Korsaranthus natalensis (Carlgren, 1938) nov. comb. (Cnidaria: Actiniaria) a mobile sea anemone attacking octocorals

Karin Riemann-Zürneck
*Forschungsinstitut Senckenberg (Zentrum für Biodiversitätsforschung), c/o Alfred-Wegener-Institut für Polar- und Meeresforschung, D-27515 Bremerhaven, Germany

Charles L. Griffiths**
Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

In-situ observations and photographs of an unusual and spectacular red and white striped, mobile anemone, which appears to feed on gorgonians on sublittoral habitats on the south and east coasts of South Africa, prompted a closer examination of two preserved specimens. The specimens are identical with *Condylactis natalensis* Carlgren, 1938, which was described from a single preserved specimen and has not since been reported. The redescription of the species indicates that a new genus, *Korsaranthus*, is required to accommodate it within the family Actiniidae. Most significant characteristics of *K. natalensis* are the lack of p-mastigophores in its cnidome and the folded, distal-most part of its actinopharynx, features that compare with members of order Ptychodactiaria, which are predators of octocorals, too.

In October 1976 one of the authors (CLG) during a SCUBA dive observed two specimens of an unusual unattached anemone feeding on the seafan *Acabaria rubra* off Miller's Point in False Bay, South Africa. The anemones, which were dubbed 'candy-striped anemones' because of their spectacular red and white vertical stripes, were collected and maintained in an aquarium at the University of Cape Town for several weeks, during which time one of them was photographed feeding. However, the specimens died before they could be preserved or identified. No further sightings of this easily recognised species were made for the next two decades, until Mr David Smeda photographed a specimen off Knysna in 1996 during a dive. This photograph was sent to one of the authors (CLG), who immediately recognized the candy-striped anemone and requested Mr Smeda to collect any subsequent specimens he might find. In January of 1997 Mr Smeda did indeed collect two further specimens from Mossel Bay, which he was able to deliver alive to the University of Cape Town, where they were photographed, relaxed and preserved.

Our article redescribes this species, which was described previously by Carlgren (1938) as *Condylactis natalensis* from a single preserved specimen. The morphological peculiarities which necessitate the establishment of a new genus, *Korsaranthus*, are discussed in relation to its peculiar way of life and to other predatory members within the Anthozoa such as the Ptychodactiaria.

Description

Genus *Korsaranthus* gen. nov.

Actiniidae with smooth column and no marginal sphincter, without marginal spherules. Actinopharynx short, horizontally divided into two regions, the upper part with deep, extensible folds. The two strong siphonoglyphs aborally prolonged, their endodermal surface with 'reticulated pads' (new term). Mesogloea fibrous in structure. One or two cycles of mesenteries perfect. Cnidome: only spirocysts and basitrichs; no 'actiniid' b-mastigophores in the messenterial filaments, no p-mastigophores. Type species: *Korsaranthus natalensis* (Carlgren, 1938) nov. comb.

Korsaranthus natalensis (Carlgren, 1938) nov. comb.

syn. *Condylactis natalensis* Carlgren, 1938: 31-32, Figure 12; p. 142: Table 1.

'Candy-striped anemone', 'Straying predator' (Riemann-Zürneck 1998: 250, Figure 3).

Material

1. The holotype of '*Condylactis natalensis*' Carlgren (1938), which was the only specimen seen by Carlgren (South African Museum, Cape Town, SAM H 4600, type Nr. 328). Carlgren also obtained the specimen from the South African Museum for his description, thus, he had not seen the anemone alive. Date and location where the holotype was collected are uncertain (p. 32: 'Durban, probably littoral'; p. 142, Table 1: '... possibly not taken in the intertidal zone. No depth was given on the label'). Carlgren included some remarks on 'colour when alive', which are probably based on some personal communication with the collector, perhaps during Carlgren's visit to South Africa between October 1935 and January 1936.
2. Two specimens collected by Mr. David Smeda 8 January 1997 in Still Bay, South Africa, 24°24'S, 21°25'E, 15 m depth. Original collector's label reads: 'One floating free, one stretched out with tentacles towards soft coral'. These specimens were kept and photographed by the junior author in an aquarium (see Figure 3 in Riemann-Zürneck 1998), then after menthol anaesthesia and preservation were deposited in the South African Museum (SAM H 4840). One of the specimens weighs 30 grams, the other is about the size of the holotype (4 grams). Part of the smaller specimen was embedded in paraffin and sectioned (horizontal serial sections and longitudinal sections). The slides were stained with Azocarmine triple staining.
3. Photograph taken by the junior author in 1976 showing one large specimen feeding on a gorgonian (Figure 1). This anemone, together with its prey, were collected at

Miller's Point in False Bay and photographed in an aquarium tank when the anemone started feeding again. The specimen perished later in 1976 and was not preserved.

