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A review of the family Sphaeronectidae (Class Hydrozoa, Order Siphonophora), with the description of three new species

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Abstract

The last reviewer of the family Sphaeronectidae (Siphonophora, Calycophorae) (Carré, 1968c) considered that it consisted of a single genus, *Sphaeronectes*, containing five species; three of which had been recently described by himself. For the other two species there had been much nomenclatural confusion in the past, as is herein reviewed. It is considered that for one of these species the name *Sphaeronectes koellikeri* Huxley (1859) has priority over the name currently in usage, that is *S. gracilis* (Claus, 1873; 1874). In addition the status of *S. brevitruncata* (Chun, 1888) is reconsidered and the species considered valid, with *S. japonica* (Stepanjants, 1967) being considered as a likely junior synonym of it. Three new *Sphaeronectes* species, *S. christiansonae* sp. nov., *S. haddocki* sp. nov. and *S. tiburonae* sp. nov., are described, and the systematic position of the genus reconsidered in the light of preliminary molecular phylogenetic data.

Key words: Siphonophora, Calycophorae, *Sphaeronectes*, Systematics, Phylogeny

Introduction

History of the family Sphaeronectidae

Presently the Sphaeronectidae is considered to be a small family of calycophoran siphonophores that are unique in that they retain into their adult, polygastric stage their larval nectophore and no further, definitive nectophores are developed. Thus, as for instance Totton (1965) had suggested, they can be considered neotenous. Totton (*ibid.* p. 201) also pointed out that "It was this beautiful and remarkable little 'monophyid' in which the stem was supposed to arise from the exumbral pole of the nectosac that gave rise to the medusoid theory of siphonophore evolution". Although in the 19th Century sphaeronectid species had been described within two genera, *Sphaeronectes* and *Monophyes*, most, but not all, more recent reviewers have considered

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that only one genus, *Sphaeronectes*, and two species were valid. Subsequently four other species have been described all of which were included by Carré & Carré (1995) in their siphonophore review. However, the nomenclatural history of those two 19th Century species has been very complicated and caused much discussion, not least as to the name that should be applied to one of them. In addition, there have been several contentious ideas as to the origin of the single nectophore. Thus, before describing three new *Sphaeronectes* species, the history of the family will be considered in some detail so as to justify the conclusions reached concerning the present taxonomic status of the genus.

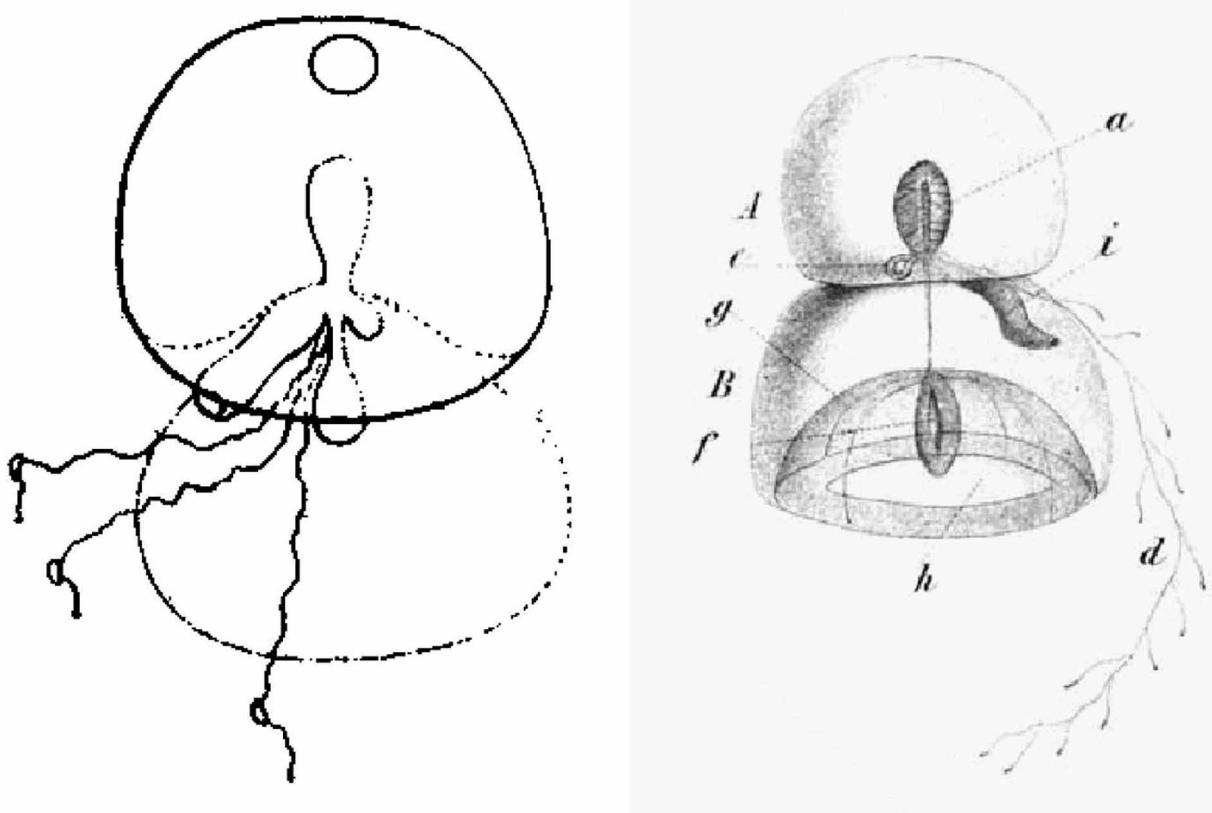


FIGURE 1, 2. 1. (Left) *Ersaea truncata*. From Plate II, Fig. XXVII of Will (1844). 2. (Right) *Diplophysa inermis*. From Plate XVI, Fig. 3 of Gegenbaur (1853)

The first description of a sphaeronectid is generally credited to Will (1844), who described the sexual, monogastric eudoxid stage, under the name *Ersaea truncata* Will (Figure 1). The whole structure consisted of a bract (A in Figure 2), a gonophore, with its sexual manubrium (B and f, respectively, in Figure 2), and a gastrozooid and tentacle (i and d, respectively in Figure 2). It was said to be $\frac{3}{4}$ of a line in length, which if 1 line = 1/12 of an inch means that it had a height of c. 1.6 mm. The phyllocyst, a caecal extension of the common gastrovascular system (a in Figure 2), was shown to rise straight up from its point of origin to about half the height of the bract. At the apex of the bract Will described an opening on the external surface, surrounded by two dark lines, but this was probably an artefact resulting from damage to the very fragile structure. The extent of the subumbrella cavity and ostial opening (g and h, respectively, in Figure 2) of the gonophore are not apparent in Figure 1, but Will (*ibid* p. 82) described the gonophore as having "sehr dicke Substanz" [very thick substance].

Gegenbaur (1853) then described a very similar eudoxid under the name *Diplophysa inermis* Gegenbaur (Figure 2). This eudoxid was said to be 1.5–1.8 lines in height, which is about twice the size of Will's specimen. The ellipsoidal phyllocyst again extended to about half the height of the bract and contained a central cavity, while the subumbrella cavity of the gonophore extended to about half its height. Gegenbaur

noted the similarity between his species and Will's *Ersaea truncata*, but distinguished it on the basis of the absence on his bract of an apical hole and of short basal lappets. As noted above the former was probably an artefact and the latter, one presumes, refers to the apparently larger hydroecial cavity of Will's bract.

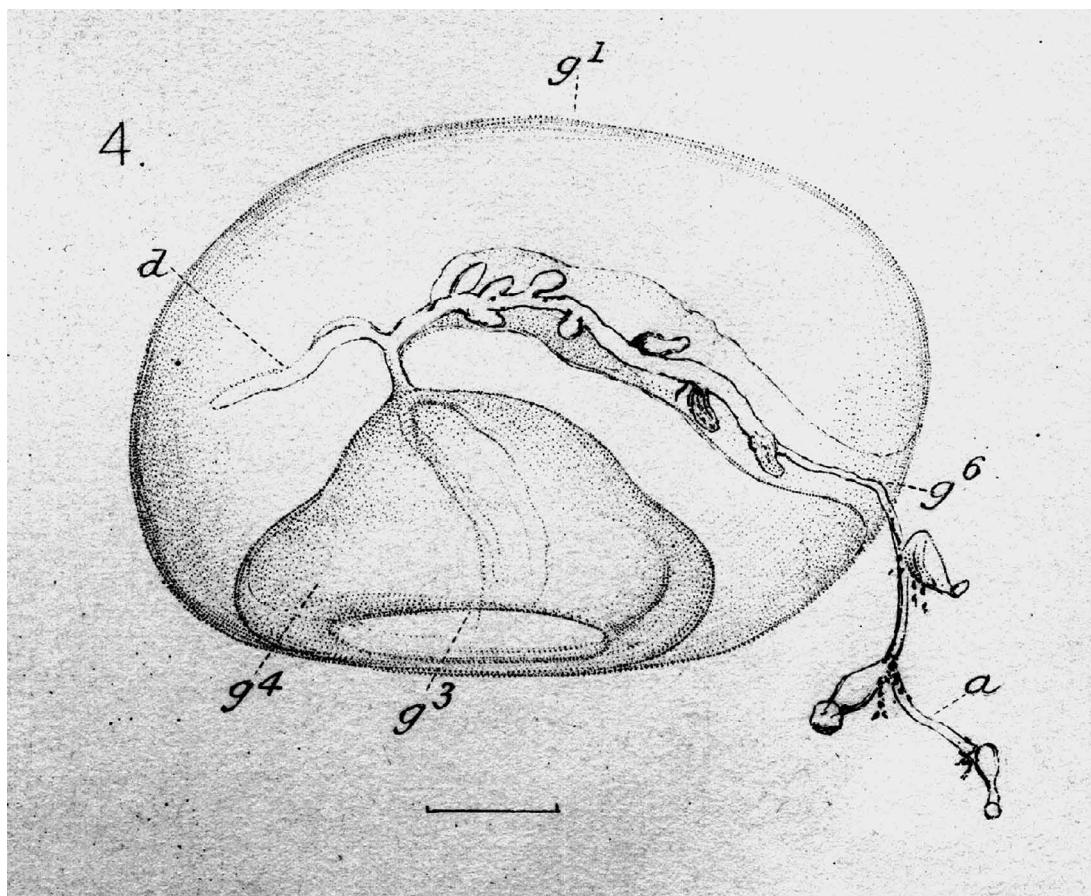


FIGURE 3. *Sphaeronectes Köllikeri* Huxley, 1859. From Huxley (1859) Plate III, Fig. 4.

The first description of a sphaeronectid nectophore was given by Huxley (1859) under the name *Sphaeronectes Köllikeri* Huxley (Figure 3), within a new calycophoran family, the Sphaeronectidae. Under Article 32(d) (i) (2) of the ICBN (1985) this name would presently have to be written as *Sphaeronectes koellikeri*. Huxley was uncertain as to the taxonomic position of both his new Family, which he defined (*ibid* p. 29) as "Calycophoridæ with probably not more than two nectocalyces [nectophores]; the proximal one being spheroidal with a complete hydroecium. No hydrophyllia [bracts]?" and his new genus, which was diagnosed (*ibid* p. 50) as "The proximal nectocalyx (which alone has been hitherto observed) is spheroidal, and of a gelatinous texture. The hydroecium is completely closed behind. Hydrophyllia (?)" Thus it was unclear to him whether eudoxid bracts were ever developed or whether a second nectophore should have been present. In the latter case, however, he found no sign of such and concluded (*ibid* p. 51) that "it does not seem easy to comprehend how any second nectocalyx could exist in this genus, at least, in its ordinary place attached to the proximal end of the cœnosarc."

The three specimens that Huxley collected, on three different occasions (in the Indian Ocean, off the east coast of Australia and in the Torres Strait) were said to have a length of $\frac{1}{4}$ inch, i.e. c. 6 mm. The very characteristic features of the species were the very long, narrow hydroecium (g^6 in Figure 3) enclosing the anterior part of the siphosome (a), and extending over the top of the nectosac (g^4), the long straight somatocyst (d) that extended from its apex, and the four straight radial canals (g^3) on the subumbrella itself.

The next person to describe nectophores of a sphaeronectid, collected in the Mediterranean, appears to have been Pagenstecher (1869), but that author clearly had no idea what he was dealing with apart from that

they were siphonophores. Indeed the identity of the specimens, because the description and illustrations (Figure 4) were inadequate, as Claus (1874) pointed out in no uncertain terms, might never have been known if Pagenstecher had not discussed his findings with Claus. Pagenstecher's figures 1 and 2 (see Figure 4) originally showed the animals at 2–3 times magnification, and from these it would be very difficult to draw any conclusions about the animal. With the benefit of hindsight, however, figures 3 and 4 of his Plate XXI, reproduced in its entirety in Figure 4, can be interpreted as showing the anterior end of the siphosomal stem (left), the somatocyst (right), and the pedicular canal (uppermost in his figure 3), giving rise to the radial canals, although there appear to be five of the latter. In his figure 4 the pedicular canal is presumed to be the descending structure, connecting to the apex of the nectosac and giving rise to the radial canals, of uncertain number. Whether these figures represent mutilated specimens, as Claus (1874) suggested, or the deliberate removal of the remainder of the nectophore, as Pagenstecher appears to indicate, remains unclear. Nonetheless the arrangement of these structures is very similar to that figured by Huxley (1859) for *Sphaeronectes koellikeri* (cf. Figure 3), and it is very probable that Pagenstecher's specimens belonged to that species. However, Claus had a different idea.

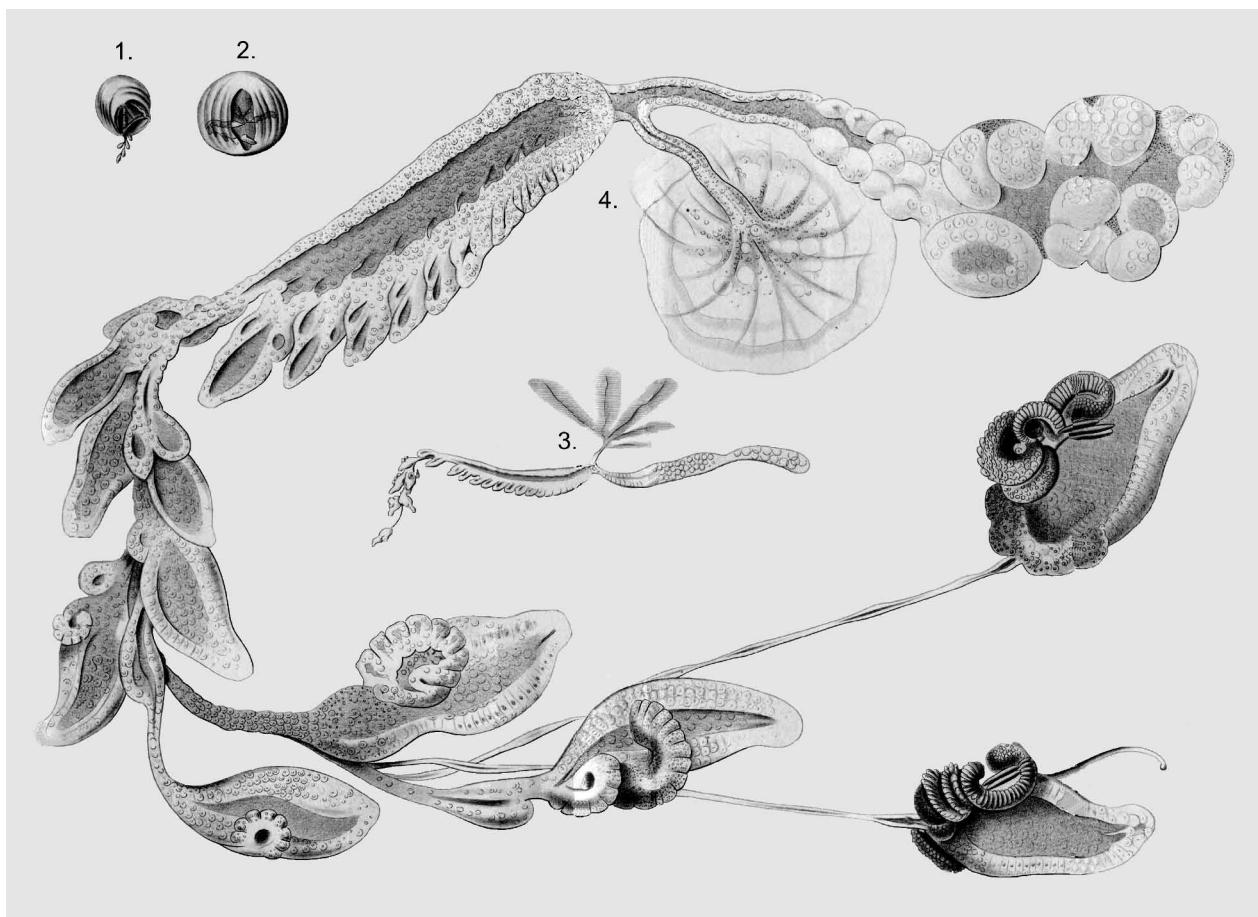


FIGURE 4. From Pagenstecher (1869) Pl. XXI.

Claus (1873, 1874) was the first person to make the connection between the eudoxids and nectophores of sphaeronectid species. Claus (1873) briefly described, without illustration, two sphaeronectid species under the names *Monophyes gracilis* Claus and *M. irregularis* Claus, both species having been collected in the Mediterranean, together with two types of eudoxid stage that probably belonged to them. In a much longer paper Claus (1874) gave further information and provided some illustrations. Firstly, he considered the eudoxids that had been described by Will (1844) and Gegenbaur (1853) and concluded that they should both be considered as belonging to the genus *Diplophysa*, which Gegenbaur had

differentiated from the genera *Ersaea* and *Eudoxia* by the fact that the bract was smooth-walled, with a simple phyllocyst, and that no special asexual swimming bell was present. Claus had found many *Diplophysas* during his studies and was the first to suggest that they were probably the eudoxid stage of his *Monophyes* species. He noted that the shape and relative size of both the bracts and gonophores that he observed varied considerably; the shape of the bract varying from hemispherical (see Figure 5 (5)) to almost spherical (Figure 5 (4)), while in other cases they were more tapered (Figure 5 (2)). From these observations Claus concluded that his *Diplophysas* belonged to two species, considering the eodoxids with small bracts and relatively large gonophores ("der grossglockigen Diplophysa" (*ibid* p. 32) [the large belled Diplophysa]) (Figure 5 (5)) to be distinct from all the other types. This distinction, he claimed, was further exemplified by the gastrozoooids having shorter peduncles together with certain differences in the tentilla. Nevertheless, these differences could merely represent growth stages as the eodoxids of the second type that Claus (1874) illustrated (Figure 5 (5), and his Plate IV, fig. 6) were, one presumes, generally smaller than the first type.

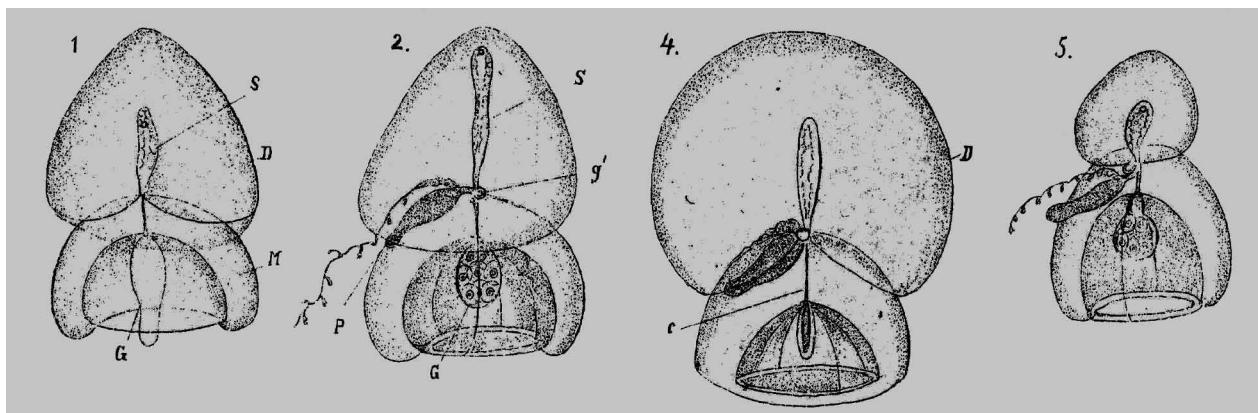


FIGURE 5. *Diplophysa*. Figures 1, 2, 4 and 5 from Claus (1874) Plate IV. No scale given.

It is interesting to note that Claus did not use the shape of the phyllocyst (Figure 5 *s*) to distinguish the two *Diplophysa* species, although he did comment that its size and shape was very variable; usually elongate, but occasionally short and wide. Also it appeared that it was the eodoxids of the second type (Figure 5 (5)), with the relatively large gonophore, that appeared to have the squatter, more rounded phyllocyst.

Claus (1874) now spent the next five pages of his text dealing with his *Monophyes* species, although in reality the relevant diagnostic parts of these descriptions extended to just three sentences in the case of *Monophyes gracilis* and four for *M. irregularis*. *M. gracilis* (Figure 6) was thus defined as being 5–6 mm in diameter and having a relatively shallow nectosac, with four straight radial canals originating from a short pedicular canal (*Cg* in Figure 6) at its apex. The hydroecium (*Tc*) was a very long tube, extending over the top of the nectosac and from whose anterior end originated the long, somewhat curved, somatocyst (*S*). This description is basically the same as that given by Huxley (1859) for *Sphaeronectes koellikeri*, and can be equated with Pagenstecher's (1869) illustrations. Claus (1874) continued with a lengthy description of the arrangement of the buds on the siphosomal stem of *M. gracilis*, probably in order to justify his contention that the *Diplophysa* with the elongate phyllocyst ("der kleinglockigen Diplophysa" (*ibid* p. 30) [the small belled Diplophysa]) was the eudoxid stage of that species. Thus he noted that the more developed gastrozoooids were borne on a peduncle of the same length as the polyp itself.

Similarly Claus's (1874) brief description of the nectophore of *Monophyes irregularis* (Figure 7) encapsulated the main characters: a deeper nectosac, a small funnel-shaped hydroecium, a short somatocyst, with the four radial canals arising directly from its base, i.e. there was no obvious pedicular canal, and the looping of the lateral radial canals. However, the size of the nectophore does not appear to have been given. Claus also drew attention to the shortness of the peduncle of the gastrozoooids, which he likened to that of his "grossglockigen Diplophysa". There is, however, one error in his description and illustrations (see Figure 7) in that he believed that there were two long, looped radial canals on the nectosac, and two short ones. In actuality

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there would be just one short one, the lower canal, while the upper canal, running over the apex of the nectosac, would be the longest.

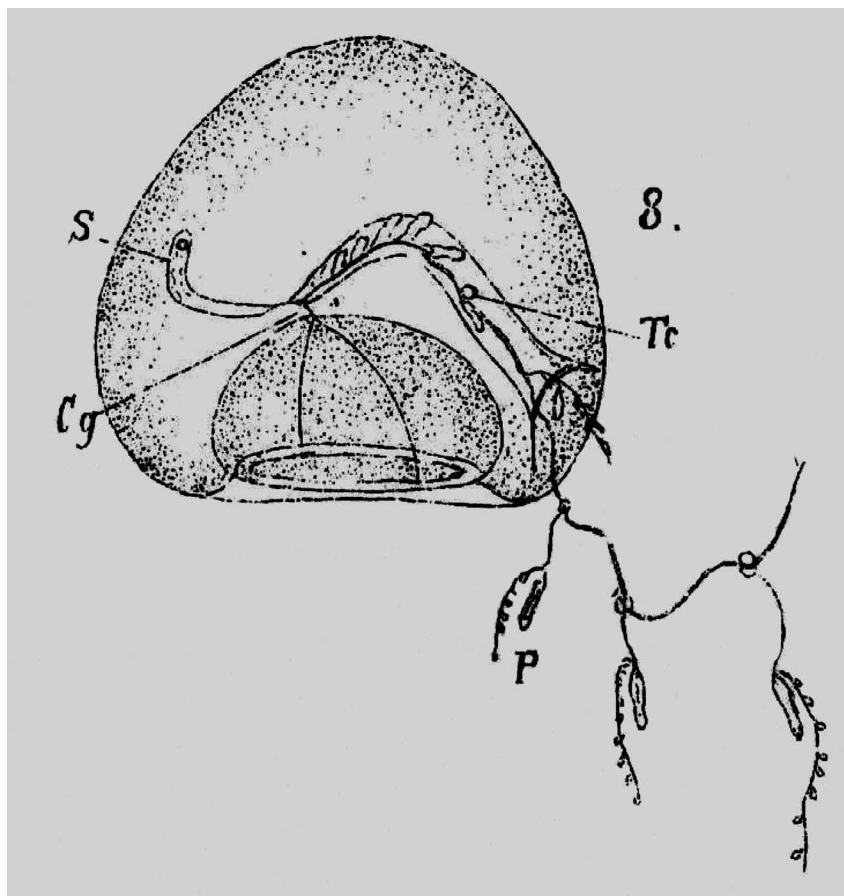


FIGURE 6. *Monophyes gracilis* Claus, 1873; 1874. From Claus (1874) Plate IV, figure 8. No scale given.

