

Description of a new lithistid sponge from northeastern New Zealand, and consideration of the phylogenetic affinities of families Corallistidae and Neopeltidae

Michelle KELLY

National Institute of Water & Atmospheric Research (NIWA) Ltd
Private Bag 109-695 Newmarket, Auckland (New Zealand)
m.kelly@niwa.cri.nz

Kelly M. 2000. — Description of a new lithistid sponge from northeastern New Zealand, and consideration of the phylogenetic affinities of families Corallistidae and Neopeltidae. *Zoosystema* 22 (2) : 265-283.

ABSTRACT

Homophymia stipitata n. sp. is described from continental shelf banks off northeastern New Zealand, and compared with the genus holotype *H. lamellosa* Vacelet & Vasseur, 1971 from Madagascar. Diagnostic morphological characters for *Homophymia* are reviewed, expanded, and compared to those of *Callipelta* Sollas, 1888, *Macandrewia* Gray, 1859 and *Daedalopelta* Sollas, 1888 in the dicranocladinid lithistid family Corallistidae. A suite of morphological characters were identified that link these genera with each other and with *Neopelta* Schmidt, 1880 presently in the monogeneric dicranocladinid family Neopeltidae. Two major diagnostic features characterize this group – the possession of monocrepid megarhizoclone desmas with a distinctive short crepis visible in the epirhabd and modified ectosomal desmas which resemble triaenes. These pseudotriaenes have a short irregularly thickened pseudorhabd in which the crepis is usually located, and the pseudoclads are disc-shaped or polyfurcate. These ectosomal desmas are granular and appear pithed as do the choanosomal desmas, and they lack the triaenose inception canals which typify triaenes. The microscleres are spined amphiasters. *Homophymia*, *Callipelta*, *Macandrewia* and *Daedalopelta* are clearly distinguished from other genera in the Corallistidae (*Corallistes* Schmidt, 1870; *Herengeria* Lévi & Lévi, 1988; *Iouea* Laubenfels, 1955 and the Cretaceous fossils *Gignouxia* Moret, 1926; *Phrissospongia* Moret, 1926; *Procorallistes* Schrammen, 1901) which have arched tuberculate dicranoclone desmas, long-shafted triaenes, and two size categories of spiraster-like streptasters. The integrity of the families Corallistidae and Neopeltidae are evaluated and suggestions put forward for the transfer of *Homophymia*, *Callipelta*, *Macandrewia* and *Daedalopelta* to the family Neopeltidae.

KEY WORDS

Porifera,
Corallistidae,
Neopeltidae,
lithistid,
Homophymia,
Callipelta,
Macandrewia,
Daedalopelta,
Neopelta.

RÉSUMÉ

Description d'une nouvelle éponge lithistide du nord-est de la Nouvelle-Zélande et remarques sur les affinités phylogénétiques des familles Corallistidae et Neopeltidae.

Homophymia stipitata n. sp., provenant de bancs du plateau continental au large du nord-est de la Nouvelle-Zélande, est décrite et comparée avec l'holotype du genre, *H. lamellosa* Vacelet & Vasseur, 1971 de Madagascar. Les caractères morphologiques diagnostiques de *Homophymia* sont revus, complétés et comparés à ceux de *Callipelta* Sollas, 1888, *Macandrewia* Gray, 1859 et *Daedalopelta* Sollas, 1888 dans la famille des lithistides dicranocladinides Corallistidae. Un ensemble de caractères morphologiques liant ces genres les uns aux autres et à *Neopelta* Schmidt, 1880 actuellement classé dans la famille monogénérique de dicranocladinides Neopeltidae, est identifié. Deux caractères majeurs identifient ce groupe : la possession de desmes mégarhizocones monocrépides avec un remarquable crepis court visible dans l'épirhabde et des desmes ectosomiques modifiés ressemblant à des triaenes. Ces pseudotriaenes ont un pseudorhabde court irrégulièrement épaissi, incluant généralement le crepis, et les pseudoclades sont discoïdes ou divisés plusieurs fois. Ces desmes ectosomiques sont granulaires et apparaissent pourvus d'une moelle, ainsi que les desmes choanosomiques. Ils sont dépourvus des canaux axiaux typiques des triaenes. Les microsclères sont des amphiasters épineux. *Homophymia*, *Callipelta*, *Macandrewia* et *Daedalopelta* se distinguent nettement des autres genres de Corallistidae (*Corallistes* Schmidt, 1870 ; *Herengeria* Lévi & Lévi, 1988 ; *Iouea* Laubenfels, 1955 et les genres fossiles du Crétacé *Gignouxia* Moret, 1926 ; *Phrissospongia* Moret, 1926 ; *Procorallistes* Schrammen, 1901), qui ont des desmes dicranoclones arqués, des triaenes à long rhabde, et deux tailles de streptasters en forme de spirasters. L'ensemble des familles Corallistidae et Neopeltidae est réévalué et des arguments sont donnés pour le transfert d'*Homophymia*, *Callipelta*, *Macandrewia* et *Daedalopelta* dans la famille Neopeltidae.

MOTS CLÉS

Porifera,
Corallistidae,
Neopeltidae,
lithistide,
Homophymia,
Callipelta,
Macandrewia,
Daedalopelta,
Neopelta.

INTRODUCTION

The family Corallistidae is considered to be one of the most cohesive of the lithistid families, all members containing monocrepid desmas of at least two different types, triaenes of various form, and a range of asterose microscleres and microxea. The genus type *Corallistes* Schmidt, 1870 is well-defined and easily recognizable, being usually cup- or ear-shaped species, and possessing simple, regular, long-shafted dichotriaenes, tuberculate monocrepid dicranoclones, two types of spiraster-like streptasters, acanthose microxea or microstyles, and long oxea-like megascleres. The genus *Iouea* Laubenfels, 1955 erected for the fossil genus *Phalangium* is similar to *Corallistes*

but elongate pedunculate with a deep central cavity. *Iouea moreti* Lévi & Lévi, 1988, the only known living species of the genus, has a pedunculate external form as in the fossil species of the genus, dicranoclones and dichotriaenes, and two forms of streptaster (Lévi & Lévi 1988). *Herengeria* Lévi & Lévi, 1988 is also well-accommodated within the scope of the family Corallistidae, having dicranoclones, spiraster-like streptasters, acanthose microxea, and tremendously long hair-like oxea that protrude in bunches from the stony, irregularly spherical body.

Callipelta Sollas, 1888, *Macandrewia* Gray, 1859, *Daedalopelta* Sollas, 1888 and *Homophymia* Vacelet & Vasseur, 1971 differ, however, from

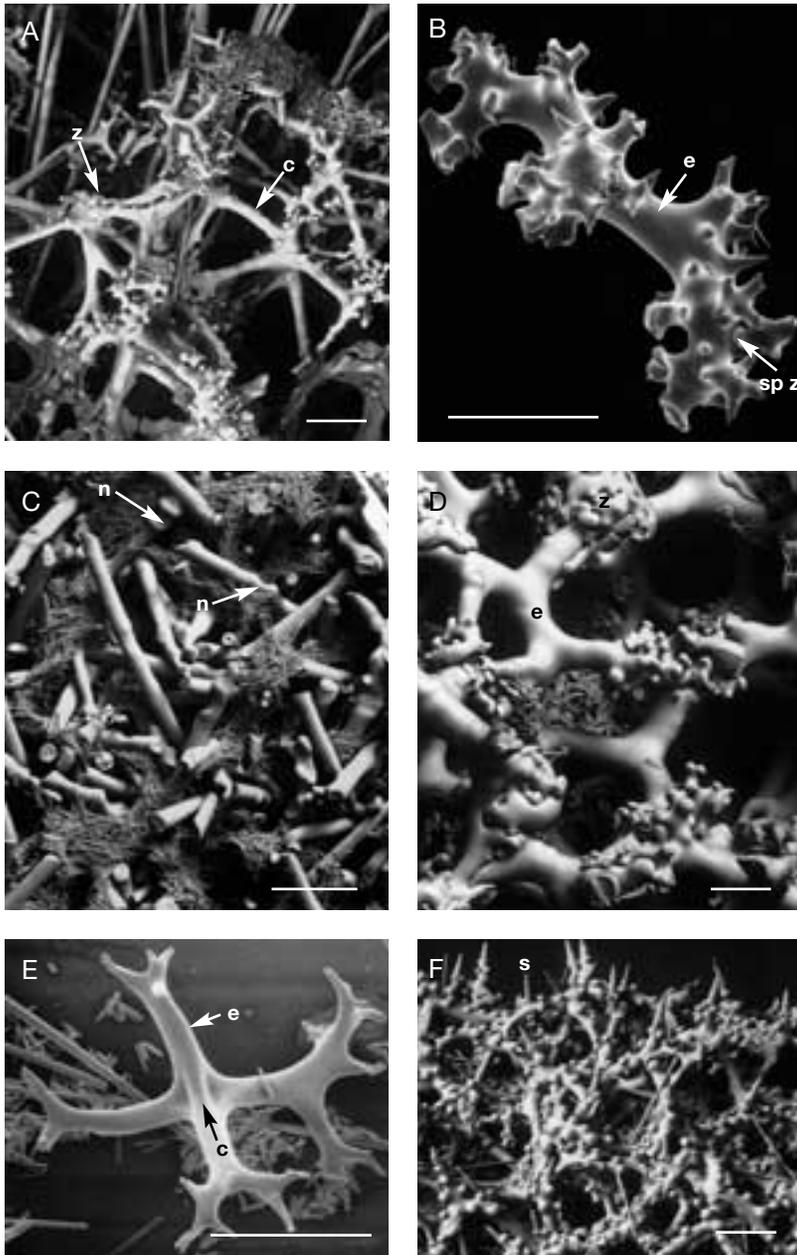


FIG. 1. — Lithistid desma morphologies; **A**, arch-shaped tuberculate monocrepid dicranoclones with terminal zygomes (**z**) and tuberculate clones (**c**), *in situ*, dicranocladinid *Corallistes nolitangere* Schmidt, Caribbean; **B**, monocrepid rhizoclone with spiny epirhabd (**e**) and spiny lateral zygomes (**sp z**), rhizomorinid *Aciculites pulchra* Dendy, New Zealand; **C**, elongate, sinuous monocrepid helo-clones, note lateral notch zygomes (**n**), *in situ*, helomorinid *Costifer wilsoni* Lévi, New Zealand; **D**, tetracrepid tetraclone with four branched epactines, *in situ*, *Discodermia verrucosa* Topsent (family Theonellidae), Azores, **e**, epactine, **z**, zygome; **E**, tetraclone with four epactines (**e**) and flanged crepis (**c**) and finger-like zygomes, undescribed tetracladinid lithistid closely related to *Siliquariospongia*, Palau; **F**, tetracrepid tripodal triders with triaenose symmetry, note ornamented apical spine (**s**) and tripod arms, *in situ*, *Kaliapsis* sp. Caribbean. Scale bars: A, 90 μ m; B, E, 100 μ m; C, 435 μ m; D, 125 μ m; F, 200 μ m.

