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A synopsis of the Family Cordagalmatidae fam. nov. (Cnidaria, Siphonophora, Physonectae)

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Abstract

The genus *Cordagalma* is reviewed and a re-description given of one of the extant species, *C. ordinatum* (Haeckel). In addition, four new species are described in the genus *Cordagalma*, namely *C. abyssorum* sp. nov., *C. bimaculatum* sp. nov., *C. isocarrei* sp. nov. and *C. rugosum* sp. nov. All these species have similar larval-type tentilla. A fifth new species, which has extraordinary tentilla, with an involucrum forming two flaps, is placed in a new genus *Cardianecta* gen. nov. as *C. parchelion* sp. nov. The significant differences that all these species have from other physonects is considered to warrant the establishment of the family Cordagalmatidae fam. nov. for them. This family is diagnosed purely on the presence of heart-shaped nectophores budded on the ventral side of the nectosome.

Key words: Siphonophora, Physonects, *Cordagalma*, Morphology, taxonomy

Introduction

In his *Challenger* Monograph, Haeckel (1888b) described and beautifully illustrated a new physonect species under the name *Anthemodes ordinata* (see Figures 1 & 2). As is always the case with Haeckel's detailed and stylised illustrations there has to be doubt concerning their veracity, particularly when dealing with small specimens such as this, which he said reached a length of only 20 cm in its fully extended state. Previously, Haeckel (1869) had established the generic name *Anthemodes* for the species *canariensis*, but in his 1888 Monograph he admitted that that species actually belonged to the genus *Cupulita* Quoy & Gaimard. Nevertheless, he (*ibid.*, p. 229) decided that "The second species, described here as *Anthemodes ordinata* ... may be retained as the true type of this species." Nonetheless, the generic name *Anthemodes* is still pre-occupied even though Haeckel's (1869) species currently is known as *Nanomia bijuga*.

Bedot (1896) and Bigelow (1911), for instance, also retained the species *ordinata* as the sole representative of the genus *Anthemodes*, while Schneider (1898) claimed to have found a small specimen of *A. ordinata* at Naples, although it had largely decayed by the time he examined it. Bigelow (*ibid.*, p. 285) noted that "the bracts are quadrangular, nearly rectangular and very characteristic, and the tentilla have numerous terminal filaments". Nevertheless, the name *A. ordinata* virtually disappeared from the literature for over 50 years before Totton (1965) quite mistakenly considered it as a junior synonym of *N. bijuga*.

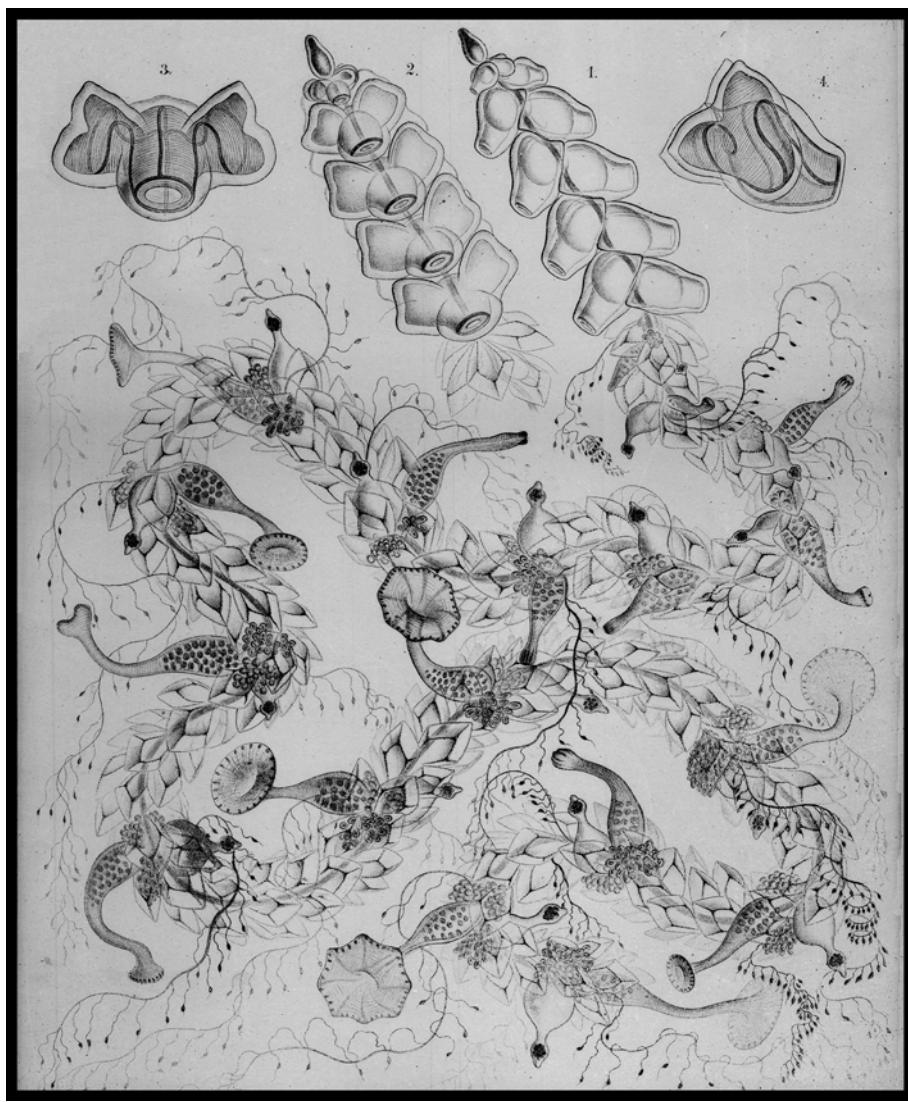


FIGURE 1. *Anthemodes ordinata* Haeckel, 1888. Reproduced from Haeckel (1888, Pl. XIV).

Meanwhile, the genus *Cordagalma* was established by Totton (1932) to encompass the species *C. cordiformis* Totton, 1932, whose description was based on just six poorly preserved nectophores collected off the east coast of Australia during the Great Barrier Reef Expedition (1928–29). Nonetheless, these nectophores, the largest of which measured 2.5 mm in height, had a very distinctive heart-shaped appearance (see Figure 3) that had never been described before. Totton (1954) gave further records for the species, but no further description, and it was another fourteen years before Carré (1968) gave a description of the entire colony of *C. cordiformis*, based on a collection of complete specimens from superficial waters off Villefranche-sur-Mer (western Mediterranean) and, critically, some nectophores and fragments of the siphosome collected in net samples, particularly during the winter, but from unstated depths. Subsequently, Cairns *et al* (1991) changed the specific name to *cordiforme* so as to be in agreement with the neuter form of the generic name but, as will be seen, that change ultimately need not concern us.

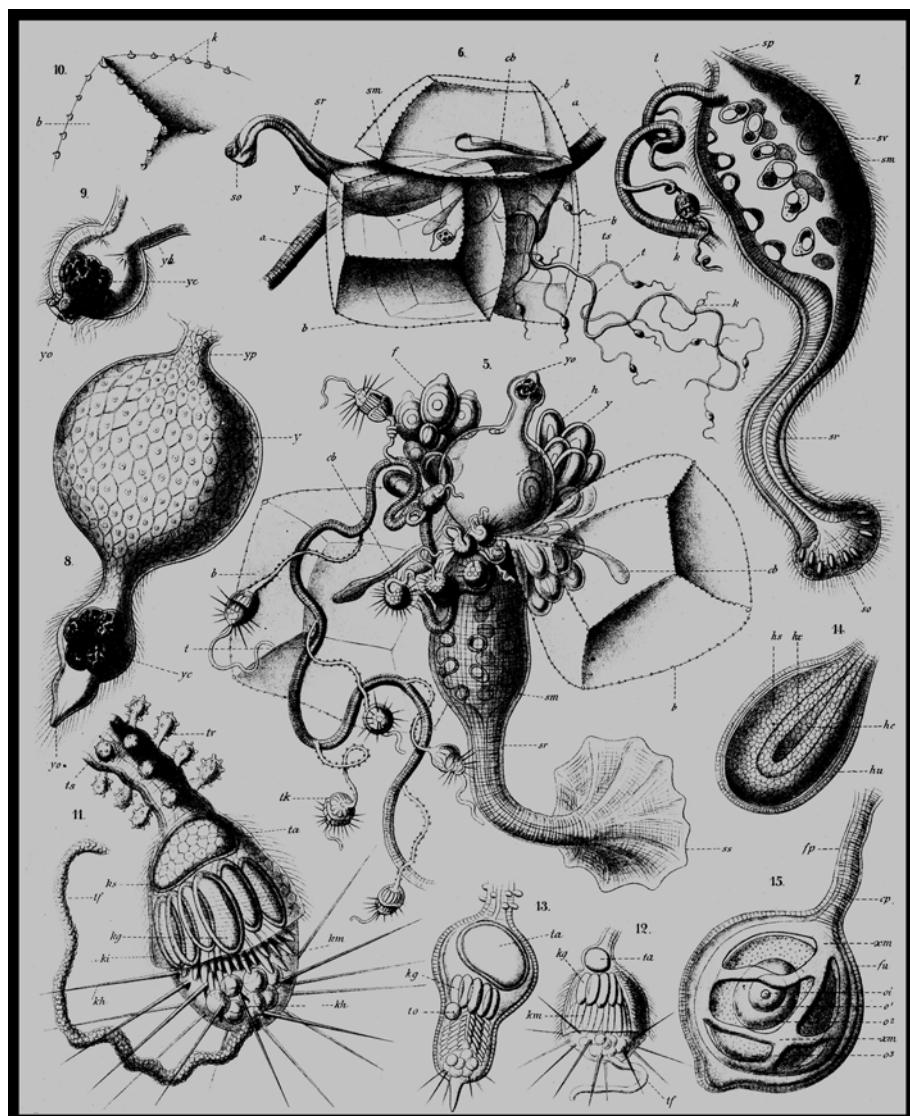


FIGURE 2. *Anthemodes ordinata* Haeckel, 1888. Reproduced from Haeckel (1888, Pl. XV).

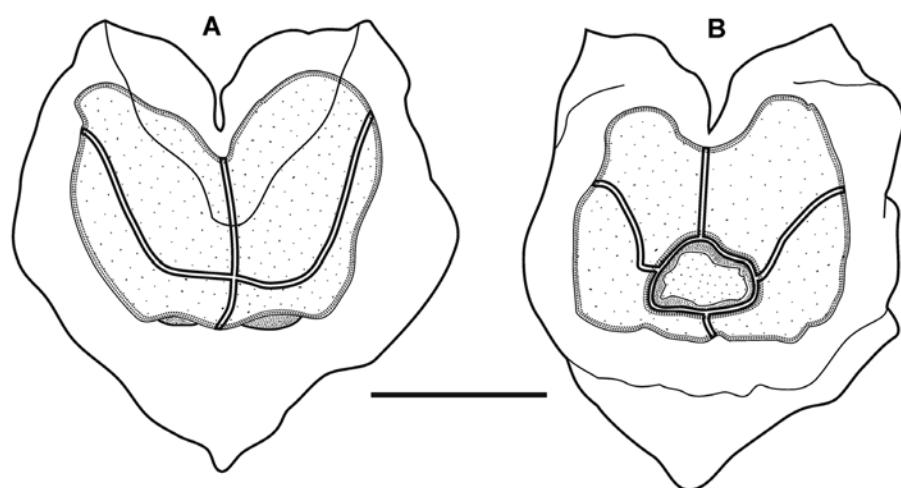


FIGURE 3. *Cordagalma cordiformis* Totton, 1932. A. Axial and B. Ostial views of nectophore. Adapted from Totton (1932) Text fig. 8. Scale bar 0.5 mm.

Although Carré (1968, p. 81) considered that the bracts of *Cordagalma cordiformis* could not be confused with those of any known “Agalmidae”, he did remark that they “proche de celles décrites par Haeckel (1888) chez *Anthemodes ordinata*, espèce énigmatique jamais retrouvée qui, par ailleurs, ne peut être confondue avec *Cordagalma cordiformis*” [resemble those described by Haeckel (1888) under the name *Anthemodes ordinata*, an enigmatic species never found again which, in addition, cannot be confused with *Cordagalma cordiformis*]. Daniel (1985, p. 79) disagreed and remarked “Except for the structure of the nectophores, *C. cordiformis* resembles *Anthemodes ordinata* Haeckel (1888) in all other characters of the siphosome, gastrozooid with its larval type of tentilla and in the characteristic prismatic pyramidal bracts.”

It is a pity that Carré (1968) did not discuss this point further in light of the fact that he also noted some “variabilité” of certain morphological characters, as is discussed below. However, he concluded (*ibid.* pp. 85) that it would be “prématur de conclure l’existence d’autres espèces du genre *Cordagalma*” [premature to conclude that another species of the genus *Cordagalma* exists]. As we shall see Carré was mistaken in coming to that conclusion.

If one compares the descriptions of *Anthemodes ordinata* given by Haeckel (1888b) and of *Cordagalma cordiformis* given by Carré (1968) (see below) it can be seen that the only major differences lie with the nectophores (cf. Figures 1 and 3), while for the siphosomal elements there are many similarities. With regard to the nectophores, Haeckel’s figures (see Figure 1) show a much more complex structure than the very simple heart-shape described by Totton (1932). In addition, Haeckel described the course of the lateral radial canals on the nectosac as having four loops while Totton illustrated only a single upward loop. Although Haeckel appears never to have noted the ubiquitous presence of the ascending mantle canal when describing any of his physonect species, it is somewhat surprising that Carré (1968) made no mention of, despite the brevity of his description, either the ascending or descending mantle canals, although both can be seen clearly in his Plate I, fig. 2.

If there is one obvious thing from Haeckel’s (1888b) *Challenger* Monograph it is that Haeckel had little interest in the structure of physonect nectophores. Leaving apart the rhodaliids, which have simple bag-like nectophores with straight or slightly curved radial canals, the nectophores of the remaining physonect species that Haeckel illustrated are generally inaccurate with regard to both the ridge pattern and the course of the lateral radial canals. There is one notable exception, *Forskalia tholoides* Haeckel, 1888, where Haeckel’s illustrations of nectophores appear to be fairly accurate (see Pugh, 2003); but given that the nectophores of this species have no major ridges, their lateral radial canals are straight, and they are so flattened as to appear almost two-dimensional, then perhaps this is not surprising. This would also apply to the ridge pattern on the nectophores of *Crystallodes vitrea* Haeckel, which currently is known as *Agalma okenii* Eschscholtz, as it is so obvious that it cannot be missed. However, for *Lychnagalma vesicularia* Haeckel = *L. utricularia* (Claus) (see Pugh & Harbison, 1986) both the ridge pattern and the course of the radial canals illustrated by Haeckel (*ibid.* Plate XVI) were inaccurate, and the latter was also the case for his illustrations of *Discolabe quadrigata* Haeckel = *Physophora hydrostatica* Forskål (see Pugh, 2005).

The present author is led to conclude that Haeckel’s (1888b) description and illustration of the nectophores of his *Anthemodes ordinata* were very likely inaccurate. It is possible that he mixed up two different species in his description, but the striking similarities between the siphosomal zooids described by Haeckel and by Carré (1968), for *Cordagalma cordiformis*, as remarked upon by Daniel (1985), leads me to conclude that they belong to one and the same species, which should be called *Cordagalma ordinatum*; a slight change from that suggested by Mills *et al.* (1996) in order to make the ending of the specific name agree with the neuter ending of the generic one.

A second species of *Cordagalma*, *C. tottoni* Margulis, 1993, was described by Margulis (1993) based on three poorly preserved nectophores and fragments of a stem that may or may not have belonged to the same specimen. The one distinguishing feature of the nectophores, which still holds true after the present identification of several new *Cordagalma* species, is that the lateral radial canals arose from the upper radial canal, and not directly from the pedicular canal. The description of *C. tottoni* will be discussed briefly below. Margulis (1993) also reported on the collection of some fragments of specimens that she tentatively ascribed to *Cordagalma cordiformis*. She noted slight differences in the shape of the nectophores and bracts from that previously described and found that the tentilla were without cnidocils. These differences were possibly significant, although the last might only indicate that the tentilla were young or had become stripped of their cnidocils during collection (see below). Margulis raised the question as to whether there were sufficient characters to separate the two forms, but concluded that the differences might only be of subspecific value.

Although *Cordagalma ordinatum* is most commonly found in superficial warm waters, and has frequently

been collected by SCUBA divers in the Sargasso Sea (North Atlantic Ocean), several other specimens of *Cordagalma* species have been collected either by submersibles or ROVs over the past 30 years. All of these appear to belong to new species and some are described herein, together with further notes on *C. ordinatum*.

Family Cordagalmatidae fam. nov.

The basic distinguishing character for all cordagalmatid species is that they possess heart-shaped nectophores, very distinct from those of any other physonect siphonophore. The taxonomic position of the family is discussed below. The species of the family Cordagalmatidae described herein can clearly be divided into two genera, one monotypic, based on the structure of the tentillum, and the presence/absence of a palpacle attached to the palpon. In the genus *Cordagalma* Totton the tentillum is of a so-called larval-type (see below), without a terminal filament bearing nematocysts or an involucrum, and has three types of nematocyst, including stenoteles in the non-spiralled cnidoband. The palpon is palpacleless. For *Cardianecta* gen. nov. the tentillum is a complex structure with an involucrum and, at some stage in its development a spiralled cnidoband. Only one type of nematocyst, probably a mastigophore, was found in the cnidoband, while the terminal process, and particularly the two horn-like appendages protruding from it contained desmonemes. The palpon bore a palpacle, although it tended to become detached from the adult, preserved ones.

The differences between the two genera appear significant, particularly with regard to the tentilla and their completely discrete cnidomes. Thus, as is discussed below, it may well be that the genus *Cardianecta* gen. nov. does not actually belong to the family Cordagalmatidae, but this can only be resolved when genetic studies are made on further material. The genus *Cardianecta* gen. nov. is monotypic for *Cardianecta parchelion* sp. nov. The genus *Cordagalma*, presently, is considered to include two species, *C. ordinatum* (Haeckel) and *C. tottoni* Margulies, 1993. However, for the latter species the only definite taxonomic character that we know is the structure of the nectophore. The tentilla, palpons and bracts described by Margulies in association with these nectophores do not conform with the same structures found in other *Cordagalma* species, but it is far from certain that they actually belong to the same specimen as the nectophores. Thus, although for convenience the species *tottoni* is included in the genus *Cordagalma* below, it must be kept in mind that it may not actually be a cordagalmatid. As well as considering all the aforementioned species, a further four new *Cordagalma* will be described herein.

Genus *Cordagalma* Totton, 1932.

Type species. *Cordagalma ordinatum* (Haeckel, 1888).

Diagnosis. Small colonies that show all the basic characters listed above for the family Cordagalmidae and are particularly distinguished by the presence, on all the tentacles, of tentilla that, as Carré (1968) remarked were devoid of desmonemes and acrophores, characteristically present in the adult terminal filaments of many monoecious physonect siphonophores, such that those of *Cordagalma ordinatum* have come to be called "tentilles de type larvaire" or larval-type tentilla. The palpons do not have a palpacle.

Cordagalma ordinatum (Haeckel, 1888).

Synonymies: For more recent papers only those that describe the species in some way have been included.

Anthemodes ordinata Haeckel, 1888a, p. 40; 1888b, p. 229, Pls. XIV, XV; Bedot, 1896, p. 409; Chun, 1897, p. 104; Schneider, 1898, p.117; Delage & Herouard, 1901, p. 225, fig. 381; Stepanjants, 1967, p. 89.

Cordagalma cordiformis Totton, 1932, p. 325, figs. 8–9; 1954, p. 69; 1965, p. 61, fig. 25; Totton & Fraser, 1955, p. 3, fig. 10; Carré, C., 1968, p. 79, Pls. 1–3 [in partim] [non Pl. II, figs. 1?, 2, ?3; Pl. III, figs. 1, 4, 7]; Carré, D., 1973, p. 113, fig. 1, Pls. 1–2; Palma, 1973, p. 27, Pl. II; Daniel, 1974, p. 49, fig. 3, K–N; 1985, p. 77, fig. 17; Stepanjants, 1977, p. 60, pl. 3a,b; Carré & Carré, 1980; p. 115, fig. 13; 1995, p. 565, figs. 171C, 175B, 181A, 188, 190; Casanova, 1980, p.21; Purcell, 1984, p. 319, fig. 4g, h, I; Mackie, 1985, p. 753; Gili, 1986, p. 268, fig. 4.49b, 4.63j,o; Mackie, Pugh & Purcell 1987, fig. 47; Pagès, 1991, p. 311, fig. 8.8; Pagès & Gili, 1992, p. 72, fig. 7; ? Margulies, 1993, p. 17, Pl. 2a–g; Kitamura, 1997, p. 20, fig. 11; Pugh, 1999, p. 481, figs. 3.9, 3.24; Zhang, 2005, p. 22, fig. 7; Bouillon *et al.*, 2006, p. 443, fig. 208A–B; Pugh, 2006b, p. 33.

Cordagalma cordiforme Cairns et al., 1991, p. 33; 2002, p. 29; Pugh, 1999, p. 481, fig. 3.9 [non fig. 3.24]; Dunn, 2005, p. 33; Dunn et al., 2005, p. 924, figs. 5–8; Cartwright et al., 2008, p. 4; Cartwright & Nawrocki, 2010, p. 463; *Cordagalma ordinata* Mills et al., 1996, p. 154; Bouillon et al., 2004, p. 211, fig. 211A,B; Pugh, 2006b, p. 33; non *Cordagalma cordiformis* Mackie, 1985, p. 753. non *Cordagalma ordinatum* Mapstone, 2009, p. 109, fig. 22a,b,d. ? *Cordagalma cordiformis* Araujo, 2006, p. 76, pl. 8, fig. 6 (non fig. 6.3). ? *Cordagalma ordinata* Araujo, 2012, p. 69.

Diagnosis. Small nectophores with relatively short and narrow basal process. Shallow apical indentation between axial wings; nectosac, in ostial view square, with rounded corners. No distinctive patches of large, darkly staining, ectodermal cells on the main body of the nectophore, but small patches, usually 3 pairs, on the lower lateral sides of the velum of the ostium. Bracts rhomboidal with weakly defined truncated upper surface. Transverse and median ridges bearing nematocysts. Bracteal canal extending onto upper side of bract proximally, and then running along the lower side to the mid-length of the bract, ending in a small swelling inflected into the mesogloea. Palpacleless palpons attached by their bases. Tentilla with terminal rostrum.

Material examined. All specimens were collected by SCUBA divers at superficial depths. BWP stands for "Blue Water Plankton" and the following numbers represent a unique dive number, according to a system used during early diving cruises out of WHOI. "OC" stands for the WHOI research vessel *Oceanus* together with its cruise number.

BWP 447		No station data available
BWP 544-8		No station data available
BWP 567-15		No station data available
BWP 752-14		No station data available
BWP 781-18	21-Jun-1979	31° 45'N, 71° 49'W
BWP 812-13	13-Jul-1979	38° 57'N, 64° 35'W
BWP 816-6	15-Jul-1979	40° 14'N, 68° 07'W
BWP 1070-7	26-Jul-1983	08° 37.3'N, 40° 22.4'W
BWP 1886-19		No station data available
OC368-22-16	12-Jul- 2001	37°59'N, 72°58.9'W
OC368-25-1	13-Jul-2001	37° 57'N, 73° 56'W
OC368-25-8	13-Jul-2001	37° 57'N, 73° 56'W
OC368-25-19A	13-Jul-2001	37° 57'N, 73° 56'W
OC368-26-9	13-Jul-2001	37° 54'N, 73° 00'W
OC368-32-13	15-Jul-2001	39° 33'N, 71° 30'W
OC370-6-6	20-Sep-2001	38° 41.83'N, 72° 54.48'W

In addition, a poorly preserved specimen collected at Villefranche-sur-Mer by Mr A.K. Totton on an unspecified date was briefly examined.

Description. *Pneumatophore:* The minute pneumatophore (Figure 4) measured c. 0.3 mm in length and 0.12 mm in diameter. There was no notable pigmentation on the preserved specimens, but Carré (1968) said it was lightly pigmented apically, although no colour was mentioned.

Nectosome. The nectophores were budded off on the ventral side of the nectosome and the maximum number found with any of the preserved specimens was 16. Carré (1968), however, noted the presence of up to 40 nectophores on the nectosome of some of his specimens, but we cannot be sure that he was referring to this species (see *Remarks* section below).

Nectophore: The preserved nectophores measured up to 3.5 mm in length and 3.25 mm in width. However, although individual specimens tended to have fairly uniformly sized nectophores their mean size varied. Thus, the *Oceanus* 368 Dive 25-1 specimen had smaller nectophores, averaging 2.32 mm in length and 1.92 mm in width; while the BWP 544-8 specimen had larger nectophores averaging 3.37 mm in length and 3.02 mm in width. Another feature was that the younger nectophores tended to be broader than long, but as they grew they increased more in length than in width. Carré (1968) stated that his nectophores measured up to 7 mm in length and 6 mm in width; the implications of which again are discussed in the *Remarks* section below.

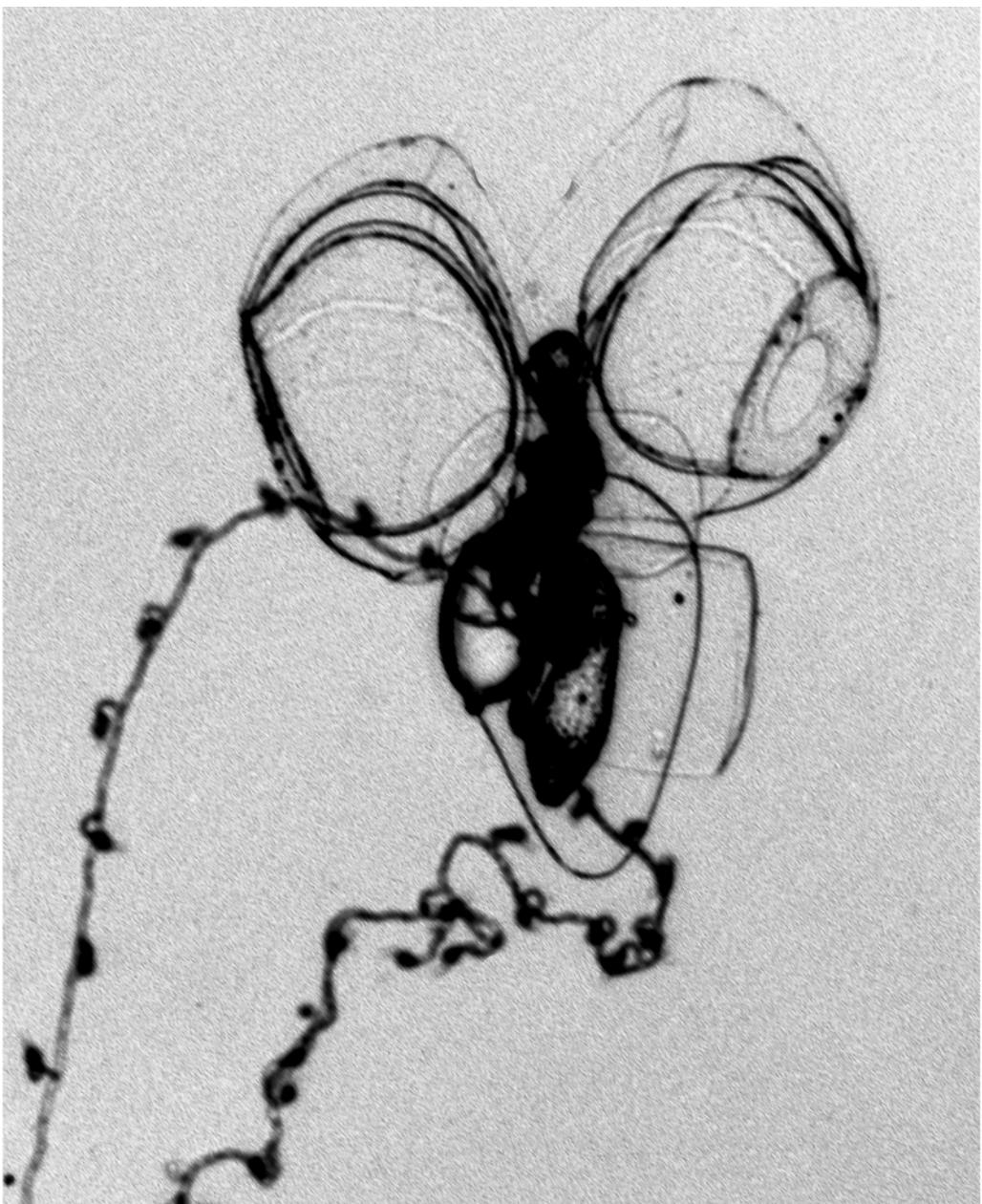


FIGURE 4. *Cordagalma ordinatum*. Young colony with larval bract. Note apparent pigment patches on the velum of the nectophore. (© C. Carré)

The hydroecium was wide on the main body of nectophore, but narrowed toward the basal process and petered out about halfway down the latter. No patches of distinctive large ectodermal cells or any sign of pigmentation were seen on the main body of the nectophore. In his notes, Claude Carré recorded the presence of spots of pigmentation on the nectophores, although he made no mention of them in his publication. Where these spots were located was also not made clear.

The nectosac was relatively small and did not extend basally, in the mid-line; with broad, shallow apical median indentation. Long ascending and descending mantle canals of approximately equal length. On the nectosac, the pedicular canal gave rise to all four radial canals. The dorsal and ventral canals ran straight to the ostial ring canal. The lateral canals, as is characteristic of cordagalmatid species, looped up and over onto the sides of the nectosac, then looped downwards, before running to the ostial ring canal (Figure 5). Typically there were three pairs of patches, made up of a few large ectodermal cells, on either side of the ostial velum at the level of, and below, the points of insertion of the lateral radial canals onto the ostial ring canal (Figure 5A,C). Occasionally there were four pairs of patches, but often they had been abraded. Also, a patch of cells, sometimes divided into two or more, was

frequently found on the velum below the point of insertion of the upper radial canal (Figure 5A). Whether these patches of cells, which are probably sites of bioluminescence, also were pigmented in life is not recorded. In addition, there was a small, discrete patch of small cells lying over the end of each lateral radial canal but, unlike the lateral ostial processes found on the nectophores of other physonects these patches did not connect to the ostium itself.

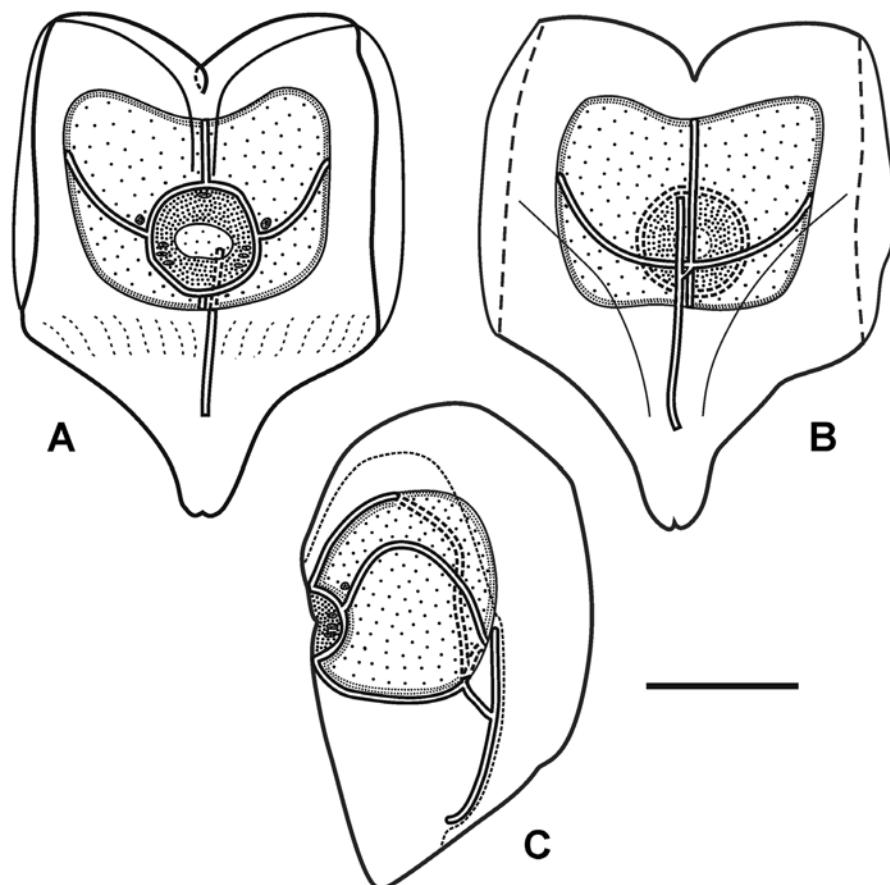


FIGURE 5. *Cordagalma ordinatum* nectophores from BWP567-15 specimen. Ostial (A), axial (B), and lateral (C) views. Scale bar 1 mm.

