

# The British Edwardsidae.

By

Oskar Carlgren

Professor, Zoological Institute, University, Lund, Sweden,

and

T. A. Stephenson, D.Sc.,

Senior Assistant, Zoology Department, University College, London.

With 18 Figures in the Text.

## CONTENTS.

	PAGE
PART 1. 1. Introduction . . . . .	1
2. Structure of the family . . . . .	4
3. Details of British species—	
<i>Edwardsia callimorpha</i> (Gosse) . . . . .	6
<i>Edwardsia delapicæ</i> n.sp. . . . .	9
<i>Edwardsia tecta</i> Haddon . . . . .	10
<i>Milne-Edwardsia carnea</i> (Gosse) . . . . .	10
<i>Milne-Edwardsia dixonii</i> Carlgren . . . . .	12
4. Note on the succession of tentacles in <i>Edwardsia callimorpha</i> . . . . .	13
5. Note on the regions of the column in Edwardsias and other Actinians . . . . .	14
PART 2. ANATOMY. <i>Edwardsia callimorpha</i> (Gosse) . . . . .	20
<i>Edwardsia delapicæ</i> n.sp. . . . .	23
<i>Edwardsia tecta</i> Haddon . . . . .	25
<i>Milne-Edwardsia dixonii</i> Carlgren . . . . .	27
LITERATURE . . . . .	30

## PART 1.

By

T. A. STEPHENSON.

### 1. INTRODUCTION.

THE genus *Edwardsia* is one known to most zoologists as an example of a primitive eight-rayed Zoantharian from which (or from a form resembling which) the higher forms are derived. It is only comparatively recently, however, that our knowledge of Edwardsias has become at all extensive, and even now it is incomplete; but it is desirable to produce a revision of the British forms since no adequate account of these exists.

In some of the textbooks best known in this country (Lankester's *Treatise*, Sedgwick, Parker and Haswell) *Edwardsia* is quoted as a form with eight mesenteries only, and the impression produced thereby has been perpetuated, although it has long been known that *Edwardsia* has more mesenteries than eight, and although this fact is recorded in the *Cambridge Natural History* and by Delage and Hérourard. There is, in fact, no Actinian which in its adult condition possesses eight and only eight of these organs, the simplest forms possessing at least six pairs of mesenteries, eight only of which are perfect. If an example of an anemone of simple structure be required, this may be found in *Gonactinia*, which represents the nearest approach to the probable primitive condition which is now extant. *Edwardsia* is in many ways an advanced and specialised form, and its limited number of mesenteries is on the whole more likely to be a reduction or an arrest of development than anything else, connected with its vermiform shape.

*Gonactinia* has eight perfect mesenteries and eight imperfect, four of the latter pairing with four of the former to make up the typical six-rayed Actinian condition. It has a very generalised structure, the ectoderm being as little differentiated in the different parts of the body as can be the case in an anemone; it retains the ectodermal muscle-sheet and nerve-net on the column and in the throat. The musculature is weak and generalised, and even on the mesenteries is very little concentrated. There is no sphincter, and the tentacles are non-retractile. The aboral end is little specialised. The filaments are simple and not trifid in their upper parts. The animal reproduces habitually by a kind of strobilisation, and it is the only known anemone, so far as I am aware, in which a tentacle alone is able to regenerate the whole of the rest of the organism.\*

In *Edwardsia*, by contrast, though the mesenteries may be as few as in *Gonactinia*, they are strongly specialised for rapid retraction, having very highly differentiated muscles. The ectoderm is by no means generalised, but is differentiated into regions even on the body (where it has lost its ectodermal muscle-sheet), on part of which it is often invaginated into the mesogloea as a series of deep pits with narrow mouths, the pits containing large nematocysts and acting as stinging batteries. The filaments are trifid in their upper parts, as in the majority of forms.

Even *Gonactinia* is possibly considerably removed from the primitive ancestral condition and may itself be a retrograde form; but it offers at least a better picture of the probable early condition than does *Edwardsia*.

The *Edwardsids* have had a varied career in the classifications; the most recent view regarding them as a distinct group being that expressed

\* This may not apply to the European form; it was worked out on a Japanese *Gonactinia* (see Okada, 1926, p. 482), which has autotomous tentacles. This form may be a *Boloceroidea*, but even so is a species with many primitive characteristics.

by Bourne in 1916, when he held that they should form a group apart from the Dodecactiniaria (Actiniaria+Madreporaria) in general, of equal rank with the latter and with the Zoanthinaria (Epizoanthus, etc.). This view was based mainly upon the mode of development of the micro-mesenteries and tentacles, as deduced from the comparative study of a series of different species. In my 1921 paper on classification I accepted this view (having studied the Edwardsias personally hardly at all), but since that time I have made a fairly detailed study of some of them, and I now agree with the view expressed by Carlgren (1921, pp. 25-6) that they are simply a family of ordinary Actiniaria with few mesenteries.

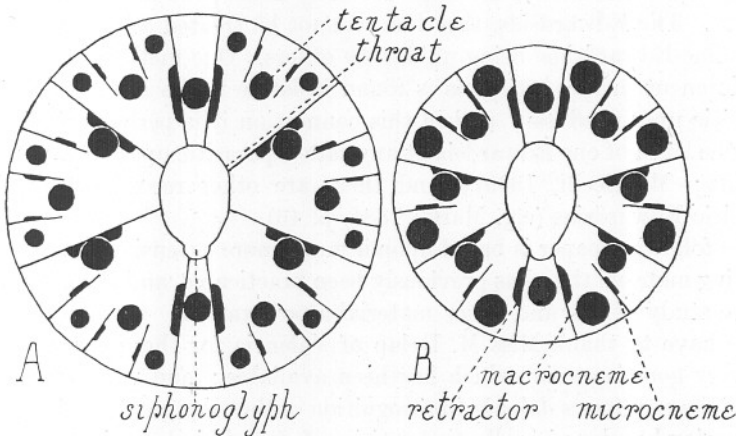


FIG. 1.—Diagrams to illustrate the arrangement of tentacles and mesenteries in *Milne-Edwardsia carnea* and *M. loveni* (A), and in *Edwardsia callimorpha* (B). The relative lengths of the tentacles are indicated by differences of size in the black spots representing them. In *M. carnea* and *M. loveni* there may be more than the 24 tentacles shown. The microcnemes have in reality no retractors, the oblong marks being inserted to show the way in which they pair.

The actual succession of tentacles and mesenteries within a single Edwardsian species has never been worked out, the notes given later on in this paper being the nearest approach to it.

The notes mentioned would appear to show at least that in *E. callimorpha* the three tentacles in the dorsolateral macrocœl do not in reality arise in the order supposed by Bourne (his *E. beautempsii* being equivalent to *E. callimorpha* from this point of view), and if this is the case for one form it may well be so for another. Carlgren has shown (and my own study of living material supports him) that in *Milne-Edwardsia carnea* (Fig. 1) the tentacles are arranged according to a plan quite different from that of *Edwardsia*, and not agreeing with Bourne's interpretation for this species. Carlgren discusses the question in the work referred to (1921, pp. 25-6, etc.), and I need not repeat him here; but I conclude

from my work that in the Edwardsids the four microcnemes adjacent on the ventral side to the lateral macrocnemes do in reality correspond to the couples 5 and 6 of the ordinary Actiniaria, that the rest of the microcnemes are to be regarded as genuine pairs and not simply as couples bilateral about the directive axis, and that in whatever way the tentacles appear there is not likely to be a difference marked enough to distinguish the Edwardsias from all other Actinians. There are, in fact, two perfectly distinct plans of tentacle-arrangement among the Edwardsids and at least two also among the Actiniaria; in the latter case it is known that the two different plans are produced by different modes of development, and in the former the same probably holds good although it is not proved. The Edwardsids, therefore, cannot be treated as a single series, the Milne-Edwardsinæ being unlike the others. One method of tentacle-development in the Actiniaria is found in larvæ which are known to be parasitic upon medusæ; and in this connection it is perhaps significant that the larva of one Edwardsia at any rate is parasitic upon a Ctenophore (Bolina; Monticelli, 1899); and there are other records of possibly parasitic Edwardsias (e.g. Mark., 1884, p. 43).

The following paper is based upon a much more extensive examination of living material than has previously been practicable, and upon morphological study of this and other material after fixation.

We have to thank Miss M. Delap of Valencia for the greater part of the very good material which has been available; and we have named one of the new forms *delapiae* in recognition of the very great service which Miss Delap has done in collecting rarities of varied kinds during a number of years.

## 2. STRUCTURE OF THE FAMILY.

The family Edwardsidæ, part of Gosse's family Ilyanthidæ, was instituted by Andres (1881, p. 333). It contains two sub-families, the Edwardsinæ (Carlgren, 1900, p. 25) and the Milne-Edwardsinæ (Carlgren, 1900, p. 25), which have sometimes been ranked as full families (Carlgren, 1893, pp. 11 and 17).

(1) *Edwardsinæ*. This sub-family contains two genera: *Edwardsia* Quatrefages, and *Isoedwardsia* Carlgren. The latter genus is non-British.

(2) *Milne-Edwardsinæ*. This sub-family also contains two genera: *Milne-Edwardsia* Carlgren and *Paraedwardsia* Carlgren, the latter being non-British.

The details are as follows:—

Family **EDWARDSIDÆ** Andres, 1881, p. 333, pro parte.

Ilyanthidæ as used by Gosse, 1860, p. 227, pro parte.

Edwardsidæ + Milne-Edwardsidæ of Carlgren, 1893, pp. 11 and 17.

Edwardsinæ + Milne-Edwardsinæ, Carlgren, 1900, p. 25.



