Suspected neoplasms in deep-sea corals (Scleractinia: Oculinidae: *Madrepora* spp.) reinterpreted as galls caused by *Petrarca madreporae* n. sp. (Crustacea: Ascothoracida: Petrarcidae)

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ABSTRACT· Hypertrophied corallites with irregular septal patterns in the Hawaiian deep-water coral *Madrepora kauaiensis* Vaughan were interpreted 30 yr ago as possible neoplasms, and this idea has persisted in comparative oncological literature. Many colonies of *Madrepora oculata* L. with similarly modified corallites are recorded herein from 233 to 604 m depth off northwestern Australia and Japan, in the Formosa Strait, and in the Banda and Arafura Seas, Indonesia. The affected corallites have a hollow space beneath the interrupted columella. Most specimens had been dried and bleached, leaving no tissue, but in some alcohol-preserved Indonesian specimens this cavity was occupied by endoparasitic petrarcid ascothoracidan crustaceans. These are described herein as *Petrarca madreporae* Grygier, new species, which is characterized by a posterior lobe on each carapace valve, poorly armed mouthparts, and a bifid penis with fixed rami. The validity of the diagnosis of the petrarcid genus *Zibrowia* Grygier, 1985 is questioned. The abnormal corallites are provisionally reinterpreted as an unusual kind of petrarcid 'internal gall.'

KEY WORDS: Neoplasms · Galls · Scleractinia · *Madrepora* · Ascothoracida · Petrarcidae *Petrarca madreporae* · KARUBAR expedition

INTRODUCTION

Tumors, neoplasms, galls, and other growth abnormalities of scleractinian corals have been the subjects of several recent studies and reviews (e.g. Loya et al. 1984, Zibrowius & Grygier 1985, Peters et al. 1986, Dojiri 1988). The study of neoplasia in corals may be relevant to medical oncology (e.g. as model systems in anatomically simple, diploblastic animals), but it is difficult, using skeletal evidence alone, to distinguish neoplasms from hyperplasia, gigantism, and proliferative lesions with extrinsic causes such as injury or parasites (Sparks 1969, Peters et al. 1986). True neoplasms (calicoblastic epithelioma) have been demonstrated histologically in only 2 corals, *Acropora formosa*

(Dana) and *A. palmata* (Lamarck) (see Peters et al. 1986). On the other hand, the first purported neoplasms in a coral, the hypertrophied corallites described by Squires (1965a) from a species of *Madrepora*, have never been confirmed as such. This is ironic since they partly inspired the establishment in 1965 of the Registry of Tumors in Lower Animals in the National Museum of Natural History, Smithsonian Institution (J. Harshbarger pers. comm.).

Squires (1965a) identified 3 hypertrophied corallites on the dried holotype of the bathyal Hawaiian oculinid coral *Madrepora kauaiensis* Vaughan as possible neoplasms. Vaughan (1907) had earlier mistaken the largest of the three for an epizoic mussid coral. The abnormal, bell-shaped corallites are from 2 to 9 times the normal diameter and have a complicated, irregular septal pattern; the porosity of the septa indicates rapid growth. White (1965) pointed out that the affected

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corallites budded normally, so 'cancer' was not a likely explanation; he noted similarities to plant galls and suggested that individual polyps had been attacked by a virus, bacterium, fungus, or invertebrate. Soule (1965) suggested that the aberrant corallites were actually epizoic ectoproct colonies, but Squires (1965b) found no evidence of overgrowth and proposed that only histological evidence could provide a decisive explanation.

Squires's neoplasia hypothesis has been discussed repeatedly in comparative oncological literature (Sparks 1969, 1972, 1985, Krieg 1973, Cheney 1975, Lauckner 1980, Dawe 1982, Bak 1983, Loya et al. 1984, Peters et al. 1986). In 1970 a photograph of the coral colony he studied even appeared on the cover of 'Cancer Research' (Vol. 30, no. 5). Most of the cited authors explicitly excluded parasite-induced tissue proliferations (i.e. galls) from their concept of neoplasia, and White's (1965) gall hypothesis has languished for lack of concrete evidence. According to the 'Occam's Razor' maxim, the discovery of parasites within the abnormal corallites would promote his explanation as the proper null hypothesis for further inquiry.

Further progress awaited the advent of corals with preserved tissues. Cairns (1984) found 2 additional hypertrophied corallites from Hawaii on *Madrepora kauaiensis* and *M. oculata* L., but both had been dried. While examining examples of similarly modified corallites on dried and bleached *M. oculata* in the Western Australian Museum, the first author noticed that broken ones were hollow and could have housed endoparasites. This inference was proven correct when the second author obtained alcohol-preserved specimens of *M. oculata* with hypertrophied corallites from Indonesia. Some of the affected corallites housed an unknown species of endoparasitic petrarcid crustacean, which is described herein.

