

With Compliments.

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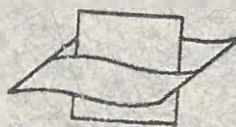
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THE MORPHOLOGY AND SYSTEMATIC  
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REPRODUCTION.

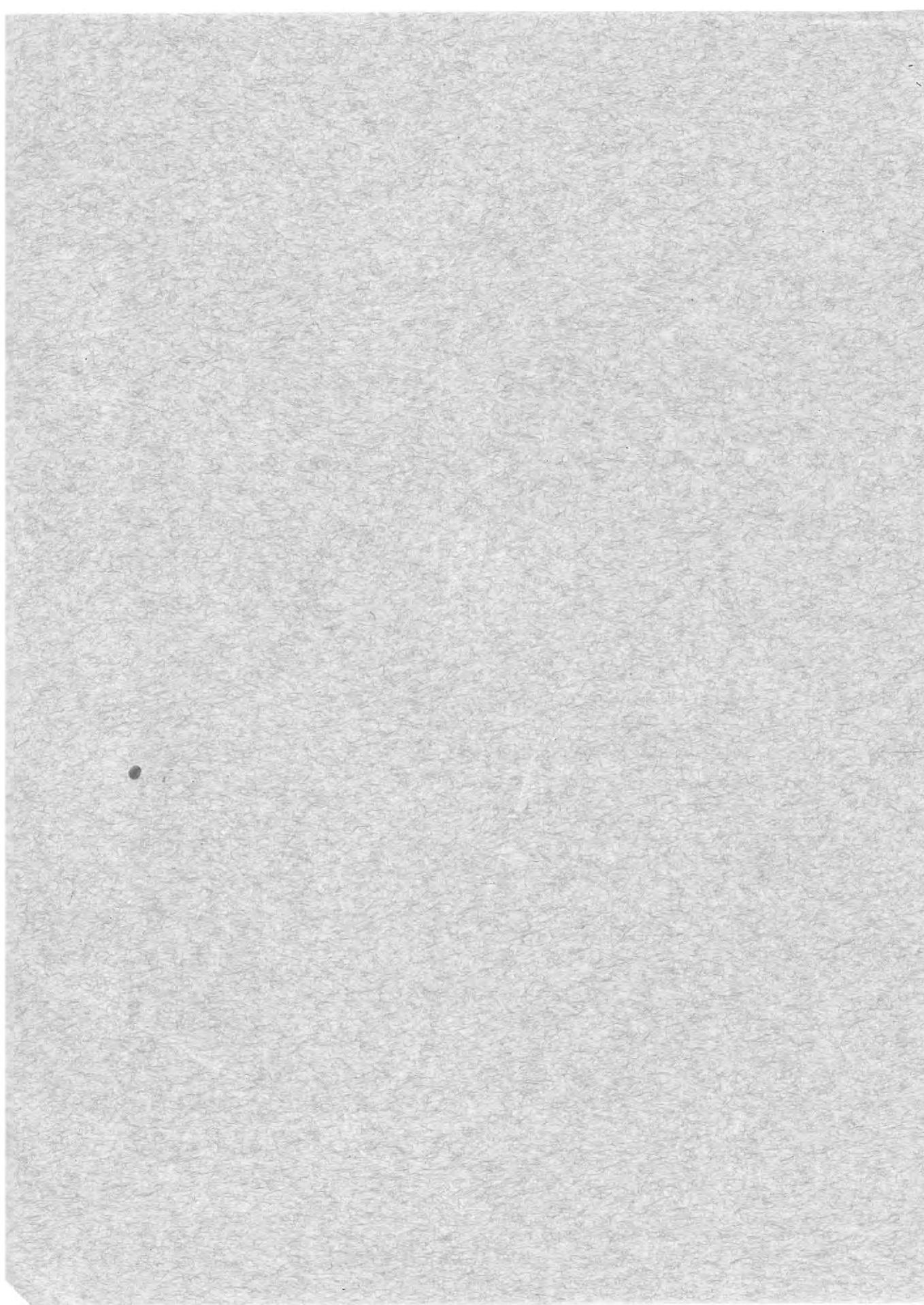
BY

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*Introduction.*

THE present communication deals with an interesting anemone, obtained from the Adyar backwaters in addition to the other brackish-water Actinians which formed the subject of two previous studies (Panikkar, 1936 and 1937). This belongs to the sub-tribe Boloceroidaria, but, as will be shown later, is different from the genera of Boloceroidaria already described. The anemone is hence referred to a new genus for which the name *Boloceractis* is suggested. The anatomy of the type species, *Boloceractis gopalai*, and the peculiar method of asexual reproduction by tentacular regeneration are described in this paper, a preliminary account of which was read before the 1936 (Indore) session of the Indian Science Congress.

*Generic and Specific Diagnoses.*

Sub-tribe	.. Boloceroidaria,	Carlgren, 1924.
Family	.. Boloceroididae,	Carlgren, 1924.

*Boloceractis*, Gen. Nov.

Boloceroididae with short column and distinct basal disc without basilar muscles. Column broader in the distal part than the proximal, smooth, without spirocysts but with a few nematocysts, and without stinging warts, vesicles or other structures characteristic of *Bunodeopsis*. Tentacles numerous; those of the innermost circle the largest. They are deciduous and provided with sphincters at their bases. Mesenteries more numerous in the distal part than in the proximal. The primary mesenteries with very weak and diffuse retractors, about six pairs or a few more in number and sterile. Distinct siphonoglyphes present. Imperfect mesenteries in large

numbers, and the gonads usually borne by them. No sharp distinction of the mesenteries into macrocnemes and microcnemes. Columnar sphincter absent. Type species *B. gopalai*.

*Boloceractis gopalai*, n.g. et sp.\*