Reference should also be made, for a history of the family, to Carlgren, 1892, p. 451, 1893, p. 8, 1900, p. 24, 1921, p. 22; Gosse, 1853, p. 157, 1860, p. 254; Faurot, 1895, p. 43; Bourne, 1916, p. 513; etc.

Athenaria with elongated body, divisible into two, three, or even four regions. Tentacles present. No sphincter or acontia. Mesenteries divided into macrocnemes and microcnemes; of the former there are eight, including two pairs of directives and four lateral mesenteries whose retractors face the ventral directives; of the latter, which are confined to the uppermost part of the body, there are four or more. Filaments trifid, the ciliated tracts sometimes discontinuous.

Sub-fam. EDWARDSINÆ Carlgren, 1900, p. 25.

Scapus with sunken batteries of nematocysts (nemathybomes) embedded in the mesogloea. Inner (endocœlic) tentacles shorter than the outer. Nematocysts of upper part of body (scapulus)\* small by comparison with those of the nemathybomes.

Genus **Edwardsia** Quatrefages, 1842, p. 68.

Edwardsiella Andres, 1883, p. 305.

Edwardsioides Danielssen, 1890, p. 100.

Edwardsinæ with the column divisible, at its highest development, into three regions—physa, scapus, and capitulum; the scapus sub-divided into scapus proper and scapulus. Physa without nemathybomes, but often (if not always) pierced by small apertures; scapus extensive, provided with a cuticular sheath and with nemathybomes containing long narrow nematocysts. Uppermost part of column cuticle-free and with small nematocysts not arranged in nemathybomes. Tentacles 12–16 or more. Throat, usually at any rate, with a single weak ventral siphonoglyphe.

The British species of *Edwardsia* are as follows:—

- (1) *E. callimorpha* Gosse, 1853, p. 157.
- (2) *E. delapicæ* n.sp.
- (3) *E. tecta* Haddon, 1889, p. 329, Pl. 33, Fig. 16, Pl. 36, Figs. 1 and 2.  
An immature form, possibly the young of *E. delapicæ*.
- (4) Apart from the above, three forms have been described, but the data available are insufficient for a determination of their status.  
*E. goodsiri* McIntosh, 1866, p. 395.  
*E. allmani* McIntosh, 1866, p. 394.  
*E. sp.* Haddon, 1886, p. 527.

Foreign species are numerous.

\* For explanation of this term, see p. 19.

Sub-fam. MILNE-EDWARDSINÆ Carlgren, 1900, p. 25.

Edwardsidæ without nemathybomes. Inner (endocœlic) tentacles longer than outer, usually hexamerously arranged. Nematocysts of upper part of body not markedly different in size from those of scapus.

Genus **Milne-Edwardsia** Carlgren, 1893, p. 17.

Milne-Edwardsinæ with column divisible into an extensive proximal region with a cuticular sheath, and an upper naked region. A physa is absent in some forms, present in others. Scapus without *Halcampapapillæ*. Nematocysts of scapus either scattered or arranged in groups; those of upper region (scapulus) occurring mainly on its longitudinal ridges, when such exist. Tentacles 12 or in several cycles. One ventral siphonoglyphe, at any rate usually.

The British species of Milne-Edwardsia are:—

(1) *M. carnea* Gosse, 1856, p. 219, Pl. IX, Figs. 1-4.

(2) *M. dixonii* Carlgren, 1921, p. 59.

There are other foreign species.

### 3. DETAILS OF THE BRITISH SPECIES.

I do not propose to give long descriptions of the species here, as I hope to publish a more detailed account with coloured illustrations, shortly. I therefore give the main points, enough for identification.

*Edwardsia callimorpha* (Gosse).

(For references, see p. 20.)

This is the commonest British species and is easily recognised. It occurs buried in sand or mud in *Zostera* beds and similar places. It cannot be called frequent, but is fairly widespread and where it does occur is sometimes common, very probably commoner than we know, being hard to find. The species has been found at Salcombe and other places in the Plymouth area, in the Clyde, Bantry Bay, Valencia (Co. Kerry), Brixham, Channel Islands; it doubtless occurs on the French coast (though in the French records it is confused with other species), and is well known at Naples as *E. clapedii*. There are other records, but those quoted are the most reliable. I have myself seen living specimens from Salcombe, Millport, Naples and Valencia, and from the latter locality many of them. The Plymouth specimens described by Walton and Rees (1913, p. 60) belonged to this species at least in part—i.e. those described as *E. clapedii* are certainly *E. callimorpha*; the one described as *E. timida* being probably the same and certainly not *E. timida*, which

is a composite species mainly belonging to *Milne-Edwardsia*. In the literature in general there is an unfortunate confusion between *Edwardsia callimorpha* and *E. beautempsii*; the two species were considered identical by Andres and Haddon, and others have followed this lead. As a matter of fact, so little is known of *E. beautempsii* that it is impossible to identify anything with it; and now that we know what the constant characters of an *Edwardsia*-species really are, it is evident that *E. callimorpha*, at any rate, is not the same as *E. beautempsii*. To take a single point only, the fact that the tentacles in *E. callimorpha* are transparent, with opaque spots and powderings in cream and maroon (one or the other, usually both), is evidently a stable characteristic of the species; in *E. beautempsii*, as described by Quatrefages, the tentacles were perfectly unmarked except for a spot at the tip, as in *E. delapicæ*; and this is one of the few definite characters of *E. beautempsii* that we have to go upon, Quatrefages' description being very incomplete. Colour alone is no reliable guide for the distinguishing of anemone species; but in a good many cases a pattern, or the structure of a pattern, is fairly trustworthy, at least as much so as most of the characters with which we have to deal in anemones. That these markings on the tentacles (not to mention others on disc and body, and quite apart from structural features) are genuinely characteristic of *E. callimorpha* I feel sure, after examination of some fifty living specimens from various localities.

*Description* :—

Body vermiform in extension. Physa well marked off from scapus, non-retractile, with microscopic adhesive rugæ. Scapus extensive, with a well-marked cuticular investment and with eight single rows of small tubercles running up it longitudinally, midway between the mesenterial insertions; each of these tubercles contains one (rarely two) nemathybome (Fig. 2). The rows usually die out gradually above, and the upper part of the body is free from both these and from cuticle. Tentacles (Fig. 1) sixteen, in two cycles (or 12–15 in young ones). Colours very variable in detail, but general plan of markings remarkably constant; allowing for individual variation, the following scheme is typical. Investment buff, rich chestnut, blackish, etc., varying from thin, smooth, and transparent to thick, rough, and opaque; often deciduous after capture. Nemathybomes and tubercles sometimes very prominent, sometimes inconspicuous and not visible till investment is removed; the rows more or less regular. Colour of upper part of body (scapulus) very variable; there is usually a coronal ring of cream spots just below the tentacles, and above this a very short transparent region, the true capitulum; there may be a second ring of cream marks a little lower down, or the latter alone may be present; there are often longitudinal cream stripes, one

to each macrocoele, below the coronal spots, or these may be broken up into irregular dots and splashes. There may also be brown or purple colour variously related to the cream. The tentacles are long and fine, transparent, with dots or powderings of opaque cream, and in adults generally with dots of blackish purple also. Sometimes the outer tentacles or all the tentacles appear sub-opaque because of a cream stripe up the oral and aboral face of each. The disc in adults (Fig. 3) is characterised by a mealy appearance, the colour being dusted on in dots; actually the colour varies indefinitely, but on the average there is a rosette of dark

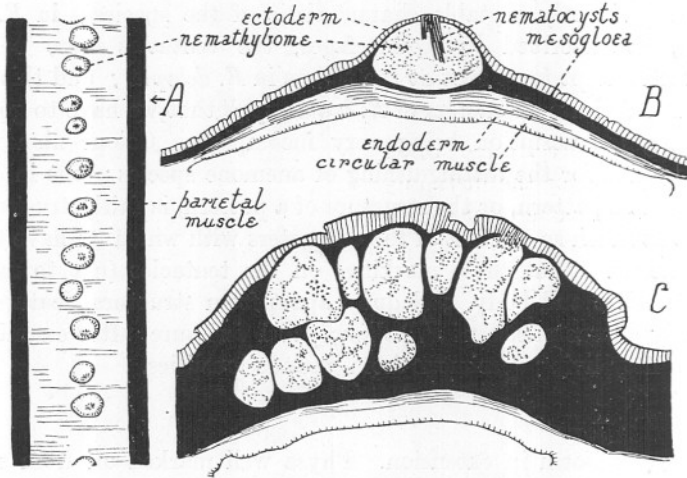


FIG. 2.—A. Part of a whole mount of a portion of column-wall from *E. callimorpha*, showing the arrangement of the nemathybomes between the insertions of two mesenteries.  
 B. Transverse section of the column-wall between two mesenteries, in *E. callimorpha*, passing through a nemathybome.  
 C. Similar section from *E. delapica*.

arches close to the mouth and a dark mark shaped like an hour-glass set transversely across the radius, near the foot of each endocœlic tentacle; sometimes the ring made by these marks is completed by similar dark spots on the exocœlic radii. Generally each outer tentacle has a cream spot on the aboral side at the base. These details will cover most specimens, but any given individual may lack some one or other of the features mentioned or may present a modification of its own upon the general theme. Young specimens usually have opaque cream discs, the other colours apparently coming later. The directive radii and tentacles may differ in colour from the others. The animal reaches a length of 10 or 12 cm., at its best.

*Edwardsia delapicæ* n.sp.

(For references, see p. 23.)

This species is so far known only from Valencia, where it was discovered by Miss Delap, and from Malahide, Co. Dublin; it is easily distinguished from *E. callimorpha*. The two species may live together.

