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First Record of a Bioluminescent Soft Coral: Description of a Disjunct Population of *Eleutherobia grayi* (Thomson and Dean, 1921) from the Solomon Islands, with a Review of Bioluminescence in the Octocorallia

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A population of alcyoniid soft corals assignable to the species *Eleutherobia grayi* (Thomson and Dean, 1931) is described from the Solomon Islands in the southwestern Pacific Ocean, a taxon previously known only from the Indonesian and Ryukyuan Archipelagos. The species is remarkable in that the anthocodiae are strikingly bioluminescent. This represents the first record of a bioluminescent soft coral, other than a dubious record for *Alcyonium*. Other octocorals for which bioluminescence has been verified are restricted to the gorgonian family Isididae and the Pennatulacea. A table of all octocorallian taxa in which bioluminescence has been recorded (along with newly presented data) is also included, along with a brief review of bioluminescence in the Octocorallia. Two additional species of *Eleutherobia*, which are presently unidentified and presumably undescribed, one from Palau, and the other from the Philippine and Mariana Archipelagos, are here reported to also bioluminesce.

Previously, bioluminescence in octocorals has been presumed to be restricted to many, but not all, sea pens (Pennatulacea) and two to four species of gorgonians (Alcyonacea: Isididae) (Harvey 1952; Muzik 1978). The present paper reports the discovery of bioluminescence in a species of the alcyoniid genus *Eleutherobia* from the Solomon Islands. The discovery represents the first record of bioluminescence in a soft coral.

The genus *Eleutherobia* was last revised by Verseveldt and Bayer (1988). Three species of *Eleutherobia* have recently been described: *E. lutea* Benayahu and Schleyer, 1995, from Natal, South Africa; *E. zanahoria* Williams, 2000, from the Tonga Islands; and *E. vinadigitaria* Williams and Little, 2001, also from Natal, South Africa. Seventeen described species of the genus (considered valid taxa) are known from southern Africa and the Indo-West Pacific—four from southern Africa and thirteen from the Indo-West Pacific (Somalia to Japan and Tonga). Bioluminescence has not been reported in any previously described species of the genus.

Material collected from a disjunct population of a soft coral species identified as *Eleutherobia grayi* (Thomson and Dean, 1931) is described from the Solomon Islands. The specimens do not differ morphologically from the lectotype (redescribed by Verseveldt and Bayer 1988), which was clearly illustrated with scanning electron micrographs of sclerites. However, the Solomon Islands material differs ecologically in one respect from the type material and other known specimens. The previously known material: type specimens from Indonesia, and a record from the Ryukyu Islands (Verseveldt and Bayer 1988:33), was collected from sandy or rubbly bottom substrata (sand with small stones and shells or pieces of dead coral), whereas specimens from the newly discovered population in the Solomon Islands have been observed only on hard substrata (floors, walls and ceilings of limestone caves, alcoves, and overhangs). The populations also differ bathymetrically. The Indonesian and Ryukyuan populations are known from 30–73 m, while the Solomon Islands population has been observed at shallower depths, 5–18 m.

Williams (2000:159) has summarized recent discoveries pertaining to natural products biochemistry and the genus *Eleutherobia*.

MATERIAL AND METHODS

Material for this study was collected by SCUBA and preserved directly in 70% ethanol. Sclerites were isolated by disassociating them from the coenenchyme with household bleach (sodium hypochlorite). Underwater photographs for Figure 1 were made with a Nikonis-V camera and Nikonis SB 103 flash unit. Other photographs and micrographs were made using a Nikon Coolpix 990 digital camera and a Nikon SMZ-10 dissecting microscope. Scanning electron micrographs were made with a Leo 1400 series scanning electron microscope. Sclerite drawings were made using an Olympus CH-2 compound microscope with an attached drawing tube. Digital images and plates of photographs, micrographs, and scanning electron micrographs were made using Adobe Photoshop software. An abbreviation used in the text is CAS (California Academy of Sciences, San Francisco).

SYSTEMATIC ACCOUNT

Family Alcyoniidae Lamouroux, 1812

Eleutherobia Pütter, 1900

Eleutherobia Putter, 1900:449. Verseveldt and Bayer, 1988:27. Williams, 1992:306; 2000:160. Williams and Little, 2001.

DIAGNOSIS. — Alcyoniid soft corals, colonies digitiform (finger-like), conical or cylindrical, rarely lobate to subglobular. Polyps monomorphic with calyces absent, however, retracted polyps may form low rounded or conspicuous and mound-like protuberances of the coenenchyme. Sclerites predominantly derived from radiates, with spindles, barrels, tuberculate spheroids, rod-like forms, or crosses sometimes present. Anthocodial sclerites present as crown and points, or as eight points only, or altogether absent. Color variable.

TYPE SPECIES. — *Eleutherobia japonica* Pütter, 1900, by monotypy.

DIVERSITY AND DISTRIBUTION. — Seventeen species in the Indo-West Pacific and South Africa (eastern and southern Africa to Japan, Saipan, and Tonga) (Fig. 10B).

Eleutherobia grayi (Thomson and Dean, 1931)
Figs. 1-10

Nidalia grayi Thomson and Dean, 1931:37, pl. 2 fig. 2. Type locality: Indonesia.
Eleutherobia grayi : Verseveldt and Bayer, 1988:33, figs. 24, 25.
Eleutherobia sp.: Williams, 1996:34 (color photographs taken both at night and during the day).

MATERIAL EXAMINED. — CAS 101096, station number 35, Solomon Islands, Mborokua Island (Murray's Island), 18 m depth, 9 November 1994, collected by G. C. Williams with aid of SCUBA, one whole specimen, 22 mm in length. CAS 147475, same data as CAS 101096, one specimen cut longitudinally into two halves, 29 mm in length. CAS 147476, station number 16, Solomon Islands,