*Diagnosis.*—Pedal disc distinct, yet variable in thickness. Tentacles 6 + 6 + 12 + 48...variable in number according to the age of the individual. The number of tentacles in each cycle may vary according to the number of mesenteries. Innermost endocoelic tentacles the largest and mostly deciduous. Oral disc narrow with prominent mouth. Actinopharynx well developed and having distinct siphonoglyphes with aboral prolongations. Pairs of mesenteries (6-8), (6-8), (12-16), (24-32).....; the mesenteries of the first order perfect and without gonads usually. Retractors very feeble. Imperfect mesenteries always fertile and with filaments; these mesenteries are more numerous near the oral disc than below. Sexes separate. Nematocysts of the tentacles curved and of the ordinary type. The sizes of the nematocysts are as follows:—

Nematocysts of the column	..	..	9-13 $\mu \times 2-4 \mu$ .
Nematocysts of the tentacles	(1)	..	46-49 $\mu \times 6-7 \mu$ .
" " "	(2)	..	19-21 $\mu \times 4-5 \mu$ .
Nematocysts of the filament	..	..	33-35 $\mu \times 6-7 \mu$ .
Spirocysts of the tentacles	..	..	27-36 $\mu \times 5-6 \mu$ .

Asexual reproduction is very common in this species.

*Morphology of the Anemone.*

The anemones are small, with short columns, from 5 to 10 mm. in height, slightly broader in the oral disc region (5 to 8 mm.) than the basal part (5 to 6 mm.). The tentacles are very prominent and surround the column making the latter look insignificant.

*The Base.*—The basal disc of the anemone, though distinct and very well developed in certain specimens, is always without basilar muscles. There is considerable variation in the general shape of the basal disc; in most specimens it is flat and adhesive, while in others it is cup-shaped.

*The Column.*—The column wall is mostly thin and some specimens reveal the insertions of the mesenteries from the outside. The column is smooth and without spirocysts so far as could be ascertained from the material available; in this respect, this species is in sharp contrast to the

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\* I have much pleasure in associating the species with the name of Prof. R. Gopala Aiyar, Head of the Zoology Department of the University of Madras,

members of the genus *Bolocerooides*. The nematocysts are very scarce on the column; they are few and scattered and are of a small size (compare diagnosis). Cincilides are absent.

There is no sphincter, either endodermal or mesogleal. The longitudinal ectodermal muscles of the column attain considerable development. In sections, they form a prominent layer lying next to the mesoglea. This musculature is uniformly developed throughout the column.

