

37. Note on the Systematic Position and Distribution of the Actinian *Sagartia lucie*. By J. PLAYFAIR McMURRICH, C.M.Z.S.

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(Text-figures 1-4.)

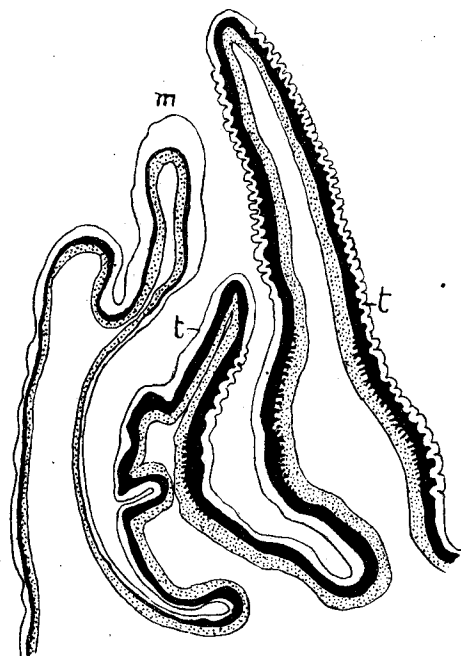
During the last twenty years the small Actinian known as *Sagartia lucie* has frequently been an object of study, and much is known as to its variations, methods of reproduction, powers of regeneration, reaction to light, locomotion, and general ecology. As yet, however, it has not been subjected to an anatomical investigation sufficiently detailed to reveal the features by which its systematic position may be determined.

It was first described in 1898 by Verrill, who gave a fairly full description of its external form and coloration, without, however, considering its anatomical structure. Later, Mrs. G. C. Davenport (1903) in a study of the variations in the number and arrangement of the vertical orange stripes, which are usually such a characteristic feature in the coloration of the column-wall, showed that reproduction by longitudinal division or by basal fragmentation was of frequent occurrence, variations in the number of the orange stripes resulting therefrom, as well as probably variations in the arrangement of the mesenteries, which, in the individuals with twelve stripes, were stated to be usually arranged in twenty-four pairs. But still there was lacking a sufficiently detailed account of the anatomy of the species to determine definitely its systematic affiliations, and other papers that have since dealt with it have not altered the situation in this respect. It may be well, therefore, to put on record some observations that were made several years ago, especially as they led to interesting conclusions not only as to the systematic position of the form, but also as to its distribution.

Concerning the disk and tentacles little need be said, further than to note the weakness of their musculature, the ectodermal fibres of the tentacles forming a simple layer on the smooth, or but slightly folded, surface of the mesogloea; on the disk they may even be absent. Between the bases of the outermost tentacles and the apparent margin of the column there is a deep fosse, which is very characteristic of the species (text-fig. 1). It is evidently equivalent to the thin portion of the column-wall that intervenes in *Metridium senilis* between the outermost tentacles and the so-called collar, this latter being the upper edge of the strong mesogloal sphincter. But whereas in *Metridium* this thin portion of the column is fully exposed in expansion, in *Sagartia lucie* it remains introverted, thus producing the characteristic fosse. The mesogloea forming its walls is very thin and smooth on both surfaces, and both the endoderm and ectoderm

are also thin, the latter containing a few scattered and almost spherical mucous glands, without distinct indication of muscle fibres. The outer wall of the fosse joins the column proper at the apparent margin, and at once a change of structure is observable. The mesogloea becomes decidedly thicker and its outer surface irregular; the ectoderm thickens and becomes richly supplied with gland cells, which, with the greater thickness of the layer, assume an oval or pyriform shape; and a weak circular endodermal musculature becomes evident. But there is no sign of a sphincter, either endodermal or mesogloæal. One would expect

Text-figure 1.



Sections through the margin and outermost tentacles of an individual from Woods Hole. *t*=tentacle; *m*=margin.

