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A description of two new species of the genus *Erenna* (Siphonophora: Physonectae: Erennidae), with notes on recently collected specimens of other *Erenna* species

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Abstract

Two new *Erenna* species, *E. insidiator* **sp. nov.** and *E. sirena* **sp. nov.,** are described from specimens collected in the vicinity of Monterey Bay, California, and also, for *E. sirena* at the southern end of the Gulf of California, Mexico. Further information on the three extant *Erenna* species is given, based on specimens collected in the same areas. These have enabled, for instance, the identification of three types of tentilla on the tentacles of *E. cornuta* Pugh, 2001, rather than the two noted on the single previously known specimen. The genus is remarkable for the presence of bioluminescent lures on the tentilla of all five species. In *E. sirena* **sp. nov.** the tentilla are also covered by a red-fluorescent layer, which was briefly described by Haddock *et al*. (2005), and further details are given herein. Another extraordinary feature of the colonies *E. sirena* **sp. nov.** is that the main part of the tentacle, with its tentilla, can be extended away from the siphosomal stem on a long peduncle. This phenomenon also appears to occur in *E. laciniata* Pugh, 2001, and has not been observed before for other physonect species.

Key words: Siphonophora, Physonectae, Erennidae, *Erenna*, taxonomy, Morphology, Lures

Introduction

The history of the little known physonect siphonophore genus *Erenna* was reviewed by Pugh (2001). Up until that time, two species of *Erenna* had been described from fragments of specimens, mainly tentilla; namely *E. richardi* Bedot, 1904 and *E. bedoti* Lens & van Riemsdijk, 1908, with the latter generally being considered a synonym of the former. However, Margulis (1991), having examined further material, concluded that the two species were valid. From material collected by the submersibles Johnson-Sea-Link I and II, Pugh (2001) was able to examine a

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much more complete specimen of *E. richardi*, and from these studies concluded that Margulis' reasons for retaining the species *E. bedoti* were unsubstantiated. However, he concluded that the unique structure of the tentillum, with its hypertrophied, uncoiled cnidoband and a terminal process devoid of nematocysts, warranted the establishment of a new physonect family to include two genera and four species. This conclusion was reinforced by the results of the study of the molecular phylogeny of siphonophores carried out by Dunn *et al*. (2005). Four other erennid specimens were also collected by the aforementioned submersibles, and Pugh (2001) described these as belonging to three new species, two within the genus *Erenna*, namely *E. cornuta* Pugh and *E. laciniata* Pugh and one in a closely related genus *Parerenna*, namely *P. emilyae* Pugh.

Since that time further specimens of *Erenna* species have been collected, mainly in Monterey Bay, California, by the ROVs *Tiburon*, *Ventana* and *Doc Ricketts* operated by the Monterey Bay Aquarium Research Institution (MBARI). These specimens have enabled us to re-evaluate the original descriptions, particularly those of *Erenna cornuta*, for which the original description was based on a single specimen, but also of *E. laciniata*, for which several additional specimens have become available, and any new information will be included herein. In addition, a further two new species belonging to the genus *Erenna* have been identified from the MBARI material and descriptions of these will be given. One of these new species was found to possess red fluorescent lures (Haddock *et al*. 2005). The characters that distinguish all these species will be discussed.

Family Erennidae Pugh, 2001.

Diagnosis. Physonect siphonophores best characterized by their uncoiled tentilla each bearing a hypertrophied cnidoband with nematocysts of three types; large microbasic mastigophores line the margins of the cnidoband, while the other types fill the central region. Terminal process, when present, devoid of nematocysts. Nectophores with basic pattern of upper-, lower- and vertical lateral ridges; with apical muscle-free zone on nectosac; radial canals straight or slightly curved; with ostium opening basally; without mouth plate. Pneumatophore without apical pore. Gastrozooids without peduncle. Dioecious.

Genus *Erenna* Bedot, 1904

Diagnosis. Nectophores flattened in the upper/lower direction, with tapering axial wings; distinct upper and lower lateral ridges respectively form upper and lower margins of lateral surface, with short, perpendicular, vertical lateral ridge connecting them. Lateral radial canals straight, with or without additional small protuberances, spikes, or 'horn' canals. Bracts of two types, with bracteal canal ending distally below a cupulate process containing ectodermal cells, including nematocysts. Tentillum large, with hypertrophied, uncoiled cnidoband and, when present, rigid terminal process devoid of nematocysts. Gastrozooid with large swollen basigaster, but no obvious peduncle.

Erenna richardi Bedot, 1904

Erenna richardi Bedot, 1904, pp 10–14, PI. 11, figs. 1–12; Totton, 1965, pp. 74–76 (*in partim*), ? fig. 38, ? Plate XIV, figs. 10–11, *non* Fig. 38; Pugh, 2001, pp. 170–175, figs. 1–7.
Erenna bedoti Lens & van Riemsdijk, 1908: 66–69; Margulis, 1977, pp. 148–151, figs. A-П; 1991, pp. 30–34, figs. 1–2.

Diagnosis. Nectophores large, up to 32 mm in length, flattened, with prominent upper-, lower- and vertical lateral ridges; upper-laterals divide close to ostium. Two pairs of incomplete lateral ridges in distal half of nectophore. Axial wings large, almost half total length of mature nectophore. Thrust block large, two lobed and, in mature nectophores, with two small digitate protuberances on its lower surface. Lateral radial canals often 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 photophores close to its distal end.

Material examined. Pugh (2001) based his redescription of *Erenna richardi* on two specimens collected by the JSL submersibles. The specimen from JSLI Dive 2889 was donated to the Natural History Museum, London, while the JSLII Dive 1456 specimen was retained and has been re-examined during the present study. In addition, thirteen specimens of *Erenna richardi*, as listed below, have been identified either from *in situ* frame grabs or from collected material (emboldened), of which the two specimens marked with an asterisk have been examined.

ROV	Dive	Date	Position	Depth (m)	T °C
Ventana	**2243***	**9 September 2002**	**36°42.44'N 122°03.62'W**	**1002**	**3.83**
Tiburon	**751***	**10 October 2004**	**36°35.89'N 122°22.23'W**	**1451**	**2.76**
Tiburon	960	4 April 2006	36°34.64'N 122°31.35'W	1368	3.07
Tiburon	**996**	**20 June 2006**	**36°33.08'N 122°30.69'W**	**970**	**4.20**
Doc Ricketts	**100**	**10 December 2009**	**36°36.49'N 122°22.95'W**	**1061**	**3.82**
Doc Ricketts	183	29 August 2010	36°36.04'N 122°20.48'W	1205	3.34
Doc Ricketts	553	21 November 2013	36°04.12'N 122°17.77'W	1280	3.17
Ventana	3762	10 February 2014	36°42.21'N 122°03.13'W	891	4.27
Ventana	3762	10 February 2014	36°42.21'N 122°03.13'W	905	4.19
Doc Ricketts	714	1 March 2015	24°18.73'N 109°12.32'W	1014	4.41
Doc Ricketts	718	2 March 2015	24°24.83'N 109°05.78'W	1320	3.58
Doc Ricketts	729	15 March 2015	24°11.07'N 109°38.04'W	978	4.44
Doc Ricketts	782	11 July 2015	36°33.90'N 122°30.4'W	1400	2.98

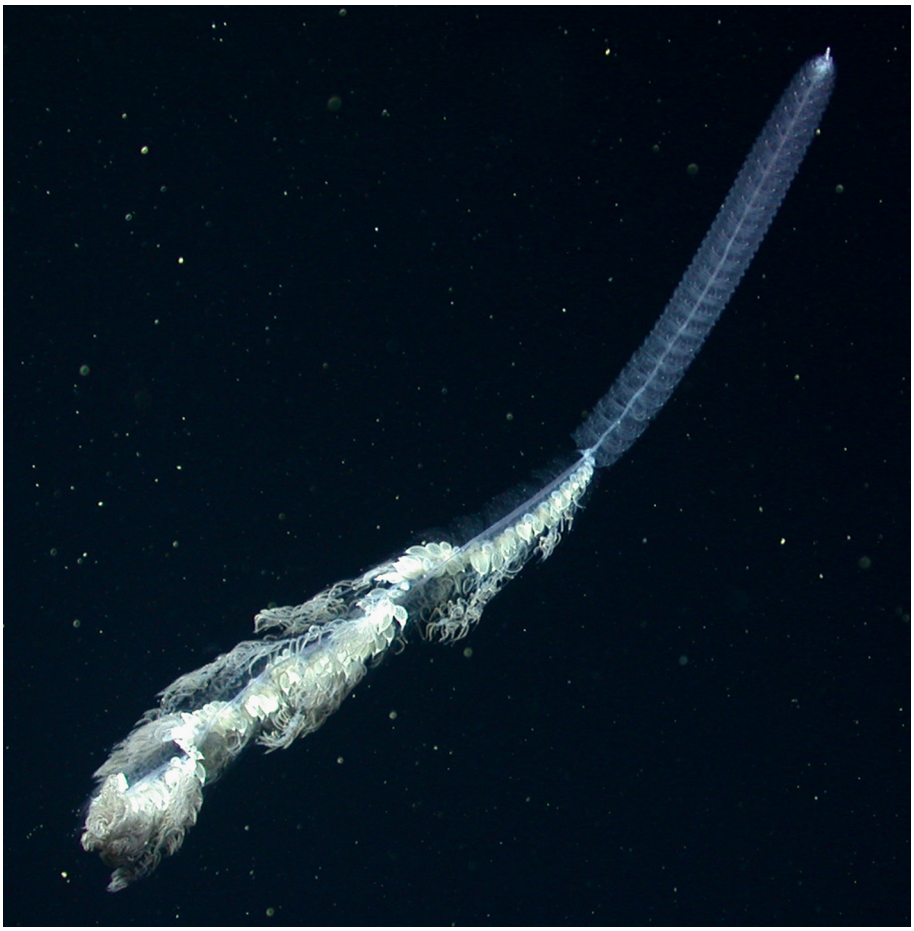
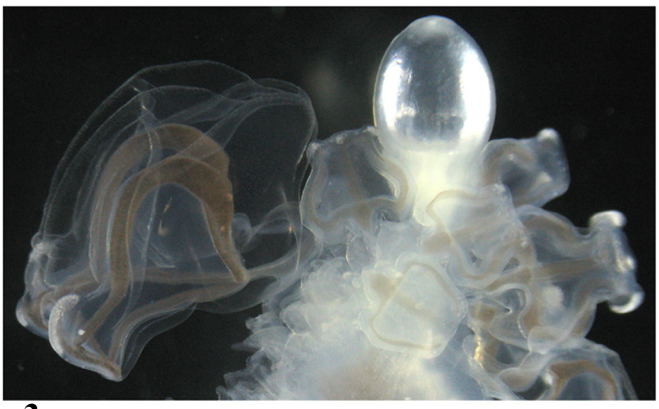


FIGURE 1. *Erenna richardi* Bedot, 1904. *In situ* frame grab of specimen observed during *Tiburon* Dive 960 at a depth of c. 1370 m. Size unknown. MBARI.

FIGURE 2. *Erenna richardi* Bedot, 1904. *In situ* frame grab of specimen collected during *Ventana* Dive 2243 at a depth of c. 1000 m. Estimated length 75–100 cm. MBARI.

Description. Pugh (2001) gave a comprehensive description of this species and here we will only add any further information that can be gleaned from the recently collected specimens. Pugh's figure 1 showed an *in situ* specimen that, with the benefit of hindsight, can be instantly recognised as *Erenna richardi*. The massive arrays of substantial tentilla, the side branches of the tentacle, are particularly obvious and clearly establish the identity of this species when observed *in situ*, as can also be seen for the specimens shown in Figures 1 and 2. The colony shown in a recent video uploaded to the web (http://www.nautiluslive.org/video/2014/06/27/stunning-siphonophore-sighting) clearly belongs to *E. richardi*, as a close up of its unmistakeable tentilla is included. Possible characters that might help to identify the other *Erenna* species *in situ* are discussed below. Another brief video sequence taken during a dive of the ROV *Doc Ricketts* shows a specimen of *E. richardi* that had ensnared a large snailfish.

Nectosome and pneumatophore: A close up of the anterior end of a colony of *Erenna richardi* collected during *Doc Ricketts* Dive 100 (Figure 3) showed a featureless pneumatophore devoid of any pigmentation. Posterior to it was a cluster of very small nectophoral buds with prominent, brown coloured, radial canals, and distinct white lateral ostial processes, on either side of the ostium. A larger nectophoral bud (Figure 3, left) showed its lateral radial canals to be much broader in their central, arched region and to contain dark brown pigmentation.



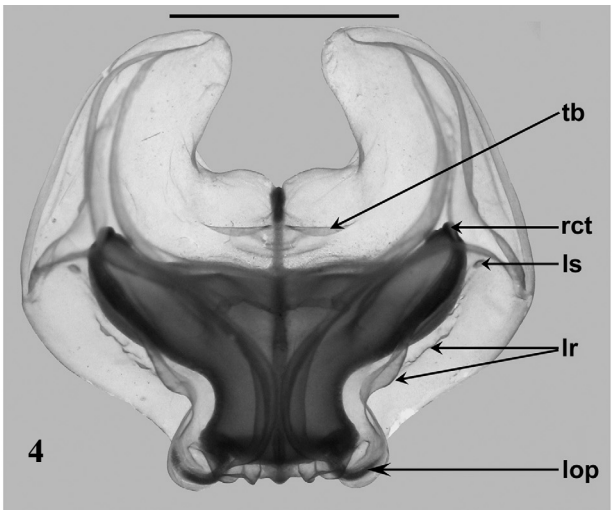


FIGURE 3. Anterior end of colony of *Erenna richardi* Bedot, 1904 collected during *Doc Ricketts* Dive 100 at a depth of c. 1060 m. By Dr Stefan Siebert.

FIGURE 4. *Erenna richardi* Bedot, 1904. Upper view of very young nectophore from JSLII Dive 1456. **lop**: lateral ostial process; **lr**: lateral ridges; **ls**: lateral spot; **rct**: radial canal thickening; **tb**: thrust block. Scale bar 5 mm.

Nectophores: The larger nectophores have been illustrated by Pugh (2001) and require no further comment, except to draw attention again to the two small conical protuberances on the lower side of the large, deeply emarginated thrust block. At that time these digitate processes characterized the species, but one of the new *Erenna* species has somewhat similar processes and detailed comparisons will be made below. Pugh (2001) also commented that these protuberances were not to be seen on the younger nectophores. One other characteristic feature that Pugh (*ibid*. p. 171) noted was that, in addition to the basic ridge system, consisting of upper and lower lateral and vertical lateral ridges, there were "at least two pairs of incomplete lateral ridges passed obliquely down the lateral facet in the basal half of the nectophore", which still remains a distinctive character for the species.

The two pairs of incomplete lateral ridges could be seen on a young nectophore (Figure 4, **lr**); the upper pair being very distinct while the lower pair was barely visible. At this stage the thrust block was only slightly developed, and there was no sign of the digitate protuberances that characterize the fully developed nectophore. The lateral radial canals still showed a distinct thickening (**rct**) at their lateral corners. The lateral patches of ectodermal cells (**ls**) just distal to the vertical lateral ridges were small and indistinct, while each of the lateral ostial processes (**lop**) was well developed. A canal ran through each process, originating from where the lateral canal joined the ostial ring canal. In their mid region these processes were overlaid by rounded ectodermal cells that included nematocysts. These cells extended round the lower half of the ostium, while the upper half was lined by a separate group of cells that were thickest in the region where the upper canal joined the ostial ring canal. A few discharged nematocysts were found that measured c. 93 x 30 µm. They appeared to have no shaft, while the long tubule had spines arranged in spirals around it. This would suggest that they were some form of haplonemes or isorhizas. However, for other species, nematocysts like these were found to have a shaft that was only slightly wider than the tubule, and so the identity of these nematocysts remains uncertain.

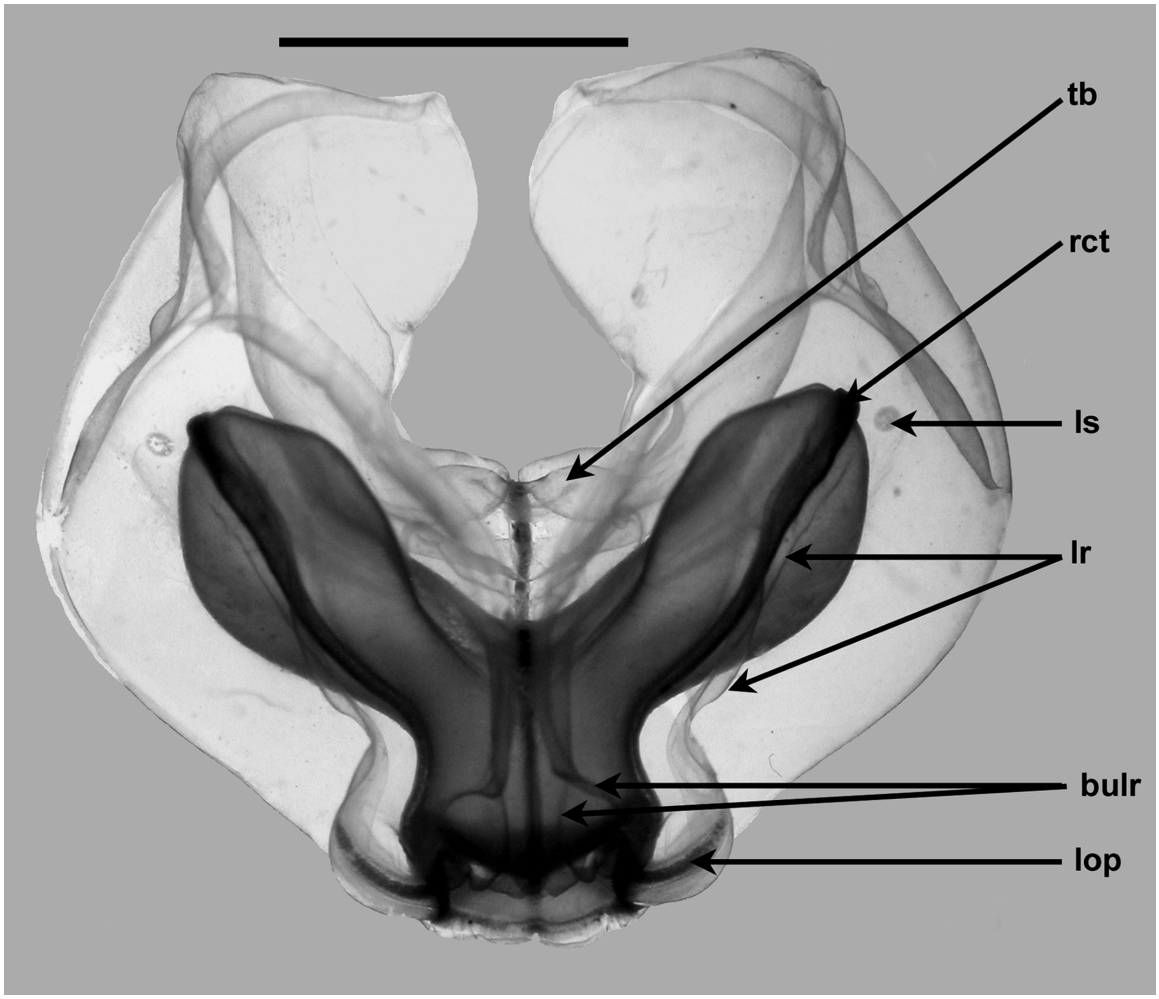


FIGURE 5. *Erenna richardi*. Upper view of slightly larger nectophore from the same specimen. See figure 6 for annotations. **bulr**: branches of the upper lateral ridge. Scale bar 5 mm.

As the nectophores grew the thrust block gradually increased in size and, for the nectophore shown in Figure 5, it consisted of two small lobes, and there was a very vague indication of the start of the development of the two small digitate processes. The lower lateral ridge, which paralleled the upper one, at first became more obvious, although not as much as the upper one. However, with further development, both ridges began to become less obvious, such that in the fully developed state they were often difficult to discern. For the nectophore shown in Figure 5 the ostial region had been tilted upwards so that the branching of the upper lateral ridges, and the ostium itself, could be seen clearly. In addition, the line of ectodermal cells on the lower half of the ostium was not as dense as it had been. In both Figures 4 and 5, the photographs gave the impression that the connection between the vertical lateral ridges and the lower lateral ones was weak. However, this was not the case and the connection between those ridges was distinct.

Siphosome: No detailed studies of the arrangement of the cormidia were possible due to the highly contracted nature of the preserved material.

Bracts: All *Erenna* species appear to have two types of bracts, with what we will call *Types A* and *B*; the former being relatively long and narrow, the latter shorter and broader. These two types were clearly illustrated by Pugh (2001), and the possible ways of distinguishing the *Type A* bracts of all the species will be discussed below. Pugh (2001) also mentioned that the canal of the bract terminated, distally, below a cupulate patch of ectodermal cells, including some nematocysts. These nematocysts (Figure 6A) measured c. 70 x 25 µm and appeared to be similar to those on the lateral ostial processes of the nectophores. On some bracts they appeared to be fairly randomly scattered amongst the other cells, which far outnumbered them, although in other cases they appeared to form an outer ring, surrounding the other ectodermal cells that were sites of bioluminescence.

Gastrozooid: As Pugh (2001) noted, Margulis (1977) was somewhat confused regarding the gastrozooid, it seemed that for her specimens the stomach region had become detached from the proximal basigaster, so that she described the tentacle as being attached to a structure with two lateral spherical dilations. This, of course, was the basigaster (see Figure 6B) that consisted of two large lateral inflations and, usually, a smaller one on the side opposite to where the tentacle was attached. There was no obvious peduncle.

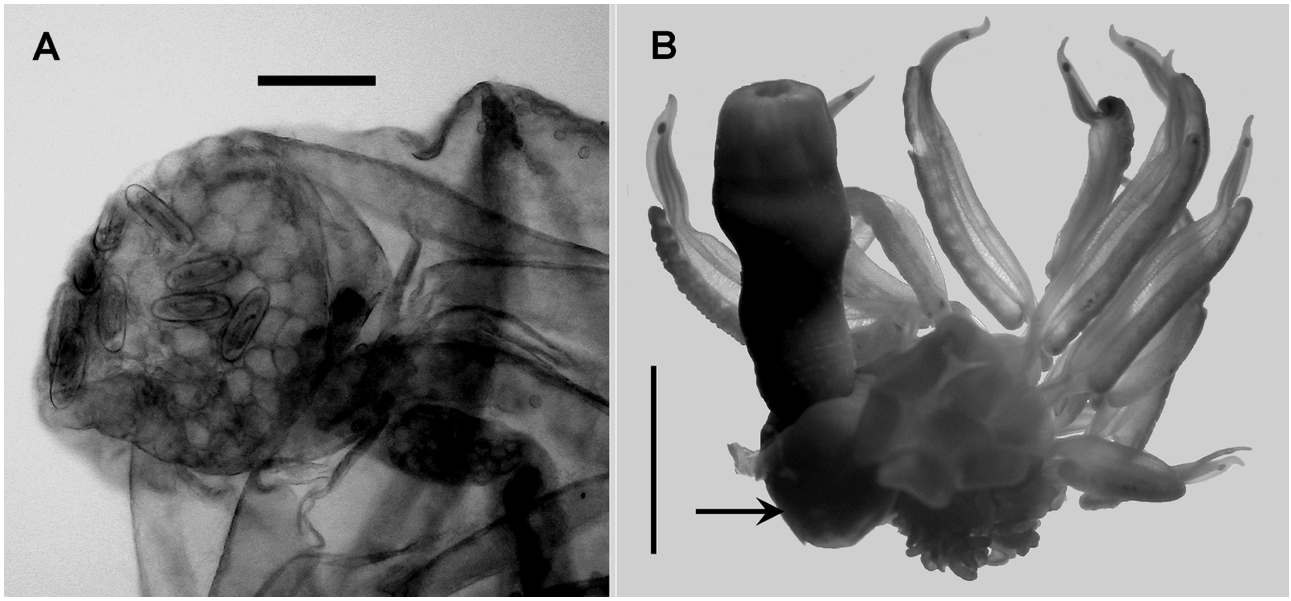


FIGURE 6. *Erenna richardi* Bedot, 1904. **A**. Patch of ectodermal cells and nematocysts at distal end of bracteal canal. Scale bar 1 mm. **B**. Gastrozooid, with large proximal basigaster (arrowed) and proximal end of tentacle, with several young tentilla. Scale bar 5 mm.

Tentilla: The basic structure of the tentillum was described in detail by Bedot (1904), and elaborated upon by Pugh (2001), particularly with regard to the developmental stages. Bedot noted the pair of bodies of ectodermal material that were present in the terminal process in the region where the diverticular canal arose. Lens & van Riemsdijk (1908) referred to them as "ocelli", but Haddock *et al.* (2005) found that they were sites of bioluminescence and were, in actuality, photophores, and were filled with calcium-activated proteins. The lateral

margins of the cnidoband were demarcated by rows, usually two, of large nematocysts measuring c. 165 x 32 µm (Figure 7A, B). Within the undischarged nematocysts of this type the shaft can clearly be seen and when devaginated that shaft was approximately the same length as the nematocyst capsule (Figure 7B). The shaft was quite narrow, but the point where the shaft ended and the tubule began can clearly be seen. These nematocysts appear to be microbasic mastigophores.