The ectoderm of the column is a comparatively thin layer, with rather sparse mucous cells. The endoderm is also a thin and compact layer, often containing zooxanthellae in large numbers. The mesoglea does not appear to contain scattered nuclei.

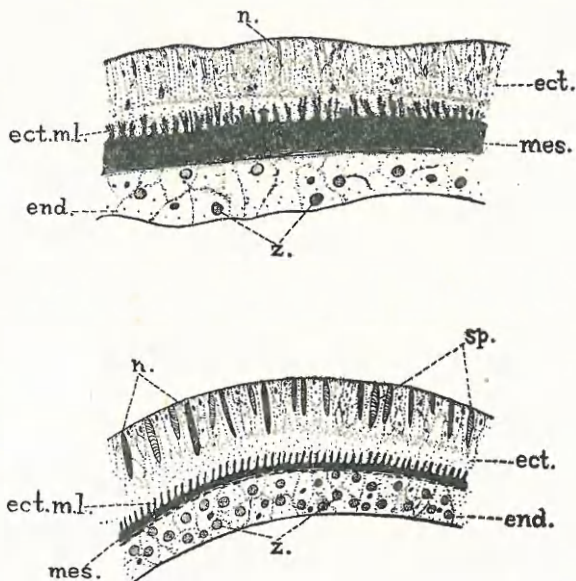


FIG. 1.

*The Oral Disc.*—The disc is thin and depressed, with the mouth placed on a central, raised, prominence. The throat is not open and the ridges are not distinct. Since the tentacles occur in crowded cycles surrounding the mouth, the margin of the disc is not clear. The oral disc is usually 6 to 8 mm. broad. The ectoderm, mesoglea and the endoderm of the oral disc are very thin and are scarcely recognizable as separate layers.

*The Tentacles.*—Large numbers of tentacles are present and they are smooth, long and pointed. They crowd at the distal extremity of the column and are usually 8 to 14 mm. in length. In younger specimens, they may be recognized as belonging to five or six cycles. The innermost

or the first cycle of six to eight tentacles corresponds to the primary endocoels and consists of the largest. The length of the tentacles gradually diminishes from the inner to the outer cycles. As the outer cycles contain large numbers of tentacles, especially in older individuals, it is not possible to distinguish the several cycles. Judged from many specimens, the theoretical arrangement seems to be  $6 + 6 + 12 + 24 + 48 + 96 \dots$ . The number varies according to the age and size of the anemone. In very young examples, all the cycles are not observed, while the asexually reproduced individuals exhibit irregularities of tentacular arrangement.

In structure, the tentacle is characterised by having a very weakly developed mesogleal layer. The longitudinal musculature of the tentacles is ectodermal. The ectodermal and endodermal layers are thin, and the cells of the latter often teem with zooxanthellæ.

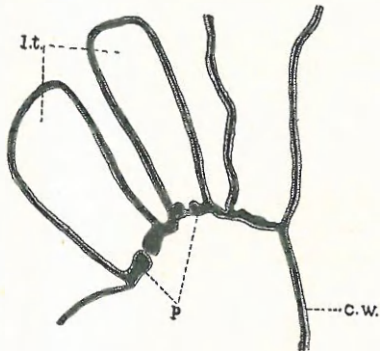


FIG. 2.

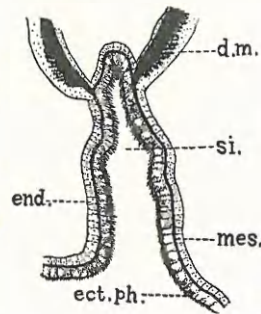


FIG. 3.

The bases of the tentacles are provided with sphincters projecting into the space where the tentacular cavities communicate with the coelenteron. The mesoglea of the sphincter is thickened towards the inner edge of the partition between the coelenteron and the lumen of the tentacle, and bears the muscle processes which control the action of the sphincter. As compared with similar sphincters described for *Boloceroideus hermaphroditica*, *Bunodeopsis globulifera* and *Bolocera tuediae* (Horton, 1934; and Stephenson, 1935), it is clear that the basal sphincter mechanism of this anemone is fairly well developed and capable of completely closing the communication between the tentacular cavity and the coelenteron. The deciduous nature of the tentacles is closely associated with the development of this sphincter. As in all tentacular sphincters, the muscle fibres impinge on the endoderm and the sphincter should hence be reckoned as endodermal.