As is noted later on (p. 23) by Carlgren, part of the specimens included by Haddon (1889, p. 329) under "*Edwardsia timida*" actually belong to *E. delapicæ*, the rest being *Milne-Edwardsia dixonii* (see p. 27).

*Description*.—

Body vermiform in extension, able to become even more attenuated than that of *E. callimorpha*. Physa well marked off from scapus, non-retractile, with microscopic adhesive rugæ, and with eight longitudinal

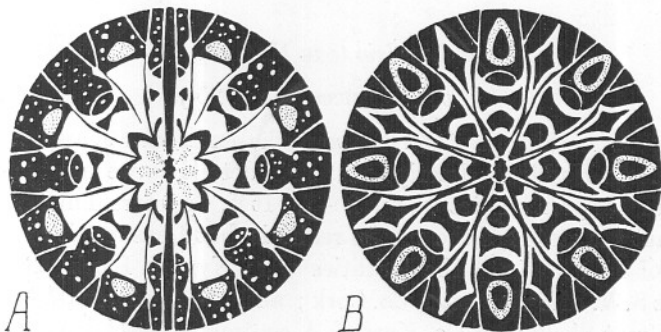


FIG. 3.—Diagrammatic representations of the pattern on the disc and tentacle-bases in *E. callimorpha* (A) and *E. delapicæ* (B). Only the lowest parts of the tentacles are shown. The shaded markings on the tentacle-bases are aboral, and are visible because of the transparency of the oral sides of the tentacles. The vertical dark stripe in A is a band of colour affecting the directive tentacles and radii. In B the aboral markings are omitted from the exocœlic tentacle-bases.  $\times$  ca. 6-7.

rows of small apertures. Scapus extensive, with a cuticular investment and with a wide band of nemathybomes along each macrocœle, the band nearly filling the space between each two mesenterial insertions; the nemathybomes are irregularly scattered, not mounted on tubercles, and not limited to a linear series as in *E. callimorpha*; in fact, some of them occur even over the mesenterial insertions, only the majority being confined to the main band; they project little, if at all, above the surface (Fig. 2). Tentacles sixteen in adults (fourteen in one case). There is a coronal ring of cream spots just below the tentacles, those corresponding to the endocœls being transparent in their centres and each sending a cream line to join a similar mark on the aboral side of the base of an endocœlic tentacle. Disc with a delicate pattern in cream and maroon



on a transparent ground, but without the mealy aspect of that of *E. callimorpha*; with very wide endocelic radii. Centre of disc with a star of eight cream rays; radii each with a cream mark of curious form on it (see Fig. 3), the marks on the exocels much farther out than those on the endocels. Tentacles long and slender, transparent, unmarked but for the basal markings and a faint brown or cream transverse bar across the tip. A cream mark with a transparent centre, shaped like the eye of a peacock's tail-feather, occurs on the aboral side of each tentacle-base. I have seen only half a dozen specimens of this species, but these exhibited very little variation, showing slight differences in the form of the cream markings on the disc, and so forth; in one a thin powdering of white on the disc obliterated some of the neat cream markings.

The animal reaches a length of about 12 cm. in extension; the diameter of the expanded flower up to about 4.5 cm.

*Edwardsia tecta* Haddon.

(For references, see p. 25.)

We know nothing distinctive about the external appearance of this species from Haddon's description; such details as we possess are contained in Carlgren's notes on pp. 25-7. It is, therefore, impossible to be sure what the status of the species really is, but I suspect it of being the young of *E. delapica*. The localities were Nymph Bank, 52 fathoms, 28 miles S.W. of Ballycotton, Co. Cork; and 70-80 fathoms, 5-8 miles W. of the Great Skellig, off Co. Kerry. A contracted specimen was 12 mm. long and 2 mm. in diameter.

*Milne-Edwardsia carnea* (Gosse).

(See Gosse, 1856, p. 219, 1860, p. 259; Carlgren, 1921, p. 62; etc.)

This small vermiform anemone (which reaches a length of 2-3 cm. only) inhabits crevices and small holes in rocks and, unlike most Edwardsids, which burrow, it has no true physa (this being essentially a burrowing organ), but an adhesive aboral end which may, it is true, assume rather the appearance of a physa if the animal be detached and left loose, but which is not histologically differentiated as such and does not function as one.

*M. carnea* is known in Britain from a number of localities—Torquay, Tenby, Plymouth, Port Erin, the Clyde, etc., and I have myself seen living specimens from three of the localities mentioned. Abroad it occurs in Sweden, but how far beyond this we cannot tell, since the various species have only been clearly recognised by Carlgren.



*Description* :—

The scapus occupies more than two-thirds of the length of the body and is sub-cylindrical, being often slightly polygonal above; its investment may be thin, or thick and rugged, pale orange-brown, dark brown, blackish, etc.; the skin beneath is orange-buff or pinkish, without nematobomes or papillæ. The scapulus is fairly long and is very sharply marked off from the scapus in partial contraction, though in full extension the division is obliterated; it bears eight sharply-marked longitudinal ridges which almost vanish in expansion, and these end sharply at its junction with the scapus; it is translucent, pinkish, generally marked by some other colour as well—the ridges may be white, or there may be a ring of opaque cream or yellow markings round the lower part. The disc may be dusted with pale yellow, which may concentrate round the mesenterial insertions; or it may be opaque cream; sometimes red round the mouth; with variants of this colouration. Throat orange or red, visible by transparency through scapulus; shorter than scapulus. Tentacles fairly long, slender, translucent pink, unmarked or with alternate bands of less and more positive colour; in 3-4 cycles—6.6.12, etc., or a close variant of this, total number up to 34 (Fig. 1). Variation not great, nor departing far from the plan indicated.

Since Carlgren describes the anatomy of all the British Edwardsidæ other than *M. carnea* in the second part of this paper, I will give here the main points in the anatomy of this species from Carlgren's 1921 paper, for comparison with that of *M. dixonii*. The retractors are similar to those of *M. dixonii* (Fig. 17), as also are the parietal muscles; the former have often twelve folds in the reproductive region and never have more than twenty. The nematocysts of the column are arranged in the ridges on the scapulus, and on the scapus itself are mainly in groups. The nematocysts in general are characterised by being short and wide as compared with those of allied species. Those of the scapus are  $29-34 (37) \times 7-8\mu$ ; those of the scapulus  $26-46 \times 7\mu$ ; of the tentacles partly  $18-24 \times 5\mu$ , partly  $27 \times 7\mu$ , the first kind numerous, the latter sparse; spirocysts up to about  $24\mu$ ; in the throat they are partly typical,  $17-20 \times 3\mu$ , partly with a distinct basal part to the spiral thread,  $22-29 \times 5\mu$ .

I have studied the nematocysts of a Clyde specimen myself, for comparison with the measurements given above; they are not quite identical in the two forms, but at the same time they are surprisingly near. Scapus,  $26-32 \times 6-7.6\mu$ ; scapulus,  $24-42.6 \times 5.4-6.6\mu$ ; tentacles partly  $17-22 \times 4-4.6\mu$ , partly  $22-26 \times 5.6-6.4\mu$ ; throat, partly  $17-22 \times 3-3.4\mu$ , partly  $20-24 \times 5-5.6\mu$ . This was a small specimen, only half the full size; the nematocysts measured preserved and unexploded.

*Milne-Edwardsia dixonii* Carlgren.

(For references, see p. 27.)

The account given here of the externals of this species is entirely taken from Dixon (1886, p. 100) and we cannot therefore personally vouch for it.

I cannot feel certain about the distinctness of this species from *M. carnea* (though I am inclined to think it is different), having never seen it alive. A good deal depends also on whether or no the tentacles are arranged as Dixon describes, and whether there is really a physa; if Dixon's account is correct in these particulars, it is probably a distinct form; especially as Carlgren shows (p. 27) that the nematocysts are considerably different from those of *M. carnea*; and in *M. carnea* their size seems to be rather constant.

*Description* :—

Physa present, provided with minute suckers, retractile into scapus. Scapus polygonal above, scapulus apparently without definite ridges. Tentacles 18–24, curiously arranged. In one specimen they ran 8+14 (or 8.12.2), and in another 10+10, and seemingly had a different relation to the mesenteries than in *M. carnea*; to judge from Dixon's figure, the inner eight in the first specimen correspond to the two directive endocoels and six symmetrical lateral chambers which do not include the four lateral primary endocoels.

Bourne (1916) gives details of two of Dixon's specimens examined by him, in each of which there were twenty-four tentacles; this account appears to confirm Dixon. It is possible that we have here a third type of Edwardsian tentacle-plan; but only a renewed examination of healthy living material can settle it. In a *Milne-Edwardsia* which is not in the best of health and at the same time very fully expanded, the real comparative lengths of the tentacles may be indistinguishable.

Physa pellucid white. Tentacles varying shades of pink or brownish red, tipped with white or not. Throat brownish red, brick-red, yellow ochre, sometimes with white longitudinal marks. Investment variable, usually tawny orange, black above. Disc usually pellucid pink, with white crescents (developed into H-marks in one case) at the tentacle bases, and a white ring round the mouth (also white specks on disc in one case); in one it was cream-white, with brownish red lines indicating the macro-insertions, white blotches at bases of directive tentacles, the other inner tentacles with a basal white bar inside which is a brownish red V, the point mouthwards. Scapulus translucent brownish red or pellucid pink, with a ring of opaque pale marks on it, arranged rather differently from those of *M. carnea*. The animal is larger than *M. carnea*, reaching a length of 6.5–7 cm. in extension. Moreover, it is different in

habit, and was found in mud among stones at extreme low water at Malahide, Co. Dublin.

