A revision of the sub-family Nectopyramidinae (Siphonophora, Prayidae)

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CONTENTS

SUMMARY

The sub-family Nectopyramidinae (Siphonophora, Prayidae) is reviewed and revised. Previously the sub-family was considered to comprise one genus, *Nectopyramis*, with four species. However, it is shown that the two types of nectophore previously ascribed to *N. spinosa* are actually the larval nectophores of two other species, namely *N. thetis* and *N. natans*. A new genus *Nectadamas* gen. nov. is erected to include the other species, *diomedeae*. The differences between the two genera are principally the arrangement of the radial canals to the nectosac and the shape of the hydroecium in the definitive nectophore; and the presence or absence of a special nectophore. A new species *Nectadamas richardi* sp. nov. is described, the eudoxid of which previously had been ascribed to *N. spinosa*.

1. INTRODUCTION

Siphonophores are highly polymorphic animals that occur in a bewildering variety of shapes and sizes. Each colony consists of a mixture of 'individuals' that may have either a polypoid or medusoid origin, which are specialized to carry out certain functions. Because of this an arcane, and thereby rather daunting, terminology has been established to describe these various parts. This situation is made even more complex by the fact that previous specialists have not always used the same terminology.

Figure 1 illustrates the complexity of a typical prayine siphonophore. The Prayinae is one of the three sub-families of the family Prayidae, which belong to the sub-order Calycophorae; that is those siphonophores that do not possess an apical, gas-filled float. In these animals it is usual for a larval necto-phore (swimming bell) to be developed from the fertilized egg. Subsequently one or more definitive

nectophores are budded off and the larval nectophore is discarded. In the Prayinae it is normal for two such definitive nectophores to form an apposed pair (figure 1a), although in another of the prayid sub-families, the Amphicaryoninae, it is believed that the larval nectophore is retained and only a single, reduced definitive one developed. In the third prayine sub-family, the Nectopyramidinae, it had been thought, with one exception, that only a single nectophore was developed, and there has been some discussion in the past as to whether this should be considered as a larval or definitive one (see Totton 1965). The present paper will clarify this situation and show that both a larval, and a single definitive nectophore are developed.

The gastro-vascular system of the nectophore usually consists of a simple canal, the somatocyst (figure 1a), but, particularly in the nectopyramidinae, it may bear several branches, which can be divided complexly. A single, pedicular canal usually joins the somatocyst to the radial canals on the walls of the sub-

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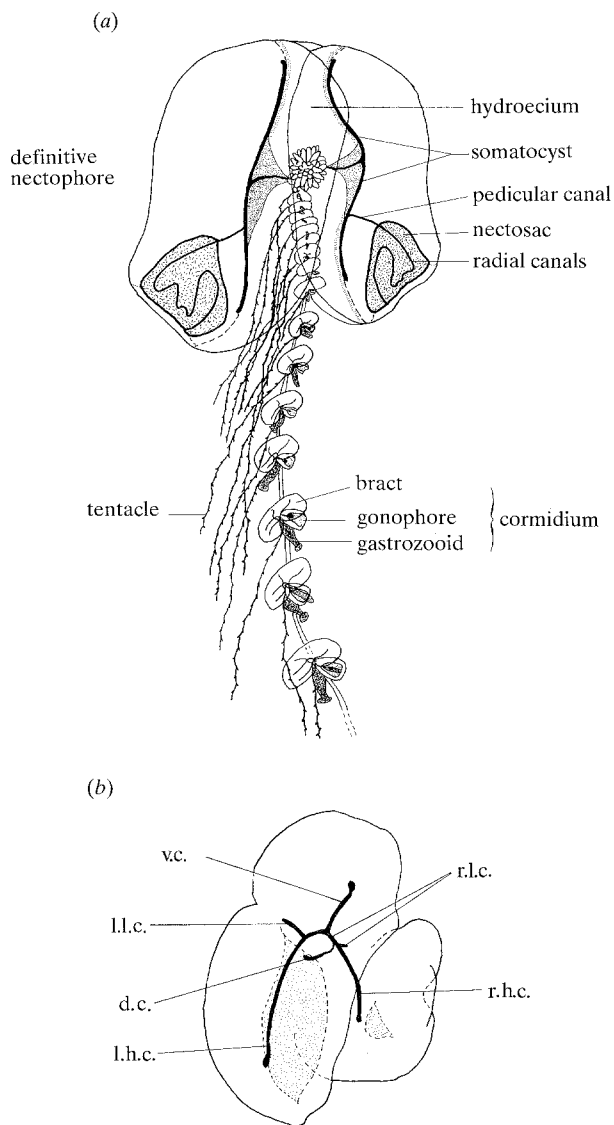*Printed in Great Britain*

281

(a)

(b)

Figure 1. General structure of a prayine siphonophore. (a) Whole colony (after Totton 1965), (b) dorsal view of bract (after Pugh & Harbison 1987). The bracteal canals are: d.c., dorsal; l.h.c and r.h.c., left and right hydroecial; l.l.c. and r.l.c., left and right longitudinal; and v.c., ventral. Note the distal extension of the r.l.c., after the r.h.c. has branched off, is reduced to a 'spur'.

umbrella or nectosac, but there are exceptions to this in the Nectopyramidinae.

Within the hydroecium of the nectophore(s) lies the budding zone for the other elements of the animal (figure 1*a*). These elements are grouped together to form cormidia, which are arranged serially along the stem. Each cormidium usually consists of a protective and flotant bract, a gastrozooid (feeding polyp) and tentacle, and the sexual elements (gonophores). Although unusual in prayine siphonophores, in the Nectopyramidinae it appears that the terminal (oldest) cormidium detaches from the stem and lives a separate life as the sexual stage or eudoxid. The gastro-vascular system of the bract (figure 1*b*) basically consists of six canals, which in some species may be complexly divided, or may be reduced or absent. The last is evident in the Nectopyramidinae where the

extensions ('spurs') to the longitudinal canals usually are absent. It should be noted that the terminology for the arrangement of the bracteal canals used in this paper is based on that used by Bigelow & Sears (1937) (see also Pugh & Harbison (1987)), and differs from that used by, for example, Totton (1965).

Although Totton (1965) recognized only four nectopyramidine species, it has become evident, as new material has become available, that the status of one of these species is doubtful. The present paper aims to clarify the situation, and to give detailed descriptions of all the species, including a new one.

2. HISTORICAL

The genus *Nectopyramis* was erected by Bigelow (1911*a*) for a new species, *N. thetis*, which he described from a single, unusual nectophore, within the hydroecium of which was attached a young eudoxid. Because of the singularity of the nectophore, Bigelow included his new genus within the family Monophyidae. However, he noted that the gastro-vascular systems of both the nectophore and the minute eudoxid bract were comparable with those found in certain species of the family Prayidae, but felt that the absence of any trace of a posterior (*sic*) nectophore forbade the inclusion of *N. thetis* in the latter family. Thus Bigelow (1911*a*, p. 338) defined the genus *Nectopyramis* as 'Monophyidae with rounded nectophore, with the somatocyst represented by a series of divergent canals: the cormidia are without special nectophores'. He precluded the presence of a special nectophore because he believed that the largest bell, attached to the very young eudoxid, contained a minute spadix, although this is not apparent in his figure (plate 28, figure 4). He did allow, however, that a special nectophore might be developed later.

Bigelow (1911*b*) described a second species, *Nectopyramis diomedeae*, which was distinguishable on the basis of the shape of the nectophore and its complexly divided somatocyst. His material consisted of two nectophores and five eudoxids, with true gonophores. He decided to place the genus in a new sub-family, the Nectopyramidinae, but retained this within the family Sphaeronectidae (the name Monophyidae having been replaced after the genus *Monophyes* had been reduced to a synonym of *Sphaeronectes*). *N. thetis* was designated the type species of the genus.

Bigelow (1911*b*) also described a single large eudoxid, with a very large special nectophore, under the name *Archisoma natans*. He considered that this species could not be allocated a systematic position among the calycophoran siphonophores until its associated polygastric stage had been found. Further eudoxids of *A. natans* were described by Bigelow (1919, 1931). Bigelow (1919) drew attention to the similarity between the arrangement of the radial canals on the sub-umbrella of the special nectophore and that on the nectosac of the nectophore of *Nectopyramis thetis*. He implied, tentatively, that the former species might be the free eudoxid of the latter, although he stated (p. 345) that 'the gaps in the chain of evidence are much more extensive than its links'. He concluded (p. 345)

that 'If my suggestion should prove correct it would be of great importance systematically, because the only other species yet referred to *Nectopyramis*, *N. albatrossi*, lacks the special nectophore, and likewise has subumbral canals of the ordinary type'. As Leloup (1932) and Totton (1954) have discussed, it is presumed that *N. albatrossi* was a manuscript name that was changed to and published as *N. diomedeae*, and thus the former name becomes a *nomen nudum*.

Moser (1925) briefly reviewed Bigelow's earlier descriptions of *Nectopyramis thetis* and *N. diomedeae*, and retained them within the family Monophyidae (Sphaeronectidae); although she did consider the possibility that they might be prayid species, despite the absence of a second nectophore. She also described a new species, under the name *Hippopodius* (?) *cuspitatus*, from a single, small nectophore that was characteristically covered in variously sized teeth. This is, almost certainly, a nectopyramid.

The fact the *Archisoma natans* was not the eudoxid of *Nectopyramis thetis* was established finally by Leloup (1932), who described the true eudoxid of the latter species. A further description of a nectophore and eight eudoxids of *N. thetis* was given by Leloup (1933), who found that all of the latter possessed a well-developed special nectophore. Bigelow & Sears (1937) described another nectophore of *N. thetis* and an eudoxid that they ascribed to that species. They noted that their eudoxid differed slightly in shape from Leloup's material, but concluded that the differences probably were caused by distortion during preservation. However, these authors were in full agreement with Leloup that a special nectophore was present. This contrasts with Bigelow's (1911*a*) original belief that such structures were absent, at least in his young specimen.

Totton (1932) reviewed the earlier classification of calycophoran siphonophores and rejected the idea that the so-called monophyid species were a single natural grouping. Therefore, he placed the genus *Nectopyramis* within the family Prayidae. Totton (1936) recorded some nectophores and eudoxids of *N.* sp. nov.(?) found in the *Beebe* collections from off Bermuda. These specimens were later (Totton 1954) ascribed to *N. diomedeae*.

Sears (1952) described another species of *Nectopyramis*, *N. spinosa*, from specimens collected during the *Dana* Expedition. The description was based on two 'nectophores', that had well-developed nectosacs, and five 'bracts', each of which had 'two threadlike branches [of the long tubular somatocyst, that] are given off dorsally and appear distally to have a globular connection.' (Sears 1952, p. 3). This author recognized the similarity between her material and that described by Moser (1925), under the name *Hippopodius* (?) *cuspitatus*. However, whereas in Moser's specimen the peculiar jagged spines appeared to be scattered over the whole surface of the nectophore, in *N. spinosa* these spines were arranged in discrete rows. Thus Sears considered *N. cuspitata* (*sic*) and *N. spinosa* to be separate species. Totton (1954), however, commented on the fact that the spinose condition was unusual, and he concluded that all the specimens probably belonged to the same species.

Totton (1954) described further material of *Nectopyramis spinosa*, and showed that the 'globular connection' in the so-called 'bract' was, in fact, an obsolescent nectosac; and the 'threadlike branches' of the somatocyst represented its dorsal and ventral radial canals. Thus the 'bract' is in actuality a nectophore. Therefore, he suggested (p. 86) that the nectophore with the obsolescent nectosac was the caducous larval one, because its somatocyst extended well beyond the nectosac, a 'characteristic of larval Prayid nectophores'; whereas, in the nectophore with a functional nectosac it 'stops short at the ventral radial canal . . ., just as it does at the pedicular canal in the definitive nectophores of Prayids'. However, these statements are in direct contrast to others he made during his discussion on the post-larvae of prayid and hippopodiid siphonophores (Totton 1954, pp. 75–77), where he noted that in the larval nectophore the 'pallial canal terminates at the inner end of the pedicular canal of the nectosac. In the definitive nectophore the pallial canal extends for some distance beyond this point'. This latter statement is certainly true for most prayid species but, as will be shown in this paper, such considerations are irrelevant as both types of nectophore are, in fact, larval ones belonging to other species.

Totton (1954) critically reviewed the earlier descriptions of what he recognized as four species of *Nectopyramis*, namely *N. thetis*, *N. diomedeae*, *N. natans*, and *N. spinosa*, and added a description of the polygastric (nectophore) stage of *N. natans*. He noted that there were several important differences in the basic arrangement of the nectophores and eudoxids between *N. thetis* and *N. diomedeae*, namely: (i) the dorsal and ventral radial canals to the nectosac of *N. thetis* do not arise in common with the lateral pair, as they do in *N. diomedeae*; (ii) the eudoxid of *N. thetis* has a special nectophore with similarly dissociated canals, whereas the largest bell in *N. diomedeae* is a true gonophore; (iii) the hydroecial cavity of *N. thetis* extends the whole length of the nectophore, while in *N. diomedeae* it is restricted to a pocket-shaped structure; (iv) there is a sharp bend in the somatocyst in the mid region of the nectophore of *N. thetis*, that is not apparent in that of *N. diomedeae*; and (v) the tentilla on the tentacles of *N. thetis* possess a terminal filament whereas those of *N. diomedeae* do not.

Totton noted that these morphological features of *Nectopyramis thetis* also were present on specimens of *N. natans*, and he concluded that these two species must be closely related. He also concluded that the overall appearance of the nectophore of *N. diomedeae*, with its simple radial canal system and the pocket-shaped hydroecium, was similar to that found in the larval nectophores of other prayid siphonophores, and thus that the animal was probably a neotenous form. He appears to have considered placing *N. diomedeae* into a separate genus, but decided against this because he considered it possible to homologize the arrangement of the somatocyst in the nectophore with that in *N. thetis*. In the present paper, it will be suggested that these two branching systems are not homologous and that *N. diomedeae* is not as closely related to *N. thetis* as Totton believed.

Totton (1965) resurrected Bigelow's (1911*b*) sub-family Nectopyramidinae, but placed it within the family Prayidae. He retained all the four species within the genus *Nectopyramis* and suggested that, with the exception of *N. spinosa*, each species only developed a single, larval nectophore. A description of a hitherto unknown eudoxid, that he ascribed to *N. spinosa*, also was given. This eudoxid was said to possess an asexual (special) nectophore.

Several records for specimens of *Nectopyramis* species have been published since Totton's (1965) monograph. In addition over 4300 specimens have been found in recent '*Discovery*' collections, mainly from the North Atlantic Ocean. The latter have enabled a critical review to be made of the earlier descriptions of the various species, and have necessitated a revision of the sub-family Nectopyramidinae. The basic conclusions reached here are: (i) that the two types of nectophore previously ascribed to *N. spinosa* are, in fact, the larval nectophores of two other species, namely *N. thetis* and *N. natans*; (ii) that there are sufficient reasons to place the species *diomedeae* into a separate genus, and consequently a new genus *Nectadamas* gen. nov. is erected. The hitherto unknown larval nectophore of *N. diomedeae* is described; and (iii) that the eudoxid that Totton (1965) ascribed to *Nectopyramis spinosa* actually belongs to a new species, *Nectadamas richardi* sp. nov., whose polygastric stage is described for the first time.

3. SUB-FAMILY: NECTOPYRAMIDINAE Bigelow 1911

Prayid siphonophores that develop only a single, definitive nectophore, bearing a pattern of ridges. The larval nectophore, where known, is relatively small and ovate and also bears ridges, as does the eudoxid bract, which resembles the definitive nectophore in general shape. True eudoxids are released. Two genera, *Nectopyramis* Bigelow 1911*a* and *Nectadamas* gen. nov., are recognized herein.

Genus: *Nectopyramis* Bigelow 1911

Nectopyramis Bigelow 1911*a*, 1911*b* (partim); Sears 1952; Totton 1954 (partim).
Archisoma Bigelow 1911*b*.
Type species: *Nectopyramis thetis* Bigelow 1911*a*.

Diagnosis

The elongate or pyramidal definitive nectophore bears a pattern of longitudinal ridges, although these may be ill-defined. The hydroecium stretches the entire length of the ventral surface, but apically has little if any depth. The somatocyst consists of a median pallial canal, which may have lateral branches and, basally, may be deflected to one side. The dorsal, lateral and ventral radial canals to the nectosac arise directly and separately from the pallial canal; the laterals also may arise separately.

The small larval nectophore bears a characteristic pattern of spinose ridges. The somatocyst is simple and the radial canals to the nectosac arise directly from it.

The somatocyst extends, basally, beyond the point of origin of the ventral radial canal.

The free-living eudoxid consists of a bract, a special nectophore, some small gonophores, and a gastrozooid and tentacle. The bract bears an apico-ventral and pairs of dorso-lateral and hydroecial ridges. The canal system conforms to the basic prayid design, but in one species is much reduced. A branch from the dorsal canal to the dorsal surface usually is present. The large special nectophore has the dorsal, lateral and ventral canals to the sub-umbrella arising separately, as in the definitive nectophore. The gonophores are small, and each eudoxid appears to be unisexual.

Discussion

Totton (1954, 1965) included four species in this genus, namely *Nectopyramis thetis* Bigelow 1911*a*, *N. diomedeae* Bigelow, 1911*b*, *N. natans* (Bigelow, 1911*b*) and *N. spinosa* Sears 1952, deeming it 'to be a better arrangement than recognition of three or four genera' (Totton 1965, p. 130). However, as is shown in the present paper, the two nectophores of *N. spinosa* are, in fact, the larval nectophores of two other species, namely *N. thetis* and *N. natans*. Also the morphology of *N. diomedeae* is deemed sufficiently different to warrant its removal to a new genus, *Nectadamas* gen. nov., within which also is included a new species, *N. richardi* sp. nov. The eudoxid of the latter species was described by Totton (1965) as belonging to *N. spinosa*. Thus the genus *Nectopyramis* is restricted to two species, *N. thetis* and *N. natans*.

The principal criteria distinguishing the genera *Nectopyramis* and *Nectadamas* are summarized in table 1. Totton (1954) also mentioned the sharp bend to the pallial canal in *N. thetis* and the absence of a terminal filament to the tentillum in *N. diomedeae*. However, the former is not always an obvious feature, and a terminal filament is present on the tentillum of *Nectadamas richardi* sp. nov. Totton's (1954) attempts to homologize the arrangement of the somatocyst canal system in *N. thetis* and *N. diomedeae*, do not appear to be sustainable, as is discussed in the section on *N. diomedeae*.

Nectopyramis thetis Bigelow 1911

Material examined

At least 646 definitive nectophores, 391 larval nectophores and 2070 eudoxids of *Nectopyramis thetis* have been identified from recent *Discovery* collections. Approximately 100 well-preserved specimens of each stage have been re-examined for this description.

Holotype

The single nectophore described by Bigelow (1911*a*), housed in the Natural History Museum under Regd. No. 1930.5.20.8, has been designated the holotype of the genotype. It came from the Bay of Biscay (47°03′N, 7°55′W) (HMS *Research* St. 36 *k* (25-vii-1900); depth range 300–0 fm (556–0 m)).

Diagnosis

Nectopyramidine siphonophore with a single pyra-

Table 1. *Principal morphological characters distinguishing the genera Nectopyramis and Nectadamas*

	Nectopyramis	*Nectadamas*
nectophore		
radial canals on nectosac	arise separately and directly from somatocyst	arise (almost) together from single pedicular canal
hydroecial cavity	extends virtually whole length	restricted to pocket-shaped structure
somatocyst	either simple or with lateral branches	three main branches lying in apico-dorsal plane. Others may be present
	lateral bend at base, usually to right side	no lateral bend at base
larval nectophore[a]	with spinose ridges	with non-spinose ridges
radial canals to nectosac	arise separately and directly from somatocyst	arise (almost) together from single pedicular canal.
eudoxid	with special nectophore	without special nectophore.

[a] Not yet found for *Nectadamas richardi.*

midal definitive nectophore, bearing indistinct ridges along the lateral margins of the apico- and baso-dorsal facets. The hydroecial opening extends the length of the nectophore, but has little depth close to the apex. The somatocyst consists of a median pallial canal which, in the region of the central organ, gives rise to a pair of hydroecial canals, from which divide dorso-lateral canals. Basally, the pallial canal usually bends towards the right side of the nectophore.

The small, ovoid larval nectophore bears a characteristic pattern of spinose ridges, including ones which form a 'figure-of-eight' on the dorso-lateral surfaces. The nectosac is greatly reduced and obsolescent. The somatocyst is simple, and gives rise directly to the radial canals to the nectosac. Usually there are only two radial canals, but from one to four can be present. The peri-hydroecial ridges, which usually are flared both basally and apically, run almost the entire length of the nectophore and surround the narrow, gutter-like opening of the hydroecium. The interior of the hydroecium is greatly expanded and houses a large bilobed central organ.

The eudoxid bears a pyramidal bract, which has a quadrangular dorsal facet edged by dorso-lateral ridges, and an apico-ventral and a pair of hydroecial ridges. There are six bracteal canals; the dorsal, which usually has a side branch to the dorsal surface, joining the right longitudinal proximal to the origin of the right hydroecial. The proximal parts of the longitudinal canals form a semicircular canal, which connects with the hemispherical central organ in three places. The hydroecial canals may or may not unite at or toward their distal ends.

The special nectophore occupies most of the hydroecium of the bract, and is strongly attached in the region of the semicircular canal. It has a long, deep hydroecium and a large nectosac, whose radial canal system resembles that of the definitive nectophore.

Description

Definitive nectophore. Only a single, highly distinctive, definitive nectophore is developed (figure 2). The maximum dimension is approximately 12 mm. Its pyramidal shape is, as Bigelow (1911a, p. 338)

described, 'so characteristic that it makes the animal noticeable at the first glance'. The mesogloea is relatively thick and the whole nectophore is rigid. It has four triangular facets, which are designated as apico-dorsal, baso-dorsal, and right and left laterals or ventro-laterals (figure 2). The margins of the facets are rounded, but a slight ridge can be discerned running along the lateral margins of the apico- and baso-dorsal facets. The dorsal margin between these two facets is rounded and usually concave in shape, although this may be the result of preservation. The nectosac lies in the middle of the basal half of the baso-dorsal facet and its opening is slightly raised above the general level of this facet. It measures up to 3.5 mm in height, but has a depth of only about 1 mm.

1. Hydroecium. The hydroecium stretches the entire length of the ventral margin but close to the apex it has little if any depth, although indistinct ridges can be discerned. These ridges form the ventral margins of the hydroecial flaps, which usually overlap each other, and peter out on the dorso-basal facet.

The depth and width of the hydroecium vary along its length (figure 2). The hydroecial opening extends onto the baso-dorsal facet, but has little depth or width. As the hydroecium passes beneath the nectosac it increases both in width and depth, reaching a maximum for both at about the mid-height of the nectophore. This depth and width is maintained in the region where the central organ is attached, before both decrease rapidly. Apical to this the hydroecium forms a narrow tube whose depth decreases to virtually nothing as the apex is approached.

2. Canal System. The somatocyst consists of a median pallial canal from which are branched pairs of hydroecial canals, which themselves give rise to dorso-lateral ones. Basally the pallial canal usually, but not always, bends toward the right lateral side of the nectophore before petering out (figure 2; Totton 1954, text-figure 37B). Additional short side branches, which run in varying directions, frequently are present in that region. Apical to this the pallial canal runs up over the dorsal wall of the hydroecium, in the mid-line until, toward the apex of the nectophore, it penetrates
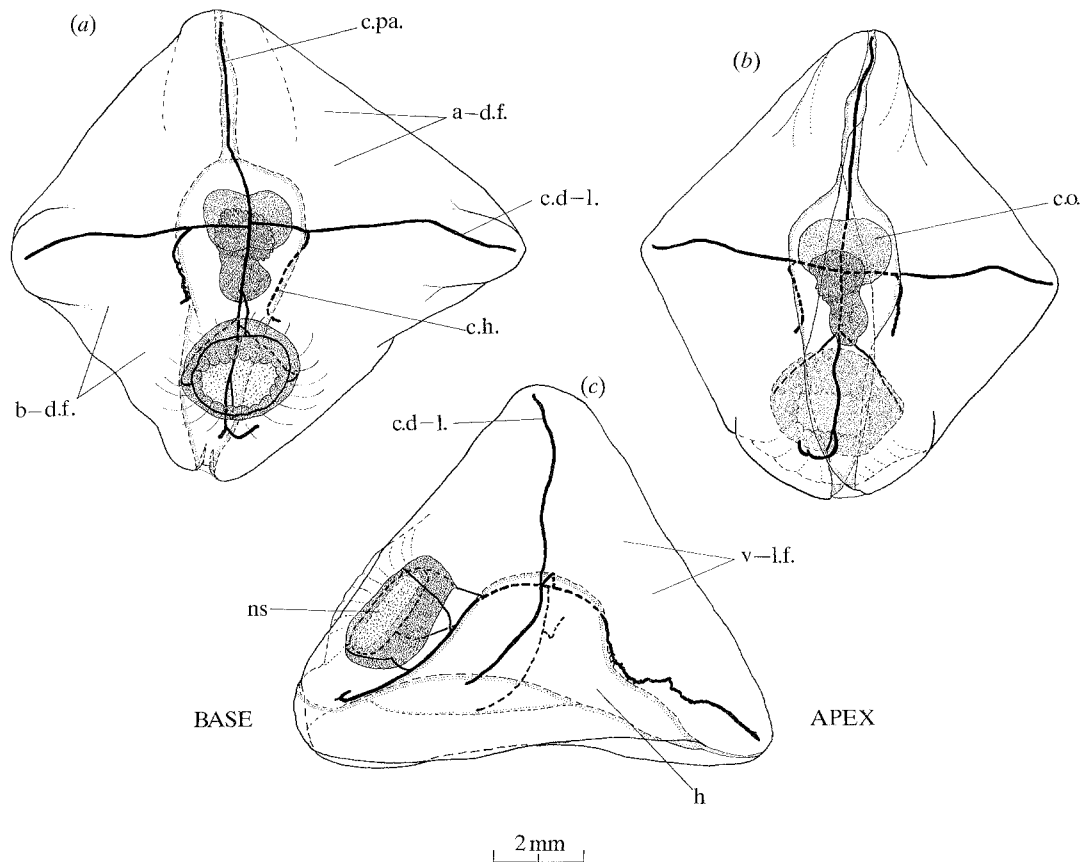
Figure 2. Definitive nectophore of *Nectopyramis thetis* Bigelow. (*a*) Dorsal, (*b*) ventral, and (*c*) lateral views of specimen from *Discovery* St. 7711#3. The central organ is omitted from (*c*). a-d.f., b-d.f. and v-l.f., apico-dorsal, baso-dorsal and ventro-lateral facets; c.d-l., c.h. and c.pa., dorso-lateral, hydroecial and pallial canals; c.o., central organ; h, hydroecium; ns, nectosac.

into the mesogloea and continues into the apical angle (figure 2*c*). Except in the mid region, the pallial canal is not always closely applied to the hydroecial wall and it may give off numerous processes, usually directed toward the hydroecial wall, which give the canal a very jagged appearance.

The radial canals to the nectosac arise directly, but separately, from the pallial canal and, as Bigelow (1911*a*) noted, join the nectosac at about its mid-depth (figure 2*c*). The order in which the two lateral canals arise, and the distance that separates them, is variable but in the majority of cases the right lateral canal arises apical to the left one, although very occasionally they arise together.

