# Three Species of Intertidal Sea Anemones (Anthozoa: Actiniidae) from the Tropical Pacific: Description of Anthopleura buddemeieri, n. sp., with Remarks on Anthopleura asiatica and Gyractis sesere1

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Abstract: A new species of sea anemone, Anthopleura buddemeieri Fautin, is described from Fiji and Papua New Guinea. Occurring high in the intertidal zone, a typical individual has a column rich brown in color and marked with longitudinal rows of red spots. Occurring in the same habitat, at least in Papua New Guinea, is a sea anemone known in the tropical Indo-Pacific from Aden to Hawai'i, the valid name of which is Gyractis sesere. Some records of Anthopleura asiatica may refer to A. buddemeieri but some clearly do not; because the name appears to have been applied to more than one species, the original description lacks critical information, and no type material exists, the name Anthopleura asiatica is considered a nomen dubium.

Anthopleura buddemeieri Fautin, n. sp., is an inconspicuous but distinctive solitary sea anemone that reaches a maximum column diameter and length of 25 mm. It lives at the level of the highest tide under stones and in holes on rocky shores. I have found it on the north and south coasts of New Guinea and in Fiii: presumably it is widespread through the tropical western Pacific. It is modestly abundant (perhaps 10-50 m<sup>-2</sup>) where I have found it but is absent in most places that appear to have suitable habitat.

Its rich brown column with vertical rows of red spots distinguish A. buddemeieri, n. sp., from other small intertidal sea anemones of the tropical Pacific, Color images are on line at hercules.kgs.ku.edu/hexacoral/anemone2/ images/05851\_05900/05882.jpg (whole ani-

mal [Figure 1]) and hercules.kgs.ku.edu/hexa coral/anemone2/images/05851\_05900/05881 .jpg (margin [Figure 2]). This color pattern is similar to that of two other species of Anthopleura, A. ballii (Cocks, 1851), which occurs in the British Isles, and A. krebsi Duchassaing & Michelotti, 1860, which occurs from the southeastern United States to Brazil, and to the species called Actinia sanguineopunctata Templeton, 1841 known from Mauritius, Details of anatomy distinguish A. buddemeieri, n. sp., from those species. It also resembles some specimens referred to the species A. asiatica Ûchida & Muramatsu, 1958, which was described from Japan and has been recorded from India, but information on it is ambiguous, making it impossible to determine what species was meant by Uchida and Muramatsu (1958) as well as others who have used the name.

Occurring with Anthopleura buddemeieri, n. sp., in some places is an anemone that was referred to by me (as Dunn [1974], Fautin [1988]) as Actiniogeton sesere and by England (1987) as Gyractis excavata. The valid name of the species is Gyractis sesere (Haddon & Shackleton, 1893).

#### MATERIALS AND METHODS

Specimens of A. buddemeieri, n. sp., were collected by hand and examined alive, then preserved in 10% formalin in seawater. His-

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tological sections 8 µm thick were stained with hematoxylin and eosin (Humason 1979). Cnidae were measured in squash preparations at 1000× with differential interfer-

ence contrast optics.

In Fiji, animals were collected in Laucala Bay, Suva, just off the campus of the Marine Studies Programme, University of the South Pacific (18° 9′ S, 178° 27′ E). They were collected at two places in Papua New Guinea (PNG): the seaward shore of Wongat Island, Madang Lagoon, Madang Province (5° 10.2′ S, 145° 50.4′ E), and the beach of the laboratory on Motupore Island, Bootless Bay, Central Province (9° 31.3′ S, 147° 17.1′ E). In all places, the anemones lived at the highest levels of the intertidal zone, attached to a rocky substratum, under stones (in Laucala Bay and Bootless Bay) or in the crevices of uplifted coral reefs (on Wongat Island).