Corallistes, *Iouea*, and *Herengeria*, in that they possess short-shafted triaene-like spicules, smooth monorepid megarhizocone desmas rather than arched tuberculate dicranoclones, and the microscleres are amphiasters rather than spiraster-like streptasters (Sollas 1888; Lévi & Lévi 1983, 1988). The discovery of a second species of *Homophymia* from continental shelf banks off northeastern New Zealand has provided an opportunity to redefine the genus *Homophymia*, to evaluate its relationship with sister taxa *Callipelta*, *Macandrewia* and *Daedalopelta*, and to evaluate the integrity of the family Corallistidae as a whole.

SPICULE TERMINOLOGY

Lithistids are fossil and recent sponges historically united within the order Lithistida Schmidt, due to the common possession of interlocking siliceous spicules (desmas) that render most species quite rigid and often stony. Frequently, additional spicules are present in lithistid sponges which resemble those in the non desma-bearing families of the order Astrophorida, and some groups within the orders Spirophorida, Hadromerida, Poecilosclerida and Halichondrida, in particular. The presence of these additional spicules has led to hypotheses of polyphyly for these enigmatic sponges (see Laubenfels 1936; Reid 1963, 1970; Lévi 1991, etc.), which have been confirmed in certain cases with molecular data (Kelly-Borges & Pomponi 1994; McInerney *et al.* 1999).

Desmas are siliceous spicules (Figs 1A-F; 2A-C) comprised of a crepis (the inceptional body of the desma), and arms that radiate in a variety of geometries from the crepis (*clones* in monorepid desmas, Fig. 1B, *epactines* in tetracrepid desmas, Fig. 1D, E), and hypertrophic terminal secretions on the arms which, in most cases, lock (zygose) the spicules together into a rigid skeleton. These terminal zygoed regions are termed zygomes (Fig. 1D).

There are three primary modes of desma development leading to the formation of a *monorepid* desma, a *tetracrepid* desma, and an *acrepid* desma. A *monorepid* desma develops from a fine thread-like monaxial crepis, contained within an epirhabd (the part of the desma formed by the

deposition of concentric layers of silica around the crepis) from which the clones arise. Monorepid desmas include various forms such as *dicranoclones* (arch-shaped tripodal, tetrapodal, or polypodal tuberculate monorepid desmas with terminal zygomes, Fig. 1A), *rhizocones* (irregular nontuberculate monorepid desmas with lateral spiny or root-like zygomes, Fig. 1B), *megarhizocones* (nontuberculate monorepid desmas with tuberculate zygomes, Fig. 7A, B), and *heloclones* (monorepid desmas with a single elongate sinuous shaft, the zygomes of which are lateral notches, Fig. 1C).

A *tetracrepid* desma derives from a tetraxon or four-rayed axial crepis from which emanate four smooth arms or epactines which may have bifurcate ends (Fig. 1D), or finger-like zygomes. The crepis region appears flanged in the tetracrones of Theonellidae (Fig. 1E). *Triders* are similar to tetracrones but have triaenose symmetry and apical ornamented spines, Fig. 1F). *Pseudodendroclones* are tetracrepid desmas with smooth arms and branched ends, one arm being very much longer than the other (Fig. 2A), forming a desma that resembles a monorepid dendroclone, occurring in some Paleozoic lithistids.

Acrepid desmas are polyaxonic in the case of *sphaerocones* which have several arms that radiate from one end of a globular, often hollow centrum that is spiny on the opposite side (Fig. 2C). *Megacones* lack a visible axial thread in the crepis, forming arch-shaped desmas with sucker-like zygomes that are elliptical or spherical in profile (Fig. 2B). The axial nature of *acrepid megacones* is uncertain. Desma terminology incorporates that of Rauff (1893), Schrammen (1910) and Lévi (1991).

The developmental pathway of the desma, whether monorepid, tetracrepid or *acrepid*, has traditionally been considered to be highly diagnostic at the subordinal level. Lévi (1991) adopted and modified the classification of Reid (1963) which subdivided the recent lithistids amongst a superorder Astrophorida, and an order Streptosclerophorida. The suborder Tetracladina Zittel contains genera with tetracrepid desmas, genera within the suborder Dicranocladina Schrammen possess tuberculate monorepid desmas, and the suborder Megamorina Zittel contains genera with

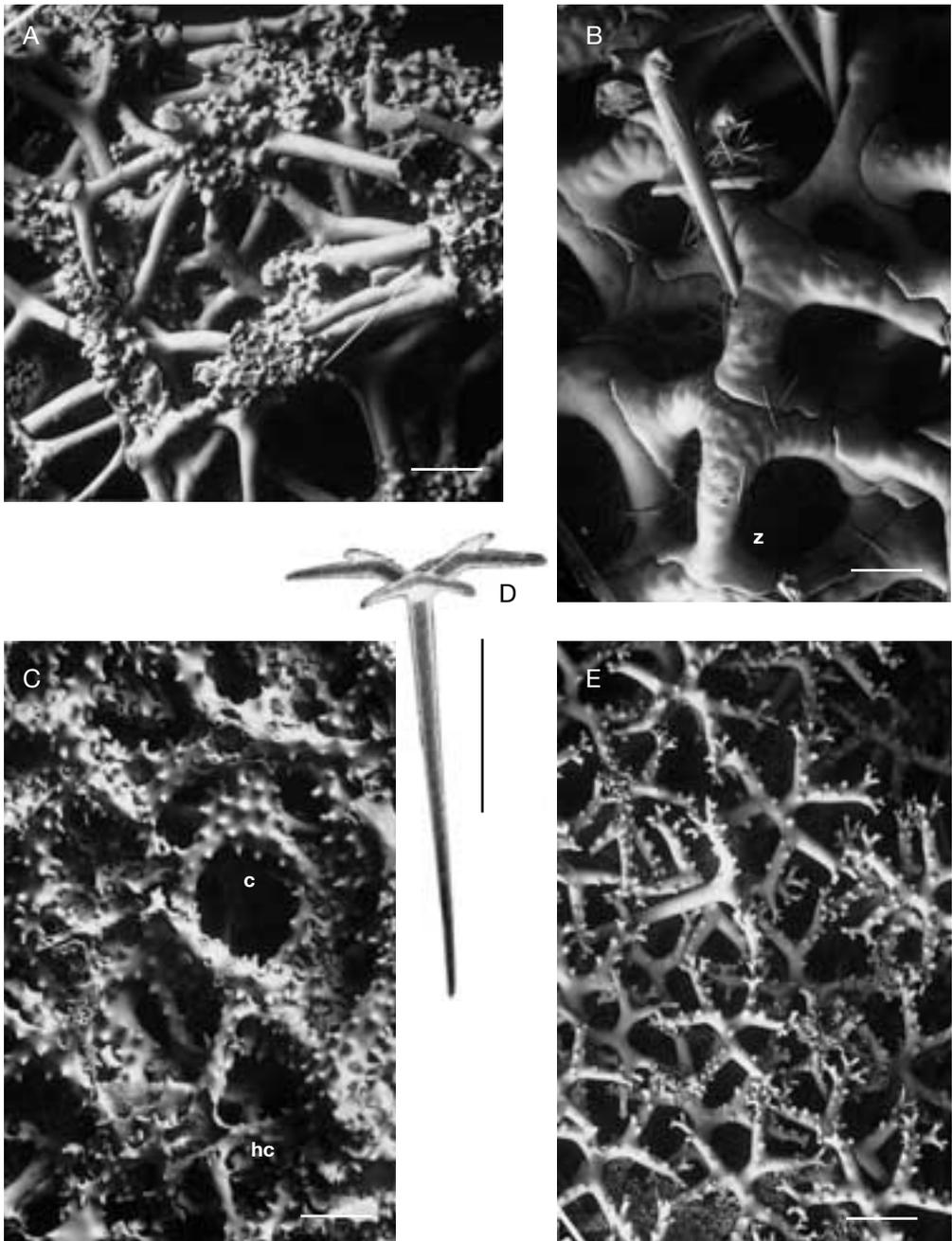


FIG. 2. — Lithistid desma and triaene morphologies; **A**, smooth tetracrepid pseudodendroclone with branched termini, *in situ*, *Racodiscula* sp., Caribbean; **B**, mammillate acrepid megaclones, note simple zygomes (z), *in situ*, undescribed species of *Pleroma*, New Zealand; **C**, sphaeroclones with several arms arising from one end of a globular spiky, hollow (hc) centrum (c), *in situ*, sphaero-cladinid *Vetulina stalactites* Schmidt, Caribbean; **D**, dichotriaene with bifurcate clads, rhabd long relative to cladome width, dicranocladinid *Corallistes typus* Schmidt, Caribbean; **E**, dichotriaenes with regular cladome but with surface ornamentation, rhabd long relative to cladome width, dicranocladinid *Corallistes nolitangere* Schmidt, Caribbean. Scale bars: A, 167 μ m; B, 208 μ m; C, 56 μ m; D, 200 μ m; E, 111 μ m.

acrepid desmas which have oblique lateral facets or tongue/hand-like terminal zygomes (Reid 1970). The suborder Helomorina Schrammen, containing genera with monocrepid desmas, is considered by Lévi (1991) to be *incertae sedis* within the order Streptosclerophorida. The suborders Rhizomorina Zittel with nontuberculate acrepid desmas, bearing spines on the entire surface as well as the zygomes, and Sphaerocladina with clones emanating from an acrepid globular centrum, are considered to be *incertae sedis* within the superorder Astrophorida. The morphology of the clones and zygomes are considered to be highly diagnostic at the genus and species level.