Since the actual body of the anemone is much smaller than the oral disc and the tentacles, the latter structures are not retractile.



*The Actinopharynx.*—The stomodæum extends to the middle of the cœlenteron. Sections of the actinopharynx show distinct siphonoglyphes accompanied by directives; but the number of directives and the siphonoglyphes is variable because of the prevalence of asexual reproduction. In structure, the siphonoglyphes do not present an advanced condition since their lining cells are not highly specialized. Mucous cells are found in the ectoderm of the actinopharynx.

*The Mesenteries.*—The number of mesenteries is highly variable according to the age and size of the anemone. They are often numerous and a sharp distinction into microcnemes and macrocnemes does not exist. The primary mesenteries, which are the prominent ones, number six to eight pairs, and they differ from others in having well-developed mesenterial filaments and long, feeble retractors. The directive mesenteries also belong to this cycle, and as mentioned above, their number varies; at least a pair is always present.

The mesenterial musculature is very weakly developed. The parietal muscles are completely absent on all the mesenteries. The retractors which

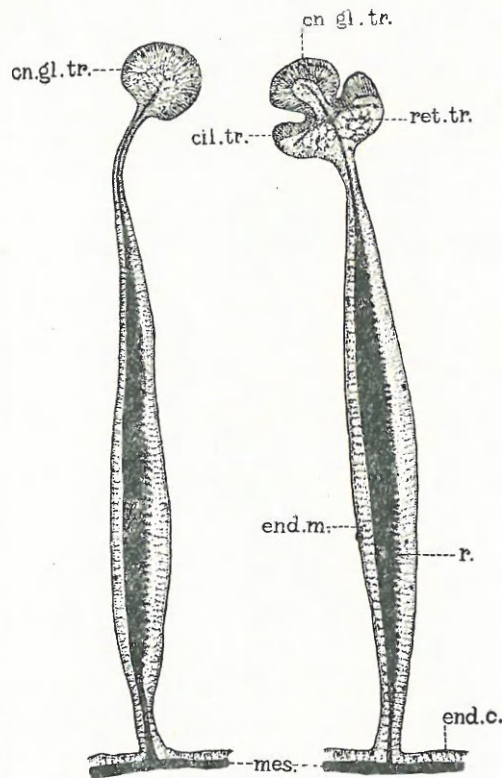


FIG. 4.



are present only on the primaries have feeble muscle processes. The mesenterial muscles are best developed near the basal part of the anemone.

As can be expected from the very large number of tentacles, the number of imperfect mesenteries increases near the oral disc of the column from what it is below. Their arrangement is not always regular. Curiously enough, most of the imperfect mesenteries near the oral disc bear well-developed mesenterial filaments which are identical in structure to that of the primaries. The tracts in the filaments are fairly well differentiated, with distinct cnidoglandular, reticulate and ciliated regions. The trifid part of the filament is very short as the ciliated tract exists only for a short distance, the remaining part of the filament consisting entirely of the cnidoglandular tract.

The gonads are borne by all the imperfect mesenteries, though rarely the perfect ones are also fertile. The usual condition is that the latter are all sterile, while a distinct reproductive region is often found even on the smallest imperfect mesentery of a fully-grown anemone. The sexes are separate. In the females, the large eggs lie in the mesoglea of the imperfect mesentery.

