



LIVE SPECIMENS OF THE PARASITE PETRARCA MADREPORAE (CRUSTACEA: ASCOTHORACIDA) FROM THE DEEP-WATER CORAL MADREPORA OCULATA IN JAPAN, WITH REMARKS ON THE DEVELOPMENT OF ITS SPECTACULAR GALLS

Hiroyuki Tachikawa

Coastal Branch of Natural History Museum and Institute, Chiba, Katsuura, Chiba, Japan

Mark J. Grygier

Lake Biwa Museum, Kusatsu, Shiga, Japan. Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung City, Taiwan, R.O.C., thecostracans@gmail.com

Stephen D. Cairns

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Follow this and additional works at: <https://jmstt.ntou.edu.tw/journal>



Part of the [Animal Sciences Commons](#)

Recommended Citation

Tachikawa, Hiroyuki; Grygier, Mark J.; and Cairns, Stephen D. (2020) "LIVE SPECIMENS OF THE PARASITE PETRARCA MADREPORAE (CRUSTACEA: ASCOTHORACIDA) FROM THE DEEP-WATER CORAL MADREPORA OCULATA IN JAPAN, WITH REMARKS ON THE DEVELOPMENT OF ITS SPECTACULAR GALLS," *Journal of Marine Science and Technology*. Vol. 28: Iss. 1, Article 7.

DOI: 10.6119/JMST.202002_28(1).0007

Available at: <https://jmstt.ntou.edu.tw/journal/vol28/iss1/7>

This Research Article is brought to you for free and open access by Journal of Marine Science and Technology. It has been accepted for inclusion in Journal of Marine Science and Technology by an authorized editor of Journal of Marine Science and Technology.

LIVE SPECIMENS OF THE PARASITE PETRARCA MADREPORAE (CRUSTACEA: ASCOTHORACIDA) FROM THE DEEP-WATER CORAL MADREPORA OCVLATA IN JAPAN, WITH REMARKS ON THE DEVELOPMENT OF ITS SPECTACULAR GALLS

Acknowledgements

We thank the fishermen Kiichiro and Akihiro Tamura of Kawazu, Katsuura, Chiba Prefecture, for providing the infected colonies of *Madrepora oculata*. MJG's work at National Taiwan Ocean University relied on support for the university's Center of Excellence for the Oceans provided under the Featured Areas Research Center Program within the R.O.C. (Taiwan) Ministry of Education's Higher Education Sprout Project.

LIVE SPECIMENS OF THE PARASITE *PETRARCA MADREPORAE* (CRUSTACEA: ASCOTHORACIDA) FROM THE DEEP-WATER CORAL *MADREPORA OCULATA* IN JAPAN, WITH REMARKS ON THE DEVELOPMENT OF ITS SPECTACULAR GALLS

Hiroyuki Tachikawa¹, Mark J. Grygier^{2,3}, and Stephen D. Cairns⁴

Key words: coral parasite, gall formation, ahermatypic coral, nauplius larva.

ABSTRACT

Grossly enlarged corallites, which had earlier been interpreted as tumors, epibionts, or parasitic galls, on colonies of deep-sea scleractinians of the genus *Madrepora* from various Indo-Pacific localities, were recognized as galls in 1996 by Grygier and Cairns on account of the new species of ascothoracidan crustacean, *Petrarca madreporae* Grygier, they had found inside enlarged corallites from a site in Indonesia. Here we report the confirmatory recovery of living specimens of *P. madreporae* from an enlarged corallite of a possibly undescribed variant of *Madrepora oculata* Linnaeus in Japan. Two affected coral colonies were taken by fishermen off Katsuura, Chiba Prefecture, at ca. 480 m depth. A fully living colony had one enlarged corallite (18.3 × 13.8 mm) containing two specimens of *P. madreporae* within its basal part, along with eggs that hatched into nauplius larvae. The first and second naupliar stages resembled those of the confamilial ascothoracidan *Zibrowia ?auriculata* Grygier. The second, partly dead colony had four slightly or considerably enlarged corallites with a spongy columella and no fossa; these lacked coral tissue at the time of collection and had only empty cavities inside. Photographs of the corals, their enlarged corallites and internal cavities, and the parasites, as well as a morpho-

logical account of the successive stages of gall formation and illustrations of the parasites' nauplius larvae, are presented here. A comparison is made to enlarged corallites in another deep-sea coral, *Lophelia pertusa* (Linnaeus), attributed to infection by sponges, along with a suggestion of a possible mutualistic benefit to the host of infection by *P. madreporae* and a full list of records of Petrarciidae and presumed petrarciid galls from Japan.

I. INTRODUCTION

Deep, cold-water coral “reefs”, with a framework of branching ahermatypic and azooxanthellate scleractinian corals of such genera as *Lophelia*, *Oculina*, *Enallopsammia*, *Solenosmilia*, and *Madrepora*, have become the subject of much recent attention (e.g., Roberts et al., 2009; Hourigan et al., 2017), especially in connection with damage caused by deep-water trawling and mineral exploration (Gianni, 2004; Cordes et al., 2016; Reed et al., 2017). While various faunistic and ecological studies concerning the communities of organisms inhabiting these reefs have been conducted (Buhl-Mortensen et al., 2010; Quattrini et al., 2015), it is not well known among zoologists that endoparasitic crustaceans infect some of these corals. In particular, ascothoracidan crustaceans of the family Petrarciidae infect many species of azooxanthellate scleractinian corals, both deep and shallow, as well as a few shallow-water zooxanthellate species of the family Dendrophylliidae. Infected corals have been found worldwide (e.g., Zibrowius and Grygier, 1985; Grygier, 1991b). Occurrences in Japanese waters have been documented by Grygier and Nojima (1995) and Grygier (1996).

