Nomenclature of *Aulactinia* (=*Bunodactis*), with description of *Aulactinia incubans* n.sp. (Coelenterata: Actiniaria), an internally brooding sea anemone from Puget Sound

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Aulactinia incubans n.sp. is an internally brooding actinian known from the San Juan Archipelago, Washington, U.S.A., and from Torch Bay, Alaska, U.S.A. Found in sheltered intertidal habitats, this sea anemone averages 25–30 mm in pedal disc diameter and has fewer than 65 tentacles. Females, hermaphrodites, sexually undifferentiated, and possibly male individuals are known. *Aulactinia incubans* releases its brooded young through the pore at the tip of each tentacle; the young are tentaculate at the time of release. This species fits genus *Bunodactis* in all respects except that the outer tentacles of some individuals contain atrichous nematocysts. We believe that this feature alone, which is not apparent in all specimens of the species, does not require naming a new genus. Rather, we broaden the definition of genus *Aulactinia*, a name that has priority over *Bunodactis*, to include this character.

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Aulactinia incubans n.sp. est une actinie à incubation interne connue de l'archipel San Juan dans l'état de Washington, et de Torch Bay, Alaska, E.U. Cette anémone de mer habite les régions protégées de la zone intertidale; le diamètre du disque pédieux est de 25–30 nm en moyenne et l'anémone porte moins de 65 tentacules. On peut reconnaître des femelles, des hermaphrodites, des individus non différenciés et peut-être aussi des mâles. Après l'incubation, *Aulactinia incubans* libère ses petits par le pore situé au bout de chaque tentacule; les jeunes portent déjà des tentacules au moment de leur libération. Cette espèce pourrait appartenir au genre *Bunodactis* puisqu'elle en a tous les caractères à l'exception de quelques individus dont les tentacules externes possèdent des nématocystes glabres. Il nous semble que ce caractère seul, qui n'est pas apparent chez tous les spécimens de l'espèce, ne suffit pas à l'établissement d'un nouveau genre. Nous préférons élargir la définition du genre *Aulactinia*, nom qui a priorité sur *Bunodactis*, de façon à englober ce caractère.

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Introduction

The sea anemone reported here, ***Aulactinia incubans*** n.sp., was first recorded in the vicinity of Puget Sound in 1976, but it is probably part of the native fauna. Its scarcity and superficial resemblance to other local actinians are likely factors in its late discovery. Most anatomical features of *A. incubans*, and its internal brooding of juveniles, ally it with species currently placed in genus *Bunodactis* Verrill 1899. Carlgren (1949) synonymized the genus *Aulactinia* Verrill 1864 with *Bunodactis* but inexplicably chose to use the junior name. Some specimens of *A. incubans* have atrichous nematocysts in their outer tentacles, a character that distinguishes it from *Bunodactis* as now defined (Carlgren 1949); we choose to broaden that definition rather than to create a new taxon based on such an apparently variable feature and to call the genus by its senior synonym, *Aulactinia*.

Materials and methods

Specimens of *Aulactinia incubans* were observed and collected on San Juan Island, Puget Sound, Washington, U.S.A. (48°32′ N, 123°05′ W) and the nearby Deadman Island. Some were maintained in running seawater tanks at the University of Washington Friday Harbor Laboratories for observation, and a number have been kept under these conditions for as long as 4 years by Dr. R. L. Fernald, during which time many have reproduced in captivity. One specimen was collected interti-

