

MARRUS CLAUDANIELIS, A NEW SPECIES
OF DEEP-SEA PHYSONECT SIPHONOPHORE
(SIPHONOPHORA, PHYSONECTAE)

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ABSTRACT

Marrus claudanielis, a new species of deep-sea physonect siphonophore, is described from material collected by the ROV TIBURON, off California (eastern North Pacific), and the submersible JOHNSON-SEA-LINK II, off New Jersey (western North Atlantic). *Marrus claudanielis* is extremely fragile and all observed specimens autotomized some of their parts during observation or collection, due to the strong contraction of the stem. The siphosomal elements, the nectophoral and bracteal canals, and the pneumatophore were all deep red in life. This species is distinguished from other *Marrus* species by the undivided apico-lateral ridges on the nectophores, and the hook-shaped arc of enlarged ectodermal cells, including nematocysts, overlying the distal branches of the bracteal canals.

Siphonophores are colonial hydrozoans found throughout the world's oceans. Most are holoplanktonic, and none are permanently attached to a substrate. They are divided into three main groups: Cystonectae, Physonectae, and Calycophorae. The Physonectae, to which the species described here belongs, are generally linear in organization. At the apical end is a small gas-filled float known as the pneumatophore. The pneumatophore is followed by a series of asexual propulsive medusae called nectophores (swimming bells), which are grouped together to form the nectosome. Immediately adjacent to the nectosome is the siphosome, of specifically variable length, bearing the other elements, such as gastrozooids (feeding polyps, siphons), bracts (protective structures), and gonophores. Most physonects are gelatinous in consistency and many are well known for their fragility (Fewkes, 1880; Pugh, 1989). Past descriptions of many species were based on only severely damaged, and often incomplete, specimens obtained from net trawls. Technological advances over the last 25 yrs, however, have made it possible to sample organisms directly from the water column and bring them to the surface intact (reviewed by Haddock, 2004). These new methods include blue-water SCUBA diving (Hamner, 1975), and the use of sophisticated samplers mounted on manned submersibles and remotely operated vehicles (Youngbluth, 1984). These techniques have not only improved our knowledge of previously described siphonophores, but have also revealed numerous undescribed species, many being extremely delicate. Here we describe one such species, *Marrus claudanielis* sp. nov. It is so fragile that all of the observed specimens autotomized most of their parts upon the approach of the submersible, during the collection process, or in the sample canisters on the way to the surface.

Marrus claudanielis new species

(Figs. 1–8)

Diagnosis.—Physonect siphonophore with unicornuate tentilla, without involucre, and with loosely coiled cnidobands. Nectophores with pairs of apico- and infra-lateral ridges, the former being undivided, and a pair of short, weak lateral ridges. Muscle-free zone at apex of nectosac in mature nectophores. Radial canals straight. Bract with divided distal facet demarcated by a median and two transverse ridges; with a distinctive line of nematocysts, and other enlarged ectodermal cells, extending along the median ridge, from the distal tip of the bract, and for most of the length of the inner transverse ridge. Palpons absent. Dioecious.

Material Examined.—Two specimens, one from the eastern North Pacific Ocean, and the other from the western North Atlantic Ocean. The Pacific specimen was collected by the ROV TIBURON Dive 596 on 19 July 2003 off Monterey Bay, California (36°36.12'N, 122°22.48'W) at a depth of 1190 m. The Atlantic specimen was collected by the submersible JOHNSON-SEA-LINK (JSL) II Dive 1411 on 16 September 1986 from a depth of 518 m at 39°56.4'N, 70°14.3'W off New Jersey. The Pacific specimen is designated the holotype and has been presented to the Yale Peabody Museum (catalog number 34789). The Atlantic specimen is designated the paratype and has been presented to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 1025949).

General Appearance In Situ.—Photographs of the type specimen, approximately 21 cm in length, taken before it was collected (Fig. 1) show the siphosome bent into an arc, but not spiraled. However, other specimens photographed in situ had a straighter posture. The siphosomal stem was never observed to be stretched out, and appeared to be under constant tension, as is the case for some other physonect species such as *Agalma okeni* Eschscholtz, 1825, so that the bracts were permanently pressed together. Nonetheless, further contraction, particularly in the nectosome, occurred while some specimens were illuminated by the white lights of the submersibles, resulting in the autotomy of many mature nectophores, as well as some bracts and gastrozooids. One specimen, recorded on videotape in situ, very rapidly contracted its nectosome, and quickly shed all of its mature nectophores before being photographed (see Youngbluth, 1989, photo 2).

The stem, pneumatophore, gastrozooids and tentacles, and gonophores were all a deep red color in life, as were the canals of both the nectophores and bracts; the latter enabling the outline of the animal to be clearly visible (Figs. 1, 2).

Pneumatophore.—The pneumatophore was elongate and in the two preserved specimens measured 5.0–5.2 mm in length and 1.6–1.7 mm in width at its widest point. There was no apical pore. In life it was pigmented an even red (Fig. 1), but after preservation this gradually faded to a pale orange color, or even became colorless. In the preserved material, the peduncle of the pneumatophore had contracted so much that it could not be discerned.

