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A review of the genus *Erenna* Bedot, 1904 (Siphonophora, Physonectae)

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SYNOPSIS. The status of the poorly known physonect genus *Erenna* is reviewed in the light of the collection, by submersibles, of specimens in excellent condition. The few previous descriptions had been based on only the tentacles, or on other parts in poor condition. Two species have been described, *E. richardi* Bedot, 1904 and *E. bedoti* Lens & van Riemsdijk, 1908, and there has been some debate as to whether they are conspecific or not. It is concluded here that they are conspecific. Two further *Erenna* species, *E. laciniata* sp.nov. and *E. cornuta* sp.nov., are described, together with a third, closely related species, *Parerenna emilyae* sp.nov. The distinctiveness of their tentilla, with uncoiled hypertophied cnidobands, and the nectophores with a basic ridge pattern and a muscle-free zone at the apex of the nectosac, is considered sufficient to warrant the transference of these species into a new physonect family, the Erennidae.

INTRODUCTION

Very little is known about the physonect genus *Erenna*, and specimens have rarely been identified. In fact, the first species, *E. richardi* Bedot, 1904, was originally described from only six tentacles found attached to the rope of a fish trap brought up from a depth of 5310 m somewhere between Portugal and the Azores. However, these tentacles bore highly distinctive tentilla of a type not previously known for any siphonophore, with uncoiled, hypertrophied cnidobands (stinging bands), and with the gastrodermal walls of the gastrovascular cavity packed with dark granules. Bedot (1904) made a detailed histological study of these tentilla and suggested that they probably belonged to a physonect siphonophore.

A second species, *Erenna bedoti* Lens & van Riemsdijk, 1908, was described from a denuded specimen collected during the *Siboga* Expedition. From the fragmented material, with many appendages containing black pigmentation, Lens and van Riemsdijk (1908) deduced that the species was a physonect siphonophore, and they assigned it to the family Forskaliidae. Although they could compare only the tentacles and tentilla with Bedot's (1904) material, they reasoned that their material could be referred to a different species because the free end of the cnidoband, on the more developed tentilla in their material, lay proximally, whereas it was distal in *E. richardi*. However, most subsequent authors have considered *E. bedoti* to be conspecific with *E. richardi*.

Bigelow (1911, p. 271) mentioned another specimen of *Erenna richardi*, in poor condition: 'In fact the condition is so bad that it is impossible to state whether or not it is specifically identical with the 'Siboga' example. Nor, for that matter, is it clear whether the latter is distinct from Bedot's *E. richardi*.'. However, he, like Lens and van Riemsdijk (1908), considered that its closest relatives were the forskaliids. Moser (1925) described a further specimen collected in the Bay of Biscay, which consisted of only a poorly preserved siphosome. She noted that the gastrozooids appeared not to have a pedicle (stalk), and that their gastrodermal lining contained black granules. On the basis of the structure of the gastrozooids and tentacles she considered that it could not be a forskaliid siphonophore and she likened it to a bathyphysid (Order Cystonectae), but noted that the latter lacked nectophores.

Tentacles, with characteristic tentilla were collected, in the north-east Atlantic on two further occasions (Leloup, 1936), but then no further specimens of *Erenna* species were recorded until Totton (1965) found three more. These were all in poor condition, but sufficient for the mature nectophores and bracts to be described and illustrated for the first time. The apex of the nectosac of the large, flattened nectophores was found to be muscle-free; and the radial canals could have more or less well-developed 'horn' canals ascending into the mesogloea. The bracts were said to have two pairs of lateral processes.

Margulis (1969) added to the description of the nectophores of *Erenna richardi*, noting that there were two small processes on the ventral side of the thrust block (the central region that abuts the stem) and that 'horn' canals were not always present on the lateral radial canals. In a later paper (Margulis, 1977) she described this specimen in more detail and concluded, from the shape of the mature tentilla, that it could be referred to *Erenna richardi*. However, she then briefly discussed possible differences from Lens and van Riemsdijk's (1908) specimen and concluded that *E. bedoti* was also a valid species. Margulis (1990) used these differences to describe a further specimen of *E. bedoti* collected in the southern Pacific. Recently, other specimens of *E. richardi* have been briefly described and/or recorded (Pugh, 1975; Musayeva, 1976; Alvariño, 1980; Leloup, 1980; Daniel, 1985).

In recent years, specimens of *Erenna* species have been collected by the submersibles Johnson-Sea-Link (JSL) I and II, and these are here used to give a more detailed description of *E. richardi*, together with descriptions of two other, previously undescribed, species that can be referred to the same genus. In addition, another JSL specimen, that is closely related to the genus *Erenna*, will be described. The taxonomic status of these species is discussed below and it is concluded that they should be separated off into a new family. The validity of *E. bedoti* also is discussed.

Family **ERENNIDAE** fam. nov.

DIAGNOSIS. Physonect siphonophores best characterised by their uncoiled tentilla bearing a hypertrophied cnidoband with nematocysts of three types: large anisorhizas and two types of smaller ones (? haplonemes). Terminal process devoid of nematocysts. Nectophores with basic ridge pattern of apico-, infra- and vertical laterals; with apical muscle-free zone on nectosac; radial canals straight or slightly curved. Ostium, without mouth plate, opening basally.

Pneumatophore without apical pore. Gastrozooids without pedicle. Dioecious.

REMARKS. As noted in the Introduction, both Lens and van Riemsdijk (1908) and Bigelow (1911) considered the genus *Erenna* might be related to the physonect family Forskaliidae, whereas Moser (1925) associated it with bathyphysid cystonects. However, Totton (1965) placed *Erenna* in the physonect family Agalmatidae. As Pugh (1998) discussed, the Agalmatidae is probably a composite family containing all those species that do not have the distinctive characters of other physonect families. There is a core of similar genera, *Agalma*, *Halistemma* and *Lychnagalma*, which have involucrate tentilla, with tightly coiled cnidobands. *Nanomia* is somewhat similar. However, the other genera are often difficult to relate to each other in any basic way.

Pugh (1999) discussed this further, with regard to the genus *Bargmannia*, which Totton (1965) had placed in the family Pyrostephidae. Among the key characters used in establishing the taxonomic position of that genus were the ridge pattern on the nectophores; the presence of a muscle-free zone on the nectosac; and the structure of the tentillum. With regard to the ridge pattern, which consisted of pairs of apico-, infra and vertical (meso-) laterals, he noted that a similar arrangement was found on the nectophores of *Pyrostephos vanhoeffeni* Moser, 1925 and *Erenna richardi*; with an even simpler arrangement, omitting the vertical laterals, being found in *Marrus* species. Similarly, all these species had a muscle-free zone on the nectosac. In addition, *Bargmannia* species, *P. vanhoeffeni* and *M. antarcticus* were known to be dioecious, whereas most other physonects are known to be monoecious. In the present study it will be shown that two *Erenna* species are dioecious, with monovan gonophores; while gonophores were not found with the other two species. These characters separate these four genera from all other agalmatids.

In *Bargmannia* spp., *Pyrostephos vanhoeffeni* and *Marrus* spp. the tentilla have simple, straight, or loosely coiled, cnidobands; with long contractile terminal filaments bearing nematocysts. However, *Erenna richardi* has a straight, hypertrophied cnidoband; and a rigid terminal process devoid of nematocysts. There are also differences in the types of nematocysts present on the tentillum. For many agalmatids four types are present: homotrichous anisorhizas (haplonemes), and either mastigophores or stenoteles on the cnidoband; desmonemes and acrophores in the terminal filament. The tentillum of *Marrus* species appears to conform with this pattern, with microbasic mastigophores included in the cnidoband. In *Bargmannia* species and *P. vanhoeffeni* large nematocysts, probably stenoteles, were present only on the proximal part of the cnidoband; with two types of smaller nematocysts present throughout the remainder of the cnidoband and terminal filament. Pugh (1999) was uncertain whether the latter were acrophores or desmonemes, but haplonemes were thought to be absent. As is shown below, the cnidobands of *Erenna* species contain mastigophores and two types of haplonemes; but, as noted above, there are no nematocysts on the terminal process.

Pugh (1999) concluded that there were sufficient similarities between *Bargmannia* spp. and *Pyrostephos vanhoeffeni* to retain the former in the family Pyrostephidae. However, despite the similarities of the nectophoral ridge pattern and the muscle-free zone on the nectosac, there are certain marked differences between these species and those of the genus *Erenna*. This particularly applies to the structure of the tentillum and its nematocysts; but also to the general structure of the nectophore. Pyrostephid nectophores have a large triangular thrust block and the axial wings are either reduced or absent; with the lateral radial canals on the nectosac arising separately from the dorsal canal. In *Erenna* spp. the thrust block is much smaller, while the apical wings are well-developed, and all four radial canals arise from the pedicular canal either together, or very nearly so. In addition, palpons with palpacles (reduced tentacles) are present in *Erenna* species, while they are totally absent in *Bargmannia* spp., or highly modified into palpacle-less oleocysts in *P. vanhoeffeni*. Also the female gonophores of the pyrostephids contain more than one ovum, while those of *Erenna*, where known, are monovan. These differences are here considered to be sufficient differences to warrant the establishment of a new family for the *Erenna* and closely related species described herein. The exact status of the genus *Marrus* remains uncertain, as Pugh (1999) discussed.

Erenna Bedot, 1904

Erenna Bedot, 1904: 10–14.

DIAGNOSIS. Nectophores dorso-ventrally flattened with tapering axial wings; apico- and infra-lateral ridges respectively form upper and lower margins of lateral surface, with short, perpendicular, vertical lateral ridge connecting them. Lateral radial canals straight, thickened on apico-lateral margins of nectosac; with or without additional small protuberances, spikes, or 'horn' canals. Bracts of two types, both with patches of epidermal cells, including nematocysts, on dorsal swelling at distal extremity. Tentillum large, with hypertrophied, uncoiled cnidoband, and rigid terminal process devoid of nematocysts. Gastrozooid with large swollen basigaster, but no obvious pedicle.

Erenna richardi Bedot, 1904

Erenna richardi Bedot, 1904: 10–14, Pl. II, figs. 1–12
Erenna bedoti Lens & van Riemsdijk, 1908: 66–69; Margulis, 1977: 148–151, 1990: 138–142.

MATERIAL EXAMINED. The description is based largely on a specimen collected during Johnson-Sea-Link (JSL) II Dive 1456 (2 xi 1987; 24° 00.9'N 82° 15.7'W; depth 871 m). In addition, parts of another large specimen collected during JSL I Dive 2889 (19 xii 1990; 26°22.3'N 78°46.2'W; depth 701 m) have been examined. These parts have been donated to The Natural History Museum, London, where they are registered as BMNH 2000.1819. Unfortunately, the remainder of the specimen, including the siphosome, has dried up.