At about the mid-height of the nectophore the pallial canal branches off the right and left hydroecial canals. These canals do not generally arise together, and usually the right canal arises apical to the left (figure 2*a*), although the gap between them is frequently very small. The hydroecial canals run out laterally and then bend ventrad, at which point each branches off a dorso-lateral canal that runs directly up into the corresponding dorso-lateral angle and ends very close to the surface. The hydroecials continue to run ventrad but shortly bend basad to run down the sides of the hydroecium. These canals usually have a very jagged appearance, with many side processes. Often, shortly before they terminate, the canals bend out laterally, away from the hydroecial wall, and

penetrate into the mesogloea. In a few specimens either the right or the left hydroecial canal gives off another side branch on the lateral wall of the hydroecium. This branch canal appears on the dorsal side, but eventually curves round to run parallel to the hydroecial. Apart from the variable branching of the basal end of the pallial canal, this was the only other additional branching of the somatocyst canal system observed. Thus, in general, the canal system is very stable and, in the larger specimens, it does not continue to ramify into the mesogloea, as is the case in the nectophores of *Nectadamas* (*Nectopyramis*) *diomedeae*, and as Leloup (1933) suggested.

The central organ is attached below the pallial canal in the region between the origin of the hydroecial canals and that where the hydroecium begins to rapidly decrease in depth. It is laterally expanded and often has a bilobed appearance

At least fifteen of the larval nectophores of *Nectopyramis thetis* have been found to contain, within the hydroecium, a very young definitive nectophore (figures 3 and 4*b*). These young nectophores do not have the pyramidal shape of the fully developed definitive nectophore, but this would not be expected. For instance, the hydroecium is widely open so as to allow for attachment to the stem. The two dorso-lateral processes are in the process of development and lie close together, overhanging the nectosac. However, the basic design of the canal system can be seen clearly
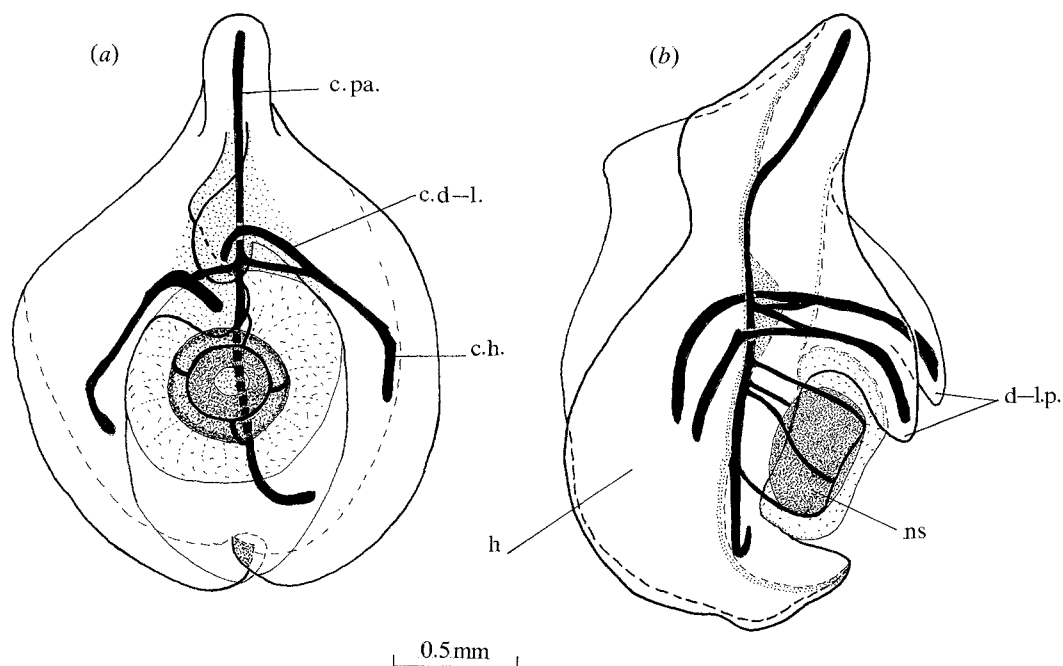
Figure 3. Developing definitive nectophore of *Nectopyramis thetis* Bigelow removed from hydroecium of larval nectophore. (*a*) Dorso-basal and (*b*) lateral views of specimen from *Discovery* St. 7711#7. The stem attachments and central organ have been removed. d-l.p., dorso-lateral processes. See figure 2 for other abbreviations.

and there can be no doubt that it is a young definitive nectophore of *N. thetis*, and, thereby, that the nectophore from whose hydroecium it was extracted is the larval nectophore of that species.

Larval nectophore (figures 4 and 5). The larval nectophore of *Nectopyramis thetis* previously was described as the 'bract' (Sears 1952) or the 'larval' nectophore (Totton 1965), with an obsolescent nectosac, of *N. spinosa*. Similarly, the larval nectophore of *N. natans*, described below, has been described as the nectophore (Sears 1952), with functional nectosac ('Totton 1965), of *N. spinosa*. The name *spinosa* thereby becomes a junior synonym partly of *N. thetis*, and partly of *N. natans*; and, indeed, partly of *Nectadamas richardi* sp. nov., as this is the species to which the eudoxid that Totton (1965) described under the name *N. spinosa* belongs.

The larval nectophores of *Nectopyramis natans* and *N. thetis* are distinguishable on the basis of characteristic differences in the ridge pattern, and on the respective presence of a functional or an obsolescent nectosac. None the less, they are very similar in basic shape and design, particularly in the presence of spinose ridges, and so it is not surprising that they have been assumed to belong to the same species. Indeed, Totton (1965) claimed to have found an early growth stage of the 'second type' of nectophore of *N. spinosa*, with a functional nectosac, within the hydroecium of the 'first type' of nectophore, with the obsolescent nectosac. However, a re-examination of Totton's material of '*N. spinosa*', housed in the Natural History Museum, did not reveal any such nectophores. It should be noted that the arrangement of the functional nectosac, and its radial canals, within the 'second type' of nectophore of '*N. spinosa*' is the same as that found in the
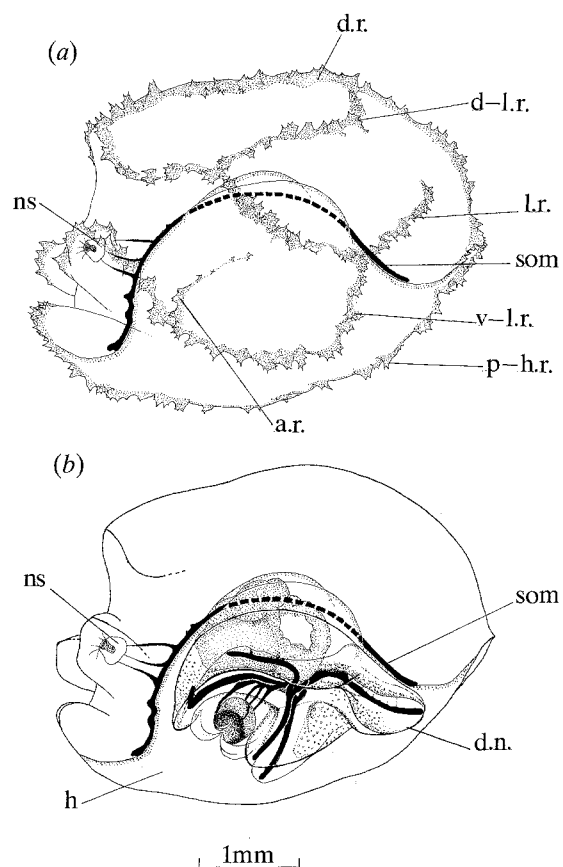

Figure 4. Larval nectophore of *Nectopyramis thetis* Bigelow. Lateral views, (*a*) showing ridge pattern, and (*b*) showing developing definitive nectophore within hydroecium of specimen from *Discovery* St. 7089#24. The ridges are: d.r., dorsal; d-l.r., dorso-lateral; l.r., lateral; p-h.r., peri-hydroecial; and v-l.r., ventro-lateral. Other abbreviations: d.n., developing definitive nectophore; h, hydroecium; ns, nectosac; som, somatocyst.
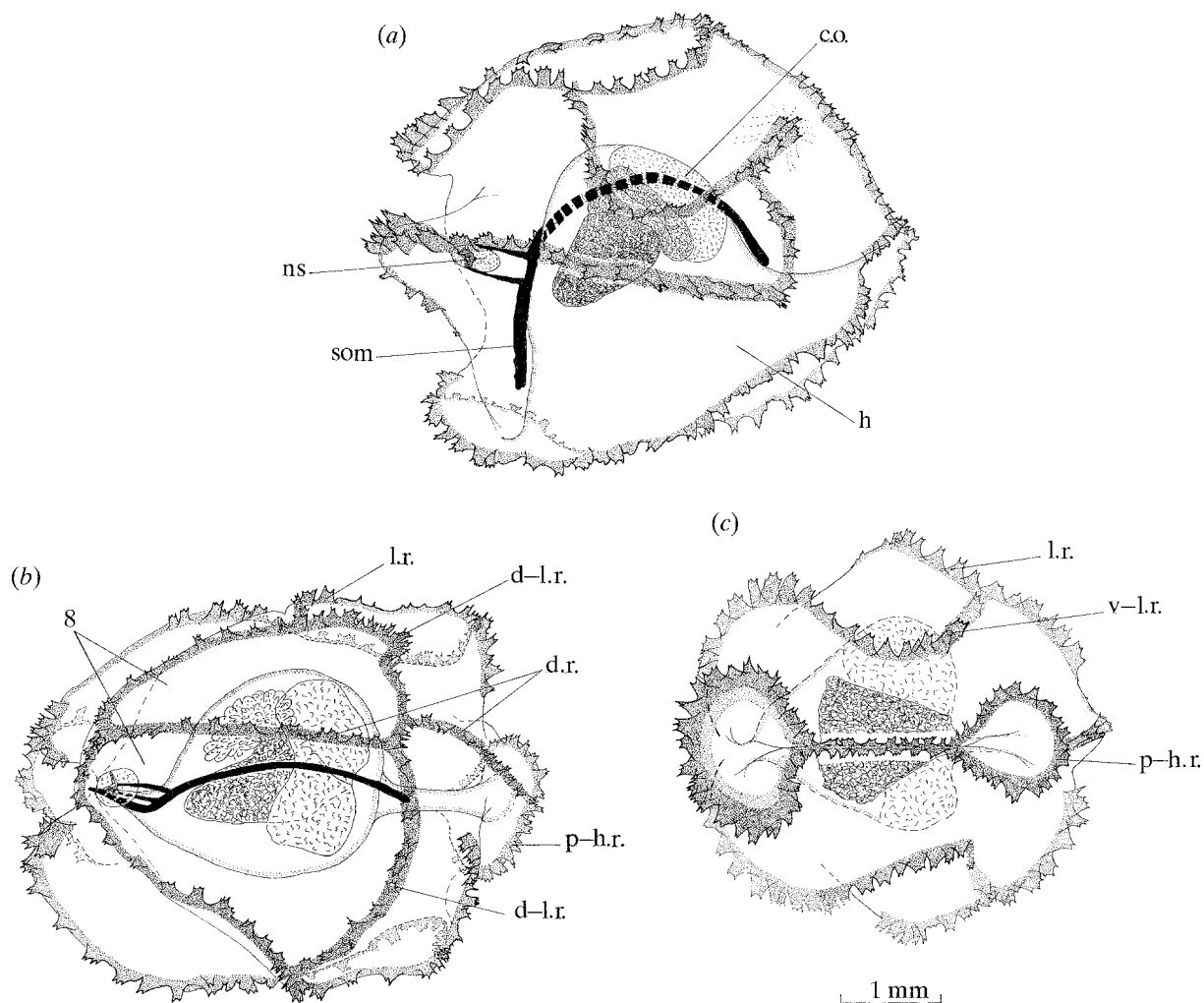
Figure 5. Larval nectophore of *Nectopyramis thetis* Bigelow. (*a*) Lateral, (*b*) dorsal views of specimen from *Discovery* St. 7716#2. (*c*) Ventral view of specimen from *Discovery* St. 8556#1, in which, for clarity, the somatocyst and nectosac have been omitted. See figure 4 for abbreviations. 8 denotes the 'figure-of-eight' pattern produced by the dorsal and dorso-lateral ridges; c.o., central organ.

definitive nectophores of both *N. thetis* and *N. natans*. Thus, unless other factors, such as the arrangement of the somatocyst, carefully are taken into account one might be easily misled, particularly if the nectophore was very small and only partially differentiated. It is concluded, therefore, that Totton (1965) was misled, by the presence of a functional nectosac, into identifying his 'early growth stage' as a nectophore of the 'second type of *N. spinosa*'.

The larval nectophore of *Nectopyramis thetis* is roughly ovoid in shape, although, to a varying degree, the basal end is indented above and below the necto-sac region (figures 4*a* and 5*a*; Totton 1954, plate V, figure 1). The dorsal indentation, shown in Totton's figure, apical to the 'figure-of-eight' ridges is unusual. The largest size recorded is 6 mm in length and 5.5 mm in height, but most specimens are smaller than this.

1. Ridge pattern. A characteristic pattern of ridges is present, and all ridges bear sawtooth-like projections or spines. Totton's (1965) description of this pattern does not appear to be complete, but his illustration (Totton 1965, figure 79B) shows it, for a

somewhat distorted nectophore. The basic pattern consists of:

(i) a median dorsal ridge (figure 4*a*), which runs from the apex of the hydroecium onto the dorsal surface where it continues as the cross ridge of the 'figure-of-eight' complex (figure 5*b*). However, it may not join the 'figure-of-eight' complex in the mid-line; the connection being displaced laterally to either side (figure 5*b*). In addition, apically the dorsal ridge may appear not to connect with either the 'figure-of-eight' or the peri-hydroecial ridges, although small connecting spines usually can be found; (ii) a pair of dorso-lateral ridges which, together with the part of the dorsal ridge, form the 'figure-of-eight' complex (figure 5*b*); (iii) a pair of lateral ridges (figures 4*a* and 5*a*), that depart from the lateral extremities of the 'figure-of-eight' and run ventrad or ventro-apically before curving round and running towards the apex of the nectophore. They may join, apically, with the median dorsal ridge, but more often appear not to; (iv) a pair of ventro-lateral ridges (figure 4*a* and 5*a*), which Totton (1965) referred to as 'buccal ridges'. These ridges usually connect with the lateral ridges in the

apical half of the nectophore, and from there run ventrad at first before curving round to run basad. However, the ventro-lateral ridges do not always appear to connect with the laterals, although this may be the result of loss of teeth by abrasion. Basally, the ventro-lateral ridges run along the margins of the two baso-lateral processes that project out on either side of the nectosac. These processes are of variable shape and may extend dorsally above the level of the necto-sac, or ventrally below it. This appears to affect the configuration of the ridges, although no consistent pattern emerges. The toothed ridges may run basad along the ventro-lateral margins of the processes and then turn dorsad to run along their basal margins before petering out, or vice versa. On those necto-phores where the baso-lateral processes are not expanded, the teeth can run basad over the lateral margins of the processes before running down their inner margins and ending close to the nectosac. However, additional teeth can be present on the baso-ventral or baso-dorsal margins; (v) a pair of peri-hydroecial (figures 4a and 5c) ridges that surround the ventral opening of the hydroecium, and connect api-cally with the median dorsal ridge. In the mid region of the nectophore these ridges are closely applied to each other, but both apically and basally they flare out laterally to enclose two rounded facets. The basal facet, particularly, can be extensive and can bend round onto the basal side of the nectophore, although this may be a preservation artifact. A comparable situation can pertain for the apical facet.

This basic pattern of toothed ridges can be seen on most of the specimens examined, but it is not infre-quent to find that some ridges are incomplete, as noted above, or that extra ridges are present. The most frequently found additional ridges are:

(i) one running between the lateral and ventro-lateral ridges, basal to their normal connection (a.r. figure 4a). Most often it is incomplete, and may then originate from either of the main ridges; (ii) one running from the ventro-lateral ridge, at the point where it usually bends dorsad, to the peri-hydroecial ridge; (iii) one running from the apico-lateral side of the 'figure of eight' towards the apical end of the lateral ridge.

Overall, the ridge pattern on the larval nectophore of *Nectopyramis thetis* differs markedly from that of *N. natans*, described below, particularly in the presence in the former of the 'figure-of-eight' complex of dorsal ridges, and the presence in the latter of an incomplete heptagon of ridges surrounding the ostium of the functional nectosac.

2. Hydroecium. The opening of the hydroecium, for the most part, is very narrow, but it opens broadly onto the basal and apical facets formed by the peri-hydroecial ridges (figure 5c). Within the nectophore, the hydroecium is greatly expanded, laterally, giving it a heart- or pear-shaped appearance when viewed dorsally (figure 5b). Much of its apico-dorsal region is occupied by a large, bilobed central organ (figure 5b) to which the stem elements are attached. As described above, a developing nectophore was found in the hydroecium of at least 15 specimens; the morphologi-

cal features of which were sufficient to establish it clearly as a definitive nectophore of *Nectopyramis thetis* (figures 3 and 4b).

3. Somatocyst. The somatocyst is a simple tube that runs over the median dorsal surface of the hydro-ecium; the latter being slightly indented in its mid region (figure 4a). Basally the somatocyst extends well beyond the origins of the radial canals to the nectosac, but does not bend laterally at its end. Although usually closely applied to the hydroecial wall, the somatocyst may deflect away slightly from it, but be connected to it by short processes.

The arrangement of the radial canals to the necto-sac is highly variable, although in the great majority of cases only two, dorsal and ventral, arise separately from the somatocyst (figure 5a). Usually they arise close together and run parallel with each other to reach the sides of the minute nectosac. However, often they arise further apart and have convergent courses. Many exceptions to this basic arrangement have been noted. These vary from only a single canal, which subsequently may divide, through to four separate canals arising from the somatocyst; with almost all possible intermediate stages (e.g. figure 4a, b). The radial canals often appear to open directly into the nectosac, although Totton (1954) observed them to connect with an ostial ring canal.

The nectosac itself varies in size from a minute knob to about 0.45 mm in height, although laterally com-pressed. In a few specimens a minute ostium is appar-ent, but in most this seems to be occluded by an amorphous mass of tissue. The whole cavity of the nectosac can be filled with this tissue and, in some specimens, the cavity is devoid of musculature. It is doubtful that the nectosac is functional.

Eudoxid. Leloup (1932) gave the first description of a well developed eudoxid, and Totton (1954) added some further notes and figures. It consists of a large, pyramidal bract enclosing a special nectophore, a gastrozooid and tentacle, and some gonophores.

1. Bract. The fully developed bract (figure 6a, b) has the shape of an inverted pyramid and the largest specimen found measures 14 mm in length and 12 mm in breadth. It bears two dorso-lateral, angular promi-nences and another which represents the ventral lobe of a typical prayid eudoxid bract. In addition the apex is angular. There are five facets (figure 6d), the most pronounced of which is flattened and quad-rangular and lies on what is here called, in accord with Totton (1954), the dorsal surface. The edges of this facet, although rounded, bear distinct dorso-lateral ridges. The pairs of triangular lateral facets on each side tend to merge into each other, being separ-ated by only a rounded margin. Frequently the left lateral side of the bract appears to be less thickened than the right and the margin between the lateral facets becomes concave. This also results in the ventral process being folded over on to the left side, and a consequent slight displacement of the hydroecial opening, such that the special nectophore appears to lie at an angle. However, this is most likely a preserva-

tion artifact as the best preserved material is symmetrical.

An apico-ventral ridge runs in the mid-line from the angular apex of the bract to the tip of the ventral lobe (figure 6*d*). It appears that this ridge may continue over this process and run down toward the hydroecium, where it joins the two hydroecial ridges. However, it is very weakly expressed and often difficult to see. The hydroecial ridges run down the lateral margins of the hydroecial opening to the base of the bract. Here they unite to close off the hydroecium, although each appears also to run over the basal margin and join up with the corresponding lateral ridge of the dorsal facet (figure 6*a*). A similar arrangement was seen in a few of the bracts of *Nectopyramis natans*.

The hydroecium occupies about two thirds the length and height of the bract (figure 6*a*), reaching a maximum depth and width in the mid region. Apical to this, in the region of attachment of the central organ, it curves downward and undercuts itself before rapidly losing depth. Most of the widely open hydroecial cavity is filled by a large special nectophore, within the hydroecial flaps of which lie the other stem components. The hydroecial cavity is speckled with patches of ectodermal cells (not illustrated for clarity), which are assumed to be sources of bioluminescence, as has been found for other prayid species (P. J. Herring, personal communication).

The bracteal canal system conforms to the basic prayid design, and consists of six canals. In accordance with modern terminology (see Pugh & Harbison 1987) these canals are referred to as a dorsal, a ventral, and pairs of longitudinals and hydroecials (figure 6). The dorsal, Totton's (1965) c^3, runs from close to the apical angle of the bract down to join the right longitudinal canal. At first it runs in the mid-line, although it may loop toward the dorsal surface, before veering to the right, at which point it gives off a side branch. The height at which this side branch appears is variable, and occasionally it is absent, as appears to be the case for the specimen described by Leloup (1932). The branch runs up to the dorsal facet and usually ends beneath a shallow depression in the latter. Occasionally, it has a sub-terminal bifurcation. On a few occasions an extra blind-ending, dorsad branch was given off closer to the hydroecium.
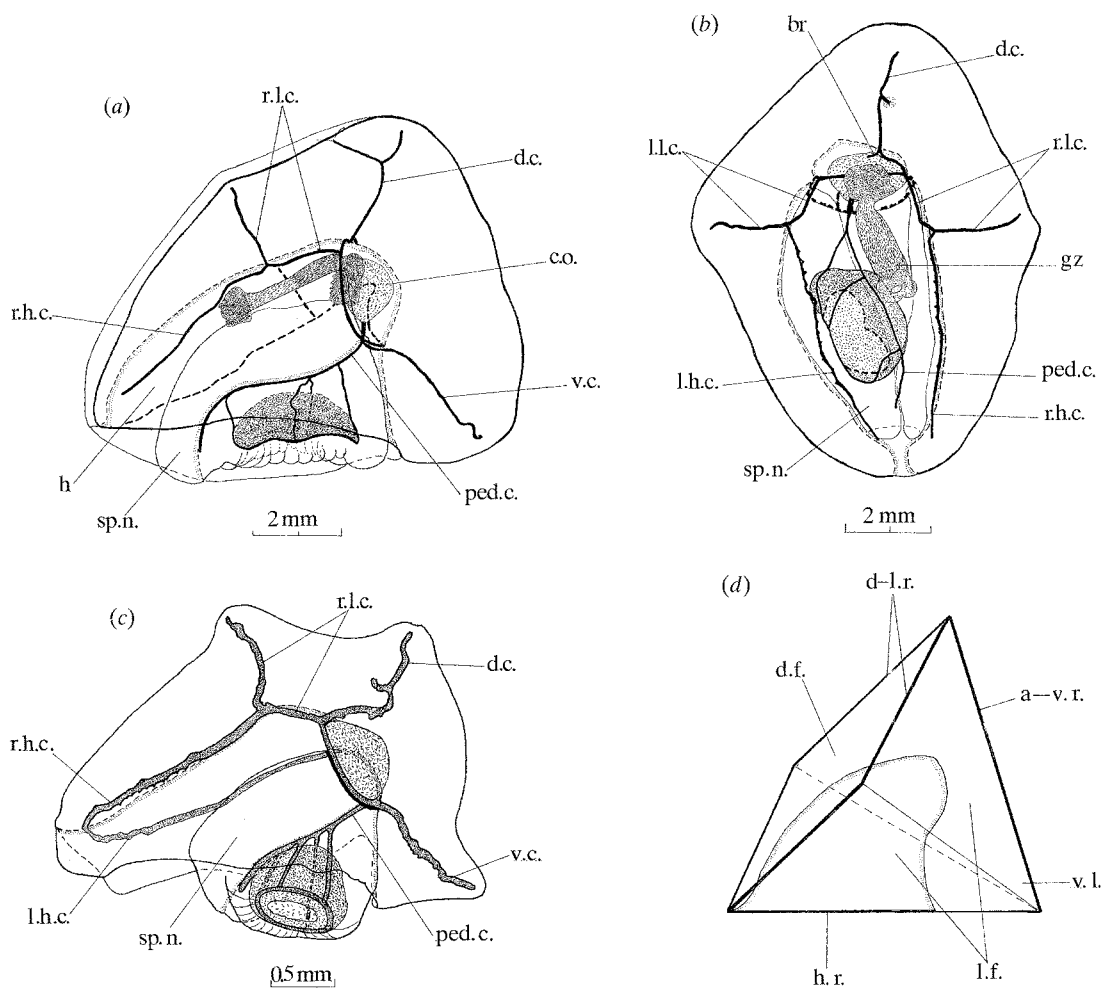

Figure 6. Eudoxid of *Nectopyramis thetis* Bigelow. (*a*) Lateral and (*b*) dorsal views of mature eudoxid from *Discovery* St. 8648#7. (*c*) Lateral view of developing eudoxid removed from hydroecium of definitive nectophore from *Discovery* St. 7711#3. (*d*) Schematic diagram of eudoxid bract showing ridges and facets. See figure 1*b* for canal system abbreviations. a-v.r., d-l.r., and h.r., apico-ventral, dorso-lateral and hydroecial ridges; c.o. central organ; d.f. and l.f., dorsal and lateral facets; gz, gastrozooid; h, hydroecium; ped.c., pedicular canal of special nectophore (sp.n.); v.l., ventral lobe.

On reaching the hydroecial wall, the dorsal canal frequently gives off a laterally (left) directed branch, of variable length (br in figure 6b). It then travels down the side of the hydroecial wall to join the right longitudinal canal, at the point where the latter bends basad. Leloup (1932, 1933), because he orientated the bract differently, called this latter canal the left longitudinal. Bigelow's (1911a, plate 28, figure 3) illustration of a very young, developing bract shows the c^3, or dorsal, canal arising from the junction of the longitudinals, in the mid-line. However, this is not the case in the youngest *Discovery* material (figure 6c).

The proximal parts of the longitudinal canals form the 'semicircular bracteal canal' (Totton 1954). In this region the special nectophore is attached and the central organ is suspended (figure 6a, b and 7). The latter has three main areas of attachment, two lateral, where the longitudinal bracteal canals turn basad, and one ventral, where the longitudinals join with the pedicular canal of the special nectophore. It appears that, at each point, a canal joins it to the semicircular canal, as Leloup (1933) described. However, probably due to preservation damage, these canals are not always apparent, particularly the lateral ones. This led Totton (1954, p. 80) to consider that 'the pedicular canal of the special nectophore . . . does not arise, as it can appear to do, from the semicircular bracteal canal, but from the central organ itself'.

The well-developed central organ is roughly hemispherical in shape, rather than bilobed (Totton 1954) or triangular (Leloup 1933), and occupies all, or most, of the overhanging part of the hydroecium (figure 6a, c). The base of the gastrozooid opens into the middle of its flattened surface, and the gonophores, at various developmental stages, are inserted on the ventral side of the gastrozooid. As Totton (1954) suggested, the central organ probably serves as a food reservoir. However, Totton (1954, p. 80) also suggested that 'the cavity of the bracteal canal system is isolated from that of the stem in the fully formed eudoxids of Prayids' and that 'in *Rosacea plicata* the central organ . . . represents a development of the remains of the stem'. This seems to imply that the bract and the remaining components of the eudoxid do not share a common gastrovascular system. This would seem unlikely and, as noted above, the central organ appears to have three connections to the bracteal canal system.

The ventral bracteal canal (figure 6a), Totton's (1954) c^4, usually joins the semicircular canal slightly to the right of, but occasionally at or to the left of, the point of insertion of the pedicular canal of the special nectophore. It runs down into the ventral process and ends very close to its tip.

The longitudinal canals, after bending basad away from their semicircular region, run down for a short distance on either side of the dorsal wall of the hydroecium before bending out into the mesogloea and running to the tips of the dorso-lateral processes (figure 6b). Whether the distal parts of these canals, because of their positioning, truly are homologous with the longitudinal bracteal canals of prayine species, which usually overlie the region of stem attachment, is uncertain. However, Totton (1954), who like

Leloup (1933) referred to them as the lateral canals, believed this to be the case.

