

NEW OBSERVATIONS ON A RARE PHYSONECT SIPHONOPHORE, *LYCHNAGALMA UTRICULARIA* (CLAUS, 1879)

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(Figs. 1–7)

A rare physonect siphonophore, *Lychnagalma utricularia* (Claus, 1879), is redescribed from 24 specimens collected in the region of the Bahamas by the submersible D.S.R.V. 'Johnson-Sea-Link II'. It was the most common siphonophore collected by the submersible, using its sophisticated sampling techniques. The paucity of previous records for the species, and thus its apparent rarity, is probably due to the extreme fragility of the animals which causes them to disintegrate on contact with nets. The status of the second species, *L. vesicularia* Haeckel, 1888, is reviewed and it is concluded that it should be reduced to a junior synonym of *L. utricularia*.

INTRODUCTION

Physonect siphonophores, i.e. those that possess a gas-filled float or pneumatophore apical to a series of swimming bells or nectophores, are poorly known from net collections. The extreme fragility of the animals results in their being torn to pieces by the netting, such that only a few damaged parts remain for identification. In contrast, during the nineteenth century, when gentler means of collecting marine animals were used, a large number of physonect species were described and the intact animals were beautifully illustrated. However, in order to show the complex organization of such siphonophores, the illustrations often were idealized or semi-schematic and recent authors (e.g. Totton, 1965) have suggested that a great deal of imagination went into their production. For this reason, and the persistent failure to find further specimens in net collections, it is difficult to assess whether some of the original descriptions are still acceptable, or should be rejected. Totton (1965), for instance, considered *Forskalia tholoides* Haeckel, 1888 to be a doubtful species 'based on a beautiful idealized figure', yet there are many recent records for this species (e.g. Biggs, 1977; Harbison, Biggs & Madin, 1977) and intact specimens appear almost exactly as Haeckel (1888) drew them (personal observation).

Another example of this dilemma is the status of species of the genus *Lychnagalma* Haeckel, 1888. Claus (1879) described, under the name *Agalmopsis utricularia*, a remarkable siphonophore characterized by the peculiar processes

on the ends of the branches (tentilla) of its tentacles. Each tentillum consisted of a stalk, a tightly coiled cnidoband heavily armed with nematocysts, and a terminal vesicle from around the base of which arose eight, regularly spaced, filaments. The number of these terminal filaments is exceptionally high as the maximum number found in other related physonects is two (gen. *Agalma* Eschscholtz, 1825, whose tentilla also each possess a terminal vesicle or ampulla). Whereas the tentilla of *Agalma* spp. hang down from the tentacles, the typical siphonophore arrangement, those of *A. utricularia* were described as being buoyant, floating upwards so that the tentacles were held out horizontally, like buoyed lines.

Fewkes (1882) created a new genus, *Calliagalma*, for Claus's unusual siphonophore, but since this generic name had already been employed for an insect, Haeckel (1888) established another generic name, *Lychnagalma*, to include the original species and another, *L. vesicularia*, which he described from a specimen collected off Ceylon (Sri Lanka). Bedot (1896) had no hesitation in synonymizing the two species, retaining *L. utricularia*, as he could find no character that was of sufficient importance to distinguish them apart. However, Totton (1965) chose to retain both species. He noted that although Claus (1879) had captured specimens of *L. utricularia* on several occasions, in the vicinity of Messina, there had been no further records for this easily identifiable animal. This absence of new material might have cast a doubt on the validity of the species, but Totton considered that both the original description and illustrations were of sufficient detail to inspire full confidence in them. Short shrift, however, was given to Haeckel's (1888) description of the other species, *L. vesicularia*, when Totton (1965, p. 73) stated 'A doubtful species. It is not clear from Haeckel's description whether *vesicularia* differs from *utricularia*. It is to be doubted whether much reliance can be placed on Haeckel's beautifully idealized figures, or the record for geographical distribution.' It is a puzzle, therefore, why Totton chose to retain *L. vesicularia* as a valid species, but perhaps he felt constrained by the widely differing type localities.

In recent years sophisticated means of collecting fragile, deep-sea gelatinous organisms have been developed using submersibles (Youngbluth, 1984). Amongst the numerous, complete specimens of siphonophores that have been captured by these means there are several of a physonect species, whose tentilla possess octaradial terminal filaments. These specimens clearly belong to the genus *Lychnagalma* and, because of their near perfect condition, they have enabled comparisons to be made with the species described by Claus (1979) and Haeckel (1888).

METHODS

The material was collected during a cruise to the Bahamas in October and November 1984 that involved the use of the submersible D.S.R.V. 'Johnson-Sea-Link II'. One of us (G.R.H.) was the organizer and principle investigator of the cruise. The 'Johnson-Sea-Link II' is a remarkable craft as the 1.7 m diameter acrylic sphere, which forms its forward compartment, allows panoramic views

of the surrounding waters. The submersible, which has been described by Youngbluth (1984), is exceptionally well equipped with sampling devices that enable even the most fragile specimens to be collected intact. Two types of such devices were used; the first, known as 'slurp guns' or 'critter-gitters', gently sucked the animals into one of 24 3.5 l containers; the second known as, 'detritus samplers' were eight vertically orientated tubes mounted on the front of the submersible into which the required animals were brought, by manoeuvring the submersible. Hydraulically operated lids, top and bottom, then enclosed the specimens in 6.5 l of water (see Youngbluth, 1984). Using these devices it was possible to collect up to 32 individual animals during each dive.

During the cruise 55 dives were made and a full station list is given in Table 1. Various depth horizons were investigated during each dive but greatest effort was put into searching the 500–700 m depth range. Most dives were of 2–2.5 h duration.

