

Archangelopsis jagoa, a new species of benthic siphonophore (Physonectae, Rhodaliidae) collected by submersible in the Red Sea

Siphonophora
New species
Physonectae
Rhodaliidae

Siphonophores
Nouvelle espèce
Physonectées
Rhodalidées

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ABSTRACT

A new species of rhodaliid siphonophore, *Archangelopsis jagoa* sp. nov., is described from three specimens collected at depths between 250 and 370 m in the Gulf of Akaba, Red Sea, by the submersible JAGO. Comparisons are made with the established species of that genus and observations, both *in situ* and on the living animals in captivity, are reported.

RÉSUMÉ

Archangelopsis jagoa, une nouvelle espèce de siphonophore benthique (Physonectées, Rhodalidées) prélevée par submersible dans la mer Rouge.

Une nouvelle espèce de siphonophore, *Archangelopsis jagoa* sp. nov., est décrite à partir de trois spécimens prélevés par le submersible JAGO entre 250 et 370 m de profondeur dans le golfe d'Akaba, en mer Rouge. Les animaux ont été observés *in situ* et en captivité et comparés aux espèces connues de ce genre.

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INTRODUCTION

The family Rhodaliidae contains a small number of species of physonect siphonophores with an unusual organization. To date, ten species belonging to seven genera have been described (see Pugh, 1983 for a detailed review). Like all physonect siphonophores, rhodaliids have an apical gas-filled float or pneumatophore; but this is unusually voluminous and, characteristically, possesses an enlarged gas-secreting area, the aurophore, protruding from its dorso-basal surface. Unlike most physonects, the swimming bells or nectophores (nectosome) and other stem appendages (siphosome) are not arranged linearly below the pneumatophore. Instead both the nectosome and the siphosome are united to form a globular corm, which can be hollowed out or solid. The budding zones for the nectosome and siphosome occur together on the ventro-basal side of the pneumatophore. The nectophores form a corona of one or more rows around the base of the pneumatophore

while the siphosomal elements, the cormidia, are generally arranged in a spiral around the remainder of the corm.

Rhodaliids, uniquely amongst the siphonophores, are benthic organisms, attaching themselves to the sea-bed by their tentacles. From the limited amount of information available it appears that individual species have limited depth and geographical ranges, although collectively specimens have been caught at depths ranging from c. 100 to 3100 m in various regions of Atlantic and Pacific Oceans, and in the East Indies. *In situ* observations from submersibles (see Ballard and Grassle, 1979 ; Hessler and Smithey, 1984; Pugh, 1983) have been made on only two species, *Dromalia alexandri* Bigelow 1911 and the "Galapagos dandelions" *Thermopalina taraxaca* Pugh 1983.

In the present paper a new species of rhodaliid siphonophore will be described on the basis of three specimens collected by the submersible JAGO at depths between 250 and 370 m in the Gulf of Akaba, Red Sea. Observations,

both *in situ* and on the living animals in captivity, are reported. This new species belongs to the previously monotypic genus *Archangelopsis*, and comparisons will be made with the established species, *Archangelopsis typica* Lens and van Riemsdijk 1908.

Material examined

Three specimens collected during dive 241 of the manned submersible JAGO on 16 November 1992 at depths of 370 (holotype), 272 and 252 m (paratypes). The location of the dive was 29°31' N, 34°56' E, off the Heinz Steinitz Marine Laboratory at Eilat in the Gulf of Akaba. The water temperature at the collection sites was 20.8 °C. The holotype has been presented to the Zoologische Staatssammlung München.

The specimens were collected with a specially constructed sampling device attached to the manipulator of the submersible. A transparent plastic cylinder was placed over the specimen, and this was gently shaken until the specimen dislodged its tentacles and floated upwards into it. The bottom of the cylinder was then closed using a rubber plug. In an attempt to minimize possible damage to the animals by rapid expansion of the gas within the pneumatophore, the submersible then slowly and obliquely ascended to the shore. On the surface the specimens were transferred to a glass aquarium filled with fresh sea water where they were observed and photographed. After they died, during the second night, they were fixed in 4 % formalin mixed with sea water.

All morphological examinations were made using a dark background binocular microscope. To the extent possible all three specimens have been kept intact, and their internal structure has not been investigated.

Diagnosis

Rhodaliid siphonophore with a small (2-3 mm diameter), smooth-walled pneumatophore that has 5-6 coloured pigment rings. The aurophore bears a large number of papilliform appendages on its external surface. The nectophores, ten or less in number, are arranged around the nectosome in a single corona, and have the typical rhodaliid form. The monogastric cormidia consist of a long stalk which divides, distally, into a single gastrozooidal and a single gonodendral branch. The former bears a type II gastrozooid (as defined by Pugh, 1983), with a long, annulated tentacle bearing spirally coiled tentilla that arise from the proximal end of each tentacular segment. Type I gastrozooids are absent. The gonodendral branch divides further and numerous gonopalpons are borne on the distal ends of these branches. The gonopalpons can stretch out, in life, to form trumpet-like tubes of extraordinary length. A single, large bract is attached at the base of each cormidial stem. The bract has a triangular shape with a large distal facet bearing tooth-like projections at its edges. It is traversed by a pigmented bracteal canal that bifurcates distally. Secondary cormidia are not developed.

Description

The specimens collected possess two major morphological characters that, in combination, are exclusive to the genus *Archangelopsis*; these are a smooth-walled pneumatophore (without gelatinous protuberances) and an aurophore with numerous external papilliform appendages (Fig. 1, Fig. 2a, c). The holotype specimen is somewhat larger than the two paratypes. In the preserved state the holotype measures about 10 mm in diameter and 12 mm in height. During fixation almost all nectophores, several bracts and many gastrozooids and gonopalpons became detached from the animals and during preservation each shrank and lost its original coloration.

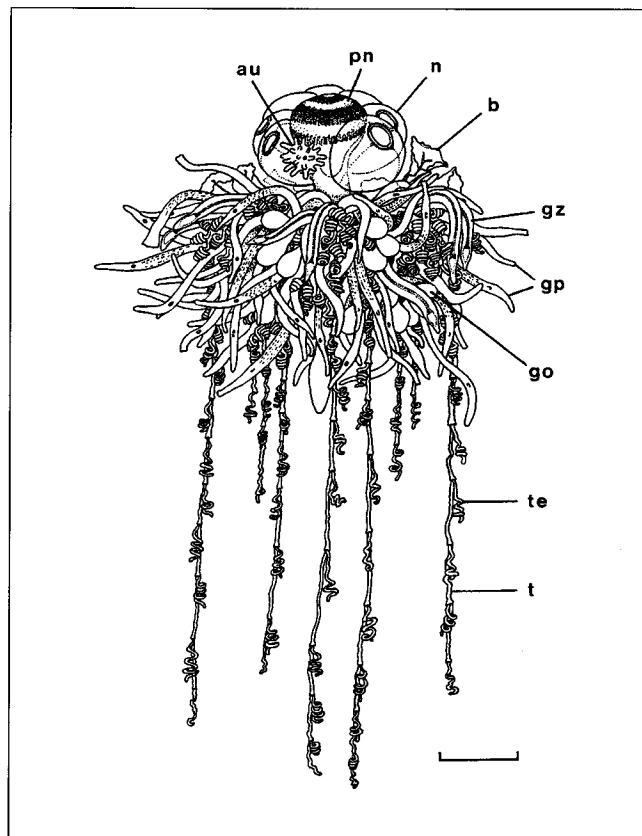


Figure 1

Archangelopsis jagoa. Lateral view of the living animal, drawn from a photograph taken in the laboratory. au = aurophore; b = bract; gz = male gonophore; gp = gonopalpon; gz = type II gastrozooid; n = nectophores; pn = pneumatophore; t = tentacle; te = tentillum. Scale = 2 mm.

