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# The first sea anemone (Cnidaria: Anthozoa: Actiniaria) from a whale fall

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## Abstract

*Anthosactis pearseae* n. sp. is the first species of sea anemone described from a deep-sea whale fall. It is a member of one of the most diverse genera of Actinostolidae, a family that dominates in the deep, and can be distinguished from its congeners based on the arrangement of tentacles, column musculature, cnidom, and aspects of its life history. To date, *A. pearseae* is known only from a single whale fall in the deep Pacific, being absent from several seep, vent, and deep-water hard substrates near this site.

**Keywords:** Deep-sea diversity, Pacific Ocean, asexual reproduction, Cnidaria, Actiniaria, new species

## Introduction

Coral reefs are the most familiar marine communities that are ecologically anchored and structurally engineered by a particular member of the habitat. An analogous phenomenon is seen in at least two kinds of deep-sea communities. Hydrothermal vent assemblages are typically anchored by vestimentiferan tube worms, with vescomyid or bathymodioloid bivalves less frequently anchoring the community. Vestimentiferans, vescomyids, and bathymodioloids all harbour the chemosynthetic bacteria upon which their communities depend, and create the structural complexity that contributes to high biodiversity (Govenar et al. 2005). The least well studied of these kinds of communities are those that depend on dead rather than living biological anchors—the communities associated with deep-sea whale falls.

The decaying carcasses of large whales provide fodder for at least three communities at different stages in their succession (Smith & Baco 2003), and have the highest species richness of any hard-substrate deep-sea habitat (Baco & Smith 2003). The distinct communities associated with whale falls include relatively short-lived scavenger dominated fauna, and two longer-lived communities: a benthic and infaunal community based on the organic material rich sediment under and around the carcass, and a chemosynthesis-based community deriving energy from sulphur liberated during decomposition of skeletal

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elements (Smith & Baco 2003). Perhaps because the long-lived communities have multiple sources of energy (i.e. carbon from the carcass and from chemosynthesis), species diversity at whale falls is among the highest in the deep sea, exceeding that of a typical hydrothermal vent (Baco & Smith 2003).

Estimates of high species richness of whale fall communities are based largely on the diversity of species living on and around bones (Baco & Smith 2003). This segment of the whale fall fauna includes some of its most spectacular members, such as the polychaete worm *Osedax*, which digests bone and marrow with the assistance of symbiotic bacteria (Rouse et al. 2004). The high diversity of whale fall communities is based on morphological diversity of the species comprising the communities rather than species counts because many of the morphotypes cannot be assigned to existing species or because expert identifications are not readily available (Dahlgren et al. 2004). Here we describe *Anthosactis pearseae*, the first species of sea anemone (Cnidaria: Anthozoa: Actiniaria) described from a whale fall and a possible whale fall endemic. The population upon which this description is based was collected from the skeleton of a whale in Monterey Canyon at about 3000 m. We have examined collections of macroinvertebrates from other hard-substrate communities in the deep East Pacific and have found no specimens that we can identify as *A. pearseae*. However, as sampling of deep-sea habitats is patchy at best and typically focuses on the more ecologically dominant members of the community, it is possible that *A. pearseae* occurs in other habitats.

## Materials and methods

Specimens were collected during a cruise of the Monterey Bay Aquarium Research Institute (MBARI) research vessel *Western Flyer* using the Remotely Operated Vehicle *Tiburon*. All specimens came from one whale skeleton in Monterey Canyon, at 36°36.8031'N, 122°26.1203'W, depth 2893 m. Specimens were collected during dive T-769 on 30 November 2004; they were either suctioned directly from the skeleton or removed by hand from bones brought to the surface. Specimens removed by hand were placed in chilled water and allowed to relax before being anaesthetized with menthol crystals. These specimens were then fixed in 4% seawater formalin and later transferred to 70% ethanol for long-term storage. Specimens suctioned from the bones were fixed immediately in 95% ethanol. Specimens have been deposited at MBARI, the California Academy of Science (CAS), and the US National Museum of Natural History (NMNH).

Preserved specimens were examined whole, in dissection, and as serial sections; serial sections were prepared using standard paraffin techniques. Histological slides were stained in Masson's trichrome (Presnell & Schreibman 1997). Pieces of tissue from tentacles, column, mesenterial filaments and actinopharynx were smeared on a slide; nematocysts in these smears were examined using DIC at 100X magnification. Cnida terminology follows Mariscal (1974).