In all about 130 specimens of siphonophores were collected, amongst which were several new and rare species. The commonest of all was a species which clearly belonged to the physonec genus *Lychnagalma*, because of the presence of octaradial filaments on its tentilla. Although this material was collected in excellent condition and could be studied in the laboratory, within a short space of time pieces began to break away from the stem and, on preservation, the specimens fell apart. Nonetheless, a description can be given of those pieces that are of greatest taxonomic value.

DESCRIPTION

Material collected

Twenty-four specimens of *Lychnagalma* were collected during fourteen dives. The station data for these specimens, given below, are arranged as follows: Dive Number, Sample Number, (Depth of Collection). Sample numbers with a prefix P or S refer to collection by the port or starboard 'slurp guns', and those without a prefix refer to the 'detritus sampler' number. The positions for these dives are given in Table 1.

960 2 (503 m); 969 P2 (640 m); 971 4 (610 m); 974 S1 (683 m); 974 S4 (686 m); 974 S11 (610 m); 974 4 (680 m); 974 7 (690 m); 974 8 (686 m); 978 P9 (610 m); 981 P6 (663 m); 984 P3 (536 m); 984 P4 (518 m); 984 P11 (610 m); 984 P12 (607 m); 987 3 (605 m); 990 P1 (670 m); 994 7 (606 m); 997 3 (595 m); 999 7 (ca. 600 m); 1003 7 (550–730 m*); 1003 S9 (550–730 m*); 1004 2 (602 m); 1004 7 (645 m).

The total depth range over which specimens were collected was ca. 500–700 m, with a mean depth of 620 m. However, this may not be representative of the depth distribution range of the species since this was the range over which sampling was concentrated.

Nectophores (Figs. 1, 2)

Claus (1879) mentioned the presence of 18–19 biserially arranged nectophores on the nectosome of his specimens, and Haeckel illustrated (1888, pl. XVI, fig. 1) 17, with three more developing ones. The 'Johnson-Sea-Link II' specimens possess between 11 and 25 nectophores, averaging about 18. The biserial, staggered arrangement of the nectophores can be seen in Fig. 3. Claus (1879) figured the nectophores in detail (see Fig. 1C–E), but his description of them is difficult to follow. The nectophores (Figs. 1A, B, 2) from the present material resemble closely those drawn by Claus, although there are certain differences in

*No precise details on depth of sampling.

Table 1. *Station data for dives of 'Johnson-Sea-Link II' during Oct./Nov. 1984 Cruise*

| Dive no. | Date (1984) | Position | | Dive time (E.S.T.) | Max. depth of dive (m) |
|----------|-------------|--------------|---------------|--------------------|------------------------|
| | | Latitude (N) | Longitude (W) | | |
| October | | | | | |
| 953 | 15 | 26° 41.2' | 79° 02.9' | 12.22-14.10 | 460* |
| 954 | 15 | 26° 33.8' | 79° 04.7' | 20.37-23.00 | 610 |
| 955† | 16 | 26° 23.2' | 78° 52.9' | 01.33-03.28 | 600 |
| 956 | 16 | 26° 23.1' | 78° 43.2' | 05.24-08.00 | 630 |
| 957 | 16 | 26° 25.5' | 78° 49.5' | 19.00-21.30 | 650 |
| 958 | 16 | 26° 25.6' | 78° 44.5' | 23.30-01.30 | 610 |
| 959 | 17 | 26° 25.8' | 78° 42.6' | 03.30-06.00 | 700 |
| 960 | 17 | 26° 25.1' | 78° 45.1' | 19.00-21.30 | 580 |
| 961 | 17 | 26° 26.7' | 78° 40.8' | 23.30-01.30 | 460 |
| 962 | 18 | 26° 26.6' | 78° 33.9' | 03.45-06.01 | 460 |
| 963 | 18 | 26° 25.0' | 78° 43.6' | 19.00-21.30 | 550 |
| 964 | 18 | 26° 28.5' | 79° 00.3' | 23.30-01.30 | 550 |
| 965 | 19 | 26° 27.2' | 78° 49.7' | 03.30-06.00 | 300 |
| 966 | 19 | 26° 28.8' | 78° 48.8' | 19.00-21.30 | 740* |
| 967 | 19 | 26° 31.5' | 78° 24.0' | 23.30-01.30 | 700* |
| 968 | 20 | 26° 35.9' | 78° 11.3' | 03.30-06.00 | 600* |
| 969 | 20 | 26° 35.3' | 78° 11.4' | 19.00-21.30 | 700 |
| 970 | 20 | 26° 33.0' | 78° 02.6' | 23.30-01.30 | 670* |
| 971 | 21 | 26° 25.7' | 77° 51.2' | 03.30-06.00 | 610 |
| 972 | 21 | 26° 24.3' | 77° 49.8' | 18.52-21.30 | 580* |
| 973 | 21 | 26° 17.5' | 77° 43.7' | 23.30-01.30 | 550 |
| 974 | 22 | 26° 03.1' | 77° 36.0' | 03.30-06.00 | 690* |
| 975 | 22 | 26° 08.5' | 77° 37.1' | 19.00-21.30 | 700 |
| 976 | 22 | 26° 02.8' | 77° 30.5' | 23.30-01.20 | 600 |
| 977 | 23 | 25° 59.0' | 77° 24.2' | 03.30-06.00 | 570* |
| 978 | 23 | 25° 58.2' | 77° 24.2' | 19.00-21.30 | 700 |
| 979 | 23 | 25° 57.8' | 77° 22.1' | 23.30-01.30 | 550 |
| 980 | 24 | 25° 58.8' | 77° 24.6' | 03.30-06.00 | 630 |
| 981 | 24 | 25° 54.5' | 77° 17.8' | 18.00-20.30 | 670 |
| 982 | 24 | 25° 54.9' | 77° 17.8' | 22.20-00.30 | 590 |
| 983 | 26 | 25° 06.8' | 77° 23.1' | 17.00-19.30 | 670 |
| 984 | 26 | 25° 05.3' | 77° 29.5' | 21.30-23.30 | 670 |
| 985 | 27 | 25° 03.1' | 77° 31.7' | 01.30-03.30 | 520 |
| 986 | 27 | 25° 22.1' | 77° 51.0' | 19.00-21.30 | 640 |
| 987 | 27 | 25° 22.7' | 77° 55.0' | 23.30-01.30 | 610 |
| 988 | 28 | 25° 23.2' | 77° 56.4' | 03.30-05.40 | 670 |
| 989 | 28 | 25° 22.6' | 77° 55.1' | 21.00-00.00 | 690 |
| 990 | 29 | 25° 22.5' | 77° 54.5' | 03.00-06.00 | 730 |
| 991 | 29 | 25° 23.0' | 77° 55.6' | 19.00-21.30 | 730 |
| 992 | 29 | 24° 49.7'? | 77° 41.4' | 23.30-01.30 | 700 |
| 993 | 30 | 25° 24.0' | 78° 00.8' | 03.30-06.00 | 550 |
| 994 | 30 | 25° 25.4' | 78° 04.0' | 19.00-21.30 | 660 |
| 995 | 30 | 25° 23.7' | 77° 57.6' | 23.30-01.30 | 550 |
| 996 | 31 | 25° 22.5' | 77° 54.9' | 03.30-06.00 | 660 |
| 997 | 31 | 25° 22.6' | 77° 54.9' | 19.00-21.30 | 610 |
| 998 | 31 | 25° 22.0' | 77° 51.6' | 23.30-01.30 | 670 |
| November | | | | | |
| 999 | 1 | 25° 22.9' | 77° 55.1' | 03.30-06.00 | 710 |
| 1000 | 1 | 25° 22.8' | 77° 54.6' | 19.00-21.30 | 700 |
| 1001 | 1 | 25° 22.9' | 77° 55.2' | 23.00-01.15 | 680 |
| 1002 | 2 | 25° 23.0' | 77° 55.3' | 03.50-06.00 | 530 |
| 1003 | 2 | 25° 22.7' | 77° 54.9' | 19.00-21.30 | 730 |