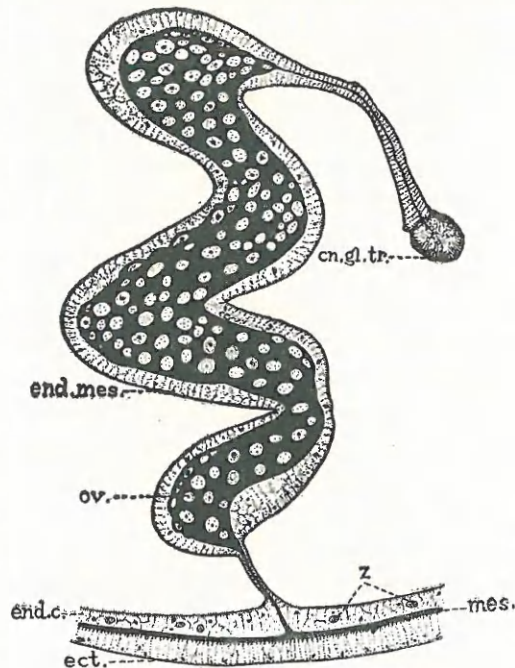


FIG. 5.

*Thread Cells.*—Cnidæ are very scarce on the base and column. Spirocysts appear to be absent on the column. Though several maceration

preparations were made and carefully examined, no evidence could be obtained to demonstrate clearly the occurrence of spirocysts on the column. These preparations showed only the small columnar nematocysts, which, as pointed out before, are rather scarce. The spirocysts and nematocysts are best developed on the tentacles. The nematocysts of the tentacles are curved in a characteristic manner and the thread of the capsule is of a forked appearance when not exploded, being similar to the capsules figured by Carlgren (1924) for *Bolocerooides* and *Bunodeopsis*. The tentacular nematocysts seem to be mostly of the penicillous type. They are indistinctly grouped on the ectoderm of the tentacles, but they do not form definite stinging warts as in *Bunodeopsis*. The spirocysts of the tentacle occur in groups at the base and middle while the nematocysts crowd near the tip.

#### *Asexual Reproduction.*

The powers of regeneration and asexual reproduction are developed to a remarkable degree in this anemone. The loss of tentacles, tears on the column, oral disc and the base, are all soon rectified by the regenerative activity of the adjacent tissues. The process of asexual reproduction is also a variant of regeneration as reproduction by longitudinal or transverse fission of the anemone has not been observed. The deciduous tentacles of the anemone regenerate new individuals as in *Bolocerooides*. The tentacles remain turgid and swollen even after their separation from the anemone. This is caused by the contraction of the tentacular sphincter which comes away along with the separated tentacle and completely closes up the opening at its base. New tentacles begin to arise from the basal part of the parent tentacle. Their orientation in relation to the column of the growing anemone is the same as in *Bolocerooides*. As the growth of new tentacles occasionally begins even before the complete detachment of the parent tentacle, the oral disc of some specimens examined bears a few developing individuals, each in association with a tentacle. This gives a characteristic clustered appearance to the discs of these anemones. The development of the young individuals does not proceed much under this condition. These 'buds' easily get detached long before they develop into young anemones. The number of such developing young ones carried by such an anemone varies from three to six. Specimens that bear asexually developing young ones do not have ripe germ cells in their mesenteries and the gonads are poorly developed. This observation seems to suggest that the asexual and sexual methods of reproduction do not take place simultaneously and that the two phases alternate.

Asexual reproduction in *Bolocerooides* has been the subject of detailed study by Okada (1926, 1930), and Okada and Komori (1932). The asexual

reproductive process in *Boloceractis* does not seem to be so highly evolved as in *Boloceroidea*. Okada and Komori discovered in the latter a regular organised process of budding whereby numerous buds are produced around the oral disc, which later grow into new Actinians after liberation. They also observed active tentacular regeneration. In *Boloceractis* we do not find budding taking place in the same way as described for *Boloceroidea*. The superior and inferior buds and their peculiar arrangement on the disc of the parent anemone are features not noted in the present form. But it was described above that occasionally, the growth of additional tentacles belonging to the new anemone takes place before the complete detachment of the parent tentacle. This phenomenon is on a small scale comparable to the budding of *Boloceroidea*. The young individuals that may develop in this manner in association with the mother anemone get detached at a much earlier stage in *Boloceractis*, as the few new tentacles are all the structures that are developed while on the parent. No mesogleal musculature has been observed in *Boloceractis gopalai* either in association with the developing 'bud' or at the base of the tentacle. The occurrence of a mesogleal musculature as described by Okada and Komori for *Boloceroidea* sp. is extremely doubtful (cf. Carlgren, 1933).

