

THE FAUNA OF BRACKISH PONDS AT
PORT CANNING, LOWER BENGAL.

PART III.—AN ISOLATED RACE OF THE ACTINIAN *Metridium
schillerianum* (STOLICZKA).

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METRIDIUM SCHILLERIANUM (Stoliczka).

Sagartia schilleriana, Stoliczka, *Journ. Asiat. Soc. Bengal*, part 2, vol. xxxviii, 1869, p 28 ; plates x, xi ; R. Hertwig, *Zool. Rep. H.M.S "Challenger,"* vol. vi, 1882, Actiniaria, p. 71.

Although Stoliczka's description of the typical form of the species is very detailed, the imperfect knowledge of the structure of the Actinians possessed thirty-nine years ago by students of the Cœlenterates, misled him as regards certain important characters, while the fact that he cut no sections prevented him from detecting others. His types are now in a bad state of preservation, the tissues being shrunk and partly decomposed, and have assumed a dark brown colour of which I have been unable to get rid. I have, however, cut sections of two of these specimens, which proved to be so far intact that the arrangement of the mesenteries could be detected. Further, I have made vertical and transverse sections of two fresh examples of this form, and have dissected two others, as well as sectioning four specimens of the new variety, dissecting six, and examining a very much larger number externally. The following description of the species and its variety is based on the material thus used. Although it differs considerably from Stoliczka's written description, it will be found to be in most respects, so far as the typical form is concerned, in accord with his figures, which, for the reasons given above, he appears to have misinterpreted in spite of the accuracy of his observations.

DESCRIPTION OF THE TYPICAL FORM OF THE SPECIES.

Colourless in spirit ; in life translucent, the column being more or less deeply tinged with green and having a variable number of semi-opaque vertical stripes arranged in multiples of six and representing the better developed of the intramesenterial spaces ; parts

of the mesenteries often of a deep purple, which may be visible externally; tentacles semi-opaque, often with irregular transverse bars of opaque white. Column cylindrical, as broad or almost as broad as high when normally expanded, broader than high when contracted; in the latter condition mound-shaped, with a considerable oval aperture as a rule remaining open above the tentacles. Tentacles elongated, tapering, perforate at the distal extremity, arranged in five cycles; the innermost cycle with six tentacles, the next with twelve the third with twenty-four, the fourth with forty-eight, the fifth with ninety-six: 186 in all (approximately). Disk ample, oval, not separated from the column when expanded; the mouth large, elongated and narrow; the lips protuberant, with six folds on either side of the mouth; the stomodæum extending more than half way down the column; the gonadial grooves distinct. External surface of the column smooth, generally with rows of suckets arranged vertically; the cinclides, which are difficult to detect in preserved specimens, scattered. Basal disk variable in outline, often extending beyond the periphery of the column, provided with a distinct sphincter, which is visible in living specimens as a thin, semi-opaque ring. Circular muscles of the column well developed, confined to the mesoderm; the sphincter elongate in vertical section, consisting of comparatively feeble folds without muscle spaces; radial muscles of the disk and tentacles situated at the base of the ectoderm and not encroaching on the mesoderm. The six primary (complete) pairs of mesenteries fertile; sometimes the first and rarely also the second secondary cycles fertile; the number of secondary cycles from three to five, each consisting of twelve mesenteries; some mesenteries in one or more of the cycles rudimentary, without fully developed retractor muscles and devoid of filaments; acontia very long. Gonads protogynous, the two elements being produced at different times and in different parts of the mesenteries, the ovaries above the testes.

DESCRIPTION OF AN ISOLATED RACE (*var. exul*) OF THE SPECIES.

Column several times as long as broad, vermiform when extended, in young specimens sausage or barrel-shaped when contracted. The walls of the column very thin, allowing forty-eight mesenteries to be visible externally as narrow, semi-opaque vertical stripes. Tentacles as in the typical form, except that there are never more than four cycles; the disk in old specimens much reduced, divided into twelve distinct parts. The stomodæum extending less than half way down the column. Basal disk devoid of a sphincter, its periphery merging gradually into the column. The folds of the subtentacular sphincter markedly deeper above than below, with a few oval muscle spaces above. The six pairs of primary mesenteries alone fully developed, the others as a rule lacking retractor muscles and filaments, but the first cycle, or some of its members, sometimes being fertile though feebly muscular. Cinclides in vertical rows on the upper part of the column.

In all other respects, so far as its taxonomic features are concerned, the characters of the variety may be regarded as identical with those of the typical form.

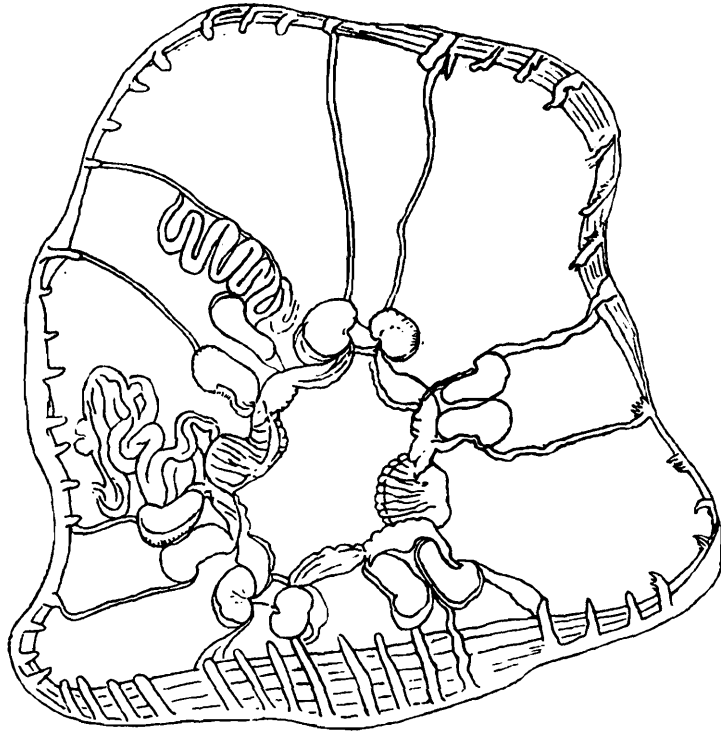


FIG. 1.—Thick transverse section of the column of *M. schillerianum* var. *exul* in the region of the stomodæum, showing the arrangement of the mesenteries, the form of the retractor muscles and the muscular strands of the wall.

COMPARISON BETWEEN THE STRUCTURE OF THE TYPICAL FORM AND THAT OF THE VARIETY.

The above is a general account of the physical characters in which the two forms agree with and differ from one another. In order to explain the manner in which it is probable that these differences have come about, it will be necessary first to compare the structure of the two forms in further detail, and then to give an account of their respective modes of life.

Column.—

The main differences between the typical form and variety are plainly connected with the differences in the form of the column. In the new variety of the species this part of the organism is a thin-walled muscular sac with a bulky lumen; in the typical form the walls are thicker and the coelenteron very much less spacious. The thinness of the walls in the variety is due to two causes, *viz.*, the nature of the ectodermal layer and the comparatively poor development of the mesoderm. In both forms the ectodermal layer consists of the usual elements, namely, epithelial and glandular cells, sense cells, and nematocysts. The cells do not differ in any feature of importance as regards form or structure from those found in the same layer in other Actinians. Stoliczka has already described and figured

the nematocysts (*op. cit.*, plate xi). The secretion of the gland cells mixed with the threads of the nematocysts forms a covering for the column, which, however, is only temporary, and has not the characters of the so-called cuticle found in some Actinians. Unless specimens are very carefully preserved, the whole of the nematocysts of the column and tentacles are forced out of the ectoderm without rupturing, and appear in transverse section to form a separate layer, bound together by slime secreted by the gland cells but external to and distinct from the ectoderm. If living specimens are examined, it will be found that there is no such layer under natural conditions, but that the nematocysts are interspersed with the epithelial and glandular cells. The temporary protective covering is not formed of the nematocysts, but only of their threads and of slime, often with foreign bodies enclosed. In the isolated race the ectoderm consists of a layer of cells parallel to the mesoderm. In the typical form, however, this layer is thrown, all round the periphery of the column, into a series of transverse folds, the function of which I will discuss later. The number of nematocysts and also of gland cells present in this region is perhaps greater in the typical form than in the variety. The suckers, which are as a rule absent in young individuals, consist, in both forms, of relatively deep folds of the ectoderm separated by a space from the mesoderm; they are oval in outline, their main axis being at right angles to that of the column. It is very difficult to detect the cinclides in preserved material, but in life they are easily distinguished as transversely elongated slits with tumid lips. In structure they closely resemble the suckers except that they are perforate; the mesogloea beneath them is much vacuolated. The vertical rows of suckers, at any rate in the variety, usually correspond to the inter-, those of the cinclides to the intramesenterial spaces; but I have been unable to convince myself that this arrangement is absolutely constant. In the typical form of the species cinclides and suckers occur on all parts of the column, the former being particularly numerous near the two disks; but in the new race both structures are confined to the upper half of the column below the region of the sphincter.