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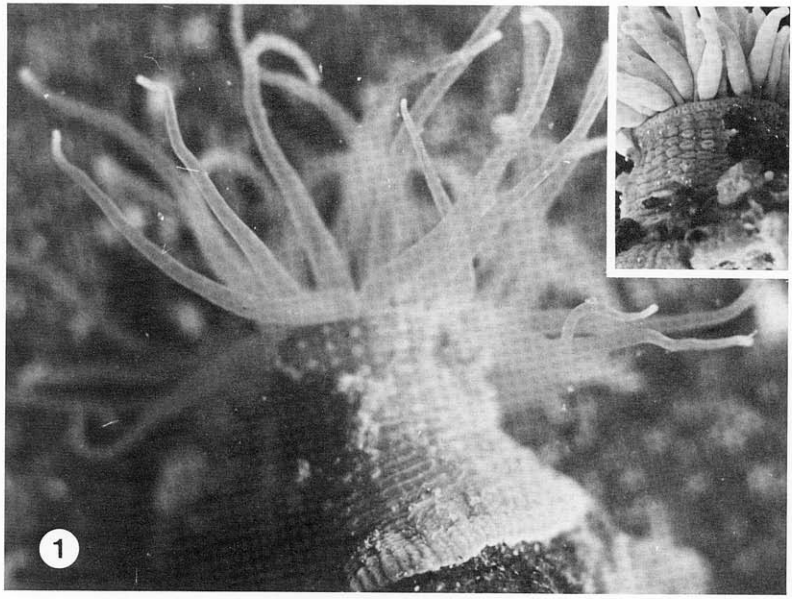

FIG. 1. Side view of live specimen of *Aulactinia incubans*. Note verrucose column, dilated pedal disc, and sinuous tentacles. Inset: Side view of fixed specimen showing the verrucae in better focus.

dally in Torch Bay, Alaska (58°18.8′ N, 136°48.0′ W), by Dr. Lisbeth Francis.

The following description is based on study of over 500 living specimens. Some were subsequently preserved for study of internal anatomy and histology. Relaxation was in seawater to which chloral hydrate (procedure in paper by Dunn (1975)) or 7.5% $MgCl_2$ had been added, and fixation was with 10% seawater formalin or Bouin's solution. Paraffin sections were cut at 5–8 μm and stained with iron hematoxylin and eosin or Mallory–Heidenhain stain (Humason 1972). Smears from 24 living animals provided data about cnidae, but not all tissues of each individual were examined. In the data on cnidae, N is the ratio of the number of animals in which a particular kind of cnida was found to the total number examined for that tissue type, and n is the number of cnidae measured; measurements in parentheses were of single capsules that fell well outside the usual range.

Description

Pedal disc

Roughly circular, typically pulled in at edge along each mesenterial insertion and shallowly scalloped; underside pale, dark mesenterial insertions may be visible. Average diameter in the live animal 25–30 mm. Strongly adherent to solid substratum. Basilar muscles strong.

Column

Diameter less than that of pedal disc, uniform for most of length, average height 12–15 mm in full extension. Contracted animal forms low dome, with tentacles completely hidden, although normally contraction is incomplete and a tuft of tentacles remains visible.

Body wall tough. In life, larger animals typically dull green or brick red color, rarely orangish; small ones cream color; pigmentation often deeper around parapet. Simple adhesive white verrucae extend from margin to limbus in longitudinal rows communicating with each endocoel (Fig. 1); larger verrucae may have dark, depressed center but smaller ones are typically domed; prominent in preserved specimens. Most rows contain about 10 verrucae, the largest of which is generally the third or fourth below margin with diameter of no more than 0.5 mm, but largest may be more proximal. Some exocoels have a few small verrucae at distal end. No marginal spherules or pseudospherules, but the most distal verrucae, situated at or just

