

**P. R. Pugh**  
Southampton Oceanography  
Centre, European Way,  
Southampton SO14 3ZH

submitted November 2003  
accepted June 2004

# A new species of *Physophora* (Siphonophora: Physonectae: Physophoridae) from the North Atlantic, with comments on related species

**Abstract** A new species of *Physophora*, belonging to the physonect family of siphonophores Physophoridae is described. It can easily be distinguished from the only other recognised species in that family, *P. hydrostatica*, by the presence of two types of bracts. The arrangement of the palpons and bracts throws new light on the cormidial organisation of the physophorids, and comparisons are made between both species. The validity of an enigmatic physophorid species, *Discolabe quadrigata*, is discussed.

**Key words** Siphonophora, Physonectae, Physophoridae, *Physophora* sp. nov., *Physophora hydrostatica*, *Discolabe quadrigata*

## Introduction

Siphonophores are complex, highly polymorphic hydrozoan cnidarians, whose ‘colonies’ are formed by many medusoid and polypoid ‘individuals’ that function physiologically as a single entity. The most famous example is the Portuguese Man O’War, *Physalia physalis* (Linnaeus, 1758), but this surface-living species, like the species of the physonect family Rhodaliidae (see Pugh, 1983) that have adopted a benthic way of life, is exceptional as most siphonophore species are holoplanktonic. Siphonophores are present throughout the world’s oceans and occur in a bewildering variety of shapes and sizes, from about 1 mm to several tens of metres in length. Because of their fragility in the past they have been difficult to study. Nonetheless they are ecologically important, as voracious carnivores, and frequently are the most numerous animals in macroplankton net catches (Pugh, 1984). In addition, with the advent of *in situ* collection, using SCUBA, submersibles or ROVs, much more is now known about individual species, and a large number of, as yet, undescribed species have been collected. The latter particularly applies to the larger, but more fragile, physonect species, and one of these, belonging to the family Physophoridae, is the subject of this paper.

Currently the family Physophoridae is considered by most authorities to contain only a single species, *Physophora hydrostatica* Forskål, 1775, even though this species has been described under at least 19 different names (see Bigelow, 1911). As Totton (1965: 83) stated the family was characterised by ‘the fact that the spiral budding zone of the siphosome, instead of elongating, expands laterally into a spiral sac, on the outer rim of the under side of which are found the cormidial groups. The single palpons of each group are proportionately very large and form a ring of active ‘feelers’, capable of co-ordinated action, and stinging badly’. No bracts, apart from

the larval one (see Haeckel, 1869), are developed. Garstang (1946), in his review of previous studies on siphonophores, concluded that there was only one palpon per cormidium in *P. hydrostatica*. So, in order to compensate for the fact that the number of palpons exceeded the number of other cormidial components (gastrozooids and reproductive elements), he considered that there were at least six, possibly one or two more, palpons, which originally overhung the protosiphon, that were developed before the secondary gastrozooids, palpons, and gonophores appeared. This assertion is considered further in the Discussion section.

A rather enigmatic physophorid species, *Discolabe quadrigata*, was described by Haeckel (1888), and was characterised by the nectosome having the nectophores arranged into four rows instead of two, as is the case for most physonect siphonophores, including *Physophora hydrostatica*. The validity of this species is readdressed.

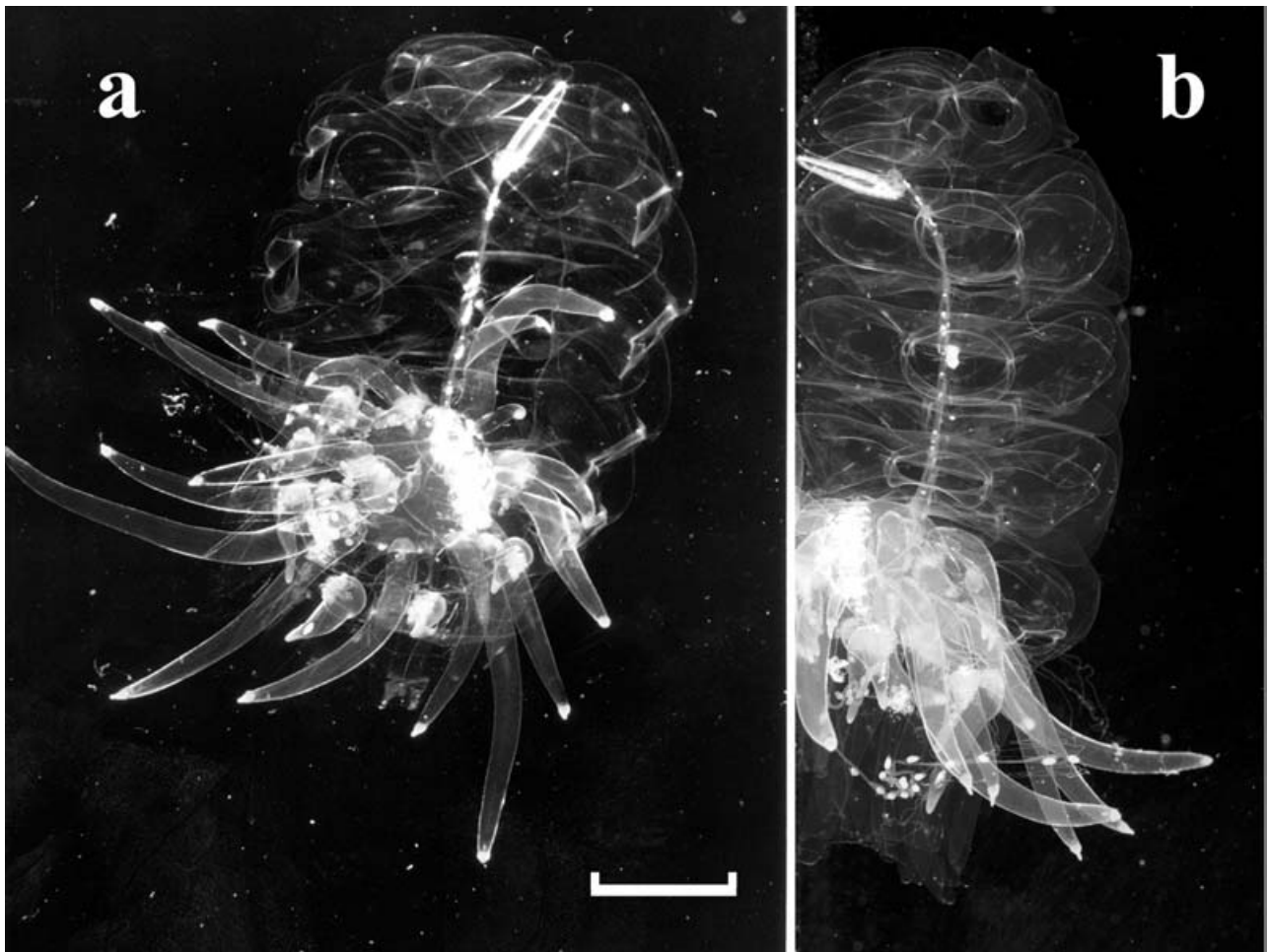
In the present paper, a second species of a physophorid siphonophore will be described, and comparisons made with the various structures of *Physophora hydrostatica*. The new species is clearly distinguished by the presence of bracts on the siphosome, and the arrangement of these throws new light on the organisation of the cormidia on the siphosomal corm.

## Taxonomic description

### *Physophora gilmeri* sp. nov.

Figs 1–11

**MATERIAL EXAMINED.** Seven specimens collected by the Johnson-Sea-Link (JSL) submersibles, all from the vicinity of The Bahamas and two from recent *Discovery* Collections, in the Northeast Atlantic. The specimen collected by JSL II



**Figure 1** *Physophora gilmeri*. Photographs of the type specimen, taken by Ron Gilmer. Scale 1 cm.

during dive 979 (25°57.8'N 77°22.1'W; 23 October 1984; depth of collection 488 m) has been designated the holotype and has been donated to the Natural History Museum (London) where it is registered as BMNH 2004.2734.

**DIAGNOSIS.** Physophorid siphonophore with a long, narrow pneumatophore. Large, broad, flattened nectophores without mouth plate. Nectosac with extensive, but narrow, lateral expansions and large baso-lateral pockets. Thin walled siphosomal corm, with cormidia each consisting of a gastrozoid, whose tentacle bears typically physophorid tentilla, and from the long peduncle of which two types of bract arise; a single blastostyle that divides immediately into two branches, with one branch bearing male and the other female gonophores; and a series of up to three palpons. One type of bract usually has a large attachment area on the corm above the gastrozoid and inserted between the palpons of successive cormidia. The other has a small attachment area on the corm below or obliquely to the side of the gastrozoid, but largely hangs from the peduncle of the latter.

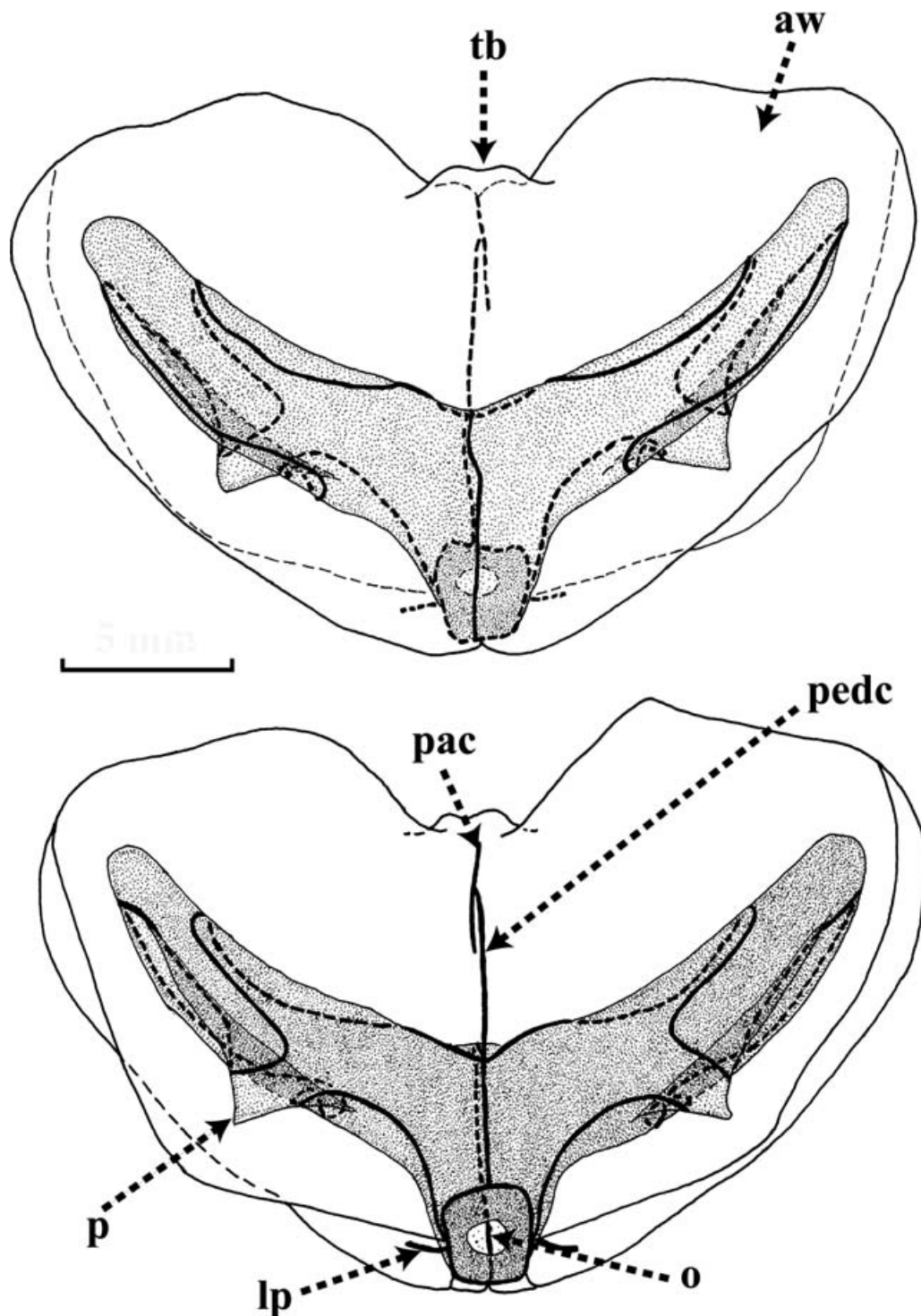
**DESCRIPTION.** Photographs of the type specimen, taken on board ship shortly after capture, are shown in Fig. 1. The bracts were very transparent and almost impossible to discern in Fig. 1a, but can be seen as vague processes hanging down from the corm in Fig. 1b.

**PNEUMATOPHORE.** Long, narrow pneumatophore that measured up to 7.7 mm in length, and 1.5 mm in width. There was a small patch of red-pigmented cells at its apex, but no other obvious pigmentation. A basal pore, as has been reported but not confirmed for the pneumatophore *Physophora hydrostatica*, could not be discerned.

**NECTOSOME** (Fig. 1). The nectophores, although attached in a single line, as is usual, to the ventral side of the nectosome, were clearly arranged into two rows.

**NECTOPHORE** (Figs 2–3). The type specimen possessed nine nectophores, eight of which were mature. The mature nectophores were broad and flattened, and measured up to 16 mm in length, 25 mm in width and 5.5 mm in depth. The axial wings (Fig. 2: **aw**) were broad, but did not extend adaxially, for any great distance. The thrust block (Fig. 2: **tb**) was small, with a shallow median indentation. There were two weak lateral ridges running, on each side, from the lateral extremities of the axial wings to the upper and lower margins of the ostium, thus demarcating a narrow lateral facet.