Size, shape, colour and gross structure

Column height of the larger preserved specimen (SAM H 4840) 5.5 cm, diameter of pedal disc 3.5–4 cm, of oral disc 4.5 cm, tentacles about 3 cm long. Carlgren's holotype and the other specimen are much smaller (about 3 cm high and 2 cm in diameter, tentacles 1–1.5 cm long). The live specimen photographed preying on a gorgonian in 1976 was larger (approx. 8–10 cm long).

The general appearance of the live specimen (Figure 1 and Figure 3 in Riemann-Zürneck 1998) is that of an actiniid anemone. As far as the tentacular crown is concerned, the tentacles number about 50 and occupy the outer part of the oral disc; they are horizontally extended except the two directive tentacles extend in a vertical direction. The mouth is circular with prominent, thick lips. The tips of the tentacles are pointed and sometimes hook-like. Shape and posture of column and pedal disc, however, are strange for a member of the actiniid family, in that the pillarlike column lies horizontally on the substratum with the more-or-less expanded unattached pedal disc resembling a mushroom. In the picture of *Korsaranthus* feeding, the extended pedal disc is very conspicuous (Figure 1).

The name 'candy striped anemone' gives a good impression of the general colour pattern of live *Korsaranthus natalensis*. The column and in particular the expanded pedal disc are brightly red and white striped, red dominating, with white stripes corresponding to the mesenterial insertions (Figure 1). The expanded tentacular crown, which is shown on the 1997 photograph (Figure 3 in Riemann-Zürneck 1998), is dominated more by white. The oral disc shows a mother-of-pearl lustre, the prominent thick lips are scarlet red, as are about 24 radial lines on the oral disc extending onto the upper side of the tentacles; the pointed, sometimes hook-like tips of the tentacles are red as well. The 1976 specimen had more white along the column and more red on the tentacles. The protruded parts of the actinopharynx are translucent scarlet and the mesenterial filaments covering part of the gorgonian are orange with white edges.

In preserved specimens body shape and colour have nothing in common with the splendid appearance and unusual body shape of live anemones. In all three preserved specimens the tentacles are extended and longitudinally fluted. The column surface is corrugated with small horizontal, parallel folds; no verrucae or other differentiations are present. Submarginally there may be a more pronounced fold but contrary to Carlgren's description there is no fossa present. In the smaller specimen (SAM H 4840) the insertions of about 24 mesenteries are visible along the column. The pedal disc is strongly