The order of appearance of the mesenteries in the asexually reproduced individuals could not be studied from the material available.

#### *Bionomics and Distribution.*

*Boloceractis gopalai* has been obtained from the Adyar and the Egnur backwaters near Madras, and from the Astamudi Lake in Travancore. From its known distribution, it would appear that the species is a euryhaline sea anemone.

Specimens have been taken from algal masses as also from the surface of the water since the anemone occasionally floats. It is capable of creeping and swimming movements; it does not, however, appear to be so actively swimming an anemone like *Boloceroidea hermaphroditica*. The tentacles are adhesive and helps the anemone to cling to algal masses. Specimens are of a yellowish brown colour in the fresh state.

The exact role played by the tentacular sphincter of the Boloceroidea and of the other Actiniid genera like *Bolocera* and *Liponema* is by no means clear (cf. Stephenson, 1935). It has been suggested by Horton (1935) that the sphincter, by strengthening the tentacular bases, may be of some advantage to swimming anemones like *Boloceroidea* (Carlgren, 1900; Komori, 1932), though he could not conceive of a definite mechanism whereby the basal sphincter helps the lashing movements of the tentacles. He was led



to this view by the greater prominence in the sphincter of the free-swimming Actinian *Boloceroides hermaphroditica*, as compared to the similar structures observed in *Bolocera longicornis* and *Bunodeopsis globulifera*. *Boloceroides*, *Boloceractis* and *Bunodeopsis* are non-attached anemones; they have comparatively short columns and the mouth is often wide and open. The partitions at the bases of the tentacles appear to be advantageous in another way. By the contraction of the tentacular sphincter, the communication between the coelenteron and the tentacular cavity is cut off, and this makes the tentacles turgid, giving it sufficient strength to execute lashing movements effectively. I have observed similar lashing movements even in a species of *Bunodeopsis* from the Madras Harbour, and it is worthy of note that this is not at all a free swimming anemone. Owing to the peculiar habit of shedding the tentacles, several circular openings are often seen on the discs of *Boloceractis gopalai* and the above-mentioned species of *Bunodeopsis*, allowing free communication between the coelenteron and the outside. Under such circumstances, it naturally suggests that the turgid state of the tentacles necessary to bring about active movements cannot be maintained but for the partitions at their bases. It should be mentioned, however, that as pointed out by Stephenson (1935) for *Bolocera tuediae*, the real significance of the "tentacle-shedding habit" of these anemones is not at all clear, though in *Boloceroides* and *Boloceractis* this habit has an important bearing on asexual propagation.

#### Discussion.

The genera *Boloceroides* and *Bunodeopsis* have occupied different positions in the schemes of classification adopted by different actinologists. Taking their many essential Protanthean characters into consideration, Carlgren (1900) referred *Boloceroides* to the Protantheæ along with *Gonactinia*. The differences between *Boloceroides* and *Protanthea* were, however, emphasised by Carlgren. The same arrangement was followed by Pax (1914) and Poche (1914). This position was questioned by Stephenson (1921, 1922) who created the new family Myonanthidæ, to include the four genera *Boloceroides*, *Myonanthus*, *Macrodactyla* and *Nevadne*. *Bunodeopsis*, on the other hand, has been classed along with *Alicia* and *Cystiactis* by Duerden (1895) in the family Aliciidæ. To this, *Thaumactis* (Haddon and Duerden, 1898), *Phymactis* (Haddon, 1898; Carlgren, 1898) and *Phyllodiscus* (Carlgren, 1898) have also been later added, though the heterogeneous character of the Aliciidæ was pointed out by Carlgren (1898). Pax (1914) placed *Bunodeopsis* along with *Alicia*, *Phymactis*, *Cystiactis*, *Rivetia*, *Phlyctenactis* and *Thaumactis* in one family. Stephenson (1921, 1922) referred it

to the Phyllactiidae, along with *Phyllactis*, *Cradactis* (inclusive of *Saccactis*), *Phymactis* (inclusive of *Rivetia* and *Bunodosoma*), *Cystiactis*, *Lebrunia* and *Thaumactis*.