The Petrarcidae belong to the Ascothoracida, a wholly parasitic subclass that is closely related to the Cirripedia, or barnacles. Petrarcids are obligate endoparasites of corals, predominantly azooxanthellate ones, belonging to 4 suborders of the Scleractinia. They are hermaphroditic and occur in groups, usually pairs, in a cavity within an 'internal gall' (usually a spongy proliferation of coenosteum involving the columella and adjacent septa of a single corallite) or an 'external gall' (involving the corallum at large rather than a single corallite). Several photographic catalogues of petrarcid galls in various corals have been, or are being, published: Zibrowius & Grygier (1985), Grygier (1991b, in press), Grygier & Nojima (1995) Recent taxonomic papers on the parasites themselves include Grygier (1985, 1991a,b); there are 10 described species in 3 genera and several partial descriptions and records of unidentified remains. Planktonic nauplius larvae have been described (e.g. Grygier 1990), but the cypridiform ascothoracid-larva stage and the earliest endoparasitic stages remain unknown.

MATERIALS AND METHODS

Forty-nine hypertrophied corallites were examined from collections of *Madrepora* spp. in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH, with USNM catalogue numbers), the Natural History Museum in London (BMNH), and the Nationaal Natuurhistorisch Museum in Leiden, The Netherlands (NNM), and among specimens loaned from the Western Australian Museum, Perth (WAM), the University of Tokyo Ocean Research Institute, Japan (ORI), and the Muséum National d'Histoire Naturelle in Paris, France (MNHN: KARUBAR Expedition); a complete list of specimens is given in Appendix 1. Some of the affected WAM corals were photographed, either bleached or dyed red. In order to check for the presence of an internal cavity and any parasites or their remains, the thecal walls of the largest corallite on Squires's (1965a) dried specimen and several large and small affected corallites from each of the other collections (including all 16 of the alcohol-preserved KARUBAR specimens) were pierced with a 0.6 mm bit in an ultra-high-speed rotary dental drill. Some of the remaining specimens had been broken or sufficiently eroded beforehand to expose the cavity. Six WAM specimens were left intact, so the presence of a cavity in them was not confirmed.

As expected, we found no tissue remains in bleached specimens, and no more than dust in dried specimens. However, petrarcid endoparasites were found in 4 of the alcohol-preserved specimens: 3 moderately enlarged corallites (10 to 11 mm wide, 6 to 9 mm high) from KARUBAR Stn CP 9 each contained a pair of parasites, while a smaller corallite (8 mm wide, 4 mm high) from KARUBAR Stn CP 19 contained 3 individuals (full collection data in Appendix 1) All the parasites, belonging to a previously unknown species, were removed from their hosts. A paratype from each station was partly dissected and examined in glycerine, then fully dissected and the body parts mounted in glycerine jelly for microscopic examination. A carapace valve was removed from the holotype in order to expose the main body for examination in a glycerine whole mount, and one of its antennules was mounted in glycerine jelly. The first author was responsible for describing the parasitic crustaceans; in conformance with the International Code of Zoological Nomenclature, Art. 50, the scientific name and diagnosis proposed herein are to be attributed to him alone. The second author was responsible for working up the corals.

