The Genus *Ilyanthus*, Forbes.

By

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With Figures 1–3 in the Text.

THE genus *Ilyanthus* was erected by Forbes (1840) for *I. scoticus*; little is known about that species, and its anatomy is undescribed. There is no evidence that any subsequently described species is really a genuine *Ilyanthus*, and the genus-name can only be used provisionally for others until *I. scoticus* can be dissected. Meanwhile the genus-name must be reserved for *I. mitchellii*, the main subject of this paper. Gosse described this species from a specimen which he saw in 1853 (see *Actinologia*, p. 232); it must have been in poor condition or semi-contracted, and his figure (Pl. 8, Fig. 6) is quite misleading. Andres erected (1883, p. 462) a genus *Mesacmæa* for his *Ilyanthus stellatus* of 1880, and, as I hope to show below, *M. stellata* is either specifically or at any rate generically identical with *I. mitchellii*; so that *Mesacmæa* now becomes a synonym; if it should prove, later on, when *I. scoticus* can be examined, that *I. mitchellii* does not really agree with it, i.e. is no *Ilyanthus*, then the name *Mesacmæa* can be revived for *mitchellii* and *stellatus*. Carlgren (Actiniaria of the Danish Ingolf—Expedition, 1921) has given a few anatomical details of *Me acmæa*, gained from notes by Andres in his possession; they agree with my description of *I. mitchellii* as far as they go, but there are not enough of them to make a full understanding of the genus possible. In Andres' 1883 monograph will be found a description of another species, *I. partenopeus* (p. 459). This has been anatomically examined by Simon (1892) and Faurot (1895), and it differs completely from *mitchellii* (and *stellatus*). I have referred to it elsewhere (*Q.J.M.S.*, Vol. 65, 1921, pp. 518, 521, etc.) and have endeavoured to show that it is not only not an *Ilyanthus*, but cannot even remain in the same family as *I. mitchellii*, being in structural grade more like an *Anemonia* which had taken to a burrowing life.

I have been acquainted with *I. mitchellii* for some time, and it is a form unique among anemones and bristling with problems, so I feel that some account of it should appear without further delay, since it has not been sufficiently described. As I shall not be able to work out the finer detail of its anatomy for some time, I now give a description

of its external characters and of a few of its habits, with such anatomical data as are needed to make these intelligible; even now, many points must be left untouched. Some young larvæ of it, which would enable us to trace its development, are badly wanted, and we can hardly hope to clear up its anatomy until these are forthcoming. My experience of the species is as follows: I found a specimen, probably of *I. mitchellii*, in an Irish collection of anemones; and Dr. Allen very kindly lent me some Plymouth specimens of it (preserved) for comparison, one of which I was able to dissect. I also, through the kindness of Mr. Chadwick, received a living specimen, which was moribund, from Port Erin in 1919: this also I dissected. Finally, in 1921, I received two beautiful and healthy living specimens from Plymouth, and these have formed the best of the material for this paper. There are some points in the anatomy which had puzzled me, and upon which preserved specimens could throw no light; but the living specimens, from their manner of holding their tentacles, and their clear display of the arrangement of the latter, solved at least some of these difficulties. As far as we know hitherto, Plymouth is the British headquarters of the species, though it is not of frequent occurrence even there. Mr. Smith tells me that it is obtained outside the Sound, off the Mewstone. Near the Eddystone and further west towards Looe some of the specimens seem to live in clean shelly gravel, and these come to hand naked as in Gosse's figure; others found on fine sandy ground invariably have the column covered by an incrustation which is not very easily removed. He also informs me that a specimen in one of the Plymouth tanks attaches itself firmly at the bottom of a glass dish containing it, and expands above the sand.

DESCRIPTION OF SPECIMENS.