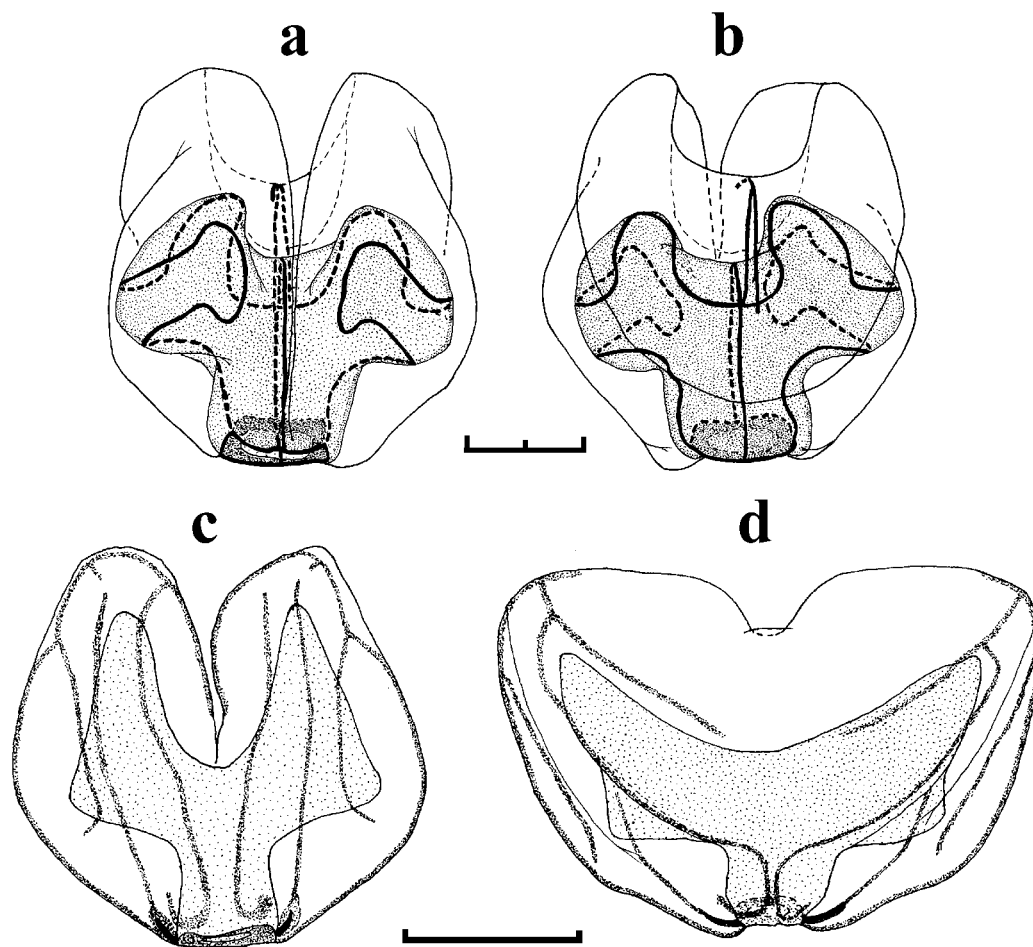
The nectosac had extensive, but narrow, lateral extensions, while in the mid-line it only extended to less than half the length of the nectophore. In the mature nectophores there were two large baso-lateral pockets (Fig. 2: **p**) on the lower side of the nectosac. The pallial canal (Fig. 2, **pac**), on the



**Figure 2** *Physophora gilmeri*. Upper (top) and lower (bottom) views of a mature nectophore from the type specimen. **aw**: axial wing; **lp**: lateral process to ostium; **o**: ostium; **p**: baso-lateral pocket to nectosac; **pac**: pallial canal; **pedc**: pedicular canal; **tb**: thrust block. Scale 5 mm.

lower side of the nectophore, ran abaxially from the base of the thrust block for some distance. At about half its length it gave off the long pedicular canal (Fig. 2: **pedc**), which continued, in the mid-line, to the lower side of the nectosac, just distal to its apex. There it directly gave rise to the four radial canals. The lower (ventral) canal ran straight to the ostial ring canal. The upper (dorsal) canal, having run over onto the upper side of the nectosac, also had a generally straight course, although

apically it could show a slight bend. The latter was, perhaps, a preservation artefact. The lateral radial canals had extensively looped courses (Fig. 2). The ostium was quite small and a mouth plate was absent. Stretching out laterally from the ostium (Fig. 2: **lp**) were narrow strips of distinctive ectodermal cells (Fig. 2). These may have been sites of bioluminescence, as is the case in many other physonecks, but no such observations were made.



**Figure 3** *Physophora gilmeri*. a, Upper and b, lower views of an immature nectophore from the JSL Dive 497 specimen. Scale 2 mm. c and d, Upper views of slightly older nectophores from the type specimen (c) and the JSL Dive 783 specimen (d) simplified in order to show the pattern of lines of ectodermal cells. Scale 5 mm.

In the very young nectophores (Fig. 3a–b) the axial wings had not yet expanded laterally, but apically were quite extensive. In consequence, the nectosac also was not laterally expanded and there was no sign of the baso-lateral pockets on its lower side. The basal section of the pallial canal was also relatively longer. As with the mature nectophores there was no mouth-plate, but the ostial opening was relatively wide. With further growth (Fig. 3c), the nectosac extended further into the axial wings and became more angular, showing laterally the processes that would ultimately become the baso-lateral pockets. At a later stage (Fig. 3d) the axial wings, and consequently the nectosac, had begun to expand laterally and the baso-lateral expansions had become more prominent.

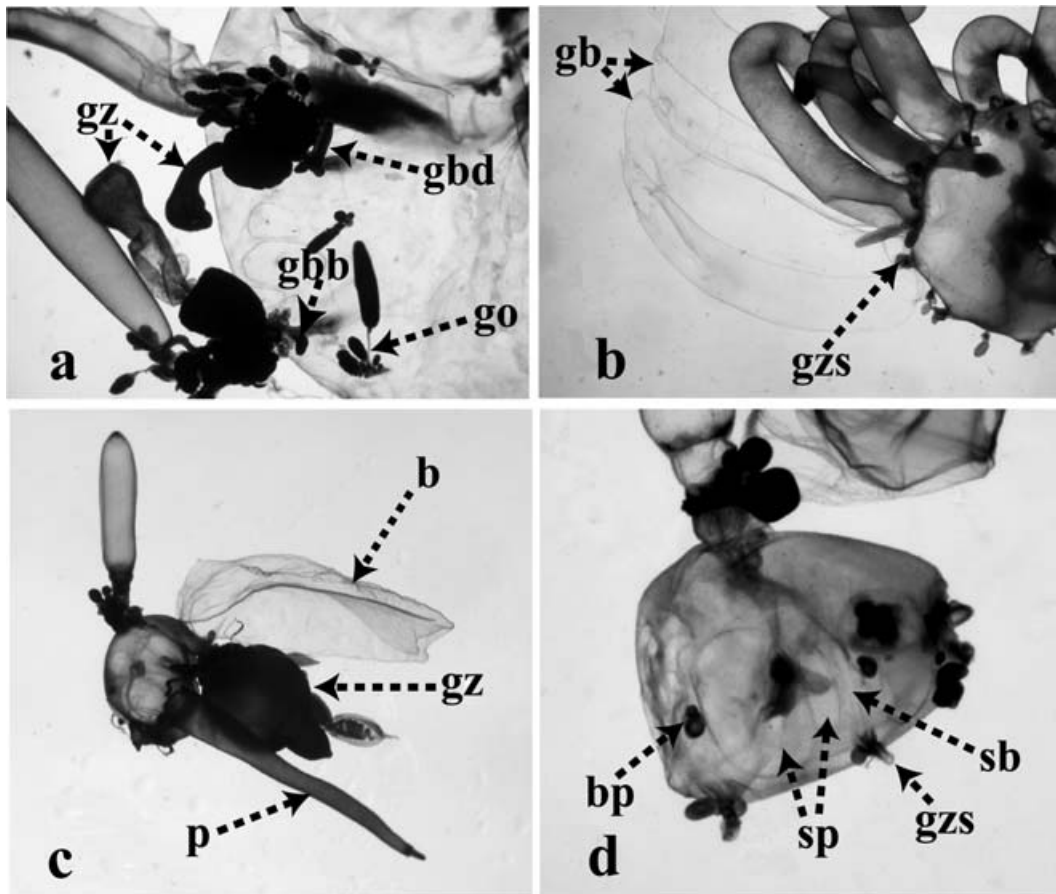
The upper surface of the nectophores, particularly noticeable on the younger ones, was mottled with relatively large ovoid, plate-like cells (not illustrated). In addition (Fig. 3c–d), there was a distinctive pattern of lines of small, darkly staining (in Steedmans Triple Stain) ectodermal cells together with the plate-like and other cells. This pattern was difficult to discern on the most mature nectophores, although parts of it could still be traced. The function of this pattern of lines is unclear.

**SIPHOSOME** (Fig. 4). The arrangement of the various elements on the siphosome was often difficult to discern. How-

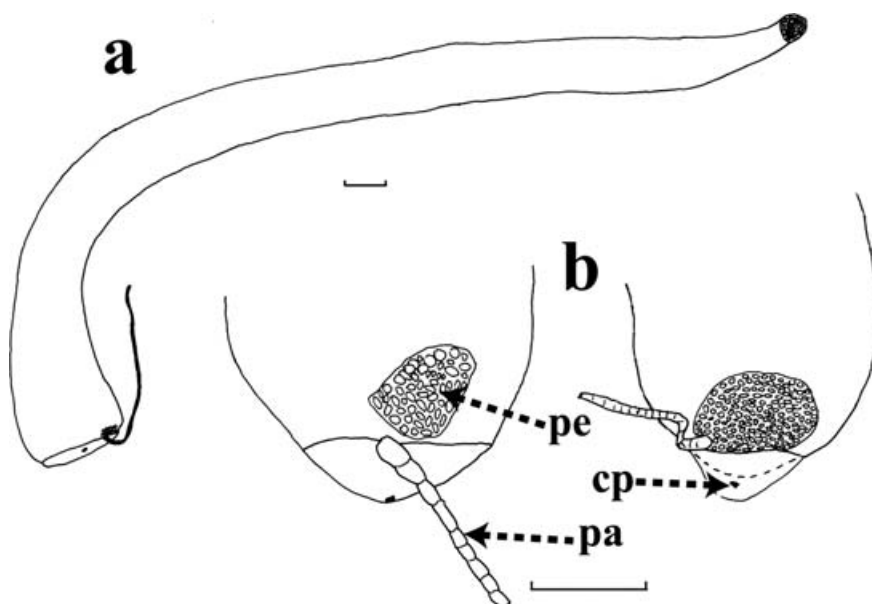
ever, careful examination revealed that each cormidium typically consisted of a gastrozoid, with its tentacle and a long peduncle from which arose two types of bract ('hooded' and 'peduncular' – see below); a blastostyle that divided immediately with one branch bearing male and the other female gonophores; and a group of up to three palpons or buds thereof.

**PALPON** (Fig. 5). Twenty-six, mostly detached, palpons of variable size were found with the type specimen, with three being very young. They were long and narrow, and measured up to c. 2.5 cm in length. Their walls were relatively thin, and largely featureless. They had a distinct, but relatively small, terminal ampulla, which often was extended out into a small proboscis, with a distal opening. In life this region contained bright orange pigmentation, while the remainder of the palpon was a pale milky-white colour.

On the base of the detached palpon or in the centre of the scar left on the corm when the palpon was detached there was a small, central pore that connected the cavity of the palpon to that of the siphosome. The palpacle was attached to the uppermost part of the base of the palpon, to one side of a distinctive pad of rounded ectodermal cells. Occasionally this pad was separated from the palpacle. The palpacle was thin and bore only weak signs of annulations, which were actually



**Figure 4** *Physophora gilmeri*. a, Part of siphosome (max. diameter 14.5 mm) of type specimen, with a developing peduncular bract (**gbd**) and a bracteal bud (**gbb**) attached to stalks of two different gastrozooids (**gz**). The male (**go**) and female gonophores are attached to a single blastostyle. b, Part of siphosome (max. diameter 8 mm) of *Discovery* St. 12188 specimen showing two mature peduncular bracts (**gb**) one of which can be seen to be attached to the stalk of a broken off gastrozooid (**gzs**). c, JSL Dive 427 specimen (diameter of siphosome 2.5 mm), with an attached palpon (**p**), showing a developing hooded bract (**b**) attached above the primary gastrozooid (**gz**). d, Denuded siphosome (diameter 2.6 mm) of JSL Dive 637 specimen showing a palpon bud (**bp**) and the scars of two detached palpons (**sp**), followed by the scar of a detached hooded bract (**sb**), with the stalk of a detached gastrozooid (**gzs**) below it.



**Figure 5** *Physophora gilmeri*. a, Palpon and b, detail of base of two palpons from the type specimen. **cp**: central pore; **pa**: palpacle; **pe**: patch of large ectodermal cells. Scale 1 mm.

gaps between patches of large rounded ectodermal cells. No nematocysts were found on the palpacle. The pads of rounded cells beside the palpacle were generally quite small, but occasionally they could be considerably larger (see Fig. 7c).

Numerous large ( $c. 85 \times 20 \mu\text{m}$ ) nematocysts were found in the terminal ampulla, but nowhere else on the palpon or the palpacle. Some loose, discharged nematocysts of a similar size to these were found with the type specimen which, judging by the figures in Werner (1965), were microbasic mastigophores.

