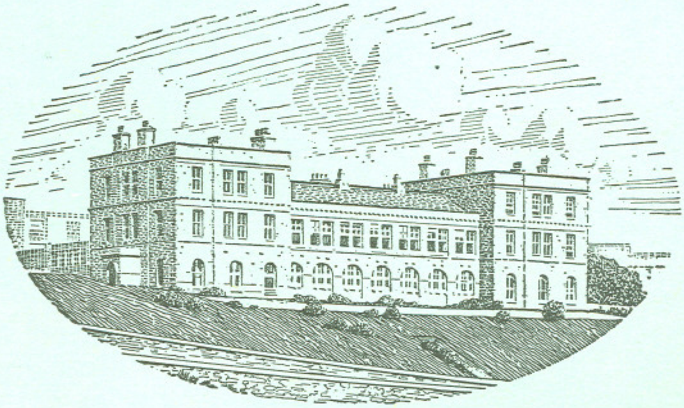
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



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MISS A. R. CLARK

Amy Rose Clark entered the service of the Marine Biological Association as clerk and typist in 1905. For a number of years she was in charge of the accounts which she kept with extreme care and accuracy, and throughout the whole of her service she acted as confidential clerk to the Director.

She also gradually undertook more work in connexion with the Library, and it was here that she chiefly came in contact with the scientific workers, who learned to value the ready help which she always gave them. The present extensive card catalogue is largely the result of her efforts. She had a remarkable memory for individual books, periodicals and even author's reprints and their positions on the shelves. She was quick too in dealing with second-hand booksellers' catalogues, discovering in what journals individual reprints had appeared, and whether or not they were already in the Library. Her work in this direction has done much to complete our literature on the different groups.

For twenty years Miss Clark has also taken a share in the scientific work, helping Mrs Sexton in caring for, examining and recording observations on living *Gammarus* which were being used in genetic work. She was a most careful observer, whose work could always be relied upon for thoroughness and accuracy. By her death, on August 12 1939, the Plymouth Laboratory has suffered a great loss, which will be felt by all who have worked there.

E. J. A.

PLANKTON PRODUCTION OFF PLYMOUTH AND THE MOUTH OF THE ENGLISH CHANNEL IN 1939

By Molly F. Mare, B.A.

Newnham College, Cambridge

(Text-figs. 1–10)

INTRODUCTION

Regular quantitative samples of phytoplankton and small zooplankton were taken near Plymouth with the Harvey measuring net from January to August 1939. Similar samples were obtained on three cruises* from the area comprising the western entrance of the English Channel and south of Ireland as far as the edge of the continental shelf. The microplankton of this area as a whole has been little investigated, the only previous quantitative records being those of Ogilvie (1923). The seasonal survey at Plymouth, though from inshore stations, forms a useful basis for comparison with the regional observations from the south-western area, and together they extend part of the work carried out in 1934 by Harvey *et al.* (1935) on plankton production and its control. The results in this paper deal only with phytoplankton in detail, and briefly with zooplankton in so far as it is necessary to the discussion of grazing intensity and for comparison with the results of 1934. Tables giving full details of the numerical data on which the following is based have been deposited for reference in the Library of the Marine Biological Association at Plymouth.

Papers by Cleve (1900), Gough (1905–7), Bygrave (1911), Bullen (1908), Lebour (1917) and records and résumés in the Bulletin Planktonique deal with the phytoplankton in this area.

METHODS

Vertical hauls were made with the Harvey measuring net (Harvey, 1934) at L4, the station used in the 1934 survey, 5 miles seaward of the Plymouth Breakwater lighthouse, and some hauls were also made at a slightly shallower station 1 mile west-south-west of Rame Head. At both stations hauls were made between the surface and 40 m. (that is to within 5–10 m. of the bottom); a measured quantity of water usually about 1 cu. m. passed through the net. The bolting silk (200 meshes to the inch) had an average pore size of $52 \times 40\,\mu$ when wet. After addition of formalin the catch was made up to 500 c.c. and

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* Cruises made in connexion with mackerel researches at Plymouth.

further diluted if necessary. The phytoplankton was allowed to settle in a cell 1·75 mm. deep and counted from a total volume varying between 0·070 and 0·232 c.c. of the catch; the zooplankton and faecal pellets were counted in 3–5 aliquot subsamples of 4 c.c. each. This gave a sufficient order of accuracy as the exact numbers of rare species are not of particular interest. A proportion of the smaller organisms will of course have passed through the net, therefore the numbers given are minimal. While these methods do not give a complete picture of the microplankton, it is thought worth while to present the results obtained as they probably indicate the main trends of production in the area.

On the cruises the same Harvey net was used as at Plymouth. The catch was made up to 500 c.c., a small subsample (1/11th of the whole) was fixed and retained for species counts, and the rest filtered and an acetone extract made of the plant pigments (Harvey, 1934). In April and June the hauls were made between the surface and 20 fathoms (i.e. to approximately the same depth as those at L4 and Rame). On the March cruise at each of the five stations they were taken to 40 fathoms; but as it was found at St. 2 that all the phytoplankton was in the upper 20 fathoms, the meter readings were halved, thus making the figures more comparable with the others given in the tables: the phytoplankton was in any case very sparse and the general picture from that cruise remains unaltered. Counts were made as above, except that when very sparse in March and June some of the phytoplankton had to be counted in 4 c.c. subsamples. Nomenclature in this paper is that used by Lebour (1925, 1930) and Kofoid & Campbell (1929). Synonyms found in other lists referring to the south-western area are shown in parentheses.

SEASONAL SURVEY AT PLYMOUTH

As pointed out by Harvey *et al.* (1935) there is movement of water masses at L4, but it is probably correct to assume that water occupying that position at the time of sampling has passed through a history similar to that previously sampled. Plankton at the Rame station was very similar to that at L4, therefore on the whole the series of samples may be accepted as a reliable indication, both qualitatively and quantitatively, of planktonic successions in the neighbourhood of these two stations. Nevertheless, some of the fluctuations in numbers of animals (see Fig. 2), particularly in February and March, may be correlated with changes in water masses and not much significance should be attached to them.

It will be seen from Fig. 1 that in the early part of 1939 the phytoplankton at L4 was very sparse. At the end of February a centric diatom, 4–8 μ in diameter and probably *Thalassiosira nana*, was found abundantly, mainly adhering to other chains; much of this will also have been lost through the net. There was some increase in numbers during March, particularly of *Chaetoceros decipiens* followed by *C. debilis*, *C. affinis* and *C. laciniosus*. The maximum was late, the highest figures being 27,000 cells per litre recorded at L4 on April 12 and 93,000 cells per litre at Rame on April 14: *C. debilis* was dominant and among a rich variety of species *Thalassiosira Nordenskioldii*, *T. gravida*, *Coscinoscira polychorda*, *Thalassiothrix Nitzschioides*, *Lauderia borealis* and other *Chaetoceros* species were abundant. After these dates there was a gap in the observations until the end of the month while the net was in use on the second cruise. The subsequent smaller peaks in the numbers mainly consisted of small-celled species: *Rhizosolenia delicatula* in May, *R. Stolterfothii* with *Guinardia flaccida* in June, *Sceletonema costatum* and *Ceratium fusus* in July and *Rhizosolenia alata*, *R. delicatula*, *R. Stolterfothii* and *Nitzschia delicatissima* in August. In 1934 phytoplankton was abundant during the first two months and the highest density, in units of plant pigment, was recorded on March 20 (numbers were actually highest on the 26th, but this was due to a dense outburst of *Sceletonema costatum*). A comparison of the distribution of the hours of sunshine in the two years (the only comparable light data yet available, obtained from the Plymouth meteorological records)

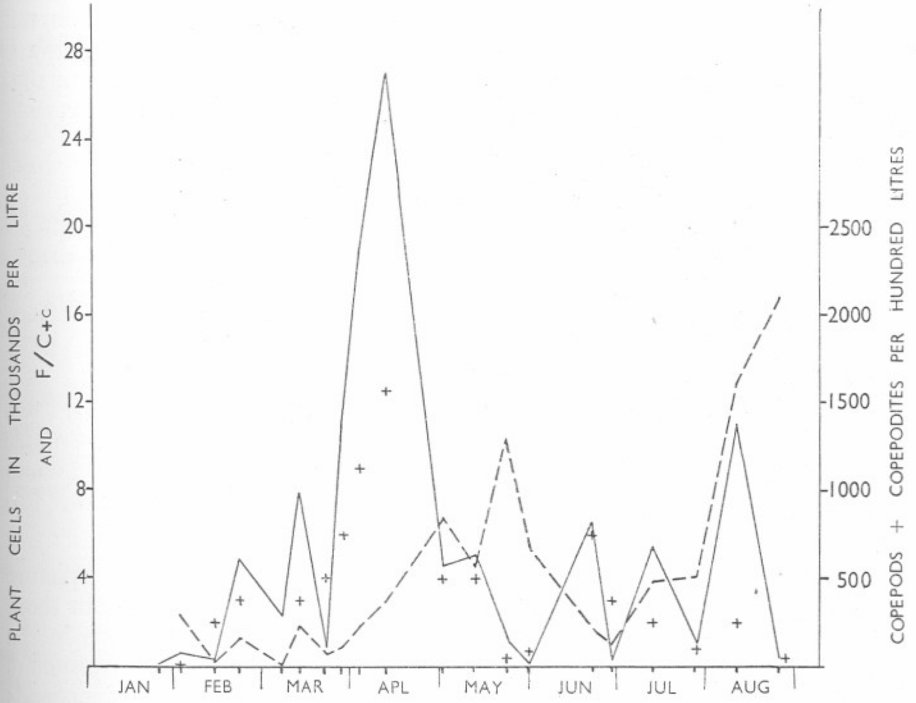

Fig. 1. Seasonal changes at L4, near Plymouth, in 1939. Numbers of plant cells, in thousands per litre (continuous line), numbers of copepods plus copepodites per 100 l. of sea (broken line) and number of faecal pellets per copepod plus copepodites, $F/C+c$ (+). This ratio shows correlation with the numbers of plant cells; the value for March 6 is anomalous—170—and is omitted from the graph. Lines joining the points have no real meaning.

suggests that light intensity may be one of many factors responsible for these differences. In 1934 January and February were very bright while March and April were rather dull. In 1939 the hours of sunshine for the first two months differed little from the mean for the past 40 years. The first part of March was very dull, bringing the total hours of sunshine for the month much below average; the latter part of March and the whole of April were bright. An apparent lag after the brightening of the weather before the phytoplankton maximum is reached has been previously recorded in this region (Atkins, 1930). The differences in the quantities of phytoplankton as shown by monthly averages of cell numbers are given in Table I, the 1934 figures being taken from the paper mentioned above (Harvey *et al.* 1935).

TABLE I. MONTHLY AVERAGES

	Plant cells per litre			Copepods + copepodites per 100 l.			Total animals per 100 l.		
	1934	1939		1934	1939		1934	1939	
	L4	L4	Rame	L4	L4	Rame	L4	L4	Rame
Jan.	2380	64	260	71	..	..	239	..	..
Feb.	1750	1940	..	119	159	..	545	580	..
Mar.	21600	5430	1850	318	106	39	2024	640	380
Apr.	3890	22900	56900	450	295	277	2518	1990	2390
May	7100	2750	5300	1028	850	797	3365	3590	1640
June	6050	3490	5740	439	175	270	2440	1380	1140
July	2320	3220	520	799	500	380	2852	2880	1900
Aug.	740	5920	..	1343	1030	..	4963	6530	..

The Harvey net used in collecting these samples is too small to give a picture of the total population of zooplankton, but it is worth while to count those animals which were caught so as to gain an idea of the variations in the population of herbivores. These include both diatom eaters and consumers of nannoplankton. On the whole it would appear that the number of copepods plus copepodites caught is proportional to the total diatom grazing population. In working up data collected with the same apparatus, Harvey used the number of faecal pellets per copepod plus copepodite as an index of the amount of grazing per animal. This ratio ($F/C+c$), the number of plant cells per litre (unweighted for size) and the number of copepods plus copepodites per 100 l. of sea are plotted together in Fig. 1. As already shown by Harvey, there is highest grazing activity at times of phytoplankton abundance (see 1935, Fig. 12, p. 424). At the spring diatom maximum the faecal pellets were green, whereas later they were brown, when probably the diet included a higher proportion of detritus. Most of the faecal pellets were too large to have been produced by the copepods caught in the net; it is therefore not surprising that there should be some anomalous results when pellets were apparently very abundant relative to the number of animals, e.g. at L4 and Rame on March 6 and 9.

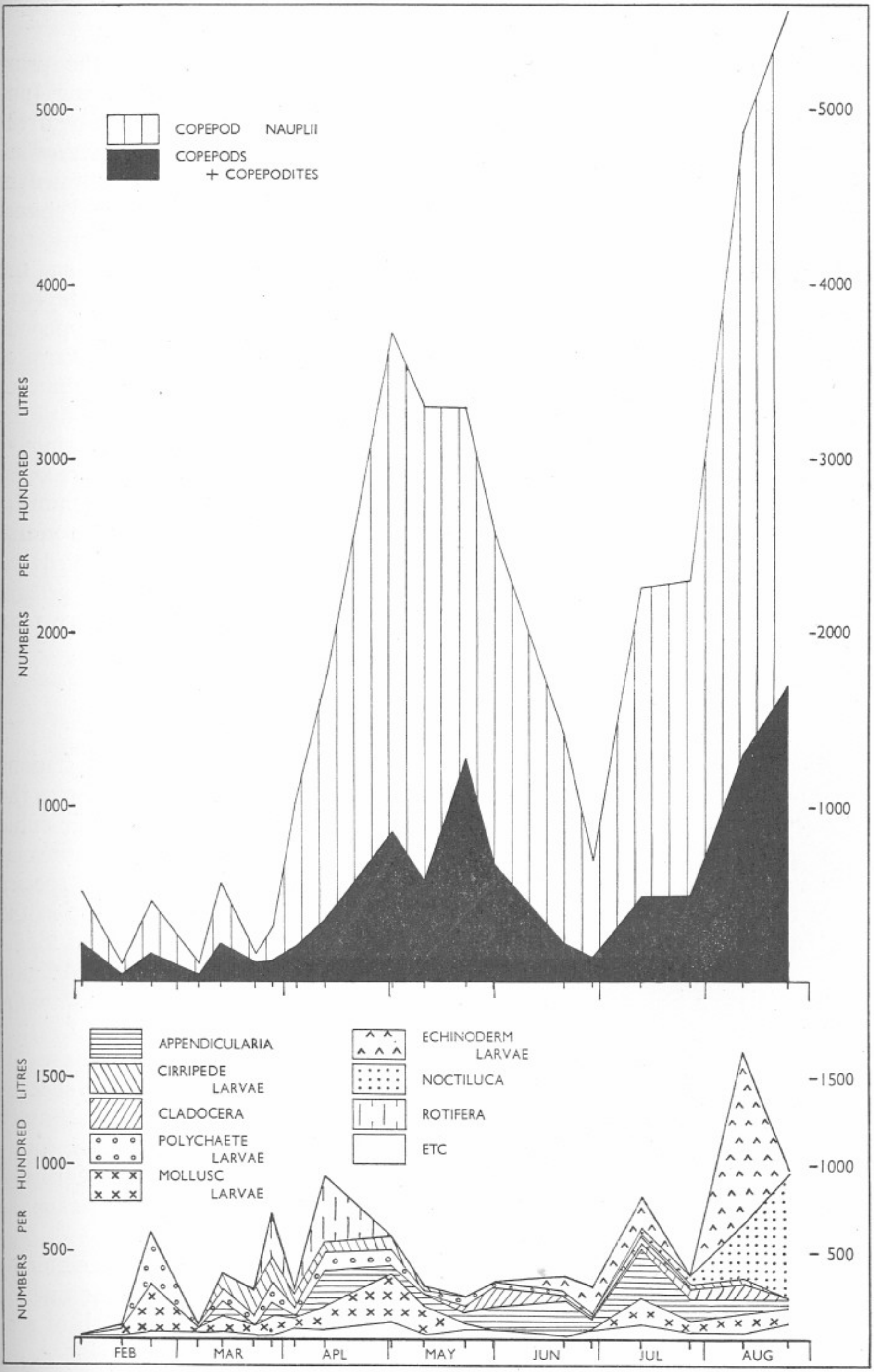

Fig. 2. Seasonal changes in the number of animals at L4, near Plymouth, in 1939.

The zooplankton numbers followed the usual course, rising after the spring phytoplankton maximum and showing reciprocal fluctuations during June and July. In the early part of the year the fluctuations were concurrent (see p. 462). The summer increase in zooplankton was still in progress when sampling had to be discontinued. The zooplankton was not identified in detail as it was required only as an indication of the abundance of animal life. Fig. 2 shows the total number of copepods with the proportion of nauplii to copepods plus copepodites, and the total of other animals and the proportions of the various groups. There is a general similarity with the 1934 data (see Harvey *et al.* 1935, Fig. 9, p. 421) particularly with regard to copepods and rotifers. Mollusc larvae were more numerous in 1939 but no swarm of *Limacina* was encountered. Numbers of echinoderm larvae were insignificant in the early part of the year and are included in the bottom group until the end of May: the outburst of ophioplutei in the latter part of the summer, though not found in 1934, has been paralleled in several previous records. Table I shows that the monthly averages of the total number of animals, including meroplanktonic forms, was of the same order in the two years; the copepods plus copepodites were, however, only about two-thirds as numerous in 1939 as in the earlier year, thus showing evidence of the general decline in quantity of zooplankton which Russell has found here since 1934 (see Russell, 1938, Table II, p. 419, for medusae and young fish).

REGIONAL SURVEY OF THE SOUTH-WESTERN AREA

On the first cruise phytoplankton samples were taken at only five stations on March 15 and 16, and at all these plants were scarce. Fig. 3 A shows the density distribution in Harvey's arbitrary units of plant pigment per cubic metre, and the positions of the stations relative to the edge of the continental shelf, as indicated by the 100 fathom line. At St. 1 and 2 nearly all species were neritic, while the three outer stations showed oceanic influence in the presence of Radiolaria, *Globigerina*, *Dictyocysta lepida* (an Atlantic and Mediterranean tintinnid, recorded as *D. templum* by Ogilvie) and the Atlantic oceanic diatom *Dactylosolen antarcticus*; *Ceratium bucephalum* and *C. lamellicorne* were also restricted to these stations.

The second cruise (April 16–26) presents many interesting features of distribution both of phytoplankton density as a whole and of individual species. Fig. 3 B shows the phytoplankton density in terms of Harvey's arbitrary pigment units; the highest values were 6250 at St. 20 on the edge of the continental shelf, and 4400 at St. 2 and 36 at the mouth of the English Channel. Fig. 4 shows all stations, but at only the numbered stations was full examination for species made.

Figs. 5 and 6 give examples of the types of species distribution encountered. They indicate the presence, in the top 20 fathoms, at the particular time of sampling, of organisms not rarer than approximately one per 10 l. of sea.

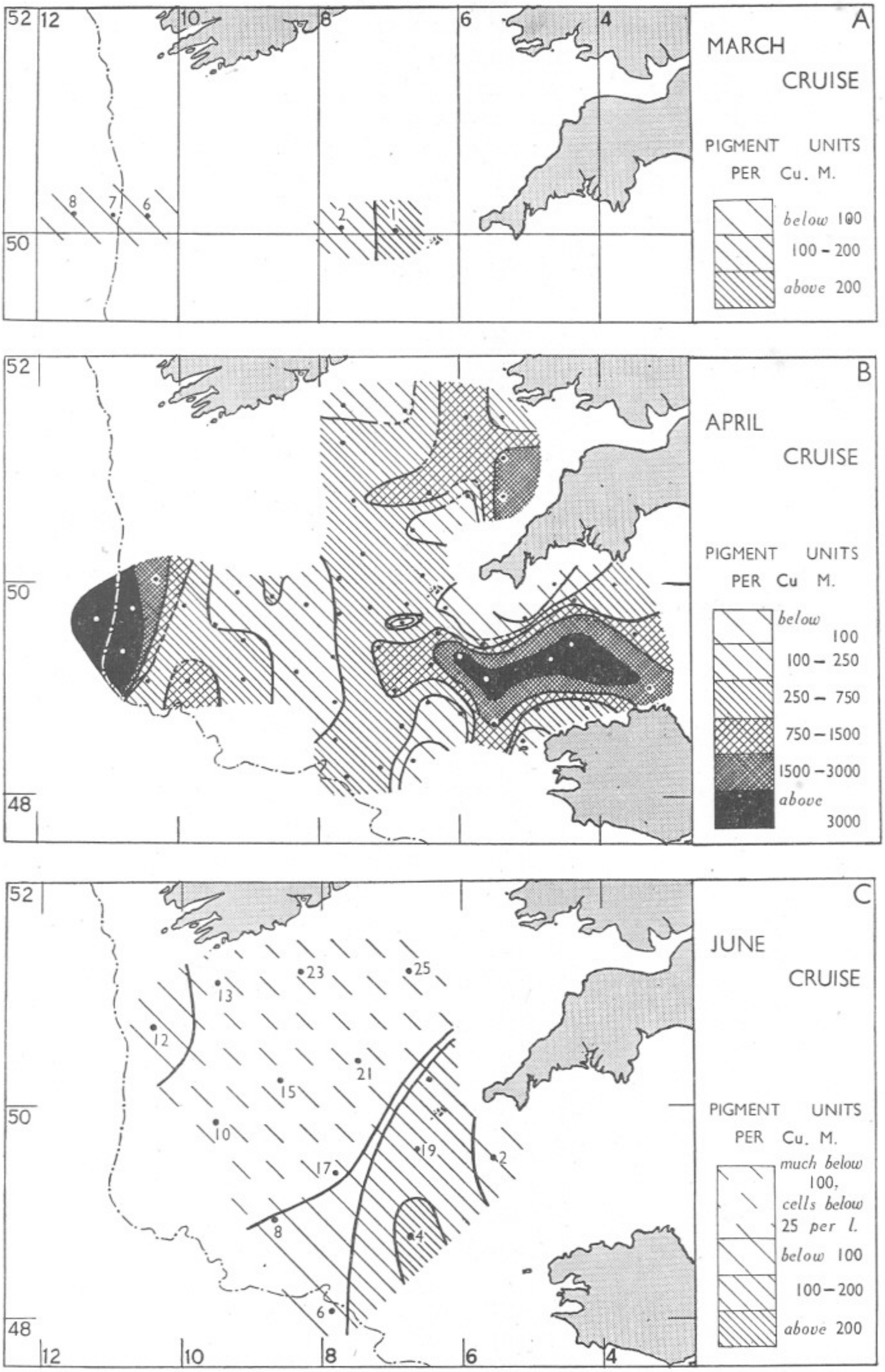

Fig. 3. Distribution of phytoplankton in Harvey's pigment units, in the south-western area in March, April and June 1939.

Small species would not have been recorded unless considerably more abundant than this, and the absence of a species from isolated stations which showed a low total density has not been regarded as significant.

The areas of distribution as they appeared at the time of sampling may be classified as follows:

(1) A region at the mouth of the English Channel was occupied by neritic species; these showed signs of spreading west or extending north to include the area off the southern entrance to the Irish Sea, e.g. *Biddulphia sinensis*, *Thalassiothrix Nitzschioides* (with sporadic occurrences to the far west), *Asterionella japonica*, *Ditylum Brightwelli*, *Phaeocystis globosa* (with which was associated *Nitzschia delicatissima*), *Lauderia borealis*, *Rhizosolenia Shrubsolei*, *R. Stolterfothii* (in part) and *Chaetoceros* spp. (in part). Some of these possibly showed indications of a north-westerly current north of the Scillies (see Fig. 5).

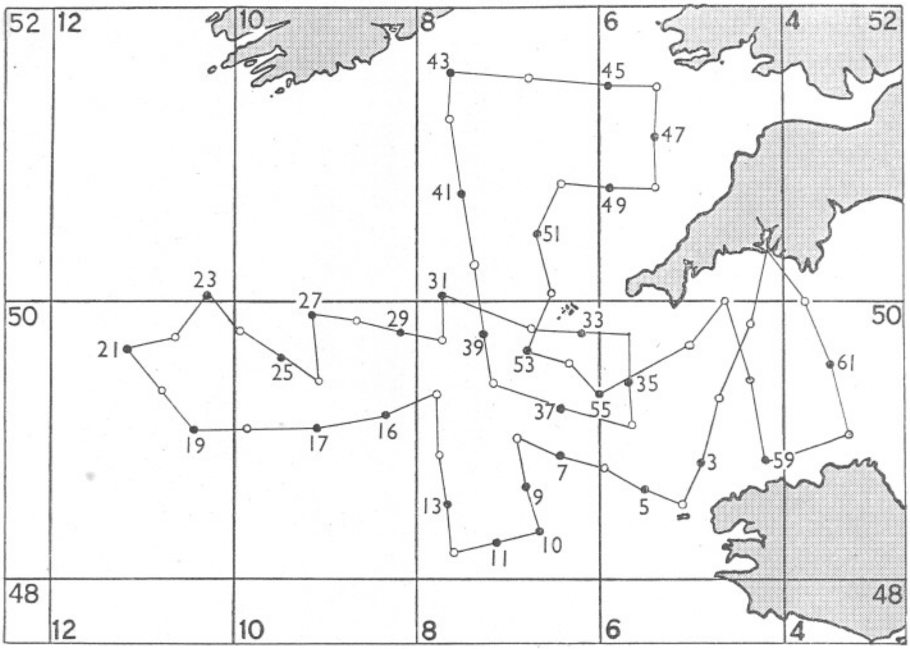

Fig. 4. April cruise. Full examination for phytoplankton was made at numbered stations; pigment extracts were made at all stations marked with a circle or spot; salinity determinations were made at all stations to St. 56 inclusive.

(2) The mid-west region, approximately 8–10° W., was occupied by *Rhizosolenia delicatula*. This neritic species was dominant and fairly abundant in an otherwise sparsely populated region (see Fig. 5 F).

(3) The region farthest west, near the edge of the continental shelf, had a dense patch of *Chaetoceros affinis* with *Guinardia flaccida* (neritic species) and also *Chaetoceros decipiens* and other oceanic species included in the next group. *Rhizosolenia Stolterfothii* found there was mainly much smaller than the normal form (see Fig. 5 E).

(4) The west and south-west region had oceanic species which showed varying degrees of penetration towards the mouth of the English Channel, e.g. *Rhizosolenia styliformis* and *R. alata*, *Ceratium bucephalum* and *C. lamellicorne*, *Globigerina* and silicoflagellates (see Fig. 6 A, D, E).

(5) Near Ushant and close to the French coast were found a group of neritic species, e.g. *Thalassiosira Nordenskioldii*, *Coscinoscira polychorda* and *Streptotheca thamensis* (three diatoms abundant at Plymouth at the same time), *Noctiluca* and *Tintinnopsis campanula* (see Figs. 5 B, 6 E).

(6) The Scilly Isles region had a mixture of oceanic and neritic forms. *Fritillaria* and rotifers were at that time confined to this area, while *Rhizosolenia styliformis* and *Ceratium bucephalum* occurred here as well as in the south-west (see Fig. 6 A, C, D). *Rhizosolenia robusta* appearing at St. 33 also occurred rarely in the south and in the Channel.

These species distributions are in reasonable agreement with previous records. Many of the species here showing only oceanic affinities have previously been recorded from the English Channel, but were not usually found far up Channel; this may be accounted for either by differences in the size of the samples examined or by the lack of penetration of oceanic water at present.

In the mouth of the English Channel *Chaetoceros decipiens* and *C. debilis* were largely responsible for the high cell numbers while *Lauderia borealis* was the most important contributor to the pigment assessment: there was also a greater variety of mainly neritic species than in the very dense patch in the west. In the latter area near the edge of the continental shelf the dominant form was the neritic species *Chaetoceros affinis* (recorded as *C. Schuettii* by Gran, 1912). These two areas were probably distinct in species and race composition (see above) as well as being separated by an area at a different stage in succession. Such indications as can be obtained from stramin net hauls suggest that a thinly populated area lies between the southern Irish coast and the area of high plant density near the edge of the continental shelf.* Species may have been transported there, perhaps from the south of Ireland as resting spores, or a wave of vegetative reproduction may have passed outwards, or resting spores may have been brought to the upper layers by vertical mixing which also provided the necessary rich supply of salts. In the middle of April 1910 the *Michael Sars* visited the same area and Gran found very dense phytoplankton to considerable depths associated with vertical mixing at the edge of the continental shelf; two stations to the east and nearer land had a less abundant phytoplankton, a further parallel to the conditions described here. Records of the repeated occurrence of two

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* For this information I am indebted to Mr G. P. Farran.

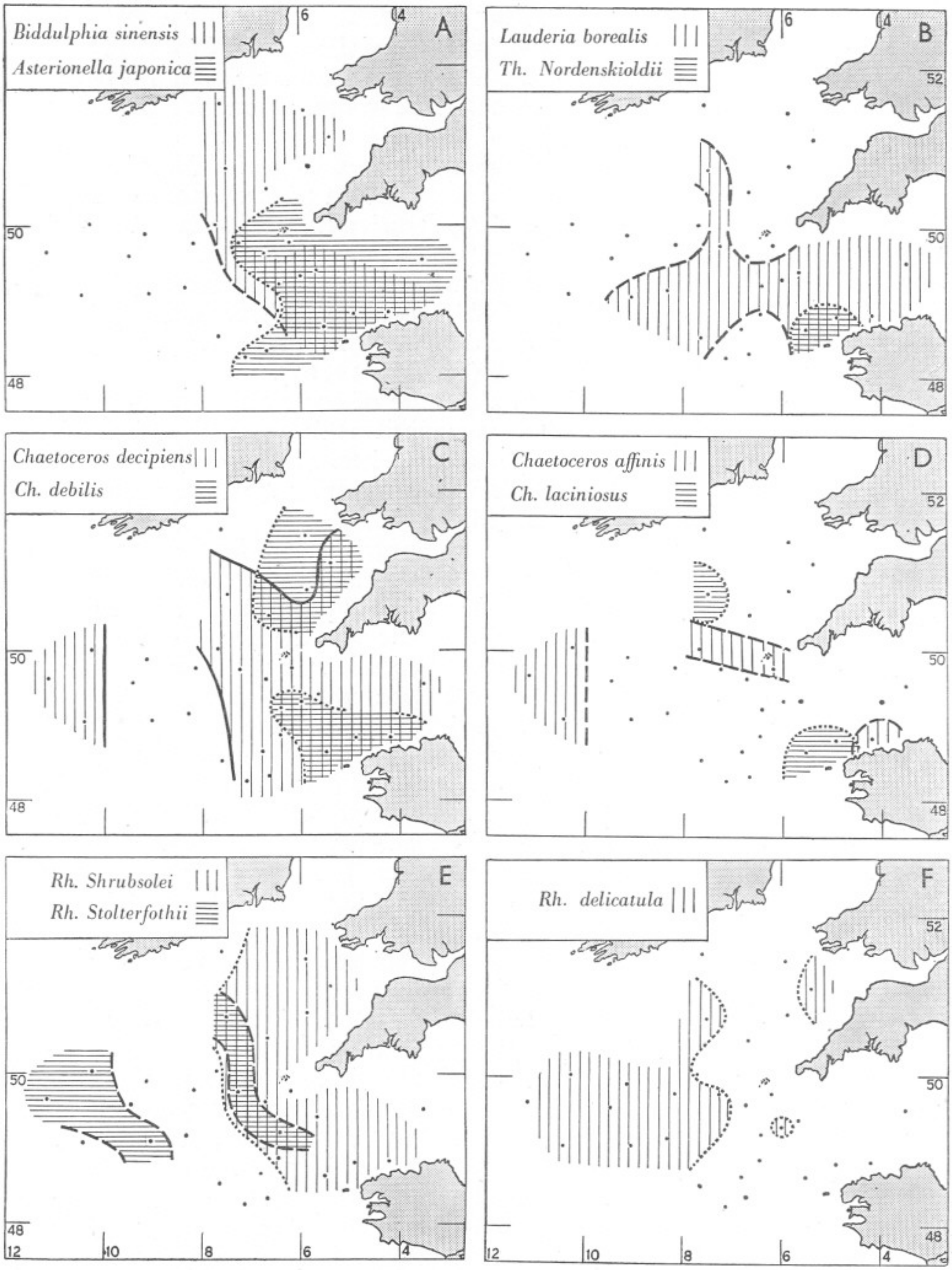

Fig. 5. Distribution of species found on the April cruise. The outer boundaries of neritic species are indicated by a broken line (— — or .....) and the inner boundaries of species generally regarded as oceanic by a continuous line (——) or by (— – —).

