

A NEW SPECIES OF *HALISTEMMA* (SIPHONOPHORA: PHYSONECTAE: AGALMIDAE) COLLECTED BY SUBMERSIBLE

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(Figs. 1-7)

A new species of physonect siphonophore, *Halistemma transliratum* sp. nov., is described from two specimens collected at mesopelagic depths in Bahamian waters by the submersibles 'Johnson-Sea-Link' I and II, and comparisons are made with the established species of that genus.

INTRODUCTION

The submersibles 'Johnson-Sea-Link' I and II have proved to be excellent vehicles for the collection of extremely delicate gelatinous organisms (Youngbluth, 1984*a, b*; Pugh & Harbison, 1986). Numerous specimens of siphonophores have been obtained and amongst these are two that clearly belong to an undescribed species of the physonect genus *Halistemma* Huxley. The general features of the nectophores and bracts have the typical *Halistemma* form, and the tentilla on the tentacles are unicornuate (i.e. have a single terminal filament) and have a vestigial involucre at the base of the cnidoband. The morphological characters of this new species are described and compared with those, where known, of the established species.

SYSTEMATICS

Halistemma transliratum sp. nov.

(Figs. 1-7)

Material examined. Two entire specimens collected by the submersibles 'Johnson-Sea-Link' (JSL) I and II in Bahamian waters.

Holotype. Single specimen collected at a depth of 472 m during Dive 628 of 'JSL' I (3 October 1981; 26° 13.5' N, 77° 41.8' W; water temperature 15.2 °C). Preserved in 5% formalin and presented to the United States National Museum (Smithsonian Institution), USNM 78496.

'Paratype'. An individual specimen collected during Dive 972 of 'JSL' II at a depth of 563 m (21 October 1984; 26° 24.3' N, 77° 49.8' W). Presented to the British Museum (Natural History), Regd. No. 1987.4.1.1.

Diagnosis. Agalmid siphonophore with unicornuate tentilla that have a vestigial involucre and have a long terminal filament ending in a characteristic ovoid process. The nectophores are of the typical *Halistemma* form but are characterized by the absence of a mouth plate, in the mature nectophores, and the branching of the apico-lateral (vk') ridges close to the ostium. The innermost of these branches continues directly to the ostium, while the outer one bends out laterally and runs, parallel with the ostium, towards the lateral (vk'') ridge, but does not join with it. Four types of bract are present, three of which have a characteristic transverse ridge on their dorsal surfaces.

DESCRIPTION

The holotype specimen is larger than the 'paratype', and has an elongated siphosome bearing several well developed cormidia. The 'paratype' specimen is at the *nectalia* post-larval stage of development, where the siphosomal stem has not begun to elongate, and it bears only a single functional gastrozoid.

A. *Nectophores* (Figs. 1-3)

Fifteen nectophores are present in association with the more developed holotype, while the 'paratype' possesses only seven. Nectophoral buds, at various stages of development, are found on the nectosomes of both specimens. The detached nectophores range in size from 5.7×5.4 mm (height \times width) to 13.0×13.4 mm. In the smaller, younger nectophores (Figs. 1, 3A), the central thrust block, which abuts the nectosomal stem, is only slightly developed, so that the squared-off, lateral 'wedge-shaped' processes extend well beyond it. As the nectophores increase in size the central thrust block enlarges considerably until it extends to approximately the same height as the lateral processes, which themselves become more rounded in appearance (Figs. 2, 3B). In the region of ostium, the opening of the nectosac, the younger nectophores possess a minute, basal mouth plate (Figs. 1, 3A) but this disappears entirely in the older ones (Figs. 2, 3B).

The basic arrangement of the ridges on the nectophores is similar to that found in other *Halistemma* species, particularly the 'e' and 'f' types of *H. rubrum* Vogt that Totton (1954) described. However, there are differences in detail that, together with the general characters of the nectophores, are sufficient to distinguish this species. The pairs of ridges present are described below and we have chosen the same notation as used by Claus (1879) and Pugh & Harbison (1986) for their descriptions of the nectophores of *Lychnagalma utricularia* (Claus).