The palpons usually were attached in groups of three between part of the attachment zone of each hooded bract (see below). However, the first and third cormidia of the type specimen appeared to have only one, as adjudged by the scars left after they became detached. Within each cormidium the size of the scars left by the detached palpons could vary considerably. In the older cormidia the central scar usually was considerably larger than the ones on either side, with the distal one being slightly smaller than the proximal one. In the younger cormidia again the central palpon was the largest, but the more distal one could be reduced to a simple bud. The number of detached palpons was consistent with the number of scars left on the siphosome.

**BRACKETS** (Figs 6–8). There were two basic types of bract that will be referred to as ‘hooded’ and ‘peduncular’. As is discussed below, both are thought to originate from the peduncle of a gastrozoid. Ten hooded and five peduncular bracts were found with the type specimen, all detached, plus the very small bud of a peduncular bract (Fig. 4a).

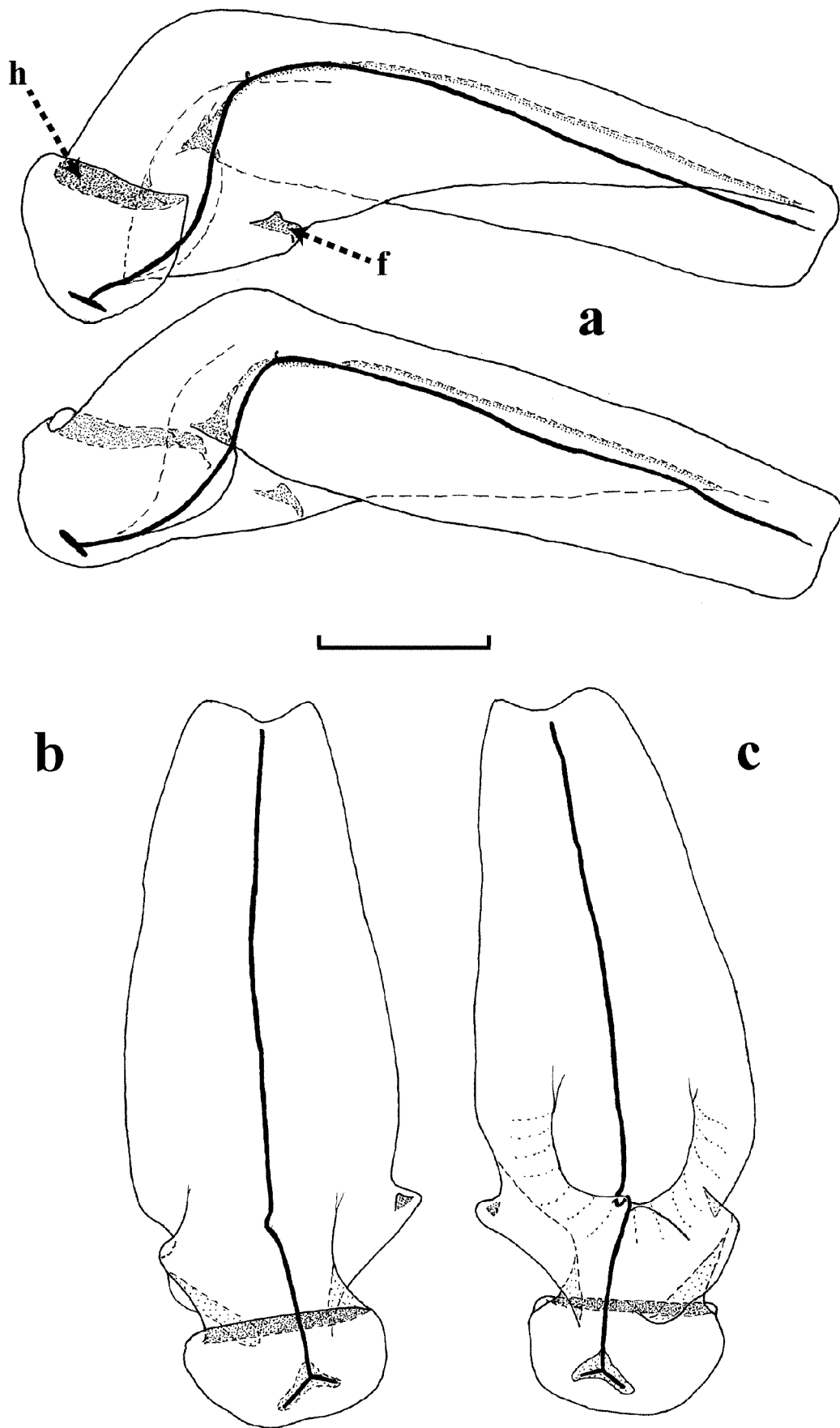
The hooded bracts (Fig. 6) of the type specimen measured up to 21 mm in length and, when mature, had a very characteristic shape. The proximal end was swollen and on its upper side it had an extension overhanging the main body of the bract, and giving the area a hood-like appearance (Fig. 6: h). Distal to this, the bract remained quite swollen for a short distance, with a pronounced swelling on the lower surface on one side (Fig. 6c). The lateral sides of the bract also extended out into more or less pronounced cusps, and on the upper side of one a small flap (fig. 6: f) was to be found, although sometimes difficult to see. The thickness of the bract was then reduced considerably by the presence, on the lower side, of a deep, but wide median furrow. This furrow ran toward the distal end of the bract and gradually lost depth, so that distally the bract was almost flat. The distal end of the bract was truncated and slightly emarginate. One of the hooded bracts, found with the type specimen, was less developed than the others (Fig. 7a). The proximal swelling was present, but the flap forming the hood and one of the lateral cusps had yet to develop, and the whole bract was more flattened.

The bracteal canal ran from the lower side of the proximal process almost to the distal end of the bract. It remained in contact with the lower median wall of the bract for almost its entire length, only penetrating into the mesogloea very close to its distal end, where it was noticeably narrower. In the mature bracts of the type specimen the proximal end of the canal was bifid (Fig. 6), but in those of some other specimens the canal often remained undivided, as was the case for the younger one of the type specimen (Fig. 7a). Judging by where the canal

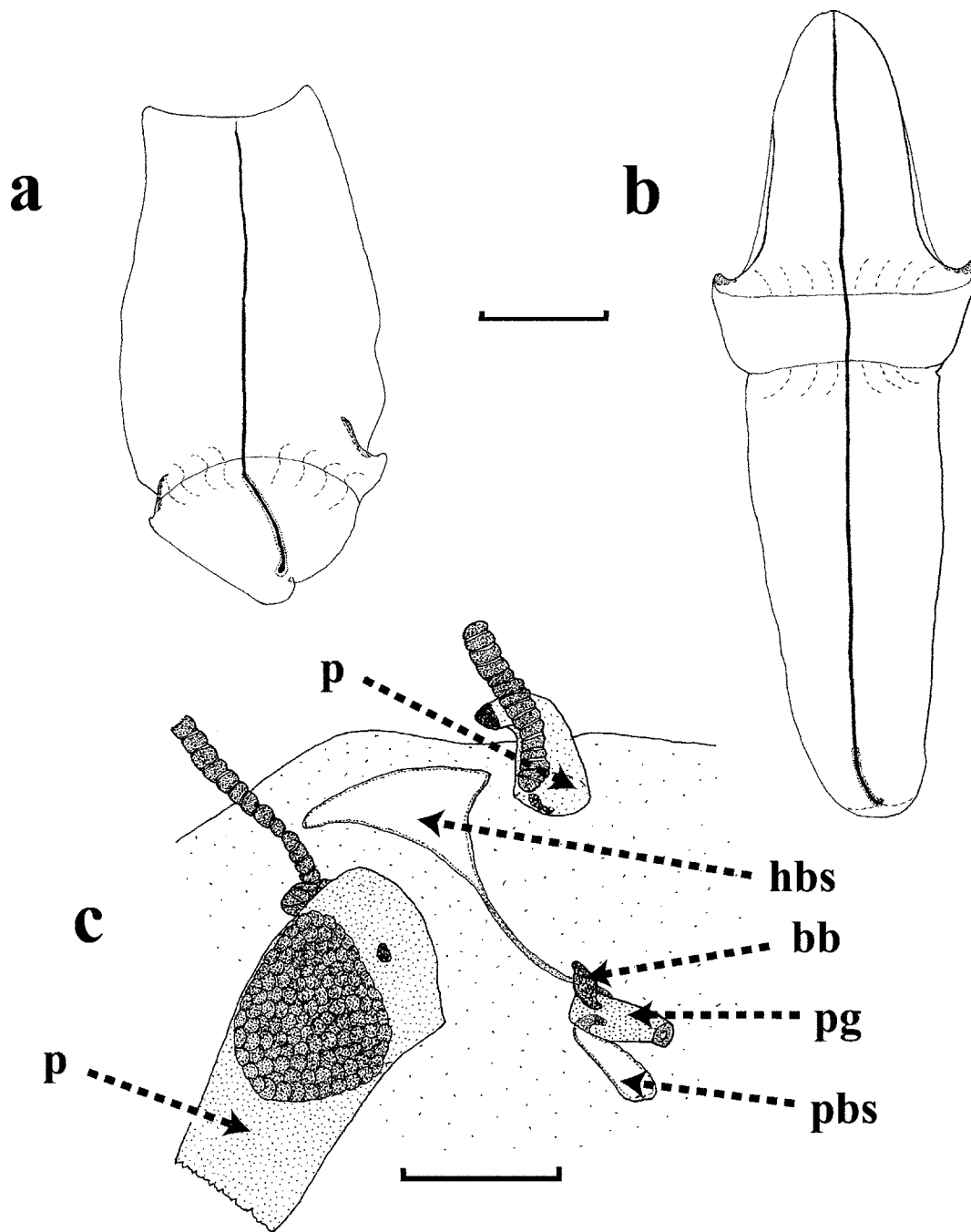
was torn it appeared that the bracteal lamella was attached from around the proximal end(s) of the canal to the proximal end of the median furrow, where the latter was deepest; the canal having curved up steeply following its contours. Around this point a short vertical branch was sometimes given off into the mesogloea (Fig. 6a–b).

All but one of the other specimens examined, even those that were very young, had hooded bracts associated with them, and one (Fig. 4c) had a young hooded bract still attached to the corm by its proximal end. One specimen, however, included five hooded bracts and five of a completely different structure, differing from both the hooded bracts and the peduncular bracts to be described below. These bracts, and indeed the specimen itself, from JSL Dive 497, were generally in a very poor state of preservation, and the siphosomal corm was torn and distorted. The hooded bracts of this specimen were relatively enormous, measuring up to 30 mm in length, although none of them showed the proximal division of the bracteal canal as seen in the type and some other specimens. The other bracts (Fig. 7b) were slightly larger, measuring up to 31 mm in length. They were generally flattened on their lower surfaces, while their upper sides were steeply convex. There was no ‘hood’ at the proximal end, which was simply rounded. However, just distal to its mid-length the bract was more swollen on its upper side, and inflated laterally, with the distal ends of each lateral extension forming a cusp. The bracteal canal was simple and, like the hooded bracts, remained in contact with the lower wall of the bract, except for a short distance, at its distal end, where it penetrated into the mesogloea. The proximal region where the bracteal lamella had been attached was comparatively short. No peduncular bracts were found with this specimen. However, the total number of both types of bracts (10) was less than the number of gastrozoids, which exceeded 12. Since, as is discussed below, the hooded bracts should be in proportion to the number of gastrozoids, it is assumed that the non-hooded bracts were a variant on the hooded ones and performed the same function. One other specimen (JSL Dive 474) possessed five immature hooded bracts, and a very small detached bracteal bud that more closely resembled the variant ones described above, having a laterally expanded region just proximal its mid-length. Thus, it appeared that the presence of these variant bracts was not necessarily unusual.

Only five of the nine specimens examined possessed peduncular bracts (Fig. 8), with the type specimen having the most, that is five. In that specimen these bracts measured up to 19 mm in length and 7.7 mm in width. They appeared to be relatively flattened, but a side view (Fig. 8c) showed that a fairly deep, wide, median furrow was present on the lower side of the bract for most of its length. At the proximal end, there was a mesogloea protuberance on the upper side that delimited a proximal facet. Slightly distal to this there was a small central protuberance on the lower side, over which the bracteal canal ran, and which demarcated the proximal end of the median furrow. The distal end of the bract was truncated and slightly emarginate and its two lateral margins bore more or less pronounced cusps on their lower sides. One of the two peduncular bracts from another specimen (Fig. 8d) was wider (13 mm), but shorter (16 mm) than the ones found with the type



**Figure 6** *Physophora gilmeri*. a, Lateral, b, upper and c, lower views of hooded bracts from the type specimen. f: flap; h: hood. For a, proximal is to the left, distal to the right. For b and c, proximal is at the bottom, distal at the top. Scale 5 mm.



**Figure 7** *Physophora gilmeri*. a, Upper view of younger hooded bract from type specimen. b, Upper view of unusual bract from JSL Dive 497 specimen. For both proximal is at the bottom, distal at the top. Scale 5 mm. c, Part of the corm of specimen from *Discovery* St. 12188#1 showing the attachment zones of a hooded bract (**hbs**), lying between two palpons (**p**), and a peduncular bract (**pbs**). Both zones connect with the peduncle (**pg**) of the gastrozoid, which also bears a bracteal bud (**bb**). Scale 1 mm.

