THREE NEW SPECIES AND ONE NEW GENUS OF FARREIDAE (PORIFERA: HEXACTINELLIDA)

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ABSTRACT
Three new species and one new genus of Farreidae are reported. The first, *Farrea herdendorfi*, is described from nearly undamaged specimens collected by robot submersible from the shipwreck of the S.S. 'Central America', 300km ESE of Charleston, S.C. The second, *Farrea seiri*, is described from a partial specimen obtained by dredge near the South East Indian Ridge in the Indian Ocean. The new genus and species *Asceptrula axialis*, is described from fragments collected by robot submersible from the Juan de Fuca Ridge, off northern Oregon.

RÉSUMÉ
Trois nouvelles espèces, dont un nouveau genre, de Farreidae sont detaillées dans cette étude. La description de la première espèce, *Farrea herdendorfi*, est basée sur des spécimens presqu'intacts, recueillis par un sous-marin robot et prélevés sur l'épave du
'S.S. Central America' (300 km à l'ESE de Charleston, Caroline du Sud). Pour la description de la deuxième espèce, *Farrea seiri*, un spécimen incomplet, obtenu par dragage de l'Océan Indien, près de la dorsale océanique sud-est indienne, est utilisé. Les fragments utilisés pour la description de la nouvelle espèce, *Asceptrula axialis* (nouveau genre: *Asceptrula*), ont été obtenus par sous-marin robot, au large du Nord de l'Orégon, dans la dorsale océanique Juan de Fuca.

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INTRODUCTION

Although discovered over 150 years ago, hexactinellid sponges, more familiarly referred to as "glass sponges", are still obscure members of the deep-sea invertebrate fauna. Due to their remote habitat, few researchers have had the opportunity to work with them, and very few have had the chance to work with live specimens. Though defined as sponges that construct either rigid frameworks or loose frameworks from six-rayed siliceous spicules exhibiting cubic symmetry, many other aspects of their biology, including reproduction, feeding and development remain relatively unknown. Even basic data pertaining to distribution and diversity have only recently surfaced. Of course, both distribution and diversity are related to taxonomy, which has been historically unstable in this group. This instability at such a basic level of knowledge has undoubtedly discouraged many workers from undertaking research on these organisms.

It is not surprising that taxonomy of the group has remained unstable until recent times and still remains so. Due to the physical inaccessibility of the group, specimens have historically been available mainly through dredging operations, which usually result in serious morphological damage, obscuring much important taxonomic information. With the advent of modern research submersibles, intact undamaged specimens have been acquired, providing a new wealth of data on delicate surface characters. This new information makes it possible to correct many historical taxonomic problems, providing a more secure foundation from which to assail more complex topics, such as local diversity or commercial exploitation (bioactive product determination).

Indeed, the possibility of developing a more coherent taxonomic scheme for the group has become a reality, in the form of "Systema Porifera". This project, a collaborative effort of over thirty spongologists around the globe, is an attempt to sort and codify the higher classification of phylum Porifera down to the genus level, making it the most thorough revision of the taxon in history. As such, any addition to the knowledge of the group, especially at the level of genus or higher, is timely.

It is the aim of this study to provide accurate descriptions of three new species of Farreidae, a very old and historically important family of Hexactinellida, placed within the suborder Hexactinosida. The Farreidae are defined by the presence of clavules **(Fig. 4D)**, or derivatives, and are typified by a two-dimensional primary skeletal framework **(Fig. 6A).** Because one of the new forms lacks the first of these two characters, it is also necessary to erect a new genus for it.

Among the objectives of this study is an assessment of some of the problems inherent in current definitions of the relevant taxa, and how strict applications of these definitions do not necessarily reflect reality. A modification of the family diagnosis is suggested. Hopefully, this study will provide new information and insight into the family Farreidae, in terms of both its diversity and its taxonomic foundations.

LITERATURE REVIEW

Currently, Hexactinellida is recognized as either a) one of three extant classes within the phylum Porifera **(Bergquist, 1978; Hooper & Wiedenmayer, 1994; Reiswig, 1994; Vacelet, 1994; Lévi, 1997;)**, or as one of two classes (Hexactinellida, Demospongiae) of the Porifera **(Borchiellini et al, 2001).** On the basis of

morphological characters, Hexactinellida differs strongly enough from its cohorts that a higher level taxonomic differentiation has been suggested (**Reiswig & Mackie, 1983**), recognizing two subphyla, Cellularia (containing Calcarea and Demospongiae) and Symplasma (containing Hexactinellida). The differences between the groups themselves can be separated into a) skeletal and b) cellular. On the skeletal level, Hexactinellida are primarily constructed from six-rayed siliceous spicules formed with cubic symmetry, a synapomorphic character not found in either of the other two classes. On the cellular level, several workers (**Schulze, 1887; Ijima, 1903; Okada, 1928; Reiswig, 1979; Mackie & Singla, 1983; Boury-Esnault & Vacelet, 1994**) have found Hexactinellida to be syncytial in organization, in striking contrast to the cellular organization of all Calcarea and Demospongiae **(Fig. 1)**. In contrast to this hypothesis which sets Hexactinellida apart, recent analysis of molecular sequences **(Borchiellini et. al, 2001)** has determined that Porifera is a paraphyletic group, with Calcarea being more closely related to Eumetazoa than the siliceous sponges (Hexactinellida, Demospongiae), supporting the upgrade of Class Calcarea to the phylum level.

Within Hexactinellida, skeletal organization is the most important character used to characterize high-level division. Those sponges with primary skeletons composed of diactine (two-rayed) megascleres, unfused or joined by simple silica bridges (synapticulae) are called lyssacine sponges; secondary fusion of their diactins never results in regular silica lattices. In others, hexactin (6-rayed) megascleres are fused permanently and rigidly into three-dimensional lattice frameworks of silica, and are called dictyonine sponges (**Reid 1964**). These two primary skeletal forms, once

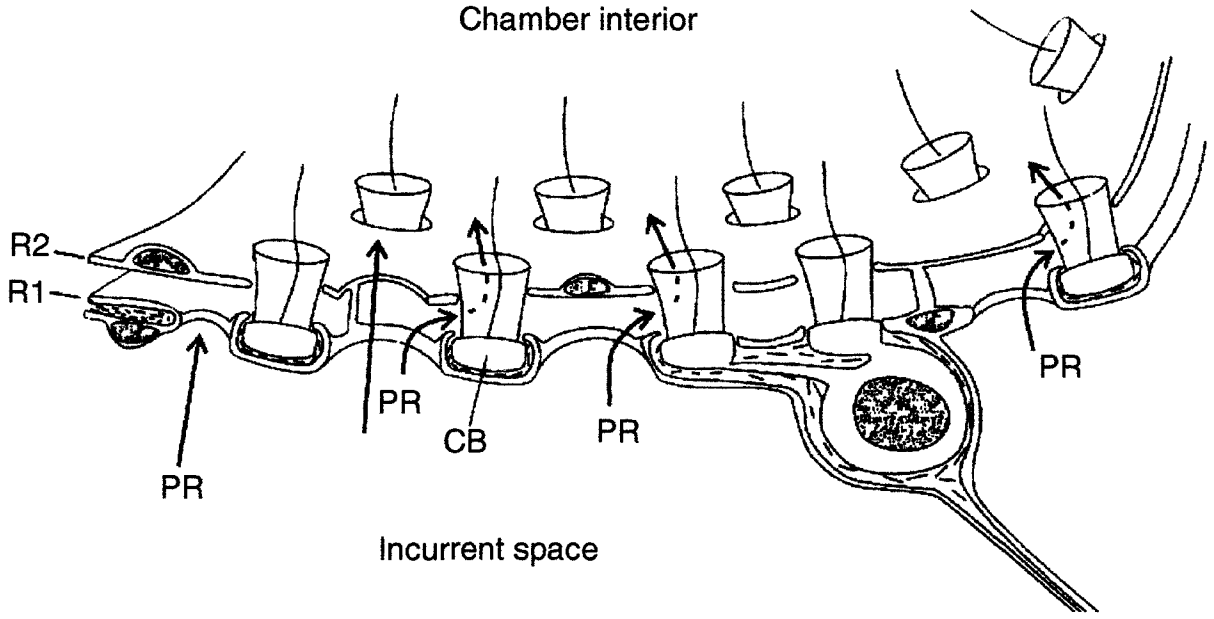

Figure 1. Cross-section of a flagellated chamber wall of a hexactinellid. Primary reticulum (R1) surrounds the enucleate collar bodies (CB). The secondary reticulum (R2) forms a thin supporting layer around the collars of the collar bodies. Water enters from the incurrent space through the prosopyles (PR). Modified from Leys, 1999.

used as the basic taxonomic division of the class Hexatinellida, are now considered grades of organization, but still form the basis, along with spicule geometry, for subclass and order definitions.

Biology

As mentioned above, the remote nature of hexactinellid habitat has rendered them difficult objects of study, and, as a result, their basic biology is not very well understood. With most species living only below 100m, as documented by **Tabachnik (1994)**, hexactinellids have often been obtained by dredge, and such specimens were rarely suitable for cellular/histological investigation. Though several authors **(Schulze, 1887, Ijima 1901)** attempted soft-tissue analysis on less-than-optimal specimens, the unique nature of the glass sponge tissue was highlighted by **Ijima (1901)**, who concluded, despite the poor condition of his specimens, the Hexactinellida were syncytial in nature.

It wasn't until the use of electron microscopy that the true syncytial nature of the Hexactinellida was confirmed. Recently, **Reiswig (1979)**, **Mackie and Singla (1983)**, and **Leys (1995; 1999)** verified this claim through TEM (transmission electron microscopy) investigation of the hexactinellid sponges, *Rhabdocalyptus dawsoni* (Lambe, 1892) and *Aphrocallistes vastus*, (Schulze, 1886) obtained from shallow water populations near Victoria, BC. These investigations not only confirmed the suspicions of past workers, but elaborated upon the unique characters of the Hexactinellida, the most prominent of which are the following: 1) the presence of collar-bearing and supporting structures, known as the choanosyncytium and

secondary reticulum respectively, which are absent in both Demospongiae and Calcarea **(Fig. 2)**; 2) secretion of their spicules intracellularly in giant multinucleate cells; 3) the presence of unique perforate septal partitions, constructed by the Golgi apparatus, inserted in intracellular bridges which join regions of specialized cytoplasm, **(Fig. 3);** and lastly 4) the absence of pinacocytes (or external "skin" cells), which follows logically from the conclusion that hexactinellids are syncytial organisms.

Indeed, this list of features has since been confirmed in *Aulorossella vanhoeffeni* (Schulze & Kirkpatrick, 1910) by **Salomon & Barthel, 1990**, *Farrea occa* (Bowerbank, 1862) by **Reiswig & Mehl, 1991**, *Dactylocalyx pumiceus* (Stutchbury, 1841) by **Reiswig, 1991** (though no secondary reticulum was found here) and *Oopsacas minuta* (Topsent, 1927) by **Boury-Esnault & Vacelet, 1994**. The most pertinent of these for the present report is the study of *Farrea occa*, a member of the family Farreidae. Extensive TEM investigations into this species uncovered yet another unique structure, known as the inner membrane, a cytoplasmic extension of the secondary reticulum, spanning the width and breadth of the choanochamber. It is hypothesized that this structure aids both in food acquisition and in the gathering of non-digestible products, packaging and releasing them into the exhalant water stream.

Feeding –

Over the last few years, and across several species **(Mackie & Singla, 1983; Perez, 1996; Wyeth et al., 1996; Wyeth, 1999),** it has been proven that the reticulum, and not the collar bodies (functional and presumed phylogenetic homologs

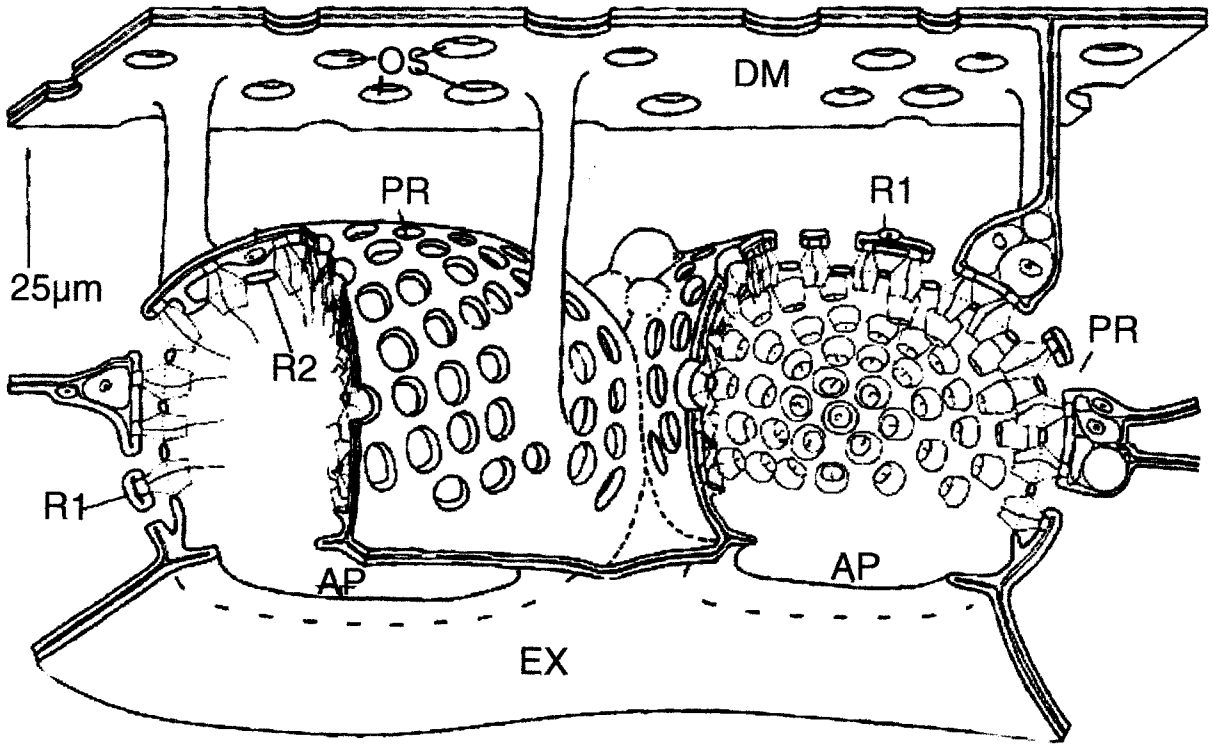

Figure 2. Diagram of two flagellated chambers in a hexactinellid, attached to the the dermal membrane (DM). Water enters the animal through ostia (OS), enters the chambers through prospyles (PR), and exits through the apopyles (AP) into the exhalant space (EX). The flagellated chambers contain a perforate syncytial perimeter, or primary reticulum (R1), an internal extension known as R2, which supports the collar bodies, and an enucleate choano-syncytium, bearing the aforementioned collar bodies/flagellar units. Modified from Reiswig & Mehl, 1991.

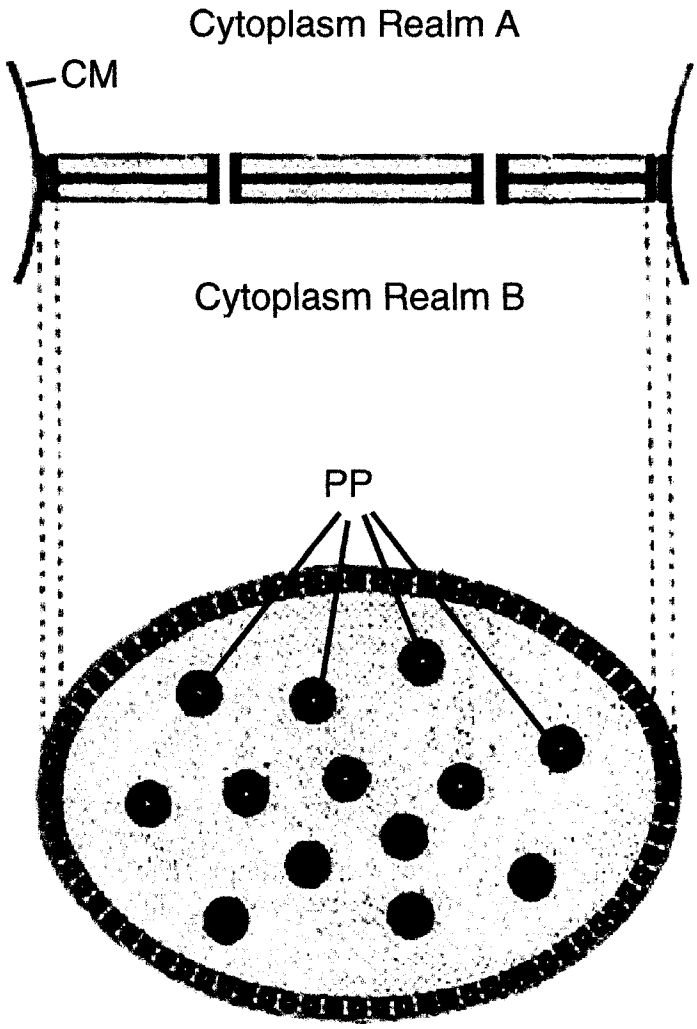

Figure 3. Diagram of a septal partition, forming an intracellular bridge joining specialized regions of cytoplasm. CM, cell membrane; PP, pore particle. Modified from Mackie & Singla, 1983.

of choanocytes), are the primary food capture structures in the hexactinellids. Unsurprisingly, this system is fundamentally different from that found in subphylum Cellularia, where food particles are captured mainly by the choanocytes, then digested and distributed by wandering amoebocytes. A potentially more efficient distribution system, that of cytoplasmic streaming, has been observed in members of the Hexactinellida **(Leys & Mackie, 1994)**, and would seem to render amoebocytes redundant. The filtration systems of hexactinellids are capable of filtering out particles down to 0.1μm in diameter **(Perez, 1996)**.

Reproduction and Development –

Though little work has been done on hexactinellid reproduction, studies done by **Boury-Esnault & Vacelet (1994)** on the lyssacine *Oopsacas minuta*, have expanded greatly on the early work done by **Okada (1928)** on the dictyonine *Farrea solasii* (Schulze, 1886). Both workers reported that the organisms in question reproduced throughout the entire year, without seasonal variation. Okada reported oocytes, spermatozoa, total and regular cleavage, a planula-like blastula, and a larval stage, the younger versions of which were without flagellated chambers. These discoveries have more recently been confirmed by **Boury-Esnault & Vacelet, (1994)**, who additionally described a new larval form termed a trichimella larva, notably different from that found in any other sponge as it contains multiflagellated cells.

On the topic of development, it should be mentioned that long segment, triple-helix structures resembling homeobox genes were recently discovered in *Ephydatia fluviatilis*, (Linnaues, 1758) a freshwater demosponge **(Coutinho et al., 1994)**. These

were found to share a 62% identity with the unclassified chicken Chox-7 homeodomain, and a 54% identity with the nematode ceh-9 homeodomain. These results are the first to indicate that homeobox genes also exist in sponges.

Conduction System –

By far and away the most interesting aspect of hexactinellid biology is the recent discovery of an electrical-potential, stimulus-conduction system in these animals, and the nature of that conduction system. It is generally recognized that all Porifera (Hexactinellida, Demospongiae and Calcarea) lack nerve cells. The drive behind the hexactinellid investigations was to determine how these sponges, without neurons, were capable of quickly propagating a signal to initiate and coordinate flagellar arrest as a response to either physical stimulus or the overabundance of particulate matter in the inhalant water **(Mackie, 1979; Mackie et al., 1983; Leys & Mackie, 1997; Leys et al., 1999)**. Though both chemical diffusion and mechanical coordination were considered as possibilities, it was eventually concluded that electrical impulse conduction through the trabecular syncytium and pinacoderm was the only possible method of coordinating flagellar arrest. This conduction system was recorded and found to be based on an all-or-nothing propagating event, dependent on Ca2+ influx, reaching conduction velocities of 0.27±0.1cm/s, with no evidence of either light sensitivity or diurnal rhythmicity **(Leys et al., 1999)**. Neurons remain undemonstrated in Porifera.

Distribution

Though some early work has been done on the topic of hexactinellid

distribution, a recent comprehensive overview was generated by **Tabachnik, 1994,** through a survey of over 300 data sources. He came to several interesting conclusions. He found clear support for the assertion made by **Lévi (1964)** that hexactinellids were primarily bathyal (200-2000m depth), as opposed to abyssal (>2000m depth) organisms. He also found that, given the available depth ranges, both bathyal and abyssal groups had the highest degree of endemism, and lowest levels of faunal overlap, leading him to conclude that the bathyal and abyssal zones served as independent foci for hexactinellid speciation.

Reid (1968) showed that distribution of modern Hexactinellids did not show a correlation with low temperatures. He proposed several other limiting factors for growth, including 1) light, 2) physical or physio-chemical disturbance, 3) high oxygen levels or 4) a combination of two or more of the above.

Spicules

The members of class Hexactinellida consist solely of species with siliceous skeletal elements (spicules), the common, but not invariable fusion of which leads to the construction of a rigid and permanent framework. Within Hexactinellida, the order Hexactinosida comprises those members that form rigid skeletal frameworks constructed by fusion of simple hexactine spicules (all six rays developed).

Traditional taxonomic classification schemes for Hexactinellida (**Zittel 1877; Schulze 1886, 1887, 1904; Schrammen 1912, 1924; Ijima 1927; Reid 1964**) have considered body shape, spicule form and skeletal organization as important diagnostic characters for higher level taxonomic division and definition.

Spicule Formation –

Within the core of almost all siliceous spicules lies an organic axial filament. The axial canal, a structure left behind by dissolution of the axial filament, is square in cross section in the Hexactinellida **(Reiswig, 1971; Hartman, 1982)**, and triangular in Demospongiae **(Hooper & Wiedenmayer, 1994; Uriz et al., 2000)**. Though it is generally believed that spicules are formed by silica deposition on the organic filament, it is often a source of confusion as to where this deposition takes place, both in demosponges and hexactinellids. For Demosponges, different sources of evidence suggest an extracellular secretion, an intracellular secretion, or, more recently, both **(Uriz et al., 2000)**. For the hexactinellids, the argument is fundamentally the same. Are the spicules secreted intrasyncytially, or inside specific cells (cytoplasmic domains), plugged to the syncytium by junctions (septal partitions)?

Recently, **Boury-Esnault and Vacelet (1994)** discovered, through their work on the development of the hexactinellid *Oopsacas minuta*, that the first indication of spicular development was the appearance of a pseudocrystalline axial filament, surrounded by a silicalemma within a sclerocyte, the cell type responsible for spicule formation. Such a situation is much like that found in Demospongiae. On the other hand, several studies investigating the soft tissues of hexactinellids **(Ijima, 1901; Schulze, 1904; Okada, 1928; Reiswig, 1991; Reiswig & Mehl, 1994)** have indicated that spicules are formed intrasyncytially.

Little is known of the order in which spicules are formed in hexactinellid ontogeny and most information comes from early studies **(Schulze, 1887; Ijima,**

1901; Okada, 1928). According to **Okada's (1928)** work on *Farrea sollasii,* the order of spicule development is as follows (see **Fig. 4** for spicule types – stauractins not included): a) smooth stauractins (2-dimensional 4-rayed) spicules, b) microdiscohexasters (small hexactins, adorned with secondary rays and spines), c) hexasters (larger hexactins, both oxyhexasters, then discohexasters), d) dermal pentactins (large five-rayed spicules positioned on the outer or dermal surface), e) uncinates, (long, thin diactin spicules), f) clavules (long monactins with a cap and recurved spines), and g) gastral pentactins (large five-rayed spicules positioned on the inner or gastral surface). Though Okada based his developmental series on subjectively determined larval stages, the development of smooth stauractins as the initial spicules was confirmed by **Boury-Esnault & Vacelet (1994)** in *Oopsacas minuta*. Stauractins are larval spicules only, and are not retained in adult skeletons.