RESULTS AND DISCUSSION

Corallite morphology of *Madrepora oculata*

A typical, uninfected corallite is about 5 mm long and has a circular calice 2.8 to 3.7 mm in diameter (several examples in Fig 1B, C, E). Each normal corallite contains 24 septa arranged hexamerally in 3 size classes (cycles). In the center of each calice is a papillose columella, and each columellar element reaches to the base of the corallite. Hypertrophied corallites are quite different, reaching up to 20 mm in length and 22.9 mm in greater calicular diameter; the smallest is 4.6 mm across. Their forms vary from dish-like (especially in smaller examples: Fig 1C) to bell-shaped (Fig. 1A, E), and there is sometimes a short basal stalk (Fig. 1D, E). Their calices are circular to quite irregular in outline, and the largest corallites have scalloped calicular edges (Fig. 1A, B). These enlarged corallites possess up to 82 septa arranged in no apparent order, and the septa are usually highly porous, not unlike those of *Letepsammia formosissima* (Moseley) (see
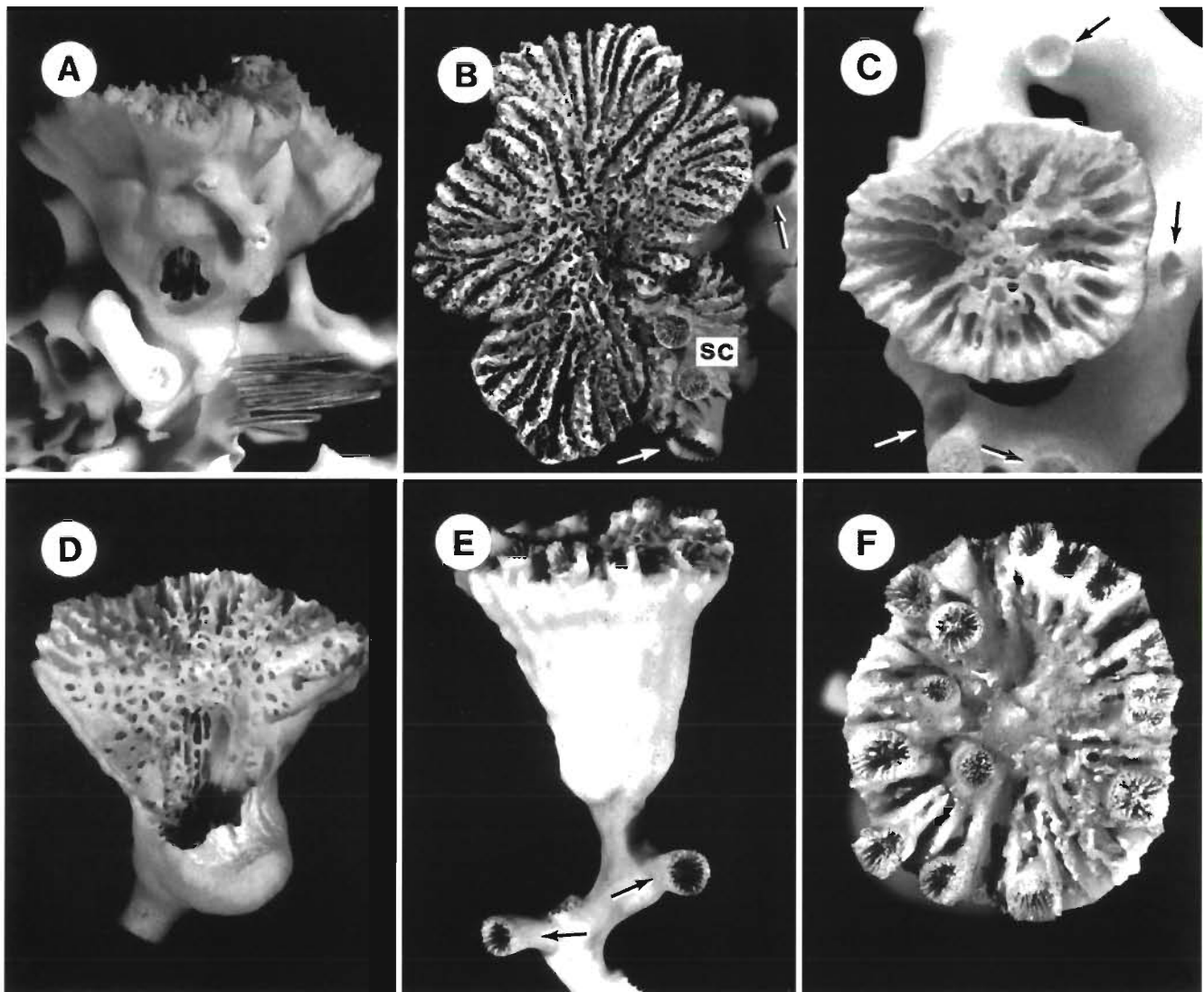

Fig. 1. *Madrepora oculata* L. Dried and bleached specimens from northwestern Australia with hypertrophied corallites that are presumed to be petrarcid galls. All specimens are housed in Western Australian Museum (WAM), some dyed to enhance contrast; normal corallites indicated by arrows in B, C, E. (A) WAM 801-84, very large irregular gall, side view, thecal wall pierced with dental drill to show internal cavity below columella, area around hole dyed yellow, ×2.3; (B) WAM 800-84, very large irregular gall, calicular view, with 2 secondary calices (sc) at lower right, dyed red, ×2.6; (C) WAM 755-84, medium-sized, bowl-shaped gall, calicular view, ×4.0; (D) WAM 801-84, medium-sized gall broken in half to show cavity beneath columella, side view, ×3.7; (E) WAM 727-84, bell-shaped gall, side view, dyed red, ×2.9; (F) same gall as E, calicular view, with many secondary corallites growing on coenosteum-covered calice, ×4.3

Cairns 1989). Furthermore, their columellae are correspondingly large and spongy in shape, not composed of solid papillae. Because of the presence of a large cavity either currently or formerly occupied by petrarcid ascothoracidans (Fig. 1A, D), the columella does not extend to the corallite base; however, there is a trabecular zone composed of porous septa between the cavity and the thecal wall. The thickness of the thecal wall varies considerably. In 10 of the 49 hypertrophied corallites examined (all 10 are WAM specimens), a thin, granular coenosteum, which is similar to and continuous with the thecal coenosteum, covers part or all of the calice, obscuring the underlying septa and columella. Up to 17 secondary corallites have been observed to bud from this overlying coenosteum (Fig. 1B, F), all of which are smaller than normal (i.e. 1.7 to 2.1 mm in diameter), but otherwise typical in morphology. These small corallites do not bud additional corallites to form branches.

