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Revisionary systematics in the gorgonian family Isididae, with descriptions of numerous new taxa (Coelenterata: Octocorallia)

> by Philip Alderslade

*Records of the Western Australian Museum* Supplement No. 55

## Records of the Western Australian Museum

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Cover: Tethrisis suzannae, from Shark Bay and the Great Australian Bight.

## REVISIONARY SYSTEMATICS IN THE GORGONIAN FAMILY ISIDIDAE, WITH DESCRIPTIONS OF NUMEROUS NEW TAXA (COELENTERATA: OCTOCORALLIA)

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Philip Alderslade

Western Australian Museum 1998

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# Revisionary systematics in the gorgonian family Isididae, with descriptions of numerous new taxa (Coelenterata: Octocorallia)

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Abstract - The work is a taxonomic treatment of a number of closely related groups of gorgonians within the family Isididae (Octocorallia: Coelenterata). The revisionary aspects of the study are centred around the genus *Mopsea* which is shown to be grossly paraphyletic. Heretofore including 17 nominal species, it is proposed that only the type species Mopsea encrinula is valid; a second, new species is added. Of the other recognised species, Mopsea dichotoma (Linné) is an unidentifiable melithaeid, and the remainder are divided amongst 1 existing and 7 new genera. These re-assignments are primarily on the basis of polyp structure, colonial branching pattern, and axial architecture, which are correlated with sclerite form and arrangement. Various states of these characters are used to define the relatedness of other genera. Taxonomic confusion is most likely to arise amongst both unbranched forms and branched forms which are predominantly planar, so the species of all known closely related genera with these morphologies are revised. The latter comprises the recognised and valid genera *Acanthoisis*, *Peltastisis*, Circinisis, Minuisis and the neglected Notisis. Although Minuisis has a generally bushy habitus, it is included because its growth form is modified to pinnate, planar branching by a commensal scale worm. It is shown that Primnoisis, Chathamisis, and Echinisis which have a bushy growth form can be distinguished as a group on this character, and individually using polyp structure, and these taxa are only considered at the generic level. Descriptions are extensively illustrated with scanning electron micrographs and all preparation techniques are detailed.

The revision of known species is based on type material borrowed from numerous Australian and international institutions. As far as can be ascertained, virtually all of the specimens mentioned in the literature that were considered to be relative to the study have been examined, together with a large suites of additional and previously undescribed material. Numerous new taxa are proposed based on these specimens. In total, 23 established species are validated, 15 as new combinations, and 30 new species are proposed along with 16 new genera. These taxa are assigned to the subfamilies Mopseinae and Circinisidinae, while Peltastisidinae is considered to be untenable. Keys to the genera of the former 2 subfamilies are given.

Lectotypes are designated for the following species *Mopsea flabellum* Thomson and Mackinnon, *M. elegans* Thomson and Mackinnon, and *M. simplex* Tixier-Durivault, and all 3 are assigned to new genera.

The history of all the relevant taxa is given inclusive of all reassignments made in the taxonomic portion of the text. Some new terms are introduced in the section on taxonomic characters and terminology, which contains a particular point of focus on polyp structure. The misuse of the terms *anthocodia* and *anthostele* is discussed, and the neglected term *anthopoma* is reintroduced for the 'opercular' region of the polyp. Each of the defined character states pertaining to polyp structure, axial architecture, and the pattern of ramification, are shown, with rare exceptions, to be consistent within the proposed generic groups.

Distribution maps are given for all species, genera, and subfamilies. A preliminary model is proposed of the broad evolutionary history of the subfamilies in an attempt to explain the disparate distribution ranges of the bushy and non-bushy forms which may have had separate subsequent lineages from a common ancestor.

#### INTRODUCTION

This study essentially comprises systematic revisions of a number of closely related octocoral genera within the gorgonian family Isididae. This family contains all of the gorgonian species where the articulated axial skeleton consists of well defined calcareous internodes which are not formed from fused sclerites and which alternate with sclerite-free proteinaceous nodes. The isidid genera are of a very diverse nature. Kükenthal (1915: 124–126; 1924: 560, 634–637) was clearly convinced the family was polyphyletic, and Bayer (pers. comm.) is of the opinion that a further accumulation of evidence may eventually justify a division into at least 2 and perhaps 3 separate familial groups.

There are 2 other families of gorgonians with articulated axes: the Melithaeidae and the Parisididae. They are both distinguished from the Isididae by the sclerite component of their axial skeleton. *Mirostenella articulata* Bayer, 1988 is an enigmatic taxon within the Primnoidae that has possible phylogenetic implications regarding the Isididae. It is the only primnoid where the scleroproteinaceous axis is partitioned at the points of bifurcation into translucent non-calcified horny 'nodes'.

The final scope of this project had its origins in a far more restricted study, which was to revise the isidid genus Mopsea Lamouroux, 1816. Such a study was considered to be of value after earlier attempts to accurately identify specimens of Mopsea (sensu lato) from Southern Australia revealed the extreme inadequacy of the literature. Unfortunately, a similar situation exists for the majority of octocoral genera, especially those of the Indo-Pacific. A student of the Australian octocoral fauna is hampered not only by the quality but also by the paucity of reports on the fauna of this part of the world. In Bayer's (1981) paper on the "Status of knowledge of Octocorals of World Seas" he placed the major geographic regions of the globe into 4 categories with respect to the levels of taxonomic knowledge: Essentially complete, Moderately well known, Poorly known, and Minimally known. The Australian octocorals were classed as Poorly known (p. 7), "where the literature is sparse and incomplete", "large numbers of species will inevitably be new to science", "the major part of the fauna remains to be described", and "distributional patterns are not clearly understood". Although a number of papers on the Australian octocoral fauna have been published since that work, the number of new Australian taxa described in the present work clearly supports Bayer's premise that much remains to be done.

The findings of the present study have shown that virtually all of the literature to date that deals with *Mopsea* (*sensu lato*) suffers from 2 major inadequacies. First, confusion over the generic characters of *Mopsea* (*sensu stricto*), and second, with the exception of Bayer and Stefani (1987a), markedly insufficient, poor quality, and often inaccurate, illustrations. As a result, the genus has become grossly paraphyletic. Of the 18 nominal species still recognised in the literature heretofore, it is proposed to retain only one, the type species *M. encrinula* (Lamarck, 1815). The inclusion of a previously undescribed taxon from the coast of New South Wales near Sydney leaves the genus at present with only two species.

It is easy with hindsight to criticise previous

authors for not recognising the paraphyletic nature of the genus. Perhaps, for example, Grant (1976) should have included M. elegans Thomson and Mackinnon, 1911, in his new family Circinisidinae where, with its cycloid scales, it surely belongs. But maybe such criticism is harsh, and that outcome would have been more likely if Thomson and Mackinnon had included a large scale figure of a polyp of *M. elegans* (as they did with other taxa) in addition to the 5 sclerite drawings. It is also harsh to criticise early authors for including, for example, both pinnately and dichotomously branched species in the genus when many other morphological characters appeared very similar and little comparative material was available. It is far more likely for patterns or groupings to emerge when large suites of specimens are available. In the present account, for instance, groups of pinnately branched colonies are shown to have other features in common which clearly differentiate them from those with 'dichotomous' branching. Pinnate groups are also differentiated from other pinnate groups, 'dichotomous' groups from other 'dichotomous' groups, and so on. In fact, in the proposed genera the branching patterns are so consistent as to possibly imply that many other gorgonian groups that include mixed colonial forms may be paraphyletic. In particular some genera of Primnoidae, a family said by various authors (e.g. Kükenthal, 1919) to have close affinities with Isididae.

When the examination of the literature during the initial identification attempts demonstrated its insufficiency, recourse was made to the type material of a number of the nominal *Mopsea* species which is housed in the Australian Museum. It was soon apparent that taxa of quite a diverse nature had been grouped within the genus, that some type series probably contained a mixture of species, and that a published revision would be essential for future workers. There is little doubt that the group is relatively important in the Australian context. Kükenthal (1924) in his synopsis of the world's gorgonians recognised 11 species (including 3 he considered doubtful). Of these, 7 were recorded solely from Australia, and Kükenthal had overlooked 2 Australian species described by Briggs (1915). Since then a further 5 species have been added to the genus; 2 from Australia and 4 from New Caledonia. Of the 53 species included in this revision, 72% are considered endemic to Australia.

During the process of reassessing and redescribing the species previously assigned to the genus, together with a re-evaluation of the associated literature, it became obvious that a necessary corollary was the appraisal of the available material of closely related groups

followed by detailed comparisons. The process of deciding which genera fell into the category of "closely related" gradually evolved as a greater knowledge of the different characteristics was gained by examining type specimens along with identified and unidentified collections from the major Australian museums and numerous overseas institutions. Bayer and Stefani (1987b: 938-940) provided the first summary of the relevant taxonomic characters since Kükenthal (1919: 606-609). They also stated that "The continuing increase in collections and discovery of new species obscures some of the taxonomic boundaries that have become accepted over the past century, making the allocation of species to genera, and genera to subfamilies, increasingly problematical". That statement, together with their summary, recognised the continued uncertainty of the value of the characters and their states, and the blurring, both perceived and real, of the discontinuities between them. A situation which, in light of my original observations regarding the nominal species of Mopsea, undoubtedly greatly contributed to the heterogeneity of the mix of taxa comprising that genus. The overall aim of the research has been to established the boundaries of the genus Mopsea (sensu stricto) and to characterise from available material all the taxonomic groups with which it is likely to be confused. The result includes revisions of the recognised genera Mopsea, Acanthoisis, Peltastisis, Minuisis and Circinisis, the validation of the neglected genus Notisis, and the proposal of 16 new genera. The study crosses the boundaries of 3 nominal subfamilies, Mopseinae, Circinisidinae, and Peltastisidinae, and proposes that the latter is not tenable as has already been intimated by Bayer and Stefani (1987b: 940). Twenty three established species are validated and redescribed, 15 as new combinations, and 30 new species are proposed. One colony with apparently malformed or deteriorated sclerites, and another consisting of a minute twig fragment with a single polyp, are both recorded as an indeterminate species.

It has become customary in octocoral systematics to include a brief species diagnosis at the beginning of each description. However, given the importance of sclerite form in distinguishing between different taxa, and the inadequacies of language as compared to illustration in describing these forms, the diagnoses of closely related species often read much the same. Correspondingly, Differential Characteristics which highlight salient features are substituted for diagnoses in the Systematics section, and these should be used in conjunction with the Figures.

Distribution maps are given both for genera and for individual species. Arrows on the maps are

designed to draw the eye to isolated stations or station groups, and to help distinguish between stations and islands.

Depth ranges quoted for each species are only guides in a number of cases as trawl or dredge stations often transversed zones of widely varying depth. They should therefore only be used with reference to the material collection data. The holotype of *Mopsea tenuis* Thomson and Mackinnon, for example was obtained from somewhere between 65–1300 fathoms.

During the course of the study it was necessary to apply to the International Commission on Zoological Nomenclature to use its plenary powers to designate *Isis encrinula* Lamarck, 1815 as the type species of the genus *Mopsea* and set aside all previous fixations (Alderslade, 1992). The existing situation was unsatisfactory because *Mopsea dichotoma* (Linné, 1758 *sensu* Lamouroux, 1816), accepted by many authors as the type species, was based on *Isis dichotoma* of Linnaeus which is an unidentifiable species of the family Melithaeidae. *Isis encrinula* was subsequently fixed as the type species by the Commission in Opinion 1738 (ICZN, 1992).

## Abbreviations

Abbieviations		
AM	Australian Museum, Sydney	
BM	The Natural History Museum, London	
MM	The Manchester Museum, The University	
MNHN	Muséum National d'Histoire Naturelle,	
	Paris	
MTQ	Museum of Tropical Queensland,	
	Townsville	
MTUF	Museum, Tokyo University of Fisheries	
NCI	National Cancer Institute of the United	
	States, Shallow Water Marine Organism	
	Contract, Australian Institute of Marine	
	Science Bioactivity Unit, Townsville	
NHMB	Naturhistorisches Museum, Berne	
NHMW	Naturhistorisches Museum, Wien	
NMV	Museum of Victoria, Melbourne	
NRS	Naturhistoriska Riksmuseet, Stockholm	
NTM	Museum and Art Gallery of the Northern	
	Territory, Darwin	
NZOI	New Zealand Institute of Water and	
	Atmospheric Research Ltd., incorporating	
	New Zealand Oceanographic Institute,	
	Wellington	
QM	Queensland Museum, Brisbane	
RMS	Royal Museum of Scotland, Edinburgh	
SAM	South Australian Museum, Adelaide	
USNM	National Museum of Natural History,	
	Smithsonian Institution, Washington, DC	
WAM	Western Australian Museum, Perth	
ZMA	Instituut voor Taxonomische Zoölogie,	
	Amsterdam	

ZMB Museum für Naturkunde der Humboldt-Universität, Berlin

#### MATERIAL

The revisionary parts of this work are based on a study of type material of all nominal species which were considered relevant. Fortunately, specimens with type status still exist for all of these taxa, and virtually every specimen has been examined. Also, with the exception of the couple of colonies from Port Phillip identified by Hickson (1890) as *Mopsea dichotoma* (Linné), all relevant material referred to in the literature from both Australian and European sources, as far can be ascertained, has been tracked down and borrowed for comparison. In addition, large amounts of comparative material from the following Australian institutions has been examined: (see Abbreviations) AM, MTQ, NMV, NTM, QM, SAM, WAM.

### **SYNONYMIES**

The synonymic listings have been made as comprehensive as possible; hopefully not to the point of redundance. One of the results of this investigation has been to show that the genus Mopsea as previously treated in the literature is grossly paraphyletic. Consequently, the majority of all the published definitions or references to the genus in keys and synopses are inherently only partially correct, and could all be legitimately cited as Mopsea (part) in the relevant generic synonymies given in this work. Many are included, but only where the author's intention can be inferred from their accompanying text. In addition, where such commonly occurring references as Kükenthal, 1919 and 1924 are continually referred to, it is done in the essence of completeness.

Amongst the lists of synonyms there is only a single entry (annotated) where the actual material identified by the respective authors has not been examined. All material will be found listed under "Type material" and "Additional material" prior to the species descriptions.

The synonymic lists includes correct identifications and misidentifications of specimens as well as the synonymy of species. Throughout the work where actual taxa have been equated, the following convention has been employed: " $\equiv$ " indicates objective synonymy, "=" indicates subjective synonymy. Where specimens have been subjectively assessed as being misidentified, new assignments are indicated by the symbol " $\Rightarrow$ ". Where the identification of specimens is assessed as correct there is no annotation.

#### TAXONOMIC COVERAGE

As a prelude to their discussion on taxonomic characters of the Family Isididae, Bayer and Stefani (1987b: 938) took the currently accepted subfamilial divisions as proposed by Kükenthal (1915, 1919,

1924) and subsequently modified by Grant (1976) and expressed them in key form, at the same time acknowledging that the "system is open to some criticism". In their key the following subfamilies were included: Muricellisidinae, Isidinae, Keratoisidinae, Peltastisidinae, Circinisidinae, and Mopseinae. The polyps of Muricellisidinae and Isidinae were characterised as retractile, the sclerites of the former being thorny spindles, and those of the latter being small rods with tubercles. The polyps of the other divisions were characterised as non-retractile. Those of Keratoisidinae having sclerites in the form of needles, spindles, and rods, and those of the remainder having exclusively scales. The scales of Mopseinae were described as transversely placed and crescentic with a dentate or serrate margin, those of Circinisidinae as irregularly arranged and cycloid with a smooth margin, and Peltastisidinae was differentiated as having polyps with an operculum. The subfamily Peltastisidinae was proposed by Grant to include Peltastisis and 2 new genera, Chathamisis and Minuisis. It was diagnosed as including colonies "having polyps with scalelike spicules, eight of these forming a fully differentiated operculum". Bayer and Stefani (p. 940) went on to point out the difficulties of sustaining this division due to the intergrading nature of the different protective arrangements of summital sclerites seen in the contracted polyps of various species from several genera. In the systematic section below, evidence is presented to fully support this view, and indeed to show that much of the material proposed by Grant to be included in Peltastisidinae does not have a "fully differentiated operculum" as was stated.

In a later discussion of taxonomic features, related primarily to Keratoisidinae, Bayer (1990: 205-207) proposed a revised subdivision of the family, and in his key to the genera of Isidinae and Keratoisidinae referred to only a third division, Mopseinae. Bayer cast doubt on the value of polyp retractility for subfamilial distinction and submerged Muricellisidinae into Isidinae on the basis of sclerite ornamentation. The proposal was placed at the end of the paper (p. 227) under the remarks on the new genus Orstomisis, and Muricellisis did not appear in the key. A reference to Circinisidinae neither appeared in the key nor was it discussed in the general text, and the only established genus, Circinisis, with its flat cycloid scales keys out in Mopseinae.

Mopseinae was defined as having "Sclerites in the form of flat plates, sometimes elongate and spindle-like but never with complex tubercular sculpture"; which must only apply to polyp sclerites in light of the complex tubercular nature of the coenenchymal spindles previously described by Bayer and Stefani (1987a) for species of *Mopsea*.

As such, Mopseinae continues to be differentiated from Isidinae, where the polyps have 6-radiates, tuberculate spindles, or are almost sclerite-free; and from Keratoisidinae where the polyps are armed with longitudinally arranged rods or spindles often ornamented with prickles.

With the aim of elucidating the complex of Mopsea-like taxa, this work therefore confines itself to isidids with polyps protected by scale-like sclerites. It is further confined to those genera where the scale-like sclerites are transversely arranged on the polyps, and where the colonial form is planar, more or less planar, or unbranched. The restriction to taxa with transverse scales eliminates from consideration the recently established genus Tenuisis Bayer and Stefani, 1987 plate-like which has elongate sclerites longitudinally arranged in the polyps. Tenuisis was adjudged to have possible affinities with Keratoisidinae (Bayer, 1990: 205) in which the larger polyp sclerites are predominantly longitudinal, and it should not be confusable with the genera described herein. This restriction also eliminates Sclerisis, whose extremely distinctive colonial growth form is well illustrated by Bayer and Stefani (1987a: Plate XXIXX; 1987b: Figure 14).

The restriction to planar and unbranched taxa eliminates Primnoisis, Chathamisis, and Echinisis, characterised by their dense bushy or bottle-brush colonial form. These genera are justifiable generically differentiated on that character which can be linked with a different polyp morphology in each case. The Scanning Electron Microscope (SEM) illustrations of the polyps of Chathamisis given by Grant (1976: 45), and those of Echinisis given along with drawings by Bayer and Stefani (1987b: 953, 961) clearly distinguish these bushy forms from the genera described below. Primnoisis can also be distinguished using the polyp illustrations which are included in this work. It should be noted that 3 recently added species of Echinisis (Bayer and Stefani, 1987b: 954-963) were founded on specimens that were not bottle-brush shaped. However, the material was fragmentary and could represent secondary branching units from bushy colonies. Although the species of Primnoisis, Chathamisis, and Echinisis are not described, remarks on these genera are included.

The revisionary aspect of this study therefore also includes the genera *Peltastisis* and *Minuisis* (colonial growth form modified by a commensal) which were formerly assigned to Peltastisidinae and are here reassigned to Mopseinae. It also includes *Circinisis* Grant, 1976, and numerous proposed new, closely related taxa which support the retention of the subfamily Circinisidinae, at least for the time being. The other established genera re-evaluated are *Mopsea, Acanthoisis,* and *Notisis,* all from the subfamily Mopseinae. The only exception to the inclusion of all of the planar taxa is that of *Stenisis*. The SEM pictures given by Bayer and Stefani (1987b: 971) show the polyp body sclerites are more spindle-like than scale-like, although not notably dissimilar from those occurring in some of the genera illustrated here. The axial architecture, on the other hand clearly prevents it from being confused with the species described below, and its occurrence in the Bahamas, as discussed later, suggest its inclusion in the Mopseinae is doubtful on zoogeographic grounds.

The following list includes all species considered valid and described in this work. The genera are listed alphabetically, as are the respectively assigned species, and in subfamilial groupings.

#### Subfamily Mopseinae

Acanthoisis dhondtae Bayer and Stefani, 1987 Acanthoisis flabellum Wright and Studer, 1889 Acanthoisis kimbla sp. nov. Acanthoisis myzourida sp. nov. Acanthoisis wrastica sp. nov. Iotisis alba (Nutting, 1910) gen. nov., new comb.

Jasminisis candelabra gen. nov., sp. nov.

Jasminisis cavatica gen. nov. sp. nov.

Jasminisis deceptrix gen. nov., sp. nov.

Jasminisis zebra gen. nov., sp. nov.

Ktenosquamisis bicamella gen. nov., sp. nov.

Lissopholidisis ampliflora gen. nov., sp. nov.

Lissopholidisis furcula gen. nov., sp. nov.

Lissopholidisis nuttingi (Grant, 1976) gen. nov., new comb.

Minuisis granti sp. nov.

Minuisis pseudoplana Grant, 1976 (emend.)

Mopsea encrinula (Lamarck, 1815)

Mopsea triaknema sp. nov.

Myriozotisis heatherae gen. nov., sp. nov.

Myriozotisis spinosa gen. nov., sp. nov.

Notisis elongata (Roule, 1907) new comb.

Notisis fragilis Gravier, 1913

Notisis charcoti sp. nov.

Oparinisis flexilis gen. nov., sp. nov.

Oparinisis parkeri gen. nov., sp. nov.

Oparinisis viking gen. nov., sp. nov.

Paracanthoisis richerdeforgesi (Bayer and Stefani, 1987) gen. nov., new comb.

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- Paracanthoisis simplex (Tixier-Durivault, 1970) gen. nov., new comb.
- Peltastisis cornuta Nutting, 1910
- Peltastisis uniserialis Nutting, 1910
- Pteronisis echinaxis gen. nov., sp. nov.
- Pteronisis incerta gen. nov., sp. nov.
- Pteronisis laboutei (Bayer and Stefani, 1987) gen. nov., new comb.
- Pteronisis oliganema gen. nov., sp. nov.
- Pteronisis plumacea (Briggs, 1915) gen. nov., new comb.
- Pteronisis provocatoris (Bayer and Stefani, 1987) gen. nov., new comb.
- Pteronisis whiteleggei (Thomson and Mackinnon, 1911) gen. nov., new comb.
- Sphaerokodisis australis (Thomson and Mackinnon, 1911) gen. nov., new comb.
- Sphaerokodisis flabellum (Thomson and Mackinnon, 1911) gen. nov., new comb.

- Sphaerokodisis tenuis (Thomson and Rennet, 1931) gen. nov., new comb.
- Tethrisis suzannae gen. nov., sp. nov.
- Subfamily Circinisidinae
- Annisis sprightly gen. nov., sp. nov.
- Circinisis circinata Grant, 1976
- *Florectisis rosetta* gen. nov., sp. nov.
- Gorgonisis elyakovi gen. nov., sp. nov.
- Pangolinisis cia gen. nov., sp. nov.
- Plexipomisis elegans (Thomson and Mackinnon, 1911) gen. nov., new comb.
- Plexipomisis thetis gen. nov., sp. nov.
- Zignisis alternata (Utinomi, 1975) gen. nov., new comb.
- Zignisis bifoliata gen. nov., sp. nov.

Zignisis lornae gen. nov., sp. nov.

- Zignisis phorinema gen. nov., sp. nov.
- Zignisis repens (Briggs, 1915) gen. nov., new comb.

In the following list, the left hand column includes references to all synonyms of the included species, including misidentifications, and the name considered valid is given in the right hand column. With the exception of two new combinations and one replacement name, the list only includes references to the literature where authors actually identified material to hand. Species names which were cited solely for the purpose of reviews or discussions are omitted here, although most are recorded in the more extensive synonymies given in the systematics section. The list is arranged alphabetically and then chronologically within.

Acabaria dakini Thorpe, 1928 Acanthoisis flabellum; Thomson and Mackinnon, 1911 Acanthoisis richerdeforgesi Bayer and Stefani, 1987a Isis encrinula Lamarck, 1815 Isis verticillata (new comb.); Schweigger, 1819 Meliteae verticillaris (nom. nud.) Lamouroux, 1812 Minuisis pseudoplanum Grant, 1976

Mopsea alba Nutting, 1910 Mopsea alternata Utinomi, 1975 Mopsea australis Thomson and Mackinnon, 1911 Mopsea australis; Briggs, 1915 Mopsea bargibanti Bayer and Stefani, 1987a Mopsea dichotoma; Wright and Studer, 1889 Mopsea dichotoma; Hickson, 1890 Mopsea dichotoma; Roule, 1907 Mopsea dichotoma; Thomson and Mackinnon, 1911 Mopsea dichotoma; Briggs, 1915 Mopsea elegans Thomson and Mackinnon, 1911

Mopsea elegans; Briggs, 1915 Mopsea elongata Roule, 1907 (and 1908) Mopsea elongata; Gravier, 1913b (and 1914) Mopsea elongata; Molander, 1929 Mopsea elongata; Grant, 1976 Mopsea encrinula; Studer, 1878 Mopsea encrinula; Wright and Studer, 1889 Mopsea encrinula; Thomson and Mackinnon, 1911

$\Rightarrow$ Zignisis sp. indet, this work
Acanthoisis flabellum Wright and Studer, 1889
=Paracanthoisis richerdeforgesi (Bayer and Stefani, 1987)
≡Mopsea encrinula (Lamarck, 1815)
(?≡, =)Mopsea encrinula (Lamarck, 1815)
(?≡, =)Mopsea encrinula (Lamarck, 1815)
part = <i>Minuisis pseudoplana</i> Grant, 1976 (emended)
part $\Rightarrow$ <i>Minuisis granti</i> this work
<i>≡Iotisis alba,</i> this work
<i>≡Zignisis alternata</i> (Utinomi, 1975)
<i>■Sphaerokodisis australis</i> (Thomson and Mackinnon, 1911)
⇒ <i>Sphaerokodisis australis</i> (Thomson and Mackinnon, 1911)
=Pteronisis provocatoris (Bayer and Stefani, 1987)
$\Rightarrow$ Jasminisis zebra, this work
(specimens not located)
$\Rightarrow$ Notisis charcoti, this work
$\Rightarrow$ Jasminisis deceptrix, this work
<i>⇒Jasminisis zebra,</i> this work
part ≡Plexipomisis elegans (Thomson and Mackinnon, 1911)
part $\Rightarrow$ <i>Plexipomisis thetis,</i> this work
$\Rightarrow$ Plexipomisis elegans (Thomson and Mackinnon, 1911)
<i>≡Notisis elongata</i> (Roule, 1907)
$\Rightarrow$ Notisis sp. indet., this work
$\Rightarrow$ Notisis charcoti, this work
⇒Notisis cf. fragilis Gravier, 1913
$\Rightarrow$ Zignisis sp. indet, this work
$\Rightarrow$ <i>Pteronisis incerta,</i> this work
$\Rightarrow$ <i>Mopsea triaknema</i> , this work

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Mopsea encrinula; Briggs 1915 part Mopsea encrinula (Lamarck, 1815) part  $\Rightarrow$  *Pteronisis incerta*, this work Mopsea encrinula; Kükenthal, 1919  $\Rightarrow$  *Pteronisis incerta*, this work Mopsea encrinula; Utinomi, 1972  $\Rightarrow$  *Pteronisis incerta*, this work Mopsea encrinula; Bayer and Stefani, 1987a Movsea encrinula (Lamarck, 1815) Mopsea flabellum Thomson and Mackinnon, 1911 *≡Sphaerokodisis flabellum* (Thomson and Mackinnon, 1911) Mopsea flabellum; Briggs, 1915  $\Rightarrow$  Sphaerokodisis flabellum (Thomson and Mackinnon, 1911) Mopsea flabellum (new comb.); Kükenthal, 1915 ≡Acanthoisis flabellum Wright and Studer, 1889 Mopsea laboutei Bayer and Stefani, 1987a ≡Pteronisis laboutei (Bayer and Stefani, 1987) Mopsea plumacea Briggs, 1915 part ≡Pteronisis plumacea (Briggs, 1915) part  $\Rightarrow$  *Pteronisis incerta*, this work Mopsea provocatoris Bayer and Stefani, 1987a ≡Pteronisis provocatoris (Bayer and Stefani, 1987) Mopsea repens Briggs, 1915 *≡Zignisis repens* (Briggs, 1915) Mopsea simplex Tixier-Durivault, 1970 *≡Paracanthoisis simplex* (Tixier-Durivault, 1970) *■Sphaerokodisis flabellum* (Thomson and Mackinnon, 1911) Mopsea squamosa (nom. nov.) Kükenthal, 1915 Mopsea squamosa; Utinomi, 1975 ⇒Mopsea encrinula (Lamarck, 1815) Mopsea tenuis Thomson and Rennet, 1931 ■Sphaerokodisis tenuis (Thomson and Rennet, 1931) Mopsea verticillata (new comb.); Lamouroux, 1816 (?=, =) Moysea encrinula (Lamarck, 1815) Mopsea whiteleggei Thomson and Mackinnon, 1911 part ≡Pteronisis whiteleggei (Thomson and Mackinnon, 1911) part  $\Rightarrow$  *Pteronisis echinaxis* this work Mopsea whiteleggei; Briggs, 1915 ⇒Pteronisis whiteleggei (Thomson and Mackinnon, 1911) Mopsea whiteleggei; Tixier-Durivault, 1970 ⇒Pteronisis provocatoris (Bayer and Stefani, 1987) Peltastisis nuttingi Grant, 1976 ≡Lissopholidisis nuttingi (Grant 1976)

The following list includes species previously assigned to the genus *Mopsea* but not included in this study. With the exception of a few entries the names refer to taxa in the subfamily Keratoisidinae or in the F. Melithaeidae. The recognised assignment is given in the right hand column, and authorities for the synonymies, where they exist, are given in square brackets. Only the material identified as *Mopsea gracilis* by Gravier (1913b and 1914) and Molander (1929) has been examined in conjunction with this study. That taxon was listed as an uncertain species of *Mopsea* by Kükenthal (1924: 441) but has never been critically evaluated.

Mopsea arbusculum Johnson, 1862 (and 1863) Mopsea bicolor Kölliker, 1865 Mopsea borealis Sars, 1869 Mopsea costata Milne Edwards and Haime, 1850 Mopsea dichotoma; Lamouroux, 1816 Mopsea eburnea Pourtales, 1868 Mopsea elongata; Philippi, 1842 Mopsea erythraea Ehrenberg, 1834 Mopsea flava Nutting, 1910 Mopsea gracilis; Dana, 1846

Mopsea gracilis Gravier, 1913b (and 1914) Mopsea gracilis; Molander, 1929

Mopsea hamiltoni; Chapman, 1912 Mopsea mediterranea Risso, 1826 Mopsea tenisoni Chapman, 1913

#### HISTORY OF THE INCLUDED TAXA

The histories of all but one of the relevant genera are comparatively short and simple. That of *Mopsea*, however, especially when combined with its associated familial and subfamilial complexities, is somewhat labyrinthine. This is primarily due to the genus originally including species of both what are now the families Isididae and Melithaeidae, together with the misplaced emphasis of subsequent early authors on nodal axial branching as a prime genetic character. In essence, the =Acanella arbusculum (Johnson, 1862) [Kükenthal, 1919: 578] most likely F. Melithaeidae
=Isidella lofotoensis Sars, 1868 [Kükenthal, 1919: 567]
Fossil of uncertain affinity
F. Melithaeidae, sp. indet.
=Acanella eburnea (Pourtales, 1868) [Kükenthal, 1919: 575–576]
Isidella elöngata (Esper, 1788) [Kükenthal, 1919: 565]
=Acabaria erythraea (Ehrenberg, 1834) [Kükenthal, 1919: 186]
Parisis sp. [Bayer, pers. comm.]
gen. indet., based on Isis gracilis Lamouroux, 1816, a decorticated axis
Primnoisis sp., this work
mixture: indeterminate decorticated axes (?Primnoisis +?Notisis) and a twig fragment of Primnoisis sp., this work
Fossil. Parisis hamiltoni (Thomson, 1908) [Hayward, 1977: 102]

Fossil. Parisis hamiltoni (Thomson, 1908) [Hayward, 1977: 102] =Isidella elongata (Esper, 1788) [Kükenthal 1919: 565] Fossil. ? Circinisidinae, this work.

problem became further exacerbated by the designation of the melithaeid species as the type of the genus, by the failure of later authors to recognise Gray's considerably accurate assessment of the situation, and by Wright's and Studer's stabilising of the situation with a completely erroneous account. Overlaying this was the more or less continual misidentification of specimens with nominal species, increasingly complicating a saga that appears to have begun about 4 years before the genus was established.

In 1812, Lamouroux published a synopsis of "Zoophytes flexibles, ou coralligènes non entièrment pierreux" which he described as an improvement on the earlier generic arrangement of Lamarck (1801). He established the family Isideae (now Isididae) for the genera Isis Linné, Melitea, and Adeona, which were characterised as having an articulated axis with segments alternatively corneous or suberous, and he proposed the new species Meliteae (sic) verticillaris, among others, without any description (a nomen nudum). Subsequently, Lamarck (1815), while agreeing with Lamouroux that Melitaea (Lamarck's spelling) should be separated from Isis, stated that the species Melitea verticillaris was in fact not a Melitaea but an Isis; the axis of Melitaea having nodes ("entrenoeds" of Lamarck) which were calcified, spongy and swollen, and that of Isis having nodes that were corneous, compact and not nodule-like. In the same publication, Lamarck went on to establish the new species Isis encrinula, quite probably using the material referred to Melitea verticillata by Lamouroux but making no mention of the fact. In 1816, Lamouroux agreed with Lamarck's remarks on axial structure, but disagreed on the inclusion of Melitea verticillaris in the genus Isis. Instead, he assigned the species to a new genus Mopsea, along with a second species Mopsea dichotoma. His description of Mopsea verticillata cited Isis encrinula as a synonym and used Lamarck's definition for that species almost verbatim. Lamarck continued to refer to the species



Figure 1 Hippuris coralloides carnea, Capensis, geniculis limosis. Redrawn original size from Petiver, 1702: pl.3, fig.10.

as Isis encrinula in later works, but all authors since Ehrenberg (1834) have used the name Mopsea encrinula.

Mopsea encrinula is a valid member of the Family Isididae, and was based on pinnately branched material collected by Péron and Lesueur in Nouvelle-Hollande (Australia). Mopsea dichotoma, the other species erected by Lamouroux, was originally established as Isis dichotoma by Linnaeus (1758) based on a brief description and drawing of "Hippuris coralloides carnea, Capensis, geniculus limosis" published by Petiver (1702). This illustration (redrawn here in Figure 1) of the decorticated axis of a melithaeid, clearly showing swollen nodes and dichotomous branching, should have been referred to Meliteae by Lamouroux instead of to Mopsea which he had defined as pinnately branched. It would seem likely that Lamouroux included Mopsea dichotoma solely on the strength of accounts of such authors as Pallas (1766), Esper (1788), and Gmelin (1791), and possibly a fragment of an articulated axis referred to Isis dichotoma by Lamarck (1815).

Lamouroux's inclusion of Isis dichotoma in the genus Mopsea undoubtedly misled many later authors who tended to focus on the fact that the branching occurred from the nodes. Thus Risso (1826) established Mopsea mediterranea (= Isidella elongata), and Ehrenberg (1834), adopting nodal branching as the premium character of the genus, included the melithaeid Mopsea erythraea (= Acabaria erythraea) along with Mopsea dichotoma and Mopsea encrinula as valid species. Similarly mistaken additions were to follow: Isis elongata Esper ( $\equiv$  Isidella elongata) assigned to Mopsea elongata by Philippi (1842); Isis gracilis Lamouroux (indet.) assigned to Mopsea gracilis by Dana (1846); Mopsea arbusculum Johnson, 1862 (= Acanella arbuscula); Mopsea bicolor Kölliker, 1865 (F. Melithaeidae); Mopsea eburnea Pourtales, 1868 (= Acanella eburnea); and Mopsea borealis Sars, 1869 (= Isidella lofotoensis).

Some of these latter authors may also have been influenced by the work of Milne Edward and Haime (1850) who designated Mopsea dichotoma as the type of the genus, and when proposing their new fossil species Mopsea costata, stated of Mopsea encrinula that "it is doubtful whether the last does in reality appertain to this division of the Isinae". If indeed they were so influenced it was in spite of Gray's (1858) accurate assessment that Mopsea dichotoma (= Isis dichotoma) was in fact not an isidid at all. Gray recognised the similarity of its axial form to that of Lamouroux's Melitea (which, like Lamarck (1816), he spelled Melitaea) and placed it in a new genus Mopsella in his family Melitaeadae (now Melithaeidae) based on that axial structure. Gray retained just one species of Mopsea, Mopsea encrinula, assigning Mopsea mediterranea, Mopsea

elongata, Mopsea gracilis, and (with uncertainty) Mopsea erythracea (Gray's spelling after Lamarck, 1836) to the new genus Isidella as Isidella elongata; both genera included in the family Isidae

With respect to Mopsea dichotoma not being an isidid, Kölliker (1865) was essentially in agreement with Gray. However, without any specimens of Mopsea (sensu stricto) before him, having only material identified as Mopsella dichotoma by Gray, along with Ehrenberg's Mopsea erythraea and a proposed new species Mopsea bicolor, all of which were melithaeids, Kölliker concluded the genus Mopsea should be in the subfamily Melithaeaceae; an example followed by Klunzinger (1877), but not by Wright (1869) who established the subfamily Mopseadinae for Mopsea and Acanella. Fortunately, Kölliker's histological analysis revealed the spiculose nature of the melithaeid axis, and all subsequent additions to the list of Mopsea species were true isidids. Unfortunately, however, although it was accepted that the actual specimens identified by Gray as Mopsella dichotoma should not be grouped in what is now the family Isididae (Mopsella eventually became recognised as a valid genus of the Melithaeidae), it was generally agreed that Gray had made an error in identifying Mopsella dichotoma with Isis dichotoma. Mopsea dichotoma still continued to be considered as a valid isidid and also as the type species of the genus in such major treatments as Kükenthal, 1915, 1919, 1924, and Grant, 1976. Nutting (1910) stated that Mopsea encrinula was the type species, presumably unaware of any earlier designation, but was ignored by later authors. Bayer and Stefani (1987a) were the first to outline the nature of the problem and to point out that the stability of the name Mopsea would depend on a ruling by the International Commission on Zoological Nomenclature on a wrongly identified type species. Subsequently, an application to this effect was made to the Commission (Alderslade, 1992) who ruled in Opinion 1738 (ICZN, 1993) that Isis encrinula Lamarck, 1815 be designated as the type species. In the latter publication mention was made of the earlier designation of Mopsea verticillata as type species by Dujardin (1846) in a natural history dictionary. That document was of apparent sufficient obscurity to have remained unnoticed by all authors in this field.

In 1870, Gray removed *Mopsea* and *Isidella* from the family Isidae, leaving only *Isis* remaining, and placed them both in a new family Mopseadae. He also created Acanelladae for a new genus *Acanella*, and Keratoisidae for *Keratoisis* Wright, 1869. In 1878, Studer reported on material collected by the *Gazelle* Expedition, and submerged all of Gray's families into Isidae. He described a decorticated specimen as a new species, *Isis antarctica*, and misidentified material from north west Australia as Mopsea encrinula (herein assigned to the genus Zignisis). In 1887, Studer was to improve on Verrill's (1883) proposal and again divide the family Isidae; this time into subfamilies: Ceratoisidinae, Isidinae, and Primnoisidinae. The latter to include part of Gray's Mopseadae, for Mopsea alone, together with 2 new genera, Primnoisis (for Isis antarctica) and Acanthoisis, both of which were to be described more fully in a report on material from the British Challenger Expedition. In that report, Wright and Studer (1889) retained the subfamilies Isidinae and Ceratoisidinae, but submerged Primnoisidinae into Mopseinae. These 3 subfamilies have been retained to date, with the spelling corrected to Keratoisidinae by Bayer (1956).

In the Challenger report, Wright and Studer gave the most comprehensive definition of Mopsea to that time, based, as they claimed, on an examination of Lamarck's specimens in Paris; those that were presumably used by Lamouroux when establishing the genus. Wright and Studer went on to describe intact colonies obtained by the Challenger that they had identified as Mopsea dichotoma and Mopsea encrinula, but their identifications were wrong and their remarks concerning the Paris specimens do not conform to the available evidence. With regard to Mopsea dichotoma they claimed that "The original specimens of Lamarck's Isis dichotoma in the Zoological Museum at the Jardin des Plantes, Paris, agrees (sic) in all particulars with our specimens, and it still has the original label attached to it, with the name written thereon in Lamarck's handwriting." In Lamarck's (1815) description of Isis dichotoma he admitted to only having seen a decorticated specimen, and the specimen labelled in Lamarck's handwriting is in fact an unbranched fragment of an articulated Adeona skeleton, which is a bryozoan. Wright and Studer also claimed of their colonies axis that "sometimes the ribs between the longitudinal furrows show sharp indented edges." This is again at odds with the smooth Adeona skeleton, which is obviously not a specimen with which their material supposedly "agrees in all particulars".

Lamarck's specimens of *Isis encrinula*, on the other hand, do have spined ribs on the internodes. However, despite Wright's and Studer's claim that "In one specimen, in the collection of the Jardin des Plantes, Paris, the origin of several branches from the calcareous joints is easily seen", which indicates the spines would also have been visible, the colonies from the *Challenger* that they identified as *Mopsea encrinula* do not have spined internodes. In their own words, the calcareous portions of the axis of their colonies only "exhibit distinct longitudinal furrows".

One could surmise that Wright and Studer

confused their notes on axial ornamentation, but their claim which indicates they saw a dichotomously branched specimen of Lamarck's complete with scleritic coenenchyme (i.e. "....agrees in all particulars") remains unexplained. Similarly unexplained is the differences in both the shape and the colour of the sclerites of the material they identified as *Mopsea encrinula* when compared to those of the Paris specimens of *Isis encrinula*. The latter specimens are orangeish and the sclerites are yellow. Wright's and Studer's white specimens of *Mopsea encrinula* are herein assigned to *Pteronisis incerta*, and their *Mopsea dichotoma* material to *Jasminisis zebra*.

Wright's and Studer's treatment of the genus complete with their validation of Mopsea dichotoma and the first illustrations of the sclerites of Mopsea encrinula, erroneous as it all was, unfortunately formed the basis for virtually all future related works. By this stage, all non fossil nominal species other than Mopsea encrinula and Mopsea dichotoma had been correctly reassigned to other subfamilial and familial groups, and the genus as defined was limited to planar isidid colonies, branching from both nodes and internodes, with non-retractile, club-shaped, incurved polyps protected by large thorny, scale-like sclerites. Correspondingly, both pinnately and dichotomously branched species continued to be added. The first of these species was Mopsea elongata Roule, 1907 (described more fully in 1908) from the material obtained by the first French expedition to Antarctica, and assigned herein to Notisis elongata. Roule also identified a colony as Mopsea dichotoma, and that specimen is assigned herein to Notisis charcoti.

Nutting (1910), reporting on the material obtained by the *Siboga* Expedition, adopted Wright's and Studer's (1889: xlv) abbreviated definition of the genus, which he then misquoted and proceeded to give scant attention. His new species *Mopsea flava* was described as having dome-shaped calyces and completely retractile polyps. The plate-like sclerites are characteristic of *Parisis*, a taxon with a scleritic axis in the family Parisididae, and this diagnosis has been confirmed by Bayer (pers. comm.). Nutting's other new species *Mopsea alba* is assigned herein to *Iotisis alba*.

In the same report, Nutting also established a new genus *Peltastisis* for 2 unbranched species *P. uniserialis* and *P. cornuta*. He identified in the polyps an opercular arrangement of 8 large triangular scales as the main character with which to distinguish the genus from *Mopsea*. The genus is maintained herein, although a re-examination of the material has failed to confirm Nutting's diagnosis for the genus.

Gravier described the results of his examination of the octocorals obtained by the second French expedition to the Antarctic in several papers

during 1913 and 1914, and he established the new genus Notisis for the species Notisis fragilis described as branching in a pseudo-dichotomous manner. He distinguished this genus from the other genera in the subfamily Mopseinae on the axial architecture, remarking that the internodes of N. fragilis were not furrowed and the spines were well spaced and not united as pronounced crests. The genus is maintained here, although reexamination has revealed the internodes are indeed furrowed. Curiously, Gravier also identified other specimens of similar appearance, having the same axial architecture, with Roule's Mopsea dichotoma. These specimens are also assigned herein to Notisis. Gravier also proposed the new species Mopsea gracilis for a number of fragments which on reexamination prove to be from a colony of Primnoisis.

The "Alcyonaria" obtained between February and March, 1898 by Her Majesty's Colonial Steamer Thetis during fisheries research off the New South Wales coast were described in 1911 by Thomson and Mackinnon. They added the new species Mopsea australis (herein assigned to Sphaerokodisis australis), Mopsea flabellum (herein assigned to Sphaerokodisis flabellum), Mopsea elegans (a mixture herein assigned to Plexipomisis elegans and Plexipomisis thetis, in the subfamily Circinisidinae), and Mopsea whiteleggei (a mixture herein assigned to Pteronisis whiteleggei and Pteronisis echinaxis). They also identified some of the material as Mopsea dichotoma which is herein assigned to Jasminisis deceptrix, and some as Mopsea encrinula which is herein assigned to Mopsea triaknema.

Further fisheries experiments were carried out off the east coast of Australia by the Endeavour between 1909 and 1914. The octocorals were described by Briggs, in 1915, who established 2 new species; Mopsea plumacea, herein assigned to Pteronisis plumacea, and Mopsea repens, herein assigned to Zignisis repens. Briggs correctly identified material with Thomson's and Mackinnon's species Mopsea elegans, Mopsea australis, Mopsea flabellum, and Mopsea whiteleggei which are herein assigned as previously indicated. Some of the specimens Briggs identified as Mopsea encrinula were correctly assessed, but the lot was a mixture containing several colonies assigned herein to Pteronisis incerta.

Kükenthal reviewed the history and classification of the family in 1915, correcting the spelling from Isidae to Isididae, as a prelude to his major work in 1919 on material from the German Deep Sea Expedition of 1898–1899. Of significance, Kükenthal erected the new subfamily Muricellisidinae for the new genus *Muricellisis*, made *Acanthoisis* a junior synonym of *Mopsea*, and expressed his doubts about the validity of *Notisis* 

suggesting it probably should be similarly synonymised. Acanthoisis was established by Wright and Studer (1889) for a rather distantly pinnate colony, Acanthoisis flabellum, collected by the Challenger off Port Jackson, Sydney, Australia. The colony has short cylindrical polyps and axial internodes with heavily spined ribs. Brushing aside the different shape of the polyps, Kükenthal equated all of the other features with those of Mopsea and placed Acanthoisis flabellum in that genus. Mopsea flabellum (Wright and Studer, 1889) predated the already existing binomial Mopsea flabellum Thomson and Mackinnon, 1911, so Kükenthal proposed Mopsea squamosa as a replacement name for the latter species. In 1911, Thomson and Mackinnon had correctly identified specimens of Acanthoisis flabellum from material obtained by the Thetis, and that was the last report of specimens referrable to this form until Bayer and Stefani (1987a) validated Acanthoisis as a distinct genus and added 2 new species, A. dhondtae and A. richerdeforgesi, from the Chesterfield Islands and New Caledonia respectively. The genus is maintained here, but A. richerdeforgesi is assigned to Paracanthoisis.

Kükenthal's (1919) massive 2 volume work on the Deep Sea Expedition, most of which was purely revisionary, extensively reviewed the family but added nothing new to the elucidation of *Mopsea*. The only new specimens of the genus described were a few colonies from Tasmania from the collections of the natural history museum in Vienna. Identified by Kükenthal as *Mopsea encrinula* they are assigned herein to *Pteronisis incerta*. Much of the information from this 1919 publication was reprinted in Kükenthal's synopsis of the gorgonians published in 1924.

Some colonies of Isididae from the Swedish Antarctic Expedition of 1901–1903 were described by Molander in 1929, and the material he identified as *Mopsea elongata* is assigned herein to *Notisis charcoti*. The specimens he identified with *Mopsea gracilis* are fragmentary and a mixture. The only piece with polyps still attached is referrable to *Primnoisis*.

Thomson and Rennet (1931) added the new species *Mopsea tenuis* from material collected by the Australian Antarctic Expedition of 1911–1914, and the species is assigned here to *Sphaerokodisis tenuis*. They also established the new genus *Echinisis* in Mopseinae to accommodate *Ceratoisis spicata* Hickson, 1907 and *Primnoisis armata* Kükenthal, 1912.

No new relevant material was reported for nearly 40 years until Tixier-Durivault (1970) described a new species from New Caledonia, *Mopsea simplex*, which is herein assigned to *Paracanthoisis simplex*. The author also identified some specimens as *Mopsea whiteleggei* which are assigned herein to *Pteronisis provocatoris*. Utinomi published 2 papers on Australian octocorals in 1972 and 1975. In the first he reported specimens of *Mopsea encrinula* from Port Phillip (which are herein assigned to *Pteronisis incerta*) perpetuating the opinion of Wright and Studer (1889) that *Mopsea encrinula* does not have an axis with pronounced spiny ridges. In the second paper Utinomi reported *Mopsea squamosa* ( $\equiv M$ . *flabellum* Thomson and Mackinnon) and a new species *Mopsea alternata* from Western Australia. The former specimen, ironically, is a genuine *Mopsea encrinula*, and the latter is assigned herein to *Zignisis alternata*.

In 1976, Grant published a large paper on Isididae from New Zealand, without including any individual sclerite illustrations, in which he established new subfamilies. The first was Circinisidinae for the new genus and species Circinisis circinata, an unbranched isidid with cycloid sclerites. The second was Peltastisidinae to include Peltastisis along with 2 new genera Chathamisis and Minuisis, both diagnosed by Grant as having polyps with an operculum of 8 scales. Grant's new species Minuisis pseudoplanum has been found to be a mixture of 2 species, neither of which has a discrete 8-scaled operculum, and part of his material is assigned herein to a new species Minuisis granti. The author's new species Peltastisis nuttingi has been assigned herein to Lissopholidisis nuttingi, and it is proposed that his subfamily Peltastisidinae cannot be sustained based as it was on an operculum of 8 scales.

The most recent paper to propose new species of Mopsea is that of Bayer and Stefani (1987a), wherein the authors describe and illustrate for the first time the nature of the sclerites and axis of the type material of Mopsea encrinula from the Lamarck Collection in Paris. Bayer and Stefani pointed out the instability of the genus in having the melithaeid species Isis dichotoma as the type species, and commented on the mixture of axial forms and colonial branching within the group. However, they declined to speculate further pending the results of this present work which had already been commenced. The authors added 3 new species from New Caledonia: Mopsea provocatoris, herein assigned to Pteronisis provocatoris; Mopsea bargibanti, herein synonymised with Pteronisis provocatoris; and Mopsea laboutei, herein assigned to Pteronisis laboutei. The Australian material they identified as Mopsea whiteleggei is herein assigned to Pteronisis incerta, and their validation of Acanthoisis has been mentioned above. In a second paper, Bayer and Stefani (1987b) published the first detailed illustrations of sclerites and axial architecture of Primnoisis antarctica and Echinisis spicata, adding new species to both genera. They also established the new genus Stenisis from the Bahamas with uncertain affinities to the subfamily Mopseinae.

#### TERMINOLOGY AND TAXONOMIC CHARACTERS

As pointed out by Bayer and Stefani (1987b), the classification and identification of the isidid octocorals has been traditionally based upon 5 morphological attributes. These are (1) polyp retractility, (2) colonial growth form, (3) characteristics of the axis, (4) characteristics of the sclerites, and (5) arrangement of the sclerites on the polyps. In 1976, Grant expanded the latter attribute to include, as a major character, the presence of an opercular-like arrangement of 8 sclerites over the oral region of the polyps. The opportunity to study hundreds of specimens during the course of this project has revealed relatively distinct character states with respect to colonial branching, axial architecture, and polyp form which, when correlated in association with sclerite shape, appear to form natural groupings of species that are treated here as distinct genera. These groupings are in contrast to the common perception of the genus Mopsea, for example, where very different character states pertaining to all 5 of the previous attributes can be demonstrated amongst the current nominal species. In the system proposed in this work, colonial branching, axial architecture, the structure of the polyp, and general sclerite form and distribution are, with rare exceptions, consistent within a genus. The rare exceptions - showing deviation from a single character state representing, in all probability, ongoing evolutionary processes - are made inclusive rather than add to the proliferation of generic names.

#### Growth form

With few exceptions, colonies are either planar or unbranched. In general, the exceptions are branched colonies where multiple overlapping fans or some minor out-of-plane branching gives the upper part of the colonies a slightly bushy appearance, and these are referred to as more or less planar. Amongst the planar colonies the following branching patterns predominate: *pinnate*, *sympodial*, and *pseudo-dichotomous*. Unbranched colonies are always filiform.

*Pinnate* branching in such genera as *Mopsea* and *Pteronisis* is for the most part plumose. The fine lateral twigs are referred to as *pinnae* (*pinna*, singular) and are generally densely arranged in a feather-like pattern. The thicker rachis of the 'feather' is usually referred to here as a *major* or *principal* branch. The branching of the plumes is commonly neat but irregular, with *pinnae* occurring in both opposite and alternate positions. *Pinnae* 

rarely subdivide except to produce lateral plumes. *Pinnate* branching in *Acanthoisis* is comparatively untidy, very irregular, and more widely spaced. In that genus, anastomoses are not uncommon, and colonial form is flabellate rather than plumose.

There are numerous definitions for sympodial branching, mostly in a botanical context. That used here is adapted from Hine (1977) as follows: a form of development wherein a lateral branch continues growth in the direction of the parent branch, and the parent branch continues growth as a lateral branch, zigzag fashion. A lateral branch which is the result of sympodial development is referred to here as a pseudo-lateral. There is often little distinction between a pseudo-lateral branch and a parent branch except in the older parts of the colony where the latter is thicker. As a variation, in some colonies the stem or main branch may repeatedly bend away in the same direction at each bifurcation instead of zigzagging, producing a series of lateral branches along one side. This is referred to as branching secundly.

In a strict sense, dichotomous branching refers to growth by repeated dichotomous forkings. That is, division into 2 equal parts with both parts identically angled away from the axis of origin. Genera with branching of this style have not been found amongst the group under study. Perhaps the closest example within Isididae is Orstomisis Bayer and Stefani, 1990, while other occurrences are found in parts of some chrysogorgiid, primnoid, and ellisellid colonies. All of the 'dichotomous' taxa in this work have bifurcations which are predominantly irregular. Regarding the 2 products of a forking, (a) they may arise at different angles, (b) they may be of different thickness, (c) only one may branch, or (d) if both re-branch they do so at different distances from the point of origin. Here, such branching is termed quasi-dichotomous. In some instances, such as in Sphaerokodisis australis (Figure 137), apparent quasi-dichotomous branching is found on closer inspection to be formed by repeated divisions that are actually lateral, and the lateral product commonly curves upwards to continue more or less parallel to the parent branch. This is referred to as *pseudo-dichotomous* branching. Neither quasi-dichotomous nor pseudo-dichotomous branching occurs consistently throughout an entire colony, but one of the modes will clearly be dominant.

Ramification in an irregularly *lateral* manner is recorded for only 4 species in this group. In 2 of these, *Annisis sprightly* and *Florectisis rosetta*, the branching is probably pseudo-dichotomous but obscured by extreme irregularity or sparseness. In *lotisis alba* and *Pteronisis oliganema* the branching is extremely sparse and may represent a distantly pinnate pattern.

Measurements of the thickness of branches, the

angle of branching, the distance between consecutive subdivisions, and the lengths of undivided branches have all been reported in the descriptive text. The distance between consecutive subdivisions has been measured from the centre of one branching point to the centre of the next. In instances where 2 consecutive twigs on the same side of a parent branch emerge so closely that they touch, the distance is recorded as zero.

#### Axis

The articulated sclerite-free axes of alternating calcareous internodes and horny nodes is the major character separating Isididae from the other families of gorgonians. Comparative studies of the internal structure of the calcareous internodes have been only briefly attempted. In more recent times Kükenthal (1919) published illustrations of thin sections of the axis of 2 species of Keratoisis, Bayer (1955) illustrated the axial structure of Isis hippuris and Primnoisis antarctica, and Grant (1970 and 1976) compared the axes of a few species covering the genera Keratoisis, Acanella, Notisis (his Mopsea elongata), Primnoisis, Chathamisis and Circinisis. However, even this sparse analysis has indicated that the arrangement of the calcareous fibres and horny lamellae of the internodal structure may possible be correlated at subfamilial, generic, and perhaps even specific levels. Isidid taxonomy would benefit from further research in this area, and the present study could form a framework in which to compare the axes of Mopseinae and Circinisidinae.

Kükenthal (1919) refuted the opinion of Gravier (1913) that the architecture of the internodal surface is an important character, stating that the longitudinal ribs and furrows, and associated tooth-like projections, are simply features of the species. In reality, if the axial surface sculpturing is divided into 2 categories it correlates more or less exactly with colonial branching, polyp structure, and sclerite form, and can be used as a generic character. The 2 categories are essentially the presence or the absence of large tooth-like spines arranged in longitudinal rows (e.g. Figure 28H), each row aligned along a ridge, or forming the ridge by the adjoining of their bases. Six genera have this axial form present, and in all cases the surface of the ridges and the spines is smooth. No members of Circinisidinae have been recorded with this style of axis, and the 6 genera are all included in Mopseinae.

In those taxa without the large axial spines, the internodes are commonly also longitudinally ridged, and the surface is either smooth or has numerous granules, denticles, or very small spines; the difference between the latter 3 states being related to the size of the irregularities and entirely subjective. Although within a species the number of ridges along an internode of given thickness is fairly consistent, the extent of granulation (or denticulation) may vary both within a colony and between specimens. Granulation can be used, however, as a species level character, as it is either always present in all specimens or always absent. Species can also be differentiated by considering whether the granulation is confined to the ridges or whether it can occur all over the internodal surface.

In order to facilitate description of the axial internodes some new terminology is introduced. The longitudinal ridges are distinguished as either primary or secondary. Most internodes only have primary ridges. They extend virtually the whole length of the internode, often have pronounced shoulders at each end, and are of equal prominence (e.g. Figures 236G-I; 125D,E). The area between adjacent ridges may be concave, forming a furrow, convex and broad, or may contain another ridge. The latter are secondary ridges and are generally lower and shorter than the primary ridges, and have reduced shoulders and less sculpturing (e.g. Figures 236E,F; 100F; 132D). They are not common in some species and are often obviously just developing primary ridges. In other species, however, they are a relatively constant feature and would appear to be present to add structural strength. The difference between a broad convexity and a broad secondary ridge is often subjective. As a general rule, ridges do not have desmocyte cavities on them, at least not on the summits. These cavities are the circular, oval, or elongate pits reported by Bayer and Stefani (1987b: 950) to mark the locations of desmocytes in the axis epithelium. They usually occur in longitudinal series between adjacent primary ridges (e.g. Figure 28H), or between primary and secondary ridges. They are often found just along the base of primary ridges that have a wide convexity between them which is then in essence a broad secondary ridge (e.g. Figures 221H; 213E,F).

It is important to note that the nature of the internodal surface varies considerably between different parts of a colony. In the finer branches, especially in the more distal parts, the internodes are often more or less 4-sided. The 4 longitudinal edges may be raised as ridges (e.g. Figure 202E) or not elevated at all (e.g. Figure 104H). The more proximal internodes may develop more ridges, but in some cases the 4-sided nature will be retained until the lower order branch is encountered, and on occasion throughout most of the colony. In pinnate forms such as Pteronisis, the principal branch of a plume usually will have more ridges than the pinnae, except at the growing tip. In general, the older, thicker internodes of a colony will have still more ridges, but the raised shoulders commonly found in finer branch internodes will often be reduced or absent.

In those species where the internodal surface is sculptured with granules or denticles, the most distal few twig internodes may be smooth. The preceding few may have the denticles restricted to ends of the internode or to the ridge shoulders, and only the proximal internodes may have irregularities extending the whole length. The reverse commonly occurs in the older parts of the colonies. Internodes in the major branches will often show a reduction in quantity and size of the irregularities which increasingly become restricted to the ridge shoulders in the lower regions, and are commonly absent altogether from the axis of the main branches and the stem. In some species, however, denticulation occurs on all colonial internodes.

Because the changes in axial architecture in the thicker, older parts of the colonies tends to reduce the appearance of these internodes from many different species to a common denominator, illustrations given here are predominantly of the internodes of the finer branches. It is in this region that the axes of different species can be more clearly differentiated.

Axial nodes do not have surface sculpturing except in a couple of species where they have longitudinal ridges in the stem and main branches which are aligned with those of the adjacent internodes. The most important feature of the nodes is their colour, together with any associated pattern, which within certain ranges tends to be characteristic for a species. The ends of the cylindrical nodes, where they cover and are attached to the often dome-like extremities of the internodes, appear to be fibrous, and the fibres are so fine that they reflect the light so as to give a satin-like sheen to this zone which is termed the border. The optical density of the main portion of a node is generally greatest for those in the stem and main branches. References to the degree of opacity of both nodes and internodes pertain to incident light, as even the densest axial material is translucent when illuminated from behind.

Within all taxa where colonies are branched, branching occurs from both nodes and internodes. In most genera of Mopseinae, however, it is predominantly from the internodes, whereas in Circinisidinae it is predominantly from the nodes. Although some colonies seem to have more or less regular distances between consecutive subdivisions, they are generally not consistent, and neither are the lengths of the internodes. Therefore, subdivisions will irregularly but repeatedly coincide with all or part of a parent branch node. Whether branching from a node or an internode, lateral branches may themselves begin with either a node or internode. Many of the styles of subdivision are common to numerous species, but a preponderance of several methods is generally found to be characteristic to individual taxa. The major variations are given in Figure 251. The effect of environmental conditions, for example current strength, on the dominant branching method adopted by a colony is unknown, but specimens of an individual species showing widely different bifurcation styles were not encountered.

There are a number of publications where fossil axial material has been attributed to the family Isididae: more recently, for example, by Voigt, 1958; Grant, 1970; Hayward, 1977; Kuz'micheva, 1980; and Grasshoff and Zibrowius, 1983. With relatively few exceptions, the research has been concerned with the palaeontology of Europe and Asia, and material has generally been assigned to Isis or the subfamily Keratoisidinae. A full analysis of the nominal isidid geological reports is outside the scope of this work, but it is apparent that internodal surface ornamentation has been used as a prime diagnostic feature with which to differentiate taxa. Despite Duncan's (1875) self directed remark that his own groupings were "of no great value, as they only refer to one portion of the organism, which in all probability is very variable", ornamentation has understandably continued to be used to place fragments in different specific, generic, and subfamilial classifications. It is hoped that the considerable details of axial architecture recorded here, along with remarks on its often extreme variability within a single colony, will not only facilitate the identification of non-fossil specimens where only colonial fragments have been obtained, but will prove valuable in the assessment of relevant palaeontological material,

#### Polyps

The form of the polyps is of major importance in differentiating between genera. The features to be considered are the orientation of the polyp, and the arrangement of the sclerites, particularly those sclerites protecting the oral region. In order to deal with the structure of the polyp, however, it is first necessary to review some of the currently accepted terminology.

The terms *anthocodia*, *anthostele*, *anthocrypt*, and *anthopoma* were introduced by Bourne (1900), and the first 2 of these, *anthocodia* and *anthostele*, have been generally adopted by subsequent authors. Unfortunately, over the intervening years their application, particularly that of *anthostele*, has been a corruption of Bourne's original intent. The term *anthocodia* was defined as the distal, total, free portion of the polyp complete with mouth and tentacles, and *anthostele* as that part of the polyp fused to its neighbours, i.e. the gastrodermal canal beneath the surface of the coenenchyme. Bourne also proposed that if the *anthocodia* was capable of retracting within the *anthostele*, and if the upper

extremity of the *anthostele* was reinforced with sclerites, then the latter coenenchymal protrusion should be called the *anthocrypt* instead of the older names of *calyx* or *verruca*; but the term never became used.

Under the pens of various authors, the gradual misuse of Bourne's terms resulted essentially in the following: 1) anthocodia became often used to refer only to the uppermost part of the polyp body, primarily the tentacles and tentacle bases, sometimes inclusive of the polyp head enclosing the pharynx; 2) anthostele became generally synonymous with calyx and verruca, which were contemporaneously used for the reinforced base of the 'polyp', and for the free part of a non-retractile polyp if it was covered in sclerites. The latter confusion would appear to be due, at least in part, to the similarity between the words calyx and calice, and the mistaken use of calices as the plural of calyx. It would seem that calice, from the Latin calix (a drinking cup) was originally employed for the domed polyp 'operculum', and calyx, from the Greek Kalyx (the cup of a flower) was employed for the structure into which a polyp retracts.

It would be a complex task to attempt to trace the full history and the possible reasons behind the change in usage of all the related terms, but it is illuminating to select isolated illustrations. Hickson (1906: 331) for example, used the term anthocodia correctly, avoided the use of anthostele, but then went on to describe contracted, non-retractile polyps with infolded tentacles as verrucae. Thomson and Ritchie (1906: 852-855) referred to the polyps of primnoids as calices, and to a single polyp as a calyx. When Sherriffs (1922) devised his coded formulae for the identification of species of Dendronephthya, he divided the polyp sclerites into 4 groups, and reserved the term "Anthocodial spicules" for those only on and just below the base of the tentacles. Subsequently his scheme was generally adopted for all genera in Nephtheidae with supporting bundles. Deichmann (1936: 28-29) correctly defined anthocodia, defined anthostele as the proximal rigid part of the polyp, defined calyx and calicle as the basal part of the anthocodia equal to verruca, and defined verruca as the contracted polyp. Hickson (1932: 501) referred to the non-retractile polyps of Acanthogorgia as verrucae, and Tixier-Durivault (1970: 329) called them calyces using the French *calice*. Verseveldt's drawing in Verseveldt and Bayer (1988: 72) clearly designates only the uppermost part of the polyp as the anthocodia supported below by a sclerite-free zone called the *introvert*. However, these authors (pp. 8-9) did retain Bourne's concept that the calyx (Bourne's anthocrypt) was a projection of the coenenchyme.

Bayer and Stefani (1987b: 939) reviewed the term calyx in the context of isidids and correctly confined its use to the retractile polyps of

Muricellisis. However, they maintained that there is no suitable name for polyps that are incapable of retraction and suggested verruca should be revived for this purpose. In actual fact, the term anthocodia as originally defined by Bourne is correct for such isidid polyps, and also for similarly constructed polyps in other families such as Primnoidae and Ellisellidae. In light of the confused history of the use of the term *verruca* it would seem preferable to return to the literal meaning of anthocodia, and also of anthostele. This would render Bayer's and Stefani's other statement (p. 938) "the polyps of Isis, although completely retractile, are not (my italics) composed of anthocodia and anthostele" as incorrect, and would maintain a greater consistency of defined structure amongst the Octocorallia. An autozooid polyp without an anthocodia is not complete. In the case of Isis, with its thick coenenchyme, there is also an anthostele within which the anthocodia can retract. Alternatively, in Chrysogorgia, for example, the structure is different, and with so meagre a covering of coenenchyme it makes no sense to speak of an anthostele. Although in Bourne's sense of the word, *polyp* (or *zooid* as he preferred) included both anthostele and anthocodia, for the purposes of morphological descriptions polyp and anthocodia are used interchangeably in this work.

In order to adequately describe the sclerite arrangement on the polyps it has been necessary to divide the anthocodia, somewhat artificially, into separate zones. Most polyps, whether erect or reclined, are more or less shaped like a capstan or a club, and for the purposes of mensuration and general morphological reference are described as having a *base*, a *neck*, and a *head*. For the description of sclerite distribution, however, it is necessary to distinguish between the protective arrangement covering the oral end, the 'operculum' of authors, and that on the rest of the polyp. The term operculum has seen various applications within several gorgonian families, but has been more traditionally associated with Primnoidae where during contraction the oral region of the polyps in a number of genera is closed by 8 triangular scales. Similar, but usually more complex arrangements found in Mopseinae and Circinisidinae are analogous but not homologous to the operculum of Primnoidae where the opercular scales are inserted mesenterially. In the material under study, the 8 sectors, or octants, of the 'operculum' are situated between the mesenteries, and each *octant* generally contains a number of sclerites in a single row or complex arrangement. No name exists in modern literature for such a structure and it seems both justifiable and appropriate to revive the generic term anthopoma which was established by Bourne for this specific purpose but never became accepted. Both the operculum of primnoids and

the crown and points arrangement found in many octocoral groups can be considered as different constructive forms of the anthopoma. The latter can be defined as the protective structure which covers the oral region of a polyp during contraction, and which is formed from the sclerites on and just below the bases of the tentacles. The remaining region of the polyp of which the sclerites and their arrangement is important, i.e. all of the anthocodia proximal to the anthopoma, is referred to as the polyp body. The division is artificial in that the anthopomal sclerites are in fact the distal sclerites of the polyp body proper. In an expanded polyp of species of Mopseinae or Circinisidinae the covering of scales would be seen to extend around and up the body, eventually becoming organised into a ring of 8 triangular sectors around the polyp head, one below each tentacle. The sclerites at the tips of the sectors would encroach little, if at all, onto the actual bases of the tentacles, which is contrary to the comments of some authors. For example, Nutting (1910) remarked of Peltastisis cornuta that the triangular scales of the "operculum" were "fitted" to the dorsal surface of the tentacles. During contraction, the tentacles deflate and shorten to but a fraction of their extended size. The oral region is pulled down and becomes concave so that the stub-like tentacles face inward, and the outer rim contracts sphincter-like above the oral disc so that the 8 triangular sclerite groups come to lie on the summit of the polyp forming the anthopoma. In most of the polyps that were dissected, the contracted tentacles were closely appressed, inverted, and filling the cavity between the anthopoma and the oral disc. In others, the tentacles were less contracted, the pharynx was open, and the tentacles protruded down into the pharyngeal space.

The orientation of the polyp in the contracted state is inextricably linked to the arrangement of the sclerites. In those genera where the sclerites are more or less evenly distributed around the polyp body, for example Primnoisis, Minuisis, or Florectisis, the contracted anthocodia stands more or less erect. In most genera, however, the polyps lie obliquely to the branch, often turning the oral end toward its surface. In order to do so the adaxial side of the polyp body, that facing the branch, has the sclerites reduced in size and number; (the abaxial side is that facing away from the branch). It is important for generic differentiation to establish the adaxial sclerite arrangement. Polyps that are able to lean or fold toward the branch surface due to fewer and smaller adaxial sclerites have been called adaxially reduced. Those polyps also described as adaxially naked have very few or no sclerites in this area. For example, the polyps of Myriozotisis (Figure 167F), Ktenosquamisis (Figure 159E,F), Sphaerokodisis (Figure 125G,J), and

*Pangolinisis* (Figure 210D,E) are all referred to as *adaxially reduced*, but only the latter 2 are also *adaxially naked*.

The extent of polyp curvature is generally reflected in the structure of the anthopoma. In those genera with erect polyps, such as Minuisis, the 8 anthopomal octants are of the same size, although not necessarily of completely identical structure, and the anthopoma is referred to as symmetrical. In those genera where the polyps curve towards the axis, the octants on the adaxial side are often smaller and the anthopoma is asymmetrical. In species with long, curving polyps the asymmetry may not be very pronounced, as the long body allows easy presentation of the anthopoma to the branch surface. In species with short, curving polyps, a marked reduction in the structure of the adaxial portion of the anthopoma is needed to facilitate positioning of the oral region against the branch. In some genera, obliquely oriented polyps always face the anthopoma away from the branch and there is little need for asymmetry. Many intermediate states occur.

In obliquely oriented polyps, the 8 anthopomal octants are designated as follows: the *adaxial* and *abaxial* octants are diametrically opposite each other, the 2 either side of these are the *adaxiallateral* and *abaxial-lateral* octants respectively, and the remaining 2 are the *laterals*. The term *minor octant* is occasionally used to designate the *adaxial* octant, and the other 7 are collectively the *major octants*.

It was stated in the section on taxonomic coverage that only taxa with non-retractile polyps are included in this work. A number of species, however, present the appearance of having retractile anthocodiae. Although the structure of their polyps may only be accurately ascertained by the study of live material or a series of relaxed specimens, it would seem that their appearance can be explained by unusual methods of contraction. Several colonies of Acanthoisis and Jasminisis are recorded here with polyps virtually flush with the surface of the branch. In the case of the Acanthoisis species, the polyps seem to be capable of extensive contraction in a telescopic fashion, with the broad body scales sliding over one another to form concentric circles, and in one species of Jasminisis, each polyp appears to be anchored within a depression in the coenenchyme into which it can contract. In this sense the processes of contraction and *retraction* can be separated if the latter term is restricted to those taxa where withdrawal of the anthocodia within the anthostele involves the process of invagination.

By extrapolation of this concept it is possible, at least in the context of Mopseinae and Circinisidinae to differentiate between a *calyx* and the reinforced base of an anthocodia, where the

latter is distinct from the extendible, non-retractile head. In the contracted, adaxially reduced polyps of the new genus Zignisis, for example, there is a suture between the sclerites of the base and those of the head (Figure 235D,E) which is confluent with naked adaxial zone. Theoretically, live colonies are capable of elevating the polyp head away from the base by virtue of an extendible sclerite-free neck zone. It is useful to differentiate this type of basal anthocodial structure - within which there is no retraction of the polyp head, no introversion - from a calyx. The latter, in the sense of Bayer and Verseveldt (1988: 8-9), and of Bourne's anthocrypt is a reinforced coenenchymal protrusion at the extremity of the anthostele, and is intimately linked with anthocodial invagination. In Zignisis and related genera, the polyp base is not involved with retraction. It is described as shelf-like - a term descriptive of function rather than shape - and appears to be flexible and capable of standing erect when the polyp is fully inflated.

As with many taxonomic features, structures occur which do not conform well to the available terminology. A case in point is *Orstomisis* Bayer and Stefani, 1990 where the anthocodia appears to be anchored at the base of a cylinder of soft epithelium into which it can withdraw by contraction and not by invagination. A somewhat exotic form, perhaps, of the method of contraction in *Jasminisis* where the anthocodia is anchored to the base of a cavity in the coenenchyme.

In the taxonomic descriptions, measurements given for the distance between consecutive polyps is taken from the centre of the base of each polyp.

#### Sclerites

In overall gross morphology, the sclerites of all species of Mopseinae are generally similar, as are those of all species of Circinisidinae. In Mopseinae, the polyp body scales are relatively large. They may be smooth, tuberculate or spined, with the distal margin dentate or thorny, and the form of the surface coenenchymal sclerites can generally be derived from that of a unilaterally spinous spindle. In Circinisidinae, the polyp body scales are relatively small, and although they may have smooth ridges or small papillae, they never have spines or complex tubercles on the exposed face, and although their free margin may be cleft or undulate, it is never dentate or thorny. The surface coenenchymal sclerites are either smooth oval scales or rooted heads; the latter derivable from the former as a scale with an exceedingly thickened blade.

Polyp body sclerites may be arranged in a definite pattern. A longitudinal line of scales is referred to as a *row*, and a line encircling the body is called a *series*. The scales in the upper part of the body are commonly arranged in 8 rows, one below

and confluent with each of the anthopomal octants. If those polyps are adaxially naked, they generally have only a few often disorganised sclerites below the adaxial octant; comparatively insufficient to constitute a row. These polyps are described as having 7 rows, which should not be taken to indicate the rows do not align with octants.

Although the form of the sclerites and their number and position in the anthopoma is often difficult to ascertain, they are important characters. Closely related species may appear to have the same anthopomal structure, but there are generally distinct differences in the architecture of the sclerites and in the number in the corresponding octants for each species. In those species where the anthopoma is markedly asymmetrical, the shape and number of the sclerites in each octant will vary considerably. There is also some variation between polyps on the same colony, and some variation between the octants of anthopomata that are symmetrical. For these reasons it is advantageous to comprehensively illustrate the structure and components of this region of the polyp.

In assessing the structure of the anthopoma, it is often difficult to decide where the upper body scales finish and the 8 octants begin, especially in colonies with tightly contracted polyps. With increased contraction, the upper body scales will tend to fold farther and farther over the summit of the polyp, and it is often moot whether to include them in the anthopomal count. The extent to which the confluence of the sclerites of the octants and those of the polyp body becomes obstructive often depends upon the ornamentation of the scales, the breadth of the scales (i.e. the number involved), and the number of rows on the body. If the upper body scales merge with those of the octants and differentiation occurs gradually through a series of sclerites, the anthopoma is said to be *continuous*. In the polyps of Pteronisis incerta (Figure 108 A,B) and Zignisis bifoliata (Figure 240A–D) for example, the anthopoma is markedly continuous with the polyp body sclerites. If the sclerites of the upper body and those of the octants are clearly not aligned and/or the differentiation is abrupt, the anthopoma cannot be said to be continuous. For example, the polyps of Myriozotisis spinosa (Figure 167A-C), Gorgonisis elyakovi (Figure 207A-C), and also Chathamisis bayeri as illustrated by Grant (1976: Figures 43-44) do not have continuous anthopomal arrangements.

The commonly convex nature of the oral region of the polyp hinders examination and accurate assessment of the anthopomal structure, and when few sclerites are involved in the differentiated series the perception of continuity becomes very subjective.

Without relaxed specimens, the arrangement of the sclerites in the tentacles is difficult to assess. In the majority of species of Mopseinae these sclerites are crescentic and are placed transversely, collarlike, in a single longitudinal series in the tentacle rachis. The arrangement in *Notisis* is slightly different, and there appear to be 2 rows of alternating scales. The tentacular sclerites in *Mopsea triaknema* are not well defined crescents, and many are knobby rodlets. In *Mopsea encrinula*, only knobby rodlets occur and they appear to be arranged in 2 rows loosely *en chevron*. There is a mixture of similar styles amongst the species within Circinisidinae.

In those species where the tentacles contain well formed crescents, between the tip of an anthopomal octant and the tentacular scales there is normally one or more sclerites of intermediate design. These sclerites, which sometimes resemble more the scales in the tentacle, and sometimes more the distal scales of the anthopoma, are referred to here as *basal tentaculars*. Their shape commonly varies from one octant to the next, but their general morphology is often characteristic for the genus if not the species. Depending on the degree of magnification, these sclerites may be grouped with the anthopomal scales or the tentacular scales in the included SEM illustrations.

When investigating the sclerites of the coenenchyme, it is important to examine both old and young branches. In pinnate colonies, for example, the coenenchyme of the pinnae may contain sclerites of a different size and shape to those found in the principal branches. Sclerites occurring in the coenenchyme of the thick stem or the main branches will usually be shorter and stouter than those in the younger portions of the colony.

In a similar context, it is important to avoid sampling juvenile polyps in order to form a consistent impression of the characteristics of the anthocodial sclerites.

#### Colour

Considerable attention has been given to specimen colour, which is a function of the colours of both the axis and the sclerites and of the translucency of the coenenchyme. Within certain ranges, axis and sclerite colours are relatively consistent for all species in a genus. As perception of colour tends to be subjective, and the application of colour names perhaps dependant upon experience, the different hues have been compared to the standards supplied in the 3rd edition of the "Methuen Handbook of Colour" (Kornerup and Warischer, 1978).

#### **METHODS**

Initially a Siemens *Autoscan*, and then its replacement, a *Philips XL 20*, were used to make virtually all of the electron micrographs of sclerites,

axial internodes, and whole mounts of twigs and polyps. A small number of images were obtained using a *Jeol T330*.

For SEM examination, sclerites and axis were separated from tissue using sodium hypochlorate solution (bleach; 125 g/l available chlorine) and hydrogen peroxide (≈ 30%). After dissolution of the tissue sample following immersion in bleach, most of the supernatant was removed and several drops of hydrogen peroxide added. The resultant violent effervescence aids in shaking loose adherent tissue remnants. The samples were then thoroughly washed in de-ionised or distilled water, dried, and then tipped into a glass slide from where sclerites were selected using a single hair 'brush'. Unless the cleaned sclerites are to be washed immediately care should be taken to neutralise the highly acidic hydrogen peroxide with dilute sodium hydroxide. Samples left in acidic peroxide will eventually dissolve.

A Leica *Kombistereo* microscope has a distinct advantage over other dissecting microscopes when selecting sclerites for SEM examination, especially when the sclerites are very small. The facility to slide in a high power objective lens allows the sclerites to be more easily checked for breakage and correct shape without having to move the sample to another instrument.

Sclerites were mounted directly onto 12 mm aluminium SEM stubs that had been previously coated with a layer of PVA glue (e.g. *Aquadhere*) and allowed to dry. The sclerites were made to adhere to the surface by briefly wafting the stub with steam. Overuse of steam will cause the sclerites to sink into the glue. Rending the surface of the stub a darker colour before applying the glue allows the sclerites to be seen more easily on the transparent coating.

It should be noted that polyp body and anthopomal sclerites are often easier to select from sclerite samples which contain only those from anthocodiae. The disadvantage being that the process of removing the anthocodiae from the colony commonly involves distortion resulting in fractured sclerites, which are often not detected prior to the scanning process.

Wet axial internodes placed directly onto the glue coating of a stub will quickly adhere to the surface. They should normally be picked up with forceps' points at each end in order to avoid damage to the surface sculpturing, but in some cases this causes fragmentation of the fibrous material remaining from the nodes which then contaminates the internode. Dried internodes can be transferred to the surface without damage by causing them to lodge between the bristles of a fine artists brush. They can then be manoeuvred with a probe or single hair 'brush' into a small drop of water placed nearby.

Twig whole mounts were carefully selected to avoid damaged polyps. The superficial tissue was removed by repeated very brief immersion first into bleach (about 1/2 strength) and then hydrogen peroxide (about 1/3 strength) followed immediately by washing in 70% ethanol. The specimens were regularly inspected under 70% ethanol in a black glass cavity block, and debris and tissue fragments eased away with a single hair 'brush'. The cleaned, dried fragments were then mounted on 12 mm SEM stubs using colloidal graphite glue. When selecting twig fragments, consideration also needs to be given to any existing contamination of the sample. Dredged or trawled material is often spoiled to various degrees by mucous residues from other captured organisms and this can be very resistant to the cleaning process. The presence of partially expanded polyps can be valuable for observing anthopomal arrangements, but parts of the extended tentacles often remain after the cleaning process, lying across the octants and obscuring many of the sclerites.

Twig whole mounts of species where the oral end of the polyps face away from the branch can be used to obtain micrographs of the anthopomal arrangement. However, in most species it is necessary to remove individual polyps and correctly orient them on a stub. For this purpose, twig fragments were selected that were longer than otherwise required, and after they had been successfully cleaned, polyps were carefully removed from the proximal portion with a sharp scalpel. By inserting a hooked probe, made from a fine entomological pin, into the exposed gastrovascular cavity of these polyps they were placed wet onto a 12 mm stub prepared with PVA glue. It is necessary to orient the polyps relatively quickly as they rapidly become fixed to the surface. Because of the difficulty of removing overlying tissue from the anthopoma where this region is closely appressed to the branch, careful selection of twig specimens is essential for good results.

It proved particularly difficult to make good whole mount preparations of many specimens from high southern latitudes, especially Primnoisis antarctica and Primnoisis deliculata. The polyps of samples treated sufficiently to remove the superficial tissue, and still apparently intact, distorted and tended to collapse upon drying. This problem could be avoided to a considerable degree if sublimation dehydration was used employing a fluorocarbon compound called Peldri. The cleaned fragments were first dehydrated from 70% ethanol through 2 changes of 100% ethanol. They were then transferred to a 1:1 mixture of Peldri and ethanol for 1 hour above 25°C, and then to 100% Peldri at the same temperature for a further hour. The preparations were then cooled to <23°C, at which

temperature *Peldri* solidifies, and left to sublime over night.

It is important to note that a certain amount of polyp distortion and disruption of sclerite arrangements is to be expected when prepared twig fragments are dried, and anthopomal structure is often better assessed in conjunction with visual inspection of uncleaned polyps, rather than relying totally on electron micrographs.

Sclerite, axis, and whole mount preparations were sputter coated with gold, with the stubs horizontally and then obliquely oriented in order to minimise charging in the SEM. With a number of whole mounts, however, some sclerites were so dissociated that the electron charge was unable to rapidly dissipate. These specimens were then examined using an environmental chamber adaptation to the Siemens SEM whereby the specimen chamber was operated under low vacuum and the scanning process performed at low magnification using a back-scatter detector. Employing this method it was also possible to examine uncoated specimens. This is useful if only a small amount of material is available, because specimens that have been insufficiently cleaned of superficial tissue can be rehydrated and further treated.

A twig whole mount can be placed vertically on a stub if it is necessary to view all sides of the specimen. In back-scatter mode especially, darker, uncluttered backgrounds for photography can be obtained if the specimen is mounted obliquely on the stub above a substrate with a high carbon content, such as clear adhesive tape. The substrate needs to be masked during the gold coating process in order to take advantage of atomic number contrast. The oblique angling of the specimen has the disadvantage that the underside is not available for viewing.

Visual assessment of anthopomal arrangements was performed on both cleared and uncleared polyps. For some species one method proved more successful than the other. Polyps were cleared in phenol-xylol, a concentrated solution of phenol crystals in xylol. The arrangement in uncleared polyps is often easier to see if they are placed in extremely dilute bleach. The solution causes the tissue to swell revealing the anthopomal structure and the orientation of the tentacular sclerites as the polyp disintegrates. Again, the Leica *Kombistereo* is the instrument of choice allowing a very large increase in magnification to be employed without need to move the carefully oriented specimen to another instrument.