DIAGNOSIS. Nectophores large, flattened, with prominent apico-, infra- and vertical lateral ridges; plus at least two pairs of indistinct and incomplete laterals in basal half; apico-laterals divide close to ostium. Thrust block large with, in mature nectophores, two small digitate protuberances on ventral surface. Radial canals black pigmented; lateral ones with thickened walls in region of lateral margin of nectosac; with small protuberances or spikes. Gastrozooids black pigmented, particularly in greatly expanded basigaster, with two prominent lateral lobes. Tentillum with hypertrophied cnidoband, and long rigid distal terminal process with a diverticular canal and a pair of 'ocelli' close to its end.

DESCRIPTION. An image (Fig. 1) taken from a video of the *in situ* JSL II Dive 1456 specimen shows the biserially arranged nectophores and the contracted siphosome.

PNEUMATOPHORE. Pneumatophore ovoid, measuring 7 by 4 mm. Margulis (1977) noted the presence of eight vertical septa on her specimen, but these were not visible on the present material.

NECTOPHORE. (Figs 2 & 3). About 45 nectophores, at various

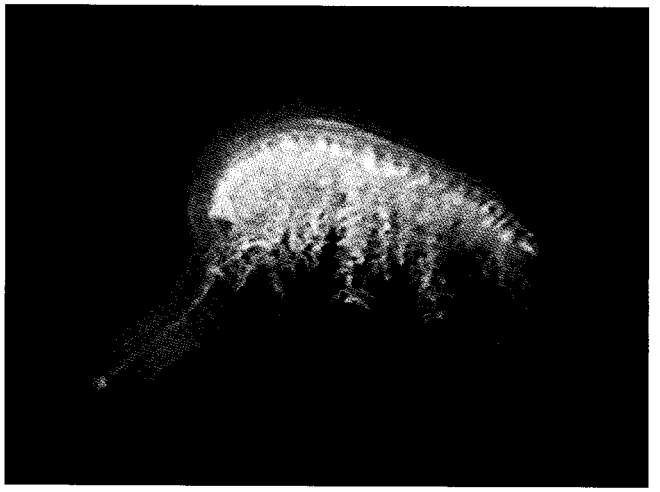

Fig. 1 *Erenna richardi*. Image from *in situ* video of JSL II Dive 1456 specimen; approximately 70–80 cm in length.

states of development, and several nectophoral buds, remained with the JSL II 1456 specimen. They were flattened, and measured up to 32 mm in length, 33 mm in width and 10 mm in height. The large axial wings tapered toward their apices (Fig. 2A *aw*). Mature nectophore had relatively large thrust block (Fig. 2C *tb*) with a broad U-shaped indentation apically. On its ventral surface there were two small conical protuberances (Fig. 2C *cp*). However, on the younger nectophores, the thrust block was small and had no protuberances (Fig. 3).

The prominent main ridge system consisted of pairs of apico- (Fig. 2A *ral*) and infra-laterals (Fig. 2B *ril*), which united close to the apex of each axial wing; and a pair of vertical laterals (Fig. 2B *rvl*) that connected the apico-laterals with the infra-laterals; although in some nectophores the junction with the latter was weak and difficult to discern. Apico-laterals branched close to the ostium, with each branch reaching the latter. In addition to these ridges at least two pairs of incomplete lateral ridges passed obliquely down the lateral facet in the basal half of the nectophore. Often these were difficult to discern without staining, but were also described by Margulis (1977), who noted 2–3 pairs of them.

Ostial opening basal with no obvious mouth plate. On each side of the ostium there were prominent lateral protuberances on which lay strips of distinctive epidermal cells. A much smaller triangular patch also was present dorsally. In addition, there was a small patch of such cells on each side of the nectophore, at about the mid-height of, and basal to, the vertical lateral ridges. All these patches of epidermal cells are believed to be sites of bioluminescence.

T-shaped nectosac (Fig. 2B *n*) with a distinct muscle-free area across the whole of its apical region. Pallial canal (Fig. 2A *pa*) was relatively short, running from the base of the thrust block over onto the ventral surface and ending just beyond the point of origin of the pedicular canal (Fig. 2B *ped*). On the nectosac the pedicular canal typically gave rise to all four radial canals, although occasionally there was a slight asymmetry in the arrangement. All four radial canals were straight. Laterals pass out, through the muscle-free zone, toward the lateral margins of the nectosac. Typically, before reaching the latter, they became thickened and could have small protuberances, or spikes extending up from them. These thickenings were particularly prominent on the youngest nectophores. All the canals had brown, but originally black, pigment in their gastrodermal walls.

SIPHOSOME. As the *in situ* video (see Fig. 1) showed, the siphosome was tightly contracted, and possibly, as in *Agalma okeni* Eschscholtz, 1825 and *Frillagalma vityazi* Daniel, 1966 (see Pugh, 1998), this was its permanent state.

BRACT. (Fig. 4). Two types of bract were present; the first long, up to 50 mm, and narrow (Fig. 4A); the second shorter and broader (Fig. 4B, C). Both possessed a pair of prominent, lateral cusps. These

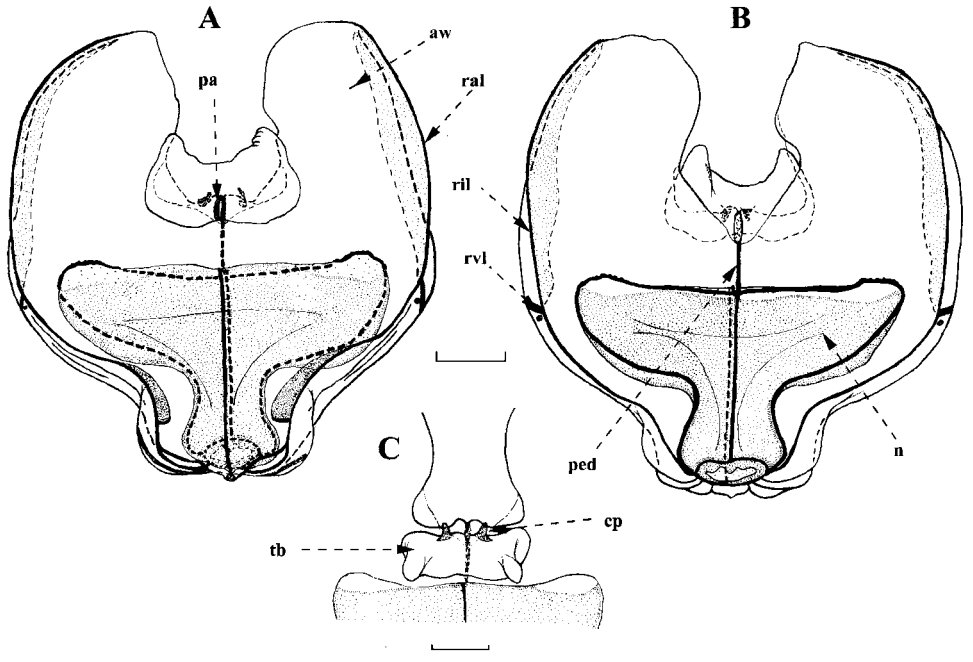

Fig. 2 *Erenna richardi*. **A**. upper and **B**. lower views of mature nectophore. **C**. detail of folded back thrust block. Scale bar 5 mm. *aw* axial wing; *cp* conical protuberance: *n* nectosac; *pa* pallial canal; *ped* pedicular canal; *ral, ril, rvl* apico-, infra- and vertical lateral ridges; *tb* thrust block.

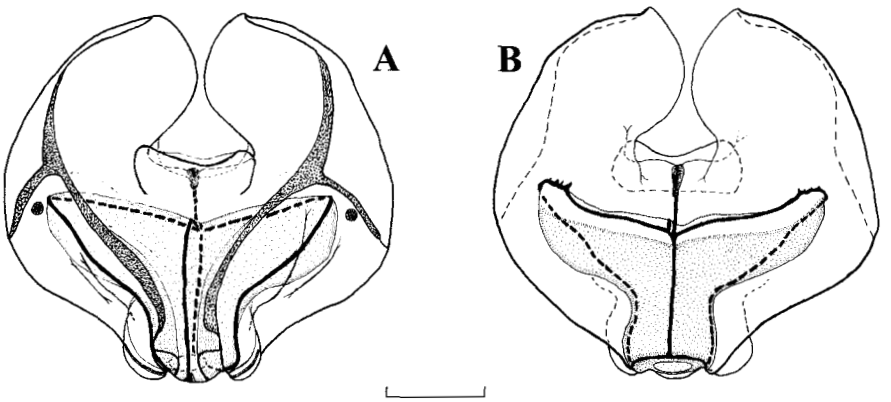

Fig. 3 **A**. upper and **B**. lower views of young nectophore. Scale bar 5 mm.

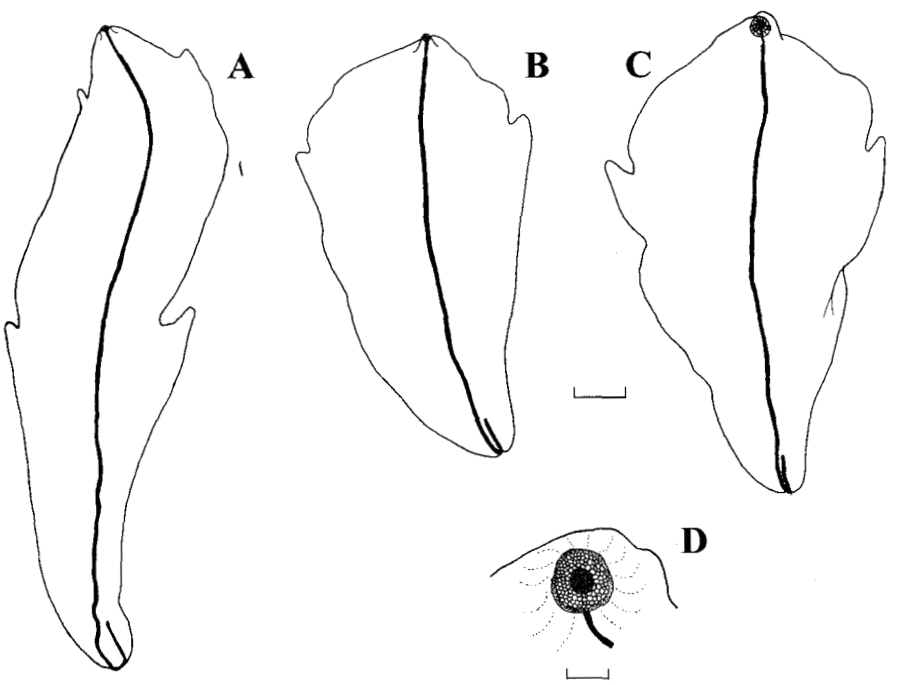

Fig. 4 *Erenna richardi*. **A**. first and **B**., **C**. second types of bract. D. detail of distal end of a bract. A–C. scale 2 mm; D. scale 0.2 mm.

were situated in the distal half of the second type of bract, but in the first type they were positioned at about 13–14 mm from the proximal end of the bract, whatever the length of the latter. Thus in the longest bracts they were situated at about one quarter to one third its length; whereas in smaller ones they could be positioned in the distal half of the bract. Longer bracts of the first type had a second pair of lateral cusps close to the distal end. For both types, the bracteal canal originated, proximally, on the dorsal surface of the bract. For most of its course it remained in close contact with the ventral wall of the bract and there were striated bands of cells on each side of it. Close to the distal end of the bract it penetrated through the mesogloea to terminate below a small cup-shaped clump of large epidermal cells sunk into the dorsal surface at the tip of the bract (Fig. 4D). Some of these cells in this clump probably produced bioluminescence; others were nematocysts measuring c. 68 × 24 μm. No patches of such epidermal cells were noted elsewhere on the bract.