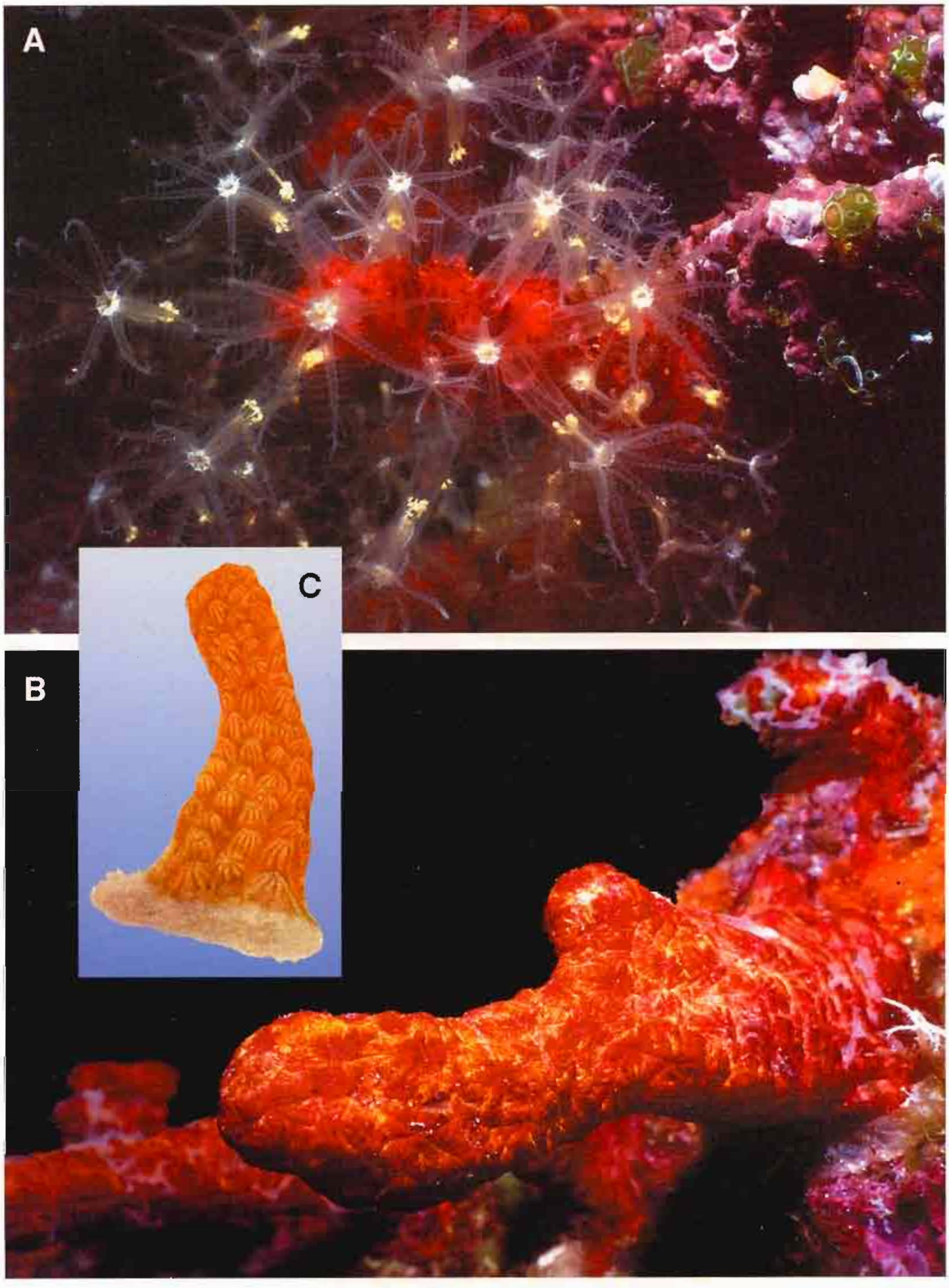

FIGURE 1. *Eleutherobia grayi*. A-B. Underwater photographs of living soft corals, Solomon Islands. Colonies (excluding polyps) are approximately 25 mm in length. A. Photograph taken at night. B. Photograph taken during midday. C. Lectotype, approximately 33 mm in length (from Thomson and Dean 1931, pl. 2 fig. 2).

Mborokua Island (Murray's Island), 10 m depth, 12 September 1998, collected by G. C. Williams with aid of SCUBA, one whole specimen, 24 mm in length. CAS 101095, station number 20, Solomon Islands, Mborokua Island (Murray's Island), 16 m depth, 4 November 1994, collected by G. C. Williams with aid of SCUBA, three whole specimens: 22 mm, 24 mm, and 27 mm in length.

DESCRIPTION. — **Growth form and size**. Alcyoniid soft corals in which the colonies are digitiform (Figs. 1A, 2E) or somewhat lobate (Figs. 1B, 2A–D), mostly cylindrical in shape (Fig. 2E), not markedly tapered, distal apex bluntly rounded (Figs. 1B, 2B–E), somewhat truncate (Figs. 1C, 2A) or somewhat clavate (Fig. 2A, C, D), not pointed. The stalk is very short, as the polyps are distributed over approximately 95% of surface of colony (Figs. 1, 2). The polyparies of most colonies arise directly from a broad holdfast (Figs. 1C, 2A). Wet-preserved colonies vary in length from 11 to 29 mm.

Polyps. The polyps are arranged uniformly over the surface of the colonies. They are monomorphic and do not have calyces, although the retracted polyps may form low rounded or mound-like protuberances on the surface of the polypary in some preserved or tightly retracted colonies (Fig. 1C). These protuberances are formed from the coenenchyme and hence cannot be defined as true calyces. In most cases, the retracted polyps are often more or less flush with the surface of the polypary (Figs. 1B, 2). Polyp sclerites are absent (Figs. 1A, 3, 4).

The living expanded polyps are colorless and translucent, 9–12 mm in length. The length of pharynx is approximately one-third the length of the body of the polyp (Figs. 1A, 3). The peristome is a lustrous and reflective opaque white, while the glandular uppermost portions of the mesenterial filaments are pale yellowish or cream-colored (Fig. 1A). The narrow elongate tentacles are mostly 6–8 mm in length, gradually taper to a point, and have two opposite rows of approximately 12–16 pinnules. (Figs. 1A, 3, 4). Wet-preserved expanded polyps are opaque white (Fig. 2B).

Sclerites. Sclerites are of several distinct types varying from 0.05 to 0.15 mm in length. In the surface coenenchyme of the polypary and holdfast are seven-radiates (Figs. 5C; 6G; 7E, O; 8I), eight-radiates (Figs. 5A, C; 6C, I; 7I, K; 8B, F, N), crosses (Figs. 7J, 8D), quadriradiates with three tubercles in one plane and one tubercle vertically disposed in the center (Fig. 6A), and triradiates (Fig. 6K). In the subsurface coenenchyme and deep interior of the colonies are tuberculate rods and irregularly-shaped, somewhat flattened, rod-like forms (Figs. 5B, D; 7G, L, P).

Color. Most colonies are brick red (Fig. 1A), but some have varying amounts of yellow coloration (Fig. 1B). Sclerite color varies from red to orange, or colorless.

DISTRIBUTION. — Solomon Islands (5–18 m depth) (present study) plus the type localities: Ceram Sea, between Misool and the western end of New Guinea; Indonesia (32 m depth) (lectotype, designated from two syntypes by Verseveldt and Bayer, 1988); and Flores Sea, northwestern end of Sumbawa, Indonesia (73 m depth) [paralectotype, designated from two syntypes by Verseveldt and Bayer (1988)]. They also reported the species from the region of Okinawa in the Ryukyu Islands, Japan (30 m depth). I have examined a large number of specimens of material assignable to the genus *Eleutherobia* from Okinawa. These specimens differ in several respects from *Eleutherobia grayi*, and are here considered to represent another (as yet undetermined) species of the genus. I therefore consider the occurrence of *Eleutherobia grayi* in the Ryukyu Archipelago as unverified (Fig. 10).

VARIABILITY. — Colony shape is variable—digitiform, or bilobate, to somewhat globular. Color is also variable depending on the proportions of red, orange, and colorless sclerites present in the coenenchyme. Some colonies are a uniform brick red, or red with yellowish polyp mounds, while others are very pale pink with cream-colored mounds created by the retracted polyps. These calyx-like mounds are usually uniformly colored, but may be bicolored in some colonies—yellow with eight radiating red stripes, or red with yellow stripes (Fig. 1).