Nectosome.—The nectophores were attached on the same side of the stem as the siphosomal elements; i.e., ventrally. Their attachment lamellae were alternately displaced to the right or left, so that the nectophores came to be biserially arranged. Photographs taken in situ indicate that the type specimen (Fig. 1) had at least a dozen mature nectophores, as well as several developing ones. This accorded with the 12 mature and at least 15 immature nectophores that were found with the preserved material.

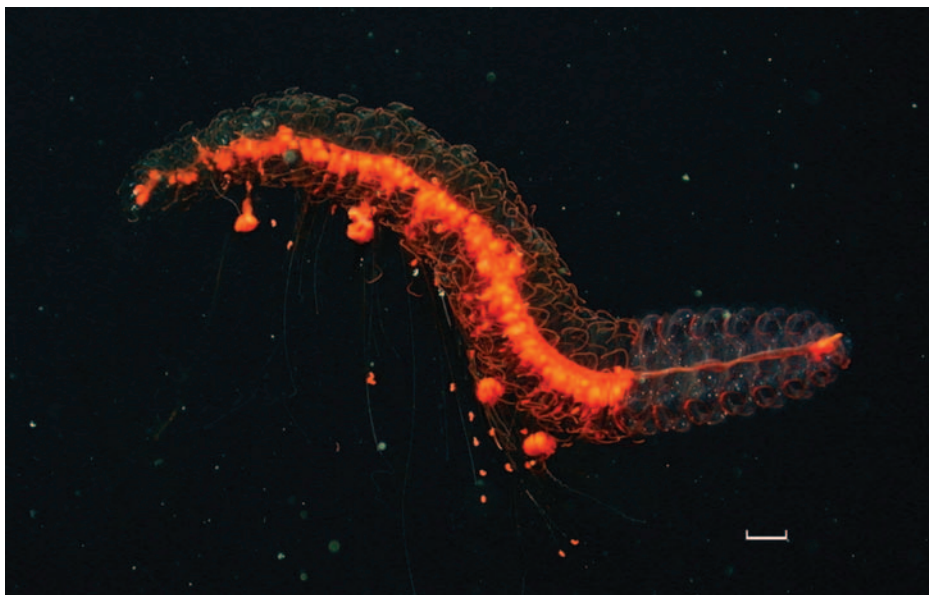


Figure 1. In situ photograph of *Marrus claudanielis* type specimen taken during ROV TIBURON Dive 596. The canals of the bracts, which appear as red arcs, make the outline of the siphosome clearly visible. Autotomized gastrozooids can be seen falling from the stem. Scale bar 1 cm.

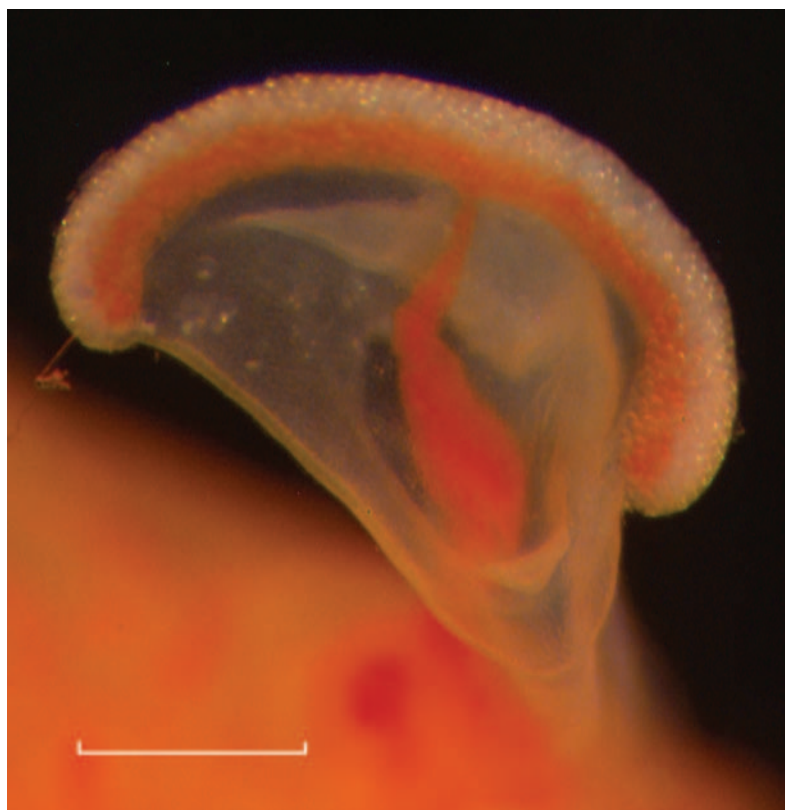


Figure 2. Lateral view of a developing bract of *Marrus claudanielis*. Scale bar 0.5 mm.