The young nectophore (Figure 6) had a short rounded basal process. The axial wings were very small and only a very shallow emargination separated them. There was a pair of marked ridges that formed the outer margins of the overhanging hydrocial flaps. They ran from the outer margins of the axial wings towards the mid-line and then down to the level of the distal end of the descending mantle canal. In that region there was a broad, but shallow trough between them. Slightly lateral to these ridges there was a row, or two, of nematocysts that ran from the axial wings to about half the height of the nectophore. Further rows of nematocysts were found on the ostial side of the nectophore, but these were not associated with distinct ridges. No lateral patches of cells could be discerned on the velum of the nectosac, but there usually was one on its upper side.

Siphosome: Haeckel (1888b) and Carré (1968) both noted that several hundred cormidia could be found on a single specimen, and that each cormidium consisted of, from posterior to anterior, a gastrozooid, a palpon without palpacle, a bunch of male, a bunch of female gonophores, and 6–8 bracts, which budded from the bases of the other zooids. However, the latter author also found that for some of his specimens the gonophores of individual cormidia were of only one sex, although both sexes were present on the whole colony. Presently it is not possible to clarify without doubt whether this is a specific character or, perhaps, whether it suggests that the specimens are protandrous or protogynous.

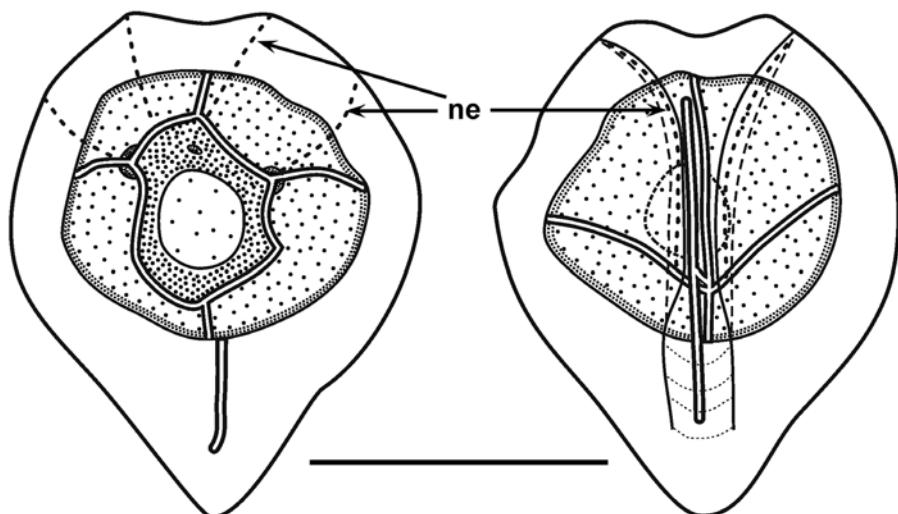


FIGURE 6. Young nectophore of *Cordagalma ordinatum* specimen from BWP Dive 752-14. Ostial (left) and axial (right) views. ne, rows of nematocysts. Scale bar 0.5 mm.

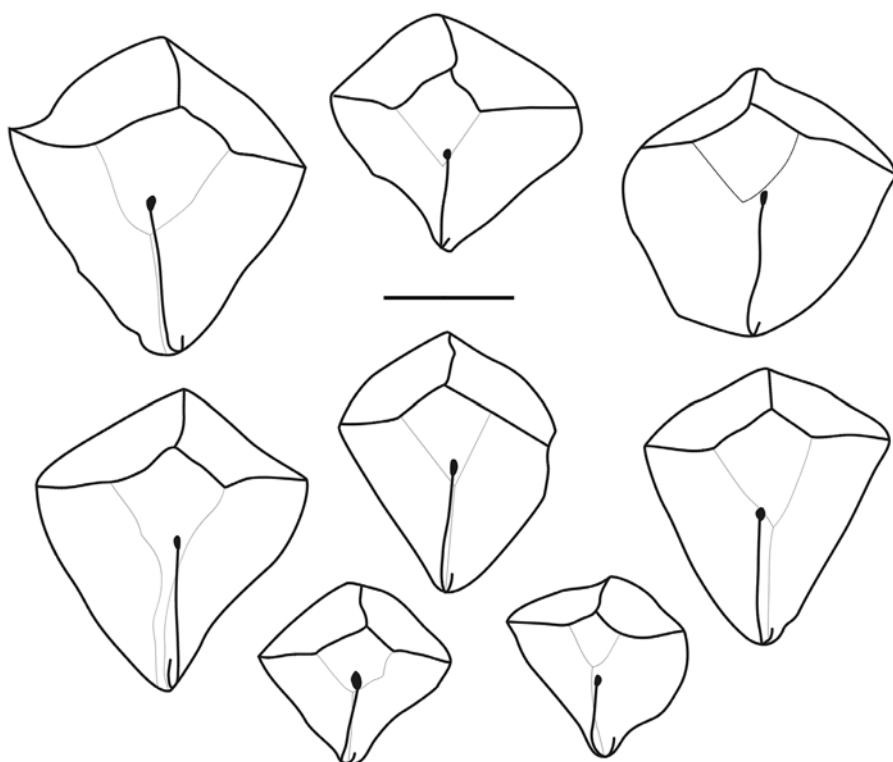


FIGURE 7. Upper views of bracts of *Cordagalma ordinatum* from BWP 544-8 specimen. Proximal at the bottom. (Nematocysts not shown). Scale bar 0.5 mm.

Bracts: For the present specimens the preserved bracts (Figures 7–9) measured up to c. 1.25 mm in length and 1.125 mm in width. They were roughly rhomboidal in shape, but the truncated part of the upper surface was only weakly defined. There was a pronounced transverse ridge and a median one that divided the distal facet into two. No patches of ectodermal cells were found on these facets. The canal extended onto the upper side of the bract and curved over its proximal end to run, in the mid-line, along its lower side. It ran to about the mid-length of the bract where it ended in a small swelling inflected into the mesogloea. This inflection was more pronounced in the younger bracts (Figure 8).

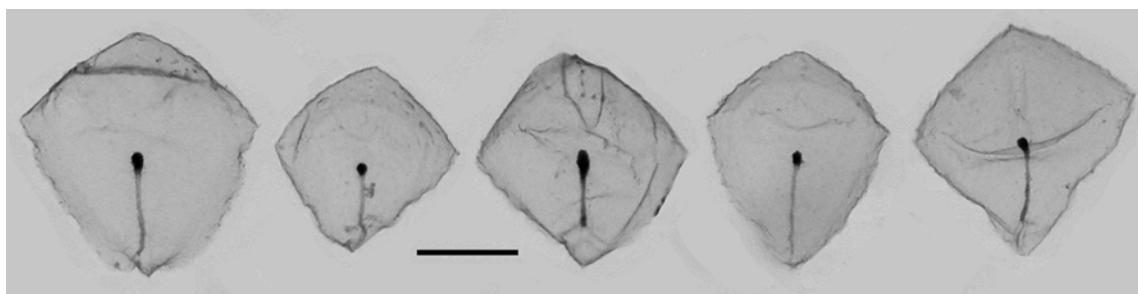


FIGURE 8. *Cordagalma ordinatum*. Upper view of young bracts. Proximal at the bottom. Scale bar 0.25 mm.

Carré (1968, p. 81) described the bracts as having "la form d'une pyramide tronquée assez régulière, avec quatre faces latérales et des crêtes garnies de petit nématocytes" [the form of a quite regularly truncated pyramid with four lateral facets and its ridges garnished with nematocysts]. The nematocysts were scattered along the transverse and median ridges (Figures 5–6) but more often than not they had been abraded. They were not investigated in detail for the present study, but Carré (1968) identified those on the "distal ridge" as being small stenoteles measuring 8.5 x 7.5 µm, while on the other ridges they were probably atrichous isorhizas. Although Carré's description of the bracts clearly indicates them as belonging to *Cordagalma ordinatum*, care must be taken when identifying the bracts from his photographs as those shown in his Plate II, fig. 2 and Plate III, figure 1 certainly do not belong to that species, although those in Plate III, fig. 5 might. (For further discussion see *Remarks* section).

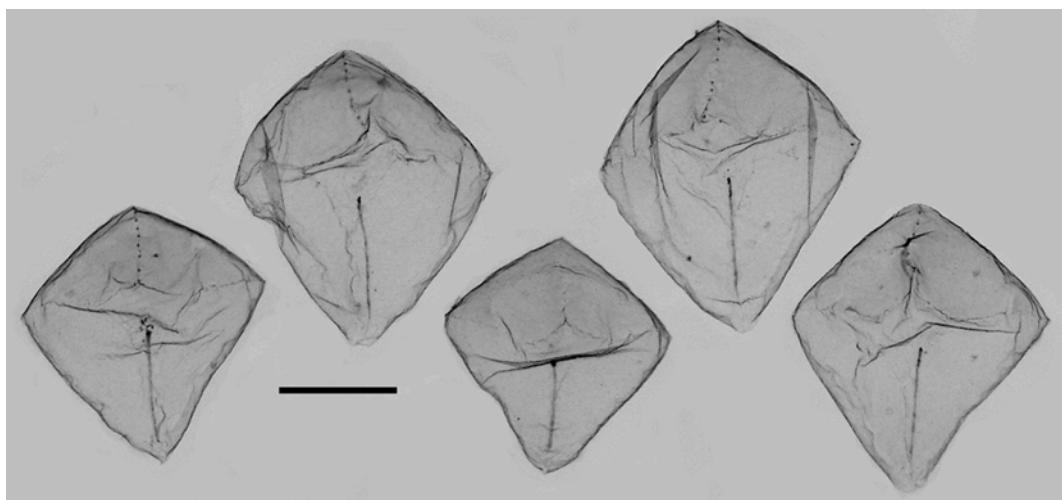


FIGURE 9. *Cordagalma ordinatum*. Upper views of mature bracts. Proximal at the bottom. Scale bar 0.5 mm.

Larval bract: No larval bracts were found with the present specimens examined, but Carré (1973), who followed the development of *Cordagalma ordinatum*, showed that a simple, almost circular caducous larval bract was developed before the nectophores appeared, but she gave no details about it, including its size. It appears that it is retained until at least the first pair of nectophores has been developed (see Figure 4).

Gastrozoid: The siphosome of the preserved specimens frequently broke into fragments consisting of a gastrozoid, a palpon, and one or two gonodendra (Figure 10), with or without bracts. The unpreserved gastrozooids (Figure 10D, gz) typically measured c. 2 mm in length and were connected to stem by a short peduncle. They were transparent and colourless except, according to Carré (1968), for two orange-red spots at their bases but these were not apparent on the current photographs. The distal proboscis section was quite long as shown by the length of the narrowed gastrovascular cavity. Hepatic stripes were present in the slightly expanded stomach region; while the basigaster was very small. After preservation (Figure 10A–C) the gastrozooids became opaque. They usually featured a pronounced proboscis region, occupying approximately a third of the total length, a slightly expanded stomach that was separated from the now very distinctive basigaster by a constriction, from one side of which the tentacle arose.

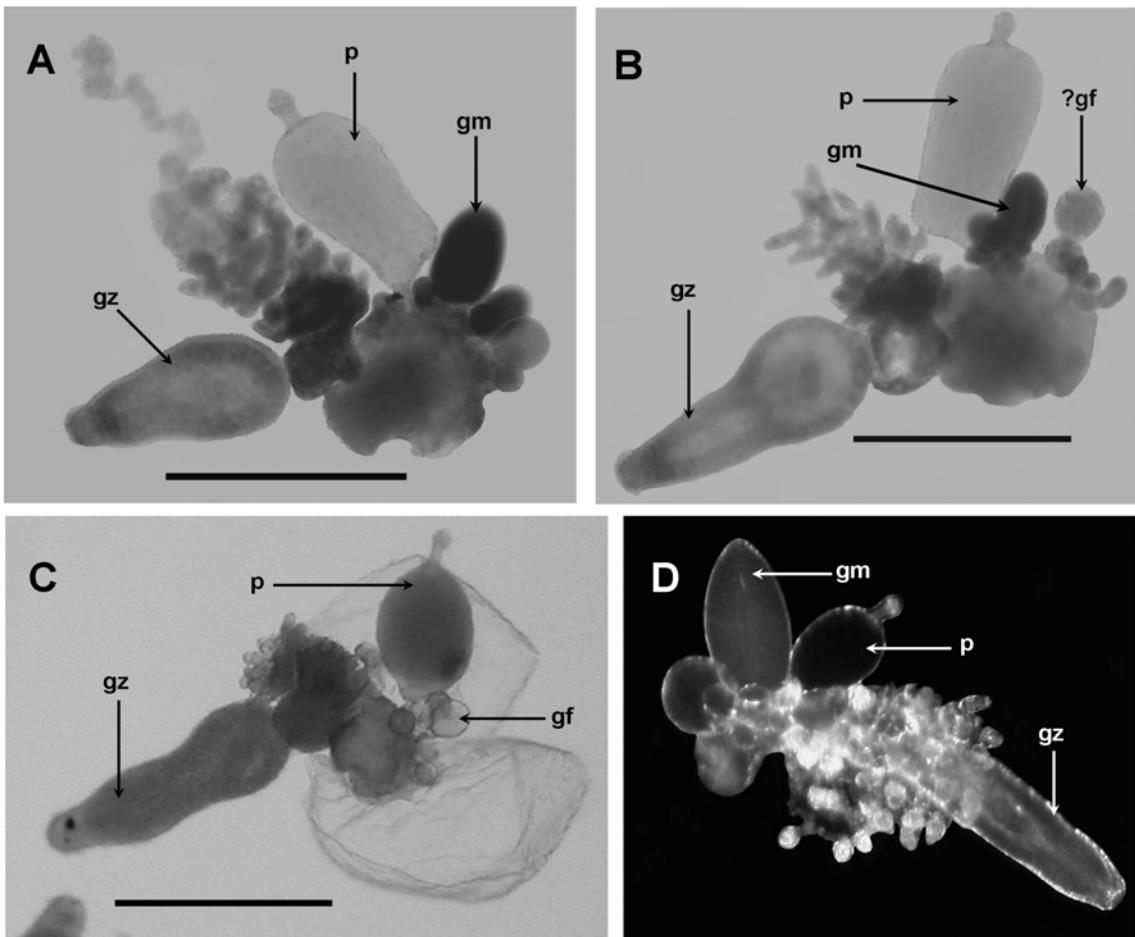


FIGURE 10. *Cordagalma ordinatum*. Detached and preserved cormidia showing: A–B. offset proximal attachment of palpons. C. proximal attachment of palpon from BWP 544-8. D. unpreserved cormidial group from *Oceanus* Dive 6-6 specimen © Casey Dunn. Arbitrary orientations. gf. and gm. female and male gonophores, respectively; gz. gastrozooid; p. palpon.

Tentilla: The tentacles could extend to considerable lengths and Carré (1968) recorded up to 100 tentilla on each, but such was impossible to gauge from the present fragmented preserved material. Each tentillum, when uncontracted, had a thin pedicle, but this was always highly contracted in the preserved ones (Figure 11A). The cnidoband formed an ovoid structure that contained three types of nematocyst. Proximally there was an incomplete ring of five large stenoteles that were somewhat variable in size. Carré's measured $15.5 \times 8.5 \mu\text{m}$, while larger ones, which measured $20 \mu\text{m}$ in length and $10 \mu\text{m}$ in diameter, were found with the present material. In the central part of the tentillum there were numerous anisorhizas ($16 \times 2 \mu\text{m}$), and a few isorhizas, possibly holotrichous, measuring $5.5 \times 5 \mu\text{m}$.

Strangely, Carré (1968) did not describe the distal part of the tentillum that consisted of several very long cnidocils stretching out in 2π directions, nor the character that, as will be shown, sets *Cordagalma ordinatum* apart from all other cordagalmatids, the "rostre" or rostrum. In our preserved specimens the "rostre" tended to be contracted and difficult to see (Figure 11A), although occasionally it was easily distinguished (Figure 11B). No nematocysts were present on the rostrum. The cnidocils also appeared much shrunken and distorted (Figure 11A). These cnidocils are presumed to be part of the isorhizas of the cnidoband, although this has not been confirmed. Carré's photograph (1968, Plate III, figure 6) clearly shows all the features mentioned above but, unfortunately, it was not one of the ones he sent to me.

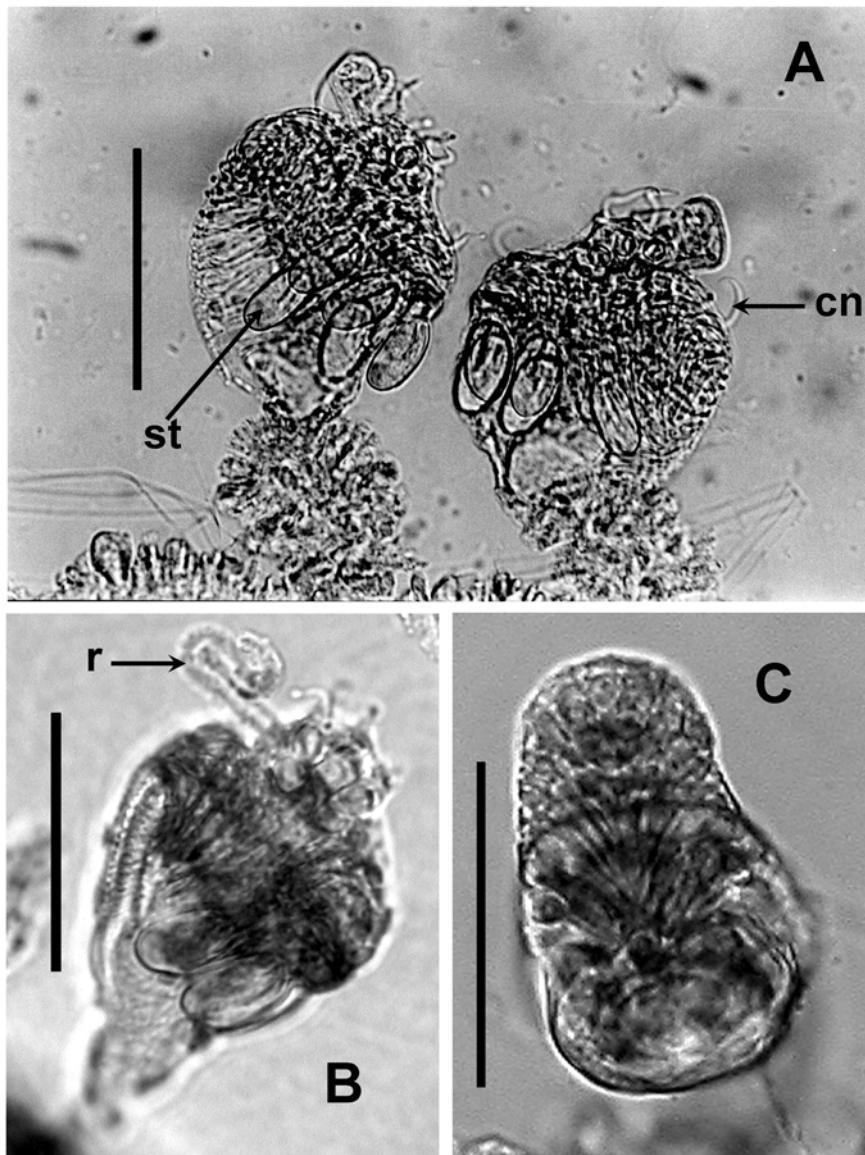


FIGURE 11. *Cordagalma ordinatum*. Mature tentillum showing **A**. large stenotele nematocysts; **B**. the "rostrum"; and **C**. Developing tentillum, without rostrum or cnidocils. cn. cnidocil; r. rostrum; st. stenotele. Proximal at bottom. Scale bars 50 µm. **A.** © Claude Carré; **B** and **C** tentilla from BWP1886-19 specimen.

Palpon: The fully developed palpons were c. 1 mm in length (Figure 10). In life they consisted of a long pedicle (see Carré, 1968, Plate II, figure 4; but not Plate III, figure 4), a globular stomach region and a short narrow distal proboscis (Figure 10D). The pedicle was inserted into the base of the stomach region so that its attachment was proximal. This arrangement could remain unaltered on preservation (Figure 10C), but more often than not considerable changes in form occurred. The stomach region becomes more elongate and cylindrical but, in particular, the pedicle contracts in such a way that it appears to be attached to one side at the base of the stomach region (Figure 10A, B). This, possibly, refers to the intermediate attachment position that Carré referred to (see below). There was never any sign of the attachment of a palpacle.

Gonophores: The gonophores were extremely small and, although it was possible to distinguish the male ones (see Figure 10), it was extremely difficult positively to identify the female ones. It is thought, by its structure, that the one shown in Figure 10B is female, but only based on the very broad anastomosing radial canals that were present. No gonophores of the sort illustrated by Carré (1968, Plate III, figs. 2 & 3) were ever observed, nor did Carré mention the presence of anastomosing radial canals.

Remarks. Although, as noted above, the nectophores of *Anthemodes ordinata* described and illustrated by

Haeckel (1888b) bear no resemblance to those of *Cordagalma ordinatum*, once a whole specimen had been, albeit briefly, described by Carré (1968), it was possible to note that their descriptions of the siphosomal elements bore close similarities.

It is not necessary to detail exhaustively these similarities here but both Haeckel and Carré noted the simplicity of each cormidium, with its gastrozooid, with a tentacle, a palpon, cyston or dactylozooid without palpacle, a male and a female gonodendron and a number of bracts. Such similarities can also be found in their descriptions of the bracts, and the presence of nematocysts on the margins of the facets; the types and distribution of nematocyst on the tentillum, and the presence of a rostrum, belatedly mentioned by Carré, and mistakenly referred to by Haeckel as a terminal filament despite the fact it bore no nematocysts.

Despite the brevity of Carré's (1968) description there are six brief paragraphs, under the heading "Variabilité" that are of great importance. Apart from some variations in pigmentation that may only be resolved by examining living material, the most important variations in characters were:

- a) In some specimens the pedicle of the palpon was attached laterally, instead of the more usual basal positioning, with some being intermediate between the two;
- b) in some specimens a terminal "rostrum" on the tentillum was absent; and
- c) in some specimens the individual cormidia included gonophores of only one sex, whereas in others gonophores of both sexes were included.

Carré (1968) considered that it would be premature to consider that these novel characters were of sufficient importance to warrant the designation of a new species mainly, it appears from his notes, because he was unable to be sure that the three characters together formed two distinct groupings.

Having looked at more recently collected specimens of *Cordagalma ordinatum*, I conclude that the first two of these characters do, in fact, form two distinct groups, and that they provide sufficient evidence to divide Carré's specimens into two different species. *C. ordinatum* has palpons that are attached by their bases to the stem, although there are some differences between the living and preserved material (see above). In addition their tentilla have a terminal "rostre". Thus, it seems that the lateral attachment of the palpons and the absence of a "rostre" on the tentillum are sufficient to distinguish a different species. Fortunately, specimens with very much the same characters, allowing for differences between Carré's fresh and our preserved material, have been collected in Monterey Bay, California and are described herein under the name *C. isocarrei sp. nov.* Comparisons will be made between that material and some unpublished pictures to which Claude Carré has kindly given me access.

Thus, one must be very careful when using any of Carré's (1968) description, and particularly his photographs, for identifying *Cordagalma ordinatum*. For instance, although the figures on Plate I probably all refer to *C. ordinatum*, at least two, and probably three, of those on Plate II refer to the new species.

Distribution. While Haeckel's (1888b) original specimen came from the Canary Islands that of Totton (1932) came from the Great Barrier Reef. The species has clearly been found in the superficial waters of the Western Mediterranean (e.g. Carré, 1968; Dallot *et al.*, 1988; Gili *et al.*, 1987) while there are no records for any *Cordagalma* in the eastern Mediterranean. However, *C. isocarrei sp. nov.* also occurs in the western Mediterranean, probably at quite shallow depths, based on the records from Monterey Bay, and a third species has been found in the Alborán Sea, which Mills *et al.* (1996) mistakenly referred to as *Cordagalma ordinata*.

Cordagalma ordinatum has frequently been found in the Sargasso Sea (N.W. Atlantic Ocean) (personal information). However, with so many new species herein described, it is difficult to be certain that the relatively sparse number of records for a *Cordagalma* species definitely refer to *C. ordinatum*. It appears to be a species that lives in superficial warmer waters, at least in the Atlantic Ocean, although its presence in other Oceans remains to be confirmed, with certainty. The record of Pagès *et al.* (2006) from Oceanographer Canyon, off Woods Hole in the North Atlantic might be dubious, although it was collected at the surface, while records from warmer waters (e.g. Biggs, 1977; Purcell, 1981; Dunn, 2005), including the Gulf of Mexico (Burke, 1975; Gasca, 1993) are likely to be of *C. ordinatum*. The only deep record for a *Cordagalma* species comes from Casanova (1980) from the 500–700m depth range near Great Meteor Bank (c. 30°N, 30°W). This might indicate that there was either surface leakage into the net, or that the species was not *C. ordinatum*.

In the South Atlantic potentially *Cordagalma ordinatum* has only been recorded in the Benguela current system off South Africa (Pagès & Gili, 1992). There are only occasional records for the species in the Indian Ocean and the Red Sea (e.g. Totton, 1954; Daniel, 1985), while in the south Pacific Ocean, it has been collected from the Great Barrier Reef, of Australia, by Totton (1932) and Russell & Colman (1935), in eastern and central regions

(Stepanjants, 1967; Margulis 1993), and in the eastern region, off Chile (e.g. Palma, 1973). In the northwest Pacific it has been collected in Japanese (Kitamura *et al.*, 2003) and Chinese (Zhang, 2005) waters.

In the northeast Pacific the only records for *Cordagalma ordinatum* appear to come from the colder waters of British Columbia, Canada (e.g. Mackie, 1985). However, the extensive studies, using ROVs and SCUBA diving, by Dr. S.H.D. Haddock and colleagues in the Monterey Bay region, northern California, have not revealed the presence of *C. ordinatum*, although several other *Cordagalma* species are present there, as described herein. It is, therefore, suspected that the records from British Columbia refer to one of the new species described below. Certainly Mapstone (2009, Fig. 14B) does not belong to *C. ordinatum* as the tentillum has no rostrum; the structure referred to as a rostrum actually represents the distal nematocysts, with their long cnidocils. Similarly, the nectophore and bract shown in her Fig. 22A, B, D actually belong to one of the new *Cordagalma* species described herein, as they were apparently drawn from one of my specimens of that species.

There are also a few other records for *Cordagalma ordinatum* that probably refer to new *Cordagalma* species. For instance, Pagès *et al.* (1996) recorded the presence of some specimens of *C. cordiformis* in Hardangerfjord, Norway and, similarly, Hosia & Båmstedt (2007) collected 27 specimens of what they called *C. ordinata* in the Korsfjord, Norway, using nets fished from close to the bottom (c. 600m) to the surface; and a single specimen in Fanafjord (0–150m). Since no specimens of *C. ordinatum* appear to have been collected in the northeast Atlantic Ocean at latitudes greater than that of the Straits of Gibraltar, it is felt that the Norwegian specimens most probably belong to a new *Cordagalma* species. Unfortunately, like those of *Sphaeronectes* sp. (see Pugh, 2009), these specimens were not retained by the authors and so their identification cannot be confirmed.

Cordagalma tottoni Margulis, 1993.

Diagnosis. Small, typically heart-shaped nectophores. Pedicular canal, on reaching nectosac, gives rise to only upper and lower radial canals. Lateral canals arise from the upper canal.

Remarks. The original description of *Cordagalma tottoni* was based on fragments of a single specimen collected, using a Juday net in the 100–0m depth zone, by the Research Vessel *Vozrozhdenia* on 18th December 1986 at 35°S 139°W, in the middle of the South Pacific Ocean. The material was said to consist of a stem, with pneumatophore and various buds, three nectophores, two gastrozooids, and several siphosomal fragments. The type specimen has been re-examined by the present author.

A problem with Margulis' (1993) description of the nectophores is that she had orientated them upside-down, such that she considered the conical lower part of the nectophore to be anterior. This apart, the only real distinguishing feature of the nectophores, the largest of which measured 3.5 mm in height and 2.5 mm in width, was that the pedicular canal, on reaching the nectosac, gave rise to only the upper and lower radial canals (Figure 12). The lateral radial canals then arose from the upper (ventral according to Margulis) canal. This, with some difficulty, was confirmed by the present author and, thus, is in contrast to the arrangement in all other *Cordagalma* species herein described where all the radial canals arise together from the pedicular canal.

It is far from certain that the siphosomal zooids described by Margulis (1993) actually belong to the same specimen as the detached nectophores. Some of the palpons were said to have palpacles (Figure 12) while others did not. This suggests their presence and subsequent loss, which would be in marked contrast to the arrangement in other *Cordagalma* species, but is in accord with that found for *Cardianecta parchelion* gen. nov., sp. nov. described below. However, the re-examination showed that the palpons, which were attached at their bases, appeared not to possess palpacles. The loose gastrozooids had the proximal part of the tentacles attached, which bore, presumably, young tentilla with long pedicles and oval cnidobands, with a beak-shaped tip. There was said to be a single row of larger nematocysts on either side of the cnidoband, enclosing numerous smaller ones. No further details could be added. These are quite unlike the tentilla of *C. ordinatum* that Margulis (1993, Figure 2E) figured but, again, those of *Cardianecta parchelion* gen. nov., sp. nov. are very different. The bracts of *C. tottoni* also were markedly different in having a transverse ridge demarcating a triangular distal facet on the upper side, and with a bracteal canal that was said to end below the middle of a strip of nematocysts running proximally from the distal tip of the bract. Finally, Margulis described the gonophores as being immature but, on re-examination, the sex of some could be determined and they all appeared to be female. It is, however, doubtful that this observation has any significance.

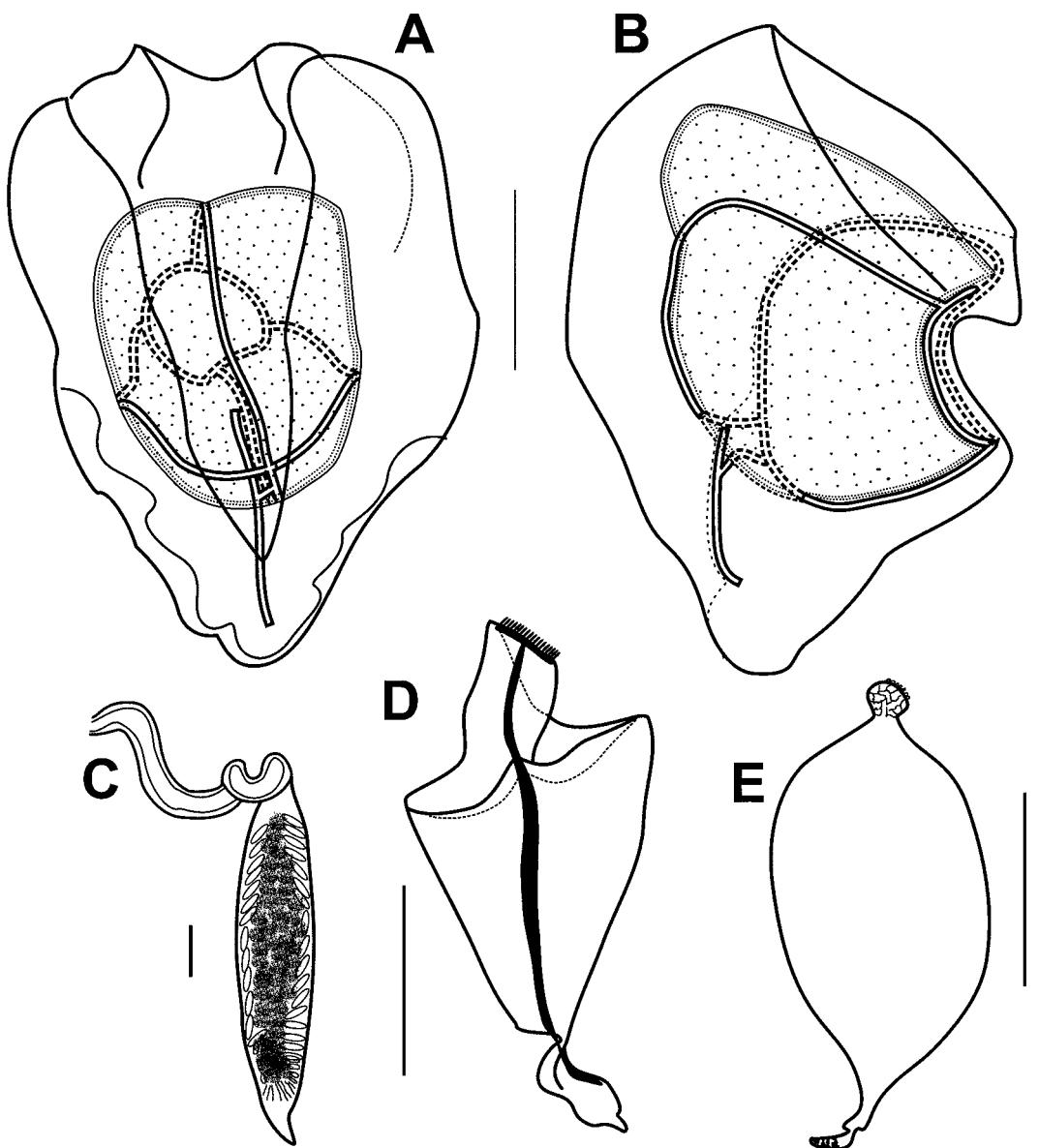


FIGURE 12. *Cordagalma tottoni* Margulis 1993. A. & B. Axial and lateral view, respectively, of a nectophore, scale bar 1 mm; C. a tentillum (proximal at top), scale bar 0.1 mm; D. bract & E. palpon (proximal at bottom), scale bars 1 mm. Redrawn from Margulis (1993).