Table 1. (*Cont.*)

| Dive no. | Date (1984) | Position | | Dive time (E.S.T.) | Max. depth of dive (m) |
|----------|-------------|--------------|---------------|--------------------|------------------------|
| | | Latitude (N) | Longitude (W) | | |
| 1004 | 2 | 25° 22.0' | 77° 50.2' | 23.30–01.30 | 650 |
| 1005 | 3 | 25° 22.5' | 77° 53.9' | 03.33–06.00 | 710 |
| 1006 | 3 | 25° 22.7' | 77° 54.5' | 19.00–21.30 | 730 |
| 1007 | 4 | 25° 22.4' | 77° 53.5' | 00.00–02.00 | 610 |

* Maximum depth of dive = depth of bottom. Generally, the depth of the bottom was between 750 and 900 m.

† No collections or observations because of failure to achieve neutral buoyancy.

detail, particularly with regard to the pattern of ridges on their surfaces. On the upper or dorsal surface (which Claus refers to as ventral) are found the prominent pair of apico-lateral ridges (Figs. 1 A, C, 2 A) (vk' in the notation of Claus). Claus failed to note that these ridges divide close to the base of the nectophore, with the inner pair of branches running directly to the ostium, the opening of the nectosac, while the outer pair curve out laterally. This latter pair may be the ridges illustrated by Claus (Fig. 1 C, 'x') which join with the pair of lateral ridges (vk''). However, in the present material they end abruptly before reaching the vk'' ridges such that a distinct gutter is formed between the two. There are thickened pads of ectoderm in the region of this furrow which appear to suspend the ostium. These pads are seen as opaque, white patches in the live specimens.

The lateral (vk'') ridges also do not extend down as far as the ostium, but curve round to join the infra-lateral (tk) ridges. This feature is more obvious in the younger nectophores (Fig. 2 A, C) than in the older ones (Fig. 1 A), where the ectodermal pads overlie these ridges. A characteristic feature of the lateral ridges, as Claus showed, is that they peter out towards the top of the nectophore before reaching the apico-lateral (vk') ridges.

In the basal half of the nectophore the infra-lateral (tk) ridges form the boundary between the lateral and ventral sides. Vertical lateral (sk) ridges branch off from these and are directed obliquely up, across the lateral surfaces, to join the apico-lateral (vk') ridges towards the top of the nectophore. Beyond the point where the vertical lateral ridges branch off, the infra-lateral ridges leave the sides of the nectophore and pass obliquely on to the lower or ventral surface (Claus's dorsal), petering out gradually. There is a vague connection, particularly in the older nectophores, between these ridges and the ventral (dk) ones, but this is more a rounded margin than a distinct ridge. Claus (1879), however, illustrated (Fig. 1 D, E) this connection as a distinct ridge which, together with the extension of the infra-lateral ridge, formed part of his so-called 'dorsal' ridge (dk).