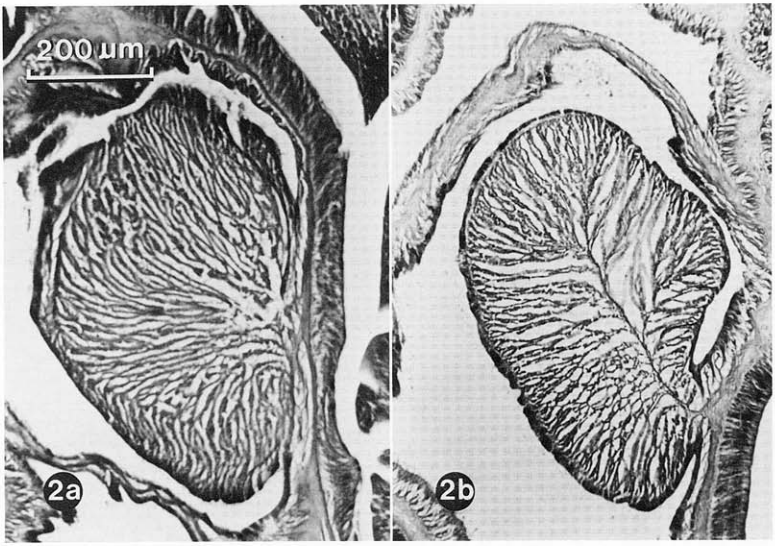

FIG. 2. Cross sections of circumscribed, endodermal sphincter muscles of *Aulactinia incubans*. (*a*) Palmate form (specimen CASIZ No. 011024); (*b*) pinnate form (specimen CASIZ No. 011025).

below margin, might be mistaken for them. Mesenterial insertions visible as dark lines at proximal end where column flares; sometimes visible as light lines above in well expanded specimens.

Fosse prominent, average depth 1 mm. Sphincter muscle arises from its marginal side near bottom; endodermal, circumscribed, and generally palmate (Fig. 2*a*), rarely pinnate (Fig. 2*b*).

Oral disc

Average diameter in live animal 12–15 mm (range 2–30+ mm), i.e., considerably smaller than pedal disc but slightly wider than column. Radial muscles ectodermal, circular endodermal.

Flat in expanded individual except for transitory low oral cone, tentacles occur only in outer half to third. Ground color usually grey, rarely green, inner portion may be tan. A white line extends over each endocoel and exocoel from just beyond oral cone to base of each tentacle, except for the two directive endocoels over which lines originating in siphonoglyphys extend across oral cone (Fig. 3). Exocoelic lines typically narrower than endocoelic, the boldness of which may be inversely proportional to their order. Dark mesenterial insertions seldom discernible. In very rare individuals, white radial lines altogether absent, or directive lines do not cross oral cone; commonly their number does not precisely correspond with that of tentacles. The two halves may have an unequal number of lines (e.g., 16 and 18, and in one animal 28 and 17) and tentacles.

Mouth typically oval, 2 mm long, lacking lips; actinopharynx white, rarely pale pink or green, shallowly sulcate, with two siphonoglyphys usually about 180° apart.

Tentacles

In expansion, longest is equal to or greater than oral disc diameter (12–20 mm in average size individual, basal diameter 2 mm), sinuous, tapering to point (Figs. 1, 3), endocoelic somewhat longer than exocoelic; length changeable. Relatively few, rarely a multiple of six (e.g., 33, 40, 47 counted), commonly 30–48, but two observed with 63 (animals were of average size). One communicates with each exocoel and endocoel. Generally first three cycles regularly arrayed; irregularities are in