Thus, until a complete specimen of *Cordagalma tottoni* is collected it is impossible to know if the siphosomal zooids described by Margulis (1993) actually belong with the nectophores. Nonetheless, the fact, since confirmed by the present author, that the lateral radial canals on the nectosac arise from the upper canal is a distinguishing feature setting this species apart from all other *Cordagalma* species.

Distribution. Known only from a single specimen collected in superficial waters in the central South Pacific Ocean (c, 35°S 139°W).

Etymology. Named for Arthur Knyvett Totton whose *Synopsis of the Siphonophora*, published in 1965, remains the most important work on siphonophores published to date.

Cordagalma abyssorum sp. nov.

Diagnosis. Nectophores with short, either rounded or truncated, basal process; without any pigmentation or lateral ectodermal process or cell patches on the velum of the ostium.

Bracts kite-shaped with a V-shaped transverse ridge and a weak median ridge dividing the distal end into two facets. No patches of ectodermal cells. Palpons attached at proximal end. Tentilla with long distal cnidocils and no rostrum.

Material examined. A total of twelve specimens have been collected by the ROVs *Tiburon* and *Doc Ricketts*; all in the region of Monterey Bay, California, U.S.A.:

<i>Tiburon</i>	Dive 678	25-May-2004	35°28.84'N	123°52.74'W	depth 2836 m
<i>Tiburon</i>	Dive 841*	06-Apr-2005	35°29.99'N	123°52.00'W	depth 3288 m
<i>Tiburon</i>	Dive 844	08-Apr-2005	35°29.78'N	123°51.79'W	depth 3261 m
<i>Tiburon</i>	Dive 846	10-Apr-2005	36°22.92'N	122°39.97'W	depth 2663 m
<i>Tiburon</i>	Dive 982	12-May-2006	35°49.99'N	122°40.00'W	depth 2682 m
<i>Tiburon</i>	Dive 985*	14-May-2006	35°37.99'N	122°43.98'W	depth 2498 m
<i>Tiburon</i>	Dive 1040*	01-Oct-2006	34°17.23'N	124°03.10'W	depth 2820 m
<i>Ricketts</i>	Dive 029*	29-May-2009	35°28.77'N	125°01.49'W	depth 2772 m
<i>Ricketts</i>	Dive 196*	08-Oct-2010	36°36.00'N	122°08.90'W	depth 3090 m
<i>Ricketts</i>	Dive 196*	08-Oct-2010	36°36.00'N	122°08.90'W	depth 2460 m
<i>Ricketts</i>	Dive 197*	09-Oct-2010	35°66.60'N	122°40.20'W	depth 2987 m
<i>Ricketts</i>	Dive 423	01-Oct-2012	36°15.p2'N	123°09.98'W	depth 3000 m

The specimens collected during the two emboldened were frozen for molecular studies.

* *In situ* frame grabs exist for these specimens but, apart from the one shown below, none is worth reproducing.

Holotype: The specimen collected during *Doc Ricketts* Dive 29 has been designated the holotype, and will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

Paratype: The specimen collected during *Tiburon* Dive 985 has been designated the paratype, and also will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

The remaining specimens will be placed in the collections of Dr Casey Dunn, at Brown University, Providence, Rhode Island, USA.

Description. The small size, fragility and great transparency of the colonies of *Cordagalma abyssorum* sp. nov. made them very difficult to locate *in situ*, let alone capture. An *in situ* frame grab of *C. abyssorum* sp. nov. is shown in Figure 13, from which it was estimated that in life, the nectosome was c. 1.7 cm in length, which would indicate that the longest specimen photographed had a total length of c. 11 cm. In several cases as the ROV approached, the specimen began to autotomise much of its siphosome, leaving only a small remnant at the anterior end. Further, they tended to totally disintegrate within the collecting device so that it was necessary to search through 6.5 (Detritus Sampler) or 6.9 (Suction Sampler) litres of water to try to find the various, often completely transparent, components of the colony. Often such a search resulted in the finding of only a few nectophores and bracts. Gastrozooids and gonophores, although they should be more visible, were rarely located, as indeed was also the case for the main stem. For this reason, the description of *C. abyssorum* has had to be based on several specimens as, for instance, good nectophores but poor bracts were found with the holotype, while the reverse was true for the paratype. Nevertheless, although the holotype specimen lost most of its siphosome during collection it remained remarkably intact and a photograph of the specimen, taken in the laboratory, is shown in Figure 14.

Pneumatophore: The denuded stem of *Cordagalma abyssorum* sp. nov. was rarely recovered from the samples. However, when found the pneumatophore was very small measuring 0.23 mm in length, by 0.14 mm in diameter. It was completely featureless and bore no signs of any pigmentation. Although the nectosome and pneumatophore obviously were present after the holotype specimen was removed from its collector (see Figure 14), they were, apparently, not preserved.

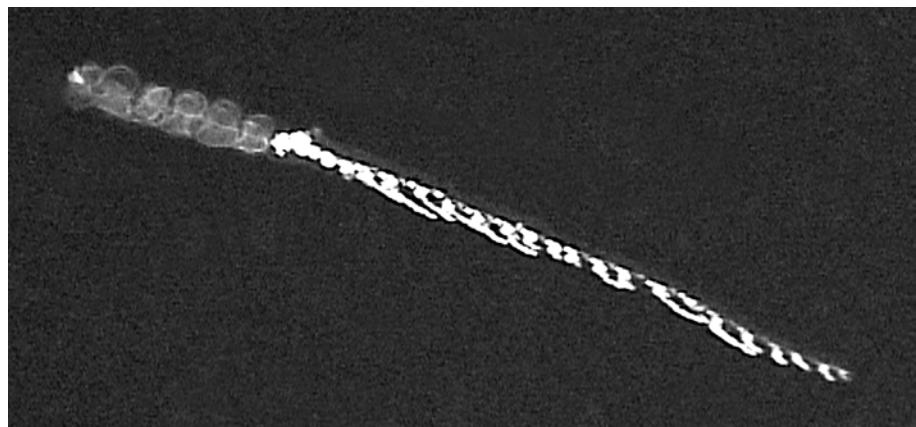


FIGURE 13. *Cordagalma abyssorum* sp. nov. *In situ* frame grab of specimen collected during Doc Ricketts Dive 197.



FIGURE 14. *Cordagalma abyssorum* sp. nov. Photograph of holotype specimen after collection. Anterior to the right. Courtesy of Dr. Stefan Siebert ©.

Nectosome: For the preserved specimens the nectosome, when found, was highly contracted and measured about 0.4 mm in length, excluding the pneumatophore. As noted above this region, including the pneumatophore was estimated to be c. 1.7 mm in length in life. The photograph of the holotype specimen (Figure 14) taken shortly after collection clearly shows the typical biserial arrangement of the nectophores, which were attached to the ventral side of the nectosome.

Nectophore: Eight small, roughly heart-shaped, nectophores, measuring up to 4 mm in height and 3.4 mm in width, were preserved with the holotype specimen, and they existed in two basic forms, characterised by the shape of the basal extension and the axial wings. In one form (Figure 15A) the short, narrow basal extension was rounded at its base, and the axial wings were small and rounded and the cleft between them was shallow and of even depth. In the other form (Figure 15B) the small basal extension was more squarely truncated, while the axial wings were larger and pointed, with a deep V-shaped cleft between them. However, for the younger nectophores (Figure 15C) the basal extension was relatively large and roughly triangular in shape. In the Tiburon Dive 678 specimen (Figure 16) the basal extension of the nectophores was small and almost squarely truncated, while the axial wings were quite small and rounded, and there was a shallow V-shaped cleft between them.

The proximal groove, demarcated by the rounded edges of the axial wings, was relatively shallow in the upper half of the nectophore and virtually non-existent in the lower half. The nectosac was rounded basally but, depending on the extent of the axial wings, had more or less pronounced lateral apical extensions. The long ascending and descending mantle canals were approximately of equal length, and the short pedicular canal arose at their junction and passed directly to the nectosac, where it divided off the four radial canals. The upper and lower

canals were straight, while the laterals to a greater or lesser extent arched upwards at first and then down to join the ostial ring canal at its mid-height. There were no signs of any tracts of large ectodermal cells arising at these latter points. No pigmentation was noted anywhere on the nectophores, and there were no patches of cells on the velum.

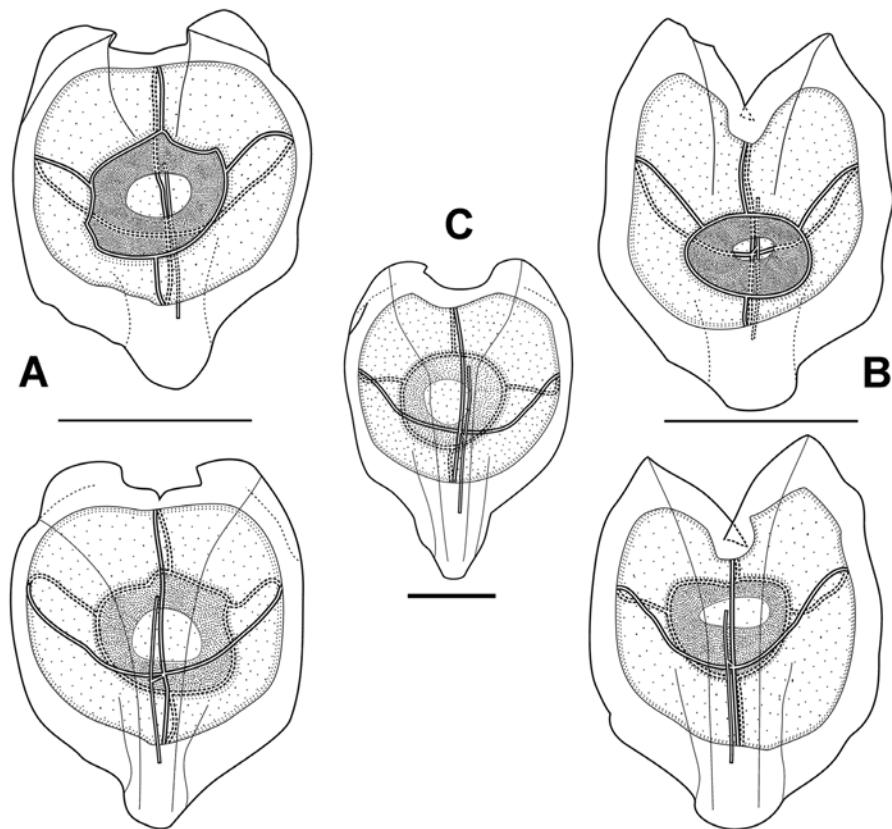


FIGURE 15. *Cordagalma abyssorum* sp. nov. Holotype specimen. A. & B. Ostial (top) and axial (bottom) views of two nectophores. Scale bar 2 mm. C. Axial view of smaller nectophore. Scale bar 1 mm.

Siphosome: Very few pieces of the siphosomal stem were found, and these were highly contracted, and generally denuded so that the exact arrangement of the cormidia could not be discerned. However, a close-up photograph of the remaining proximal part of the siphosome is shown in Figure 17. There the bracts with the terminal swelling of their canal penetrating into the mesogloea, the gastrozooids with their tentacles, and the male gonophores are obvious, but no palpon can be identified.

Bract: The minute kite-shaped bracts (Figure 18) measured up to 1.6 mm in length and 1.3 mm in width. They were flattened on their lower surface, while the highest region on the upper surface formed a flattened, rounded rhombus. The two proximal sides of the rhombus were defined by weak ridges, while the distal sides formed part of a well-defined chevron-like transverse ridge. A weak median ridge joined the centre of the transverse ridge to the distal end of the bract, demarcating two distal facets. This latter ridge, and the transverse ridge, bore widely spaced, very small, spherical nematocysts. These could also be present on the distal parts of the two other ridges, and along the central part of the inner margin of the distal facets. However, for the larger bracts particularly, these nematocysts had been lost. The narrow bracteal canal ran from close to the proximal end of the bract to approximately half its length and, in the preserved specimens, always appeared to remain in contact with its lower surface. However, this appeared to be a preservation artefact as the close-up photograph of the siphosome of the freshly collected specimen (Figure 17) clearly showed that the distal end of the bracteal canal penetrated for a short distance into the mesogloea and terminated in a slight swelling.

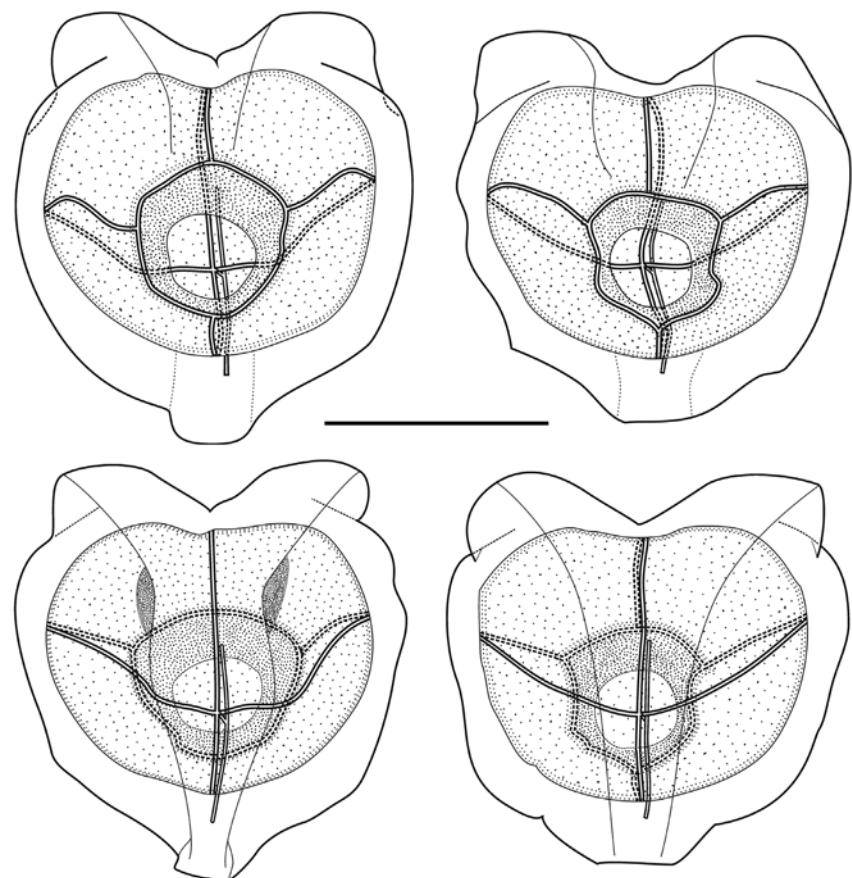


FIGURE 16. *Cordagalma abyssorum* sp. nov. Ostial (upper) and axial (lower) views of two nectophores from the *Tiburon* Dive 678 specimen. Scale bar 2mm.

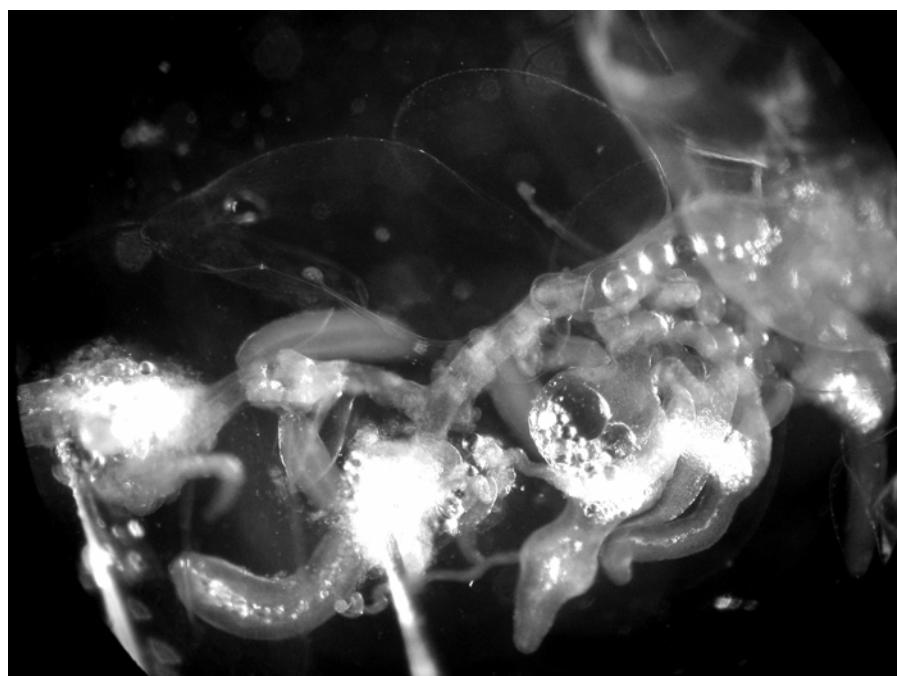


FIGURE 17. *Cordagalma abyssorum* sp. nov. Apical part of siphosome of the holotype. Courtesy of Dr Stefan Siebert©.

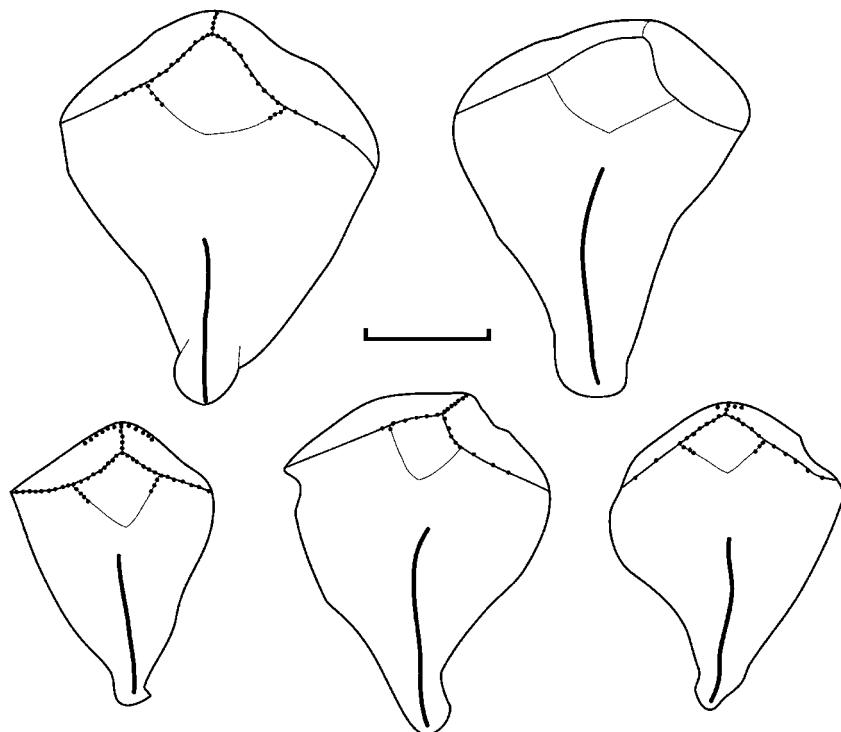


FIGURE 18. *Cordagalma abyssorum* sp. nov. Upper view of bracts from Tiburon Dive 985. Proximal at the bottom. Scale bar 0.5 mm.

Gastrozoid and tentacle: The small anterior gastrozooids of the holotype specimen measured up to c. 1 mm in length and c. 0.4–0.5 mm in maximum width in their preserved state (Figure 19A). The proximal basigaster was distinctly separated from the distal stomach region and was variable in width, but usually occupied about 1/5th the total length of the gastrozoid. Only the proximal part of the tentacle remained attached and included the very young buds of the tentilla. A close-up photograph of the siphosomal stem of the holotype specimen before preservation (Figure 19B) clearly showed a contracted distal proboscis region; an inflated stomach region and a cylindrical basigaster containing numerous, presumably oil-filled, droplets and occasionally pigmented, vesicles of various sizes. The gastrozoid was attached by a short peduncle.

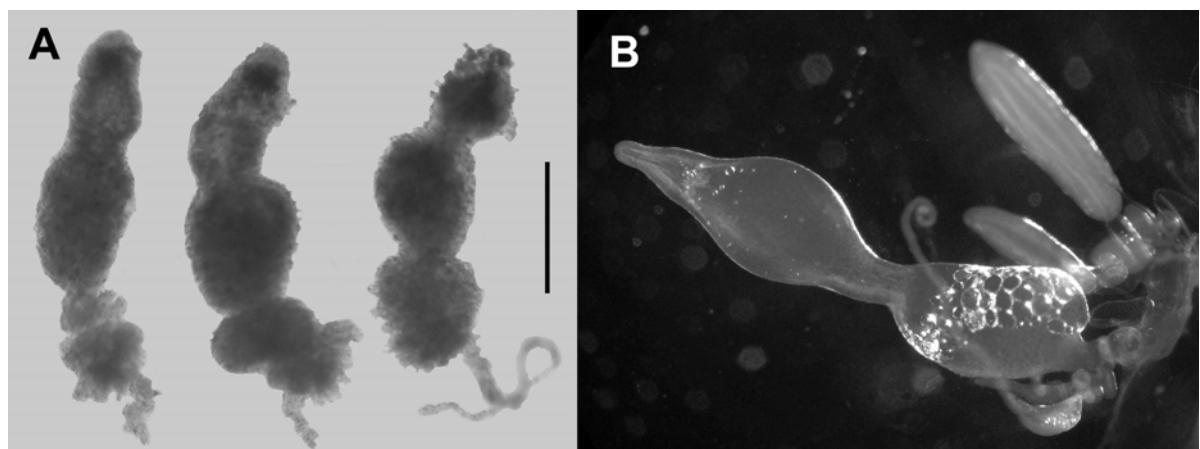


FIGURE 19. *Cordagalma abyssorum* sp. nov. **A.** Preserved gastrozooids from holotype. Proximal at bottom. Scale bar 0.5 mm. **B.** Gastrozoid and male gonophores from type specimen.

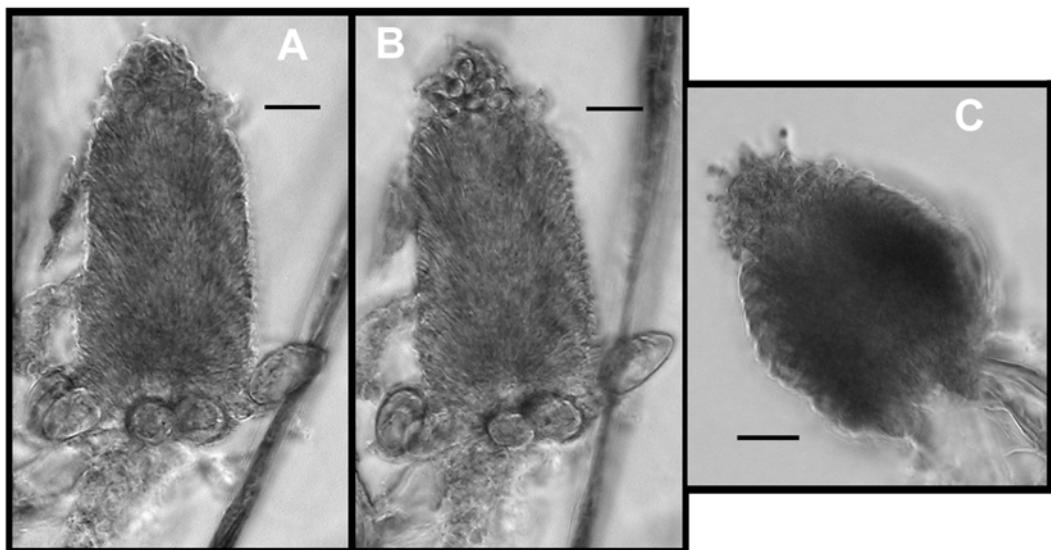


FIGURE 20. *Cordagalma abyssorum* sp. nov. Tentilla. A & B from Doc Ricketts Dive 196, C from Doc Ricketts Dive 197. Proximal at bottom. Scale bar 25 µm.

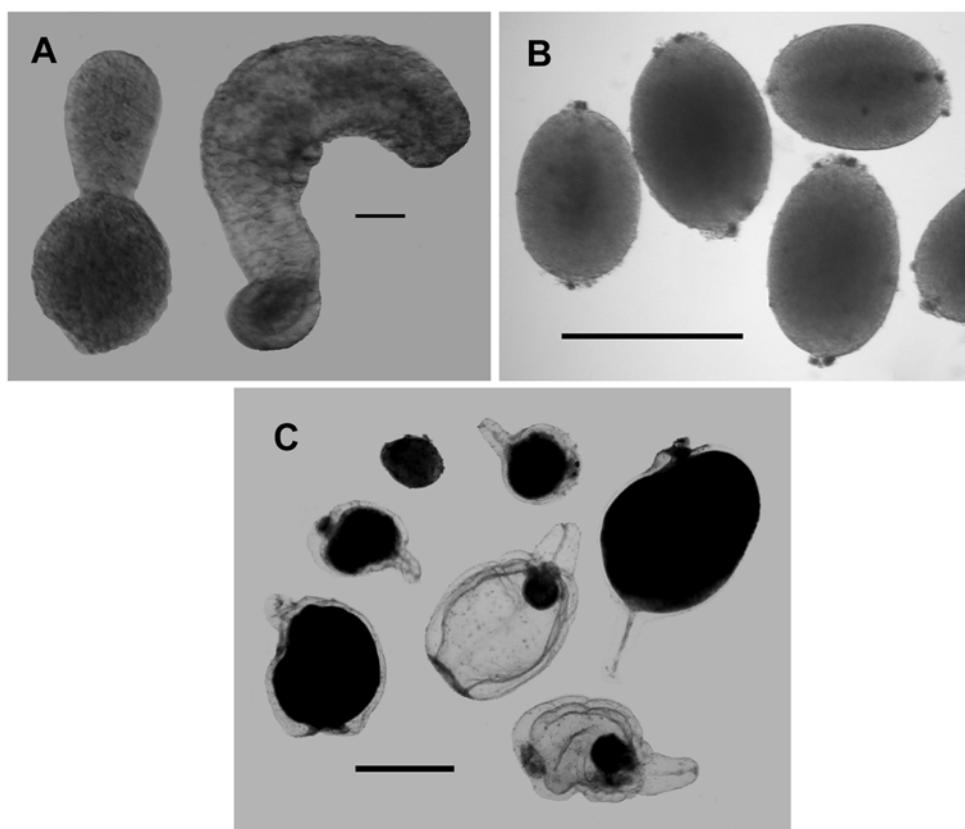


FIGURE 21. *Cordagalma abyssorum* sp. nov. A. Two palpons from Doc Ricketts Dive 197. Various views. Scale bar 0.1 mm. B. Male gonophores from Tiburon Dive 844 specimen. Various views. Scale bar 0.5 mm. C. Female gonophores from Tiburon Dive 982 specimen. Various views. Scale bar 1 mm.

Tentilla: Very few, mostly broken apart, tentilla were found with all of the specimens of *Cordagalma abyssorum* sp. nov. examined. The younger ones (Figure 20A, B) showed a semicircle of five, loosely attached stenoteles proximally, and many detached and discharged nematocysts of this type were observed entangled with debris. The majority of the cnidoband was occupied by one type of nematocyst, presumed to be anisorhizas, with a clump of a small number of presumably isorhizas at the distal end. These had short stout cnidocils projecting from

them. On a slightly more mature tentillum (Figure 20C) the stenoteles were less obvious, the central region broader and shorter, and the distal nematocysts had slightly longer cnidocils. There was some evidence, from broken fragments, that these cnidocils grew longer and broader, forming talon-like structures as the tentilla reach maturation. However, no fully mature tentilla were observed.

Palpon: The only structures that looked like they might be palpons were found with the *Doc Ricketts* Dive 196 and 197 specimens (Figure 21A). They were featureless bags with a maximum length of 0.85 mm and a maximum width of 0.28 mm. No nematocysts were found in association with them, and they would appear to have been attached by their proximal ends. Palpons could not be identified with certainty on the anterior part of the siphosomal stem (Figure 17), but there are several small buds.

Gonophores: Mature gonophores were only found for a few specimens, and in each case only gonophores of one sex were found. However, there was insufficient evidence to suggest that the species might be dioecious. The small male gonophores (Figure 21B) measured c. 0.55 mm in length and 38 mm in diameter. The manubrium could clearly be seen in some. They were borne on short, narrow peduncles and at their distal ends had a small pore. However, in the close-up photograph (Figure 19B) more mature male gonophores could be seen as elongate structures over half the length of the gastrozooids.

The female gonophores (Figure 21C) measured up to 2.5 mm in total length, with a bell length of 1.9 mm and diameter of 1.5 mm. They were quite unlike the male gonophores in that they consisted of a distinct bell, with a short but broad pedicle, within which the single egg was developed. In the most mature gonophores the outline of the bell was barely distinguishable.

Distribution. All the specimens came from a very small area in the vicinity of Monterey Bay, California, between 34°17.23' and 36°22.92'N, and 122°08.90' and 125°01.49'W. They were also found with a fairly restricted depth zone between 2498 and 3288 m, mean 2850 ± 280 m.

In addition frame grabs that were probably of *Cordagalma abyssorum* sp. nov. were taken during the following dives:

Tiburon Dive 396	36°18.96'N, 122°54.14'W	21-Feb-2002	depth 3140 m
Tiburon Dive 852	36°44.02'N, 122°41.95'W	06-Jun-2005	depth 3614 m
Tiburon Dive 852	36°44.00'N, 122°41.95'W	06-Jun-2005	depth 3055 m
Tiburon Dive 1087	36°20.29'N, 122°54.97'W	13-Apr-2007	depth 2141 m
Tiburon Dive 1088	36°33.10'N, 122°30.06'W	14-Apr-2007	depth 2818 m
Tiburon Dive 1154	35°49.97'N, 122°39.99'W	28-Nov-2007	depth 2075 m
Ricketts Dive 26	36°07.00'N, 122°46.50'W	27-May-2009	depth 3089 m

These showed that potentially specimens could be found as shallow as 2075 m and as deep as 3614 m, although the identity of these specimens is not absolutely certain.

Etymology. The specific name is derived from the Latin *abyssus* meaning the deep sea.

Cordagalma rugosum sp. nov.

Diagnosis. Small heart-shaped nectophores, usually with relatively long, narrow basal extension. Extent of the axial wings very variable, from almost non-existence to having a deep indentation between them. Distinct lateral ridges extending from outer corners of axial wings down ostio-lateral sides of the nectophore and ending approximately on a level with the ostium. Two weaker ridges divide from them and curve inwards and downwards to end above ostial level. Up to six patches of cells can be present on each side of the velum. Relatively large bracts somewhat rounded with distinct, but small distal facet divided by a ridge, with a pair of patches of ectodermal cells. The edges of the distal facet frilled, and small nematocysts are present along them. Bracteal canal to c. half the length of bract, ending in a small swelling inflected into the mesogloea. Gastrozooids with pinkish pigmentation. Palpons possibly attached by their bases or slightly to one side of it. Structure of tentillum not known.

Material examined. A total of five specimens have been collected by the ROV *Tiburon*; all in the region of Monterey Bay, California, U.S.A:

<i>Tiburon</i>	Dive 986	35°38.01'N	122°44.46' W	15-May-2006	depth 1228m
<i>Tiburon</i>	Dive 1040	34°17.23'N	124°03.10'W	01-Oct-2006	depth 1201m
<i>Tiburon</i>	Dive 1109	35°50.00'N	122°40.00'W	31-Jul-2007	depth 1120m
<i>Tiburon</i>	Dive 1154	35°49.97'N	122°39.99'W	28-Nov-2007	depth 1040m
<i>Ricketts</i>	Dive 421	35°33.74'N	123°44.97'W	20-Dec-2012	Depth 1318m

The specimen collected during the *Tiburon* Dive 1109 was frozen for molecular studies.