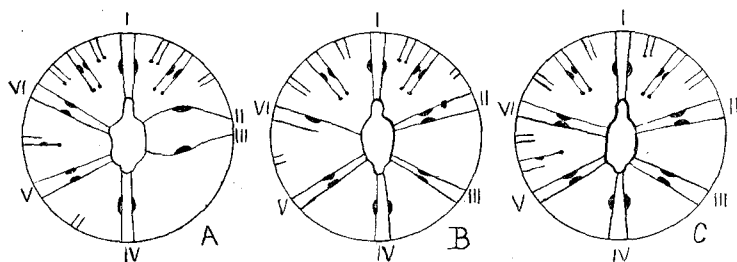
to find a mesogloæal sphincter just below the apparent margin, but in the several individuals that were sectioned I looked in vain for even traces of it.

In two particulars, then, *Sagartia luciae* differs notably from the typical members of the genus to which it has been assigned, namely, in the presence of a deep fosse and in the absence of a mesogloæal sphincter. In the one feature it shows some resemblance to *Metridium*, and in the absence of a sphincter it is

paralleled by some members of the genus *Aiptasia*; neither of these genera, however, belonging to the same subfamily as *Sagartia*.

When one comes to consider the arrangement of the mesenteries, difficulties are at once encountered, because of the tendency of the species to reproduce by longitudinal fission. Some half-dozen individuals of which serial sections were prepared all showed irregularities in the arrangement of the mesenteries that may be reasonably attributed to this process, but nevertheless, they permit of inferences as to what the arrangement may have been before fission occurred. Three individuals may be taken as examples (text-fig. 2). In each of these in sections through the middle of the column there was a deep siphonoglyph at one end of the long axis of the stomodæum, and to this a pair of directive mesenteries with well-developed muscle pennons was attached. Opposite it was a second siphonoglyph which was relatively quite shallow, and to this a second pair of directives was attached, the

Text-figure 2.



Diagrams showing the arrangement of the mesenteries in three individuals from Woods Hole, Mass.

muscle pennons of these being, however, very imperfectly developed. On either side of the fully-developed directives there were representatives of two cycles of imperfect mesenteries, and then came on either side a pair of perfect ones. So far the arrangement is quite regular except for the imperfect development of one siphonoglyph and its directives, but in two of the individuals, one member of each of the lateral pairs (II. and VI.) was decidedly less developed than the other. In these same two individuals (B and C) the pair II. is succeeded by another perfect pair (III.) poorly developed, and next this is the second pair of directives (IV.), no imperfect pairs occurring in the interspaces between II. and III. and III. and IV. Similarly, another pair of perfect mesenteries (V.) with fully-developed muscle pennons occurs between IV. and VI., and while no imperfect pairs occur in the interval between these and IV., in the interval on the other side there is in one individual a single small pair and in the

other two such pairs. These two individuals have, then, six pairs of perfect mesenteries and a number of imperfect ones disposed unsymmetrically. It is to be noted that this arrangement is that found in sections passing through the aboral half of the stomodæum; higher up, close to the bases of the tentacles, a number of additional rudimentary mesenteries may be found, but these need not be considered at present.

In the third individual (A) there were but five pairs of perfect mesenteries in sections passing through the aboral half of the stomodæum. Higher up, however, six occurred, with representatives of two cycles of imperfect ones in the intervals on either side of the fully-developed directives and in that between VI. and V., but only a single feeble pair in each of the other intervals. Following the series of sections aborally it is found that the change from the conditions showing six pairs of perfect mesenteries to that showing only five is due to the disappearance of a member of each of the pairs II. and III. together with the intervening imperfect mesenteries, the remaining members of the perfect pairs thus being brought into apposition and seeming to form a single pair.