4. NOTE ON THE SUCCESSION OF TENTACLES IN  
EDWARDSIA CALLIMORPHA.

I have been able to make out the arrangement of tentacles and mesenteries in nineteen young specimens of this species: although some of these were very small, none had fewer than 12 tentacles. The following

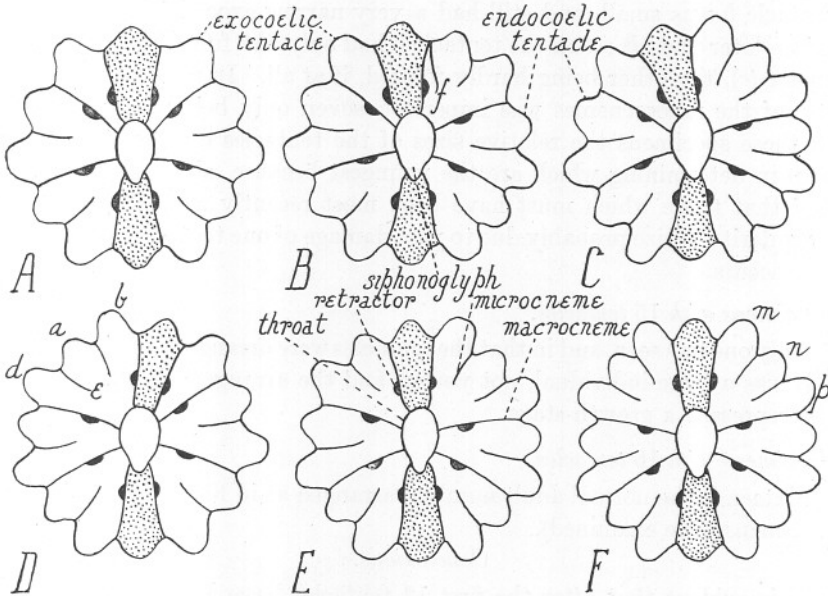


FIG. 4.—Diagrams to illustrate the mode of development of the tentacles 13-16 in *E. callimorpha*. For explanation of lettering, see text.

results were obtained, and I have added to them the case of an adult with only 15 tentacles.

*Specimens with 12 tentacles.*

Of these there were eleven, and in all of them the tentacles were arranged as in Fig. 4, A.

*Specimens with 13 tentacles.*

Only two individuals had 13 tentacles, and one of these was abnormal in one of the older sectors; if it had been normal it would have had 14 tentacles, so was of no value as an example of the 13-tentacled stage. The other specimen had the arrangement shown in Fig. 4, B. Note that

the newly added tentacle has pushed the directive axis a little out of the straight. The new microcneme (*f*) appeared to be larger than its partner.

*Specimens with 14 tentacles.*

There were six of these, three of them with the tentacles arranged as shown in Fig. 4, C, the others as in Fig. 4, D. In these, again, the directive axis is a little out of the straight, pushed to one side or the other according to the sector in which new growth has taken place. One of the specimens, arranged as in Fig. 4, D, seemed to present a stage intermediate between those exemplified by Figs. 4, B and D; in it the tentacle *b* was small, and still had a very narrow exocœl (clearly it had arisen later than *d*); and the tentacle *a* had only one fully formed microcneme (*e*), the other being hardly formed, if at all. In another specimen one of the macrocnemes was imperfect, seven only being fully formed. In these specimens the relative sizes of the tentacles do not give much help in determining which are the youngest because, although one may find that those which must have been most recently formed are small, irregularity of size probably due to past damage of one tentacle or another, also occurs.

*Specimens with 15 tentacles.*

Only one was seen, and in that the tentacles were arranged as in Fig. 4, E; this was a large individual, not young, and the arrangement shown may not represent a growth-stage.

*Specimens with 16 tentacles.*

Sixteen is the normal adult number, arranged as in Fig. 4, F (numerous specimens were examined).

*Conclusions.*

It is evident that after the first 12 tentacles have been formed, nos. 13-16 are formed asymmetrically, an endocœlic and an exocœlic appearing first, on one side or other (indifferently) of the directive axis, followed later by another endocœlic and exocœlic on the opposite side. Beyond this the paucity of observed stages with 13 or 15 tentacles prevents certainty, but it would appear that on whichever side of the directive axis growth may be taking place, the tentacle *p* (in Fig. 4, F) is the one which was in existence at the 12-tentacled stage, and that of *m* and *n* the first to be formed is *n*.

5. NOTE ON THE REGIONS OF THE COLUMN IN EDWARDSIAS  
AND OTHER ACTINIANS.

The body of an Edwardsia is usually said to be divided into three regions—physa, scapus, and capitulum. These terms are also applied to regions of the body in certain other anemones, and the usage is not

uniform. In some cases there are distinctly-marked regions present which are not accounted for in the ordinary terminology, and sometimes a region receives a name which is not its due. It is desirable that precision should be given to the terms in question and that they should be used more carefully. The following notes are an attempt towards this end, and are illustrated by Fig. 5.

(1) *Physa*. This term is accurately applicable only to the vesicular aboral extremity of a burrowing form. A physa is a digging organ; it is generally perforated by small apertures; often provided with irregular microscopic suctorial rugæ which enable it to adhere to foreign bodies; is usually marked off fairly or very distinctly from the next region of the column (scapus), this being most evident when it is contracted. If a living contracted *Peachia* or *Halcampa* be viewed from the aboral end, the physa will be seen as a rosette of tissue distinctly different from that of the scapus, and often with a deep pit in its centre. Finally, a well-marked physa has different ectoderm from the scapus above it; and in an *Edwardsia* it is further marked off by the fact that the nemathybomes cease abruptly where the physa begins.

It is often stated that a physa is "retractile within the scapus." This is sometimes actually the case (e.g. *Edwardsia vegæ*, see Carlgren, 1921, Text-fig. 62); but the statement is also due sometimes to defective observation. There is no British species which I have been able to examine alive which can retract the physa. In *Edwardsia callimorpha* and *E. delapix*, *Halcampa chrysanthellum* (= *H. arenaria*) and *Peachia triphylla*, there is a well-developed physa. It is non-retractile, but can contract into a flattened rosette and unless examined very carefully may look as if it had been invaginated because of the pit in its centre. Sometimes an anemone may be found with the end of the scapus tucked in; but this can be due to damage to the physa, which is being regenerated; and is not necessarily true retraction.

There remain the cases where an animal possesses a rounded aboral end which is sometimes inflated after the manner of a physa, and which looks like one at first sight. Such cases are *Milne-Edwardsia carnea* and *Mesacmæa (Ilyanthus) mitchelli*. In both these the aboral end may look physa-like, and in the latter can apparently be used for digging; but it is not morphologically differentiated from the scapus and it is able to adhere like the pedal disc of an ordinary anemone. *M. carnea* adheres in its normal condition, and *Mesacmæa*, when comfortable in an aquarium, sometimes adheres with very great force by a broad flat basal area. A true physa can adhere lightly by its suckers, but it is only anchored, not truly attached, and as far as I know can never become a firmly adherent base as in *Mesacmæa*.

There are doubtless intermediates between these two states, though I



cannot speak of them from personal observation. These would be very difficult to determine accurately except from living material.

(2) *Scapus*. This region includes the greater part of the body in any anemone which has a differentiated column, the other terms applying to the extremities. The only difficulty connected with the scapus is its limitation—just where does it pass into one of the other regions? Where there is a well-marked physa the boundary-line is clear enough in a contracted living specimen; where there is a rounded aboral end which is not a physa there is no definite boundary. The difficulty is greater when it becomes a question of defining the boundary at which the scapus passes into the capitulum.

(3) *Capitulum*. There is no strict homology between the regions of different anemones to which this term has been applied.

(a) In *Sagartia* there is no division of the column into regions, and nothing that can be called a capitulum; the same is true of *Bolocera*, etc.

(b) In *Calliactis* and *Stomphia* there is no actual capitulum, but there is a tendency for the submarginal region to be slightly differentiated from the rest.

(c) In *Hormathia*, *Actinauge*, *Paraphellia* (and in some of their relatives, as yet not fully described, e.g. "*Phellia*" *brodricii* and *P. gausapata*), the submarginal zone is distinctly marked off from the main part of the column (scapus) as a separate region with different ectoderm and without the tubercles and cuticle often developed by the latter (though it may have ridges instead of tubercles). It is not, however, a thin-walled region, and in fact is apt to be even more solid as to its mesoglœa than the scapus, since it contains the marginal sphincter or, at any rate, the upper part of this. The region in question is marked *sl* in Fig. 5, D and F.

(d) In *Metridium* (Fig. 5, B) there is an extensive submarginal region (*c*), limited below by the collar which terminates the upper edge of the scapus; here, however, the sphincter is in the collar, and the more delicate region above the collar is not comparable to the submarginal zone of *Hormathia*, etc. Sometimes it is even marked off from the scapus by a sharp change of colour; it is thinner-walled, with modified ectoderm, and modified endodermal circular-muscle layer. The same principle is found in *Diadumene*, where there is a delicate submarginal region above a scapal collar; but here there is no sphincter at all. The term capitulum is often applied to the submarginal regions both here and in *Hormathia*, although they are not homologous.

