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A history of the sub-order Cystonectae (Hydrozoa: Siphonophorae)

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Abstract

The siphonophore sub-order Cystonectae presently comprises just five species in three genera and two families, and includes *Physalia physalis*, the Portuguese Man O'War. Despite the smallness of the group its history has been very chequered, particularly for *P. physalis*, which has been described under more than fifty different names. Haeckel (1888) was one of the worst offenders regarding the description of questionable species, but even Totton (1965) was uncertain as to the validity of some previously described cystonect species. Herein, an attempt has been made to review the history of the sub-order Cystonectae and to clarify its taxonomy. A list of synonyms for each recognised cystonect species is given in an appendix.

Key words: Siphonophorae, Cystonectae, *Physalia*, *Rhizophysa*, *Bathyphysa*, History

Introduction

Traditionally, the order Siphonophorae has been split into three sub-orders based on the presence/absence of an anterior gas-filled float (pneumatophore) and/or the presence of swimming bells (nectophores) grouped together to form a nectosome. Species of the sub-order Cystonectae possess an apical float, but no nectosome, although asexual nectophores, as well as gonopalpons, are to be found on its gonodendra. Species of the sub-order Physonectae possess both an anterior pneumatophore and a nectosome that lies immediately posterior to it, although species of the genus *Athorybia* have secondarily lost their nectosome. Finally, the sub-order Calycophorae has lost the anterior pneumatophore, but the nectosome is retained, although it can be reduced to a single nectophore. Immediately posterior to the nectosome (Physonectae and Calycophorae) or pneumatophore (Cystonectae, except for the Family Physaliidae) there is the budding zone for the siphosome. The siphosome bears the feeding and digestive (gastrozooid and tentacle) and reproductive, with or without asexual swimming bells, zooids together with, and dependent upon several factors, protective structures (bracts) and reduced gastrozooids (palpons). By convention (e.g. Haeckel, 1888b) the side of the siphosomal stem to which the siphosomal zooids are attached is designated as ventral.

Dunn *et al.* (2005) have used analyses of 16S and 18S ribosomal RNA sequence data to study the molecular phylogenetic relationships between these three basic groups of siphonophores. These analyses showed that the Cystonectae is monophyletic andsister to a group that includes all the Physonectae and Calycophorae species, which they called the Codonophora. The Calycophorae is monophyletic and nested within the Physonectae, which is

paraphyletic. In the Codonophora the siphosomal zooids are grouped into *cormidia*, each cormidium being a simple iteration of a sequence of zooids, which includes, with the major exception of the physonect family Apolemiidae, a single gastrozooid, with its tentacle, and other types of zooids occurring in a well-defined species-specific sequence. A more detailed account of the molecular phylogeny of the Siphonophorae, mainly physonects, has recently been published by Munro *et al*. (2018) but, with regard to the Cystonectae, the results are unchanged. The arrangement of the zooids on the siphosome of the long-stemmed Cystonectae species (Family Rhizophysidae) is outwardly much simpler, with only gastrozooids, each with a tentacle, and gonodendra attached to the stem between them. The gonodendra, however, are much more complex than those found on physonect and calycophoran species. Each gonodendron has many branches and each terminal branch has a distal gonopalpon, a sub-terminal asexual nectophore, and several gonophores, all of a single sex. Indeed all the gonophores are of the same sex and so that each colony is dioecious. For the Family Physaliidae the gonodendral arrangement is further complicated by the presence of an additional reduced nectophore or "jelly-polyp" (Totton, 1960). Although Totton (1960) used the term cormidium to define the basic iteration of gastrozooid, plus tentacle, and gonodendra along the siphosome of long-stemmed cystonect species, it is far from clear that this is an accurate homology (see Dunn & Wagner (2006). Herein, they will be referred to as "cormidia", unless the word appears in a quotation.

In this paper the history of the systematics of the Sub-Order Cystonectae will be reviewed.

Morphology of cystonect siphonophores

At present, only five species generally are considered to be valid, although Totton (1965) included some *species inquirendae* whose validity will be discussed herein. These are split between two families: the short-stemmed Physaliidae, with its single genus and species, *Physalia physalis* (Linnaeus, 1758), which has a horizontal, greatly expanded, float or pneumatophore; while the Rhizophysidae, which currently is split into two genera, *Rhizophysa* and *Bathyphysa*, have a much smaller anterior pneumatophore below which the siphosoamal zooids are borne on a long, narrow stem. In all cystonect species the pneumatophore has an opening, kept closed by sphincter muscles. Nevertheless, considering how few species are currently included the sub-order Cystonectae, the history of its taxonomy has been extraordinarily complex, and that of the family Physaliidae particularly so.

The general morphology of a rhizophysid cystonect (Figure 1B) is quite simple. There is a large apical float or pneumatophore (**pn**), which has an apical pore (**ap**), and within it the gas bladder or pneumatosaccus (**pns**), which is an invagination lined with ectoderm. Hypocystic villi are found base of the pneumatosaccus, which contain giant cells responsible for gas secretion; the gas being carbon monoxide. In *Rhizophysa* species these villi may almost fill the hypocystic cavity surrounding the pneumatosaccus, while in *Bathyphysa* species they are simple tubes hanging below it. The hypovcystic cavity is in direct communication with the gastrovascular system of the siphosome that itself connects with all the siphosomal zooids. At the base of the pneumatophore, on its ventral side is the blastocrene (**bl**) or zone of proliferation where the zooids of the siphosome, the gastrozooids (**gz**), with their tentacles (**t**), and the gonodendra (**gn**). The two genera basically are separated on the basis of whether the young gastrozooids possess lateral wings or *ptera*, genus *Bathyphysa*, or not, genus *Rhizophysa*. The two species within each genus are then separated according to whether the tentacle have lateral side branches, tentilla, or not. *R. eysenhardtii* differs from all the other rhizophysids in that the tentacle arises, laterally, on the ventral side of the gastrozooid, while for the others it arises anteriorly (Dunn & Wagner, 2006). It is also somewhat confusing that *R. eysenhardtii* has filiform tentacle, i.e. without side branches, while that of *R. filiformis* bears tentilla.

The morphology of the single representative of the family Physaliidae, *Physalia physalis*, is quite different (Figure 1A). The float has enlarged greatly in size, and can exceed 12″ in length, and on the side where the main zone of siphosomal budding occurs (see below) lies a small disc-like structure that is the gland secreting the gas. The diameter of the gland increase, almost linearly, with the size of the pneumatophore (see text-fig. 4 in Totton, 1960). The narrow cavity that separates the two layers of the pneumatophore also connects with all the siphosomal zooids, i.e. it is part of the gastrovascular system. The float lies horizontally with its pore (**p**) lying at it aboral end and the protozooid, the first gastrozooid to be developed, at its oral end. This gastrozooid is the only one that initially has a tentacle attached to its base, although it later disappears. The ventral side of the siphosome, where the budding of the zooids occurs, is displaced laterally, to one side or the other. What determines this is not known for certain, but it gives rise to the clear handedness that characterises the Portuguese Man O'War. Atop the pneumatophore and

forming part of it is the sail or crest (**cr**) that can be erected above the pneumatophore, with tubes from the main cavity passing through it. It is placed along the line between the oral and aboral poles. Its size obviously is related to the size of the colony itself, and it does not appear until the developing colony is somewhere between 1 and 2 cm in length. The handedness of each colony determines the direction in which it will be driven by the prevailing winds. Thus, a left-handed specimen will drift to the right of downwind, and a right-handed on the left (see Totton, 1960, text-fig. 5)

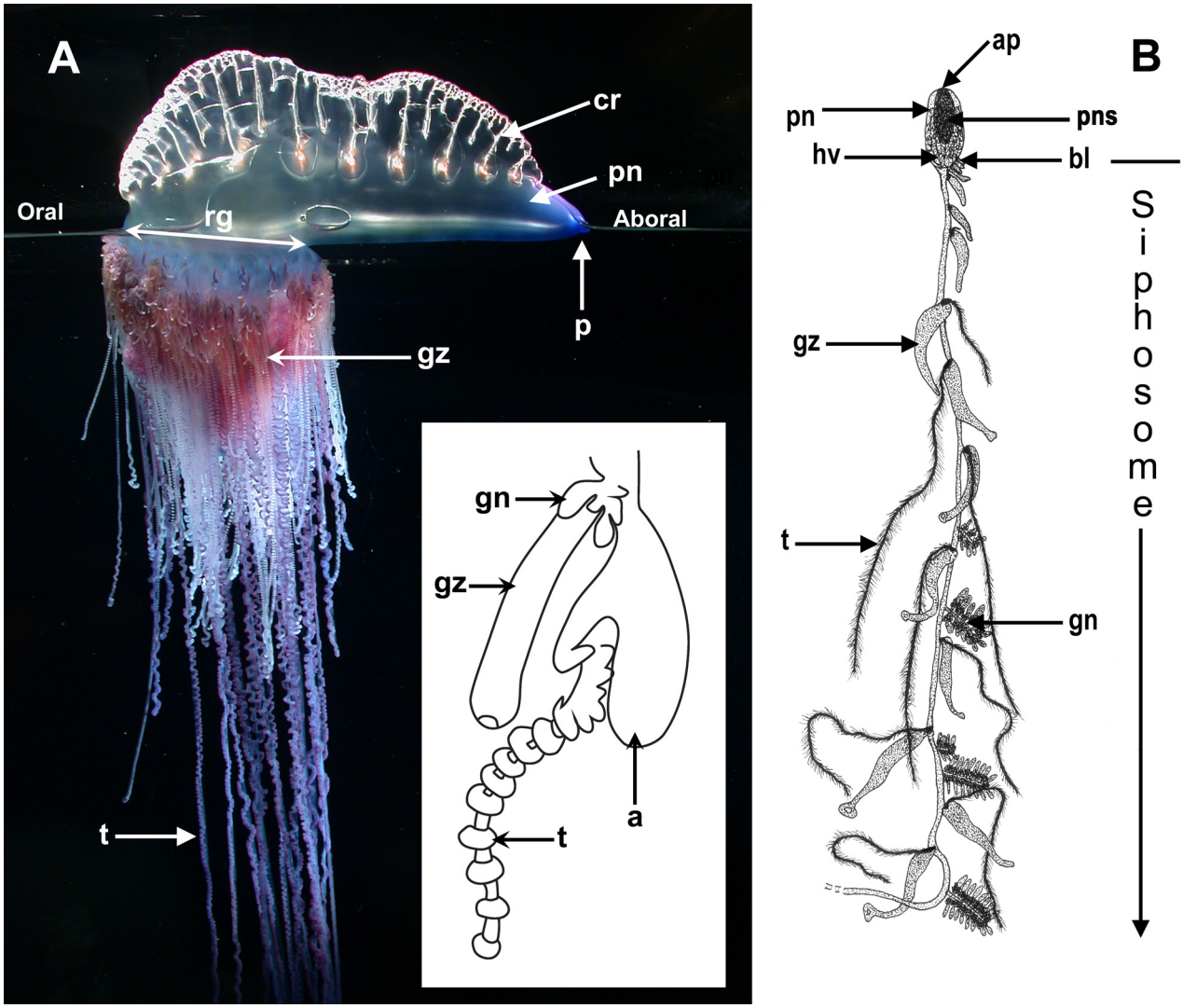

FIGURE 1. A. *Physalia physalis* Linnaeus (1758). © Casey Dunn. Insert: A single tripartite "cormidial" group. (Adapted from Totton (1960) text-fig. 16C). **B**. Generalised rhizophysid, adapted from Kawamura (1910, Plate 14, fig. 1). **a**. ampulla; **ap**. apical pore; **bl**. blastocrene; **cr**. crest; **gn**. gonodendron; **gz**. gastrozooid; **hv**. hypocystic villi; **p**. pore; **pn**. pneumatophore; **pns**. pneumatosaccus; **rg**. region of growth; **t**. tentacle.

A blastocrene, as was present in rhizophysids, is absent. Instead there are two areas, oral and main, where the zooids develop. In each zone up to seven "cormidial" units can be developed, but there arrangement is not linear, but conforms to a set pattern. Thus in the main zone, the first unit to appear will eventually be the third unit from the oral end; the second will be the first; the third the fourth, the fifth the second, etc. (Okada, 1932). Each unit is made up of several "cormidia" that, generally, are tripartite being composed of a gastrozooid, without an attached tentacle; a tentacle (**t**) attached to the base of a structure referred to as an ampulla, which is a site of nematogenesis, much like the proximal, basigaster of a non-cystonect gastrozooid; and a gonodendron. Another "cormidium" then branches from the base of the first one and, in that way up to thirteen branches (Totton, 1960) can be developed on each "cormidial" unit, thereby producing an extremely complex structure. What is abundantly clear is that the complexity of the colony increases with its size, or age. This fact, however, seems not to have occurred to many of the authorities who have pontificated on the subject of *Physalia*.

History of cystonect siphonophores

Pre-Linnaeus (1758).

As noted above, the only representative of the cystonect Family Physaliidae currently recognised is the Portuguese Man O'War and, until very recently, it was the only commonly known species of siphonophore. However, another cystonect species, *Bathyphysa conifera* (Studer) has recently been acclaimed as living proof of the existence of the "Flying Spaghetti Monster" (see, for instance*, https://www.youtube.com/watch?v=eulZ21oJbu0)* and has had much coverage in the press! A brief note on the sighting was given by Jones & Pugh (2016). Notwithstanding that, the Portuguese Man O'War probably is the only siphonophore that has been mentioned in pre-Linnaean times. For instance, it has been suggested that Aristotle (350 BCE) was referring to *Physalia* when he said: "Many creatures are unattached but motionless, as is the case with oysters and the so-called holothuria"[1] and *Holothuria* was the generic name under which Linnaeus (1758) originally described the species.

The common name, in English, the Portuguese, or very occasionally Spanish, Man O'War derives its name from its apparent likeness to Portuguese ships, in the time of Henry the Navigator, with fore-and-aft lateen sails, and which they called caravelles (Totton, 1960). It has many other colloquial names in other languages. For instance, *Agua viva* (see Totton, 1960); *Besaantjes* (e.g. Osbeck, 1857); Bluebottles (e.g. Totton, 1960); ARETUSA *Crista subrubella venosa* (Browne, 1756); *By-de-wind Seyler* (e.g. Toreen, 1757) or *By-wind-sailor* (e.g. Toreen, 1771) or *By-de-wind-zeyler* (e.g. Chun, 1897), although *Velella* is more commonly called by-the-wind-sailor in English); *Caravelle or Caravella* (e.g. Blainville, 1826); *Galere* (e.g. du Tertre, 1654, 1667); *Frégate* (e.g. Descourtilz, 1809); *Immondicites Rouges nageas sur mer* (Lery, 1578, 1594); *Kriegsschiff* (e.g. Olfers, 1832); *Moucicu* (e.g. Piso, 1648; Barrère, 1741; although Linnaeus, 1758, and in his subsequent publications, referred to *Moucicu* under the name *Holothuria denudata,* not *H. physalis* (see below)); *Ortiga de Mar* (Burmeister, 1885–1891); *Ship of Guinea* (Hakluyt c. 1598–1600, see 1904 edition, p. 319), *Urtica Marina, soluta, purpurea, oblonga, cirrhis longissimis* (Sloane, 1725); *Urtica Marina* (Barrèe, 1741); and *Vélette or Vessie de Mer* (e.g. Descourtilz, 1809), although Fleurieu (1799) considered *Vélette* to be a *Velella*.

One of the first references to *Physalia* in recent history appears to have been by Lery (1578, p. 397) who said: "I have seen on many occasions certain red impurities swimming on the sea, shaped in the same way as the crest of a cockerel, so venomous and contagious that, if we touch them, the hand will be red and swollen". Sloane (1725, p. 7) also named several other authors who had mentioned *Physalia* such as Mertens, who called it the *Sea Nettle; de Laet,* who called it *Grandes Urtica;* and, possibly, Freyère (1647) in a book, which he published anomalously, *Relation du Groenland,* where he was said to use the name *Aranees du Mer,* although he may have been referring to another animal, but no trace of that name could be found in the relevant book. For the other writers the present author has been unable to trace the relevant text. However, one other name Sloane mentioned was Ligon, who he said called it *Physalia Carvile.* Ligon (1673, p. 6) stated: *"*Yet this great Master-piece of Nature [referring to a swordfish], is not in my opinion so full of wonder, nor doth raise the consideration to such a height: as this little fish the *Carvil* who can when he pleases, enjoy himself with his neighbour fishes, under water; And when he puts on a resolution to try his fortune in another Element, the *Air*, he riseth to the top of the sea, let the billow go never so high, and there without the help of a sayler, Raises up his Main Mast, spreads his sails, which he makes of his own sinews, fits his Rudder and Ballast, and begins his voyage; But to what Coast he is bound, or what Traffick he intends, himself and He that made him only can tell. Fishes there are none to prey on, nor flies, and therefore 'tis not for food he travels. I have seen them 500 leagues from any land: if his Voyage be to any Port, he must have a long time and much patience to get thither; if to sea he's there already: in one thing he hath the advantage of any ship that ever sailed; for he can go nearer the wind by a point, than the most yare Friggot that ever was built. Which shews how far Nature can exceed Art. Another advantage he has, that in the greatest Tempest, he never fears drowning. Compass, nor Card he needs not, for he is never out of his way; whether than his voyage be for pleasure or profit we are yet to seek".

Sloane (1725, p. 8) described his specimen as no bigger than a turkey egg, with a "corrugated or curved Ledge or Band, something like a Cocks-Comb ... and Seamen do affirm that they have great skill in sailing, managing their Bladder or Sail with judgement, as may be most for their purpose, according to their different Winds and Courses; allowing them more Reason, than I, at present, am willing to do of Life". Because of its stinging nature and its pigmentation Sloane gave it the name as quoted above. Later Browne (1756) referred to the *Portuguese* Man of War under the name *Arethusa*.

1 Quote taken from D'Arcy Thompson's (1910) translation of Aristotle's *The History of Animals*.

Osbeck (1757) during his *Voyage to China* from April 1750 to June 1752, in the entry for the 17th March, 1752, mentioned the name *Physis pelagica*, but in the list of legends, for Plate 12 (see Fig. 2C) he gave the name *Holothuria velificans*. Torén (1757), a fellow shipmate, clergyman and disciple of Linnaeus, wrote a series of letters to Linnaeus, entitled *A Voyages to Suratte, China* etc., that were appended to Osbeck's article. The name *Holothuria* appeared twice, both accompanied by the name *velificans*. Both articles were subsequently translated, firstly in 1765 into German, and then into English in 1771. In the German edition Osbeck (1765) now referred to the Linnaean name *H. physalis* in the text, but in the legend to Plate 12, probably by mistake, the name *H. velificans* was retained. Nevertheless, Toreen (1765) [=Torén] again twice referred to *H. velificans*. Finally, for both authors the newly established Linnaean name, *H. physalis*, was used in the 1771 English translation. Leaving apart *Physis pelagica*, it would appear that Osbeck originally had named the species *H. velificans*, and Torén had accepted it. However, for the German edition, Osbeck now used the offficial Linnaean name *H. physalis* and so the name was altered in the text, not in the legend. Torén would have had no part in the translation of his article as, unfortunately, he died at the age of 35, just over year after returning from the voyage.

It is also worth noting that in the 1756 edition of the *Systema Naturae* Linnaeus (1756, p. 79) mentions, among the Zoophyta, the genus *Salacia* "*corpus ovato-oblongum. Tentacula per fasciculos disposita*", with one species *Physalus*[2]. It has been suggested that it might refer to a cystonect siphonophore, possibly *Physalia*, but, in Linnaeus (1758), the starting point for all binomial nomenclature, neither the generic nor specific names were mentioned. So whether the earlier name referred to *Physalia* is not relevant to any further nomenclatural considerations although, as we shall see, the name was re-established by Brandt (1835) and particularly used by Haeckel (1888a, b) to define, quite unnecessarily, a stage in the development of *Physalia* after the crest had been developed.

From Linnaeus (1758) to the late 1820s

Physalia.

The first siphonophore species to be described under the Linnaean binomial taxonomic system, which by definition is taken to have begun with the 10th edition of *Systema Naturae*, published by in 1758, was the physaliid *Holothuria physalis* Linné, 1758. Linnaeus included three other species in his genus *Holothuria*, *Thalia, caudata,* and *denudata*, all of which are now considered to be salps. Hjortberg (1769) gave a brief redescription, in Swedish, of *H. physalis* and included two extraordinary figures (see Figure 2B). The present author has been unable to translate the text and so, unfortunately, can offer no explanation as to what the two extensions (E and C) at the ends of the bladder might possibly represent. However, Olfers (1832) referred to the extension, presumably E, which he expected to be spiralled and to bear gastrozooids, although quite why is not obvious. However, he considered the "eye" (G in Figure 2B) to be superficial damage.

Forsskål (1775) only mentioned two species of *Holothuria*, *H. denudata* = *Porpita porpita* (Linnaeus, 1758), and *H. spirans* = *Velella velella* (Linnaeus, 1758), both having been removed from the Linnaean genus *Medusa*. He made no mention of *H. physalis*, but later Gmelin (1788) moved it into the genus *Medusa* and dropped the genus *Holothuria* entirely. Meanwhile, Müller (1776) gave a brief description of what he considered to be a new species, *Medusa Caravella* based on a pencil drawing apparently made by a Dr König, and sent to him six years beforehand (see Figure 2D). The drawing also included upper and lower views of a species of *Porpita*, which he referred to as *Medusa Umbella*. Before his brief description of the specimens, Müller first gave translations, in full, of the two earlier papers that had briefly described a similar species to his *M. Caravella*, namely Sloane (1725) and Browne (1756).

The description of *Medusa Caravella* by Müller (1776) was brief and really only mentions the basic characteristics of the specimens, which one supposes is all that can be expected if all that he had to go on was a pencil drawing. However, Müller (1776) had no doubt that König's specimen belonged in the same genus as that drawn by Sloane but, possibly on the basis of the presence in König's specimen of an additional long and separate tentacle that the two specimens should be considered as separate species. Of course, Sloane's name *Utriculus* has no validity under the Linnaean system, but the rules were not established until more than a century later. What is very strange, however, is that Müller made no mention of Linnaeus' (1758) *Holothuria physalis*. Also, he could not understand why Forsskål (1775) had extracted the species *denudate* and *spirans* from Linnaeus' genus *Medusa* and placed them in the genus *Holothuria*, which is indeed inexplicable.

2 Note. Throughout this text a specific name has been capitalised when that is how the original author mentioned it. It is, of course, recognised that the current ICZN rules specify that in specific name should be in lower case.

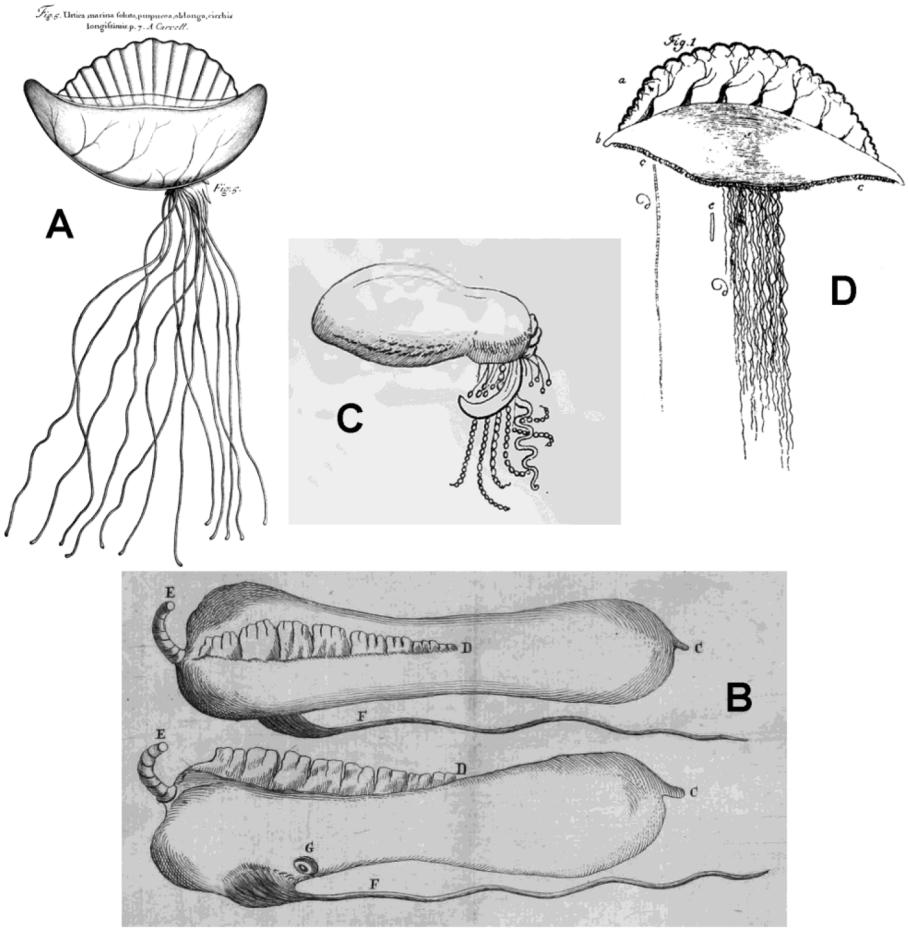

FIGURE 2. A. *Urtica marina soluta, purpurea, oblonga, cirrhis, longissmis.* From Sloane (1725, Plate III, Fig. 5); **B**. *Holothuria Physalis* from Hjortberg (1769, Plate VII (*partim*)); **C**. *Holothuria Physalis* Osbeck (1771, Plate 12); **D**. *Medusa Caravella* Müller (1776, Plate X, fig. 1).

The generic name *Holothuria*, for the Portuguese Man O'War was retained by a few authors, e.g. Gmelin (1788), Voigt (1806), and Blumenbach (1814), but in the latter part of the 18th century the generic name, *Medusa*, was often used. La Martinière (1787, p. 365), for instance, gave a brief description, and two illustrations (see Figure 3A), of an "espèce de Méduse" without giving it a name. The illustrations are notable for the fact that they were the first to show a specimen with reasonable accuracy. Gmelin (1778, p. 3155) then mentioned the species *M. utriculus* but, confusingly, he attributed the name to La Martinière. This attribution has been repeated by some subsequent authors and, for instance, Chun (1897, p.86)[3] noted: "It is only in the 13th edition of "Systema Naturae" (1788 I, part VI, p. 3155, n. 20) that Gmelin affirms the name *Medusa utriculus* to a Pacific Physalie, which La Martinière, naturalist on the expedition of La Perouse, had described in the Journal de Physique", with a footnote stating that Chun had not seen that Journal. However, Olfers (1832, page189)[4] correctly noted: "The name *M. Utriculus* does not belong to La Martinière, but to Gmelin". Modeer (1789), however, also removed Linnaeus' species *physalis* from that genus *Holothuria*, but unfortunately placed it within Forsskål's (1775) catch-all genus *Physsophora*, which contained several species belonging to entirely different families. The reason why the generic name, *Holothuria*, came to be used to derive the Class Holothuroidea, with the Phylum Echinodermata, is explained by Poche (1908).

3 Original quote: "Erst in der 13. Auflage des »Systema naturae« (1788 I, pars VI, pag. 3155, Nr. 20) legt Gmelin den Namen *Medusa utriculus* einer pacifischen Physalie bei, welche de La Martiniere, Naturforscher der Expedition von La Perouse, im Journal de Physique.

4 Original quote: "Der Name *M. Utriculu*s gehört also nicht ihm an, sondern Gmelin."

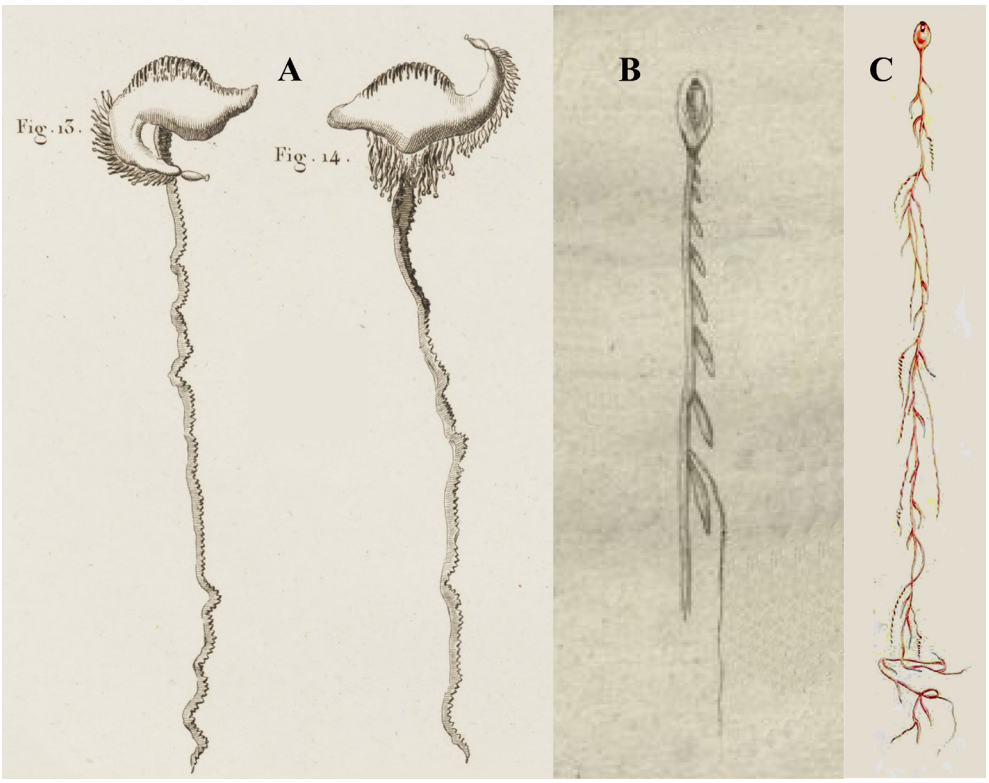

FIGURE 3. A. La Martinière (1787) Plate II, figs. 13 &14; **B**. *Physsophora filiformis* from Forsskål (1776) Plate XXXIII, figure F; **C**. *Rizophysa planestoma* from Lesueur & Petit (1807) Plate XXIX, figure 3.

The generic name *Physalia* was established by Lamarck (1801), but instead of using the original specific name, he used *pelagica*. He gave no indication as to why he chose that name but, possibly, he was trying to re-establish Osbeck's (1757) pre-Linnaean name. Bosc (1802, p. 160)[5] then gave a reasonable description and a good illustrations of, presumably, the same species, although under the slightly misspelt name, *pelasgica* (see Figure 3). He noted, justifiably, that although the species was very familiar to all sea farers: "nevertheless, it can be said that its organization is still completely ignored by the Naturalists. To convince oneself of this truth, it is sufficient to compare the figures and descriptions of the authors with the [my] description and figure on Pl. 19. It will be seen that, apart from those which are found in the Journal de Physique, November 1787, and in the Voyage de la Perouse, both by La Martinière, none gives an idea, even an approximation, of its form". However, (*ibid*. pp. 161-162)[6] he said that: "The mouth is placed inferiorly, a little to the right; and is accompanied by a great number of blue, gelatinous tentacles of five different shapes, which are united by means of a membrane with the tubercles of the anterior part". One presumes he was referring to the opening into the pneumatophore that, of course, has no connection with the gastrovascular canal system whatsoever. Bosc (1802) mentioned specimens being 5–6 cm in length, although his figures, drawn at quarter size, would suggest a length closer to 12 cm.

Bory de St. Vincent (1804, p. 288) retained Bosc's *Physalia pelasgica*, specimens of which: "n'excèdent jamais la volume d'un oeuf de poule" [never exceed the volume of a hen's egg], but caught a single much larger specimen, about six times larger than a *P. pelasgica* specimen, that he decided to call *P. gigantea*. Although Bosc (1802, p. 165) had briefly mentioned the "démangeaison violente" [violent itching] that results from touching a specimen of *Physalia*, Bory de St. Vincent (1804, p. 290)[7] added an interesting anecdote when he wrote: "Our captain assured us

5 Original quote "cependant, on peut dire que son organisation est encore complètement ignorée des Naturalistes. Pour se convaincre de cette vérité, il suffit de comparer les figures et les descriptions des auteurs avec la description et la figure de la pl. 19. On verra, qu'excepté celles qui se trouvent dans le Journal de Physique, novembre 1787, et dans le Voyage de la Pérouse, toutes deux par la Martinière, aucune ne donne une idée, même approximative, de sa forme."

6 Original quote: "La bouche est placée inférieurement, un peu à droite; et elle est accompagnée d'un grand nombre de tentacules bleus, gélatineux, de cinq formes différentes y qui s'unissent, par le moyen d'une membrane, avec les tubercules de la partie antérieure".

7 Original quote: "Notre capitaine nous assura que les *galères* écrasées sur le nombril provoquaient de grands éclats de rire. Si ce fait est vrai, ce doivent être des espèces de convulsions. qui ressemblent à ce qu'on nomme vulgairement *ris sardo-*

that *galères* crushed onto the navel provoked great bursts of laughter. If this fact is true, it must be a kind of convulsion that resembles what is commonly called *sardonic laughter*". One suspects that there were no volunteers to put this statement to the test. However, Olfers (1832) considered it a ship's legend, with no basis of truth.

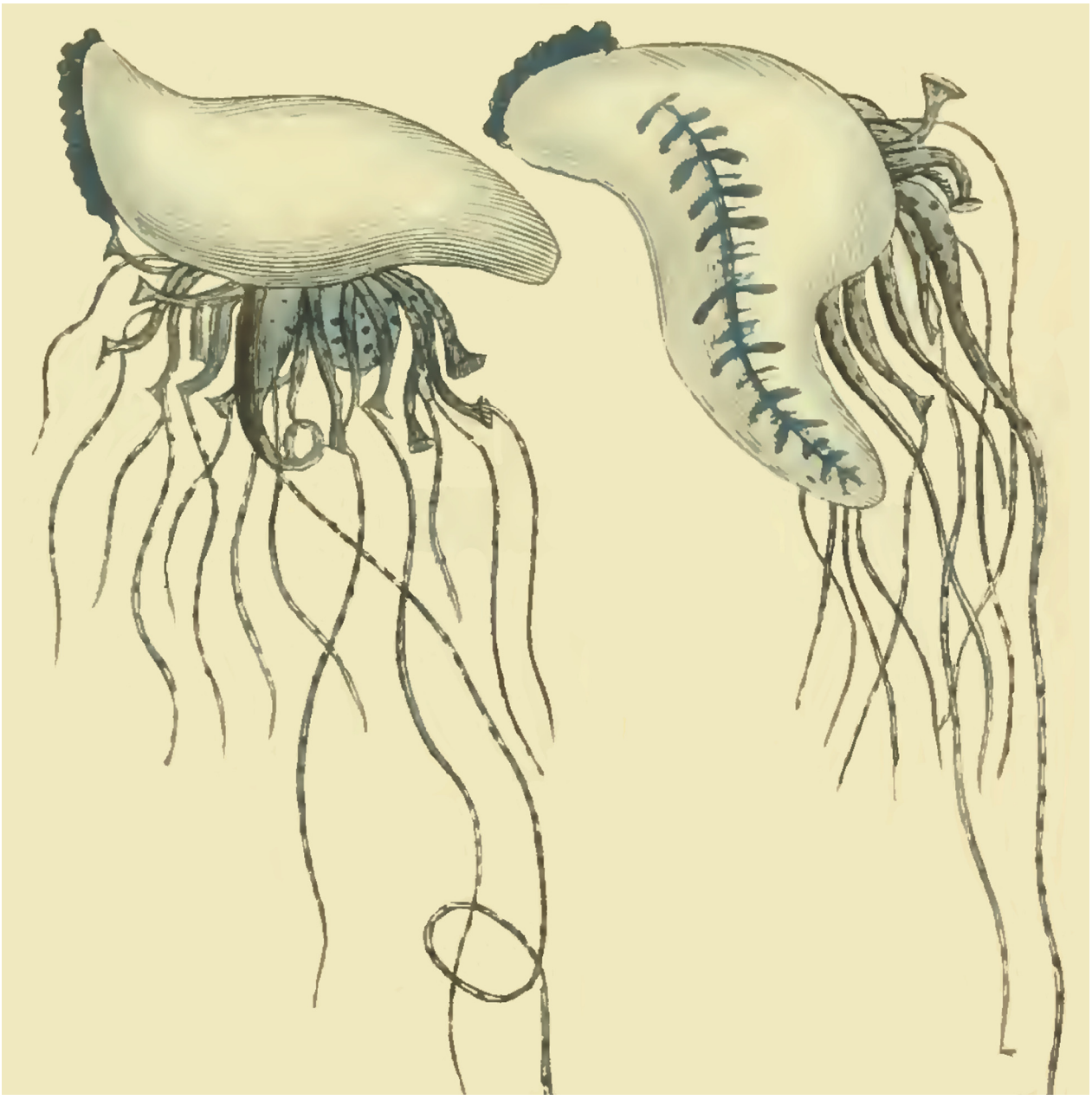

FIGURE 4. Lower (left) and upper (right) views of *Physalis pelasgica*. From Bosc (1802, Plate 16, figs. 1 and 2).

Péron (1807), in the series of tomes dealing with the *Voyage de découvertes aux Terres Australes*, added another new species, *Physalia Australis*, and referred to its illustration in Pl. XXIX, fig.1 (see Figure 5 A). However the legend on that Plate, in the Atlas by Lesueur & Petit (1807), states the species name to be "*P. megalista* N." This illustration, whose magnification is not given, showed a specimen with well developed oral and main "cormidial" groups, but still with only one main tentacle. There is no information to suggest why the authors thought the specimen represented a new species, nor any comparisons made with others.

Now one man managed to almost double the names that until then had been applied to the Portuguese Man O'War. The offender was Tilesius (1810), with seven names to his credit. It was certainly a monumental working, covering 140 pages, the vast majority of which was an extensive consideration of most, if not all, of the previous descriptions of *Physalia* that, regrettably but understandably, the present author has baulked at translating from the

nique".

original Dutch. However, the section dealing with the species covered less than twenty pages. Nonetheless, not all subsequent authors appear to have appreciated such detail, as we will return to shortly.

It appears that Oken (1815), who like Lamarck's (1801) use of the specific name *pelagica*, sought to resurrect another pre-Linnaean name when he re-established the genus *Arethusa*, a slight variant of that used by Browne (1756), to encompass both *Medusa Caravella* and *M. Utriculus*, whose specimens were said to be 3″ in length. He made no mention of the genus *Physalia*. No subsequent authority accepted the generic name *Arethusa* until, inevitably, Haeckel (1888a, 1888b) resurrected it to include *Physalia* species that had no crest or sail, but had several main tentacles. Unfortunately, we will have to return to this genus later.

Lamarck (1816), in the 2nd Volume of the *Histoire Naturelle des Animaux sans Vertèbres*, continued with the view that the species of *Physalia* had a single sub-central mouth on the lower side of the bladder, around which were numerous tentacles of various sizes. He also believed that in rough weather the colonies sank below the surface and attached themselves to whatever they could. He now included four species under the title *Physalia* but, inexplicably, when he described the species he used the generic name *Physalis*, rather than *Physalia*. Firstly, *P. pelagica*, the name he had earlier adopted for Linnaeus' species; secondly *P. tuberculosa*, which he appeared to attribute to Bosc (1802), although that author's species was named *P. pelasgica*. Thirdly, he mentioned *P. megalista* and referred to Péron & Lesueur's or actually Lesueur & Petit's (1807) species. The fourth species he named *P. elongata* apparently establishing a scientific name for the "Portugueze man-of-war" briefly mentioned by Forbes (1813, p. 200). Forbes also included a rather extraordinary illustration of his specimen (see Figure 5B) that might have made Bosc turn in his grave were he dead, which he was not at that time. Twenty six years later, in the 3rd Volume of the 2nd edition of the *Histoire Naturelle des Animaux sans Vertèbres*, Deshayes & Milne Edwards (1840) gave exactly the same description and observations as in the 1816 volume, but used the generic name *Physalia* throughout. However, they did consider the views of Eschscholtz (1829), who had actually looked at some specimens, and noted his rejection of the idea that there was just a single mouth. They included the same four species, but then added *P. utriculus*, which they ascribed to Eschscholtz instead of Gmelin. They gave a more extensive list of synonyms for each species, which is notable for the fact that he included Linnaeus' (1758) original species, *Holothuria physalis*, as a synonym of both *P. pelagica* and *P. tuberculosa*.

Eysenhardt (1821, p. 419)[8] gave a brief review of both the genera *Physalia* and *Rhizophysa*, but it was only in an Addendum that he briefly discussed the species belonging to the former genus. He appeared to be more appreciative of Tilesius' (1810) work than some, stating: "Tilesius has, with much diligence and good luck, tried to make a critical examination of the species of the genus *Physalia*; but it seems that he had not correctly stressed the same characteristics". Eysenhardt considered that there were four valid species but, like many other authors in the early, and even late, 19th Century, the concept of precedence did not appear to cross his mind. Thus, he listed, firstly, *Physalia Arethusa* Tilesius, synonyms *P. glauca* Tilesius, *P. pelagica* Lamarck, *Holothuria physalia* [sic] Linnaeus and *Medusa Caravella* Müller. Secondly, *P. Lamartinieri* Tilesius, synonyms *P. pelagica* Bory de St. Vincent, *P. Laperouse* Bory de St. Vincent, and *Medusa utriculus* La Martinière [Gmelin]. Thirdly, *P. afer* and P. *Osbeckii* Tilesius, synonyms *P. Megalista* Peron, *H. physalis* Osbeck; and fourthly, *P. pelagica* [sic] Bosc (see Figure 5C), synonyms *P. tuberculosa* Lamarck and *Arethusa Caravella* Oken. It is very difficult to decide, from Eysenhardt's brief Latin diagnoses just what separated the species, other than those that represent different stages of growth, such as the degree of development of the gonads and the "cormidial" groups themselves. It is even more difficult to gain a consensus when the *P. pelagi(s)ca* of Lamarck, Bosc, and Bory de St. Vincent were all included under different specific names. Nonetheless, for his first species Linnaeus's specific name has precedence. Similarly, for the second all of the synonymised names have precedence, although Bory de St. Vincent does not appear to have used the name *P. Laperouse*, his other species being *P. gigantea*. For the third species, *P. megalista* would have precedence, as *H. physalis* Osbeck is pre-Linnaean; and for the fourth, it would be *P. tuberculosa*.

Olfers (1822) believed that, at that time, there were four recognisable species of *Physalia*, namely *P. Arethusa*, *P. pelagica*, *P. megalista*, and *P. velificans*, the last being pre-Linnaean. However, one of the fresh specimens that he examined at sea appeared to him to differ from these four, and so he named it *P. producta* (Figure 5D). His brief diagnoses, in Latin, were very vague, concentrating on such characters as the shape and size of the float, the erectness of the sail, the length of the tentacles, and whether they stung or not. Of course, all of these could be explained by the degree of development of the colony. However, *P. producta* did appear to have an extraordinarily shaped bladder, although he described it as oval, but the distinguishing feature appeared to be the presence of a small protrusion (Figure 5D g) at the aboral end.

8 Original quote: "Tilesius hat mit vielem Fleisse und Glück sich bemüht, die Species der Gattung *Physalia* kritisch auseinander zu sezen; doch scheint es, als ob er das Charakteristische derselben nicht gehörig herausgehoben hätte."

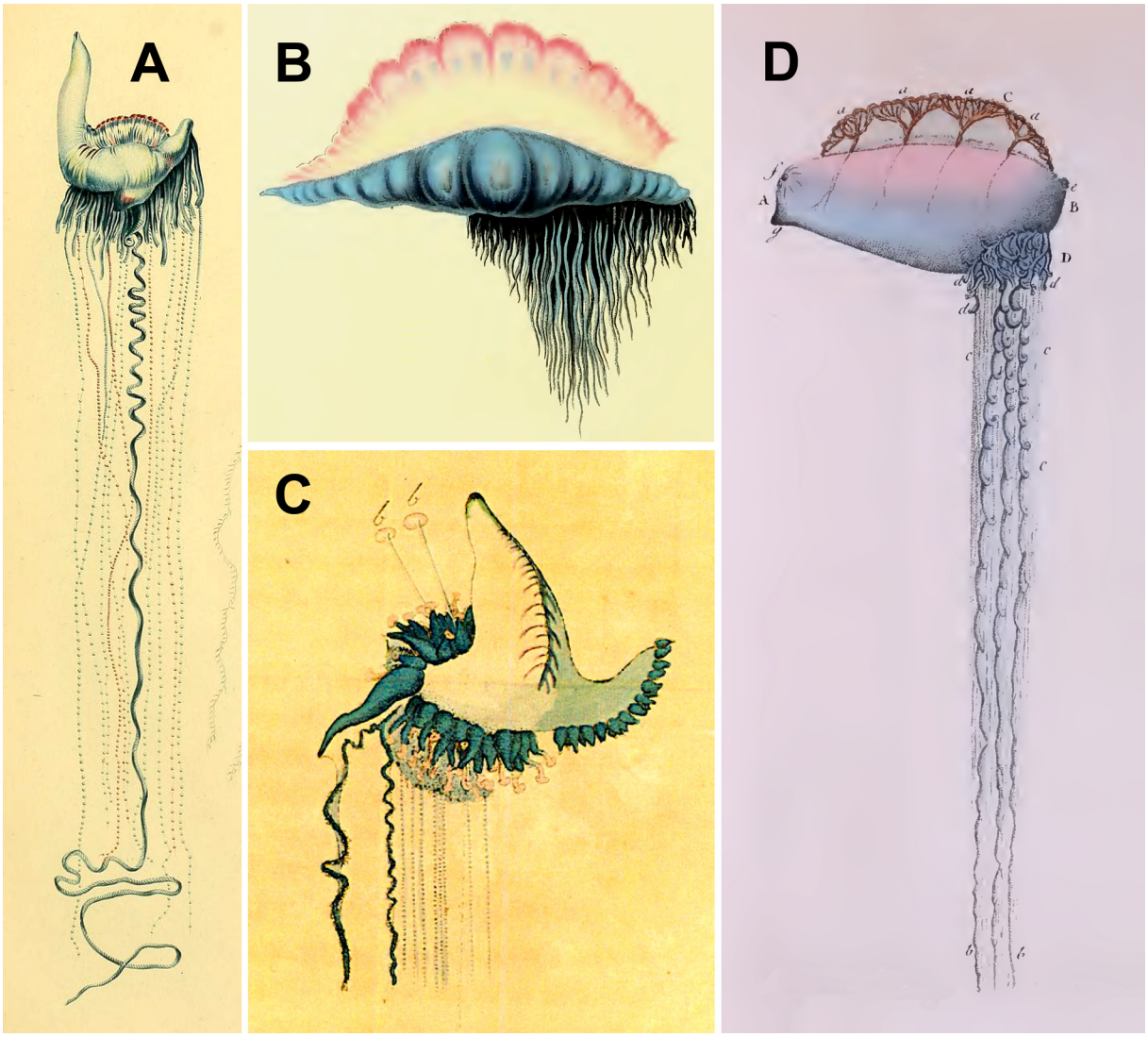

FIGURE 5. A. *Physalia Megalista* from Plate XXIX, fig. 1 of Lesueur & Petit (1807); **B**. The Portuguese Man of War, from Plate XCIII of Forbes (1813); **C**. *Physalia pelagica*, from Plate XXXV, fig. 2 of Eysenhardt (1821); **D**. *Physalia producta*, from Plate I, fig. 1 of Olfers (1822).

On the other hand, Olfers (1822) gave, it appears, the first realistic account of the morphology of a *Physalia*. He noted that the float, or pneumatophore, was double skinned and the inner chamber opened to the outside via a pore held closed by sphincter muscles. He recognised three basic structures attached to the bladder, the long, fully developed tentacles (*Senkfäden*); smaller, shorter threads (*Fühlfäden*); and the so-called catchers (*Fänger*) or stomachs. His Plate I, fig. 4 also appears to show the larger tentacle attached to an ampulla, although he did not comment on this. Olfers (1832) elucidated further on this description, as will be discussed shortly.

