Corallimorphus profundus in shallow Antarctic habitats: Bionomics, histology, and systematics (Cnidaria: Hexacorallia)

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In March 2000 and November/December 2001 thirteen specimens of *Corallimorphus profundus* Moseley, 1877, a conspicuous, anemone-like cnidarian, were hand-sampled by SCUBA diving in 30 to 40 m depth off US Palmer Station, Antarctic Peninsula. *Corallimorphus* species were formerly recorded only from deep water habitats from where they had been brought up more or less damaged, with most of their epithelia lost or macerated. The present well preserved specimens offer the opportunity to study various aspects of the species' morphology and biology, particularly as one mature female contained a full cycle of oogenesis besides two batches of brooded developmental stages.

Most of the results obtained demonstrate that the genus *Corallimorphus* shows features and bionomics that are typical of the Scleractinia. Thus, Moseley's early assumption (1877) that this genus is distinguished from certain deep-sea corals such as *Stephanophyllia* only by the absence of the calcareous skeleton is largely confirmed, although direct comparison with Moseley's material was not possible here.

Similar relationships exist for another corallimorpharian, *Nectactis singularis* Gravier, 1918. This small, discoidal, soft-bodied deep-sea species resembles the poorly skeletalized deep-sea Scleractinia *Leptopenus antarcticus* Cairns, 1980, in cnidom data and histological sections.

Introduction

Members of the genus *Corallimorphus* are rather large, solitary deep-sea Anthozoa with a world-wide distribution, but only some 50 samples have become known since Moseley described the first specimens in 1877, suggesting that they are rare animals and/or may live on surfaces not easily accessible to traditional sampling gear. All specimens collected in the past were in poor condition (see den Hartog et al., 1993) with torn bodies and tentacles and with most of their external and internal epithelia lost or macerated. Thus, knowledge of these deep-water animals remained fragmentary and there were no observations of live specimens, not to mention their ecology and reproduction.

Despite its name, *Corallimorphus profundus* is not confined to the deep sea but is known to ascend to comparatively shallow depths in the Antarctic (Fautin, 1984). Nevertheless, it was unexpected when the junior author diving near Palmer Station (Antarctic Peninsula), discovered a "club-armed anemone" in 36.5 m depth that proved to be *Corallimorphus profundus.* This was the first *Corallimorphus* specimen observed alive in its habitat and hand-sampled by a diver. It was also the first specimen obtained with almost undamaged, well preserved epithelia and, by chance, a mature female harbouring both oocytes and developmental stages. Consequently, this female, together with some additional specimens collected in November/December 2001, offer the opportunity to study various aspects of deep-water Corallimorpharia including taxonomy within the genus and its systematic relations within the Hexacorallia.

Material and methods

One specimen (preserved wet weight 45 g) was collected in March 2000 by SCUBA diving (leg. Katrin Iken, former member of the Antarctic Research Team of the US University of Alabama) from a steep rock off Janus Island (64°47'S, 64°07'W, 36.5 m depth), about 1.5 nautical miles from the US Palmer Station (Antarctic Peninsula). The specimen was fixed in 5% formaldehyde (changed once) and was transferred to 80% ethanol prior to investigation. A longitudinal sector of the specimen was embedded in Paraplast, and histological sections about 10 µm thick were stained with Heidenhain's Azan trichrome. Most of the histological results are based on this specimen which will be referred to as 'March-2000-female' in the following text.

Twelve additional specimens were collected between 16.xi.2001 and 21.xii.2001 (leg. Bill Baker and Katrin Iken) from different sites around Palmer Station, e.g. Christine Island, Norsel Point, Bonaparte Point. Nine specimens were of medium size (11.5-36 g), one was rather small (1.4 g), and two were large (76 and 87 g). Histological sections were prepared from the tiny 1.4 g specimen (serial cross sections), from the testicular tissue of the largest specimen and from the tentacles of two females containing developmental stages.

For comparative purposes, material of two deep-water Hexacorallia species was examined: *Nectactis singularis*, a deep-sea corallimorpharian, with cross sections prepared in the 1970's of two specimens originating from French deep sea cruises (see Riemann-Zürneck, 1979: 229). Two specimens of *Letepsammia formosissima*, a deep-water scleractinian coral, with tissue preserved in ethanol (donation of the Smithsonian Institution: ex USNM 96545).

Depostion of material. Four specimens of *C. profundus* (2001/3: three specimens collected 6.xii.2001; 2001/4: one specimen collected 18.xii.2001) are deposited in the Nationaal Natuurhistorisch Museum, Leiden, NL. The remaining material including the two *Letepsammia* specimens is preserved in the Zoological Museum of the University of Hamburg.

Description of *Corallimorphus profundus* Moseley, 1877

(figs. 1-8, table 1)

Corallimorphus profundus Moseley, 1877: 300-301, Plate XLV, Figures 7, 8; Hertwig, 1882: 24-25, Plate 2, Figures 2-3; ?McMurrich, 1893: 199; Fautin, 1984: 2-5, Figures 1-4.

syn. *Corallimorphus antarcticus* Carlgren & Stephenson, 1929: 7-8, Figure 1; Carlgren, 1940: 20-21; Carlgren, 1949: 13; Grebelny, 1975: 307-308, Figures 1-2. Synonymized by Fautin, 1984.

Colour, size and gross structure (figs. 1, 2, 6).— Colour in life: In its habitat (35 to 40 m depth) the specimens appeared translucent lilac, their pinball like tentacle tips (acrospheres) bright white. Brought to the surface, the colour of the larger specimens

Fig. 1. *Corallimorphus profundus*. In situ photograph of a specimen at Janus Island (36 m depth) sitting in a crevice between sponges and ascidians; note large, prominent mouth and different size of tentacles. Photo by Bill J. Baker, University of South Florida.

was pale (salmon) orange, that of the smaller ones pinkish. The specimens appeared unable to contract, but during collection and transport they shrunk to about two thirds of their original size; tentacles are always shortened in preserved specimens. Prior to preservation the specimens are quite slimy due to excreted mucus.

