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Revision of methods for separating species of *Protopalythoa* (Hexacorallia : Zoanthidea) in the tropical West Pacific

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Abstract. The genus *Protopalythoa* Verrill, 1900 (family Sphenopidae) is defined and its status discussed. As with other zoanthid genera, species are difficult to separate by traditional methods. We have developed a rigorous approach to quantitative data derived from measurements and meristic characters. In support of genetic evidence, we have utilised the relationship between number of septa and polyp column diameter, and the capsule length of nematocysts (holotrichs and *p*-mastigophores), together with the presence or absence of basitrichs in the cnidom. Using this approach, the species *Pr. mutuki* (Haddon & Shackleton, 1891*b*) and *Pr. heliodiscus*, sp. nov. are separated, described and illustrated. *Protopalythoa mutuki* is interpreted as a normal micro-carnivore with autotrophic capability, while *Pr. heliodiscus* sp. nov. is an obligate autotroph with little ability to capture prey. The latter is the only zoanthid known to have vertical transmission of zooxanthellae.

Additional keywords: Australia, Great Barrier Reef, Fiji, taxonomy, meristic characters, cnidom, nematocyst capsules, *Palythoa*.

Introduction

This paper addresses the problems posed by a lack of clear, qualitative characters with which to separate species of zoanthid generally and of *Protopalythoa* Verrill, 1900 in particular. We investigate the use of measurements and meristic characters, based on samples of meaningful size followed by statistical analysis, in a way never previously applied within the order.

Morphology of zoanthid zooids

The Zoanthidea are an order of Hexacorallia characterised by a tendency to form colonies of polyps and a distinctive arrangement of radial septa ('cnemes') within them (Fig. 1*A,B*). The actinopharynx has a single siphonoglyph (sulcus), conventionally designated ventral (Fig. 1*C*). The septa (usage following Hyman (1940)) are paired, each pair generally comprising one perfect (i.e. reaching the actinopharynx or, below it, ending centripetally in a septal filament) macrocneme and one imperfect, often almost vestigial, microcneme (Fig. 1*B,C*). However, the two ventral (sulcal) septa are perfect and their dorsal (absulcal) counterparts imperfect (Fig. 1*B*). The polyps are biradially symmetrical about the sulcal axis, any two mirror-image septa constituting a couple; the absulcal and sulcal couples are known as the dorsal and ventral directives respectively (Fig. 1*B*). As polyps increase in circumference, new septa arise in the exocoels each side of the ventral directives. Erdmann (1885) recognised two slightly (but consistently) different patterns, in which the septa of the fifth couple (i.e. in each direction from the dorsal directives) were either perfect (macrocnemic; Fig. 1*B*) or imperfect (brachycnemic; Fig. 1*C*). This distinction became the basis for Haddon and Shackleton's (1891*a*) suborders Macrocnemina and Brachycnemina respectively. Tentacles are in two cycles, the inner arising from the endocoels (the spaces within pairs) and curling upwards when extended, the outer from the exocoels (the spaces between pairs) and curling downwards (Fig. 5*G,H)*. The Brachycnemina are zooxanthellate and have, like hermatypic scleractinian corals, an essentially tropical distribution; they include the zoanthids that are abundant in the intertidal zone and shallow sublittoral of coral reefs. Macrocnemina tend to occur deeper and commonly lack zooxanthellae. A key to zoanthid genera, with pictures of several common Australian species, is provided by Ryland and Muirhead (1993).

The family Sphenopidae

Protopalythoa, together with *Palythoa* Lamouroux, 1816 and *Sphenopus* Steenstrup, 1856 constitute the Sphenopidae Hertwig (1882, emended), characterised and distinguished from Zoanthidae by: (*1*) the incorporation of sand into the mesoglea (Fig. 1); (*2*) producing a zoanthella (rather than a zoanthina) larva (see Ryland *et al.* 2000); and (*3*) the absence

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in the cnidome of *b*-mastigophore nematocysts (see next section). *Sphenopus* does not form colonies and is adapted to life on a soft substratum. In *Protopalythoa* (as currently delimited) polyps may be unitary, form small clusters or, most commonly, clone to cover extensive areas, as on many reefs and certain subtropical shores (e.g. in KwaZulu-Natal province, South Africa, and—less spectacularly—southern Queensland). In such clones, the polyps remain individually recognisable, with a well-developed erect column or scapus (Fig. 1*A*); they have a sandy appearance (taking on the colour of the dominant particles incorporated) when uncovered by the tide, but are transformed when expanded under water into a mass of flat, brown, tentaculate disks (Fig. 9*B,F*). *Palythoa* is readily distinguished from *Protopalythoa* by having the polyps wholly immersed in the colonial coenenchyme (Fig. 1*C*), the clones either spreading as large undivided sheets or broken up into small contiguous blobs a few square centimetres in size. The Hawaiian 'Limu make o Hana' (deadly seaweed of Hana (Moore and Scheuer 1971; Mebs and Gleibs 1997*a,b*)) is the palytoxin-containing *Protopalythoa toxica* Walsh and Bowers (1971)—possibly not distinct from Australian *Pr. mutuki*. In view of possible toxicity, caution should be exercised when handling live *Protopalythoa* and *Palythoa*, and certainly they should not be touched by bare hands affected with cuts or abrasions.

Genetic versus descriptive approaches to species-level taxonomy

From the confused situation surrounding at least five nominate and ill-defined species of *Protopalythoa* in the Great Barrier Reef (GBR), Burnett *et al.* (1997), using allozyme electrophoresis, showed that only two were widespread. One of these was identified as *Pr. mutuki*, described from the intertidal zone of Mabuiag, a 'high island' in Torres Strait. The second had smaller polyps but was otherwise distinguished by Burnett *et al.* mainly by being subtidal in distribution. Gametogenesis, spawning, and larval development in material from Orpheus Island had been studied earlier (Babcock and Ryland 1990; Ryland and Babcock 1991) but the species has never been identified or named. The priorities of the present study were to determine reliable morphological criteria by which the two could be distinguished, and to establish whether or not the unnamed *Protopalythoa* could be referred to any described species.

In conventional zoanthid taxonomy, some description is given of the external appearance of polyps and of their internal structure as studied in sections of wax-embedded material. The characters used, e.g. appearance (which depends on the nature of the locally available sand), lacunae (canals) in the mesogloea, and the length range of small samples of nematocyst capsules, often seem of dubious

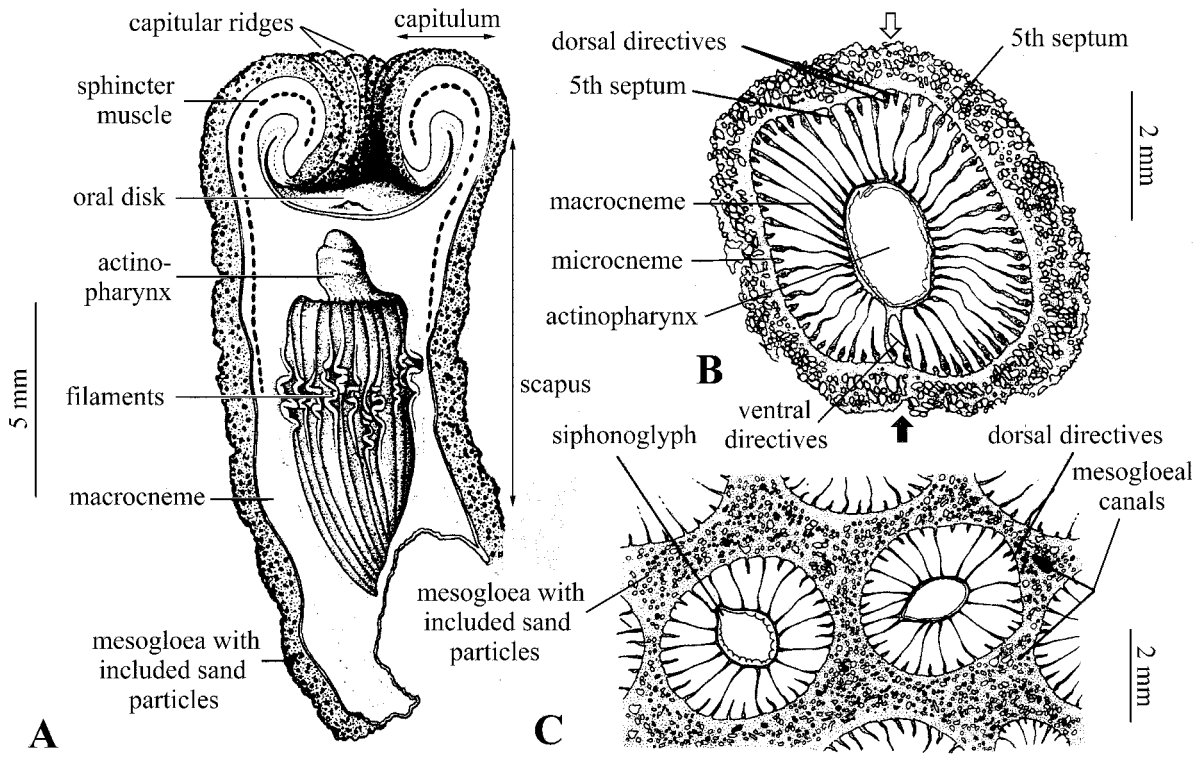

Fig. 1. Zoanthid structure. *A*, Polyp of *Protopalythoa mutuki* in LS, with two macrocnemes in the plane of the section. *B*, Zooid in TS to show arrangement of septa in *Epizoanthus* sp.—the arrangement is macrocnemic (with the 5th couple perfect); arrows mark the directive axis (black ventral). *C*, Horizontal section through portion of *Palythoa caesia*; polyps are immersed in the coenenchyme and the septal arrangement is brachycnemic. (Drawings by A. Muirhead.)

taxonomic value: the present study reveals much variation between specimens from different geographic localities. Prior to the detailed studies of the late nineteenth century, especially by A. C. Haddon and his co-workers, the information in descriptions does little more than indicate placement in one of the currently recognised genera, resulting in a plethora of ill-described nominate species. Much more detail of variation, based on samples from a spread of localities, is ideally required (though of course sometimes impossible to achieve): the provision of this has governed our approach. In view of the suggestion (Burnett *et al.* 1997) that polyp size might provide a diagnostic character in *Protopalythoa*, we first compared the number of perfect septa with column diameter (as the two should increase *pari passu*) and volume of representative polyps from Australian and Fijian collections. Then, to provide more data, we looked at the nematocysts.

The use of nematocysts in anthozoan taxonomy

Nematocyst data are used in two ways in anthozoan taxonomy: the cnidome (the types that occur, and where) and measurements of the capsules (see Fautin (1988) for a review of how they are used in Actiniaria). The value of nematocyst data, as (and if) included in descriptions written during the first part of the twentieth century, has been questioned (e.g. Herberts 1972; Muirhead and Ryland 1985) but, in other hexacoral orders, procedures have become more robust in recent years and measurement data properly quantified (e.g. Williams 1996, 1998, 2000; Chintiroglou and Simsiridou 1997). Nematocysts may be of considerable importance in species-level taxonomy but workers simply trying to identify species may be deterred by a nomenclature that has been both esoteric and inconsistent (see England 1991): thus mastigophores have been termed rhabdoids (e.g. by Schmidt 1974) and basitrichs regarded as either identical to (which they are not) or different from *b*-mastigophores (see below). We have therefore reproduced some diagrams from Schmidt (1974), which are clear, though inaccurate in showing the spines arranged in a single, rather than a triple, spiral. Schmidt (1974)—in an account of anthozoan nematocysts generally—included the array he recorded from the 'lower Zoantharia', a term of his own which appears to be equivalent to the Sphenopidae as utilised here, and from the 'upper Zoantharia', which comprise the rest of the order. Of the nematocysts present in *Protopalythoa*, 'holotrichs' or 'holotrichous isorhizas' (Fig. 2*A,A'*), which are often very large, have an undifferentiated tube with spines spread uniformly along its length, while 'mastigophores' have the base of the tube wider than the rest, forming a shaft. Mastigophores are 'microbasic' when the exploded shaft is less than three times the length of the capsule. In '*b*-mastigophores' the shaft tapers into the tube but in '*p*-mastigophores' (Fig. 2*C,C'*) the transition is abrupt, the spines at the point of transition creating a V-shaped notch in the unexploded capsule. Some authors (e.g. England 1991, though not Schmidt 1974), have separated 'basitrichs' (Fig. 2*D,D'–G,G'*) from *b*-mastigophores, the former having a long, thin shaft (<1.5× the diameter of the distal tube) appearing as a slender axis extending almost the whole length of the unexploded capsule; whereas the latter have a

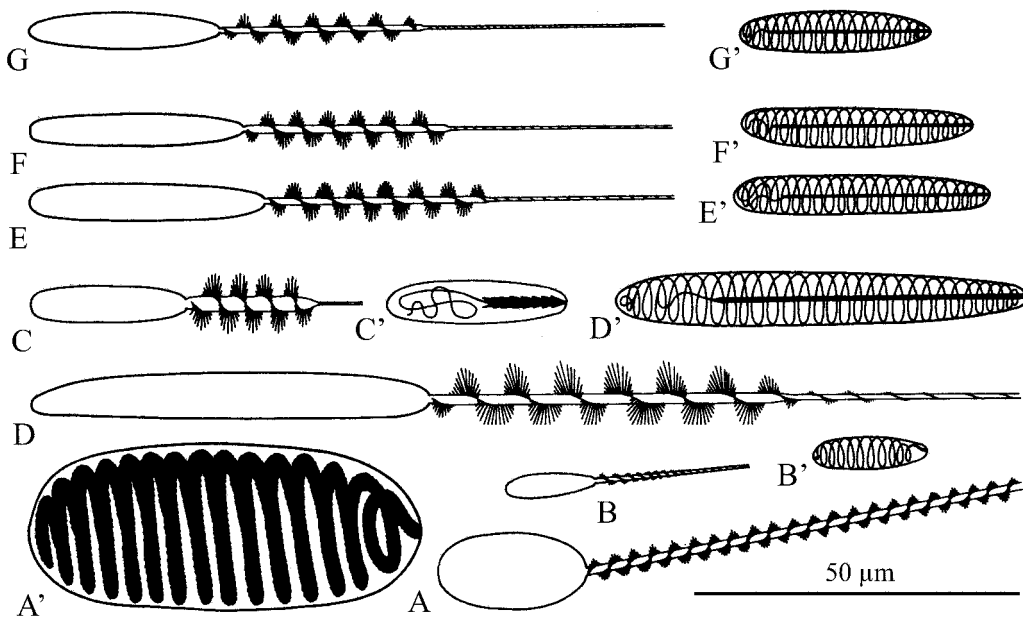

Fig. 2. Diagrammatic representations of nematocyst types in *Palythoa tuberculosa* (the same types are found in *Protopalythoa*), exploded and unexploded. *A,A'*, Large holotrich (*A* at one-third scale), scapus. *B,B'*, Small holotrich, scapus. *C,C'*, *P*-mastigophore, filaments. *D,D'*, Basitrich, filaments. *E,E'*, Basitrich, pharynx. *F,F'*, Basitrich, tentacles. *G,G'*, Basitrich, scapus. (Outlines, but not terminology, from Schmidt 1974.)

shorter, broader shaft (more than twice the diameter of the distal tube) appearing as a stubby axis within the unexploded capsule. All the microbasic mastigophores examined in this paper, so far as can be judged by light microscopy, appear to be basitrichs.