(i) *Apico-laterals* (vk') run from the apical margins of the 'wedge-shaped' processes, across the upper (abaxial) surface of the nectophore to the midline, and thence down towards the ostium. In the preserved material, these ridges overlap slightly in the midline and overhang a deep median gutter. Basally, as

these ridges run towards the ostium, they begin to curve away from the midline, and each bifurcates (Figs. 1–3). The innermost branch continues basally to reach the ostium, though often it is difficult to see, particularly in the older nectophores. The outer branch continues to bend away from the midline and runs out, parallel with the ostium, towards the lateral (vk'') ridges. This branch peters out at the

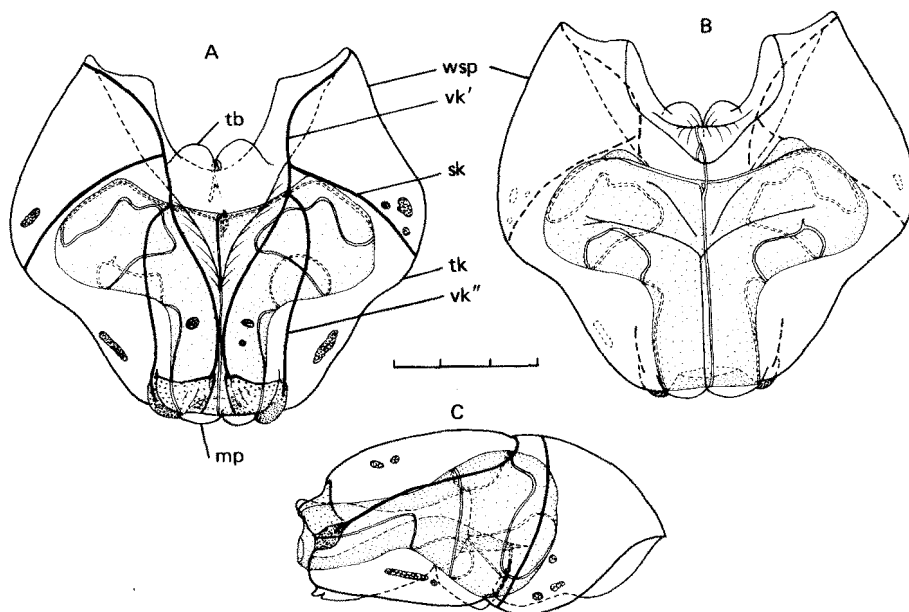


Fig. 1. Young nectophore of *Halistemma transliratum* from holotype. (A) Upper. (B) Lower. (C) Lateral views. Scale = 3 mm. mp, Mouth plate; sk, vertical lateral ridge; tb, thrust block; tk, infra-lateral ridge; vk' , apico-lateral ridge; vk'' , lateral ridge; wsp, wedge-shaped process.

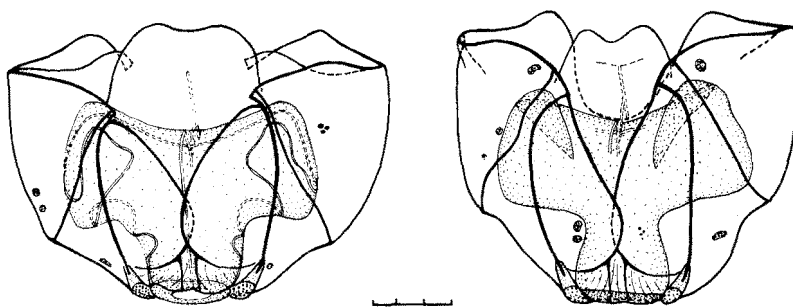


Fig. 2. Upper views of mature nectophores of *Halistemma transliratum* from holotype. Scale = 3 mm.

base of the latter ridge and does not join with it. The whole arrangement of the apico-lateral (vk') ridges is similar to that described by Pugh & Harbison (1986) for the nectophores of *Lychnagalma utricularia*.

(ii) *Lateral* (vk'') ridges that arise from the apico-lateral (vk') ridges approximately on a level with the top of the nectosac and run down the sides of the nectophore towards the ostium. However, the crests of these ridges do not reach to the ostium but end, slightly basal to the outer branches of the vk' ridges,

on enlarged lateral processes. These processes swell out from the base of the vk'' ridges and extend down to form the lateral margins of the ostium. Concentrations of small, plate-like cells are found on the basal part of these processes, which probably can be equated with the ostial chromatophores described by Totton (1965) on the nectophores of *Halistemma striata* Totton. Unfortunately, we have no record as to whether these cells were pigmented *in vivo*.

(iii) *Vertical lateral* (sk) ridges that extend from the apico-laterals, apical to the laterals, obliquely down the lateral margins of the nectophore to reach the infra-laterals (tk).