Holotype: The specimen collected during *Tiburon* Dive 1154 has been designated the holotype, and will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

The remaining specimens will be placed in the collections of Dr Casey Dunn, at Brown University, Providence, Rhode Island, USA.

Description. Specimens of *Cordagalma rugosum* sp. nov. were small and fragile and they fell apart in the collecting devices and, as with *Cordagalma abyssorum* sp. nov., it was inevitable that some pieces were missed despite a thorough search. An *in situ* frame grab of the type specimen is shown in Figure 22A. It was difficult to gauge the length of the colony, but it was certainly less than the diameter (16.5 cm) of the collector. The frame grabs indicated that the stomach region of the gastrozooids was lightly pigmented (see below), while between each gastrozooid there were one or two groups of brownish coloured appendages. It can only be presumed that one of these represented a palpon, possibly with some gonophores, and that the other represents a gonodendron.

Pneumatophore: A pneumatophore and denuded stem (Figure 22B) was present with the preserved holotype and *Tiburon* Dive 986 specimens. It was featureless and colourless, and measured c. 5 mm in length and 3.5 mm in diameter.

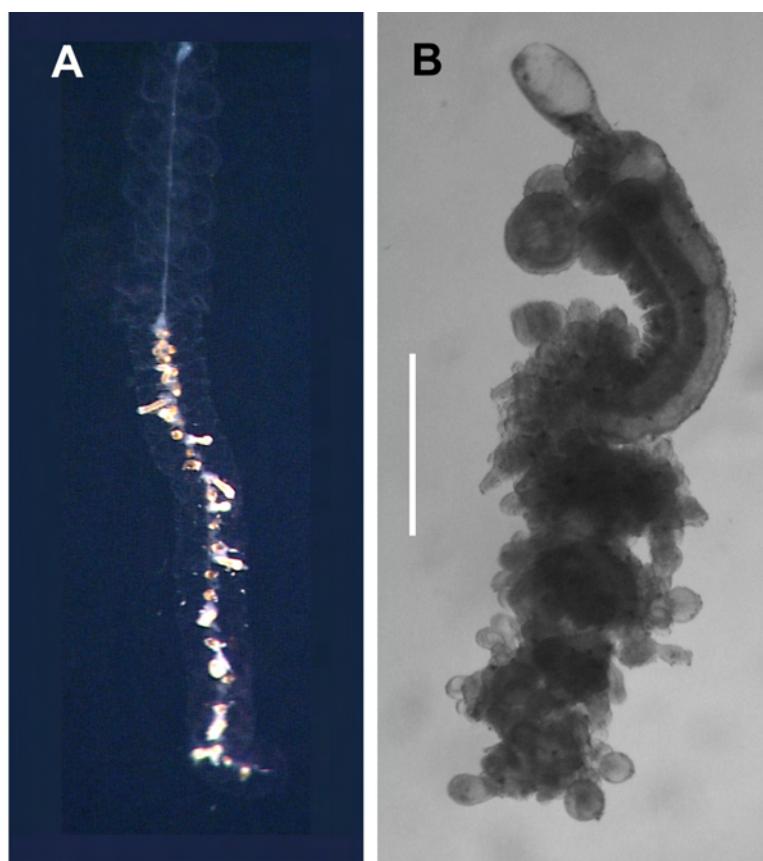


FIGURE 22. A. *In situ* frame grab of holotype specimen of *Cordagalma rugosum* sp. nov. B. Contracted stem of preserved holotype specimen. Scale 1 cm.

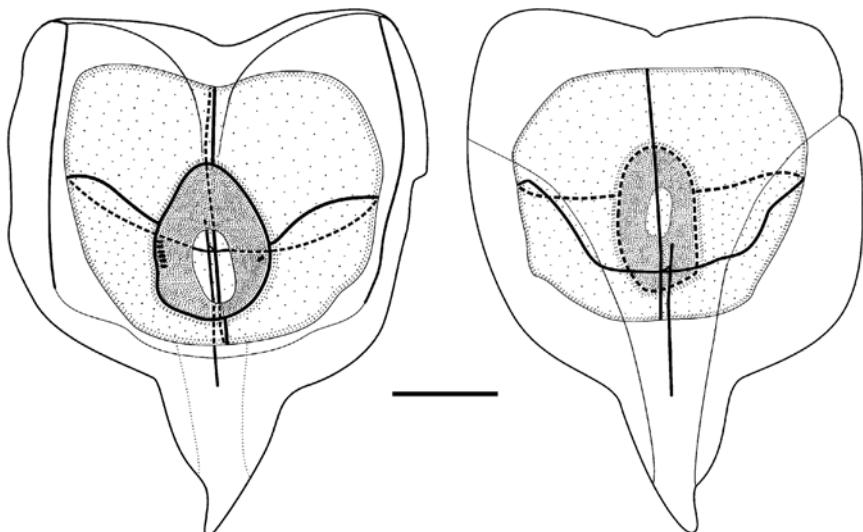


FIGURE 23. *Cordagalma rugosum* sp. nov. Ostial (left) and axial (right) views of largest nectophore from holotype. Scale bar 1 mm.

Nectosome: It was clear from the denuded stems that the nectophores were developed on the ventral side of the nectosome (Figure 22B). Several buds of nectophores were present at the apical end of the nectosome.

Nectophore: Only three nectophores were found with the holotype specimen, each of which had a characteristic form. The largest one (Figure 23) measured 5.1 mm in length and 4 mm in width. The axial wings of this nectophore were very small, with only a shallow central indentation separating them. From their lateral apices a pair of obvious ridges ran down close to the lateral margins of the nectophore, but abruptly disappeared at about the level of the base of the nectosac. Close to their origin, another pair of less distinct ridges divided from them and ran inwards and then downwards, defining the edges of a shallow furrow, to end just above the nectosac. In the region immediately below the nectosac, the nectophore narrowed considerably, while its depth, on the ostial side, decreased rapidly to c. 2/3rd its deepest. The distal process was thus quite narrow, like an inverted isosceles triangle, except that its basal tip was turned to one side. On the axial side of the nectophore there was a very shallow median furrow that narrowed and deepened considerably in the region of the pedicular canal. It then shoaled to form a broad shallow gutter, and continued down the basal process.

The nectosac, in ostial view, was almost circular and had no lateral extensions. The upper and lower radial canals were straight, while the laterals were only slightly looped. The descending mantle canal was much longer than the ascending one. The pedicular canal immediately gave rise to the four radial canals on reaching the nectosac. There were no obvious patches of ectodermal cells in the region of the junction of the lateral radial canals with the ostial ring canal. However, there were distinct patches of cells on the velum itself. A row of six such patches were found on the left-hand side of the velum, below the insertion point of the lateral radial canal, but only one was found on the right.

Outwardly, the middle-sized nectophore (Figure 24), which measured 4 mm in height and 3.3 mm in width, differed in many respects from the largest one. The nectophore had pronounced ostial wings, while the basal process was broadly triangular with a rounded base, from which hung a small appendage. The apparent asymmetry in the basal process is a preservation artefact. However, in most other respects the characteristic features of the nectophore were similar to the largest nectophore. There were distinct lateral ridges running down the nectophore on its ostial side. A weaker pair of ridges arose from them and ran inwards and downwards to peter out above the ostium. The ostial side of the nectophore rapidly lost depth just below the ostium. The margins of the hydroecial gutter, on the axial side, were weak and its depth was very shallow in the basal half of the nectophore, but increased greatly in the upper half.

The presence of axial wings was mirrored by the development of latero-apical wings to the nectosac, which resulted in the lateral radial canals being more arched than on the largest nectophore. The ascending mantle canal remained much shorter than the descending one, and the origin of the pedicular canal was similar to that in the largest nectophore. On reaching the nectosac it immediately gave rise to all four radial canals. Patches of cells were again present on the velum of the nectosac, with one large and two smaller ones on the left-hand side and six small ones on the right.

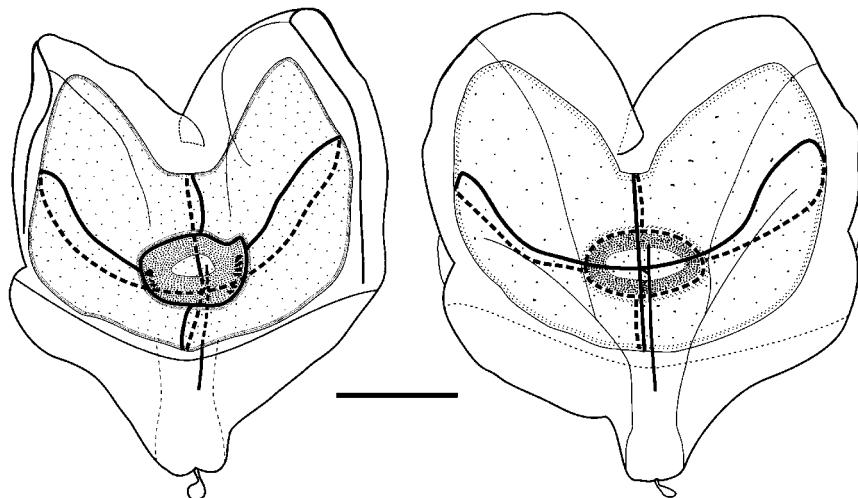


FIGURE 24. *Cordagalma rugosum* sp. nov. Ostial (left) and axial (right) views of the median sized nectophore from holotype. Scale bar 1mm.

The smallest nectophore measured 4 mm in height and 2.85 mm in width (Figure 25). It was quite similar to the largest nectophore in basic shape, but the axial wings were relatively larger and the shape of the basal process was somewhat different. Otherwise it shared the same basic characters as the other two nectophores, although the lateral ridges were relatively weak and, despite the apico-lateral extensions of the nectosac, the lateral radial canals were only slightly arched. The velum of the nectosac had four patches of cells on the left-hand side and one large and one small one on the right.

For the other specimens, nine nectophores were found with the Tiburon Dive 986 specimen, which measured up to 6 mm in length and 4.7 mm in width. All were in poor condition, with the nectosac having become completely detached in six, and partially so in another two. On the remaining one, the velum of the nectosac bore 3 spots on the left-hand side and four on the right. All these nectophores had small axial wings with a broad shallow depression between them. The form of the basal process varied between the two extremes found with the largest and smallest nectophores of the holotype. Thus in some it formed a narrow isosceles triangle, while in others the sides were almost parallel, although their width in this region was quite variable, before tapering down to a rounded base.

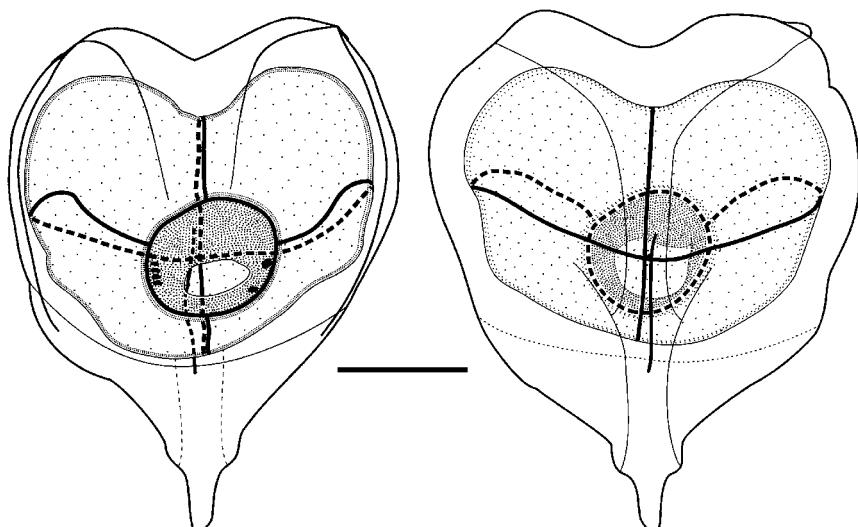


FIGURE 25. *Cordagalma rugosum* sp. nov. Smallest nectophore from holotype. Ostial (left) and axial (right) views. Scale bar 1 mm.

The eight nectophores found with the *Tiburon* Dive 1040 specimen were smaller, with maximum dimensions of 4.7 mm in length and 3.4 mm in width. They were all in reasonable condition, with their nectosacs largely intact, and were all of the form shown by the intermediate sized nectophore of the holotype, with more or less pronounced and pointed axial wings. In ostial view the inner margins of the wings came to overlap each other, leaving a narrow but deep incision between them, just above the median apex of the nectosac. They then diverged slightly and petered out above the ostium. The basal process was broad and basally rounded, with the basal protrusion much less pronounced than for the holotype nectophore; with six nectophores only showing a small pimple; one with no sign of it at all; and one with a small but distinct protrusion. The number of patches on the velum of the nectosac was quite variable, with up to six on each side.

Siphosome: The contracted siphosomal stem is shown in Figure 22. The buds of palpons, bracts and gonophores were all that remained attached to it.

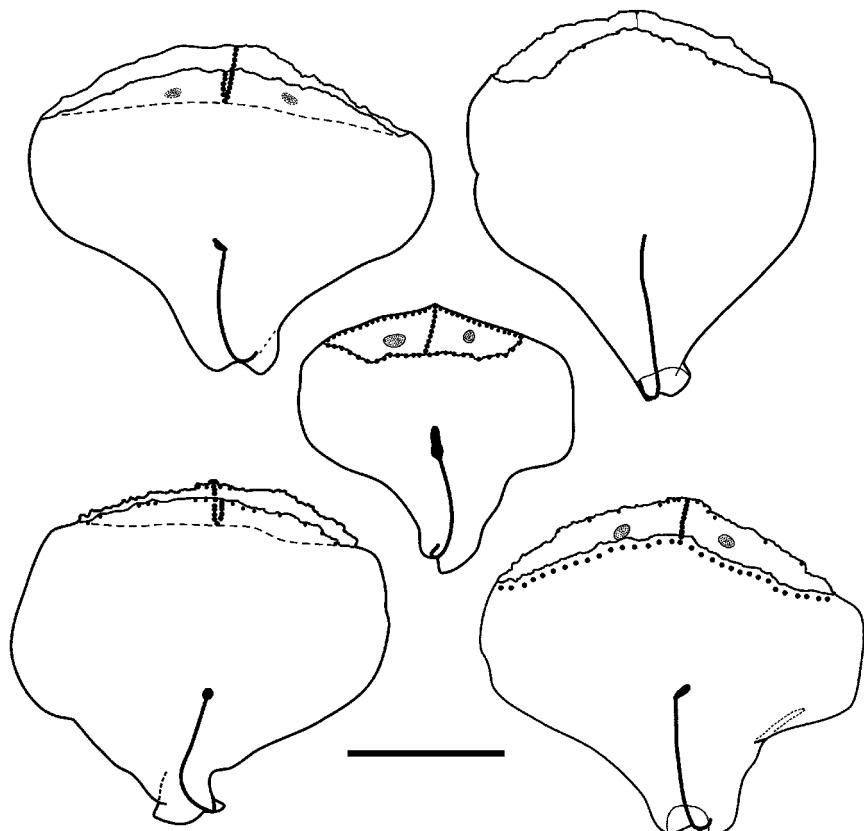


FIGURE 26. *Cordagalma rugosum* sp. nov. Upper views of bracts from holotype specimen. Proximal end bottom, distal top. Scale bar 1mm.

Bract: (Figure 26). The bracts measured up to 2.5 mm in length and 2.6 mm in width, and in general were broader than they were long. The broadest part was in the distal half to two-thirds of the bract, and proximal to this the bract narrowed rapidly. The proximal tip of the bract was turned up and formed a small process on the upper side of the bract. A narrow furrow ran along it, at the base of which was the proximal end of the bracteal canal. Occasionally in the proximal region the bracts were asymmetrical, narrowing more rapidly on their inner side, and only the outer side was turned up. The bracteal canal ran to just under half the length of the bract and usually its distal tip was swollen and inflected, often vertically, into the mesogloea for up to half the thickness of the bract itself. This was a very characteristic feature, when present, but in larger bracts it was often very difficult to discern, as was the narrow part of the canal that was in contact with the lower side of the bract.

The lower side of the bract was slightly concave, while the upper side was level for most of its length, tapering down slightly toward the proximal end. A distal facet was demarcated by a transverse ridge that arched across the upper surface just short of the distal end of the bract. The edges of both this ridge and the more rounded ridge forming the lower border of the distal facet often had a frilly appearance, but this probably was a preservation

artefact. A very indistinct median region also divided the distal facet into two. The edges of the distal facet and median ridge were overlain by small, spherical nematocysts, but frequently these had been lost. Usually on each half of the distal facet there was an opaque patch comprised of a few ectodermal cells, but like the nematocysts these were often eroded in the larger bracts, although where they had been positioned could still be seen.

Gastrozoid and tentacle: Two small gastrozooids were found with the holotype specimen, and three with the *Tiburon* Dive 968 one. They were all narrow and tubular, with the largest measuring 2 mm in length, but were only 0.2 mm in diameter in the stomach region. From the *in situ* frame grabs, this region was a very pale orange in colour, while the proximal and distal ends were white. The proboscis region was distinct, with the mouth usually turned out and back on itself. The basigaster was about twice as wide as the stomach region, but usually quite short. All bore the proximal remnants of a tentacle.

Tentilla: None of the proximal remnants of the tentacle bore any mature tentilla, but numerous small, bag-like initial buds of them were present.

Palpon: The holotype specimen, and that from *Tiburon* Dive 968, included about four small tubular structures, some with an inflated middle section, that probably were palpons. They measured up to 0.5 mm in length and 0.3 mm in diameter, but otherwise showed no characteristic features. The preserved and contracted stem of the holotype showed a number of small buds that probably represent developing palpons. Most of these buds were slightly asymmetrical in shape, but appeared to be attached at their proximal ends. However, for one or two of the buds this attachment appeared to be slightly displaced to one side, as found for the preserved palpons of *Cordagalma ordinatum*. More material will be required before the structure and arrangement of the palpons can be ascertained with certainty.

Gonophores: Only a single mature male gonophore was found with the *Tiburon* Dive 968 specimen. It was typically ovoid in shape, milky white in colour and measured 5.75 mm in length by 3.5 mm in diameter. There were no distinguishing characters. The holotype specimen possessed buds of both male and female gonophores, but no mature ones were found.

Distribution. Only five specimens of *Cordagalma rugosum* sp. nov. have been collected; one of which was frozen for molecular analyses. All five specimens came from the vicinity of Monterey Bay, California, and were found within the relatively narrow depth range of 1040 to 1318 m.

Etymology. The specific name *rugosum* is derived from the Latin *ruga*, *rugosus* meaning wrinkled, and refers to the wrinkled appearance of the edges to the basal facet on the bracts, although this may indeed be a preservation artefact.

Cordagalma bimaculatum sp. nov.

Cordagalma cordiforme Mills et al., 1996, p. 154.

Cordagalma ordinata Mapstone, 2009, Fig. 22D.

? *Cordagalma cordiforme* Mackie, 1985

Diagnosis. Nectophores heart-shaped, with a distinctive patch of large ectodermal cells at the apex of each axial wing. Broad axial wings with deep narrow incision between them. Usually two pairs of patches of ectodermal cells on lower, lateral parts of velum. Bracts roundly rhomboidal in shape, with a transverse ridge on the upper side dividing off a distal facet. Small nematocysts can line the margins of the facet, and also form a median line dividing the distal facet. A patch of ectodermal cells present on each side of the facet. Bracteal canal extends to half the length of the bract and, in younger ones, has a small swollen extension into the mesogloea. Young tentilla without long distal cnidocils. Palpon attached laterally.

Material examined. Two specimens collected by the Johnson-Sea-Link (JSL) submersibles:

JSL II	Dive 1405	39°51.6'N, 70°22.5'W	1-Sep-1988	depth 747 m
JSL I	Dive 2952	36°02.9'N, 02°48.2'W	17-Apr-1991	depth 726 m

Unfortunately the nectosome of the JSL II Dive 1405 specimen became detached during collection and was lost.

A further six specimens were collected by various MBARI submersibles, namely:

<i>Ventana</i>	Dive 209	36°42.69'N 122°01.15'W	22-Jan-1991	Depth 422 m
<i>Ventana</i>	Dive 3005	36°41.85'N 122°03.94'W	15-May-2007	Depth 372 m
<i>Tiburon</i>	Dive 843	35°29.87'N 23°51.91'W	08-Apr-2005	Depth 587m
<i>Tiburon</i>	Dive 1043	36°42.15'N 122°34.49'W	4-Oct-2006	Depth 400 m
<i>Ricketts</i>	Dive 419	36°36.00'N 122°09.03'W	28-Sep-2012	Depth 449 m
<i>Ricketts</i>	Dive 500	36°36.00'N 122°09.00'W	15-Jul-2013	Depth 302 m

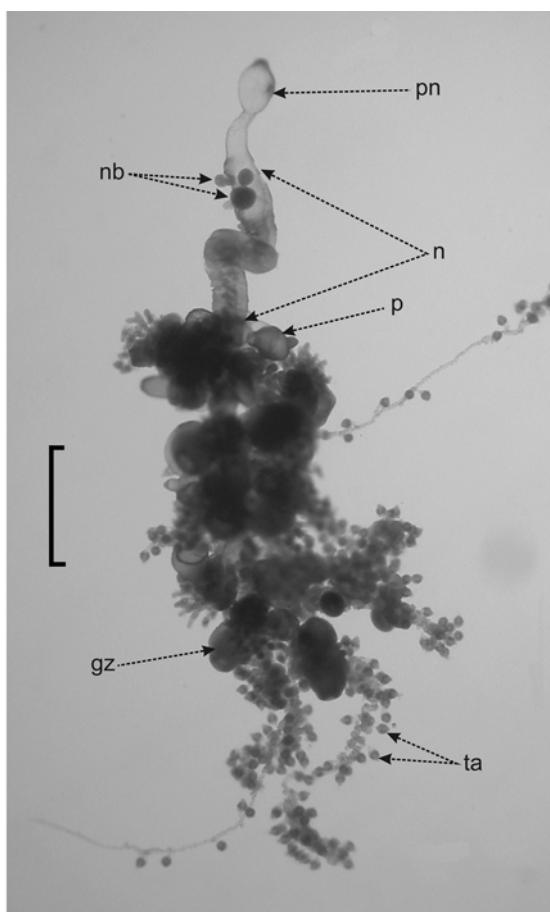


FIGURE 27. *Cordagalma bimaculatum* sp. nov. Stem of preserved holotype specimen. **gz:** gastrozooid; **n:** nectosome; **nb:** buds of nectophores; **p:** palpon; **pn:** pneumatophore; **ta:** tentilla. Scale bar 1mm.

Holotype: The specimen collected during the Johnson-Sea-Link I Dive 2952 has been designated the holotype, and will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

Description. The description of *Cordagalma bimaculatum* sp. nov. is based, for the most part, on the JSL specimens. However, there was some slight variability in the characters of certain zooids between the JSL and Monterey Bay material, to which attention will be drawn. A photograph of the preserved holotype specimen is shown in Figure 27. All the nectophores had become detached.

Pneumatophore: The pneumatophore (Figure 27, **pn**) was distorted due to rupture of its basal wall caused by gas expansion as the specimen was brought to the surface. It measured approximately 0.55 x 0.25 mm and showed no signs of pigmentation, although there was a distinctive cap of cells apically.

Nectosome: The nectosome of the preserved type specimen (Figure 27, **n**), despite the contracted state of the colony, was relatively long, and bore six nectophoral buds at its anterior end (Figure 27, **nb**). The nectophores, as indicated by their attachment lamellae, were clearly attached to the ventral side of the nectosome.

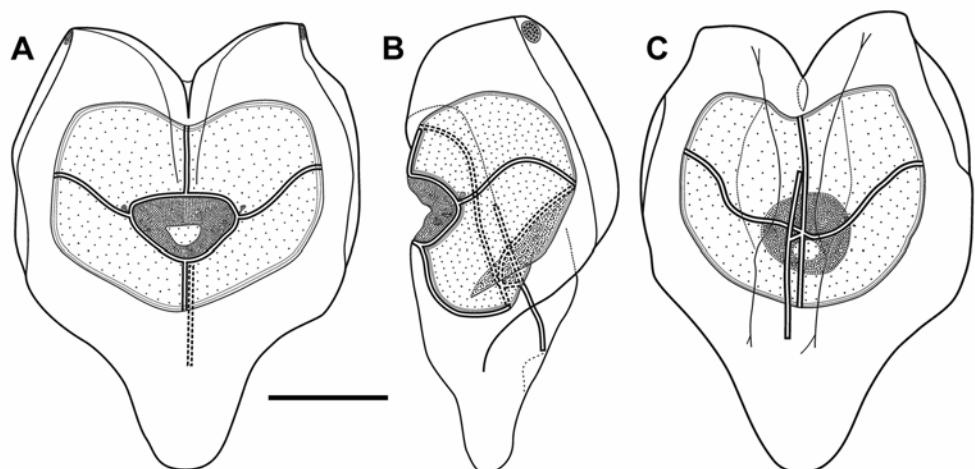


FIGURE 28. *Cordagalma bimaculatum* sp. nov. A. Ostial, B. lateral, and C. axial views of nectophore form holotype specimen. Scale bar 1 mm.

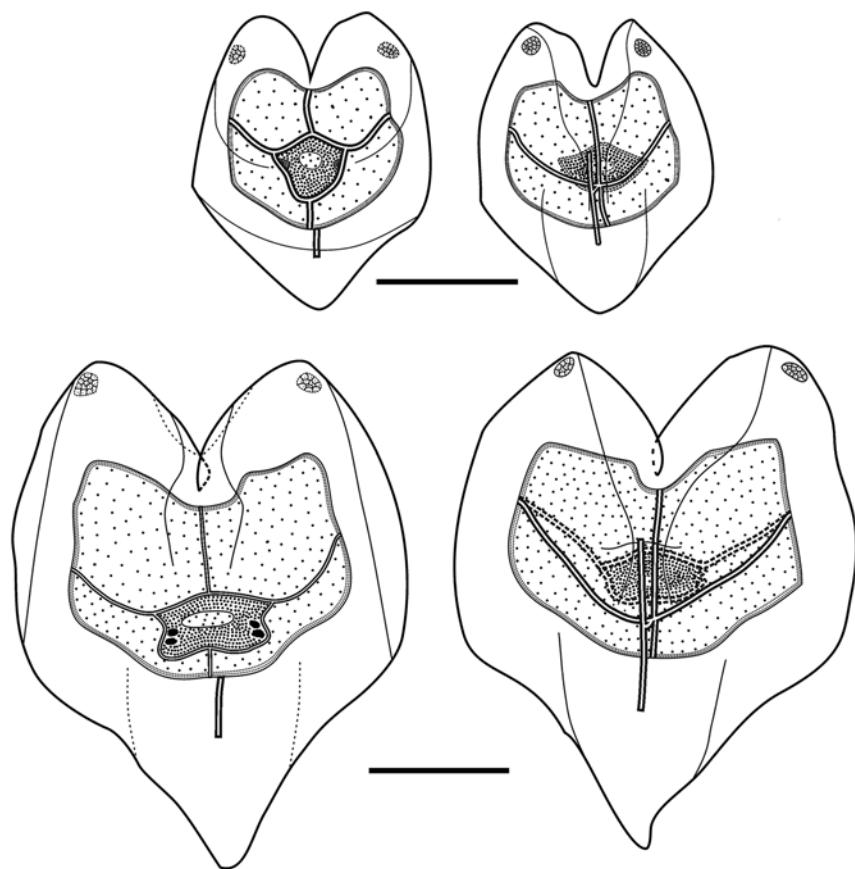


FIGURE 29. *Cordagalma bimaculatum* sp. nov. Young (top) and adult (bottom) nectophores from Doc Ricketts Dive 500 specimen. Ostial (left) and axial (right) views. Scale bar 1 mm.

Nectophore: (Figures 28, 29). Despite the apparent length of the nectosome, only seven mature nectophores, which measured up to 3.8 mm in length and 3 mm in width in their preserved state, remained with the holotype specimen. These were heart-shaped, with a pronounced basal extension. The extent and shape of this basal extension was quite variable, possibly as a result of preservation; sometimes being pointed (Figure 29A), and sometimes broadly rounded (Figure 28). The maximum number of nectophores found with any of the Monterey Bay specimens was 10 for the Tiburon Dive 843 specimen.

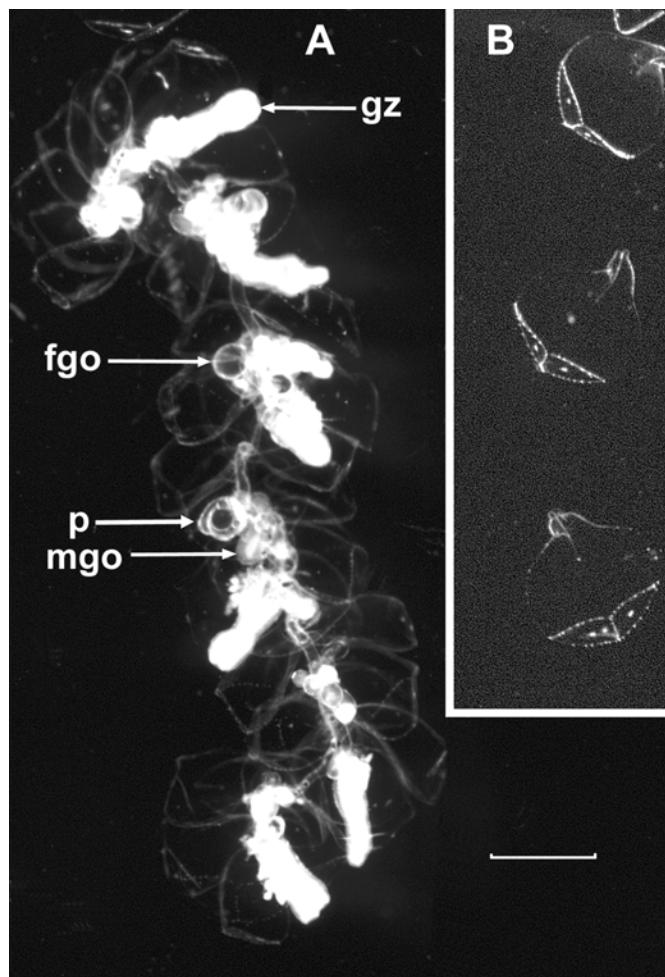


FIGURE 30. *Cordagalma bimaculatum* sp. nov. A. Siphosome of JSL Dive 1405 specimen, with B. some detached bracts. fgo, mgo, female and male gonophores, respectively. gz, gastrozooid; p, palpon. Scale bar 1 mm.

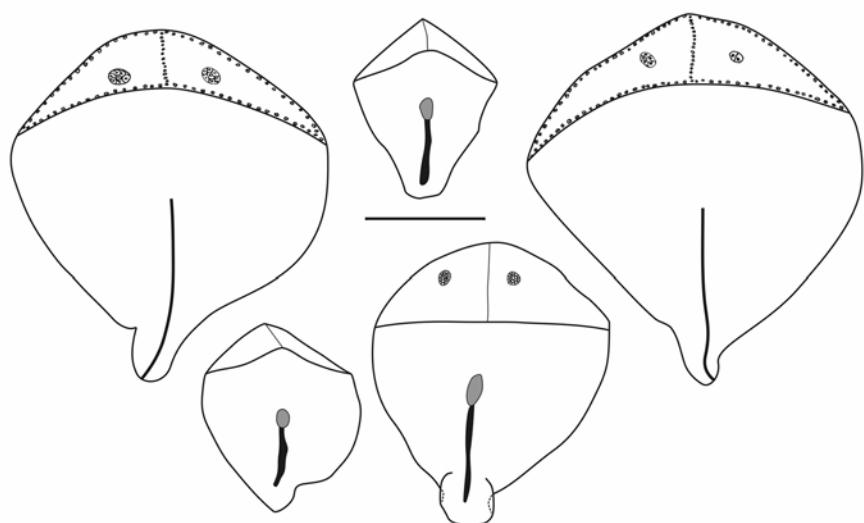


FIGURE 31. *Cordagalma bimaculatum* sp. nov. Upper views of bracts from the type specimen. Proximal at bottom. Scale 0.5 mm.

