

A revision of the family Forskaliidae (Siphonophora, Physonectae)

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The family Forskaliidae (Siphonophora, Physonectae) contains a single genus, *Forskalia*, whose species are, in general, poorly known. However, in recent years many *Forskalia* specimens have been collected by scuba divers or by using submersibles. These specimens have allowed a comprehensive review of the species within the genus to be carried out. In addition two new species are described.

Introduction

Apart from Totton's (1965) *Synopsis of the Siphonophora* little has been published on forskaliid siphonophores since the 19th century. This is probably because of their great fragility, such that they are largely destroyed during collection by nets. But, in the 19th century, when specimens were individually dipped from the surface, there was considerable discussion about them, although there was much confusion as to exactly what species individual authors were describing. Bedot (1893) discussed this confusion in detail, but several subsequent authors, including Totton (1965), have not accepted all of his conclusions.

Bedot (1893) and Totton (1965) dealt with the following specific names used in earlier descriptions:

Stephanomia ophiura delle Chiaje, 1831. Both Bedot and Totton considered this to be an indeterminate species as the description was insufficient. Schneider (1898), however, retained it along with another species, *Forskalia hydrostatica* (delle Chiaje, 1830–31), but his arguments are unconvincing. Bedot did not mention the latter species, while Totton suggested that it was a case of mistaken identity, but again the description was inadequate.

Physophora mirabilis delle Chiaje, 1841. Only Totton included this species, but again he considered it to be an indeterminate species.

Stephanomia contorta Milne Edwards, 1841 and *S. prolifera* Milne Edwards, 1841. Bedot considered the first to be valid, and the second, the original description of which had been based on a mutilated specimen, he considered probably to be conspecific with it. Totton, however, maintained that, based on the original illustration, the two species could be distinguished by the structure of the gonodendron. In *Forskalia* (*S.*) *contorta* the female gonophores were borne on an enormously

extended, terminally bifurcated protuberance; distinctly overhanging the male gonophores. In *S. prolifera*, the male gonophores overhung the female ones. Totton, therefore, considered *S. contorta* to be conspecific with *F. leuckarti* Bedot, 1893; and *S. prolifera* to be conspecific with *F. edwardsi* Kölliker, 1853. However, it should be noted that Bedot considered both *F. contorta* and *F. leuckarti* to be valid species, as is discussed below.

Bedot considered the main distinguishing feature between *Forskalia contorta* and *F. leuckarti* was the presence in the pedicular canal of the nectophores of *F. leuckarti* of a bright red-pigmented spot, which Totton called the *rete mirabile*, while in *F. contorta* it was absent. Milne Edwards (1841) did not describe such a feature in his, often detailed, description of *F. contorta*. However, with regard to the pedicular canal of the nectophore, he did state (p. 221) 'Enfin, il est encore à noter que, pendant son trajet à travers l'étui [mesogloea], ce filament présente trois petits appendices lobulaires...'. From his illustration (pl. 8, figure 4) it is clear that two of these appendages are the upper and lower branches of the pallial canal, by which the pedicular canal is connected to the gastrovascular canal of the stem. The third appendage, positioned slightly above the nectosac, has been taken by some subsequent authors to represent the *rete mirabile*. However, there is another possible explanation for this appendage in that it could represent a small part of a lateral radial canal that had become torn away from the nectosac, caused by the shrinkage of the latter. This is quite frequently seen in poorly preserved nectophores of *Forskalia* species.

Stephanomia excisa Leuckart, 1853. A *nomen nudum* as no description was given. Later, Leuckart (1854) decided that *S. excisa* was the same as *F. contorta*, and he gave a description, noting for the first time the presence of a bright red *rete mirabile* in the nectophores.

Forskalia edwardsi Kölliker, 1853. Both Bedot and Totton recognized this species as valid. It is characterized by a sulphur yellow-pigmented spot on the nectophores at the point where the upper radial canal joined the circular canal that runs around the ostium.

Forskalia formosa Keferstein and Ehlers, 1860. Bedot concluded that this species was conspecific with the *F. contorta* of Milne Edwards. Totton retained it as a doubtful species, characterized by the median incision on the stem-side of the nectophores creating two, unequal axial wings. However, rather confusingly, he also mentions *F. leuckarti* as a possible synonym.

Stephanomia atlantica Fewkes, 1882. Fewkes (1882) included this species in the genus *Stephanomia* as he considered the name *Forskalia* to be a junior synonym of it. Both Bedot and Totton considered this to be conspecific with *F. edwardsi*, based on the presence of a yellow spot on the ostium of the nectophores.

Forskalia tholoides Haeckel, 1888. Bedot accepted this species as valid, while Totton (1965: 108) considered it 'A little known and doubtful species based on a beautiful idealized figure'. Haeckel (1888) also mentioned another species, *Forskaliopsis magnifica* Haeckel, 1888, from the Indian Ocean, but as there was no relevant description it is treated as a *nomen nudum*. Neither Bedot nor Totton mentioned it.

Forskalia cuneata Chun, 1888. Both Bedot and Totton retained it as a valid species, characterized by the presence of four to six intense crimson stripes on either side of the nectosac of the nectophore. This would certainly be a striking feature, but there have been no subsequent descriptions.

Forskalia leuckarti Bedot, 1893. Bedot believed this species to be distinct from *F. contorta*, but Totton considered them to be conspecific and he united them under Bedot's name *F. leuckarti*.

The only forskaliid species to be described since Bedot's (1893) review is *Forskalia misakiensis* Kawamura, 1954. Totton concluded that it was a *species inquirenda*.

In recent years, several specimens of forskaliid species have been collected by both scuba divers and submersibles. These specimens are herein described in an attempt to sort out the complex taxonomy of the genus *Forskalia*, particularly with regard to *F. contorta* and *F. leuckarti*.

Family FORSKALIIDAE Haeckel, 1888

Genus *Forskalia* K lliker, 1853

Type species: *Forskalia edwardsi* K lliker, 1853.

Species characterized by a spirally coiled stem with the nectophores, which all arise from one meridian, arranged multiserially. Nectophores flattened in the lateral plane; with straight radial canals on the nectosac. Gastrozooids borne on long peduncles that are covered in bracts. Adult bracts usually of four types; stem, 'bolster' and two types of 'knee-shaped'. Several gonopalpons, with palpacles, present on gonodendra, which bear both male and female gonophores.

Remarks. Totton (1954) described three types of bract in *Forskalia edwardsi*, which he called 'stem', 'bolster' and 'knee-shaped'. These names will be used herein, but it should be noted that for most species there are two types of knee-shaped bract.

Forskalia edwardsi K lliker, 1853

(figures 1–8)

Totton (1965) listed the following synonyms:

Stephanomia prolifera Milne Edwards, 1841: 217–229, pl. 10.

Stephanomia contorta Leuckart, 1853: 1–95.

Forskalia Edwardsii K lliker, 1853: 2–10, pls I, II.

Apolemia contorta Vogt, 1854: 85–92, pls 13, 14, figures 1–6.

Forskalia ophiura Leuckart, 1854: 351–354, pl. XIII, figures 18–21.

Forskalia ophiura Sars, 1857: 9.

Forskalia Edwardsii Keferstein and Ehlers, 1861: 28–29, pl. V, figure 25.

Forskalia sp. 1 Claus, 1863: 545, pl. XLVII, figures 16, 20c.

Forskalia Edwardsi Bedot, 1893: 231–254.

Forskalia contorta Leloup, 1935: 3.

Forskalia edwardsii Totton, 1954: 71–72, text-figures 29, 30.

The following should be added to this list:

Stephanomia (Forskalia) Atlantica Fewkes, 1882: 264–266, pl. V, figure 1; pl. VI, figures 18–22.

Forskalia ophiura Schneider, 1898: 157.

Forskalia edwardsi Lens and van Riemsdijk, 1908: 65–66, pl. X, figures 82, 83.

Forskalia contorta Moser, 1917: 737–740.

Forskalia edwardsi Totton, 1965: 100–102, figures 52–55, pl. XX, figures 1, 2.

However, it is not absolutely clear that the species Leuckart (1854) described under the name *Forskalia ophiura* actually is *F. edwardsi*. He was well aware of K lliker's (1853) description of the latter species, which had a sulphur-yellow pigment spot on the ostium of the nectosac of the nectophore. However, he made no mention of it for his *F. ophiura* specimens; in fact he noted that pigmentation was entirely absent on the nectophores. Thus, the true identity of these specimens remains uncertain. Finally, Leloup (1935) mentioned both *Forskalia contorta* and

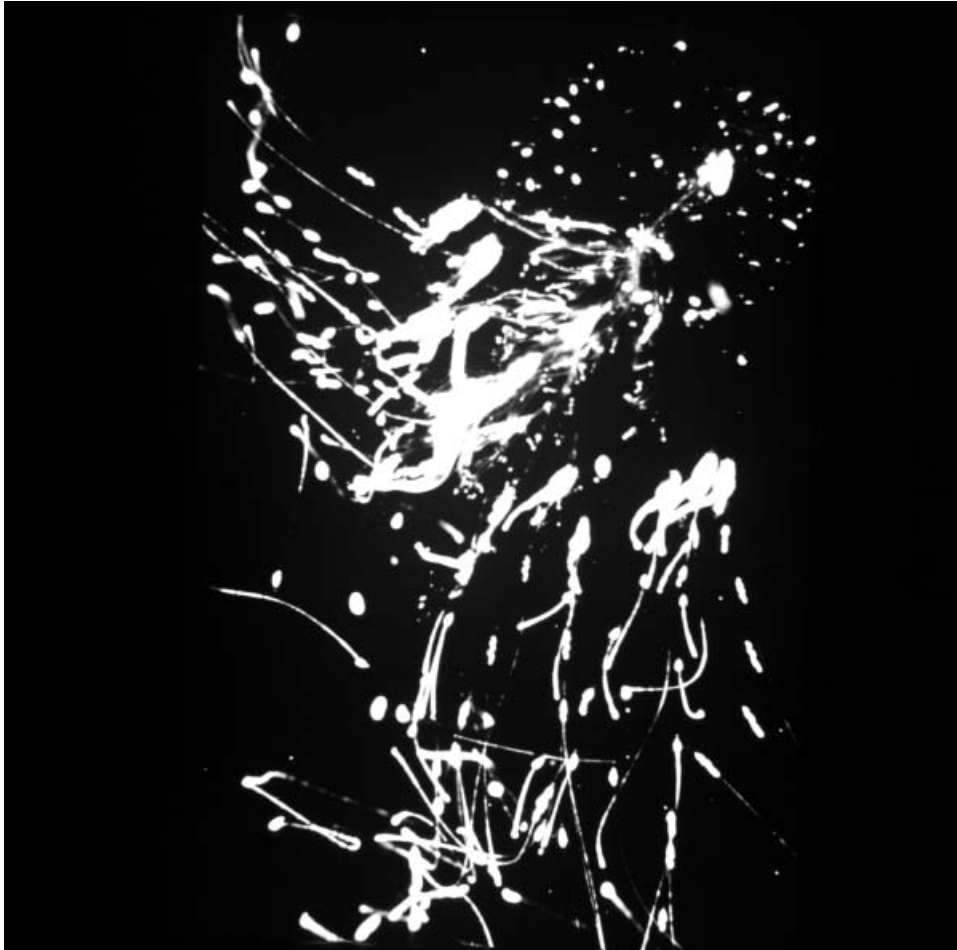


FIG. 1. *Forskalia edwardsi*. Whole animal. Photograph courtesy of Larry Madin.

?*F. edwardsi* in his paper, but described neither. Thus, it is not clear why Totton (1965) decided to synonymize the former with the latter.

Diagnosis. Nectophores with small left axial wing, and no central apical incision; with thickened mesogloea apically. Small sulphur-yellow pigment spot on ostium where dorsal radial canal joins ring canal. No *rete mirabile*. Four types of adult bract; knee-shaped ones without side branch to bracteal canal. Gonodendra with female gonophores not having elongated base. Palpacle of gonopalpon has appearance of a string of beads.

Material examined. Twenty specimens collected by scuba divers at various localities in the western North Atlantic.

Description

A photograph of a specimen *in situ* is shown in figure 1.

Pneumatophore. Up to 3.5 mm in height and 2.3 mm in diameter, but generally much smaller for the small specimens collected by scuba. Kölliker (1853) described

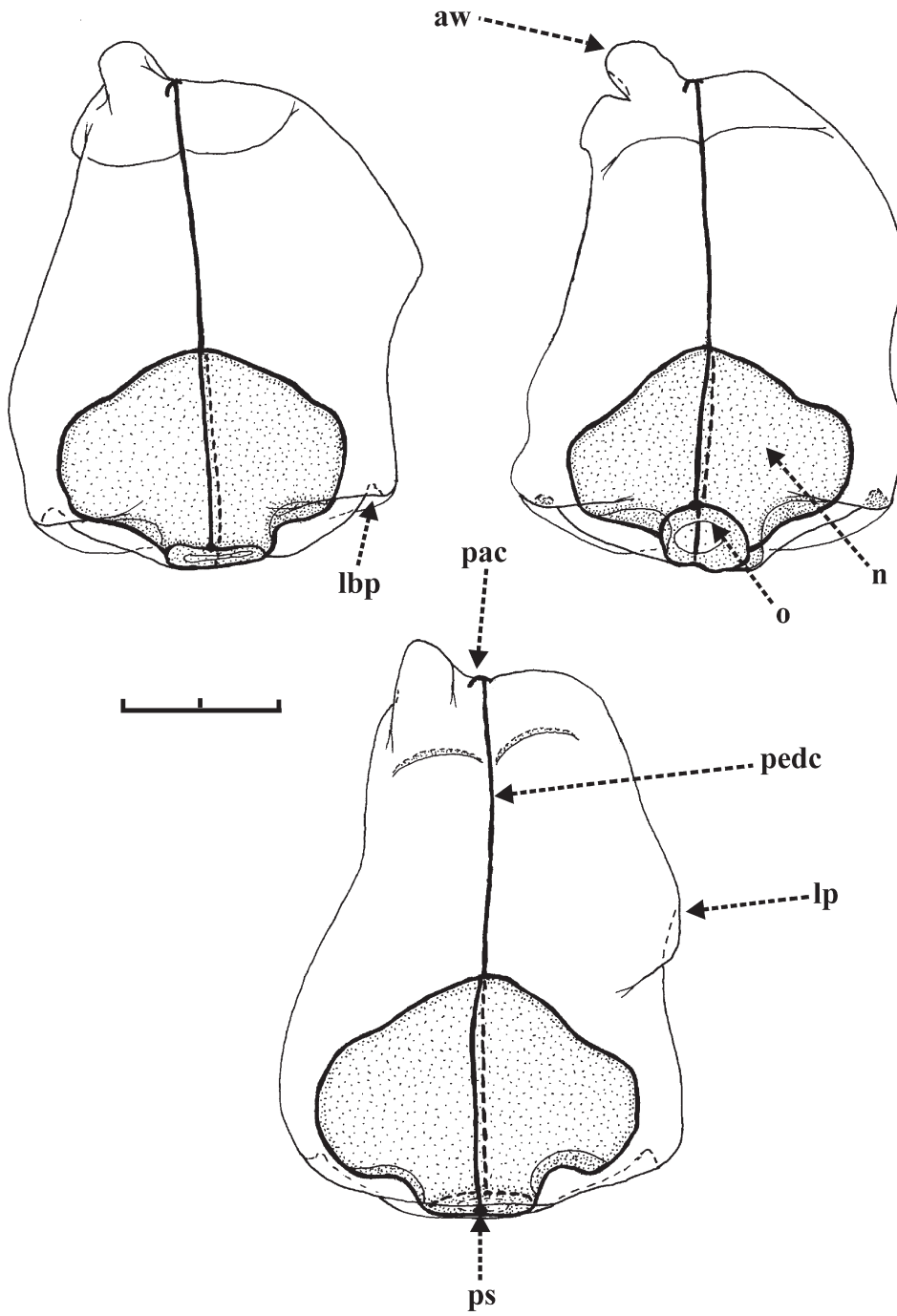


FIG. 2. *Forskalia edwardsi*. Upper views of nectophores. Scale 2 mm. aw, axial wing; lbp, lateral basal pocket; lp, lateral process; n, nectosac; o, ostium; pac, pallial canal; pedc, pedicular canal; ps, pigment spot.

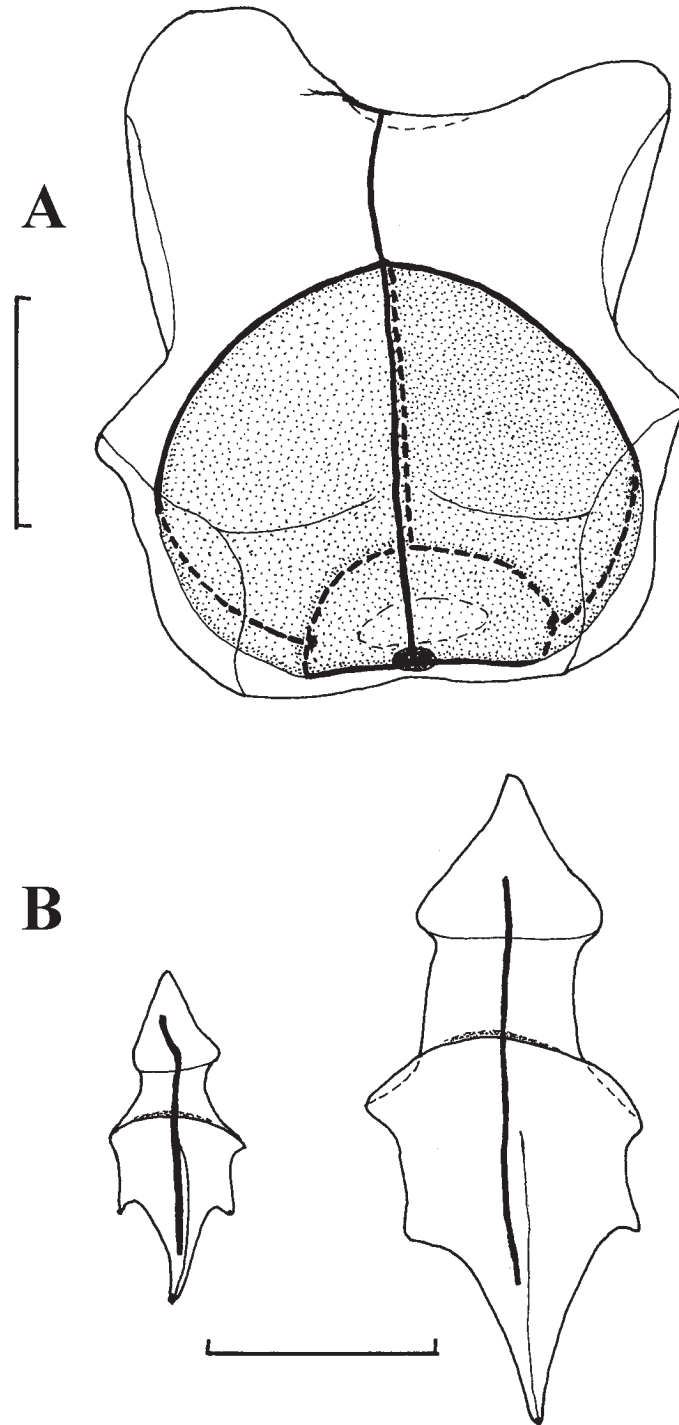


FIG. 3. *Forskalia edwardsi*. (A) Upper view of young nectophore. Scale 0.5 mm. (B) Upper view of larval bracts. Scale 1 mm.

it as having a rosy-red hue with, at its apex, larger brownish cells. This pigmentation has been lost in the preserved specimens.