The explanation which seems to fit these cases is that each is an example of an individual that has undergone longitudinal fission. The half of the body with the deep siphonoglyph and the representatives of three cycles of mesenteries shows the normal symmetrical arrangement characteristic of the species, and the irregularities and feeble development in the other half are indications of an attempt to regenerate the disturbed symmetry. It may be concluded that in the original individuals developed from ova there were three cycles of mesenteries arranged hexamerously, only those of the first cycle being perfect. The reproductive elements were not sufficiently developed in any of the individuals collected at Woods Hole to allow of a determination of their distribution, but in specimens collected at Plymouth it was found that they were limited to the pairs of the second and third cycles, *i.e.*, to the imperfect mesenteries. It may be added that both oral and marginal stomata occurred in the perfect mesenteries. Acontia are present, but are not abundant.

The structural features, then, that may be supposed to be characteristic of individuals that have not undergone fission are (1) the occurrence of a well-defined fosse; (2) the absence of a mesoglæal sphincter; (3) the occurrence of but six pairs of perfect mesenteries, which are also sterile, the reproductive elements being limited to the imperfect cycles. But before considering the significance of these features it will be well to consider the geographical distribution of the species.

Verrill's original description of *Sagartia lucia* (1898) was based on individuals collected in Long Island Sound. He states that his attention was first directed to it in 1892 and expresses his conviction that it did not occur in any quantity in that region throughout the period 1865-1890. Furthermore it was

stated to occur at Woods Hole in 1898, and Verrill collected there extensively during the period 1871-1887 without finding it. Parker (1902) added to these data observations on its occurrence at Newport in 1895 and at Nahant in 1899, it having been unknown in either of these localities before the dates mentioned, and he also records its occurrence at Salem, Mass., in 1901, that being apparently the northern limit of its distribution at that time. The records brought together by Parker seem to show clearly that the species has rapidly increased its distribution, at first eastward and then northward, until in ten years after it was first observed in Long Island Sound it had reached Salem. I have nothing to add to these records, except to state that in the summers of 1889 and 1890 I made special efforts to collect representatives of all the Actinian species occurring in the Woods Hole region and feel certain that, if *Sagartia luciæ* had occurred in that locality at that time in any considerable numbers, I could not have failed, as I did, to find it.

But whence did it come to Long Island Sound? Verrill suggests that it might have been brought from farther south on the shells of oysters that were annually brought north in large quantities and deposited in the waters of the Sound, and this possibility seems to find support in the following observations. In 1887 I described as *Sagartia pustulata* a form found on dead shells in shallow water in the vicinity of Beaufort, N.C. Its specific name was suggested by the appearance given to the column by the longitudinal and circular furrows that beset it, an appearance that may frequently be observed in living examples of *S. luciæ*, which form it also resembled in its coloration, except that the orange stripes of the column were lacking. This may seem an important difference, but undoubted individuals of *S. luciæ* without the characteristic stripes have been observed (Davenport, 1903; Walton, 1908). Unfortunately my preparations of *S. pustulata* are unsatisfactory and the preserved material has long since disappeared, so that I cannot determine the extent of its similarity to *S. luciæ*. This much, however, is certain, it has no sphincter; but there were only slight indications of the fosse, and it was not possible to determine the arrangement of the mesenteries. The points of resemblance shown by the two forms suggest their identity, but further observations are necessary to establish this and with it the extension of the distribution of the species so far to the south.

But the story of the distribution is far from being completed with the consideration of the west coast of the North Atlantic. Walton (1908) has placed on record the discovery at Plymouth in 1896 of a form which Mrs. Davenport later identified with *S. luciæ*. Previous to the date mentioned it had not been found in that locality, notwithstanding the extensive collections that had been made there, and from the Millbay Docks, where it was first observed, it has extended throughout the entire harbour and is now one of the common forms inhabiting the district. The

evidence points to its being an introduced form, possibly from the other side of the Atlantic, but Walton suggests that neither New England nor South Devon was its original home, it having been introduced into both localities at approximately the same time.