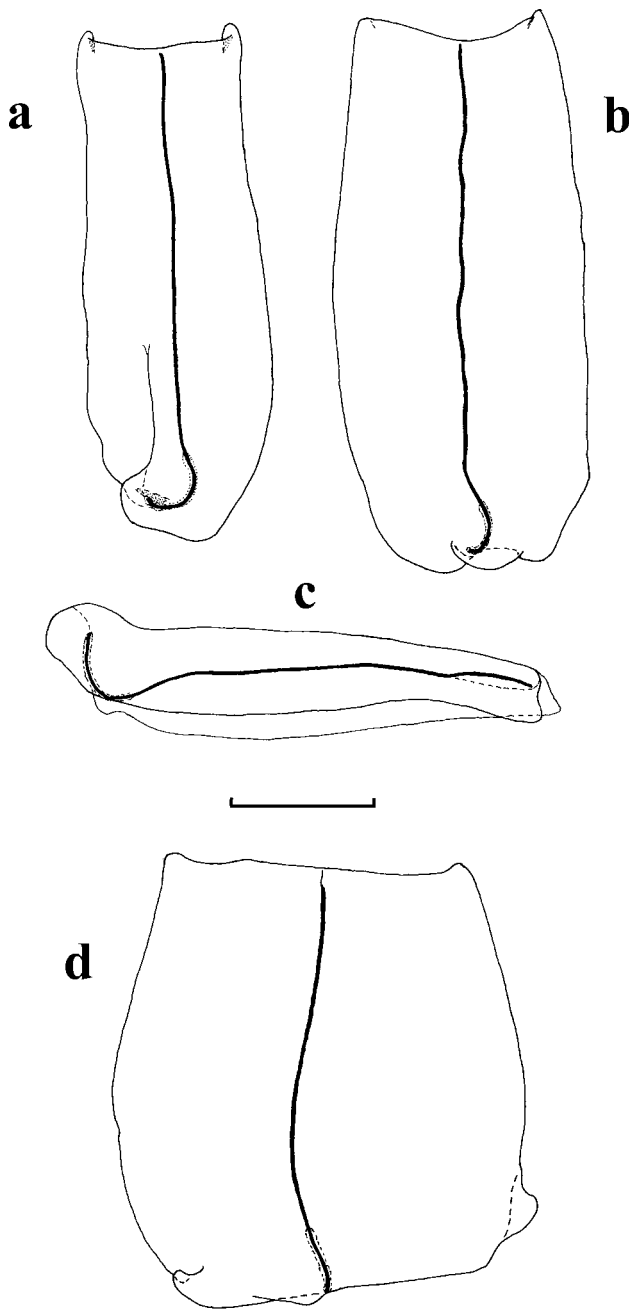
specimen. It was much flatter and the proximal protuberances on the upper and lower sides were much less pronounced, and the lateral cusps at the distal end barely visible.

The bracteal canal ran from a little more than halfway up the proximal facet over the central protuberance on the lower side and then followed the mid-line of the furrow, in close contact with its upper wall. At some distance from the distal end of the bract the canal penetrated into the mesogloea whilst continuing to run distal. In the type material there was no obvious thinning of the canal in this region, although in another

specimen (Fig. 8d) it thinned slightly, but only well after it had penetrated into the mesogloea. The bracteal attachment lamella appeared, on the basis of the scars left, to have been attached from the proximal end of the canal until shortly after it passed over the median protuberance on the lower surface of the bract.

As mentioned above, it is believed that both the hooded and peduncular bracts arose from the peduncle of the gastrozoid in each cormidium. The region of attachment of the hooded bracts was not discernible on all the specimens, but it was clear enough on several corms to make out the general





**Figure 8** *Physophora gilmeri*. a, Upper, b, lower and c, lateral views of peduncular bracts from the type specimen. d, Upper view of peduncular bract from JSL Dive 783 specimen. For a, b, d, proximal is at the bottom, distal at the top. For c, proximal is to the left, distal to the right. Scale 5 mm.

arrangement. In these an attachment area could be seen lying immediately above a gastrozoid, and inserted between the palpons of successive cormidia or, in the case of the oldest cormidium, immediately above the protozoid. The size of this area could vary from a narrow slit (Fig. 4d) to an almost triangular structure (Fig. 7c). At first it was believed that the origin of these bracts was directly from the corm. However, unlike the palpons, a canal directly connecting the gastrovascular system of the corm to the bracteal canal could not be discerned. In actuality, the attachment area of the bract could be traced, as a narrow, slightly raised, strip as far as the base

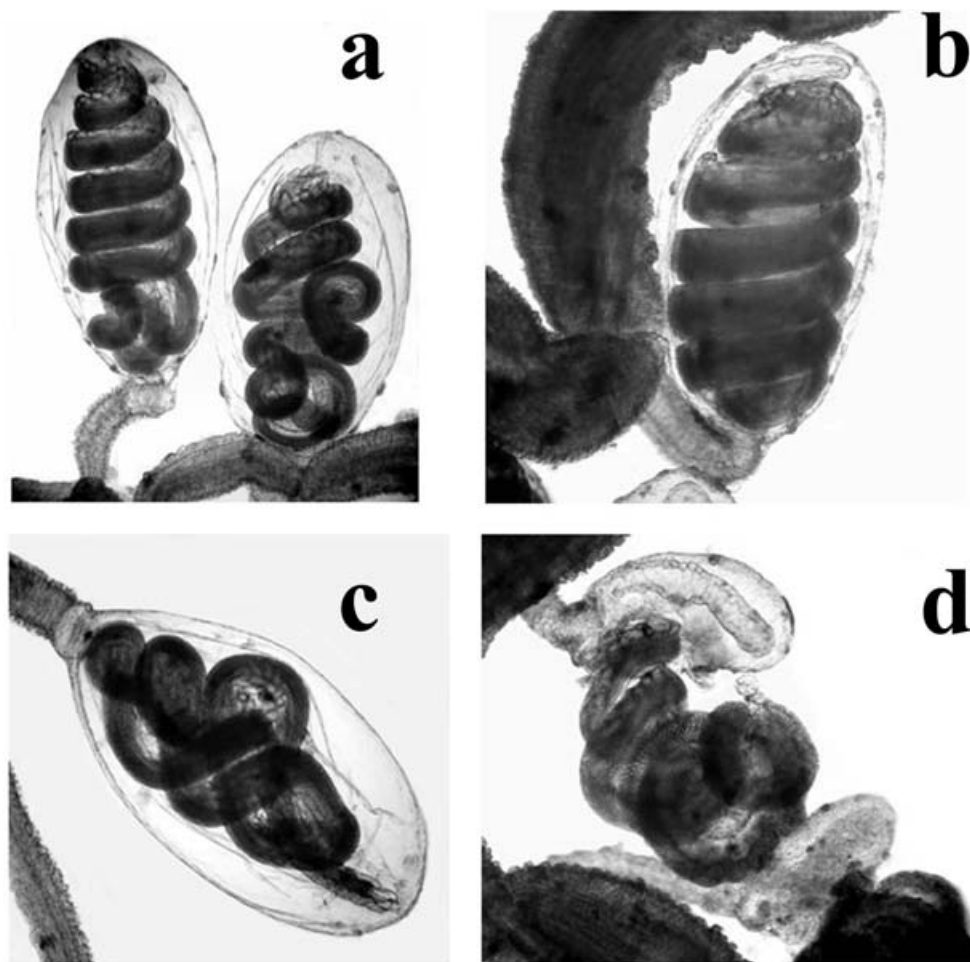
of the gastrozoid, where it continued up the peduncle, as a lamella, for a certain distance before petering out. Therefore, it was assumed that the bracteal canal was connected to the gastrovascular cavity of the peduncle although, unfortunately, no direct connection could be discerned. This connection would then lie close to the distal end of the attachment zone as described above, at the proximal end of the furrow on the lower side of the bract. The wide attachment area (Fig. 7c) area on the corm itself would then conform to the enlarged proximal region of the bract, where, in the type material at least, the bracteal canal was bifid. The young, partially detached bract in Fig. 4c gives an idea as to how well the whole structure of the bract was designed so as to partially enclose, and protect the gastrozoid when its peduncle was contracted.

The peduncular bracts clearly were attached directly to the peduncle of the gastrozoid in each cormidium (Fig. 4b), and a clear branch from that peduncle could always be seen after the bract had been detached. However, like the hooded bracts, an attachment zone to the corm itself could also be discerned, usually directly below or obliquely to one side of the gastrozoidal peduncle (Fig. 7c). This area conformed to the proximal facet of these bracts. The unusual bracts (Fig. 7b) found in one of the specimens were, as mentioned above, assumed to be analogous with the hooded bracts. However, their attachment zone was much shorter. This might explain why the area of attachment of the bract to the corm often was difficult to discern or very narrow. However, until more specimens become available, this cannot be confirmed with certainty.

In addition to the obvious attachment point of the peduncular bracts, the peduncle of the gastrozoid almost invariably also bore at least one bud, sometimes two, in the same region. The developing bud on the type specimen (Fig. 4a) appeared destined to become a peduncular bract, but whether the hooded bracts can be replaced in the same way has not been confirmed.

**GASTROZOID AND TENTACLE.** The gastrozoids of the type specimen (Fig. 4a) were quite small, and often were borne on long, thin peduncles that could reach 2.2 mm, although probably longer in life. As mentioned above these peduncles often bore one or two buds of developing bracts, as well as part of the attachment lamellae of the bracts themselves. The buds, often, were attached distal to the mid-length of the peduncle. The gastrozoid itself typically could be divided into three regions (cf. Fig. 14b). In the type specimen the large, globular basigaster, to which the tentacle was attached, was very obvious and densely staining. However, in other specimens it was transparent and almost indistinguishable from the stomach region. The stomach region itself was anything from a long, narrow tube to an inflated sphere. It was thin walled and almost totally transparent, with no obvious internal structure. The proboscis region, with its terminal mouth, was usually more opaque and bore 12 short stripes of endodermal material within. No nematocysts were noted in this region.

The tentilla, consisting of a pedicle and a 'stinging capsule' or cnidosac, branched off from the annulated tentacle in the usual manner. The 'stinging capsules' (*capsule urticante* – Vogt, 1854) were borne on relatively short, narrow pedicles, in



**Figure 9** *Physophora gilmeri* a–d. Tentilla of type specimen. Capsule size **c**, 1 mm.

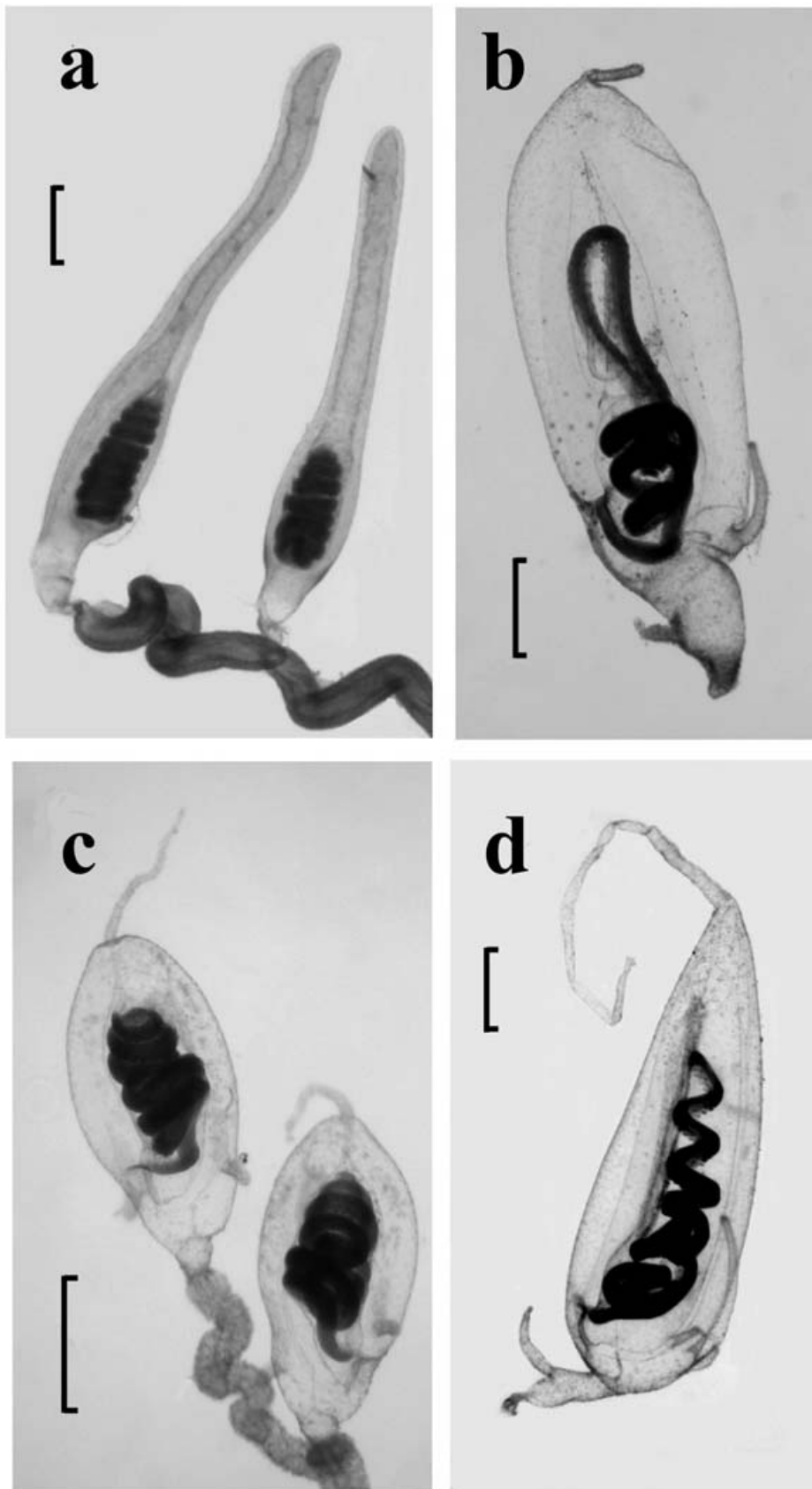
the preserved specimens. However, judging by the corrugated appearance of the gastrovascular canal (Fig. 9a) of the pedicle, it probably could have extended to much greater lengths in life. The arrangement of the stinging capsule conformed well to that previously described for *Physophora hydrostatica* by, for instance, Vogt (1854), Claus (1860) and Keferstein & Ehlers (1861). In the type specimen the ovoid capsule measured about 1 mm in length, and bore no obvious external protuberances. Inside it the cnidoband was more or less regularly coiled up (Fig. 9). Because of the extraordinary structure of the physophorid tentillum, the most proximal end of the cnidoband lay at the distal end of the capsule, and a narrow tube, running along one side of the capsule, connected the gastrovascular canal of the pedicle to it. This tube was often difficult to see, but had expanded greatly in the discharged capsule shown in Fig. 9d. The point of exit of the cnidoband, when discharged from the capsule, lay very close to the proximal end of the capsule.