Most petrarciids live in pairs in a cavity within a single calice, usually resulting in a spongy enlargement of the columella; such growths are referred to as “internal galls”. A few species in dendrophylliid corals form rounded “external galls” outside the calices, on the branches or embedded in the corallum of the colony. The absence of an aperture in most

Paper submitted 07/23/19; revised 10/31/19; accepted 11/18/19. Author for correspondence: Mark J. Grygier (e-mail: thecostracans@gmail.com).

¹ Coastal Branch of Natural History Museum and Institute, Chiba, Katsuura, Chiba, Japan

² Lake Biwa Museum, Kusatsu, Shiga, Japan

³ Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung City, Taiwan, R.O.C.

⁴ Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Table 1. List of species of Petrarciidae previously recorded from Japan, and of dry corals from Japan with galls apparently induced by unknown petrarciid ascothoracidans.

Petrarciid species	Locality, depth	Host coral(s)
<i>Introcornia conjugans</i> Grygier, 1983	Tosa Bay, 100-300 m (?)	<i>Caryophyllia quadrageria</i> (Alcock, 1902) (reported as <i>C. decapali</i> Yabe and Eguchi, 1942)
<i>Petrarca bathyactidis</i> Fowler, 1889	Challenger Stn. 241, 4209 m	<i>Fungiacyathus</i> cf. <i>marenzelleri</i> (Vaughan, 1906)
<i>Petrarca morula</i> Grygier, 1991	Amakusa; Okinawa	<i>Turbinaria frondens</i> (Dana, 1846), <i>T. stellulata</i> (Lamarck, 1816), <i>T. ?reniformis</i> Bernard, 1896
<i>Petrarca ?okadai</i> , Grygier, 1981	Tanabe Bay	<i>Tubastraea? coccinea</i> Lesson, 1829
<i>Petrarca madreporae</i> Grygier in Grygier and Cairns, 1996	Japan	<i>Madrepora oculata</i> Linnaeus, 1758 (dried; identity of parasite inferred)
<i>Zibrowia ?auriculata</i> Grygier, 1981	Tanabe Bay; Okinawa, 2-4 m	<i>Tubastraea</i> spp., <i>Dendrophyllia</i> spp.
Unknown, gall	Ise, 100 m; no data	<i>Deltocyathus vaughani</i> Yabe and Eguchi, 1932
Unknown, gall	Cape Ashizuri, 393 m	<i>Deltocyathus magnificus</i> Moseley, 1876
Unknown, gall	Suruga Bay, 123 m; SW Kyushu, 132 m	<i>Anthemiphyllia dentata</i> (Alcock, 1902)
Unknown, gall	Sagami Bay	<i>Flabellum pavoninum</i> Lesson, 1831
Unknown, gall	Amakusa, 40-60 m	<i>Truncatoflabellum ?spheniscus</i> (Dana, 1846)
Unknown, gall	Amakusa, 82 m	<i>Truncatoflabellum</i> sp.
Unknown, gall	Tosa Bay, 100-300 m (?)	<i>Endopachys grayi</i> Milne Edwards and Haime, 1848
Unknown, gall	No data	<i>Balanophyllia vanderhorsti</i> Cairns, 2001 (reported as <i>B. ?ponderosa</i> van der Horst, 1926)
Unknown, gall	Sagami Bay; Satsuma Peninsula, 270 m	<i>Enallopsammia rostrata</i> (Pourtales, 1878)
Unknown, gall	Tateyama Bay; Tanabe Bay; Amakusa; Okinawa	<i>Turbinaria frondens</i> , <i>T. ?frondens</i>
Unknown, gall	Ogasawara	<i>Turbinaria reniformis</i>
Unknown, gall	Tateyama Bay	<i>Turbinaria</i> sp.

References: Fowler, 1889; Grygier, 1983, 1985, 1990, 1996; Grygier and Cairns, 1996; Grygier and Nojima, 1995; Okada, 1938; Zibrowius and Grygier, 1985.

petrarciid galls implies lack of access to any source of food other than the host coral and supports the common view that the petrarciids' relationship with their hosts is principally parasitic (Part 3 of the Discussion herein addresses the possibility of mutualism). Especially the external galls might be mistaken for galls inhabited by other sorts of crustacean, such as gall crabs of the family Cryptochiridae (e.g., Abelson et al., 1991; Wei et al., 2013; Vehof et al., 2016) or parasitic copepods (e.g., Dojiri and Grygier, 1990; Kim and Yamashiro, 2007). In lacking an aperture, they also resemble dead, overgrown pyrgomatid coral-barnacles (cf. Chan et al., 2013) and many sorts of solid "skeletal growth anomalies" of various and often unknown etiology in corals (e.g., Work et al., 2015).

Up to now, five petrarciid species have been known from Japanese waters, as well as nine species of dry corals with galls but no preserved parasites (Table 1). The known parasites have included one species of *Introcornia* (subfamily Introcorniinae), as well as three species of *Petrarca* and one of *Zibrowia* (subfamily Petrarciinae). Here we report one more, the presence of which in Japan has only been inferred until now.

