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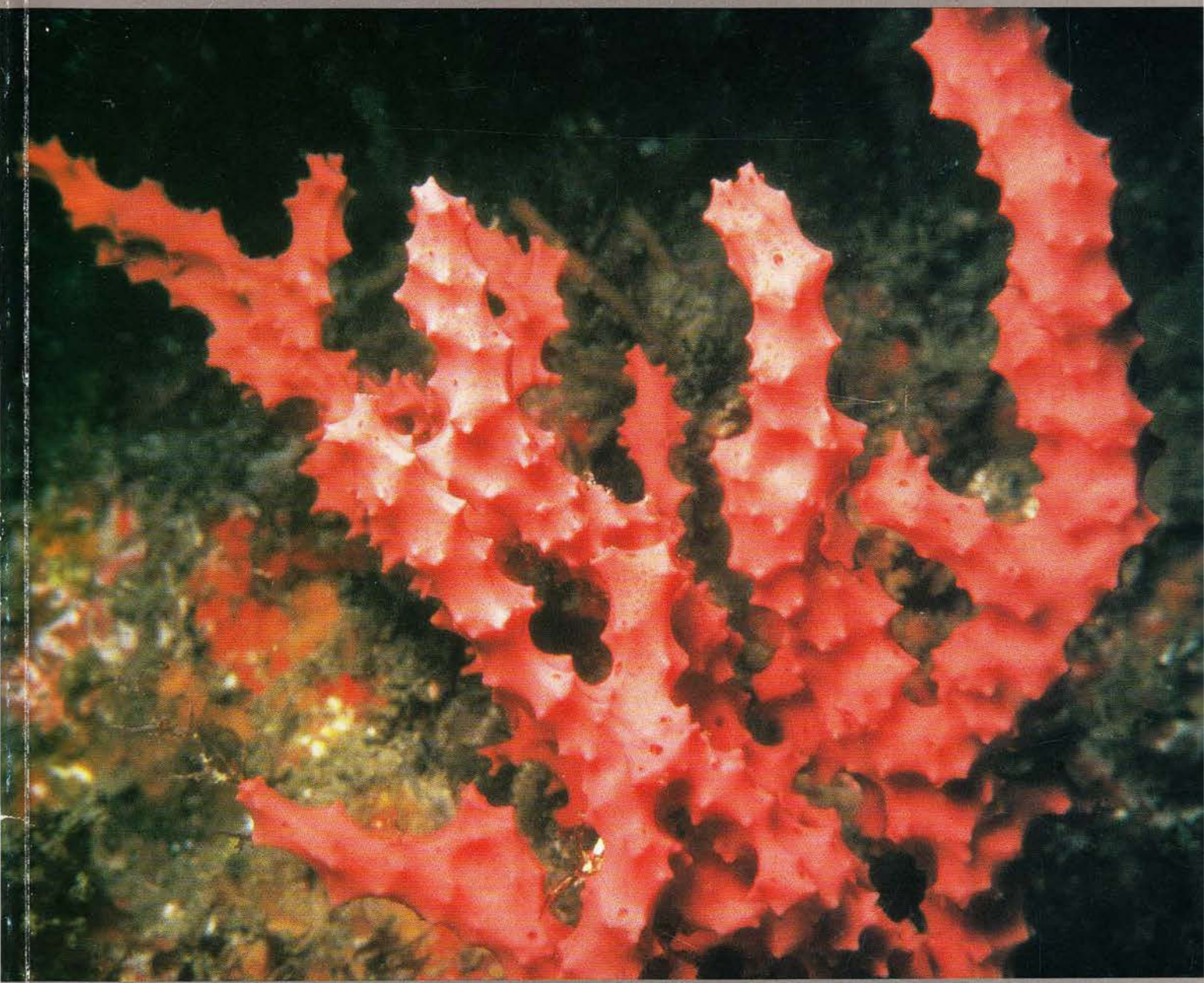

The Marine Fauna of New Zealand:

Porifera: Demospongiae Part 5. Dendroceratida and Halisarcida

Patricia R. Bergquist

New Zealand Oceanographic Institute Memoir 107

COVER PHOTO: *Darwinella gardineri* Topsent, Goat Island, Cape Rodney to Okakari Point Marine Reserve, Leigh, 15 m depth. (Photo: Chris Battershill)

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The Marine Fauna of New Zealand: Porifera: Demospongiae

Part 5. Dendroceratida and Halisarcida

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ABSTRACT

Two orders of Demospongiae are discussed and the New Zealand representatives of each are described. The Dendroceratida are represented by five species belonging to four genera, and the Halisarcida, established formally as a new order, is represented by one species in New Zealand, the cosmopolitan Halisarca dujardini. Definition of the characters used in descriptions of these sponges is given, as is a full discussion of the systematic affinities of the Dendroceratida.

Keywords: Demospongiae, Dendroceratida, Halisarcida, taxonomy, new taxa, classification, New Zealand

INTRODUCTION

This contribution is the fifth in a series which documents the demosponge fauna of New Zealand. Two orders are dealt with, the Dendroceratida and a new order, the Halisarcida. Both are numerically small groups, generally and within New Zealand, but both present significant problems with respect to their present classification and their wider relationships within the Demospongiae.

A framework for a generic and familial classification of the order Dendroceratida, which at the time included the family Halisarcidae, was established by Bergquist (1980) as part of a revision of generic and higher-order classification of the three sponge orders that lack a mineral skeleton and produce only fibrous skeletons. These are the Dictyoceratida, Dendroceratida, and Verongida. On the basis of this classification, six New Zealand species belonging to five genera fall within the Dendroceratida. Two species, *Darwinella oxeata* and *Dictyodendrilla dendyi*, are endemic. All species have been described earlier, but in this work they are fully described for the first time and recorded under their correct names.

Dendroceratid sponges are often brilliantly pigmented and are common and striking components of shallow subtidal faunas on rocky coasts around New Zealand. Consequently it is inevitable that some species have been recorded in popular works and ecological survey reports under a variety of names. Common misnomers are corrected in discussion of each species.

This contribution is primarily a taxonomic record of the New Zealand species, however the arrangement suggested here for these species raises broad issues of classification and relationships and provides opportunity to comment on current approaches to the classification of these groups of sponges.

The arrangement for the Dendroceratida proposed by Bergquist (1980) recognised three families: Aplysillidae (now Darwinellidae, recognising priority of this family name), Dictyodendrillidae, and Halisarcidae. These familial distinctions rested primarily upon skeletal content and pattern; the Darwinellidae have dendritic fibre skeletons, the Dictyodendrillidae have anastomosing fibre skeletons and the Halisarcidae have a fibrillar collagenous skeleton only, fibre not being developed.

The new element in the 1980 arrangement was that the dendritic nature of the fibre skeleton was deemphasised as the primary attribute for inclusion within the order Dendroceratida. A new family, the Dictyodendrillidae, with an anastomosing skeleton was introduced and strong argument was advanced for removing the Halisarcidae from the Dendroceratida, although that move was not formally made as further information was needed.

The monogeneric family Halisarcidae (genus *Halisarca*) was included within the Dendroceratida by De Laubenfels (1936, 1948) and Lévi (1956) as the order Myxospongida). This group, which had included all forms without any fibre or mineral skeleton, was progressively broken up and the component genera other than *Halisarca* were allocated by various authors to groups with which they had demonstrable relationships. These genera included *Oscarella*, *Bajalus*, *Hexadella*, and *Chondrosia*. The placement of *Halisarca* in a family Halisarcidae within the Dendroceratida was a convenience allocation in the absence of any clear alternative affiliation. If *Halisarca* remains within the Dendroceratida, it is impossible to frame any broad biologically based diagnosis of that order. Consequently, it is now proposed that a monogeneric order, the Halisarcida, be established. The justification for this move is included in the systematic descriptions and in the discussion.

The classification of the fibrous sponges adopted in this work, that of Bergquist (1980), was based upon a considerable body of information on ultrastructural histology, reproductive and larval biology and secondary-metabolite chemistry as well as on adult morphological attributes. This range of data was available in 1980 for many taxa within the largest order considered, the Dictyoceratida, and also for the Verongida. Almost no comparable literature was available for dendroceratid genera at that time. The only relevant works were an ultrastructural study of spermatogenesis in *Aplysilla rosea* (Tuzet *et al.* 1970), an ultrastructural description of a new type of secretory cell, the 'cellules spumeuses' (spumous cell hereafter) in *Pleraplysilla spinifera* (Donadey & Vacelet 1977), a scanning electron micrographic study of larval structure in *Darwinella oxeata* (Bergquist *et al.* 1979), a number of light-microscope and ecological studies of the reproductive biology of *Halisarca* species (Lévi 1956; Bergquist & Sinclair 1973; Chen 1976), reports of the occurrence of terpenoid metabolites in *Pleraplysilla spinifera* (Cimino *et al.* 1972, 1974, 1978) and *Darwinella rosea** (Kazlauskas *et al.* 1979), and description of the sterol profile of *Darwinella rosea** (Bergquist *et al.* 1980).

* reported as *Aplysilla rosea*

These contributions provided an indication that chemotaxonomic analysis and secretory-cell ultrastructure, which had proved useful in classification of other orders, would also assist in clarifying relationships within the Dendroceratida. In the intervening period, investigations on the chemistry, ultrastructure and histology of dendroceratid sponges have provided information which permits species and generic descriptions to be more broadly based, the existing classification to be assessed, and the Dendroceratida to be compared with other orders on a broader biological basis.

The major questions to be resolved regarding dendroceratid relationships are those raised by Bergquist (1980) and Bergquist *et al.* (1990):

(a) Should the Halisarcidae be retained within the order?
(b) Is the separation of the families Darwinellidae and Dictyodendrillidae on the basis of skeletal pattern supported by additional information from chemistry and histology?
(c) How closely are the Dendroceratida, or some members of that group related to members of the dictyoceratid family Dysideidae? Is the present dispersion of genera between the two orders supportable?

Each of these questions can now be addressed in discussion and in the context of describing of the New Zealand species.

CHARACTERS USED IN DEFINING ORDINAL, FAMILIAL, AND GENERIC TAXA

Introduction

Great difficulty has always been encountered by authors attempting comprehensive descriptions of sponges which lack a mineral skeleton. There are two major reasons for this. First, higher-order sponge classification has stressed skeletal structure and arrangement and the mineral skeleton of most Demospongiae has a diversity and structure that invite detailed description. In the absence of such a skeleton the habit has been, when dealing only with fibres, to simply describe them as primary or secondary, cored or uncored, pithed or homogeneous, and anastomosing or dendritic without carefully reporting on their structure.

Second, the need to describe carefully adult and larval soft-tissue organisation and histology in addition to skeletal attributes has only lately been rediscovered. Although workers such as Sollas (1888), Lendenfeld (1889), Schultze (1877), and Topsent (1896) recognised the importance of soft-tissue organisation in classification, most twentieth-century taxonomists dealing with Demospongiae (with the exceptions of Levi (1956), Simpson (1968), Pomponi (1976), Bergquist (1978, 1980), and Vacelet *et al.* (1989)) have ignored it and some still do. Consequently, important information is missing from most descriptions and this applies in greater measure to the Dendroceratida and to the Dysideidae than to any other groups of fibrous sponges.

A general problem with sponge descriptive terminology is that it is imprecise. For example, a fibre may have an outer concentrically laminated 'bark' and a central 'pith'; this describes most verongiid fibres, all dendroceratid fibres, and some dictyoceratid fibres. However, in each of these three groups the structure of pith and bark is distinctive in ways that indicate different morphogenetic processes during fibre development, and thus basic genetic differences. It is necessary to recognise and to specify such detail in order to permit later workers to detect affinities as new taxa are described. Failure to appreciate detailed structural differences invites misleading results when descriptions are incorporated into character matrices and subjected to cladistic analysis. Analytical methodologies are not perfect but when the data also are not ready for analysis, the exercise is destined to produce misleading results. An attempt has been made over recent years to establish a consistent terminology for sponge descriptions, but considerable refinement is needed, and also greater awareness of developmental processes involved in generating structure must underpin the exercise. The following features have been used in this work in framing species descriptions and generic, familial, and ordinal diagnoses.

Organisation of the Skeleton

Sponge-fibre skeletons are either anastomosing networks or dendritic, ramifying from multiple or single basal points or from a basal spongin plate. The latter type is by far the commonest in the Dendroceratida and is diagnostic of the family Darwinellidae.

Anastomosing skeletons exhibit three different patterns, all of which are figured in Bergquist (1980). The commonest, which is the usual one in Dictyoceratida, has a hierarchical system of stout primary ascending

fibres which are directed at right angles to the sponge surface. This organisation is most easily detected near the surface. Between these primary elements is a system of finer secondary connecting elements; even finer tertiary fibres, where developed, link secondary fibres. The arrangement of all elements of this skeleton can be regular and the consequent interlocking pattern almost rectangular or it can be irregular and tangled. All elements can be emphasised or reduced in particular genera. A second arrangement typical of many Verongida (family Aplysinidae) shows no distinction into fibres of different orientation and dimension, the meshes are polygonal, formed by interlocking fibres of almost equivalent diameter narrowing only at the surface. The third arrangement is found only in the Dendroceratida and is rectangular in construction, being composed of fibres all of almost equivalent dimension and structure (Pl. 1a). *Halisarca* lacks a fibrous skeleton.

Construction of Individual Fibres

Fibres of Dendroceratida are very uniform in construction. In transverse section a concentrically laminated spongin-fibre 'bark' invests a diffuse spongin 'pith' in which cellular elements may occur (Pl. 1b). Pith can in part be replaced by sand grains. In the Darwinellidae, where only dendritic skeletons are developed, fibres taper in diameter from base to surface. Dictyodendrillid fibres, apart from major attachment stalks, maintain constant dimensions throughout the body and attenuate sharply at the surface. Free fibrous 'spicules' supplement the skeletal fibres in two genera and these elements have distinctly different microstructures.

Soft-tissue Construction

The texture of all Dendroceratida is extremely soft and fragile, the soft tissue of the sponge collapsing at the slightest disturbance. This fragility is dictated by the construction of the tissue and the relative dominance of cellular elements over fibrous elements in the sponge body. This fragility is enhanced in forms with a continuously branching rather than an interlocking fibre skeleton. In most Dictyoceratida the fibrous skeleton is dense and dominates the cellular material, imparting a tough, flexible texture to the sponge.

Very fundamental features of sponge histology dictate the texture, which can be appraised by touch. Such features are the type of choanocyte chamber present, the density and volume of matrix in relation to canal space, the nature and spatial organisation of reinforcing matrix, and the density and localisation of the mesohyl cell population. Dendroceratida have large, oval, wide-mouthed choanocyte chambers (eurypylous) and these occupy a high percentage of the mesohyl volume leaving relatively little interchamber matrix in the choanosome (Pl. 1c). Inhalant and exhalant canal volume is high in relation to body volume in Dendroceratida and the combination of all of these factors produces a fragile collapsible sponge.

Stronger collagen reinforcing marks an ectosomal region immediately beneath the surface pinacoderm. Where this region becomes complex in its pattern of collagen deposition, zonation of particular cell types, or incorporation of foreign material, a high degree of structure can be developed. Such a structured reinforced region is referred to as a cortex (Pl. 1d). An organised subsurface region which lacks reinforcing is referred to as an ectosomal region.

Halisarca is unique in having ramifying, branching tubular choanocyte chambers, and in some species a strongly collagen-reinforced matrix and a distinct, often complex, ectosomal structure (Pl. 1e). *Halisarca* species have a delicate, slightly elastic texture.

Incorporation of Foreign Material

Incorporation of sand and other debris by sponges at their surfaces, in fibres, and to develop cortical structure is not a random event; it requires specific directed cellular activity during morphogenesis. De Laubenfels (1948) and Bergquist (1980) argued that this was so and have recognised the characters generated by such incorporation, e.g., coring of fibres and development of sandy crusts or a sandy cortex as important in generic descriptions. The elegant developmental study by Teregawa (1986) on *Dysidea etheria* supports this view. In Dendroceratida, sand is used as a surface network and cortical armour *(Chelonaplysilla)*, and can be incorporated into fibres (Pl. 1f) *(Pleraplysilla, Igernella, Acanthodendrilla)*.

Colour

Pigmentation in sponges has traditionally been devalued as a useful systematic character because of the often obvious variability of pigment expression even in a single individual depending upon environmental factors. This viewpoint is, however, too simplistic. It is true that in some groups of sponges aspect to incident light, extent of debris incorporation, and depth of occurrence may lead to variation in tissue pigmen-

tation. In other groups this is not so, most notably in the Dendroceratida; here the sponge colour is remarkably stable within the species, and arguably provides the most reliable quick field-identification characteristic at the species level. Failure to understand pigment oxidation chemistry and to observe the species in the field has led to some very questionable conclusions affecting identification of Dendroceratida.

Some fibrous sponges, including most Dictyoceratida, exhibit colour differences between superficial and deeper regions of the body. This does not occur in Dendroceratida, where pigmentation is uniformly strong throughout the soft tissue. Contrasting pigmented fibres do occur most notably in the Dictyo-dendrillidae.

Colour change after exposure to air, or following preservation, can characterise particular species as it is primarily dependent on the chemical structure and oxidation states of particular pigments. These changes are significant and need to be recorded in taxonomic descriptions.

Secretory Cell Ultrastructure

In the orders Verongida and Dictyoceratida the ultrastructure of particular secretory cells, the spherulous cells, varies and particular types characterise different families (Bergquist 1980, fig. 3 c-f). The Dysideidae are distinctive in having no such cells thus far recorded.

Very large secretory cells termed spumous cells (Donadey & Vacelet 1977, Pl. V, fig. 1) are found in most Dendroceratida belonging to the Darwinellidae but they are absent in the few Dictyodendrillidae that have been examined. Other secretory cell types are present in Dendroceratida, but have either not been studied over a range of species or have not yet been adequately characterised.

The Halisarcida have a range of secretory-cell types, of which spherulous cells like those in some Tetractinomorpha (Pl. 2b) and fuchsinophil cells of unique structure are the most abundant.

Larval Structure

All Dendroceratida incubate parenchymella larvae which are large, uniformly pigmented, histologically complex, and have long posterior cilia (Pl. 2a). *Halisarca* species incubate small parenchymellae with simple histology and uniform ciliation (Bergquist 1980, fig. 3, g). In both types of parenchymellae, anterior and/or posterior polar areas can be free of cilia.