Although the stinging capsules of the type specimen were all very similar, several other variations in shape and size were found on the other specimens examined (Fig. 10). Very young tentilla were found on one small specimen (Fig. 10a), where the tube from the pedicle could be seen to run through the developing capsule, and continuing into a long distal process.

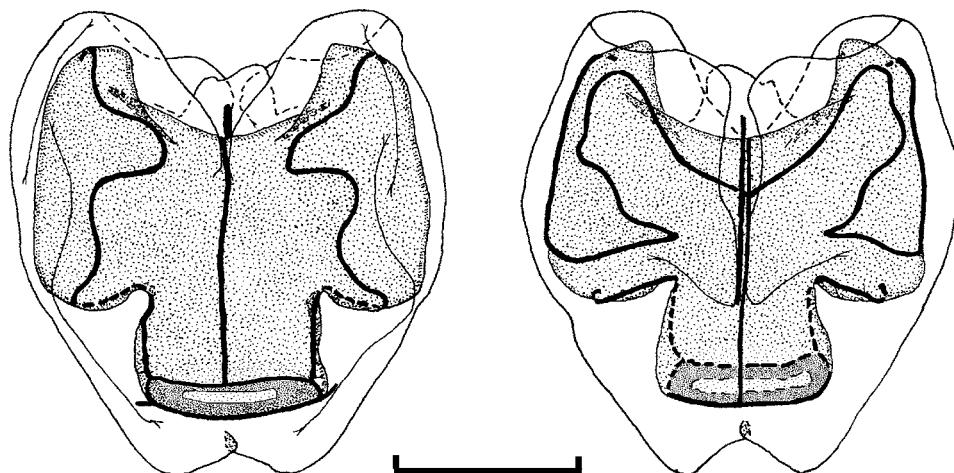
The cnidoband was tightly coiled, and connected to the tube at the distal end of the capsule. The distal process to the capsule was often retained, to a varying degree, by the tentilla of other specimens, but it was no longer hollow. The cnidoband was, generally, less tightly coiled than those in the type specimen, but the exit pore, lying close to the proximal end of the capsule, could clearly be seen. These capsules also bore lateral processes to a greater or lesser degree (Fig. 10b–d). Often there was a process at the swollen distal end of the pedicle (Fig. 10b, d), and then lateral processes on one or both sides of the capsule. The most advanced types had one process on one side, and three on the other, with the central one being much longer than those on either side (Fig. 10d).

Three types of nematocyst have been described on the cnidoband of *Physophora hydrostatica* (e.g. Vogt, 1854), and this appeared to be the case for those of *P. gilmeri*, although this was not examined in detail. Nonetheless, large nematocysts, measuring  $90 \times 30 \mu\text{m}$ , were found arranged in two rows along the sides of the cnidoband in its proximal half. These were the *fèves urticantes* referred to by Vogt (1854).

**GONOPHORES.** The gonophores were attached to the corm by a single very short blastostyle. The insertion point onto the corm usually lay below the third palpon, or below the gap



**Figure 10** *Physophora gilmeri* tentilla from a, JSL 604 specimen, b, JSL 783 specimen, c, JSL 637 specimen and d, JSL 497 specimen. Scale 0.5 mm.



**Figure 11** *Physophora hydrostatica*. Upper (left) and lower (right) views of a mature nectophore. Scale 5 mm.

between the second and third palpons, of each cornidium, and on the same level as, or slightly below, the gastrozoid. The blastostyle immediately divided into two branches, one bearing the male gonophores and the other the female ones (Fig. 4a). On most specimens where the sexual clusters were sufficiently developed only a few immature female gonophores, and one or two male ones were present. However, on the JSL 497 specimen the blastostyles were more developed. The male branch still had only a few gonophores attached, most of them at an early stage of development, but many mature ones were found loose with the specimen. These mature male gonophores, of typical shape and form, could measure up to 8 mm in length and were borne on long stalks, equal to or longer than the gonophore itself. The female branch measured up to 10 mm in length and was a single tube. Its proximal part was covered in a very tight cluster of developing gonophores, while distally it bore, each on a short side branch, ripe gonophores, about 0.55 mm in diameter, each with a single egg.

**DISTRIBUTION.** The seven specimens collected by the Johnson-Sea-Link submersibles all came from the vicinity of The Bahamas and from depths between 107 and 488 m. Two further mutilated specimens have been found in recent *Discovery* collections in the Northeast Atlantic. One was collected at *Discovery* St. 10244#6 (32°53.9'N 31°14'W; 20 November 1980; depth range 390–405 m), and the other at St. 12188#1 (17°15.2'N 23°56'W; 23 September 1990; depth range 210–240 m).

**ETYMOLOGY.** The species is named in honour of Ron Gilmer, who was the observer during the dive when the holotype was collected, and who kindly took the initial photographs.

## Discussion

### Comparisons between *Physophora gilmeri* and *P. hydrostatica*

*Physophora gilmeri* is easily distinguishable from *P. hydrostatica*, not least by the presence of two types of adult bract.

Nonetheless, there are several other differences as can be shown by comparisons with several specimens of *P. hydrostatica* collected by SCUBA divers in the Northwest Atlantic Ocean.

**Pneumatophore.** *Physophora gilmeri* has a long, cylindrical pneumatophore, up to 7.7 mm in length, and 1.5 mm in width. It is transparent and colourless throughout, in the preserved state, except for a relatively small red-pigmented spot at its apex. The pneumatophore of *P. hydrostatica* can be of a similar size, up to 7.5 mm in length, but usually is much wider (up to 4.75 mm), and always has a more obvious red-pigmented area at its apex. The shape of the pneumatophore of *P. hydrostatica* appears to change with age. In the younger specimens it is a cylindrical tube, transparent for the most part, but with a darker area at its base. In larger specimens the shape remains the same, but the dark basal area increases in size and, in the largest specimens examined it occupies almost half the height of the pneumatophore (see Fig. 17a). Above this region the pneumatophore can taper to a narrow apex, and this upper region takes on a milky white appearance, in its preserved state.

**Nectosome and nectophores.** The laterally expanded mature nectophores of *Physophora gilmeri* (Fig. 2) are very distinctive, particularly with the presence, in the most mature nectophores, of two large baso-lateral pockets on the lower side of the nectosac. Although the basic shape of the very young nectophores of *P. gilmeri* (Fig. 3a–b) is similar to that of the mature nectophores of *P. hydrostatica* (Fig. 11), the former are easily distinguished from the latter not least by their size but also by the much larger axial wings, and the total absence of a mouth-plate. No indication of the pattern of lines of ectodermal cells found on the upper surface of the nectophores of *P. gilmeri* (Fig. 3c–d) was discerned on those of *P. hydrostatica*. The course of the lateral radial canals also differed, particularly on the lower side of the nectosac where, in *P. gilmeri*, they do not have such a pronounced bend. It should be noted that the pronounced bends in the dorsal and ventral canals in the specimens of *P. hydrostatica* that Totton (1965) described and illustrated were not always

apparent in the present specimens of that species, and in several nectophores the upper (dorsal) canal only had a slight meander while the lower (ventral) one was straight. If the upper canals did have pronounced bends, then these bends were restricted to close to the apex of the nectosac. It is clear, therefore, that the degree of meandering of the upper and lower canals is a variable feature, possibly even a preservation artefact, and should not be used as a specific character.

As in *Physophora gilmeri*, the nectophores of *P. hydrostatica* are attached to the nectosome in a single line, in both cases on its ventral side. This fact, applying to most physonect siphonophores, is well known to serious investigators of the group, although often it is difficult to find it stated. Haeckel (1888: 9), for instance, briefly states that in 'the Siphonanthae [Siphonophora]... the stem... has all its appendages... budded in a row'. However, much earlier, Milne Edwards (1841: 220), while giving the original description of *Stephanomia* (*Forskalia*) *contorta*, gave more detail, noting that 'Les organes de natation forment d'ordinaire une mass ovoïde et alors se recouvrent en partie les uns les autres, de façon à simuler une disposition radiare et à paraître comme s'ils étaient imbriqués; mais ce mode de groupement tient uniquement à la courbure en spirale de la tige qui les porte, et ces appendices ne constituent dans la réalité qu'une seule série linéaire'. This was briefly summarised by Totton (1965: 97) who stated, for forskaliids in general, 'numerous, multiserial nectophores, all of which arise from one meridian of the coiled stem'.

In this regard it is appropriate to comment on some of the statements made recently by Mapstone (2003) with regard to the arrangement of the nectophores in apolemiid physonects. On p. 203 she states, 'in *Apolemia uvaria* the nectophores are attached [my italics] to the nectosomal stem in a single row, not two rows as stated by other authors (Gegenbaur, 1853a, b; Leuckart, 1854; Vogt, 1854; Trégouboff & Rose, 1957; Totton, 1965; Pagès & Gili, 1992)'. This is completely untrue as none of these authors stated that the nectophores were attached in two rows but, to quote Totton (1965: 48) with regard to the nectosome of *Apolemia uvaria*, 'About a dozen nectophores are arranged [my italics] as usual in two rows'. 'Arranged' does not mean 'attached'; similarly 'disposées' does not mean 'attachées', or, for instance 'besteht' mean 'angebracht' or 'angeordnet'.

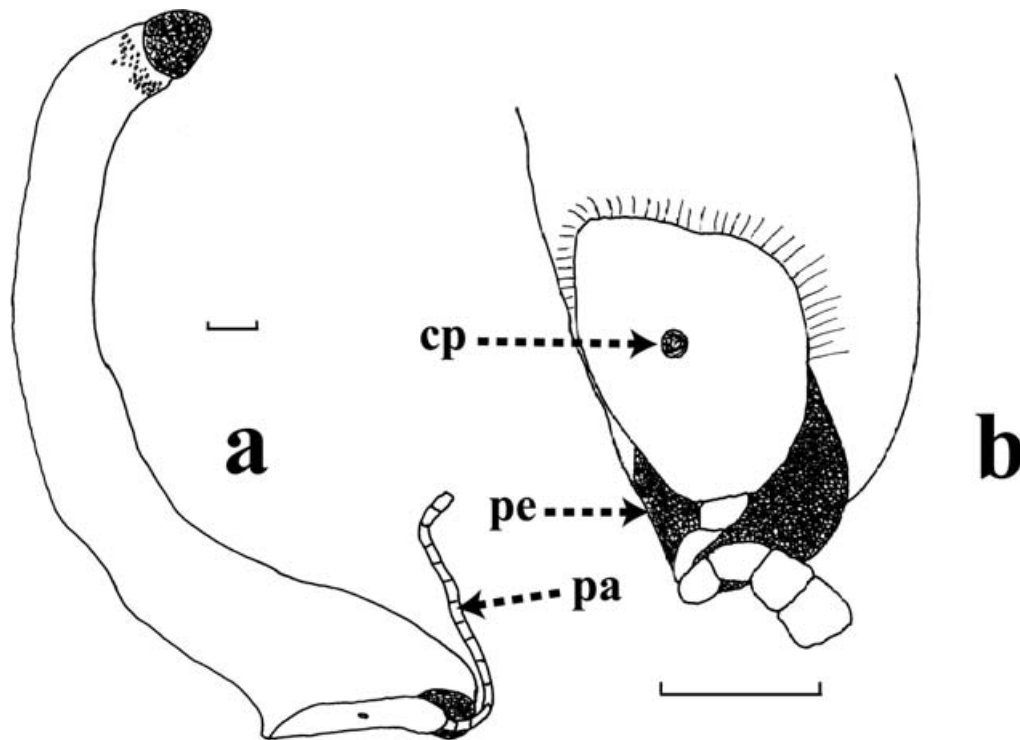
Mapstone further stated, in the same paragraph, 'It is assumed that in life the nectosomal stem is extended sufficiently to allow nectophores to take up positions around the stem in a loose spiral, and spaced sufficiently far apart to enable effective nectosac contraction during swimming'. This is an astonishing statement as all the authors that she criticised in her first statement noted that for most physonect species the nectophores are arranged in two rows down the nectosome. This is also obvious from the figure of *Apolemia uvaria* by Lesueur that she reproduced as Fig. 14, or, indeed, the excellent figure given by Vogt (1854: pl. 12). As Mackie (1964: 373) noted, when referring to *Nanomia cara* [actually *N. bijuga*] 'The nectophores are joined [interlocked] together very compactly and in a way predetermined by the morphology of their exumbrella ridges and depressions. There is only one way in

which a nectophore will fit comfortably with respect to other nectophores and to the stem'. This particularly applies to the fast moving physonects, with ridges on their nectophores, but it is also the case for the species without distinct ridges on their nectophores, such as in the genera *Physophora* and *Apolemia*. It is also relevant to the discussion below regarding the validity of *Discolabe quadrigata*. In addition, the particular biserial arrangement of the nectophores, with their large axial wings, in *Apolemia* species is very characteristic and makes apolemiids very easy to distinguish from other physonects *in situ*. One of the major exceptions to the biserial arrangement is to be found in the family Forskaliidae. Here the nectophores are flattened in the lateral plane and there is, at most, only one pronounced axial wing. This allows the nectophores to be arranged into a spiral that, nonetheless, is very regular in its disposition (see Pugh, 2003).