The mechanism of spicule formation and development is not completely understood; recent investigations into biosilicification have used demosponge models. With new techniques permitting isolation of axial filaments **(Shimizu, 1998)**, it was found that these are primarily composed of 3 types of protein, known as silicateins, with very similar molecular weights and amino acid compositions. It was also determined that the primary silicatein, silicatein-α, belongs to the cathepsin L-class papain-like protease superfamily, confirming the possibility of enzymatic function in biosilicification.

Spicule Shape –

Spicules within Hexactinellida are generally divided into two categories, megascleres and microscleres, on the basis of shape and function, but distinction

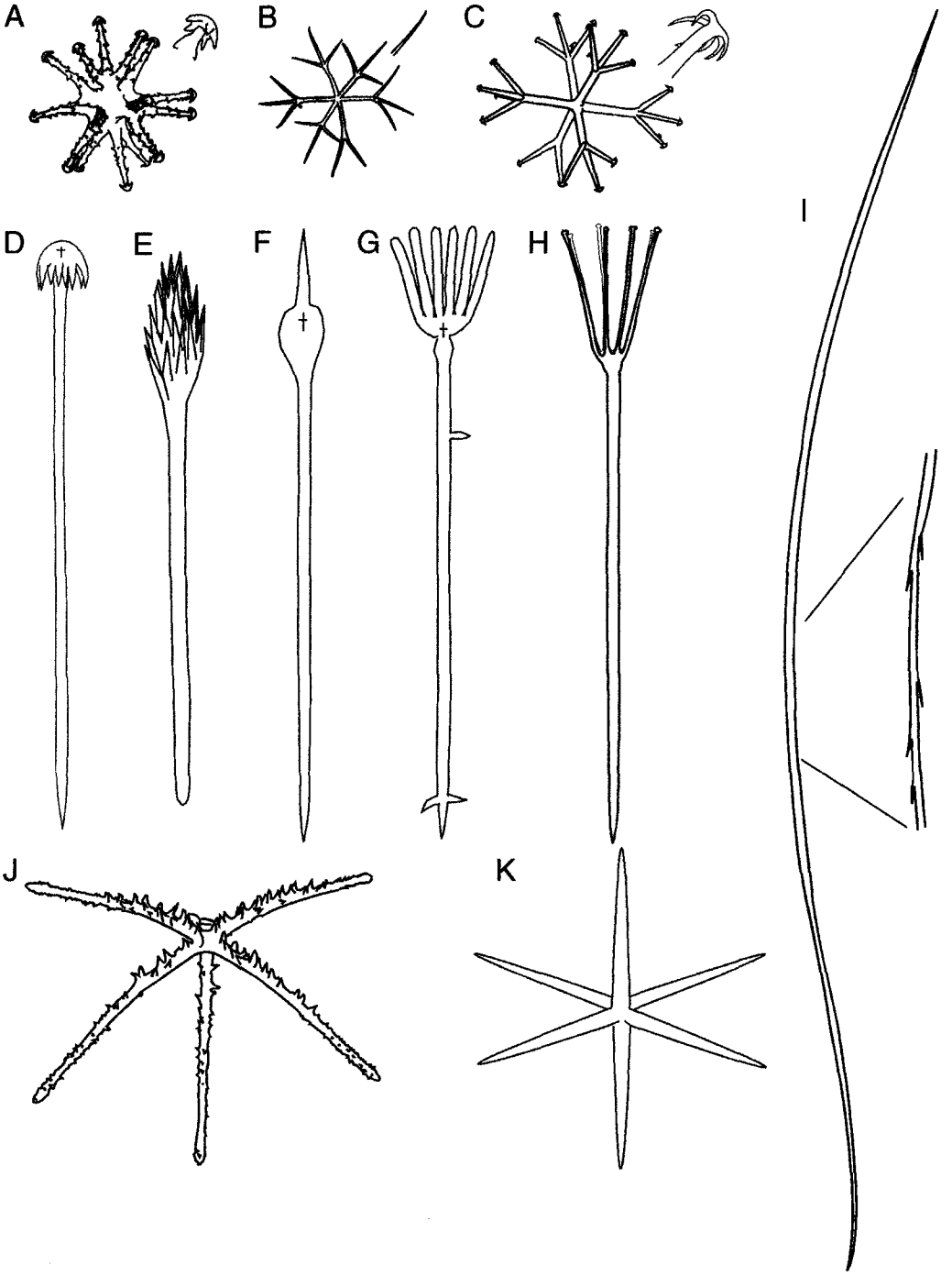

Figure 4. Spicule types of Farreidae and Euretidae, not to scale (A) discohexaster; (B) oxyhexaster; (C) onychexaster; (D) clavule; (E) sarule; (F) lonchiole; (G) aspidoscopule; (H) narrow-headed scopule (not found in Farreidae, but common in Euretidae and other hexactinosidans); (I) uncinate; (J) pentactin; (K) hexactin.

between the two categories is not always clear. The smallest spicules, known as microscleres, vary from 10's-100's of microns in diameter, whereas the larger megascleres, the primary components of the supporting skeletal framework of the animal, range from many 100's of microns to several 10's of centimeters in length. In Hexactinosida, several discrete size ranges of a single spicule type may be formed by a species **(Bergquist, 1978)**, often with specific local distribution of single size classes.

Spicule nomenclature within the two categories, microscleres and megascleres, is based on two main properties: a) the geometry of the spicule, determined by arrangement of its axial filaments, and b) the number of rays developed **(Reid, 1964)**. Indeed, the name "hexactinellid" derives from the primary type of spicule found in the class, a 6-rayed, or triaxon, spicule known as a hexactin. It is generally accepted **(Ijima, 1927; Reid, 1964)** that the hexactine template is basic to all spicule types within Hexactinellida, variations resulting from: a) reduced development of one or more rays (pentactins), b) reduction of 1 or more rays and the development of special secondary rays (astral microscleres), or c) the development of lateral spines, without the associated reduction of rays (scopules or clavules). The axial filament/canal system does not extend into the spines, but resides only in the rays **(Reid, 1964)**.

The most common form of microsclere in Farreidae, the subject of this report, is the triaxon hexaster, which is manifest as discohexasters (terminal rays end in discs), oxyhexasters (terminal rays end in points) or onychexasters (terminal rays end in a whorl of claws **(Fig. 4A, B, C).** These are believed to vary from the standard

hexactine template through the development of terminal ray appendages (= secondary rays or terminal rays).

Megascleres show much more structural variation. Within the megascleres fall the monactine, diactine, pentactine and hexactine spicules. Monactins, as their name implies, express only one ray of the possible six, with the axial cross, the spicule center, residing at the proximal end of the expressed ray. Often, the area including the axial cross bears heavy ornamentation (spines, tines, etc). As of yet, it is uncertain whether this ornamentation is homologous to secondary ray expression is astral microscleres. Typical monactins are globally referred to as sceptrules (200-600μm long, 20-60μm across the head), and, within Farreidae include: clavules and their supposed derivatives, sarules, lonchioles and aspidoscopules (**Reiswig, in press**) **(Fig. 4D, E, F, G)**. Indeed, sceptrule presence and type are a major character used in hexactinosidan taxonomy. The family Farreidae is still defined by the presence of clavules, or derivatives, and absence of narrow-headed scopules **(Fig. 4H)**.

Diactins, when present, are usually the largest spicules in the organism (1-10mm long, 1-20μm wide). In Hexactinosida, they are often manifest as uncinates **(Fig. 4I)**, long, very thin spicules, ornamented with distinctive barbs and brackets. An axial cross is not evident in these and that the interpretation they consist of two developed rays has no factual support.

Pentactins **(Fig. 4J)** are often quite large, with the unpaired ray often being the longest (0.3-0.5mm long, 0.3-0.5mm wide). The other two sets of paired rays, termed tangential rays, are usually symmetrical in both size and shape, and frequently bear ornamentation.

Hexactins **(Fig. 4K)**, as mentioned previously, are the primary spicule type in Hexactinellida (ca. 0.6mm diameter). It is through the formation and fusion of hexactins that the permanent, rigid skeletons of the dictyonine sponges are formed (mechanism discussed below).

Spicule Location –

The pattern of fusion of spicules determines the skeletal form of the sponge body. Some of the previously mentioned spicules appear rather uniformly distributed throughout a specimen, whereas others occur only in specific regions. The general body of a hexactinellid can be divided into three parts: 1) dermal - the outer surface, known or inferred to be the inhalant surface; 2) atrial (gastral in literature)- the surface of the internal axial cavity (atrial cavity) known or inferred to be exhalant; 3) parenchymal – internal sponge body between limiting surfaces.

Skeletal Formation

Although still unproven, it has been believed that all sponge spicules are separate at the time of formation, and, though some may be fused with others by silica deposition, many remain separate indefinitely. Those sponges whose skeletal construction is made up primarily of diactine and/or hexactine megascleres that remain unfused are called lyssacine; secondary fusion of diactins may occur but they do not constitute regular silica lattices. In others, hexactine megascleres are fused permanently and rigidly into three-dimensional frameworks of silica, and are called dictyonine sponges (**Reid 1964**). The skeletal frame of all living dictyonine sponges is attached directly to hard substrate for support. The order Hexactinosida, which

contains the family Farreidae, encompasses most of the dictyonine sponges. Though a complete review of the construction and features of dictyonine skeletons is beyond the scope of this project, a summary and review will be provided, as skeletal features are considered paramount topics in poriferan classification.

The fusion of two spicules, meaning the deposition of silica between two spicules lying almost in contact with one another, can occur in varying degrees. Two spicules may be cemented together, meaning that silica has been deposited between then, and, though attached, they are still recognizable as separate spicules **(Fig. 5A, B)**. More extensive deposition of silica results in full spicule fusion, the component spicules distinguished by internal surface "ghosts" and the presence of separate axial filaments, the axial components of each spicule remaining completely autonomous **(Fig. 5C)**.

Spicules undergoing fusion may have three general forms of orientation to each other **(Reid, 1964).**

1) enclosure of two parallel rays in a common depositional envelope **(Fig. 5C)**; here all junctions of rays are hexactine centers or "true nodes,"
2) attachment of tips of spicule rays to other nodal parts of other dictyonalia or to other dictyonal beams, resulting in "false nodes" ie. junctions which have no axial cross **(Fig. 5D, E)**, or
3) simple fusion of rays at arbitrary points of apposition, also resulting in false nodes **(Fig. 5F)**.

Of these three methods, the first **(Fig. 5C)** is the most common, which can lead to the development of linear series of parallel fused dictyonalia, often referred to as

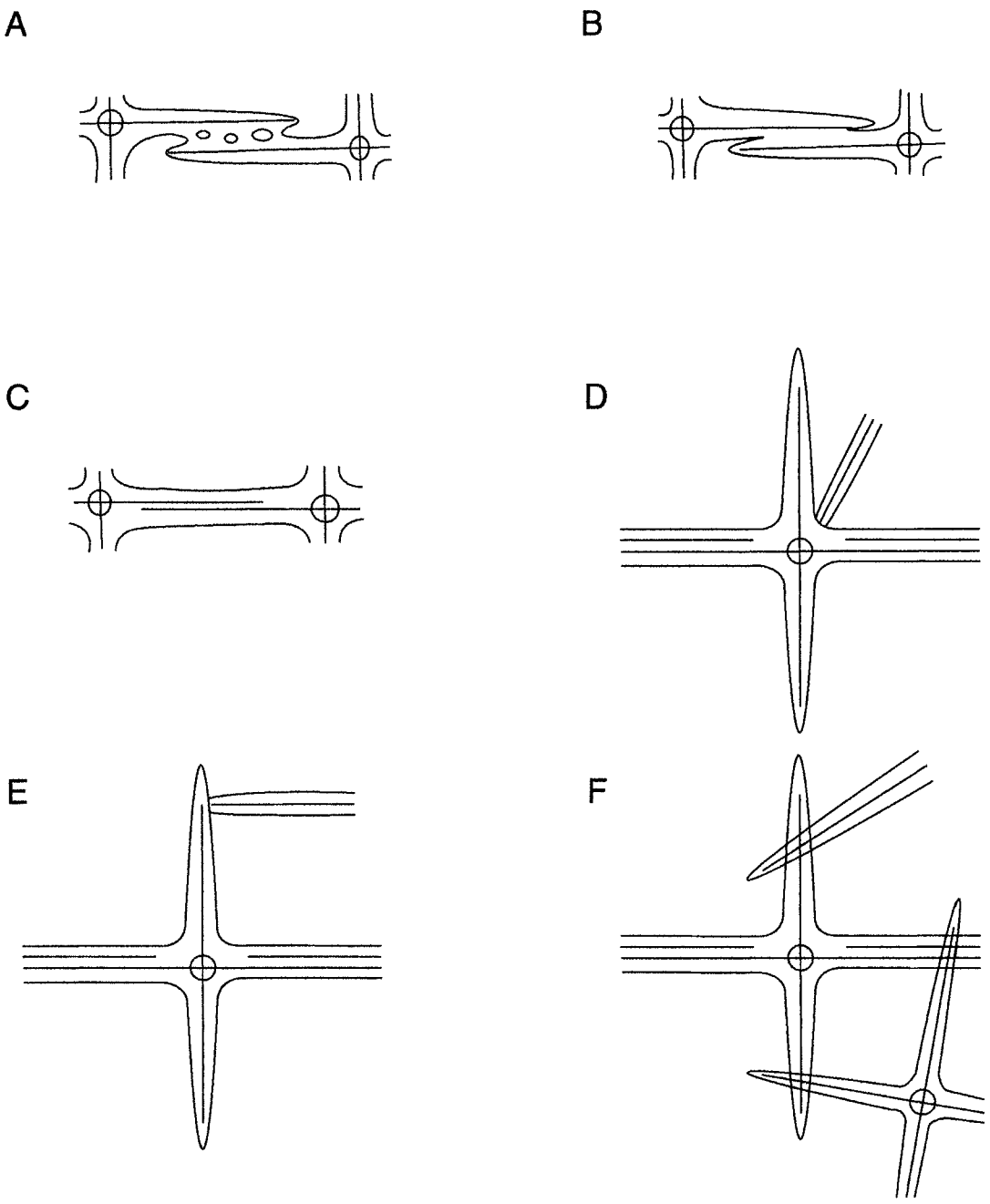

Figure 5. Diagrams of spicular fusion methods. (A) diagram of synapticular filaments; (B) partial cementation; (C) enclosure of two parallel rays in a common depositional envelope; (D) attachment of tips of spicules to nodal parts (the centres) of dictyonalia; (E) fusion of ray tips with other rays; (F) fusion of rays at arbitrary points of apposition.

dictyonal strands. These strands can be continuous throughout the entire length of the animal, and can be either primarily 2- or 3-dimensional in structure. They presumably provide a stronger basic scaffold for support of a more massive body.

Hexactinosidan classification is based mainly upon the primary aspects of skeletal growth, and thus it is important to define the difference between primary and secondary skeletal growth. The definition most often used is that of **Reid (1964:73)**:

> "All dictyonalia belonging to the series from which the dictyonal strands are formed are primary dictyonalia, and primary meshwork comprises all meshwork whose meshes are bounded by beams either belonging to dictyonal strands, or connecting strands laterally and formed from those rays of their components which project from them. In contrast, all dictyonalia which do not belong to dictyonal strands are secondary components and all meshes produced by their union with the primary framework or with one another are secondary meshes."

Within the general architecture of hexactinosidan frameworks, **Reid (1964)** recognized three distinct types: 1) farreoid, 2) euretoid, and 3) aulocalycoid, characteristic of three families, Farreidae, Euretidae and Aulocalycidae. Of these three, only the first two will be of any importance for this project.

A farreoid skeleton consists of a 2-dimensional primary grid-like framework. The dictyonalia in parallel strands are often in corresponding positions and can easily cross-link with one another, resulting in a grid-like appearance. It is the single layer, or 2-dimensional, character of this structure that is often considered distinctive for the family Farreidae. This may be maintained throughout the life of the animal, or it may be subsumed either partially or completely into a 3-dimensional construct through the

addition (fusion on) of secondary skeletal dictyonalia. The secondary components may be added by fusion in either a regular or irregular fashion, resulting either in a roughly cubic 3-dimensional latticework, or one or more completely irregular layers of dictyonal spicules superimposed on the primary meshwork. Essentially, a farreoid skeleton is primarily 2-dimensional, but may have sufficient secondary growth to make it 3-dimensional in older parts. However, the growing edge or tip of the skeleton always remains 2-dimensional **(Fig. 6A.i, A.ii)**.

Euretoid skeletons are fundamentally more complicated. Rather than a 2-dimensional growing margin, euretoid sponges have a 3-dimensional growing edge, with one to many meshes of dictyonal strands distributed throughout its depth between dermal and atrial layers. Much like farreoid skeletons, secondary components can be added to the euretoid skeleton, but its three-dimensionality is never solely the result of these secondary meshworks. The primary skeleton of a euretoid sponge is not cubic in nature, according to Reid, but consists of several dictyonal strands distributed in three dimensions. These strands then generate cross-links in the same fashion as a farreoid skeleton **(Fig. 6B.i, B.ii)**.

Farreid Taxonomy

In 1872, the family Farreadae was erected by Gray to include both *Farrea* Bowerbank (1862) and *Sympagella* Schmidt (1870). In 1877, Zittel moved *Farrea* into his new family, Euretidae. Schulze, however, disagreed with the move, and in 1885, transferred *Sympagella* out to Asconematidae Gray, and reinstated Gray's family, correcting the spelling to the modern day Farreidae, and restricting its content

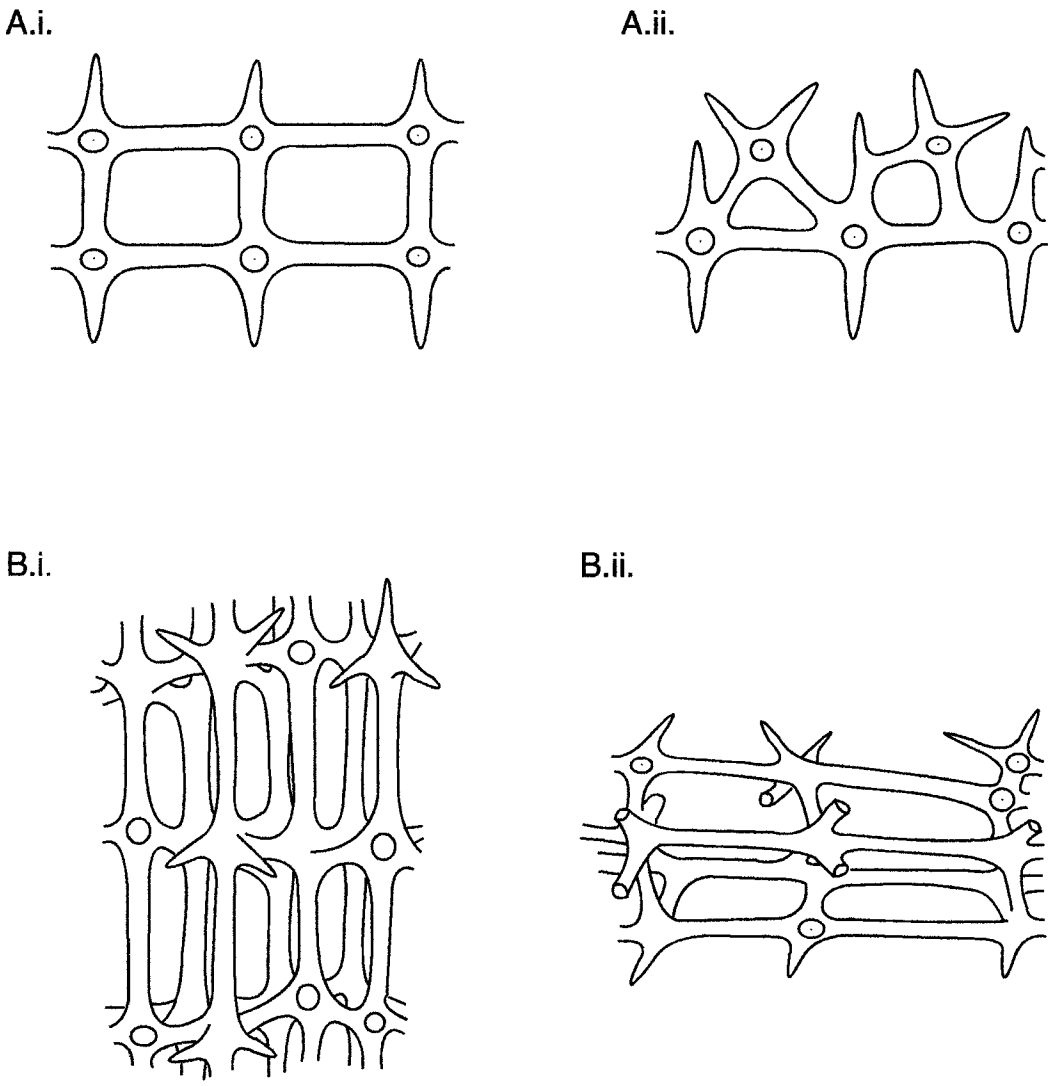

Figure 6. Hexactinellid skeleton types. A.i, farreoid plan view; A.ii, farreoid transverse section; B.i, euretoid plan view; B.ii, euretoid transverse section. (Reid, 1964)

to genus *Farrea*. Furthermore, Schulze (1886, 1887) erected a subtribe, Clavularia, solely for the purpose of supporting the genus *Farrea*.

This arrangement was widely accepted until, in 1899, Schulze himself described *Claviscopulia intermedia*, an alleged intermediate between Farreidae and Euretidae, having both farreid clavules and scopule-like spicules (sarules). As a result, he felt it necessary to withdraw his two contrasting subtribes, Clavularia Schulze (1899), then containing only Farreidae, and Scopulia, then containing Euretidae and several other families, and, renouncing his support for Farreidae, moved *Farrea* and *Claviscopulia* back to the Euretidae. During the early 1900's, the treatments accorded Farreidae and its contents, having grown to include *Sarostegia* Topsent (1904a), were highly inconsistent. In most works, farreid genera were included under the Euretidae (e.g. Schulze, 1904; Topsent, 1904c), or in Farreidae, often by the same authors (e.g. Schulze, 1902; Topsent 1904a).

In 1927, Ijima reconciled the problems created by *Claviscopulia* by erroneously stating that the sarules of this genus were diactins instead of monactins, and could not, therefore, be considered modified scopules. Ijima re-established the distinction of Farreidae, now including the new genus, *Lonchiphora* Ijima (1927), and reinstated Schulze's contrasting taxa, Clavularia and Scopularia.

The only major challenge to this arrangement has been that of **Reid 1963**, in which he suggested that *Sarostegia* be transferred to Euretidae on the basis of its framework organization. Though reasonable from a paleontological viewpoint, this was rejected for the zoological classification of recent forms, as spiculation shares prominence with framework in taxa diagnoses. **Reid, 1963** considered clavules and

farreoid frameworks to be ancestral characters. **Mehl, 1992** disputed this, arguing that the ancestral characters are sceptrules and euretoid frameworks.

In its current form, the family Farreidae consists of 5 genera containing 21 species. Of these genera, *Aspidoscopulia* Reiswig (in press), *Claviscopulia*, *Lonchiphora* and *Sarostegia* are monospecific; *Farrea* contains the remaining 17 species.