There was a deep median incision between the axial wings. On the mature nectophores, on the ostial side, a pair of weak ridges ran from the outer extremes of the axial wings toward the mid-line and continued toward the ostium, demarcating a shallow gutter between them, before petering out slightly above it. A very weak lateral ridge extended down the main body of the mature nectophore, on each side, but this could not be seen on the younger ones. Another pair of weak ridges, on the axial side of the nectophore, demarcated a relatively narrow hydroecial gutter between them, through which the nectosomal stem had once passed. At the upper end of the axial wings, just axial to the lateral ridge, there was a pair of small patches consisting of up to twenty large, ectodermal cells, probably photocytes, with darkly staining nuclei. Although characteristic these patches were unfortunately often very difficult to discern without staining, or had been abraded off in poorly preserved specimens such as the *Ventana* 209 one. They could be seen on only one of the four nectophores found with the *Ventana* Dive 3005 specimen. The more mature of these nectophores appeared to have an extensive basal process, but this probably was an illusion caused by the excessive contraction of the nectosac during preservation.

The ascending and descending mantle canals were of about equal length. The nectosac was also heart-shaped and occupied most of the main body of the nectophore. On reaching the nectosac the pedicular canal immediately gave rise to all four radial canals. The upper and lower canals ran straight to the ostial ring canal. The laterals looped up and over on to the lateral sides of the nectosac, before curving gently down and continuing to the ostial ring canal. This latter canal surrounded a large velum. In the region where the lateral radial canals joined the ostial ring canal, there was a club-shaped patch of distinctive ectodermal cells that extended out laterally for a short distance, although they could not always be discerned. In addition, on the lower lateral sides of the velum itself there were variably sized patches of cells, usually two on each side. On the younger nectophores this consisted of a single enlarged triangular patch.

Siphosome: The highly contracted siphosome of the type specimen can be seen in Figure 27, and the slightly less crowded siphosome of the other specimen in Figure 30.

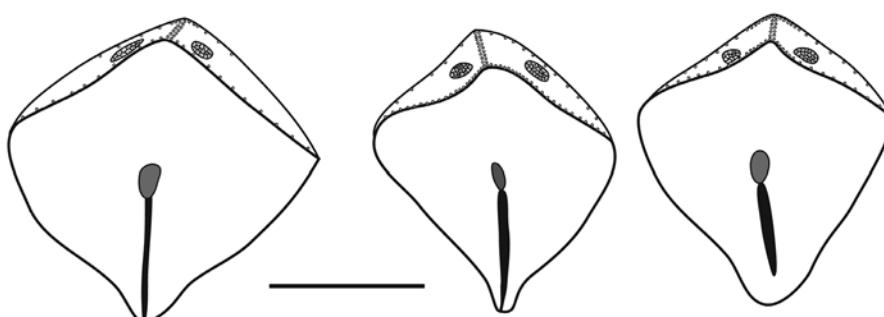


FIGURE 32. Upper views of young bracts of *Cordagalma bimaculatum* sp. nov. from the *Doc Ricketts* Dive 500 specimen. Proximal at bottom. Scale bar 0.5 mm.

Bract: Numerous small bracts (Figure 30B, 31–34), measuring up to c. 2.25 mm long and 2 mm wide, were present with both specimens. Those of the type specimen had a rounded roughly rhomboidal shape. They were slightly concave, centrally, on the lower side, and distinctly convex on the upper one. Toward the distal end a weak transverse ridge demarcated a rapid decrease in the thickness of the bract on the upper side. The whole surface of the preserved bract had a papillose appearance, particularly on the distal facet. The two sides of that facet joined, in the mid-line, forming an angle of c. 120°. On that facet there were two patches of large, distinctive ectodermal cells, which probably were sites of bioluminescence. Each patch usually consisted of 6–12 cells, but several had less. These patches were not always apparent on the younger bracts. In addition there was a median row of rounded cells, which probably were minute nematocysts, although this could not be ascertained with certainty. In life, these cells were also spaced out along all the edges of the distal facet, but after preservation many of these were abraded, and were less obvious in the JSL I Dive 2952 (holotype) specimen than the JSL II Dive 1405 one. The bracteal canal ran from the proximal end of the bract to approximately its mid-length.

For some of the specimens from Monterey Bay, the transverse ridge tended to be much more distinct and, like the younger bracts of the type specimen, it had a more pronounced V-shape. The bracteal canal, for all specimens, did not extend beyond half the length of the bract and greatly thickened in the younger bracts (Figure 32), and its distal end was swollen and inflected into the mesogloea. In the mature bract that swelling had disappeared. The

canal usually originated above the proximal end of the bracts (Figure 33), although for some bracts there was a narrow extension to the proximal tip. The array of nematocysts around the edges of the distal facet, particularly on the upper transverse ridge and in the mid-line between the two facets, was clearly to be seen on the younger bracts. This was particularly noticeable on the very young bracts of the *Ventana* Dive 3995 specimen, which had nematocysts inserted without intervals demarcating the upper and median borders of the distal facet.

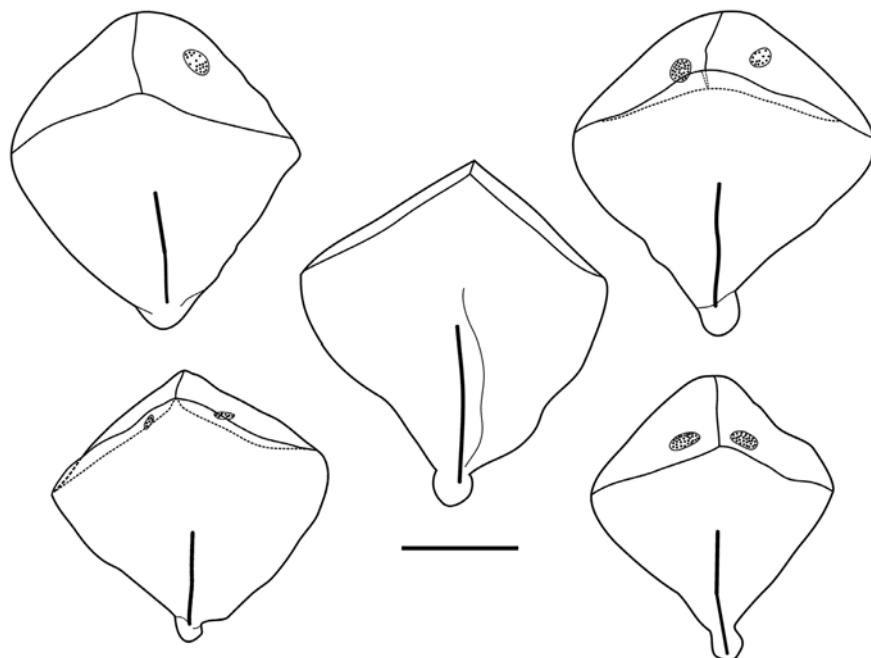


FIGURE 33. *Cordagalma bimaculatum* sp. nov. Upper views of mature bracts from *Tiburon* Dive 1043 specimen. Proximal at bottom. Scale 0.5 mm.

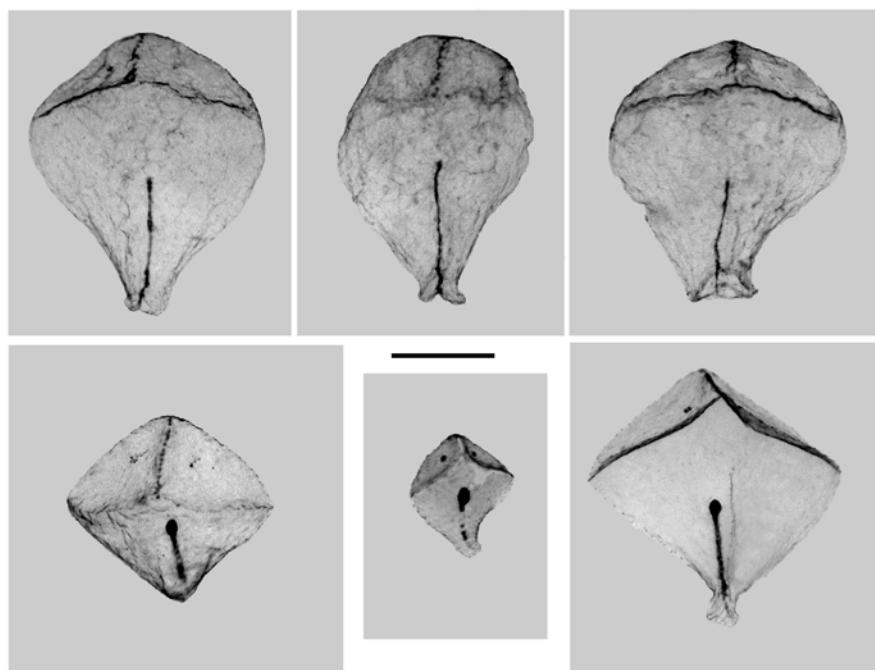


FIGURE 34. *Cordagalma bimaculatum* sp. nov. Photographs of the two types (top and bottom) of bract found with the *Doc Ricketts* Dive 419 specimen. Upper views, proximal at bottom. Scale bar 0.5 mm.

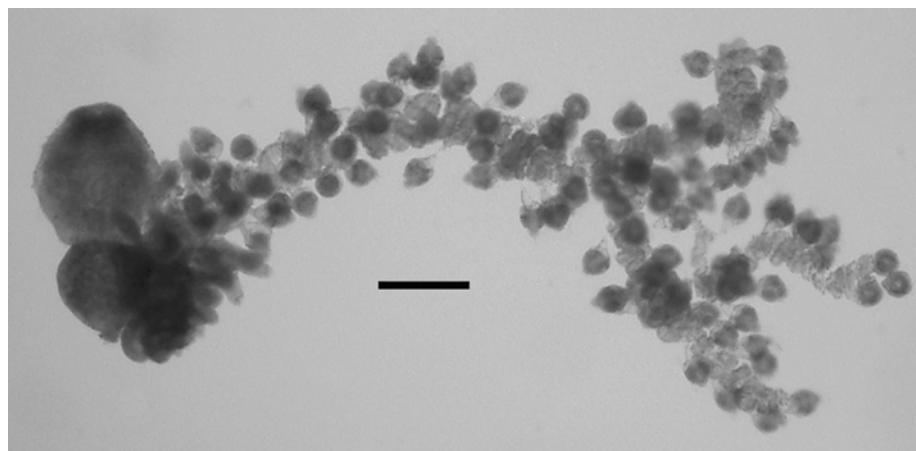


FIGURE 35. *Cordagalma bimaculatum* sp. nov. Gastrozooid and tentacle from holotype specimen. Scale bar 0.25 mm.

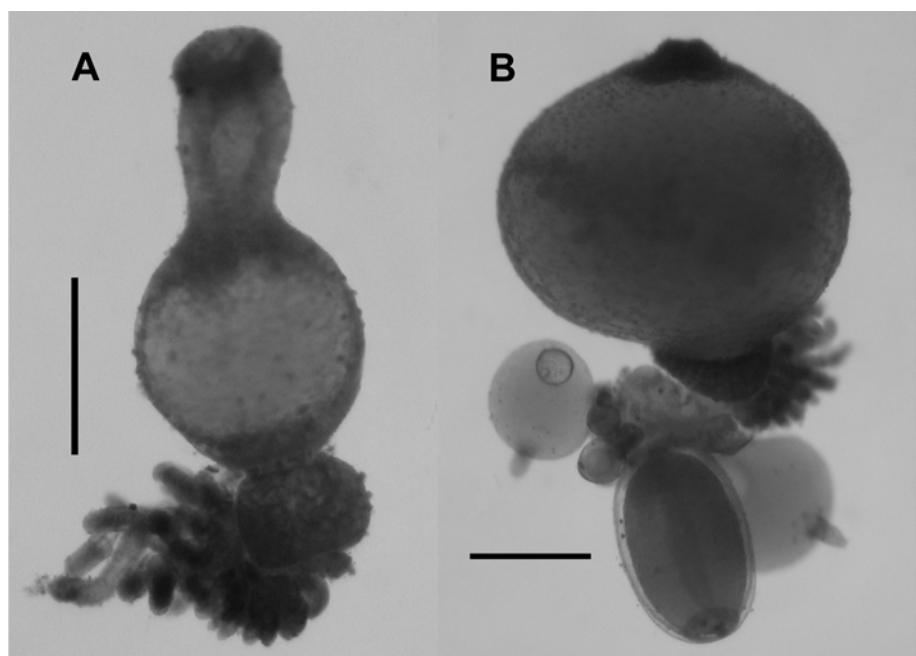


FIGURE 36. *Cordagalma bimaculatum* sp. nov. **A.** Individual gastrozooid; **B.** Small stem piece with a gastrozooid, a sideways mounted palpon and a male gonophore from *Doc Ricketts* Dive 500 specimen. Proximal at bottom. Scale bar = 0.5mm.

Amongst the Monterey Bay specimens just one, from *Tiburon* Dive 843, had only bracts resembling those found with the JSL specimens. Three others had only bracts of the type found with the *Tiburon* Dive 1043 specimen (Figure 33), while the specimen from *Doc Ricketts* Dive 419 had a combination of both types of bract in approximately equal numbers (Figure 34). With so few specimens it is impossible to speculate on any possibly reasons why these variations in the bract type occur.

Gastrozooid: The small gastrozooids measured up to 1.5 mm in length, and had a distinct basigaster measuring up to 0.3 mm in length (Figures 35–36), surmounted by an inflated stomach and a more or less extended proboscis. Dark brown droplets of oil were occasionally found at the base of the gastrozooids. The gastrozooids were, as usual, of very variable shape, not least those with the *Ventana* Dive 3005 specimen where there was a very large basigaster, a short narrow stomach that looked as if it formed the stalk for a toadstool-like proboscis region.

Tentilla: The proximal end of the tentacle was always highly contracted and it was impossible to make out the early stages in the development of the tentilla. The youngest tentilla observed (Figure 37A) were in the process of developing the cnidoband, and the cnidocils at their distal end were only rudimentary. The mature tentilla (Figure 37C, D) were very similar to the type of variant tentillum, without a rostrum, of *Cordagalma ordinatum* that Carré (1968) mentioned and figured in his Plate III, figure 7. Indeed the cnidobands of both included five proximal,

elliptical stenoteles, but for *C. bimaculatum* sp. nov. they were about twice as large, measuring 30 x 15 μm , as opposed to 17.5 x 8.5 μm for Carré's specimens. These stenoteles were grouped together on one side of the cnidoband. The other nematocysts in the cnidoband were not examined in detail, but were presumed to be the numerous anisorhizas in the middle and distal section, with a few distal isorhizas. At the distal end of the cnidoband there were numerous long cnidocytes, which in life were probably straight, but in the preserved state often twisted and distorted. No rostrum was present.

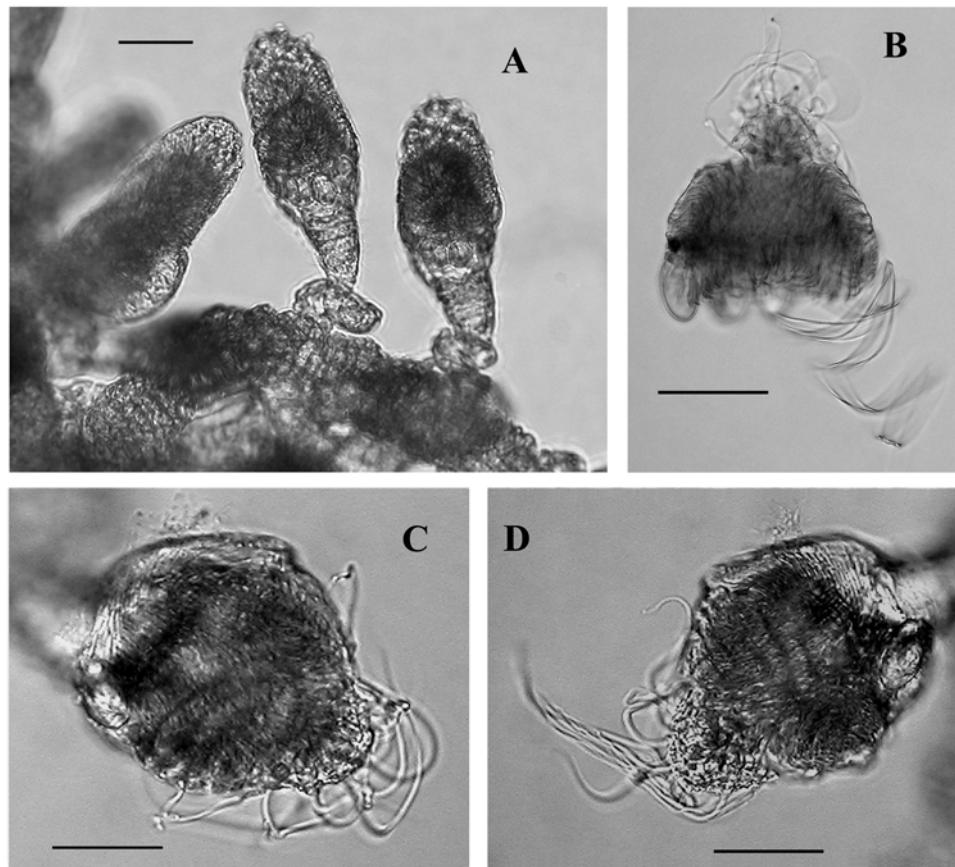


FIGURE 37. *Cordagalma bimaculatum* sp. nov. Tentilla from the type specimen. **A.** Young tentilla. Proximal at bottom.; **B.** Tentillum with concertinaed pedicle; **C & D.** Mature tentillum. Arbitrary views. Scale bars 50 μm .

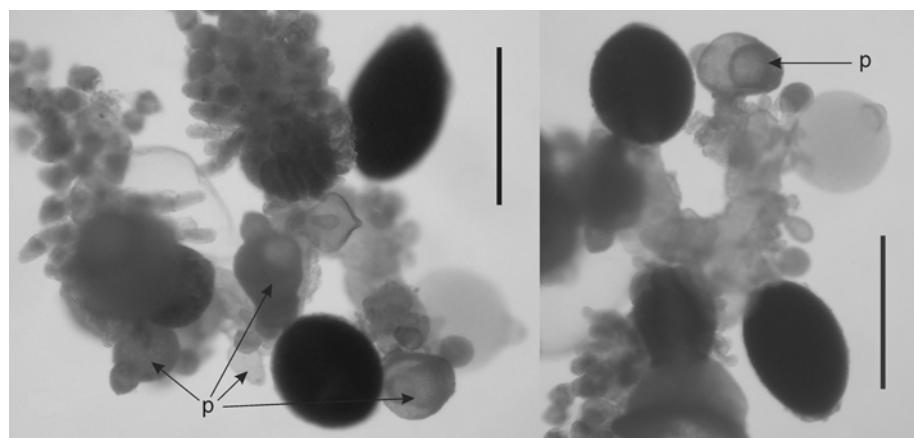


FIGURE 38. *Cordagalma bimaculatum* sp. nov. Palpons (p) from holotype specimen. Arbitrary views. Scale bars 0.5 mm.

One curious feature of the tentilla was that if pressure was applied to them the basal part of the cnidoband, with the exception of the stenoteles, became detached from the rest and was found (Figure 36B) to consist of a concertinaed, flattened tube that connected directly to the pedicle. Presumably, if fluid were to be pumped into it, it

would expand to form a long straight tube. What part this would play in prey capture is uncertain, but such an arrangement has not previously been observed in other siphonophore species.

Palpon: The palpons (Figures 38–39) were very small, up to 0.5 mm in length. They were roughly spherical in shape, with a more or less pronounced proboscis. For the larger palpons, at least, the short peduncle, which attached it to the stem, was placed laterally (see Figure 27). The exact mode of attachment of the developing palpons was difficult to discern. The palpons were without a palpacle. No nematocysts were found within the palpons. The palpons frequently contained golden or dark brown oil droplets of variable size; some occupying about a third of the interior. They were usually found laterally on the side opposite to the proboscis. Several of these were also present within the gastrovascular cavity of the stem, and many of them were released shortly after the specimens had been collected.

The *Doc Ricketts* Dive 500 specimen contained numerous stem fragments featuring several palpons, all typically with an oil droplet apposed to the proboscis. Their attachment was usually laterally, but occasionally they appeared to be at a 45° angle such that each proboscis projected outwards at a similar angle. There was no evidence to suggest that there was more than one palpon per cormidium.

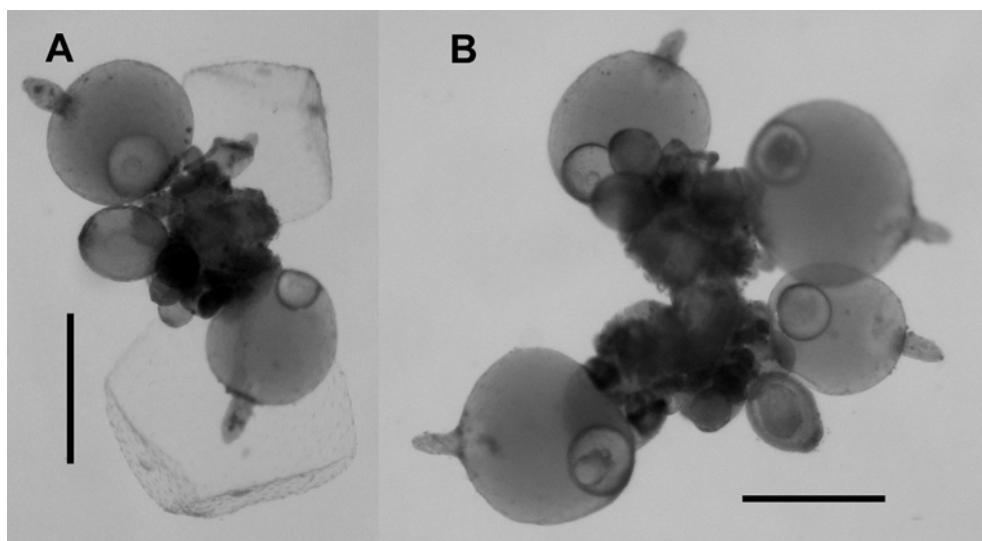


FIGURE 39. *Cordagalma bimaculatum* sp. nov. A., B. Two views of part of the siphosome of the specimen from *Doc Ricketts* Dive 500. Arbitrary views. Scale bar = 0.5 mm.

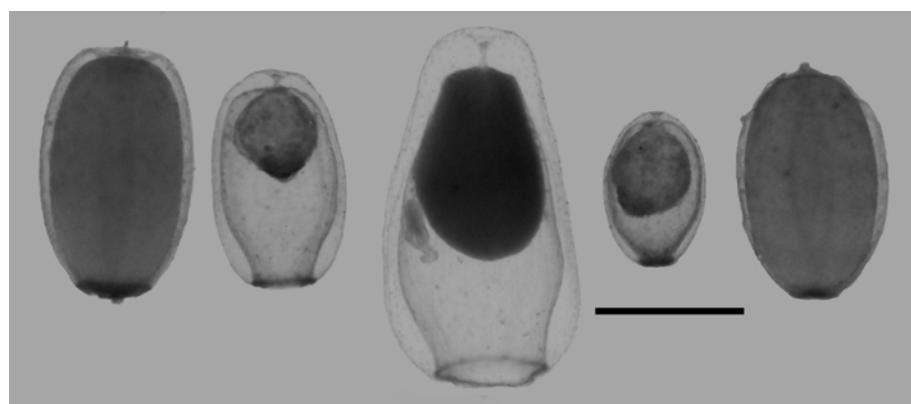


FIGURE 40. *Cordagalma bimaculatum* sp. nov. Male gonophores from *Doc Ricketts* Dive 500 specimen. Proximal at top. Scale bar 0.5 mm.

Gonophores: (Figures 38–40). Both male and female gonophores were present on each specimen, although the holotype possessed very few of them. They were more numerous on the JSL 1405 and *Doc Ricketts* Dive 500 specimens. The male ones (Figure 40) measured up to 1.2 mm in length, and 0.7 mm in diameter and had a distinct spadix, and were generally smooth-walled. The female ones were smaller and spherical, measuring c. 0.25 mm in

diameter, and the external ectoderm often showed the presence of large spherical cells. The pieces of siphosome were too contracted to be able to discern whether each cormidium possessed gonophores of both sexes, or were unisexual.

Remarks. As mentioned above *Cordagalma bimaculatum* sp. nov. is one of three *Cordagalma* species that are now known to occur in the western Mediterranean. The best known species, *C. ordinatum* is easily distinguished from the others by the presence of a rostrum on the larval-type tentilla. The differences between *C. bimaculatum* sp.nov. and the other Mediterranean species, *C. isocarrei* sp. nov, will be discussed below.

Distribution. The species is known from three widely separated sites; the Alborán Sea (western Mediterranean), the Bahamas, and Monterey Bay, California. In the warmer waters of the Mediterranean and the Bahamas the two specimens were found at similar depths, namely 747 and 726m, respectively. It should be noted that the specimen from the Mediterranean was inadvertently referred to as *Cordagalma ordinata* by Mills *et al.* (1996). In the colder waters of Monterey Bay the five specimens were found at much shallower depths, mainly between 400 and 587 m, with one specimen collected at 302 m. There are frame grabs for other *in situ* specimens of *Cordagalma* that were not collected but according to their depth probably were *C. bimaculatum* sp. nov. These were Tiburon Dives 1107 (404 m) and 1113 (470 m) and Doc Ricketts Dives 33 (494 m) and 104 (494 m).

Mackie (1985) made several observations of what he called *Cordagalma cordiforme* from British Columbian waters using the submersible *Pisces IV*. The bulk of these observations were within the 200–400 m depth range, with a few deeper records, but none shallower than c. 180 m. It is possible that some of the deeper observations refer to *C. bimaculatum* but, as we shall see, there are other *Cordagalma* species in this depth range that appear to be more common in Monterey Bay. Although Mapstone (2009) did not have any specimens of a *Cordagalma* species in her collections, she decided to include a description of *C. ordinata* = *C. cordiforme* = *C. ordinatum* on the basis that Mackie (1985) had noted its presence in British Columbian waters. The specimens used for this description were a couple belonging to the present author, of which one was actually *C. bimaculatum* sp. nov. Thus her figure 22D definitely represents a bract of *C. bimaculatum* sp. nov., as may those of the nectophores. The other bract was possibly that of *C. ordinatum*, although her interpretation of the nematocysts as "tubercles" is clearly incorrect.

Etymology. The specific name *bimaculatum* refers to the two patches of cells present on both the nectophores and the bracts.

Cordagalma isocarrei sp. nov.

Diagnosis. Small nectophores that, when mature, have a relatively short, broadly truncated basal process. A pair of small lateral ostial processes and, usually, a pair of patches of ectodermal cells on the lower lateral sides of the velum. No other patches present. Preserved specimens have a pair of furrows on the ostial side of the nectophores. The descending mantle canal is longer than the ascending one. Small rhomboidal bracts with more or less well-defined transverse and median ridges. The upper side is truncated; the distal margins formed by the transverse ridge, the proximal ones extremely vague. A pair of patches of ectodermal cells on the distal facets of younger bracts, but lost in the fully mature ones. Palpons are attached baso-laterally so that the proboscis and opening are at an angle of c. 135° to the stem.

Material examined.

<i>Ventana</i> 3557-D7	36°42'N 122°02'W	3-May-2010	Depth 214m
<i>Ventana</i> 3558-D2	36°42'N 122°02'W	3-May-2010	Depth 206m
<i>Ventana</i> 3558-D6	36°42'N 122°02'W	3-May-2010	Depth 218m
<i>Ventana</i> 3642-D1	36°42'N 122°02'W	11-May-2011	Depth 115m
<i>Ventana</i> 3629-D7	36°42'N 122°03'W	11-May-2011	Depth 357m
<i>Ricketts</i> 199-SS9	36°42'N 122°06'W	12-Oct-2010	Depth 421m

Holotype: The specimen collected during the *Ventana* Dive 3558-D2 has been designated the holotype, and will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

The remaining specimens will be placed in the collections of Dr Casey Dunn, at Brown University, Providence, Rhode Island, USA.

Description. A very poor *in situ* frame grab of the *Ventana* Dive 3558-D6 specimen, but the best available, is shown in Figure 41. It is possible to see that the siphosome was very long in comparison with the nectosome (bottom right) and that the whole structure was very delicate.

Pneumatophore: The pneumatophore was minute, measuring c. 0.35 mm long and 0.14 mm in diameter. There were no obvious signs of pigmentation.

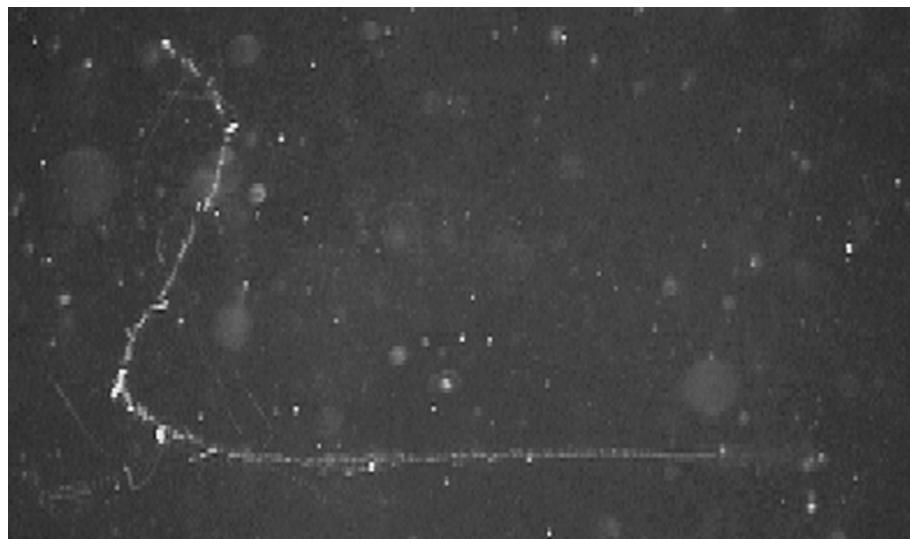


FIGURE 41. *Ventana* Dive 3558-D6 specimen of *Cordagalma isocarrei* sp. nov. at a depth of 215 m.

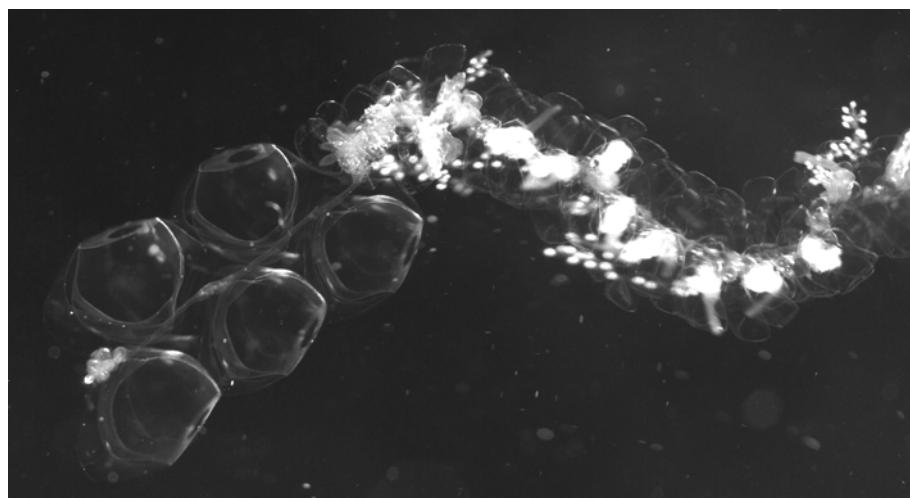


FIGURE 42. Photograph of V3629 specimen of *Cordagalma isocarrei* sp. nov., taken shortly after collection. Scale unknown. © Steve Haddock.

Nectosome: The nectosome was relatively short and the maximum number of nectophores retained with any specimens was fifteen mature, one developing and one very young. They were attached to the ventral side of the nectosome. Their alternating arrangement can clearly be seen in Figure 42, although the number of nectophores at that time had been reduced to five.

Nectophore: (Figure 43). Seventeen small nectophores were found with the type specimen, which was the largest number for any specimen. There was also a loose nectophoral bud. They measured up to 5 mm in length and 3.9 mm in width. On the older nectophores (Figure 43A) the basal process was relatively short and broad, with a broad distal portion. However, in the developing nectophores (Figure 43B, C) it was narrower and more pointed. The rounded axial wings were quite extensive and, usually, were separate by a narrow V-shaped indentation. On

the ostial side of the nectophore, a pair of ill-defined ridges was present on the inner sides of the axial wings that continued down to above ostial level and demarcated a deep gutter between them. Also on the ostial side was a pair of lateral furrows that ran obliquely out and up from the lateral margins of the ostium. They may have been preservation artefacts, but their presence was quite constant.