The assessment of axial branching modes, and nodal and internodal lengths, commonly necessitates the removal of colonial coenenchyme. This destructive practice can be limited, especially in those specimens with colourless sclerites, by 20

silhouetting the axis or viewing the material with dark field illumination.

In several taxa, in order to confirm that anthocodiae were highly contracted but not retracted, it was necessary to decalcify twig fragments.  $D \times CALCIFIER$ , a histological decalcifying preparation made by *Lerner Laboratories* was used for this purpose, and the remaining tissue sectioned with a scalpel.

The colour of colony components was compared against the standard samples in the *Methuen Handbook of Colour* under a dissecting microscope. This compensated for the small dimensions of the specimens, and allowed both to be viewed with the same light source. The colour samples were placed out of focus below the specimen to blur the printing dots. Translucent and transparent specimens should be held to one side of the colour sample to prevent coloured illumination from below. This system provided consistency but it has many inherent difficulties. Most of these are due to the size, texture, and amount of surface reflection of the specimens. Colour identity codes are therefore quoted as approximate.

Serial format keys, as have often been used in octocoral systematics in the past two decades, have been chosen here as the best way in which to present the data. The keys here have also been indented for emphasis and to make them easier to use. I believe this serial style carries more information, and it is far more amenable to keeping morphologically similar taxa together. It allows a series of optional states to be presented one after the other for which a more traditional dichotomous key needs numerous couplets; in each, the second paragraph being a denial of the first. Correspondingly, the keys are shorter, and it is easier to back track to check commonalities, especially if the paragraphs in each hierachical level address the same character.

The name of all new generic taxa incorporate the Linnaean name *Isis*, from which the family name derives, and are feminine. *Isis* was the most important goddess of ancient Egypt, principal deity in all rites connected with the dead, an enchantress who cured the sick and brought the dead back to life, a mother and life-giver, and the patroness of seafarers in Alexandria.

#### **KEY TO THE SUBFAMILIES OF ISIDIDAE Lamouroux**

Sclerites in the form of -6 or -8 radiates, clubs and tuberculate spindles: ...... ISIDINAE Kölliker

Sclerites in the form of more or less prickly rods or spindles, longitudinally arranged on the polyps: KERATOISIDINAE Gray

#### KEY TO THE GENERA OF MOPSEINAE Gray

- 1(11) Axial internodes, at least in the younger parts of the colony, with large tooth-like spines arranged in longitudinal rows, each row aligned along a ridge or forming a ridge:
  - 2(8) Polyps adaxially reduced and adaxially naked:
    - 3(6) Branching pinnate and planar:
      - 4(5) Ramification dense and markedly plumose; polyps relatively long, and curved distad; anthopoma asymmetrical, octants complex involving few to numerous scales not in a single row; polyp body scales in 7 rows; colour brownish orange with white polyps: ... *Mopsea* Lamouroux

- 8(2) Polyps erect or angled distad, sometimes squat, and completely covered with sclerites:
- 11(1) Axial internodes without rows of large spines, plain or longitudinally ridged, with or without granules, denticles, or small spines:
  - 12(17) Polyps adaxially reduced and adaxially naked, rarely flush with the coenenchyme:

    - 14(13) Branching pseudo-dichotomous and planar:
  - 17(24) Polyps adaxially reduced but **not** adaxially naked:

    - 21(18) Unbranched and filiform:
      - 22(23) Body scales oval to crescentic, tuberculate or almost smooth, with dentate margins; anthocodiae uniserial, squat, somewhat egg-shaped, and with or without very large abaxially placed sclerites; anthopoma more or less symmetrical, octants simple with one or more scales in a single row; coenenchymal sclerites tuberculate spindles; colour white: .... *Peltastisis* Nutting
  - 24(12) Polyps erect and completely covered with sclerites:
    - 25(28) Branching bushy in a bottle-brush form:

- 28(25) Branching irregularly bushy, with or without densely arranged pinnate sections:
  - 29(30) Ramification without dense pinnate sections; polyp body scales smooth, fusiform to irregular in outline with strongly scalloped margins; anthopoma symmetrical, octants simple and dominated by a single large triradiate sclerite; coenenchymal sclerites smooth, figure-8 or fusiform with scalloped margins: ... *Chathamisis* Grant

#### KEY TO THE GENERA OF CIRCINISIDINAE Grant

- 1(9) Polyps adaxially reduced and adaxially naked:

  - 3(6) Branching pseudo-dichotomous; anthopomal octants simple, with sclerites in a single row; subsurface coenenchymal sclerites in the form of stellate plates; colour white:
- 9(1) Polyps symmetrical, erect, and completely covered with sclerites; branching lateral and copious; anthopomal octants complex, involving numerous small paddle-like scales; no subsurface coenenchymal sclerites; colour terracotta: *Florectisis n.gen.*

#### Subfamily Mopseinae Gray, 1870 [nom. transl. and correct. Wright and Studer, 1889 (pro Mopseadae Gray, 1870)].

#### Diagnosis

Planar, arborescent, bushy or unbranched Isididae with non-retractile but sometimes highly contractile anthocodiae.

Polyp body with transversely arranged sclerites in the form of smooth, tuberculate, or thorny scales (generally broad, but sometimes narrow, thick, and spindle-like) with a distal margin that is dentate, tuberculate, or thorny, or rarely more or less entire. Anthopomal sclerites scale-like – generally triangular, triradiate, or crescentic – intermesenterially situated and forming simple or complex protective arrangements which enclose the deflated tentacles during contraction.

Sclerites of the surface of the coenenchyme of a form that can generally be derived from unilaterally spinous spindles, but sometimes present as irregularly shaped platelets.

Axial internodes solid, sometimes plain, but commonly sculptured with longitudinal ridges, and spines or granulations of various sizes. Branching occurs from both internodes and nodes, but is predominantly internodal.

#### Remarks

The inclusion of several new genera in the subfamily is by no means certain. On the one hand *Lissopholidisis* has an anthopomal structure typical of the group, and shares with *Peltastisis* an unbranched growth form and polyps with huge abaxially positioned supporting sclerites. On the other hand, the smooth, irregularly shaped, plate-like polyp body sclerites, and the flat, fusiform, coenenchymal sclerites are directly comparable only to *Chathamisis* – which must bring the assignment of that genus also into question.

The genus *Ktenosquamisis* shares its pinnate growth pattern, broad-scaled anthopomal structure, mode of axial branching, and axial colour, with many species of Mopseinae. However, although the body scales have ctenate margins, their general oval shape is reminiscent of those of Circinisidinae. More notable is the notion that the remarkable 'double-cup' coenenchymal sclerites are better derived from the rooted head forms of that subfamily than from unilaterally spinous spindles; in fact they bear considerable resemblance to the surface sclerites of the circinisidine *Florectisis*.

### Mopsea Lamouroux, 1816 Figure 307

Melitea (part) Lamouroux, 1812: 188.

- Isis; (part) Lamarck, 1815: 413–414; (part) Lamarck, 1816: 300–301; (part) Schweigger, 1819: Figure x; (part) Schweigger, 1820: 433; (part) Lamarck, 1836: 473–474.
- Mopsea (part) Lamouroux, 1816: 465; (part) Lamouroux, 1821: 38; (part) Deslongchamps, 1824: 557; (part) Ehrenberg, 1834: 355-356; (part) Dujardin, 1846: 342; (part) Dana, 1846: 678; (part) Milne Edwards and Haime, 1857: 193, 197; Gray, 1858: 284; (part) Dana, 1859: 144; Gray, 1870: 15; (part) Studer, 1887: 46; (part)Wright and Studer, 1889: xlv, 33; (part) Nutting, 1910: 5 (in key); (part) Thomson and Mackinnon, 1911: 673-679; (part) Briggs, 1915: 70-78; (part) Kükenthal, 1915: 117-118, 123-124 (in keys); (part) Kükenthal, 1919: 558-559 (in key), 617-618; (part) Kükenthal, 1924: 431 (in key), 437; (part) Bayer, 1956: F222; (part) Grant, 1976: 33; (part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49-51 (in key), 57; (part) Bayer and Stefani, 1987b: 940-942 (in key); Alderslade, 1992: 104-108; 240-241 (type species ICZN, 1993: designation).
- Not *Mopsea*; Risso, 1826: 332; Philippi, 1842: 38–40; Milne Edwards and Haime, 1850: lxxxi, 42; Pictet, 1853: 467; Johnson, 1862: 245–246;

Johnson, 1863: 299; Kölliker, 1865: 142; Pourtales, 1868: 132; Sars, 1869: 250; Klunzinger, 1877: 57; Studer, 1878: 665; Hickson, 1890: 137– 138; Roule, 1907: 437–438; Roule, 1908: 5; Nutting, 1910: 17–19; Gravier, 1913b: 454; Gravier, 1913c: 456–460; Gravier, 1913d: 1470– 1471; Gravier, 1914: 24–28; Molander, 1929: 79– 80; Thomson and Rennet, 1931: 16–17; Tixier-Durivault, 1970: 333; Utinomi, 1972: 15–16; Utinomi, 1975: 255–258.

#### Type species

*Isis encrinula* Lamarck, 1815, by subsequent designation ICZN, Opinion 1738, (1993: 240–241)

(?≡, =)Meliteae verticillaris (nomen nudum) Lamouroux, 1812

(?≡, =)*Mopsea verticillata* (new combination) Lamouroux, 1816

(?≡, =)Isis verticillata (new combination) Schweigger, 1819

#### Diagnosis

Colonies are planar, pinnate, plumose and grow to more than 290 mm tall. They are generally preserved as brown or brown orange with white polyps. One specimen has been found with coenenchymal sclerites that are colourless in transmitted light instead of the usual yellowish hue. The axial internodes are generally brownish and opaque in the stem and in the branches of the older parts of the colony, becoming paler, redder, or Caucasian fleshcoloured distally. They can, however, be white or yellowish and almost transparent. Internodes of the pinnae are generally brownish orange to pale yellow. Axial nodes are patterned and variously coloured. They have a transparent to translucent central band which in the older regions tend to consist of a series of patches. These patches are linked in the younger branch nodes, and form a continuous band around the nodes in the finer pinnae.

Polyps are distributed all around and occur on the pinnae and the principal branches. They are adaxially reduced, adaxially naked, and usually preserved curved over and angled distad.

The anthopoma is asymmetrical and continuous with the polyp body sclerites. In the majority of octants there are 1–2 proximal crescentic scales. Distally, several longitudinally arranged sclerites occupy most of the octant. In *M. encrinula* these are a combination of flattened spindles or clubs, triradiate, triangular, or boot-shaped forms. In *M. triaknema* sp. nov. most octants are dominated by a single triradiate sclerite with small accessory forms. Anthopomal sclerites are ornamented with tooth-like projections, and are usually <0.15 mm long. There appear to be no specialised basal

tentacular sclerites, and the rachis of each tentacle contains small scales and rodlets in a single row or more or less *en chevron*.

The polyp body is protected with transversally arranged oval or crescentic scales, generally in 7 principal rows on the polyp head. There are only 3–4 scales below the adaxial octant. The body scales have stout tooth-like projections, and are mostly <0.18 mm long.

The coenenchyme contains mostly spindles, ovals, capstans, and sub-spheroidal forms, asymmetrically developed with rounded bosses or tooth-like projections.

The axial internodes are up to 2.8 mm long, and generally have multiple primary ridges which carry a single row of large spines. Most principal branch internodes ramify and many carry 2 pinnae. Nodes may also have longitudinal ridges that line up with those of the internodes.

#### Distribution

See Figure 307.

#### Mopsea encrinula (Lamarck, 1815) Figures 2–7; 252

- Meliteae verticillaris (nomen nudum) Lamouroux, 1812: 188.
- *Isis encrinula* Lamarck, 1815: 415; Lamarck, 1816: 302; Lamarck, 1836: 476.
- Mopsea verticillata; (new combination) Lamouroux, 1816: 467, Plate XVIII, Figure 2,; Lamouroux, 1821: 39, Plate 70, Figure 4; Deslongchamps, 1824: 557; Dujardin, 1846: 342.
- Isis verticillata; (new combination) Schweigger, 1819: tab. X; Schweigger, 1820: 434.
- Mopsea encrinula; (new combination) Ehrenberg, 1834: 355; Dana, 1846: 679; Milne Edwards and Haime, 1857: 198; Dana, 1859: 114; Gray, 1858: 284; Gray, 1870: 15; (part) Briggs 1915: 71; Bayer and Stefani, 1987a: 52, 65–66; Alderslade, 1992: 104–108 (lectotype designation); ICZN, 1993: 240–241 (type species designation).
- Mopsea squamosa; Utinomi, 1975: 255–256, Figure 13; Plate 3 Figure 3.
- Not Mopsea encrinula; Studer, 1878: 665, 679. [ $\Rightarrow$  Zignisis gen. nov., sp. indet.].
- Not Mopsea encrinula; Wright and Studer, 1889: 43-44, Plate VII, 1, 1a, 1b; Kükenthal, 1919: 620-621, Plate XLVI, 86-87; Figures 281-283; Kükenthal, 1924: 438, Figure 207; Utinomi, 1972: 15-16. [⇒ Pteronisis incerta gen. nov. sp. nov.].
- Not Mopsea encrinula; Thomson and Mackinnon, 1911: 674–675. [⇒ Mopsea triaknema sp. nov.].

#### Material examined

#### Types

LECTOTYPE: MNHN, Lamarck Collection, labelled 'Isis encrinula. LK. Mopsea verticillaris. Lamx. De La N[ouv]elle Hollande par MM Péron and Lesueur 1809.'

#### Other material

MNHN, fragments, Lamarck Collection, labelled 'g.verticillaris.var?', 'Espèce nouvelle voisine des Gorgoniae mais à axe articulé', and 'Isis, Gorgonia verticillaris. LK. var? Primnoa verticillaris. Milne Edw. et J. Haime. Antilles'; MNHN, fragments, Lamarck Collection, labelled 'Isis encrinula', and 'Isis encrinule. Isis encrinula nouv. holl.'; MTUF 16001, Geographe Channel, Shark Bay, Western Australia, 110-120 m, T/S Umitaka-Maru, Tokyo University of Fisheries, 19 Dec. 1963; NTM C1175, Great Australian Bight, Western Australia, 33°14'S, 125°45'E, 62-66 m, FRV Soela, C. Wilkinson, 17 Jan. 1980; NTM C2474, Great Australian Bight, 32°58.5'S, 129°E, 72 m, FRV Soela, station 16, 3 Dec. 1981; NTM C2482, Great Australian Bight, FRV Soela, Dec. 1981; NTM C10934, off Shark Bay, Western Australia, 24°55.6'S, 112°50.8'E, 80-85 m. RV Akademik Oparin, P. Alderslade, 14 July 1987; SAM H836, Great Australian Bight, South Australia, 34°11'S, 132°38'E, 160 m, FV Comet, K. Gowlett-Holmes, 4 April 1989; SAM H837, Great Australian Bight, South Australia, 34°10'S, 132°38.6'E, 140 m, FV Comet, K. Gowlett-Holmes, 4 April 1989; AM E4382, Great Australian Bight, South Australia, 131°E (approx), 62 fm, FIS Endeavour, 26 May 1913; AM E3754, Great Australian Bight, 80-81 fm, FIS Endeavour, 1911-1914; WAM 46-74, west of Pt. Cloates, Western Australia, 23°05'S, 113°23'E, 77 fm, HMAS Diamantina, 7 Oct. 1963; WAM 212-86, 40 km west of Jurien Bay, Western Australia, 30°21'S, 114°38'E, 165 m, MV Sprightly, 15 Feb. 1976; WAM 213-86, 69 km west of Cliff Head, Western Australia, 29°35.5'S, 114°17.5'E, 163 m, MV Sprightly, 18 Feb. 1976; WAM 214-86, 105 km west of Dongara, Western Australia, 29°11'S, 113°54'E, 219 m, MV Sprightly, 18 Feb. 1976; WAM 215-86, 92 km west of Dongara, 29°7.5'S, 113°57.4'E, 110 m, MV Sprightly, 19 Feb. 1976; WAM 216-86, 92 km west of Dongara, 29°6.7'S, 113°58.5'E, 91.4 m, MV Sprightly, 19 Feb. 1976; WAM 217-86, 73 km west of Dongara, 29°7.5'S, 114°10'E, 64 m, MV Sprightly, 19 Feb. 1976; WAM 460-80, same data; WAM 398-79, south west of Rottnest Is., Western Australia, 90-91 fm, FV Blue Fin, R.W. George, 12 Aug. 1962; WAM 399-79, south west end of Rottnest Is., 65 fm, FV Blue Fin, R.W. George, 12 Aug. 1962; WAM 447-80, north west of Rottnest Is., 90-91 fm, FV Blue Fin, R.W. George, 15 Aug. 1962.



Figure 2 Mopsea encrinula (Lamarck, 1815): A-C. Lectotype: (A). Polyp; (B). Coenenchyme; (C). Axial internode. D-J. NTM C1175: (D-F). Polyps; (G). Polyp body detail; (H). Coenenchyme; (I). Axial internode; (J). Twig fragment.

#### **Differential characteristics**

Anthopomal octants contain numerous sclerites, no dominant triradiate forms; coenenchymal sclerites with 2 or more rounded, stout, knob-like projections.

#### Remarks

The specimen treated by the Muséum National d' Histoire Naturelle, Paris, as the holotype of *M. encrinula*, was redescribed by Bayer and Stefani (1987a: 65–66), and was subsequently designated as the lectotype (Alderslade, 1992: 104). The comments below, which should be read in conjunction with Bayer's and Stefani's text, have been made possible by the loan of several fragments of the lectotype by Mme Marie-José d'Hondt of the Paris Museum. A more comprehensive description of a larger, alcohol preserved, specimen follows these comments.

#### **Description of the Lectotype**

#### Colony form

The specimen has been figured by Bayer and Stefani (1987a: Plate 18, Figure 1). The fragments available to me are from both principal branches and pinnae. Much of the coenenchyme is missing. The thickest principal branch fragment is 2.9 mm in diameter (without polyps). The pinnae are 0.9– 1.5 mm thick (including polyps).

#### Polyps (Figure 2A)

Polyps are distributed all around on most fragments, sometimes appearing to be in rows. They are biserially arranged on the thinnest pinnae. The polyps are contracted, adaxially reduced, and curved upwards so as to lie against the branch surface. They are densest on the pinnae, with about 0.18–48 mm separating the head of one from the base of the next. Measured along the branch, they are 0.72–0.79 mm in length. Abaxially, they are about 48 mm across the head, and the base, about 0.36 mm across the neck, and project about 0.32 mm.

#### Colony colour

The dry coenenchyme is greyish orange to brownish-orange ( $\approx$ 5B4–5C4). The polyp heads have colourless sclerites and appear greyish white. All other sclerites are yellowish in transmitted light.

#### Axis form (Figure 2C)

All internodes have multiple, high, primary ridges. The ridges of the internodes of the pinnae and thinner principal branches each have a single row of large spines, and shoulders that may be raised. In the thickest principal branch fragments the spines are hardly discernible. Pinnae internodes 0.37 mm and 0.45 mm thick have eight and eleven primary ridges respectively. A principal branch internode 1.50 mm thick has 25 ridges. The desmocyte cavities are deep and very distinct.

Pinna internodes are mostly 2.2–2.7 mm long. Those of the principal branches are 1.8–2.8 mm in length. Nodes in the pinnae are 0.12–0.19 mm long, and in the principal branches they are mostly 0.60– 0.72 mm.

#### Axis branching

Virtually all principal branch internodes are branched, and many bear two pinnae. The pinnae may originate from very short to medium length internodal stubs as in Figure 251 example 43, or begin with short nodes as in example 44. Thicker branches may arise from shared nodes as in example 45.

#### Axis colour

The dry nodes and internodes are mostly brownish orange to light brown ( $\approx 6C4-6D4$ ). Branch internodes are translucent, and pinna internodes are almost transparent. Nodes in the thickest branch are brown ( $\approx 7E8$ ). The borders of the nodes are satin-like and greyish-white or yellowish-white, and on the pinna internodes they often appear as crescents between the shoulders of the ridges.

#### Sclerites

The sclerites have not been redescribed here. Illustrations of a polyp and surface of a twig (Figure 2A,B) are given for comparison with other specimens.

#### **Description of NTM C1175**

#### Colony form (Figure 3)

The incomplete colony consists of numerous pinnately ramified plumes that grow predominantly in one plane. The specimen is curved from bottle storage and is about 290 mm tall and 85 mm wide. The pinnae are arranged irregularly. They occur opposite, alternate, and sometimes monoserially for short distances. A few pinnae rebranch.

The holdfast and stem are missing. The colony is initially divided into two main branches, about 2.8 mm thick proximally, that taper and continue through to the apex of the colony. The pinnae are thickest, 1–1.6 mm (including polyps), slightly above their point of origin. They taper to about 0.9 mm thick, a short distance before the pointed tip, and are of various lengths from 10–60 mm. Taking only one side of a plume into account, because so many pinnae are opposite, the distance between consecutive points of branching varies from 0–5 mm. Some consecutive pinnae are touching at their



points of origin. Occasionally this occurs opposite two similarly arranged pinnae, with all four originating from a single node. Angle of branching is mostly 30–50°.

## Polyps (Figure 2E,F,J)

Polyps are densely distributed all around on the pinnae and on most parts of the principal branches. They are contracted, adaxially reduced, and curved upwards and over so that in most cases the anthopomal region faces down towards the branch making an angle of about 22–32° with the surface. Measured along the branch, polyps are 0.66–0.90 mm long, depending on how prostrate they are. Most are about 0.81 mm in length. Abaxially, the heads are 0.36–0.48 mm across, the bases 0.33–0.36 mm, and the neck regions about 0.30 mm. They project 0.33–0.36 mm above the surface. Juvenile polyps are scattered throughout the colony, and upsidedown polyps are rare.

#### Colony colour

The coenenchyme is brown ( $\approx$ 6D8); slightly paler ( $\approx$ 6C8) on the more distal pinnae. The basal few series of sclerites on the polyps are the same colour as those of the coenenchyme, yellowish in transmitted light, but above this the sclerites are colourless and the polyps are almost white. The coenenchyme is almost opaque, and only on the thick principal branches are the pale underlying nodes just discernible.

#### Axis form (Figure 2I)

All internodes have multiple, high, primary ridges. Those in the pinnae and thinner parts of the principal branches have a single row of large spines along each ridge. In the thicker areas of the principal branches the spines are reduced or absent. The most basal internode is 3 mm thick and has 68 primary ridges. A principal branch internode 1 mm thick has about 24 ridges, and a pinna internode 0.5 mm thick has 13. Nodes also have longitudinal ridges that line up with the primary internodal ridges. The desmocyte cavities in the internodes are deep and distinct.

In the principal branches the internodes are 1.8–2.5 mm long. In the pinnae they are mostly 2.3–2.5 mm in length, except at the point of origin where the proximal 1–2 internodes are only 0.8–1.1 mm long. In the thick principal branches near the base of the colony, the nodes are about 0.60 mm long, becoming shorter, 0.42 mm, distally. Pinna nodes are mostly 0.12–0.18 mm long.

#### Axis branching

The majority of principal branch internodes are branched. There are areas of non-branched internodes, but these are usually towards the proximal parts of these branches. Internodes can initiate 1–4 pinnae with 1–2 most common. Pinnae usually arise from very short internodal stubs as in Figure 251 example 44, or originate with a node as in example 38. They may also share nodes as in example 58. All combinations of styles can occur on a single internode.

#### Axis colour

The more basal main branch internodes are brown (≈7D8) and relatively opaque. In the more distal parts of the colony the branch internodes are reddish brown (≈8D8). The pinna internodes are paler, brownish orange ( $\approx 6C8$ ), and virtually transparent. The nodes of the principal branches are patterned and have an uneven surface. Forming a central band around each node is a series of transparent patches that may be separate from each other or linked. They look like pits in the node but are actually solid, although their surface is slightly concave. The surrounding matter is opaque, greyish orange (≈5B4) in the basal areas and becoming more yellowish white in the distal parts. The ridges on the nodes run from end to end between the patches. In the proximal internodes of the pinnae, the patches are linked, somewhat chain-like, and form a continuous central band around the node. In the more distal pinna internodes there is just a narrow even band of clear material between the satin-like opaque ends. The borders of all internodes are silvery and satin-like, and appear as crescents between the shoulders of the primary internodal ridges.

## Polyp sclerites (Figures 2D-G; 4)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. Each octant contains a number of irregularly shaped sclerites that fit together to form a triangular sector (Figures 2D; 4A). Although the proximal scales are usually more-or less crescentic they may be branched (Figure 4a,b). The other anthopomal sclerites may be shaped like flattened spindles or clubs, or be triangular, triradiate, boot-shaped, or some irregular form. In some instances a single triangular sclerite may dominate an octant, however, in most cases a number of sclerites combine to complete the sector and any triangular scales are generally flanked by narrow sclerites. There is no consistency in the make up of the octants, and adaxial sections, for example, have been observed with 1-6 sclerites. The anthopomal sclerites are ornamented with tooth-like projections on the upper side, and are relatively smooth underneath (Figure 4c). They are mostly 0.08-0.11 mm long, but can be up to about 0.15 mm in length. There are no specialised basal tentacular sclerites. The tentacle rachis contains 2 rows of granular, knobby rodlets (Figure 4B) arranged



Figure 4 Mopsea encrinula (Lamarck, 1815), NTM C1175, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body



Figure 5 Mopsea encrinula (Lamarck, 1815), sclerites: A. NTM C1175, branch coenenchyme; B. WAM 216-86, Polyp scales; C. WAM 216-86, branch coenenchyme; D. WAM 215-86, basal stem coenenchyme.

more or less *en chevron*. They are about 0.024–0.055 mm long with a few to 0.068 mm occurring at the apex of the anthopomal octant. Specimen WAM 216–86, whose polyps stand out from the twigs (Figure 7I) lends itself to more successful preparation of an intact anthopoma as illustrated in Figure 7A–E.

Most of the polyp body is covered with crescentic scales armed with large tooth-like projections (Figure 4C). They are arranged in 7 often indistinct rows on the polyp head (Figure 2E,F). The adaxial side of the polyp is naked except for about 3–4 narrow scales ornamented with small

tubercles (Figure 4Cd) and arranged below the adaxial octant. The scales on the lower part of the polyp body have stout, rounded projections. In some polyps many of these sclerites, especially those on the more lateral aspects, are the same as those in the pinna surface or are intermediate in form (Figure 4Cb,c). These sclerites are the same colour as those of the surface sclerites and appear yellowish in transmitted light. The scales on the upper part of the polyp have relatively sharp projections (Figure 2G). The largest of the scales are up to about 0.18 mm length, and the undersides have a few compound warts (Figure 4Ca).


Figure 6 Mopsea encrinula (Lamarck, 1815), SAM H836, natural size.

Coenenchymal sclerites (Figures 2H; 5A)

The surface of the pinnae (Figure 2H) and principal branches contains small sclerites asymmetrically developed with small rounded knobs (Figure 5Ae–g), capstans modified on one side with large irregularly shaped bosses (Figure 5Aa–d), and intermediate forms (Figure 5Ah–l). There are also a few warty forms (Figure 5Am), often somewhat flattened. Most surface sclerites are <0.10 mm long, those on the pinnae being generally smaller than those on the main branches.

There is no stem present in the colony portion. Specimen WAM 215–86 has the holdfast intact and the surface of the stem contains irregularly shaped capstans about 0.05–0.09 mm in length. A few are unilaterally developed with bosses, like some of the surface sclerites in the upper parts of the colony described above. Some have a few bluntly rounded projections on one side (Figure 5Da,b), occasionally developed as discs, but most have compound warts all around (Figure 5Dc–e).

## Variability

The other two specimens from the Lamarck Collection show the same characters as those of the lectotype. Of the additional material examined only three of the colonies have the holdfast intact. The largest has a stem about 4 mm in diameter, and the large, thick, calcareous holdfast is attached to some oyster shell fragments. The robust nature of the

P. Alderslade



Figure 7 Mopsea encrinula (Lamarck, 1815), WAM 216-86: A-F. Polyps; G. Polyp body detail; H. Coenenchyme; I. Twig fragment.

holdfast perhaps demonstrates why trawls and dredges mainly retrieve only upper colony portions. The stem, unbranched for about 23 mm, is mostly nodal material, with short partial or overgrown internodes visible mostly on one side only.

The colour of both axis and coenenchyme varies within the material available. Polyp sclerites, except the ones near the polyp base, are always colourless, but in only one colony are the coenenchymal sclerites also colourless; the colony still appearing yellowish due to the colour of the axis. Coenenchyme can be light yellow to orange yellow ( $\approx$ 4A4–4B7), or pale to deep brownish orange ( $\approx$ 6C8–7C7). Axial internodes are usually more or less the same colour as the coenenchyme, but they can be white in the thicker basal parts of the older main branches. They can also be almost transparent throughout the whole colony. The predominant colour in the nodes can vary from honey yellow ( $\approx$ 5D6) to brown ( $\approx$ 7E6). The ridging on the nodes and the pattern of clearer patches occurs in all colonies, but the patterning is more marked in some colonies. It is generally not present in stem and thick, lower, principal branches. In most colonies, relatively thick principal branches

will show it, but in a minority it is absent in branches thicker than 1.3 mm. In the more basal variegated nodes, the patches may be present as a row of transparent colourless or brownish orange dots and dashes between the nodal ridges. More distally, where the nodes are shorter, larger single patches usually occur between the ridges. The patches are sometimes cloudy instead of transparent, sometimes coloured, sometimes almost opaque, and may only occur on one side of the nodes.

Pinna internodes are always spined. The spines on the principal branch internodes are reduced or absent in the older, thicker portions. In a few spindly colonies, however, much of each principal branch is unspined, even those internodes as thin as 0.8 mm.

In a few colonies, thick basal internodes are somewhat barrel-like, being broader in the centre, and in some instances principal branch internodes are notably narrow in the middle. Usually, all internodes are more or less cylindrical, and they can be up to 3 mm long.

The two colonies from the most eastern limit of the known distribution, the eastern part of the Great Australian Bight, are both pale yellow, with white polyps and spindly growth form. The pinnae in one colony (Figure 6) are extremely flexible, up to 70 mm long, and only every third of fourth principal branch internode is ramified. This colony has greyish white internodes in most of the principal branch, and pale yellow internodes in the rest of the colony. The other specimen has all internodes pale yellow, but it may only be an upper portion of a larger colony.

There is variability amongst both polyp and coenenchymal sclerites. In the polyps the projections on the scales can be much longer than in the specimen described above and also more jagged (Figure 5B) which can give the impression that they are more densely arranged. They can also have a granular surface, and be medially swollen so as to have a somewhat ovate outline (Figure 7F,G). In the basal area of the polyp, the number of sclerites resembling those in the coenenchyme can also be quite variable, even in the same colony. There is a considerable number in the figured polyp of the lectotype (Figure 2A), and virtually none in the polyp of WAM 216–86 (Figure 7F).

In the sclerites of the coenenchyme there are 2 notable areas of variability. First, there may not be many sclerites of the form shown in Figure 5Aa,b,d, where the lateral bosses are somewhat globular and relatively undivided. Instead, many of the bosses will be divided, or replaced by several separate narrower projections, often disc-like (Figure 5Cb; 7H). Sometimes these sclerites are quite complex (Figure 5Ca). As with the polyp scales, the projections are often markedly granular

(Figure 5Cc). Second, there may be a large number of warty forms, sometimes flattened, sometimes complex, and sometimes simpler (Figure 5Cd), and occasionally up to about 0.14 mm in length. In general, the sclerites from the surface of the pinnae are smaller and less complex than those in the principal branch coenenchyme. Such distribution within a colony, however, is not totally consistent and patches of complex sclerites can occur on the pinnae, and patches of simple sclerites can occur on the principal branches.

## Distribution

See Figure 252. Depth range 62–219 m.

*Mopsea triaknema* sp. nov. Figures 8–11; 253

Mopsea encrinula; Thomson and Mackinnon, 1911: 674–675.

## Material examined

#### Types

HOLOTYPE: AM G12146, 6–8 miles off Bulgo, New South Wales, 104–115 m, HMCS *Thetis*, station 47, mud and abattoir refuse, 16 Mar. 1898. PARATYPE: AM G15593, data as holotype; AM G15594, fragments, HMCS *Thetis* station 34, 2.5–3.5 miles off Port Jackson, New South Wales, 36–39 fm, sand and mud, 10 Mar. 1898; BM 1960.12.1.61, microscope slide labelled "THETIS EXP<sup>N</sup> MEM. AUST. MUS. IV P<sup>†</sup>. 13. 1911. P.674. MOPSEA ENCRINULATA LAMARCK DET. TH. & MACK". and "11 MILES E. OF BROKEN BAY. <u>Mopsea</u> encrinula. Lamarck W. & St.".

### **Differential characteristics**

Anthopomal octants dominated by large triradiate sclerites; coenenchymal sclerites with numerous tooth-like projections.

# Description

## Colony form (Figure 8A).

The holotype consists of an incomplete planar portion of the original colony, and some twig fragments. It is curved from bottle storage, and is about 180 mm tall when stretched and 33 mm across. It is ramified in an irregularly pinnate manner. Pinnae may be opposite, alternate, or several may occur successively along only one side of a principal branch. Some incomplete 'plumes' only have twigs along one side. Much of the coenenchyme has been abraded and many polyps and twigs are either broken or missing.

The holdfast and stem are absent. The two main branches are both about 1.9 mm thick, proximally. Pinnae are about 0.58–0.72 mm thick (without



Figure 8 Mopsea triaknema sp. nov.: A. Holotype; B. Paratype, AM G12146. Both natural size.

polyps), and 15–50 mm long. Taking both sides of a principal branch into account, the distance between consecutive subdivisions is 2.75–12.25 mm (ignoring opposite pinnae). Pinnae arise at angles of 60–90°, but curve upwards so as to appear to make a more acute angle with the branch.

#### Polyps (Figure 9F,H)

Polyps are distributed all around on the pinnae and principal branches, the density being greatest on the pinnae. The polyps are contracted and adaxially reduced. Some are curved upwards and over so that the anthopomal region faces along or down towards the branch, or lies more or less against its surface. Others stand almost erect, but, as the adaxial side of the polyp is shorter, the anthopoma faces along the branch. Many polyps are swollen basally, and contain an oval body, probably a developing planula, about 0.48 mm long.

Those polyps lying against the branch surface are about 0.61–0.82 mm long. Those standing erect are about 0.72 mm tall, or 0.96 mm tall if the base is swollen with a planula. Measured abaxially, polyp heads and bases are about 0.41–0.46 mm across, and the necks are slightly narrower at 0.31–0.36 mm. Quite a few polyps are upside down, and juvenile polyps occur throughout the colony.



Figure 9 Mopsea triaknema sp. nov., holotype: A-H. Polyps; I. Coenenchyme; J. Axial internode.

## Colony colour

The coenenchyme is brownish orange (6B7–6C7), and the sclerites are yellowish in transmitted light. The polyps are colourless. The coenenchyme is just translucent enough to be able to see the underlying nodes of the principal branches. For the most part, the nodes in the pinnae are obscured by the polyps.

## Axis form (Figure 9J)

All internodes have multiple primary ridges that bear a single row of large spines. A principal branch internode 1.34 mm thick has 32 spined ridges. A pinna 0.22 mm thick has 16 ridges. Desmocyte cavities are distinct, but shallow.

Internodes in the main branches are mostly 0.84–0.96 mm in length. In the pinnae, the most proximal internode is about 1.2 mm long and the others are 1.9–2.7 mm. In the thickest of the main branches, the proximal nodes are 0.36–0.60 mm long. More distal, main branch nodes are about 0.30 mm long. Nodes in the pinnae are 0.18–0.24 mm long.

## Axis branching

The main branches intersect as in Figure 251 example 62. Pinnae originate in several styles; from a shared node as in example 58, or from a branch internode as in example 38 or 33. Many internodes bear two branches involving combinations of these styles.

# Axis colour

The internodes at the base of the thickest branch are brownish orange (≈7C6), and more or less opaque. More distally they are the colour of Caucasian flesh (~6B3-6B4). The pinna internodes are a pale yellowish white. On one face of the colony the more proximal nodes of the thickest branch have a translucent central band of reddish brown (~8E8) between opaque bands of brownish orange (≈5C5). On the other face, the nodes are mostly brownish orange, and the clearer reddish brown material is reduced to a series of patches joined together as a central band. The more distal principal branch nodes have this central patch pattern right around. The nodal borders are yellowish and satin-like. In the pinnae, the nodes are greyish orange (≈5B4) with a clear grey to colourless central band, and silvery satin-like borders.

## Polyp sclerites (Figures 9A–H; 10; 11A)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The most characteristic anthopomal sclerites have a triradiate shape (Figure 10Aa-j). In most polyps, the adaxial octant consists of a single, narrow-armed triradiate that may be quite small (Figure 10Aj) or moderately large (Figure 10Ad,e) and similar in size to those in the adaxial-lateral sectors (Figure 9A-C). In some polyps the adaxial triradiate is replaced by 2 sclerites; a proximal transverse crescentic scale representing the base of the triradiate, and a radial bar representing its distal arm. The radially arranged bar may have smaller accessory sclerites alongside it (Figure 9E). Transversally arranged crescentic scales (Figure 10Ao-w) occur at the base of each of the other octants. It is difficult to be certain of the allocation of these scales in the tightly contracted polyps, a problem exacerbated in some polyps where there is an unusually large number of series of scales on the polyp head. The distal most crescentic scale, where the body scales merge with the anthopoma, fits its convex margin into the base of the scale above, which is usually a triradiate. This crescentic sclerite often appears as an anthopomal because there is a gap between the lateral tips of the scale and those in the neighbouring octants. The preceding crescent often has its convex margin also in the anthopomal space, but the tips of the neighbouring scales touch or overlap on the polyp

body and are counted here as body scales. It is most likely that in an expanded polyp these scales (and some preceding them?) are laterally separated and form part of the anthopomal octants. In some polyps a single triradiate scale completes each of the major octants; those of the more abaxial octants being the largest. In many cases, however, there are accessory sclerites of various forms (Figure 10Al-n) that occur alongside the radially arranged arm of the triradiate, or the triradiate is replaced by sclerites of various shapes (Figure 10Ak) that combine to form a triradiate shape. This latter design can also be accompanied by accessory sclerites. Examples of these variations are shown in Figure 9A-E. The anthopomal sclerites have granular tooth-like projections on their upper surface, and the undersides are relatively smooth with areas of granules (Figure 10Ad,g). The triradiates may be up to 0.18 mm in length, but are usually smaller, up to 0.14 mm, and they often have small root structures on their basal margin.

There is a single row of crescentic scales and irregularly shaped rodlets in the rachis of each tentacle (Figure 9G). They are ornamented with groups of granules, and some have holes in them (Figure 10B). The crescents are up to about 0.057 mm long, and the rodlets are slightly longer and up to 0.065 mm.

The polyp body is protected by crescentic to oval scales ornamented with granular tooth-like projections (Figure 11A) and arranged in 7 principal rows on the polyp head (Figure 9F,H). Below the adaxial octant there can be a short row of about 4 narrow scales (Figure 11Aa) or a more disorganised group involving the lateral extensions of some adaxial-lateral scales but still about 4 sclerites deep. Below these sclerites there is a small naked patch on the polyp neck. Polyps containing planulae are raised up slightly on a swollen base which is covered in coenenchymal sclerites. Many of these sclerites close to the polyp base are like small body scales (Figure 11Bb) and are yellowish in transmitted light. Polyp body scales are relatively smooth on their underside (Figure 11Ab), and although most are < 0.18 mm long they can be as long as 0.22 mm.

### Coenenchymal sclerites (Figures 9I; 11B)

The surface of the pinnae and main branch contains a few small scales together with numerous spindles and oval or sub-spheroidal forms that are unilaterally ornamented with closely arranged tooth-like prominences (Figures 9I; 11B). The spindles are sometimes branched, often arched (Figure 11Bc), and may have one or more robust root structures (Figure 11Bd). A few small flattened spindles also occur (Figure 11Ba). Most coenenchymal sclerites are 0.04–0.18 mm long.

The colony stem is missing.



Figure 10 Mopsea triaknema sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.

## Variability

Specimen lot AM G12146 originally contained two colony portions and numerous twig fragments. The smaller portion (Figure 8B) has a different internode colour to the holotype, almost white, and no swollen polyps containing large planulae. Instead, the polyps contain several smaller irregular shaped bodies, about 0.17 mm long. This colony portion has been separated as a paratype.

AM G15594, is a small group of badly preserved twig pieces separated from the mass of fragments of Thomson's and Mackinnon's type series of *Mopsea flabellum* ( $\equiv$  *Sphaerokodisis flabellum* new comb.). The axial nodes of the principal branch pieces are patterned similarly to those of the holotype, but the end bands are pale yellow to yellowish white (4A2–4A3).

The most notable variation in sclerite architecture is seen in the coenenchymal sclerites of AM G15593. Irregularly shaped spindles up to 0.22 mm occur in this colony, and the robust root structures are very prominent, sometimes 0.05 mm long, and



Figure 11 Mopsea triaknema sp. nov., holotype, sclerites: A. Polyp body; B. Pinna and branch coenenchyme.

occasionally branched. Polyps with more series of body sclerites on the head are more common in the paratypes than in the holotype. This is particularly noticeable below the anthopomal octants where small crescentic scales of decreasing size become organised into well defined rows of about 5–6 sclerites. Only the most distal scale, however, is likely to be laterally separated and form the base of an octant.

### Remarks

Despite the apparent lack of similarity between the anthopomal sclerites of M. triaknema and those of *M. encrinula*, the two species have so many other features in common or overlapping that the decision to group both species in the same genus is quite defensible. There is little or no difference in colony colour, general form of the polyps, axis, basic sclerite architecture and colony growth form between the two species. Although coenenchymal sclerites of the style found in M. encrinula do not occur in M. triaknema the reverse is not true, and the anthopomal sclerites are better compared by considering the illustrations of them in situ. Triradiate sclerites occur in the anthopomal octants of both species, but whereas in *M. encrinula* they are few and usually occur combined with several large sclerites, in M. triaknema they are better developed and often dominate the octant. In both species, triangular or triradiate shapes are formed by the dovetailing of 2 or more sclerites. Perhaps the most significant difference between the 2 species is the architecture of the tentacular sclerites considering this character generally varies little between congeneric species.

Thomson and Mackinnon (1911:674) reported specimens they had identified as Mopsea encrinula from several locations. The whereabouts of the majority of that material is unknown. Their microscope slide preparation, housed in the Natural History Museum (London), from a specimen collected "eleven miles east of Broken Bay", appears to have been made from the tip of a pinna. It contains a small fragment of axis, numerous clumps of polyp sclerites and some incompletely macerated polyps. There are several characteristic triradiate-radiate anthopomal sclerites present, some in situ in a polyp, but virtually no coenenchymal sclerites. The sclerites are easier to see if viewed with the aid of polarising filters.

#### Distribution

See Figure 253. Depth range 66–115 m.

## Etymology

The epithet is formed from the Greek *tria*, three, and *kneme*, spoke of a wheel, in allusion to the triradiate anthopomal sclerites.

# Type species

Oparinisis flexilis sp. nov., here designated.

#### Diagnosis

Colonies grow to approximately 400 mm tall. The stem and main branches ramify secundly and sympodially, and the upper, thinner branches are pseudo-dichotomously arranged.

The sclerites are colourless and preserved colonies can be yellowish white or brownish orange. The axial internodes are greyish white and translucent proximally, becoming colourless and transparent in the finer branches. The nodes are generally yellow brown or rust brown in the older, thicker regions, and pale yellow with a clear central band in the finer twigs.

Polyps are mostly distributed all around. They are adaxially reduced, adaxially naked, and usually preserved folded down against the branch surface.

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The 7 major octants are each usually occupied by a triangular to triradiate sclerite preceded by 1–2 more or less crescentic scales. The triradiate scales can be up to 0.19 mm long and are ornamented with sharp tooth-like projections. There are 1–2 basal tentacular sclerites preceding a single row of curved scales in each tentacle rachis.

The adaxial side of the polyp body is naked except for about 1–3 narrow scales immediately below the adaxial octant. The rest of the body is covered with crescentic to irregularly shaped scales that are arranged in 7 rows on the upper part of the polyp. The scales are mostly <0.23 mm long, but can be up to 0.27 mm. They are ornamented with ridges or tooth-like projections. In one species, *O. viking* sp. nov., several of the projections on a scale may be greatly enlarged and horn-like.

The surface of the thinner branches contains predominantly unilaterally spinous spindles. The coenenchyme of the thicker, older parts contains mostly large oval forms, unilaterally developed with stout, angular, spiny projections, together with small tuberculate capstans and spindles. The largest coenenchymal sclerites are about 0.35 mm in length.

The axial internodes are up to about 2 mm long. They have multiple primary ridges each bearing a single row of large spines; except in the lower, older areas where the spines are reduced to granules.

#### Distribution

See Figure 308.

#### Etymology

Specimens of O. flexilis were obtained off the

coast of Western Australia in July 1987. This genus is dedicated to the scientific staff and the crew of the RV "*Akademik Oparin*" who welcomed me as a

> *Oparinisis flexilis* **sp. nov.** Figures 12–17; 254

guest during the Western Australian leg of their

# Material examined

#### Type

expedition.

HOLOTYPE: NTM C10928, off Shark Bay, Western Australia, 24°55.6'S, 112°50.8'E, 80–85 m, dredge, limestone rubble, sand and shell grit, RV *Akademik Oparin*, P. Alderslade, 14 July 1987. PARATYPES: NTM C10923 (4 colonies), NTM C10926, NTM C10937, NTM C10949 (2 colonies), NTM C10952 (6 colonies and some fragments), data as for holotype; WAM 384–79, 92 km west of Dongara, Western Australia, 29°07.5'S, 113°57.4'E, 110 m, dredge, sponges and stone rubble, MV *Sprightly*, 19 Feb. 1976.

# **Differential characteristics**

Branching relatively sparse; colonies with long, thick, flexible branches; sclerite form.

# Description

#### Colony form (Figure 12)

The planar holotype is curved from bottle storage and, without stretching, it is 205 mm high. The small calcareous holdfast incorporates fragments of shell and bryozoan skeleton. Nodal material has overgrown the basal stem internodes for 4-5 mm. The denuded main stem is unbranched for 45 mm. It then bends twice in the same direction giving off a broken branch each time, before bifurcating. A colonial hydroid overgrows this area. Subsequent branching is planar, sparse, and pseudodichotomous, producing relatively long, thin, flexible ramifications. The naked stem is 1.9 mm thick. The branches are mostly 1.2-1.6 mm thick (including polyps), and the polyp-free twig tips are 0.6-1.5 mm long. The distance between consecutive subdivisions is 6-23 mm, with over half >15 mm. The branching angle is consistently about 39°. The longest undivided branch is 110 mm.

# Polyps (Figure 13C,D,H)

Polyps are absent from the branched upper portion of the main stem. Near the twig tips the distribution tends to be biserial, but throughout the rest of the colony polyps are densely arranged all around the branches. The polyps are contracted, adaxially reduced, and curved so as to lie closely against the branches. The anthopomal regions are angled at about 25–38° to the branch surface, and occasionally oppressed to the base of succeeding polyps. Measured along the branch, most polyps are 0.78–0.87 mm long. They are 0.41–0.46 mm abaxially across the head, and the neck region is slightly narrower. They project about 0.27–0.33 mm above the branch. Juvenile polyps are found throughout the colony.

#### Colony colour

Brownish orange ( $\approx$ 5C4), sclerites colourless.

# Axis form (Figure 13F,G)

Internodes have multiple primary ridges, each with a single row of large spines, except on the main stem where the spines are reduced to small irregularities. There are no secondary ridges. A main stem internode 2.10 mm wide has 26 ridges. A branch internode 0.84 mm wide has 14 ridges, and, more distally, an internode 0.42 mm wide has 10 ridges. Desmocyte cavities are deep and conspicuous.

Main stem internodes are 0.47–0.79 mm long in the unbranched section and 0.63–1.30 mm in the branched region. Throughout the rest of the colony they are about 1.50 mm in length. Nodes in the main stem are 0.63–0.95 mm long. In the upper branches they are mostly 0.24–0.30 mm long becoming shorter, 0.12 mm, in the terminal regions where they are much thinner than the internodes.

## Axis branching

In the main stem and thicker branches, branching is like Figure 251 example 55. In the higher order branches it is like examples 12, 13, 14 and 29. Branching internodes have only one bifurcation.

### Axis colour

The internodes are greyish white and translucent basally, becoming colourless and transparent in the terminal regions of the colony. The nodes in the main stem are rust brown ( $\approx$ 6E8), in the lower branch regions orange ( $\approx$ 5B8), and in the upper branch regions maize yellow ( $\approx$ 4A6). All have narrow yellowish satin-like borders, often crescent-like between the ends of the internodal ridges. In the terminal regions of the twigs, the nodes are light yellow ( $\approx$ 4A4), satin-like and with a clearer dark band in the centre.

#### Polyp sclerites (Figures 13A–D,H; 14; 15)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 13A). The adaxial octant, which is very reduced, may consist of a single small, triangular sclerite preceded by a small crescentic scale (Figure 14Aj,k), but these are often replaced by 2 or 3 irregularly shaped forms, and rarely by a single, narrow, triangular sclerite. The adaxial-lateral octants contain larger sclerites, usually 1 or 2 crescentic scales preceding a distal

triangular to triradiate sclerite. The other octants usually all contain 3 sclerites. The proximal is crescentic, the medial is often more like a truncated triangle (Figure 14As,t), and the distal sclerite is more or less triangular. In some instances an octant may contain an accessory sclerite (Figure 14Ai), sometimes 2, that lies alongside the apical scale. There are 1 or 2 arrowhead-like basal tentacular sclerites (Figure 141) which precede a single row of curved tentacular scales (Figure 14B) in each tentacle rachis.

The larger of the triangular to triradiate anthopomal sclerites (Figure 14Aa–h) are usually about 0.11–0.13 mm long, but are sometimes up to 0.15 mm long. Those in the more abaxial octants are ornamented with large tooth-like projections on their exposed face, while those towards the adaxial side have small tubercles. The undersides



Figure 12 Oparinisis flexilis sp. nov., holotype, natural size.



Figure 13 Oparinisis flexilis sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-G. Axial internodes; H. Twig fragment.



Figure 14 Oparinisis flexilis sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.

are relatively smooth (Figure 14Ad). The more proximal sclerites in each octant (Figure 14Am–y) are similarly more ornate in the more abaxial sectors of the anthopoma. The larger of the tentacular scales are usually about 0.065–0.073 mm across, and have scalloped edges and small granules on the surface.

The polyp body is covered with crescentic and irregularly shaped spiny scales that are arranged in 7 rows (Figure 13C,D,H). The adaxial side of the polyp is naked except for 1 to 3 narrow scales (Figure 15a,b) arranged below the adaxial anthopomal octant. Sometimes the uppermost of these scales is quite short and may form part of the anthopoma. The upper adaxial-lateral scales are also narrow but are ornamented with tooth-like projections (Figure 15c). The other body scales have numerous tooth-like and leaf-like projections, which become stouter and ridge-like in the more basal areas of the polyp body (Figure 13B). Most of the larger scales are about 0.16–0.22 mm long, the undersides have a number of large compound warts (Figure 15d,e), and the lower margins generally have several long root-like structures.

### Coenenchymal sclerites (Figures 13E; 16A,B)

The surface of the thinner branches contains narrow spindles unilaterally developed with toothlike and leaf-like processes (Figure 13E). Amongst them are a few small spindles (Figure 16Aa–c) with tall conical warts. The bigger spindles (Figure 16Ad–k) are mostly up to 0.26 mm in length, but some are larger.

The stem of the colony is devoid of tissue, but the surface of the main branches below where the polyps begin contains an upper layer of unilaterally spiny or leafy spindles and ovals (Figure 16Bl–n,p), some of which are broad and plate-like (Figure 16Bo,q), and amongst and below these are numerous smaller warty spindles and a few



Figure 15 Oparinisis flexilis sp. nov., holotype, sclerites: Polyp body.



Figure 16 Oparinisis flexilis sp. nov., sclerites: A. Holotype, twig coenenchyme; B. Holotype, main branch coenenchyme; C. Paratype, polyp body; D. Paratype, polyp.

crosses (Figure 16Ba-k). The subsurface warty spindles are up to about 0.13 mm long, and the unilaterally developed surface sclerites are sometimes as long as 0.25 mm.

### Variability

The colony form of the paratypes agrees well with that of the holotype. The main stems are always naked, and in several cases they branch secundly, bending away at each division, as in the holotype. Branching in the upper regions of the colonies is always pseudo-dichotomous, with most branches dividing unilaterally as in the specimen in Figure 17. In this colony the coenenchyme is missing from the whole of the lower half. Unusually, this colony shows evidence of having once branched from near the base. The smallest colony is 95 mm high, the denuded stem is 0.95 mm thick, and most of the branches are 1.10 mm thick (including polyps). In this specimen, and most specimens with similarly thin branches, the polyps are not as closely oppressed to the branch surface and project about 1 mm above the surface. Twig internodes in some colonies are slightly



Figure 17 Oparinisis flexilis sp. nov., paratype, NTM C10949 (part), natural size.

longer than those of the holotype, being up to 1.73 mm in length. A small specimen of lot NTM C10923 has two downwards oriented barnacles attached, each on a separate branch. The barnacles have not altered the growth form of the colony, however the coenenchyme has overgrown their shells. Except in the lower regions of the main branches, the polyps and coenenchyme in most colonies are too thick to enable the underlying nodes to be seen.

The most notable variation between the sclerites of the various colonies is in the spininess of the polyp scales. Not markedly obvious in the anthopomal sclerites, it is extremely noticeable in the body scales of some polyps (Figure 16D) where the tooth-like projections are often extremely long (Figure 16Ca-d), and in the region of the polyp base, often very stout (Figure 16Ce). Because the tooth-like or leaf-like projections often have their apex divided in numerous points the density of the spines also appears greater (Figure 16Cd). In some of these colonies, the polyp scales may be larger than those in the holotype, up to about 0.24 mm in length.

## Distribution

See Figure 254. Depth range 80-110 m.

# Etymology

The epithet alludes to the characteristically long, flexible branches.

> Oparinisis parkeri sp. nov. Figures 18-22; 255

## Material examined

### Types

HOLOTYPE: SAM H826, 12 km off Cape Northumberland, South Australia, 62 m, S.A. Shepherd, 6 May 1975.

## **Differential characteristics**

Branching relatively dense; branches short; sclerite form.

# Description

## Colony form (Figure 18)

The species is represented by a single, much fragmented, planar colony. The main stem with the lower portions of the main branches attached is 145 mm high. The largest remaining portion of the fan is 160 mm high. The original colony may have been in excess of 400 mm tall.

All of the branches are slightly oval in crosssection. The main stem, from which much of the coenenchyme is missing, is 8 mm x 6 mm thick.

side, but a major division into a number of thick main branches occurs at a complex joint 50 mm from the base. Small calcareous protrusions are all that remain of the holdfast. The main branches and their thicker offshoots in the upper portions of the fan ramify secundly or sympodially. In subsequent branching the ramification becomes pseudodichotomous. Measured only in their broadest dimension, the main branches are 3.2-3.9 mm thick, tapering distally, and most of the thinner branches are about 1.3-2.5 mm thick (all including polyps). The growing tips are polyp-free, 1.3-3.9 mm long, and taper to a rounded point. Consecutive subdivisions occur at 5-25 mm, with 9-12 mm being most common. Branching angles vary from 25-50°, but most are about 29°. Undivided twigs can be up to 60 mm long but most are around 25-35 mm in length.

## Polyps (Figure 19B-D,H)

Throughout most of the colony the polyps are evenly and densely distributed all around the branches. The main stem, however, and its brief continuation as one of the main branches, is polypfree, as is one face of the lower regions of the other main branches. Polyp density on the main branches is slightly less than on the thinner branches and also tends to be patchy. The polyps are contracted, adaxially reduced, and curved over so as to lie more or less along the surface. The anthopomal regions make an angle of about 30-40° to the branch, often lying close to the bases of succeeding polyps. Measured along the branch most polyps are 0.9-1.0 mm long, and they are 0.48-0.54 mm across the head. They project about 0.3-0.4 mm above the branch surface. On the main branches the polyps are shorter, 0.7–0.9 mm, and a few are upside-down. Juvenile polyps occur scattered throughout the colony.

### Colony colour

The remaining coenenchyme on the main stem and lower main branches appears brownish grey ( $\approx$ 7E2) due to the dark colour of the underlying axis. The coenenchyme is actually very pale yellowish white, and this is the colour of all the thinner branches. The major branches have a banded appearance because of the underlying dark internodes. Under a low power microscope, the large surface sclerites give the coenenchyme a granular appearance. The sclerites are colourless.

## Axis form (Figure 19F,G)

The internodes have multiple rows of primary ridges, each bearing a row of spines. There are no secondary ridges. The spines are reduced to granules on the internodes of the main stem and







Figure 19 Oparinisis parkeri sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-G. Axial internodes; H. Twig fragment.



Figure 20 Oparinisis parkeri sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.

lower main branches, but in the thinner branches the spines are large. A main branch internode with diameters of 3.9 mm x 3.5 mm has 54 ridges, a thinner branch internode, with diameters of 2.5 mm x 2.1 mm thick has 32 ridges, and a thinner twig 1.7 mm thick has 10 ridges. Twig tip internodes may only have four ridges and be more or less square in section.

The stem and the beginning of its continuation as a main branch is mostly nodal material. The internodes, where present, are only lenses inserted into the side of the stem, occasionally overgrown and just visible. The internodes of the main branches are 0.3–1.6 mm long, with most being 1.1– 1.3 mm. Thick major branches from the upper regions of the colony have internodes mostly about 1.3 mm in length, and internodes of the finer branches and twigs are 1.7 mm. Main branch nodes are 0.5–1.3 mm long, commonly about 0.8 mm. In the upper major branches, nodes are mostly 0.5 mm long, and the thinner branches and twigs they are about 0.2 mm in length. Nodes are slightly narrower than internodes except near the growing tips where they are much thinner.

#### Axis branching

The branching mode where the main stem divides into main branches is like that in Figure 251 example 56. Main branches divide as in example 54, the thicker branches of the upper regions as in example 55, and the finer branches as in example 14. Branching internodes only have one bifurcation.

## Axis colour

All the internodes are grey white and translucent. The nodal material of the main stem is opaque and yellow brown ( $\approx$ 5D5). The nodes of the main branches are rust brown ( $\approx$ 6E8), and optically dense with a translucent surface region. Nodes of the higher order thicker branches are maize yellow ( $\approx$ 4A6) and more or less opaque. In the thinner



Figure 21 Oparinisis parkeri sp. nov., holotype, sclerites: A. Polyp body; B. Main branch and stem coenenchyme.



Figure 22 Oparinisis parkeri sp. nov., holotype, sclerites: Thin branch coenenchyme.

branches and twigs, the nodes are pale-yellow ( $\approx$ 3A3), opaque, and often may have a clearer central band in the thinnest sections. The main branches and thick higher order branches have nodes with narrow yellowish satin-like borders, present as crescents between the ends of the ridges of the internodes. The satin-like borders of the thinner branch internodes are also crescentic but are whitish.

# Polyp sclerites (Figures 19A-D,H; 20; 21A)

The anthopoma is asymmetrical and continuous with the polyp body scales. The structure of the adaxial octant is relatively consistent: a small, proximal, crescentic scale (Figure 20Aw,x), and a distal sclerite that is usually more triradiate than triangular (Figure 20Au,v). Occasionally there are 2 crescents, and sometimes if the triangular sclerite is a little stunted there is a very large basal tentacular sclerite at the apex. The only sclerites below this group are more spindle-like, often longer, and are treated here as polyp body sclerites. The other octants show considerable variability. In the most uniform case, each octant has a large triangular or triradiate scale at the apex, and 2 proximal scales. In the adaxial-lateral octants it is difficult to tell whether the most proximal

scale, which is long and narrow, should be included in the anthopoma. The most proximal scale in each octant is usually crescentic (Figure 20Ao-t). The middle scale tends to be boomerangshaped (Figure 20Ak-n) often becoming nearly triangular in the abaxial and abaxial-lateral octants. The distal scale is triradiate to triangular (Figure 20Aa-h). Its size seems to vary inversely to the size of the middle sclerite of the 3. There are a number of variations on this anthopomal structure, most often seen in the adaxial-lateral octants but not restricted to this area. One of the most common occurrences is for the distal triangular or triradiate scale to be replaced by 2 dovetailing sclerites arranged side by side. Occasionally, one of these sclerites is considerably larger than its partner which may be reduced to a narrow flattened rod. In some instances the triradiate sclerite along with its preceding scale are together replaced by 2 somewhat boot-shaped sclerites that fit side by side to form a long triradiate or triangular shape. In another variation the 2 proximal scales may be replaced by smaller forms combining to make crescentic shapes. Apically, it is not unusual to find irregularly shaped accessory sclerites (Figure 20Ai,j) alongside the tip of the main triradiate scale, sometimes appearing to extend onto the base

of the tentacle. The triradiate scales are generally up to 0.15 mm long, but a few are larger. They are ornamented on the upper side with thorns; the thornier scales being on the abaxial side of the anthopoma.

A single basal tentacular sclerite of triradiate form may occur in some octants in some polyps (Figure 20Be). The arrangement seems to vary greatly. In some polyps, basal tentaculars are all like that in Figure 20Bd, and in others there is a mixture often including forms transitional between those shown in Figure 20Bd and Be. The rachis of each tentacle contains a single row of curved, granular scales (Figure 20Ba–c) up to 0.077 mm long.

In many of the less uniform polyps examined, only 1 or 2 octants were irregular. It seems, however, that the extent of variation can be considerable as one polyp examined had 5 complex sectors, some appearing quite jumbled. It has not been possible to make a good electron microscope preparation of an intact anthopoma because they are closely appressed to the branch surface. Those in Figure 19A appear jumbled primarily due to their collapse during the cleaning process.

The polyp body is protected by thorny, crescentic scales that are arranged in 7 rows on the polyp head (Figure 19B); although the adaxial-lateral rows are reduced to about 3 sclerites that are elongate and narrow (Figure 21Aa,b). The scales from the lower parts of the body have thicker and blunter projections than the more distal ones (Figure 21Ad-h). There are about 14-16 series of scales down the abaxial side of the larger polyps. On the adaxial side immediately below the adaxial octant there are usually 1-2 flattened spindles. Sometimes there is a third spindle, in which case the sclerites do not form a row but are offset irregularly to each side. The underside of the body scales has compound warts (Figure 21Ac). The scales on the more abaxial aspects of the polyp are generally up to about 0.21 mm long. The lateral and adaxial-lateral scales are longer and may be up to 0.25 mm.

### Coenenchymal sclerites (Figures 19E; 21B; 22)

The surface of the finer branches contains predominantly spindles (Figure 19E). These are mostly developed unilaterally with spines or toothlike projections, and amongst them are a number of small spindles with a few conical tubercles and some large flattened sclerites with thick projections that are transitional forms to polyp body scales (Figure 22). In some samples the spindles are no longer than 0.21 mm, while in others larger ones are found to 0.25 mm.

On the stem and the main branches there is an upper layer which contains large, complexly warted oval sclerites, and a lower layer of smaller warty forms with the warts commonly in girdles (Figure 21B). The exposed face of the sclerites in the upper layer is developed with spiny tooth-like projections. Commonly up to 0.22 mm, the large oval forms may occasionally reach 0.25 mm in length. There is a larger proportion of smaller girdled sclerites in the proximal stem tissue than distad.

### Distribution

See Figure 255. Depth 62 m.

#### Etymology

This species is named in honour of Shane Parker, Curator of Lower Invertebrates, South Australian Museum. A valued friend and colleague who assisted with this project, and passed away before its completion.

## Oparinisis viking sp. nov. Figures 23–26; 256

#### Material examined

Types

HOLOTYPE: NTM C2484, Great Australian Bight, trawl, RV *Soela*, Dec. 1981, (no further data).

### **Differential characteristics**

Polyp scales with long, horn-like projections.

### Description

### Colony form (Figure 23)

The specimen is 56 mm long and is only a small branched portion of what was probably a much larger colony. Polyps are missing from some areas, and the entire coenenchyme is absent from several others. Too little of the original colony remains to accurately determine the method of ramification, but the slight zigzag nature of the main branch indicates that it was probably much the same as for other members of the genus. Most of the ramifications are oval in cross-section. Measured in the plane of the fan, the main branch is 2.4–2.8 mm thick, the major branches are 1.7–1.9 mm thick, and the thinnest twigs are about 0.9 mm thick (all including polyps). Consecutive subdivisions on the



Figure 23 Oparinisis viking sp. nov., holotype, natural size.



Figure 24 Oparinisis viking sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-H. Axial internodes; I. Twig fragment.



Figure 25 Oparinisis viking sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Branch coenenchyme.

main branch are 5.5–11.0 mm apart. Branching angles throughout the fragment are  $31-55^{\circ}$  with most around  $40^{\circ}$ .

# Polyps (Figure 24B–D,I)

Except on the main branch, polyps are evenly and densely distributed all around. On the main branch the lateral faces tend to be polyp-free. Polyps are contracted and adaxially reduced. Most arise at angles of 32–49° and curve to lie along the branch. The domed anthopomal regions are angled at 25–70° to the branch surface, and sometimes lie up against the base of a succeeding polyp. Measured along the branch, most polyps are 0.8– 1.1 mm long, and about 0.5 mm across the head. They project about 0.38–0.48 mm above the surface. There are two groups of polyps upside-down, and few juvenile polyps are occasionally encountered.



Figure 26 Oparinisis viking sp. nov., holotype, sclerites: Polyp body.

### Colony colour

Very pale yellowish white. The coenenchyme is translucent and the darker nodes can be seen underneath. The surface is granular, and the large coenenchymal sclerites are easily visible under a low power microscope. The sclerites are colourless.

### Axis forms (Figure 24F–H)

With the exception of the more terminal portions of the twigs, the only visible internodes are oval in cross-section. Internodes have multiple rows of primary ridges, each bearing a single row of large spines. There are no secondary ridges. Tip internodes may be more or less square in section. The most basal main branch internode is 1.9 mm x 1.3 mm thick and has 25 ridges. A thinner branch internode is 0.7 mm x 0.6 mm thick and has 14 ridges. Desmocyte cavities are distinct and may be deep.

Main branch internodes are mostly about 1.5 mm long. Those of the other branches are longer, up to at least 2.1 mm. Nodes on the main branch are 0.3–0.4 mm long, and slightly narrower than the internodes. In the other branches they are 0.17–0.24 mm long. On the thinnest twigs they are much narrower than the internodes.

Twigs branching from the main branch have a thick proximal internode which abruptly tapers to the diameter of the continuing narrower twig axis.

### Axis branching

Branching internodes only have one bifurcation. The modes of branching all similar to Figure 251 example 55.

## Axis colour

The internodes are grey white and translucent, becoming almost transparent when thinnest. The more basal nodes of the main branch are orange ( $\approx$ 5B7) and more or less opaque, and at the distal end they are sunflower yellow ( $\approx$ 4A7). All have narrow yellowish satin-like borders. In the branches the nodes are pale yellow ( $\approx$ 4A3) with a silky sheen and narrow whitish satin-like borders. In the thinnest ramifications the pale yellow nodes are satin-like with a clear central band.

# Polyp sclerites (Figures 24A–D; 25A,B; 26)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 24A). In general, each anthopomal octant has an apical triangular to triradiate sclerite, preceded by a single scale in the adaxial octant and by 2 scales in the other sectors. However, all polyp sclerites are extremely spiny, and in the contracted specimen it is often difficult to tell where the anthopoma begins. In the adaxial-lateral and lateral octants the 2 proximal sclerites are usually quite evident. In the 3 more abaxial octants it sometimes appears that there is only a single proximal scale, and occasionally none at all. The proximal scales are essentially crescents with a simple bilobed margin in the adaxial (Figure 25Ak) and adaxial-lateral (Figure 25Al) octants, becoming progressively developed with longer thorn-like projections in the lateral and abaxial octants (Figure 25Am-p). The apical sclerite in the adaxial octant may be somewhat triangular as in Figure 25Ai or more triradiate and similar to Figure 25Ah. In the other octants this sclerite is larger and has pronounced spines on the exposed face and lateral margins (Figure 25Aa-e), but the underside is relatively smooth (Figure 25Af). It is not uncommon to find an extra triradiate sclerite at the apex some of the octants. These are often quite large and similarly shaped to those in Figure 25Ag,h, and sometimes irregularly shaped and similar to that in Figure 25Ai, and they are overreached by the tip of the preceding sclerite. There is generally a single basal tentacular sclerite which may resemble a minute triradiate, a spiny crescent, or an intermediate form. In the rachis of each tentacle there is a single row of curved scales with granular scalloped margins (Figure 25B).

The larger apical triangular or triradiate sclerites are about 0.18–0.19 mm in length, and the tentacular scales are up to 0.073 mm across

The polyp body is protected by scales with very large horn-like projections (Figure 26). They are arranged more or less in 7 rows on the polyp head (Figure 24B–D). The adaxial side of the polyp is naked except for a couple of small thorny spindles that lie beneath the anthopomal octant. Most of the body scales have pronounced horn-like projections on the distal margin, and those near the polyp base have similar processes on the exposed face (Figure 26f–h). The underside of the scales has large compound warts (Figure 26a–e). Most of the larger scales are about 0.20–0.23 mm long, with a few longer ones up to about 0.27 mm.

### Coenenchymal sclerites (Figures 24E; 25C)

The surface of the branches contains large spindles and oval sclerites, up to 0.35 mm long, that are unilaterally developed with leafy and thorny projections (Figure 25Cd–j), together with small spindles, capstans and a few crosses that may only have small warts (Figure 25Ca–c). On the thinner branches, the small sclerites that occur amongst the large spiny forms are both spindles and capstans. On the thickest branch they are predominantly capstans.

# Distribution

See Figure 256.

# Etymology

In allusion to the resemblance of some of the

polyp scales to the two horned helmets attributed to the Vikings by romantic writers and illustrators of the 18th century. Noun in apposition.

## Tethrisis gen. nov.

### Type species

Tethrisis suzannae sp. nov., here designated.

## Diagnosis

Colonies up to 300 mm tall, planar, and sympodially branched.

The sclerites are colourless, but preserved colonies are pale to dark brown. Axial internodes are greyish white and translucent, and nodes are dark brown proximally becoming paler and much yellower in the twigs.

Polyps are generally distributed all around. They are adaxially reduced, adaxially naked, and usually preserved angled distad and folded down against the branch surface.

The anthopoma is asymmetrical and more or less continuous with the polyp body sclerites. Each octant is generally occupied by a large triradiate sclerite, up to 0.14 mm long, preceded by a crescentic scale. Accessory sclerites may occur alongside the triradiate in some octants. A single basal tentacular sclerite, or several rodlets, precede a single row of curved scales in each tentacle rachis.

The adaxial side of the polyp is mostly naked. The rest of the body is protected by very large scales that are not arranged in rows or regular series. There may be as few as 3 scales in an approximate series around the narrower parts of the polyp. The body scales are usually <0.23 mm long, but sometimes up to 0.30 mm, and are ornamented with stout ridges or tooth-like projections.

The coenenchyme contains capstans and ovals on the stem, ovals and spindles on the main branches, and narrow spindles on the twigs. Most are <0.24 mm long, and they are unilaterally ornamented with tooth-like projections.

The axial internodes are up to 1.4 mm long. They have multiple primary ridges each bearing a single row of large spines; except in the lower, older areas where the spines are reduced to granules.

## Distribution

As for Tethrisis suzannae, see Figure 257.

### Etymology

Derived from *Tethra*, the Celtic mythological king who reigns over all creatures of the sea; combined with *Isis*.

*Tethrisis suzannae* sp. nov. Figures 27–31; 257

## Material examined

### Types

HOLOTYPE: NTM C10951, off Shark Bay, Western Australia, 24°55.6'S, 112°50.8'E, 80–85 m, dredge, limestone rubble, sand and shell grit, RV *Akademik Oparin*, P. Alderslade, 14 July 1987. PARATYPES: NTM C10938, C10939, C11621, same data as holotype; NTM C2481, Great Australian Bight, trawl, RV *Soela*, Dec. 1981, (no further data).

#### Diagnosis

As for the genus.

# Description

Colony form (Figure 27)

The sympodially branched holotype is a planar colony 300 mm high and 255 mm across. The calcareous holdfast is relatively large and bulbous, about 8-11 mm thick, and like a giant internode it is faintly striated with very low ridges, and is covered with desmocyte cavities. The main stem is very irregular. It gives off a main branch 60 mm above the holdfast, but the stubs of two thinner branches remain below this. Nearly all of the proximal half of the stem is devoid of coenenchyme. Most of this lower half is nodal material. Where internodes occur, they are only partial, lens shaped, and inserted into the sides of the stem. The stem zigzags sympodially, and produces a large bulbous internodal lens at each bend. The main stem is oval in cross-section and 3.2 mm x 3.2–4.7 mm thick. The main branches are 2.5-2.8 mm thick, and most other branches are 1.1-1.7 mm thick (including polyps). Twig tips taper abruptly, most being <0.5 mm long. Branching angles are 29-46°, with 36° being the most common. Although one instance of 30 mm between branching points was measured, consecutive branchings are usually within 2.1-9.5 mm, with 4.4 mm commonly occurring. The longest undivided branch is 110 mm, though most are <60 mm.

### Polyps (Figure 28C-F,I)

The main stem is virtually devoid of polyps. Throughout the rest of the colony they are densely distributed all around the branches, with the exception of several short twigs where they are biserial. The Polyps are contracted and adaxially reduced. Although on some branches the polyps lie more or less against the surface, in most areas the base of the polyp is erect and the head is bent over through about 90°, in some instances more. The anthopomal region is then at right angles to the branch surface, or angled down towards it or to the base of a succeeding polyp. Polyps in the



Figure 27 Tethrisis suzannae sp. nov., holotype, natural size x 0.75.

P. Alderslade



Figure 28 Tethrisis suzannae sp. nov., holotype: A-F. Polyps; G. Coenenchyme; H. Axial internode; I. Twig fragment.

more peripheral regions of the colony are slightly larger than the others. Measured along the branch they are 0.70–0.80 mm in length and about 0.37– 0.41 mm measured abaxially across the head. The bases are about 0.34–0.46 mm long and the neck region is slightly narrower. Depending on the amount of curvature, polyps project 0.3–0.5 mm above the branch surface. In the lower and more central regions of the colony, polyps are mostly <0.7 mm in length. Juvenile polyps occur throughout the colony.

## Colony colour

The branches in the more peripheral parts of the colony are slightly darker than the rest. The surface of the branches is dark blonde ( $\approx$ 5D4), but the polyps are slightly darker so that the thinner branches, where the polyps are closer together, have a browner appearance ( $\approx$ 6E7). The coenenchyme is translucent and the dark nodes show through from below in most of the colony. In the still thinner branches the paler nodes are more difficult to see. The sclerites are colourless.



Figure 29 Tethrisis suzannae sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 30 Tethrisis suzannae sp. nov., holotype, sclerites: Polyp body.

# Axis form (Figure 28H)

Internodes have multiple primary ridges, each bearing a row of large spines. These are high on most of the internodes but are reduced to granules on the main stem and the lower parts of the main branches. There are no secondary ridges. A main branch internode 2.5 mm thick has 36 ridges, a branch internode 1.2 mm thick has 18, and a twig internode 0.7 mm thick has 12 ridges. Desmocyte cavities are deep and conspicuous.

Main branch internodes are mostly 0.6-1.1 mm

long, commonly about 0.9 mm, while those in the thinner branches and twigs are slightly longer, 1.3–1.4 mm. Nodes in the main branches are about 0.54 mm long. In the thinner branches they are 0.18–0.24 mm long, and in the twigs the length is 0.12–0.18 mm.

### Axis branching

In the main branches and the thicker higher order branches, divisions are of the form shown in Figure 251 examples 54 and 55. Examples 12, 13 and 14

represent the divisions involving the thinner branches. Branch internodes only have one bifurcation.

### Axis colour

The nodal material of the main stem is dark brown ( $\approx$ 6E7) and opaque. In the main branches and most higher order branches the nodes are brownish orange ( $\approx$ 6C7), opaque, and have narrow yellowish satin-like borders present as crescents between the ends of the internode ridges. In the twigs, the nodes are light yellow ( $\approx$ 4A4), opaque and satin-like, with a clearer dark band in the centre. The axial internodes are all greyish white and translucent, becoming nearly transparent near the twig tips.

## Polyp sclerites (Figures 28A-F,I; 29; 30)

The anthopoma is asymmetrical and more or less continuous with the polyp body sclerites. In a polyp where the anthopoma is relatively uniformly constructed, each octant consists of a proximal crescentic scale whose degree of complexity varies (Figure 29Am-v), and a distal triradiate sclerite of similar variability (Figure 29Aa-k). The more complex forms occur on the abaxial side of the polyp. In the adaxial-lateral octants the crescentic scale is often quite small (Figure 29Am) but it may be quite large and perhaps better considered as a body scale. More often than not, the proximal scale in the adaxial octant is also vary large and may be a marginal body scale, although it often overlaps the base of the triangular or triradiate sclerite above (Figure 29Ak). The size of the anthopomal scales diminishes from the abaxial to the adaxial side of the polyp (Figure 28A,B).

The contents of each octant vary and most polyps have one or more that contain additional sclerites. The extra sclerites are usually granular or tuberculate rods, spindles, or branched forms that lie alongside the triradiate scales. They may be as long as the triradiate scale (Figure 28A, arrowed) or short and at the apex of the octant (Figures 28B arrowed; 29Al). Rarely, the triradiate sclerite in an octant is replaced by 2 boomerang-shaped forms arranged side by side.

There is a single row of small, curved, granular scales (Figure 29Ba) in each tentacle rachis, but these are only occasionally preceded by a basal tentacular sclerite (Figure 29Bb) as several small granular rodlets often occur here instead.

The triradiate apical anthopomal sclerites are ornamented with tooth-like projections or small tubercles on their upper surface, and the larger ones may have spines on their lateral margins. Occasionally they are very ornate (Figure 29Ad). Their underside is relatively smooth (Figure 29Ai), and the largest are up to about 0.14 mm long with most <0.13 mm. The tentacular scales are often not very numerous, and are rarely larger than 0.053 mm across.

The polyp body is naked adaxially except for 1–3 narrow spindles (Figure 30b) or relatively smooth scales below the adaxial anthopomal octant. The upper most of these is often small enough to occupy the proximal position in the octant. If there is more than one sclerite they are not always in a row, but are usually offset with one or more placed towards the adaxial-lateral areas. The rest of the polyp body is protected by large, curved scales that are not arranged in rows (Figure 28C-F,I). The scales are not arranged in distinct series either, but in general terms there are about 3-4 scales in a 'series' around the polyp, depending on the part of the polyp involved. The scales are ornamented on their exposed face with stout, blunt, tooth-like or ridge-like projections with granular summits (Figures 29C; 30). The underside is relatively smooth (Figure 30a). Scales towards the base of the polyp near the abaxial midline often have a concave distal margin. Occasionally a polyp is found with generally narrower scales, having reduced and less dense projections (Figure 28F). Most of the larger scales in a polyp are <0.23 mm in length. A few towards the base of the polyp may be up to 0.25 mm, and occasionally as large as 0.30 mm.

### *Coenenchymal sclerites* (Figures 28G; 31)

The surface of the twigs (Figure 28G) contains numerous narrow spindles unilaterally developed with tooth-like projections that have small spines or granules on their summits (Figure 31A). Most are <0.22 mm but a few may be as long as 0.35 mm.

The surface of the main branches contains predominantly stout spindles and oval sclerites together with a few small spindles (Figure 31B). The large forms are unilaterally developed with blunt tooth-like and ridge-like projections with spiny summits, and are up to about 0.24 mm long.

The surface of the stem contains predominantly small spiny capstans and modified forms, and a few large oval to globose sclerites unilaterally developed with a complex of tooth-like projections (Figure 31C). Most of the capstans are about 0.080– 0.098 mm long, and the large oval forms are up to 0.220 mm in length.

## Variability

The paratypes are all portions of colonies. The 3 from the same location as the holotype are 85 mm, 135 mm, and 155 mm tall with thin branches. The specimen from the Great Australian Bight is larger, 207 mm high and 70 mm across, with a main branch that is oval in section, 3.2 x 4.0 mm thick, and internodes about 1.1–1.2 mm long. The



Figure 31 Tethrisis suzannae sp. nov., holotype, sclerites: A. Twig coenenchyme; B. Main branch coenenchyme; C. Stem coenenchyme.

specimen is badly damaged and many polyps are broken or missing.

The colour of the colonies, branching pattern, and axial architecture all agree with the characters of the holotype. The tentacular tissue in all polyps, including the holotype, remains brown and optically dense when clearing in phenol-xylol.

Colony NTM C10939 has most polyp body scales with very long projections, similar to Figure 29Ca. Also, many polyps, particularly those from younger parts of the specimen, have mainly narrow scales that are strongly curved. The basal body scales, however, are more like those of the holotype. The triradiate anthopomal sclerites are mostly like those of the holotype, but it is more common to find very ornate forms, some even more complex than that shown in Figure 29Ad and somewhat larger. The surface of one of the thicker branches, only 1.4 mm in diameter, has sclerites similar to those of the main branches of the holotype, but the stout spindles are larger and up to 0.3 mm in length. The most noticeable difference in the spiculation of the specimen from the Great Australian Bight is the larger tentacular scales up to 0.073 mm across, and the presence of a basal tentacular sclerite in each tentacle.

## Distribution

See Figure 257. Depth range 80-85 m.

### Etymology

The species is named after Ms Suzanne Horner in recognition of her tireless assistance with printing and assembling many of the photographic illustrations for this work, the compilation of the distribution maps and the bibliography, general editing, and fiddly bits too numerous to mention.

Paracanthoisis gen. nov. Figure 309

- Mopsea; (part) Tixier-Durivault, 1970: 333; (part) Bayer, 1981: 942 (in key)
- Acanthoisis; (part) Bayer and Stefani, 1987a: 49–51, 52 (in keys), 66; (part) Bayer and Stefani, 1987b; 940–942 (in key).

# **Type species**

Acanthoisis richerdeforgesi Bayer and Stefani, 1987, here designated.

≡ Paracanthoisis richerdeforgesi new combination.

### Diagnosis

Colonies are planar and pinnate, tending to be plumose, 60–110 mm tall, and cream or brownish orange when preserved. Sclerites are colourless or very pale yellow in transmitted light. Axial internodes are translucent, greyish white, or greyish white with a yellowish tint. Nodes are cream, greyish yellow, or deep orange.

The polyps are distributed all around or biserially. They are short, somewhat cylindrical, adaxially reduced, adaxially naked below the head scales, and angled distad. In the contracted state are they divided by a suture into a head and a low shelf-like base. The suture marks a sclerite-free neck zone whose visibility depends upon the extent of polyp contraction.

The anthopoma is symmetrical and only weakly continuous with the polyp body sclerites. Each octant generally consists of a triangular sclerite preceded by a single semicircular to crescentic scales. In some octants the triangular scale may be very large and stand alone, in others it may be relatively small and be preceded by 2 semicircular to crescentic scales. The larger of the anthopomal triangular sclerites are 0.09–0.15 mm long.

There is a single basal tentacular sclerite preceding a single row of curved crescentic scales in the tentacle rachis.

There are 2–3 series of scales abaxially, becoming 1–2 series adaxially, on the polyp head. The head scales are generally large, curved, and crescentic, with some very broad and irregularly shaped forms occasionally occurring in the abaxial region. The scales of the base are generally thicker than those of the head, but similar in structure. In *P. richerdeforgesi*, many are often very narrow and long. Body scales are mostly 0.13–0.35 mm long, and are ornamented with low, granular tubercles that are usually rounded but sometimes spine-like.

The coenenchyme contains predominantly ovals and spindles ornamented with rounded, granular tubercles. The spindles are sometimes branched or curved, and may have short root structures. They are generally <0.39 mm in length, but in *P*. *richerdeforgesi* those near the polyp base may reach 0.55 mm.

The axial internodes of most branches have distinct primary ridges each of which is a single series of large spines. In *P. simplex* (Tixier-Durivault 1970) some of the internodes of the pinnae are twisted, those of the main branches have unspined ridges, and those of the lower stem are smooth. Internodes are mostly 1.8–4.5 mm long, and those of the principal branches can initiate up to 4 branches.

#### Remarks

Paracanthoisis differs from Acanthoisis primarily in the structure of the polyps. Those of Acanthoisis are more or less cylindrical, often capable of extreme contraction, and, as detailed later, sometimes show slight invagination of the neck into an inflated base. Should further material be encountered of Acanthoisis flabellum, and other nominal species of Acanthoisis, that clearly demonstrates the presence of a sclerite-free neck zone as a genetic character, then it would seem advisable to reduce Paracanthoisis to a junior synonym of Acanthoisis. The polyp base in Acanthoisis is often reduced on the distal or adaxial side, and this taken to a further degree would result in a residual shelf-like base as occurs in Paracanthoisis.

# Distribution

See Figure 309.

## Etymology

The Latin *par*, equal or like, combined with *Acanthoisis*.

## Paracanthoisis richerdeforgesi (Bayer and Stefani, 1987) new comb. Figures 32–36; 258

Acanthoisis richerdeforgesi Bayer and Stefani, 1987a: 69–70, Plate XXIV; Plate XV, 1; Plate XXVI; Figure 4, b.