Nectophore (figure 2). The largest scuba caught nectophores measured *ca* 7.7 mm in length and 3.8 mm in width. Those illustrated by Totton (1965, figure 53) were slightly larger. Typically flattened in the lateral plane, with thickened mesogloea, on the upper side, apically. There was no apical incision at the median point of attachment to the stem and only a small axial wing on the left-hand side. The lateral outline was quite variable, particularly with regard to the lateral projection on the right-hand side which, for the present material, was generally much less pronounced than in Totton's illustration. A small lateral basal pocket was present on each side. The pallial canal had an obvious ascending branch, directed toward the upper surface of the nectophore, but only a very short descending one. Nectosac highest in mid-line, with sides sloping down laterally. A typical feature of the nectophores was the presence of a small pigment spot on the ostial ring canal at the point of insertion of the dorsal radial canal. This has been described as sulphur-yellow in colour in life, but the colour faded during preservation.

The young nectophore (figure 3A) was much squatter than the adult one, with the nectosac occupying over half its length and the left apical wing being relatively broader and rounder. Lateral basal pockets had not yet been developed, but the pigment spot at the junction of the dorsal and ostial ring canals was obvious.

The nectophores often were infested with up to three to four juvenile amphipods (see larger white dots in nectosome in figure 1). According to Harbison *et al.* (1977), these belong to the Family Pronoidae. Their burrows had no visible connection with the outside, but were usually situated in close proximity to the lateral radial or pedicular canals. The juvenile's mouthparts were directed toward these canals and clearly they had broken through the wall and were feeding on the gastrovascular fluids circulating within.

Bract. The small larval bract (figure 3B) is concave ventrally, and convex dorsally. It has a cross ridge at about its mid-length, proximal to which the bract is thickened dorso-ventrally, but quite thin distally. There is a patch of small nematocysts at the extreme distal point.

As Totton (1965) pointed out, there were four main types of adult bract. The stem bracts (figure 4), almost triangular in shape, were, according to Totton, attached to the main stem by their muscular lamellae, which stretched from just distal to the gastrozoid of the previous cormidium to the base of the gonodendron. A single pair was present on each cormidium. These bracts were not exact enantiomorphs as in one the proximal part of the bracteal canal approached or reached the ventral side of the bract, while in the other it remained at some distance from it. In both there was an oblique distal facet demarcated by a weak lateral ridge, and a distinct pocket beneath the latter, ventrally on the outer side of the bract.

The bolster-shaped bracts (figure 5) were, according to Totton (1965), attached in pairs at the base of the peduncle of each gastrozoid. They were triangular in cross-section and had an oblique distal facet demarcated by a weak lateral ridge on the outer side of the bract, which slightly overhung the facet. As with the stem bracts, each pair of bracts was not exact enantiomorphs, for in one the distal end of the bracteal canal was distinctly inflected into the mesogloea (figure 5B), while in the other it was not (figure 5A).

The two other types of peduncular bracts both were knee-shaped, with an obtuse bend in the bracteal canal. The first type (figure 6) had a comparatively short,

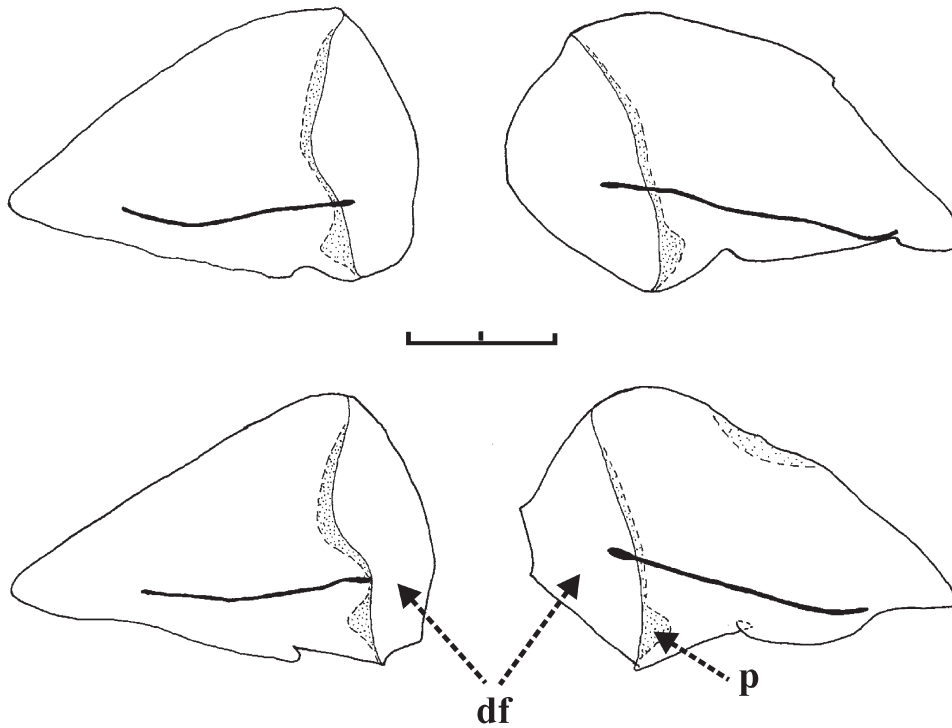


FIG. 4. *Forskalia edwardsi*. Outer views of stem bracts. Scale 2 mm. df, distal facet; p, pocket.

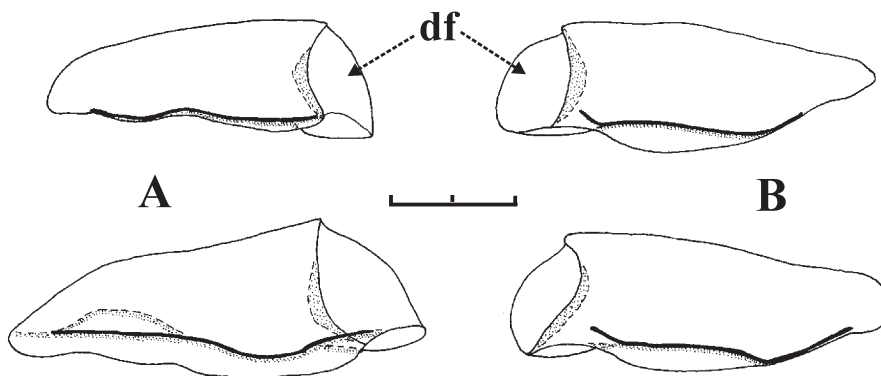


FIG. 5. *Forskalia edwardsi*. (A, B) Outer views of bolster bracts. Scale 2 mm. df, distal facet.

oblique distal facet whose lateral edges might bear small cusps in variable positions. There was a small pocket dorsally. No enantiomorphs were found for this type of bract. These bracts may be the ones that Totton (1965) referred to as being positioned toward the base of the peduncle of the gastrozoid. He made reference to his earlier figure (Totton, 1954, text-figure 30c) as an example of this bract. However, the only bract that he figured that resembles the present type is his text-figure 30a, with all the other knee-shaped bracts belonging to the second type.

The second type of knee-shaped bract (figure 7) had a much longer, oblique distal facet that could stretch up to half the length of the bract. A pocket was

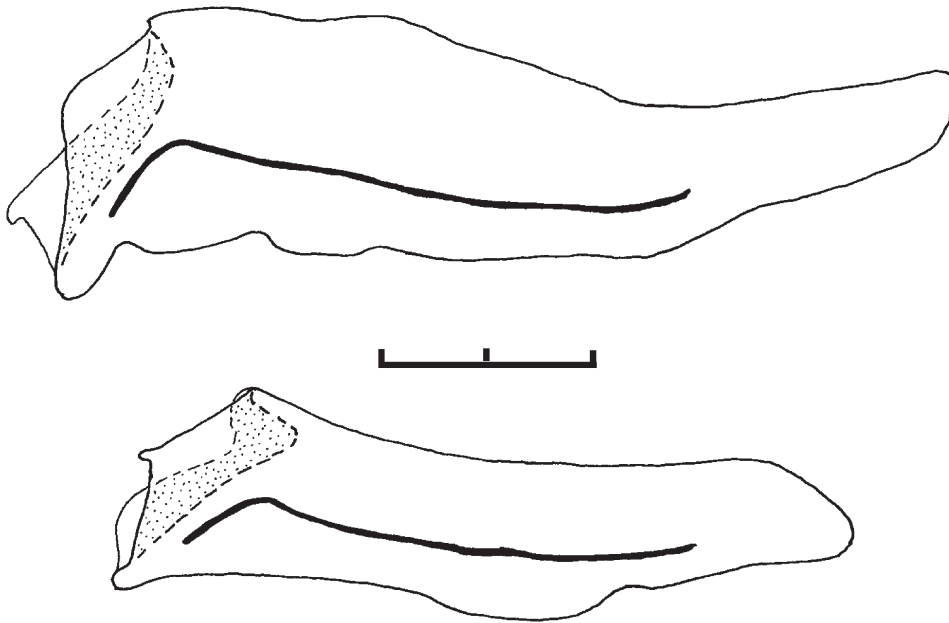


FIG. 6. *Forskalia edwardsi*. Inner views of first type of knee-shaped bracts. Scale 2 mm.

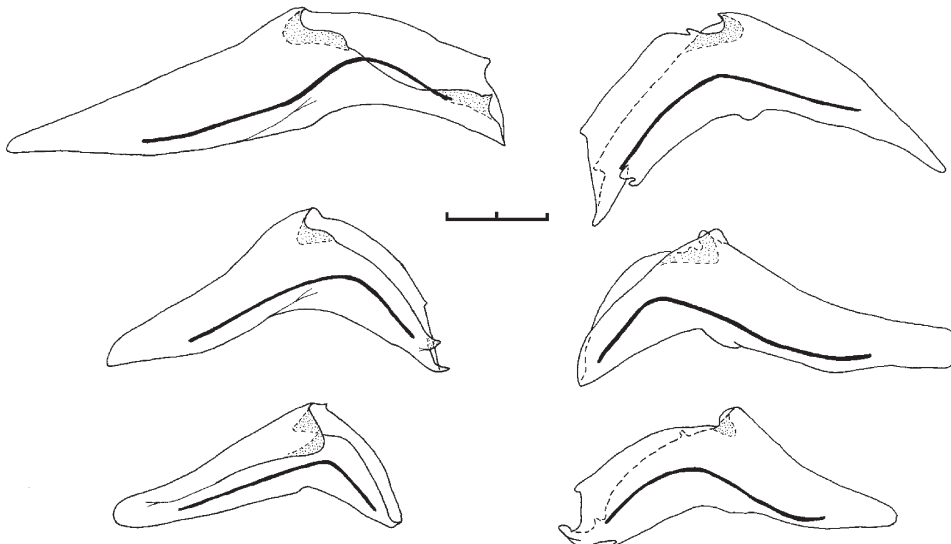


FIG. 7. *Forskalia edwardsi*. Inner views of second type of knee-shaped bract. Scale 2 mm.

present at the dorsal end of this facet. One side of this facet was always larger than the other, but both could bear cusps of varying size and disposition. These bracts occurred in enantiomorphic pairs, with no obvious differences between them. Totton (1965) noted a succession of up to ten of these bracts on the distal part of the peduncle of the gastrozoid. He also noted, almost certainly correctly, that the function of all these bracts was to give buoyancy to the peduncle of the gastrozoid which, in life, projects out from the stem at nearly a right angle.

Gastrozooids and tentacles (figure 8). The gastrozooids were borne on long peduncles, which Totton (1965) said were, in their relaxed state, over twice as long as the gastrozoid itself. There was a prominent but narrow basigaster. The tentacle bore no pronounced annulations. The tentilla had a long pedicle, a cnidoband with two to three loose spiral turns and a long terminal filament. There was a lateral row of stenoteles on either side of the cnidoband, with numerous anisorhizas, in several rows, between them. It is probable that isorhizas (?atrichous) also were present as Claude Carré (personal communication) found them in another *Forskalia* species (see below), but they were not discerned. In the terminal filament there were desmonemes and acrophores which appeared to have a fairly regular arrangement of one pair of desmonemes followed by two pairs of acrophores.

The development of *Forskalia edwardsi* was studied by Carré (1967), who noted that a tentacle, with larval-type tentilla, was developed at the base of the primary gastrozoid. Amongst the present material there were also some post-larval *F. edwardsi* specimens. The tentacles of these bore larval tentilla borne on long pedicles. The cnidoband was acorn-like, with the proximal third to half devoid of nematocysts. There was a ring of stenoteles above this, and then a multitude of anisorhizas, with distally some desmonemes; but no acrophores were noted.

Gonodendron (figure 8). There was a single gonodendron in each cormidium. The long peduncle was formed by a series of up to seven or more gonopalpons, each with a palpacle. The palpacle had the appearance of a string of beads, with each

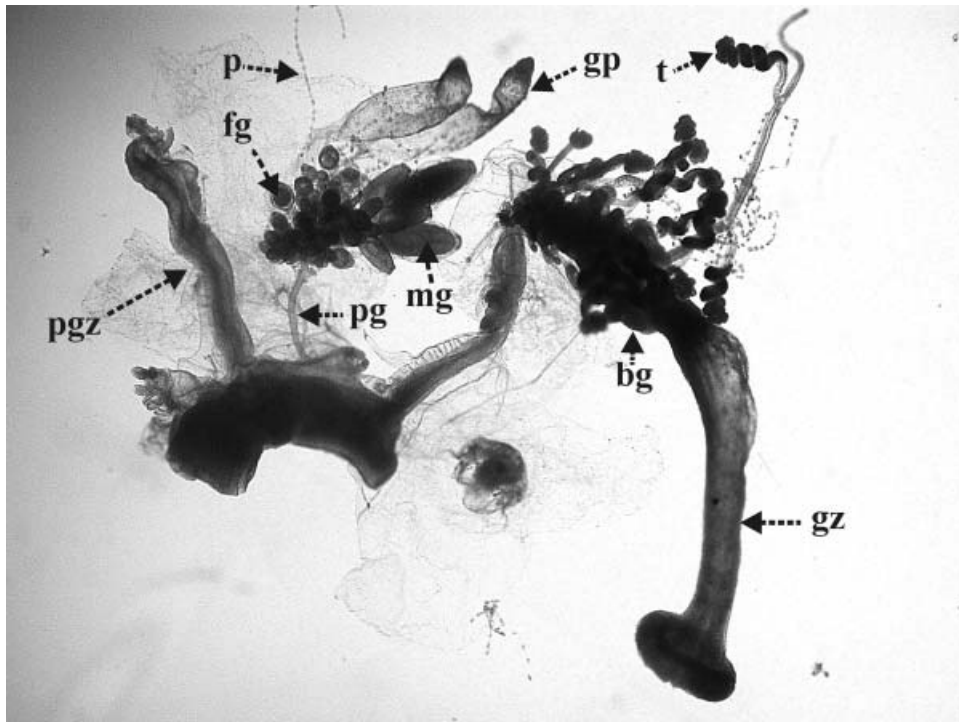


FIG. 8. *Forskalia edwardsi*. Piece of siphosomal stem (2.2 mm in length), with gastrozoid, denuded gastrozoidal peduncle and gonodendron. bg, basigaster; fg, female gonophore; gp, gonopalpon; gz, gastrozoid; mg, male gonophore; p, palpacle; pg, peduncle of gonodendron; pgz, peduncle of gastrozoid; t, tentillum.

'bead' usually comprised of two swellings. No nematocysts were found, contrary to Kölliker's (1853) assertion. However, all four (?five) of the types of nematocyst found on the tentilla were also scattered about on the surface of the gonopalpons. Up to three gonopalpons, often with additional buds, were attached close to the base of the peduncle. Then there was a long denuded section before the other palpons branched off. The male gonophores were associated with the base of the terminal gonopalpon, while the female ones were associated with the others.

Distribution

The original records for *Forskalia edwardsi* came from the western Mediterranean, where it has been recorded on many occasions since. However, it was not collected during a series of Johnson-Sea-Link (JSL) dives in the Alborán Sea (Mills *et al.*, 1996), although other *Forskalia* species were very common. There are a few records for other regions. Purcell (1980) found it in the Sargasso Sea and Gulf of California; Pugh (1974) around the Canary Islands; Totton (1954) in the Red Sea; Lens and van Riemsdijk (1908) in the East Indies; and Zhang and Lin (1997) in the South China Sea. However, it is probably much commoner than the records show as is evinced by the numerous specimens collected by scuba divers in the NW Atlantic.

Remarks

Fresh material of *Forskalia edwardsi* should be easily identifiable by the sulphur-yellow pigment spot on the dorsal side of the ostium of the nectophore. Also the shape of the nectophore, with only a small left axial wing and a lateral projection on the right-hand side, is characteristic. However, the organization of the gonodendron is not a specific character, as Totton (1965) had suggested, as a similar arrangement is found in several other species (see below). Another characteristic is the appearance of the palpacle of the gonopalpon, which looks like a string of beads.

***Forskalia contorta* (Milne Edwards, 1841)**

(figures 9–15)

Synonyms for specimens without a *rete mirabile* in the nectophore:

Stephanomia contorta Milne Edwards, 1841: 217–229, pls 7–9.

Apolemia Edwardsii Lesson, 1843: 519–526.

?*Stephanomia contorta* Leuckart, 1853: 3.

?*Forskalia ophiura* Leuckart, 1854: 351–354, pl. XIII, figures 18–21.

?*Forskalia ophiura* Keferstein and Ehlers, 1860: 261; 1861: 28.

?*Forskalia ophiura* Chun, 1888: 1171.

?*Forskaliopsis ophiura* Haeckel, 1888: 247.

?*Forskalia contorta* Lens and van Riemsdijk, 1908: 63–65, pl. X, figure 81.

Forskalia contorta Moser, 1917: 737–740.

?*Forskalia contorta* Leloup, 1935: 3; 1936a: 10; 1936b: 3; 1956: 475.

Synonyms for specimens with a *rete mirabile* in the nectophore:

Stephanomia excisa Leuckart, 1853: 1–95.

Forskalia contorta Leuckart, 1854: 340–351, pl. XIII, figures 8–17.

Forskalia contorta Keferstein and Ehlers, 1860: 261, 1861: 27–28, pl. V, figure 23.

Forskalia contorta Claus, 1863 (sp. 2): 545, pl. XLVII, figures 19, 21.

Forskalia leuckarti Bedot, 1893: 231–254.

Forskalia contorta Schneider, 1898: 157.

Forskalia leuckarti Moser, 1917: 737–740.

Forskalia leuckarti Totton, 1965: 102–108, figures 56–60, pl. XX, figures 3, 4.

Forskalia leuckarti Daniel, 1985, 111–112, figure 26.

