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All three species of Ptychodactiaria belong to order Actiniaria (Cnidaria: Anthozoa)

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Ptychodactiaria, currently recognized as an order equivalent to Actiniaria (sea anemones *sensu stricto*) and Scleractinia ('true' or hard corals) of cnidarian class Anthozoa, contains three monotypic genera, *Dactylanthus*, *Ptychodactis*, and *Preactis*, in two families, Ptychodactiidae and Preactiidae. Features that had been considered distinctive to the order among hexacorallian anthozoans were that gametes mature in protrusions from the mesenteries, as in octocorallian anthozoans, and that gametes do not mature embedded in mesogloea. However, we found that ptychodactiarian gametes develop in the mesenteries, surrounded by mesogloea, as in other sea anemones. We conclude that the three species constitute a clade, the most distinctive feature of which is medially fused mesenteries at the proximal end of the body. This clade merits subordinal status within order Actiniaria. We redefine Ptychodactiaria and its component taxa, moving *Dactylanthus* from family Ptychodactiidae to family Preactiidae.

INTRODUCTION

Ptychodactiaria, currently recognized as an order equivalent to the Actiniaria (sea anemones *sensu stricto*) and Scleractinia ('true' or hard corals) of cnidarian class Anthozoa, contains three monotypic genera in two families: *Dactylanthus* and *Ptychodactis* comprise family Ptychodactiidae, and *Preactis* belongs to family Preactiidae. At present, the order is defined by only one apomorphy, 'Gonads not enclosed in the mesogloea' (England in England & Robson, 1984, p. 315). Our histological data do not support this unusual position of the gonads: examination of all three species showed the gametes are surrounded by mesogloea, as in other anthozoans. Although our data support the three species constituting a clade, the clade does not merit ordinal status.

The systematic arrangement of sea anemones *sensu lato* (orders Actiniaria, Corallimorpharia, and Ptychodactiaria) currently used is that of Carlgren (1949). In his 1949 catalogue, Carlgren raised to ordinal level the actiniarian family Ptychodactiidae, then consisting only of *Ptychodactis patula* and *Dactylanthus antarcticus*. In 1984, England (in England & Robson) redefined the order Ptychodactiaria to accommodate the new genus and species *Preactis millardae*, which has characteristics intermediate between those of actiniarians and the other ptychodactiarians, leaving the arrangement of gonads as the only character distinguishing Ptychodactiaria. Attributes—and how interpretation of them has changed through time—of the three species that constitute order Ptychodactiaria are presented in Tables 1 & 2.

Carlgren (1949) defined the order with six characters. The first two (page 10) were 'definite base but without basilar muscles'. A definite base with no basilar muscles is characteristic of actiniarian suborders Protantheae and Endocoelantheae, as well as tribe Boloceroidaria of suborder Nynantheae (basilar muscles are found only in members of tribe Thenaria of suborder Nynantheae; another tribe of Nynantheae, Athenaria, is characterized by lack of both base and basilar muscles). England (in England & Robson, 1984) asserted that *Preactis* has basilar muscles, and therefore removed the absence of basilar muscles as a character of Ptychodactiaria, but we did not find basilar muscles in *P. millardae*. The definite base and lack of basilar muscles do characterize this group as well as some groups of actiniarians.

'Filaments without ciliated tracts' is the third attribute of Ptychodactiaria listed by Carlgren (1949). Members of Protantheae also lack them, and, indeed, ptychodactiarians had been placed among protanthean actiniarians by Appellöf (1893) and Carlgren (1911). However, the mesenterial filaments of *Preactis* have ciliated tracts (England & Robson, 1984; personal observation). Thus, neither the presence nor the absence of mesenterial filaments distinguishes ptychodactiarians from actiniarians.

The fourth character listed by Carlgren (1949), which he (Carlgren, 1911) had defined in his redescription of *Dactylanthus antarcticus*, is 'Distal end of the filaments of the imperfect mesenteries drawn out into two lobes giving this part of the filament the appearance of a bisected funnel'. This character, which is not found in any actiniarian, was omitted in England's redefinition of the order (England & Robson, 1984). It is insufficiently significant to define an entire order, we have found this feature to be a stage in mesentery development.

The fifth and sixth characters relate to the position and morphology of the gonads. Where we use the term 'gonad', it is for consistency with writings that we cite. However, zoantharian cnidarians lack discrete gonads (Fautin, 1999), and what is meant by 'gonad' is actually the gametogenic tissue of the mesenteries. Carlgren (1949) wrote of Ptychodactiaria 'Gonads below the filaments, not enclosed in the mesogloea but stalked,

Table 1. *Notable features of the Ptychodactiaria according to the original descriptions and a redescription.*