The thickness of the mesoderm is not more than moderate in the typical form; in the variety it is rather less, but the mesogloea swells out somewhat irregularly in many of the inter- and intramesenterial spaces in such a way that the whole of the layer in such spaces has a roughly spindle-shaped outline in transverse section. In both forms the nerve cells situated towards the external limits of the mesoderm are large and numerous, and in both the mesogloea itself has a distinctly reticulo-fibrillar structure and contains, especially externally, a number of irregularly placed vertical spaces and channels. In the typical form of the species, the wider folds of the ectoderm rest on slight projections and concavities in the mesoderm, while in both forms broad mesodermal 'bays' occur on the endodermal surface.

The endoderm of the column in both forms consists of consider-

ably elongated epithelial cells provided with cilia, which are particularly long and active towards the upper limits of the column. In the typical form, the number of gland cells interspersed in the epithelium is perhaps greater than in the variety. In the former, the cells lining the intermesenterial spaces are markedly longer, and contain more zooxanthellæ, than those lining the intramesenterial spaces. This difference is not so clear in the variety but appears to exist to a slight extent. In both forms the zooxanthellæ do not encroach upon the basal part of the cells.

An important point to be noted is that the differences in structure of the column are much more marked in the case of full-grown individuals of the two forms than they are in that of very young individuals of the variety and adults of the typical form. As can be seen from the figures on plate iv, young individuals of the variety measuring about 10 mm. in length when contracted, are only about four times as long as broad, their proportions being, however somewhat variable. In full-grown specimens of the same form, however, the length is at least ten times the transverse diameter. When strongly contracted the column of the young individuals assumes a barrel-shaped outline which does not differ very greatly from the conical outline of the typical form in same state, and the younger the individual is, so far as my experience goes, the less is the length in excess of the transverse diameter. It is only well-grown individuals, of over 4 cm. in length when they are contracted, which can be called wormlike, and as will be shown later, contraction takes a different course in full-grown examples of the variety than that which occurs in young examples of the variety or full-grown individuals of the original form. In the typical form and in the young of the variety, the column is able to stand vertically upright, but in larger individuals of the variety this is impossible without artificial support.

Muscles.—

The circular muscular layer of the mesoderm of the column lies within the nervous layer of the same structure and, in the variety, occupies the greater part of the mesogloea. In the typical form it is relatively less extensive. In the typical form, moreover, the muscle fibres appear to form a continuous sheet, but I am not quite confident as regards this point. In the variety, however, it is easy to see in living and even in well-preserved specimens that this muscle consists of a large number of parallel strands lying closely adjacent to one another in a vertical series. I am not referring to the sphincter, which is formed by a folding of the muscle accompanied by a parallel folding of the whole mesoderm, but to the circular muscle of the column below the sphincter.

In the typical form of the species the sphincter is not visible externally and its folds are so shallow and commence so gradually below, that it is difficult to say at what point it begins to become differentiated. This is also the case as regards young specimens of the variety less than five millimetres long; but even in these it is more powerfully developed. In full-grown specimens of the

variety, however, the sphincter region can be distinctly recognized externally, forming a somewhat corrugated and rather opaque band beneath the disk, and measuring about one-twelfth of the whole column in length. It is well shown in fig. 5, pl. iii.

The basal sphincter is formed by a few comparatively deep folds in the circular muscle at the base of the column round the periphery of the basal disk. I can find no trace of it in the variety.

Longitudinal muscle fibres can occasionally be detected in the mesoderm of the column in the typical form; in the variety they are fairly abundant in the spindle-shaped swellings of the mesoderm referred to in a preceding paragraph.

In both forms of the species, the basilar muscles of the mesenteries are well developed, surrounding outgrowths of the mesoderm at the base of these organs and having a dendritic outline in transverse section. As a rule they are developed almost equally on the two sides of the mesentery; but their exact outline varies greatly even in different mesenteries of the same individual. The basilo-retractor muscles are on the other hand somewhat feebly developed, accompanying a relatively slight folding of the mesoderm often almost indistinguishable. They, too, are very variable. The retractor muscles are stout and somewhat short in transverse section in both forms. In the variety it is possible to distinguish these belonging to the directive mesenteries from the others by their shape as well as by their position and orientation. In transverse section all have a reniform outline but those of the directive mesenteries are shorter and more nearly circular. In the typical form of the species this characteristic is not so marked as in the variety, but in the latter there is more space for the muscles to retain their natural outline than there is in the former. The retractor muscles in the variety become gradually more slender near the base of the column, and practically disappear before the base is reached. In the typical form, however, they extend along the basal disk almost to its centre, and play an important part in the muscularity of that structure.

The radial muscles of the disk and tentacles are at first sight difficult to detect, owing to the fact that they form a relatively narrow band in transverse section. In suitable longitudinal sections of the tentacles, however, they appear to be powerful and are easily distinguished.

Tentacles and disk.—

The arrangement of the tentacles is closely similar in the two forms, but the variety generally has one cycle fewer than the typical form, full-grown individuals of both being examined. Stoliczka said that he could distinguish the six primary tentacles from the others by their shape; this I have been unable to do, but, at any rate in young individuals, their position surrounding the mouth is quite distinct and they are separated from the other cycles. Typically each cycle, commencing from the primary cycle and going outwards, has twice as many tentacles as the one immediately within

it, as Stoliczka's diagram (*op. cit.*, pl. xi, fig. 2) shows very clearly ; but although this holds good as a general rule, there are many exceptions, which arise either from the suppression of some of the tentacles of a cycle or by the appearance of supernumerary tentacles. The latter phenomenon may occur in one of two ways : not infrequently an extra tentacle makes its appearance at the base of one already fully formed than which it is at first considerably smaller, and less frequently a tentacle splits longitudinally into two. I have seen both these methods of multiplication in

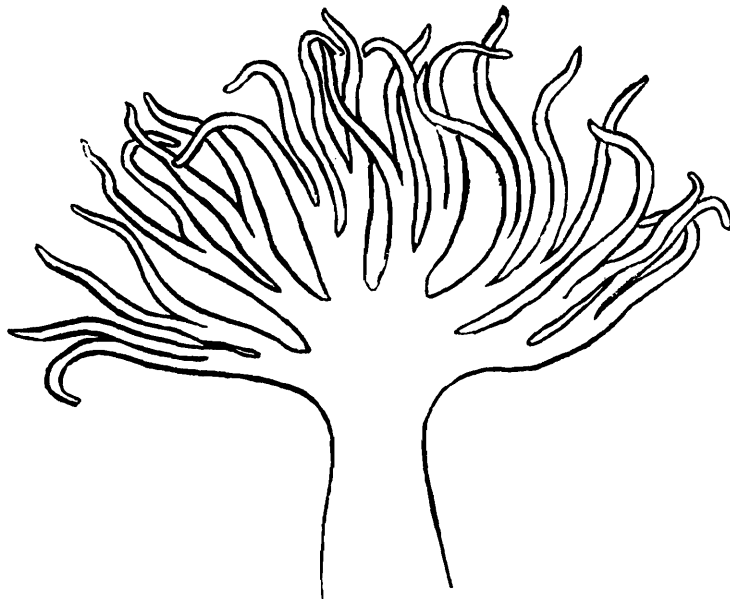


FIG. 2.—Expanded disk of *M. schillerianum* var. *exul*, oblique lateral view, nat. size.

progress in the variety, and have little doubt that they also occur in the typical form, judging from the slight divergencies from regularity which I have found in specimens.

