling phyletic relationships, and an example of *Leucopsacas scoliodocus* is explored. Hexactinellid species populations are generally thought to be sparsely distributed over fairly large geographic ranges. Historic early dredging and recent photographic sled and submersible surveys show dense hexactinellid populations of single- or multi-species communities extending over several kilometers. Factors conducive to large patch development and maintenance are under investigation.

KEY WORDS

Hexactinellida, phylogeny, larvae, post-larval development, high-density populations.

INTRODUCTION

Present understanding of the poriferan class Hexactinellida is that group of sponges, numbering slightly more than 500 known Recent species, which build a supporting skeleton of siliceous spicules of six-rayed (hexactine) symmetry, or in alternative interpretation, of 'cubic' symmetry since each ray intersects the center of a side of a bounding cube. I have chosen here to review five subject areas: high-level taxonomy, phylogeny, reproduction and development to larva, post-larval skeleton formation and high density populations.

TAXONOMY

Long before hexactinellids were recognized as a distinct group of sponges, many hexactinellid species were already, described, and assigned to groups such as Zoophytes, corals or horny alcyonid sponges. In 1868, with about 12 species of hexactinellids known, W. Thomson criticized GRAY's (1867) arrangement of Porifera and recognized that the various forms which Gray assigned to several subsections (~ orders) shared a common feature: "the [siliceous] spicules, whether of the skeleton or of the sarcode, may all be referred to the hexradiate stellate type." He named this new group Order 1. (Porifera Silicea) Vitrea and listed its membership to include all

of the then known genera and species, including within the genus *Dactylocalyx*, three species which lacked hexradiate spicules and were later transferred to lithistid Demospongiae. Shortly thereafter, O. SCHMIDT (1870) defined the group Hexactinellidae as sponges whose glass spicules follow the 3-axis type, with first examples as *Hyalonema* and *Euplectella*. He noted it was similar to Thomson's Vitrea but Thomson had failed to exclude lithistid sponges which Schmidt now recognized as a distinct group. SCHMIDT (1870) was accorded authority for the new grouping by ZITTEL (1877, and his numerous following publications) because he made the clear distinction between Hexactinellida and Lithistida, not because his concept of Hexactinellida was the first usable definition of group characters. While Triaxonia of SCHULZE (1886) is obviously a junior synonym of Schmidt's Hexactinellidae, CLAUS's (1872) Hyalospongiae, cannot be linked to any modern taxon by its original definition (REID, 1957).

Several early attempts to subdivide the Hexactinellida into natural groupings failed to receive support, but ZITTEL's (1877) recognition of soft-bodied forms with loose spicules as Lysakina, and forms with fused rigid skeletons as Dictyonina, was retained by SCHULZE (1886, 1887) for his still influential 'Challenger' Report and remains as a modified part of the present system (note: the taxonomic hierarchy levels of early schemes are converted to equivalents of the modern scheme; higher taxa names surviving to the modern scheme are bold-faced). Schulze's system was subclass **Lyssacina** with orders **Amphidiscophora** and **Hexasterophora** and subclass Dictyonina with orders Uncinateria and Inermia.

From this early scheme, the present one has evolved through a long series of realizations (hypotheses) of shared characters underlying newly recognized relationships, some of which were acceptable and others entirely or partly abandoned. Only the rearrangements which survived to the present scheme of Recent Hexactinellida are mentioned here. SCHULZE (1899) abandoned his Uncinatera / Inermia division of dictyonine sponges and recognized that both soft and hard sponges had similar microscleres, leading him to abandon Dictyonina. He concluded that primary division of hexactinellids was reflected in microsclere form, and changed the primary division to subclasses **Amphidiscophora** and **Hexasterophora**.

SCHRAMMEN (1902) recognized the distinction of the lychniscose sponges, raised them from their low level within Schulze's Inermia to equivalent of a present subclass level, and in 1903, lowered them to an ordinal group within the Hexasterophora where they remain; his scheme consisted of subclass **Amphidiscophora** without orders and subclass **Hexasterophora** with orders **Hexactinosa** and **Lychniscosa**.

SCHRAMMEN (1924) recognized division of the Amphidiscophora into fossil forms with unequal-ended amphidiscs (hemidiscs) as Hemidiscaria and those with the more common symmetric amphidiscs (all recent forms) as Amphidiscaria (spelling modified later to Amphidiscosa by REID 1964); his scheme was subclass **Amphidiscophora** with orders **Amphidiscaria** and Hemidiscaria, and subclass **Hexasterophora** with orders Inermia, Uncinateria, **Lychniscaria** and **Lyssacinaria**. IJIMA (1927) slightly rearranged the scheme to nearly that used today: subclass **Amphidiscophora** without suborders and subclass **Hexasterophora** with orders **Hexactinosa**, **Lychniscosa** and **Lyssacinosa**.

Detailed analysis of aulocalycoid frameworks by REISWIG & TSURUMI (1996) led to recognition of this as the basis of a new order, Aulocalycoida, of Hexactinosa by TABACHNICK & REISWIG (2000). Thus the present scheme as used in the Systema Porifera (HOOPER & VAN SOEST, 2002) is subclass **Amphidiscophora** with one Recent order, **Amphidiscosida**, and subclass **Hexasterophora** with four orders **Hexactinosida**, **Aulocalycoida**, **Lychniscosida**, and **Lyssacinosida**.

