The Marine Fauna of New Zealand:

Porifera: Demospongiae
Part 5. Dendroceratida and Halisarcida

Patricia R. Bergquist

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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, *Davainella oerstedi* and *Dickiodendrella denudata*, 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 Davainellidae, recognizing priority of this family name), Dictyodendrillidae, and Halisarcidae. These familial distinctions rested primarily upon skeletal content and pattern; the Davainellidae have dendritic fibre skeletons, the Dictyodendrillidae have anastomosing fibre skeletons and the Halisarcidae have a fibril-lamellar collagenous skeleton only, fibre not being developed.

The new element in the 1980 arrangement was that the dendritic nature of the fibre skeleton was emphasised 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 renaming the Halisarcidae from the Dendroceratida, although that move was not formally made as further information was needed.

The moneneric family Halisarcidae (genus *Halisarca*) was included within the Dendroceratida by De Laubenfels (1936, 1948) and Levi (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 Oscura, Bajtailus, Hesidella, 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. *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 mongeneric 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 spermatoogenesis in *Aplysilla rosea* (Tuzet et al. 1970), an ultrastructural description of a new type of secretory cell, the ‘cellules spumeuses’ (spumous cell hereafter) in *Periphrasysa spinifera* (Donadey & Vacelet 1977), a scanning electron micrographic study of larval structure in *Davainella oerstedi* (Bergquist et al. 1979), a number of light-microscope and ecological studies of the reproductive biology of *Halisarca* species (Levi 1956; Bergquist & Sinclair 1973; Chen 1976), reports of the occurrence of terpenoid metabolites in *Periphrasysa spinifera* (Cimino et al. 1972, 1974, 1978) and *Davainella oerstedi* (Kazlauskas et al. 1979), and description of the steril profile of *Davainella rosea* (Bergquist et al. 1980).

* As reported by Aplysilla rosea

These contributions provided an indication that an analysis and a superfamily ultrastructure, which had proved useful in classification of other orders, would also assist in clarifying relationships within the Demospongiae. In the intervening period, investigations on the chemistry of such 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 phylogenetic basis.

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

CHARACTERS

ORDINAL FAMILY

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 sponges classified has stressed skeletal structure as an arrangement and the mineral skeleton of most Demospongiae has a diversity and structure that invites 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, anastomosing or dendritic without carefully reporting their structure.

Second, the need to describe carefully adult larval soft-tissue organisation and histology in addition to skeletal attributes has only lately been rediscovered. Although workers such as Sollas (1887), Lendenfeld (1889), Schultz (1877), and Toppen (1979) recognised the importance of soft-tissue organisational in classification, most twentieth-century taxonomists dealing with Demospongiae (with the exception of Levi (1956), Simpson (1968), Pompini (1976), Bergquist (1973, 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 central ‘pith’; this describes most verongiid fibres.
These contributions provided an indication that characters and seta 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 Darwiniellidae 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 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, pitted or homogeneous, and anatomosing or dendritic without carefully reporting on their structure.

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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 verongid 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 spongia plate. The latter type is by far the commonest in the Dendroceratida and is diagnostic of the family Darwiniellidae.

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 tanged. 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 spongine-fibre ‘back’ invests a diffuse spongine ‘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. Dictyodendrid 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. Dendroceratidae have large, oval, wide-mouthed choanocyte chambers (euryzyous) and these occupy a high percentage of the mesohyl volume leaving relatively little inter-chamber 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 in important in generic descriptions. The elegant developmental study by Terengawa (1906) on *Dysidea etheria* supports this view. In Dendroceratida, sand is used as a surface network and cortical armour (*Chiloscyphus*), and can be incorporated into fibres (Pl. 1f) (*Pierogyphisa*, *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 pigmentation. In other groups this is not so, most notably 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 its 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 uniform throughout the soft tissue. Contrasting pigmented fibres do occur most notably in Dictyo-dendrillidae.

Colour change after exposure to air, or followed preservation, can characterise particular species and 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 spherul cells, varies and particular types characterise different families (Bergquist 1980, fig. 3c). The Dysideidae are distinctive in having no such cells thus far recorded.

Very large secretory cells termed spumous cells (Donadey & Yacelet 1977, Pl. V, fig. 2) are found in Dendroceratida belonging to the Darwinellidae; they are absent in the few Dictyodendrillidae that have been examined. Other secretory cell types are unknown.

**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 New Caledonia, Brazil, Columbia, California, and the Mediterranean by Bergquist, and by specimens sent from other sponge workers (Dr J. Vacelet, Dr G. Pullitizer-Finali, Dr Faulkner, Dr R. Anderson). As a result of this wide-ranging collection, representatives of genera
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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 Dendrillidae 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 Halisaridae have a range of secretory-cell types,
of which sphericalus cells like those in some
Tetractinomorpha (Pl. 2a) and fuscinophil 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. 5, g). In both types of parenchymellae, anterior
and/or posterior polar arms can be free of cilia.

Secondary-metabolite Chemistry
Dendroceratid sponges have as their dominant sec-
ondary metabolites diterpenoids of diverse structure,
but all are based upon a spongamer skeleton (Fig. 1).
Generic and familial patterns of occurrence of
biosynthetically distinct structural types are recog-
nisable. 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 quan-
tity 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 Auck-
land over the period 1958–1994. New Zealand material
has been supplemented by collections made in Ha-
way, 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 avail-
able 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 speci-
mens recorded are given with each taxonomic
description, and localities are indexed on Figures 2
and 3.
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 Löve

Order DENDROCRATIDA Minchin
Family DARWINELLIDAE Merejewsky
Darwinella Müller
Darwinella gardinieri Topsent
Darwinella ovata Bergquist
Chelonaplysilla de Laubenfels
Chelonaplysilla violacea Lendenfeld
Dendrilla Lendenfeld
Dendrilla rosea Lendenfeld

Family DICTYODENDRILLIDAE Bergquist
Dicyodendrilla Bergquist
Dicyodendrilla denysi nom. nov.

Order HALISARCIDA new order
Family HALISARCIDAE Vosmaer
Halisarca Johnston
Halisarca dikjardini Johnston

Fig. 1. Structure of sponge derived diterpenoids characteristic of Dendrocratida. a) aplysphurin, b) aplyssol-1, c) dendrillolide-B, d) sponge related compound from Chelonaplysilla violacea.