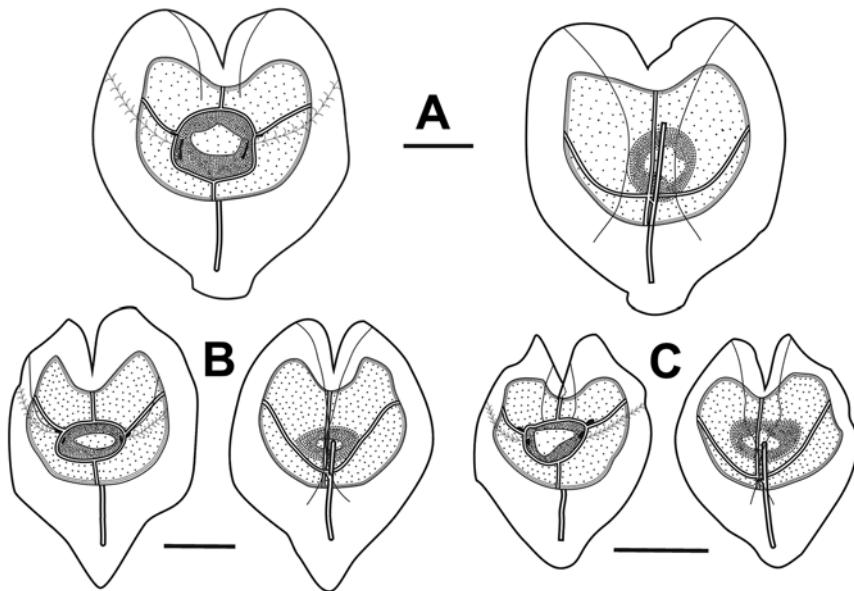


FIGURE 43. *Cordagalma isocarrei* sp. nov. Nectophores from holotype specimen. A. Large, B. medium, and C. small. Ostial (left) and axial (right) views. Scale bars 1 mm.

On the axial side of the nectophores there was a pair of lateral ridges that demarcated the margins of the hydroecium. They were very vague in the upper half of the nectophore, but more prominent basally before they petered out just below the lower level of the nectosac. In the younger nectophores they tended to approach each other more closely, while in the larger ones the mesogloea on the inner sides was thickened with the narrow hydroecial furrow running between them.

The upper lateral margins extended into the axial wings to a greater or lesser extent, while the lower margin was almost squarely truncated. The radial canals had typical courses, the upper and lower being straight, the laterals first curving out and diagonally upwards, then down to join the ostial ring canal. The long descending mantle canal extended down into the basal process, although its distal portion was very vague. The ascending canal was shorter and extended up to the mid-ostial region. The pedicular canal gave rise to all four radial canals. Above each lateral radial canal, just before it joined the ring canal there was a small patch of ectoderm cells. Another pair of patches was present on the lower lateral sides of the velum. These patches were often extensive in the younger nectophores, but in the mature ones were smaller and more rounded.

Siphosome: Part of the long siphosome is shown in a tank photograph (Figure 42) of the V3629 specimen taken shortly after collection. For the preserved specimens the cormidia tending to separate into individual cormidia, sometimes more (Figure 44). These typically consisted of a posterior gastrozooid and tentacle, bearing tentilla, followed by a palpable palpon and gonophores of both sexes, although it is not clear in what order these were attached. Some photographs (e.g. Figure 44 top left appear to show the male gonophores attached posterior to the female ones, while the reverse is possibly the case for others (e.g. Figure 44, bottom right).

Bracts: The bracts (Figure 45) measured up to 2.2 mm in length and 1.8 mm in width. They were roughly rhomboidal in shape, with the younger ones resembling a diamond, the older ones more elongate. In the preserved state they were covered in pimples, but that was probably an artefact. The lower surface was flat, while the upper one was thickest centrally. There was a more or less well-defined transverse and median ridge; often with both appearing as just a rounded processes. Spherical nematocysts were found spaced out in a single row along the median ridge and, occasionally, onto the ridge demarcating the lower side of the distal facet. Also, on the younger bracts it was sometimes possible to see much smaller nematocysts arranged along the transverse ridge, but they had been lost in the mature ones.

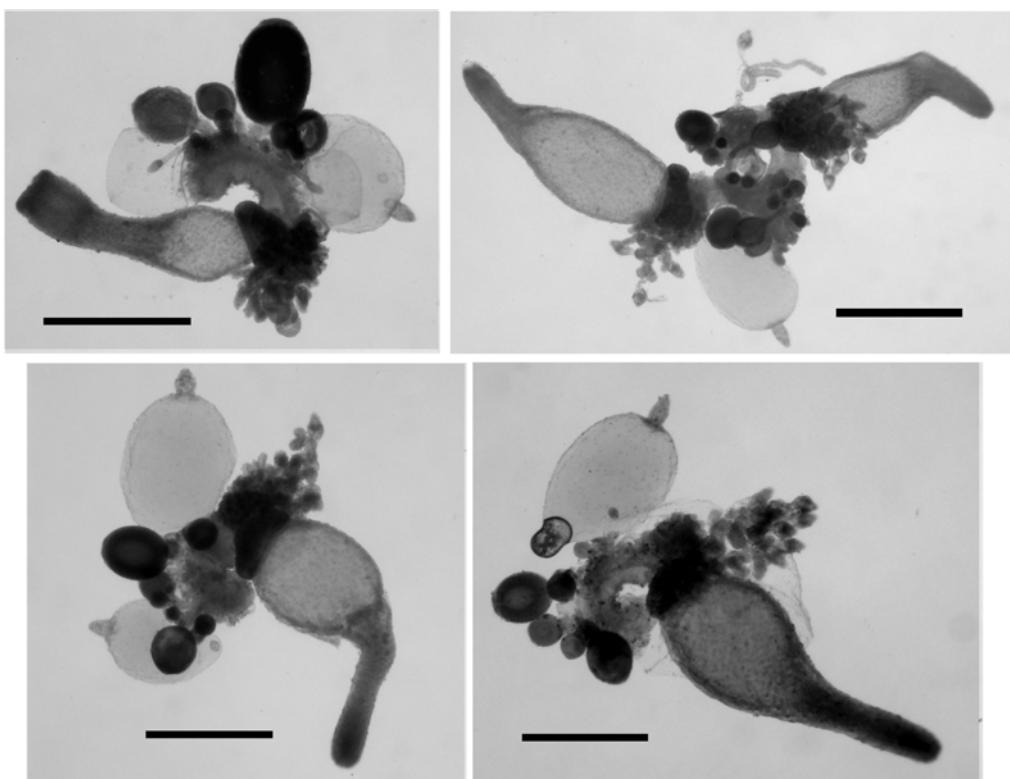


FIGURE 44. *Cordagalma isocarrei* sp. nov. Various detached cormidial groups from the type specimen. Arbitrary views. Scale bar 1 mm.

The central part of the upper surface was truncated, although the proximal margins of this truncation were often extremely difficult to see. Occasionally it was found that the truncation narrowed and stretched down to the proximal end of the bract. The bracteal canal arose close to, but not at, the proximal end of the bract and stretched up to its mid-length. It was terminated by a large ovoid swelling that was inflected into the mesogloea. The connection between this and the canal itself was sometimes very difficult to see. On the younger bracts there was a pair of patches of ectodermal cells on the distal facets, either side of the median ridge. These gradually disappeared such that there was no trace of them on the mature bracts.

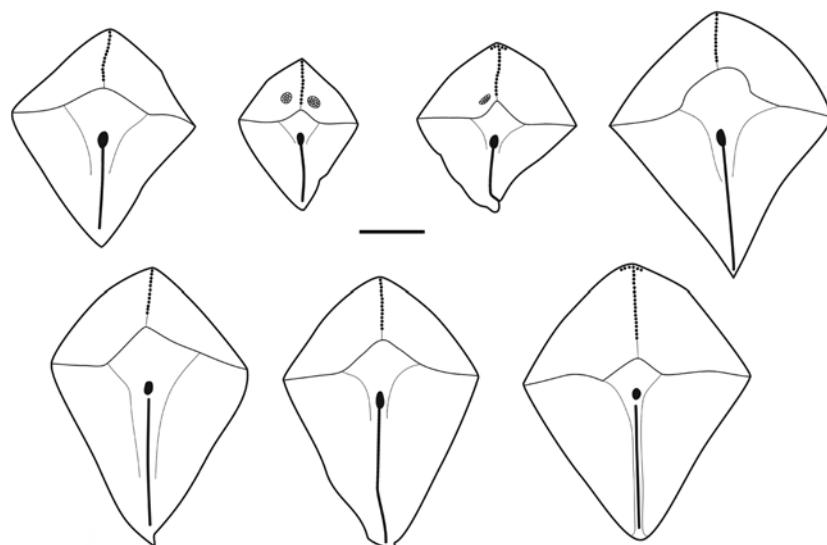


FIGURE 45. Upper views of bracts of type specimen of *Cordagalma isocarrei* sp. nov. Proximal at bottom. Scale bar 0.5 mm.

Gastrozoid: The gastrozooids (Figure 44) were small and quite variable in shape. They consisted of a long proboscis region, a more or less inflated stomach and a small, narrow basigaster. They appeared to be attached directly to the stem.

Tentilla: The mature tentillum (Figure 46) measured c. 120 µm in length and 100 µm in diameter. It had the typical *Cordagalma* organisation with five large stenoteles proximally, which measured 47 x 22 µm, partially surrounding numerous anisorhizas and surmounted, distally by a few ovoid isorhizas, with extremely long cnidocils that often were difficult to discern because of their transparency.

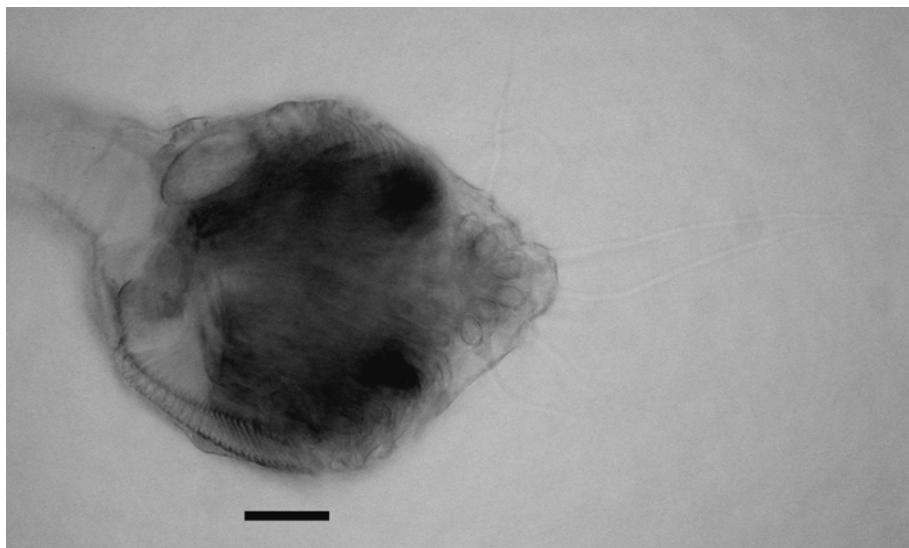


FIGURE 46. *Cordagalma isocarrei* sp. nov. Tentillum. Scale bar 100 µm.

Developing tentilla had the typical form noted in other species and were not investigated further, but see below.

Palpon: The palpons (Figures 47–48) generally measured up to 1.7 mm in maximum width and 1.0 mm in height, and were attached to the stem by a very short pedicle. The attachment point was not at the proximal end of the palpon but slightly lateral to it, so that the proboscis region stuck out at an angle of c. 135° to the stem. The proximal end of the palpon was usually marked by the presence of an oil droplet, of variable size.

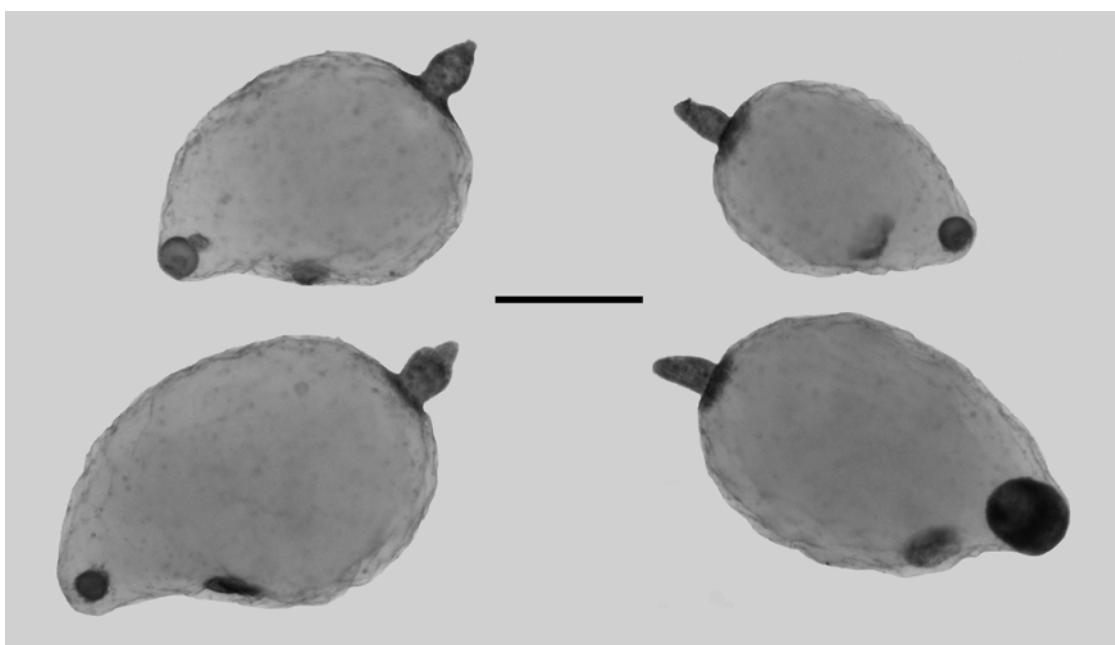


FIGURE 47. *Cordagalma isocarrei* sp. nov. Detached palpons from type specimen. Proximal at bottom. Scale bar 0.5 mm.

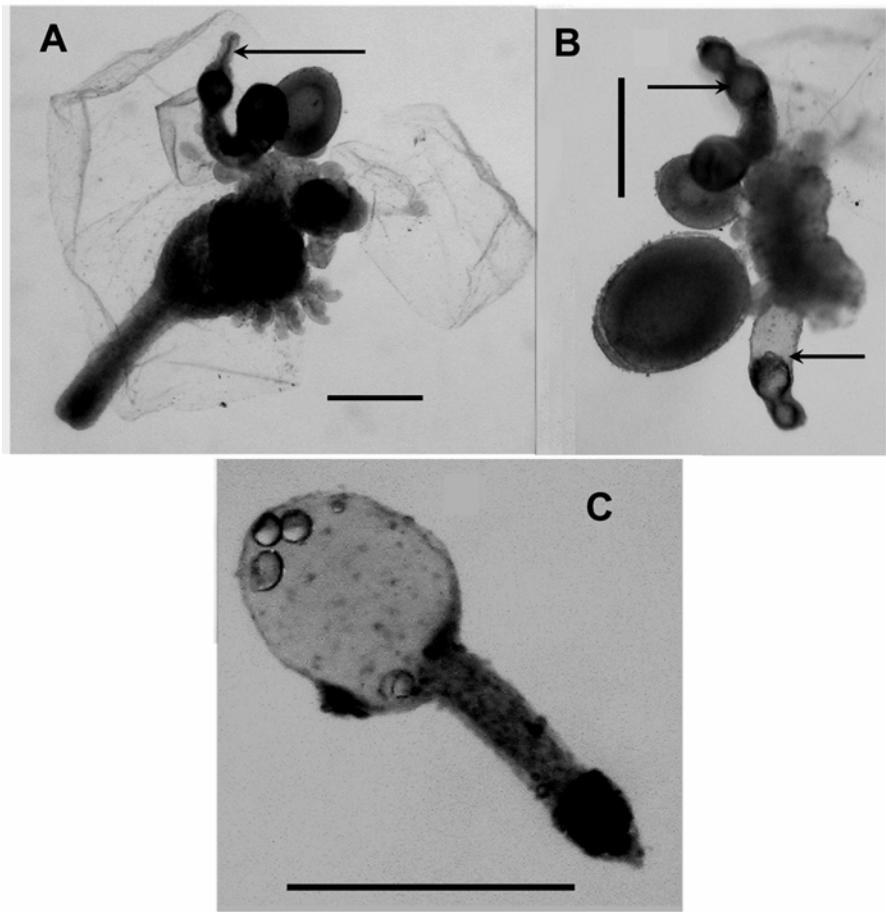


FIGURE 48. *Cordagalma isocarrei* sp. nov. **A. & B.** Odd shaped palpons (arrowed) from *Ventana* Dive 3557 specimen. **C.** Loose palpon from type specimen. Arbitrary views. Scale bars 0.5 mm.

In a few cases (Figure 48) the palpons took on a very different shape. Although this might have been a preservation artefact, most of the palpons found with the *Ventana* Dive 3557 specimen were of this kind. The proboscis region became very pronounced in relation to the main body and they were filled with droplets of oil.

Gonophores: Mature gonophores of either sex were not often found with the specimens examined. However, the male ones (Figure 49, left) were quite distinctive and measured c. 1.35 mm in length and 0.7 mm in maximum diameter. The female ones were always very small and it was not clear as to whether the largest, which measured c. 0.55 mm in length and diameter, were actually fully mature.

Remarks. *Cordagalma isocarrei* sp. nov. and *C. bimaculatum* sp. nov. are the only two species of *Cordagalma* where the palpon is known to be attached laterally and not proximally. However, the angle at which the proboscis region projects out from the main body of the palpon is quite different, being 135° in the former and 90° in the latter. The differences in the morphology of the bracts of these two species, as is discussed below, should, in association with the above, clearly distinguish the two. The mature tentilla of neither species possess a rostrum, and the other Mediterranean species, *C. ordinatum*, remains unique.

It appears that *Cordagalma isocarrei* sp. nov. is the solution to the enigma as to the identity of the second species that Carré (1968) apparently described. What we know for certain about that species is that the tentilla were without a "rostre" and that the palpons were attached laterally, although Carré (ibid p. 83) also noted "certaines colonies ont des dactylozoïdes de type intermédiaire à insertion baso-latérale" [certain colonies have an intermediate type of dactylozooid that is attached baso-laterally]. In addition, he noted that some of the cormidia included gonophores of only one sex but, in that case, we do not know to which species he was referring. As has been discussed in the description of *C. ordinatum*, it has been very difficult to establish whether the cormidia of that species were monoecious or dioecious. On the other hand, the two other characters clearly distinguish it from *C. ordinatum*.

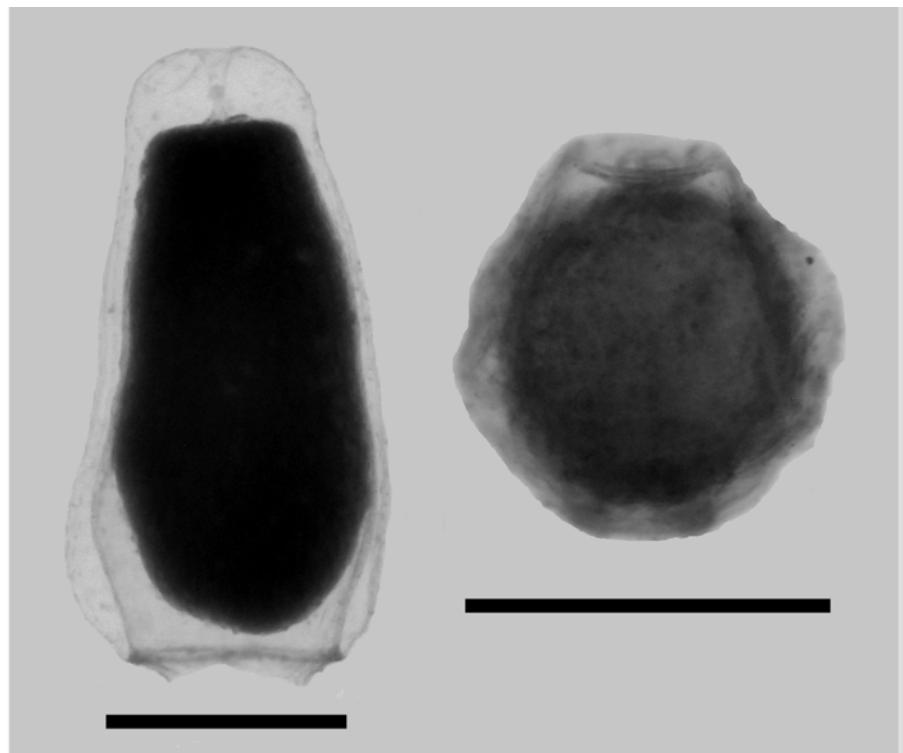


FIGURE 49. *Cordagalma isocarrei* sp. nov. Male (left) and female (right) gonophores from holotype specimen. Proximal at top. Scale bars 0.5 mm.

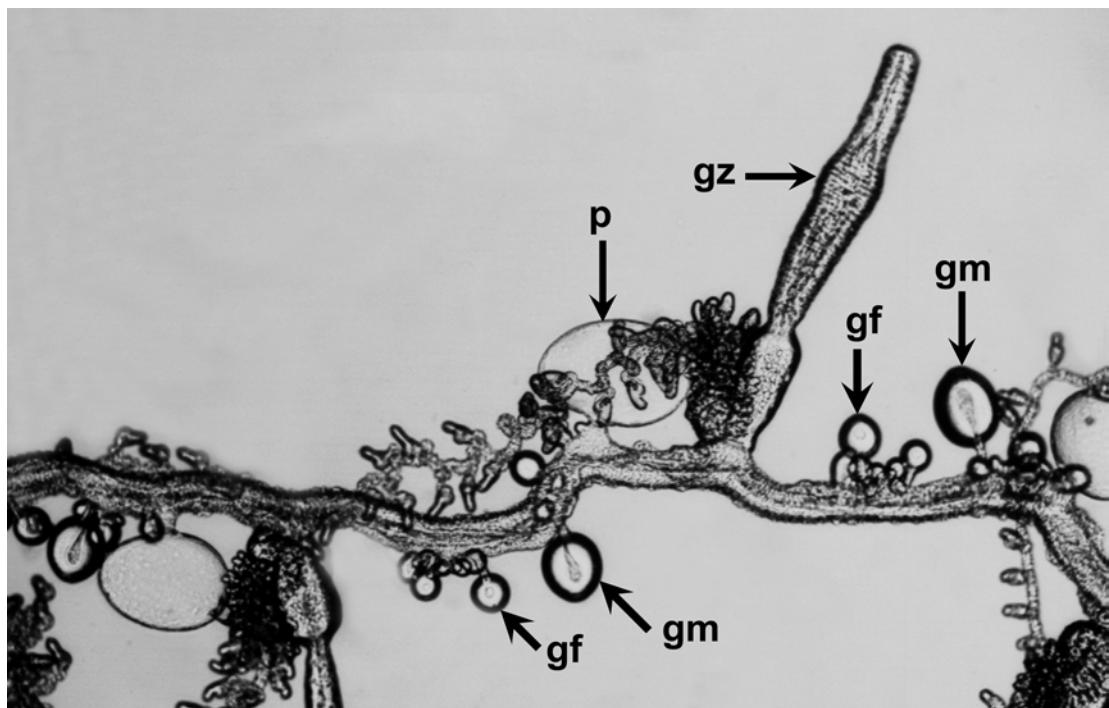


FIGURE 50. Part of siphosomal stem of Carré's other species, with all the bracts removed. Anterior to the left. Scale unknown. **gf.** and **gm.** female and male gonophores, respectively; **gz.** gastrozooid; **p.** palpon. (© C. Carré)

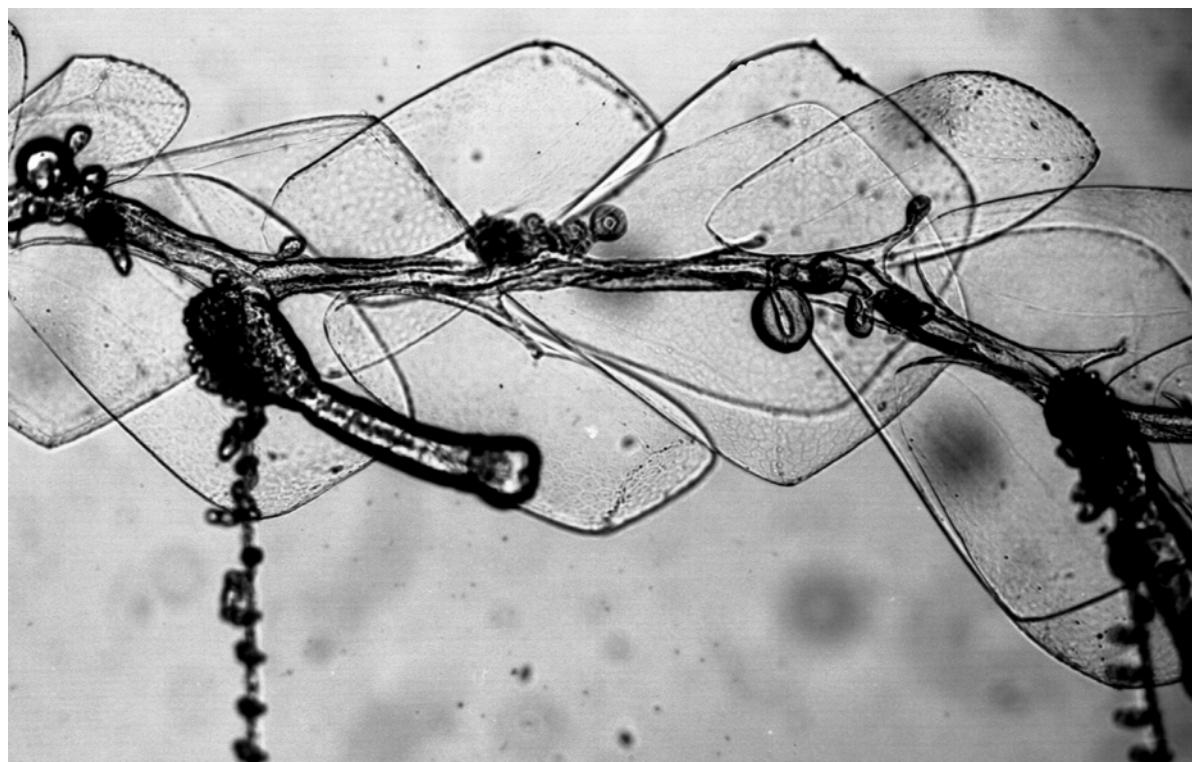


FIGURE 51. Cormidia of Carré's other species. Judging by the arrangement of the bracts proximal or anterior is to the left of the page, i.e. the female gonodendron precedes the male one. The palpons have become detached. Scale unknown. (© C. Carré)

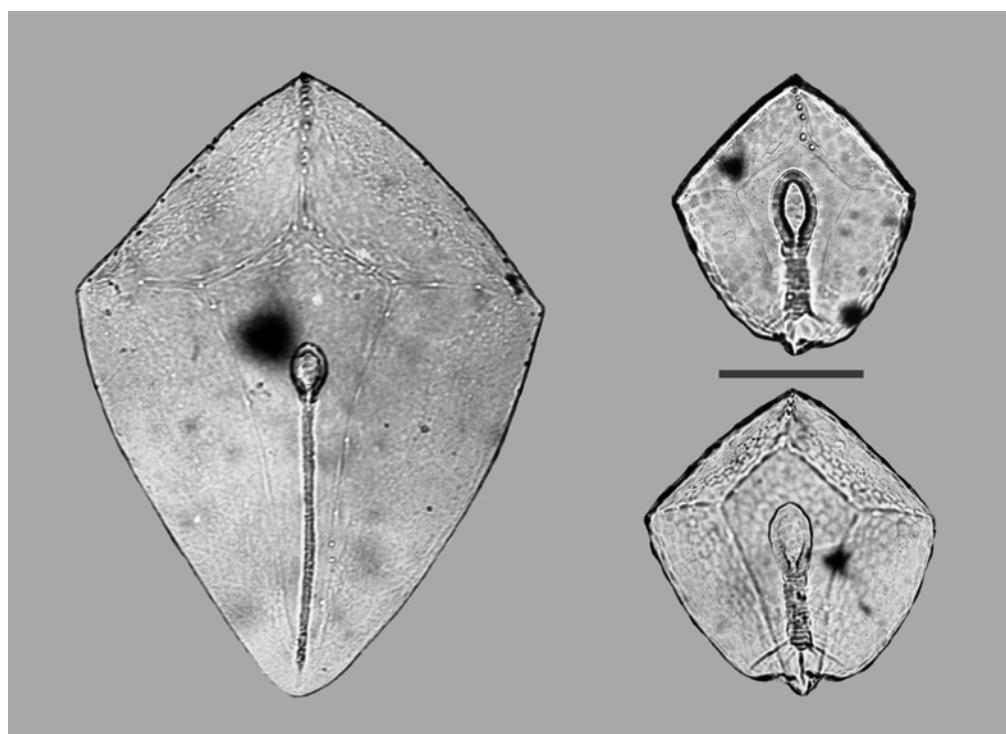


FIGURE 52. Photographs of upper views of mature (left) and very immature (right) bracts from Carré's other species. Proximal at bottom. Scale bar, for young bracts only, 200 µm. (© C. Carré)



FIGURE 53. Upper views of small bracts of *Cordagalma isocarrei* sp. nov. from type specimen. Proximal at bottom. Scale bar 0.5 mm.

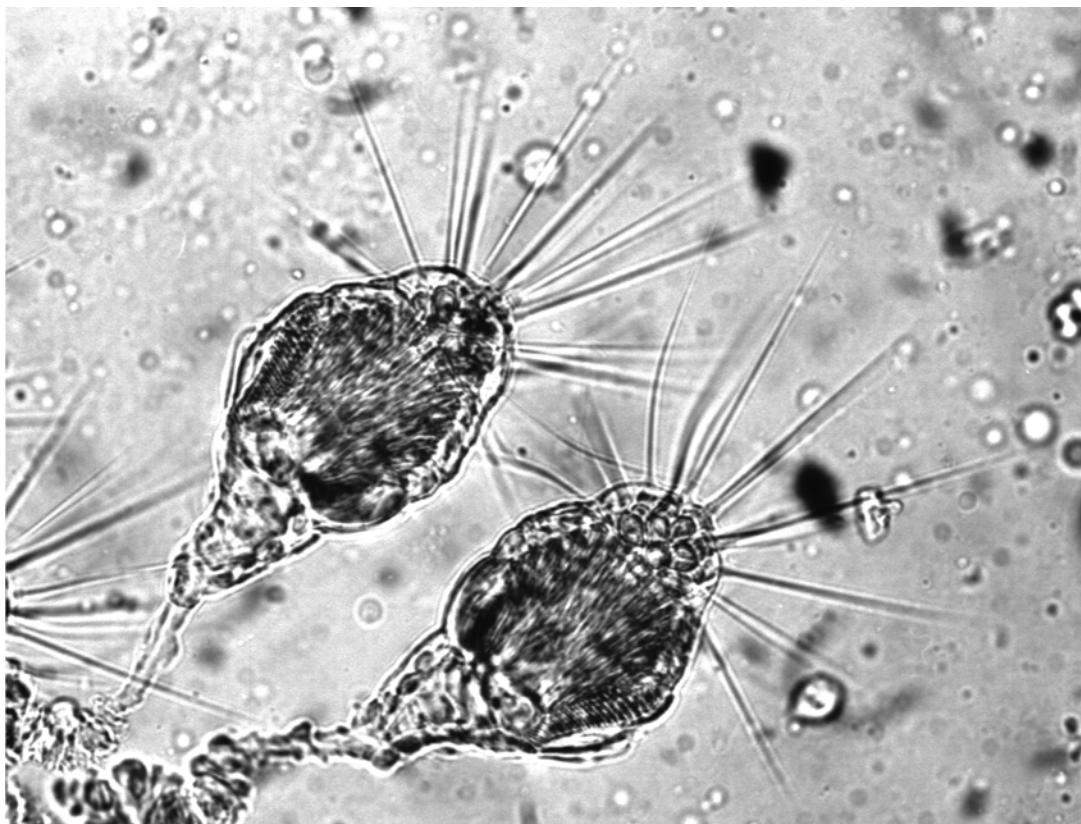


FIGURE 54. Mature tentilla from Carré's other species. Scale unknown. (© C. Carré)

Claude Carré took a number of photographs of his *Cordagalma* specimens and kindly provided some of these to me, together with some notes on his findings. Of particular interest are some fairly detailed observations and several photographs of a specimen that was collected on 14th March 1968. Having studied these in detail, we believe that there is sufficient evidence to consider that this particular specimen belongs to *C. isocarrei* sp. nov.

