ORIGINAL ARTICLE

New observations on *Dromalia alexandri* Bigelow, 1911, a rhodaliid physonect siphonophore from Southern Californian waters

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Abstract

Dromalia alexandri is a short-stemmed physonect siphonophore found regularly in bottom trawls from the shelf waters of southern California, including biannual samples taken to monitor sewage outflow from Los Angeles and San Diego. Since the last description of the species in 1983, a greater size range of specimens is here examined, some with particularly well preserved cormidial units and detached zooids. Higher abundance and larger sizes of *D. alexandri* specimens collected from the Southern California Bight might be due to increased nutrient levels derived from sewage outflow. Small and large colonies are illustrated and described, and two growth zones identified in the zone of proliferation, including the first siphosomal horn to be identified in a rhodaliid. Nectophores of *D. alexandri* are found to lack a descending surface diverticulum, and nectophoral lamellae were identified in the naked zone below the aurophore in two specimens. In the largest colony studied, a larger number of young cormidial units are present at the beginning of the first whorl than previously reported, giving a total of c. 57 in whorl one, and in the smallest specimen whorl one has only 10 units, fewer than previously found. Much larger and more complete cormidial units of *D. alexandri* are figured and described than previously published, as are also a detached mature bract and mature male and female gonophores. Cormidial units are found to comprise only three full cormidia (composed of a gastrozooid, bract, and a gonodendron with gonophores and gonopalpons) when mature, and typically one or two additional bracts. Descriptions of the colony and zooids are based on axes for siphonophores standardized by recent authors and applied here for the first time to *D. alexandri*. A revised distributional map of the species is included covering a larger geographical area than earlier maps, and based on a greater number of records than previously available. The paper concludes with a comparison and discussion of the main characters of *D. alexandri* and those of five other species in the family Rhodaliidae.

Introduction

Dromalia alexandri is a short-stemmed physonect siphonophore of the family Rhodaliidae, regularly present in sewage monitoring samples from the Southern California Bight. It is formed of an enlarged turreted pneumatophore above a near-spherical corm bearing a corona of nectophores and whorls of cormidia. The species was introduced by Bigelow (1911) for 15 specimens taken with a large open beam trawl between 572 m and the

surface, ostensibly off Hawaii but shown later by Pugh (1983) to most likely come from Albatross station 2927, off Southern California, near Pt Loma. Bigelow described a unique flattened pneumatophore with 8–11 gelatinous prominences around the outer rim, a papillate aurophore with central gas gland or funnel (pneumatochone) arising from near the base of the pneumatophore on the dorsal side, and a zone of proliferation just below the pneumatophore on the ventral side where nectophores and siphosomal cormidial units are produced. Nectophores move out laterally from this zone around the nectosome to the dorsal side, and cormidial units move along the ventral mid-line and spiral dextrally around the swollen siphosomal corm, continuing to its base. Bigelow (1911) also concluded that the corm lacks a central cavity, as found in some other rhodaliids (see Discussion).

The species *Dromalia alexandri* was described in more detail by Pugh (1983), who made the important discovery that rhodaliids are a 'truly benthic' family of siphonophores and not pelagic like all other siphonophore species. The 14 known species of rhodaliids attach to the substrate by elongate tentacles that extend from their gastrozooids, although tentacles can also detach distally to facilitate swimming over short distances. In *D. alexandri*, Pugh (1983) studied the first-formed cormidial units in the zone of proliferation and beginning of the first whorl, and found that the gonodendron of the second cormidium always subdivides at an early stage into two parts (designated $gd2_a$ and $gd2_b$), which are carried on different main branches of the common trunk of the cormidial unit. He also noted that the trunk shortens and broadens as cormidial units age. Bracts are found in most species of rhodaliids for which reasonably preserved specimens are known, and Pugh (1983) discovered that the most complex of all rhodaliid bracts occur in *D. alexandri*. He also suspected

that bracts are caducous (shed early), as he found them only on young cormidial units, whereas in older units bracts had detached, leaving the protruding scars of their attachment lamellae. Two types of gastrozooids were identified by Pugh (1983) in many species of rhodaliids, including *D. alexandri*, and these are known as type I where tentacles lack tentilla (side branches) and type II where tentacles bear tentilla. Type I gastrozooids are thought to pick off food captured by the tentilla of type II gastrozooids; they then, apparently, ingest and digest the prey themselves, at least for four other species of rhodaliids in which feeding has been observed (Hissmann 2005). Pugh (1983: p. 240, 242) also studied the internal structure of the corm and found a very small hypocystic cavity in the nectosomal region, as well as two networks of gastrovascular canals comprising a reticulum of small and large canals lying just below the corm surface, and a sparse but more extensive system of large canals penetrating throughout the mesogloea.

Material and Methods

Twenty specimens were examined in detail in this present study (Tables 1 and 2), and 143 others examined briefly; all were collected with benthic trawls. The first six specimens from JCL (2010.01–2010.06; most collected near sewage outlets off Los Angeles) deposited by GMM in the collections of the Natural History Museum (NHM), London, and the remainder (Co421–Co1852) were loaned to G.M.M. from Scripps Institute of Oceanography (SIO), California. The best preserved of the NHM specimens (Reg. No. 2010.01) was fixed in formalin and preserved in alcohol; all others were fixed and preserved in alcohol. In this new study, drawings of whole colonies, detached zooids and excised cormidial units were made

Table 1. Material examined.

Specimen Reg. Nos	Location	Coordinates	Collection date	Depth, m	No. of specimens
2010.01 and 2010.06	W of Pt Vincente, Los Angeles County, CA	c. 33°45.5′ N 118°27′ W	23 May 2006	305	2
2010.03 and 2010.05	S side Redondo Canyon, CA	c. 33°48′ N 118°31′ W	23 May 2006	305	2
2010.04	S side Redondo Canyon, CA	c. 33°48′ N 118°31′ W	28 March 2006	305	1
2010.02	Between Santa Catalina Is and Lasuan Knoll	33°36.485′ N, 118°17.795′ W–33°36.657′ N, 118°17.457′ W	16 January 2001	200+	1
Co421 (i–ix)	N of Santa Catalina Is	33°33.5′ N, 118°39′ W	9 March 1976	585–534	9
Co528	Off Bahia San Quentin, Baja California, Mexico	31°13′ N, 116°05′ W	1 April 1962	183	1
Co558	W of Pt La Jolla, CA	c. 32°50.5′ N, 117°21.35′ W	28 January 1965	311–183	1
Co1734 (i–ii)	Albatross Stn 4421	?33°11′ N, ?119°29′ W	12 April 1904	536–0 (293–0 fm)	2
Co1852	W of Pt Loma, San Diego, CA	32°41′ N, 117°21′ W	20 February1988	219.5	1

2010 Series numbers NHM, London; Co series numbers Scripps, CA.

Table 2. Summary descriptions of specimens studied.

Specimen Reg. Nos	Dimensions (mm; anterior–posterior length × max. anterior diameter in anterior view, excluding distortions)	Sex	Notable features and figures
2010.01	50 × 52	M	Rotund colony with best preserved cormidial units, two attached and 13 loose nectophores; also the largest number of units in first whorl, and many mature male gonophores; Figs 3, 7, 8 and 11A
2010.02	44 × 49	M	Large non-rotund colony; two attached nectophores and largest number of nectophoral muscular lamellae; Fig. 9A
2010.03	50 × 35	?F	Non-rotund colony
2010.04	38 × 55	M	Non-rotund colony with attached bract
2010.05	32 × 31	F	Non-rotund colony with best preserved nectophoral lamellae and excellent zone of proliferation with two growth zones discernible; Figs 5 and 6B
2010.06	25 × 31	F	Non-rotund colony with mature female gonophores; Fig. 11B
Co421(i)	12 × 14	U	Rotund colony, smallest in collection with only 12 nectophores and five whorls in life; Fig. 2A–C
Co421(ii)	20 × 22	U	Rotund colony with many well developed gastrozooids and tentacles
Co421(iii)	20 × 23	U	Rotund colony with one attached nectophore and large attached bract on a first whorl unit
Co421(iv)	28 × 22	U	Rotund colony; aurophore funnel (pneumatochone) discernible
Co421(v)	25 × 20	U	Non-rotund colony; aurophore funnel discernible
Co421(vi)	23 × 18	U	Rotund colony with two attached nectophores
Co421(vii)	29 × 20	U	Non-rotund colony
Co421(viii)	29 × 27	U	Rotund colony; aurophore funnel discernible
Co421(ix)	37 × 33	?F	Rotund colony with most aurophore papillae found and bracts attached to first whorl cormidial units; Fig. 10
Co528	61 × 54	F	Non-rotund colony with numerous aurophore papillae
Co558	54 × 55	?M	Best shaped rotund colony with numerous aurophore papillae
Co1734(i)	24 × 22	?F	Rotund colony with life-like attached nectophore; Fig. 6A
Co1734(ii)	30 × 40	M	Rotund colony with seven attached nectophores and bract on a second whorl unit
Co1852	57 × 43	F	Non-rotund colony with two attached nectophores and 12+ whorls; Fig. 4A and B

F = female; M = male; U = unknown.
Attached zooids are mature unless otherwise indicated; whorls refer to whorls of cormidial units on the siphosome.

using a camera lucida; they and the description form a taxonomic baseline for identifying *D. alexandri* in any future benthic studies, perhaps to evaluate anthropogenic change in the Southern California Bight.