Galls, not neoplasms

Examination of 49 hypertrophied corallites on colonies of *Madrepora kauaiensis* and *M. oculata* from Hawaii, northwestern Australia, the Formosa Strait, Japan, and the Banda and Arafura Seas has shown that all are similar in structure and at least 43 (probably all) have a hollow space beneath the interrupted columella. In 4 cases, representing 25% of the alcohol-preserved examples, petrarcid ascothoracidans of the new species *Petrarca madreporae* Grygier were found occupying the cavities, and no other organisms were ever found there. Most species of petrarcids discovered until now occupy a similar position in their host corals, within the columella and adjacent septa of individual corallites and often surrounded by a proliferation of the host's skeleton (Zibrowius & Grygier 1985, Grygier 1991b, Grygier & Nojima 1995). This circumstantial evidence strongly indicates that the hypertrophied corallites of *Madrepora* spp. are galls induced by *P. madreporae*. We therefore endorse the gall explanation given in White's (1965) answer to Squires (1965a). Parasite-induced galls are a well-known phenomenon in botany and zoology, including in corals (crustacean examples reviewed by Dojiri 1988). Therefore, despite the continuing absence of histological information about the host tissues, we believe that this hypothesis now takes precedence over any rare or unprecedented alternative, such as *P. madreporae* secondarily infesting endogenous neoplasms of *Madrepora* spp.

If the hypertrophied calices are galls, they are 'internal galls' in the sense of Zibrowius & Grygier (1985) because only single polyps are affected, not the corallum at large. The crustaceans presumably invade nor-

mal polyps as larvae, although no settled larvae were found and the smallest available galls had been bleached. The manner of development of the gall is unique because such a spectacular product results. Trends towards gigantism in other petrarcid-infested corals usually involve only a tendency for the columella and adjacent septa to become enlarged and spongy-looking (Zibrowius & Grygier 1985). The corallite itself is not generally enlarged, nor is the septal arrangement affected. In contrast, the corallites of *Madrepora* become enlarged many times over and the septal organization is eventually completely disrupted.

The largest alcohol-preserved galls were empty, suggesting that the parasites had died, although we do not know whether the galls continued to grow for a time afterward. It is clear, however, that the host does not recover fully. The secondary corallites that develop from newly laid coenosteum on old galls are small and seem incapable of budding further. On the other hand, the very presence of new corallites shows that the disordered growth does not continue indefinitely and argues against a neoplastic explanation for the hypertrophied corallites. Experimental study of the host-parasite relationship in the petrarcid-coral system would probably be of some interest to developmental biologists, even though the 'neoplasms' of *Madrepora* are most likely of no use as models for vertebrate cancer tumors.

The abnormal coralla were first noticed over 80 yr ago (Vaughan 1907) and the neoplasia hypothesis was proposed about 30 yr ago (Squires 1965a). It took such a long time to present a likely solution to the mystery simply because corals are routinely dried and often bleached after collection; fixed and preserved specimens, even of small, easily handled, azooxanthellate corals from deep water, have been hard to obtain, and even the present alcohol-fixed specimens could not be used for histology. In order to further the study of coral symbionts and to permit expeditious histological study of any growth abnormalities by pathologists, we urge that future collections of at least deep-water corals include both preserved and dried lots.

DESCRIPTION OF THE ENDOPARASITIC CRUSTACEAN

Ascothoracida Lacaze-Duthiers, 1880
Petrarcidae Gruvel, 1905
Petrarcinae Gruvel, 1905
Petrarca Fowler, 1889
Petrarca madreporae Grygier, new species

Diagnosis. Each carapace valve with basally constricted posterior process accounting for 40 to 55% of

total length. Entire carapace sparsely ornamented with simple, rounded papillae, plus ventrolateral array of large spines on each valve. Mandibles with a few subdivided teeth, maxillules unarmed. Thoracopods I and VI absent. Penis bifid but rami immovable; setae found on rami and along distal portion of shaft. Abdomen ending in small, rounded knob with 2 minute spines.

Etymology. Named for the host genus, *Madrepora*.

Type specimens. One of the 3 specimens from KARUBAR Stn CP 19 is designated the holotype and the other 2 are paratypes; all are deposited in the MNHN (Cat. nos. Asc2360, Asc2362, Asc2363, respectively). The 3 pairs from Stn CP 9 are also paratypes; 2 pairs, including a shriveled pair that once dried out, are deposited in the NMNH (USNM 264084, USNM 264085), and 1 pair in the Puslitbang Oseanologi — LIPI, Djakarta, Indonesia.

Description. All specimens are about twice as long as high and wide. Those from Stn CP 19 are about 2.4 to 2.9 mm long; the holotype in particular is 2.85 mm long, 1.45 mm wide, and 1.35 mm high (Fig. 2A, B). The members of one well-preserved pair from Stn CP 9 are 3.2 and 4.0 mm long, and those of the other pair are 4.4 mm long.