Fig. 2. Map of the New Zealand region showing sites.
1. Spirits Bay
2. North Cape & Kerr Point
3. Cape Brett
4. Poor Knights Islands
5. Hen Island & Whatapuuke Island
6. Whangarei Heads
7. Kent
8. Mayo
9. East Cape
10. Island
11. Makai
12. Mana
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 & Whatapoke 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
INTRODUCTION

Descriptions are given for five species of Dendrocereida and one species of the order Halisarca. Previous references relevant to New Zealand species of Dendrocereida are Lendenfeld (1883, 1886, 1889), Topsent (1905), Bergquist (1916, 1980), Pruvot (1915), Bergquist et al. (1979), Bergquist et al. (1986) and Wiidemanmayer (1989). The type species of Halisarca, *H. dauberti*, is cosmopolitan and has been the subject of many literature reviews, with very few however from the Southern Hemisphere; where only Burton (1902) has recorded the species. Bergquist and Sinclair (1973) recorded the occurrence of the genus *Halisarca* from New Zealand but have not identified the species, and Bergquist et al. (1986) described the structure of this *Halisarca* larva. An excellent, detailed study of *H. dauberti* using microscopy was published by Leví (1956).

Order DENDROCATIDA Mincin, 1906

Ceratocrinomorpha in which the fibre skeleton is present, except in one genus, is dominated by soft elements. The fibre skeleton arises from a centripetal spreading basal plate and is either densible (Darwinellidae) or anastomosing (Dictyodendrillidae). Free fibrous 'speciees' may occur in addition to the main skeleton. Fibres are always pitted and strongly laminated, usually quite stout, tapering towards the surface. At the boundary between pith and body, fibres can incorporate some free cellular elements, some of which may be microalgae, and in some cases sand and debris is incorporated into the pith. 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 eurypylla, oval and wide-mouthed and matrix volume is in relation to canal and chamber volume. The choanosal matrix is lightly reinforced with collagen; the ectosomal region contains simply strong fibres, collagen deposits and a cortical region with reinforcement elements can be present. The large canals of the choanocyte chamber space in conjunction with many sparse fibre skeleton dictates that Dendrocereidae have soft, fragile sponges.

Reproduction is viviparous; all species are parthenogenetic with relatively large size.
INTRODUCTION

Descriptions are given for five species of Dendroceratida and one species of the order Haliarcaida. Previous references relevant to New Zealand species of Dendroceratida are Lendenfeld (1883, 1886, 1888, 1899), Topsent (1905), Bergquist (1961, 1980), Ponzato (1975), Bergquist et al. (1979), Bergquist et al. (1990), Karaso et al. (1986) and Wiedenmayer (1989). The single species of Haliarca, H. dijardini, is cosmopolitan and has been the subject of many literature references, very few however from the Southern Hemisphere, where only Burton (1952) has recorded the species. Bergquist and Sinclair (1975) recorded the occurrence of the genus Haliarca from New Zealand but did not identify the species, and Bergquist et al. (1979) described the structure of this Haliarca larva. An excellent, detailed study of H. dijardini 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 choanoocyte chambers are eurypyleous, large, oval and wide-mouthed and matrix volume is low in relation to canal and chamber volume. The choano- somal 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 choanoocyte 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 spongius diterpenes as opposed to sesqui- and sesquiterpenes 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 sponge 'spicules' (Pl. 2c). Darwinellid sponges are mostly typically encrusting, but where they are erect or frondose their fibrous skeleton, like that of the encrusting forms, always arises from a flat, basal sponge 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

Darwinella Schultze, 1865

Darwinellidae in which the slightly ramified, dendritic fibre skeleton is supplemented by diactinal, trisactinal, or polycyclic 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 clathroid, lobate-digitate forms occur commonly in subtidal locations.

Type Species: Darwinella mulleri Schultze, 1865, by monotypy.

Darwinella gardneri Topsent, 1905

(Fl. 2a,d,e; Pl. 4a)

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, Cornwalls intertidal, Anawhata intertidal, Kennedy Bay 2 m, Mayor Island 2 m, Island Bay 2 m, Kaitoura 4 m, Portobello intertidal, Dusty Sound 15 m, Stewart Island 5 m.

Habitat: Darwinella gardneri 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 m². Basal mat produced into stout irregular upright lobes which may fuse to give a clathrate 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 cm², rimmed by a transparent membranous collar and slightly elevated above the surface. Poros aggregated into portal areas grouped around the base of conules giving patches of the surface a fine reticulate 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 spongian plate; the translucent fibres 0.7-3.0 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 eulites of the participating fibres remaining distinct. This type of fibre junction has been noted earlier (Lendenfeld 1889; Tsunemai 1967, Bergquist 1980) and can appear in dry skeletons as a fenestrated sheet over localised areas. Primary skeleton augmented by large, dictyal 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, 40-60 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. 2c). 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. 12).

Remarks: Darwinella gardneri has been frequently reported from New Zealand as Aplysilla rosea (Morton & Miller 1968; Doak 1971; Fricheard 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 gardneri 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 FS2065 & FS2066) but the sponge is described as deep sulphur-yellow, purple-black in ethanol, with fibres of contrasting red colour. It thus approaches Darwinella costasi in tissue pigmentation but differs from that species in having red fibres. It also differs in the structure of the dictyal spicules and in terpene chemistry (Bergquist et al. 1980). Examination of Wiedenmayer's specimens provides further points of distinction between the New Zealand specimen of D. gardneri and the Australian material; specimen FS2065 contains some tritcal spicules, as do the oxeote spicules, which are common, have a central flexure and of a recurved, almost contort tip.

Topset (1965), when describing A. gardneri, states that the sponge retained a rose pigmentation in a pod from which, by comparison with D. simplex from Banyuls with which he was familiar, he deduced a carmine pigmentation in life. There are very few records of Darwinella species which have both rose and pigmentation in life and large oxeote spongin spicules. If one ignores the unsupportable synonyms of Wiedenmayer (1989) and consults the primary literature which is well summarised by Pranzato (1975), the only available name for rose-red Darwinella with large dictyal spicules (1500-2000 x 20 µm) is D. gardneri which has been described reliably only from the Maldives Islands. Levi (1952) reaffirmed a red pigmentation for D. gardneri in the course of reviewing the species of Darwinella; however, in 1988 he described a yellow sponge from the Red Sea as D. gardneri. He has been followed in this action by Pranzato (1975) and Paltrinieri & Pranzato (1980) who applied the name to Mediterranean sponges, a range of colour without including any structural evidence in support of their identifications. The records all have to be regarded at best as dubious and almost certainly erroneous.

This work has provided extensive experience of dendrocrotalid 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 lost all oxidation reactions. This is invariable. Further electron microscopy and chemical analysis on all the New Zealand Dendrocrota has and on some from the Mediterranean, Hawaii, and Australia has been done. It can be stated that colour is not resultant from any endosymbionts of any sort, the soft tissue being markedly clear even of phaeocytes.

The novel diterpene chemistry of dendrocrotalid including Darwinella species was reported by Bergquist et al. (1990). This paper identified a group of Australian species of Darwinella which had dicyte spicules and displayed either bright rose-red, sulphur-yellow or bright orange pigmentation. Only one species, D. costasi, was named in that paper. Table summarises the major characteristics of morphology and chemistry of these species and also of Dendrocrota 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. costasi from D. gardneri.
the Australian material; specimen F52065 contains some triaxial spicules, also the oxocete spicules, which are common, have a central flexure and often recurved, almost coutort tips.

