In situ observations on benthic siphonophores (Physonectae: Rhodaliidae) and descriptions of three new species from Indonesia and South Africa

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Abstract Three new species of siphonophores (Rhodaliidae), a little known, uniquely benthic, family of Physonectae (Hydrozoa, Cnidaria), are described from specimens observed and collected at depths between 120 and 360 m off Indonesia and South Africa by the submersible JAGO. Special reference is made to *in situ* observations and video close-ups that revealed detailed information on locomotory, fishing and feeding behaviour.

Key words *Tridensa*, *Arancialia*, *Archangelopsis*, Rhodaliidae, Physonectae, Siphonophore, new species, *in situ* observations

Introduction

The Rhodaliidae, a small family of short-stemmed Physonectae, are unique among the siphonophores in that they have adopted an atypical way of life. Instead of being planktonic, as are the vast majority of their numerous relatives, they have become benthic. They attach themselves to the seabed by means of their greatly extended tentacles, while the main body floats above the substratum, like a tethered air balloon. First specimens of this unusual family were collected during the *Challenger* and *Albatross* expeditions in 1874 and 1883, respectively, and described by Haeckel (1888) and Fewkes (1886). Presently, eleven species are known to science; occurring at depths between 60 and 3100 m (for a review see Pugh, 1983; Hissmann *et al.*, 1995).

Little is known, however, about the behaviour and life history of these unique animals due to their relative inaccessibility in deep waters. *In situ* observations on benthic siphonophores using manned submersibles so far have been made on only three species, *Dromalia alexandri* (Fager, Flechsig and Vernon, 1968, 1971; recapitulated by Pugh, 1983: 254), *Thermopalia taraxaca* (Ballard & Grassle, 1979; Hessler & Smithey, 1984), and *Archangelopsis jagoa* (Hissmann *et al.*, 1995). The last two species were collected by submersibles using special sampling devices whereas all the other rhodaliid specimens, reported in the literature, have been caught in nets, mainly bottom trawls and dredges. Most of these latter specimens are, therefore, incomplete and partly damaged. The use of submersibles and ROVs, in contrast, offers the opportunity to combine *in situ* observations of deep-living animals with more gentle sampling techniques. Fragile organisms, like siphonophores, can thus be brought to the surface without severe damage and can often be kept alive, thereby facilitating further observations in captivity as was the case in the present study.

Benthic siphonophores of four different species have been found recently during dives of the manned submersible 'JAGO' at several locations in Indonesia, off the Comoro Islands (West Indian Ocean) and off the Cape Peninsula (South Africa). The submersible was equipped with a high-resolution wide-angle video camera that could be placed in very close proximity to the specimens. Thereby it provided close-ups of the organisms and allowed observations on their behaviour, much of which had never been documented before. The video images of the newly discovered siphonophores, for example, provided the first detailed *in situ* observations on the feeding behaviour of this little known family. They also gave information on the natural shape and coloration of the colonies, which can be useful taxonomically, but which can change considerably after preservation.

Three of the four species are new to science. The Comoran specimens, which are the first records for a benthic siphonophore in the entire Indian Ocean, belong to the species previously reported from the Red Sea (Hissmann *et al.*, 1995). The first part of this paper is devoted to the taxonomic description of the new species, and the second part comprises observations on living animals.

Methodology

Two different methods were used to collect the animals, which were very small in size, from the seabed. The Comoran and South African specimens were sampled with a glass cylinder that was closed at its top and open at its base. The cylinder was placed over the specimen and gently shaken until the animal dislodged its tentacles and rose up inside the cylinder. The cylinder was then stored for the remainder of the dive within a slightly larger tube with a closed bottom. The sampling device for the Indonesian siphonophores was a modified tea infuser made of two hinged halves that could be opened and closed by the submersible's manipulator arm when placed over the animal. This method guaranteed a complete sampling of the colony; the only components that were partly lost were the distal ends of the tentacles. Back on board ship, the specimens were transferred into a glass aquarium filled with cooled seawater where they were observed and photographed. Afterwards they were preserved in 4% formalin.

Two specimens of *Dromalia alexandri* and one specimen of *Thermopalia taraxaca* were kindly loaned to the author by P.R. Pugh (Southampton Oceanography Centre) and re-examined for this study.

Terminology

The terms used to describe the many types of structures ("individuals") on siphonophores are explained in detail by Pugh (1999). The typical morphology of benthic siphonophores has also been described previously by Pugh (1983) and Hissmann *et al*. (1995) and is therefore not repeated herein. Definitions are restricted here to those terms that are essential for the identification of rhodaliids but might cause confusion.

The **aurophore** (see Figs 2, 8a) is the gas-producing gland attached to the dorsal side of the apical, gas-filled float (pneumatophore); its external surface is either smooth or has numerous papilliform appendages.

A rhodaliid **cormidium** (see Figs 3, 10, 13) is a cluster of elements that typically consists of a single type II gastrozooid (feeding polyp) with a branched tentacle, one or more bracts (structures with a protective function), and **gonodendra**, branches that carry numerous gonophores (sexual structures) and gonopalpons (palpons assisting in feeding and ? excretion).

The cormidial elements can be borne on a common stem. The whole cluster is then termed a **cormidial unit**. If the cormidial unit consists of only a single cormidium, then it is termed **monogastric**, which means it carries only a single gastrozooid (see Figs 10, 13). However, the cormidial unit can become **polygastric** (see Fig. 3), if a second cormidium branches off the stem of the original one and further cormidia branch off the stems of their predecessors. The basal part of such a multiple-branched unit, formally the **stem** of the first cormidium, becomes then the **stalk** of the cormidial unit. The terms 'stalk' and 'stem', in reality synonyms, are hereafter used to distinguish between the basal stalk of a polygastric cormidial unit and the stems of the further cormidia branched off from the original. The length and thickness of the stalk is used for species recognition. The stalk of the cormidial unit is either a simple narrow tube that is directly attached to the main body of the colony (the **corm** of the siphosome) or it is swollen at its base forming pronounced elevations on the corm. These elevations are termed **cormidial bases** (Pugh, 1983). It is unclear, whether they are simply basal thickenings of the first cormidial stem or separate outgrowths of the siphosome.

A feature that distinguishes rhodaliids from all other physonect siphonophores is the possession of two types of gastrozooids; only one of these gastrozooids carries a tentilla-bearing tentacle. This latter type is termed a **type II gastrozooid** (see Figs 3, 10, 13). It is the constituent component of a cormidium (see above). The second type, the **type I gastrozooid** (see Figs 2, 7, 12) is usually enlarged in comparison with type II and possesses, at its base, and only in an early stage of development, an annulated tentacle without tentilla. This tentacle becomes detached before the type I gastrozooid is fully mature. Type I gastrozooids either form part of a cormidial unit or are attached singly to the corm on separate pedicles.

A typical rhodaliid **gonodendron** is a separate branch on the cormidial stem that bears numerous gonophores and gonopalpons on a common stalk (see Fig. 10). If gonodendra are absent and gonophores and gonopalpons are attached directly to the cormidial stem, then the latter are generally referred to as **palpons**. In most siphonophore species, palpons bear a small tentacle or **palpacle**. Rhodaliids are **dioecious**, in that all gonophores of a single specimen are of the same sex.

The **bracts** or protective structures occur singly or in multiple numbers on a cormidial unit (see Figs 6, 7, 11, 14). They are either attached to the cormidial stalk at the very base of the cormidial unit, and/or to the cormidial stems, or to the gonodendral stalks. The shape of the bract and its point of attachment are used for species recognition.

The **zone of proliferation** (see Fig. 8b) embraces two budding points; one for the nectophores and one for the siphosomal elements. Both points lie very close together apically on the ventral side of the nectosomal region, the side opposite to the aurophore. Presumably, the one for the nectophores lies immediately above the other. Nectophoral buds are passed out either to the left or right side of their budding point and move laterally on the nectosome. Buds arising from the budding point for the siphosomal elements pass directly downwards and travel on a vertical line towards the siphosomal corm.

Systematic account

Genus *Tridensa* gen. nov.

Diagnosis

Rhodaliid siphonophore with smooth-walled pneumatophore and aurophore. Pneumatophore distinctively pigmented, with irregular radial stripes of orange, red and white colour. Aurophore globular, without papilliform appendages or tubercles, but with pronounced single central pore. Nectophores colourless, nectophoral canals pigmented. Nectosomal and siphosomal corm with central cavity. Cormidial units with short slender stalk that bifurcates immediately at its base into two long and slender main cormidial stems. Large type I gastrozooids attached singly and separately to the corm on short pedicles. Bracts attached to base of cormidial units. Bracteal canal divided, on the triangular-shaped distal facet, into three distinct branches.

Tridensa sulawensis sp. nov.
Figs 1a, 1e, 2–7

Material examined

Type material. One specimen (holotype, male) collected during dive 658 of the submersible JAGO on 17 November 1999 at 205 m depth off the west coast of the volcanic island Sangihé, northeast Indonesia (03°39.34′N, 126°24.19′E). This specimen is housed in the invertebrate collection of the Natural History Museum in London, Regd. No. 2004.2103.

Second specimen (paratype, male) from JAGO dive 679, 01 December 1999, 01°24.26′N, 124°38.93′E, collected at 221 m depth on rocky ground in the Bay of Tanawangko, north coast of the northern arm of Sulawesi, Indonesia.

In addition, numerous observations on live specimens of this species were made during a series of submersible dives performed along the north and south coasts of the northern arm
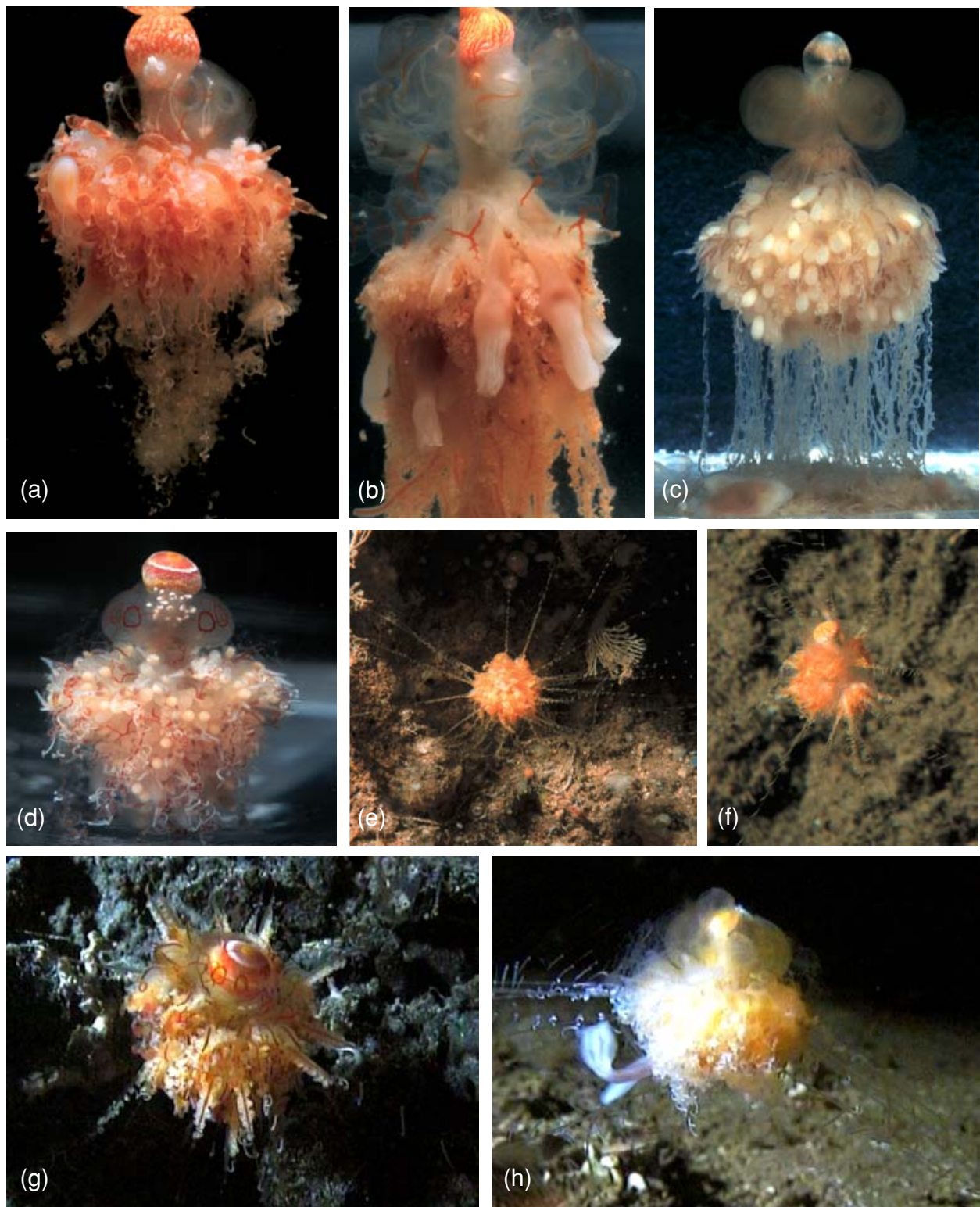
Figure 1 Benthic siphonophores. Photographs of living animals. (a) – (d) aquarium, (e) – (h) natural environment. (a) *Tridensa sulawensis* sp. nov., male holotype, note the white aurophore on the colourful pneumatophore, and two type I gastrozooids visible at left side of siphosome. (b) *Tridensa rotunda* sp. nov., male holotype, note deformed colourful pneumatophore, bracts with trifid bracteal canal visible at upper edge of siphosome, and large type I gastrozooids on siphosome. (c) *Arancialia captonia* sp. nov., male holotype, note almost transparent pneumatophore, pale orange nectophores, long cormidial stems attached to base of nectosome, and detached type I gastrozooid on bottom of container. (d) *Archangelopsis jagoa* from Grande Comore, male, note pigment rings on pneumatophore, white papilliform appendages on aurophore, dark red coloration of radial canals on nectophores, bracteal canals of bracts and tentacles. (e) *Tridensa sulawensis* sp. nov. at 239 m, Bunakeng Island. (f) *Tridensa rotunda* sp. nov. at 289 m, Bay of Tomini North Sulawesi. (g) *Archangelopsis jagoa*, female, at 174 m depth, Grande Comore. (h) *Arancialia captonia* sp. nov., male, at 125 m in Table Bay, Cape Town, note type I gastrozooid ingesting prey attached to tentillum of tentacle, and extended tentilla in fishing posture.
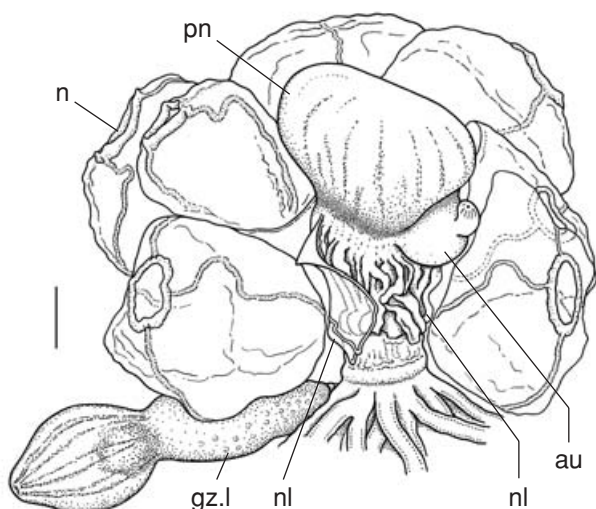
Figure 2 *Tridensa sulawensis* sp. nov. Details of the preserved holotype. Slightly deformed pneumatophore (pn), aurophore (au) with pronounced central pore, nectosome with still attached nectophores (n), transparent nectophoral lamellae without attached nectophore, shrunken nectophoral lamellae (nl) forming shrivelled ridges, and type I gastrozooid (gz.l) with food particle inside the slightly transparent proboscis. Scale 1 mm.

of Sulawesi, and Bunaken and Sangihé Islands, all in Indonesia (see below).

Diagnosis

Aurophore whitish in colour. Nectophores with four bright orange radial canals of which the two lateral ones are S-shaped. Nectosomal and siphosomal corm orange in colour. Cormidial units polygastric. No distinct gonodendra; gonophores and palpons attached directly to the cormidial stem. Proximal part of mature bracts expanded but still slightly smaller in diameter than the large triangular-shaped distal facet; corners of distal facet rounded. Bracteal canal pigmented along the upper two thirds of its length, dividing distally into three branches each of which splits again into two recurved sub-branches.