### Material examined

#### Types

HOLOTYPE: USNM 76479, Chesterfield Islands, 19°40'S, 158°27.05'E, 250 m, trawled, 18 May 1979.

### Differential characteristics

Sclerites of the polyp base and neighbouring coenenchyme often long, narrow, and curved, sometimes up to 0.55 mm long; internodes not twisted.

#### Description

Colony form (Figure 32)

The holotype is a plumate fragment of a larger



Figure 32 Paracanthoisis richerdeforgesi (Bayer & Stefani, 1987), holotype, natural size.

colony, and the holdfast and stem are missing. The piece is 60 mm tall and 45 mm across. It is ramified in an irregularly pinnate manner with the majority of the pinnae being alternately arranged.

The main branch is about 0.79 mm thick near the base, 0.63 mm mid-way, and 0.32 mm just below the tip. Most pinnae are about 0.47 mm thick and taper slightly. Consecutive pinnae occur at intervals of 0.8–4.0 mm. The angle of branching is about 57–85° with most pinnae curving slightly from their base. Unbranched pinnae are 1.7–27.0 mm in length.

#### Polyps (Figures 33; 34A–D,H)

Distribution is essentially biserial with two single opposing rows of polyps which are mostly alternately arranged. The two rows are usually within the colonial plane but there are short sections where the polyps are on the two outer faces of the pinnae. The polyps in a single row are placed at intervals of 1.2–1.5 mm. They are contracted, reduced adaxially, and angled distad at about 42–56°. The anthopomal region faces away from the branch surface and is flat to slightly



Figure 33 Paracanthoisis richerdeforgesi (Bayer & Stefani, 1987), holotype: Polyp showing naked adaxial neck region.

convex. Polyps are about 0.38–0.41 mm in diameter and project about 0.29–0.36 mm.

In most instances there is a clear constriction delineating the polyp head from a low to very low shelf-like base. In some cases the base is almost undetectable, being reduced to just a few thicker sclerites above the coenenchyme. In those polyps where the base is most pronounced it protrudes about 0.18 mm above the surface. The coenenchyme below the lateral aspects of the polyp often bulges out, merging in the abaxial region of the polyp. The constriction is often difficult to detect on the abaxial side but it is quite obvious laterally. It is in fact a suture marking a scleritefree neck zone. A small number of polyps, contracted to a lesser extent than their neighbours, have the head minimally extended from the base and the branch surface, clearly showing the transparent, membranous, lateral walls of the neck zone. This gap between polyp head and branch is in some cases 0.07 mm wide. In these widest occurrences the naked adaxial side of the neck can also be seen. There is a small region on the branch surface directly under the adaxial side of the head where the coenenchymal sclerites are missing, leaving a semi-annular transparent membrane surrounding the neck of the polyp (Figure 33).

In those polyps where the naked neck is clearly visible, only the abaxial scales of the polyp head remain continuous with those of the rim of the base. In none of these polyps is there a complete separation between head and base sclerites, but an apparent abaxial suture is visible in many other polyps and a clear impression is gained that the head region can theoretically extend well away on a sclerite-free neck.

### Colony colour

Brownish orange (~5C5), with the centre of the anthopomal region of most polyps appearing dark brown due to discoloured tissue. The coenenchyme is transparent and the pale yellowish nodes are clearly visible underneath. Sclerites are pale yellow in transmitted light.

### Axis form (Figure 34F,G)

The internodes have distinct primary ridges which each bear a single row of large spines. Desmocyte cavities are elongate and distinct, and more or less in a single row between the primary ridges.

Internodes are about 3–4.5 mm long. The nodes of the thicker region of the main branch are about 0.24 mm in length, and those on the twigs 0.12 mm.

### Axis branching

Only one internode of the main branch is unbranched. Two internodes each carry one


Figure 34 Paracanthoisis richerdeforgesi (Bayer & Stefani, 1987), holotype: A-D. Polyps; E. Coenenchyme; F-G. Axial internodes; H. Twig fragment.



Figure 35 Paracanthoisis richerdeforgesi (Bayer & Stefani, 1987), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp head.



Figure 36 Paracanthoisis richerdeforgesi (Bayer & Stefani, 1987), holotype, sclerites: A. Polyp base; B. Branch coenenchyme.

branch, and the remainder branch 2–4 times. Branch stubs are usually short throughout the colony fragment, 0.3–0.5 mm, and branching is similar to Figure 251 examples, 3, 5, 7, and occasionally example 26.

# Axis colour

The colour of the few minute axial portions visible is difficult to determine. The internodes appear translucent, greyish, with a pale yellowish tint. The nodes have broad pale yellow ( $\approx$ 4A4) satin-like borders, and a short greyish yellow central portion.

#### Polyp sclerites (Figures 34A–D; 35; 36A)

The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant is dominated by a large triangular sclerite which is usually preceded by a semicircular or crescentic scale (Figure 35Ai–k), a number of which have fallen out of the preparation illustrated in Figure 34B,D. In some cases the triangular sclerite is quite small and it is complemented proximally by an extra semicircular or irregularly shaped scale (Figure 35Ae), or laterally by an elongate sclerite (Figure 35Ad). The larger triangular sclerites are usually about 0.14–0.15 mm long (Figure 35Aa–c,f–

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h). Like the proximal anthopomal scales they are ornamented with numerous spines and have simple granular root structures.

There is a single basal tentacular sclerite (Figure 35Bb) that precedes a single row of curved crescentic scales in the tentacle rachis. The arrowhead like basal tentacular sclerites are usually about 0.106 mm long. Many of the tentacle scales are most irregularly shaped, especially the smaller ones. Those with a more characteristic form are often butterfly-shaped with several apical projections (Figure 35Ba). The tentacle scales are up to about 0.06 mm long.

The head of the polyp is covered with large curved scales (Figure 35C). Abaxially they are usually arranged in 2 series, sometimes 3, and are generally very broad and occasionally more or less triangular in order to cover the longer abaxial side of the head. Those in the lateral and abaxial aspects of the head are narrower. Adaxially there are usually 2 series of scales, but sometimes there may be only a single scale. Most of the polyp body scales are 0.25–0.32 mm in length. They are ornamented with tubercles that may be small, or tall and spine-like. Abaxial scales with long root structures occur in some polyps.

Many of the sclerites of the polyp base resemble those of the head (Figure 36Ae). Most, however, are generally not as broad, and are often quite narrow and markedly curved to conform to the contours of the base (Figure 36Aa–d). They merge imperceptibly with those of the branch surface, particularly where the coenenchyme bulges out laterally below the polyps. The bases of some polyps may also contain a few very broad scales, some of which have long root structures (Figure 36Af,g). Most basal sclerites are no longer than 0.36 mm. Coenenchymal Sclerites (Figure 34E; 36B)

The general surface of the branches contains a single layer of large spindles with the occasional plate-like form. The spindles are often branched and may have root structures. The coenenchyme that forms the lateral bulges below the polyps often contains numbers of long curved sclerites similar to those in the polyp base. Those from both sides of the polyp usually merge abaxially, often loosely forming chevrons, and become incorporated into the shelf-like bases. Although the long curved forms can be up to about 0.55 mm long, most coenenchymal sclerites are no longer than about 0.36 mm. They are ornamented with granular tubercles on their outer face.

#### Distribution

See Figure 258. Depth 250 m.

# Paracanthoisis simplex (Tixier-Durivault, 1970) new comb.

Figures 37-40; 259

Mopsea simplex Tixier-Durivault, 1970: 333–334, Figures 172–173.

### Material examined

#### Types

LECTOTYPE (here designated): MNHN, I. surprise, (presumably Atoll de Surprise, New Caledonia, 18°26.7'S, 163°09.7'E), M. Chevalier, 1962.

## **Differential characteristics**

Sclerites of the polyp base and neighbouring coenenchyme only up to 0.29 mm long; axial internodes occasionally twisted.







Figure 38 Paracanthoisis simplex (Tixier-Durivault, 1970), lectotype: A-E. Polyps; F. Coenenchyme; G-M. Axial internodes; N. Twig fragment.

## Remarks

Tixier-Durivault (1970: 333) did not designate a holotype from amongst the "Quatre echantillons conservé dans l'alcool "reported in her original description. The fragmented dry specimen described below was kindly made available to me by Mme. Marie-José d'Hondt of the Muséum National d'Histoire Naturelle, Paris. Mme. d'Hondt noted in her correspondence that she was unable to locate a colony matching Tixier-Durivault's Figure 172A. She also mentioned that the specimen label written in the handwriting of Tixier-Durivault, which states that this specimen lot is the "TYPE", specifies the collection data as "I. Surprise, M. Chevalier, 1962" in contrast to "Iles Chesterfield par M. Chevalier en 1960" recorded in the original description. This group of dried fragments labelled as the type is here designated as the lectotype. It is indeed difficult to reconcile the fragments with the original hand drawn illustration (which measures 73 x 78 mm in contrast to the 60 x 110 mm given in the text), which may only be as accurate as the remainder of the cursorily drawn figure, may only be a portion of the specimen, or could represent a different colony. Some confusion remains as to the exact locality of the collection station.

## Description

## Colony form (Figure 37)

The fragile dried lectotype fragments are consistent with the general colonial form mentioned in the original description. The ramification appears to be predominantly planar and irregularly pinnate, both alternate and opposite. Two pieces, obviously once joined, together form what appears to be the basal portion of the colony. The first main branch occurs 2 mm above the stem base. Just above this the stub of another branch remains which projects out of plane. The pinnate branching begins about 8 mm above the base. The basal 4 mm of the stem is devoid of coenenchyme and about 1.9 mm thick. Two partial nodes are inserted into one side of the internodal material. Above this the upward extension of the stem is 1.6 mm thick including coenenchyme. The diverging main branch is 1.2 mm thick. The lower coenenchyme is frosted with a white crystalline deposit, and only a few scattered polyps are present.

Most of the fragmented principal branches are about 1.1–1.6 mm thick proximally, and taper slightly. The pinnae are mostly about 0.48 mm in diameter and do not appreciably taper. The distance between consecutive subdivisions is variable with about 5 pinnae per 10 mm. The angle of branching is about 52–65°, with some pinnae diverging at nearly 90° and, like most of the others, curving upwards. Unbranched pinnae are 1.1–15.3 mm in length, the actual maximum length possible is indeterminate because many are not complete.

## Polyps (Figures 38A-E,N)

Polyps are mostly distributed all around, fewer on the thicker branches, and biserially arranged on the terminal portions of the finer twigs. They are quite regularly spaced about 0.54–0.78 mm apart, centre to centre.

The polyps lean distad making an angle of about 38–48° with the branch surface. Although most are tightly contracted, drying adding to tissue shrinkage, many show a suture dividing them into a head and shelf-like base. A few polyps are preserved with suture wide enough to just see the membranceous neck of the polyp, and a couple have the head raised sufficiently to see the naked adaxial region of the neck below the head scales (Figure 38C).

Measured abaxially, polyps are about 0.36 mm long. The more or less flat anthopomal region is about 0.31 mm in diameter. In some tightly contracted polyps the rim of the base has a greater diameter than the polyp head. Only a few juvenile polyps are present, mostly nestled between larger polyps near the ends of the pinnae.

#### Colony colour

Cream (≈4A3) to very pale greyish orange (≈5B3), like dark sand. The axial nodes can be seen through the coenenchyme. Sclerites are colourless.

## Axis form (Figure 38G-M)

The internodes of all but the lower portion of the stem have pronounced primary ridges. The lower regions of the main branches have internodes with unspined ridges. The internodes in the rest of the colony have primary ridges which each bear a single row of large spines. Some of the internodes are twisted (Figure 38G,J), and in those of the thicker branches slight signs of secondary rows of spines can sometimes be detected (Figure 38 m). The desmocyte cavities are distinct and confined to the valleys between the primary ridges where they are often predominantly in two rows leaving the trace of a secondary ridge between them.

The two basal internodes are only 0.6 mm and 0.9 mm long. Above this they are longer 2.3–2.9 mm. In other major branch fragments they are 1.9–3.3 mm in length. The internodes in the pinnae are mostly 1.8–2.4 mm long, with some up to 2.9 mm. The basal nodes are about 1.5 mm long, becoming shorter, 0.48–0.60 mm, in the upper regions of the stem and main branches. In other major branch fragments they are 0.24–0.48 mm long, and in the pinnae 0.12–0.18 mm in length.

### Axis Branching

If a branch bears pinnae then the first few



Figure 39 Paracanthoisis simplex (Tixier-Durivault, 1970), lectotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

internodes are generally unbranched and the remainder all carry 1–2 twigs (rarely, 3). In some cases there is a short branch stub (0.12–0.30 mm) as in Figure 251 example 6. In most cases there is a short node at the joint as in examples 1 and 29.

#### Axis colour

The internodes are greyish white and translucent in all branches and twigs. The nodes of the thicker branches are mostly deep orange (≈4A3) and transparent with thin white satin-like borders. The nodes of the pinnae are cream coloured (≈4A3) and mostly satin-like.

### Polyp sclerites (Figures 38A-E; 39)

The anthopoma is symmetrical and weakly continuous with the polyp body scales. Each octant generally contains a triangular sclerite which is preceded by a single rectangular, crescentic, or semicircular scale (Figure 38A-C,E); the shape of the latter (Figure 39Aj-l) mostly depends on the size of the triangular sclerite (Figure 39Aa-d). In some instances the triangular sclerite is very large and seems to occupy the whole octant, in which case the preceding scale is large enough to extend below the neighbouring octants and may occur folded down to various degrees. In other octants, extra, smaller sclerites may occur (Figure 39Ae-i). The triangular scales are mostly about 0.077-0.122 mm long. They are ornamented with globose tubercles, sometimes finely granular, and their underside is relatively smooth (Figure 39Ah). The larger triangular sclerites and their large proximal scales often have horn-like lateral basal extensions (Figure 39Aj,k).

There is a single basal tentacular scale (Figure 39Be,f) that precedes a single row of curved tentacular scales in the tentacle rachis (Figure 39Ba–d). The basal tentacular sclerites are often as long as 0.081 mm. The tentacular scales can be as long as 0.057 mm but most are <0.049 mm, and many are irregularly shaped.

The sclerites of the polyp base and head are often very similar, being predominantly large, curved, crescentic scales. Those of the head (Figure 39Ca-i) are generally thinner than those of the base (Figure 39Cj-s). The latter often more like flattened spindles, especially from the lateral regions where the base merges with the branch coenenchyme (Figure 39Cj,k). The number of series of scales on the polyp head depends upon the shape of the scales involved. When they are crescentic and mostly quite narrow there can be about 3 series abaxially. The scales of one series more or less alternating with the scales of the next. However, very broad scales of irregular shape occur in this abaxial region in many polyps allowing only 2 series to be accommodated. Similar scales (Figure 39Cn-s) also occur in some of the polyp bases (Figure 38D). There are only 2 series of lateral head scales and 1-2 series adaxially. The neck region below these adaxial scales, contracted near to the point of invisibility in most polyps, is naked. Polyp body scales are mostly 0.13-0.29 mm long. They are ornamented with rounded tubercles, sometimes finely granular, and they are relatively smooth underneath (Figure 39Cn).

## Coenenchymal sclerites (Figures 38F; 40)

The surface of the principal branches and the



Figure 40 Paracanthoisis simplex (Tixier-Durivault, 1970), lectotype, sclerites: Branch coenenchyme.

pinnae contains predominantly ovals and spindles; the latter sometimes branched or curved. The tubercles on the outer face are rounded and often finely granular, while those underneath commonly have rougher sculpturing. Some of the sclerites have small root-like structures underneath. Most sclerites are 0.07–0.29 mm long, but spindles up to 0.39 mm can occur.

# Remarks

This material demonstrates the difficulties of observing in dried material the major feature distinguishing this genus from *Acanthoisis*, i.e. the sclerite-free neck zone. The observations above were facilitated by rehydrating a specimen fragment. Such a practice may be advisable when dealing with dried colonies having characteristics of *Acanthoisis* but with obliquely angled polyps.

### Distribution

See Figure 259.

## Acanthoisis Studer [and Wright], 1887 Figure 310

- Acanthoisis Studer [and Wright], 1887: 46 (without included species); Wright and Studer, 1889: xlv, 34, 44–45; Nutting, 1910: 5 (in key); Gravier, 1913c: 456–457; Gravier, 1914: 24–25; (part) Bayer and Stefani, 1987a: 49–51, 52 (in keys), 66; (part) Bayer and Stefani, 1987b: 940–942 (in key).
- Mopsea; (part) Kükenthal, 1915:117–118, 123–124 (in key); (part) Kükenthal, 1919: 617–618; Kükenthal, 1924:437; (part) Grant, 1976:33; (part) Bayer, 1981: 942 (in key).

## **Type Species**

- Acanthoisis flabellum Wright and Studer, 1889, by subsequent monotypy, *ibidem*: 45.
- Mopsea flabellum (new combination) Kükenthal, 1915.

## Diagnosis

Colonies planar, irregularly pinnate, more flabellate than plumose, and sometimes with numerous anastomoses. Specimens up to 120 mm tall and nearly as broad.

The colour of preserved colonies is usually a shade of brown, and most species have whitish polyp summits. Sclerites are generally pale yellow in transmitted light, except those of the polyp heads which are usually colourless.

The axial internodes can be opaque to translucent, and are mostly pale grey to various shades of brown. Nodes are commonly brown and darker than the internodes.

Polyps can be distributed all around, or biserially and mostly towards one face of the colony. When not tightly contracted they are short and cylindrical and up to 0.60 mm tall. In most species they are capable of contracting until the polyp is nearly flush with the surface of the coenenchyme, and up to about 0.77 mm wide, by telescoping the body scales. In stages of intermediate contraction the polyp is seen to be divided into a head and a broader, tyre-like base. There is sometimes a slight invagination of the head into the base, but there is no evidence of a sclerite-free neck zone.

The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant is occupied by a triangular to triradiate sclerite preceded by 1–4 scales which are more or less crescentic. The triangular sclerites are mostly 0.11–0.15 mm long within the range of 0.09–0.17 mm. There is a single basal tentacular sclerite preceding a single row of curved scales in the tentacle rachis. The tentacular scales are mostly 0.07–0.09 mm long.

The polyp body is protected by large crescentic to irregularly shaped scales that often have long root-like structures. If the state of contraction permits the observation, there are usually 2–4 series of scales arranged in 8 rows on the polyp head. Body scales can be up to 0.35 mm long.

The coenenchyme contains predominantly ovals and spindles. Some of the spindles may be branched, many have small root-like structures on their underside, and they can be up to about 0.41 mm long.

The majority of the sclerites from both the polyp and the coenenchyme are ornamented on their outer face with stout, rounded tubercles that have a granular surface.

The axial internodes have multiple primary ridges, each of which is essentially a single row of large spines. The internodes are generally <4 mm long, and they may initiate up to 5 side branches.

## Distribution

See Figure 310.

## Acanthoisis flabellum Wright and Studer, 1889 Figures 41–48; 260

- Acanthoisis flabellum Wright and Studer, 1889: 45–46, Plate VIII, Figures 1, 1a. lb; platelX, Figure 12; Whitelegge, 1889: 27 (listed); Thomson and Mackinnon, 1911: 679–680; Bayer and Stefani, 1987a: 67–69, Plate XXII; Plate XXIII; Figure 4,a.
- Mopsea flabellum; (new combination) Kükenthal, 1915: 123; Kükenthal, 1919: 623; Kükenthal, 1924: 439.
- not Mopsea flabellum Thomson and Mackinnon, 1911: 676-677, Plate 1xiii, Figures 1-3; Plate

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1xvii, Figure 6; Plate 1xxi [≡ Mopsea squamosa; (nom. nov.) Kükenthal, 1915: 123–124, ≡ Sphaerokodisis flabellum (new combination)]

## Material examined

### Types

HOLOTYPE: BM 1889.5.27.103, Port Jackson, NSW, 30–35 fm, HMS Challenger.

#### Other material

AM G12154, G15595, HMCS *Thetis*, station 22, 5–6 miles offshore in Newcastle Bight, NSW, 23–63 fm, grey sand to mud and shell, 2 March 1898; AM G11747–G11749, HMCS *Thetis*, station 47, 6–8 miles off Bulgo, NSW, 57–63 fm, mud and abattoir refuse 16 March 1898.

## **Differential characteristics**

Distinctive sclerite form; polyp body scales up to 0.28 mm, outer face densely covered in low rounded projections, free margin not elaborate, root structures broad and tongue-like; sclerites of the branch coenenchyme up to 0.35 mm long and densely tuberculate.

## Description

#### Colony form (Fig 41)

The holotype was briefly redescribed for the first

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time by Bayer and Stefani (1987a: 67-69). Supplementary information on colony form and skeletal characters is given here. The holotype is 105 mm tall and 98 mm broad, planar, and pinnately branched in an irregular manner. Wright's and Studer's plate VIII, Figure 1, shows a somewhat simplified representation of the colony which is more profusely branched. The main stem is about 12 mm long, from which most of the coenenchyme has been lost, and it is 1.3-1.6 mm thick. The main branches are about 1.1 mm thick basally (1.4 mm with polyps) and their course can be followed through to the peripheries of the fan. These branches ramify pinnately producing mostly short pinnae that are sometimes opposite, sometimes alternate, and sometimes unopposed. The pinnae are 0.6-0.7 mm thick (1.1-1.3 mm with polyps). Distance between branching points is very irregular. One branch 70 mm long has 54 pinnae. Pinnae length is very variable, some as short as 1.7-1.9 mm have only 4-5 polyps. Others are up to 14 mm long, although most over 7 mm pinnately rebranch. Branching angle approaches 90° in most cases, with many pinnae curving upward near their origin making the angle appear more acute. Pinnae tips are blunt and rounded and commonly extend for only 0.18-0.30 mm beyond two more or less opposite terminal polyps as shown in Wright's and Studer's Plate VIII, Figure 1a. Anastomoses are not uncommon.



Figure 41 Acanthoisis flabellum Wright and Studer, 1889, holotype, natural size.

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## Polyps (Fig 42A-E,I)

Polyps are distributed all around except on many of the terminal twigs in the peripheries of the colony where they are generally biserial, in single rows, and arranged both opposite and alternate. The biserial nature is often disturbed by the occurrence of juvenile polyps developing on the other faces of the twigs.

Most polyps are more or less vertical to the branch or twig surface, however, many can be found slightly angled distad. Polyps are present in various stages of contraction. The tallest are about 0.30 mm high and 0.36–43 mm in diameter across the summit, slightly wider at the base. Many polyps are considerably shorter. The anthopomal sclerites and at least one row of the upper body sclerites are white, in contrast to the rest of the polyp which is brownish orange. This colour differential makes it easier to assess the state of contraction of the polyp. In the tallest polyps the anthopomal region is slightly domed and appears like a white cap at the summit. No suture is visible between the two colour zones. A smaller white zone is visible in shorter polyps. In markedly contracted polyps only the upper portion of the white anthopomal region is visible, flush with, or slightly below, the rim of the lower, coloured, portion of the polyp. Much of the outer face of the curved scale-like sclerites of the polyp body is visible in the most extended polyps. There are at least 4-5 rows of these imbricated scales, which apparently telescope as the polyp shortens or lengthens. In shorter polyps only the upper marginal areas of the scales are visible appearing like incomplete concentric rings when viewed from above. On the lower parts of the thicker branches, smaller polyps, apparently juveniles, appear as white spots where the anthopoma is flush with the surface.

## Colony colour

Light brown (≈6D8) with white polyp summits. The axial nodes can be seen through the coenenchyme in only a few places, and even here they are only faintly visible. All but the summital polyp sclerites are pale yellow in transmitted light.



Figure 42 Acanthoisis flabellum Wright and Studer, 1889, holotype: A-E. Polyps; F. Coenenchyme; G-H. Axial internodes; I. Twig fragment.

### Axis form (Figure 42G,H)

The internodes have pronounced primary ridges, each bearing a single row of large spines. The desmocyte cavities are distinct, often deep and scattered in the valleys between the ridges.

There are very few areas where the axis is visible and measurements have been estimated by silhouetting. The internodes of the lower portions of the main branches are 1.5–2.1 mm long, and those of the rest of the colony are mostly 2.7–3.3 mm in length. Nodes are mostly about 0.3 mm.

## Axis branching

Internodes usually carry more than one branch, three is not uncommon and four is seen occasionally. Branches may arise from a short stub or articulate with a node, similar to Figure 251 example 2.

### Axis colour

The internodes are pale grey and opaque. The

nodes are caramel coloured ( $\approx$  6C6) with yellowish satin-like borders.

## Polyp sclerites (Figures 42A-E; 43)

The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant is dominated by a large triangular sclerite (Figure 42C–E) which is commonly preceded by a single crescentic scale, and sometimes two. The triangular sclerites, which are ornamented with densely arranged, globose, or finger-like, granular tubercles, are mostly 0.11–0.14 mm long (Figure 43Aa–f). The smaller ones are sometimes accompanied by an additional, apically situated, triradiate scale (Figure 43Ag–i). The proximal crescentic scales also have granular tubercles, and granular, tongue-like, lateral extensions (Figure 43Aj–k). The anthopomal scales have granules on their underside (Figure 43Ad).

There is a single basal tentacular scale that precedes a single row of curved scales in the



Figure 43 Acanthoisis flabellum Wright and Studer, 1889, holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 44 Acanthoisis flabellum Wright and Studer, 1889, holotype, sclerites: A. Branch coenenchyme; B. Stem coenenchyme.

tentacle rachis. They are somewhat fish-shaped, and can be up to about 0.11 mm in length (Figure 43Bc,d). The tentacular scales have irregularly scalloped margins and can be as long as 0.09 mm (Figure 43Ba,b).

Most of the body scales are densely covered with granular, sometimes rough, tubercles (Figure 43C). A number of them have tongue-like lateral processes and root structures. The scales are mostly up to about 0.28 mm long.

## Coenenchymal sclerites (Figures 42F; 44)

The surface of the branches contains predominantly spindles, mostly 0.08–0.35 mm long. They are densely covered with rough tubercles on their outer face, and have warts and root-like structures underneath (Figure 44Ad-h,j). Around the base of the polyps the sclerites are often large and scale-like (Figure 44i,k-p), and intermediate in form to the polyp body scales.

The surface of the stem contains small spindles, arched sclerites, and oval to spheroidal forms (Figure 44B). They have tooth-like projections on their upper face and warts underneath. Most stem sclerites are <0.15 mm in length.

## Variability

It is with a small amount of hesitation that five specimens from the Australian Museum, collected by the HMCS *Thetis* Expedition and identified by Thomson and Mackinnon (1911: 679–680), are included in this taxon. The incomplete specimens

are all possibly from colonies larger than the holotype. The polyps are more densely arranged, and are contracted to a greater extent. They are broader (possibly due to the greater contraction), and there is no sign of biserial distribution on the pinnae. Upon first examination of the polyp sclerites, these specimens were thought to represent a different and undescribed species. The sclerites were found to be decidedly bigger and to have large and often branched root-like processes. However, general similarities between the electron micrographs of these sclerites and those of the A. flabellum holotype prompted a re-examination, and it was found that the variability between the sclerites of individual polyps from the same colony was occasionally great enough to believe the polyps could have been from different specimens. Colonies can have polyps with very few to very large numbers of scales with long root-like processes. The number of big sclerites in any polyp varies similarly. The percentage of polyps that have large sclerites and/or sclerites with root-like processes seems to vary between specimens. A reexamination of the holotype of A. flabellum revealed that some polyps have scales with similar root-like processes and, although never as common as those in Thomson's and Mackinnon's specimens, the number varies between polyps.

# Description of AM G12154

#### Colony form (Figure 45)

The specimen is fragmented and consists of a portion of the original fan 112 mm high and 45 mm across, a couple of pieces of the thick main branches with a few twigs attached, and numerous small fragments. The branching pattern is planar and irregularly pinnate, with the pinnae occurring both alternate, opposite, and for short sections unopposed. Anastomoses are very common. The detached main branch fragments are 1.9-2.8 mm thick. In the section of fan, the major branches which are pinnately divided are 0.9-1.1 mm thick. The pinnae are 0.6-0.9 mm thick (including polyps), they do not taper and have bluntly rounded tips. Most are 2-8 mm long but they can be up to 19 mm in length. The interval between consecutive branchings is 0.9-4.7 mm with a 70 mm branch having 41 pinnae. Most pinnae arise more or less perpendicular to the branch and then curve upwards, but the angle of branching can be as small as 50°.

### Polyps (Figure 46A-F,I)

Distributed all around and relatively crowded with polyp centres about 0.9 mm apart. On the thickest of the detached main branch portions there



Figure 45 Acanthoisis flabellum Wright and Studer, 1889, AM G12154, natural size.



Figure 46 Acanthoisis flabellum Wright and Studer, 1889, AM G12154: A-F. Polyps; G-H. Axial internodes; I. Twig fragment.

are no polyps, whilst on a small, thinner fragment, about 1.4 mm thick, a few scattered polyps can be found that are more or less flush with the coenenchyme.

The polyps in the rest of the colony are contracted to form low, flattened, discoid structures. Their brown base is inflated tyre-like and the white anthopoma sits in the centre, either flush with the rim, slightly below, or conical and slightly protruding. These polyps are mostly 0.07–0.12 mm high. Their diameter is 0.61–0.77 mm and that of the white anthopoma is 0.26–0.36 mm. Polyps that are obviously juveniles are rare.

### Colony colour

Brownish orange ( $\approx$ 5C5). The axial nodes are easily visible through the coenenchyme of the thick

main branch fragments, but can only be seen very faintly on the minor branches and twigs. Sclerites are yellowish in transmitted light.

#### Axis form (Figure 46G,H)

The internodes have pronounced primary ridges, each bearing a single row of large spines. The desmocyte cavities are distinct and confined to the valleys between the ridges.

Most internodes are 1.6–2.4 mm long, those in the pinnae being more towards the lower end of the range and those in the branches towards the upper end. A branch internode 1.3 mm thick has three primary ridges. In the main branch fragments the nodes are 0.3–0.8 mm long, in the branches of the fan they are 0.3 mm long and in the pinnae 0.18 mm.







Figure 48 Acanthoisis flabellum Wright and Studer, 1889, AM G12154, sclerites: A. Branch coenenchyme; B. Lower main branch coenenchyme.

#### Axis branching

On the pinnately ramified principal branches, most internodes initiate 2 branches, 3 occasionally. The branching style is the same as for the holotype.

#### Axis colour

The internodes are greyish white and very translucent to transparent when thin. The nodes of the thick main branch fragments are dark brown ( $\approx$ 6F8), nearly opaque, with very thin light yellow satin-like borders. The nodes of the major branches in the fan are a darker brown ( $\approx$ 7F8), very translucent with wider brownish yellow satin-like borders. In the pinnae the nodes are mostly light yellow and satin-like with a very short brown central portion.

## Polyp sclerites (Figures 46A-F; 47)

The anthopoma is constructed similar to that of the polyps of the holotype, although there are often 2 scales proximal to the apical triangular sclerite in each octant. The triangular sclerites are mostly 0.11–0.15 mm and they have smaller tubercles than are seen in the holotype (Figure 47Aa–e). Some of the proximal anthopomal scales are more rectangular than in the holotype and the tubercles are long and spine-like (Figure 47Af–i). There is a single basal tentacular scale of the same style and size as seen in the holotype (Figure 47Bc,d), and the tentacle scales are up to 0.09 mm long and relatively broad (Figure 47Ba,b).

The polyp body scales are very large, mostly up to 0.35 mm but occasionally as long as 0.40 mm, and many have stout root-like structures (Figure 47C). The tubercles on their outer face are generally smaller than those in the holotype.

## Coenenchymal sclerites (Figures 46E,I; 48)

The surface of the branches contains spindles and scale-like forms similar to those in the holotype and of the same length, up to 0.35 mm (Figure 48A).

The surface of the lower regions of the thickest main branches contains oval and spheroidal sclerites together with numerous arched forms (Figure 48B). They are up to about 0.15 mm in length but most are <0.10 mm.

## Remarks

Three of the other comparative specimens are distinctly more orange ( $\approx$ 5B5) than AM G12154, and the axial internodes are very pale orange in the thicker branches and approaching melon yellow ( $\approx$ 5A6) in the pinnae. A larger range of specimens may help to determine if more than species is involved in this material.

#### Distribution

See Figure 260. Depth range 42–115 m.

## Acanthoisis dhondtae Bayer and Stefani, 1987 Figures 49–52; 261

Acanthoisis dhondtae Bayer and Stefani, 1987a: 70– 71, plate XXV, 2; Plates XXVII–XXVIII; Figure 4,c.

## Material examined

#### Types

HOLOTYPE: MNHN, Observatory Cay, Chesterfield Islands, 150°51.2'E, 21°24.8'S, 50 m, G. Bargibant, 27 July 1984.

## **Differential characteristics**

Distinctive sclerite form; polyp body scales mostly to 0.18 mm long, narrow, and covered in stout, rounded or pointed projections; sclerites of the branch coenenchyme up to 0.2 mm long, mostly ovals and spindles with bulbous tubercles; polyp summits not white.

## Description

#### Colony form (Figure 49)

Some of Bayer's and Stefani's descriptive detail is unavoidably duplicated here, but most of the following information is supplementary to their work.

Depending along which lines the measurements are taken, the holotype is a little over 90 mm tall and 80 mm across, as stated by Bayer and Stefani in their Plate XXVII; the 15cm mentioned in their text is obviously just an oversight. The colony branches more or less in one plane (some branches overlay others), in an irregularly pinnate manner. The holdfast is missing. The broken base of the stem is about 2.4 mm thick and mostly devoid of coenenchyme. The stem divides into two main branches about 1.8 mm and 2.1 mm thick, which irregularly give off branches 0.72–0.90 mm thick (polyps not included) that ramify in a predominantly pinnate manner. The pinnae are mostly 0.36–0.48 mm in diameter (0.78–0.90 mm with polyps), and terminate in a short blunt tip 0.12–0.18 mm beyond the last polyp. Unbranched twigs are mostly 6–8 mm long, but the length varies from just over 1 mm to about 29 mm.

#### Polyps (Figure 50A-F,I)

The polyps are arranged all around on the branches, being most densely distributed on the pinnae where they are regularly spaced. They are contracted and somewhat cylindrical with a slightly convex anthopomal region. A few stand more or less perpendicular but most are angled distad. The majority of polyps have slight constriction between the basal portion and the polyp head. The distal or abaxial wall of the base does not usually extend much above the surface of the branch. The head region is quite distinct because the sclerites are arranged in rows. It is partially retracted in many instances through the slight invagination of the rim of the basal portion, which is often inflated type-like supporting the narrower head. The sclerites of the base are apparently small enough to allow the rim to roll over slightly in contraction.

Polyp bases are about 0.36–0.56 mm in diameter, the heads are narrower. Polyps extend up to about 0.36 mm above the branch surface. Most juvenile polyps occur on the terminal 5 mm of the pinnae (Figure 50F).

### Colony colour

Brown (≈7E8). Sclerites are pale yellow in transmitted light.



Figure 49 Acanthoisis dhondtae Bayer and Stefani, 1987, holotype, natural size.



Figure 50 Acanthoisis dhondtae Bayer and Stefani, 1987, holotype: A-E. Polyps; F. Coenenchyme and juvenile polyp; G-H. Axial internodes; I. Twig fragment.

## Axis form (Figure 50G,H)

Internodes with primary ridges of large spines which in the stem and basal branch areas are reduced. Basal internodes 1.7–2.2 mm thick have about 40–50 ridges, a branch internode 0.48 mm thick has nine ridges, and internodes near the pinnae tips have about 6. Desmocyte cavities are small and distinct.

Few axial portions are visible. Most internodes of the stem and main branches are 0.4–1.6 mm long, those of the thinner branches 0.9–2.8 mm long, and those of the pinnae 0.8–1.7 mm in length. Basal nodes are 0.9–1.8 mm long, branch nodes are 0.2– 0.4 mm long, and those of the pinnae are about 0.13 mm in length.

## Axis branching

In general, if a branch rebranches then its few proximal and distal internodes remain undivided and the remainder between bear 1–2 twigs each. Divisions that articulate with a node, similar to Figure 251 examples 9, 12, and 28, or those with short to medium stubs (0.19–0.29 mm) similar to examples, 3, 5, 8, and 11, are both common.

## Axis colour

The translucent internodes, are violet brown ( $\approx$ 10E8). Nodes of the stem are brownish orange ( $\approx$ 5C5) with paler satin-like borders. Those of the thinner branches and pinnae are cream coloured and satin-like with a short translucent greyish white central zone.

## Polyp sclerites (Figures 50A-E; 51)

The anthopoma is symmetrical and continuous with polyp sclerites. Each octant is occupied by 3–4 crescentic scales which precede an apical triangular to triandiate sclerite (Figure 50B–E). The triangular forms are ornamented with closely set, stout, pointed tubercles with a granular surface (Figure 51Aa–d,g). In some octants this sclerite may be replaced by 2 narrower sclerites (Figure 51Ae,f)

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Figure 51 Acanthoisis dhondtae Bayer and Stefani, 1987, holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

that sit side by side. This is quite common and can be seen at the apex of an octant on the left in Figure 50C. The apical triangular forms are mostly 0.09– 0.11 mm long. The proximal anthopomal scales are ornamented with stout, pointed, tooth-like projections that have a granular surface (Figure 51Ah–j). The lateral extensions of these scales are usually horn-like.

The basal tentacular position may be occupied by a single tuberculate sclerite (Figure 51Bb), however, it is often replaced by a couple of irregular shaped sclerites that fit together. There is a single row of curved scales in each tentacle rachis. These have rounded marginal projections that give them an irregularly scalloped appearance (Figure 51Ba), and they are up to about 0.077 mm long.

On the polyp head, below the anthopomal octants, there are about 3–4 series of scales that are mostly in rows as a continuation of the octal arrangement. The upper ones resemble the proximal anthopomal scales, while the lower ones may be slightly different with often just a single lateral extension (Figure 51Cb,d–f). Many of the

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Figure 52 Acanthoisis dhondtae Bayer and Stefani, 1987, holotype, sclerites: A. Principal branch and pinna coenenchyme; B. Stem coenenchyme.

sclerites of the polyp base (Figure 51Ch–u) resemble those of the coenenchyme, but they are generally flatter. There are also a number of small flat spindle-shaped forms that are often nearly smooth (Figure 51Ce,f). Most of the larger polyp body scales are about 0.18 mm long, but some are over 0.20 mm in length.

#### Coenenchymal sclerites (Figures 50F; 52)

The surface of the principal branches and the pinnae contains ovals, spindles, and a few plates, up to about 0.20 mm long (Figure 52A). Most of the sclerites are ornamented with stout, bulbous, granular tubercles. The tubercles on the underside are shorter and may be branched.

Similar sclerites occur in the stem coenenchyme but they have a coarser sculptured surface (Figure 52B).

## Distribution

See Figure 261. Depth 50 m.

Acanthoisis wrastica sp. nov. Figures 53–56; 262

## Material examined

#### Types

HOLOTYPE: QM GL10376, off the Gold Coast, Qld, 28°05'S, 153°54'E, 270 m, FV *Iron Summer*, Queensland Dept. of Fisheries, P. Dutton, 27 July 1982.

# Differential characteristics

Distinctive sclerite form; polyp body scales up to 0.35 mm long, free margin ctenate in one section,

outer face partly smooth, root structures somewhat elaborate; sclerites of the branch coenenchyme up to 0.41 mm long and densely tuberculate.

## Description

## Colony form (Figure 53)

The holotype is fragmented but two relatively large sections of the colony are intact, the biggest of which is 120 mm tall and 82 mm across. The fragments are more or less planar but the main stem branches out of plane indicating that the complete colony may have consisted of two or more closely oppressed fans. Branching is lateral and irregularly pinnate, pinnae occurring opposite, alternate, or for sections unopposed. Many of the pinnae are very thick and rebranch giving off both thin pinnae and thicker pinnately divided branches. Branching occurs to at least the sixth order. In a few places pinnae have laid against each other and the soft tissue has fused, but proper anastomoses, that is those involving axial material, are very rare.

The stem is somewhat oval in section, 4.6 mm at its thickest point, and 29 mm long before main branches occur, (the stubs of numerous broken branches remain below this indicating that this may not actually be part of the main stem but a major branch from a much larger colony). The stem and the lower regions of the main branches, which are about 2.4 mm thick, are denuded. Branches of the fourth order, which may be terminal, are about 0.6–0.8 mm in diameter (polyps not included). Finer terminal twigs are about 0.5 mm thick ending in bluntly rounded tips which are often occupied by one or two polyps. Consecutive subdivisions may occur within 0.8 mm or not for 17.5 mm but

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Figure 53 Acanthoisis wrastica sp. nov., holotype, natural size.

the separation is more commonly 2.4–4.7 mm. Unbranched twigs are 2.4–23.7 mm in length, and branching angles are usually 35–50° but can be up to 90°.

### Polyps (Figure 54A-F,J)

Distributed all around, sparser on the thicker branches and more densely arranged on the pinnae where they are relatively evenly spaced with about 0.9–1.23 mm between centres. Many are damaged.

The polyps are present in various stages of contraction. The tallest are about 0.39 mm high and 0.42–0.48 mm wide, with a flat, or low, conical, anthopoma. In many of these it is possible to distinguish an upper and lower region. The lower region is a short truncated cone of brown sclerites, which are often very large and thick, and the upper is a pale yellowish white cylinder of about 5–7 series of large scales. In some polyps the base is very pronounced and in others it is very reduced (Figure 54F), and as the sclerites are similar to those of the coenenchyme it can appear as part of the branch surface.

At the other extreme the polyps appear as low

domes, about 0.12 mm high and 0.66–0.72 mm diameter (Figure 54B–D), and sometimes they are almost flush with the surface (Figure 54 A,E). In these more contracted states the basal area is deflated, and the scales of the head region have slid over one another, telescoping downwards, so they appear as broken concentric circles. This occurs more commonly on the thicker branches where it may be facilitated by thicker coenenchyme. Juvenile polyps are found scattered throughout the colony.

#### Colony colour

Brown, burnt sienna ( $\approx$ 7D8), with pale yellowish white polyps. The pale nodes can be seen through the coenenchyme. In transmitted light the coenenchymal sclerites are yellowish.

#### Axis form (Figure 54G–I)

The internodes have pronounced primary ridges which each bear a single row of large spines. The desmocyte cavities are distinct and scattered in the valleys between the ridges.

Internodes of the stem are slightly oval in section,



Figure 54 Acanthoisis wrastica sp. nov., holotype: A-F. Polyps; G-I. Axial internodes; J. Twig fragment.







Figure 56 Acanthoisis wrastica sp. nov., holotype, sclerites: Branch coenenchyme.

4.6 x 4.1 mm at the base and 4.0 x 3.2 mm where the main branches diverge, and their length is 1.9-4.0 mm. Most of the internodes in the rest of the colony are 3.2-4.7 mm long, 4.0 mm being common. Basal internodes have about 74 primary ridges, a branch internode 4.1 mm thick has about 34 ridges.

Nodes of the stem are 0.8–1.1 mm long, those of the main branches about 0.60 mm, and those of the pinnae 0.24–0.32 mm in length.

#### Axis branching

Internodes may initiate 1–3 branches. With multiple branching, the products may arise all on one side of the internode. Branches may originate with a short or long calcareous stub or begin with a node as in Fig 251 example 2. Major branches virtually always begin with a node as in example 62. On the proximal part of the main branch a couple of thin, broken, lateral branches arise from the nodes as in example 58, and some of the internodes carry very long calcareous branch stubs, up to almost 5 mm in length.

### Axis colour

The internodes of the basal part of the main stem are grey white and have a frosted appearance. In the upper stem and the lower regions of the main branches they are reddish brown ( $\approx$ 8D5–8D7). In

thinner branches and in the pinnae the internodes are paler, brownish orange (≈6C8). The basal internodes are virtually opaque. The opacity decreases distad and in the finer pinnae the internodes are quite translucent. The basal nodes are opaque and dark brown (≈7F7), those of the thicker branches light brown (≈6D5), the thinner branches brownish orange (≈5C5) and the pinnae greyish yellow (≈4C4). In the branches where the nodes are brownish orange, or paler, the colour is notably not homogeneous. The central zone tends to be densely coloured and nearly opaque and is bordered either side by virtually transparent material. The very centre of the central opaque zone is mottled with a ring of dots of darker, clearer material. In some instances these dots join to a form a central disc of darker translucent material. All nodes have bright yellowish satin-like borders.

### Polyp sclerites (Figures 54A-F; 55)

The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant is dominated by a large triangular scale which is generally preceded by a single somewhat semicircular or rectangular scale (Fig 54C), though sometimes there are two. The triangular sclerites are of various sizes and both broad and narrow (Figure 55Aa–e). Most are 0.13–0.17 mm long and 92

have a rather untidy appearance. The margins are irregularly warted and the exposed face is ornamented with tubercles of various sizes that may be smooth or rough. The underside is relatively smooth (Figure 55Ab). The proximal anthopomal scales (Figure 55Af–i) are ornamented with granular tubercles. They are relatively smooth underneath and the lateral extensions may be quite pronounced.

There is a single basal tentacular sclerite preceding a single row of curved crescentic scales in the tentacle rachis. The basal tentacular sclerites (Figure 55Bd-e) are often very long, up to about 0.13 mm, and somewhat fish-shaped. The tentacular scales have pronounced granular projections along their margins and can be up to 0.09 mm long (Figure 55Ba-c).

Most of the telescoping scales of the polyp body have conspicuous, long, elaborate, root-like structures (Figure 55C). The scales are ornamented with granular tubercles that generally only occupy part of the outer face; large areas often left smooth. The granular projections on the distal margin are usually restricted to a more or less medial section. The scales are mostly 0.21–0.35 mm long and their underside is relatively smooth (Figure 55Ca,b).

### Coenenchymal sclerites (Figures 54F; 56)

The surface of the branches contains predominantly spindles, sometimes branched, and the occasional plate-like form (Figure 56a–m). Their upper face is densely covered in rough tubercles. Their underside may be relatively smooth (Figure 56a,b), but more commonly there are small warts (Figure 56f,j) and root-like projections (Figure 56h). Around the base of the polyps the sclerites are scale-like (Figure 56n–r). Although they are mostly pale yellow under the microscope, some are colourless and others are partly coloured. Coenenchymal sclerites are up to about 0.41 mm in length.

There is no stem coenenchyme preserved. The most basal coenenchyme of the thickest branch contains spindles like those on the thinner branches. Plate-like forms, though still uncommon, occur more often in this region.

#### Distribution

See Figure 262. Depth 270 m.

#### Etymology

A latinised acronym of some letters of Wright and Studer, who established the genus Acanthoisis.

> Acanthoisis myzourida sp. nov. Figures 57–60; 263

### Material examined

## Types

HOLOTYPE: AM G15597, off Moreton Bay, Qld, 27°31.5'S, 153°40'E, 76–80 m, RANS Kimbla, station



Figure 57 Acanthoisis myzourida sp. nov.: A. Holotype; B. Paratype, AM G15598. Both natural size.

1, W. Ponder, 29 March 1969. PARATYPE: AM G15598, same data as holotype.

#### Differential characteristics

Polyps biserially arranged like rows of suckers; polyp body scales up to 0.26 mm long, often platelike, a few completely smooth but most with bulbous tubercles clustered in one area; sclerites of the branch coenenchyme mostly plates and flattened spindles up to 0.18 mm long.

#### Description

#### Colony form (Figure 57A)

The small planar holotype, 75 mm tall and 88 mm across, is broken into two large pieces and some fragments. The colony is profusely branched in a lateral and irregularly pinnate manner producing a neat, close pattern of ramification. The stem, which has the top of the calcareous holdfast attached, is about 13 mm long and 1.9 mm in diameter. It gives off several main branches, about 1.3 mm thick, that rebranch irregularly. Most of the minor branches tend to branch pinnately, but this is very irregular. Some of the pinnae rebranch again, pinnately. Branches and pinnae tend to grow parallel and very close to their neighbours neatly and efficiently filling up much of the available space in the branching plane, and although numerous pinnae touch there are only about two anastomoses in the whole colony. A few minor branches protrude out of the growing plane on one side of the fan.

About half way up the colony most branches and pinnae are 1.2–1.3 mm thick (polyps included). In the upper region the pinnae are 0.8–1.1 mm thick (polyps included). Unbranched pinnae do not taper appreciably and are 1.0–16.5 mm long; most about 3–6 mm. They terminate in blunt tips with one polyp or two opposing polyps. Distances between consecutive subdivisions are commonly 1.6–4.7 mm, but can vary from 0.8–12.6 mm. Branching angles vary from 35° to more or less perpendicular.

### Polyps (Figure 58A-C,J)

The stem is free of polyps. Throughout most of the rest of the colony the polyps are arranged biserially and oriented more or less totally to one side of the fan. The 2 opposing rows of polyps are arranged in an orderly manner like the sucker discs on cephalopod arms. In a single row they are 0.48– 0.90 mm apart, measured centre to centre, with most averaging 0.60–0.65 mm separation.

The polyps are contracted to form low cylinders or truncated cones. The polyp body can be divided into a brown base and a white head. The polyps are tilted slightly distad, the adaxial or distal side of the base being the shortest and sometimes hardly projecting at all above the branch surface. The adaxial side of the head is also usually shorter, and the sclerites, which are generally shorter than those of the base and in rows, often appear to be part of the anthopoma. In other cases the base has remained more inflated on this side and the rim is slightly invaginated. Such invagination together with the marked concavity of the anthopoma is indicative of considerable development of mesenterial musculature, although how much of the appearance is artifactual may only be resolved by studying live material. A few of the polyps are so contracted that little of the white wall of the head appears above the base. Usually in these cases the diameter of the base is wider than that of the head and the rim of the base appears quite thick because it seems to have rolled over and slightly invaginated. The large sclerites would presumably prevent any extensive introversion.

It should be stated that it is possible that a study of live material or perhaps a more relaxed preserved specimen may also show that the whole of the white area of the polyp constitutes the anthopoma. Though, from the appearance of some polyps, especially those of the paratype (Figure 58D,E) where the white wall of the head may extend for 0.3 mm, this would seem unlikely.

The brown bases are mostly 0.18–0.30 mm high and 0.66–0.72 mm diameter proximally. The white summit is usually 0.43–0.48 mm in diameter. A few juvenile polyps can be found scattered throughout the colony.

#### Colony colour

Brown ( $\approx$ 7D7). In transmitted light the sclerites are yellowish, except those of the polyp heads which are colourless. The axial nodes can be clearly seen through the coenenchyme on the side of the colony without polyps.

### Axis form (Figure 58H–I)

Very little of the axial material is visible. The internodes have multiple primary ridges which each bear a single row of large spines. The thicker the axis the lower the ridges and the fewer the spines. The desmocyte cavities are distinct and scattered in the valleys between the ridges. The most basal internode of the stem has spines and ridges extremely reduced. The spines are only detectable on the side of the colony to which the polyps face. There are about 28–30 residual ridges on the internode.

Main stem internodes are 1.1–1.9 mm long. Throughout the rest of the colony they are mostly 2.4–2.7 mm in length. The most basal stem node is 3.5 mm long. The stem nodes above this are about 0.9 mm long. In most branches the nodes are also 0.36 mm long, and in the pinnae they are about 0.18 mm in length and noticeably thinner than the internodes.



Figure 58 Acanthoisis myzourida sp. nov.: A-C, F. Holotype: (A-C). Polyps; (F-G). Coenenchyme; (H-I). Axial internodes; (J). Twig fragment. D-E. Paratype: Polyps.



Figure 59 Acanthoisis myzourida sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp head; D. Polyp base.

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Figure 60 Acanthoisis myzourida sp. nov., holotype, sclerites: A. Branch coenenchyme; B. Stem coenenchyme.

### Axis branching

Internodes may initiate 1–3 branches. With multiple branching, the products may arise all on one side of the internode. The style of branching is like that illustrated in Figure 251 examples 6 and 7.

## Axis colour

The internodes of the stem are translucent and light brown ( $\approx$ 6D4). Distad they become more yellowish ( $\approx$ 5B7) and in the finer ramifications they are transparent. The stem nodes are densely coloured, slightly translucent, darker than internodes ( $\approx$ 6D6), and have pale yellow satin-like borders. The nodes of the branches are pale yellow at each end with a short, virtually transparent, strip between them. The borders are broad and satin-like. The nodes of the pinnae are mainly satin-like and pale yellow with a very fine transparent section across the middle.

## Polyp Sclerites (Figures 58A-C,J; 59)

The anthopoma is symmetrical and continuous with the polyp head sclerites (Figure 58C). Each octant contains a large triangular sclerite (Figure 59Aa-g) which is preceded by 1-3 scales that are rectangular to crescentic in shape (Figure 59Ai-k). The greater the number of crescentic scales the smaller the size of the distal triangular sclerite. There is usually a large arrow-head shaped basal tentacular sclerite (Figure 59Ah) at the apex of each octant which is oriented in a vertical position pointing down into the central aperture. If this sclerite is of a small size it is usually followed by a modified form (Figure 59Bd,e). There is a single row of curved crescentic scales in each tentacle rachis (Figure 59Ba-c). The anthopomal sclerites are ornamented on their exposed face with short, somewhat globose, finger-shaped tubercles that have a granular surface. The triangular forms are mostly 0.10–0.13 mm long. The tentacular scales have a granular surface, and the distal margin is produced into several granular, rounded processes. These scales are up to about 0.069 mm long.

The scales in the polyp head (Figure 59C) are arranged in 8 rows, with 2 and sometimes 3 scales in each row. The scales of the base generally reach a larger size (Figure 59D) and they are more irregularly arranged. Most body scales have granular, bulbous tubercles on their outer face. These are often clustered in one part of the scale leaving the remaining area covered in small granules; as is the surface of the underside (Figure 59Ca,b). On a number of the scales from the polyp base, large tubercles are very few or absent altogether (Figure 59Da-d). It is apparent that some of the body sclerites are better described as plates, their granular margins being overlapped by neighbouring scales leaving just the central cluster of tubercles exposed (Figure 59De-h). The white sclerites of the polyp head are mostly up to about 0.20 mm long, but can be larger. Those of the base are up to about 0.26 mm in length. Rarely, some of the larger scales have very long root-like processes.

## Coenenchymal sclerites (Figures 58F,G; 60)

The surface of the branches contains small plates, and flattened ovals and spindles. They have numerous bulbous, granular tubercles on their exposed face, and a few smaller tubercles on their underside (Figure 60A). Most are 0.04–0.18 mm long, with spindles to 0.27 mm occasionally found.

The surface of the stem contains small spindles and ovals with granular tubercles. Most are 0.05– 0.08 mm long (Figure 60B).

### Variability

The paratype, from the same location, is a damaged colony 115 mm tall and 80 mm across (Figure 57B). There is a light brown calcareous holdfast, and the stem together with several branches and twigs is devoid of coenenchyme. The branching is pinnate but not as profuse as in the holotype. The polyp distribution is biserial with the polyps tending to face one side of the colony and spaced, centre to centre, 0.90-1.02 mm apart; less dense than the holotype. Most of the polyps are far less contracted than those of the holotype (Figure 58D,E). Many are about 0.42 mm tall, but some are up 0.6 mm in height where the white polyp head, sometimes flared above a narrower neck, protrudes 0.18-0.30 mm beyond the base.

The colour of the colony is not homogeneous and varies from light brown ( $\approx$ 7D6) to reddish brown ( $\approx$ 8E6). Although the polyp head sclerites are colourless the polyp tissue is quite dark in some parts of the colony and so the polyp heads appear pale brown to pale yellow.

Axial internodes of the branches and pinnae are greyish orange ( $\approx$ 6B5) to melon yellow (5A6). The spines and ridges of the stem internodes are very reduced and hardly detectable on the more basal segments.

The sclerites are occasionally larger than those of the holotype with polyp scales up to 0.32 mm and anthopomal triangles up to 0.15 mm in length.

## Distribution

See Figure 263. Depth range 76-80 m.

### Etymology

The epithet indicates the species possesses suckers, a reference to the striking shape and biserial arrangement of the polyps, and is formed from the Greek *myzouridos*.

## Acanthoisis kimbla sp. nov. Figures 61–63; 264

## Material examined

### Types

HOLOTYPE: AM G15304, off Moreton Bay, Qld, 27°31.5'S, 153°40'E, 76–80 m, RANS *Kimbla*, station 1, W. Ponder, 29 March 1969.

## Differential characteristics

Distinctive sclerites; polyp body scales broad, up to 0.27 mm long, outer face tubercles not crowded; sclerites of the branch coenenchyme mostly spindles and ovals up to 0.24 mm long.

### Description

### Colony form (Figure 61)

The holotype consists of two portions of the original colonial fan. The largest fragment is 89 mm tall and 75 mm across and one half of it is overlaid by a second closely oppressed fan, the two being joined by several anastomoses. The course of a number of main branches which ramify profusely can be traced through the specimen. Branching is essentially pinnate but it is very irregularly spaced. Anastomoses, incidental fusing of branches, branches of different thickness, branches out of plane, and pinnae that rebranch, all combine to give an untidy appearance to the specimen.

The main branches in the middle region of the largest fragment are 0.95–1.42 mm thick, and throughout the colony pinnae are mostly 0.47–0.79 mm thick (polyps not included). Unbranched pinnae are 1.9–14.2 mm long, but most are <6.3 mm. The distance between consecutive subdivisions is 0.9–4.7 mm but most occur within 2.4 mm of each other. The branching angle is usually more or less 90° with the branches curving upwards after diverging, but a few arise at <50°.



Figure 61 Acanthoisis kimbla sp. nov., holotype, natural size.



Figure 62 Acanthoisis kimbla sp. nov., holotype: A-B. Polyps; C-D. Axial internodes; E. Twig fragment.

### Polyps (Figure 62A,B,E)

Although on some twigs the polyps are distributed all around, many are only visible from one side of the large fragment. They are densely arranged on all branches and pinnae in the uppermost regions of the colony, whilst the middle to lower regions of the main branches, and some of the pinnae, have far fewer polyps. Centre to centre, polyps can be 0.78–1.20 mm apart, with most at distances of 0.78–0.90 mm.

The anthocodiae are shaped like low domes with 0.60–0.72 mm basal diameter; most about 0.65 mm. The brownish orange polyp bodies are surmounted by the white sclerites of the anthopoma. Most polyps are 0.19–0.29 mm tall. Some are considerably shorter, 0.12 mm, with the anthopomal region appearing more or less as a flat white disc. Other polyps are up to 0.46 mm tall where the white polyp head forms a dome 0.12 mm high. The anthopomal region is commonly 0.36–0.41 mm in diameter. A few smaller, apparently juvenile, polyps are distributed throughout the colony.

## Colony colour

Brownish orange ( $\approx 6C6-7$ ) with white polyp summits. Nodes can be seen through the coenenchyme when not obscured by the polyps. With the exception of the apical polyp scales, all sclerites are pale yellow in transmitted light.

## Axis form (Figure 62C,D)

Internodes with pronounced primary ridges which bear a single row of large spines. Desmocyte cavities conspicuous and confined to the valleys between the ridges.

Internodes mostly 2.7–3.8 mm long. The basal internode of the thickest main branch is 1.8 mm thick and has about 36 primary ridges. The nodes of the basal region of the thickest main branch are 0.6–0.8 mm long, and those of the thicker branches throughout the colony are 0.3–0.6 mm in length. The nodes of the pinnae are 0.24–0.30 mm long. In general the nodes are noticeably narrower than the internodes. Many of the branches and pinnae show abrupt changes in diameter.

#### Axis branching

Multiple branches can arise from a single internode. Although 4–5 branches originating from a single internode can occur it is infrequent, the most common being 1–3. Depending upon the relative thickness of the originating internode and its products, the style of branching is as shown in Figure 251 examples 1–11.

#### Axis colour

The internodes of the thicker branches throughout the colony are translucent and greyish orange ( $\approx$ 6B5). Those in the pinnae are a similar colour to the coenenchyme. The nodes in the basal



Figure 63 Acanthoisis kimbla sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Thin branch coenenchyme; E. Main branch coenenchyme.

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area of the colony are brownish orange (≈5C5). They are more or less opaque with slightly translucent darker coloured centres, and thin yellowish satinlike borders. The nodes of the thinner branches are pale yellow with broad satin-like borders and thin brownish translucent to transparent centres. In the pinnae the nodes are almost entirely opaque, yellowish and satin-like with only a very short transparent brownish centre region.

## Polyp sclerites (Figure 62A,B; 63A–C)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 62B). Each octant is occupied by a single triangular sclerite (Figure 63Aa-g) preceded by 1-2 crescentic scales (Figure 63Ai-k). Proximal to these the sclerites are coloured, and may be long enough to extend below neighbouring octants. There is a single basal tentacular sclerite of various size (Figure 63Bd-f) which precedes a single row of curved scales in the tentacle rachis (Figure 63Ba-c). The triangular anthopomal sclerites have their lateral margins provided with granular spines of irregular number and size, and their exposed face ornamented with granular tubercles. They are mostly 0.12-0.15 mm long, and their underside is relatively smooth (Figure 63Ad). The tuberculate basal tentacular sclerites are commonly very long; up to 0.12 mm (Figure 63Bd). The anthopomal crescentic scales are ornamented with pointed tubercles and finger-like projections that have a fine granular surface. The lateral extensions of the scales may be pointed or tongue-like. The tentacular scales have scalloped margins, and are mostly <0.077 mm long.

The sclerites of the polyp body (Figure 63C) may be narrow or broad, and are up to about 0.27 mm in length. Their underside is relatively smooth (Figure 63Ca) and their exposed face is ornamented with granular tubercles and finger-like projections. Many of the scales have long, thick, granular, rootlike processes.

## Coenenchymal sclerites (Figures 62A; 63D,E)

The surface of the thinner branches contains spindles, sometimes branched, and a few irregularly shaped forms, 0.07–0.24 mm long. Most are slightly flattened. They are covered with rounded, granular tubercles; those on the underside being slightly warty. A few have rootlike structures (Figure 63Da,b).

The surface of the main branch at the base of the largest fragment of the colony contains predominantly small ovals, spindles, and irregularly shaped forms that are unilaterally developed with rugose, angular tubercles or tooth-like projections (Figure 63E). Most are <0.12 mm long, but larger spindles are common and they may be as long as 0.24 mm. There are small complex warts on their underside.

### Distribution

See Figure 264. Depth range 76-80 m.

## Etymology

The species is named after the expeditionary vessel, the Royal Australian Naval Survey Ship, *Kimbla*. Noun in apposition.

# Notisis Gravier, 1913 Figure 311

- Notisis Gravier, 1913a: 1015 (without included species); Gravier, 1913b: 454-455; Gravier, 1913c: 457; Gravier, 1914: 25, 43-47; Kükenthal, 1915: 124; Kükenthal, 1919: 633-634; Kükenthal, 1924: 445-446.
- Mopsea; (part) Roule, 1907: 437–438; (part) Roule, 1908: 5; (part) Gravier, 1913b: 454; (part) Gravier, 1913c: 456–460; (part) Gravier, 1914: 24–28, 34–38; (part) Molander, 1929: 79–80; (part) Bayer, 1956: F222; (part) Grant, 1976: 33–35; (part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49–51 (in key), 57; Bayer and Stefani, 1987b: 940–942 (in key).

## Type species

*Notisis fragilis* Gravier, 1913, by subsequent designation and monotypy Gravier, 1913b: 455.

## Diagnosis

Colonies grow more or less planar to somewhat bushy, up to 173 mm tall, and branched pseudodichotomously.

The sclerites are colourless and preserved colonies are generally yellowish white or grey. The axial internodes are greyish white, translucent to transparent, and the nodes are generally brown.

Polyps are usually quite crowded and distributed all around. In one species (*N. fragilis*) they are sparse and biserial. They can stand erect and appear more or less symmetrical, club-shaped or capstan-like, but are commonly preserved curved over and leaning distad. The polyp body is completely covered with sclerites.

The anthopoma is slightly asymmetrical, and the sclerites are continuous with the polyp body scales. Each octant contains about 7–9 scales up to about 0.18 mm long. The proximal ones may be crescentic and transversely arranged. The rest are irregularly shaped and arranged in 2 rows with opposing scales arranged loosely *en chevron* but alternately over-reaching other. The tentacles contain narrow, transversely oriented, curved scales, up to about 0.12 mm long. They appear to be in one row but are actually arranged in 2 rows with the scales alternately interleaved and closely overlapping so that they are often only slightly offset.

The polyp body is covered in numerous series of

oval to elongate scales, up to 0.29 mm long, ornamented with granular tubercles and tooth-like projections. The lower body scales may be very narrow, like flattened spindles.

Around the bases of the polyps the branch surface is often swollen due to the presence of what appear to be brood pouches. These areas may coalesce so that whole sections of branches may be irregularly distended. Sclerites of the surface of the coenenchyme are generally spindles, sometimes branched, ornamented with densely placed or well spaced tubercles which are often tallest on the outer face. The sclerites of the surface of the brood pouches may be modified, sometimes as narrow scales with ctenate margins. Surface sclerites are up to 0.45 mm in length.

Axial internodes may be straight or irregularly curved. They have multiple primary ridges each bearing a single row of large spines; expect in the oldest portions where the spines may be reduced or absent. Most internodes are no longer than 3.5 mm long.

#### Distribution

See Figure 311.

## Notisis fragilis Gravier, 1913 Figures 64–71; 265

- Notisis fragilis Gravier, 1913b: 455; Gravier, 1914: 43–48, Figures 52–61; Plate VI, Figures 28–29; Plate IX, Figure 49; Plate X, Figure 51; Kükenthal, 1919: 634; Kükenthal, 1924: 446.
- ? Mopsea elongata; Grant, 1976: 33–35, Figures 29– 30.

## Material examined

#### Types

HOLOTYPE: MNHN, Marguerite Bay, between

Jenny Island and Adelaide Land (most probably Adelaide Island), Antarctica, 67°45'S, 68°33'W, 254 m, French Antarctic Expedition 1908–1910, 15 Jan. 1909. PARATYPE: MNHN, colony axis only, same data as holotype.

#### Other material

NZOI station E225b, fragments identified by Grant as *Mopsea elongata*, West Young Island, Antarctica, 66°31'S, 162°26'E, 201–229 m, dredge, 12 Feb. 1965.

# Differential characteristics

Sclerite form, in particular the coenenchymal spindles which have closely arranged, tall, rounded processes with a granular surface.

## Description of the holotype

## Colony form (Figure 64)

The planar colony is pseudo-dichotomously branched, and about 67 mm tall and 43 mm across. The stem is 13.5 mm long, 0.7–1.0 mm thick, and mostly devoid of tissue. Branches and twigs taper, and are about 0.32 mm thick near the tips (polyps not included). Angle of branching is mostly about 45–70°, and the branches curve upwards from the point of division. The longest undivided branch is 40 mm.

## Polyps (Figures 65A-E,I)

The polyps are arranged more or less biserially. There are two opposing rows of alternating polyps. The polyps are spaced well apart, with about 2 mm between consecutive polyps in the middle of the colony, and 1 mm in the more terminal regions.

The polyps are contracted and somewhat clubshaped. Some stand vertical, but most are angled upwards at about 45° to the branch surface. In a number of cases the tips of the tentacles protrude



Figure 64 Notisis fragilis Gravier, 1913, holotype, natural size.



Figure 65 Notisis fragilis Gravier, 1913, holotype: A-E. Polyps; F. Coenenchyme; G-H. Axial internodes; I. Twig fragment.

from the summit of a polyp. Polyps are present in many stages of development. The largest are 1.1–1.5 mm tall, 0.54–0.60 mm across the head, and 0.30–0.42 mm across the narrower base.

Juvenile polyps occur throughout the colony. The smallest are wart-like, erect, 0.30 mm across and 0.24 mm tall.

### Colony colour

The overall appearance is yellowish brown ( $\approx$ 5D5). The polyps are darker than the coenenchyme, which is translucent and shows the white axis beneath. The colour was originally recorded as yellowish white. The sclerites are all colourless.

## Axis form (Figure 65G,H)

All internodes have multiple primary ridges. Except for the two basal internodes of the stem, there is a single row of large, widely spaced spines along each ridge. The ridges on the thinner internodes appear rounded and robust. The two basal internodes of the stem have smooth ridges. Internodes near twig tips usually have 5–6 ridges, and those in the stem have 8. Desmocyte cavities are shallow but distinct.

Internodes in the stem are 1.4–2.8 mm long. Those in the branches and twigs are 2.4–3.5 mm. Stem nodes are 0.12 mm long. Those in the middle of the colony are about 0.18 mm, and nearer the twig tips they are 0.06–0.09 mm in length.


Figure 66 Notisis fragilis Gravier, 1913, holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

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Figure 67 Notisis fragilis Gravier, 1913, holotype, sclerites: Branch coenenchyme.

#### Axis branching

All branched internodes only have one division. This usually involves a short calcareous stub as in Figure 251 example 6, but sometimes shared nodal material is involved as in the upper part of example 46.

#### Axis colour

Nodes are dark brown, opaque in the stem and translucent in the thinner twigs. The borders are cream coloured and satin-like. The internodes are greyish-white and translucent.

#### Polyp sclerites (Figures 65A-E; 66)

The anthopoma is slightly asymmetrical and the sclerites are continuous with those of the polyp body. The larger, upper polyp body scales give way to smaller forms at the base of each octant (Figure 65A,D,E). The anthopomal sclerites are scale-like, irregularly rectangular to triangular, and ornamented with tall rounded tubercles with a granular surface, and granular root structures (Figure 66A). There are about 7-9 in each octant, arranged in two rows, with opposing sclerites angled more or less en chevron but alternately over-reaching each other. Few are longer than 0.18 mm. The tentacles contain flat, narrow scales, curved to fit transversely across the back of the rachis (Figure 66B). They seem to be in a single row, but are actually in two rows, with the scales alternately interleaved, and overlapping so closely that they are only slightly offset. They are relatively large, up to about 0.12 mm.

The polyp body is covered all around with

overlapping scales (Figure 65E,I) that are ornamented on the outer surface with tall rounded tubercles (Figure 66C), and are mostly smooth with small areas of granulation on their underside (Figure 66Ca). Most are <0.29 mm long, and none were found as long as Gravier's 0.48 mm which appears to have been a misprint as it was corrected to 0.18 mm in his fuller description (1914: 46). The polyps lean distad, and there are about 8 series of scales abaxially. It is difficult to tell if there is the same number or slightly fewer series on the adaxial side.

#### Coenenchymal sclerites (Figures 65F; 67)

The surface of the branches and twigs contains flattened spindles, sometimes branched, sometimes scale-like (Figure 65F). They are unilaterally developed with closely arranged, tall, rounded tubercles with a granular surface, and are mostly 0.11–0.26 mm long, with a few to about 0.32 mm (Figure 67). No basal stem tissue remains on the holotype.

#### **Description of NZ0I E225b fragments**

#### Colony form (Figure 68)

The pieces are damaged and curved from bottle storage. The growth form is not strictly planar and the branching is lateral, but when all fragments are taken into account the ramification can be considered to be pseudo-dichotomous. Branches including polyps are up to 2.4 mm thick. Amongst the fragments, undivided branches can be as long as 80 mm, and the distance between consecutive branches is 5–55 mm.



Figure 68 Notisis cf. fragilis Gravier, 1913, NZOI E225b, natural size.

#### Polyps

Polyps are for the most part distributed all round, although on some fragments they tend to favour one or two sides of a branch, and they are often crowded. They commonly lean distad, whilst some stand erect and a few are angled downward. They commonly have a distended base that may contain a sub-spherical body up to 1.6 mm diameter. Polyps may occur in groups where the swollen bases seem to merge to form what appear to be large brood pouches. The swollen areas are covered in narrow scales and modified branch surface sclerites.

Measured abaxially, the larger polyps are about 1.5 mm tall. Some are more or less cylindrical, about 0.6 mm in diameter. Others have a narrower neck region about 0.42–0.48 mm thick, and some have a wider base 1.2 mm across. A few cylindrical juvenile polyps, 0.30–0.48 mm across and 0.12–0.42 mm tall, occur throughout.

#### Colony colour

The sclerites are colourless but the fragments are yellowish grey ( $\approx$ 4B3). The coenenchyme is translucent, and where the polyp density is low enough the dark nodes can be seen below.

# Axis form

Internodes are straight or irregularly curved,

with multiple primary ridges each with a single row of widely spaced spines. Both the ridges and spines may be reduced on the thick, older internodes. Internodal shoulders are often slightly raised. An internode 0.80 mm thick has 13 ridges, one 0.50 mm thick has 9, and one 0.26 mm thick has 6. Desmocyte cavities are shallow and form a more or less continuous narrow channel between pairs of primary ridges.

Internodes in the thicker portions are 2–3 mm long. In the thinner branches they may be as long as 4 mm but are mostly about 3.3 mm. Nodes are about 0.30 mm long in the thicker fragments, 0.24 mm in the middle of the thinner branches, and 0.16 mm near the tips.

#### Axis branching

Most bifurcations arise from expansions of the parent internodes as in Figure 251 examples 12, 13, 29 and 47. Others involve a basal stump as in example 27.

#### Axis colour

Internodes are colourless and transparent when thin, and greyish white and translucent when thick. The thick, more basal nodes are autumn leaf brown (≈6D7) and may be transparent on one side and translucent to opaque on the other. In the thinner branches the nodes are much yellower and almost

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Figure 69 Notisis cf. fragilis Gravier, 1913, NZOI E225b, sclerites: A. Anthopoma; B. Tentacles.

transparent in the middle except for a dense patch deep in the centre. Nodal borders are satin-like and whitish.

#### Polyp sclerites (Figures 69; 70; 71A)

The anthopoma is slightly asymmetrical and the sclerites of the anthopoma are continuous with those of the polyp body. The upper polyp body scales give way to somewhat triangular to rectangular shaped scales with tall rounded tubercles with a granular surface. There are about 7 of these in each octant. They are arranged in two rows, with the opposing sclerites angled more or less *en chevron* but alternately over-reaching each other. They are up to about 0.16 mm long (Figure 69A). The flattened, curved tentacular sclerites are up to about 0.12 mm long and the small tubercles near their edges give them a scalloped appearance (Figure 69B).

Most of the polyp body is covered in thorny scales (Figure 70). Despite the fact that when the polyp is leaning over, the abaxial side is longer than the adaxial, there seems to be a similar number of sclerites, about 8 series, on both sides. This is possibly because the abaxial scales are wider than the adaxials. After curving around the abaxial-lateral sides of the polyp, these scales are angled down towards the polyp base, many converging towards the abaxial centre line. When polyps stand straight out, these abaxial scales seem to slide over each other so they lie more horizontally. The scales are of varied shapes. Many have long irregularly shaped root-like processes, and long thorn-like projections that are often curved and sometimes branched. The scales are mostly 0.15–0.30 mm long, and the undersides are nearly smooth (Figure70a).

At the base of the polyp, where it adjoins the branch, are very narrow scales and spindles. Their numbers depend upon the extent of the swollen brood pouch area. The sclerites are described below.

#### Coenenchymal sclerites (Figure 71)

The surface of the branches contains spindles that are sometimes slightly flattened, and sometimes branched. They are mostly covered with closely arranged tall tubercles, simple or branched, that have a granular surface (Figure 71B). The spindles are generally 0.09–0.24 mm, with some to 0.32 mm in length.

The surface of the brood pouches contains some spindles similar to those of the branch surface, and narrow scales like those of the polyp body (Figure 71A). Amongst them are flattened forms with thorny processes arranged comb-like along the edges (Figure 71Aa–h). Sclerites in the surface of the brood pouches average longer than those in the general branch surface, and may be up to about 0.35 mm. Sclerites with comb-like edges occasionally also occur in the non-swollen branch surface.



Figure 70 Notisis cf. fragilis Gravier, 1913, NZOI E225b, sclerites: Polyp body.



Figure 71 Notisis cf. fragilis Gravier, 1913, NZOI E225b, sclerites: A. Polyp base where it adjoins a brood pouch; B. Branch coenenchyme.

#### Remarks

The paratype of *N. fragilis* is 57 mm tall, 25 mm wide, and a fragment of a larger colony. The coenenchyme is missing and some sponge tissue and other unidentified material encrusts some portions of the axis. It is not possible to tell if the specimen is conspecific with the holotype. The internodes, however, are of the same style, colour, and size, and the branching modes are as in Figure 251 examples 6 and 12.

The fragmented material identified with *Mopsea* elongata by Grant (1976) differs from the holotype of *N. fragilis* in several ways. Although the pieces branch in much the same style, the polyps are not sparse and biserial but densely arranged and distributed all around, and the polyp body sclerites are very thorny. There are also flattened spindles or narrow scales with ctenate edges which occur in the surface of brood chambers and which are not found in *N. fragilis*. In most other characters, however, the material is very similar.

The differences in polyp distribution and polyp sclerite ornamentation do not seem significant enough to warrant erecting a new species for Grant's material, despite the fact that it was found virtually 131° west of the collection site of *N. fragilis*, nearly on the other side of the Antarctic continent, as there is ample documentation of circumantarctic species in many faunal groups (Dell, 1972). Indeed, Dell (1990: 273) estimated 45% of the shelled molluscan fauna of the Ross Sea had a circumantarctic distribution. The presence of the

flattened sclerites with ctenate margins does, however, remain to be explained. These occur in Grant's material predominantly in the surface of the brood chambers. As the holotype of *N. fragilis* does not have such chambers no comparison is possible. Whether these sclerites are produced by the colony specifically during the brooding phase of reproduction is yet to be proven.

From the original material attributed to *Mopsea* elongata by Grant, besides that from station E225b, only the lots from E171, E172 and E177 have been located. The lots from the latter three stations are mixtures of both smooth, and spined, naked axial fragments from more than one genus, together with sclerite-containing tissue debris. The material is not identifiable with any certainty.

#### Distribution

See Figure 265. Depth range 201-254 m.

# Notisis elongata (Roule, 1907) Figures 72–75; 266

Mopsea elongata Roule, 1907: 438–439; Roule, 1908: 5–6, Figures 1–4; Gravier, 1914: Plate IV, Figures 18,19; Kükenthal 1919: 625 (with incorrect synonymy); Kükenthal, 1924: 441 (with incorrect synonymy); Bayer, 1956: F222, Figure 161.3.

# Not *Mopsea elongata*; Gravier, 1913b: 454; Gravier 1914: 34–38, Figures 27–38; Plate IV, Figure 17 (not Figures 18, 19) (⇒ *Notisis* sp. indet).



Figure 72 Notisis elongata (Roule, 1907), specimens from lot nº 641: A. Holotype. All natural size x 0.75.

- Not Mopsea elongata; Molander, 1929: 79-80 (⇒ Notisis charcoti sp. nov.).
- Not Mopsea elongata; Grant, 1976: 33–35, Figures 29–30 ( $\Rightarrow$  Notisis cf. fragilis Gravier, 1913: 455).

#### Material examined

#### Types

HOLOTYPE: MNHN, Booth Island (also known as Wandel Island) Palmer Archipelago, West coast of Graham Land, Antarctic Peninsula, French Antarctic Expedition 1903–1905, lot no. 641, Dr Turquet.

# Other material

MNHN (2 fragments), same data as holotype.

#### **Differential characteristics**

Sclerite form, in particular the coenenchymal spindles which have widely spaced, simple, conical tubercles; polyp head scales broader than those in the base.

# Description

#### Colony form (Figure 72A)

The holotype is a fragment of a larger colony. It is curved and compressed from bottle storage (see Gravier's life-size illustration of the more natural form, 1914: Plate IV, Figure 18), and is about 173 mm tall. The lower 50 mm is devoid of coenenchyme as are parts of several upper branches. The ramification is pseudo-dichotomous and not strictly in one plane. Many of the branches show several irregular curves.

The naked basal internodes are 1.4 mm thick, and those of the first two branches are 1.3 mm thick. In the rest of the colony, branch thickness, including polyps, is about 1.6–2.2 mm. Branches are relatively long, quite a few 80–110 mm in length, and taper very little. Angle of branching is commonly 15–40°, but occasionally there is little separation and 2 branches may grow closely side by side for some distance with some webbing of the coenenchyme. The distance between consecutive points of division can be as short as about 2.5 mm, just one internode, but is commonly 15–30 mm.

#### Polyps (Figure 73A–D,J,K)

Polyps are distributed all around. The larger ones curve upwards and over and lie against the branch surface. The density is least on the thinnest branches where about 1 mm may separate the head of one polyp from the base of the next. On the thickest branches the density may be so great that the head of one polyp may lie against the base of another. Where the lower coenenchyme is still intact there are very few polyps, which indicates the specimen may have broken off close to the base of the parent colony.

The polyps are contracted and club-shaped, and the larger ones are 1.14–1.26 mm long. Across the head most are 0.54–0.60 mm, and correspondingly project only this far above the surface of the branch. Some slightly more relaxed polyps are up to 0.70 mm across the head. Abaxially across the base most polyps are about 0.42 mm. Juvenile polyps occur scattered throughout the specimen, and are short, more or less cylindrical, and angled distad. Most are about 0.42–0.45 mm across the anthopoma and about 0.48–0.60 mm along the abaxial side.

The basal portion of most polyps, and the adjoining branch surface, is slightly distended and contains numerous spherical reproductive bodies about 0.18–0.50 mm in diameter. Where polyp density is high, lifting a section of the coenenchyme reveals larger numbers of these bodies in what appear to be continuous brood chambers.

# Colony colour

The sclerites are colourless, but the coenenchyme appears dull greyish yellow. Where polyp density is low and the surface is not distended, the underlying darker nodes can be seen.

# Axis form (Figure 73H,I)

Internodes straight or curved, with multiple primary ridges each bearing a single row of well spaced spines. Ridges and spines may be reduced or missing on the thick, older internodes, which presumably was that part of the axis figured by Roule (1908: Plate 1, Figure 2). Internodal shoulders may be raised on the thicker internodes. An internode 1.4 mm thick has about 22 primary ridges, one 0.54 mm thick has about 12, and one 0.24 mm thick has 8. What seem to be secondary ridges on some internodes appear to be only developing primary ones. Desmocyte cavities are shallow, elongate, and form a more or less continuous channel between pairs of primary ridges.

Axial internodes are mostly 2.2–3.2 mm long. Nodes are 0.20 mm long basally and 0.07 mm long apically.

#### Axis branching

Divisions commonly involve shared nodal material as in Figure 251 examples 19 and 25, while others are like examples 12 and 29. Sometimes the products of a division may not diverge very much resulting in a joint like example 41.

# Axis colour

The internodes are colourless and transparent



Figure 73 Notisis elongata (Roule, 1907), holotype: A-F. Polyps; G. Coenenchyme; H-I. Axial internodes; J-K. Twig fragments.

κ



Figure 74 Notisis elongata (Roule, 1907), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Branch coenenchyme.

when thin, becoming greyish white and translucent when older. The more basal nodes are brownish yellow ( $\approx$ 5C8), and transparent superficially but denser deep within. In the middle and upper reaches of the colony, the nodes are transparent and greyish yellow ( $\approx$ 4C6). All nodes have narrow, white, satin-like borders.

#### Polyp sclerites (Figures 73A-F; 74A,B; 75)

The anthopoma is slightly asymmetrical and the sclerites are continuous with those of the polyp body (Figure 73E). The upper polyp body scales give way to somewhat triangular or crescentic

scales ornamented with tall rounded tubercles with a granular surface (Figure 74A). There are about 7– 8 of these in each octant, but because of the continuity with the polyp body sclerites, each octant may appear to consist of about 12–14 sclerites in a microscope preparation. The more distal sclerites are arranged in 2 rows, with the opposing sclerites angled more or less *en chevron* but alternately over-reaching each other. The proximal scales may be angled or transverse. When the anthopoma is preserved slightly relaxed, the more distal sclerites often lie side by side (Figure 73A). Most of the anthopomal sclerites are <0.16



Figure 75 Notisis elongata (Roule, 1907), holotype, sclerites: A. Lower polyp body; B. Upper polyp body.

The sclerites of the abaxial side of the polyp body are wider and thornier than those on the adaxial side, and they are also slightly more numerous. This combination probably permits the marked decumbent nature of the polyps. The sclerites in the head region are more scale-like than those in the lower polyp body. The lower area contains narrower sclerites that include: spindles, mostly somewhat flattened, with widely spaced low tubercles (Figure 75Ah,i,k,l) or tall crowded prominences (Figure 75Ad-f); clubs (Figure 75Am); narrow scales (Figure 75Ag); irregularly branched forms (Figure 75Aj); small flattened rodlets with scalloped edges (Figure 75Aa-c); and sclerites intermediate in shape to these many forms. In the polyp head the scales are crescentic, oval or triangular, and ornamented with crowded tall tubercles which have a granular surface (Figure 75B). The flattened rodlets of the lower body area are 0.08-0.10 mm long. All other body sclerites are mostly <0.22 mm but can be up to 0.25 mm.

# Coenenchymal sclerites (Figures 73G; 74C)

The surface of the branches contains mostly spindles, about 0.10–0.35 mm long, with low, widely spaced simple, conical tubercles. Amongst them are spindles up to 0.15 mm long with taller prominences developed predominantly along one side.

# Variability

The two additional specimens (Figure 72) from the same locality as the holotype, but not referred to by Roule, are clearly the same species as the holotype.

#### Distribution

See Figure 266.

Notisis charcoti sp. nov. Figures 76–79; 267

Mopsea dichotoma; Roule, 1907: 438; Roule, 1908: 5. Mopsea elongata; Molander, 1929: 79–80.