Topent (1965), when describing D. gardineri, stated that the sponge retained a rose pigment 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 oxocete spongic spicules. If one ignores the unsupported synonymies offered by Wiedenmayer (1989) and consults the primary literature which is well summarised by Pronzato (1975), then the only available name for rose-red Darwinella with large diactinal spicules (1500-2000 x 20 μm) is D. gardineri which has been described reliably only from the Maldives Islands. Levi (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 dendrocereid 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 Dendrocereid and on some from the Mediterranean, Hawaii, and Australia has been done. It can be stated that colour is not resultant from endosymbions of any sort, the soft tissue being remarkably clear even of Eubacteria.

The novel diterpene chemistry of dendrocereids 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. cauta, 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. cauta from New Zealand and the unnamed species from south-eastern Australia (Pl. 5b). The letter 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 specimems 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 a new 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 Pointe and Taylor (1990) who applied the name Aphyllos tenuis. The species still requires full description but a reference specimen (Z5684) 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 synonymies based upon the narrow descriptive base available in most cases cannot be taken seriously.

Other Records: Maldives Islands.

Darwinella cauta Bergquist, 1961

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

Darwinella cauta Bergquist, 1961: 216-219, fig. 6a-c.


Darwinella cauta: Bergquist et al. 1990: 73.


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, Comwallis 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, common on steep-sloping reefs and canyon walls around 15 m depth, on southern shores it is common in the subtidal fringe. The original
<table>
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<tr>
<th>Species</th>
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<th>Soft-tissue Pigmentation</th>
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<tr>
<td><em>Darwinella oxysta</em></td>
<td>New Zealand</td>
<td>Sulphur yellow translucent</td>
<td>Pale gold</td>
<td>Diactinal with spined surface 1500-2000 μm</td>
<td>Aplysulphin® tetra hydro derivatives</td>
</tr>
<tr>
<td><em>Darwinella sp.</em> (described as <em>D. gardneri</em> by Wiedenmayer (1989))</td>
<td>Australia (SW)</td>
<td>Sulphur yellow</td>
<td>Red dark</td>
<td>Diactinal smooth, some triactinal present 1500-2000 μm</td>
<td>Aplysulphin only</td>
</tr>
<tr>
<td><em>Darwinella gardneri</em></td>
<td>New Zealand</td>
<td>Rose red</td>
<td>Translucent pale gold</td>
<td>Diactinal smooth 1500-2000 μm</td>
<td>Tetrahydro-aplysulphin*</td>
</tr>
<tr>
<td><em>Darwinella sp.</em></td>
<td>Australia</td>
<td>Brilliant orange</td>
<td>Translucent pale gold</td>
<td>Diactinal smooth 1500-2000 μm</td>
<td>Gracilin A* + 4 related compounds</td>
</tr>
<tr>
<td><em>Dendrilla rosea</em></td>
<td>New Zealand</td>
<td>Rose red</td>
<td>Translucent pale gold</td>
<td>Not present</td>
<td>Aplyroside a mixture of 10</td>
</tr>
<tr>
<td><em>Dendrilla sp.</em></td>
<td>Australia</td>
<td>Rose red</td>
<td>Translucent pale gold</td>
<td>Not present</td>
<td>Aplyroside-1® ambiofuran® plus alyroside 2-6</td>
</tr>
</tbody>
</table>

* 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 cm². 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 (YR 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 multibucculae separated by areas of smooth surface. Oscules sporadically distributed; 0.5-1.0 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 spongine 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 spongion ‘spicules’ 1.5-2.0 mm x 25 μm with a regularly notched surface, scattered throughout the tissue (Pl.2b). No zonation of ‘spicules’ in the tissue nor any specimen has 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 choanosomal by subdermal spaces. Spumous cells present throughout but are concentrated toward the choanosomal boundary.

**Remarks:** The presence of spongion ‘spicules’ notched surfaces separates *D. oxysta* from all *Darwinella* species. It falls into a group of predominantly southern hemisphere species which either do not have diactinal ‘spicules’ of relatively large size between 1500 and 2200 μm in length. Other members of this closely related group of species are *D. gardenii* Topsey and the yellow sponge from Australia referred to as *D. gardenii* 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**

**Dendrillidae** in which the fibre skeleton branches repeatedly but never anastomoses. Lateral ramifications are short, axial fibres are stout and flex. The sponges can attain large size always with a branching and/or complex lamellate bodies are from one or more small basal spongion plates. F present. C contain no foreign material.

**Type Species:** *Dendrilla rosea* Lendenfeld, 1883, by subsequent designation Topsey (1905).

**Dendrilla rosea** Lendenfeld, 1883

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

**Dendrilla rosea** Lendenfeld, 1883: 271-294, pl. 10, 3, 4, pl. 12, figs 16, 19-23, pl. 13, figs 24-27, 28. 29.

**Dendrilla rosea** Lendenfeld 1889: 716-719, pl. 44, figs 7, 8, 11, pl. 45, figs 3, 4, 7, 8, 9.

**Dendrilla rosea** Bergquist 1980: 486.

**Dendrilla rosea**: Bergquist & Skinner 1982: 49, pl. 1, (colour).

**Dendrilla tecta** Selenka, sensu Wiedenmayer 1989, fig. 98.

Dendrilla Lendenfeld, 1883

Dendrilla rosea Lendenfeld, 1883; (Pl. 3a, b, c, d, Pl. 4d)

Dendrilla rosea Lendenfeld 1889: 716–719, pl. 44, figs 4, 7, 8, 11, pl. 45, figs 3, 4, 7, 8, 9.
Dendrilla rosea: Bergquist & Skinner 1962: 49, pl. 1, fig. 3 (colour).
Dendrilla cactos Selenka, sensu Wiedenmayer 1989: 152, fig. 98.
Endopinacocytes often flagellated, bordering apoplytes, in which location they are termed apoplyal 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, dactylous growth form of *Dunedinella 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, chromosome organisation, and terpene chemistry (Table 1) are found between the genera *Dunedinella* 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 (1889) for his southern Australian material. Both significant revisors (Vasek 1959) and Bergquist (1980) regarded *Spongilla 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 *Spongilla cactos* from Bass Strait was listed in synonymy, 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 unrecognizable, 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. 1980) 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 ramosum' 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 Ari 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 *Dictyodendrilla*.

Reference should be made to *Dendrilla aerophoba* Lendenfeld (1885, 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 Aplysiniidae in which 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 claidid 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 synonymy 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 (1935) is a good species of the new genus *Dictyodendrilla* which it should take the first available appropriate species name which is *Dictyodendrilla pallasii* (Katie) this being the oldest verifiable reference to the species as indicated by Burton (1954).