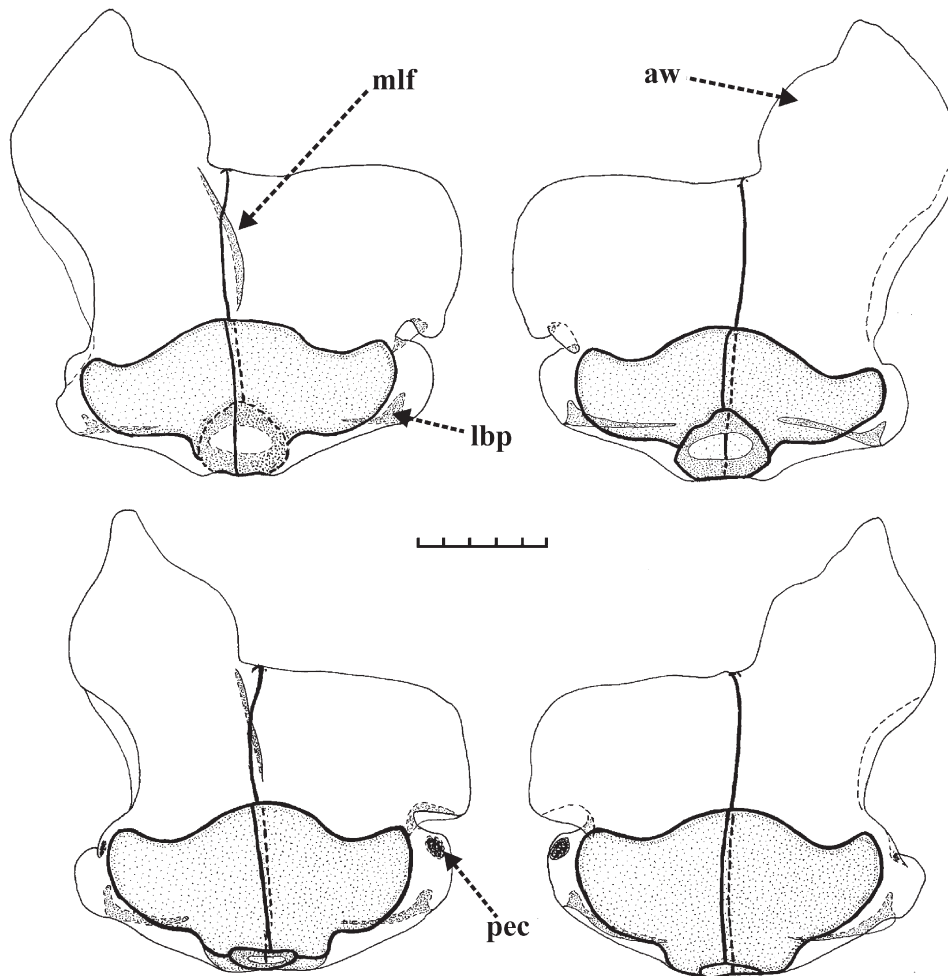


FIG. 9. *Forskalia contorta*. Upper (left) and lower (right) views of nectophores from JSL dive 2766 specimen. Scale 5 mm. aw, axial wing; lbp, lateral basal pocket; mlf, median longitudinal flap; pec, patch of ectodermal cells.

Diagnosis. Large nectophores, with large left axial wing, and no central apical incision. Longitudinal flap on upper side in apical half. Lateral basal pockets extend as flaps on to the lower surface. Nectosac with pronounced lateral wings; with dorsal and ventral canals usually not arising from pedicular canal. No pigment spots on ostium. *Rete mirabile* present or absent in pedicular canal. Three types of adult bract; with only one knee-shaped type, whose bracteal canal bends through a right angle and has a short side branch. Female gonophores, in two bunches, borne on long stalk, extending beyond male ones.

Material examined. A single specimen, without a *rete mirabile* in the pedicular canal of the nectophore, collected during JSL I dive 2766 (position: 34°01.5'N, 76°11.2'W, depth: 181 m, date: 22 August 1996). Unfortunately, the present author has not seen any complete specimens that possessed a *rete mirabile* in the nectophores.

However, such nectophores, together with some bracts, have been found, infrequently, in recent *Discovery* collections from the NE Atlantic, but these are not in a sufficiently good condition for a detailed description to be given.

Description

Fortunately, Dr Claude Carré has generously supplied me with some excellent photographs of a specimen whose nectophores bore a *rete mirabile*, and has kindly allowed me to publish some of them. Unfortunately, the specimen itself is no longer in existence.

Pneumatophore. Small, 1.9 mm in height and 0.7 mm in diameter; without any obvious pigmentation.

Nectophore (figures 9, 10). Up to *ca* 18 mm in both length and width. No apical incision at median point of attachment to the stem, but with pronounced axial wing on left-hand side which occupied about one-third the total length of the nectophore (figure 9). Median longitudinal flap on upper surface which extended from close to the point of insertion on to the stem to just above the nectosac. There was a pronounced incision of the right-hand side of the nectophore, with a much smaller one on the left-hand side. Patches of ectodermal cells generally were present in these regions, although on many nectophores they had been abraded off. The small patch on the left-hand side lay within the small incision, while that on the right-hand side lay basal to the incision and on the lower surface of the nectophore. These were confirmed to be sites of bioluminescence (P. J. Herring, personal communication), and did not contain nematocysts as Totton (1965) asserted in the case of *Forskalia leuckarti*. There were two distinct lateral basal pockets that extended, as flaps, toward the ostial region on the lower surface of the nectophore.

The nectosac was highest in the mid-line, but had pronounced lateral wings. The

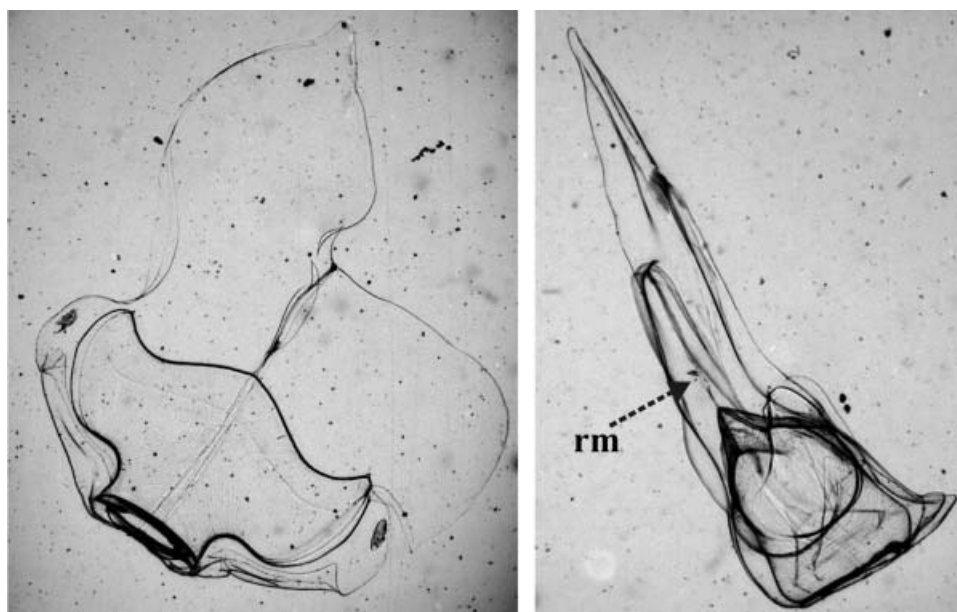


FIG. 10. *Forskalia contorta*. Two views of nectophores from Claude Carré's specimen. rm, *rete mirabile*.

pallial canal had a very short descending branch, and a longer ascending one. For the present specimen there was no *rete mirabile* in the pedicular canal. In almost all mature nectophores, the pedicular canal, on reaching the nectosac, only gave rise to the lateral radial canals. Then after a short, but variable distance, the dorsal canal branched from the left radial, and the ventral branched from the right radial. However, in small, developing nectophores all four radial canals arose directly from the pedicular canal. There were no obvious concentrations of ectodermal cells around the ostium.

If one compares figures 9 and 10 it can be seen that the nectophores are identical in almost every respect except for the absence, in the former, and the presence, in the latter, of a *rete mirabile* in the pedicular canal. This is particularly true for the shape of the left axial wing; the presence of a flap on the proximal part of the upper surface; the deep incision on the right-hand side; and the very characteristic large, baso-lateral pockets on the lower side. The extent of the nectosac is slightly greater in Carré's specimen (figure 10), but this is probably a reflection of the living versus preserved state of the nectophores. The *rete mirabile* shown in the nectophores of Carré's specimen (figure 10, rm), it is not as well developed as was found for some of the *Discovery* specimens.

Bract. Bracts of three types. Large leaf-like bracts, up to 15 mm in length, that were attached to the main stem (figure 11). They occurred in pairs but, as was the case for the stem bracts of *Forskalia edwardsi*, they were not exact enantiomorphs. One (figure 11A) had a swollen base and narrowed truncate distal end, with a more or less pronounced ventral cusp below the bracteal canal. The other (figure 11B) had none of these characters, but possessed an incomplete cross ridge, which slightly overhung the more distal part of the outer surface. In both the bracteal canal had

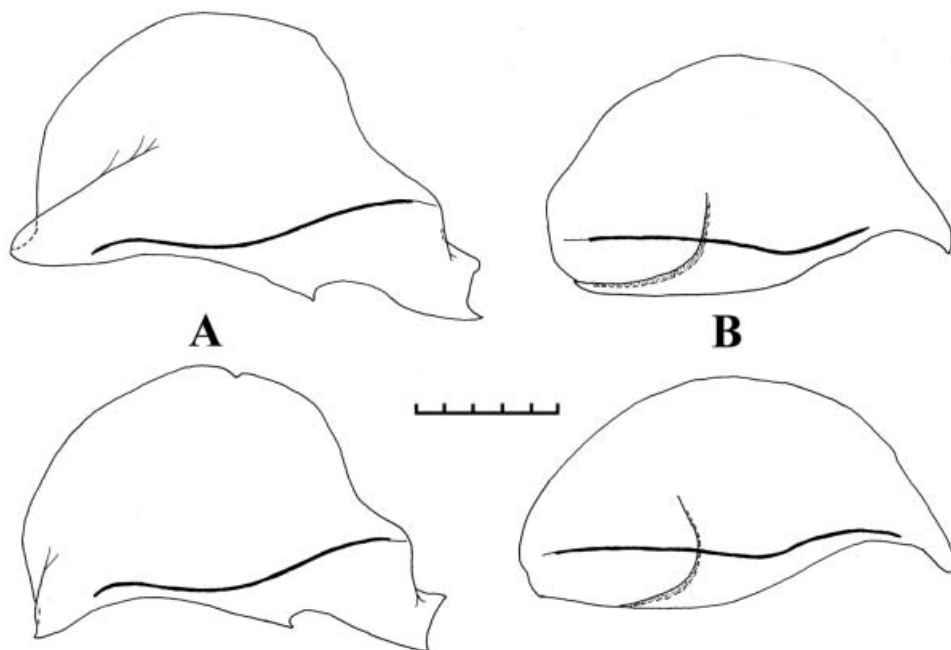


FIG. 11. *Forskalia contorta*. (A, B) Outer views of stem bracts. Scale 5 mm.

a very narrow extension at its distal end. Several hundred were present with the specimen, suggesting that more than one pair might be attached in each cormidium.

There was only one type of laterally flattened knee-shaped bract (figure 12). These were attached to the peduncle of the gastrozoid and measured up to 17 mm in length and *ca* 10 mm in height. They occurred in enantiomorphic pairs. There was a distinct thickening folded down on to the inner side of the bract, in its proximal half. In the distal half a narrow facet extended from the top of the bract down to its tip. Close to the tip the lateral margins of this facet bore several cusps of varying size and number. In the middle of the bract the bracteal canal bent at a right angle and gave off a short side branch. These bracts, often with ones at an early point in development, were only slightly more abundant than the stem bracts. It was not possible to determine how many were usually attached to each gastrozoidal peduncle. The knee-shaped bracts found with Claude Carré's specimen (figure 13) showed all the above characters, particularly the cusps near the distal end, and the side branch, of variable length, to the bracteal canal. The latter is characteristic for this species, not having been found in any other known *Forskalia* species.

A third type of much smaller bract (figure 14) was also found with the JSL specimen, but only rarely. It was flattened, with a ridge and furrow close to its distal end on its upper surface. Small cusps were occasionally present in that region. The bracteal canal was directed through the central part of the bract, and was noticeably narrower in the distal half, while proximally it bent round laterally. It is not known where this bract, of which about 30 were found, was attached.

Unfortunately, for Claude Carré's specimen, there were photographs of only the knee-shaped bracts. However, in the *Discovery* material of this species, whose nectophores possessed a *rete mirabile*, some bracts were present which resembled all

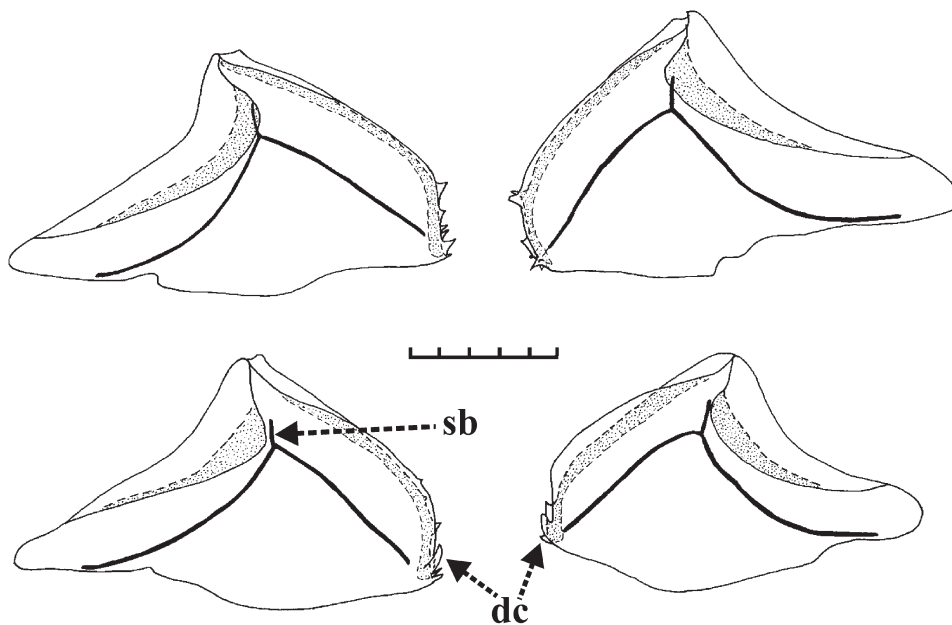


FIG. 12. *Forskalia contorta*. Inner views of knee-shaped bracts. Scale 5 mm. dc, distal cusps; sb, side branch of bracteal canal.



FIG. 13. *Forskalia contorta*. Knee-shaped bracts from Claude Carré's specimen.

three types of bract described above, particularly the third type with the central bracteal canal.

Gastrozoid and tentacle. The peduncles of the gastrozooids, in their preserved state, were highly contracted, and it is not known what their length in a relaxed state would have been. The gastrozooids had a long, narrow basigaster and a well-developed, annulated tentacle. The tentilla, which arose in the nodes of the tentacle, had a more or less loosely coiled cnidoband with from three to seven spiral turns, and a long terminal filament. There was a lateral row of stenoteles on either side of the cnidoband, with the remainder being packed with anisorhizas. Carré's photographs included ones of discharged stenoteles, anisorhizas and isorhizas, all presumably from the cnidoband, but the last type was not positively identified in the JSL specimen. The terminal filament contained desmonemes and acrophores, whose exact disposition could not be determined.

Gonodendron (figure 15). There was a single gonodendron per cormidium. It consisted of up to seven gonopalpons, each with a palpacle, and bunches of male and female gonophores. The palpacle did not have the appearance of a string of beads. Some nematocysts were associated with it, but they were irregularly disposed. The palpons had several stenoteles in the mouth region, with other types of nematocyst occasionally being present along its length. The interesting feature of the gonodendra was that the female gonophores were borne, in two bunches, on a long, and often inflated, stalk, which extended well beyond where the male gonophores were attached.

Again comparisons of the two photographs in figure 15 show that the arrangement of the gonodendron, in the specimens with or without a *rete mirabile* in the nectophore, is virtually identical.

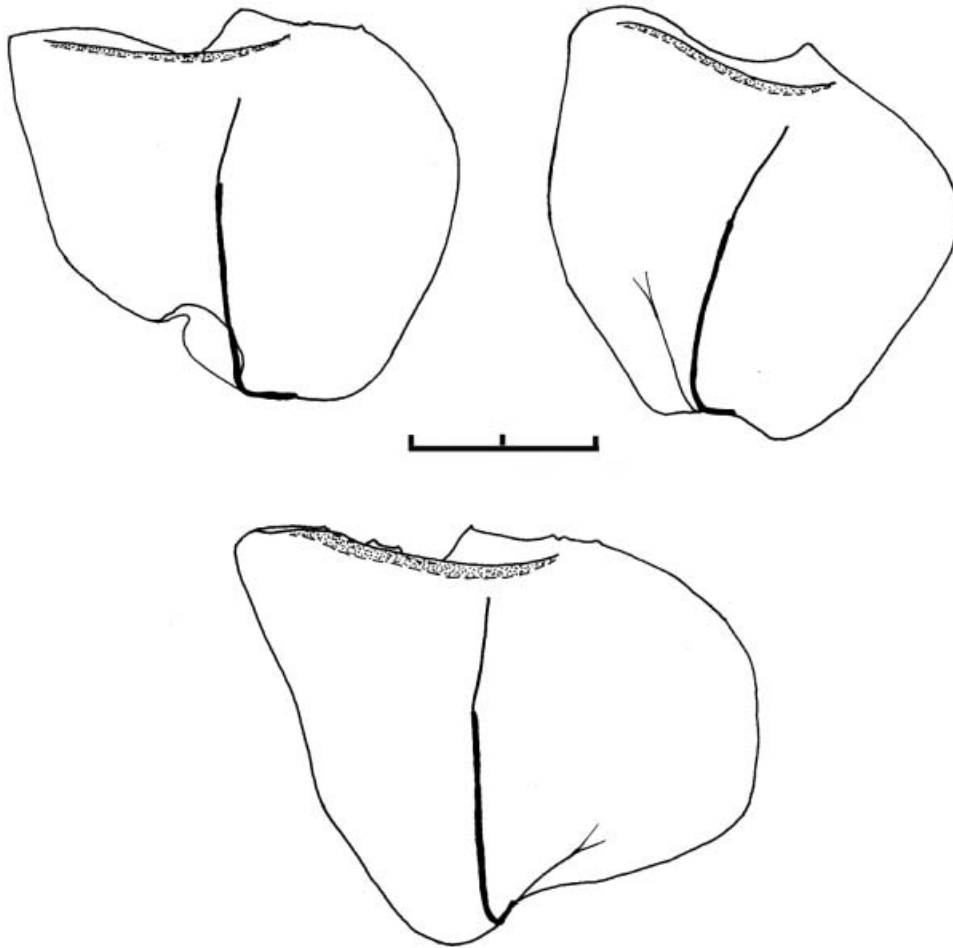


FIG. 14. *Forskalia contorta*. Upper views of third type of bract. Scale 2 mm.