Specimens of A. buddemēieri, n. sp., have been deposited in the California Academy of Sciences, San Francisco, California (cas), U.S. National Museum of Natural History, Washington, D.C. (USNM), University of Kansas Natural History Museum, Lawrence, Kansas (KUNHM), and Natural History Museum of the University of the South Pacific, Suva, Fiji (USP). Specimens of Gyractis sesere, cataloged as Actiniogeton sesere, exist in cas (catalog numbers 5327, 9963, and 16600 from Hawai'i, and 97387, 97390, and 97393 from

PNG).

Cnidae terminology is that of Mariscal (1974).

#### RESULTS

Anthopleura buddemeieri Fautin, n. sp.

DESCRIPTION: Column: Larger animals rich brown color in life, smaller ones tan to gray; mesenterial insertions visible as light lines in expanded individuals; animals of all sizes with red punctations. In proximal one-third of column, red spots scattered, varied in size but most smaller than distal ones, irregular in shape so some elongate ones appear as streaks. In distal one-third of column, red spots circular, all about equal size, in longitudinal rows, each marking a histologically specialized patch; spots aligned along endo-

coels number 5–8, with distalmost one on marginal projection; those along exocoels number 3–5 and do not extend to margin (Figure 1). Spots in middle one-third of column transitional in form, size, and arrangement

Deep fosse. Simple digitiform, brown marginal projection at distal end of each endocoel; typically, therefore, number 48 per individual. Distalmost of each row of red verrucae occupies the adoral side of the projection, and a pink acrorhagus (containing dense holotrichs and some spirocysts) bulges

from its oral side (Figures 2, 3).

Column diameter to as much as 25 mm but typically 10–15 mm; smallest animal seen 4 mm diameter. Commonly pedal and oral discs equal diameter, but column tapers from basal end to about one-half basal diameter just below oral disc; uncommonly column equal diameter entire length. Column half as long as or as long as column diameter. In contraction, distal part of column typically narrows and retracts; animal may appear dome-shaped.

Column of preserved specimens gray or tan with white verrucae and marginal projec-

tions.

Pedal disc: Color light tan (paler than column) to pink in life with red radial stripes especially pronounced at periphery; stripes may be absent in center. Lines may run distally onto limbus where they can be so dense that they appear to be a red line encircling it. Mesenterial insertions visible through expanded pedal disc as light lines.

Oral disc and tentacles: Oral disc solid brown or gray. Mouth central, in some individuals raised on oral cone. Two symmetrical siphonoglyphs; in life, tan to white (color of actinopharynx). Mesenterial insertions visible through expanded oral disc as dark lines.

Tentacles primarily near margin.

Tentacles without pattern: proximal part rich brown or gray of oral disc; distal one-third to one-half shading to red; red cast less prominent in outer than in inner tentacles. Maximum of 102 tentacles counted; smaller individuals typically with 48, larger with 96. Inner longer than outer ones (Figure 1). Slender, taper to blunt point; longest ten-



FIGURE 1. Anthopleura buddemeieri: whole animal, alive. From campus of the University of the South Pacific, Suva, Fiji. Photograph by Adorian Ardelean. Color version on line at Web site address given in text.

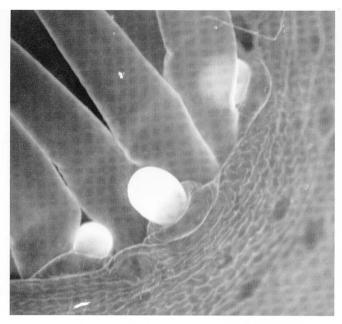


FIGURE 2. Anthopleura buddemeieri: margin of live animal showing simple marginal projection and acrorhagus. From campus of the University of the South Pacific, Suva, Fiji. Photograph by Adorian Ardelean. Color version on line at Web site address given in text.

tacles equal to column length: typically 10–15 mm long by 1–2 mm basal diameter.

In preservation, tentacles may contract greatly or have a blunt or nipplelike end; oral disc solid gray.