Fossil Record

Paleontological evidence shows hexactinellid-like forms were present in the Ediacarian (570-543 million years ago) **(Ding Wei-Ming & Qian, 1988; Gelhing & Rigby, 1996; Reitner & Mehl, 1995; Steiner et al., 1993)** fauna, before both the Burgess Shale deposits and the Cambrian explosion. The Hexactinosa themselves have been known to exist since the Paleozoic, but reached their greatest diversity in the Mesozoic. Most recent genera were present in the Upper Cretaceous **(Mehl, 1992)**.

The use of paleontological evidence in diversity studies, however, can be problematic, as fossilization will obviously skew data sets towards the rigid, more permanent skeletons of dictyonine hexactinellids, resulting in an apparent, but artifactual, decline in recent dominance of dictyonine sponges as compared to the non-fused lyssacine sponges **(Barthel & Tendal, 1994)**.

The oldest farreid known, appearing 98 million years ago, is 80 million years younger **(Benton, 1993)** than the earliest euretid, which was found in the mid-Jurassic, 178 million years ago. This sequence of first occurrence is in direct contradiction to **Reid's (1964)**, hypothesis in which the single mesh frameworks of

the farreid sponges were considered ancestral to the more complex 3-dimensional euretoid frameworks, but is in agreement with **Mehl (1992)**, claiming that the euretoid framework is ancestral.

METHODS

The specimens described here were obtained through submission by collectors to the Redpath Museum sponge laboratory for identification. Most specimens were collected by robot submersible (*Farrea herdendorfi* sp. nov., *Asceptrula axialis* sp. nov., g. nov.) and were accompanied by videotape of the collection process. Others (*Farrea seiri* sp. nov.) were collected by dredge. These are all deep-water hexactinellids with complete spicule populations, a rare situation, allowable only through technological advance. Though other non-identified farreids have been collected around the world, these samples were not searched out for several reasons:

1. Many of said specimens would have been merely new records of previously described species, and therefore of no taxonomic significance.
2. Many others would have been indeterminate, and therefore of interest only toward knowledge of Hexactinosa distribution. A complete review of other non-identified specimens from other museum collections from around the globe might have produced additional new taxa, but such study would have been too unpredictable and costly in time and funds to be justified for a Master of Science thesis project.

Sections of the sponge body wall were cut and were either whole-mounted in Canada balsam for light microscopy (LM), or were dissociated in hot nitric acid. The cleaned skeletal frameworks were picked out, rinsed and dried; the remaining acid suspensions of spicules were filtered through 25mm diameter 0.2mm pore-size, nitrocellulose filters by vacuum filtration; the filters were then thoroughly rinsed with distilled water, dried, cleared with xylene, and mounted in balsam on microscope

slides as loose spicule preparations. Framework and spicules were measured by computer using a microscope-coupled digitizer. Data are reported as mean ± standard deviation (range, number of measurements). Spicules for scanning electron microscopy (SEM) were similarly nitric-acid-cleaned, rinsed in distilled water and then directly deposited onto cover glasses mounted on SEM stubs. Acid-cleaned and rinsed fragments of body wall skeletal frameworks were mounted directly on stubs with epoxy. Following gold-palladium coating, specimens were viewed and photographed with a JEOL JSM-840 SEM. Spicule drawings were made by importing LM or SEM images into a computer image-processing program, and then tracing on screen. The extended nature of the following species descriptions is normal procedure for new Porifera. Since members of the group often change body form with size, knowledge of such shape variability is absolutely required for species identifications in faunal surveys conducted by photo or video transect. Both SEM photographs and line drawings are included to optimize communication and to conform with modern literature convention for this taxonomic group.

Systematics:

Phylum **Porifera** Grant, 1836
Subphylum **Symplasma** Reiswig & Mackie, 1983
Class **Hexactinellida** Schmidt, 1870
Subclass **Hexasterophora** Schulze, 1886
Order **Hexactinosida** Schrammen, 1903
Family **Farreidae** Gray, 1872
Genus ***Farrea*** Bowerbank, 1862

***Farrea herdendorfi* sp. nov.**
(Figs 8-17)

Materials.

Holotype: USNM #####: S.S. 'Central America' wreck, 300km S. of Charleston, S.C., 31.5°N, 77°W, September 12th, 1989, 2200m depth, coll. C.E. Herdendorf, R/S 'Nemo' from R/V 'Arctic Explorer', dive UA. **(Fig. 7)**

Paratypes: All paratypes from same sampling location and vessels;

USNM ##### (CA6), USNM ##### (CA34), USNM ##### (CA35), USNM ##### (CA36), USNM ##### (CA37), all September 12th, 1989, coll. C.E. Herdendorf, Dive UA; USNM ##### (CA8), USNM ##### (CA30), both September 21st, 1990, coll. B. Evans, dive AC.

Etymology: Named after the collector of the original holotype, Prof. Charles E. Herdendorf, who also served as Coordinator of the Adjunct Science and Education Program, S.S. 'Central America' Project, Columbus America Discovery Group.

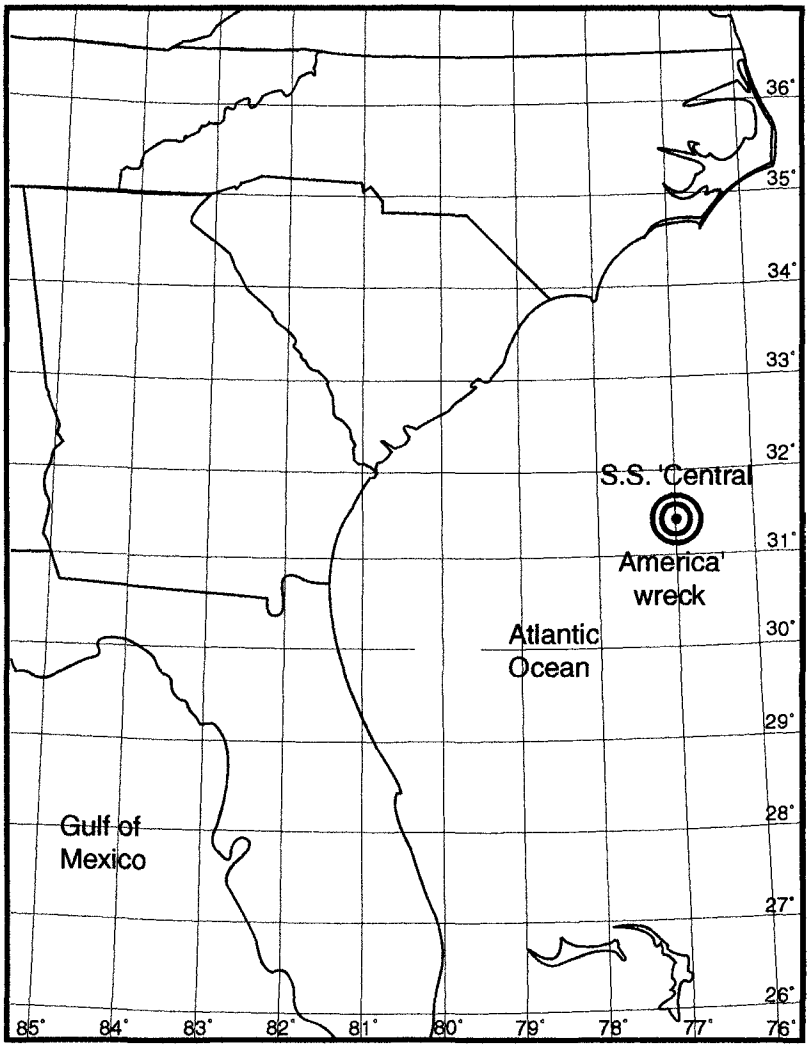

Figure 7. Collection site of *Farrea herdendorfi* sp.nov.

Description.

SIZE and SHAPE

Holotype (largest specimen) is 30cm in height, with a branching element at 16cm from the base of the specimen, extending out for 11cm at an approximately 60° angle from the primary axis **(Fig. 8)**. At their widest points, the main body is 5cm in width, and the lateral branch measures 4.2 cm in width. The body of the sponge is a highly fluted stalk. The skeleton is constructed of a central flat axial blade, which, through extensive lateral extension, with high levels of lateral curvature, fluting and fusion, forms axial and lateral tubes appended onto the central blade **(Fig. 8)**. The diameter of superficial tubular apertures of the holotype measured 6.7±2.0mm (range 5-10mm, n=12).

A sequence of growth stages is presented by the paratype series; wall thickness is assumed to reflect age or maturation stage in the series. This series is inferred to show change over time from a relatively simple blade form to the highly complex structures seen in the holotype specimen, through to senility.

The simplest of the paratypes is represented by CA35 (18.6cm x 2.0cm) **(Fig. 9A.i, ii)**. The latter **(Fig. 9A.ii)** shows a small section of the paratype facial view, illustrating one side of the blade face with lateral undulations at the marginal edges. The former **(Fig. 9A.i)** shows the entire paratype specimen in lateral view, illustrating the extreme nature of the marginal edge deformation. At this point, no self-fusion has taken place; as a result, there are no closed tube-forms.

A more complex, presumably older, paratype, CA36, (82mm x 27mm) is illustrated in **Fig. 9B.i-iii**. The original axial blade form is visible, but the structure

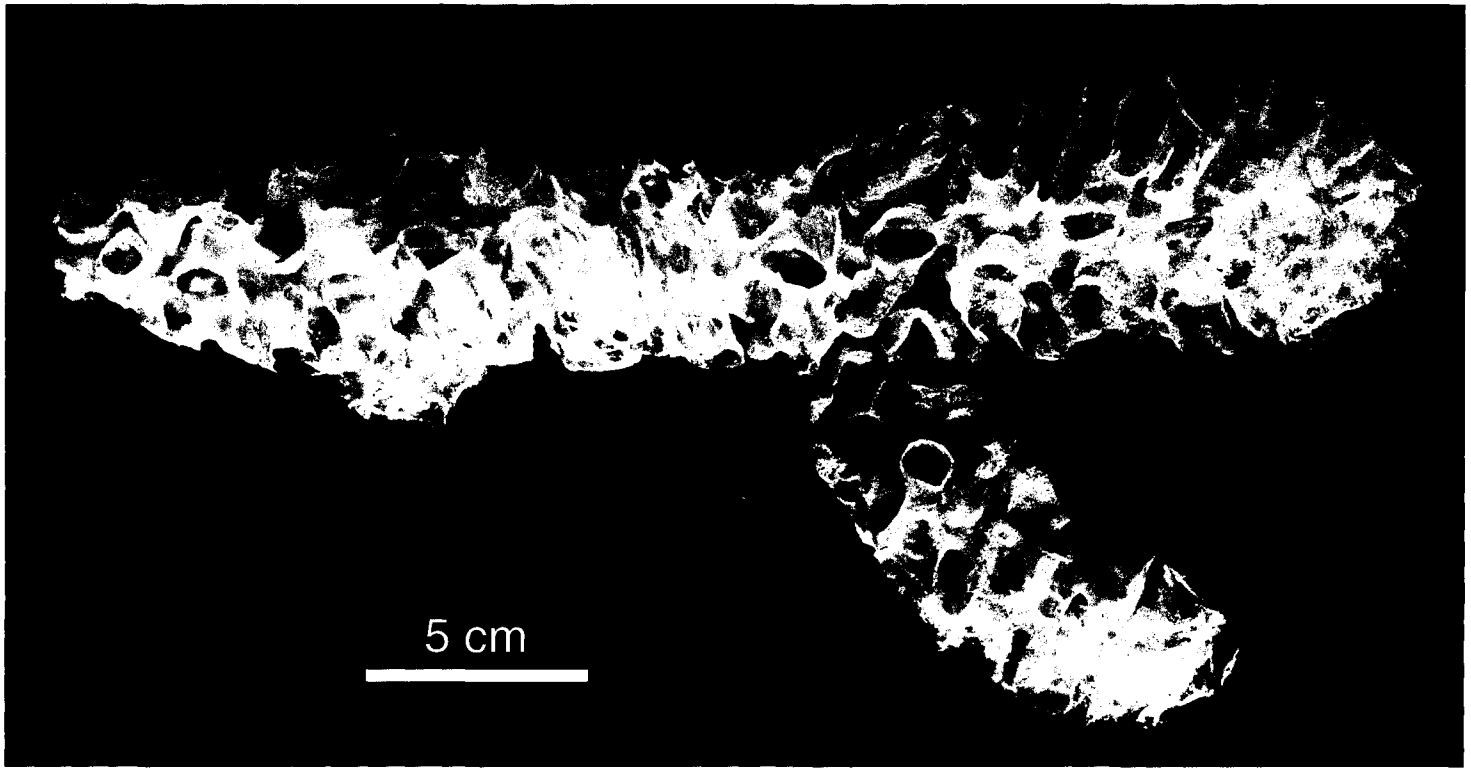

Figure 8. *Farrea herdendorfi* sp. nov. holotype, USNM XXXXX; the broken off base is toward the left.

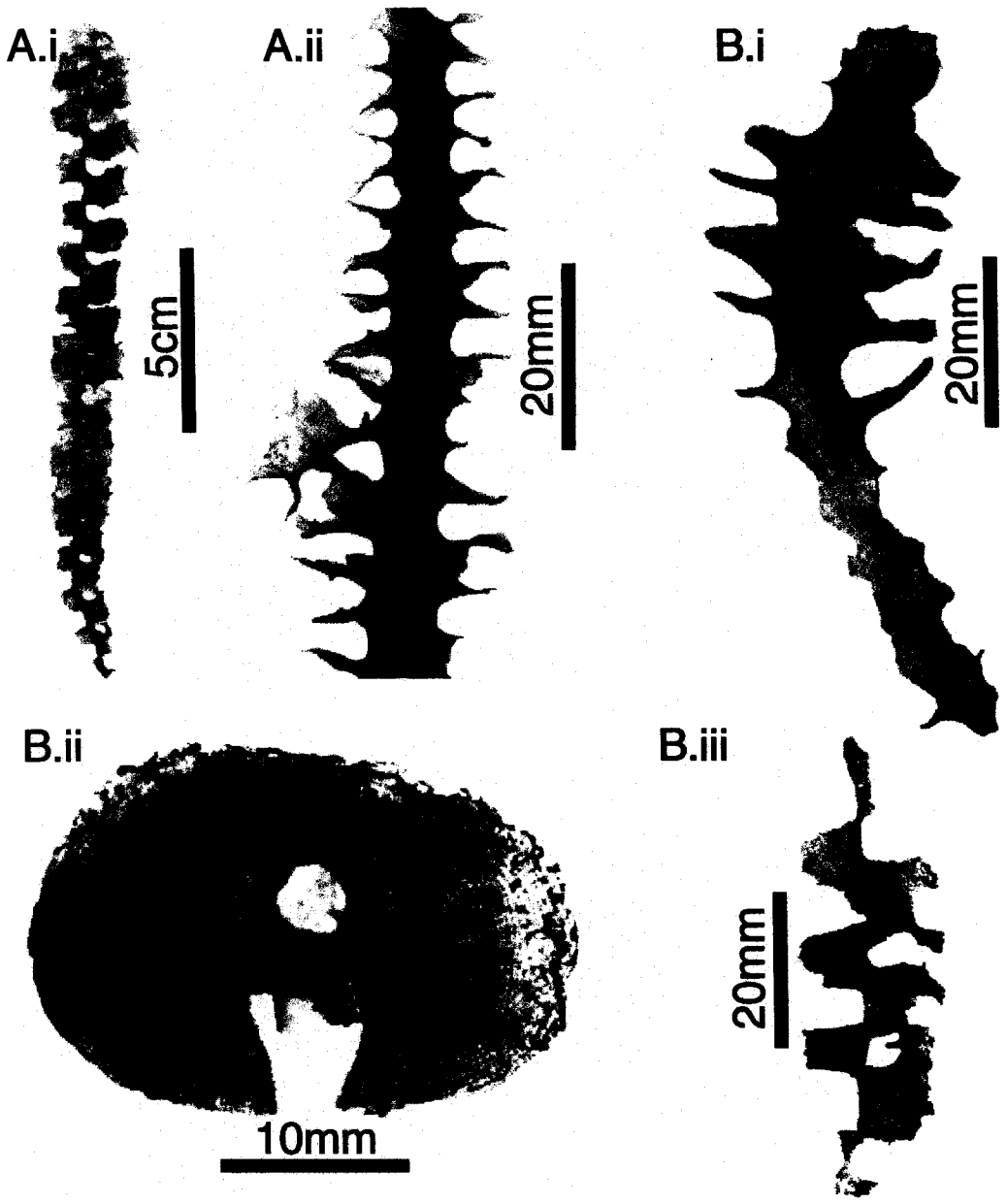

Figure 9. Macroscopic views of *Farrea herdendorfi* sp. nov. paratypes. A.i., transverse optical section of youngest paratype (CA35); A.ii., magnified facial view of youngest paratype (CA35); B.i., full face view of second youngest paratype (CA36); B.ii., view from distal tip of second youngest paratype (CA36); B.iii., transverse optical section of second youngest paratype (CA36).

has been modified by self-fusion at many points, forming short segments of an axial tube on one side of the axial blade. The tube shape can be easily seen in the apical view of the specimen, **Fig. 9B.ii**, in which several of the non-continuous tubes, **(Fig. 9B.iii)**, are aligned to form an axial tube-like formation on one side of the axial blade resulting from the self-fusing framework. This self-fusion also extends laterally, defining lateral tubes (not shown).

The basal region of the holotype, CA3, **(Fig. 10A.i)** demonstrates the massiveness of the older specimen, with thicker walls near the axis, and thinner at the edges. Though the 2-dimensional mesh is still visible at the margins, the axial blade is no longer discernible in optical section. Axial tubes are present in the main column, above and below the branch point, and in the branch itself, but they are not continuous. **Fig. 10A.ii** clearly shows the absence of continuity of the axial tube of the branch with either of those (lower or distal) in the main axis. As such, any lateral branching is not the result of the branching of an axial tube. All segments do have an axial tube, suggesting that either the axial blade extends into both segments, developing more axial tubes, or the tubes can be grown from any segments of the framework. As evidenced by the highly complex structure of the specimen, the entire framework does seem capable of self-fusion, but only one axial tube develops in the basal segment (the youngest portion of the animal). The younger specimens have axial tube formation on only one side of the axial blade. From this, it is concluded that the construction of any accessory axial tubes are accompanied by a segment of the original axial blade.

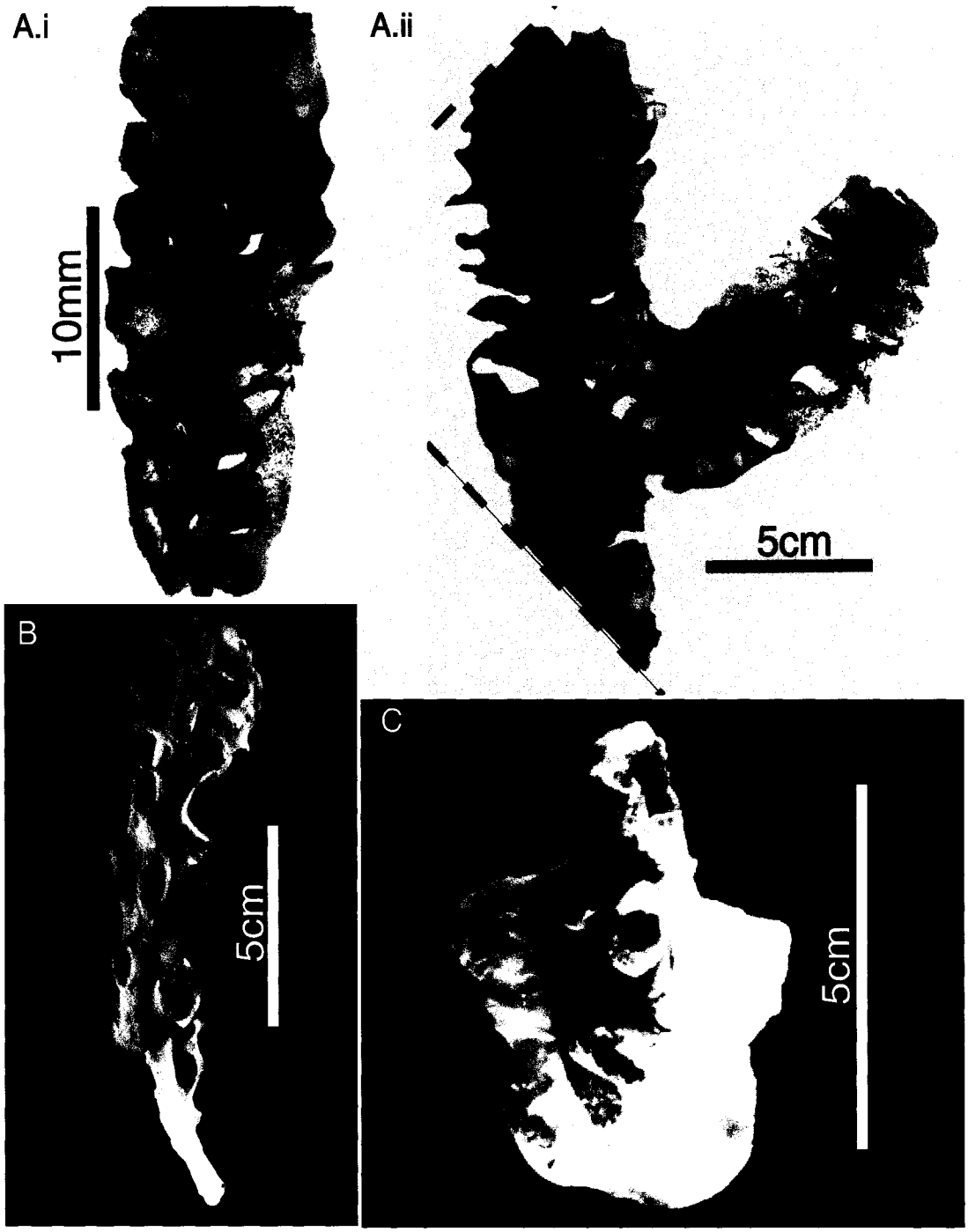

Figure 10. Macroscopic views of *Farrea herdendorfi* sp. nov. holotype and paratypes. A.i, basal segment of holotype specimen, (CA3), showing massiveness of the older portion of the skeleton ; A.ii, branch point in holotype specimen, (CA3), showing absence of a continuous tubular element connecting stalk and branch ; B, full view of second oldest paratype (CA6); C, top view of oldest paratype (CA8).

On the basis of wall thickness, paratype CA6 (14.7cm x 3.3cm) **(Fig. 10B)** represents the next oldest of the series. The marginal 2-dimensional mesh frills seen on the younger specimens are presumed to have been torn off in collection, as evidenced by the abraded edges of the lateral tubes. The thick-walled proximal tube openings occur in sets of four, occurring in alternating offset pairs.

The oldest specimen, CA8, (6.6cm x 4.9cm) **(Fig. 10C)**, consists of only a basal part of what was a larger organism. It has extremely thick-walled tube components, the walls almost as thick as the lumina are wide. The skeleton is exceedingly massive, to the point of being virtually solid.

SKELETON

Framework

The framework is an unchannelized dictyonal lattice, composed of a 2-dimensional silica mesh at the growing edge, which has been added to by secondary growth on older parts of the specimen **(Figs 11A, B; 14A, B)**. The mesh is constructed of hexactins joined permanently, their centers forming true nodes, arranged in long dictyonal stands in a highly grid-like formation. In older parts of the specimen, secondary growth has resulted in less regular 3-dimensional structures overlying the basal meshwork mesh. The frame is also heavily spurred (spurs are free unattached rays of framework hexactins). Small hexactins attached to primary and secondary dictyonal hexactins are abundant.