The *ectosomal triaene* is a spicule which is commonly believed to link those lithistids which contain them, to families of the non desma-bearing Astrophorida, such as the Geodiidae and Ancorinidae in particular. These spicules vary considerably in the architecture and ornamentation of the cladome which lies parallel to the surface of the sponge, and the length and shape of the rhabd which sits perpendicular to the sponge surface. Lithistid ectosomal megascleres include *dichotriaenes*, *discotriaenes*, *phyllotriaenes* and *pseudotriaenes*. In all of these structures except pseudotriaenes, the triaenose origin of the spicule is seen in the presence of tetractinal canals or threads that extend from the rhabd into the cladome, leading to the development of three protoclads in the cladome which usually separate into two, and rarely three deuteroclads.

In *dichotriaenes*, the cladome is regular and smooth (Figs 2D; 3C) or ornamented (Fig. 2E). In *Corallistes*, the rhabd is always long relative to the width of the cladome (Fig. 2D), but in the Phymatellidae (Fig. 3C) and Pleromidae, the rhabd is comparatively short. *Discotriaenes* have short rhabds and the cladome is a disc (Fig. 3A, B). There are many varieties of phyllotriaenes with leaf-like cladomes (Fig. 3D-H) which can be distinguished by the pattern of the cladome. All have short rhabds relative to the width of the cladome. The genus *Theonella* Gray, 1868 has simple *dichophyllotriaenes* (Fig. 3D), and a new genus of theonellid (Kelly, unpublished data) has digitate *discophyllotriaenes* (Fig. 3E). Some members of the family Phymaraphiniidae contain

spatulate *phyllotriaenes* (Fig. 3F) and indented *discophyllotriaenes* (Fig. 3G). *Daedalopelta* (Fig. 3H), and *Homophymia* spp. (Fig. 7C, D) have irregular laterally-ornamented *pseudotriaenes*. These megascleres are thought to be highly modified desmas that retain the crepis in the pseudorhabd or the pseudoclad, the desma clones forming the pseudocladome. These spicules lack the characteristic triaenose inceptual threads typical of triaenes.

ABBREVIATIONS USED

BMNH	Natural History Museum, London;
HBOM	Harbor Branch Oceanographic Museum, Florida;
MNHN	Muséum national d'Histoire naturelle, Paris;
NZNM	National Museum of New Zealand Te Papa Tongarewa;
NIWA	National Institute of Water & Atmospheric Research;
0CDN	specimen sample numbers for United States National Cancer Institute shallow-water collection programme contracted to the Coral Reef Research Foundation (CRRF). A complete collection of all 0CDN sponge specimens is located at the Smithsonian Institution (United States National Museum), and with the author.

MATERIAL AND METHODS

Sponges were collected by rock dredge from the National Institute of Water & Atmospheric Research (NIWA) research vessel RV *Tangaroa* between 1975 and 1981, and by the Coral Reef Research Foundation (CRRF) on the RV *Kaharoa* in 1999, from northeastern New Zealand (Fig. 4). On collection, specimens were preserved in 50% isopropanol and prepared for histology and scanning electron microscopy as in Kelly-Borges *et al.* (1994). Spicule dimensions are given as mean length (range of length measurements) and mean width (range of width measurements) followed by the number of spicule measurements taken. Both primary and secondary type materials are deposited at the National Institute of Water & Atmospheric Research (NIWA; formerly New Zealand Oceanographic Institute, NZOI) and Museum of

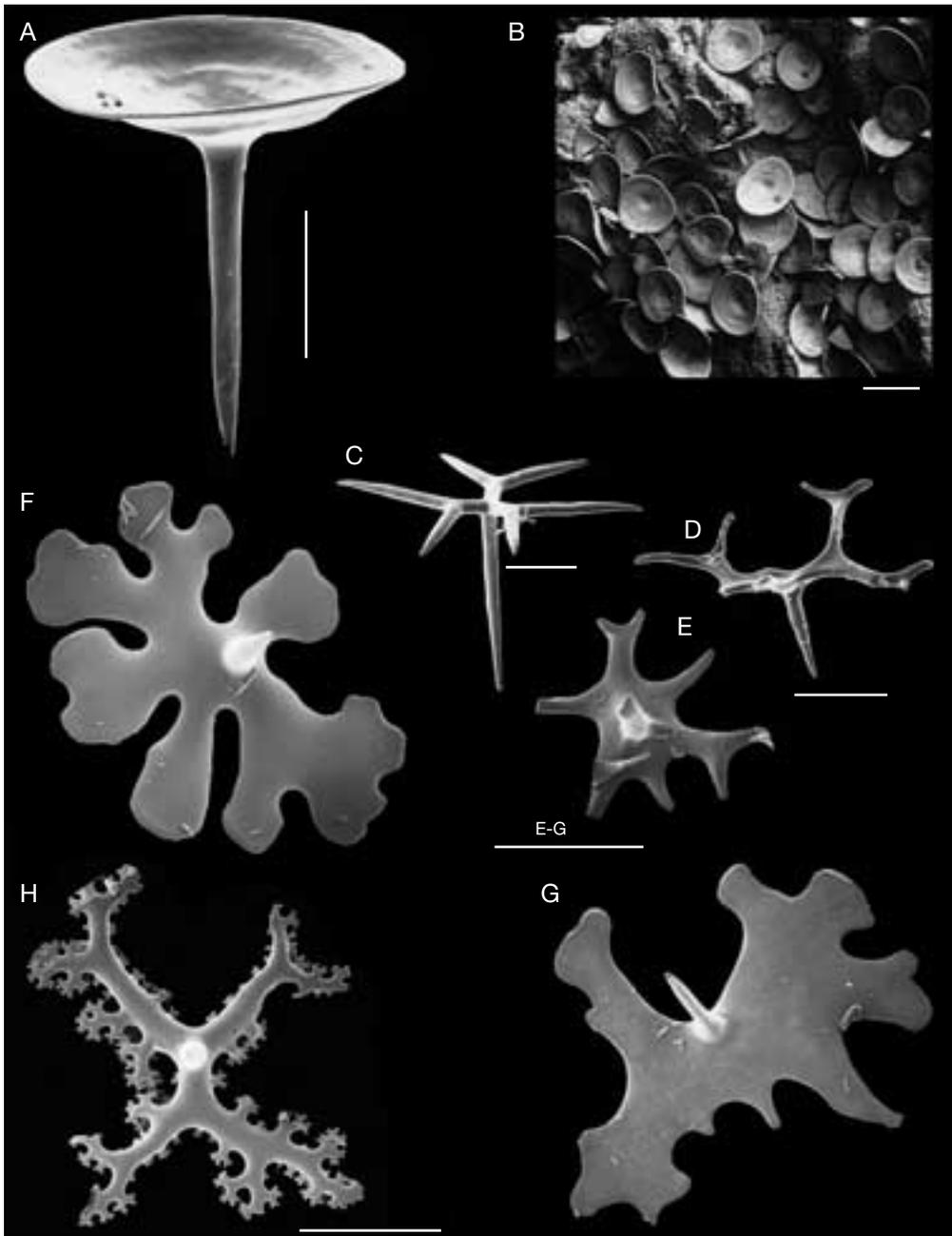


FIG. 3. — Lithistid triaene and modified ectosomal desma morphologies; **A**, discotriaene with short rhabd and cup-shaped discate cladome, undescribed species of tetracladinid *Discodermia* sp., Jamaica; **B**, discotriaenes on ectosome of sponge, *in situ*, tetracladinid *Discodermia* sp., Jamaica; **C**, dichotriaene with bifurcate clads, cladome simple and non-ornamented, rhabd short relative to cladome width, tetracladinid *Reidispongia coerulea* Lévi & Lévi, Norfolk Ridge; **D**, dichophyllotriaene, undescribed species of tetracladinid *Theonella*, Republic of Palau; **E**, digitate discophyllotriaene, undescribed new genus and species of family Theonellidae, Republic of Palau; **F**, spatulate phyllotriaene, undescribed species of tetracladinid lithistid, Caribbean; **G**, indented discophyllotriaene, undescribed tetracladinid lithistid; **H**, irregular laterally ornamented phyllospseudotriaene, dicranocladinid *Daedalopelta nodosa*. Scale bars: A, 60 μ m; B, E-G, 200 μ m; C, D, 100 μ m; H, 150 μ m.