The modern arrangement, attained through a series of discoveries at an average interval of ten years, is not entirely satisfying since it does not convincingly reflect phylogeny within the Hexactinellida, still does not allow inclusion of some fossil hexactinellids and is based in part upon unverified assumptions of skeletal organization in Hexactinosida.

PHYLOGENY WITHIN HEXACTINELLIDA

All of the arrangements noted above can be inferred to have been phylogenetic hypotheses following the stated aims and assertions of the International Code of Zoological Nomenclature, but all workers cannot be assumed to have ascribed to all particulars of the Code. Indeed few authors have pointedly published figures directly implying descent relationships between taxa. In the final section of his 'Challenger' Report, SCHULZE (1887) provided his concept of hexactinellid phylogeny which differed markedly from the arrangement used in the systematic section of the report. He recognized the two main branches as the amphidisc-bearing Amphidoscophora and the hexaster-bearing Hexasteria. Twelve years later (1899) he imported this new primary division into his revised systematic arrangement, and, with a spelling change, this concept has stood the test of time.

The first clear treatment of within-hexactinellid phylogeny was the integrated analysis of fossil and Recent taxa by cladistic analysis carried out by MEHL (1992). She accepted retention of the two main branches, Amphidiscophora, first evident in the Upper Silurian, and Hexasterophora, first found in Lower Ordovician (later evidence in MEHL, 1998, suggests Middle Cambrian occurrence). She also concluded that Lyssacinosa were paraphyletic, some members having a close relationship with Lychniscosida indicated by shared graphiocomes. She proposed a new taxon, Graphiocomida, which would replace Lychniscosida and the related lyssacine forms. This major change has not been incorporated into the arrangement for the Systema Porifera, but it is worthy of further scrutiny and testing. It directly implies that dictyonal frameworks in Hexactinosida and Lychniscosida have been independently derived and represent convergent solutions to physical support problems.

PHYLOGENY WITHIN PORIFERA

SCHMIDT (1871), shortly after his formation of Hexactinellida, proposed an arrangement of the four main taxa of Porifera, indicating the Hexactinellida as the most direct offshoot of the ancestral poriferan and, on a separate branch, Demospongiae and Calcarea sharing common descent. Using abbreviations, H = Hexactinellida, D = Demospongiae, C = Calcarea, Schmidt's arrangement shortens to H(D+C). SCHULZE (1887) was unable to support a sub grouping among Porifera classes.

While most poriferologists have recognized the three classes of Porifera as equidistantly related from some common ancestor, BIDDER (1929) hypothesized that hexactinellids had been independently derived from a different protist ancestor than that which gave rise to other sponges. He erected two new phyla in the Parazoa for these groups, Nuda, for Hexactinellida, and Gelatinosa, for the remaining Demospongiae and Calcarea. His long ignored proposal was revised later by REID (1958) who redefined Bidder's taxa as subphyla of Porifera using some cytological characters which were controversial and unverifiable at that time. Bidder and Reid thus clearly supported a relationship between the classes represented as H(D+C), although at different levels.

After the discovery of an appropriate fixation technique for fine tissue structure of Hexactinellida by MACKIE & SINGULA (1983), and clear demonstration of the syncytial nature of the first member of the class to be intensively investigated by transmission electron microscopy, REISWIG & MACKIE (1983) proposed a new division of the Porifera based upon verified differences in organization of soft tissues. The "normal" cellular sponges with relatively spacious mesohyle were designated subphylum Cellularia while the syncytial and symplasmic hexactinellida were designated Symplasma. Their treatment supported monophyly of Porifera and re-emphasized the long-held H(D+C) relationship between the classes of Porifera. MEHL (1992), in her cladistic analysis of fossil and recent Hexactinellida, supported the same conclusions: monophyly of Porifera and H(D+C) relationship between classes. She, however, suggested alternate names for the two major groups: Pinacophora to replace Cellularia, and Hexactinellida instead of Symplasma. The same conclusions of Porifera monophyly and H(D+C) class relationships were reached by REITNER & MEHL (1996) in their assessment of a new consideration of the characters defining the Porifera and each of the constituent classes. A cladistic analysis of early fossil forms by MEHL-JANUSSEN, 1999, resulted in the same conclusion of class relationships: H(D+C).

Analyses of molecular sequences have been used in the last few years to test the phylogenetic relationships between the three classes of Porifera. Five hexactinellids, *Rhabdocalyptus dawsoni, Farrea occa, Sympagella nux, Margaritella coeloptychioides* and *Oopsacas minuta*, all Hexasterophora, have been examined for sequences of one or more of the five molecules, ribosomal ribonucleic acids (18S rRNA & 26S rRNA), cytoplasmic heatshock protein (HSP70), and protein kinase C (cPKC) and compared to those of members of the other sponge classes and often to non-sponge taxa. There has as yet been no consensus in the results of such analyses. Of the ten most recent reports, five using 18S rRNA, HSP70, or cPKC support the classic H(D+C) arrangement (MEHL *et al.,* 1998; BORCHIELLINI *et al.,* 1998, 2001; KRUSE *et al.,* 1998; SCHÜTZE *et al.,* 1999) and five using 18S rRNA, 26S rRNA, and/or HSP70 support the (H+D)C arrangement (CAVALIER-SMITH *et al.,* 1996; KOZIOL *et al.,* 1997; COLLINS, 1998; ADAMS *et al.,* 1999; MEDINA *et al.,* 2001). Paraphyly of Porifera is supported by seven of the ten analyses, while Porifera monophyly is supported by only the minority of three. This is entirely expected since the Eumetazoa likely arose from within the Porifera, probably in the Calcarea lineage, and any Recent sponge deriving from an ancestor of the lineage which includes the metazoan common ancestor will necessarily share greater genetic similarity with early metazoans than with other Porifera. Such paraphyly is expected to be found in every derivation of a

