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Radianthus papillosa (Coelenterata, Actiniaria) Redescribed from Hawaii[1]

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ABSTRACT: The shallow water sea anemone that was described by Verrill (1928) as *Macranthea cookei* from specimens collected in Hawaii is redescribed and synonymized with *Radianthus papillosa*, first described by Kwietniewski (1898) as *Stichodactis papillosa* from Ambon.

IT HAS BEEN nearly 50 years since the posthumous publication of Verrill's (1928) monograph "Hawaiian shallow water Anthozoa." In it are described 21 species, all but one new to science, of 15 genera, of which four are new, in what Verrill considered to be four orders. This work is not as extensive as the title would imply, for corals are omitted altogether. Its value has been further reduced by the discovery of new species and by taxonomic changes. An up-dating of this work is badly needed, especially considering the large amount of research done on Hawaiian coelenterates (e.g., Lenhoff, Muscatine, and Davis 1971; Muscatine and Cernichiari 1969; Trench 1971), but it would now be a difficult task indeed to prepare a monographic treatment such as Verrill's. Of greater practicality, and probably utility as well, would be a series of studies on the species of areas smaller than the entire island chain, or detailed works on each of the orders or families of anthozoans. These two approaches have been employed by Reed (1971) and by Walsh and Bowers (1971), respectively, but theirs have been the only such studies published since Verrill's time.

This paper redescribes and reassigns the Hawaiian sea anemone that Verrill (1928) described as *Macranthea cookei*. Several dozen animals from Ahu o Laka (Sand Island) and the sand flats on Moku o Loe (Coconut Island), Kaneohe Bay, Oahu, were studied alive and in preserved condition. To ascertain that the species in question was indeed the one to which Verrill's description refers, I borrowed the type specimen and one of the cotypes from the B. P. Bishop Museum in Honolulu for examination. Histological sections were made from the cotype and several of the freshly collected specimens.

Radianthus papillosa (Kwietniewski 1898:415)

Stichodactis papillosa Kwietniewski 1898: 415; *Antheopsis papillosa* Stephenson 1922: 300; *Macranthea cookei* Verrill 1928: 12; *Radianthus papillosa* Carlgren 1949: 74.

Habitat

In Hawaii, this exclusively subtidal sea anemone lives in water no more than about a meter deep, buried in sand so that its oral disc is slightly above the surface of the substrate (Fig. 1). When disturbed, it contracts beneath the sand so that it is completely hidden. It is difficult to remove only if its base is attached to a firm object, but this is often not the case.

Size

The animal is capable of considerable expansion and contraction. Its usual size is very difficult to determine because, for the most part, it lies buried beneath the sand, and contracts when collected. In aquaria, however, it may expand so that its tentacular crown is 10 cm in diameter and its length is 12 cm (Fig. 2). The base of an animal this size is typically 6 to 7 cm