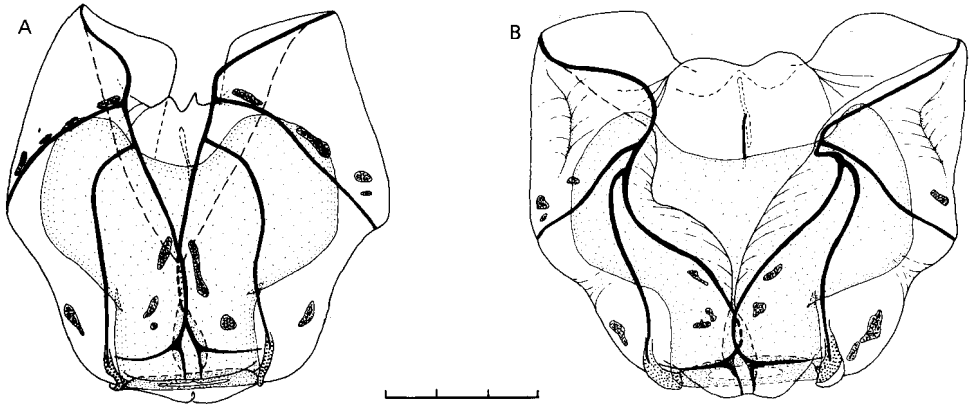


Fig. 3. Upper views of nectophores of *Halistemma transliratum* from 'paratype'. Scale = 3 mm.

(iv) *Infra-lateral* (tk) ridges that run along the entire length of the lateral edge of the adaxial (lower) surface of the nectophores, from the ostium to the outer margins of the 'wedge-shaped' processes, where they join the apico-laterals. The vk', sk and tk ridges define an apico-lateral triangular facet.

There are no distinct ridges present on the lower surface of the nectophore but, in the region below the central thrust block, the nectophore is distinctly undercut, particularly in the younger ones (Fig. 1B).

The canal system of the nectophores shows the typical *Halistemma* arrangement, which has been described and figured by Totton (1954) in *Stephanomia rubra* (= *Halistemma rubrum*). There are, however, a few morphological details that are worth mentioning. Typically, the pallial or mantle canal lies on the adaxial surface of the central thrust block in the region where the nectophore was attached to the stem. At the basal end of this canal there appears to arise a thin canal which runs down the mid-ventral line, immediately below the surface of the nectophore, and eventually joins the ostial ring canal. This canal is not always apparent, but a similar canal was described by Pugh & Harbison (1986) on the nectophores of *Lychnagalma utricularia*. The pair of lateral radial canals, on the nectosac, does not arise at the point of insertion of the pedicular canal, but from the dorsal radial canal slightly above this point (Figs. 1, 2). This feature was not noted by Totton (1954), although he did figure it. The lateral radial canals run

out laterally over the adaxial wall of the nectosac and, following the contours, curve slightly upwards (abaxially) before looping over the margins of the nectosac and continuing down its outer lateral surfaces. The loops that these canals make onto the dorsal and ventral surfaces of the nectosac are pronounced, particularly in the younger nectophores, and occasionally a short, blind-ending, branch is given off (Fig. 1A, B).

In addition to the so-called ostial chromatophores, noted above, patches of plate-like cells are found on the lateral and abaxial facets of the nectophores, and these are presumed to have been pigmented. The disposition of these patches is fairly regular but, since the cells easily flake off leaving no visible scar, the basic arrangement is not always evident. A row of up to five patches, lying close to the vertical lateral ridge (sk), is found on the apico-lateral facet, and additional spots are sometimes present on the basal corner of this facet (Fig. 3A). In the basal half of the nectophore further patches are found close to the infra-lateral ridges and on the apico-lateral facets, between the lateral and apico-lateral ridges. The former often are elongate, particularly in the younger nectophores (Fig. 1A), or may appear as several separate spots, possibly caused by the loss of intermediate cells. A more diffuse array of cells is found also on the wall of the nectophore between the lateral branches of the apico-lateral ridges and the upper margin of the ostium.

B. Bracts (Figs. 4, 5)

Twenty-one bracts are present in association with the holotype specimen, while the 'paratype' possesses only four. On the basis of their general morphology these bracts can be divided into four categories.

(i) *Type A* (Fig. 4). These bracts form the majority in both specimens, with eleven being found in the holotype, and three in the 'paratype'. They are elongate, lanceolate structures, ranging in length from 12 to 41 mm, and resemble in general form the *nectalia*-stage post-larval bracts of other *Halistemma* species (see, for example, Bigelow, 1911, plate 20, fig. 4, and Haeckel, 1888, plate XIII, figs. 1-12, both under the name *Nectalia loligo* Haeckel). However, they are distinguished easily by the presence of a conspicuous, inverted U-shaped, transverse ridge running across the dorsal surface.