new taxon from an ancestral group with modern descendants and should not be used to change the scope of diagnosable taxa. Analyses of more highly conserved molecular sequences are still needed to find a strongly supported consensus for the relationship between sponge classes, H(D+C) or (H+D)C, and identify the surviving lineage of the basal-most group of Porifera and thus Animalia (Metazoa). Presently known fossil evidence of earliest spicules and sponge body impressions (STEINER *et al.*, 1993; GEHLING & RIGBY, 1996) supports the "hexactinellid-first" and the classic H(D+C) arrangement of classes.

REPRODUCTION AND DEVELOPMENT TO LARVA

Before OKADA's (1928) classic study of *Farrea sollasi*, there were only a handful of accidental observations of a variety of reproductive stages from several hexactinellid species. SCHULZE (1880, 1887) reported sperm balls in *Euplectella aspergillum*, *Farrea occa* and *Periphragella elisae* but these were later discounted as sexual stages and considered to have been archaeocyte congeries common to all hexactinellids (IJIMA, 1901). SCHULZE (1887) also mentioned, but did not figure, oocytes up to 0.3 mm diameter in *E. aspergillum* and possible blastulae in *F. occa*, but these have never been verified as reproductive stages.

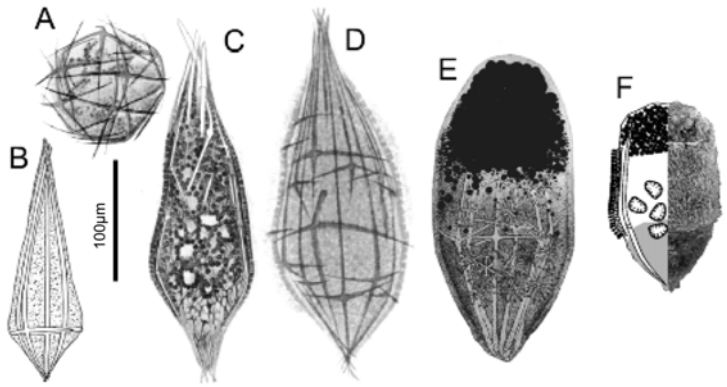

Fig. 1. Hexactinellid larval forms. **A,** a pre-larva of *Leucopsacas orthodocus* from IJIMA, 1903. **B,** larva of *L. ingolfi* from BURTON, 1928. **C, D,** larvae of *Vitrollula fertilis* from IJIMA, 1904. **E,** larva of *Farrea sollasi* from OKADA, 1928. **F,** larva of *Oopsacas minuta* redrawn from BOURY-ESNAULT *et al.,* 1999.

IJIMA gave preliminary (1901) and final (1903) reports of observations on development of *Leucopsacas orthodocus*. He had no direct information of gamete origin but was able to arrange the very few embryonic stages found into a developmental series, a solid blastula indistinguishable from archaeocyte congeries, a spherical gastrula with a single-layered epithelium of cylindrical cells, a spherical early pre-larva with hypothesized flagellated surface and stauractine spicules well below the outer epithelium. The latest stage found was a 100 µm-diameter sphere with stauractin spicules enlarged to 57 µm rays, but without obvious alignment, and sinus-like

spaces within a central cellular mass (Fig. 1A). This most developed stage was not considered a mature larva.

IJIMA also described development of *Vitrollula fertilis* in preliminary (1901) and final reports (1904). Again he had no indication of origin of gametes and was able to observe only a series of embryonic stages to a nearly mature larva. Neither ova or early cleavage stages were seen. He described an early embryo with a differentiated outer epithelium bearing indications of flagella, a later spherical stage with first formation of stauractin spicules in a layer under the flagellated epithelium, an ovoid late pre-larva] with differentiation of the central cell mass (poles reversed from the presently known pattern), and a nearly mature larval form obtained from within parental tissue and examined in sections of the parent or in microtome sections of larvae teased from the tissue. The larva (Fig. 1C, D) is spindle-shaped, 275 x 88 μm in dimensions, circular in section, with 4 μm-thick epithelium, presumed flagellated, around the middle 60 % of the body, the polar regions apparently lacking a covering epithelium. The extensively reticulated internal mass was filled with ovoid cells in the anterior end (his posterior end). The main central mass (>60 % of the total body) was filled with cells bounding lacunar spaces. Ijima first considered these as possible "anlagen" of flagellated chambers, which they almost certainly were, but abandoned that interpretation since some spaces were continuous. The stauractin spicules were arranged like a basket around the central mass, with the long rays intersecting at both anterior and posterior poles.

SCHULZE (1904) described and figured a variety of spermatocyst, oocyte and cleavage stages from *Farrea occa*, *Hyalonema apertum* and *Chonelasma lamella* but did not provide convincing evidence that these were indeed sexual and developmental stages. BURTON (1928) described ova and the nearly mature larvae of *Leucopsacas ingolfi* from near Greenland, both stages missing from IJIMA's (1903) earlier report on closely related *L. orthodocus*. The larva (Fig. 1B), like that from Ijima's *V. fertilis*, was spindle-shaped, about 200 x 55 μm, with a wide end assumed anterior as in Ijima's studies, but now known to be posterior, with a basket of stauractins with one very elongate ray extending to the tapering pointed end now known to be anterior, and all rays curved to conform to larval body contour.