The genus *Protopalythoa*

Gemmaria Duchassaing & Michelotti, 1860, was introduced for *G. Rusei* nov., *Mamillifera clavata* Duchassaing, 1850, *G. swifti* nov. [= *Parazoanthus swifti*], and *M. brevis* Duchassaing, 1850, with no designation of type species. *Protopalythoa* Verrill, 1900 was a *nomen novum* because *Gemmaria* was preoccupied by *Gemmaria* McCrady, 1857 [cited as McCready, 1859], a hydroid. Verrill designated *Gemmaria variabilis* Duerden, 1898, as type species, on the grounds that *G. riisei* [sic: *G. rusei*] was unrecognisable and Duchassaing and Michelotti's other species were not congeners. These and subsequent authors (e.g. Haddon and Shackleton 1891*b*; Duerden 1898) maintained *Gemmaria* (or *Protopalythoa*) as a genus distinct from *Palythoa* Lamouroux, 1816, type species *Alcyonium mammillosum* Ellis & Solander, 1786, because, in *Gemmaria*, the coenenchyme is less developed, such that the polyps project, and there are many more septa. Put descriptively, *Palythoa* colonies form compact sheets or blobs in which the depth of the coenenchyme exceeds (usually greatly) the free height of the polyps, which are thus wholly or largely immersed (e.g. Ryland and Muirhead 1993, fig. 17.17). *Protopalythoa* colonies, on the other hand, form carpets of contiguous—or continuous but quite distinct—polyps joined by flat, stolonate or extensive, encrusting coenenchyme of thickness less (usually much less) than the free height of the polyps. Additionally, septa and tentacles are generally few (<40) in *Palythoa* (Fig. 1*C* and Ryland and Muirhead 1993, fig. 16.6) but numerous (>40) in *Protopalythoa* (Fig. 6*A*).

Palythoa *and* Protopalythoa: *one genus or two?*

A decade after Verrill, Pax (1910) merged *Protopalythoa* into *Palythoa*, within which he created three subdivisions: (*a*) 'immersae', with the characters of *Palythoa s. str.* (i.e. excluding *Protopalythoa*) as just indicated; (*b*) 'intermediae', with the coenenchyme partly as stolons partly as a continuous layer, within which the polyps could not withdraw; and (*c*) 'liberae', in which the polyp bases were joined only by stolons. *Protopalythoa* has a tendency to form carpets, often intermingled with species of *Zoanthus* (Lamarck, 1801), which can grow between stolons and polyp clusters, and it is not necessarily easy to separate 'intermediae' and 'liberae' forms. *Palythoa s. str.* either makes extensive solid crusts or lobulates into clusters of convex, rounded blobs (illustrated, for example, by Ryland and Muirhead 1993, fig. 17.16), and may be a reef-crest (Caribbean: (Goreau 1959; Wheaton and Jaap 1988)) or reef-flat (Indo-Pacific: (Ryland and Muirhead 1993; Tanner 1997)) dominant. Pax, who was a prolific describer of species, maintained *Palythoa s. lat.* for the next half century, and Carlgren (1937, 1938, 1940, 1950, 1954), usually a fierce critic of Pax's taxonomy (e.g. 1938, pp. 3–4), in this instance followed him. Pax's three divisions are not subgenera and have no nomenclatural status.

Contemporary taxonomy favours the restriction of genera to groupings of closely similar species. With over 100 nominate species (Walsh (1967) listed 93 species of *Palythoa s. lat.* and another nine—that had not had occasion to be reclassified by Pax or Carlgren—of *Protopalythoa*; it makes little sense to follow Pax (1910) in combining two species groups that are readily separable under water or on the shore, since to do so (especially when the species often cannot be determined) results in a major loss of information. Genetic work (possibly assisted by studies on nematocysts) will ultimately clarify whether *Palythoa* and *Protopalythoa* constitute separate clades: the results of Burnett *et al.* (1997)—based on rather few species—unfortunately do not settle this question. Pending definitive clarification, discoveries such as the presence of palytoxin (PTX) (Moore and Scheuer 1971; Walsh and Bowers 1971; Kimura *et al.* 1972; Mebs and Gleibs 1997*a*,*b*) in a *Protopalythoa* (*Pr. toxica*) and a *Palythoa* (*Pa. tuberculosa* (Esper, 1809)) and of UV-absorbing mycosporine-like amino acids (Dunlap *et al.* 1986; Dunlap and Yamamoto 1995) in a *Palythoa* (*Pa. caesia* Dana, 1846), together with different ecological adaptations (e.g. Koehl 1977), make it desirable to keep the two genera separate. The natural function of PTX may be as an allelochemical enabling, for example, *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 to overgrow 'nearly every other sessile reef invertebrate' (Suchanek and Green 1981).

A practical consequence of Pax's (1910) merger of the two genera is that we now do not know how many nominate species properly belong to *Palythoa* and how many to *Protopalythoa*. In certain relatively well-studied areas, such as Bermuda–Caribbean, it should be possible to allocate nominate species to the correct genus (though it may be unclear how many actual species are involved). It is symptomatic of the present state of zoanthid taxonomy that even this has got confused (see below). However, *Gemmaria fusca* Duerden, 1898; *Pr. grandis* Verrill, 1900; and *Pa. grandiflora* Verrill, 1900 (despite the original generic attribution) are referable to *Protopalythoa*. These two Verrill species are possibly synonymous with *Pr. variabilis* and *Pr. fusca* respectively, of which Duerden provided very full descriptions. Proper revision of all West Indian zoanthids, aided by the use of allozymes or DNA, is urgently required.

Confusion involving type species

In Sterrer's (1986) important *Marine Fauna and Flora of Bermuda*, zoanthid descriptions include species of both *Palythoa* and *Protopalythoa* (Cairns *et al.* 1986), but *Palythoa* is used *sensu lato* and some names are confused. These points are important because two of the species are

types of genera and two are discussed later in this paper. We refer *Palythoa variabilis* to *Protopalythoa* and consider that their *Pa. mammillosa* (Ellis & Solander, 1786) is also a *Protopalythoa* (*Pr. grandiflora* (see their pl. 57), which as noted above is possibly *Pr. fusca*). The valid name for *Pa. caribaea* Duchassaing & Michelotti, 1864 is *Pa. caribaeorum* (as in Ryland 1992). Andres (1883) appears responsible for this particular confusion by indicating that *Pa. caribaeorum* was a synonym of *Hughaea caribaeorum* Duchassaing, 1850. This is obviously wrong: *Hughaea* Lamouroux, 1821 is an actinian or corallimorph. Although Duchassaing's descriptions are brief in the extreme, the preamble shows that he was perfectly aware of the difference between actinians/corallimorphs in which buds ('les bourgeons qui se produisent à leur surface') separate, and zoanthids in which the buds form colonies. The diagnosis of *H. caribaeorum* starts '*Corpore cylindrico...*' ('With the body [singular] cylindrical...'). Duchassaing's (1850) diagnoses of zoanthids, on the other hand, start '*Corporibus...*' ('With the bodies [plural]...'). Also, Duchassaing and Michelotti's (1860, 1861) account of *Pa. caribaeorum* is headed '*Palythoa caribaeorum* nobis [to us – not *mihi*, to me]. Though unillustrated, the description obviously refers to a colony. When Duchassaing and Michelotti later (1864, 1866, with pl. VI, fig. 11) apparently rename the species *Pa. caribaea* it seems simply to be a spelling change, either inadvertent or by design, and nomenclaturally invalid; there is nothing at all to suggest (cf. Andres 1883) a re-naming because *caribaeorum* in *Palythoa* was in some way invalidated by *caribaeorum* in *Hughaea*.

That *Protopalythoa grandiflora* (or *fusca*) has been equated with *Palythoa mammillosa* by Cairns *et al.* (1986) requires discussion. We believe there has been a misinterpretation of Ellis and Solander's figure 4 (1786, pl. 1). It must be understood that *Pa. mammillosa* occurs in nodules 3–8 cm across (see fig. 67 in Ryland (1992): these may be convex, with the tallest polyps in the centre, and separated from each other by valleys; or they may abut contiguous nodules, in which case the tallest polyps generally line the separating fissure. Ellis and Solander's pl. 1, fig. 4 shows a nodule edge that lined a fissure; the shading may exaggerate the degree of separation between the columns of the polyps (which, according to Duerden (1898), are separated in the contracted state for only the distal 4 mm or so). Verrill (1900), mentioned a thick coenenchyme (which accounts for his choice of *Palythoa* rather than *Protopalythoa*), but described the polyps as 15–20 mm high, and this is also well shown in Cairns *et al.* (1986, fig. 57).

Unfortunately, Ellis and Solander's (1786) specimen, originally in the Natural History Museum, London, has long since disappeared (Cornelius and Wells 1988) but the correctness of our interpretation of the figure is supported by the description (Ellis and Solander 1786: 179): 'Each mamilla, has a polyp within it, adhering to its base by twelve filaments [i.e. perfect septa, see their pl. 1, fig. 5], which answer to as many tentacula when they extend themselves.' The identity of Ellis and Solander's species was fully discussed by Duerden (1898), who noted 36–40 tentacles. Low numbers of perfect septa or tentacles (presumably somewhat underestimated by Ellis and Solander) are, as noted above, diagnostic for *Palythoa s. str.* and not for *Protopalythoa*. Verrill (1900) gave 52 or more for *Pa. grandiflora*. The combination of characters makes clear that *grandiflora* is best referred to *Protopalythoa* and that, whatever senior synonyms it may have, *Pa. mammillosa* is not one of them.

Protopalythoa *in the tropical west Pacific*

In the Great Barrier Reef (GBR), Coral Sea area, and subtropical coastal Australia, following Ryland and Muirhead (1993) and the genetic studies of Burnett *et al.* (1997), the following nominate species are all referable to *Protopalythoa*: *G. mutuki* Haddon and Shackleton, 1891*b*; *G. willeyi* Hill and Whitelegge, 1898; *G. arenacea* Wilsmore, 1909; *Palythoa yongei* Carlgren, 1937; *Pa. australiensis* Carlgren, 1950; *Pa. heideri* Carlgren, 1954; *Pa. singaporensis* Pax and Müller, 1956; and, from Hawaii, *Pa. psammophilia* Walsh and Bowers, 1971; *Pa. toxica* Walsh and Bowers, 1971; and *Zoanthus vestitus* Verrill, 1928 (see Walsh and Bowers 1971). The solitary *Triga philippinesis* Gray, 1867, though tentatively referred to *Gemmaria* by McMurrich (1889), seems more likely to have been an actinian, but Gray's two-line diagnosis is insufficient even to determine the order with any certainty. *Gemmaria macmurrichi* Haddon & Shackleton, 1891*b*, seems sufficiently different possibly to justify removal to a new genus but the original description first requires amplification from additional material. These species of *Protopalythoa* are discussed later in the paper: the problem is how to separate them. The use of enzyme electrophoresis (Burnett *et al.* 1997) has demonstrated the unreliability of conventional taxonomic methods: whereas genetic methods commonly reveal unexpected diversity, in *Protopalythoa* (and in *Palythoa* and *Zoanthus*) they show the opposite (Burnett *et al.* 1994, 1995, 1997)—species have been wantonly erected on nothing more than unevaluated phenotypes. In this paper we explore the quantitative use of meristic characters in trying to develop reliable criteria on which to separate species. Meanwhile, we are investigating in detail the use of nematocyst capsule size as a metric character in species level taxonomy (Ryland *et al.* (in press) data on *Acrozoanthus australiae* Saville-Kent, 1893), but we have utilised several smaller data sets from *Protopalythoa* in the present study.