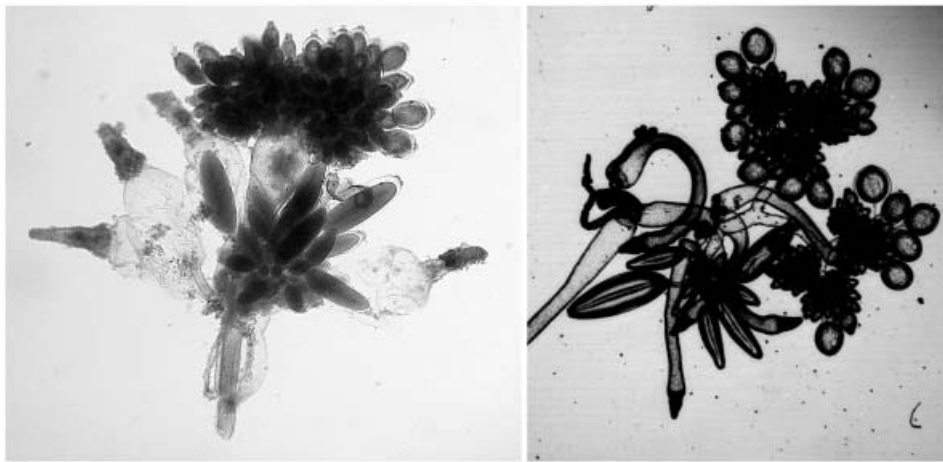


FIG. 15. *Forskalia contorta*. Gonodendra from JSL dive 2766 (left) (total length 4.2 mm) and Claude Carré's (right) specimens.

Distribution

Milne Edwards's (1841) original material came from off Villefranche (western Mediterranean). It is difficult to gauge what other records for forskaliids might belong to the form of this species without a *rete mirabile*. However, since Leloup (1935, 1936a, 1936b, 1956) would have known of the two forms it is assumed that his records for *Forskalia contorta*, which came from the western Mediterranean, south of the Azores, and off Viet Nam, respectively, refer to the form without a *rete mirabile*. The single specimen described above was collected in the vicinity of Cape Lookout (Atlantic coast of USA) at a depth of 181 m.

All the 19th-century records for the form of *Forskalia contorta* with a *rete mirabile* come from the western Mediterranean. However, it has rarely been recorded in that region since (Totton, 1965; Grimmelikhuijzen *et al.*, 1986), and was not found in the Alborán Sea (Mills *et al.*, 1996) during a series of submersible dives. Outside of the Mediterranean, Moser (1917) noted records from off Japan and at 60°N, presumably in the Atlantic. Reliable records also come from the Benguela current (SE Atlantic) (Pagès and Gili, 1992), and from various localities in the Indian Ocean (Daniel, 1985). The specimens from the Bahamas mentioned by Youngbluth (1984) probably do not belong to this form, or perhaps this species, as it is believed that their nectophores do not possess a *rete mirabile*. There are a few records from recent *Discovery* collections in the NE Atlantic, all between the equator and 20°N; together with a single nectophore from the Gulf of Guinea (5°S).

Remarks

As noted in the Introduction, it is the identity of the third appendage on the pedicular canal of the nectophore that Milne Edwards (1841) described for *Forskalia contorta* that had given rise to subsequent discussion as to whether it represented a *rete mirabile*. Bedot (1893) believed that if such a structure had been present in Milne Edwards's specimen then that author, whose description was often quite detailed, would without doubt have mentioned it. Totton (1965), however, believed that it was a *rete mirabile*, and so considered *F. contorta* and *F. leuckarti* to be synonyms. He decided to use the specific name *leuckarti* as 'it appears to be modern practise not to change a synonymy when it has remained unchallenged for a long period of years' (p. 98). However, it should be noted that the last major review of *Forskalia* species prior to his Synopsis had been given by Bedot (1893) who, as noted above, considered both species to be valid. Schneider (1898) did consider them to be conspecific but retained the name *F. contorta*.

Totton (1965) also based his argument that *Forskalia contorta* and *F. leuckarti* were one and the same by comparing the structure of the gonodendra on a specimen of *F. leuckarti* that he found at the Station Zoologique, Villefranche with the illustrations given by Milne Edwards (1841). In both cases the female gonophores were borne, in two groups, on a long stalk that considerably overhung the male ones. As was shown above, the arrangement of the gonodendron in both forms of *F. contorta*, with or without a *rete mirabile* in the nectophore, is exactly the same. Moreover, this arrangement has not been found in any other forskaliid species and thus it appears to be a good specific character. The general appearance of the nectophores and the knee-shaped bracts of both forms is also so similar that there can be little doubt that we are dealing with a single species. However, Totton's argument for retaining the name *leuckarti* is rejected and the original name *contorta* has been used.

It is not clear why some specimens of *Forskalia contorta* have a *rete mirabile* in the nectophores while others do not. However, this is not the first time that specimens without a *rete mirabile* have been found. Apart from Milne Edwards, Leuckart (1854) found this to be the case for one of his specimens. Further, it should be noted that both Moser (1917) and Totton (1965) found that in their specimens a *rete mirabile* was only present in the mature nectophores.

Forskalia formosa Keferstein and Ehlers, 1860

(figures 16–23)

Forskalia formosa Keferstein and Ehlers, 1860: 261; 1861: 29, pl. V, figure 22.

Forskalia contorta Bedot, 1893: 235, 250.

?*Forskalia hydrostatica* Schneider, 1898: 158.

Forskalia formosa Moser, 1917: 737–740.

Forskalia formosa Totton, 1965: 108, pl. XX, figure 5.

Forskalia formosa Daniel, 1985: 114–116, figure 27.



FIG. 16. *Forskalia formosa*. Specimen collected in Alborán Sea. Total length *ca* 30 cm. Photograph courtesy of Steve Haddock.

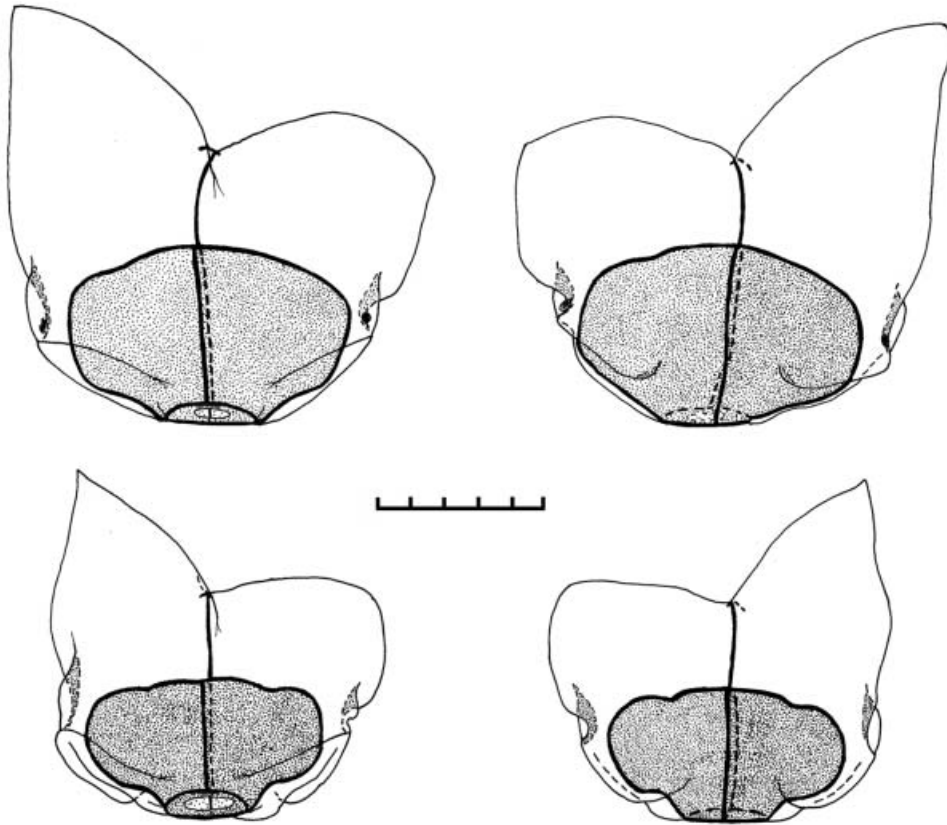


FIG. 17. *Forskalia formosa*. Upper (left) and lower (right) views of nectophores. Scale 5 mm.

Diagnosis. Nectophores with large, pointed left axial wing; and shallow, but broad and rounded right wing. Small apical incision between them. Small lateral, but no baso-lateral pockets. No *rete mirabile*. Four types of adult bract; knee-shaped ones without side branch to canal. Gonodendra with female gonophores, in two bunches, attached close to bases of gonopodons; male gonophores borne on long stalk.

Paratype. The specimen from JSL I dive 2943 (position: 35°45.6'N, 3°13.5'W, depth: 590 m, date: 14 April 1991) is designated a paratype and has been donated to the Natural History Museum, London, where it is registered as BMNH 2001.6916.

Material examined. Eleven specimens collected by the JSL submersibles, mainly from the Alborán Sea (western Mediterranean).

Description

Figure 16 shows a photograph of one of the specimens collected in the Alborán Sea.

Pneumatophore. The pneumatophore measured about 1.85 mm in height by 0.75 mm in diameter. In life it may have had an apical cap, dark red in colour, but this was not always apparent. There was also some yellow pigmentation at the base of the gas vesicle.

Nectophore (figure 17). Nectophores quite delicate and easily damaged; measured

up to 15 mm in length and 15 mm in width. There was a pronounced left axial wing, which came to a point, while the shallow right wing was rounded and broad. There was a small incision between them. Laterally, on both sides, there was a small pocket, which contained a more or less obvious patch of large ectodermal cells. The upper lateral ridge petered out, on the upper surface, slightly above this pocket, and basally it was angled obliquely toward the ostium before again petering out. The lower lateral ridge, basal to the pocket, also was angled down toward the ostium before it bent back and petered out without forming any obvious baso-lateral pocket.

The pallial canal had a very short descending and a much longer ascending branch. The extensive nectosac was highest in the mid-line, sloping down slightly toward its lateral margins. The dorsal canal usually arose from the left radial canal, but close to the point of incision of the pedicular canal. The ventral canal usually arose from that incision point. There was an obvious patch of large ectodermal cells on the dorsal part of the ostium, and two long, narrow patches laterally. There was no sign of pigmentation on any of these patches, which were presumed to be sites of bioluminescence.

Bract. Four types of bract were found. The stem bracts occurred in distinctly non-enantiomorphic pairs. On one type (figure 18A) the distal end of the bract was drawn out into a long process, each edge ending in a large cusp. A ridge ran from the ventral cusp on to the outer side of the bract. There was a small, rounded process on the ventral side, while dorsally the bract was most extensive at about its mid-length. The bracteal canal often was of variable thickness. In the other type (figure 18B) there was no pronounced distal process, while the ventral margin was distinctly emarginate. At the distal end of this a ridge ran up on to the outer side of the bract, to about half its height.

The bolster bracts (figure 19) also occurred in non-enantiomorphic pairs, with one type being slightly longer than the other. Both had flattened inner surfaces, and concave outer ones, with the mesogloea usually much thinner in the shorter type. Both had an asymmetrical distal facet, with the ventral margins of the longer type being rounded, while those of the shorter ones were usually pointed. In the mid-region of both bracts the ventral margin on the outer side was wider than the inner one; and generally more extensive in the longer type. In both the distal end of the bracteal canal penetrated for a short distance into the mesogloea. However, in the shorter type the canal curved up on to the proximal end of the bract, while in the longer type the canal did not extend to that end.

There were two types of knee-shaped bracts; one occurred in enantiomorphic pairs (figure 20), the other in distinctly different pairs (figure 21). The first type (figure 20) were long, tapering proximally and distally ending in a point, on either side of which were two cusps. The ventral one of these was usually distinct, while the dorsal one could be less well marked. The distal facet occupied the distal half of the bract on the dorsal part of the outer surface. The lower edge of this facet could be quite indistinct, particularly toward its distal end. However, there was a distinct cusp close to its proximal end. The bracteal canal was only slightly curved, and usually narrowed considerably toward its distal end.

One of the second type of knee-shaped bracts (figure 21, left) had a large triangular distal facet on its inner surface. There was a more or less pronounced flap also on the inner surface of the bract. The bracteal canal had a rounded right-angle bend, and usually narrowed distally. The other bract of the pair (figure 21, right) had a small distal facet. Its two lateral margins ended in small cusps dorsally,

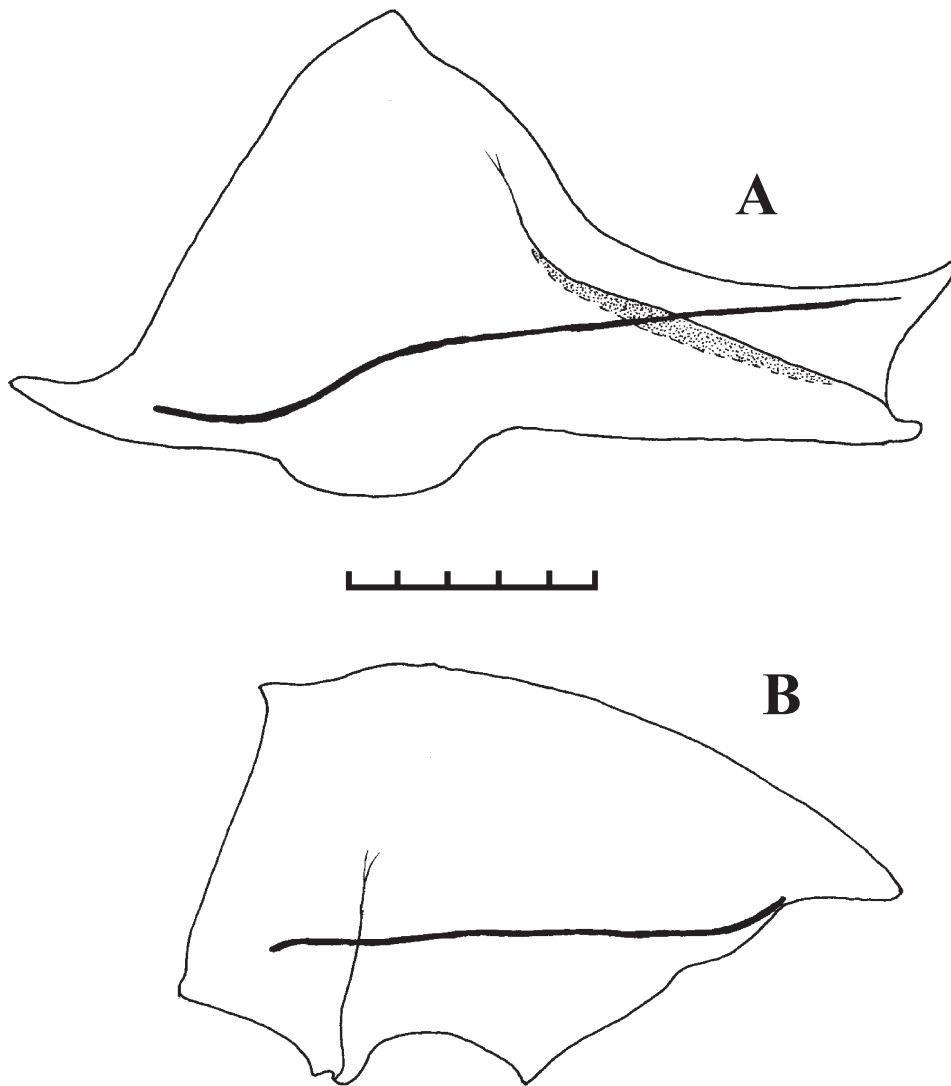


FIG. 18. *Forskalia formosa*. (A, B) Outer views of stem bracts. Scale 5 mm.

while the inner one had a distinct cusp at about mid-height. The outer margin was usually smooth, but occasionally bore a rounded cusp. The bracteal canal was bent through a right angle just proximal to the distal facet and narrowed distally.

Gastrozoid and tentacle (figure 22). The gastrozooids were borne on long peduncles and, in their preserved state, the basigaster was almost as long as the stomach region. About 16 hepatic stripes were present in the stomach and, in life, their more basal parts were coloured a bright orange. The tentacle was annulated with the tentilla arising at the internodes. In life, the orange-red coloured cnidoband of the tentillum was loosely coiled, with *ca* 2.5 spiral turns; although this number increased to up to four in the preserved material. Typically the nematocysts on the cnidoband consisted of a lateral row of stenoteles (*ca* $45 \times 22 \mu\text{m}$), surrounding several rows of anisorhizas (*ca* $25 \times 5 \mu\text{m}$). There were also some smaller nematocysts that might

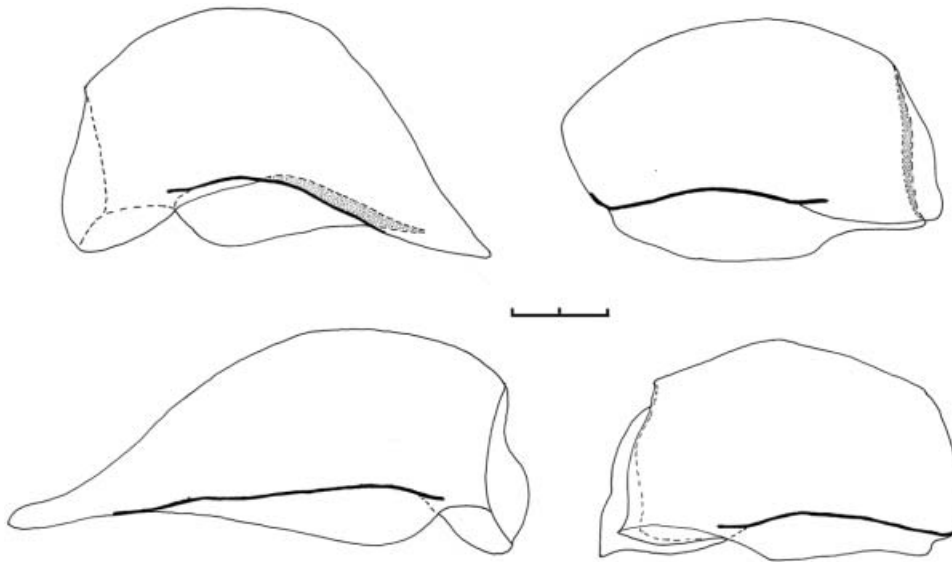


FIG. 19. *Forskalia formosa*. Inner (top) and outer (bottom) views of bolster bracts. Scale 2 mm.