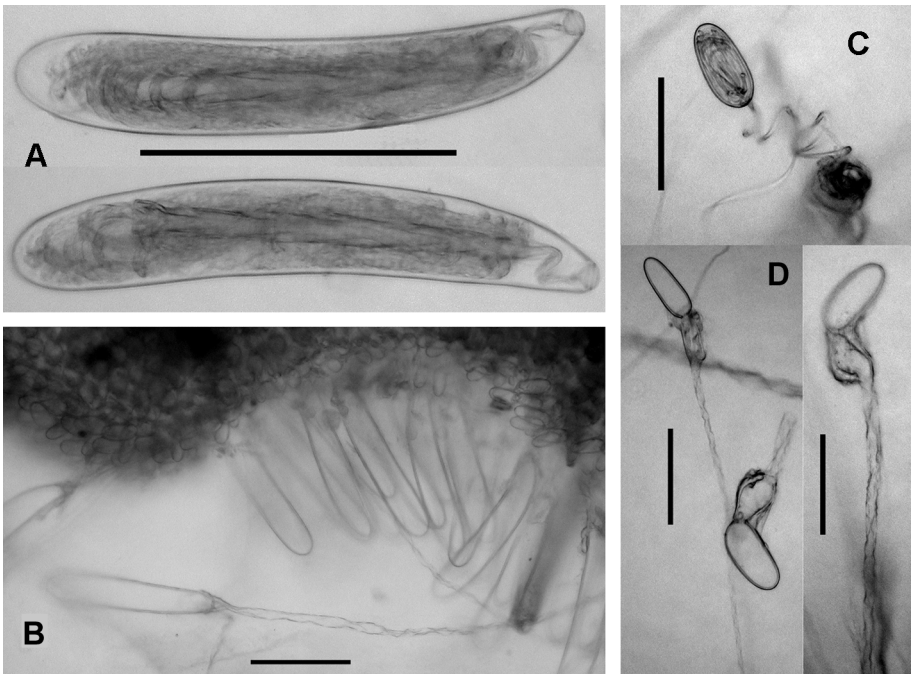


FIGURE 7. *Erenna richardi* Bedot, 1904. **A**. Separate large nematocysts of cnidoband. **B**. Large nematocysts forming lateral margins of cnidoband. **C & D**. Smaller nematocysts from central region of cnidoband. See text for details. Scale bars **A**, **B**, 100 µm; **C, D**. 50 µm.

Pugh (2001) noted two other types of nematocyst that measured c. 43 x 15 µm and c. 27 x 20 µm. However, the present re-examination suggested that there was a large variation in their sizes. Figure 7D shows some of the small pear-shaped or ovoid type that had discharged, and Figure 7C shows a nematocyst apparently preserved during the process of devagination. It can be seen that the process of devagination gave rise to a proximal, asymmetric swelling, apparently devoid of any spines. In turn, this gave rise to a distal tubule of considerable length and bearing spirally arranged spines. These nematocysts do not appear to conform to any of the basic types of nematocyst as illustrated by, for instance, Werner (1985). They somewhat resemble euryteles but the proximal vesicle does not appear to have any superficial spines, and its asymmetry is very striking. The other cylindrical type of small nematocyst was found to be very rare and was not investigated further for this particular species.

Distribution. Pugh (2001) reviewed the then known distribution of *Erenna richardi*, and considered that any nectophore where there was black pigmentation in the radial canals belonged to this species. However, we now know that this is not a character specific to *E. richardi*, since the black pigmentation is undoubtedly derived from the fish prey that the species of this genus consume. Thus, a few of the records that he gave may not have actually referred to this species.

In the intervening period there have been only a few additional records; all from the eastern North Pacific Ocean. Hung (2002), Pan (2004) and Yu (2006) all found specimens off the coast of Taiwan apparently at shallow depths. However these records were all included in M. Sc. theses, all in Chinese and from the National Sun Yat-sen University, Kaohsiung, Taiwan. Thus, there is the possibility that there has been some cross-referencing. Nonetheless, Grossmann & Lindsay (2013) found two specimens in Sagami Bay, Japan at depths between 850 & 950 m.

Of the 14 specimens of *Erenna richardi* listed in the table above ten have been sighted or collected by the MBARI ROVs in the vicinity of Monterey Bay. They had a mean depth of 1074 ± 190.0 m where the temperature was 3.612 ± 0.53°C. The remainder came from the Gulf of California (c. 24°N), with a mean depth of 1104 ± 187.9

m and a mean temperature of 4.1 ± 0.5°C. The specimens collected in the region of the Bahamas or the Gulf of Mexico (Pugh 2001) were found at a slightly shallower depth, i.e. 801 ± 92.3 m, but the temperature was not recorded.

Erenna laciniata Pugh, 2001

Diagnosis. Nectophores large, dorso-ventrally flattened, with only basic erennid ridge pattern; with apico-laterals dividing into three close to ostium. Thrust block small, with U-shaped median indentation and lower 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 photophores.

Material examined. Only two further specimens have become available for examination and, although they were large, they mainly consisted of nectophores with very little of the siphosome either collected and/or preserved. Recently, three others, see below, have been caught, but they have not been examined for the present study and are housed in the siphonophore collections at Brown University.

ROV/Sub	Dive	Date	Position	Depth (m)	T°C
JSLII	1683-CG3	11 October 1988	26°23.5'N 78°39.5'W	853	
Ventana	2570	13 September 2004	36°41.85'N 122°32.46'W	299	8.16
Doc Ricketts	344-D6	18 February 2012	24°11.01'N 109°38.03'W	1144	4.00

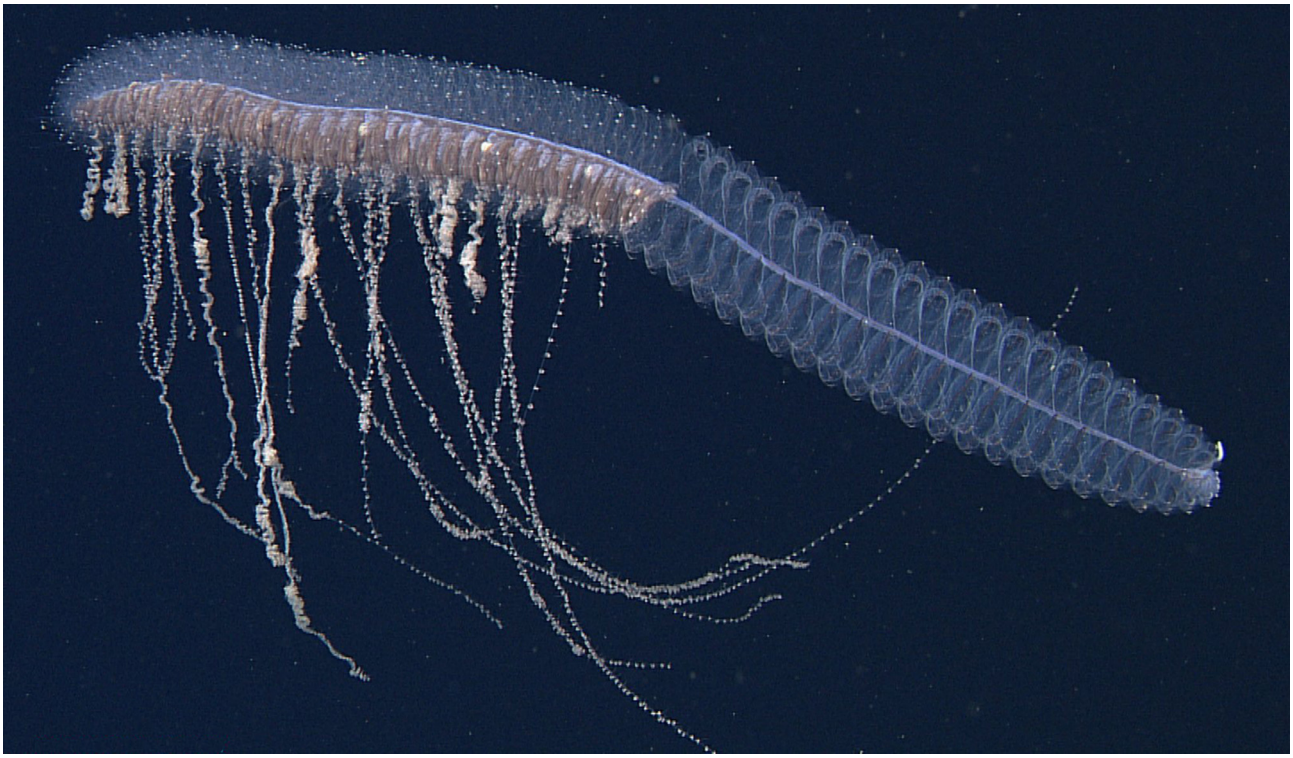


FIGURE 8. *Erenna laciniata* Pugh, 2001. *In situ* photograph of specimen from *Doc Ricketts* Dive 339 at 1581 m. MBARI.

Description. Figure 8 shows a large specimen of *Erenna laciniata* from *Doc Ricketts* Dive 339 at a depth 1581 m with 40+ mature nectophores, and some extended tentacles with their relatively small Y-shaped branches, or tentilla, that characterize this species. Figure 9A shows a smaller specimen from *Tiburon* Dive 534 at a depth of 1173 m. Here the black pigmentation in the radial and ostial ring canals can clearly be seen. In both the distal tips of the bracts are demarcated by a white patch that was filled with nematocysts. The small, circular nature of this patch clearly distinguishes specimens of *E. laciniata* from those of *E. cornuta*, which has elongated patches. This is a useful character as the two species have overlapping depth distributions.

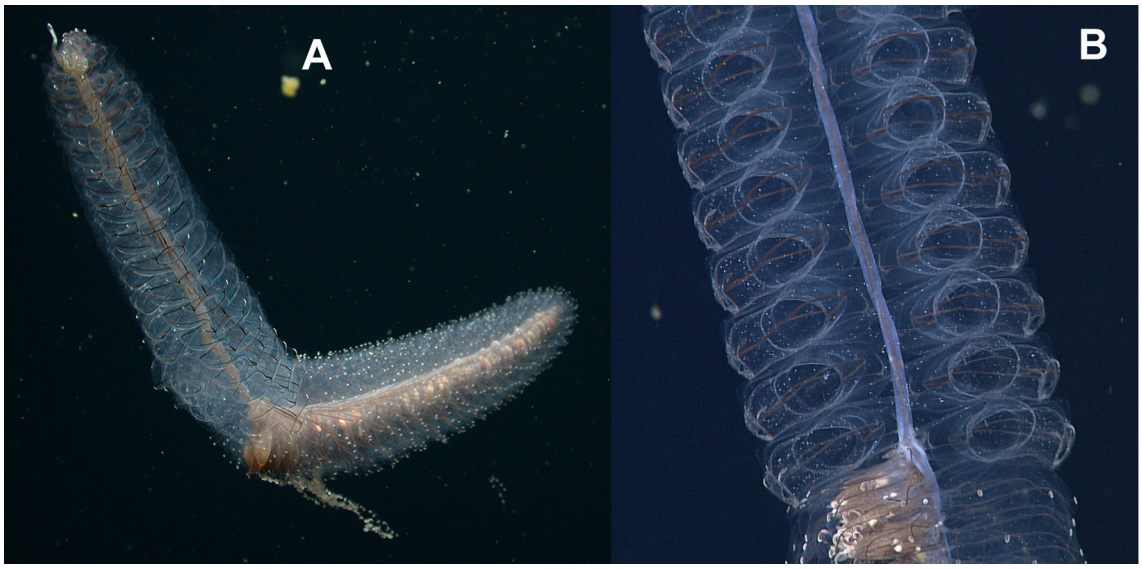


FIGURE 9. *Erenna laciniata* Pugh, 2001. **A**. *In situ* photograph of specimen from *Tiburon* Dive 534 at 1173 m. **B**. Detail of the nectosome of the specimen from *Doc Ricketts* Dive 339. MBARI.

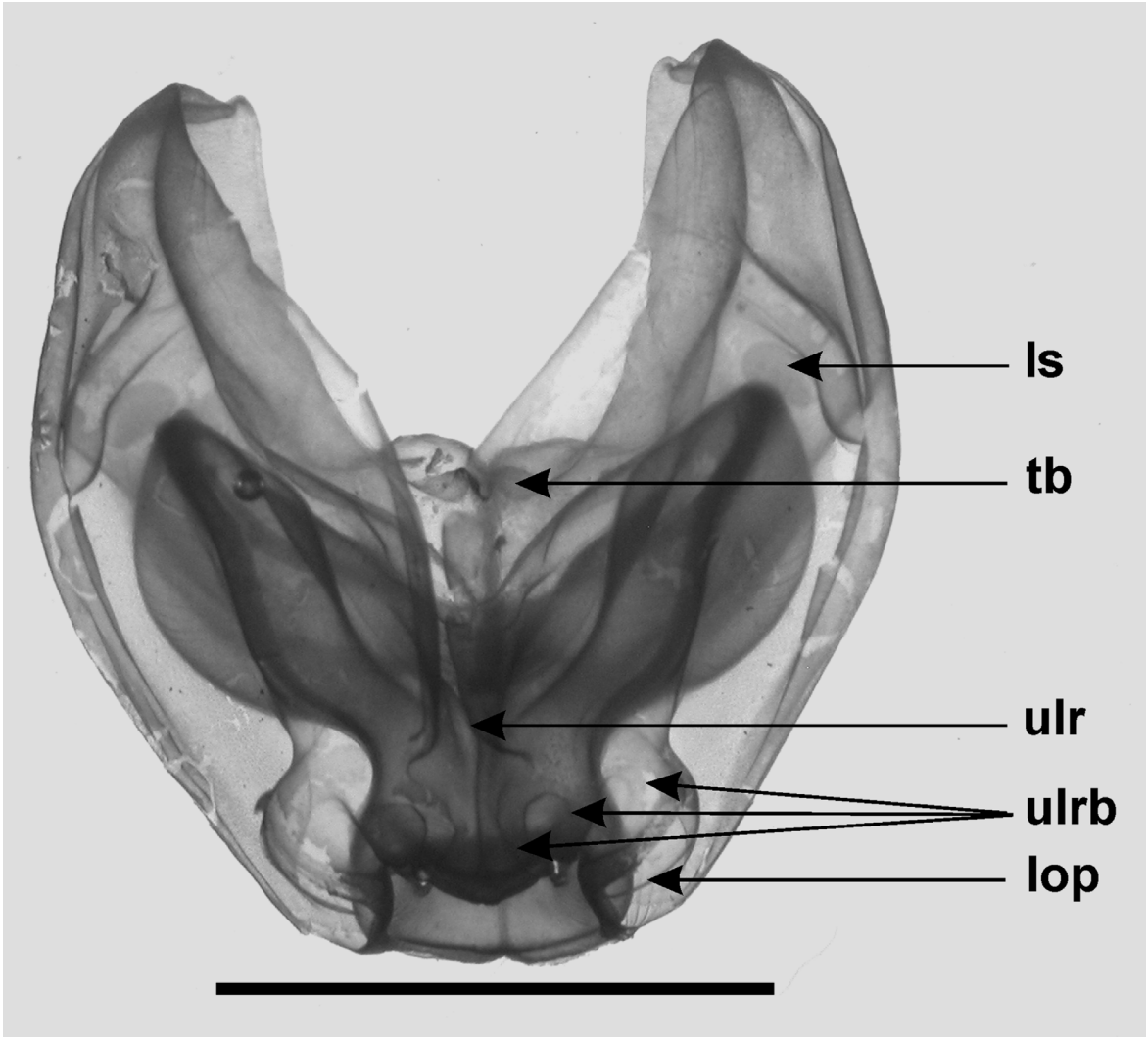


FIGURE 10. *Erenna laciniata* Pugh, 2001. Upper view of very young nectophore. **lop**: lateral ostial process; **ls**: lateral spot; **tb**: thrust block; **ulr**: upper lateral ridge; **ulrb**: distal branches of the upper lateral ridge. Scale bar 5 mm.

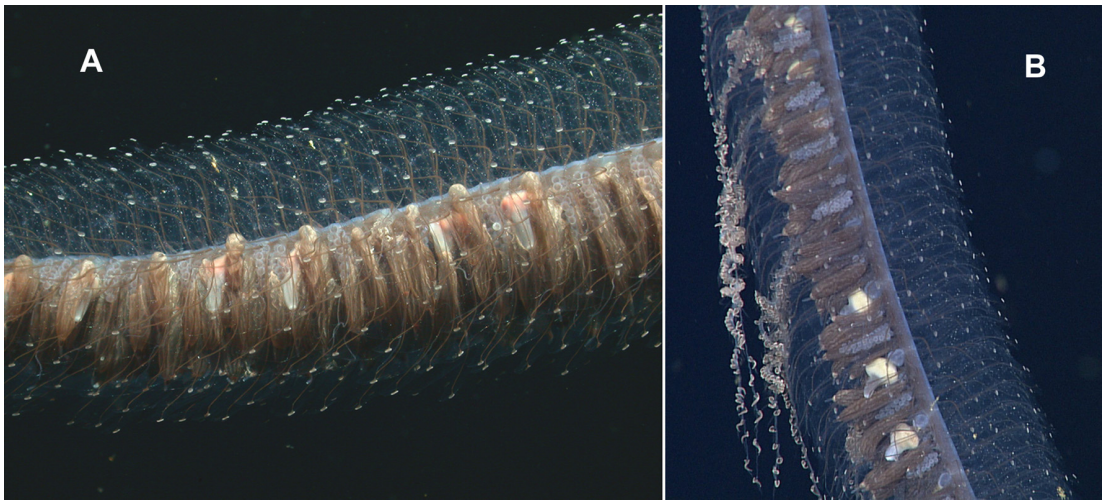


FIGURE 11. *Erenna laciniata* Pugh, 2001. *In situ* photographs of siphosome of female specimen from **A**. *Tiburon* Dive 534 and **B**. male specimen from *Doc Ricketts* Dive 339. MBARI.

FIGURE 12. *Erenna laciniata* Pugh, 2001. Part of siphosome of specimen photographed *in situ* during *Tiburon* Dive 983. See text for details. MBARI.

Nectosome: Figure 9B shows a close up of the nectosome, and the anterior portion of the siphosome, of the *Doc Ricketts* Dive 339 specimen photographed *in situ*. The pigmentation in the radial canals of the nectophores and the central gastrovascular cavity can clearly been seen, and it is also present in the canals of the bracts. Small white dots were present on the nectophores and also on the bracts. For the nectophores the majority of these were found randomly distributed on the muscular walls of the nectosac. They were round or ovoid and totally amorphous, and measured between 110 and 165 µm in diameter. Other, smaller spots, c. 90 µm in diameter, were found on the external surfaces of the nectophores and bracts, but they were far less common. The function of these spots is unknown.

Nectophores: The nectophores of the new material were slightly larger than those of the type specimen, with the *Doc Ricketts* Dive 334 ones averaging 30 mm in length and 33 mm in width, with a maximum of 33 x 39 respectively. The division of the upper lateral ridges close to the ostium was confirmed, particularly for the younger nectophores (Figure 10), whereas in the mature ones it was very vague. There appeared to be three pairs of broad branches, forming the letter "m", although the outermost one, which formed part of the lateral ostial process, was often very vague The extensive lateral ostial processes originally possessed nematocysts but by the time the nectophores were mature they had largely disappeared, either through abrasion or usage. The large lateral patches of ectodermal cells, just distal to the vertical lateral ridges, were not very distinct at this early stage of development

(Figure 10). As with other *Erenna* species, there appeared to be a black-pigmented canal through the centre of the lateral ostial process and connecting with the ostial ring canal at the same level as the lateral radial canals.

Siphosome: Figure 11 shows a close up of the *in situ* siphosome of the specimens observed during *Tiburon* Dive 534 and *Doc Ricketts* Dive 339. The black-pigmented canals of the bracts, ending in the circular white patches of nematocysts can clearly be seen. The structure of the two types of bract was sufficiently described by Pugh (2001) and nothing more needs be added here.

Gastrozooid: The *in situ* photographs (Figure 11) clearly show some gastrozooids. The distal proboscis region was pellucid and, on one specimen (Figure 11A) continued imperceptibly into the stomach, while in the other (Figure 11B) the stomach region was inflated and whitish yellow in colour. In the former the basigaster had a distinct pinkish colour, while for the other it was translucent. In the preserved state the basigaster was found to have two lateral lobes that were nowhere near as prominent as those of *Erenna richardi*.

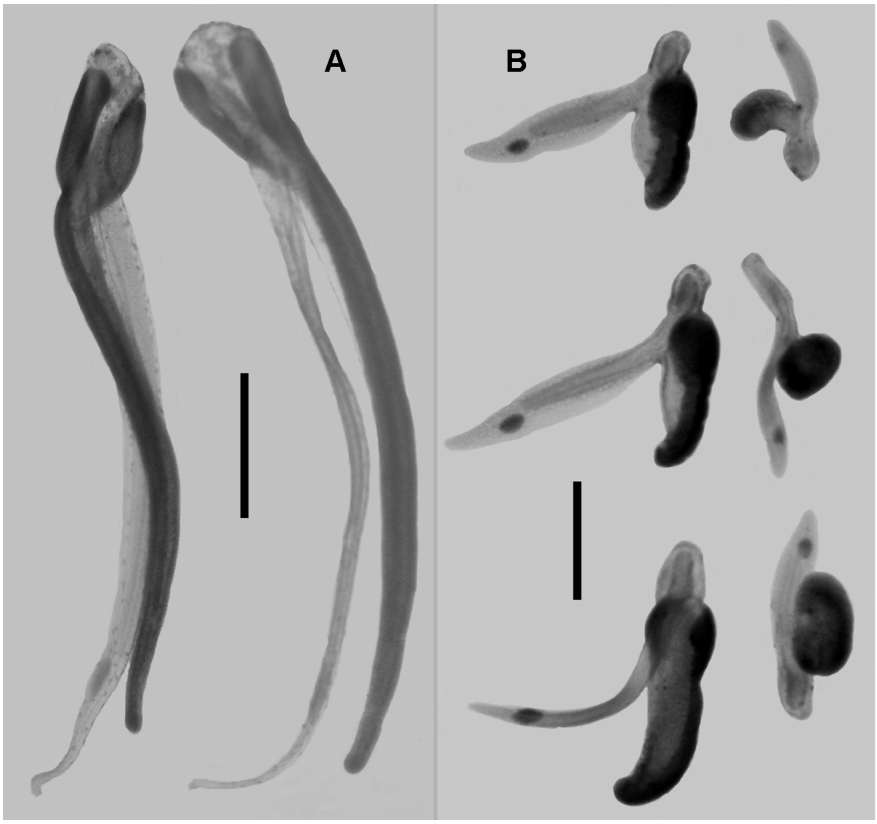


FIGURE 13. A. Mature tentilla; **B**. stages in the development of the tentillum of *Erenna laciniata* Pugh, 2001`. Scale bar 1 mm.

Tentacle and Tentilla: The *in situ* photographs often showed *Erenna laciniata* with several tentacles extended to considerable lengths and bearing small side branches that could look like a string of beads. However, on one specimen (Figure 12) the distal part of the tentacle was contracted, while the proximal part remained relaxed, with the young tentilla spaced apart. A much more pronounced manifestation of this character will be described for one of the new *Erenna* species.

The relatively small size of the tentilla can clearly been seen in Figure 12, and photographs of mature tentilla are shown in Figure 13A. The cnidoband was characteristically forked at its proximal end and encased either side of a vacuolated tissue that arose from the pedicle of the tentillum. At the point where the cnidoband forked it separated from this spongy tissue, which then formed a long, narrow tube that extended further than the cnidoband itself. Towards its distal end there was a pair of small photophores filled with calcium-activated proteins. In the shipboard laboratory these tubular processes were seen to wriggle and writhe in an apparently uncoordinated manner quite unlike the coordinated "squid jigging" movements performed by one of the new *Erenna* species (Haddock *et al*, 2005). Nevertheless, they no doubt were acting as lures. The *Doc Ricketts* Dive 334 specimen possessed only immature tentilla and a series of developmental stages in shown in Figure 13B. In general the

cnidoband and the tubular process increased in size concomitantly, and the photophores were more obvious than on the mature tentillum.

Pugh (2001) noted the presence of the three usual types of nematocysts, with large anisorhizas, which measured c. 128 x 27 µm, arranged along the lateral margins of the cnidoband. Between them were numerous smaller nematocysts of two shapes with the more cylindrical ones measuring c. 40 x 15 µm and the more ovoid ones c. 32 x 18 µm. No further investigations were carried out on the present material.

Palpon: The palpons of the new material were investigated for the presence of nematocysts, as Pugh (2001) had only noted that they were absent on the palpacles. It was found that there was a serried ring of 20–30 nematocysts surrounding the distal mouth opening. These nematocysts measured c. 98 x 27 µm.

Gonophore: No mature gonophores were found with the new material, although they can clearly be seen on the aforementioned *in situ* photographs.