Bergquist (1961) recorded *Dendrilla cactus* from the Chatham Islands. This identification was wrong and was based on a very worn specimen of the sponge belongs to a new genus within the Dictyodendrilla, 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 (Aust). *Chelonaplysilla de Laubenfels*. 1948

Bartholinidae with a distinct, separable cortex formed by a regular reticulation of sand grains (3:3). The fibres are, like those of *Aplysilla*, simple and single arising from a spongin plate, only rarely branching, concentric laminated, pitted and clear of detritus. Some sponges become lamellate or lamellodidiate from the external base and in these a more branching skeleton is developed.

**Type species**: *Chelonaplysilla noetius* (Carter, 1883).

**Chelonaplysilla violacea** (Lendenfeld) (Pl. 3e, 4c)

Aplysilla *violacea* Lendenfeld, 1883: 237, pl. 10, fig. 7, pl. 11.


Aplysilla *violacea*: Lendenfeld 1889: 704, pl. 46, fig. 15.

*Chelonaplysilla violacea* de Laubenfels 1948: 165.


*Chelonaplysilla violacea* Bergquist 1971: 100, 163.

*Chelonaplysilla violacea* Bergquist et al. 1980: 163.


**Material examined**: North Cape 0.5 m, Cape Brett 10-15 m, Poor Knights Islands 8-12 m, Whatapuke Island 10 m, Sir James Bay Whangarei Heads 0.5 m, Leigh 5-15 m, M, 0.5 m, Kaikoura Peninsula 5-12 m, Portobello 0.5 m.

**Description**: Common around New Zealand shores, being most frequent below 5 m where crusts boulders and rock faces. Particularly co...

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name should lapse within Dendrilla. Bergquist (1980) indicated that D. membranaeus 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 pallasii (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 Dictyodendrilla 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).

**Chelona*plysilla de Laubenfels, 1948**

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

**Type Species:** *Chelona*plysilla norvegica (Carter, 1876) by original designation de Laubenfels (1948).

**Chelona*plysilla violacea** (Lendenfeld) (Pl. 3e, 4g, 7c)

*Aplysilla violacea* Lendenfeld, 1883, 237, pl. 10, figs 5, 7, pl. 11.


*Aplysilla violacea* Lendenfeld 1889: 704, pl. 46, figs 13, 15.

**Chelona*plysilla violacea** de Laubenfels 1948: 165.

**Chelona*plysilla violacea** Bergquist et al. 1967: 162.

**Chelona*plysilla violacea** Bergquist 1971: 100, 163–164.

**Chelona*plysilla violacea** Bergquist et al. 1990: 74.

**Chelona*plysilla violacea** Bergquist et al. 1991: 21.

**Material Examined:**

North Cape 0.5 m, Cape Brett 10–15 m, Poor Knights Islands 8–12 m, Wataupuke 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 when 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 mm2; extending to sheets covering 0.5 m2; 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. Corules 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. Pore fields obvious microscopically between sandy deposits.

**Skeleton:** Dendritic, composed of smooth erect fibres which rise from a basal spongite plate. Fibres are concentrically laminated, 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 euryzyous choanocytes 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:** *Chelona*plysilla violacea was well described and figured by Lendenfeld (1983, 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 *Chelonophyllis* is instantly recognisable in the field by the presence of the regular dermal sand reticulation, a novel feature in the *Darwinieidae*. 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 spongin-determinate which it contains.

There are at least two other species of *Chelonophyllis* which remain to be described. One from Hawai‘i 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 *Dendrilla*. Both voucher samples have been checked and both belong to *Chelonophyllis*. The dried and damaged specimens permit no further identification.

**Other Records**: Australia, Fiji, Hawaii, Solomon Is.

**Discussion of the Family *Darwinieidae***: A comment is required regarding the preference given to the familial name *Darwinieidae* Merejkowsky (1879), over *Aplysidae* Lendenfeld (1883). This has been discussed by Lendenfeld (1889), Minchin (1900), Topset (1905), de Laubenterds (1948), and Vaecelet (1959) and most later authors followed the argument of de Laubenterds and used *Aplysidae*. Van Soest (1977) and Wiedenmayer (1989), without any supporting discussion, adopted *Darwinieidae*. Hooper and Wiedenmayer (1994) provided the argument in support of the priority of *Darwinieidae* and consequently the name should be adopted. *Aplysidae*, 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 emphasizes the thin spreading habit. The histology of *Aplysida* species remains to be documented fully, but examination of verified stained paraffin sections of *Aplysida glacialis* from Bermuda and *Aplysida polygraphis* from California confirms the presence of spumous cells in both. In terpennoid chemistry (Bobzin & Faulkner 1991) *Aplysida* contains diterpenes closely allied to those described from *Chelonophyllis* (Bergquist et al. 1990) and *Dicytoderinella* (Kornam et al. 1990). Evans and Bergquist (1977) in their study of sponge acid mucopolysaccharides included *Darwinieella gardineri*, *D. cusana* (as *Aplysida rosea*) and *A. sulphurna* respectively, and *Chelonophyllis violacea* (as *Aplysilla violacea*) in their sample. *Chelonophyllis* displayed no alcianophilia in the free mesohyl cells while this was evident strongly in both species of *Darwinieella*. 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 Vaecelet (1977). These results are consistent with those of our electron-microscope study and confirm the absence of spumous cells in *Chelonophyllis violacea*. Relationships of the aplysillids genera with others in the order are addressed in discussion.

**Family DICYTODERINIDAE**, Bergquist, 1980

*Dendroceratida* in which the skeleton is reticulate, with rectangular mesh made up of concentrically laminated and strongly pitted fibre. Pigment is partially obscured by the incorporation of detritus. Fibre skeleton can be augmented by the addition of free spongin 'spicules'. The large oval chaocyonite chambers are euryphalous. 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.

**Dicytoderinella** Bergquist, 1980

Dicytoderinellidae in which the reticulate fibrous skeleton is regularly rectangular and composed of pitted, 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, stellate or spreading with digitate projections.


**Dicytoderinella densyi** nov. nom. (Pl. 1a,c, 4f, 5a,d,e, 6a)

Megolopostes elegans Dendy, 1924: 382.

**Dicytoderinella cavernosa** Bergquist, 1980: 488 pars (reference to *M. elegans* Dendy only).

**Dicytoderinella cavernosa**: Kornam et al. 1990: 724.


**Dicytoderinella elegans**: Bergquist et al. 1995: 36.

**Holotype**: BMNH 29.10.1.163.

**Material Examined**: Spirits Bay 22 m, Poor Knights Islands 8–12 m, Leigh Island, Waiheke Channel East Cape 15–20 m, Mana Island 8–15 m.