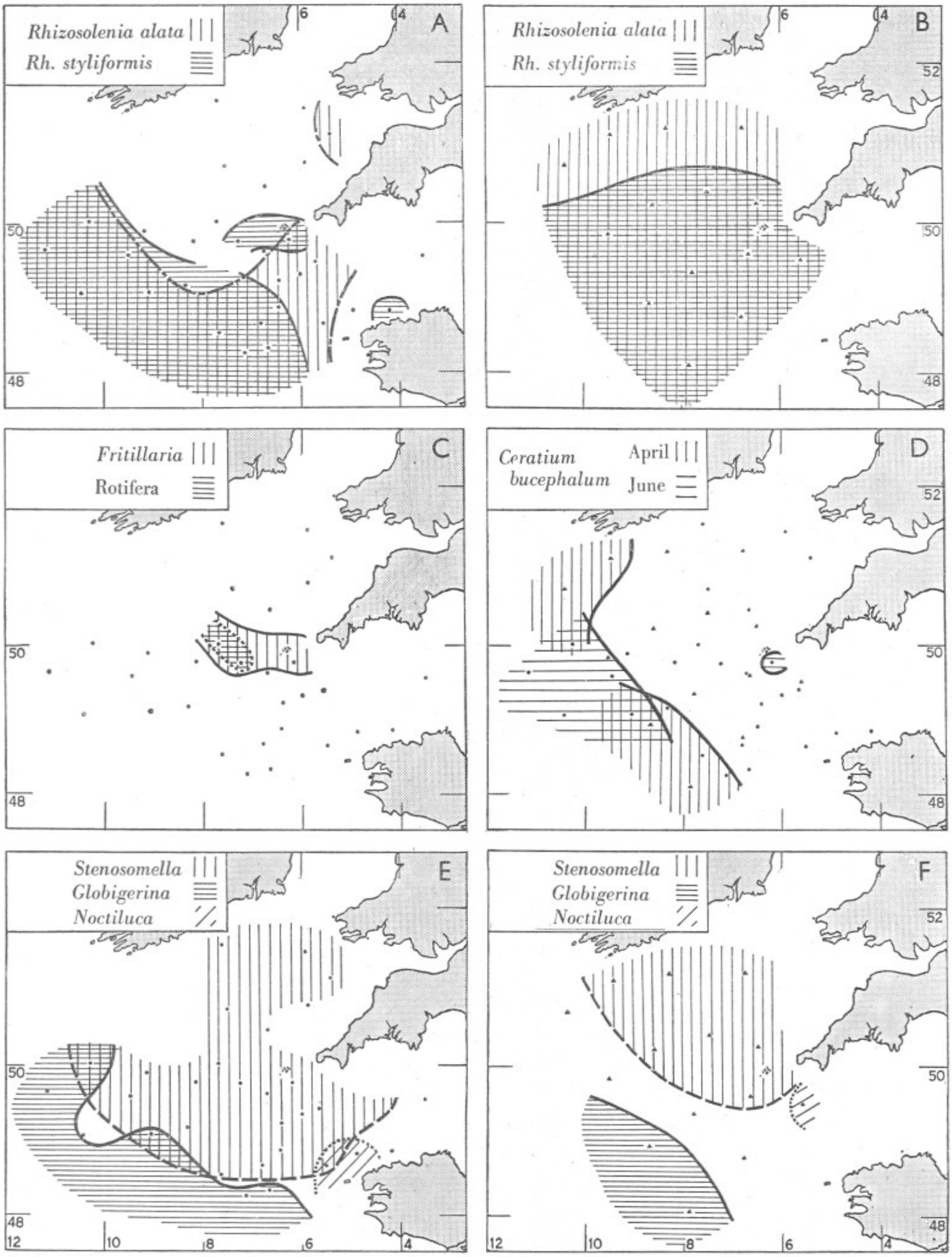

Fig. 6. Distribution of species found on the April cruise (A, C, D, E) and on the June cruise (B, D, F). April stations are indicated by circular spots and June stations by triangles.

separate maxima off the Norwegian coast, the outer associated with vertical mixing, are discussed and summarized by Gran (1929, 1930). These April samples clearly confirm that the same phenomenon may occur in the south-western area. It is noteworthy, however, that at the southern stations (9–13), also near the edge of the continental shelf, no dense phytoplankton was found at the time of sampling. Perhaps zooplankton grazing had already reduced the standing crop.

The correlation between pigment units and numbers of cells is shown in Fig. 7A. The numbers of cells are unweighted for size: hence at St. 21, 37 and 5 where *Chaetoceros* species were dominant and St. 19–39 where *Rhizosolenia delicatula* was dominant there is greatest divergence. At St. 7–13 the large celled *R. styliformis* was dominant and hence, as may be seen from the graph, one pigment unit is equivalent to less than 4000 cells. Abnormally high pigment values may also arise from the extraction of pigment from abundant green faeces. The faecal pellets collected varied considerably in

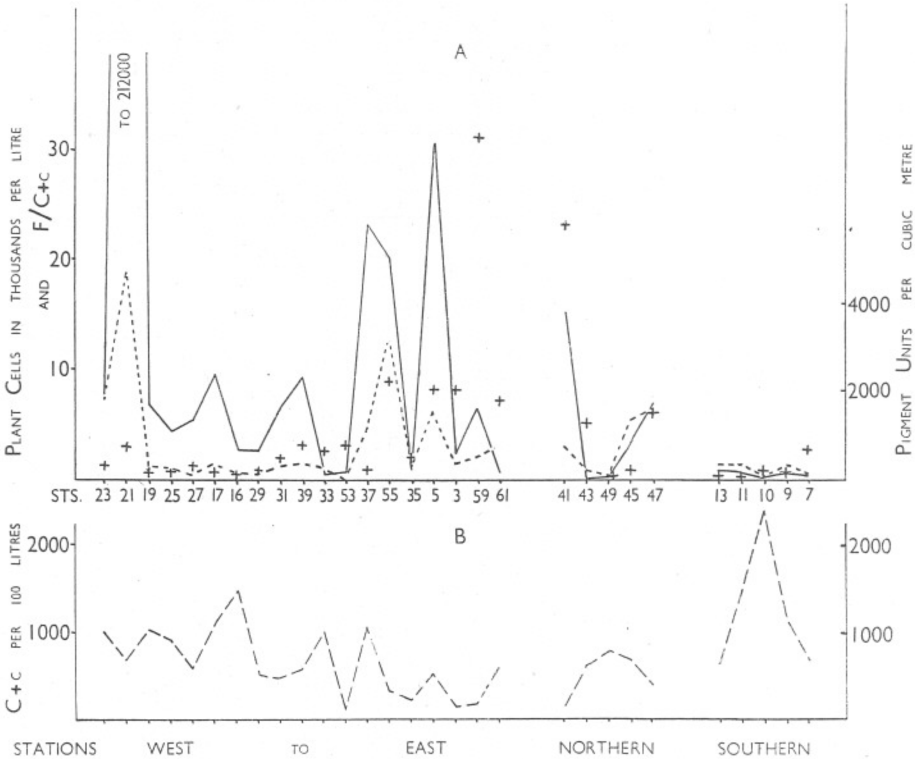

Fig. 7. Data from the April cruise in the south-western area. A, numbers of plant cells in thousands per litre of sea (continuous line), units of plant pigment per cubic metre (dotted line), and numbers of faecal pellets per copepod plus copepodite, $F/C+c$ (+). B, numbers of copepods plus copepodites ($C+c$) per 100 l. of sea (broken line). Lines joining points have no real meaning.

nature and size, nevertheless the ratio $F/C+c$ shows some correlation with the amount of available food. When cell numbers are low $F/C+c$ is also low, but there is no detailed correlation. In Fig. 7 B it is seen that the numbers of copepods plus copepodites show an inverse density relationship with the plant population between St. 23–61 and more definitely at St. 41–47 and 7–13.

The samples taken on the third cruise (June 2–7) are chiefly notable for the extreme scarcity of phytoplankton at most stations. This fact and the presence of abundant zooplankton, tingeing the acetone extract red or brown, made the assessment of colour difficult; Fig. 3 C is partly based on numbers of plant cells. The catch from which the pigment had been extracted was also examined for occurrence of species.

The mouth of the English Channel was again the area of highest cell numbers and greatest variety of species, which were mainly neritic. The central western and northern areas were again very sparsely populated with diatoms and dinoflagellates, but the zooplankton was rich (see Fig. 8). A rise in phytoplankton density was again found near the edge of the continental shelf. *Rhizosolenia alata* was present over the whole area and *R. styliformis* had spread further north and east, while *Stenosomella ventricosa*, a neritic tintinnid, appeared to have retreated north-eastward. Slight indications of more oceanic influence were seen at St. 6, 8 and 12 in the presence of *Globigerina*, *Ceratium bucephalum*, *C. lamellicorne* and *Dinophysis tripos* (*D. homun-*

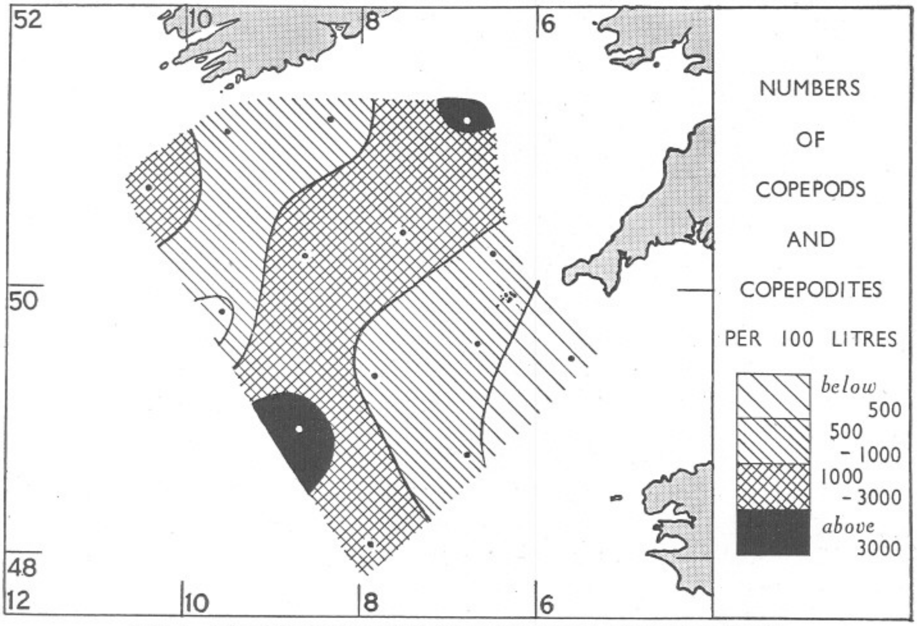

Fig. 8. The distribution of small copepods plus copepodites found on the June cruise in the south-western area.

culus var. *tripos* in Ogilvie, 1923). For charts of the distribution of some of these species see Fig. 6 B, D and F.

The faecal pellets were no longer green and the ratio $F/C+c$ was mainly below one, but it did not show detailed correlation with the low phytoplankton. The copepods plus copepodites as seen in Fig. 9 showed a reciprocal abundance with the plants at most stations, as is usually found at this time of the year.

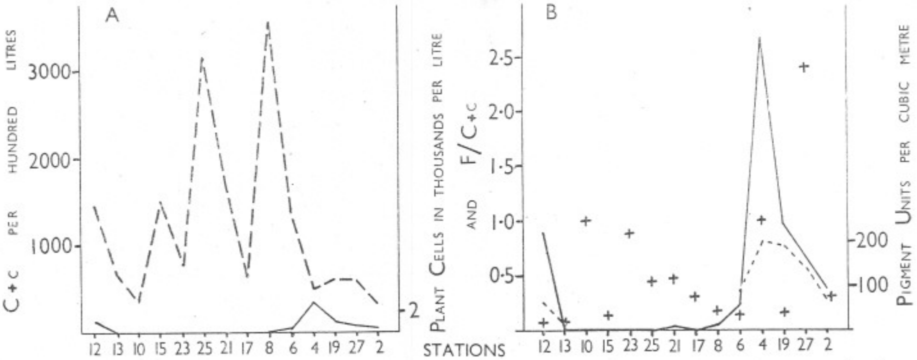

Fig. 9. Data from the June cruise in the south-western area. A, numbers of copepods plus copepodites ($C+c$) per 100 l. (broken line) and the number of plant cells per litre (continuous line). The scales are similar to those used for the April data. B, numbers of plant cells per litre (continuous line), units of plant pigment per cubic metre (dotted line), and numbers of faecal pellets per copepod plus copepodite, $F/C+c$ (+). The vertical scale is magnified ten times. Lines joining points have no real meaning.

OCCURRENCE AND DISTRIBUTION OF VARIOUS SPECIES

Chaetoceros species. The prominence of this genus in the spring maximum varies at Plymouth, and while in 1934 it was poorly represented, in 1939 (a late year) it was very important. Similar variation in importance is seen at Sevenstones in unpublished records made by Dr M. V. Lebour for the years 1913–17. In April 1939 members of the genus were abundant in all areas of dense phytoplankton (see Fig. 5 C, D).

Biddulphia sinensis did not assume its usual prominence in the spring maximum at Plymouth, only appearing as rare in April and May. A few cells were found at the Channel mouth stations on the April and June cruises (see Fig. 5 A). In April 1938 it was abundant near the Lizard. Wulff has used this species as an indicator of Channel water in the southern North Sea (Wulff *et al.* 1934).

Phaeocystis globosa. No very dense patches have been found in the waters sampled in 1939. In April 1938 two patches were encountered, one with *Biddulphia sinensis* off the Lizard and the other west of the Channel mouth, about 8° W.

Rhizosolenia delicatula. An unusual feature, both of the succession near Plymouth and of some of the stations of the April cruise, was the important part played by *R. delicatula*. Ostenfeld (1913) states that this species is "a temperate neritic species indigenous off the west coast of France, in the English Channel and in the southern part of the North Sea, where it is mostly found in the autumn". In the English Channel and Irish Sea it shows minor sporadic occurrences, usually being marked rare or very rare in available lists, and is often not recorded at all; it may occur in spring, summer or autumn, but May, October and November have the most records. Ogilvie (1923) found it to be fairly common in July off the south coast of Ireland, but only once was it recorded as very common (by Gough at Cardigan Bay Lightship in June and July 1904). From the evidence available it is not possible to place it definitely in a sequence of species, but it seems usually to be a post-maximum species. Near Plymouth in 1939 it obviously filled the stage in succession immediately after the *Chaetoceros* outburst and was followed by *R. Stolterfothii*. It may very tentatively be suggested that the sparsely populated belt which it dominated in April between 8 and 10° W. (see Fig. 5F) was at a later stage in succession than the more populous areas to east and west of it.

Rhizosolenia alata. Though this diatom apparently showed a stage in the penetration of an oceanic species up Channel in April (Fig. 6A) it must be noted that it had been present near Plymouth since February. Bygrave (1911) found it usually more abundant on the north side of the Channel mouth than on the south, and it always seems to penetrate further into coastal waters than *R. styliformis*.

Ceratium species. Several members of this genus, *C. tripos*, *C. macroceros*, *C. bucephalum* and *C. longipes* have been designated by Wulff as indicators of Atlantic water coming from the north into the North Sea. *C. tripos* and *C. macroceros* were generally present in all parts of the south western region including Plymouth. *C. longipes* was not seen. *C. bucephalum* was this year present only at the outermost stations with the addition of St. 33 in association with particularly oceanic forms (Fig. 6D). *C. lamellicorne* and also *Dinophysis tripos* (both southern species and rare in the samples) have likewise been found only at the outermost stations, though there are previous records of rare occurrences in the Channel mouth and at Plymouth.

SILICOFLAGELLATA. *Distephanus speculum* and *Dictyocha fibula* are oceanic and in the April samples showed a distribution similar to that of *Rhizosolenia alata*. Records in the Bulletin Planktonique show them to be scattered well up the Channel at all seasons. They are usually not caught in net hauls, so their presence probably indicated considerable abundance at the outer stations and at the mouth of the Bristol Channel; they may well have been present at a lower density over the whole of the area.

Globigerina. Only those stations are included in the distribution charts in which specimens showed long spines still attached (see Fig. 6E, F). They showed an outer distribution. Records in the Bulletin Planktonique show considerably more penetration up Channel. In April at St. 29 (mid-west region) very numerous dead shells, accompanied by much silt, probably indicated that there had been some upward movement of bottom water, but not necessarily at that point. Single damaged shells were found in the plankton at L4 on two occasions.

Noctiluca miliaris (see Fig. 6E, F). The distribution in April 1939 happens to be very similar to that recorded by Russell (1936, Fig. 2, p. 510) and the species did not occur at Plymouth until July; it is possible that it had come from the south. However, in previous years, including 1934, it has shown sporadic outbursts on the north side of the Channel from early in the year.

ROTIFERA. Near Plymouth there was an outburst during April (see Fig. 2B), this was a little later than a similar one in 1934. The patch of rotifers (neritic) with *Fritillaria* (oceanic) near the Scillies in April is suggestive of the mixed origin of the water there (see Fig. 6).

GASTROPOD LARVAE. Nearly all specimens collected on the cruises were very young pteropods of the genus *Limacina*. In April they showed an outer distribution and in June were present over practically the whole area. At Plymouth all specimens were dextral, i.e. gastropods other than pteropods, except a few very small ones at the end of the summer.

DISCUSSION

Prior to a discussion of the distribution of species a short account of the hydrography of the region is necessary. Matthews (1914) first suggested the existence of a cyclonic circulation in the south-western area, and drew attention to its probable biological importance. Harvey (1930) gives a general picture of the circulation at the mouth of the Channel, but emphasizes the variability of the system and the frequent occurrence of isolated patches of water at varying depths differing considerably in salinity from their surroundings. There is an inflow of water to the Channel which generally comes either from the south-west or from close to the French coast. Some high salinity water may pass north or north-west between the Scillies and Land's End; this water is joined by a variable quantity displaced out of the English Channel from eastward of the Lizard. Water coming from the Bristol Channel and from the Irish Sea is turned westward, and off the south coast of Ireland some of this is turned southward to join the eastward oceanic drift. A cyclonic circulation lying over the shallow continental plateau to the south of Ireland may thus be set up, but it is probably variable in extent and position. Russell (1939) connects it with the stable area of *Sagitta elegans* water in this region.

The salinity distributions at 5 m. in April and June are shown in Fig. 10. In April the salinities and temperatures were similar at all depths, while in June there was indication at most stations of a thermocline above or below 25 m.; vertical mixing was however particularly marked in the south at St. 6. High salinity water lay to the west and south-west in the same region as the group of planktonic species indicating oceanic influence: *Ceratium bucephalum*, *C. lamellicorne*, *Dinophysis tripos*, *Rhizosolenia styliformis*, *R. alata*, *Globigerina* and silicoflagellates. Some of these species were recorded by Ogilvie (1923) in November 1921 when there were other indications of Atlantic water reaching

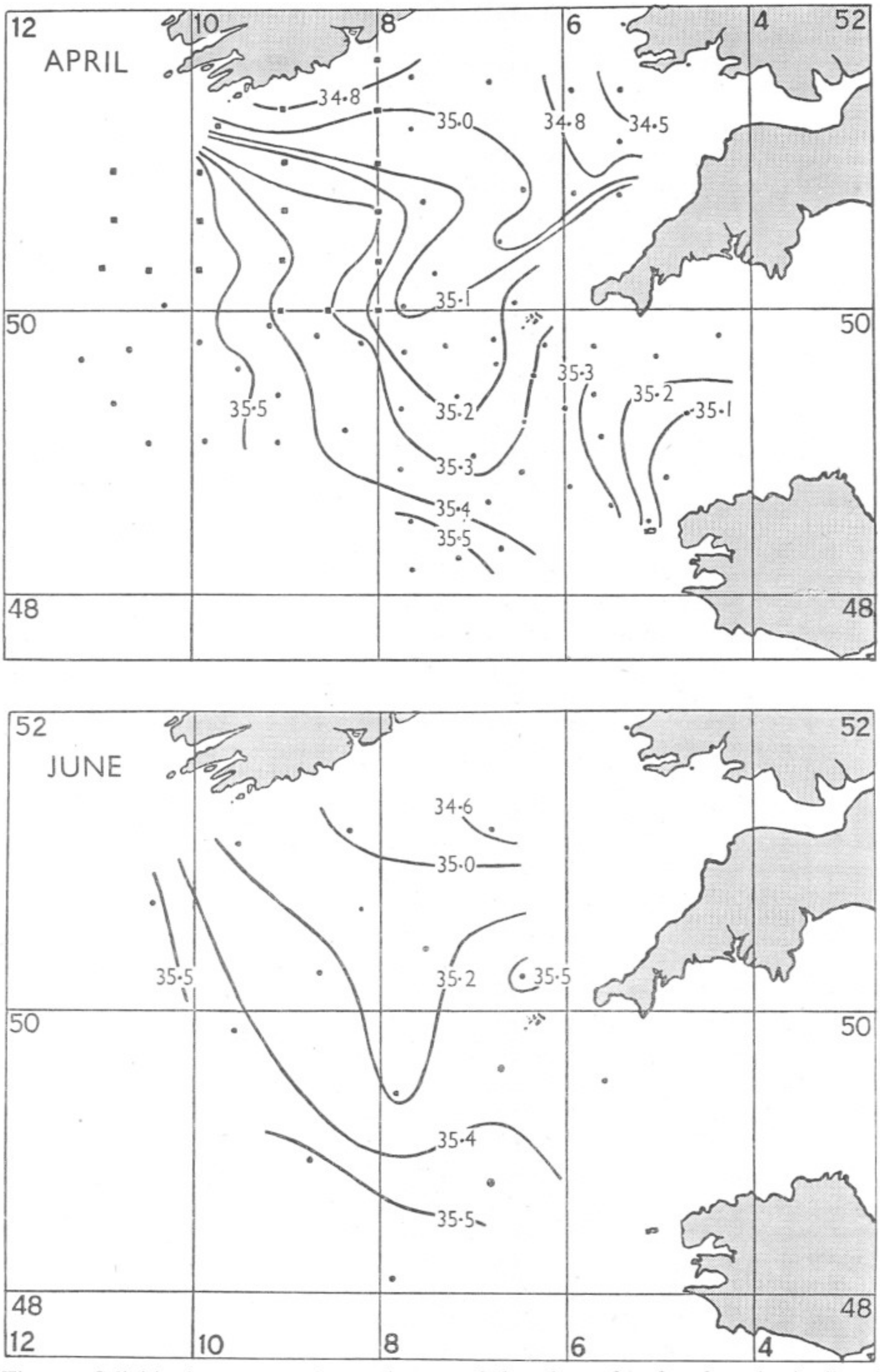

Fig. 10. Salinities in parts per thousand at 5 m. below the surface found on the April and June cruises. Stations indicated by squares on the April chart are Irish stations sampled contemporaneously but at 10 m. depth. Values at this depth differ very little if at all from those at the surface.

almost to the south-eastern Irish coast. The presence in April of oceanic species, *Ceratium bucephalum* at St. 33 close to the Scillies and of *Rhizosolenia styliformis* and *Fritillaria* in that region, together with rotifers and other neritic species, is probably indicative of the mixture of oceanic and Channel water there. In June there was again a surface patch of high salinity water north of the Scillies but there were no particular species associated with it. *Rhizosolenia styliformis* was by no means confined to high salinity water; in June it had moved much further north-east and the presence of *R. alata* over the whole area in June and in April at the mouth of the Bristol Channel, accompanied by silicoflagellates, precludes their individual use as oceanic indicators.

It has been mentioned above that some neritic species show a north-west trend north of the Scillies; it is possible that this is associated with part of the cyclonic system, otherwise these samples do not show any clear indications of it. There is a wide distribution of neritic species and much overlapping of neritic and oceanic species, which is not surprising, as the swirl is of mixed oceanic and coastal water. The tongue of low salinity water coming south-west from the mouth of the Bristol Channel is well marked (as in 1938) and the position of the swirl at the time of sampling cannot be clearly defined. It is hoped that further information, concerning the distribution of biologically distinct water masses, will be forthcoming later from work on the macroplankton indicator species of the area (as listed by Russell, 1939, pp. 179–81). In any case, from the limited amount of material available and because of the need for extreme caution in the choice of indicators from among these rapidly reproducing forms, it is not yet justifiable to erect such indicator species in the microplankton.

With only three sets of samples taken at intervals of six weeks it is difficult fully to interpret the phytoplankton density data; it is given as a record of quantitative data obtained. It is interesting but difficult to compare satisfactorily the intensity of production near Plymouth with that in the denser areas in the west. The number of plant cells, 212,000 per litre, found in April at the edge of the continental shelf, is much in excess of those found at L4 and Rame (27,000 and 93,000 cells per litre respectively) but the units of plant pigment, 6250 and 4400 units, found in the dense western areas do not differ materially from the maximum values of approximately 7000 and 4000 recorded at L4 in 1933 and 1934. There is no proof, however, that any of these figures represent the actual peak value for the standing crop and it must always be remembered that in assessing the productivity of an area the duration for which dense phytoplankton occurs is very important, and that the standing crop, even at the peak, is only a small part of the production.

By making use of the Plymouth data on the seasonal succession of species and the time of the spring phytoplankton maximum, which it will be remembered was delayed until the middle of April, it is possible to elucidate to some extent the sequence of events in the south-western area. Data collected on the March cruise suggest that over the area sampled the diatom maximum had not then been reached; the oceanic stations were at an earlier stage in succession than those nearer the Channel. It is probable that the dense patches of phytoplankton found at the mouth of the Channel and near the edge of the continental shelf in the west (see Fig. 3B) in April were part of the spring maximum, while at St. 9–13 near the edge of the continental shelf in the south the zooplankton (see Fig. 7B) had already depleted the standing crop. Possibly the mid-west zone (8–10° W.) had by the time of sampling (April 18–20) passed through a short maximal period. In June low midsummer conditions prevailed. In the middle of April 1938 a patch of "stinking water", indicating on that occasion the presence of abundant phytoplankton, was encountered in these latitudes between 8 and 9° W. It is interesting to note that this otherwise barren mid-west region was that sampled by the Irish workers in 1920–1 at seven stations in a line between 51° 40′ N., 8° 00′ W. and 49° 20′ N., 8° 00′ W. The phytoplankton at the outer southern stations was sparse at all times of that period, and only moderately dense phytoplankton was sometimes found near the coast (Ogilvie, 1923).

In April 1938 Hickling investigated the distribution of phosphates in the south-western area. It is unfortunate that no phosphate estimations were made on the 1939 cruises. As Hickling points out, high phosphate at this time of year may be due to large supplies reaching the area from vertical mixing with deep oceanic water in the extreme west, and possibly in the mouth of the English Channel, and from land drainage at the mouth of the Bristol Channel; low phosphate in the mid-west region was probably partly due to utilization by plants. Vertical circulation in the mid-west region may only involve mixing with rarely replenished bottom water. From the phytoplankton samples here reviewed the regions at the entrance to the English Channel, and to some extent at the mouth of the Bristol Channel, and also in the west at the edge of the continental shelf seem to be the most prolific. In particular the April phytoplankton density map shows considerable similarity with the surface distribution of phosphate found by Hickling (1938, Fig. 1, p. 198). The low phytoplankton density in April at St. 9–13 might be due to lack of mixing with deep waters at the edge of the continental shelf in the south or, as suggested above, to grazing.

It has been very tentatively suggested above that the mid-west region, dominated by *Rhizosolenia delicatula* in April, was at a later stage in succession than adjacent areas. This might be correlated with a poor supply of nutrient salts which would be expected to favour a rapid succession of species. Evidence from the phytoplankton mentioned by Hickling in 1938 does not run contrary to this interpretation. Only parts of the area usually thinly populated with plants had a rich zooplankton which might have been responsible for the small standing crop. Alternatively the *R. delicatula* community may have drifted eastwards from the rich zone near the edge of the continental shelf. If this mid-west region is occupied by part of the cyclonic swirl water, it is probably biologically older water than that to the east or west: it seems to be analogous to the "old" "offshore" water found by Sverdrup & Allen (1939) off the Californian coast to be poor in diatoms. Basing his argument on the conditions of plankton production on the south and west coast of Iceland, Steemann Nielson (1937) stresses the importance of oceanic upwelling, drift of water masses and the age of the water and hence the time for development of a population of plants or animals, in offering an explanation of the relative abundance of phyto- and zooplankton; the considerations are equally applicable to the area here surveyed. As a very tentative hypothesis it is suggested* that the mouth of the English Channel is a main area of phytoplankton production, that much is converted to animal substance, green faeces and other forms of detritus, and as such is carried to the west by the swirl and consumed by the large animal population there; some of the dense production at the edge of the continental shelf in the west may be added to the system. Much more data is necessary before this idea can be put forward with any certainty.

ACKNOWLEDGEMENTS

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SUMMARY

A quantitative seasonal survey of the phytoplankton and small zooplankton has been made from the end of January to the end of August 1939, at a station, L4, with supplementary observations at a station off Rame Head, both near Plymouth. The results are compared with those of a fuller survey made in 1934.

The spring maximum in numbers of plant cells was late, not being reached until the middle of April.

The monthly means of the total numbers of animals caught were of the same order in the two years, but the numbers of copepods plus copepodites in 1939 were only two-thirds of those in 1934.

The numbers of faecal pellets per copepod plus copepodite again showed

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* I am indebted to Mr F. S. Russell for the initial suggestion.

correlation with the phytoplankton density, being greatest when plant food was most abundant; there were a few anomalies.

Similar samples were collected on cruises in March, April and June in an area west of the entrance to the English and Bristol Channels and to the westward as far as the edge of the continental shelf.

Charts are given of phytoplankton densities assessed by Harvey's pigment extraction method, and of species distribution.

The distribution of various species indicated more Atlantic influence at the stations to the west and south-west, and there was a spread of some of these species north-eastward between the April and June cruises. Some other distributions are very tentatively correlated with certain phases of the complex water circulation in this region.

For the most part the numbers of copepods plus copepodites showed inverse density relationships with the numbers of plants, and the number of faecal pellets per copepod plus copepodite indicated heaviest grazing at times and places of abundant plant food. There was no detailed correlation when both this ratio and the plant numbers were low; probably detritus then formed a larger proportion of the food.

Dense phytoplankton patches were found in April at the mouth of the English Channel, the Bristol Channel and at the edge of the continental shelf in the west: this distribution was similar to that of high surface phosphate recorded in April 1938. The mid-west region (8–10° W.) is usually thinly populated with plants. It is suggested that the mouth of the English Channel is an important plant productive region, possibly supplying a wider area. An effect of vertical mixing of surface with deep oceanic water at the edge of the continental shelf in increasing plant production is demonstrated in the west.

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ON THE BIOLOGY OF THE CAPRELLIDAE. GROWTH AND MOULTING OF *PSEUDOPROTELLA PHASMA* MONTAGU

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(Text-figs. 1–6)

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Introduction, Material and Methods

This study of the growth of one species of caprellid was undertaken to see if an aberrant type of amphipod grew in a manner similar to the normal (Sexton, 1924; Le Roux, 1933). *Pseudoprotella phasma* Montagu var. *typica* (Chevreux & Fage, 1925) was selected, since this is the commonest caprellid found in the Plymouth region. The animals examined were collected at intervals during 1939 in Plymouth Sound on hydroids (mainly *Antennularia* spp.) at a depth of 6–10 fathoms. Many animals were kept in the laboratory and their moults were collected. Individual specimens were used for the measurements and drawings. These were checked against the moults except in the case of the young, where the moults were too delicate to be preserved. Individuals kept in the laboratory for several instars reproduced the measurements of the same instars straight from the sea. The measurements were made with a microscope with a calibrated micrometer eyepiece and a camera lucida was used for the drawings.

Breeding

Pseudoprotella breeds only in the spring and summer months. The young hatched at this time themselves breed the following year. The number of young in the brood varies between twenty and forty. Since ovigerous females of various sizes are found it is evident that two or more broods may occur in the life cycle. The largest growth stages are only found in any abundance in the summer months, while in the winter months only animals of intermediate unsexed stages are found. Copulation has not been observed.

Moulting

The process of moulting in *Pseudoprotella phasma* is similar to that described in *Gammarus chevreuxi* by Sexton (1924). Moulting nearly always takes place at night and an animal about to moult can be recognized many hours before ecdysis by its sluggishness and its refusal to accept food. The animal first bends itself double with a series of convulsive jerks, as if to loosen the skin. The cuticle splits on the dorsal surface just behind the head. The anterior portion is then pulled off forwards by the second pair of chelae. The animal next grasps a branch of the hydroid and kicks violently until the rest of the skin is thrown off. If this fails, it hooks the loose skin round a branch of the hydroid and attempts to crawl out, hauling itself up on neighbouring branches by its chelae. The whole process is accomplished in a remarkably short space of time; in one ecdysis moulting was completed in under 5 min. The process must be completed rapidly, for the animal quickly swells to the next moult size. Exhausted animals are often found in the morning with the posterior part of the skin still attached to them, struggling to throw it off. After the moult the animal is very sensitive, and the least movement causes it to jump into the "ready" position (Bereitschaftstellung, Wetzel, 1932). Animals that have just moulted can be thus recognized by breaking the surface film of the water in the bowl, or even by slamming the door. They do not eat the cast skin and I have not observed one animal helping another to remove it (see moulting in *Gammarus chevreuxi*, Sexton, 1924). Individuals of the later instars occasionally experience difficulty in moulting. Antennae and gills may be torn off during the moult.

NUMBER OF ECDYSES BETWEEN HATCHING AND MATURITY

Sixteen instars of *Pseudoprotella phasma* were found, which could be placed into their respective instars by visual examination. Until instar XII both sexes are alike. After this stage the females can be differentiated from the males by their developing a brood pouch. It is uncertain at which point sexual maturity is reached.

The length of the body, the length of the flagellum and the lengths of the basal segments of the antenna, the length and breadth of the second pair of chelae and the length of the third somite lend themselves admirably to accurate measurement. These data enable a particular animal to be placed in its instar at once, and for rough purposes the number of segments in the flagellum may be counted. The measurements were reproducible to within ±5% and such variations occurred mostly in the larger growth sizes. Table I gives the measure-

TABLE I

Growth stage XIV		Growth stage XVII	
Length of chela in mm.	Number of animals	Length of chela in mm.	Number of animals
2·15	2	3·98	2
2·17	10	4·08	10
2·19	15	4·18	13
2·21	10	4·28	12
2·23	3	4·38	3

ments of the length of the second chela in two growth stages (XIV and XVII). Forty specimens belonging to each stage were measured.