ROV	Dive	Date	Position	Depth (m)	T°C
Tiburon	534	16 March 2003	27°00.74'N 111°24.43'W	1171	3.69
Tiburon	541	24 March 2003	24°19.01'N 109°11.99'W	1339	3.36
Tiburon	546	30 March 2003	26°11.01'N 110°35.98'W	1242	3.59
Ventana	**2570**	**13 September 2004**	**36°41.85'N 122°32.46'W**	**289**	**8.16**
Tiburon	983	13 May 2006	35°37.99N 122°43.98'W	1341	3.02
Tiburon	998	22 June 2006	36°20.46'N 122°54.99'W	1462	2.96
Ventana	3194	22 April 2008	36°42.01'N 122°03.13'W	1010	3.96
Doc Ricketts	336	18 February 2012	24°12.72'N 109°38.36W	1207	3.84
Doc Ricketts	336	18 February 2012	24°12.72'N 109°38.36W	1303	3.52
Doc Ricketts	337	20 February 2012	23°33.49'N 106°46.99'W	1255	3.71
Doc Ricketts	339	21 February 2012	23°33.49'N 106°46.99'W	1581	2.91
Doc Ricketts	339	21 February 2012	23°33.49'N 106°46.99'W	1419	3.17
Doc Ricketts	339	21 February 2012	23°33.49'N 106°46.99'W	1313	3.40
Doc Ricketts	341	23 February 2012	24°18.90'N 109°11.95'W	1333	3.34
Doc Ricketts	**344**	**26 February 2012**	**24°30.33'N 108°14.52'W**	**1144**	**4.00**
Doc Ricketts	494	11 July 2013	35°59.92'N 122°24.98'W	1149	3.53
Doc Ricketts	553	21 November 2013	36°04.12'N 122°17.77'W	1261	3.21
Doc Ricketts	605	2 May 2014	36°43.04'N 122°00.79'W	776	4.76
Doc Ricketts	**663**	**16 September 2014**	**36°35.99'N 122°09'W**	**1242**	
Doc Ricketts	718	2 March 2015	24°24.76'N 109°03.85'W	1538	3.08
Doc Ricketts	**722**	**8 March 2015**	**27°27.0'N 109°50.99'W**	**1517**	**3.03**
Doc Ricketts	724	10 March 2015	24°19'N 109°12'W	1463	3.01
Doc Ricketts	725	11 March 2015	23°37'N 108°45'W	1073	3.92
Doc Ricketts	725	11 March 2015	23°37'N 108°45'W	1470	2.97
Doc Ricketts	725	11 March 2015	23°37'N 108°45'W	1407	3.16
Doc Ricketts	727	13 March 2015	22°55'N 108°07.00'W	1204	3.73
Doc Ricketts	727	13 March 2015	22°55'N 108°07.00'W	1081	4.15
Doc Ricketts	729	15 March 2015	24°10.99'N 109°37.99'W	1355	3.42
Doc Ricketts	780	14 July 2015	36°08.98'N 124°17.13'W	1291	3.12
Doc Ricketts	792	11 August 2015	36°32.10'N 122°35.24'W	1400	2.98

Distribution. The original specimens, as described by Pugh (2001) came from the Dry Tortugas (JSL1454 – type) and The Bahamas (JSL1688) at depths of 811 and 853 m, respectively. Some additional material may have come from the *Discovery* collections on the equator (800–900 m) and 3°N (0–1000m oblique). The only other

published records are from Sagami Bay, Japan (Kitamura *et al*., 2008; Lindsay & Miyake, 2009). The former authors included a typical *in situ* photograph of a specimen and a picture of a mature tentillum. The specimens were collected, or observed, between 690 and 860 m. We also list below the specimens of *Erenna laciniata* that have either been identified from *in situ* photographs or collected (emboldened) by the MBARI ROVs in recent years.

Thirty specimens of *Erenna laciniata*, six of which were collected, have been identified from the MBARI database of *in situ* photographs. They were observed in two main localities: Monterey Bay (MB—10 specimens) and the Gulf of California (GOC—20 specimens). For MB the mean depth for the specimens was 1145 ± 620.1 m; the result, however, being heavily skewed by one specimen (*Ventana* 2570) that was found at the unusually shallow depth of 289 m. If this specimen was excluded, then the mean depth becomes 1230 ± 75.7 m. For the GOC specimens it was 1320 ± 149.5 m. Thus, in general the Monterey Bay specimens existed at shallower depths than those in the Gulf of California, as one might expect if their depth distribution was related to water temperature. Indeed, the temperatures at these depths were 3.4 ± 0.7°C for MB (excluding the *Ventana* Dive 2570 specimen), and at GOC it was 3.5 ± 0.4°C. As the 20 specimens of *E. laciniata* from the Gulf of California were collected during just three cruises, while there have been at least an order of magnitude more cruises in the vicinity of Monterey Bay, then this would indicate that the species is much commoner in warmer fish-replete waters.

Erenna cornuta Pugh, 2001

Diagnosis. Nectophores with apico-laterals not dividing close to ostium and very weakly expressed in distal half. 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. Two types of bract both with weak transverse ridge and asymmetric pair of lateral cusps. One type with characteristic elongated ectodermal process at distal end of bract, on upper surface. Three types of tentilla; the most abundant and largest one with nematocysts, on the long cnidoband, separated into bundles, and a spherical terminal process containing a pair of photophores and a red-pigmented spot.

Material examined. Pugh's (2001) description of *Erenna cornuta* was based on a single specimen that, as will be shown, appeared to be immature. Eight further colonies, together with a fragment, have been captured by the MBARI ROVs and we have been able to study six of these, as listed below.

ROV	Dive	Date	Position	Depth (m)	T°C
Ventana	1402	8 May 1998	36°41.83'N 122°01.87'W	833	4.15
Tiburon	412-D3	23 March 2002	36°36.20'N 122°22.62'W	1673	2.47
Tiburon	964-D4	7 April 2006	36°19.78'N 122°54.02'W	1392	2.92
Tiburon	1039-D3	30 September 2006	34°17.65'N 124°03.09'W	1328	3..25
Tiburon	1039-SS11	30 September 2006	34°17.66'N 124°03.94'W	1325	3.28
Tiburon	1155-SS2	1 December 2007	35°42.24'N 122° 34.75'W	1629	

Description. Colonies of *Erenna cornuta* can instantly be recognized *in situ* by the long streak of ectodermal cells on the distal ends of the bracts (Figure 14).

Pneumatophore: c. 1.5 x 1 mm, with no pigmentation.

Nectophores: A close-up of the *in situ* nectosome (Figure 15A) showed that the white lateral ostial processes are a prominent feature as was the black pigmentation in the ostial ring canal. It was also present in the radial canals, but this was not apparent from the photograph. It may be that the prominent white lateral ostial processes are another character that distinguishes this species *in situ*, as for the other species they were generally less obvious, except for *Erenna laciniata* (see Figure 9B) where the proximal part is black, but with a distinct white distal portion.

The type material included two developing and 13 larger nectophores that measured up to 16 mm in length, 14 mm in width and 4 mm in depth. This, as with other characters discussed below, seems to indicate that the colony was quite young as the mature nectophores from the *Tiburon* Dive 1155 specimen averaged 32 mm in length and

width, with a maximum of 35 by 33 mm, respectively. Four very young nectophores, four developing and 27 mature ones from that specimen were preserved.

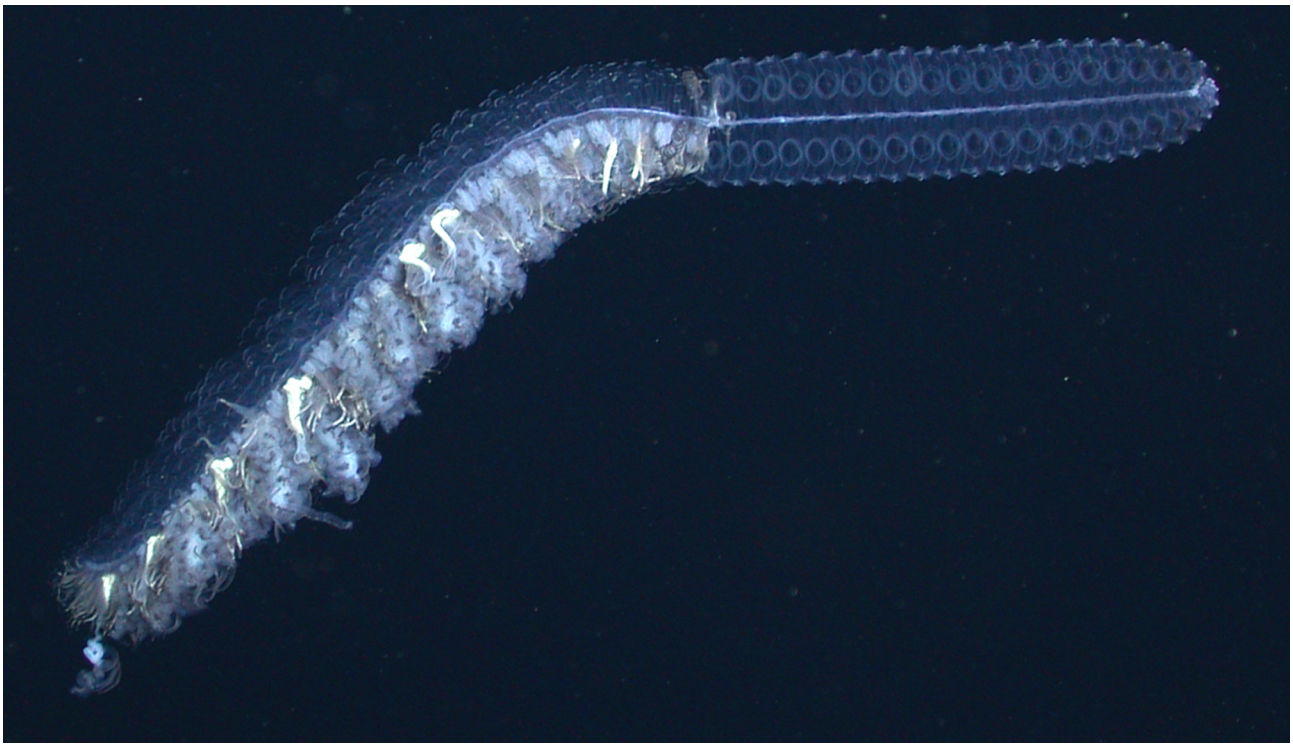


FIGURE 14. *In situ* photograph of *Erenna cornuta* taken during *Tiburon* Dive 1155 at 1628m. MBARI.

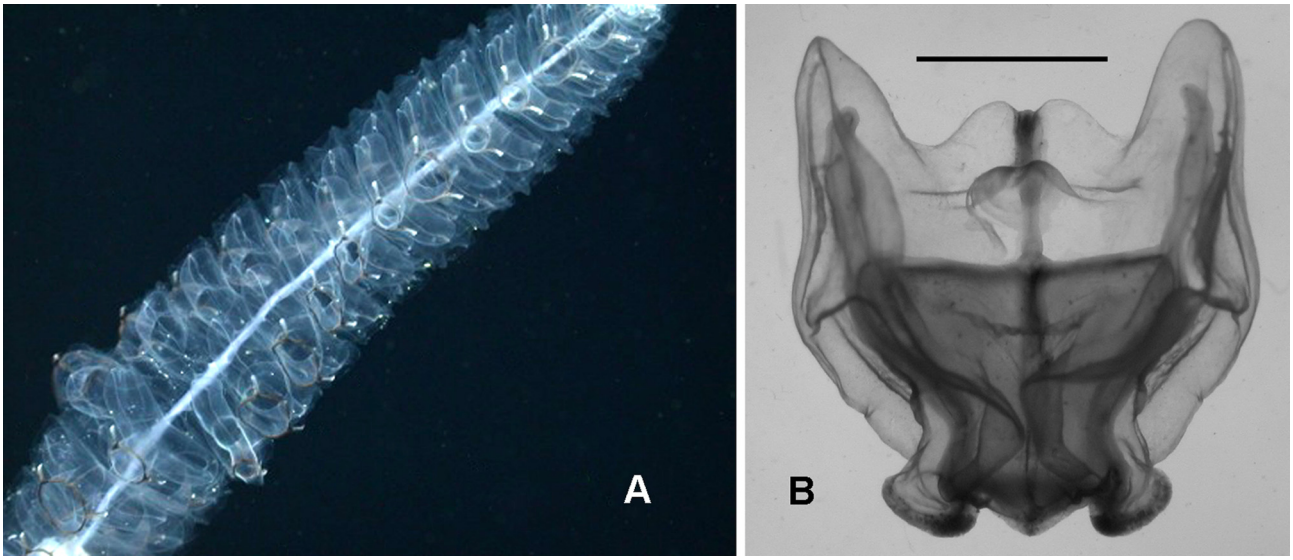


FIGURE 15. *Erenna cornuta* Pugh, 2001. **A**. Detail of nectosome MBARI.; **B**. young nectophore from *Tiburon* Dive 1155-SS2 specimen. Scale bar 1 mm.

The arrangement of the ridges on the youngest nectophores (Figure 15B) was somewhat different from the fully mature ones. Neither the upper or lower lateral ridges reached to the ostium, and the upper ones closely approached each other distally, then diverged laterally and petered out. Although they appear to do so in the photograph, the vertical lateral ridges did not join with the upper laterals at this stage. The lateral ostial processes were very obvious and were packed with nematocysts, which measured c. 110 x 35 µm. As the discharged ones did not appear to have a shaft it was presumed that they were isorhizas. The processes were penetrated by a canal that arose from the ostial ring canal at the same level as the insertion of the lateral radial canals. The thrust block

formed a small mesogloeal protuberance, slightly emarginated in the mid-line. There was no sign of a muscle-free zone on the nectosac, while the lateral "horn" canals were greatly enlarged and included a broad canal. All the canals were obviously pigmented. The patch of ectodermal cells on the sides of the nectophore just distal to the vertical lateral ridges had yet to appear.

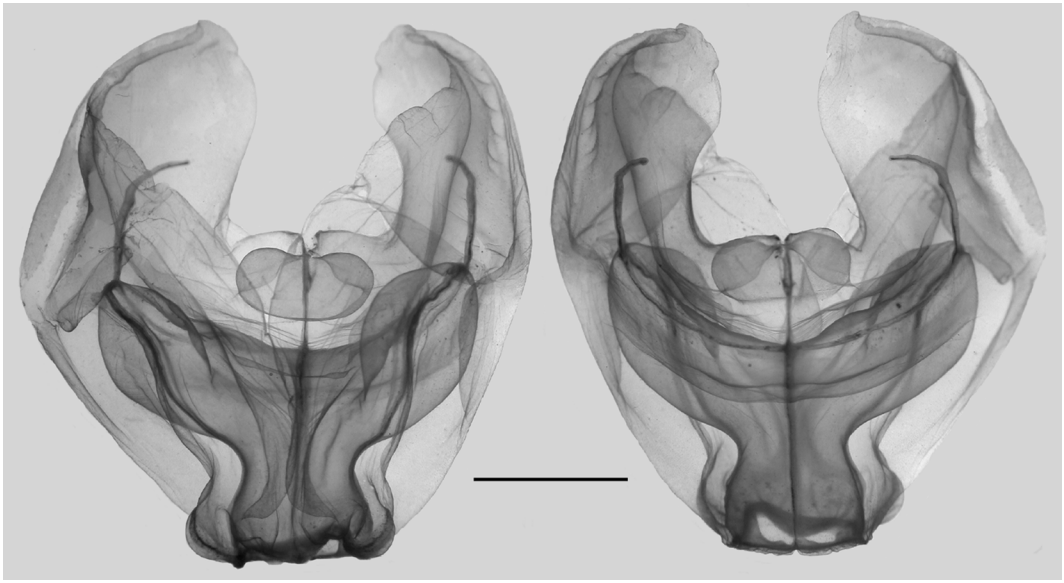


FIGURE 16. Upper (left) and lower (right) views of young nectophore of *Erenna cornuta* Pugh, 2001 from *Tiburon* Dive 1155-SS2. Scale bar 5 mm.

For the slightly larger nectophore shown in Figure 16, the axial wings had greatly increased in size as had the mesogloeal forming the thrust block. The arrangement of the ridges remained much the same, although there was now a weak connection between the vertical and upper lateral ridges. The upper lateral ridges often overlapped each other before they diverged close to the ostium, but that was probably a result of preservation. Unlike *Erenna richardi* these ridges did not divide. The nematocysts on the lateral ostial processes had by now been lost, by abrasion or usage, and so the central canal became more apparent. At this stage the lateral parts of the nectosac extended more proximally than the mid-region, but again this probably was the result of preservation. The lateral "horn" canals had narrowed to a similar diameter as that of the lateral radial canals, but there was still no sign of a muscle-free zone. The lateral photophores also had yet to appear.

The nectophores of *Erenna cornuta* illustrated by Pugh (2001, Figure 12) showed a slightly more advanced stage of development. The proximal halves of the upper lateral ridges now paralleled the lower ones, and formed the upper lateral margins of the nectophores. However, distal to the vertical lateral ridges, they still curved in toward the mid-line, and then down toward the ostium, while rapidly petering out. Often they could only be traced by staining the material. The lower lateral ridges extended down to the lower lateral margins of the ostium. The proximal end of the nectosac was almost flat, and the muscle free zone in that region was quite distinct. The lateral ostial processes remained quite prominent and the pair of lateral photophores appeared just distal to the vertical lateral ridges. In their preserved state they were brown in colour, but would have been black in life.

The new material showed that that was not the final developmental stage. For the largest nectophores (Figure 17) the upper and lower lateral ridges then almost paralleled each other throughout their length and formed the lateral margins of the nectophore. The thrust block had considerably increased in size now formed a very characteristic swollen mesogloeal process on the upper side of the nectophore. It was only attached to the main body of the nectophore by a thin strip of tissue and, thereby, formed a sort of a thickened flap, with a broad but shallow proximal emargination. The nectosac was T-shaped and had a distinct muscle-free area on either side of the proximal parts of the lateral radial canals. The thickened ascending mantle canal arose on the upper side of the nectophore, below the thrust block, and passed through a proximal groove onto the lower side where it gave rise to the narrower pedicular canal. This ran straight to the nectosac and gave rise directly to the lateral radial canals. For the type specimen no pigmentation was noted in the radial canals, but for the *Tiburon* Dive 1155 nectophores dark brown granulations could be seen in all the canals, including the "horn" canals, and particularly in the ostial ring

canal. This pigmentation was probably black in life. No nectophores were observed where the "horn" canals were absent. They usually curved inward proximally, and their walls were often irregular, occasionally with small diverticula.

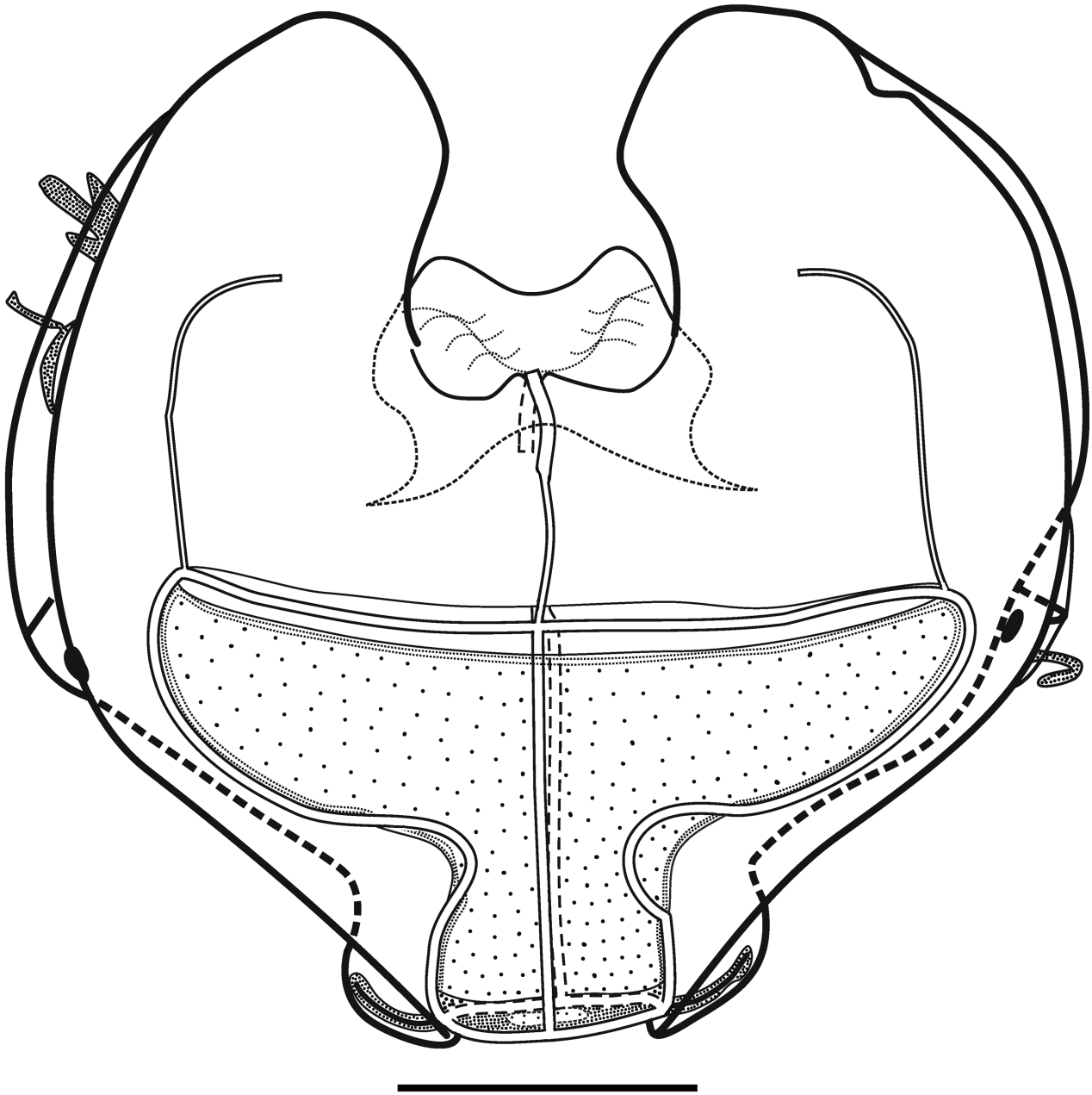


FIGURE 17. Lower view of mature nectophore of *Erenna cornuta* Pugh, 2001. Scale bar 1 cm.

One strange feature of some of the nectophores was the presence, at least in the preserved material, of thickened pieces of tissue that hung off the upper or lower lateral ridges anywhere proximal to the vertical lateral ridges or just distal to them. They appeared to be formed by a thickening of the tissue along the ridge. One end of this thickening then broke free, and gradually the free part lengthened until finally the tissue projected out from the ridge as a sort of digitate process. The size of these processes varied greatly but they could be up to 5 mm in length (Figure 17). At first they were thought to be preservation artefacts but as they were found at all stages of development, and were present on more than half of the mature nectophores of the *Tiburon* Dive 1155 specimen, it was thought that this was something that may have occurred in life, although the reason for doing so remains obscure.

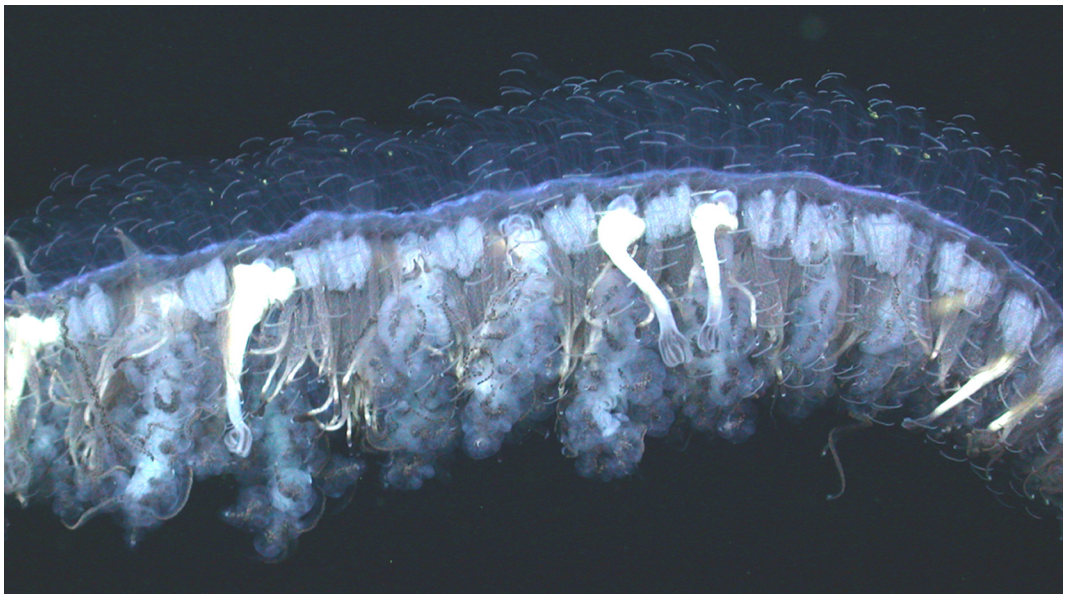


FIGURE 18. Detail of siphosome of *Erenna cornuta* Pugh, 2001 from *Tiburon* Dive 1155. MBARI.

Siphosome: The siphosome of the *Tiburon* Dive 1155 specimen *in situ* is shown in Figure 18 and clearly shows the long, white patches of cells on the upper surfaces of the bracts; the elongated gastrozooids, with their tentacles, and the gonodendral clusters of male gonophores. Because the stems were so highly contracted during preservation, it was not possible to study the organisation of the individual cormidia in detail.

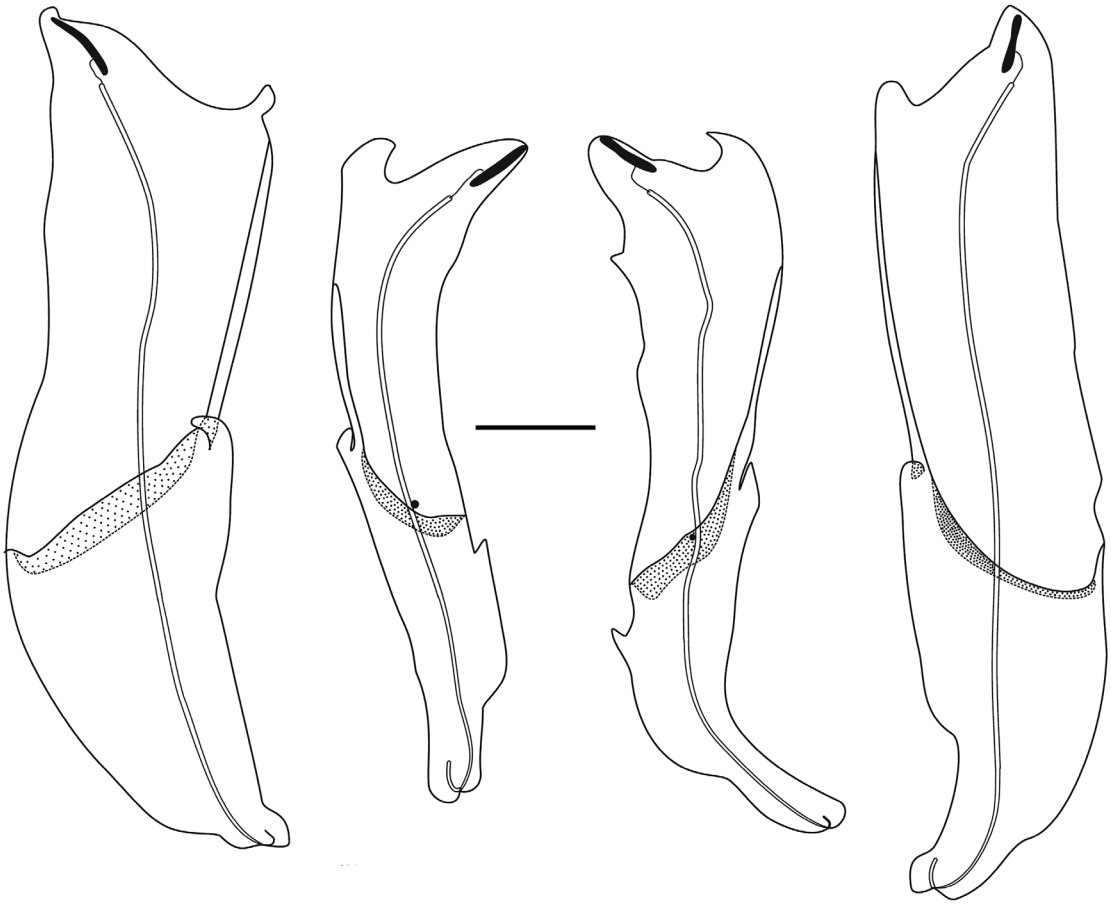


FIGURE 19. *Erenna cornuta* Pugh, 2001. *Type A* bracts. Scale bar 5 mm.