As regards the individual tentacles I can find no difference between the two forms. In both they are elongated and tapering and are perforate at the free extremity. I have on one occasion seen an acontium protruded through the pore. The nervous layer of the ectoderm is clearly marked in transverse sections and the layers are generally of typical form and structure.

The wall of the disk is thinner in the variety than in the typical form. In the latter, when the disk is fully expanded its edge makes a right angle with the column and is entire. This is also the case as regards individuals of the new race of all ages, when their disks are fully expanded. When the disk of the typical form is partly contracted, however a fold of the wall of the column containing the upper extremity of the sphincter makes its appearance, and this is also the case in young individuals of the new race less than about 2 cm. long. Even after the appearance of this "collar," the margin of the disk is entire. In larger individuals of the isolated race, for reasons to be discussed immediately, the

collar does not appear in any circumstance, and the margin of the disk is broken up by deep furrows into twelve lobes, each containing seven tentacles and every two corresponding to one of the six primary tentacles. As lobulation of the disk is generally regarded as a character of generic value in the group to which *Metridium* belongs, this is a matter of some importance. It must be noted, however, that the lobulation is not a permanent feature of the species or even of the new race, but only occurs in specimens of the latter which have attained a large size. Probably it is brought about by the nature of the radial muscles and the thinness of the wall. It is not in any way comparable to the shallower lobulation of the disk which characterizes many Actinians, but may be of interest in considering the question of the manner in which such permanent lobulation has come about.

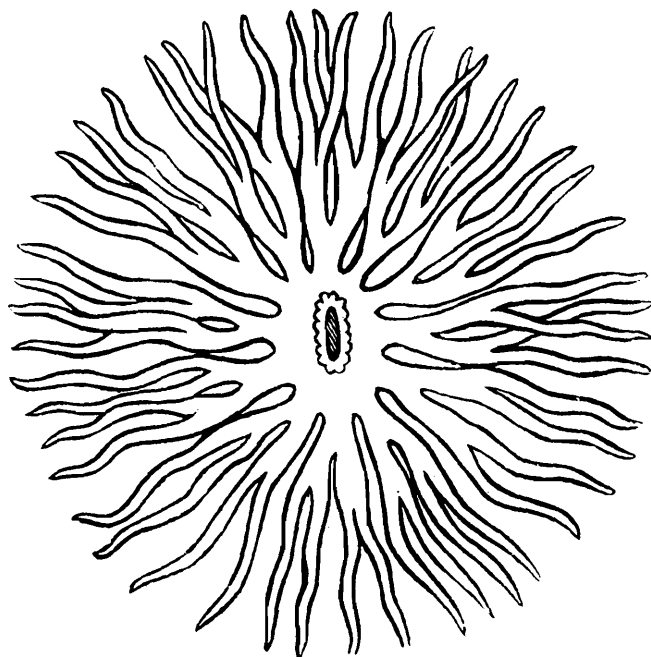


FIG. 3.—Expanded disk of *M. schillerianum* var. *exul*. from above, nat. size. Only the outermost cycle of tentacles is represented.

I have already referred to the fact that no fold makes its appearance round the disk of full-grown individuals of the var. *exul* when they are in the act of contracting, and also that contraction takes a different course in such individuals from that followed in the case of younger examples of the same variety or of either young or old examples of the typical form. When a full-grown typical individual is irritated, the whole disk is drawn downwards by the contraction of the contractor muscles, and at the same time, or a little later, the sphincter, by contracting draws in the upper part of the column above the disk, while the diameter of the disk and the length of the tentacles are reduced by contraction of the radial muscles, and the mouth is tightly closed. The tips of the tentacles are bent inwards in a broad arc. In young individuals of the variety the process

is similar, but the sphincter contracts more strongly. The space in which the disk is to be contained is therefore less, and the tentacles are forced to dispose themselves in a different manner. The outer cycles draw together in such a way that their tips are in contact or almost in contact, while the inner cycles bend downwards and enter the mouth and stomodæum. The difference between the two ways in which space is found for the bestowal of the tentacles during contraction of the disk is strikingly illustrated in bisected specimens of the two forms. In full-grown individuals of the new race, on the other hand, the tentacles and the disk are not withdrawn entirely into the column when the animal is irritated, but, after partial retraction of the disk and contraction of the tentacles, the sphincter contracts below the disk and the mouth is closed, not always very tightly. This difference is connected with a change in habits which will be discussed later.

Basal disk.—

Not the least striking difference between the two forms is that connected with the basal disk; but as in other characters, the difference in this respect is more marked in fully grown individuals than it is in the young. The base of the typical form is strongly muscular, that of the variety much more feebly so; but that of young examples of the variety resembles, in its general characters, except in the absence of a sphincter, that of the typical form. In the typical form, the main axis of the base forms a right angle with that of the column, and the edge dividing them is sharply defined. It is possible, however, for the basal disk to be extended beyond the column under certain conditions, as when the animal is stationed in a cavity the diameter of which is greater, but not very much greater than that of its column. The lower surface of the basal disk is always flat as a whole. In young examples of the new race the lower surface of the basal disk is also flat; but the edges do not appear to be extensile. In well-grown individuals of this form, however, the lower surface of the basal disk is not flat, but either concave or convex in accordance with external circumstances. In fact, it has to a great extent lost its functions as an organ of adhesion, in accordance with the change of habits already alluded to. In both forms of the species, there is a pore in the centre of the basal disk, communicating on the one hand with the coelenteron and on the other with the exterior.

In young examples of the new race there is a distinct folding of the ectoderm in the neighbourhood of the basal disk, comparable to that which occurs all over the column of the typical form; while a trace of folding can even be discovered in the former position in the adult of the isolated form. The arrangement of the inferior termination of the mesenteries is very variable in the new race, in which the two mesenteries of a pair often join together and end before reaching the centre of the basal disk, while sometimes they do not meet at all and run right to the edge of the central pore.

Mesenteries.—

The arrangement of the mesenteries in the typical form is, as is frequently the case in the family subject to many minor irregularities; but it seems to be a fixed rule in the species that only six pairs of mesenteries are complete, and that they are all, occasionally with one or two individual exceptions, fertile. The number of fertile secondary mesenteries is variable; often none of them are fertile, so that Stoliczka was right when he described specimens as having twelve ovaries. The mesenteries of the secondary cycles in this form are always smaller than those of the primary cycles, and the retractor muscles of the latter are so feebly developed that as a rule they are not visible to the naked eye. Mesenterial filaments, more or less perfect in structure, are usually present in those cases in which it is possible to recognize the retractor muscles; but some of the mesenteries, in all the specimens I have examined, consist merely of the basilar portion, with which they terminate, neither the membranous part between the proximal termination and the retractor, the retractor itself, nor the filament being represented. In the typical form of the species such imperfect mesenteries occur irregularly; in one specimen a pair was noted which seemed to represent by itself a cycle of which the other mesenteries were absent. In the new race, on the other hand, it is the rule for all the mesenteries except the six primary pairs to be in this rudimentary, or possibly vestigial condition. Only exceptionally do any of the secondary mesenteries bear retractor muscles, filaments or gonads. This condition of affairs considerably increases the lumen of the coelenteron, which is further enlarged by another peculiarity namely the thinness of the mesoderm in the mesenteries. In the typical form of the species, this layer rather increases in transverse diameter as it juts out into the mesenteries, and maintains a proportionately considerable breadth the whole way between the basilar and retractor muscles. In the new race, however, although it bulges out and takes on a dendritic form in the region in which it supports the basilar muscles, it decreases greatly in thickness between the distal extremity of the latter and the base of the retractors. Indeed, to such an extent is this the case that in what may be called the membranous part of the mesentery, the mesoderm appears in transverse sections as an extremely delicate filament. There are, of course, differences in the transverse diameter of this layer, so far as the mesenteries are concerned, in different regions of the column; but the differences just described are very much more conspicuous than any of a local nature.