There is another possibility, or rather a strong probability. In 1846 Mr. W. P. Cocks captured at St. Ives, on the north coast of Cornwall, a form which he later (1851) described as *Actinia chrysosplenium*. He sent drawings and a description of it to Johnston, who included it in his 'History of the British Zoophytes' (1847), and he conferred the same favour on P. H. Gosse, the drawing being this time the coloured one which is to be found reproduced in plate vi. of the 'Actinologia Britannica' (1860). Gosse referred it, with some doubts, to the genus *Sagartia* and added three additional localities at which it was found by Mr. Cocks, all on the Cornish coast, but neither he nor Johnston had personal knowledge of the form, their descriptions being based on notes furnished by Cocks.

Cocks's original figures do not suggest much resemblance to *S. luciae*; they show relatively large circular spots scattered over the column, looking like verrucae, but representing really, as may be gathered from the description, spots of bright yellow, the ground-colour varying "from a bright pea-green to the dark holly-leaf tint." But it is also stated that the yellow may be arranged in stripes instead of spots, and in the figure reproduced by Gosse it is so represented, the similarity to the coloration of *S. luciae* being thus very great. In Gosse's figure, however, the tentacles are shown as if very few in number and plump; Cocks's original figure, on the other hand, represents them as much more numerous and tapering, quite as they are in *S. luciae*. Combining the two figures, then, one would have a fairly accurate representation of a *S. luciae*, both as regards its external form and its coloration. It is true that no acontia were observed; but *S. luciae* is somewhat sluggish in emitting them, and the comparison that Cocks makes in a letter to Gosse of the appearance of the column-wall to that of a piece of "india-rubber when pierced with a pin" may well have been suggested by the somewhat pustulous appearance frequently presented by *S. luciae*. Indeed, making allowances for the imperfections of descriptions of Actiniae written before 1860, I do not hesitate to express the opinion that when examples of Cocks's species, taken in his localities, are studied, they will be found to be identical with *S. luciae*.

If this opinion be correct then the species has been located on the southern coast of England at least since 1846, and its appearance at Plymouth in 1896 may have been merely an easterly extension of its area of distribution, similar to what occurred on the New England coast between 1891 and 1901. This would seem a simpler explanation of the facts than the supposition that it had been introduced from some distant locality.

I have sectioned a number of examples collected at Plymouth and find that they agree in all essential points with those from the New England coast. The irregularity of the mesenteries was somewhat more pronounced, one individual (text-fig. 3), for example, showing in sections through the aboral half of the stomodæum only two pairs of perfect mesenteries, situated opposite one another, one pair being directives attached to a well-developed siphonoglyph, while in the other pair the muscle pennons were on adjacent surfaces and there was no siphonoglyph. The members of this second pair, however, were attached to the stomodæum opposite the middle of its longer axis, and, although there were no mesenteries of younger cycles intervening, it seems probable that they represent members of two different pairs, II. and VI., there having been a failure of regeneration, after longitudinal fission, of the typical mesenteries. In the intervals between the directives and each of the other perfect mesenteries there were representatives of two other imperfect cycles, symmetrically arranged, those representing the second cycle bearing reproductive elements.

Text-figure 3.

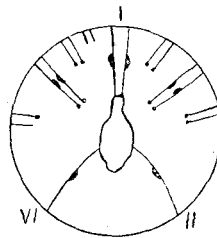
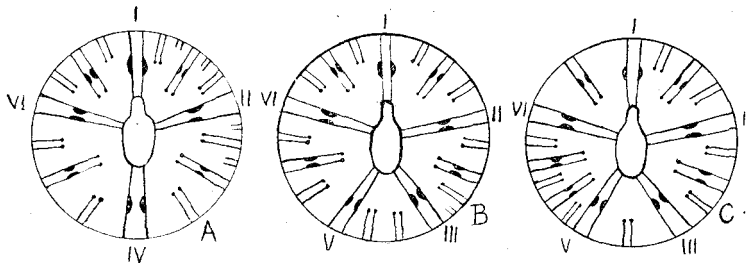


Diagram of the arrangement of the mesenteries in an individual from Plymouth.