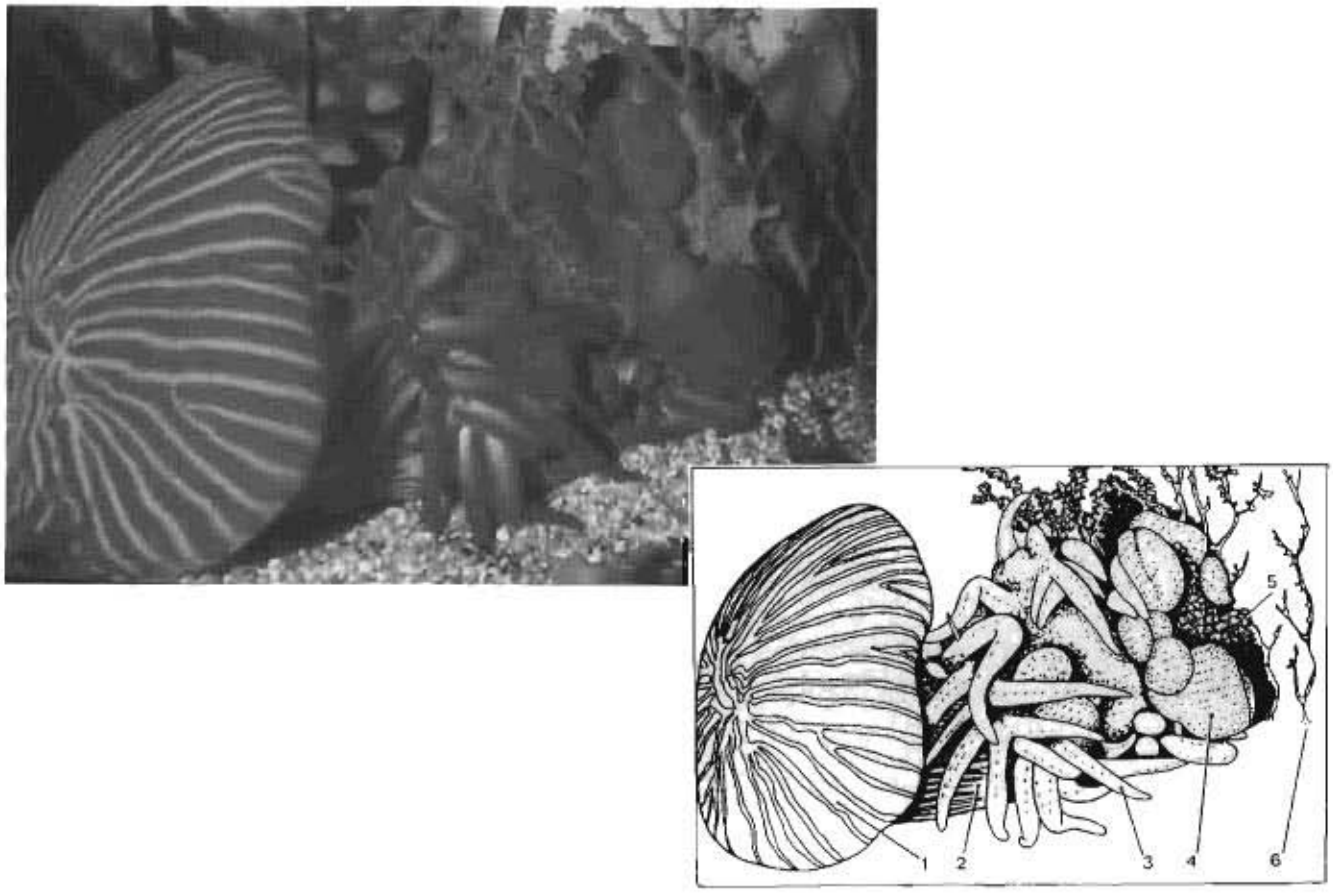


Figure 1 *Korsaranthus natalensis* feeding on a gorgonian. Photograph taken in 1976 of a specimen that was collected in the field during the act of feeding and carefully transported into an aquarium tank together with its prey. The picture was taken immediately after the anemone started feeding again. 1 – hemispherically expanded pedal disc. 2 – body wall (column). 3 – tentacle. 4 – swollen lobes of the actinopharynx outside the anemone's body covering and encircling the branches of the gorgonian *Acabaria rubra* (6). 5 – mesenterial filaments amidst the pharyngeal lobes. Length of the anemone is approximately 8–10 cm.

corrugated in all directions and gives the impression of being very muscular and extensible. The colour of the specimens in ethanol is pale to rusty brown.

The most significant character of the internal gross structure of *Korsaranthus natalensis* is the actinopharynx, which, although comparatively short, is divided horizontally into two sections. The oral portion is thrown into several deep folds, the proximal part being more normal in appearance, with numerous fine longitudinal ridges; the two siphonoglyphs are prolonged aborally. The number of tentacles and pairs of mesenteries is about 50, resulting from 4 hexamerously arranged cycles and a few small extra tentacles corresponding to small, distal extra pairs of mesenteries. In the smaller sectioned specimen (SAM H 4840), for example, each of the two directive tentacles is flanked by 2 small tentacles. In the larger specimen, one additional tiny pair of mesenteries was seen in an endocoel of the 2nd order. These tiny mesenteries are present only in the distalmost part of the body; close to the oral disc they carry trilobate filaments which become unilobate before vanishing. There are 12 perfect pairs of mesenteries in the holotype and in the larger specimen (SAM H 4840), whereas the smaller specimen has only 6 perfect pairs. This character is not easy to ascertain due to the unusual short actinopharynx.

In SAM H 4840 the endoderm of the tentacles contains a dark brown pigment but no zooxanthellae. The presence of trilobate filaments is visible at low magnification, but the site where they are most obvious is uncommon: in the larger specimen the endodermal surface of the oral disc carries three double cords of trilobate filaments in each of the 12 exocoels of the perfect pairs of mesenteries. These cords do not reach the actinopharynx; it appears that close to the pharynx they are detached over a short distance (see discussion).