		Ptychodactis patula original description Appelöf, 1893	*Cystiactis antarcticus* original description Clubb, 1908	*Dactylanthus antarcticus* redescription Carlgren, 1911	*Preactis millardae* original description England in England & Robson, 1984
1.	Mouth	Always open	No comment	Wide	Greatly expanded
2.	Actinopharynx	Rudimentary	Short, strongly plicated	Not long, extensible	Well developed
3.	Siphonoglyphs	Absent	2	2	2
4.	Cycles of mesenteries	5, irregularly arrayed	2	2	2, hexamerously arrayed
5.	No. of complete mesenteries	24	24	12 or 24	24
6.	Fertility of mesenteries	No comment	All	All	All
7.	Ciliated tracts on filaments	Absent	No comment	Absent	Present
8.	Half-funnel structures distal on incomplete mesenteries	No comment	No comment	Present	No comment
9.	Fusion of mesenteries	No comment	No comment	Proximal	Proximal
10.	Mesenterial retractor muscles	Poorly developed	Weak but well marked	Weak	Weak, 2 per mesentery
11.	Gametogenic tissue	Proximal to filaments	No comment	Proximal to filaments	Same level as filaments
12.	Gonad structure	Eggs not enclosed in mesogloea, sperm capsules as in other actiniarians	[Female illustrated; no comment about egg placement]	Eggs not embedded in mesogloeal lamella but attached to it by stalks	Not embedded in mesogloea but layered on either side of it
13.	Longitudinal column muscles	Present	Weak	Weak	Absent
14.	Sphincter muscle	Absent	Diffuse, endodermal	Absent or weak	Absent
15.	Basilar muscles	No comment	No comment	Absent	Present, very weak
16.	Parietobasilar muscles	No distinct ones	Small	Faint	Absent
17.	Column morphology	Furrowed longitudinally and circumferentially	Studded with simple vesicles	Outgrowths ('Auswuchse') in 24 columns	Covered with 'tentaculate vesicles'
18.	Tentacle array, number	Marginal, 5 rows	24	24 (distalmost column outgrowths)	None on oral disc
19.	Cnidae	Rare on oral disc, same as those in tentacles	No comment	Spirocysts in outgrowths, rare in column	Spirocysts, basitrichs, atrichs

Table 2. *Characters of* Ptychodactis patula *(columns 2–4) and* Dactylanthus antarcticus *(columns 5–7) as altered by Carlgren (1911[a], 1934[b], 1940[c], 1949[d]) by Dunn (1983[e]), and by England in England & Robson 1984[f], and in Dayton et al. 1997[g].*

	Ptychodactis patula			*Dactylanthus antarcticus*		
1. Mouth	Wide[a]	–	–	–	–	–
2. Actinopharynx	Degenerate[a]	Not as reduced as Appelöf described[b]	Short[d]	–	–	–
3. Siphonoglyphs	–	–	–	2[d]	–	–
4. Cycles of mesenteries	Irregularly arranged[d]	–	–	2[d]	–	–
5. No. of complete mesenteries	Always 12, usually 24[d]	–	–	12[d]	12, 24 in larger specimens[e]	–
6. Fertility of mesenteries	–	–	–	–	–	–
7. Ciliated tracts on filaments	–	–	–	–	–	–
8. Half-funnel structures distal on incomplete mesenteries	Present[a]	–	–	Not as prominent as usually depicted[g]	–	–
9. Fusion of mesenteries	Proximal half not fused[a]	Slightly coalesced[d]	–	Present[d]	–	–
10. Mesenterial retractor muscles	Weak[a]	–	–	Weak[e]	2[f]	–
11. Gametogenic tissue	Eggs attached to mesogloeal lamella by stems[a]	–	–	Proximal to filaments on secondary mesenteries[e]	Not entirely below filaments as stated by Carlgren (1911)[f]	–
12. Gonad structure	–	–	–	–	–	–
13. Longitudinal column muscles	–	–	–	–	–	–
14. Sphincter muscle	–	–	–	Weak, diffuse[d]	Not apparent[e]	–
15. Basilar muscles	Absent[a]	–	–	Absent[e]	–	–
16. Parietobasilar muscles	Appellöf reported them[a]	Absent[d]	–	Absent[d]	–	–
17. Column morphology	Smooth[a]	–	–	Vesicle-like outgrowths[d]	–	–
18. Tentacle array, number	Numerous[d]	–	–	Short, 24[d]	Digitiform, 24[e]	–
19. Cnidae	Spirocysts rare in tentacles and column[a]	Atrichs everywhere, spirocysts in tentacles[c]	–	Atrichs everywhere, spirocysts in tentacles[c]	Atrichs everywhere, spirocysts in tentacles and column protuberances[e]	Spirocysts, atrichs, heterotrichs[f]

recalling the arrangement of the gonads in the Alcyonaria'. In *Ptychodactis*, gametogenic tissue is proximal to ('below') the filaments on all mesenteries. However, in *Dactylanthus*, only the secondary mesenteries have this arrangement; gametogenic tissue and filaments of the primary mesenteries are arrayed as they are in actiniarians. In *Preactis*, gametogenic tissue and filaments may occur at the same level of a mesentery (Figure 1), as in typical sea anemones. Carlgren's characterization of the gonads as not being enclosed in mesogloea and being stalked is both a misrepresentation of the literature and factually in error, as we show below.

MATERIALS AND METHODS

The general morphology and cnidae in museum specimens of *Ptychodactis patula* (Figure 2), *Dactylanthus antarcticus* (Figure 3), and *Preactis millardae* (Figure 4) were studied. Cnidae were measured in squash preparations at ×1000. Histological sections 8 μm thick prepared from mesenteries, column–oral disc region, and column–base region were stained with Heidenhain's azan (Presnell & Schreibman, 1997).

Two complete specimens of *Ptychodactis patula* and one wedge of an animal were examined. One complete specimen (bearing Swedish Museum of Natural History [SMNH] catalogue number 20214) and that from which the wedge was taken (a syntype: SMNH 4887) were collected in Trondheim Fjord, Norway. The other complete specimen came from the mouth of Kotzebue Sound, Alaska (US National Museum of Natural History [USNM] 55624). Four specimens of *D. antarcticus* were examined from Darwin Canal, Chile (45°26′S 74°05′W) (USNM 96507 and 96508), and one specimen of *Preactis millardae* collected in Oudekraal, Coast of Good Hope, South Africa (California Academy of Sciences [CAS] 34038).