As the longitudinal canals bend away from the hydroecial wall they give rise to the hydroecial canals, which continue to run down the sides of the hydroecium towards its base, but end slightly above it (figure 6). Both Leloup (1932, 1933) and Totton (1954, 1965) refer to these canals as distal extensions of the longitudinals, but this is not in accord with more recent practice. In most specimens the hydroecial canals remain separate, but in a few they curve round toward the mid-line and unite (figure 6c), as Leloup (1933) noted for one of his specimens. This does not appear to be age-related, as they did not join in Bigelow's (1911a) very small specimen, whereas they did in one of the largest *Discovery* ones. In one specimen a single canal continues basad of the junction; a situation very reminiscent of that found in most of the bracts of *Nectopyramis natans*. Usually the hydroecial canals, and the mid-regions of the longitudinals, are not closely applied to the hydroecial wall, but send out numerous short processes to it. Consequently they have a jagged appearance, as was noted for the hydroecial canals of the nectophore.

The arrangement of the canals of the bract, as with those of the nectophore, appears to be remarkably stable. Apart from the additional branch to the dorsal canal, noted above, only one other specimen was found to have an extra canal. This arose from the mid-region of the right longitudinal canal and ran out toward the apico-ventral ridge, but ended well short of it.

2. Special nectophore (figure 7). The large special nectophore, measuring up to *ca.* 6 mm in length, occupies most of the hydroecium of the bract. It is strongly attached to the bract in the region of the semicircular canal. There are no obvious ridges. It has a deep hydroecial cavity, running the length of the nectophore, flanked by extensive, wing-like flaps. Much of the remainder of the nectophore is occupied by a large nectosac. The hydroecial and subumbrella cavities are speckled with patches of ectodermal cells, which are assumed to be sites of bioluminescence.

The arrangement of the canal system (figure 7) strikingly resembles that in the definitive nectophore. The pedicular canal is inserted into the base of the semicircular canal and runs down beneath the hydroecium, in the mid-line, to end close to the base of the latter. The dorsal, lateral and ventral radial canals are given off separately, and run down to meet the nectosac about half way down. In a little over half of specimens examined, the lateral canals arise together, while in the others the left usually arose first. Very occasionally only a single lateral canal leaves the pedicular canal, which subsequently divides. The special nectophore never contains a manubrium within the subumbrella cavity and, therefore, is a true asexual nectophore. Bigelow (1911a) appears to have been mistaken when he described a minute spadix in his very young specimen, and Bigelow & Sears (1937) made no mention of it, accepting Leloup's (1933) view that the nectophore was asexual. Indeed, it is difficult to imagine where a spadix could be attached as there
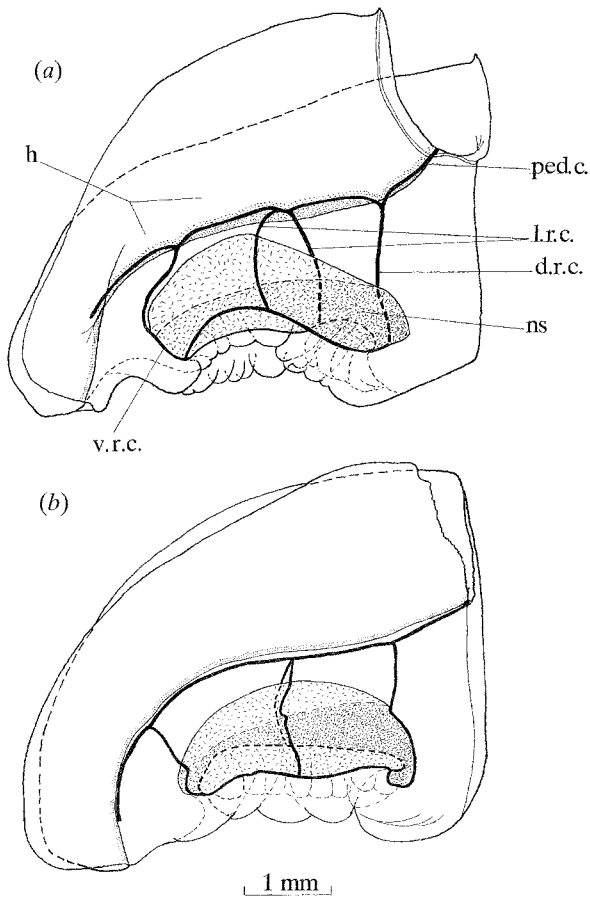
Figure 7. Special nectophore of *Nectopyramis thetis* Bigelow. (*a*) and (*b*) Lateral views of specimen from *Discovery* St. 8648#7. d.r.c., l.r.c., and v.r.c dorsal, lateral and ventral canals to nectosac (ns); h, hydroecium; ped.c., pedicular canal.

is not a singular canal running to the subumbrella. *Gonophores* (figure 8*a*, *b*). The gonophores are small, about 3 mm in length when fully developed, and attached to the central organ at the base of the gastrozooid. Up to five, at various stages of development, have been found on an individual specimen. They have a wing-like expansion at their apex, and have been well described by Leloup (1933). Each eudoxid is unisexual, as Leloup (1933) described, although this was mis-interpreted by Bigelow and Sears (1937).

3. Gastrozooid and tentacle. The gastrozooid is inserted onto the middle of the central organ. Both Bigelow (1911*a*) and Leloup (1933) describe it as having a well-developed basigaster, although this probably results from contraction during preservation, as it does not always have this appearance. The mouth opening often has four lobes. The tentillum (figure 8*c*) consists of a pedicel, a C-shaped cnidoband, and a terminal filament, which is presumed to be long, although always tightly coiled in the preserved state. The cnidoband has a row of 10 to 15 large, 80 μm × 21 μm, nematocysts on either side; and several rows of smaller, 48 μm × 8 μm, ones between. The terminal filament also bears two types of nematocysts, whose arrangement could not be discerned. One type is

elongate, measuring 22 μm × 5 μm, and the others ovoid, measuring 16 μm × 13 μm. None of the nematocysts has been examined in detail.

Distribution

Nectopyramis thetis is the best known nectopyramidine species and is well recorded in the literature (table 2). The great majority of records come from the North Atlantic Ocean and there are very few from, for instance, the Pacific. However, many authors do not record either the number of specimens or which stage was collected. In addition, in the case of records for '*N. spinosa*', many authors, particularly Alvarino, fail to state which type of nectophore they found. Thus it is impossible to know whether the author was referring to the larval nectophore of *N. thetis* or that of *N. natans*.

Over 3000 specimens (646 definitive and 391 larval nectophores; and 2070 eudoxids) of *Nectopyramis thetis* have been identified from over 450 hauls in the more recent *Discovery* collections. The data are too extensive to list here, but those for the Northeast Atlantic are summarized in table 3. A complete listing can be obtained from the author. This table shows the species to be widely distributed, but with maximum numbers in the 30–50°N latitudinal range. *N. thetis* has been collected at most depths from close to the surface down to 4000 m. However, over 80% of all stages have been found within the 300–700 m depth range (figure 9). There appears to be a latitudinal change in the depth distribution; being shallower at higher latitudes. In addition, whereas the definitive nectophores and eudoxids were most abundant in the 400–600 m depth range, the larval nectophores were mainly found between 300 and 400 m.

Nectopyramis natans (Bigelow 1911)

Archisoma natans Bigelow 1911*b*; 1919; 1931.

Hippopodius (?) cuspitatus Moser 1925.

Nectopyramis spinosa (partim) Sears 1952; Totton 1954, 1965.

Nectopyramis natans Totton 1954; 1965; Stepanjants 1967

Material examined

At least 33 definitive nectophores, 45 larval nectophores, and 70 eudoxids are present in recent *Discovery* Collections housed at the Institute of Oceanographic Sciences. Most of these have been re-examined for this description.

Holotype

Bigelow (1911*b*) designated his specimen of an eudoxid as the type specimen of his new genus and species *Archisoma natans*. This specimen was collected at *Albatross* St. 4719 and is housed in the collections of the National Museum of Natural History (Smithsonian Institution) Cat. No. 29744.

Sears (1952) designated one of her specimens of the 'nectophore' as the type of *N. spinosa*. This specimen came from *Dana* St. 3933#4, and is housed in the collections of the University Museum, Copenhagen. As is established herein, these nectophores are the
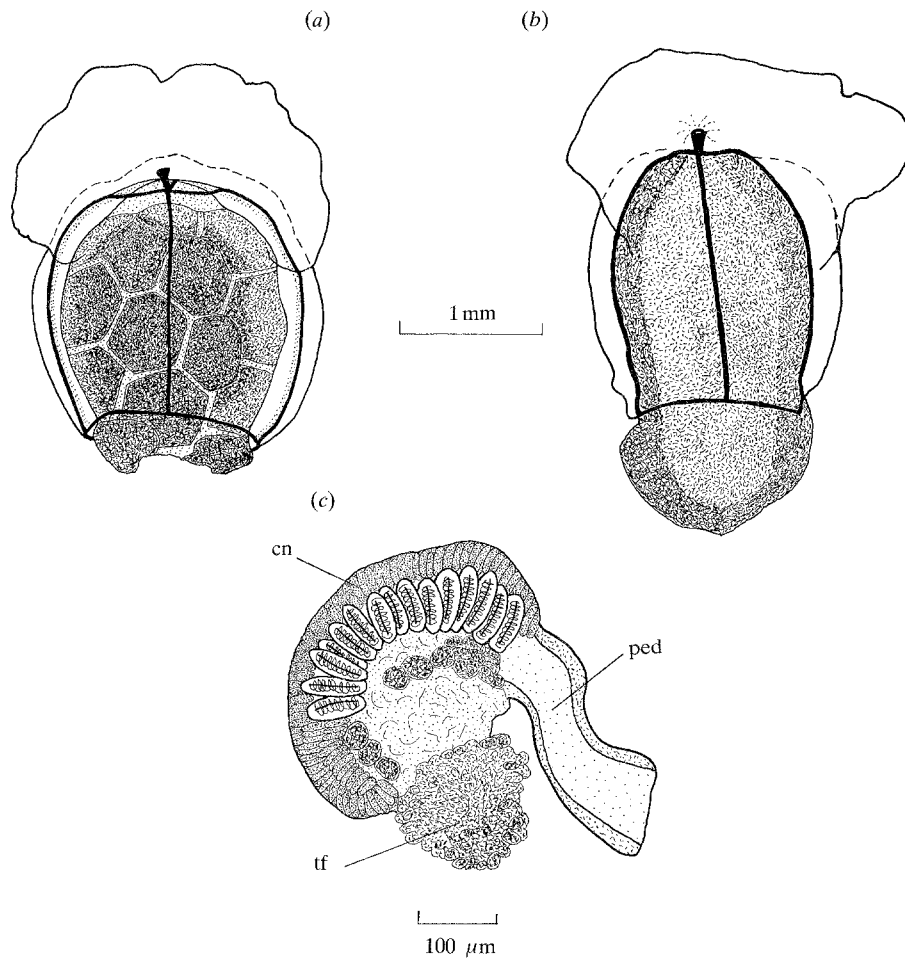
(a)   (b)

(c)

1 mm

100 μm

Figure 8. *Nectopyramis thetis* Bigelow. (a) Female and (b) male gonophores. (c) Tentillum. cn, cnidoband; ped, pedicel; tf, terminal filament.

60N   20W
10 5   5 10
0

500

depth / m   1000

1500

2000

53N   20W
10 5   5 10
0

500

1000

1500

2000

49 . 5N   14W
10 5   5 10
0

500

1000

1500

2000

44N   13W
10 5   5 10
0

500

1000

1500

2000

42N   17W
10 5   5 10
0

500

1000

1500

2000

40N   20W
10 5   5 10
0

500

depth / m   1000

1500

2000

30N   23W
10 5   5 10
0

500

1000

1500

2000

18N   20W
10 5   5 10
0

500

1000

1500

2000

11N   20W
10 5   5 10
0

500

1000

1500

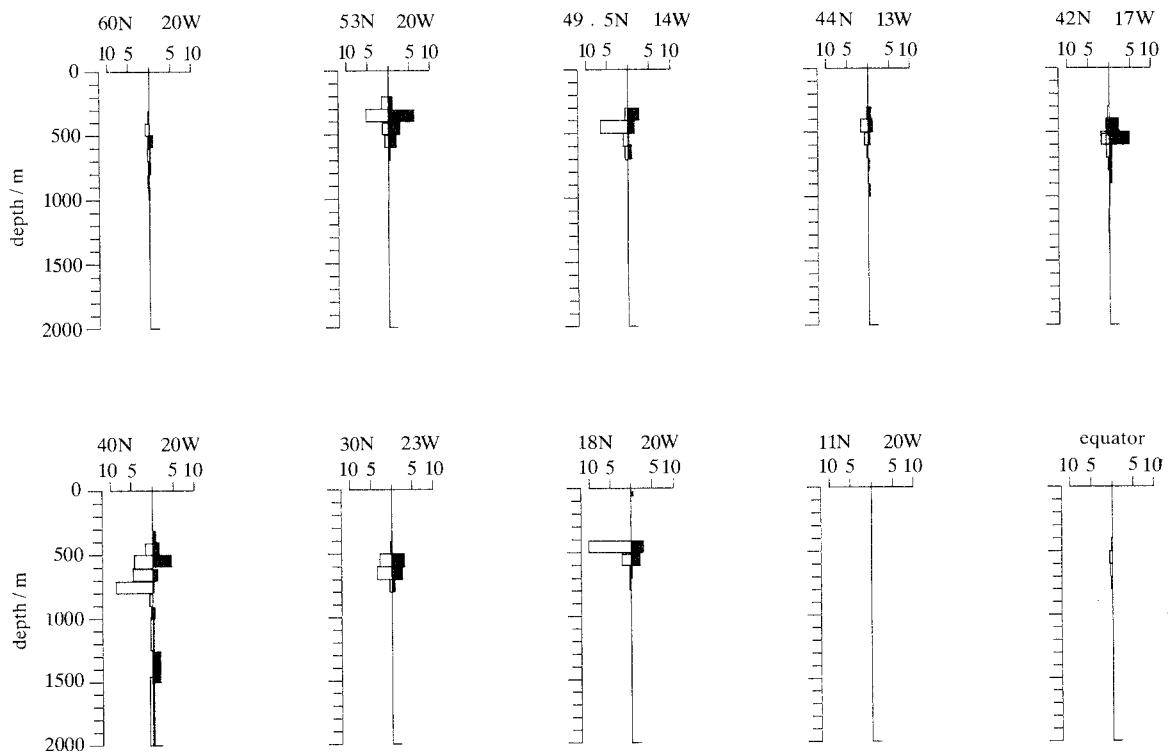2000

equator
10 5   5 10
0

500

1000

1500

2000

Figure 9. Depth distribution of *Nectopyramis thetis* Bigelow, by day and night (left and right of ordinate respectively), at various *Discovery* stations in the Northeast Atlantic. Number of specimens, of all stages, per 10⁴ cubic metres.

Table 2. *Published records for Nectopyramis thetis Bigelow*

(dn, definitive nectophores; ln, larval nectophores, e, eudoxids.)

North Atlantic Ocean

Bigelow (1911a)	1 dn (+ 1 e)	47°03′N 7°55′W
Leloup (1933, 1936)	1 dn, 10 e	28–37°N 16–43°W
Bigelow & Sears (1937)	1 dn	35°53′N 7°26′W
	1 e	47°01′N 5°48′W
Totton (1954)	2 dn, 2 ln[c], 2 e	54–58°N, 8–17°W
Leloup (1955)	3 dn, 3 e	34–48°N 13–48°W
Furnestin (1957)	?	off coast of Morocco
Fraser (1961, 1967)	?, 3 ln	54–60°N 7–16°W
Patriti (1965)	1 dn?	45°03′N 10°21′W
Totton (1965)	2 ln	
van Soest (1973)[a]	2 e	39°15′N 21°25′W
	2 e	45°N 16°W
Margulis (1974)	?	10°S–57°N, 8–31°W
Pugh (1974)[b]	77 dn, 18 ln, 118 e	ca. 28°N 14°W
Pugh (1975)	3 dn, 6 ln, 15 e	ca. 32°N, 16–60°W
Kinzer (1977)	1 e	19°38′N 17°08.5′W
Casanova 1980[a]	3 dn, 7 ln, 2 e	30°18′N 29°20′W
Pugh (1990)[a]	25 dn, 2 ln, 105 e	47°N 20°W

South Atlantic Ocean

Sears (1952)	1 ln	7°34′S 8°48′E
Totton (1954)	2 dn, 2e	ca. 3°S 4–8°W
	1 ln	12°30′S 3°42′W
	1 dn, 5e	ca. 31–34°S 6°E–30°W
Alvarino (1971)	?	32°30′S 9°04′E
	?	18°58′S 10°15′W

Indian Ocean

Sears (1952)	2 ln	5°28′S 130°39′E (Banda Sea)
	1 ln	1°12′N 62°19′E
	1 ln	25°19′S 36°13′E
Totton (1954)	3 dn, 9 e	S.E. and E. coast Africa
	2 dn, 2 e	South Indian Ocean
Alvarino (1964)	?	Central Indian Ocean
Daniel (1974)	1 ln	2°03′S 91°27′E

Pacific Ocean

Alvarino (1967)	?	30°30′N 120°W
Stepanjants (1967)	?	38°N 144°E

[a] Additional information from personal communications.

[b] Denotes amendment to published data.

[c] Also mentioned by Fraser (1961).

Table 3. *Latitudinal distribution of Nectopyramis thetis Bigelow in recent Discovery collections from the North-east Atlantic Ocean*

(No siphonophore data for *Discovery* stations between 5 and 10°N and 21–29°N.)

latitude range	no. hauls with specimens	% total stations	definitive nectophores	larval nectophores	eudoxids
0–5°N	6	13.6	2	2	9
10–15°N	5	11.9	0	0	13
15–21°N	29	48.3	67	87	154
29–35°N	94	27.7	71	60	257
35–40°N	53	39.0	124	31	215
40–45°N	173	53.1	237	139	751
45–50°N	69	43.4	103	39	522
50–55°N	12	33.3	29	28	115
55–60°N	12	38.7	11	4	26

larval nectophores of *N. natans*. Therefore, Sear's specimen is reduced to the holotype of the junior synonym.

Diagnosis

Nectopyramidine siphonophore with a single, elongate, bow-shaped definitive nectophore, with a pointed apex and a truncated base, and a characteristic pattern of seven longitudinal ridges. Only the single dorsal and the pair of hydroecial ridges unite at the apex. At the base, the hydroecial ridge on each side curves over to unite with the corresponding dorso-lateral, or occasionally ventro-lateral, ridge. The hydroecium runs the entire length of the nectophore, although in the apical third it has very little, if any, depth. The somatocyst is a simple tube, devoid of side branches.

The caducous larval nectophore is relatively small and roughly egg-shaped in outline. It bears a characteristic pattern of nine spinose, longitudinal ridges. The basal facet, within which lies the ostial opening of the small, but functional, nectosac, is surrounded by an incomplete heptagon of spinose ridges. The hydroecial opening is a narrow, ventral gutter, which extends from the base to about two thirds the height of the nectophore. The interior of the hydroecium is greatly expanded laterally and contains a large, bilobed central organ. The somatocyst is a simple, unbranched, tube from which the four radial canals to the nectosac arise directly. It bends sharply toward the right side of the nectophore at its base.

The eudoxid bears a bract and a special nectophore, and resembles an arrow-head. The bract is elongate and bow-shaped and usually is pointed both apically and basally. Occasionally, the latter may be truncated. It bears five longitudinal ridges. The apico-ventral and the pair of dorso-lateral ridges meet at the apex, whereas the pairs of dorso-laterals and hydroecials usually unite at the base. The upper part of the hydroecium is widely open to accommodate the special nectophore. The canal system is relatively simple, consisting of a dorsal, which runs apically and gives off a side branch to the dorsal surface, and two hydroecial canals. However, the proximal parts of the latter probably should be considered as the longitudinal canals, without 'spur' canals. The two hydroecial canals usually unite towards the base of the bract, but remain separate in those bracts with truncated bases.

The special nectophore is about half the length of the bract, and is rounded apically and truncated basally. The nectosac is situated on the dorsal surface and the arrangement of its radial canals is identical to that in the definitive and larval nectophores. Above the nectosac there is a median dorsal ridge, while basal to it a pair of dorso-lateral ridges define the margins of a concave dorsal facet. An apparently separate pair of dorso-lateral ridges may be present in the apical half of the nectophore.

Description

Definitive nectophore. Only a single definitive nectophore is developed. The nectophore is bow-shaped

and the maximum length and depth (dorso-ventral direction) recorded are 38 mm and 11.5 mm respectively. The apex of the nectophore is pointed, whereas the base is truncated (figure 10).

1. Ridge pattern. There are seven longitudinal ridges, which are designated as a dorsal, and pairs of dorso-laterals, ventro-laterals and hydroecials (figure 10*a*). Only three ridges, the dorsal and, usually, the pair of hydroecials, reach to the apex of the nectophore; whereas four ridges, the hydroecials and the dorso- or ventro-laterals reach the truncated base. The hydroecial ridges are the only ones that run the entire length of the nectophore, except in one specimen where they peter out before reaching the apex, and it is the ventro-laterals that unite with the dorsal. At the base they do not unite together, but each curves round to unite with the corresponding dorso- or ventro-lateral ridge.

The dorsal ridge runs down, in the mid-line, and ends over the nectosac. In several specimens, this ridge is very pronounced, particularly in its lower region, such that the nectophore appears to have a dorsal 'sail'. However, this may be an artifact resulting from shrinkage of the surrounding tissue during preservation.

There are two basic arrangements for the dorso- and ventro-lateral ridges. In the first case (figure 10*a*, *b*, *d*), which applies to most of the nectophores examined, the dorso-lateral ridges stretch from very close to the apex of the nectophore down to its base. Below the nectosac they define the margins of a flattened dorso-basal facet. At the base they do not unite with each other but curve over the truncated end and unite with the corresponding right or left hydroecial. The ventro-lateral ridges usually do not extend apically as far as the dorso-laterals, and in some cases each appears to merge with the corresponding hydroecial. They run down the sides of the nectophore and usually end below the nectosac. In some specimens, however, they extend a little further and in one specimen, from *Discovery* St. 7803#13, each appears to unite with the corresponding dorso-lateral.

In the second case (figure 10*c*), as described by Totton (1954), the dorso-laterals run down from close to the apex of the nectophore and end on the sides of the nectosac. The ventro-lateral ridges, however, extend down to the base of the nectophore. In the region of the nectosac, these ridges bend sharply, in a dorso-basal direction, before running down to the base whilst defining the edges of the dorso-basal facet below the nectosac. This arrangement has been noted on only four specimens from *Discovery* stations 101, 2064, 10380#34 and 11262#3.

2. Hydroecium. The hydroecium runs the entire length of the nectophore, but apically has very little if any depth. There the hydroecial ridges define the edges of a very slightly concave ventral facet. Basal to this the hydroecium gradually increases in depth until about half way down the nectophore, when its depth rapidly increases to accommodate the stem appendages. The hydroecium is open basally.

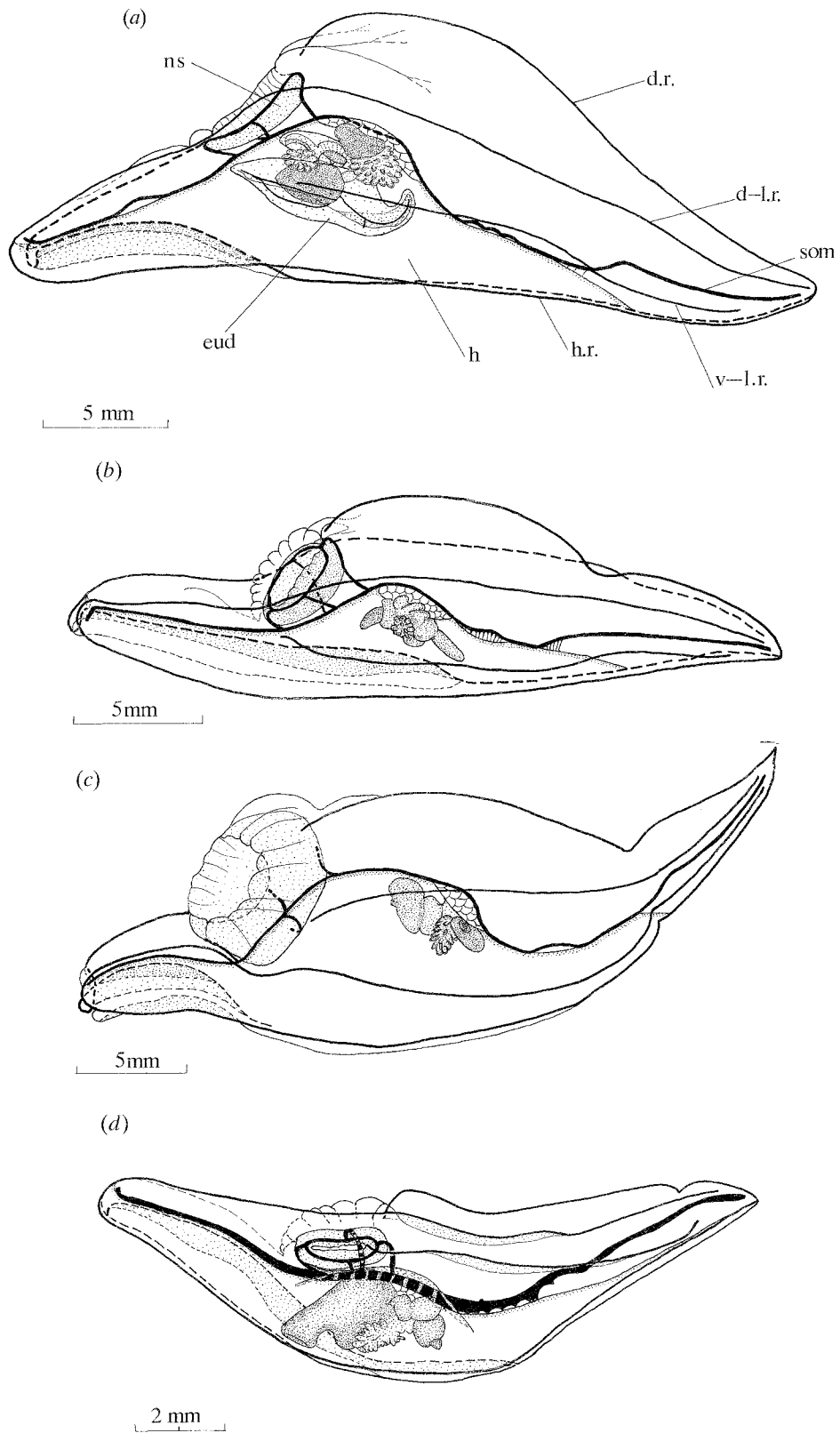The ventral margins of the hydroecial opening are demarcated by ridges, but additional flaps may be

(a)

ns

d.r.

d–l.r.

som

eud

h

h.r.

v—l.r.

5 mm

(b)

5mm

(c)

5mm

(d)

2 mm

Figure 10. Definitive nectophores of *Nectopyramis natans* (Bigelow). Lateral views of mature nectophores from (*a*) *Discovery* St. 7803#12, (*b*) *Discovery* St. 7089#9, and (*c*) *Discovery* St. 11262#3. (*d*) Lateral view of developing nectophore from *Discovery* St. 7089#15. See figure 4 for abbreviations. eud, developing eudoxid; h.r., hydroecial ridge.

developed. The flap on the right-hand side, when present, usually is small. That on the left is well developed, particularly in the basal third of the necto-phore, and overlays the other so that the hydroecium becomes a tube that opens only at its base.