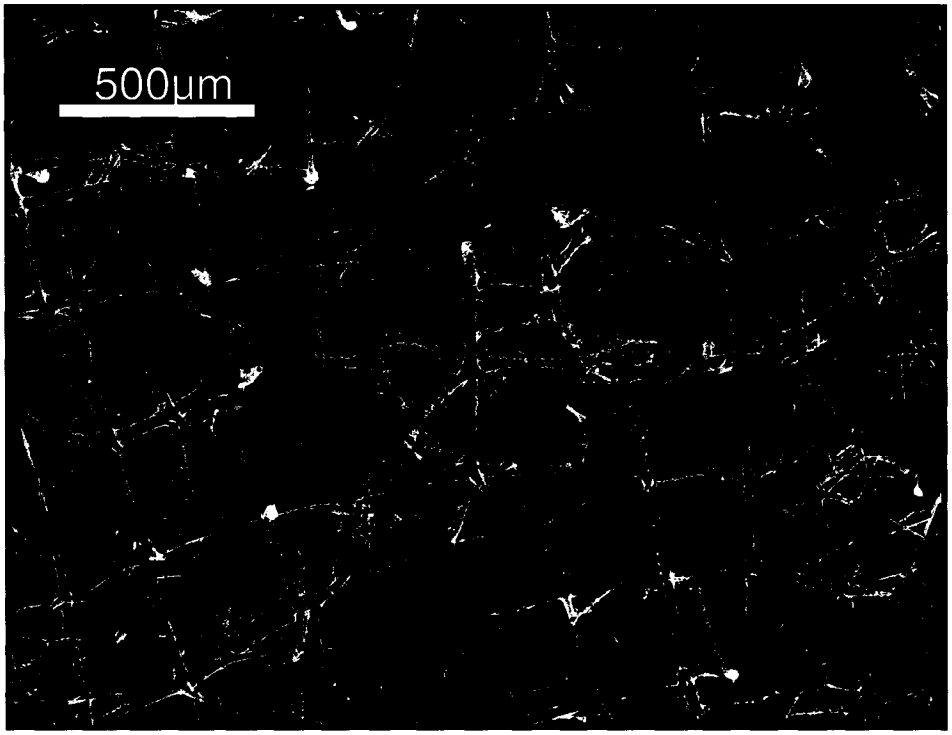

Figure 11A. SEM image of skeletal mesh of *Farrea herdendorfi* sp. nov., (CA3), showing highly grid-like structures, heavy spurring and irregular secondary skeletal elements.

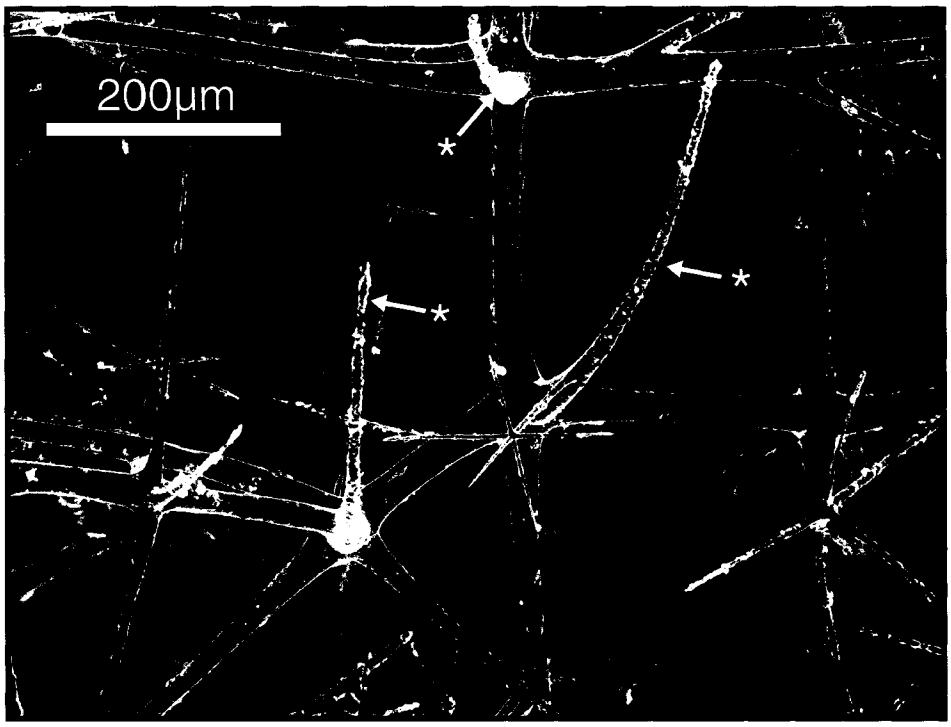

Figure 11B. Same as above at higher magnification, spurs indicated by *.

Spicules (Measurements give in **Table 1**)

Megascleres. Uncinates are very long, exceptionally thin and moderately barbed **(Figs 12A.i, ii, 13A.i, ii)**. Large pentactins have tangential rays heavily spined on outer surfaces, and a long, smooth proximal ray with slight spination near the tip **(Figs 12B, 13B)**. Two forms of clavule **(Figs 12C, 13C)** are present, both having a thin, smooth shaft ending in a slightly rough, bluntly pointed tip. The umbellate clavule, **(Figs 12C.i, 13C.i)**, has approx. 15 spines projecting down from a thimble-shaped cap, flaring slightly outward at the lower edge. The anchorate clavule, **(Figs 12C.ii, 13C.ii)**, has approx. 10 spines projecting down and out from a smoothly rounded cap, continuing on the angle of curvature without reflexion. Pentactins and clavules of gastral and dermal surfaces are indistinguishable.

Microscleres. Two types of smooth hexasters are present, distributed throughout the specimen. Oxyhexasters, **(Figs 12D, 13D),** have six long primary rays, each bearing 2-3 secondary rays ending in sharp tips. Onychexasters, **(Figs 12E, 13E)**, have 3-4 secondary rays each ending in a whorl of short claws.

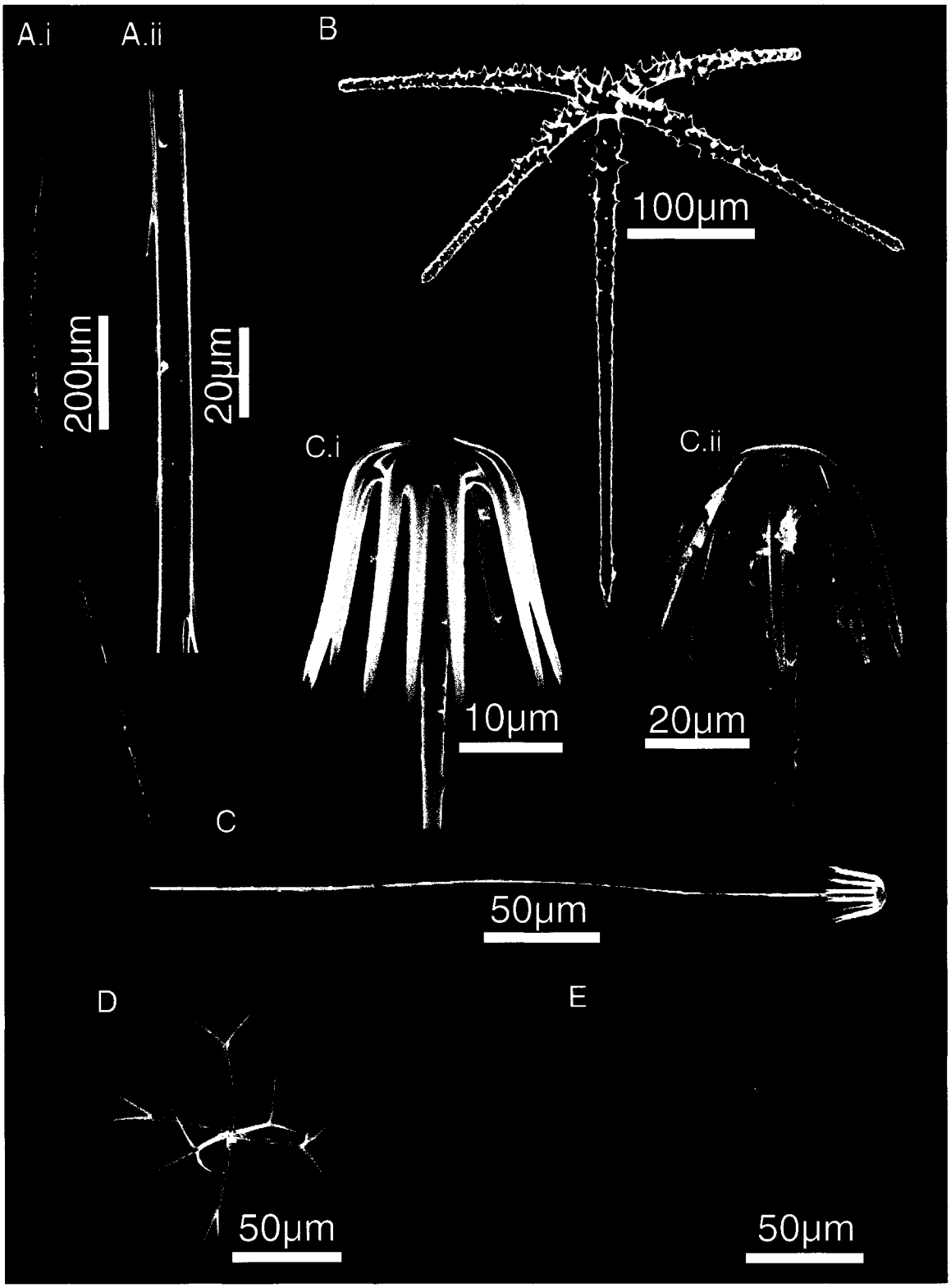

Figure 12. *Farrea herdendorfi* sp. nov. holotype spicules (SEM). A, uncinate; B, pentactin; C, umbellate clavule; C.i, umbellate clavule head; C.ii, anchorate clavule head; D, oxyhexaster; E, onychexaster.

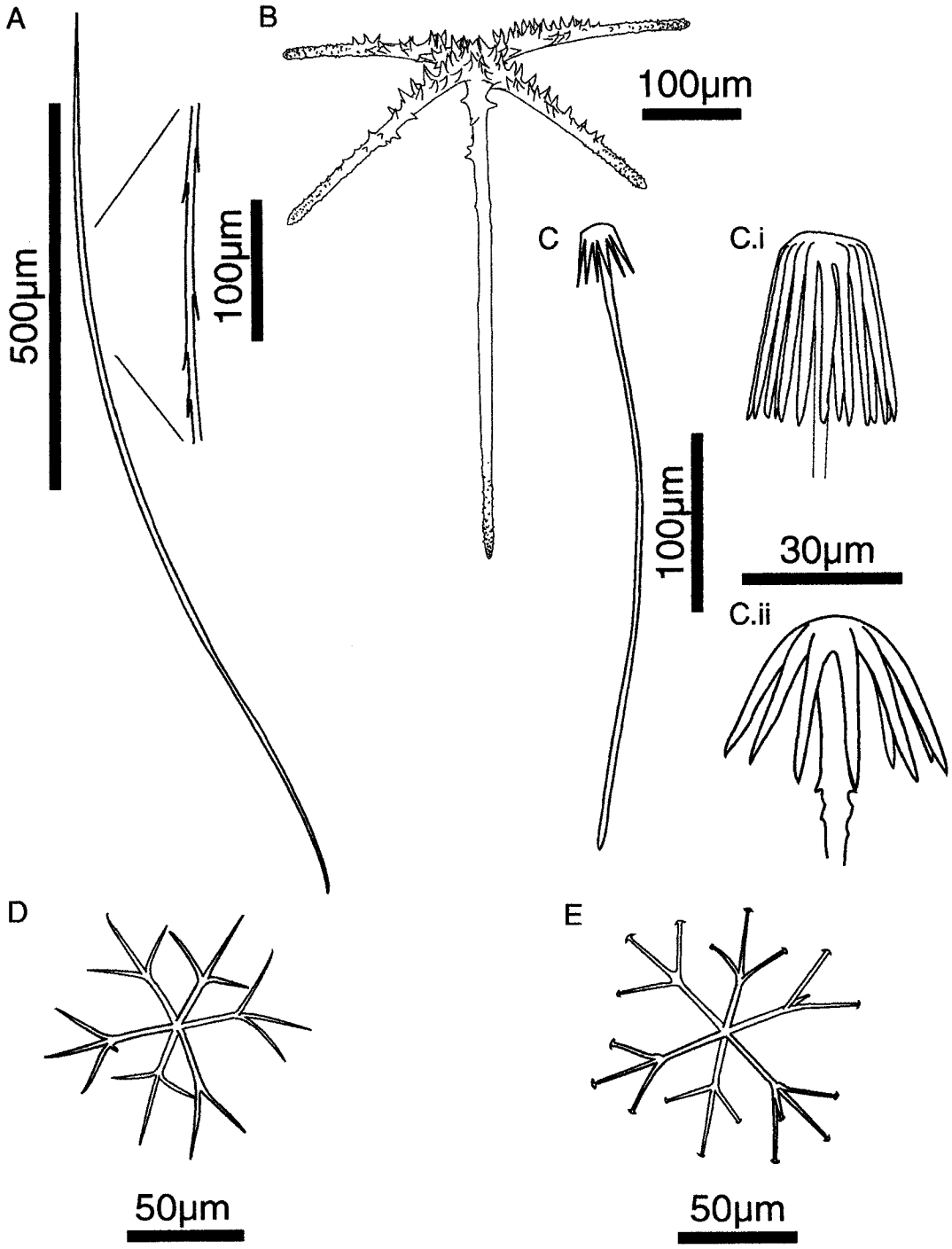

Figure 13. *Farrea herdendorfi* sp. nov. spicules of the holotype. A, uncinate; B, pentactin; C, umbellate clavule; C.i, umbellate clavule head; C.ii, anchorate clavule head; D, oxyhexaster; E, onychexaster.

Table 1. Measurements of spicules of *Farrea herdendorfi*.

Uncinate	*Length*	*Width*		
	1368±308µm (range 830-2086µm; n=50	6.1±1.4µm (range 3.5-9.9µm; n=50)		
Pentactin	*Proximal ray length*	*Proximal ray width*	*Tangential ray length*	*Tangential ray width*
	309±77µm (range 181-423µm; n=24)	11.5±2.5µm (range 7.3-17.2µm; n=24)	231±29µm (range 179-299µm; n=50)	13.1±2.9µm (range 5.2-20.1µm; n=50)
Umbellate Clavule	*Total length*	*Head length*	*Head width*	
	353±75µm(range 130-490µm; n=50)	32.7±5.5µm (range 19.9-44.8 µm; n=50)	34.9±7.9µm (range 19.7-56.2 µm; n=50)	
Anchorate Clavule	*Total length*	*Head length*	*Head width*	
	454±55µm (range 313-581µm; n=50)	36.9±4.4µm (range 28.7-48.8µm; n=50)	48.2±5.3µm (range 32.3-65.9µm; n=50)	
Oxyhexaster	*Diameter*	*Primary ray length*	*Secondary ray length*	
	59.9±6.4µm (range 43.3-72.9µm; n=50)	30.7±4.6µm (range 21.6-43.1µm; n=50)	33.1±4.7µm (range 20.7-44.3µm; n=50)	
Onychexaster	*Diameter*	*Primary ray length*	*Secondary ray length*	
	54.0±4.3µm (range 44.8-59.6µm; n=11)	25.8±2.5µm (range 22.1-29.6µm; n=11)	29.7±2.8µm (range 22.8-32.5µm; n=11)	

Remarks.

This species is differentiated from all other members of the genus *Farrea* by the presence of hemidisc clavules, (also called umbellate clavules), except for *Farrea seiri*, sp. nov., described below. It differs from *Farrea seiri* in both the presence of oxyhexasters and the absence of spiroanchorate clavules.

Discussion.

The incredible increase in thickness of the skeleton over time in this species poses an interesting question: How does the skeleton become so robust? Is it through a) addition of supplementary dictyonal strands, b) further silicification of already-occurring dictyonal strands, or c) through the accumulation of secondary structures? To answer this question, further SEM work was carried out, using skeletal fragments of several of the paratypes already discussed, as well as the holotype.

The youngest specimen, (CA35), **(Fig. 14A, B)**, shows a primarily 2-dimensional mesh, with asymmetrical secondary component growth on both sides of the grid. Some of these exhibit true nodes, but most are false.

The holotype (CA3), **(Fig. 15A, B)**, has 3-4 "layers," without clear distinction between them. The spaces in the mesh are quite large in comparison with the strand diameters, and the spaces are loosely packed with both megascleres and microscleres. There is no noticeable thickening of the dictyonal strand, and the primary meshwork is still visible.

The specimen CA6 shown in **Fig. 16A, B** has several more layers than the holotype, with distinct thickening of the dictyonal strands. The loose spicule population is still quite high, with large numbers of small hexactins attached to the framework, seemingly at random.

The oldest specimen (CA8), shown in **Fig. 17**, has undergone heavy secondary growth, completely obscuring the original farreid grid. The dictyonal strands are no thicker relative to mesh spaces than in the previous specimens, but the spicule population has dwindled. This is the result of the specimen being the basal

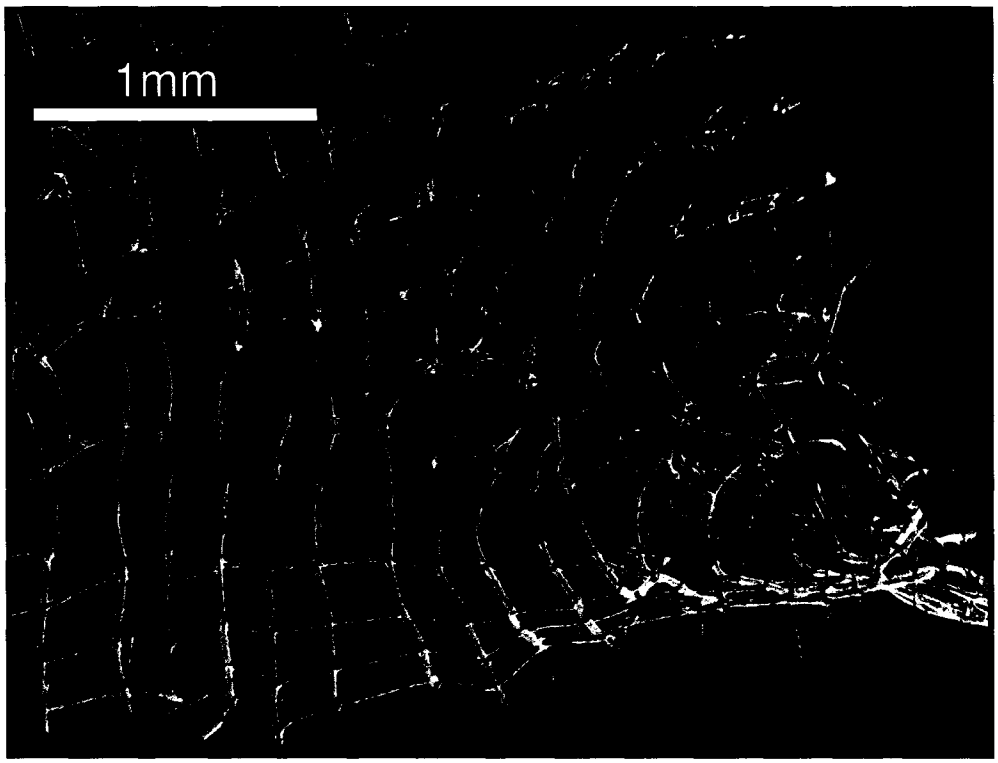

Figure 14A. SEM image of *Farrea herdendorfi* sp. nov.; youngest paratype's (CA35) skeletal mesh showing 2-dimensional grid-like nature, and minimal secondary growth.

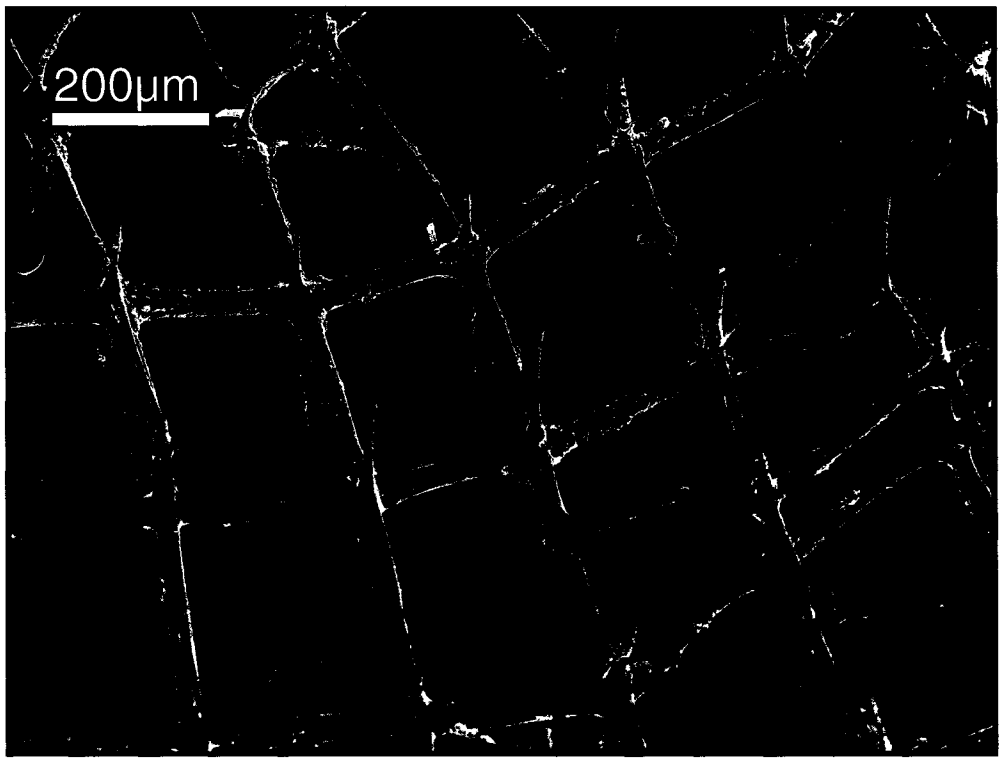

Figure 14B. Same as above at higher magnification.