Pneumatophore. The pneumatophores of the live animals ranged in size from 2 to 3 mm in diameter; shrinking to 1.7-2.6 mm after preservation. No apical pore was discernible, nor would one be expected to be present. No external damage to the pneumatophore was apparent after the specimens had been brought to the surface.

In life, the pneumatophore possessed 5-6 circular pigment rings. The two paratypes had six rings that were coloured, in sequence from the apical pole, yellow, red, white, red, yellow and red. The fourth (red) ring was absent in the

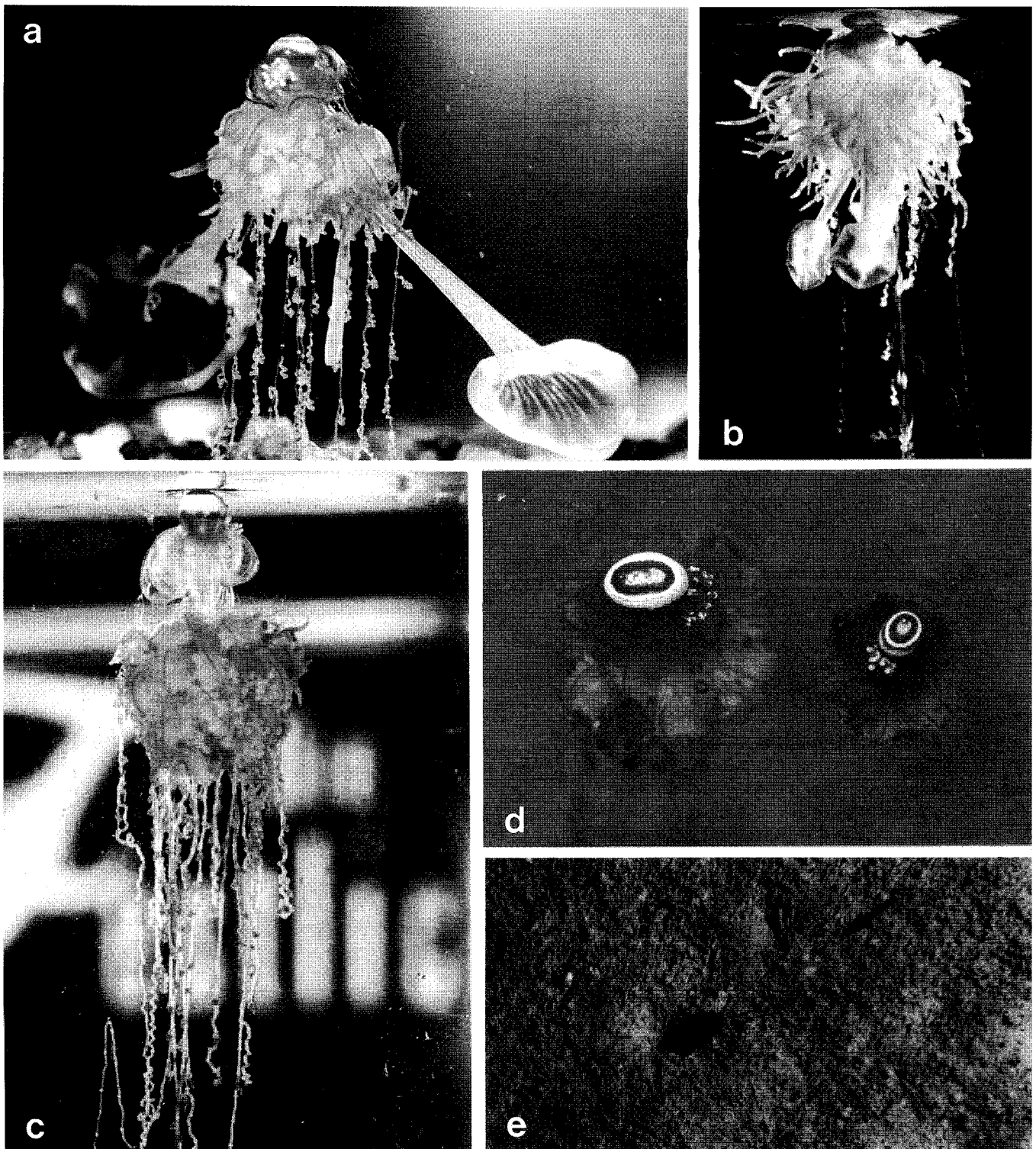


Figure 2

Archangelopsis jagoa. Photographs of the living animals. (a) Male specimen with one club-shaped [centre] and two trumpet-like elongated gonopalpons [left and right]. (b) Specimen floating under the water surface with two elongated gonopalpons. Expanded mouth regions of gonopalpons are attached to the glass of the aquarium, apparently by suction. Gonopalpons on the left side of the siphosome were actively moving. (c) The largest specimen (holotype) floating under the water surface with elongated nectosome clearly separating the nectophores from the siphosome. Flimsy bracts visible at the upper edge of the siphosome. (d) Top view of the female holotype (left) and smaller female paratype. Note the gas-bubble visible inside the aurophore of the holotype. (e) In situ photograph taken from the submersible JAGO at a depth of 300 m in the Gulf of Akaba.

larger holotype. The pigment rings varied in width and covered about three-quarters of the exposed area of the pneumatophore (Fig. 2). They were traversed by irregular radial lines. After preservation it became obvious that the

pigmentation was located in an interior cell layer, possibly the endoderm of the inner wall of the pneumatophore, the pneumatostaccus, and not in the outer wall, the pneumatocodon, which changed to a glassy pellicle. Also within the