Other nominate species of *Protopalythoa* have been described from various parts of the world, e.g. *Gemmaria canariensis* Haddon & Duerden, 1898, from the Canary Islands and Madeira (Wirtz 1995), and *G. aspera* Carlgren,

1900, *G. multisulcata* Carlgren, 1900 and *G. tubulifera* Carlgren, 1900 from Zanzibar. In view of the ocean-wide dispersal potential of zoanthella larvae (Scheltema 1971, 1989; Ryland *et al.* 2000) there seems little reason to assume that every newly discovered population will necessarily represent a new species. Probably only the use of genetic methods, so successfully applied by Burnett *et al.* (1997), will settle identities over wide geographic areas.

Material and methods

Numerous collections of *Protopalythoa* were made by JSR in Fiji, the Great Barrier Reef, and shores in southern Queensland, northern New South Wales, and Rottnest I., Western Australia (for *Pr. heideri*) between 1978 and 1995; Torres Strait was visited in 1994. In most cases colour photographs were taken *in situ* to record the site and specimen habitus and, subsequently, under water in the laboratory for disk characters of expanded polyps. The latter facilitate making measurements used in the descriptions. Preservation was in 4% seawater formaldehyde or Bouin's fluid, and storage after rinsing with water was in 70% ethanol. Because *Protopalythoa* polyps incorporate sand, material for sectioning was desilicified in 20% hydrogen fluoride for 24 h and decalcified in a solution comprising equal parts of formaldehyde and saturated formic acid made up 1:9 with water. Polyps were wax embedded, sectioned at 8 μm, and stained with Mallory's triple stain or Masson's trichrome. Representative sections (3–12 mm across) were photographed using a Wild Makroskop.

After dabbing dry, polyp diameter and height were measured with dial vernier calipers, and volume determined by accurately measuring displaced liquid in a finely graduated syringe. The polyps were rigid on account of the combined effects of fixation and the presence of sand particles in the mesogloea. Macrosepta were thus clearly displayed in hand-cut sections across the column, and were counted under a stereomicroscope in the cut surface adjacent to the oral disk. A count of tentacles or—in closed polyps—capitular ridges provided confirmation of septal counts.

To obtain nematocysts, minute amounts of tissue were removed from the septal filaments and from the tips and bases of the tentacles exposed in hand-cut transverse or longitudinal sections, using extra-fine jewellers' forceps. The extraction of nematocyst samples from the different tissues, performed on polyps immersed in water, was carried out with care to avoid cross-contamination between tissue types. The tissue was digested for 2–3 min in a few drops of 2% aqueous $KMnO_4$ on a microscope slide and excess fluid absorbed with a strip of filter paper. A single drop of glycerol was added to the preparation, which was then macerated with the forceps under ×25 magnification. The fragmented cells were spread by light, even pressure on the cover slip, which was then ringed with clear nail varnish.

Usually 100 capsule measurements were made using an Olympus BH2 microscope with bright-field (or, occasionally, Nomarski interference) illumination, ×40 objectives and ×10 oculars. The use of immersion objectives was found unnecessary for making measurements and slowed down the operation. A monochrome video camera attached via the strongest available (×6.7) photo-ocular fed images to a dedicated image-analysis computer; measurements were then made on-screen. Only capsules lying wholly in the focal plane were measured; capsules oblique to the focal plane, being foreshortened, lead to underestimates of length. We have preferred to use mainly the length measurements as widths tend to have a much higher coefficient of variation. Statistical analysis took place in Excel 2000, or in BIOMstat 3.2 (Sokal and Rohlf 1995; Rohlf and Slice 1996), with normality tested by the Kolmogorov–Smirnov test (Sokal and Rohlf 1995) or the more rigorous test of d'Agostino and Pearson (Zar 1996)—both programmed into spreadsheets.

We have used Fijian spelling for place names in Viti Levu. Preserved specimens and microscope slides of sections have been placed in the Natural History Museum, London (NHM), the Queensland Museum, Brisbane (QM) and Australian Museum, Sydney (AM) and author's private collection, Swansea (JSR).

Results of analysis of morphometric characters to achieve initial separation of species

Size and number of septa

Burnett *et al.* (1997) established that only two species of *Protopalythoa* were widespread throughout the GBR and Torres Strait. One of these was identified as *Pr. mutuki*. The other had smaller polyps but was supposedly distinguished mainly by being subtidal in distribution (an attribute which we find to be incorrect). We compared the column diameter of representative polyps from the Fijian and GBR material with their number of perfect septa (Table 1, Fig. 3). We also included *Pr. heideri* and a somewhat different looking

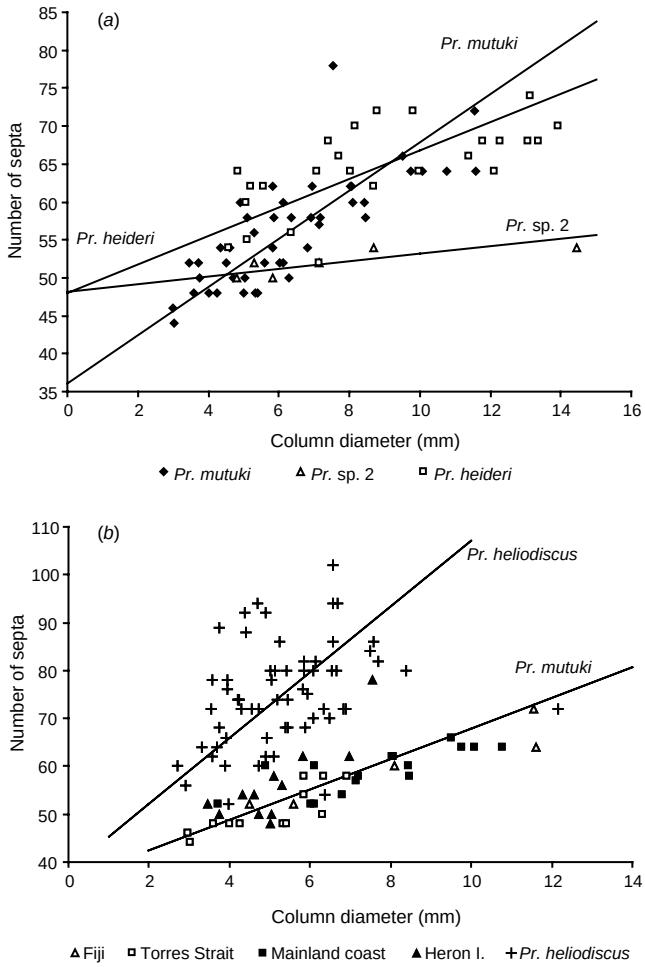

Fig. 3. Relationships between column diameter and numbers of septa. *A*, Data for *Protopalythoa mutuki*, from Fijian and Australian localities, compared with species 2 (JSR sample #136) from Heron I. and *Pr. heideri* from Rottnest I. *B*, Data for *Pr. heliodiscus* and *Pr. mutuki*. Regressions are Model II (Sokal and Rohlf 1995) and fitted lines (see Table 1) are Ricker's (1973) geometric mean.

sample from Heron I. (Capricorn Group, GBR). It was apparent that polyps within samples were linearly related with respect to the variables, generally with a high correlation ($P < 0.01$, Table 1 upper). The samples separated into four groupings: *Pr. mutuki*, *Pr. heideri*, *Protopalythoa* sp. 1 (now *heliodiscus*, sp. nov.) and *Pr.* sp. 2 from Heron I. However, probably because some lots were small and lacked large polyps, certain within-species samples were anomalous and distinguished in ANCOVA by significantly different means or slopes (Table 1, lower). Thus, Australian plus Fijian collections of *Pr. mutuki* were homogeneous only if samples from Heron I. (distinguished as form 1) were excluded; also, certain within-species samples of *Pr. heliodiscus*, sp. nov. include aberrant points. While *Pr. mutuki*, *Pr. heideri* and *Protopalythoa* sp. 2 seem rather similar, with large polyps (some >8 mm diameter, >0.5 mL) and relatively few (<35) macrosepta, *Pr. heliodiscus*, sp. nov. with small polyps (<8 mm diameter, <0.4 mL) and many (often >35) macrosepta, is hugely different ($P \approx 2.5 \times 10^{-6}$ or less).

ANCOVA shows very little overlap between *Pr. heliodiscus*, sp. nov. and the rest, so separation is clear on the scale of samples though it does not necessarily permit the identification of individual polyps. *Pr. mutuki* is also well separated from both *Pr. heideri* and *Pr.* sp. 2 (*P* for both means and slopes <0.006) though differences at a similar level within species (e.g. for the rest of *Pr. mutuki v.* its Heron I. form 1) caution against placing too much reliance on this as a sole criterion for species separation. (Form 1 is the abundant *Protopalythoa* on the reef flats at Heron I. and has been identified genetically as *Pr. mutuki* (Burnett *et al.* 1997).) At the time of collection, *Pr.* sp. 2 from Heron I. was noted as appearing distinct from *Pr. mutuki* form 1; elsewhere, prior to the genetic studies (Burnett *et al.* 1997), the similar looking *Pr. mutuki* and *Protopalythoa* sp. 1 had not been differentiated. As the regressions are based on two manifestations of polyp size, column diameter (hence circumference) and number of septa, neither being independent, they conform to Model II (Sokal and Rohlf 1995). The best descriptive relationship to characterise the species, therefore, is given by Ricker's (1973) geometric mean regression, see Table 1.

With the species separated it was possible within them to examine general morphology and nematocysts, both of which provided further diagnostic characters (see species' descriptions, and Tables 2–3). Then, with comprehensive descriptions available, we were able to establish that while *Pr. mutuki* had several synonyms (see Systematic account) the other species, now *Pr. heliodiscus*, sp. nov., was undescribed.

Cnidome and nematocyst capsule size

Only *Protopalythoa heliodiscus* sp. nov. and *Pr. mutuki* are considered in detail. Three types of nematocyst were studied, large holotrichs, basitrichs, and *p*-mastigophores, collected (when present) from the tentacles and septal filaments. The first, and remarkable, result was that whereas—as befits a carnivorous hexacoral (Van-Praët 1985)—basitrichs were abundant in the septal filaments of *Pr. mutuki*, they were completely absent from both filaments and tentacles of *Pr. heliodiscus*, sp. nov. Otherwise the occurrences of nematocyst types were broadly consistent between the species and the results address capsule sizes.

Holotrichs were usually infrequent in the tentacles, and sample sizes are small. Holotrich capsules of *Pr. mutuki* were longer than those of *Pr. heliodiscus*, sp. nov. (mean ≈ 45 μm, *v.* ≈ 32 μm; Fig. 4*B*, with details in Tables 2–3 in the species' descriptions). Holotrichs were much commoner in the

Table 1. Summary statistics for the 'Number of septa *v.* column diameter' relationship (Fig. 3)

Data shown in the upper part of the table are sample size *n*, correlation coefficient *r* and its probability *P*, standard regression *y*-axis intercept *a*, slope *b*, the means $\bar{x}$ and $\bar{y}$, and the geometric mean regression (Ricker 1973) equations used to calculate the lines shown in Fig. 3. Results from ANCOVA shown in the lower part of the table are combined samples size Σn_i, common slope, values of *F*, and their probabilities.

Species	*n*	*r*	*P*	*a*	*b*	$\bar{x}$	$\bar{y}$	Geometric regression
mutuki	45	0.7826	<<0.01	40.42	2.49	6.31	56.16	$y = 36.05 + 3.19x$
heideri	25	0.6604	<<0.01	53.56	1.24	8.83	64.52	$y = 47.93 + 1.88x$
Pr. sp. 2	6	0.7781	n.s.	49.00	0.39	7.71	52.00	$y = 48.15 + 0.50x$
heliodiscus	61	0.4575	<0.01	63.72	2.13	5.34	75.08	$y = 38.50 + 6.85x$

ANCOVA	Σn_i	Common slope	*F* (means)	*F* (slopes)	*P* (means)	*P* (slopes)
mutuki (6 samples, excluding Heron I. form 1)	33	2.25	1.74	1.14	0.1935	0.3357
mutuki (6 samples) *v.* Heron I. (form 1)	45	2.78	9.43	11.49	0.0037	0.0016
mutuki v. heideri	70	1.87	8.09	8.78	0.0059	0.0042
mutuki v. Pr. sp. 2	51	2.01	11.00	11.98	0.0017	0.0012
form 1 *v. Pr.* sp. 2	18	1.44	4.60	21.30	0.0487	0.0004
heideri v. Pr. sp. 2	31	1.05	34.68	2.16	2.47×10^{-6}	0.1535
heliodiscus (5 geographic samples)	61	2.57	5.78	1.69	0.0006	0.1669
heliodiscus v. mutuki	106	2.35	159.99	0.17	1.08×10^{-22}	0.6823
heliodiscus v. heideri	86	1.59	36.14	0.86	4.73×10^{-8}	0.3556
heliodiscus v. Pr. sp. 2	67	1.59	34.93	1.38	1.44×10^{-7}	0.2445

filaments of both species, those of *Pr. mutuki* again being much the longer (mean ≈ 52 μm *v.* 39 μm; Fig. 4*A,B*). Some samples from each species, and all the overall totals, were non-normally distributed (e.g. obviously skewed but not in any consistent direction), as in Fig. 4*A*. Under such circumstances medians have been included in Tables 2–3 and, since a parametric comparison of means is inappropriate, overlapping distributions can be compared using the Kolmogorov–Smirnov 2-sample test (Sokal and Rohlf 1995). The lengths of *p*-mastigophores from filaments were similar in the two species (≈23 μm *v.* ≈26 μm) but comparisons are obscured by the presence of an additional, larger type (p_2) in

Table 2. Nematocyst capsule lengths (μm) for samples of *Protopalythoa mutuki* and *Pr.* sp. 2 (Heron I.)