3. Canal System. The somatocyst is a simple median, longitudinal canal without any side branches (figure 10). It runs down, from close to the apex of the nectophore, and initially through the middle of the mesogloea. About one-quarter the way down the nectophore, it bends sharply, in a ventro-basal direction, to meet the dorsal wall of the hydroecium. It then continues in close contact with this wall for a short distance before, in most cases, briefly penetrating back into the mesogloea, and then returning to run just above the dorsal wall of the hydroecium. It continues to overlie the hydroecium and runs down towards the base of the nectophore, ending just before the base is reached. Basal to the nectosac, it may again briefly leave the dorsal wall of the hydroecium. At its basal end the somatocyst sometimes bends sharply towards the right-hand side of the nectophore (cf. *Nectopyramis thetis*). In most specimens numerous small processes emerge from the somatocyst and appear to connect it with the dorsal wall of the hydroecium. These are particularly obvious in the apical region, as the somatocyst leaves the dorsal wall of the hydro-ecium (figure 10).

The nectosac lies on the dorsal surface of the nectophore, immediately below the basal end of the dorsal ridge, and is angled dorso-basally. It is rela-tively shallow and has a large ostial opening also directed dorso-basally. Basally it is, to a varying degree, undercut such that there is a furrow separat-ing it from the flattened dorsal facet below. The dorsal, lateral and ventral radial canals to the necto-sac arise directly from the somatocyst. The lateral canals usually arise in close proximity to each other, but not always together, as Totton (1954) described. Either the right or left canal can arise first, and in some cases the gap between their origins is quite marked.

Larval nectophore. The larval nectophore of *Necto-pyramis natans* previously has been described as the 'nectophore' (Sears 1952) or 'nectophore of second type with a functional nectosac' (Totton 1954, 1965) of *N. spinosa*. Almost certainly it is also the nectophore described by Moser (1925) under the name *Hippopo-dius (?) cuspitatus*. It is roughly spherical or egg-shaped in outline, but the basal region, where the nectosac is situated, is truncated, while the apical region is some-what pointed (figures 11*a*, and 12*a*). The nectosac is quite small, but has a relatively large ostial opening onto the basal facet, and clearly is functional. The mean height and width of the nectophores examined are 5.2 mm and 4.4 mm respectively. The maximum sizes recorded are 8.5 mm and 7 mm respectively.

1. Ridge pattern. All the ridges bear sawtooth-like projections or spines (figures 11*a* and 12*a*). The ridge pattern is quite different from that found on the larval nectophores of *Nectopyramis thetis*, and the two are easily distinguished if the material is reasonably pre-

served. None the less there are comparable elements in the patterns, as Totton (1965) noted.

Basically, there are nine longitudinal ridges, not all of which run from the apex to the base of the nectophore. The ridge pattern is shown schematically in figure 11*b*, *c* and the ridges are designated here as: (i) a median dorsal ridge, which runs from the apex of the nectophore over its dorsal surface to join the complex of ridges that surround the basal facet, where the opening of the nectosac is situated; (ii) a pair of dorso-lateral ridges. These divide from the dorsal ridge close to the apex of the nectophore and run down the dorso-lateral margins to join the basal facet complex. At about two thirds the height of the necto-phore they give rise to: (iii) A pair of lateral ridges. These are the so-called 'buccal' ridges of Totton (1965). After branching from the dorso-laterals they run ventrad for a short distance before curving round to continue basad and to join the basal facet complex; (iv) a pair of ventro-lateral ridges. These originate at the apex of the nectophore, where they unite with the median dorsal ridge and, if present, the singular extension of the hydroecial ridges. They run down the ventro-lateral margins of the nectophore and then curve ventrad to join the peri-hydroecial ridges slightly apical to where the latter are united by a cross-ridge. In a few specimens either they do not extend as far as the peri-hydroecials, or join them at a different level. These ridges were not illustrated by Totton (1954, 1965); and (v) a pair of peri-hydroecial ridges, which surround the ventral opening of the hydroecium. Apically the ridges curve round in a broad arc and unite, while basally there is a cross-ridge that connects them. This is precisely the arrangement described by Moser (1925) for *Hippopodius (?) cuspitatus*. In addition, in several specimens there is a single serrated, median ridge that extends from the apical junction of the peri-hydroecials up towards the apex of the nectophore (figure 12*a*), and which often unites with the dorsal ridge. At the base of the nectophore, the two hydroecial ridges also may extend beyond their cross-junction and connect in with the system of ridges that surround the basal facet.

Although this basic pattern of longitudinal ridges can be seen on most specimens, it is not infrequent to find that some of the ridges are incomplete or that extra ridges are present. Also it appears that the ridges can become devoid of teeth, which makes them diffi-cult to discern. The arrangement of the ridges is not always symmetrical. In about three quarters of the specimens examined the dorso-lateral ridges do not arise from the median dorsal ridge in unison. If the right dorso-lateral ridge arises first then usually the course of the dorsal ridge is deflected towards the left side of the nectophore, before returning to the mid-line when the left dorso-lateral ridge is given off. The converse is apparent if the left dorso-lateral appears first. Additional ridges most commonly divide from the lateral ridges in the region where the course of the latter changes from ventrad to basad. These side branches run ventrad and usually are quite short, although sometimes they appear to connect with the ventro-lateral ridges.
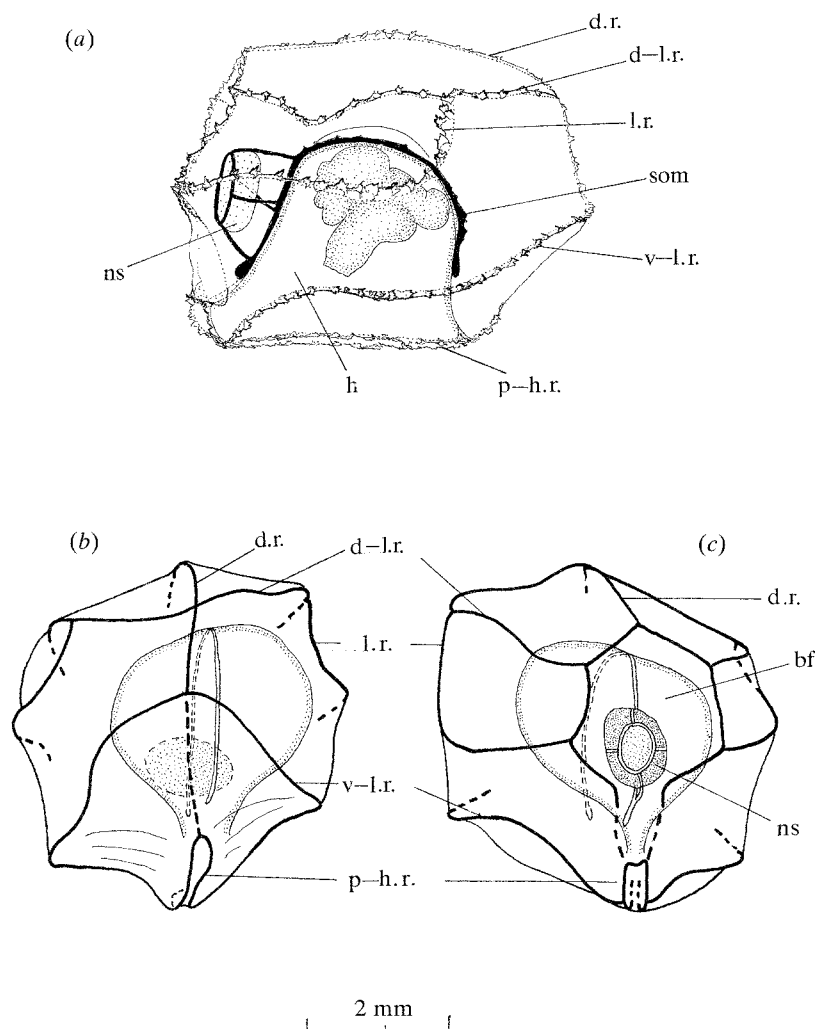
Figure 11. Larval nectophore of *Nectopyramis natans* (Bigelow). (*a*) Lateral, (*b*) dorsal and (*c*) basal views of specimen from *Discovery* St. 7089#13. The ridge pattern is shown schematically in (*b*) and (*c*). See figure 4 for abbreviations. bf, basal facet.

The basal facet of the larval nectophore, wherein lies the ostial opening of the nectosac, is surrounded by an incomplete heptagon of ridges (figure 11*c*). The missing side of the heptagon lies ventrally. The dorsal, dorso-lateral and lateral ridges join with the relevant, more dorsal angles. At the other two, ventro-lateral angles, ridges are given off that extend ventrad towards the peri-hydroecial ridges and, in about half the specimens, actually connect with them. Exceptionally one of the longitudinal ridges may not reach the basal facet, or another side of the heptagon, apart from to the ventral one, may be missing.

2. Hydroecium. The ventro-lateral walls of the hydroecium often expand to form distinct lips on either side of the hydroecial opening, which is restricted to a narrow, gutter-like groove between them. However, within the nectophore the hydroecium is greatly expanded, laterally, and occupies a considerable volume of it. Usually it contains a single large gastrozooid and tentacle, which are attached to the central organ. The latter may be extremely large and bilobed. Occasionally the bud of a definitive nectophore also can be discerned, and in at least eight

specimens this bud is sufficiently well-developed for the characteristic features of the definitive nectophore of *Nectopyramis natans* to be clearly recognizable (figure 12*b*).

3. Somatocyst. The somatocyst is a simple tube that runs over the median dorsal surface of the hydroecium. Usually it remains closely applied to the hydroecial wall, but occasionally, at its apical end, it leaves this wall and penetrates into the mesogloea. It may have a pronounced bend in this region, or a small side branch (figure 12). Basally, in contrast to Totton's (1954) description, the somatocyst always extends, for a short distance, beyond the point of origin of the ventral radial canal and generally ends in a pronounced swelling.

As in the definitive nectophore, the dorsal, lateral and ventral radial canals to the nectosac arise directly and separately from the somatocyst. The lateral canals do not always arise together, although this is true for the majority of specimens. In two specimens only a single lateral canal left the somatocyst, which in one case subsequently divided before reaching the nectosac. Other abnormalities included a blind-ending
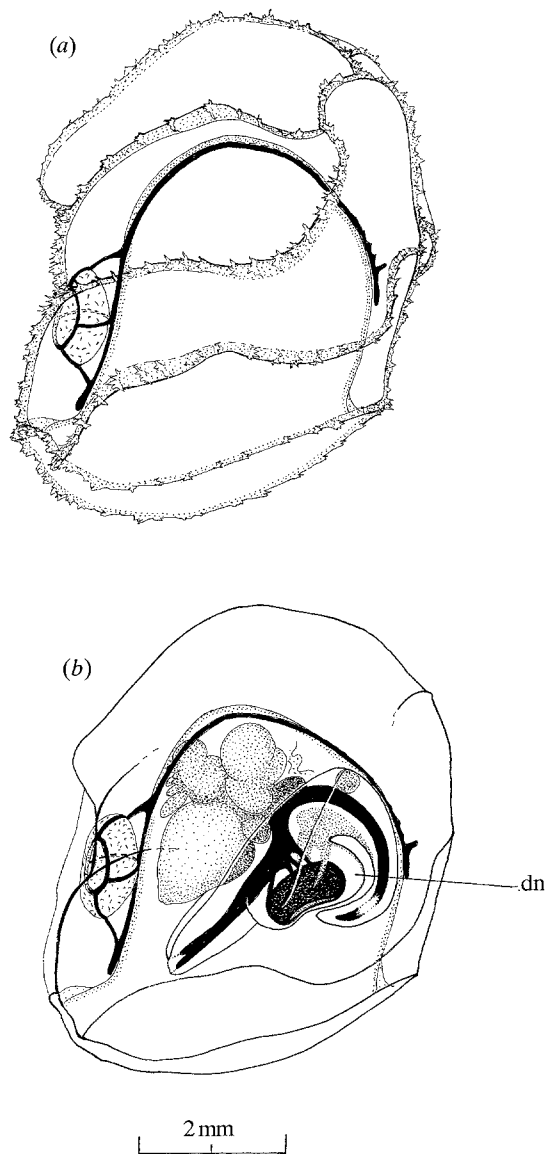
Figure 12. Larval nectophore of *Nectopyramis natans* (Bigelow). Lateral views of specimen from *Discovery* St. 7089#24, showing (*a*) the ridge pattern, and (*b*) a developing definitive nectophore (dn) within the hydroecium.

branch to the ventral radial canal, and the presence of a third, separate lateral canal.

Eudoxid. The eudoxid of *Nectopyramis natans*, which resembles an arrow head, has been described well by Bigelow (1911*b*, 1919, 1931), under the name *Archisoma natans*. It consists of a bract; a special nectophore; a gastrozooid and tentacle; and some gonophores.

1. Bract (figure 13). The bract is an elongate, bow-shaped, structure. The largest specimen in the more recent *Discovery* collections measures 42 mm in height and 11 mm in depth (dorso-ventral direction). Of the 36 specimens in reasonable enough condition to measure, the average height was *ca.* 28 mm. Some of the previously described specimens are, however, even longer. Bigelow's (1919, 1931) material measured 43 mm and 54 mm respectively, while Totton's (1954) specimen from *Discovery* St. 287 measured 45 mm.

The bract usually is pointed both apically and basally. In the apical half there are three ridges, an apico-ventral and a pair of dorso-laterals (cf. *Nectopyramis thetis*), all of which reach to the apex (figure 13*a*). The bract in this region is triangular in cross-section (see Bigelow 1931, figure 214). The dorso-laterals run the entire length of the bract and thereby delimit a dorsal facet. In most of the *Discovery* material, this facet is relatively flat, but in Bigelow's (1931) specimens it became increasingly concave basally. The apico-ventral ridge runs, in the mid-line, from the apex of the bract to the top of the hydroecium, although it may peter out before reaching it.

In the basal half of the bract there are four ridges, the pair of dorso-laterals and a pair of hydroecials. In most cases all four ridges join at the base, but in some the basal region is truncated and, as in the definitive nectophore, only the corresponding dorso-lateral and hydroccial ridges unite (figure 13*c*). The hydroccial ridges form the outer edges of the hydroccial flaps. These flaps extend slightly above the apico-lateral walls of the hydroecium, where they curve over, ventrad and then basad, before petering out. In this way two lateral pockets, the secondary recesses of Bigelow (1931), are formed. It is evident, from a study of very young eudoxids, that the siphosomal stem passes through this region.

The hydroecium occupies most of the lower half of the bract, and is deepest at its apex, where the stem components are attached via the well-developed, hemispherical, central organ. Unlike the definitive nectophore, the hydroecium of the bract is open widely to accommodate the special nectophore. Usually it has little or no depth basally, except when the base of the bract is truncated (figure 13*c*).

As in the definitive and larval nectophores, the somatocyst or canal system of the bract is relatively simple. Basically, there is an ascending or dorsal canal, and two hydroecial canals. However, it is probably more accurate to refer to the proximal parts of the hydroecials as the longitudinal canals. These usually do not extend out longitudinally as 'spur' canals, although such were seen in one specimen, from *Discovery* St. 7089#15.

The dorsal bracteal canal, which Totton (1965) referred to as the c^3 canal, runs down through the mesogloea from close to the apex of the bract to the apex of the hydroecium. At first it lies closer to the dorsal than the ventral surface. Its course is not straight and it has at least one pronounced bend, which is situated at about two thirds the height of the bract. Here a side branch is given off which runs out to the dorsal surface of the bract and usually ends there in a shallow depression (cf. *Nectopyramis thetis*). In six of the *Discovery* specimens, and in Bigelow's (1931) *Arcturus* specimen (figure 13*c*), this side branch bifurcates very close to its distal end, and both branches usually run to the dorsal facet. In four other *Discovery* specimens another, much longer, branch is given off, which usually runs basad and ends blindly (figure 13*b*), whereas in another a further, blind-ending, side branch is given off the dorsal canal closer to the hydroecium.
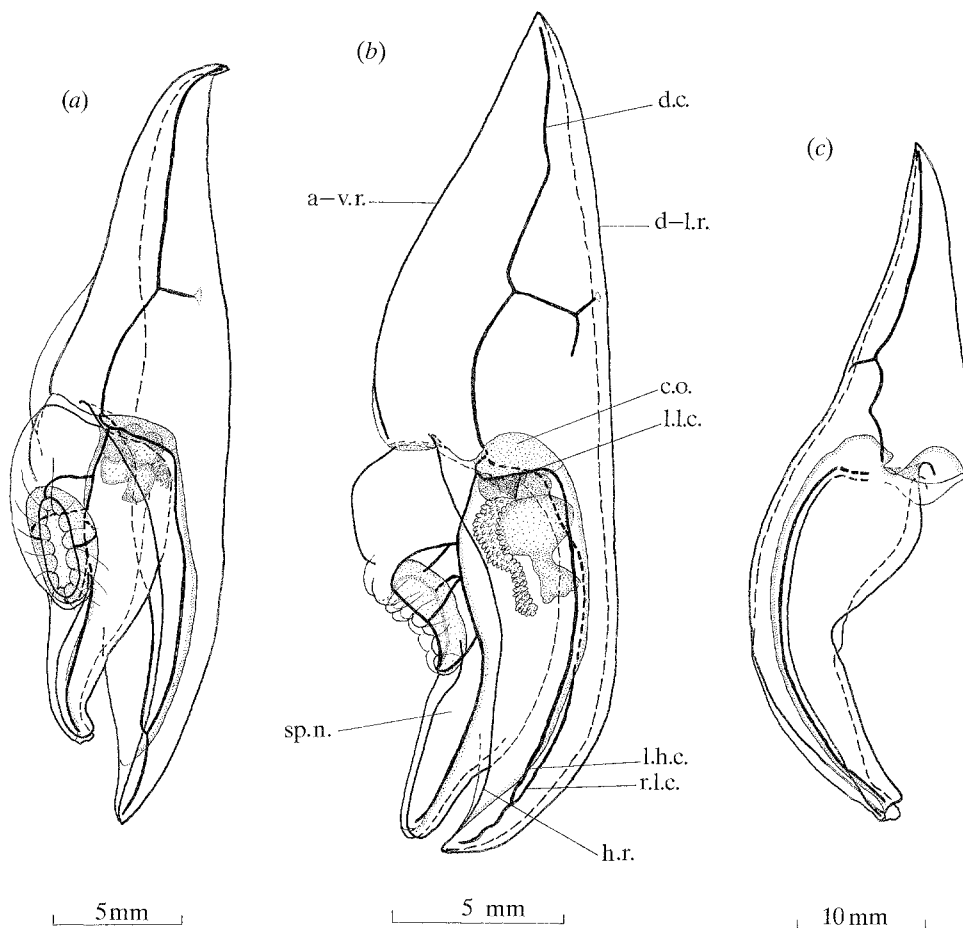
Figure 13. Eudoxids of *Nectopyramis natans* (Bigelow). (*a*) and (*b*) Ventro-lateral views of entire eudoxid from *Discovery* Sts 7089#22 and 7803#13 respectively. (*c*) Lateral view of eudoxid bract (after Bigelow 1931). See figures 1*b* and 6 for abbreviations.

As the dorsal canal approaches the hydroecium it veers toward the right-hand side of the bract and unites with the right longitudinal canal at a point that could be considered proximal to the origin of the right hydroecial (cf. *Nectopyramis thetis*). The longitudinal canals originate at their junction with the pedicular canal of the special nectophore, at which point also is inserted a canal to the central organ. It appears that the central organ, as in the eudoxid of *N. thetis*, is supplied by three canals, the other two arising from the longitudinals on each side and running to the base of the gastrozooid (figure 13*b*). However, this arrangement is not always obvious.

The longitudinal canals loop around the sides of the central organ to reach the dorso-lateral walls of the hydroecium, where they turn basad and continue, as the hydroecial canals, toward the base of the bract. These canals usually run through the mesogloea slightly above the dorso-lateral walls of the hydroecium, to which they are attached by a variable number of thin processes. As the depth of the hydroecium decreases towards the base of the bract, they leave the proximity of the hydroecial wall and penetrate into the mesogloea. Usually they then curve towards the mid-line and unite, with a single canal continuing down to end just above the base of the bract. However, in three specimens the hydroecial

canals were found to unite only very close to the base, so that the single canal was very short.

The most significant variation in the arrangement of the hydroecial canals was noted by Bigelow (1931). In this case the hydroecials do not unite close to the base of the bract, but remain separate (figure 13*c*). In these specimens the base of the bract is truncated and the hydroecium opens onto it. As noted above, the four ridges do not unite in a point, but only the corresponding dorso-lateral and hydroecial ridges on each side unite. In addition to Bigelow's specimen, this arrangement has been noted in six of the specimens in the *Discovery* collections, and is also to be seen on Totton's (1954) specimen from *Discovery* St. 100. Although two of the *Discovery* specimens were small, it does not appear to be a growth feature, for the hydroecials clearly can be seen to unite in other developing eudoxids (figure 10*a*).

2. Special nectophore. The characteristically shaped special nectophore (figure 14) was well described by Bigelow (1931). Totton (1954, footnote to p. 83) is the only person to suggest that this nectophore bears a manubrium and eggs and, therefore, should be regarded as a true gonophore. However, Totton (1965) referred to this structure only as a special nectophore and made separate reference to gonophores, without reiterating his former statement.

The specimen in question, from *Discovery* St. 287, has been re-examined and no sign of sexual products within the nectosac can be discerned. No such arrangement has been seen on any of material examined, even the youngest, developing ones, and it is concluded that Totton's footnote was added in error, and that the nectophore is a true asexual one.

The length of the special nectophore is approximately half that of the eudoxid bract; the maximum being 31 mm for Bigelow's (1931) *Arcturus* specimen. It is rounded apically and truncated basally and is attached, by the apical margins of its hydroecial walls, in the region of the longitudinal canals of the bract (cf. *Nectopyramis thetis*). The nectosac is situated on the dorsal surface, and is centred slightly above the mid-height of the nectophore. It has a relatively large opening, occupying about one quarter of the total height, but is quite shallow and resembles closely the nectosac of the definitive nectophore. As Bigelow (1931) noted, it is distinctly undercut on its ventral surface, in the mid-line.

Above the nectosac, a median, rounded dorsal ridge runs to the apex of the nectophore. In the complete eudoxid, it appears as an extension to the apico-ventral ridge of the bract. There is a pair of dorso-lateral ridges in the basal half of the nectophore. These ridges delimit a concave dorsal facet, which distinctly undercuts the base of the nectosac. Another separate pair of dorso-lateral ridges may run up the sides of the nectosac (figure 14*a*), and continue for a variable distance towards the apex of the nectophore. Bigelow (1931) noted the latter on his *Arcturus* specimen, but could not discern them on his other specimens.

The arrangement of the hydroecium seems to vary according to the size of the specimen, although this is not always the case. On the smaller specimens, but also on some of the larger ones (figure 14*b*), it runs up the ventral side of the special nectophore from the

Figure 14. Special nectophore of *Nectopyramis natans* (Bigelow). (*a*) Lateral and (*b*) dorso-lateral views from *Discovery* St. 7089#15. d.r. and d-l.r., dorsal and dorso-lateral ridges; h, hydroecium; ns, nectosac; ped.c., pedicular canal.

truncated base to slightly above the level of the nectosac. In these cases, there is a pronounced apical extension of the dorsal part of the nectophore. In the larger specimens (figure 14*a*), and as Bigelow (1931) described it, the hydroecium extends almost to the apex of the nectophore, where the lateral flaps are well-defined. The hydroecial walls more or less overlap each other, particularly in the basal half of the nectophore.

The pedicular canal follows closely the median line of the dorsal wall of the hydroecium for almost the entire length of the latter. The radial canals to the nectosac arise in a similar fashion to that described for the definitive and larval nectophores. The lateral radial canals do not always arise together, as previously described. This occurs in about a third of the specimens examined, while in approximately equal numbers of the remainder either the left or right canal arises before the other. Additional canals also can be present. In the type specimen (Bigelow 1911*b*) it would appear that not only did the lateral radial canals arise separately, but that there was an additional branch from the pedicular canal. In the *Discovery* material, no additional canals were seen to arise directly from the pedicular canal, but in one specimen the dorsal radial canal was seen to divide, and in another the left radial canal was found to have a blind-ending branch arising from it.

3. Gonophores. The small gonophores, few in number, are attached to the base of the gastrozooid. Each eudoxid appears to be unisexual, and examples of the mature gonophores of both sexes are shown in figure 15*a*, *b*. For both the male and female gonophores, the manubrium bearing the mature sexual products projects out beyond the limits of the cup-shaped bell. A large number of eggs are present on the manubrium of the female gonophore; a feature also noted by Bigelow (1931).

4. Gastrozooid and tentacle. The gastrozooid (figure 15*a*) is unexceptional. The fully-developed tentillum (figure 15*c*) has an asymmetric shape. It has been illustrated by Stepanjants (1967). The stalk or pedicel of the tentillum can be relatively long, although usually much twisted in the preserved state. It gives rise to a swollen cnidoband, the proximal part of which is devoid of nematocysts and often appears to be divided into two lateral lobes. The distal part is strongly armed with nematocysts of two main types. On each side there is row of between five and eight large nematocysts, measuring *ca.* 93 µm × 21 µm. Between these are several rows of smaller, banana-shaped nematocysts, which measure 50 µm × 10 µm. A long terminal filament is present, although it is usually highly coiled in the preserved state. It bears several small, slightly elliptical nematocysts measuring *ca.* 16 µm × 13 µm. The terminal filament arises on one side of the cnidoband, between the armed and non-armed segments. None of the nematocyst types have been examined in detail.

Distribution

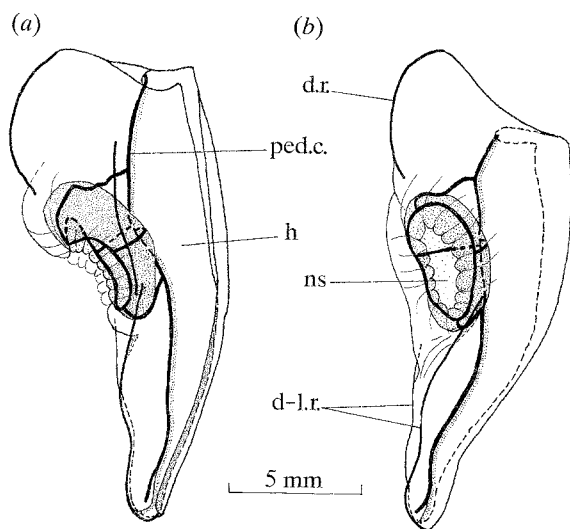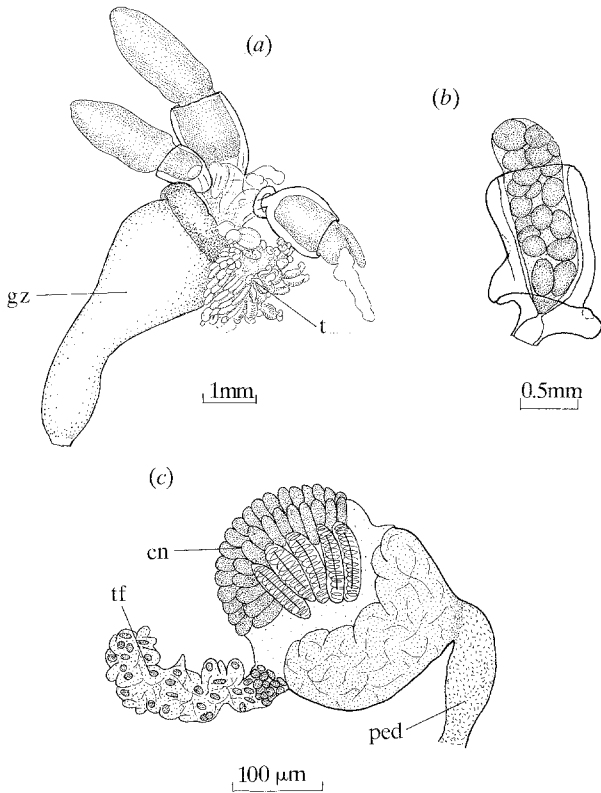Records for *Nectopyramis natans* are few and far between. There appear to be published records for

Figure 15. *Nectopyramis natans* (Bigelow). (*a*) Gastrozooid (gz) and tentacle (t), with male gonophores attached. (b) Female gonophore. (*c*) Tentillum. See figure 8 for abbreviations.

only six definitive nectophores, probably ten larval nectophores (recorded as 'definitive nectophores' under the name *N. spinosa*), and 16 eudoxids. However, several more recent authors have noted the presence of the species in their samples, but have not specified which stage was collected (cf. *N. thetis*). The most probable records for *N. natans* are listed in table 4, together with some additional information kindly supplied by various researchers. In the more recent *Discovery* Collections, 43 samples have been found to contain specimens of *N. natans*. These are listed in table 5, arranged in latitudinal order.