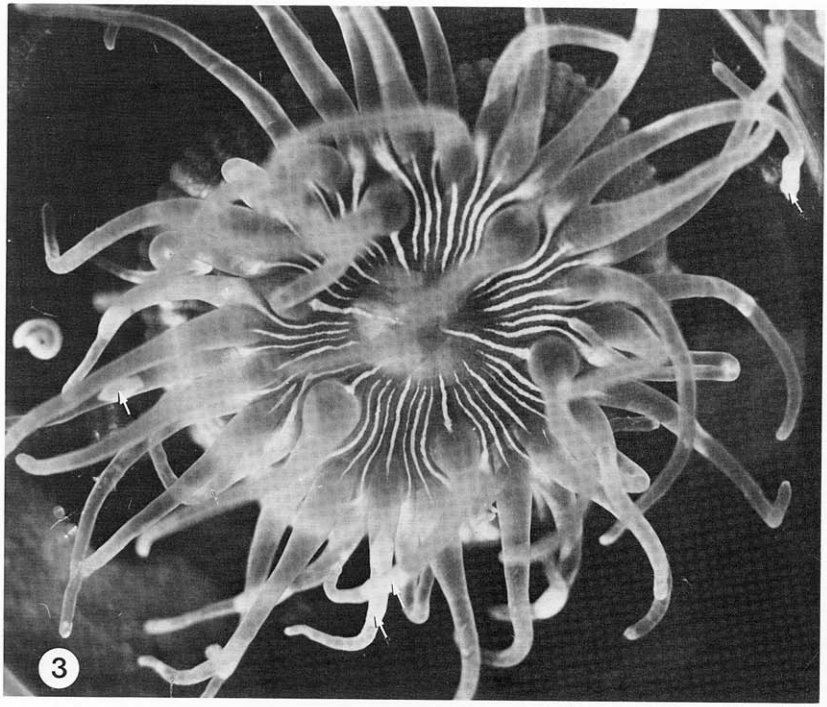

FIG. 3. Oral disc of *Aulactinia incubans*. Note that white lines over directive endocoels cross oral cone whereas others do not; planulae or juveniles (arrows) inside tentacles.

fourth and, if present, fifth cycles. Innermost six primary tentacles held vertically, outermost (exocoelic) droop downward over margin, intermediate ones held at proportionately intermediate angles. Tip perforate (Fig. 4); longitudinal musculature ectodermal, circular endodermal.

Translucent or even transparent in full extension, dove grey or rosy to lavender (independent of column color); oral side of exocoelic ones with splash of white at base upon which white radial line terminates (Fig. 3), endocoelic ones without markings. White pigmentation disappears in preservation.

Mesenteries and internal anatomy

Mesenteries regularly arrayed despite absence of strict hexametry in most individuals. At least first two cycles complete. Large marginal and oral stomata. Added from proximal end. Retractor muscles not very strong, somewhat restricted to diffuse, with moderate number of branches (Fig. 5). Parietobasilar muscles well developed and wide; may extend centrally as far as retractor muscle (Fig. 5); central edge may be slightly detached. Mesenterial filaments may be absent from mesenteries of youngest order.

All mesenteries, including directives, may be fertile except those of highest (generally fifth) order. Female, hermaphroditic, sexually undifferentiated and possibly male individuals known; in hermaphrodites, eggs and sperm may be present in the same mesentery, but more commonly one member of a pair of mesenteries has ova and the other sperm. Gonadal portion of mesentery narrow. Ova up to 800 μm diameter in section, 1 mm in preserved animals; very yolky; each has a

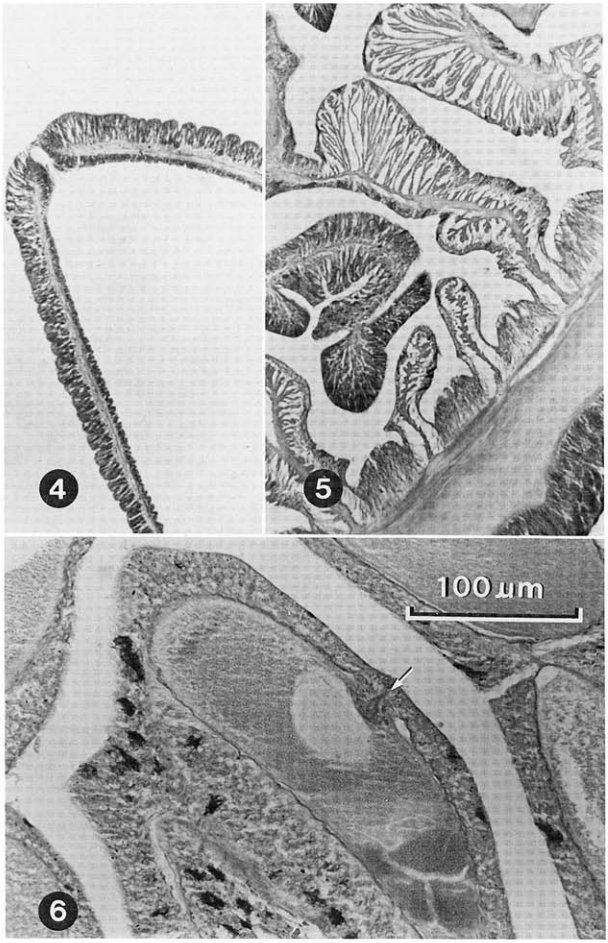

FIG. 4. Longitudinal section of tentacle tip, showing terminal pore (paratype: CASIZ No. 015672). FIG. 5. Column cross section showing parietobasilar and diffuse retractor muscles (paratype: NMCIC No. 1980–141*c*). FIG. 6. Oocyte of *Aulactinia incubans*; note trophonema (arrow) (paratype: CASIZ No. 015671).