# Material examined

#### Types

HOLOTYPE: MNHN, Booth Island (also known as Wandel Island) Palmer Archipelago, West coast of Graham Land, Antarctic Peninsula, French Antarctic Expedition 1903–1905, lot No. 641, Dr Turquet. PARATYPE: NRS, Swedish Antarctic Expedition 1901–1903, lot No. 743, station 5, off Graham Land, 64°20'S, 56°38'W, 150 m, 16 Jan. 1902.

#### Other material

NRS, Swedish Antarctic Expedition 1901–1903, lot No. 765, station 17, between the Falkland Islands and South Georgia, 54°34'S, 43°23'W, 160 m, 19 April 1902.

# **Differential characteristics**

Sclerite form, in particular the polyp body scales and coenenchymal spindles which are densely covered in thorny projections.

# Description

#### Colony form (Figure 76)

The holotype is curved from bottle storage. The holdfast, the stem, and the branched colony portion have separated from each other, but were placed together for the photograph in Figure 76. The non-planar colony is about 130 mm tall, 20 mm broad and 20 mm through, and the ramification is pseudo-dichotomous. The



Figure 76 Notisis charcoti sp. nov., holotype, natural size.



Figure 77 Notisis charcoti sp. nov., holotype: A-E. Polyps; F-G. Axial internodes.

coenenchyme is missing from most of the lower half of the colony and portions of the upper branches. The chalky coloured holdfast is about 7.5 mm x 5.5 mm. It is attached to a dark grey stone, and has incorporated small fragments of quartzlike rock. The stem, 1.5–1.7 mm thick, extends for 10 mm to the first branch. About 25 mm above the base is a complex of irregularly curving branch sections, sometimes fused together, associated with gravel particles. Although some points of branching are somewhat dichotomous, most divisions are lateral with the diverging branch curving upwards from the point of division and continuing more or less parallel to the parent branch. Such branches will usually rebranch, but will continue for different lengths before dividing. Divisions of this nature may occur in the one plane so that colony fragments could appear to come from planar colonies. However, the irregular curving of the branches, the branching into numerous directions in the lower parts of the colony, and the occasional subsequent non-planar branching have resulted in a bushy growth form.

Branch thickness varies considerably. In the

lower parts of the colony it is about 0.5-1.6 mm (without coenenchyme). In the mid-colony region it is about 0.6-1.2 mm, and in the upper parts the twigs are mostly about 0.8 mm thick (without polyps). Many branch and twig fragments are loose in the specimen container together with polyp and coenenchyme debris. The thin twig pieces are 0.6-0.7 mm thick (without polyps) and taper sharply to rounded points. Within the colony, the distance between consecutive divisions may be very short, just a couple of internodes, but is usually much longer and can be up to 60 mm. The length of undivided branches is difficult to assess due to breakages. They are relatively long and probably reach in excess of 55 mm. The angle of branching is variable, but most are 45° to almost perpendicular.

### Polyps (Figure 77A,D)

Although most polyps are missing, their points of attachment show that distribution was all around. In some regions, intact polyps are well separated, about 0.8 mm apart. In others, they are much closer, 0.15–0.30 mm, and grouped. Many polyps have markedly swollen bases, and these may touch and merge forming, apparently, large brood pouches. The swollen bases are covered with much the same sclerites as the branch surface and are therefore predominantly of coenenchymal origin. Collapsed, spherical to ovoid bodies 0.3–0.6 mm across occur in small numbers in these chambers, or individually in single polyps. Groups of polyps may consist of 3–4 or as many as 40 individuals.

Polyps are contracted and, although most are leaning distad, there appears to be as many series of scales on both abaxial and adaxial sides of the body. The largest polyps are about 1.5–1.8 mm tall, 0.6–0.7 mm across the loosely contracted anthopoma, and 0.5 mm thick in the neck region. A few juvenile polyps are present. These are more or less cylindrical, 0.5–0.6 mm tall and 0.4–0.5 mm thick, and lean distad or sit perpendicularly on the branch.

#### Colony colour

The sclerites are colourless, but the polyps and coenenchyme appear greyish yellow ( $\approx$ 4B3), and the underlying dark nodes can be seen on the thicker branches.

# Axis form (Figure 77F,G)

Internodes straight or irregularly curved, with multiple primary ridges. Each ridge has a single row of low, widely spaced spines. Both ridges and spines may be reduced or absent on the thicker internodes in the lower parts of the colony. Older internodes are often thicker at the ends than in the centre. Primary ridges extend down into the calcareous holdfast. An internode 0.39 mm thick has eight ridges, one 0.79 mm thick has 13, and one 1.50 mm thick has 24. Desmocyte cavities are shallow, elongate, and occur in a single row between the primary ridges where they often join to form long continuous channels.

Most internodes are 3.0–3.6 mm long. Those in the stem are shorter, the most basal one being only 1.50 mm long. Nodes in the thicker, more major branches are about 0.18–0.42 mm long, and those in the thinner branches and fine twigs are about 0.09 mm long.

#### Axis Branching

All branched internodes only have one division. Branching modes are mostly as in Figure 251 examples 12, 25 and 29, with a few as in example 26.

# Axis colour

Internodes are greyish white, translucent in the thinner branches and twigs and more opaque in the thicker lower regions. Nodes are dark brown ( $\approx$ 6F6) but translucent, with relatively wide, white, satin-like borders.

#### Polyp sclerites (Figures 77A-E; 78A,B; 79)

The anthopoma is slightly asymmetrical and the sclerites are continuous with those of the polyp body. The upper polyp body scales give way to a series of about 3 crescentic forms at the base of each octant (Figures 77B,C,E; 78Aa,b). Distal to these, the anthopomal sclerites are irregularly rectangular to triangular, mostly ornamented with tall rounded warts with a granular surface. These are about 7 in each octant, arranged in two rows, with opposing sclerites angled more or less en chevron but alternately over-reaching each other. Most are up to about 0.17 mm. Smaller irregularly shaped scales (Figure 78Ac) lead to the curved tentacular sclerites, up to 0.10 mm long, that occur in two closely overlapping rows in the rachis of each tentacle (Figure 78B).

The polyp body is covered all around by large overlapping scales (Figure 77A,B,D), up to 0.29 mm long and densely covered with tall spine-like prominences with a granular surface (Figure 79). Although difficult to assess, the larger polyps have about 17–20 series of body scales from polyp base to anthopomal margin.

# Coenenchymal sclerites (Figure 78C)

The surface of the branches and twigs contains spindles and the occasional multiradiate sclerite. The spindles are symmetrically and asymmetrically ornamented with tall simple tubercles. Most are 0.16–0.23 mm long. The swollen areas at the base of some polyps contain similar spindles, together with many that only have low tubercles (Figure



Figure 78 Notisis charcoti sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Branch coenenchyme.



Figure 79 Notisis charcoti sp. nov., holotype, sclerites: Polyp body.

78Ca). There are very few small forms in these areas, and most sclerites are 0.19–0.26 mm.

There are no stem surface sclerites preserved.

#### Variability

The 80 mm colony fragment from station 5 of the Swedish Antarctic Expedition, consists of about 7 upper branches that are very densely covered in polyps. The coenenchyme is very thick. A branch 1.4 mm in diameter (without polyps) has axial internodes 0.8 mm thick. With polyps included the branch is about 3 mm thick. Numerous polyps have swollen bases, and one was found to contain a sub-spherical body 1.6 mm in diameter. Visible internodes 0.8-1 mm in diameter have primary ridges with no spines. A thinner internode 0.5 mm thick in the upper branches has spined ridges. The internodes are opaque and chalky white. The nodes are virtually transparent, and orange (~5B5). The sclerites are like those of the holotype. Some polyps have more of the larger, densely ornamented scales (Figure 79, right hand column) than others.

The small fragments from the Swedish Antarctic Expedition station 17 appear to have been stored at some time in an acidic medium, possibly formalin. The general form and size of the axis and sclerites conform to the characteristics of this species, but because of the degree of corrosion some doubts as to its correct identity must remain. Two other lots from stations 6 and 59 are only fragments of naked axis with the characters of this genus.

#### Distribution

See Figure 267. Depth 150 m.

# Etymology

The species is named in honour of Dr Jean Charcot who led the first and second French Antarctic Expeditions, and who was later drowned when his research vessel the *Pourquois Pas* sank off the coast of Iceland leaving only one survivor.

# *Notisis* **sp. indet**. Figures 80; 81; 268

Mopsea elongata; Gravier 1913b: 454; Gravier, 1913d: 1471; Gravier 1914: 34–38, Figures 27–38; Plate IV, Figure 17 (not Figures 18,19).

# Material examined

MNHN (fragments), Deception Island, Port Foster, Antarctica, 62°55'S, 60°35'W, 150 m, French Antarctic Expedition 1908–1910, 9 Dec. 1909.

### Remarks

It is not possible to accurately document the characters of the species represented by this material as many of the polyp sclerites are unusually eroded and their distal margins are almost smooth. The causative agent is not obvious. The damage does not resemble that caused by storage in an acidic medium, nor that from abrasion and percussion during dredging. It is therefore likely to have a biological cause, possibly a predator or a pathogen. The gross morphological effect is that branches or branch sections carry polyps that appear smoother than others. Although the narrow aspect of the polyp scales and the design of the coenenchymal sclerites indicate this material may represent a new taxon, these may be the characters of a colony under stress.

# Description

# Colony form

The material consists of 2 branched portions and small twig fragments, originally reported by Gravier as 3 pieces. Only a small amount of material is involved and the nodes are all the same dark colour, so it is possible that the pieces came from the same colony. The 2 branched portions are about 105 mm and 85 mm tall respectively. The most basal division in the largest piece is not a natural branching point but a fusion of two crossed axial internodes. All other ramifications are lateral, with the daughter branches curving upward and growing more or less parallel to the parent branches. Most of the coenenchyme is missing from the lower portions of the branched pieces, and these broader internodes are about 0.8 mm thick. Branches only taper slightly, and some of the longer ones are about 0.8 mm thick proximally and 0.5 mm distally (including coenenchyme). Areas of branches swollen by brood pouches may be as thick as 1.6 mm (including polyps). Angle of branching is 25-67°, but 40-45° is average. The longest undivided branch is broken and would have been in excess of 87 mm.

#### Polyps

Polyps are evenly spaced, distributed all around, and usually about 1 mm apart. Commonly, where the polyp base adjoins the branch, the branch surface is swollen to form a chamber. In some sections numerous chambers merge and the whole portion of the branch is distended. Some chambers contain small spherical bodies whose number varies from 1 to several, and whose size from 0.18– 0.60 mm in diameter.

The polyps are contracted, squat, and generally lean distad. In most cases they are somewhat globular to egg-shaped, and about 0.6–0.7 mm tall and 0.5 mm across. Some are more loosely contracted with the anthopomal octants forming a conical apex from which tentacle tips protrude. On several branches the polyps are so contracted that they appear as low domes on the brood pouches,



Figure 80 Notisis sp. indet., sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 81 Notisis sp. indet., sclerites: Twig coenenchyme.

only 0.18–0.30 mm high and 0.60 mm across. A few very juvenile polyps are present between the mature forms. They are shaped like minute, squat cylinders.

# Colony colour

The sclerites are colourless, but the coenenchyme is dull greyish yellow. The dark underlying nodes can only be seen through the coenenchyme where the polyp density is low and the surface is not distended.

#### Axis form

Internodes are straight or curved with multiple primary ridges each with a single row of well spaced spines. Ridges may be reduced and spines may be irregularly distributed or missing on the more basal internodes. Internodal shoulders may be raised in the older internodes. An internode 0.6 mm thick has about 14 ridges, and one 0.2 mm thick has 7. The desmocyte cavities are shallow and elongate, and form a long continuous channel between pairs of primary ridges.

Internodes are 1.9–3.5 mm long with most being 2.4–2.8 mm. Nodes are about 0.16 mm long in the thickest parts and 0.06 mm long near the ends of the finer twigs.

#### Axis branching

Branching styles are like Figure 251 examples 6, 12, 13 and 29.

#### Axis colour

The internodes are translucent and greyish white. The nodes are dark brown (≈6F8), superficially transparent in the thicker branches and completely transparent in the finer parts. The satin-like borders are yellowish brown with white outer extremities.

#### Polyp sclerites (Figure 80)

The anthopoma is slightly asymmetrical and the

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sclerites are continuous with those of the polyp body. The upper body scales give way to smaller forms at the base of the octants, each of which contains about 9 irregular shaped scales up to 0.16 mm long. They are arranged predominantly in 2 rows with each sclerite alternately over-reaching its opposing one. "Normal" sclerites have granular tubercles and tooth-like processes (Figure 80Aa– d,l,m), while others may be eroded (Figure 80Ae– k). There are 2 rows of closely interleaved narrow scales, up to 0.12 mm long, in each tentacle rachis (Figure 80B).

The polyp body is covered with numerous series of narrow scales, mostly <0.25 mm long. The 'normal' ones have granular tubercles and toothlike processes (Figure 80Ca-h). In the smoother polyps the processes of the scale margins are mostly absent (Figure 80Ci-t).

#### Coenenchymal sclerites (Figure 81)

The surface of the branches and the brood pouches contains mostly narrow spindles, sometimes branched, up to about 0.45 mm long. They are ornamented with granular tubercles, sometimes concentrated in the middle of the sclerite (Figure 81c), and sometimes more densely arranged on the smaller forms (Figure 81a). In the areas where the smooth polyps are common the coenenchyme may also contain numerous poorly formed sclerites that are almost smooth (Figure 81b).

# Distribution

See Figure 268. Depth 150 m.

# Pteronisis gen. nov. Figure 312

Mopsea; (part) Wright and Studer, 1889: xlv, 33, 40– 44; (part) Thomson and Mackinnon, 1911: 678– 679; (part) Briggs, 1915: 70–78; (part) Kükenthal, 1915: 117–118, 123 (in keys); (part) Kükenthal, 1919: 558–559 (in key), 617–626; (part) Kükenthal, 1924: 431 (in key), 437–442; (part) Tixier-Durivault, 1970: 333; (part) Grant, 1976: 33; (part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49–52 (in key), 57–66; (part) Bayer and Stefani, 1987b: 940–942 (in key).

#### Type species

- Mopsea whiteleggei Thomson and Mackinnon, 1911, here designated.
- = Pteronisis whiteleggei new combination.

# Diagnosis

Except for one species, colonies are generally planar, pinnate, and profusely branched. [A

fragmented colony of *P. oliganema* sp. nov. indicates possible irregular lateral branching in that species, which conforms to the generic definition in all other respects, and the type series of *Mopsea bargibanti*, a species synonymised herein with *P. provocatoris* (Bayer and Stefani, 1987), are distantly pinnate and not planar]. Most colonies are smaller than 200 mm with 360 mm the tallest examined.

All species have colourless sclerites and the coenenchyme is generally yellowish white in preserved specimens. Axial internodes may also be colourless, or greyish white, and sometimes pale shades of pink or red. Axial nodes are generally light to dark brown at the base of the stem, yellowish or yellowish brown in the principal branches, and pale yellow, white, or colourless, with a darker central band, in the pinnae. Live colour data is minimal as it is only based on a few colonies. One species is greyish-red with white polyps, a second is greyish orange becoming cream coloured in the upper portions, a third is reported as light brown (cream), a fourth rose or rose orange, and a fifth is described as "vermilion red".

The anthocodiae are adaxially reduced, adaxially naked, and usually preserved curved over and lying against the surface of the branches. Distribution is all around to biserial. The anthopoma is asymmetrical and continuous with the polyp body sclerites. The apical sclerite in each octant is more or less triangular, mostly <0.11 mm long, and is generally preceded by several crescentic scales. Except for one species, the anthopomal sclerites are ornamented with prominent tooth-like projections. [Pteronisis plumacea (Briggs, 1914) has triangular anthopomal scales with a spatulate apex and a predominantly smooth upper face with a short, medial, spiny keel]. There is a single row of curved scales in the tentacle rachis, up to 0.07 mm in length. The polyp body is armoured with large transversely oriented scales arranged in 7 rows on the polyp head continuous with the anthopomal octants. There are from 1 to 3 short, narrow, more or less fusiform scales immediately below the adaxial octant (in effect an eighth row), together with the ends of the lateral arms of several large adaxial-lateral body scales. Most body scales have a distal margin with prominent tooth-like projections. In some species the margin has a medial cleft which may be sufficiently extensive to divide the edge into 2 lobes. The exposed face of the body scales may be smooth or have tubercles or tooth-like projections. In some species the projections on the lower body scales are thickened and rounded, or developed as irregular ridges. Most body scales are <0.2 mm long.

The coenenchyme contains predominantly spindles and oval sclerites that are unilaterally developed with tooth-like projections. The surface

of the pinnae contains longer and narrower sclerites than the stem, which is usually dominated by oval forms. The surface of the principal branches may contain a mixture of the 2 forms. Most coenenchymal sclerites are <0.19 mm in length.

The axial internodes in the distal portion of a pinna normally have 4 sides whose edges may be developed as primary ridges. The more proximal internodes may also have 4 sides but generally have more, and may also develop secondary ridges between the primaries. The pinna internodes are denticulated with the denticles usually restricted to the shoulders of the primary ridges but sometimes occurring along their whole length. The internodes of the principal branches have multiple primary ridges which may be denticulated on the shoulders in the younger colony parts but are usually smooth in the older portions. P. echinaxis sp. nov. is an exception regarding denticulation with virtually all internodes having denticles over their whole length including all ridges and areas between. Internodes are mostly <2 mm long and those in the principal branches may initiate 1-2 pinnae.

#### Distribution

See Figure 312.

#### Etymology

The Greek word for feather, *pteron*, in allusion to the pinnate branching; together with *Isis*.

# Pteronisis whiteleggei (Thomson and Mackinnon, 1911) new comb. Figures 82–88; 269

- Mopsea whiteleggei (part) Thomson and Mackinnon, 1911: 678–679, Plate LXVI, 2, 3; Plate LXXIII; Briggs, 1915: 75; (part) Kükenthal, 1919: 622– 623; (part) Kükenthal, 1924: 439.
- Not Mopsea whiteleggei; Tixier-Durivault, 1970: 330. [⇒ Mopsea provocatoris Bayer and Stefani 1987a: 61–63, Plate X, 2; Plates XIII–XIV, ≡ Pteronisis provocatoris (new comb.)].
- Not Mopsea whiteleggei; Bayer and Stefani, 1987a: 59–61, Plates XI–XII; Plate XVII; Figure 2, C. [⇒ *Pteronisis incerta* sp. nov.].

### Material examined

#### Types

HOLOTYPE: AM G6929 (numerous fragments). The collection locality given by Thomson and Mackinnon as "Eleven miles east of Broken Bay" does not correspond to any of the stations sampled by the HMCS *Thetis* as listed by Waite (1899: 20–22). The area 6–9 miles east of Broken Bay was

trawled on 19–21 February, 1898, at depths of 20– 84 fm. PARATYPES: AM G6882, AM G12144, HMCS *Thetis*, station 48, 7–8 miles off Wollongong, New South Wales, 56 fm, sand and mud to rock, 18 March 1898; AM G12143, HMCS *Thetis*, station 40, 3 miles off Wata Mooli, New South Wales, 52 m, sand and boulders, 12 March 1898; BM 1933.3.13.115, labelled `Schizoparatype', no further data.

#### Other material

AM E2286, 6 miles S, and 30°E of Brush Island, New South Wales, 65 fm, FIS Endeavour, 14 Feb. 1911; AM E5421, 13 miles south of Gabo Is., Victoria, 65 fm, 25 Aug. 1914; AM E6036, 36 miles south of Mt. Cann, Victoria, 70-100 fm, FIS Endeavour, 19 Oct. 1914; AM G12409, off Merimbula Pt., New South Wales, 70 m, no date; AM G12936, 10 miles north east of Montague Is., New South Wales, 128-146 m, SS Bar-ca-mue, 18 July 1925; AM G15300, 14-16 miles north east of South Head, Port Jackson, New South Wales, approx. 33°44'S, 151°38'E, 137-146 m, FS Goonambie, C.W. Malvey, May 1924; AM G15600, off Broken Bay, New South Wales, 32°52'S, 152°32'E, 144.5 m, FRV Kapala, B. Rudman, P. Coleman, K. Handley, 6 Dec. 1978; QM G4711, off Jumpin Pin, Stradbroke Islands, Queensland, 47 fm, W. Stephenson, 1 July 1961; SAM H842, H834, 57 km south east of Cape Everard, Victoria, 190 m, RV Soela, W. Zeidler, 14 Oct. 1984; RMS 1910.34.57, Australia, no further data, (? possibly a fragment from the type series retained by Thomson).

# Differential characteristics

Sclerite form, in particular the triangular anthopomal scales which have fine tubercles, and no medial ridge and keel structures; polyp body scales generally bilobed; pinna internodes with denticles only on the ridge shoulder, all other internodes without denticles.

# Description

# Colony form (Figure 82)

The labelled holotype is an assemblage of dry plumate fragments, the largest of which is 75 mm in length. Several pieces clearly match portions of Thomson's and Mackinnon's Plate LXXIII. From these, and from the author's colony dimensions of 23 x 17.5cm, it is obvious that the illustration is three quarters of the natural size and not half as stated. It is also apparent that much of the original planar specimen is now missing.

The plumes are finely and densely branched in a pinnate manner. The pinnae are mostly opposite or almost opposite, with zones of alternation irregularly occurring. According to Thomson and Mackinnon, "The stem has a maximum diameter

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Figure 82 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), holotype, natural size.

of 4 mm.; the average diameter of the larger branches is 2 mm, and of the twigs, 1 mm." The thickest remaining principal branch fragment has a diameter of 1.7 mm, while most are 0.5–0.8 mm and the pinnae are about 0.36 mm (all measured without polyps). The longest undivided pinna is 19 mm, but most are <13 mm. Angle of branching is  $40-56^{\circ}$ . The distance between consecutive subdivisions along one side of a principal branch is 1.6–2.0 mm.

#### Polyps (Figure 83B,C,H)

On the pinnae the polyp distribution varies from biserial to three sides, and may be all around on the thickest ones. Many polyps are curved so as to favour one side the of fragment. The polyps are not crowded, commonly with a space of 0.2–0.4 mm between the anthopomal region of one and the base of the next. On the principal branches, the polyps are scattered in an irregularly biserial manner with 1–2 polyps between consecutive pinnae. A number of these polyps are upside down.

Polyps are contracted and adaxially naked. The base of a polyp arises more or less erect from the surface and the head is angled through about 90° so that the anthopomal region faces along the

branch, or is angled slightly down towards it at about 55°. Measured along the branch, most polyps are 0.54–0.66 mm in length. Measured abaxially, a polyp head is about 0.36–0.42 mm across, and the neck and base are about 0.24–0.30 mm thick. Polyps project about 0.30–0.36 m above the surface. Juvenile polyps occur throughout the fragments.

#### Colony colour

The dry coenenchyme is opaque, and a very pale yellowish white (≈4A2). All sclerites are colourless.

#### Axis form (Figure 82E-G)

In short pinnae, the tip internode is 4-sided, with a primary ridge along each of the four edges and a low secondary ridge on each face. The shoulders of the primary ridges have numerous rounded denticles which may be reduced on the distal end of the internode. The more proximal internodes have the secondary ridges developed more or less to the extent of the primary ridges, complete with denticulated shoulders, while still retaining their 4sided nature. In longer pinnae the older internodes lose the 4-sided appearance and have eight primary ridges with denticulated shoulders. In the thinner upper parts of the principal branches, the internodes have multiple primary ridges and,

Figure 83 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), holotype: A-C. Polyps; D. Coenenchyme; E-G. Axial internodes; H. Twig fragment.

usually, low secondary ridges, with reduced shoulder denticulation. Proximally, the principal branch internodes have multiple smooth primary ridges only. A thick principal branch internode 1.4 mm thick has 30 primary ridges. Desmocyte cavities are shallow and indistinct.

The internodes of the principal branches are about 1.4 mm long, and those of the pinnae are 1.26–1.40 mm long. The nodes in the lower, thicker areas of the principal branches are 0.47 mm long. In the thinner more distal parts they are 0.32 mm long, and in the pinnae they are 0.18 mm long.

# Axis branching

Although some principal branch internodes support only one division, it is usual for them to initiate two pinnae, one on each side. The branching style is similar to Figure 251 example 5, with the pinnae commonly opposite or almost opposite rather than staggered. Only in the lower, thicker, parts of the principal branches do the nodes become incorporated into the divisions, as in examples 17, 57, and 58. Here, also, some diverging internodes appear to be inserted into the initiating internodes with a small amount of nodal material involved, as in the two minor twigs in example 18.

# Axis colour

The nodes in the thickest principal branch fragments are translucent and autumn leaf brown ( $\approx$ 6D7) with butter yellow satin-like borders. In the



Figure 84 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 85 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), sclerites: A. Holotype, coenenchyme; B. SAM H834, polyp and coenenchyme; C. AM G12144, paratype, coenenchyme; D. QM G4711, polyp and coenenchyme.

distal, thinner areas the nodes are also translucent, and brownish orange ( $\approx$ 5C5)) with very broad butter yellow satin-like borders. In the pinnae the nodes are more opaque, satin-like, and light yellow ( $\approx$ 4A4) with a very narrow brownish central band. The internodes of the pinnae are colourless and almost transparent. Those of the principal branches are translucent and have a faint brownish tinge. Thomson and Mackinnon stated the axis was tinged with pink.

#### Polyp sclerites (Figures 83A-C,H; 84)

The asymmetrical anthopoma is continuous with the polyp body sclerites. This is easier to observe in rehydrated material that has not been dried for electron microscopy. There are usually 3 scales in each octant, other than the adaxial one (Figure 83A). The proximal scales are crescentic and often bilobed (Figure 84Aj-m), and the distal one is a large triangular shaped sclerite with a tuberculate upper face and usually a thorny apex (Figure 84Aa-e). The triangular scale in the adaxial octant is usually smaller than the others and of simpler design (Figure 84Af). It is preceded by a small anthopomal scale and 1-2 short, narrow, marginal scales. Below this the adaxial sector of the polyp body is naked. Most octants appear to have 2 basal tentacular sclerites of various shapes (Figure 84Agi) that precede a single row of crescentic scales in each tentacle rachis (Figure 84B). The triangular anthopomal scales are up to about 0.12 mm long, and the tentacular sclerites are up to 0.077 mm.

In specimens prepared for SEM, the partial collapse of the enclosed tentacular and oral disc tissue causes the large triangular scales to dominate the appearance of the anthopoma (e.g. Figure 88D, paratype).

The polyp body, apart from the adaxial sector, is covered in large scales with thorny margins (Figure 84C). The scales in the head region are in rows (Figure 83B,C,H) and their free margins, particularly those of the upper-most series, are bilobed. The undersides of the scales have large complex warts (Figure 84Ce,h). The scales of the polyp base are thicker and less thorny than those of the head region. (Figure 84Ci–l). Body scales are mostly <0.22 mm long.

In a polyp preparation a number of small spindles are found, 0.07–0.12 mm long. They are usually asymmetrically developed, having short, irregular shaped spines on one side and being relatively smooth on the other. Some of these spindles occur at the base of the naked adaxial zone where the polyp adjoins the branch surface, and others extend onto the adaxial-lateral margins of the naked zone below the polyp head.

#### Coenenchymal sclerites (Figures 83D; 85A)

The surface of the principal branches and the pinnae contains spindles and small sub-spherical forms developed asymmetrically with flattened, somewhat foliate, tubercles. Most are 0.07–0.15 mm long. In the coenenchyme of the pinnae, the majority of sclerites are very short. A higher proportion of longer spindles occurs in the principal branch surface. Large irregularly shaped forms, like those in Figure 85Ab–f, occur where the polyp adjoins the surface.

There are no stem portions preserved.

#### Variability

From an examination of the paratypes and the additional specimens it is apparent that the branching pattern of the holotype is not typical in certain respects. In the plumate holotype fragments, branchings occur at the rate of about 40 per 40 mm of principal branch. Although some colonies have a slightly higher density, others are as low as 25 pinnae per 40 mm. Most colonies have short pinnae, but in some colonies they are up to 32 mm long. The more sparsely branched colonies tend to have the longer pinnae. The number of



Figure 86 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), paratype, AM G12143, natural size x 0.5.



Figure 87 Pteronisis whiteleggei (Thomson and Mackinnon, 1911), QM G4711, natural size.

branches per internode also varies. In the more densely branched colonies, two divisions per internode is the most common, but, unlike the holotype, the divisions are usually staggered rather than opposite. In the lesser branched colonies the system is quite irregular, with internodes supporting one or two divisions, or often none at all. In all of these colonies where the stem and/or lower main branches are present, the nodal material overgrows or replaces the more basal internodes, and above this it is common for pinnae to arise directly from the side of main branch nodes, which may be up to 1 mm in length. Colony stems are very short with main branches arising at or near the base. Paratype AM G12143 is illustrated in Figure 86.

In three of the specimens, so many short overlapping plumes are present, together with pinnae branching out of plane, that the colonies are quite thick and bushy. The most luxurious of these is that illustrated in Figure 87, from by far the most northerly collection site. The field note states that the specimen was "vermilion red" when alive, and moderately common. The specimen is 83 mm tall, 58 mm across, and 7-15 mm through. Branching begins profusely only 6 mm from the base. Pinnae often diverge at unusual angles, seemingly to avoid each other. In some instances this has failed and branch fusion has occurred. Branch density in the upper regions is 53 pinnae per 40 mm. The polyps are biserially arranged, one row per side, and most are angled towards the convex side of the colony.

In the majority of colonies, polyps are arranged biserially throughout. One row per side in the thinner pinnae and two per side in the thick ones.

Axis architecture is quite consistent, although denticulation may vary slightly within a single colony. In a few instances denticulation on the shoulders of pinna internodes is reduced so that it is not at first obvious. In other pinnae, the internodes may have denticles extending down from the shoulders onto the primary ridges, sometimes occurring along the whole length. In those colonies where the pinnae are consistently short, the pinna internodes may never evolve beyond the 4-sided phase, and secondary ridges may develop poorly.

In only two of the colonies besides the holotype is there a pinkish or brownish tinge to the colour of the stem or major branch internodes. Most are more or less colourless and translucent, or whitish and nearly opaque. Nodal colour is relatively consistent, that in the stems being light brown ( $\approx$ 7D6). The principal branch internodes in one colony are yellow ochre ( $\approx$ 5C7). In virtually all of the alcohol preserved colonies, the stem and thicker principal branches are distinctly banded due to the translucency of the coenenchyme and the underlying dark nodes.

The most consistent identifying features of the spiculation are the triangular anthopomal sclerites, the bilobed scales of the polyp head, and to a lesser extend the unilaterally developed coenenchymal sclerites. However, differences in size and ornamentation are sometimes quite marked. Both AM E6036 and SAM H834, for example, have very large triangular anthopomal sclerites, up to 0.14 mm long and 0.10 mm across the base. Polyp body



Figure 88 Pteronisis whiteleggei (Thomson and Mackinnon, 1911): A-B. AM E6036: (A). Polyp; (B). Coenenchyme. C-E. Paratype, AM G12144: (C-D). Polyp; (E). Twig fragment.

scales of AM E6036 tend to be quite broad, with the marginal thorns ridged or foliaceous (Figure 88A). The coenenchymal spindles are similarly ornamented (Figure 88B). The polyp body scales of SAM H834 also have prominent thorns and may be relatively large (Figure 85Ba,b). The aberrant feature of this specimen is the sclerites of the coenenchyme. They are all long, narrow spindles, up to 0.22 mm, unilaterally developed with thornlike tubercles (Figure 85Bc-f).

The Queensland specimen, QM G4711, also has large spindles in the coenenchyme. The thorn-like processes are thick and complex (Figure 85Dc), however the coenenchyme also contains many short forms as does the holotype. The lower polyp body sclerites may have similarly thick, thorny processes (Figure 85Dd–g), but the scales of the polyp head have margins with very long thorns (Figure 85Da,b).

The paratype AM G12144 also differs from the holotype. The coenenchyme contains very large, stout spindles, up to 0.22 mm, with very low, simple prominences on their outer face (Figures 85C; 88C). The polyp body sclerites are very robust and the bilobed nature of the upper ones is not always pronounced (Figure 88C). A large number of body scales are like Figure 84Cc,d,j–l.

There is no preserved material from the stem of the holotype, but coenenchymal sclerites are present on the stems of several of the comparative specimens. In all cases they are predominantly like the small forms occurring in the upper branches of the holotype with somewhat longer spines and foliaceous processes. The majority are often like Figure 85Aa.

#### Remarks

Lots AM G6913 and AM G12145, each labelled as a "cotype" of *Mopsea whiteleggei* have been identified as *Pteronisis echinaxis* sp. nov.

#### Distribution

See Figure 269. Depth rang 36–190 m.

# Pteronisis provocatoris (Bayer and Stefani, 1987) new comb.

Figures 89–98; 270

- Mopsea provocatoris Bayer and Stefani, 1987a: 61–63, Figure 3a; Plate X, 2; Plates XIII–XIV.
- Mopsea bargibanti Bayer and Stefani, 1987a: 58–59, Figure 2a, b; Plates VIII–X.

Mopsea whiteleggei; Tixier-Durivault, 1970: 333.

#### Material examined

Types

HOLOTYPE: USNM 76475, Récif Mbéré, outer slope, New Caledonia, 22°18'07"S, 166°11'06"E, 35-





# 50 m, G. Bargibant, 23 Jan. 1979. PARATYPE: MNHN OCT.A.1986.21, same data as holotype.

# Other material

USNM 76474, Passe de Mato, New Caledonia, 22°41'S, 166°36'07"E, 40 m, Georges Bargibanti, 10 Dec. 1981, (holotype of *Mopsea bargibanti*); MNHN OCT.A.1986.20, same data, (paratype of *M. bargibanti*); MNHN (fragments identified by Tixier-Durivault as *Mopsea whiteleggei*), Dumbea Pass, New Caledonia, M. Salvat, 1961; NTM C12040-C12043, New Caledonia, 22°33'04"S, 167°16'02"E, 45 m, G. Bargibant, 9 Dec. 1992; NTM C12044-C12046, New Caledonia, 22°30'20"S, 166°26'30"E, 50 m, G. Bargibant, 8 Sept. 1987; NTM C12047, C12048, New Caledonia, 22°33'04"S, 167°16'02"E, 45 m, G. Bargibant, 9 Dec. 1992; NTM C12047, C12048, New Caledonia, 22°33'04"S, 167°16'02"E, 45 m, G. Bargibant, 9 Dec. 1992; NTM C12219, New Caledonia, 22°30'20"S, 166°26'30"E, 40–50 m, G. Bargibant, 12 April 1994.

#### **Differential characteristics**

Sclerite form, in particular the triangular anthopomal scales which have coarse tubercles, and no medial ridge and keel structures; polyp body scales not bilobed, with coarse, thorny or ridge-like projections which are especially robust in the polyp base; most pinna internodes with denticulated ridges; some colonies sparingly branched and not planar.

# Remarks

Amongst the material reported by Bayer and Stefani (1987a) from New Caledonia were 2 specimen lots with the same general sclerite and axial architecture but clearly disparate colonial form. They assigned the planar and closely pinnate specimens to Mopsea provocatoris, and the unusual non-planar distantly pinnate specimens to M. bargibanti. When during the course of this present review, SEM images of the polyps (Figure 93) revealed no overall difference in the anthopomal structure between the 2 holotypes, contact was made with Monsieur Georges Bargibant who collected all of the specimens constituting the 2 type series. Bargibant communicated that he was no longer able to confidently distinguish the species in the field as since 1981 he had found numerous colonies of intergrading growth form occurring in the same habitats. Bargibant kindly sent more material for study (some shown in Figure 94) including 2 originally rose coloured specimens of the distinctly different growth forms attached to the same reef fragment. He added, however, that although the closely pinnate, plumose growth form was generally dominant, this is not the case in areas of strong currents. It is apparent from all the extra material that the distantly pinnate form can also occur growing in one plane, and that there are no consistent

differences in the skeletal elements between any of the specimens. In the descriptions that follow, the anthopomal arrangements in the holotype of *M. provocatoris* are recorded with slightly fewer scales than those of *M. bargibanti*, but this appearance may be due to the difference in preservation. The holotype of *M. provocatoris* is dry and the polyps are tightly contracted, while that of *M. bargibanti* is in alcohol and the anthopomal octants are separated on the majority of polyps. The paratype of *M. provocatoris* from Paris is wet preserved and the anthopomal structure agrees in form with that of *M. bargibanti*.

The new material sent by Bargibant was also accompanied by underwater photographs which showed 2 predominant colour forms; rose and brownish orange. The brownish orange forms only occur closely pinnate and plumose, and Bargibant reported that this colour morph only grows alongside the rose colonies in a few areas. It is predominantly restricted to the more sheltered parts of the lagoon as opposed to the exposed habitats of rose coloured colonies. There appear to be no other differences between these forms, both of which lose their colour when preserved, and indeed there are no distinct differences in polyp structure and both sclerite and axial architecture between any of the specimens examined. Together with Pteronisis laboutei, this assemblage forms an allopatric group, remote and apparently isolated from the other species of the genus which are concentrated in the temperate regions of south eastern Australia, and the different morphologies may be evidence of the process of speciation.

It is quite possible that the application of breeding experiments or the new techniques of the rapidly expanding field of molecular biology may reveal genetically distinct groups amongst this complex. Using traditional characters, however, and the methodology applied to this revision it is not possible to differentiate between preserved twig fragments of any of the specimens on traditional characters. It is therefore proposed to synonymise the 2 species. Because in the dominant growth form the ramification is closely pinnate and plumose, as first reviser, and with regret to Monsieur Bargibant, Pteronisis provocatoris (new combination) is chosen as the valid name for the taxon. The holotypes of both nominal species are described below.

# Description of the holotype of *Pteronisis* provocatoris

#### Colony form (Figure 89)

The dry, planar, and extremely fragile holotype is about 20cm tall and 25.5cm across. The ramification is alternate pinnate, and in several places pinnae from some of the fronds lie across



Figure 90 Pteronisis provocatoris (Bayer and Stefani, 1987), holotype: A-E. Polyps; F. Coenenchyme; G-J. Axial internodes; K. Twig fragment.

those of another. Pinnae only rebranch occasionally. The holdfast is missing, and the main stem, which is 8 mm long and 2.4 mm thick, consists of nodal material and is devoid of coenenchyme on one side. The stem gives off two main branches which are about 2.1 mm thick (polyp not included). About half way along the principal branch of each plume it is 0.95-1.10 mm thick (polyps not included). The pinnae are mostly 1.1-1.3 mm thick (including polyps) and only taper right at the tip. Pinnae branch consistently at 50-60°, and the longest undivided branch is 55 mm, with most being >20 mm. The distance between consecutive points of branching on one side of a plume is about 0.9-4.7 mm, with most being 2.7-3.6 mm apart.

#### *Polyps* (Figure 90C–E,K)

On the pinnae, the polyps are distributed all around, except in some terminal regions where they are biserial. They are densely arranged but not crowded. On the principal branches they are sparse and scattered. The polyps are contracted, adaxially reduced, and curved upwards and over so that the anthopomal region usually faces down towards the branch at about 40-50°, and occasionally lies against the base of a succeeding polyp. Measured along the branch, polyps are mostly 0.72-0.87 mm long, and project about 0.33 mm. Abaxially, the bases and the heads are about 0.42 mm across, and the necks 0.31 mm. Juvenile polyps occur throughout the colony, and a number of polyps on the principal branches are upsidedown.

#### Colony colour

The dry coenenchyme is white and opaque. The original description gives the live colony colour as rose or rose orange.

# Axis form (Figure 90G–J)

There is little of the axis visible. The internodes in the terminal regions of the pinnae are more or less square in section with four primary ridges. Only the shoulders of the ridges have rounded denticles in the thinnest internodes, while denticles occur over the length of the ridges in the thicker ones. Proximal to these, the internodes develop more faces and also a low smooth secondary ridge on each face. On still older internodes, denticles occur also on the ends of the secondary ridges. Secondary ridges develop as primary ridges in more basal internodes. Internodes of the main branches have multiple primary ridges that are smooth, and no secondary ridges. Desmocyte cavities are mostly shallow and occur between the primary and secondary ridges. A main branch internode 1.7 mm thick has about 26 primary ridges, and the internodes in a pinna 0.6 mm thick

may have eight primary and eight secondary ridges.

Main branch internodes are 0.29–0.79 mm long, most around 0.79 mm, and those of the pinna and upper parts of the principal branches are 0.47–1.26 mm long, mostly 1.26 mm. Nodes in the main branches are about 1 mm long, and those in the pinna and upper parts of the principal branches are about 0.25 mm long.

# Axis branching

Divisions similar to Figure 251 example 48, are visible on a main branch, but it seems like a small lateral internode has been overgrown by nodal material at each point of juncture. Pinnae diverge from principal branches as in examples 9, 13, 14, and 6, the latter with short to medium stubs. Internodes only branch once.

#### Axis colour

Main stem internodes are greyish red ( $\approx$ 9C5) and translucent. Translucency increases distally. Those of the upper parts of the principal branches and the proximal parts of the pinnae are a paler greyish red ( $\approx$ 9B4), and in the terminal regions they are a very pale pink and are more or less transparent. The nodal material of the main stem is dark brown ( $\approx$ 6F6) and opaque. The main branch nodes are the same colour, with paler translucent ends. The nodes in the pinnae are satin-like, opaque, pale yellow to almost white, with a narrow dark brown central band and narrow satin-like borders.

#### Polyp sclerites (Figures 90A-E; 91)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. Most anthopomal octants have a more or less triangular sclerite at their apex which is preceded by 2 or 3 crescentic scales (Figure 90A,B). In all of the polyps examined, the abaxial and abaxial-lateral octants each contained 3 crescentic scales, and there was 2 crescents in each of the laterals. The adaxial-laterals also usually contain 2 crescents before the triangular scale, but in one polyp one of these octants contained only a large triangular sclerite. In this polyp, the adaxial octant also contained only a large triangular sclerite, while in other polyps this sector contained a much smaller triangular scale preceded by 1 or 2 small crescents. In most octants the triangular scale is ornamented on the upper face and lateral margins with spines and multipointed tooth-like projections (Figure 91Aac), and on the underside with small compound warts (Figure 91Ad). The adaxial triangular scale may be similarly designed or have simple tubercles (Figure 91Ae). Most anthopomal crescents also have tooth-like projections (Figure 91Af-h). Where 2 crescents occur in an octant, the distal one is often more triangular (Figure 91Af). The crescents



Figure 91 Pteronisis provocatoris (Bayer and Stefani, 1987), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 92 Pteronisis provocatoris (Bayer and Stefani, 1987), holotype, sclerites: Coenenchyme.

in the adaxial and adaxial-lateral octants have simpler tubercles and are relatively broad. There is a single basal tentacular sclerite, which may be simple (Figure 91Bc) or quite spiny, and a single row of granular tentacle scales (Figure 91Ba–b) in the rachis of each tentacle. The larger anthopomal triangular sclerites are mostly about 0.09–0.11 mm long, and the tentacular scales are 0.025–0.045 mm across. The polyp body is covered in large oval to crescentic scales (Figure 91C) that are arranged in 7 rows on the polyp head (Figures 90C–E,K). Most of the adaxial side of the polyp body is naked. This naked area attenuates laterally and continues collar-like into the abaxial lateral zones. Immediately below the adaxial anthopomal octant is a large fusiform scale (Figure 91Cc). Below this, 2 sclerites touch or cross. These may be fusiform



Figure 93 A. Pteronisis provocatoris (Bayer and Stefani, 1987), holotype, polyp; B. Mopsea bargibanti Bayer & Stefani, 1987, holotype, polyp.

scales that extend one each side towards the adaxial-lateral zones, the lateral arms of larger adaxial-lateral scales, or a combination. The other body scales have tooth-like projections, often ridged and multipointed, on the distal margin and the exposed face. In the upper part of the polyp body the projections are sharp and relatively narrow. In the lower part of the body they are far larger and stouter, and often close together covering the whole of the exposed face of the scale. The underside of the scales has large compound warts (Figure 91Ca–b). Most body scales are 0.12–0.16 mm long with very few over 0.18 mm.

# Coenenchymal sclerites (Figures 90F; 92)

The surface of the branches contains the same style of sclerite that is found in most members of this genus. These are predominantly spindles and oval sclerites that are unilaterally developed with tooth-like projections. In the surface of the pinnae the majority of these sclerites are narrow and spindle-like. Most are 0.08–0.16 mm in length, occasionally up to 0.20 mm. In the surface of the principal branches there are both unilaterally developed spindles and oval forms with a size range the same as that of the pinna sclerites. The surface of the lower stem contains predominantly the oval forms, 0.08–0.13 with the occasional warty spindle as in Figure 92a, or irregular shaped sclerite as in Figure 92b, up to about 0.18 mm. A few small warty spindles and ovals without toothlike projections can be found amongst the coenenchymal sclerites in most samples.

# Description of the holotype of Mopsea bargibanti

# Colony form (Figure 95)

The slightly damaged holotype has a three dimensional growth form, and is about 100 mm tall, 115 mm across, and 60 mm through. The ramification is extremely unusual. Parts of the colony appear to be based on an irregularly pinnate pattern, but the main branches diverge in numerous directions. The colony may be considered to have a back and a front with regard to the direction of branching. Some branches



Figure 94 Pteronisis provocatoris (Bayer and Stefani, 1987): A. NTM C12042; B. NTM C12044; C. NTM C12041; D. NTM C12219. All natural size x 0.5.

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Figure 95 Mopsea bargibanti Bayer and Stefani, 1987, holotype, natural size.

diverge laterally from the main stem in a planar fashion, while all of the others extend away from the plane on one side only.

There is small calcareous holdfast which is about 6.3 m across its largest diameter. The main stem is about 1.3 mm thick, devoid of coenenchyme, and consists of nodal material that has overgrown all of the internodes. The main branches are about 1.9 mm thick, and most of the more or less pinnately arranged twigs are about 1.4-1.6 mm thick (including polyps). The pinnae gradually taper and the axis is bare along most of the damaged tips. At the top of the stem the main branches diverge at angles of 50-73°, one at 28°. Throughout the rest of the colony, branching angles are mostly 70-90°, while one pinna recurves at 112°. In the more pinnately ramified areas, taking pinnae on both sides of a branch, the distance between consecutive branches is mostly 4.0-8.0 mm, commonly around 4.7 mm. Undivided branches are up to 55 mm long.

#### Polyps (Figure 96B,D,H)

Distribution is dense and all around. The polyps are contracted, adaxially reduced, and curved upwards and over so that the anthopomal region usually faces down towards the branch at about 20–50°, occasionally against the base of a succeeding polyp. Measured along the branch, polyps are mostly 0.66–0.78 mm long, and project about 0.36 mm. Abaxially, the bases and the heads are about 0.48 mm across, and the necks 0.36 mm. Many polyps are upside-down, and juvenile polyps are common throughout the colony.

#### Colony colour

Pale greyish white with opaque coenenchyme.

#### Axis form (Figure 96E–G)

The internodes in the distal regions of the branches are more or less square in section, with four primary ridges. The ridges may have rounded denticles just in the vicinity of the shoulders or distributed all along their length. Proximal to these, internodes have low secondary ridges on each face. In the younger of these internodes the secondary ridges are smooth, becoming more denticulated in the older parts. In the thicker branches these secondary ridges develop shoulders and become primary ridges. In the main branches the internodes have multiple primary ridges, and the denticles are reduced to granules. A main branch internode 1.50 mm thick has about 20 primary ridges and a branch internode 0.86 mm thick has 12. A thinner internode 0.70 mm thick may have


Figure 96 Mopsea bargibanti Bayer and Stefani, 1987, holotype: A-B, D. Polyps; C. Coenenchyme; E-G. Axial internodes; H. Twig fragment.



Figure 97 Mopsea bargibanti Bayer and Stefani, 1987, holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 98 Mopsea bargibanti Bayer and Stefani, 1987, holotype, sclerites: A. Twig coenenchyme; B. Upper stem / main branch coenenchyme.

five primary and five secondary ridges, and one 0.56 mm thick may have four primaries and four secondaries. The desmocyte cavities are mostly shallow and are arranged between the primary and secondary ridges.

Internodes on the main branches can be as short as 0.30 mm, but are mostly about 0.79 mm. In the pinnae internodal length is variable, mostly 0.6–2.7 mm. Main branch nodes are 0.3–0.8 mm in length, and those of the pinnae are 0.16 mm long.

#### Axis branching

Most points of division are not visible. Modes of branching include Figure 251 examples 13, 14 and 6, the latter with medium to short stumps, and also example 51. Internodes only branch once.

### Axis colour

The holdfast is pastel red (≈8A4). The main branch internodes are greyish red (≈9C4), and translucent. Translucency increases distally. The proximal internodes of the pinnae have a very faint pinkish hue, and those in the terminal regions are colourless and transparent. The nodal material of the main stem is brown (≈6E7) and translucent enough to just detect the overgrown internodes. In the main branches the nodes have very dark brown, opaque centres with narrow translucent brown ends, and yellowish brown satin-like borders. In the pinnae, the nodes have narrow, dark brown central bands with broader, opaque ends that are satin-like and either light yellow (~4A4) or almost white. The borders are virtually colourless with a satin-like sheen.

# Polyp sclerites (Figures 96A, B, D; 97)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. A single more or less triangular sclerite occurs at the apex of each octant and is preceded by a series of crescentic scales (Figure 96A). It is difficult to tell where body scales merge into those of the anthopoma. There appear to be 4 crescentic scales in the abaxial, abaxiallateral, and lateral octants, 3 in the adaxial-laterals, and 2 in the adaxial sector. The triangular scales in all octants are ornamented with ridged, multipointed, tooth-like projections (Figure 97Aad). The 2 crescentic scales of the adaxial octant tend to have simpler tubercles (Figure 97Ag), but in all other octants they are ornamented similar to the triangular forms (Figure 97Ae-g). There is a single basal tentacular sclerite, which is commonly spiny (Figure 97Ah), preceding a single row of granular scales (Figure 97B) in each tentacle rachis. The largest triangular scale occurs in the abaxial octant of each polyp and is usually about 0.098 mm in length. The small tentacular rachis scales are mostly 0.028-0.049 mm long.

The polyp body is covered in large oval to

crescentic scales that are arranged in 7 rows on the polyp head (Figure 96B,D). Immediately below the adaxial anthopomal octant 4 sclerites cross. There are two short, narrow scales that extend one to each side towards the adaxial-lateral zones, and below them lie the extended lateral processes of 2 large adaxial-lateral scales. The rest of the adaxial side of the polyp body is naked. This naked area attenuates laterally and continues collar-like into the abaxial lateral zones. Large ridged and multipointed tooth-like projections occur along the distal margin of the scales and on the exposed face (Figure 97C). The projections are often laterally flattened, like thick leaves, and extend from the margin down onto the face of the scale. In the upper part of the polyp the tooth-like projections on the scales are relatively narrow and separate. Towards the polyp base they are larger, much thicker and closer together, and often cover the whole of the exposed face of the scale. The underside of the scales has large compound warts (Figure 97Ca,b). The largest of the body scales is usually about 0.2 mm in length, although a few may be longer.

### Coenenchymal sclerites (Figures 96C; 98)

The surface of the finer branches and twigs contains spindles or spindle-derivatives. Nearly all are unilaterally developed with tooth-like and thorn-like projections which can be densely arranged (Figure 96C). Most sclerites are <0.19 mm in length, but a few are longer (Figure 98A).

There is no tissue on the lower part of the stem. Figure 98B shows sclerites from the upper part of the stem just beyond the first 2 branches. Although the sclerites in this area are similar to those in the surface of the finer branches, most are far stouter. The majority are ornamented with spiny tooth-like projections. Amongst them are a few multiradiate forms and short girdled spindles with spiny warts. The lengths of the sclerites are similar to those on the thinner branches.

### Distribution

See Figure 270. Depth range 35-50 m.

# Pteronisis plumacea (Briggs, 1915) new comb. Figures 99–102; 271

Mopsea plumacea (part) Briggs, 1915: 76–77, Plate IV, Figure 1; Plate VII.

### Material Examined

### Types

HOLOTYPE: AM E1062, South Australian Coast, FIS *Endeavour*, no further data. PARATYPES (mixed with holotype fragments): AM G15587, data as for holotype.



Figure 99 Pteronisis plumacea (Briggs, 1915), type series: A. Portion of holotype. All natural size.

## Other material

AM G11812, AM G11851, 15 miles south of St. Francis Is., Nuyts Archipelago, South Australia, 30 fm, FIS *Endeavour*, no date; AM G12111, 58 miles south, 36 miles west of Cape Wickham, King Is., Tasmania, 132–146 m, FIS *Endeavour*, Feb. 1911?; AM G15295 (numerous fragmented colonies), 20 miles south of Tasman Head, Tasmania, 80 fm, FIS *Endeavour*, 21 March 1914; AM G15303 (numerous fragmented colonies), east north east of Maria Is., Tasmania, 57–75 fm, FIS *Endeavour*, 24 March 1914; AM G15311, off Storm Bay, Tasmania, 17 July 1909; SAM H805 (2 colonies), Bathurst Channel, southern point of Sarah Island, rock slope, Port Davey, Tasmania, 5–12 m, K. Gowlett-Holmes, 3 April 1993; SAM H825 (3 colonies), 12 km off Cape Northumberland, South Australia, 62 m, S.A. Shepherd, 6 May 1975; SAM H360, off Maria Is., Tasmania, 42°40'S, 148°27'30"E, 122 m, BANZARE Station 113, 23 March 1931; SAM H308, off Mawson Coast, Antarctica, 66°45'S, 62°03'E, 219 m, BANZARE Station 107, 16 Feb. 1931; SAM H313, off north east Tasmania, 41°03'S, 148°42'E, 128 m, BANZARE Station 115, 24 March 1931; SAM H835, 25 km west of Mutton Bird Is., Tasmania, 43°25'S, 145°40'E, 160 m, RV *Soela*, Station 60, W. Zeidler, 21 Oct. 1984.

The following specimens, housed at the NMV, are from the Victorian Institute of Marine Science's Bass Strait Survey, and are recorded in the format

'station n°/lot n°': 187/5, Bass Strait, 38°32.0'S, 142°28.6'E, 52 m, 20 Nov. 1981; 190/5, Bass Strait, 38°49'S, 142°35.4'E, 89 m, RV *Tangaroa*, 21 Nov. 1981; 191/3, 4 colonies, Bass Strait, 39°6.3'S, 142°55.6E, 84 m, RV *Tangaroa*, 21 Nov. 1981.

### **Differential characteristics**

Sclerite form, in particular the triangular anthopomal scales which have a medial ridge and keel structure; polyp body sclerites generally bilobed; most pinna internodes with denticulated ridges.

## Remarks

Lot E1062 from the Australian Museum was in two parts. The larger contained the twig-free stems and main branches of at least 3 colonies together with a large mass of fragmented twigs, and labels 'E1062' on paper and lead strip. The other portion of the lot contained smaller amounts of broken material and the label "Mopsea plumacea sp. nov. Type and Co-Type E1062". By carefully matching branch fractures and referring to Briggs' Plate VII, it has been possible to assemble six pieces of the illustrated holotype from this portion. The two remaining thick stem and branch fragments are part of a second colony whose twigs are inseparably mixed with those of the holotype.

Briggs' descriptive text indicated a number of colonies were on hand, and so all of the conspecific material from lot E1062 is treated here as the type series. Some of the fragments represent another species, *Pteronisis incerta* sp. nov. described herein. Other specimens of *P. plumacea* species also collected by the *Endeavour* are included as additional material only.

Because the type series is so fragmented and mixed, some of the descriptive account is general and not specific to the holotype, little of which has been separated. The holotype fragments retain the registration number AM E1062, while the other conspecific fragments from that specimen lot have been registered as AM G15587.

# Description

## Colony form (Figure 99)

Briggs' caption to his Plate VII states that it is a "photograph of the type, 22.5cm. in height". If the holdfast was not included in this measurement, the illustration is actually only about three quarters of natural size. The assembled portion in Figure 99A lacks the upper plumate branches and most of the twigs. The original colony was planar and pinnately branched in an irregularly alternating manner. The holdfast is spatulate, about 12 mm across and 15 mm long, and bears the short stubs from two other stems. The colony stem is 43 mm long and about 2 mm thick. Most of the

coenenchyme is missing and the axis consists predominantly of nodal material with narrow, overgrown, or partially formed internodes. The two main branches are 1.7 mm and 1.9 mm thick, proximally.

Amongst the rest of the type series material are fragments of at least 5 colonies. Most of the coenenchyme is missing from the main branch and stem portions, which appear to have broken off just above the holdfast. The stubs of the broken pinnae show that the plumate growth form began very close to the base of each colony. Stem thickness varies from 2.2-3.0 mm (without coenenchyme, which is usually about 0.12 mm thick). Pinnae that arise directly from thick main branches, or the upper sections of stems, are about 0.30-42 mm thick (without polyps). Those of the upper plumate areas are mostly about 0.30 mm. Taking both sides of plumes into account, the distance between consecutive subdivisions is mostly 1.0–1.2 mm. Many of the pinnae are broken, but the remainder are commonly about 24 mm long, the longest being around 32 mm. Angle of branching is mostly 41°.

## Polyps (Figure 100C,H)

Within the type series fragments, polyps are densely distributed all around on the pinnae. On the principal branches they are arranged biserially between the pinnae. On the lower, thicker areas of the branches there may be no polyps. Just above this, the few that occur tend to be irregularly scattered. In the upper parts of the plumes, the polyps on the principal branches are arranged biserially, a single row of up to 6 on each side between the bases of the pinnae. Remarkably, the polyps in these rows are arranged in increasing size, with the most proximal being the smallest. This arrangement is consistent over long lengths of branch giving the impression that the polyps maintain this size ratio for a very long time, and the smaller individuals may never develop to the large size. One branch 1.4 mm thick still retains such different sized polyps. Polyps are also arranged in ascending sizes on the proximal parts of the pinnae.

The polyps are contracted, adaxially reduced, and curve upwards and over so that most lie along the surface, and the anthopoma faces along the branch. In some instances the polyp bases are more erect and the adaxial side of the polyp head is raised above the branch surface. Measured along the branch, most of the larger polyps are 0.57–0.66 mm long. Measured abaxially, the heads are about 0.42 mm across, the bases 0.36 mm, and the neck zone slightly narrower at about 0.30 mm.

A number of fragments have numerous polyps containing several cream coloured, irregularly ovoid bodies of different sizes, which could be eggs



Figure 100 Pteronisis plumacea (Briggs, 1915). A-H. Holotype: (A-C). Polyps; (D-F). Axial internodes; (G). Coenenchyme; (H). Twig fragment. I-M. SAM H825 (part): (I, K-L). Polyps; (J). Coenenchyme; (M). Twig fragment.

or spermaries. One polyp had three such bodies, 0.17 mm, 0.24 mm and 0.33 mm long respectively. Other fragments bear numerous extraordinarily large polyps, about 0.7 mm long, each containing a single, yellowish, globoid body, probably a developing planula, about 0.4 mm in diameter. On some fragments nearly every polyp contains a planula, resulting in thick twigs where the polyps are closely oppressed.

### Colony colour

In all of the type material the coenenchyme is pale yellowish white and transparent, allowing the underlying nodes to show through. All sclerites are colourless.

### Axis form (Figure 100D–F)

The internodes in the pinnae are 4-sided with a denticulated primary ridge along each edge. In some instances, thicker, more proximal internodes may develop a low, wide, secondary ridge on each face which may have denticles. The internodes in the upper regions of the principal branches have multiple primary ridges, and a low, wide, secondary ridge in each valley. The younger ones of these may have denticles along the whole length of the primary ridges, but the older ones have the denticles restricted to the shoulder regions only. In the still older regions, the primary ridges are smooth and the secondary ridges are absent or extremely reduced. A principal branch internode 0.54 mm thick has nine primary ridges and eight secondaries. A stem internode 2.1 mm thick has 36 primary ridges. The desmocyte cavities are very distinct and arranged between the ridges.

In the thicker principal branches, the internodes are mostly 0.47–0.79 mm long. In the younger plumes, the principal branch internodes are 0.63–0.79, and those of the pinnae are 0.63–0.95 mm long. Thick branch nodes are 0.32–0.47 mm long, younger branch nodes are about 0.16 mm in length, and those of the pinnae about 0.12 mm.

### Axis branching

Specimens are profusely branched. In most colonies it appears that nearly each major branch internode, or, in the more basal regions, every node, bears one twig, and successive ones branch to alternate sides. Occasionally an internode bears two twigs, and in this case the following internode is commonly unbranched. Stem and main branch unions are usually complex, as in Figure 251 examples 20, 30 and 31. The pinnae commonly originate from the nodes of these thick ramifications, with the most proximal internode of a pinna more or less countersunk into the nodal material of the branch. In the higher plumate regions, the pinnae may also originate from a node, as in example 17, but more commonly they arise

from the mid or distal part of an internode, as in examples 29, 32 and 34.

### Axis colour

In general, stem and principal branch internodes are nearly white and more or less opaque, becoming more translucent in the distal regions. Pinna internodes may be translucent like milky glass, or white as in the principal branches. The nodal material in the stem of both the holotype and one of the paratypes is slightly translucent and light brown ( $\approx$ 6D5). The other stems have brownish orange nodes ( $\approx$ 5C4). The borders are very narrow, satin-like, and yellowish. The nodes in the principal branches of most colonies are brownish orange ( $\approx$ 5C4–5C5) with narrow, silvery, satin-like borders. In the pinnae the nodes are mostly satinlike, very pale whitish yellow or silvery, and sometimes with a very translucent central band.

### Polyp sclerites (Figures 100A–C; 101A,B; 102)

The anthopoma is asymmetrical and weakly continuous with the polyp body scales through a small, bilobed, marginal body scale below each octant whose flared margin slightly overreaches the anthopoma. This scale is sometimes preserved tilted towards the anthopoma to variable degrees. All octants other than adaxial are occupied by a single, large, more or less triangular sclerite whose shape suggests it could have evolved from the fusion of 2 smaller scales (Figure 100A,B). This sclerite in its most developed form has a broad flat ramp-like base, a narrow waist, and a distal half which has a serrate margin and is angled downwards (Figure 101Aa). The lateral edges of the base of the scale become ridge-like in the vicinity of the waist and converge medially to form a spiny keel-like structure on the upper surface. The sclerites in the adaxial-lateral octants are less developed (Figure 101Ab,d). In the adaxial octant, a similar but smaller sclerite (Figure 101Af) may occur alone, or a much smaller sclerite may be present (Figure 101Ai) preceded by a rectangular or crescentic scale (Figure 101Aj). A small basal tentacular scale, arrowhead-like (Figure 101Ag,h), is present in each octant and is often preserved extending vertically downwards in the centre of the anthopoma. The undersides of the triangular anthopomal sclerites usually have a few complex tubercles (Figure 101Ac,e). and the larger sclerites may be up to 0.15 mm long. The curved tentacular sclerites (Figure 101B) are up to about 0.065 mm. These have scalloped margins, and occur in a single row in each tentacle rachis.

Seven rows of body sclerites are clearly distinguishable in all but the basal portion of a polyp (Figure 100C). The abaxial rows are longest and the adaxial-laterals are the shortest. At the base of a polyp, each adaxial-lateral area has a group of



Figure 101 Pteronisis plumacea (Briggs, 1915), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Twig coenenchyme; D. Main branch coenenchyme.





3–4 warty spindles, up to about 0.23 mm long, that curve around the polyp and down towards the branch. Their tips converge in the adaxial mid-line where the base of the polyp meets the branch. Above them, the adaxial side of the polyp is naked except for a narrow scale (Figure 102e) below the adaxial anthopomal octant.

Most polyp body scales have a serrate, sometimes thorny, free margin, with a medial cleft that divides it into two lobes (Figure 102). In the basal area of the body the scales are more irregularly shaped. The few scales in the adaxial lateral rows are more elongate (Figure 102b–d) with a non-serrate lobe which may extend onto the naked area of the body. The body scales have a relatively smooth outer face, large complex warts on the underside, and the largest are commonly about 0.17–0.18 mm in length.

# Coenenchymal sclerites (Figures 100G; 101C,D)

The sclerites in the surface of the pinnae are mainly short spindles, asymmetrically developed with spines or leaf-like processes (Figure 101Ca-f). Most are <0.12 mm, but they may be larger. Amongst them a few multiradiates, and simple spindles or rods may occur (Figure 101Cj-m). Larger curved forms (Figure 101Cg-i) occur in the vicinity of polyp bases.

The surface of the principal branches contains short warty spindles, multiradiates and capstans (Figure 101Df-k), and some asymmetrically developed sclerites which are sometimes globular (Figure 101Da-g). Most are <0.12 mm.

# Variability

The other material reveals some degree of variability in several characters. The occurrence of polyps of increasing size at the proximal ends of pinnae and on the principal branches between the pinnae seems restricted to colonies with relatively dense polyp distribution and branching pattern. The distance between consecutive pinnae in some specimens is as high as 4 mm, and polyps may be up to 0.5 mm apart. In some colonies, polyps may be very close together but distributed biserially in two rows. One incomplete specimen, AM G11812, is very luxurious, and the polyps are so crowded that the pinnae are 1.6 mm thick. In this colony, the principal branch internodes are very short, 0.32-0.47 mm. Correspondingly, the distance between consecutive pinnae is also short, about 0.50-0.80 mm, and pinnae lean alternatively towards the back or front of the plume to avoid congestion. In another colony, similar branch density is achieved with longer internodes by having many of them bear two branches. Pinna internodes can be up to 1.6 mm long in sparsely branched colonies. Pinna internodes in nearly all colonies are 4-sided, but one colony has the distal internodes of some pinna

5-sided and the proximal ones with 7–9 sides. Unlike the type series, very few colonies have white internodes. Most are colourless and very translucent to transparent, and in two specimen lots the main branch internodes are pale pink. Axis branching as in Figure 251 example 38 is common.

Underwater photographs by Karen Gowlett-Holmes of the specimens in lot SAM H805 show that the live colony colour was greyish orange in the lower half fading to cream in the upper regions.

The general sclerite form is the same in all colonies examined. The sclerites of SAM H825 average slightly larger than those of the holotype and are somewhat more ornate (Figure 100I–M). The spines on the upper keel of the anthopomal sclerites are more pronounced, sometimes extending along the distal portion of the scale. The exposed margins of the polyp body scales tend to be more finely serrate, and there is a greater proportion of longer asymmetrically developed spindles in the surface of the pinnae and branches.

The colonies of the type series have no remaining basal stem tissue. Samples from other colonies indicate this area contains a thick subsurface layer of sclerites similar to Figure 101Df–k but with very spiny warts, and an upper layer of spiny and leafy spheroids. Most sclerites are 0.08–0.12 mm.

# Distribution

See Figure 271. Depth range 50–160 m, one enigmatic record from the Antarctic for 219 m.

# Pteronisis laboutei (Bayer and Stefani, 1987) new comb.

Figures 103–106; 272

Mopsea laboutei Bayer and Stefani, 1987a: 64–65, Figure 3b; Plates. XV–XVI; Plate XVII, 2.

### Material examined

#### Types

HOLOTYPE: USNM 76476, Récif de Koumac, New Caledonia, 20°34'S, 164°05'E, 60 m, G. Bargibant, 3 Nov. 1980.

# **Differential characteristics**

Sclerite form, in particular the triangular anthopomal scales with fine tubercles, and no medial ridge and keel structures; polyp body sclerites irregularly shaped; internodes narrow and without primary ridges; all internodes smooth except for the distal few in the pinnae which have knobby ends.

# Description

## Colony form (Figure 103)

The holotype is a fragile planar colony, 63 mm



Figure 103 Pteronisis laboutei (Bayer and Stefani, 1987), holotype, natural size.

across and 50 mm high, branched in an alternating pinnate manner. There is a small calcareous holdfast. The main stem, 0.95 mm thick is devoid of coenenchyme. It gives off a branch 7 mm above the base, of which only a node remains. The first intact branch is about 9 mm from the base, and the first major branch, 0.7 mm thick (without polyps) is 4 mm above this. Most pinnae are about 0.27 mm thick proximally, and about 0.13 mm near the tip (without polyps). Taking into account divisions on both sides of a branch, the distance between consecutive branching is mostly 1.4–2.3 mm, but up to 9.0 mm in two instances. Branching is consistently around 65°. A number of pinnae are over 12 mm long, the longest being 22 mm.

### Polyps (Figure 104D,E,I)

For species of this genus, the polyps are relatively widely spaced. They are arranged on the pinnae in a predominantly alternating biserial manner, but it is not regular. Polyps occasionally encroach onto the other faces of the branches, and polyps often occur opposite each other. There are about 30 polyps on a 5 mm section of pinna. Juvenile polyps are extremely common throughout the colony and add to the appearance of irregularity. On the main branches the polyps are not evenly distributed and tend to occur all around, often widely spaced.

Polyps are contracted, adaxially reduced and curved to face along the branch. Polyp bases arise erect, and the heads are bent through 90° so that the adaxial side lies against, or just above, the branch surface. The anthopomal region is more or less at right angles to the branch. Measured along the branch, polyps are about 0.51–0.57 mm in length, and their bases are 0.24–0.36 mm long. Measured abaxially, most polyps are about 0.24 mm across the base, with a slightly narrower neck zone, and about 0.30 mm across the head. The tallest polyps project 0.40 mm above the branch. There are several large, deformed, almost spherical polyps, about 0.54 mm in diameter, that each appear to contain a single egg or developing planula. Polyps growing upside down are very common.

# Colony colour

The colony is almost white. The coenenchyme is very thin and translucent, especially on the pinnae where it seems only the grainy effect of the sclerites prevent it from being totally transparent. The live colour is reported as light brown (cream).

### Axis form (Figure 104G,H)

The internodes of the main stem and main branches are more or less circular in cross-section, with multiple, very low, primary ridges. There are no secondary ridges. The internodes of the pinnae are square in section. Those more terminally situated have small knob-like processes on the shoulders (Figure 104G), while the proximal ones are smooth as figured by Bayer and Stefani (1987a: Plate XVII, 2e). A main stem internode 0.9 mm wide has about 10 ridges. The desmocyte cavities are shallow.

Internodes are mostly 1.1–1.9 mm long throughout the colony. Nodes are about 0.60 mm long near the base of the colony, becoming shorter distally. In the thicker, mid-colony branches they are about 0.30 mm long, and in the pinnae, 0.15 mm in length.

### Axis branching

Branching nodes as illustrated by Figure 251 examples 6 and 29, are the most common, with instances of example 14 occasionally encountered. Branching internodes have only one point of division.

### Axis colour

The internodes of the stem and main branches are translucent, the basal ones optically quite dense and a very faint pink colour. The other internodes are greyish white, becoming colourless and virtually transparent in the terminal regions.

The main stem nodes are light brown (≈6D8), translucent, with very narrow yellowish satin-like borders. The nodes become more yellowish distally with a central clear band and wide satin-like borders that have a bluish sheen. In most pinnae, the nodes consist of two wide, opaque bands, almost white, sandwiching a narrow, clear, greyish zone. The borders are satin-like with a bluish sheen.

#### Polyp sclerites (Figures 104A–E,I; 105)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. There are usually 2 sclerites in all octants, apart from the adaxial one



Figure 104 Pteronisis laboutei (Bayer and Stefani, 1987), holotype: A-E. Polyps; F. Coenenchyme; G-H. Axial internodes; I. Twig fragment.

(Figure 104A-C), the largest of which is the more or less triangular apical scale (Figure 105Aa-c) that dominates each sector. The proximal sclerite is crescentic in shape (Figure 105Af,g). In some polyps, some of the lateral and more abaxial octants may have 2 crescentic scales preceding the apical triangular sclerite, and some adaxial-lateral octants may contain only a large triangular scale (Figure 105Ad) and no crescents. The adaxial octant is quite variable. In some polyps it has a single large triangular scale (Figure 105Ae), while in others it may have 2 small triangular scales, or a single small triangle and a crescent or an intermediate form (Figure 105Ah,i). There is a single basal tentacular sclerite (Figure 105Bc) preceding a single row of markedly curved scales

(Figure 105Ba,b) in each tentacle rachis. The triangular anthopomal sclerites are mostly 0.07–0.09 mm long, and occasionally up to about 0.11 mm. They are ornamented on their upper face and lateral margins with small spines and tooth-like projections; those from adaxial octants having fewer and smaller tubercles. The tentacular scales are strongly curved, with a tuberculate distal margin, and up to 0.07 mm long.

The polyp body is covered in tuberculate scales, some of which have an irregular outline that is not typical of the genus. The scales are arranged in 7 short rows on the polyp head. The adaxial side of the polyp is naked except for 1–2 very narrow flattened spindles, almost smooth, that occur immediately below the adaxial octant, and which



Figure 105 Pteronisis laboutei (Bayer and Stefani, 1987), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.





meet or are crossed by the ends of the lateral arms of several large adaxial-lateral scales. In Figure 104C, a single adaxial-lateral scale extends into and dominates the area below the adaxial octant, but this is possibly an artefact induced during preparation of the specimen. The majority of body scales have small spine-like tubercles on their outer face and short tooth-like projections along the distal margin (Figure 105C). In some scales, particularly those from the lower body area, tuberculate processes make the distal margin difficult to differentiate from the lower one. Most polyp body scales are about 0.10–0.18 mm long. The underside of a scale has a few large compound warts (Figure 105Ca–b).

### Coenenchymal sclerites (Figures 104F; 106)

The surface of the pinnae and principal branches contains spindles and flattened forms, somewhat scale-like, that have an irregular outline and are sometimes branched. The sclerites are unilaterally developed with small tooth-like projections (Figure 106). Under the light microscope it is often difficult to appreciate the tooth like nature of the ornamentation on many of the sclerites because their flattened form prevents them from lying on their edge. The sclerites are mostly about 0.08–0.14 mm long, occasionally up to 0.16 mm.

Stem tissue only remains on the upper part. It contains small spindles unilaterally developed with tooth-like projections. The large ones may be arched and many have root-like legs on their lower side. Most are 0.06–0.11 mm long.

# Distribution

See Figure 272. Depth 60 m.

## Pteronisis incerta sp. nov. Figures 107–114; 273

Mopsea encrinula; Wright and Studer, 1889: 43–44, Plate VII, 1, 1a, 1b; Plate IX, 11; (part) Briggs, 1915: 71; Kükenthal, 1919: 620–621, Plate XLVI, 86-87; Figures 281-283; Kükenthal, 1924: 438, Figure 207; Utinomi, 1972: 15-16.

Mopsea plumacea; (part) Briggs, 1915: 76–77, Plate IV, Figure 1; Plate VII.

Mopsea whiteleggei; Bayer and Stefani, 1987a: 59–61, Plates. XI–XII; Plate XVII; Figure 2, c.

# Material examined

#### Types

HOLOTYPE: SAM H828, 12 km off Cape Northumberland, South Australia, 62 m, S.A. Shepherd, 6 May 1975. PARATYPES: SAM H829 (3 colonies plus fragments), data as for holotype.

#### Other material

BM 1885.11.20.10, BM 1889.5.27.32, BM 1956.9.27.1, BM 1986.9.30.1, off East Moncoeur Is., Bass Strait, 38 fm, sand and shell, HMS Challenger; NHMB, unregistered specimen, same data; NHMW, unregistered colonies (figured by Kükenthal, 1919), Tasmania, no further data; AM E2242, 36 miles south west of Cape Wickham, King Is., Bass Strait, Tasmania, 132-146 m, FIS Endeavour, 27 Nov. 1911; AM E4383, Great Australian Bight, 131°E, 80-100 fm, FIS Endeavour AM G11807-G11811, 15 miles off St. Francis Is., Great Australian Bight, 55 m, FIS Endeavour, no further data; AM G15299, off Maria Is., Tasmania, 42°35'40"S, 148°11'20"E, 82.5-91.5 m, FRV Penghana, W.F. Ponder, 25 March 1970; AM G15301, Bass Strait, 40°11'S, 144°39'E, 58 m, 23 June 1962; AM G15306 (2 colonies), off Flinders Is., Tasmania, 40°7'S, 148°30'E, scallop dredge, 35 m, CSIRO Fisheries Investigations, 4 Aug. 1938; AM G15307 (10 colonies), D'Entrecasteaux Channel, Tasmania, 43°16'S, 147°14'E, 11-13 m, dredge, CSIRO Fisheries Investigations, 22 May 1938; AM G15309 (1-2 colonies), D'Entrecasteaux Channel, Tasmania, 4-20 m; AM G15588 (fragments from amongst the syntypes of Mopsea plumacea), South Australian coast, FIS Endeavour, no further data; AM G15592 (3 colonies), 58 miles south, 36 miles west of Cape

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Figure 107 Pteronisis incerta sp. nov.: A. Holotype, natural size; B. AM G15307, natural size; C. AM E2242, natural size x 0.5.

Wickham, King Is., Tasmania, 132-146 m, Feb 1911?; NTM C2322, The Pinnacles, 1 mile off Cape Woolami, Victoria, 38°34'S, 145°21'E, 40 m, J.E. Watson, 15 Nov. 1970; NTM C2471, Great Australian Bight, 32°58'5"S, 129°00'E, 72 m, Trawl, RV Soela, cruise SO5/81, stn 26, 3 Dec. 1981; WAM 389-79, north west of Rottnest Is., Western Australia, 37 fm, dredge, FV Bluefin, B.R. Wilson, 12 Aug. 1962; SAM H806, Sisters Rocks, on rock wall, Forestier Peninsular, Tasmania, 25-30 m, K.L. Gowlett-Holmes, 18 April 1993; SAM H807, east of Governors Island, "Hairy Wall", rock slope, 25-33 m, K.L. Gowlett-Holmes, 20 April 1993; SAM H838, Thorny Passage, Hopkins Is., South Australia, 35°58'S, 136°3'E, 35 fm, RV Ngerin, L. Hobbs, K. Branden, 1 Oct. 1989; SAM H839, south east of Cape Northumberland, South Australia, 13 fm, M. Nelson, May 1975; SAM H840, off Babel Is., Tasmania, 39°57'S, 148°25'E, 40 m, RV Soela, W. Zeidler, 11 Oct. 1984; NMV Ac 75.9, off Cape Nelson, Victoria, 38°35'S, 142°33'E, 75 fm, RV Sarda, 26 Aug. 1975. NMV G3284, off Lakes Entrance, Victoria, 37°55'S, 148°21'E, 50 m, East Gippsland Scallop Survey, 5 Feb. 1971; NMV G3331 (2 colonies), The Pinnacles, 1 mile off Cape Woolami, Phillip Is., Victoria, 38°34'S, 145°21'E, 40 m, J.E. Watson, 15 Nov. 1970; NMV F72843, about 6.5 km north east of the entrance to Port Phillip Bay, Victoria, Port Phillip Survey, Station 36 of Area 59, 5 May 1963.

The following specimens, housed at the NMV, from the Victorian Institute of Marine Science's Bass Strait Survey, recorded in the format 'station n°/lot n°': 113/62, 40°23'8"S, 145°32'E, 66 m, FV Sarda, 3 Nov. 1980; 119/11 (3 colonies), 39°6'7"S, 143°28'7"E, 48-55 m, RV Hai Kung, 31 Jan. 1981; 132/? (2 colonies), 40°10'8"S, 145°44'2"E, 76 m, RV Hai Kung, 3 Feb. 1981; 140/2 (2 colonies), 40°43'9"S, 148°37'5"E, 70 m, RV Hai Kung, 7 Feb 1981; 140/13, same data; 152/8, 39°6'8"S, 144°44'6"E, 67 m, RV Hai Kung, 11 Feb. 1981; 155/4, 38°56'S, 145°16'6"E, 70 m, RV Tangaroa, 12 Nov. 1981; 160/30 (2-4 colonies), 39°43'7"S, 147°19'6"E, 59 m, RV Tangaroa, 13 Nov. 1981; 164/81, 40°40'7"S, 148°36'9"E, 67 m, RV Tangaroa, 14 Nov. 1981; 174/45 (2 colonies), 39°14'8"S, 147°31'5"E, 57 m, RV Tangaroa, 18 Nov. 1981; 185/5 (3 colonies), 38°48'S, 143°14'5"E, 47 m, RV Tangaroa, 20 Nov. 1981; 185/52 (5 colonies), same data; 187/5 (2 colonies), 38°32'S, 142°28'6"E, 52 m, RV Tangaroa, 20 Nov. 1981; 188/48 (7 colonies), 38°38'2"S, 142°35'E, 59 m, RV Tangaroa, 20 Nov. 1981; 188/5 (2-3 colonies), same data; 190/ 5 (4-6 colonies), 38°49'5"S, 142°35'4"E, 89 m, RV Tangaroa, 21 Nov. 1981; 191/3 (15 colonies), 39°6'3"S, 142°55'6"E, 84 m, RV Tangaroa, 21 Nov. 1981; 192/2 (2 colonies), 39°6'7"S, 143°7'4"E, 81 m, RV Tangaroa, 21 Nov. 1981; 196/43, 39°54'7"S, 143°43'4"E, 49 m, RV Tangaroa, 21 Nov. 1981; 198/5 (4 colonies), 40°26'7"S, 143°41'4"E, 85 m, RV

*Tangaroa*, 21 Nov. 1981; 199/3 (1–3 colonies), 40°19'5"S, 143°48'8"E, 71 m, RV *Tangaroa*, 22 Nov. 1981; 203/33 (2 colonies), 39°22'S, 144°18'3"E, 60 m, RV *Tangaroa*, 23 Nov. 1981; 205/3, 39°13'6"S, 143°55'6"E, 85 m, RV *Tangaroa*, 23 Nov. 1981.

The following specimens, housed at the NMV, from the Wilson's Promentary National Park Survey: Stn 14, Great Glennie Is., 60 ft, C. Haywood and R. Wilson, 5 Feb. 1982; Stn 24, Anser Is., 60 ft, G. Smith and M. MacDonald, 6 Feb. 1982; Stn 34, Waterloo Pt., 48 ft, R. Wilson and C. Jordan, 8 Feb. 1982; Stn 41, Hobbs Head, 55 ft, R. Wilson and L. Curtous, 9 Feb. 1982.

# Differential characteristics

Sclerite form, in particular the larger triangular anthopomal scales which a transverse medial ridge; polyp body scales sometimes bilobed; some pinna internodes with denticulated rides.

# Description

# Colony form (Figure 107A)

The holotype is planar and pinnately branched in an alternating fashion. A short axial stub at the top of the stem indicates the colony was once branched, but it is now a single plume 120 mm tall and 35 mm across. The small calcareous holdfast is 5 x 4 mm. The first 12 mm of the stem is devoid of coenenchyme, and is about 1.6 mm thick. In the vicinity of the lowest pinna, the main branch is 1.74 mm thick, and about halfway towards the apex of the colony it is 0.95 mm thick (polyps not included). In the mid to basal regions of the plume, most pinnae are about 1.2 mm thick, and those towards the apex are 0.79 mm thick (polyps included). The angle of branching is mostly 45–55°, and the distance between consecutive pinna, taking both sides of the plume into account, is 1.2-2.1 mm, with most being 1.3-1.6 mm apart. The longest undivided branch is 35 mm.

# Polyps (Figure 108C–E,J)

Polyps are densely distributed all around on most of the pinnae. Near the tip of the principal branch and on the first of the two distal pinna, the polyps are mostly biserial and arranged in single rows. Polyps are also biserial between pinnae on most of the principal branch, although they are scarce in the lower region and absent below the lowest pinna. Polyps are contracted, adaxially reduced and curved upward and over so that the anthopomal region is angled to the branch at about 35-40°, and often lies against the base of a succeeding polyp. Measured along the branch most of the larger polyps are 0.66-0.78 mm long. Smaller juvenile polyps are common throughout the colony. Measured abaxially, the base and the head of the larger polyps are about 0.39-0.42 mm across,



Figure 108 Pteronisis incerta sp. nov., holotype: A-E. Polyps; F. Coenenchyme; G-I. Axial internodes; J. Twig fragment.





with a neck region of about 0.3 mm across. Polyps project 0.30–0.36 mm above the branch, and on the lower region of the principal branch a number are upside down.

#### Colony colour

The coenenchyme is a very pale yellowish white, opaque on the pinnae but translucent enough on the main branch to be able to see the dark underlying nodes. All sclerites are colourless.

### Axis form (Figure 108G–I)

The terminal internode of each pinna usually has 4-8 primary ridges which are smooth or have denticles on the proximal shoulders. In the short pinnae at the plume apex, all of the internodes have only 4 ridges, the older ones having denticles all along the ridges, the younger ones only partially. In the longer pinnae lower down the plume, all of the internodes have 8 primary ridges, including the tip if it is not too young. Ridges on the older internodes are completely denticulated. Some of the internodes away from the tip have 8 secondary ridges, also with denticles, but these are not present, in the more proximal internodes. In the pinnae towards the base of the plume, the thick proximal internodes adjacent to the main branch have 8 primary ridges which are virtually smooth, while the distal ones have denticulated ridges. The principal branch internodes near the colony apex have denticulated multiple primary ridges. Proceeding towards the base, the internodal ridges become less denticulated, the denticles becoming restricted to the shoulders and eventually absent altogether on the internodes of the stem. One principal branch internode 0.96 mm thick has approximately 22 primary ridges, and the one just above it has about 14. A stem internode 1.50 mm thick has 29 ridges. The desmocyte cavities are usually distinct and are confined to the valleys between the internodal ridges.

Stem internodes, which are partially overgrown by the nodes, are 0.32–0.79 mm long, and those of the principal branch are 0.63–1.42 mm in length with most about 1 mm. In the pinnae, the first few proximal internodes are quite short, about 0.47 mm, while those beyond vary from 0.79–1.26 mm with 1 mm being most common. Stem nodes are about 0.32–0.79 mm long, and those on the main branch are all about 0.32 mm. In the pinnae, the proximal nodes are 0.18 mm and the distal ones 0.12 mm long.