Terminology

Most terms and axes applied to individual zooids in this work follow Mapstone (2009: p. 67–74, figs 1–3). In summary, cormidia are serially repeated groups of zooids on the siphosome. In most physonects the siphosome is extended and elongate with cormidia spread out along its length, but in rhodaliids the siphosome is spiralled because space is limited. As a result, cormidia are crowded together and zooids insert onto many stems from the corm. Such a stem can bear either one cormidium (monogastric) or several cormidia (polygastric). Most rhodaliids are polygastric with whorls of iterative tree-like structures, the cormidial units, on the corm surface. Each cormidial unit comprises a trunk with several distal branches bearing several cormidia. Each individual cormidium includes a gastrozooid, bract, and one or more gonodendra with gonopalpons and gonophores. Cormidia arise sequentially on each cormidial unit and are numbered accordingly, with most cormidial units developing three full cormidia when mature. It is important to note here that the term 'polygastric' (see Totton 1965: p. 23), which literally means 'many stomachs', is also sometimes used in a different context for the asexual colony stage in the life cycle of a calycophoran siphonophore.

Description of *Dromalia alexandri*

Five images of living colonies attached to various substrates are shown in Fig. 1. They display an orange coloured corm with paler pneumatophore surrounded by a ring (corona) of translucent pale orange nectophores (which appear grey in some images). Spirally contracted gastrozooid tentacles hang down around the siphosomal corm, whilst others extend out for some distance and attach the colony to the substrate. Both coiled and
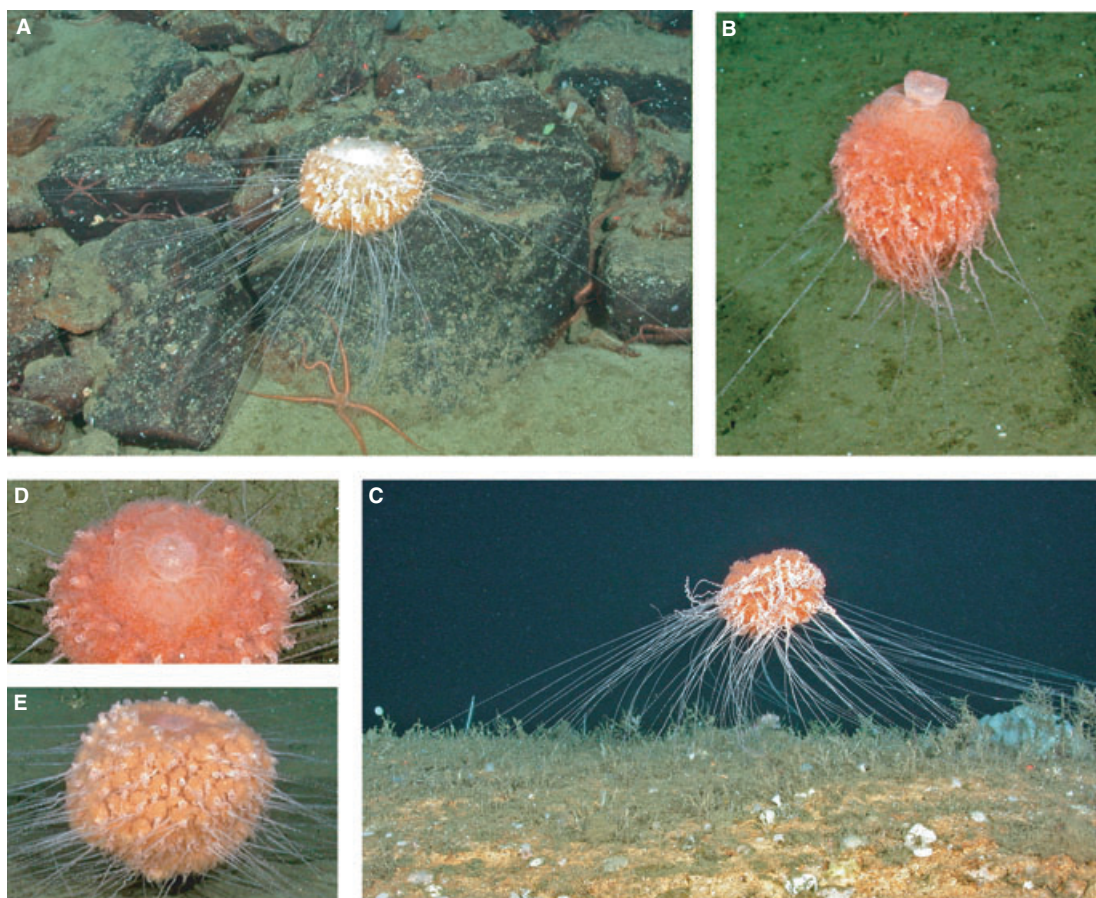
Fig. 1. Images of live colonies of *Dromalia alexandri* from the Continental Borderland area of the Southern California continental shelf. Colonies anchored by extended tentacles to a mixed boulder and sand substrate. (A) Image captured on 16 March 2005 at 345.6 m depth on 43 Fathom Bank displays corm anchored by radiating tentacles. (B) 22 March 2006 at 333.7 m depth on 9 Mile Bank shows turreted pneumatophore, corona of nectophores plus tiny tentilla on extended tentacles. (C) 18 March 2005 at 215.8 m depth on 117 Seamount demonstrates buoyant colony maintained clear of sea bed. (D) 22 March 2006 at 332.7 m depth on 9 Mile Bank shows pneumatophore, corona of nectophores and some retracted coiled tentacles. (E) 7 March 2008 at 261.7 m depth on Mission Beach Reef displays collapsed nectophores and orange cormidial units with both extended and coiled tentacles. Images slightly enhanced to reduce reflected glare from orange corm and emphasize tentacles (PHOTOSHOP: brightness/contrast and shadow/highlights). Corm diameter in live specimens c. 50 mm. All images courtesy J. Butler, NOAA.

extended tentacles appear white in Fig. 1, where extended tentacles bear numerous minute white swellings along their lengths, which are the tentilla. Tentilla include the nematocyst batteries of type II gastrozooids, which are responsible for catching the prey.

The main axes of a siphonophore colony, as defined by Haddock *et al.* (2005) and Mapstone (2009), are applied to *Dromalia alexandri* in Fig. 2A and B. An anterior–posterior axis passes from the top of the pneumatophore to the base of the corm, a dorsal–ventral axis extends through the dorsal aurophore to the ventral zone of proliferation, and a right–left axis lies in the same plane and orthogonal to the dorsal–ventral axis. The corm is divisible into an anterior nectosome bearing nectophores and a posterior siphosome bearing whorls of cormidial units. The smallest specimen studied [Co 421

(i), Fig. 2C] bears five siphosomal whorls, and the largest specimens up to 14 identifiable whorls.

Notable features of the 20 specimens studied in detail in this work are presented in Table 2. Colony sizes vary from 12 to 55 mm maximum (anterior–posterior) length and from 14 to 52 mm maximum diameter (in anterior view), a range based on only the most rotund colonies.

Pneumatophore

In *Dromalia alexandri* this structure is exceptionally large for a physonect siphonophore, with a diameter of c. 18 mm in large specimens. It has a flattened anterior surface with peripheral turrets varying from flattened and rounded to taller and more pointed, and in many specimens there are additional smaller secondary turrets
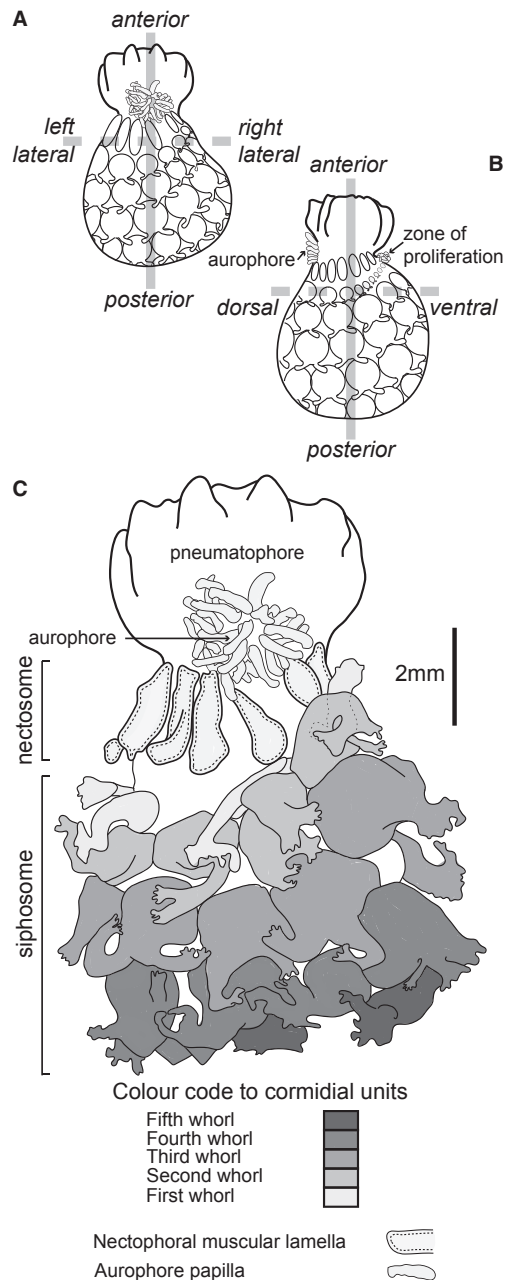
Fig. 2. *Dromalia alexandri* colony. (A) Dorsal and (B) right lateral schematic views of colony axes. (C) Morphology of immature preserved colony, dorsal view [Reg. No. Co421(i)].