Van Hasselt (1823, 1824) studied several specimens of *Physalia* and his immediate conclusion was that the four of those included by Lamarck (1816), together with five of Tilesius (1810), were all the same species that he referred to as *P. (Arethusa) megalista* Péron. The specimens of that species he had seen had varied in size by a factor of six. He noted that if a specimen was touched on its lower side then the anterior end of the bladder is raised up into the position illustrated by Lesueur & Petit (1807) (see Figure 5 A), while in the normal state, with the whole bladder in contact with the water, the specimen resembled Lamarck's fourth species, *P. elongata*. Further (*ibid*., p.117)[9] he said: "Thus the venous tissue, by which the first species (Physalia pelagica) of Lamark [sic] is supposed to be distinguished, consists only of folds, which come from the fact that the walls of the crest are internally bound

9 Original quote: "Ainsi donc le tissu veineux, par lequel on prétend distinguer la première espèce (Physalia pelagica) de Lamark, ne consiste qu'en plis, qui viennent de ce que les parois de la crête sont liées intériurement par des cloisons."

by partitions". He then remarked on how the characters that were supposed to distinguish other species could be explained as simple variations on the theme. However, he then immediately blotted his copybook, by establishing a new species, *P. obversa*, for a specimen where all the zooids were attached to the right side of the bladder, while in *P. megalista*, they were attached on the left. It is not clear if this was the first observation of the "handedness" of a *Physalia* specimen, but having dismissed variations in the shape of the bladder and the degree of elevation of the sail, it might have occurred to van Hasselt that this was just another of those variations.

Van Hasselt (1823, 1824) then laid out his interpretation of the morphology of a *Physalia* specimen. He agreed with Tilesius that each specimen was polystomatous, but disagreed with Lamarck and Tilesius as to which structure was a stomach, and actually considered the true gastrozooids or stomachs to be oviducts. Olfers (1832, p.162)[10] commented: "Weird egg duct, that sucks on everything and takes in food!" Van Hasselt considered that the ampullae at the base of the tentacles might be the organ of nutrition, which for a normal siphonophore would be true, but *Physalia* is by no means a normal siphonophore.

Two articles were published by de Fréminville (1824a, b), the latter being an abbreviated version of the former. De Fréminville (1824a, pp. 43–44)[11] briefly described some observations on *Physalia pelagica*, and commented that *Medusa utriculus* was: "*Holothuria Thalia* and the *Medusa Caravella* of Linné seem to be the same species observed at different ages". Although Linnaeus (1758) did include *H. Thalia* as one of his species of *Holothuria* but, as noted above, the species is now thought to be a salp! Also it was Müller (1776) who first used the name *M. Caravella*. De Fréminville considered that the *P. Megalista* might be distinct from *P. pelagica*, but then suggested that the artist had drawn the specimen in an attitude that is could never take (see Figure 5A). But now, having tried to reduce the number of *Physalia* species he did the same as van Hasselt and added not one but three more, *P. Thalia, P. cristallina,* and *P. hyalina*. Both the first and second were very small and otherwise distinguished by their colours. The third was the largest of all *Physalia*s, an honour previously awarded to *P. megalista*, but again it was distinguished by its colours. All this is rather difficult to swallow.

Yet another publication on *Physalia* was published in 1824, for Eichwald (1824) gave an extensive description of the species entirely in Latin, which even Google Translate has had difficulty with. He appeared to mention only the species *P. arethusa*, but Olfers (1832) remarked that Eichwald considered *P. pelagica* to be a young form of that species. Olfers also noted that Eichwald referred to the tentacles as reproductive tentacles, and that he had observed male gonophores on them. Later, Lesson (1843), who also briefly commented on Eichwald's paper, noted that it was the young rosary-like tentacles that were considered to be generative organs or *filets prolifera*. Unlike Lesson, Eichwald believed that physaliids were radiate animals, closely related to the Infusoria.

The general lack of consensus with regard to which *Physalia* species were valid continued with Blainville (1826) who, in the *Dictionnairre des Sciences Naturelles*, gave an extensive review and description of the genus *Physalia*. He criticised Bosc (1802) for not noticing a two-starred orifice, the opening of the gas bladder, that Blainville believed was a mouth. He praised Tilesius not only for having noted it, but also for describing the other orifice on the other end of the bladder that Blainville also considered to be "*orifice de l'intestin*". However, he was uncertain as to Tilesius' assertion that the tentacle functioned both to capture and to digest the prey. There was still a lot to learn!

Blainville (1826) gave a brief revue of some of the previous descriptions of *Physalia* and compared them with his own observations on a specimen preserved in wine spirit for a long time. He considered them to be related to salps (biphores) as the bladder had two openings, a mouth and an anus. The sail was considered to be a respiratory organ, and the gas gland was possibly a liver or a heart. The gastrozooids were also considered to be "*branchie*", i.e. gills. He tried to refute Tilesius' (1810) suggestion that the tentacles were the nutritive organs of the animal by noting, correctly, that their central canals connected with the cavity between the two layers of the bladder, whereas in de Blainville's mind they should connect with the "stomach", that is the inner cavity of the gas bladder. It is futile to spend further space in detailing these differences of opinion, but it is symptomatic of how entrenched various author views could become. As to the species, Blainville included three of Tilesius' species, *P. glauca*, *P. Lamartiniére* and *P. cornuta*, as well as Browne's (1756) *P. Arethusa* and Bosc's (1802) *P. pelagica*, although it was Lamarck (1801) who actually first used that name. He then added one of his own, *Physalia gaimardi* Blainville, without any illustration and with the briefest of diagnoses. He was tempted to recognise two others but, fortunately, he did not.

In the same year, Volume Two of the Atlas for the *Voyage autour du Monde … sur la Corvette de sa Majesté,*

10 Original quote: "Sonderbare Eierleiter, die sich an alles festsaugen und Nahrung einnehmen!"

11 Original quote: "*Holothuria Thalia* et la *Medusa Caravella* de Linné, semblent être le meme animal observe à différens ages."

La Coquille … was published, in which Lesson (1826) illustrated five *Physalia* species; claiming the authority for four of them although in three cases also applying earlier names to them. The description of these species, however, did not appear until 1830, and will be dealt with after considering the thoughts of Eschscholtz (1829). This also applies to an illustration, by Vauthier, of another *Physalia* species, labelled *P. cystisoma* (Figure 11A), that appeared in Volume 13 of the *Dictionnairre Classique d'Histoire Naturelle*, alongside a brief article on *Physalia* by Lesson (1828).

Rather strangely, Lesson (1827, pp. 163–164)[12] then wrote an article entitled "Considérations nouvelles sur la grande Physale, la *Caravelle*, la grande *Galère des tropiques*". He stated: "This Physalia … has long fixed the attention of the naturalists and the curious by at least its singular form. If I am not mistaken, we do not have, meanwhile, any exact description of it, or at least I know of none. That of M. de Lamarck (*Physalia pelagica*) is too short; and M. Cuvier does not say what is the species, the only one, that he has studied, and one can consider that at all those mentioned by Péron and the other voyagers as being described in an insufficient manner for the present state of science. Therefore, I think it right to attempt a description of this Physalia, remarkable for its size, shape and colour; that is based on a drawing made from nature and of natural size, as well as on the complete anatomy and an exact observation of its parts". He then gave a not particularly detailed description of the colony and, unfortunately, did not include the illustration he mentioned, nor did he actually give a name to the species that he was describing. I am sure Totton would have written "pot calling kettle black" in the margin next to Lesson's remark about Cuvier! The description is difficult to follow because it is often difficult to understand what part of the colony he was referring to, made more difficult by the absence of an illustration. Thus, Lesson believed that the posterior, oral end of the bladder bore small nipples (*petit mamelon*) that probably were slightly developed "cormidial" groupings in the oral zone. He then mentions (*ibid*. p. 165)[13]: "4 large subdivided tubers, with a cartilaginous consistency" that appear to be the bases of the "cormidial" groups in the main section. From these arose a score of tentacles, 10–40 feet long, and 30–40 (*ibid*., p. 166)[14]: "air vessels, necklace-like or in a rosary … Their function is undoubtedly to absorb from the water the air necessary for the life of the animal, which decomposes the first fluid to create the second if necessary". Quite why Lesson believed that it was necessary for a respiratory system to be present is not apparent, but what he was referring to here were the young tentacles, with their characteristic beaded appearance.

De Haan (1827) quoted in full the descripti*ons* of *Physalia* species given by Eysenhardt (1821); Olfers (1822) and Blainville (1826), and then listed those that he considered valid, namely: *P. Arethusa*, *P. producta* and *P. pelagica*, but then ruined this major reduction in species by adding another new species *P. Boiëi*. The description, if you can call it that, was extremely brief, and there was no illustration. All that can really be gleaned is that the bladder was 1″ long and bore no crest.

Rhizophysa.

Forsskål (1775) described the second cystonect species under the name *Physsophora filiformis*, and an illustration of this species was published a year later (Forsskål, 1776) (see Figure 3B). Forsskål described two other species in that genus, namely *P. hydrostatica* and *P. rosacea*; both of which are physonect siphonophores, although the second, currently named *Athorybia rosacea* has, as noted above, secondarily lost its nectosome. Thus, although all the species in the genus were siphonophores, they were all very distinct species belonging to different families in two different Sub-Orders. Forsskål's Latin description of *P. filiformis* gave little detail, but he did appear to mention that there was a cap of red pigmentation on the pneumatophore and that red coloration occurred elsewhere on the colony although it is not absolutely clear where. One other character that can be deduced from his 1776 figure (see Figure 3B) is that a well-developed tentacle only appears on the ninth gastrozooid from the zone of proliferation, and that the tentacle appears to be attached on its anterior side. This is in accord with the studies of Dunn & Wagner (2006) on the species *filiformis*, in contrast to the only other species, *eysenhardtii* Gegenbaur 1859, included in the same

12 Original quote: "Cette Physale … a depuis long-temps fixe l'attention des naturalistcs et des curieux, par sa forme au moins singulière. Si je ne me trompe, nons n'en avons cependant aucune description exacte, on du moins je n'en connais aucune. Celle de M. de Lamarck (Physalia pelagica) est trop courte; et M. Cuvier ne dit pas quelle est l'éspéce, la seule, qu'il ait étudié, et regarde toutes celles mentionnées par Péron et les autres voyayeurs, comme décrites d'une manièie insuffisante dans l'etat actuel da la science. Je crois done bien faire de tenter une description de cette Physale, remarquable par sa taille, sa forme et sa coloration; elle est fondée sur un dessin fait d'après nature et de grandeur naturelle de même que sur l'anatomie complete et une observation exacte de ses parties."

13 Original quote: "4 gros tubercules subdivisés, de consistence comme cartilagineuse".

14 Original quote: "vaisseaux aériens, moniliformes ou en chapelet … Leur fonction est sans doute d'absorber dans l'eau l'air nécessaire à la vie de l'animal, en decomposant le premier fluide pour créer au besoin le second".

genus, presently called *Rhizophysa*, where they are positioned laterally. However, the presence of red pigmentation in the siphosome, if that is indeed the case is more typical of *R. eysenhardtii,* while fully developed specimens of *R. filiformis* have green pigmentation, as Fewkes (1883) was probably the first to point out; but see Discussion section below.

Physsophora filiformis eventually came to be placed in the genus *Rhizophysa*. Most authors, e.g. Schneider (1898), Lens & van Riemsdijk (1908), Bigelow (1911), Moser (1925) and Totton (1965), have considered that Péron & Lesueur established that genus, although a few others, such as delle Chiaje (1841) cite the authority as Lamarck (1816). An illustration of the species *Rizophysa Planestoma* appeared on Plate XXIX, figure 4 in the Atlas (Volume 3) of the *Voyage de découvertes aux terres australis*, published in 1807. The specimen was also referred to, in the briefest of ways, in Volume 1, p. 43 of the same work, also published in 1807, but without actually naming it. According to the title pages, Volume 1 was "rédigé" [drafted] by Péron, while the Atlas, Volume 3 was produced by Lesueur & Petit. Thus, it would appear that these latter authors should be considered as to the authority of the name *Rizophysa*. As to who first used the modified form, *Rhizophysa*, delle Chiaje (1841) suggested it was Lamarck (1816) while Sherborn (1930) was ambiguous as on, p. 5502 he gave the authority to Oken (1815), but then, having noted that the name should be equated with *Rizophysa*, he then (p. 5531) gave the authorities as Péron & Lesueur. However, the earliest record for the generic name *Rhizophysa*, not *Rizophysa* as used by Lesueur & Petit, found in the *Biodiversity Heritage Library* was given by Tilesius (1814).

Lesueur & Petit's (1807, Plate XXIX, fig. 3) illustration of the species *Rizophysa planestoma* (see Figure 3C) clearly showed the colony to have an overall pinkish coloration, with some bluish tinges, and with a red pigment spot at the apex of the pneumatophore. Whether this is a true representation of its colour is unclear, but it might have taxonomic implications for the reasons discussed above. In addition it should be noted that well-developed tentacles are present on all but the youngest gastrozooids, and that those tentacles, although it is hard to judge, do not appear to be attached to the anterior side of the gastrozooid. However, as Eschscholtz (1829) pointed out (see below), the tentacles, which are spiralled in the mid region, appear not to have side branches, tentilla; a characteristic of *R. eysenhardtii* Gegenbaur, 1859. Thus, although most authorities have subsequently considered *R. planestoma* as a junior synonym of *R. filiformis*, here we will tentatively ascribe it to *R. eysenhardtii* although, presuming the specimen to no longer be in existence, we will never know its true identity.

Lamarck (1816) retained the genus *Rhizophysa*, but wrongly included *R. rosacea* within it. Cuvier (1817, p. 65)[15] defined the genus as: "without side bladders [nectophores], but only a long stem, along which tentacles are suspended, some conical, the others filiform", and included only one species *Rhizophysa filiformis*, considering *R. planestoma* to be a junior synonym of it. He considered Forsskål's *Physsophora rosacea* to be a mutilated form belonging to some unspecified species, but that is of no concern here.

Eysenhardt (1821) also considered that *Rhizophysa planistoma* and *R. filiformis* were the same species, and to the genus he added a new species, *R. chamissonis* Eysenhardt, that Chamisso had described and figured in manuscript form, but not published (see Figure 6). Eysenhardt stated that he had added an annotated line drawing of one of the specimens as his Pl. XXXV, Fig. 4. However, there appears to be no such figure, and so these annotations have been added, hopefully in the correct positions, to his Fig. 3B (see Figure 6). Eysenhardt's interpretation of the construction of the animal seems to be based more on fantasy than fact, as he considered it to be an intermediary form between *Physalia* and the scyphomedusan *Rhizostoma*. He suggested that the pneumatophore (Figure 6 ***a***) could have originated if the umbrella margin of *Rhizostoma* had curled upwards and inwards, thereby giving rise to an anterior pore (Figure 6 ***c***), with the surrounding pigmented part (Figure 6 ***d***) corresponding to the dark-blue umbrella margin of *Rhizostoma*. Further, he considered the "*brachia*" or "*die Arme oder Fänger*" (Figure 6 ***e***) to correspond to the tentacles of *Physalia* or the oral arms of *Rhizostoma*, and that the region anterior to them (Figure 6 ***g***) represented the mouth of a medusa, where the cavity of all the tentacles met, such that anterior to it should be found the stomach region. In addition, he considered the "*fasciculi axillares filorum rubescentium*" or "*röthlichen flockigen Fäden*" (Figure 6 ***f***) to be external sexual organs. For the present author, the "*brachia*" are the stomachs (gastrozooids), the "*fasciculi axillares filorum rubescentium*" the tentacles, and the region immediately anterior to them is the blastocrene or zone of proliferation of the siphosome. His interpretation of the origin of the pneumatophore has been known, for a very long time, to be totally incorrect.

15 Original quote: "N'ont pas de vessies latérales, mais seulement une longue tige, le long de laquelle sont suspendus des tentacules, les uns coniques, les autres filiformis."

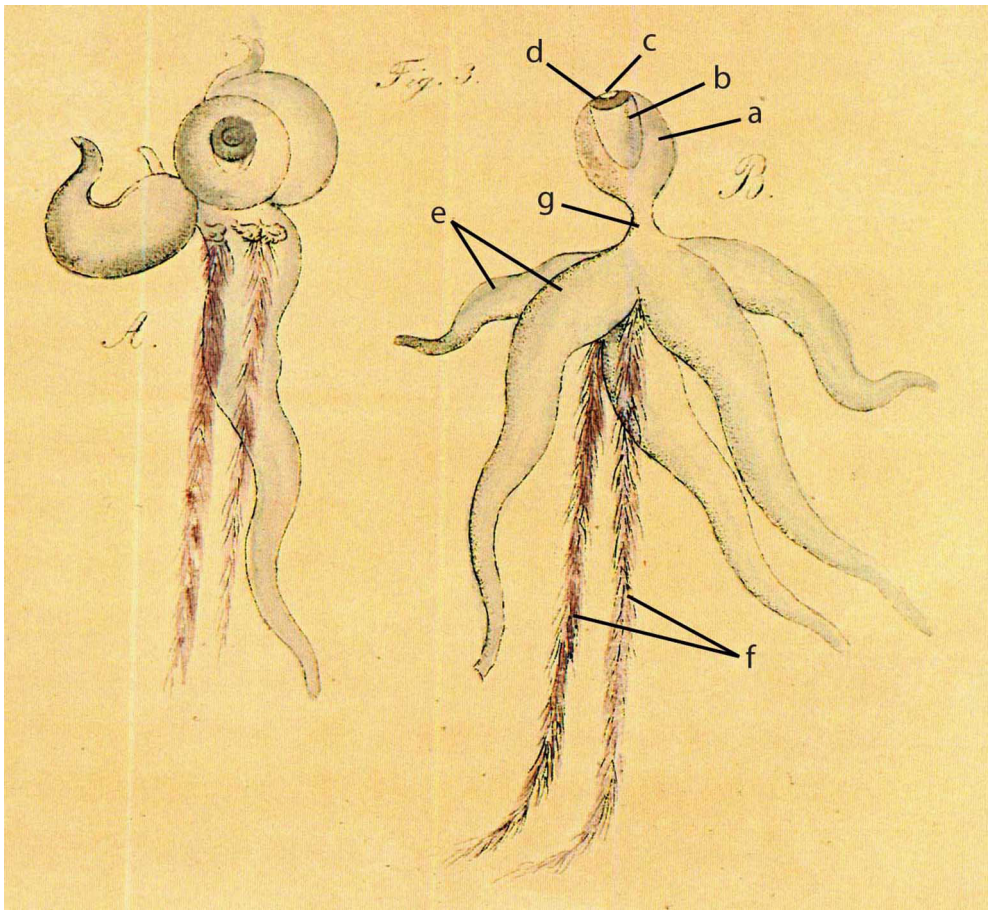

FIGURE 6. *Rhizophysa chamissonis* Eysenhardt, 1821. Reproduced from Eysenhardt (1821), Plate XXXV, with added annotations to **B**. a."den dichten Theil der Krugel" = pericystic cavity of pneumatophore; *b*. "den mit Luft gefüllten Raum" = pneumatosaccus of pneumatophore; *c*. "die Oeffnung" = the anterior opening of the pneumatophore; *d*. "den dunklen Saum derselben" = the pigmented sphincter around the anterior pore; *e*. "die Arme oder Fänger" = young gastrozooids; *f*. "die röthlichen flockingen Fäden" = tentacles; *g*. "die Stelle, wo die Fänger sich vereinigen und der Kugel adhäriren" = the base of the pneumatophore where the budding zone for the siphosome lies.

It is of interest to draw attention to certain features of Eysenhardt's illustrations of what would appear to be two different specimens. The first (Figure 6A) appears to have possessed three gastrozooids, of which one apparently has two tentacles, and the other two having a tentacular bud. This is, of course, very unlikely, but one can draw attention to the fact that the tentilla are red in colour. The second (Figure 6B) appeared to have five large gastrozooids of which two, or perhaps just one, had well developed tentacles, again with red tentilla. To which of the five gastrozooids the tentacles belong is not clear but, as drawn, they most certainly do not arise from the anterior side of the gastrozooid, that is the side closest to the pneumatophore,. Thus, in this respect, there appear to be similarities to Lesueur & Petit's species *Rhizophysa planestoma*, as well as the coloration, and this is discussed further below.

Delle Chiaje (1822, 1829, 1841) now, and later, caused some confusion, although it largely seems to have gone unnoticed by subsequent authors. His *Memorie sulla storia e notomia degli Animali senza vertebre del Regno di Napoli* was initially published in parts, starting with the Atlas in 1822, and a further four volumes (1823, 1825, 1828 & 1829), and then collectively in 1830–31. Plate 50, figure 3 in the Atlas (delle Chiaje, 1822) (see Figure 7) shows what clearly is a prayid (Sub-Order Calycophorae) siphonophore, but delle Chiaje (1829, p. 3) considered that it was the same as Forsskål's *R. filiformis*, although his description fails to mention the presence of Forsskål's (1775, p. 120) "*bullula aerea oblonga*", i.e. a pneumatophore. However, in his *Descrizione e notomia Animali Invertebrati della Sicilia citeriore osservati vivi negli anni 1822–30* delle Chiaje (1841, p. 135) defines the genus *Rhizophysa* as having a "*vesicula hydrostatica terminali*", and under *R. filiformis* he included his earlier description in a list of synonyms of Forsskål's species. Subsequently, delle Chiaje's species was rarely mentioned and eventually came to be considered as a doubtful synonym of *Rosacea plicata sensu* Bigelow, 1911.

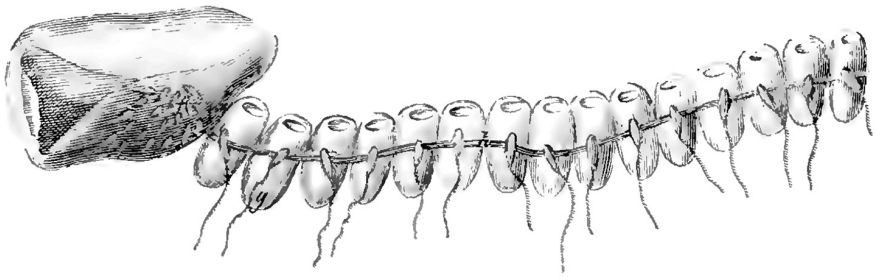

FIGURE 7. *Rhizophysa filiformis* delle Chiaje (1822, Plate 50, figure 3).

Eschscholtz.

Cuvier (1817) appeared to be the first to establish the Acalephæ as his third Class in the Zoophyta, which included some Anthozoa and Medusae, *Lucernaria*, ctenophores and siphonophores (Röhrenquallen in German); and Eschscholtz (1829) was the first to refer to the siphonophores as the Order Syphonophorae (*ibid*. p. 20) or Siphonophorae (*ibid*. p. 121). He divided the order into three families, the Diphyidae (including various species of the Calycophorae, often assigning different names to their polygastric and eudoxid stages, as the connection between them had yet to be established), the Physophoridae (including various species from all three current suborders of the Siphonophorae), and the Velellidae, which are now known to be only distantly related to the siphonophores. He included ten genera in the family Physophoridae and split them between two Divisions, based on the presence or absence of *Knorpelstöcken*, presumably nectophores. In the latter, he included just two genera, *Discolabe* gen. nov. and *Physalia*.

Eschscholtz (1829) examined several specimens of *Physalia* (see Figure 8A) and noted that, at the anterior end of the bladder, there was a pore though which gas could escape. The aboral part of the bladder was wholly devoid of attached zooids. The attached zooids consisted of gastrozooids without tentacles, separate tentacles, and occasionally small bundles of sexual organs; the tentacles being attached at their bases to elongated, pointed processes that he considered as fluid reservoirs. He was adamant that a central mouth, as Lamarck (1801), for instance, had suggested, was not present. He also noted that the gonodendra easily became detached when the specimen was disturbed, although he did not say if that applied to both sexes.

Eschscholtz (1829) was one of the first to try to make a determined effort to wrestle with the problem of just how many species of *Physalia* were valid. Unlike Blainville (1826), Eschscholtz (*ibid*. pp. 159–160)[16] was not so enamoured of the work of Tilesius by stating indirectly: "However, anyone who believes that he should be able to obtain more information about this strange species of animal from the long-winded treatise on the sea bubbles in the third volume of Krusenstern's journey around the world, will soon be deceived … One would think that a treatise as exhaustive as the one given in Krusenstern's travelogue would greatly facilitate this work; but I have seen with vexation that all my time and effort in studying it (which must have happened often, because one does not receive satisfactory information because of the confused presentation), has been in vain, although five species are placed here together". On the same subject, Chun (1897a, p. 85)[17] summarised his feelings when he said: "In ignorance of the embryonic and post-embryonic development, the astonishing variability in colour and grouping of the appendages, and in the configuration of pneumatophore, it may well be excusable if the young forms, or conspicuous states of contraction of the pneumatophore gave rise to the establishment of new genera and species. But one [Tilesius] still shot far over the target, and it almost seems as if these beautiful creatures induced a state of madness on the observer".

16 Original quote: "Wer jedoch aus der weitschweifigen, sich in Einzelnheiten immer wiederholenden Abhandlung über die Seeblasen im 3ten Bande zu Krusenstern's Reise um die Welt mehr Aufschluss über diese merkwürdige Thiergattung zu erhalten glauben sollte, wird sich sehr bald getäuscht sehen … Man sollte glauben, dass eine so ausführliche Abhandlung, wie die angeführte in der Krusensternschen Reisebeschreibung befindliche, diese Arbeit sehr erleichtern müsste; allein ich habe mit Verdruss gesehen, dass alle meine Zeit und Anstrengung beim Durchstudiren derselben (was oft geschehen musste, weil man wegen der verwirrten Darstellung durchaus kerne befriedigende Auskunst erhält) vergeblich gewesen, obgleich fünf Arten hier ans einander gesetzt werden."

17 Original quote: "Bei der Unkenntniss über die embryonale und postembryonale Entwicklung, über die staunenswerthe Variabilität in der Färbung und Gruppirung der Anhänge und in der Gestaltung der Pneumatophore mag es ja entschuldbar sein, wenn Jugendformen oder auffällige Kontraktionszustände der Pneumatophore zur Aufstellung neuer Genera und Arten Veranlassung gaben. Aber man schoss doch weit über das Ziel hinaus und es macht fast den Eindruck, als ob diese herrlichen Geschöpfe sinnverwirrend auf die Beobachter einwirkten."

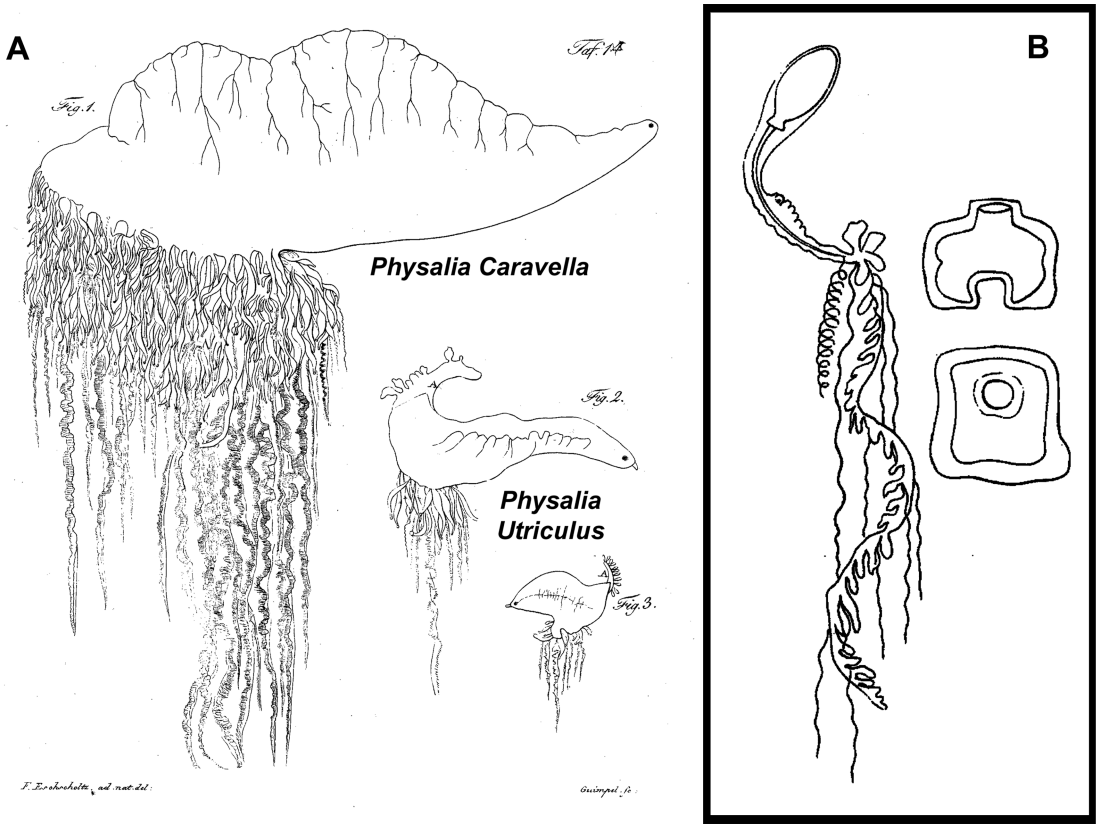

FIGURE 8. A. Eschscholtz (1829) Plate 14 (slightly modified); **B**. *Rhizophysa Peronii* Eschscholtz (1829) Plate 13, Fig. 3.

Eschscholtz (1829) concluded that, of the thirty or so species names already used for the Portuguese Man O'War, only three should be considered valid. Still two too many, but a valiant effort. Of these, at least two were found in the Atlantic Ocean, while the third was said to come from Southern Seas, but whether or not that included the Atlantic sector is not clear. The species were *P. caravella* [*Medusa caravella*, Müller, 1776], 8″ in length, which was said (*ibid.*. p. 160) (see Figure 8A, fig. 1) to have "*tubulis suctoriis pluribus ex radice communi*" that distinguished it from the other two (*ibid*, pp. 162, 163) with "*tubulis suctoriis omnibus simplicibus*". Then, *P. utriculus* [*Medusa Utriculus*, La Martinière (Gmelin)], 3.5″ in length, with its "*vesica extremitate tubulifera processu carnoso elongata*" (*ibid.* p. 163) (see Figure 8A, figs. 2–3), was distinguished from *P. pelagica*, the name based on *Physalis pelagica* Osbeck, 1757, 2.5″ in length with "*vesica extremitate tubulifera ad apicem usque aëre impleta*" (*ibid.* p. 162). Based purely on the Latin diagnoses it is often difficult to understand what exactly distinguishes these species, but fortunately Eschscholtz gave us some further information. As *Physalia caravella* was the largest species, because of its age, it naturally had "cormidial" units bearing several gastrozooids, rather than the gastrozooids being attached directly to the bladder. He also noted that the all the zooids were attached to the right-hand side of the bladder, as was the case for *P. caravella*, (see Figure 8A), and that reddish bundles of gonodendra could be seen between the gastrozooids and tentacles. For the smallest and therefore youngest species, *P. pelagica*, the gastrozooids and tentacles were attached directly to the bladder, but this time they were attached on the left-hand side. The sail, as might be expected, was not so well developed but unfortunately he did not illustrate this species. However, he noted that, for this species, the zooids were attached on the left-hand side and, for that reason, tentatively considered that *P. megalista* might be a synonym of it, but he was unsure about the accuracy of Lesueur & Petit's (1807) illustration. However, it is interesting to note that species were being differentiated on the basis of their handedness. Nonetheless, he then noted that he had collected even smaller specimens that had the gastrozooids attached either on the left- or right-hand side of the bladder, and correctly surmised that probably they were just variants of *P. utriculus*. Why he did not extend that supposition to the slightly smaller *P. pelagica* is not clear, but he seems to be the first to recognise that handiness might not be a specific characteristic.

In complete contrast to his valiant efforts to reduce the number of *Physalia* species to a reasonable number, Eschscholtz (1829) added some confusion with regard to Forsskål's *Physophora filiformis* and Lesueur & Petit's

(1807) *R(h)izophysa planestoma* that, as noted above, had both been included in the genus *Rhizophysa*. However, Eschscholtz split the genus into two dependent on whether the tentacles were simple (without side branches), genus *Rhizophysa*, or bore side-branches, genus *Epibulia*. He also believed that species of the former genus possessed nectophores, while those of the latter probably did not. For the genus *Epibulia*, Eschscholtz (1829) included the species *Physophora filiformis* Forsskål and *Rhizophysa chamissonis* Eysenhardt (see above), without actually referring to them as *Epibulia* and without any comment whatsoever regarding the fact that the former was long-stemmed while the latter was not (see Figure 6). For the genus *Rhizophysa*, he included the species *planestoma* along with a new species *P. Peronii* Eschscholtz that he also illustrated (see Figure 8B). The figured nectophores were not found attached to the denuded specimen, but it is clear that a nectosome was present, separating the pneumatophore from the siphosome, and thus that it belonged to the Physonectae not the Cystonectae. This species appears, subsequently, to have almost quietly disappeared from the literature, with Bigelow (1911) only including it amongst his list of doubtful physonect species.

1830s to 1850s

As noted above, Lesson (1830) gave a brief description of the five *Physalia* species that he had illustrated in his 1826 Atlas, although he was now aware of the work of Eschscholtz (1829). He named his largest species, with specimens measuring up to 12″ in length, *P. atlantica* Lesson (see Figure 9A) but, in the legend to the figure, be added the name *P. pelagica* Lamarck in brackets. This is in stark contrast to Eschscholtz's (1829) specimen of *P. pelagica*, which, at 2.5″ in length, was his smallest. Lesson (*ibid*. p. 36)[18] also added: "This Physalia is evidently the *physalia arethusa* of Chamisso, pl. 1 of the Voy. pittoresque de Choris. It is very certainly also the *physalia caravella* of plate 14, fig. 1, of Eschscholtz." He also considered that *Holothuria physalis* Linné, *Medusa caravella* Müller and Gmelin, *Thalia* Brugière, 1827, and *Physalis arethusa* Tilesius, 1810 were synonyms of it. This predilection for giving new names to established species, so perfected later by Haeckel (1888b), unfortunately occurred on several occasions before the ICZN rules were fully established.

Lesson's (1830) *Physalia atlantica* (= *P. pelagica*) (Figure 9A) was characterised as having "cormidial" groupings extending to almost the posterior end of the specimen, i.e. both the oral and main "cormidial" groups were well developed, and several main tentacles were present. The other four species (Figure 10) all had relatively undeveloped oral "cormidial" groups and a single developed tentacle with, usually, four "*tentacules à cils vibratoire*" or "*conduits monoliformes ou aériens*", referring to the younger tentacles that he had previously thought (Lesson, 1827) to have a respiratory function.

Lesson (1830) next largest species, at 4″ in length, was *Physalia australis* Lesson (see Figure 10, **1**), with which he equated the *P. megalista* of Lesueur & Petit (1807). As with all the remainder of Lesson's species, the sail/crest was somewhat reduced, the oral "cormidial" groupings had only begun to develop, and there was one main tentacle. Next in size, if the illustrations (Figure 10) are assumed to be drawn at the same magnification, was *P. antarctica* Lesson, which measured up to 2.5″ in length (Figure 10, **2**). It was distinguished from *P. australis* by its shorter anterior end, and the smaller size of the crest, and the fact that the main tentacle was not fully developed. It really is astonishing that authorities, such as Lesson, thought to distinguish these species based on characters that are so clearly related to the age or state of development of the colony.

Lesson also considered that *Physalis Lamartinieri* and *P. osbeckii* Tilesius, 1810, and *P. utriculus* Eschscholtz, 1829 were the same as his *P. antarctica*. His illustration (see Figure 9, 2), he said, was a copy of the illustration by Vauthier that, as noted above, Lesson (1830 p. 39), had used in the Dict. Classiq. of hist. Nat., livraison 15 [actually 13], "et on a conservé le nom de *physalis cystisoma* qu'elle portait écrit au crayon" [and we have preserved the name of *physalis cystisoma* that had been written on it in pencil]. This appears to be quite the wrong thing to do, especially as Lesson had, so shortly afterwards, given it another new name.

But now things became really confused. In the legend to his illustration, Lesson (1826) (see Figure 10) equated *Physalia antarctica* with *Physalis elongata* Lamarck, 1816. The latter species was very briefly mentioned by Lamarck, and it appears that he gave this name to a specimen of the "Portugueze man-of-war" that Forbes (1813, p. 200) briefly described and gave a rather extraordinary illustration (see Figure 5B) of, without naming it. Lamarck (1816) had included three other *Physalia* specie, namely *P. pelagica* Lamarck, 1801, *P. tuberculosa* sp. nov., and *P.*

18 Original quote: "Cette physale est évidemment la *physalia arethusa* de Chamisso, pl. 1 du Voy. pittoresque de Choris. C'est très-certainernent aussi la *physalia caravella* de la planche 14, fig. 1, d'Eschscholtz."

megalista Lesueur & Petit, 1807. Although no size was given, we shall assume that *P. tuberculosa* Lamarck, 1816 was Lesson's (1830, p. 40–41)[19] smallest bar one of his species. At the outset of his description he remarked: "The *physalia tuberculosa* originally described by James Forbes (Mem. Or.) does not exist, according to M. de Chamisso, or is confounded with the species described by this author. We do not doubt that it is distinct". This is all extremely confusing for, as we have just noted, Lamarck gave the name *P. elongata*, not *P. tuberculosa*, to Forbes' species. In addition, the quote attributed to Chamisso appears to have actually been written by Eysenhardt (1821, p. 422)[20], who stated: "Regarding Lamarck's *Phys. elongata* I cannot judge, since James Forbes Mem. Orient, to which he refers, is not at hand. However, that it belongs to one of the preceding species is not subject to any doubt". There does not appear to be any reason for these inconsistencies, but it does throw all Lesson's considerations into considerable doubt. Lesson (1830, p. 41) also noted that: "La *physalia tuberculosa* se rapproche de l'espèce précédente", that is *P. antarctica*, but he found several reasons to distinguish it, not least its peculiar shape (see Figure 10, **3**).

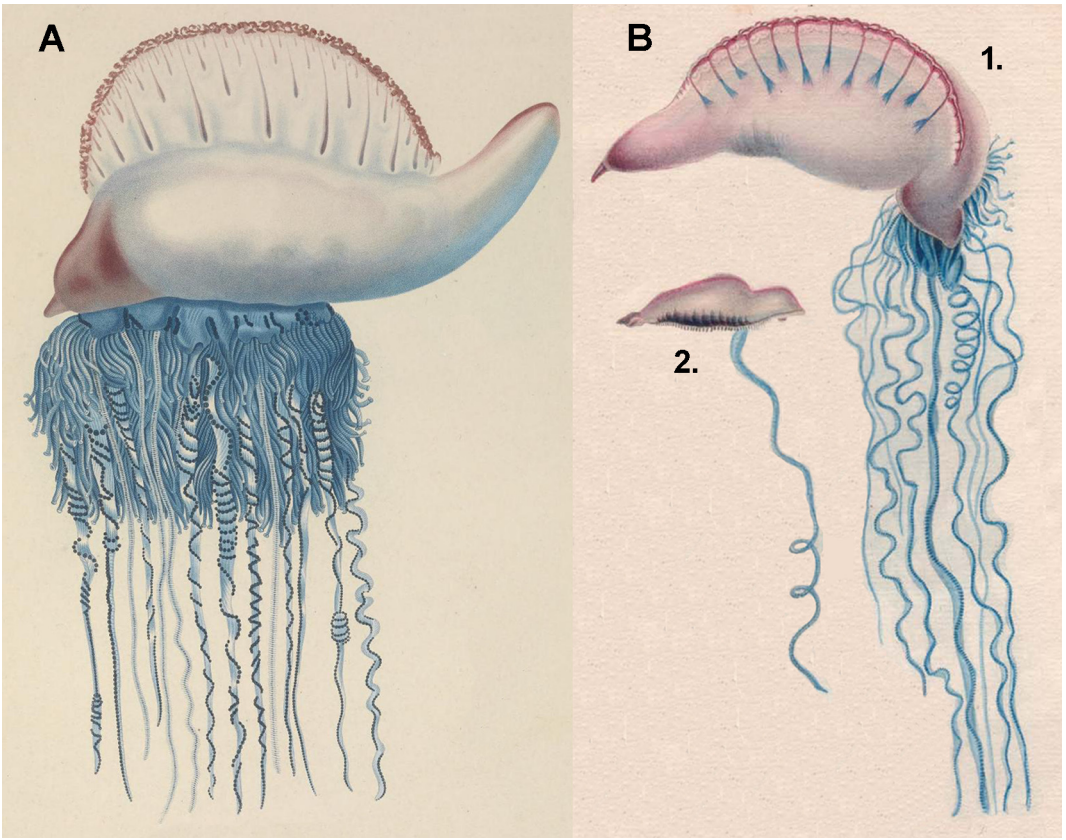

FIGURE 9. A. Physalie de l'Atlantide, *Physalia atlantica* Lesson (*P. pelagica*, Lamarck). (From Lesson (1826) Zoophytes Plate 4). **B**. Physalie de l'Atlantide, *P. caravella* = *P. pelagica*. 1. Whole specimen, with 2. one at an earlier stage of development. (From Lesson (1843) Plate 11).

The last and, presumably, smallest of Lesson's (1826, 1830) species was *Physalia azoricum* sp. nov, which measured 11–18 lines in length. He considered that it was the same as *P. pelagica* Bosc, *P. utriculus* Eschscholtz and, possibly, *P. trigona* Lamarck. The present author has not been able to trace the source of the last of these species names.

Lesson's (1830) interpretation of the morphology and, indeed, taxonomy of *Physalia* seemed to follow the typical French line adopted by Lamarck and de Blainville (1828), in that they did not believe that it was a true Zoophyte, but was somehow related to the molluscs. It was interpreted as an upside down mollusc, as the bladder and sail were equated with the foot of a mollusc; the thickened bases of the gastrozooids and tentacles the real body; and the beads that gave the younger tentacles their characteristic rosary-like appearance were thought to be external gills, which

19 Original quote: "La physalie tuberculeuse primitivement décrite par James Forbes (Mém. Or.), n'existe point, dit M. de Chamisso, ou est confondue avec les espèces que cet auteur a décrites. Nous ne doutons pas qu'elle ne soit distinct."

20 Original quote: "Ueber Lamark's Phys. elongata kann ich nicht urtheilen, da James Forbes Mem. orient., auf die er sich beruft, mir nicht zur Hand ist. Dass sie indess zu einer der vorigen Arten gehort, ist keinem weifel unterworfen."

also had the function of decomposing the seawater to produce the air that filled the bladder. Finally, Lesson considered the digestive cavity to lie between the two layers of the bladder, and did appear to recognise the gastrozooids for what they were.

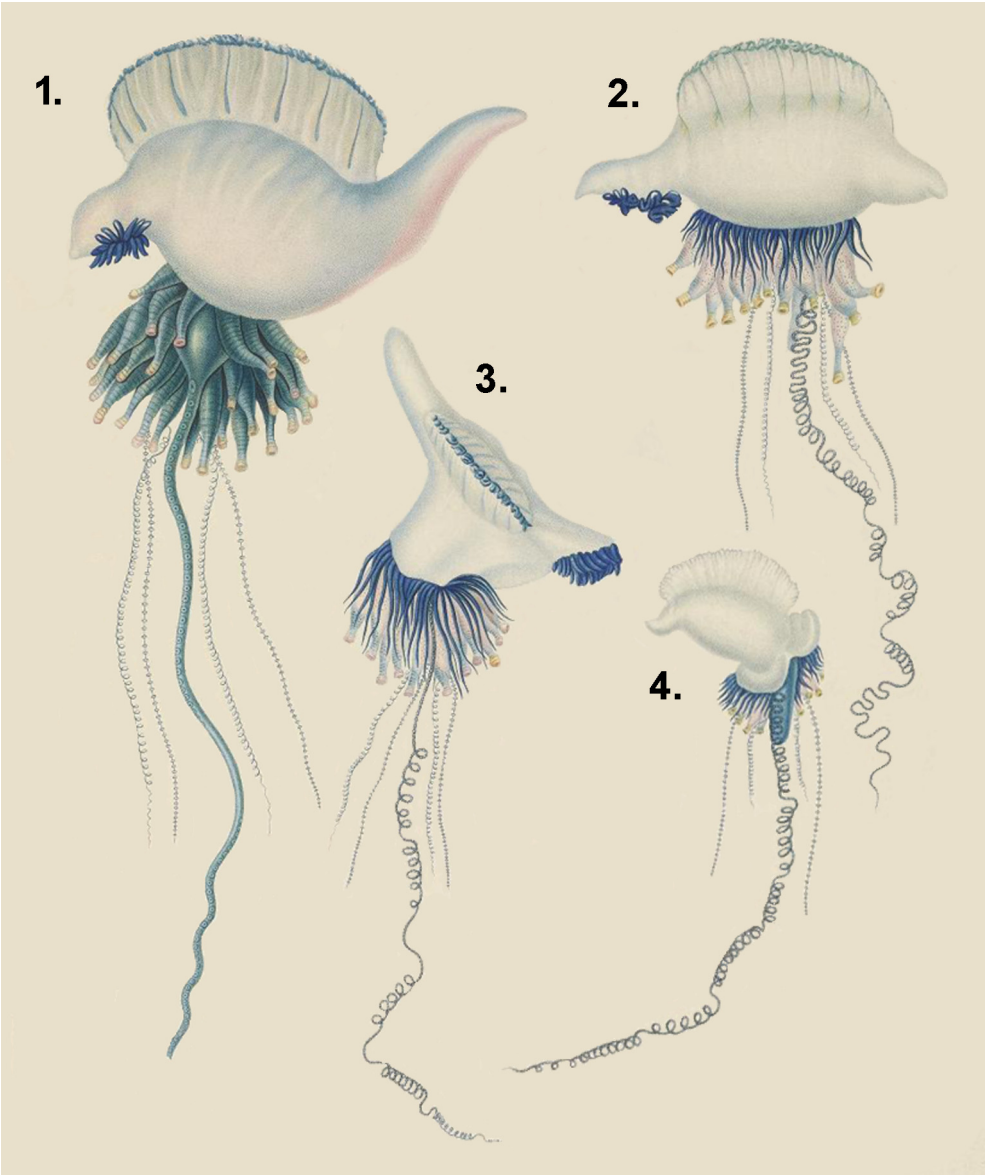

FIGURE 10. 1. *Physalia australis*, Less. (*Ph. megalista*, Péron & Les.); **2**. *Physalia antarctica* Less. (*Ph. elongata*, Lamk.); **3**. *Physalia tuberculosa*, Lamk.; **4**. *Physalia azoricum*, Less.
Reproduced from Lesson (1826), Zoophytes Plate 5.

Lesson (1830) also quoted some observations, although it is not clear whom he was quoting, concerning the effects of, firstly, feeding a fresh *Physalia* to his dog, while his servant held its mouth open. Then cutting up another specimen and feeding it to a nursing puppy; and then a chicken that he and his servant later ate! He also fed a dried and pulverised specimen to another puppy and a cat, and then to himself. One wonders what the animal rights movement might have to say about such behaviour but by report, all, apart from the roasted chicken, survived with, at most, only temporary discomfiture.

So, despite the valiant efforts of Eschscholtz (1829) to reduce the proliferating number of *Physalia* species, Lesson (1830) quickly doubled the number. However, worse was still to come. Olfers (1832) expanded on his previous description (Olfers, 1822), but this time for what he considered to be the largest *Physalia*, *P. Arethusa* (Figure 11B), although with a bladder 20 cm (8″) long, it was nowhere near the largest specimen recorded. This is in contrast to *P. Caravella* that Eschscholtz (1829) had considered to be the largest specimen, while for Lesson (1830) that species

was *P. pelagica*! He now recognised that there were two types of true tentacles, *tentaculi majore* and *tentaculi minore*, and noted some reddish bodies between the gastrozooids, which might have been the gonads. He rejected the idea that the smaller tentacles had a respiratory function. He gave a more detailed description of the bladder with its sail. He noted the presence of vertical veins running up through the sail that connect along the outer edge of the sail and there give of several side branches. By pumping gas from the bladder into these veins the sail could be raised. Further, he noted that the canals in the gastrozooids and tentacles opened into the cavity between the two walls of the bladder, which thus formed part of the gastrovascular system of the colony. He clearly figured (*ibid*. Plate II, fig. 3) that the base of the tentacles connected to an ampulla that formed a large tapering process.