**Description**: Relatively uncommon, subtidal, for large boulders, cave walls or on stable shells, bottoms between 8 and 25 m depth around New Zealand. Mostly commonly stalked, digitate, or lobate can take the form of a spreading mat with digitate projections. Colour grey-blue to blue in life (B-F); navy-blue to blue-grey (B3/2) in ethanol; fibres: Consistency delicate, soft, but not slimy.

**Surface**: Strongly concave; canules up to 1.0 mm 2–3 mm apart, and aligned to form short surface pores evenly dispersed, giving a delicate reticulate appearance to the smooth surface. Oscules flush the surface, 3–5 mm in diameter, and irregularly distributed.

**Skeleton**: A regular rectangular reticulum with a distinction between ascending (primary) and coring (secondary) elements. Fibres up to 250 mm in diameter, concentrically laminated, pitted with coring material (Pl. 5d,e).

**Soft-tissue Structure and Histology**: Ectosome a thin layer 90–120 μm thick (120 μm image) marked only by light collagen reinforcement particular cellular aggregations or arrangements in the ectosomal region which simply grades into choanoosome. Choanoosome cavernous with large occupying most of the volume. Discrete groups of euryphalous choanoocyte chambers 60–140 μm in largest dimension surrounded by a lightly collagenous matrix in which mobile cellular elements are present in moderate numbers (Pl. 1c). Archaeocyath collars dispersed throughout the choanoes no specialised secretory cells present.

**Reproduction**: Spermatogenesis observed in specimens collected from Leigh during October–November. As reported by Tuzet et al. (1994) *Aplysilla rosea* takes place by transformation of choanoocytes to form spermaticids. The process starts within a chamber but not throughout spherical eggs present in July in specimens taken from 2–7 m. Egg production not observed in New Zealand specimens but figured by Dendy (1924) in southern Australian species very similar to *D. elegans*. Typical parenchymellae produced.
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 exopylous 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 collocytes dispersed throughout the choanosome, but no specialised secretory cells present.

Reproduction: Spermatogenesis observed in specimens collected from Leigh during October and November. As reported by Tuzet et al. (1970) for Aplysina rosea, this takes place by transformation of choanocytes to form spermatooids. The process synchronous within a chamber but not throughout the sponge; many different stages occurring 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) from the southern Australian species very similar to Dendy, typical parenchymellae produced.

Remarks: Dictyodendrilla dundayi was first described from northern New Zealand as Megalopastus elegans by Dendy (1924) who also refers to its occurrence in southeastern Australia (Dendy 1905, 1924). Dendy never described his Australian specimens, simply equating them with Dictyodendrilla elegans Lendenfeld which he transferred to his new genus Megalopastus (Dendy 1905). This genus was established to receive Dictyodendrilla-like species which had reticulate rather than dendritic skeletons. Dictyodendrilla elegans Lendenfeld is, however, quite a different sponge and was correctly referred by Bergquist (1980) to the Verongiida. Dendy used Lendenfeld's species elegans as the reference for his Australian, and subsequently New Zealand, material assigned to Megalopastus. Megalopastus, with type species M. nigra, is a Spongionella, but the Australian species which Dendy and Lendenfeld were discussing fall into Dictyodendrilla. Consequently the species name elegans is preoccupied in Dictyodendrilla and the new name 'dundayi' is applied. Dictyodendrilla elegans was placed by Bergquist (1980) in Aplysina; however, recent restudy of the type material (BMNH 867.8.1) allows it to be placed in the recently described genus Suhrenia (Bergquist 1995). In discussion of the genus Spongionella, Bergquist (1980: 482) referred to Dictyodendrilla elegans Lendenfeld as aplysillid. That is incorrect, the reference should have been to Aplysina as was stated on p. 488 in discussion of Dendrylla.

In the list of described species assignable to Dictyodendrilla Bergquist (1983), Dictyodendrilla tenella Lendenfeld should also have been included.

Bergquist (1980) also suggested that Megalopastus, as evidenced by the structure of the type species (M. nigra Dendy), was not a dendrocereid sponge but rather a member of the family Dysideidae (Dictyo- coratida) 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 Dendrylla but having reticulate skeletons. The type species of Dictyodendrilla was designated as Dictyodendrilla cavernosa Lendenfeld to which Dendy's specimens, Megalopastus 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 dundayi 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. densyi* from New Zealand. *Aplysina massa* Carter from Westernport Bay, Victoria was noted by Yateel (1958) to have a reticulate skeleton of the *Megalaspis* type. Study of one specimen labelled by Carter, BMNH 87.7.11.18, confirms that it is a *Dicryophyrella*; 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 1888 : 254) reveals that the sponge he described as *A. massai* 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. massai*. It is a further species of *Dicryophyrella*, with amber fibres and very flabby texture. The type species of *Dicryophyrella* is *Dendrilla cavernosa* Lendenfeld from Port Jackson (BMNH 86.7.8.5.e). 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 *Dicryophyrella* reticulation, the sponge is large and lamellate, 25 x 25 cm high and wide. It is grey with contrasting black fibres. This spectacular sponge needs to be redescribed from living material but it certainly is a third good species of *Dicryophyrella* from southern Australia. Additional specimens are in the Australian Museum, register numbers G2551, G8910 (holotype), and Z342, a dry skeleton. An excellent specimen is also in the Macquarie Museum Sydney University, S-40hp.

The Port Phillip and Port Jackson localities from which *Dicryophyrella* 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 *Dicryophyrella* 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 *Dicryophyrella* but the New Zealand sponge *Dicryophyrella densyi* contains a range of spongian diterpenes and diterpenic aldehydes (Keman et al. 1990) closely related to those known to occur in *Aplysilla glacialis* (Bobzin & Faulkner, 1991) and *Chelonophyrella violacea* (Bergquist et al. 1990).

**Other Records:** North Cape, New Zealand, 22-40 m, Terra Nova.

**Order Halisarida new order**

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

**Family HALISARCIDAE** Voigt, 1885

Diagnosis as for the order.

**Halisarca** Johnston, 1842

**Bajulus** Lendenfeld, 1885

**Family Hypsesidae**

**Halysarca dajardini** Johnston, 1842

**(Pl. 2h, 6c, 7a, Fig. 4a,b)**

**Restricted Synonymy:**

*Halysarca dajardini* Johnston, 1842: 192-193, pl. XVI, fig. 8.

*Halysarca dajardini* Lendenfeld 1889: 729-730, pl. 50, fig. 2.4.


**Material Examined:**

Devonport Wharf 1 m, Westerme Reef 0.5 m.

**Description:** Encrusting, 0.7-1.5 mm thick, occurring in patches of 3-4 cm² on rocks and mussels (*Perum cinulicus*) 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. *Haltisca dujardini* Johnston.