OKADA (1928) examined *Farrea sollasi* samples obtained by dredge from 300 m depth off Japan and employed standard microtome sectioning and histological techniques for light microscopy. No free swimming larvae or spermatozoa were available. He found both spermatozoa and oocytes originated from archaeocyte congeries. Elliptical mature oocytes, 70-130 μm in major axis, underwent total and regular cleavage, resulting in a stereoblastula in which cells differentiated to three cell types. The youngest embryos were spherical and covered by an epithelial layer beneath which six stauractin spicules were deposited. The spicules were smooth and arrayed symmetrically around the central cell mass. The more advanced embryo was larger and slightly ovoid, 150-200 x 140 μm, and conically pointed at the position of spicule apposition -- now known to be the posterior end. The 12 stauractin spicules were enlarged to extend the entire meridional length of the embryo. In the following pre-larval stage the embryo elongated to spindle-shape and its supporting stauractins lengthened to 190 μm. Flagellated chambers developed in the inner cell mass and discohexaster spicules were formed beneath the outer epidermal cells in the posterior half. The most advanced stage (Fig. 1E), interpreted as the mature larva, was

distinctly spindle-shaped with an acute posterior end where stauractins intersected and a rounded anterior end around which the long rays of stauractins formed a tapered but not intersecting cone. Okada did not comment directly upon the extent of the outer flagellated epidermis nor state that the epidermis was flagellated at maturity, but his figures show the cellular epidermis covered nearly the entire larval surface, absent only at very small areas at both poles. He also did not observe collars and flagella in the internal choanocyte chambers and assumed that flagellated cells were to be added later after larval settlement and metamorphosis. He concluded that reproduction and development were continuous and unsynchronized in *Farrea sollasi* since reproductively active specimens could be found all year.

Recent electron microscopy observations have largely confirmed those of OKADA (1928) and have added significant new information. MACKIE & SINGULA (1983) confirmed that archaeocytes in congeries undergo spermatogenesis in *Rhabdocalyptus dawsoni*. Spermatogonia are 6-7 μm in diameter and have eccentric nuclei and large numbers of mitochondria and a single large clear vesicle. Later spermatocytes, 3.5 μm in diameter, have a single flagellum and lack the clear vesicle. Spermatocytes within a single spermatic cyst are all joined by plugged cytoplasmic bridges and develop synchronously. Mature stages of sperm were not found.

BOURY-ESNAULT & VACELET (1994) and BOURY-ESNAULT *et al.* (1999) reported the most recent and significant light and electron microscopy study of reproduction and development in *Oopsacas minuta*, a small lyssacine hexactinellid found living in a shallow-water cave near Marseille, France. Reproduction occurs all year as in *Farrea sollasi* and spermatozoa originate from archaeocyte congeries where spermatogenesis proceeds from center to periphery, with cells joined by plugged cytoplasmic junctions to each other and to the lining cells of the cyst, but all cells attain the same form in mature cysts. Although an acrosome and nuclear condensation are lacking, this is not proof of their absence since fully mature sperm may not yet have been examined. The authors also confirm that oocytes originate from archaeocytes within congeries, the earliest recognizable stages only 10 μm in diameter and barely distinct from archaeocytes, while fully mature oocytes are 100 - 120 μm in diameter, have a very large nucleate nucleus, 45 - 50 μm in diameter, and bear numerous short surface pseudopodia. Fertilization and maturation divisions have not yet been discovered.

Cleavage to 32 cells was found to be complete and equal, proving that Hexactinellida are cellular sponges in their first embryonic stages, but there was a distinct hint of spiral cleavage in blastomere orientation at the third division. The 32-cell coeloblastula begins unequal and tangential division, resulting in a bilayered gastrula formed by cellular delamination. The outer micromeres rapidly divide to form two layers, a syncytial outer epidermis and an inner layer of prismatic cells which forms the flagellated cells of the motile larva. The inner macromeres divide to fill and obliterate the blastula and differentiate into two cell types, one with lipid spherules and one with yolk granules. In the periphery of the central cell mass of the stereogastrula, the first sclerocytes differentiate from the yolk-rich cell population and form the stauractin spicules characteristic of hexactinellid larvae. The mature larval stage (Fig. 1F) has been examined in brooded position within maternal tissues and when free swimming after release from specimens in the laboratory. They are solid, biconic (spindle-form) and small, 150-180 μm in length and swim in a counterclockwise path without body spiraling, rounded or blunt end first, contrary to

previous assumptions by Ijima and Okada of larval polarity based on fixed material. The larva has three very distinct body regions, the basis of the name trichimella formed by BOURY-ESNAULT & VACELET (1994). The unflagellated anterior region is filled with lipid-rich macromeres, while the unflagellated posterior region is filled with yolk-rich choanoblast congeries budding enucleate choanocytes (collar bodies) arranged in small flagellated chambers to 30 μm diameter. Flagella and collars are present here but the supporting trabecular syncytial networks (R1 and R2) of functional adult chambers are absent. The central region is multilayered, the outermost epithelium being a thin syncytium which covers a subepithelial layer of mononucleated multiflagellated cuboidal cells. The flagella emanating in groups of up to 50 from each subepidermal cell penetrate through pores in the overlying syncytium to provide locomotion for the larva. The ciliated cells, which have accessory centrioles but lack basal rootlets, are joined to each other and the overlying epithelium by plugged cytoplasmic bridges. Inner tissues of the central body region consist of vacuolar uni- or plurinucleate macromeres forming thin strands of cytoplasm around very large fluid-filled vacuoles. Choanoblast congeries and flagellated chambers also extend through the lower half of the central body region. The supporting stauractin spicules extend through all three body regions in a basket located well below the epidermal surface, in the outer layers of the interior cell masses.