Margulis (1972, 1974) noted the dearth of information on *Nectopyramis natans*, and that, within the Atlantic Ocean, it had a fairly restricted distribution, between latitudes 2°N and 34°S. Therefore, she considered it to be an equatorial species. Most of the records from the other oceans also are from equatorial regions, although Stepanjants (1967, 1970, personal communication) found it at *ca*. 40–45°N in the Pacific Ocean. The recent *Discovery* records (table 5) are largely confined to the 0–30°N latitudinal range in the North Atlantic, possibly indicating that it is generally a tropical species, whose northern limit of distribution lies in the vicinity of the southern branch of the Gulf Stream recirculation (see Mackie *et al* 1987). However, in the southern hemisphere this species also is present at higher latitudes, possibly to 68°S. Totton (1954) recorded a larval nectophore at 58°S in the Indian Ocean; while Alvarino *et al.* (1990) gave

Table 4. *Published records for Nectopyramis natans (Bigelow)* (dn, definitive nectophore; ln, larval nectophore; e, eudoxid.)

Atlantic Ocean

Moser (1925)	?1 ln	*ca*. 1°N 19°W
Totton (1954)	1 e	2°49.5′S 9°25.5′E
	1 dn	3°35′S 32°20′W
	1 ln	21°13′S 9°25.5′E
	1 dn, 1 e	*ca*. 33°S 15–16°E (2 Sts)
Alvarino (1971)	?	32°30′ 9°04′E
Margulis (1974)	?	*ca*. 2°N–12°S 1°E–28°W (4 Sts)
Pugh (1974)[a]	3 dn, 8 ln, 6 e	*ca*. 28°N 14°W (14 Sts)
Alvarino *et al.* (1990)	?	off Brazil

Indian Ocean

Bigelow (1919)	1 e	Gulf of Boni, Celebes
Sears (1952)	1 ln	11°18′S 50°13′E
Totton (1954)	1 e	2°39.4′N 50°46.4′E
	1 ln	58°35′S 92°06.2′E (Southern Ocean)
Alvarino (1964)	?	Central Indian Ocean
Musayeva (1976)	?1 ln	0°09.2′S 77°02.0′E
Margulis (p.c.)	?	7°42′N 88°35′E
	? ln	9°06′N 63°58′E

Pacific Ocean

Bigelow (1911b)	1 e	*ca*. 6°S 102°W
Bigelow (1931)	1 e	4°56′N 84°35′W
Sears (1952)	1 ln	2°52′N 87°38′W
Alvarino (1967)	?	off San Diego, California
Stepanjants (1967)	1 dn, 3 e	30–44°N 150–170° (4 Sts)
Stepanjants (1970)	1 e	44°24′N 149°10′W
Stepanjants (p.c.)	1 c	42°25′N 149°10′W
Alvarino *et al.* (1990)	?	off Chile; Antarctic sector

[a] Denotes amendment to published data.

Table 5. *Records for* Nectopyramis natans *(Bigelow) in recent* Discovery *collections (arranged in latitude order)*

station	position	depth range (m)	defn. nect.	larva. nect.	eudoxid
9959#03	55°57.2'S, 27°11.0'E	990–2000			2
8556#03	0°22.0'S, 22°04.5'W	805–900			1
8553#01	0°21.2'S, 22°28.5'W	505–600	4	2	3
8553#02	0°20.6'S, 22°20.7'W	606–700	1		4
8556#02	0°18.5'S, 22°12.8'W	905–1000	1		1
8559#04	0°14.4'S, 22°43.7'W	1250–1500		1	
8558#01	0°08.0'S, 22°52.8'W	700–800			1
8565#03	2°50.3'N, 23°25.7'W	400–500			1
8567#02	2°52.3'N, 23°32.1'W	305–400			2
8565#02	2°56.4'N, 23°21.1'W	600–705	2		
8563#01	2°56.5'N, 22°42.6'W	806–900			3
8567#01	2°56.8'N, 23°27.5'W	505–600	2		2
8563#02	3°01.3'N, 22°52.0'W	905–1000	2	1	3
8565#01	3°03.1'N, 23°14.3'W	700–800			4
7824#19	10°53.3'N, 19°55.7'W	1000–1250			1
6662#19	10°54.7'N, 20°01.7'W	405–500	1		
6662#16	10°59.4'N, 19°52.1'W	810–890			1
6662#11	11°03.0'N, 19°52.6'W	510–590			2
7829#02	11°57.8'N, 24°39.3'W	0–1000	1		
7803#10	17°42.8'N, 24°59.3'W	405–500			2
7089#17	17°42.9'N, 25°11.9'W	505–600		1	
7803#11	17°43.4'N, 24°58.4'W	1250–1500			1
7803#17	17°44.0'N, 24°54.2'W	500–600	3		4
7089#22	17°46.3'N, 25°21.7'W	410–500		5	3
7803#12	17°48.5'N, 25°09.9'W	710–800	2		
7089#13	17°48.7'N, 25°28.7'W	515–600	1	5	2
7089#16	17°48.8'N, 25°17.3'W	610–700	1		
7089#24	17°51.7'N, 25°27.2'W	410–500		17	
7089#09	17°52.6'N, 25°25.5'W	610–700	1		2
7089#15	17°55.0'N, 25°24.3'W	700–785	2	2	3
7803#13	17°56.2'N, 24°58.9'W	1250–1500	1		3
7803#01	18°01.8'N, 25°02.2'W	0–1000			1
7802#02	18°37.9'N, 24°15.3'W	0–1000	1		1
7801#02	19°11.0'N, 23°22.1'W	0–1000		2	2
7800#02	19°46.7'N, 22°32.7'W	0–1000			2
9541#28	20°03.0'N, 21°12.9'W	510–1000	2		4
7799#02	20°25.2'N, 21°45.1'W	0–1000		1	
12181#21	20°47.8'N, 19°42.0'W	830–920			1
7782#02	27°39.4'N, 14°17.9'W	700–800			3
10380#35	29°50.5'N, 34°19.1'W	2100–2300	2		1
10380#34	29°53.1'N, 34°15.0'W	1900–2100	1		
11261#62	31°14.8'N, 25°19.1'W	700–800	1		
11262#03	31°22.8'N, 25°19.8'W	2310–2700	1		
8818#03	43°51.9'N, 12°57.0'W	500–600			1

several records for the South Pacific and Southern Ocean, but their data are difficult to interpret.

Nectopyramis natans appears to have a widespread depth distribution, as specimens have been found at most depths from close to the surface down to at least 2700 m. However, the material from the *Discovery* collections indicates that most definitive nectophores and eudoxids were collected within the 500–800 m depth range (table 5). The larval nectophores appear to have a slightly shallower distribution, but this may be biased by the fact that almost half the total number were collected in a single haul, in the 410–500 m depth range.

Genus: *Nectadamas* gen. nov.

Nectopyramis Bigelow 1911*b* (partim); Totton 1954, 1965 (partim).

Type species: *Nectadamas diomedeae* (Bigelow, 1911*b*)

Diagnosis

The definitive nectophore bears a complex pattern of lateral ridges and, in the apico-dorsal plane, a circumferential ridge that divides to circumvent the openings of the nectosac and hydroecium. The somatocyst consists of a median pallial canal, from which branch three primary canals, $C.pa^1$, $C.pa^2$ and $C.pa^3$,

that run only in the apico-dorsal plane. Additional branches are present in one species, *diomedeae*. The radial canals of the nectosac arise from, or close to, a single pedicular canal, which connects with the pallial canal. The hydroecial cavity is restricted to a small pocket-shaped structure, with a narrow ventral opening.

The small, rounded larval nectophore, only identified for *N. diomedeae*, appears to have a circumferential and lateral ridges. The arrangement of the nectosac and hydroecium are similar to the definitive nectophore, although the latter is more extensive. The somatocyst is simple, although small, median branches may be present.

The free-living eudoxid is comprised of a bract, a large gonophore, and a gastrozooid and tentacle. The bract is roughly triangular or a truncated ovoid in shape. It bears ridges, including a circumferential ridge. The canal system conforms to the basic prayid design, although the 'spurs' to the longitudinal canals are much reduced or absent. The canals may be complexly divided in one species, *diomedeae*. The large gonophore has a pedicular canal from which the canals of the subumbrella arise together. No special nectophore is present.

Discussion

The principal characters that distinguish the species of the genus *Nectadamas* from those of the genus *Nectopyramis* are listed in table 1. Based on these, it has become necessary to remove the species *diomedeae* from the genus *Nectopyramis* and place it within the new genus, *Nectadamas*, together with a closely related species, *Nectadamas richardi* sp. nov., whose polygastric stage is described for the first time. The description of *N. richardi* is given first to facilitate comparisons, as the simpler arrangement of its canals and ridges may give some clues as to the origins of the more complex, and distorted arrangements found in *N. diomedeae*.

Etymology

The name *Nectadamas* hopefully is derived from the Greek νεκτοσ, meaning swimming; and αδαμασ, also the Latin *adamas*, meaning diamond.

Nectadamas richardi sp. nov.

Material examined

There are at least 83 nectophores and 634 eudoxids of *Nectadamas richardi* present in the *Discovery* Collections, housed at the Institute of Oceanographic Sciences. All the nectophores and many of the eudoxids have been re-examined.

Holotype

One nectophore, with three developing eudoxids, from *Discovery* Station 11050#3 (7 and 8th April 1984; 45°38.3′N, 14°06.8′W; RMT8M-3; depth range 700–800 m). Preserved in Steedmann's Preserving Fluid and presented to the Natural History Museum, London, where it is entered as Regd. No. 1991.11.8.1.

Diagnosis

Nectopyramidine siphonophore with a singular, rounded definitive nectophore bearing a distinctive pattern of ridges. The somatocyst system is relatively simple, with no descending branch and with the median pallial canal giving rise to three major branches, C.pa[1], C.pa[2], and C.pa[3], which run in the apico-dorsal plane. Other short branches may be present. The nectosac bears four straight radial canals which arise together from or in close proximity to the pedicular canal. The obliquely slanted, pocket-shaped, hydroecium is deep but has a relatively narrow opening.

It is presumed that a caducous larval nectophore is developed, but this has not been identified.

The bracts have a truncated ovoid shape, with the opening of the hydroecium occupying the whole of the basal surface. The hydroecium extends to about half the total height of the bract. Each bract bears a distinctive pattern of ridges on its outer surface. The canal system basically consists of four canals, although it can be assumed six are present; the longitudinals being without 'spur'-like extensions and thereby merging directly with the hydroecials. The dorsal canal arises from the right longitudinal–hydroecial.

The gonophore is large and asymmetrical in shape, bearing two lateral asymmetric flaps on either side of a deep hydroecium.

Description

A considerable variability in certain morphological characters has been observed among the specimens examined. Although many of these variations will be noted herein, it is very likely that others will be found in subsequent specimens, and these should be carefully considered before any thought is given to describing such material as yet another new species.

Definitive nectophore. Only a single definitive nectophore is developed. In lateral view (figure 16) the nectophore is almost oval in shape, but is truncated basally in the region of the nectosac. The largest specimen (*Discovery* St. 7716#2) measures approximately 10 mm in length and 7 mm in height (dorso-ventral direction). The nectophore is laterally compressed such that its width is less than half its length. Both sides show little curvature, but in some cases the left side is flatter than the right. This asymmetry usually results in the ostial opening of the nectosac being deflected slightly towards the left side.

The nectosac is variable in size, but usually its depth is about 20% the length of the nectophore, with a range of 12 to 29%. Similarly its height (dorso-ventral direction) can vary from 30 to 70% of the maximum height of the nectophore, but averages about 40%. The nectosac is asymmetric in shape being deeper in its dorsal half. The pedicular canal is inserted between about half and two-thirds the height of the nectosac (figure 16). The lateral radial canals arise together, usually from the dorsal canal just above the pedicular canal, but sometimes at the latter's insertion point. All the canals run straight to the ostial
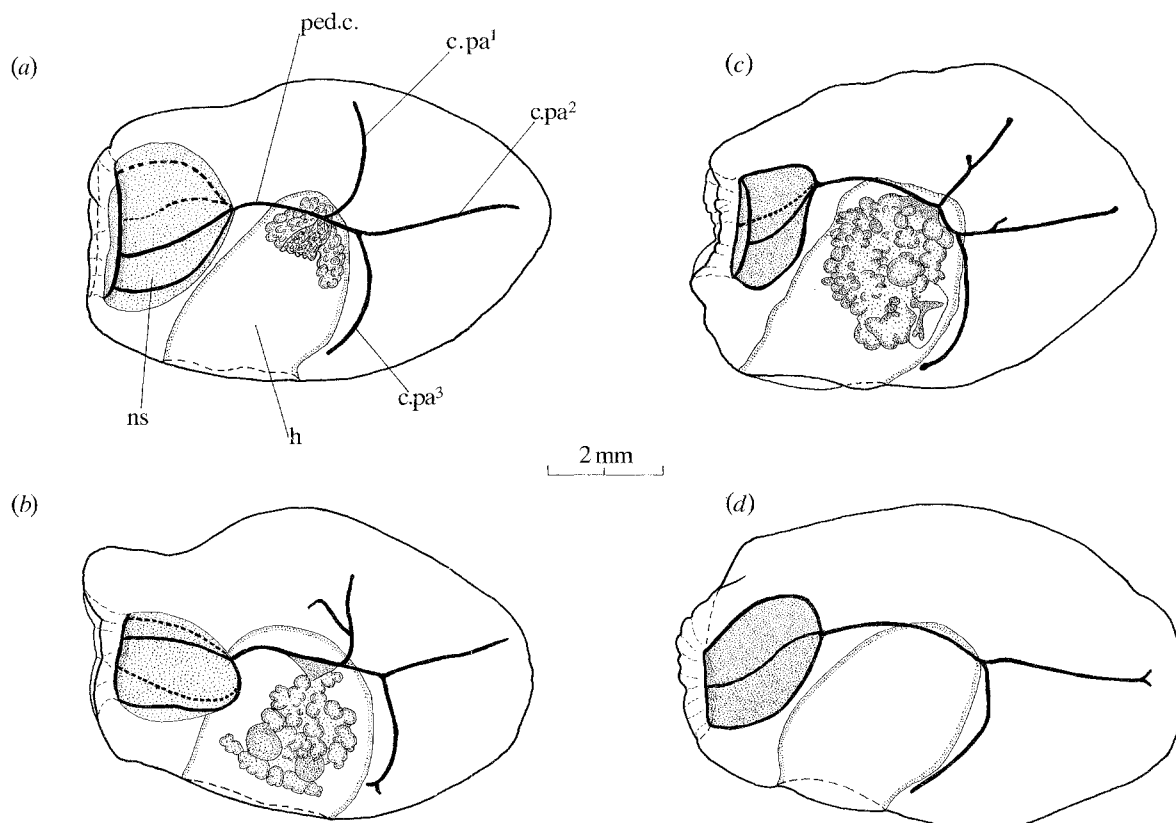
Figure 16. Definitive nectophores of *Nectadamas richardi* sp. nov. (*a*), (*b*), (*c*) and (*d*) Lateral (right) views, showing arrangement of internal structures of specimens from *Discovery* Sts. 7856#13, 8516#9, 7709#28 and 9788#2 respectively. C.pa¹, c.pa², c.pa³ the three main branches to the somatocyst; h, hydroecium; ns, nectosac; ped.c., pedicular canal.

ring canal. However, in some specimens, probably as a result of preservation, the lateral radial canals may appear to be slightly curved. There is no basal extension of the ventral radial canal as in the nectophores of *Nectadamas diomedeae*.

The hydroecium is a narrow, laterally compressed, pocket that extends diagonally up into the nectophore to about two thirds its height (figure 16). It is slightly asymmetric in shape, extending up further on the left-hand side than on the right. This results in the median longitudinal canal of the somatocyst running over the right-hand side of the hydroecium close to its top. Several round or oval patches of ectodermal cells (not illustrated) can be seen to be distributed over the internal surface of the hydroecium in a fairly regular pattern. These cell patches are assumed, as in other species, to be sources of bioluminescence.

1. Canal System. The somatocyst canal system (figure 16) is not as complicated as that in the nectophores of *Nectadamas diomedeae*, but it has the same basic arrangement. The pedicular canal runs from the nectosac to the top of the hydroecium, where it joins the end of the median longitudinal or pallial canal. No descending branch is present. The pallial canal runs over the right-hand side of the hydroecium close to its top, and it is in this region that the siphosome is attached. Although the base of the attachment zone occasionally may be inflated, it does not resemble the laterally expanded central organ found in *Nectopyramis* species. Approximately in the

middle of this region, the pallial canal gives off a branch, C.pa¹, which runs obliquely, in an apico-dorsal direction, through the mid-line of the nectophore (figure 16*a*). Ultimately it may curve dorsad. In ten of the specimens examined, this C.pa¹ canal forks just prior to its distal end, giving rise to two short branches. Further branching of the C.pa¹ canal may occur, as is discussed below.

Just apical to the siphosomal attachment zone, the pallial canal leaves the wall of the hydroecium and penetrates into the mesogloea. It then gives off another branch, the C.pa² canal (figure 16). This branch continues towards the apex of the nectophore and terminates a short distance below it. In only one specimen (*Discovery* St. 9788#2) has the C.pa² canal been observed to fork close to its distal end. However, in another (*Discovery* St. 7709#28) (figure 16*c*) a side branch was given off proximally, which ran out towards the left side of the nectophore.

After the C.pa² canal branches off, the pallial canal, which can now be referred to as the C.pa³ canal (figure 16), begins to curve round baso-ventrally and continues to parallel the apical wall of the hydroecium in the mid-line. This canal terminates just above the ventral surface of the nectophore. In only one nectophore (St. 8516#9) was this canal observed to fork close to its distal end.

This basic system of C.pa¹, C.pa², and C.pa³ canals, with or without additional branches, exists in all but five of the nectophores examined. However, in three

specimens the point of origin of the C.pa¹ canal is displaced apically, from the hydroecium region into the mesogloea above. In one of these the branching order remains the same, but an additional branch is present, basal to the C.pa¹ but still within the meso-gloea. In the other two specimens, the C.pa¹ branches from the C.pa² canal. The five exceptional specimens usually have one or more of the basic canals reduced or absent. However, by their general appearance and ridge pattern, they clearly belong to the same species. In two of these odd nectophores, there are no well-developed branches to the pallial canal, which termi-nates shortly after having left the hydroecial wall and entering the mesogloea. In both specimens this canal forks close to its end; in one case once, in the other twice. Either the C.pa¹, C.pa² or C.pa³ canal is absent in each of the other three specimens (figure 16*d*).

In addition to these oddities, several nectophores show the presence of additional branch canals. Sixteen nectophores have an extra, short branch that branches off from the pallial canal basad to the C.pa¹ canal. In twelve of these specimens, the branch canal is sited at the basal end of the zone of attachment of the siphosome, while in the remainder it is positioned close to the centre of that zone. Two other necto-phores have an additional short branch arising from the pallial canal between the C.pa¹ and C.pa² canals.

The other variations to the basic scheme all affe the C.pa¹ canal, for which two branching patteri have been noted. In the first, a canal branches o: usually in the middle region of the C.pa¹ canal, b: occasionally at its base, and runs out, laterally, t: wards the right side of the nectophore (figure 16*b*, (In the second, a branch arises close to the base of tl C.pa¹ and runs dorsad for a variable distance.

2. Ridge Pattern. All the nectophores possess : extensive and characteristic pattern of ridg(although there are several variations to the ba: scheme. In general the ridges are difficult to disce without staining, and appear as small excrescences (the surface of the nectophore. The most obvious rid, is a circumferential one that runs right around t: nectophore in the apico-dorsal plane. This rid, divides to circumvent the openings of the hydroeciu and the nectosac.

The general pattern of lateral ridges is shov schematically in figure 17*a*, *b*. Basically it is the sar on both sides of the nectophore, but it is rare to fi: an exact match for an individual specimen (figure 1; *d*). In general, the main lateral ridges (labelled figure 17*a*, *b*) do not reach the circumferential ridge the same point, as is also the case for those labelled Apart from these, the commonest variations, based (the notation used in figure 17*a*, *b*, are:
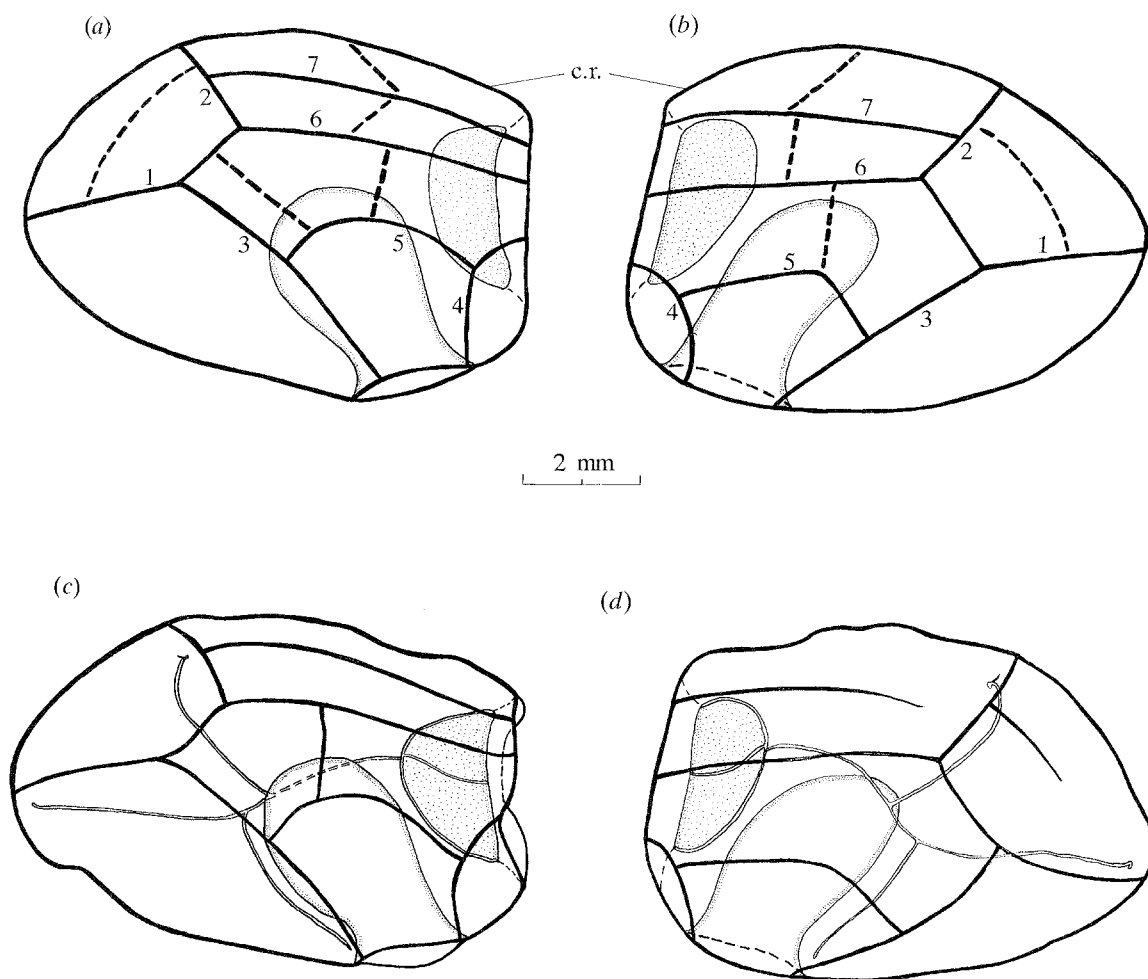

Figure 17. Definitive nectophore of *Nectadamas richardi* sp. nov.. (*a*) and (*b*) Schematic diagrams of lateral ridge pattern on left and right, respectively. c.r., circumferential ridge. See text for details. (*c*) Left and (*d*) right lateral views of pattern on specimen from *Discovery* St. 11050#3.

(i) ridge 7, extending from the circumostial ridge, does not reach ridge 2, and can be of variable length (figure 17*d*); (ii) ridge 7 often has a cross link with ridge 6, and on rare occasions with the circumferential ridge; (iii) crosslinks also occur between ridges 5 and 6 (figure 17*c*), or ridges 2 and 6. These crosslinks are not always complete; (iv) a ridge branches from ridge 2 and arcs apically towards ridge 1 (figure 17*d*), but usually does not join it; and (v) ridge 2 is absent.

Larval nectophore. The larval nectophore of *Nectadamas richardi* has not been identified. One would expect it to be of an even simpler design than that described below for *N. diomedeae*. In which case it would closely resemble the larval nectophores of *Rosacea* or hippopodiid species and, therefore, might be hard to recognize. However, a few odd, possibly aberrant, nectopyramidine-like nectophores and eudoxids, have been found in the *Discovery* collections. The nectophores have neither the characteristics expected for a larval nectophore of *N. richardi*, nor is there any other evidence to suggest this. There is too little information to suggest their affinity and so they are not described herein.

Eudoxid. The eudoxid phase was described by Totton (1965) as that belonging to *Nectopyramis spinosa*. However, there can be no doubt that these eudoxids in fact belong to *Nectadamas richardi* as developing eudoxids, up to three in number, frequently have been found attached to the stem within the hydroecium of the definitive nectophores described above.