GASTROZOOID. (Fig. 5 A, B). Large gastrozooids contained dark brown (black in life) pigment. The proboscis region often was widely open and folded back on itself exposing a mass of villi. Enormous basigaster with two large lateral lobes, and also expanded, to a lesser extent, on the side opposite to where the tentacle was attached. No obvious pedicle.

TENTACLE AND TENTILLUM. (Figs 6, 7). Bedot's (1904) original description and illustrations of the tentacle and tentilla were detailed and accurate, and need little elaboration. The annulated tentacle had a muscular lamella running down one side, with the tentilla attached on the opposite side, at the internodes.

Each tentillum consisted of a pedicle (Fig. 7*p*), a cnidoband (Fig. 7*c*) and a terminal process (Fig. 7*tp*). The largest tentilla (Fig. 6) have a pedicle of up to 4–5 mm; longer than Bedot described. However, no doubt its length can be varied in life, and photographs of the specimen before preservation showed the pedicle to be highly contracted. The cnidoband measured up to c. 15 mm long and was laterally compressed. It consisted of the cnidoband proper, where the nematocysts are attached, and what Totton (1965) called, in the case of *Pyrostephos vanhoeffeni* Moser, 1925, the saccus (Fig. 7*s*).

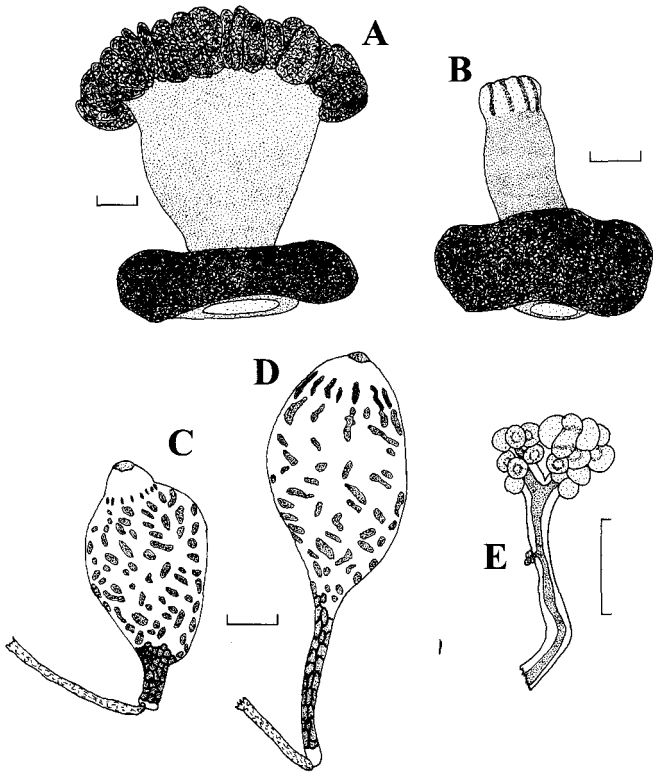

Fig. 5 *Erenna richardi*. **A**. and **B**. Gastrozooids; **C**. and **D**. palpons; **E**. Immature gonodendron. Scale 2 mm.

The bulk of the saccus was made up of a thick layer of transparent gastrodermal cells which formed a characteristic reticulate pattern (Fig. 6), through which the narrow, dark (black in life) pigmented gastrovascular canal (Fig. 7*gvc*) passed. In many preserved tentilla this canal was damaged. Figure 6 shows an undischarged and a discharged tentillum.

The numerous nematocysts formed a dense, darkly pigmented cnidoband, the sides of which undulated irregularly. On the mature tentillum the distal end of the cnidoband hung free from the main body. Three types of nematocysts were present. On the sides there were rows of larger ones, probably homotrichous anisorhizas, measuring c. 165 × 32 μm. Between these were numerous smaller nematocysts of two types, one measured c. 43 × 15 μm, the other c. 27 × 20 μm. No discharged nematocysts of these types were found, but probably they were both atrichous haplonemes, as Margulis (1977) suggested, although she noted only one type.

The rigid terminal process (Fig. 6) was up to c 10 mm in length and devoid of nematocysts. The gastrovascular canal passed through it, ending close to its distal extremity. Just proximal to the end of the canal it branched off a diverticular canal (Fig. 7*dc*) that passed back through the terminal process to end below the distal part of the cnidoband. As Bedot (1904) noted there was a band of longitudinal musculature on each side of the terminal process. Overlying the lateral sides of the diverticular canal, close to its point of origin, there was a pair of brownish-white oval structures (Fig. 7o) comprised of distinctive epidermal cells. Lens & van Riemsdijk (1908) aptly called them 'ocelli', as is discussed below.

As noted above it was the distal end of the cnidoband that hung free from the main body of the mature tentillum. However, on the young, developing tentillum (Fig. 7A), the cnidoband formed a triangular process that was slightly undercut on its proximal surface; with the pedicle and terminal process being only slightly developed. The axial and diverticular canals were prominent, and the latter opened into the saccus of the cnidoband. With further development, the saccus became closed off and began to fill with gastrodermal cells (Fig. 7B). The cnidoband remained undercut proximally. With further elongation of the tentillum (Fig. 7C, D), the proximal part of the cnidoband began to fuse with the saccus, and the 'ocelli' on the terminal process were developed, while the canal system narrowed. Finally, the distal end of the cnidoband became detached from the saccus.

PALPON. (Fig. 5C, D). Up to 15 mm in length, with a palpacle attached at the base of the pedicle. Brown (black in life) pigment throughout. Pedicle with reticulate pattern of cells. Main stomach region with an irregular pattern of patches. Distally these were concentrated to form 12–14 vertical stripes, with denser pigmentation, surrounding the base of the proboscis with its terminal opening. No obvious nematocysts present on the palpacle.

GONODENDRA. (Fig. 5E). Only female gonodendra were found on the JSL II 1456 specimen. Mature female gonodendra were comprised of small, tightly packed bunches of c.20–25 gonophores, with a milky brown coloration, connected to a relatively short stalk. Each gonophore measured c. 0.45 mm in diameter and contained a single

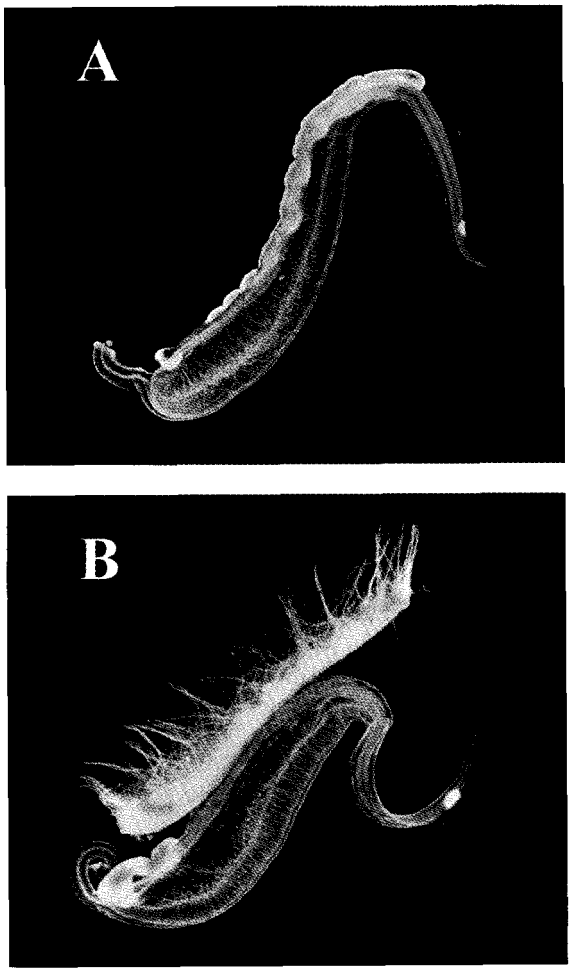

Fig. 6 *Erenna richardi*. Photographs of tentilla (c. 25–30 mm in length) before (A.) and after (B.) discharge of nematocysts.

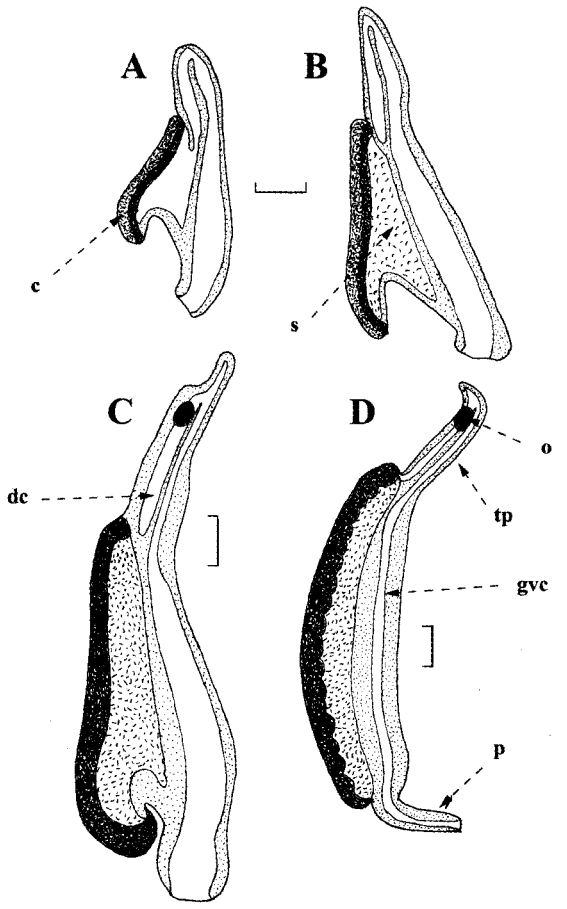

Fig. 7 *Erenna richardi*. **A–D**. Early stages in the development of a tentillum. Scale 0.5 mm. *c* cnidoband; *dc* diverticular canal; *gvc* gastrovascular canal; *o* 'ocellus'; *p* pedicle; *tp* terminal process.

egg. The immature gonodendra (Fig. 5E) were more darkly pigmented and had a relatively long stalk which typically bifurcated close to its apex, with the gonophores being developed on the branches. One of these branches could be denuded and could be mistaken for a gonopalpon. Occasionally small gonophores were budded off approximately half way up the stalk. No gonophores were found with the JSL I Dive 2889. However, two specimens from the *Discovery* collections also bore only female gonodendra.