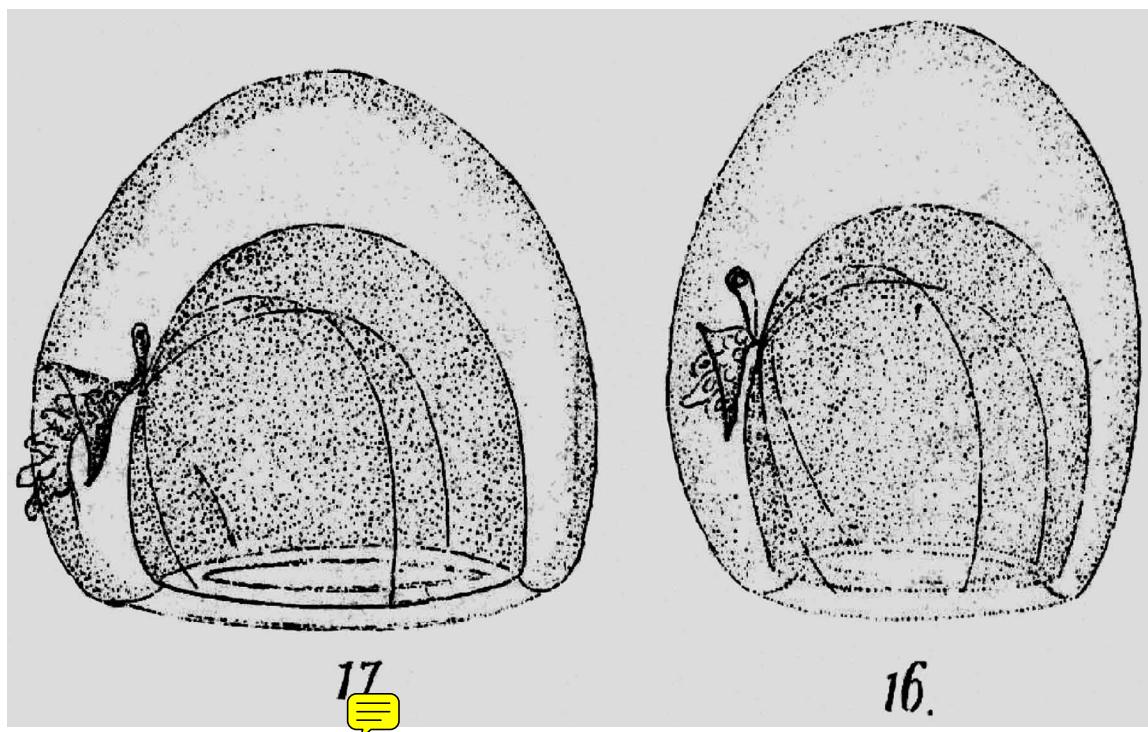


FIGURE 7. *Monophyes irregularis* Chun, 1874. From Claus (1874) Plate IV, figures 16 & 17. No scale given.

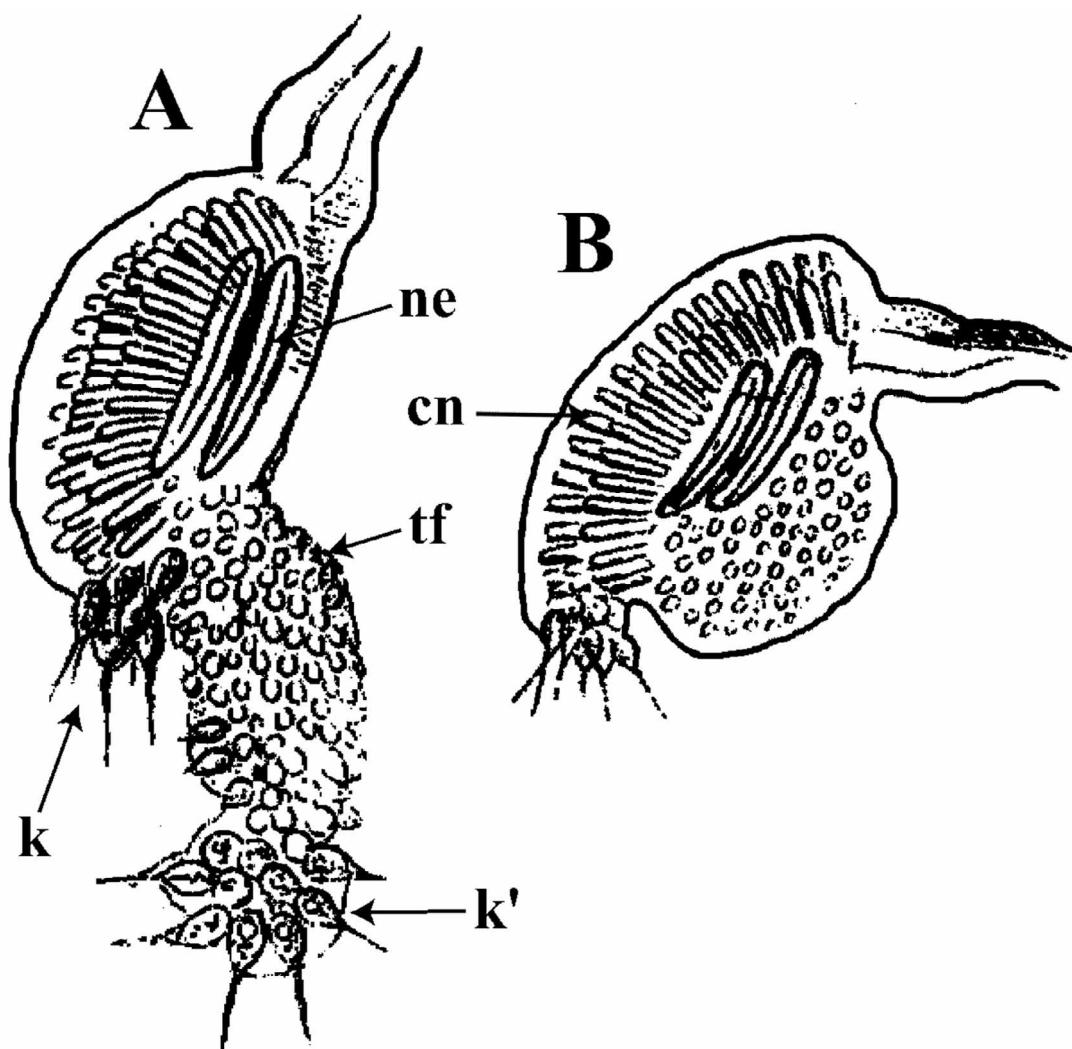


FIGURE 8. Tentilla of A. *Monophyes gracilis* and B. *M. irregularis*. From Claus (1874) Pl. IV, figures 9 (A) and 7 (B).
cn: cnidoband; **k, k'**: pear-shaped nematocysts (desmonemes); **ne:** nematocysts (mastigophores); **tf:** terminal filament.
 No scale given.

Claus (1874) also believed that he could distinguish between the two known species, and their two associated *Diplophysa* stages, by the shape of their tentilla (Figure 8). Firstly, he considered that the tentilla were distinct from all known diphyid species in that they bore only two pairs of large rod-like nematocysts (*ne*) on either side of the cnidoband, while *Praya* was characterised by a large number of such sabre-shaped nematocysts. The cnidoband itself was said to consist of seven rows of small transversely arranged nematocysts. Claus distinguished the species on the basis that the tentilla of his *M. gracilis* (Figure 8A), with its "kleinglockigen Diplophysa", bore two groups of pear-shaped nematocysts at the proximal (*k*) and distal (*k'*) ends of the terminal filament, while in *M. irregularis*, with its "grossglockigen Diplophysa", there was no distal clump (Figure 8B). However, Claus commented on the relative smallness of these tentilla, and it is apparent that for the tentillum of *M. irregularis* (Figure 8B) the terminal filament and the cnidoband still appeared to be in the process of development.

An important part of Claus's (1874) paper was his justification of his conclusion that in his *Monophyes* species only one nectophore was ever developed. He homologised this nectophore with the anterior nectophore of diphyids, but it is clear, as he later clarified (Claus, 1883), that he believed that the *Monophyes* nectophore was the larval one retained into adulthood, and that no definitive nectophore was ever developed. This conclusion was partly based on Metschnikoff's (1874) studies on the larval development of the diphyid

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Epibulia aurantiaca = *Sulculeolaria quadrivalvis* Blainville. In that species the first nectophore to be developed was a larval one, which bore a considerable resemblance to the nectophore of his *Monophyes* species. However, that nectophore was caducous and was later replaced by the first, definitive, anterior nectophore; with a second, posterior nectophore being budded off later. As we will see this conclusion proved contentious to some later authors, and the final proof of its correctness would have to wait for more than a century.

Claus (1874) also noted that neither he nor Pagenstecher (1869) was the first to describe a monophyid species and he referred to the *Sphaeronectes koellikeri* of Huxley (1859), which he noted (*ibid* p. 29) "mit *Monophyes gracilis* des Mittelmeeres nahe verwandte, vielleicht identische Siphonophore" [with *Monophyes gracilis* from the Mediterranean Sea a closely related, possibly identical siphonophore]. However, using the excuse that Huxley, as noted above, was uncertain as to the relationship between his family *Sphaeronectidae* and other calycophoran siphonophores, Claus then decided that, although he considered Huxley's well-illustrated species valid, it was not the same as his Mediterranean species. He even rejected the generic name, *Sphaeronectes*, and retained his name *Monophyes* "weil sie den von Huxley verkannten wesentlichen Charakter unserer Gattung und Familie" [because it expresses the substantive character of our genus and family, which was misjudged by Huxley,] (*ibid* p. 29), because of its appropriateness. Nonetheless, the name *Sphaeronectes* appears to be just as descriptive as *Monophyes*.

Finally, Claus (1874, p. 33) took Metschnikoff (1874) to task for his description "in einer sonst ausgezeichneten Arbeit" [in an otherwise distinguished work] of a *Praya* larva collected at Villefranche (see Figure 9), which Metschnikoff had likened to the individual parts of Gegenbaur's (1853) *Diplophysa inermis* and thus tentatively given the name *P. inermis*. Claus was far from satisfied with this conclusion, basically because Metschnikoff made no observations on the cnidoband of his specimen, which according to Claus would have proven whether it belonged to either *Praya* or *Diplophysa*.

In summary, it seems somewhat presumptuous of Claus (1874) to recognise both the validity of Huxley's *Sphaeronectes koellikeri* and that it closely resembled, even possibly was identical to his *Monophyes gracilis*, and then to retain both his species and his generic name, placing them within a new family, the Monophyidae. With regard to the eudoxid stages it is clear that he considered "der kleinglockigen Diplophysa", whose bract bore a long phyllocyst and long peduncle to the gastrozooid, belonged with *M. gracilis*, and the other ("der grossglockigen Diplophysa"), with the relatively small bract, globular phyllocyst and short peduncle to the gastrozooid, belonged with *M. irregularis*. However, he did not appear to make any statement as to which of his *Monophyes* species he considered the *Diplophysas* described by Will (1844) and Gegenbaur (1853) to belong.

From henceforth the specific names *gracilis* or *koellikeri* will be utilised according to their usage by the author under discussion. Ultimately, however, it will be concluded that the two names are synonymous and that, by precedence, the name *koellikeri* should be used, and that name will be employed whenever otherwise appropriate. The question as to whether Will's (1844) name *truncata* has precedence over both these names will be discussed later.

With regard to Metschnikoff's (1874) description of *Praya ?inermis*, he initially considered the large gelatinous upper part of his specimen (Figure 9) to be a bract, but finally concluded that the whole structure was a *Praya*-like larval nectophore with a relatively small nectosac and a large swollen somatocyst. However, if one compares Figure 9 with Figure 5, there appears to be a great similarity between *P. ?inermis* and Claus's (1874) "grossglockigen Diplophysa" (Figure 5 (5)), and thus that Metschnikoff's original inclination that he was looking at a bract, with an attached gonophore, is more likely to be correct than his later conclusion that it was a larval nectophore.

Although Claus (1874) made no attempt to associate his *Diplophysas* with those described by Will (1844) and Gegenbaur (1853), in the third edition of his "Grundzüge der Zoologie" Claus (1876, p. 239) gave a somewhat strange and brief definition of his family Monophyidae as "Nur eine halbkuglige oder thurmförmig verlängerte Schwimmglocke ist vorhanden, in deren Trichterkanal der Gallertsubstanz der Stamm mit seinen Anhängen eingezogen werden kann. Die Eudoxien-ähnlichen Abkömmlinge sind als Diplophysa bekannt.

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Monophyes Cls. *Sphaeronectes* Huxl. *M. gracilis* Cls. mit *Diplophysa inermis*, Mittelmeer" [Only one hemispherical or tower-like swimming bell exists into whose hydroecium, within the mesogloea, the [siphosomal] stem with its appendages can be withdrawn. The eudoxid-like offspring is called a *Diplophysa*. *Monophyes* Cls. *Sphaeronectes* Huxl. *M. gracilis* Cls. with *Diplophysa inermis*, Mediterranean]. Quite why he considered the nectophores to be tower-like is a mystery, particularly as he did not use the term in his earlier papers. Also, was he deliberately associating his *M. gracilis* with Gegenbaur's *Diplophysa inermis*? And why did he not mention his other species, *M. irregularis*? In the 4th edition of that work, Claus (1880, p. 274) basically repeated his earlier definition of the family, except that he then said "*Sphaeronectes* Huxl. = *Monophyes* Cls. Sp. *gracilis* Cls. mit [with] *Diplophysa inermis*." So, then, he did appear to be accepting that the generic name *Sphaeronectes* had precedence.

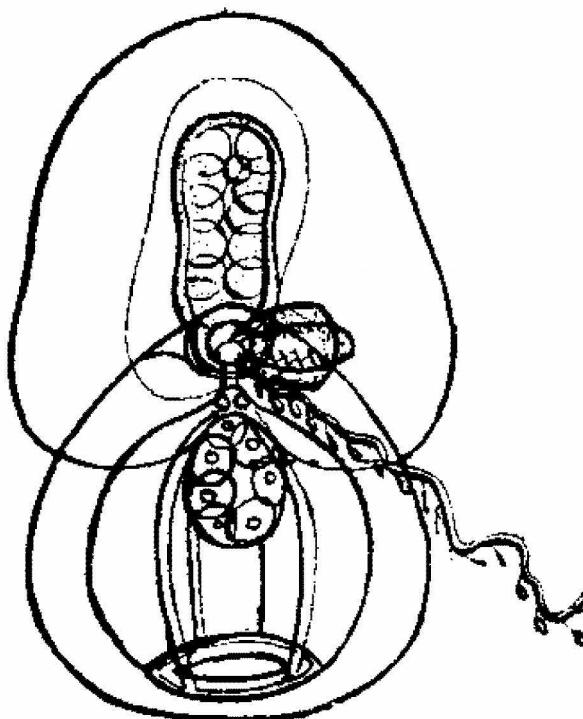
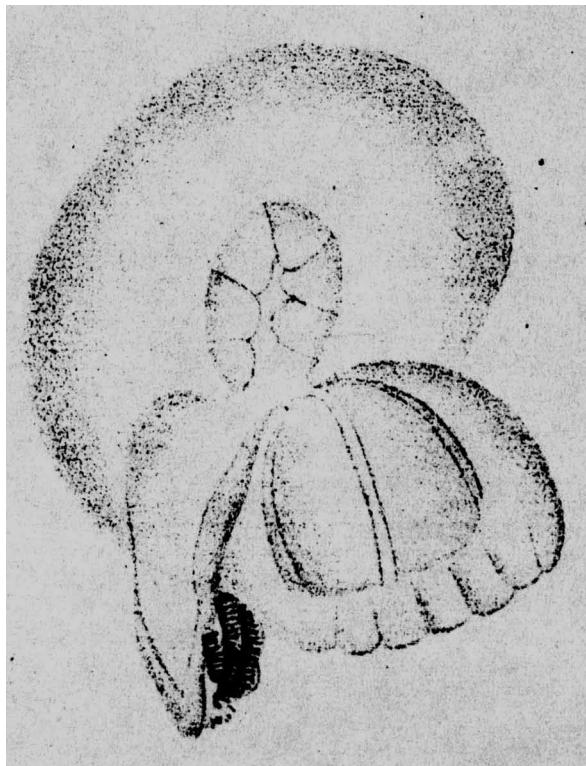


FIGURE 9–10. **9.** (Left) "*Praya inermis*". From Metschnikoff (1874), Pl. VII, fig. 16. No scale given. **10.** (Right) "*Diplophysa inermis*". From Fewkes (1881), Pl. VI, fig. 12. No scale given.

Fewkes (1880) reported the finding, in Narragansett Bay, off Rhode Island, of an eudoxid, which he identified as *Diplophysa inermis*, and later (Fewkes, 1881) illustrated it (Figure 10); in both cases without any description. Fewkes (1880, p. 145) commented that "*Praya inermis* has, according to METSCHNIKOFF, the diphyozoid *Diplophysa inermis* (Geg)". He, thus, appears to have accepted that Metschnikoff's *P. inermis* was a larval nectophore, and that *D. inermis* was the eudoxid stage released by the polygastric adult. However, this seems to be in contradiction to an earlier statement when he quoted Claus (1876) as having considered *D. inermis* to be the eudoxid stage of *Monophyes gracilis*. Presumably Fewkes (1880) thus assumed that the name *inermis* took precedence as he also figured (see Figure 11), without description, a nectophore, collected in the Mediterranean, under the name *Sphaeronectes* (*Monophyes*) *inermis*. This species is undoubtedly the same as Huxley's *S. koellikeri* and Claus's *M. gracilis*.

Fewkes (1883) briefly mentioned *Diplophysa mermis* [sic] as representing the "diphyozoid" [sic] of the genus, which he then referred to as *Monophyes*. Nevertheless a few years later, Fewkes (1889, p. 119) described "*Sphaeronectes gigantea* gen. et sp. nov." [my underlining], and so then appeared to have considered that the generic name *Sphaeronectes* also had precedence. He noted that up until then no

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polygastric, adult *Sphaeronectes* specimens had been collected either in the Atlantic or Pacific waters off the USA, although they were well known from the Mediterranean. His new species was collected at the northern end of Monterey Bay, California and was said to be so different from the Mediterranean species that he had no hesitation in considering it a new species. The specimens were described as being almost $\frac{1}{2}$ " (c. 12 mm) in diameter, truncated in the ostial region and with a shallow nectosac. Further (*ibid*, p.120), "The walls of the nectocalyx are thick, especially at its apex. In this thickened part of the nectocalyx, there lies a groove or depression, out of which hangs the stem. The somatocyst, a blindly ending tube, in communication with the point of junction of the stem with the bell at the fundus of the depression, extends parallel to the radial tubes of the nectocalyx in the thick gelatinous walls of the bell. The somatocyst is filled with 'spongy cells' as in *Diphyes*."

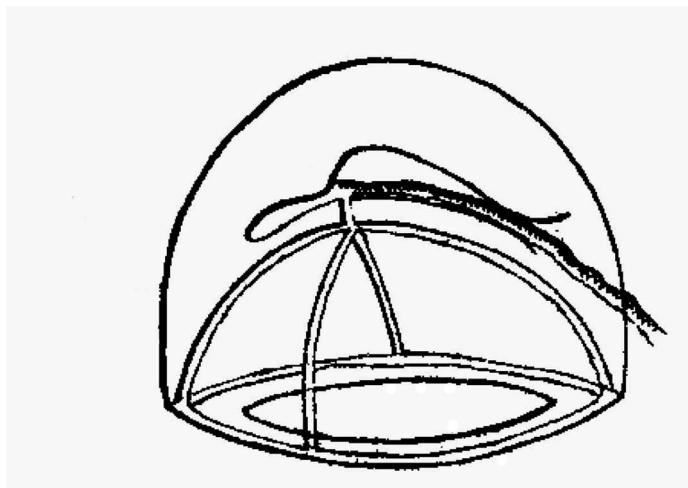


FIGURE 11. "*Sphaeronectes (Monophyes) inermis*". From Fewkes (1880) Pl. III, fig. 6. No scale given.

Unfortunately Fewkes (1889) did not provide any illustrations of *Sphaeronectes gigantea* and so we do not know what the exact arrangements of the hydroecium and somatocyst were, although the description of the former as a "groove or depression" might indicate that it was quite shallow. Nonetheless, the size of the specimens – at least twice the size of those described by Huxley and Claus – could indicate that he actually was describing a different species. Fewkes probably would have published a figure of his species later if it were not for the fact that this 1889 paper was amongst the last that he ever wrote on marine biology before, after his serious dispute with Alexander Agassiz, he became an ethnologist. Despite the probability that Fewkes specimens belong to a new species, his description is inadequate for it to be recognised and, since the specimens appear to be no longer in existence, the species name has to be treated as a *nomen nudum*. However, Bigelow (1911), Moser (1925), Palma (1973) and Daniel (1974) have all considered it as a junior synonym of what is herein called *Sphaeronectes koellikeri*.

Meanwhile, a war of words seems to have broken out between Claus and Chun as to what species should be included within Claus's (1874) family Monophyidae. Chun (1882) [a not entirely accurate English translation of which appeared in 1883], in a quite extraordinary paper, reported on the larval development of *Muggiae kochi* (Will, 1844); a species that develops only a single (anterior) definitive nectophore. Chun recognised that the eudoxids of the adult, polygastric *M. kochi* had previously been described by Will (1844), as *Ersaea pyramidalis* Will, and by Busch (1851), as *Eudoxia Eschscholtzii* Busch, and that both these authors had also described the adult stage, but without recognising the connection between the two stages, as *Diphyes Kochii* Will and *Muggiae pyramidalis* Busch. Quite illogically then Chun chose to retain the name *M. Kochii* for the adult stage and *Eudoxia Eschscholtzii*, not *Eudoxia* or *Ersaea pyramidalis*, for the eudoxid stage of his specimens.

Chun (1882) noted that during his study of the course of the larval development of *Muggiae kochi* the first structure to be developed was a nectophore that closely resembled the *Monophyes* nectophores described

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by Claus (1874). He also noted that this nectophore later was dropped and replaced by a second nectophore that to all intents and purposes resembled the anterior nectophore of a diphyid siphonophore, and was identical to that of *M. kochi*. However, rather than just accepting that a caducous (larval) nectophore was a normal stage in the development of such siphonophores, as Metschnikoff (1874) and others had already concluded, he decided that the so-called *Monophyes* stage was a unique, third stage in the developmental cycle of monophyid species, to which he gave the name *M. primordialis* Chun. He also believed that he was the first person to observe it ("welche von keinem der früheren Beobachter gesehen wurde" (*ibid.* p. 1160) [which has been seen by no previous observer]. Thus he regarded all known calycophoran species that were believed to develop only a single definitive nectophore, such as *Muggiaeae kochi*, *Diphyes chamissonis* and *Eudoxoides mitra* (although the posterior nectophore of the last was later discovered), and Claus's *Monophyes* species all belonged to the family Monophyidae. Further he considered that the *Monophyes* species described by Claus (1874) were equally just stages in the development of an as yet unknown monophyid species, each possessing a single definitive nectophore, having dropped their larval one. The logic behind such conclusions is totally unbelievable.

Not surprisingly Chun's (1882) statements drew forth a withering attack from Claus (1883). Claus pointed out that there was no reason why the nectophore of his *Monophyes* species should not be considered to be equivalent to the caducous nectophore first formed during the development of diphyid calycophoran species. Further, with regard to Chun's so-called "*Monophyes*" species such as *Muggiaeae kochi*, he pointed out that they were far more likely to be diphyid species that had lost one of their nectophores, although for some reason he was unsure whether it was the anterior or posterior one that had been lost. He also pointed out the fact that for Chun's *Monophyes pyramidalis* stage in the development of *M. kochi* only a single gastrozooid and tentacle were present, further ones not being developed until after the larval nectophore had been dropped. On the other hand, on the elongated siphosome of his *Monophyes* species numerous such structures were to be found, as well as bracts and gonophores. To him this clearly indicated that the nectophore of true *Monophyes* species was the retained larval one. He then reiterated his previous statements, as also Huxley (1859) had considered, that the structure of the deep, funnel-like hydroecium of *Sphaeronectes koellikeri* or *M. gracilis* precluded the development of a definitive nectophore. He did, however, allow that further nectophores might be developed by *M. irregularis*, with its shallow hydroecium; apparently ignoring his previous statements regarding the fact that its siphosome bore numerous cormidia.