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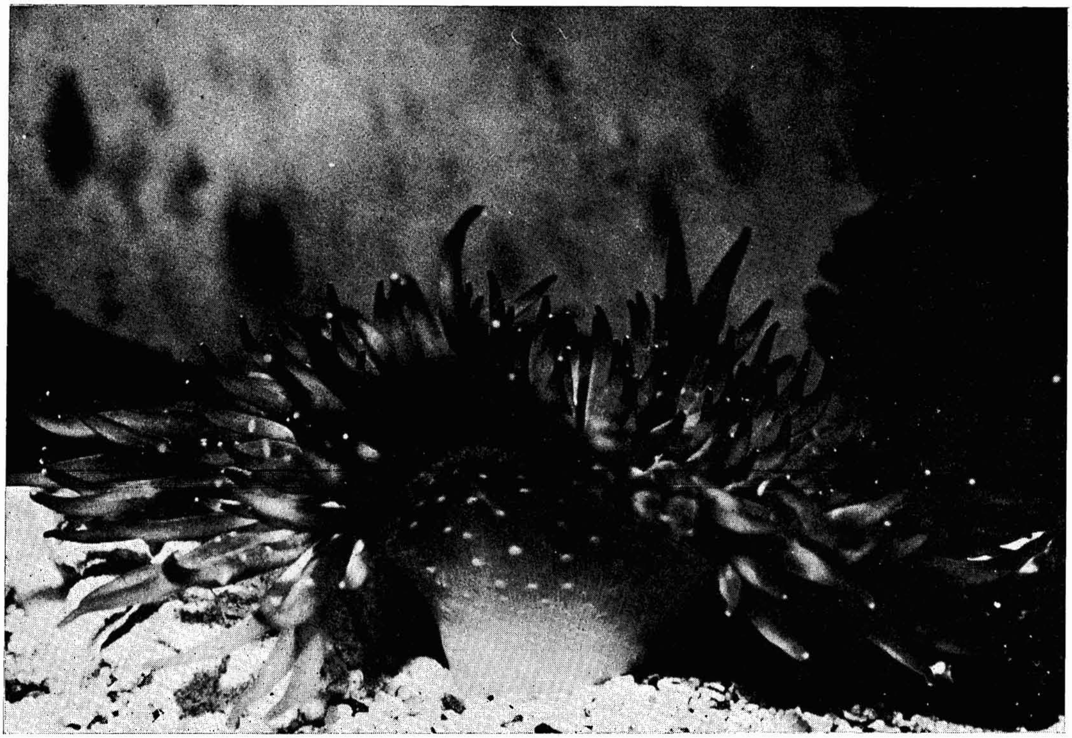

FIG. 1. *Radianthus papillosa* in its natural position, buried in sand up to its capitulum. Note verrucae and mesenterial insertions on the capitulum. (Photograph by S. Arthur Reed.)

in diameter. The column may be of uniform diameter, usually somewhat smaller than the base, occasionally with one or more constrictions, or it may taper gradually from the base upward and constrict to 3 to 4 cm just below the flared capitulum.

The type specimen has a pedal disc diameter of 3.5 cm, an oral disc diameter of 5.0 cm, and a height of approximately 4 cm. The cotype examined measures 3.0×4.5 cm across the base, 5.0×6.5 cm across the oral disc, and it is about 4 cm high. The column of the type specimen is nearly 3 cm across, and that of the cotype is equal in diameter to its base.

Base

When the animal is buried in sand, the form of its base is unknown. It will, however, adhere strongly to solid objects such as pieces of coral and shell. In aquaria, it attaches firmly to sides and bottom and is generally circular in outline (Fig. 2). The base is usually flared somewhat so that its diameter is greater than that of the column, but there is no sharp demarcation between base and column. Mesenterial insertions show through as white radial lines. The basal musculature is well developed, and the anemones may move about considerably in aquaria.

Column

The body wall is very thin (it can easily be torn during collection), and the mesenterial insertions are visible as longitudinal white lines. The upper portion of the column flares out, forming a distinct capitulum. This lies extended over the surface of the sand in the actinian's normal habitat, and may constitute a third or more of the total length of the column, depending on the animal's state of expansion. The capitulum is quite sharply demarcated from the scapus in possessing adhesive verrucae and endodermal zooxanthellae, so its appearance, in contrast to that of the smooth, pale yellow or

FIG. 2. *Radianthus papillosa* expanded in an aquarium. Mesenterial insertions are visible the entire length of the column and through the pedal disc. Note the darker color of the capitulum (due to zooxanthellae) and the verrucae on it. (Photograph by S. Arthur Reed.)

off-white, lower column, is papillate and brown, brownish-yellow, or brownish-violet. Grains of gravel and bits of shell usually adhere to the verrucae in life. These adhesive areas, the largest of which are about a millimeter in diameter, may be paler than the rest of the capitulum and are arranged in longitudinal rows between the mesenterial insertions, the endocoelic spaces having more adhesive areas than do the exocoelic ones. The only intrinsic columnar pigments are occasional small splotches of orange on the scapus, and rarely, a purplish cast to the upper capitulum. Otherwise, the color of the capitulum is due entirely to the presence of zooxanthellae.