## Results

Order Actiniaria  
Family Actinostolidae Carlgren. 1932  
Genus *Anthosactis* Danielssen, 1890

### Definition

Actinostolidae with well-developed pedal disc. Column smooth, rather low, often longitudinally sulcated in the contracted state. Sphincter strong, mesogloal. Tentacles

short, rather few, conical, robust, hexamerously or octamerously arranged. Outer tentacles on their aboral sides at the base provided with a stinging battery of nematocysts, sometimes distributed along the whole aboral side of the tentacles, though more numerous at the base. Longitudinal muscles of tentacles ectodermal, strongest on the oral side. Radial muscles of oral disc ectodermal to ectomesogloal. Actinopharynx short with two well-developed siphonoglyphs. Pairs of perfect mesenteries 6, 6+2 single, 8, or 12; two pairs of directives. Retractors rather weak, parietobasilar muscles fairly well developed. At least the younger mesenteries growing from the basal disc upwards. All stronger mesenteries fertile. Cnidom: spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores (modified from White et al. (1999); see discussion below).

***Anthosactis pearseae* n. sp.**

Figures 1–3

*Diagnosis*

Column of preserved specimens a stout cylinder, 5–8 mm in diameter, rosy pink to white, with short, bluntly conical tentacles without aboral thickenings (Figure 1 and 2). Tentacles with numerous basitrichs and holotrichs, not concentrated into discrete batteries. Mesenteries hexamerously arranged, first cycle perfect.

*Etymology*

Named for Vicki Pearse, in honour of her contributions to actiniarian systematics.



Figure 1. External anatomy and habitus of living *Anthosactis pearseae*. Note galatheid crabs, and plumes of *Osedax* protruding from bone. Photo reproduced with permission. Copyright MBARI, 2006.

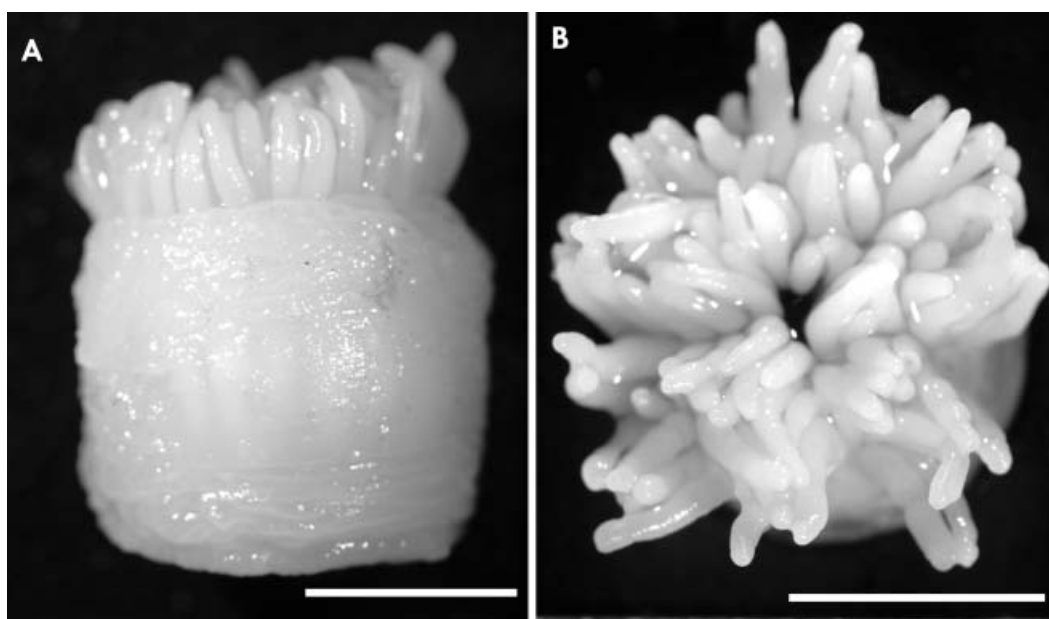


Figure 2. External anatomy of *Anthosactis pearseae*. A. Side view of holotype (NMNH 1096705). B. Three-quarter view of paratype (CASIZ 174323). Scale bar=5.0 mm.