Claus (1883, p. 6) also clarified his thoughts as to whether *Diplophysa inermis* was the eudoxid of *Monophyes gracilis*, when he said "und es bislang kaum mehr als die allerdings sehr bedeutungsvolle Identität der Nesselknöpfe war, durch welche ich mich zu dem Schlusse berechtigt glaubte, die Diplophysa inermis als die zu *Monophyes gracilis* gehörige Eudoxie zu betrachten" [and it was up to little more than the nonetheless very important identity of the tentilla by which I thought myself entitled finally to regard *Diplophysa inermis* as the eudoxid belonging to *Monophyes gracilis*]. So his identification was based solely on the structure of the tentilla but, as Gegenbaur (1853) did not describe the tentilla of *D. inermis*, and the tentilla shown in his figure (see Figure 2) cannot possibly be associated with either of the types described by Claus, it is difficult to understand how Claus came to this conclusion. Nevertheless, this assumption seems to have been followed by all subsequent authors. However, if one compares Gegenbaur's figure (see Figure 2) with those of Claus (1874) (see Figure 5) one might assume that the former bears a closer resemblance to the *Diplophysa* that Claus associated with his *M. irregularis*, with its short phyllocyst in the bract and its relatively large gonophore, rather than with the "kleinglockigen Diplophysa" he associated with his *M. gracilis*.

Undaunted by Claus's (1883) criticisms Chun (1885) then produced a truly dreadful paper purporting to prove his contention that Claus's *Monophyes* species were nothing more than a unique stage in the development of what he called monophyid species. Chun accepted that the depth of the hydroecium in *Monophyes gracilis* might be a valid reason for preventing the development of another nectophore, but he considered that there was no hard evidence to prove it, and even less in the case of *M. irregularis*. Still hell bent on justifying his "*Monophyes*" stage in the development of monophyid species Chun theorised that the *Monophyes* nectophores described by Claus were either the "*Monophyes*" stage of a more highly developed,

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as yet undescribed monophyid, or that a caducous heteromorphic nectophore preceded the development of the *M. gracilis* or *M. irregularis* nectophores. Thus Chun undertook to follow the larval development of Claus's *Monophyes* species by collecting specimens of the *Diplophysa* eudoxid stage and attempting to fertilise their ova. Unfortunately, as this approach was the only one that could truly answer his questions, he was unable to obtain fertilised ova. Having failed in this approach, Chun then made detailed studies of the anterior end of the siphosome of numerous specimens of Claus's *Monophyes* species, and reported that he could not find any bud that could develop into a replacement nectophore. However, instead of accepting Claus's conclusion that the larval nectophore was retained into adult life and that no definitive nectophores were ever developed, he resorted to his second hypothesis and concluded (*ibid.* p. 515): "Da also weder bei *Monophyes gracilis*, noch bei *M. irregularis* die Schwimmglocken abgestossen und durch Reserveglocken verdrängt werden, so können sie auch keine Larvenformen repräsentieren, sondern sie sind als selbständige Arten zu betrachten, deren medusenförmig gewölbte Schwimmglocken definitive Glocken vorstellen" [Because neither for *Monophyes gracilis* nor for *M. irregularis* are the swimming bells dropped and replaced by reserve bells, they cannot represent larval forms, but are to be regarded as independent species, with the medusa-shaped vaulted swimming bells representing the definitive bells]. Thus his sweeping conclusion was that the nectophore of these *Monophyes* species must have been preceded, developmentally, by a caducous, heteromorphic nectophore.

So now Chun began to look closely at his plankton samples in search of these caducous, heteromorphic nectophores and to nobody's surprise having seen how far Chun would go to falsify the facts he found some. Thus, in addition to finding very small versions of the *Monophyes*-type nectophores he also found two other kinds of nectophore that occurred in common with them and whose appearance Chun considered to be in a certain relationship with the monophyids. By this one assumes he meant that they somewhat resembled the definitive nectophore of *Muggiae kochi*, which in that case was preceded by a *Monophyes*-like nectophore, whereas in this case he expected the latter to give rise to the former.

With regard to these other two types of nectophore, Chun noted that the first (fig. 3 in Figure 12) had the appearance of a diphyid anterior nectophore, but was without ridges or a funnel-shaped hydroecium, which he considered a fundamental character of such species, although it did possess a somatocyst. Although most of these nectophores were denuded of their siphosome, the anterior tip of it was occasionally found still attached. From this Chun was able to deduce not only the presence of the bud of a reserve bell at its anterior end, but that the groups of buds further down the stem where identical to the corresponding groups of *M. irregularis*. So Chun immediately jumped to the outrageous conclusion that the fertilised egg of *M. irregularis* first developed into this diphyid-like nectophore and that, as the stem started to develop and the second *Monophyes*-like bell was developed, it was dropped. It is amazing that Chun could still ignore the fact, as pointed out by Claus, that the post-larva, before the second nectophore was developed and the first dropped, would have possessed only a single gastrozooid and tentacle. Yet according to Chun his larval nectophore of *M. irregularis* possessed several groups of buds that would eventually develop into cormidia. Of course, the definitive nectophore might have been detached during collection, but in that case the siphosome would more likely have remained attached to it rather than the one in question. But these points, as we will see, need not be laboured.

Thus Chun (1885) had paved the way for him to consider the second type of nectophore that he found in his plankton samples (fig. 5 in Figure 12) as the larval nectophore of the other *Monophyes* species, *M. gracilis*. This nectophore, as Chun noted, completely lacked a somatocyst and, with the benefit of hindsight, clearly resembled the second, posterior, definite nectophore of a diphyid siphonophore. However, with greater difficulty, Chun was able to show that the buds attached to the minute stem, at the anterior end of the nectophore, bore not only the bud of a replacement nectophore, but also young buds that bore a great similarity to those on the anterior end of the siphosome of *M. gracilis*, although Chun admits that he would have liked to have found more fully developed cormidia to be certain of the relationship. Nonetheless, Chun once again ignores the fact that the post-larva would be expected to possess only a single gastrozooid and tentacle.

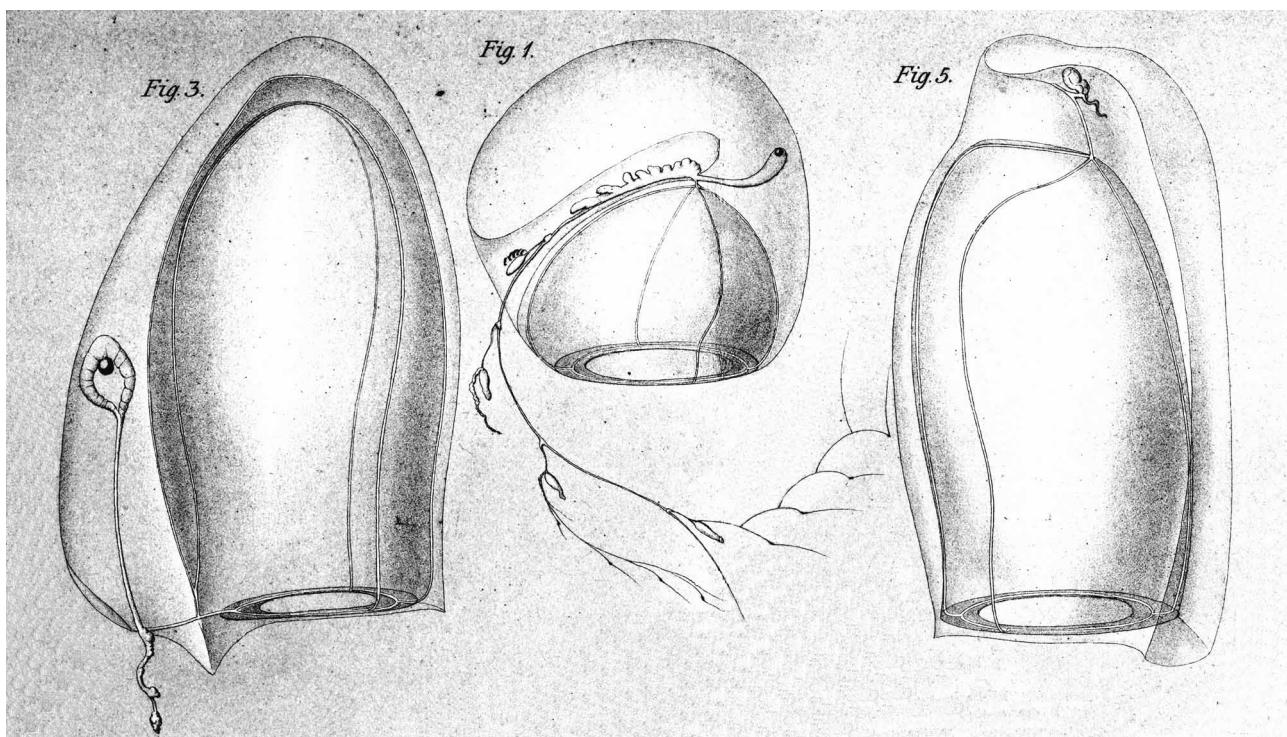


FIGURE 12. Figures 1, 3 & 5 from Chun (1885) Plate II. See text for details. Fig. 1 . *Monophyes gracilis* Claus with the initial parts of the trunk. Slightly enlarged. Fig. 3. Primary bell of *Monophyes irregularis* with a small stem. Original at x15. Fig. 5. Primary bell of *Monophyes gracilis* with the small stem inserted above the subumbrella itself. Original at x15.

It is a pity that Claus does not appear to have published a rebuttal to all this nonsense; indeed, apart from his critique of Haeckel's medusome theory (Claus, 1889a, b) he does not appear to have written any further papers on siphonophores. Nevertheless, the proof that Chun's (1885) interpretation of these two extraneous nectophores as being the larval ones of *Monophyes gracilis* and *irregularis* was completely wrong came the following year from, surprisingly, Chun (1886) himself. He then took time to collect the specimens in as good condition as possible and eventually found a specimen with the two nectophores (figs. 3 & 5 in Figure 12) still attached to each other. Thus the so-called larval nectophore of *M. irregularis* turned out to be the anterior, and that of *M. gracilis* the posterior, nectophore of a new species that he then named *Diphyes subtilis* Chun. Chun spent a great deal of time explaining how he came to make the mistake, but no time at all apologising for it! However, later (Chun, 1892) he did, briefly, admit the rectitude of Claus's criticisms. Thus all his contentions with regard to what species belonged to the family Monophyidae had come to nought and, basically, these two early papers on siphonophores by Chun (1882, 1885) are found to be deeply flawed. Chun clearly was a good observer, but his interpretations of what he saw leave something to be desired.

With this in mind, and before continuing with Chun's thoughts on the family Monophyidae, it is now, unfortunately, necessary to consider what Haeckel (1888b) had to say on the matter. Any reviewer when delving into Haeckel's *Challenger* Monograph should approach the task with extreme caution as here is a master at the art of adjusting his observations to fit his theories, and he was certainly not averse to cheating (see Richardson & Keuck, 2001). Haeckel retained the family Monophyidae, but in the sense of Chun, that is including all calycophoran species that appeared to have only a single "definitive" nectophore, rather than that of Claus who restricted it to his *Monophyes* species, which he believed retained their larval nectophore into adult life without ever developing a definitive one. Haeckel then split the family into two subfamilies, the Sphaeronectidae and Cymbonectidae. Whilst not totally relevant to the present discussion it is worthwhile looking at the species that Haeckel included in the Monophyidae as it underlines the lengths to which he

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would go to find linking species, and the fact that he apparently could not contemplate that any species he studied had been previously described. Thus he gave new names to specimens that closely resembled previously described species but had, according to him, certain differences, even if he did not deign to describe them!

Within the subfamily Sphaeronectidae Haeckel (1888b) included three genera, *Monophyes*, *Sphaeronectes*, and *Mitrophyes*; and included three species, two of his own and Claus's *M. irregularis*, within the first of these. With regard to the first of his own species Haeckel (*ibid.* pp. 128–129) said "The Atlantic species (*Monophyes hydrorrhœa*) is very similar to a small Mediterranean form figured in 1885 by Chun, who supposed it to be the "primary nectophore" of *Monophyes gracilis* (= *Sphaeronectes gracilis*), afterwards replaced by a heteromorphous secondary nectophore ... But this supposition is not very probable, and I call this form provisionally *Monophyes diptera*, provided that it does not belong to the *Cymbonectes*". This is very strange for, as noted above, Chun (1886) realised that the nectophore in question was actually the posterior nectophore of *Lensia (Diphyes) subtilis*, but Haeckel (*ibid.* p. 108) appears to have ignored this fact and frequently quoted Chun (1885) as actually proving "The peculiar metagenesis of these two forms of Calycophoridae", namely *S. koellikeri* and *M. gracilis*. So not only does Haeckel find a new species very similar to a non-existent one, which nevertheless he gives his own name to, but then he does not even bother to describe it! Thus *M. hydrorrhœa* Haeckel is a *nomen nudum*.

Haeckel's second species, *Monophyes princeps* Haeckel (Figure 13A, B), is also of interest as, to me, it exemplifies another of Haeckel's traits, as mentioned above, in that here he invents a species that is intermediate between his first *Monophyes* species, which in reality is a diphyid posterior nectophore that does not possess a somatocyst, and the true *Monophyes* species of Claus (1874). The nectophore does resemble closely the posterior nectophore of a diphyid siphonophore, with an almost completely open hydroecium on its ventral side; although one of his figures (Figure 13A) gives the allusion that it is a deep funnel-shaped structure, the other (Figure 13B) shows that it is not. Now what would be needed to link that type of nectophore to that of a true monophyid? Obvious – find that it possessed a somatocyst! Although this species is occasionally referred to as a possible *Sphaeronectes* species (e.g. Daniel, 1985) to me it is nothing more than pure invention on the part of Haeckel. There is the vague possibility that it could be an unknown species belonging to the family Clausophyidae, but there are many factors, particularly the course of the lateral radial canals, that argue against it.

Within his second genus of sphaeronectids Haeckel (1888b) included Huxley's (1859) species "*Sphaeronectes köllikeri*" and Claus's (1873, 1874) *S. gracilis*, distinguishing them by some very minor differences in shape and form. While within his third he included only one species, *Mitrophyes peltifera* Haeckel, 1888. Although Haeckel believed that this species possessed only a single nectophore to which a scale-like structure was attached, in actuality the latter is a vestigial nectophore and subsequently Totton (1965) was able to place it correctly within the genus *Amphicaryon* (family Prayidae).

Haeckel's (1888b) second subfamily, the Cymbonectidae again included three genera. Within the first, *Cymbonectes*, were included *C. mitra* (Huxley) = *Eudoxoides mitra* and *C. huxleyi* Haeckel. The former of these was later shown, by Bigelow (1911), to be a true diphyid as it budded off a posterior nectophore, but the latter (Figure 13C) seems to have been more enigmatic. The key features from Haeckel's description was that the single, anterior nectophore possessed five serrated ridges each ending, posteriorly, in a prominent tooth that surrounded the opening of the nectosac. The hydroecium was deep, but ending below the apex of the nectosac, with a large, inflated somatocyst above it. The cormidial bracts were said to be *Diphyes*-like. This species was placed by Bigelow (1911) within the genus *Muggiaeae*, presumably based on the depth of the hydroecium, although he considered its status as doubtful. This approach was followed by others (e.g. Moser, 1925; Daniel, 1974) but it appears that no one has considered it to be synonymous with any other described calycophoran. However, by the presence of three ostial teeth – the other two that Haeckel mentioned actually forming the mouth plate – of the deep hydroecium, and having *Diphyes*-like bracts, it seems to me that we are dealing with a somewhat aberrant, perhaps young, *Diphyes* species and, most likely, with *D. chamissonis* Huxley, which is known to develop only an anterior nectophore.

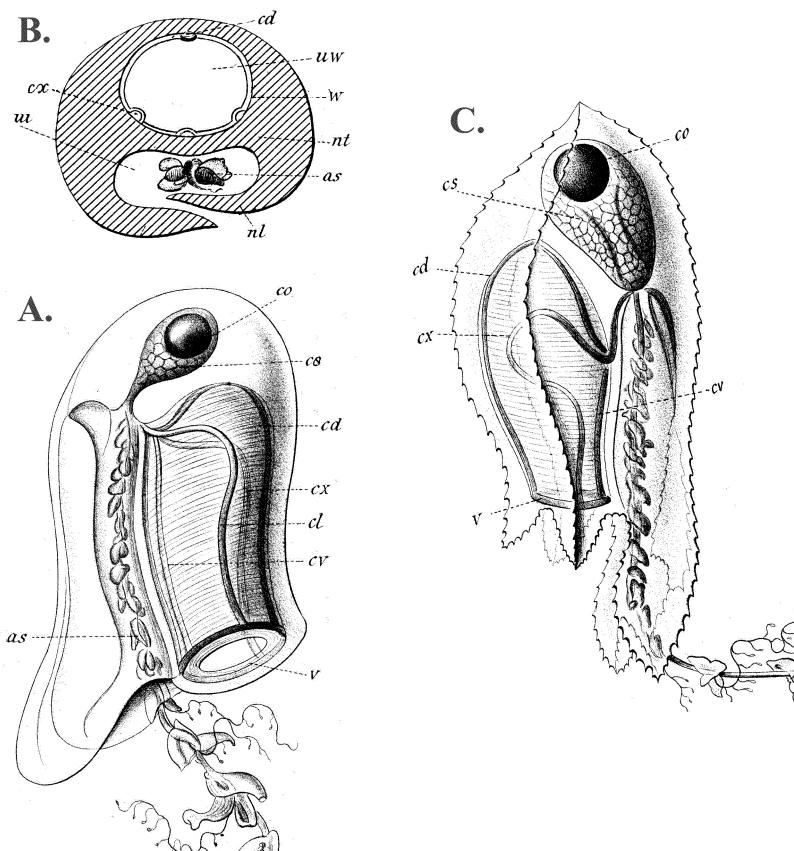


FIGURE 13. A., B. *Monophyes princeps* Haeckel, 1888; C. *Cymbonectes huxleyi* Haeckel, 1888. From Haeckel (1888b), Pl. XXVII, figs. 1 (C) (original x10), 13 (A) (original x12), and 14 (B) (original x12).

In accord with this would be the fact that Haeckel (1888b) included in his second cymbolectid genus, *Muggiaeae*, the species *M. chamissonis* = *Diphyes chamissonis*, as well as *M. kochi* and *M. pyramidalis*. Although Haeckel (*ibid* p. 127) recognised that Chun (1882), as noted above, formed the name *M. kochi* by combining Will's (1844) name *Diphyes Kochii* with Busch's (1851) name *M. pyramidalis*, nevertheless later (*ibid* p. 137) he retained the latter as a separate species. He said "A second species, slightly differing from the Mediterranean one [*M. kochi*], was observed by me in the Canary Island Lanzerote, and may retain the name *Muggiaeae pyramidalis*; it differs from the former mainly in the size of the conical hydroecium, the top of which attains half the length of the nectosac". The irony of the situation, as pointed out by Bigelow (1911) is that, although *D. Kochii* and *M. pyramidalis* are considered to be the same species, what Haeckel was describing, without realising it, was a new species. This species was later properly described by Cunningham (1891–92) as *M. atlantica* Cunningham, for Haeckel's name was pre-occupied.

Finally, Haeckel (1888b) included three species in his third cymbolectid genus; namely *Cymbenneagonum* Eschscholtz, *C. (Abyla) vogtii* Huxley, and his own *C. crystallus* Haeckel. All three of these species are now considered to be junior synonyms of *Enneagonum hyalinum* Quoy and Gaimard, which is placed within the family Abylidae.

Chun (1888a, b – the latter being an English translation of the former) **made a brief reference to the family Monophyidae and followed Haeckel (1888b) in dividing it into two subfamilies, Sphaeronectidae and Cymbolectidae.** Within the former of these Chun only mentioned two genera, *Sphaeronectes* and *Monophyes*. He noted (Chun, 1888b, pp. 224–225) that Huxley's *S. koellikeri* "possesses perfectly the characters of the form subsequently described by Claus as *Monophyes gracilis*". It would seem that Chun was, therefore, synonymising the two species and presumably adopting Huxley's specific name. However, this was not the case as he then referred to (*ibid*, p. 225) "*Sphaeronectes gracilis*, Claus (*S. Köllikeri?*, Huxl.)"! Apart

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from this, within the genus *Monophyes*, he mentioned *M. irregularis* and a new species that he named *M. brevitruncata* Chun, together with an eudoxid stage that he believed belonged to it, namely *Diplophysa codonella* Chun; the practice of giving separate names to the two stages in the life cycle of siphonophores having yet to be abolished. Amongst the species of the subfamily Cymbonectae Chun (1888a,b) mentions just *Muggiae kochi* and two new species *Doramasia picta* Chun and *Halopyramis adamantina* Chun. The descriptions of all of his new species were very brief and without illustration, but four years later he gave a much fuller description of them.

Chun (1892), in the second of his monographs on the siphonophores from the Canary Islands, dealt exclusively with the characteristics of the Family Monophyidae and the species that he considered belonged to it. He retained the subfamily Sphaeronectidae including the same three species as in his earlier paper, namely *Monophyes brevitruncata* with its eudoxid *Diplophysa codonella*, *M. irregularis*, and *Sphaeronectes gracilis* with its eudoxid *Diplophysa inermis*. He did, however, make a brief reference to *S. koellikeri* and believed that it could be distinguished from *S. gracilis* by the shape and form of the somatocyst. Thus Chun appears to be following Claus (1883) in designating *D. inermis* as the eudoxid stage of *S. gracilis*, but he also included Will's *Ersaea truncata* as a junior synonym of it.

Within the subfamily Cymbonectidae, Chun (1892) again mentioned *Muggiae kochi* with its eudoxid stage *Eudoxia Eschscholtzii*, and gave a very detailed description of the two other species, *Doramasia picta*, with its eudoxid stage *Ersaea picta*, which he compared with the eudoxid of *Diphyes bojani*, and *Halopyramis adamantina*. These need not concern us further as *D. picta* is now considered to be a junior synonym of *Diphyes dispar* Chamisso & Eysenhardt, while *E. picta* is a junior synonym of *D. bojani* (Eschscholtz) (see Moser, 1925). *H. adamantina* is yet another description of *Enneagonum hyalinum*.

However, Chun's (1892) rather brief description of *Monophyes brevitruncata*, with its eudoxid stage *Diplophysa codonella*, may be of interest. The cap-shaped nectophore (Figure 14A) was said to be 6 mm in height with a deep nectosac and a funnel-shaped hydroecium open, on the ventral side, to about half the height of its nectophore. The somatocyst was relatively long stretching up toward the apex of the bell and from the base of which arose a very short pedicular canal that connected with the nectosac and gave rise to the four radial canals. The laterals of these had a ?-like course before joining the ostial ring canal. What Chun seemed to think was characteristic of this species, and hence gave rise to its name, was the very short siphosomal stem, with almost mature cormidia at its posterior end. However, it is more than likely that most of the siphosome has become detached during collection.

From a study of these developing cormidia Chun thought he was able to associate them with some free-swimming eudoxids to which, as noted above, he gave the separate name *Diplophysa codonella* (Figure 14B). These eudoxids reached a total height of 6–7 mm. The bract was 3 mm high and possessed a long perpendicular phyllocyst reaching to almost its apex, while the gonophore was 3–4 mm in length. Chun considered the bract, by its shape and relative size, to be intermediate between those of *Monophyes irregularis*, which were smaller and had a short phyllocyst, and *Sphaeronectes gracilis*, which were larger and more spherical. The possibility that *M. brevitruncata* might actually be a distinct species is discussed below.

Meanwhile, another war of words now broke out, this time between Chun and Schneider. One bone of contention was Schneider's (1896) assertion that the siphosomal appendages were developed on the dorsal side of the stem in opposition to the nectophores. Nowadays, by convention, we define the ventral side of the siphosome to be that on which the appendages are attached, but this does not necessarily argue against Schneider's contention in that the nectophores were attached on the opposite side of the stem, which presently would be called dorsal, as the siphosomal elements. In fact, for calycophoran siphonophores, this contention still has no satisfactory conclusion (Casey Dunn, personal communication). Fortunately their disagreements need not concern us greatly, but I cannot resist giving two quotations from Schneider (1898, p. 77). Firstly, "Hier sei gleich noch einer anderen gegen mich polemisierten Stelle in Chun's Arbeit über die Plankton-siphonophoren gedacht" [Here directly is yet another polemic against me placed in Chun's work on the *Plankton* siphonophores]. Secondly, "Ich kann wohl sagen, daß mir nichts unangenehmer ist als den Werth meiner Publicationen selbst erörtern zu müssen. Aber Chun's Vorgehen zwingt mich dazu, denn ich kann nicht

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theilnahmlos zusehen, daß meine Befunde ohne sachliche Würdigung und in entstellender, nonchalanter Weise abgethan werden, als ob sie im Vergleich zu Chun's Befunden vollständig werthlos wären." [I can probably say that to me there is nothing more unpleasant than to have to discuss the value of ones own publications. But Chun's procedure forces me into it, because I cannot sit back and watch my observations be dismissed without material appreciation and in such a distorted nonchalant way as to make them appear completely worthless in comparison with Chun's observations].