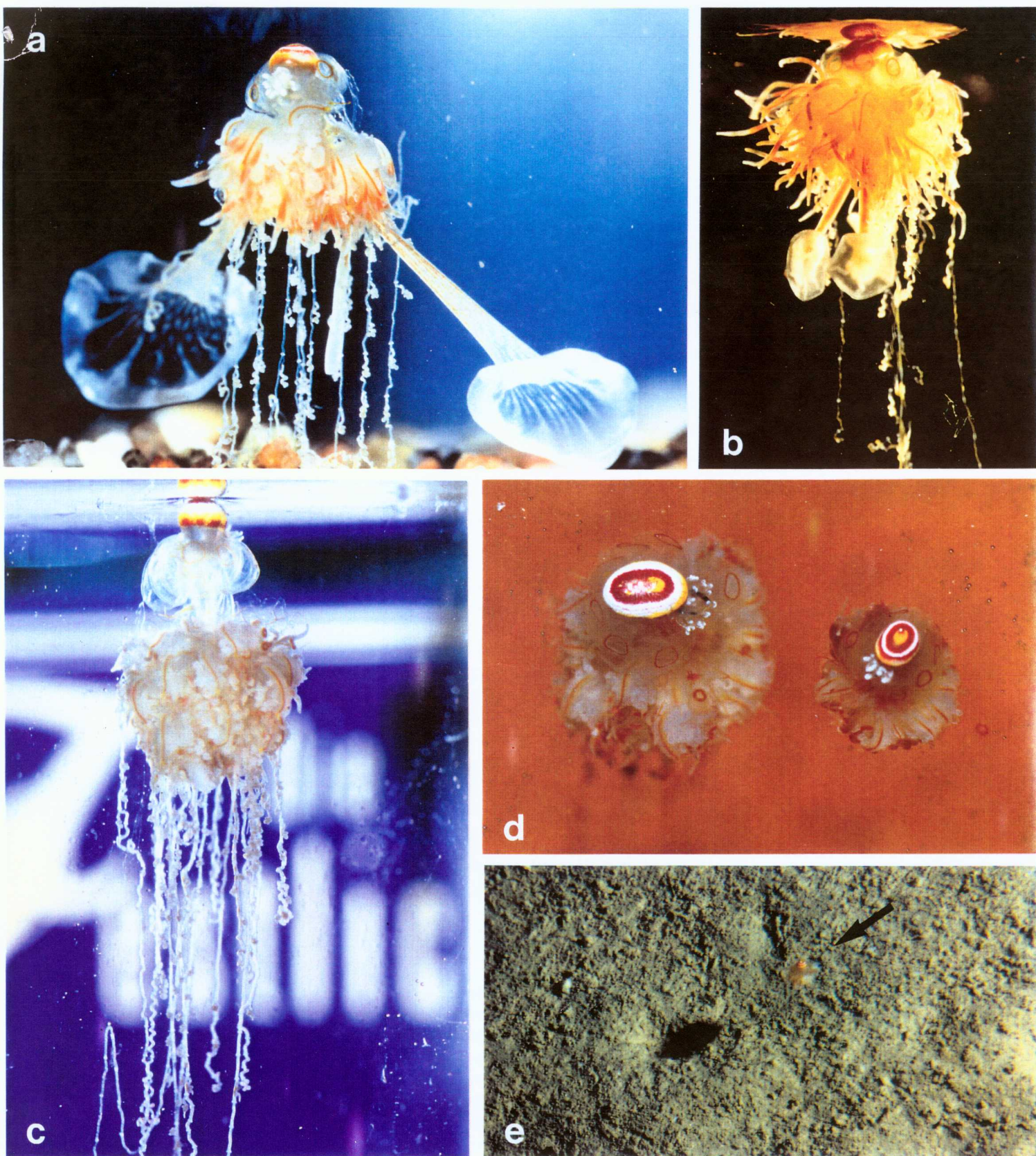


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pneumatophore, an inverse pear-shaped, silvery structure was visible (Fig. 2c) that, most probably, is the chitinous lining to the pneumatosaccus (see Pugh, 1983).

Auophore. As in all rhodaliids, the gas-secreting area projects from the basal part of the pneumatophore, on its dorsal side, to form the auophore (Figs. 1, 2a, d), and in *Archangelopsis* species the external surface of this auophore is covered with papilliform appendages. The auophore of the *A. jagoa* holotype has about 30-35 such appendages, those of the paratypes 13 and 11. In life, the tip of each appendage bears white pigmentation, while all other parts are transparent (Figs. 2a, d) so that the exterior of the auophore reminds one of a tiny sea-anemone. Initial laboratory observations on the live specimens showed that the auophore of the holotype contained a small gas bubble.

After preservation the auophores of all three specimens changed shape. For the paratypes, the auophore of one (II) retained almost its original shape, while that of the other (I) became slightly inflated. In both the appendages were arranged in an irregular band around the lateral margins of the auophore. In the holotype the auophore expanded greatly to form a sphere, 1.45 mm in diameter, and the appendages shrank to small nipples on its external surface (Fig. 3). A central papilla, in the middle of the dorsal surface of the holotype's auophore, became visible. It could not be seen on the living specimen. This papilla had a slightly different appearance from the other appendages, and was separated from them by a denuded zone. As in both paratypes, the other appendages were now arranged in an irregular band around the lateral margins of the auophore. On the paratype with the slightly enlarged auophore, an enlarged central protuberance was also visible.

We believe that this central process represents the site of the excretory pore of the auophore similar to the structure observed on other rhodaliid siphonophores. All the other appendages appear to be closed structures, without pores. Further evidence for the presence of a central pore comes from paratype II. In the centre of the dorsal surface of its auophore there is a widely open external pore from which a central canal penetrates through the auophore and opens, via a pore of similar diameter to the external one, into the

pneumatossacus of the pneumatophore. Both the external and internal pores are perfectly rounded, without any ragged edges that might be indicative of damage caused, for instance, by rupture of the pneumatophore. The inner wall of the canal has a silvery appearance, and at first sight it would appear that it represents a pneumatic duct, connecting the pneumatophore directly to the outside.

Nectosome. The region immediately below the pneumatophore is the nectosome, where the nectophores or swimming-bells are attached. The zones of proliferation for the nectosomal and siphosomal elements lie close together on the ventral side in this region, on the opposite of the pneumatophore to the auophore (Fig. 3). In the holotype one young nectophore and several very young cormidia remain attached to these zones. In the preserved state the nectosome has a height of ca. 1 mm, but observations on the living animal showed that the nectosome can expand to at least double that length (Fig. 2c). In this case the nectophores are clearly exposed and separated from the main corm. In life, the holotype specimen possessed nine large nectophores, the paratypes seven, arranged around the nectosome in a single corona (Figs. 1, 2). The nectophore itself is a rounded bag-like medusoid structure with a very thin, transparent wall. It has four colourless, straight radial canals, and a bright orange circular canal around the ostium. The largest diameter of a nectophore was 3.4 mm; the smallest, attached to the zone of proliferation, 0.6 mm. Although several of the nectophores have become detached, their muscular attachment lamellae are clearly recognizable, stretching down from the lower edge of the pneumatophore to the upper edge of the main corm (Fig. 3). Thus, nine lamellae, plus the small nectophore still attached to the budding zone, were counted on the nectosome of the holotype. However, in one of the paratypes five large nectophores remain attached, and the basal parts of these have become invaginated and surround the pneumatophore in such a way as to resemble the perianth of a flower.