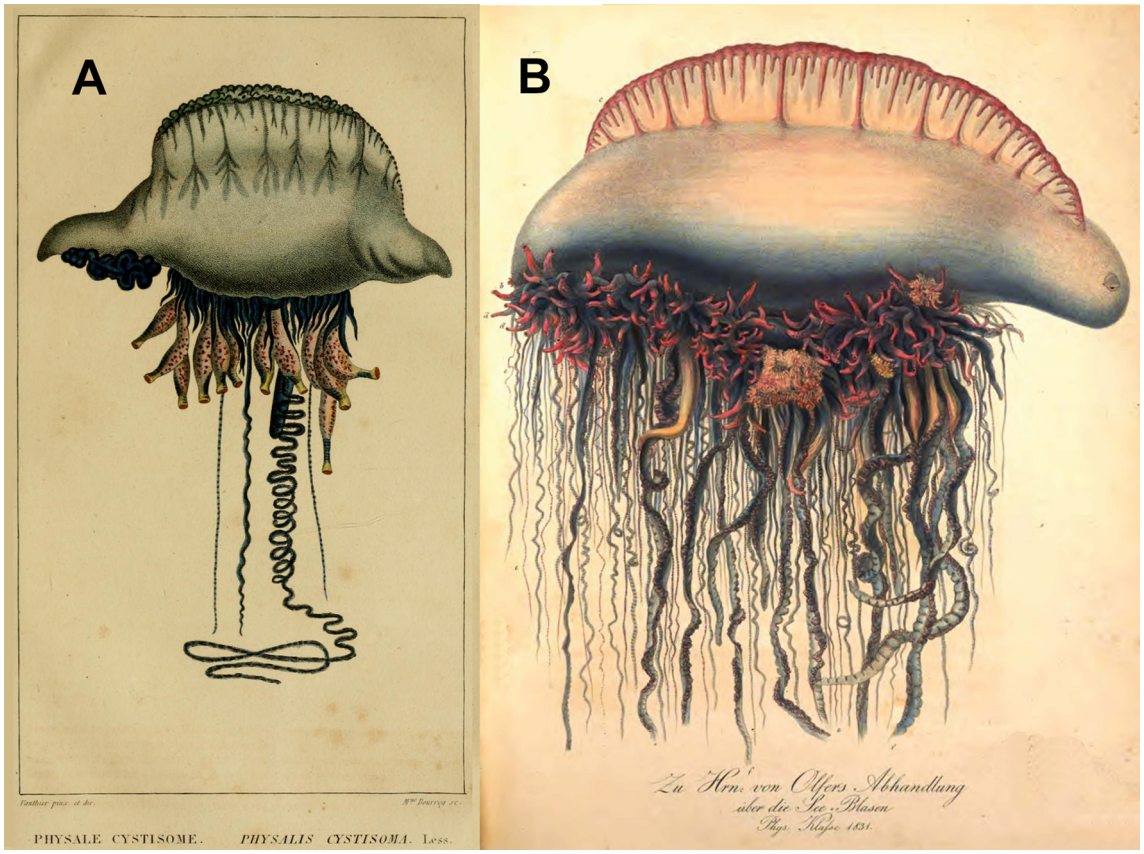

FIGURE 11. A. *Physalia cystisoma* Lesson, 1826, Plate before p. 467. **B**. *Physalia Arethusa* from Olfers (1832, Pl. I).

Olfers (1832) then compared his observations with those of previous authors. He noted that there was no central mouth, as Lamarck (1801) had suggested, and that the bladder was not a digestive organ as Deslonchamps (1828) appeared to suggest. The digestive organs were indeed the so-called *Saugröhen* and the tentacles had kidney-shaped knobs. Olfers also discussed the systematic position of *Physalia* and rejected any idea that they were related to Mollusca. He clearly established them as Physophores, in which he did not include the porpitids. Although Olfers managed to synonymise all of Lesson's (1830) species with others, he still ended up describing six species one of which, *P. producta*, was the rather dubious one he had described earlier. However, he only illustrated one, *P. Arethusa* (Figure 11B), of which he had given a detailed description, and with which he synonymised Eschscholtz (1829), *P. caravella*. He retained Lesueur & Petit's *P. megalista*, Lamarck's *P. Lamartinieri*, and Tilesius' *P. pelagica* and *P. cornuta*. To these he add one new species, *P. Eschholtzi* [sic]. [Throughout the text Olfers persistently referred to Lamarck as Lamark, and Eschscholtz as Eschholtz.] Olfers synonymised Eschscholtz's *P. utriculus* with this last species, as he believed that Gmelin's *Medusa utriculus* belonged with *P. Lamartinieri*, despite the fact that Gmelin's usage had 22 years of precedence. Once again it is not worth discussing the ins and outs of these species in detail as it will gain little, and far worse is to come!

It did not take long before the issue was further complicated when Brandt (1835) published his *Prodromus Descriptionis*. Brandt had been entrusted with the notes and numerous drawings made by K.H. Mertens after the latter's untimely early death from typhoid in 1830. Both had taken part in an extensive expedition of the Imperial

Russian ship *Seńiavine* in the years 1826 to 1829. Although Mertens, like his father, was more interested in botany, he also made a large number of drawings of various marine invertebrates, including siphonophores, with apparently extensive notes about the various species. Brandt (1835) then published a list of Merten's species, each with a brief description, but without illustration, including a few Siphonophorae, including velellids. As Brandt considered the great majority of all his species to be new, he came to be recognised as their authority, if they were deemed valid. In 1838 Brandt published an extensive treatise on the "*Schwirmquallen*" [Scyphozoa] and gave a further description of all of Mertens' manuscript species, using the latter's drawings to illustrate his 31 Plates. One might have hoped that Brandt would do the same for the other groups of invertebrates that he mentioned in his 1835 paper but, despite his numerous publications in subsequent years, it seems the remainder of Mertens' drawings remained, and still remain, unpublished. The plates were still extant until almost the end of the 19th Century as both Haeckel (1888b) and Bedot (1896) claimed to have seen them; the latter stating that they were in proof form. Totton (1965), however, tried to discover whether they still existed, but without success, and there appears to be no reference to them on the Internet.

With regard to the siphonophores, Brandt (1835) retained the same three families established by Eschscholtz, but subdivided the Physophoridae into the subfamilies Physophorae, Rhizophysidae, Agalmidae, Anthophysidae, and Physalidae. In the first he described the new species *Physophora ambigua* Brandt [undoubtedly a junior synonym of *P. hydrostatica*]; in the second he included both the genera *Rhizophysa* and *Epibulia*, but mentioned no *Rhizophysa* species. He dividied *Epibulia* into two subgenera based on whether the species were long-, *E. (Macrostoma) Mertensii* Brandt [considered to be a junior synonym of *R. filiformis* (see Bigelow, 1911, p. 318], or short-stemmed, *E. (Brachysoma) erythrophysa* Brandt, which Huxley (1859) considered it to be a mutilated physophorid. We will be returned to that species later. Apart from the last, the remaining families need not concern us here.

With regard to the family Physalidae, Brandt (1835) considered that the most important distinguishing feature among the species of *Physalia* was the presence or absence of a crest on the pneumatophore, thus portending the opinions of Haeckel (1888b), He, therefore, established the subgenera *Salacia*, with a crest, and *Alophota*, without a crest. Again pre-empting Haeckel (1888b), he referred to *P. megalista* Péron & Lesueur, 1807 as *P.* (*Salacia*) *megalista* nob*.,* and *P. pelagica* Lamarck, 1801 as *P*. (*Salacia*) *pelagica* Nob., thereby apparently claiming for himself the authority for the already described species. To these he added *P. (A.) Olfersii* Brandt. He also mentioned (*ibid*. p. 237) "Num propria species ? *Ph. ambigua*", but gave no further information. However, as noted above, Brandt also described a *Physophora ambigua*. So did he consider them the same or completely separate species? It need not concern us greatly as none of Brandt's siphonophore species is presently considered valid.

Lesson (1843) gave an exhaustive and exhausting 596 page review of the Acalephs, of which 168 pages were devoted to the siphonophores and velellids. He reviewed the some of the past history of the genus, mentioning Cuvier, Lamarck, de Blainville, Eschscholtz, Eichwald and Brandt, but notably not Olfers (1832), who, as noted above, had synonymised all of Lesson's (1826, 1830) species with others. He now divided the family Physophorae into seven tribes, but did not include the physaliids. In his first tribe, "*rhizophisae*" he included two genera, *Rhizophysa* and *Brachysoma*. In the former he included *R. filiformis*, *R. eschscholtzii* [apparently a renaming of Eschscholtz's (1829) species, *R. Peronii*, which, as noted above, is a physonect], *R. planestoma*, then *R. Peronii* again, but under its original name, and finally *R. Mertensii* Lesson [=*Epibulia (Macrosoma) Mertensii* Brandt]. A rather confusing list! For the genus *Brachysoma*, he included *B. chamissonis* Lesson [= *R. chamissonis* Eysenhardt] and *B. erythrophysa* Brandt.

Lesson (1843) was possibly the first person to separate off the Physaliidae as a separate family, which he called *Physaliæ*, distinct from what he called the *Physophoræ*, but he only included the genus *Physalia* in it. He now considered, correctly, that the gastrovascular cavity was the chamber between the two layers of the pneumatophore, with the suckers or gastrozooids hanging below and connecting with it. He talked off a *foie pyriforme* or pyriform liver to which the tentacles were attached; presumably referring to the basal ampulla, which is actually a region of nematogenesis. He also still believed that the smaller tentacles had a respiratory function

Lesson (1843) sub-divided the genus *Physalia* into three tribes, *Cystisomæ*, *Salaciæ*, and *Alophotæ*. Like Brandt, Lesson defined the last of these as being without a crest on the pneumatophore. However, the distinguishing characters of the other two tribes, and indeed all of the species, are difficult to comprehend. In the Tribe *Cystisomæ* he included just one species, *Physalia pelagica* (see Figure 10B), with which he synonymised many of the earlier specific descriptions. He said (*ibid*., p. 546)[21]: "This Physalia is distinguished from all other species of the genus by

21 Original quote "Cette physalie se distingue de toutes les espèces du genre par des caractères zoologiques très-précis. Elle est la seuie qui n'ait point d'extrémité postérieure garnie de verrues charnues; elle est aussi la seule qui ait sous le corps

very precise zoological characters. It is the only one that has no posterior extremity furnished with fleshy warts; it is also the only one that has under the body several tentacles with venom producing glands. Its size, and some other peculiarities, easily distinguish it at first sight". Its size was 11-12 inches and so was meant to be the same species as Eschscholtz (1829) had described as *P. Caravella* and Olfers (1832) as *P. Arethusa* (see Figure 11B). However, here is quite a disparity in the degree of development of the "cormidial" units between Lesson's (1843) illustration (see Figure 9B) and that of Eschscholtz (1829) (see Figure 8A) and Olfers (1832) (see Figure 11B). Indeed, there is a similar disparity between Lesson's (1826) of *P. pelagica* (see Figure 9A) and that he published in 1843 (see Figure 9B). Indeed, the disparity between the legend to the figure and the name used in the text, as noted above for Lesson's (1826, 1830) Plate 4 for *P. pelagica*, occurs again the 1843 publication. Thus, on Pl. 11 he refers to "La Physale de l'Atlantide"; the legend (*ibid*. p. 598) adds the specific name "*physalia caravella*"; while in the description the species is referred to as *P. pelagica*, although the relevant plate is said to Plate 6. Again, it is all very confusing.

Lesson's (1843) second Tribe was the Salaciæ, and contain species whose colonies bore only a single main "hepatic" tentacle and four "tracheal" ones. In this Tribe he placed his *Physalia azoricum*, Lamarck's *P. tuberculosa*, *P. utriculus*, which he attributed to Eschscholtz, and Lesueur's *P. megalista*. Finally, in his third Tribe, Alophotæ, he included *P. olfersii*, whose bladder was said to be the size of a pea.

Thus, Lesson (1843) considered six *Physalia* species to be valid; one more than in 1830. He retained *P. pelagica* and *P. tuberculosa*, but only one of his own species, *P. azoricum*. His other species became synonymised with *P. utriculus* and *P. megalista*. He appears to have reluctantly synonymised his *P. antarctica* with *P. tuberculosa*, and *P. australis* with *P. megalista*. Finally, he attributed his pea sized specimen to Brandt. All in all, it seems that Lessons (1843), for all his detailed account of the physaliids and velellids, managed to further muddle the situation and made no progress at all in trying to bring some accuracy to the morphology and taxonomy of the species included therein.

For the rhizophysids**,** which Lesson (1843) retained in the Physophoræ, he included two genera *Rhizophysa* and *Brachysoma*, for the long and short stemmed species, respectively, that had previously been described. Perhaps to try to overcome the confusion caused by Eschscholtz, Lesson ignored the genus *Epibulia*. Within the genus *Rhizophysa* he included *R. filiformis* Forsskål (Figure 12A); *R. eschscholtzii* Lesson, for a specimen from the North Atlantic that Eschscholtz had mentioned, but not named, which had rose-red tentacles; *R. planestoma* Péron & Lesueur; *R. peronii* Eschscholtz; and *R. mertensii* Lesson, to replaced Brandt's *E. (macrosoma) Mertensii*. He also gave an illustration of *R. filiformis* (Figure 12A) that shows a colony much like that of Lesueur & Petit's (1807) *R. planestoma*, with a light red stem. However, it is very difficult to interpret this figure or indeed Lesson's (p. 490)[22] brief description: "Bladder crimson, open at the top, supporting a long twisted, hollow stem, with suckers or laterally flattened tentacles, alternately bristled, bearing pedicellate suckers and packets of yellow ovaries". Huxley (1859, p. 92) gave an excellent review of this description and illustration when he commented: "Lesson ... gives a figure of *Rhizophysa filiformis,* to whose coenosarc [stem], spheroidal, granular masses are attached between the polypites. These he calls in the text 'paquets d'ovaries', and in his definition of the species these 'paquets d'ovaries' are said to be 'jaunes.' Nevertheless, in the figure they are of a lively pink hue! By way of making the confusion perfect, Lesson praises Delle Chiaje's 'description de cet Acalephe,' which he subjoins, and which obviously relates to a totally different animal." This other animal has already been referred to (see Figure 7). Within *Brachysoma* Lesson (1843) included *B. chamissonis*, for Eysenhardt's species and *B. erythrophysa* for Brandt's *E. (brachysoma) erythrophysa*. Lesson also described, very briefly, a species that he named *Angela cytherea* (Figure 12B), based on an illustration without annotations by Rand, and which has relevance to the discussion with regard to Haeckel's views (see below).

Leuckart (1851, 1852) published two, almost identical articles, the former in German, the latter in French, dealing with the structure of physaliids. Right from the start, he recognised that the knowledge of siphonophores hardly improved since the time of Eschscholtz (1829). However, with regard to morphology of *Physalia*, Leuckart (1852. p. 215)[23] stated: "Our knowledge of the structure of physaliids has been considerably extended by the researches of Eschscholtz and V. Olfers. They have established, in particular, by observation, that the suction tubes [gastrozooids]

plusieurs tentacules à glandes vénénifères. Sa taille et quelques autres particularités la distinguent aussi facilement dès la première vue".

22 Original quote: "Vessie purpurine, ouverte au sommet, supportant une longue tige tortillée, creuse, à suçoirs ou tentacules latéraux aplatis, sétacés alternes, portant des suçoirs pédicellés et des paquets d'ovaires jaunes."

23 Original quote: Nos connaissanccs sur la structure des Physalies out été considérablement étendues par les recherches d'Eschscholtz et V. Olfers. Ils ont établi, en particulier, par l'observation, que les tubes en suçoir non seulement avaleut, mais encore digèrent la nourriture reeue dans leur intérieur."

not only swallow, but digest the received food in their interior". He also noted that Olfers was quite correct in taking Blainville to task with regard to that author's suggestion that physaliids were molluscs. In addition, he considered that there was no need to establish new species according to the "handedness" of the specimen. He noted that, for the most part, his specimens were left-handed, while for those of Eschscholtz the opposite was the case. He also agreed with Olfers that the different between the large and small tentacles was merely a question of age.

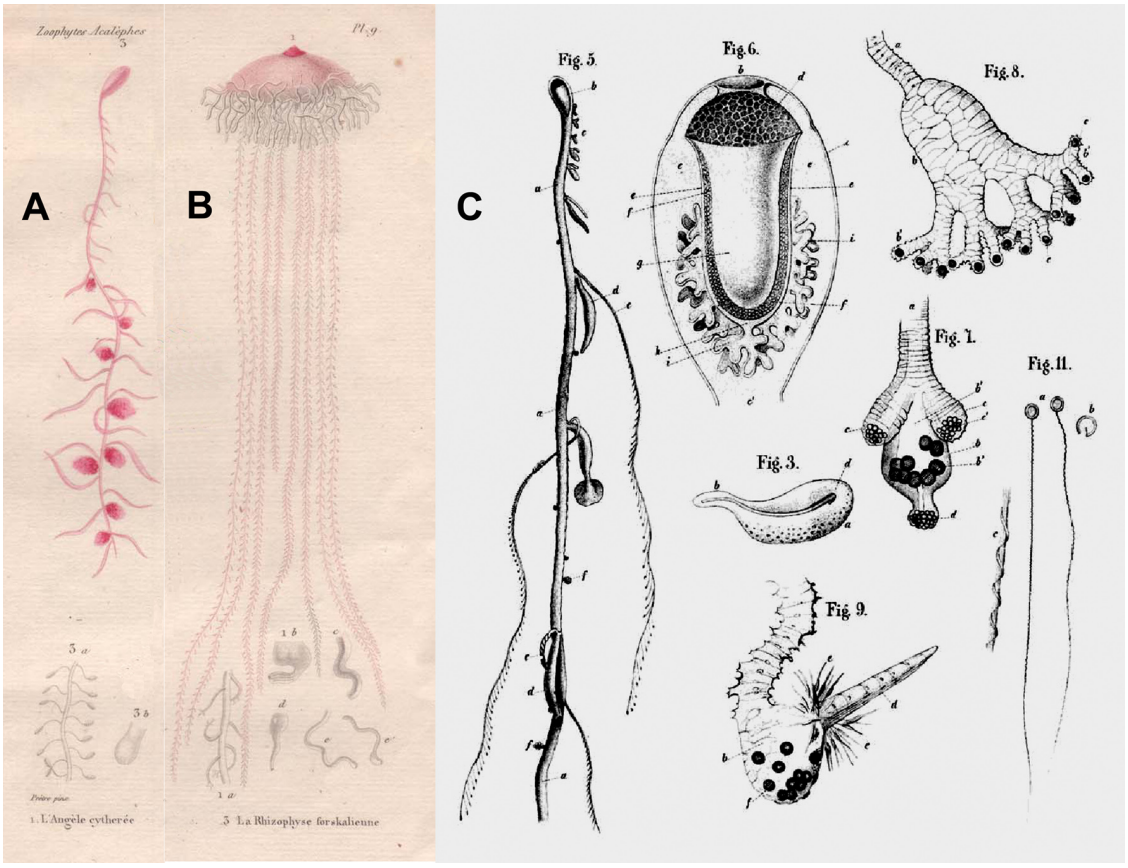

FIGURE 12. A. *Rhizophysa filiformis* and **B**. *Angela cytherea* (right) from Lesson (1843, Plate 9, figs. 1 & 3). **C**. *Rhizophysa filiformis*. Figs. 5-11 from Gegenbaur (1853) Pl. XVIII. (See original text for details.)

With regard to the number of species he only commented (Leuckart, 1852, p. 202)[24] that: "From the first, I examined *Physalia utriculus* Eschsch., or *Ph. Eschscholtzi*, which was regarded by Olfers as a distinct species from *Ph. Lamartinieri* Til. (*Medusa utriculus* (Gmel.), while Eschscholtz considered them identical, but they are distinct: the first differs even from all known species by an elongated, fleshy tube-shaped appendage, positioned on the posterior, vesicular end of the siphon". He then cited his observations on the morphology of his specimens that varied in length from 2–3.5″. Later he also mentioned *P. arethusa*.

A large part of Leuckart's (1851, 1852) memoirs were taken up with a discussion of the nature of *Physalia*. He noted that in the past researchers had largely regarded the siphonophores as simple animals with various multiple and repeated organs, which led to the assertion that there was just one central mouth, rather than the multiple ones borne by the large number of gastrozooids. He noted that Eysenhardt, in an *ex professo* manuscript, had argued that there was an analogy between these multiple gastrozooids with the situation in *Rhizostoma* whose gastrovascular cavity was said to open through a considerable number of branched tubes. Eysenhardt envisaged, as others have, that the bladder in *Physalia* was formed by an upturning and fusion of the umbrella of *Rhizostoma*. However, Leuckart reasoned that if one accepts that there are large numbers of stomachs, the siphonophores set themselves apart from all other animals. At that time, he considered that most people believed that a branching hydroid, with a stomach terminating each branch, was considered to be a colony, and, thereby, "*the suction tubes* [gastrozooids]

24 Original quote: "Des premiers j'ai examiné la *Physalia utriculus* Eschsch., ou Ph. *Eschscholtzi,* qui a été regardée par Olfers comme une espèce distincte de la. *Ph. Lamartinieri* Til. (la *Medusa utriculus* de Gmel.), tandis qu'Eschscholtlz les considère comme identiques; elles sont cependant distinctes: la première diffère même de toutes les espèces connues par un appendice allongé, charnu, en forme de trompe, disposé sur l'extrémité postérieure vésiculaire du siphon."

of the siphonophores are distinct animals, and that the siphonophores themselves are common trunks of these animals" (Leuckart, 1852, p. 217)[25]. In a footnote, Leuckart also noted that he had already expounded on his views that the siphonophores were compound animals in his *Über die Morphologie und die Verwandschaftsverhältnisse der wirbellosen Tiere* (Leuckart, 1848). He then spent much time justify the fact that the same could be applied to the nectophores, ampullae, etc., and finally concluded (*ibid.* p. 225)[26] that: "these important observations show that the *siphonophores have been wrongly considered heretofore as independent adult animals, and that they are nothing else ... than nurse larvae of the medusae*". Leuckart (*ibid*. footnote 3, p. 206) also stated that: "To my knowledge, C. Vogt (Zoolog Briefe, p.141)[27] is the only author who has put forward the idea that swimming bells are locomotory individuals of a colony of siphonophores".

Vogt (1852a, b) studied some siphonophores from Villefranche-sur-Mer and Nice but admitted that his only guide to their identification was Eschscholtz (1829), which was far from satisfactory. Among his species was one that he thought was probably the same as *Rhizophysa filiformis* of delle Chiaje (1822), which, as noted above, is most likely the same as *Rosacea plicata* (see Figure 7). He designated a related species as *Epibulia aurantiaca* Vogt, despite the fact that Eschscholtz (1829) had used the generic name *Epibulia* as an alternative to *Rhizophysa*, and based on the species *filiformis* described by Forsskål. However, for both of these genera Vogt (1852a, b) was uncertain whether an apical float, or pneumatophore, was present, while two swimming bells were.

Vogt (1852a, b) mentioned finding the species *Epibulia aurantiaca* during he stay at Nice, but in his 1854 (p. 110)[28] paper he recognised that he was mistaken stating: "Having found, during my last stay in Nice, specimens of a very delicate siphonophore that had hitherto escaped me, I looked in the System der Acalephes by Eschscholtz, the only book on the subject that was available to me, for a name that might suit my new find. The diagnosis of the genus *Epibulia* (*Tentacula ramulis simplicibus obsita, Partes cartilagineae incognitae*) appeared to me to be the most suitable to use, even if it did not specify anything. The usage of this generic name given to some incomplete and mutilated pieces had then the advantage of presenting an, up to now, perfectly useless genus with a species. I preferred this way to the invention of a new name for the genus". But Vogt (1854), having then become aware of the works of Quoy & Gaimard and Blainville, referred to his *specimen* as *Galeolaria aurantiaca*; the genus currently known as *Sulculeolaria*. He gave, in his Plate 18, a beautiful illustration of a whole specimen of what is clearly a species of *Sulculeolaria*, almost certainly *S. quadrivalvis*, which belongs to the calycophoran family Diphyidae.

It is not clear why Leuckart (1851, 1852) seemed to imply that, to his knowledge, Vogt (1851) was the first to suggest that the nectophores were individuals of a colony for, as noted above, he stated that he had already discussed the subject in his 1848 paper. Indeed, Vogt (1852b, p. 274)[29] somewhat tersely remarked: "This idea [coloniality], which I have in common with M. Leuckart, has not been borrowed from him, for it is set forth in the book I published at the end of 1847 under the title of Ocean and Mediterranean, where it is developed more extensively than in the Zoological Letters." The book he referred to, in two volumes totalling 575 pages and printed in German Gothic script, was, according to the title page, actually published in 1848, so perhaps to Vogt pre-dated it to ensure precedence over Leuckart (1848). Neither of these 1848 publications has been translated by the present author as, even if both authors did mention the subject of coloniality, there is no evidence to say if either author had read the other's work.

Actually, Vogt (1854, p. 129) considered that Lesueur (1813) was the first to consider siphonophores as "animaux composes", but it was actually Lesueur (1815, pp. 4-5, in a note added to his figure legends[30]), who made that suggestion when he said: "The analogy that I thought I had noticed between these various organs and those of

25 Original quote: "les tubes en suçoir des Siphonophores sont des animaux distincts, et que les Siphonophores eux-mêmes sont des souches communes de ces animaux."

26 Original quote: "les Siphonophores ont été considérés à tort jusqu'ici comme des animaux adultes indépendants, et qu'ils ne sont autre chose …que des larves nourrices des Médusaires."

27 Original quote: "A ma connaissance, C. Vogt (Zoolog. Briefe, p. 141) est le seul auteur qui ait émis l'idée que les cloches natatoires sontdes individus locomoteurs d'une colonie de Siphonophores."

28 Original quote: "Cette idée, que j'ai eu en commun avec M. Leuckart, ne lui a pas été empruntée, car elle se trouve exposée dans le livre que j'ai publié, è la fin de l'année 1847, sous le titre de *Ocean and Mittelmeer*, où elle est développée plus au long que dans les Lettres zoologiques."

29 Original quote "L'analogie que j'ai cru remarquer entre ces divers organs et ceux des physales, des vêllèles et des porpytes, m'a engagé à regarder les Stéphanomies comme étant très - voisines de ces radiaires, à cela près qu'au lieu d'être libres comme eux, ells sont réunies. MM. de Lamarck et de Blainville, auxquels j'ai communiqué ces observations, ont pensé avec moi que les Stéphanomies, dont je donne une ligure, n'etaient, ainsi que je vien de le dire, que des animaux réunis vivant en société."

30 Original quote: "Mais où placer alors la limite entre les organes et les individus?"

the physalias, the velellids, and the porpitids, induced me to regard the Stephanomies as being very close to these radiates, except that instead of being free like them, they are united. Messrs. Lamarck and Blainville, to whom I have communicated these observations, have thought with me that the Stephanomies, of which I give a figure, were not, as I have just said, assembled animals assembled together as a society". Vogt was emphatic that the gonophores were true medusae and, therefore, individuals, but when gathered together in a gonodendron, he considered the latter to be an organ, but then said (*ibid*., p. 136)[31]: "But where does one then place the boundary between organs and individuals?"

Nevertheless, the generic name *Epibulia* was still used in Vogt's (1852a, b) sense by several later authors, such as Chun (1882a, 1883), who referred to *Epibulia* (*Galeolaria*) *aurantiaca*, and later (Chun, 1885) to just *E. aurantiaca*. On the other hand, Fewkes (1882) used the name *G. aurantiaca*, noting that the generic name could equally be *Sulculeolaria*, but not *Epibulia*. However, later, e.g. Fewkes (1889) reverted to *E. aurantiaca*.

We owe it to Gegenbaur (1853) for the first proper description of *Rhizophysa filiformis* (see Figure 12C), although some details are lacking. He considered, correctly, that the pneumatophore was formed by an invagination and noted the apical ring of brownish-red pigmentation around what had previously been considered as an apical pore. However, interestingly, he considered that that pore had closed over and that gas release through it could no longer take place, so that the use of the pneumatophore as an hydrostatic apparatus was highly unlikely. In this, he may have been mistaken but, apart from Eschscholtz's (1829) contested observations, there remain conflicting views as to whether gas expulsion from the pneumatophore of cystonect species actually occurs, although Pickwell (1966) presumed that it occurred.

Nonetheless, Gegenbaur (1853) drew attention to several interesting characters. He noted (*ibid.* p. 325-6)[32]: "At the lower pole of the air bubble the inner layer duplicates into numerous, mostly dichotomously branched caecum-like processes that comprise almost the entire lower half of the pneumatophore" (Fig. 6*i*, in Figure 12C). These came to be known as hypocystic villi, and are characteristic of rhizophysid siphonophores. Gegenbaur also noted that the siphosomal stem had a reddish sheen, while the tentilla ended in greenish nodules. He noted that there were three types of tentillum with characteristic shapes and described them in detail. Totton (1965, p. 41) referred to these as *tricornuate* (fig. 7 in Figure 12C), *dendritic* or *palmate* (fig. 8 in Figure 12C), and *bird-headed* or *beaked* (fig. 9 in Figure 12C). For the third and rarest of these types, he noted that the "beak" or rostrum (*ibid. d*) was a rigid structure with muscles on one side that could pull the rostrum away from the pedicle of the tentillum, which would then spring back into position when the muscles relaxed. One wonders if the tentillum is thus being used as a lure, as similar behaviour has been noted in certain physonect species (Purcell, 1980; Haddock *et al.*, 2005; Pugh & Haddock, 2016).

Following on from Eschscholtz's (1829) classification of the Siphonophorae, Leuckart (1854, p. 255)[33] went one stage further when he said: "With regard now to the classification of our animals, for the presently known species, they can be distributed with tolerable accuracy into five families, Velellids, Physaliids, Rhizophysids, Physophorids and a fifth, including the diphyids and some related forms (*Hippopodius*, *Vogtia*), for which I would like to propose the name Calycophorids".

Quatrefages (1854) gave an extensive, 36 page, review of the morphology and anatomy of *Physalia*, but did not mention their taxonomy. He made a brief reference to earlier descriptions of *Physalia*, referring only to Olfers (1832) and Leuckart (1851, 1852), and believed that Vogt (1854) was probably the first to place the physaliids in a separate family. He considered that the distinction of the various *Physalia* species appeared to be extremely uncertain, but suggested that some of the characters concerned with the general shape of the bladder might have some value. He had collected just two specimens, washed up at La Rochelle, France and noted that, in many respects, they resembled *P. Arethusa*, but thought that there were sufficient reasons to establish yet another new species, and so he named it *P. Olfersii* nob. This seems a rather strange choice for, as previously noted, one of Brandt's (1835) species was *P. (Alophota) olfersii*, and which Lesson (1843) had retained and described as having a bladder the size of a

31 Original quote: "Cette idée, que j'ai eu en commun avec M. Leuckart, ne lui a pas été empruntée, car elle se trouve exposée dans le livre que j'ai publié, è la fin de l'année 1847, sous le titre de Océan and Mittelmeer, où elle est développée plus au long que dans les Lettres zoologiques."

32 Original quote: "Am untern Pole der Luftblase (h) geht die innere Lamelle der Duplicatur (e), in zahlreiche, meist dichotomisch verästelte blinddarmartige Fortsätze über, welche fast die ganze untere Hälfte der Blase becherförmig umfassen."

33 Original quote: "Was nun die Systematik unserer Thiere betrifft, so lassen sich die mit leidlicher Sicherheit bis jetzt bekannt gewordenen Arten in fünf Familien vertheilen, in die der Velelliden, Physaliden, Rhizophysiden, Physophoriden und eine fünfte mit den Diphyiden und einigen verwandten Formen (Hippopodius und Vogtia), für die ich hier den Namen Calycophoriden vorschlagen möchte."

pea. In contrast, Quatrefages specimens measured up to 25 cm in length. He disagreed with Leuckart as to where the various appendages were inserted in that, whereas Leuckart had considered them to be inserted on the inferior or ventral side of the bladder, Quatrefages said they were attached below and to the right-hand side. This seems to be somewhat semantic as, although the zooids were almost certainly attached to the ventral side, that side had become displaced to the right or, in the case of left-handed specimens, to the left.

Regarding the anterior pore on the bladder, Quatrefages (1854) noted that one of his specimens spontaneously deflated, with the gas escaping through the pore. He believed the specimen had died but, after 15 minutes, he saw that it had partially reinflated. He commented (*ibid*. pp. 116, 117)[34]: "It must, therefore, be admitted, either that the gas, which again distended the bladder after it had emptied, was secreted almost instantaneously by the very walls of this organ, or that it refilled from the atmospheric air by the pore that had served to expel the gas originally contained in the bladder, and this latter opinion is obviously the only probable one"; and "It seems difficult to me not to see a *real respiratory act* in this introduction, and this alternative expulsion of atmospheric air". He had the gas in the bladder analysed for nitrogen, oxygen and carbonic acid, and found that the first two were present in proportions almost exactly the same as in the atmosphere. Thus, he was convinced, as others before him had been, that the bladder was a sort of lung. Nonetheless, it is difficult to understand why people could believe that it was necessary for cnidarians, etc. to have a respiratory system.

Despite his lengthy details of the various appendages attached to the bladder, Quatrefages (1854) made a fundamental error in that he considered that, on each branch of a "cormidial" unit, the gastrozooid had a tentacle attached to it, with a separate "*coecum hépatiques*" or hepatic vesicles (Figure 13, figs I, II & III). He stated that Olfers and Leuckart has considered these structures as undeveloped suction tubes or gastrozooids. In fact, Olfers (1832, p. 163)[35] said: "It is certain, however, that these mouth-shaped ends of the appendages are never in such motion as those of the suction tubes, but rather remain unchanged during the most lively movements of the animal and the parts themselves; I never saw it open; in addition, the interior of these attachments differs noticeably from that of the suction tubes. If, therefore, in form and in origin, they should be regarded as modified suction-tubes, they are functionally to be compared to the blind appendages of the medusae". Similarly, Leuckart (1852, p. 211)[36] stated: "As with the suction tubes, the longitudinal canal of the tentacles (which serve not only to sting the external objects, but also to grasp and hold their prey) ends in the body cavity under the air bladder. At this mouth is a small elongate vesicle, which has the greatest analogy with a small suction tube not yet developed and lacking a mouth (Fig. 1 k); but the absence of liver cells in its interior shows that it is not an organ of this type." Also (*ibid.*, p. 212[37]): "At the base of these tentacles is also a particular cylindrical appendage ...; but here this appendage exceeds in length and in width the largest of the suction tubes; but it resembles them so much that the ancient observers to Eschscholtz have confounded them." Thus, Quatrefages appears to have totally misinterpreted what the aforementioned authors had said, particularly with regard to Leuckart's observation that no hepatic tissue was found within them in contrast to Quatrefages statement that they were *coecum hépatiques*. Quatrefages reported his observations in great detail, and made much of "*bouillie*", a porridge or chyme-like substance that was produced by digestion within the gastrozooids.

Quatrefages spent a lot of space describing the importance of these hepatic vesicles as he believed that the gastrozooids only acted like stomachs to start the digestion of the prey and to produce the "*bouillie*" that was then passed into the gastrovascular system and was acted upon by the secretions of the hepatic caeca to produce the

34 Original quote: "Il faut donc admettre, ou bien que le gaz, qui a de nouveau distendu la vessie après qu'elle s'était vidée, a été sécrété presque instantanément par les parois mêmes de cet organe, ou bien qu'il est rentré de l'air atmosphérique par le pore qui avait servi à expulser le gaz primitivement contenu dans la vessie, et cette, dernière opinion est évidemment la seule probable" ... "Il me parait difficile de ne pas voir un *véritable acte respiratoire* dans cette introduction, et cette expulsion alternative de l'air atmosphérique."

35 Original quote: "Gewiss ist aber, dass diese mundförmigen Enden der Anhänge niemals in solcher Bewegung sind wie die der Saugröhren, dass sie vielmehr bei den lebhaftesten Bewegungen des Thiers und der Theile selbst unverändert bleiben; ich habe sie niemals offen gesehen; zudem unterscheidet sich das Innere dieser Anhänge merklich von dem der Saugröhren. Wenn man sie daher auch der Form und dem Ursprung nach für veränderte Saugröhren halten möchte, so sind sie der Function nach den blinden Magenanhängen der Medusen zu vergleichen."

36 Original quote: "Comme dans les tubes ùn suçoir, le canal longitudinal des tentacules (qui servent non seulement à tâter les objets extérieurs, mais encore à saisir et retenir leur proie) aboutit dans la cavité du corps sous la vessie aérienne. A cette embouchure se trouve appendue une petite vésicule allongée, qui a l'analogie la plus grande avec une petit tube en suçoir non encore développé et dépourvu d'une bouche (fig. l *k);* mais l'absence de cellules hépatiques dans son intérieur montre qu'elle n'est pas un organe de ce genre."

37 Original quote: "A la racine des lignes à sonde existe également un appendice cylindrique particulier ...; mais ici cet appendice dépasse en longer le plus volumineux des tubes de sucoir; mais il leaur resemble tant, que les anciens onservateurs jusqu'à Eschscholtz les ont confoundu."

chyle. This lead him to suggest (Quatrefages, 1854, p. 136)[38] that: "In spite of this disposition [in *Physalia*], so different from that that exists in most animals, it follows from the anatomical arrangements, which I have described, that after having passed from the gastrozooids the chyme meets the product of secretion of the hepatic caeca, and penetrates into the large cavity of the body mixed only with bile."

Quatrefages (1854) also entered into an extensive discourse of the "*monozoïques*" or "*polyzoïques*" nature of *Physalia*, i.e. whether they were individuals or colonies. Like Vogt (1854) he thought (*ibid*., p. 137)[39] that coloniality is: "the most aptly founded in a number of cases. But has it not been pushed too far? Is there not a real exaggeration to see in each of the appendages of a siphonophore so many distinct individuals? To me, this exaggeration is obvious." Then (*ibid*., p. 139)[40]: "In the ideas of absolute polyzoicity, the answer is easy. Each of the appendages, and the bladder itself, form so many separate individuals; but it would be impossible for me to accept this view." And later (*ibid*., p. 140)[41]: "We see that as far as the *Physalias* are concerned, the doctrine of monozoïcity could very well be sustained ... If, guided by analogy, we look at the bladder as a common part supporting several animals, we shall have to search for the individual in these singular beings, I cannot, I confess, adopt the ideas here. I cannot see in each of the appendages as *many individuals* reduced to exercising a single function, and it seems to me preferable to see in them organs. Is it between a *liver*, a *liver organ*, and an *individual exclusively composed of liver and only secreting bile?* Frankly, I cannot see such. In wanting to follow logically the ideas that I contend, one could consider man as a colony, and every one of his organs known as so many *individuals*, and the principles which lead to such a consequence, seem to me rather unsuitable for placing us on a path of rational determination". There are many such anthropomorphic comparisons in Quatrefages' (1854) extensive memoir and, despite the great detail with which he made on the morphology and anatomy of the various appendages, there was a fundamental error in them, which renders much of the memoir irrelevant. However, Quatrefages did give an interesting, and brief, account of the rolling behaviour of *Physalia*.

Five years later, two relevant papers were published within a short space of time; one by Gegenbaur and the other by Huxley. Let us first consider the work of Gegenbaur (1859), although it probably appeared after Huxley's Monograph. In his paper Gegenbaur described a new *Rhizophysa* species, *R. eysenhardtii* and distinguished it from *R. filiformis* on the basis that it had filiform tentilla (fig. 49 in Figure 14A), as opposed to the complex structures that he had earlier described for *R. filiformis* (see Figure 12C). He also believed that there were some differences in the pigmentation on the pneumatophore, in that it was on the external surface rather than on the pneumatosaccus but, as noted below, the pigmentation is actually situated on the internal wall of the pneumatosaccus. Overall his description gave little detail of any value. His specimens did not appear to be in good condition as, for instance, he did not find any hypocystic villi around the lower half of the pneumatophore, and the only illustrations he gave (see Figure 14B) were of young gonophores and a single gastrozooid and tentacle. However, for this species he was convinced that an apical pore was present on the pneumatophore as he, like Huxley, observed gas escaping from it. He only found male gonophores on the one specimen he examined in detail, but also found detached apparently female ones, but did not say with which specimen they were associated. Thus the dioecious nature of the rhizophysids was still to be established with certainty.

38 Original quote "Malgré cette disposition si différente de ce qui existe chez la plupart des animaux, il résulte des dispositions anatomiques que j'ai décrites que, dès après avoir franchi les suçoirs, le chyme rencontre le produit de la sécrétion des coecum hépatiques, et qu'il ne pénètre dans la grande cavité du corps que mélangé avec la bile."

39 Original quote: "ce me semble, la plus justement fondée dans un certain nombre de cas. Mais n'a-t-elle pas aussi été poussée trop loin? N'y a-t-il pas une véritable exagération à voir dans chacun des appendices d'un Siphonophore autant d'individus distincts? A mes yeux, cette exagération est évidente."

40 Original quote: "Dans les idées de polyzoïcité absolue, la réponse est aisée. Chacun des appendices, et la vessie elle-même, forment autant d'individualités séparées; mais il me serait impossible d'accepter cette manière de voir."

41 Original quote: "On voit qu'en ce qui touelie les Physalies, In doctrine de la monozoïcité pourrait fort bien se soutenir … Je ne puis, je l'avoue, adopter ici les idées de quelques naturalists d'un incontestable mérite. Je ne puis voir dans chacun des appendices *autant d'individus* réduits à n'exercer qu'une seule et unique fonction. Il me semble préférable de voir en eux des organes. Quelle différence y a-t-il entre un *foie*, *organe hépatique*, et un *individu exclusivement composé de foie et ne faisant que sécréter de la bile?* Franchement, je n'en vois guère. A vouloir suivre logiquement les idées que je combats, on pourrait considérer l'homme luimême comme une colonie, et regarder chacun de ses organs connue autant d'*individus*. Or les principes qui conduisent à une semblable conséquence me semblent peu propres à nous mettre sur la voie d'une détermination rationnelle. Pour y arriver, rappelons ce qui existe."

FIGURE 13. *Physalia Olfersii* Quatrefages (1854, Plate 3).

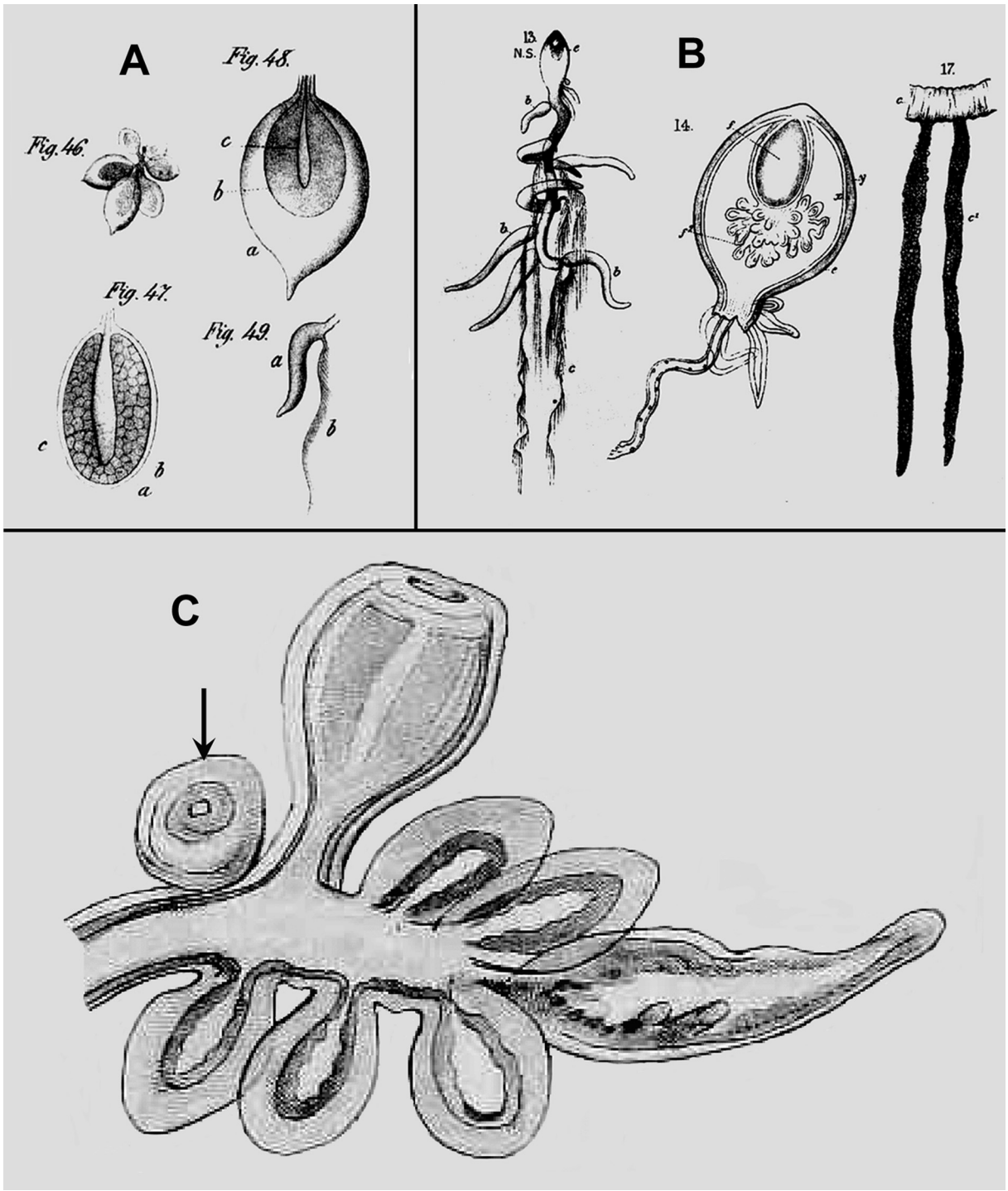

FIGURE 14. A. *Rhizophysa eysenhardtii* Gegenbaur, 1859. From Gegenbaur (1859) Plate XXXII (Legend) or actual Plate XXXI, figs. 46-49. **B**. "*Rhizophysa filiformis* ?", From Huxley (1859) Plate VIII. (For details see original) (Figs. 13, whole specimen; 14, detail of pneumatophore; and 17, part of tentacle with two tentilla). **C**. Terminal branch of gonodendron of *Physalia physalis*. From Huxley (1859) Plate X, Fig. 13.

Huxley.

Huxley (1859), in his monograph on *The Oceanic Hydrozoa*, gave a comprehensive review of the history of the Physaliadæ, as he named it, and its single genus *Physalia*. He extensively quoted from Eschscholtz (1829), and concluded (*ibid*. pp. 99–100): "Eschscholz [sic], on the other hand, is, as usual, clear and intelligible, and, as his species are founded upon personal observation of the animals in their living state, they might very advisably (if their distinctive characters are really well founded) be taken as the starting point by future observers". Like Eschscholtz, Huxley (1859, p. 95) also poured scorn of de Blainville's (1834) interpretation of physaliids when he said: "De Bla-

inville ('Manuel,' p. 113) has fallen into the most marvellous errors respecting *Physalia.* Not content with discovering its mouth and an anus, he attributes to the *Phyaliæ* a stomach (the air-bladder), a foot (the crest), branchiae (the tentacles), and generative apertures, besides a hepatic plate, vessels, and a central circulatory organ! No wonder, then, that he places *Physalia* among the Molluscs." He also thought that von Olfers (1832) had added little to what Eschscholtz described, while Leuckart's (1851, 1852) descriptions were more complex and more complete, and proceeded to quote him extensively. However, Huxley agreed with Quatrefages (1854) that, as Leuckart (1851, 1852) had suggested, the crest did not lie on the opposite side to the appendages, but that the latter were displaced to one side, or the other. But we have already considered this matter. However, he thoroughly disagreed with Quatrefages regarding the latter's assertion that the bladder had a respiratory function.

Huxley (1859) also drew attention to the useful contributions to an understanding of the anatomy of these complex animals made by Leuckart (1851) and Quatrefages (1854). However, for certain other authors Huxley (*ibid.* p. 99) had this to say: "The perusal of the works of the various writers who have occupied themselves with the establishment of specific distinctions among the *Physaliæ,* simply makes one long for the advent of a Caliph Omar[42] in this department of zoological literature. A sort of unpleasant vertigo is the only result I can report of my study of the systematic labours of Von Olfers [1832], Lesson [1843], and Lamarck [e.g. 1840]". Thus, Huxley only considered the species listed by Eschscholtz (1829), namely. *Physalia caravella, P. pelagica* and *P. utriculus*. However he stated (*ibid*., p. 101): "I must confess I feel anything but satisfied that these are really distinct species, but this is a point which can only be settled by those who study these singular animals with modern appliances and a knowledge of what has already been done." Unfortunately, he then continued (ibid.): "To such observers I would suggest that the number of primary and secondary septa in the crest, and the exact mode of grouping of the appendages, are more likely to yield good distinctions than any other characters." However, it would seem that these are merely a reflection of the age of the specimen, and have no taxonomic value whatsoever.

Huxley (1859) then gave a detailed description of his specimens, including some very young specimens as small as ⅕″ in length, but he did not attempt to study the order of development of the "cormidial" groups. He illustrated the terminal branches of young gonodendra, showing the terminal polypite, which Huxley referred to as a hydrocyst, the special nectophore, the gonophores, and what possibly is the jelly polyp (arrowed in Figure 14C), although he did not refer to it in the text. He also described both male and female gonophores, but seems not to have noted whether individual specimens were monoecious or dioecious. He concluded (*ibid*., p. 106), although it is not exactly clear how he reached it, that: "I can produce no direct evidence of the fact, but I entertain little doubt that the gynophores are detached as free swimming medusiform zöoids, as in *Velella,* and only develope [sic] their ova subsequently. The androphores, on the other hand, must dehisce while still attached. It might seem at first as if this arrangement were not very well calculated to ensure the impregnation of the ova, but when we consider in what enormous troops the *Physaliæ* are ordinarily found, the difficulty disappears".