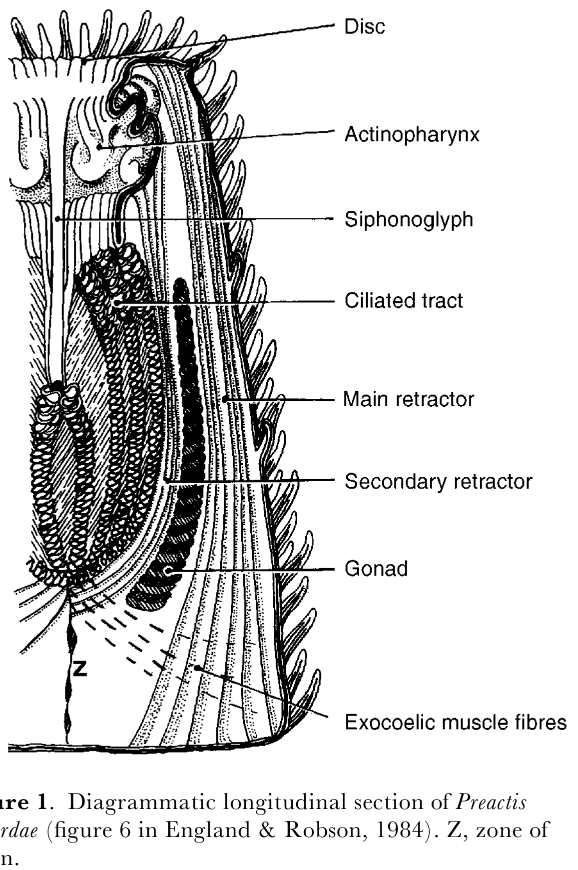


Figure 1. Diagrammatic longitudinal section of *Preactis millardae* (figure 6 in England & Robson, 1984). Z, zone of fusion.

The characters previously used to define Ptychodactiaria (Tables 1 & 2) were reassessed (Table 3) in all three ptychodactiarian species.

RESULTS

Immature females of *Ptychodactis patula* and *Dactylanthus antarcticus* have oocytes on either side of a thin lamella of mesenterial mesogloea, each oocyte surrounded by mesogloea (Figures 5A & 6, respectively). In the specimens studied, ova of *P. patula* measured 45–65 μm in diameter, and ova of *D. antarcticus* measured 25–40 μm in diameter. In a mature male *P. patula* (Figure 5B), the sperm capsules occupy the centre of the mesogloeal lamella. The sperm capsules of the specimen of *Preactis millardae* studied are enclosed in mesogloea (Figure 7). The gametes of *D. antarcticus* and *P. millardae* lie between the two bands of longitudinal retractor muscles of the mesenteries; those of *Ptychodactis patula* lie between the single retractor muscle band and the edge of the mesentery.

The gametogenic tissue of *P. patula* is proximal to the mesenterial filaments on all mesenteries, as it is on the secondary mesenteries of *D. antarcticus*. However, on the primary mesenteries of *D. antarcticus*, there is a middle region in which both filaments, which extend distally, and gametogenic tissue, which extends proximally, occur. Ciliated tracts are absent in both species. Filaments occur along the free edge of all mesenteries of *Preactis millardae*, with ciliated tracts only at the level of the actinopharynx; gametogenic tissue extends about 80% the length of the mesentery, from just proximal to the mesenterial filaments distally to just proximal to the actinopharynx. Distal to the gametogenic tissue, the two bands of retractor muscles lie side by side, thereby forming a single band, unlike in figure 6 of England & Robson (1984) (Figure 1 in this paper), which shows them remaining separate to the distal end of the animal.