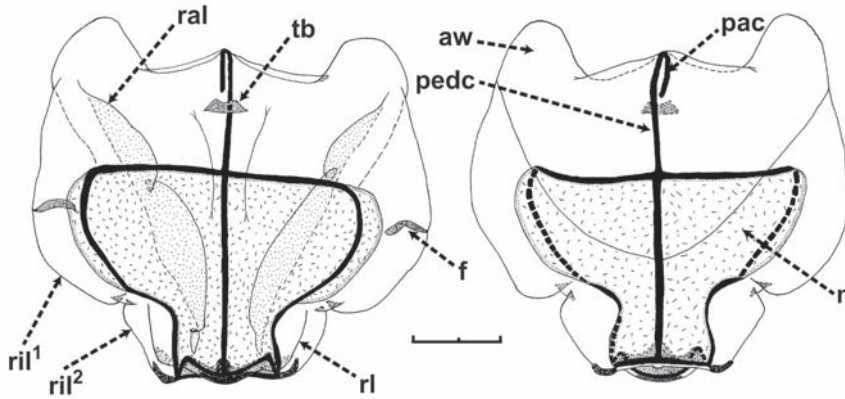


Figure 3. Upper (left) and lower (right) views of young nectophore of *Marrus claudanielis* type specimen. aw – axial wing; f – flap; n – nectosac; pac – ascending pallial canal; pedc – pedicular canal; ral – apico-lateral ridge; ril¹, ril² – infra-lateral ridges; rl – lateral ridge; tb – thrust block. Proximal up, distal down. Scale bar 2 mm.

Nectophores.—The young nectophores (Fig. 3) possessed short axial wings with rounded edges, and a minute thrust block on their upper side. The nectosac extended to slightly over half the total length of the nectophore and, at the stage figured, did not have a muscle-free zone at its apex. The ascending pallial canal arose from the pedicular canal at the point of attachment on the lower side of the nectophore, and ran to the upper side of the nectophore where it reached a point slightly proximal (i.e., adaxial) to the thrust block. The pedicular canal ran to the apex of the nectosac, in the midline, where it immediately gave rise to the four radial canals, all of which had straight courses. The ostium opened distally, and there was no mouth plate. On either side of the ostium a thickened lateral process extended along the side of the nectophore for a short distance. These processes were covered by chromatophores (sensu Totton, 1965, p. 59), which in life were red-pigmented. A smaller group of distinctive unpigmented cells was also present on the upper side of the ostium, overlying the upper (dorsal) radial canal. Other large, rounded, unpigmented ectodermal cells were found along most of the upper and lateral sides of the ostium, but none were found on the lower side. It is likely that these enlarged ectodermal cells were sites of bioluminescence as seen in other physonects, although no such observations were made. No other distinct patches of cells were found on the surface of the nectophores.

The apico-lateral ridges of the young nectophores (“ral” in Fig. 3) originated from the upper side of the main body of the nectophore, just distal to the axial wings. As they curved in toward the midline they formed extensive flaps, which folded in upon themselves in the region where they passed over the apex of the nectosac. The extent of these flaps decreased considerably as they approached the ostium, and the ridges diminished completely before reaching the latter. At no stage did the apico-lateral ridges divide.

The first infra-lateral ridges (“ril¹” in Fig. 3) arose close to the points of origin of apico-laterals, but on the lower side of the nectophore. At about the mid-length of the nectophore each connected with a flap-like extension (“f” in Fig. 3) that extended

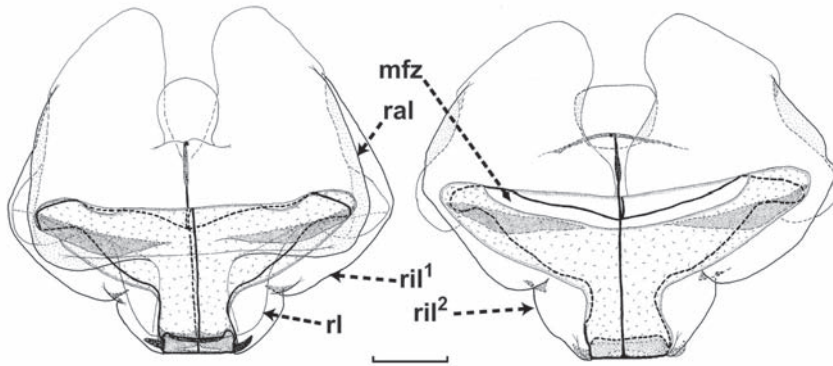


Figure 4. Upper (left) and lower (right) views of mature nectophore of *Marrus claudanielis* type specimen. ral – apico-lateral ridge; ril¹, ril² – infra-lateral ridges; rl – lateral ridge; mfz – muscle-free zone. Proximal up, distal down. Scale bar 5 mm.

perpendicularly a short distance towards the upper side of the nectophore. The infra-lateral ridges continued distally and curved inwards, and toward the lower side of the nectophore, before petering out. A second infra-lateral ridge (“ril²” in Fig. 3), unconnected with and just distal to the first infra-lateral ridge, then arose and continued distally to end on the baso-lateral sides of the ostium.

In addition to these ridges, there was also a pair of weak lateral ridges (“rl” in Fig. 3). These did not proceed, as is often the case in other species, from the lateral processes of the ostium, but from the upper surface of the nectophore, just distal to the apico-lateral ridges. They continued along the sides of the nectophore for a short distance, although occasionally they appeared to extend as far as the vertical flaps that arose from the infra-lateral ridges.

The mature nectophores (Fig. 4) measured up to 24 mm in length and 28 mm in width. They were flattened in the frontal plane, and were thickest where they were widest. They were flimsy and flaccid, and the large, pillow-shaped thrust block was weakly connected to the main body of the nectophore and in several nectophores it had become detached. In the latter case the nectophores then had a tendency to split down the midline into two halves. The axial wings were large and tapered down, both in width and depth, toward their apices.