Range is the statistic most commonly given in taxonomic descriptions. K^2 is the d'Agostino and Pearson statistic for normality (based on skewness and kurtosis) and is compared with critical values of χ^2 for 2 degrees of freedom. Preferred sample size was ~100; lower numbers indicate the relative rarity of any particular nematocyst type.

Locality	*n*	Mean ± s.d.	Median	Range	Departure from normality	
					K^2	*P*
Holotrichs from tentacles						
Mabuiag, Torres St	7	40.04 ± 3.98	38.63	34.66–44.86	–	–
Mabuiag (2)	10	43.43 ± 2.96	44.10	37.99–46.90	0.81	n.s.
Kissing Point, Qld	15	46.94 ± 5.73	44.88	39.75–62.50	13.66	<0.001
Korotogo reef, Fiji	4	52.38 ± 1.57	52.27	50.84–54.15	–	–
TOTALS	36	45.23 ± 5.63	44.63	34.66–62.50	7.22	≤0.05
Holotrichs from filaments						
Mabuiag (1)	103	49.60 ± 2.77	49.69	41.55–58.27	6.11	n.s.
Mabuiag (2)	100	55.89 ± 5.65	57.04	35.28–70.03	29.19	<<0.001
Kissing Point	103	55.99 ± 4.10	56.51	45.41–71.31	12.54	<0.005
Caloundra	100	50.01 ± 2.05	49.80	45.83–55.47	5.65	n.s.
Korotogo reef	99	49.02 ± 2.63	48.85	43.27–54.59	0.94	n.s.
TOTALS	607	52.51 ± 4.93	51.25	35.28–71.31	21.53	<<0.001
Protopalythoa sp. 2						
Heron I.	22	69.03 ± 6.46	67.12	60.03–81.88	1.79	n.s.
P-mastigophores from filaments						
Mabuiag (1)	49	19.66 ± 1.45	19.59	16.53–23.35	0.45	n.s.
Mabuiag (2)	52	22.40 ± 1.58	22.49	18.70–25.40	0.65	n.s.
Kissing Point	52	22.92 ± 1.56	23.05	18.56–25.66	3.26	n.s.
Caloundra	100	28.22 ± 3.63	26.97	22.90–38.57	13.90	<0.001
Korotogo reef, p_1	104	20.90 ± 1.81	20.79	16.58–27.29	31.03	<<0.001
Korotogo reef, p_2	96	42.95 ± 3.07	43.02	35.96–50.65	0.05	n.s.
TOTALS (< 35 μm)	253	24.28 ± 4.24	23.62	16.53–34.58	59.57	<<0.001
Protopalythoa sp. 2						
Heron I.	100	22.70 ± 1.92	22.47	17.23–28.14	0.75	n.s.
Basitrichs from tentacles						
Mabuiag (1)	51	22.92 ± 1.72	22.78	9.82–28.28	4.73	n.s.
Mabuiag (2)	51	21.86 ± 1.37	21.94	7.31–24.79	4.49	n.s.
Kissing Point	55	24.39 ± 1.47	24.24	7.55–29.21	14.09	<0.001
Caloundra	80	22.73 ± 1.91	22.49	10.48–29.80	17.64	<0.001
TOTALS	237	22.97 ± 1.87	22.95	17.47–29.80	11.21	<0.005
Protopalythoa sp. 2						
Heron I.	54	23.03 ± 1.55	23.01	20.12–27.51	2.40	n.s.
Basitrichs from filaments						
Mabuiag (1)	102	43.21 ± 2.78	43.30	35.83–52.40	2.63	n.s.
Mabuiag (2)	100	48.72 ± 2.81	48.74	15.10–55.99	3.08	n.s.
Kissing Point	55	49.68 ± 3.14	49.19	13.90–58.82	6.14	<0.025
Caloundra	100	44.58 ± 2.86	44.43	39.13–51.36	3.25	n.s.
Korotogo, Fiji	100	41.98 ± 2.74	41.88	35.49–47.57	1.89	n.s.
TOTALS	457	45.23 ± 4.05	44.80	35.49–58.82	7.36	<0.05
Protopalythoa sp. 2						
Heron I.	102	53.74 ± 3.44	53.63	45.40–61.96	0.05	n.s.

some samples of *Pr. mutuki*, most notably in that from Korotogo reef, Viti Levu, where the two types formed non-overlapping populations with means $p_1 \approx 21$ and $p_2 \approx 43$ μm (Table 2). The holotrich capsule lengths, however, provide a very reliable separation of the two species (Fig. 4*B*). The holotrichs in the filaments of one collection from Heron I. (Fig. 4*B*, Table 2) seem too large to come from *Pr. mutuki*. It seems likely that this sample represents a distinct species, henceforward referred to as *Protopalythoa* sp. 2.

Systematic account

The basic morphology of zoanthid polyps has already been described (Fig. 1 and associated text) and the descriptions that follow should be self explanatory. However, zoanthid septa display some distinctive characteristics apparently not found in actinians (see Van-Praët 1985). The actinopharynx is an involution of the body wall, so that it is lined with ectoderm. It is apparently this ectoderm that continues down the mid-column region of perfect septa as a wide, highly convoluted band, which Haddon and Shackleton (1891*a*) termed 'reflected ectoderm' (Figs 8*F,G*, 10*B,E*). The reflected ectoderm narrows basally into the filament, which, in transverse section, has at first the shape of an arrow-head (Fig. 10*B*) but becomes club-shaped towards the base (Fig. 10*C*). There is often a vertical canal in the base of each septum (Fig. 6*E*), and occasionally others centripetal to it, while there may be canals, sinuses or lacunae in the mesogloea. Sometimes, though not in *Protopalythoa* (or, at least, the species included here), there is an encircling sinus between the mesogloea and the endoderm, termed the 'ring canal' from its appearance in transverse sections.

Family **SPHENOPIDAE** Hertwig

Amended diagnosis

Brachycnemic, sand-incorporating zoanthids; undivided mesogloeal sphincter; mesogloea with lacunae and cell-islets; cnidome lacking *b*-mastigophores; larva a zoanthella.

Genus ***Protopalythoa*** Verrill

Type species: *Gemmaria variabilis* Duerden (1898) (Caribbean: Jamaica).

Table 3. Nematocyst capsule lengths (μm) in samples of *Protopalythoa heliodiscus*

Range is the statistic most commonly given in taxonomic descriptions. K^2 is the d'Agostino & Pearson statistic for normality and is compared with critical values of χ^2 for 2 degrees of freedom. Preferred sample size was ~100; lower numbers indicate the relative rarity of any particular nematocyst type. There are no basitrichs in *Pr. heliodiscus*.

Locality	*n*	Mean ± s.d.	Median	Range	Departure from normality	
					K^2	*P*
Holotrichs from tentacles						
Low Is	30	28.56 ± 3.97	27.72	23.64–39.38	15.09	<0.025
Fitzroy I.	98	29.86 ± 2.62	29.42	23.49–37.41	6.50	<0.05
Orpheus I.	101	31.66 ± 2.43	31.83	24.77–38.92	6.22	<0.025
Makuluva Pass, Fiji	100	35.54 ± 3.42	36.05	28.45–44.78	1.22	n.s.
Toberua Pass, Fiji	17	35.23 ± 3.02	36.38	30.12–40.39	1.29	n.s.
Yarawa reef, Fiji (2)	10	26.62 ± 1.54	26.13	24.72–29.53	2.11	n.s.
TOTALS	356	32.02 ± 3.96	31.69	23.49–44.78	10.24	<0.01
Holotrichs from filaments						
Goode I.	50	34.90 ± 5.98	34.82	27.18–46.37	2.47	n.s.
Low Is	30	41.42 ± 4.62	42.23	28.24–49.34	5.53	n..s.
Fitzroy I.	95	42.63 ± 5.04	42.84	32.94–54.18	2.00	n.s.
Orpheus I.	78	40.34 ± 4.13	41.04	27.19–47.89	13.94	<0.001
Makuluva Pass	77	41.55 ± 4.08	41.60	30.48–48.99	2.79	n.s.
Toberua Pass	100	40.91 ± 4.92	41.23	28.81–50.72	2.17	n.s.
Yarawa reef (1)	90	34.65 ± 5.01	34.47	24.06–44.79	1.95	n.s.
Yarawa reef (2)	100	37.89 ± 4.04	37.48	27.18–49.61	0.78	n.s.
TOTALS	620	39.33 ± 5.49	39.85	24.06–54.18	9.67	<0.005
P-mastigophores from filaments						
Low Is	11	27.63 ± 2.12	26.63	24.66–30.81	1.79	n.s.
Fitzroy I.	53	27.97 ± 2.45	27.53	21.17–36.41	17.37	<0.001
Orpheus I.	102	24.96 ± 2.40	25.25	17.58–29.76	12.17	<0.005
Makuluva Pass	103	27.79 ± 1.89	27.99	22.79–31.49	2.34	n.s.
Toberua Pass	100	23.64 ± 2.10	23.50	18.61–28.26	0.60	n.s.
Yarawa reef (1)	100	27.41 ± 1.65	27.41	23.47–32.11	1.32	n.s.
Yarawa reef (2)	100	22.51 ± 1.10	22.53	18.99–25.68	2.74	n.s.
TOTALS	569	25.57 ± 2.87	25.74	17.58–36.41	3.27	n.s.

Diagnosis

Polyps solitary or connected by thin basal coenosarc, often in the form of short stolons; perfect septa numerous (>20).

Protopalythoa mutuki (Haddon & Shackleton)

(Figs 5–6; Table 2)

Gemmaria mutuki Haddon & Shackleton, 1891*b*: 689; 1898: 405.
Gemmaria willeyi Hill & Whitelegge, 1898: 387.
Gemmaria variabilis Duerd. – Heider 1899: 280 (see Pax and Müller 1956).
Gemmaria arenacea Wilsmore, 1909: 323.
Palythoa (*Gemmaria*) *mutuki* (Haddon & Shackleton). – Carlgren 1937: 193.
Palythoa yongei Carlgren, 1937: 198.
Palythoa australiensis Carlgren, 1950: 144.
Protopalythoa australiensis. – Muirhead & Ryland 1984: 32, fig. 16.11; Bennett 1987: 178, figs top and bottom left; Ryland & Muirhead 1993: 56, fig. 17.9.

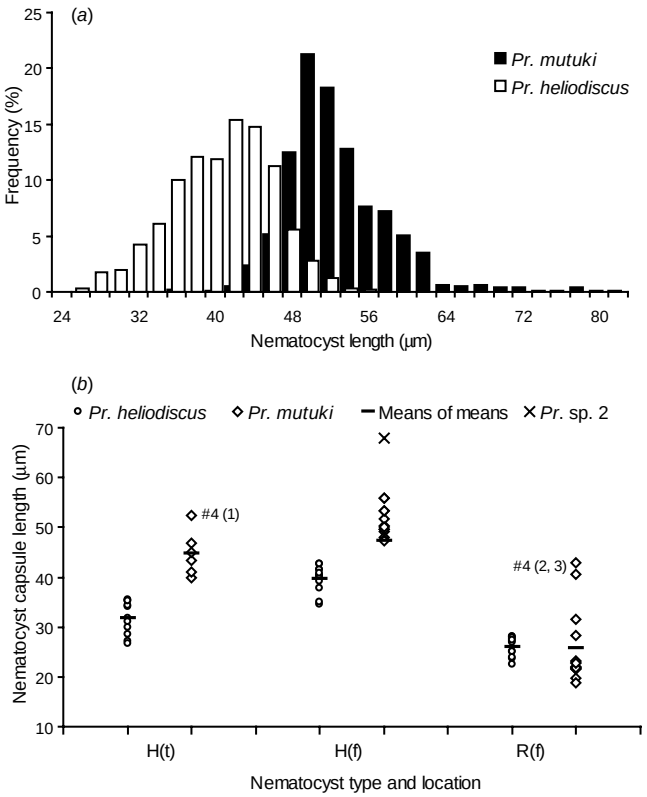

Fig. 4. Nematocyst capsule lengths in *Protopalythoa heliodiscus* and *Pr. mutuki*. *A*, Holotrichs from filaments. Both distributions are non-normal but can be compared using the Kolmogorov–Smirnov 2-sample test. *B*, Means of all samples (generally for $n = 100$, in a few cases 50; see Fig. 3 for illustrations of types), together with the means of the sample means (used because of unequal sample sizes): holotrichs in tentacles, $H_{(t)}$; holotrichs in filaments, $H_{(f)}$; and *p*-mastigophores in filaments, $R_{(f)}$. For both sets of holotrichs the ranges of the sample means in the two species do not overlap. Also shown is the sample mean for holotrichs from filaments (there were none in the tentacles) for Heron I. species 2 (JSR sample #136).

Palythoa singaporensis Pax & Müller, 1956: 233, footnote, pro *Gemmaria variabilis* Heider, non-Duerden 1898; Pax & Müller 1957: 21.
Protopalythoa. – Ryland & Muirhead 1993: [Coloured] pl. 2.
Protopalythoa mutuki. – Burnett *et al.* 1997.

Material examined

Holotype. Torres Strait, Mabuiag, coll. 6.x.1888 (NHM 1891.10.1.8).