#### Axis branching

Within the plume, virtually every principal branch internode branches once; succeeding ones to the alternate side. Pinnae may arise with a short calcareous stump as in Figure 251 example 6, or with a node as in example 38. The point of division may occur anywhere along a principal branch internode or node, such as examples 11, 57, and 58.

## Axis colour

The nodal material of the stem is brown ( $\approx 6E6$ ) and more or less opaque. About half way along the principal branch the nodes are brownish yellow ( $\approx 5C7$ ) and translucent, with yellowish satin-like borders. The proximal nodes of the pinnae have translucent brownish yellow centres and opaque, narrow, satin-like ends that are greyish orange ( $\approx 5B5$ ). The satin-like borders are colourless. The distal nodes of the pinnae are similarly coloured, but the ends are broad and the central band is narrow. The internodes of the stem and principal branch are translucent and very faintly tinged with pink. Those in the pinnae are colourless, and the more terminal ones are transparent.

### Polyp sclerites (Figures 108A–E,J; 109)

The asymmetrical anthopoma is continuous with the polyp body sclerites. There are 3-4 sclerites in each octant, other than the adaxial one (Figure 108A.B). The distal sclerite in each octant is more or less triangular with a median cleft in each lateral edge. In the abaxial, abaxial-lateral, and lateral octants this triangular sclerite has numerous thornlike and leaf-like processes which are often ridged and multi-tipped (Figure 109Aa-e). The basal half of the larger and more abaxial forms of this sclerite is commonly angled ramp-like, and the distal portion extends forward from it. The leading edge of the ramp, and the associated thorns, often form a curved ridge transversing the middle of the sclerite. Occasionally, 2 smaller triangular scales will occur in place of the single larger one. Proximal to the triangular sclerite there are 2 and sometimes 3 crescentic scales in each octant (Figure 109Ah,i). The adaxial octant is occupied by a small tuberculate sclerite (Figure 109Al) preceded by a single small crescentic scale (Figure 109Ag), and sometimes a flattened spindle below that. The triangular sclerite in each adaxial-lateral octant is intermediate in size and shape between the adaxial form and the thorny forms in the other octants. Occasionally, in the adaxial-lateral octants, 2 crescentic scales, or 1 crescentic scale and the succeeding triangular scale, will be replaced by a single sclerite (Figure 109Am). The triangular anthopomal sclerites are usually up to about 0.09 mm long, but can be up to 0.11 mm.

There is a single basal tentacular sclerite in each octant (Figure 109Aj,k) preceding a single row of tentacular scales. The latter are usually few in number, often irregularly shaped, with scalloped, granular margins, and up to about 0.07 mm in length (Figure 109B). Sometimes the basal tentacular sclerite is very large.

The adaxial sector of the polyp body is naked.



Figure 110 Pteronisis incerta sp. nov., holotype, sclerites: A. Twig coenenchyme; B. Principal branch coenenchyme; C. Basal stem coenenchyme.

The rest of the body is covered with large crescentic scales, which are arranged in rows in the head region aligned with the anthopomal octants (Figure 108D). The exposed face of each scale is relatively smooth and the distal margin has a median cleft and numerous ridged, and sometimes multi-tipped, thorn-like projections (Figure 109C). The scales on the lower part of the polyp body are thick and more irregularly shaped (Figure 109Cb-d). The body scales are mostly no longer than 0.16 mm, but can be up to 0.20 mm. The underside has

large complex warts (Figure 109Ca). There can be quite a variation in sclerite shape between polyps. Occasionally, large irregularly shaped body scales are encountered. These appear to come from the lower part of the polyp as illustrated in Figure 108C, right side.

### Coenenchymal sclerites (Figures 108F; 110)

The surface of the pinnae mostly contains spindles unilaterally developed with thorn-like and leaf-like processes (Figure 108F). Most are up to



Figure 111 Pteronisis incerta sp. nov.: A-C. AM G15588, polyps; D-E. NTM C2471: (D). Axial internode; (E). Twig fragment.

about 0.15 mm with some up to 0.20 mm in length, and amongst them are numerous short, warty spindles (Figure 110A). A few flat, multiradiate forms (Figure 110Aa,b) seem to occur in the subsurface zone where a polyp adjoins the pinna. Forms like Figure 110Ac are intermediate between the surface sclerites and those of the polyp body.

Similar unilaterally developed spindles occur in the surface of the principal branch (Figure 110B), but the thorny processes are more densely arranged.

In the surface of the stem, most sclerites are derived from capstans (Figure 110C). Many are asymmetrically developed with leafy or thorny processes, and the remainder have 8 or more tuberculate radii. Most are up to about 0.10 mm, but some complex spheroidal forms are up to 0.12 mm across.

# Variability

A large range of variability can be demonstrated amongst the material examined, which may represent a complex of closely related species. Variations exist predominantly in axial form and the nature of the polyp sclerites. However, all attempts to subdivide the specimens using morphological characters have proved unsuccessful.

Growth form in general is quite consistent. Most

colonies are relatively small, up to about 150 mm. The smaller ones consisting of a single plume, and the larger ones of one or more main plumes with a few subsidiaries (Figure 107C). One of the largest colonies, whose base is missing, is 360 mm tall. It consists of a long main plume and just two small secondary ones, others having broken off, and the largest undivided branch is 45 mm. Colony growth can occasionally be very luxurious. In one such fragment (Figure 107B), the pinnae are thin where they attach to the principal branch, but thicken distally, to about 1.6 mm, where they are densely covered in polyps. A higher branch density occurs through some internodes bearing two pinnae. Another specimen exhibits a very spindly growth form. It is 200 mm tall, sparsely branched, and the denuded main axis is only about 1 mm thick. The pinnae are about 0.95 mm thick, but appear relatively thinner due to the very low polyp density. In some places the distance between consecutive branches is >3 mm because one or two unbranched internodes occur between two pinnae. In most colonies, however, ramification is similar to that of the holotype. Polyp distribution is also usually similar to the holotype. In colony NTM C2471, however, numerous distal pinnae have polyps biserially arranged, and often many of the polyps are juveniles (Figure 111E).

Nodal colour is basically the same throughout,



Figure 112 Pteronisis incerta sp. nov., AM G15299, sclerites: A. Anthopoma; B. Polyp body.

but the coenenchyme on some colonies is quite translucent and the pinnae, stem, and main branch appear banded. A faint pinkish hue in the stem internodes is absent from many colonies, which appear nearly white.

In some colonies (particularly the smaller ones, but sometimes the larger ones), the axial internodes in the pinnae are all 4-sided. There is a denticulated primary ridge down each edge, and usually a primary ridge in the centre of each face which is also denticulated in all but the more distal parts of the pinnae (Figure 111D). In some colonies, the primary ridge on each of the four faces is quite raised and wide, but the basic 4-sided nature is still apparent if an internode is removed and viewed end on. In some cases the ridges on the faces do not develop very much, but the denticles still occur in this area. In other colonies, all ridges are of similar structure and the internodes become 8-sided. In one lush colony, the distal internodes of the pinnae have eight primary ridges, those more proximal have eight primary and eight secondary

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Figure 113 Pteronisis incerta sp. nov., AM G15307, sclerites: A. Anthopoma; B. Polyp body; C. Pinna coenenchyme.

ridges, the middle ones have 16 primaries, and the ones adjacent to the main branch have eight primaries and eight secondaries. In all colonies, the short most proximal internode (or internodes) of the pinnae always have the ridges more distinct than the distal ones, and may lose their 4-sided appearance. Very rarely, the most proximal internode has smooth ridges, but usually they are denticulated. In some colonies the internodal ridges of the pinnae are very narrow and the denticles are more or less in a single row.

The internodes of the stem and the principal branches always have multiple primary ridges only, and these are smooth throughout most of a colony. In the upper regions, they may have denticles on the shoulders of the ridges, and towards the apex where a principal branch narrows and has a higher density of polyps, the internodes will take on the aspects of the pinnae axes and may become 4 sided.



Figure 114 Pteronisis incerta sp. nov., AM G15588, sclerites: A. Polyp body; B. Main branch coenenchyme.

Underwater photographs of specimen lots SAM H806 and H807 taken by Karen Gowlett-Holmes show that the colonies were greyish red with white polyps when alive.

The main reason only a small group of specimens from the same locality have been given type status is that sclerite variability is very extensive. A continuum appears to exist from forms where the majority of polyps have sclerites with long simple spines or thorns, to colonies like the holotype where thorns are often complex, more numerous, and not predominantly confined to the margin of the body scales. The problem is exacerbated by the variability between polyps within a single colony, especially polyps of different sizes. Some measure of consistency amongst colonies can be perceived when only juvenile polyps are examined, but even here there are exceptions.

Juvenile polyps often have the majority of body scales in a 'bat-wing' design (Figure 113Ba), with a deep median cleft in the distal margin and only a few simple thorn-like projections either side of this notch. As polyps mature, most scales add more thorns to the margin. On many colonies, polyps of medium size will tend to retain this simple, open, thorny dentation. Scales on larger polyps, however, may develop ridged, complex thorns, may become excessively spiny or irregular in form, or may stay relatively simple. The proportion of each seems to vary from specimen to specimen, although there is some evidence that colonies from similar locations have similar characters. Juvenile polyps commonly have no tentacular sclerites, the number increasing with age.

In one of the colonies from AM G15307 (Figure 107B) both the anthopomal and body scales have relatively few, mostly simple, thorns (Figure 113). Many of the body scales have a pronounced cleft in both the distal and proximal margins and an exaggerated curvature (Figure 113Ba–f). Basal body scales are usually quite simple (Figure 113Bh–l), and the spindles in the surface of the pinna have tall thorns and are often slightly arched (Figure 113C).

Colony AM G15299 has more complex thorns on the anthopomal sclerites (Figure 112A) and also on some of the polyp body scales (Figure 112Bf–i), especially the lower ones which are sometimes irregular in form (Figure 112Bj–o). Tubercles on the coenenchymal sclerites often have fine spines.

In colony AM G15588 many of the polyp body scales have smooth, rounded thorns (Figures 111A; 114Ab–g), whilst the anthopomal sclerites tend to have more complex processes (Figures 111B,C; 114Aa). The polyp depicted in Figure 111B shows this specimen can have basal polyp scales that may be irregularly shaped and have long thorns. In Figure 111C, a single adaxial-lateral sclerite (arrowed) has replaced 2 anthopomal scales. The coenenchymal sclerites on the main branches

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(Figure 114B) are similar to those of the holotype, with numerous short spindles occurring amongst them (Figure 114Ba).

Attention should be drawn to colony NTM C2471, from the central Great Australian Bight, that has many of the polyp sclerites with the lower extremities developed into elongate processes. Such a characteristic is only occasionally seen in colonies from other locations (Figure 113Ah).

### Distribution

See Figure 273. Depth range 4–182 m.

### Etymology

From the Latin *incertus* describing an object whose qualities are not yet fully established.

## Pteronisis echinaxis sp. nov. Figures 115–119; 274

Mopsea whiteleggei (part) Thomson and Mackinnon, 1911: 678–679, Plate LXVI, 2, 3; Plate LXXIII; (part) Kükenthal, 1919: 622–623; (part) Kükenthal, 1924: 439.

## Material examined

#### Types

HOLOTYPE: AM G12145, (a paratype of *Mopsea* whiteleggei), HMCS Thetis, station 44, 5–6 miles off Coogee, New South Wales, 49–50 fm, fine sand, 15 March 1898. PARATYPES: AM G6913, (a paratype of *Mopsea whiteleggei*), HMCS Thetis Expedition, 11 miles east of Broken Bay, New South Wales, 73 m,



Figure 115 Pteronisis echinaxis sp. nov., holotype, natural size.

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no further data; AM G8032, off Port Jackson, New South Wales, no further data; AM G11663, G15590 (4 colonies), Broughton Is., New South Wales, 32°36'S, 152°19'E, no further data; AM G15315, HMCS *Thetis*, station 10, 2–4½ miles off Broken Head, New South Wales, 28 fm, fine sand, 22 Feb. 1898; NMV F77744, station 158/50, Bass Strait, 39°49'5"S, 146°18'5"E, 82 m, RV *Tangaroa*, 13 Nov. 1981; NMV F77745, station 159/25 (2 colonies), Bass Strait 39°46'S, 146°18'E, 80 m, RV *Tangaroa*, 13 Nov. 1981; NMV F 77746, station 158/4, Bass Strait, 39°48'6"S, 146°18'8"E, 82 m, RV *Tangaroa*, 13 Nov. 1981.

# **Differential characteristics**

Sclerite form, in particular the triangular anthopomal scales which do not have medial ridge and keel structures; polyp body scales not bilobed; all axial internodes with denticles over the whole surface.

# **Description** (Figure 115)

The planar holotype, curved from bottle storage, is about 150 mm tall. The holdfast is missing and the lower one third of the colony, consisting of stem and main branches, is devoid of coenenchyme. The axial internodes of the stem, 1.9 mm thick, are mostly overgrown with nodal material. The upper part of the colony is formed into two small and two large plumes which are pinnately branched in an alternating manner. In the middle of the larger plumes, the principal branches are 0.8 mm wide (polyps not included), and the pinnae are about 1.1 mm thick (polyps included). The distance between consecutive pinnae, both sides of the branch taken into account, is 0.95-2.37 mm, with most being 1.18-1.58 mm apart. Branching angle is 44-62°, with most around 52°.

# Polyps (Figure 116C,K)

Distribution on the pinnae is essentially biserial with two rows of alternating polyps on each opposing face (one row in the youngest pinnae). Polyps here and there encroach on the other faces. Polyps are also biserially arranged on the principal branches between the pinnae, and below the pinnae. The distribution here, however, is irregular, and on the lower part of the main branch (the continuation of the stem) polyps are scarce.

Polyps are contracted, adaxially reduced, and curve upwards and over so that most lie against the branch with anthopomal region facing along the branch or angled towards it at about 45–50°. Measured along the branch, polyps are 0.66 mm in length. A polyp head is 0.36 mm across, abaxially. There is no appreciable neck region and the polyps taper proximally to about 0.24 mm across the base. Most project about 0.30 mm above the branch. Juvenile polyps are scattered throughout the colony. All sclerites are colourless.

# Colony colour

The coenenchyme is golden blonde ( $\approx$ 5C4), opaque on the pinnae and slightly translucent on the main branches where the underlying nodes can just be detected.

# Axis form (Figure 116G–J)

The most notable feature of the internodes is the denticulation, which occurs on all stem, branch, and pinna axes and is distributed over more or less the whole of the internodal surface in all but the terminal few segments of a pinnae. Even in the developing terminal internodes the denticles are well formed and prominent. Denticles have a broad base and are occasionally complex with 2–3 points. Internodal ridges are not well developed and the valleys between them are narrow.

The tip internode of a pinna, and sometimes those just preceding it, is 4-sided with no discernible ridges. In short pinna, all of the more proximal internodes have four very low primary ridges, and a low, wide, poorly developed secondary ridge on each of the four faces. In longer pinnae, further development occurs. Older internodes still retain the 4-sided aspect but the secondary and primary ridges appear more or less equal with little room between them. Proximal to this, all eight ridges are of equal development and the internodes are no longer 4-sided. Proximal to these, the internodes have four narrow primary ridges and four wider secondaries. In still older internodes, this ridging is retained and the 4-sided nature is regained.

In the upper parts of the principal branch of a large plume, the internodes have four rounded faces and no ridges. Proximal to this, the internodes develop more faces, which are flatter. In older internodes more faces develop with primary ridges between them. Proximal to these, the valleys between the primary ridges may develop low secondary ridges. The stem and basal parts of the oldest principal branches have internodes with multiple primary ridges. A main branch internode 1.6 mm wide has 20 primary ridges. Denticles in the older parts of the colonies are prominent on the primary ridges and reduced in number and size in the valleys between the ridges. Desmocyte cavities are most distinct in the younger internodes, and often long, sparse, and less distinct in older segments.

Internodes in the pinnae are mostly 1.18–1.34 mm long; the terminal and proximal few being slightly shorter at about 0.79–0.95 mm. In the lower parts of the principal branches, internodes are 0.79–1.10 mm in length. In the plumes, the principal branch internodes are the same length as in the pinnae.



Figure 116 Pteronisis echinaxis sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-J. Axial internodes; K. Twig fragment.





## Axis branching

The stem divides off principal branches as in Figure 251 example 59, and the lower, thick regions of these branches give off pinnae as in examples 57, 58. In the plumes, branching is as in examples 12, 13, 14 and 29. Usually, each principal branch internode in a plume branches only once (succeeding ones to alternate sides). In a couple of places, internodes bear two pinna, sometimes both on one side.

## Axis colour

Nodal material in the stem base is brown (≈7E6) and slightly translucent. In the upper stem and the lower principal branches, the nodes are brownish orange (≈6C5), translucent, and have narrow yellowish satin-like borders. In the plumes, the principal branch nodes have a transparent brownish orange central band and, at each end, a narrow opaque band of light yellow (≈4A4), and silvery satin-like borders. The proximal nodes in the pinnae are opaque and light yellow, with a narrow, transparent, darker central band, and silvery satin-like borders. The distal nodes in the pinnae are satin-like and pale yellowish white with a transparent colourless to brownish central band. The internodes of the main branches are greyish white and translucent. Those of the pinnae are more or less colourless becoming transparent in the terminal regions.

## Polyp sclerites (Figures 116A–D; 117)

The asymmetrical anthopoma is continuous with the polyp body sclerites (Figure 116A,B). The distal sclerites in each octant are more or less triangular, sometimes with a marked median cleft in each of the lateral edges (Figure 117Aa-f,h). In the adaxial octant there is a single apical triangular scale, with a few small tubercles on the upper face (Figure 117Ah), generally preceded by a small crescentic scale (Figure 117Al) and 2 flattened spindle-shaped forms. Sometimes part of this proximal arrangement is taken over by the extensions of some of the adaxial lateral body scales. Below this the polyp body is naked. In the other octants there are usually 2 crescentic scales (Figure 117Ai-k) followed by a variable arrangement of triangular sclerites. The octant may be completed by a single large triangular sclerite, a moderately sized triangular sclerite followed by a smaller one, or 2 medium sized triangular forms. The size of the basal tentacular sclerite seems dependant on the make up of the octant. In general, if there is a single triangular sclerite the basal tentacular will probably be large (Figure 117Ag). If there is a moderately sized sclerite and a smaller form, the



Figure 118 Pteronisis echinaxis sp. nov., holotype, sclerites: A. Pinna coenenchyme; B. Main branch coenenchyme.

basal tentacular scale will probably be of similar design to Figure 117Ag but much smaller. If the octant contains 2 medium sized triangular scales, the basal tentacular sclerite may be of a form intermediate to a tentacular scale, with a spiny basal half like Figure 117Ag and a flat, irregular disc-shaped, granular distal portion. There is a single row of curved scales in each tentacle, up to about 0.069 mm long. They have scalloped edges and sometimes a few tubercles on the outer face (Figure 117B). The triangular anthopomal scales are usually no larger than 0.11 mm long, occasionally up to 0.12 mm, and are ornamented with relatively short, thorn-like processes. The projections on the more abaxial sclerites are the tallest and are sometimes complex. Sometimes a few tubercles are aligned ridge-like across the middle of the sclerite.

The polyp body is mostly covered in large crescentic scales (Figure 117C). Those in the head region are in 7 rows aligned to the anthopomal octants. The adaxial side of the polyp is tightly contracted and very short. There are 3-4 narrow scales immediately below the adaxial octant, and probably a naked zone below this but it has contracted to the point of invisibility. The outer face of the large body scales is relatively smooth and the exposed margin generally has an irregular arrangement of thorn-like processes, and sometimes a median cleft. Those scales on the polyp base may have thick, truncated projections (Figure 117Cb). The underside of the body scales has large complex warts (Figure 117Ca). Most of the scales are up to about 0.16 mm long, but a few of the lateral ones can be up to 0.19-0.20 mm in length.

*Coenenchymal sclerites* (Figures 116C,E; 118) The surface of the pinnae contains spindles that are unilaterally developed with thorn-like and leaflike processes (Figure 118A). Most are 0.06–0.12 mm long with a few up to 0.15 mm in length. A few warty spindles occur amongst these sclerites.

The lower stem is devoid of coenenchyme, but the surface of the upper section and the principal branches contains small, warty multiradiates and thorny spindles similar to those in the pinnae but generally stouter (Figure 118B). The multiradiates are mostly 0.04–0.06 mm across, and most of the thorny spindles are <0.13 mm long. As in the pinnae, a few warty spindles also occur.

### Variability

The general colony form of all of the paratypes agrees with that of the holotype. Polyps are distributed biserially in the majority of specimens, but in more luxurious colonies with thick pinnae the distribution can be all around.

Axial colour is variable. Principal branch and stem nodes can vary in colour from light brown to light orange to bronze, and also in translucency. One of the colonies from Bass Strait has virtually transparent nodes and internodes throughout the whole colony. Several of the Bass Strait colonies and one colony from a *Thetis* station, much further to the north, have a pinkish hue to the internodes of the major ramifications. The *Thetis* specimen, AM G6913 (Figure 119), is only a portion of a larger colony and the pinkish hue is present only in the most proximal main branch internodes. In three of the more northern specimens, internodes throughout the colonies are more or less white and they are never transparent.

Specimen lot AM G15590 from Broughton Island consists of juvenile colonies 15–50 mm tall. On one of the colonies the ornamentation of the polyp sclerites is very complex and the tubercles are



Figure 119 Pteronisis echinaxis sp. nov., paratype, AM G6913, natural size x 0.5.

ridge-like, leaf-like, or multi-tipped thorns. The tentacular sclerites are common and large, up to 0.075 mm.

The specimens from Bass Strait have some similar characters to some of the P. incerta specimens from that area, those with the simpler scales. The polyp body sclerites often have a more marked median cleft, and fewer, taller, thorns along the distal margin. The anthopomal triangular scales differ, however. They are all of the style of Figure 117Ad-f, with small tubercles, even the larger more abaxial ones, and there is no pronounced transverse ridge. Tentacular sclerites, unusually, are very few or totally absent. Coenenchymal sclerites are generally like those of the holotype, except for one unusual colony with extremely long unilaterally thorned spindles. Large numbers of these are about 0.16 mm long and 0.20 mm is not uncommon.

## Remarks

This species is not easily distinguished from *P. incerta* using sclerite morphology, although the small collar-shaped tentacular sclerites are well formed and normally in far greater abundance in *P. echinaxis*. The two species are easily separated, however, on axial architecture. Although the distal principal branch internodes of *P. incerta* have small denticles all over, this trend is never continued proximally. In *P. echinaxis* the nature of the denticles and their distribution on the internodes are quite different. Their retention even down to the internodes at the base of the stem is quite unusual.

# Distribution

See Figure 274. Depth range 51-191 m.

## Etymology

The epithet is derived from the Latin *echinatus*, spiny, and *axis*, in allusion to the axial architecture. Noun phrase in apposition.

*Pteronisis oliganema* sp. nov. Figures 120–123; 275

# Material examined

#### Types

HOLOTYPE: AM G15589 (numerous fragments), 36 miles south of Mt. Cann, Victoria, 70–100 fm, FIS *Endeavour*, 19 Oct. 1914.

#### **Differential characteristics**

Branching very sparse, apparently lateral, and not planar; branches extremely thin; triangular anthopomal scales without medial ridge and keel structures; polyp body scales not bilobed; internodes with denticulated ridges.

#### Remarks

These fine fragments were found entangled in specimen AM E6036, *Pteronisis whiteleggei*, which was collected by the FIS *Endeavour* and possibly included by Briggs amongst the type series of *Mopsea plumacea*. That specimen is labelled as *M. plumacea* but there is no indication that it has type status.

### Description

#### Colony form (Figure 120)

The holotype is badly fragmented and sparsely branched. Much of the coenenchyme and many of





the polyps are missing, and some pieces are only sections of naked axis. The 2 largest portions are about 50 mm tall, but neither are large enough to allow an accurate assessment of the branching pattern. The ramification is essentially lateral and not all in one plane. As such, it does not conform to the pinnate nature normally attributed to this genus. It is not inconceivable, however, that the pattern could be irregularly and distantly pinnate and somewhat similar to the holotype of *Mopsea bargibanti*.

The branches are mostly long and thin. The thickest is 0.33 mm and the finest 0.18 mm in diameter (polyps not included). The distance between consecutive divisions is very variable, 4.9–23.8 mm, as is the angle of branching, 32–64°. The

longest undivided branch is 34 mm. The stem is missing.

## Polyps (Figure 121A-D,J)

Polyps are biserially distributed in 2 opposing rows. The arrangement is mostly alternate, but it is irregular. They are well spaced with most of those in a single row being about 0.8–1.1 mm apart, measured centre to centre.

The polyps are more or less club-shaped. They are contracted, adaxially reduced, and curved over so as to lie close to the surface of the branches. They are present in many stages of development. Measured along the branch, the juveniles are from 0.30 mm in length and the most developed are up to 0.75 mm. Most of the larger polyps have a base



Figure 121 Pteronisis oliganema sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-I. Axial internodes; J. Twig fragment.





about 0.30 mm long and project about 0.36 mm above the branch. Measured abaxially the head is about 0.42 mm across, and there is a narrower neck zone.

# Colony colour

The polyps and coenenchyme are greyish white, and the bright axial nodes can be seen through the surface sclerites.

# Axis form (Figure 121F-I)

Internodes are more or less square in section with 4 denticulated primary ridges. The ridges have denticulated shoulders which are sometimes pronounced, and the denticles are sharper in the younger internodes (Figure 121H,I). The older internodes develop a low secondary ridge on each face which has a cluster of denticles on its shoulders and a few denticles scattered along its length (Figure 121F,G). Desmocyte cavities are deep and distinct on the younger internodes but tend to be shallow and difficult to see on the older ones.

The thickest internodes are 0.26 mm and the finest are 0.07 mm in diameter. They are mostly 0.66–1.44 mm in length, and the older internodes are generally the longest. The nodes are 0.048–0.144 mm long.

# Axis branching

All divisions are similar to Figure 251 examples 6, 12 and 14. Internodes only ever initiate a single branch.

# Axis colour

Internodes are pale greyish white, the thicker ones being translucent and the finer ones almost transparent.

The nodes are banded. The short middle section is translucent and grey to pale brown. It is flanked on each end by broader, opaque, satin-like bands of yellowish white. The narrow boarders are satinlike and silvery white.

# Polyp sclerites (Figures 121A–D; 122)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. There are normally 4 sclerites in each octant, but it is not uncommon to find fewer in the adaxial and adaxial-lateral sections. There is commonly a single more or less triangular sclerite at the apex of each octant which is preceded by several crescentic scales (Figure 121A,B). It is not unusual, however, for 2 smaller triangular sclerites to occur in place of a single larger form. The scales in the lateral and more abaxial octants have prominent thorn-like projections on their margins and upper surface (Figure 122Aa–c,k–m) and a few compound warts

on the underside (Figure 122Ad). Those in the other octants have smaller tubercles (Figure 122Aeh,n), the apical adaxial sclerites sometimes having a smooth upper surface. There are 1-2 basal tentacular sclerites in each octant (Figure 122Ai,j) which precede a single row of curved scales in the tentacle rachis (Figure 122B). The most basal of the latter is usually intermediate in form, with two proximal 'legs' and a wide spatulate distal portion, resembling an arm-less gingerbread man. The few scales above this are irregularly shaped (Figure 122Bb), but the more distal ones are typical of the genus (Figure 122Ba). The triangular anthopomal scales are mostly no longer than 0.12 mm, and the well formed tentacular scales are 0.050-0.073 mm in length.

The polyp body is covered in crescentic scales that are arranged in rows on the polyp head (Figure 121C,D). The adaxial side of the body is mostly naked, but the naked area is relatively small compared to the other species of the genus due to a short row of about 3 very narrow scales below the lateral octant. Most body scales have a relatively smooth outer face with only a few isolated tubercles (Figure 122C), and the inner face is similar. The distal scale margin has prominent thorn-like projections and sometimes a slight median cleft, and the lower margin has tuberculate root-like structures which are sometimes quite large. Most of the body scales are about 0.11–0.15 mm long, but some are larger.

# Coenenchymal sclerites (Figures 121E; 123)

The surface of the branches contains spindles and irregularly branched forms that are unilaterally developed with tooth-like projections. Those at the base of the polyps may be intermediate in form to the body scales (Figure 123a). Most of the larger sclerites are 0.15–0.17 mm long but they can be up to 0.23 mm. There is no preserved stem tissue.

# Distribution.

See Figure 275. Depth range 128-182 m.

# Etymology

The epithet employs the Greek *oligos*, small or scanty, and *nema*, thread, in allusion to the sparse, thin branching. Noun phrase in apposition.

# Sphaerokodisis gen. nov. Figure 313

Mopsea; (part) Thomson and Mackinnon, 1911: 675– 677; (part) Briggs, 1915: 72–74; (part) Kükenthal, 1915: 117–118, 123–124 (in keys); (part) Kükenthal, 1919: 558–559 (in key), 617–618; (part) Kükenthal, 1924: 437; Thomson and Rennet, 1931: 16–17; (part) Grant, 1976: 33;



Figure 123 Pteronisis oliganema sp. nov., holotype, sclerites: Branch coenenchyme.

(part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49–51 (in key), 57; (part) Bayer and Stefani, 1987b: 940–942 (in key).

# **Type species**

Mopsea flabellum Thomson and Mackinnon, 1911, here designated.

≡ Mopsea squamosa (nomen novum) Kükenthal, 1915

*≡ Sphaerokodisis flabellum* new combination.

### Diagnosis

Colonies are up to 245 mm tall. They are more or less planar, branched pseudo-dichotomously, and sometimes lyrate.

The preserved colony colour in the types of *S. australis* (Thomson and Mackinnon, 1911) and *S. tenuis* (Thomson and Rennet, 1931) is almost white. The sclerites are colourless, the axial internodes are grey-white to milky, and the nodes are shades of brown. In *S. flabellum* the colonies are brown to reddish brown and may have whitish polyps, the sclerites are generally yellow in transmitted light, axial internodes are almost white proximally becoming brown and brownish yellow in the upper colony regions, and the nodes are brown.

Polyps are distributed all around. Unless very tightly contracted they are club-shaped with a rather globose head. They are adaxially reduced, adaxially naked, and usually preserved curved over and angled distad, or lying along the branch surface.

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The major octants are occupied by an apical triangular to triradiate sclerite, up to 0.17 mm long, preceded by 1–2 crescentic scales. There is a single basal tentacular sclerite preceding a single row of curved scales in each tentacle rachis.

The polyp body is protected by large crescentic to oval scales that are commonly bilobed. They are up to 0.21 mm long, their exposed surface is generally smooth, and their distal margin has large tooth-like projections. On the polyp head the scales are arranged in 7–8 rows; the adaxial row containing up to 4 scales but sometimes none (*S. australis*).

The coenenchyme contains ovals, sometimes capstan-like, spindles, and small plates, up to 0.26 mm long. They are unilaterally developed with conical tooth-like, or leaf-like projections.

The axial internodes are up to 4.4 mm long and have multiple primary ridges. In *S. flabellum* and *S. tenuis* the internode surface is smooth, but in *S. australis* it is densely denticulated.

### Distribution

See Figure 313.

#### Etymology

In allusion to the globose polyp heads the generic hybrid name is derived from the Latin *sphaera*, ball, and the Greek *Kodeia*, head; combined with *Isis*.
# Sphaerokodisis flabellum (Thomson and Mackinnon, 1911) new comb. Figures 124A,B; 125–127; 276

- Mopsea flabellum Thomson and Mackinnon, 1911: 676–677, Plate LXIII, Figures 1–3; Plate LXVII, Figure 6; Plate LXXI; Briggs, 1915: 73–74.
- Not Mopsea flabellum; Kükenthal, 1915: 123–124; Kükenthal, 1919: 626; Kükenthal 1924: 439. [≡ Acanthoisis flabellum Wright and Studer, 1889: 45–46, Plate VIII, Figures 1,1a,1b; Plate IX, Figure 12].
- Mopsea squamosa; (nom. nov.) Kükenthal, 1915: 123– 124; Kükenthal, 1919: 625, 926; Kükenthal 1924: 441.
- Not Mopsea squamosa; Utinomi, 1975: 255–256, Figure 13; Plate 3, Figure 3. [⇒ Mopsea encrinula Lamarck 1815: 415].

## Material examined

## Types

LECTOTYPE (here designated): AM G12152, HMCS *Thetis*, station 44, 5–6 miles off Coogee, New South Wales, 49–50 fm, fine sand, 15 March 1898 PARALECTOTYPE: AM G12151, HMCS *Thetis* station 34, 2.5–3.5 miles off Port Jackson, New South Wales, 36–39 fm, sand and mud, 10 March 1898.

#### Other material

AM G5679, off Botany Bay, New South Wales, submarine cable, 91 m, registered Sept. 1906; AM G15297, off Shell Harbour, New South Wales, 34°35'S, 150°52'E, dredged, HMAS *Gascoyne*, Sydney University Geology Dept., Dr Shirley, April 1964.

## **Differential characteristics**

Branching only more or less planar; anthopomal triradiate scales relatively smooth with only a few small tubercles; coenenchymal sclerites in the form of ovals with smooth, rounded, conical or tooth like projections; axial internodes with smooth ridges. Colonies usually reddish-brown.

## Description

### Colony form (Figure 124A)

Thomson and Mackinnon (1911: 676) stated that the "species is based on one complete colony and a number of pieces", but made no type designation. In the museum storage jar there is a bundle of mostly large fragments carrying the registration number G12152, sitting amongst a mass of loose small pieces and the registration tag G12151. The label in the jar reads, "Mopsea flabellum Thom and Mck G12151–2 Co-type specimens including (very probably) also the broken up TYPE specimen". The bundle of larger fragments contains stem portions that clearly match the colony depicted in Thomson's and Mackinnon's Plate LXXI and is designated here as the lectotype. The remaining fragments are presumably from the paralectotype, and undoubtably there are pieces of the lectotype amongst them. The material is poorly preserved and macerates too quickly in bleach preventing the satisfactory removal of surface tissue from whole polyp and twig samples for electron microscopy.

From the fragile lectotype fragments it can be deduced that the colony was nearly planar and was branched in a pseudo-dichotomous manner. A few branches clearly emerge out of plane. Thomson and Mackinnon state (1911: 676), "The complete specimen rises from a slightly encrusting calcareous base to a height of 24.5 cm. Branching begins at a height of 5.5 cm. and is very luxuriant; the branches are confined almost exclusively to one plane, and there is a strong tendency to dichotomy ; they are slender throughout, and do not taper much ; the stouter branches have a diameter 2.5 mm., and the twigs of almost 2 mm., near their tips". From my own observations, the colony, like others of this general form, tends to branch dichotomously in the peripheral regions and laterally in the more central parts, with branches curving upwards and growing more or less parallel to each other. The main stem, from which most of the coenenchyme is missing, is now in 3 pieces and is about 58 mm long and 2.0-2.7 mm thick; much thinner than stated by Thomson and Mackinnon. The thick calcareous holdfast is about 8 mm x 6 mm. The stem is not straight and divides into two main branches, about 1.6 mm thick (without polyps). In the central regions of the colony the branches and twigs are about 1.4-1.7 mm thick (including polyps); again thinner than described by Thomson and Mackinnon. They do not taper greatly over their length, although the tips are very short and taper rapidly. In many cases the sharp tip of the terminal axial internode projects minutely. Unbranched twigs are between 8 mm and 55 mm long. The distance between consecutive points of branchings is about 2.4-22.0 mm, with about 10.0 mm being common. Angle of branching is 39-60°.

### *Polyps* (Figure 125B,C,F)

The polyps, many of which are badly damaged, are densely arranged all around on all branches and twigs except for the thick main branch fragments where only a few occur. Most polyps arise from the branch surface at about 31–66°, although a few are almost vertical. The polyps are adaxially reduced and curve upward and over so that the anthopomal region lies more or less against the branch surface. A few just touch the abaxial side of the base of the succeeding polyp. A









Figure 125 Sphaerokodisis flabellum (Thomson and Mackinnon, 1911). A-F. Lectotype: (A-C). Polyps; (D-E). Axial internodes; (F). Twig fragment. G-L. AM G5679: (G-J). Polyps; (K). Coenenchyme; (L). Twig fragment.

number of others have a pronounced sideways curve that has allowed them room to pull the head region down to the branch surface between succeeding polyps. The relatively heavy scales of the basal region of the polyps occasionally make this area appear as a shelf-like support for the head, but the polyp scales are continuous up the body and there is no suture between the polyp base and the head. The polyps, measured along the branch, are about 0.75-0.95 mm long. Most project about 0.36-0.48 mm above the branch. The bases are about 0.39-0.48 mm long. Above its base each polyp has a narrow neck zone about 0.31 mm thick that leads to a relatively large, somewhat globose head about 0.45 mm across, abaxially. There are a several regions where polyps are upside-down, and juvenile polyps are scattered throughout the colony.

#### Colony colour

The basal branch fragments, where the coenenchyme is intact, are brown ( $\approx$ 6D7). The upper parts of the colony are reddish brown ( $\approx$ 8E8) and the polyps are noticeably paler, the same colour as the basal branches. The axial nodes are extremely difficult and often impossible to see through the coenenchyme, except on the main branch fragments. The sclerites are yellow in transmitted light.

### Axis form (Figure 125D,E)

The internodes have multiple high longitudinal ridges, even in the twig tips, and are not spined. There are no secondary ridges. A main stem internode about 2 mm thick has 28 ridges. A branch internode about 0.5 mm thick has 8 ridges. Desmocyte cavities are shallow but distinct.

Main stem internodes are about 0.5–1.7 mm long, the lower ones covered to various extent with nodal material. Most of the upper colony regions have the coenenchyme intact, but it is estimated that the internodes of the branches and twigs are mostly 1.4–2.9 mm in length; the longest seen being 3.5 mm. The nodes of the main stem are about 0.8– 2.1 mm long. Those in the upper branches and twigs are about 0.3–0.6 mm long and noticeably narrower than the internodes.

# Axis branching

The most common form of axial branching is shown in Figure 251 examples 6 and 26. The node is sometimes shared as in example 13.

### Axis Colour

The axial internodes of the main stem and main branches are nearly white, tinted a very pale orange brown. They are quite densely coloured, but translucent. The translucency of the internodes increases in the higher regions of the colony. In the upper branches and twigs the internodes are brownish yellow ( $\approx$ 5C7). In the terminal regions of the twigs the internodes are transparent. The axial nodes of the main stem and main branches are more or less opaque, brown ( $\approx$ 7E7), with wide pale yellow satin-like borders. In the upper branches and twigs the borders are similarly coloured and very wide leaving only a narrow transparent brownish central region.

## Polyp sclerites (Figures 125A-C; 126)

The anthopoma is continuous with the polyp body sclerites and slightly asymmetrical. Each octant is usually occupied by a single large triangular to triradiate sclerite (Figure 126Aa-f) preceded by a single curved, crescentic to rectangular scale which is narrow in the adaxial and adaxial-lateral octants (Figure 126Ah,i) but relatively broad in the others (Figure 126Aj,k). Occasionally, the octant may have 2 proximal scales or a single very broad plate, in which case the distal triangular sclerite is of reduced size (e.g. Figure 126Ag). The appearance of the anthopoma depends very much on the state of contraction of the polyp. In those polyps that are very contracted (the majority) with the anthopoma lying against the branch surface, the proximal scales do not fold over very much. In this instance each octant may appear to contain just a single triangular sclerite (Figure 125A). Most of the larger triangular forms are about 0.15-0.17 mm long, and some have lateral medial processes (Figure 126Ab,d). They are smooth underneath (Figure 126Af) and have small tubercles on their exposed face.

There is a single basal tentacular sclerite preceding a single row of curved scales in each tentacle rachis (Figure 126B). The tentacular scales are up to about 0.08 mm long, and small granular tubercles give their convex and concave margins a scalloped appearance.

The polyp body is protected by large scales (Figure 126C) that are arranged in 8 rows on the polyp head. There are only about 4 scales in the adaxial-lateral rows and 3 in the adaxial row. These sclerites are narrow and of similar shape to the proximal anthopomal scales above them. Below the short adaxial row the polyp is naked. Sometimes a couple of modified stellate plates (Figure 126Cr) may occur bordering this naked area. On the rest of the polyp head the scales are bilobed (Figure 125B,C). This bilobed nature is least marked on the series of scales immediately below the anthopomal octants and on those in the lateral rows (Figure 126Ca-c). Most of those scales in the more abaxial rows of the head have a deeper medial cleft in their free margin (Figure 126Cd-g). The scales on the polyp base are usually much thicker and more irregularly shaped. They may still



Figure 126 Sphaerokodisis flabellum (Thomson and Mackinnon, 1911), lectotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

P. Alderslade



Figure 127 Sphaerokodisis flabellum (Thomson and Mackinnon, 1911), lectotype, sclerites: A. Polyp/twig adaxial juncture; B. Branch coenenchyme.

be more or less bilobed, but the free margin is often produced into large fang-like projections. Although the basal scales are not arranged in regular rows, there are about 20–23 scales in a rough line down the abaxial side of the polyp. Most of the larger body scales are about 0.15–0.21 mm long. Some of the basal scales can be extremely broad, and measured from the distal tip to the basal root they are occasionally >0.25 mm. Body scales are smooth on the underside with only a few complex warts (Figure 126Cf,g,l,m).

### Coenenchymal sclerites (Figure 127)

In the region where the adaxial side of the polyp adjoins the branch surface there are numerous platelets. Most appear to be arranged on their edge in a multilayered semicircle around the polyp base. Many are elongate or more or less figure-8 in outline (Figure 127A). They are predominantly smooth with small marginal tubercles giving them a scalloped edge. One or more smooth tubercles often occur near the centre of one face.

The rest of the coenenchyme contains predominantly ovals and the occasional platelet ornamented with smooth, rounded, conical or tooth-like projections (Figure 127Ba–p). Some have a waist and resemble capstans. Most are about 0.05–0.13 mm long. The projections on the inner face may differ little from those pointing outwards. A few have slightly more complex root structures. In some samples larger more complicated forms are found (Figure 127Bq–w), up to about 0.19 mm in length, but they are not common.

The small amount of coenenchyme remaining on the upper stem fragments contains sclerites like those in the thinner branches.

#### Variability

Amongst the mixture of lectotype and paralectotype fragments are some remnants of thick branches which have axial internodes where the longitudinal ridges are transparent, giving the

segments a stripped appearance. Polyp and coenenchymal sclerite samples taken from some of the fragments are like those of the lectotype.

In all of the other comparative specimens the polyps are extended to a much greater degree than seen in the type material. In specimen AM G5679 the polyps are about 1.4 mm long measured along the branch, and extend about 0.8 mm above the branch surface. The colony is light brown (≈6D6)) but the polyps appear very pale because their extension has rendered them relatively transparent. Under a dissecting microscope the coenenchyme is seen to be speckled. This is because many of the larger surface sclerites have optically dense centres giving them an almost white appearance. This colony lends itself better to show the arrangement of the sclerites in the polyp and coenenchyme (Figure125G-L), particularly the naked adaxial region of the polyps (Figure 125G).

Lot AM G15297 contains 3 colonies. The largest (Figure 124B) has very thick branches; up to 2.6 mm diameter including the densely arranged polyps. In the middle sized colony the coenenchyme and the very base of the polyps is brownish orange ( $\approx$  5C6). However, most of the polyp body is virtually white as the sclerites are colourless. The main stem internodes of this colony are translucent and brown ( $\approx$  7E7), and the nodes

are reddish brown (≈ 8C8) and also translucent.

There is some sclerite variability amongst the comparative material. In some polyps there up to 5 scales in the adaxial-lateral rows and as few as one in the adaxial row. Abaxial sclerites in the polyp heads in some colonies do not have very deeply incised margins, and anthopomal triangular or triradiate scales may occasionally be relatively smooth. All colonies have the smooth scalloped platelets in the coenenchyme around the base of the adaxial side of the polyp, but they are generally not as numerous as in the lectotype.

### Distribution

See Figure 276. Depth range 66-91 m.

# Sphaerokodisis tenuis (Thomson and Rennet, 1931) new comb. Figures 124C; 128–130; 277

Mopsea tenuis Thomson and Rennet, 1931: 16–17, Plate VIII, Figure 2; Plate X, Figure 4; Plate XI, Figure 4.

## Material examined

Types HOLOTYPE: AM G13251, off Maria Island,



Figure 128 Sphaerokodisis tenuis (Thomson and Rennet, 1931), holotype: A-C. Polyps; D-E. Axial internodes.

Tasmania, 65–1300 fm, Mawson Antarctic Expedition, T.T. Flynn, 12–13 Dec. 1912.

### Other material

AM G15305, 25 miles NE of Babel Island, 39°31'S, 148°39'E, NE Tasmania, edge of bank, 128–183 m, 3 April 1914.

## **Differential characteristics**

Branching only more or less planar; anthopomal triradiate scales with 1–2 rows of large tubercles; coenenchymal sclerites in the form of spiny ovals and spindles; axial internodes with smooth ridges.

## Description

# Colony form

The holotype has been reduced to a pile of very small pieces, predominantly decorticated, at the bottom of a glass vial. Most of the fragmented polyps and coenenchyme is present as a sediment at the bottom of the vial. The material was originally described by Thomson and Rennet (1931: 16) as "Broken pieces of a very delicate white colony, branching on the whole in one plane, and the most part dichotomously. The largest branch rises to a height of 15cm". Their illustration (1913: Plate VIII, Figure 2) at a magnification of X1.5 shows only a small branched portion which must have been about 57 mm tall. The branching of the parent colony was possibly pseudo-dichotomous. Amongst the now much deteriorated material the thickest axial fragments are about 1 mm in diameter and the finest twigs about 0.2 mm.

The angle of branching is 35–65°.

### Polyps (Figure 128C)

All of the polyps are damaged and only a few twig portions still have some attached. They are distributed all around and are about 0.72 mm–0.84 mm in length measured along the branch, and project about 0.30 mm above the surface. Abaxially they are about 0.40 mm thick across the base and the head, with a narrower neck region.

## Colony colour

Pale yellowish white. The sclerites are colourless but the nodes are only faintly visible through the coenenchyme.

# Axis form (Figure 128D,E)

The internodes of the finer branches, those less than about 0.18 mm diameter, are more or less square in section, with 4 smooth primary ridges. Thicker internodes have multiple primary ridges with well developed shoulders. Desmocyte cavities are shallow but distinct, and roughly circular. An internode 0.4 mm thick has a 8 primary ridges, and one 0.6 mm thick has 16. The thickest internodes, 0.9 mm diameter, also have 16 primary ridges, but 16 new ridges can be seen to have been developing between the main ones.

Most internodes are about 2.7–4.4 mm long; in some fine twigs they are only 1.7 mm in length. The nodes are about 0.16 mm long in the thin twigs and about 0.32 mm long in the thickest branches.

## Axis branching

Branching usually involves bifurcation of an internode producing a relatively long calcareous side-branch. In the thick fragments of major branches the commonest style is like that in Figure 251 example 26, with some shorter branch stubs as in example 14. Some bifurcations occur nearer the middle of the originating internode as in example 27. The latter style also occurs in the finer branches with the side-branch often reaching to the end of the originating internode as in Figure 128D, or overreaching it as in example 21.

### Axis colour

The internodes are translucent milky white. The nodes of thicker branches are virtually opaque and very dark brown (≈7F4) with thin greyish yellow satin-like borders. In the thinner branches and twigs the borders are the same colour but very wide with just a narrow transparent brownish segment between them.

### Polyp sclerites (Figures 128A-C; 129)

The anthopoma is continuous with the polyp body sclerites and slightly asymmetrical. Each octant is occupied by a large triangular scale (Figure 128A,B) preceded in most instances by a single crescentic scale that may not be preserved folded down to any great extent. Those crescents in the adaxial and adaxial-lateral octants are relatively narrow and simple (Figure 129Ai) compared to those in the other sectors (Figure 129Aj). The triangular scales are mostly 0.15–0.17 mm long and smooth underneath (Figure 129Af,g). On their outer face they have relatively large tubercles arranged more or less in 1–2 rows along the distal arm, which often has spiny lateral projections (Figure 129Aa–e,h).

There is a single basal tentacular sclerite (Figure 129Ak), which may be more pointed than that figured and have longer proximal legs. It precedes a single row of curved, broad tentacular scales, up to about 0.073 mm long. These generally have scalloped margins, the convex one being developed with rather long processes (Figure 129B).

The polyp body is covered in large scales (Figure 129Ca-z), arranged in rows on the polyp head. Most of them are bilobed with leafy or spiny



Figure 129 Sphaerokodisis tenuis (Thomson and Rennet, 1931), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 130. Sphaerokodisis tenuis (Thomson and Rennet, 1931), holotype, sclerites: Branch coenenchyme.

margins that are often robustly ribbed underneath (Figure 129Cd-g). Sometimes the undersides are heavily warted (Figure 129Cq). The basal body scales are thicker and more irregularly shaped (Figure 129Cn-v). In the vicinity of the branch surface they are occasionally very rugose and somewhat intermediate in form to the coenenchymal sclerites (Figure 129Cw). The adaxial-lateral scales are very narrow (Figure 129Cx-z) and there are about 3 in each row. The adaxial scales are of similar in shape to these and there may be 1-2 of them in a row below which the polyp body is naked. Most body scales are 0.15-0.19 mm long. Thomson and Rennet stated (1931: 17), "the abaxial rows of the calyx show about a dozen sclerites in each row". They are difficult to count, but the correct number would seem to be closer to 16.

## Coenenchymal sclerites (Figure 130)

The surface of the twigs and branches contains numerous spiny oval and spindle-like sclerites, sometimes branched, that are unilaterally developed with tooth-like or leaf-like projections. The underside has complex tuberculate roots. The surface sclerites are up to about 0.26 mm long.

### Variability

Specimen AM G15305 (Figure 124C) when complete would have consisted of several closely appressed, pseudo-dichotomously branched fans. The sclerites are like those of the holotype but the colour is completely different. The colony is brownish orange ( $\approx 6C7$ ) with slightly paler polyps. Basally the axial nodes are dark brown ( $\approx 8F6$ ) and the internodes are unusual silvery white. Distally the internodes are greyish yellow ( $\approx 5B6$ ) and relatively opaque. The branching pattern is much the same as that of *S. flabellum*.

### Distribution

See Figure 277. Depth range 128–183 m, the holotype from somewhere between 119 and 2103 m.

Sphaerokodisis australis (Thomson and Mackinnon, 1911), new comb. Figures 131–137; 278

Mopsea australis Thomson and Mackinnon, 1911: 675–676, Plate LXIV, Figures 1–2; Plate LXVI, Figure 5; Briggs, 1915: 72–73, Plate VI; Kükenthal, 1919: 625–626; Kükenthal, 1924: 441.

## Material examined

# Types

SYNTYPE(S?): AM G6917 (numerous fragments). The collection locality given by Thomson and Mackinnon as "Eleven miles east of Broken Bay" does not correspond to any of the stations sampled by the HMCS *Thetis* as listed by Waite (1899: 20–22). The area 6–9 miles east of Broken Bay was trawled on 19–21 February, 1898, at depths of 20–84 fm.

#### Other material

AM E2127, 15 miles north, 35°E of Saddle Hill, New South Wales, 34–35 fm, FIS *Endeavour*, no date; AM G11638 (3 colonies), G11652 (2 fragments), Broughton Is., New South Wales, 32°36'S, 152°19'E, (no further data); NTM C2397 (2 colonies), Boat Harbour, Sydney, New South Wales, 25 m, K. Harada, 21 Sept. 1975; NTM C5914 (at least 3 colonies, fragmented), Cronulla, Sydney, New South Wales, 24 m, N. Coleman, Jan. 1976.

## **Differential characteristics**

Branching planar and somewhat lyrate; anthopomal triradiate scales with numerous tubercles; coenenchymal sclerites in the form of ovals with sharp tooth-like projections; axial internodes covered in sharp granules.

### Remarks

Thomson and Mackinnon did not designate a holotype, and their description is so general that it could refer to all of the material they had on hand and not just the most intact piece which is presumably that figured in their Plate LXIV, Figure 1. Briggs (1915: 72, footnote) stated, "I have not been able to find, among the specimens returned to the Australian Museum by Thomson and Mackinnon, any specimen labelled as the type of Mopsea australis. I conclude therefore, that it must have been broken up. The cotype, consisting of a number of 'branching pieces of various lengths' has been preserved". There is no relevant material registered at the Natural History Museum (London), and the Australian Museum holds one box of >100 dry fragments labelled "Mopsea australis n.sp." and "Co-type" which I have assumed is the material referred to by Briggs. As Thomson and Mackinnon were probably unable to tell if the material examined by them represented more than one colony, and as a 40 mm branched 'Co-type' fragment fits nearly perfectly over part of the lower portion of their colony illustration, Plate LXIV, Figure 1, it is possible that all of their material is included in the boxed 'Co-type' lot. Similar problematic situations exist with other taxa authored by Thomson and Mackinnon.

As the material proved very difficult to clean for electron microscope examination of the polyps and







Figure 132 Sphaerokodisis australis (Thomson and Mackinnon, 1911), syntype: A. Polyp; B. Coenenchyme; C-D. Axial internodes; E. Twig fragment.

coenenchyme, especially the almost submerged anthopomata, more suitable comparative specimens are also illustrated.

## Description

#### Colony form (Figure 131)

From the dried 'Co-type' fragments it is still possible to show that the specimen(s) was probably planar and branched in pseudo-dichotomous, and somewhat lyrate manner, as illustrated by Thomson and Mackinnon (1911: Plate LXIV, Figure 1). The distance between consecutive subdivisions is 11-25 mm, (14-26 mm measured on the original illustration), and the longest unbranched twig (incomplete) is 110 mm, (140 mm on the illustration). No holdfast or main stem fragment is present. The thickest branch is 2.4 mm in diameter (including polyps). Most branches average 1.3 mm thick, and the thinnest is 0.9 mm. The angle of branching is characteristically 50°, a minority vary between 40-63°. The tips of the twigs are devoid of polyps and have a pronounced taper, as illustrated by Thomson and Mackinnon (1911: Plate LXIV, Figure 2).

## Polyps (Figure 132A,E)

Polyps are densely arranged all around the ramifications. They are relatively evenly spaced, contracted, adaxially reduced, and lie flat against the branch surface partially recessed into depressions in the coenenchyme. The abaxial side of most polyps, especially those on the thicker branches, only project above the surface about 0.2 mm. The anthopomal region of each polyp is angled at about 45° to the branch direction and faces the distal wall of the depression in which the polyp lies. Most polyps are about 0.6–0.7 mm long, and about 0.36 mm across the head and the base, with a very slightly narrower neck zone. Polyps near the growing tips are slightly smaller than the preceding ones.

### Colony colour

Each fragment shows signs of having been stored uncovered for a considerable time, as one side is darkened with grime. The cleaner under-sides are very pale yellowish white ( $\approx$ 4A2). The coenenchyme is thick and the nodes are not visible through it, even when rehydrated. The sclerites are colourless.

### Axis form (Figure 132C,D)

The internodes have multiple rows of low primary ridges, even in the twig tips. There are blunt spines, often in short transverse rows, densely distributed on and between the ridges. The shoulders of the internodes are not pronounced, but the diameter of an internode is commonly slightly narrower across the middle. One of the



Figure 133 Sphaerokodisis australis (Thomson and Mackinnon, 1911). A-B, D-H. NTM C2397: (A-B, D). Polyps; (E). Coenenchyme; (F-G). Axial internodes; (H). Twig fragment. C. AM E2127, polyp.

thicker internodes, 1.40 mm diameter, has 17 ridges. Near a twig tip, internodes about 0.57 mm thick have 7–8 ridges. Desmocyte cavities are shallow.

The internodes of the thicker branches are 1.4–1.7 mm long, while those in the terminal regions are slightly longer, 2.1–2.4 mm. The nodes of the thicker branches are 0.4 mm long and slightly narrower than the internodes. In the more terminal regions, the nodes are only 0.24 mm long, and very thin compared to the internodes.

## Axis branching

If an internode branches only a single bifurcation results. Silhouetting reveals branching nodes are similar to Figure 251 examples 47 and 52.

## Axis colour

The internodes are grey white, translucent in the thicker branches and virtually transparent in the thinnest. Most nodes are more or less opaque and yellowish brown ( $\approx$ 5C5). One visible on the thickest fragment is noticeably darker and brown coloured ( $\approx$ 6D8).

### Polyp sclerites (Figures 132A; 134)

The dried specimen proved very difficult to prepare for electron microscope examination of the polyp and surface of the coenenchyme, especially the anthopoma which in most instances is appressed to the branch. Comparative illustrations are given in Figure 133 of an alcohol preserved specimen from lot NTM C2397 in which the polyps are not so tightly contracted, and also of the dried specimen AM E2127 examined by Briggs.

The anthopoma of the polyps of the type material is asymmetrical and continuous with the polyp body sclerites. The adaxial octant is very reduced and occupied by a small more or less triradiate sclerite, often almost smooth, whose shape may vary from polyp to polyp (Figure 134Ak,l). The other octants contain crescentic and triradiate scales (Figure 134Aa-j,o-t). Generally there is a single crescentic scale followed by a single large triradiate. Sometimes there are 2 crescents and a small triradiate, or a single crescent and 2 tiradiates. In some instances an octant appears to be occupied by a single triradiate only. Occasionally there is an accessory sclerite (Figure 134Am,n) that lies alongside the distal arm of a large triradiate scale. The triradiate scales are mostly <0.12 mm long, but can be up to 0.14 mm in length. They are ornamented with small tubercles on the upper face, and are relatively smooth underneath (Figure 134Ac,d).

There is a basal tentacular sclerite and a single row of curved crescentic scales in each tentacle rachis (Figure 134B). The tentacular crescents are up to about 0.073 mm in length.

The polyp body is covered with large crescentic to oval scales (Figure 132A) arranged in 7 often indistinct rows on the polyp head. The adaxiallateral rows are very short. The adaxial side of the polyp is generally completely naked, but occasionally there is a small curved flattened spindle immediately below the adaxial anthopomal octant. Some of the adaxial-lateral scales are very narrow (Figure 134Cd,n,o), but most body scales are broader and generally have a bilobed, dentate, distal margin (Figure 134Ca-m). Many of the marginal projections have been abraded or broken. The exposed face of the scales is usually smooth, but some have a few small tubercles. The distal scales have 5-6 projections on each marginal lobe. The lower scales generally have about 3 projections each side and the medial cleft is more pronounced. The most basal scales are often quite coarse. On most polyps the larger scales are commonly about 0.12-0.15 mm in length with a few up to 0.17 mm. On some polyps 0.17 mm is not uncommon and a few very narrow scales may reach 0.20 mm in length.

## Coenenchymal sclerites (Figures 132B; 135A)

The surface of the branches contains numerous more or less oval sclerites, some capstan-like, mostly unilaterally developed with short, sharp, tooth-like projections, together with spindles with cone-like tubercles or simple warts. They are mostly 0.04–0.15 mm in length.

There is no stem coenenchyme preserved. Sclerites from the stem of a colony from lot NTM C2397 are illustrated in Figure 135B. They are mostly multiradiate capstan-like forms, commonly 0.05–0.09 mm long, occasionally unilaterally developed with tooth-like projections, and a few larger oval forms with compound warts, which may exceed 0.15 mm in length.

## Variability

The largest colony amongst lots NTM C2397, C5917, and AM G11638 is 140 mm tall. The colonies are preserved in spirit, and one illustrated in Figure 136 shows the typical growth form. The dry specimen examined by Briggs, AM E2127, is now broken into numerous pieces. Briggs reported the colony to be 37.5cm high. The fragments are illustrated in Figure 137; no attempt was made to arrange the pieces to correspond to Briggs' illustration (1915: Plate VI). From these lots it is possible to assess some degree of variability.

Holdfasts, where present, are small and calcareous, and stems are short. Even in the large specimen examined by Briggs, the holdfast is only 15 mm x 8 mm and 5 mm thick, and the stem only 25 mm long. Stems often consist predominantly of nodal material. Stem internodes are small, sometimes reduced to calcareous lenses inserted in



Figure 134 Sphaerokodisis australis (Thomson and Mackinnon, 1911), syntype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 135 Sphaerokodisis australis (Thomson and Mackinnon, 1911), sclerites: A. Syntype, branch coenenchyme; B. NTM C2397, stem coenenchyme; C. NTM C2397, branch coenenchyme; D. AM G11638, polyp body.

the stem sides, or often completely obscured by gorgonin. Stem nodal material is more or less opaque, and can be a fairly dark brown ( $\approx$ 7F8). Main branch internodes may be as short as 0.9 mm.

Branching occurs predominantly from the distal end of an internode, in the style of Figure 251 examples 47, 52, 53 and 55. A small minority of branches originate from a short stump as in examples 6 and 29. The distance between consecutive branchings ranges from 5–78 mm. The shortest distances normally occurring basally. The longest unbranched twig is 302 mm, and about 1.7 mm thick over most of its length.

The smooth polyp-free, tapered growing tips are present in all colonies. The length is variable and can be as great as 10 mm. The growth form is generally planar. It can be very dense with many branches overlapping, and occasionally somewhat bushy with branches growing out of plane. In one small colony, one half of the fan grows at right angles to the other.

Polyp distribution is consistently dense and all around, with exception of the stems and lowest regions of the first branches which are polyp-free. In some specimens the polyps are not deeply recessed into the coenenchymal cavities, and in one specimen the polyps arise more or less at right angles and curve over and down towards the branch surface. Removal of a polyp, however, always reveals a depression below. Measured along the branch, polyps can be up to 0.9 mm long, and they are up to 0.5 mm across the head.



Figure 136 Sphaerokodisis australis (Thomson and Mackinnon, 1911), NTM C2397, natural size x 0.5.

All except two colonies are shades of yellowish white. The exceptions, NTM C2397, are almost white. The colonies of lot NTM C5914 were originally preserved dry and have been rehydrated. The coenenchyme is still opaque, but the polyps, which are yellowish, appear crystalline.

From colony to colony sclerites vary in their degree of spininess, (e.g. Figure 133) perhaps mainly noticeable in the polyps. Both anthopomal sclerites and body scales may be more tubercular, and body scales may have more, and longer, marginal projections. In some colonies the polyps have numerous relatively irregular and complex scales (Figure 135D). The spindles in the coenenchyme of the branches in some colonies may be quite large, up to 0.17 mm long, and also appear more spiny due to their more complex warting (Figure 135C). The tendency towards spininess also effects axial ornamentation; compare Figure 132D to Figure 133F.

In some colonies there is usually a narrow scale below the adaxial anthopomal octant and this may be overlapped by the extensions of similar scales, one each side, that bridge between and below the adaxial and adaxial-lateral octants.

## Distribution

See Figure 278. Depth range 24-153 m.

## Jasminisis gen. nov. Figure 314

Mopsea; (part) Wright and Studer, 1889: xlv, 33, 40–41; Whitelegge, 1889: 27; (part) Thomson and Mackinnon, 1911: 673–679; (part) Briggs, 1915: 70–78; (part) Kükenthal, 1915: 117–118, 123–124 (in keys); (part) Kükenthal, 1919: 558–559 (in key), 617–618; (part) Kükenthal, 1924: 431 (in key), 437; (part) Grant, 1976: 33; (part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49–52 (in key), 57; (part) Bayer and Stefani, 1987b: 940–942 (in key).

## Type species

Jasminisis zebra sp. nov., here designated.

## Diagnosis

All colonies are planar and sparingly branched. Although in one species, *J. zebra*, both pseudodichotomy and quasi-dichotomy can occur in the same colony, the dominant branching pattern is one of pseudo-dichotomy which produces a somewhat lyrate colonial form. In 2 of the 4 described species all known specimens are relatively small; <60 mm tall. The other species are larger with colonies up to 225 mm in height.

All species have colourless sclerites, and preserved specimens are more or less greyish yellow to yellowish white. Axial internodes are white, translucent at the base of the colony becoming transparent in the twigs. The basal nodes are generally opaque and shades of brown, and those in the upper reaches are mostly pale yellow or pale orange and more translucent. Live colour data only exists for *J. cavatica* sp. nov. which was yellow.

Polyp distribution is all around or biserial. In all species the anthocodiae have the same basic structure, but they can look dissimilar because the methods of contraction differ. Polyps are adaxially reduced and angled distad. The base usually appears shelf-like and supports the head which commonly sits snugly against the basal rim. In many polyps there is a suture visible between the head and the base marking a sclerite-free neck zone. In polyps that are slightly more relaxed, the lateral and sometimes also the abaxial aspects of the neck zone can be seen. The adaxial region of the polyp body below the few adaxial head scales is also naked, but is often very short in preserved material. When probing the polyp head to widen the suture and reveal the neck zone, the head will often readily break off, displaying within the proximal end of the pharynx, which is virtually at the same level as the suture line.

The anthopoma is symmetrical in 2 of the described species (J. cavatica sp. nov. and J. deceptrix sp. nov.) and asymmetrical in the others (J. zebra n.sp and J. candelabra sp. nov.). In the latter there is a cavity in the coenenchyme below the adaxial side of the polyp. During contraction the polyp curves over and down towards the branch submerging the adaxial part of the head in the cavity. The adaxial region of the anthopoma is reduced to accommodate this activity. In J. deceptrix the adaxial cavity is more extensive. Instead of curving downwards, the polyp head tilts back in contraction, the polyp base collapses, and the head submerges into the cavity until the anthopoma is more or less flush with the branch surface. There appears to be no introversion of the neck region, and the anthopoma is symmetrical as there is no necessity to accommodate body curvature. The last species, J. cavatica, just contracts the polyp head tightly against the basal rim and





the branch, leaving the symmetrical anthopoma facing away from the branch surface at about 40°.

The anthopomal octants are dominated by a single triangular or triradiate sclerite preceded by 1–2 crescentic scales. The triradiate sclerites are ornamented with stout tooth-like or leaf-like projections, commonly have a waist, and are mostly <0.15 mm long. There is a single basal tentacular sclerite that precedes a single row of curved scales in the tentacle rachis. The tentacle scales are mostly <0.08 mm long. The anthopomal sclerites are continuous with the polyp body sclerites which are arranged in rows, sometimes loosely, on the polyp head. The body sclerites are scales or scale-like, often very thick, developed with stout leafy or angular tooth-like projections, and mostly <0.28 mm in length.

The sclerites of the coenenchyme include capstans, spheroids, and spindles, unilaterally developed with leafy or angular tooth-like projections. They are mostly <0.24 mm long, and a few warty spindles and branched sclerites, often longer, may occur amongst them.

The axial internodes in the thinner branches and twigs are generally 4-sided with small blunt spines over most of the surface. Those near the twig ends tend to have pronounced spiny shoulders. The internodes in the thicker branches and the stem have multiple primary ridges, with the small spines sometimes concentrated more on the ridges. Internodes are mostly <4 mm in length.

#### Etymology

The genus is named for Jasmine Jan, formerly a Trainee Technical Officer of the Museum and Art Gallery of the Northern Territory, who spent countless hours printing many thousands of the photographs that appear in this work, and who also did most of the line drawings. The 'e' has been dropped from 'Jasmine' to prevent confusion in pronunciation.

## Distribution

See Figure 314.

## Jasminisis zebra sp. nov. Figures 138–145; 279

- Mopsea dichotoma; Wright and Studer, 1889: 41–42, Plate IX, Figure 10; Whitelegge, 1889: 27 (listed); Briggs, 1915:70.
- ? Mopsea dichotoma; Hickson, 1890: 137–138 [specimens not located].
- Not Mopsea dichotoma; Thomson and Mackinnon, 1911: 673–674, Plate LXVII, Figure 2. [⇒ Jasminisis deceptrix sp. nov.]
- Not Mopsea dichotoma; Roule, 1907: 438 [⇒ Notisis charcoti sp. nov.].

#### Material examined

#### Types

HOLOTYPE: AM G15312, NW of Montague Island, New South Wales, 66 m, 29 Sept. 1914. PARATYPES: AM G12017, east coast (presumably of Australia), presented by Commonwealth Bureau of Fisheries, (no date); AM G15599, G15601– G15603, data as for holotype; NHMB unregistered specimen, Port Jackson, Australia, 35 fm, HMS *Challenger*.

# **Differential characteristics**

Colonies known up to 215 mm tall; anthopoma asymmetrical; polyps curved over to lay above a shallow depression in the coenenchyme; polyp sclerites with relatively short, pointed projections.

# Description

## Colony form (Figure 138)

The holotype is a planar colony branched in a quasi-dichotomous and pseudo-dichotomous manner. The colony, curved from bottle storage, stretches to 215 mm in height and 95 mm in breadth. It appears to have broken off just above the holdfast. The main stem, devoid of coenenchyme, is 19 mm long and 2.5 mm thick. Basally the first three orders of branching are more or less regularly pseudo-dichotomous. Bifurcations above this is occur more irregularly with some of the divisions towards the centre of the colony approaching a perfect dichotomy. Branching occurs to the seventh order. Branches of the second order are about 1.74-1.90 mm thick, of the third order 1.19-1.58 mm thick, and of the fourth order 1.11-1.26 mm thick (all not including polyps). Terminal twigs are about 0.8 mm thick and only taper slightly. Unbranched twigs are up to 97 mm long. Branching angles are 18–60°. The distance between consecutive subdivisions is 9.5-41.1 mm. The surface sclerites are quite large and easily seen under a dissection microscope.

## Polyps (Figure 139A–C,L)

Distribution is all around on most of the branches and twigs. The density is highest on the inside or less exposed faces of the branches with some areas on the outside faces having very few polyps. The branches at the periphery of the fan only have polyps on their inner faces, and the lowest regions of branches within the fan together with the distal parts of twigs tend to have polyps arrayed biserially. Polyps are not crowded, spaced about 0.7–1.5 mm apart, and many are damaged or have been broken off completely. Upside-down polyps are not uncommon, especially in the lower region of major branches.

The base of a polyp appears shelf-like and there

is an irregular suture, more distinct in some polyps than others, separating it from the head region (Figure 139B). It is possible to flex the head of the more extended polyps against the relatively rigid base to reveal a short sclerite-free neck zone, a character even more demonstrable in some of the paratypes.

The polyp head, with slightly conical anthopoma, generally lies more or less parallel to the branch surface. The gap, if any, between the adaxial side of the head and the branch surface depends primarily upon the angle of the lower shelf-like section of the polyp body and its amount of extension. The abaxial side of some bases is nearly perpendicular to the branch and in these cases a clear gap of about 1.8 mm is visible between the branch and the angled polyp head.

Below the adaxial side of the polyp head there is a concavity in the surface of the branch coenenchyme to accommodate it. In some polyps the head is not parallel to the branch surface but bent in towards it to such an extent that the adaxial one third of the head is tucked into this cavity and into the shelf-like base.

Polyp sizes are very variable. The tallest are 0.66–0.72 mm, the shortest developed polyps about 0.42 mm, and there are many juvenile polyps scattered throughout the colony. Polyp bases are 0.48–0.84 mm long, mostly 0.54–0.66 mm, and polyp heads 0.45–0.51 mm in diameter.



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Figure 139 Jasminisis zebra sp. nov., holotype: A-G. Polyps; H. Coenenchyme; I-K. Axial internodes; L. Twig fragment.



Figure 140 Jasminisis zebra sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp head.

### Colony colour

The coenenchyme is very pale yellowish white. It is translucent and the dark axial nodes effect distinct transverse bands to most of the branches and twigs. Sclerites are colourless.

## Axis form (Figure 139I-K)

Internodes of branches of about the fourth order and beyond are more or less square in cross section with small blunt spines over most of their surface. Developing internodes in the vicinity of twig tips have spines concentrated more towards both ends, particularly on the pronounced shoulders. Internodes proximal to these do not have the distinct shoulders and have spines more evenly distributed. Below these, internodes have four primary ridges, one along each edge. Spines occur on the ridges and on the four curved axial faces between them. Those on the ridges are larger. Internodes of lower order branches and stem have increasing numbers of primary ridges. Desmocyte cavities are shallow, and often elongate in the developing distal segments where they may be more distinct.



Figure 141 Jasminisis zebra sp. nov., holotype, sclerites: Polyp base.

Internodes of the main stem are about 0.6–0.9 mm long. Those of the main branches are 0.5–2.2 mm in length, and those of the twigs 2.1–3.6 mm. The basal axial segment is a node about 8 mm long. Stem nodes above this are 0.8–1.3 mm in length. In the thicker main branches nodes are 0.8–1.1 mm long, and 0.3–0.5 mm long in the others. In the twigs they have a length of 0.24–0.32 mm.

## Axis branching

Branching usually occurs at the distal end of an internode in the style shown in Figure 251 examples 12, and 13.

## Axis colour

The internodes are greyish white throughout the colony. They are translucent in the basal regions but densely coloured. The density of colour decreases distally with the more terminal segments appearing misty and virtually transparent. The nodes of the main stem are brown ( $\approx$ 7E6), virtually opaque, and have very thin yellowish satin-like borders which are reduced to small crescents

between the internodal ridges. In the branches the nodes are henna brown (7E8) with narrow yellowish satin-like borders that are wider between the ridges. In the thin twigs the nodes are greyish yellow, still opaque, and have yellowish satin-like borders that are wider opposite the four faces of the internodes.

# Polyp Sclerites (Figures 139A–G; 140; 141)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 139D–G). Each octant is occupied by a proximal crescentic scale (Figure 140Ah–j) that precedes a triradiate to triangular sclerite (Figure 140Aa–f). There is a single basal tentacular scale (Figure 140Bc) that precedes a single row of curved crescentic scales in the tentacle rachis (Figure 140Ba,b). Occasionally, an extra narrow triradiate sclerite occurs prior to the basal tentacular scale (Figure 140Ag). Most of the larger triangular or triradiate anthopomal sclerites have both spinous and warty marginal projections, a pronounced waist, and a small number of a stout, blunt spines on their upper face. The anthopomal sclerites in the adaxial and adaxial-lateral octants are smaller and less ornate than those in the other sectors; as shown in Figure 139E,F.

The triangular and triradiate forms are mostly 0.11–0.15 mm in length, but can be up to 0.16 mm. The tentacular scales are up to about 0.102 mm long. They have both short and long granular projections that give the convex margin an irregularly scalloped appearance. The outer face of the scales is generally smooth, but the surface of both ends may often be granular.

The polyp head is protected by large scales ornamented with stout spines and angular toothlike projections (Figure 140C). The proximal margins have both short and long, warty, root-like processes, and the undersides are relatively smooth (Figure 140Ca). The scales are arranged in 7 rows on the polyp head in irregularly alternating series (Figure 139A–C). Abaxially there are about 5 series of scales, while adaxially there is commonly only one scale below the anthopomal octant together with the overlapping lateral extensions of a couple of adaxial-lateral scales. Below this the polyp body is naked. The polyp head scales are mostly 0.2–0.3 mm in length.

The scales of the shelf-like base may be similar to those of the polyp head, but they are usually broader, have more projections, and attain a greater length (Figure 141). They are mostly 0.21– 0.28 mm long, but can be up to about 0.32 mm. A few have odd shapes and long root-like structures (Figure 141a–c), and probably occur where the base adjoins the branch surface.

## Coenenchymal sclerites (Figures 139H; 142)

The branch coenenchyme contains a layer of capstans, spheroids, spindles, and occasionally plates, that are unilaterally developed with foliaceous and angular tooth-like projections,



Figure 142 Jasminisis zebra sp. nov., holotype, sclerites: Twig coenenchyme.



Figure 143 Jasminisis zebra sp. nov., paratypes: A. AM G15599; B. AM G15601; C. AM G15602; D. AM G15603. All natural size x 0.4.

together with a few warty spindles and branched forms. Most of the foliaceous sclerites are 0.08–0.19 mm long, but a few of the spindles may reach up to 0.37 mm in length. The warty sclerites are not abundant. They seem to be subsurface forms that occur primarily around the bases of the polyp, and they may be as long as 0.3 mm.

There is no stem tissue remaining on the holotype. The coenenchyme at the base of the main branches where they diverge from the stem contains foliate capstans and spheroids similar to those in the thinner branches. Large foliate spindles and subsurface warty sclerites are rare. Instead, the subsurface layer contains small capstans and radiate forms, 0.098–0.130 mm long, with simple warts.

#### Variability

Three nearly complete colonies and a fragment, possible of a fourth, from the same location as the holotype show variations in growth form (Figure 143). The colonies are 145–





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Figure 145 Jasminisis zebra sp. nov., paratype, AM G12017, sclerites: A. Anthopoma; B. Polyp head; C. Polyp base; D. Coenenchyme.

200 mm tall and all have long terminal twigs, the longest being 130 mm. Two of the colonies (Figure 143B,D) are branched like the holotype, with outermost branches curving away from the point of bifurcation. A third colony (Figure 143C) has no curved branches, although the peripheral branches on one side are missing, and the fourth (Figure 143A) displays some pseudo-dichotomy in one half and quasidichotomy in the other. This latter colony is not flat, the two planar halves occurring at a slight angle to each other.

Sclerites samples from the topotypic specimens show similar variability to that found within the holotype. This variability is most noticeable in the polyp base and the coenenchyme. In one colony it is more common to find polyp bases with very broad, ornate scales, and in another the coenenchyme generally contains a higher proportion of foliate spindles.

Lot AM G12017 from the collections of the Australian Museum seems almost certainly that cursorily described by Briggs (1915: 70) from the material collected by the FIS Endeavour. The fragmented specimen (Figure 144) bears the labels "Mopsea dichotoma" and "East Coast. Pres. Comm. Bur. Fish.". The Fisheries Bureau of the Commonwealth Department of Trade and Customs used the Endeavour for its fishing experiments. Only two species described by Briggs did not have definite location details. One of these was Mopsea dichotoma with the location given as "South east coast of Australia". The specimen lot is a collection of dry fragments. The sclerites are colourless but the pieces have dried to a dull, pale, greyish orange. The branching pattern in the most intact fragment is like that of the holotype and the polyps are mostly arranged biserially in one or two rows. The polyps are relatively small, 0.36–0.51 mm tall, with most about 0.42 mm. There are no gaps between the polyp heads and the branch surface. The heads are angled so that the anthopoma is not at right angles to the surface but faces away from it. Branches and twigs are quite thin, 0.48-0.60 mm (not including polyps) and the axis is like that of the holotype, although some visible segments are not as heavily spined.

There are notable differences between the sclerites of Briggs' material and the other specimens of the type series. However, the material is so similar in all other aspects that it is considered conspecific. The smaller size of the polyp seems to be attributable to greater contraction and a general occurrence of much narrower, often bow-shaped, scales in both the polyp head (Figure 145B) and the polyp base (Figure 145C). Elaborate, heavily ornamented scales like those in the polyp bases of the holotype do occur, but they are never broad

(Figure 145Ca). The surface of the branches contains foliate and warty sclerites, as are found in the holotype, together with many derived forms. The latter are longer, more oval, foliate sclerites (Figure 145Da,b) and numerous forms with very long root-like processes (Figure 145Dc-f). The anthopomal sclerites, however, are much the same as those in all of the other comparative specimens (Figure 145A).

The specimens described by Wright and Studer (1889: 41–42) do not appear to be amongst the collections of the British Museum (NH) and the whereabouts of all but one small portion are unknown. Dr H.D. Volkart of the Naturhistorisches Museum Berne made available to me a small branched fragment found in the collection of Th. Studer and labelled "Mopsea dichotoma L. No 21 Port Jackson Australia 34f", the same locality data given by Wright and Studer. The specimen is about 74 mm long, 0.66–0.78 mm thick, and bears polyps that are arranged all around in some places and biserial in others. The axis is visible at the base of the main branch and is like that of the holotype, as are the sclerites.

# Remarks

Hickson (1890) reported a small amount of material from Port Phillip, Victoria, as being the same as the *Mopsea dichotoma* specimens reported by Wright and Studer (1889), but the samples have not been located.

#### Distribution

See Figure 279. Depth 64-66 m.

## Etymology

Zebra, the Abyssinian name for *Equus zebra*, the striped equine of Africa, in allusion to the banded stem and branch axes of the colonies which are visible through most of the coenenchyme. Noun in apposition.

Jasminisis candelabra sp. nov. Figures 146–149; 280

## Material examined

Types

HOLOTYPE: AM G11675, Broughton Island, NSW, 30°36'S, 152°19'E. PARATYPES: AM G8017, off Port Jackson, NSW, no further data; AM G15591 (22 colonies), data as far holotype.

## **Differential characteristics**

Colonies known only up to 58 mm tall; anthopoma asymmetrical; polyps curved to lay along the surface of the coenenchyme; polyp sclerites with stout, angular or leaf-like projections.

# Description

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#### Colony form (Figure 146a)

The holotype is a small planar colony, sparingly branched in an irregularly pseudo-dichotomous manner producing a somewhat lyrate form. The colony is 40 mm high, 30 mm broad, and has a relatively thick calcareous holdfast which is encrusted with several species of bryozoa. The main stem is about 4.4 mm long and 1.1 mm in diameter including the coenenchyme which is about 0.16 mm thick. The stem divides into two main branches 0.95-1.11 mm thick (not including polyps). About halfway up the colony, branches and twigs are 1.42-1.66 mm thick (including the densely arrayed polyps), they only taper appreciably in the last few millimetres of the blunt tips. Unbranched twigs are up to 30 mm in length. Angle of branching generally 41-63°, with two occurrences of 26°. Distance between consecutive subdivisions is 2.4-8.7 mm.

## Polyps (Figure 147C,D,I)

There are no polyps on the stem, and only a few on the first two short main branches. All other branches and twigs have densely arranged polyps, mostly all around but sometimes biserially in either

## P. Alderslade

one or two opposing rows. The polyps are contracted, reduced adaxially, and curved so that the head lies close to the lateral or abaxial side of neighbouring polyps. The basal part of a polyp is a shelf-like structure and the polyp head is angled from it so as to lie more or less parallel to the branch with the flat anthopoma angled slightly towards the branch surface. In most polyps the suture between the head and the base is quite distinct. In others the head is held tightly against the base, but the suture is easily revealed if the head is flexed with a probe. The bases of developed polyps are 0.48-0.60 mm long, the heads are 0.39-0.48 mm in diameter. Smaller, juvenile polyps are numerous and scattered throughout the colony.

### Colony colour

Dull greyish yellow. The sclerites are colourless.

## Axis form (Figure 147F-H)

The internodes of all but the stem and the basal, thicker, portions of the major branches are more or less square in section and covered in small spines. The four primary ridges that form the four edges are not pronounced and hardly discernible as ridges at all. The spines on the edges are somewhat



Figure 146 Jasminisis candelabra sp. nov., part of type series: a. Holotype; b-d, f-j. Paratypes, AM G15591 (part); e. Paratype, AM G8017. All natural size.



Figure 147 Jasminisis candelabra sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-H. Axial internodes; I. Twig fragment.





larger than those on the slightly curved faces between them. The developing internodes in the vicinity of the ends of the twigs have pronounced spiny shoulders. The stem and lower major branch internodes are also spined and have more than four primary ridges. The ridges are low and occasionally the curved faces between them are raised enough to give the appearance of broad secondary ridges. Desmocyte cavities are shallow, and are more elongate in the younger segments where they may be more distinct.

Nearly all of the internodes are covered by coenenchyme and their lengths are estimated by silhouetting. Those of the stem and main branches are 0.5–0.9 long. In the rest of the colony the internodes are 1.4–2.4 mm in length. The nodes of the stem and main branches are about 0.36 mm long, and those of the rest of the colony 0.18–0.30 mm.

#### Axis branching

The few bifurcations that are visible occur at the distal end of an internode in the style shown in Figure 251 examples 12, 13 and 14. They are all in the lower regions of the colony.

#### Axis colour

The internodes are white, densely coloured but translucent in the basal parts of the colony, becoming nearly transparent in the twigs tips. The nodes of the basal parts of the axis are approximately henna brown (7E7), virtually opaque, with thin, yellowish, satin-like borders. In the middle of the colony the nodes are brownish orange ( $\approx$ 5C6) with the satin-like borders mainly visible as crescents between the shoulders of the primary ridges. Nodes of the twig tips are paler than those in the middle of the colony and have very thin borders.

### Polyp sclerites (Figures 147A-D; 148)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 147A,B). Each octant is generally occupied by a large triradiate sclerite (Figure 148Aa–g) that is preceded by 1–2 crescentic scales (Figure 148Ah–k). The anthopomal sclerites on the adaxial side of the polyp are smaller and less ornate than those in the other octants. The triradiate sclerites usually have a narrow waist, and are ornamented with tall leaf-like or angular tooth-like processes. There is a



Figure 149 Jasminisis candelabra sp. nov., holotype, sclerites: Branch coenenchyme.

single row of curved scales in the tentacle rachis (Figure 148Ba,b), which is generally preceded by a single basal tentacular sclerite. The latter may be tuberculate Plate (Figure 148Bc,d) or a miniature triradiate form (Figure 148Be). On occasions it seems both may occur. The large anthopomal triradiates are mostly 0.11–0.13 mm long. The tentacular scales, up to about 0.077 mm long, have granular projections that produce irregularly scalloped margins.