Secondary-metabolite Chemistry

Dendroceratid sponges have as their dominant secondary metabolites diterpenoids of diverse structure, but all are based upon a spongiane skeleton (Fig. 1). Generic and familial patterns of occurrence of biosynthetically distinct structural types are recognisable. *Halisarca* species contain no terpenoid metabolites (Bergquist & Wells 1983), nor have they yielded other types of novel compound although they have as yet been little studied. It has been difficult in New Zealand and Australia to obtain sufficient quantity of *Halisarca* species to further investigate their chemistry.

MATERIALS AND METHODS

Collections Examined

All New Zealand specimens examined were collected in the shallow subtidal or using SCUBA. They were collected by sponge workers at the University of Auckland over the period 1958–1994. New Zealand material has been supplemented by collections made in Hawaii, Palau, Australia, Jamaica, New Caledonia, British Columbia, California, and the Mediterranean by P.R. Bergquist, and by specimens sent from other sponge workers (Dr J. Vacelet, Dr G. Pulitzer-Finali, Dr J. Faulkner, Dr R. Anderson). As a result of this wide-ranging collection, representatives of genera which do not occur in New Zealand have been available for comparison.

Type material from the collections of The Natural History Museum, London; the Australian Museum, Sydney; the Muséum National d'Histoire Naturelle, Paris; the Museum of Victoria, Melbourne; and the Smithsonian Institution, Washington D.C., has been examined where relevant.

Collection locations for the New Zealand specimens recorded are given with each taxonomic description, and localities are indexed on Figures 2 and 3.

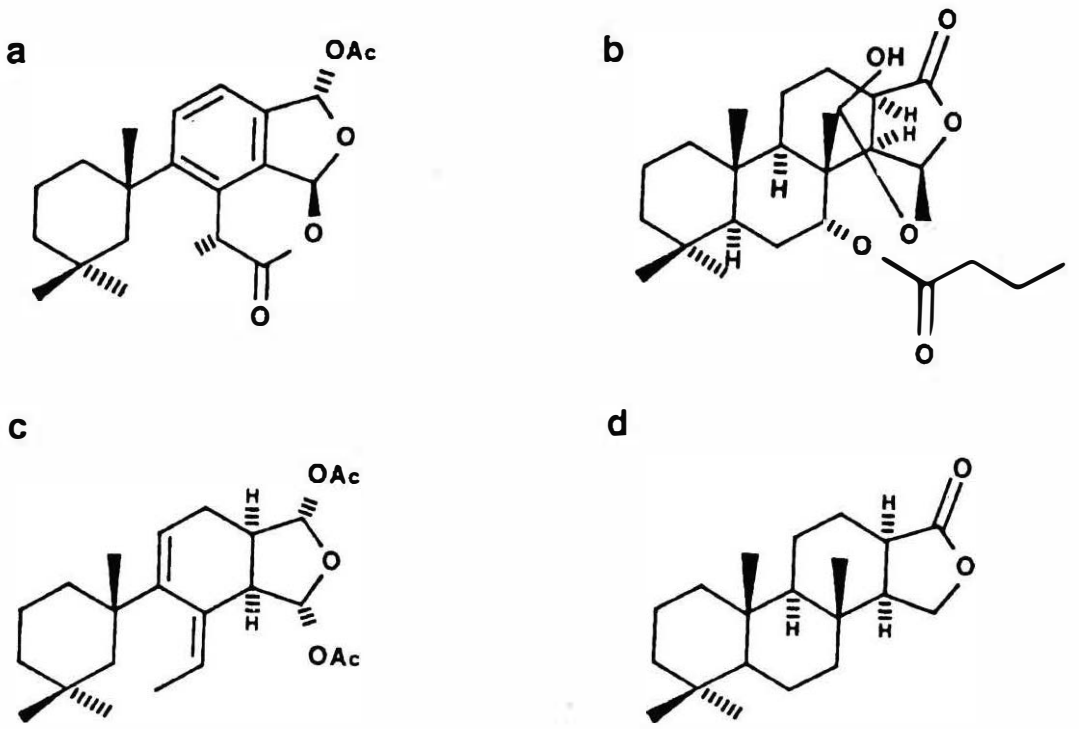

Fig. 1. Structure of spongiane-derived diterpenoids characteristic of Dendroceratida. **a**) aplysulphurin, b) aplyroseol-1, **c**) dendrillolide-B, **d**) spongiane-related compound from *Chelonaplysilla violacea.*

Methods

Methods followed were those standard for sponge taxonomy and electron microscopy. Specimens were preserved in 70% ethanol, and in 2.5% glutaraldehyde, in 0.1 molar Na-cacodylate buffer to provide for study using routine histology and for both scanning and transmission electron microscopy.

Procedures followed for transmission electron microscopy were those of Simpson *et al.* (1985). For scanning electron microscopy the preparative procedure was that followed by Bergquist *et al.* (1979) using a Phillips SEM 505 at an accelerating voltage of 20 KV using a lanthanum hexaboride crystal.

In the species descriptions all colour notations follow Munsell (1942). Museum register numbers are quoted only where it is necessary to identify a particular specimen.

LIST OF SPECIES DESCRIBED

Class DEMOSPONGIAE Sollas
Subclass CERACTINOMORPHA Lévi

Order **Dendroceratida** Minchin
Family **DARWINELLIDAE** Merejkowsky
Darwinella Müller
Darwinella gardineri Topsent
Darwinella oxeata Bergquist
Chelonaplysilla de Laubenfels
Chelonaplysilla violacea Lendenfeld
Dendrilla Lendenfeld
Dendrilla rosea Lendenfeld

Family **DICTYODENDRILLIDAE** Bergquist
Dictyodendrilla Bergquist
Dictyodendrilla dendyi nom. nov.

Order **Halisarcida** new order
Family **HALISARCIDAE** Vosmaer
Halisarca Johnston
Halisarca dujardini Johnston

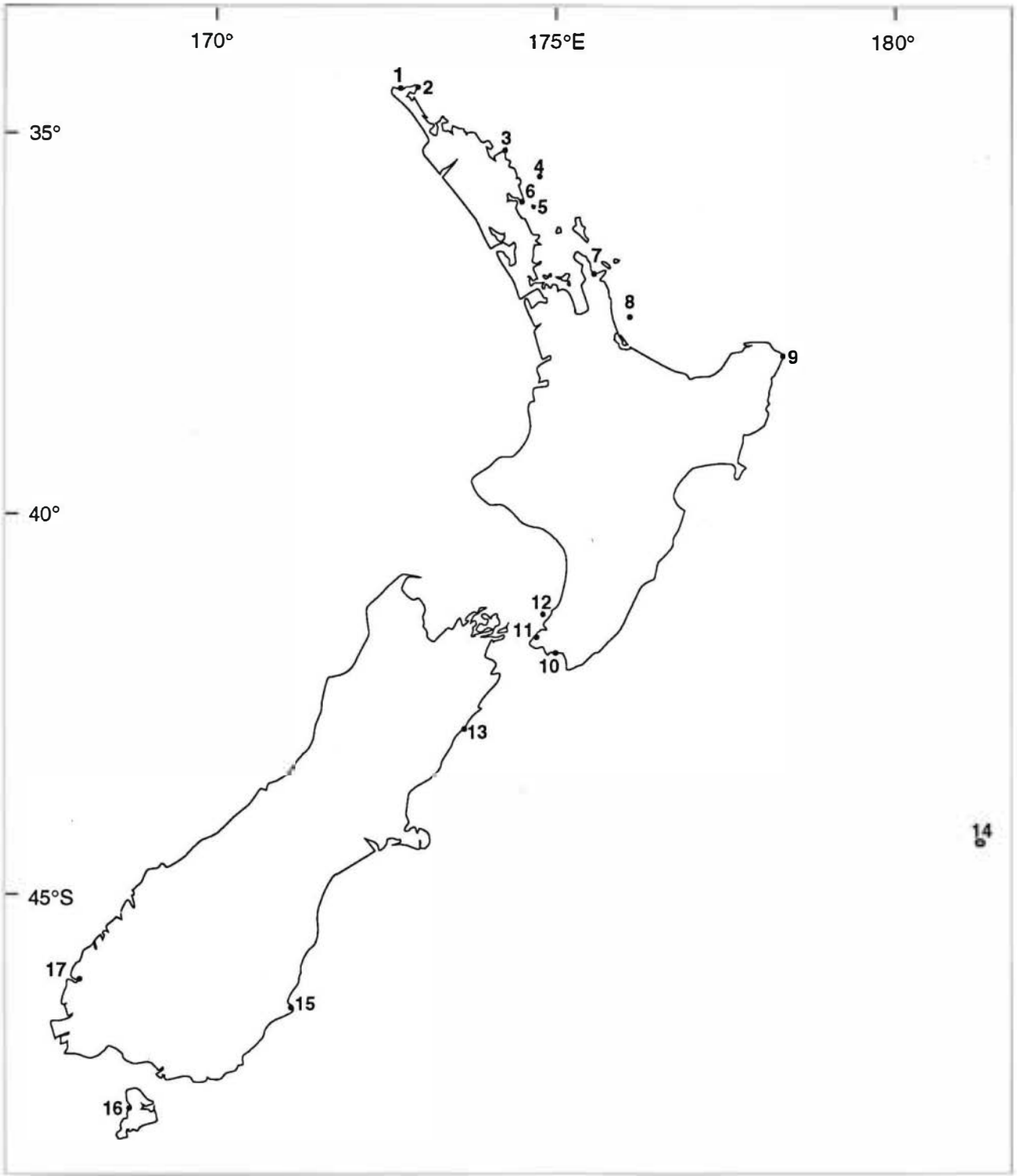

Fig. 2. Map of the New Zealand region showing sites from which material considered in this monograph was collected.

1 Spirits Bay
2 North Cape & Kerr Point
3 Cape Brett
4 Poor Knights Islands
5 Hen Island & Whatapuke Island
6 Whangarei Heads
7 Kennedy Bay
8 Mayor Island
9 East Cape
10 Island Bay
11 Makara
12 Mana Island
13 Kaikoura Peninsula
14 Chatham Islands
15 Portobello
16 Paterson Inlet
17 Dusky Sound

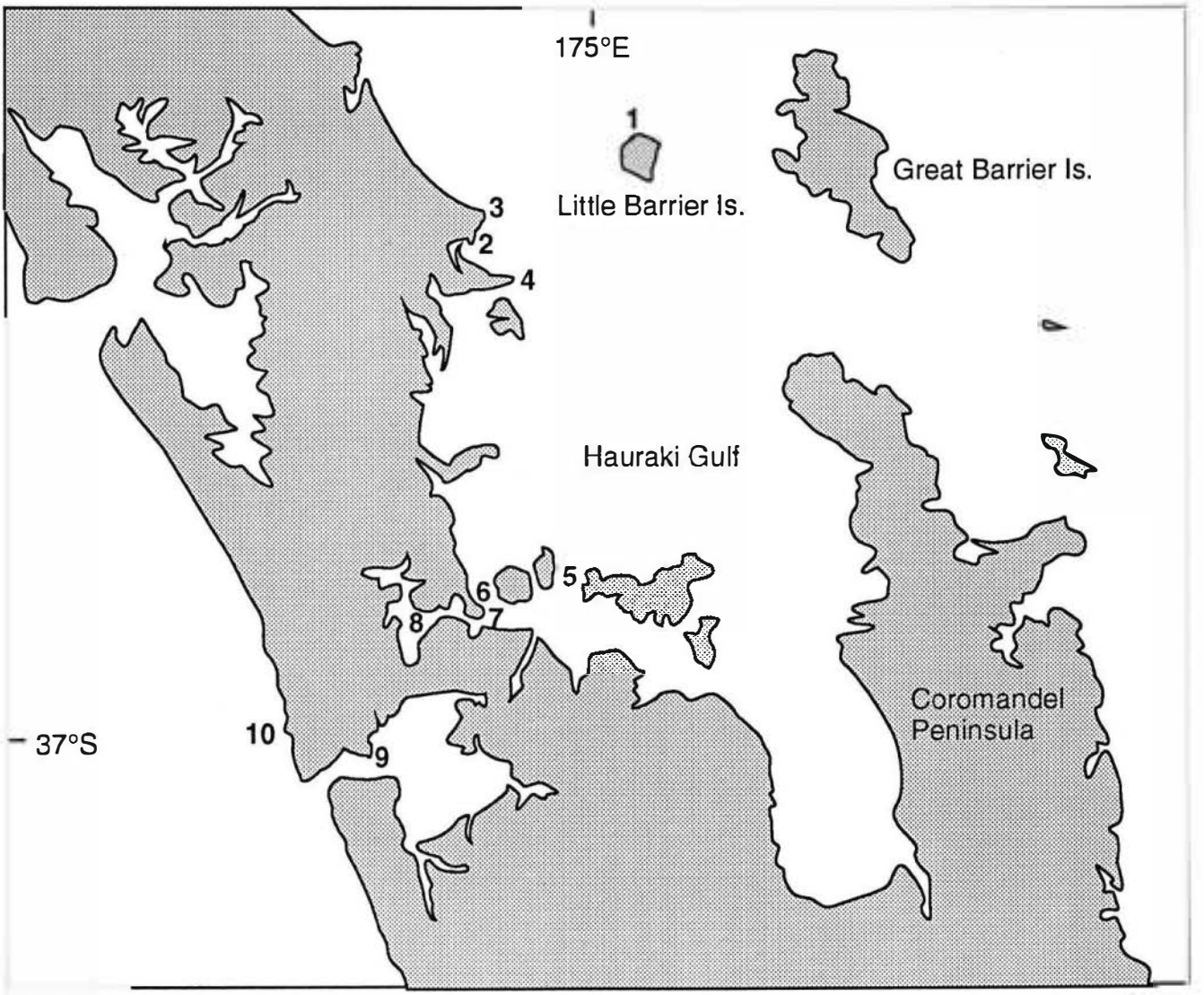

Fig. 3. Map of Hauraki Gulf and Auckland showing sites from which material considered in this monograph was collected.

1 Little Barrier Island
2 Leigh Reef
3 Leigh Marine Reserve
4 Takatu Channel
5 Waiheke Channel
6 Narrow Neck Reef
7 Devonport Wharf
8 Westmere Reef
9 Cornwallis
10 Anawhata

SYSTEMATICS

INTRODUCTION

Descriptions are given for five species of Dendroceratida and one species of the order Halisarcida. Previous references relevant to New Zealand species of Dendroceratida are Lendenfeld (1883, 1886, 1888, 1889), Topsent (1905), Bergquist (1961, 1980), Pronzato (1975), Bergquist *et al.* (1979), Bergquist *et al.* (1990), Karuso *et al.* (1986) and Wiedenmayer (1989). The single species of *Halisarca*, *H. dujardini*, is cosmopolitan and has been the subject of many literature references, very few however from the Southern Hemisphere, where only Burton (1932) has recorded the species. Bergquist and Sinclair (1973) recorded the occurrence of the genus *Halisarca* from New Zealand but did not identify the species, and Bergquist *et al.* (1979) described the structure of this *Halisarca* larva. An excellent, detailed study of *H. dujardini* using light microscopy was published by Lévi (1956).

Order DENDROCERATIDA Minchin, 1900

Ceractinomorpha in which the fibre skeleton which is present, except in one genus, is dominated by soft tissue elements. The fibre skeleton arises from a continuous spreading basal plate and is either dendritic (Darwinellidae) or anastomosing (Dictyodendrillidae). Free fibrous 'spicules' may occur in addition to the main skeleton. Fibres are always pithed and strongly laminated, usually quite stout, tapering toward the surface. At the boundary between pith and bark the fibres can incorporate some free cellular elements and some microalgae, and in some cases sand and debris is incorporated into the pith region. It is common to find dark fibre pigmentation which contrasts with the matrix; the latter is always uniformly pigmented throughout the sponge.

The choanocyte chambers are eurypylous, large, oval and wide-mouthed and matrix volume is low in relation to canal and chamber volume. The choanosomal matrix is lightly reinforced with collagen while the ectosomal region contains marked to strong fibrillar collagen deposits and a cortical region with reinforcing elements can be present. The large canal and choanocyte chamber space in conjunction with the sparse fibre skeleton dictates that Dendroceratida are soft fragile sponges.

Reproduction is viviparous; all species incubate parenchymella larvae of relatively large size, with complex structure and histology, and always with a posterior clump of long cilia.

The secondary-metabolite chemistry of the Dendroceratida is characterised by the presence of terpenes, which are dominantly spongiane diterpenes as opposed to sesqui- and sesterterpenes in the Dictyoceratida. Sterol content (Bergquist *et al.* 1980; Bergquist *et al.* 1991) shows no novel features; it is comparable to that of the Dictyoceratida and markedly distinct from that of the Verongida.

Family DARWINELLIDAE Merejkowsky, 1879

Dendroceratida in which the fibrous skeleton, where present, is strictly dendritic, very sparse, and sometimes supplemented by free spongin 'spicules' (Pl. 2c). Darwinellid sponges are most typically encrusting, but where they are erect or frondose their fibrous skeleton, like that of the encrusting forms, always arises from a flat, basal spongin plate. The fibres are comparable with, but not identical to, those of the Verongida in structure. They have a laminated bark surrounding a central diffuse pith area. The pith can incorporate debris, cells, or microalgae.

Darwinella Müller, 1865

Darwinia Schultze, 1865

Darwinellidae in which the slightly ramified, dendritic fibre skeleton is supplemented by diactinal, triactinal, or polyactinal spongin spicules. There is no sand in the fibres, but cells and microalgae mark the pith/bark boundary. The sponges are usually encrusting and small in the intertidal, but clathrous, lobate-digitate forms occur commonly in subtidal locations.

TYPE SPECIES: *Darwinella mulleri* Schultze, 1865, by monotypy.

Darwinella gardineri Topsent, 1905
(Pl. 2a,d,e; Pl. 4a)

Darwinella gardineri Topsent, 1905: 179 (not *Darwinella gardineri*: Lévi 1958: 42).
Darwinella gardineri: Pronzato 1975: 13 (not *Darwinella gardineri*: Wiedenmayer 1989: 149).
Darwinella gardineri: Bergquist *et al.*, 1991: 21.

MATERIAL EXAMINED:
Kerr Point 2 m, Cape Brett 4 m, Poor Knights Islands 4 m, 20 m, Smugglers Bay intertidal, Hen Island 20 m, Goat Island 10 m, Leigh Marine Reserve 12 m, Narrow Neck Reef intertidal, Cornwallis intertidal, Anawhata intertidal, Kennedy Bay 2 m, Mayor Island 2 m, Island Bay 2 m, Kaikoura 4 m, Portobello intertidal, Dusky Sound 15 m, Stewart Island 5 m.