#### *Material examined*

Holotype, NMNH 1096705; Paratypes CASIZ 174323–174325, and NMNH 1096706; vouchers CASIZ 174326.

**Base and column.** Column stout, of approximately equal diameter throughout in preserved specimens (Figure 2) or slightly flaring proximally, weakly ribbed longitudinally in highly contracted specimens. In life, column flares from base, being wider distally than proximally (Figure 1, V. Pearse, pers. comm.). Most specimens uniform opalescent white, a few pale pink. In all specimens, mesenteries faintly visible through column as pinkish lines. No fosse, although distal lip of column may extend beyond base of tentacles in contracted specimens (Figure 2A). Distal column of some specimens sparsely scattered with small, poorly demarcated suckers; no specimens had material adhering to these. Proximal column smooth. Limbus may extend past pedal disc, causing pedal disc to look sunken or retracted. Pedal disc adherent, muscular, same colour as column, approximately equal or slightly larger in diameter than oral disc in preserved specimens. Oral disc larger than pedal disc in well-expanded living specimens. Ectoderm of column contains small clusters of goblet-shaped basophilic (blue-staining) material without discernible nuclei or other cellular structures surrounded by deeply staining epitheliomuscular cells (Figure 3A). Column musculature strong, ectodermal and mesogloal (Figure 3E), concentrated into a mesogloal marginal sphincter distally (Figure 3C).

**Oral disc and tentacles.** Tentacles partially covered by distal column in contraction; oral disc not visible (Figure 2B). Tentacles and oral disc same colour as column. Mouth central, with two prominent siphonoglyphs; lips and siphonoglyphs slightly paler than oral disc in pink specimens, more opaque than disc in white specimens. Tentacles bluntly pointed,