II. MATERIALS AND METHODS

Two colonies and a branch fragment of *Madrepora oculata* Linnaeus, 1758 with a number of aberrant, enlarged or hypertrophied corallites were collected on 11 March 2009 by hook-and-line fishermen at the Kinme-ba fishery ground 25.7 km SE off Katsuura, Chiba Prefecture, at a depth of ca. 480 m, and brought immediately to the Coastal Branch of Natural History Museum and Institute, Chiba. There, after several hours at room temperature, they were kept in sea water in a refrigerator. That same evening, the proximal part of each aberrant corallite was opened with a Dremel (Mt. Prospect, IL, U.S.A.) rotary tool, and a pair of parasites found in one of them was removed along with parasite eggs. After being photographed alive, the coral was preserved in 70% ethanol, one parasite was fixed in 99.5% ethanol for eventual molecular systematic study, and the other was fixed in Bouin fluid for eventual histological examination. Nauplius larvae hatched from the eggs immediately; some were fixed in formalin and in 99.5% ethanol soon after hatching, and the remainder were similarly fixed 24 and (most specimens) 48 hr

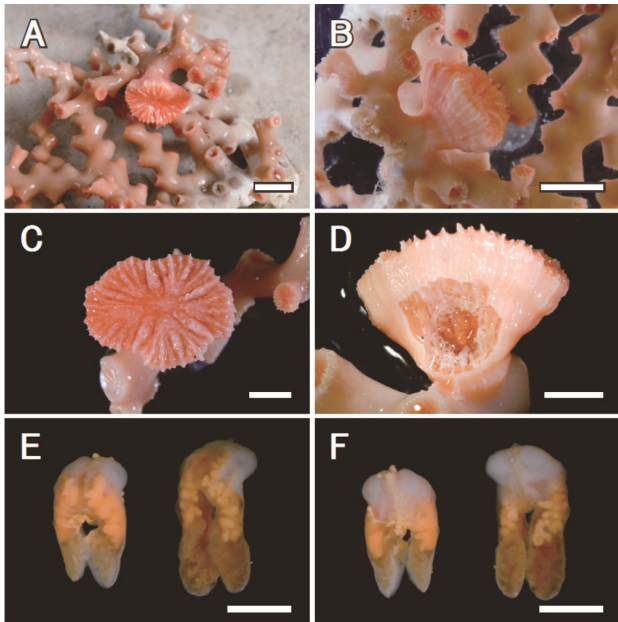


Fig. 1. Living specimen of *Madrepora oculata* (colony 1: CMNH-ZG 05408) with a greatly hypertrophied corallite containing two specimens of the petrarcid ascothoracidan *Petrarca madreporae*. A. Overview of part of colony. B. Photo of immersed coral, showing partly extended tentacles of normal and hypertrophied corallites. C. Calicular view of hypertrophied corallite. D. Lateral view of hypertrophied corallite, with part of theca removed to show internal cavity and parasites inside. E. Two adult specimens of *Petrarca madreporae* (CMNH-ZC 02533) removed from hypertrophied corallite, dorsal view. F. Same, ventral view. Scales: 10 mm in A and B, 5 mm in C and D, 2 mm in E and F.

later. Photographs of the fresh corals, their aberrant corallites, and the internal cavities of the latter were taken with a Nikon D200 DSLR digital camera fitted with an AF-S Micro Nikkor 60 mm G lens. Photographs of the living parasites were taken with the same camera fitted with a Macro Nikkor 12 cm lens mounted on a Nikon Multiphot bellows. Additional photos of corals (Figs. 2E, G, H) were taken in 2017 with a Nikon Df DSLR digital camera fitted with an AF-S Micro Nikkor 60 mm G lens. Estimates of calice area were based on these photographs, using the formula $A = \pi((GCD + LCD)/4)^2$ for these ovoid but not precisely elliptical structures, where A is the area and GCD and LCD are the greater and lesser calicular diameters, respectively. Drawings of nauplii temporarily mounted on glass slides in glycerine were made using a Nikon Optiphot-2 compound microscope with phase contrast optics and a drawing tube.

III. RESULTS

1. Aberrant Corallites of *Madrepora oculata*

Colony 1, CMNH-ZG 05408:

The color of the living polyps was orange, and the skeleton was light brown. The colony was ca. 130 × 120 × 45 mm in

