Redescription of *Aulactinia veratra* n. comb. (*=Cnidopus veratra*) (Coelenterata: Actiniaria) from Australia.

Suzanne Edmands* and Daphne Gail Fautin†

Abstract

The actinian described as Actinia veratra Drayton, 1846, and currently referred to as Cnidopus veratra, belongs to the genus Aulactinia. Discrepancies in the literature, particularly concerning ectodermal specializations of the column, led to taxonomic uncertainties about its placement. Nomenclatural re-evaluation was necessitated by recent synonymization of the genus Cnidopus with Epiactis. Cribrina vertuculata Lager, 1911, is synonymized with Aulactinia veratra.

Introduction

In this study we evaluate the taxonomic and nomenclatural status of the actiniid sea anemone originally described as *Actinia veratra* Drayton in Dana, 1846, and currently commonly referred to as *Cnidopus verater*. The genus *Cnidopus*, created by Carlgren (1934) for *Epiactis ritteri* Torrey, 1902, has been synonymized with *Epiactis* (Fautin and Chia 1986).

Carlgren (1934: 351) erected *Cnidopus* on the basis of "very numerous nematocysts present at the sides of the protuberances and between them in the lowest parts of the column", which he identified as "probably atrichs" (= atrichous isorhizas). These cnidae actually possess small spines (Bigger 1976, 1982) and so are correctly termed holotrichous isorhizas (= holotrichs). Carlgren (1949) omitted this species from his catalog of Actiniaria, but later (1950a, b) referred *Actinia veratra* to *Cnidopus*. In the process, he inexplicably changed the species name to *verater*, which Ottaway (1975) considered a deliberate emendation that should not supercede the original spelling. Carlgren subsequently (1950b, 1952) referred the Japanese sea anemone called *Epiactis prolifera* Verrill, 1869, (e.g. by Uchida and Iwata 1954) to the genus as *Cnidopus japonicus*.

Fautin and Chia (1986) returned C. ritteri to Epiactis because they found that the type species of the genus, E. prolifera, has holotrichs in the lower column. They urged that the other two species attributed to Cnidopus be studied to determine if they, too, actually belong to Epiactis. We examined Australian specimens of C. veratra to establish the

^{*}Biology Board of Studies and Institute of Marine Sciences, University of California, Santa Cruz, CA 95064 U.S.A.

[†]Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118 U.S.A. and

¹Current address: Department of Systematics and Ecology Snow Museum, Snow Hall, University of Kansas, Lawrence, KS 66045 U.S.A.

appropriate generic placement of this species; although it has not been formally reexamined, Dunn (1972) concluded from the literature and correspondence with Uchida that the Japanese species, "C. japonicus", should be returned to Epiactis.

Materials and methods

Sea anemones from the intertidal zone of Pt. Peron, Western Australia $(32^{\circ}16' \text{ S}, 115^{\circ}40' \text{ E})$, and Barwon Head, Port Philip Bay, Victoria $(39^{\circ}25' \text{ S}, 144^{\circ}50' \text{ E})$ were examined alive and then preserved. Preserved specimens for comparison were sent to us from North Beach at Wollongong, New South Wales $(34^{\circ}25' \text{ S}, 150^{\circ}52' \text{ E})$, and from Portobello, South Island, New Zealand $(45^{\circ}51' \text{ S}, 170^{\circ}39' \text{ E})$.

Cnidae measurements were made from tissue smears of 10 individuals, although not all tissues of each individual were studied. Paraffin sections cut at 8 μ m were stained with hematoxylin and eosin for histological study.

Voucher specimens in the Department of Invertebrate Zoology and Geology, California Academy of Sciences are as follows: *Aulactinia veratra* from Western Australia catalog #066250 (x4, including histological sections from three); from New South Wales #065139 (x1), #065140 (x1), #065141 (x1), #065154 (x2, including histological sections from both); unidentified actiniid from New Zealand #065138 (x7). Four voucher specimens from New South Wales, including histological sections from one, in the Western Australian Museum bear catalog number WAM 861-89.

Aulactinia veratra new combination.

Synonymy

Actinia veratra Drayton in Dana 1846: 129-130. Drayton in Dana 1848: 129-130. Dana 1849: pl.1, figure 3. Dana 1859: 6.

Phymactis veratra Milne-Edwards 1857: 275. Andres 1883: 228.

Cribrina verruculata Lager 1911: 233-234.

Bunodactis verruculata Carlgren 1949: 65.