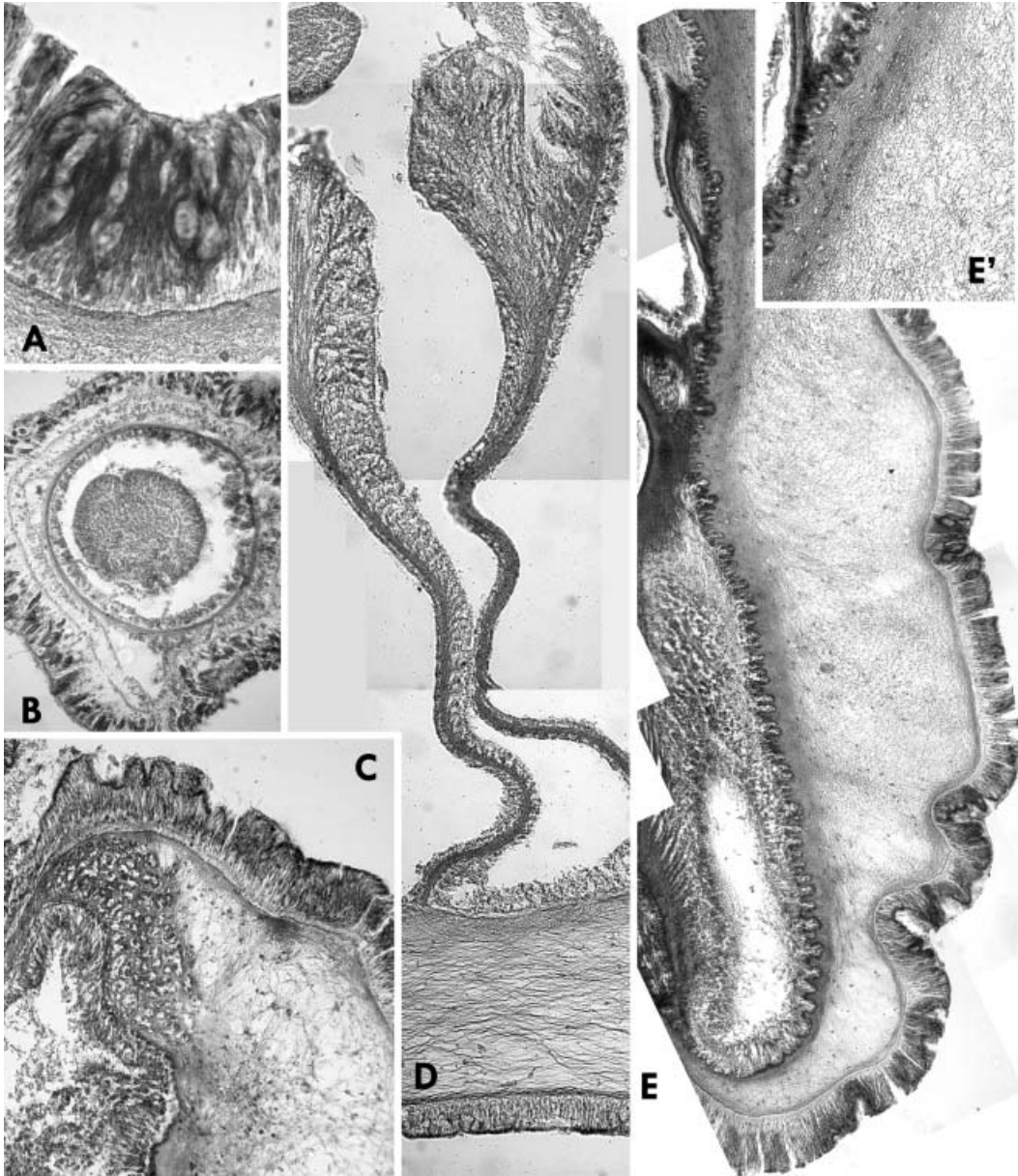


Figure 3. Internal anatomy of *Anthosactis pearseae*. A. Column ectoderm. Note hyaline, goblet-shaped structures surrounded by dense and glandular epitheliomuscular cells. B. Cross-section through a tentacle containing a brooded larva. Specimen from which this section was made is male. C. Longitudinal section through the column, showing mesogloal marginal sphincter. D. Cross-section through column of a contracted specimen, showing one pair of directive mesenteries. Note the absence of any distinct parietal or parietobasilar muscles and the relatively narrow retractory muscle. E. Longitudinal section through the column showing endodermal longitudinal muscle and mesogloal columnar muscle. The lacunae of the mesogloal muscles are visible in the inset (E'), taken at higher magnification.

longitudinally fluted in preservation, length approximately equal to diameter of oral disc, about 100 in four crowded cycles on outer half of oral disc, those of outermost cycle longest. In life, tentacle length approximately equal to column height (Figure 1). Tentacle musculature ectodermal. Because tentacles are partially retracted inside column, relative thickness of oral and aboral ectoderm at base could not be assessed.

*Mesenteries and internal anatomy.* Mesenteries arranged hexamerously in three to four cycles, only those of first cycle perfect; two pairs of directives, each attached to siphonoglyph. All mesenteries of first and second cycles including directives bear filaments and gonads; those of fourth cycle weak, lacking filaments and reproductive tissue. All specimens collected in late November sexually mature, with either female or male gametes in any single specimen, some brooding larvae (Figure 3B). Mode of larval production unclear: some specimens with male gametes bear young.

Longitudinal muscles of mesenteries weak (Figure 3D). Parietal muscle not distinct from mesenterial lamella, consisting of few short processes with no pennon. Retractor muscle circumscribed but not very broad, comprised of few, unramified branches towards the coelenteron and a few larger, more ramified branches closer to the body wall (Figure 3D).

*Cnidom.* Spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores (Figure 4). See Table I for size and distribution.

*Habitat and biology.* We see no evidence that *A. pearseae* harbours chemosynthetic bacteria, assuming instead that it feeds upon larvae, dissolved and particulate organic matter, and plankton. Although not collected until 2004, *Anthosactis pearseae* has been present at the