There appears to be little to distinguish between the sclerites of the polyp head and the base. Those of the base may occasionally be larger, or unusually shaped or plate-like where the polyp adjoins the branch surface, but they are generally very similar in design to those of the head. The body scales are mostly very thick, curved to fit the contours of the polyp, elaborately sculptured with tall leaf-like projections, and held in place by tuberculate root structures (Figure 148C). The thick and somewhat non-scale-like nature of most of the sclerites can be seen on the abaxial aspect of the polyp in Figure 147C. The body sclerites are arranged on the head in alternating series forming 7 rows; there being only 1-2 simple scales (Figure 148Ca,b) below the adaxial octant. The abaxial rows are the longest with about 5 sclerites per row. In the tightly contracted polyps the naked neck zone below the adaxial octant is very short. Most of the larger polyp body scales are 0.18-0.22 mm long, but the range is about 0.15–0.27 mm.

## Coenenchymal sclerites (Figures 147E; 149)

The surface of the branch contains predominantly capstans, clubs, spheroids, and spindles unilaterally developed with leafy projections. There are also a few small spindles with conical projections, and the occasional large warty spindle or branched sclerite. Surface sclerites can be up to about 0.025 mm long but most are usually <0.22 mm.

The stem coenenchyme contains leafy capstans and clubs about 0.06–0.13 mm long, and warty capstans up to about 0.15 mm in length.

### Variability

The paratypes consist of 22 colonies and some fragments from the type locality, and a single specimen from off Port Jackson. The latter (Figure 146e), poorly preserved, is the largest of the type series, 58 mm tall and 33 mm broad with several unbranched twigs about 34 mm in length. The branches are up to 1.74 mm thick and the polyps, many of which are damaged, are very densely arranged with no areas of biserial distribution. Of the other colonies, the smallest is 28 mm high and 16 mm across, and the largest is 46 mm high and 42 mm across. The branching patterns are much the same as the holotype, although a few are more profusely ramified. Some are shown in Figure 146. In most colonies the stem divides into two main branches. However, in one colony three branches, and in another colony four branches, diverge from the top of the stem by virtue of a complex axial internode.

One colony is nearly completely devoid of coenenchyme permitting more accurate axial measurements to be made. The nodal material of the main stem covers most parts of the short nodes, which are about 0.24 mm long. The basal internodes of the main branches are 0.4-0.9 mm and the nodes about 0.4 mm in length. In the middle and upper reaches of the colony the internodes are 0.8-1.5 mm and the nodes 0.18-0.24 mm long. The basal internodes of the thickest branches are more or less hexagonal in cross section, and above this the internodes are 4-sided. Most of the branches in the upper parts of the colony originate from short calcareous stubs as in Figure 251 example 6. The point of bifurcation occurring anywhere from the proximal to the distal parts of the internode.

In a number of the paratypes the last few millimetres of the twigs have no polyps and taper to a rounded tip. In the holotype, the polyps continue right to the apex of each twig.

In general, the sclerites of the topotypic paratypes agree very well with those of the holotype. The most notable difference is that some coenenchymal samples contain many more long leafy spindles.

The colony from Port Jackson has sclerites of somewhat aberrant form. The polyp body scales are nearly all very broad and they are very densely covered in leafy projections, but they are no longer than those of the holotype. The anthopomal triradiates are sometimes irregularly shaped, and sometimes densely covered in tooth-like projections. Others are flatter with small well spaced tubercles. The basal tentacular scales are often poorly formed.

#### Distribution

See Figure 280.

## Etymology

Candelabra is an alternative English spelling of candelabrum, from the Latin *candelabrum*, a candlestick that can be branched and it is used in allusion to the colony form of some of the more sparingly branched specimens. Noun in apposition.

## Jasminisis deceptrix sp. nov. Figures 150–154; 281

Mopsea dichotoma; Thomson and Mackinnon, 1911: 673–674, Plate LXVII, Figure 2.

Figure 150 Jasminisis deceptrix sp. nov., holotype, natural size.

- Not Mopsea dichotoma; Wright and Studer, 1889: 41–42, Plate IX, Figure 10; Whitelegge, 1889: 27 (listed); Briggs, 1915: 70. [⇒ Jasminisis zebra sp. nov.].
- Not Mopsea dichotoma; Roule, 1907: 438 [⇒ Notisis charcoti sp. nov.]

## Material examined

## Types

HOLOTYPE: AM G12153, HMCS Thetis, station 48, off Wollongong, NSW, 55–56 fm, sand and mud

to rock, 18 March 1898. PARATYPES: AM G11653 (2 fragments), Broughton Island, NSW, 32°36'S, 152°19'E; AM G8016, off Port Jackson, NSW, registered Feb. 1908; BM 1960.12.1.57 – BM 1960.12.1.60, four microscope slides prepared by Thomson and Mackinnon, which could be from the holotype.

# Differential characteristics

Colonies known up to 225 mm tall; anthopoma symmetrical; polyps may be contracted within a coenenchymal depression with the anthopoma



Figure 151 Jasminisis deceptrix sp. nov., holotype: A-G. Polyps; H. Coenenchyme; I-K. Axial internodes; L. Twig fragment.

more or less flush with the branch surface; polyp head scales relatively simple; polyp base scales elaborate with stout leaf-like projections.

# Description

Colony form (Figure 150)

The holotype, in which the branching is sparingly pseudo-dichotomous, seems to agree more or less with Thomson's and Mackinnon's (1911: 673-674) description of their largest specimen. They described it as follows: "an almost complete lyre shaped colony, rising from a slightly encrusting calcareous base to a height of 22.5 cm. The main stem, 3 mm in diameter near the base, divides to form two equal branches at a height of 2.5 cm. These two main branches give rise along one side to a number of secondary branches which run parallel to one another. As these secondary branches are nearly as thick as the main branch from which they spring, the effect of a repeated dichotomy is produced, an effect that is heightened by the tendency of the main branch to bend outward after each branch is given off, so that its course describes a series of shallow curves. The secondary branches rise straight upwards and may remain unbranched throughout their length, or may divide dichotomously. Branching is strictly in one plane". The tips of most of the twigs are now broken off leaving the extremely fragile colony 173 mm tall and 83 mm broad. The main stem is mostly devoid of coenenchyme and 2.7 mm thick at the base, (perhaps the coenenchyme was still intact when measured by Thomson and Mackinnon). The two short main branches are about 2.5 mm thick. About half way up the colony, branches and twigs are about 1.3-1.6 mm thick. The twigs do not taper markedly except at the tips, the broken fragments of which are preserved with the colony. They are long, relatively smooth, bearing only non-protruding developing polyps, and finish in a rounded tip. The longest (incomplete) unbranched twigs are up to 125 mm long. The distance between consecutive subdivisions is usually short, about 4-10 mm, but can be up to 40 mm. Angle of branching is 38–68°.

# Polyps (Figure 151C--G,L)

Distributed all around, with irregular spacing, except on the main branches in the lower peripheral regions which are virtually devoid of polyps. Most polyps are clearly separated from each other but the arrangement is not regular and a few polyps more or less touch each other.

Polyps are present in various stages of contraction. In those that are most exert the polyp head is clearly distinguishable from the small shelf-like base from which it protrudes (Figure 151E). These polyps make an angle of about 45° with the

branch surface, and the anthopomal region is either slightly domed or flat and faces away from the branch. In many there is a sufficient gap between the head and the base to clearly see the lateral aspects of a broad, naked neck zone (Figure 151D). Lifting the polyp head with a probe reveals the adaxial region of the neck zone extending down into a depression in the branch surface. The anthocodia is actually anchored below the surface of the coenenchyme, the edge of the coenenchyme forming the wall of a circular-like cavity which cradles the polyp head when it is fully contracted and more or less flush with the surface. In such a case the cavity is found to be deepest on the distal and lateral sides of the polyp, while abaxially there is a narrow region where the wall of the anthocodia is attached much closer to the surface. What appears to have happened in the most contracted polyps is that the shelf-like base has collapsed as the polyp has deflated, with the edges of its scale-like sclerites forming concentric semicircles and merging with the sclerites of the coenenchyme. The polyp head has tipped back so that the anthopoma faces directly upwards and has come to lie level with the surface (Figure 151A,B,L). If the coenenchymal sclerites surrounding the contracted polyp are prised loose, or a twig fragment is decalcified, the dome-shaped polyp head can be seen sitting in the base of the cavity. The neck zone is now so contracted that it is virtually undetectable, and, most importantly, there appears to be no introversion in the accepted sense.

It seems that during expansion the hydrostatically inflated polyp balloons outward enlarging below the abaxial region of the branch surface and lifting and stretching it upwards to form the shelf-like base.

There are polyps preserved in different states of contraction between the two extremes. The majority have the head and base well inflated. Many are partially contracted with a very short base. In some, the anthopoma is more or less level with the branch surface but a low abaxial, rim-like basal mound still remains.

Polyps sizes are varied. Most of the larger polyp heads are about 0.42–0.48 mm in diameter and when exert protrude about 0.36 mm above the branch surface. A few polyps have grown upside-down, and small, obviously juvenile polyps are scattered throughout the colony.

There are numerous polyps that look deformed. They appear as a semi-elliptical group of concentric scales around often ill-defined anthopomal octants, sometimes raised on a surface bulge, and stretched to an oval arrangement in the direction of the branch (Figure 151F,G). The adaxial or distal octants sometimes appear to be immersed beneath the coenenchyme. In fact these octants seem to



Figure 152 Jasminisis deceptrix sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp head.


Figure 153 Jasminisis deceptrix sp. nov., holotype, sclerites: A. Polyp base; B. Branch coenenchyme.

have been resorbed, the polyp being adnate to the branch in this area. There is usually a small aperture between the tips of the existing octants, and dissection reveals the tentacles are missing. Each of these polyps contains a brown subspherical mass about 0.62 mm in diameter which is probably a developing planula.

### Colony colour

Cream, the polyps appearing as very small darker spots to the naked eye, and greyish yellow under the dissecting microscope. The nodes can only be seen through the thick coenenchyme on the stem and lower regions of the main branches.

## Axis form (Figure 1511-K)

In the long twigs and branches the internodes are 4-sided and covered in small spines. The four primary ridges forming the four edges are for the most part only recognisable as ridges at the shoulders. In the more distal parts of the twigs the spines seem fairly evenly distributed over the faces, except in the developing tip region where they are concentrated more at either end and especially on the shoulders. In the lower thicker regions of the twigs and branches, the primary ridges become slightly more pronounced and spines occur predominantly on the ridges and down the centre of each curved face, sometimes to the extent of appearing like a secondary ridge. In the main branches the internodes have more than four primary ridges, and these are very pronounced. The spines are fewer in number, those on the faces quite small and granule-like, and those on the ridges larger and more concentrated at the shoulders. The stem internodes have pronounced primary ridges with spines on the shoulders. Desmocyte cavities may be very long and narrow, but for the most part they are so shallow as to virtually go undetected.

Only a few axial segments are visible and able to be measured. The basal segment is a large node about 7 mm long. The three nodes visible above this are about 1.6 mm long. The two basal internodes, partly covered with nodal material are 0.8–1.6 mm long. About half way up the colony the two internodes measured were 2.4 mm and 3.5 mm long, and the nodes were 0.32 mm in length. Nearer the twig tips the internodes measured were 2.7–4.4 mm long and the much narrower nodes 0.32 mm.

#### Axis branching

Branching occurs at the distal end of an internode in the manner of Figure 251 examples 12 or 13.

## Axis colour

The internodes are white. In the main stem they

are densely coloured and virtually opaque. In the middle to apical regions of the colony they are quite translucent, like milky glass. The basal nodes are translucent and reddish brown ( $\approx$ 8E8) with thin silver satin-like borders between the shoulders. The nodes in the middle region are apricot yellow (5B6) and virtually opaque, with thin satin-like borders on each of the flattened faces. In the more distal regions the nodes are light orange ( $\approx$ 5A4), slightly translucent, with very thin silvery borders.

## Polyp sclerites (Figures 151A-E; 152; 153A)

The anthopoma is symmetrical and continuous with the polyp head sclerites (Figure 151A–E). In general each octant contains 2 proximal crescentic scales (Figure 152Aj) that precede 2 triradiate to triangular sclerites. In most octants only the broader of the triradiate forms is obvious (Figure 152Aa,f) as the distal, narrower sclerite (Figure 152Ag,i) is often considerably overlapped by the preceding scale or is angled downwards into the central aperture. Despite its large size, it probably functions as a basal tentacular scale. There is a single row of curved crescentic scales in each tentacle rachis (Figure 152B).

The larger triradiate anthopomal scales generally have a few strong apical and lateral marginal spines, a medial waist, and a small number of stout, blunt spines on the upper face. These sclerites are mostly about 0.09–0.11 mm long. The narrow triradiate scales may be slightly longer, up



Figure 154 Jasminisis deceptrix sp. nov., paratype, AM G8016, natural size.

to about 0.13 mm. The tentacular scales have marginal tubercles giving on irregular scalloped appearance. They are up to about 0.08 mm in length and may have a few granules on the outer face.

The polyp head is protected by several series of broad scales (Figure 152C). The scales are arranged in single rows below each octant. On the lateral and adaxial aspects there are generally about 3 series of scales, below which the neck zone is naked. Abaxially, there are several extra scales arranged more or less in a single row extending the girdle of head sclerites down to the shelf-like base. Most of the head scales are 0.16–0.23 mm long and have large tooth-like projections along the distal margin and root-like processes proximally. The scales on the abaxial region of the neck zone are often not as broad as the others and they may have very long root structures (Figure 152Ca–c).

The surface of the base contains predominantly scales with stout, smooth, angular tooth-like and leaf-like projections (Figure 153A). Most are about 0.14–0.24 mm in length. Most tuberculate forms like those in Figure 153Aa,b are probably subsurface sclerites from where the base merges with the branch surface. Surface sclerites in this region are intermediates to these in the general coenenchyme (Figure 153Aa).

# Coenenchymal Sclerites (Figures 151H; 153B)

Sclerites in the coenenchyme are mostly foliate capstans and derived forms, but include a few subsurface spindles. The foliaceous sclerites are mostly 0.07–0.12 mm long, and the warty spindles, which are sometimes flattened, are longer and up to about 0.28 mm in length.

Coenenchyme is present only on the uppermost portion of the stem, and the sclerites are the same as those on the branches.

# Variability

AM G8016 is a small, pale, nearly white colony that looks very smooth relative to the holotype (Figure 154). It is curved from bottle storage and is about 90 mm tall, and 53 mm across. It appears to have been broken off just above the holdfast. A number of the branches are just naked axes. The branches and twigs are about 1.89-2.05 mm thick, tapering gradually to just over 1 mm in diameter below the bluntly rounded twig tips. The polyps are distributed all around and are all maximally contracted, hence the smooth appearance of the colony. Most polyps have a very slight elevated coenenchymal rim below the proximal side of the anthopoma. The anthopoma is slightly tilted forward, but is at the general level of the branch surface. Although the polyps are slightly darker than the surrounding coenenchyme they are not easy to distinguish, especially if there is no coenenchymal swelling or tilted anthopoma, as is often the case.

Most of the axial internodes are 1.7–2.2 mm long, the range being 1.3–2.5 mm. The coenenchyme is very thick, about 0.5 mm.

## Distribution

See Figure 281. Depth 102 m.

## Etymology

The Latin *deceptrix*, she that deceives, in allusion to the false impression that the anthocodiae are retractile.

Jasminisis cavatica sp. nov. Figures 155–157; 282

## Material examined

## Types

HOLOTYPE: NTM C919, Michaelmas Reef, Great Barrier Reef, Qld, 10 m, growing down from roof of small cave, P. Alderslade, Nov. 1978. PARATYPES: NTM C917, C918, C920, C921, data as for holotype.

## **Differential characteristics**

Colonies known only up to about 70 mm tall; cave habitat; branches very fine; anthopoma symmetrical; polyps short, cylindrical, and angled obliquely; polyp body sclerites narrow, like flattened spindles; coenenchyme without foliaceous capstans.

## Description

## Colony form (Figure 155A)

The holotype branches in one plane in a pseudodichotomous manner. The stem divides into two main branches that continue to ramify and so divide the colony into two halves which overlap in the centre of the fan. Divisions occur in each half of the fan at similar heights as though the growth plane was to produce mirror images on each side, but irregularities here and there have prevented this from happening. The overall effect is one of a dichotomous trend but the branchings are actually lateral and not symmetrically dichotomous divisions. The small, delicate colony is 68 mm tall and 35 mm broad, and is attached to a calcareous fragment of bryozoan skeleton by a small expansion of the basal axial node .

The stem is denuded and about 0.95 mm thick. The major branches are 1.3–1.4 mm thick in the lower regions, 1.1–1.3 mm thick in middle parts, and 0.9–1.1 mm thick in the upper regions (all including polyps). The twigs do not taper much and are about 0.8 mm thick just below the tip.

Branching occurs to the fourth order. Unbranched twigs can be up to 35 mm long. Distance between consecutive branchings may be as short as 2 mm but gaps as long as 10–15 mm are not uncommon. Angle of branching 35–50°.

## Polyps (Figure 156A,B,I)

Polyp distribution is biserial, with two alternating rows on each side of the thicker branches becoming virtually one row each side on the thinner ramifications with consecutive polyps leaning to alternate sides.

The polyps are short, contracted, reduced adaxially and angled at about 35–45° so that the more or less flat summit of the anthopomal region faces away from the branch. The basal portion of the polyp forms a short shelf-like structure on to or into which the heavily armoured, narrower, polyp head is contracted. The head sits snugly against the rim of the base in most polyps, whilst in others a sufficiently wide suture exits between the head and rim that parts of the sclerite-free neck zone can be seen. Polyps protrude from the branch surface about 0.29–0.36 mm, and polyp heads are about 0.41–0.48 mm in diameter. Juvenile polyps occur scattered throughout the colony.

#### Colony colour

Pale yellow ( $\approx$ 4A4–4A3) with colourless sclerites. The darker nodes of the lower regions can easily be seen through the coenenchyme, but the paler ones of the more distal regions are more difficult to detect. Yellow when alive.

### Axis form (Figure 156F-H)

Nearly all of the axial internodes are 4-sided and covered with small spines. In all but the developing terminal and sub-terminal internodes the four primary edge ridges are so low that they are more or less only recognisable as ridges at the shoulders. In the terminal regions, a shallow, wide furrow in which the shallow but distinct desmocyte cavities



Figure 155 Jasminisis cavatica sp. nov., type series: A. Holotype. All natural size.

are situated, runs down the centre of each internodal face. In the thicker regions of the twigs and branches the faces are wider, the furrow virtually disappears and spines occur across the face. The few internodes of the basal regions of the main branches have more than four low primary ridges, and the upper internode of the stem (the lower one is covered in modal material) has 14 ridges and a few small spines.

Throughout the colony most internodes are about 2.1–2.9 mm long. The nodes in the basal regions are about 0.4–0.6 mm long, and those in the finer twigs about 0.12 mm in length.

### Axis branching

The first two bifurcations at the base of the colony are similar to Figure 251 example 12, and the third and fourth are as in examples 27 and 26

respectively. Throughout the rest of the colony most points of branching are like examples 6, 4 and 29. There is only one instance where an internode initiates 2 branches.

## Axis colour

The internodes of the thicker basal regions are translucent white, like milky glass. The translucency increases in the finer parts of the axis and the more distal twig internodes are quite colourless. The basal nodes are very dark yellowish brown ( $\approx$ 5F8) gradually changing to greyish yellow ( $\approx$ 4C5) in the twigs. They all have broad yellowish satin-like borders.

## Polyp sclerites (Figures 156A-D; 157A-D)

The anthopoma is symmetrical. Each octant is dominated by a large triangular scale that lies flat

Furth Further area is a contract of the provided in the pro



Figure 157 Jasminisis cavatica sp. nov., sclerites: A-E. Holotype: (A). Anthopoma; (B). Tentacles; (C-D). Polyp body; (E). Branch coenenchyme. F. Paratype, NTM C917, surface stem coenenchyme.

on the summit of the polyp. At first glance this gives the appearance that the anthopoma contains only 8 sclerites (Figure 156C,D). However, in most octants these sclerites are preceded by a semicircular or crescentic scale (Figure 157Ae–k) that does not usually lean inwards very far but is sometimes found folded down. This is clearly seen in Figure 156C. The anthopomal sclerites are ornamented on their exposed face with stout, angular projections, sometimes flattened (Figure 157Aa,b,e,g–k). The undersides have a few small tubercles (Figure 157Ac,d,f). The triangular forms are mostly about 0.11–0.14 mm long.

There is a single basal tentacular sclerite, commonly shaped like a miniature triangular anthopomal scale (Figure 157Bb), that precedes a single row of curved scales in the tentacle rachis. These tentacle scales are few in number, smooth, 0.049–0.069 mm long, and usually have a broad concavity in the distal margin (Figure 157Ba).

The polyp head and the shelf-like base are protected by thick, curved sclerites that are often very large. Many are better described as flattened spindles than as scales. Above the neck suture the polyp head is girdled with several irregular series of scales. The scales are generally arranged in rows of about 2 per row. Extra long scales sometimes disrupt the arrangement, and, depending on the thickness of the sclerites involved, the girdle may in places be 1 or 3 scales in width. The naked adaxial region below the polyp head is very short. All body scales have short, angular, sometimes spiny projections on their outer face, and a few warts on their undersides (Figure 157C,D). Most are up to about 0.34 mm in length, but a few may be as long as 0.39 mm. The longest occur on the polyp base.

# Coenenchymal sclerites (Figures 156E; 157E)

The Surface of the branches contains predominantly spindles, some slightly curved, that are asymmetrically developed with short, spiny, angular projections which are occasionally leaf-like. The undersides have a few short, root-like warts. They are up to about 0.24 mm in length, and a few broader, plate-like forms, and some small spindles with simple tubercles may be found amongst them.

There is no stem tissue left on the holotype. A sample from a paratype reveals the stem coenenchyme contains spindles 0.09–0.21 mm in length. Most differ from the branch sclerites by having finer projections on the upper face, and longer root-like warts which also project laterally (Figure 157F).

# Variability

The paratypes are all of similar size to the holotype (Figure 155). The branching patterns are different but the general mode of ramification is

the same. A couple of axial internodes examined from the middle region of one colony were found to have a slightly raised region running down the centre of each face. There were fewer spines in this area and the desmocyte cavities were confined to rows either side of the central zone.

# Distribution

See Figure 282. Depth 10 m.

# Etymology

From the Latin adjective *cavaticus*, born or living in caves, in allusion to the type habitat.

# Ktenosquamisis gen. nov.

# Type species

Ktenosquamisis bicamella sp. nov., here designated.

## Diagnosis

Colonies are planar, pinnate, and plumose. The largest specimen is 125 mm tall, but it is incomplete.

The sclerites are colourless and the pinnae of preserved specimens are somewhat cream coloured. The principal branches, however, are pale greyish red due to the colour of the axial internodes which are like rose quartz. The internodes of the pinnae are almost transparent, with a pale milkiness. Proximal main branch nodes are translucent and dark brown, while those distad are almost transparent with a central dark zone deep within. Pinna nodes are pale yellow with a narrow, grey, middle band.

Polyps are biserially arranged on the pinnae in 2 opposing rows. They are club shaped, adaxially reduced, not adaxially naked, and usually preserved curved over and angled distad.

The anthopoma is asymmetrical, with each octant containing a single row of triangular to semicircular scales. The large apical triangular scales are up to about 0.1 mm long. There is a single, large, basal tentacular sclerite, and a single row of curved scales in the tentacle rachis.

The polyp body is protected by large, predominantly smooth, oval to semicircular scales with ctenate distal margins. Most are up to 0.12 mm long, and they are arranged in 8 rows on the polyp head. The coenenchyme contains small modified capstans, 0.035–0.050 mm long, that resemble 2 goblets fused side to side.

The internodes of the pinnae are all 4-sided with clusters of knobs on the shoulders. The principal branch internodes have multiple smooth primary ridges with smooth shoulders, and each commonly initiates 1–3 pinnae. Internodes may be up to 2.4 mm in length.

## Distribution

As for Ktenosquamisis bicamella, see Figure 283.

### Etymology

The name employs the Greek *Ktenos*, comb, and the Latin *squama*, scale, in allusion to the comb-like margins of the polyp scales; combined with *Isis*.

## Ktenosquamisis bicamella sp. nov. Figures 158–160; 283

#### Material examined

### Types

HOLOTYPE: QM GL10380, off the Gold Coast, Queensland, 27°24'S, 153°51'E, 260 m, FV Iron Summer, G. Smith, Qld. Dept. of Fisheries, 25 Sept. 1982. PARATYPE: QM GL10375, off the Gold Coast, Queensland, 28°05'S, 153°54'E, 270 m, FV Iron Summer, P. Dutton, Qld. Dept. of Fisheries, 27 July 1982.

### Diagnosis

As for the genus.

## Description

### Colony form (Figures 158)

The holotype is only a portion of the parent colony. It is about 125 mm tall and 130 mm across, planar, and pinnately branched. The pinnae are alternately arranged with occasional irregularities. The main branch is about 17 mm long, 2.2 mm thick, devoid of coenenchyme, and bears the stubs of broken pinnae. It divides into two major branches, 1.6 mm thick, which are pinnately branched and which also give off, laterally and irregularly, lower order pinnately ramified branches. The third order branches are 1.1–1.3 mm thick and the fourth 0.8–0.9 mm thick. The lower regions of the thick branches are devoid of coenenchyme. The pinnae are relatively delicate and narrow, about 0.32 mm thick, and taper only



Figure 158 Ktenosquamisis bicamella sp. nov., holotype, natural size.

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Figure 159 Ktenosquamisis bicamella sp. nov., holotype: A-F. Polyps; G. Coenenchyme; H-K. Axial internodes; L. Twig fragment.

slightly. They rarely rebranch, and most of the tips are missing. Of the intact ones the length varies from 12–28 mm. The pinnae are evenly spaced, 58 per 55 mm proximally, 58 per 50 mm distally, and arise at an angle of 40–55°. The major branches ramify at 40°. There are no portions of the main stem.

### Polyps (Figure 159D-F,L)

The polyps are biserially arranged in single rows on the pinnae, with a few occurring on the thinner more distal branches between the pinna bases. Polyps in opposing rows may be opposite or alternate and all lean slightly towards one face of the colony. There are 40–45 polyps per 15 mm of a single row.

The polyps are contracted, adaxially reduced, and curved distad with the anthopomal region angled slightly towards the branch surface. A polyp base is about 0.36–0.48 mm long, the distinct neck region 0.19–0.24 mm thick and the head 0.29– 0.36 mm across. Polyps commonly project 0.36– 0.43 mm from the twig surface, but some are as low as 0.24 mm and more erect individuals are up to 0.48 mm. Juvenile polyps are much smaller and are scattered throughout the colony.

### Colony colour

The pinnae are very pale yellowish grey to cream. The major branches are the colour of pale rose quartz, a pale greyish red (≈7B3), due to the colour of the axial internodes which are mainly naked but show through the coenenchyme where it is intact. All sclerites are colourless.

#### Axis form (Figure 159H-K)

All internodes of the pinnae are 4-sided, and the shoulder regions have clusters of knob-like processes. Internodes of the principal branches have multiple primary ridges and knob-free shoulders, except in the most distal regions where some branches undergo a dramatic reduction in thickness over one internode, and become twiglike terminally. There are no distinct secondary ridges, though the desmocyte cavities, which are shallow, are arranged in rows either side of the primary ridges in the thicker branches and leave a slightly raised area between.

Most branch internodes are 2.4–3.2 mm long. A basal internode 2.0 mm thick has 48 ridges, an upper branch one 0.6 mm thick has 10 ridges. Internodes of the pinnae are 1.3–2.4 mm long. Branch nodes are about 0.80 mm long basally, 0.32–0.47 mm long mid-colony, and 0.24 distally. Nodes of the pinnae are 0.12–0.18 mm long. Nodes are slightly narrower than internodes.

### Axis branching

Internodes commonly support 1-3 branches, and

very rarely 4. In the finer branches many pinnae grow from short internodal stubs as in Figure 251 example 5. In the thicker branches the pinnae grow from nodes that are countersunk into the internode as in example 18, and nodal material often extends just over the end of the first internode of each pinna. If a pinna emerges from a node of a thicker branch, the nodal material is shared as in example 17.

## Axis colour

Pinna internodes are glass-like, virtually transparent, with a pale milkiness. Principal branch internodes are the colour of pale rose quartz and translucent. Basal nodes are translucent, dark brown (≈7E8), with yellow brown satin-like borders. Translucency increases distad and in the upper principal branches the nodes are more or less transparent and a central dark region can be seen deep within each one. The nodes of the pinnae are pale yellow and satin-like, translucent and not transparent, with a grey, narrow, middle band.

## Polyp sclerites (Figures 159A-F; 160A-C)

Each octant of the anthopoma, apart from the adaxial one, consists of a large triangular sclerite continuous with the polyp body sclerites through a series of two and sometimes three more or less semicircular scales (Figure 159A-C). These 2-3 scales (Figure 160Ca,b) show a stepped differentiation from the upper body scales through to the more triangular terminal anthopomal scales (Figure 160A) that occupy the central area of the anthopoma. The main feature of differentiation, apart from shape, is the presence of small spines on the upper face. It would appear from the image in Figure 159A that the single differentiated scale below the adaxial octant is not able to fold down like the corresponding sclerites in the other octants. This does not seem to be the case, however, in Figure 159B. The anthopoma is asymmetrical, with sclerites in the abaxial and abaxial-lateral octants being larger than the more adaxial ones. The triangular sclerite of the adaxial octant is notably smaller and simpler (Figure 160Af) than those in the other octants which usually have a more tuberculate and spiny upper face and a more dentate margin. The triangular sclerite in the abaxial octant may be considerably expanded (Figure 160Aa). The underside of the triangular scales sclerites are tuberculate (Figure 160Ab-e), and most of the larger ones are about 0.10 mm in length, although they can be up to 0.11 mm.

There is a single basal sclerite. It is usually quite long, approaching the size of the preceding scale in many instances, but much narrower (Figure 160Be), and in some cases the two extremities of the basal margin of the sclerite may be spine-like. A single row of curved crescentic sclerites extends distad in



Figure 160 Ktenosquamisis bicamella sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Coenenchyme.

each tentacle rachis (Figure 160Ba-d). They are up to 0.60 mm across and have tuberculate margins.

The scales of the polyp head are arranged in 8 rows (Figure 159D), the adaxial scales being reduced in both size and number. The scales are curved to such an extent that the rows appear ridge-like (Figure 159F). Numerous series of scales cover the lower part of the polyp. The exposed margin of the scales is irregularly ctenate and may have a medial notch making the scale somewhat bilobed (Figure 160C). The scales are commonly about 0.12 mm across, but sclerites larger and more elongate than these, up to 0.16 mm, are not uncommon. Small forms like Figure 160Cg,h may be found where the basal polyp sclerites merge with those of the surface of the twig. The undersides of the body scales are tuberculate (Figure 160Cc-f).

### Coenenchymal sclerites (Figures 159G; 160D)

The surface of the branches (Figure 159G) contains capstans that are unilaterally modified to appear somewhat like two goblets, with tuberculate stems, fused side to side (Figure 160D). The sclerites are very small, mostly 0.035–0.050 mm. Upper and lower aspects are illustrated in Figure 160Da,b.

### Variability

The paratype is only a plumate fragment consisting of two branch segments a total of 95 mm in length. Its characteristics are the same as those of the holotype.

### Distribution

See Figure 283. Depth range 260-270 m.

### Etymology

The epithet alludes to the resemblance of the surface sclerites to the shape of two goblets, and employs a Latin word for goblet, *camella*.

## *Myriozotisis* gen. nov. Figure 315

## Type species

Myriozotisis heatherae sp. nov., here designated.

## Diagnosis

Colonies planar, up to 162 mm tall, and profusely and finely branched in a dense, pseudodichotomous and lateral manner.

Preserved colonies are greyish orange like the colour of new rust. Sclerites are yellowish in transmitted light. Axial internodes are mostly orange-white and translucent in the thicker branches, becoming transparent and orange or orange-brown in the finer ramifications. Nodes are dark brown or orange.

Polyps are distributed biserially in opposing single rows, and all angled towards one face of the colony. They are slightly club-shaped, adaxially reduced, and not adaxially naked although the sclerites in this region do not tightly dovetail and small naked patches can occur.

The anthopoma is slightly asymmetrical. Each octant is occupied by a single more or less triangular scale; the one in the adaxial octant being the smaller. There can be a single marginal body scale below each octant that may be preserved folded towards the anthopoma. The triangular scales are up to 0.18 mm long. Their upper face is ornamented with tubercles in *M. heatherae*, and with a cluster of medial spines in *M. spinosa* sp. nov. There is a single basal tentacular sclerite preceding a single row of curved sclerites in each tentacle rachis.

The polyp body is protected by large smooth scales, up to 0.24 mm long. Those in the upper body are bilobed and arranged in 7 rows. The lower body scales may or may not be bilobed.

The surface of the coenenchyme mostly contains unilaterally foliate capstans, spheroids, and spindles, up to about 0.17 mm long.

The axial internodes in the finer branches are 4sided, and those in the thicker ones have multiple primary ridges. Low, broad secondary ridges sometimes occur. Internodes rarely produce more than one branch, but are occasionally complexly branched and antler-like. They are up to 1.7 mm long in *M. spinosa* and 4.3 mm long in *M. heatherae*.

## Distribution

See Figure 315.

#### Etymology

In allusion to the profuse, dense branching the generic name is derived from the Greek *Myrios*, numberless, and *ozotos*, branched or branching; combined with *Isis*.

*Myriozotisis heatherae* sp. nov. Figures 161–165; 284

### Material examined

### Types

HOLOTYPE: QM GL10379, off the Gold Coast, Queensland, 28°05'S, 153°54'E, 270 m, FV *Iron Summer*, Queensland Dept. of Fisheries, P. Dutton, 27 July 1982. PARATYPE: QM G301210, data as for holotype.

### **Differential characteristics**

Anthopomal scales with numerous small spines



Figure 161 Myriozotisis heatherae sp. nov., holotype, natural size.

on the upper face; polyp body scales weakly bilobed.

## Description

## Colony form (Figure 161)

The holotype is an incomplete, finely branched, fragile colony 162 mm tall and 125 mm across. The colony is profusely ramified in one plane; the major branches branch laterally, and the fine branches and twigs both laterally and pseudodichotomously. The denuded main stem is 3.2 mm thick and 20 mm long. It divides into two main branches, denuded in their lower regions, 2.1 mm and 2.8 mm thick. The main branches repeatedly give off much finer branches that intricately ramify, and also major branches that by division progressively become thinner and eventually indistinguishable from the thin twigs. The fine twigs and branches that form the delicate fan-work are about 0.58–0.66 mm thick (without polyps). Unbranched twigs are 1.5–10.5 mm long. Distance between consecutive subdivisions is 1.9–6.6 mm. Angle of branching is usually 20–60°, with some twigs in the lower regions arising at near 90°.

### Polyps (Figure 162 C-G,I,J)

The polyps are biserially arranged on the fine branches and twigs in opposing single rows. Polyps are opposite or alternate, angled towards one face of the colony, and evenly spaced with about 32 polyps per 10 mm per row. On the major branches the polyps are irregularly scattered and quite a few are upside-down.



Figure 162 Myriozotisis heatherae sp. nov., holotype: A-H. Polyps; I-J. Twig fragment.

The polyps are relatively short, adaxially reduced, and angled at 22–42° distad. The anthopomal regions are mostly flat or slightly concave, and are angled away from, or nearly perpendicular to the branch surface. The bases of the polyps are about 0.36–0.48 mm wide and the anthopoma about 0.30–0.36 mm across. There is a slightly narrower neck zone. Polyps project about 0.30–0.54 mm. Juvenile polyps are few, and are most common on the terminal portions of the twigs.

## Colony colour

Greyish orange ( $\approx$ 6B6) like bright new rust, with paler greyish yellow polyp anthopomal regions ( $\approx$ 4B6). All axial nodes can be seen through the translucent coenenchyme. Sclerites are yellow to pale yellow in transmitted light.

## Axis form (Figure 163)

The internodes have low primary ridges and low, broad, secondary ridges. The finer twig and branch internodes are 4-sided. Thicker branch, major branch, and stem internodes have multiple primary ridges. A stem internode 3.2 mm thick has 56 primary ridges. The tip of a developing terminal internode is often sinuous with a concavity on one side (Figure 163C). Desmocyte cavities are very shallow.

Internodes of the stem are 1.3–2.4 mm long. Those in the rest of the colony mostly 2.7–4.3 mm

long, with those in the twigs tending to the lower end of the range. Nodes in the stem and main branch are about 1.6–2.4 mm, in the major branches 0.4–0.8 mm, and in the finer twigs and branches 0.18–0.36 mm long.

### Axis branching

Although most internodes rarely support more than one branch, a few are compound as in Figure 163A and Figure 251 example 23. Most pseudodichotomous joints in the thinner branches are like example 22, and the lateral divisions are like example 8 and 21. In the stem and thicker branches branching is like examples 19 and 20.

### Axis colour

Internodes of the stem and major branches are greyish white in the proximal regions, densely coloured but translucent, becoming pale orange white distally. In the thinner branches and twigs the internodes are orange brown ( $\approx$ 7C7) to brown ( $\approx$ 7D7), the finest ones transparent. The nodes of the stem and major branches are dark brown ( $\approx$ 8F6) and more or less opaque proximally becoming progressively more translucent in the distal regions. They have thin yellowish brown satin-like borders. In the thinner branches they are dark brown ( $\approx$ 8F3), transparent, with yellow brown satin-like borders. The nodes in the fine twigs have satin-like borders that are very wide and silvery, with a very narrow dark brown central zone.

Figure 163 Myriozotisis heatherae sp. nov., holotype: A-D. Axial internodes.





### Polyp sclerites (Figures 162A-H; 164)

Each octant of the anthopoma is occupied by a single, large, more or less triangular sclerite (Figure 162A,B). The anthopoma is asymmetrical and the adaxial sclerite is shorter, narrower, and smoother (Figure 164Ag,h) than those in the other octants (Figure 164Aa-e) which have short spines on their upper face and sometimes on the lateral margins. These sclerites are mostly 0.10-0.13 mm long, and their undersides are relatively smooth (Figure 164Af). There is normally one basal sclerite in each tentacle. It is more or less arrow head shaped (Figure 164Ba,b) and quite large, up to 0.09 mm, occasionally more rectangular and smaller. The tentacles contain a single row of curved crescentic sclerites (Figure 164Bc-e) up to 0.06 mm in length, the smaller ones often having an irregular outline.

There is usually one more or less erect marginal body scale below each octant. It is bilobed (Figure 164Ca) and appears prone to falling out during the preparation for SEM examination. One can be clearly seen in Figure162C. They may be preserved tilted towards the anthopoma. The adaxial marginal sclerite is reduced Figure 162H or absent.

The polyp body is protected by large oval to crescent-shaped scales (Figures 162E; 164C). The more distal scales are arranged in 7 rows and their exposed serrate margin is divided into two lobes. The more proximal scales are often irregular in shape with deeply incised margins. These scales occur right around the polyp and cover the basal area of the adaxial side. Above them the adaxial zone is protected by the extensions of the adaxiallateral sclerites (Figure 162H) and by other smooth, irregularly shaped scales (Figure 164D). These scales do not tightly dovetail in and small naked patches can be seen here and there, particularly just below the adaxial octant. On the abaxial side at the base of the polyp, the scales are often elongate and plate-like (Figure 164Cb,f) and extend onto the surface of the twig (Figure 162G,H). Most body scales are up to about 0.16 mm across, although those extending onto the twig surface can be up to 0.24 mm.

## Coenenchymal sclerites (Figures 162F; 165A)

The twig surface predominantly contains spheroids and spindles, which are unilaterally foliate (Figure 165A) and mostly 0.08–0.17 mm long. A few foliate capstans and tuberculate spindles also occur, the largest spindles are often slightly flattened (Figure 165Aa,b). Scale-like forms (Figure 165Ac,d) may occur near polyp bases. The coenenchyme of the stem is missing but, minute fragments remain on the paratype which contain capstans, up to 0.10 mm long, many of which are unilaterally foliate or spinous (Figure 165B) and the occasional larger flattened spindle.

#### Variability

The paratype (which may be a portion of the



Figure 165 Myriozotisis heatherae sp. nov, sclerites: A. Holotype, twig coenenchyme; B. Paratype, QM G301210, basal stem coenenchyme.

holotype) is slightly larger than the holotype, but similar to it in all other characters.

## Distribution

See Figure 284. Depth 270 m.

### Etymology

This species is dedicated to Heather Winsor of the Electron Microscope Unit, James Cook University, for her advice and assistance and for taking many thousands of the sclerite electron micrographs used in this project.

## *Myriozotisis spinosa* sp. nov. Figures 166–169; 285

## Material examined

#### Types

HOLOTYPE: QM G4708, east of Jumpin Pin, Queensland, 47 fm, dredged, W. Stephenson, 1 July 1961. PARATYPES: QM G301207–G301209, data as for holotype.

#### P. Alderslade

### **Differential characteristics**

Anthopomal scales smooth except for a medial cluster of large spines; polyp body scales strongly bilobed.

#### Description

## Colony form (Figure 166)

The holotype is a finely branched, fragile colony 145 mm tall and 125 mm wide. The ramification is a mixture of pseudo-dichotomous and lateral branching in one plane. The denuded stem is 1.6 mm thick and measures 27 mm to the first intact branch. Several branch stubs remain below this. The stem gives off numerous thin main branches that ramify repeatedly resulting in a profusely branched fan-like colony. Branch and twig thicknesses are consistent throughout the colony, the thicker branches about 0.55-1.11 mm, the terminal or subterminal twigs 0.24-0.42 mm (without polyps). The distance between consecutive subdivisions in the lower region of the colony is 4.7-10.3 mm, in the upper region 1.6-4.7 mm. Angle of branching 23-33°.



Figure 166 Myriozotisis spinosa sp. nov., holotype, natural size.

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Figure 167 Myriozotisis spinosa sp. nov., holotype: A-F. Polyps; G. Coenenchyme; H-J. Axial internodes; K. Twig fragment.

### Polyps (Figure 167D–F,K)

The polyps are biserially arranged in opposing single rows on all twigs and branches, and leaning towards one face of the colony. The polyps are contracted, adaxially reduced, mostly angled distad at about 42° and gently curved so that the anthopoma is usually slightly less than 90° to the branch surface. In some cases the polyps lie along the branch. A polyp base is 0.42–0.54 mm long and the anthopoma is 0.30 mm across. Polyps project 0.30–0.39 mm. Juvenile polyps are scattered throughout the colony.

## Colony Colour

Greyish orange ( $\approx$ 6B6). All nodes easily visible through the coenenchyme. Sclerites yellow to pale yellow in transmitted light.

### Axis form (Figure 167H–J)

Internodes have low primary ridges. with only the faintest trace of low, broad secondary ridges. The finer twig and branch internodes are 4-sided. Desmocyte cavities are very shallow. A main branch internode about 1 mm thick has 28 ridges. The tip of a developing terminal internode is often sinuous with a concavity on one side.

Internodes of the stem about 1.1–1.6 mm long, nodes slightly shorter and narrower. Throughout the rest of the colony internodes are about 1.3–1.7 mm long. Nodes in the thicker branches are about 0.60 mm long, about 0.18–0.30 mm in the thinner branches and twigs.

## Axis branching

Compound internodes like those found in *R. heatherae* are rarer and simpler in this species. Most internodal branching involving the finer branches is like Figure 251 examples 21, 22 and 8. Rarely does an internode produce more than one branch. In the lower regions of the colony where thicker branches are involved, branching is of the style shown in examples 12 and 13.

#### Axis Colour

Internodes of the stem and lower regions of the major branches are pale orangeish white, translucent but densely coloured. In the middle and upper regions of the colony the internodes are translucent orange ( $\approx$ 6B8), becoming transparent in the finer twigs and branches. The nodes of the stem and lower regions of the major branches are orange ( $\approx$ 6B8). They are virtually transparent with a dark deep central zone like a blackish air bubble and wide yellowish satin-like borders. In the thinner branches the borders of the nodes are very broad and the central orange region correspondingly shorter. In the twigs the nodes are mostly silvery satin-like, the orange central region reduced to a thin line.

## Polyp sclerites (Figures 167A-F; 168; 169A)

The anthopoma of most polyps is preserved flat or concave. Each octant is occupied by a large somewhat triangular sclerite (Figure 167A–C). The anthopoma is asymmetrical, and the adaxial sclerite is narrower (Figure 168Ag) and occasionally shorter (Figure 168Ah), and often preceded by a small rectangular scale (Figure 168Ai). The larger anthopomal sclerites (Figure 168Aa–f) are mostly 0.14–0.18 mm long, apically spatulate, and on their upper face they have a medial cluster of long spines. The distal half of each sclerite is bent slightly downwards, and the undersides are not tuberculate (Figure 168Ae).

There is usually one basal tentacular sclerite for each octant (Figure 168Bc). The other tentacular sclerites are few in number and occur in a single row. They are small, 0.07–0.05 mm, curved, crescentic and usually irregular in outline (Figure 168Ba,b).

There are small, bilobed, marginal body scales (Figure 168Aj,k) below the octants that stand more or less in a broken circle and are sometimes preserved tilted towards the anthopoma. There may be 2 marginal scales below the abaxial octant, one or two below the lateral octants, and a single reduced one adaxially.

The polyp body is protected by large scales (Figures 167D-F; 168C; 169A). The more distal ones are in 7 rows, and their bilobed margin flares outwards. The more basal scales have an irregularly toothed margin which may or may not be bilobed. The scales become very irregular in shape at the base of the lateral and adaxial lateral sides of the polyp and extend onto the lower adaxial area. The adaxial body wall above them is not naked but is protected by the extensions of the upper adaxial-lateral scales, and smooth platelets which are often branched situated between them (Figure 168D). The scales and platelets are not closely dovetailed and small naked patches can be seen here and there. The major body scales are mostly 0.12-0.19 mm across, and the undersides are usually heavily tuberculated, with keel-like ribs often associated with prominent marginal lobes (Figures 168Ca,b; 169Aa,b).

### Coenenchymal sclerites (Figures 167G; 169B)

In the surface of the twigs the majority of sclerites are capstans, spheroids, and small spindles, that are unilaterally foliate and mostly 0.08–0.12 mm long (Figure 169B). Occasionally more plate-like sclerites are found, up to about 0.15 mm, that are foliate on their upper surface (Figure 169Ba–e). Larger forms (Figure 169Bf–i) are more usually associated with the most basal areas of the polyps. A few flat multiradiate sclerites (Figure 169Bj) may be found between the bases of the surface sclerites.



Figure 168 Myriozotisis spinosa sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Small polyp body scales; D. Adaxial polyp platelets.



Figure 169 Myriozotisis spinosa sp. nov., holotype, sclerites: A. Large polyp body scales; B. Twig coenenchyme.

The sclerites in the surface of the thicker branches are like those in the twigs, but there is more of the larger foliate capstans and spheroids.

### Variability

The three paratypes are all slightly smaller than the holotype. In one colony most of the polyps lie very close to the branch surface. In the other two, the polyps tend to be much more erect than those of the holotype, projecting up to 0.63 mm, with the anthopoma facing away from the branch.

### Distribution

See Figure 285. Depth 86 m.

### Etymology

From the Latin *spinosus*, thorny, in allusion to the medial clusters of spines on the large triangular anthopomal sclerites.

## Iotisis gen. nov.

Mopsea; (part) Nutting, 1910: 17–18; (part)
Kükenthal, 1915: 117–118, 123–124 (in keys); (part) Kükenthal, 1919: 558–559 (in key), 617–618; Kükenthal, 1924: 437; (part) Grant, 1976: 33; (part) Bayer, 1981: 942 (in key); (part) Bayer and Stefani, 1987a: 49–51 (in key), 57; (part) Bayer and Stefani, 1987b: 940–942 (in key).

## Type species

Mopsea alba Nutting, 1910, here designated.

 $\equiv$  *Iotisis alba* new combination.

## Diagnosis

The only known specimen was originally 15 mm tall and 20 mm broad, planar, and sparsely branched in a lateral or irregularly pinnate manner.

Preserved colony colour is white, as are the axial nodes and internodes.

Polyps are sparse and irregularly biserial. They are more or less club-shaped, adaxial reduced, and contracted so as to be angled distad and lie close to the branch surface. The anthopoma is symmetrical and each octant contains a single row of predominantly boomerang-shaped scales, up to 0.19 mm long, preceding a single row of curved scales, up to 0.085 mm long in the tentacle rachis.

The polyp head has 8 rows of scales with toothed margins, and the polyp base is covered in unilaterally toothed spindles. The polyp body sclerites are up to 0.28 mm long.

The coenenchyme contains unilaterally toothed rods, spindles, and branched forms up to 0.19 mm long.

The axial internodes are up to 8 mm long. They are curved and twisted, have multiple primary ridges, and the surface is smooth.

#### Distribution

As for *lotisis alba*, see Figure 286.

### Etymology

Derived from the Greek letter *lota*, commonly used to mean the smallest amount, in allusion to the diminutive nature of Nutting's specimen; combined with *Isis*. The 'a' from *lota* has been dropped for the purpose of euphony.

## *Iotisis alba* (Nutting, 1910) new comb. Figures 170–173; 286

Mopsea alba Nutting, 1910: 18–19, Plate IV, Figures 2,2a; Plate VI, Figure 4; Kükenthal, 1915: 123 (in key); Kükenthal, 1919: 622; Kükenthal, 1924: 438–439.

## Material examined

#### Types

HOLOTYPE: ZMA COEL2898, south-west of the island of Waigeo, *Siboga* Expedition, station 156, 0°29.2'S, 130°5.3'E, 469 m, coarse sand and broken shells, 15 Aug. 1899.

### Diagnosis

As for the genus.

## Description

## Colony form (Figure 170)

All that remains of the holotype illustrated by Nutting (1910) in his Plate IV, Figures 2,2a, is about 13 pieces of axis with a small amount of coenenchyme attached, two intact polyps, and some fragmented tissue debris. One fragment of axis is attached by a small holdfast to a piece of olive coloured conglomerate. The colony was reported to be 15 mm tall and 20 mm broad. From the illustration the branching could be described as lateral, or irregularly and sparsely pinnate, and planar.

#### Polyps (Figure 171)

Polyps are sparse and irregularly biserial. The two remaining polyps are contracted, reduced abaxially, and have swollen bases about 0.36 mm long. The polyp heads lie close to the branch surface and are about 0.43 mm in length from the narrow neck region to the tip of the conical anthopoma, and about 0.36 mm across. Measured along the branch the polyps are about 0.7 mm long. Nutting gave the polyp dimensions as "1.6 mm. in height and 1 mm. across the margin", but the 5 times magnified illustration in his Plate IV, Figure 2a, would seem to confirm that this is incorrect.



Figure 170 Iotisis alba (Nutting, 1910). Reproduction of Nutting's pl. IV of the holotype of Mopsea alba. 2. Colony, natural size. 2a. Branch, natural size x 5.



Figure 171 Iotisis alba (Nutting, 1910), holotype: Polyp.

Colony colour White.

### Axis form (Figure 172)

The internodes have pronounced smooth primary ridges that appear uneven due to the distinct twists and curves in each axial segment. Most internodes are thickest in the middle and taper towards each end.

Internodes are 0.36–7.60 mm long and 0.18–0.45 mm thick. One internode 0.43 mm thick has 10 primary ridges. The nodes are about 0.12 mm long and considerably thinner than the internodes.

### Axis branching

Nutting reported internodes carrying up to 3 branches. Amongst the remaining fragments, branches either arise from calcareous stubs as in Figure 251 examples 8 and 16, or begin with a node as in example 15.

### Axis colour

The internodes are translucent and white. The nodes are the same colour with satin-like borders.



Figure 172 Iotisis alba (Nutting, 1910), holotype: Axial internodes.



Figure 173 Iotisis alba (Nutting, 1910), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Branch coenenchyme.

## Polyp sclerites (Figures 171; 173A–C)

Only a broken polyp base, and a fragment of a polyp head with a couple of body scales and anthopomal octants intact, were used for sclerite study. The structure of the remaining 2 whole polyps should be re-evaluated if new material thought to be conspecific is found.

The anthopoma appears to be symmetrical and continuous with the polyp body sclerites (Figure 171). Each octant contains a row of about 5 crescentic to boomerang-shaped spiny scales, up to 0.19 mm long (Figure 173A). The smaller distal forms merge with the single row of curved sclerites in the tentacle rachis. The most proximal tentacular sclerites are quite thick (Figure 173Bd–f), but the majority are thin and scale-like with long tooth-like projections on the distal margins. They are up to 0.085 mm long (Figure 173Ba–c).

There are about 6 series of scales on the polyp head arranged more or less in 8 rows. Some very large scales reach across neighbouring rows. The few scales seen were 0.22–0.27 mm long and ornamented with angular tooth-like projections (Figure 173Ca–c). The sclerites on the polyp base resemble spindles more than scales. They are unilaterally developed with tooth-liked projections, and may be up to 0.28 mm long. The adaxial side of the polyp does not appear to be naked.

## Coenenchymal sclerites (Figure 173D)

The branch surface contains predominantly rods, spindles, and branched forms, developed with rounded or angular tooth-like projections and up to 0.19 mm long.

### Distribution

See Figure 286. Depth 469 m.

## Peltastisis Nutting, 1910 Figure 316

Peltastisis Nutting, 1910: 5, 19; Gravier, 1913c: 457 (in key), 459; Gravier, 1914: 25 (in key), 28; Kükenthal, 1915: 117–118 (in key), 122; Kükenthal, 1919: 558–559, 606–607 (in keys), 609–610; Kükenthal, 1924: 431; Bayer, 1956: F222; (part) Grant, 1976: 9–10, 42; Bayer, 1981: 941 (in key); Bayer and Stefani, 1987a: 49–51 (in key); Bayer and Stefani, 1987b: 938, 940–942 (in keys).

## **Type species**

*Peltastisis uniserialis* Nutting, 1910, by original designation.

## Diagnosis

Apparently unbranched, although only one colony fragment has been collected of *P. cornuta* Nutting, 1910. The only other species, *P. uniserialis*,

is reported to grow to 85 mm in length.

Sclerites are colourless and the preserved specimens are white. Nutting recorded the polyps and "ovigerous" swellings as pale brown. Axial internodes are chalky white, and nodes are greyish yellow or pale brown, but all existing material examined is badly affected by fixation in acidic media.

Polyps are well spaced and distributed uniserially. Swellings containing ova occur midway between many pairs of consecutive polyps. Polyps are squat, adaxially reduced, not adaxially naked, and usually preserved curved over and leaning distad. In *P. cornuta* the abaxial side of the polyp is supported by a single, large, bow-shaped sclerite.

The anthopoma is continuous with the polyp body scales, and is more or less symmetrical. In *P. uniserialis* each octant is occupied by several triangular to triradiate scales, usually fewer than 5, up to 0.22 mm long. In *P. cornuta* there is generally a single, large, triangular scale in each octant, up to 0.32 mm long. Each tentacle rachis contains a single row of relatively large, curved, crescentic scales preceded by a basal tentacular sclerite.

The polyp body is protected by large scales which are oval, rectangular, crescentic, or irregular in outline, and may occur in ill-defined rows. The scales may be almost smooth, or they may have rounded tubercles like the anthopomal sclerites. They are usually <0.27 mm long in *P. uniserialis* but may be up to 0.45 mm in *P. cornuta*. The large abaxial sclerites in *P. cornuta* are up to 1.3 mm long.

The coenenchyme contains spindles, sometimes flattened and sometimes branched, up to 0.42 mm long. they are developed, mostly unilaterally, with rounded tubercles and tooth-like projections.

The axial internodes are round in cross-section and slightly flared at the ends. They are up to 3.6 mm long in *P. uniserialis* and 5.9 mm in *P. cornuta*.

#### Distribution

See Figure 316.

## Peltastisis uniserialis Nutting, 1910 Figures 174–178; 287

Peltastisis uniserialis Nutting, 1910: 5 (in key), 19–20, Plate IV, Figures 3,3a; Plate VI, Figure 3; Kükenthal, 1915: 122 (in key); Kükenthal, 1919: 610; Kükenthal, 1924: 431.

### Material examined

#### Types

HOLOTYPE: ZMA COEL3013, east of the southern tip of the island of Halmahera, *Siboga* Expedition, station 145, 0°54'S, 128°39.9'E, 827 m, hard bottom, pumice stone, 9 Aug. 1899.



Figure 174 Peltastisis uniserialis Nutting, 1910, holotype fragment.

## Differential characteristics

Polyps without large, abaxially placed supporting sclerites.

## Description

### Colony form (Figure 174)

The holotype has been reduced to numerous small unbranched fragments with a maximum length of 10 mm. According to Nutting, the original colony was 62 mm in length. The fragments vary in thickness from 0.24–0.29 mm. The colony is extremely fragile and has all the characteristics of having been stored for considerable time in an acidic medium, most likely formalin. It is difficult to pick up fragments with forceps and not accidentally crush them.

#### Polyps (Figure 174)

Polyps are uniserially distributed, not crowded, and about 1.2–1.7 mm apart. They are contracted, reduced adaxially, and angled at about 42° to the stem surface. Measured along the stem the polyps are 0.61–0.84 mm long. They rise about 0.38–0.51 mm above the surface. The polyp heads are 0.38–0.48 mm across and conical.

Between many pairs of consecutive polyps the coenenchyme is swollen forming an apparent



Figure 175 Peltastisis uniserialis Nutting, 1910, holotype: A-B. Axial internodes.

brood pouch, reported by Nutting to contain ova. Most of these pouches are 0.60–0.91 long and 0.14– 0.24 mm high. When two polyps are close together the pouch stretches virtually from base to base. If the polyps are farther apart the pouch is closer to the distad polyp and sometimes marginally confluent with its base. The pouches sometimes are extremely small and they do not occur between every pair of polyps.

Several small, cylindrical, juvenile polyps are present. They arise singly between pairs of developed polyps, and proximal to any brood pouches.

## Colony colour

White with pale greyish white polyps. The pale nodes can be seen underlying the thin coenenchyme.

## Axis form (Figure 175)

The internodes are chalky and extremely brittle. They are more or less round in cross section and slightly flared at the ends. There are no ridges but the only segment submitted to SEM examination shows some slight fluting in the shoulder regions. The desmocyte cavities are very shallow and probably rendered less distinct by the acid etching.

The internode are 0.9–3.6 mm long and 0.21–0.26 mm thick. The nodes are 0.19–0.21 mm long and 0.17–0.24 m thick.

A section of intact denuded axis consisting of eight internodes is registered under the same number as the holotype but recorded as coming from another station. The internodes are white, macroscopically smooth, slightly flared at the ends, and some are curved. They are 0.48–3.50 mm long and 0.24–0.30 mm thick, and more or less round in section. The nodes are transparent, dark yellowish brown, 0.17–0.19 mm long, and 0.19 mm thick. This axial section does not appear to have been affected by an acidic storage medium and its conspecificity with the holotype is possible but not proven.

### Axis colour

The internodes are chalk white and opaque. The nodes are greyish yellow and nearly completely transparent.

## Polyp sclerites (Figures 176; 177)

The extremely thin, fragile, eroded nature of many of the sclerites (Figure 176g,h) makes it very awkward to accurately assess their arrangement in the anthopoma. It is difficult in many instances to differentiate individual sclerites, and many of the sclerites have so little remaining calcium content that they virtually disappear in a cleared polyp. Only a few relatively intact sclerites were found suitable for SEM examination. Others are illustrated here by drawings from a slide mounted preparation where much of the ornamentation could only be guessed at because the sclerites are so transparent. Many may have originally had more tubercles than is indicated. The anthopoma is continuous with the polyp body sclerites, and appears to be very slightly asymmetrical. Nutting's (1910: 20) statement that "there is a strong operculum of the primnoid type, composed of eight flaps, each flap consisting of a single scalelike spicule", is incorrect. Most anthopomal octants within a single polyp differ slightly in their structure and none contain just a single sclerite; although some appear to at first glance. In general, the apex of each octant appears to be occupied by 2 small triangular to triradiate sclerites (Figures 176a; 177Ae-h,j-n). The proximal one is the largest and often angled sharply to the plane of the octant, lying on the summit of the polyp or angled downwards into the aperture at the centre of the anthopoma. The distal of the two is the smallest and appears to occupy the basal tentacular position, although there may be succeeding sclerites that are intermediate in design to the tentacular scales (Figure 177Ad). The major portion of the octant may be occupied by a single large triangular scale (Figures 176b; 177Ao,p), but more

commonly this is replaced by 2 scales, one following the other, with the most proximal often resembling that shown in Figure 177Ai. Occasionally, 2 scales side by side replace the larger form. Where the body sclerites merge with those of an octant there may be 1–2 narrow scales, or a single broad scale, that appear to form the proximal part of the octant (Figures 176c; 177Aq– t). In its most complex form, therefore, an octant may contain 5 scales plus a basal tentacular sclerite, but usually there are fewer.

The anthopomal sclerites are ornamented with tooth-like or rounded projections. The triangular scales are up to about 0.22 mm long. The rachis of each tentacle contains a single row of large, curved, crescentic scales with a dentate convex margin (Figure 177Aa–c), up to about 0.11 mm in length.

The polyp body is protected by large scales that are more or less oval, rectangular, or crescentic in shape (Figures 176d-f; 177B). In the abaxial region at the base of the most developed polyps the sclerites are usually largest and often irregularly arranged. Above these, sclerites are organised into often ill-defined rows, one below each octant. The number of series of sclerites differs considerably between polyps. In some polyps, above the disorganised basal zone, the abaxial rows may have 8-10 scales. In others there may only be 4-5. The basal area may be covered with a few large scales or numerous smaller ones. In some polyps the basal sclerites are not disorganised and form part of abaxial rows containing 6-7 sclerites. The adaxial side of the body is very short and is not naked. It is difficult to count the scales in this region but the maximum is perhaps 3-4. Most of the rows of body scales are well defined in the juvenile polyps. Body scales are ornamented with rounded tubercles. The



Figure 176 Peltastisis uniserialis Nutting, 1910, holotype, sclerites.



Figure 177 Peltastisis uniserialis Nutting, 1910, holotype, sclerites: A. Anthopoma; B. Polyp body.

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Figure 178 Peltastisis uniserialis Nutting, 1910, holotype, sclerites: Coenenchyme.

largest scale seen was 0.27 mm in length, but most are no larger than about 0.24 mm.

## Coenenchymal sclerites (Figures 176i-k; 178)

The coenenchyme contains a single layer of spindles, mostly narrow, occasionally with short branches, and often medially thickened. They are developed, mostly unilaterally, with rounded tubercles and short tooth-like projections. The few examined were 0.12–0.42 mm in length.

## Remarks

Nutting (1910: 20) stated that a number of unbranched specimens were dredged from station 159, the largest being 8.5cm long. It was apparent he had not seen them and there are no other specimens identified as *P. uniserialis* in the Zoölogische Museum, Amsterdam. I am indebted to Mr John Vermeulen of that institution for permission to dissociate the sclerites from a polyp and some tissue fragments from the sparse holotype material. Only a few sclerites were photographed using the SEM, the remainder being permanently mounted for light microscopy.

### Distribution

See Figure 287. Depth 827 m.

## Peltastisis cornuta Nutting, 1910 Figures 179–182; 288

Peltastisis cornuta Nutting, 1910: 20–21, Plate IV, Figures 4, 4a; Plate VI, Figures 1,2,5; Kükenthal, 1915: 122 (in key); Kükenthal, 1919: 610–611; Kükenthal, 1924: 432, Figure 204.

### Material examined

#### Types

HOLOTYPE: ZMA COEL 3012, Timor Sea, *Siboga* Expedition, station 300, 10°48.6'S, 123°23.1'E, 918 m, fine grey mud, stones and plant (?) material, 30 Jan. 1900.

#### **Differential characteristics**

Polyps with a single, large, abaxially placed supporting sclerite.

## Description

#### Colony form (Figure 179)

All that remains of the holotype is a small unbranched fragment 8 mm long with 3 attached polyps, one loose damaged polyp, several naked axial internodes, and some tissue fragments. The branch portion is 0.30–0.36 mm thick.



Figure 179 Peltastisis cornuta Nutting, 1910, part of holotype fragment.

#### Polyps (Figure 179)

Distributed uniserially about 2.1 mm apart, squat, contracted, adaxially reduced, and angled at about 48° to the surface of the branch. They rise about 0.72 mm above the surface, with a domed anthopomal region 0.54–0.66 mm wide. A single large supporting sclerite extends along the abaxial side of each polyp.

On the polyperous face of the branch fragment a single low swelling occurs about midway between each pair of successive polyps. They are apparently brood pouches, about 0.84–1.08 mm long, 0.11–0.24 mm high, and are reported by Nutting (1910: 21) to contain ova.

### Colony

White with pale greyish white polyps. The pale axial nodes can be seen underlying the coenenchyme. The polyp stays have a satin-like sheen.

### Axis form (Figure 180B)

Internodes round in cross section and flared at each end, with shallow, elongate but short desmocyte cavities scattered all over the surface. The surface has probably been eroded to some degree by formalin as the segments are extremely brittle and have the characteristic appearance of being stored for some time in an acidic medium.

The internodes are 5.1–5.9 mm long and about 0.26 mm thick. The nodes are about 0.18 mm long and 0.30 mm thick.



Figure 180 Peltastisis cornuta Nutting, 1910, holotype: A. Large abaxial polyp sclerite; B. Axial internode.

#### Axis colour

The internodes are chalk white. The only naked node is pale brown.

## Polyp sclerites (Figures 179; 181; 182A)

The anthopoma is symmetrical and some octants are more or less continuous with the body scales. The majority of octants are occupied by a single, large triangular scale (Figures 181a; 182Aj,k) up to 0.32 mm long. At the apex of each octant, lying on the polyp summit or angled downwards towards the central aperture, is a smaller scale (Figures 181b; 182Ah,i) that appears to be situated in the basal tentacular position. In a couple of instances the large triangular scale is replaced by 2 shorter scales of similar design, one following the other. Both the anthopomal scales and basal tentaculars are ornamented on their upper face with low tubercles.

The rachis of each tentacle contains a single row of large, curved, crescentic scales, up to about 0.13 mm long, with a dentate convex margin (Figure 182Aa–e). Proximally, these scales are intermediate in form to the anthopomal sclerites (Figure 182Af,g).

The abaxial side of the polyp is supported by a single, large, somewhat bow-shaped sclerite (Figures 179; 180A). The proximal half of this stay lies obliquely along the branch, over and alongside a brood pouch. Underneath the stay, both on the branch surface and the polyp body, the area is devoid of sclerites. The stays are 1.2–1.3 mm long. The section lying against the polyp has a concave inner face to allow for the curvature of the polyp body and an outer face ornamented with small tubercles. In one instance, part of the lower portion of a stay is covered with coenenchymal sclerites (Figure 179).

The remainder of the polyp body is covered with irregular shaped scales with dentate margins (Figures 181c; 182Al-x). The arrangement is different on each polyp. The most basal scales are much smaller than those above and have a tuberculate surface. The upper body scales can be very large, up to about 0.45 mm long, with those just below the anthopoma often spanning more than one octant. Although they are occasionally in rows, (there are 4–5 sclerites below the adaxial octant, for example) the scales are generally arranged irregularly. Except for those at the base of the polyp the majority of body scales have a predominantly smooth outer surface.

#### Coenenchymal sclerites (Figures 181d-f; 182B)

The surface of the brood pouches is covered in scales similar to those on the polyp body. They have dentate margins and are ornamented with few to numerous tubercles (Figures 181d,e; 182Bj– n). Through intermediate forms these scales merge

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Figure 181 Peltastisis cornuta Nutting, 1910, holotype, sclerites.

with the flattened knobby spindles of the general coenenchyme (Figures 181f; 182Ba–i), which are up to at least 0.33 mm in length.

#### Remarks

I am indebted to Mr John Vermulen of the Zoölogische Museum, Amsterdam, for permission to dissociate the sclerites from some tissue fragments and a damaged polyp, leaving only 4 polyps remaining. Only 7 sclerites were photographed with the SEM, the remainder being permanently mounted in resin for light microscopy. A large number of the sclerites are broken and many show erosion, presumably due to initial acidic preservation media. The drawings in Figure 182 incorporate some creative interpretation. The sclerites are very transparent and the margins are sometimes badly deteriorated. Dotted lines indicate missing portions of the sclerites.

### Distribution

See Figure 288. Depth 918 m.

Lissopholidisis gen. nov. Figure 317

Peltastisis; (part) Grant, 1976: 9-10, 42.

### **Type species**

Lissopholidisis furcula sp. nov., here designated.

#### Diagnosis

Colonies unbranched and thread-like, up to 335 mm long. Sclerites are colourless, and preserved colonies are more or less white. Axial internodes are translucent like milky glass in the proximal regions of the stem, becoming transparent distad. Nodes are yellowish or white.

Polyps are distributed all around or irregularly

biserial. They are relatively large, 1–2 mm long, and generally preserved angled distad to almost perpendicular. Their adaxial side is only slightly reduced and is completely covered in sclerites. In *L. furcula* sp. nov. and *L. ampliflora* sp. nov. the abaxial side of the polyp is occupied by one or more supporting sclerites. In *L. nuttingi* (Grant, 1976) these appear to be absent.

The anthopoma is more or less symmetrical and continuous with the polyp body sclerites. In *L. furcula* and *L. nuttingi* each octant is occupied by a single large triangular scale, up to 0.28 mm long. In *L. ampliflora* the polyps are very big and each octant contains about 3–5 scales in a single row, the largest up to 0.48 mm in length. Triangular anthopomal scales have dentate margins, a broad smooth base, and a tuberculate distal region. A large fish-shaped basal tentacular sclerite precedes a single row of crescentic scales in each tentacle rachis. The latter forms have markedly dentate convex margins.

The polyp body is protected by large smooth scales, usually with an irregular outline. Part or all of their distal margin may be serrate, but the remainder is usually entire. In *L. nuttingi* and *L. furcula* the scales on the polyp head are generally in rows. In *L. ampliflora* the body scales can be as large as 0.86 mm, while in the other 2 species they are about half this size.

In *L. furcula* the abaxial side of the polyp is supported by a large, forked, prop-like sclerite. In *L. ampliflora* there may be as many as 8 abaxial spindle-like forms, the largest up to 1.8 mm long.

The coenenchyme in the upper regions contains long, smooth, very narrow scales, sometimes branched, and up to 0.88 mm long in some species. In the lower regions the scales are shorter and broader, with scalloped margins and several tubercles on the exposed face.

The axial internodes in the basal regions are round in cross-section. In the upper parts they may



Figure 182 Peltastisis cornuta Nutting, 1910, holotype, sclerites: A. Polyp; B. Coenenchyme.

have multiple primary ridges but are generally square in cross-section. In *L. furcula* most internodes are about 5 mm long, in *L. ampliflora* about 2.6 mm, and in *L. nuttingi* about 1.2 mm.

## Distribution

See Figure 317.

## Etymology

In allusion to the form of the majority of the sclerites the generic name is derived from the Greek *lisso*, smooth, and *Pholidos* scale; combined with *lsis*.

# *Lissopholidisis furcula* sp. nov. Figures 183–186; 289

## Material examined

Types

HOLOTYPE: MTQ G48503, Coral Sea, 17°49.45'S, 148°39.51'E, 990–1006 m, beam trawl, FV *Cidaris 1*, 8 May 1986. PARATYPE: MTQ G48504, Coral Sea, 17°45.49'S, 148°37.52'E, 945 m, sledge, *Cidaris 1*, 9 May 1986.

## Other material

MTQ G48505, Coral Sea, 16°58.67'S, 147°11.40'E, 1545–1564 m, beam trawl, *Cidaris* 1, 13 May 1986.



Figure 183 Lissopholidisis furcula sp. nov., holotype, natural size.

#### **Differential characteristics**

Polyps with a single, large, forked, prop-like abaxial sclerite; anthopomal octants with a single scale.

### Description

#### Colony form (Figure 183)

The holotype has fragmented into more than 18 unbranched pieces 2–80 mm in length, measuring about 210–230 mm in total. The pieces are severely abraded and many polyps are missing whilst others are only loosely attached. The thickness of these fragments varies from 0.24–0.48 mm.

## Polyps (Figures 184; 185A-C,L)

Distributed all around and evenly spaced, about 12–13 per centimetre. The polyps are 1.0–1.2 mm tall and angled from 40° to more or less perpendicular to the stem surface. A polyp base is about 0.60–0.80 mm long, the narrow neck region about 0.36 mm thick, and the head with domed anthopomal region is, 0.60–0.66 mm in diameter. These measurements do not include the relatively



Figure 184 Lissopholidisis furcula sp. nov., holotype: Polyp, the abaxial stay not cradling the head.

huge abaxially placed supporting sclerites. A number of the polyp bases are ruptured and contain numerous, dull yellow, spherical reproductive bodies about 0.10 mm in diameter. A few juvenile polyps occur scattered throughout the colony.

### Colony colour

White. Viewed under a dissecting microscope the sclerites have a satin-like sheen, (caused by formalin?), and the nodes can be seen beneath the thin coenenchyme.

## Axis form (Figure 185F,G)

The internodes have pronounced, broad, smooth primary ridges. Often the ridges are alternately wide and narrow, but the ridge shoulders terminate at the same level. The finer segments are more or less 4-sided. The desmocyte cavities are shallow and elongate.

The internodes are mostly 4.5–5.3 mm long and 0.18–0.36 thick. An internode 0.30 mm thick has 10 ridges. The nodes are 0.15–0.30 mm long and of equal thickness.

## Axis colour

The internodes are white, translucent but densely coloured in the thicker parts of the stem and virtually transparent in the finest. The nodes are translucent, but densely coloured greyish yellow ( $\approx$  4B5) in the middle, with paler ends, and very narrow white satin-like borders.

## Polyp sclerites (Figures 184; 185A–D,H–L; 186A–C)

The anthopoma is symmetrical, and more or less continuous with the polyp body sclerites. Each octant is occupied by a single, large triangular scale (Figure 185D). There is a single basal tentacular sclerite (Figure 186Bd,e) preceding a row of crescentic scales in each tentacle rachis (Figure 186Ba-c). The large triangular scales (Figure 186A) have smooth, broad bases, and narrow, tuberculate distal portions. Both the apex and lateral margins of the scales are irregularly spinous. The scales are up to about 0.28 mm long, 0.17 mm across the base, and the undersides are relatively smooth (Figure 186Aa). The basal tentacular scales are somewhat fish-shaped. They have a broad head, usually with long tooth-like projections, a few large tubercles on the proximal portion, and are mostly 0.13-0.15 mm long. The tentacular scales have a markedly dentate convex margin, and are up to about 0.10 mm long.

The polyp body is supported by a large, forked, prop-like or stay-like sclerite (Figure 185A–C,L). The proximal part of the stay is bent to lie along or around the surface of the stem, and is sometimes forked. The distal portion is always forked.



Figure 185 Lissopholidisis furcula sp. nov., holotype: A-D. Polyps; E. Coenenchyme; F-G. Axial internodes; H-K. Large abaxial polyp sclerites; L. Twig fragment.



Figure 186 Lissopholidisis furcula sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Stem coenenchyme.
Sometimes there is just a simple bifurcation, but often there is complex antler-like branching that curves around and cradles the polyp head (Figure 185H–K). In only rare instances is the forked extremity of the stay not produced sufficiently to curve around the polyp head (Figure 184). The stays are up to about 1.7 mm long.

Most of the polyp body is covered with large, smooth scales. If a polyp stay is removed, the area of the coenenchyme and the abaxial side of the polyp below the stay is naked. It appears, however, that polyp head scales grow beneath the antler-like processes of the stay, and the head has some freedom of movement within the cradle.

The body scales are arranged more or less in 8 rows on the polyp head, with about 4 sclerites in each row. These scales are somewhat crescentic (Figure 186Ca-f) and curve around the head, which in some polyps is flared, trumpet-like (Figure 185B). The scales are generally quite large, even the most distal ones, and overlap with those on either side. If the distal most scale in a row is small enough, i.e. about as broad as the anthopomal sclerite, it is occasionally found folded down over that sclerite. In some polyps the rows are continued, occasionally somewhat ill-defined, on to the neck and lower regions of the polyp body. In other polyps, the scales below the head are very large and elongate, and some seem to curve about one third of the way around the narrower parts of the polyp body. Body scales can be up to 0.45 mm long, and the exposed margins are often serrate.

### Coenenchymal Sclerites (Figures 185E; 186D)

The colony surface contains a thin layer of narrow, pointed scales that fit together to form a continuous covering over the axis. They are up to about 0.6 mm in length, and the margins are finely dentate.

# Variability

The paratype consists of 3 unbranched fragments, 39 mm, 35 mm, and 65 mm in length. Many of the polyps are damaged. The axial internodes and all sclerites are colourless, and the nodes are brownish yellow ( $\approx$  5C8). The only other specimen examined is in very poor condition. It is in 2 fragments of 100 mm and 130 mm in length, and the sclerites and axial internodes are colourless.

### Distribution

See Figure 289. Depth range 945-1006 m.

#### Etymology

The epithet is the Latin *Furcula*, a forked prop, in allusion to the form of the large abaxial polyp sclerites. Noun in apposition.

# Lissopholidisis ampliflora sp. nov. Figures 187–190; 290

### Material examined

#### Types

HOLOTYPE: MTQ G48506, Coral Sea, 17°49.45'S, 148°39.51'E, 990–1006 m, beam trawl, FV *Cidaris 1*, 8 May 1986.

#### Other material

MTQ G48507, Coral Sea, 17°33.12'S, 146°55.92'E, 908 m, beam trawl, *Cidaris* 1, 16 June 1986.

# Differential characteristics

Polyps with 1–8 large, abaxially placed supporting sclerites; anthopomal octants with 2–4 scales.

# Description

### Colony form (Figure 187)

The holotype consists of two unbranched fragments 30 mm and 60 mm in length. They were badly abraded by the collection process and much of the coenenchyme is missing and the remaining polyps are damaged. The fragments are 0.31–0.36 mm thick.

### Polyps (Figure 189)

The distribution is uniserial but irregular. A few polyps appear to grow at nearly right angles to the general trend, a character possibly exaggerated by some polyps apparently being preserved bent laterally. The polyps are well spaced at irregular distances of 0.7–1.7 mm. There are 19 polyps on the 60 mm fragment and 9 on the 30 mm piece.

The polyps are contracted and are angled from 35° to nearly vertical to the stem surface. Those polyps making the smaller angles apparently do so because of damage. The polyps, notably far larger than the other known species of *Lissopholidisis*, are 1.8–2.4 mm tall. The bases are 1.2–1.3 mm long and the heads 0.9–1.1 mm across. There is a slightly narrower neck zone, difficult to measure due to



Figure 187 Lissopholidisis ampliflora sp. nov., holotype, natural size.

# P. Alderslade



Figure 188 Lissopholidisis ampliflora sp. nov., holotype: A. Large abaxial polyp sclerite; B-C. Axial internodes.



Figure 189 Lissopholidisis ampliflora sp. nov., holotype: Polyps.



Figure 190 Lissopholidisis ampliflora sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Abaxial polyp stays; D. Polyp body; E. Coenenchyme.

damage and distortion. The polyp dimensions do not include the relatively huge abaxially placed supporting sclerites. There are two small juvenile polyps.

# Colony colour

White. Under a dissecting microscope the

sclerites have a satin-like sheen, (caused by formalin?), and the pale nodes can be seen underlying the thin coenenchyme.

# Axis form (Figure 188B,C)

The internodes are 4-sided with a low smooth primary ridge on each edge. The desmocyte

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cavities are distinct, elongate ,and restricted to a narrow central tract along each side.

The internodes are 2.3–2.9 mm long, most about 2.6 mm, and 0.24–0.29 mm thick. The slightly narrower nodes are about 0.24 mm long.

# Axis colour

The internodes are translucent, like milk-white glass. The nodes are greyish yellow ( $\approx$ 4B5), translucent, and satin-like with very thin white, satin-like borders.

# Polyp sclerites (Figures 189; 190A–D)

There are only a couple of intact polyps from which the anthopomal arrangement can be assessed. The anthopoma appears to be more or less symmetrical and continuous with the polyp body sclerites. The proximal region of each octant contains 1–3 rectangular scales (Figure 190Ag–i). There are 2 per octant shown in the polyps in Figure 189 (top), but it is likely the number varies within a polyp. These scales precede a large triangular scale (Figure 190Aa–f) that dominates the octant. A smaller somewhat fish-shaped scale follows this. It is intermediate in size to the basal tentacular sclerite (Figure 190Bd,e) that precedes a single row of crescentic sclerites in the tentacle rachis.

The proximal rectangular anthopomal scales have ctenate distal margins and are up to about 0.33 mm long. The large triangular forms have spinous margins, smooth broad bases and tuberculate distal portions. They can be as large as 0.48 mm. The basal tentacular scales have a spinous apex, a tuberculate upper face, and are about 0.23–0.27 mm in length. The tentacular scales have markedly dentate, convex margins and are up to about 0.21 mm in length.

Very large curved sclerites are found supporting the abaxial side of the polyps (Figure 189), and their shape and arrangement is different in every case. In their simplest form they are unbranched or sparingly branched at one end (Figure 190C), while others are complexly ramified. One polyp has just a single stay, but the most heavily adorned has a group of 8 sclerites covering most of the abaxial region. At the base of a polyp these sclerites may extend on to the coenenchyme surface, and the upper ones may project beyond the polyp head. The sclerites are up to 2.8 mm long, and the distal ends are commonly granular (Figure 188A).

Where there is no covering of large abaxial sclerites the polyp body is protected by large, curved, smooth, irregularly shaped scales (Figure 190D). On some polyps they are loosely organised into rows (Figure 189, top), but in others very large scales disrupt this arrangement. The scales just below the anthopoma may have a serrate distal margin (Figure 190Da), but on the lower, larger

body scales the margins are usually entire, though some may have small serrate sections. Body scales may be as large as 0.86 mm in length.

# Coenenchymal sclerites (Figure 190E)

The surface of the coenenchyme contains long, narrow scales, sometimes branched, with pointed or rounded ends that fit together to form a thin covering over the axis. These scales may be up to about 0.88 mm long, and their margins have ctenate or irregularly spiny sections.

#### Remarks

Specimen MTQ G48507 is in very poor condition and its identity remains uncertain. It is an unbranched fragment, 60 mm long, with colourless sclerites and axial internodes. There are from 1–4 large abaxial sclerites. The largest polyp is just over 1.2 mm long; smaller than those of the holotype but of the same thick cylindrical form. The axial internodes are 4-sided, but the primary corner ridges are more pronounced than those of the holotype leaving a shallow valley down each face.

### Distribution

See Figure 290. Depth range 908–1006 m.

# Etymology

The epithet is derived from the Latin *amplus*, large, and *Floris*, flowers, in allusion to the very large polyps. Polyps have historically been alluded to as flowers in binomial nomenclature. When corals were still grouped with marine plants, Marsilli (1724) published his observations of polyps that he referred to as "fleurs due corail". The class name Anthozoa can be translated as flower-animals.

# *Lissopholidisis nuttingi* (Grant, 1976) new comb. Figures 191–194; 291

Peltastisis nuttingi Grant, 1976: 42–43, Figures 40– 41.

# Material examined

#### Types

HOLOTYPE: NZ0I H-129, off the west coast of South Island, New Zealand, 42°43.00'S, 169°15.50'E, 978 m, Agassiz trawl, 15 Oct. 1967.

# **Differential characteristics**

Polyps without large, abaxially placed supporting sclerites; anthopomal octants with 1–2 scales.

# Description

Colony form (Figure 191)

The holotype is a thin, unbranched, thread-like



Figure 191 Lissopholidisis nuttingi (Grant, 1976), holotype, natural size.

colony recorded by Grant to be 335 mm long, but now in two pieces. Above the small, branched, articulated root structure the naked colonial axis is about 0.43 mm thick. The colony gradually tapers and the thickness of the broken tip is 0.15 mm. The colony is not in very good condition and much of the coenenchyme is missing from the base and one side.

# Polyps (Figure 192)

Many of the polyps are missing so it is not possible to exactly determine the distribution. However, a couple of more intact areas indicate the polyps were arranged all around, evenly spaced and not crowded. At approximately a quarter of the way down from the top of the colony a lesser damaged area about 12 mm in length has 12 polyps distributed around the stem, but it is probable there were originally about 14–16.

Most of the polyps are squashed and deformed, contracted, and curved so as to lie along the colony surface. Measured along the stem they are 1.32–1.62 mm long. They project about 0.60 mm, the



Figure 192 Lissopholidisis nuttingi (Grant, 1976), holotype: Polyp.

diameter of the head. The bases are also about 0.60 mm in diameter and often swollen with 6–8 transparent, dull yellow, spherical reproductive bodies. Polyps with ruptured bases may have spilled their reproductive bodies, but, macroscopically, many intact polyps also appear to be barren. Between the polyp base and head is a slightly narrower neck region.

#### Colony colour

Very pale yellowish white with the pale nodes visible through the coenenchyme.

### Axis form (Figure 193)

The root and the basal stem internodes appear circular in cross-section and smooth, but they could not be submitted to SEM examination without further fragmenting the colony. Higher in the colony the internodes are squarer in section, without ridges but with distinct elongate desmocyte cavities. A single tip internode was examined by SEM. Further down the colony it is possible to see with a dissecting microscope that many individual desmocyte cavities appear to run the whole length of the internodes.

The first two basal stem internodes are 2.1 mm and 2.5 mm long. Above this most are about 1.2 mm long. The smaller of the two colony portions is 83 mm long and has 47 internodes. Nodes are 0.24–0.30 mm long in the basal regions, and 0.10–0.12 mm near the colony tip.