on the radii subtending the primary turrets (Figs 2 and 3). In life the anterior portion of the pneumatophore is an orange-pink colour and the posterior portion generally white (Fig. 1B and D). The external wall of the pneumatophore is tough and typically narrows posteriorly where the pneumatophore joins the nectosome (Fig. 2). A silvery gas bubble is discernible inside the pneumatophore of most specimens, and in some smaller examples

endodermal processes, which penetrate throughout the mesogloea of the pneumatophore, are also discernible in the turrets. The aurophore, or gas gland, is particularly well developed in *D. alexandri* (Fig. 4A), and comprises c. 30 papillae inserting onto a rounded gas chamber, the pneumatochone. Papillae are slender in many colonies, including most immature examples (Fig. 2), and swollen with obvious terminal pores in several larger specimens (Figs 3 and 4B).
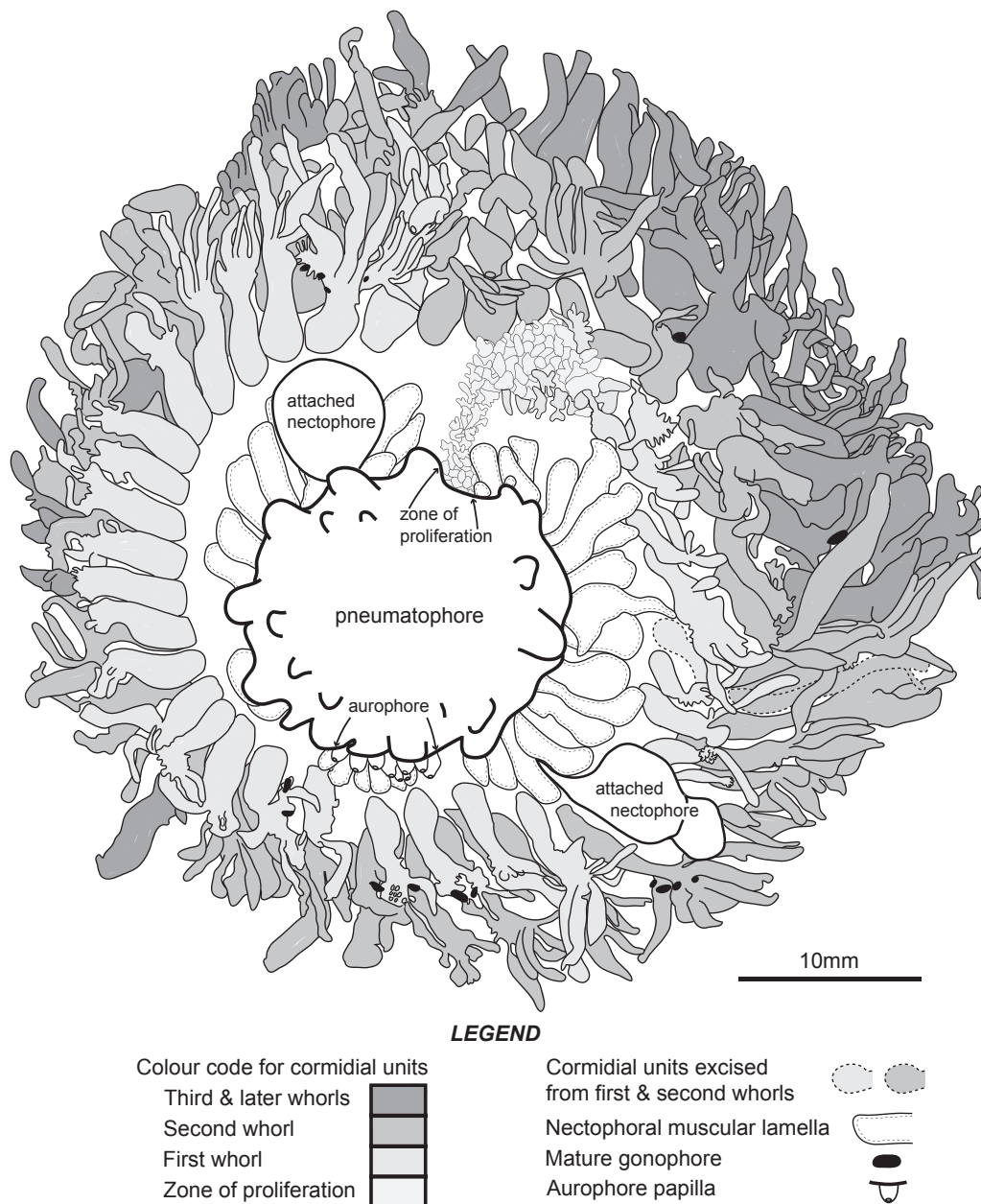
Nectosome

Nectophores form in a single corona around the base of the pneumatophore, are pale orange in life (Fig. 1B and D), and either protrude above the level of the first whorl of the siphosome (Fig. 1B) or are folded over and form a flat anterior surface to the colony (Fig. 1A and E). Nectophores develop in a nectosomal growth zone which protrudes slightly from the mid-ventral line immediately posterior of the pneumatophore, and just anterior of the siphosomal growth zone, or horn (Fig. 5). Nectophore buds move out laterally and develop rapidly into thin-walled, approximately spherical nectophores. They have an outwardly directed ostium and broad velum, and a nectosac that fills the nectophore. The latter has an ostial ring canal with four radial canals extending from it around the nectosac to the proximal surface (Fig. 6A), where they re-unite and insert onto the external pedicular canal of the nectophoral muscular lamella (Fig. 6B). This lamella is extensive and bears the gutter-like scar of an ascending surface diverticulum ('ascending pallial canal' of Haddock *et al.* 2005) along the surface, attaching the lamella to the nectophore. The diverticulum originates at the insertion point of the external pedicular canal, and extends anteriorly for some distance along the proximal surface of the nectophore. A descending surface diverticulum is not developed, and no internal pedicular canal is discernible.

Preserved nectophores are 7–9 mm in diameter (Fig. 6A), and the muscular lamellae of detached and lost nectophores in many of the present specimens indicate that nectophore numbers vary greatly from 12 to c. 80. The number of lamellae on each side of the aurophore in *Dromalia alexandri* is typically approximately symmetrical, with a noticeable gap below the aurophore in all but two colonies (including that shown in Fig. 3). Few nectophoral lamellae had detached in the present material and most have a typically elongate insertion onto the corm (Fig. 6).

Siphosome

The horn (blastocrene) is a flap of tissue projecting from the siphosomal surface and is the site for the production

Fig. 3. Mature preserved colony of *Dromalia alexandri*, anterior view, showing pneumatophore, nectosome with nectophoral muscular lamellae and two remaining attached nectophores, zone of proliferation, aurophore and first few whorls of siphosomal cormidial units including location of excised units from first and second whorls (Reg. No. 2010.01).

of siphosomal cormidial units; it is separated from the nectophoral growth zone by a trough. In *Dromalia alexandri* pro-buds for cormidial units appear at the anterior end of the horn, pass posteriorly along its outer edge to its posterior end before moving down onto the surface of the corm itself (Fig. 5). At this point (the left-hand end of the horn in Fig. 5) they are differentiated into young cormidial units, and growth continues as they extend posteriorly along the ventral mid-line towards the dextral