DISTRIBUTION. Of the four specimens of *Erenna richardi* collected by the JSL submersibles, one came from the vicinity of the Dry Tortugas, between Florida and Cuba; two from The Bahamas; and one from c. 27°N 85°W in the Gulf of Mexico (Rebeca Gasca – personal communication). The species also has been found occasionally in recent *Discovery* collections in the North Atlantic, mainly south of 35°N and at depths greater than 1000 m. Much of the material is in too poor a condition to identify to species, although it seems likely that the presence of black pigment in the radial canals of the nectophore is specific to *E. richardi*. However, one large specimen, comprising 34 nectophores, over 400 bracts and several stem pieces, from *Discovery* St. 8599 (c. 8°40'N 23°14'W; depth 3000–3500m), clearly is *E. richardi*; as is a specimen from St. 10157#3 (31°3.6'N 13°W; 650–1000 m). In addition some damaged nectophores that can be referred to this species have been collected by four hauls fished c.300 m above the bottom in the proximity of the 'Rainbow' and 'Lucky Strike' vents on the Mid-Atlantic Ridge (c. 37–38°N, 32–33°W; depth range 1793–2613 m). Better preserved material has also been collected recently in the vicinity of the East Pacific Rise (c. 12°50'N, 104°W) at depths of about 2500 m. The siphosome of one of these specimens bore numerous female gonodendra.

Leloup (1980) listed the scant published data on the geographical distribution of *Erenna richardi*, including the conspecific *E. bedoti*. The material described by Bedot (1904), Lens and van Riemsdijk (1908), Bigelow (1911), Moser (1925) and Leloup (1936, 1980) probably can be referred to *E. richardi*; but this is not the case for all of Totton's (1965) material. His figure 38, which is said to be a reconstruction, shows a nectophore with short 'horn' canals arising from the lateral radial canals on the nectosac. Re-examination of the single nectophore, in the NHM collections, shows that incomplete lateral ridges are also present and so it is referred to *E. richardi*. However, the label with it states that the *Discovery* station at which it was collected is St. 4255 not, as Totton stated, St. 2061. The reverse is true for the specimen figured in figure 39. Since figure 39 looks more like a 'reconstruction' than figure 38, it is presumed that the legends to the two figures were accidentally transposed. Totton (1965) mentioned a larger specimen from *Discovery* St. 4230, but this was not found. His other material from La Jolla, California, supplied by Dr Ahlstrom, and the Beebe collections from Bermuda, together with some bracts from *Discovery* St. 4253, which he did not mention, probably can be referred to *E. richardi*, but are in poor condition. The *Discovery* St. ?2061 material, is referred to another species, described below.

Of the other records not included by Leloup (1980) or published more recently, no description was given by Alvariño (1969, 1980) or Musayeva (1976) and so their true identity remains in doubt; particularly since Alvariño (1981) described a specimen that is probably not *E. richardi*. However, as with the description of Daniel (1985), it is difficult to decide whether or not she was largely copying the description and figures of Totton (1965). The two specimens described or mentioned by Margulis (1969, 1977, 1990) can be referred to *E. richardi*, although in the last paper the specimen was described under the name *E. bedoti*. This will be discussed in more detail below. Finally, the record given by Pugh (1975) is based on *E. richardi*.

BEHAVIOUR. The JSL II 1456 specimen was briefly observed on board the mother ship after collection. It was noted that the terminal processes of the tentilla were kept rigid and were rapidly vibrated. Meanwhile, the cnidoband might become bent into a U-shape. It has been suggested (Pugh, 1989) that vibration of the terminal process might be an example of aggressive mimicry of a swimming chaetognath. The two 'ocelli' might then be a representation of chaetognath's gonads. Equally, the vibration of the terminal process might be mimicking the swimming behaviour of a larval fish; the two 'ocelli' then representing eyes.

As Totton (1965, p.76) noted, 'What is so characteristic of *Erenna* [*richardi*] is the hypertrophy of the cnidoband, which must be a very formidable stinging apparatus'. This has certainly proved to be the case, as was demonstrated when a colleague was painfully stung when he inadvertently came into contact with a tentacle of one of the specimens collected by the JSL submersible.

REMARKS. Lens and van Riemsdijk's (1908) description of *Erenna bedoti* was based on two fragments of stem; one being the nectosome, with an apical pneumatophore, and the other a small part of the siphosome. However, they could only compare the tentacles and tentilla with those described by Bedot's (1904) for *E. richardi*. For the tentacle they stated (p. 68) that it 'reminds one exactly of the tentacle described by BEDOT'; and (p. 69) that 'the most mature

tentillum . . . reminds one at once of the tentilla described by BEDOT'. They concluded (p.69) that 'there exists undeniably the closest relationship between the tentacles and tentilla of *Erenna Richardi* and *Erenna Bedoti*.' So why did they separate them? Their earlier logic (p. 66) 'We therefore called this only specimen *Erenna*, using a new species denomination "*Bedoti*" as of course we cannot decide whether the tentacles described by BEDOT belonged to a specimen entirely identical with ours' seems very obscure.

Lens and van Riemsdijk suggested a possible difference between the tentilla of their specimen and that of Bedot. They believed that, in the largest tentillum, the free end of the cnidoband was proximal ('basal') while in *Erenna richardi* it was distal (although they referred to the latter as 'proximal'). They also noted the presence of a small black spot in the distal region of the cnidoband, which they suggested would become the 'ocelli' that Bedot described. However, the 'ocelli' of *E. richardi* are positioned toward the end of the terminal process, even in the developing tentilla (see Fig. 6C, D). Have, then, Lens and van Riemsdijk misinterpreted the structure of their tentilla? Close examination of their illustration (Plate XI, fig. 89) suggests that this is probable. It is suggested that what they call the pedicle is, in actuality, a very deformed terminal process; while the 'apical part' (terminal process) is the pedicle. Then the free end of the cnidoband is distal, as it is in *E. richardi*. For this to be so, the spot, which lay close to the *proximal* end of the cnidoband, and which they thought was equivalent to the 'ocellus' of *E. richardi*, must be considered an artefact, and that the true 'ocelli' have been destroyed. This is borne out by Lens and van Riemsdijk (1908, p. 69) statement that 'Microscopical sections have been made but the material is unfortunately absolutely insufficient, the different layers being all destroyed'. It appears that all the largest tentilla were sectioned as none are now present with the type material. However, some developing tentilla are still present with the holotype and these conform exactly with those of *E. richardi*. Thus, there does not appear to be any concrete evidence to separate specifically Lens and van Riemsdijk's material from that of Bedot.

This conclusion was reached by Totton (1965), who considered *Erenna bedoti* to be conspecific with *E. richardi*. However, Margulis (1977, 1990) resurrected the debate, when she described another specimen of *E. richardi* Margulis (1997). She correctly noted that, on the nectophores, there were two digitate processes on the ventral side of the thrust block, and 2–3 extra ridges on the lower lateral facet. On the siphosome she found, as indeed had Lens and van Riemsdijk (1908), the presence of peculiar muscular outgrowths, but did not know their function. They are, undoubtedly, the remains of the muscular lamellae to which bracts were once attached. One curious feature she described was that one detached tentacle arose from a black-pigmented formation that had a spherical dilation on each side. This was, of course, the basigaster of the gastrozooid, but she failed to appreciate this. The youngest tentillum had a digitate outgrowth in the region that was to become the cnidoband; the oldest were as Bedot (1904) described them. Margulis (1977) then made a brief comparison with Lens and van Riemsdijk's (1908) description of *E. bedoti*. The only differences she noted were that the tentacles of *E. bedoti* lacked the basal outgrowths (i.e. the basigaster), and that their young tentilla did not have a digitate outgrowth.

These points were addressed further by Margulis (1990), when she described fragments of another specimen that she referred to *Erenna bedoti*. The *key* features by which she distinguished this specimen from *E. richardi* were that:-

a) the thrust block on the nectophore was smaller, with its distal margins stretched into thread-like outgrowths; and that the two processes on its ventral surface were digitate or papillose, but not lamellate as in *Erenna richardi*;
b) there were marked differences in the structure of the gastrozooid, and;
c) the young tentilla of *Erenna bedoti* had an oval outgrowth, while in *E. richardi* it was finger-shaped.

As has been shown above, the size of both the thrust block and the digitate processes varies with the size of the nectophore of *Erenna richardi*, which, as will be seen, is the only erennid species to have such processes. Thus, judging from her illustrations, the damaged condition of Margulis's material is the most likely explanation of the differences she noted. It should be noted, moreover, that black pigment was present in Margulis's material. The differences in the gastrozooids mainly concern the basigaster. Margulis now recognised that, in *Erenna richardi*, this was the large structure, with two large rounded lobes, that she had found at the proximal end of the tentacle. However, such a structure was not found on the larger gastrozooids of her latest specimen; although it was clearly large and inflated on the younger ones. This would be a reasonable difference if Margulis had not given the impression that the basigaster had been destroyed, by describing how its outer coating began to shed until it was completely absent. Personal experience has shown that it is, indeed, easy to destroy the epidermal layers of the basigaster. Finally, the differences between the young tentilla are considered to be mere reflections of their state of growth. The important similarities between Margulis's (1990) material and *E. richardi* are that in both there is a pair of protuberances on the ventral side of the thrust block of the nectophore, and that black pigmentation is present. The former, and almost certainly the latter, of these are characteristics for only *E. richardi* and, thus, it seems inconceivable that *E. bedoti* is nothing more than conspecific with *E. richardi*.

Erenna laciniata sp.nov.

HOLOTYPE. The specimen from JSL II Dive 1454 is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1821.