Since Hexactinellida appear to be very conservative in their cytololgy, many of the characteristics established for development of any single species are very likely to be general for the class. Thus the reports by BOURY-ESNAULT & VACELET (1994) and BOURY-ESNAULT *et al.* (1999) confirm much of the earlier work carried out with much less favorable tissues on other species, but also contain many basic surprises and important observations, of which only a few are listed here. Earliest cleavages are total and equal. Multiflagellated cells, characteristic of triploblastic animals, were totally unexpected to occur in sponges. Absence of anchoring rootlets in ciliated cells is unexpected since such rootlets are ubiquitous in larvae of other Porifera. Gastrulation by cellular delamination is a pattern not seen in larvae of other Porifera. Several important aspects of hexactinellid reproduction and development remain unknown: What are the characteristics of mature sperm? Do they have an acrosome? What is their functional lifespan in terms of time and distance under natural environmental conditions? How is fertilization accomplished? When and how do maturation divisions occur in oocytes? Is the pattern of continuous reproduction in *Farrea sollasi* and *Oopsacas minuta* characteristic of all hexactinellids?

POST-LARVAL SKELETON DEVELOPMENT

Differences in early postlarval and juvenile stages of skeletal deposition are likely to be important in assessing phylogenetic relationships between hexactinellid taxa, but information is scant on these critical stages. Hexactinellid postlarval development has not been the focus of any published study, but pertinent observations are scattered through taxonomic reports, with the smallest specimens in the 10 mm range of body size. Larvae or early postlarval stages are unknown for Amphidiscophora. SCHULZE (1899) described and figured the early basidictyonal framework of the lyssacine hexasterophoran *Rhabdocalyptus mirabilis* (interpreted there

as a bud, but almost certainly a juvenile sponge), but, like many such reports, this was a single stage in an otherwise unknown sequence. Many and perhaps most lyssacine hexasterophorans form such basidictyonal skeletons, but they are known only from few species. OKADA (1928) included observations on field-collected postlarval and juvenile stages of *Farrea sollasi*, and while he reported on the sequence of spicule type formation, his description and figures on formation of the basidictyonal skeleton and early stages of the true dictyonal skeleton formation are sparse and contradictory. Here I report new observations of the sequence of postlarval (<0.5 mm body dimension) and juvenile (>0.5 mm body dimension) of the lyssacine *Leucopsacas scoliodocus* from the coast of British Columbia, Canada (Fig. 2).

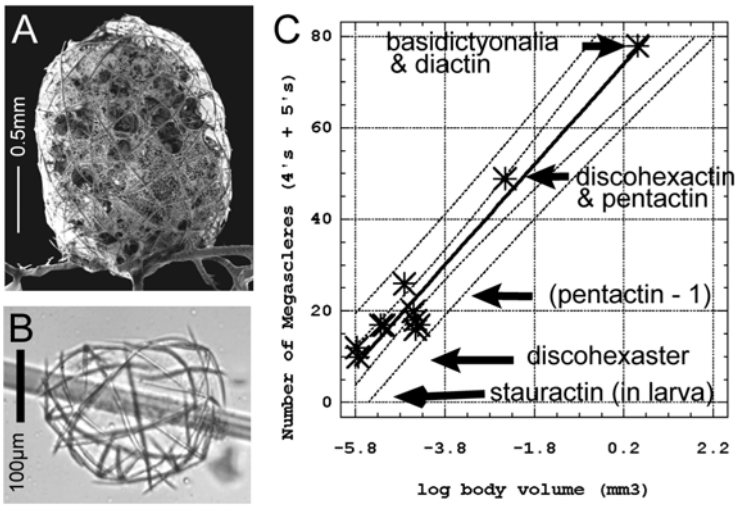

Fig. 2. Postlarval stages and spicule formation of *Lecopsacas scoliodocus*. **A,** juvenile attached to frame of *Aphrocallistes vastus* (SEM). **B,** late postlarva (LM). **C,** sequence of spicule initiation along regression line of body volume on the number of superficial megascleres (stauractins and pentactins).

A group of 15 *L. scoliodocus* were obtained from a fragment of dead *Heterochone calyx* skeleton from 428 m depth by submersible. The specimens, mostly small postlarvae, 0.18 to 0.35 mm diameter but including one 24 mm-long adult and two juveniles, 1.85 and 0.76 mm in length, were fixed in Bouin's fluid and transferred to ethanol for storage. Small stages were whole-mounted in balsam and viewed by light microscopy. The entire spicule complement of most postlarvae and both juveniles were enumerated. The smallest postlarvae have only stauractin spicules numbering from 10 to 24. The sequence of initiation of spicule types is: stauractins in larvae, spherical discohexasters (one-half adult size) in postlarvae), pentactine megascleres (begin in largest postlarva), discohexactine microscleres (in smallest juvenile), diactine megascleres and basal hexactins (first occur in the largest juvenile). Stauractins continue to be added throughout the size (age?) series, hence they are not merely larval spicules. The basidictyonal skeleton does not begin to form until the

juvenile is at least 1mm long and even at nearly 2mm body length is only beginning to form an attachment skeleton. Throughout postlarval and juvenile development, the small sponges are attached to hard substrate only by soft tissues. The largest juvenile has not yet begun formation of three adult spicule types: the choanosomal hexactin megascleres, a thin discohexactin and stellate discohexaster. The most significant difference from earlier work is precocious formation of discohexasters and early basidictyonal skeleton deposition in *F. sollasi* relative to *L. scoliodocus*. Similar studies on other hexactinellida are needed to assess relative timing of formation of comparable spicule types and, especially, the details of basal and main dictyonal framework construction.