In the present interpretation, the ' dk ' ridges run down the nectophore for a short distance from their points of origin on the outer margins of the apical thrust blocks and form the lateral margins of the ventral surface. They then bend

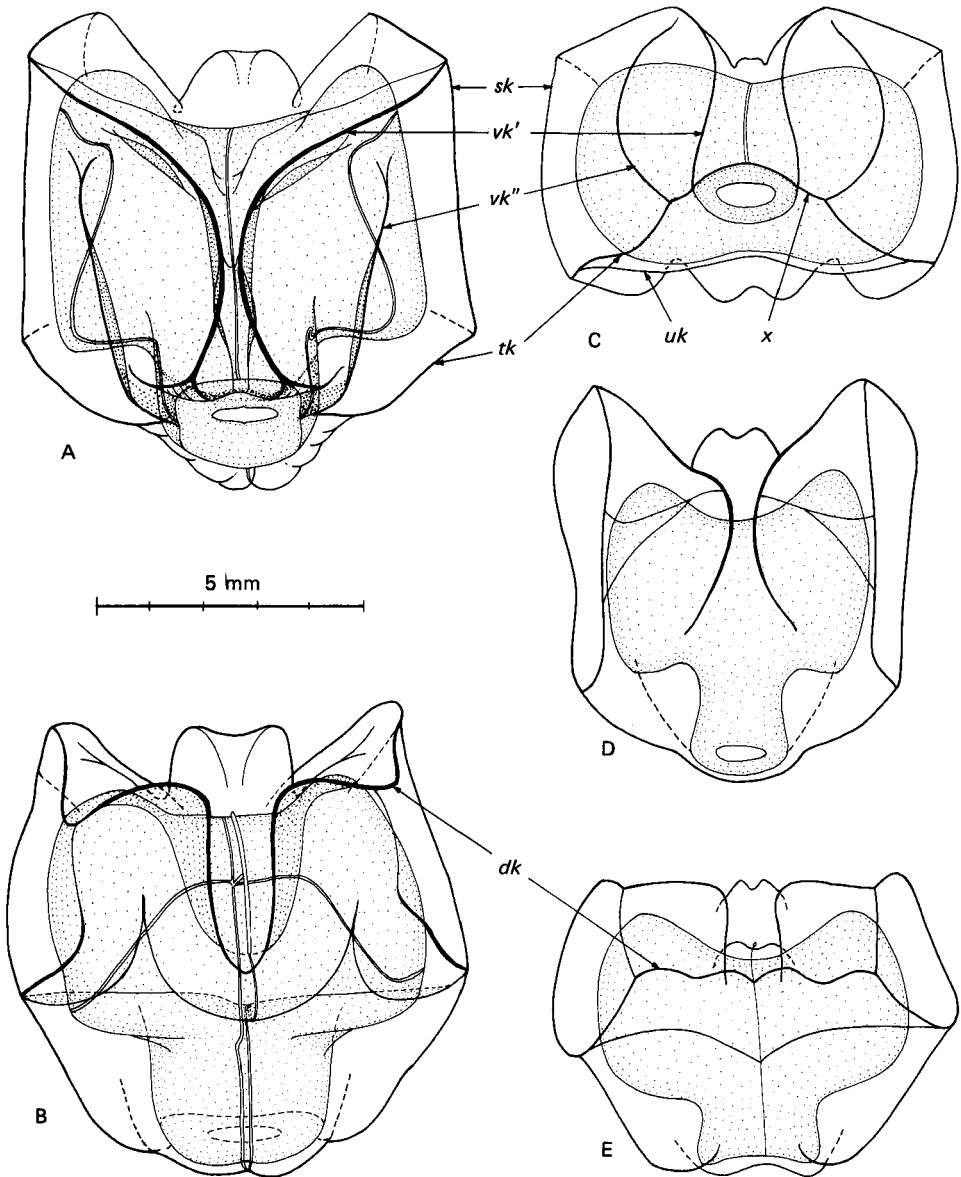


Fig. 1. Nectophores of *Lychnagalma utricularia*. (A) Upper (dorsal), and (B) lower (ventral) views of mature nectophores from JSL specimen 1004-7. Scale bars apply to these figures only. (C) Ostial and (E) lower (ventral) views of mature nectophores (D) Lower (ventral) view of immature nectophore. (Redrawn from Claus (1879), fig. 5 d, e and b respectively.) *sk*, Vertical lateral ridge; *vk'*, apico-lateral ridge; *vk''*, lateral ridge; *tk*, infra-lateral ridge; *uk*, 'untere Kante' (see text); *dk*, ventral ridge; *x*, extension of the apico-lateral ridge (see text for details).

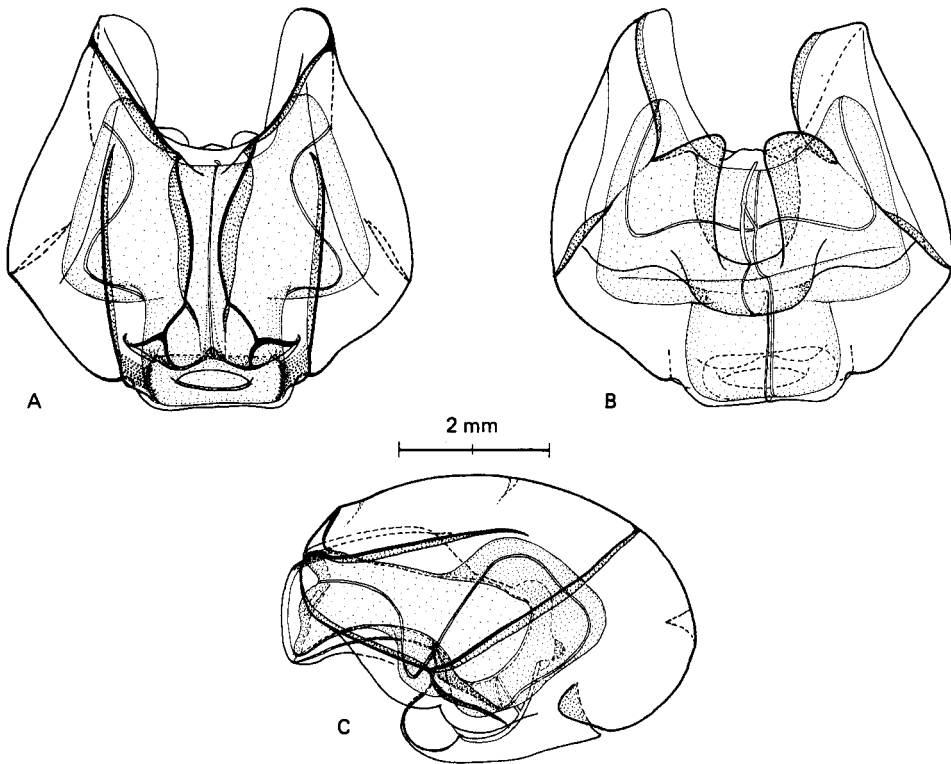


Fig. 2. Nectophores of *Lychnagalma utricularia*. (A) Upper (dorsal), (B) lower (ventral) and (C) side views of young nectophores from JSL specimen 1004-7.