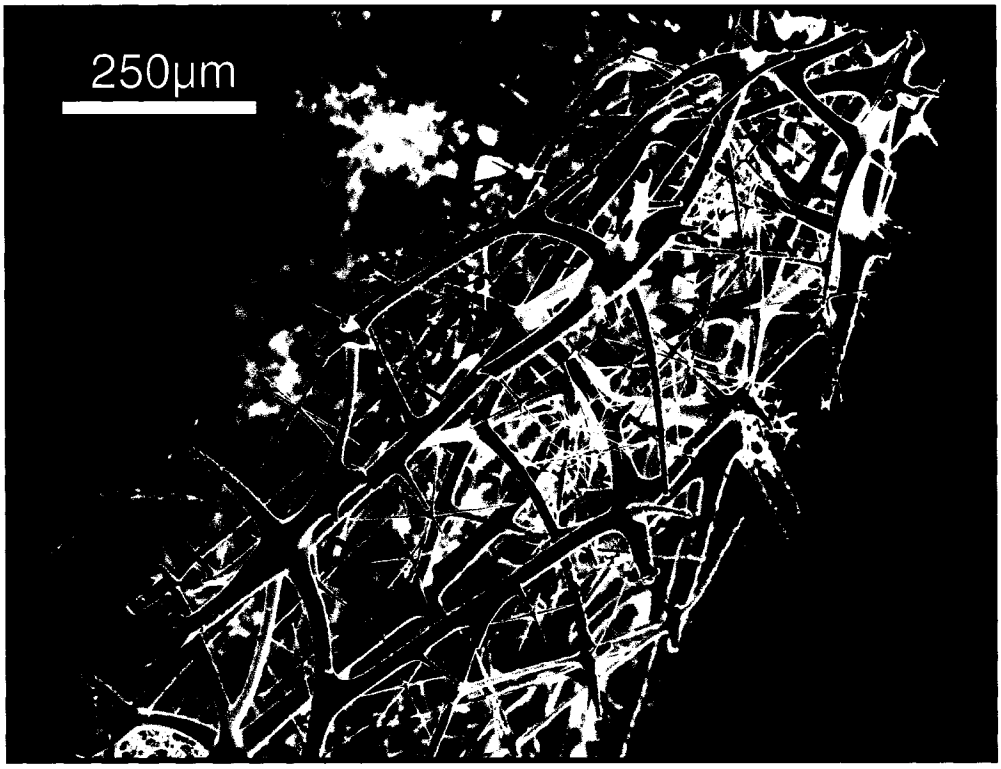

Figure 15A. SEM image of *Farrea herdendorfi* sp. nov.; holotype (CA3) skeleton edge in cross section.

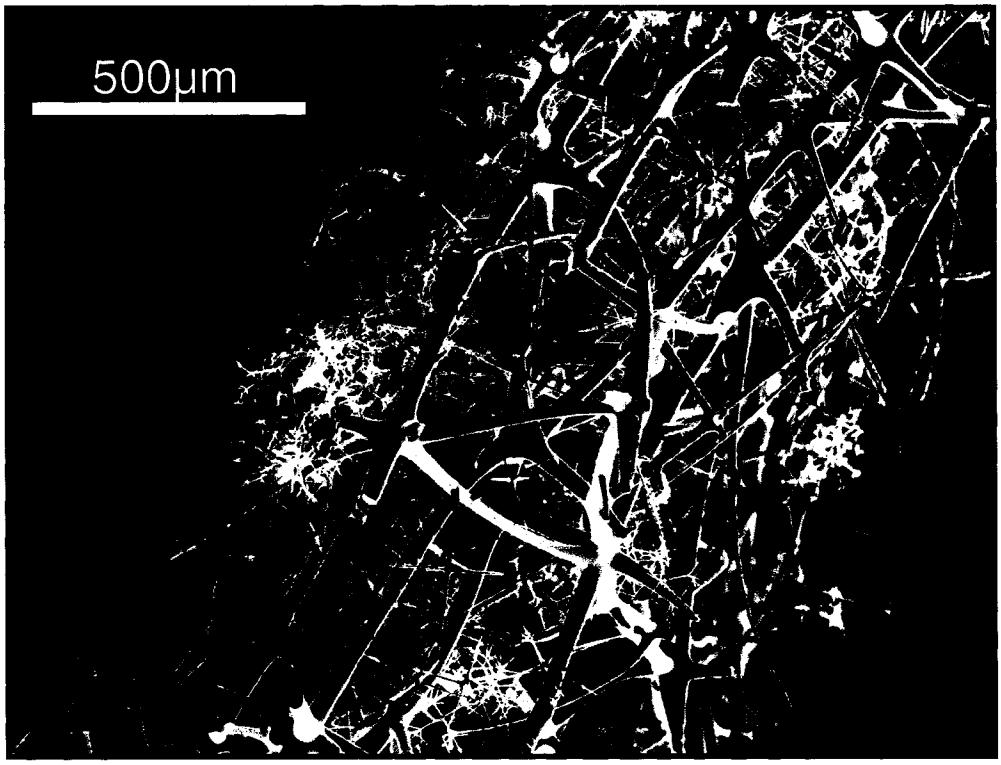

Figure 15B. SEM image of *Farrea herdendorfi* sp. nov.; holotype (CA3) skeleton center in cross section. Tangles of microscleres resisted removal from the framework during cleaning.

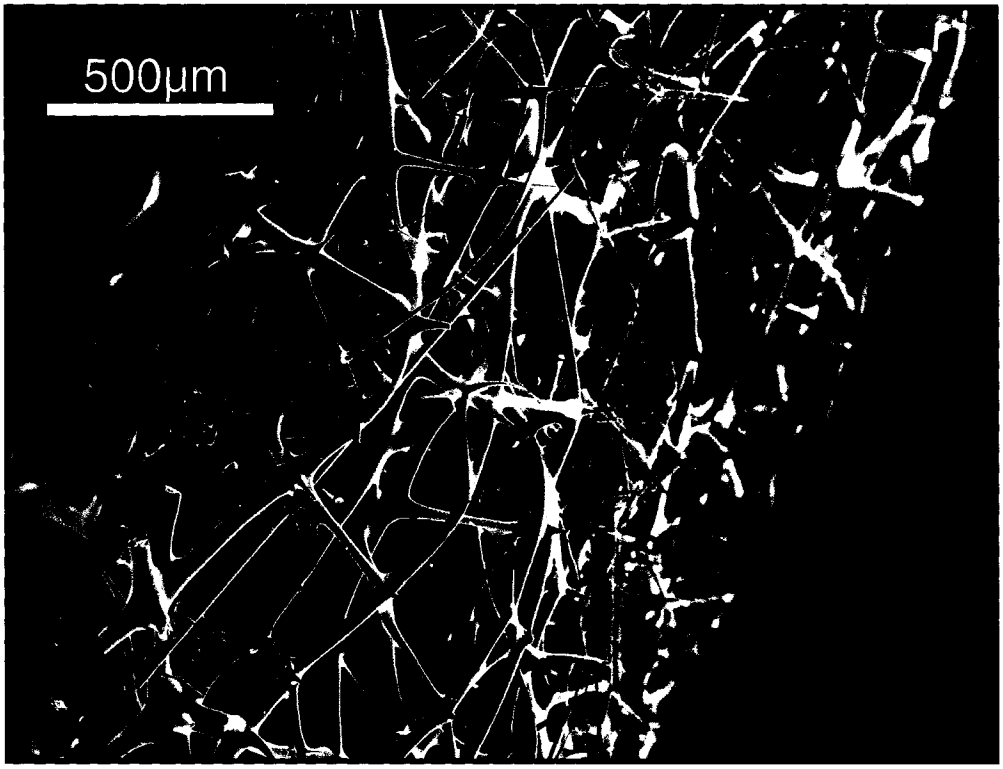

Figure 16A. SEM image of *Farrea herdendorfi* sp. nov.; second oldest paratype (CA6) skeleton in cross section.

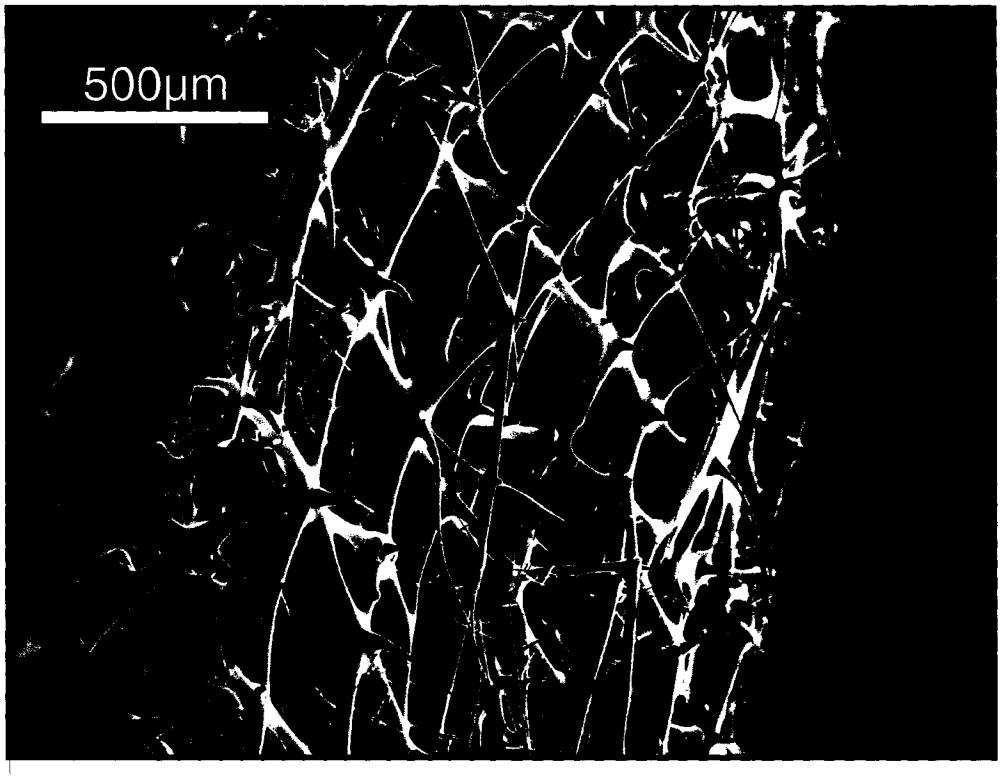

Figure 16B. SEM image of *Farrea herdendorfi* sp. nov.; second oldest paratype (CA6) skeleton showing surface features.

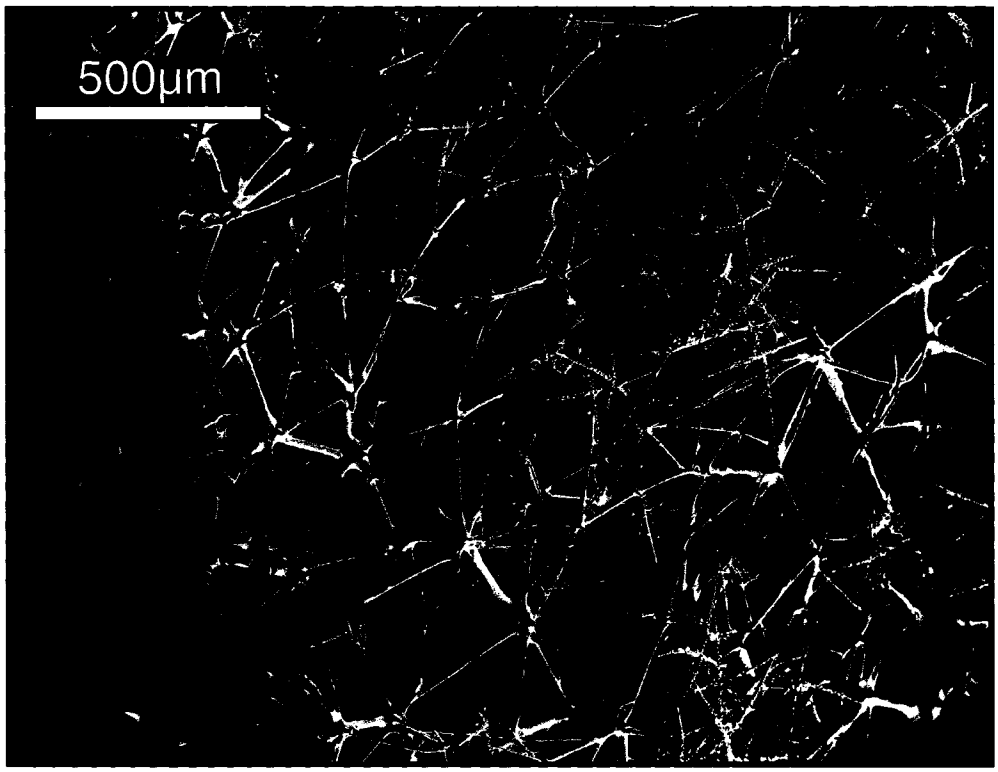

Figure 17. SEM image of *Farrea herdendorfi* sp. nov.; oldest paratype (CA8) skeleton in cross section.

segment of a very old organism, with little live tissue inhabiting this area. Regardless, there are many layers in this specimen, resulting in no discernable pattern.

This survey suggests that thickening and increasing massiveness of *Farrea herdendorfi* with aging and maturation can be attributed to a) addition of secondary structures, b) increased addition of small hexactins into mesh spaces, but only c) slight thickening of primary dictyonal strands.

Farrea seiri sp. nov.
(Figs 19-23)

Material Examined.

Holotype: USNM #####: South East Indian Ridge, Indian Ocean, 39° 12.83'S, 77°52.88'W, March 22, 1996, 1450m depth, colls D.S. Scheirer and K. Johnson, Boomerang Expedition, Leg 6, R/V "Melville," biosample #7, Site 48, Dredge 58 **(Fig. 18).**

Etymology: *Farrea seiri* is formed by abbreviation of its collection locale, the **S**outh-**E**ast **I**ndian **R**idge.

SIZE & SHAPE.

The entire sample consists of three fragments from the basal part of a single specimen **(Fig. 19A)**. The specimen was severely damaged during dredge collection, all distal parts having been lost. The largest fragment measures 95.9x42.8mm, the second largest 39.1x15.3mm, and the smallest 17.9x16.8mm. All fragments are white in colour, with fairly thick walls, 2.08±1.04mm (range 0.95-3.80mm, n=10), though all are quite delicate, easily crushed and crumbled. All 3 fragments are considered to be parts of the same specimen due to similarity in development (wall thickness), colour, and identical spiculation

The specimen is composed of fusion of two tubes (A and B), the younger being attached obliquely along the side of the older. The older tubular element (A)

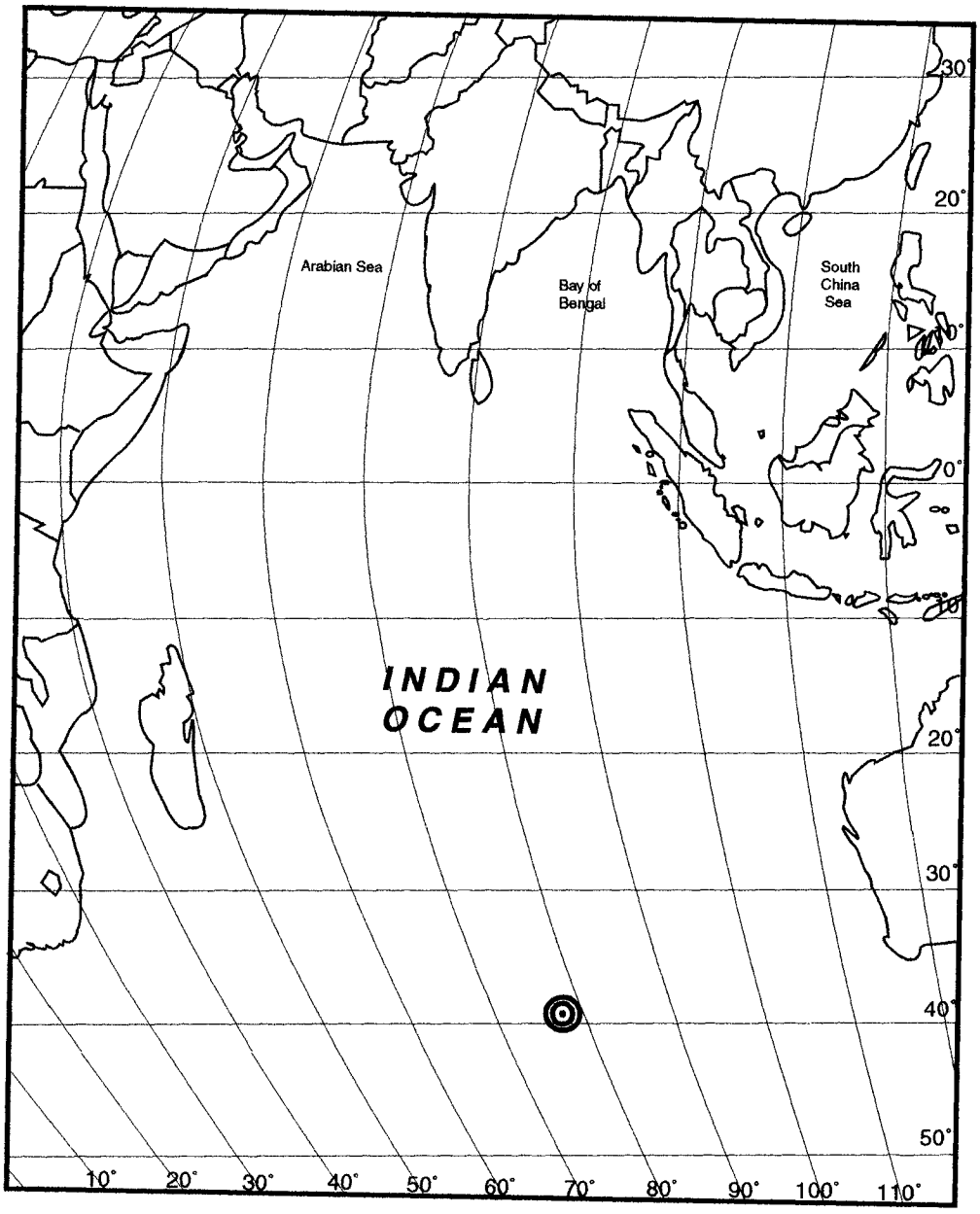

Figure 18. Sample site for *Farrea seiri*, sp. nov.

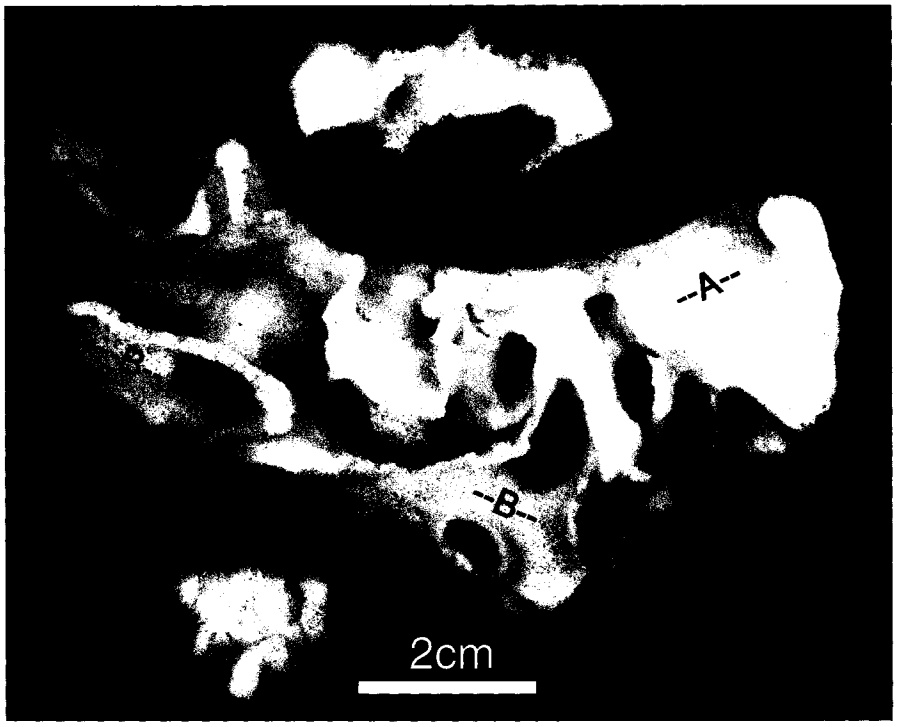

Figure 19A. Holotype of *Farrea seiri,* sp. nov. A: older tube form, B: younger tube form.

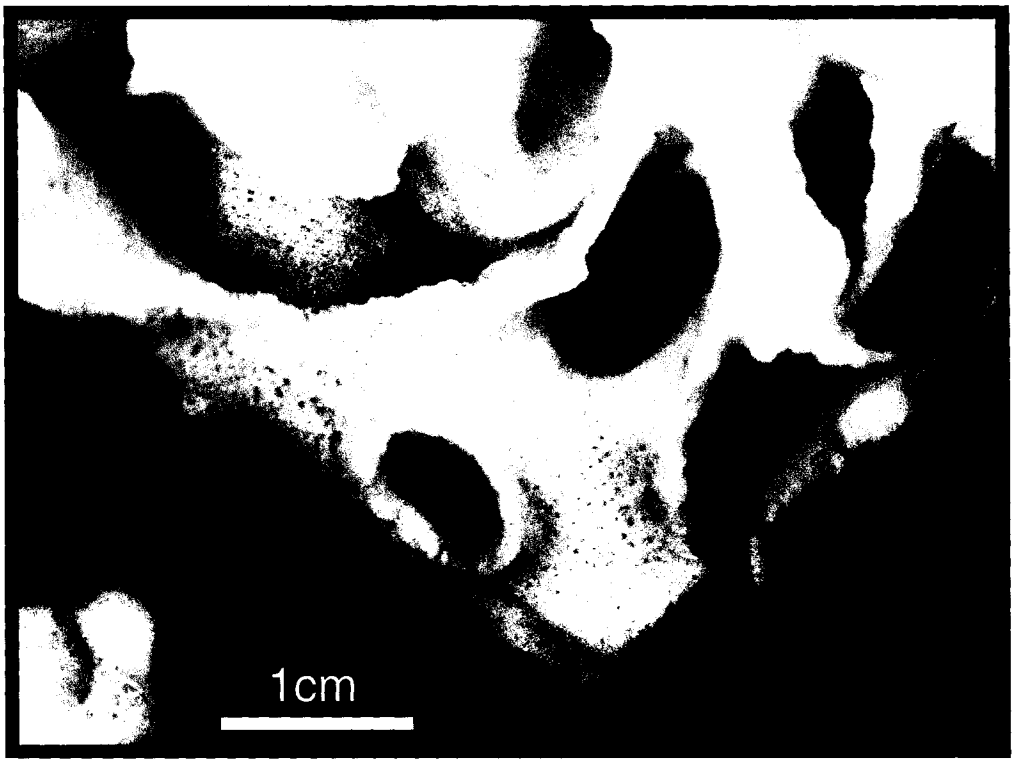

Figure 19B. Magnified view of holotype of *Farrea seiri,* sp. nov., showing surface; entrances of epirhyses are small pits scattered over surfaces.

provided basal attachment for the specimen and was dead at the time of collection. The younger tube-form (B) shows a series of paired, lateral tube openings. These openings occur in sets of two, occurring in alternating offset pairs, aperture length 9.18±0.89mm (range 8.25-10.4mm, n=5) width 5.06±0.89mm (range 4.10-6.95mm, n=5).

There is no consistent internal or external surface relative to the tubular walls of the specimen. Mapped contours show the same surface being external in one area, but internal at another. It is possible that the entire specimen is bounded by two separate surfaces, but these are contorted so that neither is consistently external or internal relative to the tubular walls throughout the specimen.

SKELETON.

Framework

The framework is dictyonal **(Fig. 20A, B)**. The outer layer is composed of a highly irregular mesh of hexactins conjoined with many synapticulae and some polyradial nodes, with channelization indicated by surface pits. These are openings of extradicytonal epirhyses, **(Figs 19B, 21A)**, with ovoid apertures, length 0.33±0.038mm (range 0.26-0.38mm, n=8), width 0.24±0.045mm (range=0.18-0.32mm, n=8). Distances between epirhyses is 0.66±0.18mm (range 0.33-1.20mm, n=32). Epirhyses extend only into the secondary framework layer; they do not penetrate into any part of the primary framework layer and thus do not pass through the entire wall.