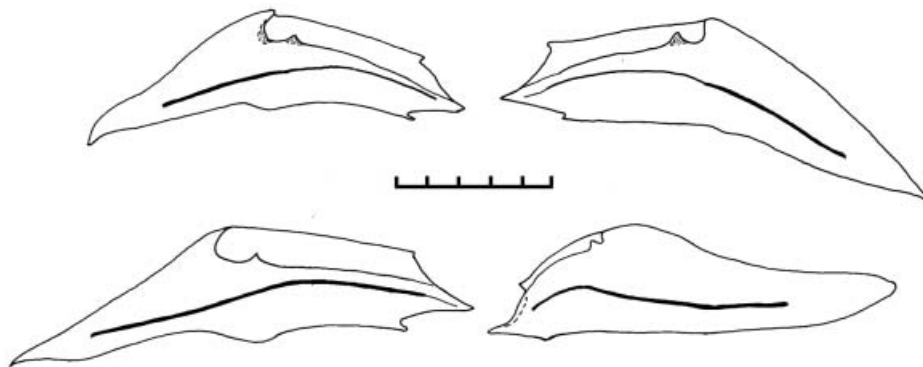


FIG. 20. *Forskalia formosa*. Outer views of first type of knee-shaped bracts. Scale 5 mm.

have been isorhizas, but this could not be determined with certainty. The terminal filament contained desmonemes and acrophores, whose arrangement could not be discerned.

Gonodendron (figure 22). The gonodendra were borne on a short peduncle in the preserved specimens. At least four gonopalpons were present, each with a palpacle. The palpons were large, typically over 10 mm long, and often were inflated. They were mostly thin walled, but in the region of the distinctive terminal ampulla there were scale-like groups of large ectodermal cells. Stenoteles were the only nematocysts seen, and these were grouped around the mouth. The palpacle had a simple structure, without any apparent nematocysts. The female gonophores were arranged in two bunches and were attached at the base of the palpons. The male gonophores, however, were borne on a long stalk that extended for a considerable distance beyond the female ones.

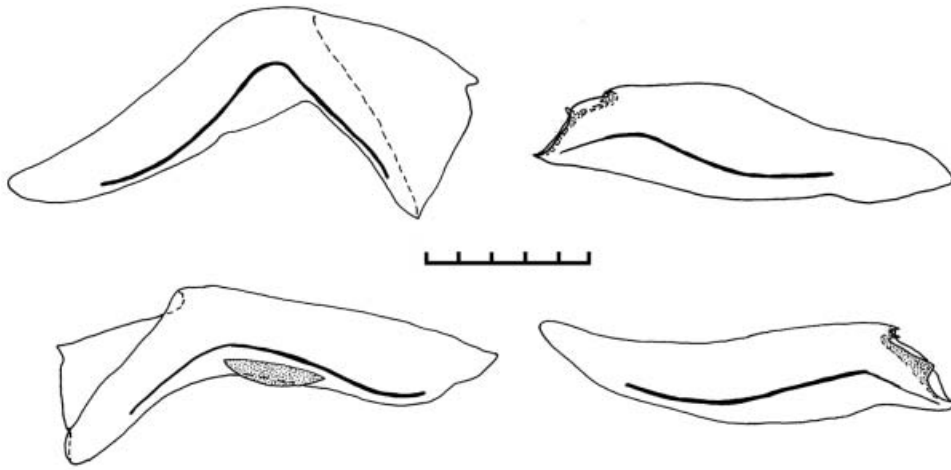


FIG. 21. *Forskalia formosa*. Outer (top) and inner (bottom) views of second type of knee-shaped bract. Scale 5 mm.



FIG. 22. *Forskalia formosa*. Piece of siphosomal stem, with gastrozoid (4.4 mm in length excluding basigaster), denuded gastrozoidal peduncle and two gonodendra.

Distribution

The original material of *Forskalia formosa*, as described by Keferstein and Ehlers (1860, 1861), was said to have been collected, infrequently, off Messina (Sicily), and presumably from just below the surface. If, as is assumed here, the present material

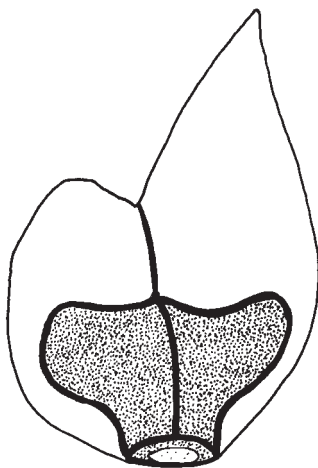


FIG. 23. *Forskalia formosa*. Nectophore. Redrawn from Keferstein and Ehlers (1861, pl. V, figure 22).

is taken to be of the same species, then the JSL I submersible collected 20 specimens, not all of which were preserved, during an expedition in June 1991 to the Alborán Sea (western Mediterranean) in the region of *ca* 35°35'N, 2°50'–5°W, which Mills *et al.* (1996) referred to as *F. (?) formosa*. The specimens were collected at depths between 355 and 590 m; mean depth 508 m. The only other forskaliid specimens collected during that cruise, which Mills *et al.* (1996) referred to as *Forskalia* sp. 1, belonged to a new species described below. In addition the JSL II submersible collected two specimens in the region of the Bahamas (position: 25°29'N, 77°24.2'W, depth: 326 m, date: 23 October 1984; and position: 26°25.6'N, 77°52.8'W, depth: 748 m, date: 5 October 1988).

Remarks

Keferstein and Ehlers's (1860, 1861) descriptions of *Forskalia formosa* were very brief. In the earlier one, the only useful characters given were that there was a deep incision between the axial wings of the nectophore, with one of the latter being consistently larger than the other. In addition, they noted that the gastrozooids were borne on short pedicles, which were consistently shorter than the palpons. Little was added in the second description, although they did state that the bracts did not differ from those of *F. edwardsi*, but no further details were given. However, they did illustrate a nectophore (see figure 23), which clearly differed from their other figured nectophores of *F. edwardsi* and what they called *F. contorta* (M. Edw.) Leuck., which clearly possessed a *rete mirabile*.

The nectophores of the present material also have a large, pointed axial wing on one side and the rounded smaller one on the other. However, the latter is much broader than illustrated by Keferstein and Ehlers. Although Keferstein and Ehlers described the incision between these wings as deep, it can be seen (figure 23) that this is not really the case. In general, apart from one of the pair of stem bracts there is also a close similarity between the bracts described above and those of *F. edwardsi*, but this is also the case for almost all the *Forskalia* species. Because the nectophores of the present material most closely resemble those of *Forskalia formosa*, it has

been decided to apply that name to them. The fact that specimens of this species were, by far, the commonest forskaliid collected by the JSL submersible in the Mediterranean, from where it was originally described, is also a mitigating factor.

Video sequences of specimens of *Forskalia formosa* showed that the animals were powerful swimmers. As they swam they rotated, usually in an anticlockwise direction, but sometimes clockwise and sometimes switching from one to the other. The cylindrical nectosome was narrower than the siphosome (figure 16); the latter, in some specimens, being about three times longer than the former. The siphosomal stem was clearly spiralled, but in such a way that the gastrozooids were arranged in four rows, which themselves had a slightly spiral arrangement.

***Forskalia tholoides* Haeckel, 1888**

(figures 24–32)

Forskalia tholoides Haeckel, 1888: 244–247, pls VIII–X.

Forskalia tholoides Bedot, 1893: 251.

Forskalia hydrostatica Schneider, 1898: 158.

Forskalia tholoides Moser, 1917: 737–740.

Forskalia tholoides Moser, 1925: 434–435, pl. XXXII, figures 1, 2.

Forskalia tholoides Kawamura, 1954: 106, pl. I, figures 1, 3–6.

Forskalia tholoides Totton, 1965: 108–109.

Forskalia tholoides Daniel, 1985: 116–117, figure 28.

Diagnosis. Nectophores bilaterally symmetrical, long and narrow, tapering apically, without axial wings. More or less pronounced lateral process. Nectosac in basal third. No *rete mirabile* in pedicular canal. Adult bracts of four types. Gonodendra with male gonophores overhanging female ones.

Paratype. The specimen collected near the surface of the Sargasso Sea by a scuba diver (position: 39°16'N, 65°30'W, date: 14 July 1979) is designated a paratype and has been donated to the Natural History Museum, London, where it is registered as BMNH 2001.6917.

Material examined. Thirty-two specimens collected by scuba divers in near-surface waters at various positions in the North Atlantic Ocean.

Description

A photograph of a whole specimen is shown in figure 24.

Pneumatophore: The pneumatophore measured up to 2.1 mm in height and 0.9 mm in diameter. It clearly bore a wide cap, dark red in colour, while the remainder of it was suffused with red pigmentation.

Nectophore (figure 25). The many hundreds of bilaterally symmetrical nectophores are arranged into a dome-shaped structure (figure 24). They were elongate, narrow and measured up to 8.5 mm in length and 3 mm in width. They tapered toward the apex and were without axial wings. More or less pronounced lateral processes, but no lateral patches of ectodermal cells. Basally, pairs of ridges were divided off on the upper and lower surfaces, which ended close to the ostium. Small baso-lateral pockets were formed between them. The nectosac occupied the basal third of the nectophore and there was a long pedicular canal. The ascending branch of the pallial canal was slightly longer than the descending one. There was a concentration of ectodermal cells on the ostium where the dorsal radial canal joined the ring canal. Other large cells were also present on the dorsal part of the ostium. Laterally, where the lateral radial canals joined the ring canal, there was a line of

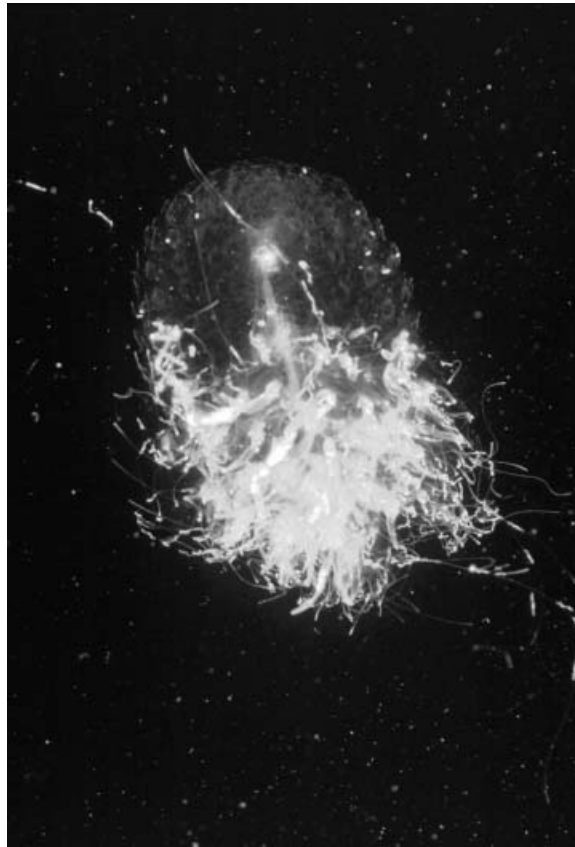


FIG. 24. *Forskalia tholoides*. Whole animal. Photograph courtesy of Larry Madin.

cells extending on to the velum, and another line extending laterally away from the ostium.

The small nectophores (figure 26) found with the post-larval specimens were not prolonged apically and the nectosac occupied about half their height. The two prominent lateral extensions lay close to the apex.

The mature nectophores often were infested with juvenile amphipods as was the case for the nectophores of *Forskalia edwardsi*. Up to five juveniles could be found in an individual nectophore, having bitten into any of the radial canals on the nectosac, or the pedicular canal.

Bract. The usual four types of bract were present in mature specimens, but some post-larvae possessed only larval bracts. The stem bracts (figure 27) occurred as almost enantiomorphic pairs. However, one form (figure 27A) was shorter than the other (figure 27B) and had a more extensive lateral process on the inner edge of the distal facet. In addition the degree of indentation of the basal facet was larger. The edges of the distal facet of both forms appeared serrate, but were made up of an irregular series of papillae which had two or more, large, darkly staining ectodermal cells at their apices. Papillae were also present on the distal facet itself; 20–30 on the form with the larger, deeper facet (figure 27A), but less on the other form (figure 27B). Additionally, a few papillae were found on the outer side of the bract

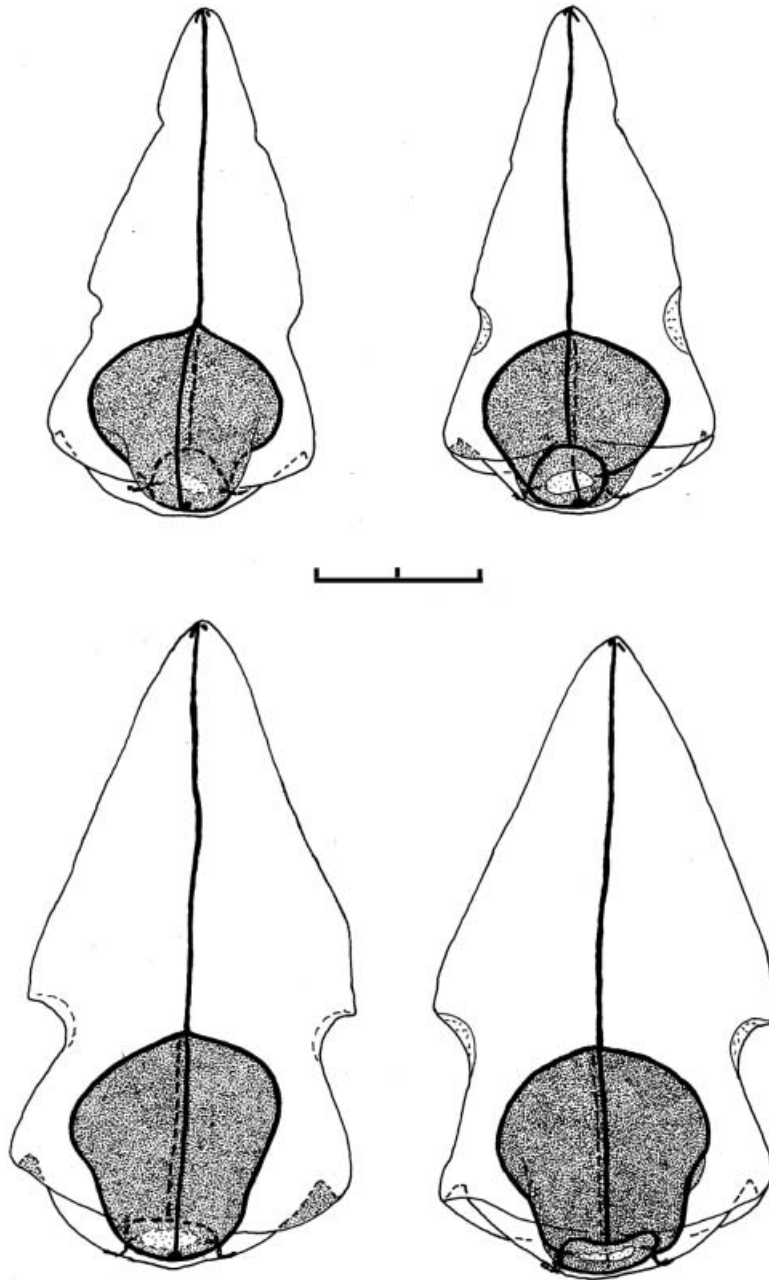


FIG. 25. *Forskalia tholoides*. Upper (left) and lower (right) views of mature nectophores. Scale 2 mm.

toward the distal end. In both forms the distal part of the bracteal canal was narrower than the proximal part, and it terminated in a small swelling.

The bolster bracts also occurred in almost enantiomorphic pairs (figure 28). However, one form (figure 28B) had a more pronounced taper, proximally, and had a more extensive ventro-lateral wing on its outer side. Both forms were triangular

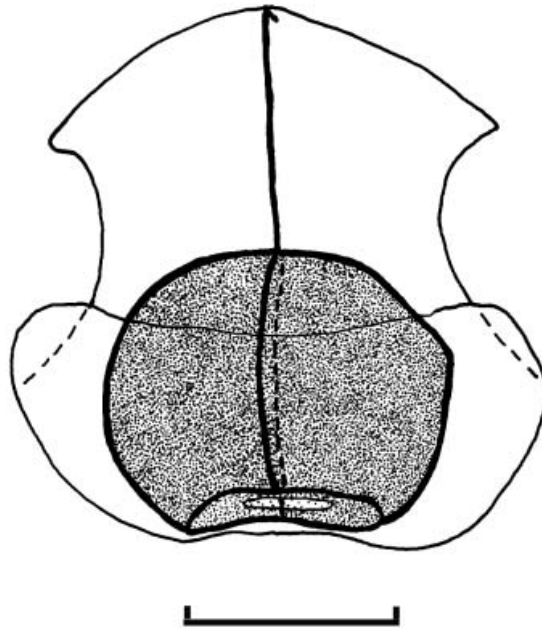


FIG. 26. *Forskalia tholoides*. Immature nectophore found on post-larval specimen. Scale 1 mm.

in cross-section. The bracteal canal became much thinner after it inflected into the mesogloea, but terminated in a small swelling. Again the edges of the distal facet were made up of an irregular series of small papillae with darkly staining ectodermal cells at their extremities. Papillae were also present on the distal facet itself. In addition, groups of darkly staining ectodermal cells were irregularly arranged along the dorsal and outer ventro-lateral edges, but no papillae were present.

There were two types of knee-shaped bracts; one occurred in enantiomorphic pairs (figure 29), the other with two slightly different forms (figure 30). The first type (figure 29) had an oblique distal facet on the outer side of the bract. There was a prominent distal cusp and large lateral cusps on either side distally, and a smaller cusp on either side proximally, close to dorsal edge. In addition there was another prominent cusp toward the distal end on the ventral side of the bract. On the inner surface of the bract the ventral wall curved up dorsally forming a small pocket. Papillae were present, particularly on the distal facet. The bracteal canal curved gently in its mid-region, and was distinctly narrower distally, apart from a terminal swelling.

The second type of knee-shaped bract (figure 30) also possessed a pocket on the inner surface ventrally. The outer margin of the distal facet in one form (figure 30A) was much more extensive than the inner one and had one prominent, and one or more indistinct, cusps. The inner margin had only one small cusp. On the other form (figure 30B) the outer margin of the distal facet was less extensive and bore several prominent cusps. Again, however, there was only a single small cusp on the inner margin. In both the bracteal canal bent through a right angle, with the distal part, apart from the terminal swelling, being thinner than the proximal part. Papillae were present on the outer surface in the distal part of the bract, and also on the distal facet itself.