Description

The holotype of *Tridensa sulawensis* measured 12 mm in greatest diameter and about 13 mm in height when preserved, the paratype about the same. The overall colour of the animals *in situ* was bright orange (Fig. 1a). However, many components lost their original coloration during preservation, and some of them, particularly the nectophores, bracts and type I gastrozooids became detached from the animals. The holotype was frontally sectioned through its middle; the paratype being left intact.

PNEUMATOPHORE. The pneumatophore was smooth-walled and generally rounded, although sometimes *in situ* slightly flattened apically. It was deformed to an ellipsoidal shape when brought to the surface and then measured about 3 × 2 mm (Fig. 2).
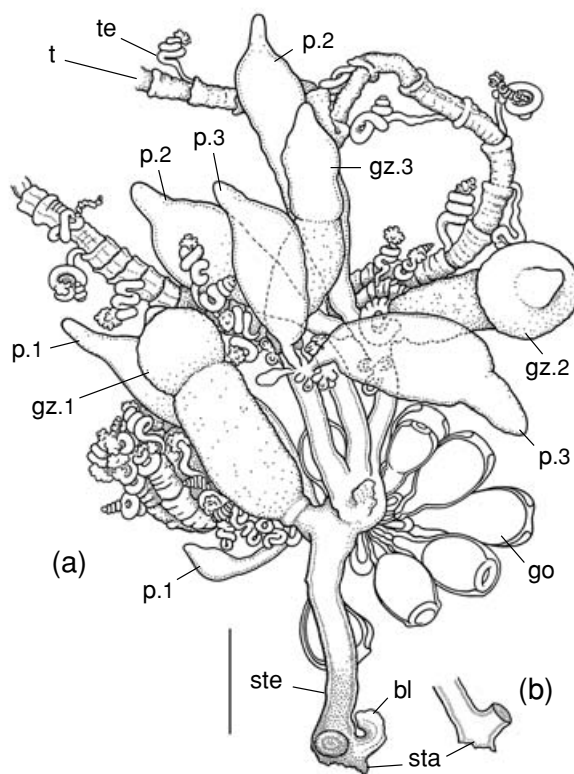
Figure 3 *Tridensa sulawensis* sp. nov. Single stem (ste) of a bifurcated polygastric cormidial unit of male holotype (second stem cut off at base, see lateral view (b)). Shrivelled bracteal lamella (bl) at base of stalk (sta), bundle of male gonophores (go), three type II gastrozooids (gz.1 to gz.3) with tentacles (t) and tentilla (te), six palpons (p.1 to p.3; numbers indicate with which gastrozooid they are associated). Scale 1 mm.
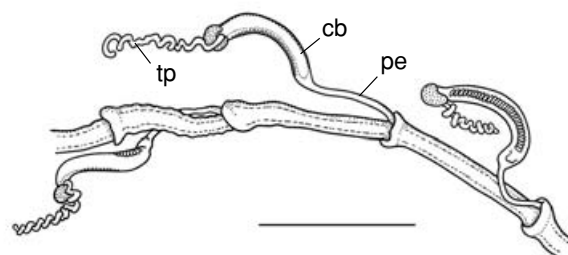
Figure 4 *Tridensa sulawensis* sp. nov. Details of an outstretched tentacle from a type II gastrozooid with tentilla attached at the proximal end of each tentacular segment. Tentillum with pedicle (pe), cnidoband (cb) with horseshoe-shaped swelling at its distal end, and terminal process (tp). Scale 1 mm.

In life, the pneumatophore was strongly pigmented (Fig. 1a). Its apical pole was usually bright orange, but in some observed specimens it was slightly translucent. The widest part of the pneumatophore was traversed by an irregular arrangement of red coloured radial lines and stripes, which alternated with shorter white stripes. The lower part of the pneumatophore
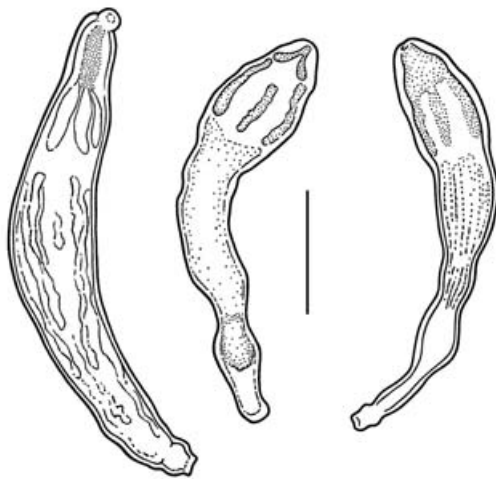
Figure 5   *Tridensa sulawensis* sp. nov. Various shapes of detached palpons (terminal region at distal ends facing upwards). Scale 1 mm.
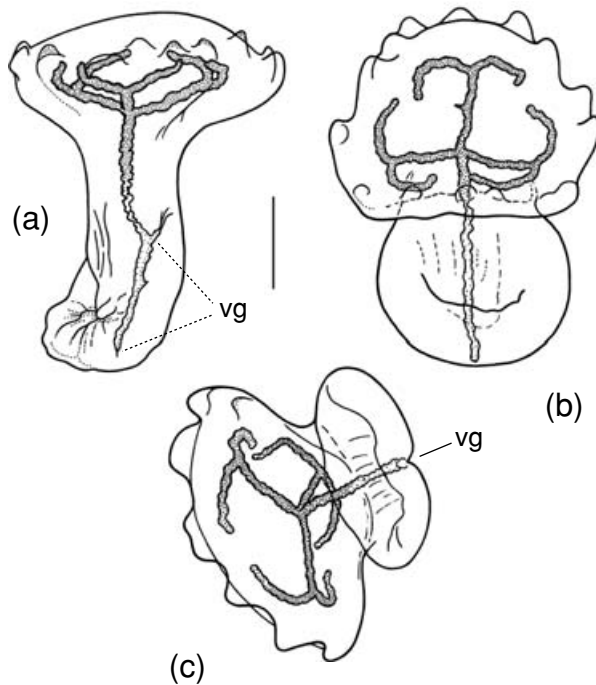
Figure 6   *Tridensa sulawensis* sp. nov. Detached mature bracts, (a) lateral, (b) dorso-apical, (c) dorso-proximal view, ventral groove (vg). Scale 1 mm.

had a whitish coloration, clearly separating the pneumatophore from the almost transparent nectosome below. When transferred into formalin, the colour of the pneumatophore changed to a uniform dark red, which after some time became light orange. The gas-filled cavity inside the pneumatophore was visible as an inverse pear-shaped structure, discernible by its chitinous silvery lining, the pneumatocyst. This layer, which was water repellent and difficult to cut through, completely lined the gas-filled cavity except in the region of the aurophore where it was covered by a milky-white coloured

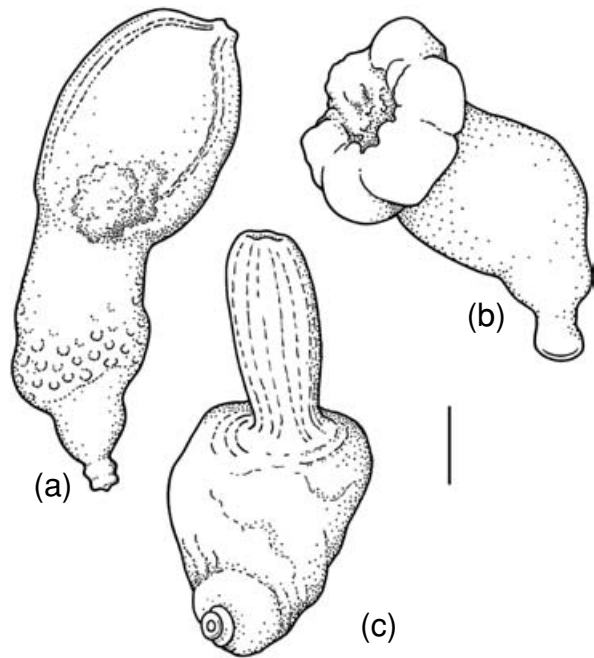**Figure 7**   *Tridensa sulawensis* sp. nov. Detached type I gastrozooids, (a) with endodermal villi visible through the outer wall of the stomach region and amorphous food particle inside the slightly transparent proboscis, (b) mouth widely open and curled back, (c) mouth region contracted. Scale 1 mm.

tissue. The basal part of the gas-filled cavity protruded into the upper part of the hypocystic cavity of the nectosome.

AUROPHORE. The aurophore, the gas-secreting area, projected dorsally from the basal part of the pneumatophore (Fig. 2). It was a smooth-walled globular structure that was attached to the pneumatophore by much of its proximal surface. It possessed a pronounced central pore and was usually whitish in colour (Fig. 1a). The diameter of the aurophore (*c*. 1.3 mm) was about one third of that of the pneumatophore. A large number of small gas bubbles escaped through the central pore of the aurophore of the holotype when it was brought to the surface, and also later when the specimen was still alive and attempted to attach itself to the bottom of the aquarium. The view from inside the pneumatophore onto the milky gas gland tissue of the aurophore revealed no obvious duct through the gland, but a translucent spot was present in its centre.

NECTOSOME. The nectosome, the region immediately below the pneumatophore, was, in the preserved state, as wide as the pneumatophore was high, so that the pneumatophore had a broad connection to the rest of the colony (Fig. 2). It had a cylindrical shape and could reach 1.3 mm in diameter and 2.3 mm in height, in life even more. The lower third of the nectosome in the holotype was free of muscular nectophoral lamellae, bright orange in colour and had a slightly thickened rim basally; clearly demarcating it from the corm of the siphosome below. The hypocystic cavity within the nectosome was voluminous in its upper part but became constricted to a narrow axial canal, by its thickened walls, below. This canal continued directly into the siphosome (see below: *Siphosome*).

The muscular lamellae of the nectophores (or swimming-bells) were long and narrow, stretching down from the lower edge of the pneumatophore to about two thirds of the height of the nectosome (Fig. 2). The lamellae to which nectophores were still attached differed considerably in shape and consistency from those that were already devoid of nectophores. When the nectophores were still attached, the lamellae were thin transparent tissue sheets, whose upper and lower ends were elongated to form a U-shaped structure that extended over the proximal half of the rounded nectophore. The two elongated tips of the lamella seemed to be only weakly attached to the surface of the nectophore. The gastrovascular canal, which branched off from the nectosomal cavity, ran through the lower part of the lamella and linked with the basal part of the nectosac where its four radial canals originated. The nectophoral lamellae shrank to shrivelled ridges and retracted their elongated tips when nectophores became detached (Fig. 2).

All the nectophores had the same rounded bag-like appearance of a medusa with very thin transparent walls (Fig. 1a, 2). The circular canal around the ostium, the opening of the subumbrella cavity, was colourless and slightly opaque, while all four radial canals were bright orange in life, but lost their coloration after preservation. The two lateral radial canals were S-shaped, while the dorsal and ventral canals had almost straight courses. The largest diameter of a nectophore was 4 mm. The holotype possessed nine nectophores and about nine nectophoral lamellae without nectophores when brought to the surface, all arranged around the nectosome in a single corona. There were no large gaps between the lamellae, some of which appeared to extend below the aurophore. They might have been pushed together by newly formed nectophores moving laterally on both sides from the ventral zone of proliferation. A tiny nectophore was found on each side of the actual budding point in the zone of proliferation. The paratype had only two nectophores attached to the nectosome when investigated in the aquarium; additional nectophores might have become detached during capture. Both nectophores were invaginated and completely covered the nectosome on both sides between the zone of proliferation and the aurophore. Two transparent tissue sheets showed that at least two more nectophores were attached to the nectosome in life, and three to four contracted nectosomal lamellae were found on each side of the aurophore. They were not as densely packed as in the holotype.

ZONE OF PROLIFERATION. In the holotype, six to seven developing type I gastrozooids and at least two to three type II gastrozooids were attached in one line from the siphosomal budding point over the entire length of the nectosomal region down towards the siphosomal corm. The most apical type I gastrozooids possessed a highly coiled tentacle that was segmented but did not bear tentilla. The lowest type I gastrozooids lacked tentacles. They were clearly recognisable as type I gastrozooids by the numerous endodermal villi within their slightly transparent stomach regions. The young type II gastrozooids possessed segmented tentacles bristling with tentilla. On the paratype this area was densely packed with young type I gastrozooids with or without tentacles.

Siphosome. The siphosome of the preserved holotype had a size of 12×6 mm; that of the paratype was about the same (including the appendages). The siphosomal corm itself was a small bulbous sac. In the preserved holotype it measured 1.5 mm in diameter and about 2 mm in height, was bright orange in colour and was well demarcated from the lower edge of the nectosome. The siphosomal corm of this specimen consisted of a thick and slightly bloated wall, which was orange throughout in colour. The lumen of the corm was restricted to a small axial cavity from where individual canals branched off into the cormidial stalks. No other canals were present within these thick walls. It is possible that the thickness of the wall and the constriction of the siphosomal cavity were due to a strong contraction during preservation.

The exact arrangement of the cormidial units around the corm was impossible to discern. Most of the larger cormidial units were arranged in two main clusters on the lateral surfaces of the upper half of the corm, close to the lower edge of the nectosome. Each cluster consisted of about five cormidial units. A few others were attached to the base of the corm. Most of the latter were smaller than the more apical ones; some of them were at an early stage of development.

The cormidial units were not borne on pronounced bases, as in several other rhodaliid species. Each mature unit had a very short and narrow common stalk that bifurcated almost immediately at its base into two equal slender stems (Fig. 3). In some units, the common stalk was so short that the cormidial stems appeared to arise directly in pairs from the corm. Their origin from a common point, however, was still discernible by the single gastrovascular canal that branched off from the siphosomal cavity and immediately split in two branches (Fig. 3b). In the holotype, both cormidial stems had a diameter of about 0.3 mm and were bright orange at their base. In older units, the first type II gastrozooid was attached by a short pedicle to the main cormidial stem at a height of about 2 mm (Fig. 3a). Immediately above the attachment point of the gastrozooid the cormidial stem was slightly thickened. Attached to this thickening were two palpons, also with short pedicles, and a cluster of mature gonophores. Above the thickening the stem divided into further cormidia. These often split off in pairs but had slightly thinner and shorter stems than the two basal ones. Each of the secondary cormidial stems (and those of higher order) carried a single type II gastrozooid at its distal end, flanked by at least two mature palpons on short peduncles, and, further below, a cluster of buds that appeared to be destined to develop into gonophores (Fig. 3a). The young cormidia at the base of the corm often had only a single type II gastrozooid attached to the distal end of the stem, while other cormidia had a type II gastrozooid, flanked by two palpons and several smaller buds. In the paratype, the main cormidial stems did not give rise to further cormidia, probably a result of age and stage of development. As in the holotype, both main stems distally formed a short pedicle that carried a type II gastrozooid and a thickening to which numerous gonophores, small buds and up to four palpons were attached. The different arrangements of elements on 'mature' cormidia compared with young cormidia can be explained as follows. The main cormidial stem gives rise to further cormidia at a point just

below the most proximal gonophoral buds. Consequently, the first type II gastrozooid, (originally the most distal element on the stem) and the part of the stem to which the palpons and gonophores are attached, are both pushed aside by the developing secondary cormidium. In this way, the original first cormidial elements come to lie proximally on the stem.

Tridensa sulawensis must be considered as polygastric, since the cormidial units possessed several type II gastrozooids. These gastrozooids had, in the preserved state, a pear-shaped proboscis, which was usually distinctly separated from the stomach region by a deep constriction (Fig. 3a). They had a total length of 2–3 mm, of which the proboscis took up about one third. The central stomach region was not translucent and usually orange in colour. A longitudinal section through this region showed that the body wall of the gastrozooid consisted of large, bloated cells that could easily be peeled off from a central tube. Endodermal villi, as present in the stomach region of the type I gastrozooids (see below), were absent. The basal basigaster was short and bore a large tentacle.

The tentacle was annulated and thinner at its base. A fine suspensory ligament ran along its ventral surface; a bright orange gastrovascular canal through its central axis. The most proximal part of the tentacle was not segmented. Buds of tentilla were attached to the dorsal surface of this part and to the first short segments. They increased in size and length with each successive segment and became spirally coiled. The tentillum was attached at the proximal end of each segment, embedded below a distal swelling of the more proximal segment (Fig. 4). Tentilla were absent on numerous segments, mainly toward the distal end of the tentacles. They either had been lost during handling, or had already become detached in life, as *in situ* video images of the specimens showed (see below). Detached tentilla did not leave stumps or any other traces of their former attachment to the segments.