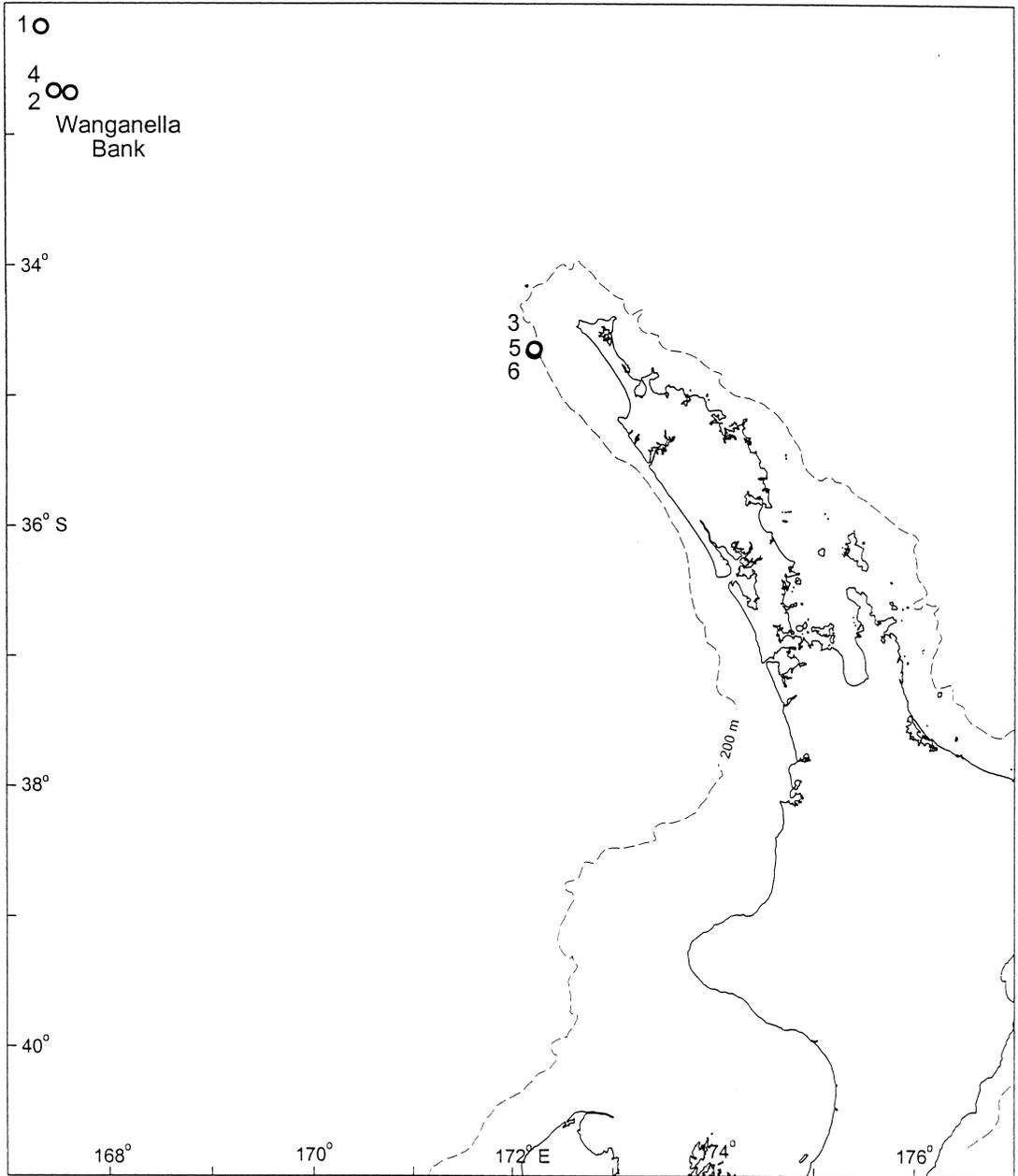


FIG. 4. — Northern New Zealand localities for *Homophymia stipitata* n. sp.

New Zealand Te Papa Tongarewa (formerly National Museum of New Zealand, NMNZ). Fragments of several paratypes have been deposited in the Natural History Museum, London. Registration numbers are cited in the text.

SYSTEMATICS

Genus *Homophymia* Vacelet & Vasseur, 1971

TYPE SPECIES. — *Homophymia lamellosa* Vacelet & Vasseur, 1971: 63.

DIAGNOSIS (EMENDED). — Stipitate, clavate, or lamellate Astrophorida with large smooth monocrepid megarhizocone desmas, epirhabd containing a distinctive short fine thread-like crepis. Two clones of variable length emanate from each end of the epirhabd, the zygome terminii are sinuous and finger-like or tuberculate, the region of the zygone extending along the clone. Ectosomal megascleres are pseudotriaenes, modified desmas that have the appearance and disposition of a triaene. Pseudocladome is polyfurcate with long sinuous fingers, the pseudorhabd is short, irregularly thickened, and curved. Crepis of the modified desma is commonly situated in the pseudorhabd, but in one species it is contained within the pseudoclad. Tips of the pseudoclad frequently partially zygose with the underlying desmas. Monaxonal megascleres are stronglyloxea-like with a central canal that dilates in the distal third of each end rendering the spicule syringe-like. Microscleres are spined amphiasters.

Homophymia stipitata n. sp. (Figs 5-8)

HOLOTYPE. — RV *Tangaroa*, NZOI stn I96(2), 32°10.8'S, 167°21.2'E, rock dredge, 356 m, 25.II.1975 (NIWA H-705).

PARATYPES. — RV *Tangaroa*, NZOI stn I96(3), 32°10.8'S, 167°21.2'E, rock dredge, 356 m, 25.II.1975 (NIWA P-1152). — RV *Tangaroa*, NZOI stn P10, 32°40.0'S, 167°28.4'E, rock dredge, 352-378 m, 25.I.1977 (NIWA P-1154). — RV *Tangaroa*, NZOI stn I96(1), 32°10.8'S, 167°21.2'E, rock dredge, 356 m, 25.II.1975 (NIWA P-1155).

Wanganella Bank. Norfolk Ridge, eastern slope, RV *Tangaroa*, NZNM stn 81889, 32°41.3'S, 167°38.1'E, rock dredge, 296-206 m, 30.I.1981 (NZNM POR615).

Eastern continental slope of Northland. RV *Tangaroa*, NZOI stn J953 (= NZOI I807), 34°39.6'S, 172°13.1'E, rock dredge, 260-270 m, 18.VI.1981



FIG. 5. — *Homophymia stipitata* n. sp.; **A**, NIWA P-1156: Specimen with double stalk and globular apex with apical depression; **B**, immature specimen with developing globular apex. Scale bar: 1 cm.

(NIWA P-1153), a voucher of this specimen has been deposited in the Natural History Museum, London (BMNH 1995.3.30.2). — RV *Tangaroa*, NZOI stn J954 (= NZOI I808-4), 34°38.8'S, 172°13.5'E, rock dredge, 192-204 m, 18.VI.1981 (NIWA P-1156), a voucher of this specimen has been deposited in the Natural History Museum, London (BMNH 1995.3.30.5).

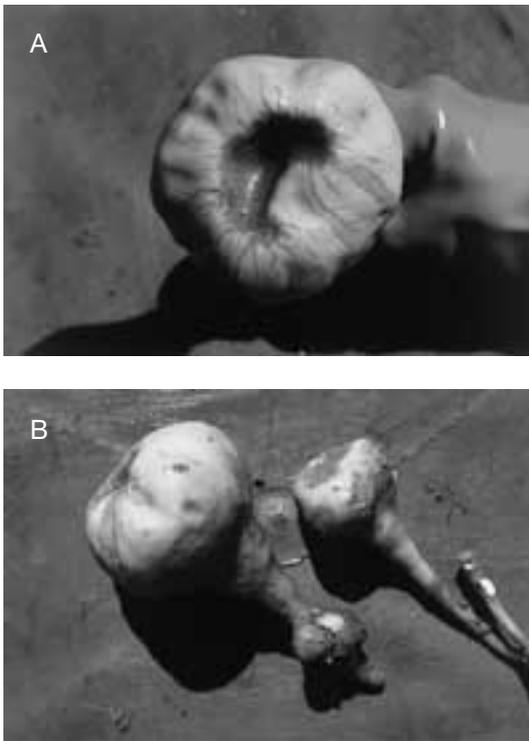


FIG. 6. — *Homophymia stipitata* n. sp. OCDN 6731-Z, collected by CRRF. Note the pigmented apical depression and bulbous subglobular body with lateral expansions, specimens are approximately 15 cm long.

West of Pandora Bank. RV *Kaharoa*, 34°38.91'S, 172°13.20'E, rock dredge, 208-198 m, 21.IV.1999 (OCDN 6731-Z).

ETYMOLOGY. — Named for the stipitate morphology of the sponge, with subglobular body supported on a long stalk that does not contain choanosome.

OTHER MATERIAL. — *Homophymia lamellosa* Vacelet & Vasseur, 1971 (MNHN D Cl 2847); *Macandrewia clavatella* (Schmidt, 1870) (HBOM 003:950); *Daedalopelta nodosa* (Schmidt, 1880) (HBOM 003:949); *Neopelta perfecta* Schmidt, 1880 (HBOM 003:00948).

GEOGRAPHIC DISTRIBUTION. — **Wanganella Bank.** West of Pandora Bank, northeastern continental shelf of New Zealand.

DESCRIPTION

Morphology

Stipitate to parsnip-shaped sponge with an irregular semiglobular body, 40-50 mm diameter, about one third of total length of 150-220 mm, elevated

upon and tapering to a relatively long fine stalk ranging from 20 mm diameter at the junction of the globular body, to 5 mm diameter at the base of the stalk (Figs 5; 6). In some specimens the globular region is faintly bulged on each quadrant of the lateral surfaces (Fig. 6). Sponge apex is depressed, forming a translucent oscular sieve through which exhalant canals are clearly visible, 20-35 mm by 10-20 mm diameter (Fig. 6). Several exhalant canals 1-3 mm diameter extend the length of the sponge, these are reinforced by extensive zygosis of the desmas around them (Fig. 7B). Specimens occasionally have double stalks (Fig. 5A) and are attached to hard substrate by a shallow skirt of variable width. Exhalant canals are visible on surface of body and stalk beneath translucent ectosome (Fig. 6). Surface is smooth but slightly undulating and irregular, granular to the touch. Texture of the globular region is firm, barely compressible, the stalk is rigid and stony, although relatively flexible along entire length. Basal third of sponge is frequently encrusted with other sponges, coralline algae, hydroids and tunicates. Immature specimens lack the apical ovate globular region (Fig. 5B) which expands with maturity.

Colour in life

Tan, in preservative light golden brown, apical depression dark grayish blue.

