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# A BROOD-CARING ACTINIAN SUBJECT TO A WIDE RANGE OF COLOUR VARIATION

BY

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(*With Plate III and 12 Text-figures*)

On the Pacific coasts from the middle part of Honshu through Hokkaido northwards to the Kurile Islands, there is commonly found a species of actinian of various colorations, generally showing a considerably flat shape with a well-expanded disc of a membraneous appearance and often bearing small embryos on the middle region of the body wall. These actinians being especially abundant in the neighbourhood of the Akkeshi Marine Biological Station, many individuals of the species were used for observation in the living state and for histological investigation. As a result of the examination it has become evident that the Japanese species is, in all probability, identical with *Epiactis prolifera* which has hitherto been known on the Pacific coasts of North America from Puget Sound to Pacific Grove, California. It seems to me very interesting that the coloration of the species is not due to environmental conditions but to the genic character as is shown later. A part of the work was carried out through a grant from the Foundation for the Promotion of Scientific and Industrial Research of Japan.

The first report on the actinian was made from Puget Sound by VERRILL (1869), who afterwards in 1899 gave a revised description with a brief anatomical note of the species. MCMURRICH (1901) gave more detailed anatomical descriptions on several preserved specimens, and cited the note of Dr. CALKINS, who collected them from Puget Sound, concerning the coloration. Following this report, TORREY

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(1902) recorded the species, together with anonther species *E. ritteri* occurring in Alaska, from Tomales Bay, San Francisco, Pacific Grove, and San Pedro, California, giving a figure of the sphincter muscle. But these reports were mostly based on preserved specimens and, therefore, no detailed remarks as to the coloration and the anatomy of the species have as yet been published.

*External aspect.* On account of the degree of extension of the pedal disc, the form is exceedingly variable; sometimes low cylindrical, usually measuring 8–20 mm high and 10–40 mm wide, but sometimes very low and nearly flat with the expanded disc over 60 mm in diameter. The pedal disc can be extended over a fair area; when it is well stretched out, the actinian takes a flat form, with the undulating margin of the pedal disc showing a membraneous appearance, and with a narrowed cylindrical distal part. The column is generally smooth, without true verrucae, but is often provided with indistinct protuberances or folds which are irregularly arranged in several (from 1–2 to about 10) rows on the middle region bearing young individuals in the female. The protuberances are sometimes very conspicuous in preserved specimens, but they are in some individuals quite indistinct (Fig. 1) and sometimes entirely absent. Their occurrence is restricted to the middle region, and the upper and lower portions of the column are bare of them. These protuberances are used to bear embryos and young individuals in the female, and are each represented by a succule-like papilla having an egg-pit in the terminal centre. The egg-pit is at first small, but as the embryo attached to the column develops, they become larger and larger, partly by a slight infolding of the ectoderm

Fig. 1. A preserved specimen having no embryo attached. ×3/2

and partly by a thinning of the mesogloea, though they remain throughout as shallow depressions. The ectodermal region to which the embryos are attached is modified to a composition of many vacuolated gland cells secreting mucus. In some individuals only two or three embryos and young actinians are found, but in others there are almost two hundred of them (Fig. 2). Some adult individuals, however, do not carry them at all. In preserved specimens longitudinal and transversal wrinkles and foldings may be observed, being especially conspicuous in the lower half. They have been caused by contraction and are not of the special histological character different from the rest of the column. There are no cinclids. A little below the margin there is a slight fosse. The tentacles are numerous, probably 96 in the adult, hexamously arranged and disposed in about 3 or 4 rows. They are moderate in length, subequal, and, when expanded, nearly of the same length as the width of the oral disc. The tentacles are not pointed at the tip, and may be easily retracted and entirely concealed in contraction.

Fig. 2. A preserved specimen bearing a great number of embryos and young actinians. ×3/2

*Colour*. As to the coloration of the actinian, McMurrich only gives the note of Dr. Calkins as "bright grass green or weed green striped with darker green". Besides, he pointed out that among the drawings of actinians made by Agassiz he found two which apparently represent this species. The column of the one is represented as bright grass green marked with longitudinal streaks of dark brown. The disc is very dark green with numerous radiating stripes of cream white, and the tentacles are buff with a distinct dark greenish-brown spot at the base of each. The column of the other

specimen is dark brown streaked longitudinally with lighter brown, and the tentacles are a dull grayish green. So far as I have observed from many living specimens at different localities from Hokkaido to Honshu, the colour is exceedingly variable in individuals. It seems to me that those of reddish brown colour without radial streaks are the most common, and those deep port-wine-coloured or dark green are the next in occurrence. Besides these plain coloured ones, there are some marked with two or three different kinds of colour. As shown in Plate III, though considerably variable and irregular in coloration and pattern as they may be, these individuals coincide in that they are always featured by somewhat similar patterns made of several irregular radial bands, different in length and width, running from the oral disc to the base. It is very interesting to note the following facts concerning the coloration:

1) Several individuals showing different colorations occur together in a limited locality which is subject to almost identical influences of sunshine and tides.