I. The two Living Specimens from Plymouth.

Body.—Form variable, short and broad like a turnip, in contraction, more elongated in expansion, but never (so far as I have seen) becoming vermiform like *Peachia* and *Halcampa*. Physa not distinctly marked off from scapus. Scapus rather corrugated, the mesenteries showing through at the lower end; above, the corrugations take the form of little horizontal projecting shelves of skin, which are rather a noticeable feature; they are not, I think, merely contraction-wrinkles, but are correlated with the presence of a good deal of rough "cuticle," some of which is easily removed; there are also bits of shell and gravel attached to the scapus. Its flesh is brownish purplish flesh-colour, the "cuticle" grey-brown. The upper end of the body is marked off as a narrow, smooth, more cream-coloured capitulum, and in expansion this forms a marked collar, which projects beyond the upper part of the scapus,

leaving a very short " neck " between it and the tentacles (only visible in full expansion) ; this " neck " shows the mesenterial insertions through its wall ; upon it, below each third-cycle tentacle, is a darker patch of colour, sending a line round either side of the tentacle-base ; *between* the bases of every two third-cycle tentacles there runs out a little dark line from the back of the base of an inner tentacle, bounded by two pale ones.

Disc and Tentacles.—In moribund individuals the tentacles may be short and thick, but in these healthy ones, though of considerable thickness, they are long, graceful, and tapering. They can be retracted with a jerk. There are three very clearly marked cycles of them, running 7, 11, 18=36. The fact that there are seven primaries, instead of the usual six of Actinians, is no casual and accidental individual feature, but regular and specific ; and, moreover, these seven are always (so far as my experience goes) held so that they point inwards, in fact they interlace and form a sort of pent-house over the mouth, springing back elastically into that position if one tries to pull them away—they seem rather stiff, and unable to spread outwards at all. Further, *only one of the seven is a directive-tentacle*, although there are two pairs of directives, the other directive-tentacle being a member of the second cycle. The seven primaries divide the others up into seven groups, which, starting from the primary directive-tentacle, run 3.5.5.3.5.5.3, the central group of three containing the secondary directive-tentacle ; the groups of three each contain one secondary and two tertiary tentacles, those of five comprising two secondaries and three tertiaries. The manner of holding the tentacles during life is most interesting. The primaries, as stated, invariably cover the mouth (Fig. 1) ; in daylight they form a rather untidy knot, at night they stretch out more gracefully and cross each other in the middle as shown in the figure. In daylight the animal lies buried up to the disc, and the secondaries and tertiaries lie spread abroad, more or less flat upon the sand, in seven distinct radiating groups. As far as one can tell, the primary tentacles are the shortest, the secondaries intermediate, and the tertiaries longest—as one expects in such a form. At night the upper end of the body is raised above the sand, the collar projects strongly, and the tentacles assume a stiffer and less flaccid habit. In my specimens those of the smaller one usually maintained seven radial groups rather decidedly (cf. Andres' figures of *I. stellatus*, Fig. 38 and Pl. IX, Fig. 5) ; those of the larger one typically spread themselves in such a way that all the secondaries pointed upwards and outwards in a regular ring, the tertiaries, in marked contrast, turning outwards and downwards, so that their tips touched the sand. I may mention that these creatures would not bury themselves, but expanded fully only when I buried them. They lived well in captivity, and ex-