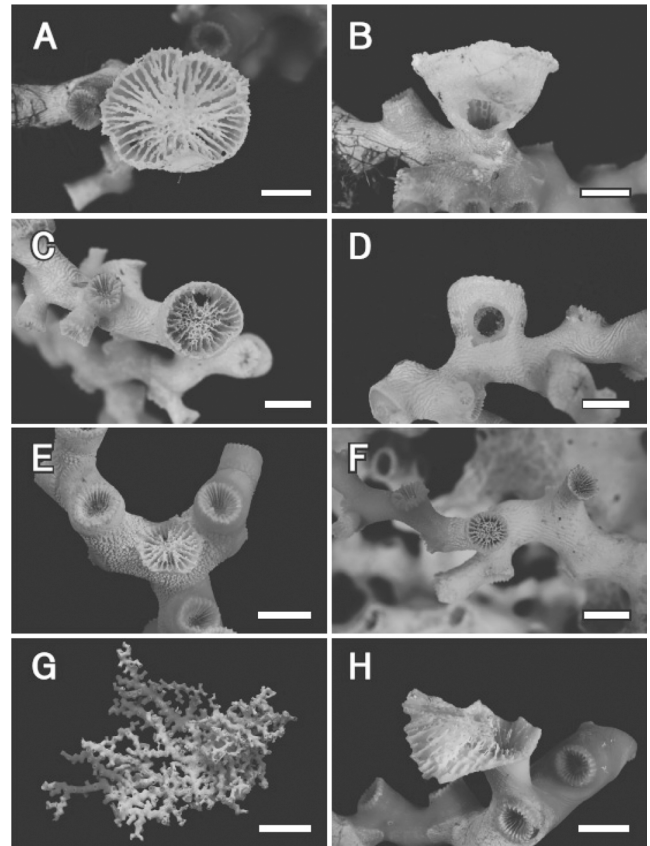


Fig. 2. Hypertrophied corallites on dead parts of *Madrepora oculata* colonies. A. Calicular view of corallite No. 1 of *M. oculata* colony 2 (CMNH-ZG 05409). B. Same, lateral view showing cavity artificially exposed within base of corallite. C. Calicular view of corallite No. 2 in same colony 2. D. Same, lateral view showing cavity artificially exposed within corallite. E. Calicular view of corallite No. 3 in same colony, in axil. F. Calicular view of corallite No. 4 of same colony, only slightly enlarged. G. *M. oculata* colony 2, source of hypertrophied corallites Nos. 1-4 shown in A-F. H. Oblique calicular view of damaged hypertrophied corallite of *M. oculata* branch fragment (CMNH-ZG 05410). Scales 5 mm, except 50 mm in G.

size and the branch diameter decreased from 8.5 mm near the base of the colony to 3.5 mm near the tips of the branches. One enlarged corallite was present.

In this colony, calices of normal corallites (Fig. 1A, B; see also Fig. 2) were rounded to slightly elliptical with a GCD of 4.5-5.0 mm and a corresponding calice area of ca. 15.9-19.6 mm². The septa of most corallites were hexamerally arranged in three complete cycles (24 septa in total), but some corallites had an additional pair of fifth-cycle septa (26 septa in all). The tentacles of the living polyps were short, conical, and orange in color (Fig. 1B). The septa were solid (not porous) with smooth margins. The fossa was moderately deep, containing a small columella composed of a few papillae.

The enlarged, conical corallite infected by *Petrarca* parasites had a slightly scalloped, elliptical calice with a GCD of 18.3 mm and LCD of 13.8 mm, a calice area of ca. 198 mm²,

and a pedicel diameter of ca. 7.0 mm (Fig. 1A-D). The septa were 48 in number, but the septal arrangement was obscured by the soft tissue covering the calice (five primary septa; possibly 5-5-10-20-6-2). The tentacles were bluntly conical and larger than those of normal corallites (Fig. 1B). The calicular surface was almost flat with no fossa. An internal cavity 3.5 mm wide and ca. 6 mm deep lying below the spongy columella was occupied by a pair of petraroid parasites (Fig. 1D).

Colony 2, CMNH-ZG 05409:

This colony (Fig. 2G) was ca. 260 x 190 x 70 mm in size. It was mostly dead when collected and only a few branches retained living tissue. Its normal corallites were of the same size and structure as in the previous colony (Fig. 2A-F). Four of the dead corallites (Nos. 1 to 4) were aberrant in structure, each having an empty cavity below a spongy columella.

Corallite No. 1 (ZG 05409a) (Fig. 2A, B): This is a large, conical corallite with an ovoid calice of 16.1 x 12.4 mm in GCD and LCD, a calice area of ca. 157 mm², and a pedicel diameter of 5.8 mm. The septa are 50 in number, hexamerally arranged in four cycles but lacking a pair of S4 and having two pairs of S5 (6-6-12-22-4). The septa are lamellar and irregularly porous, with the axial edges merging into the columella. The latter is large and spongy, its diameter being about one third of the GCD. The calicular surface is almost flat, with no fossa. An empty cavity 3.5 mm across and more than 4.5 mm deep lies below the columella (Fig. 2B).

Corallite No. 2 (ZG 05409b) (Fig. 2C, D): This is a trochoid corallite with a slightly elliptical calice of 9.0 x 8.3 mm in GCD and LCD, a calice area of ca. 58.6 mm², and a pedicel diameter of 7.7 mm. The septa are 30 in number, arranged hexamerally in three complete cycles with three additional pairs of S4 (6-6-12-6). The calicular elements are considerably damaged, but the remaining septa are highly porous, almost mesh-like, and merge into the large, spongy columella. The diameter of the latter is about half that of the GCD. An empty cavity ca. 2.5 mm across and more than 4 mm deep lies below the columella (Fig. 2D).

Corallite No. 3 (ZG 05409c) (Fig. 2E): This corallite sits immersed within a branch axil, with a nearly circular calice of 6.2 x 6.0 mm in GCD and LCD and a calice area of 29.2 mm². The septa are 26 in number, arranged hexamerally in three complete cycles with an additional pair of S4 (6-6-12-2). The septa are porous and irregularly dentate, with the axial edges merging into the spongy columella. The diameter of the latter is about one third of the GCD. The calicular surface is flat, with no fossa. An empty cavity of ca. 1.8 mm in diameter lies below the columella (not shown).

Corallite No. 4 (ZG 05409d) (Fig. 2F): This corallite is about the same size as a normal corallite, but it has a relatively large, spongy columella and a flat calicular surface (no fossa). The GCD and LCD are 4.6 and 4.3 mm, respectively, and the calice area is ca. 15.5 mm². The septa are hexamerally arranged in three complete cycles (6-6-12; 24 septa in total). The columella diameter is about a third of the GCD, and a small, empty cavity of ca. 1.2 mm in diameter lies below it (not shown).