Internal anatomy: To 48 pairs of mesenteries regularly arrayed in four cycles; only those of first cycle complete. In two specimens with two pairs of symmetrically arrayed directives 39, 44 mesenteries counted; a specimen with 27 pairs of mesenteries had three siphonoglyphs that were not evenly spaced. Each siphonoglyph attached to a pair of

directive mesenteries (Figure 4). All mesenteries except those of highest order and directives fertile; sexes separate. Equal number of mesenteries distally and proximally. Large oral, small to absent marginal stomata. Actinopharynx longitudinally ribbed, typical in appearance; siphonoglyphs slightly elongate.

Azooxanthellate.

Cnidom: Spirocysts, basitrichs, holotrichs, microbasic b-mastigophores, microbasic pmastigophores. Distribution and size of cnidae given in Table 1.

Histology and musculature: Each red patch

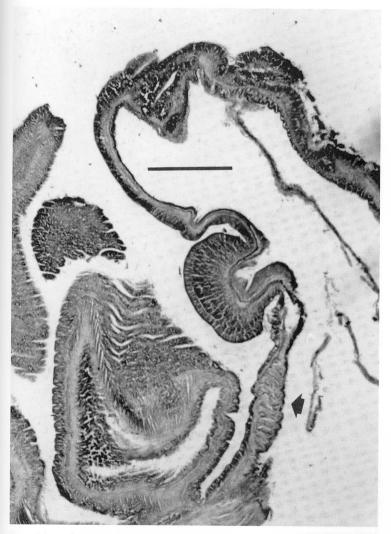


Figure 3. Longitudinal section at margin of holotype (kunhm 001992) of Anthopleura buddemeieri showing diffuse endodermal sphincter (arrow) and marginal projection with acrorhagus arising from oral side of distalmost vertuca on its adoral side. Scale bar =  $500 \ \mu m$ .

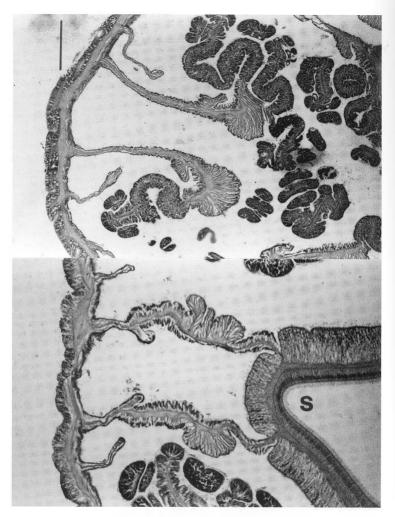


FIGURE 4. Cross section through midcolumn of *Anthopleura buddemeieri* showing mesenterial retractor muscles and parietobasilar muscles. Upper image (holotype: кимім 001992) shows fertile (female) pair of secondary mesenteries; lower image (paratype: кимім 001995) shows directive pair (s, siphonoglyph). Scale bar (which appears only in upper image) = 450 µm in upper image, 200 µm in lower image.

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TABLE 1

Distribution and Size of Cnidae of Anthopleura buddemeieri

Tissue and Cnida Type <sup>a</sup>	$Length \times Width \ (\mu m)$	Total No. of Capsules Measured	Proportion of Animals Studied That Contained Type of Cnida
Tentacles			
Spirocysts (a)	$15.9-30.1 \times 1.6-3.2$	46	4/4
Basitrichs (b)	$(16.4) 17.4-25.2 \times 1.8-3.5$	44	4/4
Acrorhagi			
Spirocysts (a)	$17.2-33.5 \times (1.4) \ 1.9-3.5$	38	4/4
Basitrichs (c)	11.1-19.5 (22.3) × $1.8-3.3$	29	3/4
Holotrichs (f)	$33.5 - 58.5 \times 2.3 - 5.7$	53	4/4
Actinopharynx			
Basitrichs (b)	$(20.8)\ 21.9-32.0 \times 1.9-3.9$	36	3/3
Microbasic p-mastigophores (d)	$20.5 - 28.2 \times 3.2 - 4.3$	3	2/3
Column (including column specializations)			
Basitrichs (c)	$(7.8)\ 10.2-17.2 \times 1.1-3.2$	51	4/4
Mesenterial filaments			
Basitrichs* (c)	$10.4-16.1 (21.9) \times 1.3-3.0$	34	4/4
Microbasic p-mastigophores* (d)	$(12.7)$ $13.3-25.9 \times 2.3-5.7$	66	4/4
Microbasic b-mastigophores (e)	$24.6 - 34.4 \times 3.2 - 5.5$	46	4/4