Thickening of beams has occurred throughout the entire available part of the specimen, and there is no single layer which could be considered as a typically

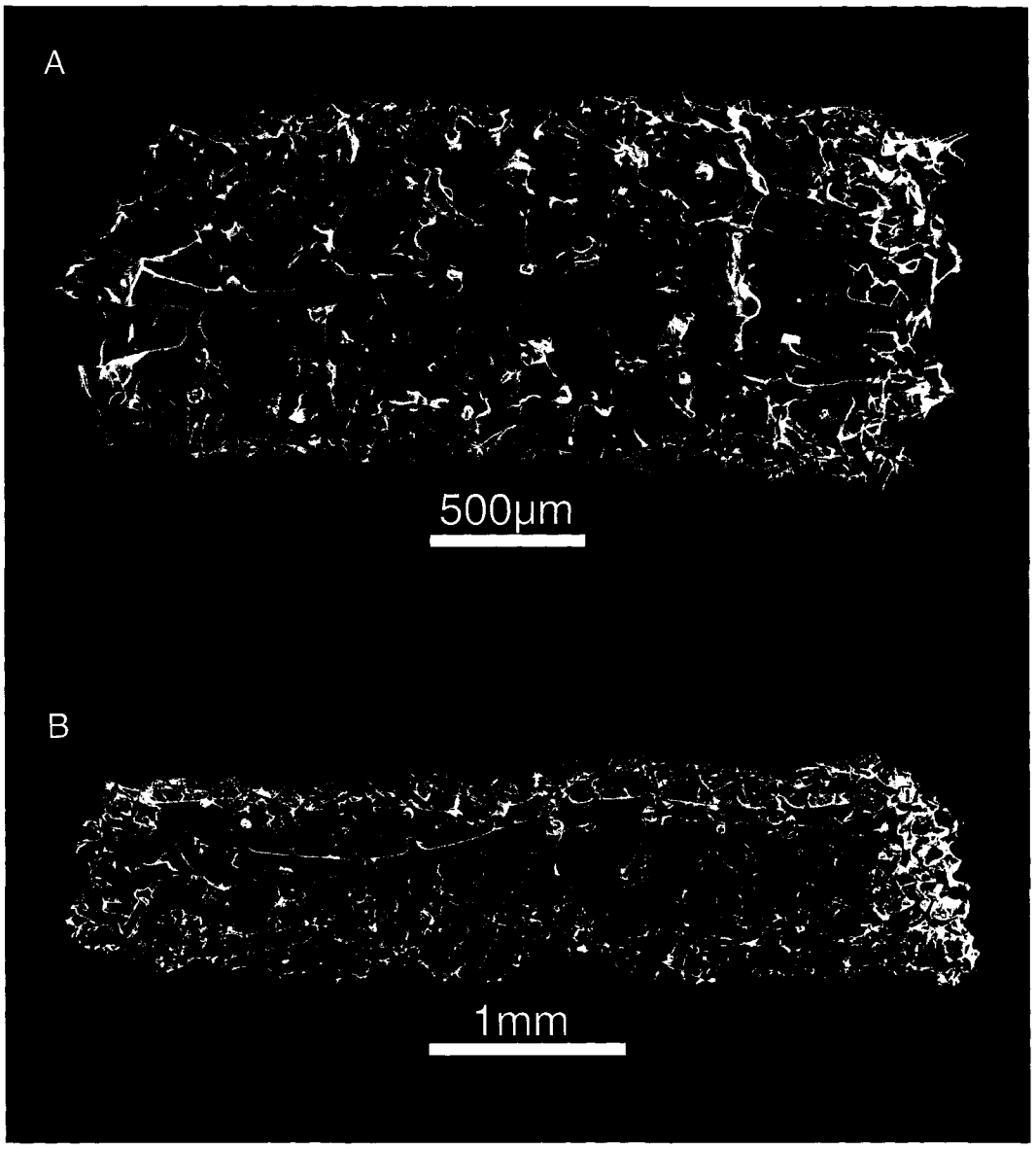

Figure 20. SEM images of *Farrea seiri*, sp. nov. framework showing massive smooth dictyonal strands and no apparent farreoid grid-like structure.

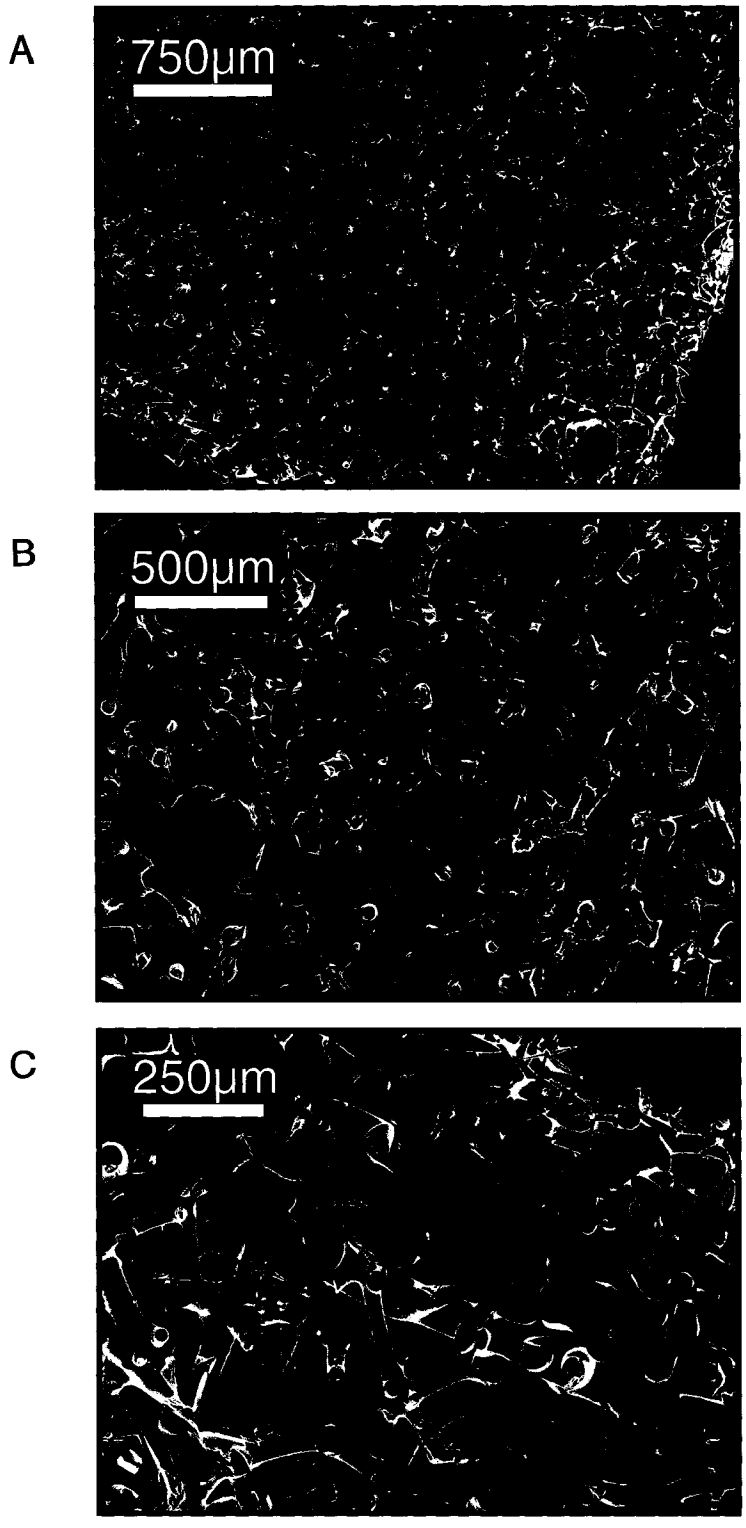

Figure 21. SEM's of *Farrea sieri,* sp. nov.; A, outer (presumed dermal) surface showing epirhyses on outer framework; B, outer surface betwen epirhyses showing highly disorganized nature of secondary framework; C, exposed inner framework showing high levels of intercalated hexactins, creating a very dense skeleton.

farreoid two-dimensional grid **(Fig. 21B)**. Long stretches of smooth dictyonal strands are hypersilicified, obscuring original hexactins. Huge numbers of intercalated hexactins obscure both the outer surfaces and internal meshes **(Fig. 21C)**. Secondary strands are smooth in texture, with a length of 287±107μm (range 89-508μm, n=50) width 52.6±14.3μm (range 21.8-81.9μm, n=50). Spurs are moderately common on both surfaces, and within the internal meshwork.

Spicules (measurements are given in **Table 2**)

Megascleres. Uncinates are very long and very thin, with moderately developed barbs, but without a distinguishable centrum **(Figs 22A.i, ii, 23A.i, ii).** Pentactins have strong spination on outer surface of tangential rays, extending almost to the tips. The proximal ray is heavily spined near the centrum, and entirely rough throughout its length, **(Figs 22B, 23B).** Two forms of clavule are present, umbellate and spiro-umbellate. Both have a thin, smooth shaft, ending in a bluntly pointed tip. The head of the umbellate form, **(Figs 22C.i, 23C.i)**, has approx. 25 spines projecting down from a thimble-shaped cap, either straight and parallel or flaring slightly outward. The spiro-umbellate form also has a thimble shaped cap, with spines projecting down but curved distally, either to the left (sinistral) or right (dextral) **(Figs 22C.ii, 23C.ii)**. Pentactins and both clavule types occur on both gastral and dermal surfaces.

Microscleres. Only one form of microsclere, an onychexaster, is present. Distributed fairly evenly throughout the specimen, these microscleres **(Figs 22D,**

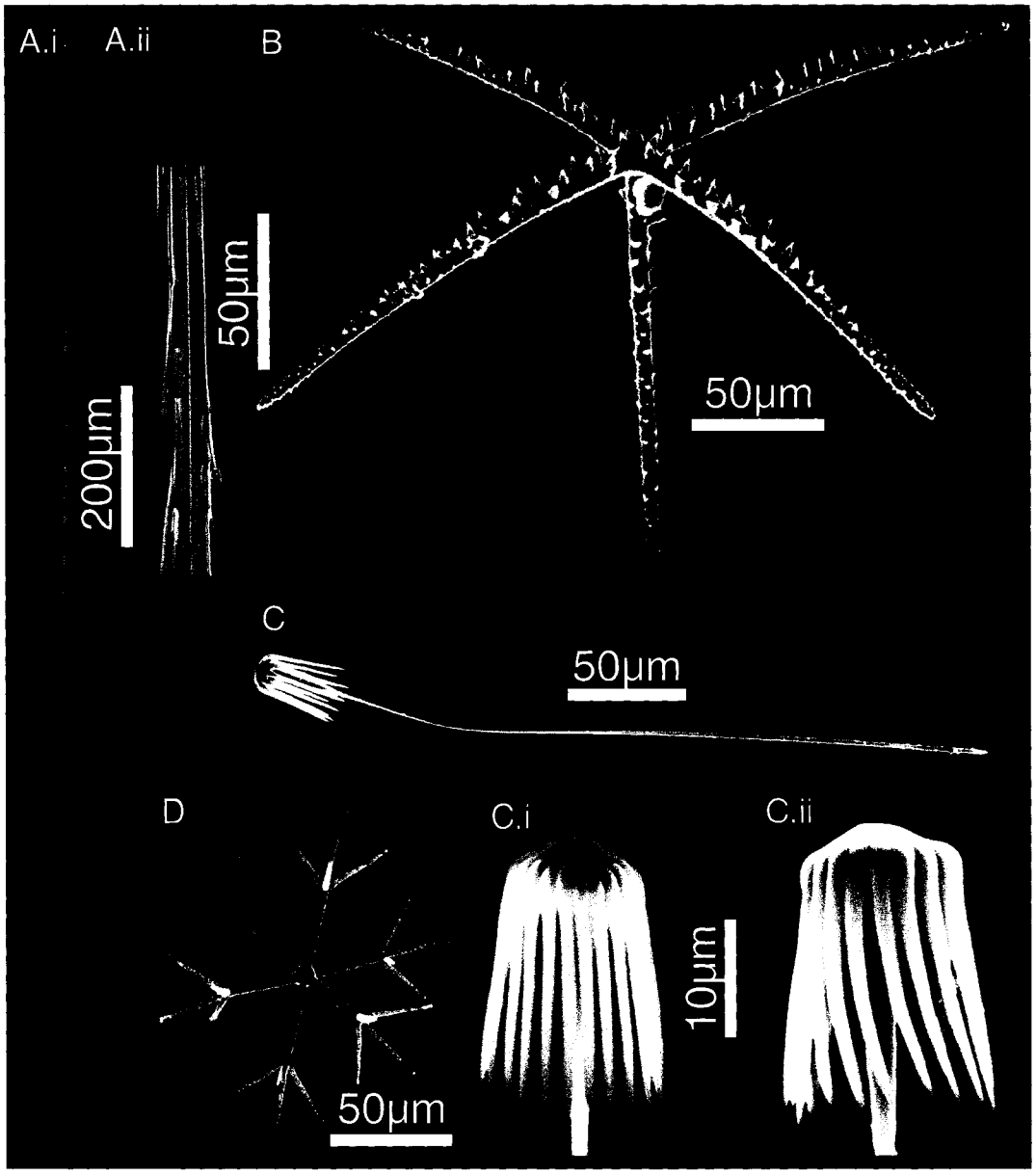

Figure 22. *Farrea seiri,* sp. nov. spicules of the holotype. A.i, A.ii, uncinate (LM); B, pentactin; C, clavule; C.i, umbellate clavule head; C.ii, spiro-umbellate clavule head; D, onychexaster.

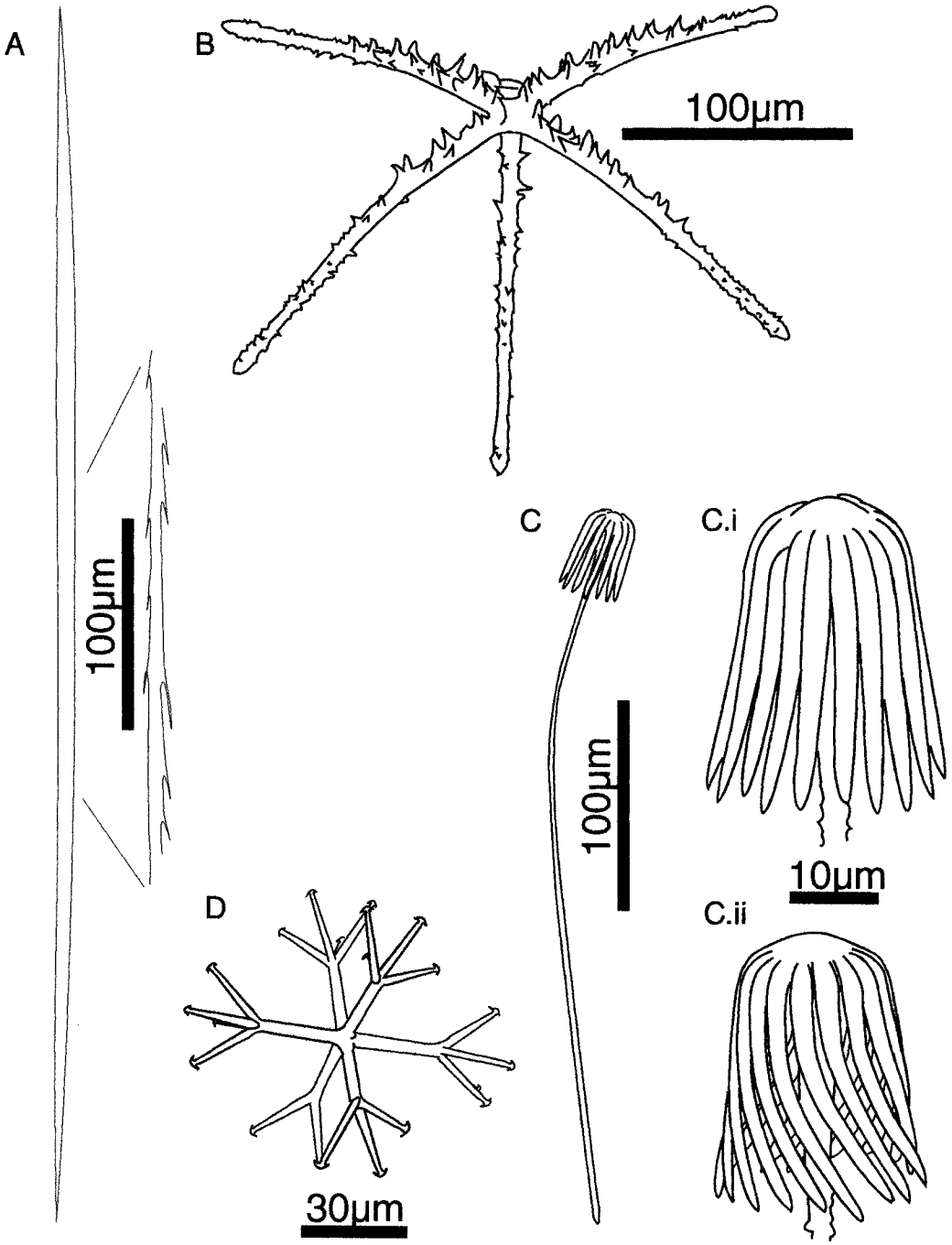

Figure 23. *Farrea seiri,* sp. nov. spicules of the holotype. A, uncinate; B, pentactin; C, umbellate clavule; C.i, umbellate clavule head; C.ii, spiro-umbellate clavule head; D, onychexaster.

23D) have with 6 finely rough primary rays, each with 4 similarly rough secondary rays ending in short, slightly reclined claws.

Table 2. Measurements of spicules of *Farrea seiri*, sp. nov.

Uncinate	*Length*	*Width*		
	802±376μm (range 520-1610μm; n=8)	6.5±2.5μm (range 3.3-10.1μm; n=8)		
Pentactin	*Proximal ray length*	*Proximal ray width*	*Tangential ray length*	*Tangential ray width*
	193±68μm (range 99-379μm; n=50)	7.9±2.3μm (range 3.1-13.3μm; n=24)	155±37μm (range 67-253μm; n=50)	8.1±2.6μm (range 3.9-12.5μm; n=50
Clavule	*Total length*	*Head length*	*Head width*	
	244±44μm (range 140-355μm; n=50)	25.6±4.9μm (range 16.4-40.5μm; n=50)	17.6±5.1μm (range 10.9-31.3μm; n=50)	
Onychexaster	*Diameter*	*Primary ray length*	*Secondary ray length*	
	108±8.6μm (range 89.6-119.2μm; n=11)	25.8±2.5μm (range 22.1-29.6μm; n=11)	29.7±2.8μm (range 22.8-32.5μm; n=11)	

Remarks

This species differs from all other *Farrea* with the exception of *Farrea herdendorfi* through its possession of umbellate clavules. It differs from *F. herdendorfi* in the presence of spiro-umbellate clavules and the absence of oxyhexasters. Also, *F. seiri* possesses much more massive dictyonal strands than *F. herdendorfi*.

Discussion

From framework appearances, *Farrea seiri* has dictyonal strands, such that, had the loose spicules not been collected in live tissue, this specimen may have been assigned to the family Aulocalycidae. It is here assigned to Farreidae, and firmly positioned in the type genus *Farrea*, on the basis of presence of clavules. This situation raises the question: which is considered a more important taxonomic indicator, the framework or the spicules? On the basis of the skeletal framework available in the basal fragments of *Farrea seiri,* the specimen does not fit the traditional definition of a farreid sponge (lacks an obvious farreoid framework), but because clavules are the only sceptrule form present, it is defined as *Farrea,* the farreoid skeleton presumably secondarily lost. More succinctly, farreid sponges are presently defined by the presence of clavules, or their derivatives. Therefore, in the case of farreids, spicules are considered by biologists to be more diagnostic indicators of phylogenetic relationships than are frameworks. This topic will be discussed more thoroughly following the description of the new genus, *Asceptrula.*

Asceptrula, g. nov.

Type species: *Asceptrula axialis* sp. nov.

Diagnosis. Farreidae, lacking sceptrules, and including uncinates and pentactins.

Etymology. The genus is named for the marked lack of sceptrules, therefore, *Asceptrula*.

Asceptrula axialis sp. nov.
(Figs 25-31)

Materials examined.

Holotype: USNM #####: 46°29.83'N, 129°35.79'W, July 19th, 1993, 2387m depth, coll.V. Tunnicliffe, R/S 'ROPOS' (Remotely Operated Platform for Ocean Sciences), dive HYS 221, North CoAxial segment, Juan de Fuca ridge. **(Fig. 24)**

Etymology: Named for visible axial condensation of the skeletal framework

Description.

SIZE and SHAPE.

Four pieces of a single organism were obtained by robot submersible. The specimen was situated in a region of recently formed basalt blocks that were sparsely clothed in bacterial mats and strands. In vivo video showed the intact organism as having been about 12 cm tall, with a branch point approximately 5 cm from the base, and with axial thickening occurring along both branches of the organism.

Overall structure is very frond-like, with thin marginal fringes, and no channelization. Growth pattern reflects very low amplitude lateral undulation of

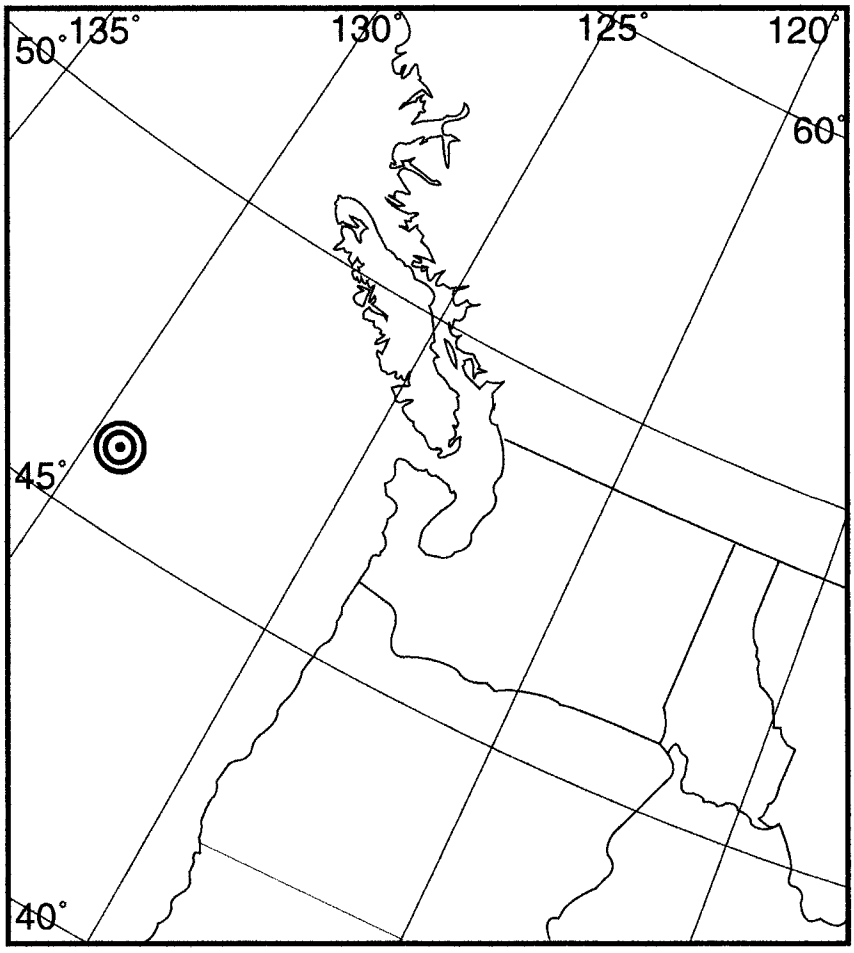

Figure 24. Sample location for *Asceptrula axialis*, sp. nov.

margins and rare extension and contact between opposite edges; self-fusion results in formation of one short tube with a diameter of 1.2 cm **(Fig. 25A)**. The framework is axially thickened, **(Fig. 26),** measuring 1.63±0.32mm (range 0.86-1.88m, n=10) in thickness at the centre of the axis.