**Palpons.** The palpons of *Physophora gilmeri* (Fig. 5) were longer and narrower than those of *P. hydrostatica* (Fig. 12), and had much thinner walls. They were largely colourless, but with a bright orange-pigmented terminal ampulla, whereas the whole of the main body of the palpon of *P. hydrostatica* is, in life, usually suffused with a purplish-blue or orange colour, while the ampulla often is white. The palpacle of *P. gilmeri* was much narrower than that of *P. hydrostatica* and was less obviously annulated. In addition it was attached to the palpon beside a distinctive pad of rounded cells (Fig. 5b), whereas in *P. hydrostatica* it is attached in the middle of that patch (Fig. 12b). Nematocysts have been found at the base of the palpacle of *P. hydrostatica*, but such were not observed in *P. gilmeri*. The scars on the siphosome left by the detached palpons are far more marked in *P. hydrostatica* (Fig. 13) than in *P. gilmeri* (Fig. 4).

**Bracts.** The presence of bracts on the cormidia of *Physophora gilmeri* clearly distinguishes it from *P. hydrostatica*, where they are totally absent. The arrangement of the hooded bracts also helps to explain the organisation of the cormidia in *P. hydrostatica*, as is discussed below. The presence, in *P. gilmeri*, of two main types of bract is not unusual amongst the physonect siphonophores, and such have been described for many other species, for instance *Frillagalma vityazi* (Pugh, 1998). However, the believed fact that their bracteal canals connect with the gastrovascular canal of the peduncle of the gastrozoid is somewhat unusual. The only other physonect species that have been described as having peduncular bracts all belong to the family Forskaliidae (see Pugh, 2003). However, recent studies (Casey Dunn, personal communication) indicate that other species may have such peduncular bracts, as he has noted their presence in *Lychnagalma utricularia*. It is quite probable that in previous descriptions of other species, often based on preserved material with highly contracted gastrozooidal peduncles, the precise attachment points of the bracts have not been investigated thoroughly, as is obviously the case for the re-description of *L. utricularia* by Pugh & Harbison (1986)!

**Tentilla.** Although the basic arrangement of the 'stinging capsule' in *Physophora gilmeri* (Fig. 9) was very similar to that



**Figure 12** *Physophora hydrostatica*. a, Palpon, with b, detail of its base. cp: central pore; pa: palpacle; pe: patch of large ectodermal cells. Scale 1 mm.

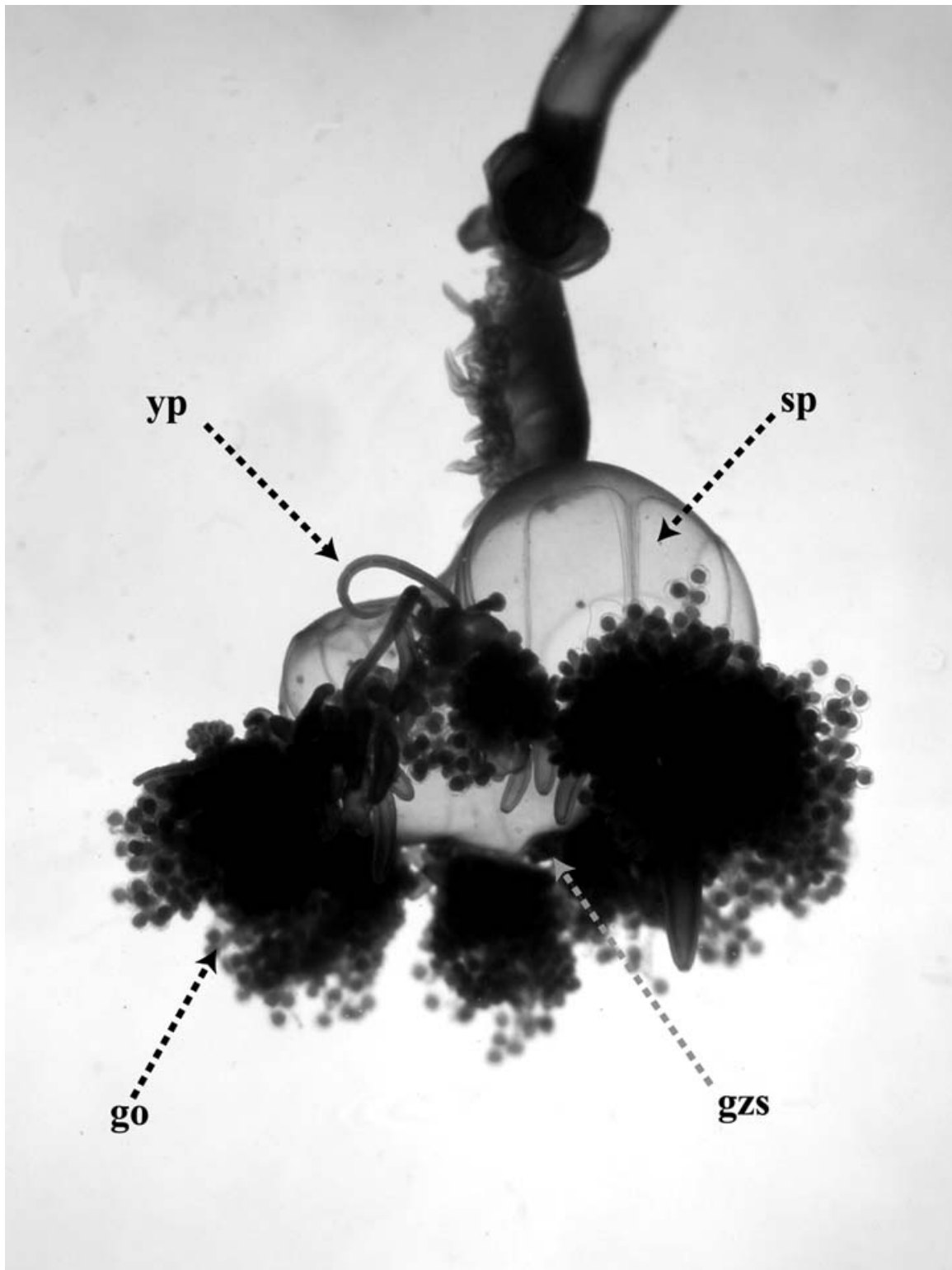
of *P. hydrostatica* (Fig. 14), the pedicles of the tentilla were very different. Whereas in *P. gilmeri* the pedicle was a short narrow tube, in *P. hydrostatica* only a short section of the pedicle, at its proximal end, was narrow. It then expanded greatly to form a long, wide muscular tube (Fig. 14b), up to 6 mm in length, with the canal occupying the central half. At the base of the stinging capsule the canal narrowed considerably and formed the tube that ran along one side of the capsule to reach the proximal end of the cnidoband, at the distal end of the capsule. The capsule itself, up to 2 mm in length, was usually egg-shaped, with a rounded point at its distal, or with a short terminal prolongation. No side processes were noted on any of these mature tentilla.

However, the tentilla of the protozoid of a very young specimen (Fig. 14a) of *Physophora hydrostatica* were slightly different. The cnidoband was less regularly spiralled, and the capsule bore two lateral processes, as well as a long terminal process. Even larger side processes were illustrated by Keferstein & Ehlers (1861, Plate IV) but were only found on the tentilla of a single tentacle. It is not clear whether such a form of tentillum only belongs to the protozoid in *P. hydrostatica*, as on other young specimens the capsule of the tentilla belonging to the protozoid showed no side processes, although the capsule itself was otherwise very similar. Nonetheless, the variety of different forms of the capsule in *P. gilmeri* clearly do not only belong to the larval tentacle, as those from the large, but poorly preserved, JSL 497 specimen, with several gastrozoids, were all of the type shown in Fig. 10d.

*Gonophores*. Many authors, including Haeckel (1888) and Totton (1965), have described the blastostyles bearing the male or female gonophores as being attached separately, but very close together, on the corm. However, many early studies, for instance by Vogt (1854), Claus (1860), and Keferstein and Ehlers (1861), have either clearly described or illustrated the male and female gonophores arising from a single blastostyle. The present studies show that this is indeed the case for both *Physophora gilmeri* and *P. hydrostatica*. However, whereas in *P. gilmeri* the female branch remains a simple tube, with the individual female gonophores branching off from it, in *P. hydrostatica* the female blastostyle has many branches, each bearing gonophores. This probably explains why the female gonophores of *P. hydrostatica* form such dense clusters (Fig. 13).

Not unexpectedly, the male and female gonophores were very similar in both species. However, in *Physophora hydrostatica* they tended to be slightly smaller, the male ones measuring 4.5 mm in length, and the female ones 0.35 mm in diameter, as compared to 8 mm and 0.55 mm, respectively, in *P. gilmeri*. The gonophores of *P. hydrostatica* have been subjected to very detailed studies by many earlier authors, for instance Vogt (1854), and no further details will be given here.

*Arrangement of cormidia*. In the past it has generally been assumed that there was only a single palpon per cormidium. Thus Haeckel (1888: 258) summarised the composition of a discolabid [physophorid] cormidium as being comprised of '(1) a large palpon with a palpacle; (2) a female gonodendron; (3) a male gonodendron; (4) a large siphon with its tentacle.

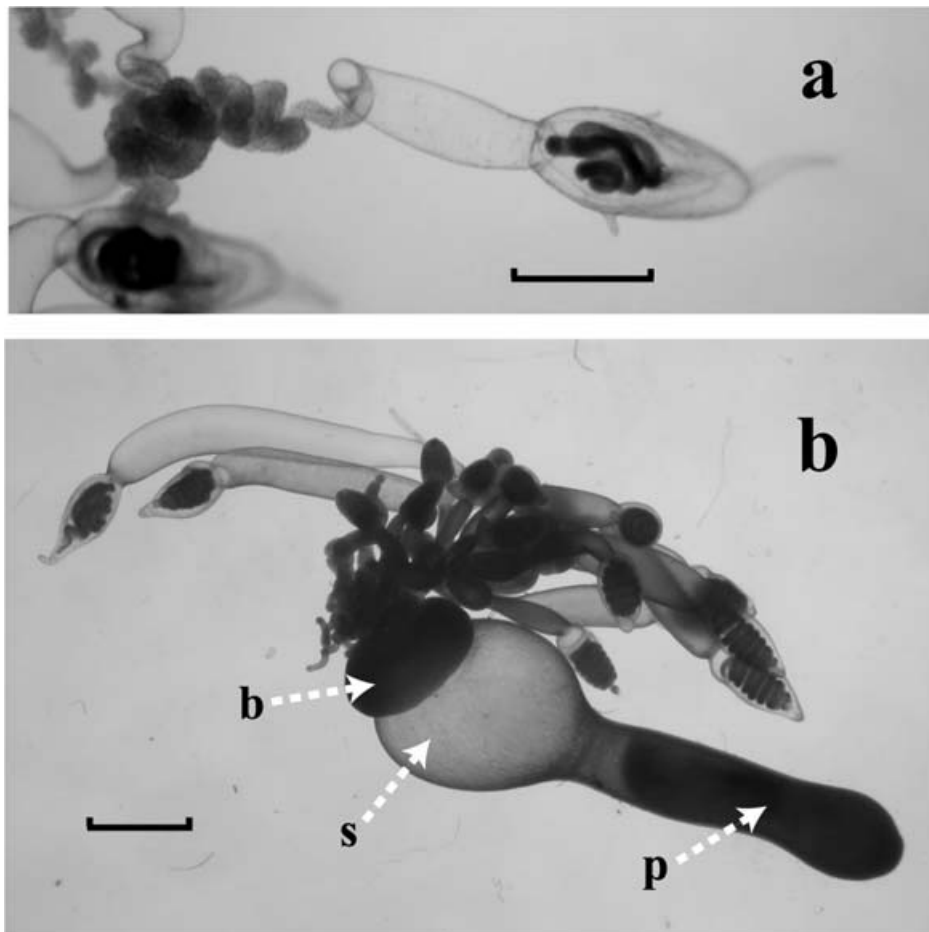


**Figure 13** *Physophora hydrostatica*. View of the siphosome, approximately 9 mm in diameter, showing a young palpon (**yp**), the attachment point (**sp**) for the mature palpons, mature gonodendra (**go**), and the stump of a gastrozoid (**gzs**).

Sometimes the number of palpons is doubled, so that a pair of them (a larger superior and a smaller inferior) belong to each cormidium; but it seems that this duplication is often accidental, and variable in one and the same species'. Totton (1965) concurred with this view. However, the fact that there is only a single blastostyle, giving rise to two branches, one

bearing the male and the other the female gonophores, has been discussed above.