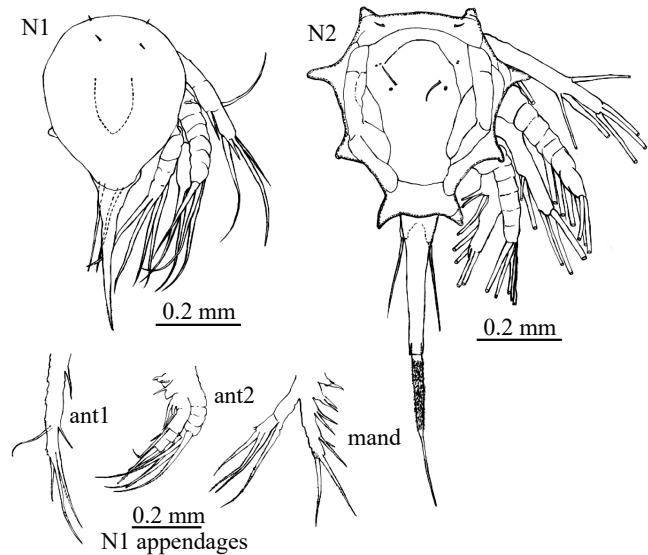


Fig. 3. Line drawings of instar I (N1) and instar II (N2) nauplius larvae hatched from eggs brooded by adults of *Petrarca madreporae* within cavity below columella of greatly hypertrophied corallite of living *Madrepora oculata* colony (see Fig. 1), and appendages of N1 (ant1, first antennule; ant2, second antenna; mand, mandible); terminal spine of N2 not fully evaginated. Scales 0.2 mm.

Branch fragment with a gall, CMNH-ZG 05410:

This specimen consists of one large but severely damaged corallite from a branch fragment collected together with the above two colonies (Fig. 2H). Only a slender pedicel of 4.4 mm in diameter and about one sixth of the corallite remain. The presumed GCD was 15 to 20 mm, with an estimated calice area of 240 mm². A deep, rounded cavity of 2.0 mm in diameter is visible in the center of the damaged calice.

2. Parasites

The two adult petraroid ascothoracidans (Reg. No. CMNH-ZC 02533) removed from CMNH-ZG 05408 were 4.3 and 5.2 mm long, and both were 2.3 mm wide (Fig. 1E, F). They were identified as *Petrarca madreporae* Grygier, 1996 based on their possession of diagnostic features noted by Grygier and Cairns (1996): the posterior lobes of the carapace valves, the ventral carapace spination, four pairs of lobular thoracopods (apparently lacking legs 1 and 6), and a terminally bifid penis with non-movable rami. Mouthparts were not examined. Previously recorded specimens from Indonesia ranged from 2.4 to 4.4 mm in length, with the posterior lobes of the carapace contributing 41-54% of the total length (Grygier and Cairns, 1996). The posterior lobes in the present specimens were distinctly longer in proportion.

The two adults were accompanied by eggs that hatched immediately into nauplius larvae. Most of the preserved nauplii were instar I with the next instar well formed within, but by the time of preservation two days later, only one individual had molted to instar II. Drawings of both instars are provided here (Fig. 3). Morphological details match those of

the same two naupliar stages of the confamilial species *Zibrowia ?auriculata* from *Dendrophyllia* and *Tubastraea* in Okinawa, as described by Grygier (1990), with the addition of a prominent pair of anterior or anterodorsal setae in instar I.

III. DISCUSSION

1. Biogeography

Madrepora oculata is a deep-water ahermatypic and azooxanthellate coral that is found throughout the world's oceans and is one of only eight cosmopolitan scleractinian species out of a total of over 1500 species (Cairns, 1999). Being so widespread and also quite common, it is a well-known species, especially in the Atlantic Ocean (Cairns, 1979; Zibrowius, 1980). Up to now, however, specimens infected by petrarcid ascothoracidans have only been found in Indonesia and, with the present find, Japan. Enlarged or hypertrophied corallites attributable to these parasites and interpreted as galls are known at low prevalences in *M. oculata* from various places in the Central and Western Pacific and Eastern Indian oceans, including Japan (Grygier and Cairns, 1996), but petrarcid infection, at least that involving massively hypertrophied corallites, appears to be non-existent in this coral in the Atlantic Ocean.

2. Identity of host coral

The morphology of *Madrepora oculata* is well studied (reviewed by Cairns and Zibrowius, 1997). The range of greater calicular diameter in almost all previously reported normal (i.e., not parasitized) colonies, including some from Japan, has been 2.5-3.8 mm, corresponding to a calice area of 5-12 mm². All of these colonies also had only 24 septa per calice, i.e., full three cycles of hexamerally arranged septa. In the present colonies from Japan, however, even the normal calices are mostly larger than this, with a GCD of up to 5.0 mm (calice area ca. 19.6 mm²); furthermore, some of the present calices have 26 septa, a condition that has not previously been reported. It is possible that the petrarcid parasites have a generalized effect on an infected colony, resulting in overall slight enlargement of calices formed subsequent to infection and with the addition of an extra pair of septa in the space thereby made available, but this should not affect calices that were formed before petrarcid infection occurred. We need to consider another possibility. Some uninfected colonies collected from the same region have a calicular size as large as the present colonies do, while others have smaller calices (Tachikawa, pers. obs.). Ogawa and Takahashi (2008) noted similar size variation in GDP in colonies from Sagami Bay, which borders the Boso Peninsula to the west – up to 3.2, 4.0, and 5.3 mm in three colonies they identified respectively as ordinary *M. oculata*, *M. oculata* forma A, and *M. oculata* forma B. Since there were very few normal-sized calices in the present colonies, and Ogawa and Takahashi (2008) considered their colony with large calices to be a distinct form, we

must consider the possibility that the population of *Madrepora* around the Boso Peninsula includes an undescribed variant distinct from *M. oculata* per se, or even a different taxon. The specific identity of the parasites may also need to be reappraised.