None of Carré's photographs of the nectosome and nectophores can be positively identified as either species, although from the pattern of patches on the velum it seems that that of a post-larval (see Figure 4) probably belongs to *Cordagalma ordinatum*. His notes suggested that the two pigment spots present on the nectophores of *C. ordinatum* were absent in *C. isocarrei* sp. nov. However, we do not know where these spots were positioned. However, Carré did remark that his nectophores measured up to 7 mm in length and 6 mm in width, which was considerably larger than the 3 mm in length and 3.2 mm in breadth that presently was found for the nectophores of

C. ordinatum. The nectophores of *C. isocarrei sp. nov.* were somewhat larger, that is 5.5 and 3.9 mm respectively, but still notably less than Carré's measurements, for which there is no obvious explanation.

Fortunately, there are several excellent photographs of the siphosomal stem and the various zooids attached to it, and representative ones have been selected here. Figure 50 shows the same arrangement of the cormidia, as was found for *Cordagalma ordinatum*, with, anterior to each gastrozooid, a palpon, some male gonophores and then some female gonophores. All the bracts had been detached. However, it is clear that the palpons were not attached basally and, although difficult to see in this photograph, the proboscis, at least the one to the lower left, has a baso-lateral attachment.

It can be seen that, in life, the gastrozooid was a long narrow tube with the proboscis region having a very narrow canal running through it. The basigaster was separated from the stomach by a constriction and was relatively long, particularly in comparison with the living ones of *Cordagalma ordinatum* (see Figure 10D), and the preserved ones of *C. isocarrei sp. nov.* (Figure 44). The gastrozooid appeared to be attached directly to the stem. The arrangement of the bracts on the siphosome is shown in Figure 51, and there appeared to be six per cormidium, although it was not clear if they were actually associated with any of the zooids.

The bracts shown in Carré's (1968, Plate II, fig. 2) look very similar to the ones in Figures 51 & 52 and so probably belong to Carré's other species (= *Cordagalma isocarrei sp. nov.*). They differed from the ones shown in Plate II, figure 1 and so one might presume that those belonged to *C. ordinatum*. This would also be true for the ones shown in Plate II, figure 4, as a small palpon attached basally by a short pedicle was shown. The only individual photograph of a bract in Carré's work (his Plate III, fig. 1) showed an extremely young bract. From Figure 52 (left), it can be seen that the mature bracts of Carré's variant species have a very distinctive shape that has all the characters described for the mature bracts of *C. isocarrei sp. nov.*, particularly with regard to the truncated region on the upper surface, the swelling at the distal end of the bracteal canal, and the presence of nematocysts on the lower part of the median ridge.

The very young bracts that Carré (1968) illustrated (Figure 52, bottom right) were very distinctive, and other photographs showed that they belong to Carré's variant species, i.e. *Cordagalma isocarrei sp. nov.* The smallest bracts that have been found with the type specimen of *C. isocarrei sp. nov.* (Figure 53) only superficially resembled them, although the smallest, which was about the same size as Carré's ones, did show some resemblance, especially in the thickening of the bracteal canal and its distal swelling. The nematocysts that can clearly be seen on the median ridges were identified by Carré (1968) as stenoteles, with a capsule size of 8.2 x 7.5 µm. On the same bracts, and so presumably belonging to *C. isocarrei sp. nov.* he described the presence of atrichous isorhizas on all the other edges, but these are not evident in the photographs, and no sizes were given. It is probable that Carré's bracts were photographed before preservation and that the clear-cut arrangement of the ridges changed after preservation.

With regard to the tentilla, Carré (1968, Plate III, fig. 7) illustrated a tentillum without a "rostre". A similar photograph is shown in Figure 54. In comparison with that of *Cordagalma ordinatum* (see above) the difference is very striking, and the similarities with that of *C. isocarrei sp. nov.* (cf. Figure 46) are very striking. It is somewhat surprising that neither Claude Carré (1968), nor Danielle Carré (1973) who studied the development of *Cordagalma ordinatum*, made any reference to the developing tentilla (Figure 55), although Claude Carré took several photographs of them. Large numbers of these can be present on mature tentacles and often they were larger than the mature ones. Basically, they were more elongate than the mature ones with the stenotele nematocysts isolated at the proximal end, while the cnidocils at the distal end were only beginning to develop.

As noted above the palpons of *Cordagalma isocarrei sp. nov.* were mostly attached baso-laterally, with the proboscis region projecting out at an angle of c. 135°. Although Carré (1968) noted that amongst his variable characters there was the fact that some palpons were attached laterally rather than basally, he also noted that the intermediate, baso-lateral, attachment position could be found. One, if not both, of the palpons shown in Figure 50 are certainly attached baso-laterally and of those shown in Figure 56 most appear to be attached baso-laterally and, interestingly, a small oil droplet often can be seen on the side opposite to the proboscis. The one on the extreme right also showed how the proboscis region can be deformed, as was noted for several of the *C. isocarrei sp. nov.* palpons. The one next to it is the only one that appears to be attached laterally. Thus there is a great similarity between the palpons of Carré's other species and those of *C. isocarrei sp. nov.* that is further evidence that these are one and the same species.

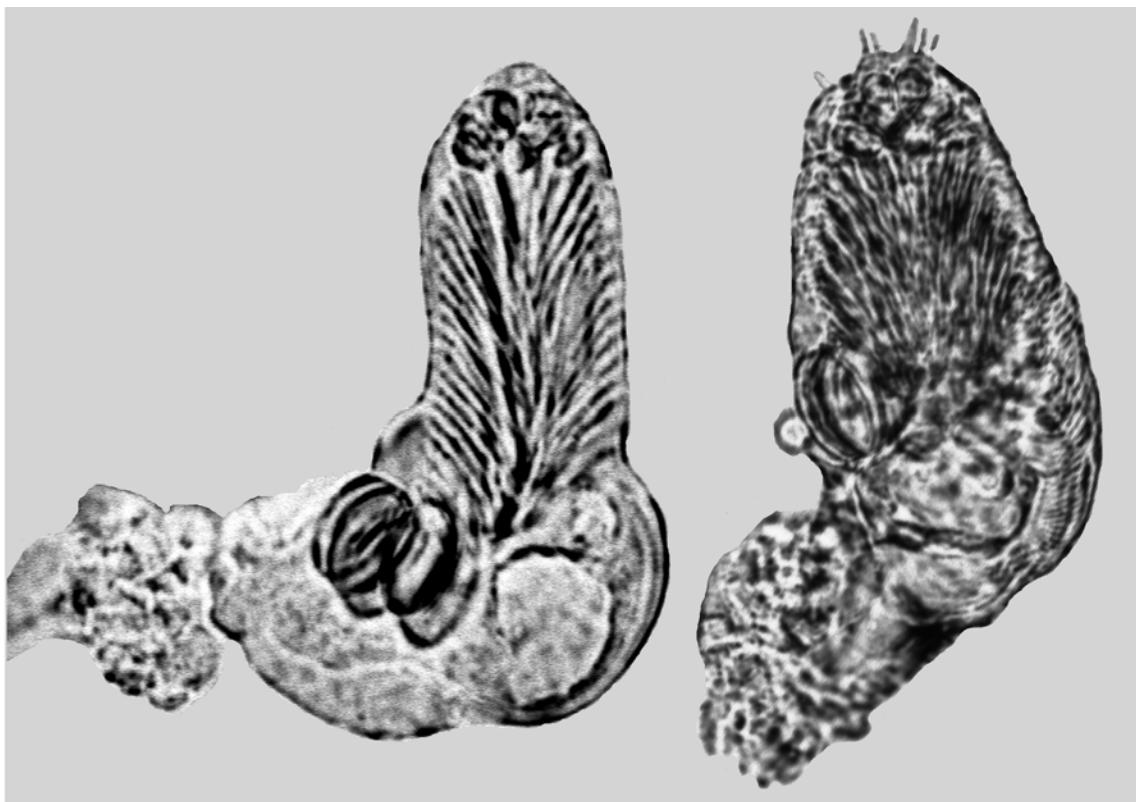


FIGURE 55. Young tentilla from Carré's other species. Scale unknown. (© C. Carré)

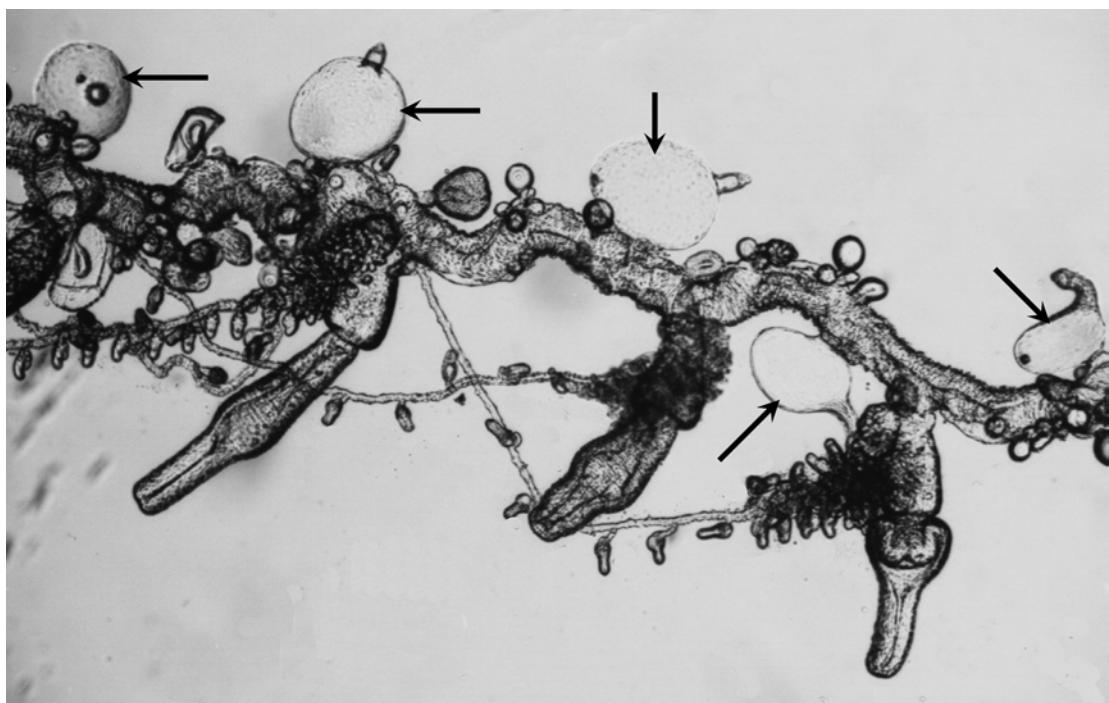


FIGURE 56. Cormidial groups from the siphosome of Carré's other species. Anterior to the left. The palpons are arrowed. Scale unknown. (© C. Carré)

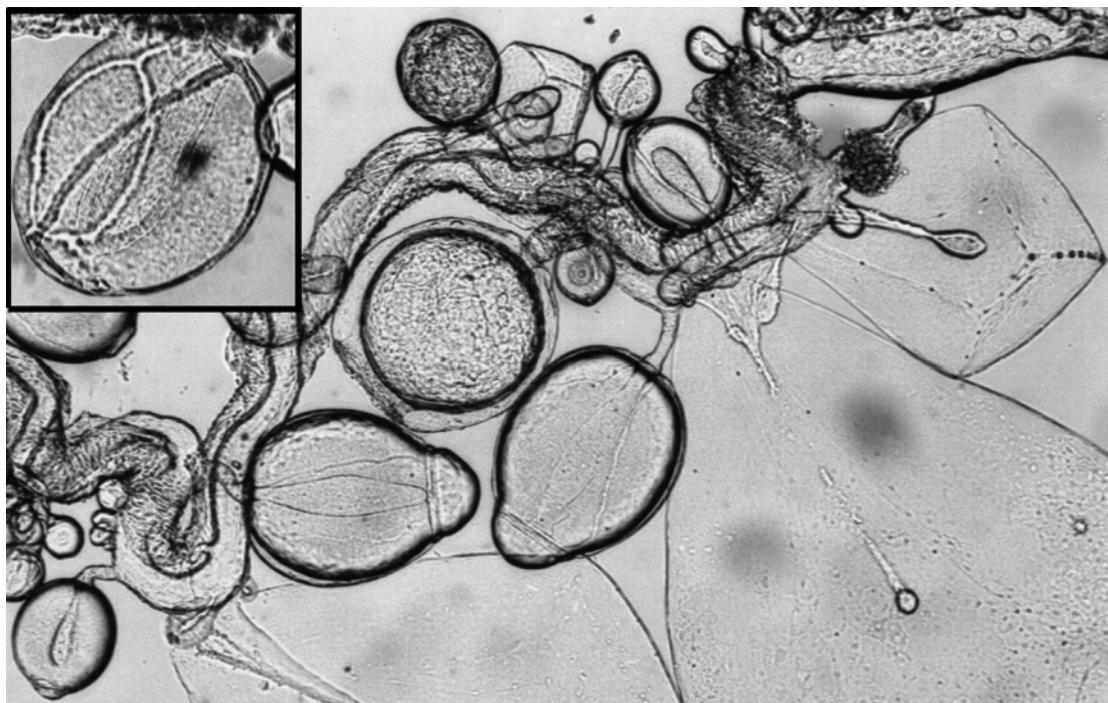


FIGURE 57. Gonophores from Carré's other specimen, with detail (inset) of female one. Scale unknown. (© C. Carré)

Finally, several of Carré's photographs show parts of the siphosomal stem with moderately well-developed gonophores (Figure 57). It can be seen that the larger male gonophores, with their distinctive spadix, were borne on long narrow pedicles, while the female gonophores had shorter ones. The presence of anastomosing radial canals on the female gonophores was somewhat similar to that drawn by Haeckel (1888b, Plate XV, fig. 15), but it probably is not a specific character.

All in all, there seems little to doubt that the species, *Cordagalma isocarrei* sp. nov., described above is the same as the one that Carré (1968) inadvertently included in his 1968 redescription of *C. ordinatum*. The general morphology of the bracts is very similar and the more often than not baso-lateral attachment of the palpons of Carré's second species supports this conclusion.

Distribution. The six known specimens of *Cordagalma isocarrei* sp. nov. come from a very limited area in Monterey Bay, California, mostly concentrate around the so-called "Midwater site". It is probable that other observations have been made of this species, but the transparency and fragility of the specimens make *in situ* specific identifications almost impossible. Three of the specimens came from a depth of c. 200 m, while one was collected much shallower, at 115 m. However, the other two were much deeper, with the deepest at 421 m. The depth range, therefore, overlaps that of *Cordagalma bimaculatum* sp. nov.

Carré's (1968) other species appears to have come from a net sample taken at an unknown depth, in the vicinity of Villefranche-sur-Mer, France, in the northwestern Mediterranean Sea.

Etymology. The specific name, *isocarrei*, refers to the fact that the species found in Monterey Bay so closely resembles the second one that Carré mistakenly described as *Cordagalma ordinatum* that there can be little doubt that they are one and the same.

Genus *Cardianecta* gen. nov.

Monotypic genus for *Cardianecta parchelion* sp. nov.

Cardianecta parchelion sp. nov.

Diagnosis. Most mature nectophores relatively large and flimsy, with typical heart-shaped appearance. Younger

ones with distinct notch on lateral wings. Long ascending and descending mantle canals of approximately equal length. No pigmentation. Bracts in enantiomorphic pairs; broad, leaf-like, tapering toward the proximal end; lower surface flat, upper domed. Indistinct longitudinal ridge from distal, median point to about half the length of the bract. Distal point, in young bracts, bearing nematocysts. Bracteal canal in contact with lower surface of the bract for about one-third its length; distal part, inflected into the mesogloea; relatively long in youngest bracts but gradually shortens to a short process in mature bracts. Tentilla of unique form, with involucrum forming two lateral flaps, and inflated terminal process bearing two asymmetrically placed horns, one terminal the other sub-terminal. At some stage in its development, the cnidoband spirally coiled and containing only one kind of nematocyst, probably mastigophores. Desmonemes (?) present in the terminal process, particularly in the horns. Proximally attached palpons possess a palpacle although often lost before the palpon becomes fully developed in the preserved state.

Material examined. 5 specimens collected by the Johnson-Sea-Link (JSL) submersibles, all in the vicinity of the Bahamas:

JSL II Dive 981	25°54.5'N, 77°17.8'W	28-Oct-1984	depth 640 m
JSL II Dive 998	25°22.0'N, 77°51.6'W	31-Oct-1984	depth 642 m
JSL I Dive 2633	26°14.8'N, 77°43.7'W	3-Nov-1989	depth 884 m
JSL I Dive 2643	26°02.3'N, 77°32.0'W	8-Nov-1989	depth 865 m
JSL I Dive 2650	26°04.0'N, 77°33.5'W	13-Nov-1989	depth 757 m

Holotype: The specimen collected during the Johnson-Sea-Link I Dive 2650 has been designated the holotype, and will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

Paratype: The specimen collected during the Johnson-Sea-Link I Dive 2633 has been designated the paratype, and will also be deposited at the United States National Museum (Smithsonian Institution), Washington, DC.

The remaining specimens will be placed in the collections of Dr Casey Dunn, at Brown University, Providence, Rhode Island, USA.

Description. *Pneumatophore:* The preserved pneumatophores were quite distorted, measuring c. 2.2 mm in length and 1.25 mm in diameter, but otherwise were quite featureless, without any obvious signs of pigmentation.

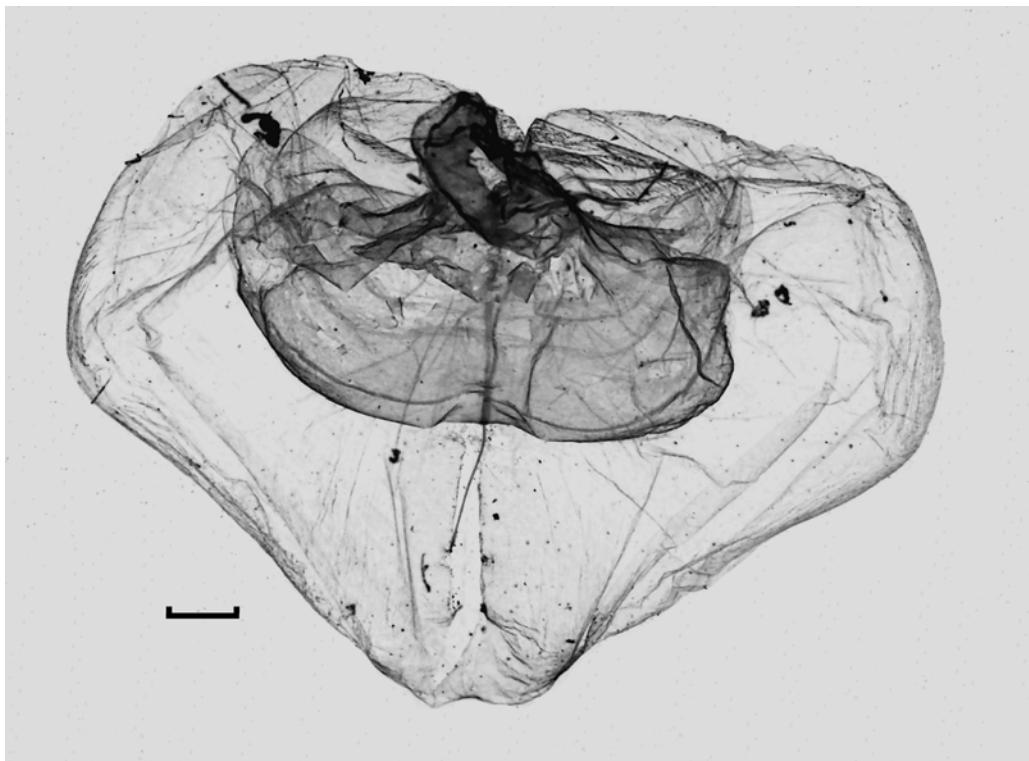


FIGURE 58. *Cardianecta parchelion* sp. nov. Ostial view of large, flimsy nectophore from paratype specimen. Scale bar 1 mm..

Nectosome: The nectophores were clearly budded from the ventral side of the nectosome.

Nectophore: The preserved nectophores were heart-shaped measuring up to 8.75 mm in length and 9.6 mm in width, without any obvious pigmentation. The largest nectophores were very flimsy and generally distorted in preservation (Figure 58), although those of the holotype specimen were better preserved. In ostial or axial view they were heart-shaped (Figure 59), with a squarish ostium measuring c. 2 mm across. The nectosac, in lateral view (Figures 60–62), was L-shaped, but deeply divided in the mid-line. The ascending and descending mantle canals were of approximately equal length. The pedicular canal passed straight to the nectosac where it gave rise to all four radial canals. The upper and lower canals were straight; the laterals were broadly looped and connected with the ostial ring canal at the upper corners of the squarish ostium, where a distinct tract of ectodermal cells extended obliquely up the sides of the nectophore (Figure 59, 61 **tec**) for a short distance.

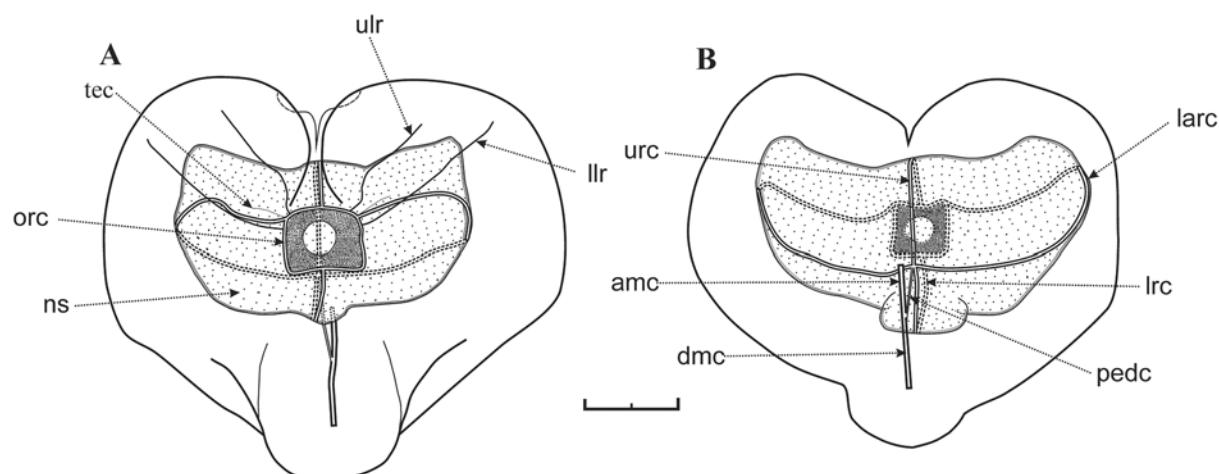


FIGURE 59. *Cardianecta parchelion* sp. nov. A. Ostial and B. axial views of larger nectophore from holotype specimen. **amc**, **dmc**: ascending and descending mantle canal, respectively; **larc**, **lrc**, **orc** and **urc**: lateral, lower, ostial ring and upper radial canals, respectively; **llr** and **ulr**: lower and upper lateral ridges respectively; **ns**: nectosac; **pedc**: pedicular canal; **tec**: tract of ectodermal cells. Scale bar 2 mm.

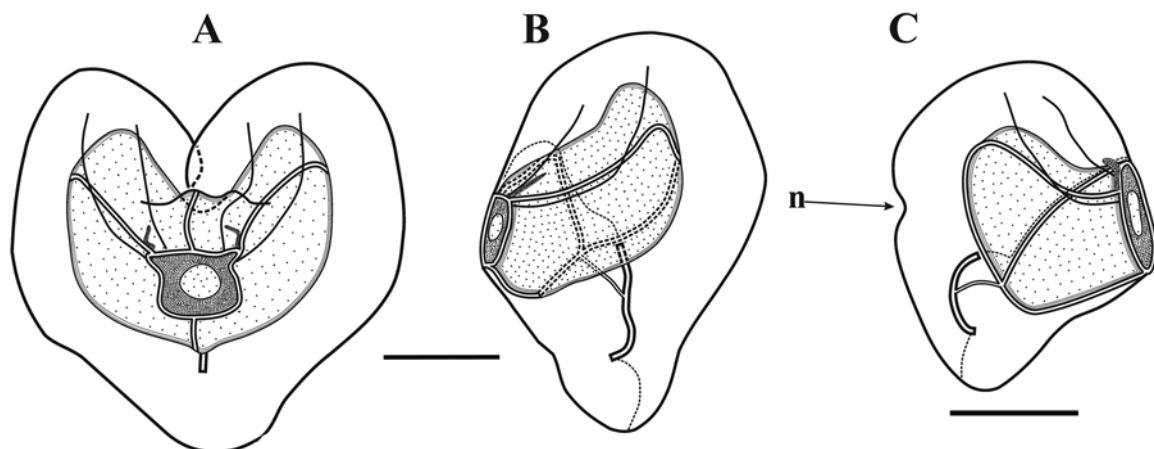


FIGURE 60. *Cardianecta parchelion* sp. nov. A. ostial and B. lateral views of larger nectophore; C. lateral view of young nectophore, both from holotype specimen. **n**: notch in lateral wings. Scale bars A and B 2 mm, C 1 mm.

One feature of the younger nectophores was that there was a distinct notch in each lateral wing (Figures 60C, 61A **n**), but the more mature the nectophore the more indistinct this notch became. Another was the presence of two pairs of lateral ridges, although they were often difficult to discern (Figures 59–61). The upper pair (Figure 59A, 61A **ulr**) stretched upwards on either side from the upper side of the squarish ostium, approximately half way between the points of insertion of the upper and lateral radial canals, toward the upper end of the nectophore, but

petered out approximately on a level with the apex of the nectosac. They were more indistinct than the lower lateral ridges and, because of damage to the ostial region it was uncertain whether they actually connected with the ostium itself. The pair of lower lateral ridges (Figures 59A, 61A IIr) was usually more distinct and often was paralleled by a furrow on their upper side, although this might have been a preservation artefact. They arose from the sides of the ostium just below the point of insertion of the lateral radial canals and followed a similar course to the upper lateral ridges.

Siphosome: The siphosomal stem, if present, was always greatly fragmented such that it was not possible to glean any information regarding the organisation of the individual cormidia.

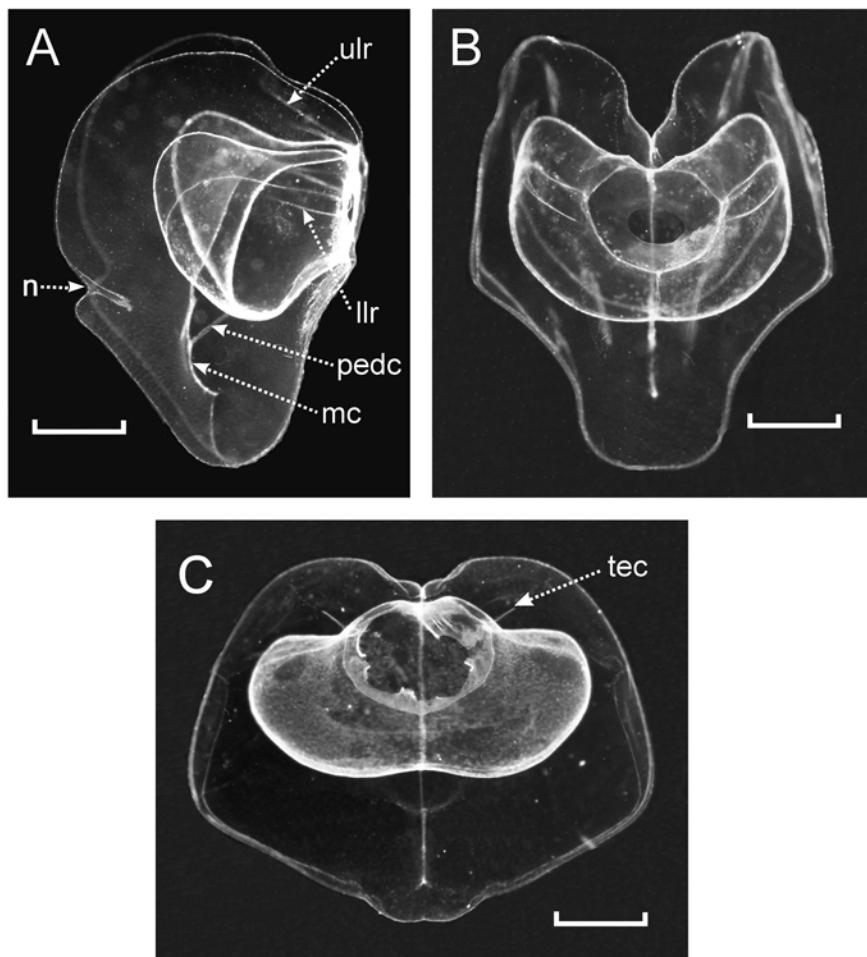


FIGURE 61. *Cardianecta parchelion* sp. nov. Lateral (A), ostial (B), and ostio–basal (C) views of younger ectophore from JSL I Dive 2643 specimen before preservation. See Figures 59 and 60 for legend. Scale bar 1 mm.

Bract: The bracts (Figures 62–63) were of a single type and occurred in enantiomorphic pairs. They measured up to 6 mm in length and 5.2 mm in greatest width. They were broadest in their distal half, rapidly tapering down to a small, ventral distal point; with a flat lower side and a domed upper one. In the younger bracts this point was occupied by an accumulation of c. 20 nematocysts, measuring $32 \times 18 \mu\text{m}$. However, in older bracts these nematocysts had usually been abraded. In the preserved specimens there was an indistinct ridge that ran from the distal point of the bract to about half its length. However, in the bracts photographed before preservation (Figure 63) this ridge can clearly been seen. In the youngest bracts (Figure 62) the ridge was quite broad and included two or three rows of distinctive ectodermal cells. The bract tapered down, proximally, more rapidly on the inner side than the outer to form a prominent protuberance at the proximal end. The length of the bractal canal varied according to the age of the bract, but it was never seen to extend the whole length of the bract. In the youngest ones the canal stretched to about three-quarters the length of the bract, and the part enclosed within the mesogloea was twice as long as the part that ran along the lower surface. The former part was also much broader, and included a

broad canal. As the bract developed the internal portion of the canal decreased in length, while the proximal part lying against the lower surface increased. Eventually, in the largest bracts the proximal part of the bractal canal extended to about one-third their length, and the part inflected into the mesogloea was very short.

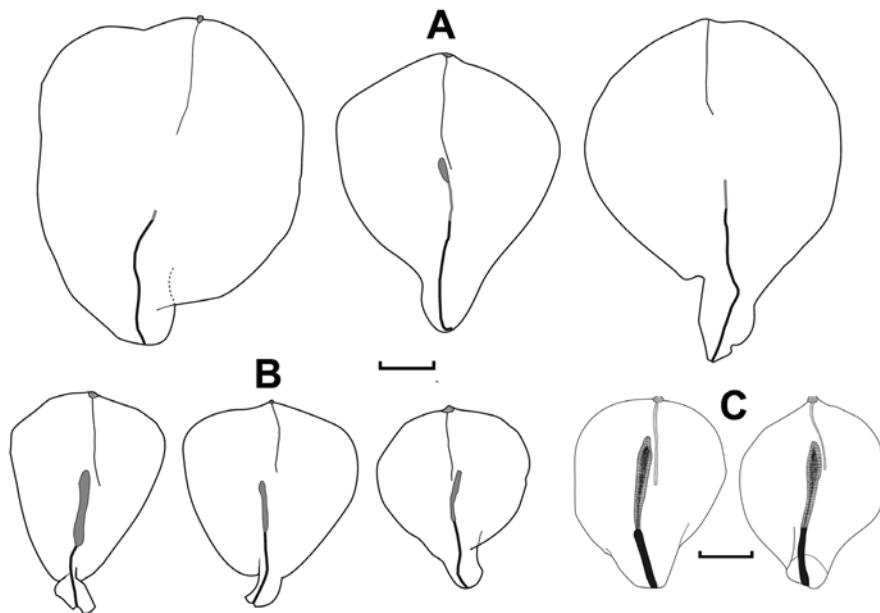


FIGURE 62. Upper views of bracts of *Cardianecta parchelion* sp. nov. **A.** mature, and **B.** developing bracts from the holotype (scale bar 1 mm). The grey part of the bractal canal is within the mesogloea. **C.** Very young bracts from the JSL I 2633 specimen. Proximal end at bottom. Scale bars 0.5 mm.