Bracts: As was described for the type material (Pugh, 2001), two types of bract were found with the specimens of *Erenna cornuta*. The longer, *Type A*, bracts of the type specimen measured up to 16 mm in length but, as with the nectophores, the bracts found with the present specimens were considerably larger, reaching more than 40 mm in length (Figure 19). They were also about twice as common as the other type. With this further increase in size the transverse ridge, which had been incomplete in the smaller examples, now became complete. It formed a distinct flap across the bract, and on the inner side it extended distally as a process thickened with mesogloea. The more proximal of the two asymmetrically placed lateral cusps, which were associated with it, disappeared, while the distal one became more prominent, as did the more distal lateral cusp, on the inner side of the bract. The central rounded spot on the upper side just distal to the transverse ridge usually could not be discerned on the largest bracts, but was quite evident on the smaller ones (Pugh, 2001, Figure 15).

The bracteal canal arose on the upper side of the bract and on passing over onto the lower side it gradually increased in diameter up to about one third the length of the bract. It then maintained that diameter until close to its distal end, where it thinned considerably as it penetrated into the mesogloea and ran at first obliquely and then perpendicularly to end below the proximal part of the elongate ectodermal process on the upper side of the bract. The canal might have extended further along beneath this process, but that could not be confirmed with certainty. The elongate distal process gave the bracts a very distinctive appearance that made it easy to identify the specimens *in situ*. Numerous nematocysts, which were anisorhizas measuring c. 130 x 38 µm before discharge but slightly smaller after, were present there.

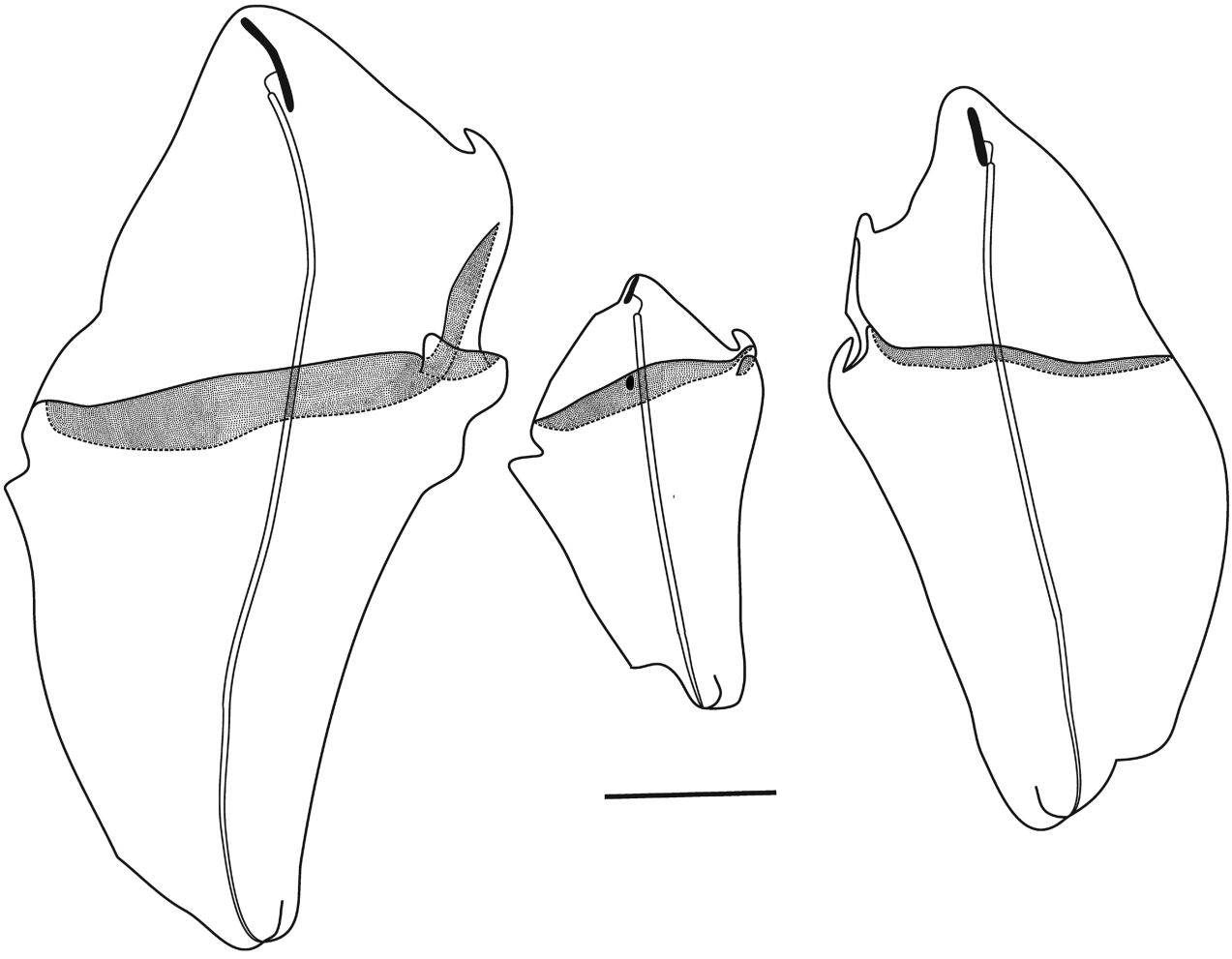


FIGURE 20. *Erenna cornuta* Pugh, 2001. *Type B* bracts. Scale bar 5 mm.

The shorter *Type B* bracts (Figure 20) were also considerably longer those of the type material. The *Tiburon* Dive 1155 ones measured up to 30 mm in length and 15 mm in width. In basic design they were very similar to the *Type A* bracts, except that the transverse ridge lay in the distal half of the bract instead of the proximal one. The

changes, as the bracts enlarged, in this ridge and the associated lateral cusps were very similar to those described for the *Type A* bracts, in that the ridge became complete and one of the cusps, the outer, was lost, while the inner one, and again the more distal lateral cusp, became more distinctive. The arrangement of the bracteal canal was exactly the same. The main change that occurred as the bracts grew was that the distal ectodermal process on the upper side of the bract became elongate, as in the *Type A* bracts. The process, as with the other *Erenna* species, was packed with nematocysts. Similarly, the median photophore, just distal to the transverse ridge, was usually not apparent on the largest bracts.

Gastrozooid: The gastrozooids can clearly be identified on the *in situ* picture (Figure 18), being swollen proximally and a long narrower stomach region, with a translucent distal proboscis region showing numerous longitudinal hepatic stripes. In the preserved state the basigaster was quite prominent and had a yellowish-orange colour.

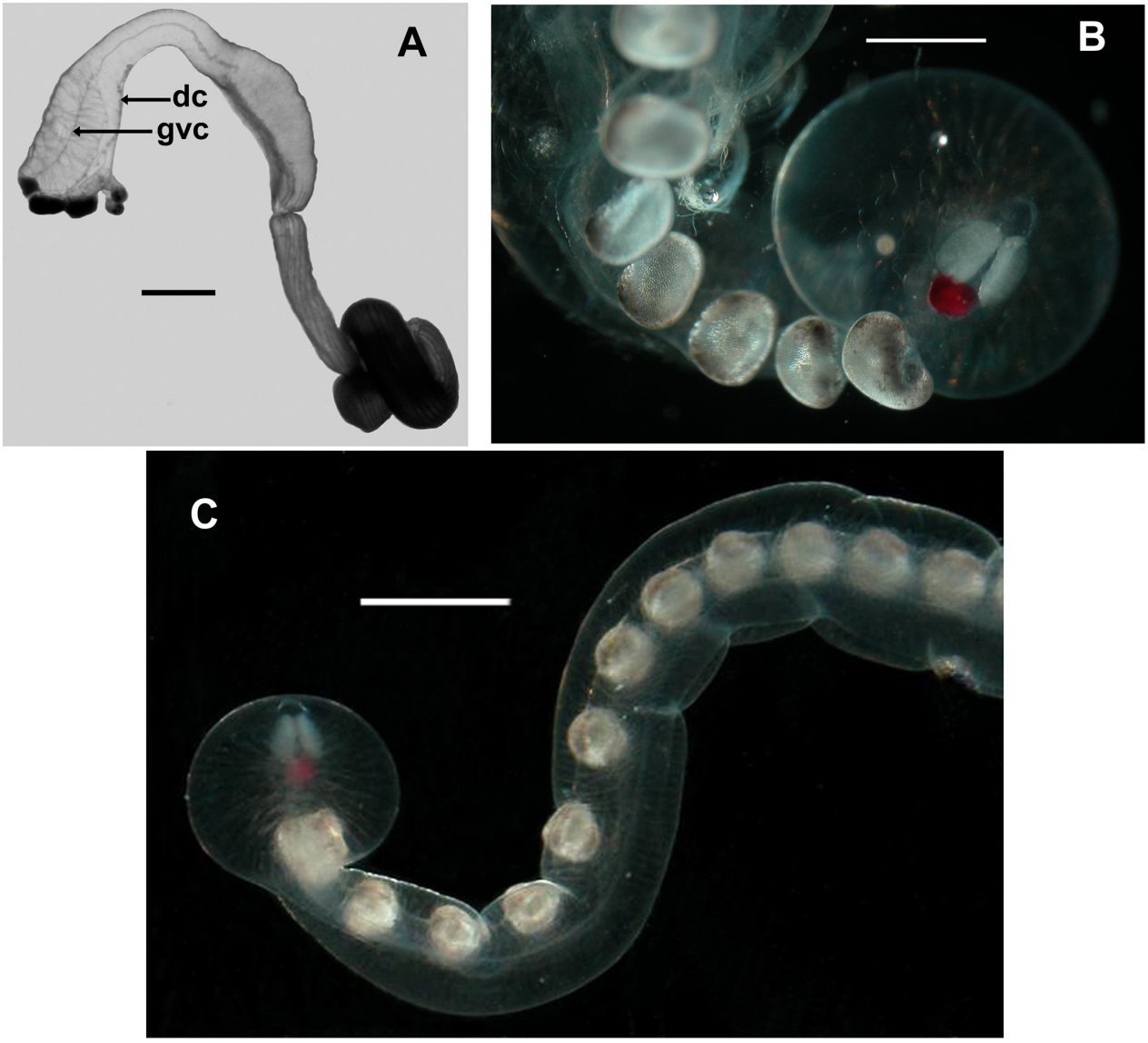


FIGURE 21. *Erenna cornuta* Pugh, 2001. **A**. Tentillum of first type. **dc**: diverticular canal; **gvc**: gastrovascular cavity. Scale bar 1 mm. **B**. Distal end of mature tentillum of second type, from *Tiburon* Dive 964-D4 specimen. Scale bar 1 mm. **C**. Distal part of cnidoband from same specimen. Scale bar 2.5 mm.

Tentilla: On the original holotype specimen Pugh (2001) described what he considered to be two different types of tentillum. However, as noted above, there are several reasons to consider the type specimen as a small, not fully developed colony, and it seems that what he considered to be the young stage of the second type of tentillum (his Figure 8A) actually belongs to a third type.

Pugh (2001) gave a detailed description of the first type of tentillum, which was relatively small, and had the nematocysts concentrated into four sub-terminal patches. This appeared to have been the commoner of the two types that he considered to be present. However, for the six further specimens presently available for examination, this type of tentillum was only found on one specimen, from *Tiburon* Dive 1039, and only three were found. These tentilla (Figure 21A) differed slightly from that originally described in that the tentillum was divided from its pedicle by a distinct annulation, distal to which the gastrovascular cavity at first ran along one side of the tentillum before abruptly moving to the mid-line. In addition there were five, not four, patches of nematocysts, three arranged in a row at the distal end of the tentillum, while the two others formed a lateral pair borne on short stalks. The nematocyst complement was not investigated further. All three of the present tentilla were detached from the tentacle, but Pugh (2001) noted both his types of tentillum were attached to the same tentacle. For the present material both the second and third types of tentillum were similarly attached to the same tentacle. It is not clear, at present, how to reconcile this apparent anomaly as to the general absence of the first type of tentillum from most of the specimens examined, but it is clear that this arrangement is highly unusual. It is unlikely that during development one transforms into another, as is the case for the two types of tentilla of *Resomia* species (Pugh, 2006), and a close examination of a tentacle with several young tentilla still attached showed that the order in which each type of tentillum was developed appeared to have no pattern. However, this phenomenon needs to be investigated further.

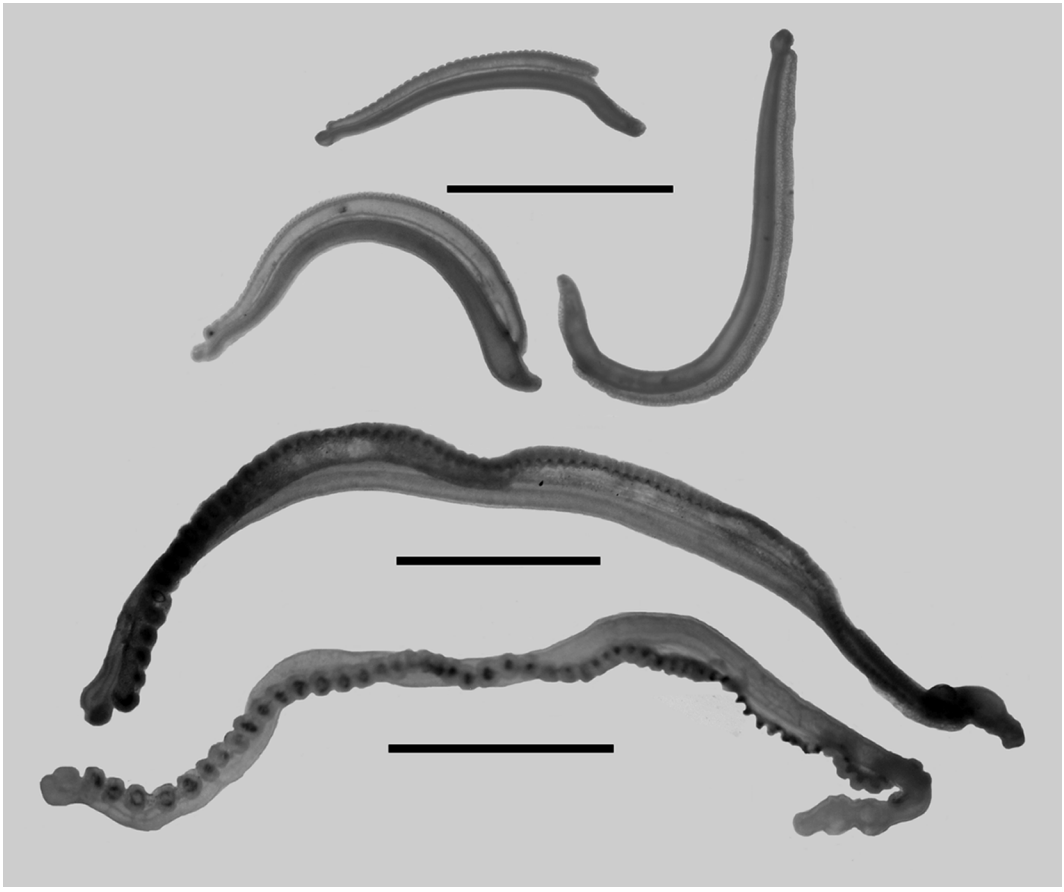


FIGURE 22. Various stages in the development of the Type 2 tentillum of *Erenna cornuta* Pugh, 2001. Scale bars 5 mm.

The holotype specimen only possessed a few mature tentilla of what we here designate as the second form. In these the broad elongate cnidoband was largely filled with large, vacuolated endodermal cells that gave it a sponge-like appearance. Many such tentilla were found with more recent specimens (Figure 21B, C) and were generally much larger. The cnidoband was penetrated by a narrow gastrovascular cavity that distally opened out into a spherical vesicle. Within this vesicle there were two photophores and a red-pigmented sphere (Figure 21B). The nematocysts were grouped into distinct domed patches along one side of the cnidoband, and as each patch was more transparent centrally, it took on the appearance of a sucker on a cephalopod tentacle. Pugh (2001) noted only

a few "mature" tentilla of this type that possessed up to 17 of these nematocyst patches. However, during an initial examination of the specimen collected during *Doc Ricketts* Dive 32, before preservation, it was noted that one tentillum had 172 of these patches arranged along the cnidoband that extended to 15 cm in length. Again this exemplified that the holotype specimen was not fully mature.

Figure 22 shows some stages in the development of the second type of tentillum of *Erenna cornuta*. At early stages the tentillum was basically a narrow tube overlain on one side, and for the most part, by the undifferentiated cnidoband. As the latter differentiated the nematocysts became grouped into distinct rounded patches, although they were tightly packed together to begin with. Towards maturity the main body of the tentillum expanded as it was filled by the spongy material surrounding the gastrovascular cavity, and the two photophores became apparent in the spherical terminal process. Unlike the other types of tentilla, there was no sign of a distal diverticular canal.

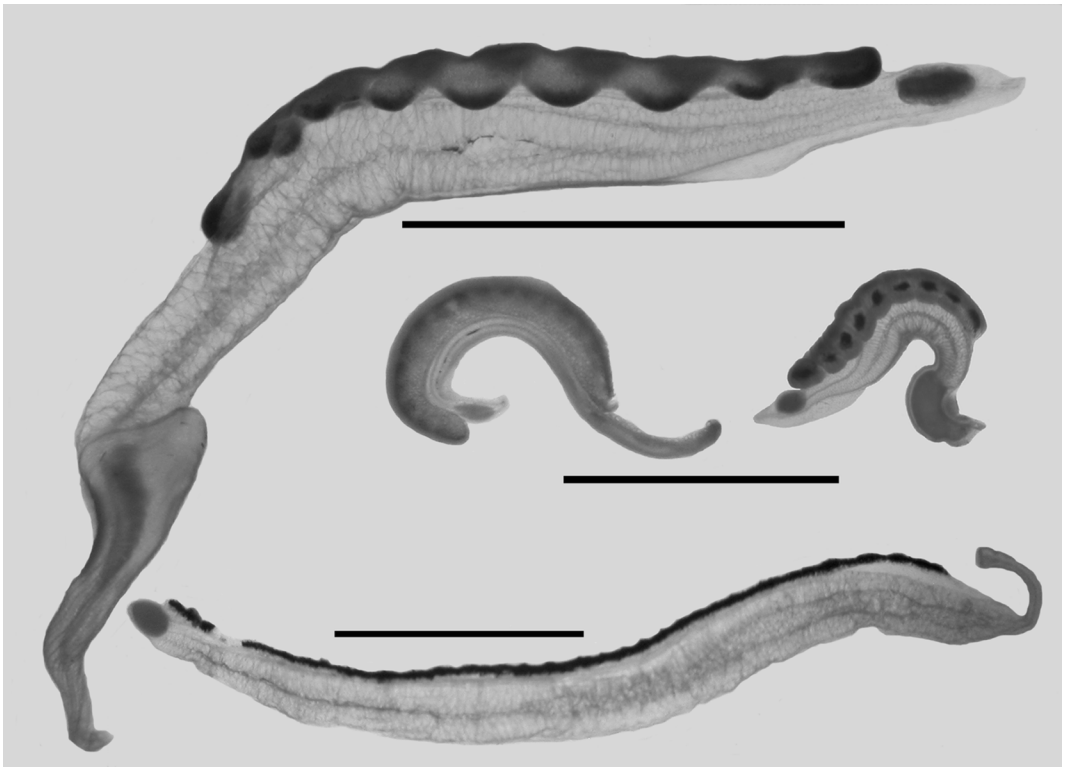


FIGURE 23. Various stages in the development of the Type 3 tentillum of *Erenna cornuta* Pugh, 2001. Scale bars 5 mm.

Stages in the development of the third type the nematocysts are shown in Figure 23. For this type, once the cnidoband has differentiated, it always formed a single patch along most of the length of the tentillum and, at its most extensive, had undulating lateral margins (Figure 23, top). The large photophores were apparent from a very early stage in the short, pointed terminal process. In life this process was observed to flick from side to side at regular intervals. The main body of the tentillum was filled with spongy material with the gastrovascular cavity running through it. This ran to almost the tip of the terminal process and gave off a diverticular canal that then ran proximally below the cnidoband to about half its length (Figure 23, top). The cnidoband of the fully developed third type of tentillum (Figure 23, bottom) appeared to be greatly reduced but, in actuality and probably during preservation, the cnidoband itself had become stripped from the tentillum leaving just a small ridge of black material. Concomitant with this stripping off, most of the nematocysts of one type in the cnidoband discharged so that the cnidoband then appeared as a fuzzy mat and these were frequently found loose in the preserved material.

The nematocysts from one of these mats of tissue were examined and found to include the three types of nematocyst that had been found in the cnidobands of other *Erenna* species. The largest measured up to 172 x 42 µm (Figure 24A), and so were somewhat larger than those found with the type specimen, namely c. 130 x 35 µm. They were the only ones that were found to have discharged and were presumed to be microbasic mastigophores. The nematocysts shown in Figure 24B were by far the most numerous and measured c. 45 x 20 µm, while the third type (Figure 24C), measuring c. 38 x 12 µm, was relatively rare. These sizes were similar to those found for the

holotype specimen. Although no discharged ones of these types were found they were presumed to be the same pear-shaped and cylindrical ones observed in other species.

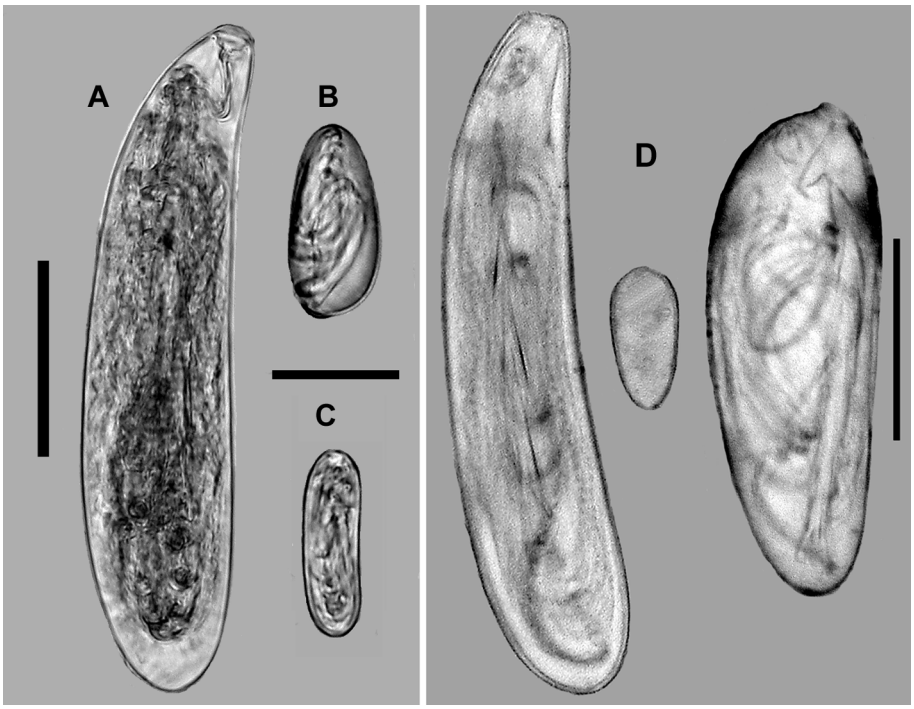


FIGURE 24. *Erenna cornuta* Pugh, 2001. **A–C**. Nematocysts from the cnidoband of the type 3 tentillum. **D**. Three types of nematocysts found on the proboscis region of the palpon. Scale bars A. & D. 50 µm; B, C, 25 µm.