MATERIAL EXAMINED. The description is based on two specimens collected by the JSL II submersible during dives 1454 (30 viii 1987; 24°30.8'N 83° 45.2'W; depth 811 m) and 1688 (11 x1988; 26°23.5'N 78°39.5'W; depth 853 m).

DIAGNOSIS. Nectophores large, dorso-ventrally flattened, with only basic ridge pattern; with weak division of apico-laterals close to ostium. Thrust block small, with U-shaped median indentation and ventral flaps, but no conical protuberances. Lateral radial canals only slight thickened at apico-lateral corners of nectosac. Bracts of two types, with lateral flap, more extensive in one type than the other. Tentilla characteristic, with terminal process arising close to base of cnidoband and bearing two distal 'ocelli'.

DESCRIPTION

PNEUMATOPHORE. The pneumatophore measured c. 2.9 × 1.9 mm; gas expansion having ruptured its base. There were no obvious striations or pigment.

NECTOSOME. Each specimen had 50–60 nectophores, which, in life, were arranged biserially.

NECTOPHORE. (Figs 8, 9). Flattened, up to 25 mm in length, 29 mm in width and c. 5 mm in height. Large tapering axial wings. On the mature nectophores (Fig. 8) the thrust block was relatively small and divided into two parts by a median U-shaped indentation.

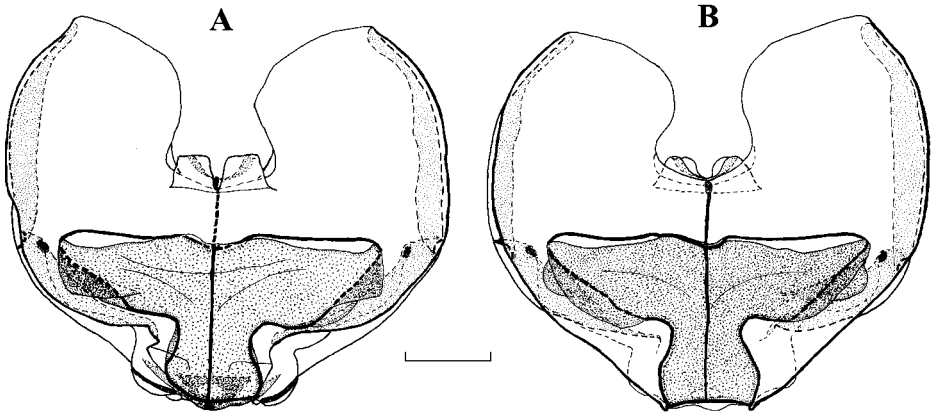

Fig. 8 *Erenna laciniata*. **A**. upper and **B**, lower views of mature nectophore. Scale 5 mm.

On each side there was a thickened flap that lay ventrally and was directed toward the mid-line. On smaller, younger nectophores (Fig. 9) the thrust block consisted of two small protuberances separated by a U-shaped indentation.

The main ridge system was well delineated, especially in the younger nectophores (Fig. 9). It consisted of pairs of infra- and apico-lateral ridges, which united close to the lateral apices of the axial wings; and a short pair of vertical laterals connecting them (Fig. 8), although, in younger nectophores, the junction with the apico-laterals was indistinct (Fig. 9). The infra-laterals ended, basally, on either side of the ostium. The apico-laterals remain prominent until just above ostial level. In younger nectophores, close to the ostium, the apico-laterals gave rise to three very vague, but broad branches (Fig. 9A). However, in mature nectophores only after staining could two very vague ridges be discerned (Fig. 8A). These would be virtually impossible to see in damaged or poorly preserved material.

No obvious mouth plate, and ostial opening basal. Prominent protuberances on each side of the ostium which bore strips of distinctive epidermal cells, and another triangular patch in mid-line on dorsal side of the ostium. In addition, a relatively large patch of such cells was present on each side of the nectophore, at about the mid-height of, and immediately basal to, the vertical lateral ridges (Figs 8A, 9A). All these patches are believed to be sites of bioluminescence.

T-shaped nectosac with a distinct muscle-free zone at its apex. Short pallial canal, originating at the base of the thrust block, with a long pedicular canal, which on reaching the nectosac gave rise to the four, straight, radial canals. In the younger nectophores there were obvious signs of thickening of the lateral radial canals in the apico-lateral region of the nectosac, but these were difficult to discern in the mature ones. No small protuberances, or 'horn' canals, were present. In the JSL material the radial canals had no obvious pigmentation, although in other nectophores, which are tentatively referred to this species, they could have an orange hue.

SIPHOSOME. On collection the siphosome of both specimens was tightly contracted. The gastrozooids and the terminal processes to the tentilla were lightish brown in colour; while the palpons were suffused with brown pigment.

BRACT. (Fig. 10). Over 1000 bracts, of two types, were found with

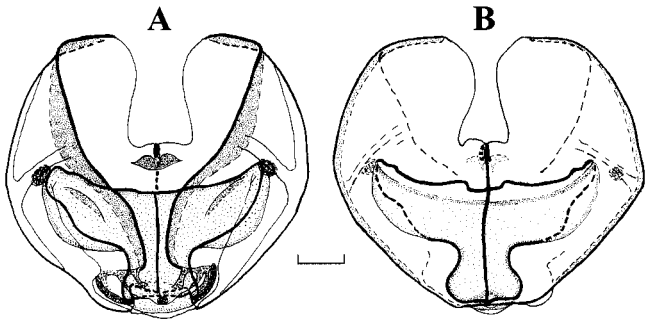

Fig. 9 *Erenna laciniata*. **A**. upper and **B**, lower views of immature nectophore. Scale 2 mm.

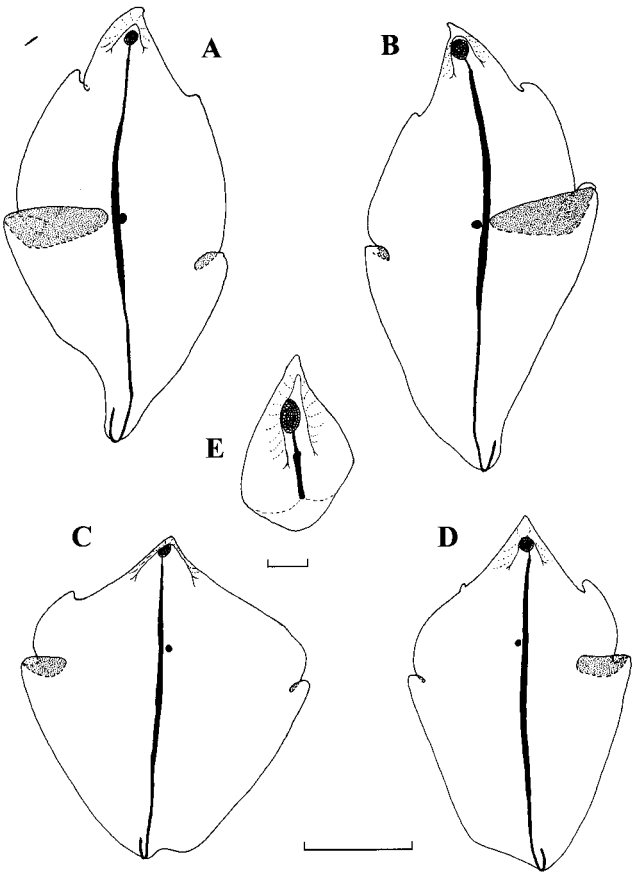

Fig. 10 *Erenna laciniata*. Bracts. **A**., **B**. dorsal views of first type; **C**., **D**. dorsal views of second type. Scale 5 mm. E. Immature bract. Scale 1 mm.

the JSL 1688 specimen, occurring as enantiomorphic (mirror-image) pairs. The first type of bract (Fig. 10A, B), which measured up to 25 mm in length, was deeply incised on one side, at about its mid-length where a large flap was formed stretching across almost to the mid-line. On the other side, slightly proximal to this level, a small cusp was present. Toward the distal end, there were two further lateral cusps, with the one on the same side as the flap tending to be more marked than the other. The distal end of the bract was pointed. Close to the tip, the dorsal surface was thickened into an oval patch of cells that surround and were interspersed with over 200 nematocysts, measuring c. 63 × 25 μm. Another small patch of such cells was found on the dorsal surface of the bract, in the mid-line, and on a level with the lateral flap. That patch, at least, is believed to be a site of bioluminescence. Proximally, the bracteal canal originated on the dorsal surface of the bract. It then curved over onto the ventral surface and continued distally in the mid-line. It appeared to be of variable thickness, but such variability was the result of variations in the thickness of the striated tissue that lay on each side of it. Close to the distal end of the bract the canal penetrated into the mesogloea and ended below the oval patch of epidermal cells.

The second type of bract (Fig. 10C, D) was similar to the first, but tended to be shorter, up to 20 mm in length, and broader. The lateral flap, however, was much reduced, although still an obvious feature. Distal to this again there was an obvious lateral cusp; but on the other side the cusp was very small or absent altogether. The first type of bract was about three times more numerous than the second. Roughly, with over a thousand bracts and approximately 25 gastrozooids, there would seem to have been about 40 bracts per cormidium. Very young bracts (Fig. 10E) were roughly pyramidal in shape with the distinctive patch of epidermal cells, including nematocysts, fully developed. The bracteal canal was short and did not extend onto the dorsal surface; while beneath the distal patch of epidermal cells it formed an extensive cavity.

GASTROZOOID. (Fig. 11A, B). The gastrozooids measured up to c. 15 mm in length. The proboscis region, which often was curled back over itself, bore some stripes of gastrodermal cells. The stomach region, externally, was featureless and had a brown colour. The basigaster was greatly expanded on all sides, except that to which the tentacle was attached, and there was no obvious pedicle.

TENTACLE AND TENTILLUM. (Fig. 12). Typically the annulated tentacle had a muscular lamella running down one side, with the tentilla attached on the other side, at the internodes. The tentilla were of an extraordinary design. Only in the very young tentilla (Fig. 12 – centre) was there any trace of a pedicle. In these the cnidoband was made up of a large saccus overlain by a horseshoe-shaped band of nematocysts. The terminal process actually arose from the base of the saccus and bore, towards its distal end, a pair of 'ocelli'. The gastrovascular canal penetrated through the terminal process, but no connection with the saccus of the cnidoband could be discerned. As the tentilla matured the cnidoband lengthened, with the terminal process still only attached close to its base. The saccus diminished in importance and distally the band of nematocyst occupied all but a narrow strip of the external surface of the cnidoband. Proximally, where the terminal process was attached, the band of nematocysts split into two parts on either side of the saccus. Three types of nematocysts were present. The large anisorhizas, which measured c. 128 × 27 μm, were arranged along the lateral margins of the cnidoband. Between them were numerous smaller nematocysts of two shapes, probably heteronemes, with the more cylindrical ones measuring c. 40 × 15 μm and the more ovoid ones c. 32 × 18 μm. Bands of musculature were present in the terminal process and extended distally to beneath the 'ocelli'. In life this process was reddish-brown in colour.