HABITAT: *Darwinella gardineri* is common from low water to 20 m on rocky coasts of New Zealand from North Cape to Stewart Island along both east and west coasts. It is particularly abundant on canyon walls at 10–12 m depth on northern coasts and in the sub-littoral algal fringe in colder waters.

DESCRIPTION: Encrusting, from 2–7 mm thick but seldom exceeding 5 mm; forming extensive mats often covering areas of 1 m^2. Basal mat produced into stout irregular upright lobes which may fuse to give a clathrous appearance. Living specimens uniform rose pink throughout the tissue (R 4/8), turning a deeper rose in ethanol (R 4/4). Texture is fleshy, compressible, rubbery and slimy to the touch.

SURFACE: The sponge exudes a slimy mucous when exposed to air. Regularly spaced sharp conules 1.5 – 3.0 mm apart and 0.5–1 mm high rise above the otherwise smooth surface; fibres frequently protrude beyond the tip of the conule. Fibre colour typical of spongin, a brownish gold (Y-R-Y 6/6).

Oscules small, 1–2 mm in diameter, spaced regularly about 1 per cm^2, rimmed by a transparent membranous collar and slightly elevated above the surface. Pores aggregated into poral areas grouped around the base of conules giving patches of the surface a fine reticulated appearance. Dermal membrane stretched between the ridges formed by the conules and easily separable from the underlying tissue.

SKELETON: Skeleton dendritic, composed of fibres that extend vertically from a continuous spreading basal spongin plate; the translucent fibres 0.7–1.0 mm in diameter, with a pronounced, concentrically laminated bark. Bark enclosing a central pith and at the pith/bark boundary some cellular material and what appear to be microalgae are incorporated. Fibres contain no detritus. In the immediate subsurface area adjacent fibres commonly merge and fuse along points of lateral contact, diverging as they approach conules. This is not anastomosis, the bark and pith entities of the participating fibres remaining distinct. This type of fibre junction has been noted earlier (Lendenfeld 1889; Tsurnemal 1967; Bergquist 1980) and can appear in dry skeletons as a fenestrated sheet over localised areas. Primary skeleton augmented by large, diactinal oxeote spongin 'spicules' 1.4–2.0 mm long and 22 µm in central dimension, lying free within the flesh and dispersed throughout the body; most abundant at the choanosome/ectosome boundary from where they can extend through the sponge surface.

SOFT TISSUE ORGANISATION AND HISTOLOGY:
Ectosome: Dense bands of collagen characterise a distinct ectosomal region 50–130 µm deep (average 90 µm). Subdermal spaces into which large exhalant canals drain are a marked feature and, with the collagen deposits, demarcate the region clearly from the underlying choanosome.
Choanosome: Mesohyl matrix is lightly infiltrated with collagen. Chambers oval, 40–80 µm (70 µm) in longest dimension and 30 µm in diameter. In the superficial regions of the choanosome significant areas of cellular mesohyl intervenes between chambers, diminishing in the deeper areas of the sponge (Pl. 2d). Spumous cells abundant throughout the mesohyl and concentrated adjacent to exhalant canals and choanocyte chambers (Pl. 2e). They are frequently observed shed into canals. Pinacocytes lining the exhalant canals are often flagellated.

REPRODUCTION: Spermatogenesis takes place in the months of September and October. Choanocytes are converted into spermatogonia synchronously within one cyst as described by Tuzet *et al.* (1970) for *Aplysilla rosea*. Larvae are parenchymellae with bare anterior and posterior poles and long cilia circling the posterior pole (Bergquist 1978, Pl. 12c).

REMARKS: *Darwinella gardineri* has been frequently reported from New Zealand as *Aplysilla rosea* (Morton & Miller 1968; Doak 1971; Pritchard *et al.* 1984). The genus *Aplysilla* has never certainly been reported from New Zealand.

It is necessary to clarify the basis upon which the specific name *gardineri* is applied to the New Zealand sponge since Wiedenmayer (1989) used the same name for an Australian species which is clearly different. His description is based on only two specimens (Museum of Victoria F52065 & F52066) but the sponge is described as deep sulphur-yellow, purple-black in ethanol, with fibres of contrasting red colour. It thus approaches *Darwinella oxeata* in tissue pigmentation but differs from that species in having red fibres. It also differs in the structure of the diactinal spicules and in terpene chemistry (Bergquist *et al.* 1990). Examination of Wiedenmayer's specimens provides further points of distinction between the New Zealand specimens of *D. gardineri* and

the Australian material; specimen F52065 contains some triactinal spicules, also the oxeote spicules, which are common, have a central flexture and often recurved, almost contort tips.

Topsent (1905), when describing *D. gardineri*, stated that the sponge retained a rose pigmentation in alcohol from which, by comparison with *D. simplex* from Banyuls with which he was familiar, he deduced a 'red carmine' pigmentation in life. There are very few records of *Darwinella* species which have both rose-red pigmentation in life and large oxeote spongin spicules. If one ignores the unsupported synonomies offered by Wiedenmayer (1989) and consults the primary literature which is well summarised by Pronzato (1975), then the only available name for rose-red *Darwinellas* with large diactinal spicules (1500–2000 x 20 µm) is *D. gardineri* which has been described reliably only from the Maldive Islands. Lévi (1952) reaffirmed a red pigmentation for *D. gardineri* in the course of reviewing the species of *Darwinella*; however, in 1958 he described a yellow sponge from the Red Sea as *D. gardineri*. He has been followed in this action by Pronzato (1975) and Pulitzer-Finali and Pronzato (1980) who applied the name to Mediterranean sponges of a range of colour without including any structural evidence in support of their identifications. These records all have to be regarded at best as dubious and almost certainly erroneous.

This work has provided extensive experience of dendroceratid sponges in the field, and pigmentation, which is uniform throughout the soft tissue, has been found to vary only in slight shades within a species. Rose-red pigmentation fades to pale rose-brown in ethanol, sulphur-yellow pigmentation turns rapidly to a deep purplish-black, the pigments having totally different oxidation reactions. This is invariable. Further, electron microscopy and chemical analysis on all of the New Zealand Dendroceratida and on some from the Mediterranean, Hawaii, and Australia has been done. It can be stated that colour is not resultant from endosymbionts of any sort, the soft tissue being remarkably clear even of Eubacteria.

The novel diterpene chemistry of dendroceratids including *Darwinella* species was reported by Bergquist *et al.* (1990). This paper identified a group of four Australasian species of *Darwinella* which had diactinal spicules and displayed either bright rose-red, sulphur-yellow or brilliant orange pigmentation. Only one species, *D. oxeata*, was named in that paper. Table 1 summarises the major characteristics of morphology and chemistry of these species and also of *Dendrilla* species with which the rose-red *Darwinellas* are easily confused. It is clear from the data in Table 1 that both diterpene chemistry and spicule morphology separate the two sulphur-yellow species, *D. oxeata* from New Zealand and the unnamed species from south-eastern Australia (Pl. 5b). The latter is probably the one reported by Wiedenmayer as *D. gardineri* and the species still requires proper description but no adequate material is available, Wiedenmayer's specimens being inadequate.

Chemistry, spicule morphology, and pigmentation separate the rose-red New Zealand sponge from the previous two species and the name *D. gardineri*, based on the characteristics of the holotype, can properly be applied to the New Zealand species.

In Table 1 there is reference to a brilliant orange *Darwinella* from New South Wales (Pl. 5b). This has very small diactinal 'spicules' (80–120 µm), very soft fragile texture, and distinctive diterpene chemistry (Bergquist *et al.* 1990). It is certainly an additional species and possibly a new genus. Specimens of this sponge were included by Wiedenmayer (1989) within a heterogeneous assemblage lumped under the name *Darwinella australiensis*. The material available to Bergquist *et al.* was not adequate for full description at the time the chemistry of the species was recorded, but a very brief description was given by Poiner and Taylor (1990) who applied the name *Aplysilla tango*. The species still requires full description but a reference specimen (Z4848) was lodged in the Australian Museum. Obviously several further species of *Darwinella* remain to be described from southern Australia and careful study of fibres, soft tissue, ecology, and chemistry is needed to define them properly. Sweeping synonomies based upon the narrow descriptive base available in most cases can not be taken seriously.

OTHER RECORDS: Maldive Islands.

Darwinella oxeata Bergquist, 1961

(Pl. 1b, 2f, 3f, 4c)

Darwinella oxeata Bergquist, 1961: 216–219, fig. 6a-c.
Darwinella oxeata: Pronzato 1975: 14–15, fig. 6.
Darwinella oxeata: Bergquist *et al.* 1990: 73.
Darwinella oxeata: Bergquist *et al.* 1991: 21.

MATERIAL EXAMINED:
Cape Brett 12–15 m, Poor Knights Islands 10–20 m, Hen Island 12 m, Smugglers Bay, Whangarei Heads 5 m, Leigh 15 m, Cornwallis shallow subtidal, Mayor Island 10 m, Kaikoura Peninsula 5 m, Portobello Aquarium Point inter-tidal, Paterson Inlet, Stewart Island shallow subtidal, Dusky Sound 15 m.

DESCRIPTION: Occurs frequently around New Zealand rocky coasts, commonest on steep-sloping reefs and canyon walls around 15 m depth; on southern shores it is common in the subtidal fringe. The original

Table 1. Summary of features of *Darwinella* and *Dendrilla* species. For structures of terpenes see Bergquist *et al.* (1990).

Species	Occurrence	Soft-tissue Pigmentation	Fibre Pigmentation	Fibrous Spicule Structure	Terpene Composition
Darwinella oxeata	New Zealand	Sulphur yellow translucent	Pale gold	Diactinal with spined surface 1500–2000 µm	Aplysulphurin* tetra hydro derivatives
Darwinella sp. (described as *D. gardeneri* by Wiedenmayer (1989)	Australia (SW)	Sulphur yellow	Red dark	Diactinal smooth, some triactinal present 1500–2000 µm	Aplysulphurin only
Darwinella gardineri	New Zealand Maldive	Rose red	Translucent pale gold	Diactinal smooth 1500–2000 µm	Tetrahydro-aplysulphurin*
Darwinella n.sp.	Australia	Brilliant orange	Translucent pale gold	Diactinal smooth 1500–2000 µm	Gracilin A* + 4 related compounds
Dendrilla rosea	New Zealand	Rose red	Translucent pale gold	not present	Aplyroseols a mixture of 10
Dendrilla sp.	Australia	Rose red	Translucent pale gold	not present	Aplyroseol-1* ambliofuran* plus aplyroseol 2–6

* Denotes major metabolite

description of this sponge by Bergquist (1961) was based upon a small piece of fixed tissue and only the peculiar, regularly notched diactinal 'spicules' permitted description as a new species. The recorded dark red-brown colour is consistent with the behaviour of all sulphur-yellow dendroceratid and verongiid pigments on fixation (Bergquist 1978). Subsequent collections now permit a better description of the species.

Sponge encrusting, with a base up to 2 cm thick often extending over areas of 25 cm^2. Erect branches arise from the base, particularly in specimens in deeper water, reaching a height of 5.0 cm with adjacent branches occasionally fusing. Colour in life sulphur yellow throughout (rY 8/10) and purple-brown (YR 3/4) in ethanol. Texture is very soft, fleshy and slimy to the touch, and mucus is exuded on damage.

SURFACE: Surface marked by conules, 1–3 mm high, 2–5 mm apart, occasionally multituberculate separated by areas of smooth surface. Oscules sporadically distributed; 0.8–1.0 mm in diameter with contractile, collagen reinforced margins. Pores microscopic and aggregated in small groups but not forming prominent pore areas.

SKELETON: Main skeleton composed of sparsely branched fibres, 0.2–0.3 mm thick, arising from a basal spongin plate. In cross section the fibres show typical laminated bark and diffuse pith structure and incorporate microalgae between laminae and in the pith (Pl.1b). Diactinal spongin 'spicules' 1.5–2.0 mm x 25 µm with a regularly notched surface, scattered throughout the tissue (Pl. 2f). No zonation of 'spicules' in the tissue nor have any specimens been found in which these elements are very rare.

SOFT-TISSUE STRUCTURE AND HISTOLOGY:
Ectosome: A thin layer, 25–120 µm deep, lightly reinforced by collagen and set off from the underlying choanosome by subdermal spaces. Spumous cells present throughout but are concentrated toward the choanosomal boundary.

Choanosome: Accounts for most of the soft-tissue volume and is made up of eurypylous choanocyte chambers 45–95 (average 64) µm long and 30–60 µm wide. Very little mesohylar space remains between the tightly packed chambers, but where mesohyl is developed the cell density of archaeocytes, collencytes and spumous cells is high. The latter are large, 9–18 µm in longest diameter, commonly localised in clusters near chambers and bordering canals into which they are often extruded, dispersing their contents. Endopinacocytes lining exhalant canals and apopyles are frequently flagellated.

REMARKS: The presence of spongin 'spicules' with notched surfaces separates *D. oxeata* from all other *Darwinella* species. It falls into a group of predominantly southern hemisphere species which elaborate solely diactinal 'spicules' of relatively large size, between 1500 and 2200 µm in length. Other members of this closely related group of species are *D. gardineri* Topsent and the yellow sponge from Australia referred to as *D. gardineri* by Wiedenmayer. The latter species requires proper description although its chemistry is known (Bergquist *et al.* 1990).

OTHER RECORDS: Chatham Islands, 15 m.

Dendrilla Lendenfeld, 1883

Darwinellidae in which the fibre skeleton branches repeatedly but never anastomoses. Lateral bifurcations are short, axial fibres are stout and flexible. The sponges can attain large size always with erect, branching and/or complex lamellate bodies arising from one or more small basal spongin plates. Fibres contain no foreign material.

TYPE SPECIES: *Dendrilla rosea* Lendenfeld, 1883, by subsequent designation Topsent (1905).

Dendrilla rosea Lendenfeld, 1883

(Pl. 3a, b, c, d, Pl. 4d)

Dendrilla rosea Lendenfeld, 1883: 271–294, pl. 10, figs 3, 4, pl. 12, figs 16, 19–23, pl. 13, figs 24–27, 29–32.
Dendrilla rosea: Lendenfeld 1889: 716–719, pl. 44, figs4, 7, 8, 11, pl 45, figs 3, 4, 7, 8, 9.
Dendrilla rosea: Bergquist 1980: 486.
Dendrilla rosea: Bergquist & Skinner 1982: 49, pl. 1, fig.3 (colour).
Dendrilla cactos Selenka, *sensu* Wiedenmayer 1989: 152, fig. 98.
Dendrilla: rosea Bergquist *et al.* 1991: 21.

MATERIAL EXAMINED:
North Cape 25 m, Cape Brett 20 m, Whangarei Heads 10 m, Poor Knights Islands 25 m, Leigh Reef 20 m, Takatu Channel 15 m, Waiheke Channel 5 m, Little Barrier Island 25 m, East Cape 30 m.

DESCRIPTION: Subtidal, inhabiting steep-sloping reefs and canyon walls usually below 10 m and extending to 25 m. It also extends onto mobile substrata where it attaches to large shells and small rocks. Sponge erect and ramose, reaching a height of 30 cm with branches 4–10 mm diameter. Colour is bright rose-pink (R 4/8) throughout the tissue, turning pale red-brown in spirit (YRY 7/4). Branching sparse and the base of attachment small; attachment and lower branch fibres thick (up to 40.0 mm), tough and flexible. Consistency slimy and the flesh soft and fragile over the tough skeleton.

SURFACE: Extremely conulose, with conules 1–5 mm high, spaced 3–5 mm apart. Between conules the pores impart a lacy pattern to the dermal membrane (Pl. 3b). Oscules dispersed randomly and are 1–4 mm in diameter.

SKELETON: Strictly dendritic. Fibres arising from a clearly evident basal plate, 1.2–1.6 mm in diameter, narrowing rapidly to 250–300 µm, a thickness retained throughout the length of any individual branch until it tapers abruptly to a point near the surface. Short lateral fibres 3–5 mm long branch out to support the surface conules. Fibre construction typical of the order with a central pith and concentrically layered bark; no foreign material is incorporated in the fibres.

SOFT-TISSUE STRUCTURE AND HISTOLOGY:
Ectosome: A distinct densely collagenous region 80–140 µm deep, set off from the choanosome by a system of sub-dermal exhalant canals. An almost tissue-like concentration of myocytes traverses the band of canals and connects ectosomal and choanosomal tissue (Pl. 3a). This tissue feature was noted in general terms by Lendenfeld (1889).

Choanosomal mesohyl densely cellular with concentrations of archaeocytes and spumous cells toward the ectosomal boundary. Choanocyte chambers oval, eurypylous, 35–80 µm (56 µm) long and 20–40 µm (35 µm) wide and distributed evenly throughout the tissue. Rarely abutting, more frequently being separated by cellular mesohyl and strong collagen tracts. Archaeocytes dispersed throughout the tissue, concentrated around choanocyte chambers and toward the ectosomal boundary. Spumous cells 9–20 µm in diameter concentrated bordering exhalant canals and at the ectosomal/choanosomal boundary.

Endopinacocytes often flagellated, bordering apopyles, in which location they are termed apopylar cells.

REPRODUCTION: Eggs (75 µm diameter), sperm, and developing and mature parenchymellae occur in specimens collected from Leigh Reef in April. Hermaphroditic reproduction was recorded for the species by Lendenfeld (1889).

REMARKS: Several points of confusion exist in the literature relating to *Dendrilla rosea*. In the popular New Zealand literature the erect, clathrous growth form of *Darwinella gardineri* has been regularly and understandably confused with the strictly bifurcating digitate flexible *Dendrilla rosea* (Pl. 3c, d). The species are almost identical in colour but *Dendrilla rosea* occurs at a slightly greater depth and on an extended range of substrata. A simple identification expedient is to tease a piece of tissue; in *D. gardineri* the long spongin 'spicules' are evident in the flesh, but are absent in *Dendrilla rosea*. Very distinct differences in fibre structure, choanosome organisation, and terpene chemistry (Table 1) are found between the genera *Darwinella* and *Dendrilla* as evidenced by the species we have studied. These features are, however, not helpful in field identification.

It is necessary to reaffirm the correct specific name for this species following the unfortunate resurrection of the name *cactos* (Selenka, 1867) by Wiedenmayer (1989) for his southern Australian material. Both significant revisors (Vacelet 1959) and Bergquist (1980) regarded *Spongelia cactos* Selenka as unrecognisable.