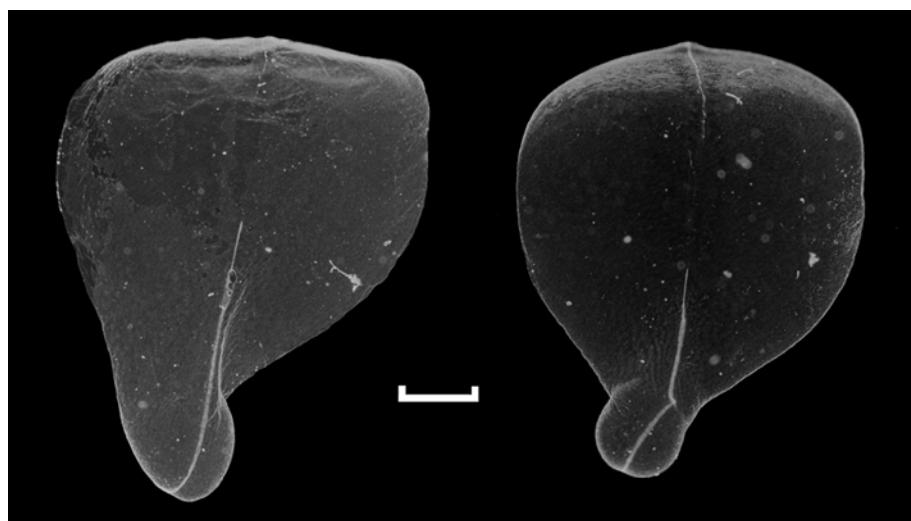


FIGURE 63. *Cardianecta parchelion* sp. nov. Photographs of upper side of bracts from paratype specimen before preservation. Proximal end at bottom. Scale bar 1 mm.

Gastrozooid and tentacle: The gastrozooids (Figure 64) typically were very variable in size and shape, particularly with regard to the stomach section. The largest measured up to 9 mm in length and 23 mm in greatest width. There was a prominent, cylindrical basigaster that measured about 2.3 mm in length and slightly less in width, which was separated from the main stomach region by a distinct constriction. There was no obvious distal proboscis region, but the mouth and much of the stomach could open widely, revealing the hepatic stripes (Figure 64 right).



FIGURE 64. *Cardianecta parchelion* sp. nov. Gastrozoooids from JSL II 998-D4. Proximal at bottom, distal at top. Scale bars 1 mm.

Tentilla: The tentilla first appeared as short, thickened, undifferentiated tubes at the proximal end of the tentacle (Figure 64). In the preserved specimens the distal end of this tube was often curved to one side, and it was part that next began to elongate and to twist itself into 2–3 spirals to form the rudimentary cnidoband, which at this stage did not appear to be covered by a membrane. At the same time the involucrum, between the pedicle and the cnidoband began to differentiate. It formed a horseshoe shaped swelling with the two loose ends closely apposed. Simultaneously the terminal process began to form as a flattened irregular swelling at the distal end of the cnidoband, with two short, broad distal protuberances (Figure 65A). The terminal process continued to enlarge into an almost spherical, relatively thick-walled swelling, bearing two, asymmetrically placed "horns"; one terminal and the other sub-terminal (Figure 65B, C). Up to this stage the pedicle remained short and broad, with a relatively wide central canal that at first was straight, but later began to twist into coils (Figure 65C), while the involucrum showed no further sign of development.

At the next stage of development the pedicle began to elongate considerably, becoming thinner walled, and with its central canal straightening out again, except at its distal end where, in the preserved state at least, it remained coiled. At the same time the cnidoband began to increase in length by the addition of further regular coils (Figures 65D; 66A, B, C) up to a maximum of six to seven. As the cnidoband reached its maximum development the involucrum began to develop further, by the lengthening of the free ends of the horseshoe and their gradual spreading apart (Figures 65E, F; 66D). Eventually these formed long lateral flaps that extended out sideways or curved distally to cover the cnidoband on two sides (Figures 65E–H; 66E, F; 67).

During this stage an external membrane began to cover the cnidoband. At first it was tight against the cnidoband, but later began to expand so as to leave a gap between. This was the ultimate stage found in most of the specimens, but in the holotype three tentilla were found that showed further development (Figure 65G, H). On these the terminal process expanded in size and its walls became thinner and indistinct from the membrane covering the cnidoband. Thus a thin-walled spherical cavity was formed that enclosed, usually in its proximal half, the cnidoband, and still retained the terminal and sub-terminal "horns". On one tentillum (Figure 65H) the cnidoband lost its regular coiling and formed a series of irregular loops. Whether this was an artefact caused by the breaking away of the proximal part of the cnidoband from the pedicle, is not clear, although other, less developed tentilla (e.g. Figure 66E) also showed a less regularly coiled cnidoband. No clear evidence for the presence of elastic or angle bands was found.

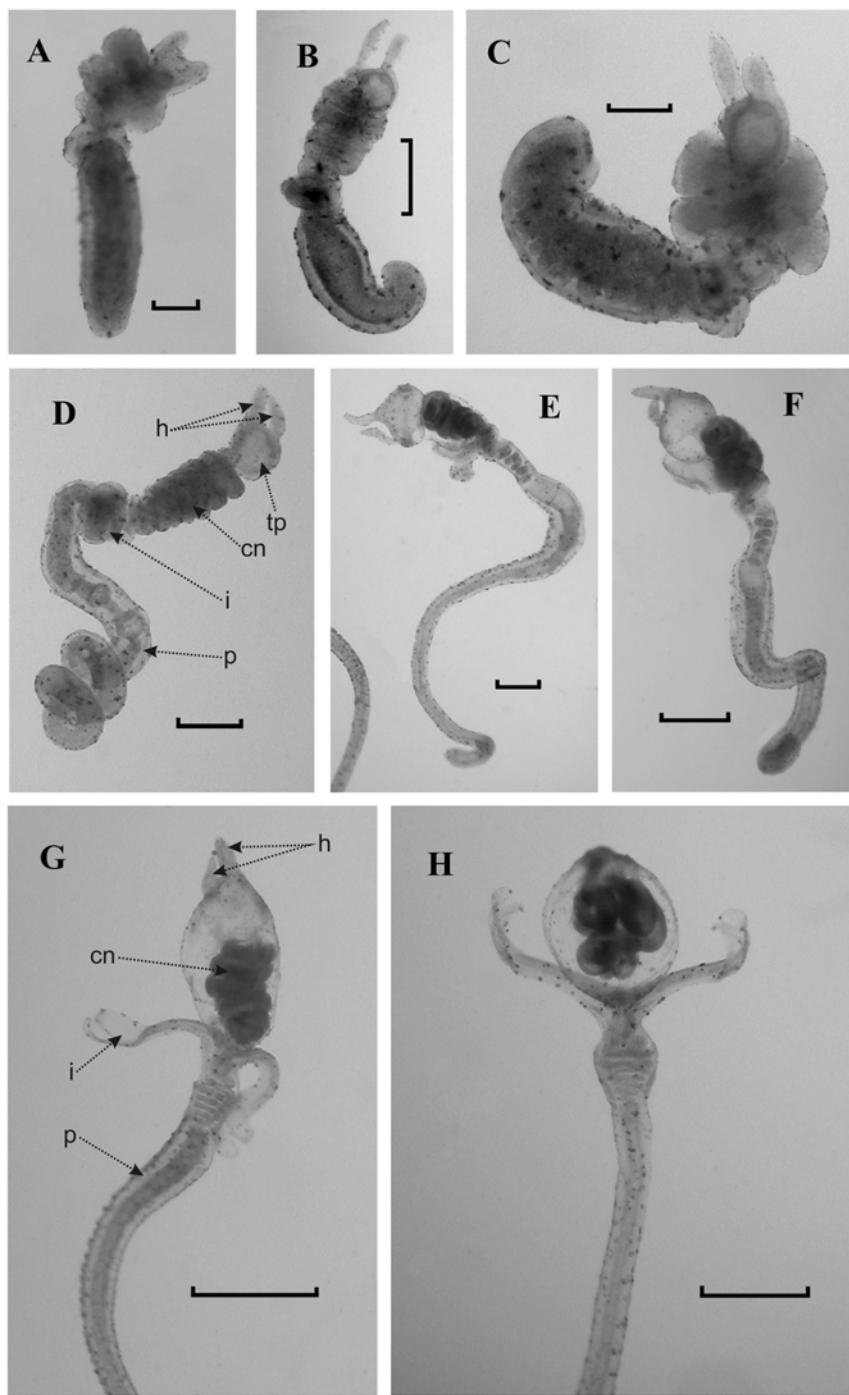


FIGURE 65. *Cardianecta parchelion* sp. nov. Stages in development of the tentilla from the type specimen. **cn.** cnidoband; **h.** horns; **i.** involucrum; **p.** pedicel; **tp.** terminal process. Scale bars: A–B 0.25 mm; C–E 0.5 mm; F–H 1.0 mm.

Only two types of nematocysts were found on the tentilla. Small rounded nematocysts, c. 14 μm in diameter where found on the terminal process and were mainly concentrated in the "horns". These appeared to be desmonemes. The cnidoband bore only elongate nematocysts, c. 42 μm long and 15 μm at their widest, which possibly were mastigophores.

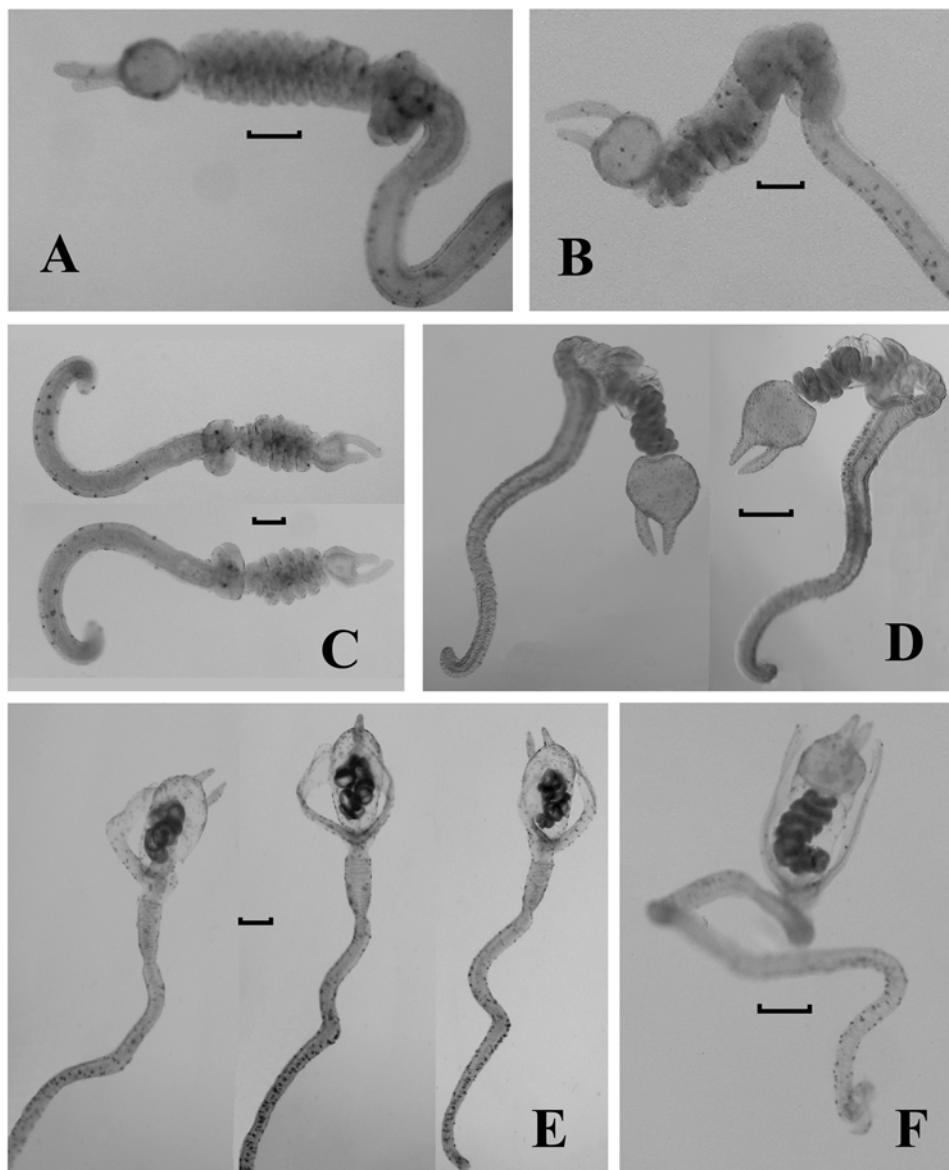


FIGURE 66. *Cardianecta parchelion* sp. nov. Stages in development of tentillum. JSLII 998-D4 specimen. Scale bars: A–C 0.25 mm; D–F 0.5 mm.

Palpon: The palpons (Figure 68A) measured up to c. 3.3 mm in length; the larger ones tending to be ovate, while the smaller ones were cylindrical or club-shaped. All possessed a small rounded proboscis region at their distal ends. Almost all of the largest palpons did not possess a palpacle, but it is clear that the latter must have been detached as such a structure was still attached to many of the younger ones (Figure 68A). The palpacle was annulated, with quite long segments between each annulation and appeared to bear a few, very small, ovate nematocysts, but these were not examined in detail. The palpon itself was thin-walled and featureless, and was devoid of any nematocysts.

Gonophores: Gonophores of both sexes were present (Figures 68B). The youngest gonophores consisted of spherical processes borne on short narrow pedicles, with the sexual products occupying the whole of the subumbrella cavity, and only a narrow distal opening. As they grew the gonophores became more elongate with a wide pedicle, through which the gastrovascular cavity passed, occupying approximately a third of its length, and the subumbrella cavity extending distal to the sexual products, and was widely open. In its lining were four straight lateral canals. Further development saw a re-shortening of the pedicle, which still remained wide, and an enlargement of the subumbrella cavity; although the overall length of the gonophore only increased slightly. No nematocysts were noted on the gonophores.



FIGURE 67. *Cardianecta parchelion* sp. nov. Tentillum from paratype specimen before preservation. Proximal at bottom. Scale bar 0.5 mm.

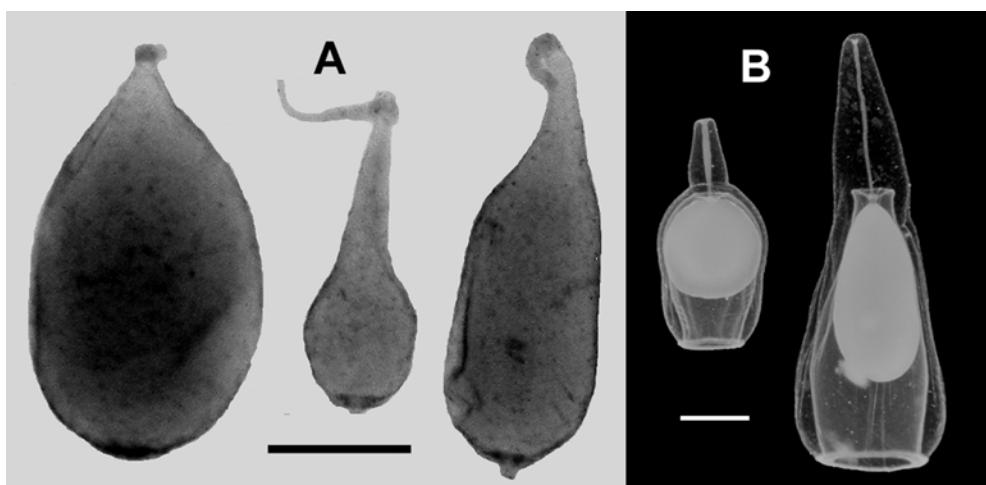


FIGURE 68. *Cardianecta parchelion* sp. nov. **A.** Palpons from JSI II 998 Specimen. Scale bar 1 mm. **B.** female (left) and male (right) gonophores from the paratype specimen. Scale bar 0.5 mm. Proximal top—distal bottom.

Distribution. All five specimens were collected in the "Tongue of the Ocean" in The Bahamas at depths ranging from 640 to 884 m.

Remarks. As noted above, it is far from certain that the genus *Cardianecta* actually belongs within the newly established family *Cordagalmatidae* fam. nov. The only character that *C. parchelion* sp. nov. and *Cordagalma* species have in common is that the nectophores are heart-shaped. Although the bracts of the former are more foliaceous and do not possess a distal facet, there are fundamental differences between the other two main

characters, the palpons and in particular the tentilla and their cnidome, that suggest that the genera may not be that closely related. All *Cordagalma* species, as far as we know, have palpons that do not develop a palpon, while such is clearly present with, at least, the younger palpons of *C. parchelion sp. nov.* Nonetheless, the fundamental differences between the simple, larval-type tentilla of *Cordagalma* species, and the complex involucrate form of those of *C. parchelion sp. nov.* is striking. This also applies to their cnidome, with *Cordagalma* species having three types of nematocysts, including an incomplete circle of usually five stenoteles, in the cnidoband, while *C. parchelion* sp nov. has just one. Meanwhile, that species possesses what appear to be desmonemes in its terminal process, with two asymmetric horns, while such a process is absent in *Cordagalma* species.

Thus it is clear that the species *parchelion sp. nov.* should be placed in a separate genus from the *Cordagalma* species but, at present, we cannot be certain whether it actually belongs within the same family. However, the two genera are both monoecious and the nectophores are developed on the ventral side of the nectosome. Molecular genetic data are now available for some *Cordagalma* species, other than *C. ordinatum* (Steve Haddock, personal communication), but until such can be gathered for *Cardianecta parchelion sp. nov.* one can only speculate on its systematic relationships.

Etymology. The generic name refers to the heart-shaped nectophore. The specific name is derived from the Greek "like a chela", and refers to the supposed chela-like appearance of the "horns" on the terminal process of the tentillum.

Discussion

With the addition of five new species, with one belonging to a new genus, it seems reasonable to establish a new family for all of them, and thus the Cordagalmatidae fam. nov. is designated. It is diagnosed solely on the presence of heart-shaped nectophores budded off on the ventral side of the nectosome. According to the molecular genetic data of Dunn *et al* (2005), the taxonomic position of *Cordagalma ordinatum* was somewhat enigmatic. This was discussed further by Pugh (2006), who noted that two characters of that species indicated that it belonged to the monoecious clade of physonects. These were the presence of a descending mantle canal in the nectophores, and the fact that individual colonies were monoecious. However, it could not be included within the family Agalmatidae, as Totton (1965) had done before, because the nectophores were budded off on the ventral side of the stem, whereas in that family they are, when present, budded on the dorsal side. Those molecular analyses also resulted in several other physonect species that Totton (1965) had included in the, then catchall, family Agalmatidae, no longer being associated with any extant siphonophore family. Of these, Pugh (2001) considered that the species *Erenna richardi* Bedot had sufficient diagnostic characters to place it in a separate family, the Erennidae, and he described three further erennid species, one in a new genus, *Parerenna* Pugh. Similarly, Pugh (2006) considered that the genus *Resomia* Pugh, derived from *Moseria* Totton, which was preoccupied, was sufficiently distinct to establish the family Resomiidae for it, and Pugh & Haddock (2009) added three new species. Finally, Pugh & Baxter (2014) re-established Huxley's (1859) Stephanomiidae for the enigmatic species *Stephanomia amphytridis* Lesueur & Petit. For the other orphaned genera *Marrus* Totton will certainly come to be placed in its own family, the Marridae (Pugh, in preparation), while the genus *Lychnagalma* Haeckel and the more recent *Frillagalma* Daniel remain unassociated with a particular family. Both are monotypic genera that have quite different characters from any other physonect genus, although the former does show some characters in common with the Forskaliidae. It is to be hoped that further molecular data will give some clues, as neither genus was included in the original genetic study by Dunn *et al.* (2005).

The two genera that are now included in the family Cordagalmatidae fam. nov. can easily be distinguished on the basis of:

- 1 The presence, where known, of larval-type tentilla with more or less-well-developed distal cnidocils; and palpons without palpacles Genus *Cordagalma* Totton
- The presence of completely different tentilla, with two-lobed involucrum; and palpons with palpacles Genus *Cardianecta* gen. nov.

As noted above, the only species that cannot be ascribed definitively to either genus is *Cordagalma tottoni* Margulis, as neither the structure of the tentillum nor the palpon is known for certain. Nonetheless, the fact that on

the nectosac the pedicular canal gives rise to only the upper and lower radials canals is a distinctive character. Otherwise *Cardianecta* gen. nov. presently is monotypic for *C. parchelion* sp. nov.

Key to the species of the family Cordagalmatidae fam. nov.

1. Lateral radial canals on nectosac arise from upper canal *Cordagalma tottoni* Margulis, 1993.
Lateral radial canals on nectosac arise directly from the pedicular canal 2.
2. Palpons without palpacles Genus *Cordagalma* ... 3.
Palpons with palpacles *Cardianecta parchelion* gen. nov., sp. nov.
3. Palpons attached basally 4.
Palpons not attached basally 5.
4. Small species living in superficial waters, tentillum with a "rostre". Bracts with truncated upper surface..... *Cordagalma ordinatum* (Haeckel, 1888).
Larger species living at deep waters >2000 m, tentillum without a "rostre". Bracts with truncated upper surface..... *Cordagalma abyssorum* sp. nov.
Relatively large species living in depth range 1000–1400 m. Bracts not truncated on upper side, but with pair of spots on divided distal facet. Tentilla not known..... *Cordagalma rugosum* sp. nov.
5. Palpon attached laterally or baso-laterally; somewhat rounded bracts not truncated on upper surface, with pair of spot on dorsal facet *Cordagalma bimaculatum* sp. nov.
Palpons usually attached baso-laterally; rhomboidal bracts with truncated upper surface, with pair of spots only on distal facet of young ones *Cordagalma isocarrei* sp. nov.

As noted in the descriptions of each *Cordagalma* species, their nectophores can vary considerably in shape, particularly with regard to the axial wings and the distal process. These variations are not necessarily related to the developmental state of the nectophore, but there can be little doubt that preservation plays a part in this. Thus, without the presence of other zooids, it would be very difficult to identify the individual nectophores of the various species, particularly if preserved. A comparison of the nectophores of cordagalmatids, at the same scale, is shown in Figure 69, and it is immediately obvious that the sheer size of those of *Cardianecta parchelion* gen. nov., sp. nov. sets them part from all the *Cordagalma* species. The smallest nectophores belong to *C. ordinatum*, *C. tottoni* and *C. bimaculatum* sp. nov. They are of a very similar sizes but, in perfect condition, they should be distinguishable. The fact that the pedicular canal, on the nectosac, gives rise only to the upper and lower canals is only found in *C. tottoni*; and the presence of distinctive patches of large ectodermal cells on the corners of the axial wings sets *C. bimaculatum* sp. nov. apart. Unfortunately, they are easily abraded and the distinctiveness of the nectophores is lost.

The nectophores of *C. isocarrei* sp. nov., *C. abyssorum* sp. nov. and *C. rugosum* sp. nov. are also of similar size, but slightly larger than the aforementioned ones. The distal process of the first two is relatively short, broad, and rounded truncated, while that of the last is narrower, elongate and triangular in shape. For *C. isocarrei* sp. nov. the nectosac occupies only the central part of the main body of the nectophore, while for *C. abyssorum* sp. nov. and *C. rugosum* sp. nov. it occupies almost all of that part. Finally, the arrangement of the axial wings is different in these three species, but the material would have to be in good condition for any accurate identification on this basis.

A comparison of certain other characters, such as the tentilla and palpons, also has limited value for identification, mainly because for some species they are incompletely known. Thus the unique construction of the tentilla in *Cardianecta parchelion* clearly distinguishes them from the larval-type tentilla of the *Cordagalma* species, apart from *C. tottoni* where the tentilla are not known for certain. The presence of a rostrum also distinguishes *C. ordinatum*. The attachment point of the palpons, and whether they also include a palpacle might be distinctive but, for several species, the exact arrangement is not known.

There is, however, one zooid, namely the bract, where comparisons between those from the various species do yield information that is an aid to their identification. Thus bracts from each cordagalmatid species, with the exception of *Cordagalma tottoni* where is has not been identified with certainty, are compared, at the same scale, in Figure 70. All *Cordagalma* species, where known, have somewhat rhomboidal bracts with a more or less distinct distal facet divided into two facets. These characters do not apply to the bracts of *Cardianecta parchelion* sp. nov. where their sheer size, and leaf-like nature clearly distinguishes them from those of *Cordagalma* species, although not necessarily those of some other physonect species. Within the genus *Cordagalma*, the size of the bracts of *C. rugosum* sp. nov., together with their more rounded nature, clearly distinguish them. For the remaining four species, the bracts of three of them are truncated on their upper surfaces. This, thus, sets the bracts of *Cordagalma*

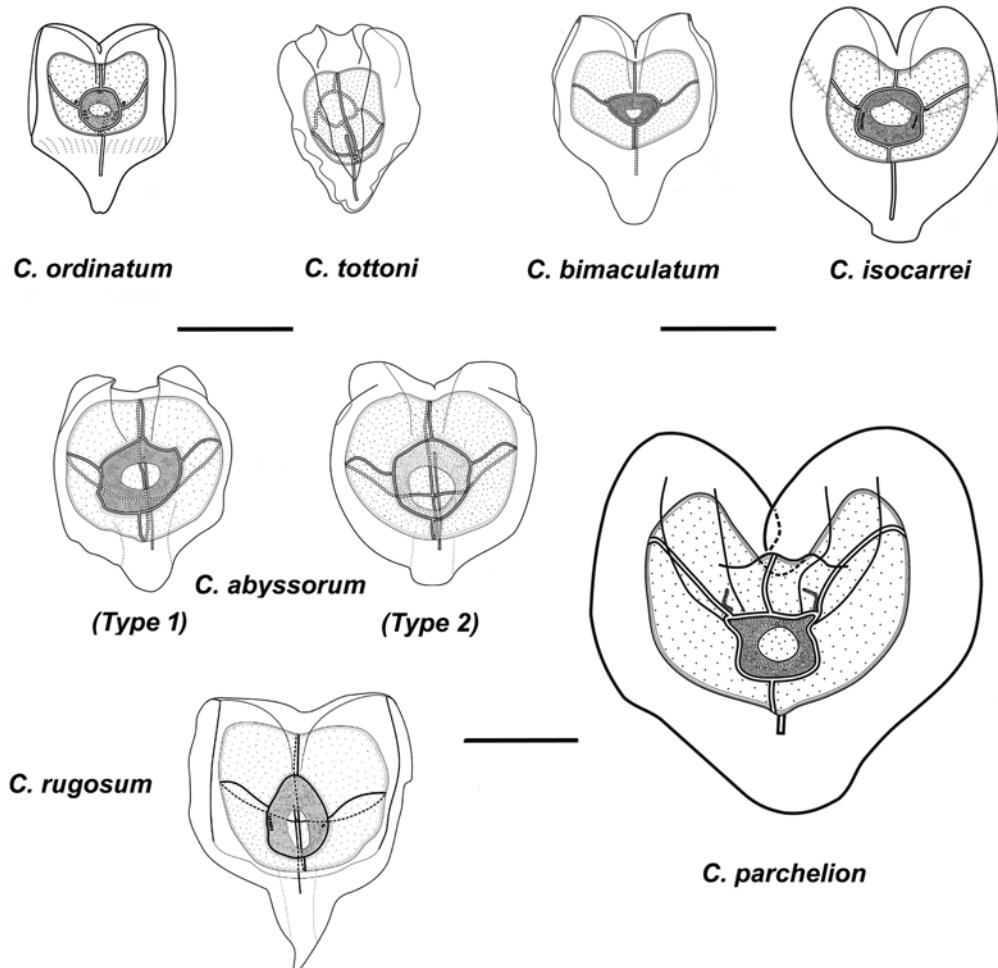


FIGURE 69. Comparison of ostial views, except for *Cordagalma tottoni* that is axial, of nectophores of the various cordagalmatid species at the same scale. Scale bars 2 mm.

bimaculatum sp. nov. apart. As noted above these bracts come in two similar forms, although only one specimen has been found to include both of them. However, it is not a regional character as specimens from Monterey Bay have been found with either type. The bracts probably can also be distinguished by the fact that nematocysts are present along the length of the transverse ridge, as well as the median ridge that divides the distal facet. The presence of bracts with truncated upper surfaces in deep waters, >2000 m, would be indicative of the presence of *C. abyssorum* sp. nov. From the characters of the bracts alone the remaining two species, *C. ordinatum* and *C. isocarrei* sp. nov. might be difficult to tell apart, although those of the latter are larger and relatively longer. However, the presence of a "rostre" on the tentilla of the former and the totally different ways in which the palpons are attached both serve as clear distinguishing characters. They have both been collected from the superficial waters off Villefranche-sur-Mer, in the Western Mediterranean and, presumably, will occur together in the warmer waters of the World's oceans. However, in the colder waters of Monterey Bay, off California, only *C. isocarrei* sp. nov. has been found.

It is interesting to note that the four *Cordagalma* species identified from Monterey Bay have fairly discrete depth ranges. *C. abyssorum* sp. nov. has only been found at depths exceeding c. 2500 m, although *in situ* frame grabs indicate that they may also occur between 2000 and 2500 m. *C. rugosum* sp. nov. occurred in the 1000–1300 m depth range, while the other two species were much shallower. For them, their depth ranges did overlap but *C. bimaculatum* was never found shallower than 300 m, with most records deeper than 400 m, while *C. isocarrei* sp. nov. was, on one day at least, clearly concentrated around 200 m, but two of the specimens were found deeper than 350 m.

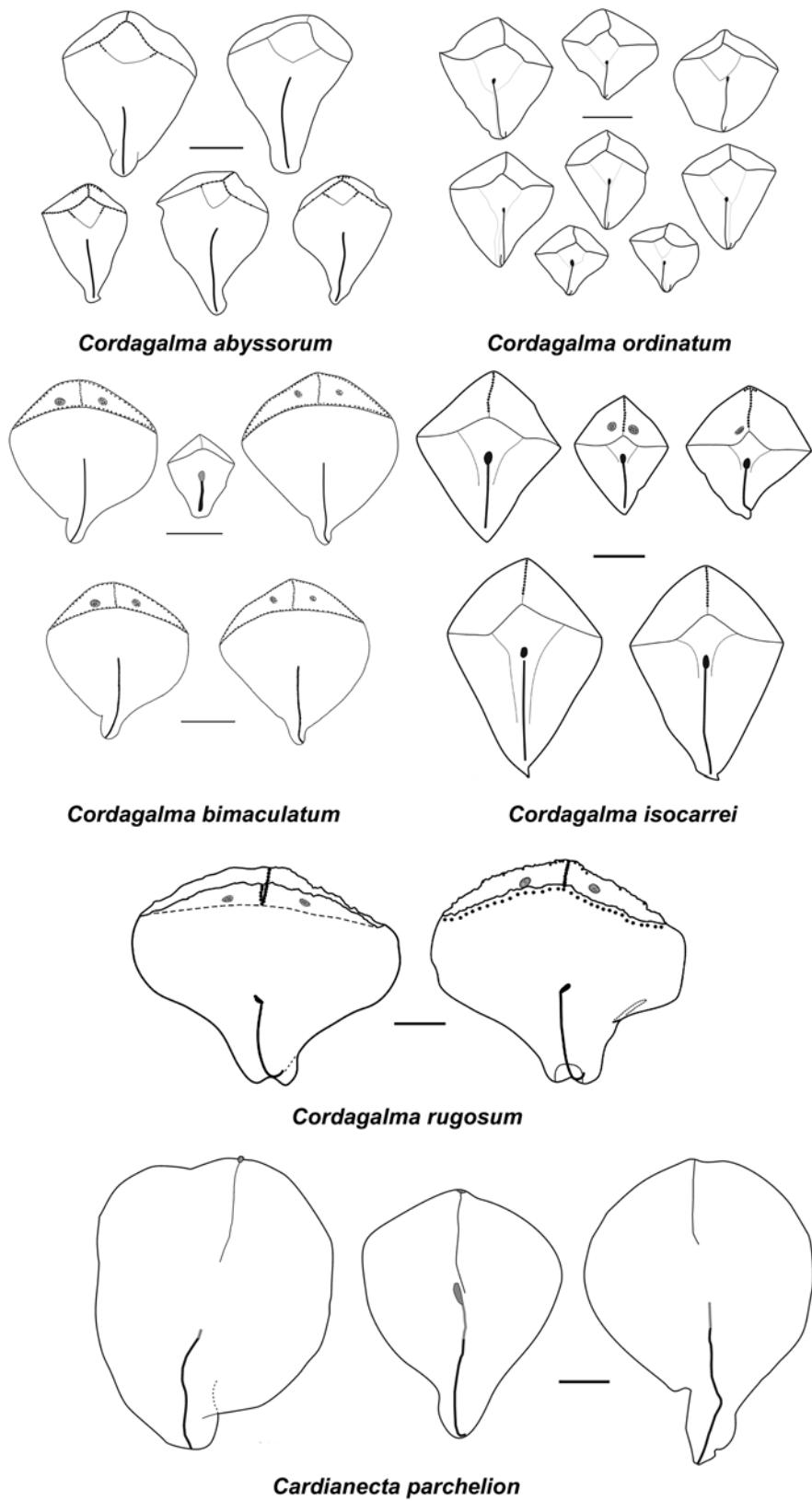


FIGURE 70. Comparison of the bracts of cordagalmatid species at the same scale. Scale bars 0.5 mm.

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