Both internal and external mesenterial stomata are present in both forms.

The structure of the mesenterial filaments calls for no special remark either as regards the species as a whole or as regards the two forms thereof. It agrees closely with that which has been described by O. and R. Hertwig (3), and subsequently by others, in the cases of different members of the Sagartiidæ. The only points in

which these organs appear to exhibit specific interest so far as *M. schillerianum* is concerned, are the extent and number of the folds into which they are thrown both horizontally and vertically, and the great length of the acontia. I can detect no difference, except those already noted, as regards the structure of the mesenteries in the two forms of the species.

Gonads.—

The nature of the gonads in this species is interesting. In most

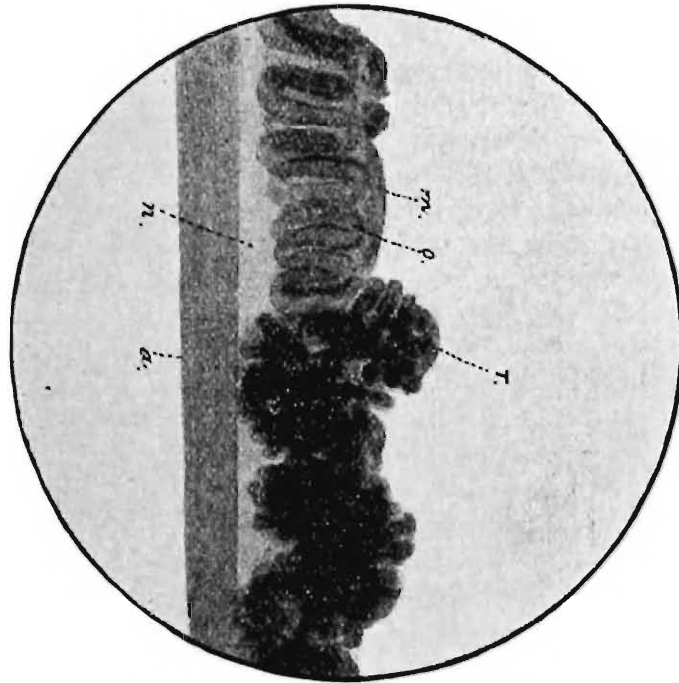


Photo by L. L. Fermor.]

FIG. 4.—Part of the mesentery of *M. schillerianum* var. *exul*, from a preparation in canada balsam, highly magnified. *m* = mesenterial filament; *t* = unripe testis; *o* = ovary; *n* = membranous part of the mesentery; *a* = retractor muscle.

of the Actinians one or other of two conditions is found—either the male and female organs are borne by different individuals, or the two are borne in the same part of the same mesentery of one individual, one sex generally taking precedence in time of the other. In *M. schillerianum*, however, neither of these conditions prevails. In specimens of the variety examined at the beginning of December, only ovaries (which were present in all individuals measuring more than about 15 mm. in length) could be found; they occupied the distal part of the mesentery, extending from the lower extremity of the stomodæum vertically downwards as far as the point at which the structure of the mesenterial filament first underwent a change. Their position on the complete mesenteries corresponded exactly, therefore, with that of the part of the filament which was trilobate in transverse section, and their lower extremity was situated exactly opposite the point at which the ciliated tracts of the filament disappeared. The lower part of the coiled portion of

the filament, on the other hand, corresponded with a region of the mesentery containing, at that date, cells with all the characters of sexual cells but as yet of an indeterminate nature. These cells were situated at the base of the endoderm covering the mesentery. The ova were already far advanced in the part of the mesentery occupied by the ovary, and this part of the mesentery had lost its purple colour; but the lower part, below the ovary, was still of a very deep purple. The structure of the ovary closely resembled (except that the whole structure was strongly folded) that of the ovary of *Calliactis parasitica* as figured by O. and R. Hertwig (3). In specimens of the new race of *M. schillerianum* killed in January, however, the condition of the gonads had altered completely. The upper part of the mesentery was now devoid of ova and was thin and colourless; the lower part, in which the indeterminate sexual cells had occurred in other individuals a month earlier, was now distended with spermatozoa arranged in approximately quadrangular follicles. Although they were already ripe, the development of the testes had not destroyed the purple colour of this part of the mesentery. The structure of the organs was identical (except for a folding similar to that of the ovaries but even more marked) with that of the testes of *Calliactis parasitica*. In a few individual mesenteries the testes appeared to have invaded that region which had been previously occupied by the ovaries, but the two regions were as a rule distinct, and corresponded to those parts of the mesenterial filaments which I have referred to above. In individuals killed towards the end of March the gonads were again in the same condition as in those killed in December.

Stoliczka states that the eggs have a chitinous covering when emitted, and that there is a dark layer beneath this covering. If his statements are correct, both these structures must come into existence at a very late stage of development, for ova which appear to be of nearly full size show no trace of either. The spermatozoa, as Stoliczka noted, have a round head and a tail of somewhat moderate dimensions. In the testes they are arranged with their heads pointing outwards towards the endoderm which encloses them, and it appears that the movements of their tails prove sufficient to drive them through this endoderm, probably between the cells. Stoliczka's specimen, which threw out part of the gonad, was evidently living under unfavourable conditions, and the process appears to have been pathological. In individuals of the form he described living in my aquarium the gonads degenerated altogether. These individuals were obtained, together with others which were killed and dissected, in the Matla estuary at the beginning of January. The gonads of those which were examined were, at that date, in exactly the same condition as examples of the isolated race from the ponds.

Skeleton.—

In his account of the species Stoliczka stated that it was remarkable in the possession of a skeleton consisting of both calcareous and silicious elements. I have examined both his own

specimens and fresh ones, in order to be in a position to discuss this skeleton ; but in vain. All that I find is that in some of the individuals examined the cœlenteron is to some extent lined with extraneous particles of silica, which also occur in the mud of the ponds and estuary, and that these particles have occasionally been taken into the cells of the endoderm or even into the mesoderm. It is well known that many Actinians protect themselves by absorbing solid extraneous particles in this way, *e.g.*, the Indian species *Myractis tubicola*, Haddon (6). The calcareous spicule figured by Stoliczka looks very much like that of an Alcyonarian, and some of my specimens of *M schillerianum* var. *exul*, which were taken from the canals of a Sponge, contain undoubted sponge spicules.

Colour.—

Such coloration as the two forms of the species possess is practically identical and is due to three factors ; two of these can be readily explained, while the origin of the third is still obscure.

The most general cause of colour is the presence of zooxanthellæ in the cells of the endoderm of the column and tentacles and of the ectoderm of the stomodæum. These bodies agree in form and structure with those found in other Actinians. In the new race of *M schillerianum*, and probably also in the typical form, they are not always present. I found at Port Canning in December that they were fairly abundant in individuals from one of the ponds, but were absent from others living in a second pond only divided from the first by a narrow bank. At the same time they were very abundant in examples of the typical form from the estuary ; they became far less numerous in the course of a few weeks in the same individuals, which were placed in an aquarium, but again reappeared in large numbers in their tissues before two months were past. The distribution of the zooxanthellæ in the tissues was found to be by no means constant. In individuals living buried in mud it was not surprising to find them practically confined to the tentacles and the upper part of the column. They were also noted occasionally in the mesoderm and even the ectoderm of these regions, and I have seen them on several occasions, as did also Stoliczka, in the cloud of slime and stinging threads shot out from the external surface when the animal was irritated. In the last instance there can be little doubt that they had been squeezed out accidentally. In individuals of the typical form they are as a rule more numerous in the endoderm underlying the sphincter and in that lining the interseptal spaces than elsewhere. They are not altogether absent from the intraseptal spaces, but are sparsely scattered in the cells. To this fact is due in part the presence of the semi-opaque vertical stripes which, in the typical form, represent the intraseptal spaces externally ; but the difference between the character of the endoderm of these spaces and that of the interseptal ones is also, to some extent, responsible for this element in the coloration. In the pond race, the scarcity of zooxanthellæ in the column renders the

wall of this region more transparent and makes it possible to distinguish the position of the mesenteries externally. The zooxanthellæ are always more numerous towards the distal end of the endoderm cells than at their base, from which, indeed, they are practically absent.