turn into the first whorl. In specimen 2010.05 (Fig. 5) there are 11 young units in the ventral mid-line beyond the horn and four in the turn to the first whorl, whereas in the smallest specimen studied [Co 421(i), Fig. 2] there are only four units (not shown), with more than 25 in the largest specimen (2010.01, Fig. 3).
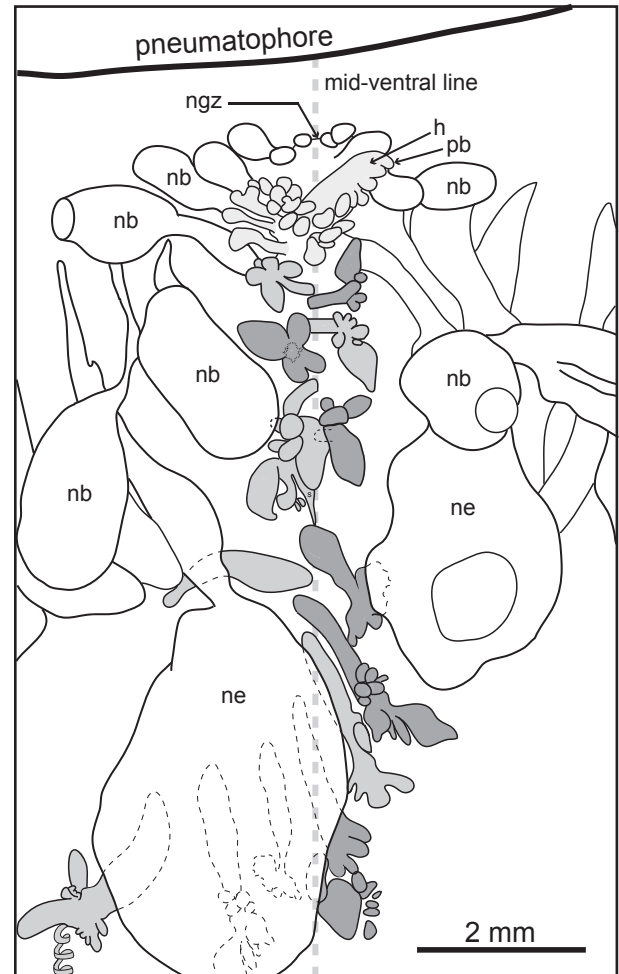
Whorls are typically delineated by a thickened white line on the corm surface in preserved material. The smallest colony has five siphosomal whorls [Co421(i),
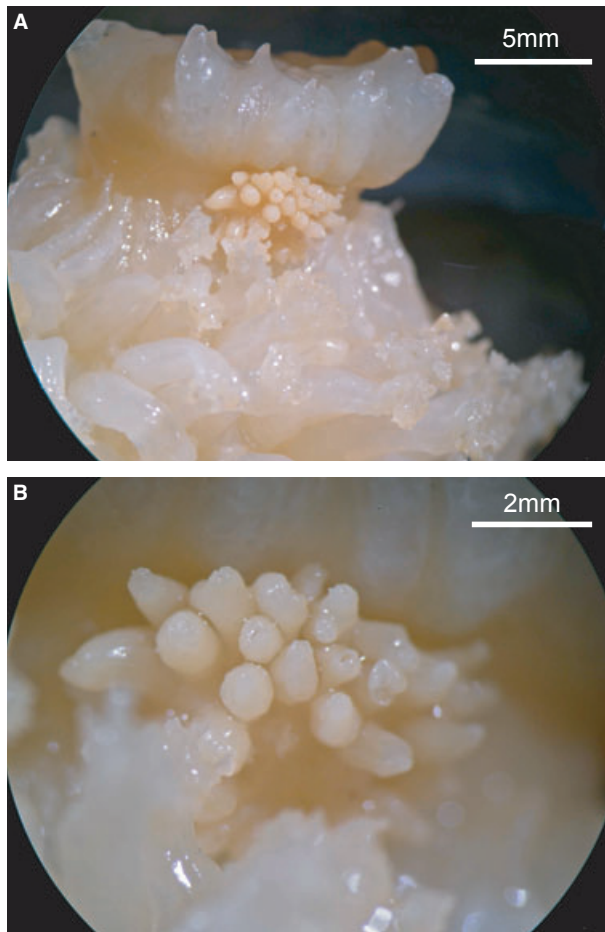
Fig. 4. Aurophore, dorsal view. (A) Upper half of specimen and (B) detail of aurophore papillae showing terminal pores (Reg. No. Co1852).


Fig. 5. Zone of proliferation, ventral view, illustrating nectophore growth zone, nectophore buds, horn of siphosomal growth zone with pro-buds along outer margin, plus 15 young cormidial units developing along the mid-ventral line and turning into the first whorl of the siphosome (Reg. No. 2010.05). h = horn; nb = nectophore bud; ne = nectophore; ngz = nectophore growth zone; pb = pro-bud.

Fig. 2C], whereas large colonies with well preserved posterior surfaces exhibit more than 12 whorls (Table 2). The largest specimen 2010.01 has about seven whorls, but only the first three to four whorls are discernible in anterior view (shown in Fig. 3). There are 10 cormidial units in the first whorl of the smallest specimen (see Table 2), and c. 57 in the first whorl of the large specimen 2010.01 (Fig. 3), including up to three abreast at the beginning of the whorl.

Three large, well preserved cormidial units were excised from two colonies (2010.01 and 2010.02) and are shown as Figs 7 and 8; nine other units were also excised from the same specimens but are not drawn. In the youngest excised unit, the leading edge (furthest from the zone of proliferation) is shown on the right (Fig. 7A). The unit trunk divides into two main branches at the level of several white buds (Fig. 7A, wb), and these branches are separated by a deep fissure. Components of the oldest cormidium (cormidium 1) arise from the main branch

nearest the leading edge and the trunk below it, on the leading side, and include a large type I gastrozooid (gz_1) with a tentacle (t_1), two elongate gonopalpons (gp_1), some partially mature gonophores at their bases, and the bracteal lamella of a detached bract (bl_1; Fig. 7A and B). The next cormidium formed (cormidium 2) is split between this main branch and the second main branch, which lies nearest the trailing edge of the unit. Zooids on the leading edge-main branch include a shorter type II gastrozooid (with narrow distal proboscis) with tentacle (t_2) and two elongate gonopalpons ($gp2_a$). Zooids on the trailing edge main branch and trunk below it include six elongate gonopalpons ($gp2_b$) and the muscular lamella of a detached bract (bl_2; Fig. 7A and B). The youngest (cormidium 3) arises exclusively from the trailing edge
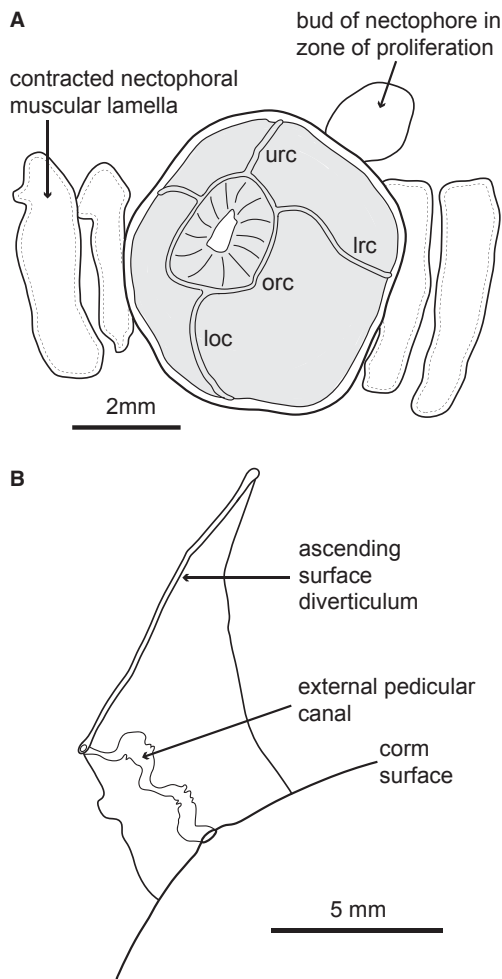
Fig. 6. Nectophore and a nectophoral muscular lamella. (A) Mature nectophore still attached to a specimen [Reg. No. Co1734(i)]. (B) Relaxed nectophoral muscular lamella with canals, left lateral side (nectophore detached; Reg. No. 2010.05). urc = upper radial canal; lrc = lateral radial canal; loc = lower radial canal; orc = ostial ring canal.

side of the trailing main branch and the trunk below it. It comprises a small and still developing type II gastrozooid (gz_3) with a swollen region proximally where the tentacle is forming, two elongate gonopalpons (gp_3), and a small attached bract (b_3; Fig. 7A and B). Some gonopalpons must have been lost during preservation.

The second excised cormidial unit (Fig. 8) from the second whorl of 2010.01 is 25% longer than the corresponding first whorl unit (Fig. 7), and whereas a large number of elongate gonopalpons remain attached, two of the three gastrozooids have detached, leaving only scars of their pedicels. The first cormidium in Fig. 8 is represented by several zooids, including a large (11 mm long) type I gastrozooid (gz_1) with detached tentacle, six elongate gonopalpons (gp_1) arising from a very short and flattened gonodendron (not labelled), a number of mature gonophores (go) on the gonodendron which are ready for release, and an elongate bracteal lamella on the trunk below (bl_1). The second cormidium is again split between the leading and trailing main branches, with the former lying immediately in front of the latter in Fig. 8, obscuring the deep furrow. The pedicel of its gastrozooid (gz_2) and five elongate gonopalpons ($gp2_a$) arise from a sub-branch of the leading edge main branch. Six more elongate gonopalpons ($gp2_b$) arise from a sub-branch of the trailing edge main branch, plus an elongate bracteal lamella (bl_2). The zooids of cormidium 3 had all detached in this unit (their pedicels are hidden from view in Fig. 8), leaving a large scar of the third gastrozooid, the stump of the third gonodendron, several attached immature gonophores and scars of gonopalpons, and a shorter lamella scar of the third bract extending down onto the trunk. The bracteal component of a fourth cormidium is evident in this cormidial unit also as a short lamella scar (bl_4) on the leading side of the first bracteal lamella (Fig. 8).