The nectosac occupied about half the total length of the mature nectophore. Its apex was flat, but there were extensive lateral processes. The upper lateral walls of the nectosac appeared, in the preserved state, to fold over themselves forming two lateral flaps, but these were almost certainly preservation artifacts. There was an extensive muscle-free zone at the apex of the nectosac, mostly on its lower side. The ascending pallial canal departed from the short pedicular canal at the point of attachment of the nectophore, and ran to the upper side of the nectophore where it terminated at the base of the thrust block. The pedicular canal ran to the lower side of the nectosac, within the muscle-free zone, and gave rise immediately to all four radial canals. All the radial canals had straight courses. The lateral canals passed obliquely out across the muscle-free zone and then over onto the upper side of the nectosac where they continued distally, eventually running along the lateral sides of the constricted part of the nectosac, proximal to the ostium, before joining the circular canal. The appar-

ent curve in their course on the upper side of the nectosac was presumably caused by the same preservation artifact that gave rise to the lateral folds in the nectosac itself. In life all the canals were red-pigmented, but after preservation, and with exposure to light, this pigmentation faded away completely.

The ostium opened distally and bore no mouth plate. The swollen lateral processes that extended from the ostium were quite small, and bore red chromatophores. Patches of large, rounded, unpigmented ectodermal cells were found on the upper side of the ostium close to the circular canal, and to a lesser extent on its lateral sides. No other distinct patches of ectodermal cells were found on the nectophores.

The apico- and first infra-lateral ridges arose close to the rounded lateral margins of the axial wings, at about half their length. These ridges formed, in the middle half of the nectophore, the edges of the narrow lateral facets. Distal to this the apico-laterals curved in toward the midline and, in the preserved nectophores, slightly overhung the main body of the nectophore on its upper side. They then curved back towards the ostium. In the vicinity of the ostium they were very weakly defined. Although they ended slightly proximal to the ostium, folds in that region often made it appear that they actually reached it.

The first infra-laterals ("ril¹" in Fig. 4), as in the younger nectophores, finally curved in toward the midline and diminished completely as they approached the region where the nectosac was constricted. A second infra-lateral ridge ("ril²" in Fig. 4) then continued to the lower lateral side of the ostium. The lower part of the lateral facet abruptly became hollowed out at the widest part of the nectophore, while above it the facet bulged out slightly. This was the point where the infra-lateral ridge, in the younger nectophores, gave off a flap-like extension (see "f" in Fig. 3). In the mature nectophores this point had become a marked, rounded corner with no hint of a vertical lateral ridge or flap being present.

The lateral ridges were very weakly defined. They ran from the upper side of the ostium along the lateral sides of the nectophore before petering out in the region where, in the preserved specimens, the apico-lateral ridge slightly overhung the main body of the nectophore.

Siphosome.—The siphosome of the preserved type specimen, still attached to the nectosome, was highly contracted and largely denuded of most of its elements. Young bracts, which could be identified even at early stages by the pronounced row of large ectodermal cells and a T-shaped canal (Fig. 2), clusters of gonophores, gastrozooids in various stages of maturation, and developing buds were still attached to the stem.

Bracts.—The bracts (Fig. 5) were of one type only, up to 18 mm in length, and occurred in enantiomorphic pairs. They were flattened on the lower side and convex on the upper, and approximately rhomboidal in outline, with a digitate, swollen process ("dp" in Fig. 5) at the proximal end, displaced slightly onto the upper side. The upper distal end of the bract was divided into two facets ("df" in Fig. 5). These facets were separated from the proximal part of the bract by two transverse ridges ("rto" and "rti" in Fig. 5). These ridges met, in the midline, to form a median ridge ("rm" in Fig. 5) that then continued to the distal tip of the bract. The transverse ridges overhung the distal facets to varying degrees. The thickest point of the bract was where the two transverse ridges united to form the median ridge. The height of the bract tapered down gradually toward the proximal end of the bract, but steeply down to the lateral sides of the distal facets.