The second factor is not very important so far as coloration is concerned. It consists of irregularly shaped solid particles and globular masses of liquid, both very minute, occurring in the cells of the ectoderm of the stomodæum and the endoderm of the mesenterial filaments. Other particles, possibly of an excretory nature and of a shining white colour, are present in certain cells of the endoderm of the tentacles, giving rise to transverse bars. I can find no confirmation of Stoliczka's statement that these bars are due to accumulations of nematocysts, for nematocysts are equally numerous throughout the ectoderm of the tentacles. When zooxanthellæ are absent from an individual, the solid particles and liquid globules in the mesenteries and stomodæum give these organs a faint pinkish tinge during life. There can be little doubt that such intracellular accumulations of matter are direct products of metabolism.

The third factor is the cause of the purplish colour noted by Stoliczka in the mesenteries of the typical form, and equally conspicuous in some individuals of the new race, but not always present either in the typical form or the other. If any part of the endoderm of an individual with purple mesenteries be examined microscopically, it will be seen to contain numerous bodies of a deep violet colour. With the aid of a fairly powerful objective such as Zeiss' apochromatic D these bodies will be seen to vary considerably in shape and size and each to be enclosed in a green and apparently structureless capsule, the colour of which does not disappear in spirit. An oil-immersion lens is necessary to throw any light on their structure, and even under the highest powers they are minute. Under favourable conditions each body can, however, be seen to contain a large number of smaller, densely pigmented spherical structures, evidently spores, surrounding a colourless central core. I have not succeeded in investigating the structure of the spores owing to their minute size and to the fact that their dense pigmentation is extremely stable. The capsule is pear-shaped or subspherical in most of the bodies, but in the largest its outline becomes irregular; in some cases it is no longer intact and the spores are scattered round it. An examination of a considerable number of sections and other preparations has elicited the following facts as regards these violet bodies.

After the spores have been set free among the cells of the endoderm, they increase in size, and a small, comparatively clear circular space appears in the middle of each. In the centre of this space is a dot so minute that I have not been able to make out its structure. At first it is difficult to ascertain the nature of the envelope in which each of the spores is enclosed, but after they have increased slightly in size it is possible to see that each lies in a capsule resembling that of the parent but exceedingly delicate and only

faintly tinged with green. At a slightly later period the capsule commences to bulge out at one pole, and finally forms a projection which may be either pointed or blunt at the free extremity, and is nearly as wide as, and several times as long as the body to which it is attached. It is apparently hollow, and a slight fold or constriction in its wall can generally be detected a short distance from the proximal end. The coloured contents of the capsule are still confined within their original limits, and as yet show no sign of subdivision. The main part of the capsule next increases in size and its contents split up, apparently by fragmentation, into numerous smaller bodies resembling the spore from which the whole structure originated but rather less minute, a colourless residue remaining. Some of these smaller bodies make their way into the hollow projection, and the main part of the capsule gradually becomes less distinct from the projection, which increases in girth; so that the whole structure assumes a pear-shaped or subspherical outline. During this process the products of division divide and become smaller by subdivision. Finally the capsule ruptures and a new generation of spores is set free.

It is obvious that much further study would be necessary before it would be possible to give a name to these violet bodies, and such study would have little bearing, so far as it is possible to see, on the subject of this paper. All that can be said is, that they appear to represent an asexual cycle in the life-history of some minute alga. It is of interest to note that if they are not phases of the same organism as the zooxanthellæ, two symbiotic, or at any rate inquiline, organisms occur together in the inner tissues of the same Actinian.

The position of the violet bodies in these tissues is practically the same as that of the zooxanthellæ, except that the former are inter-not intracellular. They are not, however, sufficiently numerous in the column to give a visible colour effect, and even in the mesenteries, in which they are far more numerous, they only colour the thin membranous part. Stoliczka believed that the deep purple, often seen in the region of the gonads, was directly due to the sexual products. So far from this being the case, I find that when the ovaries are ripe or nearly so, they lose their colour almost completely. The loss of colour, however, is due not to the entire disappearance of the violet bodies, but to the fact they are more widely separated from one another as the eggs increase in bulk and so stretch the endoderm in which the bodies are scattered. It is possible, however, that the growth of the eggs has some direct effect on these bodies, which are so scarce in the spent ovaries that the mesenteries have little colour in this region after the eggs are set free. I have not seen an immature individual with purple ovaries, and the violet bodies are always absent from the acontia.

From what has been said it is clear that neither form of *Metridium schillerianum* owes its coloration to pigment produced by its own metabolism. In both forms the colours are due to independent or semi-independent organisms, and the difference of distribution

of these organisms in the bodies of the Actinians is probably connected with biological differences in the hosts.

BIOLOGY.

Relations to environment.—

Stoliczka found the original specimens of the species living attached to logs of wood ; he therefore suggested that they should be called *Lignacalephæ*. I have recently found specimens of the typical form ensconced in the dead shells of barnacles fixed to iron posts in the Matla estuary. Stoliczka noted that the species, as he knew it, frequently inserted its basal disk into cavities in the logs to which it attached ; both in the case of my specimens and of his, the basal disk was extended somewhat beyond the periphery of the column to cover the base of the cavity in which the animal was stationed. In circumstances in which it is impossible for the Actinian to protect itself by entering a cavity already formed, for example when it is in a glass vessel, it constructs a protecting sheath for itself out of such objects as filaments of the algæ which grow in its natural habitat. This habit has been exemplified by individuals of both forms recently living in captivity in Calcutta, especially by fully grown individuals of the typical form and by young individuals of the new race. I was able, in the case of one example of the latter, to observe the production of the sheath. The animal had been removed from the aquarium and placed in a watchglass full of water, and was being examined under a fairly high power of the microscope. After a few minutes of complete contraction its column grew slightly longer and at the same time a large number of stinging-threads were emitted from the upper part of this region of the body. These were of simple structure, devoid of barbs. They did not remain still after being set free, but displayed a rapid corkscrew motion closely resembling that of many spermatozoa and were thus carried through the water for a short distance round the Actinian, from which they did not recede. A quantity of mucus was also secreted from the exterior of the column. The rapid movements of the threads did not last for more than a few minutes, but, as they ceased, the threads became matted together with the slime, which retained any extraneous substances that chanced to come in contact with it. Larger examples of the new race, examined as they were taken, had particles of the mud from which they had been removed adhering to them, probably for the same reason ; but in all cases the external coating thus formed was of an extremely evanescent and flimsy nature.

As I have already pointed out, there are few solid bodies at present to be found in the ponds at Port Canning. I have searched them in vain for specimens of the typical form of the species, which was living in one of them thirty-nine years ago, when the logs of wood were there. Representatives of the new race now abound, however, in the ponds, with the exception of the two

ponds nearest the railway station, both of which are used by the people of the settlement for such purposes as washing domestic utensils and clothes. (There is at Port Canning one large pond which is only separated from the brackish ones by a few hundred yards and yet contains fresh water; but as the fauna of this pond is of normal character and does not include marine elements, I have not referred to it hitherto and need not do so again.)