"Letters refer to components of Figure 5.

in distal part of column roughly circular, to 0.5 mm in diameter, histologically a verruca. Ectoderm of red spots in proximal part of column not histologically specialized.

Diffuse endodermal marginal sphincter muscle lies on aboral side of deep fosse (Figure 3); weak, so tentacles of even unrelaxed preserved specimens may be visible (the tentacles, however, shorten greatly in preservation).

Longitudinal retractor muscles diffuse (Figure 4). Parietobasilar muscles with short free pennon (Figure 4).

NATURAL HISTORY: When attached in crevices, this anemone is tightly adherent, but some specimens detach readily from flat or convex surfaces. Its tentacles are very sticky. The red spots on the proximal part of the column are histologically verrucae, but some are not very adhesive, and, in life, a typical individual has a small piece of gravel

stuck to only a few of them even where there is abundant gravel of appropriate size in the habitat.

There is no direct evidence that these animals reproduce asexually; although they are relatively abundant where they occur, and their occurrence is spotty, they have not been observed dividing, and most individuals have regular anatomy (one was dissected that had three siphonoglyphs and pairs of directive mesenteries).

At the type locality, A. buddemeieri occurs in the same habitat as an anemone of similar size that I (as Dunn [1974] and Fautin [1988]) have referred to as Actiniogeton seere (Haddon & Shackleton, 1893), a name that England (1987) considered a junior synonym of Gyractis excavata Boveri, 1893; the taxonomy of this other species is discussed later in this paper.

ETYMOLOGY: The species is named for

<sup>\*</sup> There may be two kinds: a more gracile sort that is typically narrower and somewhat shorter than a more robust sort, but they overlap in size and form.

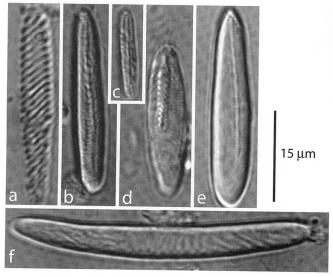


FIGURE 5. Cnidae of Anthopleura buddemeieri. See Table 1 for key to letters.

Robert W. Buddemeier, a coral reef scientist currently of the Kansas Geological Survey, and my husband, who first pointed these animals out to me on Wongat Island.

TYPE LOCALITY: High intertidal zone, seaward side Wongat Island, Madang Lagoon, Papua New Guinea (5° 10.2' S, 145° 50.4' E).

TYPE AND VOUCHER SPECIMENS: Holotype: KUNIM 001992, collected 16 June 2000, by Daphne G. Fautin, Adorian Ardelean, and John Mizeu. In preservation, 10 mm long, base 10 mm diameter. Female. Specimen longitudinally bisected: one half intact, other half transversely bisected, with histological slides (five of longitudinal sections at margin [Figure 3], five of cross sections at midcolumn [Figure 4 upper image]).

Paratypes: Collected along with the holotype. Kunim 001993 (4) uncut (so sex not determinable): one pyramidal, contracted 7 mm long, base 8 mm diameter; one contracted 4 mm long, base 4 mm diameter; one 10 mm long, flared pedal disc 12 × 17 mm, column about 12 mm diameter; one flaccid and torn 5 mm long, base ~10 mm diameter.

Collected at the type locality 27 June 1994, by Daphne G. Fautin and Kasuz. KUNHM 00191 (2) uncut: one contracted 7 mm long, base 12 mm diameter; one with actinopharynx everted 5 mm long, column 10 × 20 mm diameter.