1. Bract. The largest bracts measure *ca.* 10 mm in height, *ca.* 7.5 mm in width and *ca.* 5 mm in depth. In side view they have the shape of a basally truncated oval (figure 18). As might be expected, they are very similar in basic design to the bracts of *Nectadamas diomedeae*, but they are considerably smaller and more rounded. They have a deep hydroecium, which extends to about half the total height of the bract, and which has a wide opening occupying the whole of the basal surface. As with the hydroecium of the nectophores, the inner walls of the hydroecium of the bracts are spotted with small patches of ectodermal cells. The other siphosomal components, that is the gastrozooid and gonophore, are attached at a point close to the apex of the hydroecium. The base of this attachment zone may be inflated.
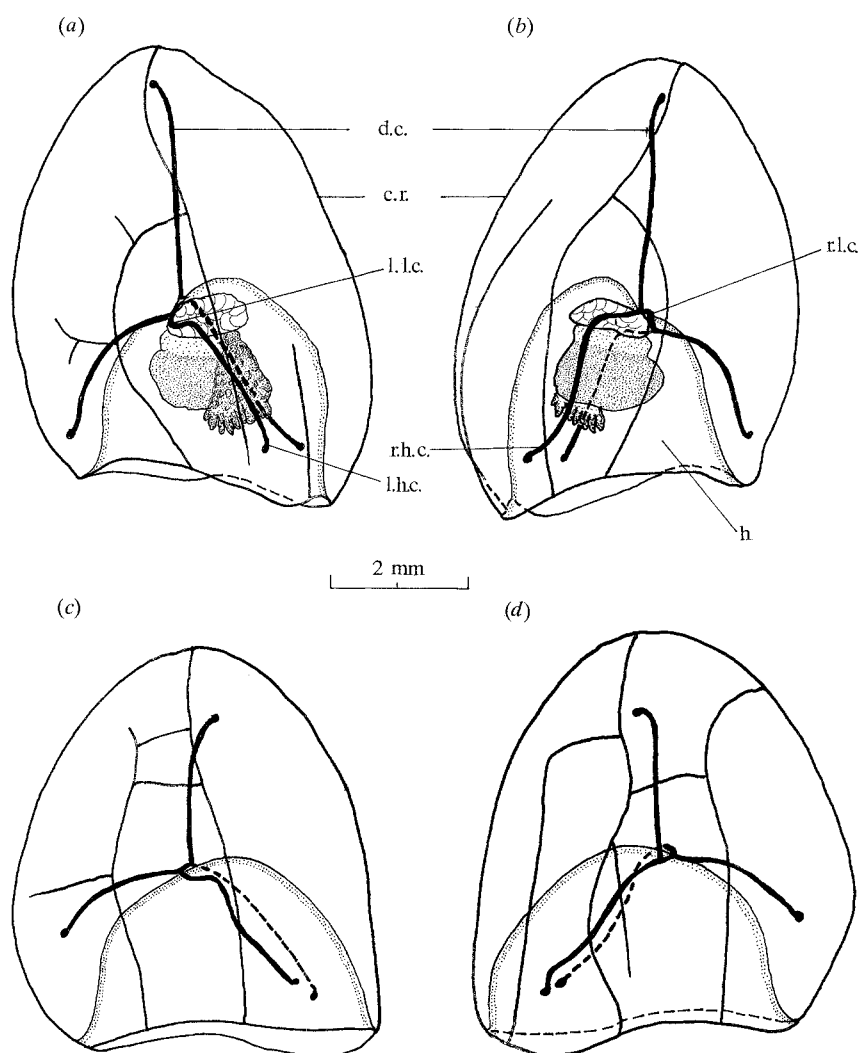
The canal system conforms with the basic prayid

Figure 18. Eudoxid bracts of *Nectadamas richardi* sp. nov. (*a*) and (*c*) Left, and (*b*) and (*d*) right lateral views of bracts from *Discovery* Sts. 7716#2 and 9795#2. Canal system (see figure 1*b* for abbreviations), thick lines; lateral ridges, thinner lines. c.r., circumferential ridge; hydroecium (*h*) with dotted outline.

design. It consists of a ventral canal, the c⁴ canal of Totton (1965), that extends from its junction with the longitudinal canals down into the mesogloea of the ventral lobe of the bract. The longitudinal canals form a semi-circular canal around the region of attachment of the other siphosomal elements. Although these longitudinal canals usually merge into the hydroecial canals, without forming 'spur canals', in one specimen from *Discovery* St. 10109#3, a very short branch was found to arise from the right hydroecial canal at a point where one might expect a 'spur' canal to be given off. The hydroecial canals run down the sides of the hydroecium, with the right canal usually being longer than the left (figure 18).

The dorsal canal, the c³ canal of Totton (1965), arises from the right longitudinal canal quite close to the mid-line. This is similar to the arrangement in *Nectadamas diomedeae*. It runs directly up towards the top of the bract, but terminates before reaching it. Often this canal curves distally. In about 5% of the bracts the dorsal canal gives off a short side branch (figure 19c), usually close to its distal end, but occa-sionally more proximal. All the bracteal canals often end in small swellings.

The bracts bear a distinctive ridge pattern on their outer surfaces (figure 18). As with the nectophores, the most obvious of these ridges is the circumferential ridge which runs around the bract in the mid-line and demarcates the edges of the hydroecium. On the lateral surfaces, the ridge pattern is very variable. Basically there is a ridge which runs from the apex of the bract to its base, and from which another ridge divides, at a varying angle. The latter ridge divides off at a level of about two-thirds the height of the bract and also runs down to the basal margin of the hydroecium. Several other ridges may be present, and examples of these are shown in figure 18c, d, figure 19c.

2. Gonophores. Totton (1965) described the large bell attached to the bract as a special nectophore, and frequently it appears to be so as no sexual products can be discerned within it (figure 19a). However, there is no doubt that, as in *Nectadamas diomedeae*, it is a true gonophore as most bells contain a sexual manu-brium (figure 19b). The gonophores occur in two,
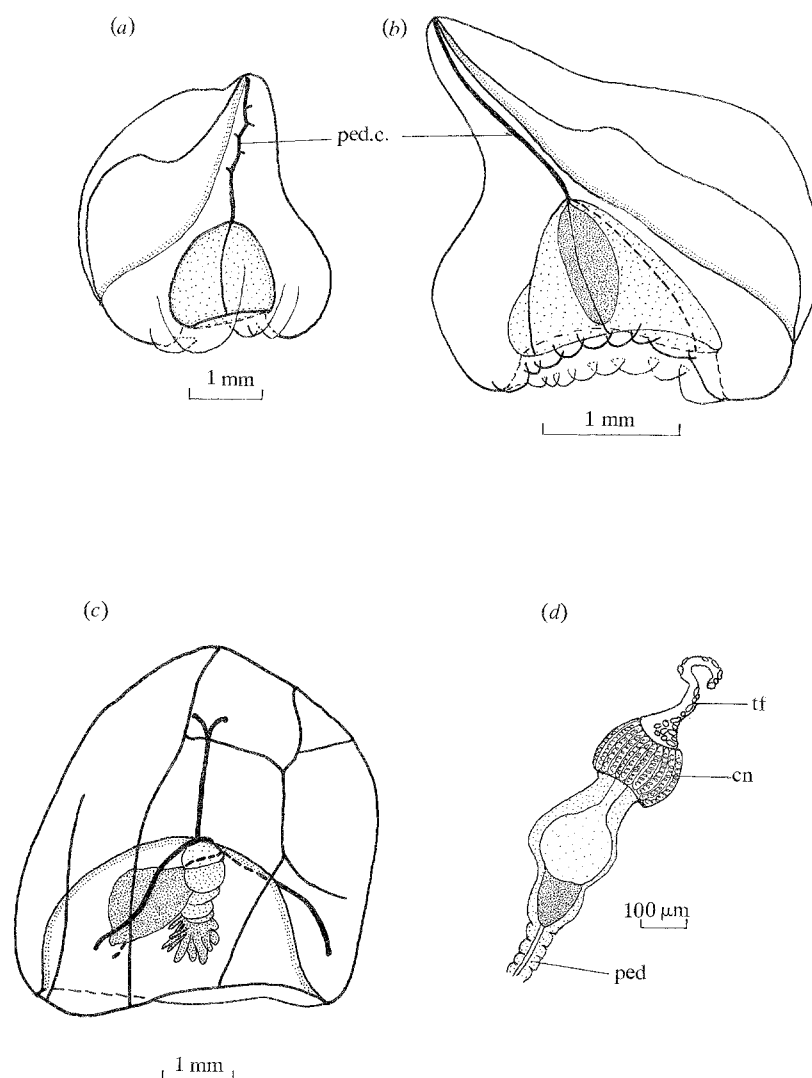

Figure 19. *Nectadamas richardi* sp. nov. (a) and (b) Gonophores from *Discovery* Sts. 10110#5 and 11074#3 respectively. ped.c., pedicular canal. (c) Eudoxid bract from *Discovery* St. 10110#5. (d) Tentillum. cn, cnidoband; ped, pedicel; tf, terminal filament.

enantiomorphic, forms. They are asymmetric in shape, being laterally expanded on one side to form two flaps which surround a deep hydroecium. The flaps themselves are asymmetric, with one being deeply indented in its upper half. No pronounced ridges have been noted on the gonophores. Small patches of ectodermal cells, similar to those noted in the hydroecia of the nectophores and bracts, are distributed over the entire surface of the gonophore. However, most often they have been abraded and usually are seen only on the inner walls of the hydro-ecium.

The subumbrella cavity is restricted to the lower half of the gonophore and has four straight radial canals. The pedicular canal usually is simple and runs up to the apex. However, in some specimens its course is slightly zigzagged and it gives off very short side branches (figure 19a). Each eudoxid usually bears only one large gonophore, with or without sexual products, although a small bud of a developing gono-phore often can be seen. It would appear, thus, that the gonophore is retained for a certain time after the release of its sexual products, but then is detached when a replacement one is developed.

3. Gastrozooid and tentacle. Totton (1965) de-scribed a dark ring of pigment around the mouth of the gastrozooids, but it has not been possible to verify this as the whole of the stomach region is a dark brown colour.

A long tentacle, bearing numerous tentilla, is attached to the lighter coloured basigaster of the gastrozooid. It has proved difficult to determine the morphology of the well-developed tentillum as, during capture or preservation, the nematocyst batteries discharge and the whole cnidoband explodes. How-ever, a few tentilla appear to be moderately intact (figure 19d). These consists of five distinct regions. Basally there is the narrow pedicel, which distally becomes slightly inflated to form a darkly pigmented region. Distal to this is an inflated, flask-shaped region which is devoid of nematocysts. The main cnidoband consists of an array of longitudinally arranged nema-tocysts, 20 to 30 in number, which measure 90 μm × 15 μm. They do not form a complete ring around the cnidoband as there is a small denuded area on one side. The terminal filament, which arise from the cnidoband, probably can be quite long, but usually is broken. It bears, on one side, an alternating series of ovoid (20 μm × 10 μm) and elongated (30 μm × 8 μm) nematocysts. None of the nematocysts has been examined in detail.

Distribution

Specimens of *Nectadamas richardi* have been identi-fied from 267 recent *Discovery* stations distributed throughout most of the Northeast Atlantic Ocean from the equator to 60°N, the northern limit of our sampling. This total includes the eight hauls men-tioned by Pugh (1990), where 16 eudoxids were collected, but excludes the SOND cruise data (Pugh 1974). These stations are too numerous to list herein, but are summarized in table 6. Further station data can be obtained from the author. A single eudoxid

Table 6. *Latitudinal distribution of Nectadamas richardi sp. nov. in recent Discovery collections from the northeast Atlantic Ocean*

(No siphonophore data for *Discovery* stations between 5 and 10°N and 21–29°N.)

latitude range	no. hauls with specimens	% total stations	definitive nectophores	eudoxids
0–5°N	10	25.0	5	15
10–15°N	15	35.7	5	34
15–21°N	17	28.3	3	34
29–35°N	36	10.6	9	51
35–40°N	20	14.7	6	28
40–45°N	81	24.8	30	216
45–50°N	71	47.0	51	229
50–55°N	11	30.6	5	20
55–60°N	6	19.4	1	11

also has been found at a site, *ca.* 32°N, 64°W, off Bermuda. Maximum numbers of nectophores and eudoxids were found at stations between 40 and 50°N, with almost half of the samples from the 45–50°N range containing specimens. However, the species was also well represented in the small number of hauls made between 10 and 15°N.

Although specimens have been found at most depths between less than 100 m and 4000 m, most have been found to occur between 600 m and 1000 m (figure 20). However, at lower latitudes it appears to have a shallower depth distribution, being mainly found in the 300–600 m depth range. There are also some indications that the eudoxids have a slightly deeper depth distribution than the nectophores. For instance, during a series of 24 hauls at a depth of 1000 m at 42°N, 17°W, almost 100 eudoxids were collected, whereas only one nectophore was recorded. The four other nectophores collected at this position were found in the 700–900 m depth range, whereas only nine eudoxids were found within this range.

The only other certain records for the eudoxids of this species, but previously ascribed to *Nectopyramis spinosa*, are given by Totton (1965) and Pugh (1974). Pugh (1974) found 22 eudoxids at the SOND site off the Canary Islands, with most being found within the 500–600 m depth range. The latter is in accord with the slightly shallower depth range for these animals found at lower latitudes in the recent *Discovery* collec-tions, as noted above. Totton's (1965) specimen was collected in the Pacific Ocean, at 31° 00.5′N, 116° 37.5′W, off the Mexican coast. The depth of collection is uncertain. In addition, there are a few, poorly preserved specimens in the collections housed at the Natural History Museum. At least one, possibly four, nectophore and two eudoxids came from a depth of 800m at *Discovery* St. 4230, 40°17′N, 12°45′W; and another nectophore was found at *Sarsia* St. C, 46°30′N, 8°00′W, at an unusually shallow depth of 250–500 m.

J.-P. Casanova (personal communication) found an eudoxid of '*Nectopyramis spinosa*' at 30°18′N, 29°20′W, and E. I. Musayeva (personal communication) states
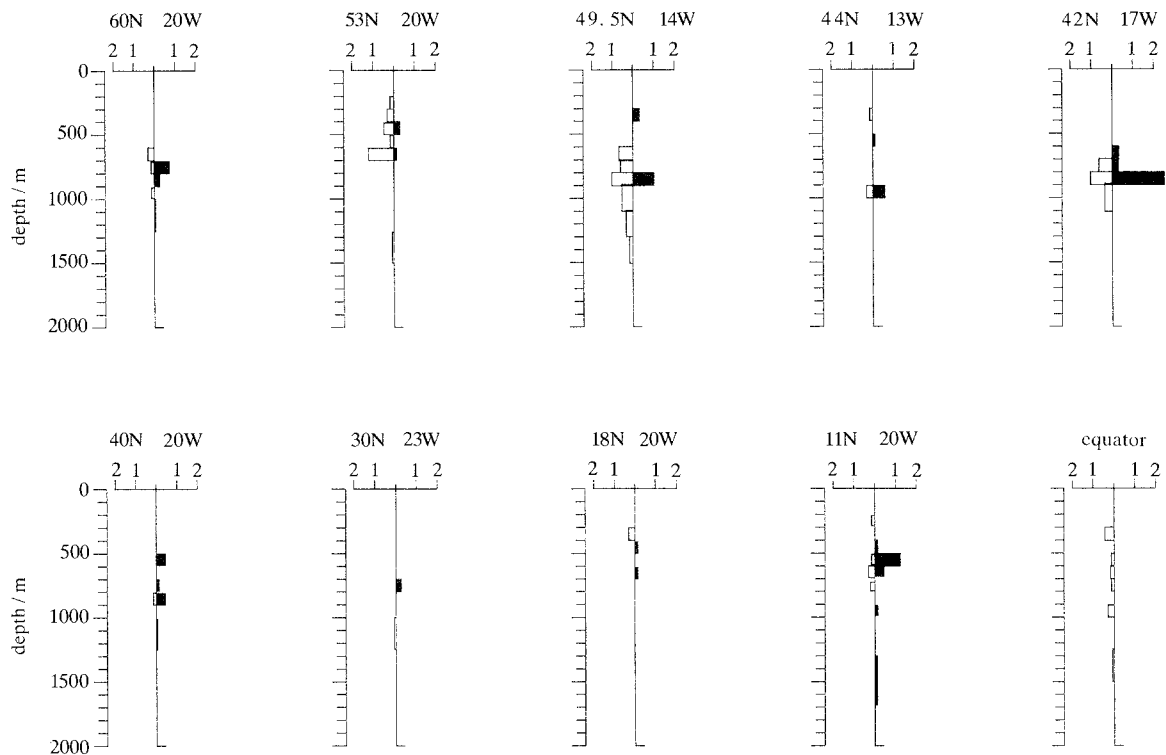
Figure 20. Depth distribution of *Nectadamas richardi* sp. nov., by day and night (left and right of ordinate respectively), at various *Discovery* stations in the Northeast Atlantic. Number of specimens, of all stages, per 10^4 cubic metres.

that some of the specimens of '*N. spinosa*' collected in the Indian Ocean (Musayeva 1976) were bracts. She refers also to nectophores, without stating which type. Because Sears (1952) referred to the nectophores with vestigial nectosacs as bracts, it is not absolutely clear whether Musayeva is referring to these or to the true bracts of *N. richardi*. The data that she provided, for R.S. *Vitiaz* stations, are:

two bracts at St. 5209 (8°10.9'S, 91°27.3'E; 225 m); one bract at St. 5220 (0°00.8'S, 91°43.5'E; 300 m); two bracts at St. 5255 (0°09.2'S, 77°02.0'E; 1500 and 1150 m); one bract at St. 5292 (5°00.0'N, 91°30.0'E; depth 1400 m).

Etymology

Named in memory of my beloved son Richard, whose brief life brought much joy, but whose death brought such sorrow; and in honour of his name-father Dr Richard Harbison, whose friendship and encouragement is much valued.

Nectadamas diomedeae (Bigelow 1911)

Material examined

At least 45 definitive nectophores, three larval nectophores and almost 300 eudoxids are housed in the *Discovery* Collections at the Institute of Oceanographic Sciences. Some of the better preserved material has been re-examined for this description.

Holotype

Bigelow (1911*b*) designated the two nectophores

taken at *Albatross* St. 4652 as the types of his new species *Nectopyramis diomedeae*. These specimens were collected at approximately 5°30'S, 82°30'W (western Pacific Ocean), in the depth range 0–732 m. The specimens are housed in the Museum of Comparative Zoology, Harvard, Cat. No. 1595.

Diagnosis

Nectopyramidine siphonophore with a singular, rhomboidal definitive nectophore, which bears a distinctive, although variable, pattern of ridges. The somatocyst canal system is complexly divided, but basically consists of a median pallial canal, from which branch the C.pa[1], C.pa[2], C.pa[3], C.h.l. and C.h.r. canals, with a descending branch extending beyond the origin of the pedicular canal. The nectophore has become distorted so that the ostium of the nectosac comes to open on its right-hand side. The obliquely slanted, pocket-shaped, hydroecium is deep, but has a relatively narrow opening.

The larval nectophore is a simple, flimsy structure. The nectosac is small, and the pedicular canal is inserted at about three-quarters its height. The lateral radial canals curve down slightly to end at about half the height of the nectosac. The hydroecium can be extensive, but has a narrow ventral opening. The somatocyst is simple, without a descending branch, and runs over the surface of the hydroecium in the mid-line. It may bear very short median branches.

The eudoxid bears true gonophores and no special nectophore. The bract is roughly triangular in shape, but with small hydroecial and ventral lobes on each side of the hydroecium. A ridge system is present on the surface of the bracts; basically consisting of a

circumferential ridge, and three lateral ridges on each side. The bracteal canal system conforms with the basic prayid design, although the longitudinal canals are short and may or may not have distal extensions ('spurs'). The other canals can be complexly branched. The dorsal canal usually originates from the right longitudinal canal. The hydroecial canals always are bifurcated, and other side branches frequently are present. One branch of the right hydroecial extends down into the hydroecial lobe.

The tentillum of the tentacle is characteristically shaped, and does not possess a terminal filament. The cnidoband consists of a large, sub-terminal, hemispherical swelling and a terminal cap.

Description

Definitive Nectophore (figures 21–24). Only a single definitive nectophore is developed, which bears a distinctive pattern of ridges and of canals. In lateral view it is roughly rhomboidal in shape. The largest specimen (*Discovery* St. 7803) (figure 24) measures 60 mm from the apical corner to the basal process, and 50 mm from the ventral to the dorsal corners. Totton (1965) referred to the two lateral sides as dorsal and ventral, apparently because of his attempts to homologize the canal systems of *Nectadamas diomedeae* and *Nectopyramis thetis*, which he outlined in an earlier publication (Totton 1954). Thus he considered that in the former species the 'ostium of the hydroecial cavity seems to have become twisted round 90% [?90°] to the right, and the original course of canal C.pa^3 readjusted' (Totton 1965, p. 133). It is presumed that Totton actually was referring to the ostium of the nectosac, as this definitely is displaced, to some extent, on to the right side of the nectophore. None the less, although it is obvious that 'during its phylogeny the

nectophore of this species [*N. diomedeae*] has become twisted and asymmetrical' and that 'what has happened . . . is not at all easy to deduce' (Totton 1965, p. 133), the distortions do not appear to necessitate a redefinition of the lateral sides of the nectophore as dorsal and ventral. This is more apparent when comparisons are made with the more simply organized nectophore of *N. richardi*.

It should be noted that the major features of the nectophores, particularly the patterns of ridges and canals, show considerable variation, such that no two nectophores exactly are alike (cf. *Nectadamas richardi*). Thus, only a generalized description can be given and, although some of the variations will be noted herein, many others can be expected.

The right-hand side of the definitive nectophore is flattened and bears a reduced ridge system. The wide ostial opening of the nectosac has become displaced on to this surface, as has, to a lesser extent, the narrow, ventro-basal, opening of the hydroecium. The left side of the nectophore is thickened, particularly in the region of the main ridge system; is irregularly convex in outline; and has a more complex ridge system. The degree of thickening varies between specimens. In some specimens thickening begins at the edges of the nectophore, whereas in others the apical and dorsal parts of the nectophore remain relatively thin, and pronounced thickening occurs only in the region of the main ridge system.

The nectosac (figures 21–24) is relatively small, usually measuring about 8–9 mm in height and 4–5 mm in depth. It has a wide, dorso-basal opening, which is displaced on to the right-hand side of the nectophore. The degree of displacement is difficult to judge, but appears to be closer to 45°, than to the ?90° (see above) suggested by Totton (1965). The ostium lies in the middle of a somewhat flattened facet, which
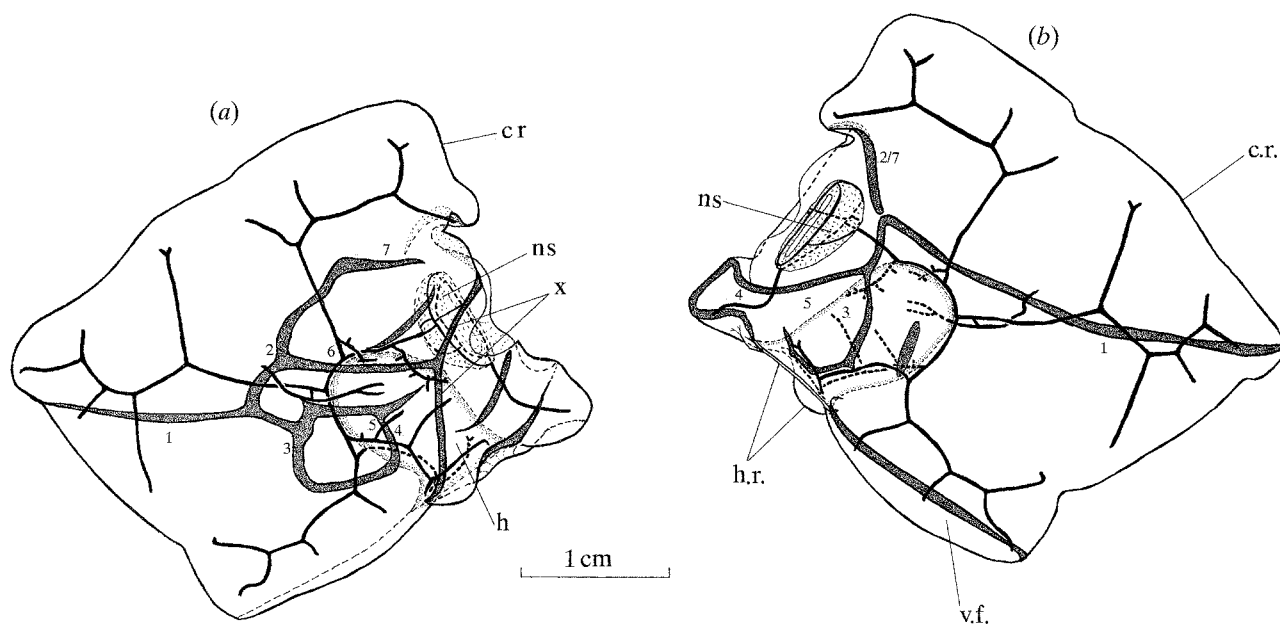

Figure 21. Definitive nectophore of *Nectadamas diomedeae* (Bigelow). (*a*) Left and (*b*) right lateral views of specimen from Johnson-Sea-Link II Dive 1004. Numbering of main lateral ridges (stippled) is an attempt to compare the arrangement with that of *N. richardi* (see text and figure 17). See figure 22 for labelling of main somatocyst canal system (thick lines). c.r., circumferential ridge; h, hydroecium; h.r., hydroecial ridges; ns, nectosac; v.f., ventral facet.
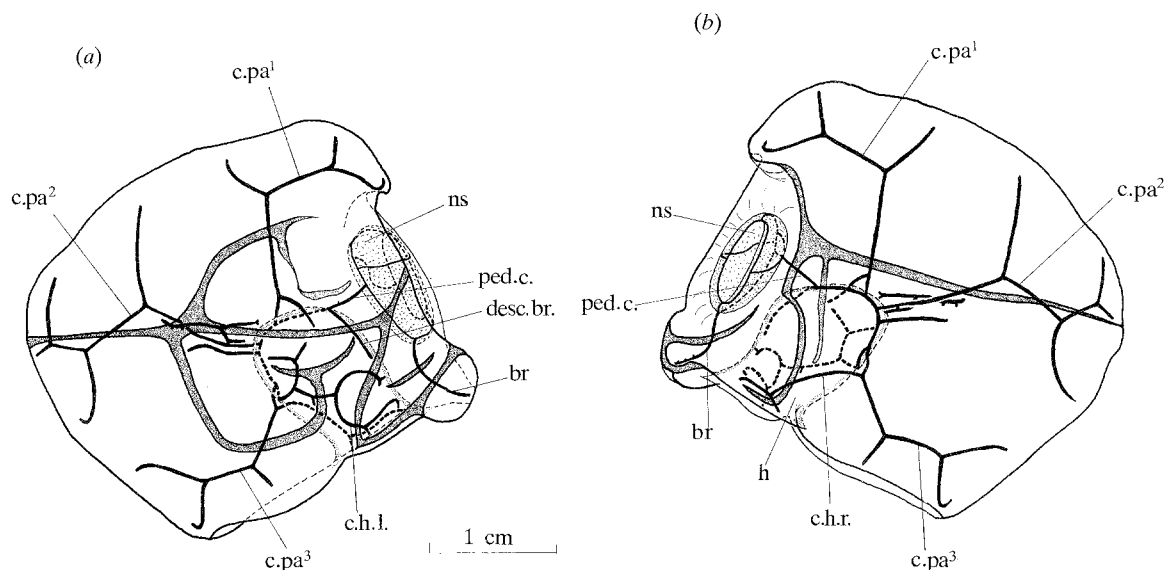
Figure 22. Definitive nectophore of *Nectadamas diomedeae* (Bigelow). (*a*) Left and (*b*) right lateral views of specimen from Johnson-Sea-Link II Dive 1680, with main somatocyst canal system (thick lines) labelled. See figure 16 for abbreviations and figure 21 for labelling of ridges (stippled). br, basal branch of ventral radial canal; c.h.l. and c.h.r., left and right hydroecial canals; desc.br., descending branch of somatocyst.

is surrounded by ridges. Often the nectosac is deeper in its dorsal half, and gradually decreases in depth ventrally.

The point of insertion of the pedicular canal lies at about two-thirds to three-quarters the height of the nectosac, and on its left side. Usually this canal gives rise to only the dorsal and ventral radial canals. These canals respectively run straight up or down the apico-lateral (left) wall of the nectosac and then curve over to join the ostial ring canal. The lateral radial canals originate close to, and occasionally at, the point of insertion of the pedicular canal. However, most frequently they arise separately from the dorsal radial canal, although one may arise from the ventral. The order in which they arise also varies. In general, the left radial canal runs obliquely across the wall of the nectosac to join the ring canal on a level with, or slightly above, the mid-height of the nectosac. The right radial canal usually is longer, running onto the right-hand side of the nectosac and then down to join the ring canal well below the mid-height of the nectosac.