In his paper on *Boloceroides*, *Bunodeopsis* and their supposed allied genera, Carlgren (1924) enters into a detailed examination of the different characters of all the allied forms and concludes that *Boloceroides* and *Bunodeopsis* are closely allied genera, while the rest of the forms go into two distinct groups: *Alicia*, *Phyllodiscus* and *Lebrunia* forming the Aliciidae; *Phymactis*, *Rivetia*, *Bunodosoma*, *Cystiactis*, *Phyllactis*, *Saccactis* and *Cradactis* constituting the Phyllactiidae. The family Myonanthidae is dropped since, according to him, it is very heterogeneous, *Myonanthus* and probably *Macrodactyla* being Actiniid genera. He creates the new group Boloceroidaria, to include the family Boloceroididae with *Boloceroides* and *Bunodeopsis* (Carlgren, 1924); and this scheme is completed by a provisional reference of *Nevadne* to a new family Nevadneidae, under the Boloceroidaria (Carlgren, 1925). Pax in his latest system (1925) accepts the families Boloceroididae and Phyllactiidae as defined by Carlgren, but retains the family Myonanthidae for *Myonanthus*, *Macrodactyla* and *Nevadne*, while in Stephenson's recent monograph (1935) the arrangement suggested by Carlgren is mainly followed.

The presence of a pedal disc without basilar muscles, longitudinal muscles and sometimes spirocysts on the column, the absence or extreme weakness of the sphincter, and the weak muscularity of the mesenteries are cited by Carlgren as the main features of the Boloceroidaria. They retain the longitudinal musculature of the body wall—an essentially Protanthean feature—but the presence of well-developed ciliated tracts on the filaments is an unmistakable Nynanthean feature, and settles once for all their position among the Nynantheæ. After a detailed study of the Boloceroidaria, Carlgren concludes, "In fact, just as there is only one opinion, that *Protanthea* is the most primitive Actiniarian we at present know, I think that *Boloceroides*, having retained the most Protanthean characters, is the most primitive Nynantheæ" (pp. 18-19, 1924). The disparity of opinion that existed on the affinity of the Boloceroidaria seems to have been set at rest as all the available evidences confirm Carlgren's contention.

It was shown in the morphological account how the new anemone described in this paper has all the features characteristic of the Boloceroidaria. This leads to a comparison with the other genera, *Boloceroides*, *Bunodeopsis* and *Nevadne*. It agrees with *Boloceroides* in having a smooth column without vesicles, and in its remarkable powers of asexual reproduction.

These resemblances are so apparent that at first sight it might appear that the anemone is a *Boloceroides*. But *Boloceractis gopalai* differs from the species of *Boloceroides* in the absence of spirocysts on the column, in the possession of distinct siphonoglyphes, and in the fertility of the mesenteries of the last orders. Of these, the last two characters are of considerable importance as they are of generic value, and are used to distinguish certain Endomyarian genera from their close relatives. It is hence necessary to consider *Boloceroides* and *Boloceractis* as distinct genera. There is very little in common between *Bunodeopsis* and *Boloceractis* save the group characters. The presence of distinct siphonoglyphes and fertile imperfect mesenteries in the new genus *Boloceractis* is in sharp contrast to the other members of the Boloceroidaria.

There is some agreement with the Nevadneidæ since the absence of spirocysts and vesicles on the column and the sterility of the primary mesenteries are characteristics of *Nevadne* (Annandale, 1915). The features of *Boloceractis* in agreement with the two families are shown in the following table :—

<i>Boloceroididæ.</i>	<i>Nevadneidæ.</i>
Column smooth.	Column without spirocysts.
Ectodermal longitudinal muscles through the column.	
Absence of sphincter.	
Deciduous nature of the tentacles.	
Weak muscularity in the mesenteries.	Feeble retractors.
No differentiation into macrocnemes and microcnemes.	No differentiation into macrocnemes and microcnemes.
	Usual sterility of the primary mesenteries.
Column short and not vermiform.	
Prevalence of asexual reproduction.	
Distinct pedal disc without basilar muscles.	Distinct pedal disc without basilar muscles.