The central part of the bract has a convex dorsal surface, in cross section, while the ventral one is concave, such that there is an extensive ventral cavity or hydroecium. In contrast, the pronounced distal extension of the bract is triangular in cross section, being delimited by a median dorsal and two ventro-lateral ridges. The dorso-lateral facets slightly overhang the ventral one at the extreme tip. The upper limit of this distal prolongation, which itself occupies the basal third of the bract, is demarcated by lateral expansions of the bract into two distinct teeth. On the inner, or stem attachment, side of the bract a third tooth is present slightly above this level. In the smaller, younger, bracts this tooth usually is folded back onto the ventral surface and often there is a ventral flap

stretching up from it to almost the apex of the bract. Towards the top of the bract another small flap, which runs transversely across the outer half of the bract and usually has a small tooth at either end, is present on the ventral side.

The dorsal, median ridge extends from the tip of the basal process to approximately two thirds the length of the bract, where it peters out a short

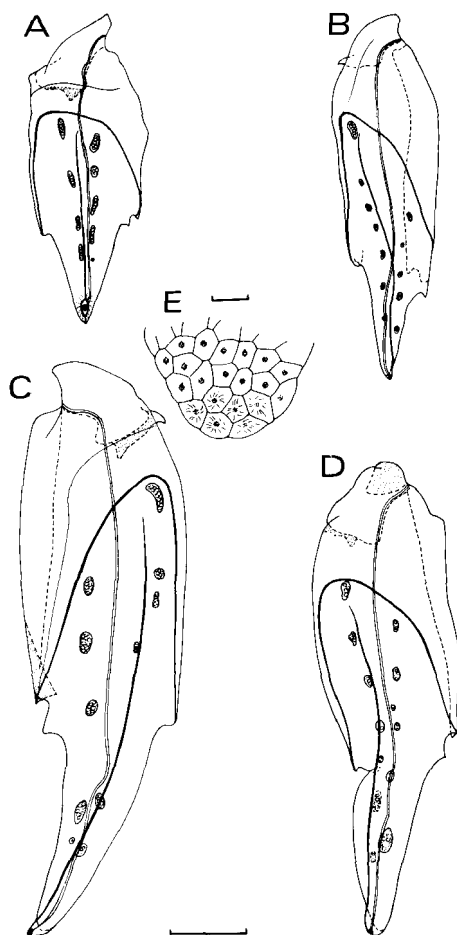


Fig. 4. Type A bracts of *Halistemma transliratum* from holotype. (A-D) Entire bracts. Scale = 5 mm.
(E) Detail of plate-like cells in dorsal patches. Scale = 0.1 mm.

distance below the transverse ridge. This transverse ridge runs obliquely away from the proximal of the two lateral teeth on the inner surface of the bract and arches over the dorsal surface, curving back down to reach the single tooth on the outer lateral margin.

The bracteal canal runs almost the entire length of the bract. It originates on the inner side of the bract, and runs transversely outwards before making a right-angle bend, approximately in the mid-line, and continuing basally. For most of its length this canal lies just under the ventral surface of the bract. However, shortly after having entered the distal bracteal process, at about one quarter the

height of the bract, it bends away from this surface and then continues to run through the mesogloea, slightly ventral to the dorso-ventral mid-line. As it approaches the base of the bract it curves up again and runs obliquely towards the dorsal surface, occasionally giving off short, blind-ending branches. Ultimately, it ends in a small, cup-shaped hollow which is recessed into the distal