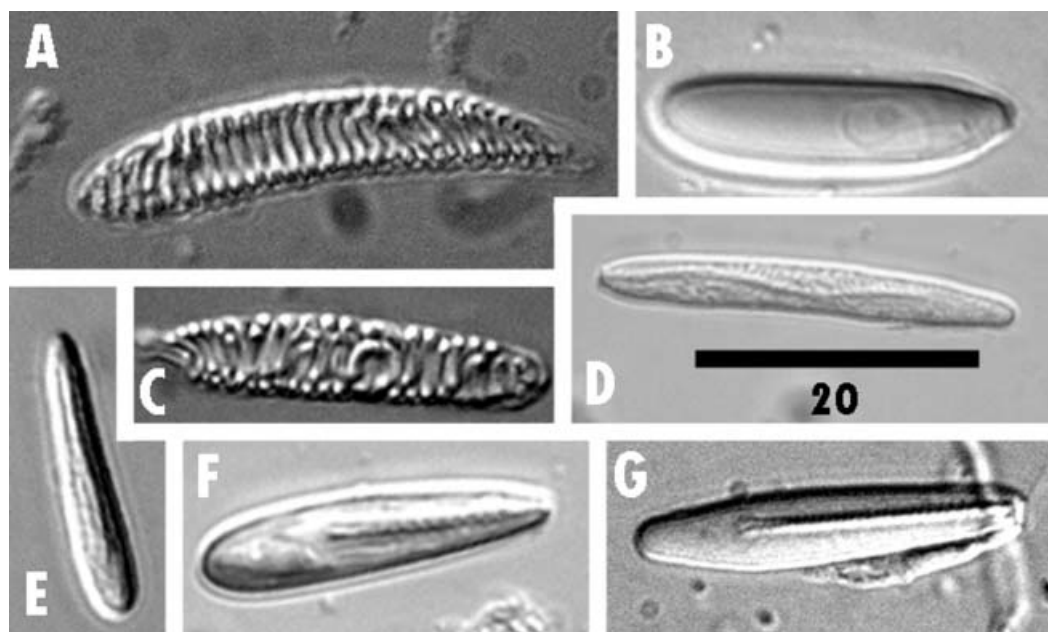


Figure 4. Cnidae of *Anthosactis pearseae*. See Table I for abundance, distribution, and size. Scale bar=20 μm. A. Robust spirocyst. B. Holotrich. C. Spirocyst. D. Microbasic *p*-mastigophore. E. Basitrich. F. Basitrich. G. Microbasic *p*-mastigophore.

Table I. Size and distribution of cnidae of *Anthosactis pearseae*, new species. Frequency of each cnidae type: +=rare; ++=common; +++=very common; *N* is the proportion of specimens examined in which the type of cnida is present; *n* is the number of capsules measured.

Tissue/Type of cnida	N	n	Size range (μm)
TENTACLES			
Robust spirocyst (A) +++	6/6	274	16.3–35.5 × 2.1–5.8
Small spirocyst (C) +++	6/6	131	11.3–19.0 × 1.3–2.7
Small basitrich (E) +++	6/6	130	16.2–29.8 × 2.2–4.6
Holotrich (B) ++	6/6	112	23.1–34.4 × 2.9–6.9
COLUMN			
Robust spirocyst (A) ++	7/7	70	19.3–38.5 × 2.9–5.9
Small spirocyst (C) ++	7/7	65	13.5–29.4 × 2.2–4.2
Small basitrich (F) +++	7/7	135	13.1–22.5 × 1.9–3.0
Holotrich (B) +++	7/7	121	16.6–27.0 × 3.5–5.5
Mic. <i>p</i> -mastigophore (F) +++	7/7	198	17.8–33.9 × 2.6–5.3
ACTINOPHARYNX			
Large basitrich (D) +++	6/6	134	25.6–44.5 × 3.0–4.3
Small basitrich (E) ++	6/6	82	16.8–26.3 × 2.0–3.3
Mic. <i>p</i> -mastigophore (F) +++	6/6	136	22.0–37.0 × 3.9–6.2
FILAMENT			
Small basitrich (E)+++	6/6	140	14.1–22.5 × 1.8–2.9
Mic. <i>p</i> -mastigophore (G)+++	6/6	204	17.5–37.6 × 3.4–6.0

type locality since at least 2002, when the carcass was first discovered (C. Braby, pers. comm.). We have examined material collected elsewhere in the northeastern Pacific, including hard substrates away from and peripheral to vents (e.g. sites in Voight et al. 2004; Voight 2005; Daly 2006), in areas of diffuse flow (e.g. sites in Collins & Daly 2005), and at active hydrothermal vents (e.g. site in Voight et al. 2004; Govenar et al. 2005) but have found no animals we can identify as *A. pearseae*. We expect this description to facilitate the identification of specimens should they occur on other whale carcasses or in other kinds of deep-sea habitats.