BIOLUMINESCENCE. — During night dives on three occasions (November 1993, November 1994, and September 1998), a vivid green bioluminescence (bright green flash) was observed immediately upon tactile contact with the fully expanded polyps of *Eleutherobia grayi*. This light seems to

FIGURE 2. *Eleutherobia grayi*. A. Wet-preserved specimen (CAS 101096); 22 mm in length. B. Wet-preserved specimen with expanded polyps (CAS 147476); 24 mm in length. C. Wet-preserved specimen (CAS 147475), external view; 29 mm in length. D. Wet-preserved specimen (CAS 147475), cut longitudinally to show internal aspects; 29 mm in length. E. Wet-preserved specimen (CAS 101095); 27 mm in length. Scale bar = 12 mm.

emanate from the region of the peristome (oral disc) and the distal-most region of the pharynx (Figs. 1A, 3, 4), although the precise origin of luminescence remains uncertain. The peristome appears lustrous white under the white-light of an underwater camera flash unit, and thus displays a striking contrast to other parts of the soft coral colony (Fig. 1A). Research using epiflourescence microscopy to determine the location of photocytes in this species is in progress.

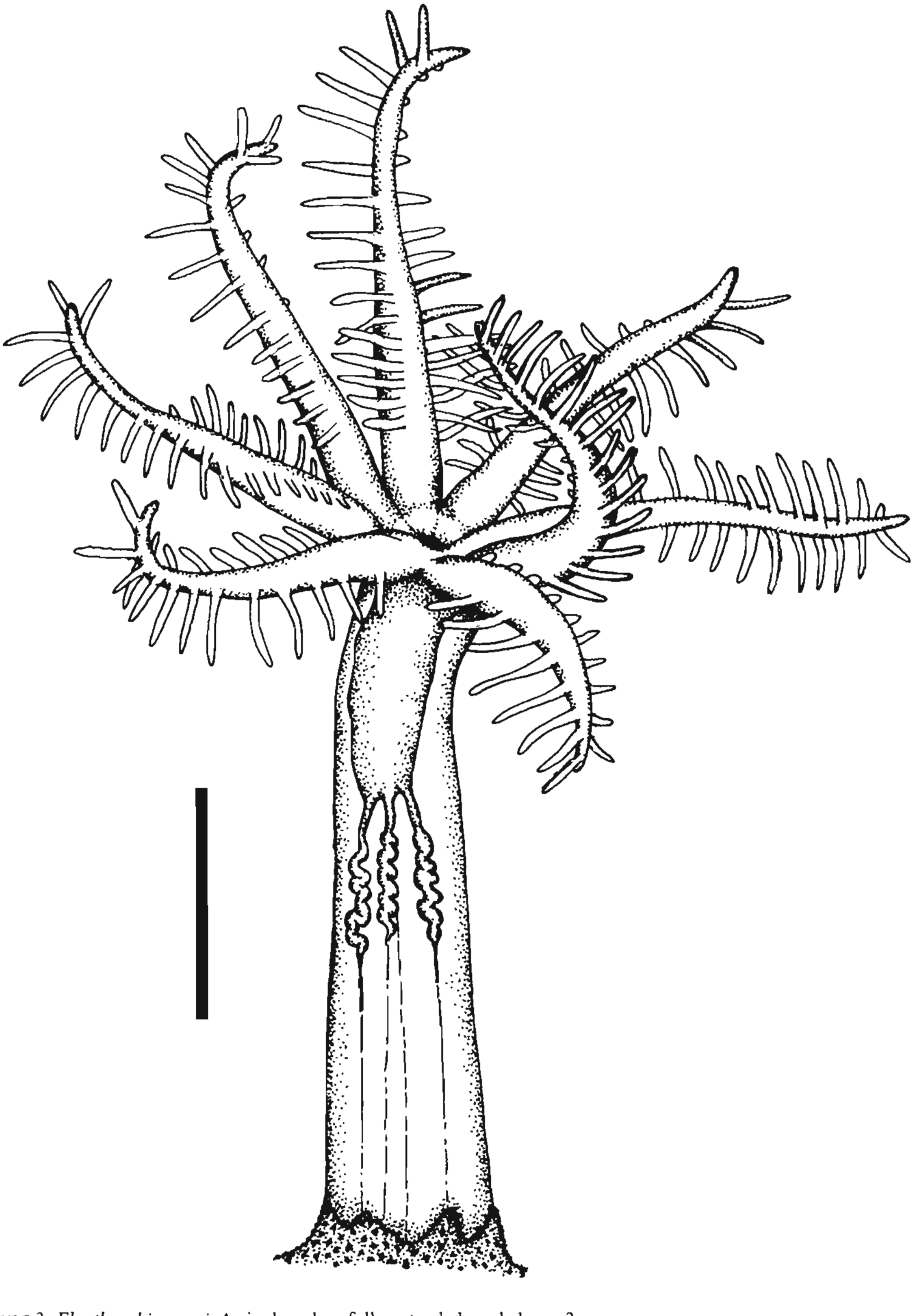

FIGURE 3. *Eleutherobia grayi*. A single polyp, fully extended; scale bar = 3 mm.