Lendenfeld (1889) designated two varieties within his earlier *Dendrilla rosea* (1883); these were *D. rosea* var. *typica*, with which Selenka's *Spongelia cactos* from Bass Strait was listed in synonomy, and *D. rosea* var. *digitata* for specimens described by Carter from Port Phillip Bay. In his description of var. *typica* Lendenfeld did not refer specifically either to Selenka's description or to the comments of Schultze (1878) on *S. cactos* which followed his study of a slide of Selenka's specimen. Lendenfeld described his own material and it is on this basis that the species must be identified.

Wiedenmayer based his argument for using *cactos* as the specific name for both varieties not upon Selenka's description, but upon Schultze's comments and their subsequent "citation" by Lendenfeld (1888, 1889). Schultze certainly stressed affinity with *Aplysilla* in fibre structure, he did not specify rigid dendritic fibre arrangement. Lendenfeld did this, but he was referring to his own material not to *S. cactos*, which he never saw. Both Lendenfeld and Schultze included within *Dendrilla* species with reticulate skeletons which are now recognised as belonging to *Dictyodendrilla*. If Selenka's figure is taken into consideration, a strong resemblance to *Dictyodendrilla cavernosa* (Lendenfeld) is evident; Selenka himself described the skeleton as reticulate. Selenka's holotype is lost, his description is unrecognisable, and his figure raises doubts as to generic identity. Schultze's comments leave the issue unresolved, consequently the name *cactos* is disregarded and priority given to Lendenfeld's name *Dendrilla rosea*.

It is probable that in Australian temperate waters there are two species of *Dendrilla*. The results of chemical studies of terpene composition (Karuso *et al.* 1986; Bergquist *et al.* 1990) indicate the existence of an Australian species which is close to, but distinct from, the New Zealand *D. rosea*. Also Wiedenmayer, like Lendenfeld, conceded that a 'terete ramose' form might be distinct from his concept of *D. rosea* (as *cactos*) which was lobose/fleshy. Wiedenmayer lost his 'terete' specimen overboard and thus could not do more than say it existed. His comparison made with Hentchel's specimens from the tropical Aru Straits is clearly mistaken. Should subsequent study demonstrate that there are two distinct species then the specific name *rosea*, type species of the genus, remains with the more fleshy lobose/lamellate form (Lendenfeld 1889, Pl. 44, figs 7, 11) and a new name should be applied to the spiky, flexible form. The New Zealand species should then receive the latter name. The varietal name *digitata* cannot be used as it is pre-occupied within *Dendrilla* by *D. digitata* Lendenfeld (1888) which is a *Dictyodendrilla*.

Reference should be made to *Dendrilla aerophoba* Lendenfeld (1883, 1888, 1889) which was described at the same time as *D. rosea*. Bergquist (1980) regarded the species as unrecognisable in the absence of type material. Apparently the holotype and two slides exist in Berlin (Wiedenmayer 1989). *Dendrilla aerophoba* can be assigned to the order Verongida, family Aplysinellidae where it may represent an additional genus. Such assessment must rest upon verifying the structure of the cortical armour, which from Lendenfeld's description is probably composed of clionid chips, and on interpreting the fibre-skeleton organisation. Until the type specimen can be examined no action should be taken; however, *D. aerophoba* is certainly not a *Dendrilla*.

A final note is necessitated by Wiedenmayer's discussion (1989 : 153–154) of Burton's extensive synonomy of *Dendrilla membranosa* (Pallas). There are major errors of assumption in Wiedenmayer's account. He states that *Spongia membranosa* Pallas could not be a *Dendrilla*. From the description cited it certainly could be a *Dendrilla*, but the identity and characters of the species will never be determined and thus the species

name should lapse within *Dendrilla*. Bergquist (1980) indicated that *D. membranosa sensu* Burton (1932) was a good species of the new genus *Dictyodendrilla* within which it should take the first available appropriate species name which is *Dictyodendrilla pallasi* (Ridley), this being the oldest verifiable reference to the species as indicated by Burton (1934).

Bergquist (1961) recorded *Dendrilla cactus* (Selenka) from the Chatham Islands. This identification was wrong and was based on a very worn specimen. The sponge belongs to a new genus within the Dictyoceratida, family Thorectidae which will be described in part six of this memoir series. Much better material of the sponge is now available.

OTHER RECORDS: New South Wales, Victoria (Australia).

Chelonaplysilla de Laubenfels, 1948

Darwinellidae with a distinct, separable cortex reinforced by a regular reticulation of sand grains (Pl. 1d, 3e). The fibres are, like those of *Aplysilla* and *Darwinella*, simple and single arising from a basal spongin plate, only rarely branching, concentrically laminated, pithed and clear of detritus. Some species become lamellate or lamellodigitate from the encrusting base and in these forms a more branching skeleton is developed.

TYPE SPECIES: *Chelonaplysilla noevus* (Carter, 1876) by original designation de Laubenfels (1948).

Chelonaplysilla violacea (Lendenfeld)

(Pl. 3e, 4e, 7c)

Aplysilla violacea Lendenfeld, 1883: 237, pl. 10, figs 5, 7, pl. 11.
Aplysilla violacea: Lendenfeld 1888: 26.
Aplysilla violacea: Lendenfeld 1889: 704, pl. 46, figs 13, 15.
Chelonaplysilla violacea: de Laubenfels 1948: 165.
Chelonaplysilla violacea: Bergquist *et. al.* 1967: 162.
Chelonaplysilla violacea: Bergquist 1971: 100, 163–164.
Chelonaplysilla violacea: Bergquist *et al.* 1990: 74.
Chelonaplysilla violacea: Bergquist *et al.* 1991: 21.

MATERIAL EXAMINED:
North Cape 0.5 m, Cape Brett 10–15 m, Poor Knights Islands 8–12 m, Whatapuke Island 10 m, Smugglers Bay Whangarei Heads 0.5 m, Leigh 5–15 m, Makara 0.5 m, Kaikoura Peninsula 5–12 m, Portobello 10 m.

DESCRIPTION: Common around New Zealand rocky shores, being most frequent below 5 m where it encrusts boulders and rock faces. Particularly common in shaded areas such as caves and archways, extending into the sublittoral fringe under boulders. Encrusting, 2–3 mm thick in tiny patches 2–3 mm^2, extending to sheets covering 0.5 m^2; short vertical lobes can be produced from the spreading base. Colour dark purple (pR 2/6) throughout, with a whitish surface sheen conferred by a patterned, organised sand reticulation. Colour in spirit identical. Texture soft, easily torn, becoming brittle in ethanol. No mucus exuded upon damage.

SURFACE: Very distinctive with a white superficial reticulation of sand and spicule fragments visible over underlying darker tissue. Conules 0.5–0.7 mm high, mainly blunt, in some cases with protruding fibres and scattered 2–4 mm apart. Oscules distributed over the entire surface 7–10 mm apart, up to 1 mm in diameter and raised on low mounds. Poral fields obvious microscopically between sandy deposits.

SKELETON: Dendritic, composed of smooth erect fibres which rise from a basal spongin plate. Fibres are concentrically laminate, composed of an outer very dense bark with cellular material between laminations, and with a central markedly diffuse pith; pigmentation deep violet. Diameter ranges from 78–198 µm (average 154 µm) at or near the base, tapering to 30 µm at the surface.

SOFT-TISSUE STRUCTURE AND HISTOLOGY:
Dermal membrane supports a reticulation of sand and spicule debris in the plane of the surface, which extends into the subdermal region as distinct cortical pillars, 36–180 µm (average 114 µm) deep; these supplemented by a compact collagenous layer to complete a highly structured cortex, clearly set off from the choanosome.

Choanosome occupies the great volume of the tissue with eurypylous choanocyte chambers abutting with little mesohyl between; chambers 60–140 µm in longest dimension. Collagen tracts localised adjacent to fibres and at the ectosomal boundary, elsewhere matrix very lightly collagenous. Melanin-containing cells occur throughout the tissue; these comparable with those described by Donadey (1982) but not identical, the cells 12–19 µm long, anucleolate with cytoplasmic vesicles containing dense inclusions. No other secretory cells present.

REPRODUCTION: Parenchymella larvae, 300 µm at maturity, in specimens collected in May from Leigh.

REMARKS: *Chelonaplysilla violacea* was well described and figured by Lendenfeld (1883, 1889) from Australian specimens. These differ from New Zealand

specimens only in their more frequent production of erect fronds or lamellae. Other characteristics of the species, including the diterpenoid chemistry reported by Bergquist *et al.* (1990), are remarkably consistent.

The genus *Chelonaplysilla* is instantly recognisable in the field by the presence of the regular dermal sand reticulation, a novel feature in the Darwinellidae. Other characters which set this genus apart within the family are the absence of spumous cells, the presence of melanin-containing cells and the diversity of spongiane diterpenes which it contains.

There are at least two other species of *Chelonaplysilla* which remain to be described. One from Hawaii is a small shiny purple-black sponge known only from a single specimen. The chemistry of this species is extremely close to that of the Australasian specimens (Karuso pers. comm.). The other species is known from Palau and Pohnpei; its chemistry was reported by Sullivan and Faulkner (1984) and the sponge was identified as a *Dendrilla*. Both voucher samples have been checked and both belong to *Chelonaplysilla*. The dried and damaged specimens permit no further identification.

OTHER RECORDS: Australia, Fiji, Hawaii, Solomon Is.

DISCUSSION OF THE FAMILY DARWINELLIDAE:
A comment is required regarding the preference given to the familial name Darwinellidae Merejkowsky (1879), over Aplysillidae Lendenfeld (1883). This has been discussed by Lendenfeld (1889), Minchin (1900), Topsent (1905), de Laubenfels (1948), and Vacelet (1959) and most later authors followed the argument of de Laubenfels and used Aplysillidae. Van Soest (1977) and Wiedenmayer (1989), without any supporting discussion, adopted Darwinellidae. Hooper and Wiedenmayer (1994) provided the argument in support of the priority of Darwinellidae and consequently the name should be adopted. *Aplysilla*, however, is more typical of the group. It exhibits the basic characters which are elaborated, added to, or lost in part in other genera, and particularly emphasises the thin spreading habit. The histology of *Aplysilla* species remains to be documented fully, but examination of verified stained paraffin sections of *Aplysilla glacialis* from Bermuda and *Aplysilla polyraphis* from California confirms the presence of spumous cells in both. In terpenoid chemistry (Bobzin & Faulkner 1991) *Aplysilla* contains diterpenes closely allied to those described from *Chelonaplysilla* (Bergquist *et al.* 1990) and *Dictyodendrilla* (Kernan *et al.* 1990).

Evans and Bergquist (1977) in their study of sponge acid mucopolysaccharides included *Darwinella gardineri*, *D. oxeata* (as *Aplysilla rosea* and *A. sulphurea* respectively), and *Chelonaplysilla violacea* (as *Aplysilla violacea*) in their sample. *Chelonoplysilla* displayed no alcianophilia in the free mesohyl cells while this was evident strongly in both species of *Darwinella*. The latter displayed slight but taxonomically insignificant differences in the spectrum of acid mucopolysaccharides present, but in both strong staining was evident in the amoebocytes. The cells which expressed the staining are the spumous cells later described by Donadey and Vacelet (1977). These results are consistent with those of our electron-microscope study and confirm the absence of spumous cells in *Chelonaplysilla violacea*. Relationships of the aplysillid genera with others in the order are addressed in discussion.

Family **DICTYODENDRILLIDAE** Bergquist, 1980

Dendroceratida in which the skeleton is reticulate, with rectangular mesh made up of concentrically laminated and strongly pithed fibre. Pith can be partially obscured by the incorporation of detritus. Fibre skeleton can be augmented by the addition of free spongin 'spicules'. The large oval choanocyte chambers are eurypylous. The reticulate structure of the skeleton allows these sponges to attain large size despite the delicate cavernous nature of the soft tissue. The fibre pigmentation often contrasts with that of the soft tissue; dark purple, red, and black are common colours with soft tissue either pale or densely pigmented but always uniform throughout.

Dictyodendrilla Bergquist, 1980

Dictyodendrillidae in which the reticulate fibrous skeleton is regularly rectangular and composed of pithed, laminated fibres which are free of any coring material. The tissue construction is delicate and cavernous, and the soft tissue frequently pale and contrasting with dark fibres. The sponges are lobate, stalked or spreading with digitate projections.

TYPE SPECIES: *Dendrilla cavernosa* Lendenfeld, 1886, by original designation Bergquist 1980.

Dictyodendrilla dendyi nom. nov.
(Pl. 1a,c, 4f, 5a,d,e, 6a)

Megalopastas elegans Dendy, 1924: 382.
Dictyodendrilla cavernosa Bergquist, 1980: 488 *pars* (reference to *M. elegans* Dendy only).
Dictyodendrilla cavernosa: Kernan *et al.* 1990: 724.
Dictyodendrilla n.sp. Bergquist *et al.* 1991: 21.
Dictyodendrilla elegans: Bergquist *et al.* 1995: 36.

HOLOTYPE: BMNH 23.10.1.163.

MATERIAL EXAMINED: Spirits Bay 22 m, Poor Knights Islands 8–12 m, Leigh 10 m, Waiheke Channel 10 m, East Cape 15–20 m, Mana Island 8–15 m.

DESCRIPTION: Relatively uncommon, subtidal, found on large boulders, cave walls or on stable shell-gravel bottoms between 8 and 25 m depth around North Island. Most commonly stalked, digitate, or lobate but can take the form of a spreading mat with digitate projections. Colour grey-blue to blue in life (B-P 6/2) dark navy-blue to blue-grey (B3/2) in ethanol; fibres black. Consistency delicate, soft, but not slimy.

SURFACE: Strongly conulose; conules up to 1.0 mm high, 2–3 mm apart, and aligned to form short surface ridges. Pores evenly dispersed, giving a delicate reticulate appearance to the smooth surface. Oscules flush with the surface, 3–5 mm in diameter, and irregularly distributed.

SKELETON: A regular rectangular reticulum with no size distinction between ascending (primary) and connecting (secondary) elements. Fibres up to 250 µm in diameter, concentrically laminated, pithed with no coring material (Pl. 5d,e).

SOFT-TISSUE STRUCTURE AND HISTOLOGY:
Ectosome a thin layer 90–140 µm deep (120 µm average) marked only by light collagen reinforcement. No particular cellular aggregations or arrangements mark the ectosomal region which simply grades into the choanosome. Choanosome cavernous with large canals occupying most of the volume. Discrete groups of eurypylous choanocyte chambers 60–140 µm in longest dimension surrounded by a lightly collagenous matrix in which mobile cellular elements are present in moderate numbers (Pl. 1c). Archaeocytes and collencytes dispersed throughout the choanosome, but no specialised secretory cells present.

REPRODUCTION: Spermatogenesis observed in specimens collected from Leigh during October and Nov-ember. As reported by Tuzet *et al.* (1970) for *Aplysilla rosea* this takes place by transformation of choanocytes to form spermatids. The process synchronous within a chamber but not throughout the sponge; many different stages occurring at at any one time. Eggs present in July in specimens taken from 25m off Gisborne. Larval production not observed in New Zealand specimens but figured by Dendy (1905) for a southern Australian species very similar to *D. dendyi*. Typical parenchymellae produced.

REMARKS: *Dictyodendrilla dendyi* was first described from northern New Zealand as *Megalopastas elegans* by Dendy (1924) who also referred to its occurrence in southeastern Australia (Dendy 1905, 1924). Dendy never described his Australian specimens, simply equating them with *Dendrilla elegans* Lendenfeld which he transferred to his new genus *Megalopastas* (Dendy 1905). This genus was established to receive *Dendrilla*-like species which had reticulate rather than dendritic skeletons. *Dendrilla elegans* Lendenfeld is, however, quite a different sponge and was correctly referred by Bergquist (1980) to the Verongida. Dendy used Lendenfeld's species *elegans* as the reference for his Australian, and subsequently New Zealand, material assigned to *Megalopastas*. *Megalopastas*, with type species *M. nigra*, is a *Spongionella*, but the Australasian species which Dendy and Lendenfeld were discussing fall into *Dictyodendrilla*. Consequently the species name *elegans* is preoccupied in *Dictyodendrilla* and the new name '*dendyi*' is applied. *Dendrilla elegans* was placed by Bergquist (1980) in *Aplysina*; however, recent restudy of the type material (BMNH 86.7.8.1) allows it to be placed in the recently described genus *Suberea* (Bergquist 1995). In discussion of the genus *Spongionella*, Bergquist (1980: 482) referred to *Dendrilla elegans* Lendenfeld as aplysillid. That is incorrect, the reference should have been to *Aplysina* as was stated on p. 488 in discussion of *Dendrilla*.

In the list of described species assignable to *Dictyodendrilla* Bergquist (1980), *Dictyodendrilla tenella* Lendenfeld should also have been included.

Bergquist (1980) also suggested that *Megalopastas*, as evidenced by the structure of the type species (*M. nigra* Dendy), was not a dendroceratid sponge but rather a member of the family Dysideidae (Dictyoceratida) under the name *Spongionella nigra*. That decision is reviewed later in this work, since better material of *Spongionella* species is now available. The genus *Dictyodendrilla* was proposed to receive species allied to *Dendrilla* but having reticulate skeletons. The type species of *Dictyodendrilla* was designated as *Dendrilla cavernosa* Lendenfeld to which Dendy's specimen, *Megalopastas elegans* from New Zealand (Dendy 1924) was referred. Collection of additional specimens and careful study of type material and descriptions indicate that the two species are distinct. *Dictyodendrilla cavernosa* is yellow in life with complex tubular habit; *Dictyodendrilla dendyi* is a deep-blue to grey-blue sponge with digitate, frondose, but solid not excavated habit. Fibre dimensions also differ between the two species.

There are several sponges from southeastern Australia which fall into *Dictyodendrilla* but none has been properly described from living material; consequently only very basic information is available. Some,

however, are very similar to *D. dendyi* from New Zealand. *Aplysina massa* Carter from Westernport Bay,, Victoria was noted by Vacelet (1958) to have a reticulate skeleton of the *Megalopastas* type. Study of one specimen labelled by Carter, BMNH 87.7.11.18, confirms that it is a *Dictyodendrilla*; however, a second specimen also labelled by Carter BMNH 87.7.11.22, has a dendritic skeleton and is a darwinellid. Careful reading of Carter's description (Carter 1886 : 284) reveals that the sponge he described as *A. massa* had a dendritic skeleton which he compared closely to his earlier description of *A. corneostellata*, which was a *Darwinella* with typical dendritic skeleton. This latter species is unrecognisable. Carter then went on in his general observations to describe "another specimen of this kind in which the skeleton appears to be more reticulate"; this is obviously specimen BMNH 87.7.11.18. Carter did not actually refer this specimen to *A. massa*. It is a further species of *Dictyodendrilla*, with amber fibres and very fleshy texture. The type species of *Dictyodendrilla*, is *Dendrilla cavernosa* Lendenfeld from Port Jackson (BMNH 86.7.8.5.6). This is a tubular sponge, yellow in life with marked, contrasting black fibres, and extremely cavernous construction.