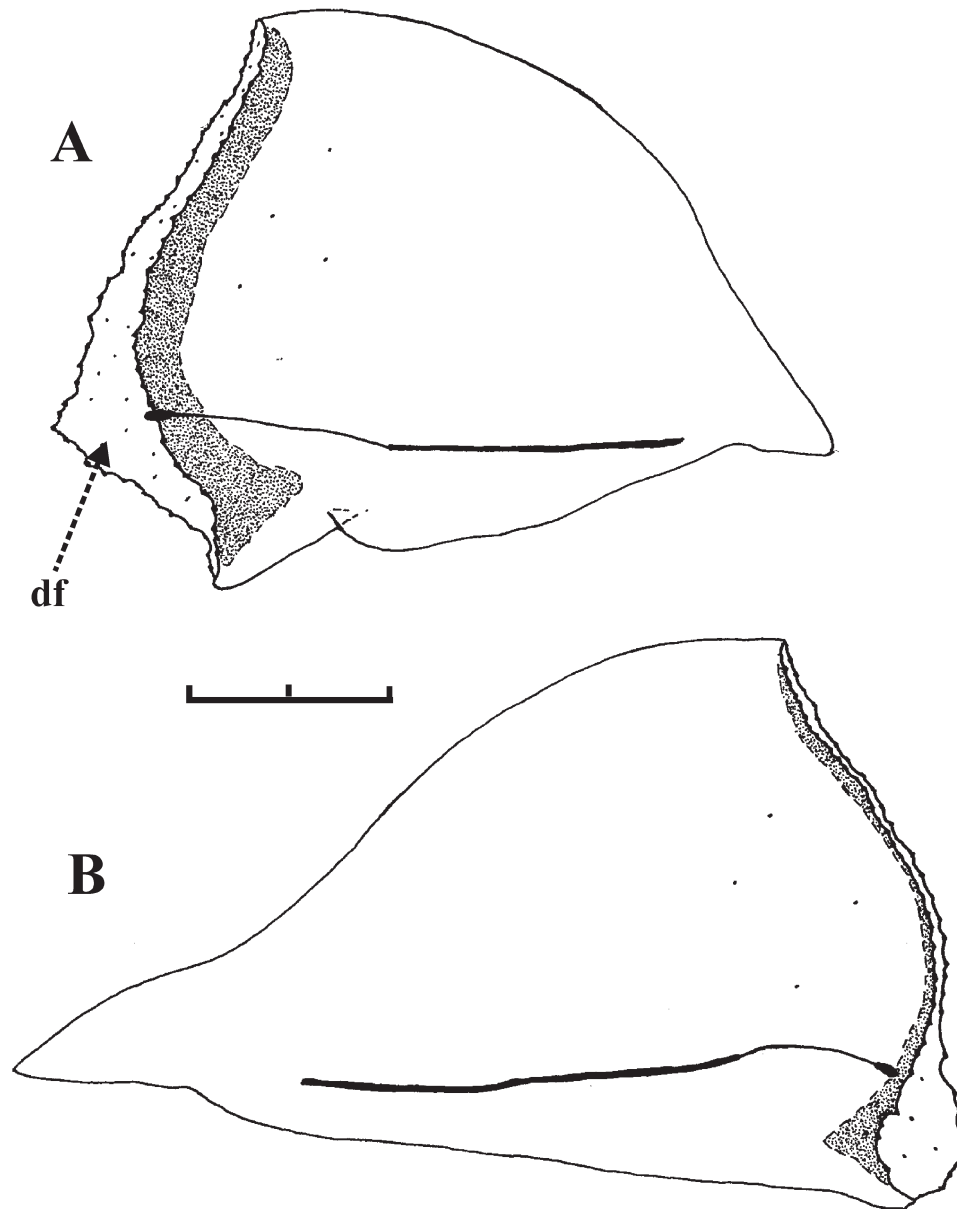


FIG. 27. *Forskalia tholoides*. (A, B) Outer views of stem bracts. Scale 2 mm. df, distal facet.

Over 20 larval bracts (figure 31) could be present on the young specimens. These were elongate structures, with the dorsal facet broadening distally and edged by an irregular series of small cusps. This facet partially overhung a smaller distal facet. The latter was also expanded ventrally and the bracteal canal curved down into it.

Gastrozoid and tentacle. The gastrozooids (figure 32) were borne on long pedicels. Each had only a relatively small basigaster, while the stomach and proboscis regions were extensive. Liver stripes were clearly visible in the latter regions, and probably were bright red-pigmented in life. Haeckel (1888) described a very precise

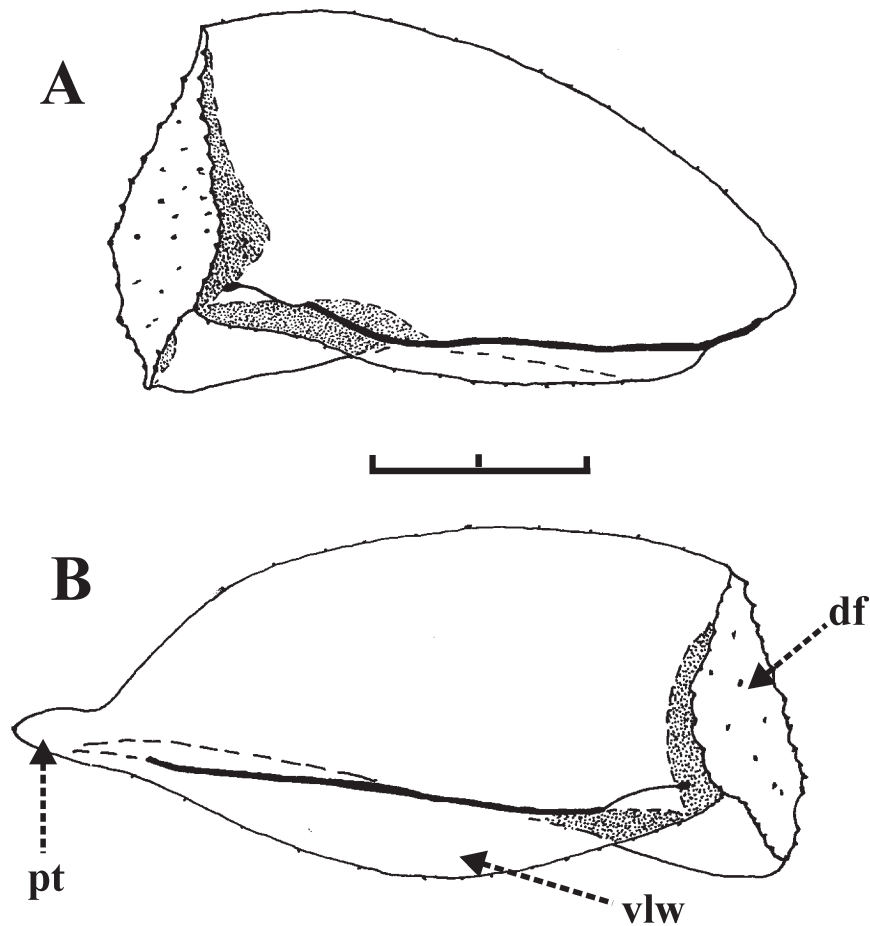


FIG. 28. *Forskalia tholoides*. (A, B) Outer views of bolster bracts. Scale 2 mm. df, distal facet; pt, proximal taper; vlw, ventro-lateral wing.

arrangement of these stripes, but this could not be verified in the present specimens. The red cnidobands of the tentilla had three to four loose spiral turns. The same types of nematocysts as found in the other *Forskalia* species were present.

The post-larval specimens of *Forskalia tholoides*, that bore the larval bracts and short nectophores, also possessed a larval-type tentacle very similar to the one described for *F. edwardsi* (Carré, 1967). Its tentilla had long pedicles surmounted by an acorn-like structure, with the proximal half devoid of nematocysts. There was a ring of stenoteles above this, and then a multitude of anisorhizas, and possibly some isorhizas.

Gonodendron (figure 32). The gonodendra bore at least four gonopalpons, each with a palpacle. The latter bore a series of swellings which, in the highly relaxed state, could give the appearance of a string of beads, although not as prominently as in *Forskalia edwardsi*. There were no nematocysts on the palpacle, but all types were found intermittently on the rather amorphous main body of the palpon. There was a concentration of nematocysts, particularly stenoteles, in the distal ampulla and mouth region, where large discrete cells also were found. As Haeckel (1888)

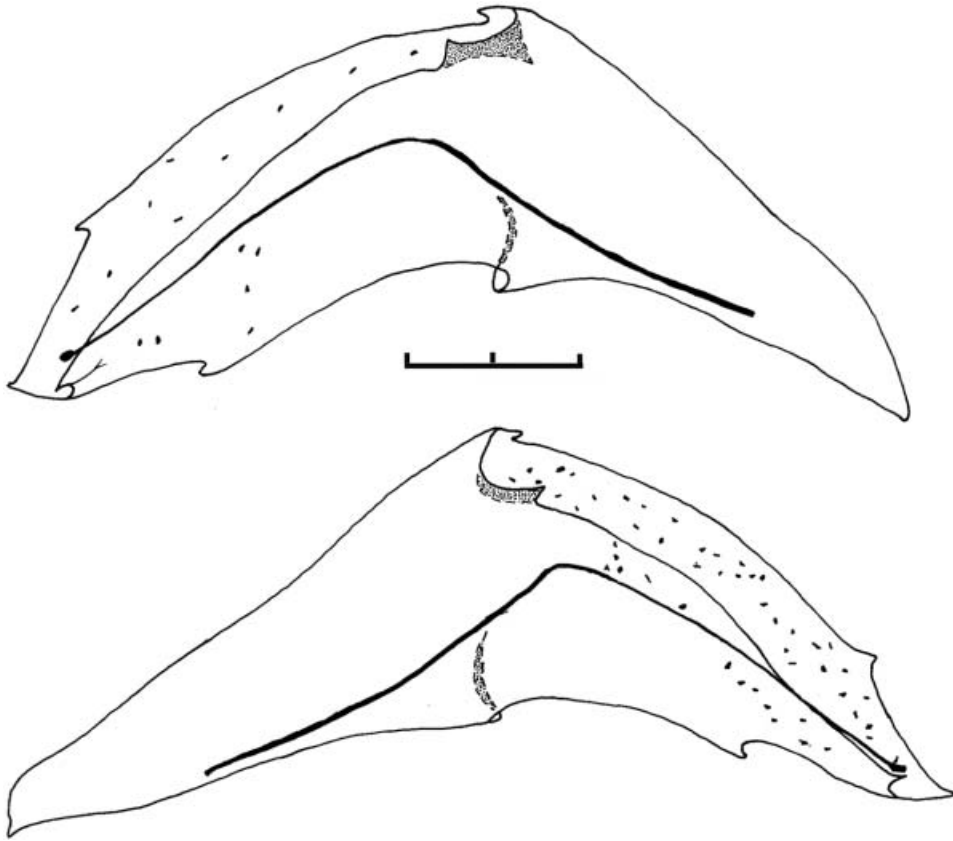


FIG. 29. *Forskalia tholoides*. Outer views of the first type of knee-shaped bracts. Scale 2 mm.

pointed out, the ampulla, in life, often is filled with a mass of red-pigmented granules, which can be discharged into the water if the animal is disturbed. It was not clear whether the female gonophores were in two bunches, but they were positioned proximal, with the male gonophores distal to them.

Distribution

Haeckel's (1888) original material of *Forskalia tholoides* was collected off Lanzarote in the Canary Islands. Since then the species has been recorded only rarely. Moser (1925) found it at *ca* 35°S, 74°E and off Natal (South Africa) in the Indian Ocean; and in the vicinity of the Tortugas off Florida. Daniel (1985) also recorded it in the Indian Ocean, from off the SE coast of India. Kawamura (1954) also briefly mentioned a specimen of *Forskalia tholoides* collected off Japan. He stated that the shape of the bracts agreed with that originally described by Haeckel (1888), but his illustrations show bracts that are very different. Thus one cannot be certain that Kawamura's identification is correct.

In recent years, several specimens have been collected by scuba divers in various parts of the North Atlantic Ocean, particularly the Sargasso Sea and Gulf Stream (Biggs, 1977; Harbison *et al.*, 1977; Purcell, 1980, 1983; present material) or in the Gulf of California (Purcell, 1980). *Forskalia tholoides* also has been identified from

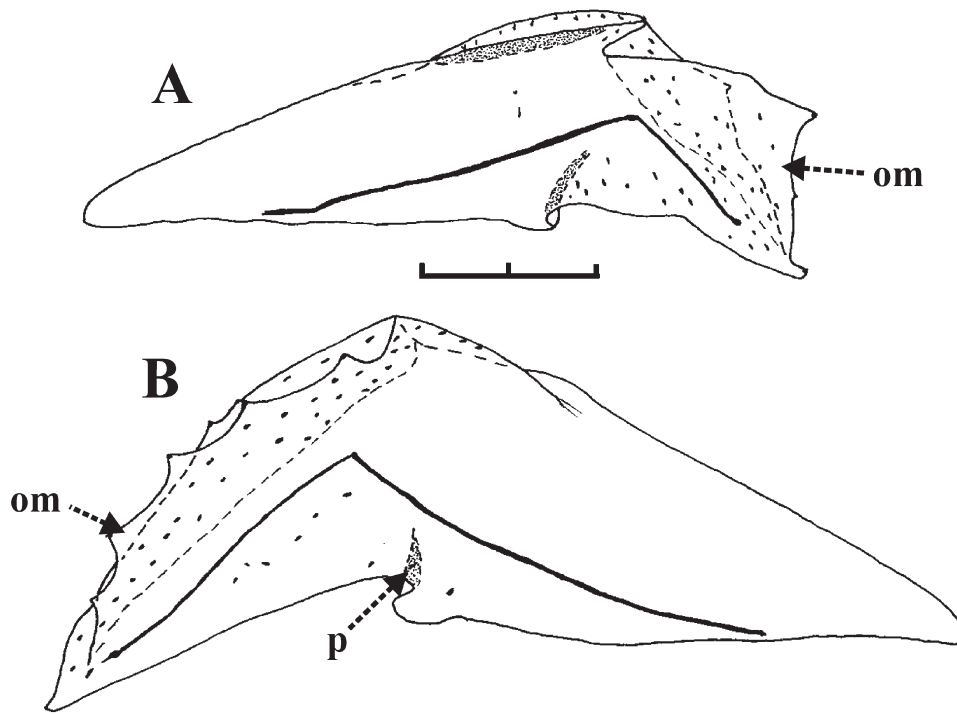


FIG. 30. *Forskalia tholoides*. (A, B) Outer views of second type of knee-shaped bract. Scale 2 mm. om, outer margin of distal facet; p, pocket.

recent *Discovery* collections at six stations in the NE Atlantic between the equator and 44°N, generally at shallow depths. Some specimens also have been identified in the collections of Harbor Branch Oceanographic Institution that were collected by the JSL submersibles, but again only at shallow depths (<100 m).

Remarks

Totton (1965) considered *Forskalia tholoides* to be a doubtful species based on a 'beautiful idealized figure'. However, if one compares Haeckel's (1888) plate VIII with figure 24 one can see that there is a great deal in common, particularly the dome-shaped nectosome. As noted above, there are some slight differences between his description of the pneumatophore and the gastrozooids from that found in the present material. However, these are of no significance. There are also some differences in the bracts, particularly the knee-shaped ones. His illustrations (plate X, figures 17, 18) of these appear a little fanciful, although one can see similarities to the present material. Nonetheless, from Haeckel's drawings of the nectophores, there can be no doubt that we are dealing with the same species. *Forskalia tholoides* is the only known forskaliid that has apically tapering bilaterally symmetrical nectophores, with no axial wings.

Forskalia asymmetrica sp. nov.

(figures 33–39)

Diagnosis. Large nectophores, with small rounded left axial wing, and small central apical incision. No lateral incisions or pockets. No *rete mirabile*. Adult bracts

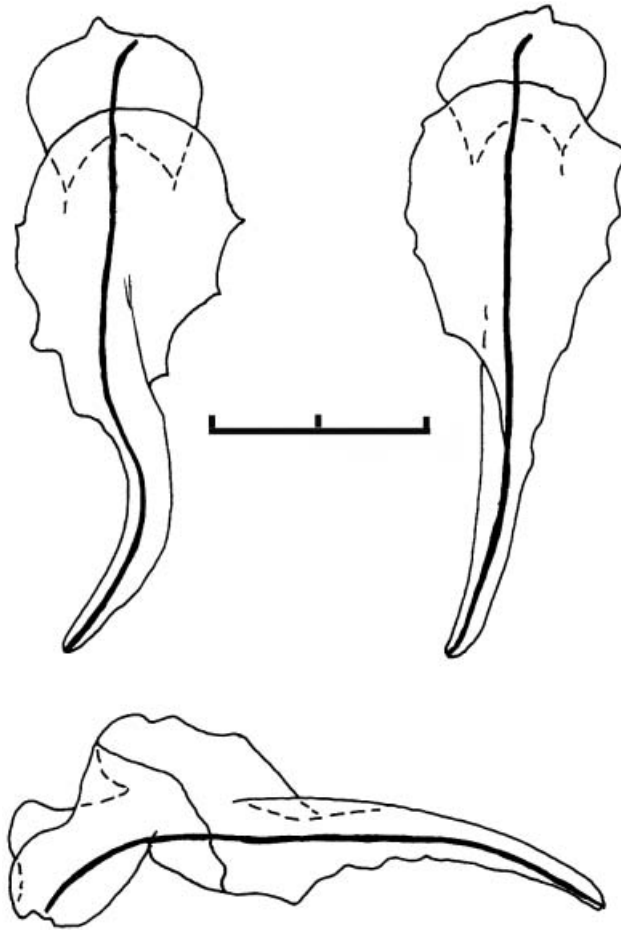


FIG. 31. *Forskalia tholoides*. Larval bracts. Scale 2 mm.

of four types. Gonodendra bearing long gonopalpons, with palpacles; with female gonophores attached close to their bases. Male gonophores attached at end of a stalk.

Holotype. The specimen from JSL I dive 2929 (position: 35°29.1'N, 4°26.4'W; date: 6 April 1991; depth: 432 m) is designated the type and has been donated to the Natural History Museum, London, where it is registered as BMNH 2001.6918.

Material examined. Thirteen of the 15 known specimens collected by JSL submersibles.

Description

A photograph of a specimen that has lost most of its siphosome is shown in figure 33.

Pneumatophore. Measuring *ca* 2.2 mm in height and 0.8 mm in diameter. The walls were suffused with an orange colour throughout, usually with an apical cap of orange-red pigmentation. After preservation such pigmentation was lost.

Nectophore (figure 34). Large nectophores that measured up to 13 mm in length and 15 mm in width. The mature ones were very flimsy and easily damaged. There

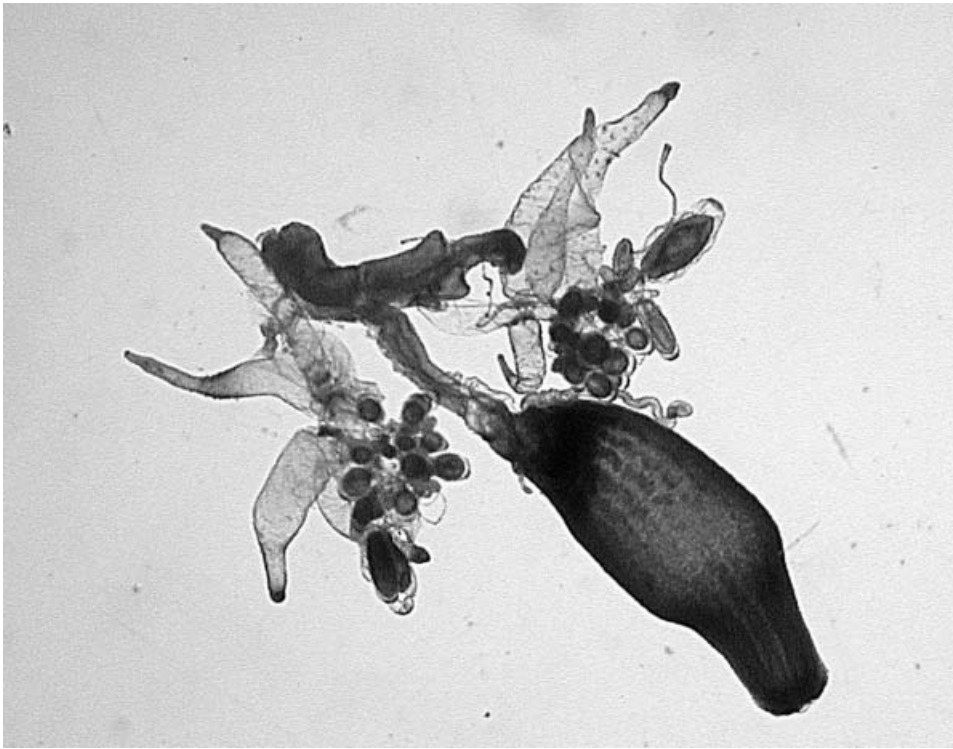


FIG. 32. *Forskalia tholoides*. Piece of siphosomal stem, with gastrozoid (4.6 mm in length, including peduncle) and two gonodendra.

was a small central apical incision, and the rounded left axial wing was only slightly pronounced. Its inner margin extended for a short distance on to the upper surface of the nectophore. There were no lateral incisions or pockets. In the basal half of the nectophore, there was a lateral facet defined by two weak ridges that petered out, on the upper and lower surfaces, close to the ostium. Occasionally the upper ridge overhung the lateral facet. At the apex of this facet, in the youngest nectophores (figure 34D), there were two small patches of ectodermal cells; presumed to be sites of bioluminescence. These were not seen on the larger nectophores; presumably having been abraded off.