Histology

Cnidome (Table 1, Figure 2). Compared to that of other actiniid anemones, the cnidome of *Korsaranthus natalensis* is poor in types of nematocysts, the most significant features being the absence of both p-mastigophores and large 'actiniid' b-mastigophores. The spirocysts are inconspicuous in number and appearance, but their capsule wall appears to be slightly more pronounced than usual. Histological sections show the basitrichs of the column to be densely aggregated along the surface of the ectoderm, occupying about one fifth of the diameter of the ectoderm.

Table 1 Size ranges of the cnidae in *Korsaranthus natalensis*. The numerals 1–5 correspond to the illustrations in Figure 2

Body region	Cnidae	Size ranges (µm)
Column	1 Basitrichs 1 (very numerous)	12–16.5 × 1.5–2
	2 Basitrichs 2 (only 2 seen)	about 5 × 1.5
Tentacles	3 Spirocysts	19–24 × 2–2.5
	4 Basitrichs 1 (numerous)	22.5–27.5 × 2
	5 Basitrichs 2	14–18 × 1.5–2

In the actinopharynx and mesenterial filaments sparse basitrichs are present in two size ranges: 13–15.5 × 1–1.5 / 20–21 × 2

Note: no p-mastigophores present; no 'actiniid' b-mastigophores present

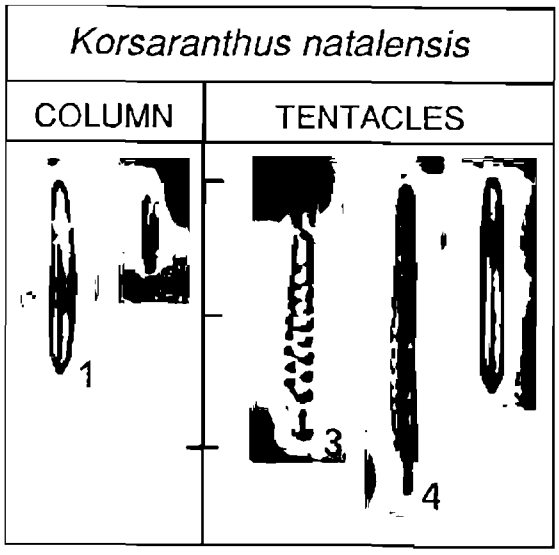


Figure 2 *Korsaranthus natalensis*. Cnidome. The numerals 1–5 correspond to cnidae listed in Table 1. Scale bars denote 10 µm

Mesogloea. Fibrous (Figure 3), laminated or cross-lattice-like, most conspicuous in column and in directive mesenteries.