The wet weight of the specimens ranges mainly between 11.5 and 87 g with one tiny juvenile weighing only 1.4 g. The diameter of the oral disc is 5 to 6.5 cm plus tentacles up to 2.5 cm long in preserved specimens and up to 5 cm in life; column height is 3 to 4 cm. The pedal disc was firmly cemented to the rock surface, and was slightly damaged in all specimens during detachment, with remnants of a brownish cuticle and protruding mesenterial filaments. The actinopharynx is large, with about 60 longitudinal furrows. The large mouth is slit-like, about 2.5 cm long, raised on a cone, with no siphonoglyphs.

The number of marginal tentacles is 60 to about 88, with a basic set that appears to be 60 (counted in the tiny 1.4 g specimen and in two more specimens). The innermost marginal tentacles are large and voluminous with smooth shafts and pronounced acrospheres up to 5 mm across; the outermost tentacles are much smaller and sometimes only knob-like. One specimen (#2001/2A, 19.5 g) has two additional tentacles emerging from one point of the column. In the March-2000-female several of the larger

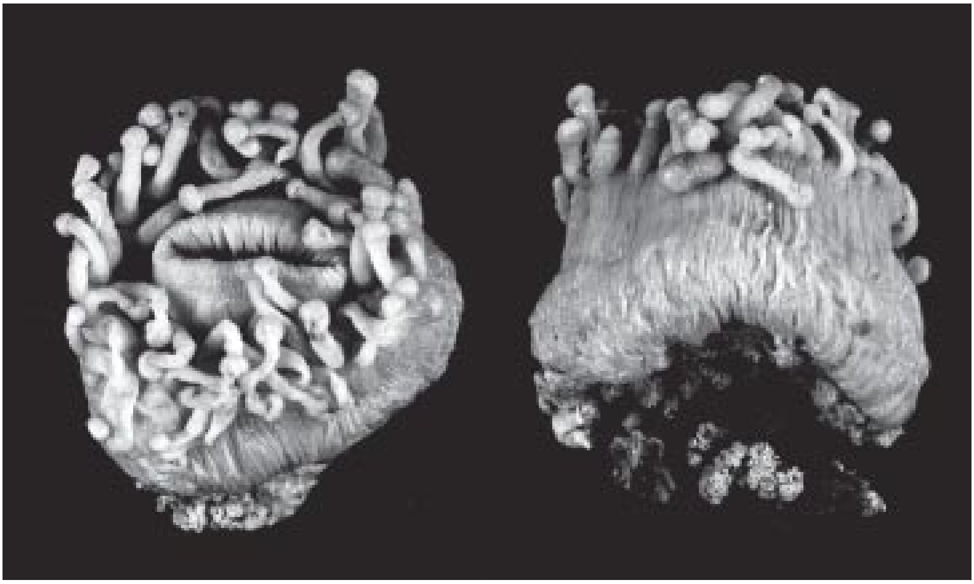

Fig. 2. *Corallimorphus profundus*. Two aspects of the March-2000-female, natural size. Note the large prominent mouth (left), the dark cuticle on the slightly damaged pedal disc with protruding mesenterial filaments, and one thick tentacle containing developmental stages in the center (right).

tentacles are unusually thick, with enlarged acrospheres. When transferred to ethanol it became obvious that they are stuffed with tiny orange-red globules which later were found to be developmental stages (blastulae).

In contrast to specimens from deeper water, which commonly have 10-20 discal tentacles (Fautin, 1984; E. Rodriguez, pers. comm.), discal tentacles are scarce or absent in the present shallow-water individuals. Only five of the 13 specimens had a few tiny discal tentacles; the maximum number was four (#2001/5B, 36.5 g), the largest specimen (#2001/1A, 87 g) had three, two specimens had two and one had only one discal tentacle. They were located close to the edges of the slit-like mouth, and in the specimen with four discals they were arranged bilaterally symmetrically (see Discussion).

Body with thick mesogloea in body wall, oral disc and actinopharynx; column with longitudinal irregular furrows.

Cnidom (tab. 1, fig. 3).—The nematocyst signature of *C. profundus* is remarkable with two of the acrosphere nematocysts exceeding 200 microns in length. Our measurements agree well with the data given by Carlgren (1940: "*Corallimorphus antarcticus*") and Fautin (1984) with the exception of the dimensions given by Fautin for the p-mastigophores of the column (104.6-123 µm: probably a scale-bar confusion) compared to 32.5-41 µm (Carlgren) and 39-49 µm (our specimens). These p-mastigophores are most abundant near the edge of the pedal disc. No cnidae were seen in the tentacle shafts, whereas Fautin found spirocysts, and Carlgren reported four different cnidae in what he called "peduncles". In the mesenterial filaments nematocysts are rare, most squash preparations containing only large holotrichs of one size class.