sharply, through 90° , and continue towards the mid-line of the nectophore. However, they do not join up, as Claus illustrated for one of his nectophores (Fig. 1 E), but make another right-angled bend and continue towards the ostium before petering out at about the mid-height of the nectophore. A faint cross-connection between these two ridges can be discerned, particularly in the older nectophores whose hydroecial groove is more pronounced.

Claus (1879) figures, but does not mention in the text, one further ridge which he labelled an 'untere Kante' (*uk*) (Fig. 1 C). It is not clear to what he was referring, but it is presumed that this ridge was the pronounced, but rounded, junction between the dorso-ventrally thickened upper part of the nectophore and the thinner basal part (Figs. 1 B, 2 C). In older nectophores this junction becomes distinctly three-lobed.

Overall, the ridge pattern found on the nectophores of the 'Johnson-Sea-Link II' specimens differs only very slightly from that described by Claus (1879) for specimens of *Lychnagalma utricularia*. Haeckel's (1888) unusually brief description of *L. vesicularia* gives virtually no information of any taxonomic significance with regard to the nectophores, and it is difficult to interpret the ridge pattern from his illustrations. Totton (1965), however, suggested that the

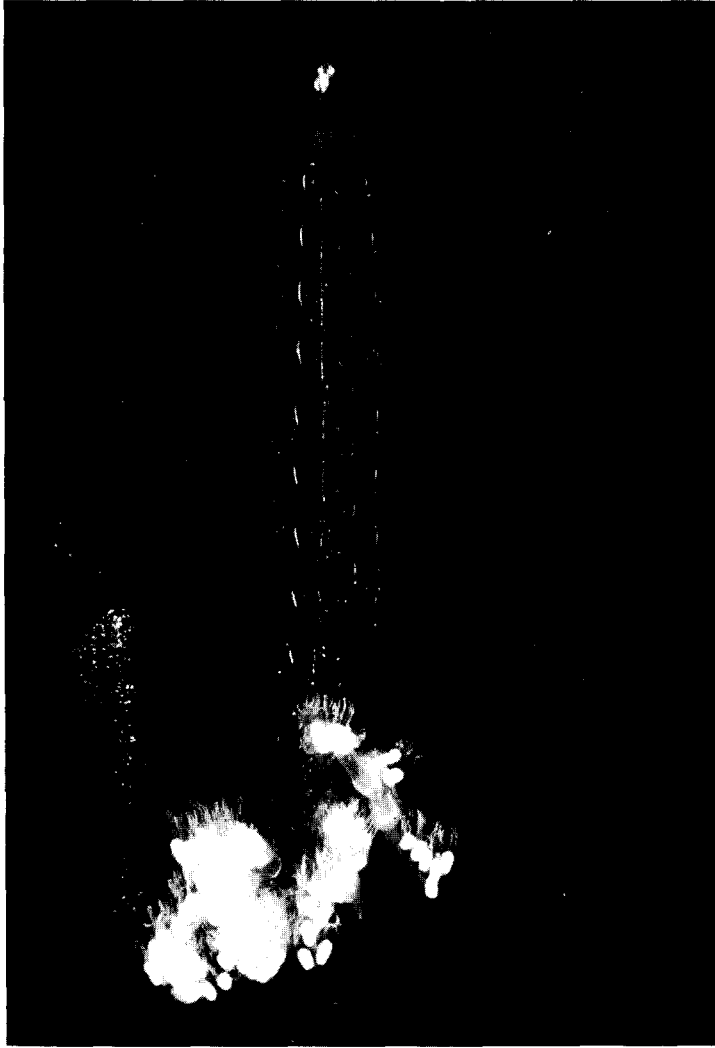


Fig. 3. Entire specimen (JSL 994-7) of *Lychnagalma utricularia*. Approximately life size.
(Photograph: R. Gilmer.)

characteristic vk' and incomplete vk'' ridges were represented. On the other hand, Haeckel did illustrate the courses of the radial canals on the nectosac of the nectophore, which Claus did not. The arrangement of these canals in the present material is very similar (Fig. 2C). The four radial canals arise together from the pedicular canal on the lower surface of the nectosac. The dorsal and ventral canals are straight, and follow the contours of the nectosac in the mid-line, connecting with the ring canal around the ostium. The lateral canals are looped in a manner reminiscent of some other agalmid physonecks. One interesting feature, not shown by Haeckel, is the mantle canal, which lies against the nectosomal stem and indicates the region of attachment of the nectophore. This canal extends down

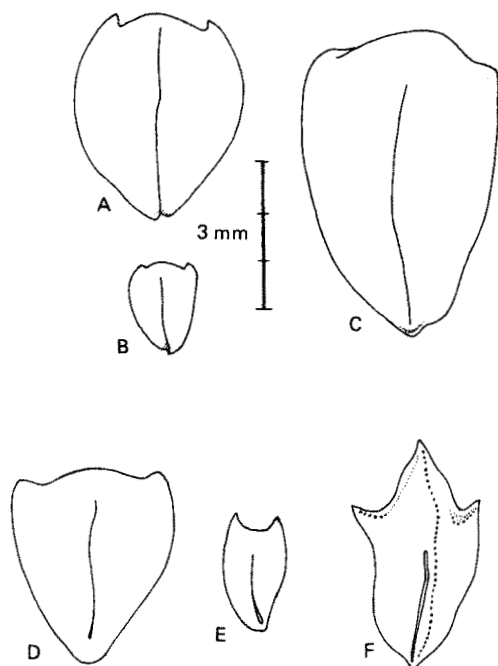


Fig. 4. Bracts of *Lychnagalma* spp. Upper views. (A-C) from JSL specimen 971-4. (D, E) Redrawn from Claus (1879, fig. 6a, b). (F) Redrawn from Haeckel (1888, plate. XVI, fig. 8) of *L. vesicularia*. Note: scale bars apply only to (A-C). Sizes of (D-F) not known.