3. Hypertrophy of infected corallites

Varying degrees of corallite enlargement are apparent in the present material. Arranged in order from normal sessile corallites through sessile corallites showing initial stages of modification (ZG 05409d, 05409c) and subsequent trochoid (ZG 05409b) and conical stages (ZG 05408, 05409a), these specimens appear to show how the abnormal corallites actually grow. Solid, smooth-margined septa mostly arranged hexamerally in three cycles and a moderately deep fossa with a small columella composed of a few papillae give way first to porous, irregularly dentate septa with the inner edges merging into a relatively large, spongy columella and a flat calicular surface with no fossa; which is followed by an increase in septa number while the septa become highly porous, almost meshlike; and eventually by the assumption of a larger, dish-like or conical form on a pedicel with even more lamellar, irregularly porous septa more or less hexamerally arranged in four cycles. The next and final stage seems to be a senescent form not observed in the present material that has secondary corallites developed on the calicular surface, as described by Grygier and Cairns (1996).

During the review process for Grygier and Cairns (1996), doubts were expressed that *Petrarca madreporae* actually induces hypertrophy of the corallites; perhaps the crustaceans are secondary invaders. Sutherland et al. (2004) furthermore noted that the attribution of hypertrophy to the ascothoracidan failed to meet Koch's postulates for proving the causation of a disease. The same can certainly be said for all petrarcid parasites so far recorded from internal and external galls on shallow- and deep-dwelling scleractinians worldwide. Koch's postulates, however, are best applied to micro-organisms, and the circumstantial evidence in favor of petraruids as the causative agent seems convincing to us, even as the physiological mechanism and the histological condition of the coral tissue in hypertrophied corallites remain unstudied. In *Madrepora oculata*, at least, no hypertrophied corallite whose interior we have exposed has failed to reveal the presence of either *P. madreporae* or an empty cavity beneath the spongy columella. This includes slightly enlarged corallites (ZG 05409c, 05409d) interpreted above to represent an earlier stage of gall formation than the smallest dish-shaped infected corallites reported by Grygier and Cairns (1996), which have correspondingly smaller cavities inside. Lacking evidence of any other macroscopic endoparasite, we assume that such cavities were formerly occupied by young individuals of this crustacean. Without trying to judge the true nature of the relationship, Rogers et al. (2015) included this association (while misspelling the generic name of the crustacean as "*Petracha*") in the section on galls in their review of diseases of deep-sea corals.

One analogous case of symbiont-related enlarged corallites involving a different deep-sea coral must be mentioned, however. In *Lophelia pertusa* (Linnaeus, 1758) (recently also called *Desmophyllum pertusum*; Addamo et al., 2016), both flared and – presumably a later stage – swollen corallites with successively larger numbers of septa than usual have been attributed to infection by several taxa of boring sponges (Beuck et al., 2007). The sponge excavates chambers not only within the base of the corallite, but also, and mainly, within its swollen walls. This very extensive excavation, together with the rather puckered, not bell-shaped look of the distal end of late-stage affected corallites, readily distinguishes the sponge-induced deformation in *L. pertusa* from that seen in *Madrepora oculata*. It may be that *Petrarca madreporae* is a secondary invader of such sponge-excavated cavities in *M. oculata*, but we think it unlikely. Not mentioned by Beuck et al. (2007), *L. pertusa* is also the host of a petrarcid, *Introcornia australis* Grygier, 1991, which was recovered from within an internal gall about 1 cm below the calice edge of a colony from the sub-antarctic St. Paul Island in the Indian Ocean (see Grygier, 1991a). There was no external evidence of infection, so it can be assumed no sponge was involved.

The hypertrophied corallites reported herein have a calice area of up to 198 mm², about 11 times greater than the largest typical corallite on the same colonies. The largest aberrant corallite reported by Grygier and Cairns (1996) had a calice area of 271 mm², or 22 times the area of a larger normal corallite on its own colony. Concomitant with the increase in size of the corallites is an increase in the number of septa: some of the hypertrophied corallites reported herein having 50 septa, and there were as many as 82 in one reported by Grygier and Cairns (1996). The apparently pentamerous rather than hexamerous symmetry of the septa in the enlarged corallite of Colony 1 herein (Fig. 1C) is very unusual. In scleractinians each septum corresponds to a tentacle (Vaughan and Wells, 1943), and tentacles are used by the coral both for protection and to capture food. These larger, hypertrophied corallites may, therefore, have an increased ability compared to uninfectious ones to obtain food and to protect the colony. If so, the relationship between *Petrarca madreporae* and its host *Madrepora oculata* may be at least partially mutualistic, although doubtlessly still highly weighted in favor of the parasite. Any advantage to the host may be offset by restriction of the gastrovascular cavity owing to the presence of the parasites and the enlarged columella, and we know nothing about the effects of petrarcid infection on host coral reproduction.

4. Petrarcid larval biology.

The immediate hatching of parasite eggs brooded within the cavity occupied by the present living pair of *Petrarca madreporae* may be usual for petraruids. This phenomenon has been observed in *Zibrowia ?auriculata* infecting various shallow-water *Tubastraea* and *Dendrophyllia* corals in Okinawa (e.g., Grygier, 1990). Natural release of nauplius larvae has been observed in petraruids inhabiting external galls on

Turbinaria corals – the larvae burrow through the spongy coenosteum to the outside (G.A. Kolbasov, pers. comm.) – but not yet in other scleractinian genera. Perhaps it also occurs as the result of damage to the host corals caused by geological cataclysms or predation. Shallow-water corals may be broken during typhoons, but not deep-dwelling *Madrepora*.