Lendenfeld (1888) also recorded *Dendrilla tenella* from Port Jackson, and BMNH 86.7.8.2 is an excellent specimen (Pl. 6b). Lendenfeld's description is recognisable; he notes 'occasional anastomoses' in the skeleton but in fact the skeleton is a classic *Dictyodendrilla* reticulation, the sponge is large and lamellate, 25 x 25 cm high and wide. It is gray with contrasting black fibres. This spectacular sponge needs to be redescribed from living material but it certainly is a third good species of *Dictyodendrilla* from southern Australia. Additional specimens are in the Australian Museum, register numbers G2551, G8910 (holotype), and Z542, a dry skeleton. An excellent specimen is also in the Macleay Museum Sydney University, S.40sp.

The Port Phillip and Port Jackson localities from which *Dictyodendrilla* and *Dendrilla* species were common in Lendenfeld's and Carter's time have been intensively collected from over the period 1960–1989. No examples of *Dictyodendrilla* have come to light and few of *Dendrilla*; these are large dramatically coloured sponges, not easily overlooked. It appears that they may have become extinct before receiving proper taxonomic descriptions.

No histological detail or chemical information is available for Australian specimens referable to *Dictyodendrilla* but the New Zealand sponge *Dictyodendrilla dendyi* contains a range of spongiane diterpenes and diterpene aldehydes (Kernan *et al.* 1990) closely related to those known to occur in *Aplysilla glacialis* (Bobzin & Faulkner, 1991) and *Chelonaplysilla violacea* (Bergquist *et al.* 1990).

OTHER RECORDS: North Cape, New Zealand, 22–40 m, *Terra Nova.*

Order **Halisarcida** new order

Ceractinomorpha in which the choanocyte chambers are tubular, branched, and wide-mouthed. Larvae are incubated parenchymellae with simple undifferentiated histology and cilia of uniform length. Skeleton is fibrillar collagen only, there are no fibrous or mineral elements present; ectosomal and subectosomal collagen is highly organised. This is, at present a monogeneric order.

Family **HALISARCIDAE** Vosmaer, 1885

Diagnosis as for the order.

Halisarca Johnston, 1842

Bajalus Lendenfeld, 1885

Diagnosis as for the order.

TYPE SPECIES: *Halisarca dujardini* Johnston, 1842

Halisarca dujardini Johnston, 1842
(Pl. 2b, 6c, 7a, Fig. 4a,b)

RESTRICTED SYNONOMY:
Halisarca dujardini Johnston, 1842: 192–193, pl. XVI, fig. 8.
Halisarca dujardini: Lendenfeld 1889: 729–730, pl. 50, fig. 2.4.
Halisarca dujardini: Burton 1932: 169.
Halisarca dujardini: de Laubenfels 1948: 175–176.
Halisarca dujardini: Lévi 1956: 1–184.

MATERIAL EXAMINED:
Devonport Wharf 1 m, Westmere Reef 0.5 m.

DESCRIPTION: Encrusting, 0.7–1.5 mm thick, occurring in patches of 3–4 cm^2 on rocks and mussels (*Perna canaliculus*) in areas not exposed to direct sunlight. Larvae recruit to settlement plates in low numbers throughout the year (Bergquist & Sinclair 1973) but the sponge becomes common only during the summer period (September to April). Colour varies slightly depending on aspect to light and state of the sponge with respect to reproduction. Most specimens exam-

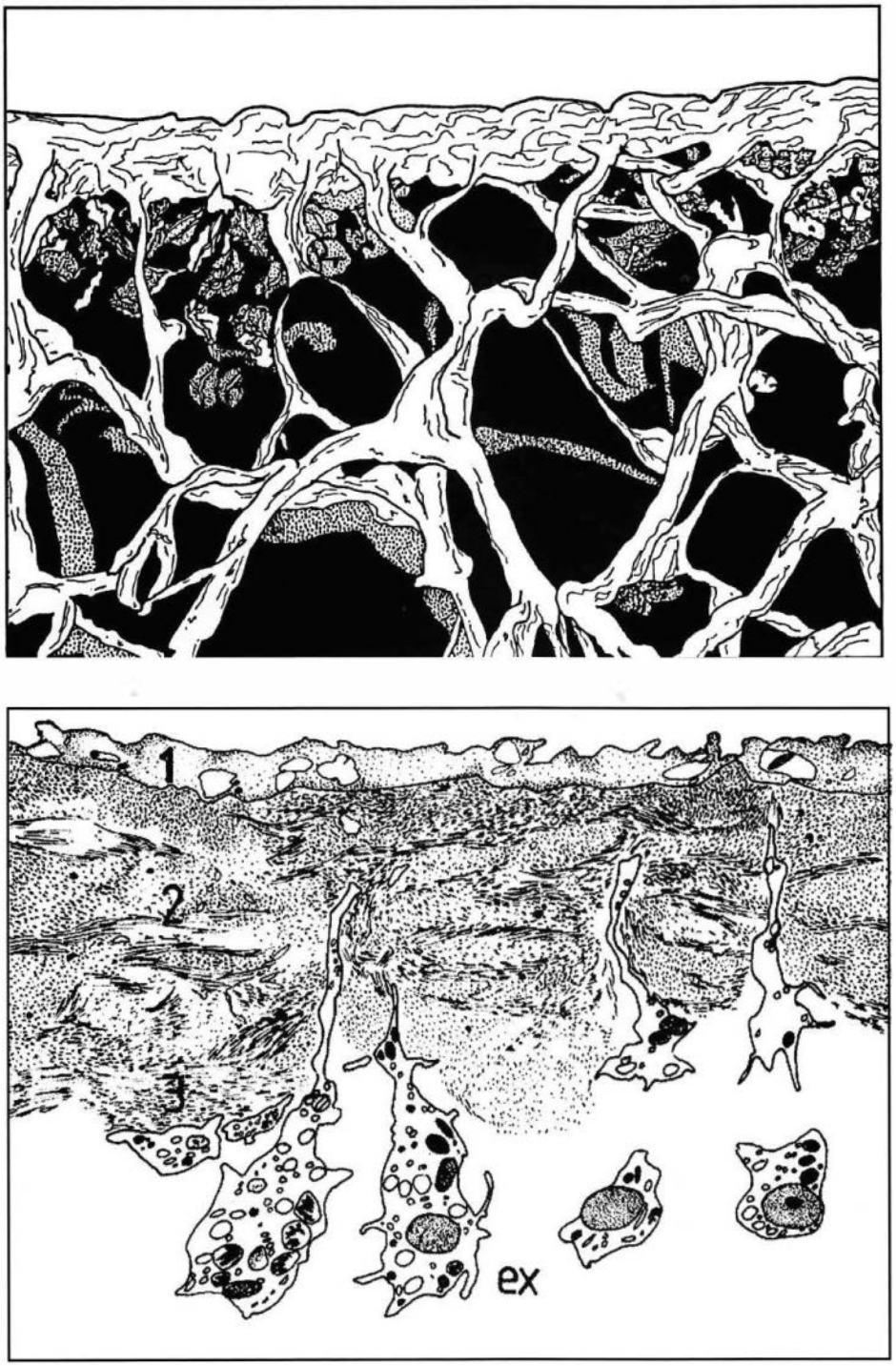

Fig. 4. ***Halisarca dujardini*** Johnston.

Upper: Diagram taken from a scanning electron micrograph showing the complex ectosomal region with superficial collagen and cellular layer; interlaced collagen fibrils organised into strong tracts form a middle layer which contains few cells.

Lower: Diagram taken from a transmission electron micrograph to show superficial pinacoderm with collagen reinforcing, a layer of organised collagen bundles, and the pendant cell bodies of the exopinacocytes connecting to the surface layer by fine extensions. **1,** cuticle; **2,** cell-depauperate, collagen-reinforced layer; **3,** concentration of pinacocyte cell bodies; **ex,** exopinacocytes.

ined contained reproductive products and were yellow-beige (YRY 8/4) in life and off white (YRY 8/2) in ethanol. Non-reproducing specimens pale yellow-brown (YRY 7/4). Consistency soft and gelatinous, slightly elastic.

SURFACE: Smooth and slimy with oscules 0.2–0.4 mm diameter scattered regularly. Pores dispersed. During reproduction a significant reduction in the aquiferous system, and surface features such as oscules and pores rarely observed.

SOFT-TISSUE ORGANISATION AND HISTOLOGY:
Ectosomal region 19–24 μm deep, consisting of three layers — a thin layer of T-shaped exopinacoctyes beneath which is a diffuse collagen and cellular layer 0.8–4 μm in thickness. The middle layer, 15 μm deep, contains interlaced collagen fibrils organised into strong tracts and is almost acellular. The inner region a condensed collagen layer 3–5 μm thick. The entire ectosomal region is traversed at intervals by an organised network of collagen bundles which provide the sponge with an organised, contractile ectosomal region (Fig. 4a, b).

Choanosome constitutes greatest volume of sponge tissue. Immediately below the ectosome is a region devoid of choanocyte chambers, composed entirely of individual mesohyl cells and collagen matrix of choanosomal rather than ectosomal density. Below this almost the entire volume is occupied by meandering, tubular choanocyte chambers 90–115 μm long and 16–22 μm wide (Pl. 6c). Choanocytes small, irregular cells, 8 μm long and 4 μm in diameter, with nucleus 3 μm in diameter containing a nucleolus 0.8 μm in diameter. On either side of the choanocyte collar are cytoplasmic extensions, the cells anchored in the matrix by long filopodia that extend from the base of the cell exactly in the manner described by Vacelet and Donadey (1987). Spherulous cells (Pl. 2b) common at the junction between ectosome and choanosome and along canals. Fuchsinophil cells scattered through the mesohyl. Oriented bundles of collagen fibrils concentrated throughout the choanosome, and lophocytes, involved in active collagen secretion, common.

REPRODUCTION: At low levels throughout the year with a peak in the period October/November. Dioecious, spermatogenesis having never been observed in sponges producing eggs and larvae. During the reproductive period a significant breakdown of choanocyte chambers with an attendant rise in free mesohyl cells, while eggs and larvae in various stages of development are concentrated toward the base of the sponge (Pl. 7a). Larvae small, spherical, translucent parenchymellae 100–200 μm from pole to pole with cilia of uniform length but absent at the bare posterior pole.

REMARKS: The specimens described above are consistent in all reproductive and histological features with *Halisarca dujardini* from Atlantic coasts (Lévi 1956; Chen 1976). The first record of the genus *Halisarca* from New Zealand was published by Bergquist and Sinclair (1973) as part of a study of sponge larval settlement in the Waitemata Harbour. They suggested that the species was probably *dujardini*, and this can now be confirmed, assisted by Chen's subsequent work (Chen 1976).

The species name *dujardini* is assigned on the basis of the light-brown colour, intertidal and shallow subtidal habitat, epizoic on mussels within a major harbour which are all features consistent with previous records worldwide (Chen 1976). Also, variation in choanosomal organisation and surface morphology with reproductive state was recorded for *H. dujardini* by Chen, and both spherulous and fuchsinophil secretory cells are present, as recorded for *H. dujardini* (Lévi 1956). Larval morphology is identical to that recorded by Lévi and Chen for *dujardini* (Bergquist *et al.* 1979) and the sponge is dioecious.

There are many quite unrecognisable descriptions of *Halisarca* species. To quote Lendenfeld (1889) referring to Carter's descriptions "these species are described in such a manner that it is impossible to criticise them, they might be anything". Carter (1886) is not the only culprit and for that reason we have described the sponge structure fully to emphasise the very advanced ectosomal structure, secretory-cell ultrastructure, and the complex matrix structure which characterises the species.

There are points of general interest to be made in relation to *Halisarca* species. The complex ectosomal structure described here has been noted by earlier authors (reviewed by Lévi 1956) but it was never described in detail or figured for *H. dujardini*. Vacelet and Donadey (1987) gave a good description of the equivalent region in *H. caerulea*, which differs from *H. dujardini* particularly in having stout collagen bundles oriented in the plane of the surface and in having fewer discrete ectosomal zones. *Halisarca ectofibrosa* (Vacelet *et al.* 1976) has very stout interlaced collagen bundles up to 400 μm in diameter in the ectosome but other details were not given in the original description. *Halisarca nahantensis* has a structured ectosome described as very similar to that of *H. dujardini* (Chen 1976).

Since *Halisarca* species have proved difficult to characterise for many authors, it is welcome to be able to point to features of ectosomal structure which distinguish species of the genus and which are constant

throughout the varying phases of growth and reproduction. The ectosome of *Halisarca* and that of *Psammaplysilla* (Verongida) display almost a tissue organisation and are unusual specialisations within Porifera.

Lophocytes are recorded as being common in the choanosome of *H. dujardini*. These very distinctive cells have not previously been reported to occur in *Halisarca* but their role in deposition of matrix collagen bundles is well documented for some hadromerid genera, for example *Chondrosia* (Pavans de Ceccatty 1957), *Tethya* (Pavans de Ceccatty & Thiney 1963, 1964), and *Suberites* (Connes *et al.* 1972). They also occur in freshwater sponges (Bergquist 1978). Early literature reports of lophocytes in sponges other than Hadromerida and Haplosclerida require verification.

Halisarca lophocytes correspond in structure with those of Hadromerida. No relationship between *Halisarca* and genera such as *Chondrosia*, which also lacks a mineral skeleton, is suggested on the basis of this cytological feature alone. However, it is of interest to note that Vacelet and Donadey (1987) drew atten-tion to possible similarities in secretory behaviour of spherulous cells in the two genera. In *H. caerulea* they identified two roles for what are obviously different categories of spherulous cell, one secretory with contents being discharged into canals, as found in *H. dujardini*, and one involving disintegration in the mesohyl with deposition of a matrix ground substance which is discrete from the matrix collagen bundles. They liken this mesohyl structure and spherulous cell behaviour to that of members of the Chondrosiidae. In addition to the histological parallels between *Halisarca* and the Chondrosiidae, a recent study involving sequence analysis of the ITSI region of the 18S ribosomal gene consistently places *Halisarca* close to *Chondrilla* and *Chondrosia* and separates it from the Dictyoceratida, Dendroceratida, and Verongida (Bergquist *et al.* 1996). While it would be tempting to find a taxonomic 'home' for *Halisarca*, it must be remembered that there are great differences in choanocyte chamber structure, ectosomal organisation and reproductive characteristics which support separation of *Halisarca* and the Chondrosiidae at the ordinal level.

It is to be expected that many more species of *Halisarca* will be described now that a clear basis for species recognition using colour, ectosomal organisation, larval structure, reproductive periodicity, secretory cell structure, and mesohyl organisation is available.

OTHER RECORDS: Cosmopolitan.

DISCUSSION

In conclusion, some comment on the questions of classification and relationship raised in the introduction can be made.

Status of *Halisarca*

Ordinal status for the Halisarcida is proposed on the grounds which were stated by Bergquist (1980). These are the possession of a choanocyte-chamber structure unique in the Porifera and the possession of an incubated parenchymella larva quite unlike any other within the Demospongiae, combining as it does the features of small size, undifferentiated histology, cilia of one size class, and a swimming habit. In addition, Bergquist and Wells (1983) noted that while all Dendroceratida investigated chemically (for which the identification could be verified) contained spongiane diterpenes as major secondary metabolites, no such metabolites were present in *Halisarca*. Many more dendroceratids have now been investigated and this statement remains true (Bergquist *et al.* 1990). Also, detailed study of histology of several species of *Halisarca* has now been completed and permits comparison with other groups of Demospongiae. There is no similarity to be found with the Dendroceratida, Dictyoceratida, or the Verongida. There are very distinctive unique histological features in *Halisarca*, such as the highly structured nature of the collagen tracts in the ectosomal region and the presence of fuchsinophil cells. Other distinctive features such as the pseudopodial choanocyte bases, nucleolate choanocytes, lophocytes, spherulous cell structure and function, condensation of granulofibrillar matrix areas which largely exclude collagen, and occurrence of dense networks of collagen bundles throughout the choanosome are shared in varying measure by species of *Halisarca* and two genera of the Chondrosiidae (order Hadromerida), *Chondrosia* and *Chondrillastra* (Vacelet & Donadey 1987), and in part with a third genus *Chondrilla* (Gaino & Pronzato 1983). Major differences in body organisation and choanocyte-chamber structure preclude any suggestion that *Halisarca* be referred to the Hadromerida. Vacelet and Donadey (1987) suggested that the features in common between the two taxa simply arise from the emphasis on

collagen as a structural skeletal element in both *Chondrosia* and *Halisarca*.

On the basis of Lendenfeld's original description, the genus *Bajalus* Lendenfeld shows some affinity with *Halisarca*, and Lévi (1958) suggested that establishing two monogeneric families, Halisarcidae and Bajalidae, within the Dendroceratida was the best indication of relationships. Bergquist (1980) examined the holotype and histological preparations of *Bajalus laxus* and suggested that the stronger relationship, if any, was to the Ianthellidae where some branching of choanocyte chambers can occur. Fresh material of Lendenfeld's sponge has now been discovered from the southern New South Wales coast where it is epizoic on *Pyura*. The sponge proves to be a distinct species, *Halisarca laxus* (Lendenfeld) (Pl. 5c) (Bergquist 1994). The relationships of the order Halisarcida within the ceractinomorph assemblage cannot be resolved with any certainty at this time.

Relationships of the Genera of Dendroceratida to Other Groups (Dysideidae & Verongida)

To discuss generic and familial relationships of present dendroceratid genera it is necessary to refer to species additional to those represented in the New Zealand fauna. Material of the following species has been examined: *Hexadella racovitzai* Topsent, *Hexadella indica* Dendy, *Hexadella purpurea* Dendy (holotypes, histological preparations only); *Pleraplysilla minchini* (slide of holotype), *Pleraplysilla spinifera* Schultze (holotype specimen and material prepared for electron microscopy, courtesy of Dr J. Vacelet); *Aplysilla glacialis* from La Jolla and Bahamas and *Aplysilla polyrhaphis* from the Gulf of California (spirit specimens, courtesy of Dr J. Faulkner); *Igernella joyeuxi* Topsent (slide of holotype) and *Igernella notabilis* Duchassaing & Michelotti (own collection, Jamaica).