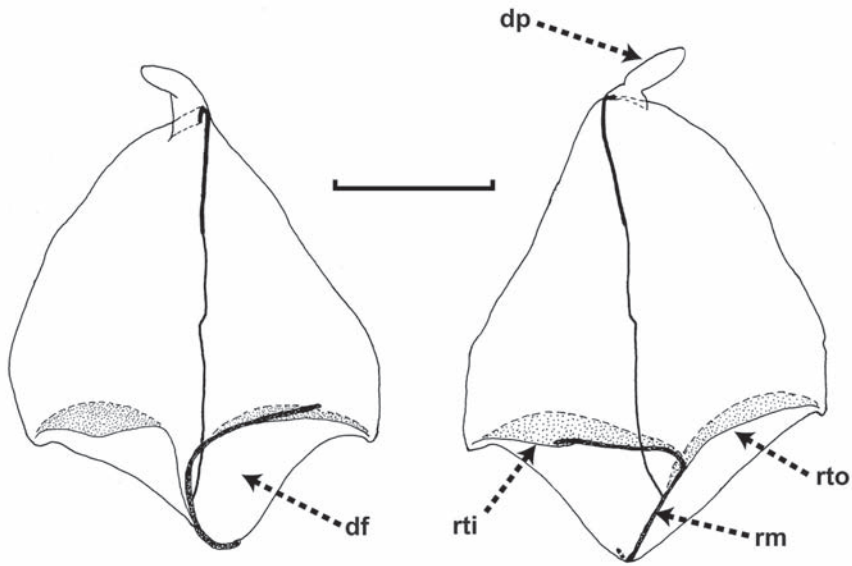


Figure 5. Upper views of an enantiomorphic pair of bracts of *Marrus claudanielis* type specimen. The line of distinctive ectodermal cells, indicated by a thickened line, can be seen extending from the distal tip, along the median and then inner transverse ridges. df - distal facet; dp - digitate process; rm - median ridge; rti - inner transverse ridge; rto - outer transverse ridge. Scale bar 5 mm.

There was a distinctive line of large ectodermal cells (thickened line in Fig. 5) running from the distal point of the bract and continuing along the median ridge, then running roughly parallel to the central part of the transverse ridge on the inner side of the bract. It was composed of rounded granulose ectodermal cells, and nematocysts of two types, one with barbs at the distal end of the shaft (Fig. 6A) and the other without them (Fig. 6B). Both types measured ca. $65\mu\text{m}$ in length and $27\mu\text{m}$ in maximum diameter. The ones with barbs at the end of the shaft were very similar to those found by Carré (1971) on the bracts of *Halistemma rubrum* (Vogt, 1852), which she called microbasic euryteles, although hers were somewhat smaller ($40 \times 25\mu\text{m}$). Carré noted that such a category of nematocysts had not previously been found in physonect siphonophores. The other type of nematocyst, without barbs, was probably a heteroneme (possibly microbasic mastigophore). No other patches of large ectodermal cells or nematocysts were found on the surface of the bract.

The bracteal canals were red-pigmented in life, but the coloration faded to yellow or disappeared altogether in the preserved specimens. The main canal ran from the lower base of the digitate process, at the proximal end of the bract, to reach approximately the middle of the median ridge on the upper side at the distal end. It remained in contact with the lower wall of the bract for only a short part of this distance, before narrowing and continuing obliquely up through the mesogloea, often narrowing further shortly before it reached the median ridge. It did not, however, end there, but divided into two canals that continued to run below the row of ectodermal cells and nematocysts in either direction. These canals were very difficult to see in the preserved mature bracts, as they had lost their pigmentation, and because they were surrounded by the rows of ectodermal cells and nematocysts. However, they

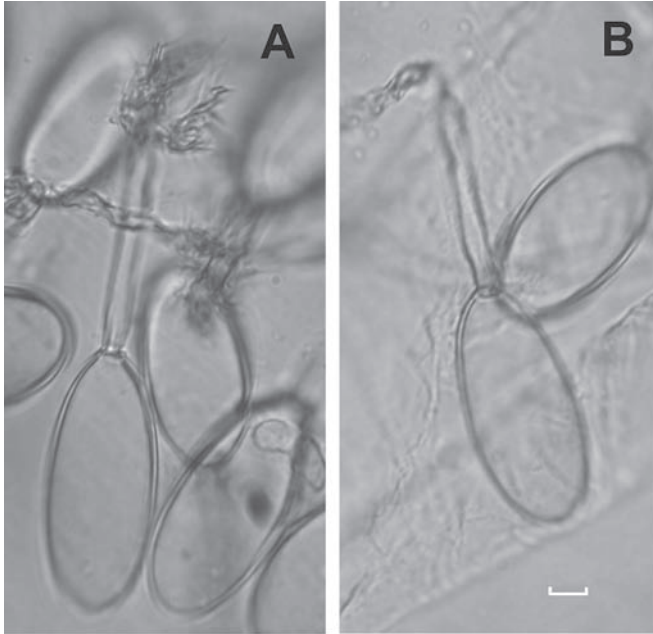


Figure 6. Exploded nematocysts from bract of *Marrus claudanielis* type specimen. Scale bar 10 μm .

were very obvious in life, when the canals were red-pigmented (Fig. 1), and in the developing bracts, where they were proportionally larger (Fig. 2). In the latter, the canal system was T-shaped, with the top of the T subtending the rows of distinctive ectodermal cells. The end of one of these branches (the one to the left as shown in Fig. 2) will ultimately lie at the distal tip of the mature bract.

Gastrozoid and Tentacle.—Gastrozooids began to detach from the specimen even before it was collected (Fig. 1), and only immature ones remained attached to the siphosome after preservation. Only a few of the detached gastrozooids retained their tentacle (as in Fig. 7A), and the proboscis region of many was everted. The detached gastrozooids that had lost their tentacle tended to become everted at both ends (Fig. 7B). Gastrozooids varied considerably in size, and the largest were at least 12 mm in length. There were about thirty mature gastrozooids with the type specimen, but over 200 developing ones. As in other species, the young gastrozooids somewhat resembled palpons, but most had a clearly defined basigaster, often occupying over a quarter of the total length, and all had a large oral opening.