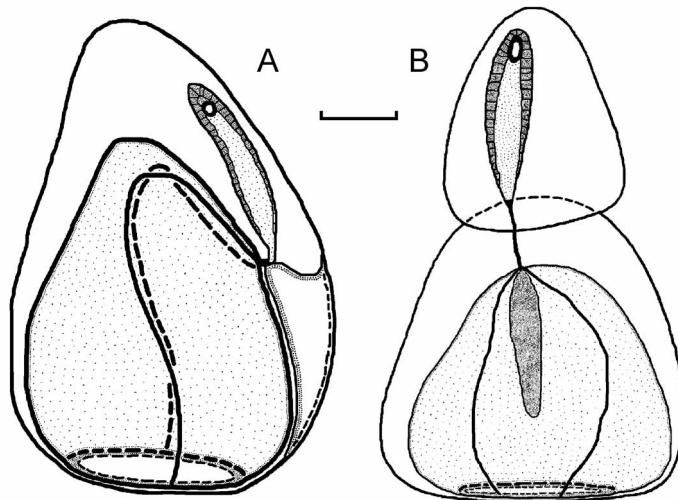


FIGURE 14. *Monophyes brevitruncata* (A) and *Diplophysa codonella* (B) Chun, 1888. Redrawn from Chun (1892), Pl. VIII, figs. 1 (A) and 2 (B). Scale bar 1mm

With regard to the genus *Sphaeronectes*, Schneider (1898) considered all three of the established species, namely *S. koellikeri*, *Monophyes gracilis* and *M. irregularis* were only varieties of a single species, noting that he had seen Huxley's species at Naples. He also considered that Chun's *M. brevitruncata* formed part of the range of variation within that single species. The name he gave to this single species was *S. truncata* quoting the recently introduced nomenclatural rules that required the oldest name, in this case that of the eudoxid stage, to be transferred to the whole. Schneider also made sweeping, and generally unacceptable, changes to the nomenclature by recognising only two families within the order Calycophorae, namely the Prayidae, within which he included the genus *Sphaeronectes*, and the Diphyidae, within which he correctly included the genus *Muggiaeaa*.

Bigelow (1911) was the next person to consider in detail what he called the family *Sphaeronectidae*, which he split into three subfamilies. With regard to his subfamily Sphaeronectinae he agreed with Schneider (1898) that only one generic name, i.e. *Sphaeronectes*, should be recognised, but thought that Schneider had gone too far in reducing the number of species to one. He did agree, however, that there was no reason to separate Claus's *Monophyes gracilis* from Huxley's *S. koellikeri*, particularly as more specimens had become available for study. Bigelow (*ibid.* p. 183) quotes Chun (1892) as having "pointed out [that] the Eudoxids of this compound species had been described by Will as *Ersaea truncata* long before the discovery of the polygastric state". However, as noted above, Chun actually used the Gegenbaur's (1853) name *Diplophysa inermis* for the eudoxid stage, and considered Will's *E. truncata* as a junior synonym of it. Thus Bigelow, like Schneider, took the earliest available specific name, i.e. *truncata*, to replace the aforementioned specific names. This acceptance that *E. truncata* was the eudoxid stage of what Bigelow called *S. truncata* has continued until the present day but, as I intimated above, I am inclined not to accept this. Rather, as I will hope to show below, that the eudoxid more likely belongs to *S. irregularis*.

With regard to the number of *Sphaeronectes* species Bigelow (1911) agreed with Schneider that the differences between *S. irregularis*, with a short somatocyst, and *S. brevitruncata*, with a much longer one, probably represented the extremes of variability seen in other calycophoran species, and so he united them

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under the former name. Finally he mentioned Haeckel's (1888b) *Monophyes princeps*, which neither Chun nor Schneider had considered, and concluded that until further material became available its status could not be determined. As noted above, to me this species is amongst the many invented by Haeckel.

The next major review of siphonophores came from Moser (1925). She decided to split the order Calycophorae into two Legions, the Mononectae and the Polynectae. Within the Mononectae she included only one family, the Monophyidae, that contained the same three subfamilies as Bigelow (1911) had established, as well as a fourth, the Heteropyramidinae, to encompass a new species, *Heteropyramis maculata* Moser. She considered that the Sphaeronectinae contained just two species, *Sphaeronectes koellikeri* and *Monophyes irregularis*, distinguishing them for the same reasons as discussed above. She rejected Bigelow's (1911) usage of the name *S. truncata*, but for the rather dubious reason that it might lead to confusion with another species *Galeolaria (Diphyes) truncata* (Sars) = *Lensia conoidea* (Keferstein & Ehlers), but correctly then used the next available name, i.e. *koellikeri*, thereby considering Claus's *Monophyes gracilis* as a junior synonym of it. She, however, continued to consider its eudoxid stage to be *Ersaea truncata*, and included *Diplophysa inermis* as a junior synonym. She also considered that Claus's *M. brevitruncata* was a young stage of *M. irregularis*, despite the fact that the nectophore of the former was described as being twice the size of the latter. She also considered that their described eudoxids were the same, again despite the considerable difference in size, but later she noted that in all cases there was no direct proof regarding to which species these free-living eudoxids actually belonged.

Totton (1932) seems to have been the first since Claus (1883) to point out that the family Sphaeronectidae, or Monophyidae, according to Chun's (1882) concept, was an unnatural grouping. Totton (*ibid.* p. 327) considered that there was evidence to suggest that the so-called "monophyism", the presence of only a single nectophore in the adult state, was "brought about along several converging lines of evolution". Thus he considered, as noted above, that *Enneagonum hyalinum* was an abylid; that *Muggiaeae* species had affinities with the diphyids; and that *Nectopyramis* species, included in the family by Bigelow (1911), were prayids. In this context he did not mention Moser's (1925) species *Heteropyramis maculata*, but later he classified it in the family Clausophyidae. Presumably Totton thus considered that the family Sphaeronectidae included just two species, although he only mentions one, namely *S. koellikeri*. However (*ibid.* p. 328) he did say that "*Monophyes* and *Sphaeronectes* themselves may be neotenous forms retaining larval features rather than modern survivors of primitive adults".

Later, Totton (1954, p. 22) appeared to have been the first to prove Claus's (1874) contention regarding the origin of the single nectophore in *Sphaeronectes* species when he said "I have bred one species of *Sphaeronectes* at Villefranche, and it is evident that the adult nectophore is the persistent larval one". However, Totton (1965, p. 19) was less positive when he said "I agree with Leloup that the single nectophore of *Sphaeronectes* is probably the larval one retained. For some years I have been collecting progressively earlier larval stages and think I now have critical stages to prove it".

Totton (1954, p. 22) continued by saying "It is interesting then, to see that although, as Garstang pointed out, the pioneers and the writer of one modern text-book, Moser, misconstrued the structure of *Sphaeronectes* as representing a medusa with an exumbrial manubrium, they were not far wrong in thinking it was the nearest approach to an archetype of the Siphonophora, since the adult is at any rate most like what we imagine the ancestor of the Calycophorae to have been. Perhaps it is a neotenous form, like *Nectopyramis diomedaeae*". This was an unfortunate comparison as it has subsequently been shown (Pugh, 1992) that *Nectadamas (N.) diomedaeae* (Bigelow) does develop a caducous larval nectophore, which is replaced by a single definitive one. Nonetheless, it appears that Totton (1954) then considered the Sphaeronectidae to be the most primitive calycophoran form, in contrast to his earlier (Totton, 1932) statement with regard to the possibility that they were neotenous.

Leloup (1954) also believed that the larval nectophore was retained in the family Sphaeronectidae, but he still maintained the two genera, *Monophyes* and *Sphaeronectes*, considering that the former was more primitive than the latter. Patriti (1964), and in his subsequent papers, also followed this approach by recognising *S. koellikeri* and *M. irregularis* as the only two sphaeronectid species.

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Although Totton (1932) had followed Moser (1925) in using the name *Sphaeronectes koellikeri* rather than *S. gracilis*, as the former had precedence, Totton (1965) inexplicably reverted back to the usage of *S. gracilis*. This is even more surprising because it is clear that Totton was loath to make even minor changes to the names of many species even though he knew that those in current usage were wrong, on the basis of precedence. Totton rejected Bigelow's (1911) suggested name *S. truncata* as, despite the work of Claus (1874), he was unsure if the eudoxid stages of the two species, i.e. *S. gracilis* and *S. irregularis*, could be distinguished. Nevertheless, he included (*ibid.* p. 202) both "? *Ersaea truncata*" and "*Diphysa inermis*" as junior synonyms of *S. gracilis*.

Stepanjants (1967) not only decided to maintain both the genera *Sphaeronectes* and *Monophyes* but, controversially, concluded that the latter did not belong within the family Sphaeronectidae, but instead placed it within the family Diphyidae as the only representative of the sub-family Monophyinae. She based this on her belief that the morphological characters, and particularly the location of the somatocyst and hydroecium, of the nectophores of *Monophyes* species more closely resembled those of diphyids, while *Sphaeronectes koellikeri* appeared to be more closely related to prayid and hippopodiid larval nectophores. She also described a new *Monophyes* species under the name *M. japonica* Stepanjants (see Figure 16), colonies of which were collected in the Japan Sea. The description was brief: nectophore height 2.8–3.5 mm, deep nectosac (2–2.6 mm), funnel-shape hydroecium to $\frac{1}{2}$ height of nectophore, and a bubble-shaped somatocyst borne on a short stalk. The species was said to be distinguishable from *M. irregularis* by the characteristic looped course of the lateral radial canals.

The fact that the single nectophore of *Sphaeronectes* species was the persistent larval one was finally proven by Danielle Carré (1969) who followed the larval development of both *Sphaeronectes gracilis* and *S. irregularis*. She noted that there were certain differences in the developmental processes of the two species in that for *S. gracilis* the bud of the nectophore arose in a distinctly ventral position, whereas in *S. irregularis* it was almost apical. From this she concluded that one should not homologise or distinguish the various structures of siphonophores purely on the basis of the location of their buds on the larva. But until the exact relationship between these two species is finally resolved, probably by molecular biological techniques, we cannot know if these observed differences have any significance.

Thus, finally, the true life cycle of sphaeronectid species was established. To illustrate its uniqueness the life cycles of all calycophoran siphonophores are summarised in Figure 15. As can be seen, these life cycles primarily depend on whether the larval nectophore is retained into adult life or is caducous, although the development of a larval bract before that of a nectophore in *Abylopsis tetragona* (Otto), as shown by Claude Carré (1967) and others before, sets this species, and by inference the whole Family Abylidiae, apart from all other calycophoran siphonophores. However, there are added complications to the individual life cycles, such as whether bracts are or are not developed, and whether the posterior cormidal groups are released as individual eudoxids. Much of our knowledge of the development of siphonophores comes from recent works by Claude and Danielle Carré, but even so the retention of the larval nectophore in species of the sub-family Amphicaryoninae (Family Prayidae), and in *Diphyes* species, as suggested by Totton (1965), is not proven. Also there have been no studies on the development of species of the Family Clausophyidae and so it is not known if the larval nectophore is retained, although it does seem possible, particularly in the case of the species of the genus *Clausophyes*.

Meanwhile Claude Carré had described three new *Sphaeronectes* species, *S. gamulini* Carré, 1966, *S. bougisi* Carré, 1968a and *S. fragilis* Carré, 1968b (see Figure 16). The nectophores of both *S. bougisi* (bell height 1mm) and *S. gamulini* (1.5 mm) were relatively small, and the former, because the nectosac occupied most of its volume, was very fragile. *S. bougisi* had a small, ventral hydroecium, somewhat like that of *S. irregularis*, but the course of the radial canals was unique amongst the known *Sphaeronectes* species in that the lateral radial canals arose separately from the upper canal at the apex of the nectosac. Although *S. gamulini* had the basic *irregularis*-like arrangement of the radial canals, its hydroecium was displaced to the left ventral side, while its somatocyst projected out horizontally toward the right-hand side.

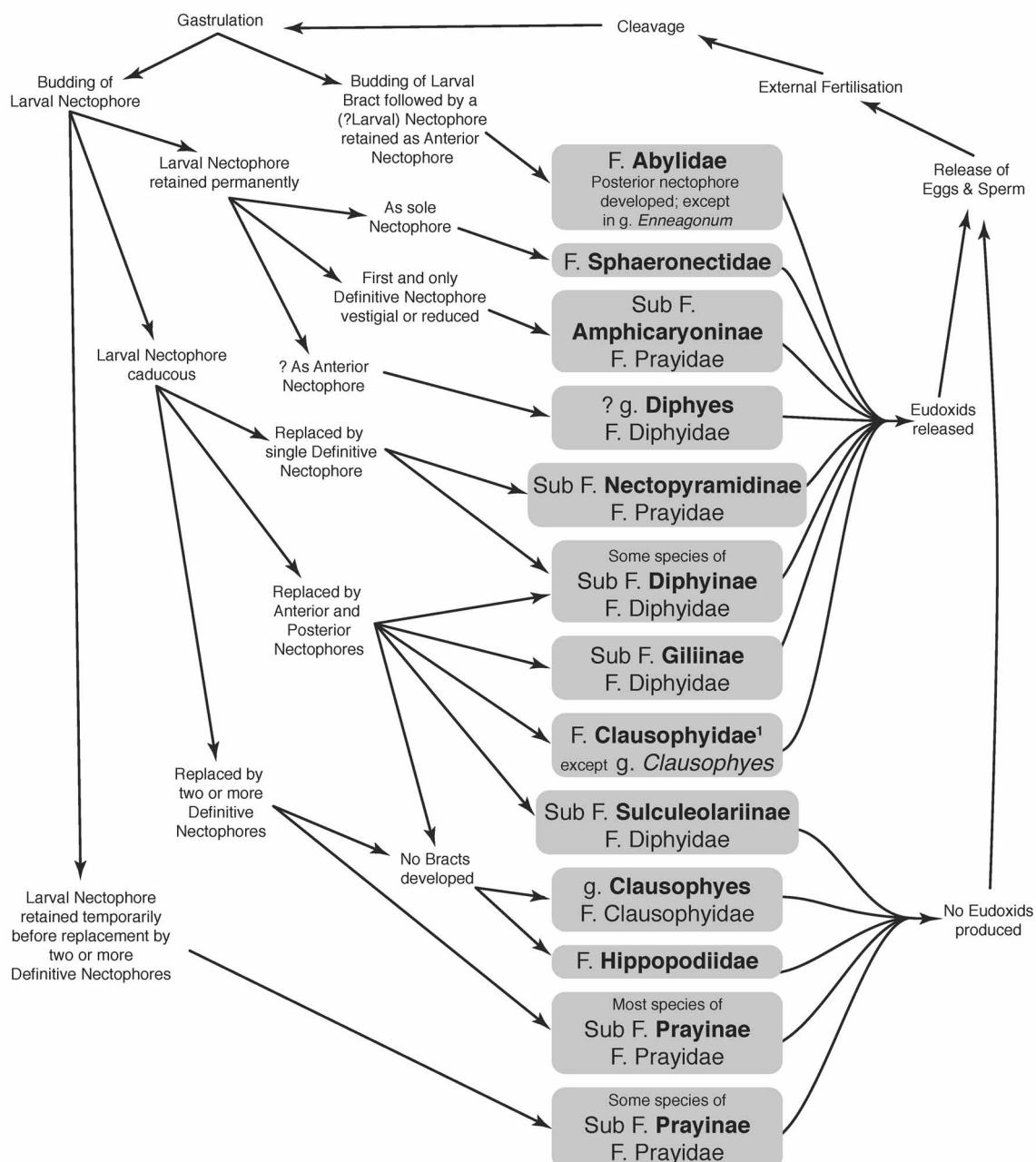


FIGURE 15. Schematic showing the life cycles of various groups of calycophoran siphonophores. (The posterior nectophore of *Heteropyramis maculata* Moser has not been identified and, indeed, may not be developed.)

The third species, *Sphaeronectes fragilis* (see Figure 16), was considerably larger, with a bell height of 5 mm, thereby exceeding that of *S. irregularis* but generally smaller than that of *S. koellikeri*. Like *S. gamulini* the nectosac occupied the great majority of the ectophore, which in consequence was very fragile; hence the name. Although the shape and size of the ventral hydroecium and the course of the radial canals was similar to that of *S. irregularis*, *S. fragilis* was distinguished by the shape of its somatocyst with a subspherical terminal swelling at the end of a long peduncle. Of these three new *Sphaeronectes* species Claude Carré was only able to keep one, *S. gamulini*, alive for a sufficient time for the specimens to develop and liberate an eudoxid group. The bract of this possessed a mushroom-shaped phyllocyst borne on a shortish peduncle (see Figure 17). Subsequently he found similar eudoxid bracts in plankton nets, but does not seem to have been able to find by such a means any eudoxid bract whose phyllocyst resemble that of the somatocyst of the ectophores of his other two species.

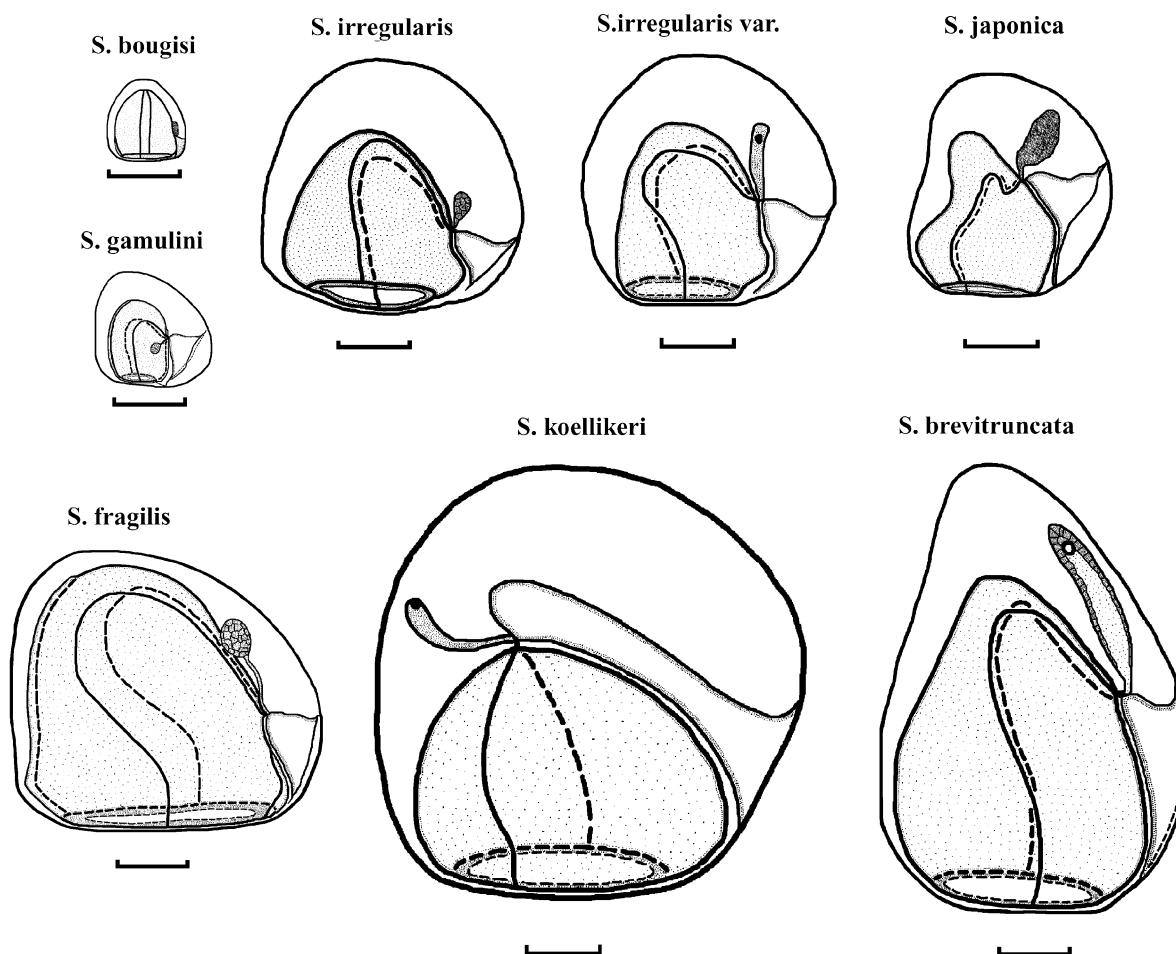


FIGURE 16. Comparison of the ectophores of the various *Sphaeronectes* species at the same scale. *S. bougisi* (redrawn from C. Carré (1968a, fig. 1A); *S. brevitruncata* (redrawn from Chun, 1892, Pl. VIII, fig. 1); *S. fragilis* (redrawn from C. Carré, 1968b, Pl. II A); *S. gamulini* (redrawn from C. Carré, 1966, fig. 1); *S. irregularis* (redrawn from C. Carré (1968c, Pl. I, fig. 3); *S. irregularis* var. (= *Monophyes brevitruncata* Chun) (redrawn from C. Carré, 1968c, Pl. I, fig. 2); *S. japonica* (redrawn from Stepanjants, 1967, fig. 99); *S. koellikeri* (redrawn from Chun, 1885, fig. 1 – as *S. gracilis*). Scale bars 1 mm.

Before looking in more detail at C. Carré's (1968c) paper, let us briefly run through the more recent and relevant papers on *Sphaeronectes* species. Daniel (1974, 1985) in her major siphonophore reviews of Indian Ocean siphonophores basically followed the line of Totton (1965) in recognising *S. gracilis* (= *S. koellikeri*) and *S. irregularis*, with which she synonymised *S. brevitruncata*. She considered both *S. japonica* and *S. princeps* as doubtful species whose existence needed confirmation, although in her later paper she appears to accept the validity of the latter species. She also included *Ersaea truncata* and *Diplophysa inermis* as junior synonyms of *S. gracilis*. Daniel (1985) figured both *S. gracilis* (her fig. 78a) and *S. irregularis* (her fig. 78b), but it is clear from the course of the radial canals and the depth of the hydroecium that the latter figure actually is of *S. koellikeri*. Several other authors have given records for various *Sphaeronectes* in various parts of the World (see Appendix) and Palma (1984) gave new illustrations of specimens of *S. gamulini* that he found off the coast of Chile. *S. fragilis* has also been found in the same locality on various occasions by, for instance, Palma (2006), but without any illustrations. There have been further records for all five of the *Sphaeronectes* species mentioned by C. Carré (1968c) in other parts of the Mediterranean (see Appendix).

In addition to the three new *Sphaeronectes* species, from Monterey Bay, California, described below, it appears that the occurrence of at least two other new *Sphaeronectes* species has already been suggested in the literature. Firstly, Pagès & Kurbjewitz (1994) and Pagès & Schnack-Schiel (1996) reported the presence of a

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new species of *Sphaeronectes* in the Weddell Sea (Atlantic Sector of the Antarctic Ocean). The nectophore of this new species was said to have a height of 1–4 mm, while that of its eudoxid was 1–3 mm. It is likely that this new species is the same as that found by Margulies (1992) in the Indian Sector of the Antarctic Ocean, which she referred to as *S. irregularis*. The Weddell Sea specimens are still extant and Francesc Pagès was working on their description before his untimely death. It is to be hoped that his information will eventually be published.

The second potentially new *Sphaeronectes* was reported on by Hosia & Båmstedt (2007) from Korsfjord, western Norway. They collected six specimens that were said to resemble the *irregularis*-type in having looped lateral radial canals, but the vertically orientated, globular somatocyst borne on a short, but distinct stalk was quite different from that of any of the previously described species. It certainly seems that they were dealing with a new species but, unfortunately, none of the specimens were retained and so, until further specimens are captured, we cannot be sure.

Returning to Claude Carré's (1968c) paper, he briefly reviewed the descriptions of most of the known *Sphaeronectes* species, although Stepanjants's (1967) *Monophyes japonica* was not included, probably because he was unaware of that recently published thesis. With information on both the nectophores and eudoxids of *Sphaeronectes koellikeri* and *S. irregularis* Carré could have drawn some important conclusions with regard to the previous muddled taxonomy of the genus, but unfortunately he did not. So in this historical review of the calycophoran siphonophore family Sphaeronectidae let us look further at Carré's information and what conclusions can be drawn from it.