Siphosome. The siphosome of the living holotype had a size of 12 × 10 mm and a strawberry-like shape (Fig. 2c). The actual size of the siphosomal corm itself was difficult to measure due to the dense crowding of the cormidia attached to it. However, it was estimated to be about 5-7 mm

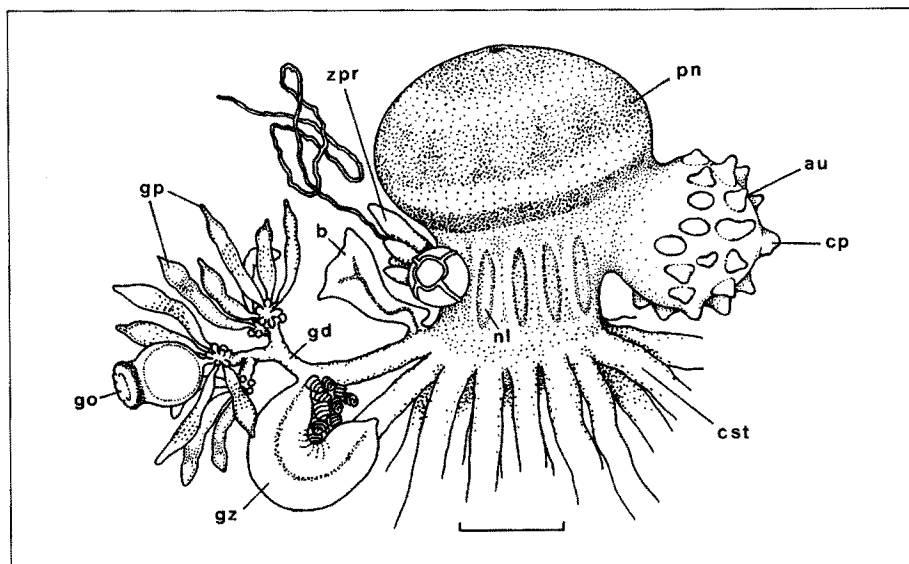


Figure 3

Detail of the preserved holotype of Archangelopsis jagoa.

au = the inflated auophore with central papilla (*cp*); *b* = bract, attached at base of cormidial stalk; *cst* = cormidial stalk, attached directly below the nectosome; *gd* = branched gonodendron; *go* = female gonophore; *gp* = gonopallions; *gz* = gastrozoid with annulated tentacle; *nl* = attachment lamellae for, now detached, nectophores; *pn* = pneumatophore; *zpr* = zones of proliferation, where a small nectophore and some young cormidial elements are attached. Scale = 1 mm.

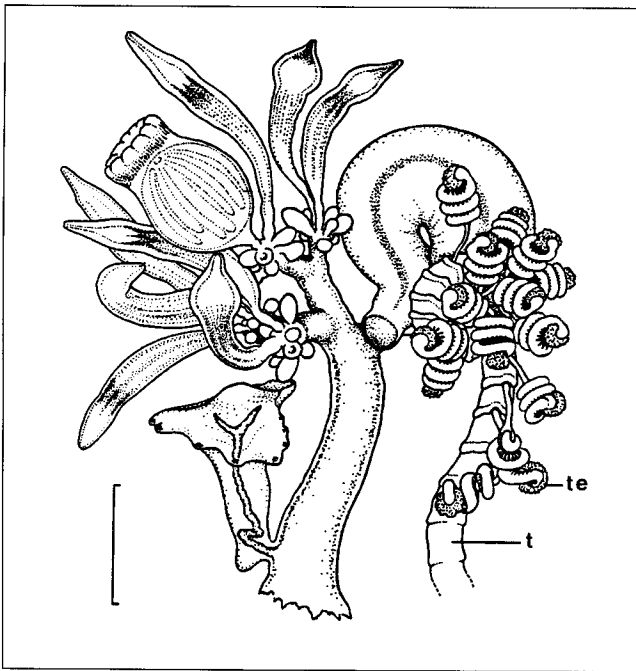


Figure 4

Detached cormidial unit of *Archangelopsis jagoa*. *t* = annulated tentacle, with spirally coiled tentilla (*te*). Other abbreviations as in Figure 3. Scale = 1 mm.

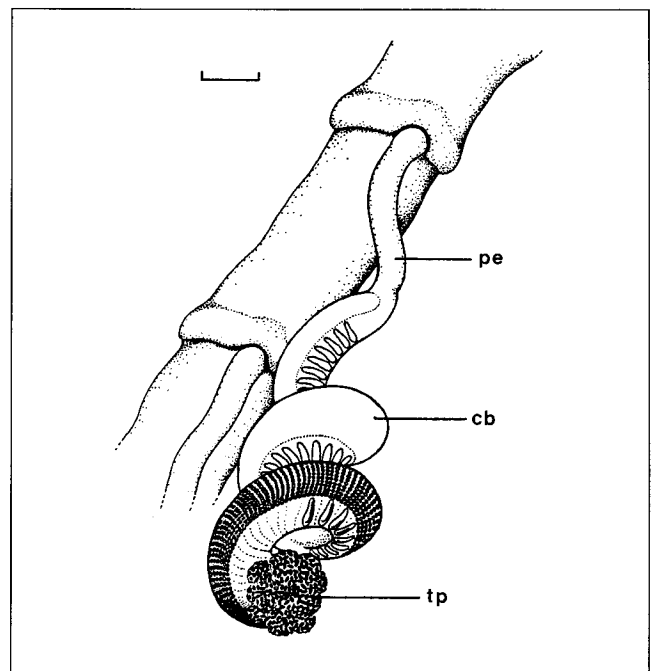


Figure 5

Detail of an outstretched tentacle from a type II gastrozoid of *Archangelopsis jagoa*. The tentillum is attached at the proximal end of a tentacular segment, and consists of three regions; pedicle (*pe*); spirally coiled cnidoband (*cb*) with dorsal and lateral nematocysts; and terminal process (*tp*) with small nematocysts. Scale = 0.1 mm.

in diameter. It is assumed, as was the case for *Archangelopsis typica*, that the corm is a thin-walled structure enclosing a voluminous sac; but as none of the specimens was dissected this remains a conjecture. Nevertheless, after preservation the corm contracted greatly, as might be expected for a thin-walled structure. This contraction led to the situation where all of the cormidia appear to be attached directly to the lower edge of the nectosome, such that it is impossible to investigate their true arrangement.

Each cormidium is borne on a long gelatinous stem that is attached directly to the corm (Fig. 3) and is connected into the central gastrovascular canal by a simple canal. It consists of a single gastrozoid, with a long annulated tentacle; a branched gonodendron which bears the gonophores, numerous gonopapils and buds; and a basal bract (Fig. 4). None of the cormidia possessed any signs of the budding off, at the base of the cormidial stem, of secondary cormidia, as has occasionally been found in *Archangelopsis typica* (see Pugh, 1983).

At a height of about 2 mm, the main cormidial stem divides into a gastrozoid and a gonodendron branch. The gastrozoid branch is a short, stout pedicle to which a large gastrozoid is attached. If the gastrozoid is dislodged, its former attachment point is easily recognizable as a round stump. The gastrozoid is made up of three main parts; the basal basigaster, to which the tentacle is attached; the central stomach region; and a terminal proboscis. In life, the stomach region is a tubular elongated structure with a single, longitudinal bright orange stripe; while the proboscis is slightly swollen and has yellow pigmentation (Figs. 1, 2c). The total length of the gastrozoid, as

estimated from photographs, is 3.7 mm. In the preserved state the gastrozoid has contracted to a length of 2 mm and is banana-shaped (Fig. 4). It still possesses the orange stripe running through the endoderm of the stomach region, but has lost the yellow coloration to the proboscis. The short basigaster is separated from the stomach region by a constriction. The well developed tentacle, which is attached to it, bears side branches or tentilla, the presence of which indicate that the gastrozoid is a type II one, according to the nomenclature adopted by Pugh (1983). The holotype possessed about 20 such gastrozoids, as assessed both from photographs of the living animal and from the preserved specimen. One paratype possessed about 20 type II gastrozoids, the other about thirteen. Since the cormidia are monogastric, no type I gastrozoids with reduced tentacles devoid of tentilla being present, the total number of cormidial units should be in accordance with the number of gastrozoids, and this has been confirmed on the preserved specimens.