For the Family Rhizophysiadæ (Huxley, 1859, p. 71) or Rhizophysidæ (*ibid.*, p. 90) he included only a single species, *Rhizophysa filiformis*, and commented (*ibid.*, p. 91) that: "The only account of any species of *Rhizophysa* which suffices the wants of the modern naturalist is the excellent description of *R. filiformis* by Gegenbaur". He put aside Eschscholtz's (1829) genus *Epibulia* as he recognised that that author's reasons for establishing the genus were incorrect, in that *Rhizophysa* species do not possess a nectosome. Also. he considered Brandt's (1835) *E. (Brachysoma) erythrophysa* as (*ibid.*, p 134): "Probably a mutilated and contracted Physophorid", but made no comment with regard to *E. (Rhizophysa) chamissonis*.

Huxley then briefly described (1859, p. 90) and illustrated a specimen of "*Rhizophysa filiformis* ?" (see Figure 14B) whose: "pneumatophore is pyriform, and, like the rest of the body, of a pale, pinkish hue, but with a very deep red patch surrounding the aperture of the pneumatocyst". He also noted the presence of hypocystic villi around the base of the pneumatophore (fig. 14 *f*[2] in Figure 14A), but the most important character he described (*ibid.*) was that: "The stem of the tentacle gives off a series of lateral branches [tentilla] in which no distinction into pedicle, sacculus, and filament is discernible" (fig. 17 in Figure 14A). He also noted (*ibid.*) that: "The polypites [gastrozooids] appear to be attached indifferently to either side of the cœnosarc [the siphosomal stem]", but unfortunately he did not mention to which side of the gastrozooid the tentacle was attached.

Finally, Huxley compared his specimen with Gegenbaur's (1853) description of *Rhizophysa filiformis*. He disagreed that the apical pore on the apex of the pneumatophore was permanently closed, particularly as he saw gas bubbles spontaneously discharged through it. He noted that the gonodendra on his specimen was situated at the

42 Omar (Umar) bin al-Kahattab was the second Muslim Caliph and an expert judge, for which he was given the tile *Al-Farooq*, meaning the one who can distinguish the right from the wrong, or between truth and falsehood.

base of and between two gastrozooids, while Gegenbaur had found possible gonodendra to be equidistant between successive gastrozooids However, the main difference between the specimens was that the tentacles on his bore filamentous tentilla that were not differentiated into "pedicle, sacculus and filament" (*ibid.* p. 90) (fig. 17 in 14A) and, thereby, were quite unlike those described by Gegenbaur. He concluded (*ibid*. p. 91): "Gegenbaur's observations agree so closely with my own that I can see no ground for supposing that we examined different species, but, in his account of the tentacles he describes structures which, I think, I could hardly have overlooked, though, as I examined but one specimen, I may have done so; or, perhaps, they were not developed in the tentacles I examined". Huxley was, unlike so many 19th Century zoologists who studied siphonophores, reluctant to establish new species on the basis of morphological differences that might have been preservation artefacts, but in this case he was too overcautious.

There can be no doubt that the species that Huxley (1859) was describing was not *Rhizophysa filiformis*, as he himself pointed out when he compared the three different types of complex tentilla that Gegenbaur (1853) had described compared with the simple filiform tentilla of his specimen. But clearly he was unaware of a new *Rhizophysa* species that Gegenbaur (1859) described as *R. eysenhardtii* Gegenbaur, 1859[43] (Figure 14B); as was pointed out by Fewkes (1879).

Although the nomenclature for the physaliids seemed to have somewhat stabilised at the time of Huxley's monograph, unfortunately L. Agassiz (1862) and A. Agassiz (1865) took a completely different view and called the species most often found off the east coast of North America *Physalia arethusa* Tilesius, 1810. This name was also, not surprisingly, adopted by Fewkes (e.g. 1880), although he did mention that *P. caravella* was rarely seen in that area and in the Mediterranean at Villefranche.

Wallich (1863) briefly reviewed all the observations that has been made on *Physalia*, but added little or no detail himself. However, he did remark on the small fish, 2-3" long, that accompanied specimens of *Physalia*, which swam freely between the tentacles without being captured. These probably were the fish that Bennett (1837) had observed. Wallich noted that, for specimens of *Physalia* collected over a wide area of the Atlantic, what he thought to be the same species of fish was always present. He also made further observations on the movement of the bladder, which he never saw deflate, and thus considered that the specimens never sank belong the surface. He noted the rolling behaviour and waxed lyrical when he stated (*ibid*., p.364): "At present, therefore, I have only to record the act of the 'Portuguese man-of-war' as one of a very frequent occurrence, leaving it to more imaginative minds to trace back the existing mode of salutation between vessels at sea designated "dipping the colours," to this primæval source." It is now well known that the fish *Nomeus gronovii* is often found in asscoiation with *P. physalis* and, according to the *Biodiversity Heritage Library*, the first person to notice that association appears to be Günther (1889)

Studer and the first Bathyphysa species

Over the next twenty years little meaningful information was published on cystonect species until Studer (1878b) gave the first description of a species of the genus *Bathyphysa*, *B. conifera* Studer. A shortened account of this paper was presented by Studer to the Bern Natural Research Society by Studer on the 11 November 1877 and published in their Reports for 1877 (Studer, 1878a). Both Bigelow (1911) and Moser (1925), in their reference lists, give the date of this latter publication as 1877 but neither, it seems, actually refer to the paper in their texts. It is likely that this paper was published in 1878, which is the date on the relevant volume.

Both papers mention three species *Rhizophysa conifera* sp. nov., *R. inermis* sp. nov., and *Bathyphysa abyssorum* gen. nov., sp. nov., that were all found attached to plumb lines, gathering data on the depth of the oceans and, often painfully, unwound from them. Twenty-four cystonect pieces were collected in this way ranging from just tentacles to extensive stem pieces. The most complete specimen (Figure 15A–C) was named *R. conifera* Studer, and came from a possible depth of 1573 fms [2876.7 m], at 35°43'N, 17°50'W; with five other less complete specimens being found at other locations in the Atlantic Ocean to as far as 24°S. The drawings (Figure 15A) were apparently drawn

43 There appear to be at least two versions of Gegenbaur's (1859) *Neue Beiträge zur näheren Kenntniss der Siphonophoren*. The manuscript was individually published by "Halle" on 2nd September 1859, but it also appeared in Volume 27 of *Novorum Actorum Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosum*. The first 19 volumes of this journal bear the title *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae* while from Volume 36 onward it was titled *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosum*.

by Dr. Weinbeck immediately after retrieval from the plumb line and before preservation. One presumes, therefore, that Studer's description is based on these drawings and not on his own personal observations on the fresh specimen. Thus, it is uncertain how much reliance can be given to the coloration of the pneumatophore and the gastrozooids, with their distinctly yellow proboscis region. Studer distinguished the species on the basis of his observation that the tentacles bore no tentilla. Studer wrote much on the subject of the pneumatophore and the internal structure of the stem, which has little if any taxonomic value; although he did note the appendix-like attachments (hypocystic villi) at the base of the sac, such as are present in *Rhizophysa filiformis*, were entirely absent"... However, as noted above, they are difficult to see in preserved rhizophysid species.

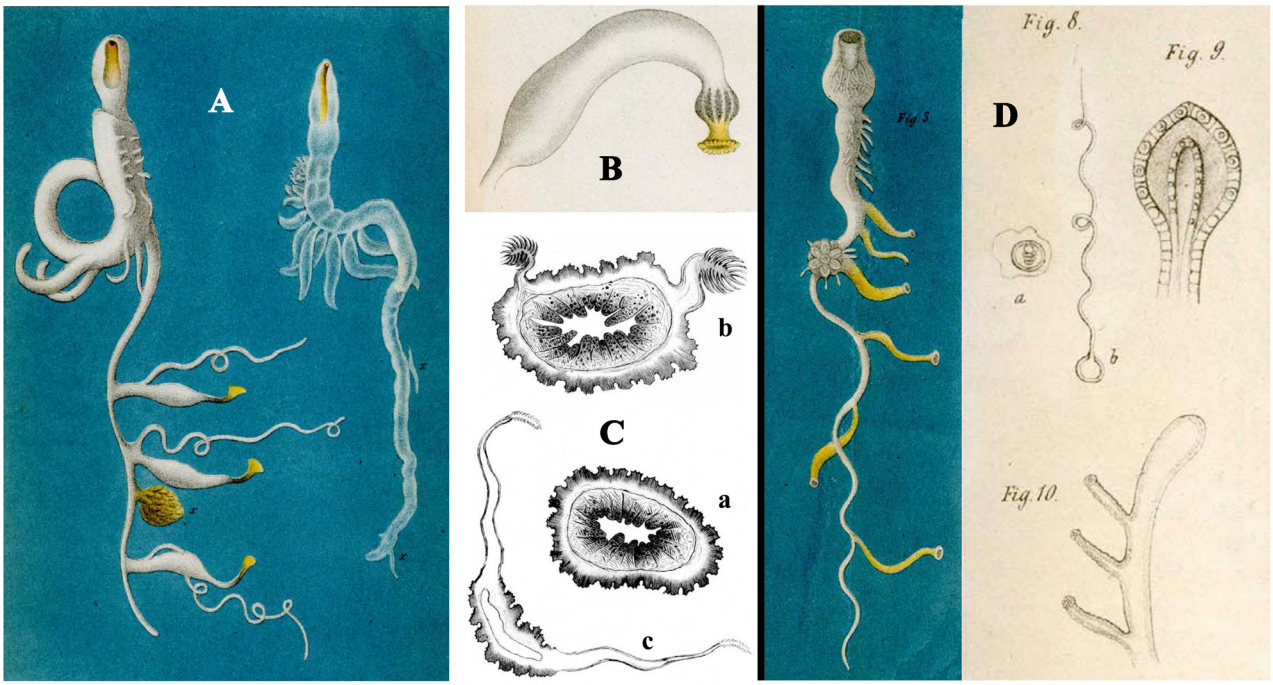

FIGURE 15. A–C. *Rhizophysa* (*Bathyphysa*) *conifera* Studer, 1878b. **A**. Two "whole" specimens; **B**. Gastrozooid (*ibid*., fig. 4); **C**. Transverse sections of a young gastrozooid – **a**. toward distal end; **b**. in middle; **c**. toward proximal end. From Studer (1878) Plate I, figs. 1–2 (**A**.), 4 (**B**.); and Plate II, figs. 16 (**C. a**), 17 (**C. b**) and 18 (**C. c**). **D**. *Rhizophysa inermis* Studer, 1878b, Plate 1, figs, 3, 8–10. Fig. 3. Whole animal; Fig. 8. Nematocyst, *a*: in its capsule; *b*: discharged; Fig. 9. Gonophore; Fig. 10. Gonophore tentacle.

Studer (1878b) devoted many paragraphs to describing the gastrozooids and tentacles, but little of value can be gleaned from them. He did note that the buds of the gastrozooids were initially arranged into two alternating rows, but later formed a single row. When the tentacles arose they were simple filiform structures without arose they were simple filiform structures without any side branches and apparently attached to the anterior side of the siphosomal stem, as the illustrations (Figure 15A) indicate. However, Studer (*ibid*, p. 10)[44] said: "Close to the attachment point of the polyp to the stem the simple tentacles arise". This was interpreted as meaning that the gastrozooid was borne on a peduncle, which has been considered an important taxonomic character by some later authors, as discussed below. However, for probably the most important feature of the gastrozooids Studer devoted just two sentences. He said (*ibid*.): "Mesoderm and ectoderm behave similarly, as in the mouth, in the posterior segment of the stomach (Fig. 17) [Figure 15C, b]; two muscular solid ridges, one dorsal and one ventral, begin to form, which now continue on the basal part of the polyp, as wing-like adhesive bands attach to the trunk (Fig. 18). (Fig. 18) [Figure 15C, c]. These ligaments consist of a solid core, a continuation of the mesoderm, send out, on its margins, numerous processes into the ectoderm, followed by the longitudinal muscle fibres, as in the main stem". Although these structures cannot be seen in his illustration of whole gastrozooids (Figure 15A, B), he is clearly describing the presence of

44 Original quote: "Mesoderm und Ectoderm verhalten sich ähnlich, wie im Mundtheil, im hinteren Magenabschnitt (Fig. 17) fangen zwei muskulöse solide Leisten, eine dorsale und eine ventrale, sich zu bilden an, die sich nun auf den Basaltheil des Polypen, als flügelförmige Haftbänder fortsetzen und an den Stamm sich anheften (Fig. 18). Diese Bänder bestehen aus einem soliden Gallertkern, einer Fortsetzung des Mesoderms, der am Rande zahlreiche Ausläufer in das Ectoderm sendet, woran sich die Längsmuskelfasern, wie am Stamm festsetzen."

what Fewkes (1886) referred to as *ptera*. Such wing-like processes or *ptera*, although actually positioned laterally, are now considered characteristic of the young gastrozooids of *Bathyphysa* species. This character, together with the filiform tentacles, are good reasons to retain the species *conifera* as a valid species, but not in genus *Rhizophysa*.

For the other species mentioned by Studer (1878b), his single specimen of *Rhizophysa inermis* was poorly described and cannot be specifically identified (Figure 15D). The description was based on brief observations on a single specimen, presumably not by Studer, that was not preserved. The pneumatophore was said to have a cap of black pigmentation, with a distinct pore, with obvious hypocystic villi being present. The gastrozooids were said to lack tentacles, but each gonodendron that was positioned close to the gastrozooid was said to have an associated tentacle bearing tentilla (fig. 10 in Figure 15D). However, that looks more like part of the stalk of the gonodendron with all the elements stripped from the side branches. Bigelow (1911) questionably treated *R. inermis* as a junior synonym of *R. eysenhardtii* but, because of the close association of the gonodendron with a gastrozooid, it seems more likely that specimen is more closely related to one of Studer's other species, *R. conifera*, which as we have seen is actually a *Bathyphysa* species.

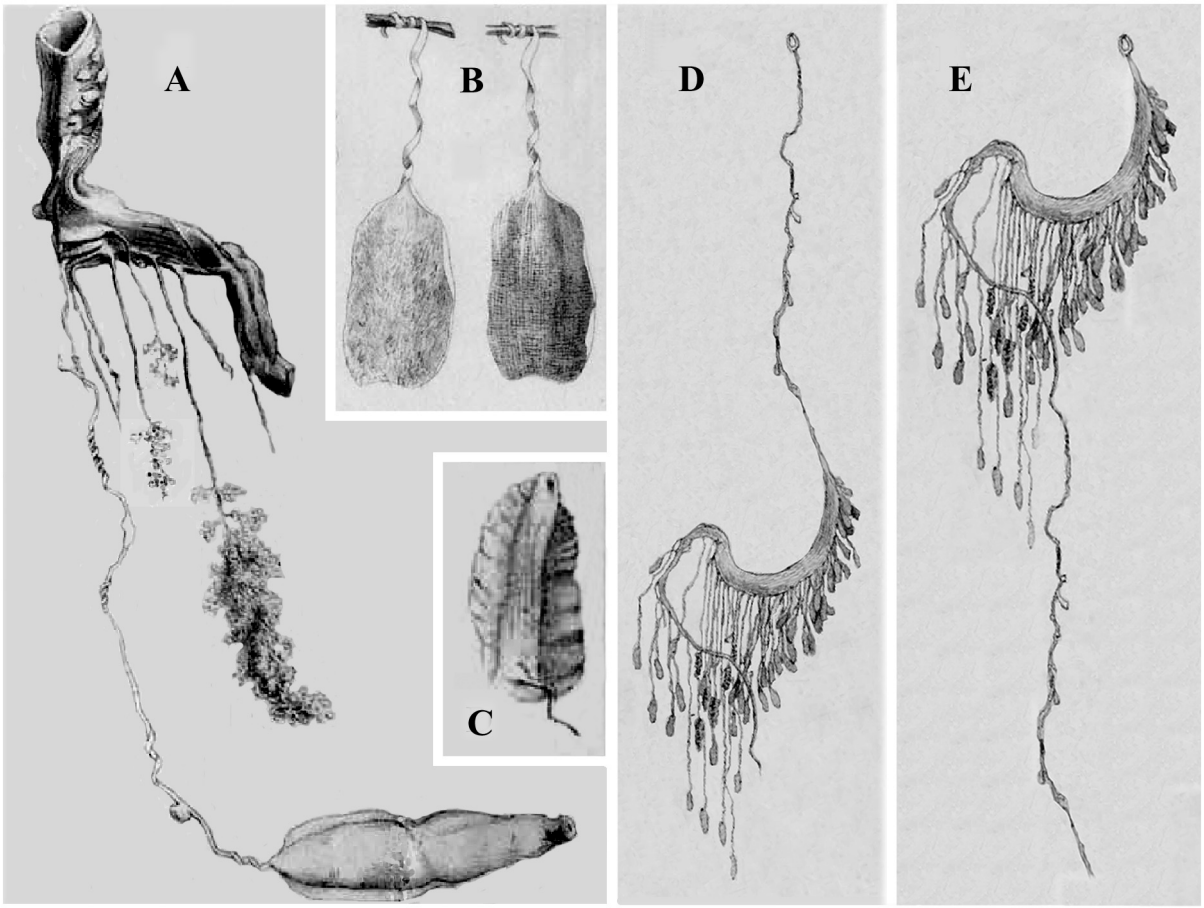

FIGURE 16. *Bathyphysa abyssorum* Studer, 1878b. **A**. Part of siphosomal stem, with "attached" appendages; B. Two gastrozooids; **C**. Bract-like structure; **D**. & **E**. Reconstructions of whole specimen; **D**. according to Studer (1878); **E**. as suggested by present author. From Studer (1978)b, Pl. III, figs. 27 (**A**), 38–39 (**B**), 25 (**C**), 28 (**D**).

The last species that Studer (1878a, b) described was *Bathyphysa abyssorum* (Figure 16). The pneumatophore, 19 mm in length, was clearly damaged when gas expansion caused it to rupture, and no mention of hypocystic villi was made. For the gastrozooids Studer (*ibid*. p. noted "zwei erhabene Kiele" [two raised keels], but this time they were lateral, not dorsal and ventral. Studer distinguished the two species, *Rhizophysa conifera* and *B. abyssorum*, on the basis of his interpretation that in *R. conifera* the gastrozooids were attached directly to the stem, and that their tentacles were without tentilla; while the gastrozooids of *B. abyssorum* were considered to be borne on long peduncles and may not have possessed tentacles although this, of course, is very unlikely, if not impossible. One glance at Studer's illustrations of the gastrozooids (see Figure 16B) should be enough to see how delusional he was. He commented that his long peduncles were wound around the main stem, and that they contained a large number of nematocysts.

What he did not comment on was that both of them clearly have a free end. The obvious answer is that the gastrozooids, without peduncles, have become detached and their tentacles have become wound around the stem. The gastrozooid shown in Figure 16A was again detached but its tentacle was wound round some other structure. Studer also suggested that bracts were present (see Figure 16C) but Schneider (1898), almost certainly correctly, interpreted them as being nothing more than young, mouthless gastrozooids. Indeed, Studer's figure clearly shows the *ptera* and a developing tentacle.

There was one suggestion that Studer (1878b) made for *Bathyphysa abyssorum* that appears rarely to have been commented on by subsequent author, although it did cause Haeckel (1888b) to reach his erroneous conclusion concerning the systematic position of this genus. This concerns his reconstruction of the arrangement of the zooids along the siphosomal stem. Once Studer had unravelled the knotted ball of interwoven pieces of the specimen he found that he had three main pieces; the pneumatophore, plus a thick and a thin piece of siphosomal stem. From these pieces he reconstructed the whole animal and illustrated it (*ibid.* Plate III, fig. 28) (see Figure 16D) with the thin piece of stem, largely deprived of any zooids, lying immediately below the pneumatophore, and the thickened stem piece, bearing many zooids of gradually increasing size, posterior to it. On the largely denuded, thinner section of the stem, immediately posterior to the pneumatophore, he noted alternating rows of wart-like polyps and depressed pores, which communicated with the gastrovascular cavity of the stem. While, on the thicker section, he illustrated what appears as a set of zooids gradually increasing in size; although that is somewhat an illusion as most of the gastrozooids seem to have been detached, while their tentacles have become wound around the stem. Nonetheless it seems to me that when Studer made his reconstruction (see Figure 16D) he positioned the two pieces of siphosomal stem in the wrong order, such that the thickened part actually lay immediately below the pneumatophore, while the thinner, largely denuded, part would have been posterior to it (see Figure 16E).

In conclusion, it is clear that several aspects of Studer's (1878b) description of the first bathyphysid species are highly questionable and resulted in, for instance, the issue of the presence/absence of peduncles to the gastrozooids being quite unnecessarily contentious It is also clear that there is insufficent detail to separate the three species from each other and so, for instance, Totton (1965) united them under the name *Bathyphysa conifera* (Studer, 1978), as that was the first species to be described.

Fewkes.

Fewkes (1879) gave some further details regarding the development of the three types of tentilla on the tentacles of *Rhizophysa filiformis* (Figure 17A), including a later stage of development of the tricornuate type, but the detail is somewhat lacking. One can note, however, that his figs. 6 & 7 (boxed in Figure 17A), clearly show a membrane connecting each lateral branch to the central one, although he, like Gegenbaur (1853) made no mention of it. In the 1880s Fewkes (1882, 1883, 1886) gave several descriptions of rhizophysid siphonophores, including two new *Rhizophysa* species, *R. gracilis* Fewkes, 1882 and *R. uvaria* Fewkes, 1886; and *Pterophysa grandis* gen. nov. sp. nov. *R. gracilis* (Figure 17B) was said to differ from *R. filiformis* by the positioning of its gonodendra, and from *R. eysenhardtii* by the presence of two types of tentilla. The pneumatophore was said to have a cap of dark brown pigment, while the lower part was yellowish green. Numerous hypocystic villi were present. Although one of his types of tentilla resembled one of those of *R. filiformis*, the other was simple and filiform. The single gonodendron that Fewkes described was very young, but was attached just below the most anterior mature gastrozooid. How this arrangement differs from that in *R. filiformis* Fewkes did not say, and so it is not possible to evaluate that comment. It is clear that Fewkes' description is inadequate, and so Schneider (1898), and subsequent authors, considered *R. gracilis* to be a junior synonym of *R. filiformis*, and there seems no reason to doubt that.

Fewkes (1883, p. 82) described and figured a single specimen of "*Rhizophysa Eysenhardti* (?)" (Figure 18A) and, possibly, was the first to contrast its coloration with that of *R. filiformis*, when he said (*ibid*. p. 83): "The axis is slender, very contractile, and has a pale pink color, while that of *R. filiformis* is greenish in color". He also noted that (*ibid.*); "The polypites [gastrozooids] arise on all sides of the axis". Although the latter is incorrect, it does mean that Fewkes noted that they did not have a linear arrangement, which is true. Fewkes made no reference to the presence of hypocystic villi in the pneumatophore, but his figure 1 (Figure 18A, left) appears to show their presence. But he drew attention to the presence of filiform tentilla on the tentacles, and that the gonodendra were attached to the stem midway between two gastrozooids. There should be no doubt that Fewkes's specimen belonged to *R. eysenhardtii*.

Fewkes (1886) gave two further rather poor descriptions of new cystonects (see Figure 18B). Firstly he de-

scribed *Rhizophysa uvaria* Fewkes that possessed a 5 mm long pneumatophore and a short piece of stem, broken off posteriorly (Figure 18B, fig. 6). He said of it (*ibid*. p. 967): "At the junction of the stem and float we find … a cluster of half-developed polypites [gastrozooids], at the base of which is a botryoidal cluster of gonophores (?). Below the first cluster of polypites there is a smooth portion of the stem, and then another cluster of polypites arising from a somewhat thickened base". Fewkes likens this to the arrangement in Studer's (1878a) *R. inermis*, which is somewhat strange as earlier he had not included that name in a list of *Rhizophysa* species. However, from the description and the primitive illustration (see Figure 18B) there can be no justification in recognising *R. uvaria* as a valid species.

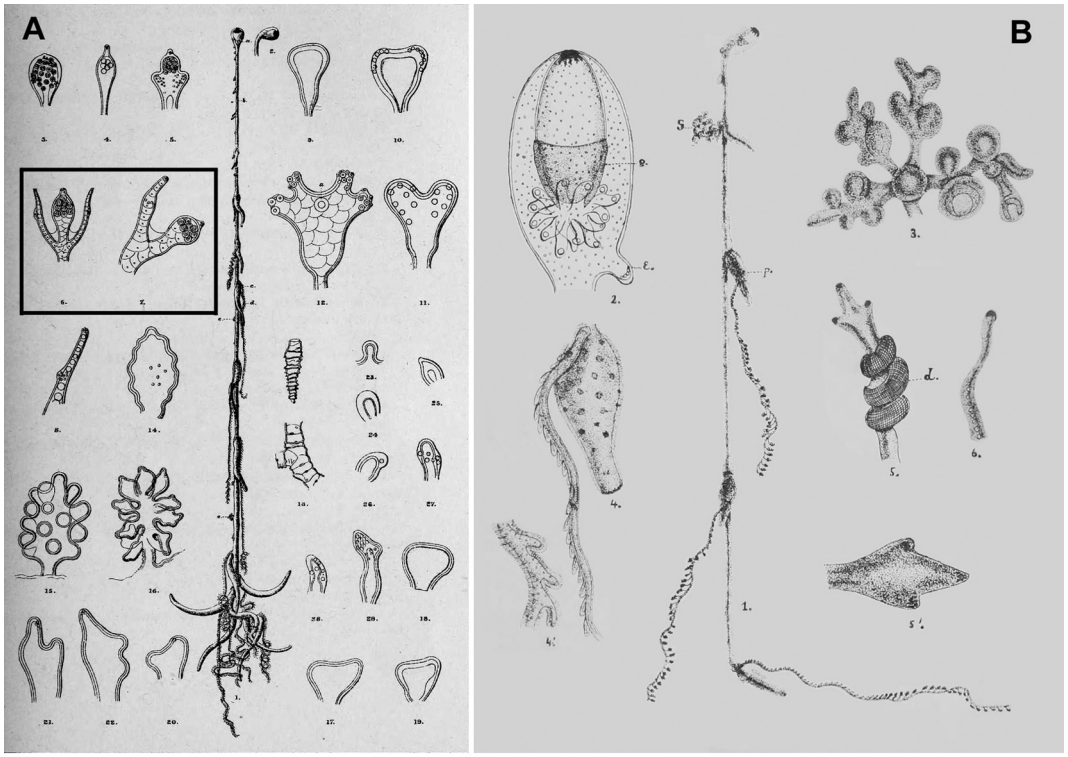

FIGURE 17. A. *Rhizophysa filiformis* from Fewkes (1879) Plate 2. B. *Rhizophysa gracilis* Fewkes (1882), Plate 6 (*partim*).

Fewkes (1886, p. 968) then described his other new cystonect *Pterophysa grandis*, from two specimens attached to a dredge rope. He characterised the genus: "by the existence on the polypites of two longitudinal wings" to which, as noted above, he had given the name *ptera*. He noted that they were also present on Studer's *Bathyphysa* species, so it is unclear why he needed to establish a new genus. He mentioned that the species had a 10 mm long pneumatophore and, for the larger of his specimens that gonodendra were present. However, he concentrated his description on the gastrozooids (Figure 18B, figs. 1–3) the detached ones of which were classically rolled up due to contraction of the muscles in the *ptera*. There followed a great deal of waffle regarding the possible function of the *ptera*, but there was absolutely no detail that could distinguish it from Studer's *Rhizophysa conifera*. However, he was correct in regarding the presence of *ptera* as a good generic character, but clearly the name *Bathyphysa* has precedence over *Pterophysa*.

Burmeister (1885–91) published and long and rather tedious study of his observations on various *Physalia* specimens, but did not appear to have added anything new to what had been published before. He did give figures of an undischarged and discharged nematocyst, but admitted that they had been copied from a paper by Chun (1882b). He also commented that Wagner (1835) was the first to describe a nematocyst from an actinian, but failed to mention that Wagner had thought it was a spermatozoon. Wagner (1841) corrected that error.

Just prior to the publication of Haeckel's (1888) *Challenger* Monograph, Chun (1887) wrote an article on the postembryonic development of *Physalia*, which gave no detail on the growth of the "cormidial" groups, and how the gas gland enlarged when the bladder grew and changed shape. He noted the division of the "cormidial" groupings into the oral and Main zones, as they are currently called, but otherwise gave little information of any value. He did, however, restrict the number of species to just two; the Indo–Pacific *P. utriculus* and the Atlantic *P. arethusa*. So,

after almost 60 years, the number of species of *Physalia* had been reduced to one less than Eschscholtz (1829) had recognised. Unfortunately, that situation was soon to change, for the worse.

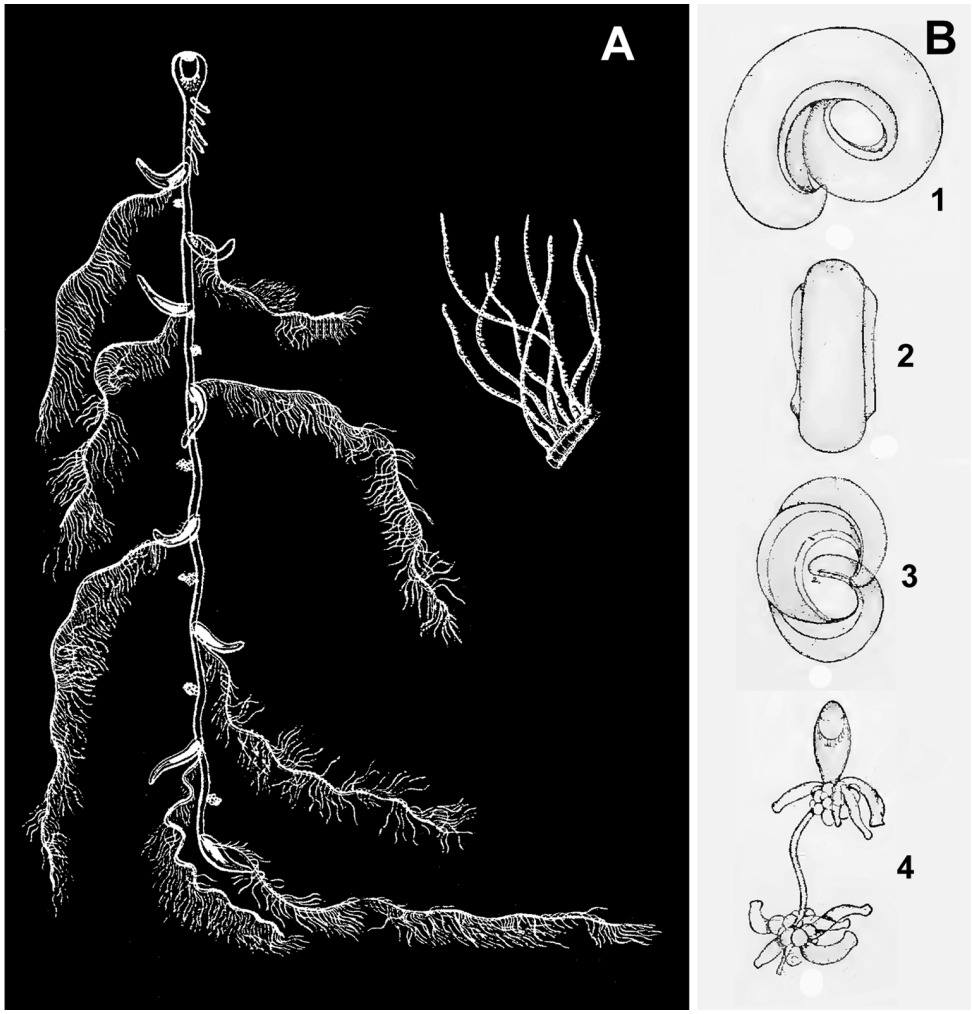

FIGURE 18. A. "*Rhizophysa eysenhardtii* (?)" from Fewkes (1883) figs 1–2. B. **1–3** *Pterophysa grandis* Fewkes, 1886; **6** *Rhizophysa uvaria* Fewkes, 1886. From Fewkes (1886), Plate X.

Pneumatophoriden or Cystonectae

Meanwhile, on a more general level, Chun (1882a, p. 1168) agreed with Vogt's (1854) view on the classification of siphonophores when he said: "Mit den Physophoriden vereinigte man vielfach die Rhizophysiden und Physalien. Von den ersteren unterscheiden sie sich jedoch in so vielfacher Hinsicht, dass ich vorschlage, beide als eine eigene Ordnung der «Pneumatophoriden» den Calycophoriden und Physophoriden an die Seite zu setzen". This was translated in Chun (1883b, p. 165) as: "The Rhizophysidæ and *Physaliæ* have been frequently united with the Physophoridæ. Nevertheless they differ so much from the latter that I prefer placing them as a distinct order, 'Pneumatophoridæ', side by side with the Calycophoridæ and Physophoridæ".

Claus (1884, footnote to p. 13)[45], however, suggested that: "The proposal by Chun that alongside the Physophorids, with closed pneumatophores, the genera with larger pneumatophore and an opening, such as *Rhizophysa* and *Physalia* should be identified as Pneumatophorids seems to me not feasible because Physophorids according to the literal meaning of the word is the same as Pneumatophorids". Claus, thus, appears to be suggesting that since at that time cystonects/pneumatophorids, physophorids, and velellids were all thought to possess a so-called pneumatophore, then the name Pneumatophorids did not clearly distinguish that order from the others.

Haeckel (1887, 1888a), in his *System der Siphonophoren*[46], possibly was the first person to separate off the

45 Original quote: "Der Vorschlag Chun's neben den Physophoriden mit geschlossenem Luftsack, die Gattungen mit grösserem offenem Luftsack wie Rhizophysa und Physalia als Pneumatophoriden zu bezeichnen, scheint mir schon deshalb nicht durchführbar, weil auch die Physophoriden der Bedeutung des Wortes nach Pneumatophoriden sind."

46 There are two versions of this paper. The 1887 one appears to have been published independently, while the 1888 one ap-

velellids from the other siphonophores; considering them a separate Legion or Subclass, the Disconanthae, of the Class Siphonophorae. At first he made several references to four orders in his other Subclass, the Siphonanthae, namely *Calycophoriden, Pneumatophoriden, Physophoriden,* and *Aurophoriden*. The last is now known to belong to the third of these groups, although Stepanjants (2014) appears to disagree. However, in his *Challenger* Monograph (Haeckel, 1888b), he noted that the Cystonectae had already been called the Pneumatophoridae by Chun, but did not explain why he thought his name should take precedence, or why earlier (*ibid.* pp. 3, 5) he had referred to the Pneumatophoridae, and not the Cystonectae, as one of his orders of the Siphonanthae, while shortly afterwards (*ibid.* pp. 10, 12) he referred to the "Cystonectae or Pneumatophoridae".

The discussion as to whether the name for the Order or Sub-Order containing the Physaliidae should be the Pneumatophoridae, as of Chun (1882a), was continued by Schneider (1896), apparently no friend of Chun based on their vitriolic exchanges in their published works. Schneider agreed with Claus (1884) that that name was inappropriate. This brought forth a detailed riposte from Chun (1897, pp. 63–64)[47] when he said: "As to the close relations that prevail between the Rhizophysids and Physaliids, despite the remarkable differences in their outward appearance and in their lifestyles, I have already mentioned it at the beginning of my *Siphonophorenstudien* in 1882. My proposal was to unite these two families into a higher category (1882, p. 14 [1168]), with which later observers - Haeckel being particularly among them - agreed. However, he does not apply the name chosen by me, »Pneumatophoridae«, but subordinates it under his new name »Cystonectae«.

"Perhaps this change of name derives from the remark by Claus (1884, p. 13) that all Physophorids, based on the literal meaning of the word, are Pneumatophorids. I do not wish to discuss this subject any further, but cannot help remarking that we can raise the same objection against the name »Cystonectae«. All Physophorids are »Cystonects«, and if the goal is to emphasise from the latter designation that the Rhizophysids, Epibuliids and Physaliids all lack swimming bells and that their locomotion (it may be active or passive) is accomplished solely by the pneumatophore, it should be remembered that the larvae of the Physophorid genera *Athorybia*, *Anthophysa* and *Athoria* also lack swimming bells. Whoever places such strict standards for our systematic names and demands that they express clearly and unambiguously the distinction from other categories will have to remove the majority of them (I draw attention from the ranks of siphonophores only to the term »Calycophoridae«).

"To meet all the objections, however, I believe that the founder of the group should be allowed to carry out a change of name and through the term »Rhizophysaliae« acknowledge the relationships between the hypocystic villi in the pneumatophore that characterise the Rhizophysids and Epibuliids on the one hand and the Physaliids on the other".

Although Chun (1897) was quite correct in pointing out that the name Cystonectae, the prefix being derived from the Greek *kystis* meaning bladder, was equally as inappropriate as Pneumatophoridae, as it equally applicable to both that sub-order and to the Physonectae. However, he was quite wrong in thinking that he could adopt a new name, Rhizophysaliae, and claim that it was originally established in 1882. It is interesting to note that the term "cyston" can be interpreted in two ways. As a term for a "bladder" it can be interpreted as referring to the pneumato-

peared in the *Jenaische Zeitschrift für Naturwissenschaft*.

47 Original quote: "Auf die nahen Beziehungen, welche zwischen den in ihrer äusseren Erscheinung und in ihrer Lebensweise sich auffällig verschieden verhaltenden Rhizophysen und Physahen obwalten, habe ich bereits bei Beginn meiner Siphonophorenstudien im Jahre 1882 hingewiesen. Meinem Vorschlag, diese beiden Familien zu einer höheren Kategorie zu vereinigen (1882, p. 14 [1168]), haben die späteren Beobachter - unter ihnen speciell auch Haeckel — zugestimmt. Allerdings wendet er nicht die von mir gewählte Bezeichnung »Pneumatophoridae«. an, sondern schafft er für die Unterordnung den neuen Namen »Cystonectae«.

Vielleicht mag zu dieser Namensänderung die Bemerkung von Claus (1884, p. 13) beigetragen haben, dass alle Physophoriden der Bedeutung des Wortes nach Pneumatophoriden sind. Ich will über die Berechtigung einer Namensänderung mich nicht weiter auslassen, mag aber die Bemerkung nicht unterdrücken, dass man denselben Einwand auch gegen die Bezeichnung »Cystonectae« erheben kann. Alle Physophoriden sind »Cystonekten« und wenn mit letzter Benennung speciell ausgedrückt werden soll, dass den Rhizophysen, Epibulien und Physalien Schwimmglocken fehlen und dass ihre Ortsbewegung (mag sie eine aktive oder passive sein) lediglich durch die Pneumatophore bewerkstelligt wird, so sei erwähnt, dass den Larven der Physophoriden und den Gattungen *Athorybia*, *Anthophysa* und *Athoria* gleichfalls die Schwimmglocken fehlen. Wer überhaupt an unsere systematischen Bezeichnungen einen so strengen Maassstab legt und verlangt, dass sie bündig und unzweideutig die Unterschiede von anderen Kategorien zum Ausdruck bringen, wird die Mehrzahl derselben (ich erinnere aus der Reihe der Siphonophoren nur an die Bezeichnung »Calycophoridae«) streichen müssen.

"Um indessen allen Einwürfen zu begegnen, so glaube ich, dass es dem Begründer der Gruppe wohl gestattet sein dürfte, eine Aenderung des Namens vorzunehmen und durch die Bezeichnung »Rhizophysaliae« den Verwandtschaftsbeziehungen zwischen den durch wurzelförmige Ausläufer der Pneumatophore charakterisirten Rhizophysiden und Epibulien einerseits und den Physalien andererseits Rechnung zu tragen."

phore, present in both cystonect and physonect siphonophores. However, Haeckel (1888b, p. 17) uses the term in a different way when he defines cystons as: "certain [types of] vesicular sacs, which have hitherto been generally confused with the palpons. They are indeed very like the latter, but are very essentially distinguished from them by a terminal aperture". Nowadays this distinction is not generally recognised as the structures that Haeckel defined as palpons have been found to have a terminal opening. Later (*ibid.* p. 184) Haeckel remarked that: "A further character common to all Physonects is the general presence of palpons or cystons; these are lacking in most other Siphonophorae, with the exception of the Cystonectae". However, within his extensive review of the Cystonectae (*ibid.* pp. 305–352) Haeckel apparently never refers to the presence of cystons, although various types of palpon are frequently mentioned and indeed, according to Haeckel's definition, no such structures are found on cystonects. Thus, one wonders how Haeckel actually came to derive the name Cystonectae.

Schneider (1898, p. 164)[48] succinctly summarised the conundrum as to what name should be ascribed to this Order or Sub-order when he said: "The older of Chun's name would be preferable to Haeckel's from the point of view of priority, but he would have to, according to the rules, convert it into the *Pneumatophorae*. Because this name is signified by a single attachment, the swim bladder, which indicates, therefore, that the use of the word pneumatophore could be misinterpreted, then the name *Cystonectae*, established by Haeckel, comes into use (my proposed modification to *Cystophora* does not correspond with the nomenclature rules). The principle embodies the fact that the latest of Chun's 97a names, *Rhizophysaliae* is of course entirely unnecessary. When Chun says that as the founder of the group he is entitled to change the name, I refer him to the Nomenclature rules that state in § 5 sub b »to a name once published the author has only the same right as every other zoologists«"

It is thus somewhat astounding that almost all of the subsequent major reviewers of the relevant sub-order, with the exception of Bedot (1893) and Kawamura (1910), referred to it as the Rhizophysaliae Chun, 1882a. These are notably Lens & van Riemsdijk (1908), Bigelow (1911), Moser (1925), Totton (1932, 1936), and Hyman (1940) (albeit as a Group within the Suborder Physophorida, that also included the Physonectae and the Chondrophorae). At last Totton (1954), in agreement with Schneider's (1898) excellent reasoning, adopted the name Cystonectae Haeckel 1888, and such has been retained ever since.

Haeckel

Introduction.

Having jumped ahead in time somewhat for the discussion of the establishment of Cystonectae as the name for the Sub-order, it is with deep regret that we have to turn the clocks back again to 1888. It is difficult not to overestimate the damage to the taxonomy of siphonophores that Haeckel (1888a, b) inflicted upon us, particularly in the latter *Challenger* Monograph, and this is truest of all, I believe, for the Cystonectae. It would be best to just gloss over it all, but since it affected the reasoning of many subsequent authorities Haeckel's thoughts will have to be considered. Even Totton (1965) retained some of Haeckel's more dubious species while, in truth, rejecting others that are valid. The species of siphonophores that Haeckel (1888b) in his *Challenger* Mongraph are considered in detail in the accompanying text (Pugh, 2019b).

There are some differences between the taxonomy established in Haeckel's two 1888 papers and so we will only consider that in the latter, in order to reduce the duplication. As can be seen from Figure 19, Haeckel (1888b) first divided his Order Cystonectae into two suborders, based on whether the colonies where mono- or polygastric.

Cystonectae Monogastricæ. Family *Cystalidæ*.

For the suborder Cystalidae, with its single genus *Cystalia*, Haeckel firstly mentioned the species *C. larvalis* Haeckel, 1888a, and then a specimen from the *Challenger* Expedition that he named *C. challengeri*. But he then

48 Original quote: "Der ältere Chun'sche Name wäre also dem Haeckel'schen aus Prioritätsrücksichten vorzuziehen, doch müßte er, den Regeln gemäß, in Pneumatophorae umgewandelt werden. Da mit diesem Namen aber bereits ein einzelner Anhang, die Schwimmblasen, bezeichnet wird, die Verwendung des Wortes Pneumatophoren also zu Mißverständnissen Anlaß geben würde, so tritt der zu zweit aufgestellte Haeckelsche Name Cystonectae (die von mir vorgeschlagene Modification in Cystophorae entspricht nicht den Nomenclatur regeln) in Verwendung. Der neueste, von Chun 97a aufgestellte Name : Rhizophysaliae ist selbstverständlich ganz überflüssig. Wenn Chun meint, als Begründer der Gruppe eine Änderung des Namens vornehmen zu dürfen, so verweise ich auf die Nomenclaturregeln, wo in § 5 sub b steht : »Einem einmal veröffentlichten Namen gegenüber steht dem Autor nur dasselbe Recht zu wie jedem andern Zoologen«."

concluded that (1888b, p. 314): "A closer comparison of them makes it very probable that these two species are identical; the more significant name *Cystalia monogastrica* may, therefore, be retained for both". Thus, Haeckel had managed to establish three different names for the same species. Haeckel (1888b, Plate XXII) gave five illustrations of *C. monogastrica* (see Figure 20), but he himself recognised that the first four of his figures represented larval stages in the development of a siphonophore with a pneumatophore, which he, at first, suggested might have belonged to an agalmatid. Indeed, he concluded (*ibid*. p. 315): "Since I was not able to recognise the origin of these pelagic larvae, nor to follow their further development, the question remains open, whether they were produced by a Physonect or a Cystonect. In the latter case they may possibly have been derived either from Cystalia or from the closely allied Epibulia". So even he was uncertain that these larvae belonged to his *Cystalia*. The fifth illustration he considered (*ibid*. pp. 314-315): "might be only a young form or a monogastric larva of the polygastric *Epibulia ritteriana*" (see below). However, he then countered that suggestion by noting that hypocystic villi where absent in his *Cystalia* but were present in *Epibulia* and, indeed in all rhizophysid cystonects.

Synopsis of the Families of Cystonectæ.

I. Suborder CYSTONECTÆ MONOGASTRICÆ (MONOSTELINIÆ).

Corm with a single large siphon, representing one cormidium only. A single tentacle on the base of the siphon. A corona of palpons around the base of the large pneumatophore. Pneumatosac without hypocystic villi, ... 20. Cystalidæ.

II. Suborder CYSTONECTÆ POLYGASTRICÆ.

Corm composed of numerous cormidia, each with one or more siphons and tentacles. Cormidia sometimes ordinate, at other times irregular. (Primary larva monogastric, *Cystonula*.)

A. MACROSTELINIÆ. Trunk of the siphosome very long and thin, tubular, with prolonged internodes.

- Cormidia monogastric, each with a single siphon and tentacle. (Pneumatosac with hypocystic villi), . 21. Rhizophysidæ.
- Cormidia polygastric, each with several siphons and tentacles. (Pneumatosac with hypocystic villi), . 22. Salacidæ.

B. BRACHYSTELINIÆ. Trunk of the siphosome short and wide, vesicular or bag-shaped, with shortened internodes.

- Cormidia in a spiral corona around the vesicular trunk, beyond the base of the subvertical pneumatophore (with hypocystic villi), . 23. Epibulidæ.
- Cormidia in a multiple series along the ventral side of the trunk, the dorsal side of which is occupied by the subhorizontal pneumatophore (without hypocystic villi), . . . 24. Physalidæ.

FIGURE 19. Haeckel's (1888b, p. 314) classification of the Cystonectae.

From his description of *Cystalia monogastrica*, based on his figure 5 (see Figure 20A), we can note the prevalence of red pigmentation, especially in the gonodendron. Haeckel (1888b, p. 317) said: "Gonodendron (fig. 5, *gd*).—The single large clustered gonodendron, which is attached to the base of the siphon, on its ventral side, is similar to that of the Rhizophysidæ. The gonostyle is richly branched, and each ultimate branch bears a single gonopalpon on its distal end (PI. XXIII, fig. 8, *gq*) and above it a single medusiform gynophore (f) and a cluster of several (four to eight) ovate androphores (h)". However, the gonodendron that Haeckel was referring to was that of another of his new species, *Nectophysa wyvillei*, which will be discussed below. Nevertheless, it is clear that Haeckel's interpretation is completely wrong. What he referred to as the female gonophore (gynophore, **f**) is actually the asexual medusoid that is subterminal on all the branches of either the male or female gonodendron of rhizophysid cystonects.

The tentacle of *Cystalia monogastrica* bore simple filiform tentilla, and there was also a (*ibid*. p. 316) a "corona of palpons". Thus, as we will discuss further with regard to the Family Epibulidae, we have a specimen that, in its coloration and the structure of the tentilla, greatly resembles a much contracted specimen of *Rhizophysa eysenhardtii*, where the corona of palpons are simply young gastrozooids that have not yet developed their tentacles. On

the other hand there are no hypocystic villi below the pneumatophore, a feature particularly noted by Haeckel. It is possible, as the specimen is so young, that they have yet to develop, and further observations on young specimens are needed before this can be resolved, but all mature specimens of the rhizophysid species currently recognised possess these structures.