Skeleton

Skeleton of globular region is composed of huge smooth monorepid megarhizoclones, very long slender clones render the overall structure fairly porous and the sponge almost compressible (Fig. 7A), exhalant canals are reinforced by heavy zygome development (Fig. 7B). In the stalk zygosis is more developed and the clones are shorter. Isolated tracts of large oxeads 7-10 spicules wide arise in the stalk and radiate towards the surface of the globular apex. Ectosome is packed with pseudotriaenes, the sinuous fingers (Fig. 7C) of which are partially zygosed with neighbouring ectosomal megascleres and choanosomal desmas below the surface (Fig. 7D). Pseudorhabds are orientated perpendicular to the surface (see Fig. 7A). Amphiasters (Fig. 8) are abundant and regularly disposed throughout the choanosome, but are more abundant in the ectosomal region.

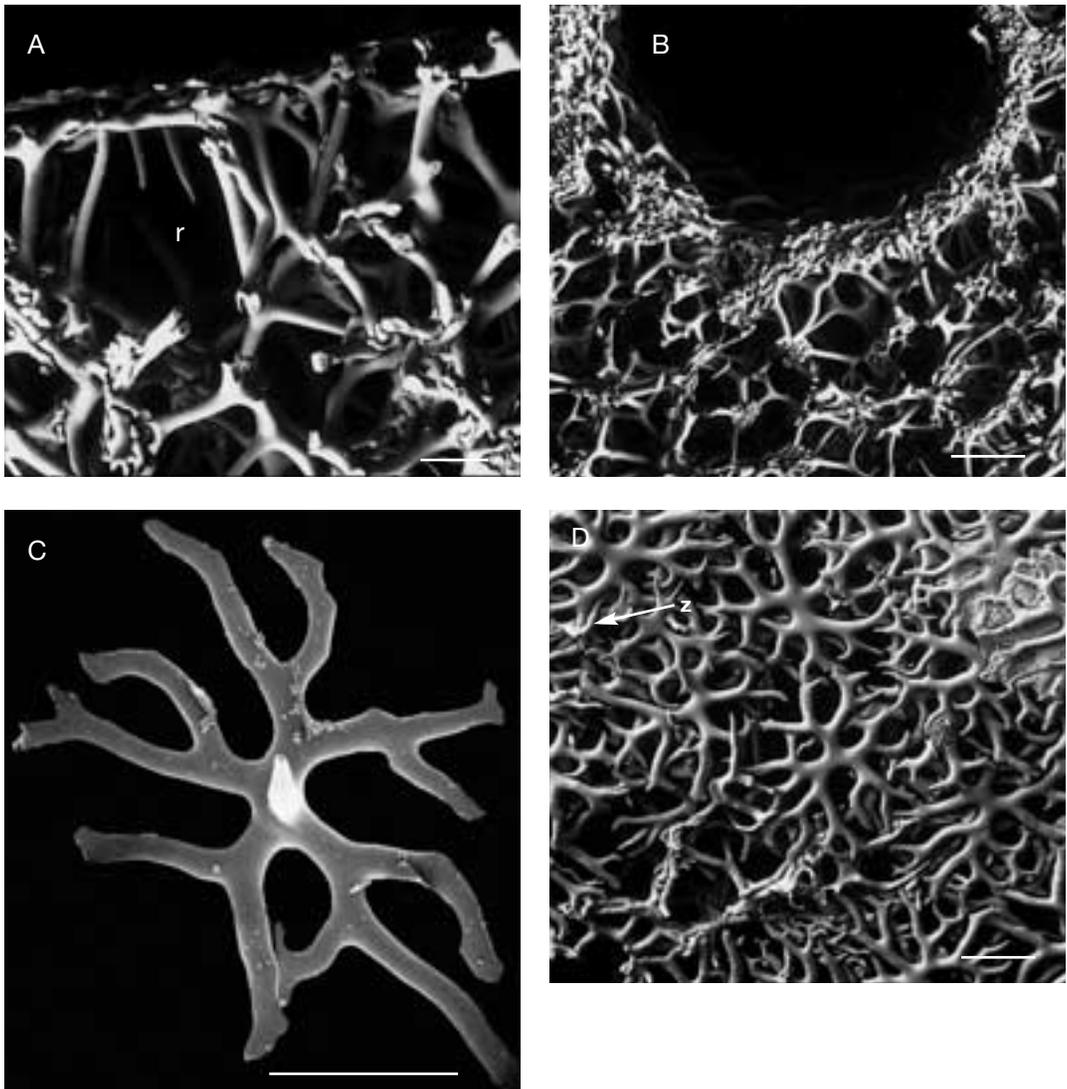


FIG. 7. — Desma and pseudotriaene morphology and architecture in *Homophymia stipitata* n. sp. (NIWA P-1156); **A**, monocrepid megarhizoclone desmas *in situ*, note rhabds (r) of pseudotriaenes protruding through sponge surface; **B**, heavy zygome development around exhalant canals; **C**, pseudotriaenes with sinuous dichotomous and trichotomous arms with bifurcate tips; **D**, pseudotriaenes *in situ* in ectosome, note intricately meshed partially zygosed cladomes. Scale bars: A, 167 μm ; B, 323 μm ; C, 250 μm , D, 217 μm .

Spicules

Choanosomal desmas. Highly irregular monocrepid megarhizoclones with a relatively short epirhabd and 2-3 clones arising off each end, the termini of which are root-like and sinuous. Clones and zygome are smooth, zygome is a tightly wrapped oval structure composed of the sinuous interlocking fingers of the desma ter-

minii which can extend along the clones a short distance (Fig. 7A). Desmas appear laminated and pithed with a faint granular interior: maximum and minimum overall dimensions of desma: 682 (588-857) \times 399 (176-612) μm ; length and thickness of individual arms: 427 (147-588) \times 42 (20-59) μm , $n = 10$; epirhabd length: 193 (147-225) μm , $n = 10$.

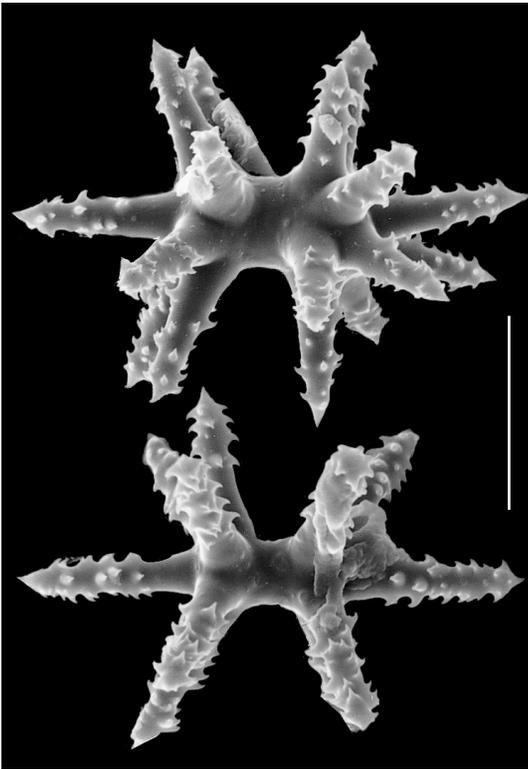


FIG. 8. — Amphiaster morphology in *Homophymia stipitata* n. sp. (NIWA P-1156). Amphiasters with recurved spines. Scale bar: 6 μ m.

Ectosomal polyfurcate pseudotriaenes.

Pseudorhabd is irregular in shape and thickness, and is slightly sinuously curved, and the whole spicule has a laminated and granular appearance as in the choanosomal desmas. Pseudoclads are polyfurcate with sinuous branches. Immature pseudotriaenes are discate with irregularly indented margins, they are granular and rough, often with small rounded projections on one surface, crepis is often visible in one of these projections (Fig. 7C, D): maximum and minimum diameter of pseudocladome 664 (514-711) \times 590 (465-686) μ m, n = 10; length of pseudorhabd 254 (186-323) μ m, n = 10.

Strongyloxeas. Slightly curved, occasionally abruptly curved, fusiform, hollow except in the centre, with a syringe-like appearance, two size categories: 1) length 1055 (809-1372) μ m, width 8 (6-10) μ m, n = 10; 2) length 472 (308-617) μ m, n = 10.

Amphiasters. Acanthose, oxeote, with recurved spines on the distal two thirds of rays, 5-9 rays on each end of spicule, 6-7 rays most typical (Fig. 8): length 15 (12-19) μ m, width 8 (6-9) μ m, ray length 2-5 μ m, n = 10.

Substrate, depth range, ecology

Little is known about the ecology of this species as it was collected by a dredge. The shallow flanged base of the stalk on two specimens suggests that the sponge attaches to hard substrate, which is probably coralline rubble or shell debris. That the sponge may be partially buried in sand is evident from sand-grains attached to the stalks of some specimens; a stalked morphology seems to allow this sponge to cope with shifting unstable substrate of sand and shell rubble, typical of continental shelf banks.

It can be deduced from the accompanying dredge haul that the invertebrate community in which this sponge lives is very rich, consisting of hydroids, soft corals, bryozoans, ascidians, and other sponges, many of which use the stalk of *Homophymia stipitata* for support (Fig. 5). Several other lithistid species were dredged with *Homophymia stipitata* including *Aciculites pulchra* Dendy, *Discodermia proliferans* Lévi & Lévi, and several new and known species of *Corallistes* and *Pleroma* Sollas, 1888. In the central tropical Atlantic where these genera have been observed *in situ* in manned-submersible by the author, they are typically attached to hard substrate on vertical rock faces, or on rocky outcrops surrounded by sand or sediment. This diversity of lithistid species confirms the importance of these continental shelf banks as habitats for lithistid sponges. The sponge has been collected from a depth range of 192-378 m.

REMARKS

Homophymia stipitata n. sp. is distinguished from the type species *H. lamellosa* Vacelet & Vasseur, 1971 by gross morphology and spiculation; the holotype of *H. lamellosa* is lamellate and convoluted whereas *H. stipitata* is subglobular and stalked. However, descriptions of *H. lamellosa* from deeper water (100-159 m) around La Réunion, kindly provided by Professor Claude Lévi indicate that *H. lamellosa* is also pedunculate

or clavate with a rigid stalk in this environment. The apex of this sponge can be convex as in *H. stipitata*, but the oscules are not necessarily confined to an apical depression. The sponges are further differentiated by the much larger size and more complex form of the pseudotriaenes, and by the larger size of the desmas and the smoother zygomes in *H. stipitata* n. sp.