The length of the chela of stage XIII is 1·60 mm., that of stage XV is 2·60 mm. and that of stage XVI is 3·30 mm. Since measurements of other parts show as little variation as those shown in Table I for the chela it can be seen that little difficulty is experienced in placing an animal in its instar by measurement, there being no overlap.

Table II gives the measurements of the body and other parts in millimetres. In nearly all cases twenty to fifty animals were measured; where only a few specimens were available their number is indicated in brackets by the measurement.

TABLE II

All measurements in millimetres

Growth stage	Chelae		Antennae		Third somite	Body length	Przibram constant
	Length	Breadth	Length first segment	Total length			
UNSEXED							
I	0·20	0·10	0·13	0·89	0·13	1·17	..
II	0·22	0·10	0·18	0·89	0·16	1·35	1·13
III	..	..	..	..	..	..	..
IV	0·32	0·16	0·22	1·40	0·23	1·90	..
V	0·38	0·18	0·25	2·09	0·28	2·18	1·12
VI	0·44	0·19	0·30	2·29	0·33	2·57	1·17
VII	0·60	0·25	0·35	2·70	0·41	3·00	1·16
VIII	0·70	0·26	0·40	2·99	0·53	3·50	1·17
IX	0·84	0·32	0·50	3·32	0·60	4·10	1·20
X	1·00	0·46	0·60	3·71	0·77	4·95	1·19
XI	1·20	0·50	0·70	5·10	0·82	5·70	1·14
XII	1·35	0·55	0·80	5·95	0·94	6·40	1·12
MALE							
XIII	1·60	0·60	0·90	6·55	1·12	7·80	1·21
XIV	2·20	0·78	1·20	7·85	1·50	8·80	1·13
XV	2·60	0·85	1·30	8·95	1·72	10·4	1·18
XVI	3·30	1·00	1·60	11·5	2·10	12·6	1·20
XVII	4·20	1·30	1·90	14·4	2·65	14·4	1·13
FEMALE							
XIII	1·60 (4)	0·70 (4)	0·90 (5)	6·45 (5)	1·10 (9)	7·40 (9)	1·10
XIV	2·05 (15)	0·90 (15)	1·10 (15)	7·50 (15)	1·44 (15)	8·60 (15)	1·14
XV	2·50	0·95	1·40	9·90	1·69	9·80	1·14
XVI	3·00	1·00	1·50	10·2	2·01	11·5	1·17
XVII	3·80	1·05	1·60	12·0	2·40	13·0	1·13

If the logarithms of the lengths obtained from the sixteen known growth stages be plotted against the instar number a straight line is obtained (Fig. 1). It will be seen that the third stage is missing. When kept in the laboratory the mother lifts the young out of her brood sac with her first pair of chelae and places them upon her antennae and second pair of chelae where they feed on her food (Montagu, 1802). The young live in this manner for about three weeks, then one by one they fall off and sink to the bottom of the bowl. Attempts to rear the young beyond this stage have failed. Both the young obtained from the laboratory broods and young so far found attached to females taken from the sea have never been larger than stage II. The smallest animals found in the sea free-living on the hydroids have been stage IV. It would appear that the young either jump stage III and moult straight from stage II to stage IV or that there may be a change in the mode of living. Stage III has not been obtained by fine tow nets, netting dragged over the hydroid bed or by dredging.

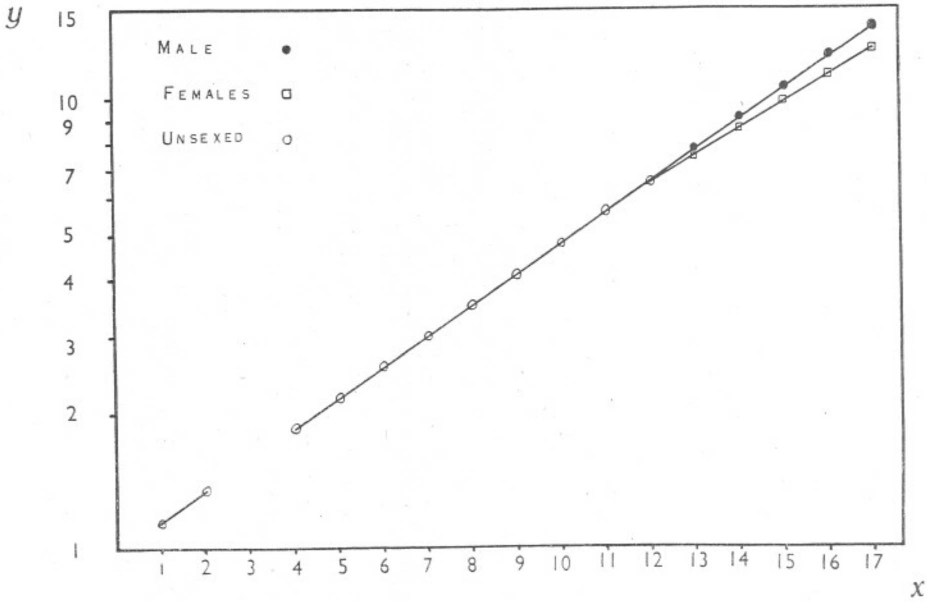

Fig. 1. Logarithms of body lengths (y) as a function of the growth stage (x).

It will be seen (Fig. 1) that the logarithm of the length of the $(n+1)$th stage differs from that of the (n)th stage by 0·068. Or

$$\log L_{n+1} - \log L_n = 0{\cdot}068.$$

From this

$$\frac{L_{n+1}}{L_n} = 1{\cdot}169.$$

The figure 1·169 is the common ratio of the geometric series obtained from the body lengths and is known as the Przibram quotient, see Table II, (Przibram, 1931). By a coincidence the length of the first stage is 1·17 mm.; so that the approximate length in millimetres of any specimen of *Pseudoprotella phasma* found in Plymouth Sound can be determined, knowing its growth stage, by means of the following equation:

$$y = 1{\cdot}169^n,$$

where y is the length of the nth stage measured in millimetres. For the females from the twelfth stage onwards the equation differs slightly from this:

$$y = 6{\cdot}51 \times 1{\cdot}48^{n-12},$$

where

$$6{\cdot}51 = 1{\cdot}169^{12}.$$

For any different scale of measurement a correcting constant k must be introduced.

If the logarithm of the length of the growth stage be plotted against the logarithm of the length of a part or an appendage straight lines are obtained. These graphs fit the simple allometry equations,

$$y = bx^a,$$

where y is the length of the part or appendage and x the length of the body, b a constant depending on the unit of measurement and a the *constante de croissance* (Teissier, 1937) or the constant differential growth ratio (Huxley, 1932). This equation has been criticized in that it is not dimensionally equivalent (Needham, 1934). But it must be realized that the term length of an instar or appendage is not an absolute mathematical dimension but the visible result of many complex internal processes producing growth. The equation formulated above is that which best fits the practical results and it must not be considered as a basic formula of growth. If the formula is written

$$\frac{y}{y_0} \doteq b\left(\frac{x}{x_0}\right)^a,$$

the criticism can no longer be made, for both sides of the equation are dimensionless. For a further mathematical treatment of the equation see Lumer (1939).

TOTAL AND RELATIVE GROWTH

Table II and Fig. 1 show that after stage XII the length of the body and appendages are shorter in the females than in the males of the same instar. The constant a obtained by $\log y/\log x$ indicates the ratio of the rate of growth of a part or appendage to the rate of growth of the body. If the value of the constant is <1 the body is increasing in length faster than the part. If the constant is >1 the part is increasing in length faster than the body, while if the constant $=1$ the growth rates are equal and growth is isometric.

Table III A gives the constants for the parts measured in the unsexed, male and female animals. The constant for the third somite remains unaltered throughout the life of both sexes (Fig. 2 B), while in other parts the value changes after stage XII. Table III B shows the constants recalculated relative to the third somite constant to enable the relative growth rate changes to be understood more easily.

TABLE III A

Values of the constant $a = \log y/\log x$, where x is the body length and y is the length of the part.

				Antenna		
	Third somite	Chela length	Chela breadth	First segment	Second segment	Total length antenna
Unsexed	1·15	1·14	1·00	1·07	1·16	1·12
Male	1·16	1·41	1·22	1·10	1·25	1·12
Female	1·16	1·41	1·26	1·00	1·00	1·00

TABLE IIIB

Values of the constant a relative to the third somite constant.

	Third somite	Chela length	Chela breadth	Antenna First segment	Antenna Second segment	Total length antenna
Unsexed	1·00	1·00	0·87	0·93	1·00	0·90
Male	1·00	1·22	1·06	0·95	1·09	0·90
Female	1·00	1·22	1·09	0·87	0·87	0·87

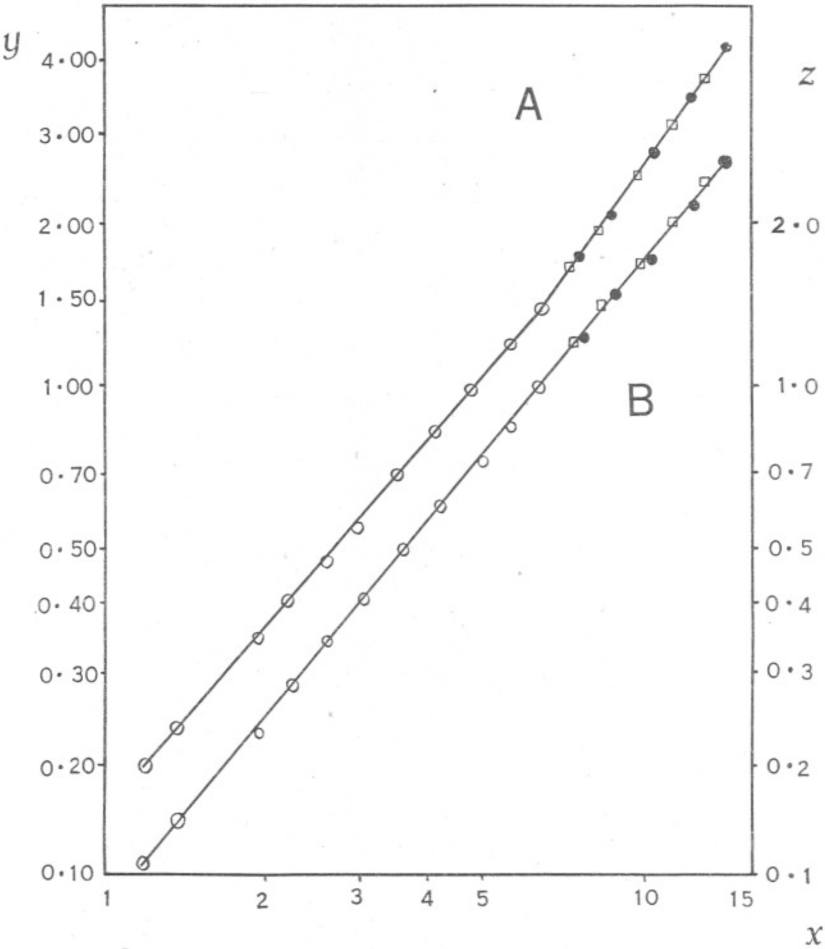

Fig. 2. A, The logarithm of the length of the second chela (y) against the logarithm of the body length (x). B, The logarithm of the length of the third somite (z) against the logarithm of the body length (x). Males, females and unsexed indicated as in Fig. 1.

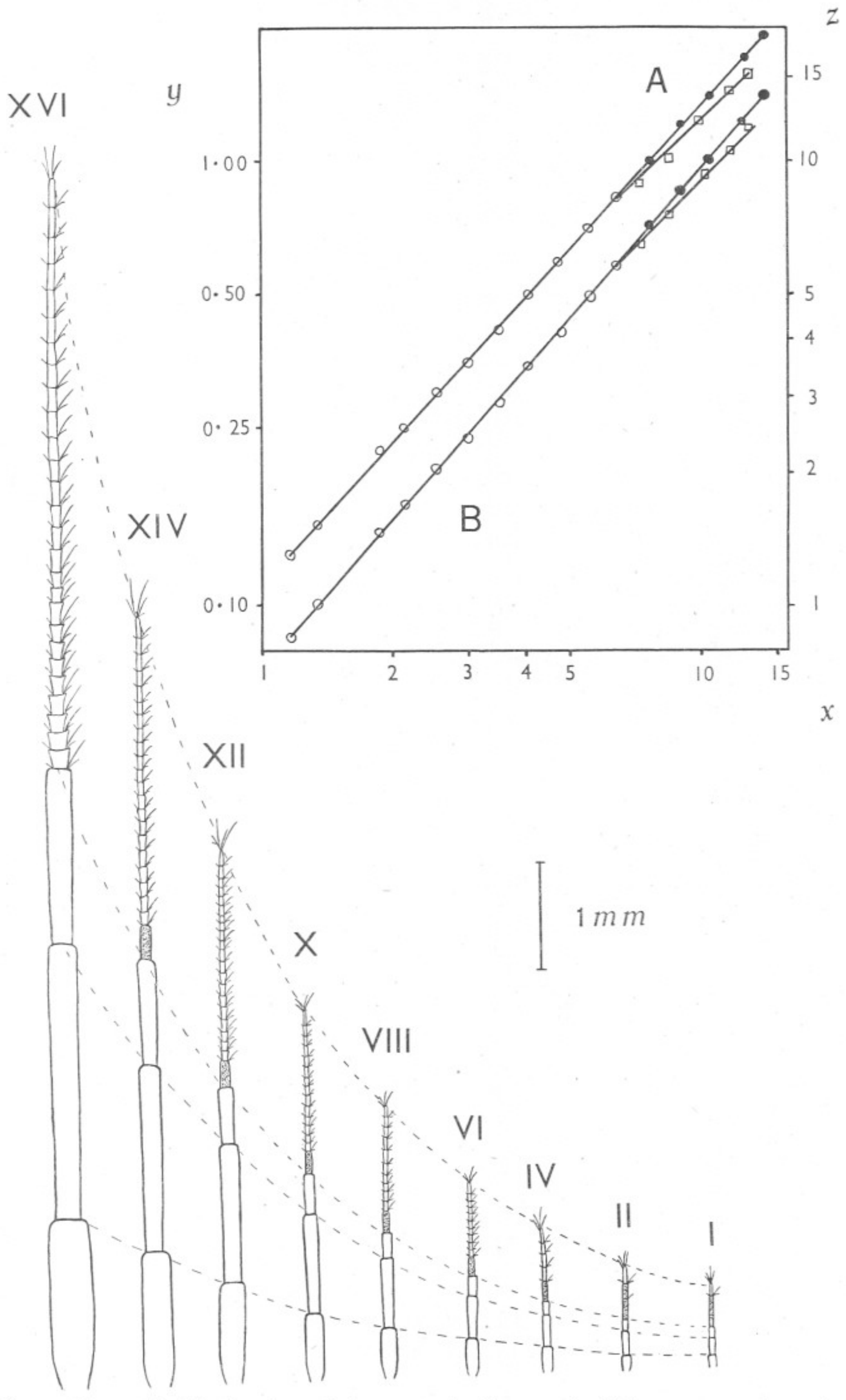

Fig. 3. Camera lucida drawings of nine stages in the growth of the antennae; the region of growth of the flagellum is shaded. The graph shows A the logarithm of the length of the first antennal segment (y) against the logarithm of the body length (x). B, The logarithm of the length of the whole antenna (z) against the logarithm of the body length (x). Males, females and unsexed indicated as in Fig. 1.

In the male both the chelae (Fig. 2A) and the antennae (Fig. 3A, B) increase in relative growth rate after stage XII. In the female the chelae increase in growth rate and at a similar rate as the increase in the growth rate of the male chelae. But the growth rate of the antennae in the female is less than that of the antennae in the unsexed animals and is the same as the growth rate of the body, so growth is isometric (Table III A).

CHANGES IN SHAPE DURING GROWTH

Such slight morphological changes as occur during development are confined to the chelae, first antennae, and body spines.

The first antenna consists of a three-segmented peduncle which remains the same throughout life and a long many-segmented flagellum arising from it. In the first stage the flagellum has two segments, the proximal segment being the region of growth of the flagellum (Fig. 3). In some stages the next segment to be formed may be seen dividing off from the proximal segment. Each segment has a large seta with several hairs at its distal end. The distal segments of the flagellum are long and thin while the proximal segments are short and stout.

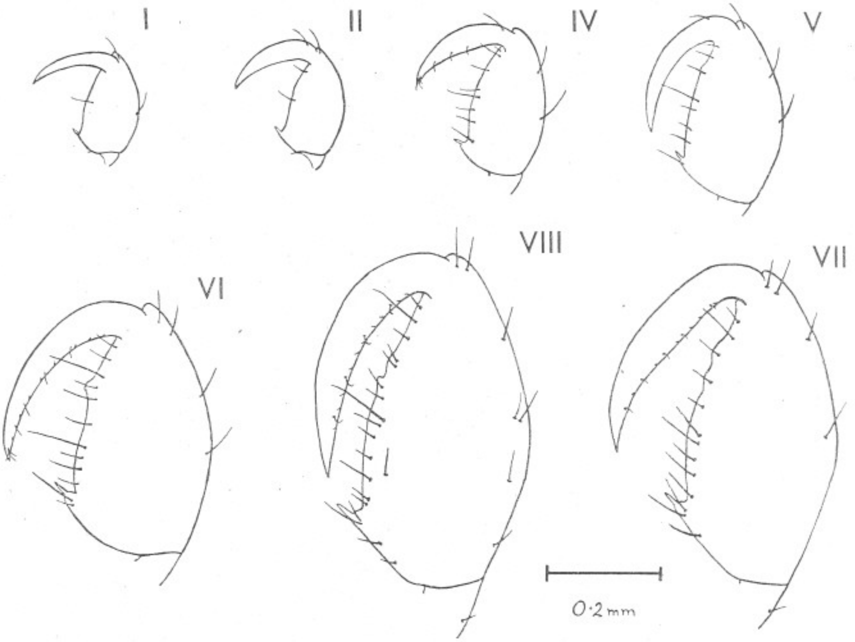

Fig. 4. Camera lucida drawings of the left side of the second left chela of growth stages I–VIII.

As early as stage V (Figs. 4, 5) the chelae begin to develop indentations on their palmar margins (Sexton, 1924, p. 361). A strong spine is present at the base of the palm. This becomes well developed and strong, helping to secure

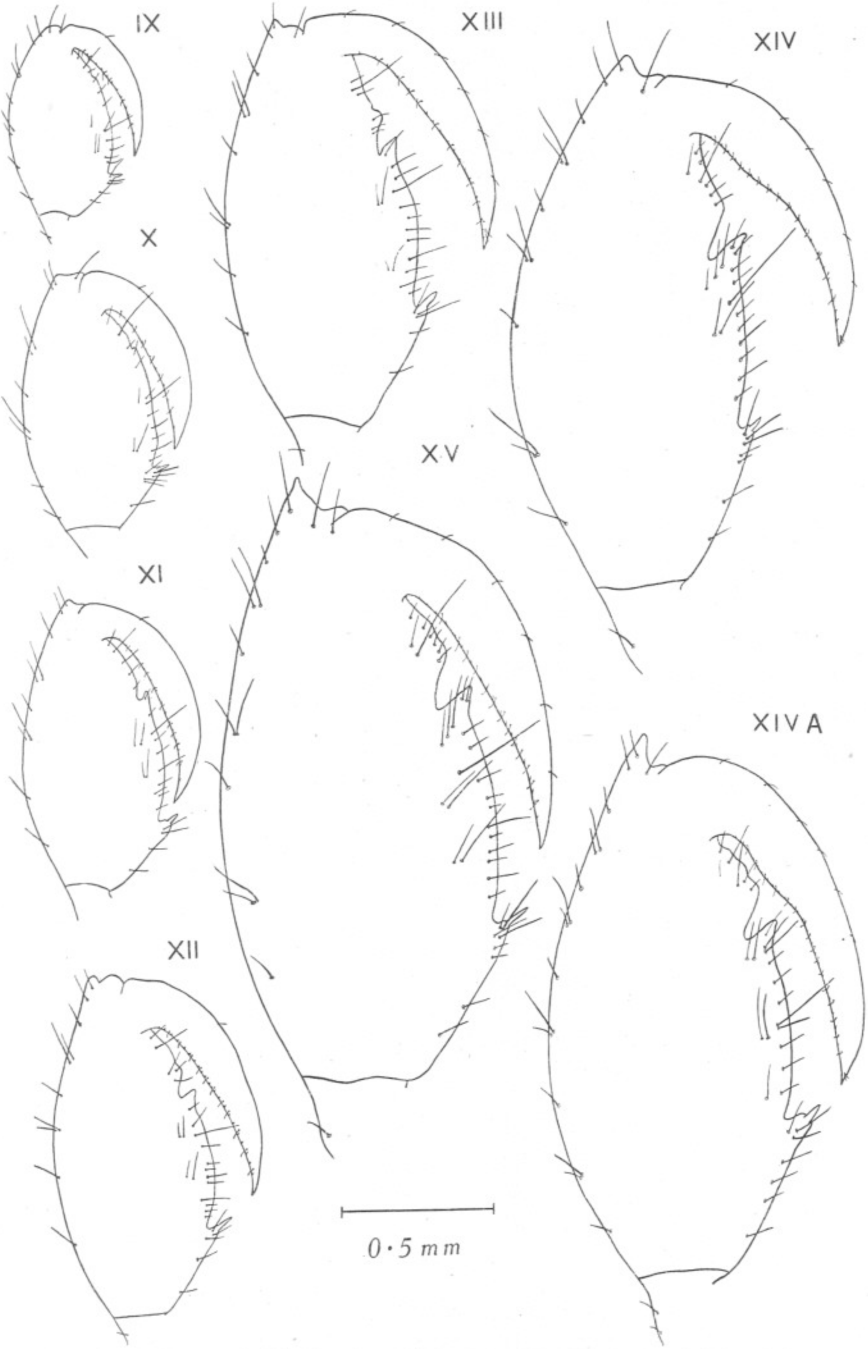

Fig. 5. Camera lucida drawings of the right side of the second right chela of growth stages IX–XV. XIV A is a female of growth stage XIV.

the grip of the chela on the food. In other caprellids (Haller, 1879) it is said to be poisonous and it is true that there is a large-celled gland at its base. Small chitinous thickenings appear on the inner edge of the dactylopodite which increase the cutting power of the joint. The rounded distal end of the palm in the younger stages becomes distinctly pointed in the adult. Hairs arise in a manner similar to the origin of tentacles in medusae. At first two hairs appear some distance apart; at a later ecdysis a third hair appears between the first two and secondary hairs may develop close to the primaries.

From stage X onwards large spines appear on the dorsal surface of the body (Fig. 6), one on the head, one on the segment fused with the head, two together in the middle of the third segment and another at the posterior end. Other smaller spines and tubercles appear in different positions on the body and are very constant in every stage, both male and female. There are no external morphological differences between the sexes except that the females possess a brood pouch.

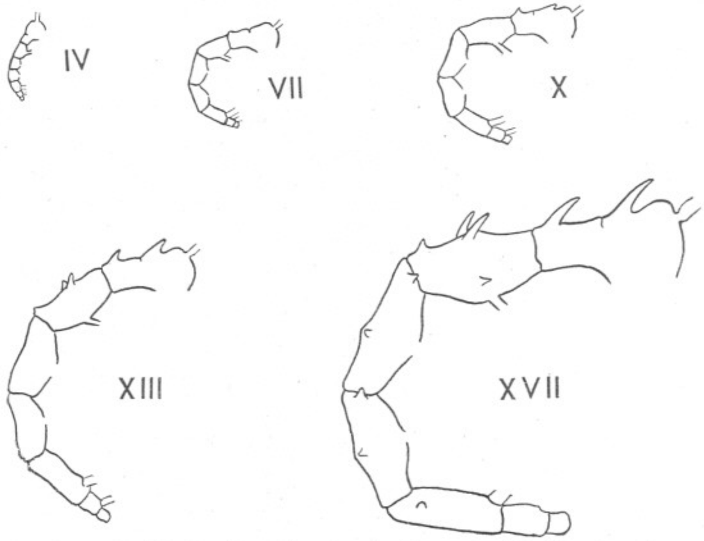

Fig. 6. Camera lucida drawings showing development of body spines in several growth stages. These drawings are not accurately to scale.

My thanks are due to Dr Stanley Kemp, F.R.S., for so kindly giving me every facility to work at the Plymouth Laboratory. I wish also to express my thanks to Mr F. S. Russell, F.R.S., for his great help and advice and to the staff of the Laboratory for collecting and supplying the material.

SUMMARY

The process of moulting in *Pseudoprotella phasma* is described. Sixteen instars have been found with a discontinuity in growth at the third stage. The

instar lengths differ by a common ratio of 1·169 in the male and 1·148 in the female, the animals becoming differentiated at the twelfth stage. There are no secondary sexual characteristics except the brood pouch. The growing parts display simple positive allometry. The growth rates of the chelae and antennae alter after stage XII but remain the same in the third body segment. Changes in shape in the chelae, antennae and spinous armature are described.

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NOTES ON THE OSTRACOD FAUNA OF PLYMOUTH

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(Text-figs. 1–13)

On June 15 and 20, 1938 Mr W. J. Rees of the laboratory of the Marine Biological Association, Plymouth, collected some mud samples at Mewstone and Rame Mud near Plymouth for Mr J. Hult, Uppsala. By kind permission of the director of the laboratory and of Mr Hult I have examined the Ostracoda contained in the samples.

The samples proved to contain seventeen species of Ostracoda. They will all be mentioned here in view of the uncertainty of the older identifications of these animals:

Philomedes interpuncta (Baird)
Polycope areolata G. O. Sars
Pontocypris trigonella G. O. Sars
Erythrocypris mytiloides (Norman)
Bairdia inflata (Norman)
Xenocythere cuneiformis (Brady)
Cythereis villosa G. O. Sars
Cythereis runcinata (Baird)
Cythereis emaciata (Brady)
Cythereis antiquata (Baird)
Cythereis jonesi (Baird)
Loxoconcha impressa (Baird)
Loxoconcha guttata (Norman)
Loxoconcha tamarindus (Jones)
Bythocythere turgida G. O. Sars
Xestoleberis depressa G. O. Sars
Paradoxostoma ensiforme Brady

Of these species only two have not been recorded before from the Plymouth district (Marine Biological Association, 1931, p. 150), viz. *Xenocythere cuneiformis* and *Xestoleberis depressa*. Both of these are, however, found in other parts of the English Channel (Norman & Scott, 1906, pp. 119, 121).

Three of the above-mentioned species have been very insufficiently described, since their appendages were not examined. These are *Cythereis runcinata*, *C. emaciata*, and *Loxoconcha guttata*; they are here described in greater detail.

The material on which this paper is based has been deposited in the museum of the Plymouth laboratory.

Genus Cythereis Jones, 1849

Cythereis runcinata (Baird), 1850

1850	*Cythere runcinata*, Baird, p. 254.
?1869	*Cythere stimpsoni*, Brady, p. 48.
1880	*Cythere stimpsoni*, Brady, p. 85.
1889	*Cythere runcinata*, Brady & Norman, p. 160.

Description. The structure of the shell and the appendages agree to a large extent with the diagnosis given for the subgenus *Cythereis* (Jones) by

Skogsberg (1928, p. 126). The following alterations and additions may be made.

Female. Shell (Fig. 4): with the same characteristics as in the subgenus *Cythereis*. The bristles along the margin usually with several branches.

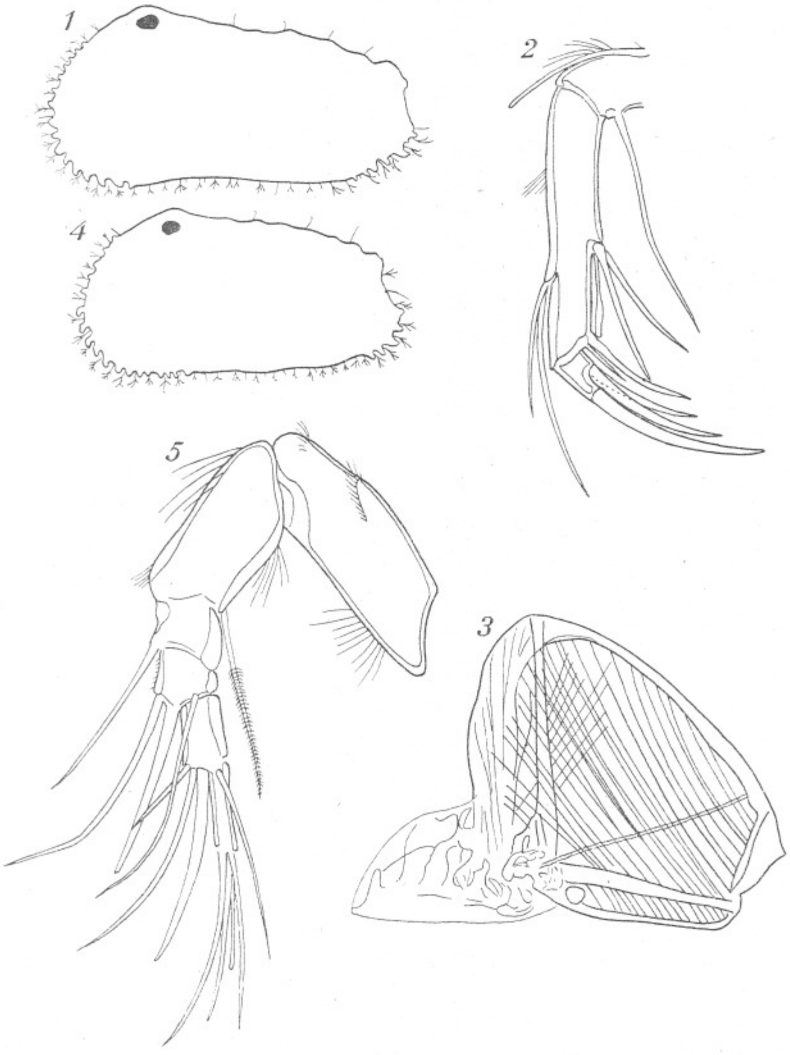
First antenna (Fig. 5): six-segmented. Of moderate strength. The relative lengths of the segments are about as follows: $\frac{16}{16}:\frac{15}{9}:\frac{4}{4{\cdot}5}:\frac{5}{2{\cdot}5}:\frac{4}{5}:\frac{6{\cdot}5}{6{\cdot}5}$. Bristles comparatively long. Bristle of second segment about twice as long as posterior side of the segment. Bristle of third segment three times as long as posterior side of the segment. Anterior bristle of fourth segment longer than its claw; its lateral bristle reaches with its point nearly to the point of the claw of the fifth segment. Anterior bristle of fifth segment as long as on the preceding segment; near this bristle a small spine-like bristle of the same length as that of the distal segment; it is directed more forward than the other bristles. Lateral bristle of about the length of the claw. Close by the end claw, the distal segment has two bristles of the same type and of about the same position and relative length as the two long and narrow bristles of the fourth segment. Sensorial bristle somewhat longer than the segment. The pilosity is about the same as in the subgenus *Cythereis*.

Second antenna: of moderate size. Exopodite thick, two-segmented, with the end broader, of the same length as half the anterior side of the second endopodite segment. Relative lengths of the segments of the endopodite about as follows: $\frac{7{\cdot}5}{4}:\frac{21}{17}:\frac{4{\cdot}5}{4{\cdot}5}$. Bristle of first segment of about the same length as the posterior side of the second segment. The two bristles on the anterior side of the second segment situated at a distance of nearly a third of this side from its distal end; one of them reaches to the point of the distal segment, the other much farther. The three posterior bristles are situated about two-thirds of the way from the distal end of the segment. The sensorial bristle reaches the distal end of the segment. The remaining two strong, extend beyond the point of the third segment. One of the postero-distal bristles claw-like, somewhat more than twice as long as the anterior side of the distal segment. The other bristle weak, less than half the length of the claw-like bristle. Antero-distal claw of end segment three and a half times as long as the anterior side of the segment. The two others much shorter.

Mandible: masticatory segment strong, short, wedge-shaped, without a hump on the anterior side. Epipodial appendage with three long and two short bristles. The relative lengths of the endopodite segments are about $\frac{4{\cdot}5}{3}:\frac{6{\cdot}5}{6}:\frac{5{\cdot}5}{5{\cdot}5}$. Dorso-distal bristle of first segment with long hairs. The two long ventro-distal bristles of this segment very thinly set with hairs.

Maxilla: without any special characteristics.

Fifth limb: proximal bristle of the anterior side of the protopodite very short and weak. Bristle on the posterior side swollen at the base, non-annulated, furnished with long hairs, thinly set, of nearly the same length as the dorsal side of the segment. Relative lengths of the segments of the endopodite segments about as follows: 10: 6·5: 6. Bristle of first segment half as long as second segment. End claw as long as first segment.



Figs. 1–3. *Cythereis runcinata* (Baird). Male. 1. Left shell. 2. Second antenn 3. Penis.
Figs. 4, 5. *Cythereis runcinata* (Baird). Female. 4. Left shell. 5. First antenna.