Nor is the story of the distribution yet complete. In the summers of 1909 and 1911 I collected at the Canadian Biological Station at Departure Bay, on the east coast of Vancouver Island, an Actinian whose superficial resemblance to *S. lucie* of New England was most striking, the only noticeable difference being a somewhat greater average size. They were of the same green colour, the column was adorned with the same characteristic longitudinal stripes of yellow or orange, and the tentacles showed the same form and coloration. They were found on Jesse Island, not far from the station, among the barnacles that closely covered the face of a large rock, in such a situation that for hours each day they were exposed by the tide. This was the only location in which they were observed in these years; but on a third visit to the station in 1912, I found them quite abundant in slight depressions and crevices in the sloping rocks forming

the shore at the station, again well above low-water mark, so that they remained exposed to the air for several hours at each tide. I am confident that they did not occur on these rocks in the earlier years; had they then secured foothold upon them they could hardly have escaped observation. The rock on Jesse Island is not far from the station, but their extension to the latter locality is of interest in connection with the migrations of *S. lucie* on the New England coast and at Plymouth. Many years ago Mr. Alexander Agassiz gave me a number of drawings of Actinians that he had collected in the Gulf of Georgia in 1859, and among these there were two that were unmistakably representations of the form under consideration. The drawings were made from specimens collected on Galliano Island, and furnish certain proof that the form has been in existence on the Canadian Pacific coast for over sixty years at least.

Text-figure 4.



Diagrams showing the arrangement of the mesenteries in three individuals from Departure Bay, British Columbia.

As has been stated, these Pacific forms resemble *S. lucie* in their external form and coloration; their anatomical structure is also the same. They show a similar fosse, complete absence of a sphincter, and a similar arrangement of the mesenteries. The irregularities of the mesenteries were not so marked as in the Plymouth examples, but were nevertheless quite evident, as may be seen from the diagrams (text-fig. 4), which represent the arrangement observed in three individuals. In each case the individual was monoglyphic, with but a single pair of directives, and in one case there were only four pairs of perfect mesenteries, in the other two five pairs. Two cycles of imperfect and fertile mesenteries were present, in one case arranged symmetrically with regard to the four perfect pairs, but in the others showing some irregularity, and in the example with four pairs of perfect mesenteries representatives of a third imperfect cycle, without mesenterial filaments or reproductive elements, occurred in two of the interspaces. Acontia were present, but not abundant.

There can be no doubt as to the specific identity of the

Vancouver Island forms with those from New England and Plymouth, so that we now know of three areas inhabited by the species, separated from one another by wide intervals, two of them by the North Atlantic Ocean and the other from these by the whole width of the North American Continent. Furthermore, there is the certainty that the species has been "in residence" on the Canadian Pacific coast for over sixty years, and if the suggestion be correct that it has been secondarily introduced into the other two areas, the Pacific may have been its original home. But Mr. Cocks's discovery of his *A. chrysosplenium* on the Cornish coast dates back seventy-five years, and this lessens the probability of the introduction hypothesis. There is another possibility, however, namely, that originally the species had a circumpolar distribution, like *Metridium senilis*, *Urticina felina*, and a number of other Cœlenterate forms, and that its present areas of distribution are but separated remains of a much larger area. If further observations should reveal its presence on the Asiatic side of the Pacific the probability of this suggestion would be greatly increased*; in the meantime it is merely offered as an alternative to the introduction hypothesis.

But no matter what the original home of the species may have been, the evidence is clear that in each of its known localities it has in recent years more or less markedly extended its distribution. The cause of this is also obscure. It scores largely in favour of the introduction hypothesis, but is not necessarily a proof of it. It may be a phenomenon in some respects and on a lesser scale comparable to the migration of the Colorado Potato Beetle many years ago, but as to the influences that determine it in three widely separated areas I have no suggestion to make.