The carapace has a bivalved form but no dorsal hinge (Fig. 2A, B). The antennules often protrude and the entire abdomen and penis are exposed. In side view, the main portion of the carapace is more or less rounded with a somewhat irregular ventral margin. Each valve is produced into a posterior lobe with a marked proximal constriction and a somewhat expanded distal part, the height of which is at least half that of the valves proper. These lobes usually constitute 41 to 45% of the total carapace length, measured from the front end of the constriction, but 50 to 54% in one pair of paratypes. In some specimens, the dorsal and ventral margins of the lobes are sinuous; the anterodorsal portion of each lobe may even be produced into a subsidiary lobe (Fig. 2C). The ventrolateral portion of the valve proper is armed with a row of strong, often elongate and multifid spines (Fig. 2A, E). Dorsal to these are some smaller spines, and there are sparse papillae on the remainder of the carapace, including the posterior lobes.

The testes and diverticula of the midgut extend into the tissues of the carapace. There seem to be 3 pairs of gut diverticula but this needs to be checked histologically. The shortest pair extends anterodorsally from the anteroventral part of the stomach (i.e. anterior midgut) and a second pair extends in an arc from the anterodorsal part of the stomach downward and posteriorly, parallel to the ventral margins of the valves (not illustrated). The largest and widest pair extends to the tips of the posterior lobes and gives off

a variable number (8 to 16 in 3 specimens) of short branches (Fig. 2D).

The body proper (Fig. 2F) consists of: the nondescript cephalon very broadly attached to the carapace and bearing the antennules and mouthparts; the thorax divided into a poorly segmented, posteriorly tapering part with vestigial thoracopods and a male genital somite (thoracomere 7) bearing a disproportionately large penis; and the vestigial abdomen with perhaps 3 small somites. A pair of lateral adductor muscle tentoria (not illustrated) contributes in joining the cephalon to the carapace.

The subchelate antennules have 5 distinct segments (Fig. 2G). A weak chitinous band crosses the medial face of the second segment (Fig. 2F). The third segment is triangular. The fourth segment sometimes bears a very short seta on its anterior margin. The fifth segment bears a strongly sclerotized distal claw with up to 3 short setae at its base (one marginal, one on each face) and a claw guard behind. The latter is similar in size to the claw and lightly curved, and it slightly overlaps the claw laterally; sometimes there is a seta on the posterior edge, and the tip bears 2 small spines or a single multifid spine in front of a long seta that is sometimes accompanied by a tiny setula (Fig. 2F–I).

The mouthparts comprise a compact oral cone, sheathed anteriorly and to some degree laterally by a keel-shaped, unornamented labrum and backed by the blunt, massive maxillae (Fig. 2F). The short hypopharynx and the anterior parts of the maxillae are flanked by flattened, leaflike mandibles and maxillules. Only 1 of the very delicate mandibles was recovered from the 2 dissected specimens; its short working edge bears 4 delicate, usually multifid teeth (Fig. 2J). The somewhat more robust maxillules have a sclerotized, unarmed working edge (Fig. 2K). A pair of lobes posterior to the oral cone contains hollow organs that are probably the end-sacs of the maxillary glands (Fig. 2F).