Other material examined. **Australia, Queensland:** Torres Strait, Mabuiag (type locality), 25.iii.1994, coll. J. S. R. (JSR #528); Townsville, Kissing Point, 10.iv.1992 (JSR #321), 10.iii.1994 (JSR #529–530), coll. J. S. R.; Magnetic I., Cockle Bay, 18.vii.82, coll. J. S. R. (NHM 2002.167); Masthead I., Capricorn Group, coll. J. P. Hill (NHM 1910.6.4.2, 1904) (Type of *Gemmaria arenacea*); Heron I., 10.xi.1985, coll. J. S. R.; Caloundra, 18.viii.1982, coll. J. S. R. (QM GL1581) (NHM 2002.164); Cape Woora, 17.vii.1982, coll. J. S. R. (NHM 2002.178), (QM M318685). **New South Wales:** Hastings Point, 28.viii.1985, coll. J. S. R. (NHM 2002.177) (QM G319683); Sandon Bluffs, v.1985, coll. I. Bennett (QM G319684); Diggers Camp, 29.viii.1985, coll. J. S. R. (NHM 2002.166); Nambucca Heads (Type of *Pa. australiensis*), 28.viii.1946, (QM G15226). **Fiji, Viti Levu:** Nukubuco reef, 6.v.1982, coll. A. Muirhead (NHM 2002.162); Deuba, 9.ix.1979, coll. J. S. R. (NHM 2002.159), 1.vi.1980, coll. J. S. R. (NHM 2002.173); Tagaqe fringing reef, 16.vi.1980, coll. J. S. R.; Malevu fringing reef, 22.v.1982, coll. A. Muirhead; Korotogo fringing Reef, 7.ix.1979, coll. J. S. R. (NHM 2002.160) (QM G319211), 6.x.1979, coll. J. S. R. (NHM 2002.158); (no other data) (NHM 2002.175) (QM G 319677). **Tuvalu:** Funafuti atoll (AM G3146) (Type of *Gemmaria willeyi*), no date stated but coll. by C. Hedley between 21st May and very early August, 1896, while he was on the atoll (Etheridge 1896).

Diagnosis

Generally intertidal *Protopalythoa* with large zooids (15–20 × 10 mm) and about 35 capitular ridges or tentacles per cycle; tentacle length about half expanded disk diameter. Microcnemes in transverse section often bulbous, with a conspicuous basal canal. Septal filaments with abundant basitrichs, and the holotrichs up to ~80 µm in length. Zooxanthellae not transmitted via the oocytes.

External appearance

Colony extensive (Fig. 5*A*); polyps appearing crowded together (Fig. 5*B–C*) though sometimes separated by spaces (which are often occupied by *Zoanthus coppingeri* Haddon and Shackleton, 1891*b*: see Fig. 5*E–F*). Polyps joined basally but their closeness and flaring columns obscuring the bases, very variable in size; about 35 per 25 cm^2 of substratum, apparently occupying most of the available space. Polyps stumpily cylindrical, gradually widening from a basal diameter of 8–10 mm; 14–21 mm high, sometimes with transverse corrugations; the capitulum smoothly rounded, 10–11 mm in diameter, dome-like, topped by a small, slightly sunken opening; capitular ridges variably distinct, radiating from this opening; in other samples the opening larger, rounded or flattened, showing the mouth in the centre of the disk below. Column and ridges heavily sanded, colour depending on locality; or lightly sanded,

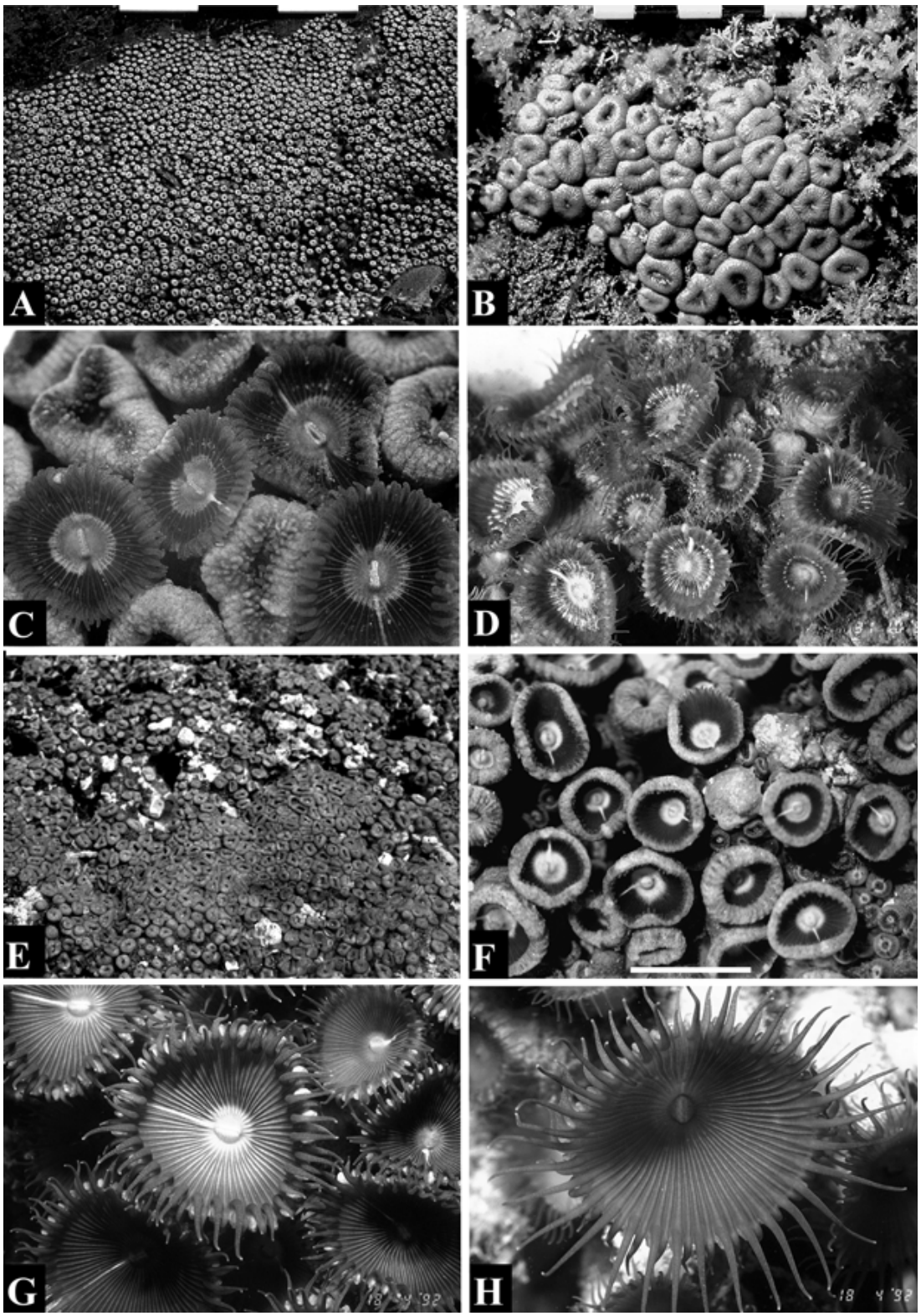

Fig. 5. *Protopalythoa mutuki*. *A*, In an intertidal pool, Hastings Point, NSW, 16.ii.1972; scale at top = 3 × 5 cm. *B*, On intertidal rock, Cape Ferguson, Qld., 17.vii.1982; scale at top = 5 × 1 cm. *C*, Open polyps, C. Ferguson. *D*, Open polyps, intertidal flat, Yule Point Reef, Qld., 19.viii.82. *E*, Seaward edge of reef, Korotogo, Viti Levu, Fiji, 6.x.1979. *F*, Polyps in close-up, as *E*; note interspersed *Zoanthus coppingeri*. *G*, Polyps from the shore, Kissing Point, Townsville, 18.iv.92. *H*, Single polyp, Kissing Point.

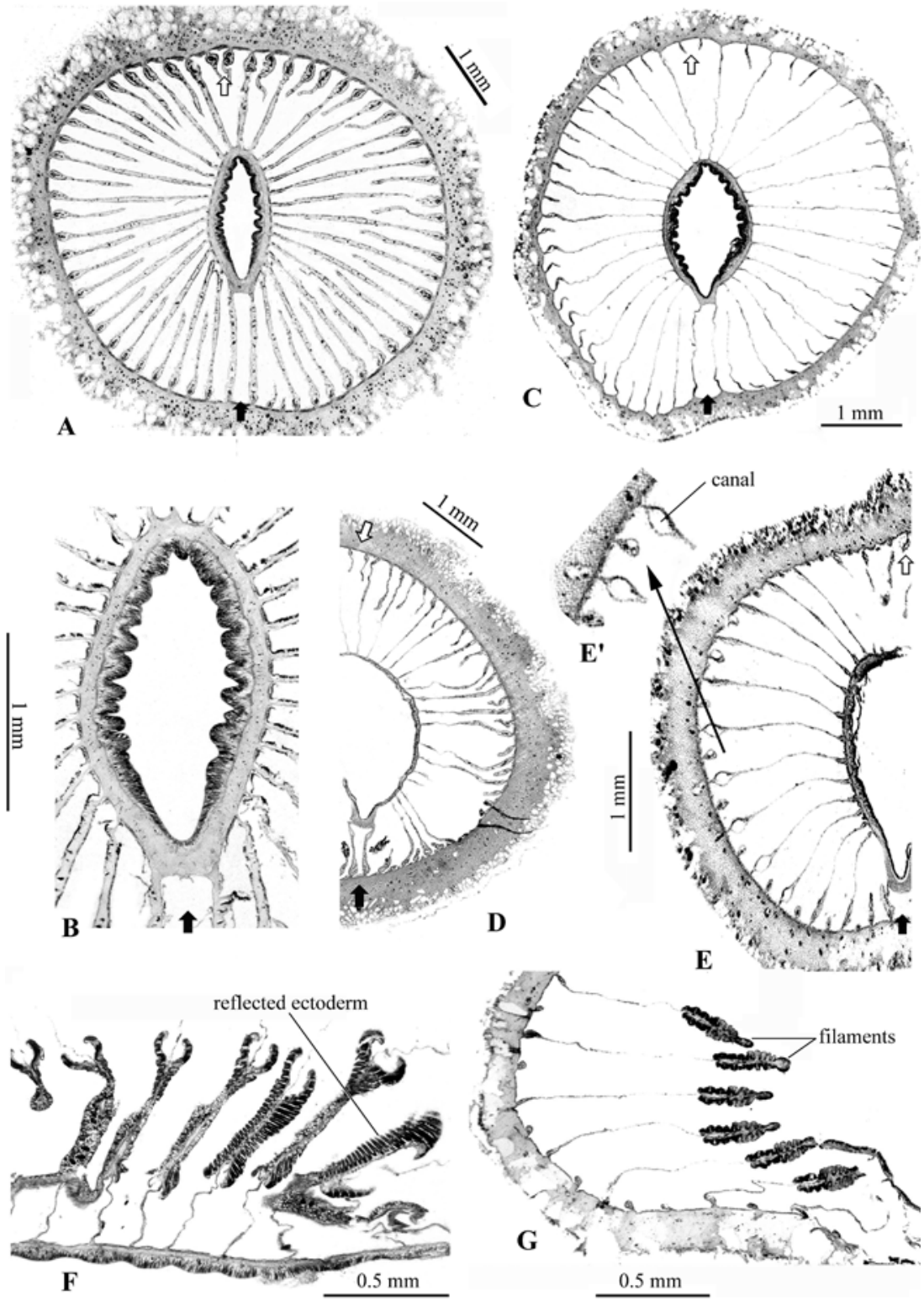

Fig. 6. *Protopalythoa mutuki*. Photomicrographs of transverse sections. *A*, Upper part of actinopharynx, Hastings Point, NSW, 28.viii.1985. *B*, Same polyp, actinopharynx, slightly lower. *C*, Mid-actinopharynx, Heron I., 8.xi.1985. *D*, Lower part of actinopharynx, Cape Woora (Cape Ferguson), 17.vii.1982. *E, E'*, Lower part of actinopharynx, Cockle Bay, Magnetic I., 18.vii.1982; note septal canals. *F*, Reflected ectoderm, almost below the actinopharynx, Deuba, Viti Levu, 1.vi.1980. *G*, Septal filaments, Nukubuco, Viti Levu, 6.v.1982. ➡ Ventral directives; ⇨ dorsal directives; see Fig. 1*A* for additional labelling.

rather smooth, without strong capitular ridges. Expanded disks variable in colour, often uniformly dark brown (with green fluorescence under water) or mainly dark or buff-brown; then often with pale radii (marking positions of septa), a bold white line in the ventral directive axis (Fig. 5*G*), white 'knobs' (inner ends of capitular ridges) between the exocoelic tentacles (Fig. 5*G*), with one or both of those marking the directive endocoels noticeably broader; or a paler central region, and/or a white or pale mouth, all with brown tentacles; or there may be a strong pattern, such as khaki background and tentacles, whitish-blue centre and white mouth (Fig. 5*D*). Disk size variable with degree of expansion but the largest disks in a colony 12.5–17 mm diameter. Tentacles up to almost one-half of expanded disk diameter (Fig. 5*H*).