The nectosac occupied most of the basal half of the nectophore. It was highest in the mid-line, but only sloped slightly toward the apico-lateral margins. The pedicular canal did not contain a *rete mirabile* and, as in some other species, on reaching the nectosac usually only branched off the lateral radial canals. The dorsal canal then arose from the left lateral, and the ventral canal from the right lateral. Along the dorsal margin of the ostium a row of large, but variably sized, ectodermal cells overlaid the ring canal. On each side a narrow band of cells extended laterally for a short distance. The pallial canal had a relatively long descending branch, although it was slightly shorter than the ascending one. The lower nerve tract, that extended from the end of the descending branch down to the ostium was particularly obvious after staining but, for clarity, has not been illustrated.

Bract. Four types of bract were found. The stem bracts (figure 35) occurred in pairs, which were by no means enantiomorphs. Both kinds had an incomplete ridge



FIG. 33. *Forskalia asymmetrica*. Photograph of live specimen.

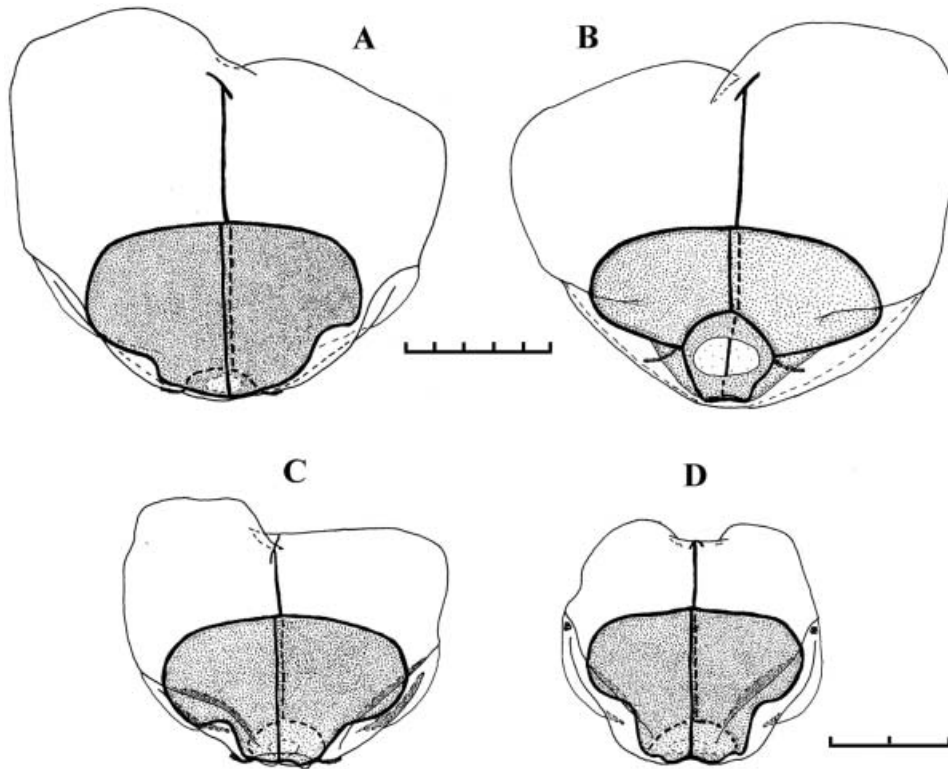


FIG. 34. *Forskalia asymmetrica*. (A) Upper and (B) lower views of mature nectophore; (C) upper view of younger nectophore. Scale 5 mm. (D) Upper view of developing nectophore. Scale 2 mm.

on the outer side, close to the distal end. In one kind (figure 35, left) the distal end was more or less roundly truncated, while in the other (figure 35, right) it was prolonged and thickened into a process with more or less pronounced cusps laterally, and centrally. In the latter kind the bracteal canal extended beyond the cross ridge.

Bolster bracts again occurred in non-enantiomorphic pairs, but both with slightly concave distal facets. One kind (figure 36, right) was shaped like an isosceles triangle in cross-section, and was thickened with mesogloea throughout. A cusp was occasionally found on the ventro-lateral margin of the distal facet, on the inner side. There were two lateral flaps ventrally which enclosed a gutter of variable depth. The bracteal canal ran along the ventral margin of the central region of the flap on the left-hand (inner) side, and distally was inflected, at an angle of *ca* 45°, for a short distance into the mesogloea. The other kind (figure 36, left) was only thickened distally, and had only a single ventro-lateral flap, on the left-hand (outer) side. However, the bracteal canal did not run along its margin, but at its base. Proximally, this canal curved up and ran along that margin for a short distance. Distally, it curved up into the mesogloea and continued for a variable distance, but always further than in the other kind, toward the distal end of the bract. These bracts were presumed, as in *Forskalia edwardsi*, to have been attached at the base of the peduncle of the gastrozoid.

There were two types of knee-shaped bracts, both of which occurred in

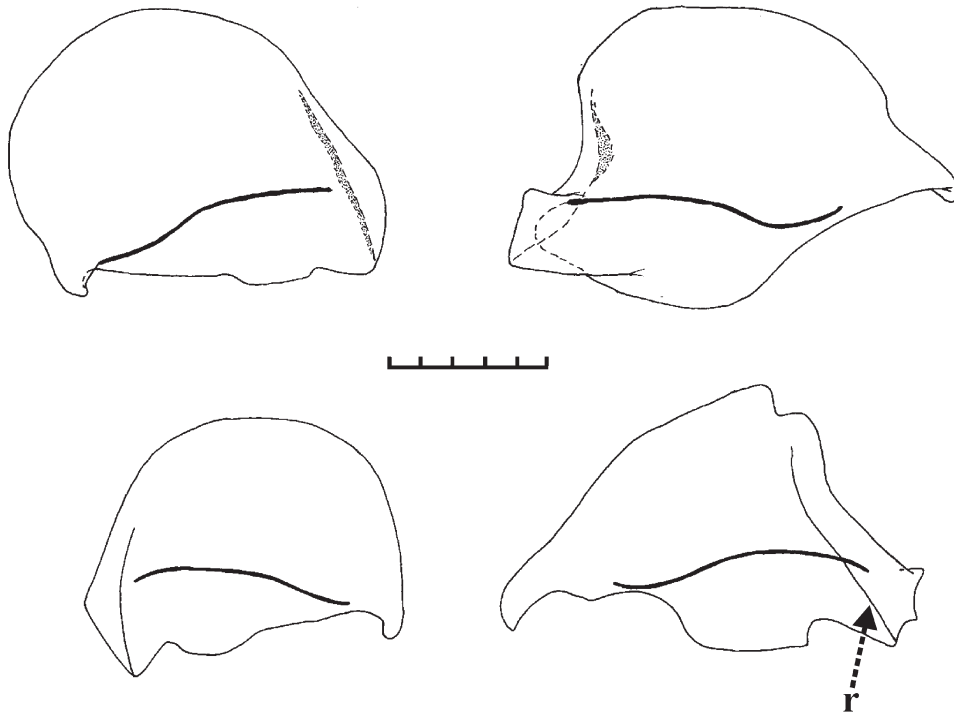


FIG. 35. *Forskalia asymmetrica*. Inner (top) and outer (bottom) views of stem bracts. Scale 5 mm. r, ridge.

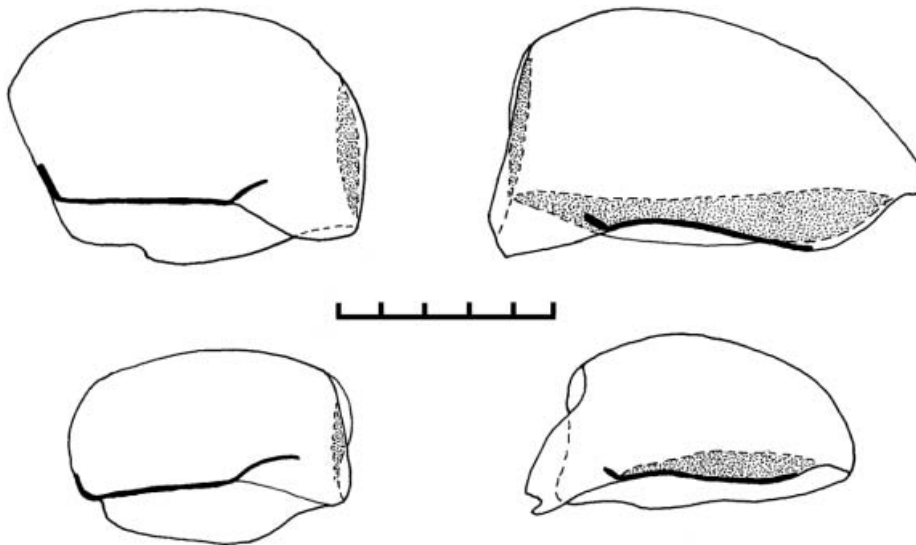


FIG. 36. *Forskalia asymmetrica*. Inner views of bolster bracts. Scale 5 mm.

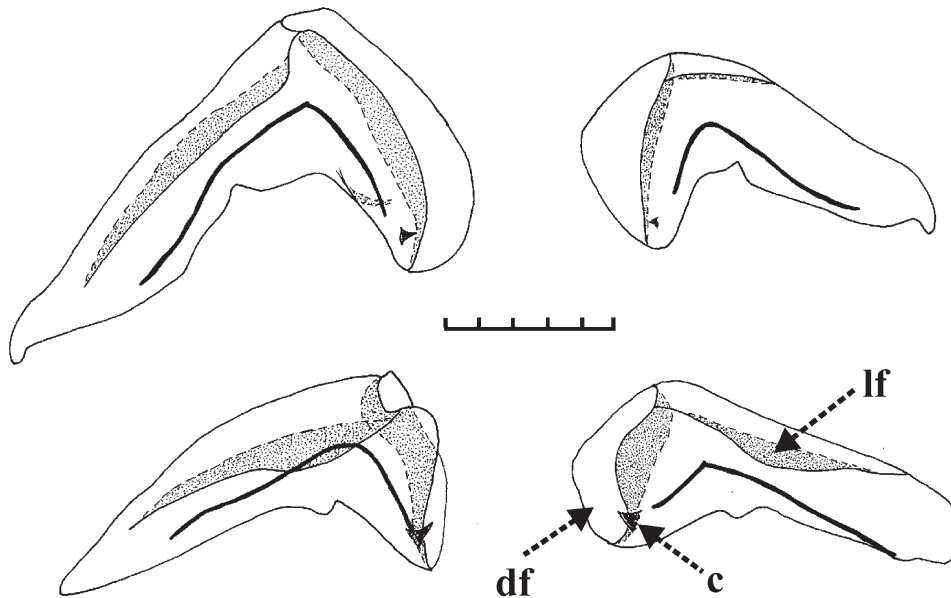


FIG. 37. *Forskalia asymmetrica*. Inner views of first type of knee-shaped bract. Scale 5 mm. c, cusp; df, distal facet; lf, lateral flap.

enantiomorphic pairs. The first type (figure 37) had a broad, concave distal facet, and a more or less pronounced lateral flap along its inner side. There was a cusp just proximal to the baso-lateral margin of the distal facet, on the inner side. The sharpness of the bend in the bracteal canal was variable, but occasionally, when it was close to a right angle, there was a small protuberance, but no distinct branch canal. The canal remained in close contact with the surface of the bract throughout its length.

The structure of the second type of knee-shaped bract (figure 38) varied according to its size. The smaller, younger bracts were thin with a broad, notched lateral flap overhanging the upper part of the inner surface, and two prominent cusps distally. There was a distinct, but short, cross ridge on the upper surface, and another flap that extended from below this obliquely down toward the distal end, on the outer surface of the bract. In older bracts both these features became less distinct. Also the proximal part of the lateral flap began to merge with the main body of the bract, which became thickened in that region. Meanwhile, the distal part of the flap opened out to form part of the main body of the bract, with its distal margin having a more or less pronounced cusp. The curved bracteal canal did not have a pronounced bend.

Gastrozoid and tentacle. The gastrozoid showed no specific characters. It was borne on a long peduncle, which, even in its contracted state, measured up to 4.5 mm in length. Numerous bracteal lamellae were attached along its length. The saddle-shaped basigaster was long and expanded. Obvious liver stripes were present in the stomach region. These were orange-coloured toward the mouth, but basally the density of pigmentation increased so that they appeared deep red close to the basigaster. The tentacle was annulated. The cnidobands were a pale orange colour in life and consisted of about six loose coils. The types of nematocysts were the same as in other *Forskalia* species.

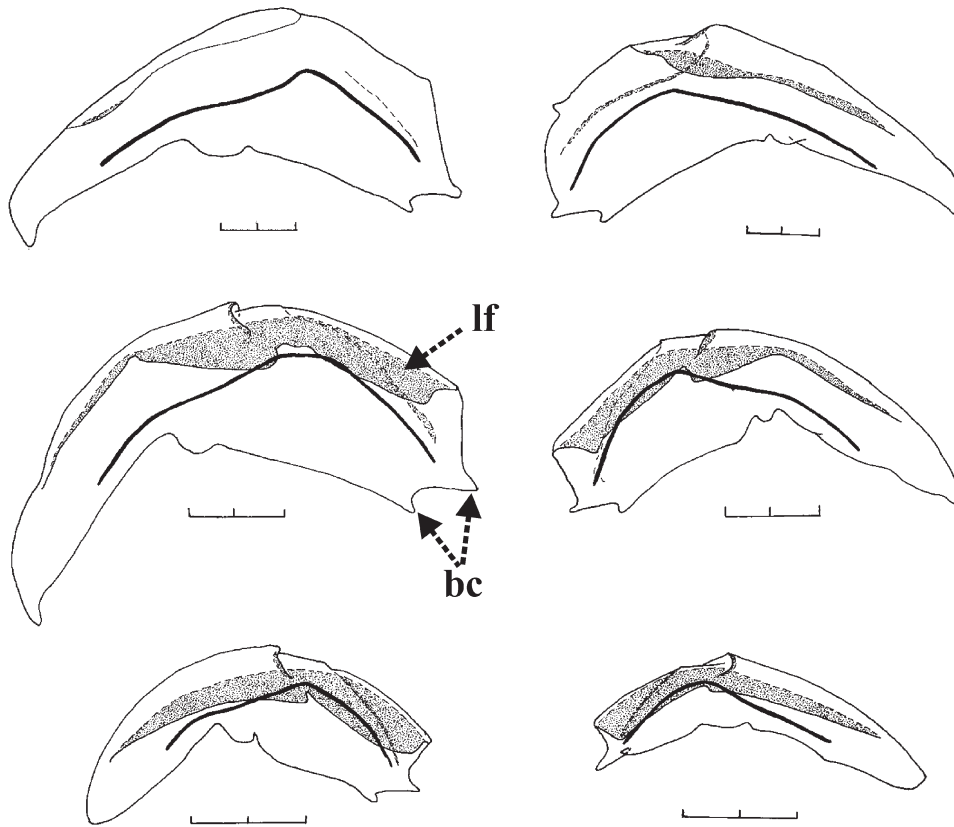


FIG. 38. *Forskalia asymmetrica*. Inner views of second type of knee-shaped bract. Scale 2 mm.

Gonodendron (figure 39). The gonodendra bore very long gonopalpons, measuring up to 13 mm in length, in their preserved state. At the base of each palpon was a small cupulate process to which the palpacle was attached, although for many palpons the latter had broken off close to its base. The palpacle was a simple structure, not like a string of beads, and no nematocysts were found associated with it. However, in the mouth region of the palpon numerous small nematocysts, probably acrophores, were present. Below this, in the region of the ampulla, which was quite distinct in some examples, the surface of the palpon was covered in large, scale-like ectodermal cells. In life the ampulla could contain a bright red fluid. The remaining surface of the palpon appeared quite amorphous.

A maximum of three gonopalpons were found associated with each gonodendron, although it is likely that more could be developed as the gonodendra enlarged. Two clusters of female gonophores were attached close to the base of the palpons, while the male gonophores were borne on a long stalk.

Distribution

A total of 15 specimens are known to have been collected by the JSL submersibles, two of which were not re-examined during the present study. Eight of these came from the vicinity of the Bahamas (ca 25–26°N, 77°W); three from the Alborán Sea



FIG. 39. *Forskalia asymmetrica*. Gonodendron. Length of longest palpon 3.1 mm.

(western Mediterranean, ca 35°N, 3–4°W); and four from the canyons off Woods Hole (USA, ca 40°N, 70°W). The specimens were collected at depths between 191 and 823 m, with a mean depth of 598 m.

Remarks

The nectophores of this species are distinguished from those of other *Forskalia* species by the smallness, but broadness, of the left axial wing, and the absence of lateral indentations or baso-lateral pockets. The gonodendra, with the male gonophores borne on a long stalk overhanging the female gonophores, resembles that of *Forskalia formosa*. However, in the *F. formosa* the male gonophores appear to be attached along the length of the stalk, while in *F. asymmetrica* they are attached at its end.

In situ videos of *Forskalia asymmetrica* showed that both the nectophores and the cormidia on the siphosome were obviously arranged into a spiral, with the gastrozooids held well away from the stem. The gastrozooids also appeared to be arranged in rows, which themselves were slightly spiralled.

Etymology

The species name *asymmetrica* is chosen to represent the asymmetric shape of the nectophores.

Forskalia saccula sp. nov.

(figures 40, 41)

Diagnosis. Small nectophores, with extensive (up to 30% of total length), pointed left axial wing, and no central apical incision. Deep lateral basal pockets. No *rete mirabile*. Extensive nectosac, highest at apico-lateral margins. Four types of adult bract; with canal of knee-shaped type having right-angled bend, but without side branch.

Material examined. A single, young, specimen collected by a scuba diver close to the surface in the Sargasso Sea (position: 31°45'N, 71°49'W; date: 21 June 1979). This specimen is designated the holotype and the specimen has been donated to the Natural History Museum, London, where it is registered as BMNH 2001.6919.