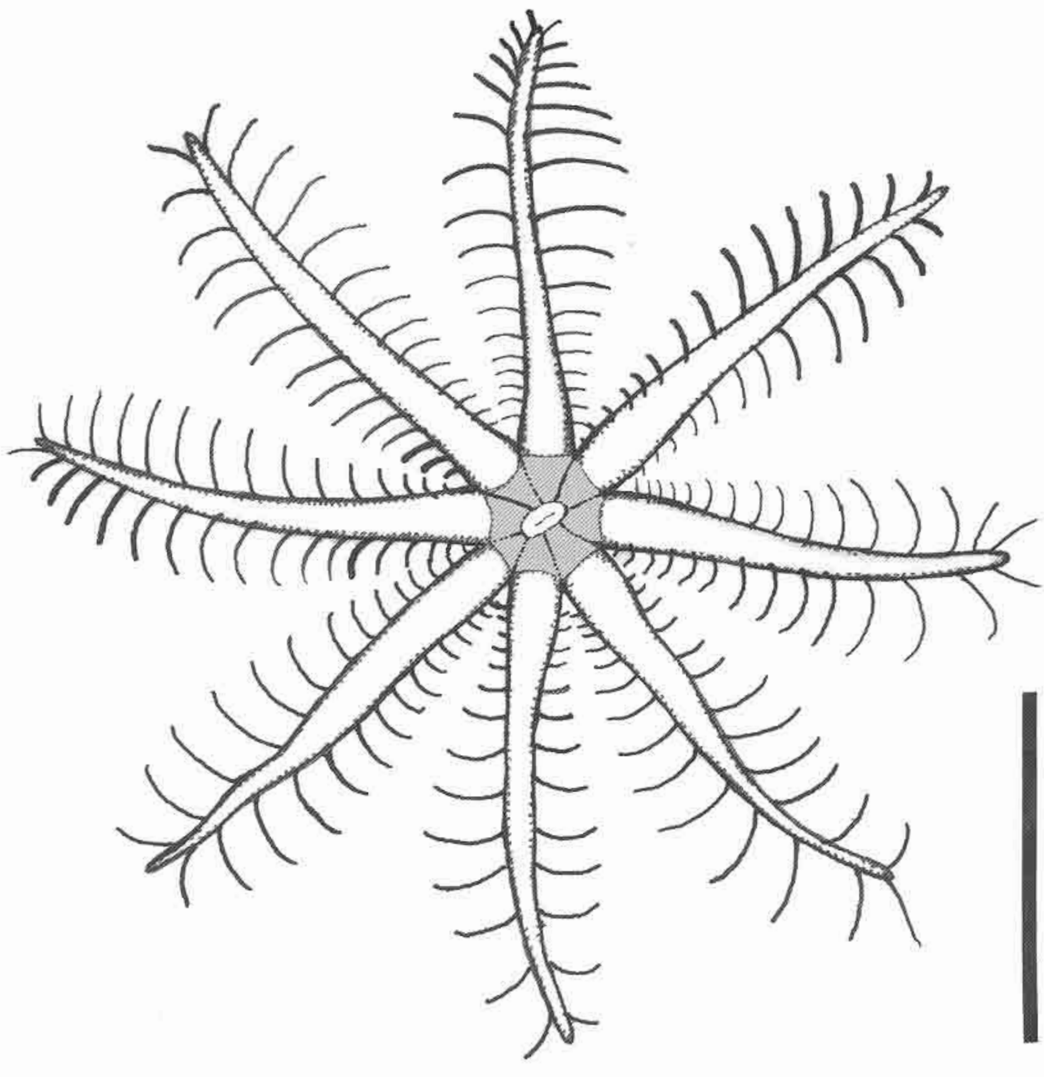

FIGURE 4. *Eleutherobia grayi*. Mouth and tentacles showing oral disc surrounding the mouth (peristome), which is the suspected region of bioluminescence; scale bar = 5 mm.

Since the polyps of *Eleutherobia grayi* are bioluminescent and devoid of scleritic armature as well, it is possible that the attribute of bioluminescence precludes the need for anthocodial armature, and may be regarded as a defense against potential predators of the soft coral polyps. Only one other described species of *Eleutherobia* (*E. zanahoria* Williams, 2000) is known to lack polyp armature, but the presence or absence of bioluminescence in this taxon is not known.

ECOLOGICAL OBSERVATIONS. — Much of the shallow water, hard coral cover at the type locality was dramatically altered between 1994 and 1998, presumably by a combination of warming events and a series of severe storms. Physical decimation of hermatypic as well as ahermatypic scleractinians took place, together with a substantial amount of bleaching (predominantly on the distal-most extremities of the coral colonies). On the exposed reef flats and slopes, replacement of hermatypic scleractinians by soft corals such as *Paralemnalia* spp. and various taxa of coralline algae, was observed during this period. In the limestone caves, alcoves, and overhangs (Fig. 9), a physical replacement of *Tubastraea faulkneri* Wells, 1982 (which provided the dominant cover in 1993 and 1994) by the soft coral *Eleutherobia grayi*, was also observed during the same period.

The polyps of the soft coral are retracted into the body of the soft coral during daylight hours (Fig. 1B), gradually expand at dusk, and remain fully expanded (in feeding mode) for the duration of the night (Fig. 1A).

Several colonies of *Eleutherobia grayi* were observed to have minute epizoites (mostly tunicates or bryozoans) growing on the surface of the polyparies, between the polyps.

REMARKS. — Morphologically, material from the Solomon Islands population fully agrees with the original description of *Eleutherobia grayi* by Thomson and Dean (1931), and the well-illustrated redescription of the designated lectotype by Verseveldt and Bayer (1988). Several important points of concurrence are listed below.

1. Total lack of sclerites in the anthocodiae.
2. Red or yellow coloration due to varying amounts of red and yellow sclerites.
3. Deep interior of colonies with many sclerites, almost exclusively rod-like forms.
4. Size range of sclerites: 0.05–0.15 mm (present study); 0.03–0.18 mm (Verseveldt and Bayer, 1988).
5. Sclerite types: Eight-radiates, seven-radiates, triradiates, crosses, quadriradiates with three tubercles in one plane and one tubercle arising vertically from the center, and irregularly-shaped tuberculate rods.

DISCUSSION

BIOLUMINESCENCE IN OCTOCORALS (Table 1). — For the sake of the following discussion, the various groups of octocorals are defined as follows. **Stoloniferous octocorals** have separate polyps connected at their bases by membranous or ribbon-like stolons. **Soft corals** have polyps embedded in a common coenenchyme and are attached to hard substrata by basal holdfasts, they have no axial development, and only free sclerites comprise the skeletal elements. **Gorgonians**, like the soft corals, have polyps embedded in a common coenenchyme and are attached to the substratum by basal holdfasts, but unlike soft corals, in addition to free sclerites, have some form of internal axial development composed of calcium carbonate, gorgonin, or a combination of the two. **Sea pens** or **pennatulaceans** have the coral colony divided into a proximal muscular peduncle that is anchored in soft substrata, and a distal rachis that contains several kinds of polyps. They may or may not have a calcareous axial skeleton.

Williams (1999:23, 49–50) provided a historical review and comprehensive bibliography pertaining to pennatulacean bioluminescence. The scientific literature regarding bioluminescence in octocorals is relatively rich, extending back to the sixteenth century with the works of Gesner, Boussuet, Imperato, Rondelet, and others. Important modern contributions include: Panceri (1871, 1872a, b); Parker (1920); Harvey (1940, 1952); Nicol (1958); Titschak (1965, 1966); Morin (1974, 1976); Muzik (1978); and Herring (1991). Harvey (1952:168) stated, "... but among the Alcyonaria are to be found some of the most brilliant and striking luminous animals. Of the three groups of Alcyonaria, the Alcyonacea, the Gorgonacea, and the Pennatulacea, only luminescence of the Pennatulacea has been carefully studied." Pertaining to alcyonaceans, only a few species in the gorgonian family Isididae have been known to luminesce. Mangold's (1910) record of Leuckart's luminescent *Alcyonium* is considered by Harvey (1952:169–170) to be "very dubious." No subsequent records of bioluminescence in the genus *Alcyonium*, or any other soft coral taxon for that matter, are known in the previous literature.

The only records of bioluminescent soft corals are represented by new data presented here of *Eleutherobia grayi* from the Solomon Islands, as well as observations made on two other species of

TABLE 1. Records of bioluminescence in octocorals.