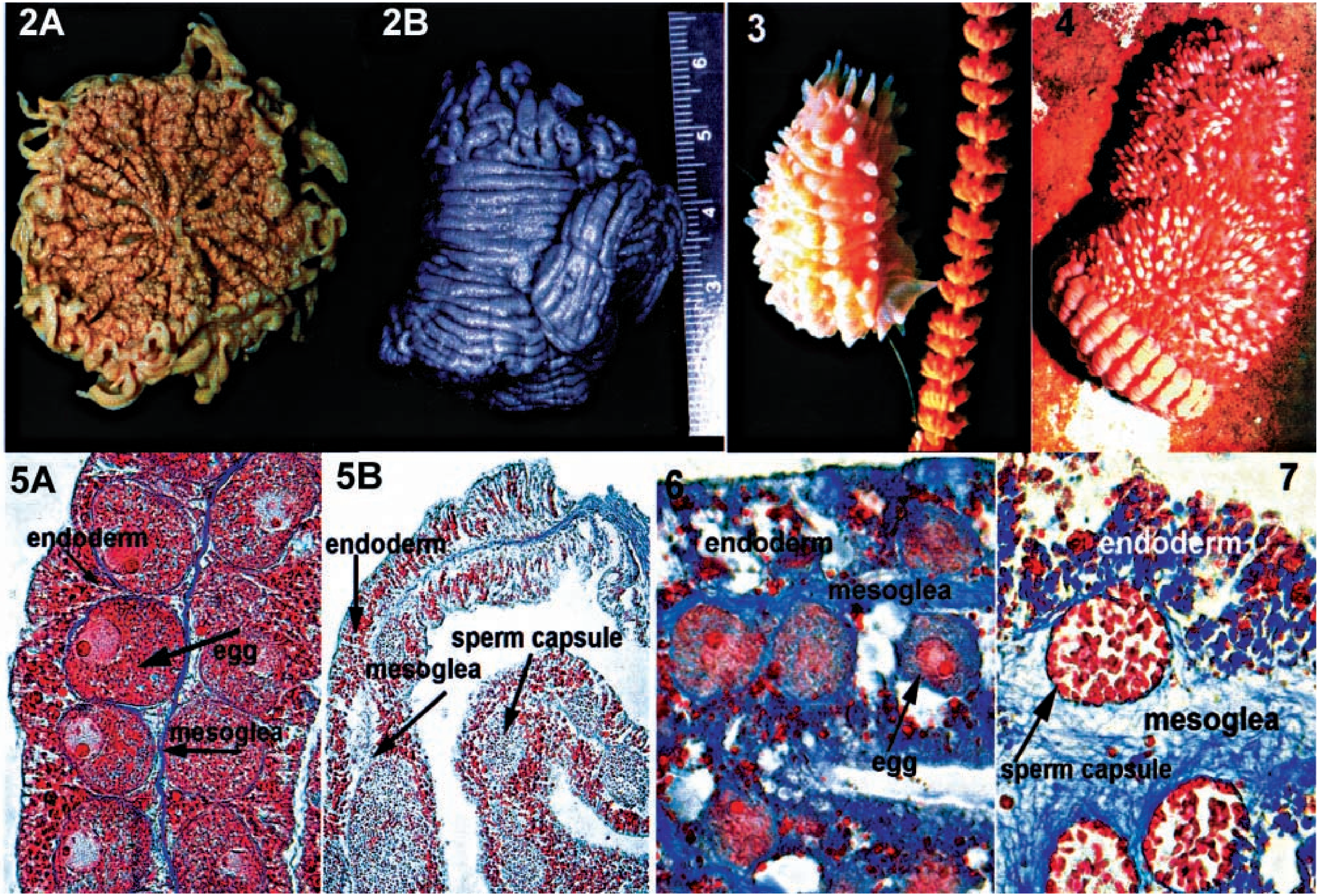
The mesenteries of *Ptychodactis patula* are regularly arrayed, contrary to what Appellöf (1893) reported. They are also regularly arrayed in the other two species. The members of each pair and couple of mesenteries are fused medially, which produces separated pockets of coelenteric space at the proximal end of the animal. In *P. patula* the mesenteries are fused only at their extreme proximal ends, whereas fusion occurs along a quarter their length in *D. antarcticus* and a third their length in *Preactis millardae*. Individuals of the latter two species are highly extensible in length, so the extent of the fusion may differ in life and in preservation.

The structures described by Carlgren (1911) were interpreted by us as bisected funnels on the incomplete mesenteries of *D. antarcticus* to be the distalmost portion of the mesenteries—that part attached to the underside of the oral disc. Such structures are also present in *Ptychodactis patula* but are absent in *Preactis millardae*, in which all the mesenteries are complete in the specimen examined.

Table 3. *Features of the Ptychodactiaria from re-examination of all three species.*

	Ptychodactis patula	*Dactylanthus antarcticus*	*Preactis millardae*
1. Mouth	Capable of opening wide	Capable of opening wide	Capable of opening wide
2. Actinopharynx	Very short, strongly folded	Short, strongly folded	Short, strongly folded
3. Siphonoglyphs	Absent	2	2
4. Cycles of mesenteries	4 (*or 5), regularly arrayed	2, regularly arrayed	2, regularly arrayed
5. No. of complete mesenteries	24	12 or 24	24
6. Fertility of mesenteries	All	All	All
7. Ciliated tracts on filaments	Absent	Absent	Present
8. Half-funnel structures distal on incomplete mesenteries	Developmental stage	Developmental stage	Developmental stage
9. Fusion of mesenteries	Proximal end	Proximal quarter of body	Proximal third of body
10. Mesenterial retractor muscles	Single, weak	Double, weak	Double, weak
11. Gametogenic tissue	Proximal to filaments	1°, some at same level as filaments; 2°, proximal to filaments	Same level as filaments
12. Gonad structure	Enclosed in mesogloea	Enclosed in mesogloea	Enclosed in mesogloea
13. Longitudinal column muscles	Absent	Absent	Absent
14. Sphincter muscle	Absent	Diffuse endodermal or absent	Absent
15. Basilar muscles	Absent	Absent	Absent
16. Parietobasilar muscles	Absent	Absent	Absent
17. Column morphology	Furrowed longitudinally and circumferentially	24 columns of tentaculate vesicles	Covered with tentaculate vesicles
18. Tentacle array, number	Marginal, ~100	24 (distalmost tentaculate vesicles)	Distalmost tentaculate vesicles†
19. Cnidae	Spirocysts, atrichs	Spirocysts, atrichs	Spirocysts, basitrichs, atrichs

*, indicates a feature that has been reported but that did not occur in the specimens we examined; †, indicates an inference.