In life, the tentacles can reach enormous lengths, many times the diameter of the main corm (Fig. 2c). The tentacle is annulated and mature ones consist of at least 50 segments, each of which can stretch out to a length of ca. 2 mm, so that the total length of the tentacle exceeds 10 cm (see *in situ* observations, below). A fine suspensory ligament is attached along the ventral surface of the tentacle; while the large tentilla are inserted on the dorsal surface at the proximal end of each segment, embedded beneath a distal swelling of the more proximal segment (Fig. 5). Both the tentacles and the tentilla had an orange coloration in life. Tentilla are present on the proximal and middle parts

of the tentacle, but are absent from most of the distal segments although scars where they would have been attached can often be seen. This has been found in other rhodaliids, for instance *Dromalia alexandri* and *Thermopalia taraxaca* (Pugh, 1983), and presumably they have become detached during life, or during collection and handling.

The tentillum is a distinctive, filiform structure, whose diameter is somewhat less than that of the tentacle itself. Each consists of three regions (Fig. 5); a slender, elongated basal pedicle; a relatively long, spirally-coiled cnidoband; and a terminal filament. The spirally-coiled cnidoband is tightly coiled in the contracted state (Fig. 4), but more loosely coiled in life when the tentacles hang down below the siphosome (Fig. 2a). The cnidoband bears at least two different types of nematocysts. A large number of (?) haplonemes ($28 \times 4 \mu\text{m}$) arranged in about a dozen rows along its dorsal surface and individual rows of large sabre-shaped (?) heteronemes ($56 \times 17 \mu\text{m}$) on the flanks of the others. The terminal filament of the younger tentilla, i.e. those on the proximal part of the tentacle, is coiled into a neat spiral in the preserved state. In older tentilla this coiling becomes more erratic and in some cases it appears that the filament has become agglomerated into a single irregular mass (Fig. 5). Two types of small nematocysts are present, probably acrophores and desmonemes, measuring $11 \times 6.5 \mu\text{m}$ and $13 \times 4 \mu\text{m}$.

The other main branch of the cormidial stem is the gonodendral one. This continues to branch dichotomously, at least once and sometimes as many as three times. The resulting 2 to 8 gonodendral branches bear at their distal ends several simple gonopalpons and many gonophoral buds. In addition mature gonophores are attached here, although their number per gonodendron appears to be restricted to one. The gonopalpons are variable in shape, both in life and after preservation. In the holotype, there are two basic types of preserved gonopalpons both c. 2-3 mm in length. Firstly, simple, banana-shaped whitish tubes with a short peduncle and a narrow distal end. Secondly, dumb-bell-like tubes with 5-6 whitish longitudinal streaks and, towards the distal end, a yellowish, optically dense swelling (Fig. 4) with patches of nematocysts distributed over its surface. Nematocysts also seemed to be present on its proboscis region. However, in the preserved paratypes only the second type of gonopalpon was found, and so the two different types in the holotype are considered to be preservation artifacts.

A simple central gastrovascular canal is easily recognizable through the transparent outer wall. Although many gonopalpons became detached after preservation, from 10-20 remained attached to each gonodendron. A maximum of seven was found on a single gonodendral branch. In accordance with the total number of cormidia, one specimen would possess at least 200 gonopalpons, an enormous number considering the relatively small size of the entire colony.

In life, the gonopalpons are elongated, narrow tubes which are permanently in motion amongst the siphosomal elements (Fig. 2b). They possess a single red spot close to their distal end, probably identical with the optically dense area found on some of the preserved ones. Their mid-region is flecked orange-red, with the pigments arranged in irregular longitudinal streaks. They can

extend to enormous lengths and their terminal region can expand so much that its mouth opening has a diameter greater than that of the entire siphosome (Fig. 2a). As they expand, the orange-red coloration of the mid-region breaks up into a series of thin stripes reminiscent of the hepatic stripes often described in the gastrozooids of other physonects. Whitish streaks, usually five in number and symmetrically disposed, become visible around the mouth opening of these trumpet-shaped gonopalpons (Fig. 2b). When the gonopalpon retracts the mouth sometimes curls back on itself.

Like all rhodaliid siphonophores, *Archangelopsis jagoa* is dioecious, in that the gonophores on all of the gonodendra of a single specimen are of the same sex. The holotype is female, as is paratype I, while paratype II is male. Almost all cormidia that were examined possessed only a single maturing gonophore attached to the distal end of one of the gonodendral branches. However, very young gonophores, and in the female specimens the egg pouch, are present on all the branches. The mature female gonophore is a rounded bell borne on a short, narrow stalk (Fig. 4) and has a total length of c. 1.3 mm. It has a bright orange bulge around the opening of the sub-umbrella cavity (Figs. 2c, d), and longitudinal streaks are sometimes recognizable on the surface of the exumbrella. The mature male gonophore on each gonodendron is a simple white, sac-like structure (Fig. 1) borne on a narrow stalk which is slightly longer than that of the female gonophores. The opening of the sub-umbrella cavity is not pigmented, thereby making it easy to distinguish at a glance between male and female individuals.

A single, large bract, measuring 2-2.5 mm in length, is attached at the base of the main cormidial stem (Fig. 4). On the living specimens the bracts were visible as flimsy and highly transparent "leaves" between the upper edge of the siphosome and the nectophores (Figs. 2a, c). The individual bract is a triangular structure with an expanded convex distal facet (Fig. 6), emarginated on its dorsal side. The edges of this facet are recurved and are made up of about 15 tooth-like projections, each of which has a pad of small oval cells, that appear to be nematocysts, on its distal side. These structures had the same greenish coloration as the nematocysts found in the terminal process of the tentillum. The bracteal canal is orange-coloured in life. It runs from the proximal tip of the bract, originally in contact with the ventral surface in the region of attachment, before bending abruptly through two right angles and continuing along the central axis of the bract toward the distal facet. After entering the distal facet it branches, one branch continuing toward the convex centre of the facet, and the other, at a right angle, runs up toward the dorsal surface of the bract.

Etymology

The specific name *jagoa* refers to the name of the submersible JAGO which collected the specimens, itself named after a deep-sea shark, *JAGO omanensis*, living at depths around 400 m in the Red Sea.