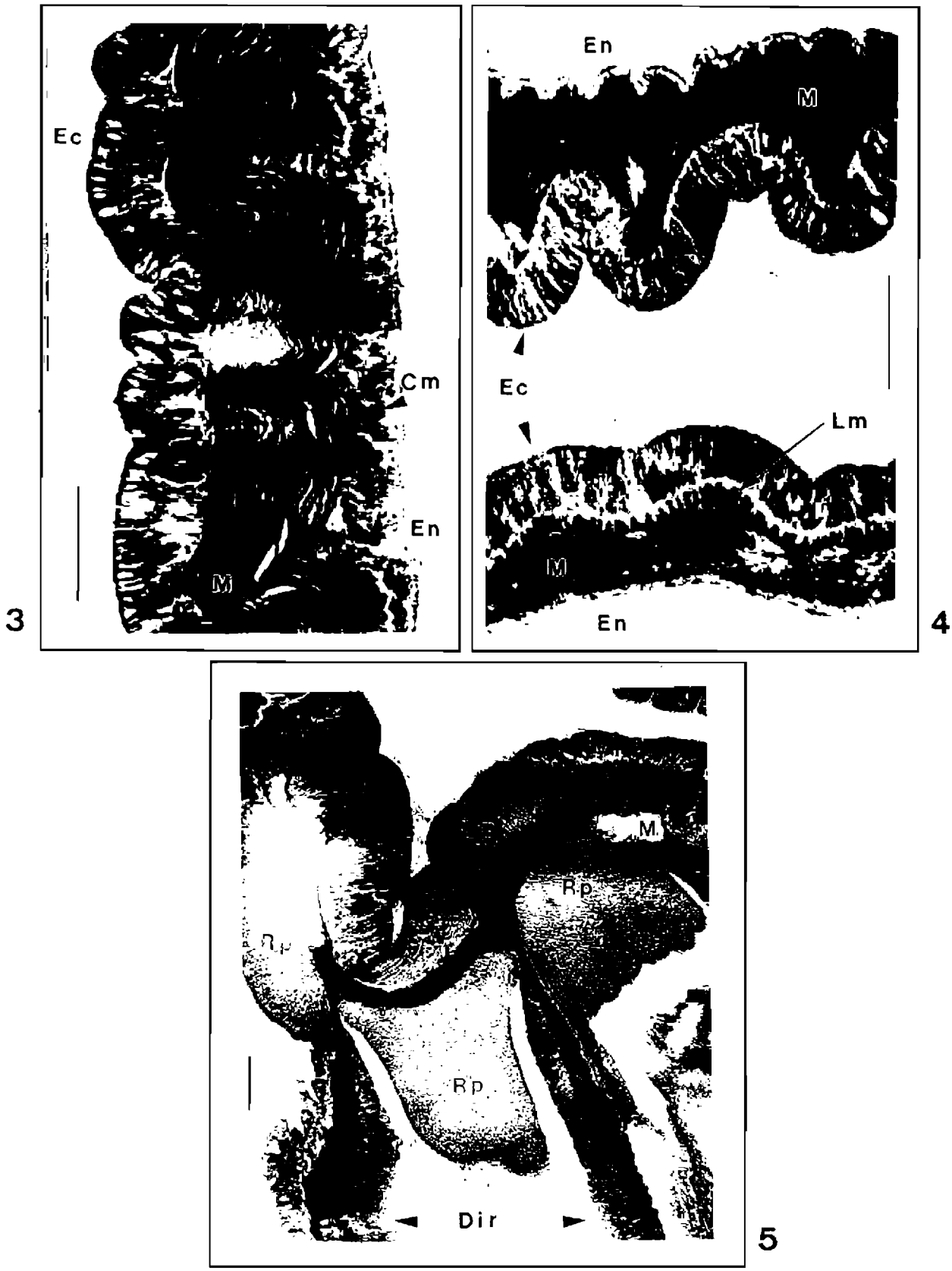
Musculature. Circular musculature of body wall evenly developed throughout (Figure 3). Longitudinal musculature of tentacles extodermal, well developed along their oral side only (Figure 4). Oral disc with thickened mesogloea and sheets of muscle fibres on both sides, rather strong along its endodermal surface. Retractors of mesenteries diffuse on thick mesogloea. Weak parietobasilar musculature present only on directive mesenteries below actinopharynx. Basilar musculature well developed.

Actinopharynx. Deeply folded distal part of the actinopharynx is lined with thick epithelium consisting of a variety of strongly staining gland cells. The epithelia of the two siphonoglyphs are thicker and histologically different on each surface; inner surface is like that of most siphonoglyphs with long cilia and comparatively few gland cells, whereas the endodermal surface – in between the directives and adjacent to both – carries 'reticulated pads' (Figure 5), which are 350 to 500 µm thick in transverse section. This strongly vacuolated, peculiar tissue is a common, although often neglected, feature of most members of the family Actiniidae.

Mesenterial filaments. As stated above, double cords of trilobate mesenterial filaments along the endodermal surface of the oral disc are a striking feature in *Korsaranthus natalensis*. Histologically, they exhibit the classic trefoil with well-developed reticulated tracts. Below the actinopharynx, the trilobate filaments are replaced by their unilobate counterparts together with the gonads.

Gonads. The sectional specimen is female, with oocytes in all mesenteries except the directives and the tiny mesenteries of the last cycle. Diameter of the largest oocytes about 140 µm.

Other histological characters. A trait which we have not seen in other sea anemones is the vacuolated border of the endodermal epithelia in both tentacles and endoderm. As the general preservation of the sectioned specimen is excellent,



Figures 3–5 *Korsaranthus natalensis*. Histology (Azocarmine triple staining, scale bars 100 µm). 3 – Longitudinal section of column showing fibrous, laminated structure of mesogloea, circular musculature and a variety of mucous cells in the ectoderm. 4 – Transverse section of two adjacent tentacles showing oral and aboral parts of tentacles respectively. Below – oral face with well-developed ectodermal longitudinal musculature. Above – aboral face lacks strong ectodermal musculature. 5 – Transverse section of a siphonoglyph showing thick 'reticulated pads' along the endodermal surface. Abbreviations: Cm, circular musculature of column. Dir – pair of directive mesenteries; En, endoderm; Ec – ectoderm; Lm, ectodermal longitudinal musculature of tentacle; M, mesogloea; Rp: reticulated pads

we believe that this character may perhaps be part of the food utilization regime in *K. natalensis* (see discussion). The epithelium of the pedal disc is thick with cilia or stereocilia that appear to be arranged in small cones; this feature is not unusual.