panded permanently save when irritated, and then did not retract for long. The colouration of disc and tentacles is complicated, and would be easier to represent in a drawing than in words ; I hope to be able to illustrate the species fully, at a later date. The colours and markings form an intricate and beautiful pattern, softly shaded, and comprising varying tints of straw-colour, light purplish grey, browner shades, purplish browns, and so on, which vary to some extent according to the degree of distension of the tissues. The most striking point about the tentacles in general is that there is a dark median stripe running longitudinally down the oral face of each, from the tip to about half-way down ; besides this their oral faces are marked, roughly speaking, by a series of alternately light and dark transverse marks, which, towards the tentacle-base, are more or less V-shaped, the V pointing towards the mouth. No two V's on any one tentacle are quite alike, and there are differences between the patterns of the three cycles of tentacles, further complicating details coming in about the tentacle bases ; but in so unique a species it seems superfluous to write down every detail, and that will be done better in a figure later on. The aboral faces of the tentacles are not much marked, save in the case of the primaries, where the *backs* of the tentacles are, apparently, permanently exposed to the light, and here there is a certain amount of pattern—quite an unusual feature. The most striking feature in the colouration of the larger specimen was the conspicuous marking out of the directive-tentacles by large patches of opaque white, quite distinguishing them from the rest. The primary directive-tentacle was white at the base, on its back ; the secondary directive-tentacle was white over most of its basal part, at least on the inner face. In the smaller specimen the secondary directive-tentacle was almost wholly dull purple, the primary being a little purple at the base, and having a white aboral stripe.

The disc is also patterned. The reddish mouth is surrounded by a pale ring, followed by a rather narrow dark one, which is made up of a series of dark marks on the inter-radii, these being darker on the tertiary inter-radii than on the others ; the former break into the pale ring as little points, giving it a star-like effect. Next there comes a broader pale ring, all the inter-radii sharing in its formation. The tertiary inter-radii have no other markings till the base of the tentacle is reached, where there is a pale diamond, save that their outer parts are less pale than the inner. The primary and secondary inter-radii have a dark transverse mark shading off at the four corners into the radii, and this is farther from the mouth on the secondaries than on the primaries ; between this mark and the tentacle base is a pale roughly triangular mark, much larger for the secondaries than for the primaries.

The above details of colour are compiled from the two specimens, there

being differences of detail but the same general plan in both ; the larger had the colours less well defined than the smaller.

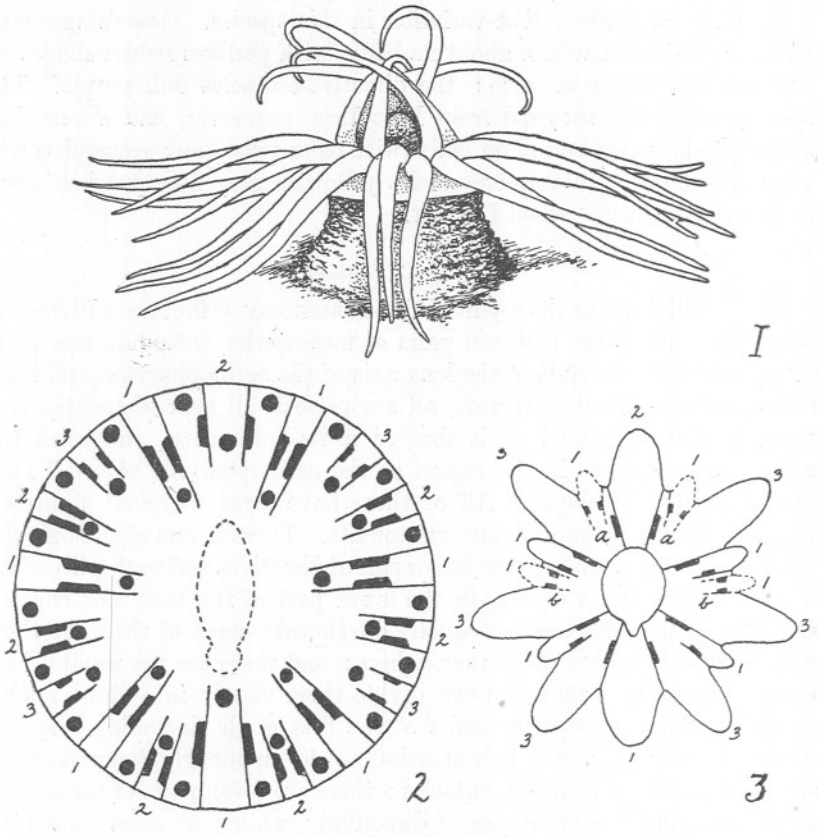
II. Variation.