Taxon	Depth	Color of light	References on bioluminescence
Order Alcyonacea			
Soft corals			
ALCYONIIDAE			
Eleutherobia grayi	5–18 m	green	present study
Eleutherobia sp. indet. #1 (Luzon and Saipan)	12–23 m	green	Gosliner and Starmer - pers. commun.; Williams - pers. observ.
Eleutherobia sp. indet. #2 (Palau)	20 m	—	Starmer - pers. commun.
Gorgonians			
ISIDIDAE			
Lepidisis olapa	400–450 m	white	Muzik (1978:735; 1981[82]:56)
Isidella elongata	564 m	—	Muzik (1978:735)
Keratoisis sp.	—	—	Harvey (1952:169)
Primnoisis sp.	—	—	Harvey (1952:169)
Order Pennatulacea			
Sea Pens			
VERETILLIDAE			
Cavernularia habereri	—	—	Harvey (1917)
Cavernularia pusilla	65–75 m	—	Panceri (1872a)
Veretillum cf. *manillense*	10–25 m	green	Williams - pers. observ.
Veretillum cynomorium	13–91 m	—	Bujor (1901); Titschak (1965)
ECHINOPTILIDAE			
Actinoptilum molle	12–333 m	green	Williams (1990:63)
RENILLIDAE	0–70 m		
Renilla muelleri	—	—	Parker (1920)
Renilla koellikeri	—	—	Morin (1976:632)
Renilla reniformis	—	—	Ward and Cormier (1978)
FUNICULINIDAE			
Funiculina quadrangularis	60–2600 m	lilac	Thomson (1874:149); Herring (1991)
PROTOPTILIDAE			
Distichoptilum gracile	650–4300 m	—	Herring (1991)
UMBELLULIDAE	210–6100 m		
Umbellula huxleyi	—	—	Herring (1991)
Umbellula thomsoni	—	—	Tizard et al. (1885:49)
VIRGULARIIDAE			
Stylatula elongata	9–50 m	—	Morin (1976:632)
Acanthoptilum gracile	10–146 m	—	Morin (1976:630)
Virgularia mirabilis	9–400 m	—	Herdman (1913); Nicol (1958)
PENNATULIDAE			
Ptilosarcus gurneyi	0–68 m	—	Morin (1976:630)
Pennatula phosphorea	300–3609 m	—	Herdman (1913); Titschak (1966)
Pennatula rubra	—	—	Panceri (1871); Titschak (1966)
Pteroeides spinosum	—	—	Panceri (1871); Titschak (1966)

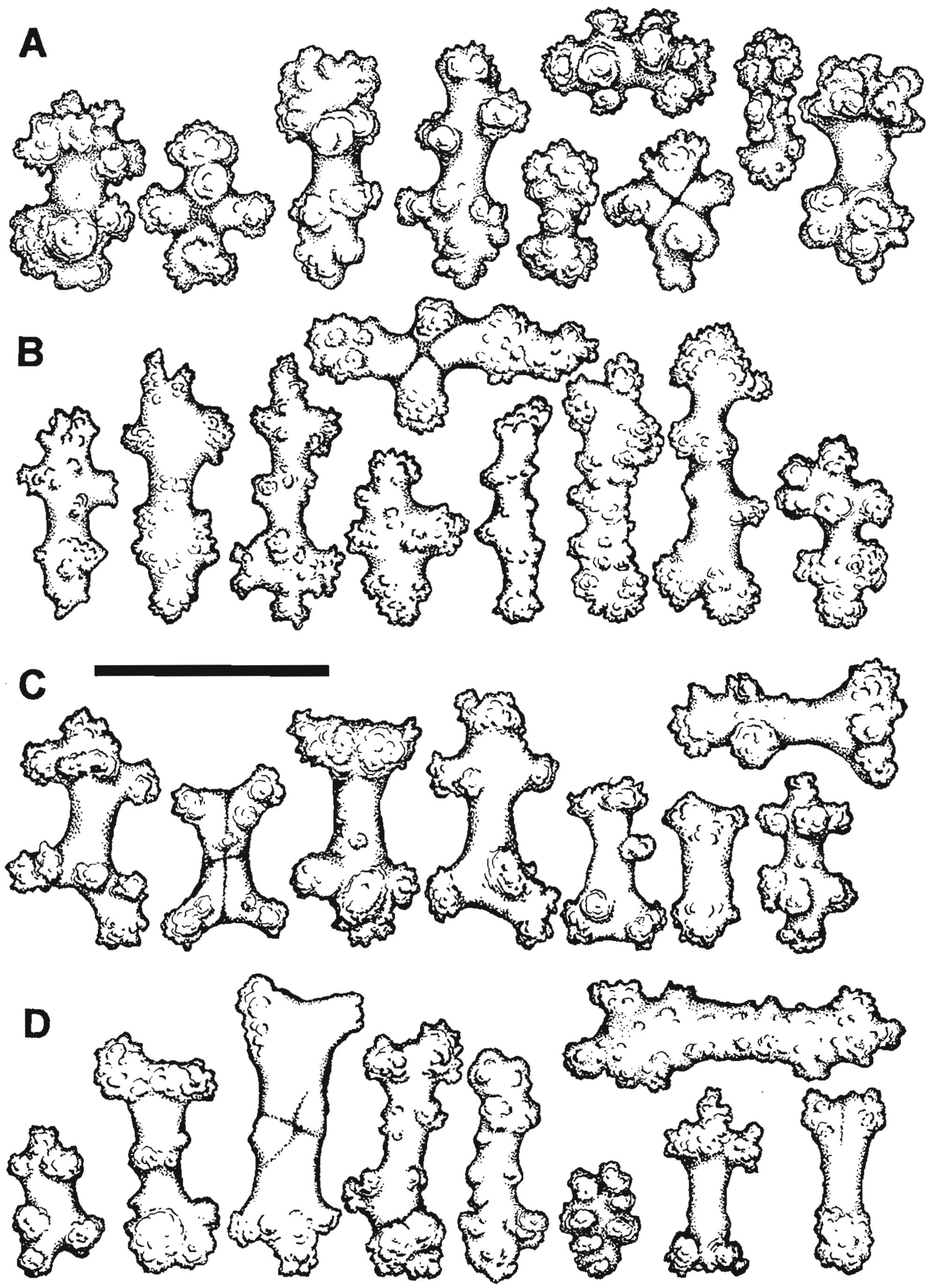

FIGURE 5. *Eleutherobia grayi* sp. nov. Sclerites. A. Polypary surface. B. Polypary interior. C. Stalk surface. D. Stalk interior. Scale bar = 0.1 mm.