Collected at the type locality 30 October 1987, by Daphne G. Fautin, John Mizeu, and R. W. Buddemeier. cas 065197 (11), histological sections made from some, some dis-

sected: most 12-15 mm long, 10-12 mm diameter.

Collected at Motupore Island, Bootless Bay, Central Province, Papua New Guinea (9° 31.3′ S, 147° 17.1′ E), 9 June 2000, by Daphne G. Fautin and Adorian Ardelean. KUNHM 001995 (2), ~7 mm long, column 12 mm diameter, dissected, with histological slides (four of longitudinal sections at margin, four of cross sections at midcolumn from one specimen, five of the former and five of the latter from the other specimen) (Figure 4 lower image). KUNHM 001996 (3) uncut: one 8 mm long, base  $5 \times 8$  mm; one 9 mm long, base 9 mm diameter; one 11 mm long, base 17 mm diameter. USNM 1026643 (2) uncut: one 10 mm long, 8 mm column and basal diameter; one 10 mm long, base 7 × 15 mm.

Collected in the high intertidal zone, shore near the campus of the University of the South Pacific Marine Studies Programme (18° 9' S, 178° 27' E), 25 May 2000, by Johnson Seeto, Daphne G. Fautin, and Adorian Ardelean, KUNHM 001989 (2) uncut: one 3 mm long, base 5 mm diameter; one 4 mm long, base 7 × 8.5 mm. KUNHM 001990 (1) female almost completely sectioned histologically (five slides of longitudinal sections at margin, five of cross sections at midcolumn. USP 5306 (3): one uncut 4.5 mm long, base 6 mm diameter; one uncut 2.5 mm long, base 4.5 mm diameter; one transversely bisected, 9 mm long, base 8 × 11 mm, sex unknown. USP 5307 (3): one uncut 8 mm long, base 5 × 6 mm; one uncut 3 mm long, base 6 mm diameter; one longitudinally bisected, sex unknown, intact half 4.5 mm long, base 5.5 mm diameter, with histological slides of other half (four of longitudinal sections at margin, four of cross sections at midcolumn).

Voucher specimens: Collected at the type locality 27 June 1994 by Daphne G. Fautin and Kasuz. KUNHM 001994 (2) uncut (so sex not determinable); (4) (two female, one male, one sexually undifferentiated) sectioned histologically.

Collected at the type locality 24 October 1987, by Daphne G. Fautin, T. L. Frohm, and R. W. Buddemeier. cas 065198 (6), histological sections made from some: one uncut

10 mm long, base  $11 \times 17$  mm; one transversely bisected 8 mm long, basal diameter 10 mm, oral disc diameter 15 mm; four others in pieces about 8–14 mm long, 14–20 mm diameter.

Collected in the high intertidal zone, shore near the campus of the University of the South Pacific Marine Studies Programme (18° 9′ S, 178° 27′ E), 25 May 2000, by Johnson Seeto, Daphne G. Fautin, and Adorian Ardelean. USP 5311 (17), most uncut.

DIFFERENTIAL DIAGNOSIS: Three known species have the rich brown column with red spots of Anthopleura buddemeieri: A. ballii (British Isles), A. krebsi (southeastern United States to Brazil), and Actinia sanguineopunctata (Mauritius). Some specimens of A. asiatica are similarly colored. Tentacles of A. sanguineopunctata have pinkish tips, the oral disc has white radii, and the mouth is surrounded by blue patches. Anthopleura ballii is zooxanthellate. All verrucae of A. krebsi conform closely to Carlgren's definition of those structures, in contrast to those of A. buddemeieri (and A. ballii), and the oral face of each tentacle of A. krebsi is marked with a white longitudinal stripe and white crossbars, in contrast to the unmarked oral face of a tentacle of A. buddemeieri. Nematocysts of A. krebsi have the following distinguishing attributes (Daly and den Hartog 2004): holotrichs of two size classes in the acrorhagi, microbasic pmastigophores of the actinopharynx smaller, column with holotrichs, and mesenterial filaments with both basitrichs and microbasic bmastigophores of two distinct classes, the larger basitrichs and the smaller microbasic b-mastigophores not overlapping those of A. buddemeieri in size. Nematocysts of A. asiatica have the following distinguishing attributes (Uchida and Muramatsu 1958): holotrichs of two size classes in the acrorhagi (although the size range of the two combined corresponds to the range in A. buddemeieri); column with holotrichs and three size classes of basitrichs, the largest of which are larger than any I found; and mesenterial filaments lacking microbasic b-mastigophores altogether and having basitrichs that do not correspond in size to those of A. huddemeieri.