Distribution and ecology

The four localities where *Korsaranthus natalensis* was collected (off Durban, Knysna, Still Bay, False Bay) imply that this anemone may be distributed along the whole south and east coast of South Africa. The fact that it was collected only four times during 60 years documents its rarity. Nevertheless, it may well be that *K. natalensis* is more abundant below diving depths.

There are no formal records or notes describing environmental conditions at the times of collection, or detailing the composition of the benthic communities associated with the specimens collected. Surface temperatures within the range of the species, which appears to span both the warm-temperate south and subtropical east coasts of South Africa, vary seasonally between about 22 to 27°C in KwaZulu-Natal and 14 to 19°C in False Bay. The coastline throughout this region is exposed to strong currents and wave action. This is particularly the case in the southwest, where wave heights frequently exceed 6 m. As a result of this extreme water movement, shallow subtidal communities are characteristically dominated by dense growths of filter feeders, particularly mussels, sponges, ascidians, crinoids, soft corals and sea fans. These would provide ideal opportunities for an unattached anemone to locate and drift between food items.

In aquaria, one of the 1976 specimens was seen to attach to the glass with its pedal disc, suggesting that this species is not necessarily always detached. Field observations, however, together with the morphological peculiarities described above, imply that *Korsaranthus natalensis* is enabled to lead the life of a 'straying predator' (Riemann-Zürneck 1998). Although its body shape and gross structure is that of an actiniid anemone, in the field it has been found lying on the ground with its column in a horizontal position and its pedal disc unattached. As shown in aquarium photographs the anemone can extend its pedal disc to form a large, hemispherical balloon, similarly to the behaviour of anemones able to escape adverse conditions (Riemann-Zürneck 1998). If the expanded pedal disc increases overall surface area, this will encourage drifting of *Korsaranthus* and increase chance encounters with its prey.

Feeding. As illustrated by Figure 1, *Korsaranthus natalensis* preys on gorgonians. The specimen shown in the picture was seen feeding on *Acabaria rubra* in its habitat and was carefully transported into an aquarium tank together with its prey. The photograph was taken immediately after the anemone started feeding again. The large expanded pedal disc is to the left. The tentacles (centre) are extended and relaxed but do not appear to be involved in the feeding process. Largely protruded and expanded translucent lobes covering and encircling the branches of the octocoral are certainly produced by the deeply folded upper part of the antinopharynx. Also visible on the gorgonian between these actinopharyngeal lobes is an accumulation of mesenterial filaments. Thus, together with the protruded actinopharynx, unilobate filaments have been applied to the prey organism.

Diagnosis of *Korsaranthus natalensis*

Brightly coloured red and white actiniid sea anemone of 3 to 10 cm height that may be mobile and unattached, the extended free specimens lying horizontally on the ground in sublittoral habitats. Hitherto it has been found only off South African shores. Column smooth. No marginal sphincter. Actinopharynx comparatively short, its upper part deeply folded. About 50 tentacles, their tips pointed and sometimes hook-like. One or two cycles of mesenteries perfect, distally a few more small mesenteries present than proximally. Mesogloea fibrous. Musculature inconspicuous, longitudinal ectodermal musculature of tentacles well developed only along oral side of each tentacle. Cnidome most significantly characterised by absence of both p-mastigophores and 'actiniid' b-mastigophores; spirocysts rare and rather small; column ectoderm furnished with a dense layer of small basitrichs. Presumed to prey on gorgonians.

Discussion

Lifestyle and correlated morphological and histological characters

Nothing has been known about the lifestyle of *Korsaranthus natalensis*, as Carlgren's description (1938) was based on a preserved specimen from the South African Museum. The present observations of live specimens in the field and in aquaria reveal for the first time its unique lifestyle as a mobile predator of gorgonians. Several morphological and histological characters can be related to this unusual behaviour.