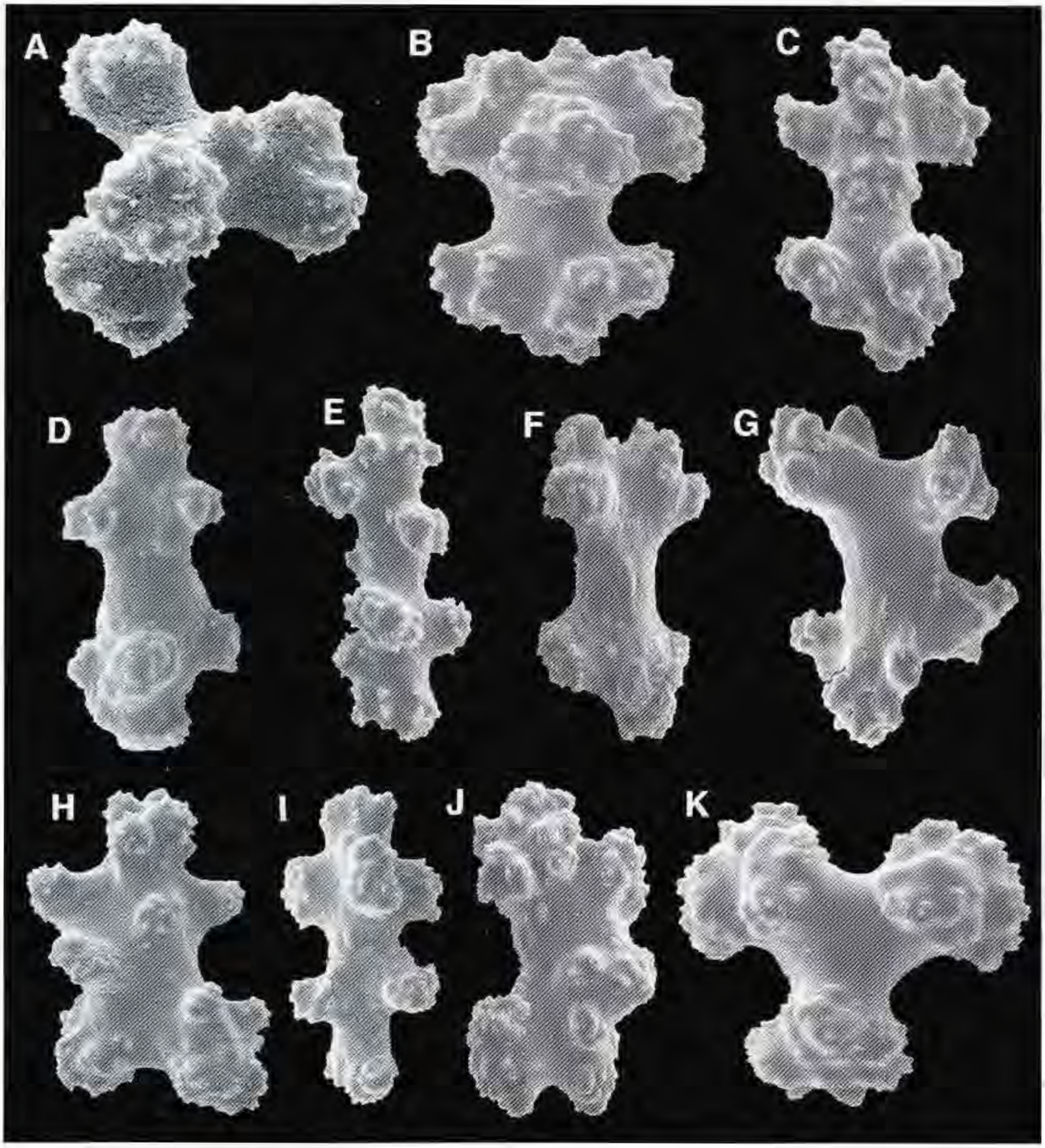

FIGURE 6. *Eleutherobia grayi* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the mound-like protuberances formed by the retracted polyps. A. 0.04 mm. B. 0.05 mm. C. 0.06 mm. D. 0.05 mm. E. 0.07 mm. F. 0.06 mm. G. 0.07 mm. H. 0.07 mm. I. 0.07 mm. J. 0.07 mm. K. 0.04 mm.

Eleutherobia (*Eleutherobia* spp. indet.). One of these is found on vertical surfaces at 12 m depth in southern Luzon, Philippines (pers. observ., and pers. commun. T. M. Gosliner), and Saipan (pers. commun. J. Starmer), and the other has been collected from Palau (pers. commun. J. Starmer). These observations presented here are the first records of bioluminescent soft corals (outside of the dubious record of Leuckart's *Alcyonium*).

The phenomenon of bioluminescence in the Pennatulacea, although commonly encountered in bathymetrically diverse habitats and supported by a relatively rich literature, is by no means universal.

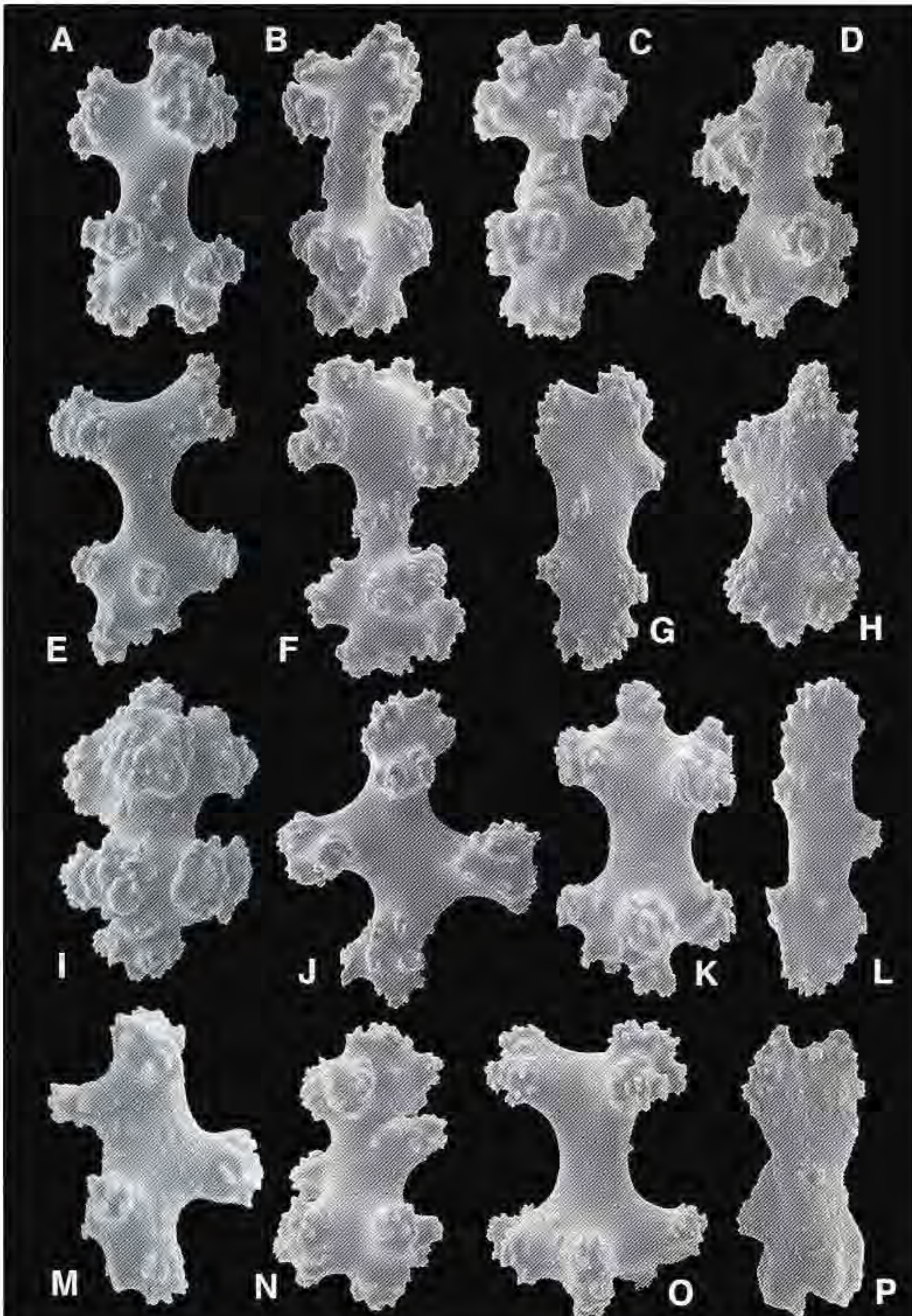

FIGURE 7. *Eleutherobia grayi* sp. nov. Scanning electron micrographs of coenenchymal sclerites from the surface and subsurface of the polypary. A. 0.09 mm. B. 0.08 mm. C. 0.05 mm. D. 0.08 mm. E. 0.09 mm. F. 0.08 mm. G. 0.08 mm. H. 0.07 mm. I. 0.06 mm. J. 0.10 mm. K. 0.08 mm. L. 0.09 mm. M. 0.05 mm. N. 0.05 mm. O. 0.08 mm. P. 0.07 mm.