Internal structure

In longitudinal sections (LS) zooids comprise a thick column, widening upwards, into which the capitulum is rolled (Fig. 1A), with the tentacles above the disk, often cut transversely; sphincter muscle well developed. Capitular ridges prominent; present in transverse sections (TS) above the oral disk as a ring of long, jagged, centrally-directed teeth; in LS appearing as vertical stripes between the two sides of the capitulum. In TS the tentacles are outside the ridges, often cut through their free extent; endoderm almost nil, ectoderm well developed, with abundant zooxanthellae and spirocysts, even at the tentacle bases, the spirocysts forming an almost unbroken layer distally. Columnar and capitular surfaces well separated in the contracted state, up to 80 septa forming 'boxes', undifferentiated, fairly thin, outer insertion triangular, with elongate canal centripetal to it; sometimes with lacunae. Zooxanthellae on inner and outer surfaces of the 'boxes', with a few scattered along the septa. Actinopharynx often large in sections, the ectoderm then thin and without ridges; sometimes smaller (more contracted) and the ectoderm then ridged; basitrichs present; siphonoglyph in TS a tapering U-shape supported by a thick H of mesogloea (Fig. 6*A–D*). At level of actinopharynx the septa lack the triangular base, the radial canal now separated from the base by a short narrow neck; then very thin. Above the reflected ectoderm the microcnemes quite long in TS, 10–30% of the radius; radial canal long in macro- and microcnemes, giving a double-walled appearance (Fig. 6*A*). Column mesogloea about 10% of radius, inner part with lacunae containing cells and zooxanthellae; similar lacunae also in centripetal part of perfect septa, without zooxanthellae, though these present along the septal ectoderm. Reflected ectoderm bands lateral to actinopharynx, long (in TS) or at each free end of incomplete septa (Fig. 6*F*). Centripetal margin clavate below the ectoderm bands, with rounded filament separated by grooves; widening abruptly at the column mesogloea, with 1–2 lacunae and oval radial canal; microcnemes shorter than the 'shaft' of macrocnemes, the canal more rounded (Fig. 6*E*,*E'*), or slender (Fig. 6*C*).

Cnidome

See Fig. 2 for types, Table 2 for measurements. Tentacles with few *p*-mastigophores and holotrichs but an abundance of banana-shaped, distally-tapering basitrichs. Septal filaments with abundant cigar-shaped basitrichs, holotrichs and *p*-mastigophores; the *p*-mastigophores sometimes with bimodal capsule length distribution (Korotogo sample, Table 2) but consistent shaft percentage length (mean ± s.d.: $p_1 = 43.2 \pm 3.8\%$, $p_2 = 41.9 \pm 3.5\%$).

Reproduction

In all the collections, gravid zooids have been found only once: Korotogo Reef, Fiji, 6.x.1979, with an abundance of oocytes 210–420 μm diameter. There is no evidence that zooxanthellae are transmitted via oocytes. Haddon and Shackleton (1891*b*) recorded ripe sperm in the one Torres Strait polyp (collected 6.x.1888) they sectioned; Hill and Whitelegge (1898) found small oocytes in material from Funafuti (collected some time between late May and early August, 1896).

Biology

All the material unquestionably referred to this species has been intertidal. Its long tentacles and abundant basitrichs are consistent with micro-carnivory as a major nutritional mode (see under *Pr. heliodiscus*, sp. nov.).

Distribution

From Torres Strait, along shores of tropical Queensland, with sporadic occurrences in southern Queensland and northern New South Wales (Fig. 7). The most southerly locality is

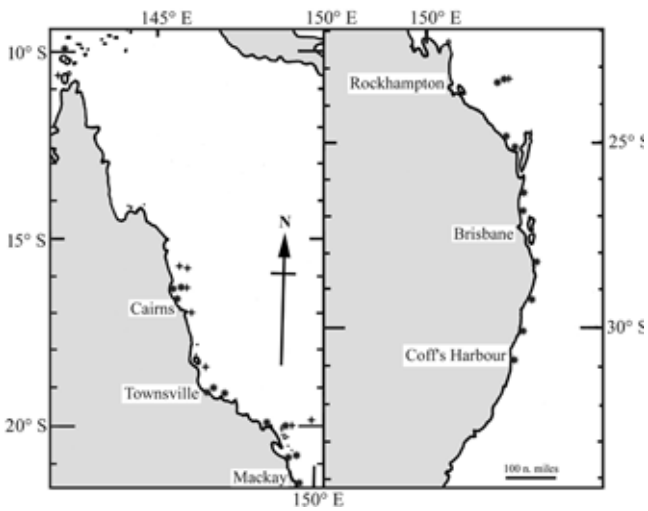

Fig. 7. The Australian distribution of *Protopalythoa mutuki* (✱) and *Pr. heliodiscus*, sp. nov. (✦).

Nambucca Heads, where it was found in 1946 (and described as *Palythoa australiensis* by Carlgren (1950)); it persisted here for some years (I. Bennett, pers. com.) but had disappeared by August 1985. Offshore, it is present on Low Is. (Carlgren 1937, as *Palythoa yongei*; Burnett *et al.* 1997) and on Masthead (as *Gemmaria arenacea* (Wilsmore, 1909)) and Heron I. reefs (xi.1985) in the Capricorn Group. It is probably the species present at Singapore and in Viet-Nam (as *Pa*. *singaporensis* (Pax and Müller, 1956, 1957)). In Fiji (records 1979–80) it is distributed (at least) from the Laucala Bay reefs, via the 'Coral Coast' (Ryland 1981) to Vuda Pt (near Nadi) (Fig. 8). In Tuvalu it was recorded from Funafuti as *Gemmaria willeyi* (Hill and Whitelegge, 1898). The notes on colour 'drawn by Mr. C. Hedley on the spot' seem most unlike any *Protopalythoa* and perhaps refer to the *Zoanthus* from the same locality.

Remarks

Samples from some collection sites displayed occasional anomalies. A single polyp from a Heron I. sample (JSR #140, polyp 9668) stands out in Fig. 3*B* as having an unusually high number of septa (78) for its diameter (7.55 mm). Polyps from Korotogo Reef (the only Fijian specimens examined) tended to have fewer nematocysts in both tentacles and filaments. They also included a wider range of types, including some bent and tapered basitrichs in the filaments, along with short-shafted (?)basitrichs and an unidentified type of cigar-shaped nematocyst. The *p*-mastigophores were present in the filaments as two totally separated populations, the larger kind

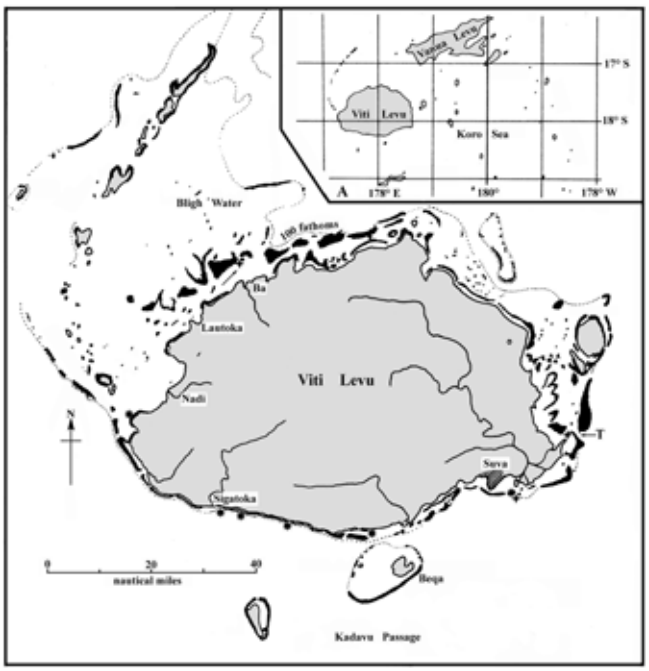

Fig. 8. The distribution of *Protopalythoa mutuki* (✱) and *Pr. heliodiscus*, sp. nov. (✦) around Fiji. T, type locality of *Pr. heliodiscus*.

(mean length ≈ 43 μm) either not represented in the other material or perhaps indicated by a tail (as at Caloundra) in the size distribution (Table 2). The mean sizes of holotrichs and basitrichs were slightly less than from other sites.

This is the common intertidal *Protopalythoa* in tropical and subtropical eastern Australia, the GBR and the South Pacific islands. In consequence, the same species has been collected and redescribed several times: an indication of how difficult it has been to provide recognisable descriptions of species. Polyp size may be variable but some are usually large, 15–20 × ~5 mm (volume 1 mL) with about 35 macrocnemes, capitular ridges, or tentacles per cycle; in contraction, the capitulum is rounded, and the sphincter muscle well developed; in TS the microcnemes may be bulbous, with a basal canal (Fig. 6*E,G*); septal filaments contain abundant basitrichs. The polyps of *Pr. willeyi* (Hill and Whitelegge, 1898), described from Funafuti Atoll, are smaller, but still larger than found in *Pr. heliodiscus*, sp. nov.; Hill and Whitelegge's (1898) statement that there were 80 tentacles appears to have been a misleading 'guestimate', for his drawing shows 32 in a half TS, exactly what would be predicted in a polyp of 0.65 mL (derived from his linear measurements). The TS (pl. 27, fig. 2) shows the same bulbous microcnemes that we find characteristic of *Pr. mutuki* (see Fig. 6*E*), a species with which Hill and Whitelegge made no comparison. The largest polyps of *Pr. arenacea* (Wilsmore, 1909), from Masthead I. (placed by Walsh and Bowers (1971) in the New Hebrides!), were about 0.55 mL with 28–29 capitular ridges, clearly in conformity with *Pr. mutuki*, with which it was not compared. The microcnemes were not mentioned but their appearance in TS (fig. 18), fairly high in the actinopharynx, is as we have described above. *Pr. yongei*, from Low Isles, 'reminds one of *Palythoa* (*Gemmaria*) *mutuki*, but seems to be different' (Carlgren 1937). The polyps were small, 0.3 mL, but 25–30 capitular ridges is correct for *Pr. mutuki*, too few for *Pr. heliodiscus*, sp. nov. Carlgren (text-fig. 26) illustrates a side-view of the canal system which complements our Fig. 6*E*. Carlgren thought that the nematocyst capsules of *Pr. yongei* were larger than those of *Pr. mutuki*, but their dimensions are virtually identical with those of our specimens from Mabuiag (holotrichs in tentacles 43–47 μm, in filaments 53–60 μm; cf. Table 2); 'microbasic mastigophors' (our basitrichs) were present (in tentacles ~24 μm, in filaments 36–38 μm). The authors of the above three species, it should be said, were provided with very small (manifestly inadequate) samples. That was not a constraint with *Pr. australiensis* (Carlgren, 1950), from Nambucca Heads. The polyps are very large, owing to their great length, with 60–70 septa, about the maximum we have recorded in *Pr. mutuki*; the quoted dimensions of holotrichs (in tentacles 41–49 μm, in filaments 49–58 μm; cf. Table 2) conform perfectly with our data; 'microbasic *p*-mastigophors' (our *p*-mastigophores) were 'numerous' in the filaments.

Protopalythoa heideri (Carlgren, 1954), from Rottnest I., Western Australia, separates from *Pr. mutuki* on our graph of macrocnemes *v.* polyp diameter (Fig. 3) with $P \approx 0.005$ (Table 1) but not on nematocyst capsule sizes. On present evidence we regard the two species as separate but it would be desirable to examine collections from tropical Western Australia, which would fill the long gap between Torres Strait and Rottnest I. Heider (1899) obtained a *Protopalythoa* from Singapore, which he tentatively identified as *Pr. variablilis* (Duerden, 1898) but which Pax and Müller (1956) later named *singaporensis* new species. Pax and Müller (1957) amplified the description of the latter with material from Viet-Nam (Cap St Jacques, No. 37, 1908, and [no locality] No. 63, 1910). Contracted polyps were 7–17 (mean 13) mm high, reaching 20 mm (Heider 1899), with a distal diameter up to 12 mm. These are large polyps of volume ~1 mL. Well-grown polyps had 21–29 (mostly 28) capitular ridges, and a sectioned polyp had 74 septa. This relationship could apply to either *Pr. mutuki* or *Pr. heideri*. Pax and Müller unfortunately do not describe the septa at all but do include some cnidome data. Holotrichs were not found in the tentacles but capsules from filaments had mean measurements of 52×20 μm; 'microbasic *b*-mastigophores' (basitrichs) in filaments had a mean length of 52 μm or 20 μm (the latter clearly being *p*-mastigophores). These measurements fall centrally within those of *Pr. mutuki*. These collections may have been subtidal; that from Singapore was on the 'Coral Bank', those from Viet-Nam were not properly localised; however, on the basis of the descriptions it is impossible not to regard them as belonging to *Pr. mutuki*.

Three nominate species of *Protopalythoa* have been described from Hawaii (Walsh and Bowers 1971) which, from their polyp size and number of septa, could be referable to *Pr. mutuki*. The three seem morphologically distinct, though they might fall within the range of variation we have observed. The septa are not properly described, save in respect to their canal system. There seem to be more canals in the macrocnemes than in either *Pr. mutuki* or *Pr. heliodiscus*, sp. nov. (perhaps more like our *Protopalythoa* sp. 2). Unfortunately, Walsh and Bowers seem to have been unable to identify nematocyst types, and interpreting their data involves a degree of guesswork. Their methodology is vague and suggests that origins would get mixed; 'holotrichs' are very small indeed and true holotrichs seem to have been called macrobasic *p*-mastigophores; ranges are quoted without either mean or sample size and seem very large, again suggesting mixed origins. For the present we do not synonymise any of the Hawaiian species with *Pr. mutuki*. Differences from *Pr. heliodiscus*, sp. nov. are summarised in Table 4.