The tentilla of the preserved tentacle were filiform structures. Those at the proximal end of the tentacle were often highly coiled, while those at the distal end were less coiled and even sometimes fully stretched out. Each tentillum consisted of three regions (Fig. 4); a slender, elongated basal pedicle, a cnidoband, which bore large nematocysts, and a terminal filament, which was also armed. The first two regions were penetrated by an orange-coloured canal. The basal pedicle, which bore no nematocysts, was highly contractile; its length could be less than one tenth the length of the cnidoband. In life, however, it could extend to three times the length of the cnidoband. The cnidoband was either loosely coiled or stretched out to 1 to 1.5 mm when unwound, but it seemed not to be as extensible as the other two regions of the tentillum. It was slightly flattened laterally and bore at least two types of nematocysts: large elongated nematocysts on both flanks (length c. 85 µm), and several rows of smaller rounded ones along its dorsal surface. Distally it ended in a horseshoe-shaped structure covered with rounded cells, which may be either small nematocysts or just platelets of chitinous appearance. The proximal end of the terminal filament was embedded ventrally in this structure. In its contracted state the terminal filament formed a coiled mass but when extended it reached 3 to 4 times the length of the cnidoband (see below). It was heavily armed with small rounded nematocysts, apparently all of the same type.

The palpons are termed palpons and not gonopalpons since they were attached directly to the cormidial stem and not on gonodendra. They were elongated thin-walled simple tubes with a short narrow proximal region and a pronounced terminal region that could extend to enormous length (Fig. 5). In the preserved state they could reach 4.5 mm in length and were thus slightly longer than the type II gastrozooids. Their terminal region was dark red in life and the edges of the mouth opening bore numerous small rounded nematocysts; below this red region there were four elongated stripes, which became optically dense areas of yellowish coloration after preservation. The mid-region of the palpon was partially transparent but also had many small orange-red flecks arranged in irregular longitudinal streaks. On the preserved specimens, the palpons could be roughly distinguished from the type II gastrozooids by their transparent mid-region and the lack of the constriction between the proboscis and the stomach region. On the living animal, both components were difficult to distinguish.

GONOPHORES. Both specimens were male, and none of the specimens videoed *in situ* could be clearly identified as female. The mature male gonophore was a simple white sac-like structure borne on a narrow stem, which was about as long as the rounded or square-shaped umbrella region (up to 1 mm). The numerous male gonophores formed dense tufts that could be easily recognised on the siphosome. Each bundle could consist of 7 to 18 gonophores at similar stages of development and, in between, small rounded buds. Mature gonophores were only found on the first cormidium. They were attached to the area where the main cormidial stem was thickened (Fig. 3). Gonodendra were absent on both specimens.

BRACTS. The large bracts had a very characteristic shape (Fig. 6). They measured 3–4 mm in length and were attached singly at the base of the cormidial unit on the short stalk. The attachment lamella was a simple long spur that fitted into a long groove on the ventral side of the bracteal stalk. The most proximal part of the bract was thickened and recurved dorsally, which resulted in a pocket-like depression on the dorsal surface. In the largest bracts, the diameter of the expanded proximal part was only slightly smaller than that of the distal facet. The greatly expanded distal facet was slightly convex and triangular in shape with rounded corners. It measured up to 3 mm in diameter and had recurved edges with 10 to 15 cusp-like projections (depending on the size of the bract). Each projection bore a pad of rounded cells (? nematocysts).

The bracteal canal ran straight up the ventral groove on the proximal part to about one third of the length of the bract. Up to this point, the canal was colourless. Distal to this point, it bent towards the centre of the bract where it became slightly zigzagged and dark red in colour as it then continued toward the centre of the distal facet. When it reached the distal facet, the canal divided into three branches of equal length. Each of these branches then split again into two recurved horns (Fig. 6).

No bracts were present on the holotype when investigated in the aquarium (Fig. 1a) and only a single small young bract was found among the detached components. Bracts are

one of the siphosomal elements that easily become detached; they might have been lost during the collecting procedure, or already had been lost during life. Several *in situ* video close-ups of different individuals showed that some of them lacked bracts (see below). Structures that were clearly identifiable as attachment lamellae at the base of the cormidial units were almost absent in the holotype; it is possible that the spur-shaped bracteal lamella first became shrivelled and then degenerated, like the nectophoral lamellae, when the bract was detached. An indistinct structure, which might be a bracteal lamella was found at the base of a cormidial unit that was cut off from the main corm (Fig. 3a). On the same unit, a similar but smaller structure, possibly a degenerated bracteal lamella, was observed at the base of the second pair of cormidia branching off the main cormidial stem (Fig. 3a). It was the only indication that more than one bract could be attached to a cormidial unit.

The *in situ* close-ups and the investigations of the paratype showed that the bracts were usually equally distributed over the entire siphosome. Six detached bracts and four younger ones still attached to the siphosome were found on the paratype. Very young bracts were found at the base of some well‑developed cormidial units on the apical part of the siphosome. It is likely that lost bracts are replaced after some time.

TYPE I GASTROZOOIDS. The type I gastrozooids were large elongated structures that were the most obvious components of the siphosome in life (Fig. 1a). They could measure up to 7 mm in the preserved state, but stretched out to a considerably longer length when actively moving around among the components of the siphosome of the live specimen (see below). Each type I gastrozooid consisted of a short, narrow, white basigaster; a large expandable stomach region, which was usually light orange in colour; and a large whitish, slightly transparent proboscis (Fig. 7). The proboscis was very variable in shape when preserved; it could be bulbous when the mouth was tightly closed; pear-shaped when the mouth was pronounced; or curled back over its own external surface when the mouth was widely open. The endoderm of the proboscis formed six ridges, which became exposed when the mouth was everted. These ridges were usually visible as longitudinal stripes through the transparent ectoderm when the proboscis was pronounced. In the stomach region, the internal wall of the gastrozooid bore numerous, conical, endodermal villi, which were visible through the outer wall in younger type I gastrozooids or through the mouth opening when everted. None of the mature type I gastrozooids showed any traces of a tentacle attached to them.

The type I gastrozooids were not attached to cormidial units but were borne on short bright-orange stems, which were attached directly to the corm. The distal end of the stem was slightly enlarged and pan-shaped, best visible when the gastrozooid was detached. In the holotype, eight large type I gastrozooids were attached to the corm of the live animal, and at least six smaller ones to the region between the zone of proliferation and the siphosome. Seven of these 14 gastrozooids became detached during preservation and handling. It was obviously easy for them to break off from their short stems. In the holotype, five of the mature large type I gastrozooids were

attached to the ventral region of the corm, forming a narrow cluster passing spirally down from the lower edge of the nectosome to the base of the corm. The others were dispersed on the dorsal region – as observations on the live animal showed. The paratype possessed four large type I gastrozooids of which one was extremely enlarged and contained a 8 mm long fish larva (see below). These large gastrozooids were arranged in a single vertical row from immediately below the lower edge of the nectosome down to half the height of the corm. Four smaller type I gastrozooids were attached to the region between the zone of proliferation and the edge of the siphosome. These all possessed, at their bases, a very thin, annulated, segmented tentacle without tentilla. Since none of the larger type I gastrozooids on the corm possessed a tentacle, it seems that the older type I gastrozooids lose the tentacle entirely.

NUMBER OF COMPONENTS. Each of the mature cormidial units on the holotype split into two equal main cormidial stems. Thus, at least 10 large cormidial stems were found on the holotype, and the number of bracts should roughly correspond to that. If each stem then divided into three to four branches, each bearing a type II gastrozooid and double the number of palpons, a total of at least 30 to 40 type II gastrozooids and 60 to 80 palpons should be present on the siphosome. The total number of gonophores, 6 to 18 per cormidial stem, may lie between 60 to 180 for a single specimen. The number of type I gastrozooids attached directly to the corm were found to be relatively small; eight in the holotype and four in the paratype.

Habitat and abundance

Tridensa sulawensis was occasionally sighted during a submersible survey along the slopes of the Bunaken and Sangihé Islands, and along the north and south coasts of the northern arm of Sulawesi, North-East Indonesia, in November–December 1999. Thirty-four specimens were found at 11 different dive sites at water depths between 165 and 278 m and temperatures ranging from 12–20 °C. The submersible had a maximum diving depth of 400 m, and most dives took place in the zone between 200 and 300 m. Thus, it was quite possible that *T. sulawensis* also occurred in shallower or deeper waters. However, no specimens were sighted between 300 and 400 m depth; and the vertical distribution clearly showed a peak at 240 m. The slopes of these islands consisted mainly of carbonate and volcanic rocks, gravel and sand, and varied in angle between 20 and 80 degrees. *T. sulawensis* was most commonly found on the steeper carbonate slopes in crevices (Fig. 1e), between single rocks, and sometimes on sandy sediment. Currents could reach 2–3 knots in these areas, appearing suddenly as strong surges that shook the animals back and forth. They obviously caused a strong pull on the tentacles that were used to tether the animal to the substratum. These strong currents might be a reason why most individuals were found in small crevices and among overhangs that served as shelters. Attaching tentacles sometimes were stretched out in all directions, even above the corm, when there was substrate above. In this case the animal looked like a spider sitting in the centre of its web that had been set up between the surrounding rocks. At these locations, sometimes up to 10 individuals were
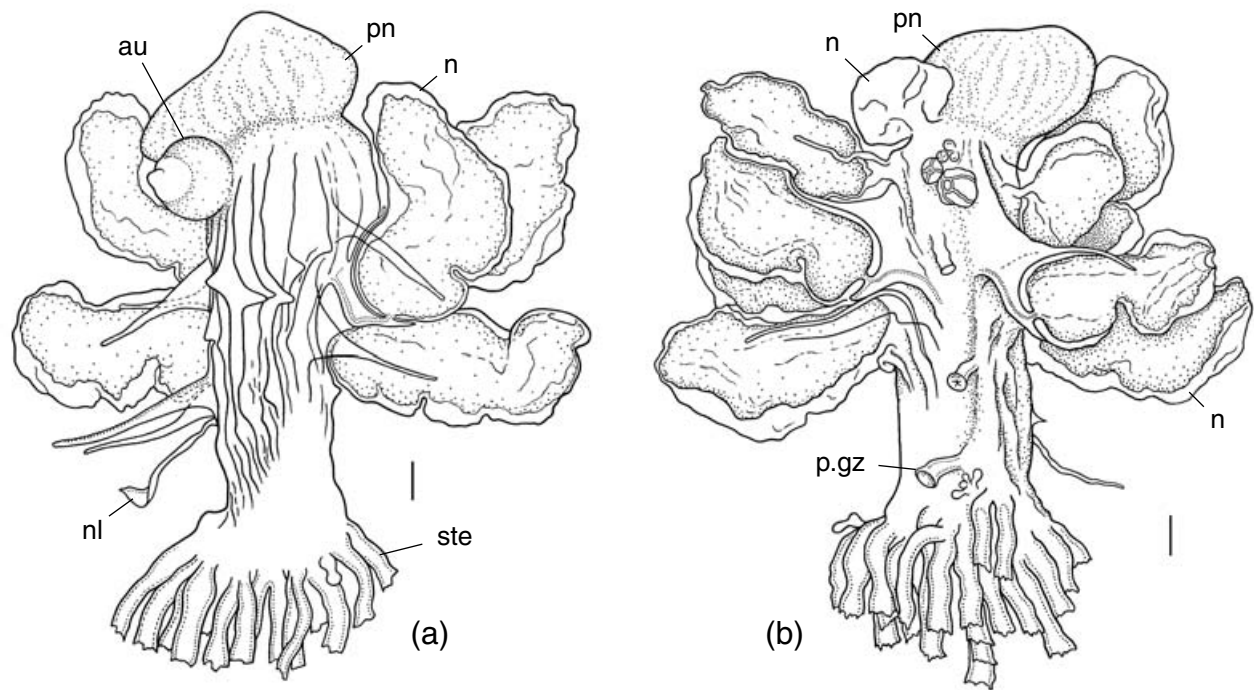
Figure 8 *Tridensa rotunda* sp. nov. Preserved holotype with deformed pneumatophore (pn). (a) Dorso-lateral view of aurophore (au), nectosome with nectophores (n) still attached, transparent nectophoral lamellae (nl) with pointed tips and shrunken nectophoral lamellae forming shrivelled ridges. All cormidial stems (ste) have broken off. (b) Ventral view of zone of proliferation with nectophoral buds on the upper part of the zone and three pedicles of detached type I gastrozooids (p.gz). Scale 1 mm.

found in 1 m³ with distances of less than 30 cm between each other. Aggregations of such high density, however, were rare and restricted to single locations, which probably provided optimal conditions. However, usually *T. sulawensis* occurred only sporadically and scattered over large areas. Some of the single specimens that were found on plain sandy bottoms, had stretched out their tentacles to lengths of more than 12 times the diameter of the siphosome.

Etymology

The generic name *Tridensa* refers to the trifid branching of the bracteal canal in the middle of the distal facet of the bract, and the specific name to the habitat of the collected specimens.

Tridensa rotunda sp. nov.
Figs 1b, 1f, 8–9

Material examined

TYPE MATERIAL. One specimen (holotype, male) from JAGO dive 663, 20 November 1999, at 01°41.26′N, 124°45.95′E, collected at 246 m depth on a sandy bottom off the south coast of Manterawu/Bunaken Islands, North Sulawesi. The specimen was also presented to the Natural History Museum in London, and registered as BMNH 2004.2104.

Diagnosis

Aurophore in some specimens pale-orange. Nectophores with orange coloured circular canal and straight colourless radial canals except for one that is S-shaped and orange coloured.
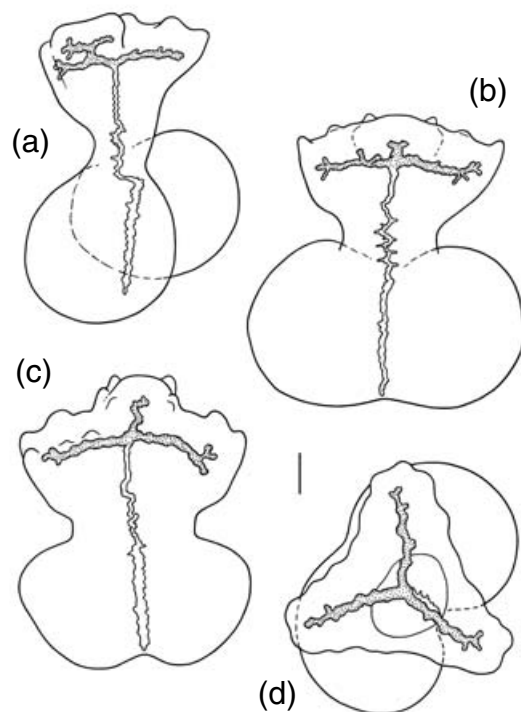
Figure 9 *Tridensa rotunda* sp. nov. Detached mature bracts, various aspects: (a) lateral, (b) dorsal, (c) ventral, (d) apical view. Scale 1 mm.

Nectosomal and siphosomal corm whitish. Bracts with distinctive neck between proximal and distal part; proximal part of mature bracts largely inflated and bigger in diameter than the distal facet; triangular-shaped distal facet with three well separated corners. Bracteal canal divided distally into three branches each of which terminates close to a corner of the distal facet, but without splitting again into major sub-branches; only the three branches are pigmented.

Description

The description given here is based largely on photographs and video footage of the single collected specimen made after it was transferred into an aquarium (Fig. 1b). After it was brought to the surface, the specimen was exposed for a short time to air temperatures of more than 30 °C, and it obviously suffered a 'heat shock' and became stressed. It was gently cooled down in the aquarium, but the water quickly became milky white, probably due to release of spermatozoa (from the gonophores) and augmented with tiny grains, possibly nematocysts. The tentacles became heavily entangled, and the ectodermal surface of the components took on a denatured appearance. After a while most nectophores, all bracts, and the distal halves of all cormidial stems fell off the corm. At this stage, the components were transferred into formalin, but after one night they were found to have completely disintegrated. Even the large bracts, which contained a large quantity of mesogloea and were thought to be quite robust, dissolved, but fortunately drawings of them were made before preservation. What remained was only the pneumatophore, attached to the large nectosome, which still bore several nectophores.