HIGH DENSITY HEXACTINELLID POPULATIONS

Hexactinellida are not generally regarded to be very significant components of deep-sea communities. They are often large, but generally rare. In some regions, however, they may be one of the main faunal elements or even the clearly dominant group. Even at the time Hexactinellida was being recognized as a taxon by THOMSON (1868) and SCHMIDT (1870), such massive populations of *Pheronema* (then *Holtenia*) *carpenteri* (Amphidiscophora) were reported from 820-1000 m depths by the 'Porcupine' in the area between Scotland and the Faeroe Islands, that the area was dubbed "Holtenia ground" (CARPENTER *et al.,* 1870). Recent investigations with camera mounted sled in the adjacent Porcupine Seabight SE of Ireland at depths of 1000-1300 m (RICE *et al.,* 1990) and collections off the coast of Morocco, NW Africa (BARTHEL *et al.,* 1996) suggest that the population extends as a continuous dense band varying in depth over this very large region.

Dense populations of hexactinellids, mainly (lyssacine) Rossellidae, have long been known from Antarctic shelf waters in reports from numerous early oceanographic cruises to the region, and especially in shallow depths at McMurdo Sound (DAYTON *et al.,* 1970). More recent photographic, trawl and grab sampling have documented the high abundance of hexactinellids in several Antarctic shelf waters, particularly in the Weddell Sea (BARTHEL *et al.,* 1990; BARTHEL, 1992). Unlike the NE Atlantic population, the Antarctic communities consist of mixture of several species of very large hexactinellid species and a comparable component of demosponges.

Large bioherms constructed by a few species of dictyonine hexactinellids have recently been discovered at ca. 200 m depth on the continental shelf of British Columbia, Canada (CONWAY *et al.,* 1991, 2001; KRAUTTER *et al.,* 2001). Individual reefs are several km in dimensions and are argued to serve as a living analogue to the large reefs also built by dictyonine hexactinellids of the Late Jurassic and Cretaceous which extended across much of present Europe and parts of North America.

Another dense monospecific population of an amphidiscophoran hexactinellid, *Sericolophus hawaiicus*, has been discovered by YOUNG & MALDONADO (pers. comm.) off the west coast of Hawaii, in a narrow depth band between approximately 350 and 450 m. The most recent report of a high-density population of hexactinellid (FULLER, 2002) is the large monospecific bed of *Vazella pourtalesi* (lyssacine, Rossellidae) long known to fishermen working the banks off Nova Scotia, eastern

Canada. Studies of bycatch records by FULLER (pers. comm.) indicate the sponges are being decimated at the rate of tons per trawl.

In view of the new discoveries of massive hexactinellid populations in regions not previously expected, it is likely that such densities will be encountered elsewhere as we continue to expand our knowledge of shelf and deep-sea benthos. The most fascinating questions of why they are developed at that location, and what limits them from range expansion are common to all of these examples. The alternate question of why and how hexactinellids can survive and persist at very low population densities over much of the deep-sea bottom is less likely to be amenable to testing for some time.

REFERENCES

ADAMS C.L., MCINERNEY J.O., KELLY M., 1999 - Indications of relationships between poriferan classes using full-length 18s rRNA gene sequences. *Mem. Queensl. Mus.,* **44**: 33-43.

BARTHEL D., TENDAL O.S., PANZER K., 1990 - Ecology and taxonomy of sponges in the eastern Weddell Sea shelf and slope communities. *Ber. Polarforsch.,* (**68**): 120-130

BARTHEL D., 1992 - Do hexactinellids structure Antarctic sponge associations? *Ophelia*, **36**: 111-118.

BARTHEL D., TENDAL O.S., THIEL H., 1996 - A wandering population of the hexactinellid sponge *Pheronema carpenteri* on the continental slope off Morocco, Northwest Africa. *P. S. Z. N. I Mar. Ecol.,* **17**: 603-616.

BIDDER G.P., 1929 - Sponges. Encyclopaedia Britannica. 14th ed., **21**: 254-261.

BORCHIELLINI C., BOURY-ESNAULT N., VACELET J., LE PARCO Y., 1998 - Phylogenetic analysis of the Hsp70 sequences reveals the monophyly of metazoa and specific phylogenetic relationships between animals and fungi. *Mol. Biol. Evol.,* **15**: 647-655.

BORCHIELLINI C., MANUEL M., ALOVON E., BOURY-ESNAULT N., VACELET J., LE PARCO Y., 2001 - Sponge paraphyly and the origin of Metazoa. *J. Evol. Biol.,* **14**: 171-179.

BOURY-ESNAULT N., VACELET J., 1994 - Preliminary studies on the organization and development of a hexactinellid sponge from a Mediterranean cave, *Oopsacas minuta*. In R.W.M van Soest, T.M.G. van Kempen, J.C. Braekman (eds), *Sponges in Time and Space.* Biology, Chemistry, Paleontology. Balkema, Rotterdam: 407-415.