Garstang (1946) in his review of the earlier literature also concluded that in *Physophora hydrostatica* there was a single palpon per cormidium. He believed that the cormidial components were arranged in a regular, dextral sequence in



**Figure 14** *Physophora hydrostatica*. a, Tentillum from young specimen. Scale 0.5 mm. b, Gastrozoid and tentacle from a larger specimen. b, basigaster; p: proboscis; s: stomach. Scale 2 mm.

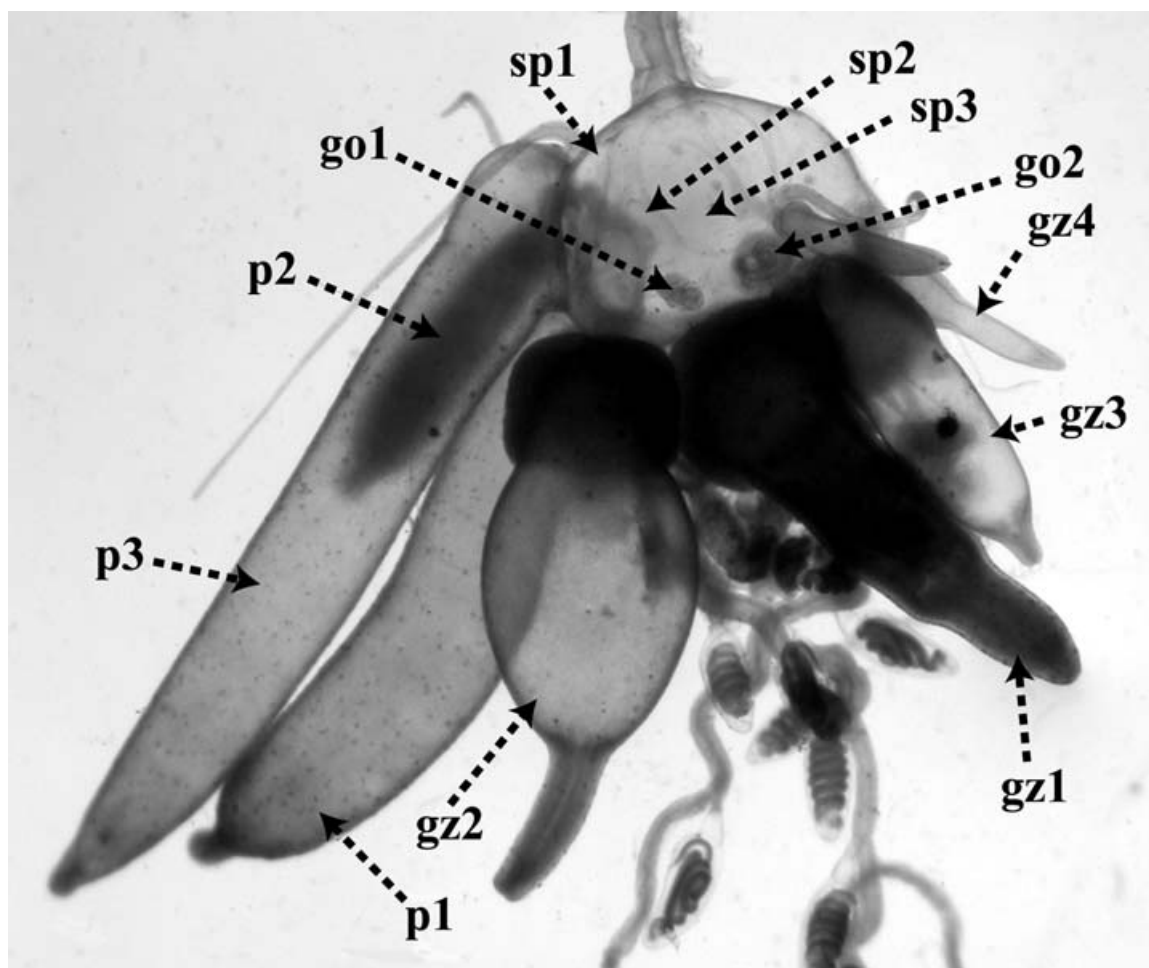
a trimorphic series, that is palpons, blastostyles and gastrozoids. In addition, he suggested that, because the palpons were crowded together in the nascent lobe (that closest to the zone of proliferation), the palpons were squeezed into two rows, with the palpon of one row alternating with one from the other row. However, he did note that, in earlier descriptions, more palpons than gastrozoids had been reported, and mentioned an illustration by Kölliker (1853) that showed nine palpons and three gastrozoids. In order to account for this discrepancy Garstang (p. 160) concluded that, at an early stage of development, after the appearance of the protosiphon 'the larval whorl probably includes at least six palpons, possibly one or two more, before the secondary siphons and gonodendra begin to appear'.

Totton (1954), after some detailed studies on young specimens of *Physophora hydrostatica*, came to doubt Garstang's (1946) conclusions concerning the origin of the arrangement of the siphosomal cormidia. He illustrated a sequence of possible steps by which the basic, long-stemmed physonect arrangement of the cormidial elements might have become transformed into the arrangement in *P. hydrostatica*. He noted that Garstang's interpretation appeared to be incompatible with the basic arrangement. However, he agreed that the palpons probably were arranged in two rows, on the nascent lobe, but concluded that the lower row of palpons was a secondary one,

and had not been caused by deformation of a single row, as Garstang suggested. Also that the primary row itself was not a single series. Totton then continued to make some rather confusing statements about the arrangement of the palpons, assuming that the order of their origin was quite variable. This appears to be based on (a) his belief that there was only one palpon per cormidium and (b) that the sizes of the palpon, or their buds, indicated the order in which they arose. However, Totton also noted that the second gastrozoid was budded quite early on, after only two or three palpons had been developed.

The conclusions reached by Garstang (1946) and Totton (1954) need to be re-examined in the light of the present observations on *Physophora gilmeri*, where each cormidium normally included a hooded bract, attached both to the gastrozoid and to the corm immediately above it, followed by three palpons. An examination of some young specimens of *P. hydrostatica* showed that a similar situation pertained, with the obvious difference in that there were no bracts. The siphosome of the young specimen shown in Fig. 15 was almost spherical, with the protosiphon or primary (larval) gastrozoid (**gz1**) attached in the middle of its base. However, the first three palpons (**p1**, **p2**, **p3**), which presumably belonged to the first cormidium, were attached on the upper side of the siphosome. The middle palpon (**p2**) of these three was much



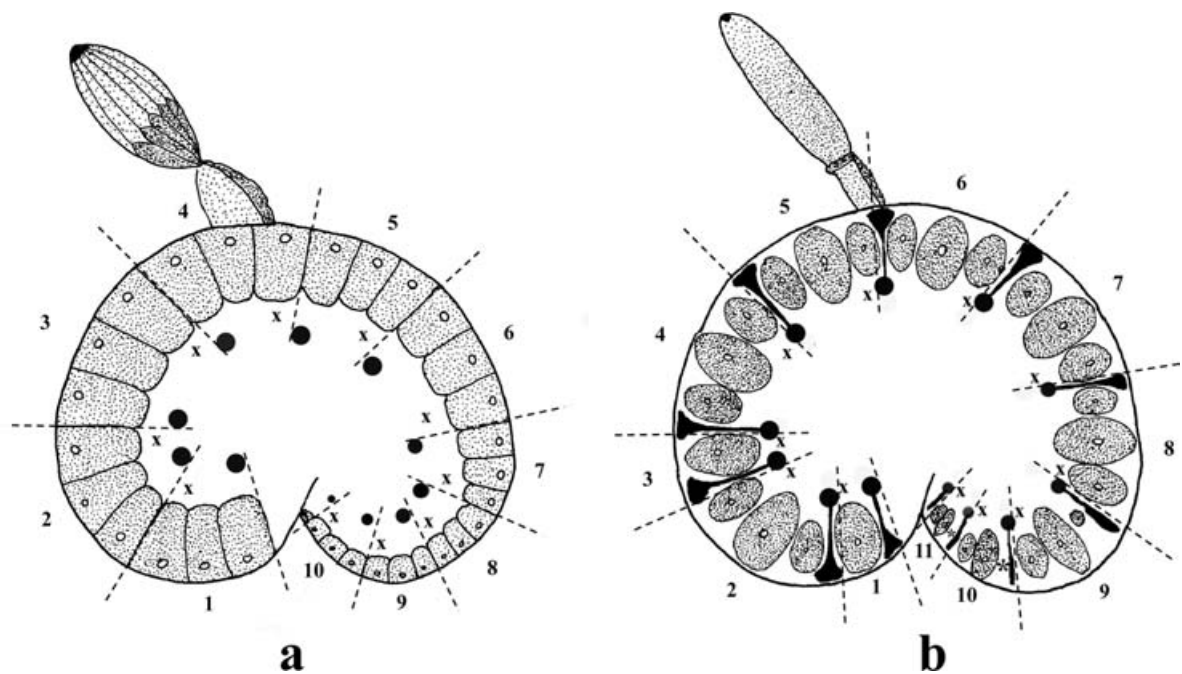


**Figure 15** *Physophora hydrostatica*. Siphosome, diameter *c.* 4 mm, of a young specimen. **gz1, gz2, gz3, gz4**: gastrozooids of the 1st, 2nd, 3rd and 4th cormidia; **go1, go2**: gonophore clusters of the 1st and 2nd cormidia; **p1, p2, p3**: 1st, 2nd and 3rd palpons of the 1st cormidium; **sp1, sp2, sp3** scars of 1st, 2nd and 3rd palpons of the 2nd cormidium.

smaller than the others. The second gastrozooid (**gz2**) was attached below the large scar (**sp1**) of the first palpon of the second cormidium. The scar of the second palpon (**sp2**) of that cormidium was much smaller, while that of the third palpon (**sp3**) was of a similar size to the first. Two more gastrozooids (**gz3** and **gz4**) were also visible, and in their cormidia the first and third palpons were small, while the scars of the second were large. The second cormidium appeared to have two sets of gonophore clusters (**go1** and **go2**). It was presumed that the first (**go1**) actually belonged to the first cormidium, and that as the siphosome enlarged and its base became flattened the primary gastrozooid and the gonophores would come to lie below the palpons of that cormidium. The second set of gonophores (**go2**) lay in the typical position below the third palpon of the second cormidium. Close to the zone of proliferation, the cormidia usually include palpon buds and/or immature palpons (Fig. 13: **yp**), so that often there were only two fully developed ones, with a bud or immature palpon inserted between them, close to their bases.

It would thus appear that the arrangement of the cormidia in both *Physophora hydrostatica* and *P. gilmeri* is very similar, with normally three palpons present in each. This is

illustrated in the schematic drawings in Fig. 16 that show the basic arrangement of the cormidia in the two species. Thus, as each cormidium is developed, the gastrozooid is budded off first. In *P. gilmeri* this bud will be accompanied by ones for the hooded and peduncular bracts, although the buds of the latter may not develop further until the cormidium is fully developed (Fig. 16b). Three palpons are then budded off in succession, and one or two of these, particularly in *P. gilmeri*, may, likewise, not develop further until the cormidium is fully developed. It was noted that the first and third cormidia of the type specimen of *P. gilmeri* appeared to have only one palpon present, and this is reflected in Fig. 16b. It is not clear whether the blastostyle, bearing the gonophores of both sexes, arises before or after the appearance of the third palpon. Its point of attachment to the corm differs in the two species. In *P. hydrostatica* the blastostyle is attached between the spirals of palpons and gastrozooids, whereas in *P. gilmeri* it is attached on the same level as, or slightly below, that of the spiral of gastrozooids. However, the position with relation to the nearest gastrozooid remains the same, in that it lies just distal to the one belonging to the next, more proximal, cormidium, approximately below the third palpon of its own cormidium.



**Figure 16** Schematic basal view of the corm of a, *Physophora hydrostatica* and b, *Physophora gilmeri* showing the arrangement of the various cormidial components. The scars of the palpon attachment areas (stippled) are arranged around the outer edge of the corm and, for *P. gilmeri*, the attachment zones of the hooded bracts (black) are shown connecting to the gastrozooids (●). The positions of the blastostyles (x) and of palpon buds (\*), in the two youngest cormidia (10 and 11) of *P. gilmeri*, are indicated. The cormidia are numbered from the oldest (1), with its protozooid, to the youngest, nearest to the zone of proliferation.

It is not clear whether any component of the cormidium, apart from the peduncular bracts, can be replaced once the cormidium has been developed, but it is clear, particularly in *Physophora gilmeri*, that the full development of some palpon buds can be delayed. The schematic arrangement of the cormidia as shown in Fig. 16 can be compared with Kölliker's (1853) illustration of a specimen of *P. hydrostatica* with three gastrozooids and nine palpons, indicating that three cormidia had been developed. From this one must infer that previous statements regarding the arrangement of the cormidia, such as Garstang's (1946) interpretation, are generally in error.