(e) In *Tealia* (Fig. 5, A) there is a strong marginal fold (*p*) bearing the sphincter, and above this a definite and clearly marked region (*c*) of delicate structure between sphincter and tentacle bases; this region is not generally called a capitulum, but it is comparable to the similar but



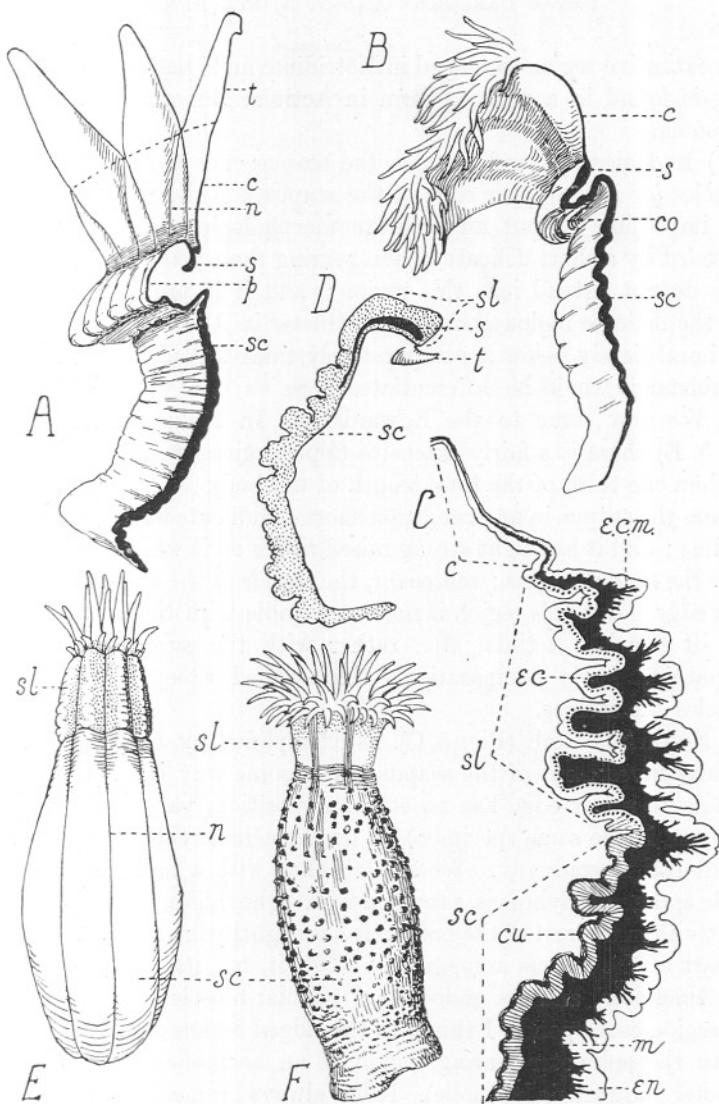


FIG. 5.—The regions of the column wall in Actinians.

- A. Sector of column, with tentacles, from *Tealia*. In this and in B, the cut edge is black. The dotted line indicates upper edge of capitulum.  $\times 1$ .  
 B. Sector of column, with tentacles, from *Metridium*.  $\times 1$ .  
 C. Longitudinal section of upper part of column of *Edwardsia callimorpha*. The mesogloea and the processes of the endodermal muscle-sheet are black. This section did not pass through any nemathybomes.  $\times 15$ .  
 D. Vertical section through the body-wall of *Actinauge richardi*. Sphincter black. The thickness of the wall is here largely composed of mesogloea.  $\times 1$ .  
 E. Entire specimen of *Milne-Edwardsia carnea*, in a contracted condition.  $\times 6\frac{1}{2}$ .  
 F. Living specimen of *Phellia gausapata*.  $\times 1$ .

c, capitulum; co, collar; cu, cuticle; ec, ectoderm; e.c.m., endodermal circular muscle; en, endoderm; n, mesenterial insertion; m, mesogloea; p, parapet; s, sphincter; sc, scapus; sl, scapulus; t, tentacle.

more extensive region so named in *Metridium* and *Diadumene*. The same thing is found in a reduced form in *Actinia*, *Bunodactis*, and even in *Anemonia*.

(*f*) In *Halcampa* and *Peachia* the scapus ends very little below the tentacles (or if the upper edge of the scapus is to be placed lower down it is impossible to put an accurate morphological limit to it) and is succeeded by a short delicate region bearing these; the imperfect mesenteries do not extend into this region; and it is probably homologous with the delicate region above the sphincter in *Actinia* and *Tealia*. The part immediately below is comparatively thick-walled, and if there were a sphincter it would be differentiated here.

(*g*) We now come to the *Edwardsiæ*. In *Milne-Edwardsia carnea* (Fig. 5, E) there is a fairly extensive upper region (*sl*), though it occupies less than one-third of the total length of the body; it is sharply marked off from the scapus in any condition short of full extension, by a recognisable line; and it has eight strong raised ridges on it which cease abruptly where the scapus begins; moreover, the cuticle of the scapus ceases at its lower edge. But this region is not comparable with the tentacle-bearing neck of *Peachia*, *Actinia*, etc., rather with the submarginal zone of *Hormathia*. It is comparatively thick-walled except just below the tentacles themselves.

In *Edwardsia* itself (Fig. 5, C), as exemplified by *E. callimorpha*, the cuticular investment of the scapus ceases some way below the tentacles (though its upper edge has no constant position, varying from time to time even in the same specimen), so do the nemathybomes, though these die out rather gradually. We are left then with a region (*sl*) devoid of cuticle and nemathybomes, provided with eight ridges, and coloured more brightly than the rest of the body; it has slightly different ectoderm than the part of the scapus immediately below it, but its mesogloea is of the same thickness, and its endodermal circular-muscle is well developed. This region corresponds, I think, to the ridged region of *Milne-Edwardsia* and to the sphincter-bearing region of an anemone which has a true sphincter (*Edwardsia* has none). It has always been called the capitulum. At the same time, *Edwardsia* possesses, in fact, above this "capitulum" another region (*c*)—a narrow, delicate, thin-walled, colourless part bearing the tentacles; in it the mesogloea and endodermal circular-muscle are reduced as compared with the part below, and the ectoderm thins out somewhat also; moreover, the microcnemes are practically confined to this region and do not penetrate far into that below. This region is no doubt comparable to the tentacle-bearing region of *Peachia* and *Halcampa*, but we have in *Edwardsia* two kinds of "capitulum" one above the other. Moreover, there is the difficulty that in *Edwardsia* the lower capitulum is not always marked off at all clearly from the scapus—there may be a

distinctive ring of colour at about the point where they join, and at this point the ridges may rise into crests; but sometimes the colour fades off gradually from above downwards and it is very difficult to separate one region from the other—i.e. the coloured region is morphologically part of the scapus.

(h) We have then at least two types of capitulum. The first is a comparatively thick-walled region, containing the sphincter (or, in the absence of a sphincter, well-developed mesogloea and endodermal muscle-sheet); the second is a region above the sphincter and more delicate in structure than the scapus. These two types of region are clearly not homologous, especially as in *Edwardsia* both are developed. It is necessary to introduce a new term for one of them, or else to continue to use "capitulum" for two different things. The latter course would seem to be undesirable. I therefore propose that the matter be regarded as follows:—

The body-wall in Actinians tends to differentiate into regions; in some cases a delicate submarginal region above the sphincter (or above the place where the sphincter would lie if it existed) can be recognised; this is a true capitulum. In other cases the scapus itself differentiates into regions; an upper part, containing the sphincter or the head of it, but at the same time differentiated from the part below; and a distinct lower region; or, in sphincterless forms the upper part is differentiated but is morphologically part of the scapus. The upper portion of a differentiated scapus such as this I propose to call a *scapulus*. In *Hormathia*, therefore, the column is divided into scapus and scapulus, and there is no capitulum. In *Edwardsia* we have both scapulus and capitulum present; in *Milne-Edwardsia* the upper part is a scapulus, but perhaps has a feebly marked capitular region above it also.

The proposed restriction of the term capitulum does not carry out the original intention of the term to the letter, but to my mind it fulfils the spirit of that intention. It should not be thought from the above discussion that the regions of an Actinian body-wall have the degree of distinctness attained by the segments of an Annelid—far from it; but they are none the less recognisable entities.

## PART 2. ANATOMY.

By

OSKAR CARLGREN.

## EDWARDSIA CALLIMORPHA (Gosse).

*Scolanthus callimorphus* n.sp., Gosse, Ann. Mag. Nat. Hist. (2) 12, p. 157, Pl. 10.

*Edwardsia callimorpha* Gos., Gosse, 1860, Actin. Britan., p. 255, Pl. 7, Fig. 7.

*Edwardsia claparedii* Panc., Andres, Mitt. zool. Stat. Neapel. 2, 1880, p. 123, Pl. 8; Le Attinie, 1883, p. 303, Pl. 11, Figs. 1-5 (pro parte).

*Edwardsia claparedii*, Carlgren, Zool. Anzeig., 27, p. 543; The Danish Ingolf Exp., 5, 9, Actiniaria, pp. 23-25, Figs. 6, 7, 8, 10.

*Edwardsia beautempsii* Quatr., Haddon, 1889, Sci. Trans. R. Dublin Soc. 4 (2), p. 327, Pl. 33, Fig. 17, Pl. 36, Fig. 4.

*Diagnosis.* Physa well developed. Scapus-periderm of ordinary thickness. Nemathybomes rather large, arranged in eight longitudinal rows. Tentacles (12)-16. Pennons of the macrocnemes in the upper part of the reproductive region with numerous folds, often profusely branched, especially in the outer and innermost parts. Outer lamella of the mesenteries attached to the pennons rather far from their outer edge. Parietal muscles in the same region more or less triangular, with numerous folds which are mostly not ramified. Extension of the parietal muscles on to the column-wall only slight. Microcnemes comparatively well developed, but weak as in other *Edwardsia*-species. Nematocysts of the nemathybomes partly (72)  $84-113 \times 4.5-6\mu$ , partly (53)  $60-82 \times 2.5$ -almost  $3\mu$ ; those of the scapulus  $10-12 \times 1.5\mu$ ; those of the tentacles  $18-26 \times$  about  $2-2.5\mu$ ; those of the actinopharynx partly  $24-31 \times 2.5-3\mu$ , partly  $29-41 \times 5-6.5\mu$  (the latter broader at the basal end and with a visible basal part to the spiral thread). Spirocysts of the tentacles  $10 \times 1$  to about  $22 \times 3\mu$ .