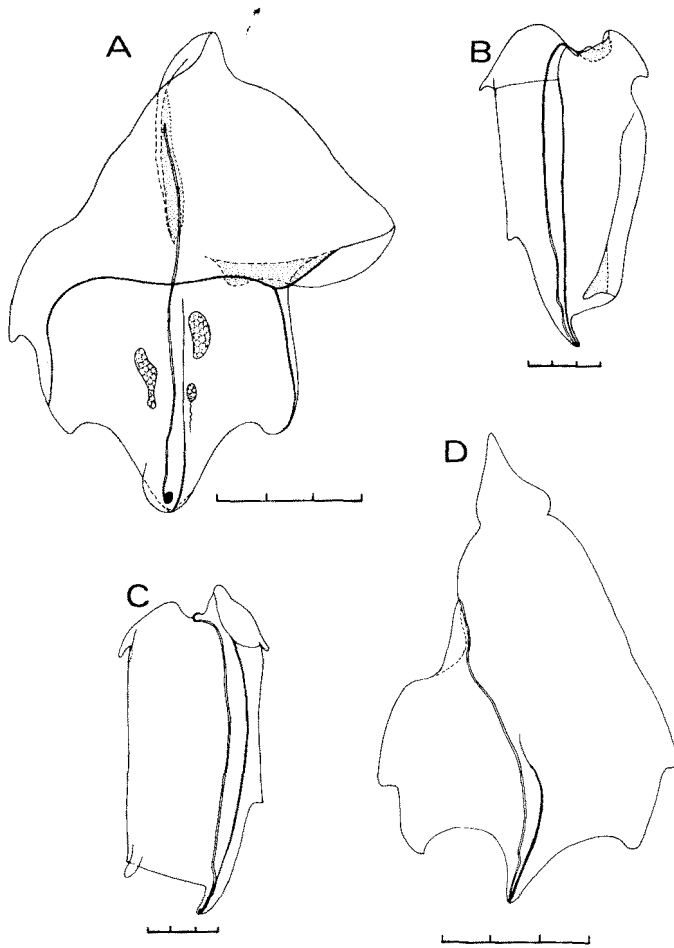


Fig. 5. Bracts of *Halistemma transliratum* from holotype. (A) Type B. (B-C) Type C. (D) Type D. Scale = 3 mm.

extremity of the bract. This hollow is packed with small cells, some of which might have been nematocysts as they have been described from the bracts of *Halistemma rubrum* (Kölliker, 1853; Totton, 1954) and identified as microbasic euryteles by Carré (1971), but none was identified in a detailed study of a few bracts.

In the distal half of the bract there is a biserial pattern of milky-white patches arranged down the dorsal surface, similar to those seen on the nectophores. These patches comprise thin, straight-sided cells (Fig. 4E), which are clearly not

nematocysts but which may once have contained pigment. As on the nectophores, these cells flake away easily.

(ii) *Type B* (Fig. 5A). Seven of this type of bract are present with the holotype, ranging in height from 8.2 to 12.6 mm, and the remaining bract of the 'paratype' is of this type. Typically, the bracts form enantiomorphic pairs as result of their relative positioning on the siphosomal stem, i.e. whether their attachment zone lies on their right- or left-hand sides. The bracts are distinctly asymmetric and are concavo-convex in outline, although this curvature is more pronounced in the proximal-distal direction than from side to side. The mesogloea of the basal half of the bract is much thicker than proximally, where it tapers down so that, at the apex, it forms only a thin sheet.

As with the Type A bracts, there is a distinctive transverse ridge running across the dorsal surface, but it is more rectangular in shape and does not connect with either of the lateral teeth on the inner surface of the bract. On the outer side of the bract it branches with one ridge running out laterally and the other turning down towards the lateral tooth on that side. A dorsal ridge runs up, in the midline, from the distal extremity of the bract towards this ridge but, as in the Type A bracts, peters out before reaching it.

The basal extension of the bract is comparatively small and the two distal, lateral teeth are rounded. The more proximal, third tooth, on the inner lateral margin, is more conspicuous. Again, as in the Type A bracts, there is a transverse fold on the outer ventral surface of the bract. In addition, in the proximal half of the bract, there is a thin flap projecting from the ventral side, through part of which runs the bracteal canal.

The bracteal canal, for most of its course, lies just under the ventral wall of the bract. It inflects into the mesogloea at a point approximately on a level with the distal lateral teeth and runs obliquely towards the dorsal surface, where it ends in an oval indentation just above the extreme tip of the bract. Again, this hollow is filled with cells.

Patches of flattened cells again are present on the dorsal surface of the bract. Generally they are more elongate than on the Type A bracts and, usually, two pairs are present on either side of the dorsal ridge, although the arrangement is quite varied.

(iii) *Type C* (Fig. 5B, C). Only two bracts of this type are present with the holotype, and they probably represent an enantiomorphic pair, though their shapes are not exact mirror images. They measure about 13.5 mm in length. Distally there are only two lateral teeth, which are arranged asymmetrically. Proximally there are two further lateral teeth, which usually are folded back ventrally. An indistinct transverse ridge stretches from the outer of these teeth and joins the dorsal ridge, which runs from the top to the bottom of the bract but is only vaguely defined proximally.

The bracteal canal arises in a central indentation at the apex of the bract and runs down to the tip of the distal process, ending on its dorso-basal surface. The canal inflects away from the ventral wall at a point slightly above the distal process. No superficial patches of cells were found.

(iv) *Type D* (Fig. 5D). Three bracts of this type are present in the holotype. Two of these, measuring 8.5 mm in height, formed an enantiomorphic pair, while the third was 13.1 mm in length. In outline the bracts are almost symmetrical, but the course of the bracteal canal belies this. This canal arises on the inner lateral margin of the bract, at about half its height, and curves down into the short distal process, where it inflects away from the ventral wall and ends at the extreme tip. Two pairs of lateral teeth are present. The median dorsal ridge is distinctive only in the distal third of the bract and there is no sign of a transverse ridge. A single superficial patch of cells was found only on the dorsal surface of the largest bract.