At early stages in their development, the tentilla were completely straight; becoming slightly curved at their tips as they elongated and the cnidoband began to differentiate (Fig. 7C). With further development, first the terminal filament and then the cnidoband began to coil up. No mature tentilla were found with the type specimen, but the distal ends of some of the immature ones were partially coiled. The mature tentilla of the JSL Dive 1411 specimen (Fig. 7D) had a loosely coiled cnidoband, about 3 mm in length, with up to nine regular turns. The single terminal filament, however, was usually chaotically spiraled. There was no involucre covering any part of the cnidoband. The cnidoband contained many rows of innumerable nematocysts, measuring ca. $65 \times 9 \mu\text{m}$. These appeared to be heteronemes, though no discharged ones

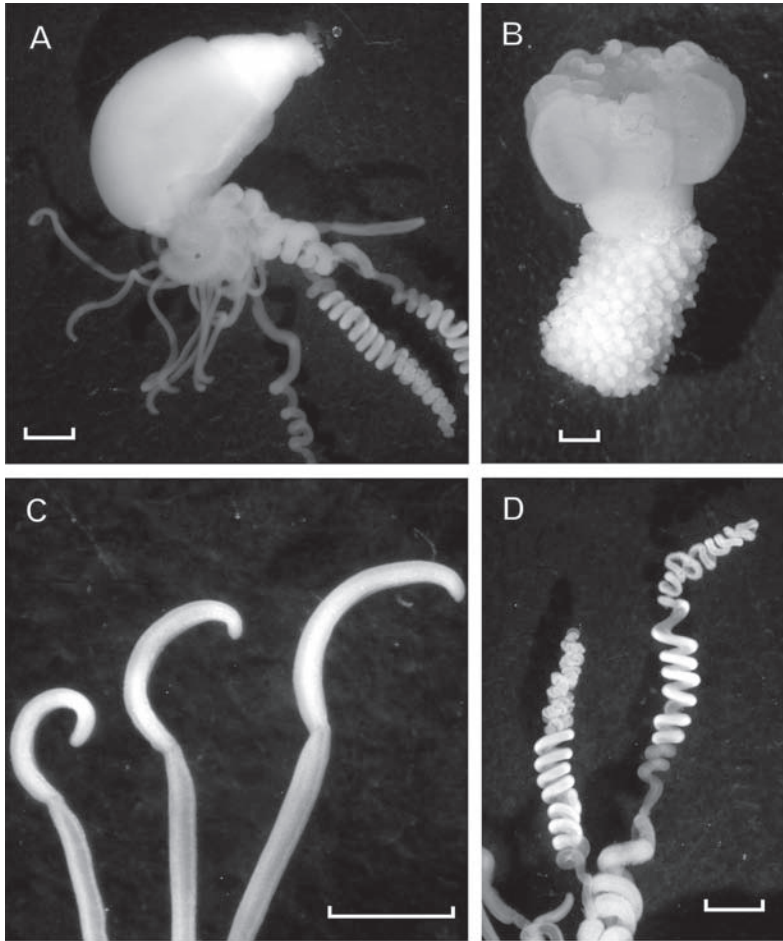


Figure 7. (A) Gastrozoid and tentacle; (B) everted gastrozoid; (C) young tentilla; and (D) mature tentilla of *Marrus claudanielis* from (A, D) JSL Dive 1411; (B, C) type specimen. Scale bars 1 mm.

were found. They differed in size and shape from those found on the bracts (Fig. 6). Two rows of larger nematocysts ($125 \times 28 \mu\text{m}$), presumed to be haplonemes (anisorhizas), flanked them laterally. The terminal filament bore two sizes of nematocysts that were assumed to be desmonemes ($25 \times 14 \mu\text{m}$) and smaller acrophores ($12 \times 12 \mu\text{m}$).

Palpons.—Palpons not present.

Gonophores.—Borne in clusters, each cluster attached to the stem by a single short gonostyle. The species is assumed to be dioecious as all the observed gonophores of the type specimen were female (Fig. 8A), while those of the JSL Dive 1411 specimen were male (Fig. 8B). The gonophores of both specimens were immature and of variable sizes.

Organization of Zooids in the Siphosome.—It was not possible to observe the exact arrangement of all the zooids in the siphosome because many parts were dissociated from the stem in the examined material. It was possible, though, to establish the relative positions of some of the zooids that were still attached. Young bracteal