The most conspicuous morphological character is the deeply folded upper part of the actinopharynx, which can extend to form large lobes that may protrude from the mouth during feeding, drawing with them the edges of perfect mesenteries, so that mesenterial filaments join the lobes and feed on the octocoral externally. To date no similar pharyngeal structure or behaviour is known among true sea anemones (Actiniaria), but there are two species of order Ptychodactiaria, *Dactylanthus antarcticus* (Clubb 1908), and *Preactis millardae* England & Robson (1984), which have a similarly short actinopharynx with 'deep sulci', (Dunn 1983), or 'pocket-like protuberances' (England & Robson 1984) in the upper part close to the mouth. There are observations of live specimens of both species (England & Robson 1984; Dayton, England & Robson 1997) showing that they are predators of gorgonians and alcyonarians. Unlike *Korsaranthus*, no actinopharyngeal lobes were seen outside the two Ptychodactiaria species during feeding. Instead, *Dactylanthus* wraps its oral disc around a whip-like gorgonian, whereas *Preactis* was seen to engulf its prey by putting its whole body over an alcyonarian colony, which can be almost the size of the predator. We suggest that the finger-like extensions of the upper actinopharynx cover the whip-like or arborescent colonies and help to suck the polyps, which may be also true for *K. natalensis*. The predominance of mucous cells in the epithelium of the upper actinopharynx in both *Korsaranthus* (as described above) and *Dactylanthus antarcticus* (Riemann-Zurneck: unpublished histological investigation) also reflects their probable role in breaking up and digesting prey organisms: mucous is considered the means to transport both enzymes and nutrients in

particulate and dissolved form (Sedmak 1984; Shick 1991), which must be paramount when the prey is outside the coelenteron.

Another conspicuous character of *Korsaranthus* is the absence of two significant types of nematocysts, which is surprising given its status as a predator. Firstly, there are no large b-mastigophores in the mesenterial filaments, although these are typical of most members of the family Actiniidae, and secondly, there are no p-mastigophores, which usually occur in the actinopharynx and mesenterial filaments. To our knowledge this is the first species within the family Actiniidae lacking p-mastigophores. Only the actiniarian genera *Anemonactis* and *Haloclava* (Family Haloclavidae; Carlgren 1949), the species '*Alfredus lucifugus*' (family Edwardsiidae; Schmidt 1979), and the family Actinodendronidae (Carlgren 1949) lack p-mastigophores. It may be that this type of nematocyst was lost in anemones such as *Korsaranthus natalensis*, which are specialized in preying on soft cnidaria. The above mentioned Ptychodactiaria, too, have no p-mastigophores.

A feature that may also correlate to the uncommon feeding regime of *K. natalensis* is the noticeable abundance of vacuolated tissues: the trilobate filaments, which are particularly well developed and abundant in the distal part of the body; the 'reticulated pads' along the endodermal surface of the siphonoglyphs; and the vacuolated endoderm of tentacles and gastrocoel. According to Van Praët (1985) 'vacuolar cells absorb macromolecules'; thus, these vacuolated tissues may help to process large quantities of macromolecules during and after feeding by this predatory anemone.

Taxonomic status and systematic relations

In his brief description of the holotype, Carlgren (1938) noted the morphological characters which we consider the most significant of the species: 1. 'Sphincter absent'; 2. 'Actinopharynx rather short ... the upper part was irregularly folded'; 3. 'Nematocysts ... all probably basitrichs'. The present investigation of two additional specimens establishes that these features are real. The absence of the marginal sphincter obviously prompted Carlgren (1938) to place the species within the genus *Condylactis*, but we consider the absence of two significant nematocyst types, p-mastigophores and 'actiniid' b-mastigophores in the mesenterial filaments as taxonomically significant. Cnidae are high ranking characters with respect to taxonomic status and systematic relations, so we establish a new genus, *Korsaranthus*, for the species. Whether these characters warrant a rank higher than genus remains to be seen in the future.

Our reasons for keeping this anemone a member of the family Actiniidae are its general appearance and gross morphology, and the very pronounced 'reticulated pads' along the endodermal surface of the siphonoglyphs, which we consider a consistent character of the family. The most significant features of *K. natalensis*, its 'poor' cnidome, the extensible upper part of the actinopharynx, and its mobile and predatory lifestyle, are characteristics that are strange for the family Actiniidae and rather compare to members of the order Ptychodactiaria. It is tempting to speculate on these peculiarities as perhaps being a first step towards the Ptychodactiaria, but we value them as being convergently evolved properties.

There are also some analogies of *Korsaranthus* with members of the family Haloclavidae, for example *Peachia*, as juveniles, the *Peachia* species are non-sedentary and parasitic, feeding on medusae. Their lip region is differentiated to form the conchula, finger-like extensions at the entrance to the single siphonoglyph. Feeding behaviour of adult *Peachia* specimens is also similar to *Korsaranthus*, as both the protruding conchula and swollen lobes of the actinopharynx were seen to encircle and draw in large food particles, whereas the tentacles do not appear to be involved (aquarium observation of Haddon & Dixon 1885, see Stephenson 1935). Features that may also compare with the lobes produced by the upper part of the actinopharynx in *Korsaranthus* are the labial tentacles in order Ceriantharia, structures that are known to perform preoral digestion (Tiffon 1975, Shick 1991).