Sixth limb: the swollen bristle on the protopodite as on the fifth limb. Proportions of the lengths of the segments of the endopodite about 13 : 7·5 : 7·5.

Bristle of the first segment of the length of half the second segment. End claw as long as second and third segment together.

Seventh limb: bristle on the posterior side of the protopodite narrow, annulated, with fine hairs, of the length of half the anterior side of the protopodite. The segments of the endopodite have the following relative lengths: 20 : 8 : 9. Bristle of the first segment as long as the second segment. End claw much longer than first segment.

Furca: with two bristles, furnished with fine hairs.

Male. Second antenna (Fig. 2): exopodite narrow, indistinctly segmented, of the same length as in the female.

Fifth limb: the thick bristle on the posterior side of the protopodite as in the female.

Sixth limb: the same bristle shorter than in the female, with longer hairs. Bristle on first endopodite segment weak, as long as two-fifths of the second joint.

Brush-shaped organ: about three times as long as wide. Distal bristles about as long as stem.

Penis (Fig. 3): basal part triangular. Terminal part comparatively small with a straight ventral side. Its dorsal margin curved. Vas deferens with spiral thickenings. Free tube of ductus ejaculatorius not observed.

Dimensions.

	Length mm.	Height mm.	Breadth mm.
Female	0·84–0·86	0·43–0·44	0·40–0·41
Male	0·91–0·93	0·42–0·43	0·39–0·40

Distribution. English Channel, Vigo Bay and Mediterranean.

Remarks. In the second part of his studies, Skogsberg (1928) has begun to divide the genus *Cythereis* Jones into subfamilies on the basis of a number of new species from the Arctic regions and California. To these subfamilies Procter (1933) has added two more. *Cythereis runcinata*, like the following species, does not belong to any of the subfamilies referred to. They certainly represent two different subfamilies. But it is at present too early to define these subfamilies, because most of the species described by authors previous to those mentioned above are too insufficiently known, and the two species under notice are so far the only representatives of their subfamilies.

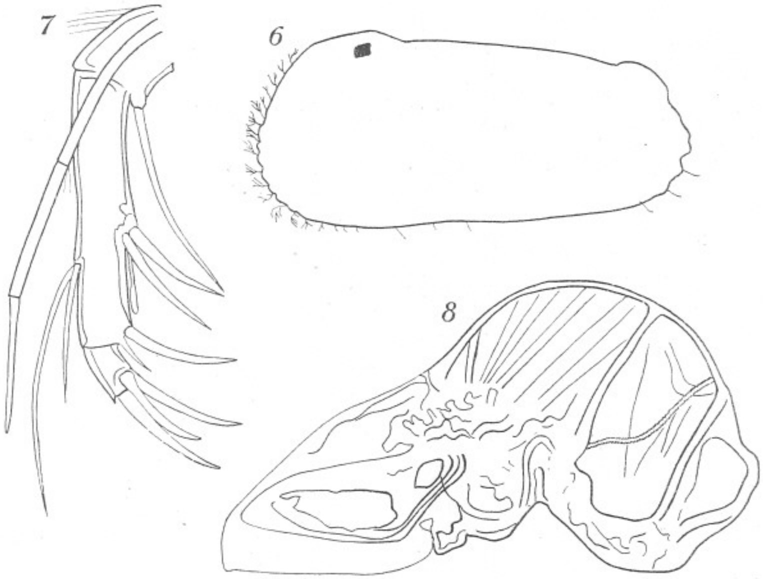
Cythereis emaciata (Brady), 1867

1867 *Cythere emaciata*, Brady, p. 210.
1868 *Cythere emaciata*, Brady, p. 413.
1874 *Cythere emaciata*, Brady, Crosskey & Robertson, p. 161.
1889 *Cythere emaciata*, Brady & Norman, p. 159.

Description. As in the preceding species, the structure of the shell and the appendages agrees to a large extent with Skogsberg's (1928) diagnosis for the subfamily *Cythereis* Jones. The following alterations and additions may be made.

Male. Shell (Fig. 6): bristles along the anterior margin long, with several branches.

First antenna: six-segmented, of the same type as in *C. runcinata*. Relative lengths of its segments about as follows: $\frac{14}{13}:\frac{14}{8}:\frac{3\cdot5}{5}:\frac{4}{2}:\frac{2\cdot5}{3}:\frac{5\cdot5}{6}$. Bristles long. Bristle of second segment twice as long as posterior side of the segment, reaches beyond the point of the distal segment. Bristle of third segment a little more than three times as long as anterior side of the segment. Claws of fourth and sixth segments of the same length as the posterior side of the two distal segments, the one of the fifth segment a little longer. The other bristles of fifth and sixth segments as in the preceding species. Pilosity also identical; apparently, however, no dorso-distal bunch of hairs on the first segment.



Figs. 6–8. *Cythereis emaciata* (Brady). Male. 6. Left shell. 7. Second antenna. 8. Penis.

Second antenna (Fig. 7): of about the same breadth as in the preceding species. Exopodite long, divided into three segments, reaches beyond the distal point of the antenna. The relative lengths of the segments of the endopodite are about as follows: $\frac{7\cdot5}{4}:\frac{18}{15}:\frac{3\cdot5}{3\cdot5}$. Bristle of first segment somewhat shorter than posterior side of the segment. Situation of anterior and posterior bristles of second segment and the length of the former as in *C. runcinata*. The posterior bristles, except the sensorial one, the postero-distal bristles and the bristles of the third segment shorter and thicker than in that species. All these bristles, except the little postero-distal one of the second segment, the sensorial one and one of the posterior bristles of the last segment, claw-like, about two-fifths of the length of the posterior side of the second segment. Antero-distal claw of third segment about twice as long as the anterior side of this segment. Pilosity as in the preceding species.

Mandible: as in *C. runcinata*. Relative lengths of the endopodite segments as follows: $\frac{4}{3} : \frac{6}{5{\cdot}5} : \frac{5{\cdot}5}{5{\cdot}5}$. Dorso-distal bristle of first segment with short hairs.

Maxilla: without peculiarities.

Fifth limb: bristle on posterior side of protopodite swollen at the base, thin, covered with long hairs, as long as half the anterior side of the segment. Proportional lengths of the segments of the endopodite about as follows: 9·5 : 6·5 : 5. End claw as long as second segment. Other bristles as in the preceding species.

Sixth limb: bristle on posterior side of protopodite not swollen, annulated, with short hairs, as long as half the segment. Relative lengths of the endopodite segments are: 12 : 7·5 : 7. Bristle of first segment nearly as long as second segment. End claw as long as first segment.

Seventh limb: bristle on posterior side of protopodite as in the sixth limb but with only very short hairs. Relative lengths of the endopodite segments: 18 : 8·5 : 9·5. Bristle of first segment longer than second segment. End claw much longer than third segment.

Brush-shaped organ: as in the preceding species.

Penis (Fig. 8): terminal part big, triangular, with a rounded point. Vas deferens has spiral thickenings.

Female unknown.

Dimensions. The shells of the few specimens which were contained in the samples were in a very bad condition. Yet, the length seemed to be about 0·83 and the height about 0·37 mm.

Distribution. Around the British coasts, Bay of Biscay, Mediterranean.

Remarks. See *Cythereis runcinata*.

Genus Loxoconcha G. O. Sars, 1865

Loxoconcha guttata (Norman), 1865

1865	*Cythere guttata*, Norman, p. 19.
1865	*Cythere guttata*, Brady, p. 192.
1868	*Loxoconcha guttata*, Brady, p. 436.
1874	*Loxoconcha guttata*, Brady, Crosskey & Robertson, p. 186.
1880	*Loxoconcha guttata*, Brady, p. 120.
1889	*Loxoconcha guttata* (partim), Brady & Norman, p. 184.
1906	(*non Loxoconcha guttata*, Cushman, p. 370).

There were ten specimens in the samples, the shells of which agreed in all respects with the descriptions of *Loxoconcha guttata* (Norman). The following additions may be made.

Description. Female. Shell (Fig. 9): anterior and posterior margins with simple marginal pores and thinly set with fine hairs. Other pores on the shell few in number. Line of concrescence and inner line coincide except on the anterior and posterior margins.

Eyes: separate.

First antenna (Fig. 10): six-segmented. Proportional lengths of the segments about as follows: $\frac{10\cdot5}{10}:\frac{10}{8}:\frac{3}{3}:\frac{4}{4}:\frac{6}{6}:\frac{6\cdot5}{6\cdot5}$. Bristle of second segment thick at the base, suddenly growing narrower and in the middle provided with long hairs. Bristle of third segment and dorsal bristle of fourth segment thicker than the other bristles and as long as the fourth and fifth segments put together. Lateral bristles of fourth segment somewhat shorter. Of the bristles of the fifth segment two are but slightly longer than the segment. The remaining two and the two longest bristles of the sixth segment about the length of the two distal segments put together. The short bristle of the last segment and the sensorial one of about the length of the segment.

Second antenna (Fig. 11): exopodite three-segmented, reaches to the points of the end claws. Relative lengths of the segments about as follows: $\frac{10\cdot5}{10}:\frac{6}{2\cdot5}:\frac{17\cdot5}{17}:\frac{2}{2}$. Bristle of first endopodite segment as long as one-third of the anterior side of the second segment. The two bristles on the anterior side of this last segment situated on the middle of this side, the three on the posterior side at a distance of three-sevenths of this side from its distal end. Of these latter, one is very short, one reaches to the end of the segment, only the sensorial bristle reaches beyond the distal end of the antenna. Of the bristles of the anterior side one is about as long as the middle bristle of the posterior side, the other shorter. End claws long, nearly two-thirds of the second segment.

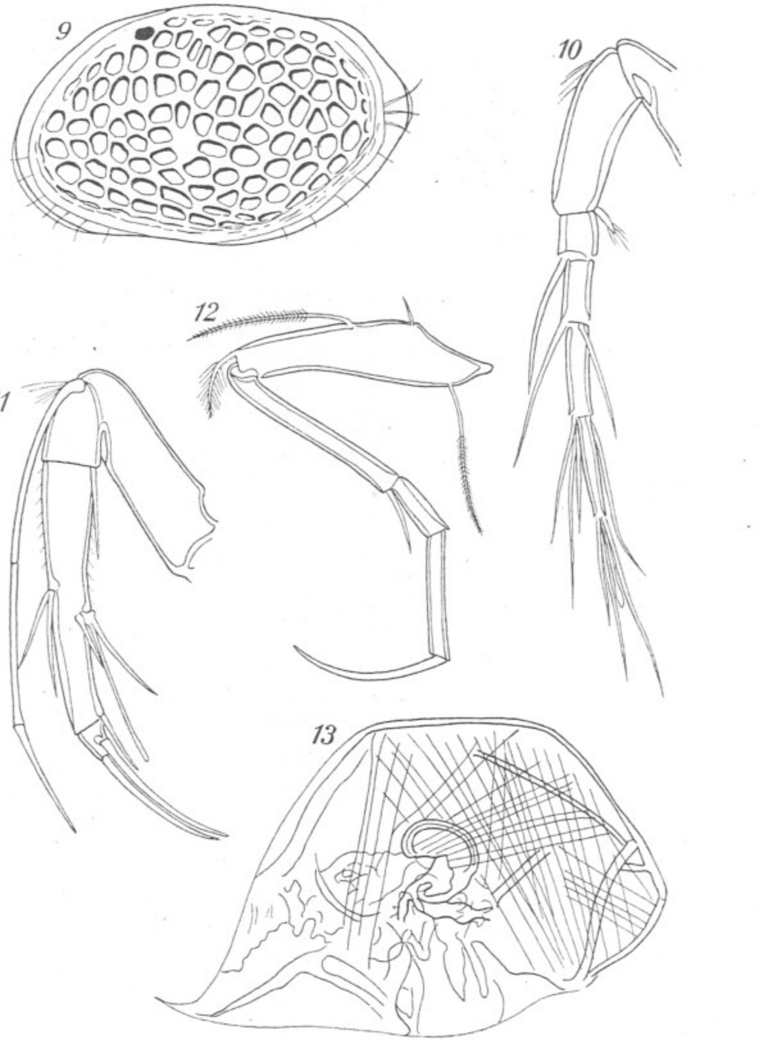
Mandible: epipodial appendage with three very long and one short bristle. Endopodite indistinctly three-segmented.

Maxilla: with the first segment of the endopodite rather prolonged. Epipodial appendage with one "aberrant" bristle.

Fifth limb: protopodite with two anterior, two antero-distal bristles and one posterior bristle. The antero-proximal bristle on all the three of the last limbs very short. The other anterior bristle reaches beyond the distal end of the segment, the posterior of about the same length. Proportional lengths of the segments of the endopodite about as follows: 13 : 5·5 : 7·5. Bristle of first segment shorter than second segment. End claw, as on the other legs, about as long as distal segment.

Sixth limb: (Fig. 12): protopodite with two anterior bristles and with one antero-distal and one posterior bristle. The distal of the two anterior bristles and the posterior one relatively longer than on the fifth limb. Relative lengths of the endopodite segments about 17 : 5·5 : 10. Bristle of first segment as long as second segment.

Seventh limb: protopodite as on the sixth limb. The long anterior bristle and the posterior one shorter than the distance from the base of the first to the end



Figs. 9–12. *Loxoconcha guttata* (Norman). Female. 9. Left shell. 10. First antenna. 11. Second antenna. 12. Sixth limb.
Fig. 13. *Loxoconcha guttata* (Norman). Male. Penis.

of the segment. Relative lengths of the segments of the endopodite: 25 : 6 : 13. Bristle of first segment longer than distal segment.

Posterior part of the back of the body with hairs.

Furca: with two bristles.

Male. Brush-shaped organ: of usual *Loxoconcha*-type.

Penis: (Fig. 13): subtriangular. Terminal part large, not clearly defined from the basal part, with prolonged, somewhat upturned point.

Dimensions.

	Length mm.	Height mm.	Breadth mm.
Female	0·60–0·63	0·35–0·36	0·33–0·35
Male	0·56–0·58	0·28–0·29	0·27–0·28

Distribution. Difficult to know exactly for reasons stated below. The species seems, however, to occur from Shetland and the British coasts down to the Bay of Biscay and Spain, probably also in the Mediterranean.

Remarks. After having regarded *Loxoconcha guttata* (Norman) and *L. granulata* G. O. Sars as two different species, Brady & Norman in their monograph (1889) united them as *L. guttata*, believing them to be only different stages of the same species, and most other authors have followed them in so doing. However, that this view is not right is already evident from the fact that the former species is not known from Scandinavia, where the latter is very common. And G. O. Sars (1928, p. 220) pointed out that these species can scarcely be identical, as the differences in the sculpture of the shell are considerable.

The resemblance between these species as regards the structure of the limbs (relative lengths of the segments, situation and length of the bristles) is, however, striking. Even the penis, which usually exhibits easily detectable and reliable characteristics, shows no noticeable differences here. The differences observed thus refer almost entirely to the shells. But since the shells of these species, belonging to a genus with very slight individual variations within the species, show very easily observable and quite constant differences, since only one of the species occurs on the Scandinavian shores, and since both occur quite constantly in the same British districts, there are nevertheless good reasons for classing *L. guttata* and *L. granulata* as two separate species.

Besides the material of *L. guttata* mentioned above, I have also examined material of *L. granulata* from the west coast of Sweden in my own collection, and of both species from the British coast. The British material is kept in the Hancock Museum at Newcastle-upon-Tyne and has been identified by G. S. Brady. I have great pleasure in thanking the keeper of this museum for his kindness in placing the material at my disposal.

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THE LARVAE OF THE BRITISH SPECIES OF *SPIRONTOCARIS* AND THEIR RELATION TO *THOR* (CRUSTACEA DECAPODA)

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(Text-figs. 1–4)

The general larval characters of the genus *Spirontocaris* are summarized by Gurney (1937*b*), but since his paper was written there have been published descriptions of *S. spinus* var. *lilljeborgi* (see Lebour, 1937) and of *S. pusiola* (see Bull, 1938). The four British Columbian species described by Needler (1933) must also be taken into consideration. With our present knowledge of all these species the description must be slightly modified. We now know the larvae of all the British species of this genus with the exception of the typical form of *S. spinus*. The specimen from which the larvae were hatched was intermediate between the typical *S. spinus* and the var. *lilljeborgi* and was regarded as the latter. The following species are British: *S. polaris*, *S. spinus* and its var. *lilljeborgi*, *S. gaimardi*, *S. pusiola*, *S. occulta* and *S. cranchi*. *S. polaris* is a northern form, the only British records being from the Shetlands. It has an abbreviated development, described by Stephensen (1912*b*, 1916, 1935).

S. spinus var. *lilljeborgi*; the first larva is described from Millport (Lebour, 1937).

S. gaimardi, the first larva is described from Millport in the present paper.

S. pusiola, the first larva is described by Bull (1938) from Cullercoats.

S. occulta, all the larvae are described from Plymouth (Lebour, 1932*a*, 1936*a*).

S. cranchi, all the larvae are described from Plymouth (Lebour, 1932*a*, 1936*a*).

The British Columbian species *S. paludicola*, *S. tridens*, *S. herdmanni* and *S. brevirostris*, unlike the British species, have the antennal scale without segmentation, or indistinctly segmented, and there are no marginal spines on the carapace of two of them. Otherwise they agree with *S. occulta* and *S. cranchi* which are hatched without a rostrum. The northern species described by Stephensen all have an abbreviated development. *S. spinus* var. *lilljeborgi*, *S. gaimardi* and *S. pusiola* are hatched with a rostrum and there is an accessory spine on the antennal endopod in *S. spinus* var. *lilljeborgi*. Bull (1938) gives a key to the known larvae of the British species (excluding *S. polaris*) but this will have to be modified to include *S. gaimardi*:

KEY TO THE KNOWN LARVAE OF THE BRITISH SPECIES OF *SPIRONTOCARIS* (EXCLUDING *S. POLARIS*) IN STAGE 1

- I. Dorso-lateral spines at hinder end of fifth abdominal somite.
  - *a*. Rostrum well developed.
    - * Accessory spine on antennal endopod ... ... *S. spinus* var. *lilljeborgi*
    - ** No accessory spine on antennal endopod ... ... *S. gaimardi*
  - *b*. Rostrum absent ... ... *S. cranchi*
- II. No dorso-lateral spines at hinder end of fifth abdominal somite.
  - *a*. With distinct but small rostral spine, dorsal side of fifth abdominal somite without denticles ... ... *S. pusiola*
  - *b*. Rostrum absent, dorsal side of fifth abdominal somite with a row of fine denticles ... ... *S. occulta*

We may now define the larvae of the known species in the following way: Rostrum present or absent in stage 1, pointed in front. Carapace with small supra-orbital spines and with or without denticulate margin. Abdominal somite 5 with or without dorso-lateral spines. Telson rather deeply indented, in late stages with two pairs of lateral spines and twelve terminal. Anal spine present from stage 1. Antennal scale segmented or not, endopod spine-like, with or without an accessory spine. Maxillule without outer seta. Exopod of maxillipede 3 with three terminal setae in stage 1. Exopods on two, three or four pairs of legs. Legs 3–5 long, slender, functional. The development of certain northern species is greatly abbreviated, others may have nine larval stages.

Spirontocaris gaimardi (Milne Edwards) (Fig. 1 *a–d*)

Hippolyte gaimardi Milne Edwards.

This species has been taken several times in the neighbourhood of Millport by Mr R. Elmhirst and Dr A. G. Nicholls. Dr Nicholls has kindly sent me the newly hatched larvae to describe. The adult resembles *S. spinus* var. *lilljeborgi* in having a large and conspicuous mandibular palp and in having no central tooth on the hind margin of the telson. It has epipods on the first and second legs only, thus resembling *S. occulta* and *S. cranchi*.* The larvae were hatched in April 1935. They come in between those of *S. spinus* var. *lilljeborgi* and *S. pusiola*. Thus there is a fairly long rostrum but no accessory spine on the antennal endopod, the antennal scale has only one external seta and there are denticulations antero-ventrally on the carapace.

Description of the newly hatched larva (Fig. 1 *c*, *b*). Length 2·9 mm. The rostrum is long and slender ending in a point and reaching beyond the eyes. The carapace ends anteriorly in a point and there are three teeth behind this on the margin. The fifth abdominal somite has a pair of dorso-lateral spines. The telson is fairly deeply excavated posteriorly with the usual fourteen spines. The antennal scale is segmented and has one outer seta; the endopod is a simple rod ending in a spiny seta. The exopods of the maxillipedes bear

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* The setobranch on leg 3 referred to by Lebour (1936 *b*) is here disregarded.

4, 5, 5 setae, the endopod of the second having four segments, of the third, five segments. There are rudiments of legs 1–4. An anal spine is present.

It is shown that the larvae of the species of *Spirontocaris* vary in several ways, more than do the larvae of the species of *Hippolyte*. They can, however, always be distinguished from *Hippolyte* by the absence of the outer seta on the base of the maxillule and in the presence of an anal spine in the early stages; in the later stages the legs are always longer and functional and there are usually more exopods on the legs. The characters of the larvae of *Hippolyte* are summarized by Gurney (1937*b*).

Attention has been drawn (Lebour, 1936*a*) to the great similarity between *Spirontocaris cranchi* and the genus *Thor*, both of which have lost the mandibular palp, but *Spirontocaris cranchi* in other ways resembles *S. occulta* so strongly that it seems impossible to remove it from that genus. Zariquiey (1935) has actually attributed *S. cranchi* to the genus *Thor*, but it is inadvisable to follow him in this respect, especially as we now almost certainly know the larvae of *Thor* which show generic differences from those of *Spirontocaris cranchi*.

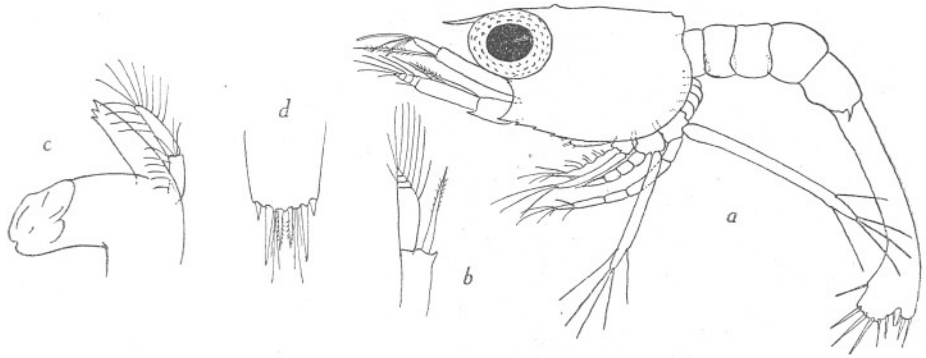

Fig. 1. *Spirontocaris gaimardi: a*, newly hatched larva, 2·8 mm. long; *b*, antenna; *c*, mandible of adult; *d*, end of telson of adult.

Whilst working at the Bermuda Biological Station in 1938–9, I found a conspicuously coloured and very small Hippolytid larva which occurred commonly in the plankton from fairly shallow water. The first stage was caught in the Reach at night, but it also occurred with the other stages outside Castle Harbour. The last larva changed to the post-larva in the laboratory, and the post-larva to the first young stage. In this last, the latest stage obtainable, the rostrum was very short; there was a leaf-like process, apparently movable, on the distal segment of the antennular peduncle; the external ramus of the antennule was very much swollen, and the carpus of the second leg was divided into four segments. There were no traces of epipods on the legs. From these characters it seemed almost certain that here was the missing larva of *Thor*. Verrill (1922) has recorded *T. paschalis* from Bermuda, having dredged berried females in the shallow waters of the Reach among weed, but subsequent efforts to obtain it have been unsuccessful. It is a common species on the Florida coast and in many other parts of the world, but the Bermuda form according to Verrill, differed slightly from the type, having only five segments in the carpus of the second leg and a shorter rostrum with fewer teeth. As the larvae were obtained both in the Reach (early stages only) and outside (all stages) commonly in spring and summer, it is very probable that one at least of the habitats of the adult is in the shallow water outside among the weeds and rocks where it is almost impossible to dredge.

The chief peculiarity of the larva is its extremely broad rostrum which is triangular, slightly broader at the base than at the sides and ending in a rounded angle anteriorly. This rostrum is unlike that of any known larva. No teeth had appeared even in the first young stage, although the rostrum had become more pointed and very much the shape of a young form figured by Verrill, which, however, had three teeth.

All the larvae were coloured bright red with many chromatophores on a yellow ground, there being two red streaks from the thorax right along the abdomen.

THE LARVAL AND YOUNG STAGES OF *THOR* (Figs. 2–4)

First larval stage (Fig. 2*a–g*). Length 2 mm. or less. The eyes are not free. The rostral region is rounded, but there is no true rostrum. The carapace ends anteriorly in a point, and there are three denticles behind it on the ventral margin. The dorsal organ is conspicuous behind the eyes, and there is a small prominence in front of the posterior end of the carapace dorsally. There are no spines on the abdominal somites, and there is no anal spine. The telson is indented in the centre and has the usual fourteen spines. The antennule is short with an unsegmented peduncle bearing at its end a long seta internally, representing the endopod, with a thin hair, and a thick terminal process bearing three aesthetes and a hair. The antennal scale is segmented at the tip with two outer setae and nine inside and round the tip, the endopod being represented by a short thick rod bearing a long seta with a short accessory seta. The mandible has the molar process already beginning to be separated from the incisor portion. The maxillule has no seta on its base; the endopod has five setae. The maxilla has a setose endopod with three lobes, bearing three setae terminally and 2, 2, 2 setae on the lobes, and five setae on the exopod. The exopods of the maxillipedes bear five setae, three terminal. There is a rudiment of the first leg.

The second larval stage. Length *ca*. 2 mm. (sometimes slightly less or more). This is very like the first, but has the eyes and rostrum free and the usual extra pair of spines internally on the telson. There are no supra-orbital spines, but the antennal spine is present.

The third larval stage (Fig. 2*h–k*). Length 2–2·8 mm. The larvae vary in size and development, but none of them have the base of the uropods separated.

The telson is cut off from the sixth abdominal somite. There are rudiments of the second to the fourth legs, the first being functional. The exopods of the second and third maxillipedes and the first leg have four terminal setae, the second maxillipede with one lateral, the third and leg I with two. In the larger specimens the pleopods show beneath the cuticle. The inner uropod

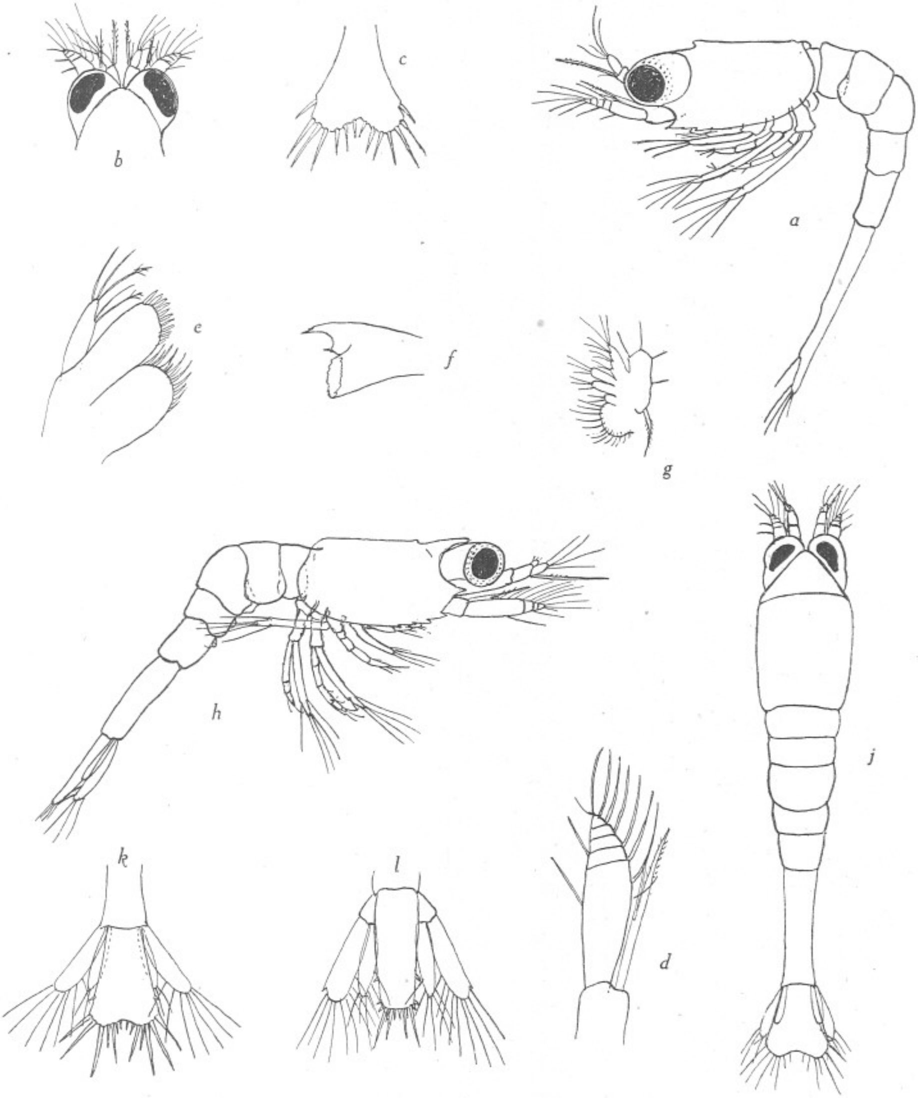

Fig. 2. *Thor: a*, first larval stage, 2 mm. long; *b*, head region; *c*, telson; *d*, antenna; *e*, maxillule; *f*, mandible; *g*, maxilla; *h*, third larval stage, 2·5 mm. long; *j*, dorsal view; *k*, telson of more advanced third stage; *l*, fourth larval stage, telson.

has no setae in the smaller forms but in the larger specimen there are two, and in these the outer seta of the telson has become tooth-like.

The fourth larval stage (Fig. 2*l*). Length *ca.* 2·7 mm. or rather longer, varying much. Small pleopods are now present, the second leg is functional, the other three rudimentary. Legs 1 and 2 bear exopods, but the others are simple rods. The telson is nearly straight-sided and the uropods have a distinct base. There is a spine each side just above the posterior third, the following one tooth-like near the angle, and ten terminal spines. The antennal endopod has lost the accessory spine.

The fifth larval stage (Fig. 3*a*, *b*). Length 3·6 mm. The rostrum is still a blunt triangle, the carapace is pointed in front with the three antero-ventral denticles. There are no supra-orbital spines but there is an antennal spine. The first and second legs are chelate, their exopods bear eight setae, the third to the fifth legs are not functional and are scarcely jointed and held under the abdomen. The pleopods are long but without setae. The telson has two pairs of lateral spines and ten terminal spines, the second from the outside being the longest, and the hind margin is slightly convex. There is now an anal spine. The mandible is distinctly cleft.

The sixth larval stage. Length 4 mm. This stage moulted to the post-larva. It was very little larger than stage 5 and very similar, but slightly farther advanced in development. All the legs are longer and jointed, but the third to the fifth are hardly functional. The pleopods are long but not setose.

The post-larva from the last larva (Fig. 3*c*–*g*). Length 4 mm. The anterior angle of the carapace is rounded and there are no ventral denticles. The antennal spine alone remains. The antennule shows rudiments of the distal plate. The rostrum is still a broad triangle, rounded, but rather more pointed, in front. There are remains of exopods on legs 1 and 2, but no epipods. The carpus of the second leg is divided into three segments. Legs 3–5 are long and slender, the dactyl ending in a tooth with two inner teeth. The pleopods are setose. The telson has two pairs of lateral spines and six terminal with two hairs. The fifth abdominal somite has a very small postero-lateral tooth, and the fourth ends sharply almost in a tooth and there are hairs at the edges of these somites.

The post-larva moulted to a first young stage.

The first young stage (Figs. 3*h*, *j*, 4*a*–*g*). Length 3·6 mm. In this stage there is a distinct hinged plate on the distal segment of the antennular peduncle. The outer antennular flagellum is very thick at the base and composed of seven segments. The antennal flagellum is about twice as long as the carapace. The rostrum is short, pointed, with a very broad base, but has no teeth. The appendages closely resemble those of *Thor paschalis* in shape. The carpus of the second leg has four segments. Legs 3–5 end in toothed dactyls. The telson is convex terminally with six terminal setae and a pair of long hairs, but no central tooth. There are no epipods and there is no trace of a mandibular palp.