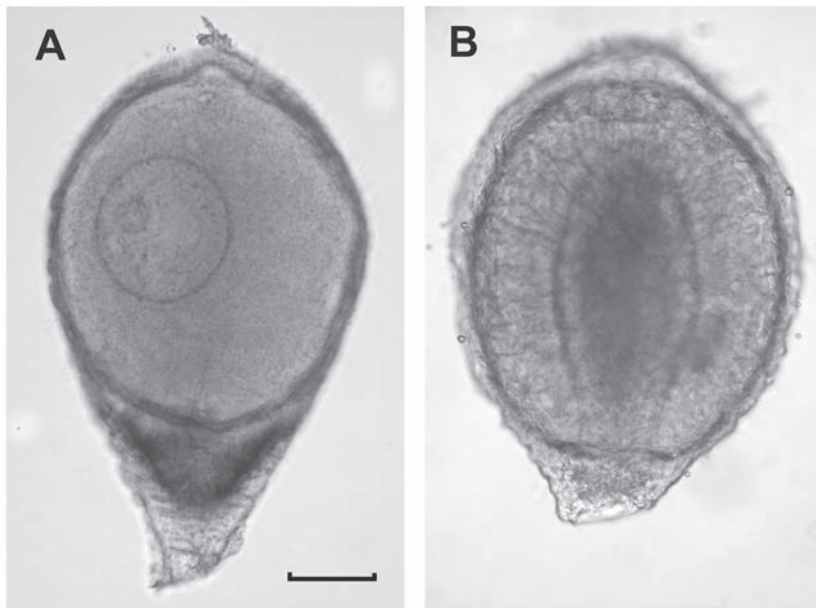


Figure 8. (A) Female gonophore of *Marrus claudanielis* from type specimen; and (B) male gonophore of *Marrus claudanielis* from JSL Dive 1411 specimen. Scale bar 100 μ m.

buds could be distinguished easily by their unique T-shaped canals (Fig. 2). The large lamellae where mature bracts had been attached, located farther from the midline than all the other zooids, were also obvious. Each of these large lamellae had, on its inner side, a younger bract that ranged from a small bud to a well differentiated, but still immature, bract. Siphonophores lose bracts throughout their life (Mackie et al., 1987), and it is likely that the inner, younger bract is in reserve to replace older bracts that are autotomized or torn away. These lamellae/young bract complexes occurred in regular pairs along the length of the siphosome and bracketed the other siphosomal elements. In the type specimen, lamellae on the right side of the stem tended to be larger than those on the left side, while the young bracts on the left were at a later stage of development than those on the right.

Distribution.—In addition to the two specimens examined here, which came from off Monterey Bay, California (eastern North Pacific Ocean) and off New Jersey (western North Atlantic), eight other specimens are known to have been observed and photographed in situ (Table 1). One such photograph has been published (Youngbluth, 1989, photo 2), and those taken during the VENTANA and TIBURON dives are in the photographic database at the Monterey Bay Aquarium Research Institute.

The Pacific specimens generally were collected deeper than the Atlantic ones. This may be related to temperature, as in the relevant Pacific area the temperature decreases below 4 °C at depths greater than 1000 m, while in the relevant Atlantic area it sinks below 5 °C at about 550 m.

Etymology.—This species is named in honor of Claude and Danièle Carré in recognition of their important contributions to siphonophore biology.

Table 1. Known records of *Marrus claudanielis*.

Vehicle dive	Date	Location	Depth	Notes
TIBURON 596	July 19, 2003	36°36.12'N, 122°22.48'W	1,190 m	Holotype
JSL II 1411	September 16, 1986	39°56.4'N, 70°14.3'W	518 m	Paratype
VENTANA 1575	March 11, 1999	36°42.24'N, 122°02.52'W	767 m	
VENTANA 1777	June 16, 2000	36°42.60'N, 122°02.70'W	934 m	
VENTANA 2243	September 9, 2002	36°42.48'N, 122°03.84'W	1,001 m	
TIBURON 515	November 24, 2002	36°42.00'N, 122°01.98'W	1,156 m	
TIBURON 531	March 13, 2003	24°19.02'N, 109°12.18'W	1,144 m	
TIBURON 547	March 31, 2003	24°14.04'N, 109°40.02'W	1126 m	
JSL II 930	August 18, 1984	40° 05.03'N, 69°03.01'W	686 m	Youngbluth (1989)
JSL II 3457	September 26, 2003	40°17.77'N, 68°06.68'W	862 m	Pagès (pers. comm.)

DISCUSSION

Marrus claudanielis can easily be distinguished from the other three species presently included in the genus by the fact that the apico-lateral ridges on the nectophore do not divide and by the presence of weak lateral ridges. The distal facet of the bract is divided, as in *Marrus orthocanna* (Kramp, 1942), but the line of nematocysts, and other ectodermal cells, on the upper side of the bract is considerably more extensive than in that species. The bracts of the other two species have an undivided distal facet and do not show the lines of nematocysts.

Totton (1965, p. 62) defined the genus *Marrus* as "A group of three unicornuate Agalmidae known only from fragments, whose nectophores have straight (unlooped) lateral radial canals." These two characters together do appear sufficient to distinguish the genus. The presence of unlooped lateral radial canals on the nectosac of the nectophore immediately separates the genus *Marrus* from some other long-stemmed physonect genera, such as *Agalma*, *Halistemma*, *Nanomia*, *Lychnagalma*, and *Pyrostephos*, as their nectosacs bear markedly looped lateral canals. The species of the genera *Cordagalma* and *Frillagalma* have only slightly looped lateral radial canals, but have very distinctive, non-unicornuate tentilla; while those of the families Apolemiidae and Forskaliidae, the latter having straight lateral canals, are quite distinct for several other reasons. The other relevant long-stemmed genera with straight lateral radial canals are *Erenna*, *Parerenna*, *Bargmannia*, and *Moseria*. The first two genera have very peculiar tentilla with a hypertrophied cnidoband that so distinctly sets them apart that recently Pugh (2001) has placed them in a separate family, the Erennidae. Similarly the nectophores of *Bargmannia* species cannot be confused with those of any other genus. The presence of stenotele nematocysts at the proximal end of the straight or loosely coiled cnidoband of *Bargmannia* species also