Considering that members of the Ceriantharia, Ptychodactiaria, Corallimorpharia and Scleractiniaria all show some kind of pharyngeal and/or extragastral digestion, it seems possible that this type of food uptake is an ancient feature of the Anthozoa which was lost in most members of the present order of true sea anemones (Actiniaria), but is retained in a few species highly specialized in their food requirements.

Acknowledgements

Our special thanks to David Smeda, who not only collected the specimens on which this article is based, but made a special trip from Mossel Bay to Cape Town to deliver them live to the University of Cape Town. We are also indebted to Elaine A. Robson for her commited efforts to improve the final version of the manuscript. During her 1976 visit to South Africa, she was one of the witnesses who saw the first live specimens of *Korsaranthus natalensis* in aquaria. An anonymous referee kindly contributed to clarifying and shaping the manuscript. The assistance of the collection managers at the South African Museum, Michelle van der Merwe and Liz Hoensen in loaning material to the senior author is gratefully acknowledged. Financial support in South Africa was provided by a Foundation for Research Development grant to CLG. This is contribution no. 1599 of the Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven, Germany.

References

CARLGREN, O. 1938. South African Actiniaria and Zoantharia. *K. svenska Vetensk.Akad. Handl.* (Ser. 3) 17: 1–148.

CARLGREN, O. 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *K. svenska Vetensk.Akad. Handl.* (Ser. 4) 1: 1–121.

CLUBB, J.A. 1908. Coelentera IV. Actiniae. *Nat. Antarct. Exped. 1901–1904, Nat. Hist.* 4: 1–12.

DAYTON, P.K., ENGLAND, K.W. & ROBSON, E.A. 1997. An unusual sea anemone, *Dactylanthus antarcticus* (Clubb, 1908) (Order Ptychodactiaria), on gorgonians in Chilean fjords. In: Proceedings of the 6th International Conference on Coelenterate Biology, (ed.) J.C. den Hartog. 1995. Natl. Nat. Hist. Museum, Leiden. 1358142.

DUNN, D.F. 1983. Some Antarctic and Sub-Antarctic sea anemones (Coelenterata: Ptychodactiaria and Actiniaria). In: Biology of the Antarctic seas XIV. Antarctic Research Series Washington 39: 1–67. (ed.) Kornicker, L.S.

ENGLAND, K.W. & ROBSON, E.A. 1984. A new sea anemone from South Africa (Anthozoa, Ptychodactiaria). *Ann. S. Afr. Mus.* 94: 305–329.

HADDON, A.C. & DIXON, G.Y. 1885. The structure and habits of *Peachia hastata* (Gosse). Part I. *Scient. Proc. R. Dublin Soc.*, Dublin 4: 399–405.

VAN PRAET, M. 1985. Nutrition of sea anemones. *Adv. Mar. Biol.* 22: 65–99.

RIEMANN-ZURNECK, K. 1998. How sessile are sea anemones? A review of freeliving forms in the Actiniaria (Cnidaria, Anthozoa). *Marine Ecology* 19: 247–261.

SCHMIDT, H. 1979. Beitrage zur Differentialdiagnose, Morphologie und Evolution der Edwardsiidae (Actiniaria, Anthozoa) I. Die Gattung *Alfredus* nov. gen. mit der Typusart *A. lucifugus* (Fischer, 1888). *Z. zool. Syst. Evolut. forsch.* 17: 211–220.

SEDMAK, B. 1984. The determination of proteolytic activities in the sea anemone *Condylactis aurantiaca*. *Biol. Vestn.* 32: 93–104.

SHICK, J.M. 1991. A functional biology of sea anemones. Chapman & Hall, London, New York.

STEPHENSON, T.A., 1935. The British sea anemones, II. The Ray Society, London.

TIFFON, Y. 1975. Hydrolases dans l'ectoderme de *Cerianthus lloydi* Gosse, *Cerianthus membranaceus* Spallanzani et *Metridium senile* (L.). Mise en évidence d'une digestion extracellulaire et extracorporelle. *J. exp. mar. Biol. Ecol.* 18: 243–254.