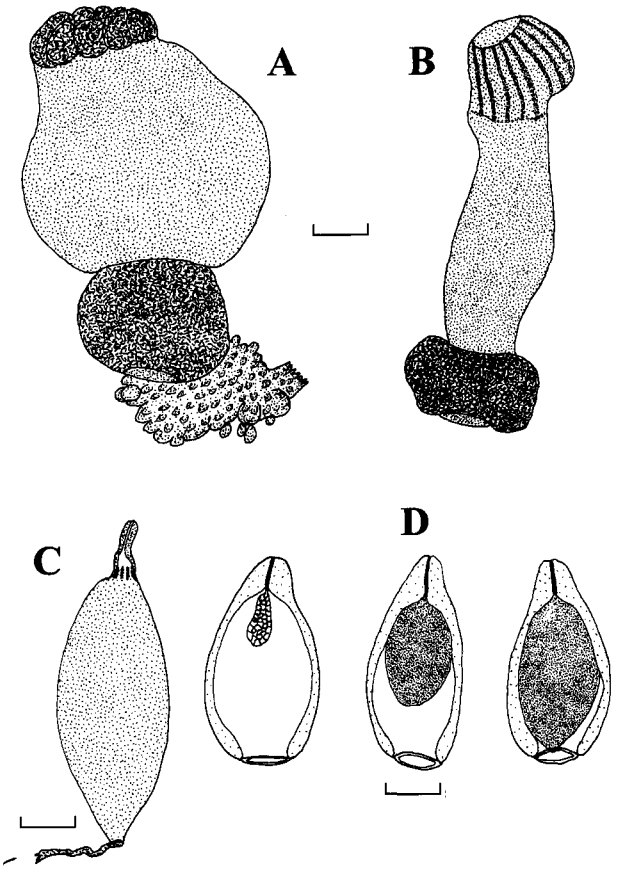

Fig. 11 *Erenna laciniata*. **A.**, B. gastrozooids; **C.** palpon. Scale 2 mm. **D.** male gonophores. Scale 1 mm.

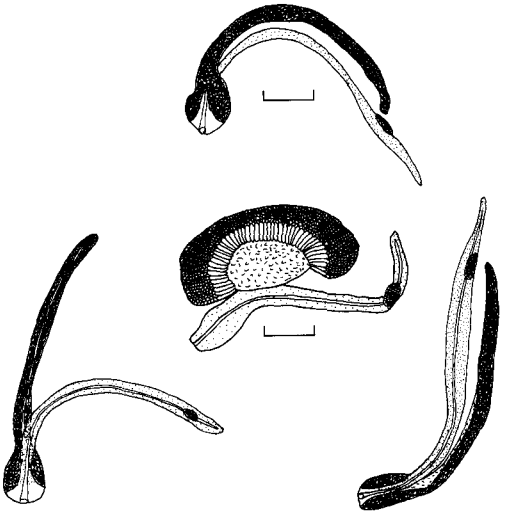

Fig. 12 *Erenna laciniata*. Three mature tentilla (Scale 1 mm), with (centrally) an immature one (Scale 0.5 mm).

PALPON. (Fig. 11C). Numerous palpons, up to c. 15 mm long, were present with the specimens. They were featureless thin-walled sacs filled, with a milky-white amorphous substance, although in life they were suffused with a brownish hue. The extent of the proboscis was variable, but typically, at its base, there were some

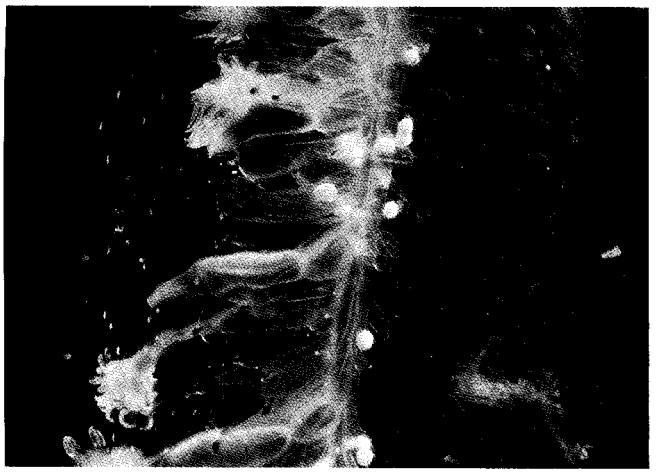

Fig. 13 *Erenna laciniata*. Photograph of part of siphosome showing male gonophores.

short, brown-coloured stripes. No nematocysts were found on the palpacle.

GONODENDRA. (Figs 11D, 13). The JSL 1688 specimen was female and the gonodendra were arranged in a very similar fashion to that described in *Erenna richardi*. The JSL 1454 specimen was male, with the individual gonophores apparently scattered randomly down the stem (Fig. 13). Each was a relatively large medusoid, whose manubrium progressively filled with spermatozoa until it occupied almost the entire subumbrella cavity (Fig. 11D) and had a milky-white colour.

DISTRIBUTION. The JSL II Dive 1454 specimen came from the region of the Dry Tortugas between Florida and Cuba, while the Dive 1688 specimen came from the region of The Bahamas. In addition, some damaged nectophores that can be referred to this species have been found in the *Discovery* collections from individual hauls on the equator at 22°W (805–900 m) and at 3°N 23°W (0–1000m).

BEHAVIOUR. In life the terminal process of the tentillum was reddish-brown in colour. It was kept rigid and was vibrated rapidly presumably, as was suggested for *Erenna richardi*, as a form of aggressive mimicry.

ETYMOLOGY. The specific name, being Latin for a 'flap', refers to the lateral flap-like process on the bracts.

Erenna cornuta sp.nov.

HOLOTYPE. The JSL II Dive 1451 specimen is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1818.

MATERIAL EXAMINED. The description is based on a single specimen collected during JSL II Dive 1451 at a depth of 896 m. (29 viii 1987; 24°30.6'N 83°45.6'W). In addition, a few specimens that apparently can be referred to this species have been found in recent *Discovery* collections, but always in a poor state of preservation.

DIAGNOSIS. Nectophores relatively less dorso-ventrally flattened, with only the basic ridge pattern; with apico-laterals not dividing close to ostium. Thrust block small, with no median indentation or conical protuberances. Lateral radial canals typically have 'horn' canals branching off at apico-lateral margins of nectosac. Bracts

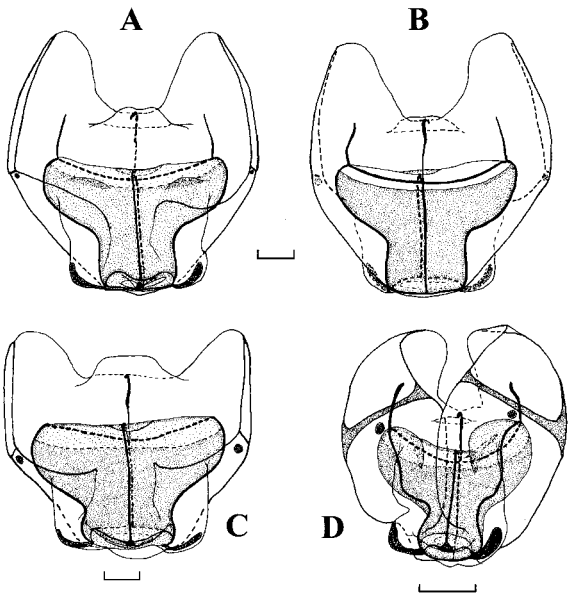

Fig. 14 *Erenna cornuta*. **A**. upper and **B**. lower views of nectophore with 'horn' canals; **C**. upper view of nectophore without 'horn' canals. **D**. upper view of young nectophore. Scale 2 mm.

with weak transverse ridge. Tentilla of two characteristic types; one with a long pedicle and no terminal process, with nematocysts grouped into four circular processes; the other with shorter pedicle and a small vesicular terminal process; with nematocysts, on the long cnidoband, more or less separated into c. 17 bundles.

DESCRIPTION

PNEUMATOPHORE. Measured c. 1.5 × 1 mm, but its base has been ruptured by gas expansion. No obvious pigmentation.

NECTOPHORE. (Fig. 14). Thirteen large nectophores, plus two developing ones and some nectophoral buds, were found with the specimen. They measured up to 16 mm in length, 14 mm in width and 4 mm in depth. The ridge pattern comprised pairs of apico-, infra- and vertical laterals. The apico- and infra-laterals unite close to the apices of the axial wings. The infra-laterals extended basally to end below the ostium. The apico-laterals, on mature nectophores, were only prominent in the upper half of the nectophore and, unlike the two species described above, basal to the vertical lateral ridges, they curved in toward the mid line (Fig. 14A, C). They could be traced, usually only after staining, down further toward the ostium, but did not divide. On the youngest nectophore the apico-laterals rapidly approached and then overlapped each other, ending just above ostial level (Fig. 14D).

No obvious mouth plate and the ostium opened basally. On each side of the ostium there were prominent lateral processes with obvious strips of epidermal cells; with a smaller triangular patch of cells found dorsally. In addition, there was a pair of small patches of cells on either side of the nectophore; above the mid-height of and basal to the vertical lateral ridges. All these patches were believed to be sites of bioluminescence.