C. Other stem components

(i) *Pneumatophore*. The pneumatophore is borne on a relatively long, thin stalk which, even in the preserved specimens, measures from 2 mm (holotype) to 3.7 mm ('paratype') in length. The pneumatophore of the holotype was much distorted by gas expansion during collection, while that of the 'paratype', which measures *ca.* 1.6×0.4 mm (height \times diameter) is better preserved but shows no remarkable features. No apical pigmentation remains, although there is a distinct cap to the pneumatophore that may have been pigmented.

(ii) *Gastrozooids* (Fig. 6A). The siphosome of the holotype bears two developing and four mature gastrozooids, of which the older, distal one (Fig. 6A, *gz*¹) is much smaller than the one proximal to it (*gz*²). This distal gastrozoid may be the protozoid (larval gastrozoid) as it resembles closely the single developed one present on the 'paratype'. Both measure about 4.5 mm in length, after preservation, and have a long, thin-walled gastric region in which numerous hepatic stripes can be seen. The basigaster is shorter and relatively narrow. In both specimens this ?protozoid is attached to a comparatively narrow piece of stem that bends away from the main line of the siphosome. This configuration results in the second gastrozoid assuming the basal position, with the protozoid on a short side shoot. Such side tracking appears to be common in agalmid siphonophores and has been described for at least two other species (Totton, 1956).

The simple tentacle, which is attached to the base of the basigaster of these ?protozooids, bears only one or two tentilla, but these bear a close resemblance to those found attached to the tentacles of the other gastrozooids. This is somewhat surprising in view of the extraordinary larval tentilla developed by *Halistemma rubrum* (see Carré, 1971) that are very different from the adult ones. The larval tentilla of other agalmid siphonophores also differ markedly from the adult ones (Totton, 1956). This may argue against the terminal gastrozoid being the protozoid, despite the other evidence in favour of this supposition.

The three other mature gastrozooids on the holotype are much expanded laterally and distally, such that they have very wide mouths which, in the preserved state, are curled back over the external surface exposing the hepatic stripes to view. The basigaster is large and prominent, and to this is attached a long tentacle.