The live and stretched out animal measured 26 mm in height (from the apical pole of the pneumatophore down to the lowermost tips of the cormidia on the base of the siphosome) when kept in the aquarium, almost twice as high as *Tridensa sulawensis*.

PNEUMATOPHORE. In life, the smooth-walled pneumatophore was a large spherical structure whose outer wall contained thin lines of bright pigmentation (Fig. 1f). These lines radiated out from the apical pole to the lower edge of the pneumatophore. Red lines alternated apically with yellow lines, which turned to white in the lower half of the pneumatophore. When the animal was brought to the surface, the pneumatophore became strongly deformed and took on an ellipsoidal shape (Fig. 1b). In the preserved state, its widest diameter was 7 mm, its height 4 mm, and its colour was milky orange.

AUROPHORE. The smooth-walled aurophore (Fig. 8a) was globular and had a size of about one quarter of the diameter of the pneumatophore, to which it was attached by much of its proximal surface. The central pore was pronounced and looked like a small bud. The aurophore was slightly orange in coloration in some specimens observed *in situ*.

NECTOSOME. The white-transparent nectosome was highly stretched when the animal, still alive, was observed in the aquarium (Fig. 1b). After preservation, it still measured 10 mm in height and 4–5 mm in diameter. The animal possessed 16 nectophores when brought to the surface, and numerous necto-

phoral lamellae (*c.* 10), densely arranged around the upper two thirds of the nectosome. The nectophores were partly invaginated, a feature that was also observed in other specimens and on *in situ* video close-ups. Each nectophore had a collar-like ostium surrounded by a bright orange circular canal. Only one of the four radial canals was coloured and S-shaped (Fig. 1b). The other three canals were almost transparent and straight. The diameter of the highly folded, preserved nectophores was about 7 mm. They were attached to the nectosome via thin muscular lamellae that embrace the nectophores in the typical mode described above for *Tridensa sulawensis* (Fig. 8). The lamellae of the younger nectophores to the left and right of the zone of proliferation stretched down from the lower edge of the pneumatophore to about half the height of the nectosome; the oldest to the left and right of the aurophore stretched down the entire nectosome (Fig. 8a). This situation gave the impression that the nectophores might be arranged in a spiral around the nectosome, however, they rather formed a single corona.

ZONE OF PROLIFERATION. Some indefinable buds and three nectophoral buds were found at the zone of proliferation between two smaller nectophores (Fig. 8b). Three pedicles, probably of detached type I gastrozooids, were attached at about the same distance from each other in a vertical line along the ventral side of the nectosomal region down toward the siphosomal corm; small dark-orange polyps that appeared to be young type I gastrozooids without tentacles were observed in this area when the animal was still alive.

SIPHOSOME. The siphosome of the live animal had a height of about 17 mm (including all appendages). The base of the main cormidial stems and the corm itself were of whitish colour (Fig. 1b) and not orange pigmented as in *Tridensa sulawensis*.

The cormidial units bifurcated immediately at their base into two main cormidial stems – as in *Tridensa sulawensis*. At least 20–30 of these stems were found still attached around and at the base of the basally flattened corm. They were all broken off at a length of about 2 mm (Fig. 8). Each thin-walled stem was penetrated by a wide gastrovascular canal that branched off from the vast cavity within the siphosomal corm. This cavity seemed to occupy the whole of the interior of the corm and there was no separation between it and the nectosomal cavity. Both were surrounded by a thin wall that was not penetrated by any network of canals.

Since they were all broken off, the arrangement of the elements on the long and slender cormidial stems could not be investigated in detail. It is, however, supposed that their arrangement was very similar to *Tridensa sulawensis*. The video footage clearly showed numerous palpons, bright red in colour, with a very pronounced terminal region and a dark-red pigment spot below (Fig. 1b). They were similar to those found in *T. sulawensis*. Type II gastrozooids were not explicitly distinguishable on the images. Also the tentacles were of similar colour and shape as those in *T. sulawensis*. Most of the tentilla were detached during the capture and handling procedure. The caught specimen was a male as it possessed numerous sac-like gonophores seen as dense tufts around the siphosome. The photographs and video footage also showed eight large type I

gastrozooids that were distributed all around the siphosome (Fig. 1b). The largest had a length of 13 mm. They had a dark orange-red stomach region and the typical whitish, striped proboscis. Some of them contained food remnants, visible through their slightly transparent body walls.

At least 15 extremely large bracts were visible at the upper edge of the siphosome (Fig. 1b). They were probably attached to the base of the cormidial units, as a small degenerated lamella was found between the two main stems of several cormidial units. The mature bracts had a total length of 6.5 mm (Fig. 9). Their proximal part was largely inflated and occupied about half the height of the entire bract, had a diameter of 7 mm and a characteristic curvaceous shape. It continued distally into a short narrow neck that further extended into a triangular shaped distal facet that measured 5 mm in diameter. This facet had three well-separated corners and several small cusp-like projections on its edges. The bracteal canal ran straight up in the centre of the ventral side of the inflated proximal half of the bract; then, in the mid-region of the bract, it bent abruptly through a right angle (Fig. 9a). It then continued through the centre of the bract, firstly in a zigzagged fashion and later straight up through the centre of the narrow neck towards the distal facet. In the middle of this facet the canal divided into three bright-red branches each of which terminated close to a corner of the facet (Fig. 9d). The branches could have irregular short and very narrow side-branches. On some of the *in situ* images, the bracteal canals were clearly visible as bright-red tridents: a character that was used to identify the species in the field.

Habitat and abundance

Tridensa rotunda occurred in the same habitat as *T. sulawensis* around the Sangihé and Bunaken Islands and along the coast of North Sulawesi. Five different individuals were documented at four different dive sites at depths of 226–289 m and water temperatures between 11.6–15.5 °C.

Etymology

The specific name *rotunda* refers to the rounded and extremely enlarged proximal part of the bracts.

Genus *Arancialia* gen. nov.

Diagnosis

Rhodaliid siphonophore with smooth-walled pneumatophore and aurophore. Apical and basal part of pneumatophore translucent, widest part traversed by irregular red lines and white dots. Aurophore globular, colourless, with pronounced single central pore; additionally it can have up to six small tubercles on its margins. Basic colour of nectophores pale orange; circular and radial canals dark orange. Nectosomal and siphosomal corm colourless, both with central cavity. Cormidial units monogastric, consisting of a single cormidium. Cormidial stem slender, divided, distally, into a single gastrozooidal and from one to several gonodendral branches. Large type I gastrozooids attached singly to the corm on separate pedicles. Single large bract and up to two bracteal buds attached to base of each cormidial stem. Distal facet of bracts round. Bracteal canal

bright orange, almost straight and without major branches. Distal end of bracteal canal bent over, giving off a very short branch that runs up to a small depression in the middle of the distal facet.

Arancialia captonia sp. nov.
Figs 1c, 1h, 10–12

Material examined

TYPE MATERIAL. Three specimen (one male, two female) collected during JAGO dive 537 on 31 December 1997 between 123 and 125 m depth at Table Bay off Cape Town, South Africa, on a soft sandy bottom; location 33°55.37′S, 18°10.34′E. The male specimen has been designated as the holotype. It is housed at the Natural History Museum in London as BMNH 2004.2105.

Fourth specimen (young male) from JAGO dive 398, 31 October 1996, at 359 m on soft sediment southwest off Cape Point, South Africa; location 34°31.30′S, 17°58.96′E.

Diagnosis

As for genus.

Description

The size of the four collected specimens ranged from 4.5 mm to 22 mm in greatest diameter. The height was variable in life depending on the degree of contraction; in the preserved state it was about the same as the diameter, since by then the nectosome and the siphosomal elements were strongly contracted. The overall colour of the live animals was orange (Fig. 1c, h), which faded away after preservation. Almost all the type I gastrozooids, many nectophores and bracts, and numerous tentilla and male gonophores became detached after preservation.

PNEUMATOPHORE. The round pneumatophore was thin- and smooth-walled and became slightly ellipsoidal after preservation. It measured, at its greatest diameter, 3–4.5 mm in the mature specimens collected in 1997, and 2 mm in the younger specimen from 1996. The coloration in life was very typical for this species (Fig. 1c). The apical and basal parts of the pneumatophore were devoid of pigmentation and transparent; the widest part (at about one third the height of the pneumatophore) was traversed by irregular radial red lines that were separated by flocky dots of white pigment. These flocky dots were also found, as a circular line, around the lower edge of the pneumatophore. The transparent parts had a silvery appearance, probably caused by light reflection off the chitinous lining of the inner pneumatosaccus. The pneumatophore became whitish after preservation.

AUROPHORE. The aurophore of *Arancialia captonia* was a globular smooth-walled structure, which was attached to the dorso-basal part of the pneumatophore by much of its proximal surface. Its diameter ranged from 1.2–1.3 mm. It was completely transparent, and had a pronounced central pore, which, in comparison with the species described above, was slightly more apical in position. One to six small tubercles were found on its lateral margins in three of the four preserved
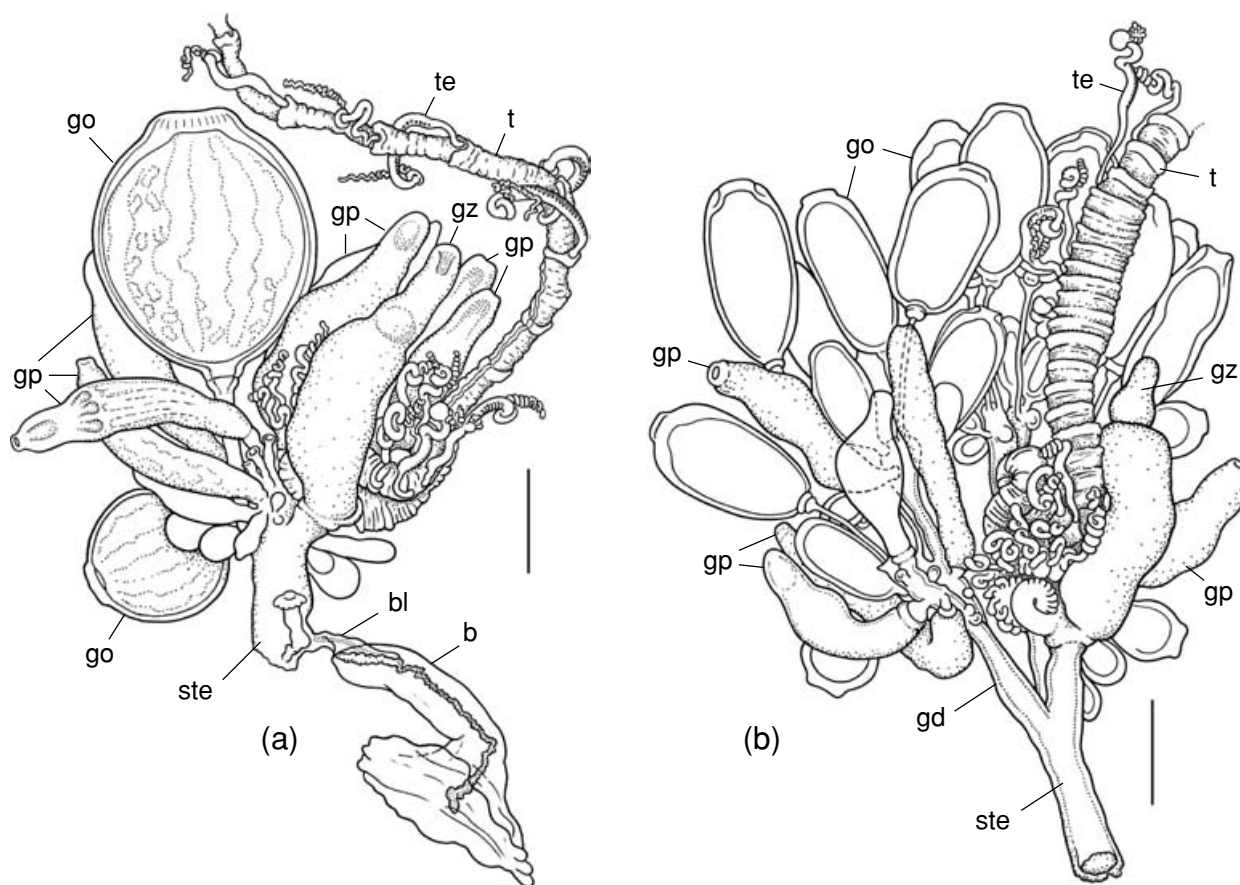
Figure 10 *Arancialia captonia* sp. nov. Detached cormidial units. (a) female, (b) male cormidium, both monogastric. Bract (b), bracteal lamella (bl), type II gastrozooid (gz) with tentacle (t) and tentillum (te), gonodendron (gd) with numerous gonopalpons (gp) and gonophores (go), cormidial stems (ste). Scales 1 mm.

specimens; these tubercles were not clearly visible in life. Because they were relatively small, they were not considered as true appendages like the papilliform structures found on the aurophore of the rhodaliid species *Archangelopsis typica*, *A. jagoa* and *Dromalia alexandri*.

NECTOSOME. The nectosome was contracted in the preserved specimens and only 2 mm high. In life, however, it could expand to 3–4 mm in height (Fig. 1c). It then had the shape of a slender cylinder that raised the pneumatophore and the nectophores clear of the siphosomal corm. The nectosome was transparent in life with a slight pale orange hue that disappeared after preservation. The internal organisation is described below.

In life, the nectophoral lamellae stretched down from the lower edge of the pneumatophore over about two thirds of the nectosome. They were thin transparent tissue sheets traversed, in the lower half, by a gastrovascular canal. The distal corners of the sheet were slightly elongated, but not as much as in the genus *Tridensa*. The lamella linked with its distal edge to the dorso-basal surface of the nectophore. On some detached nectophores, this connection was still recognisable as an opaque longitudinal streak.

The nectophores were typically large rounded bags with a thin transparent wall that was pale orange in life (Fig. 1c).

This over-all pale coloration of the nectophores was a typical feature for *A. captonia*. The circular canal and the four radial canals were more darkly coloured. Two of the radial canals had a straight course, the other two were slightly curved. The diameter of the mature nectophore was slightly larger than that of the pneumatophore; it ranged from 4–5 mm in the larger specimens, and 3 to 4 mm in the smaller one. All nectophores were arranged in a single corona around the upper two thirds of the nectosome. The large male possessed at least 20 nectophores when brought to the surface, the young one about five, and the two females 16 and 14. Much smaller nectophores and nectophoral buds were also found on both sides of the ventral zone of proliferation.

ZONE OF PROLIFERATION. A succession of developing cormidia and type I gastrozooids, in a series of developmental stages, passed down from the zone of proliferation at the nectosomal region and connected with the units on the siphosomal corm. The developing cormidia consisted of a single stalk topped by a type II gastrozooid that had a prominent but typical tentacle, bristling with tentilla. The young type I gastrozooids were also borne on thin-stemmed stalks, but only the youngest ones possessed an unbranched tentacle. The tentacle obviously was detached before the type I gastrozooid reached the siphosome (see below).
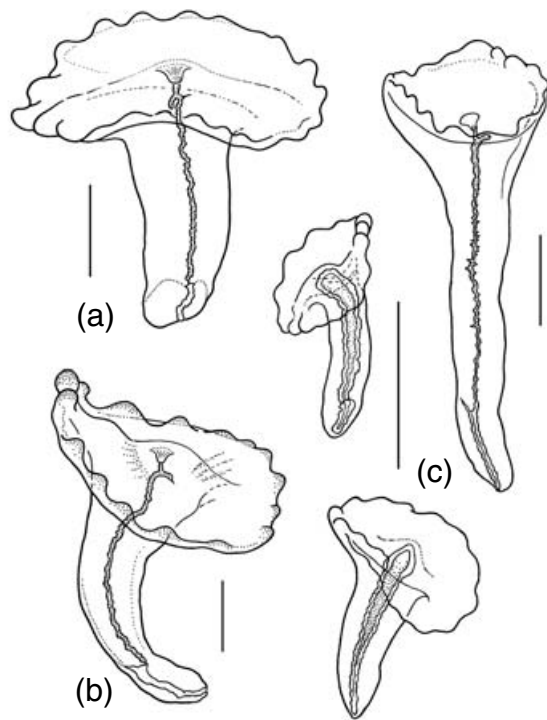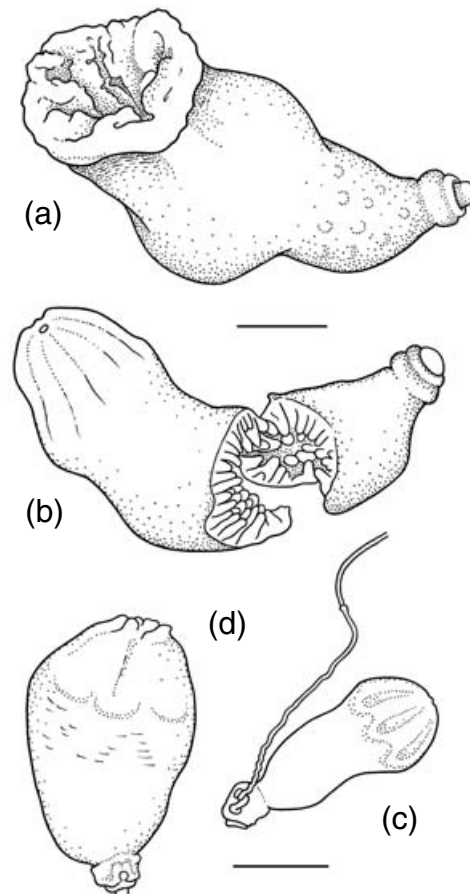
Figure 11 *Arancialia captonia* sp. nov. Detached bracts, various aspects and stages of development: (a) mature, dorsal view, (b) mature, lateral view, (c) young, lateral views. Scales 1 mm.