trophonema (Fig. 6) (see paper by Dunn (1975) for definition).

Zooxanthellae lacking.

Cnidom

Spirocysts, basitrichous isorhizas (basitrichs), atrichous isorhizas (atrichs), microbasic *p*-mastigophores.

Size and distribution of nematocysts

The letter following each cnida type refers to illustration of it in Fig. 7.

Tentacles			
Spirocysts (*a*)	13.0–28.0 μm × 2.0–3.2 μm	$n = 121$	$N = 17/17$
Basitrichs (*b*)	(16.5)19.0–28.0 μm × 2.5–3.8 μm	$n = 157$	$N = 17/17$
Atrichs (*c*)	17.0–27.5 μm × 2.3–3.5 μm	$n = 26$	$N = 5/17$
(Only in outermost tentacles)			
Actinopharynx			
Basitrichs (*d*)	10.5–23.0 μm × 2.0–3.3 μm	$n = 30$	$N = 9/14$
Basitrichs (*e*)	22.0–37.0 μm × 3.0–4.8 μm	$n = 96$	$N = 14/14$
Microbasic *p*-mastigophores (*f*)	16.0–24.0 μm × 4.0–6.0 μm	$n = 33$	$N = 8/14$
Mesenterial filaments			
Basitrichs (*g*)	11.5–22.0(25.0) μm × 2.0–3.0 μm	$n = 65$	$N = 11/11$
Basitrichs (*h*)	29.0–44.0 μm × 3.5–4.8 μm	$n = 58$	$N = 11/11$
Basitrichs (*i*)	24.0–40.5 μm × 3.5–7.0 μm	$n = 48$	$N = 11/11$
(May be mistaken for microbasic *p*-mastigophore because heavy basal spines form V-shaped notch in unfired state, but butt is not dilated)			
Microbasic *p*-mastigophores (*j*)	18.0–26.0(29.0) μm × 4.0–6.0 μm	$n = 51$	$N = 11/11$
Column			
Basitrichs (*k*, *l*)	8.0–21.0 μm × 1.8–3.5 μm	$n = 159$	$N = 15/15$
(Generally separable into two size classes, 8.0–12.0 μm (*k*) and 13.5–21.0 μm (*l*) long, but intermediates may occur)			

Habitat

Occurs in sheltered habitats on exposed (west) sides of San Juan Island and Deadman Island. Inhabits crevices and tide pools as high as +2 m, particularly where shaded by seagrass (*Phyllospadix*), overhanging rock, or logs; in such situations generally surrounded by sand and gravel in which it may be buried to the margin. Also occurs atop rocks, especially at lower levels (to about −1 m) where algal cover dense. Found both above and below other sea anemone typical of these habitats, *Anthopleura elegantissima* (Brandt 1835). Generally several specimens of *Aulactinia incubans* occur near one another, but nowhere are they abundant.

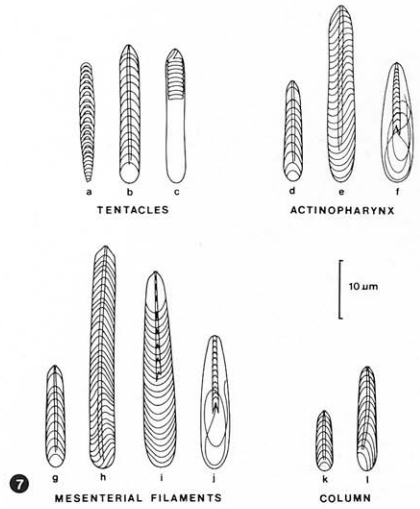

FIG. 7. Nematocysts of *Aulactinia incubans*; see text for explanation.