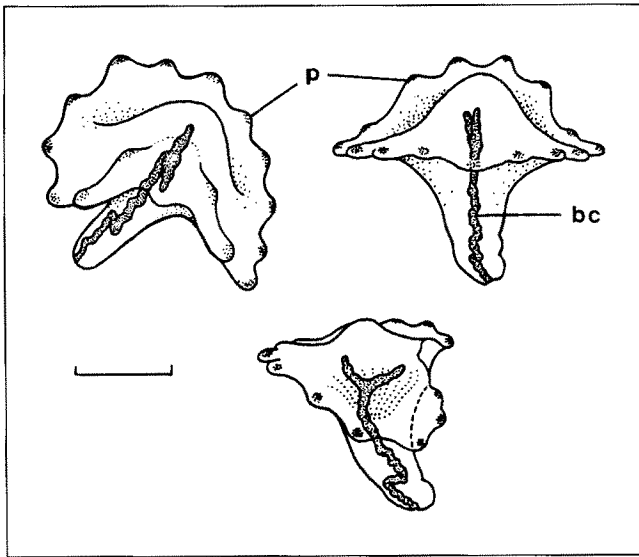


Figure 6

Various aspects of a mature bract of *Archangelopsis jagoa*. bc = branched bracteal canal; p = projections at the edges of the distal facet. Scale = 1 mm.

Observations on the live animals

In situ observations. *A. jagoa* is one of the smallest known rhodaliid species, in that its volume is little more than 1 cm³. Because of this it was difficult to make *in situ* observations or photograph these almost transparent animals from the submersible; and it is not surprising that they were overlooked during previous dives in the same locality. They only became apparent when the powerful lights of the submersible threw their star-shaped silhouettes onto the pale sediment below (Fig. 7), or if the rings of colour on the pneumatophore were observed (Fig. 2e).

All observed specimens were tethered to the soft sediment by their thin tentacles (Figs. 2e, 7), which were stretched out to lengths of at least six times the diameter of the corm, thereby maintaining the animal like a small hot-air balloon at a height of 10–15 cm above the substratum. The number of these attachment tentacles was estimated, from photo-

graphs taken of their radiating shadows on the sea floor, to range from 7 to 11. Tentilla could be seen dangling down from them. If the number of gastrozooids and tentacles is taken to be twenty, then it would appear that not all tentacles are involved in attaching the animal to the substratum. However, no non-attached tentacles were seen, although this could be due to the minute size of the animals and the poor contrast of the photographs.

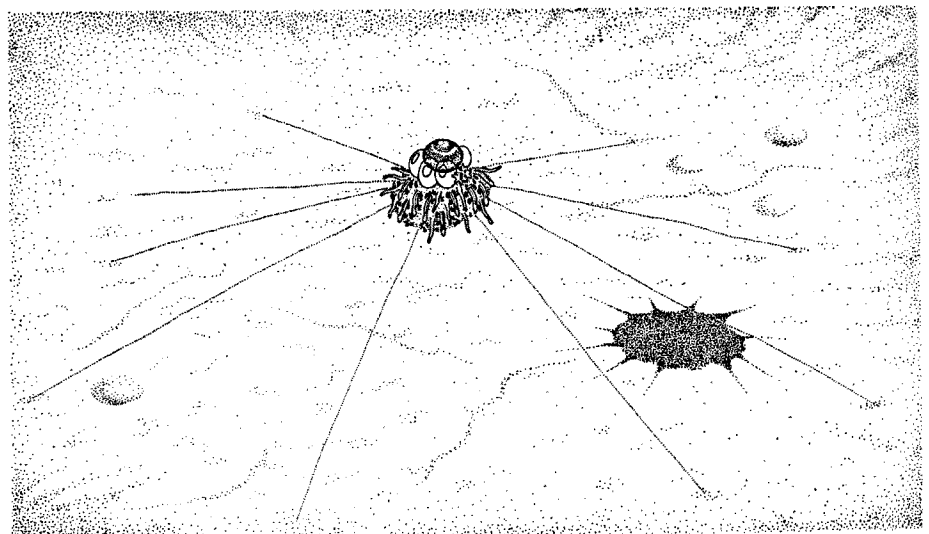
If the animal was disturbed, the tentacles contracted, thereby pulling the corm down toward the sea floor. When an animal was gently dislodged, it floated slowly upwards to a maximum height of approximately 50 cm above the sea floor and then started active swimming by rhythmic and fairly coordinated contractions of its nectophores. This resulted in the animals moving directly downwards at a rate that was estimated to be c. 3 cm s⁻¹. However, free-floating or actively swimming animals were never observed under natural conditions.

The animals were first sighted during dives carried out in July 1992, at depths between 240 and 400 m (the maximum diving capacity of the submersible). They were distributed over large areas, with an average population density of c. 1–2 m⁻² and with each specimen well separated from its neighbours. However, during a second diving period in November 1992, it was difficult to find any specimens. Perhaps the population undergoes seasonal changes; but without a full seasonal coverage of dives and *in situ* observations this can only remain a conjecture. At depths between 240 and 400 m in Gulf of Akaba the slope angle is c. 18–25°. Apart from sporadic rocks surrounded by depressions, the sea floor is covered with soft muddy, occasionally sandy sediment. These sediment planes are poorly structured but not devoid of life, as was indicated by many superficial tracks, small mounds, burrows and craters. Many tracks were generated by irregular sea urchins (*Pericostmus akabanus*) that moved over the seabed in dense aggregations feeding on the superficial deposit. It is probable that such bioturbating animals easily could disturb the benthic siphonophores, but such contacts were never observed.

Laboratory observations. Observations on the live, but obviously stressed, animals were continued after transfer-

Figure 7

Tracing, from a photograph, of a live specimen of *Archangelopsis jagoa* attached to the sediment with its long tentacles, and with the main corm at a distance of approximately 10–15 cm from the sea bed.



ring the collected specimens into a glass aquarium. For most of the time they were positively buoyant and floated in contact with the water surface, although the pneumatophore did not penetrate through it (Figs. 2b, c). However, the holotype specimen became negatively buoyant after a small gas-bubble, in the middle of the aurophore, was removed with a fine pipette. The specimen sank to the bottom of the aquarium and was not able to rise up again, indicating that positive buoyancy is achieved only if a sufficient volume of gas is enclosed within the pneumatophore.

The other specimens were able to swim, and this was achieved by strong, rhythmical contractions of the flimsy nectophores. The ostium of each nectophore was directed upwards, so that the jet-propulsive effect, from the contraction of the nectophores, moved the whole animal directly downwards if all nectophores of the corona were involved, or diagonally downwards if only the nectophores of one side were contracted. In the latter case the pneumatophore became slightly tilted. The tentacles trailed behind before they started to retract. When the animal reached the aquarium bottom, which was covered with coarse gravel, the nectophores did not stop contracting. Unsuccessful attempts to attach the tentacles to the substratum were noted. After several seconds at the bottom the contractions of the nectophores decreased and the animal ascended to the surface; the reduced thrust of the nectophores, whose contractions became uncoordinated, apparently being able only to reduce this upward motion.

Shortly after transference into the aquarium, several nectophores, female gonophores and gonopodpalps became detached. For a while, the detached nectophores continued to contract rhythmically, pushing themselves through the water. Similarly, the detached gonopodpalps were seen to contract and extend on the aquarium bottom. The attached gonopodpalps moved actively among the other elements of the siphosome, sometimes elongating into large dumbbell-like structures dangling below the siphosome or extending to form trumpet-like tubes of enormous lengths (Fig. 2a). In the latter case the mouth region reached a diameter larger than that of the entire corm, and this region could attach itself to the glass or to the small gravel stones on the bottom of the aquarium. However, mouths of the extremely elongated gonopodpalps were not observed to come into contact with the tentilla of the tentacles. Such a "feeding behaviour" was observed for *Thermopalia taraxaca*, but in that case it involved the type I gastrozooids (Pugh, 1983). When a small *Artemia larva* was placed, with a pipette, amongst the tentacles it was obviously paralysed but did not stick to them. Extension of the gastrozooids was never observed, and they appear to be relatively passive elements on the corm.