5. Conservation biology.

Petrarca-infected *Madrepora* colonies provide a good example of a “hidden” part of the deep-water reef community that is frequently overlooked by biodiversity researchers. Not only *Madrepora oculata*, but other larger deep-water (> 200 m) scleractinians of branched colony form also serve as hosts of described species of Petraridae or have been recorded as bearing a gall attributed to petrarcid infection: *Enallopsammia rostrata* (Pourtalès, 1878), sometimes reported as *E. amphelioides* (Alcock, 1902); *E. profunda* (Pourtalès, 1867); and *Lophelia pertusa* (see Grygier, 1985, 1991a; Zibrowius and Grygier, 1985; Grygier and Nojima, 1995). These parasites, along with other, less obvious associates such as copepods, are at least as vulnerable to human activities as their coral hosts are (Buhl-Mortensen and Mortensen, 2004), and should be borne in mind as part of the rationale for preserving deep-water “reefs”.

ACKNOWLEDGMENTS

We thank the fishermen Kiichiro and Akihiro Tamura of Kawazu, Katsuura, Chiba Prefecture, for providing the infected colonies of *Madrepora oculata*.

MJG's work at National Taiwan Ocean University relied on support for the university's Center of Excellence for the Oceans provided under the Featured Areas Research Center Program within the R.O.C. (Taiwan) Ministry of Education's Higher Education Sprout Project.

REFERENCES

- Abelson, A., B. S. Galil and Y. Loya (1991). Skeletal modifications in stony corals caused by indwelling crabs: hydrodynamical advantages for crab feeding. *Symbiosis* 10, 233-248.
- Addamo, A. M., A. Vertino, J. Stolarski, R. García-Jiménez, M. Taviani and A. Machordom (2016). Merging scleractinian genera: the overwhelming genetic similarity between solitary *Desmophyllum* and colonial *Lophelia*. *BMC Evolutionary Biology* 16, 108.
- Beuck, L., A. Vertino, E. Stepina, M. Karolczak and O. Pfanckuche (2007). Skeletal response of *Lophelia pertusa* (Scleractinia) to bioeroding sponge infestation visualized with micro-computed tomography. *Facies* 53, 157-176.
- Buhl-Mortensen, L. and P. B. Mortensen (2004). Symbiosis in deep-water corals. *Symbiosis* 37, 33-61.
- Buhl-Mortensen, L., A. Vanreusel, A. J. Gooday, L. A. Levin, I. G. Priede, P. Buhl-Mortensen, H. Gheerardyn, N. J. King and M. Raes (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* 31, 21-50.
- Cairns, S. D. (1979). The deep-water Scleractinia of the Caribbean and adjacent waters. Studies on the Fauna of Curaçao and Other Caribbean Islands 57, 1-341.
- Cairns, S. D. (1999). Species richness of Recent Scleractinia. *Atoll Research*