The first whorl cormidial unit from specimen 2010.02 (fixed in alcohol, Fig. 9A) was excised from near the end of the first whorl (not illustrated) and shows a contracted main trunk with zooids, two shorter and more widely spaced leading and trailing main branches, and gonophores represented mostly by the scars of their pedicels. The leading edge main branch lies on the right in Fig. 9A (not labelled) and the trailing main branch on the left. The first cormidium (on the right) comprises a large type I gastrozooid (gz_1) with short contracted tentacle (too small to label), a large gonodendron (gd_1) denuded of all zooids except one small gonopalpon (gd_1), and an elongate scar of the first bract (bl_1) passing onto the posterior surface of the main trunk. The second cormidium bears a well preserved type II gastrozooid (gz_2) with elongate attached tentacle and denuded gonodendron gd_{2a} on the leading edge main branch. Gonodendron gd_{2b} is borne on a sub-branch of the trailing edge main branch and bears three elongate gonopalpons (gp_{2b}), with an elongate bracteal canal scar (bl_2) extending from this main branch onto the trunk (Fig. 9A). The third cormidium has a gastrozooid represented only by a pedicel scar (gz_3), and a gonodendron (gd_3) on its trailing side, with three attached elongate gonopalpons (gp_3) and a shorter bracteal lamella (bl_3). A fourth cormidium is again represented in this unit by a small bracteal lamella (bl_4) but here the lamella occurs on the opposite side of the leading edge main branch to the left of the first bracteal lamella (Fig. 9A). Similar bracteal lamellae representing later cormidia are found in the same position in several other excised units (not illustrated) and, in one cormidial unit from the third whorl, a fourth bracteal lamella
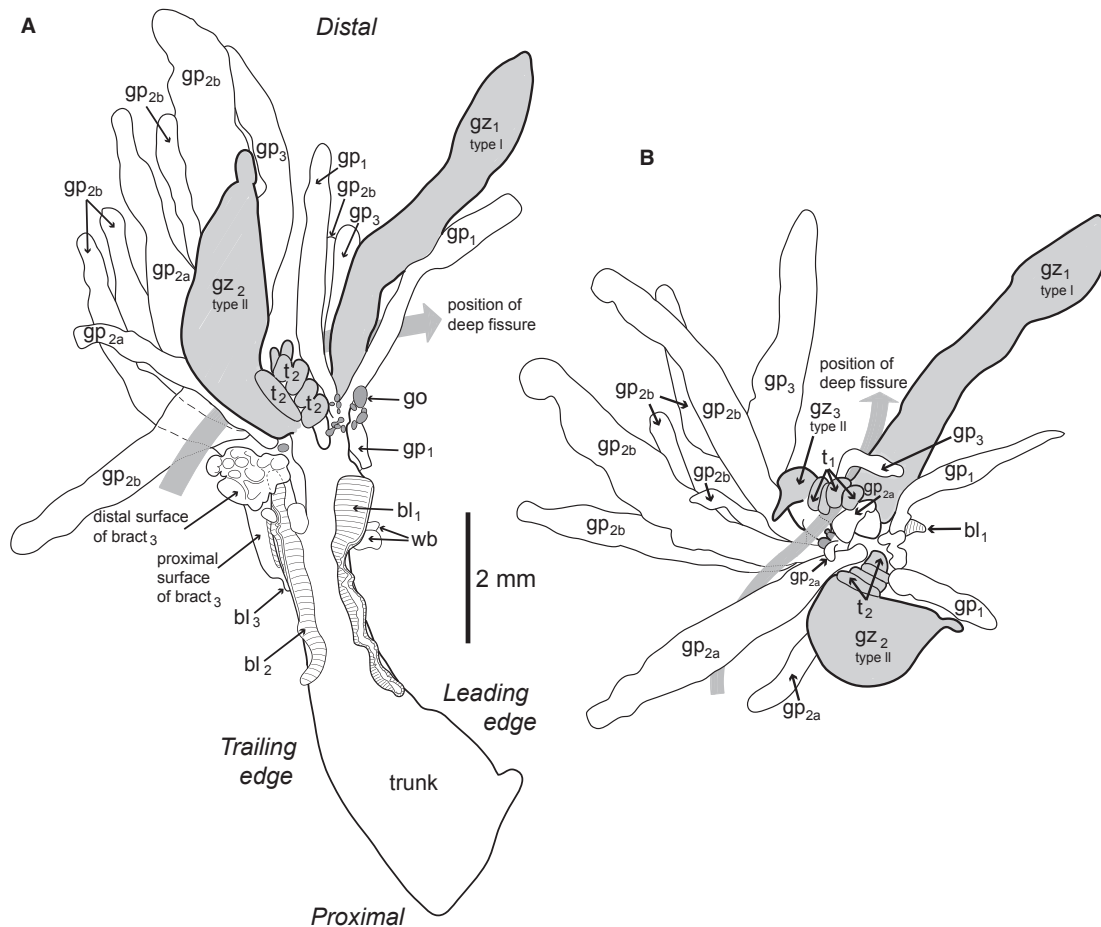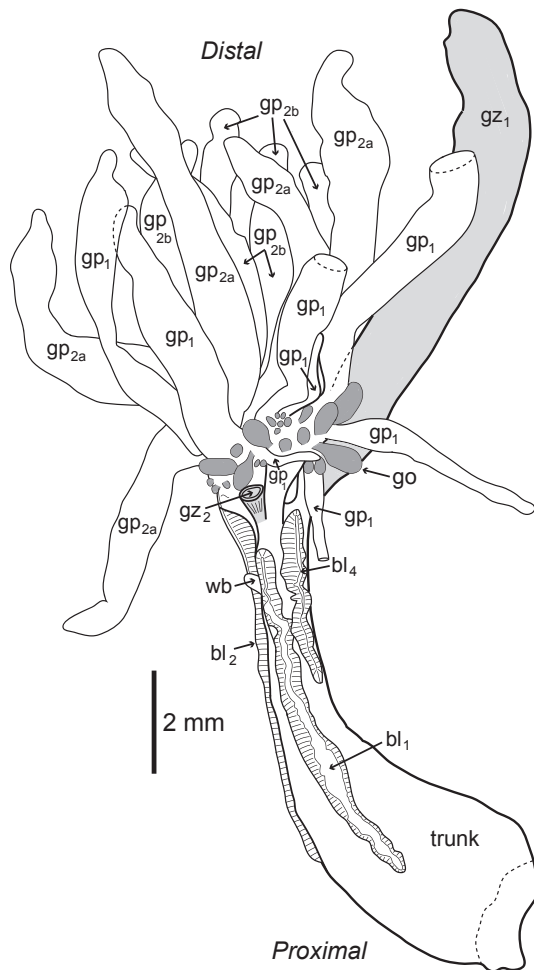
Fig. 7. Cormidial unit excised from near end of the first whorl (Reg. No. 2010.01, see Fig. 3). (A) Anterior view. (B) Distal view of splayed zooids. bl = bracteal muscular lamella; go = gonophore; gp = gonopalpon; gz = gastrozooid; t = tentacle of gz; wb = white bud.

(representing a fourth cormidium) is present on the leading edge main branch with a small fifth bract on the trailing edge main branch. No representative zooids of fourth and fifth cormidia other than bracts are identifiable on any excised units.

The annulated tentacle of the second gastrozooid of specimen 2010.02 shows developing tentilla proximally (Fig. 9A). The proximal portion of this tentacle is attached to the proximal end of the gastrozooid (gz_2) by an extensive suspensory ligament (sl), whereas distally the tentacle is free, and where relaxed annuli are spaced further apart, the tentilla themselves have detached. Mature tentilla were found on a portion of tentacle from another type II gastrozooid, and arose from the annuli of the tentacle (Fig. 9B). Each tentillum comprises an elongate pedicel (ped), a small bilobed cnidoband (bcb) and a single terminal filament (tf; Fig. 8B). Tentilla are white in life, and carried on a translucent pale pink tentacle which is thickened proximally by the similarly coloured suspensory ligament (Fig. 1D).
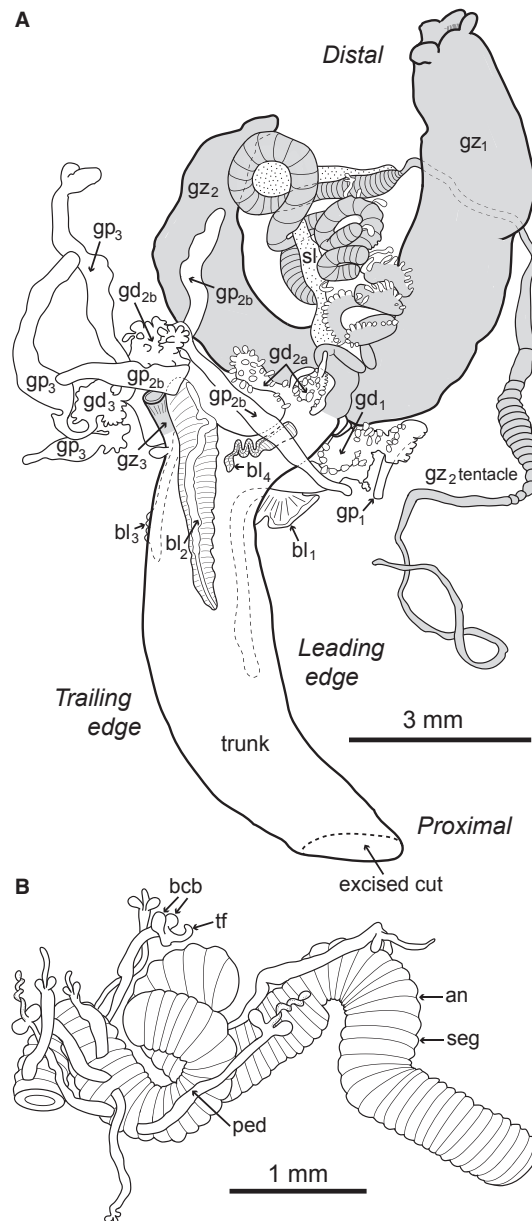
Several bracts remain attached to cormidial units in the first and second whorls of *Dromalia alexandri* specimens Co421 and Co1734 from the Scripps collection (Table 2), and a particularly mature detached bract is present in the jar with specimens of Co421. This bract (Fig. 10) is 4 mm long, approximately triangular in shape, with an angled proximal end and a broad distal surface subdivided into 10 small lobes; the bracteal canal has many branches and sub-branches. When opened out to expose the lower surface, a centrally located scar marking the region where the bract was attached to the bracteal lamella is discernible (bcs), and from this scar extend two branches of the bracteal canal, one proximally and the other distally (Fig. 10, pbc, dbc). The proximal branch (pbc) lies close to the lower surface of the bract with many T-shaped side branches arising from its upper side at regular intervals. The distal branch rises upwards to just below the upper bracteal surface and gives rise to several short lateral branches proximally on each side, before subdividing into two elongate right and left lateral

Fig. 8. Cormidial unit excised from second whorl (Reg. No. 2010.01, see Fig. 3), leading edge view. bl = bracteal muscular lamella; go = gonophore; gp = gonopalpon; gz = gastrozooid; wb = white bud.