Type locality and specimens

HOLOTYPE: Half of a longitudinally bisected female specimen and three slides (one of longitudinal and two of cross sections) made from the other half; deposited in the Department of Invertebrate Zoology, California Academy of Sciences (CASIZ catalog No. 015670); collected 6 August 1979, by D. F. Dunn (who collected all type specimens).

TYPE LOCALITY: Grandmother's Cove, American Camp, San Juan Island, Washington, U.S.A.

PARATYPES: At the California Academy of Sciences, two similarly sectioned, CASIZ catalog No. 015671 (a hermaphrodite, also collected at Grandmother's Cove on 6 August 1979) and CASIZ catalog No. 015672 (a female, collected from False Bay, San Juan Island, on 8 August 1979), and a third, whole and therefore of unknown sex, CASIZ catalog No. 015673, collected from a surge channel roofed over by drift logs on the west side of Cattle Point, San Juan Island, 15 August 1979; two in the United States National Museum, USNMNH No. 59290 (a hermaphrodite from Grandmother's Cove, collected 6 August 1979, and three slides

from half of it), and USNMNH No. 59289 (a whole specimen collected from the surge channel on the west side of Cattle Point on 15 August 1979); one in the National Museum of Natural Science, Ottawa, No. NMCIC 1980–141*a* (a female collected at Grandmother's Cove on 6 August 1979) and four slides from it (NMCIC 1980–141*b*, *c*, *d*, and *e*). Some of the other specimens studied are in the collection of the Department of Invertebrate Zoology, California Academy of Sciences, as voucher material.

Etymology

The specific name "*incubans*" is derived from the Latin, and refers to the brooding of juvenile sea anemones in the coelenteron of the parent. Fully tentaculate, pale colored young are released through the tentacle tip pores of the brooding adult.

Taxonomic and nomenclatural considerations

This species clearly is a member of Actiniidae and, according to Carlgren's (1949) key to that family, belongs in genus *Bunodactis* Verrill 1899. The diagnostic characters of the genus apply well to this species except for the cnidom. *Bunodactis* is not known to possess atrichous isorhizas. *Anthopleura* does have atrichs and is so similar in many respects to *Bunodactis* that numerous species have been shifted from one genus to the other, but it is distinguished by its acrorhagi (marginal spherules) that are absent in *Aulactinia incubans*. Its atrichs occur only in the outermost tentacles, but were not found in those of every individual anemone, possibly because they are indeed absent, possibly because they are very sparse. Moreover, they are the same size as tentacle basitrichs and could be confused with them. Thus it is possible that their presence in some or all of the other species assigned to *Bunodactis* may have been overlooked, and the conservative approach would be to revise the generic definition to include the possibility of atrichs occurring, rather than to erect a new genus on the basis of a character that may not be present in all individuals.

Carlgren (1949) listed 37 species under genus *Bunodactis*, 3 of them with a query. Eight have been formally removed from the genus: *B. minima*, *B. elegantissima*, and *B. nigrescens* actually belong to *Anthopleura* (according to Parry (1951), Hand (1955), and Dunn (1974), respectively); as do *B. duregnei*, *B. rigidus*, *B. sabelloides*, and *B. steinitze*, which are all synonyms of *A. rubripunctata* according to Schmidt (1972); and *B. pluvia* is the type species of *Phymanthea* (Carlgren 1959). Uchida (e.g., Uchida 1938; Uchida and Iwata 1954) discussed synonymizing *B. japonica* with *Epiactis prolifera*; the latter is specifically distinct from the North American actinian of that name (Dunn 1975), and thus the species should be known as *E. japonica*. Cadet Hand (personal communication to D. F. Dunn, May 1977) believes that *B. rosea* belongs to *Anthopleura*, and *B. altifossa* to *Pseudohormathia*. Since the publication of Carlgren's (1949) catalog, three new species of *Bunodactis* have been described: *B. chrysobathys* Parry 1951, *B. taxaensis* Carlgren and Hedgpeth 1952, and *B. marplatensis* Zamponi 1977. Carlgren (1959) recognized *B. hermafroditica* [sic] (McMurrich 1904) as distinct from *Anthopleura hermafroditica* [sic] (Carlgren 1898) although he had previously (Carlgren 1949) synonymized them. Clubb's (1908) name *Cribrina hermaphroditica* must refer to McMurrich's species because Clubb's specimens had pseudoacrorhagi; Carlgren (1949) synonymized Clubb's species with *B. aucklandica*, but his 1959 discussion made no reference to it. Thus there seem to be 29 nominal species of *Bunodactis*, although the situation is still very confused, and other synonymies probably exist, e.g., *B. elongata* and *B. conica*.