Firstly, the question as to what name should be applied to each of the species described in the 19th Century could easily have been resolved. As all current authorities accept that the names *Sphaeronectes koellikeri* and *Monophyes gracilis* are synonyms, then Huxley's name *S. koellikeri* must have precedence both as the generic and specific name. In actuality, if in the future this species comes to be considered as generically distinct from the *irregularis*-like species, the name *Monophyes* should not be applied to the latter as *M. gracilis* was the species first described by Claus (1873, 1874) and thus *Monophyes* would have to be considered as a junior synonym of *Sphaeronectes*.

C. Carré (1968c) clearly established the identity of the eudoxids of the two main species under consideration, namely *Sphaeronectes koellikeri* (as *S. gracilis*) and *S. irregularis* (see Figure 17), thereby confirming Claus's (1874) original belief as to which of his *Diplophysas* belonged to which polygastric stage. Basically the bract of *S. koellikeri* has a long, fusiform phyllocyst, and corresponds (*cf.* figs. 2, 3, & 4 in Figure 5 with the eudoxid of *S. koellikeri* Figure 17) closely to the "kleinglockigen Diplophysa" of Claus (1874). The eudoxid bract of *S. irregularis* has a short and spheroidal phyllocyst and corresponds (*cf.* fig. 5 in Figure 5 with the eudoxid of *S. irregularis* Figure 17) to Claus's "grossglockigen Diplophysa". Even the relative sizes of the gonophores testify to this. The question then is to which of these two species do the eudoxids described by Will (1844) and Gegenbaur (1853) most likely belong? To me Gegenbaur's *Diplophysa inermis* (see Figure 2) is almost identical to Claus's "grossglockigen Diplophysa", which he established belonged to *S. irregularis*. For Will's *Ersaea truncata* (see Figure 1) the bract and gonophore are of almost equal size, but the phyllocyst of the bract, being swollen and occupying less than half the height of the bract, again more closely resembles that of *S. irregularis* than that of *S. koellikeri*. So why did Chun (1892) and Bigelow (1911) consider that both these eudoxids belonged to *S. koellikeri*? The answer appears to lie in the fact that they both blindly followed Claus's (1883) belief, based on the most tenuous of evidence, that *D. inermis* was the eudoxid stage of *S. koellikeri*.

Thus it is the present author's conclusion that Bigelow's (1911) contention that the name *truncata* should be used in place of *Sphaeronectes koellikeri* and *Monophyes gracilis*, as it had precedence, can no longer apply as the eudoxid described by Will (1844) clearly differs from that illustrated by C. Carré (1968c) for *S. koellikeri*. However, the question then arises as to whether Will's name *truncata* should be applied to the species *S. irregularis* as the eudoxid of the latter species, as illustrated by C. Carré (1968c), is somewhat similar to it? In reality, this question is unanswerable as there is no way of knowing to which of the species, whose description is based on their polygastric stage, they belong. In addition the eudoxid stages of only three

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Sphaeronectes species are positively known and since, as will be contended, there are at least two other *Sphaeronectes* species present in the Mediterranean whose nectophores are of a similar size to that of *S. irregularis*, then it would seem inappropriate to arbitrarily apply the name *truncata* to any one of them. Even if the *Ersaea truncata* of Will (1844) does belong to *S. irregularis*, the use of the former specific name, in complete opposition to the way that Bigelow (1911) used it, would cause confusion, and it seems safest to retain the name *S. irregularis*. However, it is clear that, on the basis of the shape of the phyllocyst, the *E. truncata* of Will (1844), the *Diplophysa inermis* of Gegenbaur (1853), and probably the *Praya ?inermis* of Metschnikoff (1874) and the *D. inermis* of Fewkes (1881), can no longer be considered as junior synonyms of *S. koellikeri*, as has usually been the case in the past. For the present they will be considered as questionable synonyms of *S. irregularis* (see Appendix).

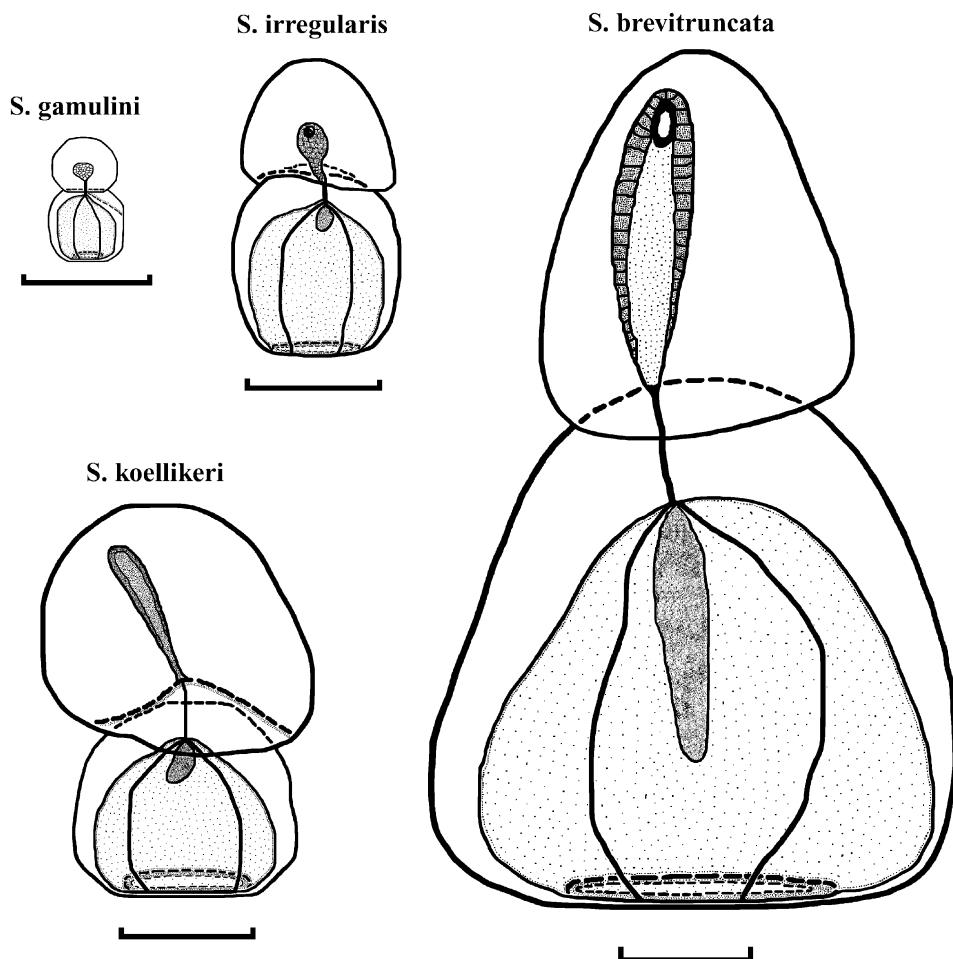


FIGURE 17. Eudoxids of various *Sphaeronectes* species at the same scale. *Sphaeronectes brevitruncata* (redrawn from Chun, 1892, Pl. VIII, fig. 2 – as *Diplophysa codonella*); *S. gamulini* (redrawn from C. Carré, 1966, figure 4); *S. irregularis* (redrawn from C. Carré, 1968c, Pl. II, fig. 6); *S. koellikeri* (redrawn from C. Carré, 1968c, Pl. II, fig. 4 – as *S. gracilis*). Scale bars 1 mm.

Claus (1874) had noted that the gastrozoooid of the *Diplophysa* that he associated with *Sphaeronectes koellikeri* had a much longer peduncle than that of *S. irregularis* and this was confirmed by C. Carré (1968c) who found that the peduncle of the gastrozoooid of *S. koellikeri* was the same length as the gastrozoooid itself, while in *S. irregularis* it was only about half the length. For his new species, Carré found that the peduncle was short but quite distinct in *S. fragilis* and very short and difficult to distinguish in *S. gamulini* and *S. bougisi*.

It is of interest to note that until C. Carré's (1968c) paper the only published figure, as far as I can ascertain, of *Sphaeronectes irregularis* was the original one by Claus (1874) (see Figure 7), if one ignores the

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one given by Daniel (1985), which appears to be of *S. koellikeri*. There are certain differences between these figures (cf. Figures 7 and 16), mainly with regard to the positioning of the hydroecium, but in both the hydroecium is small and the somatocyst is very short. Subsequently, Gamulin and Kršinić (2000) have provided a figure of a very small nectophore (1.3 mm bell height), with a relatively deep hydroecium and a globular somatocyst, under the name *S. irregularis* (see Figure 18B). If it does belong to that species then, judging from its size, it would be at a very early stage in development. Nonetheless, it does show certain differences, particularly in the arrangement of the somatocyst and hydroecium, to a much larger, but still very young, nectophore of *S. irregularis* that was photographed by D. Carré (1969) (see Figure 18A). In view of the fact that we know of the larval development of only two of the *Sphaeronectes* present in the Mediterranean it may well be that Gamulin and Kršinić's (2000) specimen might not belong to *S. irregularis*.

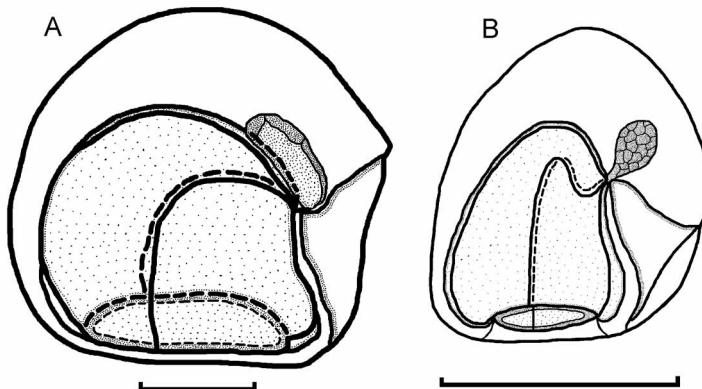


FIGURE 18. *Sphaeronectes irregularis* young nectophores. A. Redrawn from D. Carré (1989); B. Redrawn from Gamulin & Kršinić (2000). Scale 1 mm.

So just how many *Sphaeronectes* species currently should be recognised? C. Carré (1968c) included five species, but appeared unaware of Stepanjants's (1967) *Monophyes japonica*. Stepanjants's illustration (see Figure 16) appears to show that the nectosac was distorted from what, one presumes, was its normal relaxed state. This distortion probably resulted in the lateral radial canals assuming what Stepanjants considered to be a characteristic bend. C. Carré (1968c, Pl. I, fig. 2) included a photograph of a slightly distorted nectophore, of a similar size to Stepanjants's species, that had a somewhat similar arrangement of the somatocyst and the hydroecium, but which did not appear to have the characteristic bend in the lateral radial canals. This photograph was captioned as "*Sphaeronectes irregularis* var. (= *Monophyes brevitruncata* Chun)", and Carré (*ibid.* p. 91–92) briefly commented "Nous donnons une photographie d'un spécimen (Pl. 1, fig. 2) qui diffère de la forme typique et commune de *S. irregularis*, par son somatocyste plus long et qui correspond à la figure donnée par CHUN (1892) pour *Monophyes brevitruncata*. CHUN attribue à cette espèce une eudoxie (= *Diplophysa codonella*) différente de celle que nous décrivons pour *S. irregularis*. Cependant, nous suivons, pour l'instant, l'opinion de BIGELOW et TOTTON, et nous pensons que l'espèce décrite par CHUN est une variété de *S. irregularis*" [We show a photograph of a specimen (Pl. 1, fig. 2) that differs from the common and typical form of *S. irregularis*, by its longer somatocyst, which corresponds with the figure given by CHUN (1892) for *Monophyes brevitruncata*. CHUN attributes an eudoxid to that species (= *Diplophysa codonella*) that differs from what we have described for *S. irregularis*. However, we follow, for the moment, the opinions of BIGELOW and TOTTON, and we think that the species described by CHUN is a variety of *S. irregularis*]. This nectophore is schematically shown as it possibly might have looked when relaxed in Figure 16.

Although C. Carré (1968c) recognised the similarity between his variety and the species that Chun (1892) described as *Monophyes brevitruncata*, and the clear differences from his specimens of *Sphaeronectes irregularis*, he merely followed the established course in considering them both as varieties of *S. irregularis*. Nevertheless, the basic characters that separate the *irregularis*-like species are the shapes of the hydroecium and the somatocyst, and the size of the nectophore itself. Thus it seems to me that there is a greater

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similarity in the first two of these characters between Carré's "variété", Stepanjants's *M. japonica* and Chun's *M. brevitruncata*, than any have with *S. irregularis*, where both the somatocyst and hydroecium are relatively small. The only major difference between them is that the height of the nectophore of *M. brevitruncata* was said to be twice that of the other two, which were similar in size to *S. irregularis*. Although I believe that size does matter there is some evidence (see next paragraph) that Chun's measurements are inaccurate. Nonetheless, it seems to me that there is sufficient evidence, based on the two other main characters, to justify separating them from *S. irregularis* and thereby to refer to them as *S. brevitruncata*. It is to be hoped that further specimens showing these characters will be collected and allow for better comparisons with *S. irregularis* to be made.

With regard to the *Diplophysa codonella*, which Chun (1892) described as the eudoxid stage of *Sphaeronectes brevitruncata*, I am inclined to think that it is actually the eudoxid of *S. koellikeri*, because of the shape of its phyllocyst (see Figure 17). However, Chun stated that the bract was 3 mm in height, which appears to be approximately twice that of *S. koellikeri*, judging from C. Carré's (1968c, Pl. II, fig. 6) photograph. Nonetheless, Chun (*ibid.* p. 81) stated "Die genannten Diplophysen stehen an Grösse hinter jenen von *Sphaeronectes gracilis* nicht zurück, insofern sie eine Länge von 6–7 mm erreichen" [The diplophysas mentioned are approximately the same size as those of *Sphaeronectes gracilis*, in so far as they reach a length of 6–7 mm]. Thus I believe that there must be some anomaly in the dimensions given by Chun for the nectophore and eudoxid of *S. brevitruncata*, although the sizes indicated for the figures, based on their magnification, do accord with what Chun quotes in the text. If indeed this is the case then it is even more likely that Chun's *D. codonella* is the eudoxid stage of *S. koellikeri*.

Having re-established *Sphaeronectes brevitruncata* as a probably valid species, there remains the questions of the validity of C. Carré's species *S. gamulini*, *S. bougisi* and *S. fragilis* and how accurate are past identifications of all *Sphaeronectes* species. As mentioned above it is quite likely that the specimens, from the Indian sector of the Antarctic Ocean, described by Margulis (1992) as *S. irregularis* actually belong to a new species mentioned by Pagès & Kurbjewitz (1994) and Pagès & Schnack-Schiel (1996). In addition, the records from Monterey Bay for *S. koellikeri*, as *S. truncata*, published by Bigelow & Leslie (1930) also appear suspicious. Although *S. koellikeri* does occur inshore off south California (Purcell, 1981; Purcell & Kramer, 1983), and had been found by Bigelow (1911) in Acapulco harbour, there are no other records for the occurrence of this species in the cold California Current waters to the north of Point Conception. Indeed there are no records for this species in the extensive records of the Monterey Bay Aquarium Research Institute, based on HD video recordings made by ROVs, or from serendipitous SCUBA dives that have been made in the same area. Nonetheless, one would have expected Bigelow to be able to identify this species, but in actuality the siphonophore identifications for the Bigelow & Leslie paper were made by Mary Sears, in whom the present author would have far less confidence.

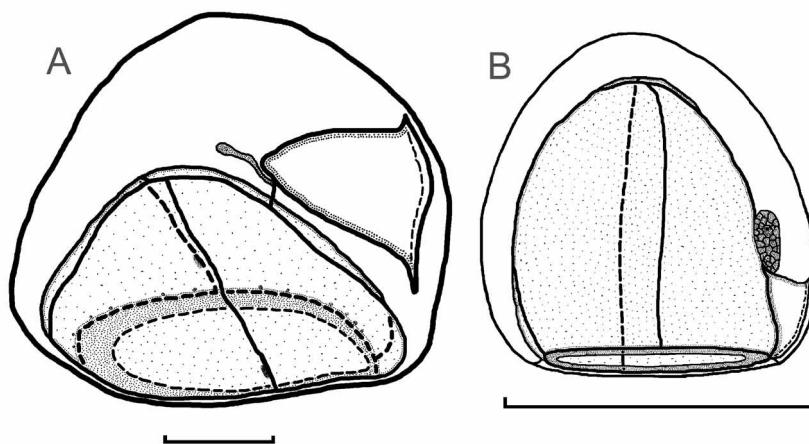


FIGURE 19. A. Calyconula stage of *Lilyopsis medusa*. Redrawn from C. Carré (1969) fig. 3A. B. *Sphaeronectes bougisi*. Redrawn from C. Carré (1968a) fig. 1A). Scale bar 1 mm.

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So if *Sphaeronectes koellikeri* is, as it appears, not present in Monterey Bay then what species might Mary Sears have identified it as? The specimens were unlikely to be of any other *Sphaeronectes* species because they are all, including the three new species described herein, of the *irregularis*-type, which should be clearly distinguishable from *S. koellikeri*, if not from each other. The obvious candidate would appear to be *Lilyopsis medusa* Metschnikoff, 1870¹ as this species has frequently been collected by SCUBA divers in that area. This thought was further enhanced when, by chance, I came across some old correspondence from my late and much lamented friend Francesc Pagès. He, whilst working in Japan, believed that he had found a new species of *Sphaeronectes* but, on thorough examination, found it to be the calyconula stage, i.e. the larval nectophore, of *L. medusa*. A quick glance at C. Carré's (1969) figure (see Figure 19A) clearly shows the resemblance between this calyconula and a *Sphaeronectes* species, particularly *S. koellikeri*. Indeed, C. & D. Carré (1969, p. 363) commented "Par ailleurs, il est intéressant de remarquer que le développement de *Lilyopsis rosea* et celui de *Sphaeronectes gracilis* ..., bien que se déroulant suivant des modalités différentes, aboutissent à des calyconulas âgées, très proches morphologiquement" [Moreover, it is interesting to note that the development of *Lilyopsis rosea* and of *Sphaeronectes gracilis* ..., although taking place according to different modalities, leads to some morphologically very similar older calyconulas]. So even they recognised the similarity between the larval nectophores of these two species. It is thus concluded that the specimens mentioned by Bigelow & Leslie (1930) as *S. truncata* most likely belonged to *L. medusa*.

In his paper redescribing *Lilyopsis rosea* [= *L. medusa*] C. Carré (1969) noted the very striking feature that for both the larval and definitive nectophores the lateral radial canals did not arise directly from the pedicular canal, but from the upper canal close to the apex of the nectosac. Further these lateral canals did not branch off together, but at two closely associated positions (Figure 19A). In the larval nectophore these canals have a straight course to the ostial ring canal, while in the definitive nectophore they follow an S-shaped course. C. Carré (*ibid.*, p. 78) even went as far as to say "Les quatre canaux radiaires ne sont pas concourants, caractère exceptionnel pour les nectophores de Siphonophores" [The four radial canals are not convergent, an exceptional character for the nectophores of siphonophores]. So, one asks oneself, if this character was so unusual, why did C. Carré (1968a) not draw greater attention to the fact that exactly the same arrangement of the radial canals was found on the nectophores of his new species *Sphaeronectes bougisi*? Although his six specimens of *S. bougisi* are small (1mm in height) (see Figure 19B) compared with the larval nectophore of *L. medusa* (2–3 mm), and the arrangement of the somatocyst and hydroecium is quite different, one is led to suspect that what C. Carré (1968a) actually described is a calyconula larva of a *Lilyopsis* species. However, there are two arguments against such a conclusion. Carré described the siphosomal stolon as being very short, but bearing 3–4 cormidial buds and, posteriorly, a reasonably well-developed cormidium. Certainly several siphosomal buds can be seen in his photograph (Carré, 1968a, figure 2) of one of the specimens. This would suggest that no further nectophore was developed, as one would have expected if it belonged to a *Lilyopsis* species, and thus, as is characteristic for *Sphaeronectes* species, the larval nectophore is retained into adult life as the sole nectophore. Secondly, Carré described the terminal cormidium as bearing a hemispherical bract with a globular phyllocyst. This again is more characteristic of a *Sphaeronectes* species than a *Lilyopsis* one, whose bracts have the characteristic prayid arrangement of bracteal canals rather than a phyllocyst.

1. This is another example of where Totton (1965) has failed to use precedence in establishing a specific name. Totton recognised two species in the genus *Lilyopsis*, namely *L. rosea* Chun, 1885, which he designated the type species of the genus, and *L. gracilis* (Fewkes, 1883); although he doubted that the two species could co-exist in the Mediterranean. Subsequently C. Carré (1969) showed that the latter species represented the larval nectophore of the former and he followed Totton in retaining the name *L. rosea*. However, not only does the name *gracilis* have precedence, but it too is preceded by two other names, namely, *diphyes* (for *Praya diphyes* Graeffe, 1860) and *medusa* (for *P. medusa* Metschnikoff, 1870). Although Graeffe's (1860) description and illustrations are excellent, and clearly show the species in question, the name cannot be used as it is pre-occupied. However, although Metschnikoff's (1870) illustrations are not good, there is no reason not to use his name, *medusa*, as Bigelow (1911) and Moser (1925) had previously suggested.

In conclusion it is considered that presently six species of *Sphaeronectes* should be recognised, namely: *S. koellikeri*, *S. irregularis*, *S. brevitruncata*, *S. gamulini*, *S. fragilis*, and *S. bougisi*, although the present author still has some lingering doubts about the validity of the last of these. Three more species will herein be described from material collected in Monterey Bay, California. It is likely that one of these is the species that Fewkes's (1889) "described" as *S. gigantea* but, as noted above, the description was inadequate and the name must be treated as a *nomen nudum*, especially as the original material has not been traced.

Descriptions

Sphaeronectes christiansonae sp. nov.

Diagnosis: Large hemispherical nectophore, c. 10 mm in height, with nectosac extending to 80% of it. Deep hydroecium stretching to half height of nectosac. Small, up to 1.5 mm in length, cylindrical, upright somatocyst, without obvious pedicle. Lateral radial canals looped, with secondary curve on descending part. Somatocyst and phyllocyst deep red in colour.

Material examined: Two specimens collected by the ROV *Tiburon* during Dives 842 (7th May 2005; 35°29.96'N, 123°51.99'W; depth of collection 508 m) and 987 (16 May 2006; 35°30.86'N, 122°39.73'W; depth of collection 840 m). The specimens were initially fixed in 5% formalin, and latter transferred to Steedman's preserving fluid. The specimen from *Tiburon* Dive 987 has been designated the type and is deposited at the Smithsonian's National Museum of Natural History (USNM1124194).

Description: Each specimen, when collected, consisted of a single nectophore, and the proximal part of the siphosome, which was contracted into the hydroecium. The main part of the siphosome was, unfortunately, broken off during collection.

Photographs of the type specimen, taken on board the R.V. *Western Flyer*, are shown in Figure 20.

Nectophore: The single nectophore (Figure 21) was approximately hemispherical in shape, and in life measured 10–11 mm in height and 9.5–10 mm in greatest diameter. After preservation the nectophores shrunk in size and became distorted. For the type specimen this resulted in a considerable decrease in the diameter of the specimen, particularly in the anterior and distal parts, where the mesogloea was much thinner, resulting in the nectosac appearing to occupy virtually all of that space and the whole nectophore appearing almost conical. The hydroecium, on the proximal side of the nectophore, extended from the base of the bell up to about two fifths of its height. It was widely open at its base but rapidly narrowed in its upper half. It had a maximum depth of 2.5 mm and was open, proximally, for all its height. In the living specimen its upper, anterior surface was not straight, being deflected posteriorly by a bulge of mesogloea. However, in its preserved state this surface became almost flat, in the type specimen, or bulged convexly up into the mesogloea in the other specimen.

The somatocyst arose from the point of insertion of the siphosomal stem at the distal apex of the hydroecium and, in the live specimens, was directed upwards. For the type specimen, the proximal end of the somatocyst rapidly increased in diameter, and then formed a cylindrical process, 0.5 mm in diameter and 1.1 mm in length. In the *Tiburon* Dive 842 specimen (Figure 20) the somatocyst was more club-shaped and reached a length of 1.5 mm. Although in both the living specimens the somatocyst was directed anteriorly, after preservation the somatocyst tended to lie more obliquely, slanting towards the proximal side. The most characteristic feature of the somatocyst, however, was its pigmentation (Figure 20). It was mainly filled with pigmented granulated material that, where densest, appeared dark, almost brownish, red, but where less dense, at the proximal and toward the distal ends, appeared more yellowish. However, the distal end of the somatocyst appeared to be devoid of any granules and thereby pigmentation. This was particularly noticeable on the *Tiburon* Dive 842 specimen (Figure 20, middle right) where there was a clear patch surrounding a central core of pigmented material, but it could also be seen across the whole of the distal end of the type specimen (Figure 20, upper right). None of this pigmentation was retained after preservation.