The ventral canal, at the base of the nectosac, gives rise to a branch canal, which runs down, baso-ventrally, through the mesogloea into the basal process. This branch canal usually is undivided, but occasionally it bears small side processes or has a distinct side branch (see Bigelow 1911*b*, Pl. 1, fig. 1). Surprisingly, neither Bigelow (1911*b*) nor Totton (1954) describe this canal, although they both figured it. Totton (1965 p. 133–134), however, referred to it when he stated 'we see the longitudinal pallial canal extending from above down beyond the radial canals of the nectosac'. Totton, presumably, was attempting to draw homologies with the arrangement of the canals in *Nectopyramis thetis*, as is discussed in more detail below.

The narrow, laterally compressed, pocket-shaped,

hydroecium extends diagonally up into the necto-phore (figures 21–24). It is asymmetrical in shape, in accord with the general asymmetry of the nectophore itself, being deeper on the left-hand side than on the right (see also Bigelow (1911*b*, plate 1, figure 2)). Its narrow, slit-like, ventral opening also is displaced slightly, on to the right side of the nectophore. This asymmetry also results in the displacement of the pallial canal on to the right-hand side of the hydro-ecium, but close to its dorsal margin. The lateral borders of the opening to the hydroecium are marked by two ridges.

1. Ridge pattern. The nectophores bear a characteristic pattern of ridges, but there are many variations on it, and no two nectophores have been found to have exactly the same arrangement (figures 21–24). The system of numbering of these ridges (figure 21*a*, *b*) represents a preliminary attempt to compare their arrangement with that found on the nectophores of *Nectadamas richardi* (see figure 17*a*, *b*). However, such comparisons are not entirely satisfactory, and the subject will not be discussed in detail.

As in *Nectadamas richardi*, there is a circumferential ridge that runs around most of the nectophore in the apico-dorsal plane (figure 21*a*, *b*). It can become quite rounded in the apical half of the nectophore, particularly in those where thickening of the mesogloea extends to the margins. This ridge divides at the ventral corner of the nectophore, and two ridges run basally on top of rounded processes, which delimit a shallow, concave ventral facet (figure 21*b*). The width of this facet narrows considerably as the more apical part of the hydroecial opening is approached. The ridges then appear to run on to form the margins of this opening, although the linkage is not always easy to discern. Basal to the hydroecial opening, the ridge on the right-hand side connects in with the lateral ridge system, while that on the left usually peters out
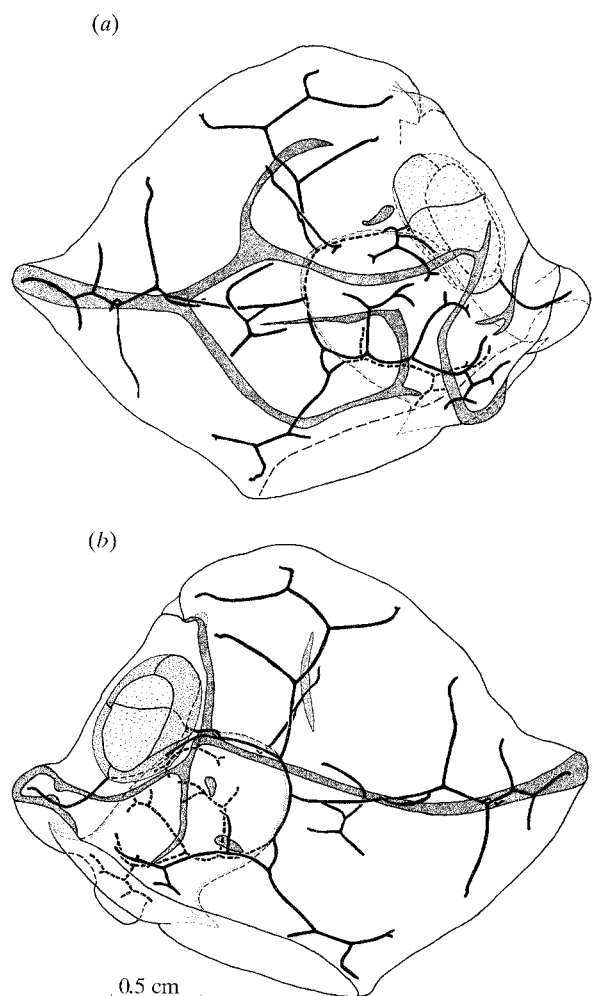
(a)

(b)

0.5 cm

Figure 23. Definitive nectophore of *Nectadamas diomedeae* (Bigelow). (a) Left and (b) right lateral views of specimen from *Beebe* specimen no. 31942.

(figure 21*b*), but occasionally it appears to connect in with the ridge system on that side of the nectophore.

The circumferential ridge, in accordance with the arrangement in *Nectadamas richardi*, also would be expected to divide and circumvent the opening of the nectosac. Indeed the ostium is surrounded by ridges but, because the nectosac has been displaced on to the right-hand side of the nectophore, it is uncertain whether these ridges are equivalent to those of *N. richardi* or whether, in part at least, they are derived from the lateral ridge system. It is tentatively suggested that the ridge running along the left lateral margin of the ostial facet ancestrally was the right-hand branch of the circumferential ridge, and that the ancestral left-hand branch has been displaced on to the left side of the nectophore (X, figure 21*a*). Further, it is suggested that the ridges (2/7 and 5, figure 21*b*) that now form the right-hand margin to the ostial facet are derived from the ancestral right lateral ridge system.

The main lateral ridges usually are very prominent, but variable in their arrangement (figures 21–24). Although a basic pattern usually can be discerned (see figure 21), in the largest specimen (figure 24) the ridge pattern is much reduced. Because of this variability

the lateral ridge system will not be described in detail. The ridge system on the left-hand side of the necto-phore (figures 21*a*, 22*a*, 23*a* and 24) is more complex than that on the right (figures 21*b*, 22*b* and 23*b*), but it appears to show greater conformity with that found on the nectophores of *Nectadamas richardi* (cf. figures 17*a* and 21*a*).

The complex of ridges on the left side of the nectophore, in the mid-ventral region, which some-times encloses a squarish raised facet (figure 21*a*) with either a flattened or concave surface, is particularly variable in its arrangement (figures 21*a*, 22*a*, 23*a* and 24). It is also difficult to compare with the ridge pattern on the nectophores of *Nectadamas richardi*. However, it is tentatively suggested that it might be equivalent to ridges 3, left hydroecial, 4 and 5 of *N. richardi* (cf. figures 17*a* and 21*a*). The present arrange-ment might have been brought about by the distor-tion of the nectophore, with the opening of the hydro-ecium being displaced, slightly, onto the right lateral side. In this case, the present left hydroecial ridge, with its extension to the ventral corner, would have to be considered as of novel formation.

The remaining baso-ventral ridge complex on the left side of the nectophore also is difficult to compare with the arrangement found in *Nectadamas richardi*. A tentative solution might be to suggest that the baso-ventral region on the right-hand side of the necto-phore has expanded and pushed the original ridges over on to the left side. Thus the left circum-ostial ridge (X, figure 21*a*) now runs obliquely from the middle of the ostial facet toward the apico-ventral corner of the hydroecial opening. However, it does not always reach to the base of the nectophore (figure 23*a*), nor does it join the present left hydroecial ridge but bends sharply basad before reaching it.

The ridge pattern on the flattened right-hand side of the nectophore (figures 21*b*, 22*b*, 23*b*) is much simpler than that on the left. Despite this, it is difficult to draw comparisons with the ridge pattern found on
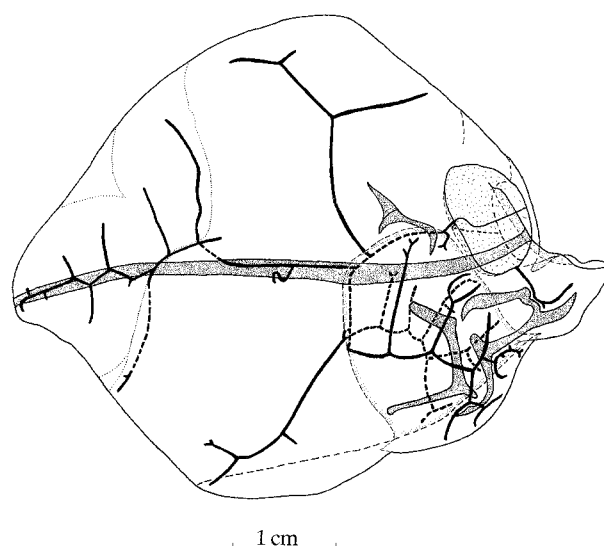

1 cm

Figure 24. Definitive nectophore of *Nectadamas diomedeae* (Bigelow). Left lateral view of specimen from *Discovery* St. 7803#7.

the nectophores of *Nectadamas richardi* (figure 17*b*); and the numbering system in figure 21*b* is suggested only tentatively. Additional ridges (figure 23*b*), with no obvious counterparts on the nectophores of *N. richardi*, sometimes are present. The possible derivation of the ridges on the right-hand side of the ostium was mentioned above, but it should be noted that the connections between these ridges are not always complete (figure 22*b*). Also it is suggested tentatively that the distal part of ridge 3, which runs basad, parallel to the hydroecial opening (figure 21*b*) on some but not all of the nectophores, is comparable with the right hydroecial ridge of *Nectadamas richardi*. In which case the present right hydroecial ridge, like that on the left, would have to be considered a novel formation.

2. Canal system. The basic canal system of the somatocyst is very similar to that found in the necto-phores of *Nectadamas richardi*. There is a median, longitudinal pallial canal from which branch, in the apico-dorsal plane, the C.pa^1, C.pa^2 and C.pa^3 canals (figure 22). In addition, there are three other canals which Bigelow (1911*b*) described as the right (C.h.r.) and left (C.h.l.) hydroecial canals, and a descending branch to the main pallial. However, as is discussed below, Totton (1954, 1965) drew a different conclusion as to the identity of these canals, whilst attempting to homologize this somatocyst canal system with that of *Nectopyramis thetis*. None the less, it should be noted, as Totton (1954) pointed out, that the labelling to Bigelow's figures (1911*b*, plate 1, figures 3 and 4) is in error.

The pedicular canal, from the nectosac, joins the pallial canal on the right side of the hydroecium, close to the latter's basal wall and slightly below its dorsal apex. At this point the descending branch is given off, which runs over the hydroecial wall onto the left side, and then ventrad. The degree of complexity of this descending branch is very variable, ranging from entirely simple to bearing several side branches (figures 21–24; Totton 1954, text-figure 39A). Assuming this is the true descending branch of the pallial canal, as is seen in many prayine siphonophores, then its unusual disposition can be considered to be the result of the general distortion of the nectophore. However, in one nectophore (*Beebe* 29286) there are two 'descending' branches; the more basal branch running ventrad on the right side of the hydroecium, whereas the other, which is comparatively thick, runs over onto the left side and has two side branches.

The main pallial canal runs apically, close to the dorsal apex of the hydroecium but on its right side. Approximately in the middle of the hydroecium, it gives off the C.pa^1 canal. This canal, at first, usually runs dorsad and then, as it bends basad, it gives off one, sometimes two, branch canals, directed towards the apico-dorsal edge of the nectophore. The main C.pa^1 canal continues basad and then branches; one branch running towards the dorsal corner of the nectophore, and the other running into the beak-like process that marks the dorsal junction of the ridges that surround the ostial facet. Any one of these branches may have a further, sub-terminal bifurcation, or may be reduced or absent. Additional

branches also may be present. The simplest, and least typical, arrangement of the C.pa^1 canal is found in the largest nectophore (figure 24).

In eleven of the specimens examined, the C.pa^1 canal also gives off one or more additional canals from its proximal, dorsally directed part. In these speci-mens, there are two basic arrangements for these canals, with one specimen having both types. In the first case, a canal arises close to the base of the C.pa^1 and runs baso-ventrally and laterally to pass over the left side of the hydroecial wall. It may be simple or bear several side branches (figures 21–22). Totton (1954, p. 84) suggested that this canal, which he referred to as the C.h.l.^{2}, was the 'true left hydroecial canal, and that Bigelow's [1911*b*] C.h.l. is a secondar-ily developed canal'. This contention will be discussed later, after the full canal system has been described.

In the second case, the branch canal usually arises further along the C.pa^1 canal and runs out, laterally, towards the left side of the nectophore. This branch canal usually is simple but may divide, close to the lateral wall of the nectophore, to produce two further branches which run in opposite directions (figure 23). In addition, one specimen also had a basally directed branch arising from half way up the proximal part of the C.pa^1 (figure 23).

The main pallial canal usually is thickened between the C.pa^1 and C.pa^2 branches. This is the region where the siphosomal stem is attached. No pro-nounced central organ was observed in any of the specimens examined. The C.pa^2 canal arises just after the pallial canal has curved round on to the apico-lateral (right) wall of the hydroecium. This canal, at first, runs straight toward the apex of the nectophore, but later it has a zigzag course, giving off dorsad or ventrad branches at each zig and zag, before termi-nating close to the apex of the nectophore (figures 21–24). In only two specimens was this basic pattern not adhered to. There may be up to eight of these side branches, but the average number is four. In all but one of the specimens examined, it is a dorsad branch that appears first. The length of the side branches decreases in accord with the decrease in width of the nectophore as the apex is approached. The longest branches may bear short side branches or bifurcate sub-terminally. In the distal region of the C.pa^2 canal, short lateral branches also may be given off either to the right or left (figures 23–24).

In the proximal region of the C.pa^2 canal another lateral (left) branch always is present, except possibly in one specimen (*Beebe* 311767) where it may arise from the pallial canal itself. This lateral branch may be simple (figure 24), but most often, close to the lateral margin of the nectophore, it divides to produce two canals which run in opposite, but variable, direc-tions. Either one of these canals may then bifurcate (figures 21–23). A further branch, directed basally, may leave the lateral at about half its length (figure 22). In addition there may be an extra lateral branch, to the right side, which usually arises apical to the left lateral branch. Finally, there may be an extra branch from the pallial canal itself, in the vicinity of the C.pa^2 canal (figure 22).

After giving rise to the $C.pa^2$ canal, the pallial canal continues ventrad on the apico-lateral (right) wall of the hydroecium. It branches off the left hydroecial canal (C.h.l.) and continues ventrad, but away from the apical wall of the hydroecium, which curves round baso-ventrally in this region. Shortly after the appearance of the C.h.l., the right hydroecial canal (C.h.r.) is branched off at an acute angle. The pallial canal then continues, as the $C.pa^3$, to curve down towards the ventral corner of the nectophore, and then up, for a short distance, towards its apex (figures 21–24). Typically, the $C.pa^3$ gives off a branch, which runs down towards the ventral corner of the nectophore. Either branch may have a sub-terminal bifurcation. In addition, up to three other canals, directed towards the ventral facet, may branch from the $C.pa^3$. In one nectophore an apico-ventrally directed branch also was present.

The right hydroecial canal (C.h.r.) usually has a much simpler organization than the left. Basically, after leaving the $C.pa^3$ canal at an acute angle, it runs basad on to the right-hand wall of the hydroecium. It then curves round and runs ventrad. As it approaches the hydroecial opening it bends sharply basad and runs, for a variable distance along the hydroecial wall parallel to its opening. There may be a sub-terminal bifurcation, or the canal may bend ventrad again close to its end. In about half of the specimens examined, a branch canal is given off where the main canal bends sharply basad. This branch canal, which runs towards the apico-ventral part of the hydroecial opening, usually is short, although it may divide further (figure 23).

In three specimens a more complex arrangement of the C.h.r. was found. In one (figure 23) there was an extra branch in the proximal part of the canal, which ran dorsad and paralleled one of the branch canals of the C.h.l.. In the second specimen, there were two extra, dorsally directed, branches, and in the largest specimen the C.h.r. was almost as complexly divided as the C.h.l. (figure 24).

The C.h.l. canal is branched complexly, but there seems to be a basic scheme to this branching. It divides from the pallial canal usually at a point where the latter still lies on the apico-lateral (right) side of the hydroecium, but occasionally after the latter has left this wall and penetrated into the mesogloea. It then travels over on to the left side of the hydroecium and descends towards the hydroecial opening, giving off a series of side branches. Close to this opening it divides to produce, usually, a short ventrad branch and a longer basad one, which parallels the opening of the hydroecium and may have a sub-terminal bifurcation. There are many exceptions to the latter arrangement, usually associated with a considerable shortening of the basad branch, but in general it resembles that found for the C.h.r.. The number of side branches is variable, but usually there are two or three (figures 21–24). The first runs dorsad and may be simple or have extensive side branches. The second runs towards the nectosac, but often then curves round to run down the basal side of the hydroecium. Again it can be simple or bear side branches. The third, present in

most of the specimens examined, runs basad and usually is simple, but in one specimen (figure 24) was complexly divided. Occasionally a very short side branch is present, either before the first main branch or after the last. In addition, short, laterally directed branches may be present (figure 22).

3. Comparisons of the somatocyst canal systems in the genera *Nectopyramis* and *Nectadamas*. Despite the fact that the somatocyst canal system of *Nectadamas diomedeae* is complexly divided, Totton (1954) considered it possible to homologize this system with that found in the nectophores of *Nectopyramis thetis*. He suggested: (i) that the $C.pa^2$ canal of *N. diomedeae* nectophores represented the apical extension of the pallial canal in *N. thetis*; (ii) that the $C.pa^3$ canal of *N. diomedeae* represented the right dorso-lateral canal of *N. thetis*, which divides from the right hydroecial canal (C.h.r.); (iii) that the $C.pa^1$ canal of *N. diomedeae* represents the left dorso-lateral canal of *N. thetis*, and that its proximal branch, which he referred to as $C.h.l.^2$, is equivalent to the left hydroecial canal of the latter species; (iv) that the left hydroecial canal (C.h.l.) of *N. diomedeae* is a secondarily developed canal; and (v) that, to account for the present disposition of the canals in *N. diomedeae*, 'the whole nectophore is twisted, so that the nectosac opens on one side instead of dorso-basally, and the branches of the somatocyst have become secondarily displaced.' (Totton 1954, p. 84.)

In addition, it would seem necessary to consider the basal extension of the ventral radial canal in *N. diomedeae* as equivalent to the descending branch of the pallial canal in *N. thetis*. However, Totton (1954) makes no mention of this, nor does he label it as such in his figure (text-figure 39A). Instead he labelled one of the two branches of the canal which extends, basally, beyond the origin of the pedicular canal as *C.desc.* This is the same as Bigelow's (1911b) descending branch. However, Totton (1965, pp. 133–134) appears to correct this when he states 'we see the longitudinal pallial canal extending from above down beyond the radial canals of the nectosac'.

Totton (1965, pp. 133–134) noted that the canal system of the somatocyst of *Nectadamas diomedeae* was not always as complex as previously described (Bigelow 1911b, Totton 1954), perhaps to allow for the fact that his $C.h.l.^2$ is not always present. Further he equated the 'upper branch' of the pallial canal with the $C.pa^3$ canal. This would seem more logical as it is this canal, and not the $C.pa^2$, that runs over the apical part of the hydroecial wall, as does the 'upper branch' of the pallial canal in *N. thetis*. However, later he contradicts this by stating 'In *N. diomedeae* I homologize Bigelow's $C.pa^3$ with *C.D.R.* (right dorsal canal) in *N. thetis*, and his $C.pa^1$ with C.D.L. in *N. thetis*. In *N. diomedeae* the right canal $C.pa^3$ sends branches to both sides of the twisted hydroecium, and the left branch sends only small ones'. Thus, there appears to be some confusion here.

It is difficult to sustain Totton's efforts to establish a close relation between the somatocyst canal systems in *Nectadamas diomedeae* and *Nectopyramis thetis*, particularly if the very basic arrangement in *N. richardi*,

where there is no obvious distortion of the nectophore, and *N. natans* are taken into account. In the genus *Nectadamas* the radial canals to the nectosac do not arise directly from the pallial canal, but from a separate pedicular canal. The main pallial canal runs around the pocket-shaped hydroecium, which has a restricted opening on the ventral side of the nectophore. It gives rise to three median branches, C.pa[^1], C.pa[^2] and C.pa[^3], which run in the *apico-dorsal* plane of the nectophore and not laterally, as the pair of dorsolaterals in *N. thetis* do. This basic arrangement is found in *N. richardi*. However, in *N. diomedeae* a pair of hydroecial canals also is present, as well as what appears to be a descending branch to the pallial canal, extending beyond the origin of the pedicular canal. Also all the main branch canals are complexly divided.

To homologize the canal system of the nectophore

of *Nectadamas diomedeae* with that of *Nectopyramis thetis*, it would require that the whole nectophore be twisted on its axis such that the ancestral dorsal and ventral sides lie laterally, as indeed Totton (1965) suggested. However, although the nectosac has been displaced, there is little other evidence for this. The opening of the hydroecium remains ventral, although slightly displaced to the right side, and the C.pa[^1], C.pa[^2] and C.pa[^3] canals lie in the same plane as those in the undistorted nectophores of *N. richardi*. Further the canal (C.h.l.[^2]), which Totton (1954) equated with the left hydroecial canal in *N. thetis*, is not always present and, when it is, it does not always run down on to the left side of the hydroecium. Thus, it is concluded that the somatocyst canals systems in the genera *Nectopyramis* and *Nectadamas* are not homologous, and that, although the species are quite closely related, this does not warrant their inclusion in a single genus.
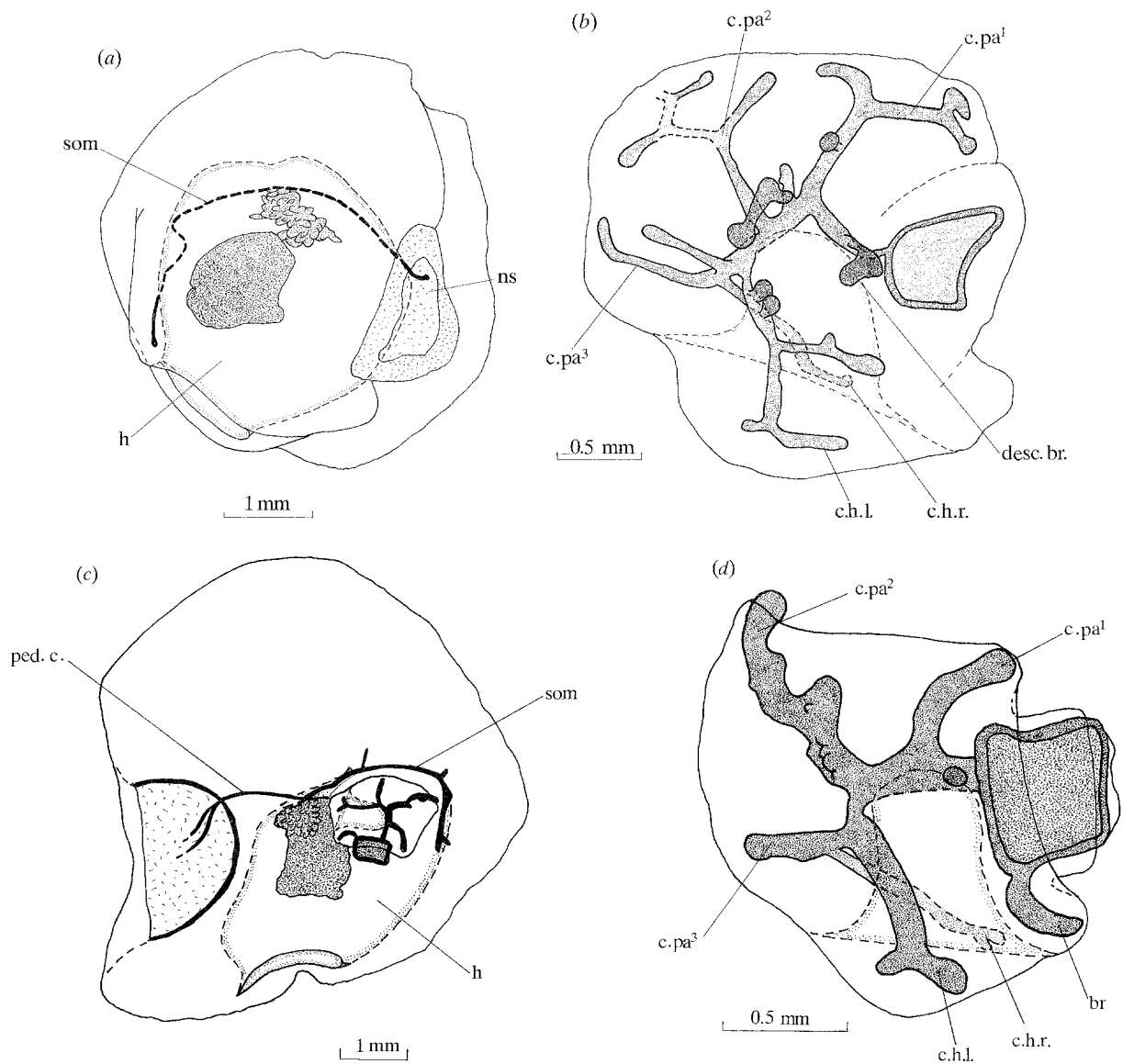

Figure 25. *Nectadamas diomedeae* (Bigelow). (a) and (c) Larval nectophore, and (b) and (d) developing definitive nectophore, extracted from its hydroecium, from *Discovery* Sts. 10378#15 and 7803#1 respectively. The hydroecial contents of the developing definitive nectophores have been omitted for clarity. See figures 16 and 22 for abbreviations. som, somatocyst.

Larval nectophore (figure 25*a*, *c*). Three larval necto-phores of *Nectadamas diomedeae* have been identified from the *Discovery* collections. They are flimsy struc-tures, measuring up to 6.5 mm in length, and 7.5 mm in height, although they appear to have shrunk during preservation and probably are larger in life. Two of them contain a developing definitive nectophore (figure 25*b–d*).

In basic construction they resemble the definitive nectophores of *Nectadamas richardi*. However, the pres-ence of a developing definitive nectophore or of characteristic tentilla clearly establish their prov-enance. A lateral ridge system appears to be present, although the distortions of the nectophore make this difficult to discern. However, there is a circumferential ridge running around the nectophore in the apico-dorsal plane.

The nectosac opens basally, and measures up to 3 mm in height and 1.8 mm in depth. The pedicular canal is inserted at about three-quarters its height, and appears to give rise directly to four radial canals. The hydroecium is extensive and can occupy a great deal of the interior of the nectophore (figure 25*a*), depending on the degree of development of the defini-tive nectophore. None the less, it has a relatively narrow opening which can be considerably smaller than length of the definitive nectophore developing within it.

The somatocyst consists of a simple pallial canal running over the dorsal and apical walls of the hydro-ecium, but displaced slightly on to its right-hand side, as it is in the definitive nectophore. In two of the specimens, it gives off three short side branches, and in one of these the pallial canal had a sub-terminal bifurcation (figure 25*c*). There is too little information to decide whether this arrangement is homologous with the C.pa[1], C.pa[2] and C.pa[3] canal system of the definitive nectophore, particularly as no side branches were noted in the third specimen (figure 25*a*). The pedicular canal arises from the basal end of the pallial canal, and no descending branch is present. This point also represents the region of attachment of the gastro-zooid and tentacle, and the definitive nectophore. In one specimen, this region of attachment is slightly inflated.

The developing definitive nectophores are of inter-est in themselves. The smaller one (figure 25*c*, *d*) has the basic *Nectadamas diomedeae* somatocyst canal sys-tem, with the descending branch to the pallial canal present only as a small knob; while the extension to the ventral radial canal of the nectosac is pronounced. The nectosac itself appears to open basally and, therefore, its displacement on to the right-hand side of the nectophore must occur at a later developmental stage.