SKELETON

Framework

The framework, constructed of a 2-dimensional mesh, **(Fig. 27),** has an average mesh size of 249±45μm (range 177-324μm, n=10). The thick axial region is composed of up to nine dictyonal layers, the extra skeletal components being added to one side of the primary framework, **(Fig. 28).** The two differentiated body surfaces are presumed to be the atrial or exhalant surface with thicker beams, 81.3±31.2μm (range 54-134μm, n=5), and the dermal or inhalant surface with thinner beams, 41.1±14.8μm (range 28.0-64.5μm, n=5). Differentiation of the two surfaces is based on the supposition that secondary dictyonalia addition occurs mainly on the dermal surface of the primary framework. This is supported in **Fig. 29A, B**, where construction of secondary skeletal structures has begun. This image shows heavy spur formation on each side of the grid, at virtually every node. All spurs appear long and straight, but all atrial spurs have a rough texture and are unmodified, whereas those on the dermal side are often extended and variable in texture. Many of the dermal spurs are fused to centres of secondary dictyonalia or tips of their rays. The secondary structures are a mixture of true and false nodes, with cross connections occurring between grid levels by synapticula.

Spicules (Measurements given in **Table 3**)

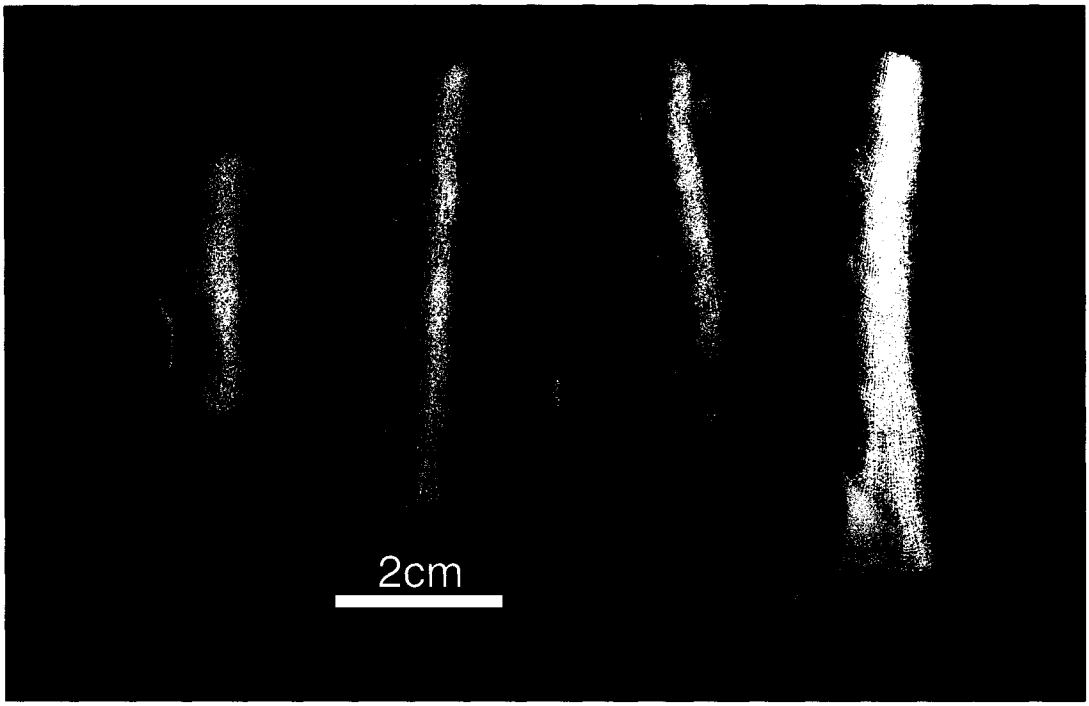

Figure 25A. Face view of cleaned framework of holotype fragments of *Asceptrula axialis*, sp. nov.

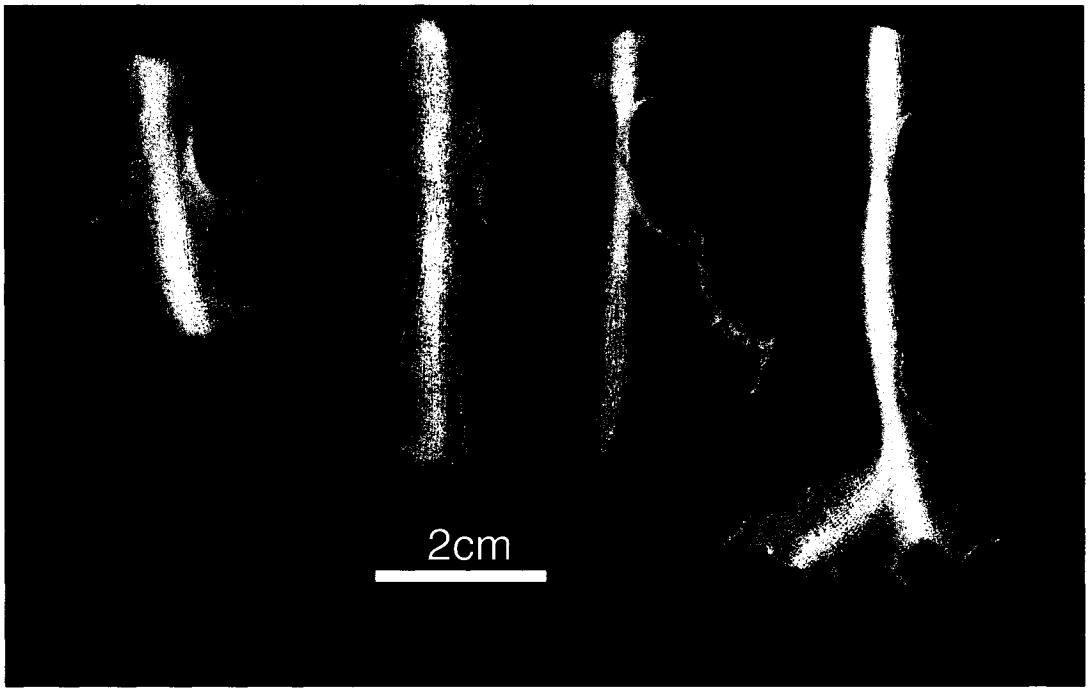

Figure 25B. Reverse side faces and nearly edge views of two fragments (right) of holotype of *Asceptrula axialis*, sp. nov.

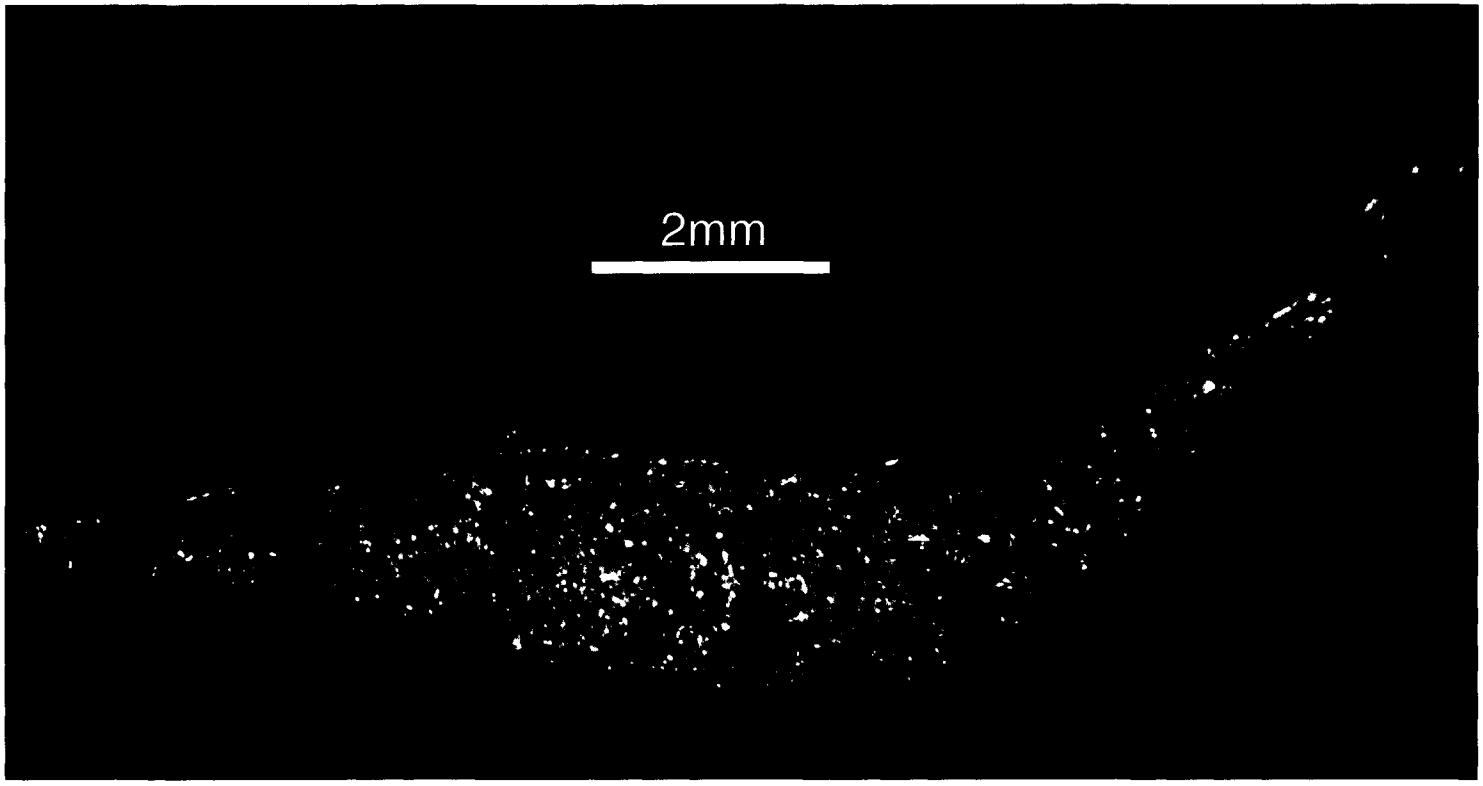

Figure 26. Cross-section of a *Asceptrula axialis*, sp. nov. framework, showing axial thickening in central 5 mm wide axis of frond.

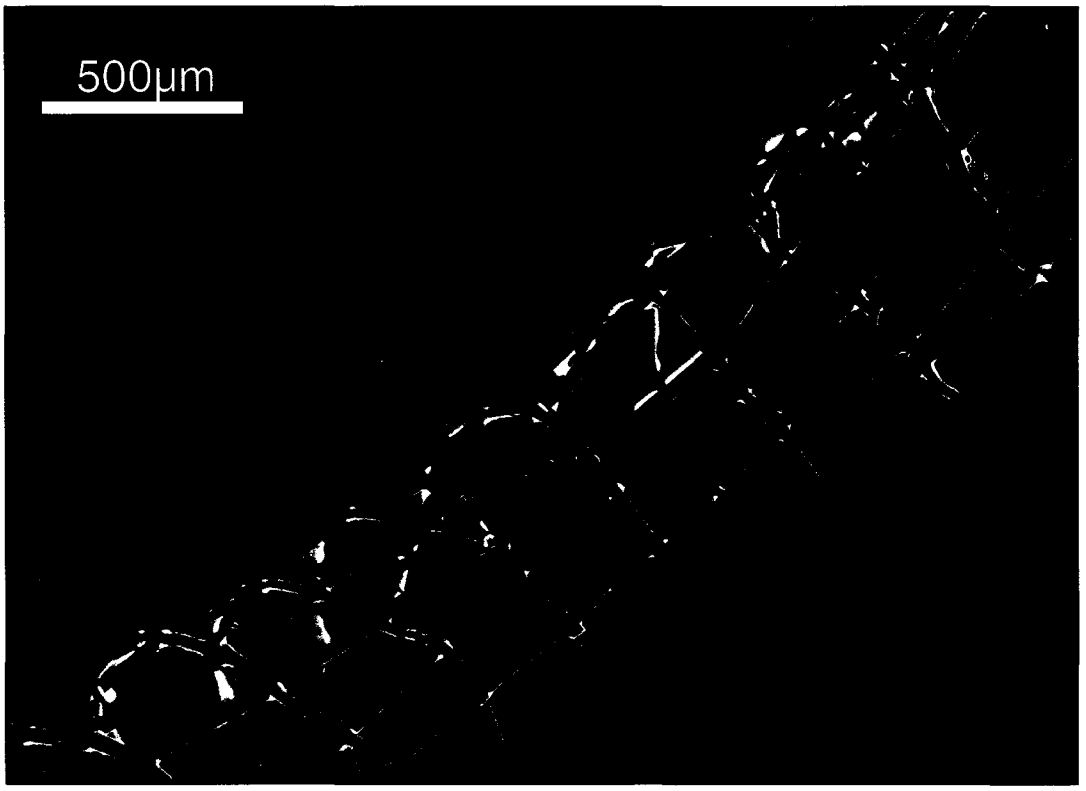

Figure 27. Edge view of marginal skeletal framework of *Asceptrula axialis* sp. nov., holotype, showing farreoid nature of skeletal grid (SEM).

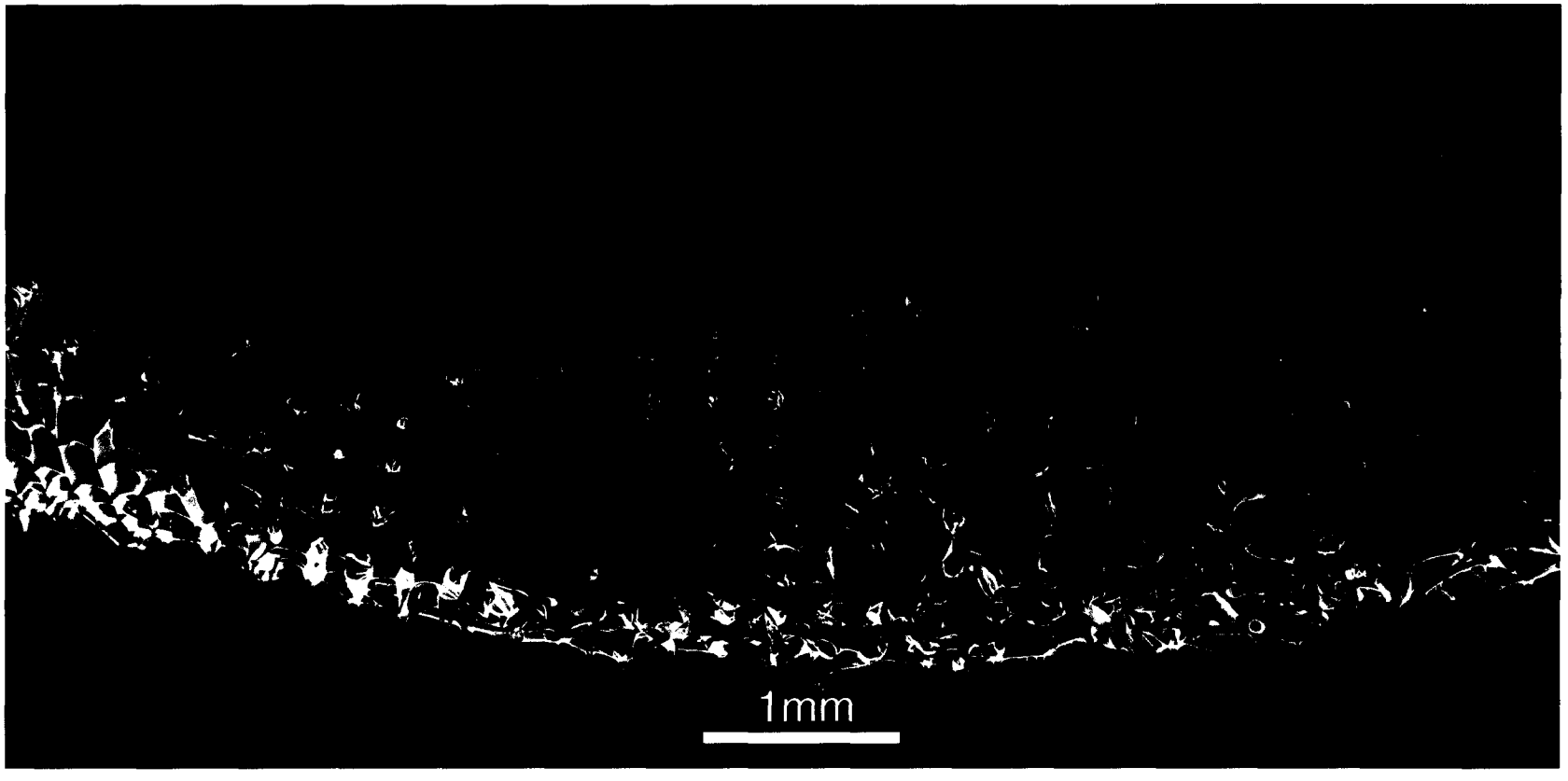

Figure 28. Skeletal SEM of *Asceptrula axialis* sp. nov., holotype, cross-section through axially thickened region.

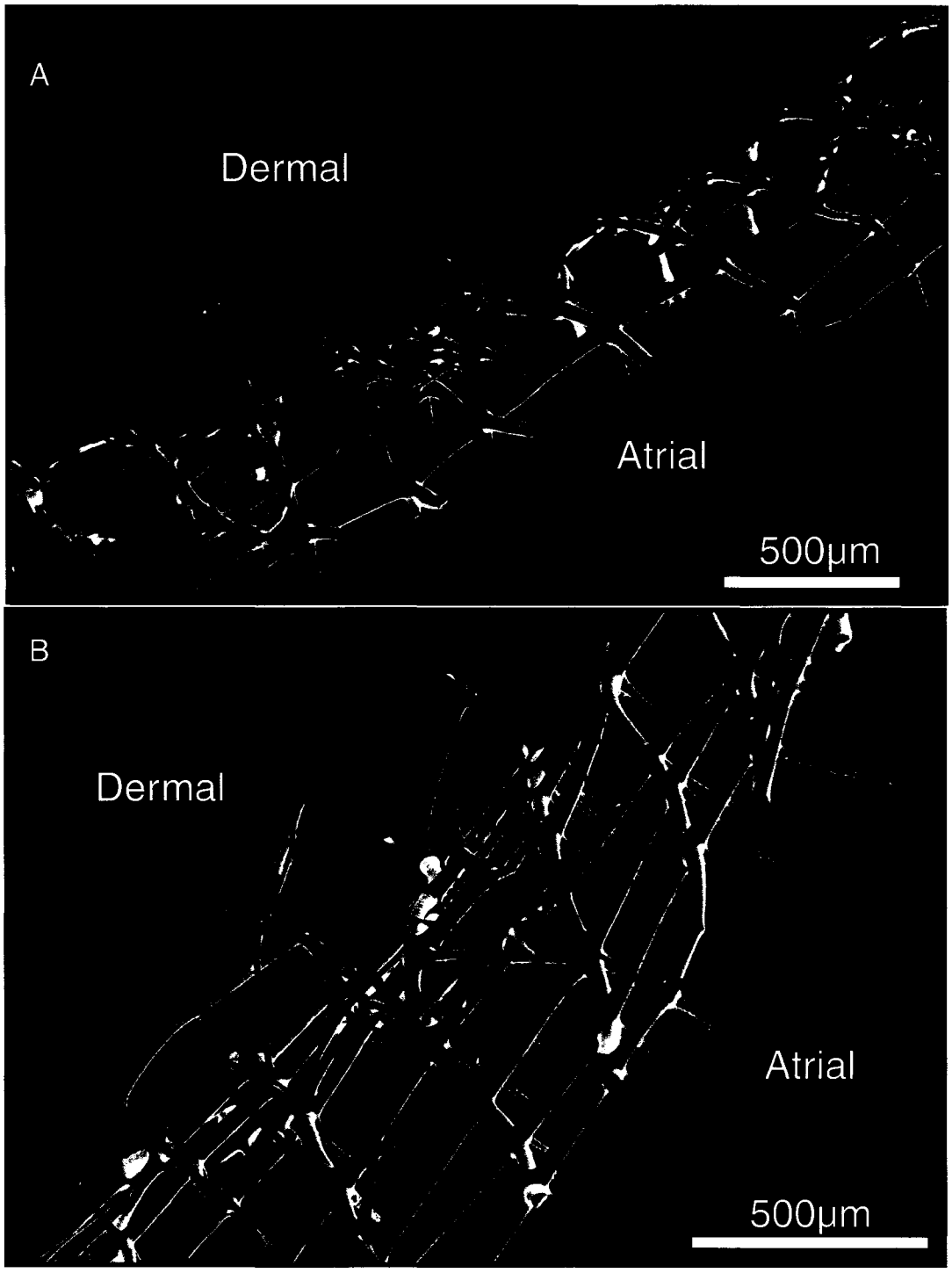

Figure 29. SEM skeletal images *Asceptrula axialis* sp. nov., holotype, showing addition of secondary skeletal components on the dermal side. Specimen fragment in A is younger than in B as indicated by differential addition of secondary skeletal components.

The specimen has both low diversity and density of loose spicules. Megascleres consist of long, thin uncinates **(Figs 30A.i, ii, 31A.i, ii)**, and large, robust pentactins **(Figs 30B, 31B)**. Uncinates are very long and very thin, with well-developed barbs, brackets, and no visible central tyle. Pentactins, present on the dermal and gastral surfaces, have heavy spination on outer lateral surfaces of tangential rays. The proximal ray is coarsely tuberculate near its root, and is very sparsely spined through most of its length.

Discohexasters **(Figs 30C, 31C)**, the only microsclere type, are scarce and distributed evenly throughout the wall thickness. Their six primary rays are short, thick and smooth, each supporting three secondary rays that are heavily spined. Each of these ends in a disc, bearing 5-6 recurved marginal spines.

Table 3. Measurements of spicules of *Asceptrula axialis*.

Uncinate	*Length*	*Width*		
	1641.1±250.4µm (range 1173.7-1967.3µm, n=11)	10.4±2.7µm (range 5.5-15.2µm, n=11)		
Pentactin	*Proximal ray length*	*Proximal ray width*	*Tangential ray length*	*Tangential ray width*
	445.8±107.8µm (range 261.0-751.6µm, n=50)	15.1±4.5µm (range 8.6-27.1µm, n=50)	216.8±28.8µm (range 141.2-279.1µm, n=50)	16.8±4.4µm (range 7.9-25.1µm, n=50)
Discohexaster	*Diameter*			
	66.0±7.0µm (range 52.6-80.6µm, n=50)			

Discussion.