Siphosome. The siphosomal corm to which the cormidial units and the type I gastrozooids were attached was, in comparison with the voluminous appendages of the cormidia, relatively small (Fig. 1c). In life, it appeared to be very thin-walled and colourless. The 1996 specimen was sectioned sagittally. It had one large cavity within its corm. There was no internal separation between the relatively large hypocystic cavity of the nectosome and the small siphosomal cavity. The surrounding walls of the siphosomal cavity were relatively thick but they were not penetrated by a network of gastrovascular canals. Those canals that ran through the cormidial stalks branched off directly from the siphosomal cavity. The relative thickness of the walls, in comparison with the live animal, might be due to contraction and shrinkage during preservation.

The mature specimens possessed about 15 to 20 cormidial units. Their arrangement around the crowded corm was impossible to discern without cutting off most of the cormidial elements, which was avoided. All cormidial units consisted of a single cormidium, i.e. were monogastric (in this situation the stalk of the cormidial unit is identical with the stem of the cormidium – see terminology). Each cormidium had a slender stem that divided, further distally, into at least two branches, one of which bore a type II gastrozooid, while the other bore one to several gonodendra. A large bract was attached basally to the main stem (Fig. 10a).

The thin-walled main cormidial stem could have a pale orange coloration in life, but became whitish after preservation, as was the case for almost all of the transparent parts

Figure 12 *Arancialia captonia* nov. Detached type I gastrozooids, (a) with mouth widely open and curled back, (b) mouth closed, stomach region broken open, endodermal villi visible, (c) young one from apical part of zone of proliferation with segmented tentacle attached to basigaster, (d) young one from lower part of zone of proliferation, basigaster already without tentacle. Scales 1 mm.

on the specimens. The stem reached a length of 1–1.5 mm in the preserved state before it branched for the first time. On the live animal, however, it could expand to 4–5 mm (Fig. 1c). The first short distal branch bore the well-developed type II gastrozooid, which was of the typical rhodaliid shape with a slightly separated proboscis, a large stomach region, and a well-developed basigaster (Fig. 10a,b). In life, the centre of the stomach region was orange, a good feature to distinguish type II gastrozooids from gonopalpons. After preservation, the stomach region became whitish. The large tentacle, which was attached to the basigaster, was very similar to the one described above for *Tridensa sulawensis*. Its gastrovascular canal was bright orange in life. Each tentacular segment bore, at its proximal end, a well developed tentillum. Again the tentilla strongly resembled those described of *T. sulawensis*. Even the horseshoe-shaped structure at the distal end of the cnidoband was present. A stretched cnidoband, 1.5 mm in length, bore on each flank about 50 large elongated nematocysts. The most proximal part of the tentacle, which carried tentilla of

successive stages in development (Fig. 10b), was slightly longer than in *T. sulawensis*. It was usually highly coiled.

The second main branch of the cormidial stem was the gonodendron. In the younger cormidia it was just a thickening to which numerous gonopalpons, gonophores and buds were attached (Fig. 10a). In the older cormidia the main gonodendral branch could split dichotomously into further long branches (Fig. 10b). Each of these slender stems carried at its distal end gonopalpons and gonophores, and sometimes a further branch with further gonopalpons and gonophores. The oldest cormidia thus could carry a large number of distal components. A cormidium of the large male specimen with 4 gonodendral branches, collected in 1997, carried 15 gonopalpons, 23 matured gonophores and numerous buds. Some gonodendral stems had lateral buds.

The simple thin-walled gonopalpons looked like the (stem) palpons of *Tridensa sulawensis*. They possessed a narrow basal region, a red-flecked stomach region, and an elongated terminal region with four optically dense stripes (Fig. 10a). In life, all gonopalpons had a bright-red pigment spot located between these stripes and the stomach region. The spot broke up into several red stripes as the terminal region expanded. The gonopalpons were restricted to the gonodendral branches, to which they were attached by short pedicles. They were very numerous (10–15 per cormidium), but also were easily detached.

GONOPHORES. The female gonophores were borne on long thin stalks, which were attached mainly to the basal part of the first gonodendral branch (Fig. 10a). The mature female gonophore was a large rounded structure of 2 to 2.5 mm in diameter. Its coloration, in life, was pale orange. The opening of the sub-umbrella cavity was not pigmented, as in some other rhodaliid species. Irregular longitudinal streaks, slightly more strongly pigmented, ran down the surface of the exumbrella. A longitudinal section through a preserved mature gonophore showed that the sub-umbrella cavity contained numerous loose polygonal granules. Each cormidium generally possessed only one maturing gonophore attached to the main gonodendral branch, and additionally, several younger female gonophores at different developmental stages. The youngest were whitish and were borne on short stalks. One of the two female specimens possessed 17, the other 28 mature gonophores.

The mature male gonophore was generally smaller than the female gonophore. It was a simple white sac, also borne on a thin stalk that was slightly shorter than that of the female gonophore (Fig. 10b). The umbrella region could have a length of 1.5–2 mm and thus was more elongated than, for example, the roundish umbrella region of male gonophores in *Tridensa sulawensis*. Granular structures inside the sub-umbrella cavity were visible through the umbrella walls of the most mature gonophores. Mature male gonophores were attached to all gonodendral branches, even to the most distal ones (Fig. 10b). They formed dense bundles that could consist of 15 to 25 individuals per cormidium; a large number in comparison with the relatively small size of the corm.

BRACTS. The large transparent bracts (Fig. 11) were attached to the base of the main cormidial stems and measured 3–4 mm

in length when mature. The proximal part of the bract could be slightly recurved and had, ventrally, a longish groove that embraced the attachment lamella. The large distal facet was almost round, slightly convex (or concave in the young ones) and had recurved edges with 15–18 rounded projections. The facet could reach 3 to 4 mm in diameter. The bracteal canal was simple. It first ran up from the proximal tip of the bract in contact with the ventral groove. Up to the distal end of the ventral groove, it was colourless. Then, now bright orange, it bent towards the centre of the bract and travelled, without branching, to the vaulted centre of the distal facet, which could have a small depression at that point. In the mature bract, the very distal end of the canal was bent over like a walking stick towards the dorsal surface of the bract; the small bend gave off a very short branch that ran up to the small depression in the middle of the distal facet.

The attachment lamella branched off from the base of the main cormidial stem. It was a thin transparent tissue sheet of triangular shape (Fig. 10a). The free edge of the triangle fitted into the ventral groove at the proximal part of the bract. A canal that branched off from the gastrovascular canal of the cormidial stem ran straight through the centre of the lamella and ended in the middle of its distal edge where it presumably connected with the bracteal canal.

The larger cormidial units that were investigated usually possessed one mature bract and, next to it, 1–2 bracteal buds or a bract at a very early stage of development (Fig. 10a). The oldest bracteal component at the base of the cormidial stem was always the most proximal one. Detached bracts were obviously replaced by younger ones. About 50 bracts were found among the components of the mature specimens, almost double the number of estimated cormidial units, which appeared to mean that most of the cormidial stems must have borne at least 2 mature bracts.

TYPE I GASTROZOOIDS. The large type I gastrozooids (Fig. 12) were of the same shape as described in the species above. They were the largest and most obvious components on the corm. In the preserved, contracted state, they measured 5–6 mm in length, in life much more. The proboscis possessed about 7–8 longitudinal stripes, which were probably identical with the endoderm ridges visible through the mouth opening when expanded. The stomach region was orange-red in life, and the endodermal villi, restricted to this region, were clearly visible through the outer wall (Fig. 12a,b). The basigaster was short and narrow. A thin, segmented tentacle, without tentilla, was attached to it at early stages of development, when the type I gastrozooid was still attached to the region immediately below the zone of proliferation (Fig. 12c). The tentacle was lost when the gastrozooid had a length of 2.5 to 3 mm and before it passed down onto the siphosomal corm (Fig. 12d). The detached tentacle left a rounded stump on the basigaster. This stump obviously degenerated after some time, since the mature gastrozooids did not possess any traces of a tentacle.

Each type I gastrozooid was borne on a long, thin stem that was attached directly to the corm; it had no association with a cormidial unit. The distal end of the gastrozooidal stem

was slightly enlarged. The large male specimen possessed nine type I gastrozooids when brought to the surface, the small male three. Four and seven type I gastrozooids were found on the female specimens. All type I gastrozooids of the large male were detached after transfer into the aquarium. Eight stumps that looked like contracted gastrozooidal stems were later found on the basal side of the corm. As in *Tridensa sulawensis*, the type I gastrozooids of *Arancialia captonia* appeared to be arranged in a cluster on the corm.

Some of the type I gastrozooids contained prey fragments or an amorphous, mucoid mass consisting of sand grains and detritus (see below).

Habitat and abundance

Arancialia captonia was sighted during submersible dives performed to document the deep-water benthic community around the Cape Peninsula, South Africa, in October 1996 and December 1997. The encountered specimens had settled on relatively plain substrates made up of soft, sandy sediment, or on rocky substrates made of pebbles and cobbles. They were present at depths between 123 and 361 m at water temperatures of 7.5–9 °C. The upper and lower limit of their distribution is not known since dives were not carried out at shallower and greater depths. The animals were exposed to bottom currents that frequently exceeded 1 knot (51 cm/s) and to the influence of high swell that reached down to the seabed even at 200 m depth. The sea around the Cape of Good Hope is famous for being rough at most times of the year.

Twenty-five individuals were counted along a transect of 250 m, a population density of 0.1 individuals per m^2. They were more abundant on soft bottoms than on hard substrate. Sometimes two individuals were found within 30–50 cm of each other, but usually they did not occur in clusters and were well separated. They may also be disturbed by other benthic organisms that move around on the sea bed, particularly Echinodermata, such as sea urchins, star fish and brittle stars.

The coastal stretch in which siphonophores were recorded off the Cape Peninsula had a total length of 120 km. Several dives carried out in the Cape Canyon 130 km north-northwest of Cape Town, at a depth of 310 to 370 m, and on soft sediment plains off the west coast of South Africa and South Namibia, between 100 and 140 m depth, revealed no siphonophore sightings. Rhodaliids were also not encountered during numerous dives between 50 and 400 m depth within and at the edges of submarine canyons in the St Lucia Marine Protected Area off the northeast coast of South Africa. It is therefore possible that *Arancialia captonia* is generally restricted to the Cape Peninsula. This, however, remains an assumption since dives in False Bay and along the south and east coast of South Africa were not performed.

Etymology

The generic name *Arancialia* refers to the over-all orange coloration of the animals ('arancia' means 'orange' in Italian), the species name *captonia* refers to their distribution around the South African Cape Peninsula.
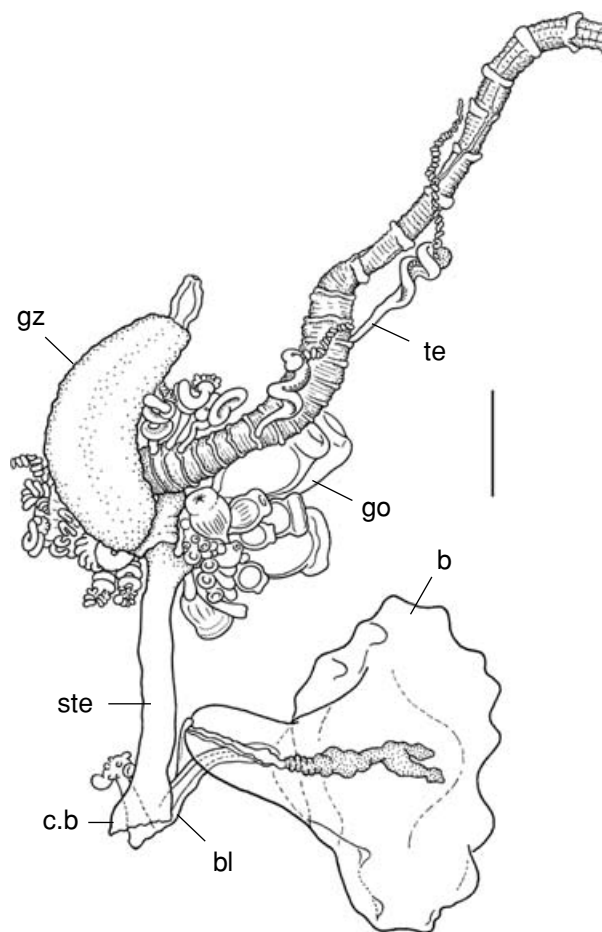
Figure 13   *Archangelopsis jagoa*. Detached female cormidial unit, monogastric, with large bract (b) attached to bracteal lamella (bl) at base of cormidial stem (ste) with? cormidial bud (c.b); all gonopalpons broken off. Scale 1 mm.
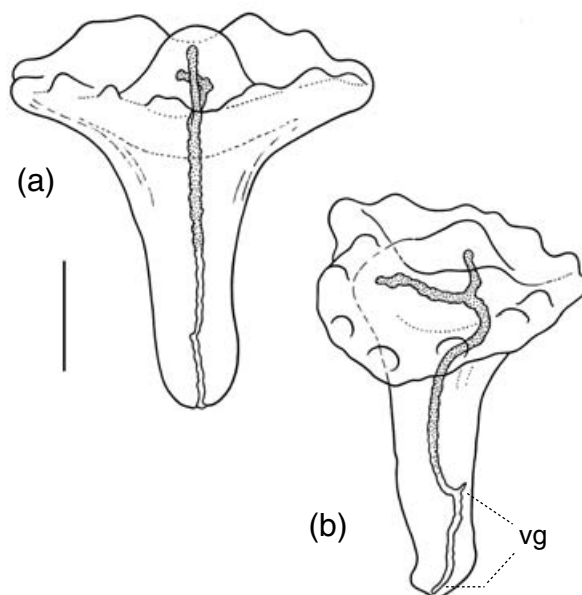
Figure 14   *Archangelopsis jagoa*. Detached mature bracts, (a) dorsal and (b) lateral view, ventral groove (vg). Scale 1 mm.

Further information on *Archangelopsis jagoa* Hissmann, Schauer and Pugh, 1995
Figs 1d, 1g, 13–14

Archangelopsis jagoa was first observed and described from material collected in the Gulf of Akaba, Red Sea in 1992 (Hissmann *et al.*, 1995). Further specimens were then discovered during submersible dives off the volcanic island Grande Comore in the Comoro Archipelago (western Indian Ocean) in 1994, 1995 and 2000 (11°51.6′S, 3°21.2′E). Three specimens were collected: the first (female) on 28 November 1994 during JAGO dive 297 at 256 m depth in front of a volcanic cave (16 °C); the second (female) during the same dive at 178 m depth on loose gravel below a cliff (22 °C); and the third (male) during dive 308 on 05 December 1994 at 196 m (24 °C) again in front of a volcanic cave. In addition, numerous *in situ* observations and video close-ups helped to gain a better understanding of rhodaliid life history.