Investigating relationships of present members of the family Dysideidae to the Dendroceratida required that we examine species of *Dysidea* and *Spongionella*. Light- and electron-microscopic studies were made of two undescribed New Zealand *Dysidea*, cosmopolitan *Dysidea fragilis* which is the type species for the genus, three tropical species (*Dysidea herbacea* and *D. chlorea* from Palau and Great Barrier Reef, and a new species similar to *D. avara* (own field collections)), and *D. tupha* from the Mediterranean (courtesy Dr J. Vacelet). Material of *Spongionella gracilis* (Vosmaer) was made available by Dr G. Pulitzer-Finali, the holotypes of *Spongionella pulchella* (Sowerby) and *Spongionella nigra* Dendy were examined, and newly collected specimens of *S. pulchella* were made available by Dr Bernard Picton.

No descriptions of these additional species are provided, rather comment is given on relevant attributes which arise either from existing literature or from new observations. For all genera except *Hexadella* the terpene chemistry of some representatives has been reported in the literature (Bergquist *et al.* 1990) and can be considered in conjunction with other features. The only reports of secondary-metabolite chemistry for *Hexadella* are those by Morris and Andersen (1989, 1990) who worked with collections from the Pacific coast of Canada, and these present a confusing picture. They report the presence of bromotyrosine derivatives typical of all Verongida in the one collection from shallow water (40 m) and tryptophan-derived metabolites related to topsentin in a second collection from deep water (100–200 m). A later, shallow-water collection yielded bromotyrosine metabolites and further tryptophan-derived compounds. It is clear that neither sponge was *Hexadella* and inadequate voucher material remains to permit further taxonomic investigation. Morris and Anderson, on the basis of their results, state that *Hexadella* belongs to the Verongida; perhaps their specimens, or some of them are verongiids, but *Hexadella*, based on the features of the type species *H. racovitzae*, belongs in the Dendroceratida and its chemistry remains unknown.

With the Halisarcidae removed, the Dendroceratida as evidenced by the New Zealand representatives becomes a closely cohesive group. However, the situation for the group as a whole and its possible dysideid relationships are less clear cut.

The decision to establish the family Dictyodendrillidae for species with a regular reticulate skeleton composed of fibres with identical structure to those of the Darwinellidae, which have a strictly dendritic skeleton, is upheld despite suggestion to the contrary by Vacelet *et al.* (1989) who suggested that the Dysideidae be transferred to the Dendroceratida and take precedence as a family for species with reticulate skeletons. These authors completely overlooked significant differences in fibre structure and organisation. There is only one New Zealand dictyodendrillid, *D. dendyi*, and this is the only species which has been studied carefully for chemistry and histology. The chemistry of a second, undescribed species from the Great Barrier Reef has been reported (Cambie *et al.* 1988). In both species the chemistry is extremely close to that of *Chelonaplysilla* (Bergquist *et al.* 1990) and *Aplysilla* (Bobzin & Faulkner 1991). Both species lack the spumous cells that occur in all Darwinellidae except *Chelonaplysilla*. Skeletal pattern thus remains the only exclusive familial characteristic separating the Darwinellidae and the Dictyodendrillidae.

The Dictyodendrillidae as originally constituted contained two genera: widespread *Dictyodendrilla*, and Caribbean and Indian Ocean *Igernella* (Pl. 7d). A third genus, *Acanthodendrilla*, was added by Bergquist (1995). *Dictyodendrilla* has a regular reticulate skeleton made up of stratified uncored fibres of typical dendroceratid structure with extremely strongly developed pith. *Igernella* has a reticulate skeleton made up of stratified fibres that incorporate a variable amount of coring debris. The matter of presence or absence of a strong pith component in *Igernella* fibres was not clearly addressed in early descriptions and could not be resolved with certainty from material available in 1980. Topsent (1905) indicated that the fibres of the type species *I. joyeuxi* were "of *Dysidea* type" and certainly the heavy load of foreign material in the superficial fibres made this an appropriate comparison, particularly since Topsent was working with a sun-dried specimen. Topsent's slides have been examined in the course of this work. Van Soest (1978) redescribed the holotype of *Igernella notabilis* Duchassaing & Michelotti, with which *I. joyeuxi* was synonomised, but did not clarify the precise structure of the fibres. His diagram (Fig. 26a) does however suggest that a strong pith is present; he also verified the presence of a continuous basal spongin plate. Study of freshly collected material from Jamaica permits me to confirm that pith is present and that it is a strong component of the fibre. On this basis, and supported by the presence of spongiane diterpenes (Schmitz *et al.* 1988), *Igernella* shows clear affinity to the family Dictyodendrillidae. No spumous cells have been seen in *Igernella*, but no electron microscopy has been done on the sponge.

In addition to the features already mentioned, *Igernella* species augment their skeleton with tri- to polyactinal fibrous 'spicules'. These are very similar in gross structure to those found in *Darwinella* species, and to some authors (Van Soest 1978) this similarity dictates a very close relationship between the two genera. Garrone (1978), in a comprehensive review of connective tissue and matrix structure in sponges, reported results of his ultrastructural study of fibrous 'spicules' in both genera. The microstructure of the collagen and its organisation prove to be quite different. *Darwinella* 'spicules' have a concentric laminate structure and a distinct, less dense core, they are flexible and elastic; *Igernella* 'spicules' are brittle, homogeneous in section, and have a helical orientation of microfibrils that incorporate deposits of lepidocrocite. They somewhat resemble *Ircinia* filaments in their microstructure (Garrone *et al.* 1973). These fibrous spicular structures are clearly not homologous. This underlines the importance of resolving structure before using it in cladistic analyses. Bergquist (1980) drew attention to the presence of free fibrous 'spicules' in *Aplysinella* (Verongida) and noted that this tendency to produce free fibrous elements had obviously arisen more than once in the evolution of the groups under consideration. *Igernella* and *Darwinella* with the differing patterns of skeletal construction, distinctly different microstructure of the fibrous spicules, and distinct differences in histology are well separated at the family level.

The genus *Pleraplysilla* was established by Topsent (1905) for *P. minchini* from the Atlantic coast. The species was interpreted by Vacelet (1959) to be identical to *Spongelia spinifera* Schulze although the latter, Mediterranean species was thicker with more branching fibres. Vacelet designated *P. spinifera* as the type species. Very few *Pleraplysilla* species have been described but all have an axial core of debris in their fibres; this never occludes the whole fibre as it does in most *Dysidea* species. The feature 'cored fibres' has been held to indicate relationships with the Dysideidae, but the existence of genera such as *Acanthodendrilla* and *Igernella* demonstrates that this feature is common in both dictyoceratid and dendroceratid species.

It has been difficult to determine from published reports and museum collections whether the fibres of *Pleraplysilla minchini* and *P. spinifera* have the marked, clearly separate pith component that characterises all other Dendroceratida. Study of Topsent's original slides confirms the presence of a typically dendroceratid pith (Pl. 7b). Vacelet's figures (1959) of *P. spinifera* do not resolve the fibre structure clearly but infer the presence of a marked pith. Examination of a specimen from Naples, BMNH 33.3.1.14 confirms the presence of pith.

Histological characters other than choanocyte-chamber structure point to affinity with the Dendroceratida rather than the Dysideidae. *Pleraplysilla spinifera* has an abundant mesohyl cell population which includes the spumous cells found in many other Dendroceratida. This contrasts with *Dysidea* species which have a mesohyl depauperate of mobile cells and of secretory cells in particular. Only isolated secretory cells have been observed in the *Dysidea* species studied in this work, and others who have studied the histology of the genus confirm this (Lévi, Boury-Esnault & Vacelet pers. comm.). *Pleraplysilla minchini* appears to lack spumous cells.

A problem arises with the reports on terpene chemistry. These relate only to *Pleraplysilla spinifera* from the vicinity of Naples, and the sponge yielded a range of sesquiterpenes such as are found in all *Dysidea* species (Bergquist & Wells 1983). No chemistry is known for *P. minchini*, which, with its typical *Aplysilla*-like thin habit and sparse skeleton, is here considered a distinct

species. It is possible that the sponge extracted for chemistry was a very small *Dysidea*. However, no voucher specimens are available to confirm the identification of the specimens from which the chemistry derives. There is sufficent ambiguity surrounding this matter to base an assessment of the taxonomic position of *Pleraplysilla* only on the features of *P. minchini*, the original species described in the genus, and thus by monotypy the type species.

Another genus which has proved difficult to assign with certainty is *Spongionella* Bowerbank. The genus was long known only from the dry type specimen *S. pulchella* (BMNH 30.7.3.454); the regular reticulate skeleton and lamellose form were well depicted, but soft tissues and internal fibre structure were not resolvable. Vacelet (1959) recorded some small specimens of the species from the Marseilles region and Vacelet *et al.* (1989) described the choanocyte-chamber structure from scanning electron microscopy. Ackers *et al.* (1992) have provided some excellent photographs and some spirit specimens which have been examined (Pl. 6d,e).

During the period that *Spongionella* could not be characterised completely, other species were added to the genus simply on the basis of similarity in skeletal pattern and presumed choanocyte-chamber structure. The earliest was *Spongionella gracilis*, described as *Velinea gracilis* by Vosmaer (1883). Topsent (1928) added the species *repens* and *ramodigitata* under the latter generic name. Topsent later (1929) referred all of these Mediterranean species to *Spongionella*. Vacelet (1959) gave a good review of the various taxonomic assessments of the species assigned to *Spongionella* in the broadest sense and he decided with respect to the Mediterranean ones that all could be referred to *S. pulchella*. With better-preserved and more numerous specimens of *S. pulchella* now available, as well as excellent material of *S. gracilis*, it is apparent that the intersecting lamellose form of *S. pulchella* is a consistent feature in all but the smallest specimens while the tubular ramodigitate habit is consistent within *S. gracilis* (including *repens* and *ramodigitata*), (Fig. 5). There are small differences also in the skeletal pattern and surface conulation (Ackers *et al.* 1992, fig p. 161). Both are good species of *Spongionella*, both have eurypylous choanocyte chambers, stratified fibres with typical, but slightly reduced dendroceratid pith, a tight evenly reticulate skeleton, mesohyl with moderate mobile cellular population, and a microconulose surface. Ultrastructural histology remains unknown except for scanning electron microscopy of the choanocyte chambers (Vacelet *et al.* 1989).

Mayol *et al.* (1985) reported that the major secondary metabolite of *Spongionella gracilis* was gracilin-A, gracilin-A, a spongiane diterpene also known to occur

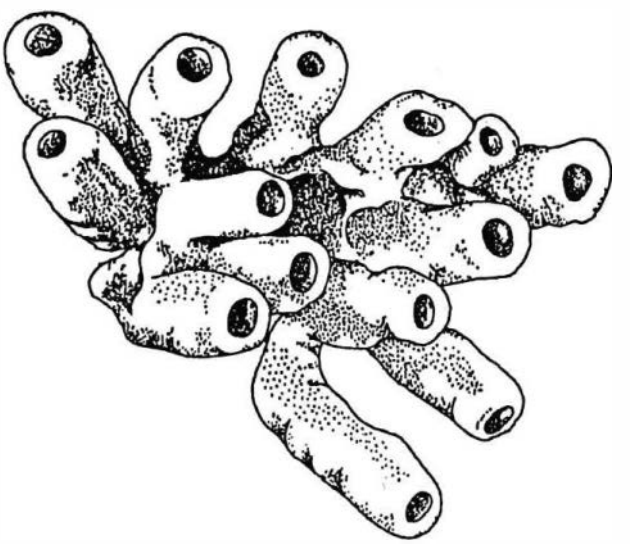

Fig. 5. *Spongionella gracilis* (Vosmaer). Illustration of whole sponge to show tubulodigitate habit (natural size).

in the unusual *Darwinella tango* from Australia and closely related to the metabolites of *Darwinella oxeata* from New Zealand (Bergquist *et al.* 1990; Poiner & Taylor 1990) (Table 1). Nothing is known of the chemistry of *S. pulchella*.

On balance, *Spongionella* as evidenced by the features of the type species and *S. gracilis*, falls easily into the family Dictyodendrillidae. It is a genus in which the fibre structure is finer and more regular than in *Dictyodendrilla*. The pith elements are major components of the fibres but are not as developed as in *Dictyodendrilla*, the fibres are clear of coring material, and the surface is microconulose, differentiating the genus from *Acanthodendrilla* and *Dictyodendrilla*. The lack of coring material, regularity of the skeleton, and absence of free fibrous 'spicules' distinguishes it from *Igernella*.

Other species re-examined during this study which fall into *Spongionella* are *Spongionella nigra* Dendy (Pl. 6f), with which *Spongionella pulvilla* Dendy (as *Megalopastas*) is synonymous, and *Spongionella tubulosa* Burton.

Spongionella chondrodes de Laubenfels was referred to *Fasciospongia* (Bergquist 1965) but it may yet be better referred to *Lendenfeldia*. *Spongionella frondosa* Hentschel belongs to the genus *Lendenfeldia*. *Spongionella foliascens* Kelly-Borges *et al.* (1993) has not been examined but is certainly congeneric and, in the superficial irregularity of its skeleton, recalls the organisation of *Igernella*. Kelly-Borges *et al.* refer to a *Spongionella hermanni* (for *Pseudobasta hermanni* Topsent) and infer that Bergquist (1980) thought this to be a *Spongionella*. In fact it was stated to be recognisable

only as belonging to the Dictyodendrillidae not as being a *Spongionella*.

Review and Proposed Taxonomic Arrangement

As the previous discussion has revealed, a state of considerable indecision has surrounded the problem of how best to resolve the boundary between the Dysideidae (Dictyoceratida) and the whole assemblage of sponges grouped within the Dendroceratida. Much of the difficulty stems from the paucity of characters that can be attested to with certainty across the whole generic assemblage. Many of the sponges concerned are small, encrusting, or very collapsible, losing many identifiers on removal from the substratum. Thus descriptions of new species with consequent re-evaluations of classification are often inadequate and the recommendations premature or wrong.

It has been emerging in the literature since 1979 (Bergquist 1979) that terpenoid chemistry has considerable potential as a taxonomic indicator for the Dictyoceratida and Dendroceratida. Gathering taxonomically verified information on the chemistry of these sponges has been a time-consuming exercise. Bergquist reported on current data in 1985, but conference proceedings were delayed in publication until 1990. This report (Bergquist *et al.* 1990) gave an appraisal of the existing classification, made some suggestions for revision, highlighted remaining problems, and indicated possible future rearrangements. Attention was drawn to the need for further information on the histology and chemistry of a number of species before deciding whether the family Dysideidae should be transferred in whole or in part to the Dendroceratida as Dendy (1905) foreshadowed. A tentative new scheme was put forward but this is materially revised in this work.

Vacelet took up these ideas and pursued his investigation of choanocyte morphology and chamber structure of a number of species using scanning electron microscopy and provided some interesting data (Vacelet *et al.* 1989). These authors decided formally to propose the transfer of the Dysideidae to the Dendroceratida and suggested that since the skeleton of dysideiids, in which they included *Spongionella*, was reticulate, the family Dictyodendrillidae could be viewed as a junior familial name. In making these transfers Vacelet *et al.* overlooked several important points. They stressed the similarity of the eurypylous chambers in Dysideidae (*Dysidea*, *Euryspongia*, and for them *Spongionella*) and Darwinellidae (Aplysillidae for them), stating that these are unique in ceractinomorph demosponges. This is not the case — *Ianthella* and *Anomoianthella* have eurypylous chambers (cf. Bergquist 1995, fig. 26). This, plus their skeletal pattern, fibre structure, and chemistry differentiate the family Ianthellidae from the other two families of the Verongida. In making chamber structure an ordinal rather than familial discriminator, Vacelet *et al.* lose sight of the dramatically different fibre structures to be found within the Dysideidae, Darwinellidae, and Dictyodendrillidae.

In all Dendroceratida, the marked diffuse pith bears most resemblance to that of the Verongida (Pl. 5f) than to that of Dysideidae (*Dysidea* and *Euryspongia*) where the closest structural comparison is with some Thorectidae (Dictyoceratida). One other fact which was overlooked is that, apart from the ambiguity over *Pleraplysilla spinifera* mentioned earlier, all Dendroceratida studied contain spongiane diterpenes while all *Dysidea* species studied contain sesquiterpenes among a range of other secondary metabolites, some of microalgal origin. Diversity of structure and biosynthesis within these sesquiterpenes offers some guidance toward subdivision of this large genus. No terpene chemistry has been reported for *Euryspongia*.

In using a "broad brush" and transferring all Dysideidae to the Dendroceratida, Vacelet *et al.* overlooked the very obvious fact that the genus *Dysidea* is not homogeneous. This was made clear on the basis of structure and chemistry by Bergquist and Wells (1983) and commented on further by Bergquist *et al.* (1990). Exactly how to subdivide *Dysidea* needs careful study but at least four generic groups can be recognised. It is conceivable that some species presently in *Dysidea* could be placed within the Dictyodendrillidae, or a new family within the Dendroceratida for forms with irregular reticulate skeletons, but none examined by the present author falls into this category nor do any of the known species of *Euryspongia*. What is unarguable is that the family Dysideidae, based on the characters of the type species of *Dysidea* (*D. fragilis* Montagu, well figured by Ackers *et al.* (1992)), belongs in the Dictyoceratida. One problem which makes a complete revision of *Dysidea* extremely difficult is the very summary nature of many descriptions, understandable given the tendency of these sponges to incorporate debris in both fibres and matrix. A preliminary subdivision of the genus which takes terpene chemistry into account will be published in conjunction with descriptions of some new tropical species. Since *Dysidea sensu stricto* is not a member of the Dendroceratida, further treatment is out of place here.

Table 2 provides a summary of the major characters used to distinguish the orders and families discussed above. A number of other characters such

as reproductive mode, larval structure, mesohyl cell density, body construction, ratio of skeletal fibre to soft tissue, pigmentation, and surface features could be added. However, the table includes all frequently used descriptors and makes one thing clear — one cannot define the orders, let alone the families, except on the basis of reproductive mode and secondary- metabolite chemistry, without taking care to distinguish between various types of pith and stratification in fibres as was done in the introduction. Similar attention to detail of secretory-cell structure is also necessary. It was stressed in the introduction that different morphogenetic processes are involved in producing the various forms of pith and fibre lamination patterns and reticulate skeletons, and that a mere reference to pith absent/present, skeleton reticulate for example, is seriously misleading. These groups can be distinguished as the ordinal and familial diagnoses in the text indicate, but only by properly understanding and defining structure.