Description

Pneumatophore. Small pneumatophore that measured *ca* 1.2 mm in height and 0.45 mm in diameter. There was some obvious dark red pigmentation at its apex.

Nectophore (figure 40). Twenty-nine nectophores, plus some buds, were found with the specimen. They were small, measuring up to 3.1 mm in length and 3.4 mm in width. No apical incision at median point of attachment to stem, but with large (*ca* 30% of total length) and pointed left axial wing. The inner margin of this wing extended down on to the upper surface of the nectophore, ending just above the apex of the nectosac. Very deep incision on right-hand side, while on the left-hand side the lateral margin was emarginated. Small patches of ectodermal cells, probably producing bioluminescence, were present slightly basal to those regions. These patches were often abraded. Two deep lateral basal pockets that did not extend toward the ostium as flaps.

The nectosac was extensive and highest at its apico-lateral margins. The pallial canal had a short descending branch and a longer ascending one. There was no *rete mirabile* in the pedicular canal. The latter, on reaching the nectosac usually gave off the two lateral and the dorsal radial canals, although the origin of the dorsal one sometimes was slightly displaced on to the left radial canal. The ventral canal usually

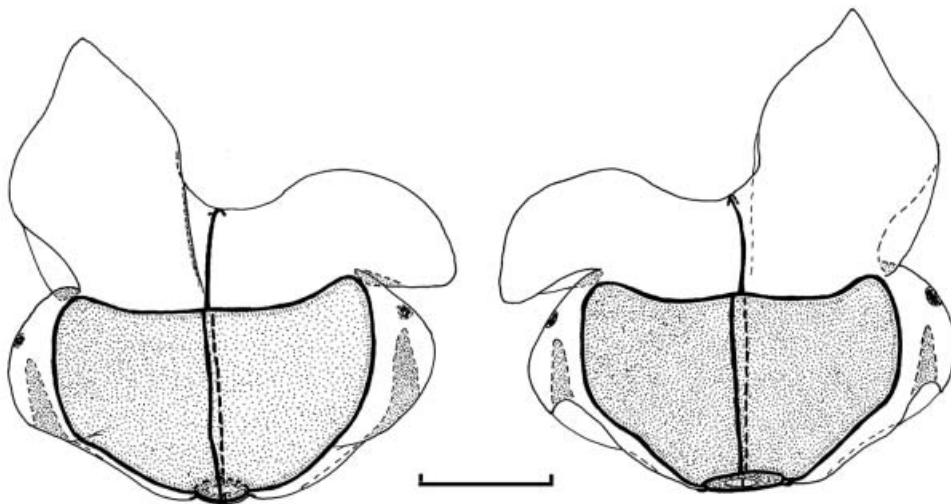


FIG. 40. *Forskalia saccula*. Upper (left) and lower (right) views of nectophore. Scale 1 mm.

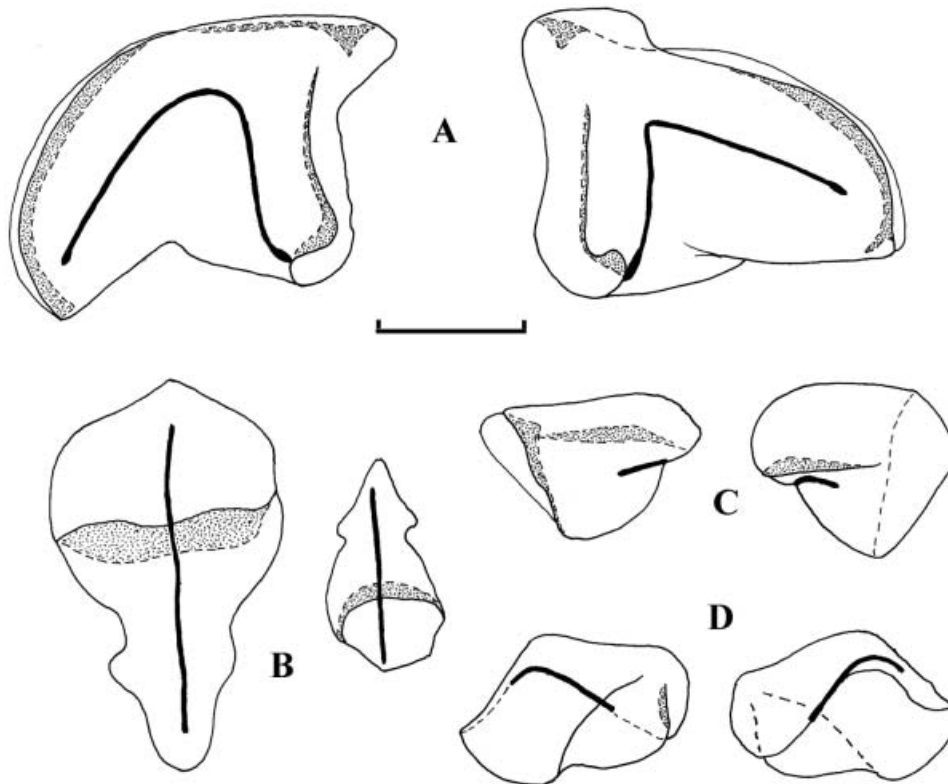


FIG. 41. *Forskalia saccula*. Bracts: (A) inner views of two knee-shaped bracts; (B) upper views of two of second type; (C) outer (left) and inner (right) views of third type; (D) outer (left) and inner (views) of single bract of fourth type. Scale 1 mm.

arose from the right radial canal, a short distance from the insertion of the pedicular canal. Two small concentrations of ectodermal cells extended laterally away from the ostium, slightly below its mid-height. In addition, a row of large ectodermal cells was present along the velum, close to the ostial ring canal, on the lower side of the ostium.

Bract (figure 41). Only 32 bracts were found with the specimen, and it was not possible to determine their disposition. They were of four kinds of which by far the commonest, 22 in all, were those of the knee-shaped kind (figure 41A) which occurred as enantiomorphic pairs. However, only the bracteal canal was knee-shaped; bending, roundly or abruptly, through a right angle, but without a side branch. There were small pockets at both ends of the dorsal facet. It is presumed these bracts were attached to the peduncle of the gastrozoid.

There were five bracts, that probably were attached to the stem, which had a convex appearance in lateral view (figure 41B). There was a cross ridge on the upper surface which slightly overhung the more distal part of the bract. The third type (figure 41C), four only, were more akin to the bolster bracts of *Forskalia edwardsi*, and had a very short bracteal canal. Only one of the fourth type of bract (figure 41D) was found. It was asymmetrical, with a canal much longer than that of the previous type.

Gastrozoid and tentacle. Only seven gastrozooids were found with the specimen, which showed no specific characters. Their peduncles were highly contracted. They had long, usually narrow, basigasters and obvious hepatic stripes in the stomach region. Tentacle with no obvious annulations, although there was little material to examine. Tentilla with short pedicle and about four turns to the loosely spiralled cnidoband; with long terminal filament. The types of nematocysts present were not investigated.

Gonodendron. Fourteen palpons, with palpacles, were found with the specimen, but the gonodendra were very immature and the arrangement of the male and female gonophores could not be determined.

Distribution

Known only from a single specimen collected close to the surface in the Sargasso Sea.

Remarks

The nectophores of *Forskalia saccula* bear a superficial resemblance to those of *F. contorta*, particularly the large left apical wing and the lateral incision on the right-hand side, but they are much smaller. In addition, the nectosac is proportionally much larger, and there were no baso-lateral flaps on the lower surface. Instead, there were very distinctive, deep baso-lateral pockets.

The bracts are also quite different from those of *Forskalia contorta*, although in both species there appears to be only one type of knee-shaped bract. In *F. saccula* it is only the bracteal canal that is knee-shaped, and it has no side branch. It is possible, because of the smallness and apparent youngness of the specimen, that one of the other types of bracts (figure 41B) may be of the larval type, but without further specimens this cannot be confirmed.

Etymology

The species is named for the small pouch-like baso-lateral pockets on the nectophores; derived from the Latin *sacculus*.

Species inquirenda

Forskalia cuneata Chun, 1888

Chun's (1888) description of his specimen(s), collected in the vicinity of the Canary Islands, was brief and there were no illustrations. He stated that the subumbrella of the nectophore had four to six intense crimson pigment stripes on each side. The gastrozooids were remarkably large, and arranged in distinct right-hand spirals. Their liver stripes were red-brown in colour. The cnidobands of the tentilla were bright red. The bracts were wedge-shaped, with their outer margins truncated at a right angle. They entirely filled the interstices between successive spiral turns of the siphosome. The bracteal canal had a right-angled bend. The larval tentacle bore acorn-shaped tentilla, with numerous short sensory hairs.

Of these characters, the only one that would appear to have any specific significance is the presence of the pigment stripes on the nectophore. However, this may

only represent an intraspecific variation, as Schneider (1898) suggested, as is the case for the *rete mirabile* in the nectophores of *Forskalia contorta*. Totton (1965) illustrated some bracts that he thought might possibly belong to this species. However, subsequently Mackie *et al.* (1987) and Pugh (1998) have shown that they actually belong to *Frillagalma vityazi* Daniel, 1966. The name, *Forskalia cuneata*, also appeared in a list of species from the South China Sea (Zhang and Lin, 1997), but the source of their information is not clear. It may be a reference to the bracts as described by Totton, although these were collected off Somalia (00°06'S, 49°45.4'E).

As no specimens that meet the description of this species have been collected by scuba divers or submersibles, or found in recent *Discovery* collections, it is concluded that *Forskalia cuneata* must continue to be considered as doubtful.

Forskalia misakiensis Kawamura, 1954

Kawamura's (1954) description of *Forskalia misakiensis* also was very brief, but did include a photograph and some illustrations. The adult nectophores were said to be quadrangular, 7–8 mm in length and 8–9 mm in width; with a relatively small nectosac. The illustration, indeed, shows an almost square nectophore, with no axial wings or apical incision. The other main character described was that the bracts were 'lobate or spoon-shaped, with smooth margins, no denticulation at all'. The illustrations show them to be quite unlike any bract found in other *Forskalia* species. The tentillum was said to be simple, with the cnidoband spiralled, and a long, slender terminal filament. He also illustrated a cormidium, showing a gastrozoid and a gonophore, but there is nothing to distinguish it. The single specimen was collected in Aburatsubo Bay, Japan.

The specimen is known to still exist and has been re-examined by Dr Francesc Pagès (in press), who informs me that Kawamura's description is inaccurate and that the poor state of preservation of the specimen means that there are insufficient characters to distinguish it from other *Forskalia* species.

Discussion

Although there are specific differences in the shapes of the bracts, these would be difficult to discern in poorly preserved material, and might be difficult to use as the basis for a specific identification. However, the presence of a side branch to the bracteal canal of the singular type of knee-shaped bract in *Forskalia contorta* does make this species easily distinguishable. There are also differences in the structure of the gonodendra of the various species. *Forskalia contorta* is the only known species where the two bunches of female gonophores have been found to greatly overhang the male ones. The reverse situation pertains in both *F. formosa* and *F. asymmetrica*. In the former, the male gonophores were attached all along a long stalk, while in the latter they were attached at its end. These may be specific differences, but more material is needed to verify this. For the other species, although the arrangement in *F. saccula* has not been elucidated, there appear to be no specific differences in the structure of the gonodendron. However, the bead-like appearance of the palpacle in *F. edwardsi* is quite characteristic.

It appears that the best character to distinguish the species of *Forskalia* is the structure of the nectophore. A key to their identification is given below, not including the *species inquirenda*:

- 1 Nectophore elongate bilaterally symmetrical, without axial wings. *Forskalia tholoides*
- Nectophore asymmetrical, with more or less developed left axial wing 2
- 2 Nectophore with small left axial wing 3
- Nectophore with extensive left axial wing 4
- 3 Nectophore elongate, with small, narrow left axial wing. Yellow pigment spot, dorsally,
on ostium *Forskalia edwardsi*
- Nectophore with broad, but shallow left axial wing. No yellow pigment spot, dorsally,
on ostium *Forskalia asymmetrica*
- 4 Nectophore with no baso-lateral pockets *Forskalia formosa*
- Nectophore with baso-lateral pockets present 5
- 5 Nectophores large, with extensive baso-lateral pockets, extending as flaps toward
ostium; shallow nectosac *Forskalia contorta*
- Nectophores small, with discrete, deep baso-lateral pockets, not extending toward
ostium; extensive nectosac *Forskalia saccula*

References

- BEDOT, M., 1893, Revision de la famille des Forskaliidae, *Revue Suisse de Zoologie*, **1**, 231–254.
- BIGGS, D. C., 1977, Field studies of fishing, feeding, and digestion in siphonophores, *Marine Behaviour and Physiology*, **4**, 261–274.
- CARRÉ, D., 1967, Etude du développement larvaire de deux Siphonophores: *Lensia conoidea* (Calycephorae) et *Forskalia edwardsi* (Physonecte), *Cahiers de Biologie Marine*, **8**, 233–251.
- CHUN, C., 1888, Bericht über eine nach den Canarischen Inseln im Winter 1887/88 ausgeführte Reise, *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften*, **1888**, 749–781.
- CLAUS, C., 1863, Neue Beobachtungen über die Structur und Entwickelung der Siphonophoren, *Zeitschrift für Wissenschaftliche Zoologie*, **12**, 536–563.
- DANIEL, R., 1985, Coelenterata: Hydrozoa Siphonophora, *The Fauna of India and Adjacent Countries* (Zoological Survey of India), 440 pp.
- FEWKES, J. W., 1882, Notes on the Acalephs from the Tortugas, with a description of new genera and species, *Bulletin of the Museum of Comparative Zoology at Harvard College*, **9**, 251–289.
- GRIMMELIKHUIJZEN, C. J. P., SPENCER, A. N. and CARRÉ, D., 1986, Organization of the nervous system of physonectid siphonophores, *Cell and Tissue Research*, **246**, 463–479.
- 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.
- HARBISON, G. R., BIGGS, D. C. and MADIN, L. P., 1977, The associations of Amphipoda Hyperiidea with gelatinous zooplankton, II. Associations with Cnidaria, Ctenophora and Radiolaria, *Deep-Sea Research*, **24**, 465–488.
- KAWAMURA, T., 1954, A report on Japanese siphonophores with special references to new and rare species, *Journal of the Shiga Prefectural Junior College, Series A*, **2**, 99–129, 7 pls.
- KEFERSTEIN, W. and EHLERS, E., 1860, Auszug den Beobachtungen über die Siphonophoren von Neapel und Messina angestellt im Winter 1859/60, *Nachrichten von der Georg-Augusts Universität und der Königlichen Gesellschaft der Wissenschaften zu Göttingen*, No. 23, 254–262.
- KEFERSTEIN, W. and EHLERS, E., 1861, Beobachtungen über die Siphonophoren von Neapel und Messina, *Zoologische Beiträge Gesammelt im Winter 1859/60 in Neapel und Messina* (Leipzig: Wilhelm Engelmann), 34 pp.
- KÖLLIKER, A., 1853, *Die Schwimmpolypen oder Siphonophoren von Messina* (Leipzig: Wilhelm Engelmann), 28 pp.
- LELOUP, E., 1935, Les siphonophores de la rade de Villefranche-sur-Mer (Alpes Maritimes, France), *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **11**(31), 11 pp.

- LELOUP, E., 1936a, Siphonophores calycophorides (suite) et physophorides provenant des campagnes du Prince Albert 1er de Monaco, *Résultats des Campagnes Scientifiques accomplies par le Prince Albert I. Monaco*, **93**, 1–36.
- LELOUP, E., 1936b, Siphonophores récoltés dans la région de Monaco, *Bulletin de l'Institut Océanographique*, No. 703, 15 pp.
- LELOUP, E., 1956, Siphonophores Calycophorides de la Baie de Nhatrang-Cauda, *Bulletin de Muséum*, **28**, 474–475.
- LENS, A.D. and VAN RIEMSDIJK, T., 1908, The Siphonophora of the Siboga Expedition, *Siboga-Expeditie (Siboga Expedition)*, **9**, 1–130.
- LESSON, R.-P., 1843, *Acalèphes. Histoire Naturelle des Zoophytes* (Paris: Librairie Encyclopédique de Roret), pp. 1–596.
- LEUCKART, R., 1853, *Zoologische Untersuchungen, I. Die Siphonophoren*, 95 pp. + 3 pls.
- LEUCKART, R., 1854, Zur nähern Kenntniss der Siphonophoren von Nizza, *Archiv für Naturgeschichte*, **20**, 249–377.
- MACKIE, G. O., PUGH, P. R. and PURCELL, J. E., 1987, Siphonophore biology, *Advances in Marine Biology*, **24**, 97–262.
- MILLS, C. E., PUGH, P. R., HARBISON, G. R. and HADDOCK, S. H. D., 1996, Medusae, siphonophores and ctenophores of the Alborán Sea, south western Mediterranean, *Scientia Marina*, **60**, 145–163.
- 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, Ser. 2*, **16**, 193–232.
- MOSER, F., 1917, Die Siphonophoren der Adria und ihre Beziehungen zu denen des Weltmeeres, *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse, Wien*, **126**, 703–763.
- MOSER, F., 1925, Die Siphonophoren der Deutschen Südpolar-Expedition, 1901–03, *Deutsche Südpolar-Expedition*, **17** (zool 9), 1–541.
- PAGÈS, F., The status of three rare siphonophores (Cnidaria, Hydrozoa) described by Tamiji Kawamura: *Bathyphysa japonica*, *Athorybia longifolia* and *Forskalia misakiensis*, *Scientia Marina* (in press).
- PAGÈS, F. and GILI, J.-M., 1992, Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic), *Scientia Marina*, **56** (Suppl. 1), 65–112.
- PUGH, P. R., 1974, The vertical distribution of the siphonophores collected during the SOND Cruise, 1965, *Journal of the Marine Biological Association of the United Kingdom*, **54**, 25–90.
- PUGH, P. R., 1998, A re-description of *Frillagalma vityazi* Daniel 1966 (Siphonophorae, Agalmatidae), *Scientia Marina*, **62**, 233–245.
- PURCELL, J. E., 1980, Influence of siphonophore behavior upon their natural diets: evidence for aggressive mimicry, *Science. New York*, **209**, 1045–1047.
- PURCELL, J. E., 1983, Digestion rates and assimilation efficiencies of siphonophores fed zooplankton prey, *Marine Biology*, **73**, 257–261.
- SARS, M., 1857, Bidrag til Kundskaben om Middelhavets Littoral-Fauna, Reisemaerkninger fra Italien, *Nyt Magazin for Naturvidenskaberne, Kristiana*, **10**, 1–99.
- SCHNEIDER, K. C., 1898, Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen, *Zoologischer Anzeiger*, **21**, 51–53, 73–93, 114–133, 153–173, 185–200.
- 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* (London: British Museum (Natural History)), 230 pp.
- 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 pls.
- YOUNGBLUTH, M. J., 1984, Water column ecology: *in situ* observations of marine zooplankton from a manned submersible, *Memorial University of Newfoundland Occasional Papers in Biology*, **9**, 45–57.
- ZHANG, J. and LIN, M., 1997, Study on the ecogeography of Siphonophora in the South China Sea, *Acta Oceanologica Sinica*, **19**, 121–131 (in Chinese).