These 29 species were originally described in 13 genera, including *Bunodactis*. The generic names *Bunodes* Gosse 1855 and *Bunodella* Verrill 1899 are junior homonyms in actinians, having priority in Xiphosura (Neave 1939). The names *Actinia* Linnaeus 1767, *Tealia* Gosse 1858, *Anthopleura* Duchassaing and Michelotti 1860, *Epiactis* Verrill 1869, and *Parantheopsis* McMurrich 1904 are all currently in use for animals that are generically distinct from species included in *Bunodactis* as it is now defined. The type species of *Tealiopsis* Danielssen 1890 belongs to *Stomphia* Gosse 1859 (Carlgren 1949). None of the 10 species listed under the original description of *Cribrina* Ehrenberg 1834 was specified as type, although the first is *verrucosa*, type species of *Bunodactis* (Verrill 1899; Carlgren 1949); there was no diagnosis of the genus and its 10 species are now assigned to diverse genera. None of the three original species of *Cystiactis* Milne-Edwards 1857 was designated type; Verrill (1869, p. 473) found the genus "imperfectly defined," and of the three original species, the only one listed by Carlgren (1949), *C. reynaudi*, was included in *Bunodactis*. Neave (1940) stated that *Urticina* was described by Ehrenberg (1834) but we have been unable to find reference to it; Verrill (1899) said that that name is synonymous with *Tealia* Gosse 1858, over which *Urticina* has priority. Species described as belonging to *Urticina* are now included in *Actinostola*, *Antholoba*,

Bunodactis, and *Tealia*. Thus these generic names, which have been applied to species now considered to belong to *Bunodactis*, properly belong to other genera, or are ambiguously defined.

The only other name that has as its type a species included by Carlgren (1949) in *Bunodactis* is *Aulactinia* Verrill 1864. *Bunodactis* was proposed as a replacement name for *Bunodes*, which predates *Aulactinia*. According to Article 60(*b*) of the International Code of Zoological Nomenclature, replacement names "compete in priority with any synonym recognized later." Verrill (1864) distinguished *Bunodes* from *Aulactinia* and was agitated (Verrill 1899) by Andres' (1881) astute suggestion that they might be the same, but Carlgren (1949) combined them and, for unexplained reasons, called the genus by its junior synonym. Thus the name *Aulactinia* Verrill 1864, should be used rather than *Bunodactis* Verrill 1899. *Aulactinia* was employed most recently by Schmidt (1967) for *A. crassa*, although he later (1972) placed the species in *Cribrinopsis*.

McMurrich (1889) modified the original description of *Aulactinia* to deemphasize the importance Verrill (1864) had attached to the character of the upper verrucae, but also stated that verrucae are restricted to the upper column and that only six pairs of mesenteries are perfect. Verrill (1899) created the genus *Bunodella* on the basis of only six pairs of complete mesenteries, realizing that if specimens with more complete mesenteries were found, the genus would be synonymous with *Bunodactis*. This character varies through ontogeny and is not of taxonomic value in this group.