The larger one (figure 25*a*) measures about 2.5 mm in length and height, while the opening of the hydro-ecium of the larval nectophore measures only 1.5 mm. The surface of the nectophore is covered in a patch-work of large, ectodermal cells. A pattern of ridges also is present, but its arrangement could not be discerned. This specimen has begun to distort so that the opening of the nectosac lies slightly to the right.

There appears to be no extension to the ventral radial canal, but this is the result of damage caused during extraction of the nectophore from the hydroecium of the larval nectophore. The descending branch to the pallial canal is obvious, and lies on the left side of the hydroecium. The C.pa[1] and C.pa[2] canals have begun to branch, in a typical fashion, and both have a lateral (left) branch present. However, between them there is an extra canal running towards the right side of the nectophore. Another additional canal, running api-cally, branches from the pallial canal between the C.pa[2] and C.pa[3]. In only two of the large definitive nectophores was one or the other of these additional canals found to be present. Thus, the presence of both these canals in a single nectophore is exceptional, but does not detract from the fact that the specimen belongs to *Nectadamas diomedeae*, particularly as its tentilla are identical to those found in the definitive nectophore.

Eudoxid. The eudoxid stage of *Nectadamas diomedeae* was briefly described, but beautifully illustrated, by Bigelow (1911*b*). It consists of a roughly triangular bract; a large gonophore, with buds of successive ones; and a gastrozooid and tentacle, with characteristically shaped tentilla.

1. Bract (figure 26). The bract has the approximate shape of an isosceles triangle. However, the apex is rounded and the two longer sides usually have convex outlines and extend basally to form the hydroecial and ventral lobes. These lobes usually are fairly pro-nounced, but can be greatly reduced. The largest specimen measured 43 mm in height and 23 mm in width. The hydroecium occupies the middle of the basal region and has a narrow slit-like opening. In smaller specimens, it reaches to about one third the total height of the bract, but its size does not increase commensurate with that of the bract, so that in the largest specimens it reaches only to one quarter the total height. In poorly preserved material, the lateral sides of the bract may be compressed. However, for the better preserved, larger material either one or both of the sides may be thickened, particularly in the basal half.

Each bract has a system of ridges on its surface, the most obvious of which is a circumferential ridge running around the outer margins (figure 26). This ridge passes over the ventral lobe and then splits to form the sides of the hydroecial opening. About half way across this opening each ridge splits again. The inner ridges continue as the margins of the hydroecial opening and subsequently unite, with a single ridge continuing down onto the hydroecial lobe (i, figure 26*a*). The outer pair (o figure 26*a*), which are more prominent, run on to form the basal edges of the hydroecial lobe and unite with the circumferential ridge at its base.

There are three ridges on each side of the bract (figure 26), although they are not always easy to discern. A central ridge runs from the apex down towards the hydroecium. In the basal half of the bract it is slightly deflected towards the hydroecial lobe and
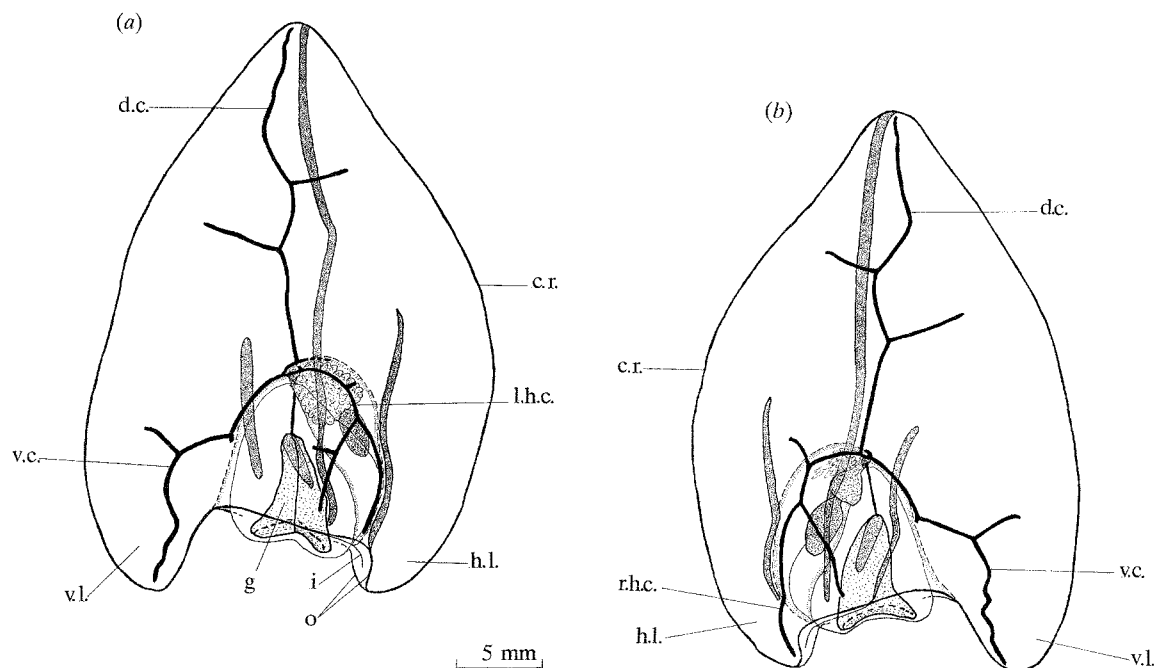
Figure 26. Eudoxid of *Nectadamas diomedeae* (Bigelow). (*a*) Left- and (*b*) right-hand views, showing ridge pattern (stippled) and canal system (thick lines). See figure 1*b* for abbreviations for canals. c.r., circumferential ridge; g, gonophore; h.l. and v.l., hydroecial and ventral lobes; i and o, inner and outer hydroecial ridges.

may end just short of the hydroecial ridge or join with it. The other two ridges are present only in the basal half of the bract, and the one on the hydroecial lobe side is usually longer than the other. They may or may not join the hydroecial ridge. On a few specimens a weak cross connection was found between the central ridge and the one on the ventral lobe side. On one specimen, on the left-hand side only, the central ridge was relatively short and did not reach to the apex of the bract, whereas the other two ridges were long and joined the circumferential ridge close to the apex. In addition, there was a weak cross link between all the ridges.

The bracteal canal system conforms with the basic prayine arrangement, and is a more complex version of that found in the bracts of *Nectadamas richardi*. This complexity does not appear to be a function of size, as Bigelow (1911*b*) suggested, as it is evident even in the youngest specimens; thereby allowing the two species easily to be distinguished. The ventral canal, from its junction with the longitudinal canals on the apex of the hydroecium, at first runs down the wall of the hydroecium. About half-way down the latter it bends sharply away into the mesogloea, and may give off a short basad branch. It continues towards the side of the bract for a short distance and then usually branches. The main branch continues down into the ventral process and ends close to its tip, whereas the side branch, if present, is of variable length and may branch further (Bigelow 1911*b*, plate 1, figure 5). Additional branches also may be present, as in Bigelow's specimen. An extra branch may arise from the ventral canal before it inflects away from the hydroecium, or as the ventral canal enters the ventral process. The most complex arrangement noted had five side branches.

Longitudinal bracteal canals are assumed to be present as several, but not all, of the bracts examined had very short 'spur' canals extending out longitudinally from the ends of the zone of attachment of the other eudoxid components. This zone of attachment is semi-circular in shape, but does not appear to be inflated into a central organ. The dorsal canal usually arises from the junction of the right longitudinal and hydroccial canals. However, in two of the bracts examined it actually arose on the left side. It runs up towards the apex of the bract and usually has a zigzagged course. At each change of direction a side branch is given off, in a similar fashion to that noted for the C.pa^2 canal of the definitive nectophore. The length of these side branches is very variable. This arrangement is not always adhered to, and occasionally extra longitudinally directed branches may be present.

The two hydroecial canals curve over the hydroecial wall on each side and, more often than not, proximally give off a side branch, of variable length (figure 26). Occasionally a second side branch is present. Each hydroecial then bifurcates, with one branch running diagonally basad across the wall of the hydroecium, and the other running down toward the hydroecial lobe. The former branch may be simple, or give off side a branch (figure 26), or bifurcate towards its distal end (Bigelow 1911*b*, plate 1, figure 5). The one on the right side of the hydroecium is usually longer than that on the left. This is also true for the other main hydroccial branch. The one on the left side usually ends at the base of the hydroecium, while that on the right inflects away from the hydroccial wall and continues down into the hydroccial process, to end close to its tip. At the point of inflexion, a short basad branch may be given off.

(a)

1 mm

(b)

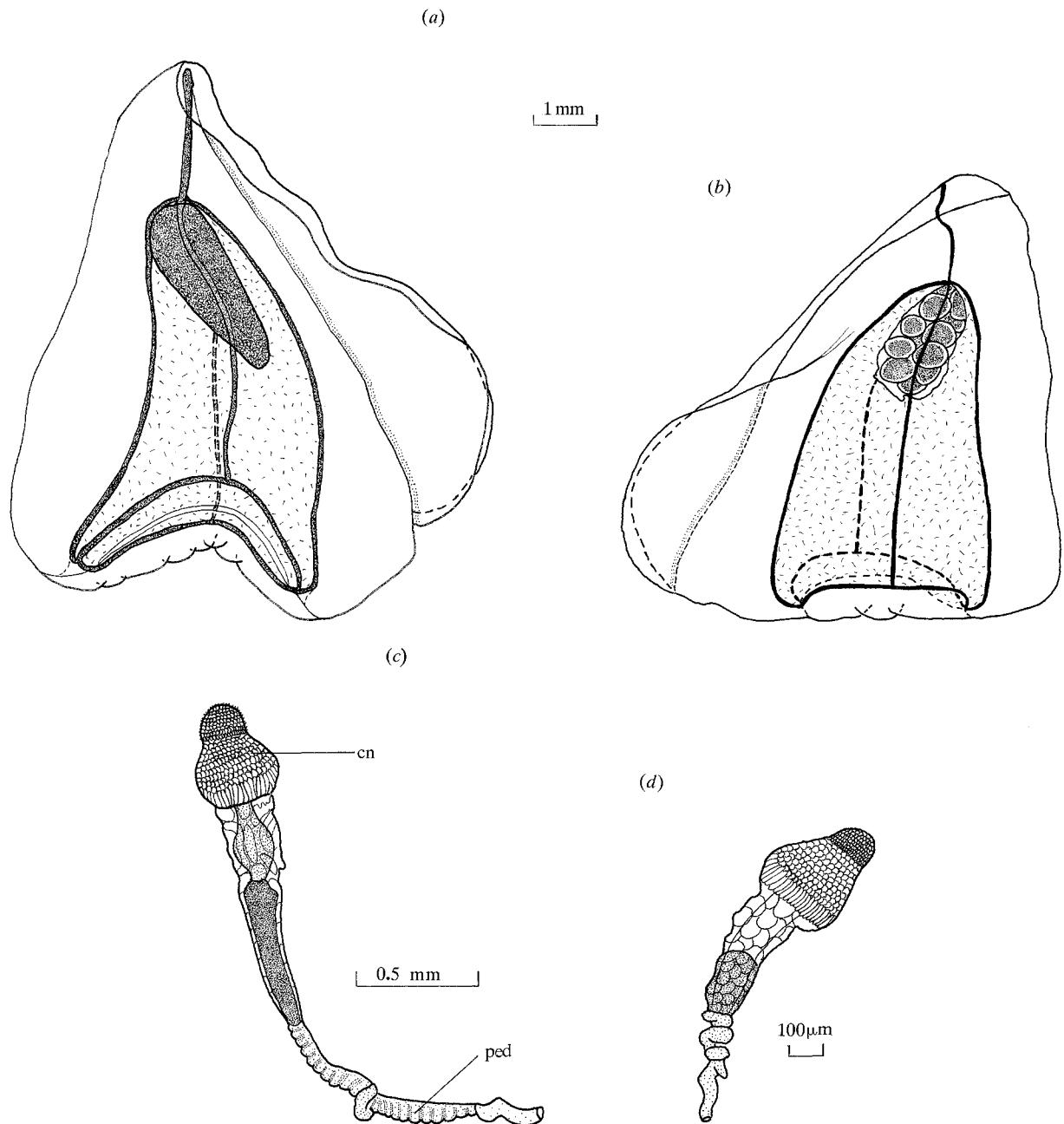*(c)*

cn

(d)

0.5 mm

ped

100 μm

Figure 27. *Nectadamas diomedeae* (Bigelow). (a) Male and (b) female gonophores. (c) and (d) Tentillum. See figure 8 for abbreviations.

Other side branches also may be present. In two specimens the branch on the left side also was found to extend down beyond the hydroecium, but not as far as that on the right.

2. Gonophore (figure 27a, b). The mature gonophore can occupy most of the hydroecial cavity of the bract, and extend from its opening. It measures up to 10 mm in height and 8.5 mm in width. The radial canals in the walls of the subumbrella cavity have straight courses, and the pedicular canal is simple. Each eudoxid has only one large gonophore, either male or female, although small buds of successive ones can be discerned in the region of the zone of attachment. No special nectophore is present.

The lateral flaps that flank the hydroecial cavity of the gonophore are of approximately equal size, although one tends to be thinner than the other and

consequently may undergo more distortion during preservation. Small patches of ectodermal cells, probably sites of bioluminescence, are scattered over the internal walls of the hydroecium and the subumbrella cavity. They are also present on the outside of the gonophore, particularly in the basal region.

3. Gastrozooid and tentacle. The gastrozooid shows no unusual features worthy of note. The tentilla of the tentacle, however, are distinctly different from those of other nectopyramidine species in that they do not have a terminal filament (figure 27c, d). Their structure was described well by Totton (1954). They are relatively large and borne on long pedicels, which clearly can extend to a considerable length. Distal to this is a region where the endoderm is thickened and opaque. In the mature tentillum, this region can be about 0.7 mm in length, but in the immature one it is

much shorter. This is superseded by a region, about 0.4 mm in length, where the endodermal canal is flask shaped. In both regions the long, irregularly twisted, structureless, and presumably doubled, elastic cord clearly can be seen.

The main nematocysts batteries are to be found at the distal end of the tentillum, and are clearly divided into two regions. The larger, hemispherical, proximal battery has a diameter of between 0.3 mm and 0.4 mm. Two sorts of elongate nematocyst are present. The larger, and less numerous, ones measure ca. 100 × 18–20 μm and are roughly cylindrical, with rounded ends. The slightly smaller, but much more numerous, ones measure ca. 90 × 10 (max) μm and usually have a curved appearance, and distinctly

taper towards one end. The terminal cap of nematocysts measures from 0.1 to 0.25 mm in diameter, depending on the degree of development of the tentillum. Only one type of nematocyst, 50–70 in number, appears to be present. This has a darkly pigmented centre and measures about 27 × 19 μm. Totton (1954) presumed that they were stenoteles, but no further, detailed studies of any of these nematocyst types have been made.

Distribution

The published records for *Nectadamas diomedeae* (table 7), as *Nectopyramis diomedeae* or *N.* sp. nov.? (Totton 1936), indicate that this species has a poorly known, but widespread distribution in the Atlantic,

Table 7. *Published records for Nectadamas diomedeae (Bigelow).*
(dn, definitive nectophore; e, eudoxid.)

Atlantic Ocean

Totton (1936)[b]	3 dn, 1 e	centred around
& Totton (1954)	4 dn, 11 e	32°12′N 64°35W
Totton (1954)	7 + e	26–40°S 18–38°W
	1 e	64°55.9′S 22°08.1′W
Fraser (1961)	?	54–60°N 8–15°W (2 Sts)
Totton (1965)	1 e	45°51′N 8°43′W
Fraser (1967)	?	60°23.5′N 7°49.5′W
Stepanjants (1975)	?	ca. 19°N 68°W
Stepanjants (p.c.)	?	82°16′N 5°56′E (Arctic)
Alvarino (1971)	?	31–34°S 0–16°E (3 Sts)
van Soest (1973)	2 e	45°N 16°06′W
Margulis (1974)	?	ca. 39°N 14°W
	?	ca. 15°S 30°W
Casanova (1980)[a]	1 dn, 1 e?	30°18′N 29°20′W
Pugh (1974)	4 dn, 4 e	ca. 28°N 14°W
Pugh (1975)	2 dn, 7 e	ca. 32°N 34–60°W
Pugh (1990)[a]	2 e	47°N 20°W
Alvarino et al (1990)	?	off Brazil

Indian Ocean

Totton (1954)	2 dn	34–38°S 34–36°E (2 Sts)
	2 dn	00–06°N 49–52°E (2 Sts)
	2 dn	32°S 62–78°E (2 Sts)
Margulis (p.c.)	1 dn, ? e	7–9°N 63–88°E

Pacific Ocean

Bigelow (1911b)	2dn + (1e), 4 e	ca. 5–12°S 80–94°W (4 Sts)
	1 e	16°32.5′S 119°59′W
Bigelow (1913)	1 e	between San Francisco & Unalaska
	1 e	east of Kurile Islands
Bigelow (1931)	1 dn	3°52′N 86°43′W
Stepanjants (1963)[a]	1 e	80°39.1′N 163°01′W
	3 e	59–61°N 175–180°W (3 Sts)
Alvarino (1964)	?	W.Pacific/Indo-Pacific
Alvarino (1967)	??	ca. 30°30′N 120°W
Stepanjants (1970)	? e	45–47°N 152–154°E (2 Sts)
Stepanjants (1977)	1 dn	10°N–20°S 155°E–140°W
Stepanjants (p.c.)	?	83–86°N 164–175°W (3 Sts)
	?	56°05.5′N 174°32′E
	?	45–46°N 152–154°E (2 Sts)
	?	7°33′N 162°38′W
Alvarino et al. (1990)	?	ca. 36–43°S 75–79°W
	?	44°S 148°38′E

[a] Additional information from personal communication (p.c.).
[b] Published as *Nectopyramis* sp. nov.?

Table 8. *Latitudinal distribution of Nectadamas diomedeae (Bigelow) in recent Discovery collections from the northeast Atlantic Ocean*

(No siphonophore data for *Discovery* stations between 5 and 10°N and 21–29°N.)

latitude range	no. hauls with specimens	% total stations	definitive nectophores	eudoxids
0–5°N	9	20.5	4	34
10–15°N	15	35.7	8	38
15–21°N	29	48.3	7	68
29–35°N	51	15·0	10	75
35–40°N	17	12.5	1	19
40–45°N	22	6.7	3	21
45–50°N	10	6.3	2	8
50–55°N	4	11.1	0	5
55–60°N	1	3.2	0	1

Pacific and Indian Oceans, as well as occurring in the Antarctic and Arctic Oceans. Stepanjants (1963), who reviewed the known records, considered that it was encountered most often in tropical regions, and that it had a mainly bathypelagic depth distribution. Apart from the records mentioned in table 7, specimens have been found in about 175 hauls from more recent *Discovery* cruises. These are too extensive to detail herein, but the records from the northeast Atlantic are summarized in table 8. Full details can be obtained from the author.

These *Discovery* records indicate that the great majority of specimens have been collected in tropical and sub-tropical waters, between the equator and *ca.* 35°N. There are also several records from the region off Bermuda, which corresponds to the many *Beebe* records cited by Totton (1954). However, specimens have been found at more northerly latitudes, up to 60°N, the northerly limit of our sampling, where a single eudoxid was found in the 1250–1500 m depth range. In addition three definitive nectophores and three eudoxids of *Nectadamas diomedeae* have been caught by Johnson-Sea-Link submersibles, all in the Bahamas region, at depths between 572 and 803 m.

Specimens of *Nectadamas diomedeae* have been collected by *Discovery* at most depths between 50 and 3910 m. However, the great majority of specimens were found within the 300–800 m range. There appears to be little latitudinal change in this depth distribution, except that north of *ca.* 44°N the comparatively rare specimens were, in general, collected at deeper depths, that is between 1000 and 2000 m.

The station data for the three larval nectophores is as follows:

Discovery St. 7803#01 18°01.8′N, 25°03.1′W 0–1000 m;

Discovery St. 10378#15 32°22.2′N, 29°50.7′W 600–705 m;

Discovery St.10380#30 30°00.6′N, 33°56.0′W 500–600 m.

REFERENCES

Alvarino, A. 1964 Report on the Chaetognatha, Siphonophorae, and Medusae of the MONSOON Expedition to the Indian Ocean. *Rep. Scripps Instn Oceanogr. SIO Ref. Ser.* **64/19**, 103–108, 209–212.

Alvarino, A. 1967 Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae and Ctenophorae off San Diego, California. *Pacif. Sci.* **21**, 474–485.

Alvarino, A. 1971 Siphonophores of the Pacific with a review of the world distribution. *Bull. Scripps Instn Oceanogr. tech. Ser.* **16**, 1–432.

Alvarino, A., Wojtan, J.M. & Martinez, M.R. 1990 Antarctic siphonophores from plankton samples of the United States Antarctic Research Program. *Antarct. Res. Ser. Wash.* **49**, 1–436.

Bigelow, H.B. 1911*a* Biscayan Plankton collected during a cruise of H.M.S. 'Research', 1900. Part XIII. – The Siphonophora. *Trans. Linn. Soc. Lond. (Zool.)* **10**, 337–358.

Bigelow, H.B. 1911*b* The Siphonophorae. *Mem. Mus. comp. Zool. Harv.* **38**, 173–402.

Bigelow, H.B. 1913 Medusae and Siphonophorae collected by the U.S. Fisheries Steamer 'Albatross' in the northwestern Pacific, 1906. *Proc. U.S. natn. Mus.* **44**, 1–119.

Bigelow, H.B. 1919 Contributions to the biology of the Philippine Archipelago and adjacent waters: Hydromedusae, siphonophores, and ctenophores of the 'Albatross' Philippine Expedition. *Bull. U.S. natn. Mus.* **100** (vol. 1, part 5), 279–362.

Bigelow, H.B. 1931 Siphonophorae of the 'Arcturus' Oceanographic Expedition. *Zoologica, N.Y.* **8**, 525–592.

Bigelow, H.B. & Sears, M. 1937 Siphonophorae. *Rep. Dan. oceanogr. Exped. Mediterr.* **11** (Biology), H. 2, 1–144.

Casanova, J-P. 1980 Campagnes du 'Meteor' dans l'Atlantique N-E. Siphonophores, Méduses et Thécosomes. Distribution verticale et comparaisons faunistiques avec la Méditerranée. *Meteor ForschErgebn. Reihe* D **32**, 15–32. (In French.)

Daniel, R. 1974 Siphonophora from the Indian Ocean. *Mem. zool. Surv. India* **15**(4), 1–242.

Fraser, J.H. 1961 The oceanic and bathypelagic plankton of the North-east Atlantic. *Mar. Res.* **1961**(4), 48 pp.

Fraser, J.H. 1967 Siphonophora in the plankton to the North and West of the British Isles. *Proc. R. Soc. Edinb.* **B70**, 1–30.

Furnestin, M.-L. 1957 Chaetognaths et zooplancton du Secteur Atlantique Marocain. *Revue Trav. Inst. Pech. marit.* **21**, 1–356. (In French.)

Kinzer, J. 1977 On the vertical distribution of siphonophores in the upwelling area off NW Africa (Auftriebs-Expedition R.V. 'Meteor', cruise 26, 1972). *Meteor Forsch-Ergebn. Reihe* D, **26**, 21–27.

Leloup, E. 1932 L'eudoxie d'un siphonophore calycophoride rare, le *Nectopyramis thetis* Bigelow. *Bull. Mus. r. Hist. nat. Belg.* **8**, 1–8. (In French.)

Leloup, E. 1933 Siphonophores calycophorides provenant des campagnes du Prince Albert 1er de Monaco. *Résult. Camp. scient. Prince Albert I* **87**, 1–66. (In French.)

Leloup, E. 1936 Siphonophores calycophorides (suite) et physophorides provenant des campagnes du Prince Albert 1er de Monaco. *Résult. Camp. scient. Prince Albert I* **93**, 1–36. (In French.)

Leloup, E. 1955 Siphonophores. *Rep. scient. Results Michael Sars N. Atlant. deep-Sea Exped. 1910* **5**(11), 1–24. (In French.)

Mackie, G.O., Pugh, P.R. & Purcell, J.E. 1987 Siphonophore biology. *Adv. mar. Biol.* **24**, 97–262.

Margulis, R.Ya. 1972 Factors determining the large-scale distribution of siphonophores of the suborders Physophorae and Calycophorae in the Atlantic Ocean. *Oceanology* **12**, 420–425.

Margulis, R.Ya. 1974 On the distribution in the Atlantic Ocean of the siphonophore families Hippopodiidae, Prayidae and Abylidae (Suborder Calycophorae). *Trudy vses. gidriobiol. Obshch.* **20**, 144–170. (In Russian.)

Moser, F. 1925 Die Siphonophoren der Deutschen Südpolar-Expedition, 1901–03. *Dt. Südpol.-Exped.* **17** (zool 9), 1–541. (In German.)

Musayeva, E.I. 1976 Distribution of siphonophores in the eastern part of the Indian Ocean. *Trudy Inst. Okeanol.* **105**, 171–197. (In Russian.)

Patriti, G. 1965 Contribution à l'étude de siphonophores calycophores recucillis dans le Golfe de Gascoigne. Note preliminaire 2. *Recl Trav. Stn mar. Endoume* Fasc. 54, Bull. **38**, 15–31. (In French.)

Pugh, P.R. 1974 The vertical distribution of the siphonophores collected during the SOND Cruise, 1965. *J. mar. biol. Ass. U.K.* **54**, 25–90.

Pugh, P. R. 1975 The distribution of siphonophores in a transect across the North Atlantic Ocean at 32°N. *J. exp. mar. Biol. Ecol.* **20**, 77–97.

Pugh, P.R. 1990 Biological collections made during Discovery CR 175 to BIOTRANS site (c.47°N,20°W). *Inst. Ocean. Sci. Rep.* **277**, 1–78.

Pugh, P.R. & Harbison, G.R. 1987 Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by a submersible, with notes on related species. *Bull. Mar. Sci.* **41**, 68–91.

Sears, M. 1952 Notes on siphonophores. 3. *Nectopyramis spinosa* n. sp.. *Breviora* **3**, 1–4.

Stepanjants, S.D. 1963 A finding of Syphonophora, *Nectopyramis diomedea* Bigelow, 1911 in the Arctic Basin. *Zool. Zh.* **42**, 1866–1869. (In Russian.)

Stepanjants, S.D. 1967 Siphonophores of the seas of the USSR and the north western part of the Pacific Ocean. *Opred. Faune SSSR* **96**, 1–216. (In Russian.)

Stepanjants, S.D. 1970 Siphonophora of the southern part of the Kurile-Kamchatka Trench and adjacent marine areas. *Trudy Inst. Okeanol.* **86**, 222–236. (Translation of Russian text, 234–249.)

Stepanjants, S.D. 1975 Species composition and distributional pattern of Siphonophora of the Caribbean, Gulf of Mexico and adjacent waters of the Atlantic. *Trudy Inst. Okeanol.* **100**, 96–126 (in Russian).

Stepanjants, S.D. 1977 Siphonophora of the central part of the Pacific Ocean. In *Explorations of the fauna of the seas* XX (XXVIII) Marine plankton (systematics and faunistics), pp. 54–81. (In Russian.)

Totton, A.K. 1932 Siphonophora. *Scient. Rep. Gt. Barrier Reef Exped.* **4**, 317–374.

Totton, A.K. 1936 Plankton of the Bermuda Oceanographic Expeditions. VII. Siphonophora taken during the year 1931. *Zoologica, N.Y.* **21**, 231–240.

Totton, A.K. 1954 Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Rep.* **27**, 1–162.

Totton, A.K. 1965 *A synopsis of the Siphonophora*. London: British Museum (Natural History).

van Soest, R.W.M. 1973 Planktonic coelenterates collected in the North Atlantic Ocean. *Bijdr. Dierk.* **43**, 119–125.