Cnidopus verater Carlgren 1950a: 124-125. Carlgren 1950b: 137-138, figure 7, 8; pl. III, figure 3. Carlgren 1952: 387. Dakin *et al.* 1952: 136, 137, pl. 22. Carlgren 1954: 571, 576, 593. Ottaway 1975: 58-59. Bennett 1987: 175.

Cnidopus veratra Ottaway 1975: 58-59.

Description

Pedal disc

Well developed, more or less circular, pale tan. Diameter approximately equal to that of column; to 35 mm in specimens examined.

Column

Height 8-15 mm in preserved specimens, average 20 mm in live specimens. Typically green, less commonly brown or reddish brown in color; lighter adhesive areas in longitudinal rows run entire length of column. Histologically adhesive areas composed

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Figure 1. Sections through adhesive areas on column: A) vertucae in upper column; B) sucker in lower column. (CAS 066250). Scale bar = $360 \ \mu m$.

of less vacuolated and more tightly packed cells than regular ectoderm (figure 1); some appear as true complex verrucae (figure 1A), others as suckers (figure 1B). No spherules or pseudospherules at margin.

Endodermal sphincter muscle strong, circumscribed to circumscribed-diffuse, generally palmate, on marginal side of distinct fosse (figure 2).

Oral disc

Flat, mouth central. Tentacles restricted to marginal half.

Redescription of Aulactinia veratra

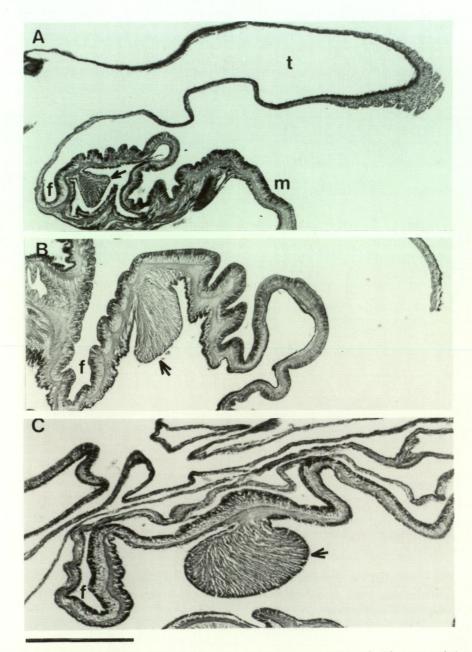


Figure 2. Longitudinal sections through upper column illustrating variability of sphincter muscle (arrow). Sphincter is consistently on marginal side (m) of fosse (f) (CAS 066250). Scale bar = 645 μm for A; 345 μm for B, C. S. Edmands, D.G. Fautin



Figure 3. Cross section showing mesenteries (CAS 066250). Scale bar = 720 μ m.

Tentacles

Conical, blunt-tipped, regularly arrayed, same color as rest of animal. Central ones held erect; marginal ones droop over edge. Fairly short: 5-12 mm in preserved specimens; all of one individual approximately equal length. Observed number varied from 24 to 96, but may be more numerous (Carlgren [1950b] counted 152 in a large specimen, and Hand [unpub.] recorded as many as 150, consistent with a developing fifth cycle of mesenteries that we observed). Longitudinal muscles ectodermal.

Mesenteries and internal anatomy

Maximum five orders of mesenteries (figure 3); first three complete, highest order may be rudimentary and confined to proximal end; two pairs of directives. Mesenteries mostly hexamerously arrayed, with occasional irregularities. Stronger mesenteries except directives fertile; sexes presumably separate (all four fertile individuals sectioned female). Mesenteries added from proximal end, so narrower distally; oral and marginal stomata large. Retractor muscles diffuse (figure 3); parietobasilar muscles wide with short free flap. Actinopharynx ribbed; rose colored in one specimen, cream in others. Directive mesenteries attached to two distinct, symmetrical siphonoglyphs.

No zooxanthellae.

Cnidom

Spirocysts, basitrichs, holotrichs, and microbasic p-mastigophores.

Size and distribution of cnidae

See Table 1 and Figure 4. Column holotrichs were primarily in the lower portion, but occurred occasionally in the mid-column. Nematocyst size did not appear to correlate with animal size.

Table 1. Distribution and size of nematocysts. Measurements are in μ m; values in parentheses indicate nematocysts that fell outside the typical size range. Letters refer to illustrations in Figure 4; n is total number of animals examined; N refers to the ratio of animals possessing a particular cnidae type to the total number examined for that type.