### Comparisons between *Physophora hydrostatica* and *Discolabe quadrigata*

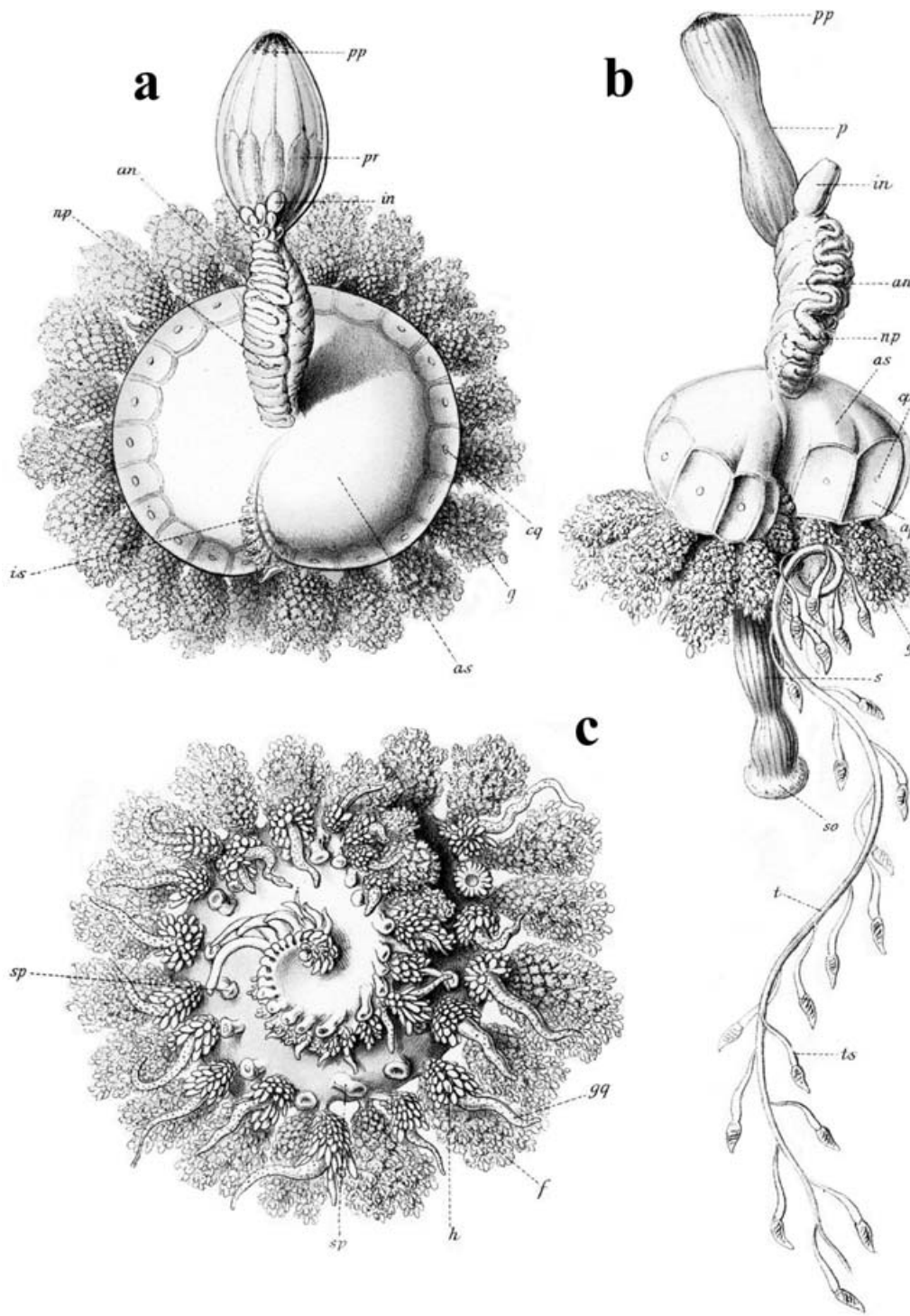
The species *Discolabe quadrigata* was established by Haeckel (1888) as a discolabid [physophorid] species whose nectophores were said to be arranged into four rows as against the two rows in *Physophora hydrostatica*. Totton (1965: 83) stated that he was 'in no way satisfied by the evidence published by Haeckel (1888b) for the existence of a rather different species *Discolabe quadrigata*, alleged to have a quadriserial nectosome'. Garstang (1946), however, had earlier considered that there were sufficient grounds for the retention of this species. His reasons will be briefly considered here.

Garstang based his reasoning, not on the reported presence of four rows of nectophores, but on the basic structure of the corm. He pointed out that, although Haeckel had described the cormidia of all physophorids as being arranged in a dextrotropic (clockwise) spiral, four out of five of his figures of corms of *Discolabe quadrigata* (Haeckel, 1888: Pl. XX) (see Fig. 17) showed the arrangement to be a laeotropic

(counter-clockwise) spiral. Garstang (1946: 164) considered this to be 'one of many similar lapses from accuracy which disfigure Haeckel's 'Challenger' Report when he deals with matters of Right and Left, Dorsal and Ventral, Dextrotropic and Laeotropic... in complete disharmony with his illustrations, which are always the right way up. In these the artist was wiser than the philosopher'! Garstang, therefore, concluded that Haeckel's description, but not his figures, was wrong, and he provisionally restricted the name *D. quadrigata* to those specimens with a laeotropically spiralled siphosome, and retained the name *Physophora hydrostatica* for those specimens with a dextrotropic one.

The present author finds it difficult to sustain this argument, particularly as Haeckel (1888) clearly stated that all physophorids, including both *Physophora hydrostatica* and *Discolabe quadrigata*, possessed a dextrotropically spiralled siphosome. Indeed, Haeckel (p. 265) made direct comparisons between the spiral arrangement of the corm in *D. quadrigata* and *P. hydrostatica*, and clearly stated that they were both dextrotropic. Even if, as Garstang (1946) suggested, Haeckel cannot tell his left from his right, nonetheless Haeckel was adamant that the spiralling was the same direction in both species.

Looking at the various structures that Haeckel described for *Discolabe quadrigata*, it is very clear that many closely resemble those of *Physophora hydrostatica*. The pneumatophores are very similar, particularly in the shape of the radial septa, as Haeckel described them, that comprise the lower half of the pneumatophore. Haeckel said that there were eight such septa, but from his illustrations and observations on the present material of *P. hydrostatica*, the number is more likely to be twelve. With regard to the nectophores, it is of interest



**Figure 17** Three views of the trunk of *Discolabe quadrigata* taken from Haeckel (1888: Pl. XX). a, Apical view showing laetotropic spiralling of siphosomal corm. b, Ventral view showing corm with dextrotropic spiralling. c, Basal view of corm showing two laetotropic spirals. For legend see Haeckel (1888, Pl. XX).

to compare Haeckel's (1888, Plate XIX) illustrations of the nectophores with those of *Physophora hydrostatica*. They are very similar, particularly with regard to their general shape and the winding courses of the lateral radial canals. However, that being said, for many other species Haeckel's illustrations of nectophores are entirely inaccurate.

All the cormidial elements that Haeckel described for *Discolabe quadrigata* are virtually identical to those seen on

the present specimens of *Physophora hydrostatica*, particularly the obvious scars left by the detachment of the palpons and the large clusters of female gonophores. One of Haeckel's illustrations (Pl. XX, fig. 12) (see Fig. 17c) purports to show a basal view of the corm, with the laetotropic spiralling forming two complete turns. This is considered to be extremely unlikely, based on the general arrangement of the corm in physophorids. In addition and again only visible in this figure,

Haeckel stated that the size of the cormidia was greatest in the middle of the series, and decreased both toward the zone of proliferation and toward the oldest, most distal, cormidia on the corm. Garstang (1946: 167) interpreted this as meaning that the older cormidia 'undergo degeneration, with the loss of their articulating facets, as they turn the ventral corner of the senescent lobe'. However, Garstang defined the senescent lobe as the hemisphere of the corm containing the older cormidia, and the nascent one as the hemisphere including the zone of proliferation. Since there are said to be two complete spirals of cormidia, then this definition cannot apply. It is, thus, very difficult to believe in the accuracy of Haeckel's illustration.

All in all, the present author concurs with Totton's (1965) view, and believes, unlike Garstang, that Haeckel's description is, by and large, more accurate than the illustrations, which would appear to have become reversed during production. The only reason, then, for distinguishing *Discolabe quadrigata* from *Physophora hydrostatica* would be the quadriserial arrangement of the nectophores. However, as discussed above, it is very difficult to imagine how the nectophores, as described, could be fitted neatly together into four rows. Thus, this arrangement is believed to be yet another example of Haeckel's all too furtive imagination, and that there is no reason to consider the name *D. quadrigata* as anything other than a junior synonym of *P. hydrostatica*.

## Conclusion

The presence of bracts on the siphosome of *Physophora gilmeri*, and the new information of the arrangement of the cormidia makes it necessary to apply a new diagnosis to the family Physophoridae, thus:

Physonect siphonophores with a vertical nectosome, whose nectophores have complexly contoured lateral radial canals. The siphosome is expanded laterally into a spiral sac, on the outer rim of which are placed the cormidial groups, arranged approximately in three spirals, with the palpons forming all or part of the uppermost spiral. Each cormidium is comprised of a gastrozoid, with a tentacle bearing characteristic tentilla, and with or without bracts attached to its peduncle; three large palpons or buds thereof; and a single blastostyle that immediately divides into two branches, one bearing male and the other female gonophores.

## Acknowledgements

I am very grateful to Dr Richard Harbison who invited me participate in the cruise, and many others, during which the type specimen was collected; and to Dr Marsh Youngbluth for providing the other specimens collected by the JSL submersibles. It is also a pleasure to thank Ron Gilmer for all his help. I also thank the reviewers for their helpful comments on the manuscript.

## References

- BIGELOW, H.B. 1911. The Siphonophorae. *Memoirs of the Museum of Comparative Zoology, at Harvard College* **38**, 173–402.
- CLAUS, C. 1860. Ueber *Physophora hydrostatica* nebst Bemerkungen über andere Siphonophoren. *Zeitschrift für Wissenschaftliche Zoologie* **10**, 295–332.
- GARSTANG, W. 1946. The morphology and relations of the Siphonophora. *Quarterly Journal of the Microscopical Society* **87**, 103–193.
- GEGENBAUR, C. 1853a. Ueber einige niedrige Seethiere. *Zeitschrift für Wissenschaftliche Zoologie* **5**, 103–117.
- GEGENBAUR, C. 1853b. Beiträge zur näheren Kenntniss der Schwimmpolypen (Siphonophoren). *Zeitschrift für Wissenschaftliche Zoologie* **5**, 285–344 +3 pls.
- HAECKEL, E. 1869. Zur Entwicklungsgeschichte der Siphonophoren. *Utrechter Gesellschaft für Kunst und Wissenschaft gekrönte Preisschrift*, 1869, 119 pp, 14 pls.
- HAECKEL, E. 1888. Report on the Siphonophorae collected by HMS Challenger during the years 1873–1876. *Report of the Scientific Results of the voyage of H.M.S. Challenger. Zoology* **28**, 1–380.
- KEFERSTEIN, W. & EHLERS, E. 1861. Beobachtungen über die Siphonophoren von Neapel und Messina. *Zoologische Beiträge Gesammelt im Winter 1859/60 in Neapel und Messina*. Wilhelm Engelmann, Leipzig, 34 pp.
- KÖLLICKER, A. 1853. *Die Schwimmpolypen oder Siphonophoren von Messina*. Wilhelm Engelmann, Leipzig.
- LEUCKART, R. 1854. Zur nähern Kenntnis der Siphonophoren von Nizza. *Archiv für Naturgeschichte* **20**, 249–377.
- MACKIE, G.O. 1964. Analysis of locomotion of a siphonophore colony. *Proceedings of the Royal Society of London B* **159**, 366–391.
- MAPSTONE, G.M. 2003. Redescriptions of two physonect siphonophores, *Apolemia uvaria* (Lesueur, 1815) and *Tottonia contorta* Margulis, 1976, with comments on a third species *Ramosia vitiazii* Stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae). *Systematics and Biodiversity* **1**, 181–212.
- MILNE EDWARDS, H. 1841. Observations sur la structure et les fonctions de quelques Zoophytes, Mollusques et Crustacés des côtes de la France. *Annales des Sciences Naturelles Series 2* **16**, 193–232.
- PAGÈS, F. & GILI, J.-M. 1992. Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina* **56** (Suppl. 1), 65–112.
- PUGH, P.R. 1983. Benthic Siphonophores. A review of the Family Rhodaliidae (Siphonophore, Physonectae). *Philosophical Transactions of the Royal Society of London B* **301**, 165–300.
- PUGH, P.R. 1984. The diel migrations and distributions within a mesopelagic community in the North east Atlantic. 7. Siphonophores. *Progress in Oceanography* **13**, 461–489.
- PUGH, P.R. 1998. A re-description of *Frillagalma vityazi* Daniel 1966 (Siphonophorae, Agalmatidae). *Scientia Marina* **62**, 233–245.
- PUGH, P.R. 2003. A revision of the family Forskaliidae (Siphonophora, Physonectae). *Journal of Natural History* **37**, 1281–1327.
- PUGH, P.R. & HARBISON, G.R. 1986. New observations on a rare physonect siphonophore, *Lychnagalma utricularia* (Claus, 1879). *Journal of the Marine Biological Association of the United Kingdom* **66**, 695–710.
- TOTTON, A.K. 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Reports* **27**, 1–162.
- TOTTON, A.K. 1965. *A Synopsis of the Siphonophora*. British Museum (Natural History), London.
- TRÉGOUBOFF, G. & ROSE, M. 1957. Siphonophores. In: *Manuel de Planctologie Méditerranéenne*. Centre nationale de la Recherche Scientifique, Paris, pp. 335–377.
- VOGT, C. 1854. Recherches sur les animaux inférieurs de la méditerranée. I. Mémoire sur les Siphonophores de la Mer de Nice. *Mémoires de l'Institut National Genevois* **1**, 1–165 +21 plates.
- WERNER, B. 1965. Die Nesselkapseln der Cnidaria, mit besonderer Berücksichtigung der Hydroida. 1. Klassifikation und Bedeutung für die Systematik und Evolution. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **12**, 1–39.