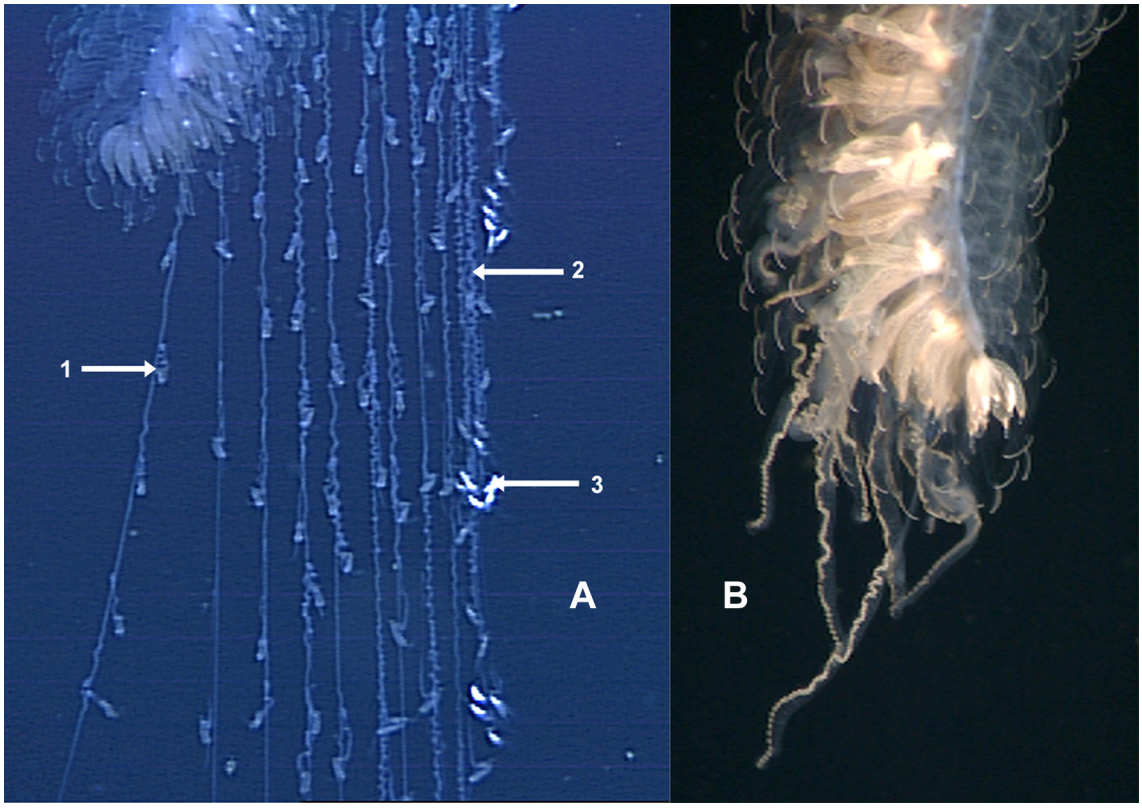


FIGURE 25. A. *In situ* frame grab showing some tentacles of *Erenna cornuta* Pugh, 2001 from *Tiburon* Dive 333. See text for details. **B**. *In situ* frame grab of posterior end of *Tiburon* Dive 1155 colony, showing the extremely long type 2 tentilla. MBARI.

One of the *in situ* frame grabs taken during *Tiburon* Dive 333 of a colony of *Erenna cornuta* is shown in Figure 25 (left). The characteristic long distal patches on the upper sides of the bracts can clearly be seen as can, with close inspection, the three types of tentilla on the tentacles. The small Type 1 ones appeared to be more common on the posterior-most tentacles, being supplemented by the long irregular type 2 ones more anteriorly and then by the type 3 ones with the distal "ocelli" clearly showing up as white spots. On the other hand the *Tiburon* Dive 1155 colony showed the total dominance of the type 2 tentilla that reached extraordinary lengths (Figure 25 right).

Palpon: The palpons of the *Tiburon* Dive 1155 specimen were also much larger than those of the type specimen, measuring up to 19 mm long and 7 mm in diameter. They consisted of a very short pedicle to which a short palpacle was attached; an inflated stomach region the internal walls of which were covered with irregular patches of gastrodermal cells; and a short proboscis. The ring of pigmented spots of gastrodermal cells found in the smaller palpons of the type specimen at the proximal end of the proboscis had coalesced into a solid darkly pigmented region. No nematocysts were found on the palpacles, but at least three different types (Figure 24D) were found to be present in the proboscis region. The two larger types were by far the most common, but as well as the smallest, whose contents appeared to be completely transparent, a few very small nematocyst, 14 x 10 µm, were occasionally observed. What type any of them were was not ascertained as no discharged ones were found.

Gonophore: For all the specimens examined no mature gonodendra were found, although some minute, very immature ones were found with the *Tiburon* Dive 1155-SS2 specimen that were too young to sex.

Distribution. Including the material examined, the following specimens have been either identified from *in situ* frame grabs or collected (emboldened).

ROV	Dive	Date	Position	Depth (m)	T°C
Ventana	**1402**	**8 May 1998**	**36°41.83'N 122°01.87'W**	**833**	**4.15**
Tiburon	333	16 July 2001	36°19.49'N 122°54.04'W	1830	2.28
Tiburon	412-D3	23 March 2002	36°36.20'N 122°22.62'W	1673	2.47
Tiburon	479	23 September 2002	36°20.19'N 122°54.47'W	1483	2.81
Tiburon	480	24 September 2002	36°34.53'N 122°31.38'W	464	6.323
Tiburon	514	23 November 2002	36°34.29'N 122°31.36'W	1381	3.09
Ventana	2394	1 July 2003	36°41.91'N 122°02.93'W	995	3.87
Ventana	2572	15 September 2004	36°42.47'N 122°04.11'W	1060	3.91
Tiburon	543	26 March 2005	23°37.73'N 108°46.99'W	1340	3.17
Tiburon	**964-D4**	**7 April 2006**	**36°19.78'N 122°54.02'W**	**1392**	**2.92**
Tiburon	964	7 April 2006	36°19.78'N 122°54.02'W	1320	3.02
Tiburon	965	8 April 2006	36°34.35'N 122°31.25'W	1526	2.77
Tiburon	**1039-D3**	**30 September 2006**	**34°17.65'N 124°03.09'W**	**1334**	**3.25**
Tiburon	**1039-SS11**	**30 September 2006**	**34°17.66'N 124°03.94'W**	**1324**	**3.28**
Tiburon	**1106-D1**	**28 July 2007**	**36°07.00'N 123°38.00'W**	**1608**	**2.61**
Tiburon	**1109-D3**	**31 July 2007**	**35°50.00'N 122°40.00'W**	**1766**	**2.44**
Tiburon	1115	9 August 2007	36°19.87'N 122°56.02'W	1567	2.76
Tiburon	1152	6 November 2007	36°38.09'N 122°08.98'W	1282	3.07
Tiburon	1152	6 November 2007	36°38.09'N 122°08.98'W	1366	2.91
Tiburon	1155	1 December 2007	35°42.24'N 122° 34.75'W	1542	2.63
Tiburon	**1155-SS2**	**1 December 2007**	**35°42.24'N 122° 34.75'W**	**1629**	**2.55**
Doc Ricketts	**32-SS9**	**31 May 2009**	**36°15.00'N 123°10.00'W**	**1715**	**2.56**
Doc Ricketts	310	2 November 2011	36°33.01'N 122°30.10'W	1407	2.85
Doc Ricketts	326	3 December 2011	36°04.27'N 122°16.98'W	1396	2.85
Doc Ricketts	343	25 February 2012	24°21.71'N 109°15.34'W	1418	3.32
Doc Ricketts	**725**	**11March 2015**	**23°37'N 108°45'W**	**1590**	**2.87**
Doc Ricketts	725	11March 2015	23°37'N 108°45'W	1323	3.27
Doc Ricketts	**728**	**14 March 2015**	**23°41.5'N 108°49'W**	**1419**	**3.20**
Doc Ricketts	728	14 March 2015	23°41.5'N 108°49'W	1404	3.22

All but six of these specimens of *Erenna cornuta* were seen or collected in a very small area in Monterey Bay, California and, as with other *Erenna* species, over a relatively narrow depth range of 833 to 1830 m, mean 1426 ± 207.3 m; ignoring the one anomalously shallow value. The mean temperature was 2.9 ± 0.16°C. In the 1000–1500 m depth range *E. cornuta* co-occurred with both *E. richardi* and *E. laciniata*, but it was easily distinguished from them by the long patch of cells at the distal end of the bracts. The six specimens from the Gulf of California came from similar depths, mean 1438 ± 105.8 m, with a mean temperature of 3.17 ± 0.16°C.

The type specimen came from off the Dry Tortugas, in the Gulf of Mexico at a depth of 896 m. As previously reported (Pugh, 2001) four specimens have been found in the *Discovery* collections, two at 30°N, 23°W between 1250–1500 and 1500–2000 m, and two from off Bermuda (c. 31°45'N, 63°45'W) at depths of 1250–1500 m. In addition, Totton (1965) mentioned a specimen with horns collected at *Discovery* St. 4255 from a depth of 1000 m (between 36°31'N, 11°24'W and 36°22'N, 11°15'30"W, to the west of the Straits of Gibraltar). Thus, it is probable that this rare species has a worldwide distribution, but it has not yet been found off Japan although its sister species *E. laciniata* has (Dhugal Lindsay, personal communication).

Erenna insidiator sp. nov.

Diagnosis. Nectophores basic erennid ridge pattern. The upper laterals do not divide nor extend as far as the ostium. Two types of bract, both with pair of lateral cusps in proximal half; larger ones with rectangular distal ectodermal process on upper side, containing nematocysts. Very characteristic tentilla, consisting of a long pedicle and a long tube mostly filled with spongy tissue through which passes the endodermal canal. The tube tapered distally and there enclosing a photophore. Cnidoband itself forms the corrugated outer perimeter on a distinct process from the outside of the distal part of the cylinder.

Material examined. Only two colonies of *Erenna insidiator* **sp. nov.** are known to have been collected and their station data are given here.

ROV	Dive	Date	Position	Depth (m)	T°C
Tiburon	1040	1 October 2006	34°17.23'N, 124°03.10'W	3098	1.59
Doc Ricketts	779	9 July 2015	35°37.97'N 123°08.9'W	2800	1.68

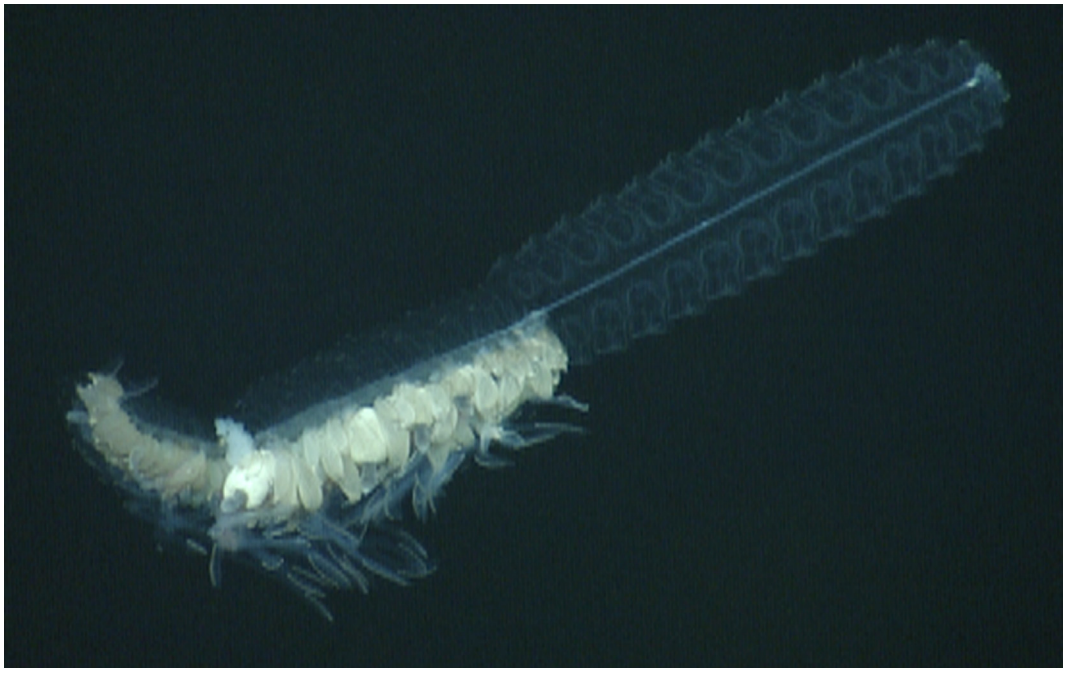


FIGURE 26. *Erenna insidiator* **sp. nov.** *In situ* frame grab of type specimen from *Tiburon* Dive 1040. The specimen is estimated to have been c. 30 cm in length. MBARI.

Part of the specimen from *Tiburon* Dive 1040 is designated the holotype and will be donated to National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A., while the remainder, and the other specimen will be maintained, in the siphonophore collections at Brown University, Providence, R.I.

Description. An *in situ* frame grab of the type specimen is shown in Figure 26, and a more detailed one of the recently collected specimen from *Doc Ricketts* Dive 779 is shown in Figure 27.

Pneumatophore and *Nectosome*: *In situ* the nectosome of the type specimen occupied over half the total length with c. 29 mature nectophores and a number of nectophoral buds, together with the anterior pneumatophore. However, this region, having become denuded of its larger nectophores, does not appear to have been preserved.

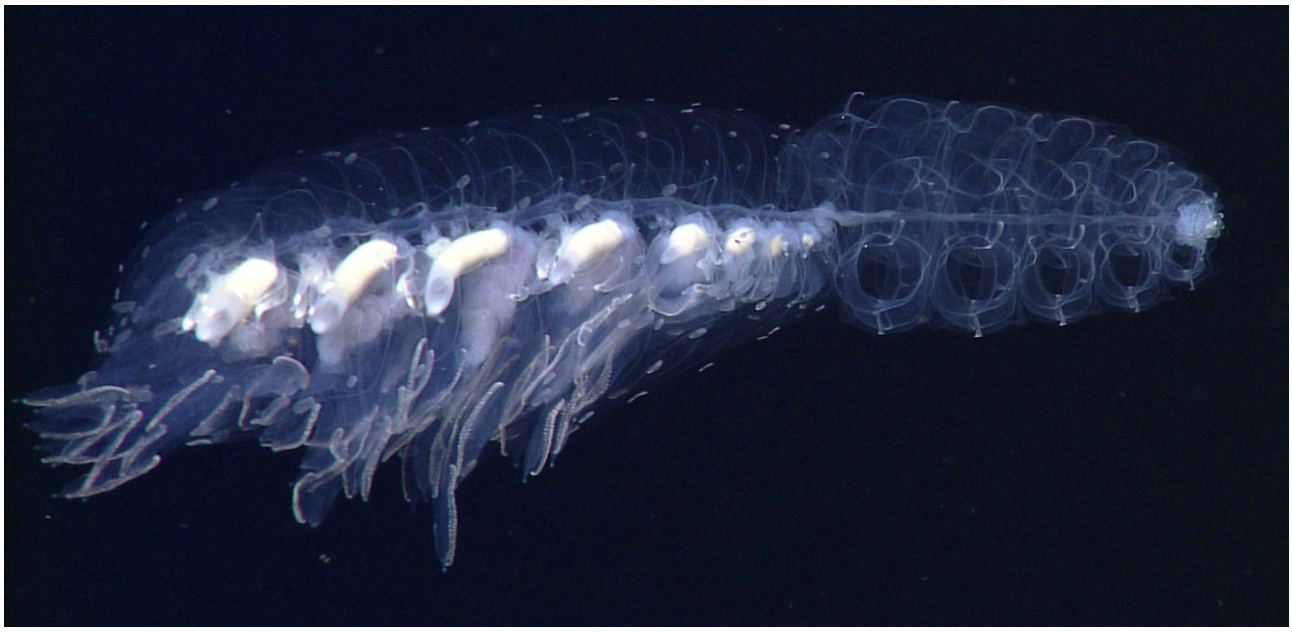


FIGURE 27. *Erenna insidiator* **sp. nov**. *In situ* photograph of small specimen collected during *Doc Ricketts* Dive 779. MBARI.

Nectophores: Twenty seven nectophores were found with the preserved type specimen that ranged in size from 12 to 30 mm in length and 6 to 29 mm in maximum width. The small nectophores (Figure 28 A) had yet to take on the flattened, in the upper/lower plane, appearance of the mature ones. The sides were folded up so that the upper lateral ridges ran parallel with each other and only a short distance apart. They defined the edges of a deep median furrow that was deepest proximally and gradually shallowed distally, as is indicated by the course of the upper radial canal in Figure 28 A. Proximally the combined upper and lower lateral ridges originated in the region where the nectophore was attached to the stem. The latter branched from the former at about half the height of the nectophore, and each was divided into two sections, proximal and distal, with the distal part appearing as an extension of the vertical lateral ridge (Figure 28 A). At this stage, the vertical lateral ridge did not join with the upper lateral ridge and, at all stages, neither the upper nor lower lateral ridges reached the ostium, nor did the former divide. The vertical and lower lateral ridges stood out from the surface of the nectophore. A small, elongate patch of ectodermal cells was present on each side of the nectophore just distal to the vertical lateral ridge. In the preserved state it was brown in colour but, as with other *Erenna* species, almost certainly it was black in life. The nectosac was deeply divided in the mid-line by the upper furrow (Figure 28 A), but had extensive lateral wings in the proximal half of the nectophore. The mantle canal was thick and U-shaped, and gave rise to the short pedicular canal that, in turn gave rise to all four radial canals. For the most part the lateral canals followed the contours of the nectosac, except distally where they continued to the lateral margins of the ostium. All the canals were a brownish-black in colour in the preserved state, but almost certainly were black in life. There was a small muscle-free zone just distal to the lateral radial canals, where they ascended from their origin from the pedicular canal.

On the slightly larger nectophores (Figure 28 B, C) the upper lateral ridges still remained close together in the distal half of the nectophore, but the furrow between them was much shallower. The lower lateral ridge then appeared as a single entity and the vertical lateral ridges joined with the upper laterals. The muscle-free zone now consisted of a narrow band on either side of the proximal part of the lateral radial canals. The most interesting

feature was the start of the development of the very characteristic thrust block. The central, proximal connection between the combined upper and lower lateral ridges, which formed the margins of the axial wings, consisted of two hemispherical mesogloeal thickenings that lay each side of a deep groove through which passed the ascending mantle canal. Distal to these, on the upper side of the nectophore, there were two further pairs of roughly hemispherical mesogloeal thickenings. The more distal pair was the larger and partially overhung the other pair.

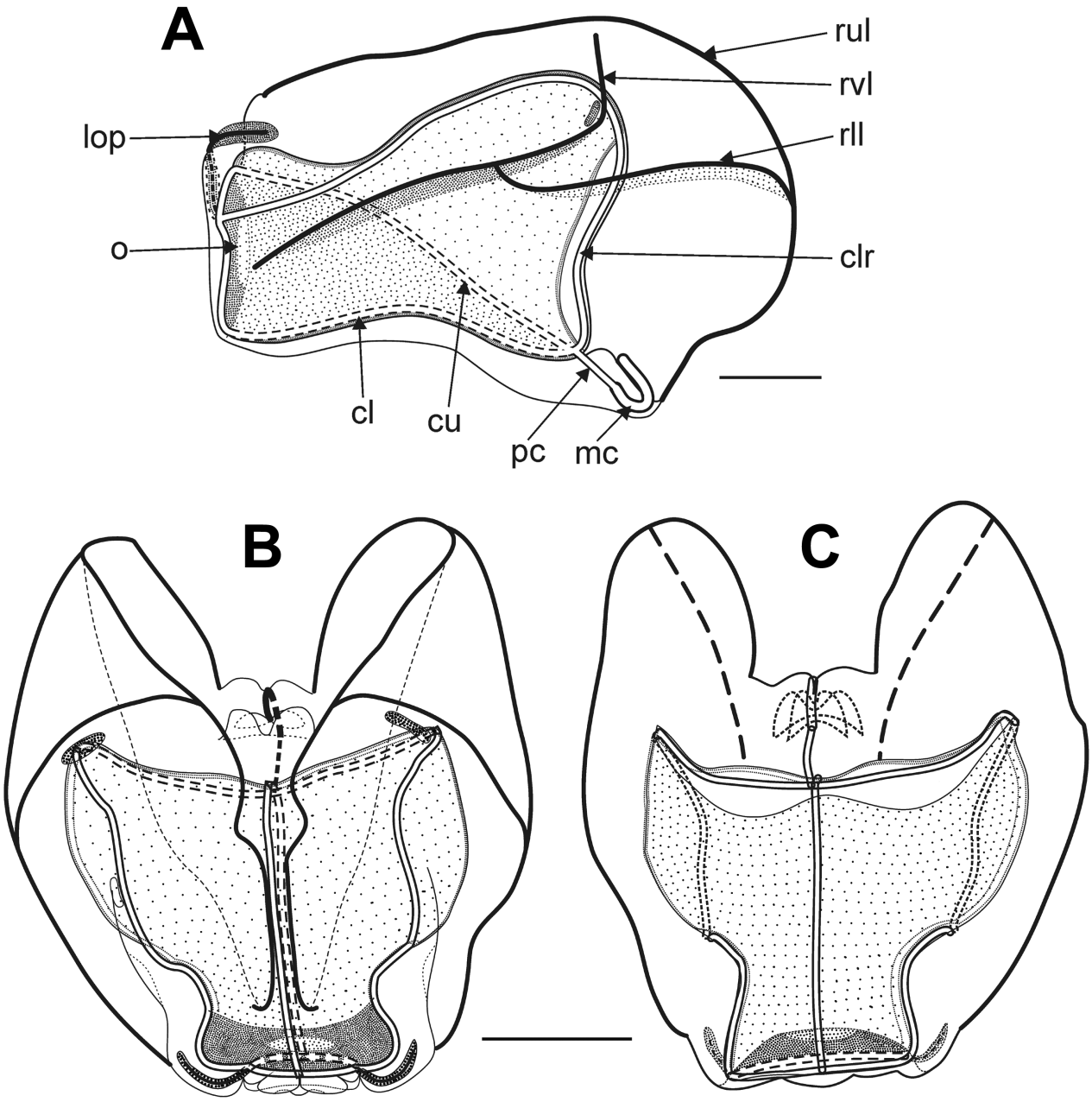


FIGURE 28. *Erenna insidiator* **sp. nov. A**. Lateral view of young nectophore. **cl**, **clr**, **cu**: lower, lateral and upper radial canals; **lop**: lateral ostial process; **mc**: mantle canal; **pc**: pedicular canal; **o**: ostium; **rll**, **rul**, **rvl**: lower, upper and vertical lateral ridges. Scale bar 2 mm. **B**. upper and **C**. lower views of intermediate-sized nectophore. Scale bar 5 mm.

On the fully developed nectophores (Figure 29 A, B) the upper lateral ridges had now moved out toward the lateral margins. As before they did not quite reach to the ostium. The lower lateral ridges branched from the upper ones on the lateral margins of the axial wings, and these too did not quite reach ostial level. The vertical lateral ridges were distinct and there were small patches of, presumably, cells producing bioluminescence on the distal margins. Proximally the apex of the nectosac was almost flat and there was a clear muscle free zone, mainly on the lower side, but occasionally extending on to the upper one. The thrust block had expanded considerably and now

formed two rounded lobes on the upper side of the nectophore. Below these and extending further proximally, was the pair of rounded thickenings that were deeply divided in the mid-line with the ascending mantle canal running through the furrow. The lateral ostial processes were well developed and even by the mature stage still contained nematocysts that appeared to be isorhizas (Figure 29 C).

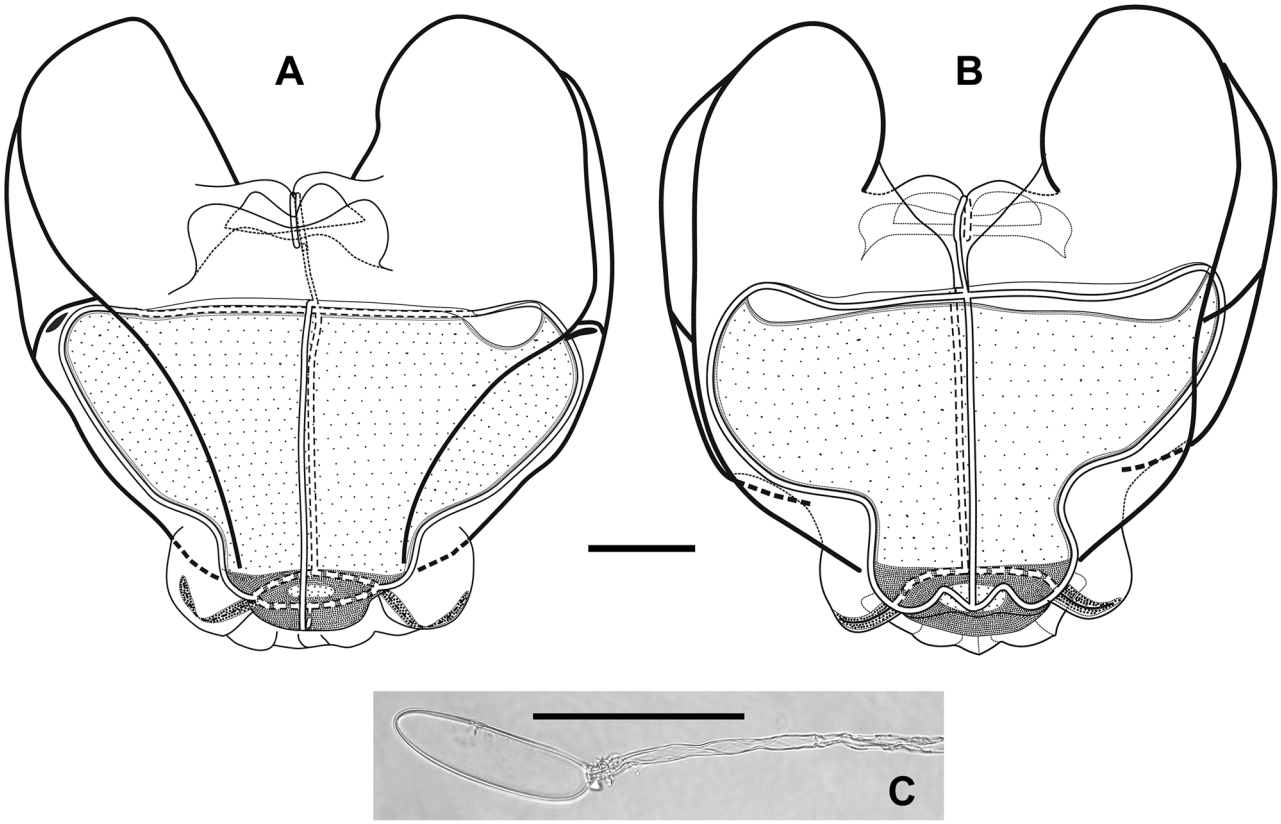


FIGURE 29. *Erenna insidiator* **sp. nov. A**. Upper and **B**. lower views of mature nectophore. Scale bar 5 mm. **C**. Discharged nematocyst from lateral ostial process on nectophore. Scale bar 100 µm.