The oral disc and capitulum can be fully retracted, although such retraction is rare. The subcapitular sphincter is weak, endodermal, sessile, and more or less diffuse. In cross section it is quite variable: it may be oval (Fig. 3), in which case there is one major mesogleal lamella that branches quite symmetrically and several smaller ones, often more on one side than the other; in some individuals the subsidiary lamellae may be quite well developed (Fig. 4), making the sphincter bilobed; and in others the two lobes may be set apart (Fig. 5), forming essentially a double sphincter.

In the extremely contracted state the animal is slightly taller than it is broad, and its column is girdled by numerous folds.

A shallow fossa separates the top of the column from the oral disc. The uppermost verrucae are situated on the rim of the fossa and contain cinclides, through which jets of water escape when the animal contracts suddenly (unusually forceful contractions may rupture the body wall).

Oral Disc

Although usually flat, the oral disc may be thrown into undulations when the anemone is partially contracted. Its underlying color is the

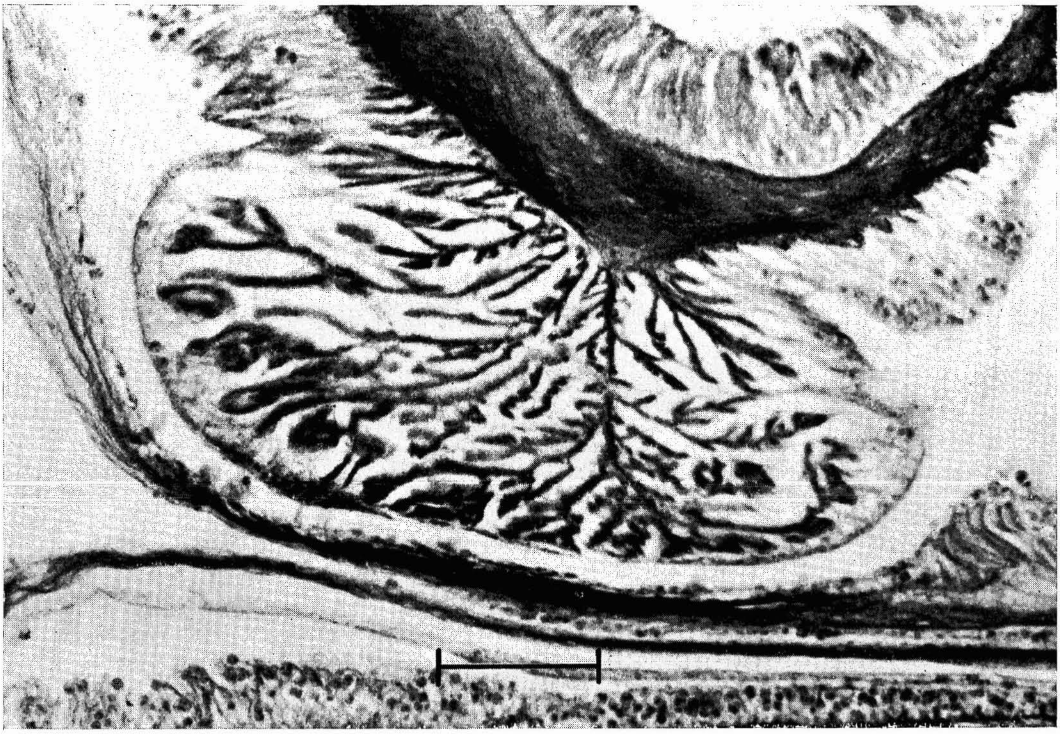

FIG. 3. Cross section of the most circumscribed variant of the sphincter muscle of *Radianthus papillosa*. Scale is 100 μm.