Figures 2–7. (**2**) Preserved specimens of *Ptychodactis patula*: (A) expanded (SMNH 20214) (diameter about 40 mm); (B) contracted (USNM 55624). (**3**) Live specimen of *Dactylanthus antarcticus* photographed by L. Peck, British Antarctic Survey. Specimens we studied were as long as 50 mm. (**4**) Live specimen of *Preactis millardae* (CAS 34038). In preservation, the animal is 100 mm long. Photograph by T.M. Gosliner. (**5–7**) Gametogenic region of mesenteries showing that mesoglea (stained blue) surrounds developing gametes, both male and female. (**5**) *Ptychodactis patula*: (A) female (SMNH 20214) (diameter of the indicated egg is about 55 μm); (B) male (USNM 55624) (width of the indicated sperm capsule is about 40 μm). (**6**) Female *Dactylanthus antarcticus* (USNM 96057) (diameter of the indicated egg is about 25 μm). (**7**) Male *Preactis millardae* (CAS 34038) (diameter of the indicated sperm capsule is about 40 μm).

Table 4. *Cnidae of the three species of Ptychodactiaria. Number following species name is number of specimens in which capsules were measured. Capsule measurements are range of length×width in μm; number of capsules measured follows in parentheses. Measurements for the oral disc of* Ptychodactis patula *are absent because one specimen was gaping so wide its oral disc was obliterated, and no cnidae were found in the other; measurements for the column of* Preactis millardae *are absent because it is so densely covered with tentaculate vesicles that contamination was unavoidable. Atrichs of all species varied in appearance; figure 10 A.c., B.b., and B.e in England & Robson (1984) illustrate some variants.*

	Ptychodactis patula (N=2)	*Dactylanthus antarcticus* (N=4)	*Preactis millardae* (N=1)
Tentacles			
Spirocysts	11.6–18.9×2.5–3.2 (21)	15.3–26.6×2.3–3.3 (54)	16.2–21.8×2.9–4.0 (13)
Basitrichs	–	–	13.3–22.7×2.8–3.5 (17)
Atrichs	13.7–24.9×3.0–4.9 (30)	18.4–31.0×2.7–5.0 (78)	17.0–33.1×3.0–4.0 (19)
Tentaculate Vesicles	None in this species		
Spirocysts	–	14.9–25.0×2.0–3.4 (45)	16.3–21.5×2.9–3.4 (10)
Basitrichs	–	–	15.8–18.7×2.3–3.3 (11)
Atrichs	–	16.3–33.5×2.7–4.3 (69)	19.4–30.5×2.8–4.2 (21)
Oral Disc			
Spirocysts	–	–	15.7×3.0 (1)
Atrichs	–	13.7–24.6×2.0–4.4 (63)	15.3–19.0×2.1–3.1 (18)
Actinopharynx			
Basitrichs	–	–	17.9×2.3 (1)
Atrichs	11.7–19.1×2.0–4.1 (15)	14.8–27.5×2.7–4.7 (70)	14.8–25.9×2.6–4.3 (20)
Mesenterial Filaments			
Atrichs	15.1–25.0×2.3–4.1 (14)	12.5–24.4×2.5–4.3 (one was 4.9 μm wide) (64)	14.1–25.7×2.0–3.3 (19)
Column		Measured in 3 specimens	
Atrichs	14.9–20.6×2.5–4.6 (21)	16.3–23.7×2.7–4.4 (29)	–

The actinopharynx of all species is proportionally shorter than is typical of sea anemones, and is highly plicate. The siphonoglyphs of *D. antarcticus* and *P. millardae* are prolonged aborally, as has been reported (e.g. Clubb, 1908; England & Robson, 1984, respectively). The fine transverse ridges on the siphonoglyph of *D. antarcticus* were first noted by Carlgren (1911). As has been reported (for example by Appellöf, 1893), *Ptychodactis patula* lacks siphonoglyphs. It has a unique crinkled sheet of tissue where some (but not all, in our experience) of the complete mesenteries attach to the aboral end of the siphonoglyph. This structure was described by Appellöf (1893, p. 5) as resembling 'eines Grunkohlblattes'—a leaf of kale. To us, each resembles a fully extended folding fan.

We could not find ectodermal longitudinal muscles in the column of any of the three species, despite reports of it in *P. patula* (according to Appellöf, 1893) and *D. antarcticus* (according to Clubb, 1908; Carlgren, 1911). Such musculature is clear in sections examined from *Gonactinia prolifera*, a protanthean actiniarian, and *Corallimorphus* sp., a corallimorpharian. Examining both whole animals and histological sections, we were unable to find basilar muscles in any species including *Preactis millardae*, the only ptychodactiarian species in which they had been reported (England & Robson, 1984). Nor did we find parietobasilar muscles, which have been reported for *Ptychodactis; patula* (by Appellöf, 1893) and *D. antarcticus* (by Clubb, 1908; Carlgren, 1911).

Size and distribution of cnidae are given in Table 4. Cnidae resemble those illustrated in figure IV of Carlgren (1940) and figure 10 of England & Robson (1984), except that every basitrich of *Preactis millardae* we found had a visible tubule so it resembled that illustrated by England & Robson as B.c. (termed a heterotrich) rather than that illustrated as A.b. (termed a basitrich).

DISCUSSION

Gametogenic tissue

The single apomorphy ostensibly distinguishing Ptychodactiaria from other anthozoans of subclass Hexacorallia, and uniting its three genera, is the structure of the gametogenic tissue (England & Robson, 1984). In other anthozoans, gametes arise in the endoderm but move into the mesogloea, which surrounds them as they mature (Hyman, 1940; Fautin, 1999). Gametes in members of order Ptychodactiaria are supposedly not surrounded by mesogloea, presumably maturing in the endodermal tissue from which they arise. We found ptychodactiarians not to differ from other anthozoans in this regard; their maturing gametes are enclosed in the mesogloea of the mesenteries. This misconstruction of the nature of the gametogenic tissue of these species seems due to the thinness of the mesenterial mesogloea, perhaps the maturity of the specimens studied, but mainly misinterpretation and overgeneralization of the literature.