Although the typical and the new forms of *M schillerianum* are alike in producing a temporary sheath of matter secreted by their own cells and mixed with extraneous substances, the new form is not in the habit as a rule of attaching itself by its base to the few inanimate solid bodies to be found in the ponds. *Spongilla cerebellata*, however, often occurs in masses of considerable size in the ponds, and in its canals I have found enormous numbers of young individuals of the Actinian. In the majority of cases these were situated in such a way that their long axes were parallel to those of the canals, to the walls of which they adhered by means of the external surface of their columns. In some cases, however, their basal disks were attached to the shells of small Lamellibranchs (*Corbula* spp.) which also frequent the canals of the Sponge. In situations in which no Sponges were present, the young of the Actinian were generally found attached to the filaments of algæ which formed more or less dense cloud-like masses, and many were also found among the matted roots of grasses. None, however, were found attached to the stems or branches of upright plants such as *Naias*, and it was clear that among the algæ and grass roots a considerable amount of lateral support was given them. When they were placed in a vessel of water without any such artificial support, they proved able to adfix themselves to the bottom by their bases and to stand upright with fully expanded tentacles. In this position they closely resembled the young of the common European *Sagartia troglodytes* and could only be distinguished from small examples of the typical *M schillerianum* by the greater elongation of their columns and by the thinness of the walls of this region—a feature quite apparent owing to the transparency of the tissues, which permitted the exact position of the internal organs and the movements of the acontia to be observed with ease. Individuals even in this stage, however, rarely lived for long in an aquarium, and at once gathered round them filaments of algæ.

The full-grown individuals of this new race were invariably found buried in mud, in which they were sunk as far as the base of the tentacles, and into which they retreated completely on being disturbed. When removed from the mud their long, vermiform columns were unable to support them in an upright position, and they lay in a glass vessel with their main axes parallel to the bottom, but with the extreme distal end of the column slightly curved upwards. Their attitude and appearance were in fact closely similar to those of many species of *Cerianthus* in similar circumstances. And yet every intermediate stage was to be found

between the typical *Sagartia*-like young and the *Cerianthus*-like adult, while the internal anatomy, allowing for differences due to maturity, was found to be identical in large and small individuals. Moreover, although the basal disk had almost disappeared, it had not altogether lost its function as an organ of adhesion, for many large individuals dug from the mud were found on close examination to be adherent by their bases to shells and other small objects. In preserved specimens it would often appear on superficial examination that the basal disk is in much the same condition of atrophy as it is in *Edwardsia* and other burrowing forms, but in living examples it is always clear that this is not the case; in fact, a distinct disk is present (plate iii, fig. 3), but it is relatively small and in other respects degenerate.

Stoliczka noted that the typical form of the species was able to survive exposure to the sun out of water for some hours—a phenomenon which has been recorded in other Actinians—and I am able to confirm his observation. When exposed at low tide the animals remain with their tentacles extruded, and the whole organism has a particularly flabby appearance. A close examination of living specimens under these and other conditions, and a comparison with dead and carefully preserved material, enables me to suggest a reason for the powers of endurance possessed by the typical *M schillerianum*; possibly this explanation will be found to apply to other species also. I have already remarked on the comparatively thin walls of the column of the new race of *M schillerianum* as compared with those of the same part of the body in the typical form of the species, and on the fact that it is possible to gauge the thickness of the wall in small living specimens of the former owing to its transparency. The wall of the column in the typical form is usually less transparent than it is in the variety, owing to the large number of zooxanthellæ present in the endoderm; but this very fact makes it possible to estimate the extent to which the thickness of the wall is due to the layers other than the endoderm. This can be done most easily by watching an acontium which is being thrust out of one of the cinclides. It is not difficult to see that the thin white thread has to traverse a considerably greater extent of transparent tissue outside the coloured endoderm than could be accounted for if the thickness of the ectoderm and mesoderm seen in a transverse section of a preserved specimen were the same as the thickness of these same layers during life. The shrinkage, which is inevitable in preserved specimens, is very much more marked in the case of the typical form than in that of the pond race; it is less evident, in the case of the former, if specimens are killed and preserved in weak formol than if they are treated with reagents, such as corrosive sublimate and alcohol, which give a more satisfactory result as regards cellular histology. The reason for this apparently is that an aqueous solution of formol while causing intense muscular contraction during life, does not dehydrate the tissues after death. If a specimen of the typical form which has been preserved in formol be cut in two

with a razor, so as to disturb the tissues as little as possible, it will be found that the ectoderm is not closely folded as it is in a specimen preserved in spirit or even in one which has been killed in formol and then dehydrated in alcohol and embedded in paraffin; but that there are large spaces between this layer and the mesoderm, the two layers being only in contact at widely separated points and there being a considerable amount of liquid enclosed between them. The same condition, but not nearly to the same extent, will be found to exist in young individuals of the new form, while, except in the lower part of the column, it will not be detected in full-grown examples of this form. In the neighbourhood of the basal disk of these, however, it exists to a slight extent. In specimens of the typical form which have been long in alcohol, as I found in the types of the species, the ectoderm shrinks very greatly (apparently more so than the mesoderm does) and therefore comes to be nearly smooth again, lying parallel to the mesoderm. From these considerations I conclude that there is naturally a layer of water between the ectoderm and the mesoderm in the typical but not in the new form of *M. schillerianum*—there are traces of it even in the adult, and much more clearly in the young, of the latter—and further that the folds of the ectoderm which are so striking a feature of this layer in sections of the typical form (plate iii, figs. 5, 6) of the species, are artificial.

As to the function of this layer of water, which is confined to the column: I would suggest that it is to enable the Actinian to endure exposure to the sun out of water. The form is one which haunts tidal waters and, as Stoliczka noted, has a great tendency to maintain its position near the surface and to return to that position if removed from it. In the small cavities in which it is frequently found ensconced, a certain amount of water remains when the object in which they occur is left dry as a whole by the retreating tide. If the animal is able to make use of this water by drawing it into its body, as it may do by means of the cinclides, the habit of living in such cavities must benefit it in more ways than one. My reason for saying that it is possible that other species make use of subectodermal spaces in the same way as the typical form of *M. schillerianum* is that I have observed in specimens both of this form and of *Sagartia troglodytes*, *Actinia mesembryanthemum* and other British species (especially when they are living under unnatural conditions in foul water) that blister-like projections appear on the column, most commonly towards its base, and that in the case of the Indian form these projections, which remain in specimens preserved in formol, are due to accumulations of liquid below the ectoderm. It is difficult to make observations as regards the exact relation of one layer of the body to another on living material, for the whole organism is so highly contractile that such relations are distorted immediately on the application of a sharp instrument to the external surface; but water certainly exudes in considerable quantities from the wall of the column of a living example of the typical *M. schillerianum* which is cut with a razor.

The pond race of the Actinian is not subject to the same periodical exposure as the typical form of the species, for under ordinary conditions it lives beyond the reach of the tides. It is, however, exposed to gradual changes in the salinity of the water to which it is restricted. To what extent it is able to survive such vicissitudes is still uncertain¹; if Stoliczka is right as regards the chitinous nature of the membrane which covers the egg of the typical form, and if the egg of the pond race has a similar covering, the egg is well fitted to withstand chemical changes in the environment, and even desiccation. Adults of the pond race are able to live for some hours lying on the ground exposed to the sun. Under such conditions their behaviour is totally different from that of examples of the typical form. I have found individuals of moderate size lying on the mud at the edge of a tank. Their tentacles were completely retracted and the sphincter was tightly closed; their columns were, however, distended with water, which was contained in the coelenteron.

Under natural conditions both forms of the species are diurnal in habit, the typical form remaining with its disk fully expanded when exposed to the direct rays of the sun. The new race, however, is usually found below or among floating algæ according to its age, and these provide considerable shade. Young and half-grown individuals in my aquarium became practically nocturnal after a few days' exposure to bright light in a glass vessel. At night and early in the morning they expanded their tentacles, which were withdrawn as soon as the day became warm (*cf.* Fleure and Walton (12), p. 217). Individuals of the typical form living under identical conditions exhibited a similar tendency, but to a less marked degree; full-grown examples of the race never lived for at most more than three days in these conditions. Young examples of this form showed less power of resistance to the unnatural conditions of a small aquarium than did adults of the typical form, the latter living for over three months in water which was always kept of the same salinity, while those from the pools, in the same vessel, as a rule died in about a fortnight. The water in which they were, was taken from one of the ponds at Port Canning and was brought to Calcutta in a stoppered bottle.