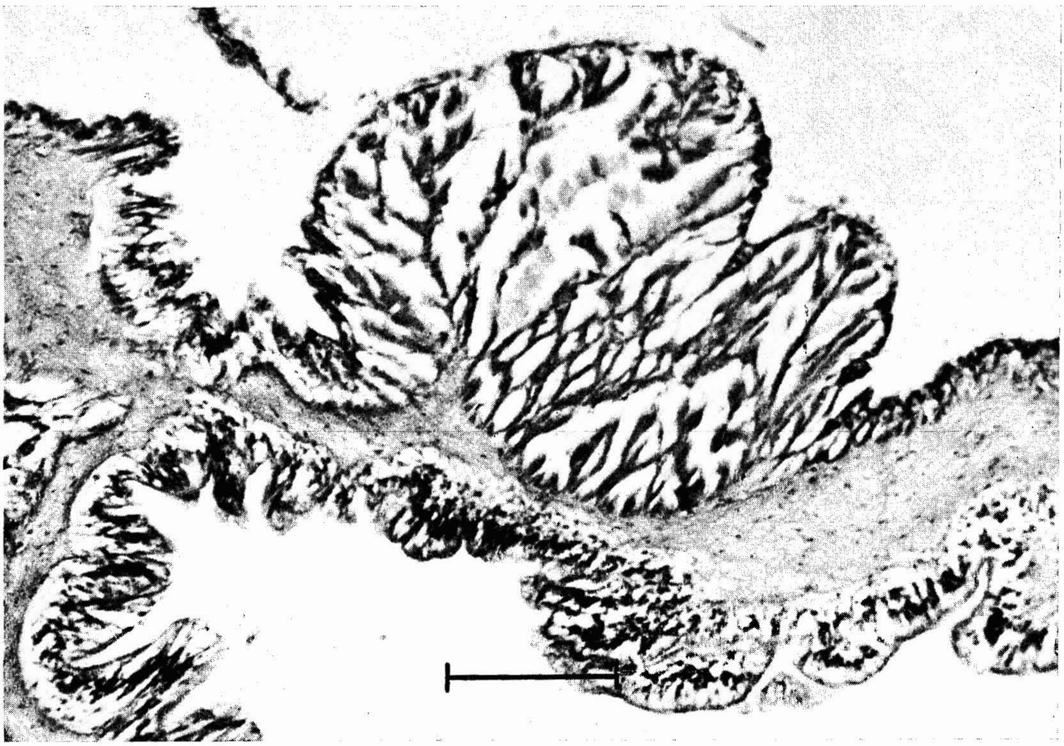

FIG. 4. Cross section of the bilobed type of *Radianthus papillosa* sphincter. Scale is 100 μm.