the surface of the nectophore for some distance beyond the point of origin of the pedicular canal. At its basal end arises a thin canal which runs down the mid-ventral line of the nectophore, immediately below its surface and follows its contours. It curves over the mouth plate and joins the ostial ring canal at the same point as the ventral radial canal on the nectosac. It is not clear whether such an extension of the mantle canal has been reported before for any physonect siphonophore, although the nectophores of some other species do possess it (personal observation).

Bracts (Fig. 4)

The bracts of the 'Johnson-Sea-Link II' specimens (Fig. 4A-C) resemble closely those drawn by Claus (Fig. 4D, E), who described them as being relatively broad with two or three (distal) points. Haeckel illustrated the bracts (Fig. 4F) somewhat differently, with 3-5 prominent distal points, or teeth, and with rows of ?nematocysts (labelled as a cnidoband) present on the dorsal surfaces. Totton (1965) suggested that the bracts of *L. utricularia* measured 1.5 mm in length, but the source of this information is unclear as neither of the original descriptions gave any exact indication of size. The bracts of the present material measured from 2 mm, for the very youngest, up to 7 mm in length. The larger bracts are very flimsy and, on preservation, many partially or totally disintegrated. The two

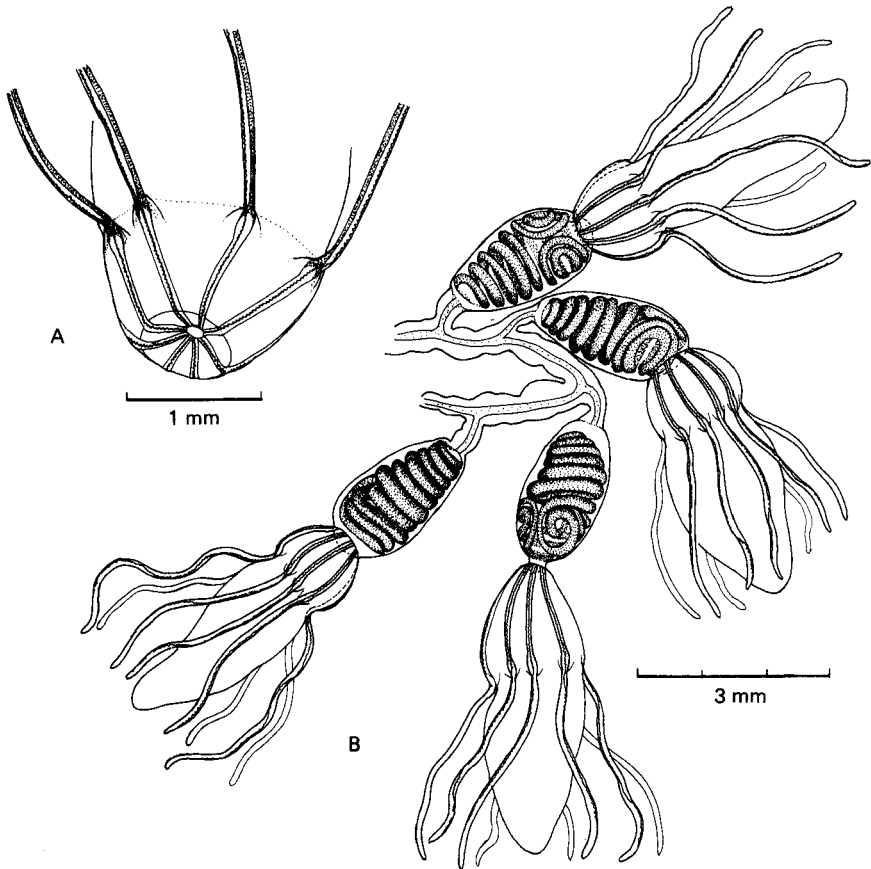


Fig. 5. Tentilla of *Lychnagalma utricularia*. (A) Detail of the base of a detached terminal vesicle. (B) General view of four tentilla.

distal, lateral teeth are clearly defined only in the younger bracts, while the central process becomes more prominent with age, although it always remains rounded.

Tentilla (Fig. 5)

Both Claus (1879) and Haeckel (1888) provided beautiful illustrations of a tentillum, and there are few basic differences apart from Haeckel's addition of an apical oil globule in the terminal vesicle. Both authors described the cnidoband as having 4 or 5 proximal transverse coils, while the distal coils were inclined towards the vertical. The whole structure was enclosed within an involucre. Although outwardly this is the basic arrangement, the actual configuration of the distal end of the cnidoband in the present material is much more complex. The proximal part of the cnidoband (Fig. 5 B) usually consists of five or six transverse (horizontal) spiral coils, but in certain specimens there appears to be a great deal of variability. Viewed from one angle the distal part seems to consist of four transverse coils, but from another the arrangement appears very convoluted. A