JSR sample #136 (species 2) from the north-east reef, Heron I. 10.xi.1985, has a distinctive appearance, a different septa *v.* diameter relationship (Fig. 3), larger holotrichs in the filaments (Fig. 4), and canals in the septa. We have not yet identified it. Burnett *et al.* (1997) also found aberrant polyps (their *Pro*. form 3) among *Protopalythoa* from Ross reef: 'When treated as a separate population in the UPGMA analysis, they cluster closer to *Pro*. *mutuki* than to *Pro*. sp. 2 [*heliodiscus*, sp. nov.]'. We hope to examine these at a later date.

Table 4. Distinguishing features of two species of *Protopalythoa*

Character	*Pr. mutuki*	*Pr. heliodiscus*
Habitat	Intertidal (?always)	Low intertidal and subtidal
Polyp size (volume after preservation)	Up to >1 mL	Up to 0.3 mL
Macrosepta (1/2 number of tentacles)	44–72	~50 up to ~100
Length of tentacles	Up to ~45% of disk diameter	Up to ~10(–20)% of disk diameter; masked by light tubercles
Disk colour	Brown, sometimes with a white stripe; or variegated	Dark brown (brown disks may fluoresce green under water)
Length of holotrichs in tentacles	Range 29–51 ($\bar{x} = 45$) [A] μm	Range 23–45 ($\bar{x} = 37$) [A] μm
Length of holotrichs in filaments	Range 35–82 ($\bar{x} = 52$) [A] μm	Range 24–52 ($\bar{x} = 40$) [A] μm
Length of *p*-mastigophores in filaments	Range 17–51 ($\bar{x} = 27$) [A,B] μm	Range 17–34 ($\bar{x} = 26$) [A] μm
Basitrichs in tentacles	Present	Absent
Basitrichs in filaments	Abundant	Absent
Spirocysts in tentacles	Abundant	Sparse
Presumed dominant mode of nutrition	Hetero- and autotrophic	Essentially autotrophic
Spawning	No evidence of eggs being 'bundled'	Egg (or egg/sperm) bundles
Oocyte maximum diameter	>400 μm (formalin fixed)	≈300 μm (unfixed); ≈240 μm processed[C]
Transmission of zooxanthellae	Not via oocytes	Vertical (via oocytes)

[A]Grand mean of sample means (unequal sample sizes); [B]sometimes with bimodal length frequency distribution; [C]Babcock and Ryland (1990), Ryland and Babcock (1991).

Protopalythoa heliodiscus, sp. nov.

(Figs 9–10; Table 3)

Protopalythoa sp. – Muirhead and Ryland 1984: 32, fig. 16.14 and 15; Babcock and Ryland 1990; Ryland and Babcock 1991; Ryland & Muirhead 1993: 56, fig. 17.14 and 15; Burnett *et al.* 1997.

Palythoa sp. – Allen and Steene 1994: fig. (centre right), p. 63; Ryan 1994: fig., p. 51.

Protopalythoa sp. – Schuhmacher and Hinterkircher 1996: fig. (top right), p. 73.

Palythoa vestitus – Colin and Arneson 1995: 124-125 [not *Pa. vestitus* Walsh and Bowers, 1971].

Protopalythoa spp. 1, 3. – Gosliner *et al.* 1996: 66, fig. 201; 67, fig. 203.

Material examined

Holotype. Fiji: east Viti Levu, Toberua Pass, 18.00ºS, 178.70ºE, 0.5–5 m, coll. J. S. Ryland, 3.vii.1980 (NHM 2002.157) (QM G319675).

Paratype. Specimen from same collection as holotype (QM G319678).

Other material examined. **Queensland:** Torres Strait, Goode I., 28.iii.1994. coll. W. J. Burnett; Fitzroy I., intertidal reef, 16.viii.1982, coll. J. S. R. (NHM 2002.165/170); Low Isles, intertidal reef, 17.viii.1982, coll. J. S. R. (NHM 2002.171); Orpheus I., Pioneer Bay, low intertidal, 20.vii.1982, coll. J. S. R. (NHM 2002.169) (QM G319680), 10.xi.1985, coll. C. Shelley (NHM 2002.176) (QM G319681), 30.xi.1985 (QM G319682), North-East Reef, 22.vii.1982, coll. J. S. R. (NHM 2002.168). **Fiji, Viti Levu:** Toberua Pass, 2–3 m, 3.vii.1980, coll. J. S. R.; Yarawa Reef, reef edge, 30.vii.1980, coll. J. S. R. (NHM 2002.161/174) (QM G319676); Makuluva Pass, 5–7 m, 14.ii.1982, 4.iv.1982, 31.v.1982, coll. A. Muirhead (NHM 2002.163) (QM G319676).

Diagnosis

Very low intertidal or subtidal *Protopalythoa* with smallish zooids (11–17 × 4–6 mm), somewhat knobbed in contraction and often of tricorn appearance in semi-expansion. Tentacles minute, 35–40 per cycle. Microcnemes in TS lacking a conspicuous basal canal. Septal filaments without basitrichs, and the holotrichs not above ~50 µm in length. Zooxanthellae transmitted via the oocytes (vertical transmission).

External appearance

Colony (of holotype) comprising loose but extensive mats of polyps. Polyps in basally joined clumps of about 5 (commonly 2–4), shortly separated from similar clumps or joined by slender stolons. New (smaller) polyps occasionally present in clumps. About 35 polyps per 25 cm^2 of substratum; in the contracted state apparently occupying about one-half of the space. Contracted polyps in form of knobbed pillars, 11–17 (mean 14) mm high (Fig. 9*A,C*), columns 3.5–6 (mean 4.5) wide, sanded, transversely wrinkled; taller and thinner when expanded; capitula loosely closed, about 6 mm across but not necessarily circular; the rolled-over margin consisting of fine, sanded capitular ridges, that marking the ventral directive axis notably broader; short, transparent, downwards-directed exocoelic tentacles arising between the ridges; longer, lightly sanded endocoelic tentacles prolonging the ridges toward the mouth. The semi-open state of the capitula characteristic (Fig. 9*D,E*), with much of the disk visible, the margins partially inrolled to create a triangular outline; this seen on the shore or in specimens recently brought into an aquarium.

Expanded disks typically dark brown with fine, pale radiating lines marking the position of the perfect septa, at least up to ~15 mm diameter (mean of 10 largest disks in Fig. 9*B* = 14.5 s.d. ± 0.8 mm); surrounded by a ring of pale knob-like capitular ridges, one or both of those marking the directive endocoels often broader and more conspicuous. Several colour morphs noted at Orpheus I., but 'never a white line on the disk' (cf. *Pr. mutuki*). Tentacles extremely short, often virtually invisible (Fig. 9*B,D*).

Internal structure

In sections (LS, TS) of the type and paratype, retracted zooids typically comprise a slender column and a broader, loosely closed capitulum, in which the oral disk is saucer to goblet-shaped, below an acutely angled capitular inflection. Tentacles inrolled, cut through their bases but, owing to their shortness, rarely cut through their free portion. Capitular ridges inconspicuous. Mesogloeal sphincter muscle (in LS) long and slender. Column ectoderm continuous, with zooxanthellae. Mesogloea of column heavily impregnated with sand in its outer portion, thick, 20–35% of column radius in Fijian material but only 10% in collections from Orpheus I. (possibly a consequence of incorporating siliceous rather than calcareous particles); with lacunae containing cells and zooxanthellae toward the coelenteron. Ectoderm of disk with zooxanthellae; cnidae rare. Ectoderm of tentacles with abundant zooxanthellae, spirocysts and holotrichs only in the short free portion; endoderm thin, with sparse zooxanthellae, not along the septa in the 'boxes' between the flaring column and inflected disk. Siphonoglyph in TS a tapered U-shape in the upper pharynx, with supporting H-shaped mesogloea, but not forming a gutter lower down (Fig. 10*D*). Ectoderm of actinopharynx vertically ridged, cnidae lacking or rare in sections; underlying mesogloea forming a smooth cylinder or (in the type) pectinate in TS, supporting the ectodermal ridges. Septa 70–80, the numbers not necessarily equal each side of the directive axis; imperfect septa near the capitular inflection finger-like in TS, becoming shorter proximally and finally minute abreast the reflected ectoderm in the column. Perfect septa of uniform thickness near the capitular inflection, then regionated, mainly very thin (membranous); the peripheral end thicker, with a slit-like cell-filled basal canal near the capitulum, this end becoming shorter and more triangular at the level of the reflected ectoderm, with a conspicuous basal canal. Reflected ectoderm bands present centrifugal to the lower part of the actinopharynx, corrugated

in TS, attached to the actinopharynx orally, free from it basally, with the ends of both sides flaring away from the septum (Fig. 10*B*). The band of reflected ectoderm narrower toward the inner opening of the actinopharynx, first (in TS) as an arrowhead and then as a clavate thickening terminating in a rounded filament delimited by grooves (Fig. 10*C*); no lateral lobes. Some macrocnemes, particularly toward the directive axis, imperfect and lacking the bands of reflected ectoderm. Microcnemes in TS often bulbous, without an obvious basal canal.

Cnidome

See Fig. 2 for types and Table 3 for measurements. Tentacles with variable numbers of holotrichs and virtual absence of all other types. Filaments with variable numbers of holotrichs and *p*-mastigophores but a total absence of basitrichs.

Reproduction

The reproductive biology of this species in the GBR is well established (Babcock and Ryland 1990; Ryland and Babcock 1991). Oogenesis commences in mid-year, spermatogenesis somewhat later. Mature oocytes measure ~300 μm in diameter and are spawned about 3–5 nights after the full moon in October (Magnetic I.) or November (Orpheus I.), each probably with a small spawning one month later. *Pr. heliodiscus*, uniquely among zoanthids so far studied (Ryland 1997), has both vertical transmission of zooxanthellae, making the eggs buff-coloured rather than

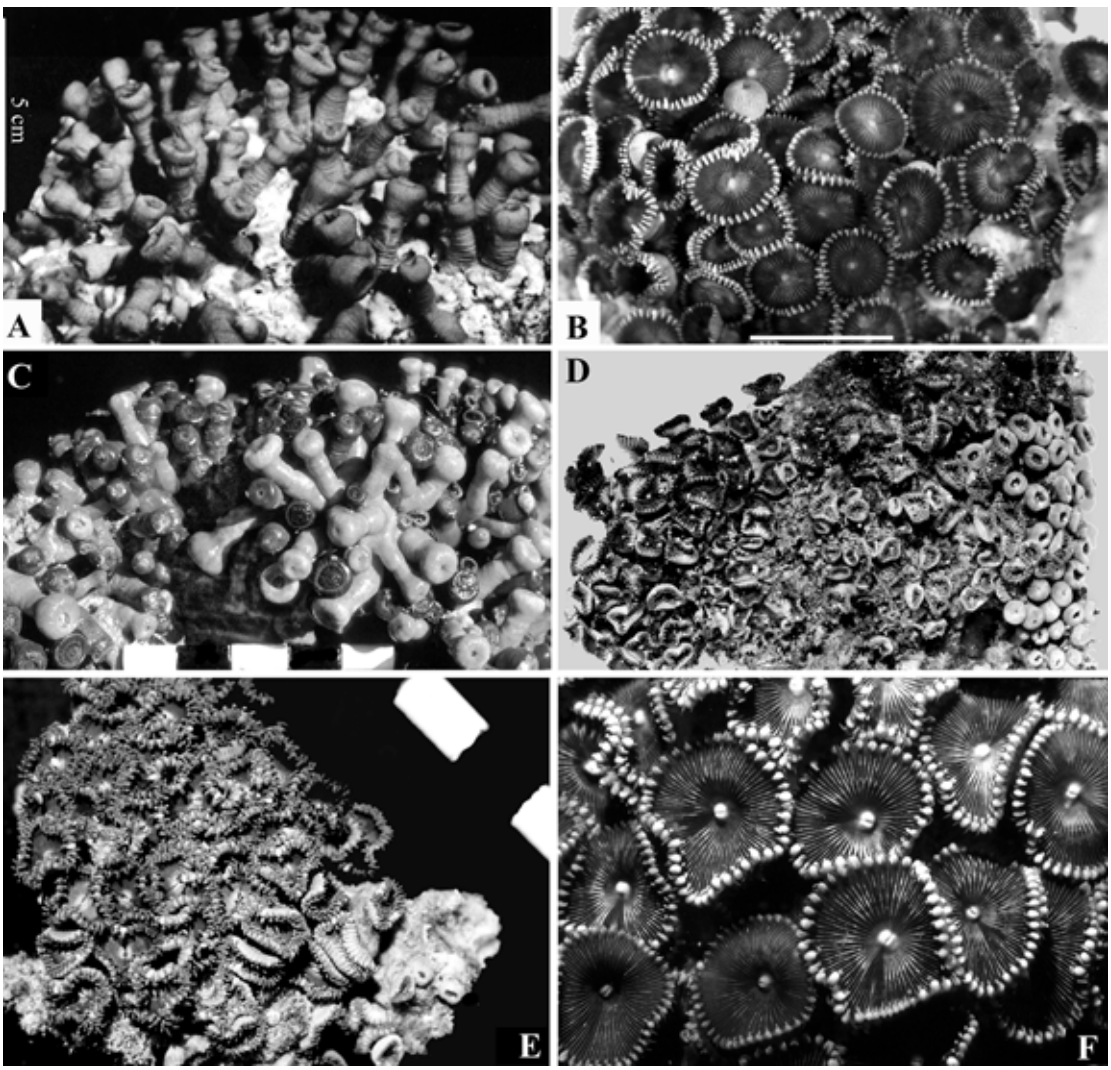

Fig. 9. *Protopalythoa heliodiscus*, sp. nov. Holotype. Collected from Toberua Passage, Viti Levu, 3.vii.80, 2–3 m. *A*, After preservation. *B*, Polyps open after collection; scale bar = 2 cm. *C*, Intermingled with *Zoanthus coppingeri*, Goode I., Torres Strait, 2–3 m, 28.iii.94; scale 5 × 1 cm. *D*, From low shore, Pioneer Bay, Orpheus I., 20.vii.82. *E*, Same specimen as *B*; scale bar segments each = 1 cm. *F*, Open polyps, Makuluva Passage, Viti Levu, 5–7 m, 16.iv.82 (A. Muirhead).

yellow or white, and eggs compacted into egg (or egg/sperm) bundles instead of being shed individually. A sample collected 1.xii.85, four days after full moon, contained a few mature oocytes between septa and in the actinopharynx: they appeared left over from spawning. The only account of development from fertilised egg to fully formed larva (a zoanthella) for any zoanthid is for this species (Babcock and Ryland 1990).