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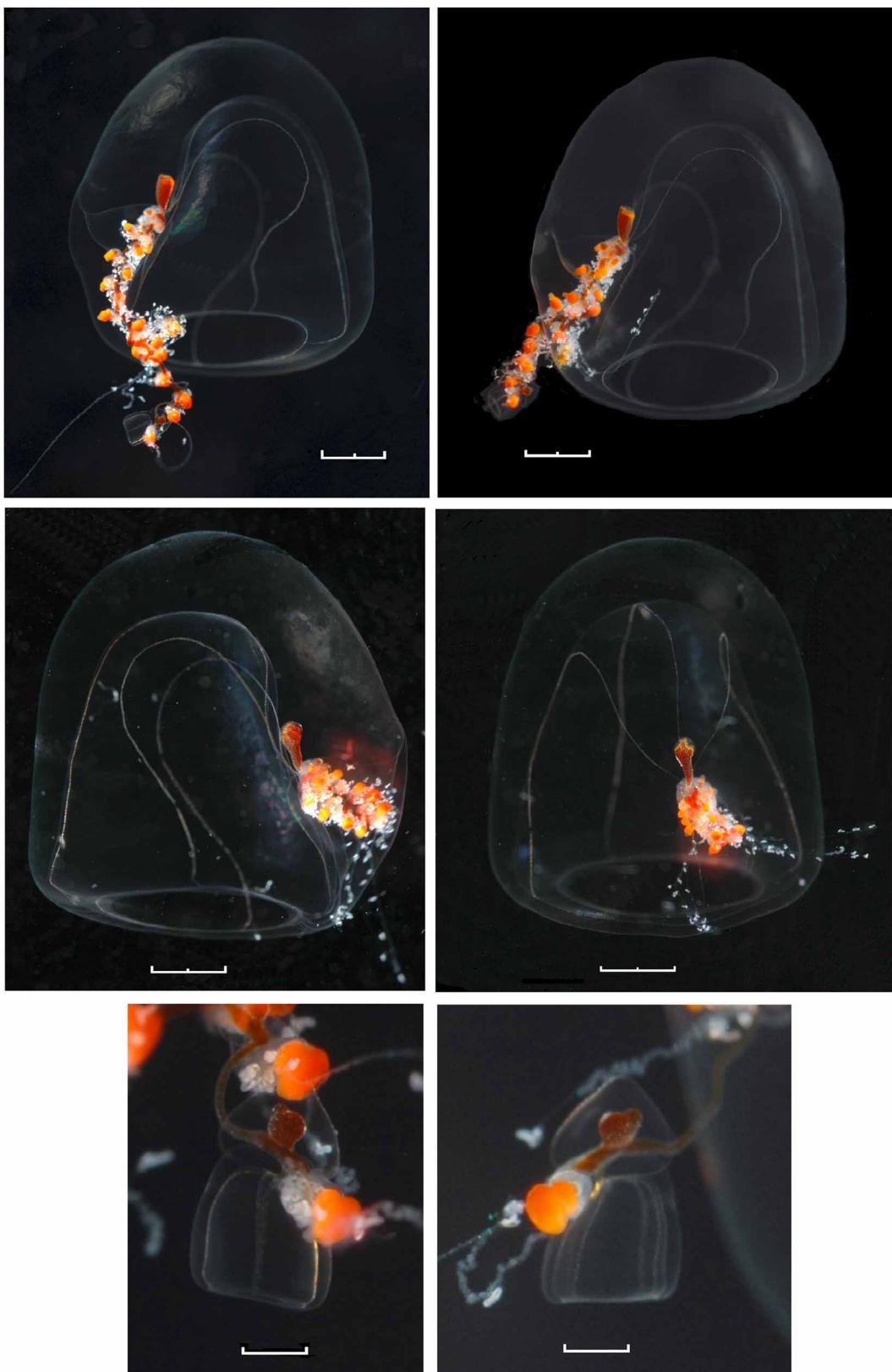


FIGURE 20. *Sphaeronectes christiansonae* sp. nov. Top. Two views of entire type specimen. Scale bar 2mm. Middle. Two views of Tiburon Dive 842 specimen. Scale bar 2 mm. Bottom: Close-ups of oldest stem group of type specimen. Scale bar 0.5 mm. Photographs taken by Dr. S.H.D. Haddock, and reproduced with his kind permission.

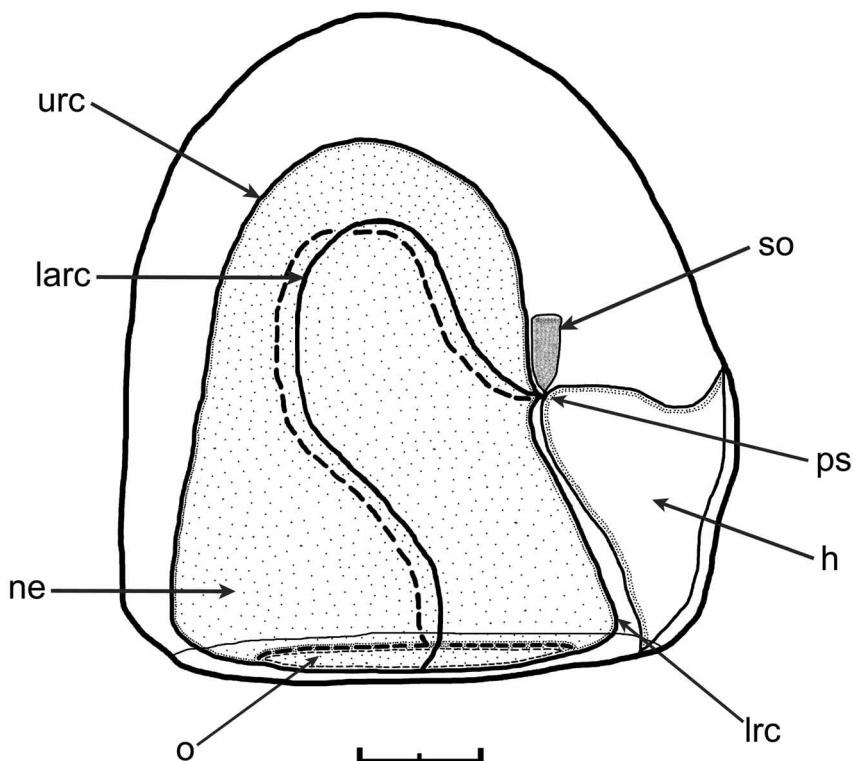


FIGURE 21. Lateral view of *Sphaeronectes christiansonae* sp. nov. nectophore. **h:** hydroecium; **larc:** lateral radial canal; **irc:** lower radial canal; **ne:** nectosac; **o:** ostium; **ps:** point of insertion of siphosomal stem; **so:** somatocyst; **urc:** upper lateral canal. Scale bar 2 mm.

In the living specimens, when relaxed, the nectosac extended to almost four fifths the height of the bell and occupied most of its volume apart from on its proximal (ventral) side. However, during normal contractions or when under stress the nectosac could become considerably distorted. As noted above, that is also the case for the preserved specimens. Close to the ostial opening both the nectophore and the nectosac narrowed considerably so that the broad ostial opening measured c. 5.5 mm in diameter, and was equipped with a narrow velum. From the origin of the somatocyst, and the point of attachment of the siphosome, a very short pedicular canal ran to the nectosac. There it gave rise directly to all four radial canals (Figure 21). The lower radial canal ran directly to the ostial ring canal, while the upper canal passed over the apex of the nectosac and then straight down to the ring canal. The lateral radial canals arched up toward the apex of the nectosac, curved round close to this apex and back toward the mid-line before continuing down to the ostial ring canal, forming a ?-like shape. Close to the ostium, they followed the narrowing of the nectosac and curved inwards toward the ring canal. When observed from certain angles, this could appear as an extra lateral curve.

Siphosome: Unfortunately only the anterior end of the siphosomal stem of both specimens was collected and, for the Tiburon Dive 842, this consisted only of gastrozooids and their tentacles. Fortunately, for the type specimen, a single developing cormidial group, consisting of a bract and gonophore, as well as a gastrozooid and tentacle, was present when the photographs of the living specimen were taken. Unfortunately, this part of the siphosome was then removed and frozen before the specimen was preserved.

The endoderm of the siphosomal stem was chocolate brown in colour (Figure 20 bottom). The proximal half of the endoderm of the most anterior, immature gastrozooids bore pigmentation very similar in colour to that of the somatocyst, while the distal half was a lighter yellowish-orange colour. The whole was surrounded by a relatively thick layer of mesogloea, encase by the ectoderm, with a milk-white appearance (Figure 20). For the more mature gastrozooids, the proximal half was entirely orange in colour, while the distal half was a deeper orange-red. As usual their size and proportions varied greatly according to the degree of contraction or

relaxation. No pigmentation could be seen in the preserved gastrozooid, whose proximal half appeared clear, while in the distal half there were two bands of denser material separate by a constricted part, with less dense material. The cnidobands and terminal filaments of the tentilla appeared milky white in life (Figure 20 bottom). The gastrozooid was attached directly to the stem that, on the more posterior remaining cormidia, was often slightly swollen in its preserved state. Immediately posterior to the gastrozooid was a distinct node. The buds of the bract and gonophore lay just anterior to the gastrozooid and could be seen on most of the remaining cormidia; indicating that their development lagged considerably behind that of the gastrozooid. The tentacle bore numerous lateral excrescences, and the small tentilla were borne on long contractile pedicles (Figure 22). The tentilla were of the basic calycocephoran form with two large mastigophores lying on each side of the proximal part of the cnidoband, and large desmonemes, with distinct spines, at its distal end. The other nematocysts were not examined in detail, but it is presumed that anisorhizas constituted the great majority of nematocysts on the cnidoband itself, while smaller desmonemes and anacrophores were present on the terminal filament.

The single cormidial group of the type specimen that included a bract and gonophore can be seen at the posterior end of the siphosomal stem in Figure 20, and is represented, without the gastrozooid and tentacle in Figure 23. The bract was conical in shape and measured about 1.1 mm across and 0.9 mm in height, and on its proximal side there appeared to be a deep groove through which the siphosomal stem passed. The phyllocyst, which was spherical, with an asymmetrically placed excrescence toward its distal apex, occupied the central region of the bract and was c. 0.3 mm in diameter. It had the same granulated appearance as the somatocyst and was pigmented a deep, brownish red.

The immature gonophore, which bore no sign of a manubrium, was about 1.2 mm in height and diameter. Two of its lateral radial canals appeared to be slightly arched close to their point of origin, before passing directly to the ostial ring canal. The photographs (Figure 20, bottom) seem to indicate that the canals initially arose in pairs, but unfortunately this cannot be confirmed at present. It is presumed that this very young cormidial group would grow considerably in size before being released as an eudoxid.

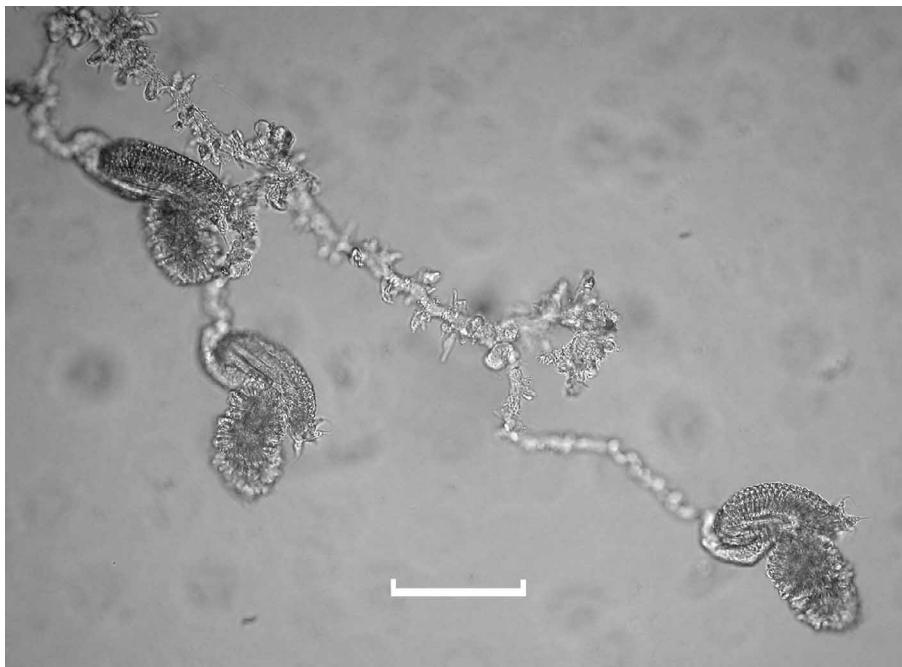


FIGURE 22. *Sphaeronectes christiansonae* sp. nov. Part of tentacle from type specimen. Scale bar 100 µm.

Distribution: With only two known specimens, both from a limited area of Monterey Bay, California, we can say very little about its geographical distribution. However, given that many of the species described from the Mediterranean have also been found in very different locations, for instance off Chile (see Appendix), *Sphaeronectes christiansonae* may yet be found in other areas. The main problem for studying *Sphaeronectes*

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species is their fragility, which means that they are rarely collected in coarse meshed nets. Even if caught, after preservation the general distortion of the nectophore may conceal important morphological characters. The specimens of *S. christiansonae* were caught at depths of 508 and 840 m. The only *in situ* frame grabs of the species that could be found in the VARS Library at MBARI were for the *Tiburon* Dive 987 specimen. These pictures, although of poor quality, clearly showed the dark red pigmented stem and somatocyst that are so characteristic of this species.

Remarks: *Sphaeronectes christiansonae* is clearly distinguished from all previously described species not only by its sheer size, although as will be seen that also applies to the two other new species described herein, but by the presence of the deep red, even brownish pigmentation in the somatocyst, phyllocyst and gastrovascular cavity. No such pigmentation has ever been noted on any other *Sphaeronectes* species.

The surface of the nectophore emitted a bright green fluorescence under blue excitation (S.H.D. Haddock, personal communication).

Etymology: Named for Lynne Christianson of the Monterey Bay Aquarium Research Institute whose help, whether it be during my visits to MBARI or in answering numerous questions, has been so invaluable to me.

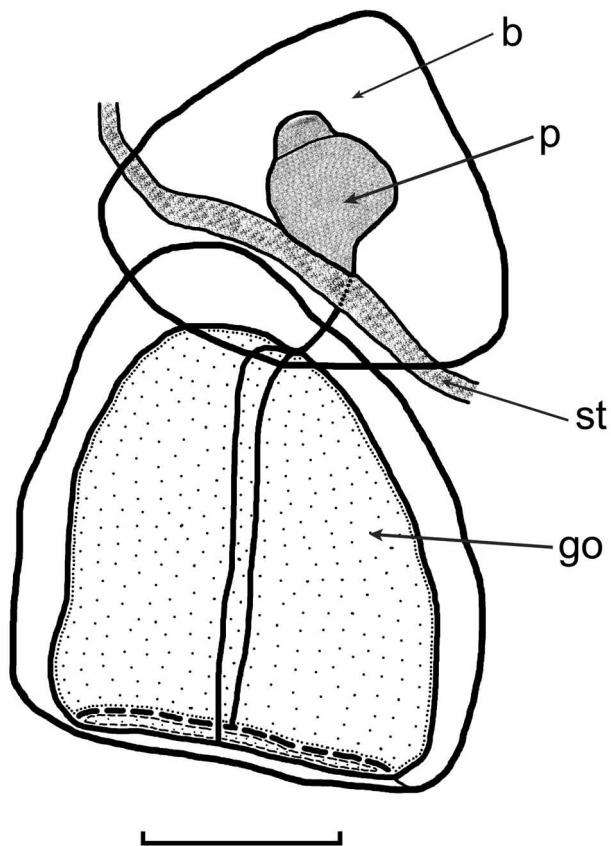


FIGURE 23. *Sphaeronectes christiansonae* sp. nov. Developing stem group originally on the type specimen of *Sphaeronectes christiansonae*. b: bract; go: gonophore; p: palpon; st: stem. Scale bar 0.5 mm.

***Sphaeronectes haddocki* sp. nov.**

Diagnosis: Large cylindrical nectophore, with rounded apex, up to 11.5 mm in height. Nectosac extensive, occupying 87% of height of nectophore. Hydroecium extending to 45% height of nectosac, but not fully open on proximal side. Ovate vertical somatocyst, without pigmentation, with characteristic, mainly horizontal, pedicle. Lateral radial canals looped, with secondary curve on descending part.

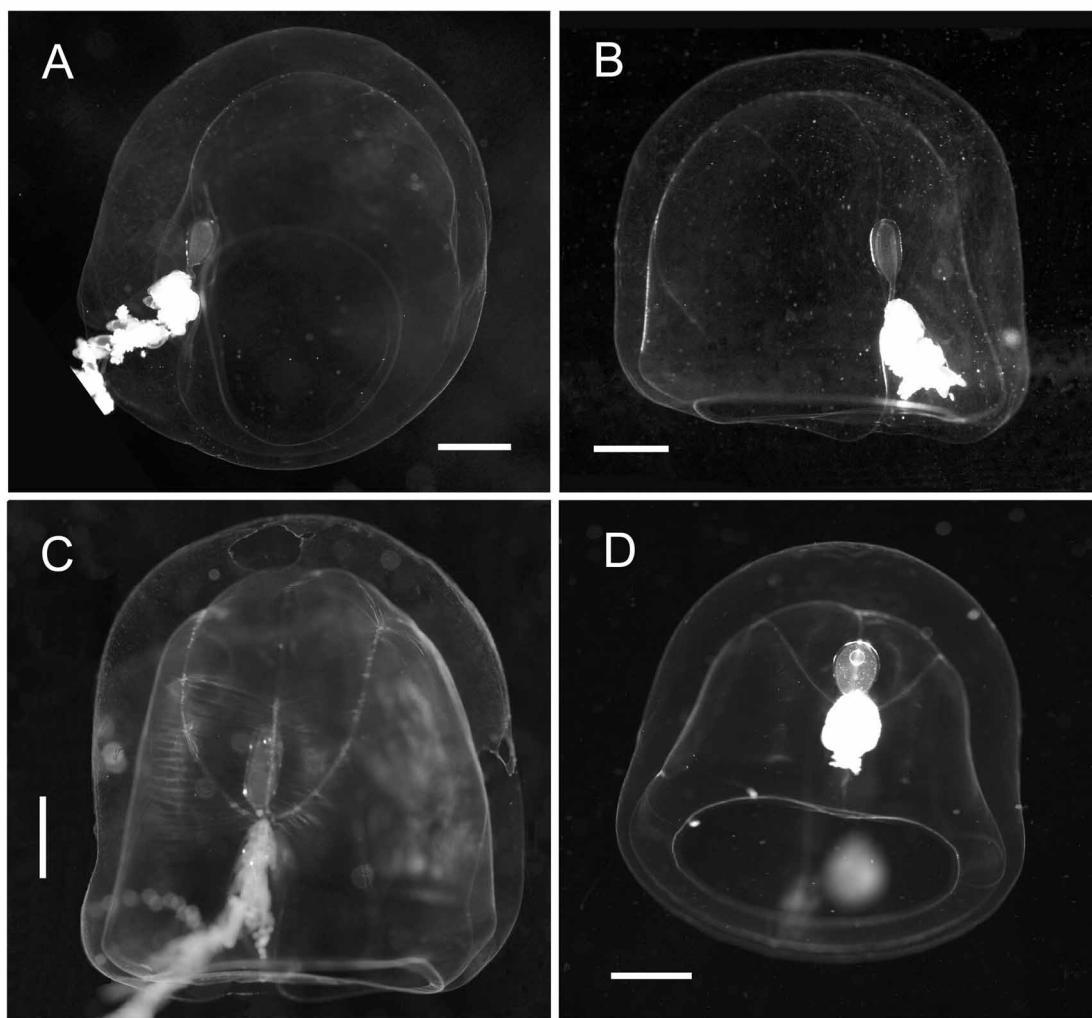


FIGURE 24. *Sphaeronectes haddocki* sp. nov. Laboratory photos of specimens from A. & B. *Tiburon* Dive 987; C. *Tiburon* Dive 1156 (type specimen); and D. *Tiburon* Dive 1157. Photos taken by S.H.D. Haddock (A. & B.) and C.W. Dunn (C. & D.), and reproduced by their kind permission. Scale bar 2 mm.

Material examined: Four specimens collected by the ROVs *Ventana* and *Tiburon*. *Ventana* Dive 2623 (7th February 2005; 36°41.87'N, 122°03.49'W; depth of collection 354 m); *Tiburon* Dive 987 (16th May 2006; 35°30.86'N, 122°39.73'W; depth of collection 397 m); *Tiburon* Dive 1156 (1st December 2007; 35°42.24'N, 122°34.75'W; depth of collection 412 m); and *Tiburon* Dive 1157 (2nd December 2007; 36°41.76'N, 122°04.98'W; depth of collection 433 m). The specimens were initially fixed in 5% formalin, and latter transferred to Steedman's preserving fluid. The specimen from *Tiburon* Dive 1156 has been designated the type and is deposited at the Smithsonian's National Museum of Natural History (USNM1124195).

Description: Each specimen, when collected, consisted of a single nectophore, and the proximal part of the siphosome. The main part of the siphosome was, unfortunately, broken off during collection. Photographs of various specimens, taken shortly after recovery of the ROV, are shown in Figure 24.

Nectophore: The single nectophore (Figures 24 & 25) present with each specimen was cylindrical in shape with a rounded, convex apex and in life measured from 9 to 11.5 (type specimen) mm in height and c. 10.5 mm in diameter. The nectosac occupied the great majority of the nectophore, and extended to 0.87 of the nectophore height. On its proximal side it was indented toward its mid-line to afford space for the hydroecium and the somatocyst. Slightly above the ostial opening both the nectophore and the nectosac narrowed considerably so that the broad ostial opening measured about 7 mm in diameter but, according to the degree of contraction of the nectosac, occasionally was smaller. It was equipped with a narrow velum. After preservation the nectophores shrunk considerably in size and became distorted. There was a considerable

decrease in the diameter of the type specimen, particularly in its upper and distal regions, where the mesogloea was much thinner, resulting in the nectosac appearing to occupy virtually all of that space.

The hydroecium had a maximum depth of 2.5 mm and extended to about two fifths the height of the bell, on its proximal side. It was widely open at its base, forming two large lateral flaps that, in the preserved specimens, tended to fold down and extend below the ostial level. It gradually decreased in width up to its apex and, in the living specimen, it was open on its proximal side for only about two-thirds of its height. The siphosomal stem was attached at the upper distal corner of the hydroecium of the nectophore. Here too was the point of origin of the somatocyst. However, no obvious pedicular canal arose at this point; the wall of the nectosac being closely applied to the apex of the hydroecium in this region. Several other *Sphaeronectes* also have what Carré (1969c) described as a "virtuel" pedicular canal. The four radial canals arose together from this point with the lower canal running directly to the ostial ring canal down the median indentation of the nectosac. Similarly the upper canal passed up this median indentation then over the apex of the nectosac and then straight down to the ring canal. The lateral radial canals arched up toward the apex of the nectosac, curved round close to this apex and back toward the mid-line before continuing down to the ostial ring canal. Close to the ostium, they followed the narrowing of the nectosac and curved inwards toward the ring canal. Their course was very similar to that described above for *Sphaeronectes christiansonae*.

The somatocyst had a very characteristic shape. A broad pedicle arose from its point of origin and, at first, followed the contours of the hydroecium, running a short distance up its distal side to its apex and then bending through 90° and running proximally for a short distance before bending up, again through 90°, and giving rise to the main part of the somatocyst. In all, the pedicle was c. 0.8 mm in length. The main part of the somatocyst expanded into a large ovate structure up to 2 mm in height and 1.3 mm in diameter. In life it had a very pale whitish hue, with apparently homogeneous contents, although occasionally oil droplets were present (Figure 24D). It was covered with a honeycomb of large, but indistinct cells.