Discussion

The majority of deep-sea actinarians belong to one of two families: Hormathiidae or Actinostolidae (Fautin & Barber 1999). All species of sea anemone known from chemosynthetically-active habitats (vents, seeps and whale falls) also belong to either Hormathiidae or Actinostolidae (López-González et al. 2005; Fautin 2006; *contra* Wolff 2005), with most species belonging to Actinostolidae (Table II). Despite this gross similarity, the fauna of the chemosynthetically active sites should not be considered reflective of that of the deep sea in general. For example, although Hormathiidae and Actinostolidae are the most diverse families at depths greater than 100 m, at least 15 other families include species restricted to deeper waters. The actinarians of chemosynthetically-active habitats exhibit a relatively high degree of endemism; with five genera and eight species (out of a total of 11 genera or species) known only from these kinds of habitats. Although only the symbiont-harboring species *Cyanthea hydrothermala* Doumenc and Van Præet 1988 is known to have an obvious adaptation to life in chemosynthetically-active habitats, the degree of endemism and distinctiveness of the fauna at these sites suggest that the habitat is inhospitable to the majority of deep water species of sea anemones, and argues



Table II. Sea anemones known from hydrothermal vents, cold seeps, and whale falls. Species also reported at non-chemosynthetically active sites are indicated by an asterisk; those belonging to monotypic genera are in bold. Sources listed are those reporting original locality information; for other records for each species, see Fautin (2006).

Taxon	Habitat	Localities and sources
Actinostolidae		
<i>Actinostola callosa</i>	Vent *	East Pacific Rise, Pacific Ocean: Doumenc and Van Präet 1988
<i>Anthosactis pearseae</i>	Whale fall	Monterey Canyon, Pacific Ocean: Daly & Gusmão 2006 (this paper)
<b>Cyanththea hydrothermala</b>	Vent	East Pacific Rise, Pacific Ocean: Doumenc & Van Präet 1988
<i>Hadalanthus</i> aff. <i>knudseni</i>	Seep	Middle America Trench, Pacific Ocean: López-González et al. 2003
<b>Maractis rimicarivora</b>	Vent	Mid-Atlantic Ridge, Atlantic Ocean: Fautin & Barber 1999
<b>Marianactis bythios</b>	Vent	Mariana Back Arc Basin, Pacific Ocean: Fautin & Hessler 1989
<b>Pacmanactis hashimotoi</b>	Vent	Manus Basic, Pacific Ocean: López-González et al. 2005
<b>Paranthosactis denhartogi</b>	Vent	Guaymas Basin, Pacific Ocean: López-González et al. 2003
<i>Parascicyonis ingolfi</i>	Vent	Mid-Atlantic Ridge, Atlantic Ocean: Segonzac 1992
Hormathiidae		
<i>Chondrophella coronata</i>	Vent*	East Pacific Rise, Pacific Ocean: Doumenc & Van Präet 1988
<i>Phelliactis</i> sp.	Vent*	East Pacific Rise, Pacific Ocean: Doumenc & Van Präet 1988

for a closer examination of the anatomy, physiology, and biology of those species which are capable of flourishing in chemosynthetically-active habitats.