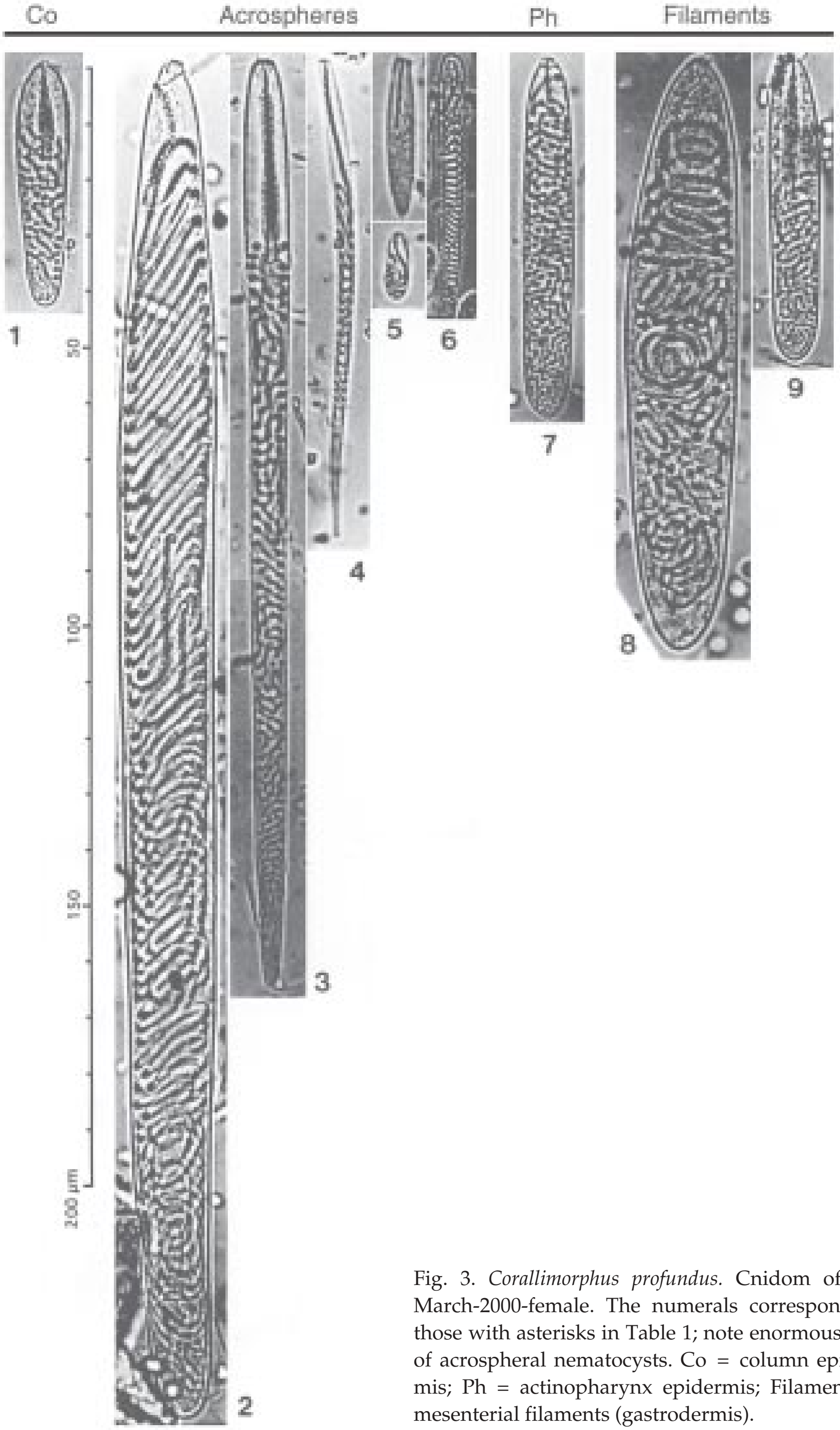

Fig. 3. *Corallimorphus profundus.* Cnidom of the March-2000-female. The numerals correspond to those with asterisks in Table 1; note enormous size of acrospheral nematocysts. Co = column epidermis; Ph = actinopharynx epidermis; Filaments = mesenterial filaments (gastrodermis).

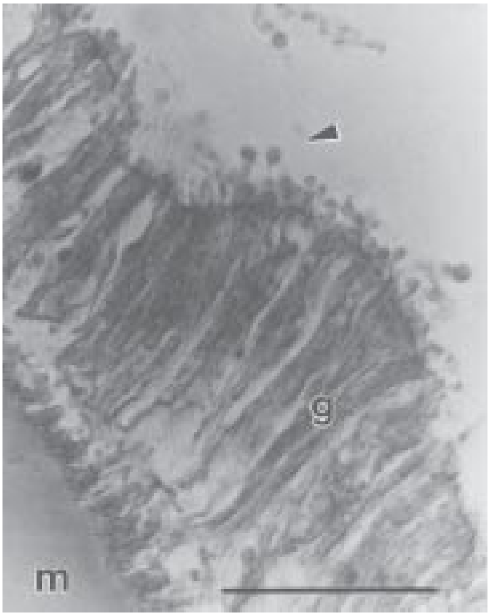

Fig. 4. *Corallimorphus profundus*. Longitudinal section of column with 'villous' gastroderm presumably releasing vesicles 3-8 µm in diameter into the gastrocoel (Heidenhain's trichrome staining). g = gastrodermis; m = meosogloea with circular musculature. Scale bar = 100 µm.

Size variation of cnidae. The size range of the long p-mastigophores in the tentacle acrospheres of the March-2000-female is exceptionally large at almost 100 µm. Measurements in two further specimens confirmed this range but also indicated that two size classes may be involved. This long p-mastigophore is also the nematocyst type that shows some size dependent variation within one individual with regard to large and small acrospheres and also between specimens of different size. The cnidae of the acrospheres in the tiny 1.4 g specimen are as follows: holotrichs: 170-215 µm; long p-mastigophores: 116-145 µm; lanceolate basitrichs: 52-64 µm; spirocysts 43.5-55 µm. One discal tentacle acrosphere of the largest specimen (87 g) was checked against the marginal tentacle acrospheres and was found to have only slightly smaller p-mastigophores.

Table 1. Size ranges of the cnidae in *Corallimorphus profundus* (March-2000-female). The numerals with asterisks correspond to fig. 3.

Body region	Cnidae	Size ranges (µm)
Column	1* p-mastigophores	39-49 x 8-9
Tentacle acrospheres	2* holotrichs	220-248 x 14-17.5
	3* long p-mastigophores	128-212 x 6-9
	4* lanceolate basitrichs	55-88 x 3-4
	5* small basitrichs (rare)	29x5.5 and 12x4
	6* spirocysts	50-78 x 3.5-5
Actinopharynx	7* holotrichs	58-73 x 8.5-11
Mesenterial filaments	8* holotrichs	95-125 x 14.5-20
	9* p-mastigophores (rare)	44-60 x 8-9.5

Musculature.— Contrary to Moseley's (1877) and Stephenson's (1920) statements, no ectodermal longitudinal musculature is present in the column. The weak circular musculature of the column is evenly developed throughout. The tentacle shafts are provided with weak endodermal circular musculature and comparatively strong ectodermal longitudinal musculature.