The spiculation of the dicranocladinid genus *Homophymia* and the tetracladinid genus *Manihinea* Pulitzer-Finali, 1993 (family Phymaraphiniidae) are superficially very similar and differences can quite easily be overlooked. Prior to this study, the author had mistakenly transferred *Manihinea conferta* Pulitzer-Finali, 1993 to *Homophymia* in Li *et al.* (1999) due to this superficial similarity. The major difference between *Homophymia* spp. and *Manihinea conferta* is the presence of a tetraxonal crepis in the desmas, and the triaenose inceptional canals in the phyllotriaenes of *Manihinea*, which are pseudotriaenose in morphology with a short rhabd and foliate cladome. The triaenes of *Manihinea* are slightly more regular, however, as the cladome emanates from regularly spaced protoclads. The microscleres in *Manihinea* were originally described as spherasters (Pulitzer-Finali 1993) but examination of several specimens collected recently by the Coral Reef Research Foundation, Micronesia, and others, have revealed that these are actually amphiasters which are frequently infilled with silica.

The morphology, and to a lesser extent, the spiculation of *Homophymia* spp. resembles that of the Cretaceous fossil sponge *Pachinion scriptum* (Römer, 1864) [family Pachionidae Schrammen (= Corallistidae Sollas)]. This fossil species is abundant in the Upper Chalk formation of Flamborough, Yorkshire (Hinde 1883) and throughout Germany (Römer 1864; Zittel 1878; Schrammen 1910). *Pachinion scriptum* has an inverse conical form, the lower portion of the body tapering to a slender stem, the summit rounded with an apical depression (Hinde 1883). Unlike *Homophymia* spp., the central cavity of *P. scriptum* is shallow and cylindrical, and at the base of the cavity several vertical tubes continue to the base of the stalk (Zittel 1878; Schrammen 1910). In *H. stipitata* n. sp. these vertical canals

extend from the base to the depressed apex where they emerge. The sponge ranges in size from 100–380 mm in length and 55–68 mm in width (Hinde 1883).

The spiculation of *P. scriptum* is best known from Schrammen's material in which the spicules are extremely well-preserved. Lagneau-Hérenger (1962) describe the choanosomal desmas as large irregular tuberculate, "forked" dicranoclones (see Zittel 1878: table 5, fig. 2A, B), which determine the size of the large meshes surrounding the central aquiferous tube. Large, relatively smooth megarhizoclones are associated with the dicranoclones (Lagneau-Hérenger 1962). The ectosome consists of a layer of small strongly branched and ornamented desmas (see Zittel 1878: table 5, fig. 2C) between which are situated the cladomes of regular dichotriaenes (see Zittel 1878: table 5, fig. 2D), the shaft sitting perpendicular to the sponge surface, as in recent *Corallistes* spp.

This stipitate morphology in lithistids is not restricted to the suborder Dicranocladina, however, as the tetracrepid fossil genera *Phymatella* Zittel, 1878, *Siphonia* Parkinson, 1822 and *Hallirhoa* Lamouroux, 1821 (family Phymatellidae) all have stalked morphologies. This morphology is most probably an adaptation to the environment in which these sponges lived. Hinde (1883) provides beautiful illustrations of these fossil species recovered from chalk which indicates that the palaeoenvironment was soft fine calcareous sediments such as would occur in some deep offshore waters.

Very similar ectosomal triaenes to those of *Homophymia stipitata* n. sp. (Fig. 7C) have been described from beds of siliceous or siliceo-calcareous material from Lower Tertiary strata near Oamaru, Otago, New Zealand (Hinde & Holmes 1892: pl. 14, fig. 1). This material contains a mixture of radiolarians, diatoms and sponge spicules; the absence of coarse arenaceous materials in the Oamaru rock suggests that it was also a deep-sea soft sediment formed at considerable distance from the land (Hinde & Holmes 1892). The inferred palaeoenvironment of the Oamaru deposits concurs with our knowledge of the distribution of the *Homophymia stipitata* today.

DISCUSSION

The diagnostic characters of *Homophymia* Vacelet & Vasseur have been confirmed with the discovery of a second species of the genus from New Zealand. Both species have monocrepid megarhizoclone desmas with a distinctive short crepis visible in the epirhabd. The ectosomal megascleres are polyfurcate pseudotriaenes, the monaxonal megascleres are syringe-like strongyloxea, and the microscleres are spined amphiasters.

The ectosomal megascleres of *Homophymia lamellosa* were originally described as dichotriaenes but Vacelet & Vasseur (1971) noted the lack of a triaenose inception canals in the cladome. Examination of the holotype of the genus and *H. stipitata* n. sp., confirms that the spicules are most likely modified desmas. Typically, triaenes have easily recognizable and characteristic inception canals that extend into protoclad and then deuteroclads, and along the length of the rhabd. Silica deposition is usually laminated and uniform around these canals. In *Homophymia* spp; the pseudotriaenes lack these canals and the rhabd is short, curved and irregular, containing a fine line or thread the same length and morphology as the crepis in the choanosomal desma, suggesting that the pseudorhabd most likely originates from the desma epirhabd. In *H. stipitata* n. sp., the lengths of the epirhabd of the choanosomal desma and the pseudotriaene rhabd are approximately equal as are the overall diameters of the pseudocladome and the choanosomal desma. Further clues to the origin of these ectosomal spicules include partial zygois of the tips of the branches in the cladome with desmas below in the choanosome, and with each other (Fig. 7D), and the entire pseudotriaene has a "pithed" or granular appearance, as in the choanosomal desmas. Although these pseudotriaenes appear superficially to possess three protoclads, it is more common for there to be four "protoclads" each of which splits into three to four arms.

Callipelta Sollas, currently recognized within the Corallistidae, also has modified ectosomal desmas in the shape of phyllotriaenes. These pseudotriaenes differ from those of *Homophymia* in that they are more discate in shape with crenulate

margins. Sollas (1888: 309) described these ectosomal spicules as discostrongyles, "with a short conical strongylar rhabdome, expanding into a horizontal disc with incised crenulate denticulated margins and tuberculate distal surface". Sollas remarked that although the monocrepid nature of the desma is obvious, the nature of the discostrongyle is not as clear. He could find no trace of the expected triaenose inception canals typical of triaenes, and concluded that the disc must be uniaxial as in *Neopelta*, although in those rare discs that have rhabds in *Neopelta*, the rhabd was observed to be oblique to the disc. Sollas considered the ectosomal pseudotriaene of *Callipelta* to be intermediary in the evolution of triaenes to the ectosomal disc in *Neopelta*, and thus more like the triaenes in *Corallistes* than *Neopelta*, hence the family assignment of Corallistidae for his new genus. It was his consideration that, as the crepidial axis of the ectosomal discs of *Neopelta* lay in the plane of the cladome, and never in the rhabdome, these spicules had a completely separate origin from the triaenes of *Corallistes*. It should be noted that in *Homophymia lamellosa* the crepis is occasionally in the pseudoclad near the inception of the pseudorhabd.

Callipelta cavernicola (Vacelet & Vasseur, 1965), *C. thoosa* Lévi, 1964 and *C. punctata* Lévi & Lévi, 1983 are all consistent in their possession of pseudotriaenes, a term first used by Lévi (1964) in describing the ectosomal spicules of *C. thoosa*. He also described and illustrated them as being "pithed" and granular like the desmas. The pseudotriaenes of *Callipelta* are often tuberculate, a feature evident only in immature spicules of *Homophymia*. This feature led Vacelet & Vasseur (1965) to compare the triaenes of *C. cavernicola* to those of *C. nolitangere* which are apically ornamented, but in a much more regular pattern. The spicules of *C. nolitangere* are triaenes, however, unlike those of *Callipelta*, and are more closely reminiscent of those of the fossil genus *Gignouxia*. The pseudotriaenes of *Callipelta mixta* Vacelet, Vasseur & Lévi, 1976 are very similar to those of some specimens of *Homophymia lamellosa*, but this species contains acanthomicroxeas as in *Neopelta*. The genus *Callipelta* is clearly related to *Homophymia* in the possession of pseudotriaenes, albeit discate, monocrepid

megarhizoclones that resemble tetracloones, and amphiasters. These genera are primarily distinguished on the form of the pseudotriaene.

Macandrewia Gray was established for species that were essentially similar to *Callipelta*, but which lacked amphiasters and possessed microrhabds of various forms. The desmas are monocrepid megarhizoclones with short clones and heavily tuberculate zygomeres. The epirhabd of the majority of desmas contains a clear monaxonal crepis, but very occasionally, a tetractinal crepis can be observed in *Macandrewia clavatella* (HBOM 003:00950) as described in Sollas (1888: 342) and illustrated in Schmidt (1870). Illustrations of the desmas of *Macandrewia rigida* Lévi & Lévi, 1989 also reveal an unusual tetractinal crepis (Lévi & Lévi 1989: 49). In these crepii, three very short incipient canals extend off one end of a typically long fine crepis. Schmidt concluded from this that the desmas were tetracrepid, but Sollas (1888) considered them to be monocrepid, and thus corallistid in affinity, viewing the rare tetractinal crepii to be transitional from monocrepid to tetracrepid desmas.

Interestingly, the pseudotriaenes of *Macandrewia azorica* Gray, 1859 and *M. clavatella* (Schmidt) contain a very similar structure, a long fine "crepis" in the rhabdome, and three very short fine or inflated canals emanating from the proximal end of the rhabdome canal. This structure could easily be misconstrued as the inceptional canals of a triaene, as did Schmidt (1870), but there are no deuteroclads and the inflated canals are very irregular and foliate. The similarity in size and proportions of the "tetractinal" crepis of the choanosomal desmas and the foliate "inceptional canals" in the pseudotriaene suggests their common origin as in *Callipelta* and *Homophymia*. The morphology of the discopseudotriaene, with denticulate and pseudoinceptional canals, and spinulate microrhabds in *Macandrewia*, differentiates this genus from *Homophymia* and *Callipelta*, but the remaining features of spiculation in *Macandrewia* suggests that they belong to the same general group.