BOURY-ESNAULT N., EFREMOVA S., BEZAC C., VACELET J., 1999 - Reproduction of a hexactinellid sponge: first description of gastrulation by cellular delamination in the Porifera. *Invertebr. Reprod. Dev.,* **35**: 187-201.

BURTON M., 1928 - Hexactinellida. *Danish Ingolf Expedition Reports,* **6** (4): 1-18.

CARPENTER W.B., JEFFRIES J.G., THOMSON.C.W., 1870 - Preliminary Report of the Scientific Exploration of the Deep Sea in H.M. Surveying vessel 'Porcupine' during the summer of 1869. *Proc. R. Soc. London,* **18**: 397-492.

CAVALIER-SMITH T., ALLSOPP M.T., CHAO E.E., BOURY-ESNAULT N., VACELET J., 1996 - Sponge phylogeny, animal monophyly, and the origin of the nervous system: 18S rRNA evidence. *Can. J. Zool.,* **74**: 2031-2045.

CLAUS C.F.W., 1872 - Grundzuge der Zoologie. 2nd ed., N.G. Elwert, Marburg und Leipzig, 1170 pp.

COLLINS A.G., 1998 - Evaluating multiple alternative hypotheses for the origin of Bilateria: an analysis of 18S rRNA molecular evidence. *P.N.A.S.,* **95**: 15458-15463.

CONWAY K.W., BARRIE J.V., AUSTIN W.C., LUTERNAUER J.L., 1991 - Holocene sponge bioherms on the western Canadian continental shelf. *Cont. Shelf Res.,* **11**: 771-790.

CONWAY K.W., KRAUTER M., BARRIE J.V., NEUWEILER M., 2001 - Hexactinellid sponge reefs on the Canadian continental shelf: a unique "living fossil". *Geosci. Can.,* **28** (2): 71-78.

DAYTON P.K., ROBILLIARD G.A., PAINE R.T., 1970 - Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. In M.W. Holgate (ed.), *Antarctic Ecology,* Vol. **I**, Academic Press, N.Y.: 244-258.

FULLER S.D., 2002 – Analysis of trawl survey and observer reports of sponge by-catch in the northwest Atlantic: what are we losing? *Boll. Mus. Ist. Biol Univ. Genova,* **66-67**: 71.

GEHLING J.G., RIGBY J.K., 1996 - Long expected sponges from the neoproterozoic ediacara fauna of South Australia. *J. Paleontol.,* **70**: 185-195.

GRAY J.E., 1867 - Notes on the arrangement of sponges, with the description of some new genera. *Proc. Zool. Soc. London,* **1867**: 492-558.

HOOPER J.N.A., SOEST R.M.W. VAN, 2002 - Systema Porifera. A Guide to the Classification of Sponges. Kluwer Academic / Plenum Publishers, New York, (2 vols) 1708 pp.

IJIMA I., 1901 - Studies on the Hexactinellida. Contribution I. (Euplectellidae). *J. Coll. Sci. Imp. Univ. Tokyo,* **15**: 1-299.

IJIMA I., 1903 - Studies on the Hexactinellida. Contribution III. (*Placosoma*, a new Euplectellida; Leucopsacidae and Caulophacidae). *J. Coll. Sci. Imp. Univ. Tokyo,* **18**: 1-124.

IJIMA I., 1904 - Studies on the Hexactinellida. Contribution IV. (Rossellidae). *J. Coll. Sci. Imp. Univ. Tokyo,* **18** (7): 1-307.

IJIMA I., 1927 - The Hexactinellida of the Siboga Expedition. *Siboga Expedition Reports,* **6**: 1-383.

KOZIOL C., LEYS S.P., MÜLLER I.M., MÜLLER W.E.G., 1997 - Cloning of Hsp70 genes from the marine sponges *Sycon raphanus* (Calcarea) and *Rhabdocalyptus dawsoni* (Hexactinellida). An approach to solve the phylogeny of sponges. *Biol. J. Linn. Soc.,* **62**: 581-592.

KRAUTTER M., CONWAY K.M., BARRIE J.V., NEUWEILER M., 2001 - Discovery of a "living dinosaur": globally unique modern hexactinellid sponge reefs off British Columbia, Canada. *Facies,* **44**: 265-282.

KRUSE M., LEYS S.P., MÜLLER I.M., MÜLLER W.E.G., 1998 - Phylogenetic position of the hexactinellida within the phylum Porifera based on the amino acid sequence of the protein kinase C from *Rhabdocalyptus dawsoni*. *J. Mol. Evol.*, **46**: 721-728.

MACKIE G.O., SINGULA C.L., 1983 - Studies on hexactinellid sponges. I. Histology of *Rhabdocalyptus dawsoni* (Lambe, 1873). *Philos. Trans. R. Soc. London (B),* **301**: 365-400.

MEDINA M., COLLINS A.G., SILBERMAN J.D., SOGIN M.L., 2001 - Evaluating hypotheses of basal animal phylogeny using complete sequences of large and small subunit rRNA. *Proc. Natl. Acad. Sci. USA,* **98**: 9707-9712.

MEHL D., 1992 - Die Entwicklung der Hexactinellida seit dem Mesozoicum. Palaeobiologie, Phylogenie und Evolutionsoekologie. *Berl. Geowiss. Abh. (E)*, **2**: 1-164.