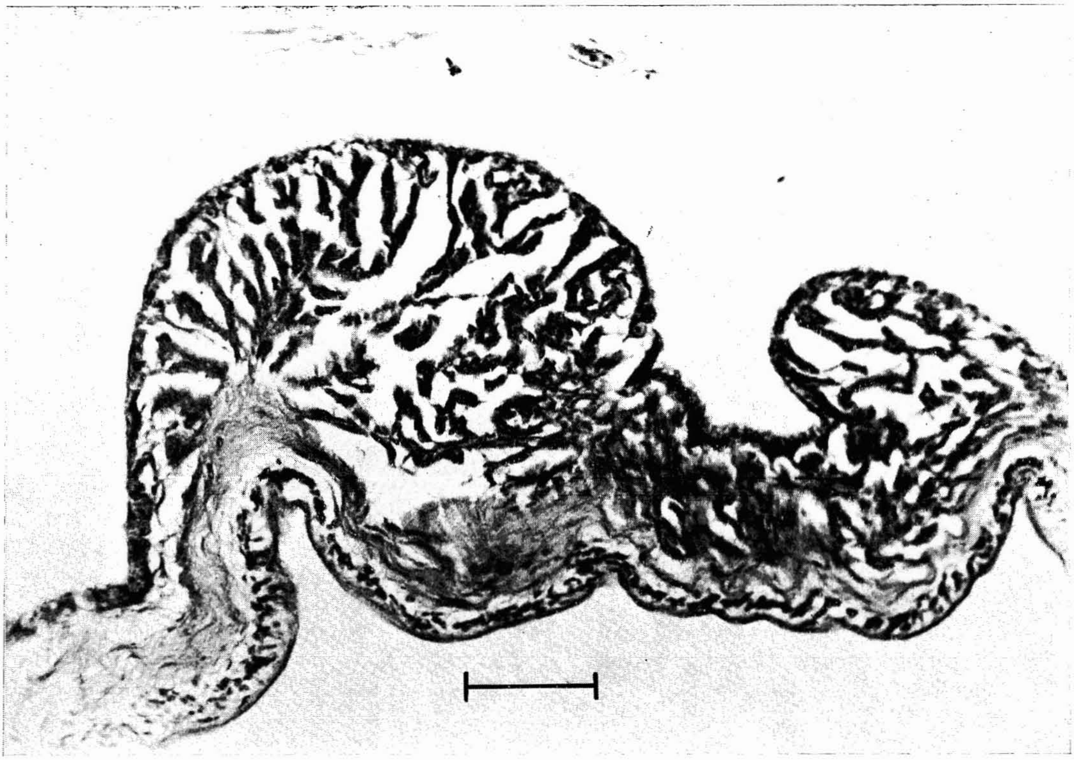

FIG. 5. Cross section of the variant of *Radianthus papillosa* sphincter that is essentially double. Scale is 50 μm.

same as that of the capitulum and is also due to the presence of abundant zooxanthellae in the endoderm. The mesenterial insertions show through as radiating white lines. In addition, the inner part of the disc has a white pigment which disappears in preserved specimens. Surrounding the mouth are 24 radiating white bars several millimeters long. There may be a white dot at the outer end of each bar, separated from it by a pigment-free gap about a millimeter wide. The six tentacles comprising the inner circlet arise just distal to this and so are nearly a centimeter from the mouth. Several successive rings of increasing numbers of tentacles extend to the edge of the oral disc, where the tentacles become very dense. The white pigmentation, which extends about halfway across the oral disc from the mouth to rim, is interrupted by a pigmentless line surrounding each tentacle and leading from it peripherally. The whiteness may increase in intensity near the mouth due to the combined effects of the pigment and the mesenterial insertions showing through.

The slitlike mouth lacks protrusive lips in life, although they may be evident in preserved specimens. Openings of the siphonoglyphs are not differentiated. The slightly ribbed throat is the same yellowish or off-white color as the lower column.

The circular musculature of the oral disc is endodermal and the radial musculature is ectodermal.

Tentacles

Although they are capable of considerable inflation or contraction, the tentacles are usually all about 15 to 20 mm long and 2 to 3 mm in diameter. Their tips are perforate (water also escapes through them during contraction). The tentacles are of simple digitiform shape except for a few on each animal that are bifid. Their color is generally the same as that of the capitulum, but the tips are often paler, and sometimes each one is ringed with several narrow white bands. In the absence of zooxanthellae, an intrinsic pink or lavender pigmentation may be