Daedalopelta, erected by Sollas (1888: 342) for *Discodermia clavatella* var. *nodosa* Schmidt (1880) from the Gulf of Mexico is, at first glance, barely distinguishable from *Callipelta* s.s. Examination

of *Daedalopelta nodosa* (Schmidt, 1880) (HBOM 003:00949) from Jamaica reveals that the crepis of the desma is monocrepid but difficult to distinguish in the granular pith of the desma. The microscleres are amphiasters, rare spirasters and larger metasters, and the ectosomal spicules are pseudotriaenes. These latter spicules have very narrow denticulate pseudoclads, and the pseudorhabd contains a crepis in the axis. The proximal end is usually granular or "bubbled," unlike *Callipelta* and *Homophymia* which lack any canals at the rhabdome-cladome junctions, and *Macandrewia*, which has a foliate crepidial canal.

Macandrewia, *Homophymia*, *Callipelta* and *Daedalopelta* are thus clearly linked by common characters. These four genera all possess megarhizoclone desmas and ectosomal pseudotriaenes, and various combinations of amphiasters, metasters and microrhabds. They differ from other genera that are typically included in the family Corallistidae, and Lévi (1991: 80) expressed doubt as to their inclusion in this family. *Corallistes*, *Herengeria* and *Iouea* (family Corallistidae) contain tuberculate, often tridentate, monocrepid dicranoclones, long-shafted dichotriaenes with smooth or ornamented clads, and microscleres which are two categories of streptoscleres, and in some species microxea.

It is tempting to speculate on the evolution of this group of fossil and recent sponges, as the recent genera appear to possess subsets of morphological characters present in certain fossil genera. The fossil genus *Pachinion* (Lower-Upper Cretaceous) had megarhizoclone and dicranoclone desmas, subectosomal rhizoclonoid desmas ("dermal plaques" of some authors) and dichotriaenes, while recent genera *Homophymia*, *Callipelta*, *Macandrewia* and *Daedalopelta* have megarhizoclones and pseudotriaenes (possibly derived from spicules similar to the subectosomal rhizoclones of *Pachinion*). In these genera dicranoclones and dichotriaenes are absent or "lost". The fossil genera *Procorallistes* (Upper Cretaceous-Miocene), *Iouea* (Cretaceous), *Gignouxia* (Upper Cretaceous) and *Phrissospongia* (Upper Cretaceous), on the other hand, had the same general megasclere complement as the fossil *Pachinion* and the Jurassic fossil genus *Dicranoclonella* (with arched tuberculate dicran-

oclonal) but lacked megarhizoclonal. Recent genera *Corallistes* and *Herengeria* may have evolved within this second group of fossils having lost the subectosomal rhizoclonal developed in the recent "*Homophymia*" group. This Cretaceous fossil group represented by *Procorallistes-Iouea-Gignouxia-Phrissospongia* has been further subdivided into two subgroups by Brimaud and Vachard (1986) that reflect a natural division in Recent *Corallistes* spp. (Lévi 1991). The first group (subfamily Corallistinae) contains *Procorallistes* and *Iouea* with regular non-ornamented dichotriaenes, and the second (subfamily Gignouxinae) contains *Gignouxia* and *Phrissospongia*, with ornamented dichotriaenes.

Another fossil family also included in the suborder Dicranocladina, the family Megarhizidae Schrammen, is best known from the genus *Megarhiza* Schrammen, 1901 (Cretaceous), and the very rare genus *Chalaropegma* Schrammen, 1910 (Upper Cretaceous), both of which exclusively contain megarhizoclonal. No dermal spicules are known from these fossils. Although dermal microscleres may simply not have been recovered in the fossils, it seems less likely that the megarhizid group is ancestral to the corallistid and neopeltid groups as they lack the majority of desma and megasclere types found in *Pachinion* and the potentially derived groups.

Unfortunately, with the exception of microxea-like spicules in *Pachinion scriptum* (Schrammen, 1910), these fossils give no indication of the microsclere component of the skeleton, having been lost in the process of fossilization. However, the microspiculation of fossil genera may be deduced from the spiculation of recent groups given the previous scenario. In the "*Homophymia*" group, *Callipelta* and *Homophymia* possess amphiasters, and *Neopelta* and *Daedalopelta* possess amphiasters with metastar modifications. Thus, *Pachinion* might be expected to have had amphiasters and metastars in addition to microxea. Living Corallistidae, such as *Corallistes nolintangere*, *C. thomasi* and *C. microstylifer*, which have ornamented dichotriaenes as in the fossil "*Gignouxia*" group, possess amphiasters, streptasters and microxea. *Corallistes* species, on the other hand, only have spiraster-like microscleres and spined microxea.

Assuming the acknowledged close phylogenetic affinity of fossil *Pachinion* with the "*Procorallistes*" fossil group (Hinde 1883; Zittel 1878; Moret 1926; Lagneau-Hérenger 1962; Lévi 1991), the presumed loss of ectosomal rhizoclonal, megarhizoclonal, and amphiasters in the living "*Corallistes*" group, suggests that this group is the most derived within the family Corallistidae. Similarly, megarhizoclonal and amphiasters, and hypothesised retention of ectosomal rhizoclonal, in the living "*Homophymia*" group, suggests that they are less derived and thus older than modern *Corallistes* species as they contain a greater proportion of the spicule complement of its hypothesised *Pachinion*-like ancestor. The high numbers of *Corallistes* spp. within the central tropical Atlantic Ocean (Wiedenmayer 1994; Kelly & Pomponi unpubl.) and the Southwest Pacific (Lévi & Lévi 1983; Wiedenmayer 1994) compared to those of the "*Homophymia*" group, adds weight to this hypothesis. Lithistid genera *Theonella* and *Discodermia* (tetracladinid family Theonellidae) parallel this general evolutionary pattern of rapid speciation, coupled with a loss of desmas, ectosomal triaenes, and microscleres (McInerney *et al.* 1999).

While the desmas of *Macandrewia*, *Homophymia*, *Callipelta* and *Daedalopelta* are always monocrepidial, they are quite different from the dicranoclonal of *Corallistes*, *Iouea* and *Herengeria*, and more closely similar to the desmas found in *Neopelta*. *Neopelta* is the only member of the family Neopeltidae, and this family is the second and only other family included in the suborder Dicranocladina by Lévi (1991). The genus and family were erected for taxa with monocrepidial desmas, ectosomal monocrepidial discs, acanthose microxeas and streptoscleres (Sollas 1888). Examination of *Neopelta perfecta* (HBOM 003:00948) reveals a remarkable similarity in general spiculation to *Homophymia* and *Callipelta* in particular. The desmas are monocrepid megarhizoclonal with a slender crepis in the middle of a short epirhabd (see Schmidt 1880: pl. 5, fig. 3), and at least two smooth long rhizome-like clones emanating from each end of the epirhabd, as in *Homophymia* and *Callipelta*. The microscleres are acanthose microxea and asterose microscleres are fundamentally amphiasters

which may have an additional ray on one side of the elongate centrum giving the superficial impression of a spiraster or metastar as in *Daedalopelta*. The characteristic ectosomal discs of *Neopelta* are more or less oval in outline. The crepis can be wholly or partly immersed in the disc, or according to Sollas (1888), occasionally found in an oblique rhabdome projecting from the lower surface.

A third species of *Neopelta*, *N. plinthosellina* Lévi & Lévi, 1988 was recently described from New Caledonia. The desmas are described as being tuberculate and monocrepid, but their overall morphology is more similar to the tuberculate tricanoclones of the fossil genus *Scheiella thesaurium* Finks, 1971 (suborder Eutaxioclada, family Hindiidae) (see Lévi & Lévi 1988: pl. VI, figs a, b), than to the smooth megarhizoclones of Neopeltidae as presently recognized. *Scheiella thesaurium* also had megarhizoclones; perhaps the desmas in Lévi & Lévi (1988: fig. 4 of pl. VI) are more reminiscent of these later spicules. Finks (1971) hypothesised that *Scheiella* was a transitional genus between eutaxioclades *Hindia* (Ordovician-Devonian) and *Scheiella* Tschernychew & Stepanov, 1916 (Mesozoic), and the dicranocladines *Dicranoclonella* Schrammen, 1936 (Jurassic) and *Pachinion* (Cretaceous), which are hypothesised to have led to the family Corallistidae and Neopeltidae, respectively (Lévi 1991; this work).

The ectosomal spicules of *Neopelta plinthosellina* are also different from that of the genus holotype; they are multifaceted plaques rather than smooth circular discs. These plaques are also modified desmas, however, as evidenced by the crepis visible in the plaque. These desmas may also be viewed as modifications of the subectosomal rhizoclonid desmas found in many fossil dicranocladinids, as are the pseudotriaenes of the "*Homophymia*" group. The microscleres are amphiasters with spiraster modifications which differs from *Neopelta* s.s. The phylogenetic affinities and identity of the species *plinthosellina* may require further examination and reconsideration in the light of this work and the fossil genus *Scheiella*.

It is clear that *Homophymia*, *Macandrewia*, *Daedalopelta*, *Callipelta*, *Neopelta*, and the species

plinthosellina form a group that possesses megarhizoclone desmas, pseudotriaenes derived from subectosomal desmas, amphiasters and modifications of these, and in some genera, microxea. Many of these characters are shared with the Cretaceous fossil genus *Pachinion*, and its hypothesised earlier ancestors *Dicranoclonella* and *Scheiella*. *Corallistes*, *Iouea* and *Herengeria*, and the fossil genera *Gignouxia*, *Procorallistes*, *Phrissospongia* in the family Corallistidae, clearly differ from the above group however and it is suggested that the former group be transferred to the family Neopeltidae. An emended diagnosis for the family Neopeltidae is given below.