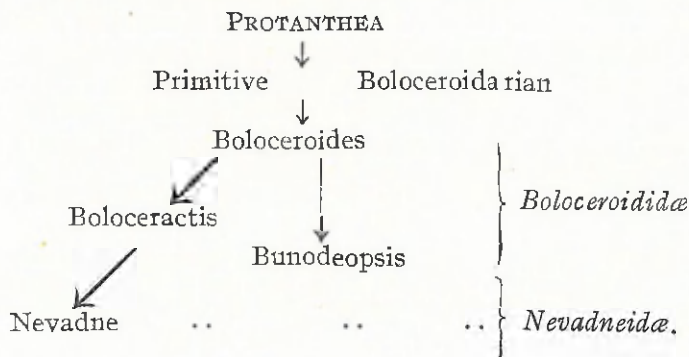
This comparison makes it clear that we have to refer *Boloceractis* to the Boloceroididæ as there is great agreement with this family in several important features. In the presence of siphonoglyphes and fertile imperfect mesenteries, the genus shows deviation from the typical Boloceroidid



condition. The arrangement of the tentacles in *Boloceractis* is on the fundamental actinian plan and does not present any peculiarities; but the very curious arrangement of tentacles and later sets of micromesenteries is the most important feature of *Nevadneidæ* which is represented by the solitary species *Nevadne glauca*. Hence we cannot pay so much attention to the features wherein *Boloceractis* and *Nevadne* are in agreement as to consider them as belonging to the same family.

In the evolution of this new genus, the spirocysts on the column wall observed in *Boloceroides* may have been lost; but neither the vesicles as seen in *Bunodeopsis*, nor stinging spots have developed here. The power of regeneration and the sphinctered nature of the tentacles are present as in the Boloceroididæ. Siphonoglyphes have developed and the imperfect mesenteries have become progressively fertile, while there has been a gradual reduction in the reproductive organs in the perfect mesenteries. The *Boloceractis*-stage possibly represents a definite landmark in the evolution of the *Nevadneidæ*. If so, the development of the vermiform column with stinging spots and the atypical arrangement of tentacles would be later acquisitions of *Nevadne*.

The evolutionary tendencies indicated by the Boloceroidaria have been discussed by Carlgren (1924) who rightly maintains that the Boloceroidaria have arisen from the Protantheæ as an independent off-shoot in which some of the primitive Protanthean features have been retained. *Boloceroides* must be reckoned as the most primitive genus of the group as it shows the closest resemblance to *Protanthea*. *Bunodeopsis* may have descended from a *Boloceroides*-like ancestor (cf. Carlgren, 1924; Stephenson, 1922). *Boloceractis* must also have descended from a *Boloceroides*-like ancestor but independent of *Bunodeopsis*. The genus *Nevadne* has perhaps evolved from a form closely related, if not very similar, to *Boloceractis*. The scheme may be represented as follows:—



*Summary.*

1. The morphology and asexual reproduction of a brackish-water Boloceroïdarian from Madras, have been studied.
2. As the anemone differs from other known members of the Boloceroïdaria in certain features of generic value, it is referred to a new genus, *Boloceractis*, under the family Boloceroïdidae.
3. Generic and specific definitions of *Boloceractis gopalai* are given and the anatomy of the anemone is described.
4. The mesenteries of *Boloceractis gopalai* are not sharply differentiated into macrocnemes and microcnemes; and the gonads are usually borne by the later cycles of imperfect mesenteries, the perfect mesenteries being typically sterile.
5. Asexual reproduction takes place in the anemone by a process of regeneration of the deciduous tentacles, the sphinctered partitions at the bases of the tentacles playing an important rôle in this process.
6. An account of the habits of the anemone is given and the rôle of the tentacular sphincter of the Boloceroïdaria is discussed.
7. The systematic relationships of the genus *Boloceractis* are discussed.

*Acknowledgments.*

In conclusion, I wish to thank Professor R. Gopala Aiyar for the constant help, encouragement and advice that I have received from him in the preparation of this paper. I am deeply indebted to Professor T. A. Stephenson of the University of Cape Town, for numerous suggestions and helpful criticism. Finally, I have to thank the University of Madras for giving me facilities for this work by awarding me a research studentship.

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