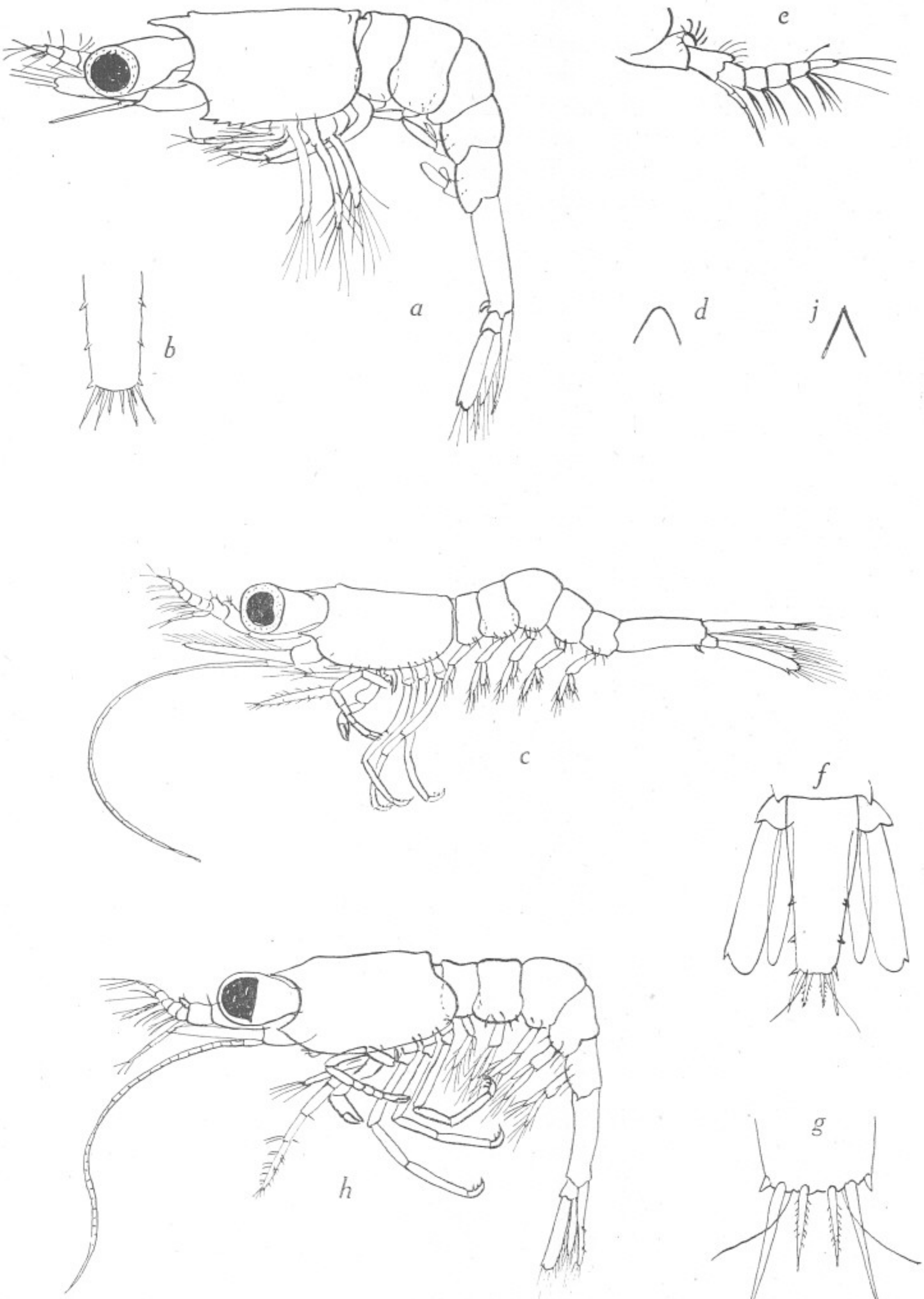

Fig. 3. *Thor: a*, fifth larval stage, 3·6 mm. long; *b*, telson; *c*, post-larva from last larva, 3 mm. long; *d*, rostrum; *e*, antennule; *f*, telson; *g*, end of telson; *h*, first young stage from post-larva, 3·6 mm. long; *j*, rostrum.

No later stages were procurable but it seems certain that this is the larva of *T. paschalis*. This species (or possibly a variety) has been recorded from Bermuda and there cannot be a doubt of the truth of the record, judging by Verrill's figures. No species of *Spirontocaris* have ever been found there and it is here shown that the larva differs from both that genus and from *Hippolyte*. The characters of the first young stage show that it is very close to *Thor*, having the characteristic plate on the distal segment of the antennular peduncle, no supra-orbital spines, no epipods, the carpus of the second leg divided into four segments (there being five in the Bermuda form of *Thor* according to Verrill), a very broad and short rostrum and no mandibular palp (this last character is not significant, as it has been shown that in *Spirontocaris occulta* the palp does not appear in the first young stages (Lebour, 1936*a*).

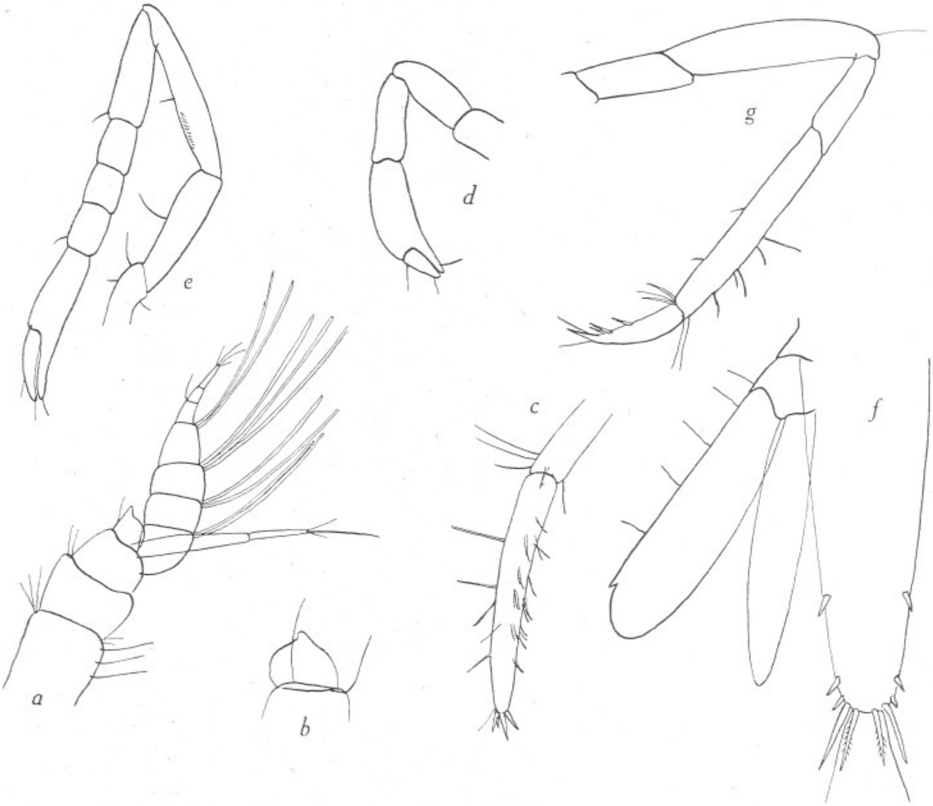

Fig. 4. *Thor*, first young stage: *a*, antennule; *b*, leaf-like process on antennule; *c*, end of third maxillipede; *d*, first leg; *e*, second leg; *f*, telson; *g*, last leg.

The differences in the larva fully warrant the separation of *Thor* from *Hippolyte* and *Spirontocaris*, although it is obviously related to them and has certain characters of both. The rostrum is unlike that of any known decapod larva.

The adult *Thor* closely resembles *Spirontocaris cranchi*, but the larva differs much more from this species than it does from *S. spinus* var. *lilljeborgi*, having an accessory spine on the antennal endopod as in that species. The fact that there are no epipods on the legs at once separates it from *S. cranchi*, the only species of *Spirontocaris* in which the mandibular palp is wanting and which has epipods on legs 1 and 2. Those species of *Spirontocaris* which lack epipods (see Rathbun, 1926) are of an entirely different type, having the usual two-segmented mandibular palp.

The larval characters of *Thor* may now be given in order to compare them with the other genera of the Hippolytidae:

Rostrum absent in stage 1, the front margin rounded; in the following stages it forms a broad triangle, the front being rounded. Carapace without supra-orbital spines; denticles on the antero-ventral margin.

Abdominal somite 5 without dorso-lateral spines. Telson fairly deeply indented, in late stages with two pairs of lateral spines and ten terminal. Anal spine not present in early stages but present in the two last.

Antennal scale segmented with two outer setae, endopod spine-like with accessory spine. Maxillule without outer seta. Exopods on legs 1 and 2, exopods of third maxillipede with three terminal setae. Six larval stages.

KEY TO THE LARVAE OF THE GENERA *SPIRONTOCARIS*, *HIPPOLYTE* AND *THOR*

A. Rostrum pointed.
   1. No external seta at base of maxillule [dorso-lateral spines on fifth abdominal somite present or absent; accessory spine on antennal endopod present or absent; supra-orbital spines small; anal spine present in all stages] *Spirontocaris*
   2. External seta at base of maxillule [dorso-lateral spines on fifth abdominal somite present, no accessory spine on antennal endopod; supra-orbital spines absent or minute in early stages; anal spine present only in later stages] *Hippolyte*

B. Rostrum very broad, triangular, rounded in front [no dorso-lateral spines on fifth abdominal somite; antennal endopod with accessory spine; no external seta at base of maxillule; no supra-orbital spines; anal spine present only in later stages] ... ... *Thor*

The genera *Hippolyte*, *Spirontocaris*, *Thor*, *Chorismus* and *Caridion* are all included in the group of the Hippolytidae as defined by Calman (1906) and Kemp (1914) which have no arthrobranchs on the peraeopods and possess an incisor process on the mandible. The larvae give additional evidence that the existing classification of these forms is a natural one. *Caridion* approaches nearest to the Pandalidae and also has certain characters which approach *Lysmata*. *Chorismus* (see Gurney, 1937*b*) has an abbreviated development but in essentials it is not unlike the others, except in having more spines on the telson. All in this group agree in having a compact body, not specially elongated, the fifth leg not unusually long and never prematurely developed, in having the exopod of the third maxillipede in stage 1 ending in three setae, in the telson being broad and somewhat indented in the posterior margin, in the absence of dorsal spines on any of the abdominal somites and in the absence of posterior spines on the ventral margin of the carapace or in the centre, the eyes being normal and not specially long. This group of larvae differs very appreciably from all the other Hippolytid larvae known. Gurney (1937*b*), in summarizing the larval characters of the Hippolytid genera, has shown that there are four types of larvae in *Lysmata*, *Hippolysmata*, *Tozeuma*, *Saron* and *Latreutes*, those of *Lysmata* and *Hippolysmata* being very similar, all four for the most part differing greatly from one another and that it is not as yet possible to group these further in any natural system. The finding of the larva of *Thor*, one of the desiderata mentioned in his work, has, however, advanced us a step in showing that this genus undoubtedly takes its place near *Spirontocaris* and *Hippolyte*.

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ON THE NEMATOCYSTS OF HYDROMEDUSAE. III

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Naturalist at the Plymouth Laboratory

(Text-figs. 1–32)

The present paper is a continuation of the observations on the nematocysts of Hydromedusae and includes descriptions of the nematocysts of twelve species that I have not previously examined.

In two only of these species, *Turritopsis nutricula* and *Aglantha digitalis* var. *rosea*, was examination made on living material. For the remainder it has been necessary to use specimens preserved in formalin. Amongst these are a number of species whose classificatory position has a special interest. These species are not found at Plymouth and would in any event be difficult to obtain living as most of them are from deep water.

I am grateful to Mr J. H. Fraser, Dr H. B. Moore, and Mr W. J. Rees for kindly supplying me with some of these specimens. Certain of the other deep sea medusae were found among the collections of the late Mr E. T. Browne.

ANTHOMEDUSAE

Turritopsis nutricula McCrady

Observations were made on living material from Plymouth. There were two kinds of nematocysts, microbasic euryteles and desmonemes (Figs. 1–4).

Euryteles: 8–10 × 4μ undischarged.

Desmonemes: 6–7 × 4–4·5μ undischarged, 4–5 × 3μ discharged.

Both kinds of nematocysts were present in the marginal tentacles and in the nematocyst clusters along the margins of the mouth lips. In the tentacles there were only a few isolated euryteles, the desmonemes being very much the more numerous. In the margin of the mouth, however, the euryteles were abundant and the desmonemes a little less so.

Bythotiara murrayi Günther

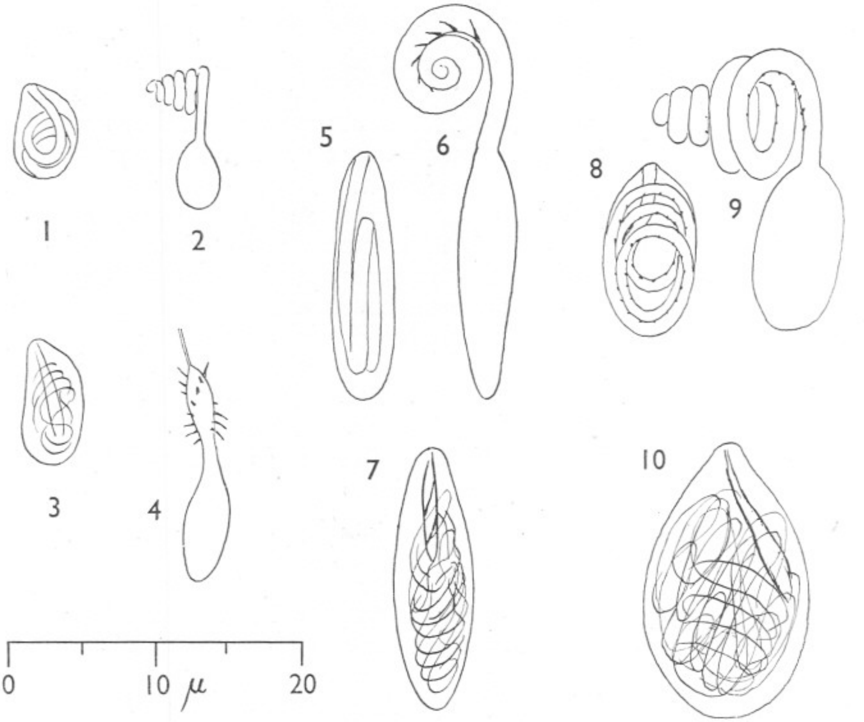
I found in Mr Browne's collection a number of specimens collected by Dr Stanley Kemp from 1000 fm. at a position 50 miles north-west of Inishtearaght, Co. Kerry, on the west coast of Ireland, on November 3 1904.

Two kinds of nematocysts were found, ? microbasic euryteles and desmonemes (Figs. 8–10). Although many of the desmonemes were discharged, unfortunately none of the other kind of nematocyst were discharged; I could not therefore be absolutely certain whether they were microbasic euryteles.

? *Euryteles:* 17–20 × 10–11 μ undischarged.

Desmonemes: 13–14 × 6 μ undischarged, 10–11 × 5–6 μ discharged.

The distribution of the nematocysts was peculiar. On the primary marginal tentacles no nematocysts were to be seen along the whole tentacle until the terminal knob was reached. This large terminal cluster of nematocysts consisted entirely of desmonemes, most of which were discharged.



Figs. 1–4. *Turritopsis nutricula:* 1, 2, desmonemes; 3, 4, microbasic euryteles. × *ca.* 2000
Figs. 5–7. *Heterotiara anonyma:* 5, 6, desmonemes; 7, ? microbasic eurytele. × *ca.* 2000.
Figs. 8–10. *Bythotiara murrayi:* 8, 9, desmonemes; 10, ? microbasic eurytele. × *ca.* 2000.

The secondary marginal tentacles were covered with nematocysts of both kinds over their whole length.

On one side of a secondary tentacle I saw one small discharged microbasic eurytele 6 × 4 μ, but as I could find no others of this size I concluded that it had become attached to the tentacle from another medusa.

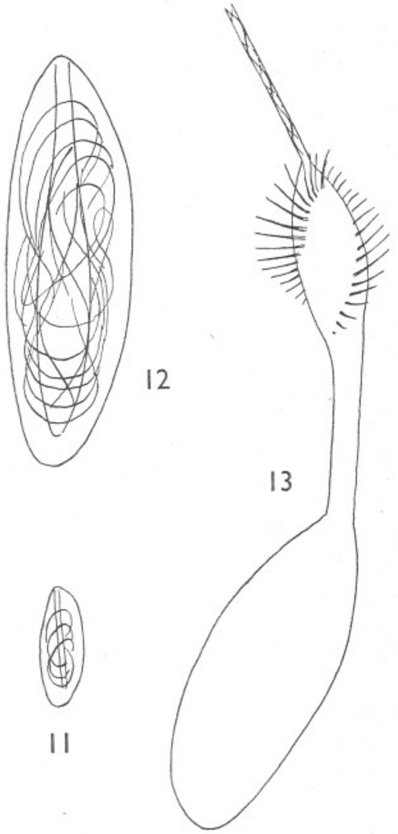
Heterotiara anonyma Maas

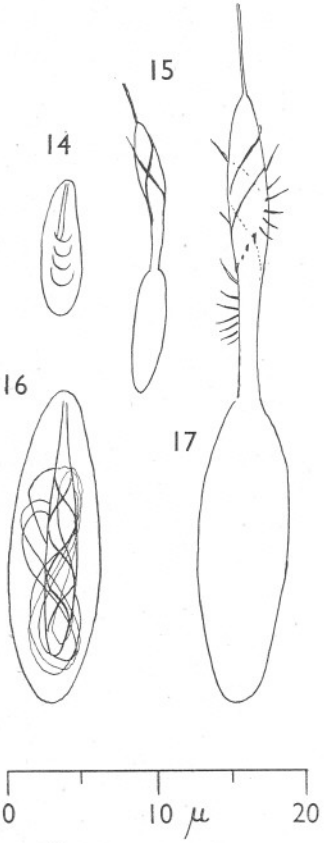
Dr H. B. Moore kindly gave me a very perfect specimen of this medusa caught near Bermuda. The specimen was 9 mm. in height and had all eight tentacles intact. I examined the terminal cluster of one tentacle. It had nematocysts very similar in type to those of *Bythotiara murrayi*, namely,

? microbasic euryteles and desmonemes (Figs. 5–7). As with *Bythotiara*, I could not be certain of the euryteles since none were discharged.

? *Euryteles:* 16–18 × 4·5–5 μ undischarged.

Desmonemes: 17–18 × 4 μ undischarged, 16–17 × 3·5 μ discharged.





Figs. 11–13. *Tiaranna rotunda:* microbasic euryteles. × *ca.* 2000.

Figs. 14–17. *Chromatonema rubrum:* microbasic euryteles. × *ca.* 2000.

Tiaranna rotunda (Quoy & Gaimard)

Mr W. J. Rees kindly allowed me to examine fragments of two specimens sent to him by Mr J. Hult and caught in Trondhjeimsfjord on August 23 1937.

Both in the marginal tentacles and in the marginal cordylus-like structures only one kind of nematocyst could be found, microbasic euryteles (Figs. 11–13). These were, however, of two sizes, large and small.

Euryteles: two sizes.

Large: 24–27 × 8–9 μ undischarged.

Small: 8–9 × 3 μ undischarged.

Chromatonema rubrum Fewkes

I found one specimen of this species in Mr Browne's collection. It was taken from 1000 fm. at a position 50 miles north-west of Eagle Island, Co. Mayo, on the west coast of Ireland by Dr Kemp, on August 11 1904. None of the mouth was available for examination but there were a few marginal tentacles. These contained nematocysts of only one kind, microbasic euryteles (Figs. 14–17). As in *Tiaranna rotunda* these were of two sizes, large and small.

Euryteles: two sizes.

Large: 19–20 × 6 μ undischarged.

Small: 9–10 × 2·5–3 μ undischarged.

ON THE AFFINITIES OF *TIARANNA* AND *CHROMATONEMA*

The fact that *Chromatonema rubrum* possesses only microbasic euryteles and that these resemble so closely those of *Tiaranna rotunda* is of considerable interest. It seems to imply that the affinities of *Chromatonema* are closer to the Anthomedusae than to the Leptomedusae.

That *Chromatonema* belongs to a borderline group between the two is fully realized (see e.g. Kramp, 1919, 1920; Bigelow, 1938), and the difficulty has been to decide whether it should be placed with the Pandeidae in the Anthomedusae or the Laodiceidae in the Leptomedusae. The form of its nematocysts strengthens the argument that *Chromatonema* would be nearer its right position if placed in the Anthomedusae, but I do not think it should be put in the Pandeidae. Bigelow (1938) suggests that it may deserve a separate family, but there is another genus which also requires to be considered and that is *Tiaranna*, which has up till now been included among the Pandeidae. This genus, like *Chromatonema*, is remarkable in having medusae with marginal cordylus-like structures, and the two genera likewise agree in the form of their marginal tentacles. I suggest that *Tiaranna* and *Chromatonema* are placed together in a new family, the Tiarannidae. In doing this it is necessary to reiterate with Kramp (1926, p. 69) that *Tiaranna affinis* should not belong to the genus *Tiaranna*. In the form of its marginal tentacles it resembles more closely *Leuckartiara*, but from the form of its stomach and gonads it is probably necessary to make a new genus for which I propose the name *Annatiara*, which was suggested to me by Dr G. P. Bidder.

Ranson (1936) has already placed *Chromatonema* in the Anthomedusae, but his inclusion of the genus in the Williidae cannot stand. Kramp (1939) has shown the probable relationship of the Williidae with the medusae of his newly erected Limnomedusae. In spite of the fact that the nematocysts of *Willia* are so remarkable* I agree with Kramp that we cannot as yet place too much stress on the use of nematocysts as classificatory characters. But if the characters of the nematocysts reinforce indications that are already supplied by other characters I think we are quite entitled to use them as

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* I have seen in preserved material that the nematocyst patches on the exumbrella of the medusa *Willia stellata* contain the macrobasic mastigophores characteristic of the hydroid.

corroborative evidence. In this respect the differences between the nematocysts of *Chromatonema* and *Laodicea* are quite conclusive. The nematocysts of *Laodicea* are typically Leptomedusan (see below), and in no species of Leptomedusae have microbasic euryteles as yet been found, except for the doubtful form in the aberrant *Dipleurosoma* described below. The further descriptions given below also show that the nematocysts of *Ptychogena* and *Staurophora* are Leptomedusan in character, although they appear to lack the atrichous haplonemes which are present in so many other species.

LEPTOMEDUSAE

Ptychogena crocea Kramp & Damas

Mr W. J. Rees kindly allowed me to see specimens of this medusa which he had collected in Norway. They had only one kind of nematocyst, microbasic mastigophores (Figs. 18–19).

Mastigophores: 14–15 × 2·5 μ undischarged.

Laodicea undulata (Forbes & Goodsir)

The examination was made on preserved specimens collected in the English Channel. There were two kinds of nematocysts, microbasic mastigophores and atrichous haplonemes (Figs. 28–31).

The mastigophores were of two sizes, large and small.

Mastigophores: two sizes.

Large: 16–18 × 5·5 μ undischarged.

Small: 11–13 × 3–4 μ undischarged, 10–11 × 2·5 μ discharged.

Atriches: 10–12 × 4·5–5 μ undischarged.

The large mastigophores were extremely rare, and at most only an occasional one or two were to be found in the proximal region of a tentacle. In general appearance all the nematocysts were typically Leptomedusan.

Staurophora mertensi Brandt

Some specimens were kindly sent to me by Mr J. H. Fraser, collected from 56° 02′ N., 2° 30′ W., on July 21 1937. Both on the mouth lips and marginal tentacles there was only one kind of nematocyst, microbasic mastigophores (Figs. 20–21).

Mastigophores: 10–11 × 3–3·5 μ undischarged.

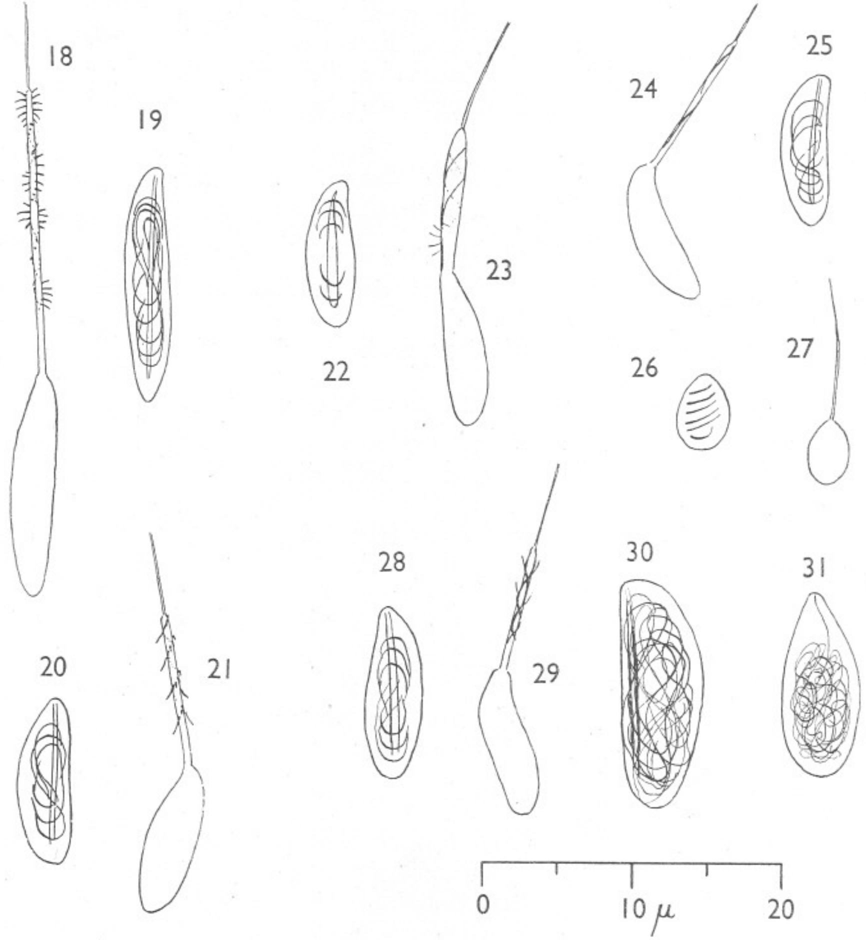
Dipleurosoma typicum Boeck

Examination was made on material in Mr Browne's collection from Valentia. There was only one type of nematocyst so far as I could see, ? microbasic euryteles (Figs. 22, 23). The hamp of the discharged nematocyst was only very slightly expanded distally and its sides were very nearly parallel, so that it might almost as well have come under the category of microbasic mastigophores.

? *Euryteles* or *mastigophores:* 9–10 × 3 μ undischarged.

Melicertum octocostatum (M. Sars)

Examination was made on material in Mr Browne's collection from Lamlash Bay, Isle of Arran. There were two kinds of nematocysts, microbasic mastigophores and what appeared to be atrichous haplonemes of rather an unusual form (Figs. 24–27). In their undischarged state the atrichous haplonemes showed six well defined coils of the basal part of the thread, differing from



Figs. 18, 19. *Ptychogena crocea:* microbasic mastigophores. × *ca.* 2000.

Figs. 20, 21. *Staurophora mertensi:* microbasic mastigophores. × *ca.* 2000.

Figs. 22, 23. *Dipleurosoma typicum:* ? microbasic euryteles or mastigophores. × *ca.* 2000.

Figs. 24–27. *Melicertum octocostatum:* 24, 25, microbasic mastigophores; 26, 27, atrichous haplonemes. × *ca.* 2000.

Figs. 28–31. *Laodicea undulata:* 28–30, microbasic mastigophores; 31, atrichous haploneme. × *ca.* 2000.

the usual irregular coiling shown in typical Leptomedusan nematocysts of this kind.

Mastigophores: 10–11 × 3 μ undischarged.

Atriches: 5 × 3–3·5 μ undischarged, 4 × 3 μ discharged.

Aequorea floridana (L. Agassiz)

Dr H. B. Moore kindly gave me a specimen of this medusa caught near Bermuda. The structural details of the specimen were as follows: diameter of umbrella, 23 mm.; diameter of stomach, 5 mm.; number of radial canals, 16; number of marginal tentacles, 3–5 per sector, or *ca.* 64 in all.

There were two kinds of nematocysts, ? basitrichous haplonemes or microbasic mastigophores (none were discharged) and atrichous haplonemes.

? *Basitriches:* 10–11 × 2·5–3 μ undischarged.

Atriches: 13–14 × 6·5–7·5 μ undischarged.

The nematocysts were quite similar in shape to those I have described for *Aequorea forskalea* and *A. vitrina* (Russell, 1939), but the atrichous haplonemes were smaller than in either of those species.

TRACHYMEDUSAE

Aglantha digitalis (O. F. Müller) var. rosea (Forbes)

Examination was made on several living specimens 5–11 mm. in height collected at Plymouth in January and February 1939. The mouth only was examined, and unfortunately I have seen no more specimens since; a close study of their nematocysts might prove interesting. There are apparently two kinds of nematocysts, stenoteles and microbasic euryteles, but there are also a number of nematocysts intermediate between the two kinds of which the fully formed stenoteles were usually the larger (Fig. 32).

Stenoteles-Euryteles: 8–13 × 6–11 μ undischarged, 7–10 × 5–9 μ discharged.

The stenoteles were quite typical of this kind of nematocyst (Fig. 32*a*, *b*), and the fully formed microbasic euryteles would likewise have been classified as such if seen alone (Fig. 32*f*). But the euryteles were apparently formed as a result of the reduction of the stenoteles. This seems to have been accomplished by a reduction of the dilated portion of the hamp between the large basal spines and the capsule, so that these spines were contiguous with the capsule itself (Fig. 32*c*). In more advanced stages of reduction these large spines show signs of contortion (Fig. 32*d*) or incomplete development (Fig. 32*e*) and in some they had entirely disappeared.

These nematocysts of *Aglantha* have an interesting bearing on the possible lines of evolution among nematocysts in general. Weill (1934, p. 98 *seq.*) has sketched the possible evolution of nematocysts in which he suggests that the evolution of the stomocnides has been in general in the direction of increased complexity. In these specimens of *Aglantha* we have an indication of the evolution of a microbasic eurytele from a stenotele actually taking place by a reduction of the basal portion of the hamp of the stenotele and its spines, with a consequent decrease in size of the nematocyst as a whole. Weill has already concluded that it is not possible to say whether atrichous haplonemes are derived from holotrichous haplonemes by progressive reduction of spines or the holotriches from the atriches by progressive development of spines. It seems that the nematocysts of *Aglantha* afford definite evidence that evolution may have proceeded as well by reduction as by elaboration in other kinds of nematocysts.

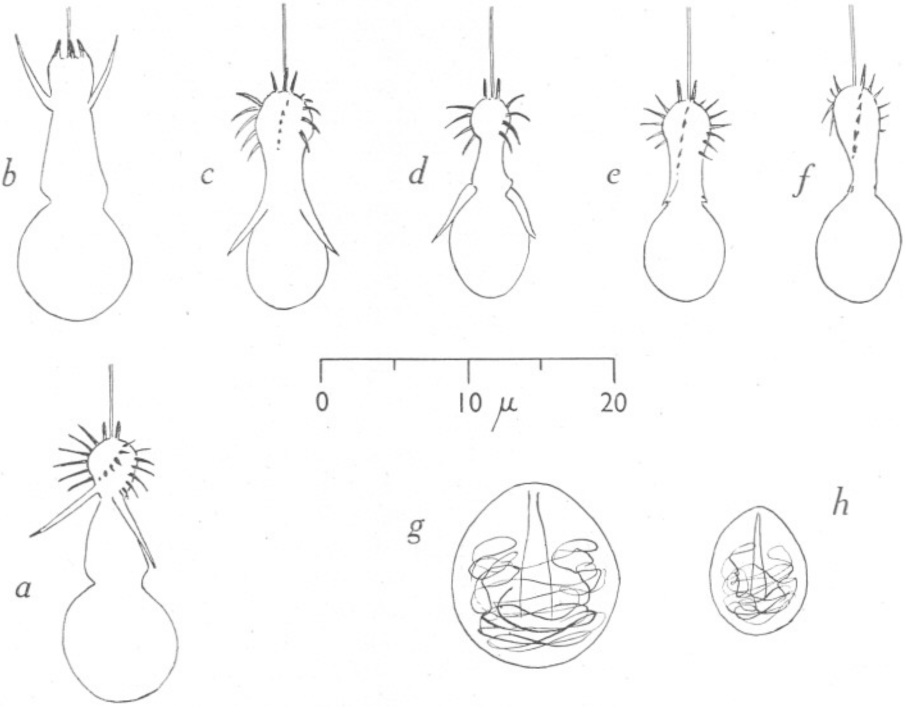


Fig. 32. *Aglantha digitalis* var. *rosea:* stenoteles and microbasic euryteles and transitional forms. × *ca.* 2000

SUMMARY

The nematocysts of five species of Anthomedusae, six species of Leptomedusae, and one Trachymedusa are described.

In view of the additional support supplied by characters of its nematocysts it is suggested that the genus *Chromatonema* should be placed with *Tiaranna* in a new family, the Tiarannidae, in the Anthomedusae.

Evidence on the possible evolution of microbasic euryteles from stenoteles is afforded by the nematocysts of *Aglantha*.

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ON SOME MEDUSAE OF THE GENERA *PODOCORYNE* AND *PHIALOPSIS*

By F. S. Russell, F.R.S.

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(Text-figs. 1–3)

It is generally assumed that there are two species of the genus *Podocoryne*, in northern waters, in which free swimming medusae are produced, *P. carnea* M. Sars and *P. areolata* Alder. Of these, the hydroid of *P. carnea* is known for certain, and that of *P. areolata* is thought to be the hydroid described by Alder under that specific name. Recently, I have found that there are two more species of *Podocoryne* medusae in British waters, *P. hartlaubi* Neppi & Stiasny and *P. minima* (Trinci). There are, therefore, two more hydroids to be found and it will be shown that the identity of the hydroid of the so-called medusa *P. areolata* must remain in doubt.