MEHL D., 1998 - Porifera and Chancelloriidae from the Middle Cambrian of the Georgina Basin, Australia. *Palaeontology,* **41**: 1153-1182.

MEHL D., MÜLLER I., MÜLLER W.E.G., 1998 - Molecular biological and paleontological evidence that Eumetazoa, including Porifera (sponges), are of monophyletic origin. In Y. Watanabe, N. Fusetani (eds), *Sponge Sciences Multidisciplinary Perspectives*. Springer Verlag, Tokyo: 133-156.

MEHL-JANUSSEN D., 1999 - Die fruehe Evolution der Porifera: Phylogenie und Evolutionsoekologie der Poriferen im Palaeozoikum mit Schwerpunkt der desmentragenden Demospongiae (>>Lithistide<<). *Muenchner Geowiss. Abh.,* **37**: 1-72.

OKADA Y., 1928 - On the development of a hexactinellid sponge, *Farrea sollasii*. *J. Fac. Sci. Imp. Univ. Tokyo Sect. IV Zool.,* **2** (1): 1-27.

REID R.E.H., 1957 - On Hexactinellida, "Hyalospongea", and the classification of siliceous sponges. *J. Paleontol.,* **31**: 282-286.

REID R.E.H., 1958 - A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part I. *Paleontogr. Soc. Monogr. London,* **111**: i-xlvi.

REID R.E.H., 1964 - A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part IV. *Paleontogr. Soc. Monogr. London,* **117** (3): xlix-cliv.

REISWIG H.M., MACKIE G.O., 1983 - Studies on hexactinellid sponges III. The taxonomic status of Hexactinellida within the Porifera. *Philos. Trans. R. Soc. London (B),* **301**: 419-428.

REISWIG H.M., TSURUMI M., 1996 - A new genus and species of Aulocalydicae, *Leioplegma polyphyllon*, (Porifera: Hexactinellida) from the Blake Ridge off South Carolina, U.S.A. *Bull. Mar. Sci.,* **58**: 764-774.

REITNER J., MEHL D., 1996 - Monophyly of Porifera. *Verh. Naturwiss. Ver. Hambg.,* **36**: 5-32.

RICE A.L., THURSTON M.H., NEW A.L., 1990 - Dense aggregations of a hexactinellid sponge, *Pheronema carpenteri*, in the Porcupine Seabight (northeast Atlantic Ocean), and possible causes. *Prog. Oceanogr.,* **24**: 179-196.

SCHMIDT O., 1870 - Grundzüge einer Spongien-fauna des Atlantischen Gebietes. Engelmann, Leipzig, 88 pp.

SCHMIDT O., 1871 - Das naturliche System der Spongien. *Mitt. Naturwiss. Ver. Steiermark,* **2** (3): 261-269.

SCHRAMMEN A., 1902 - Neue Hexactinelliden aus der oberen Kreide. *Mitt. Roem. Mus. Hildesh.,* **15**: 1-26.

SCHRAMMEN A., 1903 - Zur Systematik der Kieselspongien. *Mitt. Roem. Mus. Hildesh.,* **19**: 1-21.

SCHRAMMEN A., 1924 - Die Kieselspongien der oberen Kreide von Nordwestdeutschland. III. und letzter Teil. *Monogr. Geol. Paleoent. Ser. 1 H.,* **2**: 1-159.

SCHULZE F.E., 1880 - On the structure and arrangement of the soft parts in *Euplectella aspergillum*. *Trans. R. Soc. Edinburgh,* **19** (2): 661-673 + pl. 17.

SCHULZE F.E., 1886 - Über den Bau und das System der Hexactinelliden. *Abh. König. Akad. Wiss. Berl. (Physik.-Mathem.),* **1886**: 1-97.

SCHULZE F.E., 1887 - Report on the Hexactinellida collected by H.M.S. "Challenger" during the years 1873-1876. *Rep. Sci. Res. H.M.S. Challenger 1873-76, Zool.,* **21**: 1-513.

SCHULZE F.E., 1899 - Amerikanische Hexactinelliden nach dem materiale der Albatross-Expedition. G. Fischer, Jena, 129 pp.

SCHULZE F.E., 1904 - Hexactinellida. *Wiss. Ergeb. Deutsch. Tiefsee Exped. Valdivia 1898-1899,* **4**: 1-266.

SCHÜTZE J., KRASKO K., CUSTODIO M.R., EFREMOVA S.M., MÜLLER I.M., MÜLLER W.E.G., 1999 - Evolutionary relationships of Metazoa within the eukaryotes based on molecular data from Porifera. *Proc. R. Soc. London (B),* **266**: 63-73.

STEINER M., MEHL D., REITNER J., ERDTMANN D., 1993 - Oldest entirely preserved sponges and other fossils from the Lowermost Cambrian and a new facies reconstruction of the Yangtze platform (China). *Berl. Geowiss. Abh. (E),* **9**: 293-329.

TABACHNICK K.R., REISWIG H.M., 2000 - Porifera Hexactinellida: on Euryplegma auriculare Schulze, 1886, and formation of a new order. *Mem. Mus. Natl. Hist. Nat.,* **184**: 39-52.

THOMSON C.W., 1868 - On the "vitreous" sponges. *Ann. Mag. Nat. Hist. (4),* **1**: 114-132.

ZITTEL K.A., 1877 - Studien über fossile Spongien. I. Hexactinellidae. *Abh. König. Bayer. Akad. Wiss. (Mathem.-Physic.),* **13** (1): 1-63.