#### DISCUSSION

By virtue of having basilar muscles, an endodermal sphincter muscle, and one tentacle per intermesenterial space, individuals of A. buddemeieri clearly belong to the actiniarian family Actiniidae. Each marginal projection has an acrorhagus on its oral side and a verruca on its adoral side. This terminology is that of Daly (2003), who distinguished among the structures that may be present at the margin of a sea anemone. Although they are not very adhesive, the ectodermal specializations in the distalmost column most closely correspond to verrucae, defined by Carlgren (1949:10) as "more or less ampullaceous, adhesive evaginations of the column, simple or more rarely compound; with modified ectoderm, without nematocysts in their central part." According to Carlgren (1949), an actiniid with acrorhagi and verrucae is a member of the genus Anthopleura. England (1987, 1992) considered the presence of "heterotrichs" (holotrichs) in the column to be a requisite for membership in the genus, but they are lacking in some species of Anthopleura (e.g., A. ballii), and the most recent definition of the genus (Daly and den Hartog 2004) does not include that character.

The Mauritian species Actinia sanguineopunctata Templeton, 1841, has not been recorded under that name since its description, nor has the species been referred to by any other name to my knowledge. It was described at a time when most sea anemones were referred to the genus Actinia, so it should be studied to determine the genus to which it properly belongs. If it still exists, it should not be difficult to identify; Templeton's (1841) color illustration is sufficiently detailed to distinguish it from A. buddemeieri.

The genus *Pseudactinia*, according to Carlgren (1949), is similar to the genus *Anathopleura* but has vesicles rather than verrucae. Vesicles were defined by Carlgren (1949:10) as "ampullaceous, non-adhesive evaginations of the column, simple or compound; with more or less numerous nematocysts of various categories." The distinction between verrucae and vesicles, and how they differ

from other similar structures, has been debated (e.g., England 1987, den Hartog 1987, Riemann-Zürneck and Gallardo 1990). Clearly, neither definition precisely fits the column patches of *Anthopleura buddemeieri* because some are adhesive but most are not. Considering that the nature of column specializations is less clear-cut than Carlgren's definitions imply, and that the definition of the genus otherwise fits this new species so well, I place it in *Anthopleura*. According to M. Daly (pers. comm.), some other species of *Anthopleura*, such as *A. ballii*, also have column structures of both or ambiguous types.

Some aspects of Anthopleura asiatica are reportedly similar to those of A. buddemeieri, but because the name seems to have been applied to more than one species, critical information on internal anatomy (e.g., nature of sphincter and retractor muscles) is lacking in the original description, and no type specimens were designated or are known (Fautin 2004), I find the name Anthopleura asiatica to be a nomen dubium. Some records of A. asiatica may be of A. buddemeieri, but without specimens it is impossible to ascertain which. According to the original description by Uchida and Muramatsu (1958) from animals collected in Japan, some categories of nematocysts of A. asiatica are identical in size to those of A. buddemeieri, the size of the animals is similar, and at least some individuals are brown with red spots. As pointed out by England (1992), the reported number of tentacles is half that of the mesenteries, which would preclude the species belonging to Anthopleura, but this is clearly a lapsus: Uchida and Muramatsu (1958:117) reported 48 tentacles and 48 pairs of mesenteries, stating that the "48 pairs ... are divided into 12 primary, 12 secondary and 24 tertiary cycles. Only the primary 12 are perfect," so the numbers refer to individual mesenteries, not pairs. Parulekar (1968:142) used the name A. asiatica for some "grevish-green" animals found at Chaupatty, Bombay, India, but den Hartog and Vennam (1993) were unable to obtain specimens in an effort to confirm the identity of the animals. The size of an individual and habitat notes given by Pei (1998)