Movements.—

Notwithstanding what appears to be an avoidance of bright light in the case of the variety, neither form of the species exhibits any marked heliotropism, negative or positive, in its movements. When individuals are placed in a glass vessel lighted from one side, they remain, other conditions being suitable, where they are placed, neither moving towards the light nor away from it. Stoliczka noticed, however, that his specimens showed a tendency to move upwards towards the surface of the water, and I find that mine prefer

¹ Almost at the end of the hot weather, the Actinian is still abundant in the ponds. May 27th, 1907.

to become stationary on the sides rather than at the bottom of the aquarium, unless they are given empty shells, in which they ensconce themselves at the bottom.

Both forms possess considerable powers of progression, but they do not habitually move in the same way. The only method I have seen the typical form adopt is that observed by Stoliczka *viz.*, by crawling slowly on the basal disk along a vertical or horizontal surface. This method of progression is effected partly by alternate contractions and expansions of the disk, and partly by a copious secretion of very tenacious mucus from the glandular cells which abound on this disk and round the base of the column. It is a slow and feeble one, as it generally is in Actinians; Stoliczka records that a specimen in his aquarium moved 7 inches in 24 hours, while one in mine took three days and nights to move half the distance.

Possibly the young of the pond race may adopt the same method of progression occasionally, but as a rule they drag themselves along by their tentacles—a much more rapid method. A tentacle is stretched out to its greatest length, until it becomes filamentous. Some part of its surface is then applied to a fixed object, and a gland cell in the neighbourhood secretes a drop of mucous secretion, which fixes the tentacle to the object. The tentacle thus fixed contracts, dragging the whole animal forward as it does so; the strain on its surface being considerable, the cells in the neighbourhood of the gland are drawn out into irregular projections at the points at which they are held by the mucus. Lately I have observed the same phenomenon in the tentacles of *Hydra*, and I have little doubt that this is the true explanation of Zykoff's statement that the ectoderm cells of the tentacles of *Hydra* put out pseudopodia which are used in progression (*Biol. Centralblatt.*, xviii, p. 272, 1898). When the tentacle is dragged away after a forward movement of the organism, the false pseudopodia naturally appear in an exaggerated form; they are not due directly to movements of the protoplasm of the cells, but to a mechanical strain on the external surface of these cells. I have been able to observe this method of progression in the case of very young individuals of the Actinian under a fairly high power of the microscope. Although the tentacles play in it the most important part, the walls of the column are also adherent to the surface along which the animal is travelling, and if it is moving vertically up the walls of an aquarium, as I have occasionally observed it to do, the "suckers" can be seen to be applied to the glass very closely. They do not appear to be at all markedly concave on the surface, however, as would be the case if they actually functioned as suckers.

In addition to this mode of progression with the aid of the tentacles and the surface of the column, individuals of the variety exhibit, at all ages, strongly marked muscular movements of the column wall. It is evident that the separation of the circular muscle of this region into separate circular strands is physiological as well as anatomical, for it is possible for each strand to contract independently of the others, so that the column appears just as though an extremely

fine thread were drawn tightly round it at one point (see plate iv, figs. 3, 4). Although any one of the strands can contract in this way without affecting the others, I have observed under the microscope that they very frequently contract rhythmically and in regular succession from below upwards. What happens is this: The pore in the centre of the basal disk is opened and water is drawn into the lumen of the disk, which becomes bulbular, the circular muscle strands at the base of the column being strongly contracted above it. Then the pore is closed, the lowest muscle strand relaxes and the second one above it contracts. Then the second strand relaxes and the first contracts again, and, as the process is continued up the column, the water is gradually driven up towards the mouth, just as though it were being squeezed upwards in an indiarubber bag by drawing tight and loosening in regular succession a series of elastic rings. I have little doubt that it is by such means that the Actinian is able to rise to the surface again after it has sunk into the mud; but I have only been able to observe such movements in the case of young individuals which had not yet begun to burrow. In their case the movements assisted them in making their way through a tangled mass of alga filaments. The foot of adult individuals of this variety is probably used for burrowing, aided by contractions both of the circular and the retractor muscles; but owing to the difficulty experienced in keeping such individuals in a healthy condition after they have been removed from their natural habitat, I have no direct observations to offer on this point. When large individuals are removed from the mud, the contractions of the column which take place are very marked, but entirely lack co-ordination.

Food.—

Judging from dissected specimens, the food of the pond race consists very largely of minute univalve Molluscs, the shells of which are ejected after the animal has been absorbed, and of small fish such as *Haplochilus melanostigma* and *Gobius alcockii*. Stoliczka found that the typical form eat Crustacea in captivity, but I have no information as to its natural food.

RELATIONS OF THE VARIETY TO THE TYPICAL FORM.

In order to make this question clear it will be well to commence its discussion by summarizing the resemblances and differences between the two forms (*a*) as regards their physical structure, and (*b*) as regards their habits.

Physical resemblances between the two forms.

1. The coloration is practically identical.
2. The arrangement of the tentacles and mesenteries is the same.
3. The position of the circular and radial muscles is the same.
4. The structure and nature of the gonads are the same.
5. The retractor muscles are closely similar.

6. The outline of the sphincter is almost the same.
7. The number and position of the mesenterial foramina are the same.

Physical differences between the two forms.

1. The column is much longer in the variety than in the typical form.
2. Its wall is thinner during life.
3. There is one cycle of tentacles and mesenteries less in the variety than in the typical form.
4. A larger number of mesenteries are usually rudimentary in the variety than in the typical form.
5. The mesoderm of the mesenteries is thinner in transverse section in the variety than in the typical form and a larger number of mesenteries are degenerate.
6. There is no basal sphincter in the variety.

In these lists only the resemblances and differences which appear to be constant throughout life are noted. The following are differences which are only apparent in full-grown individuals :—

1. There are no muscle spaces in the sphincter of the typical form, while these spaces occur in small numbers in the adult of the variety but are absent in its young.
2. The adult of the variety is unable to withdraw its tentacles into its body, while the young of the same form and the adult of the typical form can do so.
3. The adult of the variety is unable to stand upright on its base, while the adult of the typical form and the young of the variety can do so.
4. The disk of the adult of the variety is broken up into lobes; but this is not the case in the young of the same form or the adult of the typical one.

Biological differences between the two forms.

The habits of the two forms are totally unlike. The typical form lives in tidal waters, attached to solid objects; but it was also found formerly in an isolated pond. The variety is apparently confined to isolated ponds, the water of which sometimes contains as little as 0·22 % of soluble solids; the young live among grass-roots and filamentous algæ, or in the canals of Sponges, the adults buried in the mud. Individuals of the typical form can live in water of the same salinity as that of the isolated ponds in which the variety occurs but are not now found in these ponds, from which the solid objects to which they were formerly attached have disappeared. The movements of the variety are more active than those of the typical form, in accordance with the different mode of life adopted.

The most striking differences externally visible between the two forms are the great relative length of the column and the

degeneracy of the basal disk in the pond race. I do not know of any other form of the genus in which these characters are so strongly marked; but many instances among the Actinaria could be adduced in which there is a considerable tendency to variation as regards them. Anyone who has observed living examples of the common British *Sagartia troglodytes* from different parts of the country, or even from different situations in the same locality, must have been struck by the differences they exhibit as regards the form of the column and the relative proportions of its base. Those individuals which have been extracted from small crevices in rocks have a long, thin column and a base with a small transverse diameter, while those from pools with smooth bottoms are short and squat. In Gosse's *History of the British Sea-Anemones* (1) figures are given of the species in the latter condition. As regards outline at any rate, these figures are accurate; but they are as unlike as they could well be to some individuals I have seen. Moreover, I have noticed that in such cases the column cannot adapt itself, except to a limited extent, to new conditions, even although the individuals may be kept alive for many years in captivity. Those individuals which have been living in small round holes such as are a favourite station for the species, cannot assume the depressed conical form that characterizes those which have been fixed to a smooth surface; but those which have been taken from the latter situation are able to elongate their columns considerably and to draw in the projecting margin of their bases. In other British species differences, which may be local, have been recorded, e.g., Dixon (5) states that specimens of *S. nivea* from the east coast of Ireland are much longer and more attenuated than those described from Torquay, on the south coast of England, by Gosse. From Indian seas Alcock (7) has described a variety of *Sphenopus arenaceus* in which the base of the column is drawn out into a relatively long and narrow peduncle.