Podocoryne hartlaubi Neppi & Stiasny

While on a cruise on the S.S. *George Bligh* in the mouth of the English Channel in April 1938 I obtained a specimen of *Podocoryne* about whose identity I was in doubt. The medusa had thirty-four marginal tentacles, but its mouth lips were undivided and each had a single terminal nematocyst cluster. The medusa thus agreed with *P. carnea* in the characters of its mouth, but with *P. areolata* as regards the number of marginal tentacles, for no undoubted *P. carnea* have yet been recorded from European waters with more than eight tentacles.

On looking through the collections of the late Mr E. T. Browne I came across a medusa labelled *Cytaeandra* n.sp., caught at Valentia on August 11 1899. I saw at once that this was the same species that I had found, and the specimen was quite perfect, the stomach being torn in my own specimen. In Mr Browne's medusa (Fig. 1*a*) it could be seen that each gonad extended for a short distance along the proximal portion of the radial canal. In this respect it resembled exactly the medusa figured by Neppi & Stiasny (1913) as *Podocoryne hartlaubi* from the Gulf of Trieste.

Mr Browne's specimen and mine had forty-four and thirty-four marginal tentacles respectively, of which the four perradial and four interradial were large and approximately of the same size, the remaining tentacles being small and of different sizes (Fig. 1*b*). Neppi and Stiasny in their description give the number of tentacles as *ca.* 18; in their figure, however, these authors show two to three small tentacles between every two large tentacles, making a total of between twenty-four and thirty-two. I think there can be no doubt that the British specimens are *P. hartlaubi*, and it might be expected that the medusa should have more tentacles in northern waters than in the Mediterranean.

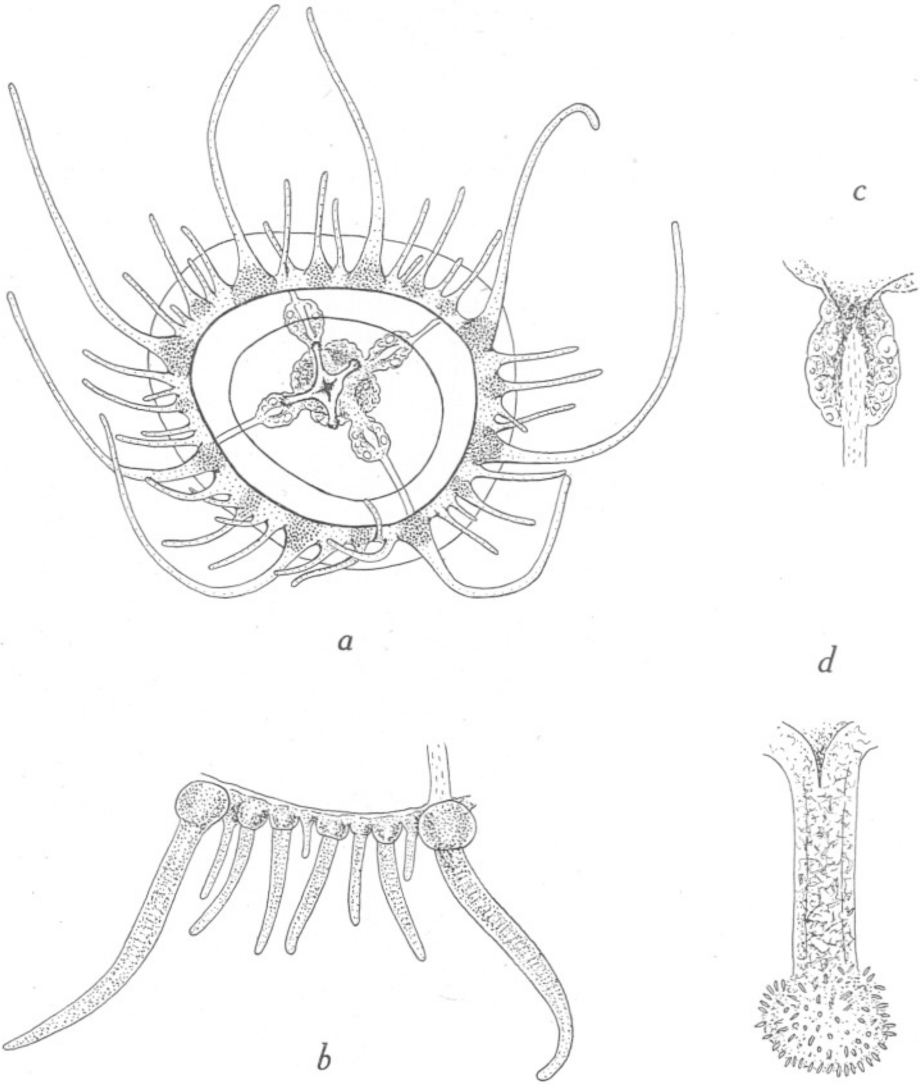

Fig. 1. *Podocoryne hartlaubi: a*, 2 mm. diameter, Valentia, Aug. 11 1899; *b*, octant of margin of specimen 3·8 mm. diameter; *c*, gonads on proximal portion of radial canal; *d*, mouth lip.

Mr P. G. Corbin kindly allowed me to look through a ring trawl catch taken in the same position as that in which I caught my original specimen. I found two more specimens, with forty-eight and fifty-seven tentacles respectively, and in each a characteristic feature was the large size of eight only of the tentacles. These medusae were obviously the same species as mine, but in one the stomach was badly torn and in the other it was completely missing.

The details of these four specimens were as follows:

Diameter of umbrella mm.	Numbers of marginal tentacles: Large	Numbers of marginal tentacles: Small	Locality
2*	8	36	Valentia
3	8	40	50° 30′ N., 6° 49′ W.
3·5	8	26	,, ,,
3·8	8	49	,, ,,

* This specimen had been preserved for 40 years: it has probably shrunk.

In their original description Neppi and Stiasny said as regards the gonads "Gonaden nur am Magen oder sowohl an demselben als am Manubrium". This expression is not quite clear, but their figure leaves no doubt that the gonads are present on the proximal portions of the radial canals as well as on the stomach.

In view of the above observations the species can now be redescribed as follows.

Umbrella bell shaped, about as high as wide; no apical process; jelly thin, thicker in apical region. Velum broad. Stomach cylindrical, about half height of subumbrellar cavity in length; with very slight peduncle. Four radial canals and ring canal narrow. Mouth with four elongated perradial lips each with single terminal nematocyst cluster. Gonads interradial on stomach wall and perradial for short distance along proximal portions of each radial canal. Up to fifty-seven solid marginal tentacles with swollen basal bulbs; four perradial and four interradial tentacles large and approximately of same size, remaining tentacles small and of different sizes. No ocelli. Diameter of umbrella 2·0–3·8 mm. Colour of basal bulbs of larger tentacles yellow or brownish; stomach and gonads flecked with yellow or brown.

I was able to make colour notes of the living medusa; the basal bulbs of the eight large tentacles were brilliant yellow, and yellow pigment was also present in the bulbs of the larger tentacles of the series of small ones. In this respect the medusa differed from typical *P. areolata*, in which the colour is much redder and in which most of the tentacle bulbs are pigmented.

Each mouth lip is continued outwards to form a solid tentacle with several rows of endoderm cells and a single large terminal nematocyst cluster (Fig. 1 *d*).

The gonads on the proximal portions of the radial canals are situated on the sides of the canals and are not continuous over the lower walls of the canals. Each of these gonads appears to be continuous with its neighbouring portion on the interradial wall of the stomach (Fig. 1 *c*).

Since the stomach appears often to be badly torn in preserved specimens it is possible that it may be necessary to rely for identification on the number of marginal tentacles and the fact that only eight of these are large. This note is therefore written in the hope that others may re-examine their collections of *P. areolata*, in which the tentacles appear to be usually of more uniform size. It is, for instance, interesting to note that Kramp & Damas (1925, p. 270) mention a specimen 2·5 mm. in height with forty-one tentacles of which only eight were large, the remainder being small.

The hydroid *P. areolata* Alder has generally been assigned to the medusa now known under that name because of the large number of marginal tentacles in the newly liberated medusa. It seems now that there is an equal likelihood that it may belong to *P. hartlaubi*, if this species can also be shown to occur in North Sea or Norwegian waters.

Podocoryne minima (Trinci)

I have found in Mr Browne's collection a number of specimens labelled *Cytaeis* sp. (?), together with manuscript notes. The medusae were referred to by Browne (1898) as *Cytaeis* sp. (?), but were never described. They were found in Plymouth Sound and Cawsand Bay.

These medusae agree in every respect with the medusa described by Trinci (1903) as *Cytaeis minima*, and discussed by him later (Trinci, 1904), having four perradial marginal tentacles and medusa buds on the stomach. The four perradial mouth lips each terminated in a single nematocyst cluster and were typical of *Podocoryne*. The only difference is in size, the Plymouth specimens being up to about 1 mm. in height and Trinci's being 0·27–0·33 mm. In size they thus resemble more closely Kramp's *Podocoryne simplex* from Japan, which was 0·75 mm. in height (Kramp, 1928). It seems possible that all three are the same species.

The medusa has not been seen here since and its hydroid is not known.

Phialopsis diegensis Torrey

Four specimens undoubtedly belonging to this species were given to me by Mr P. G. Corbin who found them in a ring trawl catch taken in 49° 40′ N., 11° 10′ W., 120 miles south-west by south from Fastnet, on April 20 1939.

Phialopsis diegensis was first described by Torrey (1909) from San Diego. It has been described by one or two authors under the name of *Eirene viridula*, and these erroneous identifications have been cleared up by Kramp (1936) in his synonymy of that species. The best figures of the species are those given by Bigelow (1909, as *Eirene*) from a single specimen. Since this medusa has not often been recorded and since its identification may at first give some difficulty, it seems worth while to give some figures of the specimens I have seen and mention a few minor structural details not given in previous descriptions.

The specimens were about 10–15 mm. in diameter. Of these, two specimens, 10 and 15 mm.* in diameter, had ten and thirteen large marginal tentacles

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* This specimen had two young actinians attached to the stomach.

respectively. In both the peduncle was very slight and scarcely perceptible at first glance. In the 10 mm. specimen (Fig. 2*a*) in which almost the whole of the umbrella margin was intact I counted the following numbers of marginal organs between every two tentacles:

Rudimentary marginal bulbs	2–6
Marginal cirri	3–9
Marginal vesicles	2–5, with 1–6 concretions, usually 4

The 15 mm. specimen had fifty-seven rudimentary marginal bulbs. In both these specimens the gonads were only slightly developed.

The other two specimens, each about 14 mm. in diameter, had fully formed peduncles. In one specimen (Fig. 2*b*) there were eighteen marginal tentacles, but the other was too damaged to count. In both, the gonads were well developed. The umbrellas had obviously contracted much more than in the other two specimens, and in life their diameters would have been larger. The distal ends of the gonads were thus thrown into sinuous folds.

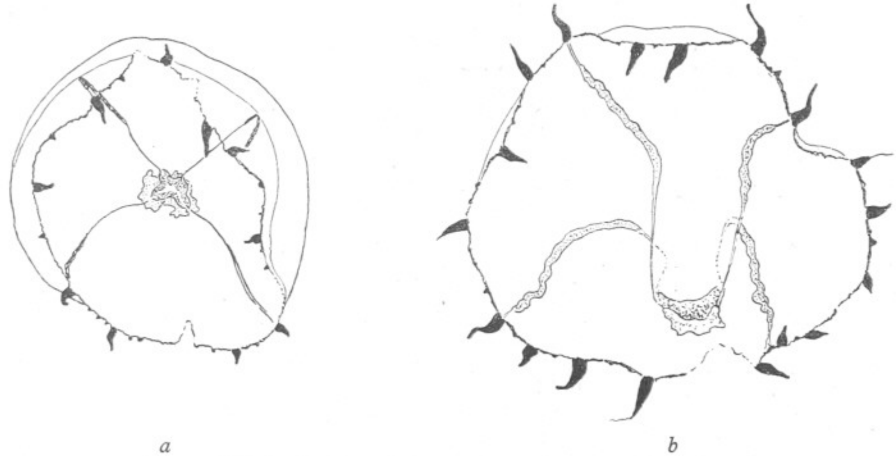

Fig. 2. *Phialopsis diegensis:* appearance of preserved specimens; *a*, 10 mm. diameter; *b*, 14 mm. diameter.

The gonads ended a short distance before the ring canal, and, as far as I could see from hand sections, the gonadial tissue was continuous over the lower wall of the radial canal and there was no median furrow.

The base of the remarkably short stomach appears to be characteristic (Fig. 3*a*, *b*). It is attached to the end of the peduncle along the arms of a small perradial cross, and there is a distinct dilatation at each of the four points where a radial canal enters, though not quite so pronounced as in *Eirene viridula*. Four well marked shoulders are thus formed, which run down to the mouth lips and give the appearance of a raised cross when viewed from above (this appearance is indicated in Bigelow's figure, 1909, pl. 36, fig. 3).

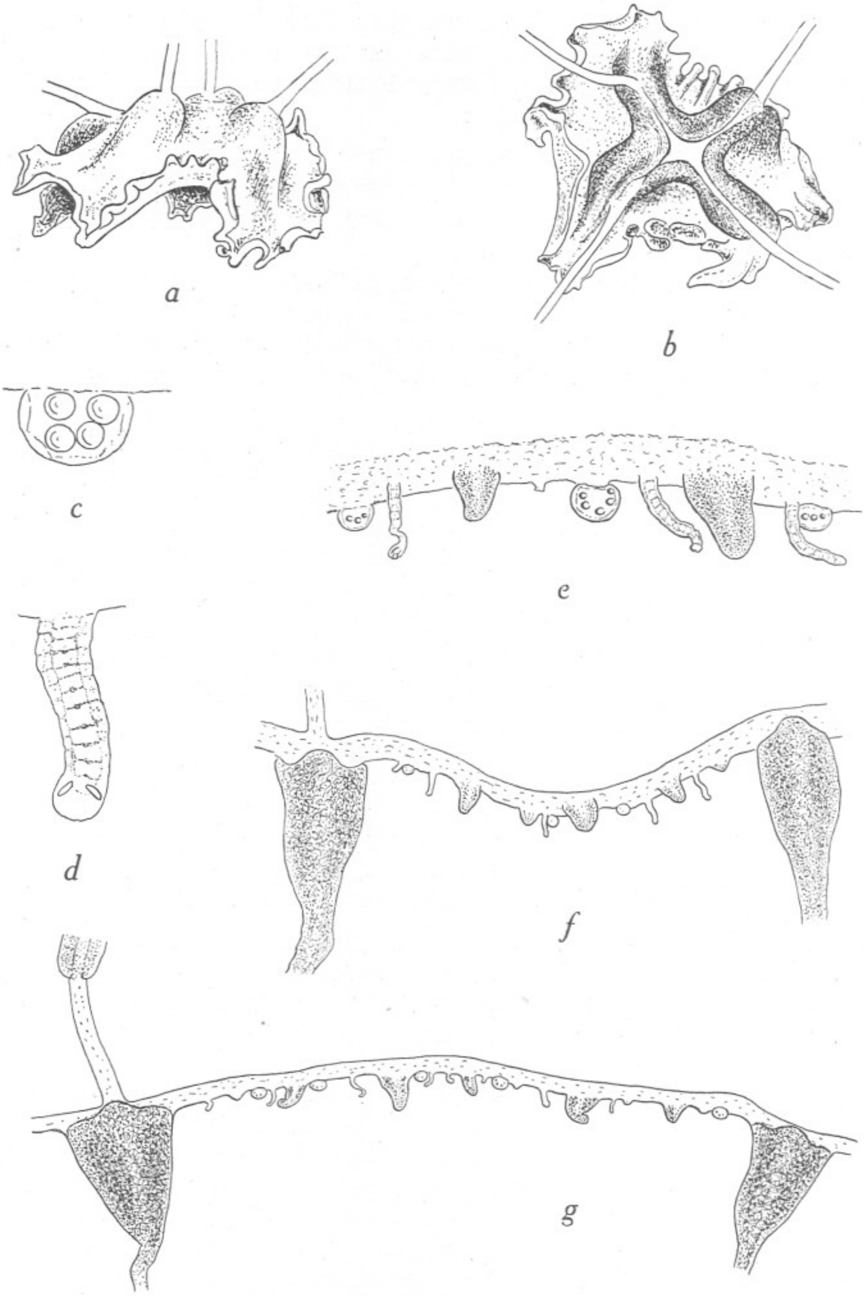

Fig. 3. *Phialopsis diegensis: a, b*, stomach of 10 mm. specimen viewed from side and above; *c*, marginal vesicle; *d*, marginal cirrus; *e*, portion of umbrella margin of 15 mm. specimen, enlarged; *f, g*, umbrella margin between two adjacent tentacles in 13 and 15 mm. specimens.

The basal bulbs of the marginal tentacles are large and conical, and appear elongated or short and broad according to their degree of contraction. Each bulb has a slight rounded median spur clasping the umbrella margin (Fig. 3*f*, *g*). I could see no excretory pores.

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THE OCCURRENCE OF A MARINE LEECH, *ABRANCHUS BLENNII* N.SP., RESEMBLING *A. SEXOCULATUS* (MALM), IN NORTH WALES

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(Text-figs. 1–2)

Occurrence

In April 1939 two small leeches were found on two shannies, *Blennius pholis*, which had been collected from rock pools near Rhosneigyr on the west coast of Anglesey. Earlier in the year another leech was reported to have been found at the same place, free on the underside of a stone, and subsequently lost. In May a *B. pholis* was found which bore two leeches, one on each side. All the parasites were attached just behind the base of the pectoral fin.

Further search during the summer failed to reveal any more specimens although, in all, about a hundred shannies were examined. There is no doubt that all the leeches examined belong to the same species, which closely resembles that described by Malm (1863) as *Platybdella sexoculata* and put into the genus *Abranchus* by Johansson (1896). *A. sexoculatus* has only been recorded from the west coast of Sweden, where it is rare. Malm and Johansson were indefatigable collectors who captured large numbers of other species, yet up to 1896 only three of this one had been found, all on different hosts—*Gadus morrhua*, *Cyclopterus lumpus* and *Zoarces viviparus*. In 1929 Johansson says that this small rare leech occurs by preference on *Z. viviparus*, so it seems likely that further specimens have been found on this fish.

A comparison of the Anglesey leech with this species must be incomplete owing to the fact that no description of the internal anatomy of *Abranchus sexoculatus* has ever been published. The external resemblance is great but certain differences, which will be discussed later on, make me hesitate to identify them as the same. In this difficulty I propose to put forward the name *A. blennii* for the leech described below. If it is not a distinct species I hope that the account may yet be of interest as being the first adequate description of the structure of this form.

Generic Characters

The genus *Abranchus* was created by Johansson (1896, 1898) to include four species, *A. brunneus*, *A. scorpii*, *A. microstomus*, and *A. sexoculatus*. Later (1929) he separated the two former from the others and put them into the genus *Ottonia*. We still owe our knowledge of these forms to his work and to that of Selensky (1915).

There are many characters common to both *Ottonia* and *Abranchus*. Of these the coelomic system, which is of great systematic value in the Ichthyobdellidae (Selensky, 1931), must be mentioned first, for it completely marks off these two genera from other forms. It is represented by tubular ventral, lateral and dorsal lacunae. The ventral lacuna, which contains the ventral blood vessel and the nerve cord, has no segmental communication with the others. The dorsal, which contains the dorsal blood vessel, communicates with the lateral lacunae in each segment of the testicular region by a transverse tubular connexion. There are no testicular lacunae and no pulsating vesicles or corresponding structures.

Other features which distinguish them from some or all other Ichthyobdellidae are six eyes, hypodermis with large dermal cells crowding out the fibrous connective tissue, ducts of prae-clitellar glands opening along a narrow line on each side, feeble musculature of the body wall, sphincters between the caeca of the stomach, blind guts, i.e. the long posterior pair of stomach caeca, separate or almost separate from one another, nephridial network confined to the dorsal and lateral parts of the body, testes tending to be irregular in form and arrangement, simple bursa.

With all these points in common, it is not surprising to find that the dividing line between these two genera is not very sharp. Johansson only describes the anatomy of two species at all fully, i.e. *Ottonia brunnea* and *Abranchus microstomus* (1896). He mentions many differences between them, but taking all these into consideration and comparing the internal as well as the external characters it is impossible to say that *A. blennii* is more closely related to one than to the other. In some respects it resembles *O. brunnea*, in others *A. microstomus*, in others it differs from both. Hence it is only possible to regard the division into two genera as one of convenience, based on the following considerable external differences unsupported by many other anatomical features.

Ottonia. Body rounded and almost uniformly thick along its whole length. Anterior sucker large. Skin opaque.

Abranchus. Prae-clitellar region smaller than and distinct from the flattened abdomen. Anterior sucker very small. Skin transparent.

DESCRIPTION

Habits. *A. blennii* does not appear to swim but can move energetically by looping. If put into a dish it attaches itself by the posterior sucker and if undisturbed assumes a resting position, with the body very flattened and usually curled into a zigzag shape. A slight movement of the water or a shadow falling across it causes it to stretch itself to more than twice its resting length and to execute random searching movements, swinging its attenuated rigid body in all directions as though attached to the posterior sucker by a universal joint. If a fish is presented to it and it is able to secure a hold by its anterior sucker it lets go the dish and immediately takes a firm hold upon its host by the large posterior sucker. Fresh specimens readily attach themselves to shannies in this way, and one was induced on two occasions to attach itself to *Centronotus gunnellus*. It would not attack a small *Cottus* similarly presented to it. When the *Centronotus* was put into a tank with other fish the leech on each occasion transferred itself to a shanny within a few days. It appeared to prefer the shelter provided by the shanny's large pectoral fin. Later, however, in a tank that contained only shannies it disappeared from off its host and must have been eaten by one of the fish.

External characters. The external appearance was carefully examined in only three of the specimens.

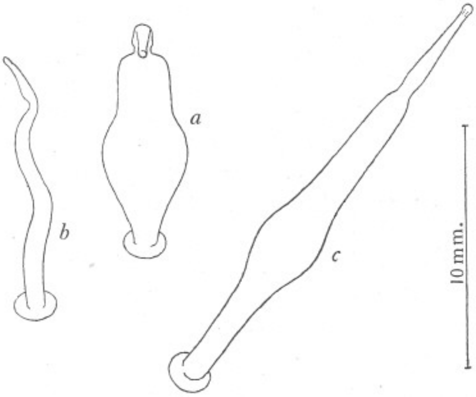

Fig. 1. *Abranchus blennii* n.sp.: *a*, resting with head thrown back, dorsal view; *b*, resting, side view to show flattening; *c*, moderately extended, dorsal view.

The length when fixed or resting is about 12 mm. A well-marked clitellar constriction divides the small front portion of the body, or "neck", from the large flattened abdomen. The body is broadest just behind the middle. The anterior sucker is minute. In the resting condition it is very little broader than the anterior end of the neck, but the animal is able to dilate it to twice this breadth (Fig. 2*b*). The posterior sucker is about 1·7 mm. across, that is, never as broad as the body at its broadest part, even when the leech is stretched out. When the body is shortened and flattened in the resting position it may be twice as broad as the posterior sucker (Fig. 1*a*). There are six eyes, two pairs on the head and one pair on the second annulus of the neck (Fig. 2*a*). The skin is smooth and transparent, and the annuli are obscure. The latter are plainer after fixation but still difficult to count. The genital openings are very difficult to make out. The caeca of the stomach show through the body wall, being usually dark red with blood. Numerous yellow or cream-coloured granules, the dermal pigment cells, lie in the skin. They are 40–150 μ across, round or oval in shape. The dorsal surface and the sides of the body are marked with dark brown pigment, arranged in a series of transverse stripes interrupted in the middle line. In the posterior part of the abdomen the whole of the dorsal surface is pigmented and the posterior sucker often bears a radial stripe in the dorsal mid-line. The clitellum is particularly pale and opaque. In one specimen a few small black spots occurred near the edge of the posterior sucker.

Internal anatomy. This was studied by a single series of transverse sections, cut at 10μ and stained with Ehrlich's haematoxylin and eosin.

Body wall (Fig. 2*c*). The epidermis, which secretes a smooth strong cuticle, consists of cells with their inner ends rounded and of the usual ichthyobdellid type. It is unlike that of *A. microstomus*, which consists of flattened cells. Large epidermal gland cells are common.

The dermal pigment cells, which are conspicuous in the living animal as yellow flecks, occupy the hypodermis. They are rounded or flattened and 40–150μ across, with large nuclei. Because of the large size of these cells the fibrous connective tissue in this layer is correspondingly reduced.

The musculature, although weak, is stronger than that of *A. microstomus*. Its thickness varies somewhat, but it usually consists of a single layer of circular muscle fibres, one or two layers of oblique fibres, and one or two layers of longitudinal fibres. The oblique fibres are particularly small and weak. Dorso-ventral fibres occur in the post-clitellar parts of the body and must be responsible for the flattening of this region. They are also numerous in the clitellum, especially around the genital openings.

Skin glands. Most of the space between the internal organs is occupied by the unicellular gland cells, the cell-bodies of which lie within the muscle layer though their ducts open on to the surface of the skin.

There appear to be two types of clitellar gland cell resembling those described by Badham (1916) in *Austrobdella*. One has a coarsely granular secretion the globules of which when first formed are scattered throughout the cytoplasm of the cell. The other type, to which the largest cells belong, has a denser cytoplasm and an homogeneous secretion which is confined to the lumen of the cell body and duct. The secretions stain brightly with eosin and both types remain distinctive right up to the openings of the ducts. All the clitellar gland cells belong to one of these two types and there are no intermediate forms. Both occur mixed together throughout most of the length of the body. Near the clitellum the cells are numerous and measure 30–60μ across. Further away they are less numerous and larger. The largest cells which occur behind the testicular region measure up to 200μ. All the ducts open on to the clitellum so that those of the posterior cells have to traverse a considerable distance. For the greater part of this they are arranged in eight adradial bundles, two dorsal, two ventral and two lateral on each side (Fig. 2*d*, *e*). The ducts of the cells anterior to the clitellum have no such regular arrangement. The clitellum itself is packed with the ducts which open to the exterior over the whole surface.

The prae-clitellar gland cells, which are numerous in the three segments anterior to the clitellum, are all fairly large (about 80 μ across) and are distinguished by their faintly basophil staining. Their secretion, if any was present, was quite unstained and their ducts were best seen after the light had been cut down. Johansson says that in *A. microstomus* and *O. brunnea* the ducts of these cells open along a narrow line on each side, and are confined to the second prae-clitellar segment. In *A. blennii* a large proportion of the ducts open in clumps arranged along the lateral edge in the manner Johansson

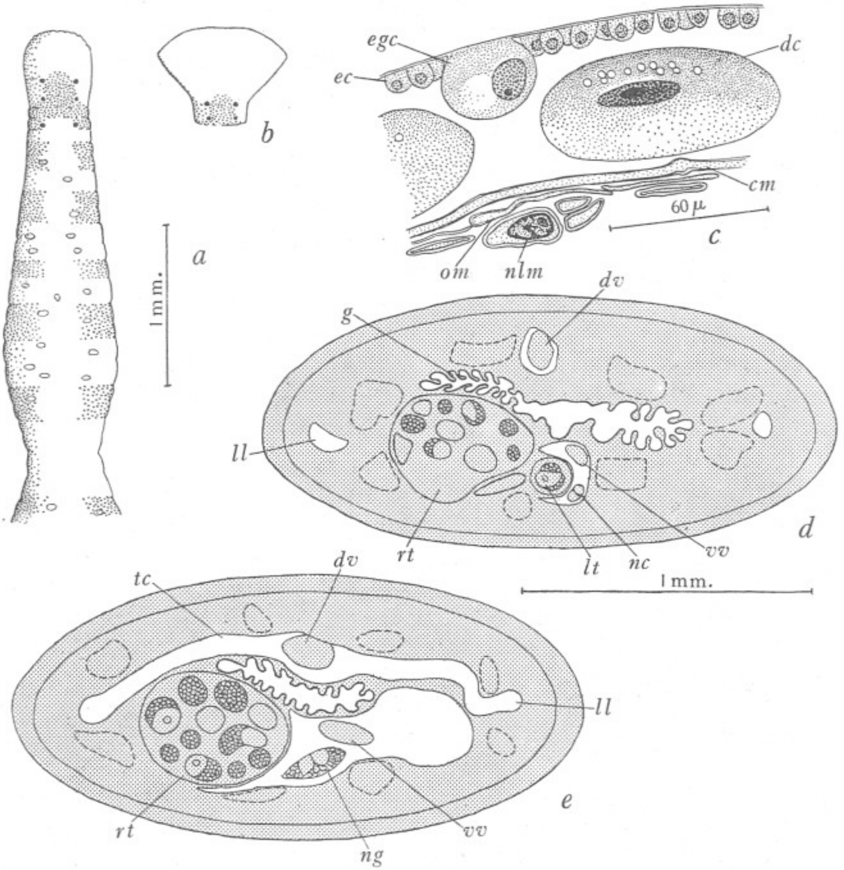

Fig. 2. *Abranchus blennii* n.sp. *a*, anterior end, dorsal view. *b*, head with sucker dilated. *c*, transverse section body wall; *cm*, circular muscle fibre; *dc*, dermal pigment cell; *ec*, epidermal cell; *egc*, epidermal gland cell; *nlm*, nucleus of longitudinal muscle fibre; *om*, oblique muscle fibre. *d*, transverse section body between 2nd and 3rd post-clitellar ganglia, shaded except for coelom and gut cavity, bundles of clitellar gland ducts bounded by interrupted lines; *dv*, dorsal vessel in dorsal lacuna; *g*, gut; *ll*, lateral lacuna; *lt*, left testis shifted over to right side; *nc*, nerve cord; *rt*, right testis; *vv*, ventral vessel in ventral lacuna. *e*, transverse section through 3rd post-clitellar segment, as *d*, in addition *ng*, ganglion; *tc*, transverse communication.

describes, but the remainder open all over the dorsal surface of the body. Moreover, the openings occur on all segments of the prae-clitellar region.

Nervous system. The nerve cord lies for the whole of its length in the ventral lacuna. It is terminated anteriorly by the large suboesophageal ganglionic mass which gives off a nerve ring round the proboscis sheath, and posteriorly by the ganglionic mass associated with the posterior sucker. Between these there are in the majority of leeches twenty-one separate ganglia marking a corresponding number of segments which Johansson and other authorities group as follows:

Prae-clitellar region	3	segments
Clitellum	3	,,
Testicular region	6	,,
Region of the blind gut	6	,,
Anal region	3	,,

In *A. blennii* three of these ganglia have disappeared, probably by fusion with the anterior or posterior ganglionic masses, for there are only eighteen separate ganglia. In the series of sections the clitellum, as indicated by the openings of the clitellar glands, includes the 3rd, 4th, 5th and 6th ganglia, owing to the contraction which occurred on fixation having thrown the nerve cord into a loop in this region. The genital openings occur between the 5th and 6th ganglia so it seems probable that the 4th, 5th and 6th ganglia belong to the three segments of the clitellum. If this is so, ganglia 7–12 must correspond with the testicular region. The last pair of testes does in fact occur between ganglia 11 and 12 and the segmental communications between the dorsal and lateral lacunae occur opposite ganglia 8–12. On the other hand the blind guts open into the stomach in front of the 12th ganglion, whereas in most Ichthyobdellidae, including *A. microstomus* and *O. brunnea*, this occurs between the last segment of the testicular region and the first of the blind gut region.

Most of the evidence, however, is in favour of ganglia 4, 5 and 6 belonging to the clitellum. This leaves the full number of three separate prae-clitellar ganglia, indicating that it is a fusion of the three anal ganglia with the posterior ganglionic mass that is responsible for the reduction from the typical condition.

Gut. The pharynx is short and has a very narrow lumen. The proboscis, retracted within the proboscis sheath, has the typical ichthyobdellid structure with radial, circular and longitudinal muscles. It differs from that of *A. microstomus*, in which the radial muscles are reduced and the circular muscles particularly powerful. There are about sixty salivary gland cells scattered throughout the prae-clitellar region, from the suboesophageal ganglion to the clitellum itself. They are 50–150μ across and closely resemble clitellar gland cells of the granular type. However, they can be readily distinguished from these by the fact that their secretion is more finely granular. The ducts run into the base of the proboscis and traverse its length, lying alongside the longitudinal muscle fibres. A few open into the lumen on the way, but the vast majority open at the extreme tip. According to Johansson this is unusual and in *A. microstomus* all the ducts open at the base of the proboscis.

The oesophageal glands are sacs, which were large but practically empty in the specimen sectioned. They open posteriorly into the gut, in the front part of the clitellum, by a short duct with a minute lumen. The duct is provided with a small sphincter muscle for closing it and radial muscles for dilating it. So far as I am aware, no such muscles have been mentioned previously in relation to this type of gland.

The stomach gives off a pair of caeca in the front part of each segment of the testicular region. The caeca extend forward so as to lie inter-segmentally. The first pair is small. There are sphincter muscles round the stomach behind the 3rd, 4th and 5th pairs. The caeca of the 6th pair are relatively huge and not only send lobes forward like the others, but extend backwards alongside the intestine almost as far as the anus. There can be little doubt that they are homologous with the blind guts of *A. microstomus* and other forms, and it is remarkable that they are, as in *O. brunnea*, completely separate from one another throughout their whole length.

Coelom and vascular system. The coelomic spaces are extremely thin walled.

The ventral lacuna runs the whole length of the body. It contains the nerve cord and the ventral blood vessel. The paired lateral lacunae can be distinguished from just behind the clitellum to about half-way along the region of the blind guts.