2) Young individuals attached to a mother have always a nuance in colour similar to the latter, though patterns may be indistinct.

3) As to coloration, the actinians are divided into two groups, plain coloured and radially streaked. In the latter forms, patterns coincide broadly with each other, as shown in Plate III.

4) In both the plain-coloured and radially-streaked individuals colour variations appear in several ways, but instead of these variations being at random, they seem to be constant; each variation is not represented by a single specimen, but at least a few individuals occurring in the same locality are observed of similar coloration and pattern.

Judging from these facts it is probable that the colorations of the actinian are not due to the environmental effects but are of a genic character.

The colour of tentacles agrees generally with that of the column, but in some individuals they are quite different (Pl. III).

*Anatomical description.* The tentacles are composed of the three layers, thick ectoderm containing supporting cells, spirocysts and gland cells, fibrillated mesogloea and thin endoderm. In the ectoderm the cells are arranged in about two alternate rows, the upper ones being wedged between the lower. The spirocysts are generally, except in a few cases, situated near the surface and thickly set, while the gland cells are located in the inner part with a narrow canal leading outside. The mesogloea is of about 1/2 the thickness of the ectoderm, fibrous, and provided with a ring muscle giving rise to arborescent branches outwards and showing the form of a palisade. The endoderm layer consists of cylindrical cells, which are vacuolated in the part adjacent to the mesogloea, but granulated in the axial portion containing a nucleus.

The ectoderm cells of the column are high and cylindrical, being composed of supporting cells and granulated gland cells. These cells are about alternate in position and have each a nucleus in the basal portion. The ectoderm cells corresponding to the protuberances are not especially differentiated from the normal ectoderm cells, but the ectoderm to which the embryos are attached is slightly vacuolated

Fig. 3. Radial section of an embryo attaching to the ectoderm of the column of the mother, which is especially modified, composed of high cells secreting mucus. ×60

and becomes somewhat higher than the rest, secrecting mucus on the surface, as shown in Fig. 3. In the basal disc the ectoderm cells are exceedingly modified, very high, and are arranged in a row, containing vacuolated cells, gland cells and supporting cells. The ectoderm cells bordering the inner wall of the actinopharynx are narrow, very high, all ciliated, consisting of supporting cells, gland cells and granulated cells and folding into manifold ridges innerward in well-developed individuals. The actinopharynx of young actinians is simiply round in cross section and comparatively larger than that of the adult. There are two distinct deep siphonoglyphs of which the ectoderm consists of granulated cells.

The mesogloea of the column is thick and finely fibrillated throughout, but generally bare of nuclei, while that of the mesenteries, also fibrous in structure, contains nuclei sparsely distributed. On the inner wall of the fosse is situated the circumscribed sphincter. Though somewhat different in individuals, as shown in Figs. 4–6, it is always sessile and circumscribed, taking an almost elliptical form in cross section. The mesogloeal lamellae forming it are fine, sparsely branched and rather arborescent, but more or less anastomose in places. Out of the three figures here given, Fig. 4 is quite similar

Fig. 4. Cross section of sphincter in a individual. ×48

Fig. 5. Cross section of sphincter in a individual. ×48

Fig. 6. Cross section of sphincter in a individual. ×48

to the figure of the sphinter for *E. prolifera* made by TORREY (1902), while Fig. 5 broadly accords with that of *E. ritteri* also made by him (1902). Fig. 6 represents a sphincter of a quite different form. Concerning variations occurring in form of the sphincter in an

actinian species, CARLGREN (1924) pointed out the fact with figures for *Epiactis mortenseni*[1] collected from the Auckland Islands.

The endoderm is universally formed by vacuolated cells with a nucleus and granula near the inner portion, containing a few finely granulated gland cells.

The mesenteries of the actinian are different in number according to degree of development. In the youngest actinians with 12 tentacles, just developed from the embryo, only 6 pairs of the perfect mesenteries are found. Young individuals, about 2 or 3 mm in diameter, still attaching to the column of the mother are provided with 12 pairs of mesenteries, 6 of them being perfect and 6 imperfect (Fig. 7). In these individuals the tentacles are 24 in number and arranged in two circlets. Larger specimens still attached to the mother actinian, or those already separated from it, measuring less

Fig. 7. Diagram of transverse section of a very young actinian attaching to the mother, showing mesenterial arrangement. DI; directive mesentery pair, I; perfect mesentery pair of the first cycle, II; mesentery pair of the second cycle.