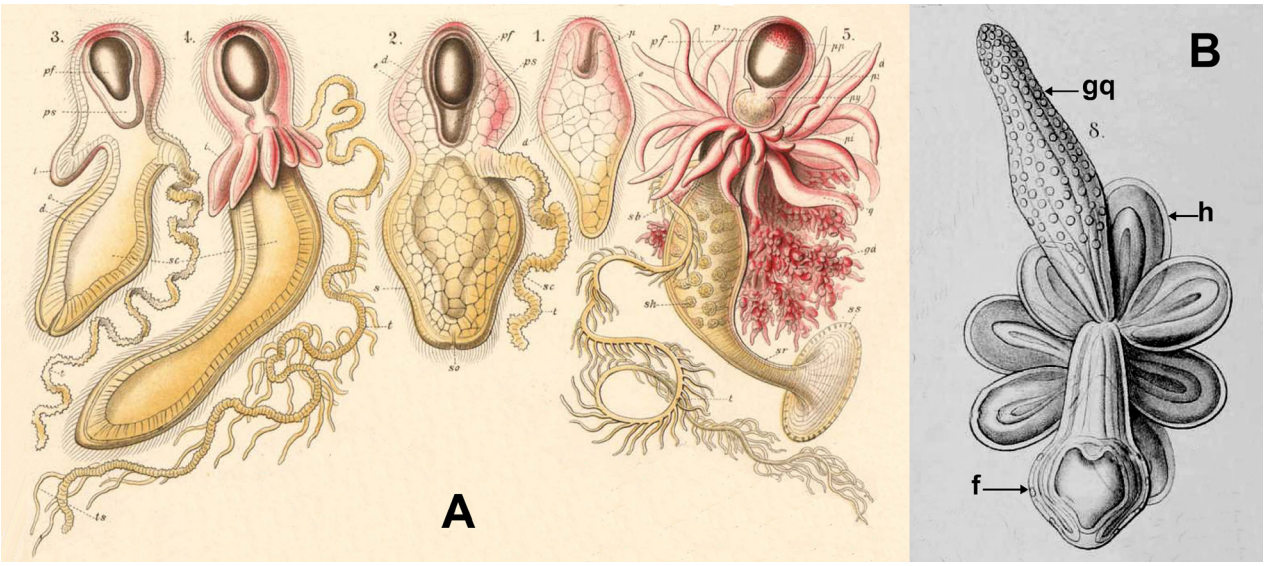

FIGURE 20. A. *Cystalia monogastrica* Haeckel, 1888; from Haeckel (1888b) Plate XXII, figs. 1-5. For annotations see original legend. **B**. Gonodendron of Nectophysa *wyvillei* Haeckel (1888b) Plate XXIII, fig. 8. **f**: female gonophore; **gq**: gonopalpon; and **h**: male gonophore.

Nonetheless, there appears to be little reason to consider *Cystalia monogastrica* a valid species and so, in order to remove it from any further discussion, let me summarise the considerations of later authors, although in actuality, Haeckel's (1888b) description of *Cystalia monogastrica* has aroused very little interest. Schneider (1898, p. 172)[49],[50] merely remarked: "The fact that *Cystalia monogastrica* shows itself as nothing more than a young stage of *Epibulia erythrophysa*, probably requires no detailed discussion". Bigelow (1911) rather strangely included both *C. monogastrica* and *C. challengeri* as junior synonyms of *E. ritteriana*, but included *C. larvalis* as only a questionable synonym; despite the fact that Haeckel had stated that they were all the same species.

Finally Totton (1965, p. 18) said: "I must point out that the only certainly known cystonect larva is that of *Physalia.* No reliance should be placed, except with great reserve, on certain figures of Haeckel's purporting to be of this nature …. This specific name [*monogastrica*] is applicable only to figure 5 of Haeckel's (1888b) plate XXII. The larvae, which he took in a tow net, Haeckel thought might belong to this species. Certainly no phylogentic [sic] arguments should be based on larvae of such doubtful parentage and identity … I have grave doubts about the existence of Haeckel's Epibuliidae". That is quite suffient for the present author to say goodbye to *Cystalia monogastrica*!

Cystonectae Polygastricæ.

As Figure 19 shows, Haeckel (1888b) divided this suborder into two depending on whether the species had long, Macrosteliniæ, or short siphosomal stems, Brachysteliniæ, with each containing two families. For the former he divided the families according to whether the "cormidia" were monogastric, Family Rhizophysidæ, or polygastric, Family Salacidæ; and for the latter by whether the "cormidia" were spiralled around the base of of a subvertical pneumatophore, Family Epibulidæ, or were in a multiple series along the ventral side of a subhorizontal pneumatophore, Family Physalidæ.

***Cystonectae Polygastricæ.* Macrosteliniæ. Salacidæ.**

Let us look at potentially the easier one first; namely the Salacidæ, which are long-stemmed but were said to

49 Original quote: "Daß *Cystalia monogastrica* nichts als eine Jugendform der *Epibulia erythrophysa* vorstellt, bedarf wohl keiner eingehenden Erörterung."

50 Delage & Herouard (1901, p. 244) appeared to attribute that statement to Chun (1897), but no such reference has been found in that paper.

possess polygastric "cormidia", in which Haeckel (1888b) included only one genus and described only one species. The generic name *Salacia* was used, according to Haeckel, by Linnaeus (1746), but the date appears to be 1748, for the Portuguese Man O'War. However, Haeckel decided to revive it rather than give a new name to the genus. Haeckel, as noted above, suggested that the *Rhizophysa uvaria* of Fewkes (1886) probably belonged in the genus. As with *Cystalia monogastrica*, we will follow the subsequent history of *Salacia polygastrica* in the hope that we can make an end of it. Chun (1897) retained Haeckel's species and questionably equated Fewkes's *Salacia uvaria* with it, while Schneider (1898), unsurprisingly, did the reverse by retaining *Rhizophysa uvaria* and synonymising *S. polygastrica* with it; for which Schneider was correct on the basis of precedence. Delage and Hérouard (1901) pointed out that the name *Salacia* was already pre-occupied by a calyptoblastic hydrozoan that Lamouroux (1816) had described in the early years of the 19th Century, and thus they substituted the name *Salacella* for it. Bigelow (1911, p. 317), it seems, did not know of this, and considered the genus *Salacia* was monotypic for *S. uvaria* (Fewkes), but all he said about it was: "I have not had the opportunity to study [it]". After Bigelow the generic name *Salacia/Salacella* appears to have almost completely disappeared from the literature. However, Totton (1960, p. 346) in his Monograph on *Physalia*, stated that: "The only other siphonophore at all like *Physalia* is a remarkable specimen, now lost, taken by H.M.S. 'Challenger' and described by Haeckel (1888b) as *Salacia polygastrica.* … Haeckel not only named this delicate specimen - the stem measured only half a millimetre in diameter - which was "much contracted in the spirit bottle", but he softened "it gradually with water to make it so elastic that it could be extended to that degree which is figured in (his) plate xxv, fig. 1" [quoted from Haeckel, 1888b, p. 331]. Haeckel's idealized figure [see Figure 21] showed a truly remarkable animal. No other specimen has ever been seen, but if such animals do exist they have many features in common with *Physalia,* from which they differ strikingly in the nature of their air-sac and by the fact that the "cormidia" are borne on a long stem. The existence of *Salacella,* if confirmed, would demonstrate conclusively that *Physalia* retains characteristics of larval forms such as are also found in physonect genera". Totton made no reference to Fewkes's specimen of *S. uvaria*.

Haeckel's (1888b, p. 330) fascination with this "remarkable species" (Figure 21) was probably because, as is very evident throughout his Monograph, he was hell-bent on finding or, in retrospect, inventing, intermediate species. Thus (*ibid*.): "The family Salacidae is an interesting group intermediate between two very dissimilar families of Cystonectæ, the macrostelious Rhizophysidaæ ... and the brachystelious Physalidæ ... It agrees ... with *Physalia* ... in the polygastric structure of the cormidia ... and ... especially in the structure of the siphons and the simple tentacles, bearing a series of reniform cnidonodes". This is a somewhat strange statement for, although the gastrozooids and tentacles of the two species might resemble each other, *Physalia* is unique among siphonophores as most of its tentacle arises from a separate ampulla and not from the base of the gastrozooid. The specimen of *Salacia polygastrica* that Haeckel described was one of the few that were actually collected during the *Challenger* Expedition, and (*ibid*.): "The single specimen examined was so well preserved that it was possible by staining and dissecting it to recognise the essential structure of all the different organs".

However, in Haeckel's (1888b pp.331-332) short, seven paragraph description there is a certain lack of detail that belies the detailed illustrations (see Figure 21 Left). Two of these paragraphs deal with the *pneumatophore* and the *pneumatocyst* and contain no information of taxonomic importance apart from the fact that hypocystic villi were present. The three paragraphs on the *cormidia, siphons* and *tentacles* tell us that (*ibid*.): "each ordinate polygastric cormidium ... is a botryoidal cluster composed of about ten to twenty siphons and gonodendra, each siphon provided with a long simple tentacle"; that palpons were "possibly" present, although the difference between them and the gastrozooids "does not seem as sharp, as in *Physalia*"; the tentacles bore no tentilla; while the *gonodendra* were monoecious, as both "gynophores" and "androphores" were present. The remaining paragraph contained details of the *corm*, and it will be quoted below.

However, having apparently waxed so lyrical, although one must note the quotes form Haeckel that he made, Totton (1965, p.8) later said: "Haeckel's Salaciidae [Salicidæ in Haeckel] for *Salacia polygastrica* … should be dropped. I have mentioned (1954) the difficulty of accepting *S. polygastrica*". This again is rather strange as there does not appear to be any reference to *S. polygastrica* in Totton (1954), and presumably he was referring to his 1960 monograph. Evenso, Totton's 1965 statement does not seem to follow on from his earlier one, unless one appreciates the extreme subtlety of his sarcasm, which we will return to shortly. Totton (1965) then makes no further reference to the species or genus. Stepanjants (1967) also commented that if the existence of *S. uvaria* were to be confirmed, then the link between Physaliidae and Rhizophysidae through *Salacella* probably would become obvious. Daniel (1974, p.27), however, noted that: "Totton (1960) doubted the validity of this genus and later he omitted it from the

list of valid species of Siphonophora in his Synopsis (1965). The validity of *Salacella* will remain problematic and doubtful until fresh material is obtained".

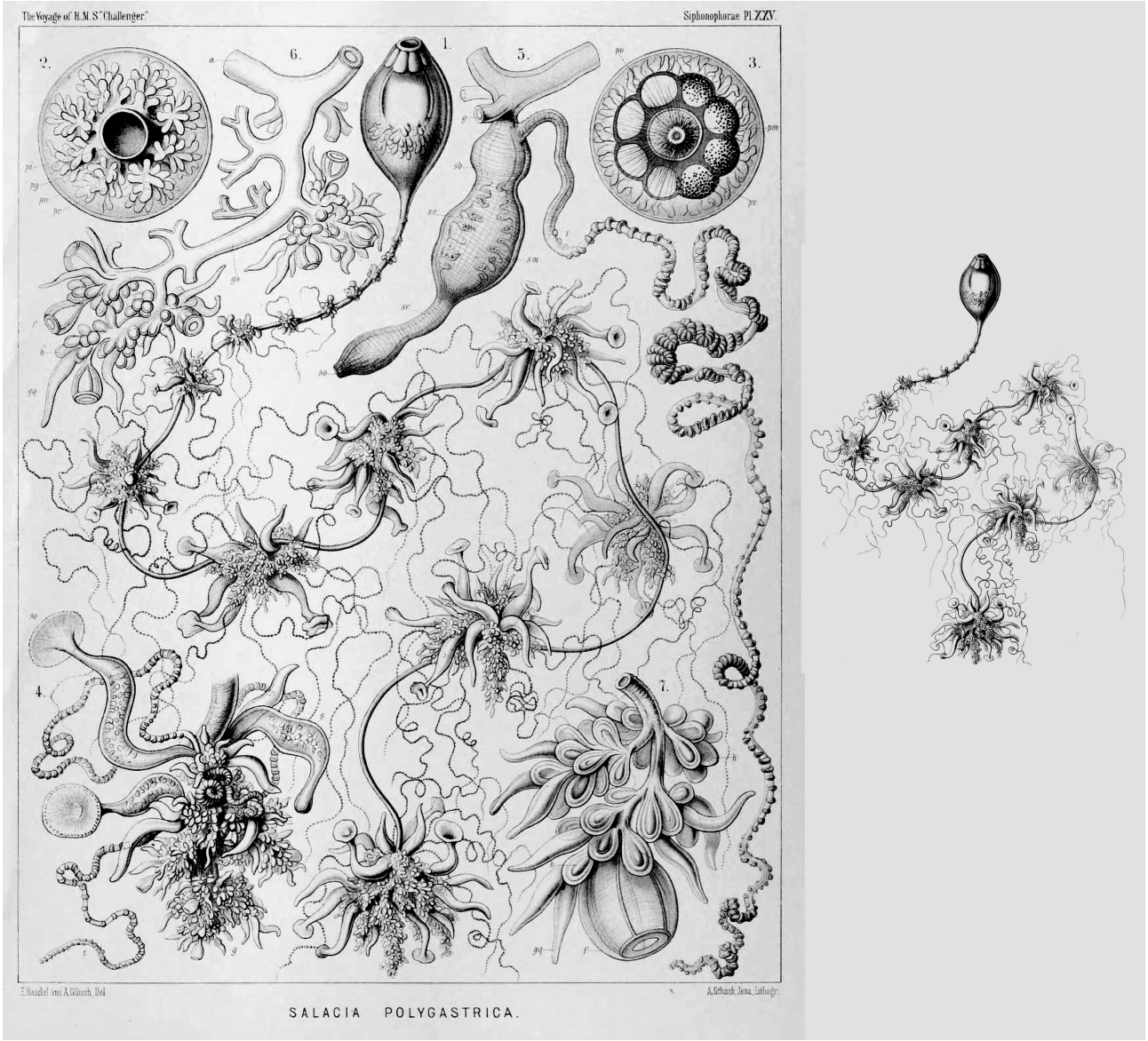

FIGURE 21. Left. *Salacia polygastrica*. Left. Reproduction of Haeckel (1888b), Pl. XXV. Right. Figure 1 from Plate XXV reproduced at approximately actual size.

So are there any features of Haeckel's (1888b) description and illustration of *Salacia polygastrica* that might help one to decide whether they are factually correct or just pure fantasy? Firstly, it should be remembered that Haeckel did not observe the living specimen as it was collected in a dredge that sampled the bottom fauna at a depth of 1990 fathoms during the *Challenger* Expedition. With such a sampling technique one would not expect that such a specimen would be in such a fine condition, as the above quote implied. However, it is likely that the specimen was caught close to the surface shortly before the dredge was retrieved and so may have suffered little damage.

Secondly, as Totton (1960) pointed out, the specimen was very small and had been preserved in alcohol. Although it was much contracted, Haeckel, by the means quoted above, managed to stretch it out; but even then its total length was then only 12–15 cm. To show just how truly remarkable, if not miraculous, was Haeckel's feat of teasing out the specimen, Figure 21 (Right) shows it approximately at actual size, as stated by Haeckel. Apart from the fact that it is very doubtful that one could in any way tease out a highly contracted specimen preserved in alcohol, to have achieved such perfection as Haeckel illustrated is wondrous!

Haeckel's (1888b, p. 332) description of the terminal branches of the gonodendra was also rather strange in

that he said that there was: "a single large gynophore (medusiform umbrella … the manubrium of which develops after the detachment), a clustered group of smaller club-shaped androphores ... , and a number of gonopalpons". Firstly, how could he possible know that the manubrium of the "gynophore" developed after its release, when he was dealing with a preserved specimen? We have already pointed out that Haeckel was mistaken in considering this subterminal medusoid as a female gonophore (gynophore) rather than what it actually is, an asexual nectophore that never develops a manubrium, which would, at least, make the specimen dioecious, as are all cystonects.

As in all of Haeckel's (1888b) descriptions, that of *Salacia polygastrica* is totally unsatisfactory and, although the illustrations are beautiful, as are many others in his *Challenger* Monograph, they appear to be the result of Haeckel's intent on finding an intermediate species, in this case linking the Physaliidae and the Rhizophysidae, such that their veracity and accuracy must be called into question. But can the species be synonymised with any currently recognised cystonect? Because Haeckel did not describe the presence of ptera on the gastrozooids and, because of its small size, one could assume that the specimen was probably a young *Rhizophysa* species. However, neither *Rhizophysa. filiformis* or *R. eysenhardtii* have tentacles without tentilla; this character having been found only for *Bathyphysa conifera*. Nonetheless, the tentilla are fragile structures and can easily break off or "dissolve" in the preservative, as the present author has witnessed for specimens of *R. filiformis*, and there are many descriptions of species whose tentacles are said to be without tentilla that subsequently have been shown to be incorrect. In that case, the presence of well-developed gonodendra, even on the more anterior region of the siphosome, would suggest that *S. polygastrica* could be synonymised with *R. eysenhardtii*. However, the one major difference is that the "cormidia" were said to be polygastric. This does set *Salacia* apart from all rhizophysids, while showing a close relationship with *Physalia.* Nonetheless, the present author is led to the same conclusion as Totton (1965) in that Haeckel's description of *S. polygastrica*, like Fewkes' (1886) *Rhizophysa uvaria*, is too unreliable for it to be considered as valid species.

Cystonectae Polygastricæ. **Family *Rhizophysidæ***.

With regard to Haeckel's (1888b) Family Rhizophysidæ, the first thing ones notes is the absence of any reference to the genera *Bathyphysa* or *Pterophysa*. This is because he placed those genera in his physonect family Forskaliidae. He seems to have linked his statement (*ibid*. p. 237) that: "the Forskalidæ are the largest and most splendid of all Physonectae" with another (*ibid*.) stating that a: "very remarkable and gigantic deep-sea Physonect, which probably belongs to this family, was described in 1878 by Studer", namely *B. abyssorum*. Haeckel stated that he re-examined Studer's specimen and commented that (*ibid*. p. 248): "The proximal or superior half is only 3 to 5 mm. in diameter and is the trunk of the nectosome; it bears at its apex an ovate pneumatophore of 20 mm. in length, and beyond it numerous lateral apophyses (not mentioned by Studer, but figured by him in fig. 28, *loc. cit*.), which are probably the bases of the pedicles of the detached and lost nectophores". This unlikely interpretation is made even more so if one accepts the present author's suggestion that Studer assembled his two pieces of siphosome in the wrong order, as illustrated above!

Haeckel suggested that Fewkes (1886) *Pterophysa grandis* probably belonged to the same genus and mentioned some fragments of a large forskaliid from the *Challenger* Expedition that he provisionally called *B. gigantea*, which is a *nomen nudum* as he never actually described it. He believed that these species bore bracts not only on the stem itself but also on the long peduncles of the gastrozooids; hence the link to the family Forskaliidae. The pea-shaped bumps that Studer had noted on these peduncles and which he found to be filled with nematocysts were interpreted by Haeckel as the attachment points for bracts. Haeckel also hypothesised that not only had nectophores once been present, but that palpons probably had existed between them. Such flights of fancy, based on no evidence whatsoever, are, unfortunately all too prevalent in Haeckel's (1888b) *Challenger* monograph. Presumably, this one derived from the fact that *Forskalia* species do have bracts attached to the peduncles of the gastrozooids, and Haeckel's false belief that palpons or tentacles were attached to the nectosome in his genus *Forskaliopsis*; rather than what happens in actually, in that the palpacles, attached to siphosomal palpons, stretch up between the nectophores.

Although so far we gave got away lightly with regard to the genus *Bathyphysa*, we will not be so lucky with the genus *Rhizophysa* that, with the exclusion of the former genus, should have been the only one in the family Rhizophysidae. Not so, Haeckel (1888b) included six genera! The following key shows how he distinguished between them:

1. "Cormidia" ordinate, separated by free internodes. Gonophores attached to the stem immediately on the base of the siphons .

. . . . . .Subfamily **Cannophysidae** 2
- "Cormidia" loose. Gonostyles attached to the internodes of the stem, scattered between the siphons. . . . . Subfamily **Linophysidae** 3
2. Tentilla simple, not branched . . . . . Genus *Aurophysa*
- Tentilla trifid, with 3 terminal branches . . . . . Genus *Cannophysa*
3. Tentacles simple, without tentilla; or with simple, unbranched tentilla 4
- Tentacles always with a series of tentilla, all or some branched 5
4. No tentilla, tentacles simple . . . . . Genus *Linophysa*
- Tentilla simple, unbranched . . . . . Genus *Nectophysa*
5. Tentilla all trifid, with three terminal branches . . . . . Genus *Pneumophysa*
- Tentilla polymorphous, partly simple, partly branched or palmate . . . . . Genus *Rhizophysa*

The first characters that he used to split the family into two sub-families are basically what divide the genus *Rhizophysa* into its two species, *R. filiformis* and *R. eysenhardtii*. The same could be said about the genera said to have trifid or polymorphous tentilla and those with simple tentilla. However, the total absence of tentilla would be very distinctive, if true. For the genus *Aurophysa* Haeckel simply mentions one species *A. ordinata*, from Ceylon, whose pneumatophore was capped with brown pigmentation; whose gastrozooids were orange; and whose gonophores were yellow. He compared his species with Studer's (1878a) *Rhizophysa inermis* and noted (*ibid*. p. 324): "Studer tells us that this deep-sea form has no tentacles, but he describes and figures tentacles with a series of simple tentilla (fig. 10), apparently attached one to the base of each gonophore. I have no doubt that this was the usual tentacle, arising from the base of the siphon, strongly contracted and twisted around the base of the neighbouring gonophore". As noted above the characters given suggest that the species is *R. eysenhardtii*, but as it was neither described in detail nor illustrated it is yet another of Haeckel's *nomina nuda*.

The other genus included in that subfamily was *Cannophysa*, in which he described the species *C. murrayana* Haeckel, and likened it to the species Fewkes (1882) described as *Rhizophysa gracilis*, which subsequent authors have considered to be a junior synonym of *R. filiformis* (e.g. Bigelow, 1911; Totton, 1965). Haeckel (1888b) gave a brief description, based on two specimens that he himself had collected off Lanzerote (Canary Islands), the smaller of which (see Figure 22, fig. 3) measured c. 15 cm in length. For the larger one he, yet again, produced stunning illustrations (see Figure 22). The pneumatophore was of the basic rhizophysid type, with an anterior pore, and numerous hypocystic villi. The gastrozooids and tentacles were rose in colour, and the latter were attached to the former on its dorsal or outer side; regarding which one might assume he was mistaken. Although Haeckel's primary distinction of his cannophysid species was that the each gonodendron was attached close to the base of a gastrozooid, he gave very little information about it apart from saying (*ibid.* p. 326) that: "Each smallest group (or secondary gonodendron) is composed, as usual, of a single medusiform gynophore and a corona of club-shaped androphores, with a distal (rose-coloured) palpon". With regard to their positioning, Haeckel said (*ibid.*) that each was: "attached to each node of the stem, immediately beyond the insertion of each siphon"; i.e. posterior to each gastrozooid. The key feature of his description and illustrations is the fact that tentacles bore tentilla with distinctly trifid distal ends. Haeckel made no reference to their similarity to the *tricornuate* type described by Gegenbaur (1853) on the tentacles of *R. filiformis* (compare Figures 12C, fig.8 and 22, fig. 9), but one should be in no doubt that that was the species Haeckel was describing, although, surprisingly, some later reviewers did not reach that conclusion.

Haeckel (1888b) included four genera in his other sub-family, the Linophysidæ, which included those species whose gonodendra were attached in the internodes between each gastrozooid. The first two genera were distinguished by the fact that tentilla were either absent, *Linophysa*, or were simple and unbranched, *Nectophysa*. Haeckel devoted just thirteen lines to the genus *Linophysa*, which contained only a single species, namely the *Rhizophysa conifera* of Studer, 1878. As usual Haeckel ignored the fact that, despite the change of genus, Studer was still the authority for the species that (i*bid* p. 271) he referred to it as "*Linophysa conifera* Hkl. (= *Rhizophysa conifera*, Studer". Nevertheless, since the young gastrozooids of that species possess *ptera* it, thereby, belongs to the genus *Bathyphysa*, as has been discussed above. Thus we need not consider it any further.

The genus *Nectophysa*, with simple tentilla, contained two species, *N. wyvillei* Haeckel 1888b (see Figure 23) and *N. eysenhardtii* (Gegenbaur, 1859). Again the description of the former is brief. He noted that the stem was rose-coloured, as were the gastrozooids, tentacles and gonodendra. The tentilla were simple, and the gonodendra were attached midway between the gastrozooids. As usual, Haeckel made no comparisons with Gegenbaur's species*,* except to note that they were closely allied. But really there is only one possibly good character that Haeckel described and that is the presence of filiform tentilla. There can be no doubt, as all subsequent reviewers agree upon, that Haeckel's *N. wyvillei* is a junior synonym of Gegenbaur's *R. eysenhardtii*.

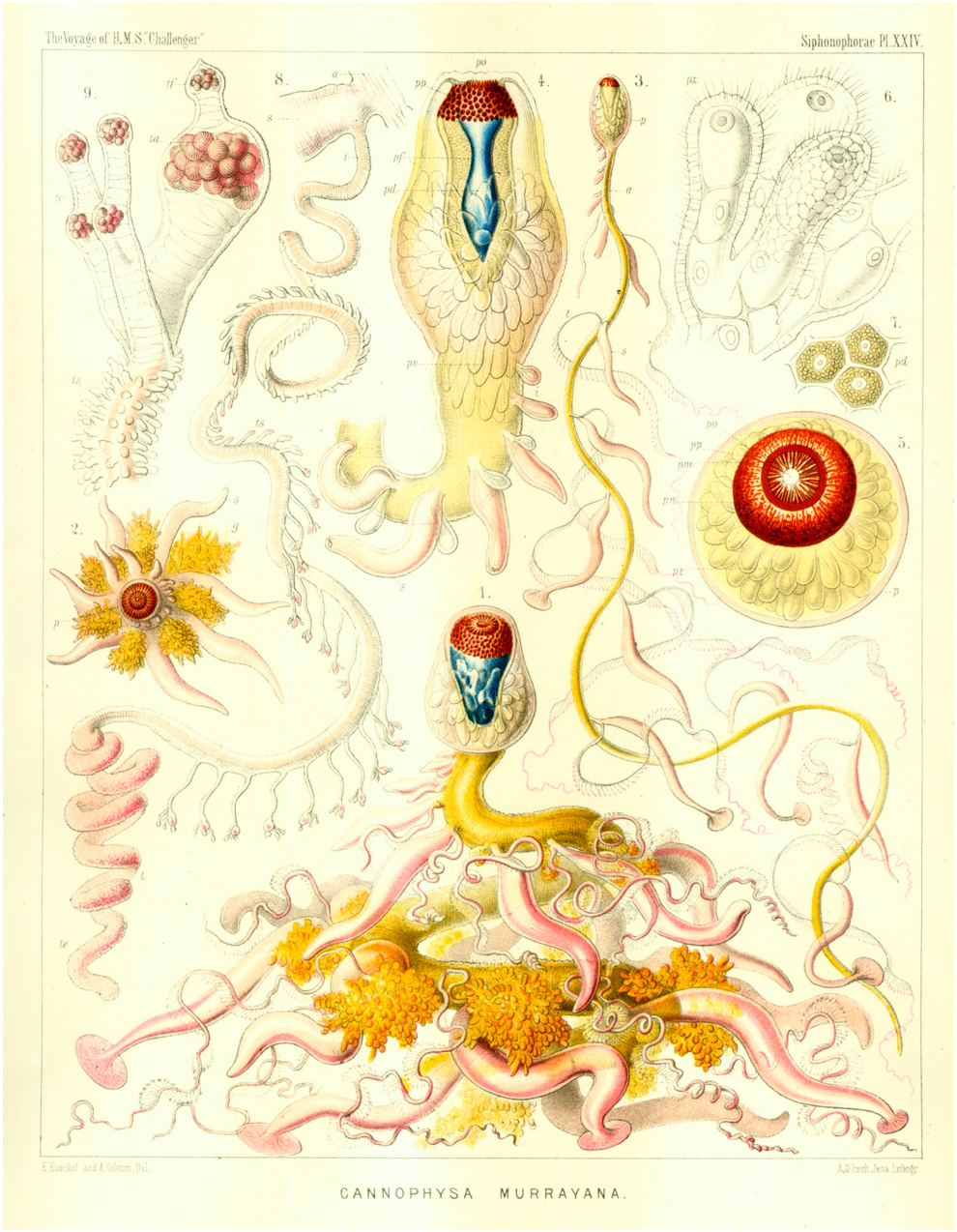

FIGURE 22. *Cannophysa murrayana* Haeckel, 1888b Plate XXIV.

The second group of Haeckel's linophysids again included two genera, *Pneumatophysa* and *Rhizophysa*. For the genus *Pneumatophysa* Haeckel (*ibid.* p. 328) said: "The single known species of this genus, *Pneumophysa gegenbauri* [Haeckel, 1888a], was observed by me in December 1881 in the Indian Ocean, and will be described on another occasion. A second species, similar to this, was noticed in my System der Siphonophoren … as *Pneumophysa mertensii* (= *Epibulia mertensii*, Brandt, 25, p. 33). But a closer examination of the excellent figures which its discoverer, Mertens, has left of this species, taken in the Tropical Pacific, has convinced me that it belongs to the following genus, *Rhizophysa*". Since Haeckel was one of the last to see these drawings by Mertens that shortly afterwards appear to have been lost and never seen again. Also, since Haeckel did not describe his *P. gegenbauri* then the species must become a *nomen nudum*.

Finally, in the genus *Rhizophysa*, the only rhizophysid genus that Haeckel did not himself establish, he included three species, Forsskål's *R. filiformis*, Lesueur and Petit's *Rhizophysa planostoma* [sic], and the aforementioned *R. mertensii*. There can be no doubt about the validity of Forsskål's *Rhizophysa filiformis*, and we have already commented on *R. planestoma*, and suggested that it might be the same as *R. eysenhardtii*. However, Haeckel (1888b, p. 329) collected a specimen, off the Canary Islands, that he considered to be the same as the latter species, and he

commented: "The structure of this Atlantic species, for which I retain Péron's name, was very similar to that of the well-known Mediterranean form, the best description of which was published in 1854 [1853] by Gegenbaur [*R. filiformis*] … The Atlantic *Rhizophysa planostoma* [sic] differed, however, in the peculiar coloration (the pneumatophore, the stem, and the tentacles being rose-coloured, the siphons violet), and in the special form of the tentilla; the majority of these were trifid, with an odd median club and two paired lateral horns (similar to those of *Cannophysa murrayana*) but scattered between them was a number of very large palmate tentilla, differing from those figured by Gegenbaur … mainly by a large purple ocellus on the convex outside; the peculiar calcarate tentilla, which Gegenbaur compared with a bird's head in the Mediterranean *Rhizophysa filiformis* … were absent". There can be little doubt, despite Haeckel's reservations, that what he was describing was *R. filiformis*, if we accept the observation that *R. planestoma* had filiform tentilla. As for Brandt's (1834) species *mertensii* was distinguished by Haeckel as having two different kinds of branches tentilla but, apart from that vague observation, no proper description has been published and, as noted above, it is not known if the illustrations of Mertens still exist.

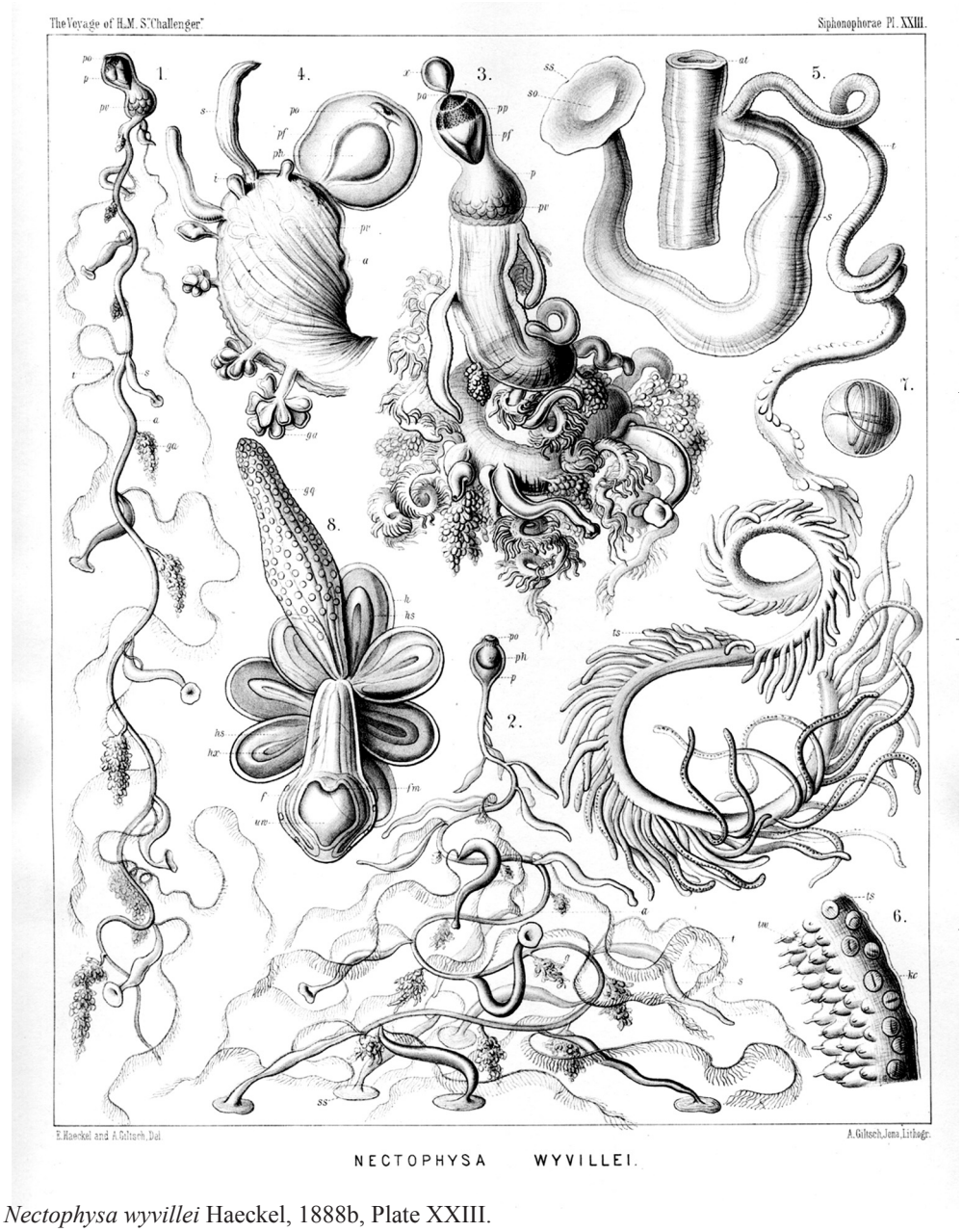

FIGURE 23. *Nectophysa wyvillei* Haeckel, 1888b, Plate XXIII.

Finally, the present author suggests that the fate of the eleven species that Haeckel (1888b) placed in the family Rhizophysidae is as follows:

Family **Rhizophysidae** Brandt, 1835
Sub-family **Cannophysidae** Haeckel, 1888a
Genus *Aurophysa* Haeckel, 1888a
Aurophysa ordinata Haeckel, 1888a — *Nomen nudum*
Aurophysa inermis = *Rhizophysa inermis* Studer, 1878 — ? = *Rhizophysa eysenhardtii*
Genus *Cannophysa* Haeckel, 1888a
Cannophysa gracilis = *Rhizophysa gracilis* Fewkes, 1882 — = *Rhizophysa filiformis*
Cannophysa murrayana Haeckel, 1888a — = *Rhizophysa filiformis*
Sub-family **Linophysidae** Haeckel, 1888a
Genus *Linophysa* Haeckel, 1888a
Linophysa conifera = *Rhizophysa conifera* Studer, 1878 — = *Bathyphysa conifera*
Genus *Nectophysa* Haeckel, 1888a
Nectophysa eysenhardtii = *Rhizophysa eysenhardtii* Gegenbaur, 1859 — = *Rhizophysa eysenhardtii*
Nectophysa wyvillei Haeckel, 1888a — = *Rhizophysa eysenhardtii*
Genus *Pneumophysa* Haeckel, 1888a
Pneumophysa gegenbauri Haeckel, 1888a — *Nomen nudum*
Genus *Rhizophysa* Péron & Lesueur, 1807
Rhizophysa filiformis = *Physophora filiformis* Forsskål, 1775 — = *Rhizophysa filiformis*
Rhizophysa planostoma [sic] Lesueur & Petit, 1807 — ? = *Rhizophysa eysenhardtii*
Rhizophysa mertensii = *Epibulia mertensii* Brandt, 1835 — ? = *Rhizophysa filiformis*

***Cystonectae Polygastricæ.* Family *Epibulidæ*.**

We come now to Haeckel's (1888b) short-stemmed grouping of cystonects, the Brachysteliniæ, which included the families Epibulidæ and Physalidæ. The species *Epibulia* was briefly discussed earlier and for all the descriptions Haeckel was the most muddled. In Haeckel (1888a) he consider the genus *Epibulia* to belong to the calycophoran family Diphyidae, and even established the Subfamily Epibulidae to include it, noting that the genus *Epibulia* was the same as Blainville's *Galeolaria*, which currently is referred to as *Sulculeolaria*. Another diphyid subfamily was the Prayidae, which has long been known to be a distinct family. However, in his *Challenger* Report Haeckel (1888b, p. 151) remarked that the genus *Galeolaria* had been: "confounded by later authors with *Epibulia*", apparently forgetting that he was one of them. He again placed the genus in its own family, the Epibulidæ, but now returned it to its original placed amongst the cystonect siphonophores. He (*ibid*, p. 332) defined the family as: "Cystonectæ polygastricæ with a short inflated trunk of the vesicular siphosome, which is spirally convoluted beyond the basal side of the large subvertical pneumatophore. Cormidia ordinate in a spiral ring, protected by a corona of palpons. Pneumatosaccus without radial septa and pericystic radial pouches, but with eight or more radial groups of hypocystic villi". He included two genera *Epibulia* and *Angela*, for the species *A. cytherea* Lesson. He devoted just twelve lines to the latter genus, in which he noted that the tentilla were trifid, which is a classic character for species of the genera *Agalma*, *Athorybia* and *Melophysa*. Bigelow (1911) considered Lesson's species in some detail and concluded that it belonged to the physonect family that he called the Anthophysidae. Indeed, there can be very little doubt that, despite the poorness of the illustration the species name *cytherea* is a junior synonym of *Athorybia rosacea* (Forsskål, 1775), which currently is included in the physonect family Agalmatidae (see Pugh, 2006); and so need not concern us any further.

Within the genus *Epibulia* Haeckel (1888b) included *Epibulia chamissonis* Eysenhardt and *E. erythrophysa* Brandt but, as noted above, despite Haeckel's statement that he saw the original manuscript drawing of Mertens, those drawings remain unpublished and so that species name must be treated as a *nomen nudum*. As Haeckel also had what he identified as an *Epibulia* specimen, collected off Sri Lanka, of course he described it as a new species, *E. ritteriana* Haeckel, and illustrated it in his Plate XXII (see Figure 24A). Like so many of Haeckel's illustration, this is a work of art but, as always, the question remains as to just how accurate was it? As noted above, Haeckel keenness to find intermediary species was also applied to *Epibulia*, which he considered to be a prime example of an intermediate between the Physaliidae and the Rhizophysidae.

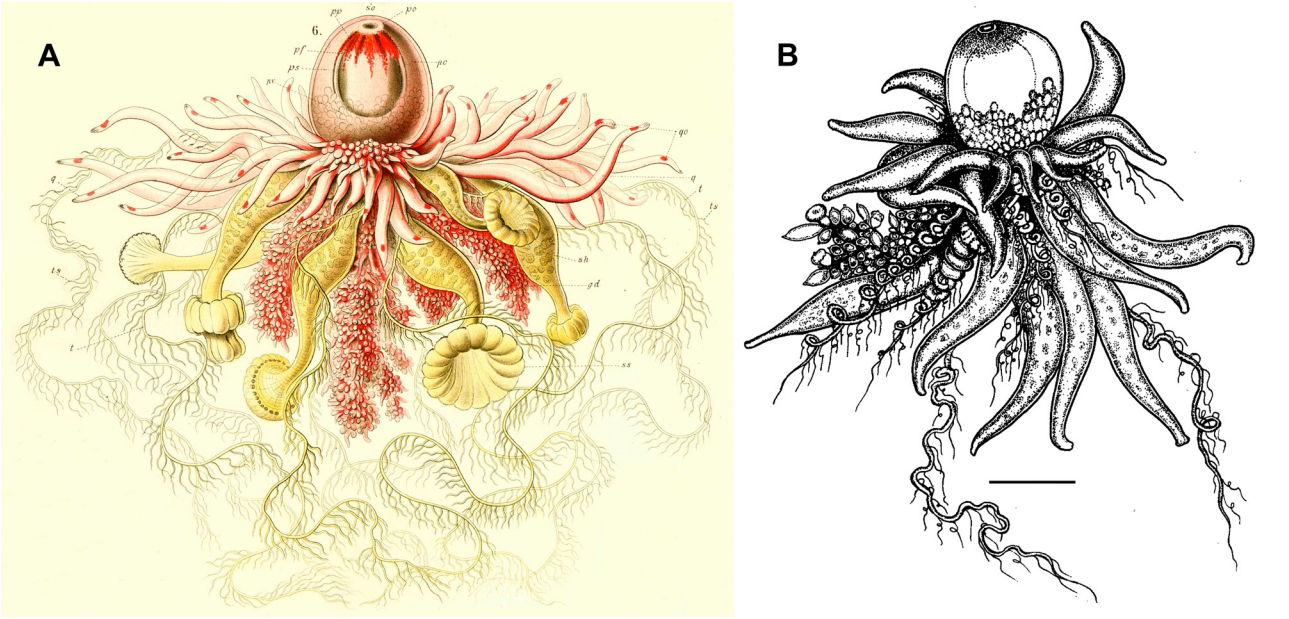

FIGURE 24. *Epibulia ritteriana*. **A**. Reproduced from Haeckel (1888) Plate XXII (*partim*). **B**. Adapted from Alvariño (1972, fig. 1). Scale bar 5 mm.

Haeckel (1888b), in his comparatively lengthy (88 lines) description of *Epibulia ritteriana*, spent a great deal of space (40%) describing the pneumatophore with its hypocystic villi that, as Haeckel noted, were also found in his Rhizophysidæ. The critical part of the description, however, is the description of the siphosome. Haeckel considered that this was made up by 40–60 palpons, as well as many young buds. He counted eight "cormidia" of which "four siphons and tentacles, and four large gonodendra were fully developed, two others (smaller) half developed, and two very small and young" (*ibid.* p. 335). By dividing the number of palpons by the number of "cormidia", he suggested that each "cormidium" bore 6–10 palpons. However, despite the fact that he himself had captured the specimen and watched its "vivid motions", he noted (*ibid*.): "Unfortunately, I was not able to examine closely the form of the central trunk of the siphosome, and the mode of attachment to the cormidia; probably it is similar to that of the Anthophysidæ, Discolabidæ, and Nectalidæ; all that I could observe of the trunk was that it represented a shortly conical or ovate bladder, coiled up in a spiral, with a single dexiotropic turning". Thus once again it appears that we were being given pure speculation rather than hard fact.

Schneider (1898), rather mysteriously, retained *Epibulia erythrophysa*, which must be considered as a *nomen nudum*, as the only species of the genus and synonymised Haeckel's *E. ritteriana* with it, on the rather dubious grounds that they both came from the Indo–Pacific. He thought that *E. chamissonis* probably also belonged to the genus. He suggested that Haeckel's description should be interpreted with some caution as Haeckel was describing features not known in cystonect species, i.e. stem palpons. Further, he noted that the descriptions of the pneumatophore, tentacles and genital clusters also equally applied to *Rhizophysa* species. However, Bigelow (1911, p. 320) considered that: "one species, *E. ritteriana* Haeckel, from the Indian Ocean, has been carefully described and beautifully figured. Two others from the Pacific, *E.* (*Rhizophysa*) *chamissonis* Eysenhardt, the type, and *E. erythrophysa* Brandt, are known, but from such incomplete accounts that their relationship to Haeckel's form remains doubtful".

Stepanjants (1967) retained all three species in her systematic list (see below), but otherwise made no mentioned of the genus. Totton (1965, p. 44) wrote of the "? Epibulidae Haeckel, 1888" that the chief characteristic was the presence of a ring of palpons below the pneumatophore so that (*ibid*.): "it seems best to regard these animals, if they exist, as forming a quite separate family Epibulidae Haeckel". He included both *E. chamissonis* and *E. ritteriana*, and for the latter he was (*ibid*.): "not satisfied of the existence of a siphonophore such as was figured by Haeckel. If it was indeed a cystonect it could hardly have a ring of palpons under the float. The description is incomplete and unconvincing. It seems possible that Haeckel had worked up notes and sketches of an incompletely examined specimen of *Athorybia rosacea*". Indeed, Totton included as a synonym of *E. ritteriana* "? *Athorybia rosacea* (Forskål) 1775". However, that seems to be a rather strange conclusion and perhaps Totton was actually thinking of the other species, *Angela cytherea*. It is also strange that Totton, who must have studied several specimens of *Rhizophysa*

filiformis during his visits to Villefranche-sur-Mer, appeared not to have noticed the fact that in that species the youngest gastrozooids, close to the pneumatophore, have yet to develop their tentacles; the buds of which gradually appear and enlarge as the gastrozooids move posteriorly in accordance with the growth of the stem. The reason for the presence of the so-called palpons would then become apparent. They are nothing more than young gastrozooids. Daniel (1974, p. 33) also elucidated this point when she said: "As pointed out by Totton ... the species of the family Epibuliidae will have to be treated as *species inquirendae.* The alleged presence of 'palpons' below the float may be really young gastrozooids, for if it were really palpons this family may have to be removed from the Suborder Cystonectae and placed before the Suborder Physonectae".

Since Totton's (1965) Synopsis, Alvariño (1972) reported the second record for *Epibulia ritteriana* (Figure 24B), from off California, and gave a "description" of the specimen. This description is remarkable for the fact that it reads almost exactly as though it had been copied directly from that of Haeckel (1888), as follows:

Alvariño (1972)	Haeckel (1888b)
"The pneumatophore is an ovate chitinous case, 8 mm x 10 mm in size. According to Haeckel (1888) the size of the pneumatophore ranged from 10 mm x 12 mm in the expanded stage to a spheroid of 3 to 4 mm after the emission of the gas through the apical pore. The structure of the pneumatophore, according to Haeckel (1888) includes the pneumatocodon or outer wall of the pneumatophore, which is separated from the inner wall, or pneumatosac, pneumatocyst or air sac, which contains the gas gland; and the hypocystic villi (giant cells) protrude from the air sac into the pericystic space. The apical pore is closed by the stigmatis sphicter [sic] (ring muscle).	"The great float filled with air is ovate, and has a diameter of 10 to 12 mm. in the expanded state; in the contracted state, however, after the emission of gas through the apical pore, it represented a depressed spheroid of 3 to 4 mm. only. The pneumatocodon or the outer wall of the pneumatophore is separated from the inner wall, or the pneumatosaccus, by a wide cavity. This pericystic cavity opens below into the stem-cavity of the siphosome, whilst it is closed above, surrounding like a ring the apical pore where both walls are connected. The distal or inferior half of the pericystic cavity is filled by the numerous finger-shaped hypocystic villi, arising in eight radial bunches from the airfunnel.
"The palpons (feelers or testers) are slender, cylindrical tubes, smaller than the siphons, with a thick muscular wall. They connect into the vascular trunk, and the outer end is armed with cnidocysts. The palpons are consequently then both sensory and protective organs.	"The palpons are slender, very movable, cylindrical tubes with a thick muscular wall. Their cavity opens at the proximal end into the vesicular trunk, whilst the closed distal end is armed with cnidocysts and a purple ocellus. Their function is not only sensory, but also protective and capturing.
"The siphons or gastrozoids [sic] are large ... rod-shaped tubes of thick muscular wall.	"Siphons [are] ... spindle-shaped tubes with a thick muscular wall.
"The largest part is the stomach with the hepatic villi, and the outer opening a muscular proboscis. The opening of the mouth may be expanded in a kind of disc or sucker, divided into several lobes.	"The largest part is the dilated stomach, covered inside with numerous yellow hepatic villi. The distal proboscis is very muscular; its mouth-opening may be expanded in the form of a circular suctorial disc, the margin of which is divided into sixteen lobes.
"The tentacle arising from the base of each gastrozoid [sic] consists of a long cylindrical tube reaching to 80 mm or more than 100 mm long when fully extended.	"The single tentacle which arises from the base of each siphon is a long cylindrical tube, in the fully expanded state 80 to 120 mm. long or more.
"The concave side of each tentillum has sensitive papillae, and the convex side is armed with cnidocysts.	"The concave ventral side of the tentilla bears sensible papillae; the convex dorsal side is armed with spherical cnidocysts.
"The gonodendra are attached by a short pedicle to the periphery of the vesicular trunk, between the palpons and the siphons or gastrozoids [sic]. The gonostyle is branched, and each branch has at the end a gonopalpo [sic] and a medusoid gynophore (female gonophore) and below a bunch of roundish androphores (male gonophores). "	"Gonodendra [are] attached by a short pedicle to the periphery of the vesicular trunk, between the superior palpons and the inferior siphon. The gonostyle is richly branched, and each ultimate branch ... bears a large, distal, medusiform gynophore and a bunch of club-shaped androphores with small gonopalpons scattered between them."