Fig. 9. (A) Cormidial unit excised from first whorl of Reg. No. 2010.02, anterior view. (B) Detached length of type II tentacle, with tentilla (Reg. No. 2010.01). an = annulus; bcb = bilobed cnidoband; bl = bracteal muscular lamella; gd = gonodendron; gp = gonopalpon; gz = gastrozooid; ped = pedicel; seg = segment; sl = suspensory ligament (stippled); tf = terminal filament.

side branches (rls, llb) which extend to the outer edges of the bract, giving rise to more side branches, which again further subdivide (Fig. 10).

Colonies are dioecious. Mature gonophores are attached to the gonodendra of six specimens examined, including four males and two females (Table 2; Fig. 8, go). Mature detached male and female gonophores are illustrated in Fig. 11, and both reach c. 3 mm in length including their pedicels. The male gonophore (Fig. 11A) is filled with sperm, and the female (Fig. 11B) contains a single large ovum with much yolk and a nucleus situated near the margin; the ovum is surrounded by endodermal outgrowths (spadicine canals) from the manubrium. Radial canals are not discernible in either gonophore but both possess a cap which may contain a reduced circular canal.

Geographical distribution

A new distributional map for *Dromalia alexandri* is shown in Fig. 12, and includes 328 sighting records made between 1889 and 2008. These include the six specimens from one of the present authors (J.C.L.; most from biannual sewage monitoring samples) now deposited by G.M.
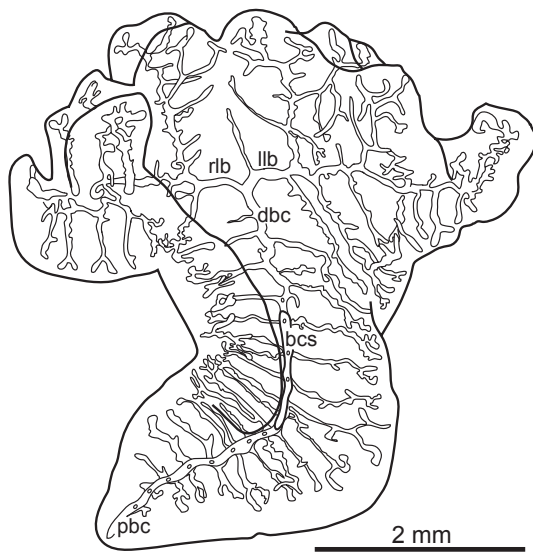
Fig. 10. Detached mature bract, lower view, with left wing (right in Figure) opened out (Co 421). bcs = bracteal canal/lamella scar; dbc = distal branch of bracteal canal; llb = left lateral bracteal canal branch; pbc = proximal branch of bracteal canal; rlb = right lateral bracteal canal branch.
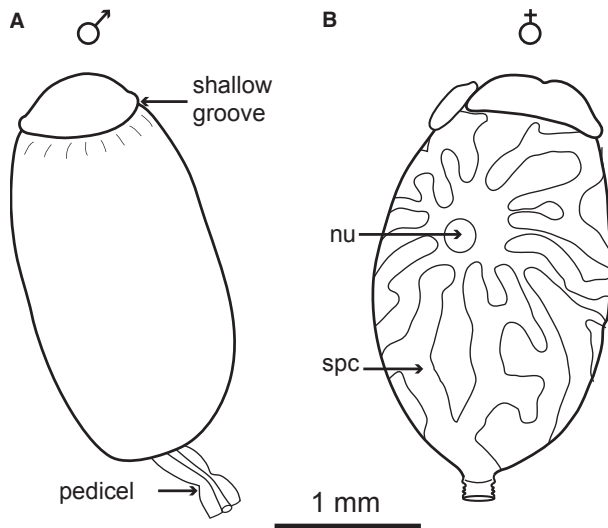
Fig. 11. (A) Male (Reg. No. 2010.01) and (B) female (Reg. No. 2010.06) gonophores. nu = nucleus; spc = spadicine canal.

M. in the collections of the Natural History Museum, London, all material of *D. alexandri* held in the benthic collections of Scripps Oceanographic Institution and inspected by G.M.M., material listed by Pugh (Table 1 in Pugh 1983) including the deduced Type specimen (but excluding Scripps specimens previously noted), all material reliably identified as *D. alexandri* from the remotely

operated vehicle (ROV) archives of the Monterey Bay Aquarium Research Institute (MBARI) and observed above 750 m (see Discussion), all material similarly identified from the ROV archives of the Southwest Fisheries Science Center (NOAA), and specimens of *D. alexandri* observed by Vetter & Dayton (1999) and by Brueggeman (2005).

Dromalia alexandri distribution density in Fig. 12 is strongly influenced by the availability of the Scripps specimens (examined by GMM) and the ROV observations from MBARI; both group records are from deep submarine canyons cut into the near-shore continental shelf in the Californian borderlands basins area (specifically La Jolla Canyon and Redondo Canyon). Other frequently sampled *hotspots* visited by underwater vehicles are the exit of the Santa Barbara Channel adjacent to Hueneme Canyon and Monterey Canyon further north. The largest red circles in Fig. 12 indicate in excess of 50 sightings located close together, hence necessitating considerable red circle overlap. Single sightings or group records up to five or 10 sightings are variously dispersed throughout the borderland basins area, including further offshore on the Cortes Bank, Northeast Bank and elsewhere, with a minority of records stretching along the narrow continental shelf off Baja California. The distribution is strongly biased by active centres of research, so more activity along the Baja California shelf and on the shallower banks across the borderlands basins area would substantially increase records. Figure 12 could be used to evaluate future changes in distribution, for example from anthropogenic influences, provided these biases are properly taken into account.
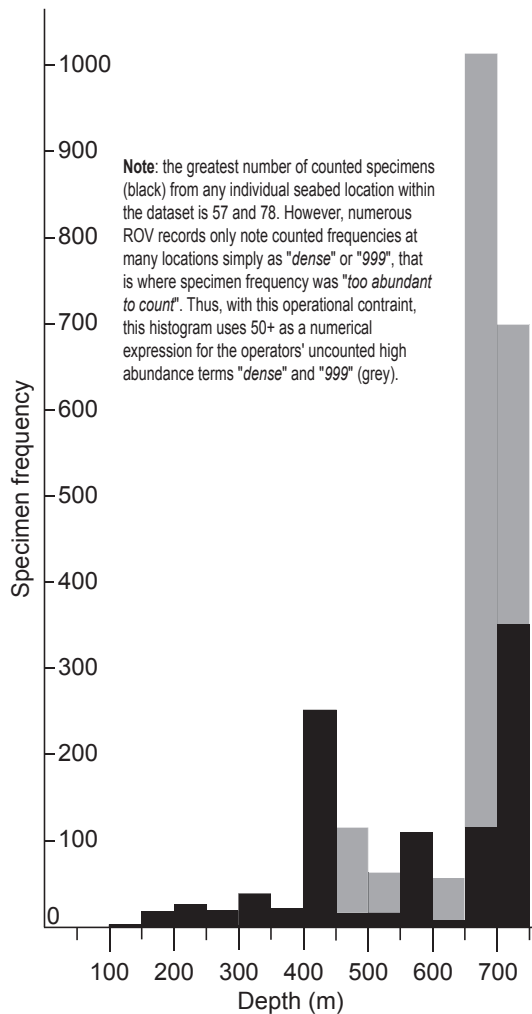
The location of the Type specimen, which is held in the Invertebrate Collections of the National Museum of Natural History, Smithsonian Institutions, USA (catalogue number 29696), is also shown in Fig. 12, as are the locations of photographic images in Fig. 1.