Stephenson has identified one of the species from Valencia with Gosse's *Edwardsia callimorpha*, and suggests that this species is identical with *Edwardsia claparedii*, figured by Andres in his work of 1883. A close examination of the anatomy of both these species shows clearly that at least the common form of *claparedii* belongs to *callimorpha*; but probably this does not apply to all the varieties figured by Andres in his Pl. XI, Figs. 1-5. Whether *callimorpha* and Quatrefage's *beautempsii* are identical, as Haddon supposed, it is hardly possible to decide. On the other hand, Haddon's *beautempsii* is certainly the same form as the

*callimorpha* from Valencia. From the Dublin Museum I have received a specimen labelled *Edwardsia beautempsii*, Berehaven (one of Haddon's localities). The upper part of the body has been cut off, and only the lower part remains. It is certainly the specimen examined by Haddon. The nematocysts of the nemathybomes agree well with those of *callimorpha*. Also, the parietal muscles examined by me on Haddon's slides

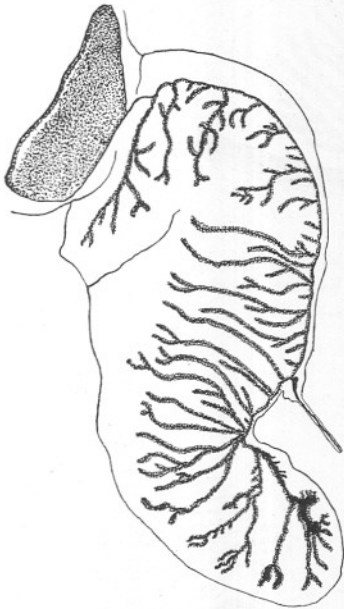


FIG. 6.—*E. callimorpha*. Transverse section of retractor in upper part of fertile region. The dotted area is part of a gonad. Valencia specimen.

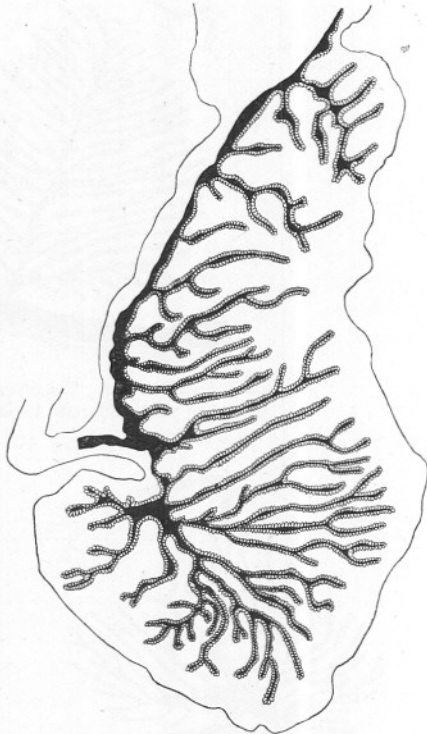


FIG. 7.—*E. callimorpha*. Transverse section of retractor in upper part of fertile region. Naples specimen.

show rather good agreement with those in Gosse's species. Haddon's slides of the pennons are very bad, and the figure of such a one in Haddon's paper is quite useless for identification of the species.

*Anatomical Description.* The anatomy of this species recalls that of other *Edwardsia*-species, so that it is not necessary to go into details. The physa is perforated by pores—"cinclides" (observed on slides of *claparedii*). I have already (1904, 1921) given figures of the arrangement of the mesenteries and of the actinopharynx with the weak ventral

siphonoglyph. The pennons of the macrocnemes are not concentrated, but more diffuse, in the upper part of the reproductive region, the folds numerous and especially richly branched in the outer and innermost parts. The outer lamellar portions of the mesenteries issue rather far from the outside edges of the pennons. In Figs. 6 and 7 I have reproduced pennons

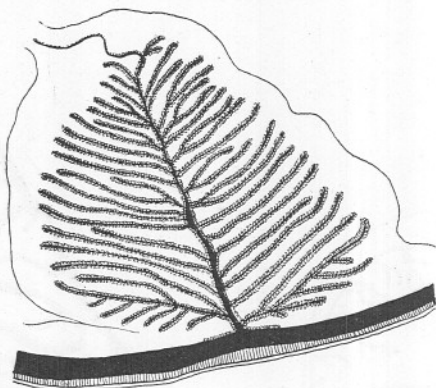


FIG. 8.—*E. callimorpha*. Transverse section of parietal muscle in upper part of fertile region. Valencia specimen.

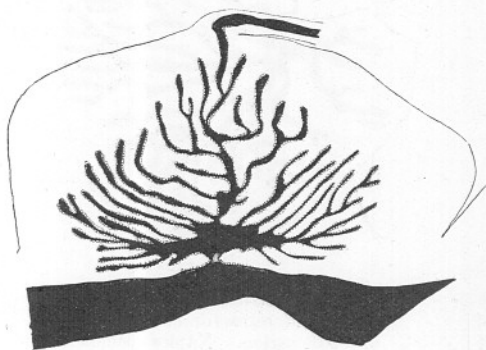


FIG. 9.—*E. callimorpha*. Transverse section of parietal muscle in middle part of fertile region. Naples specimen.



FIG. 10.—*E. callimorpha*. Transverse section of parietal muscle in upper part of fertile region. Haddon's "*beautempsii*" specimen.

from one Naples specimen and from one Valencia specimen. The parietal muscles are strong and triangular in the upper part of the fertile region, and are provided with numerous but little-branched folds. Figs. 8-10 show parietal muscles from the Valencia specimen, from *claparedii*, and from Haddon's "*beautempsii*."

The size of the nematocysts from the different regions agrees very well



in the three "species," as is evident from the following table (A, B, *claparedii*; C, *callimorpha*; D, Haddon's *beautempsii*):—

*Nemathybomes.*

- A.  $84-106 \times 4.5-6\mu$ ;  $62-82 \times 2.5-3\mu$ .
- B.  $84-94\mu$ ;  $65-74\mu$ .
- C. (75)  $84-113 \times$  about  $5\mu$ ;  $63-82 \times$  about  $2.5\mu$ .
- D.  $72-105 \times$  about  $5\mu$ ; (53)  $60-74 \times$  about  $2.5\mu$ .

*Tentacles.*

- A.  $18-23 \times$  almost  $2\mu$ .
- B.  $17-23 \times$  almost  $2\mu$ .
- C.  $22-25 \times$  almost  $2(2.5)\mu$ .
- D. . . . .

*Actinopharynx.*

- A.  $26-31 \times$  about  $2.5-3\mu$ ;  $29-34 \times$  about  $5-6\mu$ .
- B. . . . .
- C.  $24-30 \times$  about  $3\mu$ ;  $31-41 \times 5-6.5\mu$ .
- D. . . . .

EDWARDSIA DELAPLÆ n.sp.

*Edwardsia timida* Quatref., Haddon, 1889, Sci. Trans. Dublin Soc., 4 (2), p. 329, pro parte; Pl. 36, Fig. 3; p. 331.

*Diagnosis.* Physa well developed. Scapus-periderm of ordinary thickness. Nemathybomes scattered, rather numerous, varying in size but not large. Tentacles (14)–16. Pennons of the macrocnemes in the upper part of the fertile region with numerous (between 20 and 30) folds, which are rather well branched, especially in the outer and innermost parts of the pennons. Outer lamellar portions of the macrocnemes attached to the pennons rather far from their outer edges. Parietal muscles in the same region more or less elongated, considerably weaker than in *callimorpha*, with fewer folds which are only slightly branched. Extension of the parietal muscles on to the column wall about as usual. Nematocysts of the nemathybomes partly  $59-77 \times 5.5-5.5\mu$ , partly  $46-58 \times 3-3.5\mu$ ; those of the scapulus  $10-12 \times 1-1.5\mu$ ; those of the tentacles  $19-22 \times 1.5-2\mu$ ; those of the actinopharynx partly  $26-34 \times 2.5(3)\mu$ , partly  $19-22 \times 1.5$ –almost  $2\mu$  (sparse); spirocysts of the tentacles about  $11 \times$  almost  $2\mu$ – $22 \times 3\mu$ .

Of the Valencia specimens I have seen only one. I have also examined slides of the species described by Haddon in 1889 as *Edwardsia timida*. The appearance of the pennons and parietal muscles in "*timida*" agrees

rather well with that of the same organs in our present species; the nemathybomes are scattered and their nematocysts (measured only from slides) are partly  $60-67 \times 5\mu$ , partly  $43 \times 2\mu$ . The last-mentioned nematocysts are a little smaller in "*timida*" than in *delapiae*; but as the nematocysts mostly shrivel a little during the treatment of the slides this small difference is unimportant.