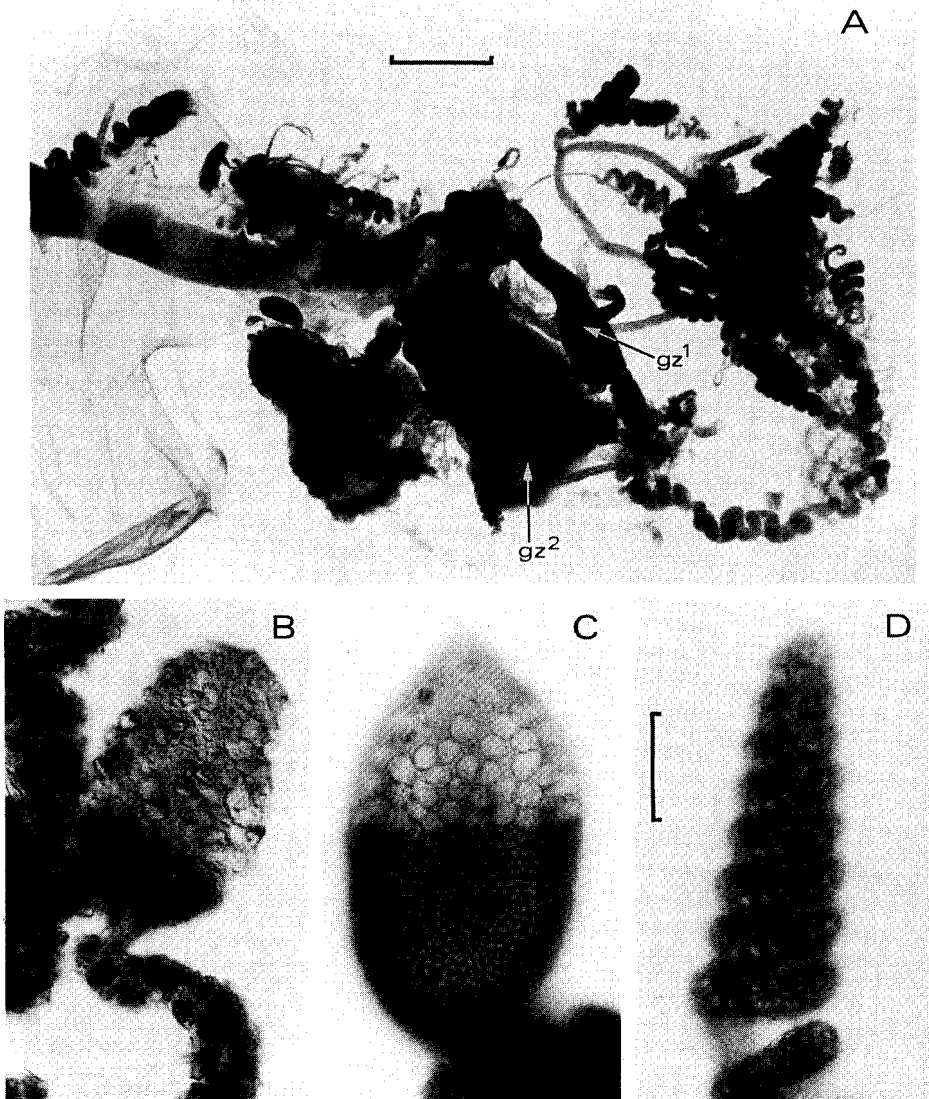


Fig. 6. (A) Part of holotype of *Halistemma transliratum*. Scale = 2 mm. (B-D) Detail of distal end of tentillum of *Halistemma transliratum* (B), *H. cupulifera* (C), and *H. rubrum* (D). Scale = 50 μ m.

(iii) *Tentillum* (Figs. 6B, 7A). Each tentillum consists of a long peduncle, a coiled cnidoband and an extremely long terminal filament ending in a characteristically shaped terminal process. At the junction between the peduncle and the cnidoband there is a cup-shaped structure that represents the vestigial involucre, which is characteristic of the tentilla of *Halistemma* species. The cnidoband is a loosely coiled structure of five to six coils, usually six, and is strongly armed with nematocysts. In life the cnidoband was a deep orange-red colour somewhat reminiscent of the vermillion coloration noted by Totton (1965)

on the tentilla of *H. rubrum*. The nematocysts consist of a few stenoteles, mainly confined to the proximal one or two coils, and numerous anisorhizas. The stenoteles are cylindrical in shape and measures $76\text{ }\mu\text{m}$ in length and $29\text{ }\mu\text{m}$ in diameter. The banana-shaped anisorhizas measured from 47 to $63\text{ }\mu\text{m}$ in length and from 8 to $12\text{ }\mu\text{m}$ in diameter, being wider at the apex than the base.

The terminal filament of the tentillum (Fig. 7A) has a very characteristic form that sets it apart from all other *Halistemma* species whose tentilla have been

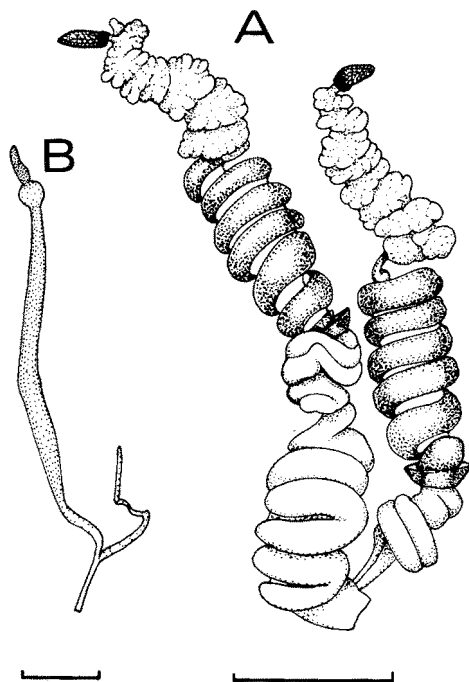


Fig. 7. *Halistemma transliratum*. (A) Two tentilla. (B) Palpon, from holotype. Scale = 1 mm.

described. It is obviously extremely long, probably reaching to several centimetres in length when extended, but in its contracted state forms a coiled mass of about the same size as the cnidoband. It bears numerous nematocysts of two types; acrophores, measuring between 29 and $35.5\text{ }\mu\text{m}$ in length and 10.5 to $12\text{ }\mu\text{m}$ in diameter, and desmonemes, 20 – $21\text{ }\mu\text{m}$ long and $10.5\text{ }\mu\text{m}$ in diameter. At the distal end of the terminal filament there is a distinctive process (Fig. 6B) somewhat reminiscent of that originally described for *H. cupulifera* Lens & van Riemsdijk but, as will be discussed in more detail later, it is of different shape. This process is ovoid, measuring *ca.* 280 – $300\text{ }\mu\text{m}$ in height and 150 – $170\text{ }\mu\text{m}$ in width, and is divided into two distinct parts. At its base, i.e. proximally, there is a band of nematocysts, similar to those on the terminal filament itself, which usually occupies about 20 – 25% of the total height of the process. The remaining, distal part of the process is devoid of nematocysts and is covered with platelets, measuring *ca.* $20 \times 25\text{ }\mu\text{m}$, which have a chitinous appearance (Fig. 6B).