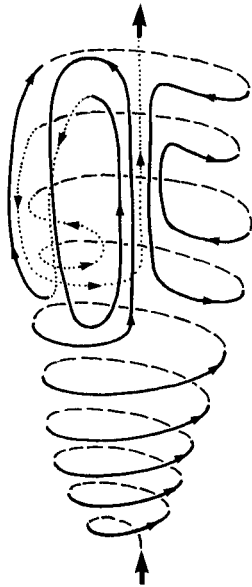


Fig. 6. Schematic representation of the coiling pattern of the cnidoband on the tentillum of *Lychnagalma utricularia*. The dotted line indicates the coils that are hidden within the structure. The two side branches are not shown.

schematic representation is shown in Fig. 6. Furthermore, coiled within the main cnidoband there are two thin side branches, which arise in the region of the fourth to sixth transverse spiral coil. The author can recall no other siphonophore whose cnidobands possess such side branches. Observations on a partially uncoiled cnidoband indicate that the terminal vesicle remains attached to the pedicle of the tentillum by both the main cnidoband and the suspensory ligament that has become straightened by the action of the angle bands. As the cnidoband uncoiled, the two side branches were exposed, but they do not appear to be armed with nematocysts and so their function remains obscure.

There appear to be two rows of relatively large, ensiform nematocysts, probably heteronemes (stenoteles), on the margins of the inner surface of the cnidoband. These are present throughout its length and are not restricted to the four or five proximal coils as Claus (1879) stated. The cnidoband also possesses a very large number of banana-shaped nematocysts, probably haplonemes (homotrichous anisorhizas).

The terminal vesicle is a large, thin-walled, fluid filled sac, which acts as a hydrostatic apparatus lifting the tentillum up and away from the tentacular stem. It is presumed that the density of the fluid content is reduced, possibly by ionic means such as sulphate regulation (Bidigare & Biggs, 1980), as there is no sign of the apical oil globule mentioned by Haeckel (1888). However, Dr G. O. Mackie (personal communication) has sectioned some of these terminal vesicles and found that the vesicles are indeed fluid filled, but the endoderm in their walls is very thin and does not appear to be an ion-transporting epithelium. So unless there

is a specialized part of the epithelium that has not yet been located the density of the fluid may not be under ionic control. Distressed animals, in laboratory tanks, released large quantities of a mucous-like substance from the tentilla (see Fig. 3), and so a special low density fluid may be secreted in the terminal vesicles.

Claus (1879) mentioned the presence of pronounced stripes of reddish pigmentation on the involucrum enclosing the cnidoband of the tentillum, but in the present specimens it is the cnidoband itself that is pigmented. This pigmentation is not equally disposed on the cnidoband, as the proximal coils are virtually colourless. However, pigmentation is gradually enhanced to form a deep orange colouration in the more distal coils. This colour turned a pale red on preservation.

The tentilla are unusually large, with the cnidoband and terminal vesicle measuring up to 7.5 mm in length. Claus (1879, pl. 1, fig. 3) illustrated a tentillum that was said to be enlarged *ca.* 100-fold. This would mean that its length was only 1.5 mm, extremely small in comparison with the present material. It is possible that the original illustration was reduced for publication, but it is doubtful whether the few indications of size given by Claus are reliable.

Gastrozooids (Fig. 7)

Claus (1879) mentioned only that the gastrozooids had long stalks or pedicles, but Haeckel (1888) in his brief description of the whole structure noted that there were eight hepatic ridges on the spindle-shaped stomach section. The gastrozooids of the present specimens (Fig. 7) show a clear distinction between the four component sections; namely (*a*) the long thin pedicle; (*b*) the enlarged, thickened but transparent basigaster, to the base of which is attached the tentacle, and separated by a constriction from; (*c*) the opaque stomach; and (*d*) the tapering proboscis region with its terminal mouth opening. The stomach region has a pale yellowish colouration, but it bears no hepatic stripes. These stripes are seen only on the proboscis, and can be either eight or twelve in number. They connect into a circular ring that runs around the mouth opening. The distal three segments of the large gastrozooids measured up to *ca.* 10 mm when contracted, but *in situ* observations showed that they could be extended considerably.

Palpons (Fig. 7)

As Haeckel (1888) stated, these are long, slender tubes with extremely long and very thin palpacles attached to their bases. The presence of nematocysts at their distal ends could not be confirmed and there was no sign of any pigmentation. The contracted palpons measured up to 5 mm in length, but, as with the gastrozooids, in life they could be extended greatly.

Gonophores

The gonodendra are small and difficult to make out and no detailed studies have been carried out. The female gonodendra are made up of a large number of minute gonophores, looking like bunches of grapes. Male gonophores on the same animal