In describing the first ptychodactiarian known to science, *Ptychodactis patula*, Appellöf (1893, p. 14) distinguished the gametogenic tissue in a passage translated from German as follows: 'In the latter [other actiniarians]—as far as we know—the eggs displace the mesogloea so that they are entirely embedded in it. Only the youngest eggs are an exception to this, in that they are accompanied [or attached] by a short and wide stalk [or stem] of mesogleal lamella. In *Ptychodactis* by contrast, the very thin [mesogleal] lamella (ms) [reference to a figure] continues unbroken through the entire ovary and the eggs (o) [reference to a figure] are arrayed on both sides of it, all connected by longer or shorter stalks to the lamella. The stalks are branches of the mesoglea and form a fibrous capsule around the egg'.

Appellöf (1893) noted the capsule is so thin in some places that it is indistinguishable from the egg membrane. He differentiated between what he considered unusual female gonads and normal, actiniarian-like male gonads, which are completely enclosed in mesogloea and lack stems. He illustrated (plate II, figure 5) an enlarged view of a developing oocyte with a 'stiel'—a stalk or stem. The direction the stalk extends is unclear in the enlarged view; in a low-power view (plate II, figure 1), connections of eggs to both mesogloea and mesentery edge are apparent. If it extended between egg and mesogloeal layer of the mesentery, the stalk is a strand of mesogloea that surrounds the egg, so the egg is clearly enclosed in mesogloea. If it extended between egg and edge of the mesentery, the stalk resembles a trophonema (Nyholm, 1943; Dunn, 1975), a tube through which nutritive material passes from the gastrovascular cavity to the developing egg in some anthozoans (Larkman & Carter, 1982; Fautin, 1999).

Dactylanthus antarcticus was described in actiniarian family Aliciidae as *Cystiactis antarctica* by Clubb (1908), who illustrated ova on both sides of a thin lamella of mesogloea but did not comment on the structure of the gametogenic tissue. In redescribing the species and transferring it to the new genus *Dactylanthus*, Carlgren (1911) compared the gonads to those of *P. patula*. He concluded that in both species, the gonads are proximal to the filaments and the eggs are not embedded in the main part of the mesogloea but are attached with mesogloeal stalks to the mesogloeal lamella. Carlgren (1949, p. 10), in creating order Ptychodactiaria, asserted the gonads are 'not enclosed in the mesogloea but stalked, recalling the arrangement of the gonads in the Alcyonaria', and did not distinguish between the sexes. In redefining the order, England (in England & Robson, 1984, p. 315) asserted only 'Gonads not enclosed in the mesogloea'. Carlgren may have meant that the gametes do not lie in the centre of the mesentery, in the mesogloeal lamella, but the implication is that they are not surrounded by mesogloea. England (in England & Robson, 1984, p. 325) clearly considered there to be no mesogloea around the gametes, stating, in regard to the taxonomic position of ptychodactiarians, 'As the gonads are not enclosed in the mesogloea of the mesenteries, the Actiniaria are precluded'.

Thus, as ptychodactiarians were described and redescribed, accounts of the gametogenic tissue (Tables 1 & 2, character 12) became less precise. Although he recognized that each oocyte is surrounded by mesogloea, Appellöf (1893) considered that different from the situation in actiniarians with which he was presumably familiar—an actiniarian oocyte is clearly embedded in mesogloea if the mesogloeal lamella is thick, but in sea anemones without a thick mesogloeal lamella, developing gametes lie lateral to the lamella, with mesogloea stretched around them (see e.g. Wedi & Dunn, 1983). Moreover, gametes of the female ptychodactiarians we examined appeared to be immature, and it is possible that they move into the centre of the mesentery as they mature, as is true of other sea anemones and of the mature male specimens of *P. patula* we examined (Figure 5B).

Carlgren (1949) seems to have interpreted Appellöf as meaning the gametes lie outside the mesentery, attached to it by a stalk, as is true in members of anthozoan subclass Alcyonaria (see figure 177A in Hyman, 1940; figure 1A in Benayahu, 1991). Thus, Carlgren's (1949) defining character of order Ptychodactiaria appears to have been a misinterpretation of Appellöf (1893), the word 'stiel' being considered to refer to a pedicle, as in the Alcyonaria, rather than perhaps to a trophonema, as in some sea anemones. Moreover, the distinction Appellöf had made between the sexes was lost. Finally, gametes were regarded not as maturing in the mesogloea, where, even in the Alcyonaria, their development occurs. Stalked gonads, differences between the sexes in mode of gamete maturation, and development outside the mesogloea would be unique among hexacorallian anthozoans.