**Upper:** Diagram taken from a scanning electron micrograph showing the complex ectosomal region with superficial collagen and cellular layer; interfaced collagen fibres 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.
tred contained reproductive products and were yellow-
beige (YR V 8/4) in life and off white (YR 8/2) in
ethanol. Non-reproducing specimens pale yellow-
brown (YR 7/4). Consistency soft and gelatinous,
slightly elastic.

**Surface:** Smooth and slimy with oscules 0.2-0.4 mm
diameter scattered regularly. Pores dispersed. Dur-
ing reproduction a significant reduction in the
aqueous system, and surface features such as oscules
and pores rarely observed.

**Soft-tissue Organization and Histology:**
Ectosomal region 19-24 μm deep, consisting of three
layers — a thin layer of T-shaped exopinacocytes be-
neath 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 or-
ganised network of collagen bundles which provide
the sponge with an organised, contractile ectosomal
region (Fig. 4a, b).

Chaoosome constitutes greatest volume of sponge
fissure. Immediately below the ectosome is a region
divid of choanoocyte 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 choanoocyte chambers 90-115 μm long and
16-22 μm wide (Pl. 6c). Choanosomes 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 choanoocyte collar are cytoplas-
mic 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). Spherules (Pl. 2b) common at the jun-
tion between ectosome and choanosome and along
canals. Fuchsinophil cells scattered through the
mesohyl. Oriented bundles of collagen fibrils concen-
trated 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,
sporogonogenesis having never been observed in
sponges producing eggs and larvae. During the repro-
ductive period a significant breakdown of choanoocyte
chambers with an attendant rise in free mesohyl cells,
while eggs and larvae in various stages of develop-
ment are concentrated toward the base of the sponge
(Pl. 7a). Larvae small, spherical, translucent parenchy-
matulæ 100-200 μm from pole to pole with cilia of uni-
form length but absent at the bare posterior pole.

**Remarks:** The specimen described above are consis-
tent in all reproductive and histological features with
_Halioura dugardini_ from Atlantic coasts (Lévi 1956; Chen
1976). The first record of the genus _Halioura_ from New
Zealand was published by Bergquist and Sinclair (1973)
as part of a study of sponge larval settlement in the
Wairarapa Harbour. They suggested that the species
was probably _dugardini_, and this can now be confirmed,
assisted by Chen's subsequent work (Chen 1976).

The species _name dugardini_ is assigned on the basis of
the light brown colour, intertidal and shallow sub-
tidal 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.
dugardini_ by Chen, and both spherical and fuchsinophil secre-
tory cells are present, as recorded for _H. dugardini_ (Lévi
1956). Larval morphology is identical to that recorded
by Lévi and Chen for _dugardini_ (Bergquist et al. 1979)
and the sponge is dioecious.

There are many quite unrecognisable descriptions of
_Halioura_ species. To quote Lendenfeld (1889) refer-
ing to Carter's descriptions "these species are
described in such a manner that it is impossible to criti-
cise them, they might be anything". Carter (1986) is
not the only culprit and for that reason we have de-
scribed 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 _Halioura_ 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. dugardini_. Vacelet
and Donadey (1987) gave a good description of the
equivalent region in _H. caroula_, which differs from _H.
dugardini_ particularly in having stout collagen bundles
oriented in the plane of the surface and in having fewer
discrete ectosomal zones. _Halioura ecklonis_ (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.
_Halioura mahanthesia_ has a structured ectosomal
described as very similar to that of _H. dugardini_.

Since _Halioura_ 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 repro-
duction. The ectosome of _Halioura_ and the
_Pannaptyphsia_ (Verongida) display almost a
similar organisation and are unusual specialisations with
Porifera.

Lophocytes are recorded as being common
choanosomal of _H. dugardini_. These very distinctive
are not previously been reported to occur in _Halioura_
but their role in deposition of matrix collagen is
well documented for some hadromerid genera as an
example _Chondrilla_ (Pavans de Ceccatty 1957),
(Pavans de Ceccaty & Thiney 1963, 1964), and _Sia-
cones_ (Cornes et al. 1972). They also occur in fresh
sponges (Bergquist 1978). Early literature reports
lophocytes in sponges other than Hadromerida
Haplosclerida require verification.

_Halioura_ lophocytes correspond in structure to those of Hadromerida. No relationship be-
_Halioura_ and genera such as _Chondrilla_, which
lacks a mineral skeleton, is suggested on the basis
of the morphological evidence. However, it is of
interest to note that Vacelet and Donadey (1987)
att irr to possible similarities in secretory func-
tion of spherical cells in the two genera. In _Hali-
ours_ they identified two roles for what are onero
different categories of spherical cells.

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

**Status of Halioura**

Ordinal status for the _Halioura_ is proposed
based on the evidence that it is the only species in
the family _Haliouridae_ and has some features of size, undifferentiated histology of
one size class, and a swimming habit. In addi-
tion Bergquist and Wells (1983) noted that whereas
_Dendroceratida_ investigated chemically for
the identification could be verified contained spon-
dipiones as major secondary metabolites, no
metabolites were present in _Halioura_. Many
_Dendroceratida_ have now been investigated and
the statement remains true (Bergquist et al. 1990).
A detailed study of histology of several spec-
ies...
throughout the varying phases of growth and reproduction. The echinocyte of Halisarca and that of Pseudocystella (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 Chondresia (Pavans de Ceccatty 1957), Tetrapyle (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 Chondresia, 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 attention to possible similarities in secretory behaviour of spherulous cells in the two genera. In H. coerulea 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 ITS1 region of the 18S ribosomal gene consistently places Halisarca close to Chondrella 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 (1986). 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 spongine 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. 1996). 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 Chondrella (Gaino & Fronzato 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 Bajalites Lendenfeld shows some affinity with Halisarca, and Lévi (1958) suggested that establishing two monogenic families, Halisarcidae and Bajalitidae, within the Dendroceratida was the best indication of relationships. Bergquist (1980) examined the holotype and histological preparations of Bajalites laxus and suggested that the stronger relationship, if any, was to the Jathellidae 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 Pusula. The sponge proves to be a distinct species, Halisarca laxus (Lendenfeld) (PL 5c) (Bergquist 1994). The relationships of the order Halisarcidae within the ceractinimorph 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 racovitzae Topsent, Hexadella indica Dendy, Hexadella purpurea Dendy (holotypes, histological preparations only); Phrontispylla minchini (slide of holotype), Phrontispylla spinifera Schultz (holotype specimen and material prepared for electron microscopy, courtesy of Dr. J. Vacelet); Aplysilla glaciata from La Jolla and Bahamas and Aplysilla polyglyphus from the Gulf of California (spirit specimens, courtesy of Dr. J. Faulkner); Igerella jouseni Topsent (slide of holotype) and Igerella 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 Spongianella. 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 herdmanii and D. choris from Palau and Great Barrier Reef, and a new species similar to D. acutus (own field collections)), and D. tapha from the Mediterranean (courtesy Dr. J. Vacelet). Material of Spongianella gracilis (Vosmaer) was made available by Dr. P. Pulitzer-Finali, the holotypes of Spongianella pulchella (Sowerby) and Spongianella 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. 1980) 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 tosptin 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 verongids, but Hexadella, based on the features of the type species Hexadella 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. densid, 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 Chelonerita (Bergquist et al. 1990) and Aplysilla (Bolitin & Faulkner 1991). Both species lack the spumous cells that occur in all Darwinellidae except Chelonerita. 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, Caribbean and Indian Ocean Igerella (PL 7d). A third genus, Acanthodendrilla, was added by Bergquist (1980). Dictyodendrilla has a regular reticulate skeleton made up of stratified uniced fibres of typical dendrillid structure with extremely strongly developed 'joeyzani' fibres which incorporate a variable amount of cuticle. The matter of presence or absence of a stiff pith component in Igerella fibres was not clearly resolved in early descriptions and could not be resolved with certainty from material available in 1980. Toy (1985) indicated that the fibres of the type species Igerella joeyzani were "of Dysidea type" and certainly the high load of foreign material in the superficial fibres suggested this was an appropriate comparison, particularly as 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 Igerella notabilis Duchassaing & Michelotti, which he also described as being "of Dysidea type" and certain that the precise structure of the fibres. His diagram (26a) does however suggest that a strong pith is present, but he also verified the presence of a continuous spongin plate. Study of freshly collected material from Jamaica permits me to correct this: that it is a strong component of the fibre. On this basis, and supported by the presence of spongin fibres (Schmitz et al. 1986), Igerella shows strong affinity to the family Dictyodendrillidae. No species have been seen in Igerella, but no electron microscopy has been done on the sponge.