The dorsal blood vessel can be distinguished over most of the length of the body. The dorsal lacuna is confined to the testicular region, where it contains the dorsal blood vessel (Fig. 2*d*, *e*). In each segment, except the first, it is joined to the lateral lacunae on either side by a transverse communication (Fig. 2*e*). The species which Johansson describes have these communications in all six segments of the testicular region, but in *A. blennii* the ducts of the clitellar cells occupy so much space in the first post-clitellar segment that there is no room for the segmental communication. In fact at this point the dorsal lacuna itself is not yet distinguishable.

Excretory system. The nephridial tubules stained very lightly and were difficult to follow. They could be observed beside the lateral lacunae in many places, and occasionally beside the dorsal lacuna.

Reproductive system. The testes occur in all six segments of the testicular region. They vary greatly in size and are somewhat irregular in shape. In the specimen sectioned their arrangement was asymmetrical, for the left testes of some segments were displaced to the right side. The bursa has a simple structure and the sexual organs are otherwise unremarkable.

COMPARISON WITH ALLIED SPECIES

The genus *Abranchus* when amended by Johansson (1929) contained only two species, i.e. *A. microstomus* and *A. sexoculatus*, and up to the present time no further species have been described. Certain points in which *A. blennii* differs from *A. microstomus* have already been mentioned. In addition *A. microstomus* is wholly unpigmented and about twice as large as our leech.

A. blennii resembles *A. sexoculatus* in size, general body form and pigmentation, but it is necessary to point out some differences which suggest that they are distinct species.

Johansson says that *A. sexoculatus* has a circle of small spots round the edge of each sucker. None of the three leeches examined alive had any spots, other than eye-spots, on the anterior sucker, but I do not think much importance can be attached to this point as Malm does not mention such spots in his careful original description. The posterior sucker lacked spots altogether in two of our specimens. In the other it bore four spots near the edge, two placed laterally and two dorsally one on each margin of the mid-dorsal stripe. Malm says that the two most median spots of the circle are situated one on each margin of a mid-dorsal band, but this point of resemblance does not outweigh the fact that our specimens had no circle of spots on the posterior sucker. This character is the more important because not only *A. sexoculatus*, but also the other species of *Abranchus* and *Ottonia*, possess a complete circle (Johansson, 1898).

Another point of difference lies in the relative and absolute size of the posterior sucker. Malm gives this as being 2·5 mm. across. Johansson says that it is broader than the body at its broadest point, and describes the body as being 2–2·5 mm. across. Our specimens had suckers measuring only 1·6–1·8 mm. across and, as has already been mentioned, the body when fully broadened out is twice as broad as the sucker. The posterior sucker then is definitely smaller than that of the Swedish form. It is interesting to note that Johansson (1898) separated the two species *Ottonia brunnea* from Sweden and *O. scorpii* from Spitzbergen solely because the posterior sucker of the latter had a diameter twice that of the former. Selensky's study of the internal anatomy of *O. scorpii* later (1915) upheld the view that they were distinct species.

In the same way, though the external differences described above do not in themselves constitute a very good specific distinction, they indicate that *Abranchus sexoculatus* and *A. blennii* may prove to be separate species. Doubtless sections of the Swedish form would decide the question.

Summary

Several specimens of an ichthyobdellid leech were found on *Blennius pholis* collected on the coast of Anglesey.

The leech resembles *Abranchus sexoculatus* (Malm), a rare form only recorded previously from Sweden and not yet adequately described. Slight differences, however, indicate that it may be a distinct species and the name *Abranchus blennii* is provisionally put forward for it.

A short review of the genus *Abranchus* and a description of the appearance and structure of the leech follow.

My thanks are due to Prof. F. W. Rogers Brambell for his encouragement and advice; and to Mr W. H. Leigh-Sharpe for advice regarding the literature.

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THE BREEDING OF OYSTERS IN TANKS

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(Text-fig. 1)

The following paper is a record of certain work which was carried out at the River Yealm during 1939. No claim is made for original work, but it may serve some useful purpose as a record.

Oysters from the River Yealm have been used in most of the experimental work carried out on the breeding of oysters at Conway. But, for some unknown reason, there has never been any relevant growth of native oysters in the Yealm. The beds are stocked every year with three-year-old Brittany oysters. These oysters thrive well in the Yealm and are of considerable commercial value.

Certain old tanks at the Fisheries have been altered and repaired for the purpose of cleansing prior to their despatch to the London market. These tanks are in use for this purpose approximately from the end of August until the beginning of May. Therefore they are unused for approximately four months during the breeding season.

Description of the Tanks

The accompanying diagram (Fig. 1) shows the lay-out of the tanks. Two old storage pits have been subdivided into three sections and rendered watertight. They may be described as A, B and C. Tank A is approximately 10 ft. deep and holds 32,000 gallons when filled to a depth of 8 ft. 6 in. The wall between A and B is 10 ft. high, and the wall between B and C is 8 ft. high. Tank B holds 9000 gallons at 3 ft. Tank C has a larger superficial area and the surrounding walls are 8 ft. high; it holds 32,000 gallons when filled to a depth of 5 ft.

Tanks B and C can be filled to the stated depth on the flowing tide via the sump marked in the diagram. The water in tank A is topped up to a depth of 8 ft. 6 in. by means of a petrol pump, except on very high tides.

The walls of the tanks are of brick rendered with concrete, and the floors are of concrete. All tanks are watertight. It will be noted that these tanks are considerably smaller than those in use at Conway.

It may be mentioned at this juncture that the owner, Mr J. Kingcome, made several attempts at oyster breeding in 1927, 1928 and 1929, in conjunction with the Experimental Station at Conway, but at that time the conditions necessary for ensuring a settlement of oysters in tanks were not known, and the attempts were unsuccessful.

BREEDING

On June 1 1939 200 healthy four-year-old oysters from the river were placed in single layers on slatted frames on the floor of tank A. These frames were about 9 in. from the bottom, being supported by two widths of common brick. The oysters were covered by large slates, as advised by Cole (1938). All slates and bricks were treated with the prescribed mixture of sand and lime. Seventy bouquets of limed tiles were arranged round the floor of the tank. The tank was then filled to a depth of 8 ft. (30,000 gallons) on a high spring tide.

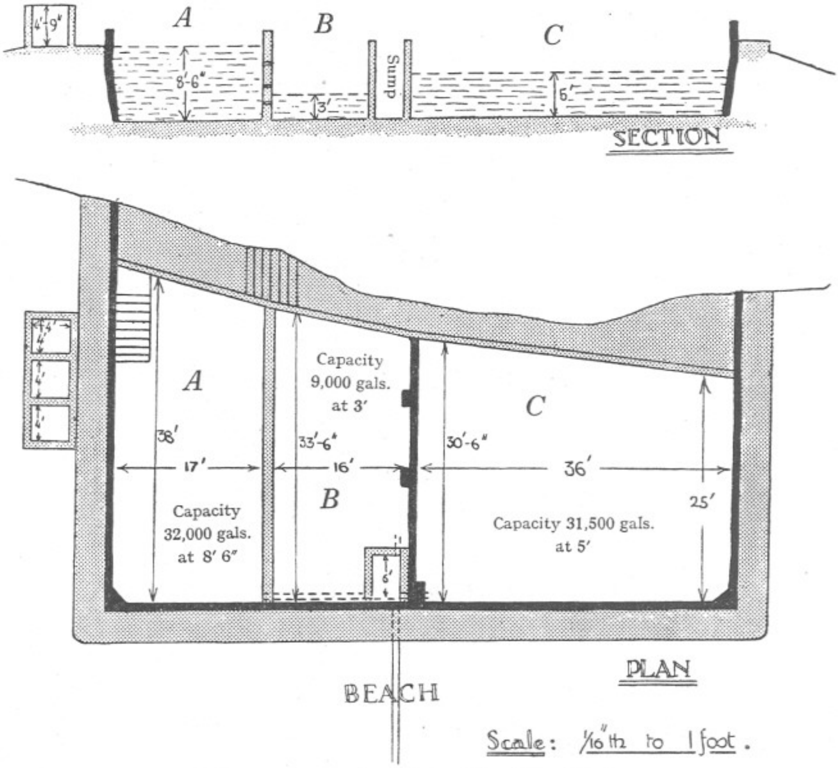

Fig. 1. Oyster cleansing tanks, River Yealm

Enrichment of the water by crabmeat minced up with sand was then commenced. The sand was subjected to preliminary heating in order to kill any littoral organisms. The rate of enrichment was three medium minced crabs on alternate days.

About this juncture, Mr D. P. Wilson, of the Marine Biological Laboratory, Plymouth, very kindly examined a sample of tank water. He reported the presence of an abundance of suitable flagellates. Daily nettings were taken in order to ascertain the presence of free-swimming larvae. *p*H readings were taken twice a week. With the exception of one reading of 8·5 (corrected) on June 21, the *p*H values appeared stationary at 8·3 (corrected). On June 23 free-swimming larvae were noted for the first time.

On June 24 a further eighty bouquets of tiles were lowered down the sides of the tank, to rest on the floor. At the same time a few oyster shells, in net bags, were lowered to a depth of 3 ft.

On July 5 settlement of spat was noticed on these shells, and on July 7 spat was visible on the tiles. Enrichment at the rate of three crabs on alternate days was continued.

On July 7 after perusal of the article by Cole & Jones (1939) forty bouquets were taken up from the floor of the tank and placed about 1 ft. below the surface of the water, being suspended from pieces of wood placed across the top of the tank A.

Tank B was filled to a depth of 3 ft. 6 in. on July 17 and allowed to warm by the heat of the sun.

On July 19 the temperature of the water in tanks A and B was the same, and forty bouquets of tiles which had been suspended in A were transferred to B. There was a heavy settlement of spat on these tiles. At the same time tank C was filled and the water allowed to warm in the sun.

The water in B was completely replaced by water from C on alternate days until July 23. Enrichment of B was continued with four medium crabs per day.

On July 23, tanks A and B were emptied at the same time and the walls well cleaned down. Seventy-five bouquets were placed in each of A and B and each tank was filled to a depth of 3 ft. 6 in. from C, in which the water had been warmed by the sun. At this period there was a difference of 10° F. between the temperature of the river water and that of the tanks. Up to this period, the air temperature was relatively low for the time of the year, and we were concerned lest a sudden change in water temperature would prove harmful to the young spat.

After July 23, there was a distinct improvement in the air temperature with a consequent increase of the temperature of the river. Thus, it was possible to effect several partial changes of the water in A and B direct from the river, and finally after August 1 it was possible to effect almost daily changes direct from the river. By this time the river temperature was only 5° below that of the tank water, and the spat had grown to the size of a sixpenny piece.

Enrichment of tanks A and B was continued at the rate of four minced crabs per day between July 23 and August 1.

On July 23 it was noticed that the spat on the forty bouquets which had been suspended in A and subsequently transferred to B and given partial changes of water, were appreciably larger than those which had remained on the floor of A without change of water until July 23.

Growth continued steadily, and there appeared to be a definite risk of overcrowding on the tiles. During the week August 7–14 a few of the larger oysters, which were a little larger than a sixpenny piece, were detached from the tiles and placed in cages, lined with stiff muslin, inside the tanks. About 600 were detached in this way.

Mr Cole visited the tanks on August 14. On his advice the detachment of oysters was stopped on account of the danger of exposing patches of bare tile on to which the remaining oysters would be liable to grow. The subsequent detachment of such oysters without considerable damage presents great difficulty.

Owing to the necessity of utilizing tanks A and B for purification purposes, all the tiles were transferred to tank C on August 16. Here, they are given practically daily changes of tidal river water to a depth of 3 ft. 6 in. and at the time of writing (October 26 1939) they are making good progress. The tiles are covered with a heavy settlement of young oysters, many of which are the size of half a crown.

The spat which were detached from the tiles during the week August 7–14 were placed in the river estuary on August 16 and 17.

They were housed in suitable cages which are exposed on a low spring tide. At first, the growth of spat appeared to be slower than that on the tiles in tank C, but during the last two weeks they have improved, and at present are larger than those inside the tank.

Discussion

I understand that there are variations in the spatting of oysters, both in regard to the time of spatting and the abundance of spat. The year 1939 was considered a fair year for oyster breeding. The factors which contribute to these variations appear to be uncertain, but must be borne in mind when considering the success of this experiment in its first year.

The Yealm is a sheltered Devon river, free from gross sewage pollution and, so far, free from animal life which is inimical to oysters. The temperature of the water is relatively high, certainly higher than that at Conway. This factor in itself should favour successful attempts at oyster breeding. The following table gives the list of temperatures, taken at midday:

Date	Temperature ° F.	Date	Temperature ° F.
June 2	59	June 16	65
3	60	18	66
4	61	20	67
5	63	21	67
6	65	22	68
7	66	23	68
8	65	24	70
9	65	25	69
10	65	27	71
11	65	29	69
12	65	July 4	68
13	65	8	68
14	65	9	69
15	66	13	70

Cole (1938) has stated that he does not consider it practicable to breed oysters in tanks which are smaller in size and depth than those at Conway. It is interesting to note that the tanks at the Yealm in which the spat settled are approximately one-third the size of those at Conway, although the depth of water is greater. The number of oysters and tiles used, and the rate of enrichment were "scaled down" from the Conway data.

Our experience confirms the view (see Cole & Jones, 1939) that the best results are obtained by suspending the tiles just below the surface of the water. The growth of spat on the tiles which were suspended in this manner was definitely superior to that on tiles which were left at the bottom of the tank. When the experiment is repeated next year, we shall place a few bouquets on the bottom of the tank, and suspend the remainder approximately a foot below the surface of the water about a week after free-swimming larvae are first noted.

Cole has stressed the importance of instituting several partial changes of water at an early date. Experience confirms the value of this procedure. Next year we propose to commence partial changes of water about a week after the spat has settled. In doing this we shall have to avoid the occurrence of a sudden drop in temperature of the water in the breeding tank. This can probably be effected by allowing for a preliminary period of warming for a day or two in the shallow tank C. As a working rule we propose to try to avoid a decrease in temperature of more than 5° F. In our work this year we have found that it is possible to allow for a change of about one-third of the volume of water by this method. Cole has suggested that spat should be placed in the river estuary about one month after settlement. Unfortunately, Mr Kingcome did not have sufficient cages to do this, but it is hoped to remedy this deficiency by next year. I have already reported the superior growth of the oysters which were placed in the estuary of the river.

Unfortunately, events will not allow the writer to continue his contact with this work next year, but it is hoped that this brief paper will serve as a record of work which can be done outside an experimental station. The absence of data which will interest the keen scientist is only too obvious.

ACKNOWLEDGEMENTS

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It is a pleasure to acknowledge the great help and co-operation of Mr J. Kingcome. His practical experience has played a great part in the success of this experiment.

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THE MANTLE CAVITY OF SOME OF THE ERYCINIDAE, MONTACUTIDAE AND GALEOMMATIDAE WITH SPECIAL REFERENCE TO THE CILIARY MECHANISMS

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(Text-figs. 1–26)

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INTRODUCTION

Despite various accounts of the occurrence, habits and general anatomy of several species of the order Leptonacea, there exists no general account of this group, unique amongst the Lamellibranchia in that it is composed largely of commensal species. In particular, little is known of the structure and mode of functioning of the organs in the mantle cavity, while little attempt has been made to correlate the various peculiarities of structure found in these animals with their specialized mode of life.

Descriptions of the shells of these species were early recorded. All except *Devonia* were described by Forbes & Hanley (1853) and Jeffreys (1863), and later accounts have been given of the external appearance and habits of these species. There are many descriptions of *Kellia* and *Lasaea*, the most complete being that of Pelseneer (1903) who investigated the general anatomy of *Lasaea*, and later (1911) of the whole order (the Lucinacea according to his classification). Pelseneer (1891) also described the anatomy of *Montacuta ferruginosa*, and later accounts of *Montacuta* (Marshall, 1891), and also of *Mysella* (as *Montacuta bidentata*) were given by Winckworth (1923, 1924), Gardiner (1928) and Salisbury (1932). The external appearance and habits of *Devonia* were recorded by Jeffreys (1863), but erroneously identified as *Montacuta donacina* (S. V. Wood) and by Malard (1903) and Winckworth (1930), and the general anatomy by Anthony (1916, as *Entovalva*) and Ohshima (1930, 1931). *Galeomma* has been described by Mittre (1847) and Fischer (1887), but again the most complete account of the anatomy is given by Pelseneer (1911). But apart from Ridewood (1903), who has described the structure, and Atkins (1937), who has described the appearance and mode of functioning of the gills, no previous general investigation of the ciliary mechanisms of the mantle cavity of these members of the Leptonacea has been recorded.

Acknowledgements are due to Prof. C. M. Yonge for his supervision of the preparation of this paper, to the Director and members of the staff of the Plymouth Laboratory for their kindness and help during the time spent there in connexion with this work, and also to Mr R. Winckworth for valuable criticisms.

MATERIAL

Two members of the family Erycinidae, *Kellia suborbicularis* (Montagu) and *Lasaea rubra* (Montagu), and four members of the family Montacutidae, *Montacuta ferruginosa* (Montagu), *M. substriata* (Montagu), *Mysella bidentata* (Montagu) and *Devonia perrieri* (Malard), were examined alive. All these are included in the family Leptonidae (Marine Biological Association, 1931). *Galeomma turtoni* Sowerby, of the family Galeommatidae, was also examined. This family is included with the Leptonidae in the order Leptonacea. The general anatomy and ciliary currents of the mantle cavity were studied and special attention paid to the feeding mechanisms.

Several of each species were examined alive and the ciliary currents in the mantle cavity were observed using powdered carmine. Others were fixed in Bouin's fluid, serial sections were cut at about 6–8 μ and the sections stained in Delafield's haematoxylin and eosin for examination of the general anatomy and details of the ciliation.

The ciliary currents in the mantle cavity of *Lasaea rubra* were difficult to determine owing to the small size of this species. Some were fixed in Bouin's fluid, cleared in clove oil and examined as whole mounts as they were perfectly transparent when treated in this manner.

Montacuta substriata is small and fragile, and was easily damaged during dissection. *Mysella bidentata* is also small, but partial dissection was possible without much damage, and the chief ciliary currents were determined.

Devonia perrieri is rare, and it is also fragile and easily damaged during dissection. Although a preliminary examination of the mantle cavity was made, the study was not complete.

Lepton squamosum, *L. nitidum* as well as *Epilepton clarkiae* are reported from Salcombe (Marine Biological Association, 1931). Many unsuccessful attempts were made to procure them, for they have apparently disappeared from Salcombe during the last few years.

Kellia suborbicularis (Montagu)

K. suborbicularis is free-living. At Plymouth it was found in crevices and holes bored by *Pholadidia* and *Saxicava* in soft red sandstone dredged from the Revelstoke Grounds. It was also frequently found in the dead shells of boring molluscs, or in crevices with such small openings that it could only be removed by breaking up the rock. The larvae or small adults must have entered these holes and early settled down there. Some small adults were found crawling on the rock and also in the fine red sand and grey mud which had collected in the crevices (Lebour, 1938). *Kellia* is also fairly common on all rocky shores near Plymouth.

K. suborbicularis is the largest member of this group. The average size is from about 8 × 6·5 to 11 × 10·5 mm. It has a smooth white glossy shell, oval in shape, with faint concentric striations. The embryonic shell is still visible in the adult near the umbo, and the whole shell has a rounded appearance, being very wide from valve to valve across the thickest part. The shell valves can be closed completely and the foot, mantle and siphons withdrawn. There is therefore no permanent gape.

There are three distinct pallial openings; the anterior inhalent opening which is in the form of a definite siphon, the ventral pedal opening, and the posterior exhalent opening which is also in the form of a siphon. With the exception of the inhalent siphon (Fig. 1, *i*) the tissues do not extend beyond the shell in life. The opening has lips formed by the free edges of the mantle, and is surrounded by a band of circular muscle. The exhalent opening is at the same level but posterior. The siphon is shorter and the opening much smaller than that of the inhalent opening (Figs. 1, 2, *e*). The pedal opening extends along the whole of the ventral side and allows extensive movement of the foot.

The foot is hatchet-shaped and large (Fig. 2, *f*), the ventral surface acting as a creeping sole. It is solid and not very extensile. The anterior portion has a blunt tip; the posterior portion forms a definite heel, although it does not trail behind as the posterior border is vertical. The ventral surface of the foot is flat, with a byssal groove which opens near the anterior end. The byssal gland is situated in the heel portion of the foot, and this region has a denser appearance than the general mass of pedal muscle.

K. suborbicularis is not so active as the other members of the group, it usually lives in a confined space, and the foot is probably rarely used for movement in the adults which are often found attached to the rock by several byssus threads. It is, however, capable of active movement, using its foot as a creeping sole.

Mantle cavity and ciliary currents

There are two complete demibranchs on each side (Atkins, 1937). The inner demibranch is larger, and extends farther anteriorly and ventrally than the outer (Fig. 1, *i.d*). The outer demibranch has a narrow supra-axial extension (Fig. 1, *s.e*) (Atkins, 1937). The axis of the ctenidium runs diagonally from immediately below the umbo towards the posterior ventral border of the shell (Fig. 2, *c.a*).

The adductors are large, the posterior adductor being larger than the anterior and slightly more ventral in position (Figs. 1, 2, *a.a*, *p.a*).

Gills. The ciliation on the inner demibranchs is normal. Particles are passed down from the axis towards the free edge of the ctenidium and along the food groove at this edge to the labial palps and the mouth (Fig. 3). On the outer demibranch, however, the particles pass down the outer, ascending lamella to the free edge, in under this edge and up the inner side of the outer demibranch, i.e. the descending lamella, towards the axis. This is contrary to the normal direction, and has been observed by Atkins (1937). There is no food groove at the distal or free edge (Fig. 1). Nevertheless, owing to the presence of a thickening of the filaments at the distal edge of this demibranch, this is regarded as a complete outer demibranch consisting of a descending and an ascending lamella rather than as a single lamella which has been reflected. This is clearly seen in sections. Except for the absence of the groove, the ventral margin is similar in appearance to that of the inner demibranch and is

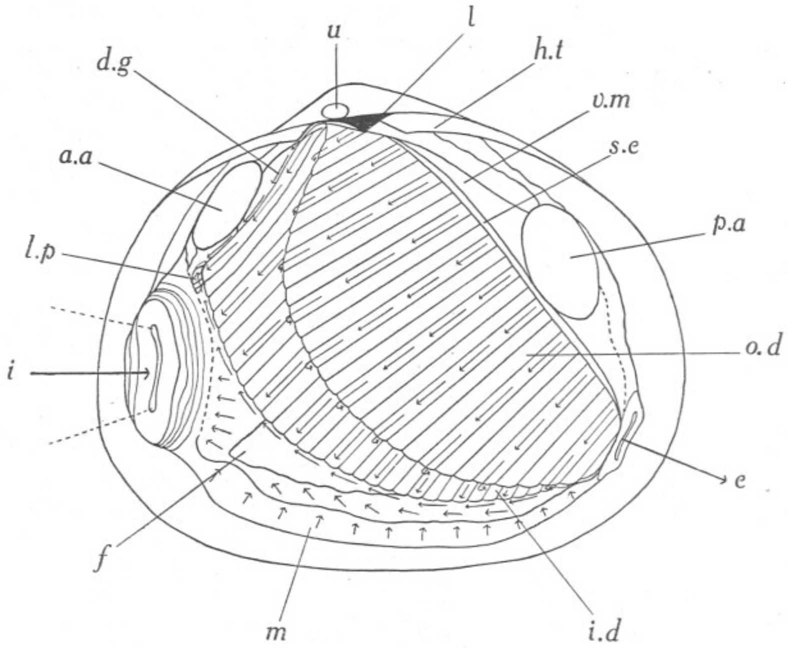


Fig. 1. *Kellia suborbicularis* with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. × 10. *a.a*, anterior adductor; *d.g*, distal oral groove; *e*, exhalent current; *f*, foot; *h.t*, hinge tooth; *i*, inhalent current; *i.d*, inner demibranch; *l*, ligament; *l.p*, labial palp; *m*, mantle; *o.d*, outer demibranch; *p.a*, posterior adductor; *s.e*, supra-axial extension; *u*, umbo; *v.m*, visceral mass.

strongly ciliated. In the region of the axis some particles are drawn across and passed down the descending lamella of the inner demibranch to the food groove, but there is also a current along the ctenidial axis between the two demibranchs which carries particles towards the mouth. At the anterior end they pass down the anterior border of the inner demibranch in the distal oral groove (Kellogg, 1915) and so to the labial palps where they are sorted (Fig. 2, *l.p*). Only very small particles go to the mouth, larger particles are passed off the palps on to the mantle and collect below the inhalent opening. No orally directed currents were observed along the junction of the ascending lamella of the inner demibranchs with the visceral mass, or along the junction of the ascending lamella of the outer demibranchs with the mantle. This was also found by Atkins (1937).

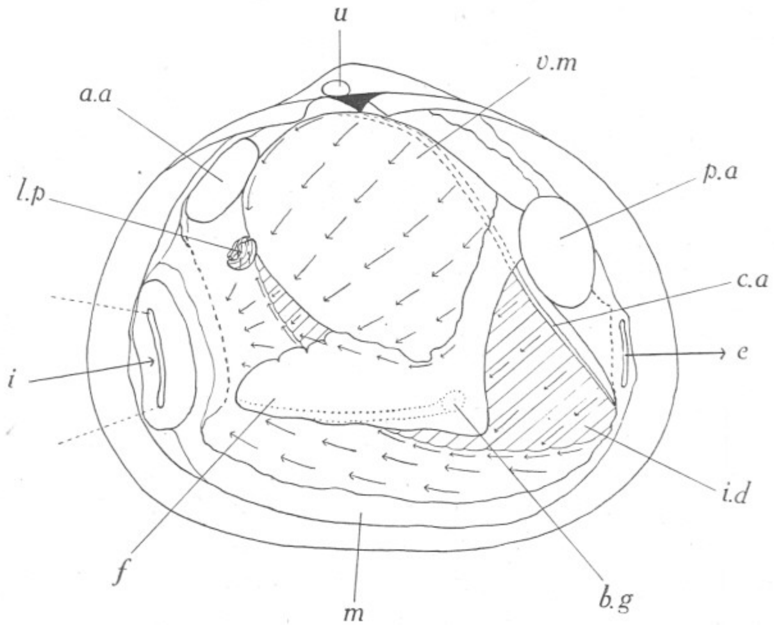


Fig. 2. *K. suborbicularis* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 10. *a.a*, anterior adductor; *b.g*, byssal gland; *c.a*, axis of ctenidium; *e*, exhalent current; *f*, foot; *i*, inhalent current; *i.d*, inner demibranch; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *u*, umbo; *v.m*, visceral mass.

Labial palps. There are two pairs of small labial palps (Fig. 3). They are fused anteriorly to form the lips of the mouth (*mo*), but the free parts are curved away from each other. The opposed surfaces are diagonally ridged. Particles of food and other material are swept on to the palps from the food groove of the inner demibranch which lies between each pair of palps, and from the distal oral groove (Fig. 1, *d.g*). The ciliation of the labial palps is normal (Fig. 3). They act as sorting organs. Large particles and masses of waste material entangled in mucus are passed off the palps on to the mantle and are rejected from the mantle cavity. Only the finest particles pass along the proximal oral groove (*p.g*) at the oral end of the base of the palps into the mouth. Particles pass diagonally across the ridged surface of the palps from the tips to the outer side of the lips of the mouth, and collect in mucus-entangled masses (Fig. 3, *w*) which are removed by the ciliary rejection currents of the mantle. There is also a current up the outer edges and over the smooth outer surfaces of the palps from the base towards the tips, i.e. contrary to the movement over the ridged surface. Particles which do not pass into the mass of waste material, or which become detached from it, pass up to the tips of the palps in this current and down over the ridged surface where they are sorted further. There is an additional sorting in the grooves of the ridged surface. Moderately fine particles are detached from the main mass, pass up these grooves and into the current passing up the free edge. No current was observed in the middle of each ridge passing in the opposite direction to that in the grooves, as mentioned by Kellogg (1915), but that was probably owing to the relatively small size of the palps. The fine particles sorted out from the main mass pass slowly into the mouth along the short proximal oral groove (Fig. 3, *p.g*).

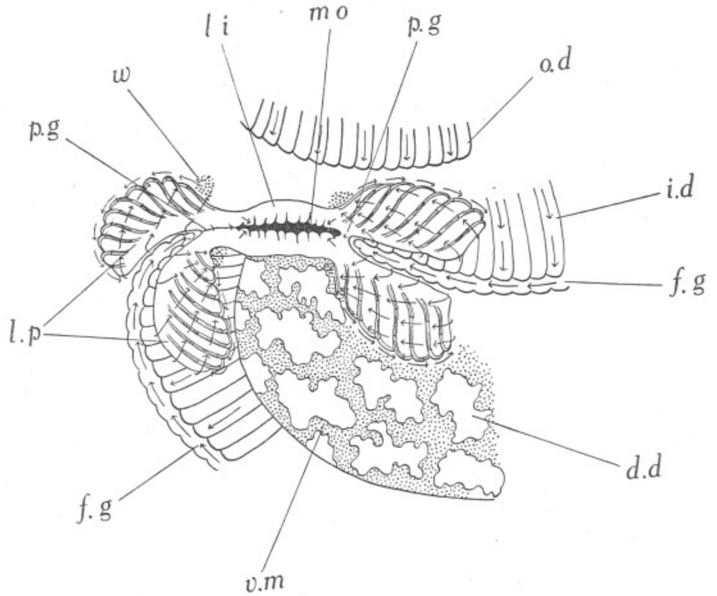


Fig. 3. *K. suborbicularis*. Ciliary currents on the labial palps. × 20. *d.d*, digestive diverticula; *f.g*, food groove; *i.d*, inner demibranch; *li*, lip; *l.p*, labial palp; *mo*, mouth; *o.d*, outer demibranch; *p.g*, proximal oral groove; *v.m*, visceral mass; *w*, waste.

Visceral mass and foot. The surface of the visceral mass is ciliated and concerned with the rejection of waste material (Fig. 2). The direction of the currents on the visceral mass is the same as that of the ascending lamella of the inner demibranch which lies over it, from the line of the axis of the ctenidium towards the mouth. Particles of waste material are passed downwards and forwards over the surface of the visceral mass and collect immediately inside the inhalent opening. They also pass forwards along the dorsal region of the foot at its junction with the visceral mass into the main mass of waste material. This appears to be the only ciliated region on the foot.

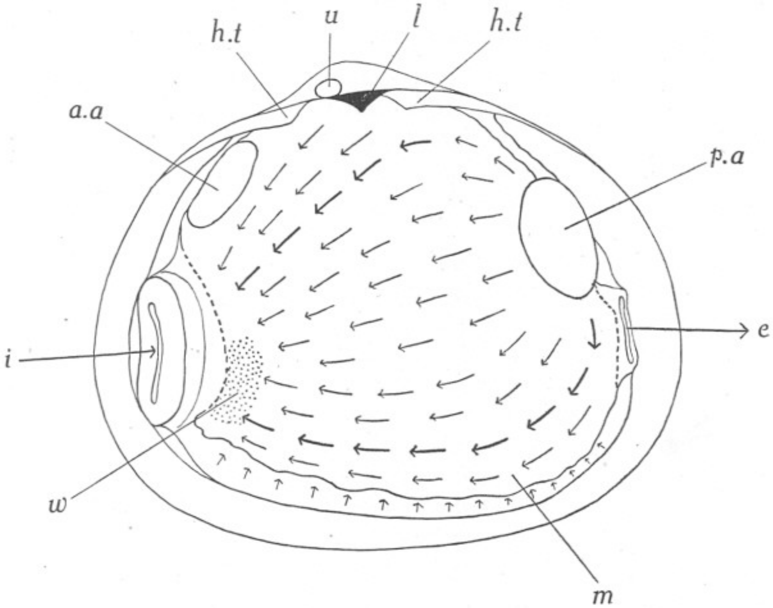


Fig. 4. *K. suborbicularis*. Ciliary currents on the mantle. × 10. *a.a*, anterior adductor; *e*, exhalent current; *h.t*, hinge tooth; *i*, inhalent current; *l*, ligament; *m*, mantle; *p.a*, posterior adductor; *u*, umbo; *w*, waste.

Mantle. There is an active ciliation of the mantle surface concerned with the rejection of waste material. The general trend is forwards from the posterior adductor towards the inhalent opening (Fig. 4). The cilia are active and the currents are strong over the whole surface, but there are two main currents, one from below the posterior adductor which follows the ventral curve of the shell to the "collecting ground" of waste material inside the inhalent opening, the other passes forwards dorsally but farther from the dorsal border of the shell. The free edges of the mantle around the pedal opening are ciliated. Particles falling on them are passed up into the mantle cavity, they are swept over the mantle edge into the rejection current on the ventral part of the mantle. A large mass of waste material collects inside the inhalent opening entangled in mucus (Fig. 4, *w*). It is passed out through the inhalent siphon by a sudden violent contraction of the adductor muscles, and is shot out against the normal inhalent stream as in other lamellibranchs (Kellogg, 1915). *Kellia* is the only member of this group in which this has been observed.

The exhalent current is normal, water passes out from the suprabranchial cavity through the short exhalent siphon.

The active ciliation of the mantle and the removal of waste through the inhalent opening by muscular contraction prevent silting up of the mantle cavity in this species which usually lives a practically sedentary existence in an environment where there may be a considerable amount of mud.