The present working definition of the family Farreidae **(Reiswig, in press)**, is that group of hexactinosidan sponges "bearing, as loose spicules, sceptrules, including at least one form of clavule or sarule, and without narrow-headed

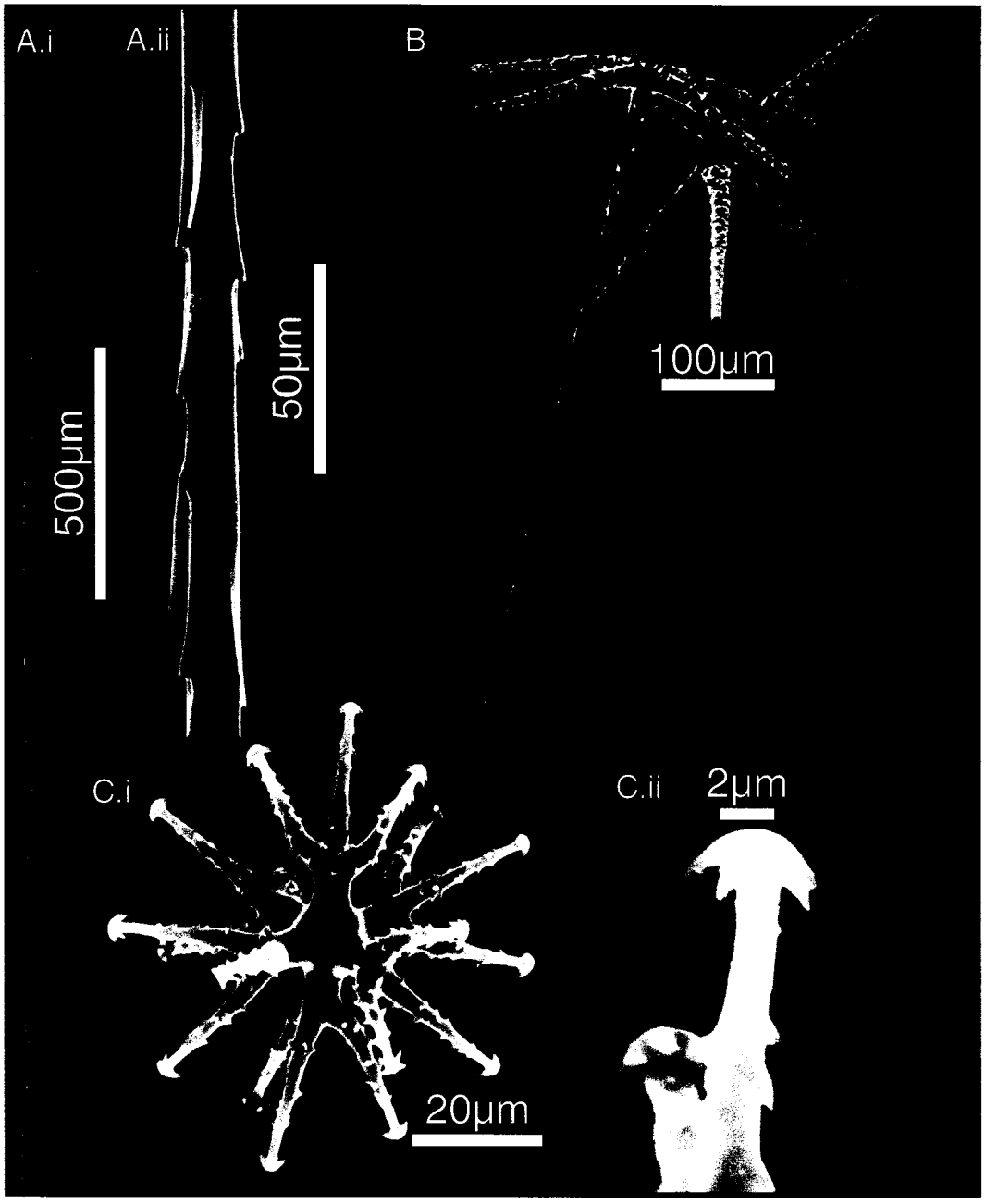

Figure 30. *Asceptrula axialis*, sp. nov. holotype spicules (SEM). A.i, uncinate; A.ii, uncinate (zoom); B, pentactin; C.i, discohexaster; C.ii, magnified tip of discohexaster.

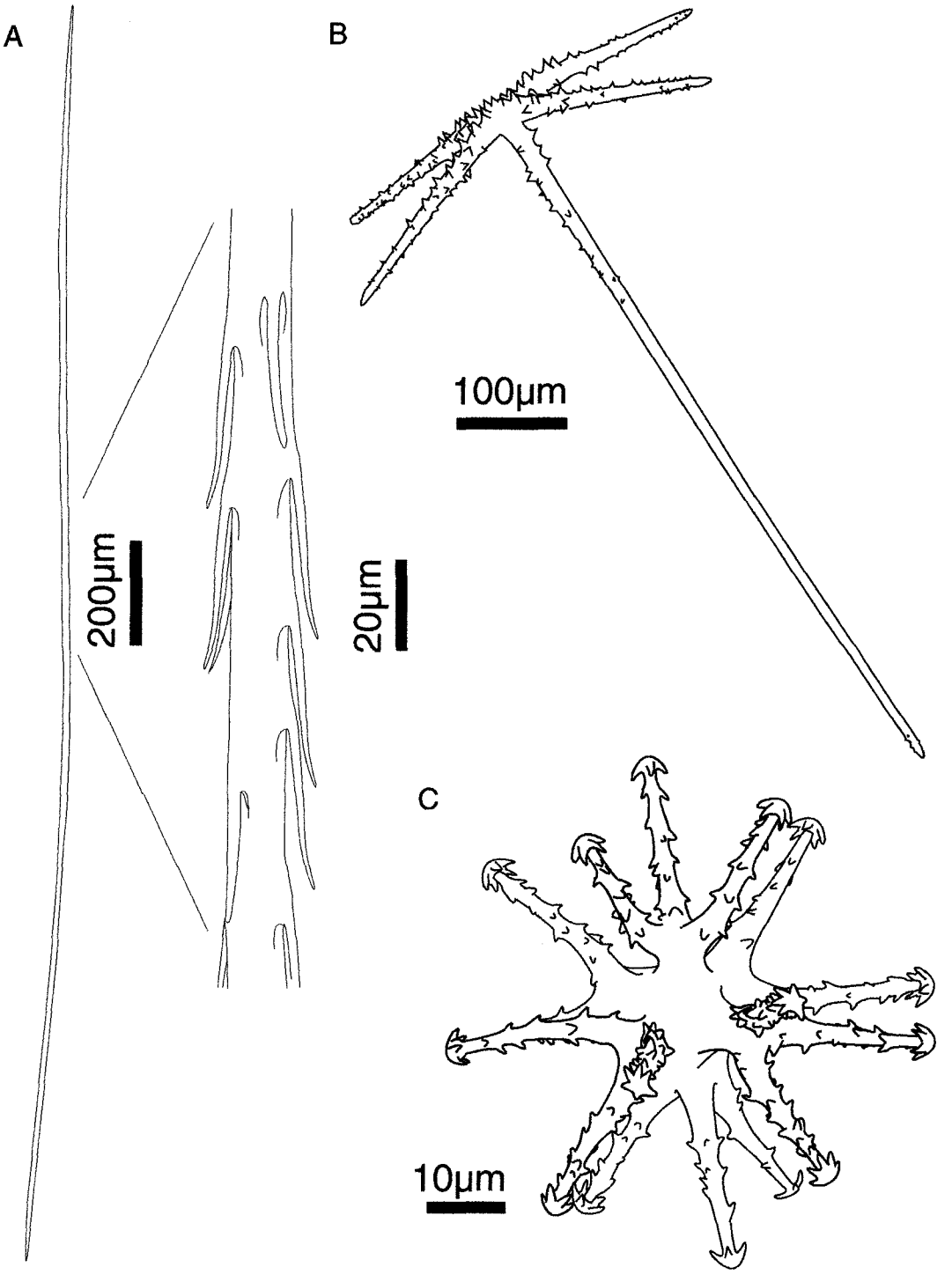

Figure 31. *Asceptrula axialis* sp. nov. spicules of the holotype. A, uncinate; B, pentactin; C, discohexaster.

scopules." From this, it is clear that the possession of sceptrules and, less importantly, the absence of narrow-headed scopules are the defining characteristics of Farreidae. Five genera, *Aspidoscopulia*, *Claviscopulia*, *Farrea*, *Lonchiphora* and *Sarostegia* are currently included in the family. Though defined solely on the basis of their sceptrules, many farreids share other similarities. For instance, all possess uncinates, pentactins and either oxyhexasters or discohexasters, and all farreids, except *Sarostegia*, have a farreoid framework **(Reid, 1964)**. Farreoid frameworks, as defined in the introductory section of this paper, consist of a two-dimensional primary grid-like scaffold. The dictyonalia in parallel strands are often in corresponding positions and are cross-linked with one another by tangential rays fused side to side, resulting in a grid-like layer of fused framework. It is the single layer, or two-dimensional, character of this structure that is considered by some authors to be distinctive for the family Farreidae. This alternate definition of Farreidae is extremely important for paleontologists, since loose spicules are unavailable in fossil material.

The present working definition of Euretidae **(Reiswig, in press)** is that group of Hexactinosid sponges "with basic three-dimensional dictyonal framework several dictyonalia in thickness even at the growing edge; primary dictyonal frame consists at least in part of four-sided (square or rectangular) meshes; rays of dictyonalia extend only one-mesh in length to the next adjacent dictyonal centrum; dictyonal rays composed of series of short beams aligned to form a single strand; dictyonal beams typically composed of two (sometimes one) dictyonal ray." Channelization of the framework is also considered central to Euretid taxonomy. It is important to note that

while the farreid definition was spicule-centered, the euretid definition is much more concerned with framework organization. Sixteen genera in two subfamilies are currently included in Euretidae.

The most prevalent common characteristic spanning these genera, with the exception of *Bathyxiphus* Schulze (1899) is the presence of a three-dimensional euretoid framework **(Reid, 1964)**. Euretoid frameworks, as defined in the introductory segment of this paper, consist of a 3-dimensional growing edge, with one to many meshes of dictyonal strands distributed throughout its depth between dermal and atrial layers. Much like farreoid skeletons, secondary components can be added to the euretoid skeleton, but its three-dimensionality is never solely the result of these secondary meshworks. The primary skeleton of a euretoid sponge is not cubic in nature, but consists of several dictyonal strands distributed in three dimensions. These strands then generate cross-links in the same fashion as a farreoid skeleton.

Two specimens discussed earlier in this paper were assigned to the family Farreidae, under genus *Farrea*. *Farrea* is defined as members of "Farreidae with clavules as the only sceptrule form" **(Reiswig, in press)**. Both *Farrea herdendorfi* and *Farrea seiri* contain sceptrules in the form of clavules only, and are without narrow-headed scopules. For this reason, they were assigned to *Farrea*.

Sarostegia is assigned to Farreidae **Ijima (1927)**, despite its typically euretoid framework, based on its relation to *Claviscopulia* by assumed homology of the sarules present in both genera, establishing a clear precedent of spicular importance over framework. Though *Asceptrula axialis* has a farreoid framework, this is insufficient in and of itself to legitimate assignment to Farreidae. Without sceptrules,

it simply cannot presently be considered a member of Farreidae as the definition of that family now stands. *Asceptrula axialis* does not, however, have narrow-headed scopules, lacking a positive character to support exclusion from Farreidae.

The only alternate hexactinosidan family into which *Asceptrula axialis* might fit is Euretidae. On the basis of its loose spicules, *Asceptrula axialis* could be easily accommodated in Euretidae, which often has pentactins, scopules and uncinates, but can be lacking any of these; microscleres are often either oxyhexasters or discohexasters. The monospecific genus *Bathyxiphus* is poorly known in terms of its loose spiculation. Although it has a farreoid framework, it is presently placed within Euretidae on the basis of poorly substantiated possession of narrow-headed scopules, the few clavules found with the original type being considered extrinsic in origin. Though the axial region of *Asceptrula axialis* has a 3-dimensional structure, the margins are quite obviously 2-dimensional in nature.

Decision on the placement of *Asceptrula axialis* can be assisted by analysis of the differences between Farreidae and Euretidae and whether or not some characters might be plesiomorphic or apomorphic. Which type of framework arrangement is ancestral: 2-dimensional or 3-dimensional? Which spicule type is ancestral: clavule, scopule, no sceptrule or an undifferentiated sceptrule? Is *Asceptrula* itself possibly ancestral?

Several trees were constructed to reflect these basic assumptions of the ancestral condition. A table of the taxa to be involved in the analysis and their character states is constructed below.

Table 4. Character states for taxa to be used in analyses.

Characters	Asceptrula	Sarostegia	Farrea	Bathyxiphus	"2 genera" of Euretidae	Most Euretidae
2-d framework	present	absent	present	present	absent	absent
3-d framework	absent	present	absent	absent	present	present
scopules	absent	present	absent	present	absent	present
clavules	absent	absent	present	absent	absent	absent
uncinates	present	present	present	present	absent	present
sceptrules	absent	absent	absent	absent	absent	absent

Aseceptrula is placed in the farreid lineage, the lower branch in most of the following trees, because a placement in the Euretidae lineage would necessitate branching off of the *Bathyxiphus* line. Such a branch, though superficially equally parsimonious to branching from the Farreidae, presents the following difficulties: besides the absence of scopules, *Asceptrula* also differs from *Bathyxiphus* in the absence of pileate clavules, dermal and atrial pinular hexactine megascleres, and the presence of large heavily spined pentactins. General body form also differs; though both have primarily 2-dimensional frameworks, *Bathyxiphus* shows no signs of self-fusion or tube formation, as seen in *Asceptrula*. Derivation of *A. axialis* by branching from any of the existing Farreid genera would necessitate further state changes; as such, assignment of the species *axialis* to a new monospecific genus, *Asceptrula*, is the most parsimonious solution. Due to the limited scope of this project, a total character state/cladistic analysis of all sister taxa is not feasible.

Table 5. Basal condition in trees representing phylogenetic hypotheses.

Tree	Basal Condition
1	2-d framework, uncinates, clavules
2	2-d framework, uncinates, scopules
3	2-d framework, uncinates, no sceptrules

Tree	Basal Condition
4	3-d framework, uncinates, scopules
5	3-d framework, uncinates, clavules
6	3-d framework, uncinates, undifferentiated sceptrules

The first phylogenetic hypothesis considered, **Tree 1 (Fig. 32)**, is derived from **Reid, 1964** and illustrates contemporary zoological view: that Farreidae is more primitive than Euretidae and is, in fact, basal to it. This assumes the ancestral organism to have had a 2-dimensional framework and both uncinates and clavules. This tree requires 7 state changes, 2 in the Farreidae and 5 in Euretidae.

The second set, **Tree 2 (Fig. 33)**, is a hypothetical one not investigated in the literature. It places *Bathyxiphus* in the basal position with a combination of 2-d framework and scopules. The resulting tree requires 6 state changes, 3 in Farreidae, and 3 in Euretidae.

The third set, **Tree 3 (Fig. 34)**, places *Asceptrula* in the basal position; the primitive characters are a 2-d framework and absence of sceptrules. The resulting tree requires 6 state changes and assumes the independent generation of scopules and clavules.

The fourth phylogenetic hypothesis, **Tree 4 (Fig. 35)**, a mirror to the basal position of *Farrea* in set 1, places typical euretid characters in the basal position: a combination of a 3-d framework and the presence of scopules. These characters are typified by the Euretid genus, *Eurete* Semper (1868). The resulting tree requires 7 state changes, 3 in Euretidae and 4 in Farreidae.

The fifth phylogenetic hypothesis, **Tree 5 (Fig. 36)**, reflects a combination of a 3-d framework with clavules as seen in the Farreid genus *Sarostegia* as the

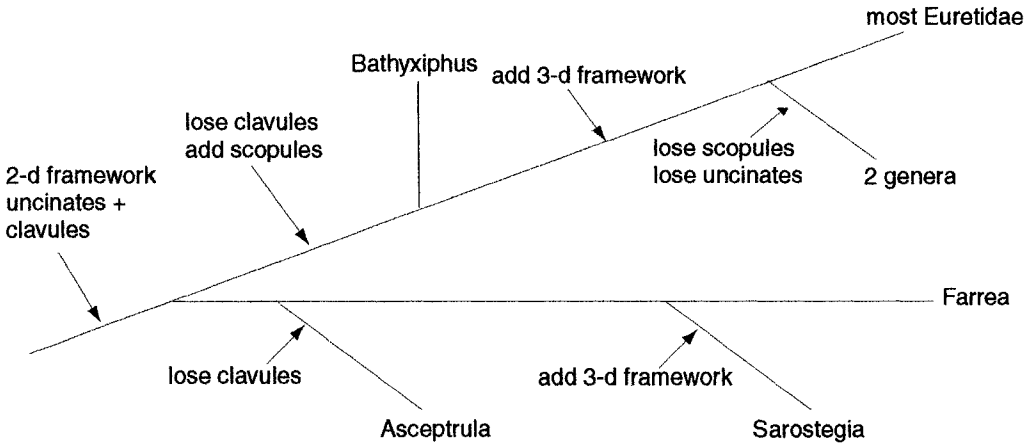

Figure 32. Tree 1: 2-d framework, clavules ancestral (Reid 1964)

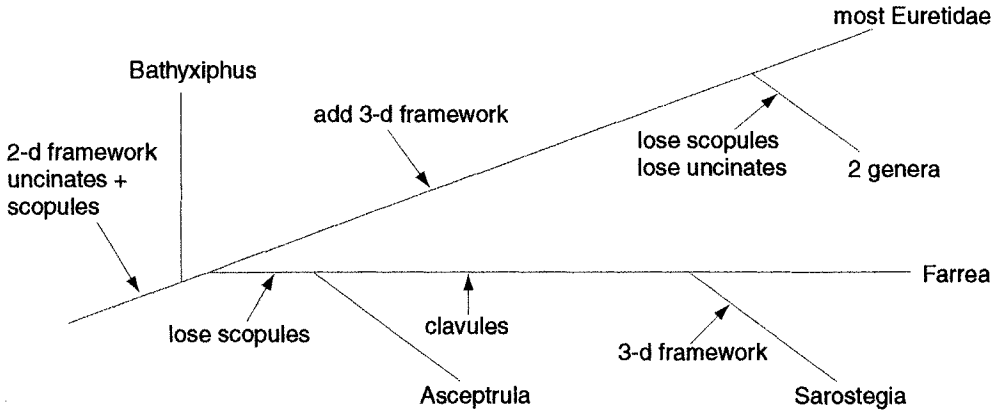

Figure 33. Tree 2: 2-d framework, scopules ancestral (*Bathyxiphus*)

primitive condition. This resulting tree requires 7 state changes, 5 in Euretidae and 2 in Farreidae.

The sixth phylogenetic hypothesis, **Tree 6 (Fig. 37)**, is derived from **Mehl, 1992**. This assumes the ancestral organism to have had a 3-d framework and sceptrules, though of an undifferentiated type, neither scopule nor clavule. The tree resulting from these assumptions requires only 5 state changes for resolution.

From this general analysis, Mehl's (1992) hypothesis, represented by **Tree 6**, is the most parsimonious among the alternate ancestral relationships presented here for the Euretidae-Farreidae clade. It is also in conformity with the known temporal sequence of occurrence of Farreidae and Euretidae in the fossil record. It is both possible and logically consistent to define *Asceptrula* as a mono-specific genus within Farreidae with the unique feature of lack of sceptrules.

A revised definition/diagnosis of the Farreidae is offered here: Hexactinosida typically with sceptrules in the form of clavules, or their derivatives, sarules, lonchioles or aspidoscopules, and typically with a farreoid framework. Where sceptrules are lacking the framework is farreoid. Where the framework is euretoid, sarules are present.

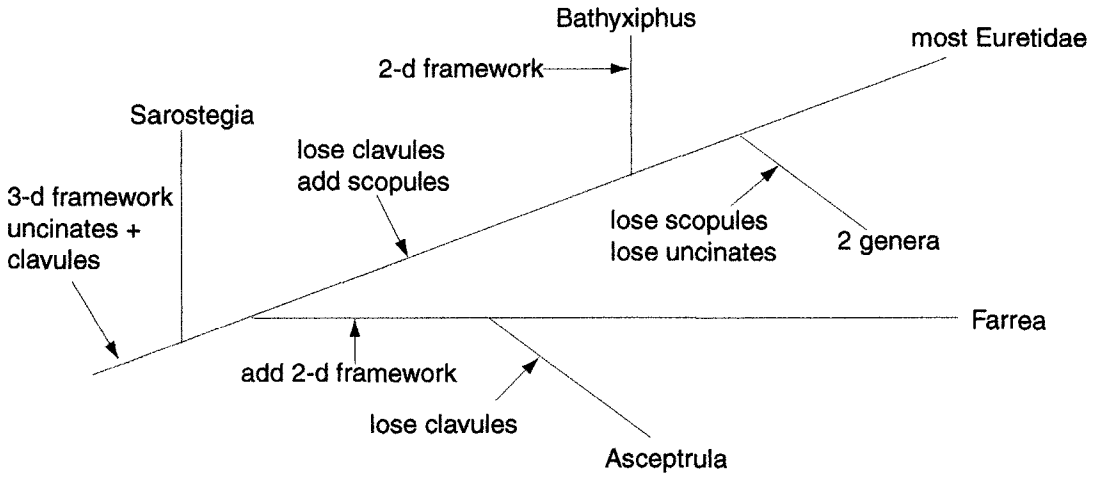

Figure 36. Tree 5: 3-d framework, clavules ancestral (*Sarostegia*)

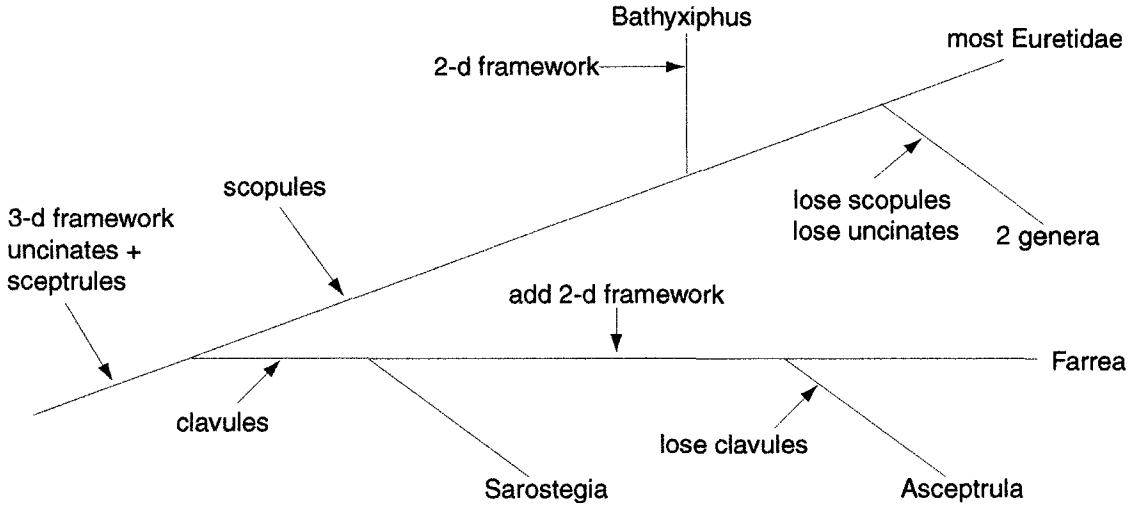

Figure 37. Tree 6: 3-d framework, sceptrules ancestral (Mehl 1992)

Conclusion.

Among the problems associated with the discussed taxa is that individual workers have used different criteria for taxa definitions. Zoologists place precedence on spicules, whereas paleontologists, with usually only the dictyonal framework available give precedence to structure. As a result, Hexactinosida is sometimes defined by its spicules and other times defined by its framework. As such, the supposed precedence of characters used by biologists is not yet internally consistent. Since spicules are not central to the definition of Euretidae, that family is still used as a catch-all taxon.

It is inevitable that different workers will choose different defining characters for a given taxon, but to solve the myriad problems associated with Hexactinosida, it is imperative that an objective re-assessment of the defining characters be undertaken. A complete cladistic overhaul of the group is absolutely necessary. The analysis would be based primarily on physical characters; though it would be useful to have genetic material, it is quite difficult to obtain.

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