1) According to CARLGREN, this species must be named *Bunodactis* (*Cribrina*) *mortenseni* on account of the presence of verrucae on the column (CARLGREN, 1924, Postscript, p. 261).

than 10 mm in diameter, are provided with 24 pairs of mesenteries, of which 6 are perfect and 18 imperfect, as shown in Fig. 8. In full-grown specimens there are 96 mesenteries arranged in 48 pairs, including 24 perfect mesenteries (in 12 pairs) and 72 imperfect ones (in 36 pairs) (Fig. 9). The appearance of new mesenteries in each

Fig. 8. Diagram of transverse section of a young actinian still attached to the mother, indicating mesenterial arrangement. DI; directive mesentery pair, I; perfect mesentery pair of the first cycle, II; mesentery pair of the second cycle III; mesentery pair of the third cycle.

hexant seems to be nearly synchronous, but it often occurs independently in each hexant. There are, therefore, several intermediate stages between those indicated in Figs. 5–7. In specimens standing in these intermediate stages, several kinds of disparity in the number of the mesenteries are found in each hexant according to the different degrees of development in each hexant. The full-grown specimens are furnished with the fifth cycles of mesenteries; 6 (perfect), 6

(perfect), 12 (imperfect), 24 (imperfect) and 48 (imperfect). Of the mesenteries of the first cycle, two opposite pairs are the directive, each corresponding to a siphonoglyph and extending in the coelenteron deeper than the others to near the base. Though mesenteries of the second cycle are also perfect in well-developed actinians, they do not

Fig. 9. Diagram of transverse section of a full-grown specimen, denoting mesenterial arrangement. DI; directive mesentery pair, I; perfect mesentery pair of the first cycle, II; perfect mesentery pair of the second cycle, III; mesentery pair of the third cycle. Mesentery pairs of the fourth and fifth cycles are not indicated by figures and present between the older ones.

extend in the lower portion so far as those of the first cycle. There are, therefore, twelve pairs of perfect mesenteries in the upper part of the body, but a little farther down only the six primary pairs reach the stomodaeum. The gonads do not develop in these perfect mesenteries, but they are borne by all the imperfect mesenteries in well-developed individuals.

The perfect mesenteries are all provided with diffused muscle pennons which are situated on the entocoelic sides (in the directives

on the exocoelic sides only) near the wall of the actinopharynx, with the best-developed part in the axial portion. The muscle pennons, at first somewhat circumscribed in the young actinian (Fig. 10), become gradually enlongate (Fig. 11), and finally take the diffused form (Fig. 12). At an abaxial part and on the opposite side of the muscle pennons is found an arborescent parieto-basilar muscle giving rise to several processes. The mesenteries of the

Fig. 10. Horizontal section of a hexant of column of a youngest actinian attaching to the mother. DI; directive mesentery pair, I; mesentery pair of the first cycle, II; mesentery pair of the second cycle.

Fig. 11. Horizontal section of a hexant of column of a young actinian still attached to the mother. DI; directive mesentery, I; mesentery of the first cycle, II; mesentery pair of the second cycle, III; mesentery pair of the third cycle.

third cycle are generally similar in structure to the mesenteries above mentioned, but the muscle pennons and parieto-basilar muscles are not so developed as in the former. Furthermore, they are, in the inner part, provided with mesenterial filaments which, in cross section, are composed of a head of a trefoil-leaf-form and a thin filamentous proximal part made of narrow endodermal layers with a thin mesogloeal axis. The ova and testicular succules are very few in number, large in size and arranged in a row along the middle length of the axial portion of the filaments. In the mesenteries of the fourth and fifth cycles there is generally found only one well-developed ovum embedded in the mesogloea near their distal part. The terminal portion of the filaments is tri-lobed and is divided into

three regions, a cnidoglandular tract, ciliated tracts and a reticular tract. The cnidoglandular tract is composed mostly of granulated gland cells, which are especially thickly set in the central lobe. No

Fig. 12. Horizontal section of 1/12 part of column of an adult. DI; directive mesentery pair, II; mesentery pair of the second cycle, III; mesentery pair of the third cycle, IV; mesentery pair of the fourth cycle, V; mesentery pair of the fifth cycle.

spirocysts could be found there. The ciliated tracts, situated on both sides of the central lobe forming two lateral lobes, are distinctly marked by the presence of slender cells which are thickly arranged into two alternate rows, containing only spindle-shaped cells of a similar structure. The reticular tract located adjacent to the ciliated tract consists mostly of vacuolated cells, containing a few gland cells. The reticular tracts on both sides unite in the middle portion and are connected with the narrow lamellar part composed of vacuolated cells. The mesogloeal core running through the axial part of the lamellar part extends into the axial portion of the median cnidoglandular and two lateral ciliated tracts. The terminal end of the

mesenterial filaments destitute of the ciliated tract is, in cross section, represented only by a somewhat heart-shaped cnidoglandular tract containing a great number of highly granulated gland cells. Behind the base of the tract are arranged vacuolated endoderm cells, which are especially high near the base, and are known as digestive cells. The mesenteries of the fourth cycle are generally of a structure similar to that of the third, with the exception of the presence of more feebly developed parieto-basilar muscles. The mesenteries of the fifth cycle are small and devoid of parieto-basilar muscles, but are furnished, in well-developed specimens, with feebly-developed muscle pennons and small mesenterial filaments. The basilar muscles of the species are branched into several processes.