Siphosome: Because of the highly contracted nature of the preserved stem and the dense clusters of zooids, it was not possible to glean any useful information concerning the organisation of the individual cormidia.

Bracts: Although very similar, the bracts could be divided into two types. The *Type A* (Figure 30A) were slightly more abundant than the *Type B* ones (Figure 30B). They were elongate, measuring up to c. 45 mm in length and 20 mm in width. They bore a pair of asymmetrically placed lateral cusps in their proximal half, with the cusp on the inner side usually being the more distal of the pair and more pronounced. There was a small circular patch of ectodermal cells on the upper side in the mid-line slightly distal of the mid-length. The inner side, at the proximal end, was distinctly thickened with mesogloea so that the bracteal canal ran over a sort of keel. The canal arose on the upper side of the bract and shortly after passing on to the lower side it usually thickened slightly. It continued distally and in contact with the lower wall until close to the distal end. There it thinned as it penetrated into the mesogloea and ran diagonally upwards to reach the upper surface toward the proximal end of a distinct raised patch of ectodermal cells, and then continued distally for a short distance immediately below the patch. Throughout its length the canal contained, in the preserved state, dark brown pigmentation that probably was black in life.

This distal patch of cells (Figure 31) was roughly rectangular in shape with rounded corners. Its upper side consisted of a honeycomb of ectodermal cells interspersed with a few nematocysts. This probably was the result of abrasion as the more protected sides of the patch were packed with nematocysts. These nematocysts (Figure 31, insert) measured c. 100 x 28 µm and were probably of the same type that were found on the lateral ostial processes of the nectophores. However, no evaginated ones were observed.

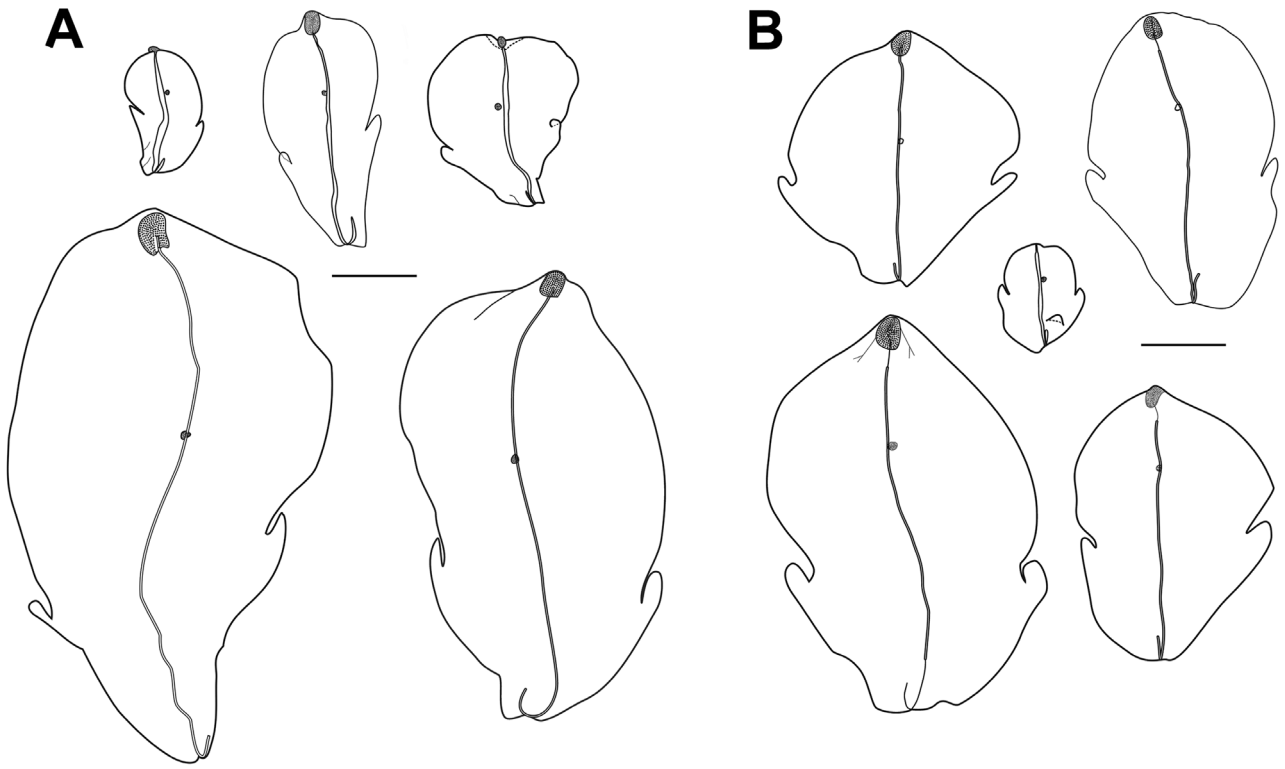


FIGURE 30. *Erenna insidiator* **sp. nov.** Bracts at various stages of development. **A**. *Type A*; **B**. *Type B*. Scale bar 5 mm.

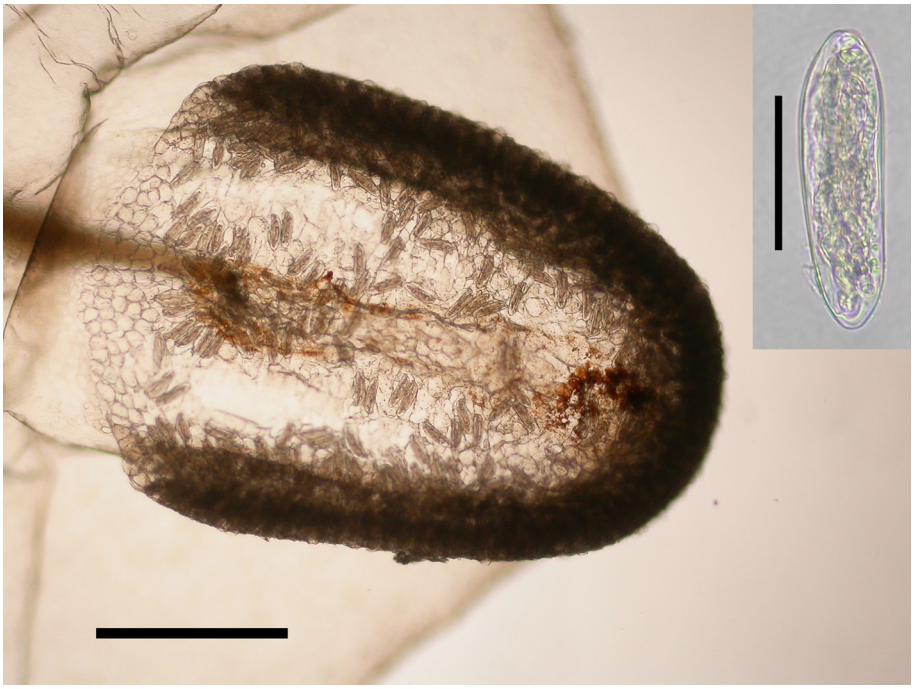


FIGURE 31. *Erenna insidiator* **sp. nov**. Upper side of distal tip of young bract (scale bar 500 µm), with (insert) detail of nematocyst (scale bar 50 µm).

The bracts of the second type (Figure 30B) were shorter, measuring up to 25 mm in length and 17 mm in width. They also possessed a pair of lateral cusps in their proximal half, but in this case the cusps were almost symmetrically arranged. Again, there was a small central patch of ectodermal cells, and the course of the bracteal canal was the same as for the other type of bract. However, on the inner side of the bract, at the proximal end, the mesogloea was uniformly thickened and so there was no pronounced keel. In the very youngest bracts there was a

conical protuberance on one side of the bract, proximally, but this disappeared as the bracts enlarged. The distal ectodermal thickening on the upper side of the bract was basically the same as for the other type of bract, although in general it was less extensive.

Gastrozooid and tentacle: The large gastrozooids (Figure 32) were largely black in colour and, in both life and after preservation, had an asymmetrical shape. The small, ring-like basigaster was attached directly to the stem and was separated from the main stomach region by an annulation. The stomach was usually laterally expanded and the distal proboscis region arose at an oblique angle on one side. The distal region was paler than the others and numerous endodermal, longitudinal "hepatic stripes" could be seen. The tentacle arose from one side of the basigaster, and was annulated and bore strong musculature.

FIGURE 32. *Erenna insidiator* **sp. nov**. Gastrozooid and proximal part of tentacle from specimen before preservation. Scale bar 1 cm.

Tentillum: The tentillum (Figure 33) was of a unique morphology, although typical for an *Erenna* species. It consisted of an obviously highly extensile, but in its preserved state a highly contracted pedicle, as exemplified by the corrugated nature of the gastrovascular cavity. The remainder of the tentillum was a cylindrical tube, but flattened on its inner side. It was U-shaped in its preserved state and measured c. 55 mm in length, but in life was quite straight (see Figure 27). Its ectoderm consisted of irregularly shaped small cells, below which was an amorphous layer of mesogloea, and then a spongy internal layer of pentagonal or hexagonal-shaped cells surrounding the narrow gastrovascular cavity (Figure 33B). This spongy layer decreased in size distal to the cnidoband itself, forming a narrower, short terminal process that terminated in a spherical photophore (Figure 34D). There the gastrovascular cavity gave rise to a diverticular canal that ran proximally, above the main gastrovascular cavity to the middle of the cnidoband (Figure 33C, D). Whether it then gave rise to two branches that ran distally and proximally along the base of the cnidoband could not be discerned. Young tentilla, at various stages in development are shown in Figure 34A. The outer process that forms the cnidoband is distinct at a very early stage in development. No details with regard to the ocellus and its potential luminescent properties are presently available.

The cnidoband itself, as with other *Erenna* species (see Pugh, 2001) was a discrete structure that measured c. 12.5 mm in length in its preserved state (Figure 33B, C). The nematocysts were concentrated around the outer lateral margins of the cnidoband in a much folded sequence giving the outer edge a scalloped appearance. The large nematocysts, presumably microbasic mastigophores (Figure 36 B), which measured c. 142 x 23 µm, were present in relatively large numbers compared with the other *Erenna* species. The smaller ones (Figure 34C), which were quite variable in size, measuring c. 39–42 x 16–20 µm, appeared to be all of the ovoid, pear-shaped type. No discharged ones of either type were found. Whether the small cylindrical type of nematocyst was absent or so rare that it was not noted was unclear.

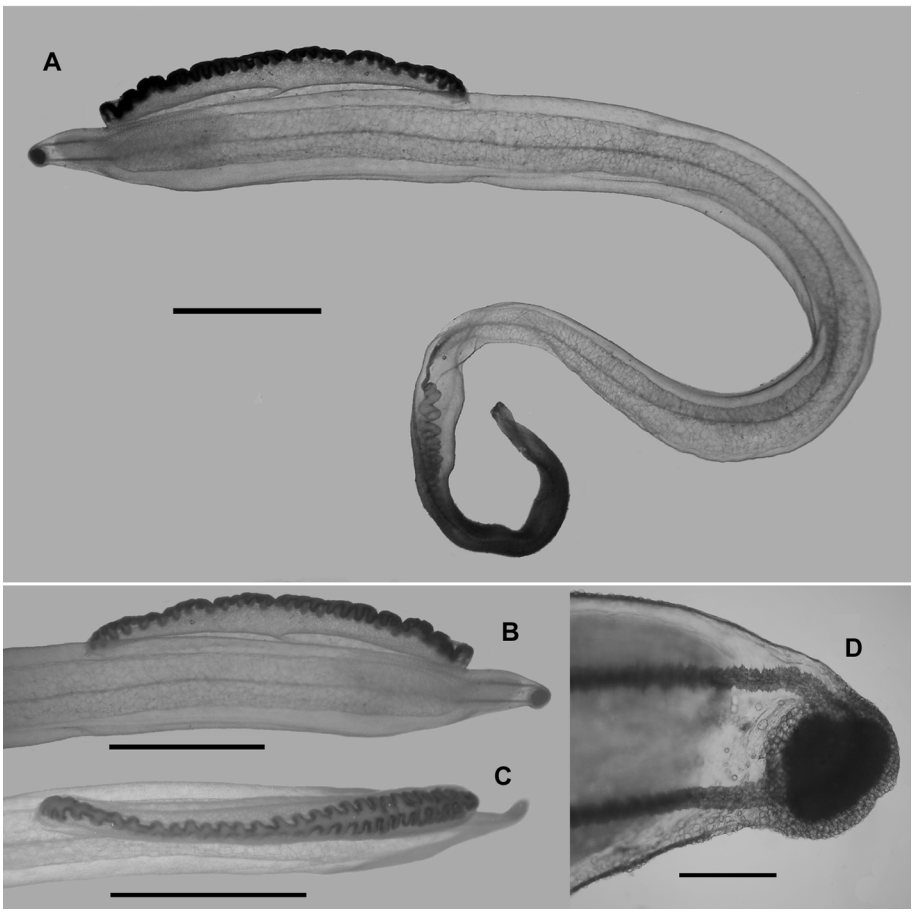


FIGURE 33. *Erenna insidiator* **sp. nov. A**. Tentillum. Scale bar 5 mm. **B–D**. Detail of distal end of tentillum. **B**. Lateral, and **C**. outer views of cnidoband. Scale bars 5 mm. **D**. Lateral view of ocellus. Scale bar 1 mm.

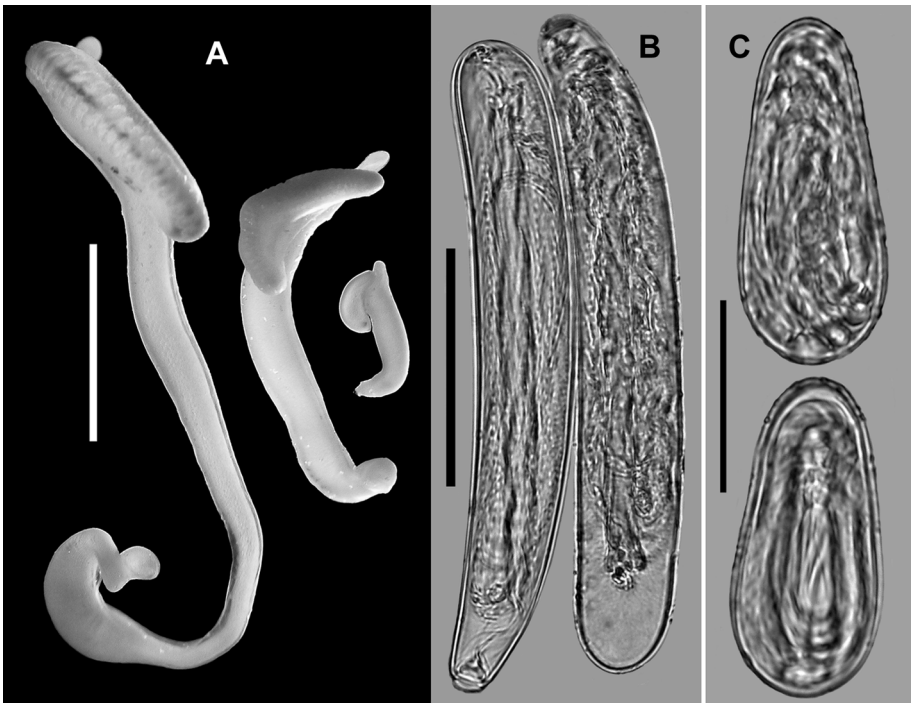


FIGURE 34. *Erenna insidiator* **sp. nov. A**. Young tentilla. Scale bar 5 mm. **B–C**. Nematocysts on cnidoband. Scale bars **B**. 100 µm; **C**. 50 µm.

FIGURE 35. *Erenna insidiator* **sp. nov.** palpons, prior to preservation. Scale bar 5 mm. Inset. Nematocyst from mouth region of palpon. Scale bar 50 µm.

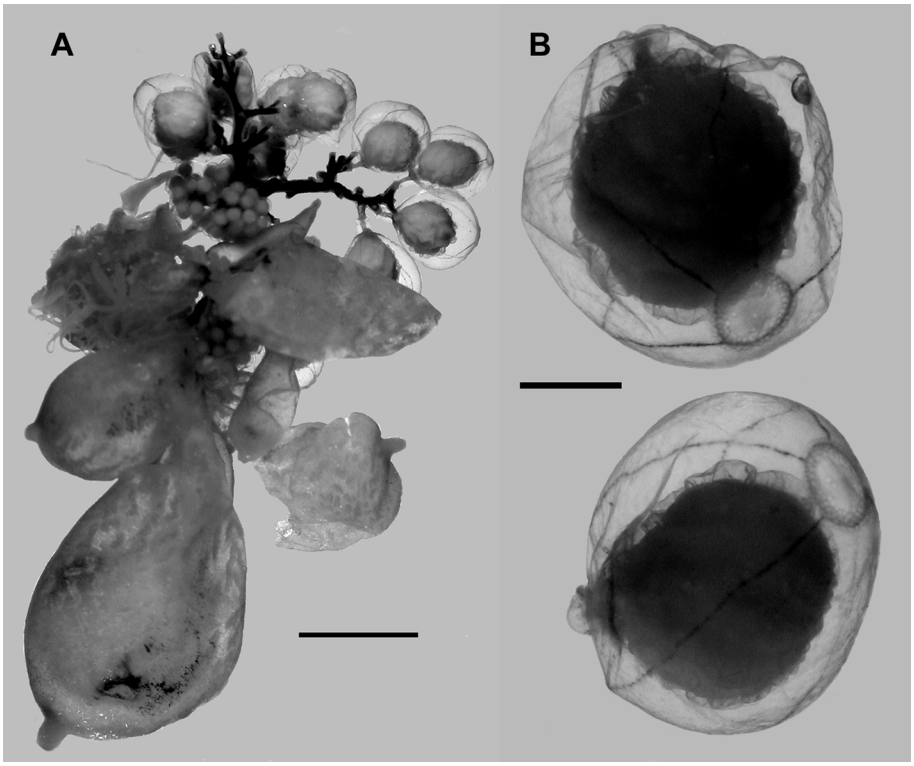


FIGURE 36. *Erenna insidiator* **sp. nov. A**. Gonophores at various stages of development. Scale bar 5 mm. **B**. Individual male gonophores. Scale bar 1 mm.

Palpon: Each palpon (Figure 35) consisted of a short pedicle, a slightly broader part, separated from the more distal parts by a constriction, to which the palpacle was attached. The latter was often lost, but when present, was very short and possessed no nematocysts. The main part of the palpon consisted of a large, flimsy bag-like structure, together with a distinct, narrow, whitish proboscis region. The main body was covered in an array of long irregular patches of large ectodermal cells interspersed with or overlaying more homogeneous smaller cells. The

largest palpons measured up to c. 20 mm in length and 10 mm in diameter. Groups of palpons arose from a common pedicle and these were usually closely associated with the gonodendra. However, the highly contracted nature of the preserved stem did not allow for the exact arrangement to be elucidated.

From 30 to 50 nematocysts were found around the distal mouth opening that measured c. 92 x 28µm (Figure 35 inset). Although of similar size to those found on the nectophores and bracts they did not appear to be of the same type. Possibly they were mastigophores, but this could not be confirmed as no discharged ones were found.

Gonodendron: The type specimen was male and gonophores, in various stages of development, were found attached to several gonodendra (Figure 36A). There appeared to be more than one of these per cormidium, but due to the highly contracted state of the preserved specimen, this could not be verified with certainty. Each gonodendron appeared to be associated with a cluster of palpons, but again the highly contracted nature of the preserved siphosome did not allow an accurate assessment of their disposition. The younger gonophores were clustered closely together, but as they matured they became more separated, being borne on rigid, brittle, almost twig-like, stalks.

Each gonophore, up to c. 3.5 mm in diameter, was a spherical, bag-like structure with a somewhat amorphous but spherical, central manubrium containing the sexual products that occupied only part of the subumbrella space. Typically four straight radial canals could be discerned, but they were not arranged symmetrically (see Figure 36B). Their arrangement suggested that there should have been five canals, spaced approximately 72° apart, but with one canal missing. Occasionally (see Figure 36B) this fifth canal was present, while on rare occasions there were only three canals that reached the ostial ring canal. The ostium was completely closed by a circular membrane comprised of an outer ring of large, roughly circular cells surrounding smaller cells.

Distribution. Known from only two specimens, one collected from a depth of 3098 m at 34°17.23'N, 124°03.10'W, west of Point Conception, California, where the water depth was c. 3450 m, and the other west of the Davidson Seamount, California at a depth of 2800 m, where the water depth was c. 3770 m.

Etymology. The specific name *insidiator* is derived from the Latin *insidia*, and means an ambusher as, although not proven, its tentillum probably, in some way, acts as a lure.

Erenna sirena sp. nov.

Diagnosis. Flattened nectophores with pairs of upper lateral, lower lateral and vertical lateral ridges. The upper laterals do not divide and end at some distance above the ostium. Two types of bract; the *Type A* being distinguished by their relatively small size and absence of any transverse ridges or flaps. Very characteristic tentilla where the terminal process is modified to form a red bioluminescent appendage that acts as a lure.

Material examined. Thirteen specimens of *Erenna sirena* **sp. nov**. are known to have been collected and six of these have been examined for the present description, namely:

ROV	Dive	Date	Position		Depth (m)
Tiburon	594-SS7	17 July 2003	36°12.99'N	122°32.00'W	1935
Tiburon	678-D5	25 May 2004	35°28.84'N	123°52.74'W	2428
Tiburon	681-D3	27 May 2004	36°33.81'N	122°11.65'W	2262
Tiburon	981-D3	11 May 2006	36°36.13'N	122°22.57'W	2188
Tiburon	1040-D3	1 October 2006	34°17.23'N	124°03.10'W	2061
Tiburon	1154-SS1	28 November 2007	35°49.97'N	122°39.99'W	1920

Holotype: The specimen from *Tiburon* Dive 1154-SS1 has been designated the holotype and will be donated to National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Description. In general the *in situ* specimens were up to c. 70 cm in length, with the siphosome usually slightly longer than the nectosome (Figure 37). The cell patches, including nematocysts, at the distal ends of the bracts were prominent, but would not serve to identify the species *in situ*. However, the thick clusters of tentilla were quite distinctive, and absolutely so if they could be seen in close-up so that the red lures could be observed (Figure 38).

FIGURE 37. *In situ* photograph of specimen of *Erenna sirena* **sp. nov.** seen at a depth of 1662 m during *Tiburon* Dive 538. MBARI.

FIGURE 38. *Erenna sirena* **sp. nov.** In situ photograph of colony seen during *Tiburon* Dive 647 at a depth of 2213 m. MBARI.

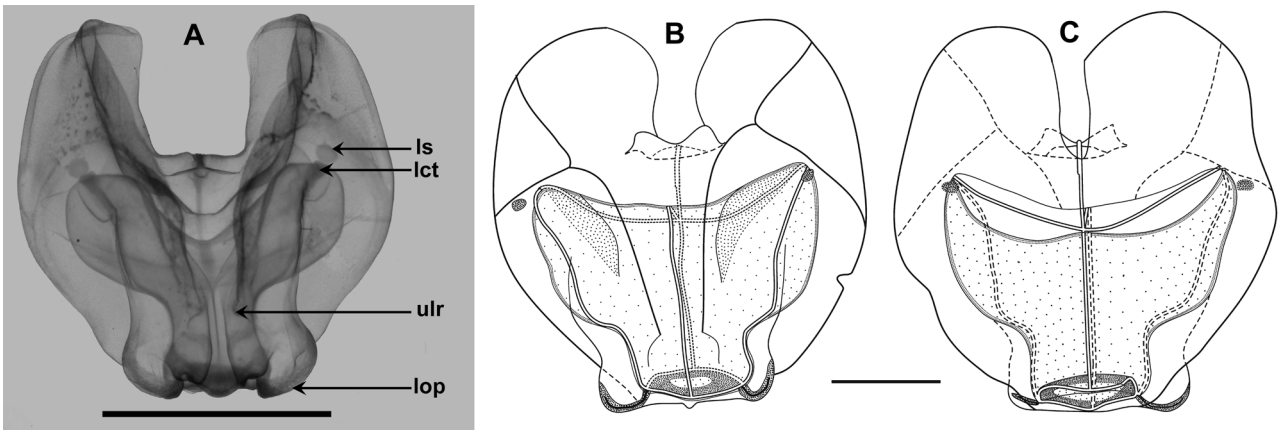


FIGURE 39. *Erenna sirena* **sp. nov**. **A**. Very young nectophore from *Tiburon* Dive 681-DS3. **lct**: later canal thickening; **lop**: lateral ostial process; **ls**; lateral spot; **ulr**, distal extent of upper lateral ridge; **B**. Upper and **C**. lower views of a mature nectophore of the type specimen of *E. sirena*. Scale bar 5 mm.