Remarks

The new species described herein clearly belongs to the rhodaliid genus *Archangelopsis*, as the specimens possess the characteristic combination of a smooth walled pneumatophore and an aurophore bearing numerous papilliform appendages. The presence of monogastric cormidia, bearing only type II gastrozooids, and borne

on long, stout stalks is also characteristic of the genus. In order to establish the morphological differences between *A. jagoa* and the only other species in the genus, *A. typica*, the specimen of the latter described by Bigelow (1913) and collected to the south of Japan during an Albatross expedition in 1906 was examined. This specimen is housed in the collections of the National Museum of Natural History, Smithsonian Institution, as catalogue number U.S.N.M. 32993, and we are grateful to the Museum for generously loaning the material. The three specimens of *A. typica* that were described by Lens and van Riemsdijk (1908), from material collected in the Dutch East Indies, have all been sectioned, but the resulting histological slide collection has not been located (see Pugh, 1983).

It should be noted that whereas the specimens of *Archangelopsis jagoa* were collected intact by submersible, all those of *A. typica* were collected in trawls and consequently were greatly damaged. Therefore, not all of the morphological characters of *A. jagoa* can be compared directly with those of *A. typica*. In addition, many of the external features of *A. jagoa* changed during fixation and preservation, mostly due to shrinkage, which in extreme cases impeded detailed investigations of the preserved material. However, this was also the case for the specimen of *A. typica*.

The pneumatophore of *Archangelopsis jagoa* (diameter 1.7-2.6 mm after preservation) is distinctly smaller than that of *A. typica* (diameter 4.5-10 mm). Such differences in size might be considered as being related to the age of the specimens, but observations on the size distribution of the population of *A. jagoa* in the Gulf of Akaba indicate that the two paratypes are of average size, while the holotype is amongst the largest observed. In addition, the size difference between the pneumatophore of the smallest specimen of *A. jagoa* and the largest of *A. typica* is far in excess of that found for any other individual rhodaliid species (see Pugh, 1983). Further, although the development of the corm of the rhodaliid species is not fully understood, it would appear impossible, on the basis of the discussion of this subject by Pugh (1983), for the specimens of *A. jagoa*, the holotype of which appears to be fully mature, to expand sufficiently to reach the size of the largest *A. typica* specimen. Besides which a concomitant increase in the size of the pneumatophore would be extremely unlikely.

Although such comparisons may appear only relative, there are other corroborative features demonstrating that we are dealing with different species and not with size differences within the same species. For instance, the holotype of *Archangelopsis jagoa* (pneumatophore diameter 2.6 mm) has 30-35 papilliform appendages on its aurophore, as compared with 27 on the *A. typica* specimen (pneumatophore diameter 9 mm). This similarity in the number of appendages, together with the great difference in size of the specimens, cannot be reconciled with any suggestion of growth stage differences of the same species. Also, the fact that the two smaller paratypes of *A. jagoa* have only eleven or thirteen such appendages indicates that, as the animals expand, further appendages can be added. The difference in the number of nectophores, ten or

less in *A. jagoa* as compared with c. 26 in *A. typica*, would also appear to be too great to be age-related.

Bigelow (1913) stated that each appendage on the aurophore of his Albatross specimen of *Archangelopsis typica* had a terminal pore. However, we were unable to confirm this after a re-examination of the specimen. In *A. jagoa* we believe that the only pore present is the central excretory pore. However, final proof of the presence or absence of pores on the other appendages would only come from sectioning the specimen. Nonetheless it appears, from the sections through *A. typica* figured by Lens and van Riemsdijk (1908), that they only found a central excretory pore. Indeed re-examination of the Albatross specimen, despite the fact that the aurophore has been cut in half, reveals that a central pore probably is present.

One of the paratypes of *Archangelopsis jagoa* shows a feature that is unique amongst all the known specimens of rhodaliid siphonophores. This is the presence on the aurophore of a widely open external pore, with a canal extending from it that connects directly with the pneumatostomus of the pneumatophore. At first sight, the canal would appear to represent a pneumatic duct allowing the venting of excess gas from the pneumatophore directly to the outside. Haeckel (1888) believed that such a structure was present in his specimens of *Rhodalia miranda* Haeckel, 1888, but those specimens do not show a widely open external pore. Nonetheless, the presence of such a canal was discounted by Bigelow (1913) and, as discussed by Pugh (1983), it is generally believed that a pneumatic duct is absent. The external pore is thought to be an excretory opening only into the pericystic cavity of the aurophore. This is the arrangement that Lens and van Riemsdijk (1908) illustrated for their specimens of *A. typica*, although it should be noted that they considered the papilliform appendages on the outside of the aurophore to be the zones of proliferation of the nectosome and siphosome. In the present case, the canal certainly has the appearance of a pneumatic duct but we cannot exclude that it is an artifact caused by the rupture of the pneumatophore. The silvery lined canal is considered to be the chitinous tube that lines the gas-secreting area of the pneumatophore and which, in rhodaliids, lies within the aurophore itself. It is suggested that the distal end of this tube has been ruptured, by excessive gas expansion within the pneumatophore, as Pugh (1983, Fig. 36) found to be the case in *Thermopalia taraxaca*. Somehow the distal end of this tube then came in contact with and was surrounded by the excretory pore, and the contents of the gas gland were blown out by the expanding gas. If this is the case, then one might expect to find some damage to the external end of the canal, but the opening was found to be smooth, without any signs of tearing.

The total number of siphosomal cormidia on the Albatross specimen of *Archangelopsis typica* was estimated to be c. 30, while the *A. jagoa* specimens possess about 13-20. In both species a bract was originally attached at the base of the stout cormidial stalk, although the evidence in the former species was based largely on the presence of attachment lamellae, and Pugh (1983) found only a single small bract in the fragments of the Albatross specimen. This bract appeared to be either young or vestigial and so it is difficult to make comparisons with those of *A. jagoa*

although, in general appearance, it does resemble them. However, in *A. typica* there was evidence for the development of a secondary cormidium, with an associated bract, at the base of the main cormidial stalk (Pugh, 1983). Such secondary cormidia were never observed on the specimens of *A. jagoa*.