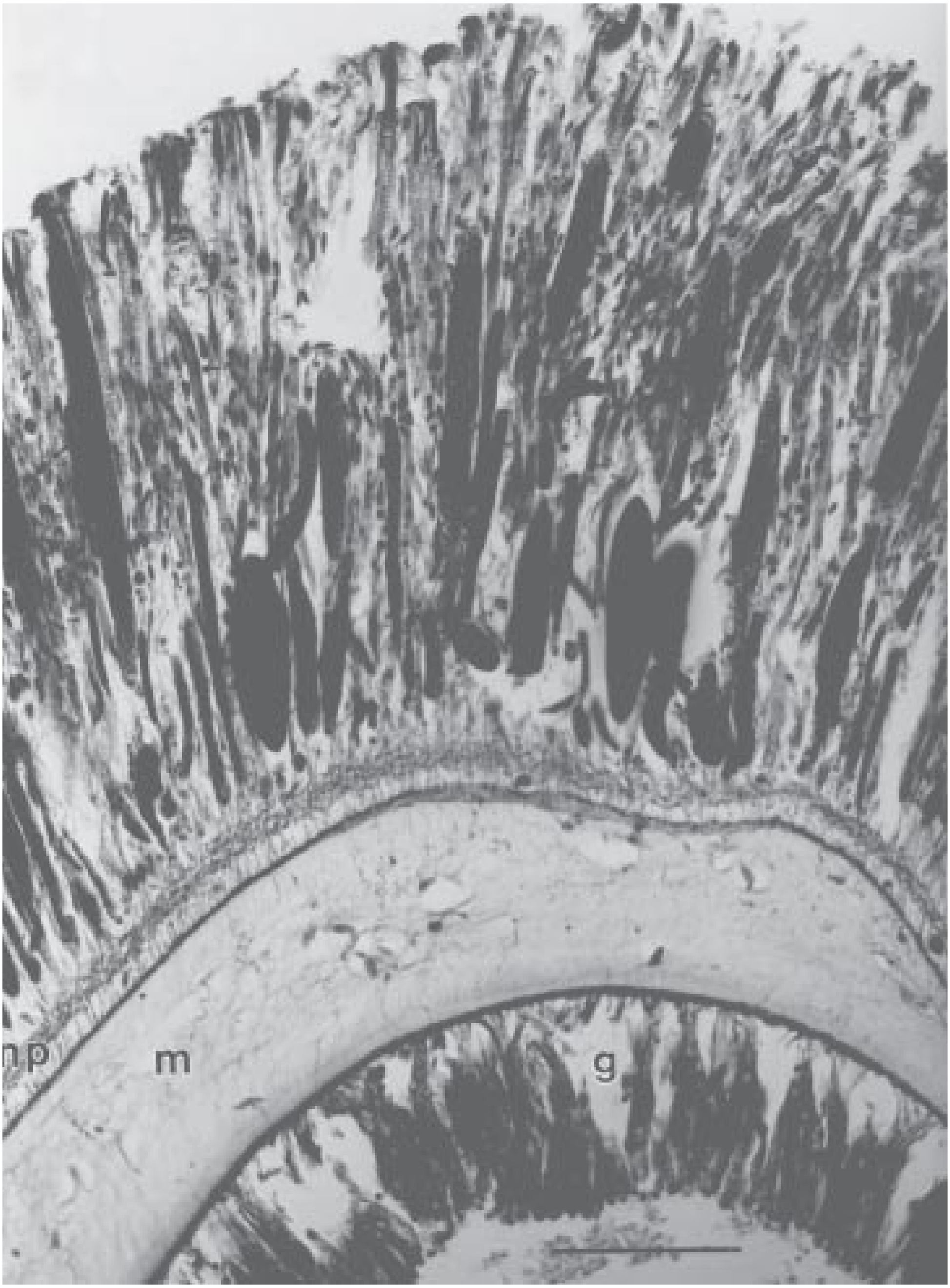

Fig. 5. *Corallimorphus profundus*. Histological section of the tentacle acrosphere (Heidenhain's trichrome staining). In the acrospheral epidermis large holotrichs, large p-mastigophores and small spirocysts are present close to the surface, whereas the lower region shows the plainly coloured sticks (presumably the precursors of the large nematocysts). g = gastrodermis; m = mesogloea, condensed along both faces; np = nerve plexus. Scale bar = 100 µm.

Fig. 6. *Corallimorphus profundus*. *In situ* picture of a female at Hermit Island (35 m depth) with several thousand eggs or early developmental stages in its tentacles. This photo was taken on January 28, 2003 by Bill Baker, University of South Florida. The specimen is attached to an almost vertical wall; the fact that only the uppermost tentacles contain eggs suggests that they are positively bouyant. About natural size.

Gonads.— *C. profundus* is dioecious with profusely developed gonads in all specimens except the tiny juvenile (see below and Discussion).

Mesogloea.— Column, oral disc and actinopharynx with thick, clear mesogloea, more condensed (a darker blue) along both faces, with reticulated substructure in the column close to the pedal disc (fig. 7), but no inclusive cells. The mesogloea of the tentacular shafts is very subtle in places, most obvious close to the acrospheres. We suppose that these are preformed rupture points, as mesenterial filaments emerge from them in two specimens.

Epithelia.— Several specimens collected by SCUBA divers have well preserved epithelia and thus are the first of their genus to show this vulnerable structure. The most conspicuous feature in the large brooding female is the villous surface of the gastrodermal layer, particularly pronounced in the gastroderm of the column. As depicted in fig. 4, the gastrodermal cells seem to release their apical parts into the coelenteron (see Discussion).

The acrospheres (fig. 5) are covered by an unusually thick epidermis, 300 to 400 µm compared to about 100 µm along the shafts. This thick acrospheral epidermis is

Fig. 7. *Corallimorphus profundus*. Longitudinal section of the column of the March-2000-female with six planulae arranged along the lower part of the column, five showing epidermal evaginations (arrows). e = epidermis; f = mesenterial filaments; g = 'villous' gastrodermis; m = mesogloea of column close to the limbus, condensed along both faces and with reticulate substructure (Heidenhain's trichrome staining). Scale bar = 500 µm.

composed of several layers. Lining its surface are the large p-mastigophores and the spirocysts, while the large holotrichs rarely touch the surface. The deeper layer contains plainly coloured and partly broken large sticks, some giving the impression of immature nematocysts, others that of nematocyst waste. These parts overly an uncoloured horizon resembling a nerve plexus (see Discussion).