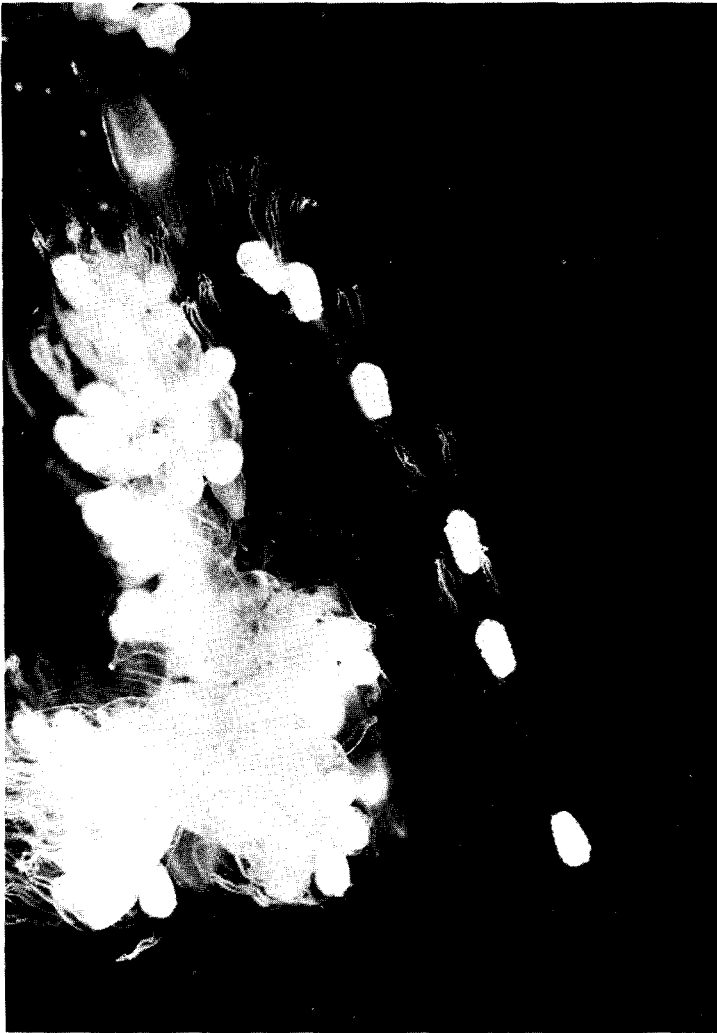


Fig. 7. Part of the siphosome of *Lychnagalma utricularia* showing the buoyant tentilla and a large gastrozoid (at top). JSL specimen 994-7, approximately 3.5 times life size. (Photograph: R. Gilmer.)

are much larger, and are disposed in small groups, or perhaps individually along the stem. Claus (1879) described the ripe male gonophores as being the same size as the terminal vesicles of the tentilla.

Pneumatophore

Haeckel (1888) gave great prominence to the description of the pneumatophore of *Lychnagalma vesicularia*, as he did with many physonects. However, the pneumatophore may not provide useful taxonomic characters and, in any case, is rarely collected in good condition as it becomes highly distorted when the animal is brought up from any depth. Nonetheless, in the present specimens the

structure is in accord with Haeckel's description, apart from the absence of an octa-radial red-brown pigment star on its apex. The pneumatophore is 3–5 mm in height and, in life (Fig. 3), is borne on a relatively long stalk such that it is raised well above the nectosomal budding region. *In situ* observations show that the pneumatophore imparts little lift to the animal as a whole.

Behavioural notes

In addition to the *in situ* observations of the animals, video recordings were made of several specimens before they were collected. Almost all the specimens had their siphosomes contracted when observed, possibly as a response to the bright lights of the submersible. Thus the characteristic fishing posture figured by Claus (1879), with the tentacle held out horizontally like a buoyed line, was not seen. It may be that the siphosome of *Lychnagalma* is relatively short as only four to six well-developed gastrozooids and tentacles usually were observed. The tentacles, no doubt, could be extended to a considerable length and they could bear thirty or more widely spaced tentilla. In the laboratory, although the terminal vesicles of the tentilla clearly were positively buoyant (Fig. 7), they provided insufficient buoyancy to lift the whole tentacle, casting doubt as to whether the horizontal fishing posture actually could be achieved.

The terminal part of the tentillum underwent periodic contractions and the terminal filaments themselves were greatly extensible. The outward appearance and orientation of the whole structure gives the impression of a minute medusa. This might be another instance of aggressive mimicry, which has been suggested for the tentilla of other siphonophores, e.g. *Agalma* spp. (Purcell, 1980). However, in these *Lychnagalma* specimens the gastrozooids were either empty or their contents too digested for recognition so that their preferred diet could not be analysed.

The animals were extremely active swimmers and often proved difficult to capture. However, there appeared to be no synchrony to the contractions of the nectophores. Occasional waves of contraction spread down the nectosome but in general the contractions were asynchronous and resulted in the whole nectosome moving from side to side, sometimes quite violently.

DISCUSSION

The very close similarity between the nectophores, bracts and tentilla of the 'Johnson-Sea-Link II' material and those described by Claus (1879) for *Lychnagalma* (*Agalmopsis*) *utricularia* leaves no doubt that we are dealing with the same species. Haeckel's (1888) poorly described specimen of *L. vesicularia* appears to differ only slightly, in the structure of the bracts and the presence of an oil droplet in the terminal vesicle of the tentillum. These differences are considered insufficient to distinguish a separate species and so *L. vesicularia* here is synonymized with *L. utricularia*. Totton's (1965) retention of the two species may have been based largely on the widely different localities of collection, but

since the present material came from a third, quite different, locality this apparent zoogeographical patchiness may be an artifact produced by sampling difficulties and so prove to be irrelevant. Moreover, the possible record for *L. utricularia* given by Casanova (1980) for the N.E. Atlantic Ocean may represent a connecting link between the Bahamian region and the Mediterranean, where Claus caught his specimens. Unfortunately it has not proved possible to verify Casanova's record.

Although the specimens of Claus (1879) and Haeckel (1888) appear to have been collected at the surface, *Lychnagalma utricularia* seems to be a deep living physonect, only brought to the surface by local upwelling events. Nevertheless, the 500–700 m depth range over which the 'Johnson-Sea-Link II' collected material is not necessarily indicative of its true depth range, as it represents only the region given closest scrutiny during the dive programme. On one of the dives (JSL 974), when six specimens were captured and several others seen, the animals were concentrated very close to the bottom.

Despite the dearth of records for *Lychnagalma utricularia* in the literature it is clear that this physonect is relatively abundant, at least in the Bahamas region, since it was the siphonophore most commonly caught by the submersible. The general failure to observe this species in net collections clearly is due to its great fragility. However, many siphonophore species that are too small to be observed from submersibles, such as many calyphorans, are adequately sampled by nets. Thus it is clear that only with a combination of *in situ* observations and net collections can all the types of siphonophore be studied. Since the net collected calyphoran species are one of the dominant micronektonic groups in the oceans, the present observations of numerous physonect species, even in such an oligotrophic region as the Bahamas, can serve only to emphasize the important role that siphonophores play in the marine ecosystem. This role, for all types of gelatinous organisms, is all too often ignored or severely underrated.

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