TENTACLES			
Spirocysts (A)	9.0-22.0 x 1.9-4.0	n = 94	N = 8/8
Basitrichs (B)	10.0-21.0 x 2.0-4.0 (5.0)	n = 85	N = 8/8
Basitrichs (C)	21.0-31.5 x 2.0-4.0 (5.0)	n = 88	N = 8/8
ACTINOPHARYNX			
Basitrichs (D)	9.7-17.3 x 1.6-3.8	n = 25	N = 4/8
Basitrichs (E)	18.2-32.1 x 2.2-5.2	n = 75	N = 8/8
MESENTERIAL FILAM	ENTS		
Microbasic p-mastigop	hores (F)		
	9.9-19.8 x 1.8-4.0	n = 42	N = 5/7
Basitrichs (G)	20.1-48.7 x 2.2-5.4	n = 68	N = 7/7
Microbasic p-mastigop	hores (H)		
	15.5-30.4 x 2.9-5.5	n = 45	N = 7/7
COLUMN			
Basitrichs (1)	7.5-19.9 x 2.0-4.0	n = 95	N = 8/8
Basitrichs (J)	20.0-32.0 (36.0) x 2.0-4.0	n = 55	N = 7/8
Holotrichs (K)	21.1-35.0 x 3.7-7.4	n = 37	,

Geographical and ecological range

Aulactinia veratra is known from the intertidal zone of Australia and New Zealand; we observed it in the middle and lower reaches of this zone, Carlgren (1950a) reported it in the upper part. It may be locally abundant on rocky shores, often in the same areas as *Oulactis muscosa* (see Dakin *et al.* 1952, Bennett 1987). It occurs in areas "of moderate wave energy" (Thomas and Shepherd 1982: 167), particularly in rock pools, crevices, and the undersides of ledges.

In New Zealand it has been reported from Auckland (Carlgren 1954), Kaikoura Peninsula (Ottaway 1975), and Otago Peninsula (Ottaway 1975). If it has been confused with *Isactinia olivacea* and possibly other actinians, it may actually be more widespread

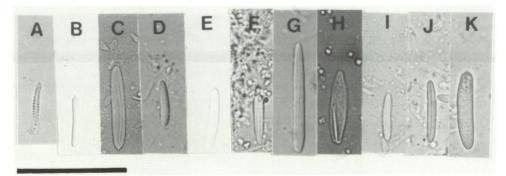


Figure 4. Cnidae types. Letters refer to categories in Table 1. Scale bar = $36 \mu m$.

in New Zealand (Ottaway 1975). This is likely, since "it is found all round the temperate Australian coasts", according to Bennett (1987: 175).

Discussion

Taxonomy

The specimens examined, including those from Wollongong, type locality of Actinia veratra, conform well to the most complete descriptions of the species in terms of size, color, external morphology, musculature, and internal anatomy (Carlgren 1950a), b; Hand unpub.) except that Carlgren (1950b) recorded fertile directives. Carlgren (1950b) failed to list spirocysts, which is certainly an omission since those cnidae are characteristic of most actinians, and definitely of actiniids. We (Table 1) found a somewhat greater size range in several categories of cnidae than did Carlgren (1950a, b), although our range for holotrichs is narrower. Considering that, from what we know of Carlgren's work, his data probably came from small numbers of both cnidae and animals, the agreement is excellent. Mesenterial filaments contain, according to Carlgren (1950b), basitrichs of two sizes and microbasic *p*-mastigophores, whereas we found the reverse. It is difficult to ascertain detail in such small structures, so we deem it likely that we all confounded small basitrichs and small microbasic *p*-mastigophores, both of which occur.

There is confusion in the literature concerning the nature of the column projections of *A. veratra.* Carlgren stated (1950b: 138) that the "outgrowths could possibly be interpreted as verrucae . . . [but] certainly are vesicles". Subsequently (1950a: 124) he "correct[ed] [this] mistake . . . In fact the outgrowths *seem* [emphasis added] to be verrucae, though perhaps not so strong as usually in the verrucous genera". Still, he did not alter his generic assignment of *A. veratra*, although he (1949: 61) had defined *Cnidopus* as having a "[c]olumn smooth in its upper part, in its lower, from the limbus upward, provided with transverse and longitudinal rows of low protuberances square at the base". Similarly, according to Hand (unpub.), anemones of the genus *Cnidopus* have "low protuberances" on the column "which are not identical to verrucae", yet he defined

C. veratra as having "numerous warts". Verrucae are, by definition, warts (Latin for wart is verruca) (Stephenson 1928). Dakin et al. (1952) and Bennett (1987) described C. veratra as papillose. This uncertainty, and the related conflicting information about whether debris adheres to the outgrowths (vide Carlgren 1950a), is not surprising. In our specimens, the projections were clearly identifiable as verrucae in life. Their ambiguous character when preserved is probably because both verrucae (figure 1A) and adhesive spots (figure 1B) — which do not project in life — are present. Debris attaches at least to the adhesive spots (figure 1B). [We agree with den Hartog (1987) that the definition of verrucae should be based on histological structure, and that adhesiveness should not be considered, if for no other than the pragmatic reason that structure can be determined in preserved specimens, whereas adhesiveness cannot always be.]