To return now to a consideration of the systematic affinities of the species. The possession of acontia marks it as a member of the family Sagartiadæ, a family in which several subdivisions are now recognized. From the subfamily Phellinæ it is excluded by the thinness of the column-wall and by the fact that acontia may be extruded through the wall, and it finds no place among the Sagartiinæ, since it has not more than six pairs of perfect mesenteries, these being also sterile. This leaves only the Metridiinæ and the Aiptasiinæ for its reception, and it is very doubtful if the separation of these two groups can be maintained. For the Aiptasiinæ differ from the Metridiinæ only negatively, in the lack of a mesogloæal sphincter, and since it may be supposed that they are descendants of forms possessing that structure, its absence in them is due to a process of reduction and is of less importance than the arrangement of the mesenteries. Furthermore, I have found in *Aiptasia (Heteractis) lucida* faint indications of a mesogloæal sphincter, and, I may add, since this

* Since possibilities are being discussed I may suggest that perhaps the form collected by Stimpson in Hong Kong Harbour and described by Verrill (1869) as *Sagartia lineata* may be the Asiatic representative of *S. luciæ*.

observation has not been confirmed by others (Duerden, Pax) who have studied that species, that a quite distinct though feeble mesogloal sphincter occurs in *A. pallida*. In the arrangement of the mesenteries the Aiptasias agree with the Metridiinae, so that their separation from that subfamily seems to be artificial and unnecessary.

S. luciae agrees with the majority of the Aiptasias in lacking a mesogloal sphincter and in the possession of not more than six pairs of perfect mesenteries, and, with the Aiptasias, should be assigned to the subfamily Metridiinae. That means that it is not entitled to the generic term *Sagartia*. When Gosse (1855) established the genus *Sagartia* he included in it all the forms known to him to possess acontia, with the exception of *Adamsia palliata*, which had already been assigned to a special genus by Forbes. In the list of the forms belonging to the new genus, Gosse placed *viduata* (*effeta*) first, and it might therefore be taken as the type species, but later, in the 'Actinologia Britannica' (1860), Gosse proposed the subdivision of *Sagartia* into a number of subgenera, retaining the original name for a group of forms of which *miniata* is the type, while *viduata* is referred with *troglodytes* (*undata*) and *parasitica* (*polypus*) to a subgenus *Cylista*. This complicates matters; for *miniata* and the other forms that Gosse associated with it are, apparently, referable to the older genus *Cereus*, and if this be the case *Sagartia* becomes merely a synonym, unless *viduata* (*effeta*) be accepted as its type species. This seems the proper thing to do, for otherwise the confusion that now exists in Actinian nomenclature would become still worse confounded.

Sagartia viduata, or, to give it its more correct name, *S. effeta* L., has no fosse and a well-developed mesogloal sphincter; my preparations from specimens collected at Plymouth do not allow of certainty as to the arrangement of the mesenteries, though the indications were that more than six pairs were perfect, but Carlgren (1893) has shown that this is the case. *Sagartia*, then, as is seemly, belongs to the subfamily Sagartiinae, and our *S. luciae* cannot be referred to it. What, then, is the proper generic term for this species? It has some resemblance to *Aiptasia*, but, lacking the characteristic double row of permanent cinclides of that genus, it cannot well be included in it. It has already been pointed out that there is a strong probability, indeed, I believe it is more than a probability, that it is identical with the *A. chrysosplenium* of Cocks, and that form Gosse recognized as a *Sagartia*, referring it to a special subgenus *Chrysoela*. If my belief as to its identity is well founded, *S. luciae* should be known as *Chrysoela chrysosplenium* (Cocks) Gosse. At all events it is not a *Sagartia*, nor can it be assigned to any of the genera now recognized.

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