In addition to the features already mentioned, Igerella species augment their skeleton with polyvalent fibrous 'spicules'. These are very strong and in a great number of species the 'spicules' have been evidence by the presence of spongin fibres. Study of freshly collected material from Jamaica permitted me to confirm this: that it is a strong component of the fibre. On this basis, and supported by the presence of spongin fibres (Schmitz et al. 1986), Igerella shows strong affinity to the family Dictyodendrillidae. No species have been seen in Igerella, but no electron microscopy has been done on the sponge.
The Dicytodontellidae as originally constituted contained two genera: widespread Dicytodontella, and Caribbean and Indian Ocean Igerella (Pl. 7c). A third genus, Acanthodendrilla, was added by Bergquist (1985). Dicytodontella has a regular reticulate skeleton made up of stratified uncorrelated fibres of typical dendroceratid structure with extremely strongly developed pith. Igerella 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 Igerella 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. foeyi were "of Dysoidea 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 Igerella notabilis Duclaux & Micholot, with which I. foeyi was synonymised, 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 spongillean diterpenes (Schmitz et al. 1988), Igerella shows clear affinity to the family Dicytodontellidae. No spumous cells have been seen in Igerella, but no electron microscopy has been done on the sponge.

In addition to the features already mentioned, Igerella species augment their skeleton with tri- to polyaxial 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; Igerella 'spicules' are brittle, homogeneous in section, and have a helical orientation of microfibrils that incorporate deposits of lepidocrocite. They somewhat resemble triina 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 Aphyriella (Veronica) and noted that this tendency to produce free fibrous elements had obviously arisen more often than once in the evolution of the groups under consideration. Igerella 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 Plerapsyllina was established by Topsent (1905) for P. minchini from the Atlantic coast. The species was interpreted by Vacelet (1959) to be identical to Spongilla spinafrons Schultze although the latter Mediterrenean species was thicker with more branching fibres. Vacelet designated P. spinifera as the type species. Very few Plerapsyllina 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 Dysoidea species. The feature 'cored fibres' has been held to indicate relationships with the Dysoidea, but the existence of genera such as Acanthodendrilla and Igerella demonstrates that this feature is common in both dendroceratid and dendroceratid species. It has been difficult to determine from published reports and museum collections whether the fibres of Plerapsyllina minchini and P. spinafrons 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. spinafrons do not resolve the fibre structure clearly but infer the presence of a marked pith. Examination of a specimen from Naples, BMNH 353.3.14 confirms the presence of pith.

Histological characters other than choanoocyte-chamber structure point to affinity with the Dendroceratida rather than the Dysidea. Plerapsyllina spinafrons has an abundant mesohyl cell population which includes the spumous cells found in many other Dendroceratida. This contrasts with Dysoidea species which have a mesohyl deaperature 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 (Levi, Boursy-Esnault & Vacelet pers. comm.). Plerapsyllina minchini appears to lack spumous cells.

A problem arises with the reports on terpene chemistry. These relate only to Plerapsyllina spinafrons from the vicinity of Naples, and the sponge yielded a range of sesquiterpenes such as are found in all Dysoidea species (Bergquist & Wells 1982). No chemistry is known for P. minchini, which, with its typical Aphyriella-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 sufficient ambiguity surrounding this matter to base an assessment of the taxonomic position of Platyphyllosia only on the features of P. minutini, 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 lamelllose 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 choanoocyte-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 choanoocyte-chamber structure. The earliest was Spongionella gracilis, described as Valosia gracilis by Vosmaer (1883). Topsent (1928) added the species repens and ramadigita 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 lamelllose form of S. pulchella is a consistent feature in all but the smallest specimens while the tubular ramadigita habit is consistent within S. gracilis (including repens and ramadigita), (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 euryphyleous choanoocyte 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 choanoocyte chambers (Vacelet et al. 1989).

Mayo et al. (1985) reported that the major secondary metabolite of Spongionella gracilis was gracillin-A, gracillin-A, a spongiane diterpene also known to occur in the unusual Darwiniella tangei from Australia and closely related to the metabolites of Darwiniella oxasta from New Zealand (Bergquist et al. 1996; 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 true fibrous 'spicules' distinguishes it from Igermella.

Other species re-examined during this study which fall into Spongionella are Spongionella nigra Dendy (Pl. 6d), with which Spongionella pulvella Dendy (as Megalopotas) is synonymous, and Spongionella tubulosa Buxton. Spongionella chondrodas de Laubenfels was referred to Fasciospongia (Bergquist 1985) but it may yet be better referred to Lendenfeldia. Spongionella francoda Hentschel belongs to the genus Lendenfeldia. Spongionella foliacea Kelly-Borges et al. (1995) has not been examined but is certainly congeneric and, in the superfcial irregularity of its skeleton, recalls the organisation of Igermella. Kelly-Borges et al. refer to a Spongionella hermanni (For Pseudodemos 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 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 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 are small, encrusting, or very collapsible so many identifiers on removal from the substratum have not been possible. Thus descriptions of new species with consequent re-evaluations of classification are often incomplete, and the recommendations premature or wrong.