At most 5 segments can be distinguished in the anterior part of the thorax (Fig. 2F); their correspondence to the basic 6 somites of that region in the Ascothoracida is unclear. The first 2 segments can be distinguished only with difficulty. The third segment is clearly delineated from the second by a cuticular fold. The third and fourth segments bear dorsal tergites that may be fused or partly distinct from each other, as in the holotype (Fig. 2F). The fifth segment has a large tergite and sometimes a few dorsolateral pores. Within the thorax, the intestine (posterior midgut) ends blindly (Fig. 2F). The animals are hermaphrodites; in the holotype oocytes occupy much of the cephalon and the paired vasa deferentia coming from the testes in the carapace run ventrolateral to the gut (Fig. 2F). Several long, thin
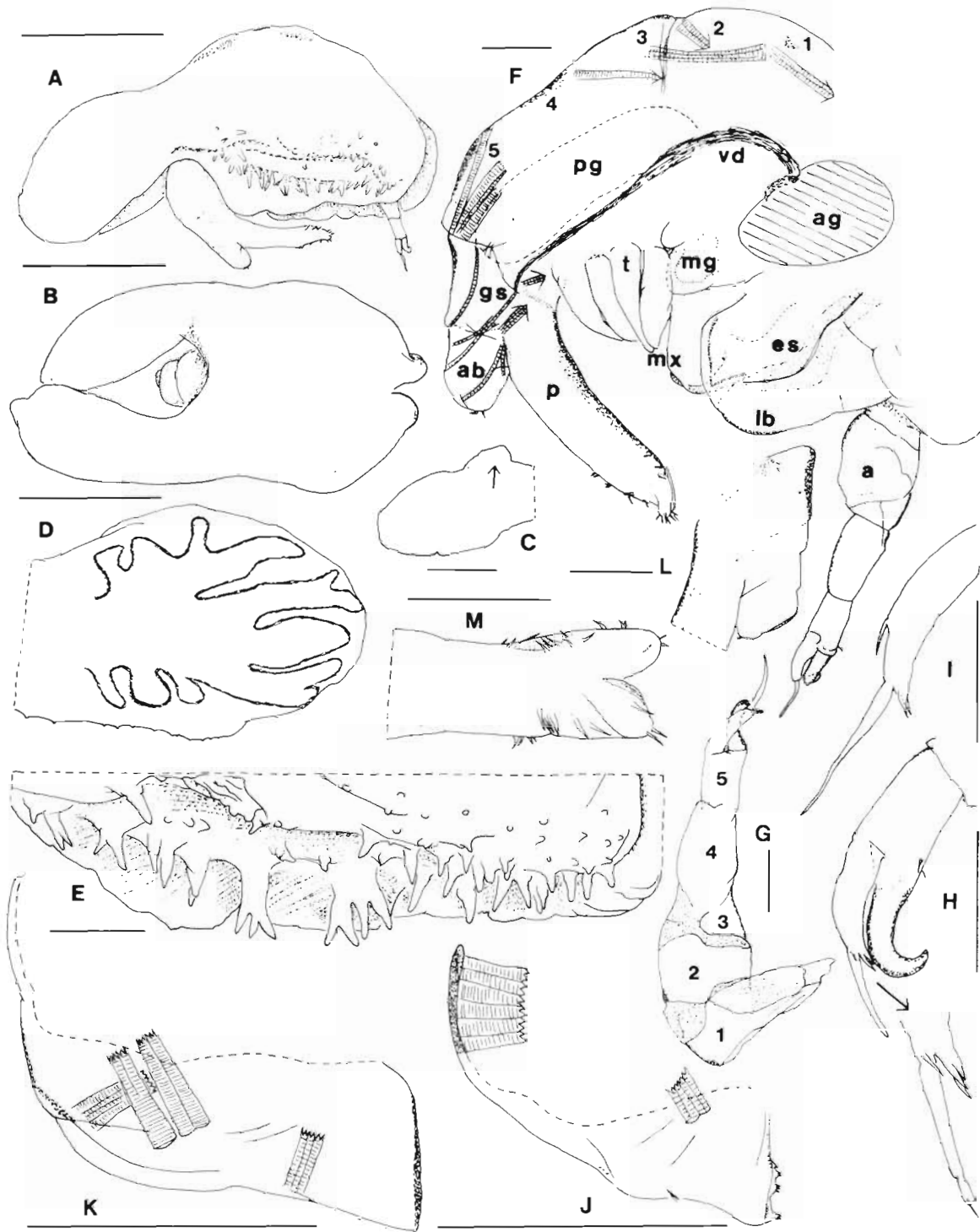
Fig. 2. *Petrarca madreporae* Grygier, new species. (A, B) holotype in lateral and dorsal views; (C) right posterior lobe of undissected paratype (Stn CP 9), with subsidiary dorsal lobe (arrow); (D) left posterior lobe of dissected paratype (Stn CP 9), showing ramifications of internal midgut diverticulum; (E) lateroventral spines and papillae on right carapace valve of dissected paratype (Stn CP 19), anterior end right; (F) holotype, main body with right antennule removed, some trunk musculature shown to locate segment boundaries, apparent thoracic segments numbered; (G) right antennule of dissected paratype (Stn CP 9), outer view, segments numbered; (H) holotype, fifth article of right antennule, with detail of apex of claw guard; (I) claw guard of left antennule of dissected paratype (Stn CP 9); (J,K) mandible and maxillule, respectively, of dissected paratype (Stn CP 9); (L) male genital somite and abdomen of dissected paratype (Stn CP 19); (M) distal part of penis of dissected paratype (Stn CP 19), ventral view. Abbreviations: a, antennule; ab, abdomen; ag, anterior midgut; es, esophagus; gs, male genital somite; lb, labrum; mg, maxillary gland; mx, maxillae; p, penis; pg, posterior midgut; t, thoracopods; vd, vas deferens. Scale bars = 1.0 mm in A–D, 0.2 mm in E–M

seminal receptacles are present in the thorax, and a few shorter ones sometimes occur within the more anterior thoracopods (not illustrated).

Thoracopods II to V are present but the first and sixth pairs are absent (Fig. 2F) All 4 pairs are simple, unsegmented lobes and lack any significant cuticular ornamentation. Thoracopod II is the thickest and the more posterior ones become narrower; all are equally long.