Family NEOPELTIDAE Sollas, 1888: 344

DIAGNOSIS. — Stipitate, clavate, pedunculate, lamellate, or plate-like Astrophorida with monocrepid megarhizoclone desmas consisting of sinuous, smooth or tuberculate zygomes, four smooth clones emanating from a short epihabd with a distinctive fine monaxonal crepis; other megascleres include large fusiform oxea with strongylar modifications and ectosomal pseudotriaenes with morphology and disposition reminiscent of dichotriaenes; ectosomal pseudotriaenes are modified desmas which can be digitate, bifurcate, phyllamentous, or discate, with crenulate or denticulate margins, which are pithed and laminated, occasionally with blunt conical projections. The pseudorhabdome is short, curved and irregularly thickened when it is present. These megascleres lack the triaenose inceptional canals of the triaene. In *Macandrewia*, three minute tetractine-like canals emanate from one end of the thread-like crepis in leading to foliate expansions at the proximal end of the rhabdome, these expansions are granular in *Daedalopelta* and *Callipelta*, and *Homophymia* lack all such canals. Microscleres are spined amphiasters in *Homophymia*, and *Callipelta*, with metastar-like modifications in *Neopelta* and *Daedalopelta*, these are absent in *Macandrewia*. Acanthose microxea are present in *Neopelta* and smooth spinulate microxea are found in *Macandrewia*.

REMARKS

The genus *Plinthosella* (family Plinthosellidae Schrammen) was initially created for tetracladine fossil lithistids with superficial siliceous plaques in the ectosomal region of the sponge. Lévi (1991) considers that the tetracrepidial nature of the desmas of species described within the genus is not always easy to demonstrate, and that they

could very well be more reminiscent of megarhizoclones of *Neopelta* and indeed, *Macandrewia*, *Callipelta* and *Homophymia*. Thus, as suggested by Lévi (1991), a thorough comparison of spicules in Mesozoic species will need to be made before family Plinthosellidae Schrammen, 1910 can be confirmed as a synonym of Neopeltidae in the suborder Dicranocladina.

The separation of the suborder Dicranocladina into two families containing predominantly Recent taxa, family Corallistidae and family Neopeltidae is upheld, but it is suggested that *Callipelta*, *Homophymia*, *Daedalopelta* and *Macandrewia* be transferred to family Neopeltidae, the group appearing to share a common origin with fossils such as *Pachinion*, but having lost the ancestral dicranoclone and dichotriaene skeletal components. Recent genera *Corallistes* and *Herengeria*, on the other hand, are retained in the family Corallistidae, having potential common ancestry with *Procorallistes*, *Iouea*, *Gignouxia* and *Phrissospongia*, and also sharing a possible common origin with *Pachinion* and *Dicranoclonella*-like ancestors that have reduced the megarhizoclonal component of their skeletons. Ongoing molecular systematics research by the author and colleagues is focused upon verification of the above hypothesis.

Acknowledgements

The author thanks Dr Andrej Pisera for constructive comments on desma terminology, and Klaus Borges for histological sectioning and scanning electron microscopy carried out at the Natural History Museum, London. Dr Steve O'Shea, NIWA, Dr Bruce Marshall, National Museum of New Zealand Te Papa Tongarewa, Wellington, assisted with access to New Zealand deep-water sponge collections, and Prof. Patricia Bergquist provided some photographic material of the new species. Prof. Claude Lévi, MNHN, Paris, provided comparative histological slides of *Homophymia lamellosa* and his personal notes on several additional specimens to the holotype. This research was facilitated by the Lottery Science Grants Board of New Zealand, the Biological and Biotechnological Research Council (BBSRC), UK, British Airways Conservation Travel Awards, and support from

The Natural History Museum, London, and NIWA, New Zealand is gratefully acknowledged. This is a contribution from the Coral Reef Research Foundation, Micronesia, and is Harbor Branch Oceanographic Institution Contribution N° 1294.

REFERENCES

- Brimaud C. & Vachard D. 1986. — Les Spongiaires siliceux du Tortonien des Bétiques (Miocène de l'Espagne du Sud): espèces nouvelles ou peu connues. I: Choristides et Lithistides. *Bulletin du Muséum national d'Histoire naturelle* 4 (8) C3 : 293-341.
- Hinde G. J. 1883. — *Catalogue of the Fossil Sponges in the Geological Department of the British Museum (Natural History) with Descriptions of New and Little Known Species*. Taylor & Francis, London, 237 p.
- Hinde G. J. & Holmes W. M. 1892. — On the sponge remains in the Lower Tertiary strata near Oamaru, Otago, New Zealand. *Journal of the Linnean Society (London)*, Zoology 24: 177-262.
- Finks R. M. 1971. — A new Permian Eutaxiclade demospone, mosaic evolution, and the origin of the Dicranocladina. *Journal of Paleontology* 45 (6): 977-997.
- Kelly-Borges M. & Pomponi S. A. 1994. — Phylogeny and classification of lithistid sponges (Porifera: Demospongiae): a preliminary assessment using ribosomal DNA sequence comparisons. *Molecular Marine Biology and Biotechnology* 3: 87-103.
- Kelly-Borges M., Robinson E. V., Gunasekera S., Gunasekera M., & Pomponi S. A. 1994. — Species differentiation in the marine sponge genus *Discodermia* (Demospongiae, Lithistida): the utility of secondary metabolites as species-specific markers. *Biochemical Systematics and Ecology* 22: 353-365.
- Lagneau-Héranger L. 1962. — Contribution à l'étude des Spongiaires siliceux du Crétacé inférieur. *Mémoires de la Société géologique de France*, NS, 41 : 1-262.
- Laubenfels M. W. de. 1936. — A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for the revision of the families and orders of the Porifera. *Publications of the Carnegie Institution*, No. 467, *Papers from the Tortugas Laboratory* 30: 1-224.
- Lévi C. 1964. — Spongiaires du Canal de Mozambique. *Bulletin du Muséum national d'Histoire naturelle*, 2^e série (36) 3 : 384-395.
- Lévi C. 1991. — Lithistid sponges from the Norfolk Rise: Recent and Mesozoic genera: 72-82, in Reitner J. & Keupp H. (eds), *Fossil and Recent Sponges*. Springer-Verlag, Berlin.

- Lévi C. & Lévi P. 1983. — Éponges Tetractinellides et Lithistides bathyales de Nouvelle-Calédonie. *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, 5 A (1) : 101-168.
- Lévi C. & Lévi P. 1988. — Nouveaux Spongiaires Lithistides bathyales à affinités crétacées de la Nouvelle-Calédonie. *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, 10 A (2) : 241-263.
- Lévi C. & Lévi P. 1989. — Spongiaires (Musorstom 1 & 2), in Forest J. (ed), *Résultats des Campagnes Musorstom*. Volume 4. *Mémoires du Muséum national d'Histoire naturelle A* 143 : 25-103.
- Li C. J., Schmitz F. J. & Kelly M. 1999. — Aurantoside C, a new tetramic acid glycoside from the lithistid sponge *Homophymia conferta* (Pulitzer-Finali). *Journal of Natural Products* 62: 170-172.
- McInerney J. O., Adams C. L. & Kelly M. 1999. — Phylogenetic resolution potential of 18s and 28s rRNA genes within the lithistid Astrophorida, in Hooper J. N. A. (ed.), Proceedings of the 5th International Sponge Symposium. *Memoirs of the Queensland Museum* 44: 343-352.
- Moret L. 1926. — Contribution à l'étude des Spongiaires siliceux du Crétacé Supérieur français. *Mémoires de la Société géologique de France*, NS, 5 : 1-322.
- Pulitzer-Finali G. 1993. — A collection of marine sponges from East Africa. *Annali del Museo Civico di Storia Naturale "Giacomo Doria"* 89: 247-350.
- Rauff H. 1893. — Palaeospongiologie. *Palaeontographica* 40: 233-346.
- Reid R. E. H. 1963. — A classification of the Demospongia. *Neues Jahrbuch für Geologie und Paläontologie*, Monatshefte 4: 196-207.
- Reid R. E. H. 1970. — Tetraxons and demosponge phylogeny: 63-89, in Fry W. G. (ed.), *The Biology of the Porifera*. Academic Press, Symposia of the Zoological Society of London 25, London.
- Römer F. A. 1864. — Die Spongitarier des nord-deutschen Kreidegebirges. *Palaeontographica (Stuttgart)* 13: 1-64.
- Schrammen A. 1910. — Die Kieselspongien der oberen Kreide von Nordwestdeutschland. I Teil: Tetraxonia, Monaxonia und Silicea incert. sedis. *Palaeontographica*, suppl. 5: 1-175.
- Schmidt O. 1870. — *Grundzüge einer Spongien Fauna des Atlantischen Gebietes*. Wilhelm Engelmann, Leipzig, 84 p.
- Schmidt O. 1880. — *Die Spongien des Meerbusens von Mexico und des Caraibischen Meeres*. Gustav Fischer, Jena, 90 p.
- Sollas W. J. 1888. — Report on the Tetractinellida collected by H. M. S. *Challenger*, during the years 1873-1876. *Reports on the Scientific Results of the Voyage of the H. M. S. Challenger, Zoology* 25 (63): 1-458.
- Vacelet J. & Vasseur P. 1965. — Spongiaires des grottes et surplombs des récifs de Tuléar (Madagascar). *Recueil des travaux de la Station marine d'Endoume* 4 : 71-123.
- Vacelet J. & Vasseur P. 1971. — Éponges des récifs coralliens de Tuléar (Madagascar). *Téthys*, suppl. 1: 56-126.
- Wiedenmayer F. 1994. — Contributions to the knowledge of post-Palaeozoic neritic and archibenthal sponges (Porifera). *Schweizerische Paläontologische Abhandlungen* 116: 1-147.
- Zittel K. A. 1878. — Studien über fossile Spongien. 2. Lithistidae. *Abhandlungen der Königlich bayerischen Akademie der Wissenschaften, Mathematisch-Physische Klasse* 13: 65-154.

Submitted on 7 June 1999;
accepted on 24 September 1999.