In none of these cases has the basal disk become degenerate to the same extent as it has done in the tank form of *M. schillerianum*, for there is no basal disk in the genus *Sphenopus*; but in other respects the variation seems to be of a similar nature. It must be remembered, moreover, that there is a great difference, in respect to the condition of the base, between the young and the adult of *M. schillerianum* var. *exul*, as well as in respect to the proportions of the column. It must further be borne in mind that this Actinian lives in a medium the chemical constitution of which is different from that of the medium proper to its class, and there is very good reason to believe that a chemical stimulus may be a powerful one in matters of variation. The particular direction which evolution has taken in respect to this isolated race, moreover, is one which has not been uncommon in the history of the sub-class to which *M. schillerianum* belongs, for we get forms as distinct from one another morphologically as *Edwardsia*, *Cerianthus* and *Peachia* all adapted in a similar manner to become burrowing animals, and

all in consequence having a considerable external resemblance both to one another and to the form under consideration.

The differences which the two forms of *M. schillerianum* exhibit as regards their muscles and mesenteries are perhaps of more importance, from the point of view of the systematist, than the differences in the general appearance and shape of the animals. The muscular differences, however, all seem to be what may be called rather dynamical than morphological. The position of the muscles as regards the layers of the body is identical in the two forms, but in var. *exul* they appear to have become strengthened in certain directions and weakened in others, in accordance with a complete change in the mode of life. Although the mesoderm of the mesenteries is much thinner in the new than in the typical race, and the secondary mesenteries are in a much earlier stage of development as regards their whole form and structure, I think that a similar explanation is possible, for this change is, like that of the muscles, one of development. The mesenteries have not evolved new characters in the isolated race but remain throughout life in a condition through which they pass at an early age in the typical form, and it is obviously a convenient condition as regards the bionomics of the race. This explanation does not quite apply to the thinness of the mesoderm in mesenteries which are just as long as they are in the typical form of the species; but seeing that one of the most striking biological modifications of the isolated race is the use to which it puts the liquid contained in its coelenteric cavity, it is not difficult to see that the pressure of this liquid must have, in the case of the individual, considerable influence on the growth of the mesenteries.

It is noteworthy that those structures which have the same function in the two forms have undergone very little change in the isolated race. This is particularly true of the tentacles and stomodæum. Indeed, the last-named structure offers so little of interest in connection with the special line of study embodied in this paper, that I have barely referred to it except in the brief systematical description of the two forms. I ought to say, however, that while it is actually longer in the case of a full-grown example of var. *exul* than it is in one of the typical form of the species, the elongation is by no means proportionate to that of the columns as a whole. The reduction in the number of tentacles and mesenteries exhibited by the isolated race, is clearly related to its narrow, elongated form.

In dealing with the question of the modifications which the Actinian of the Port Canning ponds has undergone, it is not by any means easy to apportion the degrees in which these modifications have affected (a) the individual and (b) the race. It is known that individuals of the same family (e.g., in *Sagartia troglodytes*) have lived for over fifty years (see Ashworth and Annandale [9]), but such instances, as Hickson (II) has recently pointed out, are only known in the case of captive specimens, which have received regular food and lived a sheltered life. Considering the

vicissitudes to which they are exposed in the ponds at Port Canning, it is very improbable that any of the individuals now living in these ponds have survived for so long a period, while the presence of numerous young in the ponds and of ripe gonads in the adults proves that we are dealing with a race and not merely a collection of infertile individuals. The modifications are undoubtedly less marked in the young than they are in their parents, between which and the typical form the young are intermediate. This is true as regards biological as well as structural characters. The youngest individuals of the typical form I have seen (measuring about 4 mm. in height) have had a considerably shorter column than examples of the isolated race with disks of a smaller diameter.

Variation has been little studied in the Actinians, which do not make satisfactory specimens either for the museum or the laboratory; but the stony corals, in which the skeleton preserves in many respects a complete diagram of the living tissues, prove how variable certain genera and species of *Zoantharia* can be (for example see Bernard on *Porites* in the *Catalogue of the Madreporarian Corals in the British Museum*, vol. v, 1905). I doubt whether Gosse was so far from the truth as later systematists believe him to have been when he laid stress on the importance of the study of the living organism in the case of the Actinians. It is worthy of note that, at any rate as regards the *Sagartiidæ*, the descriptions of genera have recently shown a tendency to become more rather than less indefinite. Compare, for example, Hertwig's (4) definition of *Sagartia*, published in 1882, with Haddon's (8), published in 1898, or with McMurrich's (10), published in 1905, having regard to the fact that these authors are in substantial agreement as to the species which should be included in the genus. As the three diagnoses are short, they may be quoted in full :—

“ *Sagartiidæ* with smooth walls and numerous powerful tentacles arranged in several rows; with circular oral disk; without anatomically perceptible cinclides.” (Hertwig, 1882.)

“ *Sagartiinæ* with a smooth body-wall, or with small verrucæ in the upper portion of the column; moderately long tentacles in several cycles around the margin of the oral disk, which is not greatly expanded.” (Haddon, 1898.)

“ *Sagartiinæ* with the column smooth or provided with verrucæ in its upper portion; cinclides more or less scattered; acrorhagi wanting; margin not lobed.” (McMurrich, 1905.)

The diagnoses of the family and sub-family given by these authors are still more diverse, but the point I wish to bring out is the way in which various descriptions illustrate the necessity felt by recent authorities for broadening the diagnoses of Actinian genera.

Granted that *Metridium schillerianum* var. *exul* is an isolated race of the species to which I have referred it, it still remains to be discussed whether this race has become differentiated in the ponds at Port Canning, and how long the process of its evolution has taken to reach the present stage. The historical evidence on these points, although it cannot be called absolutely conclusive, is much stronger than such evidence usually is. Stoliczka's account of the typical form of the species was written in 1868 (at which date the extent and number of the ponds were probably not the same as they are today) and was more detailed than any dealing with the Sagartiidæ which had previously appeared, although it contained a number of misconceptions rather than errors of observation. Its author was a trained and cautious observer and apparently examined the ponds at more than one time of year. It is improbable that he only did so on occasions when the water had been rendered turbid by rain. Except under these conditions he could not have failed to see the Actinians, had they occurred in the ponds; nowadays they are the most characteristic feature of the fauna to which they belong, and strike even a casual observer. Native fishermen at Port Canning volunteered the information, when I asked them about the fish in the ponds, that there was in the mud "an animal just like a flower." It is unfortunate that we do not know in which of the ponds Stoliczka found the Actinian, but I suspect that it was the one nearest to the railway station. Its usage for domestic purposes has now rendered the water of this pond foul. Stoliczka said that the Actinian did not live in the other ponds at Port Canning because they did not contain logs of wood, and because their water was unsuitable. The last statement is not explained. The logs of wood no longer exist, and their place has not been taken by other solid substances to which the animals might have attached themselves. It has been shown that the race of the Actinian now found in the ponds does not attach itself to fixed bodies, but has become adapted for a burrowing life. So far as the neighbourhood of Port Canning is concerned, I feel sure that this new race is only to be found in the ponds; but our ignorance of the Actinarian fauna of the Indian seas makes it impossible to deny that an identical form may occur elsewhere. Even should this prove to be the case, however, it would not necessarily be uncritical to argue that similar causes have produced convergence among the offspring of different individuals.

However, it is perhaps better not to introduce questions of possibility; my object in this paper has been to give an unbiassed account of the differences and resemblances between two Actinians which I take to be no more than races of a single species. One of these races has been isolated in certain small ponds, in which it appears to have responded to its environment to such an extent as to have altered very considerably both its structure and its mode of life.

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(Only those works which are directly referred to in the text are noted in this list. Full bibliographies on the group will be found in papers Nos. 8 and 10, while several species are recorded for the first time from Indian seas by Southwell in Herdman's "Faunistic Results" in *Ceylon Pearl Oyster Fisheries and Marine Biology*, part v, p. 441 (1906)).