There is evidently colour-variation in this species. Gosse's specimen had a good deal of scarlet about its body, with perhaps redder shades on the disc also, than in mine ; the directive-tentacles dull purple. The specimen which I received from Port Erin, moreover, had a beautiful softly vivid, orange-vermilion body (with paler collar) and actinopharynx, general colours of disc and tentacles yellowish grey and purplish grey. It had no " cuticle " when I saw it.

III. Anatomy.

First I will describe the essentials in the anatomy of the larger Plymouth specimen. There are eighteen pairs of mesenteries, including two pairs of directives at the ends of the long axis of the actinopharynx ; all have strong circumscribed retractors, all are perfect, all bear filaments (save perhaps a single one which is aborted in its lower part), and when the animal is cut across in the region of the actinopharynx, they all look about equally developed. All of them have large marginal stomata ; but I could not be sure about oralstomata. There is one siphonoglyphe only, and it corresponds to the larger pair of directives and to the directive-tentacle of the inner cycle. In the lower part of the body one can see that the mesenteries are not equally developed ; some of them, or their muscles, reach farther down than others ; and there are the usual differences in breadth ; thus one can divide them clearly into three grades or cycles. There are seven pairs of the first grade, including *only one* of the directive pairs (the pair attached to the siphonoglyphe) and corresponding to the seven inner tentacles ; there are seven pairs of the second grade, including the other pair of directives ; while four pairs constitute the third grade ; the eleven tentacles of cycle 2 belong to the endocoels (7+4) of grades 2 and 3 of the mesenteries, while the 18 tertiary tentacles correspond to the 18 exocoels. In other words, the arrangements of mesenteries and tentacles exactly correspond, and are symmetrical about the long axis of the throat ; but while the tentacles run 7, 11, 18, the mesenteries run 7 p., 7 p., 4 p. (7+4=11), the remaining 18 tentacles being exocoelic. The accompanying Fig. 2 shows a diagrammatic transverse section taken below the level of the actinopharynx, which is dotted in simply to show the relationships of the mesenteries to the siphonoglyph ; it would not actually appear in such a section. All three mesenterial grades are fertile, grade 3 being but sparsely so, grade 2 intermediate, grade 1 richly fertile ; the grade 2 directives are well supplied. Ciliated streaks are present on the filaments.

I think it may be assumed that the type of structure above described is specific and not an individual freak. It is perfectly regular. The Port Erin specimen agreed exactly with what I have recorded for the Plymouth



Ilyanthus mitchellii.

Fig. 1.—Sketch of a living specimen with most of its body buried, showing some of the characteristics of its way of holding the tentacles. This is the smaller Plymouth specimen, perhaps a little enlarged.

Fig. 2.—Diagrammatic transverse section below the level of the actinopharynx. See text. The relations of the tentacles to the mesenteries are shown by including black spots for the tentacles.

Fig. 3.—Reconstruction designed to illustrate the theory proposed in the text, with regard to the development of the species. In this figure the numbers indicate the cycles to which the tentacles will eventually belong. In Fig 2 numbers refer to the mesentery-cycles.

specimen, as far as I could get details from it; also, another Plymouth specimen I dissected some time ago would, so far as I remember, agree also in essentials, though I have not the details at hand. The second of my living Plymouth examples, having the same arrangement of tentacles as the one dissected, is bound to have the same arrangement

of mesenteries, for this is a case in which the one can be deduced from the other. Moreover, in Andres' specimens of *I. stellatus*, there was the same state of affairs—seven inner tentacles bent over the mouth, and seven bunches of outer ones in two cycles. In his examples they ran 3.5.3.3.3.5.3 or 3.3.5.3.5.3.3, giving two tentacles less on each side than in mine ; but that is only because his individuals were less fully developed ; I have seen cases myself with fewer than 36 tentacles, one, I believe, having 28 only. Deducing the arrangement of mesenteries in Andres' examples from that of their tentacles it is evident that the third-grade mesenterial pairs can appear first in *either* the asulcar or in the lateral members of the six main exocoels which lie nearest the siphonoglyphe.