The male genital somite (thoracomere 7) is set off anteriorly by a wide dorsal zone of arthrodial membrane (Fig. 2F, L). Its tergite sometimes has a few pores. The anteroventrally directed penis reaches approximately to the level of the maxillae and in ventral view it is narrowest a little distally of midlength. The tip is bifid, but the 2 'rami' are not movable (Fig. 2M). Numerous small setae adorn the 'rami' and the dorso- and ventrolateral parts of the distal part of the shaft.

The musculature and weak cuticular folds seem to show that the extended abdomen is 3-segmented (Fig. 2F), but in specimens in which the segments' dorsal sides are telescoped into each other and into the genital somite, this fact is obscured (not illustrated). The first 2 supposed segments are similar in size and unarmed, while the third is much smaller and rounded and bears a pair of minute spines (Fig. 2F, L).

Brood. The spaces between the septa surrounding all 4 petrarcid-occupied coral cavities were filled with eggs, and in one case also with some hatched first-stage nauplii similar to those described by Grygier (1985, 1990). Adult exuviae were not found. The eggs are 140 to 290 μm in diameter and vary considerably in size within a clutch.

Remarks. The rather long and slender antennular claw and the apical position of the claw guard's longest seta in Petrarca madreporae are most similar to those of P. azorica Grygier (1985). In all other petrarcines this seta is situated far proximally of the apical spines or is separated from them by a distal broadening of the claw guard. The mandibles and maxillules of the present species have the simplest armament yet noted in the subfamily.

Of all the hitherto described petrarcids, only Zibrowia auriculata Grygier, 1985, the type of a monotypic genus, has a posterior lobe on each carapace valve. Such lobes are one of Grygier's (1985) proposed diagnostic features of Zibrowia, in contrast to simple valves in Petrarca. The lobes are relatively shorter in Z. auriculata than in P. madreporae and lack a distinctly constricted zone at the base (see Grygier 1985, Grygier & Nojima 1995). As a result, the abdomen and usually the penis are hidden by the carapace in side view in Z. auriculata, unlike the present case.

The other supposedly diagnostic features of Zibrowia do not apply well to P. madreporae. The third abdominal (post-genital) somite of Z. auriculata tapers posteriorly as a single massive spine. The present small lobe with 2 short spines may represent an incipient version of this, but it is also reminiscent of the various species of Petrarca thus far described (see Grygier 1985, 1991b), in which abdominal segmentation is somewhat obscure (1, 2, or 3 post-genital segments reported) and 2 spines or 2 small groups of spines appear to arise from a pair of vestigial furcal rami. Another supposedly diagnostic feature of Zibrowia is a penis with an undivided tip and its setae restricted to the distal end. The penis in the known species of Petrarca has a bifid tip with small, movable rami, and there are numerous ventral setae along its whole length or at least the distal half. The penis of the present species is intermediate, being bifid with unarticulated rami, and with only distal setae.

The carapace lobes and the intermediate morphology of the penis and abdomen suggest that the present new species should be assigned to Zibrowia. However, while the subfamily Petrarcinae is monophyletic, recognition of Zibrowia has always posed the danger of leaving Petrarca paraphyletic, diagnosed mostly by the plesiomorphies mentioned above. Grygier (1985) included 2 supposed autapomorphies in his diagnosis of Petrarca. One of them, the possession of ventral setae along the penis, is actually plesiomorphic since similar setae are found on the penis of the synagogid ascothoracidan Waginella sandersi (Newman) (see Grygier 1987). A counter-example to the second feature, the near loss of thoracic segmentation, is provided by an unnamed Australian species of Petrarca (see Grygier 1991b). These circumstances dictate the provisional assignment of the present species to Petrarca. They also suggest that Z. auriculata may have to be subsumed within Petrarca as well, if suspicions that it represents a number of similar species (Grygier 1985, Grygier & Nojima 1995) prove unfounded. A generic level revision of the Petrarcidae is beyond the scope of this paper, however

Appendix 1. List of infested coral specimens

NMNH[a] specimens. Hypertrophied corallites on the following 3 dry lots from the Hawaiian Islands have already been reported by Squires (1965a) and Cairns (1984):
(1) *Madrepora kauaiensis*, holotype, USNM 20780 (corallum) and Registry of Tumors in Lower Animals RTLA #54 (photographs only), 'Albatross' Stn 4136, 22°05'10"N, 159°19'05"W, 538–644 m, 1 Aug 1902, 3 affected corallites.
(2) *M. kauaiensis*, USNM 60564, SANGO 14, Stn 1, 21°18'N, 157°32.9'W, 362 m, 18 Jan 1972, 1 affected corallite.
(3) *M. oculata*, USNM 60563, MIDWAY Stn 13, 21°24.9'N, 168°38.3'W, 627–750 m, 29 Jul 1972, 1 affected corallite.
BMNH specimen. *Madrepora oculata*, BMNH 1885.12.30.20, Japan (no other data), dry with 1 affected corallite.

NNM specimen. *Madrepora oculata*, NNM 22728, Danish Expedition to the Kei-Islands Stn 50, 5°34'S, 132°25'40"E, 233 m, 4 May 1922, dry with 1 affected corallite.