Type I gastrozooids, with simple unbranched tentacles, are absent in *Archangelopsis jagoa*, as is the case for *A. typica*. In both species the type II ones are similar in design. However, certain important differences are found in the detailed structure of the tentacles. In *A. jagoa* the whole of the tentacle is segmented and tentilla are attached along its entire length, except at the distal end. As the latter is the region of the tentacle that is attached to the substrate, it is probable that, in life, the tentilla have been abraded off, as stumps of the pedicles can still be seen. In the Albatross specimen of *A. typica* the proximal part of the tentacle is not segmented, but bears a series of knobs, of varying sizes, on its dorsal surface. These may be young tentilla buds, but such an arrangement was not seen on the *A. jagoa* tentacles. Most of the tentilla originally attached to the Albatross specimen have been lost but, judging from the stumps of their pedicles, they were mainly attached to the mid region of the tentacle. Although there may be differences in the structure of the tentilla in the two species, the most important taxonomic feature is their point of attachment on the tentacle segments. In *A. jagoa* the tentilla are attached to the proximal end of each segment, embedded beneath a distal swelling of the more proximal segment (Fig. 5). In *A. typica* they are attached to the distal end of a highly contracted segment (Fig. 8). This is a very distinctive feature.

The preserved gonopapils of both *Archangelopsis* species look very similar and it is unfortunate that we cannot compare their coloration in life. The most impressive feature of the living gonopapils of *A. jagoa* is their ability to

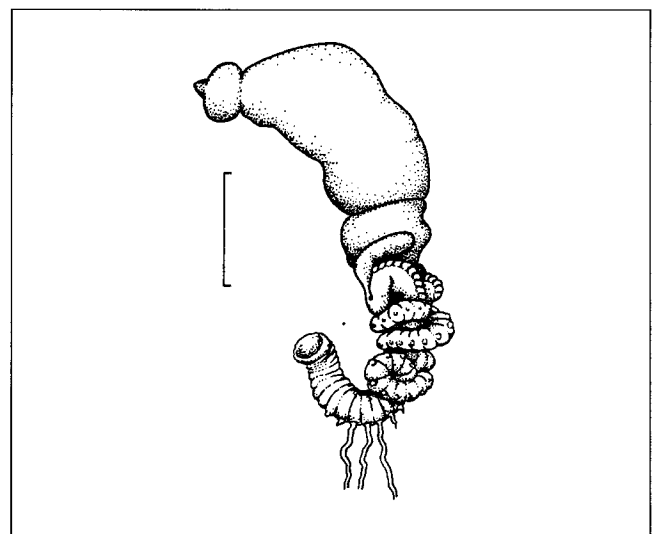


Figure 8

Archangelopsis typica. Type II gastrozooid with annulated tentacle. Proximal part of tentacle with knobs; each tentacle segment with pedicle stump of detached tentilla; distal end of tentacle is broken off. Scale = 1 mm.

expand to form trumpet-like structures of enormous length. Although the mouths of the expanded gonopalpons were observed to attach themselves to the aquarium walls, or to pebbles, it is doubtful whether attachment is their main function. It is more likely that the gonopalpons play an important role in the feeding behaviour of the animals. In holoplanktonic siphonophores transference of food items, ensnared or paralysed by the nematocysts on the tentacles/tentilla, to the mouth of a gastrozoid is generally achieved by the contraction of the tentacle. However, in the benthic rhodaliids, where the tentacles are used to tether the animal to the substrate, the release of a tentacle might prove precarious. Pugh (1983) suggested, from studies of videos of in situ specimens of *Thermopalia taraxaca*, that the role of food transference had been taken over by the type I gastrozooids. Greatly extended examples of these gastrozooids were seen to move actively amongst the tethering tentacles, as if searching for captured food items, and also to arch back to touch the corm, as if in the process of transferring the food.

Although this may be feeding behaviour for the species in other rhodaliid genera, it cannot be the case for *Archangelopsis* species as type I gastrozooids are absent. In these species, it appears that the role of food transference is carried out by the numerous gonopalpons. However, we never observed the mouth regions of the gonopalpons of *A. jagoa* to be placed directly onto the tentilla of the tentacles. In addition, no food items were found inside the gonopalpons, but clusters of (?) nematocysts were. Nevertheless, a comparison of the video-tape recordings of *Thermopalia taraxaca* and the observations on the living specimens of *A. jagoa* revealed an impressive similarity in the activity of the type I gastrozooids of the former and the gonopalpons of the latter. If the gonopalpons of *A. jagoa* have the role of food transference, then this species is the first rhodaliid known to use this technique. However, Pugh (1983) did note that some of the preserved gonopalpons of *Rhodalina miranda* Haeckel 1888, possessed a distinct terminal chamber that appeared to open to the exterior by a highly expandable mouth. Thus it is possible that they may play a similar role to those of *A. jagoa*, but there are no in situ observations to demonstrate this. The probability that the various rhodaliid species use different structures for food transference opens the interesting question as to which was originally evolved for the role, the gonopalpon or the type I gastrozoid.

In summary, *Archangelopsis jagoa* is distinguished from *A. typica* by the smaller size of its pneumatophore in combination with, in the largest specimen at least, a similar number of papilliform appendages to the aurophore; by the fact that its tentilla are attached to the proximal end of the tentacular segment; by the smaller number of nectophores; and by the absence of secondary cormidia. The structure of the bract may also be characteristic, but we know little about those of *A. typica*. In addition, the geographical separation between the sites of collection is indicative of species separation. The four known specimens of *A. typica* were collected either in the region of Indonesia (Lens and van Riemsdijk, 1908) or at the southern tip of Japan (Bigelow, 1913). The c. 41.5° latitudinal difference between these localities is the largest range of distribution for any of the known rhodaliid species. Nevertheless, the Gulf of Akaba is separated from these localities by c. 80-90° of longitude; over twice the distance between the *A. typica* collection sites. Furthermore, the *A. jagoa* material represents the first record for a benthic siphonophore not only in the Red Sea, but for the entire Indian Ocean. Both facts suggest that the specimens of *A. typica* and *A. jagoa* belong to different species. In addition *A. typica* was collected at depths between 100 and 183 m (Pugh 1983), while *A. jagoa* was never found at depths shallower than 200 m. However, although each rhodaliid species appears to have a fairly limited depth range, the actual distribution within this range might be influenced by local differences in, for instance, the type of the bottom sediment or the slope angle. Thus the small differences between the depth distribution of the two *Archangelopsis* species may not be significant.

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REFERENCES

- Ballard R.D., J.F. Grassle (1979). Return to oases of the deep. *Natn. geogr. Mag.* **156**, 689-703.
- Bigelow H.B. (1913). Medusae and Siphonophorae collected by the U. S. Fisheries Steamer "Albatross" in the northwestern Pacific, 1906. *Proc. U. S. Natn. Mus.* **44**, 1-119.
- Haeckel E. (1888). Report on the Siphonophorae collected by H.M.S. Challenger during the years 1873-1876. *Rep. Sci. Res. H.M.S. Challenger (Zool.)* **28**, 1-380.
- Hessler R.R., W.M. Jr. Smithey (1984). The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. In : Rona, P. A., Bostrom, K., Laubier, L., Smith jr., K. L. eds. Hydrothermal processes at seafloor spreading centers. Plenum Publishing Corporation, p. 735-770.
- Lens, A.D., T. Van Riemsdijk (1908). The Siphonophora of the Siboga Expedition. *Siboga-Expeditie (Siboga Expedition)* **9**, 1-130.
- Pugh P.R. (1983). Benthic Siphonophores. A review of the Family Rhodaliidae (Siphonophore, Physonectae). *Phil. Trans. R. S. London B* **301**, 165-300.