The actinopharynx epithelium is about 180 µm thick, crowded with mucus cells and again with an uncoloured basal layer resembling a nerve plexus.

Pedal disc epithelium. The epidermis of the pedal disc contains fibres that seem to originate from the mesogloea although they stain orange rather than blue with the Heidenhain colours. These fibres are fixed to the cuticula produced by the pedal disc and seem to be equivalents of the "desmoidal processes" known in Scleractinia and other Corallimorpharia (Muscatine et al., 1997; Pinto & Belém, 1997), elements that are believed to be responsible for the firm cementation to the rock surface. The cuticula of the pedal disc shows an acidophilic reaction with the Heidenhain colours as it stains bright red.

Gonadal tissue, gametogenesis, and early development

The March-2000 specimen is a mature female with profusely developed ovarial tissue forming packages along the proximal parts of the larger mesenteries. They contain all stages of oogenesis. Mature oocytes have retained their orange colour through the processes of fixation and preservation.

In histological sections mature oocytes are rich in yolk and up to 750 µm in diameter. The yolk consists of two distinct types of tiny spheres as described from Scleractinia ("heterogeneous yolk granules": Harrison & Wallace, 1990: 158), one type being plain pink lilac and the other bright red with lighter inclusions. Oocytes are surrounded by thin mesogloeal cysts and the common gastrodermal epithelium. There is a minute opening in the mesogloeal cyst where a number of thick cells seem to encroach (already noted by Schäfer in scleractinians, 1983: 345). This epithelial structure appears to be analogous to the trophonema in sea anemones, but in *Corallimorphus profundus* the nucleus was never seen to be close to this structure (in contrast to observations by Schmidt & Schäfer, 1980; Schäfer, 1983). There are also a few oocytes that appear to be in a state of dissolution, in two cases the red yolk spheres are incorporated in the surrounding gastroderm, suggesting that part of the oocytes serve a nutritional purpose (see Schäfer, 1983: 426; Harrison & Wallace, 1990: 158). In most of the mature oocytes the nucleus is close to the egg surface which shows a marked depression (indentation) that also involves the outline of the nucleus, a feature already seen and discussed in scleractinian oocytes by Szmant-Froelich et al. (1985). As observed in one female in the field (fig. 6) and one in the laboratory (#2001/5B), eggs are released into the tentacles and gastrodermal pharyngeal compartments; whether fertilisation occurs prior to or after release of the mature oocytes is not known.

Spermatogenesis. The largest specimen (87 g) collected in November (16.xi.2001) is a male with profusely developed testicular follicles harbouring different stages of spermatogenesis with a high percentage of follicles containing mature sperm. The development of sperm appears to be similar to the description given by Szmant-Froelich et al.

(1985) for the scleractinian *Favia fragum*. As no empty or partially empty cysts were seen in this specimen we suggest that the onset of sexual reproduction is probably November (late Antarctic spring, see Discussion).

Development. *C. profundus* is a brooding species as evidenced by the presence of both blastulae and planulae in the March-2000-female. In the longitudinal total section blastulae were found in the tentacles and in the gastrodermal compartments of the large, prominent actinopharynx, whereas planulae were found lined up along the column gastroderm, close to the pedal disc (fig. 7).

Blastulae are spherical, similar in size to mature oocytes (750 µm), and with the blastoderm (70-100 µm thick) bordered by a thin lamella of mesogloea (1 µm). Both blastoderm and blastocoel are rich in yolk, the lilac component of the yolk being more prominent in the blastocoel. In some blastulae the yolk granules seem to concentrate in the centre leaving a concentric free space around. Whether the layer inside the mesogloeal lamella can already be considered endoderm is not clear; in about 50 sectioned blastulae we have seen only one showing something that could be described as invasion.

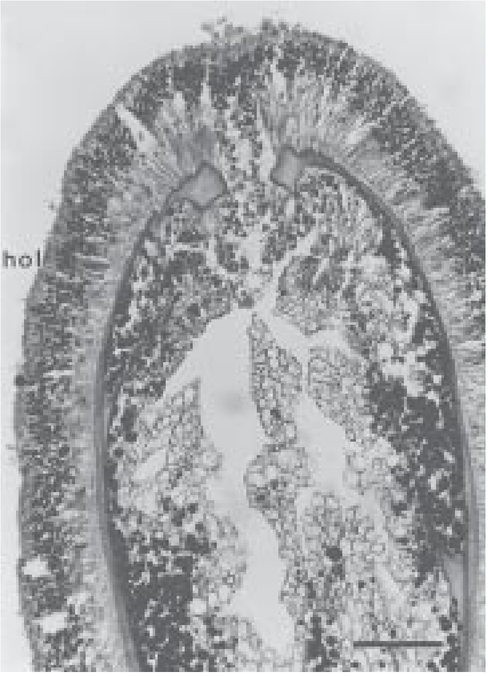

Fig. 8. *Corallimorphus profundus*. Longitudinal section of a planula showing oral opening, intruding ectodermal cells and two of the four larval mesenteries. The interior is filled with yolk (black globules) and a clear foamy substance. hol = holotrichous nematocyst (Heidenhain's trichrome staining). Scale bar = 100 µm.

Developmental stages between blastulae and planulae were not found, suggesting that the larvae inside the female represent two different broods, originating from two different reproductive events (see Discussion).