It has been emerging in the literature since Bergquist (1979) that terpenoid chemistry has considerable potential as a taxonomic indicator beyond Dictyoceratida and Dendroceratida. Gatt et al. (1990) taxonomically verified information on the chemistry of these sponges has been a time-consuming exercise. Bergquist reported on current data in 1985; subsequent proceedings were published in 1990. This report (Bergquist et al. 1990) gave a proper description of the existing classification, made suggestions for revision, highlighted remaining gaps in the literature, and indicated possible future rearrangements of the family. Attention was drawn to the need for further investigation on the histology and chemistry of a range of sponges before deciding whether the family Dysidea should be transferred to the order Dendroceratida or to a separate family as currently considered. The tentatively new scheme was put forward but not fully revised in this work.

Vacelet took up these ideas and pursued his investigation of choanoocyte morphology and the structure of a number of species using scanning electron microscopy and provided some interesting results (Vacelet et al. 1989). These authors decided for the taxonomic status of the Dysideidae Dendroceratida and suggested that since the family is in some sponges which fall within the genus Igermella, in which they included Spongionella, the family Dictyodendrillidae could be considered as a junior familial name. In making this transfers Vacelet et al. overlooked several important points. They stressed the similarity of the euryphyleous choanoocyte chambers in Dysideidae (Dysidea, Euprosoporia, and Spongionella) and Darwiniellidae (Alphillia) and stated that these are unique in euryphyleous demosponges. This is not the case — large choanoocyte chambers are also found in the Dictyodendrillidae being a Spongionella.
only as belonging to the Dictyodendrillidae not as being a Spongiosella.

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 taxonomy 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 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 dysideids, in which they included Spongiosella, 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 euryphyllous chambers in Dysideidae (Dysidea, Eurypogonigia, and for them Spongiosella) and Darwinellidae (Aplysillidae for them), stating that these are unique in ceractinomorph demosponges. This is not the case — Ianthella and

Aroniaanthelia have euryphyllous 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 (P. S.) than to that of Dysideidae (Dysidea and Eurypogonigia) where the closest structural comparison is with some Thoeretiidae (Dictyoceratida). One other fact which was overlooked is that, apart from the ambiguity over Piripetesella spinifera mentioned earlier, all Dendroceratida studied contain sponginete diterpenes while all Dysidea species studied contain sesquiterpenes among a range of other secondary metabolites, some of microbial 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 Eurypogonigia.

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 recognized. 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 Eurypogonigia. 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            | DENDROCRATIDA             | VERONGIDA                 |
|                           | 1  2  3  4                | 5  6  7  8  9             |                           |
| Diplodal chambers         | ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Eurypylos 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     | ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Sesintercerpes present    | ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Sesqueropes present       | ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Spongiane diterpenes present | ✓ ✓ ✓ ✓               | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Brominated tyrosines present | ✓ ✓ ✓ ✓           | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Reproduction oviparous    | ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| Reproduction ovooviviparous| ✓ ✓ ✓ ✓                   | ✓ ✓ ✓ ✓ ✓                | ✓ ✓ ✓ ✓ ✓                 |
| 1 Spongidae               | 4 Dysideidae              | 7 Athysideidae            |                           |
| 2 Theoctidae              | 5 Durvillidae             | 8 Athysideidae            |                           |
| 3 Icnelidae               | 6 Dictyodendrillidae      | 9 Ianthellidae            |                           |

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

<table>
<thead>
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<th>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.</th>
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<tbody>
<tr>
<td>DENDROCRATIDA</td>
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<td>Darwinellida</td>
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<td>Aphysida</td>
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<td>Chlorophylla</td>
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<td>Paraphylla</td>
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<td>Hexadilla</td>
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<td>Dendrilla</td>
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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-, seco-, ses) 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 sterol components of membranes, the question was raised as to whether terpenes in certain sponges could substitute for sterols in cell membranes. Lichfield and Morales (1976) had considered the same possibility with regard to the unusual long-chain fatty acids found in some sponges. This idea has been pursued through a long series of cell-fractionation, radioactive-labelling, ultrastructural and biosynthetic experiments (Garrison et al. 1988; Lawson et al. 1988) and it is now possible to affirm that these terpenes do indeed play a role in cell membranes.

ACKN

I wish to acknowledge the assistance of Ms K. Sutton, who prepared the line diagrams and some of the scanning micrographs, Mr I. MacDonald for photography and preparation of plates, Ms B. Derry for historical advice, and my many colleagues worldwide who have provided helpful comments and insights.


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, (dr-, 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 (Gannon et al. 1976, Lawson et al. 1986) 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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I wish to acknowledge the assistance of Ms K. Sutcliffe who prepared the line diagrams and some of the scanning micrographs, Mr I. MacDonald for photography and preparation of plates, Ms B. Davy for histology, my many colleagues worldwide who have provided material, Dr C.N. Battershill for many diving hours, collections, and a colour illustration, and Mr K.R. Grange, Dr P. Karuso, and Dr A. Davis for colour illustrations.

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PLATE 1

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

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

C. *Dictyodendrilla densata* nom. nov.; Photomicrograph of choanosome to show fibres, eucyphalous chambers, and matrix (x 120).

D. *Cheirimaphysilla 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 octosomal structure. E, superficial octosomal 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. *Halocera dejardinii* 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;
   sc = spumous cell. Scale bar 10 μm.
E. *Darwinella gardineri* Topsent: Scanning electron micrograph to show choanocyte chambers (x 600).
F. *Darwinella axceata* 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 100μm.

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 'tere' specimen (x 0.25).

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

F. *Darseimella axiata* Bergquist: Light micrograph to illustrate choanosomal and fibre structure and parenchymella larvae (x 120).
COLOUR PLATE 4

A. *Darwinella gardineri* Topsent.
B. *Darwinella garudina* Topsent.
C. *Darwinella oceata* Bergquist.
D. *Dendrilla rosea* Lendenfeld
E. *Chelonaaptinaea violacea* Lendenfeld
F. *Dictyoendrilla dendyi* comb. nov.
COLOUR PLATE 5

A. *Dictyodendrilla dendyi* nom. nov.
B. *Druveinella tango* (Poiner and Taylor) and an unnamed *Druveinella* 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 dasyi* nom. nov.: Preserved specimen showing the prominent surface comules (x 1.0).
B. *Dictyodendrilla tenella* (Lendenfeld): Preserved specimen showing the frondose lamellate habit. BMNH 86.7.8.2 (x 0.25).
C. *Halisarca djuardinii* Johnston: Photomicrograph to show organisation of the choanosomal 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 choanosomal chambers (x 40).
F. *Spongionella nigra* (Dendy): Photomicrograph of the fibre skeleton (x 40).
PLATE 7

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

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

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

D. *Igerella notabilis* (Duchassine & Michelotti): Preserved specimen (x 0.25).
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