Actinostolidae comprises 25 genera, most of which have only one to three species. The taxonomy of the family is convoluted, with genera distinguished by mosaics of traits rather than unique attributes (Fautin & Hessler 1989; Häussermann 2004). *Anthosactis* is one of the most variable genera in Actinostolidae. The geographic range is extensive, ranging from the Arctic to Antarctic oceans, with species also reported from lower latitudes in the Pacific and Atlantic (Fautin 2006). *Anthosactis* has the broadest bathymetric range in the family, with species reported from water as shallow as 90 m and as deep as 2515 m (Fautin 2006). With the finding of *Anthosactis pearseae*, the bathymetric range is extended to almost 3000 m. The arrangement of mesenteries varies among species of *Anthosactis*: according to Carlgren (1949), there are six, eight, or 12 pairs of perfect mesenteries, or six pairs plus two singletons. As with bathymetry, this range of variation exceeds that of any other genus in Actinostolidae. The extent of variability among species of *Anthosactis* in terms of the arrangement of mesenteries is especially notable because mesenterial arrangement is often used to distinguish genera of Actiniaria (Carlgren 1949). The description of *Anthosactis pearseae* requires that the diagnosis of the genus be further broadened because in this species the tentacles of the outer cycle are slightly longer than those of the inner cycle. In doing so, however, we reinstate conventions of the original description removed by subsequent authors. Danielssen (1890) initially described *Anthosactis* as having tentacles “about uniform in size”. Carlgren (1921) emended this to include “Tentacles...inner longer than the outer ones...” In their description of *Anthosactis nomados*, White et al. (1999) re-emphasized Danielssen’s original definition, which Carlgren (1949) omitted in the entry for *Anthosactis* in his catalogue of Actiniaria, Corallimorpharia, and Ptychodactaria. In *A. pearseae*, the tentacles of the outer cycle are only slightly longer than those of the inner cycle, and so can be interpreted as “about uniform in size”, thus conforming to Danielssen’s (1890) description. We chose to include *A. pearseae* in this genus rather than erect a new one because Danielssen’s original description does not preclude the condition seen in *A. pearseae*, and because at least one species already in the

genus, *Anthosactis excavata* (Hertwig 1882), has slightly longer tentacles in the outer cycle (White et al. 1999). Because all possible combinations of tentacle lengths are seen in *Anthosactis*, the trait is not informative for the genus, and we have stricken mention of this feature from the definition of the genus.

In addition to its unusual tentacle arrangement, *A. pearseae* is distinguished from its congeners in the extreme development of its marginal sphincter and in brooding young. In all species of *Anthosactis*, the musculature of the column is most developed at the margin, where it constitutes a mesogloal marginal sphincter muscle (Figure 3C). In *A. pearseae*, small lacunae of the muscle extend to the limbus (Figure 3E), rather than tapering off mid-column; these mesogloal muscles are in addition to, rather than in place of, endodermal column muscles. These muscles regulate the circumference and height of the column (Batham & Pantin 1951). The increased musculature in the column of *A. pearseae* does not seem to make individuals unusually contractile or robust.

The only other species of *Anthosactis* in the deep Eastern Pacific is *Anthosactis nomados* White, Wakefield Pagels, and Fautin 1999. This species differs from *A. pearseae* in all of the features described, and can be further distinguished based on the types and sizes of cnidae. The tentacles of *A. pearseae* have numerous holotrichs, which are absent in the tentacles of *A. nomados*, but the cnidom of the latter may not be fully documented. Furthermore, *A. nomados* lives on scaphopod shells, a habitat dissimilar from that of *A. pearseae* in many respects, but one that supports the conclusion that biological substrates may be critical in deep-sea habitats where hard substrates are patchily distributed or absent altogether. López-González et al. (2003) described *Paranthosactis*, a new genus of Actinostolidae, to accommodate a species discovered in the deep East Pacific. *Paranthosactis* has sparse *p*-mastigophores in the tentacles, lacks holotrichs in the column and tentacles, lacks the tentacular nematocyst batteries characteristic of *Anthosactis*, and has tentacular musculature that is equally developed on the oral and aboral sides. *Anthosactis pearseae* differs from *Paranthosactis denhartogi* López-González, Rodríguez, Gili and Segonzac 2003, the type species of *Paranthosactis*, in all characters ascribed to the genus. *Paranthosactis denhartogi* and *A. pearseae* broadly co-occur, but seem to differ in their preferred habitat: *P. denhartogi* is known only from active hydrothermal vents; *A. pearseae* is known only from a whale fall.

The presence of planula-like propagules in the coelenteron and tentacles of male specimens indicates that these may be asexually produced. Asexually produced, internally brooded young are known from some species of *Actinia* (e.g. Black & Johnston 1979; Orr et al. 1982; Monteiro et al. 1998), in species of *Bolocerooides* and *Bunodeopsis* (Cutress 1979; Pearse 2002), and in *Megalactis comatus* (Ardelean & Fautin 2004); all of these are shallow water species. No other species of *Anthosactis* has been reported to brood. The patchiness of suitable habitat in the deep sea has led to unusual reproductive strategies in many marine invertebrates, including Actiniaria (e.g. Riemann-Zürneck 1976), and may help explain this attribute.

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