Planulae (figs. 7, 8). In the longitudinal sections of the March-2000-female only two planulae are found inside a tentacle, the others (9 planulae) are lined up along the lower part of the 'villous' column gastroderm down to the corner between column and pedal disc; a similar position of brooded planulae was observed in the solitary scleractinian coral *Balanophyllia elegans* by Fadlallah & Pearse (1982). The planulae are all the same cylindrical shape and size (1100 µm long, diameter 600 µm) thus presenting the same stage of development; their ectodermal layer is free of yolk, about 130 µm thick, with conspicuous nuclei and already differentiated into oral and aboral region. The oral pole is distinguished by a number of holotrichs (45-60 µm long), whereas the aboral pole shows the fibrillar, obviously mesogloeal structures called desmoidal processes in Corallimorpharia and corals. The surface of the larval epidermis looks rather corrugated but not villous like the gastroderm of the adult; cilia were not seen.

The mesogloea is 5-10 µm thick. Both the oral and aboral pole may show evaginations of the epidermis, a feature also seen in scleractinian planulae (Rinkevich & Loya, 1979; Tranter et al., 1982: 851; Harrison & Wallace, 1990: 178) and in brooded planulae of an actiniarian (Riemann-Zürneck, 1975: Figure 2e, g). The interior of the planula is still rather unorganized, with yolk globules of the red type concentrated along the mesogloea and a foamy, clear substance filling most of the rest. Cross-sectioned planulae show four rudimentary mesenteries in their oral region but no other internal differentiation; four primary mesenteries were also described by Shlesinger & Loya (1991: 104) for the planulae of two corals. Two longitudinally sectioned planulae show the oral opening and intruding ectoderm, but no actinopharynx is present (fig. 8).

Distribution and ecology

Originally, *C. profundus* was known as a deep-sea species with the type locality in the South Pacific (39°S, 105°W) being the deepest known (3700 m). Around Antarctica the species ascends to shallower depth (Fautin, 1984), one location off Queen Mary Coast (Haswell Archipelago) being as shallow as 30-42 m (Grebelny, 1975: "*Corallimorphus antarcticus*").

SCUBA diving observations on the west coast of the Antarctic Peninsula again proved that *Corallimorphus profundus* occurs in depths of only 30 to 40 meters. The area around Janus Island and the other collection sites are exposed, with moderate currents, and are characterised by large rocks and steep walls densely populated with sponges and octocorals. Specimens of *C. profundus* are not rare in this habitat, but both their translucency and their preference for cracks and crevices, often hidden between other sessile organisms, ask for a trained eye.

Life observations.— As discussed by den Hartog et al. (1993) nothing precise was known of the life of *Corallimorphus* species. They speculated that (p. 49) "*Corallimorphus* can only thrive under rather special conditions, in locations or areas with a relatively high food supply" and that "the composition of the cnidom… suggests that these anemones can easily hold substantial prey that may accidentally come in touch with them." Indeed, the Janus-Island area has a high biological productivity year round. In November 2001 one of the specimens (#2001/1 B, 30 g) was observed in the field feeding on a sea star about the size of the corallimorpharian with two arms of its prey still visible in the large mouth. The tentacles were used to pull the prey to the mouth. This feeding method, called "raptorial feeding" (Muscatine, 1973: 80; Lawn & McFarlane, 1991: 595) is known from solitary corals (other than fungiids) with large polyps and relatively small skeletons. In other specimens of the present material remnants of phyto- and zoodetritus were found in the gastrocoel, indicating that *C. profundus* exploits a wide range of food organisms.

Discussion

The study of well preserved and sexually mature specimens of *Corallimorphus profundus* has revealed morphological and reproductive characters new for the Corallimorpharia. Considering that *C. profundus* usually is a deep-sea species, the carefully collected shallow water specimens provided an exceptional chance to study histology and reproduction of these vulnerable animals. The results are exciting for the sea anemone specialist but presumably less so for the coral specialist, as virtually all features (habit and gross structure, cnidom, mesogloea, musculature, gametogenesis, early development, brooding, structure of planulae, ecology) are similar to, or identical with, those known for some Scleractinia.

Taxonomy.— Although the present shallow-water specimens are exceptional in having either no discal tentacles or only a few tiny ones, we have no hesitation in ascribing them to *Corallimorphus profundus*, a species already known to show some variation in the development of the discal tentacles. Fautin (1984) described 27 specimens from depths between 132 and 3660 m with commonly 10-20 discal tentacles, but one of her individuals had only four discals; similarly, E. Rodriguez (2002, pers. comm.) investigated 17 specimens from 278-589 m along the Scotia Arc and Antarctic Peninsula and found one individual with only three discals contrasting with the common number of 10-21. Grebelny's drawing (1975: Figure 1: *"Corallimorphus antarcticus"*) seems to depict a specimen without any discal tentacle (in contrast to his Figure 2 which neither corresponds to this drawing nor to his description). The variation in number and the occasional absence of discal tentacles is not uncommon in other Corallimorpharia and Scleractinia (den Hartog et al., 1993: 60; Lang, 1984: 22). Nevertheless, the extreme scarcity of discal tentacles in our shallow-water population may be indicative of some genetic separation from the deep-water populations due to the oceanographic regime and the brooding of larvae.

Cnidom.— In his original description of *Corallimorphus profundus* Moseley (1877) reported on the large size of the nematocysts of this species ("apparently the largest nematocysts known"). Carlgren & Stephenson (1929), Carlgren (1940), Grebelny (1975), and Fautin (1984) complemented the nematocyst data; Fautin also presented drawings. What this impressive nematocyst equipment meant taxonomically speaking was not known until den Hartog et al. (1993) studied *Corallimorphus cf. atlanticus* Carlgren, 1934 and *Corallimorphus ingens* Gravier, 1918. Although there is some variation between specimens (partly due to the poor condition of the material), it is now obvious that the cnidom is of specific diagnostic significance. We further assume that the long, lanceolate, delicate basitrich of the acrospheres (No. 4 in fig. 3) ("spirulae c2" of den Hartog et al., 1993; "microbasic b-mastigophore" of Carlgren, 1940; Grebelny, 1975; Fautin, 1984) is of generic significance, as this particular nematocyst is not known to date elsewhere (Schmidt, 1974; Pires, 1997). However, this often delicate, inconspicuous nematocyst may have been overlooked in the past.