Additional ambiguity may have been created by confusion with Isactinia olivacea. Parry (1951) characterized two species under that name; Carlgren (1954: 593) believed there to be "at least three" among her specimens, one of them "undoubtedly Cnidopus verater". Ottaway (1975: 59) concluded that "Isactinia olivacea... is easily confused with Cnidopus veratra . . . and possibly also with Isanemonia australis Carlgren, 1950[a]". The specimens sent to us from New Zealand, and tentatively identified as Isactinia olivacea by P.K. Probert (Portobello Marine Laboratory, University of Otago), have adhesive verrucae, but the genus Isactinia is characterized by a smooth column (Carlgren 1949). Ottaway (1975: 56) described the column of Isactinia olivacea as "smooth, but with verrucae in longitudinal rows", while quoting Carlgren's (1949) definition of the genus. Members of Isactinia have spherules (sensu England 1987) at the margin; our New Zealand specimens lack them. Isanemonia australis (as defined by Carlgren 1950a; see also Ottaway 1975) is smooth-columned, too. The sphincter and parietobasilar muscles of our New Zealand specimens differ from those of A. veratra. Intertidal New Zealand actiniids clearly still need study, and we do not feel qualified at this time to list either of these species as partial and/or erroneous synonyms of A. veratra.

Nomenclature

Because specimens of "C. veratra" have verrucae, they fit neither within the genus Cnidopus nor Epiactis (Carlgren 1949), with which Cnidopus has been synonymized (Fautin and Chia 1986). They can, however, be assigned to the actiniid genus Aulactinia (Dunn et al. 1980: 2078):

All or most of column with more or less distinct adhesive vertucae... No marginal spherules . . . Sphincter more or less circumscribed, sometimes circumscribed-diffuse . . . All stronger mesenteries fertile, although directives sterile in some species . . . Mesenteries grow from proximal end and therefore may be more numerous proximally than distally. Cnidom: Spirocysts, basitrichs, microbasic p-mastigophores, atrichs in some.

Holotrichs (= atrichs), which were not present in all individuals we sampled, may be inducible (Fautin and Chia 1986), and therefore probably should not be considered a character defining a taxon (Fautin 1988). Our specimens also conform to England's (1987) redefinition of *Aulactinia*, which includes those species previously called *Bunodactis* that lack marginal spherules. Indeed, Carlgren (1950b: 138) noted that individuals of "*C. verater*" "recall specimens of the genus *Bunodactis*... There [sic] is, however, impossible to refer them to this genus as I have never found any atrichs there and the outgrowths of the specimens certainly are vesicles". We found both "atrichs" and verrucae in them.

Aulactinia veratra does not differ appreciably from the species described by Lager (1911) as Cribrina verruculata, except that she said the latter had "Randsäckchen" (acrorhagi). She listed smaller cnidae from the column and larger from the "Randsäckchen". The former fall within the range of our small column basitrichs and the latter of our large column basitrichs. In our experience of this animal, verrucae at or near the margin may be misinterpreted as spherules. Lager admitted that her specimens were poorly preserved and that her descriptions were, in some cases, incomplete. Of 18 species she recorded from Southwest Australia, she described 15 as new, but many have since been synonymized (see, for example, Dunn 1981). Carlgren (1949), whose student Lager was, assigned C. verruculata to Bunodactis. The type locality of C. verruculata is within 45 km of the Western Australian site where we collected specimens for this study. There are no type specimens of B. verruculata at the Western Australian Museum (where some of Lager's types are), nor in the Swedish Museum of Natural History and the Zoological Museum in Lund, Sweden. Carlgren (1954: 571) asserted "that it is not easy to identify Lager's species" because type specimens of "the species described by Lager were probably lost during the war" except for some in Stockholm (presumably he was referring only to those kept in Europe). Even so, we have no reservations in synonymizing Cribrina verruculata with Aulactinia veratra.

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