#### Axis colour

The internodes are translucent like milky glass in the basal regions and nearly transparent towards



Figure 193 Lissopholidisis nuttingi (Grant, 1976), holotype: A-C. Axial internodes.



Figure 194 Lissopholidisis nuttingi (Grant, 1976), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Upper stem coenenchyme; E. Basal stem coenenchyme.

the tip of the colony. The basal nodes are golden yellow with white satin-like borders. In the distal regions they are mostly white and satin-like.

### Polyp Sclerites (Figures 192; 194A–C)

All of the polyps are so badly damaged that the exact nature of the anthopomal arrangement could not be seen. It appears that each octant is generally occupied by a single, large triangular scale (Figure 194A), with a single basal tentacular sclerite (Figure 194Ba,b) preceding a row of crescentic scales (Figure 194Bc-f) in the tentacle rachis. Dissociating a polyp, however, may reveal more than 8 triangular scales, of various sizes. This suggests some octants may contain more than a single sclerite, and those in the more adaxial sectors may be of a slightly smaller size.

The triangular anthopomal scales have a rounded apex, and irregularly spined lateral margins. The broad basal portion of the exposed face may have fine granulations or be almost smooth, and the distal half has large tubercles. There are fine granulations on the underside (Figure 194Aa). Grant's recording of the size of these sclerites as "length 0.35 mm, width across the base 0.1 mm" appears to be incorrect as such long, narrow forms have not been observed. They are usually much shorter and wider; up to 0.25 mm long and 0.20 mm across the base.

The basal tentacular scales are quite large, somewhat fish shaped, narrow, and ornamented with tubercles and granules. They are about 0.14–0.18 mm long. The tentacular crescents are also granular. They have ctenate convex margins and are up to about 0.09 mm in length.

The polyp body is covered with large, almost smooth scales (Figure 194C). The arrangement in Figure 192 is an approximation. On the polyp head the scales appear to be aligned in 8 rows, approximately 6-9 scales per row, and are more or less rectangular in outline. The distal margin of the scales is often serrate, commonly with a medial notch. The lower part of the polyp has scales of more irregular outline, often lobed, that become very elongate where they merge with the sclerites of the coenenchyme. They are loosely arranged in rows on some polyps. The adaxial side of the polyp is not naked, but the scales in this region seem to be smaller. Those similar to Figure 194Ca-c probably come from the adaxial side of the neck to accommodate the curvature of the polyp. The largest body scale seen was 0.4 mm long.

The large abaxial stays characteristic of the other species in this genus appear to be absent. It was at first thought they may have been torn away during dredging as several polyps were noted to have naked patches on the abaxial side of the neck region. However, many polyps are crushed and folded in this area so naked patches could just be where body scales have become detached, and several polyps that are more intact clearly show a complete covering of abaxial scales. Although there are not many polyps on the colony now, Grant's figure of the holotype (1976: Figure 40) shows that he had many more to examine. It is unlikely that every abaxial stay would have been torn free during collection, and that Grant would have missed those remaining.

# Coenenchymal sclerites (Figures 192; 194D,E)

The coenenchyme is missing from much of the colony, particularly in the lower regions. In the upper part of the colony the surface contains predominantly long, narrow scales, almost smooth, with finely dentate margins, and up to at least 0.45 mm in length (Figure 194D). Smaller forms occur amongst them and the scales fit neatly together to form a thin layer completely covering the axis.

The coenenchyme of the lower part of the colony contains shorter, broader forms. They have markedly granular, scalloped margins, several large tubercles on their outer face, and are up to about 0.26 mm long (Figure 194E).

## Distribution

See Figure 291. Depth 978 m.

# Minuisis Grant, 1976 Figure 318

*Minuisis* Grant, 1976: 9–10, 45–47; Bayer, 1981: 941 (in Key); Bayer and Stefani, 1987a: 49–50 (in key); Bayer and Stefani, 1987b: 938, 940–942 (in keys).

### Type species

*Minuisis pseudoplana* Grant, 1976 (emended), by original designation and monotypy.

# Diagnosis

Colony growth form is severely modified by a commensal scale worm in all know examples. The main branches, of which there are only 1-2, are induced to produce sections of close pinnate branching with web-like expansions of axial material and coenenchyme between the pinnae. The worm further induces the branches to grow in a curved manner towards one side of the colony so that the closely arranged bases form a gutter. Some branch bases may fuse to form a hollow sphere or tube. Colony portions apparently unaffected by the worm indicate that worm-free colonies, should they exist, may be branched in a bottle-brush manner. Twigs rarely rebranch and are often irregularly curved. Maximum known colony height is 70 mm.

Preserved colony colour is white. Axial internodes are translucent, like milky glass, to

almost transparent. Nodes are brown in the proximal parts of the colony becoming paler distad and greyish yellow in the twigs. Sclerites are colourless.

Polyps are well spaced and arranged all around on the twigs and non-modified branch portions. They are erect, tall, and capstan shaped. The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant contains a single row of 2–7 more or less semicircular to triangular sclerites. There is a single basal tentacular scale preceding a single row of crescentic scales in each tentacle rachis. The large triangular anthopomal scales are mostly <0.22 mm long.

The polyp body is protected by large irregularly shaped scales that are not usually arranged in regular series or rows. Up to at least 0.4 mm long, their size is very variable. Like the anthopomal scales they have short granular spines on their exposed face.

The coenenchyme is very thin and contains a single layer of irregularly shaped plates, sometimes branched, up to 0.3 mm long and ornamented with short spines.

The axial internodes are smooth, often curved and twisted, and up to 9.5 mm long. Those in the twigs are 4-sided and those in the rest of the colony have multiple faces. The edges of the internodes are rounded and not often ridge-like. Main branch internodes can initiate up to 24 branches each in worm affected regions.

# Distribution

See Figure 318.

## Minuisis pseudoplana Grant, 1976 (emended) Figures 195–197; 292

Minuisis pseudoplanum (part) Grant, 1976: 45, Figures 45-47.

### Material examined

## Types

HOLOTYPE: NZ0I H-131, station E859, Norfolk Ridge, 32°01'S, 168°03'E, 500 m, 18 March 1968.

#### **Differential characteristics**

Anthopoma with 5–7 scales in each octant

### Remarks

Upon examining specimens of the type series recorded by Grant, it became apparent that two species of *Minuisis* were involved. Grant designated "No. 131" as the holotype. Lot "No. 131" contained one complete and two incomplete colonies. The largest two are illustrated in Grant's Figure 47, which is 2x natural size. The beginning of his descriptive text, "Type specimen 60 mm

high, span 27 mm...", obviously refers to the left most colony of this figure. Unfortunately, Grant's electron microscope images in his Figures 45–46 were not made from the holotype which has a distinctly different anthopoma. Hence, his comment, "Operculum of eight triangular scales...", as applied to the figured holotype is incorrect (and is in actual fact an erroneous interpretation anyway). Two of Grant's paratypes, one of which was sampled for his electron micrographs, form the type series of *Minuisis granti* sp. nov., described later. The paratypes from stations E841 and E868 were not returned to the New Zealand Institute of Oceanography after the study and their whereabouts is unknown.

Grant's forming of the epithet *pseudoplanum* is incorrect. *Planus* is a common Latin adjective with the endings *us*, *a*, and *um*. The hybrid compound with the Greek *pseudos* should be *pseudoplana* to agree in gender with *Minuisis*, which is feminine.

### Description

### Colony form (Figure 195)

The holotype is curved from bottle storage and straightens to about 70 mm tall. It is about 30 mm across at its widest point. The stem arises from a very thin, polygonal, calcareous holdfast, about 4 mm x 2.5 mm, attaching the colony to a small piece of rock. The stem is 9 mm long and is decorticated. A single main branch extends above this, where the colonial form has obviously been modified by the growth of a commensal scale worm. Along the main branch, a large number of twigs have been produced in a close, irregularly pinnate manner. The adjacent bases of the twigs are joined by weblike expansions of coenenchyme. About half way along the branch, even the axial internodes are expanded web-like between the twig bases. Because the twigs curve towards one side of the colony, the basal expansions either side of the main branch form a gutter for the scale worm. This curvature of the twigs causes the colony to be densely bushy on three sides, and sparsely branched on the fourth where a number of twigs emerge that have been unaffected by the worm. Nearly all of the twigs are somewhat irregularly curved and the general appearance of the colony is quite untidy. The six lower-most twigs on the main branch appear to be only partially affected by the worm and are not pinnately arranged. It is likely that if worm-free colonies exist the branching mode would be lateral and non-planar, perhaps in a bottle-brush form.

The stem is about 0.7 mm thick. The twigs are 0.39–0.63 mm thick at their base, tapering to a distal point, and they are unbranched. They are longest on the opposite side of the colony to the gutter, being up to 17 mm in length. On the bushy,



Figure 195 Minuisis pseudoplana Grant, 1976, holotype, natural size x 3.

gutter side they are up to 11 mm long, but most are <8 mm. In the middle region of the colony there are 20 twigs on each side of the main branch within a distance of 17.5 mm.

### Polyps (Figure 196A,B,H)

The polyps are arranged all around on the twigs and are well spaced. There are 7 polyps within about 12–13 mm. The polyps are contracted and stand more or less at right angles to the twig surface, some leaning distal. Most polyps are 1.2– 1.5 mm tall. Shorter ones are found mainly towards the twig tips, as are a few very juvenile forms. The base of most polyps is swollen, about 0.72–0.84 mm thick, and transparent, containing up to 20 spherical, yellowish reproductive products. The polyps are somewhat capstan-shaped and have a narrow neck region about 0.47 mm thick and a head about 0.6 mm in diameter.

### Colony colour

The colony is more or less white. The



Figure 196 Minuisis pseudoplana Grant, 1976, holotype: A-D. Polyps; E. Coenenchyme; F-G. Axial internodes; H. Twig fragment.

coenenchyme is translucent and the underlying nodes show through.

#### Axis form (Figure 196F,G)

The internodes are irregularly curved and often twisted. In the twigs they are more or less 4-sided, especially at the tips, and relatively smooth. In the thinner internodes and the proximal part of the tip internode, there is a very low wide ridge on each face. The four edges of the internodes are rounded and not raised ridge-like except in older internodes. The stem internodes are twisted and have eight spiralling faces with low rounded edges between them. Desmocyte cavities are distinct and elongate.

The three stem internodes are 1.3 mm, 1.3 mm and 1.9 mm in length. In the main branch there are nine internodes, 5.4–9.5 mm in length. There are 2– 4 internodes in each twig and they may be up to 7.9 mm long. The stem and branch nodes are about 0.48 mm long, and those of the twigs are 0.12–0.3 mm.

#### Axis branching

Branching is from the calcareous internodes as in Figure 251 example 50. One main branch internode



Figure 197 Minuisis pseudoplana Grant, 1976, holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Branch coenenchyme.

in the most developed region of the gutter has 11 twigs branching from one side and 13 from the other. At the point of insertion of each twig base, a crescent of pale milky colouration can be see within, but no nodal material is visible.

# Axis colour

The internodes of the stem and main branch, and the twig bases in the lower regions of the colony, are translucent like milky glass. The translucency increases distally, with only fine milky transverse irregularities in the axial substance preventing the internodes from being completely transparent. The basal nodes are dark brown ( $\approx$ 6F8), becoming paler brown ( $\approx$ 6D8) distally in the main branch. In the twigs the nodes are pale brown proximally and greyish yellow towards their tips. All nodes have yellowish satin-like borders.

## Polyp sclerites (Figures 196A-D; 197A-C)

The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant contains

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5–7 sclerites in a single row (Figure 196C,D). The apical sclerite in each row is in the basal tentacular position and is slightly modified (Figure 197Ba–d). Of the other 4–6 scales in each sector (Figure 197A) the proximal ones are crescentic to semicircular, and those more distal, of decreasing size, are more or less triangular. The 2 most distal sclerites in each octant generally occur within and on the lip of the aperture at the centre of the anthopoma. The anthopomal scales have numerous short, granular spines on their exposed face, and also a few on the distal portion of the underside (Figure 197Aa). The triangular forms are occasionally up to 0.21 mm long, but most are <0.17 mm.

There is a single row of large, curved, crescentic scales in each tentacle rachis. Their concave basal margin is more or less entire, sometimes with a medial notch, and their convex margin is markedly dentate (Figure 197Bg,h). The largest are about 0.12–0.14 mm long. The proximal tentacular scale may be intermediate in form to the basal tentacular scale (Figure 197Be,f). Its structure seems to depend on the size of that preceding sclerite.

The polyp body is protected by large scales, mostly irregularly shaped (Figure 197C). Those at the base of the polyp are generally the largest (Figure 196A,B). The upper few series are often narrow and arranged in rows below each octant, some forming a continuation of the crescentic scales of the anthopoma (Figure 197Ca). This is variable, however, with the amount of scales involved differing from polyp to polyp, and from one side of a polyp to the other. The body scales have numerous short, granular spines on their exposed face. They are for the most part smooth underneath (Figure 197Cc), and their margins have blunt, granular spines or tooth-like projections. Most body scales are about 0.18-0.28 mm long, with a few of the larger basal sclerites being as large as 0.43 mm. Around the base of the polyp some of the scales are intermediate in structure to the coenenchymal sclerites (Figure 197Cb,d). In general the body scales are not arranged in regular series or rows, but counting from base to upper margin in more or less a straight line about 14 scales are encountered.

#### Coenenchymal sclerites (Figures 196E; 197D).

The surface of the branches contains a single layer of irregularly shaped platelets that are sometimes branched. The majority are 0.08–0.18 mm long, but they can be up to 0.25 mm. Their upper face is ornamented with short, granular spines, and their underside is mostly smooth (Figure 197Da).

### Distribution

See Figure 292. Depth 500 m.

*Minuisis granti* sp. nov. Figures 198–200; 293

Minuisis pseudoplanum (part) Grant, 1976: 45, Figures 45–47.

### Material examined

## Types

HOLOTYPE: NZOI H-593, station E859, Norfolk Ridge, 32°01'S, 168°03'E, 500 m, 18 March 1968. PARATYPE: NZOI P-946, data as for holotype.

#### **Differential characteristics**

Anthopoma generally contains 2 large scales in each octant.

## Description

#### Colony form (Figure 198A)

The holotype is about 45 mm tall and 33 mm across. Its general appearance is of a bushy untidy mass of twigs. The stem and holdfast is missing. The main branch passes into a confusion of twisted basally fused twigs that form a calcareous mass with a hollow tubular central cavity. As in M. pseudoplana, this growth, about 6.4 mm long and 3.2 mm wide appears to have been induced in the colony by the commensal scale worm. Further distortion of twig growth, together with web-like expansions of the coenenchyme between twig bases, has formed a 6.3 mm gutter-like distal extension of the tubular cavity. Another main branch protrudes from the centre of one side of the fused tubular mass and extends upwards for about 32 mm. Its middle section is also gutter-like and, as in M. pseudoplana, it is formed from adjacent closely arranged twig bases. It appears that the worm not only causes gutter-forming twig curvature and coenenchymal webbing, but also induces the multiple pinnate branching from the axial internodes. The majority of twigs arise from fused or gutter areas. Two other major branches have very few twigs, and these twist and curve irregularly and are not densely arranged.

The main branch at the base of the colony is 0.79 mm thick. Main branches where no guttering occurs are about 0.60 mm thick. A main branch gutter 12.5 mm long is formed from 14 twigs on one side and 13 on the opposite side. Most twigs do not rebranch. Many are >12.5 mm long, and the longest is 23.7 mm. The twigs are 0.40–0.48 mm thick proximally and taper to a distal point.

#### *Polyps* (Figure 199F,G,J)

Polyps are well spaced and distributed all around on the twigs and branches. They are contracted, and more or less at right angles to the surface or leaning slightly distad. They are more cylindrical than those of *M. pseudoplana* and





virtually transparent. Many contain numerous spherical reproductive bodies 0.07–0.14 mm in diameter. Most polyps are about 1.2 mm tall and 0.60–0.72 mm across the base. The heads are about 0.60 mm in diameter and the polyp is only slightly narrower. There are no juvenile polyps.

#### Colony colour

The colony is more or less white. The coenenchyme is translucent and the underlying nodes show through.

### Axis form (Figure 199I)

Axial architecture is similar to that in *M. pseudoplana*. Main branch internodes have multiple faces with low rounded edges between them, and twig internodes are 4-sided with rounded, sometimes ridge-like edges. The very low, wide ridge down each face is often just a general convexity of that face. Internodes are often curved and twisted. Desmocyte cavities are distinct and elongate.

Main branch internodes are not of consistent lengths, and vary from 2.8–9.2 mm. Those of the twigs are 4.7–6.3 mm long, and the most proximal one is usually the longest. Main branch nodes are 0.16–0.47 mm long, and those in the twigs 0.12–0.30 mm.

### Axis branching

Branching is from the internodes, commonly as in Figure 251 example 50.

#### Axis colour

Virtually the same as *M. pseudoplana*. Basally, the nodes are brown ( $\approx 6E8$ ) becoming paler ( $\approx 6D8$ ) distally. The smaller twig nodes are greyish yellow. All nodes have yellowish satin-like borders. Internodes are translucent, like milky glass, or almost transparent with fine milky transverse irregularities.

### Polyp sclerites (Figures 199A–G,J; 200A–C)

The anthopoma is continuous with the polyp body sclerites and essentially symmetrical (Figure 199A–E,J). Each octant is occupied by a large more or less triangular sclerite (Figure 200Aa–h) usually preceded by a somewhat rectangular scale (Figures 199B–G,J; 200Aj–n). In the most uniform arrangement, there are 8 rectangular sclerites of approximately equal dimensions that form the periphery of the anthopoma, and often stand fairly erect. Distal to these, 8 triangular sclerites complete the anthopoma, each followed by a basal tentacular sclerite (Figure 200Ba–e) and a single row of small crescentic scales in each tentacle rachis (Figure 200Bf–j). Most polyps, however, are not uniform, and several octants may have scales of different sizes. The proximal rectangular scale may be quite short or absent and the following sclerite may be longer than usual to compensate, or may remain of average size. If the latter, the octant may not have closed properly, revealing a large basal tentacular sclerite at the apex of the octant and angled downwards into the aperture at the centre of the anthopoma (Figure 199A). In other instances, the rectangular scale may be very tall and followed by a correspondingly small triangular scale. More rarely, the single large triangular scale is replaced by 2 smaller scales. In this case, if the proximal one is the smaller of the 2 then it may be shaped as in Figure 200Aj, and if it is the larger, then it may be like Figure 200Ab,f.

The anthopomal scales and basal tentaculars are ornamented with short spines that have a granular surface. Most of the triangular anthopomal scales are about 0.18–0.22 mm long, but they can be up to 0.28 mm, and the rectangular scales can be up to 0.24 mm but are often not longer than 0.16 mm. The undersides of the scales have both smooth and tuberculate areas (Figure 200Ah,I). The basal tentacular sclerites can be as large as the smaller anthopomal sclerites. The curved tentacular sclerites, up to 0.12 mm across, are often butterfly-shaped and have a dentate distal margin.

The polyp body is covered with irregularly shaped overlapping scales (Figures 199F,G,J; 200C). They are ornamented with short granular spines on their outer face, and are mostly smooth on the underside (Figure 200Cc,d). They have long granular, root-like spines on the basal margin, and short, often complex, granular spines along the exposed margin. In some polyps the scales are nearly all <0.24 mm long. In others, the scales are fewer in number and correspondingly larger, up to about 0.35 mm in length; rarely, one or two are even as large as 0.4 mm. The scales are not in regular series or rows, but counting from base to upper margin in a more or less straight line about 11 body scales are commonly encountered. The scales at the base of the polyp (Figure 200Ca,b) are intermediate in character between those of the polyp body and those of the branch surface.

#### Coenenchymal sclerites (Figures 199H; 200D)

The surface of the branches contains irregularly shaped plates, often branched, up to 0.31 mm long but usually shorter. They have numerous granular spines on their exposed face, and smaller, isolated ones on the underside (Figure 200Da).

#### Variability

The paratype is only a colony fragment. It is essentially a hollow ball of fused twig bases, presumably worm induced, on a short section of main branch. Irregularly curved twigs protrude in



Figure 199 Minuisis granti sp. nov., holotype: A-G. Polyps; H. Coenenchyme; I. Axial internode; J. Twig fragment.



Figure 200 Minuisis granti sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Branch coenenchyme.

numerous directions, and the ball is enveloped by a white ophiuroid.

#### Distribution

See Figure 293. Depth 500 m.

### Etymology

The species is named after Dr Ralph Grant who established the genus *Minuisis*.

# Primnoisis Studer [and Wright], 1887 Figures 201; 202; 319

Isis; Studer, 1878: 661.

Primnoisis Studer [and Wright], 1887: 46; Wright and Studer, 1889: xlv, 33–35; Bayer and Stefani, 1987b: 942–944 (synonymy and history).

# **Type species**

Isis antarctica Studer, 1879, by monotypy, Studer [and Wright] 1887: 46.

### Remarks

Bayer and Stefani (1987b) detailed the history of the genus Primnoisis and pointed out that its diagnostic characters are based on the material obtained by the Challenger Expedition, not the indeterminate decorticated axis taken by the Gazelle which was identified by Studer (1879) as Isis antarctica sp. nov. Given the similarities of the sclerites, the character which has been used to differentiate the genus from Mopsea (sensu lato) is the bushy, commonly bottle-brush, growth form. The Challenger material was briefly redescribed by Bayer and Stefani (1987b: 944–948) who gave SEM illustrations of sclerites and axial sculpturing. The polyp drawings in their Figure 3a show that the nature of the anthopomal octants is complex. This arrangement, and the form of the scales involved, is further illustrated here with SEM images (Figure 201B,C), and so far it appears to be unique to this genus.

In view of the importance of the anthopomal structure as a diagnostic feature, much of the material that has been assigned to Primnoisis by numerous authors should be reassessed. A bottle-brush styled specimen in the collection of the Museum and Art Gallery of the Northern Territory, has polyps that show a similar anthopomal arrangement (Figure 201E,F), and appears to be attributable to the genus. Primnoisis deliculata Hickson, 1907, considered by Bayer and Stefani (1987b: 944) to be more appropriately assigned to Mopsea, also has polyps with this same basic structure and appears to be a valid nominal species (Figure 202) although the coenenchymal sclerites are very thorny. Bayer's and Stefani's drawings (1987b: Figure 3c,d) of their new species P. mimas also shows anthopomal octants of

similar design, although the architecture of the individual scales was not illustrated. In the same paper these authors reassigned several species of Primnoisis to the genera Echinisis and Stenisis, but maintained P. sparsa Wright and Studer, 1889, P. ambigua op. cit., P. rigida op. cit., and P. fragilis Kükenthal, 1912, as valid. To be certain, the type material should be re-examined along with that of P. formosa Gravier, 1913. The original descriptions of P. sparsa and P. rigida indicate the octants have scales in more than 1 row, and therefore the assignment to the genus may be correct. No such detail is given in the description of P. ambigua, P. fragilis or P. formosa. The large number of small anthopomal scales illustrated for a polyp of *P. antarctica* by Kükenthal (1912: Figure 55), from a specimen taken by the Deutschen Südpolar-Expedition, clearly indicates а misidentification, possibly at the generic level. Reexamination of the type material of Mopsea gracilis Gravier, 1913, has shown that this material should be assigned to Primnoisis.

# Distribution

See Figure 319. Depth range 18–1097 m. The type localities for all of the species mentioned above are plotted on the map in Figure 319, as well as the locality for a specimen of *P. antarctica* from the Antarctic Peninsular identified by Bayer and Stefani (1987b). However, as outlined, some of the nominal species may not be valid.

### Chathamisis Grant, 1976 Figure 320

- ?Ceratoisis; Hickson, 1904: 224; Thomson, 1911: 877; Stiasny, 1940: 35.
- ?Primnoisis; (part) Kükenthal, 1919: 611; (part) Kükenthal, 1924: 432.
- Chathamisis Grant, 1976: 9, 10 (in key), 43; Williams, 1992a: 282.
- ?Chathamisis; Bayer and Stefani, 1987b: 938 (in key), 941 (in key), 966.

#### Type species

*Chathamisis bayeri* Grant, 1976, by original designation and monotypy.

### Remarks

The genus was established by Grant for several colonies of a bushy growth form collected to the east of New Zealand on the Chatham Rise. Grant figured scanning electron micrographs of a single polyp with the superficial tissue still intact (1976: Figures 43,44), but the characteristic anthopomal arrangement of 8 triradiate sclerites was well displayed. Unfortunately, no individual sclerites were figured in the description, and their true



Figure 201 A-D. Primnoisis antarctica (Studer, 1879), holotype: (A-C). Polyps; (D). Coenenchyme. E-F. Primnoisis sp., NTM C12329, polyps.



Figure 202 Primnoisis deliculata (Hickson, 1907), syntype: A-C. Polyps; D. Coenenchyme; E. Axial internode.

nature was obscured by epithelium in the SEM picture. This possibly contributed to Bayer and Stefani (1987b: 966–969) identifying material from the vicinity of Durban, South Africa, with the genus; material with quite a different sclerite architecture.

An examination of the holotype of *C. bayeri* revealed the scales of the polyp body and coenenchyme to be thin, and predominantly smooth with little tuberculation. The small scales in the coenenchyme are somewhat figure-8 and the longer ones are narrow and fusiform. The polyp body scales are often also fusiform, but curved to fit the body wall. All scales have strongly scalloped

edges, and there is little to distinguish between the distal and proximal margins of those which are from the polyp body. This is in keeping with the form of the sclerites illustrated by Williams (1992a: Figure 70, 71C–F) for material identified as *Chathamisis ramosa* (Hickson, 1904), but not with the thick, tuberculate sclerites illustrated by Bayer and Stefani (1987b: Figure 17) for material also attributed to that species. Bayer's and Stefani's specimens may not be congeneric, so the holotype of *Ceratoisis ramosa* Hickson, 1904 needs to be reexamined to establish its affinities. William's material would seem to be closer in form to that described by Hickson.

## Distribution

See Figure 320. Depth range 146–900 m.

# Echinisis Thomson and Rennet, 1931 Figure 321

### Ceratoisis; (part) Hickson, 1907: 4-5.

- Primnoisis; (part) Kükenthal, 1915: 122; (part) Kükenthal, 1919: 611; (part) Kükenthal, 1924: 432.
- *Echinisis* Thomson and Rennet, 1931: 15; Grant, 1976: 9, 10 (in key), 47; Bayer and Stefani, 1987b: 938 (in key), 941 (in key), 952–954.

### **Type species**

*Ceratoisis spicata* Hickson, 1907, by subsequent designation, Grant, 1976: 47.

### Remarks

The genus Echinisis was established for colonies with a bushy growth form, and stellate polyp body scales; those in the upper one or more series having one ray developed as a strong projecting spike. The included species were E. spicata (= Ceratoisis spicata Hickson, 1907) and E. armata (= Primnoisis armata Kükenthal, 1912). The characters of the genus were discussed by Bayer and Stefani (1987b: 952) as a preface to their proposal of the 3 new species E. eltanin, E. vema, and E. persephone. These authors also described material from the Ross Sea, Antarctica, which they attributed to E. spicata, the type of the genus. The type locality of E. spicata is also in the Ross Sea, but the holotype has never been comprehensively illustrated. Grant's Antarctic material which he identified also as E. spicata came from north of the Ross Sea, but as no sclerites were illustrated it is not recognisable from his description.

### Distribution

See Figure 321. Depth range 33–2350 m.

# Subfamily Circinisidinae Grant, 1976

### Diagnosis

Planar or unbranched Isididae with non-retractile anthocodiae.

Polyp body sclerites in the form of oval to cycloid scales whose external face is generally smooth but occasionally ridged or minimally papillate, and whose free margin is predominantly entire, but occasionally notched or undulate especially if the scale is radially ribbed underneath.

Anthopomal sclerites generally small, in the shape of platelets, clubs, or crescentic scales, intermesenterially situated and forming complex protective arrangements which enclose the deflated tentacles during contraction. Sclerites of the surface of the coenenchyme in the form of smooth scales with entire free margin, or rooted heads.

Axial internodes solid, sometimes plain, but commonly sculptured with longitudinal ridges and granulations of various sizes. Branching from the internodes is not uncommon, but lateral branches predominantly share a parent branch node at the point of origin.

### Remarks

*Circinisis* appears to differ from all the other included genera by not having a differentiated, octate anthopoma.

### Circinisis Grant, 1976

*Circinisis* Grant, 1976: 9–10, 40; Bayer, 1981: 941 (in key); Bayer and Stefani, 1987a: 49–50 (in key); Bayer and Stefani, 1987b: 938, 940–942 (in keys).

### **Type species**

*Circinisis circinata* Grant, 1976, by original designation and monotypy.

#### Diagnosis

Colonies unbranched, thin, and up to at least 310 mm in length.

The sclerites are colourless and the preserved colour of specimens is pale yellowish white. The axial internodes are translucent like milky glass, and the nodes are golden yellow.

Polyps are densely placed and distributed all around over most of the colony. They are fingershaped, adaxially reduced, adaxially naked, and usually preserved lying along the stem surface.

There appears to be no anthopoma. The tentacles contain a single row of sclerites; tuberculate plates proximally, differentiating to curved, crescentic scales distad.

The polyp body is protected by numerous, small, smooth, oval scales with entire margins. Most are about 0.106 mm long, and they are not arranged in rows. In the lower polyp body there is a subsurface layer of stellate plates, up to 0.085 mm long, with 2 warts on one face.

The coenenchyme contains 2 layers of sclerites like those in the polyp body.

The axial internodes are up to at least 2.5 mm long, and have multiple, smooth, pronounced primary ridges.

### Distribution

As for Circinisis circinata, see Figure 294.

Circinisis circinata Grant, 1976 Figures 203–205; 294

Circinisis circinata Grant, 1976: 41-42, Figures 37-39.

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Figure 203 Circinisis circinata Grant, 1976, type series: A. Holotype. All natural size.

# Material examined

### Types

HOLOTYPE: NZOI H–128, approximately 20 km NNE of Three Kings Islands, New Zealand, 34°00'S, 172°15'E, 88 m, bryozoan shell debris, algal/bryozoan accretions, and probably glauconite, 11 April 1965. PARATYPES: NZOI P– 943, P–944, P–945, data as for holotype.

### Diagnosis

As for the genus.

## Description

Colony form (Figure 203A)

The holotype is a single unbranched specimen about 160 mm long. The distal portion of the colony (probably quite long judging by the thickness at the break) is missing. In the basal region, the large nodes, the small internodes, and (where the coenenchyme is intact) the lack of polyps indicates that the specimen appears to have broken from quite near the colonial base. It is not definite that the species is unbranched as it is not uncommon to find the main branches from ramified isidids to have a similar structure proximally. However, the three badly damaged paratype fragments are also unbranched and one is nearly twice as long as the holotype. Although the specimens all came from the same station and could be portions of the one colony, no jointed portions are present so it seems likely the species is not branched.

The colony is about 1.5 mm thick near the base where the coenenchyme is intact. At the mid-point the colony is 1.8–2.1 mm thick (including polyps).

### Polyps (Figure 204A,D)

Distributed all around, except in the basal region. They are contracted, adaxially reduced, and curved so as to lie flat along the stem surface. They are densely arranged and angled so that the oral region of each polyp lies against the stem just below or beside the base of the succeeding polyp (Figure 204D). Measured along the stem the polyps are about 1.44 mm long. Abaxially, the heads measure 0.54–0.66 mm across. In the thickest part of the colony there about 5 irregular rows of polyps, and near the tip about 3–4 rows. The polyps contain numerous reproductive bodies about 0.04–0.08 mm in diameter. There are no obvious juvenile polyps.

#### Colony colour

Very pale yellowish white. The coenenchyme is translucent and the nodes are visible through the surface.

# Axis form (Figure 204B,C)

The internodes have multiple, smooth, pronounced primary ridges. There are no secondary ridges. Desmocyte cavities are shallow and distinct. The four basal internodes are 0.8–1.1 mm long. The three visible above this are 2.1–2.4 mm long. The internode visible at the tip of the colony is 2.5 mm long, 0.9 mm thick, and has 8 longitudinal ridges. There are 51 internodes in the fragment, the longest being 4.4 mm. The nodes are about 0.7 mm long.

#### Axis colour

The internodes are translucent like milky glass. The nodes are golden yellow ( $\approx$ 5B7).



Figure 204 Circinisis circinata Grant, 1976, holotype: A. Polyp; B-C. Axial internodes; D. Twig fragment.



Figure 205 *Circinisis circinata* Grant, 1976, holotype, sclerites: A. Tentacles; B. Polyp body; C. Sub-surface of the twig coenenchyme.

# Polyp sclerites (Figures 204A,D; 205A,B)

The polyps appear to be completely naked below the adaxial tentacle base and are preserved indented along this line which is confluent with the similarly depressed tentacular region (Figure 204A). Consequently, it is very difficult to assess the summital sclerite arrangement. It seems, however, that there is no anthopoma, no octoradiate arrangement of differentiated scales as described for the other genera in this work. An examination of the paratypes, where some polyps have the tentacles partly protruding, supports this view. Nevertheless, specimens with expanded polyps are needed for a more accurate evaluation.

The tentacles, armed with large scales, are fusiform; the largest sclerites occurring more or less midway along the rachis. There is change in sclerite morphology from tentacle base to tip. Proximally, the first 1–2 sclerites are tuberculate plates (Figure 205Aa–e). There is then a change in form to crescentic scales of increasing size (Figure 205Af–h), and then of decreasing size becoming poorly formed towards the tentacle tip (Figure 205Ai–m). The largest of the crescents is about 0.116 mm.

The polyp body is protected by numerous, small oval scales (Figure 204D). These scales have an entire convex margin, a smooth exterior, and complex warts on the underside (Figure 205B). They are 0.073–0.164 mm long, but most are about 0.106 mm. Beneath these scales in the lower part of the polyp body there is a layer of stellate plates that interlock with one another like gear wheels. Similar sclerites occur in the coenenchyme (Figure 205Ca–c).

#### Coenenchymal sclerites (Figure 205C)

The coenenchyme contains 2 layers of sclerites. Those in the surface are smooth scales which are of the same form as those of the polyp body. The subsurface layer contains stellate plates that usually have 2 warts on one face (Figure 205C). Most are of relatively simple design, 065–0.085 mm long, like those illustrated in Figure 205Ca–c. However, more complex forms occur that may be up to 0.118 mm in length.

#### Variability

The three paratype fragments are all badly damaged. They are 115 mm, 260 mm and 310 mm in length. Most of the coenenchyme is missing and only a few polyps remain. Two specimens are heavily encrusted with sponges. The axial and sclerite characteristics of the three fragments agree well with those of the holotype. The proximal internodes in the longest specimen have 20 primary ridges, and the most distal have 8.

### Distribution

See Figure 294. Depth 88 m.

#### Gorgonisis gen. nov.

### Type species

Gorgonisis elyakovi sp. nov., here designated.

# Diagnosis

Colonies up to 340 mm high, sparsely branched, planar, with long whip-like branches arranged in a pseudo-dichotomous manner.

Sclerites are colourless and preserved colonies are yellowish white. Axial internodes are white proximally, becoming colourless and transparent in the twigs. Axial nodes are dark brown in the stem, becoming paler in the middle of the colony and yellow in the distal regions.

Polyps are distributed all around on most branches, becoming biserial near the ends of the twigs. They are adaxially reduced and adaxially naked, and contracted so as to lie along the branch surface. The neck zone is only slightly narrower than the rest of the body. The anthopoma is asymmetrical and not continuous with the body scales. The major octants are occupied by knobby, tuberculate scales that can be in a row of 3, or be up to 5 when some lie side by side. There are numerous granular platelets in the tentacle base which are transitional forms to the granular curved scales in the tentacle rachis. Anthopomal scales are up to 0.077 mm long, and tentacular scales are up to 0.053 mm.

The polyp body is protected by numerous smooth, ovate scales, up to 0.14 mm long, that often have a medial cleft in their distal margin. The scales are not arranged in rows.

Scales similar those in the polyp body form a surface layer on the thinner branches over a lower layer of spiny capstan-like sclerites which are mostly 0.065–0.090 mm long. Small stellate plates with 2 tubercles on each face also occur, but they are uncommon. The coenenchyme of the thicker branches and the stem contains a surface layer of smooth rooted heads, mostly 0.07–0.09 mm long, over a layer of capstans up to 0.11 mm in length.

The axial internodes are mostly <2 mm long and have multiple, smooth, primary ridges with pronounced shoulders.

#### Distribution

As for Gorgonisis elyakovi, see Figure 295.

#### Etymology

In allusion to the long whip-like branches, the epithet is derived from the Gorgons, the 3 mythical sisters with serpents instead of hair; combined with *Isis*. The generic name *Gorgonia* is similarly derived.

> Gorgonisis elyakovi sp. nov. Figures 206–208; 295

### Material examined

### Types

HOLOTYPE: NTM C10953, off Shark Bay, Western Australia, 24°55.6'S, 112°50.8'E, to 24°56.5'S, 112°53.5'E, 80-85 m, trawled, RV Akademik Oparin, P. Alderslade, 14 July 1987.

#### Diagnosis

As for the genus.







Figure 207 Gorgonisis elyakovi n.sp., holotype: A-E. Polyps; F-H. Axial internodes; I. Twig fragment.

### Description

# Colony form (Figure 206)

The sparsely branched planar colony is curved through bottle storage but can be straightened to a height of 340 mm. The branches are long and whiplike, and arranged in a pseudo-dichotomous manner. Branches curve from their point of origin and continue to grow more or less parallel to each other.

The main stem is bent, about 60 mm in total length and attached to a substantial calcareous holdfast. The stem is 2.4–3.0 mm thick at the denuded base. It divides into two main branches 1.9 mm and 2.4 mm thick. Branching occurs to about the sixth order. About mid-way up the colony the branches and twigs are 1.2–1.6 mm thick

(including polyps). They taper gradually over their length, the finest twigs being about 0.8 mm thick below the tip (including polyps). Twig tips sharply pointed, occasionally with a protruding axial internode. Unbranched twigs 40–250 mm in length. Distance between consecutive subdivisions 10–45 mm. Angle of branching 35–55°mm.

### Polyps (Figure 207D,E,I)

Rare on stem and lower portions of the main branches. Densely arranged and all around in the rest of the colony, except the terminal 1.5–8.0 mm of most twigs where they are biserial in single rows.

Polyps are contracted, adaxially reduced, and curved to lie along the branch bringing the anthopomal region to lie close to the branch surface

or to the base of a succeeding polyp. Measured along the branch most polyps are 0.72–0.90 mm long, with bases about 0.36 mm in length. Abaxially the polyp heads measure 0.36–0.38 mm across and there is a slightly narrower neck zone. Polyps project about 0.30–0.36 mm. Juvenile polyps are only common in the terminal twig regions.

### Colony colour

Yellowish white.

### Axis form (Figure 207F-H)

Internodes have pronounced, multiple, smooth primary ridges. The faintest trace of secondary ridges present only in terminal developing internodes, the last one or two of which may be 4sided. All others have numerous ridges with pronounced shoulders. A branch internode 0.58 mm thick has 12 ridges, a stem internode 1.08 mm thick has 43.

The basal 8 mm of the stem is mostly nodal material with two, short, partially covered internodes about 0.9 mm long on their longest side. Above this several internodes are visible 0.5–4.0 mm long. Very few axial portions above this are visible and segment lengths are estimated. The remainder of the stem internodes are mostly 0.8–1.1 mm long, with one measuring 3.6 mm. Internodes of the main branches are about 0.8–1.9 mm, and those in the rest of the colony about 1.3–2.1 mm long, with a few up to 2.7 mm. Nodes in the stem are 0.8–1.3 mm long, and in the main branches 0.3–0.6 mm. In the rest of the colony the nodes are about 0.2 mm long and considerably narrower than the internodes.

#### Axis branching.

Axial divisions often involve shared nodal material, particularly in the stem and thicker branches where branching is of the style shown in Figure 251 examples 60, 61 and 62. In the thinner branches, most joints are like example 52, with example 14 occurring more rarely.

#### Axis colour

Stem internodes white and only faintly translucent. Translucency progressively increases distally and the internodes in the thinner parts of the twigs are transparent and colourless. The colour of the nodes is variable. In the stem they are dark brown ( $\approx$ 6F8) with extremely narrow silvery satin-like borders. About half way up the colony, branch nodes are paler, rust brown ( $\approx$ 6E8), with yellowish satin-like borders. In the more distal regions of the twigs the nodes are maize yellow ( $\approx$ 4A6) with bluish opalescent borders reduced to nearly transparent narrow crescents between the shoulders of the primary internodal ridges. In the

terminal twig regions the borders are of similar design, while the opposing ends of the nodes are pale yellowish white either side of a thin, nearly transparent, central zone.

### Polyp sclerites (Figures 207A-E,I; 208A-C)

The anthopoma is asymmetrical and not continuous with the polyp body scales. The adaxial octant is weak and consists of 1-2 granular or tuberculate plates in a single row. They are usually figure-8, ovate (Figure 208Ak), or rectangular in outline (Figure 208Ag). The other octants are much stronger. They may be occupied by a row of about 3 sclerites whose shape can be oval or triangular or somewhere in between. The proximal scale is the largest and its upper face has smooth knobs and ridges, and granular tubercles (Figure 208Aa-d). The more distal scales are of decreasing size and are more tuberculate (Figure 208Ae-j). Some octants are more complex with the proximal and/ or the succeeding sclerite being replaced by 2 smaller scales arranged side by side. The largest anthopomal scales are about 0.077 mm long.

There seems to be a gradual transition of form through butterfly-shaped scales in the base of each tentacle to a single row of curved granular scales, up to 0.053 mm long, in the tentacle rachis (Figure 208Ba–d).

The polyp body is protected by numerous, smooth, generally ovate scales up to about 0.14 mm long (Figure 208C). They are not arranged in rows (Figure 207D,E,I). Those in the more basal region of the polyp tend to have an exposed margin that is entire except for a small, more or less medial, notch. In some polyps, like those illustrated, the notch in the more distal scales is quite marked. In others, however, it remains slight and in many scales it is absent altogether.

The circle of about 11–12 body scales that form the rim of the anthopoma often appear somewhat jumbled, but there is a general tendency for them to be imbricately arranged in both directions around the rim away from the most abaxial scale. Small accessory scales, sometimes modified (Figure 208Ca,b) may occur partially folded down within this rim.

The adaxial side of the polyp is short and naked below the adaxial anthopomal octant.

#### Coenenchymal sclerites (Figures 207D; 208D,E)

The surface of the thinner branches and the twigs (Figure 207D) contains an upper layer of scales similar to those of the polyp, and a lower layer of capstan-like sclerites (Figure 208D). The scales are mostly 0.10–0.14 mm across, occasionally up to 0.18 mm, with the exposed margin more or less entire. The capstan-like forms are mostly 0.065–0.090 mm long and many are flattened (Figure 208Da,b). Stellate plates with two tubercles on each



Figure 208 Gorgonisis elyakovi sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Twig coenenchyme; E. Main branch coenenchyme.

side (Figure 208Dc) and tuberculate plates (Figure 208Dd) are both present but very uncommon.

The surface of the main branches contains blocklike rooted heads, and capstans (Figure 208E). The rooted heads are mostly 0.07–0.09 mm across but a few to 0.14 mm are encountered. The capstans are 0.05–0.11 mm long with most occurring at the larger end of the range. The surface of the stem is similar to that of the main branches, but the rooted heads tend to be more mushroom-like.

# Distribution

See Figure 295. Depth range 80-85 m.

### Etymology

The species is named after Professor Georgy Elyakov, Director of the Pacific Institute of Bioorganic Chemistry, Vladivostok, expedition leader of the 1987 cruise of the RV *Akademik Oparin*, and amiable host who made it possible for me to join the vessel off the coast of Western Australia.

### Pangolinisis gen. nov.

#### Type species

Pangolinisis cia sp. nov., here designated.

#### Diagnosis

Colonies up to about 160 mm tall, sparsely branched, more or less planar, and ramified in a pseudo-dichotomous manner.

Sclerites are colourless and preserved colonies are yellowish white. Axial internodes are white and densely coloured in the stem, becoming more translucent in the distal parts of the colony. Axial nodes mostly brown becoming brownish orange in the thinner twigs.

Polyps are distributed all around. They are adaxially reduced, adaxially naked, and are contracted and curved so as to lie arch-like against the branches. The neck zone is only slightly narrower than the rest of the polyp body. The anthopoma is asymmetrical and continuous with the body scales, the last 1-2 series of which may occur folded over. The proximal sclerite in the major octants is usually a modified body scale with a smooth basal portion and a ridged apex. The scale which follows generally has a ridged base and a tuberculate apex. There may be a small basal tentacular scale, and each tentacle rachis has a single row of curved crescentic scales. The larger anthopomal sclerites are up to about 0.13 mm long, and the tentacular scales can be as long as 0.081 mm.

The polyp body is protected by smooth oval scales, up to 0.17 mm long, which commonly have a medial cleft in their otherwise entire distal margin. The scales are arranged in 7 rows on most

of the upper part of the polyp body, there being only a few irregularly arranged scales below the adaxial octant.

Scales similar to those in the polyp body form a surface layer in the branches, but many are anchored by a centrally placed cluster of warts. There is a subsurface layer of stellate plates with 2 tubercles on each face, together with spiny capstans and spheroids up to about 0.067 mm long. The surface layer of the stem coenenchyme contains many thicker scales which approach the form of rooted heads.

The axial internodes are mostly 2–4 mm long and have multiple, smooth, pronounced primary ridges.

### Distribution

As for the Pangolinisis cia, see Figure 296.

#### Etymology

From the Pangolins, the scaled mammals of Africa and Asia (O. Pholidota), in allusion to the appearance and orderly arrangement of the polyp scales; combined with *Isis*.

*Pangolinisis cia* sp. nov. Figures 209–211; 296

### Material examined

Types

HOLOTYPE: AM G15314, off Botany Bay, New South Wales, on submarine cable, 91 m, registered 18 Feb, 1906. PARATYPE: AM G15596, off Shell Harbour, New South Wales, 34°35'S, 150°52'E, HMAS *Gascoyne*, Sydney University Geology Dept., Dr Shirley, April 1964.

### Diagnosis

As for the genus.

## Description

### Colonial form (Figure 209)

The holotype is a broken specimen consisting of a sparsely branched basal fragment, complete with holdfast, and several smaller fan portions. The main fragment is 145 mm tall and 40 mm across. The large, thin, calcareous holdfast is about 12 mm x 10 mm and covered in thin coenenchyme. It is attached to some black, dense material and a tuft of thin string-like fibres, both of which are probably from the submarine cable on which the colony was growing. Branching is pseudo-dichotomous, and the branched fan portions indicate the colony would have been more or less planar. Some branching occurs slightly out of plane but the colony is only about 10 mm thick at the bushiest



Figure 209 Pangolinisis cia sp. nov., holotype, natural size.

section. The main stem is 2.1–2.2 mm thick (including coenenchyme) and 33 mm long. It divides into two main branches that are 1.6 mm and 1.9 mm thick (without polyps). Most branches in the middle region of the colony are about 2.1–2.2 mm thick (polyps included), and the twigs are about 1.6 mm thick. The branches and twigs in the upper regions of the colony are about 1.3–1.6 mm thick (polyps included). Many of the twigs terminate in a bare axial internode as the result of damage to the colony. Intact twig tips are blunt, polyp-free, and about 1.6 mm long. Unbranched twigs are 10–30 mm in length. Most consecutive branchings occur 10–30 mm apart, but the distance can be as great as 65 mm. Angle of branching is 39–52°. The colony fragments have a somewhat untidy appearance due to the slightly sinuous nature of the branches.

# Polyps (Figure 210E,F,L)

Polyps are distributed all around on the main stem and all twigs and branches. Polyp density is low on the main stem but high in most other parts of the colony. The contracted polyps are reduced adaxially, arising more or less vertically and then curving upward and over so that the anthopomal region faces the branch and is preserved just above or just touching the surface. Measured along the branch, polyps are about 0.90–1.08 mm long. They project from the branch surface about 0.42–0.48



Figure 210 Pangolinisis cia sp. nov., holotype: A-F. Polyps; G-H. Coenenchyme; I-K. Axial internodes; L. Twig fragment.

mm. Polyps bases are about 0.54–0.66 mm long, polyps heads about 0.45 mm wide, and there is a narrower neck zone. Juvenile polyps are common and scattered throughout the colony.

### Colony colour

The sclerites are colourless and the colony is a pale yellowish white. The nodes can be faintly seen through the coenenchyme only on some of the thinner twigs.

# Axis form (Figure 210I-K)

The axial internodes have numerous, very pronounced, smooth, longitudinal primary ridges. Even the axial tips have many ridges. Secondary ridges are absent. Desmocyte cavities are deep. The colony has very few visible axial segments. The internodes of the main stem are about 0.8-2.1 mm long and 1.9–2.1 mm thick. In the rest of the colony they have been estimated at about 2.7-4.3 mm in length. The internode at the tip of a twig, or that preceding a small developing tip, abruptly tapers (Figure 210I). A tip internode 0.69 mm at its widest has 11 longitudinal ridges. A main stem internode 2.05 mm thick has 33 ridges. Axial nodes in the main stem are about 1.3–1.6 mm long and slightly narrower than the internodes. In the rest of the colony they have been estimated at 0.3-0.5 mm long and, particularly in the upper reaches of the colony, are noticeably narrower than the internodes.

#### Axis branching

Branched internodes only initiate one division, and this is usually similar to Figure 251 examples 6, 14, 12 or 13.

### Axis colour

Internodes are white, translucent in the stem but densely coloured, and becoming progressively more translucent in the upper regions of the colony although never becoming transparent. In the stem and thicker twigs and branches the nodes are all more or less the same brown colour ( $\approx$ 7E6), slightly translucent, with thin yellowish satin-like borders. In the thinner twigs they are paler, brownish orange ( $\approx$ 5C6) with broader satin-like borders.

### Polyp sclerites (Figures 210A–F,L; 211A–C)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. Depending on how tightly the tentacles are infolded, one or more series of the upper body scales may or may not fold over the anthopomal region and appear to be incorporated into the octants. Where this folding over is minimal (Figure 210A), the major octants are dominated by a modified body scale with a more or less triangular shape and, commonly, an

irregularly ridged apex (Figure 211Ad-j). If this scale is relatively large and extensively modified (Figure 211Ai,j) the sclerite which follows and completes the octant will be mainly tuberculate (Figure 211Ak-n). If the scale is smaller and little modified (Figure 211Ad,e) the succeeding sclerite will be mainly ridged and generally have a tuberculate apex (Figure 211Aa-c). Most octants contain complementing pairs of an architecture between these 2 extremes. The major anthopomal scales (Figure 211Af-j) are mostly <0.13 mm long. The adaxial octant usually contains a single row of 3 tuberculate sclerites of decreasing size, and of similar form to those in Figure 211Ak-n. There is a single row of curved crescentic scales in each tentacle rachis, which are up to about 0.081 mm long (Figure 211Ba,b), and these are preceded by a single basal tentacular sclerite (Figure 211Bc,d).

The polyp body is protected by numerous, smooth, oval scales (Figure 210E,F,L). They have a distal margin that commonly has a medial cleft or concavity, but is otherwise entire (Figure 211C). The scales are arranged in 7 rows on the polyp head and neck, although the adaxial-lateral rows are very short. A few small scales, which are almost circular, are irregularly arranged in the area immediately below the adaxial octant, and there is a large naked area below this (Figure 210D). Body scales are 0.08–0.17 mm long, and they have complex warts on the underside.

# Coenenchymal sclerites (Figures 210G,H; 211D,E)

The surface of the branches contains 2 layers of sclerites. The outermost layer consists of oval to circular scales (Figure 210G,H), mostly about 0.07–0.13 mm across. Some are rooted by one edge (Figure 211Da), especially where the branch surface merges with the base of the polyps. However, many are only anchored by warts that are positioned more or less centrally on their underside (Figure 211Db). The subsurface layer contains thick stellate plates that usually have 2 tubercles on each face (Figure 211Dc,d), together with spiny spheroids, capstans, and intermediate forms (Figure 211De–h). The sclerites are about 0.045–0.067 mm long.

The sclerites in the coenenchyme of the stem are similar to those found in the branches. However, although many of the scales in the surface layer are thin (Figure 211Ee,f), some are very thick and unevenly swollen (Figure 211Eg–j) and stand more or less erect in the coenenchyme. The sclerites in the subsurface layer of stem coenenchyme are like those found in the branches, but they are larger and up to about 0.08 mm in length, and the spiny processes are notably longer (Figure 211Ea–d).

#### Variability

The paratype is a small, relatively delicate colony



Figure 211 Pangolinisis cia sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Twig coenenchyme; E. Stem coenenchyme.

from which much of the lower coenenchyme is missing. Apart from the thinner branches and the paler, whiter colouration the characters agree well with those of the holotype.

### Distribution

See Figure 296. Depth 91 m.

# Etymology

The specific epithet is a combination of letters not totally irrelevant to the fact that the holotype was found connected to a telephone cable.

# *Plexipomisis* gen. nov. Figure 322

Mopsea; (part) Thomson and Mackinnon, 1911: 677– 678; (part) Kükenthal, 1915: 117–118 (in key); (part) Kükenthal, 1919: 558–559 (in key), 617– 618; (part) Kükenthal, 1924: 437; (part) Grant, 1976: 33.

# Type species

Plexipomisis thetis sp. nov., here designated.

#### Diagnosis

Colonies up to 340 mm tall, more or less planar, and branched in a predominantly quasidichotomous manner.

Preserved specimens are pale yellow to pale orange, with paler or white polyps. Sclerites are colourless to pale yellow in transmitted light. Axial internodes are white and very translucent in the basal regions, becoming transparent and colourless distad. Axial nodes in the lower parts of the colonies are opaque and shades of brown, becoming yellower with a brown central band in the thinner twigs.

Polyps are generally biserially distributed with up to 4 rows on each side of the thicker branches. Polyps are more or less club-shaped, adaxially reduced, adaxially naked, and contracted to lie against the branch surface. The anthopoma is asymmetrical and continuous with the polyp body sclerites. The major octants are each occupied by a complex of small, ridged or leafy sclerites, fitting closely together and up to 0.07 mm long. There is a single row of curved scales in the rachis of each tentacle.

The polyp body is protected by numerous, small, oval scales, up to 0.12 mm long, that are not arranged in rows. The scales are ornamented with ridges or papillae, and the distal margin is undulate or has a medial cleft. In *P. thetis* sp. nov. there is a subsurface layer of stellate plates over most of the polyp body. In *P. elegans* (Thomson and Mackinnon, 1911) such forms only occur in the most basal regions of the polyp.

The coenenchyme of most branches has a surface layer of either thick oval scales (*P. elegans*) or dimpled rooted heads (*P. thetis*). There is a subsurface layer of stellate plates, capstans, and intermediate forms, up to 0.057 mm long. The coenenchyme of the stem contains rooted heads over a subsurface layer of capstans and spheroids that are up to about 0.07 mm long.

The axial internodes have multiple primary ridges and low, broad, secondary ridges. The surface is either granular (*P. elegans*) or relatively smooth (*P. thetis*). Internodes are up to 2.7 mm long.

### Distribution

See Figure 322.

#### Etymology

The combining form of the Latin *Plexus*, a figurative term for intricate, with the Greek *poma*, a lid or cover, in allusion to the complex anthopomal structures; combined with *Isis*. The 'a' from *poma* has been dropped for the purpose of euphony

### *Plexipomisis thetis* **sp. nov.** Figures 212–215; 297

Mopsea elegans (part) Thomson and Mackinnon, 1911: 677–678, Plate LX1V, Figures 3–4, Plate LXV111, Figure 5, Plate LXX11; (part) Kükenthal, 1919: 624; (part) Kükenthal, 1924: 440.

#### Material examined

#### Types

HOLOTYPE: AM G12147, exact location not specified, HMCS *Thetis*, station 34 or 41 or 42 or 47 or 48, between Port Jackson and Wollongong, New South Wales, 39–78 fm, March 1898. PARATYPES: AM G12148, AM G12150, BM 1933.3.13.114, data as for holotype; AM G11750–G11752, AM G11755– G11756, HMCS *Thetis*, station 47, 6–8 miles off Bulgo, New South Wales, 104–115 m, mud and abattoir refuse, 16 March 1898.

#### Differential characteristics

Coenenchymal sclerites in the form of dimpled rooted heads.

# Remarks

In the taxonomic account of their new species *Mopsea elegans*, Thomson and Mackinnon did not designate a holotype or differentiate a type series, and, unfortunately, confused two different species in their report. The labelled type series apparently consists of six lots; four from the Australian Museum collection and two from the Natural History Museum (London). The latter are only



Figure 212 Plexipomisis thetis sp. nov., holotype, natural size.

small fragments and most probably portions of the former, one being labelled "Schizo-cotype". Of the Australian Museum material, specimen G12147 is labelled "Type" and specimens G12148–G12150 are labelled "Co-Types". Of these, specimen G12149 is a different species to the other three, and Thomson's and Mackinnon's sclerite drawings (1911: Plate LXV111, Figure 5) and their descriptive comments about polyp size, sclerite architecture, and a median line on the surface of the branches, clearly refer to this species. However, it is apparent that the authors selected a different colony to be photographed for their Plate LXX11, and portions of specimen AM G12147 labelled 'Type', clearly match this illustration. Which fragment is

illustrated in Plate LX1V, Figure 3, is not determinable. Most, or all, of the HMCS *Thetis* Expedition specimens constituting the type series of the numerous new species created by Thomson and Mackinnon are held by the Australian Museum. Although in most instances a single specimen bears the label "Type", it is by no means clear whether this was done by the authors or even at their instigation. Upon reading their descriptions it becomes apparent that in some cases they appeared to base their species primarily on one specimen, usually the largest; for example *Plumarella corruscans*, (pp. 684–686). In others they do not appear to have singled out any particular colony; for example *Plumarella thetis*, (pp. 683–684).

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Figure 213 Plexipomisis thetis sp. nov., holotype: A-C. Polyps; D. Coenenchyme; E-F. Axial internodes; G. Twig fragment.

In the case of *M. elegans* the text indicates that their largest colony may have initially been selected as the specimen upon which to base their description, but, although this is quite probably the illustrated colony, all of the type series specimens are now so fragmented that it is impossible to be certain which was the largest. It is clear, however, that their microscopical investigation of colony surface ornamentation, polyps and sclerites was carried out on a specimen of the species represented amongst the syntypes by G12149 and the three small fragments of BM 1933.3.13.113. The syntype AM G12149 is here designated as the lectotype of Mopsea elegans Thomson and Mackinnon, 1911, and the species group is transferred to Plexipomisis gen. nov. and described later.

The other specimens, paralectotypes of *M*. *elegans*, form part of the type series of the new species *Plexipomisis thetis* described below.

Thomson and Mackinnon gave five collection stations for *M. elegans*. Assuming the British Museum fragments are pieces off the four labelled types, they must have used other material as well. There are five more specimens in the Australian Museum collected by the HMCS *Thetis* expedition from station 47 that are the same species as the majority of the labelled types. These may have been seen by the authors, however, they have no labels indicating they were identified. Also, some of them are nearly white which contradicts Thomson's and Mackinnon's statement that the colonies were "golden brown". It seems prudent not to include
them as original syntypes of *M. elegans*. They are included here as part of the type series of the new species *Plexipomisis thetis*.

## Description

## Colonial form (Figure 212)

The holotype consists of numerous sparsely branched fragments. The branching pattern appears to be more or less in one plane and quasidichotomous with some lateral divisions. The branches grow nearly parallel to each other and are closely oppressed, a state probably exaggerated by storage in a tied bundle. The holdfast and basal portion of the colony is missing. The preserved upper section of the main stem is 3.5 mm thick, 26 mm long and divides into two main branches 3.3 mm and 2.2 mm thick. Most of the coenenchyme, 0.23–0.32 mm thick, is missing from the lower part of the fragment. Most of the branches and twigs in the remaining fragments are about 1.26–1.58 mm thick (including polyps). They do not taper noticeably over their length. In the upper regions the twigs are 1.11–1.26 mm thick with blunt tips. Terminal axial internodes protrude minutely in some instances. The longest unbranched twig is 135 mm, but most are less than 70 mm. The distance between consecutive subdivisions is mostly 25–40



Figure 214 Plexipomisis thetis sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Adaxial polyp margin.

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mm, but can be as great as 80 mm. Branching angle is  $10-40^{\circ}$ .

## Polyps (Figure 213B,C,G)

Predominantly arranged biserially, especially in the upper regions of the colony. In some of the thicker lower branches there may be four irregular rows on each of the two opposing sides, which tend to encroach on the other faces. On some branches only one face is free. In the middle regions of the colony there are two or three rows on each side, in the terminal regions two, and on the finest twigs occasionally one row. There are very few polyps on the fragment of stem and main branches.

The polyps are slightly club-shaped, adaxially reduced, contracted, and curved upwards against the surface of the branch so that the anthopomal region lies close to the base of the succeeding polyp. In a number of cases there is a shallow depression in the branch surface to receive the anthopomal region. Measured along the branch the polyps are about 0.90–0.96 mm long, the bases 0.48–0.60 mm long. The heads are about 0.45–0.48 mm across, abaxially. There is a slightly narrower neck zone that is more noticeable in the longer polyps. The polyps project about 0.30–0.33 mm above the branch. Juvenile polyps occur scattered throughout the colony.

#### Colony colour

The stem and main branches are light yellow ( $\approx$ 4A4). The main polyp bearing regions are light orange ( $\approx$ 5A5), the polyps slightly paler. The coenenchyme is translucent with the underlying dark nodes of the main stem and main branches easily seen, and the paler nodes of the upper regions just visible. Sclerites are colourless to pale yellow in transmitted light.

## Axis form (Figure 213E,F)

Internodes have pronounced primary ridges and broad, low, secondary ridges. Surface granulation like that in *P. elegans* sp. nov. is almost imperceptible. Internodes in the thinner apical regions of twigs are 4-sided. The number of ridges increases proximally. A stem internode 3.2 mm thick has 50 primary ridges, a branch internode 1.1 mm thick has 11.

Very little of the axial segments are visible and measurements are estimates. The stem internodes are about 1.3–1.7 mm long, and those in the main branches 1.6–2.7 mm long. In the rest of the colony they are 2.4–2.7 mm in length. The stem nodes are 1.6–1.7 mm long, and those of the main branches 0.8–1.1 mm long. In most branches and twigs they are about 0.3 mm long, shorter near the twig tips where they are noticeably thinner than the internodes.

### Axis branching

In the thinner branches and twigs, most of the lateral divisions occur from the distal end of an internode involving the nodal material of the parent branch as in Figure 251 example 13. The more dichotomous bifurcations involve shared nodal material as in example 19. Similar but more complex joints are formed in the main stem and major branches like that illustrated in example 20.

#### Axis colour

The internodes of the stem and main branches are white and very translucent. Translucency increases distad and the internodes of the terminal twigs are virtually transparent. The nodes of the stem and main branches are virtually opaque and light brown ( $\approx$ 6D5) with thin silvery satin-like borders. The nodes of the thicker branches are also opaque, and brownish orange ( $\approx$ 5C5) to brown ( $\approx$ 7E7) with broad yellowish satin-like borders. The nodes of the thinner branches and twigs have very broad yellowish borders with a brownish central band. Terminally the nodes are mostly satin-like with very thin pale brown central zones.

#### Polyp sclerites (Figures 213A–C; 214; 215A,B)

The anthopoma is asymmetrical and continuous with the polyp body sclerites (Figure 213A). At the periphery of the anthopoma, small modified body scales with very uneven margins give way to a complex arrangement of more elongate, crescentic, or club-shaped sclerites within each octant. These sclerites (Figure 214A) are up to about 0.07 mm long, and often unilaterally developed with ridges and leafy processes. Their arrangement and architecture differs in each octant. At the apex of an octant a few spindle or club-shaped sclerites (Figure 214Aa-c) are arranged in chevrons on to the base of the tentacle where they merge with the proximal tentacular sclerites. The latter are tuberculate crescents (Figure 214Bb,c), and sometimes rods (Figure 214Bd). They precede a single row of curved scales with tuberculate margins, up to 0.065 mm long, in the tentacle rachis (Figure 214Ba). The adaxial octant contains far fewer ridged or leafy sclerites than is found in the other sectors; about 7 compared to about 15. The proximal portion of the adaxial octant contains numerous figure-8 scales (Figure 214C). Occasionally up to 0.05 mm long, most are exceedingly small, 0.028-0.033 mm, and they extend onto the upper part of the polyp body. Below these scales the adaxial neck region of the body is naked.

The scales of the polyp body are very small, numerous, and not arranged in rows (Figure 213B,C). The largest are about 0.12 mm across. They have a more or less ovate outline (Figure 215A) and the upper face has smooth granules, and



Figure 215 Plexipomisis thetis sp. nov., holotype, sclerites: A. Polyp body; B. Sub-surface of polyp body, stellate plates; C. Twig coenenchyme; D. Sub-surface of stem coenenchyme.

ridges which are mostly transverse. The undersides are tuberculate and radially ridged (Figure 215Aa,b). Beneath these scales is a layer of stellate plates (Figure 215B), mostly 0.05–0.07 mm across, which commonly have two complex tubercles on both faces.

## Coenenchymal sclerites (Figures 213D; 215C,D)

The surface of the twigs and branches contains an upper layer of rooted heads (Figure 215Ca-d), and a subsurface layer of capstans (Figure 215Ce,f), and other sclerites (Figure 215Cg-k) that are flattened and intermediate in form between capstans and the stellate plates of the polyps. The rooted heads have a smoothly dimpled upper surface and are mostly 0.024–0.057 mm across. The capstan and flat-capstan forms are mostly 0.041– 0.057 mm long.

The surface of the main stem contains rooted heads of a similar size to those in the branches, but

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with shallower dimples, and many subsurface capstans and spheroids (Figure 215D) up to 0.07 mm across.

## Variability

Seven of the paratypes are groups of colony fragments. The eighth, from the Natural History Museum (London), is a single portion 130 mm long labelled "Schizo-cotype", and is therefore a piece off G12148 or G12150. Except in colour, the character of all the specimens agree well with those of the holotype. Four of the colonies have colourless sclerites and are a very pale yellowish white. In some of the paratypes some of the axial internodes have ridges with pronounced shoulders.

## Distribution

See Figure 297. Depth range 71–142 m.

## Etymology

The species is dedicated to the HMCS *Thetis*, the expeditionary vessel. Thetis was one of the mythological nereids and mother of Achilles. Noun in apposition.

## Plexipomisis elegans (Thomson and Mackinnon, 1911) new comb. Figures 216–219; 298

Mopsea elegans (part) Thomson and Mackinnon, 1911: 677–678, Plate LXIV, Figures 3–4; Plate LXVIII, Figure 5; Plate LXX11; Briggs, 1915: 74; (part) Kükenthal, 1915: 123 (in key); (part) Kükenthal, 1919: 624; (part) Kükenthal, 1924: 440.

## Material examined

Types

LECTOTYPE (here designated): AM G12149, HMCS *Thetis*, station 47, 6–8.5 miles off Bulgo, New South Wales, 60 fm, 16 March 1898. PARALECTOTYPE(?): BM 1933.3.13.113, no data, labelled "Cotypes = Syntype?", possibly fragments of the lectotype.

## Other material

AM E142, no data; AM E2288, 6 miles SE of Brush Head Island, New South Wales, 65 fm, F.I.S. Endeavour, 14 Feb. 1911.

#### **Differential characteristics**

Coenenchymal sclerites in the form of smooth oval scales.

## Description

Colony form (Figure 216)

The lectotype now exists as numerous branched

fragments. The branches are more or less parallel to each other and are closely oppressed, a state undoubtedly exaggerated by being stored in a tied bundle like a bunch of thin sticks. The fragments indicate the colony was planar. The longest of the sparsely branched fragments are about 190 mm. The ramification is mostly quasi-dichotomous with some lateral divisions. There are no recognisable main stem portions preserved. A short 30 mm fragment, with very few polyps and the stubs of two relatively thick branches, appears to be a portion of a main branch, and it is about 1.7 mm thick. In what was apparently the middle regions of the colony the branches and twigs are 1.0-1.8 mm thick (including polyps). They taper only very slightly over their length, being about 0.9-1.1 mm thick below the tips which are sharply pointed. The tip of the terminal axial internode generally protrudes beyond the coenenchyme. Unbranched twigs are 8-65 mm in length with most about 20-40 mm long. Consecutive branchings occur 15-70 mm apart with the distances in the lower parts of the colony being generally shorter than in the upper regions. The angle of branching is 11–35° with most being >30°.

#### Polyps (Figure 217B,I)

Distribution is for the most part biserial but very variable. There are from 1–3 rows along each side of a branch or twig. The rows may be regular or irregular, and their number may vary on different parts of the branch which is not necessarily correlated with its thickness. In some areas the polyps are distributed all around.

The polyps are club-shaped, adaxially reduced, contracted, and curve upward and over so that anthopomal region makes an acute angle with the branch, usually <45°. Sometimes the anthopoma is nearly parallel to the surface. The polyps are very close together and the head of one may lie just beside the base of the next. Juvenile polyps occur scattered throughout the colony fragments. The larger polyps are mostly 0.72–0.90 mm measured along the branch and may project 0.27–0.33 mm. Each polyp has a broad base 0.48–0.54 mm long, a distinct neck zone, and a bluntly rounded head 0.36–0.42 mm across.

#### Colony colour

Most of the colony fragments are light yellow ( $\approx$ 4A4) with the polyp heads much paler, nearly white. Part of a thick branch fragment is a darker colour, greyish-orange ( $\approx$ B5). On the bare faces of many branches there is a thin, sinuous, shiny median line caused by the ridge-like arrangement of the surface sclerites (Figures 217E). The coenenchyme is translucent on the thinner branches and twigs where the pale underlying nodes can just be seen. The sclerites are colourless to pale yellow in transmitted light.



Figure 216 Plexipomisis elegans (Thomson and Mackinnon, 1911), lectotype, natural size.

## Axis form (Figure 217F-H)

The axial internodes have conspicuous primary ridges and wide, low secondary ridges. The whole of the internode surface, including the ridges, is finely granular. Desmocyte cavities are shallow. In the thinner more distal regions of the twigs the internodes are 4-sided. The number of ridges and sides increases proximally. A branch internode 1.32 mm thick has 16 primary ridges. The shoulders of the ridges are often very pronounced.

Very little axial material is uncovered and the sizes of the segments are mostly estimates. Throughout the fragments the internodes are about 2.1–2.7 mm long. In the thicker branches they are

about 1.3–1.6 mm thick, and about 0.3 mm thick just below the twig tips. The nodes in most of the colony regions are about 0.3 mm long. They are slightly shorter near the twig tips where they are much thinner than the internodes.

### Axis branching

Branched internodes only initiate one division. Bifurcations involve shared nodes as in Figure 251 examples 19 and 25, and short calcareous stubs as in examples 6, and 12–14.

## Axis colour

The internodes of the thicker branches are

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Figure 217 Plexipomisis elegans (Thomson and Mackinnon, 1911), lectotype: A-D. Polyps; E. Coenenchyme; F-H. Axial internodes; I. Twig fragment.



Figure 218 Plexipomisis elegans (Thomson and Mackinnon, 1911), lectotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

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translucent and white, like milky glass. The translucency progressively increases distally and in the terminal regions of the twigs the internodes are transparent. The more proximal nodes are more or less opaque, brownish orange ( $\approx$  5C5) with yellowish satin-like borders. In the thinner twigs the nodes are mostly yellowish and satin-like with a very thin brownish central band.

## Polyp sclerites (Figures 217A–D; 218)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The adaxial octant contains 2 small tuberculate platelets of irregular shape, about 0.06 mm long. The major sectors are more complex, each containing numerous overlapping scales in several series (Figure 217A,C). Within an octant the scales decrease in size distad, the apical few being in a single row. There is a gradual change in the form of the upper body scales from those with a few small papillae (Figure 217D) to those with irregularly arranged ridges (Figure 218Ca-e) which merge into the peripheral parts of the anthopoma. The succeeding sclerites are more elongate with more pronounced ridges (Figure 218Ai,j), and they give way through intermediate designs to ridged and knobbed distal forms with incised margins Figure 218Aa-h,k-m). The anthopomal scales are mostly about 0.045-0.073 mm long.

There is a small tuberculate basal tentacular scale (Figure 218Bc,d) preceding a single row of large, curved, crescentic scales, up to 0.077 mm long, in the tentacle rachis (Figure 218Ba,b).

The polyp body is protected by numerous oval scales that are not arranged in rows (Figure 217B;

218C). They have a medial cleft in the distal margin, clusters of warts on the underside, and are mostly 0.045–0.102 mm long. Those merging with the anthopoma are ridged, and while the majority of those remaining are ornamented with a few small papillae a few are smooth (Figure 218Cg–l). The adaxial side of the polyp body is naked below the adaxial octant.

#### Coenenchymal sclerites (Figures 217E; 219A)

The coenenchyme on the branches has a surface layer of scales similar to those found on the polyp, but slightly thicker (Figure 219Aa–c). Instead of being imbricately arranged in the direction of the branch, they are lying in 2 lateral directions (Figure 217E), the zone of change of direction appearing as a bright line meandering along the face of the branch, and faintly visible in Figure 217I.

The subsurface layer contains capstans (Figure 219Af–i), stellate plates with 2 tubercles or tubercle clusters on one side (Figure 219Ad,e), and intermediate forms. Many of the capstans have flattened processes (Figure 219Ah,i), and the stellate plates are mostly found around the polyps where they extend as a subsurface layer on the very base of the polyp body. The capstans and plates are mostly 0.041–0.057 mm long.

There is no stem material preserved. The coenenchyme from a fragment of AM E142, that appears to be main branch or upper stem, contains a surface layer of thick scales and rooted heads up to 0.09 mm long (Figure 219Be,f) and subsurface capstans and spheroids up to 0.07 mm (Figure 219Ba–d).



Figure 219 Plexipomisis elegans (Thomson and Mackinnon, 1911), sclerites: A. Lectotype, twig coenenchyme; B. AM E142, upper stem coenenchyme.

### Variability

Specimen lot AM E142 is a large number of dry branched fragments representing a very big colony, assuming all the material originated from one specimen. The coenenchyme is light orange ( $\approx$ 6A5) and the polyp heads are white. The internodes are light yellow ( $\approx$ 4A4). One unbranched twig is 100 mm long while most are much shorter. Polyp distribution is mostly all around with areas where they are concentrated more on two sides, but some of the thinner twigs have two single rows biserially arranged.

#### Distribution

See Figure 298. Depth range 71-142 m.

Zignisis gen. nov. Figure 323

Mopsea; Studer, 1878: 665, 679; (part) Briggs, 1915: 70-78.

Acabaria; Thorpe, 1928: 521-523.

## **Type species**

Mopsea repens Briggs, 1915, here designated.

*≡ Zignisis repens* new combination.

#### Diagnosis

Colonies grow in excess of 200 mm tall. They are more or less planar; some flabellate, and others slightly bushy and formed from several closely oppressed fans. All colonies are sympodially divided, and branching is usually profuse.

The colonies are generally a shade of brown, with sclerites that are yellowish in transmitted light. Some colonies have pale yellow to white polyps, and a few colonies are totally white. The axial internodes may be, yellowish, orangeish, brownish or grey-white. They are opaque to translucent in older parts of the specimens becoming increasingly transparent distad. The nodes are generally shades of brown, orange, or yellow.

The polyps are usually arranged all around most branches, but they may be biserial on the thinner twigs or their terminal portions. They are adaxially reduced and adaxially naked below the polyp head. They are usually preserved with the polyp base arising shelf-like from the branch, and the head angled distad so that the anthopoma faces along the branch or down towards its surface. There is a suture between the head and the base marking the position of an extendible sclerite-free neck zone.

The anthopoma is asymmetrical and continuous with the polyp body sclerites. Its structure varies from species where the octants contain several transverse scales preceding a complex arrangement of tubercular rods, clubs, and branched forms, to species where each octant is occupied by just a single row of scales of decreasing size. In the latter, the most distal scales may resemble 2 clubs laterally fused head to head. The structure of the anthopoma is of major importance when differentiating between species.

The tentacle rachis contains small granular rods, sometimes flattened, whose exact arrangement is usually difficult to ascertain. They are generally arranged transversally. In some species they occur in 2 close rows with the sclerites alternately interleaved. It is uncertain if the apparent single rows in other species are a result of their tightly contracted state, as some rods may be found longitudinally arranged, jumbled, or *en chevron*.

The polyp is protected by numerous, mostly smooth, oval to crescentic scales, commonly no more than 0.17 mm long. Their distal margin is more or less entire, sometimes undulate, and sometimes with a medial cleft. The underside of the blade is usually radially ribbed. The scales may be arranged in 7 rows on the polyp head. There are usually only a few narrow scales or flattened spindles immediately below the adaxial octant.

There are 2 layers of sclerites in the coenenchyme. The upper layer contains rooted heads. The head portion may be laterally compressed, like a thick scale, and have prominent ribs down the sides. More often, however, the ribs are not as prominent, the head is bulbous and cushion-like, and the summit is smooth or has a few simple tubercles. The subsurface layer usually contains ovals and spindles with complex tubercles often in girdles, tuberculate plates, and capstans. Capstans are more common in the older, thicker parts of the colonies. The rooted heads may only be as large as 0.08 mm, but in most species they are commonly twice as long as this.

Most axial internodes are <1.9 mm long. They have multiple primary ridges, usually with pronounced shoulders, and secondary ridges (developing primaries) are not uncommon. Internodes in the finer portions of the twigs may be 4-sided. In the thicker, older parts of the colonies the primary ridges are continued as ridges along the nodes. In some species the internodes are all smooth, while in others the ridges are denticulated. In the latter case, the older internodes and those near the twig tips will usually be smooth. Axial branching commonly involves shared nodes.

#### Remarks

Acabaria dakini Thorpe, 1928 is almost certainly a species of Zignisis. Unfortunately, Dakin's collection from the Abrolhos Islands, Western Australia, is lost, and Thorpe's description is so imprecise and full of errors and inconsistencies that it is not possible to identify her material with any 292

of the species described below. For example, Thorpe described the anthopoma as consisting of 8 "calyx lobes" each containing "from five to six spicules", whereas her Plate 32, Figure 12 shows the number of spicules in the "lobes" at approximately 12–15.

## Distribution

See Figure 323.

## Etymology

In allusion to both the zigzag nature of the branching, and the reptile-skin appearance of the smooth-scaled polyps, the generic name is derived from the Greek Zignis, a kind of lizard; combined with Isis.

## Zignisis repens (Briggs, 1915) new comb. Figures 220–224; 299

Mopsea repens Briggs, 1915: 77–78, Plate iv, Figure 2; Plate viii.

## Material examined

Types

HOLOTYPE: AM E2243, 36 miles south west of Cape Wickham, King Island, Tasmania, 72–80 fm, FIS Endeavour, 27 Feb 1911. PARATYPES: AM E1015, E1018, G11800, G11801, 15 miles south of St. Francis Island, South Australia, 30 fm, FIS Endeavour registered 15 Sept. 1909; AM G12112, same data as holotype.

## Other material

NTM C10917, C10920, C10921, C10925 (3 colonies), C10930 (6 colonies), C10931 (3 colonies), C10932 (3 colonies), C10936, C10940 (2 colonies), C10941 (2 colonies), C10947 (3 colonies), C10950, off Shark Bay, Western Australia, 24°55.6'S, 112°50.8'E, 80-85 m, RV Akademik Oparin, P Alderslade, 14 July 1987; WAM 25-74, north west of the western end of Rottnest Is., Western Australia, 37 fm, FV Blue Fin, B.R. Wilson, 12 Aug. 1962; WAM 1-95, west side of Sandy Hook Is., Recherche Archipelago, Western Australia, 80 ft, on rock wall, C. Bryce, 8 April 1977; AM G15308, Great Australian Bight, 34°29'S, 133° 58'E, 95 m, RV Courageous, P. Alderslade, 31 Jan. 1979; SAM H827, 12 km off Cape Northumberland, South Australia, 62 m, S. Shepherd, 6 May 1975.

The following specimens housed at the NMV from the Victorian Institute of Marine Science's Bass Strait Survey, recorded in the format 'Station n°/lot n°': 185/53, 38°48'S, 143°14.5'E, 47 m RV *Tangaroa*, 20 Nov. 1981; 191/4, 39°6.3'S, 142°55.6'E, 84 m, RV *Tangaroa*, 21 Nov. 1981.

## **Differential characteristics**

Colonies flabellate and profusely ramified with

delicate thin branches; characteristic anthopomal sclerites mostly in the form of leafy or tuberculate clubs and rods; axial internodes without denticles.

## Description

## Colony form (Figure 220A)

The holotype, designated by Briggs in the caption to his Plate viii, is a delicate, planar colony about 135 mm tall and 120 mm wide. It comprises a number of sympodially branched fans which are profusely ramified and overlap each other, but the colony is no more than 7 mm thick. The holdfast is missing, and the stem is 2.1 mm in diameter and devoid of coenenchyme. The first 12.5 mm of the stem is predominantly nodal material which is longitudinally ridged like the internodes above it. The stem branches twice, forming 3 main branches which repeatedly divide in a zigzag manner, producing major branches and pseudo-lateral twigs that branch again to a high order. In the upper reaches of the colony the sympodial manner of branching sometimes becomes irregular, and occasionally breaks down completely when the axis fails to zigzag and gives off lateral twigs on one side only. Most of the longer twigs are about 0.54-0.60 mm thick. Shorter twigs are only about 0.42 mm in diameter. The coenenchyme is missing from the tips of most terminal twigs leaving one or more axial segments exposed. Where the main branches diverge from the stem they are about 1.50-1.62 mm thick, gradually becoming narrower as they ramify throughout the colony. Unbranched terminal twigs are relatively short. They may be as long as 25 mm but most are <20 mm, with some as short as 10 mm. The zigzagging branches give off pseudo-laterals about every 3-4 mm, but intervals of up to 8 mm do occur. Angle of branching is 35-50°.

## Polyps (Figure 221D,J)

For the most part polyps are distributed biserially, but it is not consistent. On the thinner ramifications there is usually a single row of polyps down each side in a more or less alternating manner. On the slightly thicker branches the rows become irregular, with polyps occasionally occurring out of line. On still older branches polyps also occur all around, but they are densest on the lateral aspects. Polyps are scarce on the main branches and especially rare in the lowest regions. There are about 5 polyps for every 2 axial internodes on the thinner twigs and branches.

The polyps are contracted and adaxially reduced (Figure 221J). The head is supported by a shelf-like base that is quite small and not as pronounced as in other species of the genus. There is a suture between the head and the base visible in a small number of polyps. In most colonies the head is



angled so that the adaxial side touches the surface of the branch, the anthopoma facing along the branch or tilted towards it, sometimes making an angle as small as 30°. Polyp heads are about 0.43– 0.46 mm across abaxially, and about 0.34–0.41 mm in length. The total length of a polyp is about 0.65– 0.72 mm, and most project about 0.36 mm. A few polyps are more erect, with a small gap between the adaxial side and the branch, and stand up to 0.48 mm above the surface. A few juvenile polyps occur scattered throughout the colony, and polyps growing upside-down are not uncommon.

#### Colony colour

The wet coenenchyme is light brown ( $\approx$ 6D6) and polyps are pale yellow. As the specimen begins to dry the colour of the coenenchyme becomes much paler, changing to greyish orange ( $\approx$  5B4). This is because the colour of the colony when wet is determined primarily by the axial internodes and



Figure 221 Zignisis repens (Briggs, 1915), holotype: A-F. Polyps; G. Coenenchyme; H-I. Axial internodes; J. Twig fragment.

the subsurface layer of coenenchymal sclerites which are mostly brownish orange. The surface layer sclerites and those of the polyps are colourless to very pale yellow in transmitted light. The pale axial nodes can be seen through the coenenchyme.

#### Axis form (Figure 221H,I)

The internodes of the stem, main branches, and all but the narrowest of the other zigzagging major branches have multiple smooth primary ridges. The nodal material of the stem is also ridged. The internodes of the twigs are more or less square with a primary ridge along each edge. The shoulders of the ridges are often pronounced and they have a slightly lumpy surface, but true denticles never develop. Twig internodes, especially those at the proximal ends of the longer twigs, may show a developing primary ridge on each face. A branch internode 0.36 mm thick has 8 primary ridges, and one 0.60 mm thick has 14. A stem internode 1.86 mm thick has 36 primary ridges. The desmocyte cavities are relatively deep and quite distinct.

Most of the stem is constructed from modal material. In the lower part, overgrown internodal masses can be seen within the translucent nodal substance. Above this the internodes are very short and uneven, 0.12–0.60 mm long, separated by nodes 0.60–1.02 mm in length. In a section of naked main branch axis in the middle of the colony, internodes are about 0.72–1.12 mm long and the nodes are about 0.30 mm long. In the terminal twigs most internodes are 0.84–1.32 mm long, and the length of the nodes is 0.12–0.18 mm.

## Axis branching

Where the stem and the main branches bifurcate and give off thick branches the joints involve complex nodes as in Figure 251 example 59. Where narrower major branches generate branches of similar diameter, or slightly thinner pseudolaterals, the node is shared as in examples 24, 25, 42 and 45. Thick lower branches produce thin



Figure 222 Zignisis repens (Briggs, 1915), paratype, AM G11801: A-E. Polyps; F. Coenenchyme; G. Twig fragment.

pseudo-laterals from nodes as in example 57. Amongst the finer branches and twigs, bifurcations are generally of the form shown in examples 13 and 14, and sometimes 26.