Thus, there appeared to be no new observations in Alvariño's description, and the only difference from that of Haeckel is that she, probably inadvertently, at one point equated the palpons with young gastrozooids. Alvariño also gave a presentation concerning this species at the Third International Conference on Coelenterate Biology, which took place in Victoria, B.C. in 1976. She showed some photographs of the specimen and both Dr. D.C. Biggs and myself were present and were immediately convinced that what we were seeing was a highly contracted *Rhizophysa* species. Thus we contend that *Epibulia* species are merely young, highly contracted specimens of a *Rhizophysa*. Because of the pink and red pigmentation and the simple, filiform nature of the tentilla, the most obvious candidate for both Eysenhardt's (1821) *E. chamissonis* and Haeckel's (1888b) *E. ritteriana* is *R. eysenhardtii.* However, personal observations (see below) have shown that the young gastrozooids of *R. eysenhardtii* quickly develop their tentacles, so that the sixth gastrozooid from the zone of proliferation has a well-developed one. In contrast, for *R. filiformis* the first 30 developing gastrozooids have no sign of a tentacle. This again raises the question, possessed above, as to whether all *R. eysenhardtii* specimens are red and *R. filiformis* ones green. Nonetheless, the large number of palpons, i.e. young gastrozooids, illustrated by Haeckel for *E. ritteriana* should be put down to the artistic licence that Haeckel (ab)uses all too often. It is concluded that there is no reason to continue to consider the family Epibuliidae, including its genera and species, as having any validity.

***Cystonectae Polygastricæ.* Family *Physalidæ*.**

And so we come to Haeckel's (1888b) final cystonect family, the Physalidæ. Haeckel begins by reviewing the history of the family and noted (*ibid*. p. 338) that: "All recent authors have accepted the genus *Physalia* as the only type of this family". Ones hopes are raised that Haeckel will do the same! But those hopes are quickly dashed. First of all he re-established Brandt's (1835) genera *Salacia* for species with a dorsal crest, and *Alophota* for those without one. He said (*ibid*. p. 339): "The family Physalidæ was established in 1835 by Brandt ... He first distinguished two different subgenera in the genus *Physalia*, viz., (1) *Salacia* (or *Physalia* proper), with a chambered dorsal crest of the float; and (2) *Alophota*, without crest. This distinction, although not accepted by later authors, is very important, since the crestless state of the pneumatophore, regarded from a phylogenetic point of view, must necessarily precede the crested state". Of course, it also applies from a developmental point of view. However, as noted above, Haeckel had already used the generic name *Salacia* as the basis of a completely different cystonect family. Haeckel (*ibid*.) continued: "We establish for these [the so-called species without a crest] the subfamily Alophotidæ, and oppose it to the crest-bearing subfamily Caravellidæ". In each sub-family Haeckel then uses the presence of only a single large tentacle or of many such tentacles to divide each into two genera.

Haeckel (1888b, p. 339) succinctly summarised the problems arising from many of the previous descriptions, but then made the situations even worse. He said: "The distinction of species in these four genera of Physalidæ is a very difficult task, since the entire family is transformistic, and all the so-called "good species" are connected by Darwinian intermediate forms. Nevertheless, there exist a number of "geographical species" as local forms in the different seas. In the majority of the numerous descriptions the species of Physalidæ are founded upon slight differences in the variable coloration, or different states of contraction of the very variable pneumatophore and other parts ... A better and more natural distinction of "relatively good species" will be got when the future observers carefully regard the following anatomical structures:— (1) the grouping and composition of the monogastric or polygastric cormidia; (2) the relation of the basal protosiphon (at the distal end of the float) to the secondary siphons (or metasiphons) on its ventral face; (3) the difference in structure and form of the pneumatophore, mainly at its apical and basal poles; (4) the structure of the crest, the number of its chambers, &c".

Having established the sub-family Alophotidæ for the physaliids without a crest, eight pages later Haeckel very confusingly changed the name of the sub-family to the Arethusidæ, and included in it the genus *Alophota* with a new genus *Arethusa*. The genus *Alophota*, defined as being without a crest and with a single large main tentacle, was originally established by Brandt (1835) as a sub-genus of the genus *Physalia*. However, the Latin diagnosis of *Physalia* (*Alophota*) *Olfersii* (*ibid*. p. 238) stated "Tentacula 2". Typically, Haeckel (1888b) did not mention, in the section on *Alophota* Brandt's subspecies by name, although he did include it in his final list of siphonophore species. He decided that he had two other related species, *A. giltschiana* and *A. mertensii*, the description of the latter being left for his fabled *Morphology of the Siphonophoræ*.

There is little point into going into any detail of Haeckel's (1888b) descriptions of *Alophota giltschiana* or *Arethusa challengeri* (see Figure 25), the only two physaliids he illustrated. One could note that the maximum size of the float of the former "species" was 2 cm, with four "developed cormidia" in the main group; while for *A. challeng-*

eri the float measured up to 5 cm and the number of tentacles, which unsurprisingly were larger than for the former species, was six to eight. This is only interesting because of its inexactitude as Totton (1960), and others before him, clearly established was that the maximum number of groups in each zone was seven. To put this into context let us remember that the pneumatophore of *Physalia physalis* can reach at least 30 cm in length, so Haeckel's specimens were mere babies. As there is no value in continuing to discuss Haeckel's misguided ideas on the family Physaliidae, it is simplest to list in full the species he included in the family (Haeckel, 1888b, p. 372); all of which, apart from the *nomina nuda*, are considered by the present author to be junior synonyms of *Physalia physalis*:

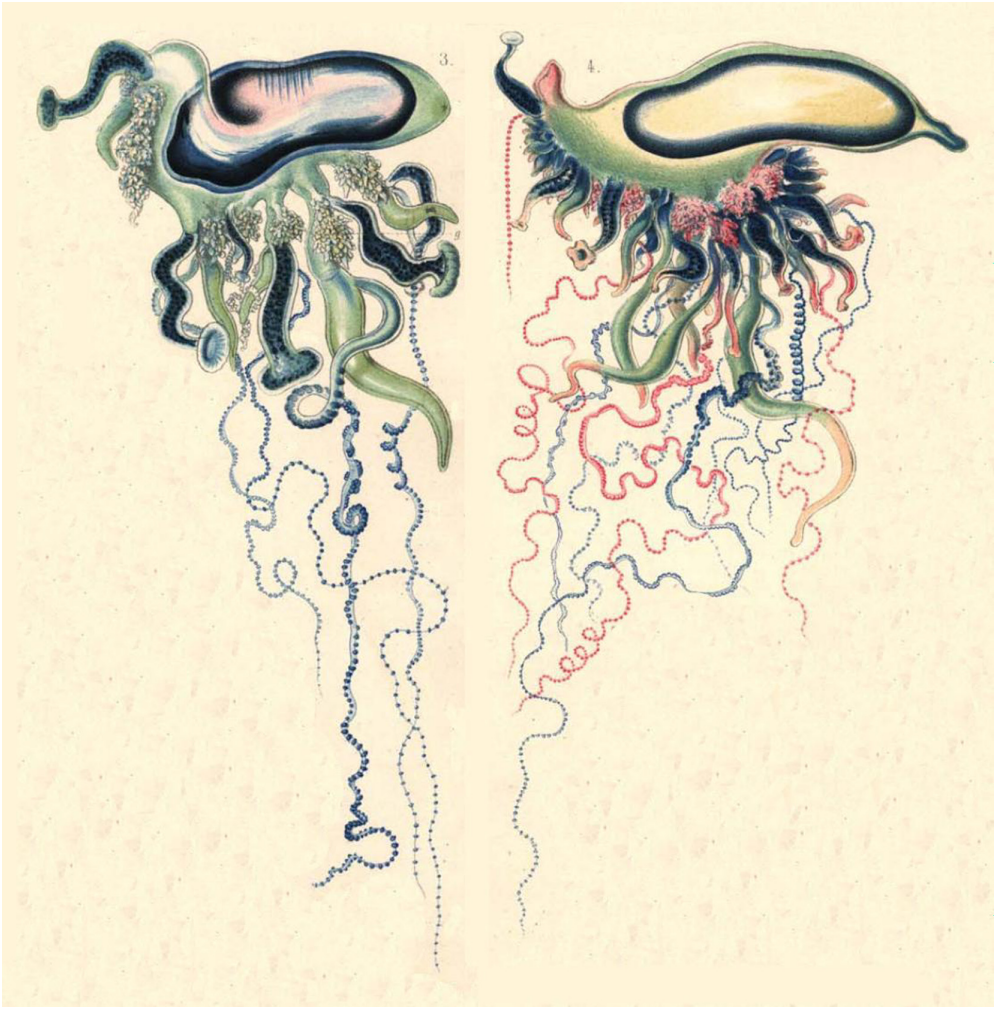

FIGURE 25. Left. *Alophota giltschiana* Haeckel, 1888b – corm diameter 1.5–2 cm; and Right. *Arethusa challengeri* Haeckel, 1888b – corm length 4–5 cm. Figures 3 and 4, respectively, from Haeckel (1888b) Plate XXVI.

Family **PHYSALIDÆ** Brandt, 1835
Sub-family **Arethusidae** Haeckel, 1888b (Pneumatophore simple, without dorsal crest).
Genus ***Alophota*** Brandt, 1835 – A single large main tentacle.
Alophota olfersii Brandt, 1835
Alophota giltschiana Haeckel, 1888b
Alophota mertensii Haeckel, 1888b *Nomen nudum*
Genus ***Arethusa*** Haeckel, 1888b[51] – Several large main tentacles.

51 Haeckel (1888a) attributes the generic name *Arethusa* to Browne, but no date was given. However, Haeckel (1888b, p. 349) attributes the name to himself as "The genus *Arethusa* was established a century ago (in 1789) by Patrick Browne, for that gigantic Physalid of the Tropical Atlantic, which is known to the sailors as the "Portuguese Man-of-War," and which O. F. Müller and Gmelin had called *Medusa caravella* ... Since the generic name *Arethusa* was afterwards given up and replaced by Lamarck's name *Physalia*, we employ here the former for the designation of those Physalidæ which agree with *Caravella* in the possession of numerous large main tentacles, but differ from it in the absence of a polythalamous crest on the pneumatophore". Nonetheless, the species that Haeckel (1888b) includes in this genus are very different from those that Haeckel (1888a) included.−

Arethusa challengeri Haeckel, 1888b
Arethusa thalia Haeckel, 1888b — *Nomen nudum*

Sub-family **Caravellidae** Haeckel, 1888b (Pneumatophore with dorsal crest).
Genus ***Physalia*** Lamarck, 1801 – Single large main tentacle
Physalia pelagica Bosc, 1802[52]
Physalia cornuta Tilesius, 1813[53]
Physalia utriculus Eschscholtz, 1829[54]
Physalia megalista Lamarck, 1816[55]
Genus ***Caravella*** Haeckel, 1888b – Several large main tentacles.
Caravella gigantea Haeckel, 1888b = *Physalia cystisoma* Lesson *partim*
= *Physalia gigantea* Bory de St. Vincent, 1804
Caravella maxima Haeckel, 1888b = *Physalia caravella* Eschscholtz, 1829[56]
= *Physalia arethusa* Olfers, 1831

Physalia post-Haeckel

At last, we can return to sanity! Or, to paraphrase Merrill (1949, referring to Rafinesque, as quoted by Endersby, 2009, p. 170): "in taxonomy and nomenclature we would have been infinitely better off today had Haeckel never written or published anything appertaining to the subject". It did not take long for Claus (1889a, b), the latter being an English translation of the former, to give a critical review of Haeckel's 1888 contributions. Claus particularly took issue with Haeckel's nomenclature for the parts and appendages of siphonophores. However, in actuality that probably had more to do with the translator than Haeckel himself, since the original text was written in German. Claus wrote a great deal in regard to Haeckel's Medusome Theory, which he debunked very successfully and regarded it as "fiction"! Indeed it attracted few followers. With regard to Haeckel's classification of the cystonects, Claus (*ibid*. p. 196-7) stated: "There are numerous novelties in connexion with the division of pre-existing genera into two or more, and, indeed, on the ground of trifling distinctions scarcely applicable as generic characters. As examples may be cited the division of *Physalia* into *Physalia* and *Caravella* and of *Alopleota* [sic] into *Aloploeota* [sic] and *Arethusa* as also the establishment of two subfamilies associated therewith; further the breaking up of *Rhizophysa* by its different species into the genera *Aurophysa*, *Cannophysa*, *Linophysa*, *Nectophysa*, *Pneumophysa*, and *Rhizophysa*, and the distinction of two subfamilies as Cannophysidæ and Linophysidæ upon differences which perhaps justify generic separation". Indeed, Claus (*ibid*., pp 195-6) had earlier remarked: "That Haeckel makes a very extensive, indeed almost unlimited, use of his skill in making new and suitable names, is certainly intelligible from the fact that he possesses this faculty in a very high degree and has developed it, by many years' practice, into a speciality, in which at present no other naturalist can hope to equal him"!

Chun (1897) was one of the last 19th century reviewers of the family Physaliidae, He, like Huxley, drew attention to a couple of the main offenders, Tilesius, Olfers and Lesson, who had done so much to muddle the already confused taxonomy of the family; and, correctly, also added Louis Agassiz (1862) to this list but, being an adherent to Haeckel's Medusome Theory, he was reticent to criticise that particular author. However, Chun clearly did not consider that Haeckel's division of the family Physalidæ into sub-families, dependent on the presence or absence of a crest, was valid. In fact he believed that there were only two valid *Physalia* species; one living in the Atlantic and the other in the Indo-Pacific. The main difference between the two species was the other Haeckelian character, in that the Atlantic form had numerous main tentacles, while the other had only one. So Chun, like Huxley (1859), adopted the specific name for the Indo-Pacific species, *Physalia utriculus* (La Martinière) [but actually, Gmelin, see above]. For the Atlantic species Chun applied what he considered to be the principles of priority and gave it

52 The name *P. pelagica* was first used by Lamarck (1801, p. 356). Bosc (1802, p. 166) used the misspelt form *P. pelasgica*. Haeckel (1888a) attributed this name to Osbeck (1757), but that is pre-Linnaean.
53 Haeckel (1888b) used Tilesius (1813) as the authority although, as discussed above, it appears to be Tilesius (1810).
54 Haeckel (1888b) quotes Eschscholtz (1829) as the authority for *Physalia utriculus*, but Gmelin (1788, p. 3155) was the first to use the specific name for *Medusa utriculus* (see above).
55 Although Haeckel (1888b) quotes Lamarck as the authority, but in brackets he says "Péron ... pl. xxix, fig.1. Lesueur & Petit (1807) should be the authority.
56 O.F. Müller (1776) is the original authority for this species, under the name *Medusa caravella*.

the name *P. Arethusa*, based on the description and name given by Browne (1756). However, that was contrary to the then emerging International Rule of Nomenclature, as Schneider (1898, p. 190)[57] pointed out when he said: "Linnaeus established in the 10th edition of Systema Naturae, the Atlantic Physaliid as *Holothuria physalis*. It follows, therefore, that as a species name *physalis*, but not *arethusa* or *Caravella*, is preferable over both. Chun (97, p. 87) violates the principles of priority (which he believed to be following), when he designated our form: *Physalia arethusa* Browne (see also the rules of nomenclature)." Thus, after 140 years since it was first named by Linnaeus, Schneider finally established the name *Physalia physalis* by which the species is known today.

Although Schneider (1898, p. 87)[58] also retained the name *Physalia utriculus* for the "smaller and less luxuriously developed" Indo-Pacific form, he commented (*ibid*.)[59]: "If there are no morphological differences in the construction of the individual appendages between the two forms, it seems to me that it should be understood that the Pacific form is only a variety of the Atlantic one." As noted above, it was clear that Schneider was not a friend of Chun, judging by their comments about each others' work, some of which are definitely worth reproducing. For instance, Schneider (1898, p. 51)[60] began his review of the systematics of siphonophores by stating: "For the present communication I am induced by the two Chun works of 1897 [a, b]. To my regret, I have found that Chun, when judging my second communication of 1896, 'Grundriß der Organisation der Siphonophoren,' had very little objective preoccupation, and spoke so disparagingly about many points - without thereby substantiating his opposite opinion or my opinion against earlier statements to acknowledge the grounds for refutation - that in the interest of my own work I consider a detailed criticism of Chun's recent communications to be useless." However, he was more forthright (*ibid*., p. 162)[61] when he stated: "I cannot refrain from expressing my satisfaction that Chun now finally recognizes the extra-capsular attachment of the stinging tube in the young nematocyst. Chun still said '92 on p. 156 against my statement of '91: 'I regret having to contradict almost all of Schneider's information.' Perhaps the time will come when Chun will no longer have to contradict the information I have provided. Incidentally, a statement of the incorrectness of my findings is just as welcome as a confirmation, because I work in the interest of science. Only then must the inaccuracy be 'explained' in detail; empty sarcastic phrases are not enough in scientific studies."

Schneider (1898) gave a quite detailed account of the morphology of rhizophysids, particularly with regard to the structure of the pneumatophore and the gonodendra, and made many comments, not all positive, about Chun's (1897) description, and, with regard to the giant cells of the pneumatophore, he stated (*ibid*., p. 167)[62]: "The interpretation that Chun presents for the giant cells appears completely untenable to me. He regards them as "buffers," that "prevent vigorous contractions of the stem and the pneumatocodon above it from rupturing the pneumatophore." If there is any element that would appear to be inappropriate to fulfil such a function it is precisely these giant cells,

57 Original text: "Linné führt in der 10. Auflage des Systema naturae die atlantische Physalie als *Holothuria physalis* auf. Als Speciesnamen ergiebt sich summit *physalis*, nicht aber *arethusa* oder *caravella,* die beide bevorzugt werden. Chun (97 p. 87) verstößt gegen die Grundsätze der Priorität (denen er doch zu folgen glaubt), wenn er unsre Form: *Physalia arethusa* Browne benennt (siehe darüber die Nomenclaturregeln)."

58 Original text: "kleiner und weniger üppig entwickelt"

59 Original text: "Falls nicht morphologische Differenzen im Bau der einzelnen Anhänge zischen beiden Formen bekannt werden sollten, scheint mir die pacifische Form nur als Varietät der atlantischen aufgefaßt werden zu können."

60 Original text "Zu der vorliegenden Mittheilung Averde ich durch die beiden Chun'schen Arbeiten von 1897 veranlaßt. Ich habe zu meinem Bedauern constatieren müssen, daß Chun bei Beurtheilung meiner zweiten Mittheilung von 1896: »Grundriß der Organisation der Siphonophoren «sehr wenig objectiv vorgieng und sich über manche Puncte derart abfällig aussprach - ohne dabei seine entgegengesetzte Auffassung zu begründen oder meine gegen frühere Angaben vorgebrachten Gründe einer Widerlegung zu würdigen - daß ich im Interesse meiner eigenen Arbeit eine ausführliche Kritik der Chun'schen neueren Mittheilungen für nüthig erachte."

61 Original text "Ich kann hier nicht unterlassen, meine Genugthuung darüber auszudrücken, daß auch Chun nun endlich die extracapsuläre Anlage des Nesselschlauches in den jungen Nesselzellen anerkennt. Sagte doch Chun noch 92 auf p. 156 gegenüber meinen Angaben von 91: »Ich bedaure, fast sämmtlichen Angaben von Schneider widersprechen zu müssen.« Vielleicht wird auch die Zeit kommen, wo Chun den von mir 96 gemachten Angaben nicht mehr widersprechen zu müssen bedauert. Übrigens ist mir eine Darlegung der Unrichtigkeit meiner Befunde ebenso willkommen, wie eine Bestätigung, denn ich arbeite ja im Interesse der Wissenschaft. Nur muß die Unrichtigkeit dann auch eingehend »dargelegt« werden; leere sarcastische Phrasen genügen nun einmal bei wissenschaftlichen Untersuchungen nicht.

62 Original text: "Ganz unhaltbar erscheint mir die Deutung, welche Chun für die Riesenzellen aufstellt. Er betrachtet sie als »Puffer«, die »bei energischen Contractionen des Stammes und des ihm aufsitzenden Luftschirmes ein Sprengen des Luftsackes verhüten«. Wenn irgend welche Elemente dazu ungeeignet erscheinen müßten, so sind es gerade die Riesenzellen, die von äußerst zart spongiöser Beschaffenheit und außerdem nur von einer sehr dünnen Stützlamelle umgeben sind. Mit demselben Recht könnte man Blätterteig als Puffer zwischen Eisenbahnwagen für geeignet halten."

which are extremely delicate and of a sponge-like texture and, in addition, are surrounded only by a very thin supporting lamella. With the same reasoning one could argue that puff pastry is suitable as a buffer between railway carriages".

Schneider (1898) was possibly the first person to make a detailed study of the development of the "cormidial" units in *Physalia*. On his most developed specimens, he found 11 "cormidial" groups, five in the oral zone, and six in the main one. With regard to the gonodendra, he noted (*ibid*., p. 187)[63]: "The findings generally show that the genital groups are being detached *in toto*. In addition to the tentacle and its associated polyp you will find, if the genital group is no longer detectable, a short rounded stump, to which the genital group was originally attached. Since, as is well known, no medusa bud on *Physalia* itself reaches maturity, and rather here germ cells are completely lacking, thus the detached genital group seems to be the site of maturation, and in the future, in order to find more advanced stages, one must look for free-swimming groups when a swarm of *Physalia* occurs." As Schneider noted male gonophores on the gonodendra he examined, one presumes, therefore, that he considered both the male and female gonodendra to be detached before both the special swimming bells and the gonophores became mature.

Steche (1910) made a much more detailed study of the order of development of the various "cormidial" groups, based largely on the same material that Chun had looked at. He followed Schneider (1898) in designating the Atlantic species, *Physalia physalis*, but was adamant that it was distinct from *P. utriculus*, mainly on the more complex nature of the arrangement of the various zooids in the former, and that there were marked differences in the development of the young zooids. He reviewed the other studies on developing larvae by Huxley (1859), Chun (1887) and Schneider (1897). He criticised the description by the last of these authors on several counts. In one instance he considered that Schneider's conclusion that the ampulla at the base of the tentacle was very similar to the basigaster of a physonect gastrozooids, since in contained innumerable numbers of developing nematocysts, and which Schneider considered to have separated itself from the gastrozooid in order to give greater freedom to the tentacle, as his findings gave no support to that idea although it is not quite clear what these findings were. He also noted that the "cormidial" groups did not arise in a linear order and, thus, (*ibid.*, p. 369)[64] he concluded: "This proves that at an early stage germinative material must be distributed over the entire stem zone, which is then activated one after another".

Bigelow (1911) followed Steche in recognising the two species, *Physalia physalis* in the Atlantic, and *P. utriculus* in the Indo-Pacific. He pointed out that although the Pacific species, with its single main tentacle, resembled the immature stage of the Atlantic species; nevertheless of all the specimens from the Pacific that he, and previous authors, had examined none possessed more than one main tentacle. However, a year earlier Kawamura (1910), in a somewhat obscure paper in Japanese, had already shown that of his specimens from near Izu Oshima, Japan, two had two major tentacles while one had four. Kawamura, thus, considered *utriculus* to be a variety of *P. physalis*.

Moser (1925), having studied a large collection of physaliid specimens from the *Gauss* and other expeditions, came to the same conclusion in that the Atlantic and Indo-Pacific forms were merely varieties of one species, which would thus be called *Physalia physalis*. Nevertheless, she still recognised the possibility of two varieties that she referred to as the Atlantic *arethusa* and the Indo-Pacific *utriculus*.

The final nail in the coffin for the idea that there were two species of *Physalia* should have come from Okada (1932, 1935) who examined a large number of *Physalia* specimens from Japan with a pneumatophore ranging in length from 2 to 100 mm. He also made very detailed studies of the order of origin of the various zooids and, helpfully, used the same system of annotations as Steche (1910) had used. Unlike Steche, however, he finally concluded from his studies (*ibid* p. 19)[65]: "It is wrong, as was believed until now, that the Indo-Pacific Ocean *Physalia* has only one main tentacle, and that is because we had never observed a fully developed *Physalia*. The specimen, whose pneumatophore reached 95 to 100 mm long, has as many long and major tentacles as the species living in the Atlantic Ocean."

63 Original text "Die Befunde lehren ganz allgemein, daß die Genitalgruppen in toto abgestoßen werden. Neben dem Fangfaden und seinem zugehörigen Polypen findet man - falls die Genitalgruppe nicht mehr nachweisbar ist - einen kurzen abgerundeten Stummel, an dem ursprünglich die Genitalgruppe festsaß. Da nun, wie bekannt, keine Medusenknospe an der Physalia selbst zur Reife gelangt, alle vielmehr hier der Keimzellen vollständig entbehren, so scheint die abgelöste Genitalgruppe die Reifungsstätte zu sein, und man wird künftig, um weiter vorgeschrittene Stadien zu finden , bei Auftreten eines Physalia-Schwarmes nach frei schwimmenden Gruppen suchen müssen."

64 Original text "Dies beweist, daß schon frühzeitig Keimmaterial über die ganze Stammzone verteilt sein muß, das nacheinander aktiviert wird."

65 Original text: "C'est à tort que l'on a cru jusqu'à présent que la Physalie de l'Océan Indo-Pacifique n'avait qu'un tentacule principal, et cela parce que l'on n'avait jamais observé la Physalie en parfait développement. Le spécimen dont le pneumatozoïde atteint 95 à 100 mm. de long, possède de longs et nombreux tentacules principaux, comme l'espèce vivant dans l'Océan atlantique."

Totton (1960, p. 304), who made very detailed studies of the budding patterns of the "cormidial" groups, was clearly not particularly impressed with the studies on this subject, made by earlier authors when he stated: "The methods employed had to be purely exploratory to begin with, because previous accounts of the arrangement of the groups of buds in *Physalia* were too superficial and illustrated either not at all (Schneider, 1896) or so inadequately (Steche, 1910; Okada, 1932, 1935) that they could not be checked and built upon. In fact it was necessary to start *de novo*". However, he did commend Steche (1907) for possibly being the first person to recognize that the gonophores, usually assumed to be always male, while the special nectophores were assumed to be the female, could also be female; and that all gonophores on a single gonodendron were of the same sex. Was this the first recognition that cystonects were dioecious? It is not clear.

Totton (1960) also was adamant that there was only one *Physalia* species, namely *P. physalis*. In fact, all major reviewers since Bigelow (1911) have recognised only the one species. However, there are still a few exceptions to be found in the literature. Collins (2002) used material from an Atlantic (as *P. physalis*) and a Pacific (as *P. utriculus*) specimen in his analyses of the molecular phylogeny of the Medusozoa. In one instance (*ibid.* Fig.1) he found that that the "Bootstrap indices under maximum parsimony and minimum evolution criteria" for distinguishing the species were both 100; indicating that there was a high degree of likelihood that those two specimens were more closely related to each other than to anything else included in the analysis. However, although the likelihood is high, one cannot use these data to prove that one is dealing with a single species (Dr Casey Dunn, personal communication).

As Dr Dunn has also commented that the more recent papers that have suggested that there is more than one *Physalia* species have largely been peripheral to the core siphonophore literature, as for more than 70 years siphonophore systematists have agreed that there is just one. For instance, at least two teams of medics have suggested ways to distinguish more than one species of *Physalia*. Fenner *et al.* (1993) suggested that the response to the experimental exposure of *Physalia* tentacles, from different regions of Australia, to vinegar indicated that there must be at least two *Physalia* species, although they do not appear to provide any statistical evidence for this conclusion. They (*ibid*., p. 500) continued with the description of: "A newly differentiated specires of *Physalia physalis*"! This "species" was differentiated from the Atlantic *P. physalis* by its smaller size, up to 15 cm, and the number of "main" tentacles, up to five, with up to ten developing ones. They then stated (*ibid*.): "We suggest that the smaller, single-tentacled jellyfish commonly known as the "bluebottle" should be referred to by its original name *Physalia utriculus,* despite the suggestion in 1960 by Totton that all *Physalia* species are the same and should all be referred to as *Physalia physalis.* (This question has remained taxonomically unresolved, and Totton's suggestion has since been ignored by some workers in this field.)"; this field being medicine!

Before continuing the discussion on Australian *Physalia* species, let us consider the other team of medics mentioned above. Yanagihara *et al.* (2002) studied the cnidome of specimens of a *Physalia* caught off Hawaii, and compared their data with that of previously published information on *P. physalis*. They noted (*ibid.* p. 140) that, for the latter species: "Totton & Mackie (1960) … reported large and small holotrichous isorhizas along the tentacle, isorhizas along the stomach lip-region and stenoteles in its gastrozooids and dactylozooids palpons and float." However, Weill (1934) had identified the isorhizas as atrichous, while others variously had identified them as anisorhizas; and the stenoteles as euryteles. Yanagihara *et al.* (*ibid.*) considered that: "Accurate identification of the cnidome is essential in the analysis of venoms and understanding the potential plasticity of predator-prey relationships" but clearly they also thought that it had taxonomic importance, as they were convinced that their specimens belonged to *P. utriculus*. They made detailed measurements of the discharged threads of the tentacular nematocysts and came to the conclusion that, for their *Physalia* specimens, they were two sizes of heterotrichous anisorhizas, rather than isorhizas. However, they did not resolve whether the other, non-tentacular, nematocysts where euryteles or stenoteles.

But do the findings of Yanagihara *et al.* (2002) have any taxonomic significance? It seems, to the present author, that the answer has more to do with semantics than with taxonomy. They found that for both their types of "heterotrichous anisorhizas" the tubule decreased in diameter from base to tip, but that the most rapid decrease in diameter occurred in the distal half of the tubule. From this they concluded that the nematocysts should be considered to be anisorhizas, although they do not state why they came to that conclusion, except to say (*ibid.* p. 147) that they: "arbitrarily interpreted tapering of more than 30% to be significant".

Werner (1965, p. 8) described isorhizas as "Faden isodiametrisch"; and anisorhizas as "Faden an der Basis deutlich erweitert". Similarly, Mariscal (1974, p. 136) defined isorhizas as "thread of the same diameter throughout"; and anisorhizas as "thread slightly dilated toward base". Östman (2000, p. 44) gave a very similar definition for anisorhizas, but enhanced the definition of isorhizas as: "tubule isodiametric or nearly isodiametric proximal to the

mid-point and tapering thereafter". Thus, using the data of Yanagihara *et al.* (2002) one finds that, for the smaller type of nematocyst, the diameter of the thread has reduced to just 89% of its proximal value by its mid-length, but to 50% at it distal tip. For the larger for the values are 88 and 65% respectively. Thus, according to Östman's definition, they should be considered as isorhizas, and the complete absence of any basal swelling on the tubules attests to that conclusion. Thus, on this basis it appears that the conclusions reached by Yanagihara *et al*. (2002) do not conform with Östman's definitions.

Pontin (2009), in his Ph.D. thesis, used CO1 and ITS1 DNA molecular sequencing on tissues from specimens of *Physalia* collected from various locations in New Zealand. He concluded that there appeared to be at least three species of *Physalia* present, of which only one was likely to be a named species, namely *P. utriculus*, and neither of the others was *P. physalis*. However, in the published version of these results, Pontin & Cruickshank (2012) were more cautious in their conclusions, and considered that there was substantial cryptic diversity amongst the specimens of *Physalia* from New Zealand coastal waters. Nevertheless, they still considered the possibility of there being more than one *Physalia* species, unless there was an extraordinary level of intra-specific diversity for *P. physalis*.

Unfortunately, Gershwin *et al*. (2010) again used morphological characters, such as size and the number of tentacles, to establish that there were four different forms of *Physalia* in Australian waters. Three of these possessed a single main fishing tentacle, but differed as to whether the crest on the pneumatophore was absent, incomplete or complete. One of these, the commonest of all, the one with a prominent but incomplete crest, they suggested was *P. utriculus*, with which they synonymised *P. megalista* (Lesueur & Petit, 1807). The other two were thought to have been previously unrecognised species, although it is difficult to believe that a similar one could not be found among the more than fifty *Physalia* species that have been described to date. The fourth type had multiple tentacles, with or without a crest, but they did not definitively name this as *P. physalis*. These conclusions do not agree with the conclusion reached by Fenner *et al*. (2003) who called the last, not the first, *P. utriculus*. It is difficult to believe these conclusions, in rather the same way as Haeckel's (1888b) numerous varieties have all been rejected. In addition, their photographs of the various "species" raises the same questions of interpretation with regard to the number of main tentacles as was discussed above with regard to Haeckel's species.

Bardi & Marques (2007) made detailed morphological and histologival studies of *Physalia physalis* from the Brazilian waters. The question as to whether the nematocyst batteries tentacles of *P. physalis* should be considered as tentilla was raised recently by Munro *et al*. (2018). On the young tentacles these batteries form semi-annular horseshoe-shaped buttons appparently attached directly to the siphosome, but for the mature relaxed tentacles they are arranged along the axis of the siphosome; thereby suggesting that they where ectodermal swellings. However, they noted that Bardi & Marques (2007) had found that the buttons actually contained a cavity, lined with endoderm, that connected with the gastrovascular cavity of the tentacle; thereby suggesting that they were reduced tentilla.

Bardi & Marques (2007) noted that there were regional differences in the morpholoy of their specimens, mainly regarding the number of mature tentacles, which harks back to the results from Australia and New Zealand. They then discussed the possibility that there were more then one *Physalia* species, but noted that their specimens with more than one main tentacle were longer in length than those with one. Thus, they concluded that the addition of new tentacles was just a stage in the growth of the colony. They also considered the size and types of nematocyst present on the tentacles and noted the results of Yanagihara *et al*. (2002) that suggested a difference between the Atlantic *P. physalis* and the Pacific *P. utriculus*. However, we have already discussed this above and concluded that is just a matter of definition.

Bedot and *Bathyphysa*

Having brought the history of *Physalia physalis* up to the present, let us now turn to the rhizophysid cystonects. As noted above we got away lightly with Haeckel's (1888b) interpretation of the genus *Bathyphysa* as belonging to the family Forskaliidae. However, this interpretation caused great confusion to Bedot (1893) when he described a bathyphysid species under the name *Bathyphysa Grimaldii* Bedot. Firstly, Bedot adopted Haeckel's terminology, dividing the stem into the anterior nectosome and posterior siphosome, and he noted that for his specimens the former was reduced to just the pneumatophore, which had hypocystic villi at its base (see Figure 26C). Instead of nectophores, Bedot believed that the upper part of the stem bore peculiar and specialised zooids, which he name *pneumatozoïdes* (see Figure 26A, B, *pz*), which were said to be borne on short peduncles. These zooids were de-

scribed as consisting of a tube, closed at both ends and lined by endodermal cells, and curved into a C-shape by a transparent ectodermal membrane united to its walls (Figure 26 E, F). Bedot considered that the endodermal tube was filled with air, attributing to them a hydrostatic function; hence their name.

Posterior to these so-called *pneumatozoïdes* Bedot (1893) described the siphosome with a great number of gastrozooids, although it would seem that all the latter were detached. The gastrozooids were said to be similar to those described by Studer (1878a) for *Bathyphysa abyssorum*, i.e. with two longitudinal *replis* or *ptera*, and borne on long peduncles, which bore small swellings filled with nematocysts. Bedot rejected Haeckel's idea that these swellings represented the sites of attachment of bracts, and considered that bracts were totally absent, noting that the so-called bract that Studer described for *B. abyssorum* was nothing more than a small gastrozooid. Tentacles were also present, which had exactly the same structure as the peduncles of the gastrozooids. Bedot concluded that his *B. Grimaldii* was actually more closely related to *Rhizophysa* than to *Forskalia*, but he considered that there were sufficient differences, particularly the presence of *pneumatozoïdes*, to warrant the establishment of a new family, the Bathyphysidae, as Haeckel (1888b) himself had suggested; but in Bedot's case within the Cystonectae. Bedot considered that the presence of *ptera* on the gastrozooids was an important taxonomic character and thus included Studer's *B. abyssorum* and Fewkes's *B.* (*Pterophysa*) *grandis* within the genus. However, Bedot, like Fewkes, considered that there was only one genus and he chose Studer's original genus *Bathyphysa*, as opposed to Fewkes' substitute one *Pterophysa*. Nonetheless, although Bedot also noted the presence of *ptera* on the gastrozooids of Studer's *R. conifera*, for some unexplained reason he excluded this species not only from the genus *Bathyphysa*, but also from his family Bathyphysidae. He did not mention Studer's *R. inermis* at all.

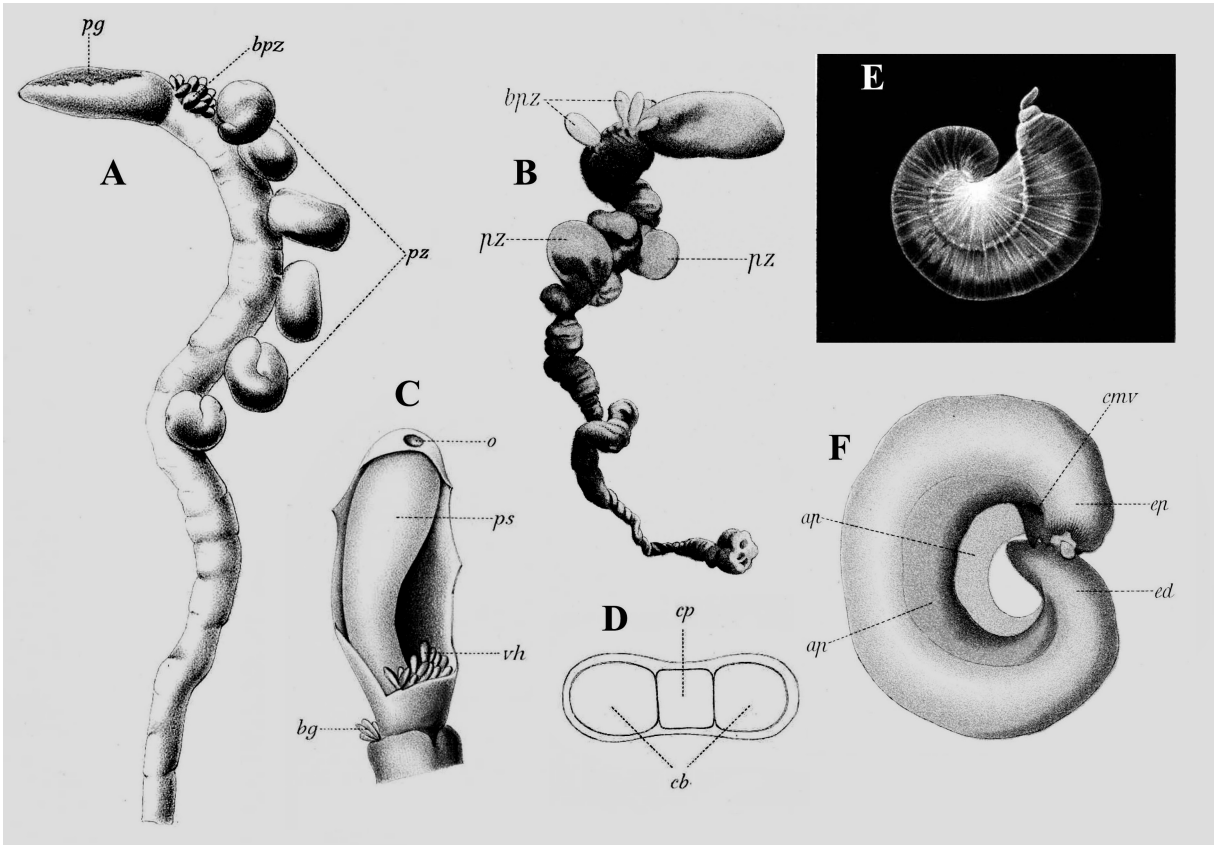

FIGURE 26. *Bathyphysa grimaldii* Bedot. **A**. "Nectosome"; **B**. Fragment of colony; **C**. Pneumatophore with part of external wall removed; **D**. Schematic section through a *pneumatozoïde*; **E**. and **F**. *pneumatozoïdes*. *ap*: *ptera*; *bg*: buds; *bpz*: young *pneumatozoïdes*; *cb*: cavity of *pneumatozoïde*; *cmv*: median ventral crest; *cp*: median cavity; *ed*, *ep*: distal and proximal ends of *pneumatozoïde*; *o*: aperture; *pg*: pigment spot; *ps*: pneumatosaccus; *pz*: *pneumatozoïde*; *vh*: hypocystic villi. From Bedot (1893), Pl. I, figs, 1 (**A**), 4 (**C**), 8 (**E**), 9 (**D**); and Bedot (1904), Pl. III, figs. 1 (**B**), 8 (**F**).

With regard to bathyphysid species Schneider (1898) was remarkably brief. To him they were all cystonect siphonophores and he placed them all in the genus *Pterophysa*. He separated off *P. conifera* from his other species on the basis that its gastrozooids were not borne on long peduncles, and its tentacles were simple, without tentilla.

However, he did not explain why he considered the gastrozooids as sessile. He also recognised *P. abyssorum*, with gastrozooids borne on long peduncles, but without tentacles, and suggested that *P. grandis* and *Bathyphysa grimaldii* were most probably junior synonyms it. With regard the so-called *pneumatozoïdes*, described by Bedot (1893), he correctly identified them as nothing more than young gastrozooids.

Unfortunately, Schneider's (1898) contention goaded Bedot (1904) into publishing a further paper on his *Bathyphysa grimaldii*. Most of this paper is taken up with detailed descriptions of the anatomy of the so-called *pneumatozoïdes*, which Bedot believed contained a specialised organ of unknown function. However, Bedot changed his mind with regard to two features of the *pneumatozoïdes*. Firstly, what he had previously thought was a short peduncle, he now interpreted as a short filament, said to be on the dorsal side, and that the *pneumatozoïde* was, thus, attached directly to the stem. Secondly, he decided that he was wrong to consider the endodermal cavity as having contained "air". He also changed his mind with regard to the presence of a peduncle on the mature gastrozooid, now regarding it as a tentacle such that the gastrozooid was attached directly to the stem. Attention was also draw to the fact that this tentacle was positioned on the gastrozooid in exactly the same position as the filament on the *pneumatozoïde*. But he was still quite adamant that the two structures were entirely different. Thus he took issue with Schneider stating (*ibid.* p. 22)[66]: "If the *pneumatozoïdes* were young gastrozooids, they should have smaller dimensions than the latter. However, this is not the case and I studied a great number of pneumatozooids whose length varied between 30 and 40 mm, which is the size of the largest gastrozooids. In addition - and this is the most important point - the pneumatozooids are never open at the distal end, while it is easy to distinguish the mouth of the gastrozooids even when they are very young". The question of size of a zooid appears to be similar to the question – "how long is a piece of string?", but he was entirely wrong with regard to his believe that young gastrozooids should always have a mouth opening, because it is now clear that the so-called *pneumatozoïdes* are indeed the developing gastrozooids, and the youngest ones have yet to develop a mouth opening. As for the strange organ that these zooids were supposed to contain, Lens & van Riemsdijk (1908, p. 107): "looked in vain for the apparatus ... We made microscopical sections of the base of siphons in different specimens but there was not the slightest indication of any such structure". However, photographs of *B. conifera* in a tank, taken by Rob Sherlock clearly show that a small white sphere usually is present at the distal end of the gastrovascular canal, just below the tapered tip of the young gastrozooid, which has a mauve tinge (see below). This may be what Bedot was referring to.

So, returning to Schneider's (1898) classification, the species *Bathyphysa grimaldii* would now appear to be more closely allied with *Pterophysa conifera*, as both had now been described with gastrozooids without, or at least only short, peduncles, but with simple tentacles, without tentilla. As Fewkes's (1886) specimen of *P. grandis* consisted of a denuded stem and pneumatophore, and some young detached gastrozooids with *ptera*, but without tentacles and, presumably, a peduncle, then it is impossible to categorise the species on this basis. This leaves *B. abyssorum* as the only species to have been described with gastrozooids borne on long peduncles, and possibly without tentacles. However, as discussed above, it is extremely likely that what have been interpreted as peduncles are more likely to be tentacles, and that a peduncle, if present, is likely to be quite short. The presence/absence of a peduncle seems, therefore, to be a complete red herring.

Mayer, Chun and Schneider

Mayer (1894, p. 239) considered that: "Dr. Fewkes [1879] gives a good description and a very poor sketch, which is apparently intended to represent *R. Eysenhardtii.* In our opinion it would be better to adopt the nomenclature of Haeckel, and give to this species the name of Cannophysa, as it is evidently very closely allied to, if not identical with, *Cannophysa Murrayana* from the Canary Islands". This appears to be a slightly arrogant on Mayer's part as a) Fewkes's paper predates Haeckel's monograph; b) Fewkes described and, admittedly poorly, illustrated the tentilla of *R. filiformis* not *R. eysenhardtii*; and c) Mayer should have synonymised *C. Murrayana* with *R. eysenhardtii*, and not the other way round. Mayer then goes on to give a description of specimens of what he calls *C. Eysenhardtii*,

66 Original quote: "Si les pneumatozoïdes étaient de jeunes gastrozoïdes, ils devraient avoir des dimensions inférieures à celles de ces derniers. Or, cela n'est pas le cas et j'ai étudié un grand nombre de pneumatozoïdes dont la longueur variait entre 30 et 40mm**,** ce qui est la dimension des plus gros gastrozoïdes. En outre - et c'est là le point le plus important – *les pneumatozooids n'ont jama s d' ou erture à leur extr m t d stale,* tandis que l'on distingue facilement la bouche des gastrozoïdes lors même qu'ils sont très jeunes."