T-shaped nectosac with a distinct apical muscle-free area, particularly on its ventral side. Pallial canal short, extending from the base of the thrust block over on to the ventral surface of the nectophore, where it gave rise to the pedicular canal. On the nectosac the latter immediately divided to form the four straight radial canals. No pigmentation was noted in any canals. The lateral

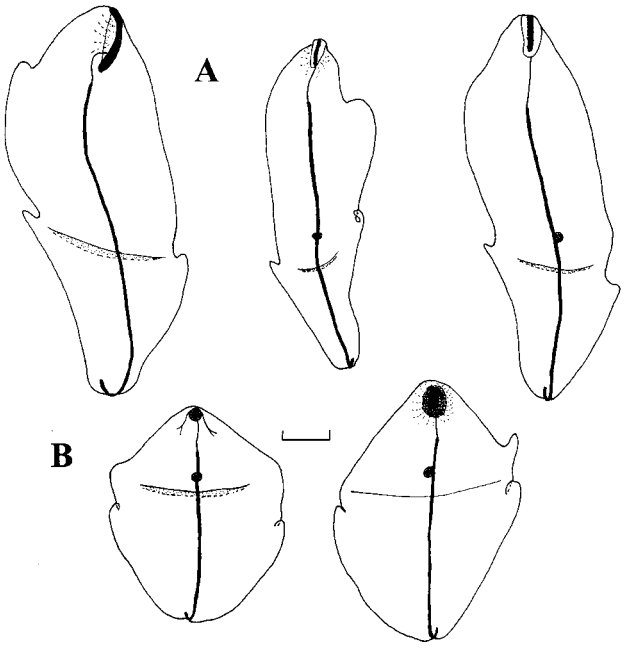

Fig. 15 *Erenna cornuta*. **A**. Three bracts of first type; **B**. two bracts of second type. Scale 2 mm.

radial canals passed through the middle of the muscle-free zone to reach the apex of the nectosac just short of its lateral margins. At that point the narrow 'horn' canals may or may not be given off. When present these 'horn' canals extended up for a variable distance, toward the apex of the nectophores, typically terminating on a level with the central thrust block. Eight nectophores (Fig. 14A, B) had well-developed 'horns', as did the two immature ones (Fig. 14D). In three others the 'horn' canals were ill-defined and short; while in the remaining two (Fig. 14C) there was no trace of them whatsoever.

The mature nectophores varied slightly in shape apparently in association with the extent of the 'horn' canals. The tapering axial wings were more extensive on those with well developed 'horn' canals; while the central thrust block typically was slightly smaller than those without 'horn' canals. The ones with ill-defined 'horn' canals tended to be intermediate. Of the 23 damaged nectophores collected at *Discovery* St. 7856#54 the 'horn' canals were prominent in all but the two smallest, but mature ones. The others were larger than the JSL II Dive 1451 ones, measuring c. 20 mm in length and width, and had denser musculature on the nectosac. The 'horn' canals also were more extensive, and there were traces of orange-brown pigment in the basal parts of the radial canals and, particularly, the ostial ring canal.

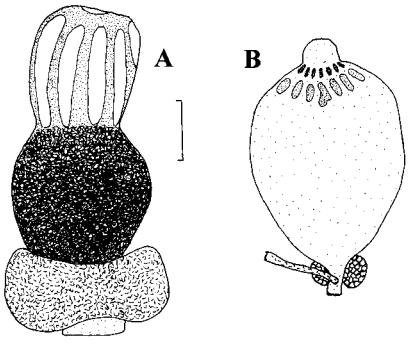

Fig. 16 *Erenna cornuta*. **A**. gastrozooid, and **B**. palpon. Scale 1 mm.

BRACTS. (Fig. 15). Two types of bract were present; the first (Fig. 15A), and considerably more numerous, being longer, up to 16 mm in length, and narrower than the second (Fig. 15B), which was up to 10 mm in length. Both types possessed a pair of lateral cusps. In the first type, as was the case with *Erenna richardi*, these seemed to lie at a fixed distance from the proximal end of the bract, and were asymmetrically disposed. Along the axis between these two cusps, on the dorsal surface of the bract, there was a rounded transverse ridge or process, that marked a change in the thickness of the bract, which was thinner distally. This ridge did not connect with the cusps, and its extent and distinctiveness was variable. Just distal to the ridge, in the mid-line, there was a small patch of cells; although often these has been abraded away.

On the second type of bract the lateral cusps were positioned, almost symmetrically, at about the mid-length of the bract. Just distal to these cusps there was a more or less pronounced cross-ridge which again demarcated a change in the thickness of the bract. Again a small patch of cells was situated distal to this ridge, in the mid-line. On the distal half of both types of bract, there could be an additional lateral protuberance of variable shape. At the distal tip of both types the dorsal surface was raised up in the mid-line to form an elongate or elliptical process on which were found a concentration of small epidermal cells, with brownish-red pigment. Centrally, these cells included some nematocysts, which measured c. 68 × 32 μm.

The bracteal canal originated, proximally, slightly over on the dorsal surface of the bract. It passed down the middle of the bract in close contact with its ventral wall, with striated bands of cells lying on either side of it, indicating where the muscular lamella was attached. At some distance from the distal end of the bract, in comparison with *Erenna richardi*, the canal penetrated into the mesogloea and curved up to end beneath the proximal part of the concentration of cells on the dorsal surface.

GASTROZOOID. (Fig. 16A). Only three well-developed gastrozooids remained with the specimen. The largest was 6 mm in length. The basigaster formed a horseshoe-shaped, laterally expanded structure around the base of the gastrozooid, with the tentacle attached in the open zone. It was a light brown colour. No obvious pedicle. The expanded stomach was externally featureless and had a dark brown colour. The proboscis region, which was about the same length as the stomach, had distinct stripes.

TENTACLE AND TENTILLUM. (Figs 17, 18). The tentacle was annulated, with a muscular lamella running down one side, and the tentilla attached, on the opposite side, at the internodes. There were two types of tentilla, both of which were found attached to the same tentacle. Early on in the development of the first type (Fig. 17A), the tentillum consisted of a long pedicle and a minute cnidoband devoid of nematocysts. The gastrovascular canal was seen, at the end of the pedicle, to turn back and continue down to open into the cavity of the saccus of the cnidoband. With further development the connection with the saccus cavity was closed, and the cavity filled with gastrodermal cells. A remnant of the diverticular canal seemed to persist, passing through a relatively dense band of gastrodermal cells. In the mature tentillum (Fig. 17B), the proximal part of the pedicle was expanded, typically tapering towards its base. The gastrovascular canal could occupy most of the interior, or could remain as a narrow tube, which became twisted and folded up on one side of the pedicle. Distally the pedicle was narrower, with the canal often having a zigzag appearance, probably indicating some

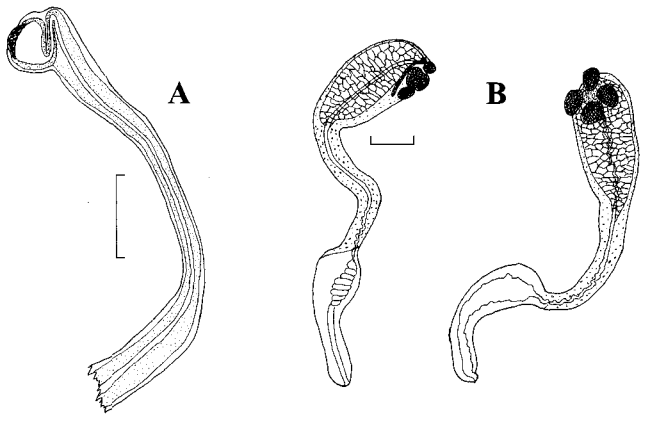

Fig. 17 *Erenna cornuta*. **A**. young tentillum of first type. Scale 0.5 mm. **B**. Two views of mature tentillum of first type. Scale 1 mm.

contraction in the length of the pedicle itself. The canal penetrated through the saccus of the cnidoband to its tip. The saccus was largely filled by large, vacuolate gastrodermal cells that formed a reticulate pattern. The nematocysts were restricted to four circular swellings; two lateral, one proximal, one distal. Three types of nematocysts were present and arranged so that the larger anisorhizas, measuring c. 130 × 35 μm, surrounded the smaller (?) haplonemes; the more cylindrical ones measuring 32 × 11 μm, and the more ovoid ones 41 × 14 μm.

The youngest of the other type of tentillum (Fig. 18A) comprised a short, thickened pedicle, a long cnidoband, and a short terminal process, which had a circular spot of distinctive epidermal cells on one side. The broad gastrovascular canal was present throughout and, in the terminal process, it appeared to bend back and continue, for a short distance, toward the saccus of the cnidoband. However, even in the smallest tentilla examined, the saccus had already been occluded by gastrodermal cells. The nematocysts had begun to accumulate into an undulating series of connected swellings on one side of the saccus.

Only a few mature tentilla (Fig. 18B) of the second type were found with the specimen. In these the pedicle remained short and broad and was largely filled by the gastrovascular canal. The cnidoband had increased greatly in length and was largely filled by large, vacuolated gastrodermal cells. The narrow gastrovascular canal passed through its middle and opened into the cavity of the small, spherical, thin-walled terminal process. The patch of cells persisted on one side of the latter. No diverticular branch of the main canal could be discerned. On the cnidoband the rounded swellings containing the nematocysts became more or less separated one from another. On the two best preserved mature tentilla there were 17 of these patches. The nematocysts were of the same type and size as on the other type of tentillum.

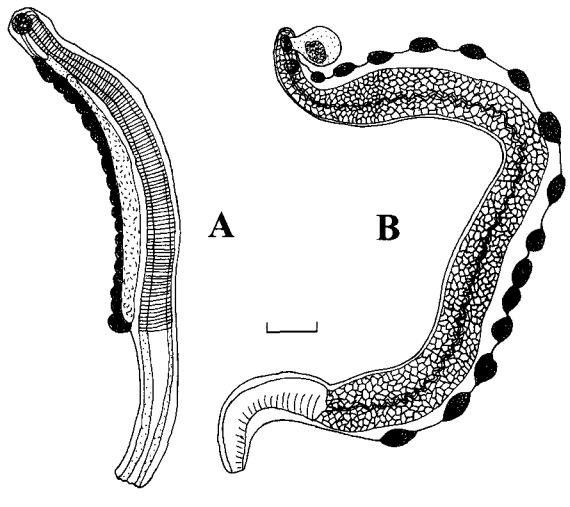

Fig. 18 *Erenna cornuta*. **A**. Young tentillum of second type. Scale 0.5 mm. B. Mature tentillum of second type. Scale 1 mm.

PALPON. (Fig. 16B). The globular, thin-walled palpons measured up to c. 4 mm in length. There was a short, narrow proboscis, at the base of which was a ring of pigmented gastrodermal cells, often organised into distinct spots. Other concentrations of gastrodermal cells sometimes were visible, particularly on the distal part of the stomach region. The base of the stomach region was almost surrounded by a small, loosely attached, horseshoe-shaped region of large, vacuolated epidermal cells, with the palpacle being attached in the open region. No nematocysts were found on the palpacle.

GONODENDRON. No gonodendra were found on the small piece of siphosome that remained with the specimen.

DISTRIBUTION. The type specimen came from the region of the Dry Tortugas, between Florida and Cuba. Nectophores with 'horn' canals, which presumably can be referred to this species, have been collected at four recent *Discovery* stations. Two of these were at c. 30°N 23°W at depths of 1250–1500 m and 1500–2000m, and the other two from off Bermuda (c. 31°45'N 63°45'W) at depths of 1250–1500m.

ETYMOLOGY. The specific name, meaning 'horned' in Latin, refers to the 'horn' canals present in most of the nectophores.