Siphosome: Of all the photographs of the living specimens only those of the Ventana Dive 2623 specimen show any signs of well-developed cormidia, but these pictures are too poor to reproduce. However, they do show a barrel-shaped gonophore, but with little sign of a manubrium, and a hemispherical bract whose phyllocyst appears to be small and globular. Unfortunately that posterior part of the stem was not preserved and so no further details on the arrangement of the bract and gonophore could be elucidated. The other specimens, however, retained quite long pieces of the anterior siphosomal stem that, in the case of the type specimen, included more than twenty cormidia. Most of these consisted of a gastrozoid, with its tentacle, attached directly to the stem and just anterior to it two buds, side by side, which represented the primordial bract and gonophore. However, the posterior most four cormidia on the siphosomal stem of the type specimen showed the beginnings of the development of the bract. The oldest of these is shown in Figure 26. Here the mesogloea of the bract has yet to expand to its full extent and its ultimate shape cannot be gauged. The phyllocyst appears as a slightly asymmetric globular process. The gonophore at this stage remains a bud1.

In the preserved specimens, the stem was slightly narrower at the point where each gastrozoid was attached, but there was no sign of the distinctive node seen in *Sphaeronectes christiansonae*. The gastrozooids were, as usual, very variable in shape and, in life, appeared to be colourless. Those of the type specimen were narrow and elongate, measuring 1.5–1.8 mm in length. The basigaster, which was the widest part, occupied the proximal quarter of the gastrozoid, while the small distal proboscis region also was slightly inflated. However, the gastrozoid of the Ventana Dive 2623 and the Tiburon Dive 1157 specimens were much shorter, with the main stomach region greatly expanded. In life the cnidobands of the tentilla were pale yellow in colour. The cnidoband (Figure 27) was of the typical calyphoran form, with a pair of large mastigophores on each side of the proximal part, and some large desmonemes distally. The nematocysts of the long, but highly contracted and convoluted in its preserved state, terminal filament were not examined in detail but were presumed to be the desmonemes and anacrophores typical of other calyphoran species. Both the pedicle of the tentillum and the tentacle itself bore numerous large lateral excrescences.

Distribution: The four specimens of *Sphaeronectes haddocki* that have been examined, together with a further known specimen from Tiburon Dive 1157, all came from a very limited area in the region of Monterey

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Bay, California. They were also collected within a relatively narrow depth range between 354 and 488 m. Further specimens can almost certainly be identified from the *in situ* frame grabs, taken during various dives of *Ventana* and *Tiburon*, in the VARS Library at MBARI. These were all taken within the 391 to 498 m depth range; further suggesting that this species has a limited depth range.

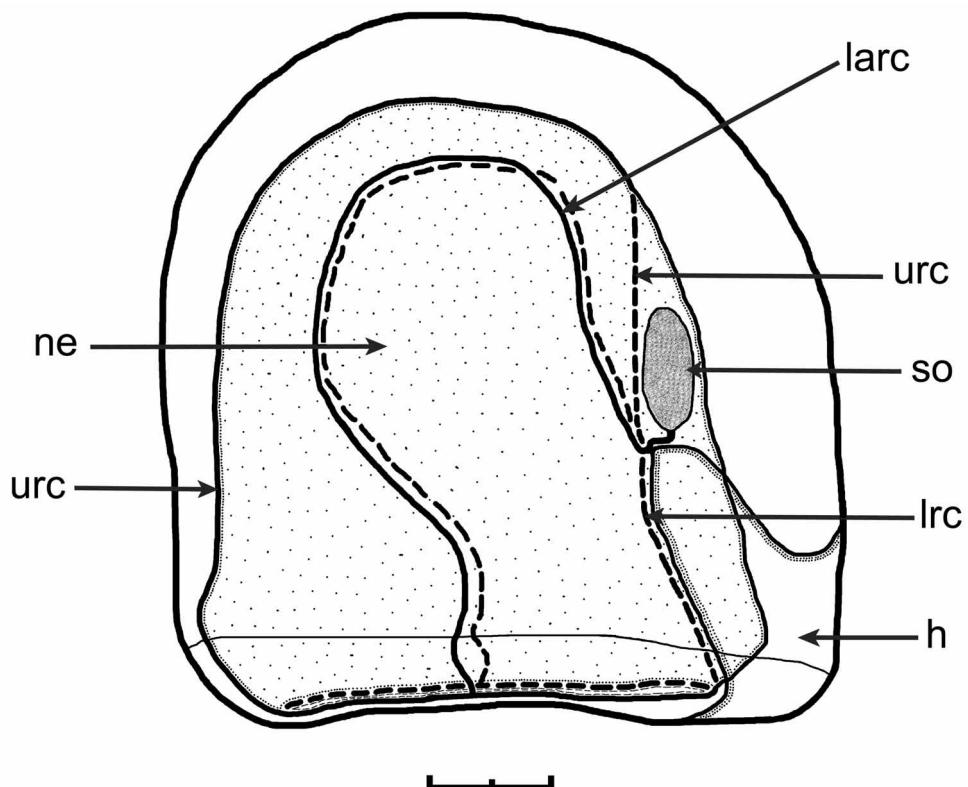


FIGURE 25. *Sphaeronectes haddocki* sp. nov. Lateral view of nectophore. For annotations see legend to Figure 21. Scale bar 2 mm.

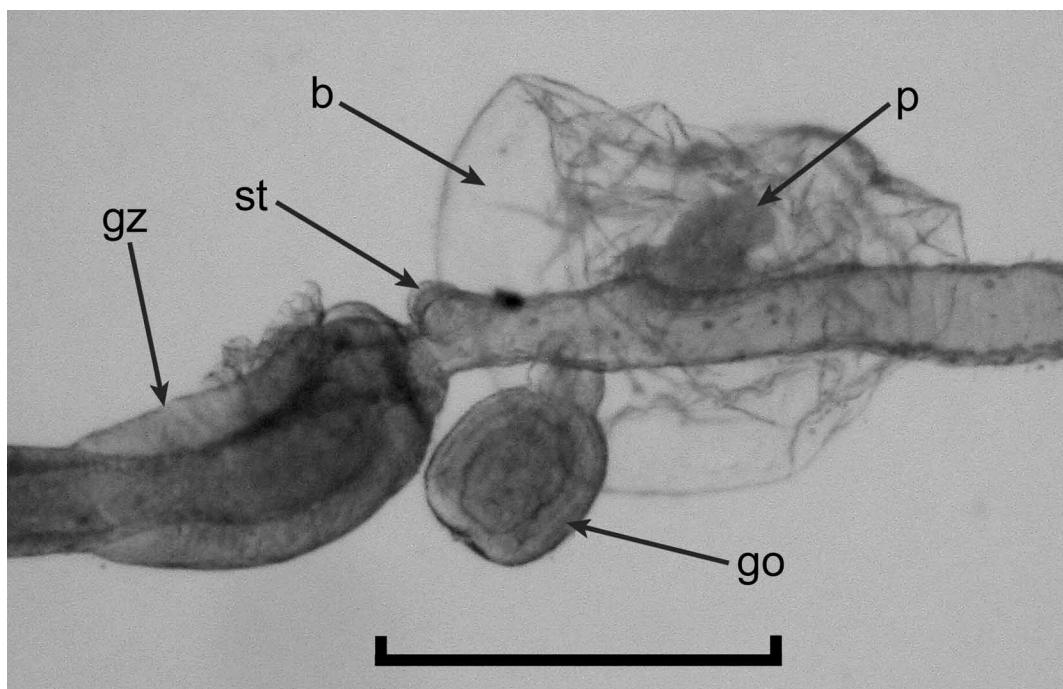


FIGURE 26. *Sphaeronectes haddocki* sp. nov. Part of siphosomal stem of type specimen of *Sphaeronectes haddocki* sp. nov. showing a gastrozooid (gz), anterior to which is a developing gonophore (go) and a bract (b), with its phyllocyst (p). st represents the point where the stem was broken. Scale bar 0.5 mm

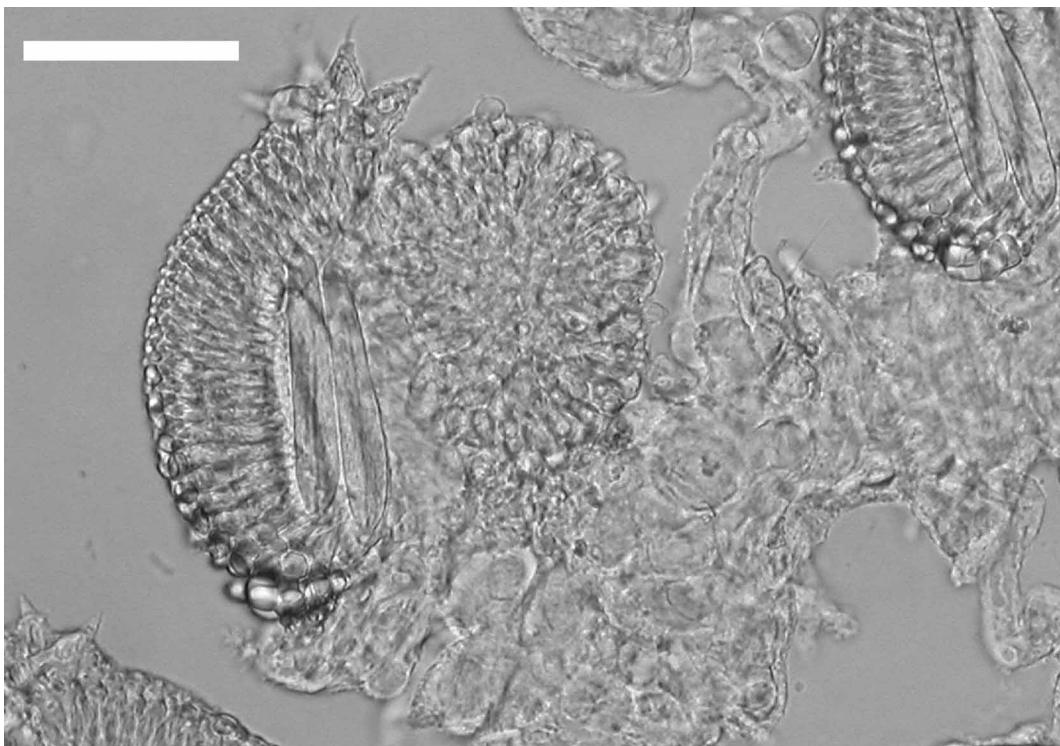


FIGURE 27. Tentilla of *Sphaeronectes haddocki* sp. nov. Scale bar 50 µm.

Remarks: Although of similar size to *Sphaeronectes christiansonae*, *S. haddocki* is easily distinguished from it not least by the absence of deep red pigmentation. In addition, the general shape of the nectophore is different and the presence of the large pale milky-white somatocyst can clearly be seen in some of the *in situ* frame grabs. The arrangement of the somatocyst is very characteristic of this species. Like *S. christiansonae*, the surface of the nectophore of *S. haddocki* was found to emit bright green fluorescence (S.H.D. Haddock, personal communication).

Etymology: *Sphaeronectes haddocki* is named in honour of Professor Steven Haddock of the Monterey Bay Aquarium Research Institute who has not only kindly invited me to participate in several of his cruises, but has always taken a keen interest in siphonophores.

Sphaeronectes tiburonae sp. nov.

Diagnosis: Large hemispherical nectophore, somewhat truncated on its proximal-basal side, 8 mm in height. Nectosac restricted to lower two-thirds of nectophore. Hydroecium small and tubular, up to one-third height of nectosac. Minute globular somatocyst, 0.25 mm in diameter. Lateral radial canals extending up to close to apex of nectosac, but then curving and running directly to ostium.

Material examined: A single specimen collected during *Tiburon* Dive 981 (11th May 2006; 36°36.13'N, 122°22.57'W: depth of collection 1896 m). The specimen was initially fixed in 5% formalin, and later transferred to Steedman's preserving fluid. It is designated the type and is deposited at the Smithsonian's National Museum of Natural History (USNM1124196).

Description: The specimen consisted of a single nectophore, and a short part of the anterior region of the siphosome, which was tightly contracted into the hydroecium. The posterior part of the siphosome was broken off during collection. Photographs of the somewhat stressed specimen, taken shortly after recovery of the ROV, are shown in Figure 28.

Nectophore: The fragile nectophore (Figures 28 & 29) was hemispherical in shape with a rounded, convex apex, rather *Sphaeronectes haddocki*, although it was obliquely truncated on its proximal side between the top

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of the external opening of the hydroecium and the base of the nectophore. In life it measured 8 mm in height and 8 mm across, in the proximal-distal direction, and 7.8 mm in the lateral direction. There was a slight decrease in the diameter of the nectophore above the ostium, but nowhere near as marked as in the two species described above. Nonetheless the ostial opening was quite narrow, measuring 4.5 mm in diameter. Typically it was equipped with a narrow velum.

The animal, when being photographed in the laboratory on board ship, was clearly stressed, probably as a result of temperature shock, and its nectosac underwent a number of violent contortions, such that it was difficult to establish its true relaxed condition. Some of the photographs showed the nectosac to be conical, with a pointed apex, but the configuration shown in Figure 28 (bottom) appeared to closest to the relaxed state. Based on this, the height of the nectosac was c. 5.5 mm, and thus it stretched to approximately two-thirds the height of the nectophore itself. After preservation the nectophore shrank considerably in size and became greatly distorted, with the only obvious features being the hydroecium packed with the siphosomal stem, and the minute somatocyst, while the nectosac was very shallow and difficult to distinguish, with no signs of any radial canals.

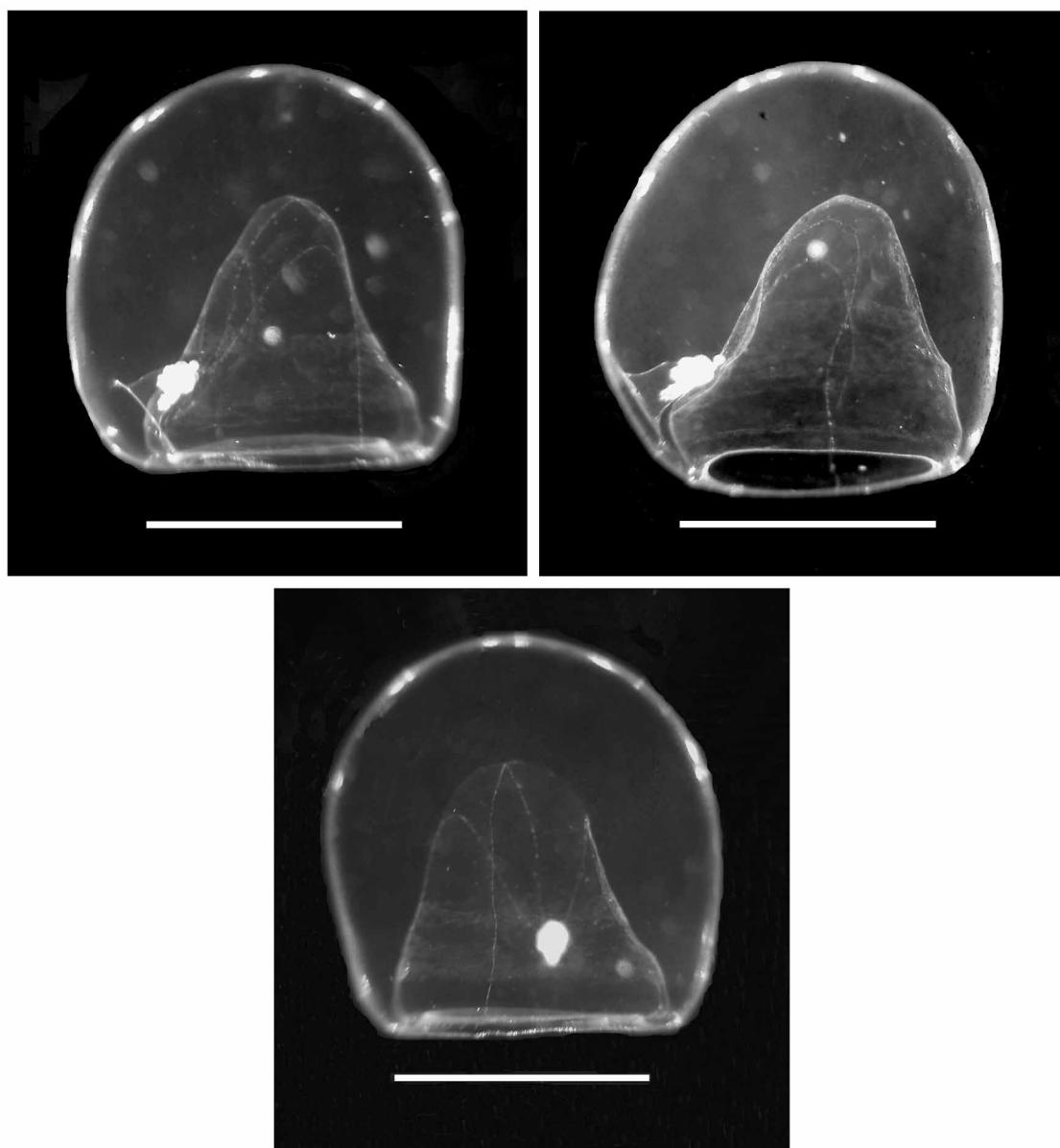


FIGURE 28. *Sphaeronectes tiburonae* sp. nov. Three views of the somewhat stressed nectophore of shortly after recovery of the ROV. Scale bar 5 mm.

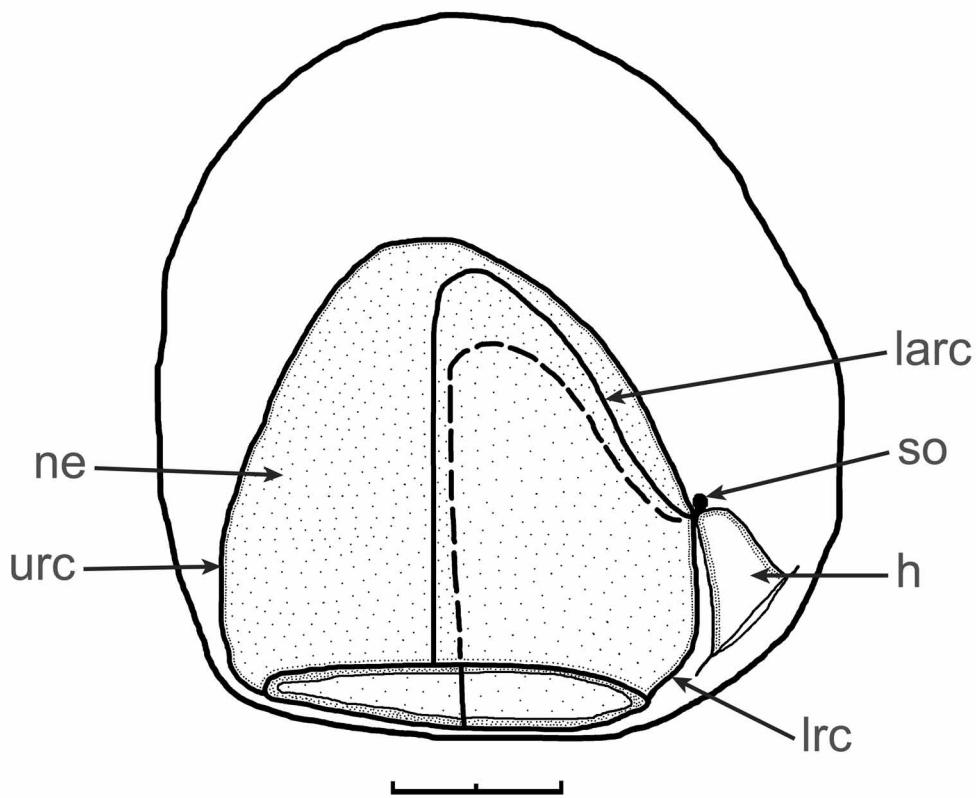


FIGURE 29. *Sphaeronectes tiburonae* sp. nov. Lateral view of nectophore. For annotations see legend to Figure 21. Scale bar 2 mm.

The hydroecium was small and tubular, with only a relatively small opening onto the proximal side of the nectophore, and extended up to about one third the height of the nectosac. Typically the siphosomal stem was attached to the nectophore in the upper distal corner of the hydroecium, and at that point arose the somatocyst, which was without an obvious pedicle. The somatocyst was globular in shape and minute in size, measuring only 0.25 mm in diameter. In relative terms, with regard to the size of the nectophore, the somatocyst of *Sphaeronectes tiburonae* is by far the smallest of any *Sphaeronectes* species. No pigmentation was observed in the somatocyst, but it was seen to contain numerous oil droplets of varying sizes. As with *S. haddocki*, there was no obvious pedicular canal connecting the somatocyst to the nectosac. The four radial canals arose together, with the upper canal running over the apex of the nectosac and then down to the ostial ring canal, and the lower canal running directly down to it. The lateral radial canals looped upwards to close to the apex of the nectosac, but then curved down and ran directly to the ostial ring canal, without forming the additional loop that was found on the nectophores of the species described above. On the proximal side of the nectosac the angle between the upper canal and each of the lateral canals was c. 30°.

Siphosome: As noted above only the very anterior most part of the siphosomal stem remained with the specimen, and this was greatly contracted into the hydroecium. The cormidia were at a very early stage of development and no useful observations could be made concerning them.

Distribution: The species is known from a single specimen collected in the vicinity of Monterey Bay, California, at a depth 1896 m. There are several *in situ* frame grabs of probable *Sphaeronectes* specimens in the VARS database at MBARI that were taken between depths of 1385 and 2764 m. This depth range is very different from that known for the other two species described herein and so the records may refer to *S. tiburonae*, although one cannot discount the possibility that yet another *Sphaeronectes* species might be present at deeper depths.

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Remarks: Although the nectophore of *Sphaeronectes tiburonae* is only slightly smaller than those of *S. christiansonae* and *S. haddocki*, the former can easily be distinguished on the basis of its minute somatocyst, its less curved lateral radial canals, and the small tubular hydroecium.

Etymology: *Sphaeronectes tiburonae* is named for the ROV *Tiburon* whose pilots so skilfully collected most of the specimens of the species described herein, and a great number of other siphonophore species beside. Unfortunately the ROV is now decommissioned, and it remains to be seen whether its replacement can be manoeuvred as skilfully.

Discussion

Phylogenetic position of the family Sphaeronectidae

As noted above there has been much discussion as to the phylogenetic position of the family Sphaeronectidae amongst the calycophoran siphonophores. Bigelow (1911), summarising the thoughts of previous authors, considered that the sphaeronectid-like species were the ancestral calycophorans from which the other calycophoran families, Hippopodiidae, Prayidae, and Diphyidae plus Abylidae, were separately derived. Of the two species, which are currently considered to belong to the family Clausophyidae that were known at that time, Bigelow placed one of them (*Kephyses ovata* (Keferstein & Ehlers, 1860)) within the diphyid genus *Galeolaria* (= *Sulculeolaria*) and the other (*Clausophyes galeata* Lens & van Riemsdijk, 1908) he doubtfully included within his sub-family Nectopyramidinae. Nonetheless, Bigelow placed the latter sub-family, and the sub-family Muggiinae, alongside the Sphaeronectinae, within the family Sphaeronectidae.

Moser (1925) also maintained these three sub-families within what she called the Monophyidae, and added a fourth sub-family, the Heteropyramidinae. She also agreed that the monophyids were the most primitive calycophorans and that their ancestors gave rise to all the other calycophorans, and indeed to the Physonectidae. It was Totton (1932) who finally showed that the grouping together of these sub-families was unnatural, considering the family Sphaeronectidae to include only the genus *Sphaeronectes*, but Totton (1954) still considered the genus to be of the ancestral calycophoran type. Leloup (1954) on the other hand believed that sphaeronectids were neotenous monophyids that had evolved, as an offshoot, from precursors to the family Prayidae, which themselves were a descendant of hippopodiid-like ancestors. Later Totton (1965) changed his opinion and considered the sphaeronectids to be descended from precursors to the family Abylidae, which he considered to be the most advanced of all calycophoran families.

Stepanjants (1967) was the only recent author to consider not only that the recognised *Sphaeronectes* species should be split amongst two genera, but that these genera were by no means closely related to each other. Thus she considered that the ancestors of *Sphaeronectes koellikeri* were to be found amongst the family Prayidae, while those of *Monophyes irregularis*, although her illustration (*ibid.* fig. 53) is actually of *S. brevitruncata*, was a neotenic form close to the larvae of the family Diphyidae.

Molecular phylogenetic data will no doubt throw some light on the position of the family Sphaeronectidae. To date the only published data are those for *Sphaeronectes koellikeri* (as *S. gracilis*) given by Dunn *et al.* (2005). For the Calycophorae as a whole, their data indicate that the ancestral calycophoran family is the Prayidae, which gave rise, on the one hand, to the family Hippopodiidae, and on the other to all the other calycophoran families; firstly the Clausophyidae, then the Sphaeronectidae and finally the Diphyidae plus Abylidae, with the latter not being clearly distinguishable from the former. However, only one abylid species was included in that analysis. More recently preliminary data for the 18S gene of *Sphaeronectes christiansonae* have become available (S.H.D. Haddock, personal communication), and these show that this species is sister to *S. koellikeri*. This would appear to indicate that it is appropriate to include all known sphaeronectid species in a single genus, and that Stepanjants's (1967) separation not only into different genera, but also different families, is invalid. Nonetheless, we await more molecular data for both further genes and other species.