clearly separates them from *Marrus* species. The distinguishing characters of the genus *Bargmannia* were discussed in detail by Pugh (1999) who followed Totton (1965) in retaining the genus within the family Pyrostephidae. Finally, the species of the genus *Moseria* have some characters in common with those of *Marrus* species, but the shape of the nectophores is distinctly different. In addition, there is no muscle-free zone on the nectosac, although this is also the case for *Marrus orthocannoides* Totton, 1954, and there is a descending pallial canal; the possible significance of which is discussed below. Further, *Moseria* bears two forms of tentilla, both on the same tentacle (P.R.P, pers. obs.) and both involucrate, one of which was described and figured by Moser (1925) and the other described by Totton (1965). Existing evidence suggests that the tentilla of all *Marrus* species do not possess an involucre.

There are important variations in some of the more general characters across the species of *Marrus* (Table 2). The absence of a muscle-free zone at the apex of the nectosac in *M. orthocannoides* clearly differentiates this species from the others, and Pugh (1999) concluded that this species might eventually be excluded from the genus. In *Marrus antarcticus* Totton, 1954 and *M. orthocanna*, the apico-lateral ridges branch well before the ostium, although, as Totton (1965) notes, they are very difficult to see without staining. In *M. claudanielis*, the apico-lateral ridges do not divide. There is also a pair of weak lateral ridges in this species. Norden Andersen (1981) described a pair of short lateral ridges on each side of the nectophore of *M. orthocanna*, but the structures he figured were not true lateral ridges. We believe that they were probably preservation artifacts, as no such ridges were apparent on the nectophores of *M. orthocanna* we examined.

There are also some important differences in the siphosomal elements of *Marrus* species. Totton (1954, 1965) described the presence of palpons, mostly or wholly on the gonodendra, in *M. antarcticus*, whereas long, thin stem palpons were said to be present in *M. orthocannoides*. This contrasts markedly with the situation in both *M. orthocanna* and *M. claudanielis* where palpons were found to be entirely absent. Similarly, the bracts of *M. antarcticus* and *M. orthocannoides* are somewhat similar, with an undivided distal facet. In contrast, in *M. orthocanna* and *M. claudanielis*, the distal facet is divided and the median ridge is covered in lines of nematocysts, which also extended along the inner transverse ridge in the latter species.

Two of the species, *M. antarcticus* and *M. claudanielis*, were found to be dioecious, bearing only male or female gonophores, and only male gonophores were found with the specimen of *M. orthocannoides* (Totton, 1954, 1965) so that, too, may be dioecious. However, Norden Andersen (1981) described both male and female gonophores on his specimen of *M. orthocanna*, and we have confirmed this observation on our material of that species.

The tentilla of *M. orthocannoides* have not been described, but for all other *Marrus* species they are without an involucre and possess a single terminal filament. Totton (1954) described the cnidoband of the tentillum of *M. antarcticus* as having three coils, but he did not mention how tight the coiling was. Kramp (1942) described the few tentilla of *M. orthocanna* as slightly coiled. In contrast, Norden Andersen (1981) described the cnidobands of tentilla of the same species as being loosely and irregularly coiled. Present observations on additional material of *M. orthocanna* show that the cnidobands are either straight, slightly bent, or loosely coiled. It is thought that the latter two conditions are probably preservation artifacts. In *M. claudanielis* the cnidobands of the young tentilla are straight, while the mature cnidobands are

Table 2. Diagnostic characters of the species of *Marrus*.

	<i>Marrus claudanieliis</i>	<i>Marrus antarcticus</i>	<i>Marrus orthocanna</i>	<i>Marrus orthocannoides</i>
Nectophores	Present	Present	Present	Absent ²
MFZ ¹ on adaxial wall of nectosac	Straight	Straight	Straight	Straight
Radial canals	Absent	Absent	Absent	Absent ³
Descending to pallial canal	Undivided	Bifurcated	Bifurcated	Bifurcated
Apico-lateral ridge	Weakly Present	Absent	Absent	Absent
Lateral Ridges	Absent	Mainly Gonopalpons ²	Absent	Present ²
Palpons	Yes	No	Yes	No
Distal facet of bracts divided in mid-line	Dioecious	Dioecious	Monoecious	?Dioecious ²
Sex	Loosely coiled	Loosely coiled	Mostly straight	Undescribed
Tentillum Cnidoband	Absent	Absent	Absent	Undescribed
Involucrum				

¹ Muscle Free Zone.² According to Totton (1965).³ Kindly confirmed for us by Dr. G. Mapstone.

fairly regularly, but loosely, spiraled, which probably represents their normal, but contracted, condition.

One interesting feature of the nectophores of *Marrus* species is the lack of a descending pallial canal. Whether this character has any taxonomic relevance remains to be seen, but in many agalmatid genera, as we presently know them, there is a descending pallial canal. However, in the Pyrostephidae (*Bargmannia* and *Pyrostephos*) and Apolemiidae it is not present. This is also, to a large extent, applicable to the Erennidae, where there is a very short pallial canal. Although these three families are in other ways clearly distinct from the Agalmatidae, the arrangement of the pallial canal may be another indicator of their distinctiveness and informative for resolving higher level relationships among these taxa.

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