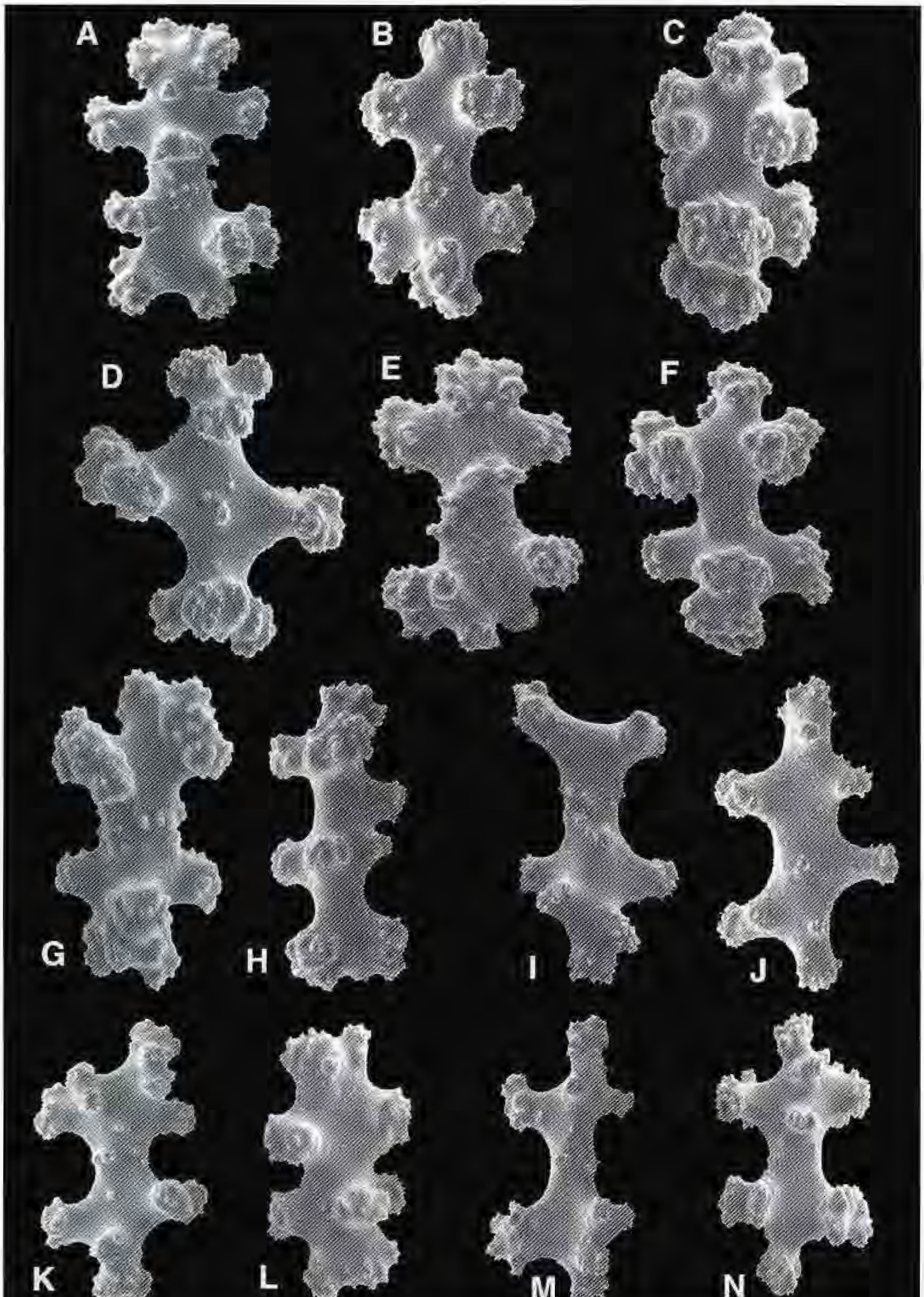

FIGURE 8. *Eleutherobia grayi*. Scanning electron micrographs of coenenchymal sclerites from the surface of the holdfast region of the stalk. A. 0.09 mm. B. 0.08 mm. C. 0.07 mm. D. 0.08 mm. E. 0.08 mm. F. 0.08 mm. G. 0.05 mm. H. 0.08 mm. I. 0.10 mm. J. 0.11 mm. K. 0.10 mm. L. 0.07 mm. M. 0.13 mm. N. 0.11 mm.