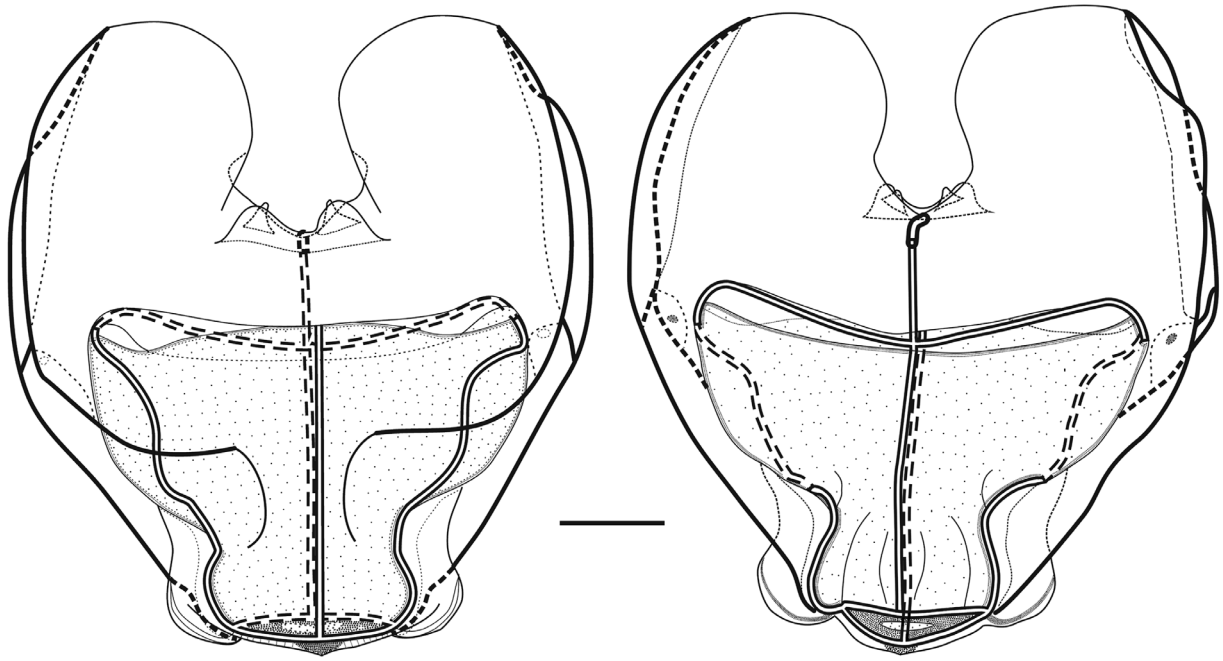


FIGURE 40. Upper (left) and lower (right) views of larger nectophore of *Erenna sirena* **sp. nov**. Scale bar 5 mm.

Pneumatophore. The preserved, and partially exploded, pneumatophore measured c. 3.5 mm in length and 1.75 mm in diameter, and was completely featureless.

Nectosome: Up to eighteen pairs of mature nectophores were observed on *in situ* specimens.

Nectophores: There were 26 detached mature and three young nectophores included with the type specimen, and one nectophoral bud. These nectophores measured up to 30 mm in width and length. One of the distinctive characters of the very young nectophores (Figure 39A) was the fact that the upper lateral ridges ended, distally, well above ostial level and without dividing. Both the upper and lower lateral ridges were well-defined while the vertical laterals were less so, although they clearly joined with the other two ridges. There was a prominent lateral spot on either side of the nectophore just distal to the vertical lateral ridges and as the lateral radial canals passed over the lateral apices of the nectosac they were considerably thickened. The lateral ostial processes were not prominent at this stage, and the canal running through them was ill-defined. However, they bore nematocysts measuring c. 90 x 25 µm. There also was a prominent patch of ectodermal cells on the upper side of the ostium, where the upper canal joined the ring canal.

As the nectophores enlarged, the muscle-free zone on the proximal part of the lower side of the nectosac became apparent, and the thrust block began to develop and, at that stage, consisted of two small lobes (Figure 39B, C).

The fully developed nectophores (Figure 40) had the typical *Erenna* form, i.e. compressed in the upper/lower plane and with a distinct triangular lateral facet in the proximal half of the nectophore, delimited by the upper, lower and vertical lateral ridges. Distally, the upper lateral ridges turned inwards and ran directly toward the mid-line, before turning back toward the ostium and becoming much less distinct and gradually petering out. The lower ones continued to the ostium. Just distal to the vertical lateral ridge there was a small patch of ectodermal cells. The axial wings increased further in size and formed a pair of extensive lobes. The thrust block remained relatively small but now took on its characteristic form, consisting of two rounded lobes, on the upper side of the nectophore, behind which where two smaller digitate flaps.

The nectosac occupied the distal half of the nectophore and had a distinct muscle-free zone at it proximal end. The ascending mantle canal was quite short and gave rise to a long pedicular canal that ran to the lower wall of the nectosac just below its apex. It gave rise directly to all four radial canals, the upper and lower running directly to the ostium, while the laterals followed the contours of the lateral walls of the nectosac. Two long, but narrow lateral ostial processes extended out from the ostium.

Siphosome: A very unusual, if not unique, situation was noted on the siphosome of *Tiburon* Dive 1040 specimen observed *in situ* (Figure 41). Here the tentacles, particularly toward the posterior end of the colony, appeared to possess long contractile pedicles, such that the tentacle itself was hanging loose at some distance from the siphosomal stem.

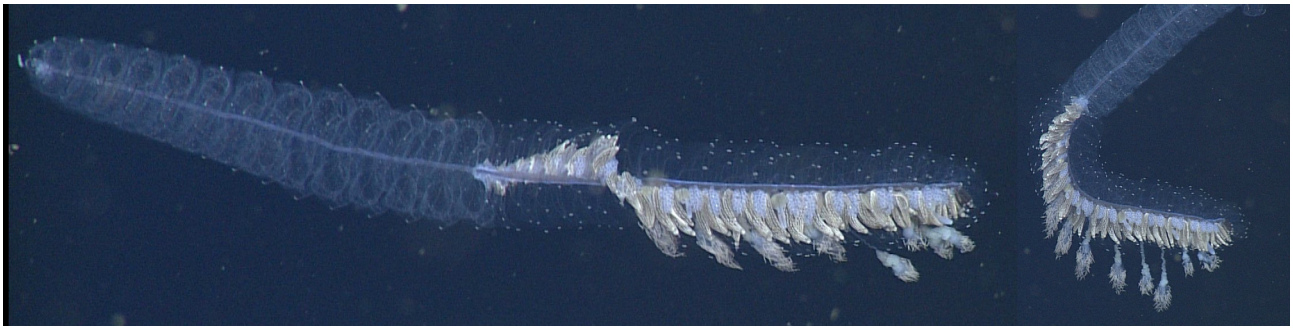


FIGURE 41. *In situ* photographs of specimen of *Erenna sirena* **sp. nov.** from *Doc Ricketts* Dive 723 showing the extraordinary elongation of the pedicle of the gastrozooidal tentacles toward the distal end of the colony. MBARI.

Bracts: Typically there were two types of bracts, with the *Type A* (Figure 42A) being longer and thinner, and the *Type B* (Figure 42B) shorter and fatter. The *Type A* bracts measure up to 27 mm in length and 14 mm in maximum width. They possessed two pairs of lateral cusps, with the distal pair being almost symmetrical, while the proximal pair were distinctly asymmetrical, with the cusp on the inner side being considerably more distal than the other. The distal end of the mature bracts was pointed and formed a right-angle. Proximally the inner side was thickened. The bracteal canal arose on the upper side of the bract and, once it had passed over to the lower side, remained in contact with the lower wall of the bract for most of its distance. However, distally it narrowed considerably and ran obliquely through the mesogloea to end below a large patch of cells, including nematocysts, that was raised above the upper surface of the bract just prior to its distal end. In the youngest bracts, this cluster of cells was formed into a ball that projected beyond the distal tip of the bract. A small circular patch of ectodermal cells was present in the mid-line on the upper side of the bract, usually approximately on a level with the more distal of the proximal pair of lateral cusps. This was not always to be seen on the younger bracts.

The nematocysts (Figure 42C) in these clusters were of one type, although somewhat variable in size ranging from 90–103 μm in length and 25–30 μm in diameter, and presumably were the same as those on the lateral ostial processes of the nectophore.

The *Type B* bracts (Figure 42B) measured up 20 mm in length and 16 mm in width. They also possessed two pairs of lateral cusps, but the proximal pair was much closer to being symmetrical than those on the *Type A* bracts. The course of the bracteal canal was the same as for the *Type A* bract, as was the proximal thickening on the inner side of the bract itself. The distal patch of nematocysts, etc, on the upper side of the bract, was similarly raised above the surface, but generally smaller in size, especially in the mature bracts where the number of nematocysts was reduced, either by erosion or usage.

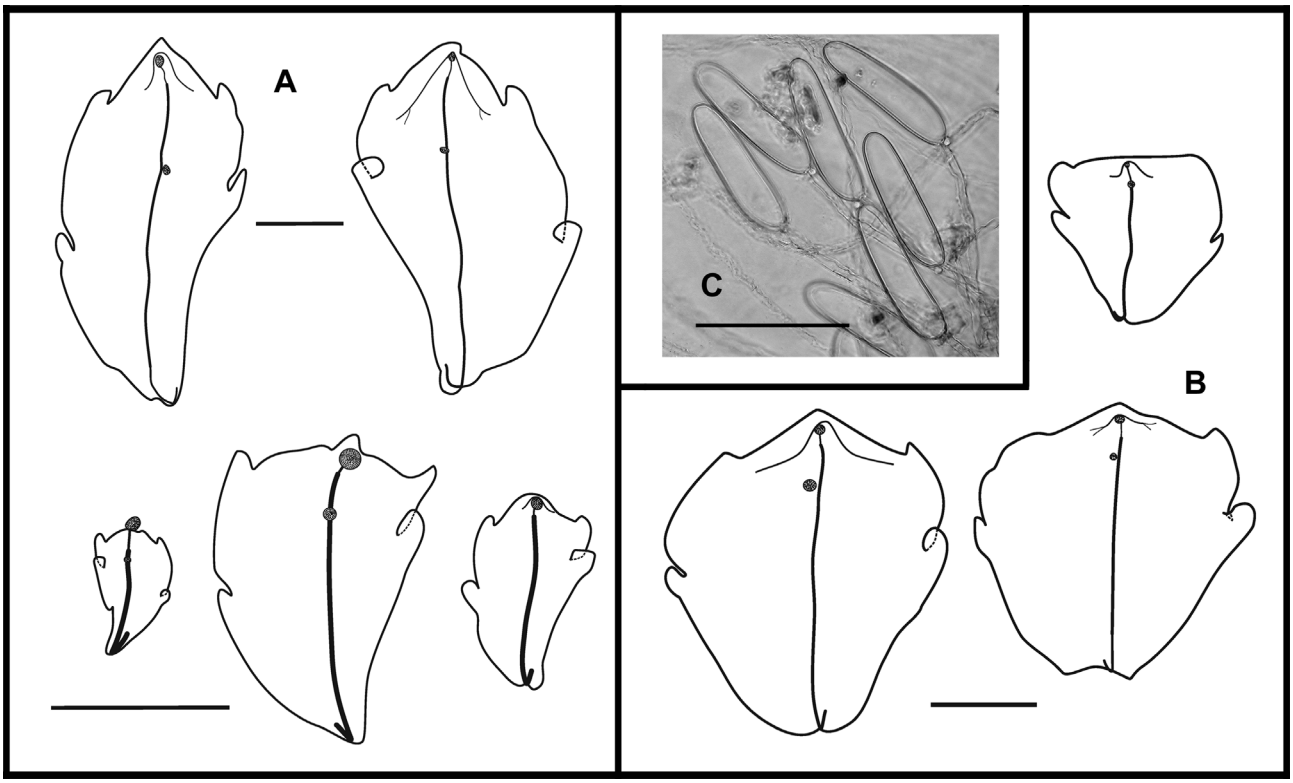


FIGURE 42. A. Mature (upper) and immature (lower) *Type A* bracts of *Erenna sirena* **sp. nov.; B**. *Type B* bracts. Scale bars 5 mm. **C**. Discharged nematocysts from distal patch of cells on bract. Scale bar 100 µm.

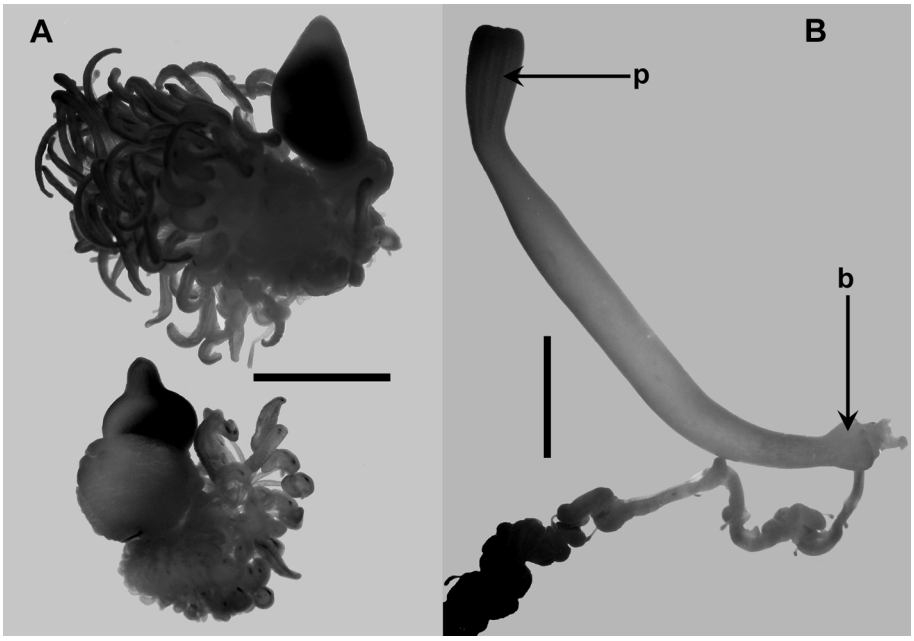


FIGURE 43. *Erenna sirena* **sp. nov**. **A**. Young and **B**. mature gastrozooids. Scale bar 5 mm. **b**: basigaster; **p**: proboscis.

Gastrozooid and tentacle: The younger gastrozooids (Figure 43A) had a relatively small stomach and proboscis region and a large basigaster, to which the young tentacle with developing tentilla was attached. The mature gastrozooids (Figure 43B) often were more elongate, up to 3 cm in length, with a small slightly inflated basigaster, a long stomach region, and a narrow proboscis within which the so-called hepatic stripes were apparent.

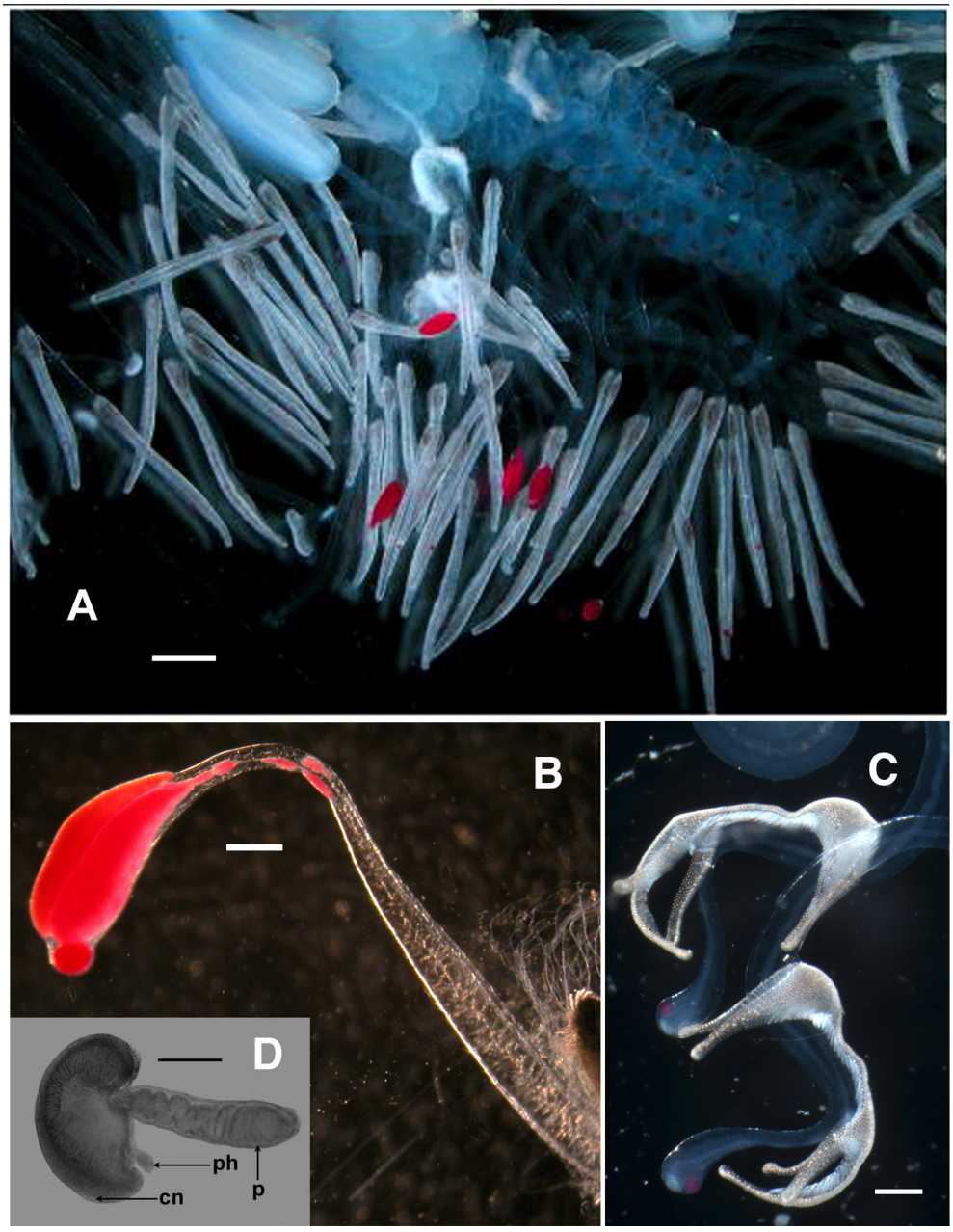


FIGURE 44. *Erenna sirena* **sp. nov.** Tentilla. **A**. Cluster of tentilla from *Tiburon* Dive 981 specimen; **B**. Detail of lure of mature tentillum from *Tiburon* Dive 981 specimen; **C**. Two larval tentilla from *Doc Ricketts* Dive 727; **D**. Very young tentillum. Scale bars **A**. 1 mm; **B**. 0.25 mm; **C**, **D**. 0.5 mm.

Each tentacle bore a considerable number of tentilla (Figures 37, 44A) at various stages of development (Figures 44B, D, 45). Although, for many, the cnidoband was of about the same length, the degree to which the lure was developed varied considerably. Only a few had the fully developed red-pigmented lure (Figure 44A), while in many the lure remained small and whitish in colouration. As Haddock *et al*. (2005) showed the milky-white appearance of the younger lures was due to the presence of bioluminescent material that later became covered in a red fluorescent material with multimodal emissions. The relative sizes of the cnidoband and the lure varied during the development of the tentillum. At the very youngest stage (Figure 44D), in its preserved state, it consisted of a highly contracted pedicle, with the relatively wide gastrovascular canal concertinaed. The cnidoband formed a hemispherical partial covering to an inflated cavity, with the very small stalkless photophore projecting out from the other side. The earliest stage photographed in life (Figure 45A), however, showed the milky-white bioluminescent lure, again without a stalk, to be considerably larger than the ill-developed cnidoband. As development progressed (Figure 45B–E) the size of the cnidoband increased rapidly, while that of the photophore

remained the same or even slightly decreased. At first (Figure 45B–C) it developed a short free stalk, but later this seems to have been resorbed (Figure 45E). Only at the final stages in the development of the tentillum did the photophore, with its covering of fluorescent material, greatly increase in size and the vacuolated stalk considerably elongate. At all stages of development the tip of the stalk could be flicked through strong contractions of the stalk itself. One young specimen, with only sixteen nectophores, was found to have retained the larval tentacle at the posterior end of the siphosome (Figure 44C). The eight attached tentilla had a unique "anteater-shaped" cnidoband and the lure was more bulbous-shaped than a typical mature lure. It was flicked in a similar manner to the adult one, through contractions of the stalk, and the photophore consisted of a small hemispherical protuberance from close to its distal end.

FIGURE 45. Stages in the development of the living tentillum of *Erenna sirena* **sp. nov. cn.** cnidoband; **ph**. photophore. Scale bars 1 mm.

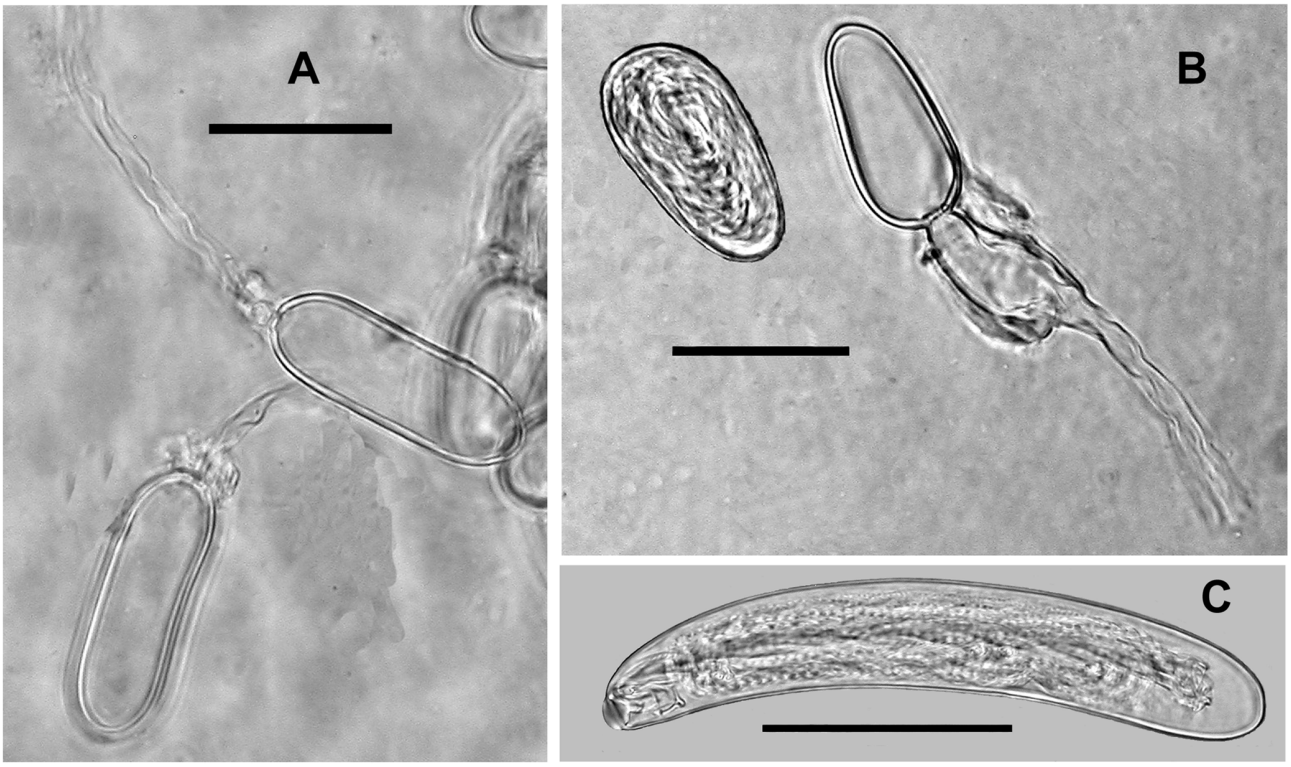


FIGURE 46. *Erenna sirena* **sp. nov.** Nematocysts on cnidoband. Scale bars **A**., **B**. 25 µm; **C**. 50 µm.

The bioluminescent and fluorescent properties of the lure have been dealt with by Haddock *et al*. (2005) and further details can be found on the web. One of these, http://www3.mbari.org/news/news_releases/2005/lures.html, contains a figure showing the red distal tips of the lures, with an inset showing the side view of one of these, which was considered closely to resemble a copepod..

The usual three types of nematocyst were found on the cnidoband (Figure 46). On each side there were several rows of, what were presumed to be, large microbasic anisorhizas (Figure 46C) that measured c. 135 x 21 µm before discharge, but were longer after discharge as the capsule straightened out. Very occasionally, a smaller version of this type of nematocyst, which measured c. 85 x 25 µm, was observed. The bulk of the cnidoband consisted of two, smaller types of nematocyst. A cylindrical form (Figure 46A), whose tubule was without a shaft and possibly atrichous, had a capsule that measured c. 39 x 12 µm; and a pear- shaped form (Figure 46B) that measured c. 31 µm in length and 15 µm in maximum diameter. The latter were considerably more abundant than the former and, when discharged, they showed the peculiar asymmetrical proximal swelling with a long tubule extending from it that has been described above for *Erenna richardi*.

Palpon: The palpons (Figure 47A) were very similar in morphology to those described above for *Erenna insidiator*. The mature ones had a short pedicle, to which the palpacle was attached, that gradually expanded into the main body region, covered in an array of long irregular patches of large ectodermal cells interspersed with or overlaying more homogeneous smaller cells, and then rapidly narrowing into the long distal proboscis. The largest palpons measured c. 15 x 5 mm. Unlike those of *E. insidiator* no clusters of elongate nematocysts were found around the distal mouth region. Occasional ones were observed, but it was not clear if these were definitely positioned there or were being ingested or egested.