Generally speaking, the cnidom of the Corallimorpharia is useful for the discrimination of families, genera and most probably also species (Schmidt, 1972: 437; Pires, 1997: 179). Although the cnidom of Corallimorpharia looks simpler and more uniform than it does in Actiniaria (den Hartog, 1980: 63), further research will certainly reveal more structural differences between cnida types. In *Corallimorphus profundus* for example, the undischarged, 240 µm holotrich of the acrospheres (no. 2 in fig. 3) presents a coiled tube that tapers gradually into a presumably spineless (naked) distal tip (similar to the observations of den Hartog et al., 1993: 47 and Pires, 1997: 170).

Villous surface of the gastroderm.— Although there are some hints and illustrations in the scleractinian literature suggesting microvilli and other surface structures of the gastroderm in corals (e.g. Gladfelter, 1983: 625), the presumed release of vesicles 3 to 8 µm across, as seen along the column gastroderm of the March-2000-female, was never observed by the senior author in any actiniarian and appears to be a novelty for both Corallimorpharia and Scleractinia. The other dissected specimens did not show this feature as clearly as the first specimen. Possibly this character is evident only in specimens that were in prime condition prior to and after preservation, which is almost impossible to achieve with the conventional methods of collecting and processing.

We can only speculate on the significance of the substances released into the gastrocoel. One possibility is that they have a role in the support of brooded developmental stages (see below). If we conceive these substances as mucus, another well-known feature of corals comes to mind with a wealth of literature describing the amount of mucus produced by corals (Lang, 1984; Crossland, 1987). For large, almost non-contractile polyps like *C. profundus* mucus release may contribute to clearing their inner and outer surfaces; this had already been suggested for some corals (Crossland, 1987: 42).

Acrospheres (also called "nematospheres" in older publications).— Acrospheres are a diagnostic feature of the family Corallimorphidae, and their specific cnidae have been well studied in the past. On the contrary, their histology remained widely unknown and reference was made only to the genera *Corynactis* and *Pseudocorynactis* (den Hartog et al., 1993, Figures 10, 12, 37; Haddon, 1898: 467, Plate XXX, Figure 1; Carlgren, 1900, p. 41). The histological features generally agreed upon are: unusual thick epidermal layer, no musculature, an accumulation of spirocysts and nematocysts. Carlgren (1900) also reported on a "well developed nerve layer".

The acrospheral cnidae of *Corallimorphus profundus* are remarkably large, and to accommodate these cnidae, the acrospheral epidermis is thick (300-400 µm). Histologically, it is composed of several layers. The layer with the undifferentiated, partly broken and heavily staining sticks is most conspicuous and looks like a dump or spare parts store. In the largest specimen (#2001/1 A, 87 g) some tiny tentacle knobs almost without shafts emerge from the margin. When investigating these budding acrospheres we found no nematocysts, but an abundance of sticks, suggesting that they may be the precursors of the large acrospheral nematocysts.

Reproductive ecology.— *Corallimorphus profundus* is the first deep-water corallimorpharian where gametogenesis and early development could be studied. As found in the March-2000-female, it is a brooding species with multiple gametogenic cycles, simultaneously presenting various developmental stages of oocytes and two larval stages in the form of blastulae and planulae. Also, there is evidence that part of the mature oocytes degenerate and provide nutrient for the remaining oocytes and probably also for the embryos.

Similar features are known from scleractinian species (Fadlallah, 1983; Szmant-Froelich et al., 1985; Harrison & Wallace, 1990). *C. profundus* is unique in brooding two broods simultaneously. This implies that they originate from different reproductive events. Fadlallah & Pearse (1982) found overlapping gametogenic cycles in scleractinian coral species, where the planulae released shortly after fertilization are believed to be the result of an earlier reproductive event. But two batches of larvae brooded simultaneously in different parts of the polyp were never reported before.

The position of the planulae along the villous gastroderm of the column wall suggests some 'brood care' where planulae receive nutritional support from the parent polyp. Uptaking of particles by planula ectoderm is shown by one planula inside the tentacle of specimen 2001/1B: it incorporated yolk spheres from some adjoining decaying oocytes. Among scleractinians, planulae of *Porites porites* are known to take up particulate matter by pinocytosis (Hayes & Goreau, 1977a and 1977b, as cited by Fadlallah, 1983) and *Favia fragum* planulae were "found abutted to the parental endodermal tissues" (Szmant-Froelich et al., 1985) to achieve transfer of zooxanthellae. Whether the observed evaginations of the planula epidermis contribute to nutrition is not known (see Kojis, 1986; Wright, 1986); a function in settlement has also been suggested (Fadlallah, 1983).

Whether sexual reproduction in *C. profundus* is seasonal or year-round is difficult to answer as all females from late spring/early summer (November-December 2001) and from autumn (March 2000) harbour all stages of oogenesis. Also, besides the March-2000-female carrying two broods of larvae, two females collected in November and December contained a few planulae in the tentacles amidst mature oocytes. Maturity in male gonads can be more indicative of the timing of sexual reproduction (Fadlallah & Pearse, 1982; Szmant-Froelich et al., 1985: 889). Accordingly, the sexual condition of the large male collected November 16th, 2001 carrying testicular follicles with developing and mature sperm but no empty follicles, suggests that the peak of sexual reproduction is correlated with austral spring/summer when successive gametogenic cycles produce several broods. As brooded planulae are believed to develop more slowly (at least in corals: Szmant-Froelich et al., 1985: 887) and certainly more so under Antarctic conditions (Pearse et al., 1991) with development times of up to 20-fold (Stanwell-Smith et al., 1999), it is conceivable that a few planulae of last year's reproductive season are still being brooded when the new season begins. In this context it is significant that at Signy Island pelagic and demersal larval sampling showed that planulae are the only larvae that tend to be present year-round at low densities (Stanwell-Smith et al., 1999: 482).

In general, brooding is believed to benefit species like *C. profundus* with specialized environmental preferences to settle in crevices and cavities (Shlesinger et al., 1998: 700). Brooded coral planulae were found to have a longer competency period than free-living planulae (Richmond, 1990).