WAM specimens. All the affected specimens are identified as *Madrepora oculata*. They are fully dried and bleached and no traces of tissue or endoparasites remain. They were collected by S. Slack-Smith during the Northwest Shelf Survey in February 1984, aboard FV 'Soela' Each of the following lots includes at least 1 coral with 1 or more hypertrophied corallites:
(1) Stn SO 01/84/051 (WAM 801–84), WNW of Lacepede Archipelago, 15°40.2–42.6'S, 120°37.3–34.6'E, 500–540 m, 10 Feb 1984, 2 affected corallites (Fig. 1A,D).
(2) Stn SO 01/84/052 (WAM 544–84 and WAM 802–84), WNW of Lacepede Archipelago, 15°46.4–43.8'S, 120°39.9–39.8'E, 446–450 m, 10 Feb 1984, 2 affected corallites.
(3) Stn SO 01/84/075 (WAM 797–84), NW of Augustus Is., 13°51.4–52.8'S, 123°01.8'–122°59.0'E, 308–306 m, 14 Feb 1984. 1 affected corallite.
(4) Stn SO 01/84/078 (WAM 800–84), NW of Augustus Is., 13°27.6–25.0'S, 122°44.4–47.0'E, 444–440 m, 14 Feb 1984, 4 affected corallites (Fig. 1B).
(5) Stn SO 01/84/080 (WAM 722–84), NW of York Sound, 12°48.1–50.90'S, 122°56.7–55.2'E, 496–504 m, 15 Feb 1984, 1 affected corallite.
(6) Stn SO 01/84/081 (WAM 763–84), N of York Sound, 12°54.4–50.6'S, 123°00.2–00.4'E, 452–462 m, 15 Feb 1984, 1 affected corallite.
(7) Stn SO 01/84/099 (WAM 755–84), W of Lacepede Archipelago, 16°56.8–56.3'S, 119°51.0–53.4'E, 430–432 m, 20 Feb 1984, 3 affected corallites (Fig. 1C).
(8) Stn SO 01/84/105 (WAM 734–84(1)), W of Lacepede Archipelago, 16°56.9–55.8'S, 119°52.0–53.8'E, 432 m, 21 Feb 1984, 1 affected corallite.
(9) Stn SO 01/84/108 (WAM 727–84), W of Lacepede Archipelago, 16°54.1–55.2'S, 119°55.6–53.1'E, 434 m, 21 Feb 1984, 3 affected corallites (Fig. 1E,F).
(10) Stn SO 01/84/109 (WAM 7–87), W of Lacepede Archipelago, 16°57.4–56.6'S, 119°51.8–54.2'E, 433–434 m, 22 Feb 1984, 3 affected corallites.
(11) Stn SO 01/84/112 (WAM 776–84), W of Lacepede Archipelago, 16°55–56'S, 119°56–53'E, 434–432 m, 22 Feb 1984, 1 affected corallite.
(12) Stn SO 01/84/118 (WAM 781–84), W of Lacepede Archipelago, 16°54–59'S, 119°52–47'E, 440 m, 23 Feb 1984, 1 affected corallite.
ORI specimen. One dried branch of *Madrepora oculata*, already dead before collection. 'Hakuhô-Maru' Stn KH 73-2-44-2, southern Formosa Strait, 21°42.1'N, 117°36.9'E, 412–430 m. 19 Mar 1973, 3 affected corallites.

KARUBAR specimens. The following lots were collected in 1991 by the French-Indonesian KARUBAR Expedition in the Banda and Arafura Seas and all are identified as *Madrepora oculata*. Each lot includes at least 1 corallum with 1 or more hypertrophied corallites; some of the coralla are dry and the others were preserved in ethanol. When a taxonomic study of all the KARUBAR Scleractinia is completed (Cairns & Zibrowius unpubl.), these corals will be deposited in the NMNH, the MNHN, and the Puslitbang Oseanologi — LIPI in Djakarta, Indonesia.
(1) KARUBAR Stn CP 9, near Kai Is., Banda Sea, 5°19'21"–22'49"S, 132°30'35"–29'16"E, 361–389 m, 23 Oct 1991, 9 affected corallites.
(2) KARUBAR Stn CP 13, near Kai Is., Banda Sea, 5°26'27–34"S, 132°37'37–48"E, 393–417 m, 24 Oct 1991, 5 affected corallites.
(3) KARUBAR Stn CP 19, near Kai Is., Banda Sea, 5°15'52"–17'23"S, 133°00'01"–132°59'16"E, 604–576 m, 25 Oct 1991, 1 affected corallite.
(4) KARUBAR Stn CP 77, south of Tanimbar, Arafura Sea, 8°55'38"–56'46"S, 131°29'12"–26'46"E, 347–351 m, 3 Nov 1991, 1 affected corallite.
[a]See 'Materials and methods' for full names of institutions

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