The Significance of Terpene Content

Frequent reference has been made to the secondary-metabolite chemistry of the Dendroceratida and particularly to the basic terpenoid metabolite structures and their relationship to similar compounds which occur in the Dictyoceratida. Affinity or otherwise of terpene structure has provided an additional systematic character when comparing families in particular.

Table 2. Major characteristics of orders and families of fibrous sponges.

	Dictyoceratida				Dendroceratida		Verongida		
	1	2	3	4	5	6	7	8	9
Diplodal chambers	✔	✔	✔				✔	✔	
Eurypylous chambers				✔	✔	✔			✔
Skeleton reticulate	✔	✔	✔	✔		✔	✔		✔
Skeleton dendritic					✔			✔	
Fibres stratified		✔	✔	✔	✔	✔	✔	✔	✔
Fibres homogeneous	✔								
Pith present		✔	✔	✔	✔	✔	✔	✔	✔
Pith absent	✔								
Fibrous spicules present					✔	✔		✔	
Fibrous filaments present			✔						
Fibres cored	✔	✔	✔	✔	✔	✔			
Spherulous cells present	✔	✔	✔				✔	✔	✔
Spumous cells present					✔				
Sesterterpenes present	✔	✔	✔						
Sesquiterpenes present				✔					
Spongiane diterpenes present					✔	✔			
Brominated tyrosines present							✔	✔	✔
Reproduction oviparous							✔	✔	✔
Reproduction ovoviviparous	✔	✔	✔	✔	✔	✔			

1 Spongiidae
2 Thorectidae
3 Irciniidae
4 Dysideidae
5 Darwinellidae
6 Dictyodendrillidae
7 Aplysinidae
8 Aplysinellidae
9 Ianthellidae

Table 3 summarises the recommended taxonomic arrangement of the genera discussed in this work.

Table 3. Arrangement of genera proposed in this work. The additional dysideid genera are currently being described and notice is simply drawn to this fact.

Dendroceratida		Dictyoceratida
Darwinellidae	Dictyodendrillidae	Dysideidae
Darwinella	*Igernella*	*Dysidea*
Aplysilla	*Dictyodendrilla*	3 new genera
Chelonaplysilla	*Spongionella*	*Euryspongia*
Pleraplysilla	*Acanthodendrilla*	
Hexadella		
Dendrilla		

The dominance and ubiquity of terpenes as secondary metabolites in these sponge groups has caused questions to be raised about their function. Bergquist (1978, 1979) drew attention to the relationship between elaboration of a range of terpenes, (di-, sester-, sesqui-) and possession of an extremely low content of sterols (0.07–2.00% total lipid) in the Dictyoceratida and Dendroceratida. Given the accepted role of sterols as components of membranes, the question was raised as to whether terpenes in certain sponges could serve instead of sterols in cell membranes. Litchfield and Morales (1976) had considered the same possibility with regard to the unusual long-chain fatty acids in some sponges. This idea has been pursued through a long series of cell-fractionation, radioactive-labelling, ultrastructural and biosynthetic experiments (Garson *et al.* 1988; Lawson *et al.* 1988) and it is now possible to affirm that these terpenoid constituents are membrane components.

This is indicative of a very basic metabolic and functional divergence between the Dictyoceratida and Dendroceratida, in which synthesis of terpenes is emphasised, and the Verongida which emphasise synthesis of sterol lipids (Bergquist *et al.* 1980). These biosynthetic alternatives both underpin membrane function and probably would have been adopted as alternatives very early in the evolution of the sponge groups we are considering. Other groups of sponges may prove to have the same emphasis on membrane terpenes, but all others that have been studied utilise sterols (Bergquist *et al.* 1980; Bergquist *et al.* 1986). This is the first time that a functionality can be ascribed to a secondary-metabolite profile of a lower invertebrate group and that profile at the same time can be shown to correlate with the higher-order systematics of the group.

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PLATE 1

A. ***Dictyodendrilla dendyi*** nom. nov.: Preserved specimen showing the complex reticulate skeleton composed of fibres of approximately equal dimensions (x 0.5).

B. ***Darwinella oxeata*** Bergquist: Photomicrograph of a fibre to show incorporation of cellular material and clearly demarcated bark and pith regions (x 400).

C. ***Dictyodendrilla dendyi*** nom. nov.: Photomicrograph of choanosome to show fibres, eurypylous chambers, and matrix (x 120).

D. ***Chelonaplysilla aurea*** Bergquist: Photomicrograph to illustrate the structured sandy deposition marking the cortical region. Clear pith/bark demarcation in the fibres is also shown (x 400).

E. ***Halisarca dujardini*** Johnston: Scanning electron micrograph to illustrate the complex ectosomal structure. E, superficial ectosomal layer; ct, connective tissue tracts. Scale bar 50 μm.

F. ***Acanthodendrilla australis*** Bergquist: Photomicrograph of fibre in cross section to show incorporated sandy material, laminate bark and distinct pith region (x 120).

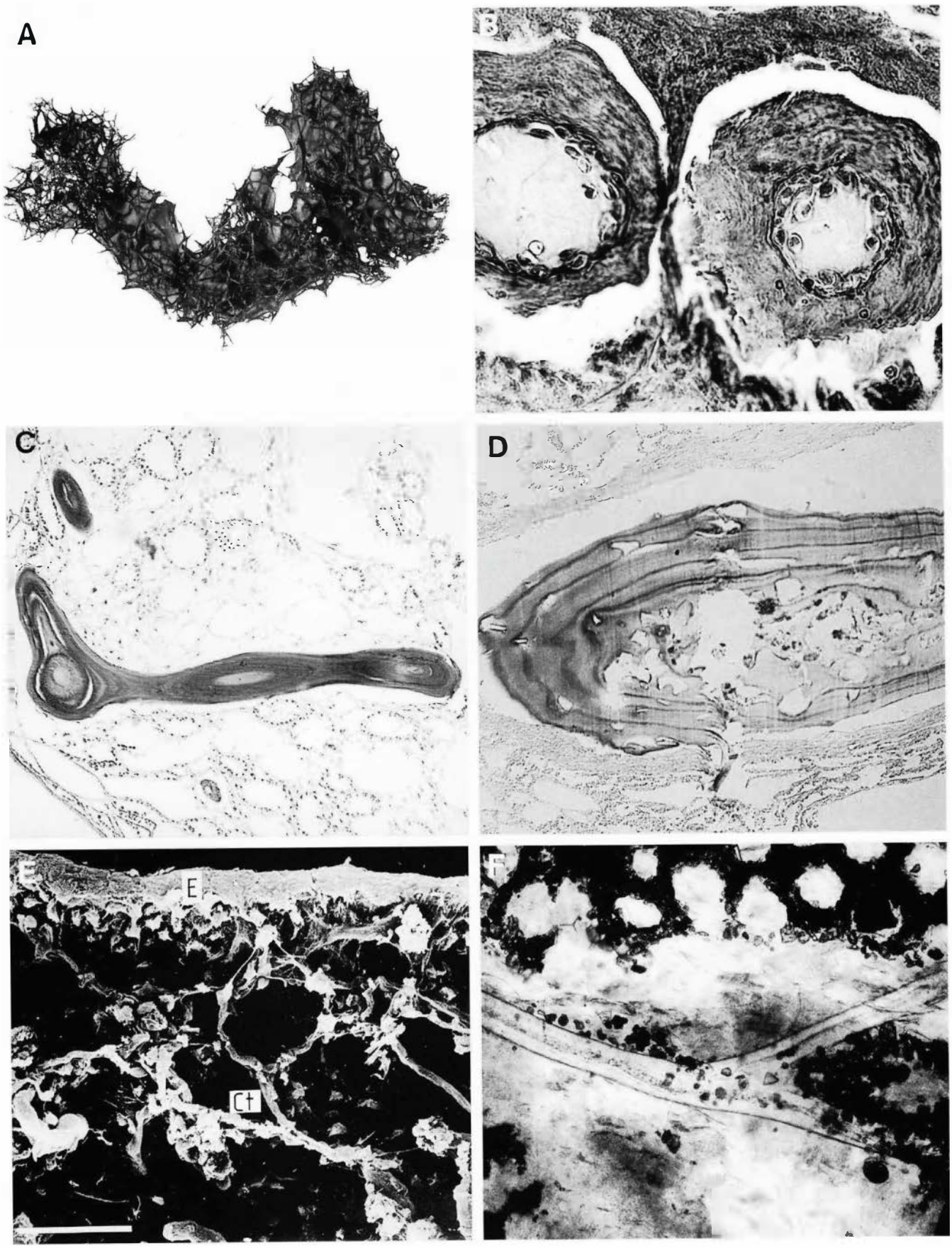


PLATE 2

A. ***Darwinella gardineri*** Topsent: Scanning electron micrograph of the larva (x 400).
B. ***Halisarca dujardini*** Johnston: Transmission electron micrograph of a spherulous cell. Scale bar 1 µm.
C. ***Igernella notabilis*** (Duchassaing & Michelotti): Free fibrous spicules (x 40).
D. ***Darwinella gardineri*** Topsent: Scanning electron micrograph of the choanosomal region; se - spumous cell. Scale bar 10 µm.
E. ***Darwinella gardineri*** Topsent: Scanning electron micrograph to show choanocyte chambers (x 600).
F. ***Darwinella oxeata*** Bergquist: Section of free fibrous spicule to show notched surface (x 400).

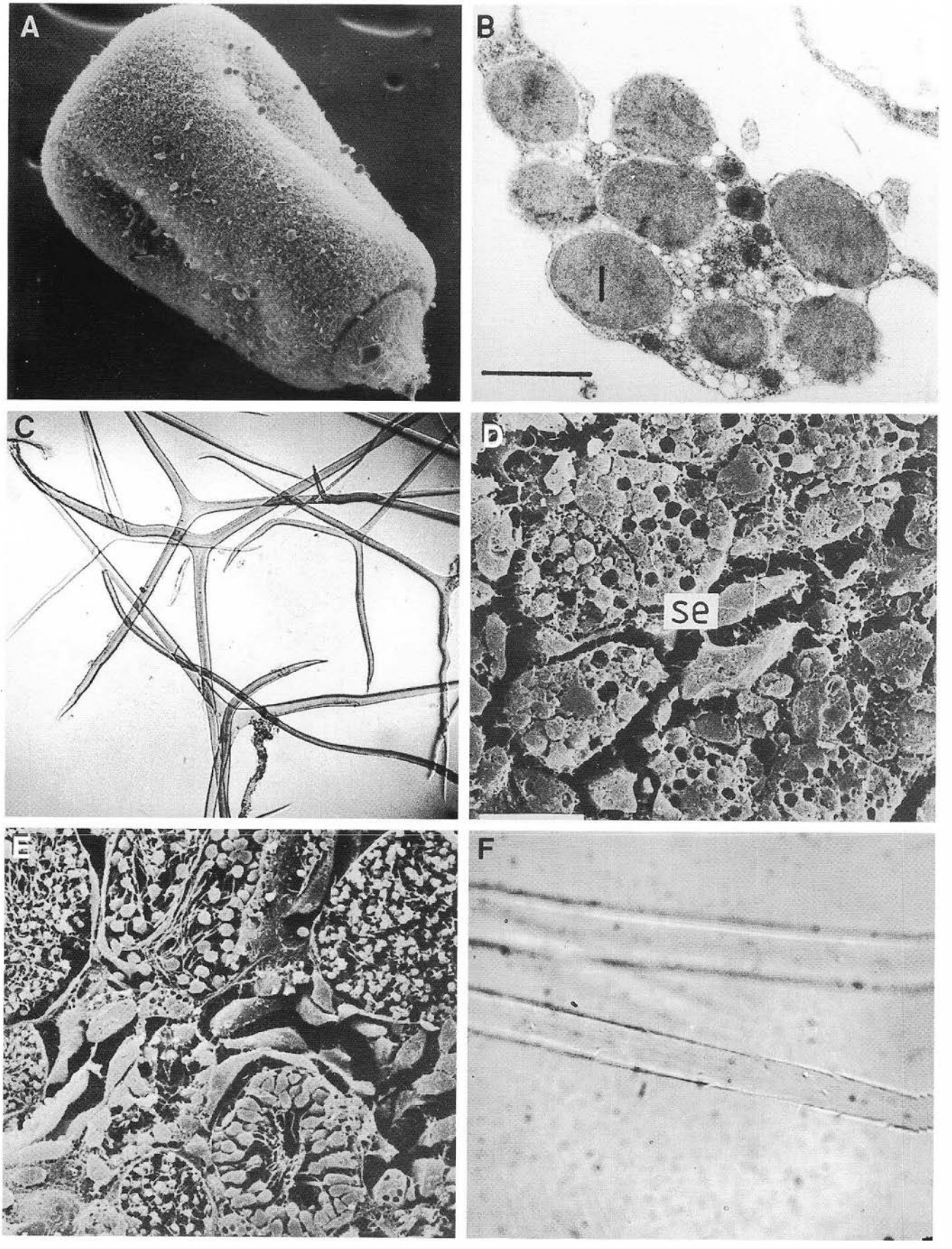


PLATE 3

A. ***Dendrilla rosea*** Lendenfeld: Electron micrograph to illustrate myocyte concentrations between choanosome and ectosome; my - myocyte. Scale bar 100 µm.

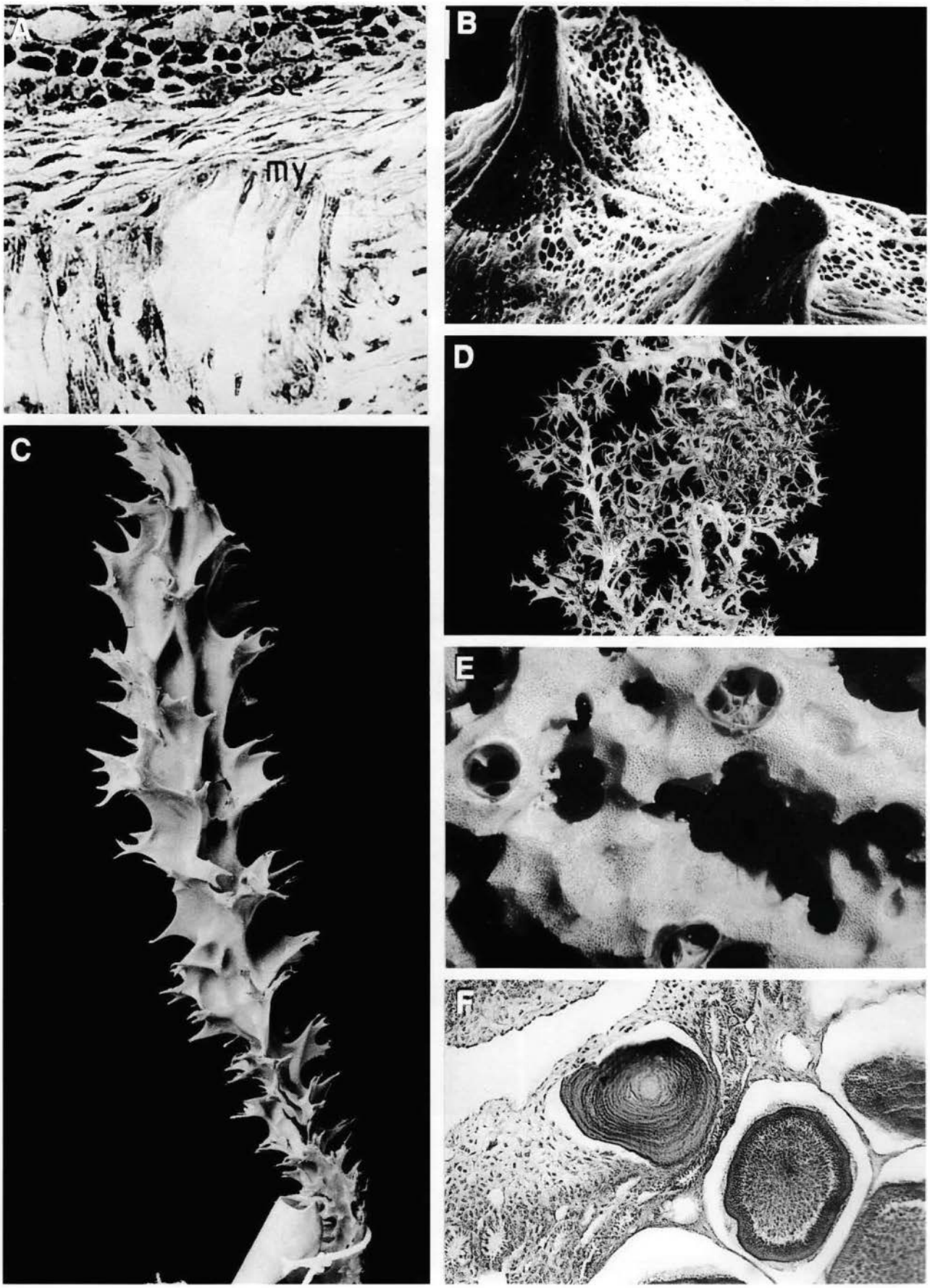
B. ***Dendrilla rosea*** Lendenfeld: Surface aspect to show pore arrangement and surface texture (x 50).

C. ***Dendrilla rosea*** var. ***digitata*** Lendenfeld. South coast of Australia, J.B. Wilson collection, BMNH 1887.7.11.16 (x 1.0).