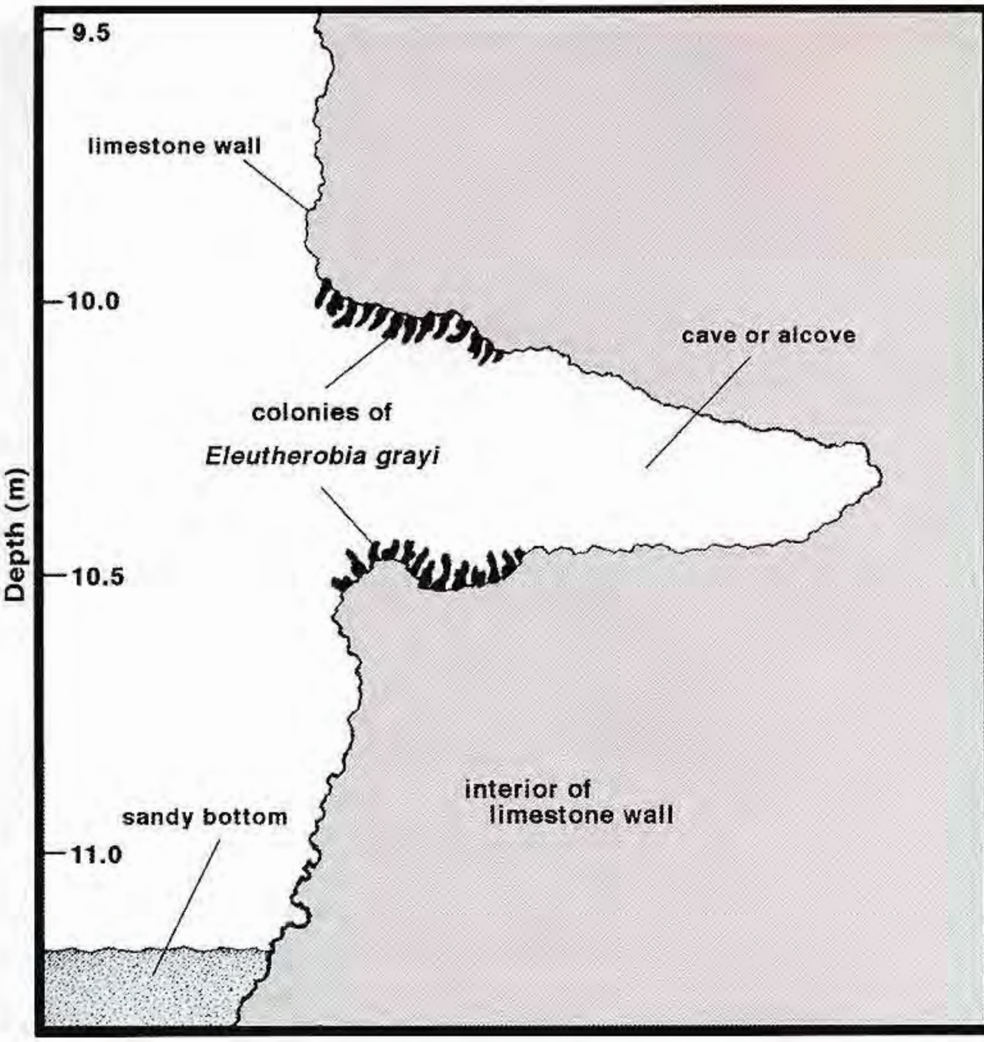

FIGURE 9. Habitat Section. Diagram of longitudinal section through a limestone wall at approximately 10 meters in depth, Mborokua Island, Solomon Islands, showing disposition of densely-set colonies of *Eleutherobia grayi*. Depths shown at left are in meters.

as some taxa are definitely not luminescent. For example, Herring (1978:204) stated that some species of *Virgularia* have been shown to be non-luminous.

Bioluminescence has thus far been recorded in only 53% of the pennatulacean families (8 of 15), 40% of the genera (13 of 32), and 10% of the estimated number of valid species (19 of 186). If the total number of described species in the literature are taken into account, then the latter percentage drops to approximately 4% (19 of 436). These estimates represent minimum values, but could be much higher, and are based on numbers of taxa in Williams (1995:93) and Table 1 of the present paper.

It is surprising that after nearly 450 years of published observations resulting in more than eighty published accounts of pennatulacean bioluminescence, a mere nineteen species (or approximately 10% of the valid species) have been recorded. This number seems especially low considering the introduction of modern technological means to make observations—such as SCUBA, remote operational vehicles (ROV's), and manned deep-sea submersibles. Only a few sea pens are diurnal and/or

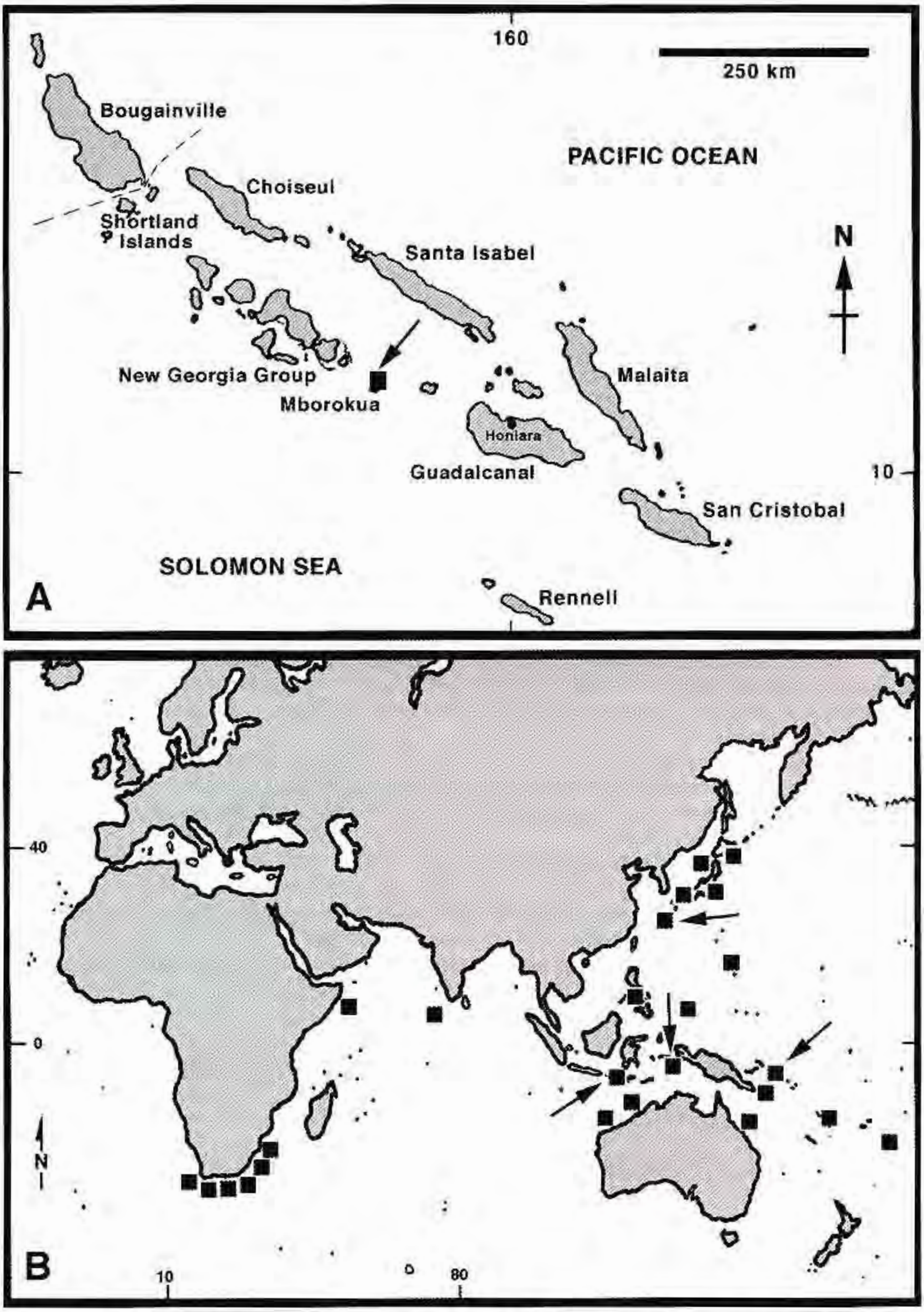

FIGURE 10. A. Map of the Solomon Archipelago, southwestern Pacific Ocean; dotted line marks the political boundary between Papua New Guinea (upper left) and the Solomon Islands. B. Map of the Indo-West Pacific showing geographic distribution of the genus *Eleutherobia*; ■ = collecting stations; arrows show collecting stations for *Eleutherobia grayi*.

zooxanthellate, and are not known to bioluminesce. The majority of shallow water species (at least in the Indo-Pacific) are nocturnal and azooxanthellate (Williams, pers. observ.). One South African species, *Actinoptilum molle*, appears to be active both during the day and night, and is at the same time azooxanthellate and bioluminescent (Williams, 1990:63). In addition, a remarkable diversity of deep-water taxa are known (Williams 1993:733–734; 1997:499, 503) that live in perpetual darkness. It is therefore assumed that the actual number of bioluminescent sea pens could be much higher than is presently documented.

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