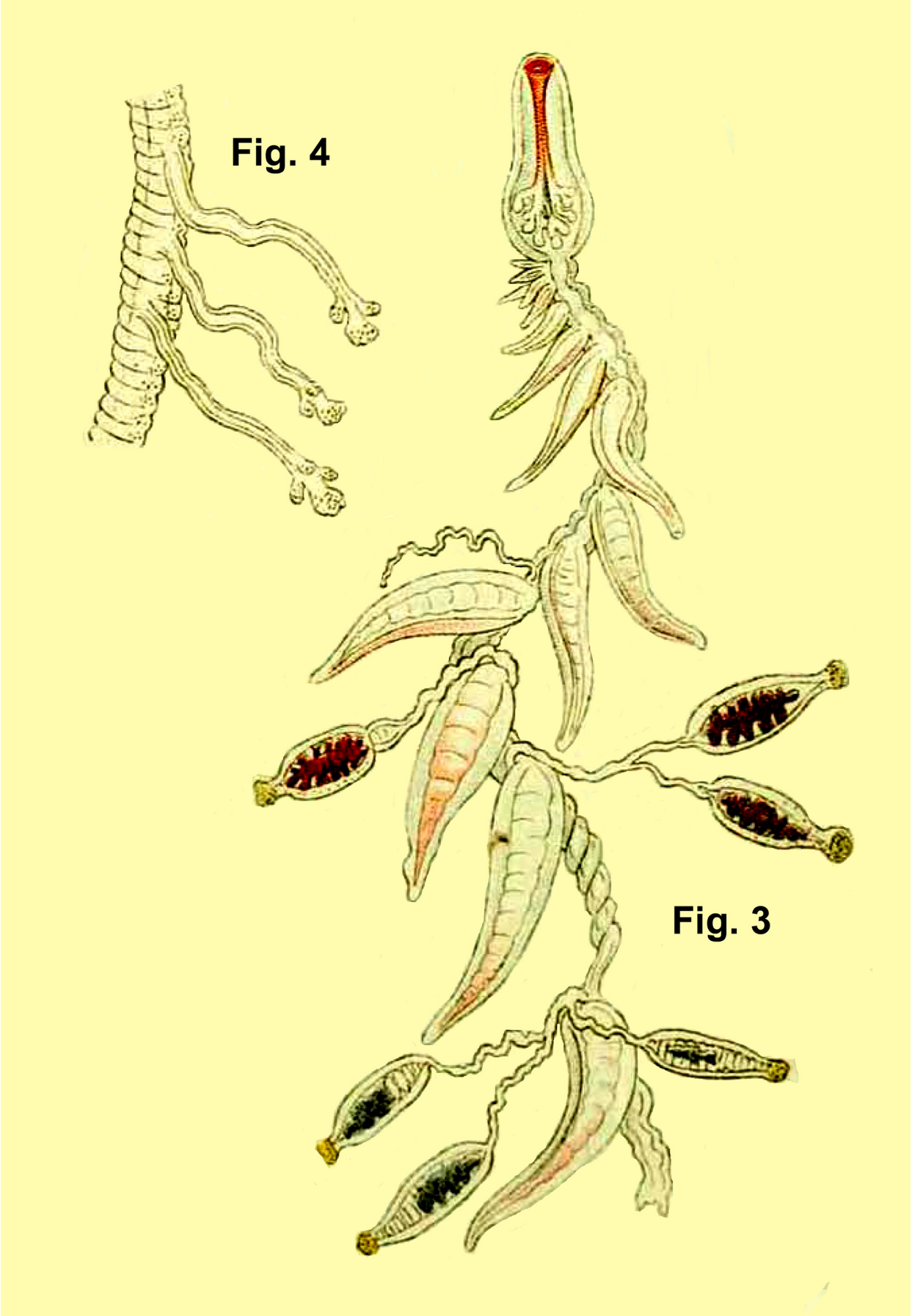

FIGURE 27. *Cannophysa filiformis* from Mayer, 1894 (Plate III, fig. 3), with detail of tentillum of *C. Eysenhardtii* (Plate III, fig. 4).

which contains virtually no characters of any worth, together with three poor illustrations. With regard to the tentilla all he said was (*ibid.* p. 240): "The secondary filaments are fine hair-like structures terminating in a bunch of nematocysts (see Plate III, Fig. 4)". However, that figure (see Figure 27) clearly shows that distally they are divided into three lobes, from which one would conclude that they are very young tentilla of the *tricornuate* type of *R. filiformis*. Thus, clearly Mayer appears not to know his *eysenhardtii* from his *filiformis*. Also included in his Plate III was a figure (see Figure 27) of what he referred to, in the legend, as *C. filiformis*, although Mayer made no reference whatsoever to it in the text. The specimen clearly is deformed as the stem is highly twisted, but it gives the impression that the tentacles bore extremely large tentilla of a type not previously described. One wonders, therefore, why Mayer gave it the specific name *filiformis*, presumably likening it to the well-known *filiformis* or perhaps, from the above, *eysenhardtii*. We will return to this figure shortly.

Chun (1897, p. 83)[67], for once did not agree with Haeckel, and considered, with regard to the family Rhizophysidae, that the two basic characters that Haeckel had used to subdivide the family, i.e. the positioning of the gonodendra and the structure of the tentilla, were untenable. Regarding the former he said: "A principle of classification, which applies to not only numerous genera, but also to two subfamilies, in my opinion should be based on structural features that in all cases allow a clear and unambiguous decision to be made." Chun believed that the positioning and number of the gonodendra was more related to the age of the specimen. With regard to the number of types of tentilla present he said (*ibid.*)[68]: "Whomever now attached generic value to the structure of the tentilla would have to split [specimens of] *R. filiformis*, dependant on their age, into no less than three genera, characterised by mono-, tri- and bimorphic tentilla … [thus] the structure of tentacles and stinging buttons should not be given too high a systematic value". Finally, he split his Order Rhizophysaliae into two sub-orders, the Rhizoidea, including the families Epibulidae and Rhizophysidae, and the Physaloidea, for the family Physalidae.

Among the *Plankton Expedition* samples Chun (1897) found only two *Rhizophysa* species, which he called *R. eysenhardtii* and *R. murrayana*. But he also listed all the siphonophore species previously found in the Atlantic Ocean and which apparently he considered to be valid. For the family Rhizophysidae be included the following species:

Rhizophysa Eysenhardtii Gegenbaur.
Rhizophysa (Cannophysa) Murrayana Haeckel.
Rhizophysa clavigera Chun (= *Cannophysa filiformis* Mayer).
Rhizophysa (Linophysa) conifera Studer.
Rhizophysa gracilis Fewkes.
Rhizophysa filiformis Forsskål.
Bathyphysa abyssorum Studer.
Bathyphysa Grimaldii Bedot.
Pterophysa grandis Fewkes.
Salacia polygastrica (= *S. uvaria* Fewkes?) Haeckel.

Although Chun (1897, p. 84)[69] recognised that there was a close similarity between the tentilla of *Rhizophysa eysenhardtii* and *R. murrayana*, he believed that there were some differences as he said, with regard to *R. murrayana*: "As I will describe them in more detail at another time, I only remark that in the case of the latter species, in the angle at the base of the weaker [side] branches are muscle fibres which run along the middle of the main branch to the base these branches." However, this description apparently never appeared in print and, as noted above, the structure referred to had already been illustrated by Fewkes (1879), and is now known to be characteristic of the mature tricornuate tentilla of *R. filiformis*.

We have already dealt with most of the species in the list above. However, Chun (1897) did not describe *Rhi-*

67 Original quote: "Ein Eintheilungsprincip, welches nicht nur zur Aufstellung zahlreicher Gattungen, sondern auch zweier Unterfamilien Verwerthung findet, sollte meines Erachtens an Strukturverhältnisse anknüpfen, welche in allen Fällen einen klaren und unzweideutigen Entscheid gestatten."

68 Original quote: "Wer nun der Gestaltung der Seitenfäden generischen Werth beilegt, müsste die *Rh. filiformis* je nach ihrem Alter in nicht weniger denn drei Genera zerspalten, welche durch monomorphe, trimorphe und bimorphe Seitenfäden charakterisirt wären … der Struktur von Tentakeln und Nesselknöpfen keinen allzu hohen systematischen Werth beizulegen."

69 Original quote: "Da ich dieselben an einer anderen Stelle noch eingehender schildern werde, so bemerke ich nur, dass ebenso wie bei der letzteren Art in dem Winkel zwischen dem Ansatz der schwächeren Seitenäste Muskelfasern entwickelt sind, welche längs des mittleren Hauptastes bis zur Basis der Seitenäste verstreichen."

zophysa clavigera (= *Cannophysa filiformis* Mayer), and one can only presume that he considered it to be a new species, distinct from *R. filiformis*. He had earlier rejected Mayer's placement of it within the genus *Cannophysa* as it was impossible to use Haeckel's key to identify that genus since no gonodendra were present. Bigelow (1911, p. 318) also provided a very reasonable explanation with regard to this species when he said: "Whether *R. clavigera* is really a distinct species can hardly be determined from Mayer's very confused account, or from his figure which was evidently drawn from a fragmentary specimen. My opinion is that it was probably *R. filiformis,* with siphons and tentacles twisted together". Thus the suppose tentilla are actually gastrozooids. Although I am not sure what Bigelow means by "very confused account" for, as mentioned above, no description of this species was actually given. However, like many of Mayer's new siphonophore species, this one is best ignored and, as Bigelow (1911) suggested, treated as a synonym of *R. filiformis*.

Of course, Schneider (1898, p. 164)[70] rejected Chun's classification of his order Rhizophysaliae when he said: "In my view, the relationships of all the relevant forms are so close that a division of the same family into 3 and even 2 Suborders (the whole group of Cystonects being considered only as a Suborder, as the Siphonophora as a whole was considered only as an Order) does not appear justified". However, with regard to the genus *Rhizophysa*, Schneider entirely agreed with Chun that care must be taken for specific identifications based on the structure of the tentilla but, based on this, he expressed his surprise, correctly in our opinion, that Chun (1897) had retained the species *R. murrayana* and *R. gracilis*. Nonetheless, Schneider's (1898) choice of species that he believed belonged to the genus *Rhizophysa* is itself rather strange. Firstly, he considered (*ibid.* p. 170)[71] that: "The type of this genus is generally considered to be Gegenbaur's 53 *R. filiformis* from Messina". He noted that Forsskål's (1776) illustration of *R. filiformis* (see Figure 3B) showed no side branches to the tentacles, but contemplated that they might have been lost, or simply overlooked.

However, Schneider (1898) then did just that for his second rhizophysid species, which was *Rhizophysa Mertensii* Brandt, 1835. He considered the tentacles of this species to bear simple tentilla, and thereby likened it to Gegenbaur's (1859) *R. eysenhardtii* and Haeckel's (1888b) *Nectophysa Wyvillei*. As Bigelow (1911, p. 318) pointed out: "Schneider ('98) used the name *R. mertensii* Brandt to replace *eysenhardtii* Gegenbaur, evidently supposing that Brandt's ('35, p. 33[233]) description of the tentilla as "Tentacula composita ramulis, i.e. tentaculis porpriis, simplicibus" meant that they were filiform. But Haeckel ('88b, p. 329) who examined Mertens' unpublished figures of this species expressly states that it "exhibits distinctly two different kinds of branched tentilla"". Thus Bigelow (*ibid.*) concluded that: "there seems to be only one course open, namely, to consider *mertensii* a synonym of *filiformis,* on the strength of its having two kinds of tentilla". In fact, what Bigelow quoted was Brandt's description of the genus *Epibulia*, while that for the species *E*. (*Macrosoma*) *Mertensii* itself, Brandt stated (*ibid.* p. 233): "*Corpus longissimum, pallidissime fuscescens, Vesica natatoria ovata corpori concolor. Tentacula composita plurima*, *alterna, corpori concolora. Proboscides suctoriae plures in trunco secundae, pallide roseae, apice in peltam dilatabiles*". In addition, Brandt's (*ibid.*) description of the species also stated: "*Corpus longissimum, pallidissime fuscescens*". So the long stem was said to be of the palest brown colour, while the gastrozooids were pale pink, thus indicating that Mertens' specimen could have been *R. eysenhardtii*. However, as we only have Brandt's description, without illustration, to go by it really is best to consider the species name *Mertensii* as a *nomen nudum*

The third species that Schneider (1898) included in the genus *Rhizophysa* was *R. uvaria* Fewkes, 1886. As noted above, this species, supposedly had polygastric "cormidia" and, thus, would belong in Haeckel's (1888b) genus *Salacia* - the sheer inventiveness of which we have already considered. As for the genus *Epibulia*, we have already dealt with the views of Schneider.

Lens and van Riemsdijk (1908)

This last point was discussed further by Lens & van Riemsdijk (1908), who reviewed all the descriptions of rhizophysid and bathyphysid species. They included two genera in the family Rhizophysidae, and with regard to *Rhizophysa* species, they said (*ibid*. 100): "So far as we can judge by the litterature [sic] ... we can only accept two species, *Rhizophysa filiformis* Forsk. 1775 and *Rhizophysa Eysenhardtii* Ggbr. 60 [59]. We cannot admit the validity of any

70 Original quote: "Meiner Auffassung nach sind die Verwandtschaftsbeziehungen aller hierher gehörigen Formen so enge, daß eine Auseinanderreißung derselben zu 3 Familien und gar 2 Unterordnungen (die ganze Gruppe der Cystonecten ist nur als Unterordnung zu betrachten, wie die Siphonophoren insgesammt nur als Ordnung) nicht berechtigt erscheint."

71 Original quote: "Als Typus dieser Art betrachtet man allgemein die *R. filiformis* Gegenbaur's 53 von Messina."

of the new genera which Haeckel has proposed (*Cannophysa*, *Linophysa*, *Aurophysa*, *Pneumophysa*, *Nectophysa*): their characteristics are based on differences too slight to permit us to look upon them as more than two species of the same genus″.

Lens & van Riemsdijk (1908, p. 100) stated: "Haeckel also often repeats that he will describe the specimens in a future work (see 88b *Pneumophysa* p. 328). His descriptions of *Aurophysa* and *Linophysa* are quite insufficient. *Cannophysa* and *Nectophysa* have been treated somewhat better, but we cannot find any difference from the original *Rhizophysa Eysenhardtii*, looking through the description of *Cannophysa Murrayana*, from *Rhizophysa filiformis* or comparing it with *Nectophysa Wyvillei*. Haeckel writes simply of the latter (88b p. 327) "Another closely allied species seems to be *Rhizophysa Eysenhardtii* described by Gegenbaur"". They then gave quite detailed descriptions of both *R. filiformis* and *R. eysenhardtii* (Figure 28) of which they had several specimens.

For the bathyphysid species, Lens & van Riemsdijk (1908) gave a detailed summary of what had been published to date, but they fell into the trap with regard to the presence/absence of a peduncle on the gastrozooids. With regard to *Bathyphysa abyssorum* they noted that in Studer's (1878a) Plate III figures 38-39 (see Figure 16B) the so-called peduncles to the gastrozooids appeared to be wound around the stem rather than connecting with it. Thus, they reached the preliminary conclusion that these filaments were more likely to be tentacles than peduncles. They attempted to resolve this point by looking at the original and still extant material but apparently, because of the large size of the specimen, they were only able to re-examine one of the original gastrozooids from the original specimen. Clearly, this was insufficient to resolve the point and so they ultimately decided against this option as they interpreted Studer's (see Figure 16A) illustration as clearly showing that the gastrozooids were attached to the stem by long peduncles. As has already been discussed, this conclusion is almost certainly wrong.

Thus, Lens and van Riemsdijk (1908) divided the known bathyphysid species among the genera *Pterophysa*, with sessile, and *Bathyphysa*, with pedunculate gastrozooids. They agreed with Schneider that *Rhizophysa conifera* and *P. grandis* were closely related, but maintained them as separate species. However, they never referred to the former species as *P. conifera* presumably because they considered that the gastrozooids were borne on short peduncles, while those on *P. grandis* were sessile. They reached the latter conclusion based on the examination of some additional material that Fewkes had subsequently identified as that species. This uncertainty as to the exact status of the species *conifera*, also applies to one of Lens & van Riemsdijk's new species, as is discussed below. However, they also moved Bedot's *B. grimaldii* into the genus *Pterophysa*, and considered that it was probably identical with *P. grandis*.

Lens & van Riemsdijk (1908) then gave an extensive re-description of *Pterophysa grandis* (see Figures 29, 30A) based on their own material. They could not find any hypocystic villi at the base of the pneumatophore, but stated that such might have been obscured by the opacity of the walls. However, they noted that the young gastrozooids did not possess tentacles, and that this structure did not begin to develop until the c. 60th gastrozooid from the anterior end of the siphosome. Gonodendra also were not present between the most anterior gastrozooids, but buds of them, apparently just anterior to a gastrozooid, began to appear well before the tentacle began to be developed on the gastrozooid. All the gastrozooids, at whatever degree of maturity, were attached directly to the stem.

A small part of the large specimen from *Siboga* St. 52, and the smaller specimens from Sts. 185 and 284 have been re-examined by the present author, thanks to the kindness of Elly Beglinger (Zoological Museum, University of Amsterdam). All of Lens and van Riemsdijk's specimens were initially fixed in formalin and later, perhaps after they had examined them, transferred into alcohol. The portion from the St. 52 specimen, although in poor condition, clearly came from toward the posterior end as it included many mature gastrozooids and a well-developed gonodendron. However, what was most striking was that many of the long, tubular gastrozooids were borne on short peduncles, up to 2.5 mm in length. The other two specimens were more contracted so that often the gastrozooids appeared to be attached directly to the stem, but evenso a short peduncle occasionally could be discerned. The only conclusion that could be reached was that the gastrozooids did possess a short peduncle, but that preservation may have resulted in it becoming severely contracted so as to give the appearance that it did not exist. With regard to the gonodendron, there were approximately forty side branches from the central gonostyle, each of which bore a terminal gonopalpon, a primordial asexual nectophore and about eight gonophores. The exact distribution of the gonophores with respect to the asexual nectophore could not be assessed accurately due to the poor state of preservation.

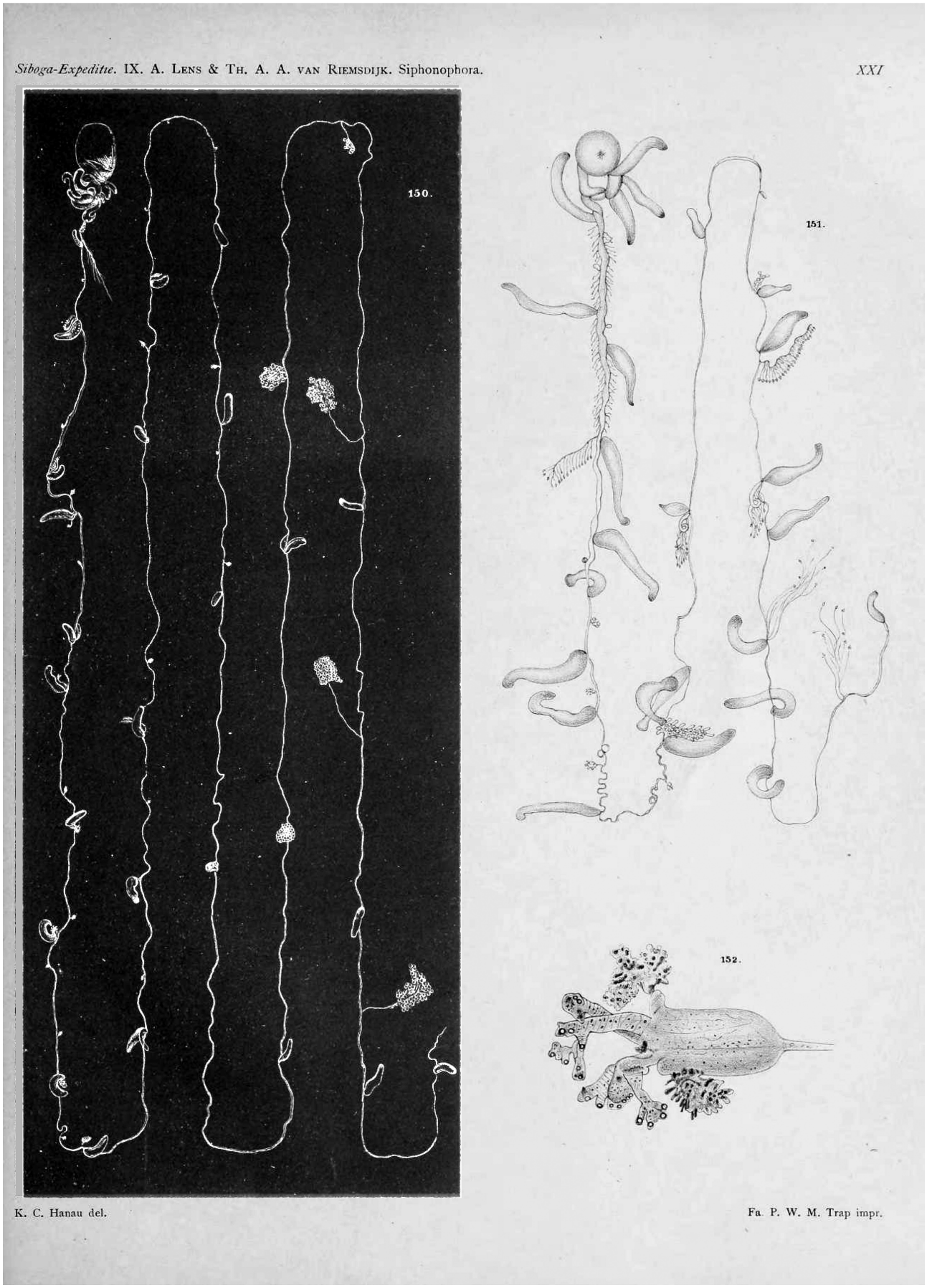

FIGURE 28. Specimens of *Rhizophysa eysenhardtii* (left) and *Rhizophysa filiformis* (right), with palmate tentillum of latter (bottom right). From Lens & van Riemsdijk (1908) Plate XXI.

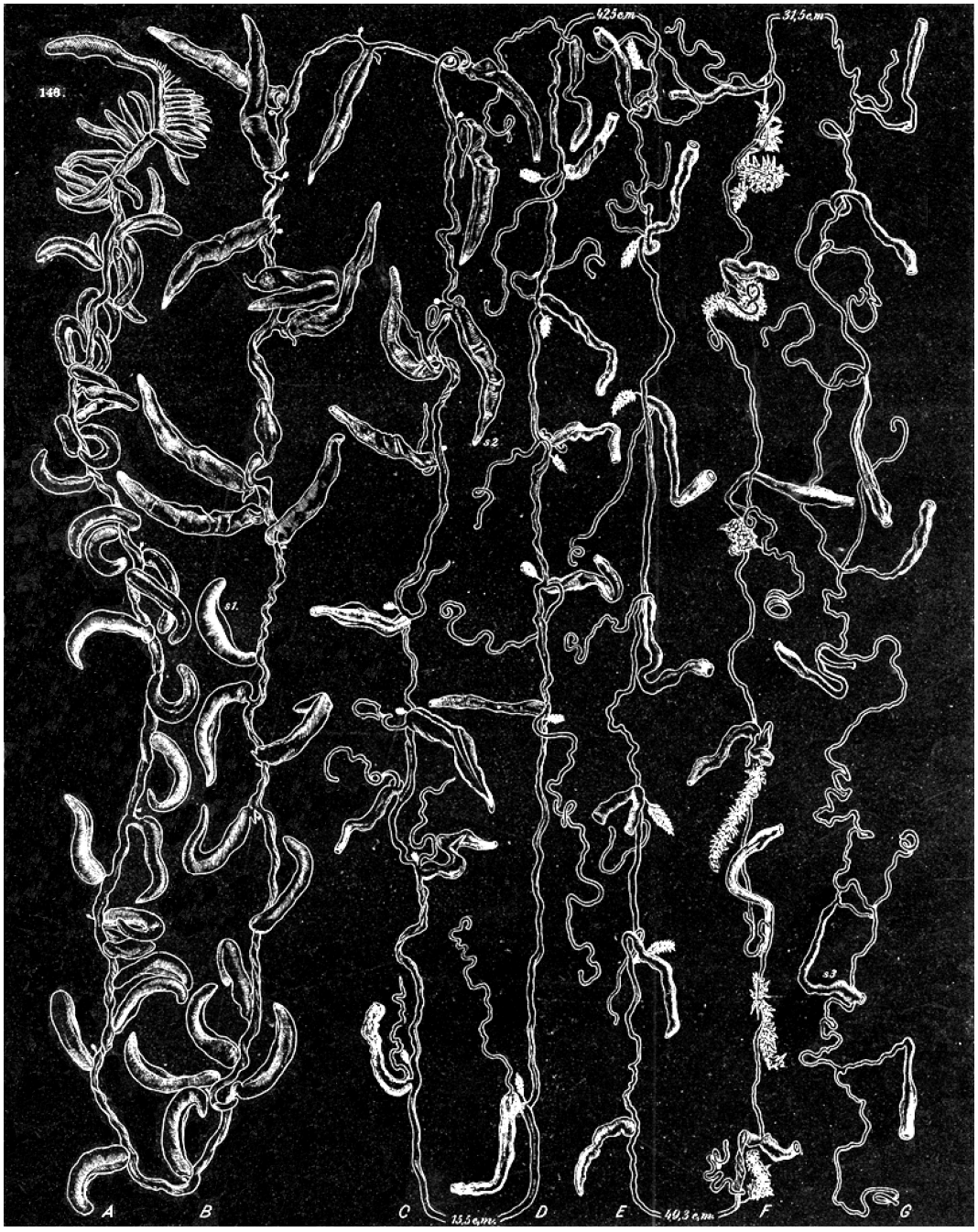

FIGURE 29. *Pterophysa grandis* Fewkes, 1886. From Lens & van Riemsdijk (1908, Pl. XIX., fig. 149).

Next, Lens & van Riemsdijk (1908) described their two "new" bathyphysid species. For *Pterophysa* (*Bathyphysa*) *Studeri* Lens & van Riemsdijk (see Figure 30 B) they described the presence of hypocystic villi at the base of an enormous (35 mm long) pneumatophore, and they devoted a large part of their description to their structure. Only three gastrozooids remained attached to the stem, situated at 28, 52 and 64 mm from the anterior end of the siphosome. They were all considered to be mature, but it is clear that all of them were young as they possessed obvious *ptera*, but no tentacles, and only one was said to have a mouth opening. Another three gastrozooids and: "a vast amount of tentacles, and stems and other appendages, impossible to determine" (*ibid.* p. 114) were also found with the specimen. The authors were unable to ascribe the species to either of the genera discussed above, because they believed that the gastrozooids were borne on short peduncles, and thereby, like *Rhizophysa (P.) conifera*, possessed a character that was intermediate between the two genera as they had earlier defined them. Although they noted that their specimen closely resembled Studer's *B. abyssorum*: "To call our specimen *Bathyphysa* we thought too daring" (*ibid.* p. 113). However, if one compares their illustration of one of the attached gastrozooids (see Figure 30 B, cen-

tre), with those of young gastrozooids of *P. grandis* (see Figure 30 A) it is clear that in both the *ptera* continue right to the base of the gastrozooid. Since Lens & van Riemsdijk considered the gastrozooids of the latter species to be attached directly to the stem, it is unclear why they considered those of *P*. (*B*.) *studeri* to have a short peduncle.

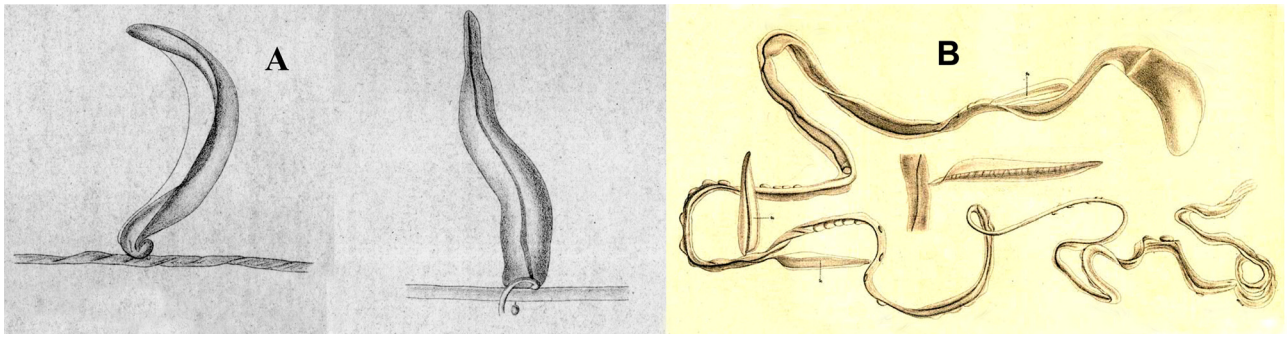

FIGURE 30. A. Two young gastrozooids of *Pterophysa grandis*. From Lens & van Riemsdijk (1908, Pl. XXIV, figs. 167 & 168); **B**. *Pterophysa* (*Bathyphysa*) *studeri*. *s*: siphon. From Lens & van Riemsdijk (1908), P. XXII, figs. 153-4.

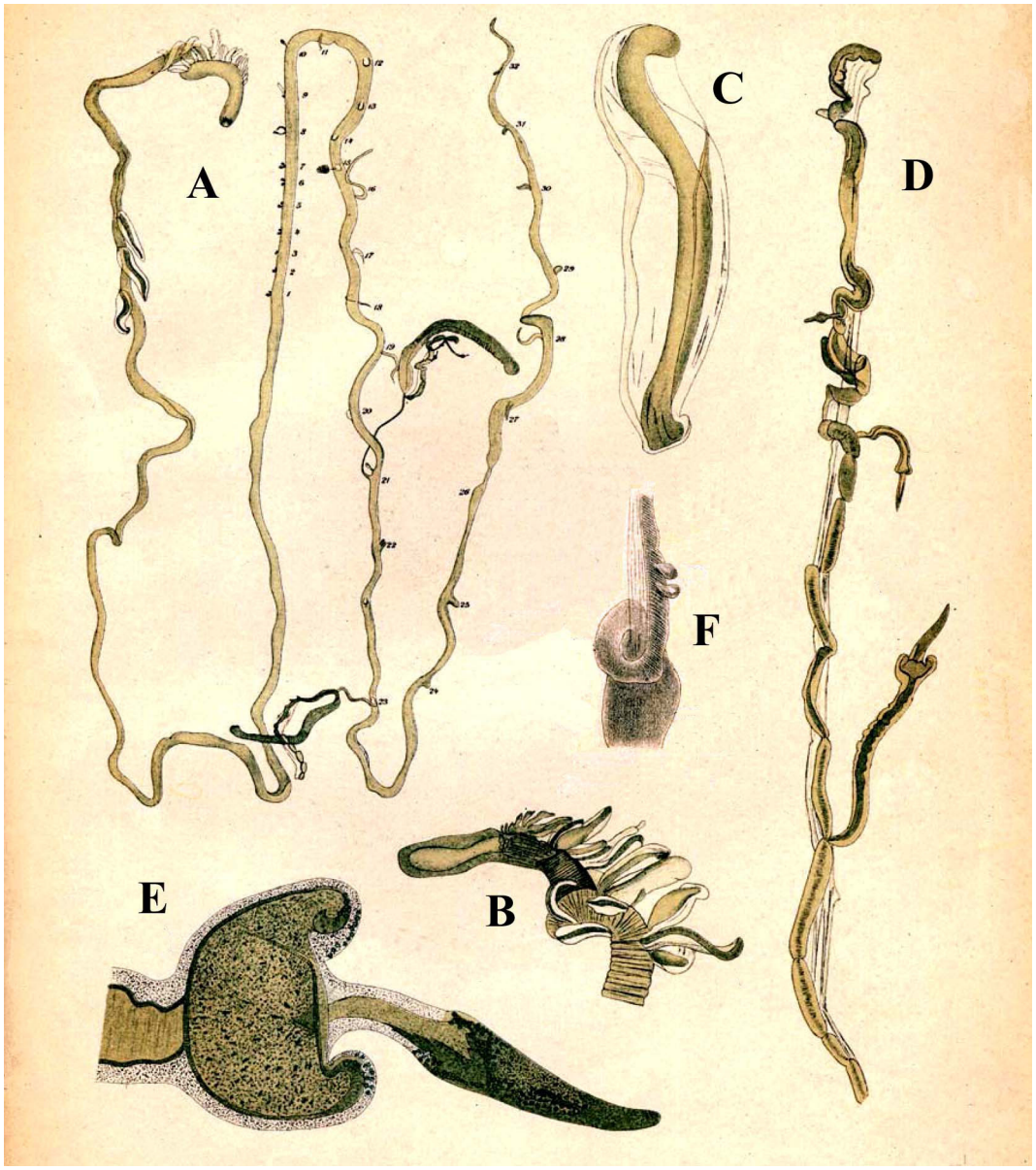

FIGURE 31. *Bathyphysa sibogae* Lens & van Riemsdijk, 1908. **A**: Entire specimen, with **B**: detail of pneumatophore and anterior part of siphosome; **C**: Young gastrozooid; **D**: Tentacle with tentilla; **E**: detail of distal end of tentillum; **F**: Proximal parts of gastrozooid and tentacle, with buds of tentilla. From Lens & van Riemsdijk (1908), Pl. XXIII, ex. fig. 165, inc. fig. 173 from Pl. XXIV.

What remains of Lens & van Riemsdijk's material of *Pterophysa (Bathyphysa) studeri* from *Siboga* St. 126 has been re-examined by the present author, but it consists of only a few pieces of denuded siphosomal stem, some of which are flattened and ribbon-like, as noted by Lens & van Riemsdijk. Thus, we can only rely on their description for further consideration of this species.

Finally, Lens & van Riemsdijk (1908) described *Bathyphysa sibogae* Lens & van Riemsdijk, based on two specimens that bore mature gastrozooids with distinct peduncles (see Figure 31). Small hypocystic villi were present around the base of the pneumatophore. The young gastrozooids, at the anterior end of the siphosome, clearly bore *ptera* (Figure 30A) and were attached directly to the siphosomal stem. The shape of these gastrozooids was said to; "resemble more or less a foliaceous bract of *Physonecta*" (*ibid.* p. 115). The first bud of a gonodendron was found at some distance from the budding zone. Most of the siphosomal stem was denuded of gastrozooids, but the authors found one mature one that was borne on a long peduncle, with a small gonodendron attached just anterior to it. From the base of the gastrozooid arose an annulated tentacle with a tentillum attached at each internode. The tentillum had a very distinctive shape (see Figure 31 D, E).

In summary, Lens & van Riemsdijk (1908) considered that two bathyphysid genera should be distinguished: *Bathyphysa* characterised by the mature gastrozooids being borne on long peduncles (*B. abyssorum* and *B. sibogae*); and *Pterophysa* with "sessile" gastrozooids attached directly to the siphosomal stem (*P. grandis* and *P. grimaldii*). On this basis Lens & van Riemsdijk were unable to place two other species, Studer's *Rhizophysa conifera* and their own *Pterophysa* (*Bathyphysa*) *studeri*, into either genus as they believed that for these species the gastrozooids were borne on short peduncles. Nonetheless, as noted above, some of the gastrozooids on Lens & van Riemsdijk's specimens of *P. grandis* have been found to have short peduncles, while the supposed peduncles to the young gastrozooids on their *P. (B.) studeri* are considered to have been imagined, since the *ptera* stretched down to the very base of the gastrozooid, although it was still uncertain as to whether the mature gastrozooids of this species were borne on peduncles. From this it would seem that there is very little, if anything, that separates the species *R. conifera*, *P. grandis*, *P. grimaldii* or *P. (B.) studeri*.

The Last 110+ Years

We owe a debt of gratitude to Bigelow (1911), in his Monograph on the Siphonophorae, for his attempts to sort out the disastrous state of the taxonomy of this group in the aftermath of Haeckel. Unfortunately, he was not always successful and, indeed, introduced further confusion in the case of certain genera, such as the physonect *Athorybia*. We have already discussed his thoughts regarding species of *Physalia*. For the rhizophysids and bathyphysids, Bigelow (1911) largely followed the views of Lens & van Riemsdijk (1908) and others. For the former, the only genus he recognised was *Rhizophysa* and he included in it just *R. filiformis* and *R. eysenhardtii*. For the latter, he retained both the genera *Bathyphysa* and *Pterophysa*. He concluded *(ibid*. p. 321): "In *Pterophysa* there are *P.* (*Rhizophysa*) *conifera* Studer, *P.* (*Bathyphysa*) *grimaldi* Bedot, and *P. grandis* Fewkes. These three are so closely allied that I doubt whether they can be distinguished". However, he did not include the species *studeri* in this category, noting only that Lens & van Riemsdijk were unable definitively to place it in either genus. Within the genus *Bathyphysa* Bigelow retained the two species, *B. abyssorum* and *B. sibogae*.

A huge monograph concerning the siphonophores caught by the *Gauss* during the Deutsche Südpolar-Expedition 1901-1903 was eventually published by Moser (1925). Within the collections there were a few fragments of rhizophysids, including what Moser considered to be a larval form (see Figure 32, 1), consisting of a relatively small pneumatophore, 5 mm in length, and a very short fragment of the siphosome to which were attached some gastrozooids, one of which was considered to be at the terminal end. Moser noted the presence of hypocystic villi and also claimed that an apical pore was absent; speculating that it might appear later in development. Whether this really is a post-larval form of a *Rhizophysa* species or just the extreme anterior end of a larger specimen remains uncertain; but we need not considered it any further as it is totally unrecognisable.

Moser (1925) also found fragments of two rhizophysid specimens that she considered had sufficient characters to warrant a specific designation, provisionally in the genus *Rhizophysa*. The first of these she named *R.* (?) *tricornuta* Moser (see Figure 32, 2, 2a) that was collected in the vicinity of the Cape Verde Islands. There is very little detail in the general description of this species, and it is difficult reconcile Moser's fig. 2 (see Figure 32, 2) with a pneumatophore, as she described it. The main portion is clearly a gastrozooid, but it is uncertain as to what the

attached part might be. Apart from the detail regarding the tentilla, the only other character that Moser mentions is that the gastrozooids were borne on long peduncles, in contrast to the arrangement for *R. filiformis*. However, it seem, likely, as was the case for *Cannophysa filiformis* described by Mayer (1894) that the so-called peduncles were actually the tentacles of the detached gastrozooids that have become entangled around the stem. Moser spent much time comparing the structure of the tentilla, firstly with the "birds head" like ones described by Gegenbaur (see above) and then the tentilla of *Athorybia*; noting that the central, terminal ampulla was devoid of nematocysts. However, she decided that in both cases there sufficient differences to distinguish her species. She stated that she would describe the tentilla in more detail in a later publication, but this never appeared. So, given the lack of detail, its seems best to consider this species as another *nomen nudum*.

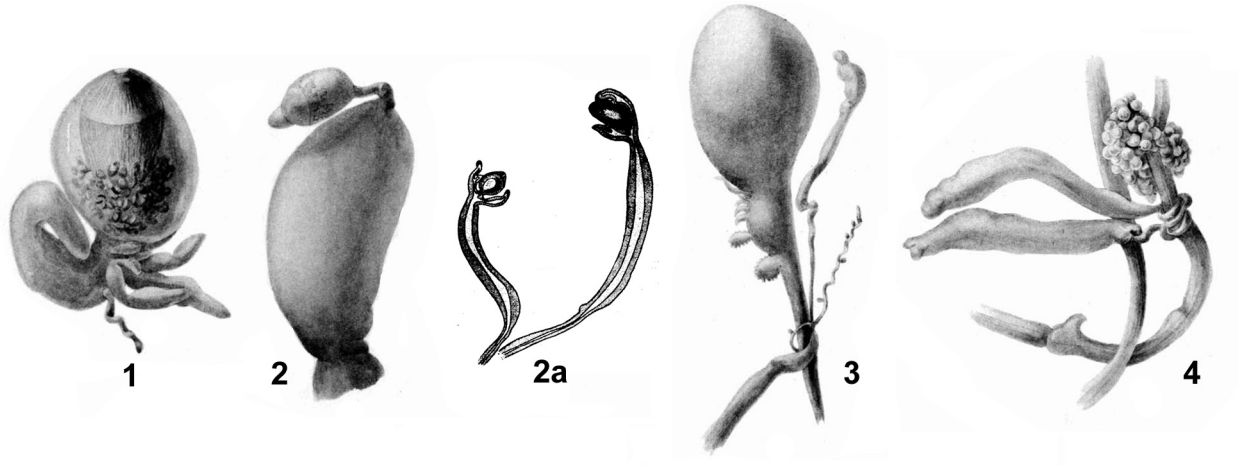

FIGURE 32. Moser (1925) Plate XXXIII (partim). 1. "Larval Rhizoidarum"; 2. Pneumatophore of *Rhizophysa* (?) *tricornuta* n. sp.; 2a from Textfig. 59 showing 2 tentilla; 3–4. *Rhizophysa* (?) *megalocystis* n. sp.: 3. showing the anterior end of the specimen, and 4. a "cormidium" with gonodendron, gastrozooid and (?) palpon.

The other species, of which Moser (1925) had three specimens, she named *Rhizophysa* (?) *megalocystis* Moser (see Figure 32, 3–4). The pneumatophore was relatively large, up to 7–8 mm in diameter, and had an apical pore, but no mention was made of hypocystic villi. Immediately below the pneumatophore there were five buds, increasing in size posteriorly, arranged in a single sequence. Moser considered that the siphosomal stem divided, which is extremely unlikely (see the discussion below regarding *Bathyphysa japonica* Kawamura). The remainder of her description is very confusing and lacking in detail, although it does appear that Moser considered that, as well as gastrozooids with their tentacles, and gonodendra, there was the possibility that palpons were present. A close examination of Moser's Plate XXXIII (Figure 32, figs. 3-4) appears to show that she fell into the same trap as Studer (1878) in that the long narrow peduncles of the gastrozooids actually might be their tentacles that have become wrapped around the siphosomal stem and which might explain the division in the stem that she described. Nonetheless, there is so little detail that, again, it is felt that this species must be considered as a *nomen nudum*.

The only subsequent authors that have commented on these two species of Moser appear to be Bigelow & Sears (1937, pp. 64–65). They remarked that: "*R. tricornuta* like *R. filiformis,* has "vogelkopfartigen Tentakelknopfen" [bird-headed tentacle buttons] (Moser, 1925, p. 445). According to Moser, the terminal median beak of her new species corresponded more closely to the terminal ampulla in the young tentillum of *Anthophysa* (Bigelow, 1911, P1. 20, Fig. 8), or of Agalmidae before the cnidoband has become spirally coiled, than to the terminal median structure in the beak-like tentilla of *R. filiformis.* But comparison of Haeckel's (1888b, P1. 24, Fig. 9) figure of the trifid tentillum of *R. filiformis,* and of the 'Thor' examples of the latter, with Moser's (1925, Textfig. 59) illustration of tentilla of *tricornuta* fails to show any essential difference: the terminal structure is, in fact, only slightly more dilated in Moser's figure than it is shown by Haeckel, or than in the 'Thor' example ... And the lateral filaments show the same indication of incipient subdivision. We are, therefore, inclined to refer *tricornuta* to the synonymy of *filiformis.*

"Moser's *R. megalocystis* is set apart by the possession of palpons ("Tentakeltaster", Moser, 1925, p. 447) bearing giant nematocyst capsules. As no corresponding structures have ever been described for *Rhizophysa,* it cannot be referred to that genus, but may belong to the genus *Salacia,* in which the polygastric cormidia are described by Haeckel (1888b, p. 332) as bearing thin spindle shaped tubes, "perhaps palpons which remain permanently mouthless", as well as siphons". The present author does not agree with this conclusion, as noted above.

From henceforth the number of *Rhizophysa* species was stabilised at two, *R. filiformis* and *R. eysenhardtii*, but Leloup (1936) gave an extensive review of the genus *Bathyphysa* and the six species that Bigelow (1911) had included in his sub-family Bathyphysinae. Unfortunately, Leloup started badly by resurrecting Bedot's (1893, 1904) contention regarding the presence of *pneumatozoïdes*. Leloup agreed with Bedot (1904) that the term *pneumatozoïde* was inappropriate, as the zooids had no hydrostatic function, but still considered that they were not the first stages of the development of the gastrozooids proper, but had a totally different function. He reached this conclusion because he contended that no intermediary stages between the *pneumatozoïdes* and full grown gastrozooids had been found. We now know (see Biggs & Harbison, 1976) that the young gastrozooids, with *ptera*, but without tentacles, do gradually transform into the mature gastrozooid, with a well tentacle, but with the *ptera* reduced or totally resorbed. Fortunately, however, this erroneous assumption did not greatly affect the remainder of Leloup's discussion.

For Studer's *Rhizophysa conifera* Leloup (1936) believed that as the gastrozooids matured they came to be borne on small peduncles, and possessed a tentacle without tentilla. He likened the apparent disappearance of the *ptera* on these mature gastrozooids to that which Lens & van Riemsdijk (1908) had described for the gastrozooids of *Pterophysa grandis*. With regard to Studer's other species, *Bathyphysa abyssorum*, Leloup was able to examine numerous detached gastrozooids from the original specimen. These led him to conclude that the filaments that appeared to attach the gastrozooids to the stem were actually tentacles that had become wrapped around the latter, as Lens & van Riemsdijk had initially suggested. He was able to discern the scar left from where the gastrozooid had been attached to the stem, although he described this as lying at the distal end of the gastrozooid. Leloup, therefore, concluded that the gastrozooids were sessile, being attached directly to the stem and bearing a simple tentacle, without tentilla. Unfortunately the present author has been unable to ascertain whether Studer's specimens are still in existence.

For *Pterophysa grandis* Leloup (1936) noted that, from Lens & van Riemsdijk's (1908) redescription, all the gastrozooids were attached directly to the stem and bore simple tentacles, without tentilla. For both *Bathyphysa grimaldi* and *P.* (*B.*) *studeri* Leloup was able to examine some of the original material. Although he considered that the presence of the special organ that Bedot (1904) had described at the distal end of the *pneumatozoïdes* set these structures apart, he considered that the mature gastrozooids in both species were both attached in the same way, presumably directly to the stem or perhaps on a small bud-like excrescence. Finally he was able to re-examine the material of *B. sibogae* and concluded that Lens & van Riemsdijk were wrong to describe the gastrozooids as being borne on long peduncles, having found numerous loose gastrozooids, bearing a tentacle with tentilla, but without any sign of a peduncle. Thus, he concluded that for all species the gastrozooid was attached directly to the stem and that Lens and van Riemsdijk's (1908) division of the bathyphysid species into two genera was not justified. He, therefore, retained the older generic name, *Bathyphysa* and, based only on the presence or absence of tentilla on the tentacles, he recognised just two species, namely *B. conifera*, with simple tentacles, and *B. sibogae*, with tentacles bearing tentilla.

Although most recent authors, with the notable exceptions of Stepanjants (1967) and Carré & Carré (1995), concurred with this conclusion, despite Leloup's (1936) justifications for his conclusion that the gastrozooids of *Bathyphysa sibogae* were sessile being untenable.. This is because Biggs & Harbison (1976) have largely confirmed Lens & van Riemsdijk's (1908) original description of *B. sibogae* and have shown that the mature gastrozooids are indeed borne on long peduncles, each bearing a tentacle with distinctive tentilla. With regard to *B. conifera*, including its four junior synonyms, it has been suggested that the mature gastrozooids may be borne on a short peduncles that, on preservation, strongly contract so as to give the appearance of their total absence. However, examination of numerous photographs of a living specimen of *B. conifera* taken by Rob Sherwood, who has kindly given the present author access to them, seem to indicate that there is no peduncle to the gastrozooid.

Subsequent to Leloup's (1936) review another bathyphysid species, *Bathyphysa japonica* Kawamura 1947, was described. The original description appeared in an obscure Japanese publications (see Pagès, 2002) but, fortunately, Kawamura (1954) published a further description in English. He took no account of Leloup's (1936) review as he recognised six *Bathyphysa* species; but these are not the same as the six discussed by Leloup. He omitted Studer's *B*. (*Rhizophysa*) *conifera* and Lens & van Riemsdijk's *Pterophysa* (*B*.) *studeri* and replaced them with Haeckel's (1888b) *B. gigantae* [sic] and *B.* sp. from Bigelow (1911), both of which are *nomina nuda*. As well as the description of the new species, Kawamura also gave details on a further specimen of *B. grimaldii*. Unfortunately, both descriptions are short in detail, and Kawamura described both species as having branched stems (see Figure 33), which is, of course, theoretically impossible.

For *Bathyphysa grimaldii* Kawamura (1954) noted the absence of hypocystic villi at the base of the pneumatophore. He considered this to be a character distinguishing the genera *Bathyphysa* and *Rhizophysa*, but it is not in accord with previous descriptions and, indeed, is incorrect. He also described the presence of many "pneumatosiphons" or "pneumatozoides", without specifically mentioning the presence of *ptera*, thereby adopting the erroneous terminology of Bedot (1893), but perhaps acknowledging that they were in fact siphons/gastrozooids, which Bedot did not. Like Bedot (1893), Kawamura (*ibid.* p. 121) described these "bladder-like siphons" as having a short peduncle: "while the kidney-shaped gastric portion is converted into an airbladder-like structure, embracing a gas bubble in their interior". However, as pointed out above, in his later paper Bedot (1904) corrected both of these interpretations, stating that the peduncle was actually a tentacle-like structure attached at the base of the sessile *pneumatozoïde*, and that the structure did not enclose an air bubble and, thus, was not a flotation device. Although Kawamura referred to Bedot's paper in his references, he did not appear to have cited it anywhere in the text.

Kawamura (1954) also described "hook-shaped siphons", presumably more mature ones, which he interpreted as being borne on long, slender peduncles. He also noted the presence on these of thin lateral membranes, i.e. *ptera*. Although Bedot (1904) observed greatly reduced *ptera* on his mature gastrozooids of *Bathyphysa grimaldii* he was unable to observe their mode of attachment, although he considered it most likely that they were attached directly to the stem. In addition, Kawamura mentioned two or three "zooids" that he believed were pairs of "pneumatosiphons" fused together. Finally, he illustrated a gonodendron apparently attached to a "pneumatosiphon". There are thus many peculiarities in Kawamura's description of *B. grimaldii*, not least the presence of a branching stem, many of which are not in accord with the redescription of the species by Bedot (1904). Unfortunately, according to Pagès (2002), the whereabouts of the specimen cannot be traced. However, the present author considers that Kawamura's interpretations of various structures on this specimen were probably grossly inaccurate. The apparent branching of the stem must be a preservation artefact (see below) where various parts of the stem have become entangled with each other. The apparent fusion of the young gastrozooids (pneumatosiphons), again is a preservation artefact, while with regard to the attachment of the mature gastrozooids it can also been seen from Kawamura's figures that if one interprets the singular structure at the proximal end of the gastrozooid as a peduncle, then a tentacle would be absent. As with many prior descriptions, it is most likely that what has been interpreted as a peduncle is in actuality a tentacle that has become wrapped around the stem. Thus there seems no reason not to consider Kawamura's specimen as belonging to *B. conifera*.