Ecology

Visual frequency of *Dromalia alexandri* observed on the seabed above 750 m water depth (see Discussion) and benthic trawl data, is plotted against water depth in Fig. 13, which shows a frequency maximum in the depth range 650–750 m, and a secondary peak between 400 and 450 m. Elsewhere the histogram shows a steady increase in numbers with depth. Specimen observations within this maximum zone (650–750 m) is clearly influenced by the numerous imprecise ROV records that note counted frequencies at many of the deeper localities simply as '*dense*' or '*999*', that is, where specimen frequency was '*too abundant to count*' (S.H.D. Haddock, personal communication). Thus the histogram construction uses 50+
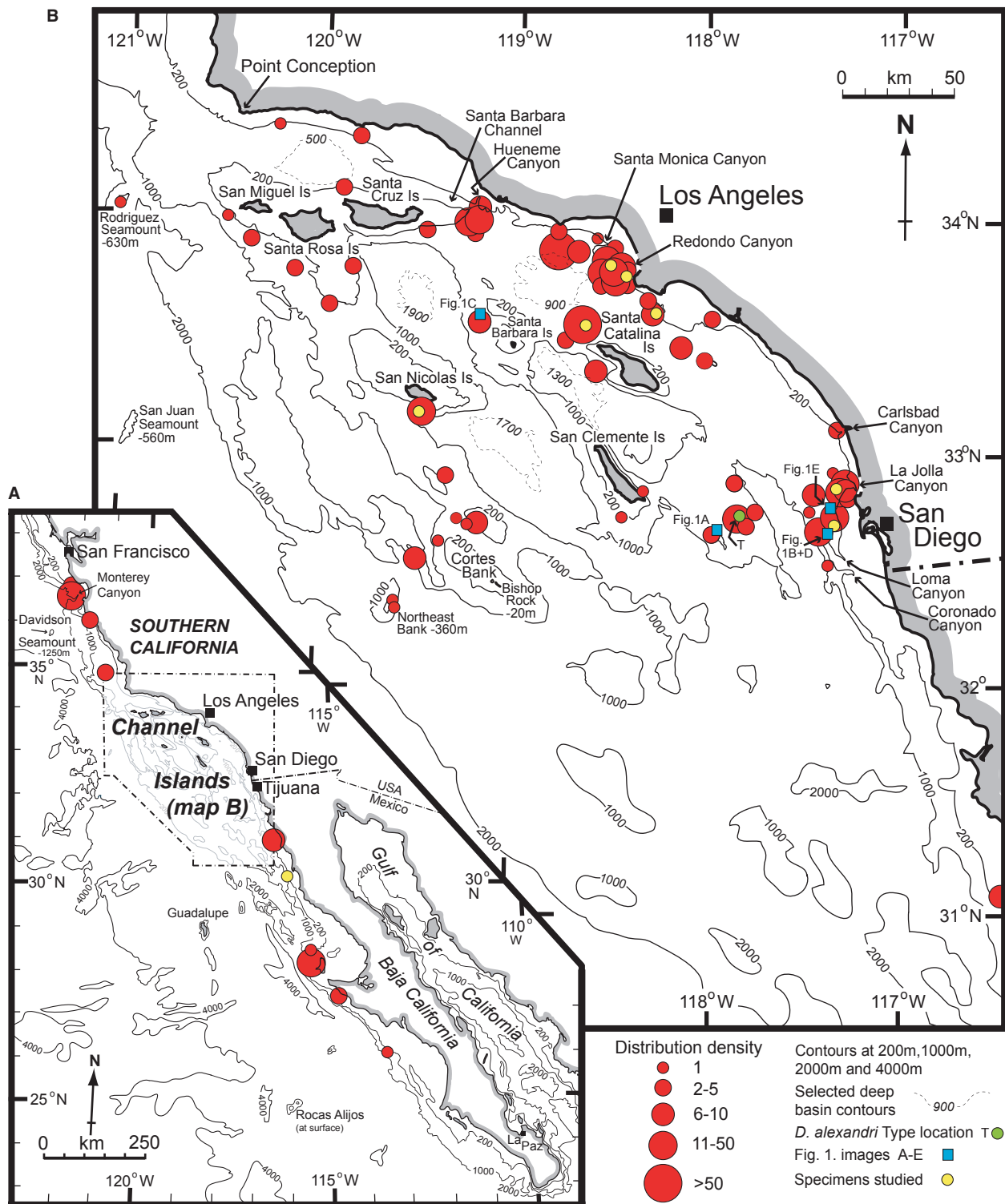
Fig. 12. Distribution of recorded sightings of *Dromalia alexandri* (<720 m water depth). (A) Southern California–Baja California Pacific continental shelf. (B) California Channel Islands and borderland basins. Bathymetry on the continental shelf north of 32°N derived from NOAA preliminary maps B14 (Western United States) and B15 (Southwestern United States), south of 32°N and in the Gulf of California derived from the global seafloor topography project of Smith & Sandwell (1997), deep water contour data (*i.e.* 4000 m) derived from NOAA maps supplemented by world atlas.

concentrations in deeper water (650–750 m) lie within the numerous submarine canyons that obliquely cut the continental shelf, where down-slope or down-canyon currents provide a richer concentration of suspended food particles sourced from shallower nutritious shelf areas. No identifiable items of prey were found in any preserved gastrozooids during the present taxonomic work.

Discussion

The new information for *Dromalia alexandri* presented in this work is related below to previously published information on the species. Its overall morphology is also compared below with that of species in the five other genera of the Rhodaliidae most similar to *D. alexandri* (Table 3).

Application of the standardized axes of long-stemmed physonects (Haddock *et al.* 2005; Mapstone 2009) to *Dromalia alexandri* (Fig. 2A and B) shows the anterior–posterior axis to be only slightly greater than, or of similar length to, the dorsal–ventral and left–right axes. This is evident in Table 2, and not unexpected for a short-stemmed siphonophore.

The morphology of *Dromalia alexandri* is particularly complex with so many attached zooids and zooid-complexes (the cormidial units), and the reader is referred to Pugh (1983) for descriptions and figures of the early growth stages of young cormidial units, the morphology of type I and II gastrozooids, the internal structure of the pneumatophore, aurophore and corm, and a full synonymy of *D. alexandri*. A turreted pneumatophore is unique to *D. alexandri* (Table 3), and the only other rhodaliids with a papillate aurophore are species of the genus *Archangelopsis* (*Archangelopsis typica* Lens & van Riemsdijk, 1908 and *Archangelopsis jagoa* Hissmann *et al.* 1995; Table 3), albeit with a terminal pore only on one central papilla. Like *D. alexandri*, these species inhabit relatively shallow depths on continental shelves. Pugh (1983: p. 285) suggests that papillae may aid the control of gas expulsion at these depths, but the more recent discovery of three shallow-living species with smooth aurophores (Hissmann 2005) indicate that other factors are likely involved. Bigelow (1911) concludes that the number of papillae on the aurophore does not increase with age, as confirmed in the present study. Aurophores of almost all specimens presently examined have c. 30 papillae, either slender or swollen, where swollen papillae are c. 2 mm long with a clearly discernible terminal pore, originally noted, but not illustrated, by Pugh (1983: p. 241).

Internally, the corm of *Dromalia alexandri* is filled with mesogloea penetrated by a sparse system of canals. However, at the anterior end in the nectosomal region of younger specimens, a reduced hypocystic cavity is recognized and makes the corm quite soft (Pugh 1983: p. 251).

Fig. 13. Depth-frequency distribution of ROV and benthic seabed trawl records for *Dromalia alexandri* on the Southern California continental shelf.

as a numerical expression for the operators' uncounted high abundances.

From photographic images generally available to the authors (Fig. 1 and many others), benthic colonies of *Dromalia alexandri* are observed to live on varied substrates including crevices between exposed rocks and along bedding planes, on areas of mixed rock, boulder, pebble and finer grained sediment, flat rocky bedding planes with thin sediment cover, and on deeper water muddy sediment.

More observational work is needed to interpret the high density *Dromalia alexandri* areas, particularly in relation to underwater topography and currents supplying food. It could be that the general population of *D. alexandri* with frequencies of tens to a hundred or more observations occur on the slopes of the basins within the Continental Borderlands, whilst the higher *D. alexandri*

Table 3. Main characters of *Dromalia alexandri* compared with five other rhodaliid genera.

Character	Dromalia	Archangelopsis	Rhodalia	Stephalia	Thermopalia	Tridensa
Max. length × diameter, mm	50 × 52	17 × 10	40 × 60	20 × 24	33 × 18	>13 × 12
Pneumatophore	Turreted	Smooth	Smooth	Typically smooth	Smooth	Smooth
Aurophore	Papillate	Papillate	Smooth	Smooth	Smooth	Smooth
Corm shape	Near spherical	Near spherical	Near spherical	Near spherical	Conical	Near spherical
Hypocystic cavity	In nectosome only or absent	Throughout corm	In nectosome only	In nectosome only	Throughout corm	Throughout corm
No. of nectophores	12–78	10–24	27–80	17–30	11–17	8–18
Siphosomal whorls	<15	Only 1 after preservation	2 whorls	2 (S. corona)	4–7	2 lateral clusters
Cormidial type	Polygastric	Monogastric	Polygastric	Polygastric	Polygastric	Polygastric
Cormidial bases	Swollen	Not swollen	Swollen	Swollen	Not swollen	Not swollen
Cormidial unit production	Continuous	Ceases after 1+ whorls	Ceases after 2–3 whorls	Ceases after 2–3 whorls	Ceases after 7 whorls	Probably ceases
Gonodendra	<3 per unit with 2nd deeply divided	1 per stem	3+, with 1st deeply divided	4+, deeply divided with gz_1, 2nd and 4th cormidia on one branch, gd_1 and 3rd cormidium on other branch	Up to 4, with stems very short	Probably only 2, each with stalk fused to pedicel of gz_1
Gonophores	Female probably from egg pouch	Female from egg pouch (*Archangelopsis jagoa*)	Female from egg pouch	Female from egg pouch	Female from egg pouch	Unknown
Gonopalpons	Present	Present	Present	Present	Absent	Present
Secondary gastrozooids on posterior surface	No	Yes, type 1 gastrozooids	Yes, type 1 gastrozooids probably secondary	Yes, type 1 gastrozooids probably secondary	Probably present	Probably present
Bract attachment	On stalks of gonodendra and main trunk	On base of cormidial stem	On stalks of gonodendra	On stalks of gonodendra	On very short gonodendral stalks	On very short common main trunk

Angelopsis, Arancialia and *Sagamalia* excluded as most characters dissimilar to *Dromalia*. Data sourced from present paper, or derived from Hissmann (2005), Hissmann *et al.* (1995), or Pugh (1983), based on mature specimens.