#### Axis colour

The nodal material of the stem is brown (≈7F7) and translucent, and the internodes are relatively opaque and pale greyish orange (≈5B4). Nodal borders are very narrow, white and satin-like, and present as semi-circles or crescents between the internodal ridges. Higher in the colony the nodes become paler and the colour of the internodes intensifies. About one third of the way up the colony the internodes of the main branches are light orange or salmon coloured (≈6A4), and the nodes are autumn leaf brown (≈6D7) with borders like those in the stem but slightly broader. Higher up the centre of the main branch nodes become transparent. The internodes of most all of the finer branches and twigs are brownish orange (≈6C8) and translucent, becoming almost transparent at the tips. The nodes generally have an almost transparent, short, central band which is flanked by bright white bands (the visible ends of the internodes) and the usual white satin-like borders.

### Polyp sclerites (Figures 221A-F,J; 223)

The anthopoma is asymmetrical and continuous with the polyp body scales. The adaxial octant is often weak and may consist of only 2 sclerites, but up to about 4 may occur in this sector. They are tuberculate plates of irregular shape (Figure 223Aw–z). There may be 1–3 of the larger forms arranged transversally followed by 1–2 lying longitudinally.

The other octants are each occupied by a row of proximal crescentic scales which precede several clubs and small platelets. In each of the adaxiallateral octants there are about 3 proximal scales (Figure 221A,E). They are tuberculate on their exposed face and their convex margin is generally half leafy or blade-like and half warty or dentate (Figure 223At-u). In each of the other octants there are about 4 proximal crescentic scales in a row. Their outer face is sculptured with knobs and ridges (Figure 223Aq-s) and their convex margin may have a medial cleft. The most distal of the these may occasionally be very narrow (Figure 223Av) or divided into 2 leaf edged clubs. Scales which are modified as clubs (Figure 223Am-p) often occur in preparations of polyp sclerites. All major octants are completed distally by several clubs and platelets (Figure 223Aa-l) whose arrangement is difficult to define in the contracted polyps (Figure 221A-C,E,F).

The knobby and leafy clubs are mostly about 0.07–0.09 mm, but can be as long as 0.11 mm. The tuberculate platelets can be as small 0.05 mm, and

are intermediate in form to the tentacular scales (Figure 223B). The latter are small, elongate platelets, sometimes curved, and ornamented small warts. They are about 0.04–0.05 mm long and are arranged somewhat irregularly in the tentacle rachis. Some lie across the tentacle while others are staggered and arranged loosely *en chevron*.

The polyp body is covered with oval to crescentic scales that are not arranged in rows (Figure 221D,J). Their exposed face is predominantly smooth, and their distal convex margin is gently scalloped and may have a medial cleft (Figure 223Ca–g). Scales from the polyp base are thicker than those from the head, and the more proximal ones are intermediate in form to those in the surface of the coenenchyme (Figure 223Ci). Most body scales are <0.15 mm long but they can be up to about 0.18 mm. The underside of the blade margin is radially ribbed above large complex warts and tuberculate root structures.

The adaxial side of the polyp is naked apart from a couple of flattened spindles below the adaxial octant (Figure 223Cj,k) and the lateral extensions of some of the adaxial-lateral body scales (Figure 223h).

### Coenenchymal sclerites (Figures 221G; 224A)

The surface of the coenenchyme contains a layer of rooted heads (Figure 221G). The heads have relatively smooth summits but are ridged and indented laterally (Figure 224Aa-i). Below the rooted heads is a layer of warty spindles (with the warts tending to be in girdles), capstans, and a few crosses and irregularly shaped flattened forms (Figure 224Aj-z). The rooted heads are mostly 0.06-0.16 mm long. The larger forms, especially those with a narrow waist (Figure 224Ad,i), occur mostly in the proximal parts of the thicker, older branches. The subsurface layer in these regions contains predominantly capstans (Figure 224Awz) and oval forms (Figure 224Ar), mostly 0.060-0.114 mm in length. In the thinner branches and twigs, the majority of subsurface sclerites are spindles, mostly 0.08-0.12 mm long. The occasional flattened form (Figure 224Ao,p) may be up to 0.16 mm long, but they are usually smaller. Narrow, sparsely warted spindles (Figure 224Au,v) seem to occur around the base of the polyp on the adaxial side.

There is no stem coenenchyme preserved.

#### Variability

There are few differences in morphological characters between the paratype colonies, three of which are for the most part complete. The largest colony is 110 mm tall and still has the holdfast intact, which is calcareous, about 8.5 x 7 mm and 3 mm thick, and mottled orange and reddish brown. In all colonies the polyps are predominantly



Figure 223 Zignisis repens (Briggs, 1915), holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.



Figure 224 Zignisis repens (Briggs, 1915), sclerites: A. Holotype, twig coenenchyme; B. Paratype, AM G11801, polyp & coenenchyme.

biserial in the peripheral parts of the colony, becoming all around or arranged on 3 sides in the older parts. Three colonies are a slightly darker colour than the holotype because a larger proportion of the coenenchymal sclerites are of similar brownish orange tones to the branch internodes. In one paler colony all the sclerites of the white polyps are completely colourless, as are many of the coenenchymal sclerites. In AM E1018 all sclerites are colourless and the colony's somewhat pinkish hue is attributable to the internodes which are brownish orange fading to pale greyish orange in proximal parts of the colony.

In the 3 specimens where the stems are present, both the nodes and internodes of the stem are longitudinally ridged. In the 2 smaller colonies where the stems are only about 1.25 mm thick, the first 3–4 mm are mostly nodal material. In the largest specimen, where the stem is 1.7 mm thick, the proximal 29 mm is mostly nodal material. Some internodes are uncovered but most are completely overgrown.

Most of the material from the area of Bass Strait and the western part of the coast of South Australia is similar to the holotype. Some have darker axial tones, with stem internodes reddish brown ( $\approx$ 8E8) and those of the finer branches far more redder ( $\approx$ 9E8). One specimen has a thick stem (2.7 mm) completely constructed of brown, opaque nodal material. Dissection reveals no buried internodes.

The material from the Great Australian Bight and from the southern and middle latitudes of Western Australia is for the most part morphologically similar in that the polyp distribution is neatly biserial all over the polyp bearing areas (Figure 220B). The colour of much of this material is darker than the holotype, but similar variability occurs as in the other specimens mentioned above. Some colonies have white polyps while others have all the sclerites reddish brown, and some have dark axes while others have pale. In one colony the internodes of the stem and most major branches are almost white, and the nodes in the major branches and the internodes in the finer branches and twigs are golden yellow (~5B7).

Assessing sclerite variability between colonies is complicated by inherent variability between samples taken from the same colony. This is more marked amongst the polyps, where the number and form of the anthopomal clubs is often inconsistent.

Some colonies show a tendency towards spinier sclerites, such as the paratype AM G11801. The polyps of this colony are contracted to a greater degree than those of the holotype, and this has allowed better illustration of the proximal anthopomal scales (Figure 222A–D,G). Figure 222B,C also shows some clubs in the adaxial-lateral octants. Anthopomal clubs in this specimen tend to

be far more foliaceous or spiny than those of the holotype (Figure 224Bc-h) and the warts on the small platelets are often taller (Figure 224Ba). Crescentic anthopomal scales are similarly affected, where heavier scalloping may produce spiny margins with pronounced radial ribbing underneath (Figure 224Bn,o). Adaxial-lateral anthopomal scales (Figure 224Bi,j) and body scales (Figure 224Bk,l) show similar characteristics. Even the rooted heads from the coenenchyme show increased lateral ridging (Figure 224Bm) which may encroach on to the summit of the head (Figure 222F).

Other colonies may have a preponderance of anthopomal clubs and platelets with dense, fine sculpturing, or clubs with broad, terminal leafy projections, like that in Figure 224Be, that are radially ribbed underneath.

A noted character of the material off central Western Australia is the predominance of small rooted heads in samples from the coenenchyme. A fragment may contain hardly any rooted head longer than 0.08 mm. In instances where the sclerites of the surface are mainly small the subsurface layer will consist mainly of capstans, even on the thin ramifications.

The specimen from Bass Strait station 191/lot 4 is remarkable for several reasons: many branches project out of plane giving the colony a bushy appearance; the anthopomal clubs are commonly quite large, 0.09-0.11 mm long, unusually broad, and very ornate with multiple small leaf-like projections; the subsurface layer of the coenenchyme contains large numbers of very big spindles and flattened forms, up to 0.19 mm long, and the rooted heads have the short ridges that commonly occur on the lateral aspects also scattered over their summit. In contrast, the Bass Strait specimen from station 185/lot 53, a luxurious colony with thick branches and densely arranged polyps, has sclerites more like those of the holotype.

There is no coenenchyme remaining on the stem of the holotype. Samples from stems of several of the comparative specimens contain rooted heads and subsurface capstans. The rooted heads often have a narrow waist; in one instance so pronounced that the heads of many of the sclerites were divided into 2 bosses. In small colonies, the stem coenenchyme is usually very thin and the subsurface layer reduced to a few scattered capstans. In the larger colonies with thicker coenenchyme the capstans are numerous. In the Bass Strait colony from station 185, many of the capstans have extremely warty projections and a very short waist, some being so modified as to have no waist at all and are quite globose.

### Distribution

See Figure 299. Depth range 24–146 m.

Zignisis alternata (Utinomi, 1975) new comb. Figures 225–228; 302

Mopsea alternata Utinomi, 1975: 256–258, Figure 14; Plate IV, Figure 4.

#### Material examined

#### Types

HOLOTYPE: MTUF 16000, Geographe Channel, Shark Bay, Western Australia, 110–120 m, T/S *Umitaka-Maru*, Tokyo University of Fisheries, 19 Dec. 1963.

## Other material

NTM C10924 (2 colonies), C10927, C10929, C10942, C10943, off Shark Bay, Western Australia, 24° 55.6'S, 112° 50.8'E, 80–85 m, RV Akademik Oparin, P. Alderslade, 14 July 1987; WAM 24–74, north west of the western end of Rottnest Is., Western Australia, 37 fm, FV Blue Fin, B.R. Wilson, 12 Aug. 1962.

## **Differential characteristics**

Colonies plumose, branches relatively thick and well spaced; characteristic anthopomal sclerites mostly in the form of small, densely arranged leafy platelets; the more proximal internodes in the twigs with denticulated ridges.

## Description

## Colony form (Figure 225A)

The largest piece of the holotype is a planar colony portion that ramifies sympodially producing 2 plumes of unbranched pseudo-lateral twigs. The specimen was 100 mm tall when figured at a reduced magnification by Utinomi (1975: Plate IV. Figure 4). It is now 80 mm high, 26 mm across, and is accompanied by numerous small fragments that have broken away. The material is not in good condition. The tissue is very friable and many of the polyps are damaged. There is no stem. The naked main branch is about 1.20 mm diameter and the twigs are about 1.25-1.65 mm thick (including polyps). None of the twigs are complete but it would appear some were originally longer than 50 mm. Utinomi recorded twig lengths of 25 mm, 30 mm, and 50 mm. He also recorded the angle of branching as 20-30°, but most are 35-45° with the majority around 40°. There is about 4-6 mm between consecutive subdivisions.

## Polyps (Figure 226 D–F,K)

The polyps are distributed all around, densely arranged and evenly spaced. They are contracted and adaxially reduced. The polyp head is supported by a prominent shelf-like base that stands erect from the surface. The heads are mostly angled so that the flat anthopoma makes an angle of about  $35^{\circ}$  with the branch surface. In some instances the head is more elevated so that the anthopoma faces along the branch. There is a clear suture between the head and the base in most polyps. Polyp heads are about 0.48 mm across abaxially, and about 0.38 mm long. The total length of a polyp is about 0.77–0.89 mm and they project about 0.40 mm above the surface.

#### Colony colour

Very pale yellowish white. The sclerites are colourless but the nodes cannot be seen through the coenenchyme.

## Axis form (Figure 226G–I)

The internodes have multiple primary ridges. The most distal 1-2 twig internodes do not have any denticles, while the preceding couple have denticles only on the shoulders (Figure 226G). The more proximal ones have denticles all along the ridges and a few scattered between them (Figure 226H). In the older, thicker parts of the specimen, however, the ridges and shoulders are more or less smooth. In intermediate parts the internodes may have a few tiny granules on the ridge shoulders. Internodes near the twig tips, about 0.19-0.26 mm thick, have 5-6 primary ridges. Some more proximal internodes about 0.41 mm thick have 8 ridges, and some 0.51 mm thick have 12. The internodes at the base of the fan portion are 1.2 mm thick and have 23 primary ridges. The desmocyte cavities are relatively crowded and distinct.

The internodes of the main branch are about 1.44–1.56 mm long. Those of the twigs are about 1.62–1.92 mm. The main branch nodes are 0.32–0.40 mm long and those of the twigs are about 0.12 mm.

#### Axis branching

In most cases the pseudo-lateral twigs originate from a shared node as in Figure 251 example 24. In the distal, finer ramifications there are a couple of joints as illustrated in example 29. There are usually 3 internodes, occasionally 4, between each bifurcation.

#### Axis colour

The internodes are pale greyish white, like cloudy glass. They are translucent when thick, but become semi-transparent near the ends of the twigs. The nodes in the naked main branch are greyish yellow ( $\approx$ 4B5), somewhat opaque, with thin satin-like borders. In the thinner ramifications the nodes are yellowish white ( $\approx$ 4A2), sometimes with a thin translucent greyish band across the centre, and with silvery borders present mainly as crescents between the shoulders of the internodal ridges.



#### P. Alderslade

## Polyp sclerites (Figures 226A-F; 227; 228A)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The adaxial octant is composed of tuberculate platelets (Figure 227Am– t). The larger, proximal ones, whose number varies, are crescentic to oval (Figure 226C), and the apical ones are small and irregularly shaped. Medially, a platelet may be somewhat triangular, or it may be replaced by 2 elongate sclerites arranged side by side. The other octants are of a different structure, but they are so complex that it has not been possible to determine the exact arrangement of sclerites. Proximally, they appear to have 2–3 relatively large scales. In the adaxial-lateral octants the most distal of these scales is relatively simple and tuberculate. In the other octants the scales have a ribbed, irregularly undulate margin that may have a medial cleft (Figure 227Au–y). The rest of the octant is made up of small leafy platelets (Figure 227Aa–l) mostly 0.07–0.09 mm across.



Figure 226 Zignisis alternata (Utinomi, 1975), holotype: A-F. Polyps; G-I. Axial internodes; J. Coenenchyme; K. Twig fragment.

Each tentacle rachis contains 2 closely aligned rows of alternating, curved, granular scales up to 0.065 mm long (Figure 227B).

The polyp body is protected by large oval to crescentic scales that are not in distinct rows (Figure 226D,E). The distal margin of the scales of the polyp head is more or less entire, although some have a medial notch (Figure 228Aa-f). The scales of the lower part of the body are thicker and the margin is often scalloped conforming to the ribs on the underside of the blade (Figure 228Agi). The adaxial-lateral scales have a lateral extension (Figure 228Aj-l) which reaches towards the adaxial side of the polyp. Immediately below the adaxial octant there are about 3 flattened spindles (Figure 228Am) which are overlapped by the adaxiallateral scale extensions. Below this, the adaxial side of the polyp is naked. Apart from the adaxial and adaxial-lateral body sclerites, which may have tubercles, most scales have a more or less smooth outer face. On the underside the blade is ribbed, and the proximal portion has large compound tubercles (Figure 228Ab,c,f,k). Most of the body scales are 0.14-0.18 mm long.

A number of polyps have the heads covered in sclerites that appear to be quite deformed (Figure

226F). The sclerites are more like rooted heads than scales and most are not arranged in an imbricate manner. Perhaps these are the result of regrowth following damage.

### Coenenchymal sclerites (Figures 226J; 228B)

The branch surface contains an upper layer of rooted heads, most of which have distinctly ribbed sides. Beneath the heads are complexly warted capstans, ovals, a few irregularly shaped plates, and a small number of spindles with sparse granular tubercles. The small spindles are particularly common in the region where a polyp body adjoins the branch surface. The rooted heads are mostly 0.06–0.12 mm long. The subsurface capstans are mostly >0.06 mm in length. The bigger ones do not have a distinct waist and are intermediate to the larger ovals that can be up to 0.12 mm in length. The warty plates may be as long as 0.15 mm.

None of the stem of the holotype was preserved. Samples from the stem coenenchyme of comparative specimens contain an upper layer of rooted heads, often as small as 0.06–0.09 mm, of which a high proportion have the head modified into 2 bosses similar to the stem sclerites of *Zignisis* 



Figure 227 Zignisis alternata (Utinomi, 1975), holotype, sclerites: A. Anthopoma; B. Tentacles.





*lornae* sp. nov. (Figure 238C). If this upper layer contains numerous large rooted heads, up to about 0.15 mm, the subsurface layer usually contains warty capstans, ovals, and plates as seen in the branch coenenchyme. When the upper layer contains predominantly very small heads the underlying layer may contain only capstans, some modified as double stars, about 0.05–0.10 mm in length.

### Variability

The most obvious difference between the holotype and the comparative material is the colour. All of the other specimens are shades of brown, somewhat rust-like. The palest is more or less autumn leaf brown ( $\approx$ 6D7) and the darkest is close to henna brown ( $\approx$ 7E8). The axes are, however, similarly coloured to that of the holotype. The internodes are greyish white to colourless, and the nodes are yellowish, often with more prominent banding in the finer branches.

A couple of specimens are for the most part complete, and still have holdfasts. One colony (Figure 225B) is 140 mm tall with a stem 1.2 mm thick and a small, smooth calcareous holdfast about 5 mm across and 5 mm thick. The other colony is 190 mm tall, the stem is 1.9 mm thick, and the holdfast is 5 x 8 mm across, 5 mm thick, and ridged like the axial internodes of the stem. The first 3–7 mm of the stems of these colonies is predominantly nodal material, coloured dark brown ( $\approx$ 7F7) like the rest of the stem nodes.

Colony WAM 24–74 (Figure 225C) is remarkable because everything about it is bigger. Apart from the specimen size, however, the colony fits the characters of the species, even though it was collected about 1000 km farther south than all the other specimens. The colony is about 220 mm tall and 50 mm across. The stem is missing. The main branch is 2.7 mm thick at the base and can be traced to the middle of the colony where it is 1.6 mm thick. The twigs are up to 1.7 mm thick (including polyps) and 75 mm long. The polyps are about 1.13 mm long, the head measuring 0.46 mm, and they project about 0.54 mm above the branch. Polyps are distributed all around on the twigs but biserially on the main branch. The thin axial internodes are denticulate and the thick ones are smooth as in the holotype.

There is little significant sclerite variability amongst the comparative material. Differences in size of the polyp scales and the rooted heads of the coenenchyme is encountered between colonies, but this also occurs between samples from the same colony. It was noticed, however, that in some colonies the flattened spindles below the adaxial portion of the anthopoma are consistently stouter and quite bar-like. This is at its most extreme in the remarkably robust colony WAM 24–74, where it is also not unusual to find polyp scales 0.20 mm long, occasionally up to 0.28 mm. Tentacular scales up to 0.08 mm are also found in this colony and one other specimen. The presence of warty plates in the subsurface layer of the branch coenenchyme seems to be another variable feature, as they do not appear in every sample taken from a colony.

## Distribution

See Figure 302. Depth range 68–120 m.

Zignisis phorinema sp. nov. Figures 229–233; 300

#### Material examined

#### Types

HOLOTYPE: NTM C5218, Transect Reef, Rottnest Is., Western Australia, 32°3'S, 115°25'E, R. Roberts, 16 Dec. 1985. PARATYPES: WAM 419–80, north west of Rottnest Is., 110 ft, C. Bryce, Dec. 1979; NTM C12335 (4 colonies), 1.3 km north of Abraham Pt., Rottnest Is., 32°0.25'S, 115°28.02'E, 12–16 m, on cave floors and under ledges, NCI, 14 March 1989.

#### **Differential characteristics**

Colonies forming compressed bushy fans, profusely ramified with relatively thick branches; characteristic anthopomal sclerites mostly in the form of tuberculate platelets; axial internodes in most branches with denticulated ridges.

## Description

## Colony form (Figure 229)

The holotype is about 205 mm tall, including the calcareous holdfast, and 110 mm across. The zigzagging main stem is devoid of coenenchyme and consists predominantly of nodal material. Small partial internodes are inserted into the side of the stem or are completely overgrown. The stem is 3 mm thick and 50 mm long to the first intact branch, below which are numerous old encrusted branch stubs. It produces two main branches, 2.4 mm thick, which ramify sympodially and continue more or less to the apex of the colony. Branching is profuse. Those arising from the main branches may remain undivided, but most rebranch irregularly in a mixture of sympodial and lateral branching, and many of the twigs produced diverge out of plane. The result is a compressed, somewhat bushy fan about 20-30 mm thick. Unbranched twigs are commonly up to 50 mm long. They are 1.5-1.7 mm thick (including polyps) and gradually taper to about 0.7-1.2 mm before the rounded tips. The zigzagging branches give off pseudo-laterals about every 2.3-4.0 mm. Angle of branching is about 40-55°.



Figure 229 Zignisis phorinema sp. nov., holotype, natural size.

## Polyps (Figure 230D-G,K)

On one of the main branches polyps are scattered all around, scarce proximally and denser in the younger regions. The lower half of the other main branch has virtually no gorgonian polyps, but they are quite dense in the upper half. Several large hydroid polyps of the Family Tubulariidae are growing on the lower part of this branch, and the coenenchyme grows ridge-like over the basal portions and extends to 7 mm up the polyp stalks.

On the minor branches and twigs which lie more or less in the central plane of the colony, the polyps are densely distributed all around. Those twigs that branch out of plane notably have most of their outer face polyp-free, all the polyps facing towards the colony.

Polyps are contracted and adaxially reduced. Polyp bases are relatively large, and they extend



Figure 230 Zignisis phorinema sp. nov., holotype: A-G. Polyps; H. Coenenchyme; I-J. Axial internodes; K. Twig fragment.

## shelf-like and more or less erect from the surface. Each base supports a polyp head which in most cases is angled down towards the branch so that the anthopomal region lies flat against the surface. In some areas, the polyps are slightly more extended and there is a gap between the adaxial side of the head and the branch surface. In many of these less contracted polyps there is a slight gap, up to 0.05 mm, between the polyp head and the base where a narrow, white, sclerite-free neck zone is visible. The heads are quite moveable and their sclerites are clearly not continuous with those of the relatively rigid bases. The bases of the least contracted polyps project about 0.60 mm, whereas they more commonly protrude 0.36-0.41 mm. Measured along the branch, polyps are 0.84-0.96 mm long. The shelf-like bases are about 0.72 mm across where they adjoin the branch. Abaxially, polyp heads are about 0.52 mm across. There are a number of upside-down polyps on the secondary branches, and juvenile polyps occur sparsely on the branches and twigs being more common in the terminal 1-2 mm.

## Colony colour

The coenenchyme is opaque and brown ( $\approx$ 7D8), and the polyp heads are golden yellow ( $\approx$ 5B7).

## Axis form (Figure 230I,J)

All internodes have well developed primary ridges. The ridges on the internodes of the stem and the basal area of the two main branches are smooth. In the rest of the colony they are denticulated and have high shoulders. In one 37 mm twig of 31 segments, the internodes towards the tip (0.15-0.36 mm thick) have six primary ridges, those near the centre and towards the proximal end (0.36-0.60 mm thick) have eight, and the proximal two (0.63 mm thick) have nine and ten ridges respectively. A branch internode 2 mm thick has 35 primary ridges. In a few twigs, the more terminal internodes are 4-sided with only four primary ridges. Developing primary ridges occasionally occur on internodes. Each appears as a low secondary ridge with high shoulders between two primary ridges. There may only be 1-2 of these on an internode, and sometimes the



Figure 231 Zignisis phorinema sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.

ridge is absent leaving one or both of the shoulders only. The nodes of the stem also have ridges, which line up with those on the internodes. The desmocyte cavities are distinct and overlap.

Where the axis is exposed on the two main branches the internodes are 0.72–0.84 mm long. Twig internodes are 0.6–1.3 mm long, commonly about 0.96 mm. Nodes in the two main branches are 0.33–0.42 mm long, and in the twigs they are mostly about 0.12 mm in length.

## Axis branching

Branching involves shared nodes. In the thinner

branches it is similar to Figure 251 example 25. In the thicker branches it is like examples 24 and 45. There are 2–3 internodes between each branching point.

## Axis colour

The internodes of the stem and lower parts of the main branches are translucent and brownish red ( $\approx$ 8C8). Those of the twigs are virtually transparent and much redder ( $\approx$ 9D8). The nodal material of the stem is brown ( $\approx$ 6E4) and is virtually opaque. In the proximal area of the two main branches the nodes are brownish orange ( $\approx$ 5C4), and in the twigs



Figure 232 Zignisis phorinema sp. nov., holotype, sclerites: Polyp body.

they are pale yellowish white with very translucent greyish central bands. All nodes have narrow silvery satin-like borders, crescent-like between the shoulders of the internodal ridge.

## Polyp sclerites (Figures 230A–G; 231; 232)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The adaxial octant, like the major octants, is variable in structure. At its strongest it is occupied by a triangular to triradiate sclerite preceded by 1-2 crescentic scales (Figure 231Ar,s). In other instances the triangular scale is replaced by a small spindle (Figure 231Aq), and often there is no apical sclerite at all, only 1-2 proximal crescents. The other octants are occupied predominantly by tuberculate platelets of various shapes (Figure 231Aa-p), many more or less triangular or triradiate, that combine to form the triangular sectors of the anthopoma (Figure 230A-C). Proximal to these, each octant contains several sclerites of irregular shape (Figure 231At-z) that are transitional forms between the scales of the polyp head and the anthopomal platelets; those in the adaxial lateral octants being tuberculate. In general, the adaxial-lateral and lateral octants contain fewer but larger platelets than the other octants. However, this is not consistent. The sectors appear to contain about 5-8 tuberculate platelets (the smaller forms usually being apical), but it is not possible to determine the exact number in the contracted polyps. The platelets are mostly <0.114 mm long.

Each tentacle rachis contains numerous small granular rods (Figure 231B). In the tightly contracted tentacles they are irregularly arranged; sometimes across the tentacle, sometimes *en chevron*, and sometimes jumbled. The tentacular rods are mostly 0.033–0.057 mm in length. The smallest often have a smooth waist and tuberculate ends.

The polyp body is protected by thick sclerites that in some polyps are loosely arranged in rows. Although scales more characteristic of other members of this genus occur (Figure 232a-g), the body sclerites often resemble rooted heads more than scales, even those on the polyp head. Their distal margin is often deeply incised, and on some polyps the lower margin of the 'blade' or 'head' of the sclerite has projections also which are oriented towards the base of the sclerite (Figures 230F; 232h-l). These thick sclerites can appear quite deformed (Figure 232 m), and the head of one polyp on the twig fragment selected for electron microscopy was completely covered in sclerites of this form (Figure 230G). In those polyps where the sclerites are more or less in rows, and this may only involve the upper 3-4 series, the architecture of the sclerites is more scale-like. Where the sclerites are irregularly arranged they are thicker

and more like rooted heads. Below the adaxial octant there are several spindles (Figure 232n,o) usually interleaved with the lateral extensions of some adaxial-lateral sclerites. They tend to form a jumbled array about 4–5 sclerites deep. Below this, the adaxial side of the polyp is completely naked.

The sclerites in the adaxial-lateral region of the polyp head are tuberculate (Figure 230F), unlike those on the rest of the body which have a smooth exterior, and they are often more like flattened spindles than scales (Figure 232p–r). Intermediate forms of these occur where the upper margin of the sclerite is blade-like at one end. The larger polyp body sclerites are about 0.13–0.15 mm long, but they can be up to 0.20 mm in length.

#### Coenenchymal sclerites (Figures 230H; 233)

The coenenchyme of the finer branches contains a surface layer of rooted heads, and a lower layer of large warty sclerites (Figure 233A). The warty forms are commonly ovals with the warts more or less in girdles, but irregularly shaped bodies also occur along with some spindles and platelets. The subsurface forms are mostly 0.08–0.15 mm long, sometimes to 0.20 mm and the rooted heads may also be up to about 0.20 mm in length. In some areas the upper surface of the heads is ornamented with small conical tubercles (Figure 230H).

On the major branches the coenenchyme contains an upper layer of large block-like rooted heads, up to 0.20 mm long, and a subsurface layer of warty capstans and sub-spheroids to about 0.12 mm (Figure 233B). The coenenchyme of the continuation of the stem, where the branching begins, contains rooted heads of similar design and a lower layer predominantly of capstans (Figure 233C) to about 0.114 mm in length.

#### Variability

All of the paratypes show the same dense branching in a characteristically flattened, bushy growth form, with twigs protruding out of plane. These twigs are commonly amongst the longest in the colony. One specimen has relatively short twigs throughout, up to 35 mm with most <20 mm long.

Polyp distribution in a number of colonies tends to be biserial for much of the distal part of each twig. Towards the centre of the colonies, the polyps are still distributed all around.

Nodal material of stem axes can be very dark brown ( $\approx$ 6F6). There is also some variation in axial denticulation. In some colonies the denticles are reduced on many of the internodes, particularly those in the terminal regions of the twigs. In all colonies, the terminal 1–2 internodes of each twig generally have only the shoulders of the ridges denticulated, but they can be smooth. In some twigs slightly more than the first 2 internodes may have this style of architecture. Older internodes are



Figure 233 Zignisis phorinema sp. nov., holotype, sclerites: A. Thin branch coenenchyme; B. Main branch coenenchyme; C. Stem coenenchyme.

always denticulated, but occasionally some have narrow ridges with few denticles, while those in the remainder of the colony are more like those of the holotype.

With regard to the sclerites there are two main areas of variability. First, specimens of lot NTM C12335 have more polyps with scale-like sclerites, and these sclerites are more often arranged in rows, although, many polyps still have an irregular arrangement. Second, several of these specimens also have very large warty subsurface sclerites. In some samples from thinner branches the subsurface layer contains mainly warty spindles similar to Figure 233Aa, together with broader forms, and these may be up to 0.21 mm in length.

## Distribution

See Figure 300. Depth range 12–33 m.

## Etymology

The epithet employs the Greek word *phorinema*, thick skinned, in allusion to the thick polyp sclerites.

Zignisis lornae sp. nov. Figures 234–238; 301

## Material examined

Types

HOLOTYPE: WAM 26–74, north west of western end of Rottnest Is., Western Australia, 37 fm, FV *Bluefin*, B.R. Wilson, 12 Aug. 1962. PARATYPES: WAM 23–74, same data as holotype; WAM 395–79, same data except collector, R.W. George; WAM 443–80, west side of Sandy Hook Is., Recherche Archipelago, Western Australia, 80 ft, on rock wall, C. Bryce, 8 April 1977; NTM C2485, western part Great Australian Bight, RV *Soela*, Dec. 1981, (no further data).

#### **Differential characteristics**

Colonies more or less planar, and profusely branched with relatively thick branches; characteristic anthopomal sclerites mostly in the form of leafy crescentic scales; axial internodes of the twigs and thin branches with denticulated ridges.

## Description

## Colony form (Figure 234)

The holotype is in two fragments, the main portion of which is 190 mm tall and about 48 mm wide halfway up. The zigzagging stem, arising from a small calcareous holdfast, is about 2.5 mmx2.8 mm thick proximally. It is about 50 mm long to the first intact branch, below which are numerous stubs of lost branches. Most the of coenenchyme is missing from the lower portion, and the first 10 mm of the axis is predominantly nodal material. The stem can be traced as a main branch to the upper parts of the colony. It zigzags, sympodially producing numerous pseudo-lateral branches. Some of these remain unbranched, and others divide sympodially producing small plumes which overlap to form a more or less planar colony about 7 mm thick. In the upper half of the colony, the main branches are about 1.9 mm thick (including polyps) and the twigs are 1.5-1.6 mm thick tapering to about 0.9 mm below the rounded tips, most of which are broken. Undivided branches are 10-35 mm long, with most about 15-20 mm. The distance between consecutive points of branching is mostly 3.5-5.0 mm, and the angle of branching is 45-78°.

#### Polyps (Figure 235D-F,H)

The polyps are distributed all around throughout most of the colony except in the terminal regions of the thinnest twigs where they are biserial, a single row along each side. There are only a few polyps on the main stem and they are in the upper region where the intact branching begins.

Polyps are contracted and adaxially reduced. The polyp heads are each supported by a prominent shelf-like base. In most cases, the abaxial side of the base is angled so that the polyp head is more or less parallel to the branch, or angled down towards it with the anthopomal region pressed against the surface. In a few cases, the abaxial side of the base is about 90° to the branch and the polyp head is directed upward and outwards. A sclerite-free neck zone can clearly be seen in a few polyps, although in most polyps the head sits snugly against the supporting base which is about 0.60 mm across where it adjoins the branch. Polyp heads are 0.43-0.46 mm across abaxially and about 0.38-0.41 mm in length. Polyps which lie along the branch are 0.60-0.94 mm long, the base included, and project about 0.48 mm. Those that are angled away from the branch project about 0.6 mm. A few polyps are upside-down and juvenile polyps seem to be absent.

#### Colony colour

The colony has a mottled appearance because the polyp heads are white, and the polyp bases and coenenchyme are brownish orange ( $\approx$ 5C6) on the thicker parts of the main branches, mainly in the lower parts of the colony, and brown ( $\approx$ 7D8) on the finer branches and twigs. The coenenchyme is opaque and has a speckled appearance in close-up because the glass-like surface sclerites have yellowish borders and brownish orange centres.

#### Axis form (Figure 236C,F)

The more distal internodes of the twigs are



Figure 234 Zignisis lornae sp. nov., holotype, natural size.

usually 4-sided. The terminal 1–2 do not have primary ridges, but rounded edges. Throughout the rest of the colony the internodes have prominent primary ridges. Those on the more proximal internodes of the twigs and on the minor branches are denticulated and have pronounced shoulders. Internodes thicker than about 1 mm have very reduced denticulation which may be difficult to detect even on the shoulders. The ridges of the stem internodes are smooth and the shoulders are not pronounced. The 1–2 terminal twig internodes may only have denticles on the shoulders, but they are commonly along the edges as well. The stem nodes also have ridges and they line up with those of the internodes.

In a 23.5 mm twig of 20 internodes, one near the tip (0.26 mm thick) has five primary ridges, one near the middle (0.38 mm thick) has six, and the proximal internode (0.56 mm thick) has eight. A branch internode 1.0 mm thick has 16 primary ridges, and a stem internode 2.4 mm x 2.7 mm thick has 48. Developing primary ridges are common and appear as a low secondary ridge with high shoulders between two primary ridges. There



Figure 235 Zignisis lornae sp. nov., holotype: A-F. Polyps; G. Coenenchyme; H. Twig fragment.

may only be 1–2 on an internode, and sometimes the ridge is absent and only one or both shoulders are present. Desmocyte cavities are distinct.

Main stem internodes are 0.6–1.1 mm long, those in the thinner branches are 1.2–1.3 mm, and those in the twigs 0.72–1.40 mm. The stem nodes are 0.6– 1.1 mm long, those of the thinner branches are 0.12–0.18 mm, and in the twigs they are mostly about 0.06 mm.

## Axis branching

Of the visible branching points, one is like Figure 251 example 27. The others all involve shared nodes as in examples 24, 25, 42 and 45.

#### Axis colour

The internodes of the stem and branches are reddish brown (≈8D7–8D6), more or less opaque in the thicker ramifications and becoming very translucent distally. The twig axes are multicoloured. The proximal twig internodes are reddish brown and the distal ones are colourless. The gradation of colour from proximal to distal regions goes through pale yellow, and the internodes are mostly transparent and are usually unevenly coloured. The nodal material of the stem and main branches is light brown ( $\approx$ camel colour 6D4) and opaque. In thinner branches it is also opaque but golden blonde ( $\approx$ 5C4). In the thinnest branches and in the twigs the nodes are mostly satin-like and white with a greyish central band. All nodes have silvery satin-like borders, crescentlike between the primary ridges of the internodes.

# Polyp sclerites (Figures 235A-F,H; 237; 238A)

The anthopoma is asymmetrical and continuous with the polyp body sclerites. The ornate nature and small size of the more distal sclerites in the major octants make it extremely difficult to distinguish one from another. In the much smaller adaxial octant there is generally 2 sclerites (Figure 235B,C). The distal one is usually triangular to triradiate (Figure 237Au,v) and is preceded by a small crescentic scale (Figure 237Ay,z). There appear to be about 4 sclerites in each of the adaxial lateral octants. The most proximal is a more or less crescentic scale with an irregular dentate or leafy margin (Figure 237Aw,x). This is followed by a





scale of characteristic shape (Figure 237Ar,t), having the blade more or less marginally divided into 2 unequal portions. Succeeding this is a scale of irregular form ornamented with tooth-like projections (Figure 237An-q). The apex of the octant is occupied by a small tuberculate, crescentic scale similar to those occurring towards the tips of the other octants (Figure 237Aa-c). The other octants consist of a single row of what appears to be about 5 crescentic sclerites. The more proximal and less ornate of these generally have a marked medial cleft in the blade margin (Figure 237Af,g,j-1), and these are followed by scales with the upper face developed into leafy processes (Figure 237Ah,i) and finally by smaller forms ornamented with tooth-like tubercles (Figure 237Aa-e). Occasionally, a single scale may be replaced by 2 club-shaped sclerites (Figure 237Am) arranged en chevron. The crescentic scales with the cleft margin have large compound warts and radial ribs on their underside (Figure 237Ak) and are mostly <0.13 mm long, with many of the larger ones being about 0.10 mm in length. The smaller, tuberculate

forms near the apex of each octant can be as small as 0.045 mm.

The tentacular sclerites are very conspicuous in a preparation because of their large numbers. They are flat, granular rods (Figure 237B) up to about 0.050 mm long and 0.018 mm wide. They are often slightly curved and for the most part lie across the tentacle in a single row along the rachis, although several instances were noted where 2 rods were arranged *en chevron*.

The polyp head and base are covered in oval to crescentic scales (Figure 235D–F). Those on the head are arranged in 7 rows aligned with the major anthopomal octants. Below the adaxial octant the arrangement is irregular, with generally 1–3 narrow scales (which are essentially flattened spindles) interleaved with the lateral extensions of some of the adaxial-lateral scales (Figure 235C). There are about 5 scales in each adaxial-lateral row and only about 3 of the upper ones reach beneath the adaxial octant. The adaxial side of the polyp below these extended scales is mostly naked, but where this side of the polyp body adjoins the



Figure 237 Zignisis lornae sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.



Figure 238 Zignisis lornae sp. nov., holotype, sclerites: A. Polyp body; B. Branch coenenchyme; C. Stem coenenchyme.

branch there are several series of small scales and spindles, most of the latter having small tubercles or being nearly smooth (Figure 238Al-n). The sclerites below the other anthopomal octants are in well defined rows; the abaxial row of about 9 scales being the longest. The scales of the adaxial-lateral rows are of a different style to the others. The scale immediately below the octant is elongate with tooth-like projections (Figure 238Ai,j), and the one below this commonly has a blade on the abaxial end (Figure 238Ak). Those further down are more like the lateral and abaxial scales but are somewhat more elongate (Figure 238Ah). The other body scales generally have a smooth exposed face or a few simple tubercles (Figure 238Aa-e). Those on the head are thinner than those on the polyp base, and generally have radially arranged ribs on the underside of the periphery of the blade (Figure 238Af). Where the base merges with the branch surface some of the scales may be very large (Figure 238Ag). Most of the body scales are up to about 0.17 mm long.

#### Coenenchymal sclerites (Figures 235G; 238B,C)

The surface of the coenenchyme of the branches contains rooted heads. The summits of the heads are smooth or may have a few simple tubercles, the sides have raised ribs (Figure 235G), and the roots are a complex of compound warts (Figure 238Ba-d). Below the rooted heads are numerous warty oval and sub-spheroidal forms (often with warts in girdles), together with spindles and platelets (Figure 238Be-l). The rooted heads are mostly 0.09-0.16 mm long. The warty forms in the lower layer are mostly 0.08-0.14 mm in length; a few are longer.

The surface of the middle of the stem has similar sclerites to the branches, but the heads are often divided into 2 bosses and the subsurface forms are mainly girdled ovals or sub-spheroids (Figure 238C). Although the rooted heads may be as large as 0.14 mm most are smaller, about 0.06–0.12 mm long, and the warty subsurface forms are about 0.08–0.11 mm in length.

## Variability

All of the paratypes are smaller than the holotype. Most of them are also paler and have polyps which are totally white. WAM 443–80 is the palest with most of the sclerites colourless and the axial internodes greyish red ( $\approx$ 8C4) basally and yellowish in the twigs. In some colonies the stem nodes and internodes are almost transparent, and the coenenchyme is quite translucent. Only one colony does not have a similar colour gradation in the twig internodes as is seen in the holotype. Most twigs have relatively densely coloured proximal internodes and pale yellow to colourless distal ones. In NTM C2485, however, most internodes

are deep red ( $\approx 10D8-10E8$ ). In several colonies, the distal internodes of the twigs are 4-sided and only denticulated on the shoulders (Figure 236A,D), but the more proximal ones are like those in holotype (Figure 236B,E).

### Distribution

See Figure 301. Depth range 24-68 m.

## Etymology

This species is dedicated to Lorna Gravener who typed the manuscript, in recognition of her word processing skills, and her infinite patience in contending with re-writes, seemingly endless corrections, and the general trials and Sysyphean labour associated with assembling a document of this size.

## Zignisis bifoliata sp. nov. Figures 239–242; 303

#### Material examined

## Types

HOLOTYPE: NTM C10935, off Shark Bay, Western Australia, 24°55'S, 112°50.8'E, 80–85 m, RV Akademik Oparin, P. Alderslade, 14 July 1987. PARATYPE: NTM C10933, same data as holotype.

## **Differential characteristics**

Colonies plumose, branches fine and densely arranged; characteristic anthopomal sclerites in the form of bilobed scales resembling 2 leaf clubs laterally fused; internodes not denticulated.

### Description

### Colony form (Figure 239)

The holotype is 120 mm tall and about 110 m wide. The colony is planar and consists of a number of neat symmetrical plumes, each formed by sympodial branching. The holdfast and stem are missing. Just above the base, the colony bifurcates into two main branches of about equal thickness, 1.1 mm, which sympodially produce numerous pseudo-lateral twigs, and originate other main branches that in turn sympodially divide. The twigs rarely rebranch. Near the centre of the colony the twigs are 0.48-0.54 mm thick, and at the apex they are 0.24 mm thick (without polyps). Twigs of the first generation plumes are 35-45 mm in length, and those of the second and third generations are about 25 mm long. At the top of the colony the twigs are only 10 mm long. The angle of branching is 28-42°, and the distance between the origin of each consecutive branch is commonly 2.5–3.0 mm.

#### Polyps (Figure 240D,E,I,J)

On the distal portion of the twigs at the apex of


Figure 239 Zignisis bifoliata sp. nov., holotype, natural size.

the colony, the polyps are arranged biserially. On the rest of the twigs the polyps are all around. They spiral irregularly around the twigs which causes them to be lined up in rows over short distances. In the lower to middle regions of the colony there are 4 'rows', but only 3 'rows' in the younger parts. Polyps are less densely arranged on the main branches, particularly in the lower part of the colony where there are very few.

Polyps are contracted and adaxially reduced. The base of a polyp arises erect and somewhat shelflike from the surface, and the head is angled so that the anthopomal region faces along the branch and more or less at right angles to it, leaving a gap between the branch and adaxial side of the polyp. In a number of polyps there is a clear suture between the head and the base. Measured along the branch, polyps are 0.62–0.77 mm long. Abaxially, the heads and bases are 0.41–0.46 mm across and the neck region about 0.29–0.34 mm. Polyps project 1.1–1.3 mm above the surface. Juvenile polyps are few and are found mostly near the base of the twigs.

#### Colony colour

The coenenchyme and the polyps are reddish brown ( $\approx$ 8E8). The underlying nodes are only faintly visible through the coenenchyme. The sclerites are yellowish to brown in transmitted light.

### Axis form (Figure 240G,H)

The internodes of the twigs are mostly 4-sided, with a primary ridge down each edge which is often mainly distinguishable only at the shoulders and is difficult to see on internodes near the tips. In the older twig internodes, a secondary ridge usually develops on each face. Internodes near the origin of longer twigs may have the secondary ridges developed as primary ridges and become 8sided. Main branch internodes have multiple primary ridges, with secondary ridges occasionally developed. A basal main branch internode 1.2 mm thick has 22 ridges. Desmocyte cavities are very distinct.

Internodes of the main branches are about 0.84– 1.14 mm long, and those of the twigs are mostly



Figure 240 Zignisis bifoliata sp. nov., holotype: A-E. Polyps; F. Coenenchyme; G-H. Axial internodes; I-J. Twig fragments.

1.0–1.4 mm. The nodes of the basal main branch are about 0.30–0.36 mm long, and those of the main branches near the middle of the colony are 0.18–0.21 mm. Twig nodes are about 0.12 mm long.

## Axis branching

In the younger plumes, where the main branch and the twigs are of similar thickness, branching is as in Figure 251 example 12 and 26. In the older parts, where the main branch is thicker than the twigs, branching is like examples 24 and 39, with mostly two internodes, but often three, between each branched node.

#### Axis colour

Internodes of the main branches and proximal parts of the longer twigs are pale yellow ( $\approx$ 4A3) and translucent, like cloudy-glass. Those of the short twigs and distal parts of the longer twigs are the same colour and transparent. The nodes are greyish orange ( $\approx$ 5B5) with silvery satin-like borders.

#### Polyp sclerites (Figures 240A–E,I,J; 241)

The anthopoma is slightly asymmetrical, and continuous with the polyp body sclerites. In the contracted polyps it is very difficult to tell exactly



Figure 241 Zignisis bifoliata sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body.

where the upper polyp body scales begin to become organised into the anthopomal octants (Figure 240A,C,I). There appears to be about 5–6 scales in each octant except for the adaxial sector where there seems to be one less. The adaxial scales are slightly smaller than those in the other octants.

The larger, more proximal anthopomal scale in each octant has a wide crescentic blade with a dentate margin which is slightly bilobed (Figure 241Ai–k). Distad, the bilobed nature of the scales becomes increasingly developed along with their warty root structures (Figure 241Af–h) until the most distal scales resemble 2 leaf clubs joined laterally (Figure 241Aa–e). The anthopomal scales are about 0.041–0.114 mm across. They have a few radially arranged spines and short ridges on both their outer (Figure 240B) and inner (Figure 241Af– h) faces.

Each tentacle contains a single row of flattened, granular sclerites, up to about 0.05 mm in length, that lie across the rachis. Some are rod-like and others are slightly crescentic or irregularly formed (Figure 241B).

The polyp body is covered with broad crescentic to oval scales which are arranged in 7 relatively distinct rows on the polyp head, aligned with each of the major anthopomal octants (Figure 240D,E,J). Below the adaxial octant the scales are not regularly organised, but in general there are 2 alternating rows of 3 scales. Below each of the other octants there is a single row of scales, with the abaxial row being the longest and consisting of about 9–10 sclerites. The scales on the polyp base only occasionally form rows, and these are usually somewhat indistinct. The short adaxial side of the polyp base immediately below the scales of the polyp head is naked. The outer face of the body scales is predominantly smooth with a few simple tubercles or short ridges, but the underside has prominent radial ribs (Figure 241C). Most of the larger scales are about 0.14–0.16 mm, but they can be as long as 0.19 mm.

#### Coenenchymal sclerites (Figures 240D,F; 242)

The surface of the coenenchyme contains rooted heads. The heads are flattened, like thick scales, and have a narrow summital ridge and prominent lateral ribs (Figures 240D,F; 242a–e). Below the ridged heads, between their warty roots, are numerous small sclerites that are predominantly capstans (Figure 242f–i) or capstan derivatives (Figure 242j–l). There are also a few spindles, crosses, and irregularly shaped flattened forms (Figure 242 m–q) which are encountered mostly in the thinnest branches. The rooted heads are usually about 0.045–0.081 mm across, and the subsurface capstans and other forms are generally <0.075 mm in length.

#### Variability

The paratype is of similar size to the holotype, but with fewer plumes. The lower half of the



Figure 242 Zignisis bifoliata sp. nov., holotype, sclerites: Branch coenenchyme.

colony is devoid of coenenchyme showing axial branching of the same styles as the holotype, but commonly with 3–4 internodes between each divided node on the main branches. The colony is bi-coloured. The coenenchyme is brownish orange ( $\approx$ 6C7), and the polyps are almost white having colourless sclerites. The most basal nodes are brown ( $\approx$ 7E8) and those above are caramel ( $\approx$ 6C6). Polyps density is relatively high. It is not possible to distinguish rows, and in most areas there are about 5 polyps around a branch.

#### Remarks

The nature of the anthopomal octants, which each contain a single row of scales, sets this species apart from all others in the genus. The growth form is also distinct, but it is sympodial and conforms to the generic definition. Given that the number of crescentic scales in the anthopomal octants of the other species of *Zignisis* varies, and the distal scales in the octants of *Z. bifoliata* resemble fused sclerites, the species is included in the genus for the present.

#### Distribution

See Figure 303. Depth range 80-85 m.

#### Etymology

The epithet alludes to the foliaceous nature of the anthopomal sclerites, many of which are 2-leaved

and characteristic of the species. The name uses the Latin *foliatus*, meaning leaved or leafy.

## Zignisis sp. indet. Figures 243; 304

Mopsea encrinula; Studer, 1878: 665, 679.

#### Material examined

ZMB, off north west Australia, 19°42.1'S, 116°49'E, 50 fm, SMS *Gazelle*.

## Remarks

All that could be traced of Studer's original specimen, recorded as 20cm long, was a mostly decorticated twig fragment about 7 mm in length with a single attached polyp. The whole specimen was submitted to non destructive SEM examination without being cleaned of superficial tissue, of which little is in evidence. Some details of the specimen are illustrated in Figure 243. The sclerites of the coenenchyme and the appearance of the anthopoma bear similarities to *Z. lornae*, although the large scale in the adaxial octant of the polyp from Studer's specimen is somewhat more robust. However, the axial internodes are not denticulate as internodes of comparative size in *Z. lornae* would be, and the collection area is far to the north of the region where that species is known to occur.



Figure 243 Zignisis sp. indet. Details of Studer's Mopsea encrinula specimen obtained by the SMS Gazelle: A. Anthopoma; B. Adaxial octant; C. Polyp; D. Coenenchyme; E. Axial internode.

## Distribution

See Figure 304. Depth 91 m.

#### Annisis gen. nov.

## Type species

Annisis sprightly sp. nov., here designated.

## Diagnosis

Colonies in excess of 190 mm tall, sparingly branched in a lateral and possibly pseudodichotomous manner, and not necessarily planar. Branches are long relative to *Zignisis*.

The stem of preserved specimens is white to pale yellow proximally, becoming orange-brown distad the same colour as the coenenchyme of the branches. Polyps are more or less completely white. The axial internodes are greyish white in the older parts of the specimens and yellowish orange distad. The nodes are greyish orange to greyish yellow.

The polyps are sparse on the secondary branches but much denser and distributed all around on the higher order ramifications. They are adaxially reduced, and adaxially naked. They are usually preserved with the polyp base arising shelf-like from the branch, and the head angled distad so that the anthopoma faces along the branch or down towards its surface. There is a suture between the head and the base marking the position of an extendable sclerite-free neck zone. The polyp head is relatively long compared to Zignisis.

The anthopoma is markedly asymmetrical, and is continuous with the polyp body scales. The adaxial octant is devoid of sclerites. The other octants contain up to 7 small, irregularly shaped platelets, preceded by about 3 scales intermediate in design to the polyp body sclerites.

The tentacle rachis contains small granular rodlets loosely arranged in 2 rows.

The polyp body is protected by numerous irregularly alternating series of overlapping scales not arranged in rows. Between the numerous abaxial-lateral scales the long length of the adaxial area of the polyp head is naked. The body scales are smooth, more or less oval, and generally <0.16 mm long. The distal margin often has a medial cleft and may be scalloped between the radial ribs of the underside.

The coenenchyme contains 2 layers of sclerites. The upper layer contains rooted heads with lateral ribs. The heads are broad in the older parts of the specimens and narrow in the finer branches. The subsurface layer contains warty capstans and multiradiates in the basal regions, and spiny branched sclerites and plates in the finer branches.

The axial internodes of the thinner branches are 4-sided, and those of the thicker ramifications have

multiple smooth primary ridges. The desmocyte cavities are unusually profuse and occupy the whole of the internode surface between the ridges. Internodes can be up to 2.7 mm long.

## Distribution

As for Annisis sprightly, see Figure 305.

### Etymology

In dedication to my wife Ann, in appreciation not only for editing the manuscript but also for her support during its compilation and the years of associated research.

> Annisis sprightly sp. nov. Figures 244–247; 305

## Material examined

#### Types

HOLOTYPE: WAM 385-79, 92 km west of Dongara, Western Australia, 29°6.7'S, 113°58.5'E, 91.4 m, MV Sprightly, 19 Feb. 1976. PARATYPES: NTM C2473, central Great Australian Bight, 32°58.5'S, 129°E, 72 m, RV Soela, 3 Dec. 1981; SAM H307, Great Australian Bight, Western Australia, 35°18'S, 118°15'E, 62 m, BANZARE Station 76, 21 Mar. 1930; SAM H841, Great Australian Bight, South Australia, 34°10'S, 132°38'E, 140 m, FV Comet, K. Gowlett-Holmes, 15 April 1989.

### Diagnosis

As for the genus.

### Description

Colony form (Figures 244A)

The holotype may be a portion of a larger colony, but the principal branch is devoid of polyps and may be most of the colonial stem. The colony is curved from bottle storage and can be stretched out to about 190 mm tall and 25 mm across. Because the fragment is sparingly branched, it is difficult to accurately assess the form of ramification. Branching is not in one plane and it is lateral, but there is an aspect of regularity about it that gives the impression of a pseudo-dichotomous pattern. The basal main branch is 1.6 mm thick and devoid of polyps, the two secondary branches are 1.3 mm and 1.6 mm thick, and the higher order branches are 1.3-1.6 mm thick proximately tapering to about 1.1 mm near their tips (polyps not included). Intact undivided branches are 40-85 mm long, branching angle is 12-25°, and the distance between consecutive branching points is mostly 12-27 mm.

### Polyps (Figure 245B,C,G)

Polyps are distributed densely, but evenly



Figure 244 Annisis sprightly sp. nov.: A. Holotype; B. Paratype, NTM C2473. Both natural size.

spaced, all around on the tertiary and higher order branches, and sparsely on the secondary branches . The polyps are contracted and adaxially reduced. Polyp bases arise shelf-like from the branches and there is a fine sclerite-free suture between a polyp head and base easily demonstrated in cleared preparations. Polyp heads are relatively large, and are angled so as to lie parallel to the surface or angled down towards it. Even when the head lies parallel to the branch the anthopomal region is angled downwards. Measured along the branch, polyps are 0.78–0.90 mm in length. Abaxially, the heads and bases are 0.36–0.46 across, and the narrow neck region is 0.24–0.29 mm across. Polyps project about 0.95–1.10 mm above the surface.

There are large areas on the secondary branches where polyps appear to be regenerating or resorbing. Apart from a few bases that support very small polyp heads, there are many short bases without heads. These are closed tightly against the branch surface like the upper valve of an oyster. Amidst these are bases reduced to just a patch of colourless sclerites. A few juvenile polyps occur throughout the colony.

#### Colony colour

The coenenchyme is palest in the basal parts of the colony where it is pale yellow ( $\approx$ 4A3) and the underlying internodes are just discernible. Mid colony it is brownish orange ( $\approx$ 5C5) and distally it is light brown ( $\approx$ 7DC). The first few series of polyp base sclerites are the colour of the coenenchyme and appear yellowish in transmitted light. Above this the remainder of the polyp is white.

#### Axis form (Figure 245E,F)

Little of the axis is exposed. It seems that the internodes throughout the lengths of most of the

thinner branches are 4-sided, with a primary ridge along each edge and with raised shoulders. In the lower, thicker, portions of these branches a single secondary ridge (a developing primary) may occur on some faces. The internodes of thicker branches are multiple sided with multiple primary ridges. A branch internode 0.63 mm thick has 8 primary ridges and two developing ridges. Near the base of one of the secondary branches, an internode 1.14 mm wide has 11 primary ridges and a developing ridge between most of them. The basal internode of the colony is 1.32 mm wide and has 19 primary ridges only. Axial nodes also have ridges that line up with those on the internodes. None of the internodes have denticles, but the desmocyte cavities are distinct and unusually profuse.

Exposed internodes are 1.5 mm long at the base, 1.4 mm mid colony, 1.7 mm near a branch tip, and the estimated common range is 1.4–1.9 mm. Nodes in the basal primary branch are about 0.66 mm long, in the secondary branches they are about 0.48 mm, and in the finer branches about 0.18 mm long.



Figure 245 Annisis sprightly sp. nov., holotype: A-C. Polyps; D. Coenenchyme; E-F. Axial internodes; G. Twig fragment.

#### Axis branching

All bifurcations involve shared nodes as in Figure 251 examples 19, 25, 40, 42 and 60.

## Axis colour

The internodes of thicker and more basal branches are quite translucent and greyish white. Those of the thinner branches are virtually transparent and partially coloured yellowish-orange. The colour is present as an interior rod up the centre of the internode, sometimes confined mainly to the ends, and sometimes present in the shoulders of the primary ridges. The nodes of the thicker branches are slightly translucent, and greyish orange ( $\approx$ 5B5). Those of the younger branches are light yellow to greyish yellow ( $\approx$ 4A4–4B5). All nodes have wide silvery satin-like borders.

## Polyp sclerites (Figures 245A-C; 246; 247A,D)

The anthopoma is continuous with the polyp body sclerites, complex, and markedly asymmetrical. The adaxial octant and the area below it are completely devoid of sclerites. At the proximal end of each of the other octants a few small scales like those of the polyp body, but with irregular margins (Figure 246As-z), give way to a number of platelets (Figure 245A). These platelets are mostly irregular in shape and may be tuberculate or almost smooth (Figure 246A-r). The transition from polyp body scale to tuberculate anthopomal platelet occurs through a very short series of sclerites. The more proximal platelets are the largest and broadest and may be angled loosely en chevron. The more distal forms tend to be elongate and granular (Figure 246Al,r) and are transitional forms to the tentacular sclerites. The



Figure 246 Annisis sprightly sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles.



Figure 247 Annisis sprightly sp. nov., holotype, sclerites: A. Polyp body; B. Thin branch coenenchyme; C. Primary branch coenenchyme; D. Large scale from polyp base.

platelets are mostly <0.10 mm in length. A specimen preserved in a relaxed state will be required to accurately determine the arrangement within each octant. There are perhaps 3-5 platelets in the adaxial-lateral octants, which are relatively smooth, and 5-7 in the other sectors. These platelets appear to be preceded by about 3 transitional scales with irregular margins. The tentacular sclerites are granular rodlets (Figure 246B) that loosely form 2 rows in each tentacle rachis. Their size is very variable, as is their orientation. Some are more or less en chevron and others lie across the rachis, but there appears to be no regular arrangement. They are generally 0.043-0.073 mm in length, and some of the smallest are very narrow with a smooth waist and tuberculate ends.

The polyp body is protected by numerous series of irregularly alternating overlapping scales that are not arranged in rows (Figure 245B,C). On the head, these series of scales do not reach completely around the polyp. In the contracted polyp there is a naked area about 0.04 mm wide running the length of the head below the adaxial anthopomal octant bordered by the lateral extensions of about 7 scales on each side. Sometimes there is a sclerite arranged more or less longitudinally in one or both border areas that may be shaped like a flattened spindle or a branched plate (Figure 247Ak), or some intermediate form.

The abaxial side of the polyp head is the longest and about 9-12 scales can be encountered in a line between the neck suture and the anthopomal margin. The body scales are more or less oval in shape and there is generally a medial cleft in the distal margin, often more pronounced in the thinner head scales (Figure 247Ae,f) than in the thicker scales of the base (Figure 247Ag-i). There is commonly also a conspicuous medial "bullet hole" cleft in the warty basal margin of the body scales (e.g. Figure 247Ag,j). There is some variability between polyps as can be seen in Figures 245B,C where scale margins differ considerably on the heads. In general, the bases of the polyps have numerous scales, mostly <0.16 mm, as illustrated in Figure 245B,C. However, several polyps have their base covered by a few, massive, thick scales, up to 0.21 mm across, with deeply incised margins (Figure 247D). The scales on the polyp head are generally smaller than those on the bases, with most being up to about 0.14 mm in length. The undersides have radial ribs on the blade and complexly warted bases (Figure 247Aa). The ribs on the underside of the basal scales are less pronounced (Figure 247Ai).

#### *Coenenchymal sclerites* (Figures 245D; 247B,C)

The surface of the coenenchyme on the thinner branches contains rooted heads (Figure 245D). The

head portion is somewhat narrow, with low lateral ribs, and the sclerites may resemble thick scales. Their upper surface is mostly smooth with a few small simple tubercles, and the roots have complex warts (Figure 247Ba–f). Below the heads is a layer of spiny sclerites that are often branched (Figure 247Bh–n) and a few branched plates (Figure 247Bg). The rooted heads and spiny sclerites are up to about 0.13 mm long.

The surface of the primary, basal, branch also contains 2 layers. The upper layer consists of robust, broad rooted heads up to about 0.2 mm across (Figure 247Ca-c) and the lower layer contains warty capstans and multiradiates about 0.065–0.114 mm long (Figure 247Cd-f).

Branches of intermediate diameter contain subsurface coenenchymal sclerites of intermediate form. A sample from a tertiary branch, for example, contained multiradiates similar to those on the basal branch but with spines instead of compound warts.

### Variability

The largest of the paratypes is NTM C2473 (Figure 244B). The coenenchyme on the lower portions of the main branch, where intact, is almost white, and on the thinner branches it is brownish orange. Axial internodes are up to 2.7 mm long, and greyish white with no internal tinting. One of the bifurcations is unlike those of the holotype and is similar to Figure 251 example 8. A similar joint is found in specimen SAM H841. SAM H833 has the characteristics of being stored for some time in acidic formalin and the fragmented branches are nearly as flexible as string. The specimen is valuable, however, as some of the polyps have the tentacles protruding showing arrangements of the tentacular rods. These rods usually lie across the back of the tentacle in a single row up the rachis, but in some preparations they appear jumbled and in others they are more longitudinally arranged.

#### Distribution

See Figure 305. Depth range 62–140 m.

#### Etymology

The species is dedicated to the MV *Sprightly*, the expeditionary vessel used when the holotype was collected. Noun in apposition.

#### Florectisis gen. nov.

#### Type species

*Florectisis rosetta* sp. nov., here designated.

#### Diagnosis

Colonies laterally and profusely branched, and more or less planar.

Preserved colony colour is terracotta, and the sclerites are pale yellow in transmitted light. Proximal axial internodes are greyish white, becoming brownish orange in the upper regions. Nodes are light brown.

Polyps are widely spaced and irregularly arranged, mostly on one side of the colony. They are erect, tall, and capstan shaped. The anthopoma is symmetrical and continuous with the polyp body sclerites. Each octant is occupied by 2 rows of paddle-shaped scales, up to 0.11 mm long, and there is a single row of curved, crescentic scales in each tentacle rachis. The latter sclerites are unusually large, up to 0.10 mm long.

The polyp body is covered in an irregular arrangement of small elliptic scales, up to 0.13 mm long, whose free margins are entire and undulate.

The coenenchyme contains small rooted heads, about 0.03–0.05 mm long. Their summit has smooth ridges and cavities, and the underside usually has 2 root-like legs.

The axial internodes have multiple, smooth, pronounced primary ridges, and are up to 2.7 mm long. Fine twig internodes are 4-sided.

## Distribution

As for Florectisis rosetta, see Figure 306.

#### Etymology

The name is derived from the Latin *Floris*, flower, and *erectus*, upright, in allusion to the form of the polyps; combined with *Isis*.

*Florectisis rosetta* sp. nov. Figures 248–250; 306

## Material examined

Types

HOLOTYPE: AM G5680, off Botany Bay, New South Wales, on submarine cable, 90 m, registered 18 Sept. 1906.

## Diagnosis

As for the genus.

## Description

#### Colony form (Figure 248)

The copiously branched species is based on a single broken colony consisting of a large more or less planar fragment with a small holdfast, several smaller broken fan portions and some branch and twig fragments. The main fan fragment is 110 mm x 65 mm. A number of the smaller fragments can be



Figure 248 Florectisis rosetta sp. nov., holotype, natural size.

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Figure 249 Florectisis rosetta sp. nov., holotype: A-E. Polyps; F. Coenenchyme; G-I. Axial internodes; J. Twig fragment.



Figure 250 Florectisis rosetta sp. nov., holotype, sclerites: A. Anthopoma; B. Tentacles; C. Polyp body; D. Twig coenenchyme.

matched to the main piece indicating that the original colony was at least 130 mm across. The holdfast is calcareous, about 6 mm x 10 mm, and attached to a lump of intense black friable material that is probably a piece of the coating of the submarine cable on which the colony was growing. The main stem is about 8 mm long, devoid of coenenchyme, and about 1.4 mm thick. It divides into two main branches about 1.3 mm thick, one of which immediately rebranches out of the general plane of the colony, but only a stub of this ramification remains. The lower regions of the main branches are also devoid of coenenchyme. At about 12 mm from the base of the colony the two main branches both rebranch slightly out of plane, and again only stubs remain. Branching in the main fan is generally lateral and irregular, however, there is an illusion of dichotomy because many neighbouring branches arise at more or less the same height in the colony. Branching occurs to about the sixth order. Branches in the mid-region of the colony are about 0.54-0.66 mm thick (without polyps). In the upper regions branches and twigs are about 0.36-0.54 mm thick. Unbranched twigs vary from about 3-28 mm in length. The distance between consecutive subdivisions is also variable, 1.6-33.2 mm, although usually it is about 4.7 mm. A few branches and twigs have laid over each other and fused together. The angle of branching is about 30-60°. A number of branches diverge out of plane but curve and grow close and more or less parallel to the main fan so that the colony is only about 10 mm thick.

#### *Polyps* (Figure 249A,B,J)

One face of the colony is almost entirely free of polyps which are irregularly arranged and not crowded. In the middle region of the colony 33 polyps were counted on a 10 mm section of branch. Polyps are symmetrical, tall and capstan shaped. Most arise at nearly right angles to the branches, although in the upper regions many are angled distad at about 45°. Most polyps are contracted so that the anthopoma is more or less flat or slightly concave. A few are less contracted with tentacle tips slightly protruding. The polyps are mostly 0.84–0.90 mm tall. Polyp heads are 0.39–0.45 mm across, polyp bases 0.42–0.48 mm thick, and neck regions 0.30–0.33 mm in width. A few juvenile polyps occur scattered throughout the colony.

## Colony colour

More or less the colour of terracotta (≈7D7). The nodes can be seen through the translucent coenenchyme. Sclerites are pale yellow in transmitted light.

#### Axis form (Figure 249G–I)

Internodes have multiple, smooth, pronounced,

primary ridges. Those in the finer twigs are 4-sided with a ridge along each edge. A main branch internode 0.78 mm thick has 10 longitudinal ridges.

Throughout the colony most internodes are 0.8–2.7 mm long, with those in the middle regions being mostly 2.1–2.4 mm in length and 0.6 mm thick, and those in the fine twigs about 1.3 mm long and 0.3 mm thick. Basally the nodes are 0.6–0.9 mm long. In the middle regions of the colony they are about 0.3 mm long, and in the twigs about 0.2 mm. The nodes are slightly narrower than the internodes. Desmocyte cavities are quite distinct and arranged in rows alongside the primary ridges.

## Axis branching

Most branching occurs from the distal ends of internodes in the style shown in Figure 251 examples 11, 12 and 14.

#### Axis colour

In the more basal regions internodes are greyish white, translucent but densely coloured. In the upper regions of the colony the internodes are brownish orange ( $\approx$  6C5). Basally the nodes are light brown ( $\approx$ 6D6) with narrow pale yellow satinlike borders. Distally the borders become progressively wider until, in the twigs, only a narrow light brown central region remains.

## Polyp sclerites (Figures 249A–E; 250A–C)

Each octant of the anthopoma is continuous with the polyp body sclerites and consists of 2 rows of angled, somewhat paddle-shaped, overlapping scales (Figure 249C–E). At the proximal end of each octant, the scales become larger and more transversely placed and there is no regular arrangement of body scales in rows below this. The more distal anthopomal scales have a single serrate blade and resemble the rooted leaves of some species of Echinogorgia. The medial to proximal scales are far more elongate and not serrate (Figure 250Ab). Anthopomal scales are up to about 0.11 mm long. There does not appear to be a specialised basal tentacular scale. The terminal anthopomal scales are small and quite tuberculate, as in Figure 250Ac. There are one or two scales intermediate in form between these and the curved crescentic scales which form a single row in the rachis of each tentacle. The tentacle scales are relatively large, occasionally up to 0.10 mm across, and their distal margin carries long, granular, tooth-like projections (Figure 250B).

The elliptic polyp body scales are up to about 0.13 mm across. They have entire, often undulate, distal margins and a more or less continuous transverse ridge across their exposed face (Figure 250C). There are complex tubercles on the undersides of the scales (Figure 250Ca,b).



Figure 251 Modes of axial branching, (continued next page)



## Coenenchymal sclerites (Figures 249F, 250D)

The sclerites in the surface of the twigs, branches, and stem are rooted heads. The upper surface of the head has smooth ridges and concavities, and the lower side commonly carries two or more leglike structures. Most of the heads are about 0.033– 0.050 mm across. Larger flattened forms which grade into polyp body scales occur in the vicinity of the base of each polyp.

### Distribution

See Figure 306. Depth 90 m.

### Etymology

In allusion to the rosette-like arrangement of the anthopoma.

## DISTRIBUTION AND ITS IMPLICATIONS FOR PHYLOGENY

Any theoretical explanations for the distribution of the taxa studied are hampered by the paucity of reports on these animals from the Southern Ocean, and the virtual absence of any geological record. With such little data it is possible to conceive numerous models with perhaps equal validity. What data there are divides the fauna into 2 relatively distinct morpho-geographical groups: Australasian and Southern Ocean. The differences in distribution correlated with morphological characters may indicate a major evolutionary branching probably from the same ancestral stock.

The Australasian Group comprises Circinisidinae (Figure 324), and the genera of Mopseinae that have a non-bushy growth form (Figure 325). Its members are predominantly endemic to the southern, south western, and south eastern regions of Australia, with small numbers of taxa occurring in New Zealand, New Caledonia, the Coral Sea, and Indonesia. The exception is a single anomalous record of *Pteronisis plumacea* off the Mawson coast of Antarctica which is difficult to account for.

The Southern Ocean Group comprises the bushy members of Mopseinae, Primnoisis, Echinisis, Minuisis, and Chathamisis, together with Notisis which is known primarily from colony fragments both planar and non-planar in growth form. The genera in this group have not been extensively reported, and are found predominantly in Antarctic and Subantarctic waters (Figure 326). They are more common around the west coast of the Antarctic Peninsula (an area relatively well collected), with isolated occurrences right around the Antarctic continent, and off the west coast of southern South America. Two endemic species are found off Southern Africa, and there are scattered occurrences of other species westwards from South America in the vicinity of several Subantarctic islands including New Zealand, and a single record

from the South Pacific Basin. With the exception of the South African component, virtually no occurrences of this group have been recorded north of the Subtropical Convergence. The Falkland Current extends the Subantarctic water mass as far north as the isolated occurrence of Primnoisis rigida of Rio de la Plata, but the type locality of Minuisis lies just beyond the northern limit of a tongue of the Convergence where it is straddled by New Zealand. However, the North Island of New Zealand, usually considered to be a warm temperate zone, retains faunistic features of the cold temperate south as it is bathed by the mixture of Subantarctic and Subtropical waters of the Tasman current (Knox, 1963). The genera in this group have in common not only a bushy growth form, but also erect, minimally contractile polyps which are covered all around with sclerites. This latter feature, which can possibly be considered plesiomorphic, is rarely seen in the Australasian Group. If Notisis and Chathamisis are disregarded, the remaining genera also have in common the possession of coenenchymal sclerites in the form of small spinous platelets; a feature not shared by any of the Australasian group.

Both *Chathamisis* and *Notisis* deserve special attention. The 2 closely related taxa, *Chathamisis ramosa* of Williams (1992a) and of Bayer and Stefani (1987b) occur only in Southern Africa. They are the only representatives of Mopseinae in Africa (there are no Circinisidinae), and the only known record of *Chathamisis* outside of New Zealand. These 2 taxa, especially *C. ramosa* of Williams, have quite a different sclerite form to the other Southern Ocean genera, which might be explained by the present oceanographic isolation of this coast of Africa from the Southern Ocean as is discussed later.

Notisis is mainly included in the Southern Ocean Group on distributional grounds. Morphologically, it is much closer related to the members of the Australasian Group with which it shares pseudodichotomous branching, often with a planar aspect, and axial internodes with longitudinal rows of large tooth-like projections; and although the polyps are covered all around with sclerites, these may be narrower on the adaxial side allowing the polyps to be curved distad. It also appears to reproduce by brooding the larvae, an activity which has not been reported for the other genera within the Southern Ocean Group, but which as has been found in a number of the Australasian taxa during the course of this revision. The relatively restricted distribution of the Australasian Group, in a global sense, can possibly be attributed to this more conservative mode of dispersal, and it may be found that the larger circum-polar Antarctic and Subantarctic range of the Southern Ocean Group (other than Notisis) has been possible because those genera have long living planktonic

larvae and may even be broadcast spawners. Although *Notisis* is also circum-polar, its distribution is much more confined, only being reported once outside of the limits of the winter ice shelf. Of course, the Southern Ocean group may also prove to be brooders, whose distribution is for the most part continuously peri-polar and driven by the westward drift of the water mass.

On first appearance it could be suggested that the faunal origins of both of these isidid groups were the ancestors of the Southern Ocean Group; that this group was radiating after the break up Gondwanaland when the regions that are now South America, the Antarctic Peninsula, and South Africa were in close proximity; and that the Australasian component rafted on the Australian plate to which it had dispersed before or after it had broken away from the Antarctic/Australian Supercontinent. As Southern Ocean taxa occur from 18-2350 m it could be hypothesised that the population that remained with the Antarctic land mass became increasingly cold water adapted, dispersing into both shallow and deep waters as that region became colder. On the other hand, marked environmental gradients would have been generated in the shelf waters of the Australian land mass as it moved into overall increasingly warmer waters, and this would have provided opportunities for the selection pressures that drive speciation, resulting in the large diversity seen in the Australasian Group.

There are two obvious problems with such a model. First, there are no bottle-brush or irregularly bushy colonial forms in the Australasian Group, nor any branching patterns obviously derived from this form. One could postulate this could possibly be attributed to the requirements for existing in the different habitats. Gage and Tyler (1991:105-106) state that in shallow water, suspension feeders may employ flat, fan-like catching structures held at right angles to tidal or oscillating currents, or a radial or bushy form in more turbulent conditions, and the latter commonly occurs in deep water environments. If this were the sole criterion, however, the completely disparate distributions of the 2 morphogroups would presuppose a homogeneity of environment in the 2 regions that would seem unrealistic. Also, Southern Ocean taxa occasionally occur in shallow water and retain their bushy body form, and some isidids and many gorgonians of other families having a planar, pinnate, or dichotomous colonial form are found in deep water.

Second, Williams (1992b) reports that only 4% of the South African octocoral fauna has affinities with that of the Southern Ocean, and of these only 2 species are from these isidid groups. One explanation for this could be that the radiation of the Southern Ocean forms was a much more recent event, occurring well after the South African land mass had separated from Gondwanaland. Williams even suggests that this coast of Africa may have been biogeographically linked to the Antarctic and Subantarctic faunas as recently as the late Pliocene and early Pleistocene, and dispersion of Southern Ocean forms could have occurred then. The region is now well to the north of the Subtropical Convergence, possibly placing the representatives of this group at the extreme of their temperature tolerance which, together with the relatively short period of isolation may account for the low diversity.

One model incorporating these ideas is to place the origins of the present Australasian Group around the end of the Cretaceous in the oceans surrounding the Antarctic/Australian Supercontinent. The ancestral stock may have been circum-polar, but as there so few forms similar to the Australasian Group remaining in the region today, it could be proposed that the ancestral fauna was restricted to the eastern part of the supercontinent, that destined to become Australia, and as the Australian land mass moved away adaptive radiation occurred to the newly available coastline. With the movement into lower latitudes, the higher water temperatures may have led to the attenuation of species on the more northern Australian coastal regions, and their concentration in the temperate and cold temperate regions as is seen today. In the present situation the only genera that occur above the Tropic of Capricorn (Peltastisis, lotisis, and Lissopholidisis) are found in relatively cold waters at depths of 500-1000 m, while virtually all other genera are restricted to depths of <270 m. Species of Peltastisis and Lissopholidisis are unbranched, which would seem to be a plesiomorphic character. They are very rare, and it could be argued that they are the closest examples yet found to the ancestral form. The low number of representatives of the group in New Zealand may possibly be attributed to the very early separation of this region from the Australasian land mass, and its subsequent oceanographic isolation from the viviparous Australian taxa. Indeed, the only 2 Australasian Group genera that occur in New Zealand, Circinisis and Lissopholidisis, are both unbranched.

The only known remnant of the Australasian Group in the Antarctic today is *Notisis* and perhaps *Pteronisis*. (There is one specimen lot of *Pteronisis plumacea* amongst material of the British and New Zealand Antarctic Research Expedition reputed to have come from off the Mawson Coast. All other occurrences of the species are in the vicinity of Tasmania, the western portion of Bass Strait, and the Great Australian Bight, and several of these records are also from the BANZARE collections. It is difficult to explain this distribution considering there are no other records of *Pteronisis* other than those on the Australian continental shelf, and indeed difficult to reconcile it with present ocean current régimes. The enigma may simply be due to a mix up of labels).

This alternative distribution model further necessitates that the present Southern Ocean Group evolved and dispersed much later. Some evidence for this may have been provided by Grant (1970 and 1976) who equated numerous lower Miocene New Zealand fossils with the axial internodes of Primnoisis ambigua. Although Grant's conclusion is somewhat equivocal, as his comparative fresh specimen was a decorticated bushy axis and therefore of uncertain generic identity, it seems quite probable that the fossil material may be from early Southern Ocean taxa. If this group were indeed dispersing in the Tertiary equivalent of the westward flowing peri-polar Subantarctic water mass, the model needs to explain their absence from Australia. During that period the southern coastal zones of that continent would have been about 15° further to the south than they are at present, and it seems likely that early Southern Ocean forms would have had the opportunity to colonise these regions. It could simply be postulated that they were out-competed by the existing Australasian fauna, but perhaps it is more likely they were unable to cope with the general rise in water temperature associated with the Miocene Oscillation. The events comprising this oscillation permitted subtropical faunal assemblages to extend their range into Southern Australia (McGowran and Li, 1994).

Evidence to support this model would be the existence of Cretaceous fossils, reliably linked to the present Australasian Group, in the Australasian and east Antarctic regions. Similar occurrences in southern South America, South Africa, or the Indian subcontinent, however, would require considerable changes to the hypothesis.

To further substantiate the theory, South American, South African, Australasian and circumantarctic regions should only have fossils of a much younger age representing ancestors of the present Southern Ocean Group. At present such data are lacking.

Some isidid fossils have been reported from Australia by several authors, but only *Mopsea tenisoni* Chapman, 1913 is recognisable as possibly being closely related to present forms. Chapman's illustration (1913: Plate XIX, Figure 39) of a section through an internode resembles the structure given by Grant (1976: Figure 5a) for the axis of *Circinisis circinata*, and therefore possibly represents an Australasian Group element. No stratigraphic detail is given in Chapman's account, but the material came from the Murray Basin in South Australia at a relatively shallow depth and is probably from the mid Cainozoic carbonates (Megirian pers. comm.).

In conclusion, although the Australasian and Southern Ocean Groups would appear to have a common ancestor, their distinctly differing distributions may indicate two subsequently diverging lineages. This may justify separating the Southern Ocean Group (minus *Notisis*) into the revived subfamily Primnoisidinae on phylogenetic considerations, but this may be unsatisfactory in the current classification which is morphologically based.

As mentioned earlier in the section on Taxonomic Coverage, the genus *Stenisis* shows morphological similarities to some genera of Mopseinae. However, as the taxon was established on material from the Bahamas, zoogeographic considerations suggest that a closer examination should reveal characteristics which will support its exclusion from Mopseinae.

## CONCLUSION

It is not uncommon to find in invertebrate groups that current taxonomic difficulties can be attributed to the inadequacies of older literature. This has been the case with the majority of the genera revised here, particularly *Mopsea*, where it is proposed that, of the numerous nominal species, only the type species *M. encrinula* be retained as valid. It is not an exaggeration to state that prior to 1987 none of the nominal species could be recognised from the literature with any degree of certainty.

In establishing the proposed generic groups, several character sets proved very reliable. These were: the branching pattern; the structure of the polyp; and the sculpturing of the axial internodes. All 3 of these can be correlated with sclerite architecture. This is not to say that sclerite shape is not of great importance, but many genera do share common forms. Sclerite form is the character upon which the subfamily Mopseinae is distinguished from Circinisidinae; it is of prime importance for differentiating between species; the same general form occurs amongst all members of a genus; and if 2 groups of species had the same branching pattern, polyp structure, and axial architecture, but markedly different sclerite shape, then they would be separated as distinct genera. However, in this study differentiation between both the new and revised genera was rarely dictated by sclerite form. Two exception are Peltastisis and Lissopholidisis. Both genera comprise species which are unbranched and filiform, and which commonly have very large abaxially placed polyp sclerites. Nevertheless, the general form of all of the other sclerites in Peltastisis is quite similar to that found in other groups within Mopseinae, whereas that in *Lissopholidisis* are relatively quite different. *Primnoisis, Chathamisis, Echinisis, and Minuisis, all* with bushy colonial form, are also separated on sclerite shape, primarily using the sclerites of the polyps.

It has been found that colonial branching form can be categorised into a number of distinct patterns which, with rare exceptions, are consistent for all species within a proposed generic group, and similar remarks can be said to apply to both polyp structure and axial architecture. Polyp structure can be more specifically defined as the polyp sclerite arrangement, and is inherently linked with sclerite form. In the past, too little attention has been paid to the structure of that part of the polyp termed the anthopoma, which is here proved to be of prime importance.

Because of the prior confused state of the taxonomy of the nominal species of Mopseinae, it seems that the disparate distributional patterns of the bushy and the planar forms have been obscured, as up until now some species of Mopsea were thought to occur in Antarctic waters. On the evidence presented it can be seen that there are in fact 2 quite separate distribution ranges, with minimal overlap in the region of New Zealand. With little fossil evidence, and few records from high southern latitudes or the deep waters of the Australian plate, any theories about the history of this distribution are very conjectural. There are clearly 2 morpho-geographical groups, Australasian and Southern Ocean, and they are sufficiently alike to be considered to have come from a common ancestral form. However, it could be hypothesised that they may have evolved along separate lineages, with the older Australasian Group rafting on the Australian plate after the break up of Gondwanaland, and before the dispersive radiation of the Southern Ocean taxa.

It is certain that the geologically based models proposed to explain the distribution will be altered

by future authors, but this study has indicated where evidence for such reappraisals is likely to be found. With regards recent material, this necessitates more collecting. There is comparatively little material yet recorded from the Southern Ocean, and no records from off the coast of Chile which is washed by a northerly flow of Subantarctic waters whose westward drift is interrupted by the South American land mass. Closer to Australia, the recent reports (Gowlett-Holmes, pers. comm.) of huge populations of isidids in the deep waters of the South Tasman Rise hold much promise. The Australasian area is the region of highest species richness on available data, but this undoubtedly reflects to some extent the concentration of collecting effort. Nevertheless, it seems likely that many more new taxa relevant to the problem will be found in the relatively untouched regions of the deep waters of the Indonesian archipelago, south to the Australian continent, and in the Coral Sea. Perhaps richer still is the Australian continental slope outside of the Great Barrier Reef and as far south as Sydney, and the vast area between Australia's east coast and the line drawn south through New Caledonia, the Norfolk Ridge, and New Zealand.

Should material from these regions be forthcoming it would greatly facilitate an in-depth analysis of the phylogeny and zoogeographic history of the group. With the uncertainty of the subfamilial assignments and affinities of a number of isidid genera, as detailed by Bayer and Stefani (1987), Bayer (1990), and herein, perhaps only Keratoisidinae and Circinisidinae are close to 'natural' groupings of genera, while Isidinae and Mopseinae are likely to be polyphyletic as they stand at present.

Any studies of the phylogeny of the subfamilies covered in this work (Mopseinae and Circinisidinae) should preferably include Isidinae and Keratoisidinae, for which a thorough revision of a number of genera is an unavoidable prerequisite.



Figure 252



Figure 254





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Figure 253

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### P. Alderslade

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Figure 258

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Figure 263

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## P. Alderslade

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Figure 306

AUSTRALIA BRISBANE SYDNEY PERTH SYDNEY BADELAIDE MELBOURNE PHOBART Mopsea Lamouroux, 1816

Figure 307

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Figure 309

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Figure 311

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Figure 318

## P. Alderslade

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Figure 322

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Figure 324

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Figure 325

#### P. Alderslade

![](_page_359_Figure_1.jpeg)

Figure 326

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### **Revisionary systematics in Isididae**

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# Guide to Authors

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Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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