DISCUSSION.

I. Ilyanthus and Mesacmæa.

I do not think anyone who reads Andres' account and looks at his figures can doubt that these two genera are identical (using the name *Ilyanthus* as applying to *I. mitchellii*). The unique arrangement of tentacles that occurs in both, and the unique way of holding them, are too striking resemblances to be overlooked ; and they are borne out by almost everything else. There may be colour-differences, but only such as one expects between British and Mediterranean varieties, and even among our British specimens there are such differences : and there are also several resemblances, such as the axial stripe on the oral faces of the tentacles (rather an important detail), and so on. I am inclined to think that not only are the two genera identical (so much I think is certain), but very likely the species *mitchellii* and *stellatus* also. There is certainly one curious difference between them—in *stellatus* the tentacles of the middle series seem to be a little longer than the others ; but, as the number of tentacles seems to show that these specimens were not quite fully grown, I am not sure that it is impossible for the tertiary tentacles to be considered as being a little short of their eventual length ; they might in the end outgrow the secondaries—although the probable order of tentacle-succession in this genus might not fit in with that idea. But the specific identity of the two is of minor interest, it is the generic identity which is of most importance.

II. Problems connected with Ilyanthus.

Is it possible to make suggestions which will help us to understand the curious state of affairs in *Ilyanthus?* We cannot know anything for certain until its development has been worked out, and it is, of course, always quite possible that the larvæ when examined will reveal something

quite unexpected ; but it does seem worth while to make at least some attempt to think out, quite tentatively, a conceivable explanation. It is possible to think of various schemes by which the result might have been obtained, but as far as I have been able to carry my study, the following seems the likeliest.

In the first place, if *Ilyanthus* is to be compared, for enlightenment, with any other genus, the form indicated seems to be *Peachia*, which, although very different from *Ilyanthus* and less strange, is at any rate probably one of its nearest relatives. In the development of *Peachia* there is the usual 8-rayed Edwardsia-stage, and later on a 12-rayed stage with six pairs of mesenteries. The eight tentacles of the Edwardsia-stage, however, give way to the twelve of the next stage, in a way differing from that of the more usual anemones, the added four arising in connection with the four lateral primary endocoels, so that of the eight original tentacles, six become exocoelic, the other two being the directive-tentacles ; and the exocoelic six are persistently larger than the endocoelic ; just as in the adult *Ilyanthus* the exocoelic tentacles are the largest. It seems that in thinking of *Ilyanthus* it would be unwise to suppose that it had no Edwardsia-stage and no 12-rayed stage ; that would be stretching the case too widely away from the normal, without evidence for doing so. The safest plan to follow, perhaps, would be to postulate for it both these stages ; also, it seems a fairly probable supposition that it develops its tentacles according to the *Peachia* plan. By a slight modification of the history of *Peachia*, moreover, the state of affairs exhibited by *Ilyanthus* can be obtained. Let us suppose that early in the 12-rayed stage, for some reason, two pairs of secondary mesenteries (which should in a normal case come later) appear in two of the exocoels, and grow so fast that they outstrip the asulcar directives, which tend to be rather backward. They bring with them two endocoelic tentacles ; and it may be that both they and their tentacles grow so strongly that they take their places in the first cycle ; while the asulcar directives themselves are relegated to a second grade of size as compared with the interlopers, and their tentacles to the second cycle. So much being admitted, we have accounted for the 7-rayed condition just as it is actually represented in the adult, and the subsequent development offers no difficulty. All this would regularise itself later on, assuming adult proportions, as it does in any anemone. It may be that my suggestion is rather bizarre, but not more so than certain other suggestions which have actually proved correct, in the cases of Endocoelactidæ and of *Tealia*. In *Tealia*, in fact, the 10-rayed adult condition *does* arise from an earlier 6-rayed state, by the precocious growth of four secondary mesenterial pairs which assume primary rank ; and *Ilyanthus* may only be a more extreme case of the same sort of thing.