The anatomy of this species agrees with that of other *Edwardsia*-

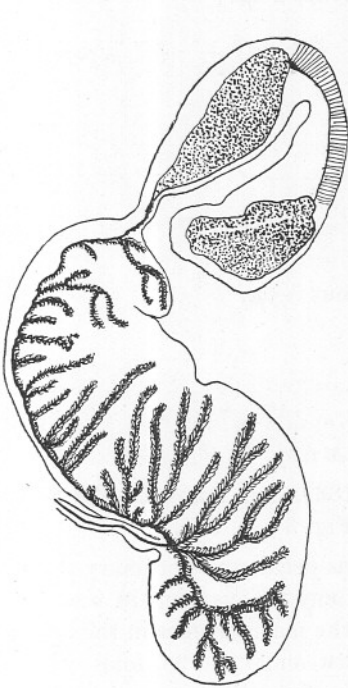


FIG. 11.—*E. delapiae*. Transverse section of retractor in upper part of fertile region. The dotted areas represent gonad. Valencia specimen.

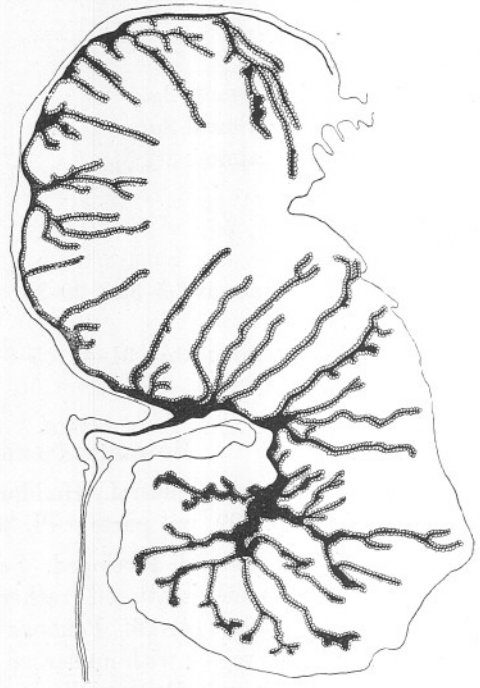


FIG. 12.—*E. delapiae*. Transverse section of retractor in the fertile region. Haddon's "*timida*" specimen.

species. I have figured for comparison two pennons, one from the Valencia specimen, and one from Haddon's "*timida*" (Figs. 11 and 12). The slide of "*timida*" is taken from the fertile region, but I cannot decide whether or not it is from the uppermost part of this tract because the upper part of this animal was not sectionised by Haddon. Fig. 13 shows the appearance of the parietal muscle in the upper part of the fertile region in the Valencia specimen.

The species is closely related to *Edwardsia danica*, but in this latter form the nematocysts of the nemathybomes are smaller.

## EDWARDSIA TECTA Haddon.

*Edwardsia tecta* n.sp., Haddon, 1889, p. 329, Pl. 33, Fig. 16; Pl. 36, Figs. 1-2.

*Diagnosis.* Physa small, delicate, completely retractile within the scapus. Scapus with eight shallow longitudinal grooves, with few scattered nemathybomes not forming tubercles on the surface. Periderm of the scapus thin, translucent, easily deciduous. Scapulus delicate. Tentacles at least 14 in number. A distinct ventral siphonoglyph present. Pennons of the eight macrocnemes (in the upper part of the cnido-glandular tract) with few (about 10-12) high folds, which are unbranched or but slightly forked, except for the outermost fold, which is large and more branched. Outer lamellar part of the macrocnemes attached not far from the outer edges of the pennons. Parietal muscles in the same region triangular, with few but rather high folds; their extension on to the column wall about as usual. Nematocysts of the nemathybomes partly  $34-43 \times$  about  $3.5\mu$ , partly  $55-72 \times 4.5\mu$ ; those of the scapulus about  $10 \times 1.5\mu$ ; those of the tentacles about  $17\mu$ ; those of the actinopharynx  $24-31 \times 2-2.5\mu$  (size of the nematocysts measured only on slides). Specimens not sexually ripe.

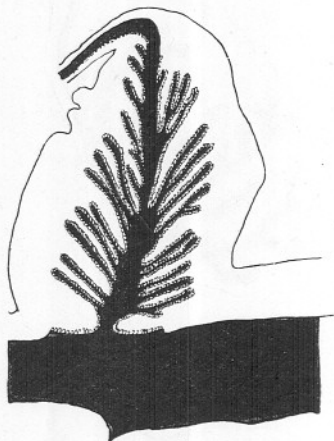


FIG. 13.—*E. delapicæ*. Transverse section of parietal muscle in upper part of fertile region. Valencia specimen.

*Colour, dimensions, and occurrence;* see Haddon, 1889, and this paper, p. 10.

I have examined Haddon's slides of this species. The slides of the specimen from Nymph Bank were well preserved. It is certainly this specimen which Haddon described and figured. A slide including sections of the undermost part of the actinopharynx and of the ciliated tract and also sections of the physa I have, however, not examined. Several other slides labelled *E. tecta* were also present in Haddon's collections. These were, however, very badly preserved; and some longitudinal sections showing numerous very close nemathybomes certainly do not belong to this species.

*External characters.* According to Haddon, the physa is small, delicate, and completely retractile; he has not observed any terminal pore in it. Probably the pores were overlooked by him, as I have found pores in all the physæ which I have examined in the genus *Edwardsia*. The periderm of the scapus is thin and easily deciduous; in the preserved specimens it is quite loose from the ectoderm. Haddon states that the

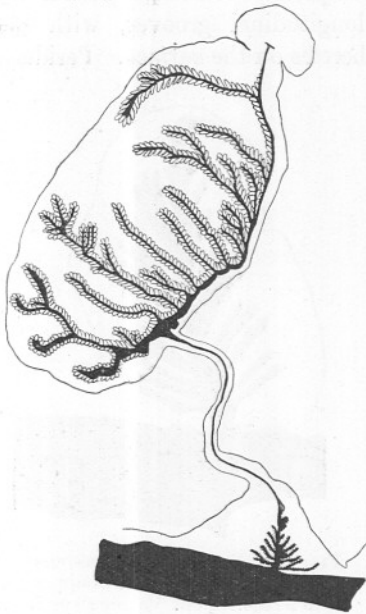


FIG. 14.—*E. tecta*. Transverse section of macrocneme in the region of the cnido-glandular tract.

species lacks tubercles on the scapus. It is true that there are no visible tubercles, but in the mesogloea nemathybomes are present. They are of ordinary size, scattered and few in number. Some of them are situated exactly in the middles of the intervals between the insertions of the mesenteries, others lie nearer to the insertions themselves. On the whole, the arrangement of the nemathybomes recalls that of *E. danica* (Carlgren, "The Actinaria of the Ingolf Expedition," 1921, p. 32, Fig. 17), although the nemathybomes here are more sparse than in that species. The uppermost part of the introverted anterior end is polygonal. The boundary between the scapus and scapulus is not distinct, but the scapulus is certainly considerably longer than the microcnemes. Haddon states that there are only 8 tentacles in the single

specimen examined by him. As far as I can discover, 14 tentacles are present in the specimen sectionised, arranged as in the *Edwardsia*-species with 16 tentacles, except for the fact that only one tentacle issues from one of the dorso-lateral compartments. The single ventral siphonoglyph is distinct (see also Haddon's Fig. 1, Pl. 36).

*Anatomical description.* The ectoderm of the scapus is of average height, its periderm only a little incrustated; the mesogloea not much wrinkled. The nematocysts in the nemathybomes are numerous. In the introverted part of the scapus the mesogloea forms ridges between the insertions of the mesenteries. The ectoderm of the actinopharynx is very thick; the siphonoglyph is provided with longer cilia than the other parts of the actinopharynx, but its ectoderm is thinner.

The pennons of the macrocnemes are provided with 10-12 high folds

in the upper part of the cnido-glandular tract. The innermost fold is higher than those in the middle of the pennon. The outermost fold is coarse and branched, the other folds are unbranched, or more or less branched (Fig. 14). The parietal muscles are triangular, with about half a dozen folds on each side, which are some of them unbranched, some a little branched (Fig. 14); see also Haddon's Fig. 2, Pl. 36. The microcnemes are six in number in the sectionised specimen, two microcnemes being absent from one of the dorso-lateral compartments. The four microcnemes forming pairs with the lateral macrocnemes are comparatively well developed, the two other microcnemes very weak. The specimens show no traces of reproductive organs.

*Remarks.* As the form is a young one it is difficult to say to which species it belongs, or whether it is a distinct species. In many respects it recalls *E. danica* Carlgr., although the nemathybomes of that species are more numerous than they are in "*tecta*." It is possible that the species is the young of *E. delapiev*.

#### MILNE-EDWARDSIA DIXONII Carlgren.

*Edwardsia timida* Quatref., G. Y. Dixon, Sci. Proc. R. Dublin Soc., 5 (N.S.), 1886, p. 100, Pl. 6; not *Edwardsia timida* of Haddon.

*Milne-Edwardsia dixonii* n.nom., Carlgren, The Ingolf Exp., 5, 9, Actiniaria, p. 59.

*Diagnosis.* Physa well developed, retractile. Scapus long, cylindrical in the lower part, higher up polygonal, at least in contracted state; provided with a rough and opaque but thin periderm, which easily falls away. Nematocysts in the lower part of the scapus arranged in groups, in the upper parts on the ridges between the insertions of the mesenteries. Scapulus cylindrical. Tentacles 18-24 in two (?) cycles. Actinopharynx probably with a ventral siphonoglyph. Pennons of the macrocnemes of average development, forming in the upper part of the cnido-glandular tract about 12-18 high folds, which are branched little or not at all. Outer lamellar portions of the mesenteries attached not far from the outer edges of the pennons. Parietal muscles triangular with few but branched folds. Extension of the parietal muscles on to the column wall about as usual. Nematocysts of the scapus 25-31 × 5-6 (7)μ, broader at one end and often curved; those of the scapulus 15-25 × 2.5-3.5μ. of the same appearance as those of the scapus; nematocysts of the tentacles partly about 24 × 3-3.5μ, partly 14 × 1.5-2μ (probably also intermediate forms); those of the actinopharynx 17-24 × 5-3.5μ.