All nominal species of *Aulactinia* clearly differ from *A. incubans* in color, pattern, presence or absence of zooxanthellae, musculature, nematocysts, and (or) sexual and reproductive features. Many characteristics of the new species are shared with other species of the genus (e.g., pigmented oral disc rays of *A. biscayensis*; habitat of *A. capitata*; posture of *A. duregnei*) but that would be expected of congeners, and the particular combination of features is otherwise unknown. Nor does *A. incubans* closely resemble any species of the similar genera *Anthopleura* and *Actiniogeton*.

Shuffling of species among these and other genera resembling them is partly because some features of contemporary taxonomic significance were not noted in early species descriptions, partly because the taxonomic and biological significance of structures such as acrorhagi and pseudoacrorhagi, which are a criterion for separating some genera, remain unclear, and partly because some such characters are not rigorously defined. For example, if the distalmost verruca of a row is large and at the margin, it may be mistaken for or called a pseudospherule. Carlgren's (1949) definition of *Bunodactis* includes anemones with and without marginal pseudospherules. We follow the more conservative course by retaining the possibility of pseudospherules in *Aulactinia*, although the type species, *A. capitata*, lacks them, and this might create confusion with *Actiniogeton*. Accurate generic assignment of species can be done only after restudy and redefinition of the genera on the basis of biologically meaningful criteria.

Interestingly, among the species of *Aulactinia* that most closely resemble *A. incubans* are *A. capitata* and *A. stelloides*, which were originally described in that genus. Two specimens of *A. capitata* from USNM lot 51245 appeared to have atrichs in their tentacles, although it is difficult to differentiate them in preserved material. (Lots 51244 and 51245, cataloged as *Bunodactis capitata* (Verrill), have recently been identified as *Anthopleura capitata* by J. C. den Hartog, Rijksmuseum, Leiden, according to labels in the jars, although they clearly lack acrorhagi.)

The following diagnosis of *Aulactinia* is somewhat reworded from Carlgren's (1949) diagnosis of *Bunodactis*, and the possibility of atrichs is added:

Aulactinia Verrill, 1864

Actiniidae with well developed pedal disc. All or most of column with more or less distinct adhesive verrucae which are often simple but sometimes lobed in distal part of body. They may or may not be arranged in obvious vertical rows, and foreign bodies are commonly attached to them. No marginal spherules but there may be pseudospherules. Sphincter more or less circumscribed, sometimes circumscribed–diffuse. Tentacles short to intermediate length, simple; longitudinal muscles ectodermal or mesoectodermal. Commonly two well developed siphonoglyphs. Usually mesenteries numerous, with two pairs of directives. All stronger mesenteries fertile, although directives sterile in some species. Retractors commonly strong, more or less restricted. Mesenteries grow from proximal end and therefore may be more numerous proximally than distally. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, atrichs in some.

Discussion

Aulactinia incubans is the sixth species of the genus reported to brood its young internally (the others are *A. bunodiformis*, *A. chrysobathys*, *A. stella*, *A. stelloides*, and *A. verrucosa*). It is appar-

ently unique in releasing them through the pores at the tips of its tentacles. An additional six species, all polar, brood externally. The internal brooders inhabit temperate (*A. verrucosa*) and tropical (*A. stelloides*) waters as well as cold. Whether this high proportion of brooding species results from the primarily cold temperate to polar distribution of *Aulactinia*, or from some sort of predisposition, is an evolutionary–ecological question that invites analysis.

Of 14 sexually ripe specimens examined, 10 were female, 3 were hermaphroditic, and 1 was possibly male. The average pedal disc diameter of females was 19 mm, and that of hermaphrodites 15 mm, the same as that of the questionable male. The largest animals were female, but so were the smallest. The sex of brooding individuals is currently unknown.

The actinian fauna of the Puget Sound area has been the subject of a number of surveys (e.g., Verrill 1869; McMurrich 1901, 1913; Fraser 1932) but new species continue to be found there (e.g., Siebert 1973; Siebert and Spaulding 1976). The late discovery of *Aulactinia incubans* may be attributable to its scarcity, its burial in sand, and the superficial resemblance of its radially lined oral disc to that of *Epiactis prolifera* Verrill 1869.

Acknowledgements

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