Musculature

Among the features Appellöf (1893) considered demonstrated *Ptychodactis* is related to the protanthean actiniarians were ectodermal nervous system and longitudinal musculature of the column. England (in England & Robson, 1984) placed *Preactis* in its own family, Preactiidae, based partly on the presence of basilar muscles and the lack of ectodermal longitudinal muscles. Perhaps the intersection of the ectoderm with the rather fibrous mesogloea of these animals was misinterpreted as longitudinal musculature. The column of all specimens of *Ptychodactis patula* we examined had circumferential wrinkles: we infer the bunched tissue gave the impression of longitudinal muscles, because this is where Appellöf (1893) stated the musculature was particularly prominent. The longitudinal ectodermal musculature of the tentaculate vesicles (tentacle-like protrusions from the column) of *Preactis millardae* 'continues for . . . a short distance on to the column' (England & Robson, 1984, p. 317); such muscles could have been misinterpreted in *D. antarcticus* as being associated with the column.

Our finding that basilar muscles are absent confirms Carlgren's (1949, page 10) statement that ptychodactiarians have a 'definite base but without basilar muscles,' but that is not unusual among hexacorallians. Perhaps the ridges we observed along the base of some mesenteries were misconstrued as basilar muscles. There was no evidence of musculature in these ridges, which might be the result of bunching of tissue in contraction.

Reports of parietobasilar muscles in *Ptychodactis patula* and *D. antarcticus* were equivocal. Appellöf (1893) stated they occur in the former species but Carlgren (1949) reported them absent. In the latter species, Clubb (1908) described them as small and Carlgren (1911) as faint. We did not find them.

Mesenteries

Among the features of the mesenteries Appellöf (1893) considered allied *Ptychodactis* with protanthean actiniarians were the lack of ciliated tracts and stomata. Carlgren's (1949, p. 10) feature 'filaments without ciliated tracts' applies to the species he was including in order

Ptychodactiaria (*P. patula* and *D. antarcticus*), but not to *Preactis millardae*. Oral stomata are present in *P. millardae*; if stomata are taxonomically important in sea anemones, it is at the species level.

A feature by which Carlgren (1949, p. 10) defined Ptychodactiaria is 'distal end of the filaments of the imperfect mesenteries drawn out into two lobes giving this part of the filament the appearance of a bisected funnel'. He (Carlgren, 1911) analogized these structures with the ciliated tract in the mesenterial filaments of other actiniarians. We interpret this structure, which we observed in *Ptychodactis patula* and *D. antarcticus* (specimens of *Preactis millardae* we examined lack incomplete mesenteries), as a stage in mesentery development. England's description of mesentery development in *P. millardae* (see England & Robson, 1984) is consistent with this interpretation.

The proximal fusion of mesenteries, which is the most distinctive feature of these animals, may be associated with behaviour. *Preactis millardae* and *D. antarcticus* are elongate, flexible animals that undergo peristalsis, crawl along the substratum with the column, and prey on octocoral colonies (England & Robson, 1984; Dayton et al., 1997, respectively). Their form and behaviour caused Dayton (Dayton et al., 1997) and L. Peck (British Antarctic Survey; personal communication to D.G.F.) initially to mistake individuals of *D. antarcticus* for holothurians. We agree with England & Robson (1984) and Dayton et al. (1997) that the distinctively short and extensible actinopharynx allows the animals to engulf octocoral prey, which may be large relative to the anemone; the large amount of tissue necessary for such flexibility forms pockets and folds in contraction. Although *Ptychodactis patula* is not elongate, the first specimens of it reported were associated with octocorals (Appellöf, 1893). Appellöf (1893) remarked that *P. patula* gaped so much even when alive that the mesenterial filaments were exposed, and, in extreme cases, the body assumed the form of a disc, exposing the entire gastrovascular cavity (Figure 2A). However, the mouth of some specimens we studied (Figure 2B) was closed and the gastrovascular cavity was not exposed, just as in other actiniarians.

The South African actiniarian *Korsaranthus natalensis* (Carlgren, 1938) also crawls along the substratum and preys on octocorals, and has an unusually short, deeply folded actinopharynx and a simple cnidome (Riemann-Zürneck & Griffiths, 1999). Thus these morphological features appear to be related to behaviour, as Riemann-Zürneck & Griffiths (1999) speculated, rather than to phylogeny—*K. natalensis* is a member of the largest sea anemone family, Actiniidae.

Tentacles

The protrusions on the column of members of family Preactiidae have been termed outgrowths ('Auswuchse' in *D. antarcticus* by Carlgren, 1911) and 'tentaculate vesicles' (in *Preactis millardae* by England & Robson, 1984). Their histological structure and complement of cnidae are identical to those of tentacles, but since tentacles are defined as arising from the oral disc (e.g. Stephenson, 1928), we adopt the term tentaculate vesicles for them.

Cnidae

Sizes of cnidae we found in *Ptychodactis patula* agree with data given by Carlgren (1921, 1940). Our data on *D. antarcticus* are identical to those of Carlgren (1940) and agree very closely with those reported by Dunn (1983) and England & Robson (1984), although England & Robson also reported heterotrichs and possibly holotrichs. The holotrichs might have been developing atrichs (England & Robson, 1984). Based on the variability we observed in the appearance of atrichs in all three species (Table 4), we infer the 'heterotrichs' were also atrichs. It is likely there is more than one type of atrich, but we could not sort them easily: the tubule of some was neatly wound in contrast to that of others, and a few capsules had a tubule that was neat only at one end; and the width of some short capsules was greater than that of some long capsules. Data on *Preactis millardae* agree with published figures except for minor differences; for example, we found some atrichs in the filaments smaller than any reported by England & Robson (1984), and they did not find spirocysts on the oral disc (we found one).