Archangelopsis jagoa is recognisable by the striking circular pigment rings on its smooth-walled pneumatophore and the large number of papilliform appendages on the aurophore (Fig. 1d). Most structures were described in detail by Hissmann *et al.* (1995). However, some new observations have been made on the living and subsequently well-preserved Comoran specimens that are worth mentioning. The colour sequence of the six rings on the pneumatophore was identical in all observed Comoran specimens: yellow at the apical pole, red, white, red, yellow and red. The numerous appendages on the aurophore had white pigmentation and most had a red pigmented tip (Fig. 1d). The largest specimen had a pneumatophore with a diameter of 3.8 mm, 25 appendages on the aurophore, and 25 nectophores arranged in a single corona around the nectosome. In life, the nectophores were clearly visible due to their bright red pigmented circular canals (Fig. 1d); the four radial canals were also pigmented but less strikingly.

The siphosomal corm was a small, thin-walled sac. Dissection of one specimen revealed a single relatively vast central cavity that occupied the entire nectosome and siphosome and from which a single gastrovascular canal was given off to each cormidial stem. There was no obvious network of canals in the necto- or siphosomal walls; the latter not being as thickened as in *Tridensa sulawensis*.

Each cormidial unit consisted of a single cormidium, i.e. was monogastric in that it possessed a single type II gastrozooid, with an annulated tentacle (Fig. 13). The main cormidial stem (in this situation identical with the stalk of the cormidial unit – see terminology) was, in comparison with other rhodaliid species, relatively long and thin (Fig. 13). The gonodendron bore numerous well-developed gonopalpons and a whole bunch of gonophores, either female (Fig. 1g, 13) or male (Fig. 1d), at different stages of development. The attachment lamella for the single bract arose from the base of the main cormidial stem. It was a large, but thin, transparent tissue sheet with a triangular shape (Fig. 13). The mature bract was also relatively large (Fig. 14), and its heart-shaped distal facet could reach 3 mm in diameter. Thirty-five bracts were counted on the largest specimen. Proximally the bracteal canal was colourless and ran straight up along the ventral groove (to

which the bracteal lamella was attached). It then bent toward the centre of the bracteal stalk, where it became pigmented dark red, while a short narrow branch continued to the ventral surface. When it entered the distal facet the canal divided into two branches at right angles to each other: one branch continued towards the convex centre of the facet, while the other (which was usually slightly longer) ran out toward the dorsal surface of the bract. The bracts could also be clearly seen *in situ* because of their red bracteal canal. Small buds and contracted structures were sometimes also found at the base of the main cormidial stems, but it was unclear whether these were secondary cormidia at an early stage of development or retracted bracteal lamellae of detached bracts (Fig. 13).

Hissmann *et al.* (1995) assumed that *Archangelopsis jagoa* lacked type I gastrozooids since none were found on the holo- and paratypes. Pugh (1983) also did not find type I gastrozooids on a specimen of *A. typica*, and so it was speculated that in the genus *Archangelopsis* the role of food transference was carried out by the gonopalpons. However, all specimens collected at the Comoros possessed well-developed type I gastrozooids of the typical rhodaliid shape, without tentacles in the mature stage. They were mainly found to be attached on the flattened base of the corm, each borne on a long, thin stem, and quite separate from the usual cormidial units that bore a type II gastrozooid. Type I gastrozooids became easily detached from their stems when handled and that might explain why none were found on the Red Sea specimens or on *A. typica*. Nine type I gastrozooids, all without tentacles, were counted on the siphosome of the first and largest specimen. Four smaller type I gastrozooids were found attached to the region below the zone of proliferation of the second specimen. Each of them possessed a thin, segmented tentacle without tentilla. Three slightly larger type I gastrozooids, still with tentacles, were found at the upper edge of the siphosome below the zone of proliferation, all in a vertical row. They were followed by a large type I gastrozooid that had no tentacle. The tentacle obviously detaches when the gastrozooid is passed down onto the siphosomal corm.

An unusual observation was made on a bundle of detached fragments of the third Comoran specimen, which mainly consisted of entangled and already slightly denatured tentacles and of gonopalpons. Some of these gonopalpons had an expanded mid-region which was clearly separated from the long and narrow peduncle. It turned out that these gonopalpons contained parts of a tentacle including tentilla. One end of the incorporated tentacle was highly coiled inside the expanded mid-region, and clearly visible through the transparent outer wall, while the free end of the tentacle was still tightly embraced by the gonopalpon's mouth. Tentacle fragments were found to have been incorporated either from their distal or their proximal end.

Habitat and abundance

Specimens of *Archangelopsis jagoa* were sighted during submersible surveys for coelacanths, archaic fish, off the Comoran island of Grande Comore. This volcanic island is relatively young. Its steep submarine slopes are mainly covered by highly structured lava rocks, while sandy slopes are rare. *A. jagoa* was

found at sheltered locations such as in front of submarine caves, or under overhangs and niches, always being attached to rocky ground (Fig. 1g) and never on pure sand as in the Red Sea. The fragile animals obviously avoided settling on ground that was exposed to submarine avalanches, sliding sand or rocks. Specimens were present at depths between 174 and 256 m and at water temperatures of 16–23 °C. They were not found at shallower or deeper depths (surveys were conducted to 400 m depth maximum). During the three years during which dives were made, sightings were restricted to a total of eight different individuals, all within a stretch of coastline of less than 3 km. The closest observed distance between two individuals was 40 cm, while a group of three other animals were separated by 2 and 5 m, respectively.

Observations on the living animals

Ground attachment and locomotion

All specimens of the species described above observed *in situ* were tethered to the substratum by the tentacles of their type II gastrozooids. The number of tentacles that were used to attach the animals to the ground varied between 10 and 25 (Fig. 1e–h), with about the same number floating freely below the siphosome. The number of attaching tentacles may depend on the type of substrate and the current strength. The tentacles were greatly extended in all directions around the corm, even sometimes above it when the animal had attached itself under a rocky overhang or inside a niche. These tentacles could extend to at least 12 times the diameter of the siphosome. The distance between the siphosome and the substratum varied according to the degree of contraction of the tentacles. If the bottom current was strong, the attaching tentacles were more contracted and the siphosome floated at a distance to the ground that was sometimes not much more than the diameter of the siphosome itself. On the other hand, heights of up to 10 cm and more were observed in calm water or when the animals were sheltered in crevices.

The detachment and reattachment of tentacles was observed very rarely. Once the animal had taken a stable position it clearly retained it for quite some time. A Comoran specimen was found in the same posture and at exactly the same spot after a period of seven days. It had not moved at all. However, this does not mean that the animals are sessile. If there was a massive disturbance, such as being repeatedly nudged with the submersible's manipulator arm, they detached all their tentacles from the substrate, rose up from the sea floor to a height of about one meter, and drifted with the current. Usually they quickly returned to the bottom by rhythmical contractions of their nectophores, whose ostia were directed upwards, so that the jet propulsive effect pushed the animal downwards. If the nectophores on only one side of the nectosome contracted then this caused the animal to rotate around its vertical axis. Similarly, if the ostia were pointing sideways, then the animal moved horizontally or diagonally. The contractions of the individual nectophores were not performed simultaneously. They seemed to contract independently and it was difficult to judge

whether they were at all synchronised. The most important factor appeared to be to return to the bottom as quickly as possible. When the animal touched the bottom reattachment took place relatively quickly, and the nectophores continued to contract until the first few tentacles were reattached to the substratum. The nectophores were mostly inactive and sometimes partially invaginated (see above) when the animal was tethered to the substratum. Long periods of detachment are obviously to be avoided since the animals risk unpredictable transportation by the current and an uncontrolled rise in the water column.

'Walking' along the bottom by detaching and reattaching tentacles, cited by Pugh (1983: 255) according to submersible observations on *Dromalia alexandri*, was not recorded. The supposed detachment and reattachment of tentacles by this species might just have been the shortening and lengthening of the tentacles that freely float below the siphosome (see below).

The animals responded to direct tactile contact by immediate contraction of the nectosome, the cormidial stems, the type I gastrozooids, and the attaching and floating tentacles. The pneumatophore was then sometimes completely withdrawn among the siphosomal components. The animals also appeared to be sensitive to water-borne vibrations and sudden illumination since both stimuli caused contractions.

Fishing and feeding behaviour

Fishing. Since benthic siphonophores are stationary, to feed they depend upon prey bumping into their tentacles. To improve the chance of prey capture, rhodaliids spread out their tentacles like a three-dimensional fishing net, comprised of both the more or less static attaching tentacles and the freely floating ones (Fig. 1e–f). The size and shape of the space into which the tentacles extend depends on where the animals are attached. If the animals are attached to more or less flat bottoms, the tentacles are mainly spread out horizontally or angled below the siphosome so as to occupy a hemispherical space, which can be enlarged further by the activities of the floating tentacles. Those individuals that are tethered within a niche stretch their tentacles into an almost spherical space.

When there was no current the floating tentacles usually dangled below the siphosome. However, they could extend to enormous lengths when relaxed and drawn out by any current. The outstretched tentacles, both the attaching and floating ones, could reach lengths of more than 15 cm (see also above), so that the actual fishing space around the stationary colony could measure up to 30 cm in diameter, an enormous size for an animal whose corm measured not much more than 1 cm^3. The tentacles could rapidly contract and lengthen again in a regular rhythm. Retraction either involved only the tentacle itself or both the tentacle and the cormidium to which it was attached. Retraction could be very fast, lasting less than 1–2 seconds.

The tentacles served as the radial strands of the 'spider's web' to which were attached the tentilla that actually capture the prey. These side branches are armed with thousands of nematocysts that, on contact with the prey, discharge and either inject toxins or entangle it. In still water the tentilla

dangled from the floating and attaching tentacles like lures on a fishing line. They were either coiled up when inactive, or stretched out when in the fishing posture (Fig. 1h). In the latter case, the basal pedicle and particularly the terminal filament were highly expanded and the entire tentillum easily reached a total length of more than 10 mm. The most distal end of the terminal filament often remained contracted and thus formed a thickening at the end of the extremely thin and almost invisible filament. This thickened end obviously served, together with the cnidoband, as a 'weight' to increase drag at the end of the tentillum and thereby aid in 'casting'. The water current obviously played an important role in spreading the tentilla. If there was a current, they floated almost horizontally and parallel to each other downstream of the current. From time to time, they were completely or partially retracted, either only the terminal filament or the basal pedicle, or both parts at the same time, before they expand again. The contractions of the tentacles and tentilla seemed to alternate more or less randomly. Also the proximal part of the attaching tentacles contracted from time to time causing their tentilla to move without detaching the entire tentacle.

Feeding. The most important components involved in feeding were the tentacles of the type II gastrozooids and the large type I gastrozooids, devoid of tentacles. When inactive the latter were contracted down among the other siphosomal components. Usually, however, they dangled below or to the side of the siphosome (Fig. 1b), and actively moved among the other components and tentacles (Fig. 1a). They could stretch out or retract, perform pendulum and writhing movements, and occasionally touch the proximal part of the tentacles and their tentilla. While moving they often changed their shape; the proboscis could be elongated to an enormous length or contracted into a bell-shape and the stomach region could be stretched or inflated. When touching the tentacles, the mouth formed a narrow tip and the entire gastrozooid performed movements as if to pick off small items attached to the contracted tentilla, apparently either to clean the tentacle from indigestible particles or to feed on small prey organisms.

When a larger prey organism, like a fish larva or an amphipod, contacted a tentacle and became entangled, only the tentacle attached to the prey contracted bringing the prey closer to the siphosome and the mouths of the type I gastrozooids. The remainder of the colony continued fishing. If the contacted tentacle was a floating tentacle, it was completely retracted. If it was an attaching tentacle, only the proximal segments were contracted while the tentacle remained attached to the ground. Thus a stable anchorage was maintained at all times. The type I gastrozooids next to the contracted tentacle began to writhe about but did not immediately touch the prey if it was still moving. When the prey was completely immobilised and pulled close to the siphosome, the type I gastrozooids slowly started to touch it. The next step depended on the type and size of the prey. Smaller prey, of 1–2 mm and rounded shape, like some amphipods, were engulfed relatively quickly. The widely open mouth of the gastrozooid completely surrounded the prey (Fig. 1h) and pulled it into the upper part of the proboscis by rhythmical contractions of its lower part and by the closure

of the mouth. The tentillum to which the prey was attached was ripped off by this action and ingested together with the prey. Further contractions and stretching transported the ingested particles through the elongated proboscis region and down into the stomach. The time between capture and complete ingestion was about 1 to 2 minutes. This period was much longer when large prey was captured. The South African specimens were observed catching fish larvae of 10 mm in length – as long as an extremely elongated type I gastrozooid. The fish larvae trembled for a few minutes until the toxin, injected by the nematocysts, acted. Only once the larva was completely immobilised, did the type I gastrozooids start to touch it and then one of them clung to it. Its mouth opening docked with the prey and then the distal part of the proboscis started to expand over the prey's surface like an ever-increasing funnel. Finally this "funnel" completely embraced the head, or the tail, of the fish, which was then completely ingested by rhythmical contractions of the proboscis. The initial ingestion procedure took more than 20 minutes, but the length of time it took for the prey to be passed down into the stomach prior to digestion was not recorded *in situ*. Food fragments, which were found inside the stomach of several dissected type I gastrozooids (see Fig. 7a), and the presence of large endodermal villi (see Fig. 12b) suggested that the type I gastrozooids were responsible for the entire digestive process.

The type II gastrozooid behaved completely passively, showing no conspicuous activity, when its tentacle retracted after having come in contact with a prey item. The gonopalpons and palpons, however, were frequently in motion as *in situ* close-ups showed. They performed writhing movements, similar to the type I gastrozooids, and extended their mouth regions into a narrow trunk which could come in contact with the tentilla of any retracted tentacles. They were not observed to ingest any large prey items, but small amorphous particles, consisting mainly of detritus and sand grains, were found in the region proximal to the terminal part.

Diets. The *in situ* observations showed that the rhodaliids described above were capable of capturing relatively large, active prey, such as hard-bodied amphipods and soft-bodied fish larvae, whose length could equal that of the diameter of the corm itself, as well as much smaller prey items. One of the dissected type I gastrozooids contained an 8 mm long fish larva, while another had several fragments of different crustacean species (probably amphipods and mysids). Others contained a brownish mucus, which partly consisted of detritus and sand grains. This material probably was derived from the large fluffy amorphous particles that were borne by the currents. These particles are particular abundant in the relatively strong bottom currents, as noted above, in the region where the South African specimens were caught. They frequently drifted into and stuck to the outspread tentacles, without causing them to contract. They were then 'sucked off' by the ever-searching type I gastrozooids. This probably indicates that the type I gastrozooids were also being used to clean the tentacles of indigestible particles, and that the tentacles themselves were able to differentiate between prey and non-prey items, as not every tactile impulse led to a tentacle retraction.

Loss of components and autotomy

Structures like the bracteal canal of the bracts or the circular and radial canals of the nectophores are conspicuous features on the living animals if brightly pigmented (see Fig. 1b, g, f). It is, therefore, striking when they are absent. Some of the specimens videoed in Indonesia obviously had no or only a few nectophores and bracts whereas other individuals had a luxuriant corona of nectophores, and easily visible bracts dispersed all over the siphosome. The tethered animals may lose bracts and nectophores when a larger organism bumps into them by accident or when struck by strong bottom currents. The *in situ* images also showed that some segments on the tentacles, particularly at the distal, had no tentilla. Single tentilla were also missing on the proximal part. These might have broken off when prey escaped from entanglement or they were ripped off by the type I gastrozooids and eaten together with the prey. Thus, some specimens already had, in life, experienced a reduction in the number of certain components that obviously detach easier than others.

Detachment of certain components like nectophores, bracts, tentilla, gonopalpons, type I gastrozooids and male gonophores also happened frequently during capture and transfer of the living animals in the aquarium (Fig. 1c). Detachment always occurred at the same point, e.g. for the bract between the bracteal lamella and the groove at the proximal part of the bract, or for the type I gastrozooid between its pedicle and its basigaster. All the components that broke off easily obviously had a kind of weak link that resulted in them being rapidly discarded.

The loss of certain components during life is obviously not a serious threat to the survival of the animals since at least some of them are replaced. New nectophores are generated at the nectosomal budding point, and detached bracts might also be replaced since bracteal buds and young bracts were found at the base of the cormidial stems, at least in *Arancialia captonia*. Numerous buds and young tentilla were present on the most proximal segments of the tentacles suggesting that the tentacles are continuously growing and thus generating new tentilla.

Detached nectophores were observed to swim autonomously through the aquarium for quite some while; and detached type I gastrozooids sometimes performed rhythmical pumping movements or even attached themselves to the glass bottom with their funnel-shaped expanded mouths. Siphonophores are known to use the active shedding of nectophores and bracts as a kind of defensive reaction when touched, e.g. by a potential predator (Mackie *et al.*, 1987), and these movements might serve as a distraction.