- Bulletin 459, 1-46.
- Cairns, S. D. and H. Zibrowius (1997). Cnidaria Anthozoa: Azooxanthellate Scleractinia from the Philippine and Indonesian regions. *Mémoires du Muséum National d'Histoire Naturelle* 172, 27-243.
- Chan, B. K. K., Y.-Y. Chen and Y. Aчитuv (2013). Crustacean Fauna of Taiwan: Barnacles, Volume II (Cirripedia: Thoracica: Pyrgomatidae). Biodiversity Research Center, Academia Sinica, Taipei.
- Cordes, E. E., D. O. B. Jones, T. A. Schlacher, D. J. Amon, A. F. Bernardino, S. Brooke, R. Carney, D. M. DeLeo, K. M. Dunlop, E. G. Escobar-Briones, A. R. Gates, L. Genio, J. Gobin, L.-A. Henry, S. Herrera, S. Hoyt, M. Joye, S. Kark, N. C. Mestre, A. Metaxas, S. Pfeifer, K. Sink, A. K. Sweetman and U. Witte. (2016). Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. *Frontiers in Environmental Science* 4, 58, doi: 10.3389/fenvs.2016.00058.
- Dojiri, M. and M. J. Grygier (1990). *Pionomolgus gallicolus*, gen. et sp. nov. (Poecilostomatoida: Lichomolgidae), a gall-inducing copepod of a scleractinian coral from Australia. *Australian Journal of Zoology* 37, 695-703.
- Fowler, G. H. (1889). A remarkable crustacean parasite, and its bearing on the phylogeny of the Entomostraca. *Quarterly Journal of Microscopical Science, New Series* 30(118), 107-120, Pl. VIII.
- Gianni, M. (2004). High Seas Bottom Trawl Fisheries and their Impact on the Biodiversity of Vulnerable Deep-Sea Ecosystems: Options for international action. IUCN, Gland, Switzerland.
- Grygier, M. J. (1983). *Introcornia conjugans* n. gen. n. sp., parasitic in a Japanese ahermatypic coral (Crustacea: Ascothoracida: Petrarciidae). *Senckenbergiana Biologica* 63(5/6), 419-426.
- Grygier, M. J. (1985). New ascothoracid crustacean endoparasites of Scleractinia. *Journal of Natural History* 19, 1029-1043.
- Grygier, M. J. (1990). Early planktotrophic nauplii of *Baccalaureus* and *Zibrowia* (Crustacea: Ascothoracida) from Okinawa, Japan. *Galaxea* 8, 321-337.
- Grygier, M. J. (1991a) [dated 1990]. *Introcornia* (Crustacea : Ascothoracida : Petrarciidae) parasitic in an ahermatypic coral from Saint Paul Island, Indian Ocean. *Vie et Milieu* 40(4), 313-318.
- Grygier, M. J. (1991b). Additions to the ascothoracid fauna of Australia and South-east Asia (Crustacea, Maxillopoda): Synagogidae (part), Lauridae and Petrarciidae. *Records of the Australian Museum* 43, 1-46.
- Grygier, M. J. (1996). A world list of coral reef-associated Ascothoracida (Crustacea), with remarks on Lauridae, Petrarciidae, and Dendrogastridae from Okinawa, Japan. *Galaxea* 13, 15-33.
- Grygier, M. J. and S. D. Cairns (1996). Suspected neoplasms in deep-sea corals (Scleractinia: Oculinidae: *Madrepora* spp.) reinterpreted as galls caused by *Petrarca madreporae* n. sp. (Crustacea: Ascothoracida: Petrarciidae). *Diseases of Aquatic Organisms* 24, 61-69.
- Grygier, M. J. and S. Nojima (1995). Petrarciid galls and Petrarciidae (Crustacea: Ascothoracida) in some scleractinian corals from Japan. *Galaxea* 12, 83-101.
- Hourigan, T. F., P. J. Etnoyer and S. D. Cairns (eds.) (2017). The State of Deep-Sea Coral and Sponge Ecosystems of the United States. NOAA Technical Memorandum NFS-OHC-3. NOAA., Silver Spring, MD, U.S.A. Available: <https://deepsceacoraldata.noaa.gov/library/2015-state-of-deep-sea-corals-report>.
- Kim, I.-H. and H. Yamashiro (2007). Two species of poecilostomatoid copepods inhabiting galls on scleractinian corals in Okinawa, Japan. *Journal of Crustacean Biology* 27, 319-326.
- Ogawa, K. and K. Takahashi (2008). A revision of Japanese hermatypic corals around the coastal region with guide to identification – XIII. *Rhizop-sammia, Madrepora, Cyathelia, Enallopsammia, Goniocorella, and Rhizosmilia*. *Nankiseibutu* 51, 65-71.
- Okada, Y. K. (1938). Les Cirripèdes Ascothoraciques. *Travaux de la Station Biologique de Wimereux* 13, 489-514.
- Quattrini, A. M., M. S. Nizinski, J. D. Chaytor, A. W. J. Demopoulos, E. B. Roark, S. C. France, J. A. Moore, T. Heyl, P. J. Auster, B. Kinlan, C. Ruppel, K. P. Elliott, B. R. C. Kennedy, E. Lobecker, A. Skarke and T. M. Shank (2015). Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic habitats and diverse communities. *PLoS ONE* 10(10): e0139904.
- Reed, J., S. Farrington, C. Messing and A. David (2017). Distribution and habitat use of the golden crab *Chaceon fenneri* off eastern Florida based on in situ submersible and ROV observations and potential for impacts to deepwater coral/sponge habitat. *Gulf and Caribbean Research* 28, 1-14.
- Roberts, J. M., A. J. Wheeler, A. Friewald and S. D. Cairns (2009). Cold-Water Corals: The biology and geology of deep-sea coral habitats. Cambridge University Press, Cambridge, U.K.
- Rogers, A. D., K.M. Kemp, A. J. Davies and M. L. Taylor (2015). The diseases of deep-water corals. In: Woodley, C. M., C. A. Downe, A. W. Bruckner, J. W. Porter and S. B. Galloway, editors. *Diseases of Coral*, John Wiley & Sons, Hoboken, N.J., USA, 416-441.
- Sunderland, K. P., J. W. Porter and C. Torres (2004) Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. *Marine Ecology Progress Series* 266, 273-302.
- Vaughan, T. W. and J. W. Wells (1943). Revision of the suborders families, and genera of the Scleractinia. *Geological Society of America Special Publication* 44, 1-363.
- Vehof, J., S. E. T. van der Meij, M. Turkay and C. Becker (2016). Female reproductive morphology of coral-inhabiting gall crabs (Crustacea: Decapoda: Brachyura: Cryptochiridae). *Acta Zoologica (Stockholm)* 97, 117-126.
- Wei, T.-P., H.-C. Chen, Y.-C. Lee, M.-L. Tsai, J.-S. Hwang, S.-H. Peng and Y.-W. Chiu (2013) Gall polymorphism of coral-inhabiting crabs (Decapoda, Cryptochiridae): a new perspective. *Journal of Marine Science and Technology* 21(Suppl), 304-307.
- Work, T. M., L. T. Kaczmarzsky and E. C. Peters (2015). Skeletal growth anomalies in corals. In: Woodley, C. M., C. A. Downe, A. W. Bruckner, J. W. Porter and S. B. Galloway, editors. *Diseases of Coral*, John Wiley & Sons, Hoboken, N.J., USA, 291-299.
- Zibrowius, H. (1980). Les Scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Océanographique, Monaco* 11, 1-284, 107 plates.
- Zibrowius, H. and M. J. Grygier (1985). Diversity and range of scleractinian coral hosts of Ascothoracida (Crustacea: Maxillopoda). *Annales de l'Institut Océanographique (Paris), Nouvelle Série* 61(2), 115-138.