Many years ago I received three specimens of this species from Mr.



Dixon. Unfortunately they were not well preserved, so that the description here given is somewhat incomplete. I think, however, that it will prove sufficient for the identification of the species. As I have pointed out before (p. 23), the form which Haddon has called *Edwardsia timida* is not identical with Dixon's species. It is very doubtful whether Dixon was right in his opinion that his form was Quatrefages' "*timida*"; as a matter of fact, it is impossible to identify that species on the basis of Quatrefages' description. Therefore in 1921 I proposed a new name, *Milne-Edwardsia dixonii*, for Dixon's form.

*Colour, dimensions, and occurrence.* See Dixon, 1886, and this paper, p. 12.

*External characters.* I have made slides of two specimens; one is sectionised in the lower part, the other in the upper. I cannot determine

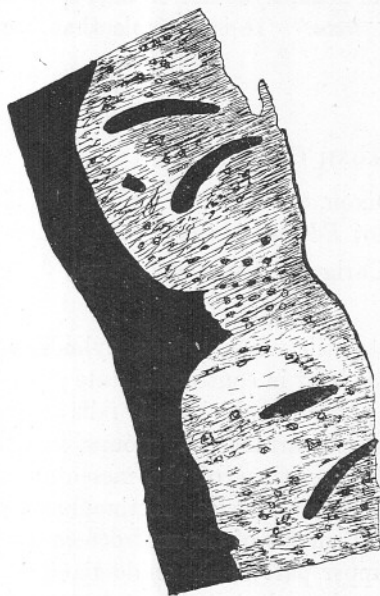


FIG. 15.—*M. dixonii*. Section of part of the scapus-wall. Mesogloea and nematocysts black, ectoderm shaded.

whether the physa was perforated by pores, as it is badly preserved. The lower part of the scapus is cylindrical, the upper polygonal by virtue of the fact that the ectoderm is considerably higher in the middles of the compartments than at the insertions of the mesenteries. The periderm of the scapus is thin and easily falls away. In the specimen of which I have cut the upper part, the periderm has mostly disappeared from the ectoderm. This species can probably, as in *M. carnea*, form a free tube into which the distal part of the animal can be withdrawn; and because of this fact the boundary between the scapus and the scapulus is not distinct. Since, however, the uppermost cylindrical part of the column, introverted in the sectionised specimen, certainly lacks a periderm, and moreover is provided with smaller nematocysts than the

scapus, this part may be the real scapulus. Probably Dixon (see 1886, p. 102) has mistaken part of the scapus for the scapulus. The tentacles are of ordinary length, according to Dixon 18–24 in number and arranged in two cycles, the inner of which should have 8 or 10 tentacles. I cannot confirm this statement, but I think that Dixon's statement as to the arrangement may be incorrect. The outer tentacles are probably



shorter than the inner (see Dixon's Figs. 2 and 3). The specimen examined by myself had 24 tentacles. The actinopharynx is probably provided with a single and ventral siphonoglyph.

*Anatomical description.* The ectoderm of the scapus is high and contains large nematocysts which are often curved, and in the lower part

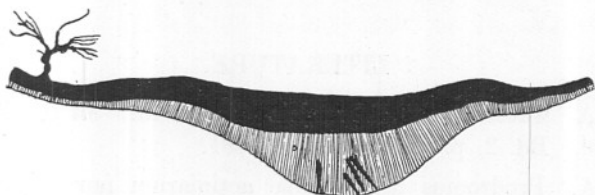


FIG. 16.—*M. dixonii*. Transverse section of a sector of the uppermost part of the wall of the scapus, between the insertions of two macrocnemes. Mesoglea, nematocysts, and part of a parietal muscle, black; ectoderm shaded.

of the scapus are concentrated into groups (Fig. 15). In the upper polygonal part of the column the ectoderm forms rather high ridges between the insertions of the mesenteries, and the nematocysts are here collected on the ridges, but are absent or very sparse in the furrows

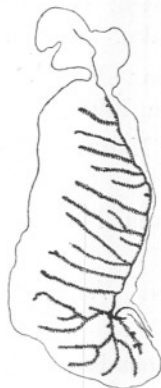


FIG. 17.—*M. dixonii*. Transverse section of retractor near the level of the ciliated tracts of the filaments.



FIG. 18.—*M. dixonii*. Transverse section of parietal muscle in the region of the actinopharynx.

(Fig. 16). The ectoderm of the scapulus, which is introverted in the sectioned specimen, is thin, and not thickened in the middles of the compartments. The nematocysts here are smaller than in the scapus. The structure of the tentacles agrees with that of other Edwardsias. The ectoderm of the actinopharynx is very thick, but the cilia are not well preserved.

The pennons of the eight macrocnemes (Fig. 17) recall those of *M. carnea*, and form rather few (12-18) folds, issuing from the main lamella. The parietal muscles are also of the same type as those of *M. carnea* (Fig. 18). The microcnemes are present, but not well preserved. The sectionised specimens were not sexually ripe.

## LITERATURE.

- ANDRES, A. Intorno all' Edwardsia Claparedii. Mitth. Zool. Stat. Neapel. Bd. 2, p. 123. Leipzig, 1881.
- ANDRES, A. Prodromus neapolitanæ actiniarum faunæ, etc. Mitth. Zool. Stat. Neapel. Bd. 11, p. 305. Leipzig, 1881.
- ANDRES, A. Le Attinie. Mem. R. Accad. Lincei, Rome, Ser. 3, Vol. XIV, p. 211. 1883.
- BOURNE, G. C. A Description of Five New Species of Edwardsia, Quatr., from New Guinea, with an Account of the Order of Succession of the Micro-mesenteries and Tentacles in the Edwardsiæ. Journ. Linn. Soc., Vol. XXXII, Zool., p. 513. London, 1916.
- CARLGREN, O. Beiträge zur Kenntnis der Edwardsien. Öfv. af K. Vetenskaps-Akad. Förhandl., 1892, p. 451. Stockholm.
- CARLGREN, O. Studien über Nordische Actinien. K. Svenska Vet.-Akad. Handl., Bd. XXV, No. 10. Stockholm, 1893.
- CARLGREN, O. Ostafrikanische Actinien. Mitth. Naturhist. Mus. Hamburg, XVII. Hamburg, 1900.
- CARLGREN, O. Kurze Mitteilungen über Anthozoen, 1-3. Zoologischer Anzeiger, Bd. 27, p. 534. Leipzig, 1904.
- CARLGREN, O. Actiniaria. Danish Ingolf. Exped., Vol. V, 9. Copenhagen, 1921.
- DANIELSSEN, D. C. Actinida. Den Norske Nordhaus-Expedition, Vol. 5. Christiania, 1890.
- DIXON, G. Y. Notes on two Irish Specimens of Edwardsia timida (Quatrefages). Sci. Proc. R. Dublin Soc., N.S., Vol. V, p. 100. Dublin, 1886.
- FAUROT, L. Études sur l'anatomie, l'histologie, et le développement des Actinies. Arch. Zool. expér. et gén., Sér. 3, t. 3, p. 43. Paris, 1895.
- GOSSE, P. H. Notes on some new or little-known Marine Animals. Ann. Mag. Nat. Hist. (2), XII, p. 153. London, 1853.

- GOSSE, P. H. Ann. Mag. Nat. Hist. (2), XVIII. London, 1856 (for *E. carnea*, see p. 219).
- GOSSE, P. H. A History of the British Sea-Anemones and Corals. London, 1860.
- HADDON, A. C. Preliminary Report on the Fauna of Dublin Bay. Proc. R. Irish Acad. (2), IV, p. 523. Dublin, 1886.
- HADDON, A. C. A Revision of the British Actiniæ: Part I. Sci. Trans. R. Dublin Soc., Ser. 2, Vol. IV, p. 297. Dublin, 1889.
- MARK, E. L. Drawings from an unpublished paper by E. L. Mark. Mem. Mus. Comp. Zool. Harvard, IX, No. 3, p. 43; Pl. XII, Figs. 24-33. Cambridge, Mass., 1884.
- MCINTOSH, W. C. Note on two New Species of the Genus Edwardsia. Proc. Roy. Soc. Edin., Vol. 5, p. 394. Edinburgh, 1866.
- MCINTOSH, W. C. The Marine Invertebrates and Fishes of St. Andrews. Edinburgh and London, 1875.
- MONTICELLI, F. S. Sulla larva di Edwardsia claparedii Panceri. Mitth. aus der Zool. Station zu Neapel, 13 Bd., p. 325. Berlin, 1899.
- OKADA, Yô K. Aktinienregeneration aus abgeworfenen Tentakeln. Archiv. zür Entwicklungsmech., Bd. 108, p. 482. Berlin, 1926.
- QUATREFAGES, A. DE. Memoire sur les Edwardsies (*Edwardsia*, Nob.) nouveau genre de la famille des Actinies. Ann. des Sci. Nat. (2), XVIII, Zool., p. 65. Paris, 1842.
- STEPHENSON, T. A. On the Classification of Actiniaria. Part 2. Quart. Journ. Micros. Sci., Vol. 65, 4, p. 493. London, 1921.
- WALTON, C. L., AND REES, O. M. Some Rare and Interesting Sea Anemones from Plymouth. Journ. Mar. Biol. Assoc., Vol. X, p. 60. Plymouth. 1913.