In older colonies this cavity is occluded and the corm is turgid. Discrete hypocystic cavities and solid siphosomes also occur in species of the genera *Stephalia* and *Rhodalia* (Table 3).

The size range of the preserved specimens of *Dromalia alexandri* examined in this study exceeds that of Pugh's specimens (1983: p. 240) in both maximum corm diameter and anterior–posterior length (Pugh's 'height'), with two exceptions: one smaller colony 14 mm diameter by 12 mm length found in this study (Fig. 2C, Table 2), and a larger live colony 'ca. 100 mm in diameter' found by Pugh (1983). The overall orange pigmentation of live rhodaliid colonies is universal, where known, with a bright colour shown by most species. The size range exhibited by *D. alexandri* in this work is similar to that recorded for *Rhodalia miranda* (Pugh 1983: p. 229), but colonies of other species are mostly smaller (Table 3).

The nectophores of *Dromalia alexandri* are thin-walled sacs with few characters of taxonomic significance. Their radial canals do not follow sinuous curves, as also in most other rhodaliid species (Pugh 1983; Hissmann *et al.* 1995). However, in *Tridensa sulawensis* and *Tridensa rotunda* one or more of the radial canals are s-shaped (Hissmann 2005). Nectophore numbers vary between different rhodaliid species (Table 3).

New observations presented here include the first descriptions and figures of mature cormidial units (from the first and second whorls of a well preserved colony of *Dromalia alexandri*, Figs 7–9) and of a siphosomal horn in the zone of proliferation of a rhodaliid (Fig. 5). Probuds of cormidial units form along the outer edge of the horn, a flange-like projection from the corm surface, which somewhat resembles that described by Dunn & Wagner (2006) for *Nanomia bijuga*. Horns have also been identified in two other physonects: *Bargmannia elongata* (Dunn 2005) and *Agalma elegans* (Dunn & Wagner 2006).

Figured here also are the first full interpretations of both a small preserved *Dromalia alexandri* specimen (only five whorls), and a much larger preserved specimen (with the most cormidial units per whorl yet found in any rhodaliid; Figs 2C and 3), as are the course of the external pedicular canal through the expanded muscular lamella of a mature nectophore (Fig. 6B), a figure of a mature bract and figures of male and female gonophores (Fig. 11A and B). The large number of small cormidial units at the beginning of the first whorl in the specimen shown in Fig. 3 suggest a maximum corm size has been reached, although cormidial units are still being produced. As a result, a back-up of young cormidial units has developed at the beginning of the first whorl.

Dromalia alexandri forms only one type of cormidial unit in the zone of proliferation, with further units produced continuously throughout life. Conversely, cormidial unit production ceases in other rhodaliids before the colony becomes adult so cormidial units immediately below the zone of proliferation are already mature, and the first whorl has no 'young' units. In these species later produced reduced cormidia, including type I gastrozooids, are secondary (Table 3), and pass either directly down the corm in a ventral or other meridional tract to the posterior surface or may move there after formation from labile buds in between the mature cormidial units of the last whorl. Both Pugh (1983) and Hissmann (2005) suggest extra type I gastrozooids are needed to increase feeding efficiency.

The cormidial units of *Dromalia alexandri* observed in this work bear three cormidia with gastrozooids so are designated polygastric. Polygastric units also occur in four other rhodaliid genera (Table 3), whereas in others cormidia are monogastric, as discussed by Hissmann (2005: p. 225). Amongst polygastric rhodaliids, the bases of the cormidial units are swollen in some genera (Table 3). The specimens studied here display three full cormidia per unit (see Terminology above) with bracteal lamellae representing two possible additional cormidia which never completely develop. White buds noted adjacent to bracteal lamellae (Fig. 6A) may give rise to these extra bracts, but further evidence is needed to support this speculation, and some buds are probably resorbed later (Pugh 1983).

The bracts of rhodaliids, where known, are all distinctive (Table 3), and a good external character for distinguishing species (Pugh 1983; Hissmann 2005: p. 243) when present. *Dromalia alexandri* bracts have the most complex structure of any rhodaliid yet mature bracts are scarce because they are caducous. A more mature bract is described and figured here from the present study specimens than found previously by Pugh (1983). Its bracteal canal has distinct proximal and distal main branches and these exhibit many more subdivisions (Fig. 10).

Gonodendra are branched complexes on the siphosome of physonects and cystonects (Mapstone 2009) where gonophores are produced. In rhodaliids gonodendra arise from discrete cormidia, and each typically bears gonopalpons (Table 3) which in *Dromalia alexandri* are orange (Fig. 1). Gonopalpons are thought to void undigested fragments of food from their tips, as in long-stemmed physonects (Mackie & Boag 1963).

The gonodendral branches of *Dromalia alexandri* are short, and each gonodendron bears several elongate gonopalpons and numerous gonophore buds and maturing gonophores (Fig. 8). Such mature gonodendra have not been described previously in this species. Gonophore pedicels are short and the most mature gonophores were always found on the oldest cormidium in cormidial units

with zooids still attached. Large numbers are probably produced by all three gonodendra of each cormidial unit as it progresses around the corm (beyond the first whorl), but probably not all simultaneously, although it is impossible to assess this accurately in the present specimens. Release of gametes from the gonophores still remains unobserved.

The male gonophores of *Dromalia alexandri* are similar in shape to those figured for other rhodaliids by Hissmann (2005). Female gonophores are probably formed in egg pouches in all rhodaliids, as described and figured by Brooks & Conklin (1891) for a specimen from the Galapagos Islands (probably *Stephalia dilata*), with ova passing into separate gonophores when mature (Table 3). A mature female rhodaliid gonophore contains a single ovum enclosed within a network of nutritive spadicine canals (Fig. 11B).

A large number of specimens of *Dromalia alexandri* were either collected by trawl or positively identified from ROVs in Southern Californian waters (Fig. 12), and clearly reflects the relatively shallow depth range occupied by this species, and the research effort in these waters. Off Baja California records are fewer, and there are also unconfirmed reports of *D. alexandri* from the Gulf of California, but it has not been possible to locate the specimens collected from this area to verify their identity. *D. alexandri* may possibly have been muddled with the deeper water *Stephalia dilata* by some observers, especially where their ranges overlap. *S. dilata* is also bright orange in colour, and has been observed from the Galapagos to the Davidson Seamount (Bigelow 1911 as *Angelopsis dilata*, Dunn *et al.* 2005; Burton & Lundsten 2008), but lives below 750 m (Pugh P.R, personal communication) down to 2805 m (Burton & Lundsten 2008) and has a smooth aurophore. Another species recorded from the geographical area inhabited by *Dromalia alexandri* is *Thermopalia taraxaca*, which has also been identified on the Davidson Seamount (Burton & Lundsten 2008). However, this species should be easily distinguished by its paler orange colour and smaller colony size, and occupies a deeper depth range than either *D. alexandri* or *S. dilata*.

The vertical distribution of *Dromalia alexandri* in Southern Californian waters shows two peaks of abundance using the present dataset. These animals are thought to utilize food rolling down the slopes of canyon walls and Borderlands basins (J.C.L., personal communication). The peaks at 400–450 m and 650–700 m (Fig. 13) may reflect varied currents at these depths which are related to diverse underwater topography. Currents might carry the food deeper into canyons than basins, but further investigation of this theory is beyond the scope of the present paper. For *D. alexandri*, a maximum species density of three individuals per m^2 was suggested by Pugh (1983), and this figure is similar to that estimated for *Thermopalia taraxaca* from the Galapagos Rift (Crane & Ballard 1980) and *Archangelopsis jagoa* from the island of Grand Comore in the Indian Ocean (Hissmann *et al.* 1995). However, the MBARI ROV observations indicate that *D. alexandri* may be much more abundant at some sites, perhaps even reaching the 10 individuals per square meter suggested by Hissmann (2005) for *Tridensa sulawensis* off Sulawesi. In Southern Californian waters several environmental issues from human activities extend throughout the Bight, including regional and local changes in benthic and planktonic communities due to nutrient enrichment by waste waters [National Research Council (U.S.) Marine Board, 1990]. An increased food availability at all trophic levels and depths along the shelf, ultimately boosting growth and reproduction of benthic suspension feeders and invertebrate predators, like rhodaliid siphonophores, might result in the observed higher abundance and wider size range of *D. alexandri* specimens. This hypothesis needs validation, with new investigations based on quantitative sampling along transects at decreasing distances from the outfall. Our observations, including the re-description of a poorly known morphology and extension of the phenotypical variability and distributional range of this species, will be of interest not only to hydrozoan taxonomists, but also to the scientific community interested in monitoring eutrophication effects along marine shelf and slope areas.

Conflicts of Interest

None of the authors have any potential conflicts of interest.

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