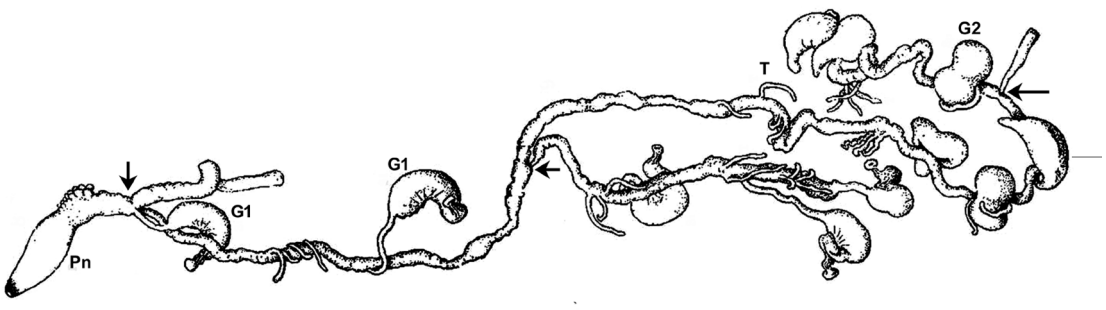

FIGURE 33. *Bathyphysa. japonica* Kawamura, 1943. (Figs 8-9.) G1: gastrozooid; G2: Pneumatosiphon; Pn – pneumatophore. The arrows indicate the supposed branching of the stem. Adapted from Kawamura (1954), Pl. VII, figs 8 & 9.

For the other species, *Bathyphysa japonica*, Kawamura again believed that its stem was branched (Figure 33), and he made no mention of the presence of hypocystic villi at the base of the pneumatophore. Otherwise he gave little information of any descriptive value whatsoever, merely stating that "hook-shaped" and "bladder-shaped" gastrozooids, each with simple a tentacle, were present, as well as two fused siphons. However, it can be seen from his figure that the siphons closest to the pneumatophore are gastrozooids, not pneumatosiphons. Kawamura made no mention of the presence of *ptera* or the mode of attachment of the gastrozooid to the stem, and he distinguished his specimen from other *Bathyphysa* species on the basis of the smaller size and shape of the siphons, and the form of the pneumatophore. He then came to some strange generalised conclusions, which need not be considered here.

Totton (1965) agreed with Leloup (1936) that there were only two valid species, *Bathyphysa conifera* and *B. sibogae*, but he included Kawamura's *B. japonica* as a *species inquirenda* because of the apparent presence of stem branches. Referring to both of Kawamura's *Bathyphysa* descriptions Totton said (*ibid.* p, 43): "My tentative

interpretation is that these branches are gonodendra. The fact that they bear gastrozooids may perhaps be explained in the following way: Physonect gonodendra develop by successive budding of palpons from the bases of their predecessors. These palpons are reduced gastrozooids. In *Bathyphysa* gonodendra appear to develop from unreduced gastrozonoids [sic], though there is a terminal gonopalpon on the ultimate branchlets".

Fortunately, the specimen of *Bathyphysa japonica* is still extant and was re-examined by Pagès (2002). Although Pagès did not mention whether hypocystic villi were present at the base of the pneumatophore, he was able to clearly show that the so-called branching of the stem was an artefact caused by the detachment of the posterior part of the stem, and its subsequent entanglement with the anterior part. Thus the stem part illustrated by Kawamura (see Figure 33) between the most anterior and the next branching (arrowed) was actually two parts of the stem ravelled around each other. For the gastrozooids Pagès noted that the youngest ones, which included Kawamura's fused siphons, bore *ptera* and were attached directly to the stem, but he made no mention of *ptera* on the older gastrozooids. Although the tentacles appeared simple, without tentilla, Pagès was uncertain as to whether this could be a preservation artefact, in that tentilla had been lost. This argument could, of course, be applied to all previous descriptions of *B. conifera*. In addition, as no mature gastrozooids actually were attached to the stem, he was uncertain as to whether they were borne on a peduncle or not, noting that although it was known that *B. sibogae* had mature gastrozooids borne on long peduncles the young gastrozooids were sessile. However, he erroneously stated that Lens & van Riemsdijk (1908), with regard to *B. grandis*, considered that peduncles were present on all gastrozooids although, as noted above, Lens & van Riemsdijk statement that the gastrozooids of this species were all sessile itself is incorrect.

Although Pagès (2002) was unsure as to whether Kawamura's (1954) of *Bathyphysa japonica* could, with certainty, be associated with either *B. conifera* or *B. sibogae*, the information that he provided was quite sufficient enough to show that there were no specific characters by which one could continue to consider *B. japonica* as a valid species. For my part, it seems that there is every reason to consider the species as a junior synonym of *B. conifera*, based on the general construction of the preserved young gastrozooids, the absence of any tentilla on the tentacles (as even if they are lost some remnant of their attachment often remains), and the probability that the mature gastrozooids were attached to the stem by, at most, short peduncles.

Thus the ultimate conclusion is that of the seven species, excluding Haeckel's *Bathyphysa gigantea* as it was never described, that have previously been considered for inclusion in the genus *Bathyphysa*, only two are valid, namely *conifera* and *sibogae*. The two species are, if the material is good enough, easily distinguished by the fact that the mature gastrozooids of *B. sibogae* are borne on long peduncles and bear tentacles with tentilla, while in *B. conifera* the gastrozooids have, at most, short attachment peduncles and their tentacles do not bear tentilla. In both species hypocystic villi are present at the base of the pneumatophore, although Totton (1965, p. 42) mistakenly said, in his diagnosis of the genus, that they were absent.

CONCLUSIONS

We have seen that the mayhem created by Haeckel (1888a, b) was gradually sorted out by subsequent authors. The Table below shows a list of the cystonect species that the major reviewers of the 20th Century considered as valid or questionable. We have omitted Moser (1925) as she did not consider the sub-order in any detail, only describing some rather dubious species, as noted above. However, Stepanjants (1967) is included although she only listed what species she considered valid or dubious, but did not consider any cystonect species in the systematic section of her thesis. Also Daniel (1974, 1985), largely followed Totton (1965). Thus Bigelow (1911) was the last to consider that there was more than one species of the Portuguese Man O'War and, despite recent efforts to try to re-establish other species, or indeed establish new ones, there appears to be no sound reason to believe that such is the case. Indeed, to sort out the differences between the c. 50 junior synonyms[72] that have been used to described a *Physalia physalis*, and still be able to establish a new one, would seem miraculous.

While the number of species within the genus *Rhizophysa* has remained stable at two, that for the genus *Bathyphysa* has varied considerably, although no other author has ever included either of Moser's (1925) species. As Stepanjants (1967) did not give any details about cystonect species, it is unclear why she retained so many *Bathyphysa* species, but it would appear that the vast majority of her thesis was written without any knowledge of Totton (1965), for although Totton's monograph appears in her bibliography, there are no references to it in the text. Carré & Carré

72 A list of synonyms for all five of the currently recognised cystonect species is given in the Appendix.

(1995) also gave no reasons as to why they retained four species in the genus *Bathyphysa*, but the supposed re-description of *Epibulia ritteriana* by Alvariño (1972) led them to include that species, as well as *E. chamissonis*.

TABLE. Species of Cystonectae recognised by the main 20th Century reviewers.

Cystonectae	Bigelow (1911)	Totton (1965)	Stepanjants (1967)	Daniel (1974)	Carré & Carré (1995)	Pugh herein
Family Physaliidae						
Physalia physalis (Linné, 1758)	✓	✓	✓	✓	✓	✓
P. utriculus (La Martinière, 1787)	✓					
Family Rhizophysidae						
Sub-family Bathyphysinae						
Bathyphysa abyssorum Studer, 1878	✓		✓		✓	
B. japonica Kawamura 1943		?		?	✓	
B. sibogae Lens & van Riemsdijk, 1908	✓	✓	✓	✓	✓	✓
B. conifera (Studer, 1878)	✓[74,75]	✓	**?**[76]	✓	✓	✓
Pterophysa grandis Fewkes, 1886	✓[74]		✓			
P. (B.) grimaldi Bedot, 1893	✓[74]		✓			
P. (B.) studeri L.& v R., 1908	✓		✓			
Sub-family Rhizophysinae						
Rhizophysa filiformis (Forsskål, 1775)	✓	✓	✓	✓	✓	✓
R. eysenhardtii Gegenbaur, 1859	✓	✓	✓	✓	✓	✓
Salacia uvaria (Fewkes, 1886)	✓		✓[77]			
S. (Salacella) polygastrica Haeckel, 1888a				?		
Sub-family Epibuliinae						
Epibulia chamissonis Eysenhardt, 1821	✓	**?**	**?**	**?**	✓	
E. erythrophysa Brandt, 1835	✓		?			
E. ritteriana Haeckel, 1888	✓	?	✓	?	✓	

74 Bigelow (1911b) doubted that these three species could be distinguished.
75 As *Pterophysa (Rhizophysa) conifera*.
76 As *Pterophysa conifera*.
77 As *Salacella uvaria*.

Haeckel's fame, whether justified or not, has inspired a number of books about him. However, the taxonomy of siphonophores by these biographers is usually, and rightly, given short shrift, because it was a complete and utter disaster, the repercussions of which are still reverberating around well over a century later. Richards (2008), in his panegyric of Haeckel, for instance, devoted just 8 pages, out of 551, to Haeckel's siphonophores, and the vast majority of this was concerned with his earlier, embryological work (Haeckel, 1869), which Richards (*ibid*., p.163) said: "yielded a magificent monograph ... that won a gold medal from the Utrecht Society of Arts and Sciences". Unfortunately, many of Haeckel's observations were extremely inaccurate, as he believed that when the gastrovascular canal was formed it ran from the mouth of the protozoid into the pneumatophore. This, of course, is an imposibility since the lining of the gastrovascular canal is endoderm, while that of the pneumatophore is ectoderm.

With regard to the *Challenger* Monograph (1888b), Richards (2008, p. 188) devoted it just nine lines and noted: "that his analysis of some 240 species confirmed that his earlier conjecture concerning the medusoid origin of the siphonophores. Today this theory has been extended to encompass all of the Cnidarians – namely, that a free-floating medusoid form constitutes the primitive pattern of the phylum [e.g. Brusca & Brusca, 1990]". This in astonishing statement and completely untrue for we have already noted how Claus (1889a, b) comprehensively debunked the medusome theory and there is not a shred of evidence to support it so, as Professor Casey Dunn (personal communication) remarked, it cannot even be used as a null hypothesis.

In actuality, Brusca & Brusca (1990) only referred to the medusa theory, the more basic theory from which Haeckel's derived his medusome theory. For this theory they suggest that the egg develops into a planula, then an actinula and a sexual medusa as seen in certain hydrozoanns, but certainly not siphonophores. With regard to the opposite, polyp theory, Brusca & Brusca (1990, p. 255) said: "Some zoologist hold the polyp to to be the original cnidarian body form; they view the medusa as a derived disperstal stage that could have evolved independently among the hydrozoans and scyphozoans. We view this idea as an unneccessary complicated hypothesis with little supporting evidence". A lot of water has passed under the bridge since 1990 and recently Zapata *et al*., 2015 have shown that it is now quite clear that the medusa is derived within cnidaria, not the ancestral state. This is because there is strong support for Anthozoa as sister to Medusozoa. Since Anthozoa entirely lacks medusae, it seems that the medusa arose within Cnidaria along the branch that gave rise to Medusozoa.

In a more general way, Gould (2000, p. 43) succinctly summarised Haeckel when he said: "No character in the early days of Darwinism can match Haeckel for enigmatic contrast of the admirable and the dubious. No one could equal his energy or the extent of his output - mostly of high quality, including volumes of technical taxonomic description (concentrating on microscopic radiolarians and on jellyfishes and their allies), and not merely theoretical effusions. Yet no major figure took so much consistent liberty in imposing his theoretical beliefs upon nature's observable factuality". And later on the same page: "Haeckel also prepared his own illustrations for his technical monographs and scientific books - and here he did claim fidelity to nature, as standard practice and legitimate convention also required. Yet Haeckel's critics recognized from the start that this master naturalist, this more than competent artist, took systematic license in "improving" his specimens to make them more symmetrical or more beautiful … This practice cannot be defended in any sense." He also talks of Haeckel's well known embryological "forgeries", and it is the present author's personal view that such a name should be applied to some, if not many, of Haeckel's drawings of siphonophores, particularly as he drew so many from memory rather than from actuality. This subject is discussed in more detail in the accompanying paper (Pugh, 2019b).

Discussion

In this paper we only recognise one species of the family Physaliidae, i.e. *Physalia physalis*. Although there is, presently, a push by mainly Australian and New Zealand workers to establish several more species they would need to establish definite morphological differences from *P. physalis* and, indeed, any of the c. 50 synonyms (see Appendix) that cannot be accounted for by changes occurring during the various stages of development of the species. It does not seem appropriate to distinguish a new species as it has a more powerful sting than another specimen found in a different region of the same country, as Fenner *et al*. (1993) have suggested. It was also long been held that specimens found in the Pacific Ocean only possessed one major tentacle, and these have been referred to as *P. utriculus* but, for instance, Okado (1933) have found specimens of *P. physalis*, around Japan, with a gas bladder up to 10 cm in length and possessing many main tentacles.

With regard to species belonging to the Family Rhizophysidae only four are currently recognised. The following key is a simple way to distinguish them:

Key to the species of the Family Rhizophysidae

It should be noted that all four recognised rhizophysid species possess relatively large pneumatophores, compared with Physonectae species, and, uniquely have finger-like processes from the gas gland, called *hypocystic villi*, hanging down from the base of the pneumatophore.

1. Young gastrozooids with lateral wing-like structures, *ptera* . . . . . Genus *Bathyphysa* ...2.
   Young gastrozooids without lateral wing-like structures. . . . . Genus *Rhizophysa* ...3.
2. Tentacles without side branches, tentilla . . . . . *Bathyphysa conifera*
   Tentacles with side branches, tentilla . . . . . *Bathyphysa sibogae*
3. Tentacles with simple tubular tentilla. . . . . *Rhizophysa eysenhardtii*
   Tentacles with three types of complex tentilla . . . . . *Rhizophysa filiformis*

Additional observations

Rhizophysa filiformis. In younger specimens the pneumatophore was ovoid, almost spherical, with the gas cavity, the pneumatosaccus, usually having an inverted pear-shape and occupying the top half of the pneumatophore. There were extensive patches of red pigmentation within the pneumatosaccus wall, around the apical pore. The hypocystic villi, of various shapes and sizes, attached to the base of the pneumatosaccus extended in all directions so as to virtually fill the gastrovascular cavity of the pneumatophore. Older pneumatophores were considerable larger, often elongate, twice as long as wide, with the pneumatosaccus extending down to ¾ its height. For preserved specimens the hypocystic villi were often obscured by the opaqueness of the outer lining.

The first buds of the gastrozooids arose on the ventral side of the siphosome, immediately below the pneumatophore, and, in preserved specimens, these first buds were all crowded together, but soon formed themselves into a straight line. There could be up to 30 gastrozooidal buds before the bud of the tentacle appeared on its anterior side. Before the distal mouths of these young gastrozooids opened, some of them had a small white somewhat spherical spot at the distal end of the gastrovascular cavity. The tentacles then grew rapidly on successive gastrozooids and soon had functional tentilla. Internodes now appeared between the gastrozooids and, at first, a single gonodendral bud arose there, although it position along the internode varied. However, further down the siphosomal stem there could be up to eight of these buds, with the most developed being the posteriormost. The gastrozooid always remained directly attached to the stem, i.e. it was sessile.

Although fully grown colonies of *Rhizophysa filiformis* usually were green in colour, with the pigmentation concentrated in the tentilla, there has been some doubt as to the coloration in the younger specimens, as mentioned above. The present author has been unable to find a good photograph of a mature specimen, but the young one shown in Figure 34A may throw so light on the matter. It can be seen that the tips of the tentilla are at first white, then pink before finally turning green. On another specimen some of the tentilla were entirely yellow. Thus, further material, preferably of all ages, needs to be studied before this matter can be fully resolved. In addition, the tentilla of the relatively large specimen with some yellow also had others that were suffused with pink, and had intense red spots on a) the smallest branch of the developing dendritic tentilla, and b) the tip of the major branch of the tricornuate tentilla, surrounding the short terminal filament.

With regard to the gonodendron, Totton (1965) suggested that there were 6+ gonophores on each of the terminal branches. Photographs of a maturing gonodendron taken by Casey Dunn show that, from their distal end, there was a large gonopalpon followed by 3-4 gonophores and then the asexual nectophore. Proximal to that there appear to be 4-6 gonophores, but it is difficult to be sure as the branches are all crowded together. Many of the gonophores were a bright yellow in colour.

Rhizophysa eysenhardtii. The young pneumatophore of *Rhizophysa eysenhardtii* tended to be longer than that of *R. filiformis*, but otherwise it was quite similar, with internal red pigmentation around the apical pore and hypocystic villi hanging from the base of the pneumatosaccus, some of which surrounded most of the latter. The number and size of the villi increased with age. One clear difference between the two species was that, as Dunn & Wagner (2005) observed, on the siphosomal stem the buds of the gastrozooids were arranged in two alternating rows on either side of the ventral line. This was difficult to see on the youngest gastrozooidal buds, but soon became obvious. The bud of the tentacle, which was attached on the ventral side of a gastrozooid, had already appeared on the first or second youngest of them. The gastrozooid was always sessile. Internodes then appeared between successive gastrozooids and each had a bud of a gonodendron. Further down the stem there could be two gonodendra per internode, but never more. Younger gastrozooids were often suffused with yellow, but this had disappeared in the older ones. These gastrozooids often had a white sphere in them, but it did not lie at the end of the gastrovascular cavity, but at some distance from its distal end. Meanwhile, the filiform tentilla took on a pink coloration. No mature gonodendron have been seen and so it has not been possible to assess the arrangement of gonophore on the terminal branches.

Although no rhizophysid species is bioluminescent, Haddock & Dunn (2015) have shown that *Rhizophysa eysenhardtii* have found green fluorescent spots on the tips of the tentacles and along the gastrozooids.

So, apart from the character used in the above key, *Rhizophysa filiformis* and *R. eysenhardtii* can further be distinguished by the biserial arrangement of the gastrozooids in *R. eysenhardtii*, together with the ventral position of the tentacle on the gastrozooid. Also, the tentacular buds and the gonodendra appear to arise much earlier in *R. eysenhardtii*. Coloration should help, but there still remain some uncertainties in this regard.

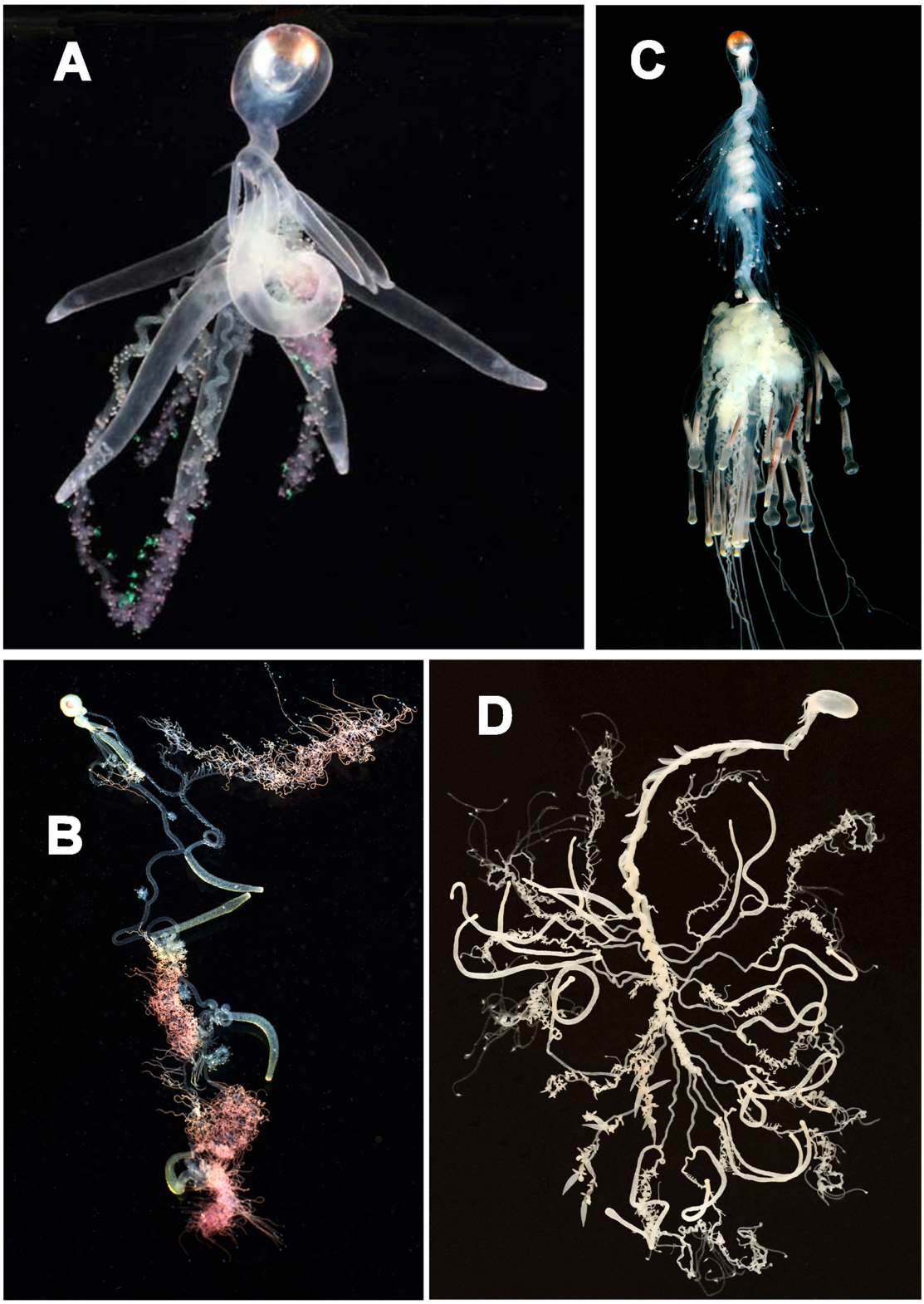

FIGURE 34. Photographs of specimens of the four species preaently included in the Rhizophysidae. **A**. Young specimen of *Rhizophysa filiformis*; **B**. *Rhizophysa eysenhardtii*; **C**. *Bathyphysa conifera*; **D**. *Bathyphysa sibogae*. All photographs are copyrighted: **A.** © Denis Riek; **B**. © Steve Haddock; **C**. © Rob Sherlock; **D**. © P.R. Pugh. The present authors thanks these people for allowing him to reproduce their photographs.

Bathyphysa conifera. For the living specimen (see Figure 34C) the gastrozooid was large and spherical, with the pneumatosaccus occupying the anterior third. Most of pneumatosaccus was covered, internally, in red pigmentation, which darkened around the apical pore and lightened posteriorly. Numerous long hypocystic villi hung down

below the pneumatosaccus, reaching to almost the base of the pneumatophore, but did not rise up to surround the pneumatosaccus as in *Rhizophysa* species. These villi were less numerous and shorter in younger colonies.

The first buds of gastrozooids appeared in the mid ventral line immediately below the pneumatophore. Side processes or *ptera* quickly appeared on these developing buds and developed quickly. These developing gastrozooids that were at that time without a mouth opening also had a spherical white structure at the distal end of the gastrovascular cavity. These may be what Bedot (1893) called *pneumatozoïdes* but they have not been investigated in detail and, as noted above, have also been seen on the young gastrozooids of *Rhizophysa* species. On a large preserved specimen, there were c. 15 buds before a tentacular bud appeared on its anterior side. The next c. 18 gastrozooids gradually increased in size, but without any sign of the development of the tentacle. The first internode then appeared, but there a further c. 20 gastrozooids before the first gonodendral bud was developed, immediately anterior to them. It was estimated that there were c. 100 gastrozooids before there was any sign of the development of the tentacle.

The mature gastrozooids measured more than 5 cm in length and were clearly divided into two parts, with proximal region slightly longer than the distal one. The proximal part was a simple tube that in the living colonies could appear to be a long peduncle, but in preserved ones it clearly formed the stomach region of the gastrozooid, as the tentacle arose at its base. Thus the gastrozooids were always sessile. In preserved specimens, the distal part, the proboscis, was a narrow tube, sometimes swollen toward it distal end. In life (see Figure 34C) the distal half of the proboscis was always swollen, but sometimes constricted in the mouth region. It was large colourless except around the mouth where it was a light purple. The proximal half, however, was deeply pigmented with a purplish red coloration. The filiform tentacle, when coiled up, had a pale yellowish colour. Contrary to Totton's (1965) statement, the *ptera* could still be discerned on the mature gastrozooids. They arose slightly above the base of the gastrozooid and continued onto the proboscis region, petering out at about 2/3rd its length.

The terminal branches gonodendra had between 15 and 19 gonophores. However, because of their crowded nature, it was difficult to ascertain exactly how many were attached between the asexual nectophore and the terminal gonopalpon. There seemed to be at least 5 and occasionally more in this region, with the remainder being attached proximally.

Bathyphysa sibogae. For young specimens the pneumatophore was relatively small and variable in shape, with red-violet pigmentation around the apical pore (Biggs & Harbison, 1976). The pneumatosaccus was relatively large with the hypocystic villi hanging down from its base, but never along its sides. These villi increased in number and size with the age of the colony. For both small and large colonies the first buds of the gastrozooids arose in a single line on the ventral side of the pneumatophore itself, up to c. ½ the length of the pneumatophore. Eleven or twelve buds could be found in this region, and they quickly increased and length distally, with the lateral processes or *ptera* appearing on the fifth bud. At that stage there was no sign of a tentacular bud on its anterior side.

Once on the siphosomal stem internodes appeared between successive gastrozooids and the bud of a gonodendron soon was formed at its mid length. Very small protuberance began to appear on the anterior side of the gastrozooid, at its base. However, these tentacular buds did not begin to develop until the c. 30th gastrozooid. For the two young specimens looked at in detail, the first 20 or 32 gastrozooids were sessile after which a peduncle began to develop at the base of the gastrozooid and, simultaneously, its tentacle began to grow and developed rapidly, as did the single internodal gonodendron. As the peduncle of the gastrozooid elongated the *ptera* began to disappear and had totally vanished after a further eight gastrozooids. The mature gastrozooids were often suffused with pink, and the pedicle of the tentilla on their tentacles was regularly annulated.

The single gonodendron was always attached in the middle of each internode. The terminal branches of each of these bore, proximally, from 4-9 gonophores followed by the asexual nectophore. There were then a further 2-3 gonophores before the large terminal gonopalpon.

Thus the two *Bathyphysa* species are distinguishable not only by the absence of tentilla in *B. conifera* but also by the absence of a peduncle to the mature gastrozooids. In addition, while the *ptera* can be seen on the mature gastrozooids of *B. conifera* they have completely disappeared on those of *B. sibogae*. The appearance of the first gastrozooidal buds on the side of the pneumatophore of *B. sibogae* would also be a distinguishing feature. Whether there are differences in pigmentation remains to be established with any certainty.

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Appendix

Synonymies of existing species of the sub-order Cystonectae.

NOTE: The only more modern references that are included are those that illustrate and/or describe a species, although it is expected that many have been omitted. Most general textbooks from all centuries have been excluded, and also many dealing with the nematocysts and their venom.

Bathyphysa conifera (Studer, 1878)

Rhizophysa conifera Studer, 1878a, p. 4, Pl. 1, figs, 2, 4–7, Pl. 2, figs. 13–18; 1878b, p. 89; Lens van Riemsdijk, 1908, p. 106; Leloup, 1936, p. 19.
Bathyphysa abyssorum Studer, 1878a, p. 21, Pl. 3; Haeckel, 1888b, p. 248; Chun 1897a, p. 104; Schneider, 1898, p. 171; Lens & van Riemsdijk, 1908, p. 105; Bigelow, 1911, p. 321, 351; Leloup, 1936, p. 19, Pl. I, fig. 7–8; Carré & Carré, 1995, p. 561.
Pterophysa grandis Fewkes, 1886, p. 969, Pl. 10, figs. 1-3; 1889, p. 515 Chun, 1897, p. 104; Lens & van Riemsdijk, 1908, p. 107, Pl. 19, Pl. 34, figs. 167–170; Bigelow, 1911, p. 321; Leloup, 1936, p. 20
Bathyphysa grandis Haeckel, 1888b, p. 249.
Linophysa conifera Haeckel, 1888a, p. 45; 1888b, p. 326.
Bathyphysa grimaldii Bedot, 1893, p. 4, Pl. 1; 1904, p. 14, Pls. 3–4; Chun, 1897, p. 104; Bigelow, 1911, p. 321, 351 Leloup, 1936, p. 21, Pl. I, fig. 1, 3–4; Kawamura, 1947, p. 95, figs. 1–5; 1954, p. 120, text-fig. 2, Pl. V, fig. 1–, Pl. VI, fig. 1–2, Pl. VII, fig. 1–7; Patriti, 1970, p. 75, fig. 106.
Pterophysa abyssorum Schneider, 1898, p. 171.
Pterophysa conifera Schneider, 1898, p. 171; Lens & van Riemsdijk, 1908, p. 106; Bigelow, 1911, p. 321.
Pterophysa grimaldii Lens & van Riemsdijk, 1908, p. 107
Pterophysa (Bathyphysa) studeri Lens & van Riemsdijk, 1908, p. 111, Pl. 20, fig. 149, Pl. 22, figs. 153–155, 157–159, Pl. 23,

fig. 165, Pl. 25, fig. 171; Bigelow, 1911, p. 321, 351; Leloup, 1936, p. 21.
Bathyphysa conifera Leloup, 1936, p. 23, Pl. I, fig. 2, 5–6, Pl. II; 1955a, p. 14, fig. 4–6, 1955b, p. 17; Totton, 1965; p. 43, Pl. V, fig.3, Pl. VI, fig. 1–4; Janssen *et al* 1989, p. 198; Jones & Pugh, 2016, p. 1.

Bathyphysa sibogae Lens & van Riemsdijk, 1908

Bathyphysa sibogae Lens & van Riemsdijk, 1908, p. 114, Pl. 20, fig. 148. Pl. 23, figs. 160–164, Pl. 24; Bigelow, 1911, p. 321, 351; Leloup, 1936, p. 22, Pl. I, fig. 9; Totton, 1965, p. 43, Pl. V, fig. 2; Biggs & Harbison, 1976, p. 14, fig. 1–4; Dunn & Wagner, 2006, p. 745, fig. 3;

Physalia physalis Linné, 1758

Holothuria physalis Linnaeus, 1758, p. 657; 1759, p. 254, Pl. III, fig. 6; 1760, p. 657; 1767, p. 1090; 1772, p. 198; Osbeck, 1765, p. 371 (non Plate 12 legend); 1771, p. 105, Pl. 12, fig. 1; Hjortberg, 1769, p. 226, Pl. VII (*partim*); Torén, 1771, p. 166, 262; Gmelin, 1788, p. 3139; Voigt, 1806, p. 507; Blumenbach, 1814, p. 443; Bennett, 1834, p. 6; Griffith & Pidgeon, 1834, p. 490, Zoophytes pl. 5, fig. 1; Chun, 1897a, p. 86; : Burmeister, 1885–1891, p. 2.
Holothuria velificans Osbeck, 1765, Pl. 12, fig. 1; 1771 (Part 1, Pl. 12, fig. 1; Part 2, pp, 74; Torén, 1865, p. 166, 263; De Haan, 1827, p. 496; Chun, 1897a, p. 86.
Medusa caravella **O**. F. Müller, 1776, p. 190, Pl. 2, fig. 2; Gmelin, 1788, p. 3156; de Frémenville, 1824a, p. 44; 1824b, p. 321 [both citing Linné as the authority]; De Haan, 1827, p. 500; Spagnolini, 1869, p. 642; 1870, p. 40.
Meduse La Martinière, 1787, p. 365, Pl. 2, figs. 13–14;
Medusa utriculus Gmelin, 1788, p. 3155; La Perouse, 1797, atlas, Pl. 20, figs. 13–14; Blainville, 1830, p. 102; 1834, p. 113; Lamarck, 1840, p. 94; Fenner *et al*., p. 500, fig. 1; Gershwin et al, 2010, p. 79, Fig. 4 A–C; Chun, 1897a, p. 86.
Physsophora physalis Modeer, 1789, p. 285, Pl. 10, figs. 1-2.
Physalia pelagica Lamarck, 1801, p. 356; 1816, p.480; 1840, p. 92; Tilesius, 1810, p. 184; Eysenhardt, 1821, p. 421, Pl. 35, fig. 2; de Fréminville, 1824a, p. 42; 1824b, pp. 320; de Haan, 1827, p. 496; Deslonchamps, 1828, p.468; Eschscholtz, 1829, p. 162; Olfers, 1832, p. 38; Bennett, 1837, p.43; 1860, p. 5; Lesson, 1843, p. 545; Thompson, 1844, p. 281; Huxley, 1859, p. 100; Chun, 1887, p. 557; 1897a, p. 87; 1897b, p. 8; Haeckel, 1888b, p. 351; Burmeister, 1885-91, p. 13; Mayer, 1900, p. 73.
Physalia pelasgica Bosc, 1802, p. 159, Pl. 19, figs. 1-2; 1830, p. 198, Pl. 16, figs. 1-2; Bory de St Vincent, 1804, Vol III, p. 288, Pl. 54, fig. 1 (Atlas); Blainville, 1830, p. 103; Bennett, 1834, p.6;1837, p. 43; Chun, 1897a, p. 87.
Physalia gigantea Bory de St. Vincent, 1804, Vol III, p. 289.
Physalia Australis Péron, 1807, p. 210; Lesson, 1826, Pl. 5, figs. 1-2; 1830, p. 38; Chun 1887, p. 558; 1897b, p. 8.
Physalia megalista Lesueur & Petit, 1807, Pl. 29, fig. 1; De Haan, 1827, p. 496; Lamarck, 1840, p. 94; Olfers, 1832, p. 32.
Physalis arethusa Tilesius, 1810, p. 298; Eysenhardt, 1821, p. 420, Pl. 35, fig. 1; Blainville, 1826, p. 131; De Haan, 1827, p. 497; Chun, 1897a, p. 558.
Physalis glauca Tilesius, 1810, p. 300; Blainville, 1826, p. 131; 1830, p. 103; 1834, p. 113; De Haan, 1827, p. 496.
Physalis pelagica Tilesius, 1810, p. 302; Lamarck, 1816, p. 480; Blainville, 1826, p. 132; 1834, p. 113; Lesson, 1830, p. 41.
Physalis lamartinieri Tilesius, 1810, p. 309; Eschscholtz, 1825, p. 744; Blainville, 1826, p. 132; 1830, p. 103; 1834, p. 113 De Haan, 1827, p. 496; Olfers, 1832, p. 36.
Physalis cornuta Tilesius, 1810, p. 314; Blainville, 1826, p. 132; 1834, p. 113; De Haan, 1827, p. 496.
Physalis osbeckii Tilesius, 1810, p. 314; De Haan, 1827, p. 496.
Physalia afer Tilesius, 1810, p. 314, Pl. 1, figs. 14, 16; De Haan, 1827, p. 496.
Arethusa caravella Oken, 1815, p. 128.
Physalis pelagica Lamarck, 1816, p. 480.
Physalis tuberculosa Lamarck, 1816, p. 480; 1840, p. 93; Lesson, 1826, Pl. 5, fig. 3; 1830, p. 40; Blainville, 1834, p. 113; Chun, 1887, p. 558; 1897b, p. 8.
Physalis megalista Lamarck, 1816, p. 481.
Physalis elongata Lamarck, 1816, p. 481.
Physalia arethusa Eysenhardt, 1821, p. 420, Pl. 35, fig. 1; Eschscholtz, 1825, p. 744; De Haan, 1827, p. 496, Blainville, 1830, p. 103; Lesson, 1830, p. 41; Olfers, 1832, p. 3, Pl. I, II; van der Hoeven, 1856, p. 112, L. Agassiz, 1862, pp. 335, 367, Pl. 35; A. Agassiz, 1865, p. 215, fig. 351; Fewkes, 1880, p. 139; 1883, p. 79; 1889, p. 518; Burmeister, 1885–91, p. 13: Chun, 1882b, p. 55; 1887, p. 557; 1897a, p. 89; Vanhöffen, 1906, p. 36, figs. 55-57; Koeppern, 1913, p. 18, figs. 1-3.
Physalia lamartinieri Eysenhardt, 1821, p. 421; De Haan, 1827, p. 496; Blainville, 1830, p. 113; Lesson, 1830, p. 41.
Physalia osbeckii Eysenhardt, 1821, p. 421; De Haan, 1827, p. 496; Lesson, 1830, p. 41.
Physalia Laperouse Eysenhardt, 1821, p. 421; *Non* Bory de St. Vincent, 1804.
Physalia producta Olfers, 1822, pp. 347-356, Plate I; 1832, p. 32; De Haan, 1827, p. 498.
Physalia obverse van Hasselt, 1823, p. 1414; 1824, p. 118; Olfers, 1832, p. 177.
Physaliae Eichwald, 1824, p. 453, Pl. XV, figs. 1–7.

Holothuria Thalia de Frémenville, 1824a, p. 43; 1824b. p. 321.
Physalia Thalia de Frémenville, 1824a, p. 44; 1824b, p. 322.
Physalia cristallina de Frémenville, 1824a, p. 44; 1824b, p. 322.
Physalia hyalina de Frémenville, 1824a, p. 44; 1824b, 323.
Physalia gaimardi Blainville, 1826, p. 132; 1830, p. 103; 1834, p. 113; De Haan, 1827, p. 498
Physalia atlantica Lesson, 1826, Pl. 4, figs. 3–4; 1830, p. 36; Griffith & Pidgeon, 1834, Pl. 5, fig. 1; Burmeister, 1885–91, p. 13; Chun, 1887, p. 557; 1897b, p. 8.
Physalia antarctica Lesson, 1826, Pl. 5, fig. 2; 1830, p.39; Burmeister, 1885–91, p. 13.
Physalia azoricum Lesson, 1826, Pl. 5, fig. 4; 1830, p. 42; 1843, p. 555.
Physalia Boiei De Haan, 1827, p. 502.
Thalia Brugière *et al.* 1827, p. 159, P. 89, fig. 1.
Physalis cystisoma Lesson, 1828, Pl. after p. 466; 1830, p. 39; 1843, p. 557.
Physalia elongata Lessons, 1828, p. 468; Lamarck, 1840, p. 9.
Physalia caravella Eschscholtz, 1829, p. 160, Pl. 14, fig. 1; Gegenbaur, 1853, p. 340; Huxley, 1859, p. 100; Spagnolioni, 1869, p. 642; Carus, 1885, p. 49; Chun, 1887, p. 557; 1888a, p. 1173; 1888b, p. 245;1897b, p. 8; Bigelow, 1891, p. 90.
Physalia utriculus Eschscholtz, 1829, p. 163, Pl. 14, fig.2; Blainville, 1834, p. 113; Lamarck, 1840, p. 94; Lesson; 1843, p. 557; Leuckart, 1851, p.190, Pl. 6, figs. 1-6; Huxley, 1859, p. 101, Pl. 10, Pl. 12, fig. 12; Haeckel, 1888b, p. 351; Burmeister, 1885–91, p. 13; Chun 1887, p. 558; 1897a, p. 86; 1897b, p. 8; Agassiz & Mayer, 1902, p. 169, Pl. 10, figs. 43-44; Browne, 1904, p. 744; Lens & van Riemsdijk, 1908, p. 118, Pl. 24, figs. 175–175; Steche, 1910, p. 361,figs.1–8; Bigelow, 1911, p.321; 1919, p. 347; Browne, 1926, p. 84; Kawamura, 1954, p. 120; Barnes, 1963, p. 7, figs. 1-6; Halstead, 1965, p. 300; Williamson *et al*., 1996, p. 137; Alam *et al*, 2002, p. 9; Collins, 2002, p. 420; Yanagihara *et al*, 2002, p. 139.
Physalia eschholtzi Olfers, 1832, p. 37.
Physalus arethusa Blainville, 1834, p. 113.
Physalia (Salacia) megalist*a* Brandt, 1835, p. 237
Physalia (Salacia) pelagica Brandt, 1835, p. 237
Physalia (Alophota) olfersii Brandt, 1835, p. 237; Lesson, 1843, p. 559.
Physalia olfersii Quatrefages, 1854, p. 109, Pl. 3–4.
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Physalia tuberculosa Lamarck, 1840, p. 93
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Physalia elongata Lamarck, p. 94.
Physalia aurigera McCrady, 1857, p. 74; Fewkes, 1880, p. 144;
Alophota olfersii Haeckel, 1888a, p. 46
Alophota giltschiana Haeckel, 1888a, p. 46; 1888b, p. 348, Pl. 26, figs. 1-3; Chun, 1897a, p. 87.
Arethusa challengeri Haeckel, 1888a, p. 46; 1888b, p. 349, Pl. 26, figs. 4-8; Chun, 1897a, p. 87.
Alophota mertensii Haeckel, 1888b, p. 348.
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Physalia physalis **var.** ***utriculus*** Kawamura, 1910, p. 449, text-figs. 4–6, Pl. XIV, figs.2-6; Dakin & Colefax, 1933, p. 198; 1954, p. 124; Hong, 1964, p. 117, Pl. IX, fig. 1; Tokioka, 1970, p. 183; 1973, p. 141; Park & Song, 2004, p. 34, fig. 2A-D.
Physalis physalis Birsa *et al*., 2010, p. 429.

Rhizophysa eysenhardtii Gegenbaur, 1859

Rhizophysa eysenhardtii Gegenbaur, 1859, p. 408, Pl. 32, figs. 46–49; Fewkes, 1883, p.82, Pl. 1, fig. 1; Chun, 1897, p. 83, Pl. V, fig. 9; Mayer, 1900, p. 72; Lens & van Riemsdijk, 1908, p. 103, Pl. 20, fig. 47, pl. 21, fig. 150, Pl. 24, fig. 172; Kawamura, 1910, p. 445, Pl. XIV, fig. 1–2; 1954, p. 118; Bigelow, 1911, p. 320; Leloup, 1934, p. 2; 1936, p. 15; 1956, p. 475; Daniel & Daniel, 1963, p. 190, fig. II, 1–2; Totton, 1965, p. 42, Pl. I, fig. 3, Pl. V, fig. 1, Pl. VII; Daniel, 1985, p. 53, fig. 10; Pagès, 1991, p. 305, fig. 8.2; Pagès & Gili, 1992, p. 68, fig. 2; Pugh, 1999, p. 480, fig. 3.3; Dunn *et al*, 2005, p. 922, fig.5–9.
Nectophysa wyvillei Haeckel, 1888a, p. 45; 1888b, p. 327, Pl. 23; Agassiz & Mayer, 1902, p.169, Pl.8, fig. 36.
Aurophysa ordinata Haeckel, 1888a, p. 44; 1888b, p. 323.
Pneumophysa mertensii Haeckel, 1888a, p. 45; 1888b, p. 328.
Rhizophysa mertensii Schneider, 1898, p. 170.
? *Rizophysa planestoma* Lesueur & Petit, 1807, Pl. 39, fig. 3; Eschscholtz, 1829, p. 147; Blainville, 1834, p. 118 [spelt *planostoma*]; Lamarck, 1840, p. 83; Lesson, 1843, p. 491.
? *Rhizophysa planestoma* Eschscholtz, 1829, p. 147; Blainville, 1834, p. 118; Lesson, 1843, p. 491.
? *Rhizophysa filiformis* Huxley, 1859, p.90, pl. 8, fig. 13–20.
? *Rhizophysa inermis* Studer, 1878a, p.13, Pl.1, figs. 3, 8–10.
? *Aurophysa inermis* Haeckel, 1888a, p.44; 1888b, p. 324.

Rhizophysa filiformis (Forsskål, 1775)

Physsophora filiformis Forsskål, 1775, p. 120; 1776, Pl. 33, fig. F; Modeer, 1789, p. 282; Gmelin, 1790, p. 3159; Lamarck, 1816, p. 478; 1840, p. 82; Eysenhardt, 1821, p. 416; Blainville, 1826, p. 151; 1834, p. 118; Bosc, 1830, p. 200; Griffiths & Pidgeon, 1834, p. 491;
Rhizophysa filiformis Oken, 1815, p. 127; Lamarck, 1816, p. 478; Risso, 1826, p. 305; Blainville, 1827, p. 392; 1816–1830 Pl. 49, fig. 1; 1830, p. 108;1834, p.118; delle Chiaje, 1829, p. 3, 29; Lesson, 1843, p. 490; Gegenbaur, 1853, p. 42, Pl. 18, figs. 5–10; Keferstein & Ehlers, 1861, p. 32, Pl. II, fig. 18–25; L. Agassiz, 1862, p. 370; Vogt, 1862a,b fig.3; Claus, 1863, Pl. 47, fig. 20b; Spagnolini, 1869, p. 641; 1870, p. 39; Fewkes, 1879, p. 292, Pl. 2; 1883, p. 79; Bedot, 1881, p. 122; Carus, 1885, p. 46; Haeckel, 1888b, p. 329; Chun, 1897a, p. 79, Pl. V, figs. 1–8; 1897b, p. 82, fig. 17, fig. 26a, 27; Schneider, 1898, p. 170; Lo Bianco, 1899, p. 463 Richter, 1907, p. 559, text-figs. 1-6, Pl. 27, figs. 1-13; Kawamura, 1910a, p. 447, Pl. XIV, fig. 3; 1954, p. 118; Lens and van Riemsdijk, 1908, p. 100, Pl. 18, figs. 141-145; Bigelow, 1911b, p. 319; 1915, fig. 81; 1918, p. 427; Leloup, 1955a, p. 17; Bigelow & Sears, 1937, p. 65, fig. 50; Totton, 1965, p. 41, Pl. I, fig. 2, Pl. II-IV; Patriti, 1970, p. 75, fig. 105; Daniel, 1974, p. 28, fig. 1, H-N; 1982, fig. 1 (4–6); 1985, p. 49, fig. 9; Stepanjants, 1977, p. 56, fig. 2,А,Б; Bonnemains & Carré, 1991, p. 50, fig. 1; Pagès, 1991, p. 306, fig. 8.3; Pagès & Gili, 1992, p. 69, fig. 3; Pugh, 1999, p. 480, fig. 3.4; Gao et al, 2002, p.66, text-fig. 24; Dunn, et al., 2005, p. 922, fig. 5-8; Zhang, 2005, p. 16, figs. 1C, 12; Dunn & Wagner, 2006, p. 747, figs. 2, 7; Araujo, 2012, p.58.
Rizophysa filiformis Bruguière *et a*l. 1827, p. 139, Pl. 89, fig. 12;
Epibulia filiformis Eschscholtz, 1829, p. 148.
Rhizophysa sp. Fewkes 1881, p. 773, fig. 11
Rhizophysa gracilis Fewkes, 1882a, p. 269, Pl. VI, figs. 1–6;
Cannophysa gracilis Haeckel, 1888a, p. 44.
Cannophysa murrayana Haeckel, 1888a, p. 44; 1888b, p. 324, Pl. 24.
Pneumophysa gegenbauri Haeckel, 1888b, p. 328.
Cannophysa eysenhardti Mayer, 1894, p. 239, Pl. 3, figs. 1,2,4.
Rhizophysa murrayana Chun, 1897a, p. 84; Mayer, 1900, p. 72.
? *Epibulia (Macrosoma) mertensii* Brandt, 1835, p. 233
? *Rhizophysa mertensii* Lesson, 1843, p. 492; Haeckel, 1888b, p. 329.
? *Pneumophysa mertsensi* Haeckel, 1888b, p. 45
? *Cannophysa filiformis* Mayer, 1894, p. 241, Pl. 3, fig. 3.
? *Rhizophysa clavigera* Chun, 1897b, p. 104; Mayer, 1900, p. 72;
? *Rhizophysa (?) tricornuta* Moser, 1925, p. 445, 533 textfig. 59.
? *Rhizophysa (?) tricarnuta* Moser, 1925, Pl. 33 (legend).
non Rhizophysa *filiformis* Huxley, 1859, p. 90, Pl. VIII, fig. 13 = *Rhizophysa eysenhardti*

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