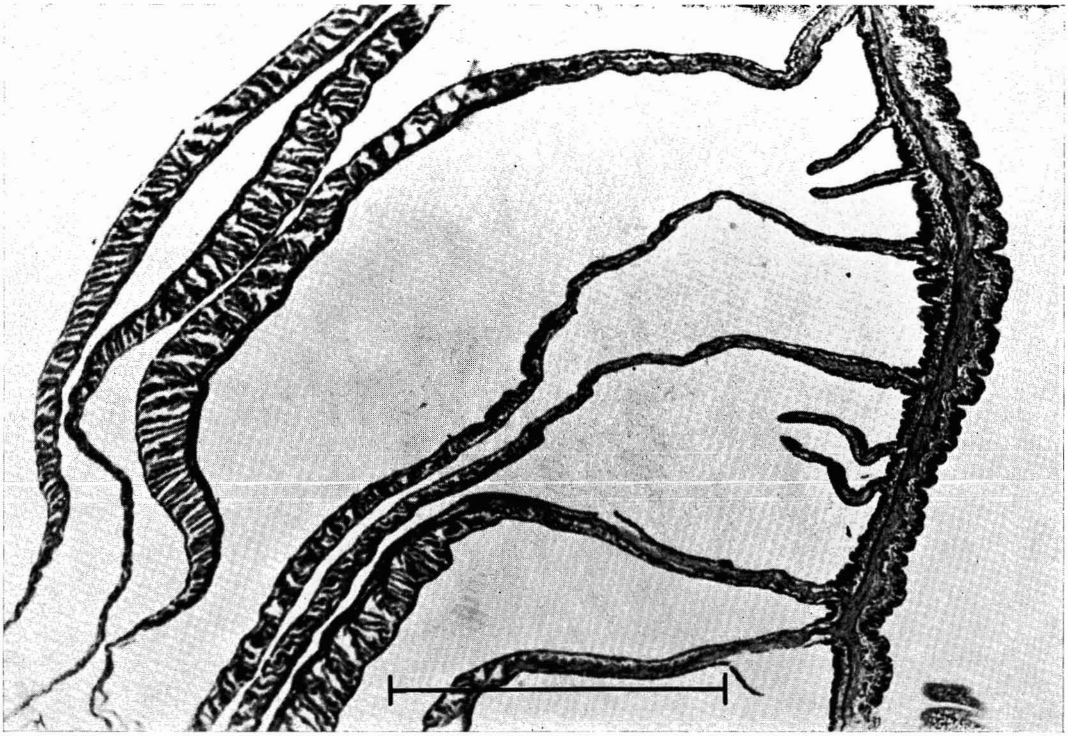

FIG. 6. Cross section through the upper column of *Radianthus papillosa*. Note the regular arrangement of mesenteries, the character of the diffuse retractor muscles, and the relative widths of the three body layers. Scale is 800 μm.

unmasked toward the base of each tentacle. The type specimen has 327 tentacles, one of the cotypes has approximately 385, and another individual has about 330.

The six tentacles nearest the mouth communicate with the endocoels of the primary mesenteries, and the circlet distal to that apparently represents those of the second cycle. Thereafter the arrangement is indistinct. Only one tentacle communicates with each exocoel. The cotype with 385 tentacles has 96 pairs of mesenteries; this is an average of three tentacles per endocoel. Although it is possible that younger endocoels may have fewer tentacles than do older ones, the type specimen has three tentacles in one of its directive endocoels, and it appears that most endocoels have an equal number. The radial arrangement of tentacles is obscure.

Longitudinal muscles of the tentacles are ectodermal, and circular muscles are endodermal.

Mesenteries and Internal Anatomy

The several average-sized individuals examined, including a cotype, have 96 pairs of mesenteries arranged in a very regular fashion. All except the fifth order are perfect, the older mesenteries attaching lower on the throat than the younger ones. All have tripartite mesenterial filaments, although those of the youngest mesenteries are developed only near the top. At least all the stronger mesenteries are fertile, including the directives, and the species appears to be dioecious. Retractor muscles are diffuse and moderately well developed, with the mesogleal laminae up to five times as long as the mesogleal strand is wide (Fig. 6). Very small peripheral stomata and larger oral ones are present. The well-developed parietobasilar musculature forms a broad detached sheet at its free extremity along the larger mesenteries, but in smaller mesenteries only a narrow portion is detached.

The siphonoglyphs (two per animal) are histologically differentiated from the rest of the throat. The actinopharynx extends perhaps half the length of the animal, although the siphonoglyphs are slightly longer.

The mesoglea contains scattered nuclei. In the lower part of the column the mesoglea is about twice the thickness of each of the two body layers, but in the upper portion the ectoderm, mesoglea, and endoderm are of approximately equal thickness (Fig. 6).

Cnidom

Spirocysts, basitrichs, and microbasic p-mastigophores constitute the cnidom.