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TABLE 1. Principal characters of the nectophores of the species of the genus *Sphaeronectes* Huxley. Adapted and extended from Carré (1968c)

Species	<i>S. christiansonneae</i>	<i>S. haddecki</i>	<i>S. tiburonae</i>	<i>S. koeilkeri</i>	<i>S. frigilis</i>	<i>S. irregularis</i>	<i>S. brevitruncata</i>	<i>S. gamulinii</i>	<i>S. bougisi</i>
(Scale bars 1 mm)									
Height of nectophore	10-11 mm	9-11.5 mm	8 mm	6 mm	5 mm	3 mm	2.8-3.55 mm ⁱⁱ	1.5 mm	1 mm
Diameter of nectophore	9.5-10 mm	10.5 mm	7.8-8 mm	6 mm	5 mm	3 mm	6 mm ⁱⁱⁱ	2.4-2.7 ⁱ	0.8 mm
Shape of nectophore	Hemispherical	Cylindrical, with rounded apex	Hemispherical	Spheroidal	Asymmetric	Hemispherical	Spheroidal	Asymmetric	Hemispherical
Height of nectosac relative to nectophore	0.8	0.87	0.67	0.5	0.9	0.67	0.7 ²	0.75	0.8
Pedicular canal	Short, but visible	Virtual	? Virtual	Short, but obvious	Virtual	Virtual	? virtual	Short, but visible	Virtual
Position of insertion of pedicular canal onto nectosac	Proximal, at 1/2 height of nectosac	Proximal, at 0.45 height of nectosac	At apex	Proximal, at 1/3 height of nectosac	Proximal, at 2/5 height of nectosac	From pedicular canal	Proximal, at 1/2 height of nectosac	Proximal, at 1/2 height of nectosac	At apex
Origin of lateral radial canals	From pedicular canal	From pedicular canal	From pedicular canal	From pedicular canal	From pedicular canal	From pedicular canal	From pedicular canal	From pedicular canal	Separately from upper canal
Course of lateral radial canals in ventral view	Looped, with a secondary curve on the descending branch	Looped, with a secondary curve on the descending branch	Curved	Straight, with a slight curve close to the origin	Looped, with a secondary curve on the descending branch	Curved	Looped, with a secondary curve on the descending branch	Curved	Straight

to be continued.

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Species	<i>S. christiansenae</i>	<i>S. nattostaki</i>	<i>S. turronae</i>	<i>S. koellikeri</i>	<i>S. jaglits</i>	<i>S. irregularis</i>	<i>S. brevistruncata</i>	<i>S. gamatum</i>	<i>S. boungisi</i>
angle of two lateral radial canals with upper canal, at origin	45°	45°	30°	90°	45°	60°	?	45° for right and 90° for left	90°
shape of hydroecium	Conical	Conical	Tubular	Tubular, flattened laterally in the proximal region	Conical	Conical, flattened laterally	Conical, flattened laterally	Conical, flattened laterally	Conical
arrangement of hydroecium	In sagittal plane. Deep	In sagittal plane. Intermediate	In sagittal plane. Shallow	In sagittal plane. Deep	In sagittal plane. Shallow	In sagittal plane. Shallow	In sagittal plane. Deep	To left of sagittal plane.	In sagittal plane.
shape and length of somatocyst	Swollen, cylindrical or club-shaped, w/o distinct pedicle	Swollen, ovate with distinct swollen pedicle	Minute, spherical, w/o distinct pedicle	Swollen fusiform with pedicle ≈ same length	Swollen sub-spherical with a very long pedicle	Swollen, pyriform without pedicle	Swollen, cylindrical, (?) with a short pedicle	Intermediate	Shallow
length of somatocyst	1.1-1.5 mm	2 mm	0.25 mm	1.5 mm	1.5 mm	0.3 mm	1 mm	0.35 mm	0.18 mm
position of somatocyst	Vertical in life. Extending obliquely away from nectosac in preservation.	Vertical, extending along proximal border of nectosac	Immediately above apex of hydroecium	Horizontal, extending above apex of nectosac	Vertical, extending along proximal border of nectosac	Vertical, or extending along proximal border of nectosac	Vertical, or projecting into mesogloea away from nectosac.	Horizontal, extending along right lateral side of nectosac, at mid-height	Vertical, extending along proximal border of nectosac

ording to Palma (1984)
ording to Stepanjants (1967) for *Monophyes japonica*
ording to Chun (1892),

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In summary, therefore, the family Sphaeronectidae is considered to include a single genus, *Sphaeronectes*, which presently includes nine species, although the exact status of *S. bougisi* remains to be properly established. The characteristics of the nectophores of these species are summarised in Table 1, and a key to their identifications follows. The Appendix lists the synonymies for the six previously described species, and summarises what is known about their geographical distribution.

Key for the identification of the nectophores of *Sphaeronectes* species.

1	Lateral radial canals straight	2
-	Lateral radial canals curved	3
2	Lateral radial canals arising from upper canal, hydroecium restricted to one side of nectosac. Nectophore minute, c. 1 mm in height	<i>S. bougisi</i>
-	Lateral radial canals arise from pedicular canal, hydroecium extending over apex of nectosac. Nectophore large, up to 8 mm in height	<i>S. koellikeri</i>
3	Somatocyst horizontal, ovoid with a distinct peduncle. Hydroecium asymmetrical. Nectophore small, up to 2.7 mm in height	<i>S. gamulini</i>
-	Somatocyst vertical. Hydroecium symmetrical	4
4	Somatocyst cylindrical.....	5
-	Somatocyst not cylindrical	6
5	Somatocyst long, > 1/6 th height of nectophore	<i>S. brevitruncata</i>
-	Somatocyst short, < 1/9 th height of nectophore	<i>S. christiansonae</i>
6	Somatocyst with distinct pedicle	7
-	Somatocyst without distinct pedicle	8
7	Somatocyst spheroidal with very long, vertical pedicle. Nectophore c. 5 mm in height	<i>S. fragilis</i>
-	Somatocyst large & swollen with distinct, mainly horizontal pedicle. Nectophore large 9–11.5 mm in height.....	<i>S. haddocki</i>
8	Somatocyst pyriform. Nectophore small c. 3 mm in height	<i>S. irregularis</i>
-	Somatocyst minute and globular. Hydroecium small and tubular. Nectophore large c. 8 mm in height ..	<i>S. tiburonae</i>

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Appendix. *Sphaeronectes* species: their synonymies and geographical distribution.

Within the lists of synonymies only those papers that discuss, describe or illustrate the species are included. Undoubtedly the lists are incomplete.

***Sphaeronectes koellikeri* Huxley, 1859 (see Figures 16 & 17)**

Sphaeronectes köllikeri Huxley, 1859, p. 50, Pl. 3 fig. 4; Pagenstecher, 1869, Pl. 21; Chun 1885, p. 513; Agassiz & Mayer, 1899, p. 177, Pl. 16 figs. 51,52; Moser, 1924, p. 5, fig. 6; 1925, p. 97, text-fig. 4d; Trégouboff & Rose, 1957, p. 372, Pl. 76, fig. 9 [non fig. 10 copy of Fewkes, 1881, Pl. 6, fig. 12 as *Diplophysa inermis*]; Smith, 1977, Pl.30 fig. 164.

Monophyes gracilis Claus, 1873, p. 258; 1874, p. 30, Pl. 4 figs. 8–15; Chun, 1885, p. 514, Pl. 2 figs. 1–2 [non figs. 5–7 = *Lensia subtilis*]; Mayer, 1900, p. 73, Pl. 27, fig. 89; Lo Bianco, 1904, p. 57, Pl.36, fig. 148.

Diplophysa sp. Claus, 1874, p.27, Pl.4 figs. 1–4.

Sphaeronectes (*Monophyes*) *inermis* Fewkes, 1880, p. 143, Pl. 3, fig. 6.

Sphaeronectes gracilis Chun, 1892, p. 84, text-fig. 5; 1897a, p. 60, fig. 4; Schneider, 1896a, p. 603, text-fig. AA, Pl. 43 figs. 6, 9, 10; Mayer, 1900, p. 73, Pl. 27 fig. 89; Delage & Herouard, 1901, p. 283, fig. 423; Vanhoeffen, 1906, p. 12, fig. 5–6; Totton, 1965a, p. 202, text-fig. 138, Pl. 36 fig. 1, ?text-fig. 137; C. Carré, 1968c, p. 86, Pl. I, fig. 1, Pl. II, figs. 1–4; D. Carré, 1969a, p. 32, Pl. I, 1–8; Palma, 1973, p. 52, Pl. 29; Daniel, 1974, p. 173, text-fig. 14C, D; 1985, p.291, text-fig. 78a,b; Kirkpatrick & Pugh, 1984, p. 126, fig. 56; Purcell, 1984, p. 315, figs. 3A, B; Pages & Gili, 1992, p. 100, fig. 44; Carré & Carré, 1995, p. 577, figs. 177B, 180H, 199; Pugh, 1999, p. 493, figs. 3.43, 3.54; Gamulin & Kršinić, 2000, p. 122, fig. 75; Bouillon *et al.*, 2004, p. 230, fig. 142E; 2006, p. 484, fig. 231E; Zhang, 2005, p. 31, text-fig. 26.

Monophyes köllikeri Haeckel, 1888a, p. 34.

Diplophysa truncata Haeckel, 1888a, p. 32 (*in partim*).

Diplophysa köllikeri Haeckel, 1888a, p. 32; 1888b, p. 108; ? Agassiz & Mayer, 1899, p. 177, Pl. 17 fig. 53.

Sphaeronectes truncata Schneider, 1898, p.75 (*in partim*); Bigelow, 1911b, p. 184.

Sphaeronectes sp. Totton, 1954, text-fig. 2B.

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? *Diplophysa codonella* Chun, 1888, p. 1154; 1892, p. 79, Pl. 8, fig. 2, Pl. 9, fig. 4; 1897b, p. 102.
non Sphaeronectes gigantea Bigelow, 1911b, p. 185; Moser, 1925, p. 97; Daniel, 1974a, p. 173; Palma, 1973, p. 53.
non Sphaeronectes gracilis [eudoxid] Bouillon *et al.*, 2004, fig. 142F; 2006, fig. 231F (copy of Fewkes, 1881, Pl. 6, fig. 12 of *Diplophysa inermis*).

Distribution: *Sphaeronectes koellikeri* was first described by Huxley (1859) from three individual specimens collected in the Indian Ocean, off the east coast of Australia, and in the Torres Strait south of New Guinea. It is the best known of all the *Sphaeronectes* species and has been found throughout the Mediterranean (see Gamulin & Kršinić, 2000), with numbers exceeding 18 m⁻³ in the Adriatic, and the Atlantic, Pacific and Indian oceans. Like all *Sphaeronectes* species, *S. koellikeri* is very fragile and is most often collected in coastal regions, either by hand or in fine mesh nets fished at shallow depths. However, the species does occur in open water as it has been collected there, particularly close to the surface by SCUBA divers (Dunn *et al.*, 2005; Pugh, personal data). Nevertheless observations of its presence in the Atlantic Ocean are few, ranging from the Gulf of Maine (Pagès *et al.*, 2006) and off the west coast of Scotland (Fraser, 1967), the Canary Islands (Chun, 1885), to off South Africa (Pagès & Gili, 1991), where it was the predominant siphonophore species in the 20–100 m depth range. There appear to be no records for the South-west Atlantic but this probably is due to the lack of studies on siphonophores in that area. Mayer (1900) found it in the Gulf of Mexico, in the vicinity of the Dry Tortugas.

The records for *Sphaeronectes koellikeri* in the Pacific Ocean are similarly disparate. There are many records from off Chile (e.g. Apablaza & Palma, 2006; Palma, 2006, and references therein), where the species is abundant in superficial waters, with up to 3 specimens m⁻³. It also has a widespread distribution in the China Sea (e.g. Zhang & Lin, 1997; Zhang, 2005) and off Japan (Kitamura *et al.*, 2003). Margulis & Vereshchaka (1994) have collected it in the Central Pacific, as did Bigelow (1911). The species was found to be abundant off south and Baja California, with large numbers being found off Santa Barbara and Santa Catalina Island (Purcell, 1981; Purcell & Kramer, 1983), and in Acapulco harbour (Bigelow, 1911). It is likely that, in these cases, the species has been carried north in warm inshore currents.

As previously discussed it is very likely that the records for this species, as *Sphaeronectes truncata*, in Monterey Bay given by Bigelow & Leslie (1930) actually refer to larval specimens of *Lilyopsis medusa*. However, Mackie (1985) has also observed "Sphaeronectes gracilis" from the submersible *Pisces IV* off British Columbia, Canada, but only at one of the 21 sites where dives were made. It was noted during both the winter and spring at depths between 70 and 140 m. One cannot say whether these observations actually refer to larval nectophores of *L. medusa* as if any specimens were collected none still exist (Mackie, pers. com.). However, the most likely conclusion is that his specimens belong to the shallowest living of the new species described herein.

Apart from Huxley's (1859) records *Sphaeronectes koellikeri* has been recorded in the Indian Ocean by Daniel (1985), who listed sporadic records for the Arabian Sea, Bay of Bengal, and off the west coast of Australia, and by Gibbons & Thibault-Botha (2002) and Patriti (1970) who found occasional specimens off South Africa and Madagascar, respectively. Pagès *et al.* (1990) also found it off Papua New Guinea.

***Sphaeronectes irregularis* (Claus 1873, 1874) (see Figures 16 & 17)**

Monophyes irregularis Claus, 1873, p. 259; 1874, p. 32, Pl. 4, figs. 5–6, 15–18; Chun, 1888, p. 1154; Haeckel, 1888b, p. 128; Chun, 1892, p. 82; 1897b, p. 102; Trégoüboff & Rose, 1957, p. 372, [*non* Pl. 83, fig. 11 copy of *Sphaeronectes brevitruncata* (Chun, 1888)].

Diplophysa sp. Claus, 1874, p. 27, Pl. 4 figs. 5–7.

Diplophysa truncata Haeckel, 1888a, p. 32 (*in partim*).

Sphaeronectes truncata Schneider 1898, p. 78 (*in partim*).

Sphaeronectes irregularis C. Carré, 1968c, p. 86, Pl. I, fig. 3, Pl. II, figs. 5–6; D. Carré, 1969, p. 34, Pl. I, figs. 9–11.

? *Ersaea truncata* Will, 1844, p. 82, Pl. 2 figs. 28, 29, 31; Moser, 1925, p. 97.

? *Diplophysa inermis* Gegenbaur, 1853, p. 291, Pl. 16 fig. 3; Fewkes, 1881, p. 166, Pl. 6 fig. 12; Haeckel, 1888b, p. 107; Chun, 1892, p. 85.

? *Praya inermis* Metschnikoff, 1874, p. 46, Pl. 7, fig. 16.

? *Sphaeronectes ptacilis* Vanhoeffen, 1906, fig. 13 [copy of Fewkes, 1881, Pl. 6, fig. 12 as *Diplophysa inermis*].

? *Sphaeronectes köllikeri* Trégoüboff & Rose, 1957, Pl. 76, fig. 10 [copy of Fewkes, 1881, Pl. 6, fig. 12 as *Diplophysa inermis*].

? *Sphaeronectes irregularis* Gamulin & Kršinić, 2000, text-fig. 81.

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- ? *Sphaeronectes gracilis* [eudoxid] Bouillon *et al.*, 2004, fig. 142F; 2006, fig. 231F [copy of Fewkes, 1881, Pl. 6, fig. 12 as *Diplophysa inermis*].
non Sphaeronectes irregularis Moser, 1925, p. 93, text-fig. 19 [copy of *Sphaeronectes brevitruncata* (Chun, 1888)]; Stepanjants, 1967, text-fig. 53(I); 1973, text-fig. 1A [copy of *Sphaeronectes brevitruncata* (Chun, 1888)]; Daniel, 1985, p. 293, text-fig. 78b [= *S. koellikeri*]; Bouillon *et al.*, 2004, Fig. 142G [copy of *Sphaeronectes brevitruncata* (Chun, 1888)].
non Sphaeronectes irregularis var. C. Carré, 1968c, Pl. I, fig. 2 [= *Sphaeronectes brevitruncata* (Chun, 1888)].

Distribution: The records for *Sphaeronectes irregularis* are far fewer than those for *S. koellikeri*, and mostly come from the Mediterranean, from whence it was first described (see Gamulin & Kršinić, 2000), with the great majority of specimens having been collected within the top 200 m of the water column. It often co-occurs with *S. koellikeri* but in considerably fewer numbers. The records for *S. irregularis* by Chun (e.g. Chun, 1892) from the Canary Islands appear to be the only published ones for the whole of the Atlantic Ocean. However, it has been collected by SCUBA divers off Bermuda (Pugh, personal data), and Margulies (1992) maps an unpublished record from Josephine Bank (c. 36°N, 14°W).

For the Pacific Ocean there are again numerous records from off Chile (e.g. Apablaza & Palma, 2006; Palma, 2006, and references therein), and Kitamura *et al.* (2003) have recorded it off Japan, but there are no records for the China Sea. Margulies (1992), in her Figure 2, shows many records for the South-East Pacific, but the only record for the North-East Pacific appears to come from Margulies & Vereshchaka (1988) from off California, although the exact position is unclear.

This last record again raises the question as the accuracy of identification as, like *Sphaeronectes koellikeri*, *S. irregularis* has not been collected by SCUBA divers off California. Of the six *Sphaeronectes* species, excluding the new ones described herein, only *S. koellikeri* can be readily distinguished by the shape of its hydroecium, extending over the top of the nectosac, and the straight radial canals all arising together from the pedicular canal. All the other species have a relatively small hydroecium confined to the ventral side of the nectophore and, apart from *S. bougisi*, looped lateral radial canals. The shape of the somatocyst and the size of the nectophore are then the main characters distinguishing the species. However, the differences between the structures of the somatocyst for what are obviously distinct species can be slight. Thus I am inclined to believe that the record for *S. irregularis* given by Margulies & Vereshchaka (1988) for off California actually pertains to another species. The same also probably applies to the records of *S. irregularis* given by Margulies (1992) for the Antarctic Sector of the Indian Ocean. These, as noted above, may well belong to the new *Sphaeronectes* species mentioned by Pagès & Kurbjewit (1994) and Pagès & Schnack-Schiel (1996) from the Weddell Sea (Atlantic Sector of the Antarctic Ocean). Margulies (1992) Figure 2 also shows the presence of "*S. irregularis*" off New Zealand and to the south of Tasmania.

Margulies (1992) also records *Sphaeronectes irregularis* in the Indian Ocean, in the region of the Maldives, and Patriti (1970) has found it off Madagascar. Daniel (1985) has also recorded the species from the Bay of Bengal but, judging by her illustration (*ibid*, Fig. 78b), she may actually have been referring to *S. koellikeri*.

***Sphaeronectes brevitruncata* Chun, 1888 (See Figure 16)**

- Monophyes brevitruncata* Chun, 1888a, p. 1153; 1888b, p. 225; 1892, p. 79, Pl. 8, fig. 1, Pl. 9, figs. 1–3; 1897b, p. 102.
Sphaeronectes truncata Schneider 1898, p. 78 (*in partim*).
Sphaeronectes irregularis Bigelow, 1911b, p. 346 (*in partim*); Totton, 1965a, p. 203 (*in partim*); Bouillon *et al.*, 2004, Fig. 142G.
Monophyes irregularis Moser, 1924, p. 5, fig. 5; 1925, p. 93 (*in partim*).
Sphaeronectes irregularis var. C. Carré, 1968c, p. 91, Pl. 1, fig. 2).
? *Monophyes japonica* Stepanjants 1967, p. 157, fig. 99.
? *Sphaeronectes japonica* Daniel, 1974, p. 172; 1985, p. 290; Carré & Carré, 1995, p. 577.
non Diplophysa codonella Chun, 1888, p. 1154; 1892, p. 79, Pl. 8, fig. 2, Pl. 9, fig. 4; 1897b, p. 102.

Distribution: Chun's (1888) specimens of *Sphaeronectes brevitruncata* came from Oratava (Tenerife) in the Canary Islands, presumably from superficial waters; Stepanjants's (1967) specimens of *Monophyes japonica* came from the Japan Sea (39°21'N, 134°36'E) in hauls made over 0–100 and 100–200 m depth ranges; and C. Carré's (1968c) specimen of *S. irregularis* var. presumably was collected off Villefranche-sur-Mer (western Mediterranean). It is here assumed that Chun's *Diplophysa codonella* is actually the eudoxid stage of *S. koellikeri*.

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***Sphaeronectes gamulini* Carré, 1966 (See Figures 16 & 17)**

Sphaeronectes gamulini Carré, 1966, p. 1070, fig. 1, Pl. 1; 1968c, p. 91, Pl. 1, figs. 5–6, Pl 2, fig. 7; Palma, 1984, p. 83, fig. 1; Gamulin & Kršinić, 2000, p. 134, fig. 84; Bouillon *et al.* 2004, p. 230, fig. 142A–D.

Distribution: *Sphaeronectes gamulini* was originally described by C. Carré (1966) from specimens caught in the entrance to the Rade Villefranche-sur-Mer in non-closing nets fished at 50 m or between 50 and 100 m. It has also been found elsewhere in the western Mediterranean by Specchi *et al.* (1976) [off Sardinia], Ianora & Scotto di Carlo (1981) [Bay of Naples], and Dallot *et al.* (1988) [Alborán Sea]. In the eastern Mediterranean it has been found often in the Adriatic Sea by Rottini & Gamulin (1969), Batistić *et al.* (2004), Gamulin (1979), and in all the relevant papers quoted below for *S. fragilis*, except for Gamulin (1977). It has also been found off Chile by Palma (1984), who gave a further description of both the polygastric and eudoxid stages, and by Apablaza & Palma (2006).

***Sphaeronectes fragilis* Carré, 1968 (See Figure 16)**

Sphaeronectes fragilis Carré, 1968b, p. 1, Pl. 1–2; 1968c, p. 84, Pl. 1, fig. 4; Bouillon *et al.* 2004, p. 230, fig. 141F,G; Gamulin & Kršinić, 2000, p. 137, fig. 87.

Distribution: *Sphaeronectes fragilis* was described by C. Carré (1968b) from a score of specimens collected in a non-closing net fished at 10 m depth in the entrance to the Rade de Villefranche-sur-Mer. Dallot *et al.* (1988) also found specimens at two stations in the western Mediterranean (Alborán Sea) and, apparently, on the Atlantic side of the Straits of Gibraltar, in vertical nets hauled from a maximum of 200 m. Ianora & Scotto di Carlo (1981) also found 12 specimens in the Bay of Naples between 50 and 300 m. In the eastern Mediterranean the species has been found in the Adriatic by Rottini (1966a,b), Gamulin (1977, 1982), Gamulin & Kršinić (1993a,b, 2000), and Lučić *et al.* (2005); the last authors finding it mainly concentrated at a depth of c. 100 m.

Apart from record from Dallot *et al.* (1988), for just west of the Straits of Gibraltar, there appear to be no other Atlantic Ocean records for this species. However, it has been found on a number of occasions at various locations off the coast of Chile by Sergio Palma and his co-workers, e.g. Palma (2006), Palma & Rosales (1995, 1997), Apablaza & Palma (2006), and by Pagès & Orejas (1999). Sergio Palma (personal communication) informs me that he has been able to identify the eudoxid stage of this species.

***Sphaeronectes bougisi* Carré, 1968 (See Figure 16)**

Sphaeronectes bougisi Carré, 1968a, p. 446, figs. 1–2; 1968b, p. 89, Pl. 1, fig. 7; Gili, 1986, p. 278, figs. 4.50e; 4.65l; Bouillon *et al.* 2004, p. 229, fig. 141D,E.

Distribution: As noted above, because of the peculiar arrangement of the radial canals on the nectosac that resemble closely that found in *Lilyopsis* species, there is some doubt as to the validity of this species; although the few buds on the siphosomal stem appear to have a greater affinity with *Sphaeronectes* species. *S. bougisi* was described by Carré (1968a) from six specimens collected in non-closing nets fished at depths of 50 (4 specimens) and 100 m (2 specimens) in the entrance to the Rade de Villefranche-sur-Mer (Western Mediterranean). Gili (1986) appears to be the only other person to record this species from two specimens caught in the 50–200 m depth zone off Barcelona.