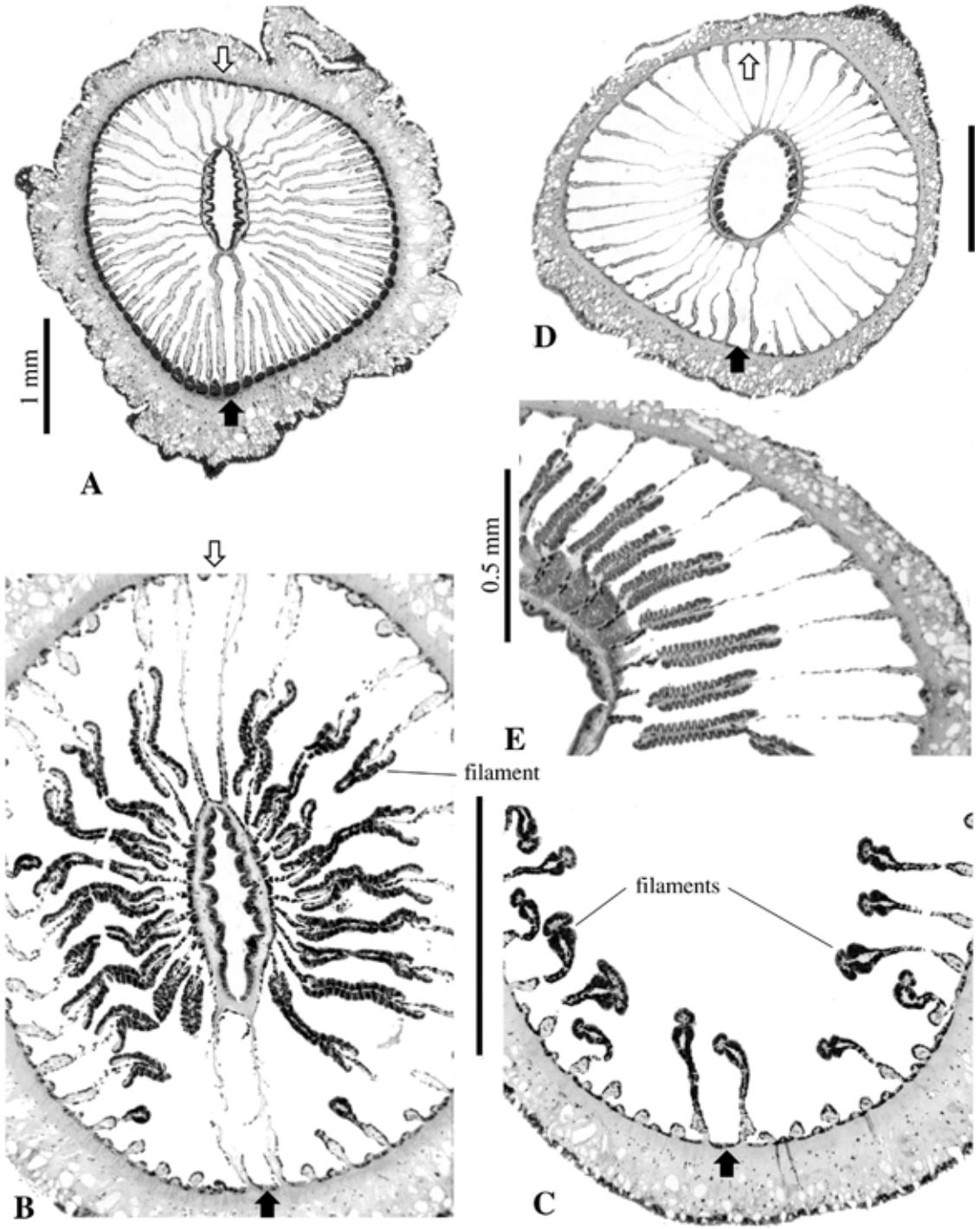

Fig. 10. *Protopalythoa heliodiscus*, sp. nov. Photomicrographs of transverse sections. *A–C*, Holotype, Toberua Pass, east Viti Levu, 30.vii.1980. *D–E*, Yarawa outer reef flat, north Viti Levu, 30vii.80. *A, D*, Upper part of actinopharynx. *B, E*, Lower part of actinopharynx. *C*, Below the actinopharynx, perfect septa ending in filaments. Unmarked scale bars = 1 mm; ➡ ventral directives; ⇨ dorsal directives; see Fig. 1*A* for additional labelling.

Biology

Although Burnett *et al.* (1997) described this species as characteristically subtidal, that is not correct. Most of the GBR specimens seen by us, and all used in the study of reproduction (Babcock and Ryland 1990; Ryland and Babcock 1991), were from the intertidal, but collectable only at low water of spring tides. At Pioneer Bay, Orpheus I. (20.vii.82) its habitat was noted as 'often in silt, on all microatolls or mounds formed by soft corals. Usually in small patches, many of them within 30 m of the low tide (predicted height –0.2 m)'. Toward the north end of the bay it was noted as being 'very common at low water, about a colony every metre in every direction'. However, it certainly is abundant in shallow water where swathes of open disks make it conspicuous (Fig. 9*D*). The large oral disks, minuscule tentacles, and lack of basitrichs (total absence in the filaments) suggest that carnivory is nutritionally insignificant in this species, and it must be an obligate autotroph.

Distribution

We have found *Protopalythoa heliodiscus* in Torres Strait (off Goode I.) and tropical Queensland (Fig. 7). Burnett *et al.* (1997) obtained the species from East Hope I. and Endeavour reef (off Cooktown), down to Heron I. (Fig. 7). It occurs in the passes between the Laucala Bay reefs in Viti Levu, and intertidally on Yarawa reef, off Ba (Fig. 8). Allen and Steene's (1994, fig. on p. 63) photograph was taken in the Russell Is (Solomon Is). *Protopalythoa heliodiscus* is presumably widely distributed in the tropical Indo-West Pacific, since underwater pictures feature in several coral-reef guides (Muirhead and Ryland 1984; Allen and Steene 1994; Ryan 1994; Colin and Arneson 1995; Schuhmacher and Hinterkircher 1996; Gosliner *et al.* 1996) generally without indication of where the photographs were taken.

Remarks

Only one set of oral disk diameter measurements is available, none of the published photographs having an indicated scale. The disks in Fig. 9*B* do not appear to have reached maximum expansion, so the mean (14.5 mm) of the 10 largest is conservative. It suggests that the expanded disks are as large as those of *Pr. mutuki*, despite being associated with much smaller polyps. In the cnidome the *p*-mastigophores appeared variable in shape (and the difference in diameter between shaft and tubule was less abrupt, making the V-notch less distinctive than in *Pr. mutuki*). Holotrichs from both tentacles and filament tissue were often misshapen and appeared shrunken and wrinkled in appearance. While this may have been due to preparative methods, the same techniques were applied throughout and holotrichs from *Pr. mutuki* were rarely affected.

Any collection of this species, provided it adequately samples a range of polyp sizes, can be readily separated from *Pr. mutuki* on the basis of polyp size and number of septa, by checking the filaments for presence or absence of basitrichs, and by measuring a few holotrichs. If seen expanded on the reef it is unmistakable, with its large brown oral disks and conspicuous tubercles almost concealing the minute tentacles. The differences between *Pr. mutuki* and *Pr. heliodiscus* are summarised in Table 4.

It is interesting to note that the two sympatric species of *Protopalythoa* in Bermuda and the Caribbean, *Pr. grandiflora* (which probably should be subsumed in *Pr. fusca*) and *Pr. variabilis*, appear to differ from each other in their meristic characters exactly as do *Pr. mutuki* and *Pr. heliodiscus*. *Pr. grandiflora* has 44–56 longish tentacles (Ryland 1992, figs 55–57) and Duerden (1898) implies 48–64 in *Pr. fusca*, *Pr. variabilis* has 60–80 minute tentacles surrounding a large oral disk (Duerden 1898; Ryland 1992, figs 52–54). Unfortunately the cnidome and reproductive processes of these species are unknown and clearly need to be investigated.

Etymology

Heliodiscus refers not only to the large, circular expanded oral disk but to the observation that closed polyps rapidly opened in response to direct sunlight falling upon their container.

Discussion and conclusions

Burnett *et al.* (1997), using enzyme electrophoresis, found that all but one sample of *Protopalythoa* from the GBR belonged to one of two species, *Pr. mutuki* and the one now named *Pr. heliodiscus*. We have examined various morphological criteria that separate these, seeking non-traditional, quantitative and statistically testable, methods of separation. Using samples with a range of polyp sizes, we have plotted number of septa against column diameter. Variation between samples was quite high, and the usually accepted significant probability level of 0.05 frequently exceeded (Table 1, Fig. 3). However, the regressions between the species were different at probabilities of 1×10^{-6} or less, readily separating within-species and between-species variability.

We used a similar approach with the length of nematocyst capsules (holotrichs and *p*-mastigophores), again recording small between-sample differences and large between-species differences (Tables 2,3, Fig. 4). Zoanthid polyps are small (much smaller than most anemones) and trying to prepare adequate samples of all nematocyst types from every structure in which they occur would be excessively time-consuming. Accordingly, since our objective was to find reliable methods of distinguishing the species, we have concentrated on two clearly visible structures only: tentacles and filaments. We used large sample sizes, usually $n = 100$.

Williams (1996, 1998) found in anemones that $n \geq 40$ was adequate for establishing standard deviation and range, but capsule lengths in his samples were always normally distributed. Since great care was taken to avoid cross-contamination and all samples had a single source, we do not know why several of our samples were non-normal, especially since there was no consistent pattern to the departure from normality. In many cases the non-normality was associated with kurtosis rather than skewness, affecting the variance rather than the mean; nevertheless, we have included medians as well as means in Tables 2 and 3. With such variability, data transformations are not an option and comparisons have been made between distributions, using the non-parametric Kolmogorov–Smirnov 2-sample test (Sokal and Rohlf 1995), rather than between means and variances. For this reason we prefer the larger samples. We intend to return in subsequent papers (Ryland *et al.* in press.) to this and various other issues concerning the use of nematocysts in zoanthid taxonomy; it would be unfortunate if zoanthid taxonomists were unable to take advantage of the methods proposed by Williams (1998, 2000) for extracting the maximum information from data in the form of capsule size ranges conventionally given in mid-20th century literature (e.g. Carlgren 1937, 1950).

Even more striking in the cnidome than the differences based on capsule size was that basitrichs were abundant in the filaments and usually numerous in the tentacles of *Pr. mutuki* but completely absent from both in *Pr. heliodiscus*. This unusual feature makes *Pr. heliodiscus* very distinct. Study of expanded polyps showed another large difference: *Pr. mutuki* has long tentacles, and *Pr. heliodiscus* very short ones. The white line, when present, on the disk of *Pr. mutuki* also appears to be species specific. Finally, the reproductive biology of the two species is hugely different, with *Pr. heliodiscus*—at least in the Great Barrier Reef sea area—adapted to participate in the mass spawning events that characterise reef scleractinians and soft corals (Babcock *et al.* 1986; Alino and Coll 1989). Ova are spawned in egg or egg–sperm bundles, and zooxanthellae have vertical transmission (Ryland and Babcock 1991; Ryland 1997). *Protopalythoa mutuki*, though we found only one sample reproducing (Korotogo reef, Fiji, 6.vi.1979), has neither of these features. We thus have a suite of biological characters that would have been largely or completely overlooked in descriptions published during the nineteenth century and most of the twentieth. Using more conventional criteria, seen in transverse sections, it is difficult to find characters that reliably separate the two species.

Zoanthid taxonomy is difficult on account of the range of variation found within species and the lack of methods for distinguishing infra- and inter-specific variation without the use of genetic methods. Colonial morphology in *Palythoa* is highly variable: wherever species of this genus occur they range from extensive spreading sheets to clusters of small lumps (for processes of fission and fragmentation, see Acosta *et al.* 2001). Yet, at least in the GBR, it seems that these morphologies represent a single, variable species (Burnett *et al.* 1994). Similarly, numerous nominate species of *Zoanthus* from the GBR, including the apparently very distinctive *Z. pacificus* Walsh and Bowers, 1971 (see Muirhead and Ryland 1984; Ryland and Muirhead 1993) seem merely variants of *Z. coppingeri* (Burnett *et al.* 1995, 1997). We have shown the value of both meristic macro-characters and of nematocyst capsule measurements when based on adequate samples and proper statistical analysis. In the latter our results agree with those from other hexacoral taxa (Pires and Pitombo 1992; Chintiroglou and Simsiridou 1997). It remains to be seen whether other species of *Protopalythoa*, and those of *Palythoa* and *Zoanthus*, can also be characterised in this way.

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