from Chinese specimens agree with what I found for A. buddemeieri, but nematocyst sizes are very different from those given by Uchida and Muramatsu (1958) and from what I found for A. buddemeieri, and Pei (1998) reported that the tentacles are patterned. Uchida and Muramatsu (1958) noted that acrorhagi may be absent in small individuals of A. asiatica, but they were present in all individuals of A. buddemeieri I examined. The lower photograph of A. asiatica in the book on Japanese sea anemones by Uchida and Sovama (2001:55) shows animals that resemble A. buddemeieri, but the other two photographs, ostensibly of the same species, do not. The name A. asiatica was mentioned by Dunn (1974:381) and by England (1987:239) (Fautin 2004).

Clearly, a column with bright red punctations is not sufficiently distinctive to be used alone to identify sea anemones. In addition to those listed above, the South African species described by Carlgren (1938) as Anthostella stephensoni has such markings, although the column is typically yellowish or white. Carlgren (1938) created the genus Anthostella for this species because of the nature of its column specializations and marginal structures; Branch et al. (1994) placed it in the genus Anthopleura, an action that has not been formally justified, to my knowledge.

The sea anemone known most recently as Gyractis excavata and Actiniogeton sesere is widespread in the tropical Pacific, having been described from Sri Lanka and Torres Straits, respectively, and being known from as far east as Hawai'i (Dunn 1974) and as far west as Aden (England 1987). England (1987) convincingly showed that this species was described in 1893 under three names, Gyractis excavata and G. pallida by Boveri (1893), and Actinioides sesere by Haddon and Shackleton (1893). Clearly, G. excavata has "position precedence" (International Code of Zoological Nomenclature Recommendation 69A.10 [International Commission on Zoological Nomenclature 1999]) over G. pallida. England (1987) provided no reason for selecting the name G. excavata rather than A. sesere for the species (he died in 1991: see notes at the end

of England [1991] and [1992]). The cover of the brief publication in which Haddon and Shackleton (1893) described the genus Actinioides and two new species of it states "Read December 21; Received for publication December 22, 1892; Published March 25, 1893." The issue of Zoologische Jahrbücher containing the article by Boveri describing the genus Gyractis and what he considered to be two members of it was published on 15 August 1893, according to the journal's table of contents. Thus, the genus name Actinioides has priority over the name Gyractis, and the species name A. sesere has priority over the name G. excavata. Carlgren (1938) considered the "genotype" of Actinioides to be A. dixoniana, a species he assigned to Anthopleura, an assignment with which England (1987) concurred. Carlgren (1938:32) therefore created the generic name Actiniogeton as a provisional name "for sultana, and probably for certain other species referred to Actinioides by Haddon and Shackleton (1898)" [the paper by Haddon and Shackleton was published in 1893; in 1898, Haddon alone published a paper redescribing many of the species briefly covered in 1893 by Haddon and Shackleton and describing some others]. Despite that, Carlgren redescribed in the same publication the species he called Actinioides sultana Carlgren, 1900. England (1987) considered Actinioides sultana to be another synonym of what he referred to as Gyractis excavata. Of the generic names that have been applied to that species, Actinioides, which was described in 1893, is a junior synonym of Anthopleura; Gyractis was created in 1893; and Actiniogeton was created in 1938. Because the precedence of names can be objectively determined, the species described as Actinioides sesere Haddon & Shackleton, 1893; Gyractis excavata Boveri, 1893; and G. pallida Boveri, 1893, should be properly termed Gyractis sesere (Haddon and Shackleton, 1893).

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