There is one important point which my suggestion has so far left untouched—in *which* pair of exocoels do the precocious mesenteries appear ? We may perhaps dismiss the sulcar exocoels as being too far away from the scene of action ; and if the sulcar lateral primary pairs (as the fact that they are, in the adult, the most fully developed of all, seems to suggest) in the adult include the sulco-lateral couple of the larva, it is impossible for the precocious pairs to have appeared in the sulcar exocoels. We have, therefore, to choose between the asulcar and the lateral exocoels. In *Peachia*, *Eloactis*, and *Haloclava* there is a backwardness or growth-atrophy about the asulcar region : no metacnemes are formed there, the asulcar directives tend to be less developed than the sulcar, and there is no asulcar siphonoglyphe ; in this *Ilyanthus* resembles them. If the reduction of the asulcar directives, etc., indicate a general (relative) growth-reduction in the asulcar region, precocious or quickly growing mesenteries would be unlikely to develop in that very area, and it would seem more natural to expect them in the lateral exocoels, in a position lateral to the long axis of the actinopharynx, and the region in which, according to the adult, most of the mesentery-formation has taken place. This is actually the spot in which the first of the precocious pairs in *Tealia* make their appearance. This would seem to involve a growth stage at which two endocoelic tentacles, destined to belong to the same cycle, would be adjacent to each other on each side of the axis, until a new exocoelic tentacle came between them. For most of the above suggestions in favour of the lateral exocoels I am indebted to Dr. Gemmill, and agree with him in preferring them, though I do not think we need rule out the other possibilities altogether in the present state of our knowledge. In Fig. 3 I have tried to illustrate both the likelier possibilities ; in this figure the continuous lines represent the actual state of affairs in a *Peachia* larva ; the dotted portions represent the suggested additions for *Ilyanthus ;* but *both* alternatives are included to economise space. Of course, only *one* of the alternatives would actually take place, *either* the pairs a, a would be the precocious ones, *or* the pairs b, b, there would not really be four pairs involved.

Finally, it may be of interest to make a brief comparison of *Peachia* and *Ilyanthus*. I cannot feel that they need separate families (any more than *Tealia* does by reason of its decamery) ; they fit in well enough with the genera *Eloactis* and *Haloclava* (and probably also *Harenactis*), and together constitute the true Ilyanthidæ ; each of the genera is peculiar in some way. *Peachia* is unique, as well as *Ilyanthus* (though not so markedly unusual), by virtue of its conchula ; and its mesenterial and tentacular arrangements are also peculiar. It has twelve tentacles and twenty mesenteries ; *Ilyanthus* has up to thirty-six tentacles and thirty-six mesenteries (sometimes more ?), and no conchula ; *Peachia* has six

primary mesenterial pairs, including both pairs of directives, *Ilyanthus* seven primary pairs, including *one* of the pairs of directives only ; *Peachia* carries its tentacles, when alive, in an ordinary way, *Ilyanthus* in quite an unusual way. *Peachia* shares with *Ilyanthus* a single siphonoglyphe and a predominance of the sulcar directives over the asulcar, and also its general form and that of its tentacles. It is becoming evident, from the observations of Elmhirst (*The Zoologist*, Jan., 1915, p. 3) and others, that *Peachia* is at least to a considerable extent a current-feeder, and does not make a great deal of use of its tentacles. About *Ilyanthus* in this connection we so far know nothing. It typically keeps its mouth raised on a very steep little cone or spout, within the tent formed for it by the inner tentacles (Fig. 1).