Additional observations

Sex ratio and movement of gonophores. The species described above are all dioecious, as are all rhodaliids. Male gonophores were simple white sacs, which usually occurred in large numbers on the siphosome, while female gonophores were usually larger, less abundant and often had a bright orange bulge around the opening of the sub-umbrella cavity (see Fig. 1g). These differences were usually very obvious and enabled sex determination *in situ*.

Both, *Arancialia captonia* and *Archangelopsis jagoa* were found to have a well balanced sex ratio of about 1:1. *Tridensa sulawensis* and *T. rotunda*, however, were difficult to sex *in situ*. Most of the observed specimens were considered to be males, while others could not be sexed because their gonophores were not clearly visible. *A. captonia* possessed extremely large female gonophores (see Fig. 10a) that reached a diameter of up to 3 mm, while the female gonophores of *A. jagoa* barely reached a diameter of 1 mm.

Both the male and the female gonophores of the Comoran specimens were observed to pulsate periodically, *in situ* as well as in the aquarium. Usually three to four pulses were followed by a longer period of inactivity. Not all gonophores of a single cluster pulsated at the same time. Mackie *et al*. (1987) suggested that these movements might serve for ventilation or dispersal of sexual products. In the aquarium, clouds of a milky sperm were ejected vigorously by some of the pulsating male gonophores. Female gonophores were observed to expel a single large ovum through their widely open manubria.

Malformations. Malformations of single components were found on two different specimens, one female *Arancialia captonia* and one male *Archangelopsis jagoa* from the Comoros. In both cases a gonopalpon was affected in that it possessed two separate terminal regions, i.e. two mouth openings. However, malformations seemed to be exceptional, since they were found only twice among the hundreds of components studied.

Discussion

Characters for systematics of Rhodaliidae

The following components of rhodaliid siphonophores were found to be relatively uniform among the species described above and assumed to be uniform in all rhodaliids. They are therefore not suitable for species recognition:

(a) the shape of the nectophores
(b) the general morphology of tentacles and tentilla
(c) the shape of the type I gastrozooids
(d) the general shape of the type II gastrozooids
(e) the shape and coloration of the gonopalpons, and
(f) the general morphology of the male gonophores.

The major morphological features that have been used by Pugh (1983) and earlier workers to distinguish the rhodaliid species are:

(a) the shape of the pneumatophore
(b) the shape of the aurophore
(c) the internal structure of the corm
(d) the structure of the bracts (if still present after collection).

Most of the known species, however, possess both a smooth-walled pneumatophore and a smooth-walled aurophore without papilliform appendages. Additional characters are, therefore, needed to distinguish between genera and species and to establish new ones. The internal structure of the corm is, according to Pugh (1983), a good systematic character to define distinct groups among rhodaliid species. However,

investigation of the internal structure requires sagittal sectioning of the specimens, but if only a single specimen is available, then the researcher may want to avoid this in order to maintain the animal intact. Also, the lumen of cavities inside the nectosome and siphosome and the thickness of their surrounding walls are strongly affected by contraction and shrinkage due to preservation, which makes it difficult to distinguish between specific and individual differences. The walls of a siphosomal cavity, for example, might be thin in life, but become thicker when contracted after preservation, as suggested for *Tridensa captonia*. Useful for systematics is merely the general internal constitution of the siphosomal corm, i.e. whether the corm is solid (and then penetrated by a network of gastrovascular canals), as in *Rhodalia* and *Dromalia*, or has a cavity that is surrounded by a wall of varying thickness. The wall itself can also be penetrated by a network of gastrovascular canals, as in the genus *Angelopsis* and maybe also in *Thermopalia taraxaca* (Pugh, 1983); it then can serve as an additional distinguishing character.

Morphological characters that might change during death and after preservation are not sufficient for distinguishing genera and species, e.g. the size, shape and colour of the pneumatophore; and the bracteal and nectophoral lamellae which shrink to shrivelled ridges. The actual number of components like bracts, nectophores and type I gastrozooids is not useful either since their abundance depends on size and, presumably, age of the specimen; they are also often lost during collection.

The following external features were found to be good characters for generic and species identification if the internal structure of the corm is not used as one of the prime characters; some of them, however, depend on the animals being intact and viewed immediately after capture:

(a) the shape of the stalk of the cormidial units (narrow at its base and usually tube-shaped, or thickened at its base forming pronounced elevations on the corm)

(b) cormidial units mono- or polygastric, i.e. consisting of one or more cormidia

(c) the point of attachment of the type I gastrozooids (on cormidial units or singly to the corm on separate pedicles)

(d) the shape of the bracts and their point of attachment (on cormidial stalk or on gonodendra)

(e) the number of branches of the bracteal canal and additionally, if colours are not faded:

(f) the coloration of the pneumatophore

(g) the coloration and shape of the circular and radial canals of the nectophores.

Pneumatophore and aurophore. None of the specimens described above had a pneumatophore with gelatinous protuberances as is the case for *Dromalia alexandri*, nor an aurophore with papilliform appendages as in both the genera *Dromalia* and *Archangelopsis*. The small tubercles found on the aurophore of *Arancialia captonia* were not comparable in shape and number to the papilliform appendages of these two genera.

Cormidial units and siphosomal corm. The three new species also do not belong to the group of rhodaliids where the basal part of the main cormidial stalk is largely inflated forming pronounced elevations on the siphosomal corm, as in the genera *Angelopsis*, *Stephalia* and *Rhodalia*. Instead, their cormidia are borne on long and narrow stalks that are attached directly to the corm. *Tridensa sulawensis* and *T. rotunda* have cormidial units that immediately subdivide into two long cormidial stems each of which is polygastric, at least in *T. sulawensis* but unclear in *T. rotunda*. This basal bifurcation of the units set both new species apart from all the described species, except perhaps *Sagamalia hinomaru*, where the arrangement of the cormidia is uncertain. The cormidial units of *Arancialia captonia* also have narrow stalks that arise directly from the siphosomal corm, but they do not subdivide immediately and each unit consists of a single cormidium, i.e. it is monogastric, as in the genus *Archangelopsis*. *Archangelopsis* species also have long and narrow cormidial stalks, but as mentioned above, they also have papilliform appendages on their aurophores.

The shape and length of the cormidial stalks and branches are obviously connected to the size of the siphosomal corm. In *Thermopalia taraxaca*, known as the 'Galapagos dandelions', the cormidial elements seem to be attached directly onto the corm or to very short common stalks (Pugh, 1983). The siphosomal corm of this species is elongated and cone-shaped providing a large surface for the direct attachment of elements. *Angelopsis* and *Stephalia* species, *Rhodalia miranda* and *Dromalia alexandri* also have relatively large corms and their cormidia are bundled on thick stalks forming pronounced elevations on the corm. The siphosomal corm in the genus *Archangelopsis* and the newly described species, in contrast, is relatively small. There is insufficient space on such a small corm for a direct attachment of the numerous cormidial elements or for inflated cormidial stalks. The small size of the corm is probably a reason why the cormidia are bundled on such long and narrow stalks. None of the newly described species had a solid corm or a thick siphosomal wall penetrated by a network of gastrovascular canals clearly distinguishing them from the eight known species of the genera *Angelopsis*, *Stephalia*, *Rhodalia*, *Dromalia* and *Thermopalia*.

Type I gastrozooids. In all the new species described above, the type I gastrozooids were found to be distinct units without any association with the cormidial units, and each consisting solely of a pedicle and the gastrozooid itself. Pugh mentions isolated scars and stumps at the base of the corm in *Angelopsis euryale* and *Rhodalia miranda* to which type I gastrozooids might have been attached, and he found concentrations of these gastrozooids on the base of the corm in *Stephalia corona*. This situation appears to be the more typical one for rhodaliid siphonophores since clear evidence for type I gastrozooids as part of cormidial units has been given only for *Dromalia alexandri* (Pugh, 1983).

Bracts. Another evident character to distinguish between rhodaliid species is the structure of the bract. Bracts are known for 10 of the 14 presently recognised species (including the three new ones presented here), although only barely known in *Archangelopsis typica*. In most species, as in those described above, the bracts are attached to the base of the main cormidial stalk, and in some of them also to the stems of the

more distal cormidia on the cormidial unit. *Stephalia corona*, *Rhodalia miranda* and *Thermopalia taraxaca* have their bracts attached to the stalk of the gonodendron. The distal facet of the bract is either round, as in *T. taraxaca*; heart-shaped, as in the genus *Archangelopsis*, or triangular with three pronounced corners as in *S. corona*, *R. miranda* and *Sagamalia hinomaru*. The bracteal canal can be straight and without any branches (*R. miranda, T. taraxaca*); straight but bent at a right-angle at the distal end (*S. corona*); or its distal end is bifid- (*A. jagoa*) or trifid-branched (*S. hinomaru*). *Dromalia alexandri* has bracts with the most unique construction; they are triangular in shape, flattened dorso-ventrally and their bracteal canal is divided into many branches. In *Tridensa sulawensis* and *T. rotunda* the bracteal canal divides, on the broad distal facet, into three branches of equal length; in *T. sulawensis* each branch then subdivides into two further branches, a very distinctive character that separates the two species. The trifid branching of the bracteal canal is here considered a generic character of *Tridensa*, shared also with the genus *Sagamalia* from Japan (Pugh, 1983). The general shape of the bracts in both genera, however, is quite different. The Indonesian species do not have the lateral wings on the mid-region of the bracteal stalk like *S. hinomaru*, and their proximal parts are much larger inflated. There is unfortunately very little information available on the Japanese specimen, but nonetheless, it appears that this species might be the closest relative to *Tridensa* species. *Arancialia captonia* possesses bracts that are similar to those of *R. miranda* and, especially, *T. taraxaca*. All three of them have a bracteal canal without major branches. The bracts of *R. miranda* and *T. taraxaca*, however, are attached to the gonodendra of polygastric cormidial units that have, at least in *R. miranda*, thick bases (see above), whereas those of *A. captonia* are attached to the base of monogastric cormidial units with thin stalks. Furthermore, mature bracts of *R. miranda* possess a swollen, recurved proximal end in the form of a process, which is missing in *A. captonia* and *T. taraxaca*. The bracts of the latter two species have cusps around the margins of the distal facet, which are tooth-like in *T. taraxaca* but less pronounced in *A. captonia*. Also the distal end of the bracteal canal differs in that it is straight in *T. taraxaca* and bent in *A. captonia*. On the other hand, both species have pale orange coloured nectophores in common. The shape of the corm and the entire construction of the siphosome, however, are generally so different in both species that they are considered to belong to two different genera.

Gonodendra. In all but one of the rhodaliid genera so far described the cormidial elements include at least one gonodendron. This multi-branched structure is attached to the main stem by a single stalk, and bears the single-sexed gonophores as well as palpacle-less palpons, that are generally referred to as gonopalpons. Secondary, and higher order, cormidial branches do not always develop a gonodendron, but always bear a type II gastrozooid. In *Tridensa sulawensis*, however, a gonodendron is absent, and the gonophores and palpons, still palpacle-less, are attached separately to the main stem. Unfortunately, presently it is not certain that this is also the case for

T. rotunda, although supposed to be so. The lack of gonodendra sets *Tridensa sulawensis* apart from all other rhodaliid species so far described.

In summary, the genus *Tridensa* can be clearly distinguished from other rhodaliid genera on the basis of the bracts, the basal bifurcation of the cormidial units and the lack of gonodendra (assuming that they are also absent in *Tridensa rotunda*). The morphological differences between *Tridensa sulawensis* and *T. rotunda* are sufficient to establish both as distinct species that are probably closely related. The most notable differences between both species are the proximal part of the bracts, which is largely inflated in *T. rotunda*, and the bracteal canal which has no secondary branches in *T. rotunda*. The status of the monotypic genus *Arancialia* can definitely be established by a combination of characters that is not found in other rhodaliid genera: a globular aurophore with small tubercles, monogastric cormidial units and bracts that are traversed by a simple bracteal canal without major branches.

Key to the genera and species of the family Rhodaliidae

1 (a) Pneumatophore and aurophore smooth-walled 2

(b) Pneumatophore smooth-walled, aurophore with papilliform appendages, bifid branching of distal end of bracteal canal . . . . Genus *Archangelopsis*

(c) Pneumatophore apically flattened and bearing several gelatinous protuberances, aurophore with papilliform appendages . . . . Genus *Dromalia* (*D. alexandri*)

2 (a) Stalks of cormidial units thickened at base forming pronounced elevations on the corm 3

(b) Stalks of cormidial units tube-shaped, no pronounced thickened bases 5

3 (a) Siphosomal cavity vast and thick-walled . . . . Genus *Angelopsis*

(b) Siphosomal corm solid 4

4 (a) Bracts attached to base of cormidial stems, bracteal canal bent by 90° at distal end, distal facet triangular . . . . Genus *Stephalia*

(b) Bracts attached to gonodendra, bracteal canal not bent but straight, distal facet heart-shaped . . . . Genus *Rhodalia* (*R. miranda*)

5 (a) Trifid branching of distal end of bracteal canal 6

(b) Bracteal canal without major branches at distal end . . 7

6 (a) Lateral wings at the mid-height of the bract . . . . Genus *Sagamalia* (*S. hinomaru*)

(b) Bracts without lateral wings at mid-height . . . . Genus *Tridensa* **gen. nov.**

7 (a) Cormidial units without a pronounced stalk, cormidial elements attached directly to cone-shaped corm or to very short common stalks ; units polygastric; type I gastrozooids attached to first cormidium . . . . Genus *Thermopalia* (*T. taraxaca*)

(b) Cormidial units consisting of single cormidium, attached directly to small corm by narrow stems, monogastric; type I gastrozooids attached singly to the corm on separate pedicles . . . . Genus *Arancialia* **gen. nov.** (*A. captonia* **sp. nov.)**

Genus: *Archangelopsis*

(a) Pneumatophore large, nectophores numerous, tentilla attached to mid-region of tentacular segment .... *A. typica*
(b) Pneumatophore with circular pigment rings, tentilla attached to proximal end of tentacular segment ...*A. jagoa*

Genus: *Angelopsis* (see Pugh 1983)

(a) Walls of siphosomal cavity penetrated only by radial gastrovascular canals, with a peripheral reticulum of longitudinal and latitudinal canals; connection between siphosomal and hypocystic cavities reduced or absent.....*A. euryale*
(b) Walls of siphosomal cavity (?) with a reticulum of gastrovascular canals through-out; (?) distinct opening connecting siphosomal and hypocystic cavities ......*A. globosa*

Genus: *Stephalia* (see Pugh 1983)

(a) Hypocystic cavity per se restricted to upper part of nectosome, the remainder of the nectosome being filled with many large, intercommunicating chambers; up to *c*. 20 nectophores present which are arranged in a single corona; reticulum of small gastrovascular canals throughout siphosomal corm ....*S. corona*
(b) Hypocystic cavity probably occupies whole of nectosomal region; reticulum of small gastrovascular canals restricted to periphery of siphosome (number of nectophores not known) ....*S. dilata*
(c) Internal structure of corm inadequately known but there is either an axial cavity or a system of gastrovascular canals that includes a very large canal; between 20 and 30 nectophores present, which may be arranged in a double corona...............................*S. bathyphysa*

Genus: *Tridensa*

(a) Nectophores with four pigmented radial canals, two of them S-shaped; circular canal not pigmented; distal facet of bract triangular with rounded corners; bracteal canal distally divided into three branches each of which splits again into two recurved sub-branches..................
.........................*Tridensa sulawensis* **sp. nov.**
(b) Nectophores with one pigmented and S-shaped radial canal; circular canal pigmented; distal facet of bract triangular with more distinct corners; proximal part of bract largely inflated; bracteal canal distally divided into three branches, but with no further branches................
.........................*Tridensa rotunda* **sp. nov.**

Methods of growth

Nectophoral and siphosomal buds were found on all of the investigated animals showing that the zone of proliferation probably retains the potential to generate new elements at any age. This is reasonable if elements become detached during life and need to be replaced.

The classical growth pattern of the siphosome in rhodaliid siphonophores was described by Pugh (1983), in accordance with earlier researchers, as follows: 'The growth of the siphosome is a continuing process with the spiral arrangement of the cormidia being extended by the addition of new cormidia from the apical zone of proliferation'. Consequently, '…a progressive series of developing cormidial units can be found in the most apical whorl of the siphosome'(most rhodaliids possess cormidial units that are arranged in spiral whorls around the surface of the corm). The youngest units on the siphosome are hence found on the ventral side of the corm just below the zone of proliferation, the oldest on the base of the corm.