Distribution and Size of Nematocysts

TENTACLES: spirocysts, 17.7–27.1 × 3.0–4.1 μm (24); basitrichs, 12.4–21.2 × 2.4 μm (23).

COLUMN: spirocysts, 16.5–24.8 × 2.4–4.1 μm (18); basitrichs, 5.9–9.4 × 1.8–2.4 μm (21); basitrichs, 13.0–18.9 × 1.8–3.0 μm (33); microbasic p-mastigophores, 21.2–29.5 × 5.3–10.6 μm (21) (butt 23.6–40.1 × 2.4 μm).

BASE: spirocysts and large and small basitrichs falling within the same size range as those of the column. Spirocysts and small basitrichs very sparse.

FILAMENTS: spirocysts, 17.7–26.0 × 2.4–4.7 μm (15); basitrichs, 9.4–16.5 × 1.8–3.0 μm (28); basitrichs, 17.7–30.7 × 2.4–4.1 μm (25); microbasic p-mastigophores, 22.4–28.3 × 4.1–8.3 μm (10).

Distribution

I have collected this anemone in central and southern Kaneohe Bay but have been unable to find it in similar shallow water habitats at the extreme north end of the bay. It also appears to be absent from sandy environments off the shore along Diamond Head, and I failed to find the species in brief searches along the north and northeastern coasts of Oahu. Verrill's type material came from Laie, Oahu, but I did not find this anemone in the bay east of Laie Point.

This actinian may harbor the anemone fish *Dascyllus albisella*, according to Richard N. Mariscal (personal communication), and is the only species of sea anemone in Hawaii to do so.

Discussion

Verrill (1928) described *Macranthea cookei* as a new genus and species but failed to compare it with previously described actinians. His description, although quite accurate, is based almost entirely upon the external appearance of the animal. Perhaps Verrill, if he had lived longer, would have elaborated on it and given a differential diagnosis. His findings concerning the number and size of the tentacles are not in agreement with mine, for he stated that an individual may have 600 or more tentacles, and that "the outer ones are much shorter and smaller" (p. 12). This may be the case with very large individuals, but I have never seen such an animal. He also stated, as a generic character, that the animal seems unable to involute its disc, and he assigned it to family Anemonidae partly on the basis of its lack of a sphincter. As described above, this species has a very small, weak sphincter, and, although it covers its crown entirely only under the most extreme conditions, it is able to do so. The sphincter is noteworthy for its variability, and, according to Cadet Hand (personal communication), is unique among endodermal sphincters in being nearly double.

Although Carlgren (1949) made no mention of either the genus or the species in his monograph of the actinians of the world, one can, by using his key, assign this anemone unambiguously to the family Stoichactiidae [*sic*]. Stephenson (1922) recognized three genera among the Stoichactidae; these genera form a series from a single tentacle (*Antheopsis*) to a single row (*Radianthus*) to multiple rows of tentacles (*Stoichactis*) per endocoel. He added, however, "I do not feel perfectly confident that they do not all form one large genus" (p. 297). Carlgren (1949) combined *Radianthus* and *Antheopsis* under the former name, recognizing 12 certain and three possible species, compared with the 12 certain and one possible listed by Stephenson (1922) in the two genera combined. In either case, "*Macranthea cookei*" is clearly a *Radianthus*.

In trying to determine whether this Hawaiian actinian belongs to a species that has been described from other localities, one can easily eliminate several of the 15 possibilities from consideration, despite the fact that the earliest descriptions of some species now considered as belonging to *Radianthus* are so archaic and vague as to be virtually worthless for taxonomic purposes (e.g., Ehrenberg 1833; Quoy and