*Embryos.* The embryos are found attached to the column of the adult during summer. Their number on a mother actinian is very variable, as stated above. There are many large specimens which do not bear the embryos in the summer. It is surmised that they are male individuals. From the fact that the youngest embryo adhering to the mother is furnished with the ectoderm and the endoderm, it is possible that the eggs fertilized in the mother's coelenteron are thrown out from it by a contractive movement of the column, and are attached to the wall by means of mucus secreted from the surface of the ectodermal protuberances. These embryos develop *in situ* to a small actinian at first provided with 12 tentacles and 6 mesentery pairs, and then with 24 tentacles and 12 mesentary pairs. After that they become gradually large and consequently leave the mother's column to begin their independent life.

*Distribution.* Pacific coasts of North America, from Puget Sound to Pacific Grove, California. In Japan the following localities are known: southern Kuriles, Hokkaido (Akkeshi, Muroran, Oshoro, Hakodaté), Honshu (Asamushi, Ôarai, Misaki). Considering the distribution of these localities, the actinian seems to be one of the most common inhabitants of the North Pacific.

*Remarks.* TORREY (1902) reported *E. ritteri* from Alaska together with *E. prolifera* from Pacific Grove, California. According to him,

*E. ritteri* may be distinguished from *E. prolifera* by its larger size, the shape of its sphincter, and the absence of the habit of carrying the young externally. In Japanese specimens the size is quite different and some specimens in my hands are larger than those photographed and described as *E. ritteri* by TORREY. The habit of carrying the young is not constant character in both sexes of the actinian and probably disappears after the breeding season. The form of the sphincter, the most important among the characters pointed out by TORREY to distinguish *E. ritteri* from *E. prolifera*, is somewhat variable in the species, as stated above, some quite resembling that of *E. prolifera*, while some resemble that of *E. ritteri*. Furthermore, CARLGREN (1924) described several different forms of the sphincter in a species, *E. mortenseni*=*Bunodactis* (*Cribrina*) *mortenseni*. Such being the case, the difference in the sphincter to this degree is of no significance for distinguishing the species. Besides, the description and figures made by TORREY coincide exactly with the Japanese actinian, so there is no room for doubt in identifying *E. ritteri* with *E. prolifera*.

Furthermore, it seems to me that the actinian found in Hakodaté and described by VERRILL (1868) as *Bunodes japonica* is probably identical with the present species. His description of the actinian is as follows: "Column with *very prominent warts* or *verrucae;* when contracted taken the form of a *thin fleshy membrane*, with verrucae arranged around a central depression. The tentacles arranged in two rows, so crowded as to encroach on each other and placed very near the margin of the disc; twelve are more prominent than the rest and nearer the mouth. *Disc broad, flat. Mouth small. Color variable*, but generally uniform on all parts of the same specimen. Some are *dark green*, others *olive*, *vermilion*, or *dark red*. One was *radiated with two colors*. Hakodati[1] Bay, Island of Jesso[2], Japan, on stones at and just below low-water mark, June, 1855. Dr. William STIMPSON." His description, probably based on Dr. W.

1) Hakodati=correctly Hakodaté.
2) Jesso=the ancient name of Hokkaido.

STIMPSON's note, thus concerns only external features, and is not sufficient for the specific diagnosis of an actinian. It shows, however, several remarkable characters of *E. prolifera*. In the first place, STIMPSON presumably mistook embryos attached to the column for "*very prominent warts or verrucae*. In the second place, *E. prolifera* often takes the form of a *thin fleshy membrane*, with embryos attached around the middle depression. The disc, moreover, is generally broad and flat, with a small mouth in the centre. In the third place, the description of the colorations quite agrees with my observations on Japanese specimens, including those found at Hakodaté. From these facts it would seem that the identification of *Bunodes japonica* with *E. prolifera* is highly probable.

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# Plate III

## Explanation of Plate III

(*Epiactis prolifera* VERRILL)

11 individuals showing different colorations and colour pattterns. All drawn from life in Akkeshi, Hokkaido, natural size. For details see pp. 19-20.

*T. Uchida: A brood-caring actinian.*

*Y. Uchida del.*