Systematic relations.— The name *Corallimorphus* implies that it was obvious from the very beginning that members of this genus bear a strong resemblance, if not a real relationship, to deep-sea Scleractinia, e.g. *Stephanophyllia* (see Moseley, 1877: 301, 304; Hertwig, 1882: 20; Duerden, 1898: 635; Stephenson, 1921: 510; see also the historical survey by den Hartog, 1980: 4 and 70). Later, it became more difficult to compare members of the Corallimorpharia and Scleractinia, basically because the morphological features used in taxonomy were not the same. The soft-bodied Corallimorpharia were studied and described by sea anemone taxonomists who rely on histological characters (musculature, cnidae) besides external features of the polyp, whereas coral taxonomy and systematics are almost exclusively based on the architecture of the skeleton, thereby neglecting the living polyp (Lang, 1984; Pires & Castro, 1997). The exceptional status of the Corallimorpharia was assessed by Carlgren (1936: 16; 1940: 52), who elevated it to the rank of a separate order, but this action did not help to elucidate the systematic relationships.

A new approach to this issue was to compare the cnidom of Corallimorpharia and Scleractinia in more detail (Schmidt, 1972, 1974; den Hartog, 1980; den Hartog et al., 1993; Pires & Pitombo, 1992; Pires, 1997; Pires & Castro, 1997; Pinto & Belém, 2000). These investigations showed that both groups share the same categories of cnidae, although comparison of species, genera and families is still hampered by nomenclatural confusion (den Hartog, 1980; den Hartog et al., 1993; Pires, 1997).

Other attempts to resolve taxonomic and/or systematic relations were made by Schmidt & Zissler (1979: sperm morphology), Fautin & Löwenstein (1992: radioimmunology), Chen et al. (1996: rRNA transcription unit), Berntson et al. (1999: nuclear 18S rDNA), Cappola & Fautin (2000: mitochondrial 16s rDNA and nuclear 28s DNA), and Romano & Cairns (2000: nuclear and mitochondrial DNA). Fautin & Löwenstein (1992) concluded that "Corallimorpharia does not constitute an order distinct from and equivalent in rank to Scleractinia" and that some of the Corallimorpharia may be more closely related to certain Scleractinia than to each other. This statement is a return to beliefs of the early days (Gosse, 1860: 292; Hertwig, 1882; Duerden, 1898).

The question is no longer whether the two orders are related, but rather how to accommodate the about 40 extant species of Corallimorpharia within the Scleractinia or Madreporaria *sensu* Stephenson (1920, 1921) and Schmidt (1972, 1974). Answers may propose useful alternative soft-part characters for the Scleractinia which obviously call for complementary characters to reevaluate the systematic implications of the skeletal characters (Veron et al., 1996; Pires, 1997; Pires & Castro, 1997; Berntson et al., 1999: 418; Romano & Cairns, 2000: 1057).

Moseley's (1877) provocative statement that specimens of the non-skeletalized *Corallimorphus* and the coral *Stephanophyllia* can only be distinguished by touch deserves to be tested. It would be consistent to compare deep-sea members of both groups, especially since some authors already suspected the scleractinian genera *Fungiacyathus* and *Leptopenus* to be fairly close to the Corallimorpharia. In particular, members of the family Micrabaciidae have their skeleton more or less reduced with the fleshy polyp totally investing the rudimentary corallum (den Hartog, 1980: 73; Owens, 1984; Cairns, 1989, 1990; Fautin & Löwenstein, 1992; Pires & Castro, 1997).

This suggests a hypothetical corallimorpharian final stage with no corallum at all. In fact, it seems that such a soft-bodied coral without a skeleton is already known to science in the form of *Nectactis singularis* Gravier, 1918, a small discoidal, free-living corallimorpharian inhabiting abyssal plains of the eastern North Atlantic (Gravier, 1918, 1922; Riemann-Zürneck, 1979). The cnidom of this species, as reported by Riemann-Zürneck (1979) and by den Hartog et al. (1993), is similar in distribution and size of nematocyst types to the cnidom of deep-sea corals *Leptopenus antarcticus* Cairns, 1989 and *Fungiacyathus sp*. as listed by Pires & Castro (1997: table 1).

Histologically, *Nectactis singularis* presents a peculiar, acidophilic substructure of its mesogloea (Riemann-Zürneck, 1979: 232). Heidenhain stained, the bright red structures resemble the matrix of a very rudimentary *Leptopenus* skeleton with pores and spines besides a reinforcement of the body wall and mesenteries (compare Cairns 1982: pl. 2, Figures 1-3). Should this ghost skeleton correspond to the organic matrix of coral skeletons as postulated by some authors (Wainwright, 1963; Johnston, 1980; Fautin & Mariscal, 1991: 300)?

The genera *Nectactis* and *Corallimorphus* were united in the family Corallimorphidae by den Hartog et al. (1993: 72), but *Corallimorphus profundus* has a quite different appearance. In contrast to the discoidal, free-living *Nectactis*, *Corallimorphus* species are low-cylindrical, rather large, fleshy animals that are firmly attached (cemented) to hard surfaces (in the deep sea this may be small stones or other hard particles). Still, as suggested by Moseley (1881: pl.16, Figures 8 and 9), the polyp of *Stephanophyllia* looks the most similar to *Corallimorphus.*

Unfortunately, we did not succeed in obtaining specimens of *Stephanophyllia* but were able to investigate (courtesy of Stephen Cairns, Smithsonian Institution) two specimens of *Letepsammia formosissima*, a related micrabaciid taxon (see Owens, 1986). However, this species is discoidal and free-living and also shows a pronounced marginal shelf. The shafts of the tentacles are covered with clusters of spirocysts and the comparatively small acrospheres contain only inconspicuous nematocysts. Thus, this species seems to have little in common with *Corallimorphus*. Nevertheless, we still expect that relatives of *Corallimorphus* will be found among solitary, firmly attached corals that have pronounced acrospheres. We consider these histologically rather complex ‘organs’ to be systematically more significant than hitherto believed.

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