Gaimard 1833, revised by Pax 1912). R. *kükenthali* (Kwietniewski 1896) has 10 to 15 tentacles per endocoel, thick lips, and a lobed oral disc; R. (described as *Helianthopsis*) *mabrucki* (Carlgren 1900) lacks papillae on its body wall; R. *lobatus* (Kwietniewski 1898) has a lobed oral disc and lacks tentacles near the mouth. Others of the 15 species differ in more subtle ways. The sphincter of R. (*H.*) *ritteri* (Kwietniewski 1898) is different from that of the Hawaiian species, and the animal has too many tentacles per row and too many septal pairs. Of the four species now assigned to the genus *Radianthus* that were first described by Lager (1911), the sphincter muscles of both R. (*Antheopsis*) *carlgreni* and R. (*Stichodactis*) *kwietniewskii* are more diffuse than that of "*M. cookei*"; R. (*A.*) *concinnata* has too few pairs of mesenteries and too few complete ones; and R. (*S.*) *glandulosa* has too few central tentacles, too long an actinopharynx, and too strong a sphincter. Although the description of R. (*Bunodes*) *koseiriensis* by Carlgren (1900), based on poor material, is confusing, and that of Haddon (1898) is very brief, the species differs from the Hawaiian anemone at least in having more mesenteries. R. (*Discosoma*) *macrodactylus* and R. (*D.*) *malu* (Haddon and Shackleton 1893, redescribed by Haddon 1898) (each description based upon a single specimen) differ from "*M. cookei*" in size and color. Of the three species questionably assigned to *Radianthus*, R. (*Myractis*) *tubicola* (Haddon 1888) forms a tube; not even the size of R. (*Actinia*) *parvitentaculata* (Quoy and Gaimard 1833, redescribed by Pax 1912) is given, but its color differs from that of "*M. cookei*"; and the description of R. (*Actinia*) *crispus* (Ehrenberg 1833) is too poor for meaningful comparison.

Of the 15 species, therefore, the one first described as *Stichodactis papillosa* by Kwietniewski (1898) from a single, fairly well-preserved specimen collected by Semon on the island of Ambon (3°35′ S, 128°20′ E) most closely resembles the Hawaiian species. R. *papillosa* has fewer tentacles per row over progressively younger endocoels (from at least six to three), but this may also be true of "*M. cookei.*" The lack of filaments on the fifth-order mesenteries of R. *papillosa* is almost certainly ascribable to age or individual variation. The figures in Kwietniewski's paper greatly resemble the species found in Hawaii. Unfortunately there is no discussion of how the animal differs from closely related species, although Lager (1911) did provide a differential diagnosis between R. (*S.*) *papillosa* and R. (*S.*) *glandulosa* on a few points. I therefore propose synonymizing *Macranthea cookei* with *Radianthus papillosa*.

The possibility remains that one or more of the very early and incomplete descriptions also refer to this species, and that *Radianthus papillosa* may not be the most senior synonym. In some descriptions the only detail of internal anatomy is the form of the sphincter, and even that detail may be absent, so that the species description is based largely or entirely upon external appearance (e.g., R. *macrodactylus* and R. *malu*). Color generally is not a useful taxonomic character in sea anemones (Stephenson 1928) but, in the absence of other information, it must be considered. It is difficult to evaluate the taxonomic importance that should be attached to size. Related to this, at least to some extent, is the number of mesentery pairs and also, perhaps, the number of tentacles. With our limited knowledge of the life history of any member of the Stoichactidae, we cannot know if two tentacles per row (as in R. *glandulosa*) is significantly different than the three in "*M. cookei*," or if the 10 of R. *ritteri* and 15 of R. *kükenthali* should be regarded simply as indicating a more mature condition or a manifestation of individual variation. For the time being it would seem prudent to consider variation within two or three tentacles as representing variability due to age or other conditions not related to taxonomic position, but two- or three-*fold* differences as being taxonomically significant.

It is likely that some synonymy exists among the dozen or so described species of *Radianthus*, and this is probably also the case with *Stoichactis*. Resolution of these questions is not possible by means of a literature search, and a sorting out of the taxonomy of the Stoichactidae necessitates a redescription of each species from its type locality, with a complete differential diagnosis. In this connection, it is also imperative that the natural history of these species be studied to resolve questions about developmental changes within the individual, and the extent of intraspecific variation.

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