(iv) *Palpons* (Figs. 6A, 7B). Interspersed between the gastrozooids are some long, thin, transparent palpons, borne on long pedicels. Many of these palpons have a small swelling towards their distal ends, but otherwise are quite featureless. The palpacle, attached to the base of the palpon, can be of considerable length.

(v) *Gonophores*. Only male gonophores were found attached to the siphosomal stems. It is probable that the female gonophores have not yet been developed, as both specimens have few cormidia, rather than suggesting that the species is dioecious. The structure of the male gonophores is typical of that described for other *Halistemma* species and Vogt (1854) gave a detailed account of them.

Etymology

The specific name *transliratum* refers to the transverse ridge present on most of the bracts.

Distribution

Known only from Bahamian waters at mesopelagic depths.

REMARKS

Totton (1965) defined the genus *Halistemma* as agalmid siphonophores with unicornuate tentilla, i.e. with a single terminal filament, whose cnidobands lacked a marked basal involucre. He noted that previously only two species, *H. rubrum* and *H. cupulifera*, definitely had been established, but to these he added another, *H. striata*. He also mentioned a fourth species, *H. amphytridis* (Lesueur and Petit), which he considered to be indeterminate, since previous descriptions had been based on only pieces of the siphosome. However, he commented that a great deal of similar material with associated nectophores was present in more recent collections, but unfortunately did not describe it. Nonetheless, as Mackie, Pugh & Purcell (1987) concluded, it is very likely that *H. amphytridis* will be confirmed as a valid species.

Detailed descriptions exist for only one of these four *Halistemma* species, that is *H. rubrum*. *H. striata* is known only from its nectophores, which have a distinctive ridge pattern with several vertical lateral (sk) ridges present on each side. This contrasts with the single 'sk' ridge found in both *H. rubrum* and the new species described herein. In the case of *H. amphytridis*, although the specimens were incomplete, we know from the descriptions of Huxley (1859) and Bigelow (1911) that these specimens were relatively enormous and possessed large (2 to 5 cm long) foliaceous bracts. Also, there was no terminal process on the tentillum, which itself possessed a relatively distinct involucre covering the proximal spiral of the cnidoband. Therefore, the structure of the tentillum alone serves to distinguish *H. amphytridis* from *H. transliratum*.

The description of *Halistemma cupulifera* given by Lens & van Riemsdijk (1908) is based largely on the structure of its tentilla that possess a peculiar acorn-

shaped terminal process. As noted above, these processes bear a superficial resemblance to those found on *H. transliratum*, but there are distinct differences. Fortunately, specimens with tentilla that closely resemble those described for *H. cupulifera* have been found in 'Discovery' and other collections, and the terminal process of one of these is shown in Fig. 6C. It can be seen that the terminal processes of *H. transliratum* (Fig. 6B) and *H. cupulifera* are easily distinguished. In *H. cupulifera* the basal, cupulate part of this process, which is also armed with nematocysts, occupies over half the total height of the process, whereas in *H. transliratum* it occupies less than a quarter. The plate-like cells on the upper 'acorn' part of the terminal process of *H. cupulifera* also are more numerous and more regularly arranged than in *H. transliratum*, and the whole structure is larger and more globular. There can be no doubt that these differences are of specific importance and, in this context, we compare these terminal processes with the terminal filament of *H. rubrum* (Fig. 6D), which is a tightly coiled, cone-shaped structure without a terminal process.

Halistemma transliratum can be distinguished from other species on the basis of its nectophores and bracts. Totton (1954) described three types of nectophore which he ascribed to *H. rubrum*. These nectophores types differ mainly in the structure of the mouthplate and the completeness of the ridges. However, none of these had the apico-lateral (vk') ridge bifurcating close to the ostium, as seen on the nectophores of *H. transliratum* (Figs. 1-3). The mature nectophores of the two Indian Ocean forms of *H. rubrum* had distinct, albeit in one case small, mouth plates, while such a structure was absent in the Mediterranean form as it was in *H. transliratum*. However, the Mediterranean form of *H. rubrum* has incomplete lateral ridges that easily distinguish it.

The foliaceous bracts of *Halistemma rubrum* and *H. cupulifera* also are quite different from those of *H. transliratum*, the most notable difference being the presence, on most of the latter's types, of a transverse dorsal ridge. No other *Halistemma* species is known to have such a variety of bract types. Thus, in combination the unique characters of the nectophores, bracts and, in particular, the tentilla serve to establish *H. transliratum* as a valid species.

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