Cormidial units, at a very early stage of development, were also found at the base of the corm in *Tridensa sulawensis* and *Arancialia captonia*. They occur directly adjacent to mature cormidia. These young units were similar to those that were developing below the siphosomal budding point. They consisted merely of a short stem, a type II gastrozooid on a pedicle, and some small buds at the distal end of the stem. There was, however, no evidence for a connection between the young cormidia at the nectosomal region and those at the base of the corm, as mistakenly described by Pugh (1983) for *Angelopsis euryale* (see below). The young cormidia at the base of the corm therefore must have had another origin. They might emanate from latent buds between fully developed cormidia that only start growing at an advanced age of the entire organism. Also Pugh (1983) reported on less developed cormidia on the base of the corm in *Stephalia corona*. The arrangement of these cormidia were different from those around the sides of the corm and he suggested that they were secondarily developed.

Additionally, further growth can be achieved by budding of secondary cormidia within each cormidial unit, either at the base of the main cormidial stalk or distally on the cormidial stems (Pugh, 1983). In this study, budding of secondary cormidia on the distal part of the cormidial units were found in *Tridensa sulawensis*, and at the base of the main cormidial stem in *Archangelopsis jagoa* (see Fig. 13a).

The type I gastrozooids clearly are essential to the animal, as they are the principal digestive elements. However, they can easily be detached and new ones must be generated continuously. All specimens of the new species described herein had separate developing type I gastrozooids attached to the region immediately below the siphosomal budding point. They still possessed an annulated tentacle, but without tentilla (see Fig. 12c). The tentacle became detached before the gastrozooid was passed down onto the main siphosomal corm. From the apical part of the siphosome the type I gastrozooids travelled straight down to the base of the corm as clearly seen on *Tridensa sulawensis*. Also Pugh (1983) observed in *Angelopsis euryale* a series of 'young buds' passing down between pairs of well developed cormidial bases from immediately below the nectosomal region to the base of the corm. He interpreted these buds as young cormidia. A re-examination, however, revealed that these elements were most likely type I gastrozooids (Pugh, pers. comm.); they joined up with large scars on the base of the corm that obviously belonged to type I gastrozooids.

Thus, additional type I gastrozooids seem to be added to the corm in a different way as young cormidial units. As mentioned above, both are obviously generated by the same budding point, but as clearly separated units. What predestines a particular bud to become a type I gastrozooid while the next may become a cormidial unit is so far not understood.

Function of gastrozooids, gonopalpons and palpons

Unlike all the other known siphonophores, rhodaliids possess two different types of gastrozooids. Type I, which is not known from other taxa, loses its tentacle at an early stage of development and plays, as shown above, the main part in feeding and digestion; whereas type II always bears a well developed tentacle with tentilla, but behaves surprisingly passively if prey items become entangled in its tentilla. A transfer of food by the type I gastrozooids to the type II gastrozooids, as suggested by Pugh (1983), was never observed. As mentioned above, no endodermal villi were found within the stomach region of the type II gastrozooids. These observations suggest that the type II gastrozooids, at least of the four species described above, do not play any part in feeding or digestion. Thus it seems as if a functional separation has taken place in rhodaliids in which the type II gastrozooid is merely the structure that supplies the prey catching device (the tentacle) while type I carries out the digestive function. Since this separation is exclusively found in rhodaliids, it is presumed to be a special adaptation to the benthic life-style. The tentacle operates largely in independence of the gastrozooid to which it belongs. The attachment of a large tentacle to the basigaster of the gastrozooid may limit the motility of the gastrozooid, particularly if it is used for tethering the colony to the substratum and not released when prey bumps into it. A gastrozooid without a tentacle, like type I, is much more flexible in all directions and highly manoeuvrable among the elements of the closely crowded siphosome. A concentration of these large specialised type I gastrozooids at the base of the corm has the advantage that all parts of the siphosome can be reached from this position. The arrangement of the type I gastrozooids in clusters, in particular on the ventral region of the corm or at its base, was also found in other rhodaliids (e.g. *S. corona*, *R. miranda*; Pugh, 1983).

The *in situ* observations of the species described above suggest that, unlike type II gastrozooids, gonopalpons and rhodaliid palpons may assist in feeding. These numerous structures were almost permanently in motion between the cormidial elements. Their mouth region was highly expandable, but could also stretch to a narrow trunk that was used like a pipette or forceps. The amorphous particles found inside their distal regions suggest that gonopalpons probably mainly picked up small items, either for digestion or to clean the tentacles of indigestible material. The observation on gonopalpons of a Comoran specimen of *Archangelopsis jagoa*, which incorporated tentacle fragments, indicated that gonopalpons were capable of also engulfing larger items. Mackie *et al.* (1987) described palpons as accessory digestive organs that, in some cases, can excrete waste products. It is probable that the rhodaliid gonopalpons have this similar additional function.

Selectivity for certain prey items is thought to be correlated to the size of the gastrozooids involved in digestion (Purcell, 1980). Weakly swimming siphonophores, which have fewer and larger gastrozooids than strongly swimming species, are known to capture relatively large, less common prey. The species described above, although benthic, might fit into this scheme since their type I gastrozooids are relatively large and

few in number. Small and light prey items, like the flocculent material floating close to the seabed off South Africa, evoked no response from the tentacles (see above). Mackie *et al.* (1987) found a specialisation for soft- or hard-bodied prey in certain siphonophore species linked to the type of nematocysts borne by the tentilla. The tentilla of the species described above contained nematocysts of different types; they caught soft- (fish larvae) as well as hard-bodied (crustacean) prey that would indicate a relatively wide range in prey type.

The contractions and relaxations of both the tentilla and the floating tentacles strongly resembled the casting of fishing lines as, for example, practised in fly-fishing. The thickened end of the terminal filament in the tentilla might serve as a kind of lure that could attract zooplankton, suggested also by Purcell (1980) for pelagic siphonophores.

Buoyancy control

While floating above the substratum and tethered to it like an air balloon, rhodaliids are positively buoyant. Consequently they would slowly float upwards if they release themselves or become accidentally dislodged. If detached, specimens normally swim rapidly back down to the bottom and reattach before the gas pressure inside the pneumatophore could increase by a significant amount. An increase in buoyancy would only become a problem if a detached animal was lifted too far up, e.g. by an unpredictable upwelling, and the jet propulsive action of the swimming bells could not reverse the ascent. As the ambient pressure decreases, the gas inside the pneumatophore would try to expand, but the relatively rigid chitin, lining the pneumatosaccus, would act to prevent this. While rising upwards the pressure inside the pneumatophore would potentially double with each halving of the ambient partial pressure. The situation would become more and more critical for the animal as it approached the surface, and the float would probably burst if the animal did not have a means of venting excess gas.

The exact mechanism and extent to which rhodaliids can control the gas pressure inside the pneumatophore, either by expulsion through the pore of the aurophore, diffusion or resorption, is not yet known. Pugh (1983) discussed this matter in detail (pp. 278–285). The *in situ* observations of the species described above showed that specimens that became dislodged always used their nectophores to return to the bottom, without any obvious venting of gas. On the other hand, none of the animals described here, which were brought up from 120 m depth or more to the surface without using a pressure chamber, had a ruptured pneumatophore or aurophore or any other severe damage. That means they must have released or absorbed gas on the way up and thus could keep the pressure inside the float adjusted to the ambient partial pressure. Some specimens had a slightly deformed pneumatophore with signs of over-inflation or collapse as if over-deflation had occurred (Fig. 8), others had a slightly enlarged aurophore with the prominent central pore pointing upward (Fig. 1a). One Indonesian specimen released several gas bubbles through the pronounced central pore of the aurophore while being observed in the aquarium. These observations indicate that the animals were able to maintain a certain overpressure inside the pneumatophore for a while and to release gas intermittently. This in turn requires a constrictor

that functions like a pressure sensitive valve, a pneumatic duct. The only part of the pneumatosaccus which is not covered by the rigid chitinous lining is where the pneumadenia, the gas-secreting glandular tissue of the aurophore, connects to the gas-filled cavity of the pneumatophore. Thus, this is the only area where gas could be released. Pugh (1983: 218) summarised the different theories about how the gas could be vented at this point, either by rupture or extrusion through the cells, or via a pneumatic duct that might pass through the gas gland tissue and thus connects the gas-filled cavity with the exterior. Authors have disagreed about the presence of such a duct, and even the findings of the present study are contradictory. One of the South African specimens had an aurophore with a widely open external pore, as also did one of the *Archangelopsis jagoa* specimens from the Red Sea (Hissmann *et al.*, 1995). Sagittal sectioning through the aurophore and pneumatophore of the South African specimen revealed a silvery lined duct with no signs of tearing or rupture. In one of the Indonesian specimens the gas-gland tissue between the aurophore and the pneumatophore was found to be translucent in the centre but there was no clear evidence for a duct. The question of whether rhodaliids, or at least some of them, possess a pneumatic duct should be reinvestigated on recently sampled specimens.

Under normal circumstances, however, there is no need for a regular disposal of gas since rhodaliids are more or less sessile. Venting gas is probably restricted to cases of emergency. The majority of the species known to date live at water depths of at least 100 m (see below). At these depths, a rise of 1–2 m above the bottom would have little effect on the gas pressure inside the pneumatophore. It only becomes critical at depths where the ambient partial pressure decreases quickly within small vertical distances and that is from about 50 m upwards.

Geographical and depth distribution

Benthic siphonophores, collectively, have been found at many offshore regions of the World's Oceans (see Addendum), and it seems that, in general, they are not restricted to certain areas. Rhodaliids occur in tropical and temperate waters as well as in the subantarctic; in deep (3000 m) and in relatively shallow (60 m) waters; at cold (2 °C) and warm (23 °C) temperatures; and on sandy and rocky substrata. All specimens described above, however, were found below 100 meters, and also among the other known species there is only a single record from a shallower depth. Rhodaliids seem to avoid the sub-tidal zones, probably because of high water temperatures (exceeding 25 °C), difficult conditions for buoyancy control (see above), and disturbances caused by stronger water movements and higher densities of other benthic and epibenthic organisms.

The geographical distribution of most individual species, however, is relatively restricted (Pugh, 1983) and rather patchy, although this might also be attributed to a dearth of data. Some species are known only from a single record. The most widely distributed species are *Stephalia corona*, found in the Atlantic northwest of Scotland, off Iceland and west Africa; *Rhodalia miranda* along the southeast coast of South America; *Archangelopsis typica* off Java and Japan; and *A. jagoa*. The last species was at first described from the Gulf of Akaba/Red Sea (Hissmann *et al.*, 1995) and now has been found around the Comoros, which was the first record of benthic siphonophores for the Western Indian Ocean. However, even within these relatively large areas, rhodaliids tend to have a disjunctive distribution pattern with large gaps in-between locations, where they are apparently not present (e.g. *R. miranda*, Riemann-Zürneck, 1991).

Some species live geographically relatively close to each other but at different depths, such as *Stephalia corona* and *Angelopsis euryale*. However, *Tridensa sulawensis* and *T. rotunda* are so far the first sympatric species to be found co-occurring within the same habitat and depth range. They are probably closely related as their morphological similarities suggest (as discussed above).

Rhodaliid populations also might undergo temporal changes, but up to now there is nothing known in detail about the life span, life cycles and population dynamics of benthic siphonophores. Hessler *et al.* (1988) reported from the Rose Garden hydrothermal vent in the eastern Pacific that the so-called 'Galápagos dandelions' *Thermopalia taraxaca* were virtually absent when the site was revisited 5 years after its discovery. Thereafter they were again sighted during another visit in 2002 (T. Shank, pers. comm.). These fluctuations might have been caused by changes in the physical milieu at the vent site, which is naturally quite unstable. The few studies on pelagic species indicate seasonal fluctuations in the presence of certain species. It is, however, difficult to separate fluctuations attributed to population dynamics of individual species from differences in their distribution generated by seasonally changing hydrographical conditions (Mackie *et al.*, 1987). *Archangelopsis jagoa* was relatively abundant when first discovered in the Red Sea but hard to find 4 months later (Hissmann *et al.*, 1995). At Grande Comore, the same species was first found in a small, restricted area at the southwest coast of the island. Then, after an absence of 5 years, only a single animal was encountered in that area, although dives took place at the same time of the year. Also, intensive submersible surveys along different stretches of coastline revealed no further siphonophore records. The environmental conditions at the Comoros are relatively stable in deeper water throughout the entire year and seasonal fluctuations caused by hydrographical conditions are rather unlikely. If individuals are widespread and very low in numbers, species must be equipped with sophisticated dispersal mechanisms and efficient chemoattractants for reproduction to guarantee the survival of the population. Although generally rare, specimens were sometimes found in small accumulations with distances of less than 40 cm between individuals. These aggregations did not seem to be accidental and might suggest the possibility of mutual attraction.

With the three new species described above the total number of rhodaliid species recognised to date is increased to 14 (see Addendum). What explains this small number is the fact that rhodaliids are extremely beautiful but, unfortunately, often tiny and flimsy creatures that are easily overlooked when surveying the sea floor. Without doubt, however, more records will follow as explorations of coastal zones, by submersibles and ROVs, continue. They will reveal more challenging

images and information on how these 'beautiful, deadly predators' (Mackie, 2002), which mostly shrink to unalluring objects when preserved, really look and behave.

Acknowledgements

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Abbreviations used in figures

au – aurophore
b – bract
bl – bracteal lamella
cb – cnidoband of tentillum
c.b – cormidial bud
gd – gonodendron
go – gonophore
gp – gonopalpon
gz.I – gastrozooid of type I.
gz – gastrozooid of type II.
n – nectophores
nl – nectophoral lamella
p – palpon
pe – pedicle of tentillum
p.gz – pedicle of type I gastrozooid
pn – pneumatophore
sta – stalk of cormidial unit
ste – cormidial stem
t – tentacle
te – tentillum
tp – terminal process of tentillum
vg – ventral groove of bract

Addendum

Species of rhodaliid siphonophores

1. *Angelopsis globosa* Fewkes, 1886. Original specimens untraced – no further specimens known. East coast off North America, 2553 m.
2. *Angelopsis euryale* Pugh, 1983. Three specimens exist, but are in poor condition. Off Mauretania, West Africa, 3089–3109 m.
3. *Stephalia corona* Haeckel, 1888. Original specimens destroyed. Further specimens known – see Pugh (1983) and Schuchert (2000). Scotland, Iceland, NW-Africa, 666–1658 m.
4. *Stephalia dilata* Bigelow, 1911. Original specimen sectioned, but slide collection untraced. One specimen, possibly of this species, has been collected recently (Pugh, pers. comm.). Galapagos, 495–1158 m.
5. *Stephanalia bathyphysa* Haeckel, 1888. Original specimens destroyed. No further specimens known. New Zealand, 503 m.
6. *Sagamalia hinomaru* Kawamura, 1954. Original specimen exists – see Pugh (1983), and at least one new specimen has been collected recently (Pugh, personal communication). Japan, 450 m.

7. *Archangelopsis typica* Lens and van Riemsdijk, 1908. Only a few pieces of the original three specimens exist, but another specimen in poor condition, described by Bigelow (1913), still exists – see Pugh (1983). Tomir, Japan, 100–112 m.

8. *Archangelopsis jagoa* Hissmann, Schauer and Pugh, 1995. Several specimens in good condition exist. Golf of Akaba (Red Sea), Comoro Islands, 240–400 m.

9. *Rhodalia miranda* Haeckel, 1888. Three of four original specimens exist, others known to exist (see Pugh, 1983; Riemann-Zürneck, 1991). South Argentina, 455–1098 m.

10. *Dromalia alexandri* Bigelow, 1911. Specimens exist – see Pugh (1983). South California, 64–752 m.

11. *Thermopalia taraxaca* Pugh, 1983. Original and other specimens exist – see Pugh (1983). Galapagos Rift, 2500–2600 m.

12. *Tridensa sulawensis* **sp. nov.** Hissmann 2004. Two specimen exist. Sulawesi, Sangihé (Indonesia), 165–289 m.

13. *Tridensa rotunda* **sp. nov.** Hissmann 2004. One specimen in poor condition exists. Sulawesi, Sangihé (Indonesia), 226–289 m.

14. *Arancialia captonia* **sp. nov.** Hissmann 2004. Four specimens exist. Cape Peninsula, South Africa, 120–360 m.