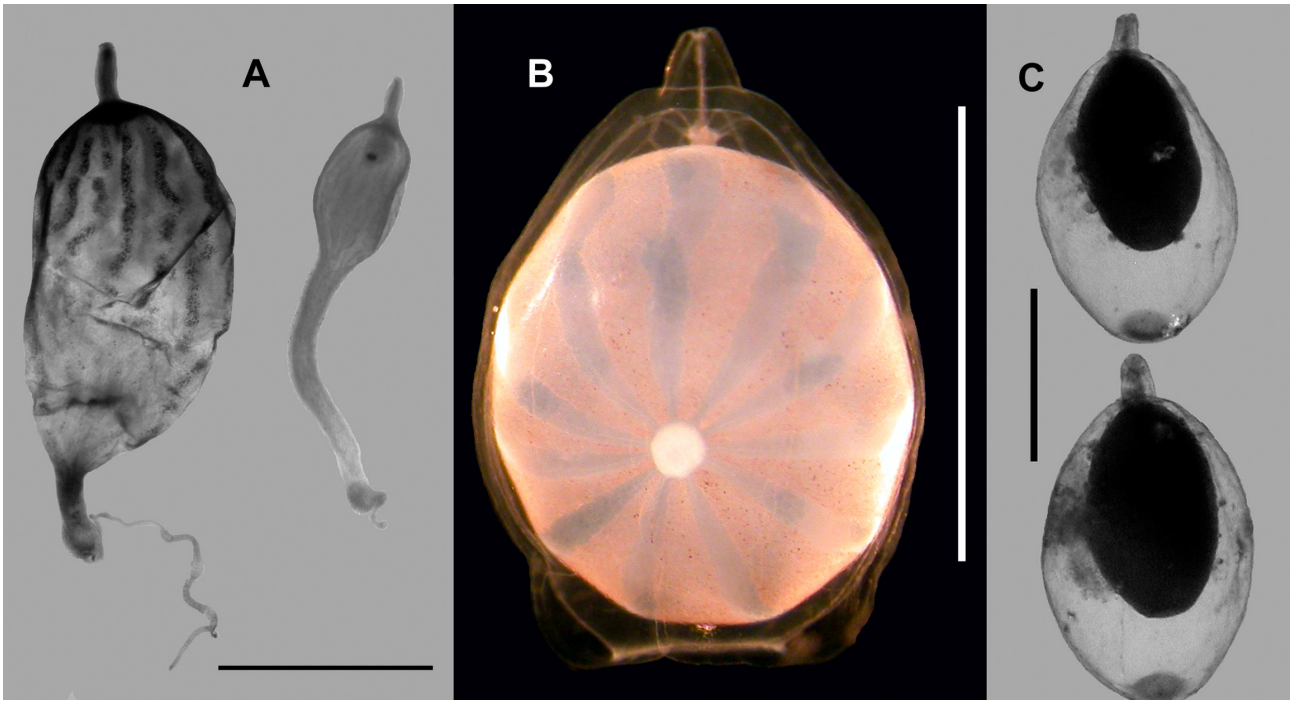


FIGURE 47. *Erenna sirena* **sp. nov**. **A**. Palpons; **B**. *In vivo* picture of female gonophore from *Tiburon* Dive 678 specimen; **C**. Young male gonophores from *Tiburon* Dive 1040 specimen. Scale bars **A**. & **B**. 5 mm; **C**. 1 mm.

Gonophore: The female gonophores were of a considerable size (Figures 38 & 47B) and, in their preserved state, measured c. 6 mm in length and 4.5 mm in diameter. They had a short triangular pedicle through which passed the pedicular canal. On reaching the subumbrella this canal initially gave rise to five radial canals and, after a short distance, three of these divided so that eight canals ran down to the ostial ring canal. Whether this was also the case for the male gonophores could not be elucidated. After preservation the egg turned a dark brown colour and no superficial structures could be seen. However, in life there were 11 bluish ribbon-like structures which connected with the region that was presumed to contain the nucleus (Figure 49B). Female gonophores at all stages of development were found on the colonies.

FIGURE 48. *In situ* photograph of specimen of *Erenna sirena* **sp. nov**. from *Tiburon* Dive 981 showing the large clusters of male gonophores, some of which were being released. MBARI.

FIGURE 49. Close up of siphosomal region from same specimen as shown in Figure 48, showing the clusters of male gonophores and of tentilla, with red "lures". MBARI.

The male gonophores (Figure 47C, 48–49) were borne on elongate gonodendra that were only developed on the older, more posterior, cormidia. Each gonophore (Figure 47C) measured c. 2.1 mm in length and 1.25 mm in diameter, including a short narrow pedicle. As the gonophores matured the sexual products increased in volume so as to completely filled the subumbrella cavity, and the mouth opening broke through and widened considerably. No nematocysts were found around the opening.

Remarks. The tentilla of *Erenna sirena*, although resembling those of *E. laciniata*, as noted above, more closely resemble those of *Parerenna emilyae* (see Pugh, 2001), particularly in the presence of what appears to be a lure, although the colour of that of *P. emilyae* is unknown. Since all the other species *Erenna* have highly distinctive tentilla it is reasonable to examine the possibility of these species might be one and the same. The

original material of *P. emilyae* was not in pristine condition, having been examined for bioluminescence before preservation, and indeed has deteriorated further since it was originally described, through poor curation. However, there are striking differences in the relative size of the various zooids of the two species. For, instance, the nine nectophores of *P. emilyae*, which appeared to be mature, had maximal dimensions of 13 mm in length and breadth. That compares with the 30 x 30 mm, respectively, for *E. sirena*. Indeed, a youngish nectophore of the latter, with typically thickened lateral radial canals, was larger than any of those of *P. emilyae*. The young tentilla of *E. sirena* also were considerable larger than those of *P. emilyae*. For these reasons we have decided to maintain the two as separate species, and hope that better material of *P. emilyae* will be collected in the future in order to confirm or not the original description.

Distribution. *Erenna sirena* **sp. nov**. has been collected in the two main MBARI ROV sampling regions, namely Monterey Bay (MB) and the Gulf of California (GOC). All known specimens that have been identified from *in situ* photographs or collected (emboldened) are listed below.

ROV	Dive	Date	Position	Depth (m)	T°C
Tiburon	239	17 November 2000	36°35.08'N 122°31.02'W	2424	1.80
Tiburon	538	20 March 2003	25°27.16'N 109°50.17'W	1661	2.61
Tiburon	**594**	**17 July 2003**	**36°12.99'N 122°32.00'W**	**1934**	**2.20**
Tiburon	647	27 January 2004	36°34.41'N 122°31.43'W	2215	1.89
Tiburon	678	25 May 2004	35°28.84'N 123°52.74'W	2428	-
Tiburon	**681**	**27 May 2004**	**36°33.81'N 122°11.65'W**	**2262**	**1.90**
Tiburon	763	17 November 2004	36°19.80'N 122°54.05'W	2352	1.85
Tiburon	**981**	**11 May 2006**	**36°36.13'N 122°22.57'W**	**2211**	**1.91**
Tiburon	**986**	**15 May 2006**	**35°38.01'N 122°44.46'W**	**2179**	**1.95**
Tiburon	**1040**	**1 October 2006**	**34°17.23'N 124°03.10'W**	**2063**	**2.06**
Tiburon	**1154**	**28 November 2007**	**35°49.97'N 122°39.99'W**	**1920**	**2.00**
Doc Ricketts	336	18 February 2012	24°12.72'N 109°38.36W	1773	2.68
Doc Ricketts	336	18 February 2012	24°12.72'N 109°38.36W	1926	2.31
Doc Ricketts	337	20 February 2012	23°33.51'N 108°46.96'W	1772	2.60
Doc Ricketts	340	22 February 2012	23°41.56'N 106°05.00'W	1751	2.55
Doc Ricketts	341	23 February 2012	24°18.90'N 109°11.95'W	1609	2.84
Doc Ricketts	410	14 July 2012	36°32.67'N 122°29.98'W	2237	1.86
Doc Ricketts	547	16 November 2013	36°32.71'N 122°30.79'W	2003	2.22
Doc Ricketts	**723**	**9 March 2015**	**27°27'N 109°50.99'W**	**1697**	**2.65**
Doc Ricketts	**723**	**9 March 2015**	**27°27'N 109°50.99'W**	**1721**	**2.64**
Doc Ricketts	724	10 March 2015	24°18.99'N 109°11.98'W	1610	2.68
Doc Ricketts	726	14 March 2015	23°41.5'N 108°49'W	1815	2.42
Doc Ricketts	**727**	**13 March 2015**	**22°55'N 108°7'W**	**2353**	**1.88**
Doc Ricketts	**728**	**14 March 2015**	**23°41.5'N 108°49'W**	**2239**	**2.01**
Doc Ricketts	**728**	**14 March 2015**	**23°41.5'N 108°49'W**	**1894**	**2.42**
Doc Ricketts	**728**	**14 March 2015**	**23°41.5'N 108°49'W**	**2103**	**2.16**

There are numerous records for *Erenna sirena* sp. nov. from both the regions of Monterey Bay and the southern part of the Gulf of Mexico. Those from the former region had a mean depth of 2188 ± 175 m, while that for the latter was somewhat shallow at 1849 ± 231.3 m. This difference was also notable for the mean temperatures that were 1.97 ± 0.15°C for the former and 2.46 ± 0.28°C for the latter. However, this may be a reflection of the water depth that, for the latter was c. 3000 m, while for the former it was often > 4000m. Although the known distribution of *E. sirena* sp. nov. presently is quite restricted it is probable that it has a much broader distribution, but the dearth of studies of the deeper waters of the world's oceans means that it has, to date, been overlooked

Etymology. The specific name *sirena* is derived from the sirens of Greek mythology, who lured sailors to their death, in reference to the function of the bioluminescent tentilla this species uses to attract its prey.

Genetic results. Molecular sequences for the nuclear 18S and 28S ribosomal RNA genes were largely invariant between the *Erenna* species, but 16S mtDNA and COI sequences showed a enough variation to potentially aid in identification. There was variation in the 16S and COI between the California and Mexico samples of *E. sirena*, but otherwise each species was closest to others of the same species, as expected. Sequences were obtained from the following specimens, and have been deposited with GenBank under the accession numbers given below.

Species	Dive	18S	28S	16S	CO1
Erenna cornuta	D728-SS5_GOC	KX752699	KX752708	KX752718	KX752726
Erenna cornuta	T964-D4	-	KX752710	-	KX752728
Erenna cornuta	T1106-D1	KX752700	KX752709	-	KX752727
Erenna insidiator	D779-SS4	KX752701	KX752711	KX752719	KX752729
Erenna insidiator	T1040-SS2	KX752702	KX752712	KX752720	KX752730
Erenna laciniata	D663-SS2	KX752703	KX752713	-	KX752731
Erenna laciniata	T594-SS7	-	KX752714	KX752721	-
Erenna laciniata	V3194-D6	KX752704	KX752715	KX752722	KX752732
Erenna richardi	T751-D3	KX752705	-	KX752723	-
Erenna sirena	T531-D3_GOC	KX752707	KX752717	KX752725	KX752734
Erenna sirena	T1040-D3	KX752706	KX752716	KX752724	KX752733

Conclusions

The description here of two new *Erenna* species increases the number of erennids to six. *Parerenna emilyae* Pugh, 2001 is now the rarest, being known from only a single specimen. However, it is easily distinguished from the *Erenna* species by the lack of compression of the nectophore in the upper/lower plane, and the indistinctiveness of the ridge system. For the *Erenna* species, *E. insidiator* **sp. nov.** is only known from two specimens, but is clearly distinguishable by the long wing- or fish shaped cnidoband on the tentillum. The maximum size of the nectophore is approximately the same in all species, except *Erenna laciniata* where they appear to be slightly smaller. However, there are certain characters that should easily distinguish them and these are used in the following key:

Key to *Erenna* species based on their nectophores.

1 Long "horn" canals arising from lateral radial canals; thrust block without median indentation . . *Erenna cornuta* Pugh, 2001
- No "horn" canals. Thrust block with median indentation 2
2 Mature nectophores with digitate processes on thrust block. 3
- Mature nectophores without digitate processes on thrust block 4
3 Upper lateral ridges divide close to ostium. Incomplete lateral ridges present . . . . . *Erenna richardi* Bedot, 1904
- Upper lateral ridges undivided. No lateral ridges . . . . . *Erenna sirena* **sp. nov**.
4 Upper lateral ridges divide close to ostium forming broad "m"-shaped branches. Thrust block consisting of one pair of lobes . . . . . *Erenna laciniata* Pugh, 2001
- Upper lateral ridges undivided. Thrust block with two pairs of lobes . . . . . *Erenna insidiator* **sp. nov**.

All five *Erenna* species have two types of bracts of which one, *Type* B, is a squatter form of the other, *Type* A. The *Type* A bracts of the five species are compared in Figure 50, and a key to their identification follows.

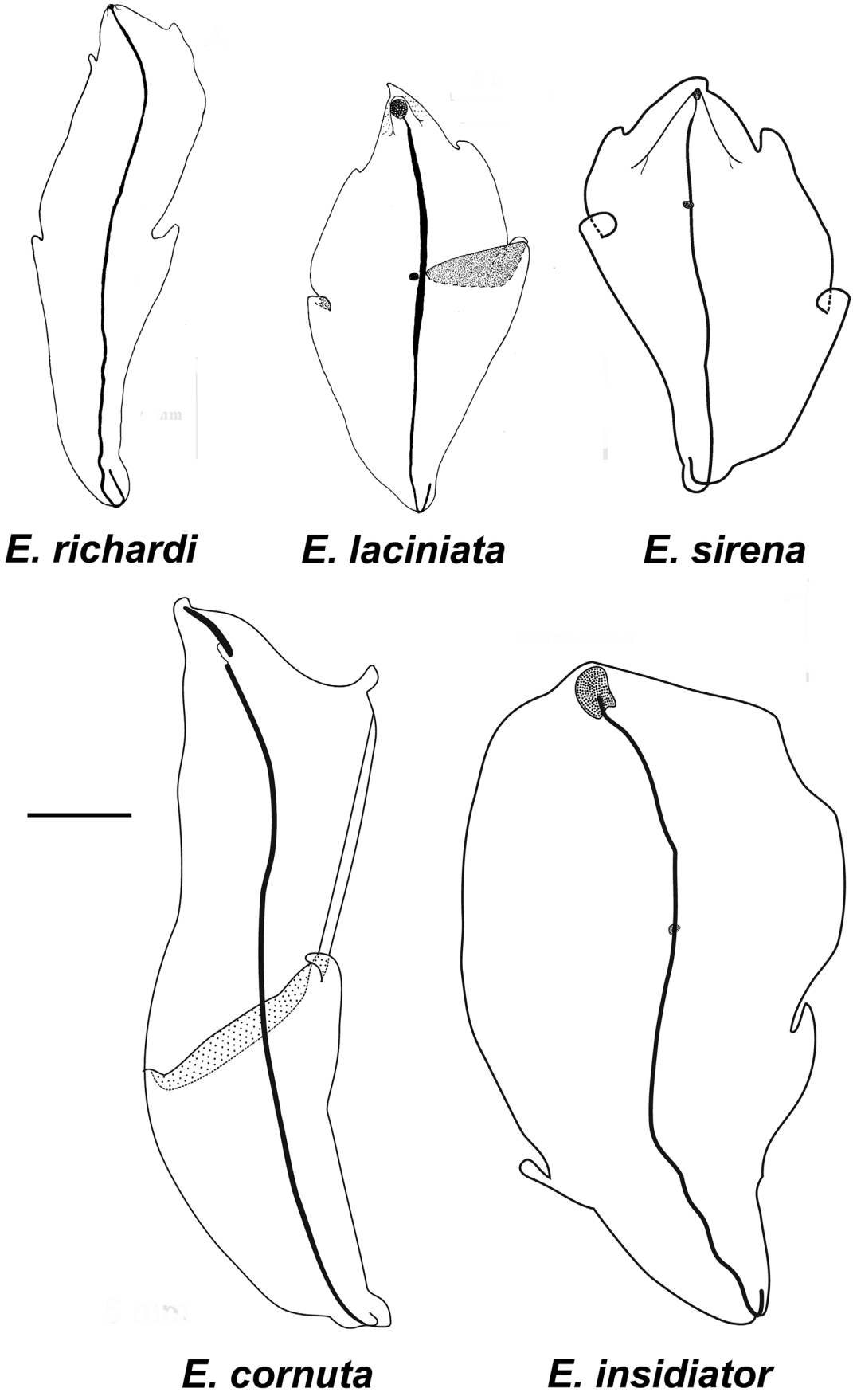


FIGURE 50. Comparison of the *Type* A bracts of *Erenna* species at the same scale. Scale bar 5 mm.

Key to *Erenna* species based on their *Type* A bracts

1 Largest bracts > 35 mm in length 2
- Largest bracts < 35 mm in length 3
2 Mature bracts with complete transverse ridge between proximal pair of cusps; elongate patch of cells, including nematocysts, distally . . . . . *Erenna cornuta* Pugh, 2001
- Bracts without transverse ridge between proximal pair of distinctly asymmetrical cusps; large squarish distal patch of cells . . . . . *Erenna insidiator* **sp. nov.**
3 Bracts with one of proximal cusps forming a distinct flap . . . . . *Erenna laciniata* Pugh, 2001
- Bracts without distinct flap formed by one of proximal cusps 4
4 Bracts relatively narrow. Proximal pair of cusps symmetrical, 13–14 mm from proximal end of bract . . . . . *Erenna richardi* Bedot, 1904
- Bracts relatively broad. Proximal pair of cusps distinctly asymmetrical . . . . . *Erenna sirena* **sp. nov.**

The bracts of *Erenna cornuta* are the easiest to identify, particularly *in situ*, as the elongate patch of cells, including nematocysts, at the distal end of the upper side of the bract is very distinctive. Its bracts and those of *E. insidiator* **sp. nov.** are distinctly larger than for the others. For the others, the half transverse fold across the middle of the bract distinguishes *E. laciniata*, while the others are distinguished by their relative proportions and the positioning of the lateral cusps.

The tentilla of the various *Erenna* species are compared in Figure 51, and each should be easily distinguishable when closely examined. They are also a useful guide for *in situ* identification. The small size of those of *Erenna laciniata* give the extended tentacle a beaded appearance (see Figure 12), and the forked Y-shaped base of the cnidoband of the tentillum is readily seen. In comparison, the often densely packed tentilla of *E. richardi* are larger and have a spiky appearance (see Figure 1). Despite *E. cornuta* having three types of characteristic tentilla, the colonies are best identified *in situ* by the long patches of cells at the distal ends of the bracts. Although the tentillum of *E. sirena* **sp. nov.** bears a very distinctive red lure, it is often difficult to see in the *in situ* photographs and it is often easier to deduce the identity of the colony by the absence of the characters of the other species. Nonetheless, the species has acquired the nickname of the "pompom *Erenna*" as a result of its ability to extend the base of the tentacle so that cluster of tentilla are positioned well away from the siphosomal stem (see Figure 41). It appears that *E. laciniata* also has this ability, but not to such a great extent (see Figure 12). However, as with the red lures, this feature is not to be seen on every colony observed. Finally *E. insidiator* **sp. nov.** tentilla can clearly be identified from the long wing-like cnidoband that is very prominent on the small specimen shown in Figure 38.

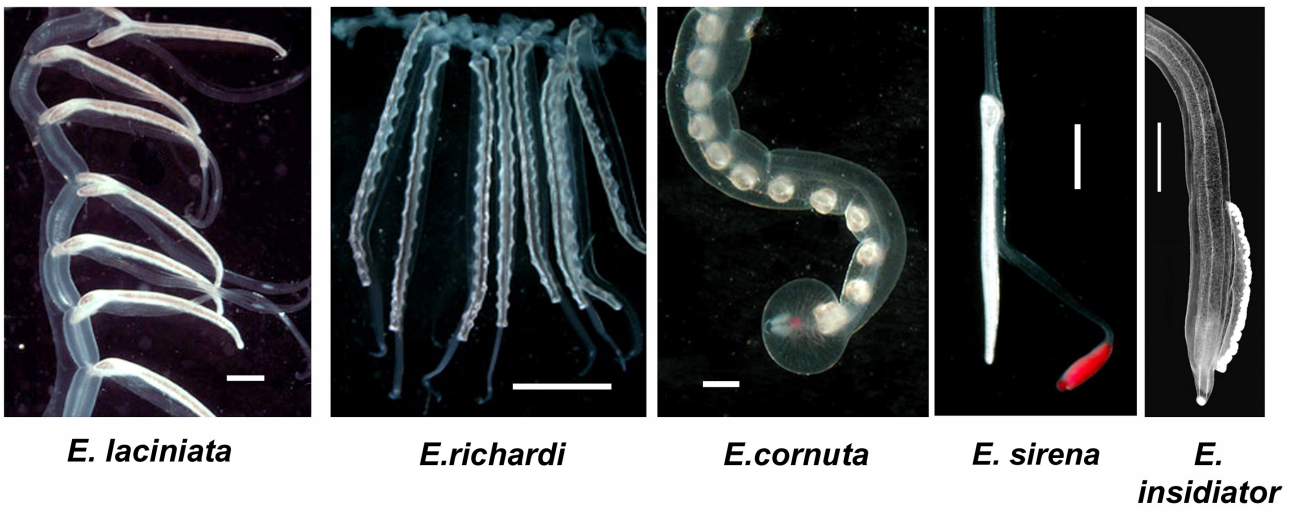


FIGURE 51. Comparison of the tentilla of *Erenna* species. Scale bars: 1 mm for *E. laciniata, E. cornuta & E. sirena* **sp. nov**.; 5 mm for *E. richardi* & *E. insidiator* **sp. nov**.

Finally, the depth distribution for each species in the vicinity of Monterey Bay and the Gulf of Mexico are compared in Figure 52. The two known colonies of *Erenna insidiator* **sp. nov.** both occurred in Monterey Bay and at depths (< 2800 m) distinctly deeper than any other *Erenna* species. *E. sirena* **sp. nov.** also occurred there over a quite separate depth range that did not overlap with any other (i.e. c. 1900-2450 m). For the other three species the

depth ranges for *E. richardi* and *E. laciniata* were very similar and coincided with the upper half of that of *E. cornuta*. Between c. 1600 and 1850 m *E. cornuta* was the only species found.

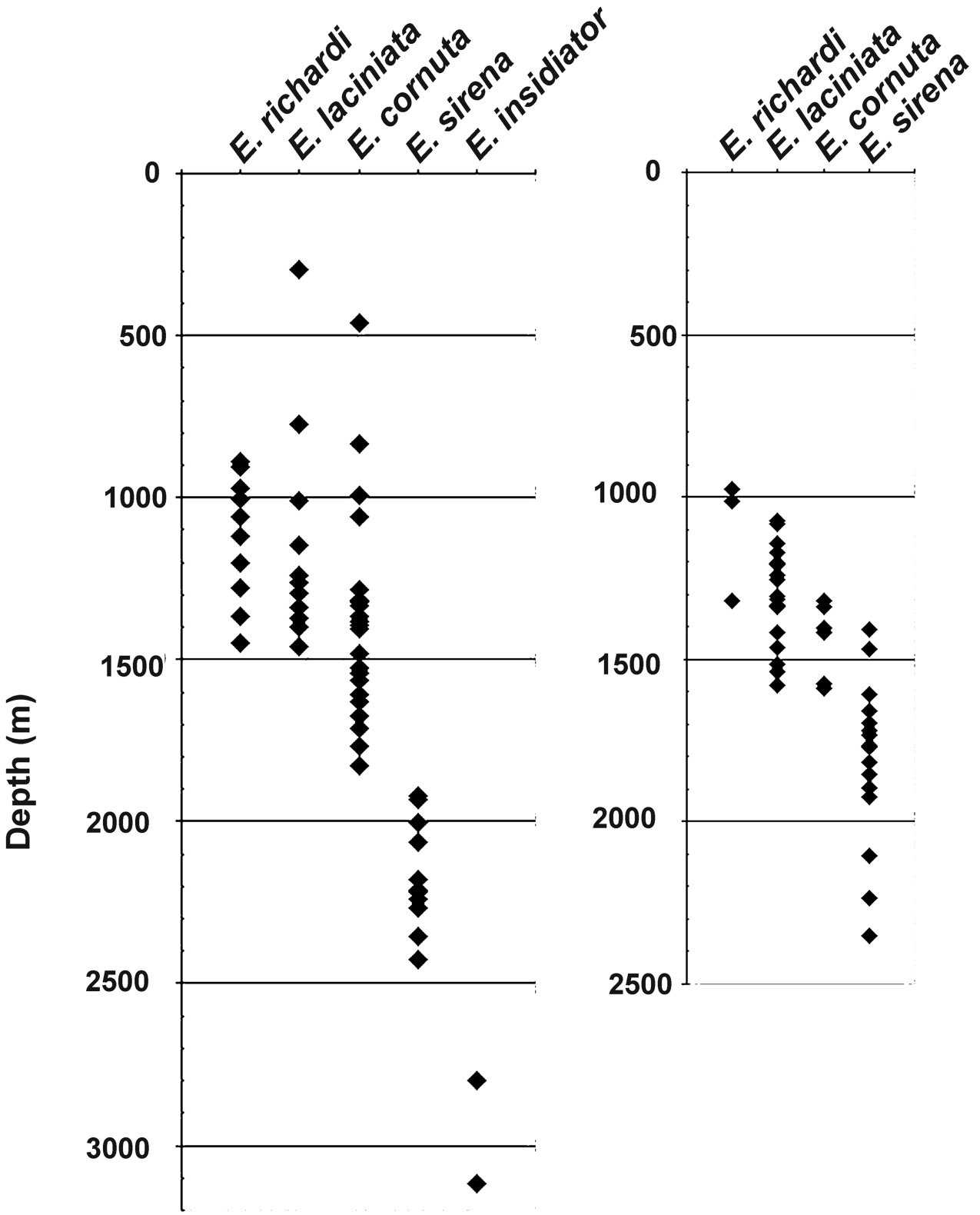


FIGURE 52. Depth distributions of *Erenna* species in Monterey Bay (left) and the Gulf of California (right).

The situation in the generally shallower waters of the Gulf of Mexico was somewhat more complex. Both *Erenna richardi* and *E. cornuta* were relatively rare and their depth distributions were similar to those in Monterey

Bay. The number of observations of *E. laciniata* was very similar at both localities and so, considering that the Gulf of Mexico has only been investigated on three occasions, one would presume it is much more common at that site than in the vicinity of Monterey Bay. As noted above, this species tended to live, on average, at depths 90 m deeper in the Gulf of California than in Monterey Bay. In contrast the depth distribution of *E. sirena* **sp. nov.** was generally shallower in the Gulf of California than in Monterey Bay, and the upper part of its range overlapped the lower parts of other species ranges. It was suggested earlier that this may be the result of the shallower depth of water at the former.

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