D. ***Dendrilla rosea*** Lendenfeld: Typical 'terete' specimen (x 0.25).

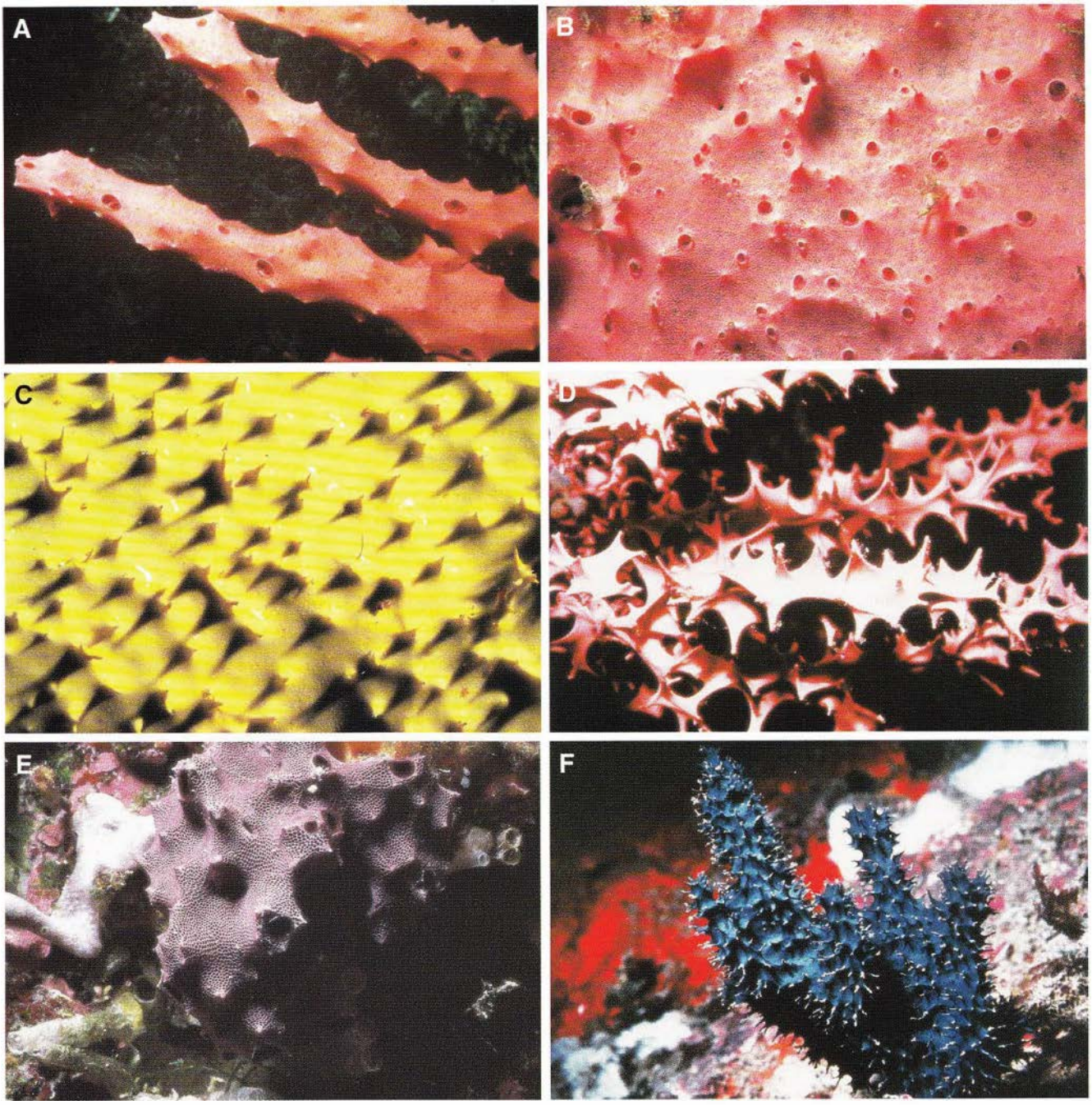
E. ***Chelonaplysilla aurea*** Bergquist: Surface morphology to illustrate the sand-reticulated surface diagnostic of the genus (x 5).

F. ***Darwinella oxeata*** Bergquist: Light micrograph to illustrate choanosomal and fibre structure and parenchymella larvae (x 120).



COLOUR PLATE 4

A. ***Darwinella gardineri*** Topsent.
B. ***Darwinella gardineri*** Topsent.
C. ***Darwinella oxeata*** Bergquist.
D. ***Dendrilla rosea*** Lendenfeld
E. ***Chelonaplysilla violacea*** Lendenfeld
F. ***Dictyodendrilla dendyi*** nom. nov.



COLOUR PLATE 5

A. ***Dictyodendrilla dendyi*** nom. nov.
B. ***Darwinella tango*** (Poiner and Taylor) and an unnamed ***Darwinella*** sp. from southeastern Australia.
C. ***Halisarca laxus*** (Lendenfeld)
D. Cross section of main fibre of ***Dictyodendrilla dendyi*** nom. nov.
E. Cross section of connecting fibre of ***Dictyodendrilla dendyi*** nom. nov.
F. Cross section of fibre ***Suberea (Dendrilla) elegans*** (Lendenfeld).

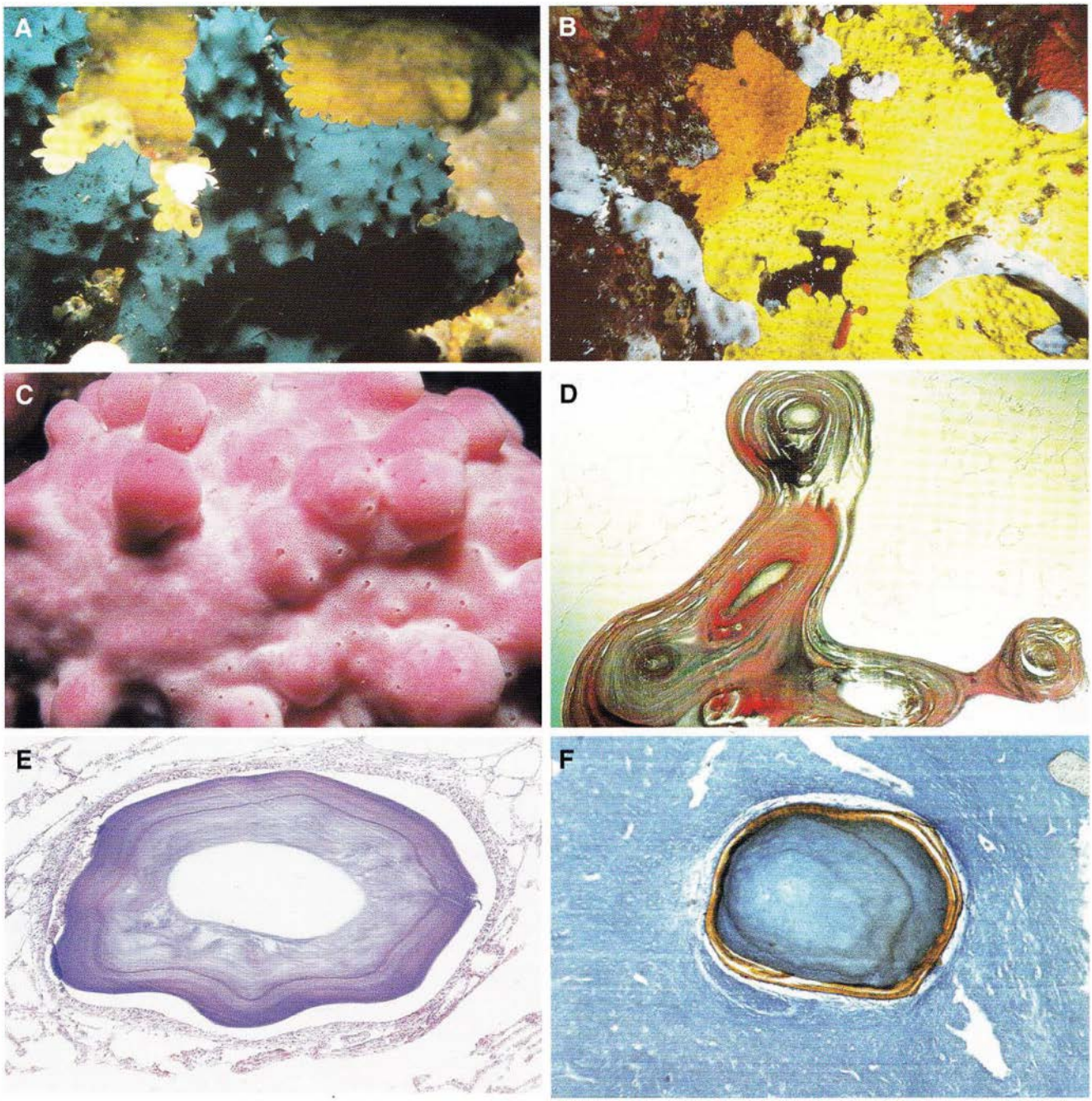


PLATE 6

A. ***Dictyodendrilla dendyi*** nom. nov.: Preserved specimen showing the prominent surface conules (x 1.0).

B. ***Dictyodendrilla tenella*** (Lendenfeld): Preserved specimen showing the frondose lamellate habit. BMNH 86.7.8.2 (x 0.25).

C. ***Halisarca dujardini*** Johnston: Photomicrograph to show organisation of the choanocyte chambers (x 120).

D. ***Spongionella pulchella*** (Sowerby): Preserved specimen showing the frondose habit (x 1.0).

E. ***Spongionella pulchella*** (Sowerby): Photomicrograph showing structure of fibres and choanocyte chambers (x 40).

F. ***Spongionella nigra*** (Dendy): Photomicrograph of the fibre skeleton (x 40).

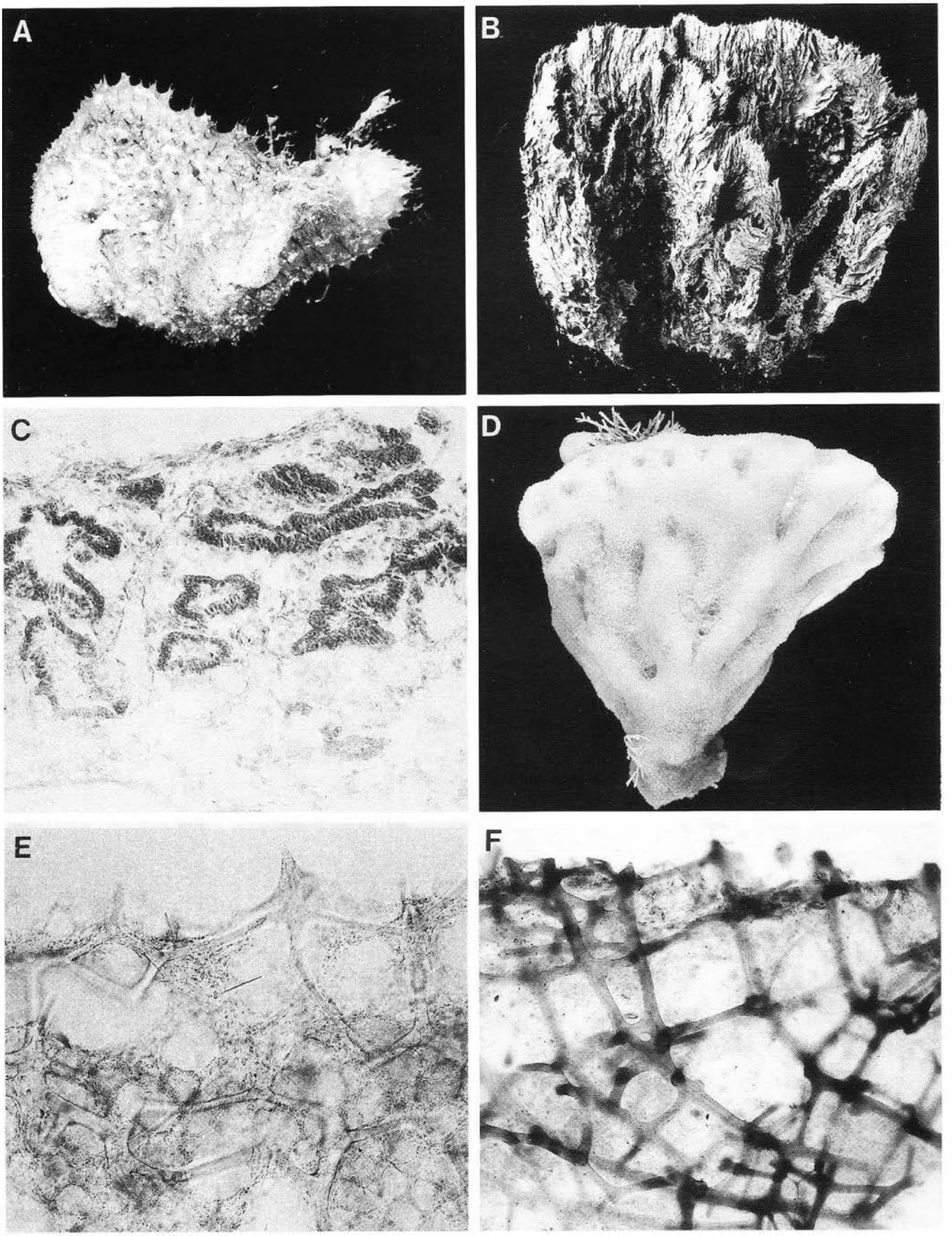


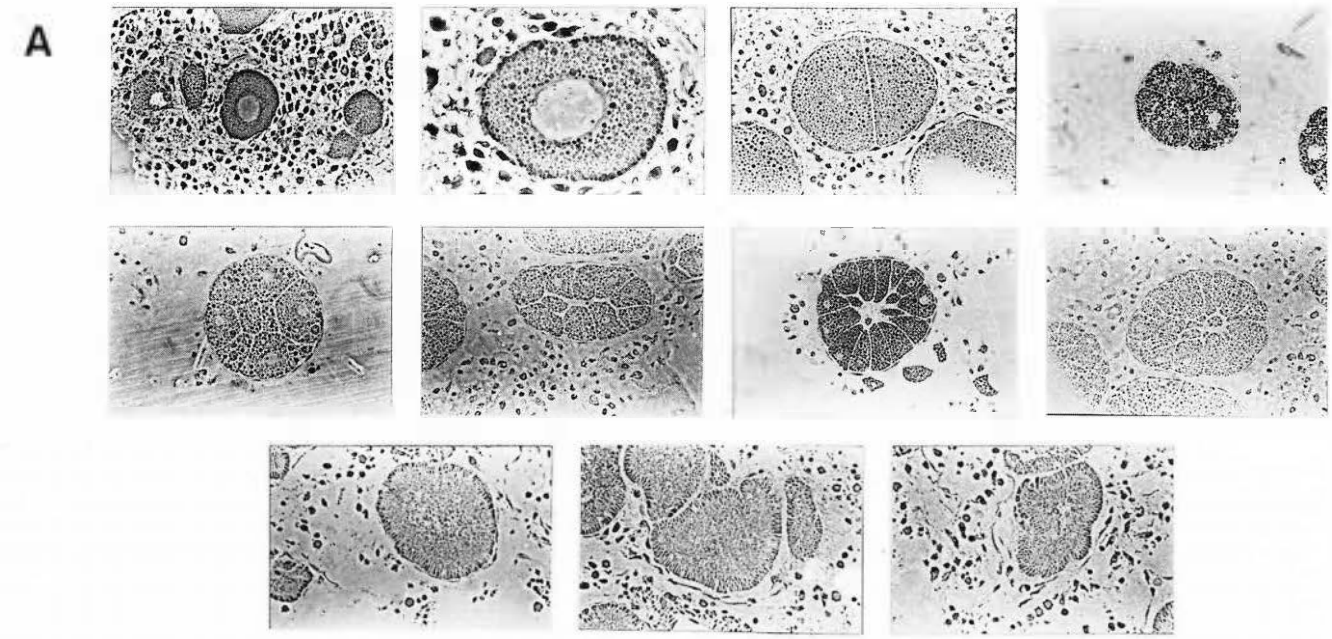
PLATE 7

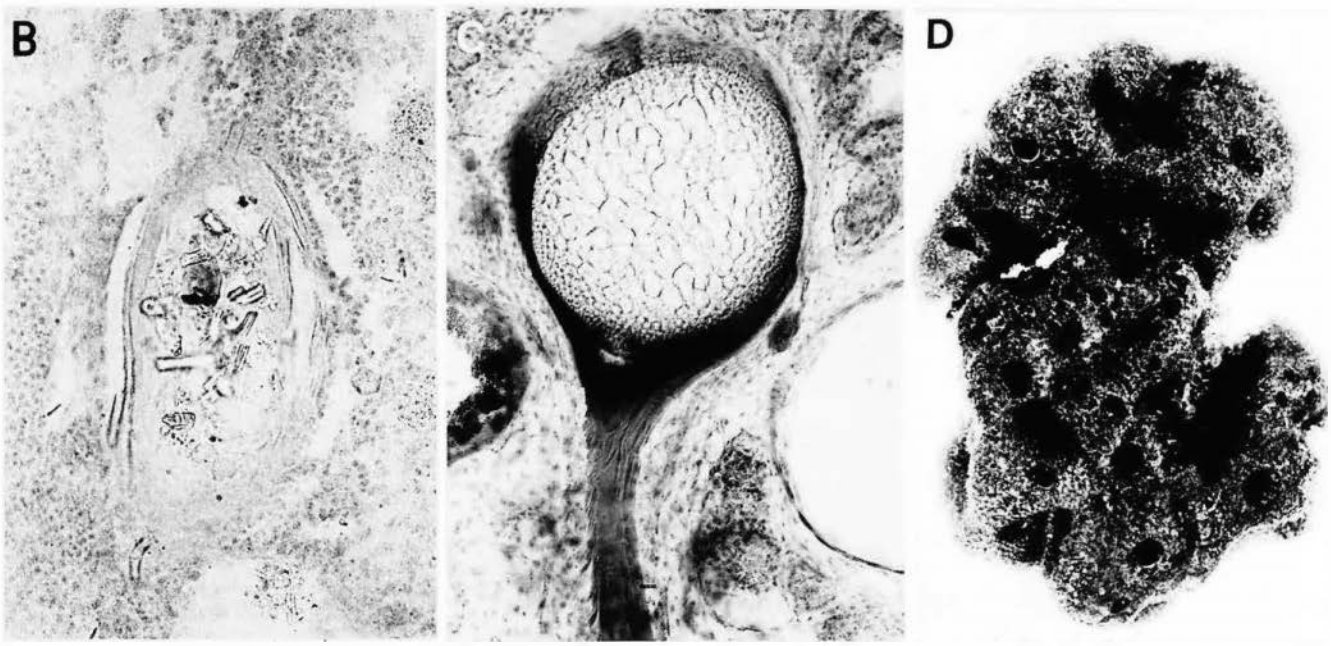
A. ***Halisarca dujardini*** Johnston: Photomicrographs showing stages in the development of the parenchymella larva (x 400).

B. ***Pleraplysilla minchini*** Topsent: Holotype. Transverse section of fibre to show bark, pith, and axial debris (x 120).

C. ***Chelonaplysilla violacea*** (Lendenfeld): Section of fibre to show marked vesicular pith (x 120).

D. ***Igernella notabilis*** (Duchassaing & Michelotti): Preserved specimen (x 0.25).





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