Parerenna gen. nov.

DIAGNOSIS. Nectophores not dorso-ventrally compressed; with muscle-free zone on nectosac mainly on lower surface adaxially. Vertical lateral and incomplete infra-lateral ridges very indistinct; the latter not forming the lower margin of lateral surface. Apico-laterals peter out well above ostial level. Gastrozooid with minute basigaster. Tentillum with long pedicle; with cnidoband extending beyond terminal process, which has a small spherical distal swelling.

Monotypic genus to accommodate *Parerenna emilyae* sp.nov.

Parerenna emilyae sp.nov.

HOLOTYPE. The specimen from JSL I Dive 2886 is designated holotype, and has been donated to the Natural History Museum, London where it is registered as BMNH 2000.1820.

MATERIAL EXAMINED. A single specimen collected during JSL I Dive 2886 (18 xii 1990; 26°31.8'N, 78°05.6'W; depth 823 m). Before preservation in 5% buffered formalin, the bioluminescence of the specimen was studied which, unfortunately, resulted in the loss of some parts.

DIAGNOSIS. As for genus.

DESCRIPTION

PNEUMATOPHORE. The base of the pneumatophore has exploded due to the expansion of the gas contents while bringing the specimen to the surface. Pneumatosaccus spherical, c. 1 mm in diameter, with a small cap of cells, which may have been pigmented in life.

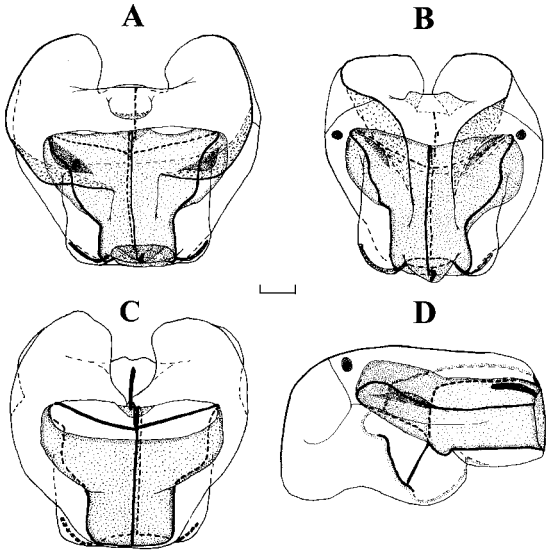

Fig. 19 *Parerenna emilyae*. Nectophores. **A.**, **B.** upper, **C.** lower, and **D.** lateral views. Scale 2 mm.

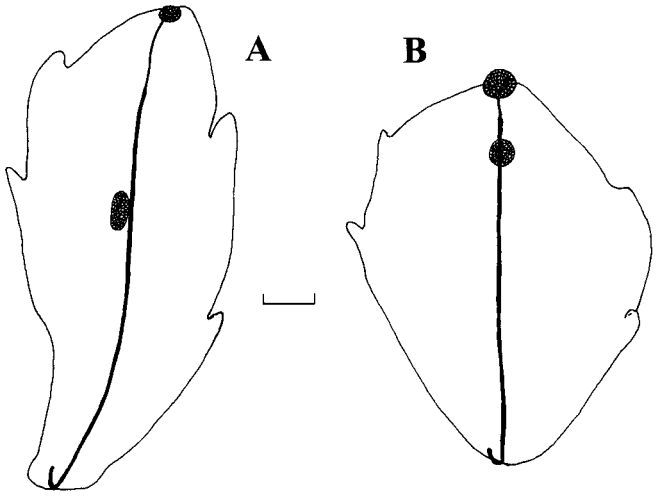

Fig. 20 *Parerenna emilyae*. Bracts of **A.** the first and **B.** the second type. Scale 1 mm.

NECTOPHORE. (Fig. 19). Eight fully developed and two developing nectophores were found with the specimen; plus a few nectophoral buds at the apex of the highly contracted nectosome. Mature nectophores were not dorso-ventrally flattened and measured up to 13 mm in length and width and 6 mm in height, and had well developed tapering axial wings. The central thrust block was broad, but of little height. The only obvious ridges were the apico-laterals (Fig. 19A, B), running down from the apices of the axial wings toward the ostium, but petering out well above that level. Only by staining were the pairs of complete vertical lateral and incomplete infra-lateral ridges revealed. The latter did not form the lower margins of the lateral surface of the nectophore (Fig. 19D). Two small patches of cells were found on each side of the nectophore, just basal to the vertical lateral ridges, although for many nectophores they had been abraded away. In addition there were three distinct strips of small epidermal cells, one dorsal and two lateral, stretching up from the ostium; the lateral pair being more extensive and pronounced than the dorsal one. These were all believed to be sites of bioluminescence. Mouth plate absent. Ostiun opened basally.

The nectosac was Y-shaped in the younger nectophores, but the median apical indentation was less pronounced in the larger ones, and may disappear altogether; the nectosac then being T-shaped. There was a large muscle-free zone on the apical, adaxial part of its lower side. The pallial canal was quite long, extending from the base of the thrust block to beyond the point of origin of the pedicular canal. The long pedicular canal was inserted onto the nectosac either at the point of origin of the lateral radial canals, or slightly basal to it. On half of the fully developed nectophores there was a slight asymmetry in the origin of the lateral radial canals with either the left or the right branching off before the other. The dorsal and ventral canals were straight and ran directly to the ostial ring canal. There was, however, a slight loop in the lateral radial canals as they curved over onto the lateral surface of the nectosac slightly above its mid-height. These canals then curved down to the mid-level and continued to the ostial ring canal.

SIPHOSOME. The remaining piece of siphosome was highly contracted, with four gastrozooids and four palpons still attached. There were no signs of any gonodendra.

BRACTS. (Fig. 20). Twenty-two bracts, up to 9 mm in length, remain with the specimen. Two basic types, present in approximately equal numbers, could be distinguished. The first (Fig. 20A) was longer, but narrower, than the second (Fig. 20B). Both types

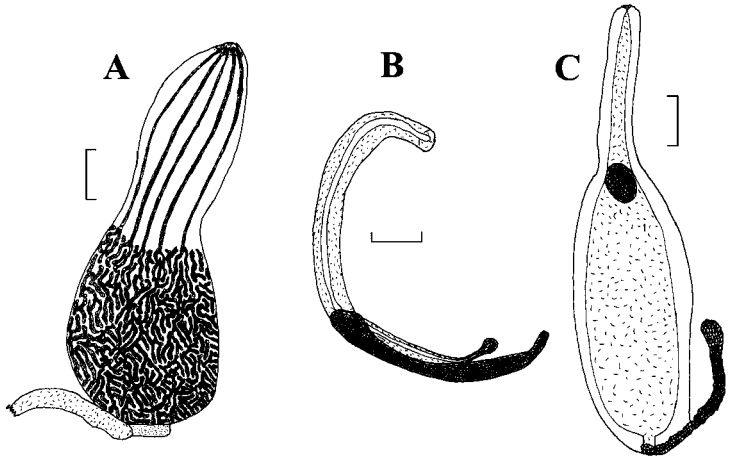

Fig. 21 *Parerenna emilyae*. **A.** Gastrozooid. Scale 1 mm. **B.** Tentillum and **C.** Palpon. Scales 0.5 mm.

have two pairs of lateral cusps; although in the shorter, more rounded bracts, one or both of the more distal pair could be difficult to discern. Both types had a patch of small epidermal cells on the dorsal surface, but the positioning differed (Fig. 20). Often these patches had been abraded away. Proximally the bracteal canal originated on the dorsal surface of the bract. It passed down the middle of the ventral side bract and, for the most part, lay in close contact with its surface. A short distance from its distal end it narrowed and penetrated through the mesogloea to terminate beneath a hemispherical clump of epidermal cells sunk into the mesogloea. Some of these cells, as with the patches on the dorsal surface of the bract, probably produced bioluminescence; others were nematocysts measuring 80 × 20 μm.

GASTROZOOID. (Fig. 21A). Up to 7.5 mm long, with no obvious pedicle. The basigaster, to which the tentacle was attached, was minute. The gastrodermal lining of stomach region bore a complex pattern of villi; while the proboscis was broad and elongate, with a distinctive arrangement of eight stripes.

TENTILLUM. (Fig. 21B). The tentillum was very distinctive, with a thickened pedicle, occupying about half its length, through which the broad gastrovascular canal passed. The distal half of the tentillum consisted of an extensive cnidoband and a process, containing a canal, that bent away, occasionally at a right-angle, from the base of the cnidoband and was terminated by a small spherical swelling. The cnidoband appeared to have two rows of large nematocysts on either side, measuring 120 × 20 μm, that, judging by those that had been discharged, probably were homotrichous anisorhizas. The remainder of the cnidoband bore numerous smaller nematocysts of two sizes; the more cylindrical ones measuring c. 21 × 12 μm, and the more ovoid ones c. 26 × 15 μm. These were the only nematocysts to be found on the distal tip of the cnidoband.

PALPON. (Fig. 21C). Up to 4 mm long, with a palpacle, without nematocysts, at its base. Proboscis region long and narrow with broad gastrovascular canal.

DISTRIBUTION. Known only from a single specimen collected in the region of The Bahamas.

REMARKS. Although *Parerenna emilyae* possesses the general erennid characters, there are certain differences from those of the genus *Erenna* that warrant its placement in a separate genus. Primarily, the nectophores are not flattened dorso-ventrally and only the apico-lateral ridges are distinct. The weak infra-lateral ridges do not demarcate the lower margins of the lateral facets, and the weak vertical lateral ridges have an oblique course. Further, the lateral radial canals on the nectosac are slightly curved. In addition the basigaster of the gastrozooid is minute, especially in comparison with the greatly expanded basigasters of the *Erenna* species.

ETYMOLOGY. The species is named for my daughter Emily.

KEY FOR THE IDENTIFICATION OF ERENNID NECTOPHORES

1 Nectophores dorso-ventrally flattened with distinct, short vertical lateral ridges, and apico- and infra-lateral ridges joining apically. Genus *Erenna* 2

Nectophores not dorso-ventrally flattened; indistinct vertical lateral ridges; indistinct infra-lateral ridges not joining apico-laterals apically. Genus *Parerenna* ..... *P. emilyae*

2 Two digitate processes on ventral side of thrust block ..... *Erenna richardi*

No digitate processes on ventral side of thrust block 3

3 Apico-lateral ridges divide close to ostium; thrust block with V-shaped median indentation; no 'horn' canals ..... *Erenna laciniata*

Apico-lateral ridges do not divide close to ostium; thrust block without median indentation; 'horn' canals usually present ..... *Erenna cornuta*

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