We found in *Ptychodactis patula*, as noted by Carlgren (1921, p. 11), 'Spirocysts in the column and in the oral disc extremely rare, also in the tentacles not common. Nematocysts not especially numerous . . .' Indeed, nematocysts in specimen USNM 55624 were nearly absent.

Distribution

Ptychodactis patula is arctic–boreal (Carlgren, 1939) and possibly panarctic (Dayton et al., 1997). It has been reported from latitudes of 63–70°N: in Norway, it has been collected at depths of 188–350 m (Appellöf, 1893; Carlgren, 1939); north of Iceland it was collected at 80 m (Carlgren, 1921); and it has been collected in Kotzebue Sound, Alaska, at unspecified depth (Carlgren, 1934).

Dactylanthus antarcticus has a south circumpolar distribution. Dredged specimens have been reported from around Antarctica at latitudes of 64–78°S and depths of 37–610 m, and from the southern tip of South America (54°22–23′S 64°42–52′W) at 106–110 m (Dunn, 1983). Live specimens were observed by SCUBA divers in the Chilean fjords of Canal Darwin (45°23.5′S 74°0.80′) and Estrecho Collingwood (51°52′S 73°43.6′W) at 25–40 m (Dayton et al., 1997).

Preactis millardae is known only from the Western Cape of South Africa (34–37°S): divers have found it at 10–20 m at Oudekraal on the Cape Peninsula and at Roman Rock in False Bay; stranded specimens have been collected from Maclear's Beach near Cape Point and near Cape Point and near Hermanus (England & Robson, 1984).

Systematics

The three species *Ptychodactis patula*, *Dactylanthus antarcticus*, and *Preactis millardae* do not constitute an order; their common characters do not differentiate them from actiniarians. The three species do, however, form a clade supported by proximally fused mesenteries, all mesenteries being gametogenic, lack of basilar and parietobasilar muscles, and weak retractor muscles. Only the first of these four characters is unique to this clade.

Based on 18S rDNA sequences and neighbour-joining analyses, Berntson et al. (1999) found that *D. antarcticus*, the only ptychodactiarian they considered, lies within Actiniaria. We found the same thing in a parsimony analysis of sequence data from 28S rDNA obtained in our laboratory by T.R. White. The nearest relative of *D. antarcticus* in the analysis by Berntson et al. (1999) was *Haloclava* sp., an athenarian anemone (suborder Nynantheae). In our analysis, the nearest relatives of *D. antarcticus* were some species of family Actiniidae (suborder Nynantheae); our analysis did not include any athenarian species, but did include members of six thenarian families and some species of order Scleractinia.

In referring to Carlgren's (1911) family-level taxon, Stephenson (1921, p. 508), stated 'the Ptychodactidae must be kept apart from the ordinary Actinians . . . in a group of their own and of higher rank than a family'. We consider this assessment still accurate, and therefore restore Stephenson's (1921) taxon Ptychodacteae, which he considered one of three tribes of Actiniaria, the others being Protantheae and Nynantheae. Those taxa are now considered to be suborders, and a third has been recognized, the Endocoelantheae (Carlgren, 1949). We consider Ptychodacteae a fourth suborder of Actiniaria.

We recognize both described families, Ptychodactiidae and Preactiidae, but move *Dactylanthus* from the former to the latter. We redefine all taxa of this clade below.

Suborder Ptychodacteae Stephenson, 1921
Diagnosis. Actiniaria with a definite base, lacking basilar and parietobasilar muscles. Mesenteries of each pair and couple fused medially at animal's proximal end. One or two weak retractor muscles per mesentery. All or almost all mesenteries fertile. Filaments with or without ciliated tracts. Actinopharynx short, highly folded. Sphincter muscle weak or absent. Cnidome: spirocysts, atrichs, and basitrichs.

Family Ptychodactiidae Appellöf, 1893
Diagnosis. Column short, smooth (or wrinkled in contracted specimens) without outgrowths. Tentacles simple, numerous, not retractile. Gametes develop proximal to filaments on all mesenteries. As many as five cycles of mesenteries; those of first and second cycles complete. One weak retractor muscle per mesentery. Sphincter muscle absent. Actinopharynx little differentiated from the oral disc; siphonoglyphs absent. Cnidome: spirocysts and atrichs.

Genus Ptychodactis *Appellöf, 1893*
As for family; with about 100–122 tentacles that are longitudinally ridged, at least in preserved specimens.

Family Preactiidae England (in England & Robson), 1984
Diagnosis. Column elongate with vesicular outgrowths (tentaculate vesicles) that are histologically identical to tentacles. Tentacles absent on oral disc or only at margin. Gametes and filaments at same level on at least primary mesenteries; on higher-order mesenteries, gametes may be proximal to filaments. Twelve pairs (two cycles) of mesenteries, one or both cycles complete. Two weak retractor muscles per mesentery. Sphincter muscle weak or absent. Actinopharynx well developed with two distinct siphonoglyphs that are prolonged aborally. Cnidome: spirocysts, atrichs, and basitrichs.

Genus Dactylanthus *Carlgren, 1911*
Column with 24 longitudinal rows of tentaculate vesicles; 24 marginal tentacles on oral disc. Sphincter muscle very weak, diffuse. All mesenteries or only primary ones complete. Cnidome: spirocysts and atrichs.

Genus Preactis *England (in England & Robson), 1984*
Column covered with tentaculate vesicles that are not clearly arrayed in rows or columns; no tentacles on oral disc. Sphincter muscle absent. All mesenteries complete. Cnidome: spirocysts, atrichs, and basitrichs.

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