Lasaea rubra (Montagu)

L. rubra is found among dead barnacle shells between tide-marks. It occurs in the dead shells or between them, but it has not been observed actually within the shell of living barnacles. It is often attached to the rock or shells by means of a byssus, but is sometimes found crawling on the surface of the rock. The barnacles are so closely packed together that the movements of *L. rubra* must be restricted.

It occurs on all rocky shores in the neighbourhood of Plymouth and is most abundant a few feet below high-water mark. It was collected from Drake's Island and the G.W.R. wharfs at Plymouth, and from the rocks on the shore at Chapel Porth on the North coast of Cornwall.

L. rubra is small, the largest specimens collected measured only 1·4 × 1·2 mm. and these were fully mature. The shell is a dark reddish brown in colour and is darkest in the region of the umbo. The largest specimens are heavily pigmented, while the shells of the young are practically transparent. The shell is oval, in the young it is only slightly longer than it is broad, but in the large specimens the asymmetry is increased. The umbo is raised above the level of the hinge, and the embryonic shell is still clearly visible in the adult (Fig. 5, *em*). The surface of the shell is smooth with striations following the curve of the shell. The edge is entire. There is no permanent gape between the shell valves.

There are three pallial openings, the anterior inhalent siphon, the ventral pedal opening and the posterior exhalent siphon. The inhalent opening is a definite siphon and extends for a considerable distance beyond the shell valves in life (Fig. 5, *i*). When fully expanded it is bell-shaped. The mantle is fused for a short distance below the inhalent siphon and so separates the inhalent from the pedal opening. The large pedal opening extends along the whole of the ventral side. This large opening makes possible the rapid and active pedal movements characteristic of *Lasaea*. The exhalent opening is the smallest of the pallial openings. The mantle lobes are fused to form a short but distinct siphon which is not visible from the exterior as it never extends beyond the shell valves (Fig. 5, *e*).

The foot is long and slender with a rounded tip. It is very extensile and when fully extended it may exceed the length of the shell (Fig. 5, *f*). The anterior end of the foot is cylindrical in shape, the whole foot becoming wider towards the shell and flattened dorso-ventrally. It is capable of active movement and when moving about the foot is first pushed out in an anterior and slightly ventral direction. The anterior tip of the foot appears first and seeks about, the heel or posterior portion of the foot then appears and the whole animal moves forward with a gliding motion using the ventral surface of the foot as a creeping sole. The anterior tip of the foot becomes attached, apparently by a sucker-like action, and the whole animal is pulled forward by a contraction of the pedal muscles and tilted slightly forwards over the foot. During this movement the foot is partially withdrawn between the shell valves. The anterior part is then pushed out again and the animal moves forward by a series of short violent movements. These movements are arhythmic, like those which occur in certain Gastropoda such as *Aporrhais* (Yonge, 1937). The direction of movement is determined by the tip of the foot which can be turned in all directions.

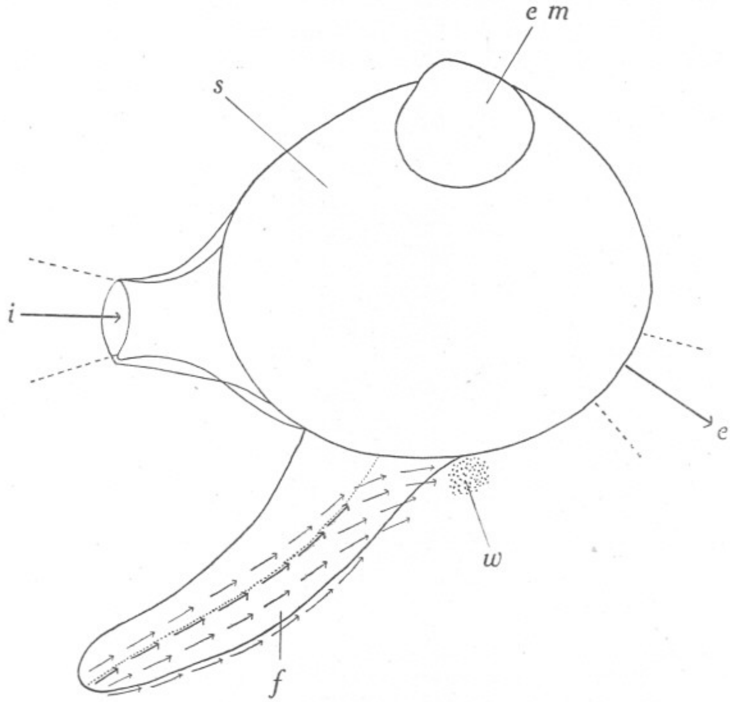


Fig. 5. *Lasaea rubra*. External appearance. × 60. *e*, exhalent current; *em*, embryonic shell; *f*, foot; *i*, inhalent current; *s*, shell; *w*, waste.

The byssal gland is situated in the posterior portion of the foot. There is a byssal groove along the ventral surface of the foot which opens out just behind the anterior tip. This groove becomes a closed duct posteriorly. Several strong threads are produced, their position being determined by the direction of the anterior tip of the foot, and the angle between the threads usually varies from 30 to 45°. The byssal gland is very active and if several animals are left in a dish they become bound together by a network of byssal threads so that they are difficult to separate.

Mantle cavity and ciliary currents

Each ctenidium consists of a complete inner demibranch consisting of a descending and a very short ascending lamella, and an outer demibranch consisting of a descending lamella only, the distal edge of which is attached to the adjacent mantle lobe (Fig. 6). When this mantle lobe was removed the outer demibranch came away with it, thus causing damage and obscuring the normal ciliary currents. The axis of the ctenidium runs diagonally. The morphologically anterior end of the axis is dorsal in position and immediately below the umbo. The morphologically posterior end is anterior to the posterior adductor, and just inside the exhalent opening (Fig. 7, *c.a*).

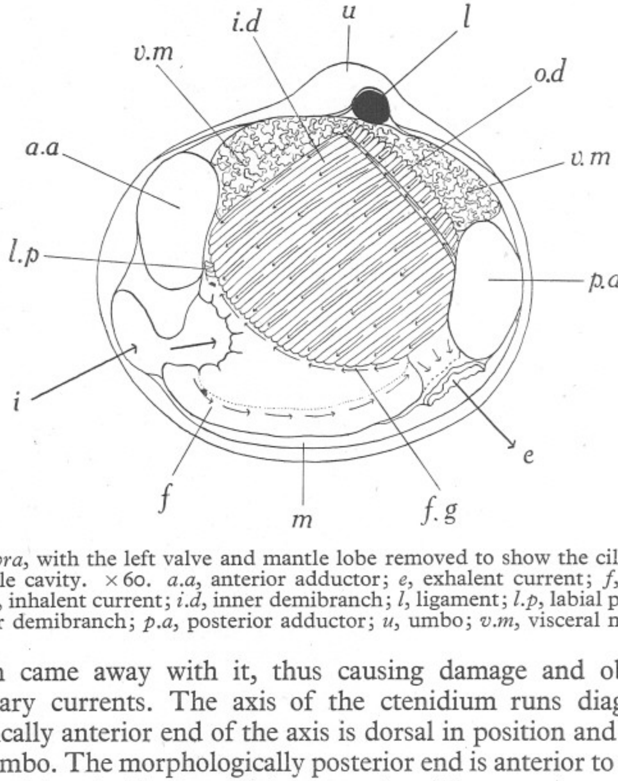


Fig. 6. *L. rubra*, with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. × 60. *a.a*, anterior adductor; *e*, exhalent current; *f*, foot; *f.g*, food groove; *i*, inhalent current; *i.d*, inner demibranch; *l*, ligament; *l.p*, labial palp; *m*, mantle; *o.d*, outer demibranch; *p.a*, posterior adductor; *u*, umbo; *v.m*, visceral mass.

The adductor muscles are large and approximately equal in size. The posterior is rather more ventral in position (Fig. 6, *a.a*, *p.a*).

Gills. The ciliation on the inner demibranch is normal. Particles are passed down both the descending and ascending lamellae towards the free edge of the demibranch. There is a food groove along the free edge with an orally directed current (Fig. 6, *f.g*). On the descending lamella of the outer demibranch, in this case the only lamella, particles are passed up from the distal edge which is fused with the mantle, towards the axis and into the current passing forwards along the groove between the two demibranchs (Fig. 6).

Palps. There are two pairs of labial palps (Fig. 6, *l.p*). They are so minute that the direction of the currents over their surface could not be followed, but they certainly act in a normal manner as sorting organs and prevent large particles passing to the mouth.

Visceral mass and foot. There was also difficulty in following the currents on the surface of the visceral mass owing to the small size and the amount of damage done during dissection.

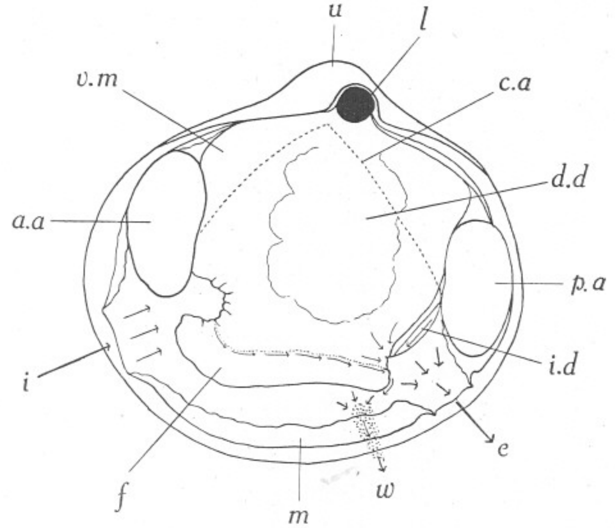


Fig. 7. *L. rubra* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. ×60. *a.a*, anterior adductor; *c.a*, axis of ctenidium; *d.d*, digestive diverticula; *e*, exhalent current; *f*, foot; *i*, inhalent current; *i.d*, inner demibranch; *l*, ligament; *m*, mantle; *p.a*, posterior adductor; *u*, umbo; *v.m*, visceral mass; *w*, waste.

The portion of the foot which extends beyond the shell is strongly ciliated (Fig. 5, *f*). This is in marked contrast to *Kellia*. Particles are passed rapidly over the surface of the foot from the tip in a posterior direction even when it is extended. The ventral surface of the foot is most strongly ciliated. The ciliation is continued for a short distance up the sides, but there appears to be no ciliation on the dorsal surface of the foot. Only the finest particles are passed up into the mantle cavity, all larger particles are passed off the posterior portion of the foot entangled in mucus and join the main mass of waste material which is passed out behind the foot in a posterior and ventral direction (Figs. 5, 7, *w*).

Mantle. The ciliation of the mantle has not been determined in detail, but it appears to be normal and is concerned entirely with rejection. The main trend is from the anterior end in a ventral and posterior direction, i.e. in the reverse direction to the mantle currents found in *Kellia*. Waste material is passed out over the border of the mantle ventrally. This mass of waste material is entangled in mucus and is joined by the waste material from the foot and left behind in strings as the animal moves forward. Contractions of the free edges of the mantle surrounding the pedal opening also help in the removal of this waste material (Figs. 5, 7).

Montacuta ferruginosa (Montagu)

M. ferruginosa always occurs in association with *Echinocardium cordatum*. The larger specimens were found in the sand of the burrow opposite the anal siphon of the *Echinocardium*. There were usually several *Montacuta* grouped together, and the sand surrounding them was coloured reddish brown probably owing to an iron pigment among the faecal material from the *Echinocardium*. The red colour of the *Montacuta* may be due to this pigment. Some smaller specimens were found attached to the spines on the under side of the *Echinocardium* in a position similar to that of *Montacuta substriata* on *Spatangus purpureus*. A few specimens were collected in the muddy sand below the Marine Hotel, Salcombe, but they were not numerous, and small in size. The majority were collected from the cleaner sand at Mill Bay, Salcombe, where they are abundant.

M. ferruginosa varies greatly in size from 9 × 4·8 to 1·5 × 1 mm. The shell is a light reddish brown in colour, darkest in the region of the umbo, and often almost pure white at the edge of the valves. The young specimens are the lightest in colour. The shell is oval in shape and asymmetrical, in the large specimens it is almost twice as long as it is broad. The umbo is raised slightly above the level of the hinge. The embryonic shell is still visible in the adult. The surface of the shell is smooth with faint concentric striations and the edge is entire.

The mantle edge and foot normally extend beyond the shell valves in life, but both can be completely withdrawn and there is no permanent gape between the shell valves. There is no definite inhalent siphon, but the free edges of the mantle normally extend beyond the shell anteriorly and form a temporary siphon. There are only two pallial openings. One of these is very large, extending for three-quarters of the anterior side and the whole of the ventral side except for the extreme posterior part where there is fusion of the mantle lobes for a short distance below the exhalent siphon. This large pallial opening is a combined inhalent and pedal opening and it permits a wide angle of movement of the foot. The exhalent opening is in the form of a short siphon situated on the mid-line of the posterior end (Fig. 8, *e*). It does not extend beyond the shell valves in life. The mantle lobes are fused dorsal to the exhalent opening.

The free edge of the mantle which extends beyond the shell and surrounds the large antero-ventral pallial opening has many papillae (Fig. 8, *pp*). These are small on that portion of the mantle which forms the inhalent opening and sides of the pedal opening, but they are larger posteriorly on the mantle surrounding the exhalent siphon, and there are two very large unpaired papillae or "tentacles", one dorsal and the other ventral to the exhalent siphon. These are very extensile. The papillae, like the mantle, are pinkish in colour, they are numerous and regular in arrangement.

The foot is large and wedge-shaped, with a thickened ventral surface used as a creeping sole (Figs. 8, 9, *f*), the upper part is dark red in colour, the sole is paler. The anterior end has a bluntly pointed tip which is pushed out first when the animal is moving. It seeks about and then becomes temporarily fixed down. The whole animal is tilted forward over the foot. The thin posterior part, or heel, of the foot then emerges, and the animal walks forward on the broad ventral surface of the foot, with the posterior portion trailing behind. The ventral surface of the foot is lubricated by the secretion of mucus.

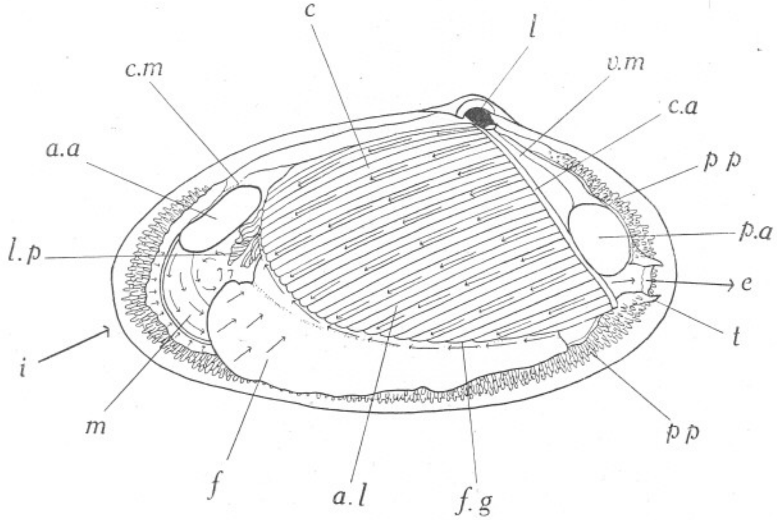


Fig. 8. *Montacuta ferruginosa* with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. × 10. *a.a*, anterior adductor; *a.l*, ascending lamella; *c*, ctenidium; *c.a*, axis of ctenidium; *c.m*, cut edge of mantle; *e*, exhalent current; *f*, foot; *f.g*, food groove; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *pp*, papillae; *t*, "tentacle"; *v.m*, visceral mass.

The byssal gland is embedded in the posterior portion of the foot. A duct leads from it into a deep groove which runs along the ventral surface of the foot and opens out just behind the anterior tip. The young specimens are attached to the spines of *Echinocardium* by means of byssal threads, but the byssal gland can have little function in the adult which lives in loose sand and has no permanent attachment. None of those kept in dishes in the laboratory was seen to produce byssal threads. The adults are capable of very active movement.

Mantle cavity and ciliary currents

There is a single complete demibranch on each side with descending and ascending lamellae (Fig. 8, *c*). This is the inner demibranch, the outer has disappeared completely. The axis of the ctenidium is almost dorso-ventral in position but with the upper, or morphologically anterior end of the axis slightly anterior to the lower or posterior end (Fig. 8, *c.a*). The axis is in this case even more vertical in position than it is in *Lasaea*.

The adductor muscles are well developed, the anterior is slightly larger than the posterior (Figs. 8, 9, and 10, *a.a*, *p.a*).

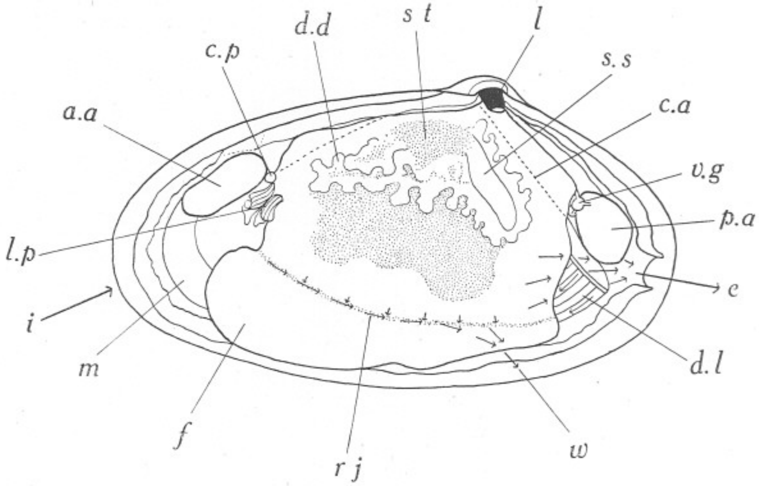


Fig. 9. *M. ferruginosa* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 10. *a.a*, anterior adductor; *c.a*, axis of ctenidium; *c.p*, cerebro-pleural ganglion; *d.d*, digestive diverticula; *d.l*, descending lamella; *e*, exhalent current; *f*, foot; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *r.j*, rejection current; *s.s*, style sac; *st*, stomach; *v.g*, visceral ganglion; *w*, waste.

The whole mantle is tinged pink, and the visceral mass is dark red with greenish digestive diverticula. The ganglia are bright pink in colour and show up clearly in the mantle cavity.

Gills. The ciliation of the demibranch is normal. Particles are passed down both lamellae towards the free edge and along it to the palps and the mouth (Fig. 8, *f.g*).

Palps. The labial palps are relatively larger than in most members of this group (Figs. 8, 9, *l.p*). They are similar in appearance and ciliation to those of *Kellia* and appear to be quite normal in function. Only small particles are passed into the mouth. Large masses of waste material entangled in mucus are passed off the palps on to the mantle, or back along the sides of the foot and out of the mantle cavity (Fig. 9, *w*).

Visceral mass and foot. There is no ciliation on the surface of the visceral mass, and only a slight ciliation causing a slow movement of particles along the sides of the foot at the level of its junction with the visceral mass (Fig. 9). This current is concerned with rejection. The particles of waste material form strings and are bound together by mucus (Figs. 9, 10, *w*). They are passed backwards across the foot more by the cilia on the surface of the mantle lying outside the foot and close over it than by the cilia on the foot itself.

Mantle. The actual surface of the mantle is strongly ciliated along definite tracks (Fig. 10), particularly at the anterior end. The whole of the free edge of the mantle forming the antero-ventral pallial opening is ciliated, so that particles falling on this are passed into the mantle cavity, except at the region where waste material is rejected from the mantle cavity. In this region the current is in the reverse direction. There is a band of strong cilia stretching from the mid-line of the anterior end to the posterior end of the pedal opening where the mass of waste material is passed out. It follows the curve of the shell ventrally, and a mass of waste particles and mucus is rejected behind the foot and left behind in strings as the animal moves forward. There are contributory currents on either side of the main stream, and there is a collection of particles on to one track which stretches from the centre of the mantle to a point on the ventral edge in line with the umbo. The general trend is therefore ventrally and *posteriorly* as in *Lasaea*; not anteriorly as in *Kellia* and most lamellibranchs (Kellogg, 1915).

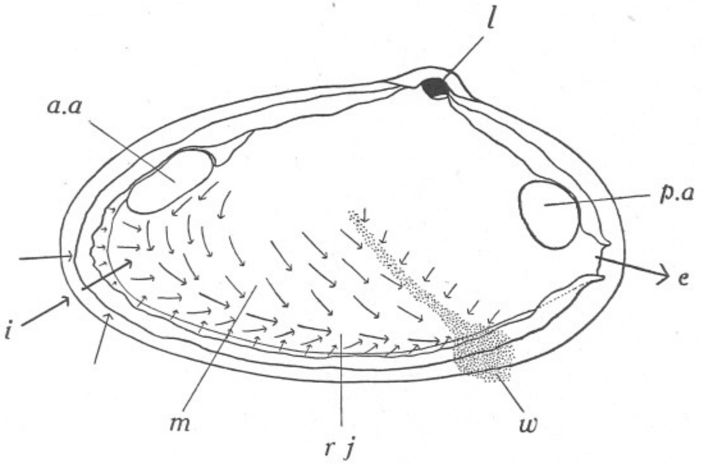


Fig. 10. *M. ferruginosa.* Ciliary currents on the mantle. × 10. *a.a*, anterior adductor; *e*, exhalent current; *i*, inhalent current; *l*, ligament; *m*, mantle; *p.a*, posterior adductor; *rj*, rejection current; *w*, waste.

The absence of cilia on the visceral mass is probably correlated with the removal of waste material from the mantle cavity by sudden violent contractions of the whole of the free part of the mantle, aided by the contraction of the adductors, which has been observed at irregular intervals, apparently depending upon the amount of material entering the mantle cavity. There was no sign, however, of any removal of waste through the anterior inhalent opening as in *Kellia*, because the inhalent opening is closed temporarily and all waste material is shot out through the ventral pedal opening as in other members of the group. This muscular movement must be a more efficient mechanism than the gradual removal of particles by the action of cilia, as occurs in *Lasaea*. It is probably connected with the sandy, and often muddy environment in which *Montacuta ferruginosa* occurs. *Kellia*, which is often found in a muddy environment, has in effect a similar mechanism to prevent silting up of the mantle cavity.

Montacuta substriata (Montagu)

M. substriata is commensal with *Spatangus purpureus*. It was collected by dredging in shell gravel in Stoke Bay, Plymouth, and in deep water south-west of the Eddystone. It is always found attached to the spines of *Spatangus* and never free living. It is usually on the under side and attached to the anal spines by two or three byssal threads. Three or four may be found on one *Spatangus*, each attached to a different spine, but many of the *Spatangus* collected were without *Montacuta*. All the specimens collected were small, but they were fully mature.

The specimens collected varied in size from 0·6 × 0·5 to 1·75 × 1·5 mm. The shell is whitish in colour and so transparent that the brownish coloured visceral mass is visible through the shell. There is no pigment deposited in the shell as in *M. ferruginosa*. The shell is symmetrical in comparison with other members of the group. In the smallest specimens it is only slightly longer than it is broad, and even in the largest it is only slightly asymmetrical. The umbo is prominent and raised above the level of the hinge, and the embryonic shell is clearly visible (Fig. 11, *em*). Fine lines radiate from the umbo and there are also concentric striations, presumably indicating growth stages. The shell resembles that of *Kellia*, but the valves are flatter and more transparent than in the adult *Kellia*. The edge is entire.

The free edges of the mantle do not extend beyond the shell valves and there are no definite siphons. The foot can be extended for a considerable distance, so that the portion of the foot outside the shell is greater in length than the shell, i.e. in a specimen with a shell 1·5 mm. in length, the foot was extended for a length of 2 mm. beyond the shell, but it can be completely withdrawn and the shell valves closed.

As in *M. ferruginosa* there are only two pallial openings and there is little fusion between the mantle lobes, but in this species there are no papillae on the free borders of the mantle.

The foot is roughly cylindrical in shape, but flattened ventrally to form a creeping sole (Figs. 11, 13, *f*). It is in two parts; the anterior is very extensile and has a rounded tip, the posterior forms a heel and trails behind.

The animal is capable of rapid motion and exhibits a curious and characteristic rocking movement. The anterior tip of the foot is pushed out first; it can be turned about in all directions and determines the direction in which the animal travels. The tip of the foot seeks about and then becomes temporarily fastened down, apparently by a sucker-like action. The heel of the foot then appears. Muscular contractions follow, by which the animal is first tipped forwards over the point of the foot, and then rocked back so that the shell is in a normal position and the heel of the foot is in contact with the substratum. It then moves forwards by a slow gliding movement on the flat ventral surface of the foot. The violent rocking movement is repeated at irregular intervals. There is a considerable gape between the shell valves during movement. The extensive movement is possible owing to this and to the large size of the pedal opening.

The byssal gland is situated in the posterior portion of the foot, and opens into a groove on the ventral side. Two or three threads are produced and the angle separating them is not great (Fig. 11, *by*).

Mantle cavity and ciliary currents

There is a single complete demibranch on each side consisting of a descending and an ascending lamella. As in *M. ferruginosa*, it is the inner demibranch. The ascending lamella is deeper than the descending, and has a supra-

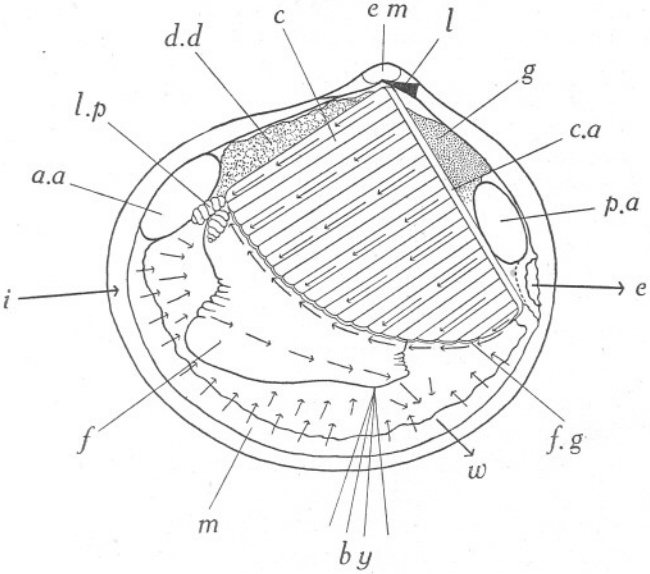


Fig. 11. *Montacuta substriata* with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. ×40. *a.a*, anterior adductor; *by*, byssus; *c*, ctenidium; *c.a*, axis of ctenidium; *d.d*, digestive diverticula; *e*, exhalent current; *em*, embryonic shell; *f*, foot; *f.g*, food groove; *g*, gonad; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *w*, waste.

axial extension as has the outer demibranch of *Kellia*. The axis of the ctenidium again runs diagonally and is similar in position to that of *M. ferruginosa* (Fig. 11, *c.a*).

The adductor muscles are well developed (Figs. 11, 13 and 14, *a.a*, *p.a*).

Gills. The ciliation of the demibranch is normal (Fig. 11) and the same as that found in *M. ferruginosa*.

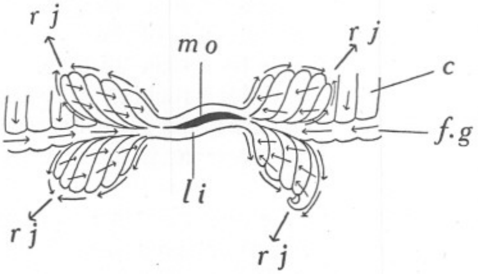


Fig. 12. *M. substriata.* Ciliary currents on the labial palps. ×80. *c*, ctenidium; *f.g*, food groove; *li*, lip; *mo*, mouth; *rj*, rejection current.

Palps. The labial palps are small, and the details of the currents on the surface were difficult to follow, but the ciliation appears to be quite normal (Fig. 12). When large quantities of waste material were being dealt with, the palps were raised so that the tips touched the overlying mantle folds, and waste material was passed off into the main rejection current passing out over the mantle surface.

Visceral mass and foot. The visceral mass is only slightly ciliated (Fig. 13). There is a movement of particles below the line of the axis of the ctenidium along the dorsal surface of the visceral mass towards the palps, and there is also some movement below this, but no definite stream of particles was observed. The surface of the foot is strongly ciliated (Figs. 11, 13). Particles move rapidly across the sides of the foot from the tip to the heel, and are passed off into the main rejection current which passes out between the shell valves in a posterior and ventral direction immediately behind the foot (Figs. 13, 14, *w*). This current is concerned entirely with the rejection of waste material.

Mantle. There is a clearly defined band of strong cilia concerned with rejection on the mantle (Fig. 14). The free edge of the mantle surrounding the inhalent and pedal opening is also ciliated. Particles falling on this edge are passed into the mantle cavity. The area of the mantle corresponding to an inhalent siphon occupies the central part of the anterior end below the anterior adductor muscle. It is ciliated and particles are passed into the mantle cavity in this region. The ciliation is particularly strong in a line passing from the middle of the inhalent opening to a point on a level with the anterior adductor. From this point the band of cilia runs diagonally downwards and backwards to the ventral border of the mantle. This is the chief rejection area where waste

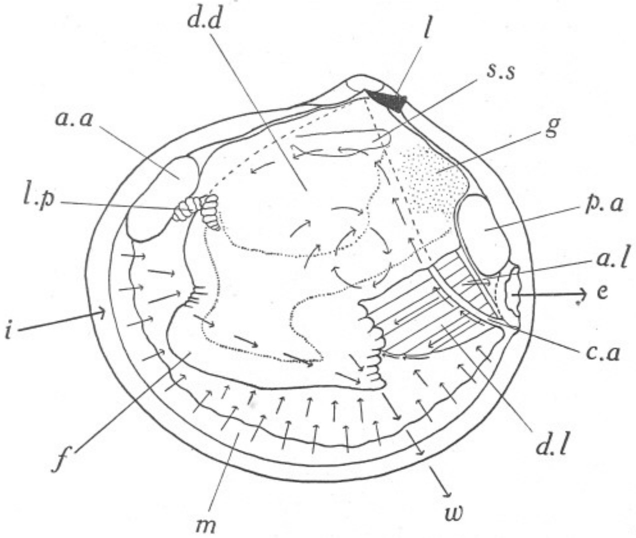


Fig. 13. *M. substriata* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 40. *a.a*, anterior adductor; *a.l*, ascending lamella; *c.a*, axis of ctenidium; *d.d*, digestive diverticula; *d.l*, descending lamella; *e*, exhalent current; *f*, foot; *g*, gonad; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *s.s*, style sac; *w*, waste.

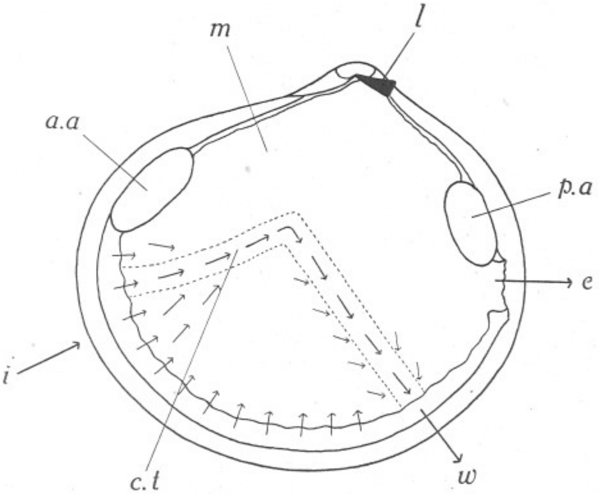


Fig. 14. *M. substriata*. Ciliary currents on the mantle. × 40. *a.a*, anterior adductor; *c.t*, ciliated tract; *e*, exhalent current; *i*, inhalent current; *l*, ligament; *m*, mantle; *p.a*, posterior adductor; *w*, waste.

material is passed out between the shell valves. The ciliation of the mantle edge is very strong at this point and particles are passed over it in the reverse direction, i.e. out of the mantle cavity instead of into it. There are slight contributory currents on the anterior side of the main stream, but the main ciliary action is confined to this definite band.

M. substriata has a most efficient ciliary mechanism for the removal of waste material and can cope with large quantities. Much waste material is passed out over the foot and never reaches the gills, while that which does reach the gills is sorted by the palps and passed out along the band of strong cilia on the mantle. The waste material is passed out entangled in mucus. The action of the cilia is assisted by sudden violent contractions of the adductor muscles, which shoot water out through the exhalent opening, and water carrying waste material out through the pedal opening. The greater part of the waste material is expelled at the normal rejection position. None was seen to pass out through the anterior end of the pallial opening in the position of the inhalent current.

Mysella bidentata (Montagu)

M. bidentata is commensal with *Ophiocnida brachiata*. A few were collected from the muddy shore below the Marine Hotel, Salcombe. They are rare and can only be reached at low water springs. One or two *Mysella* were found in the mud with each *Ophiocnida*, but they were never attached to it in any way. It is also reported to live in association with *Phascolosoma elongatum* (Winckworth, 1924; Gardiner, 1928; and Salisbury, 1932).

M. bidentata is small, the largest specimen collected measured 7 × 5 mm. The shell colour varies from a yellowish white to a dark reddish brown and is darkest in the region of the umbo. It is approximately rectangular in shape and only slightly rounded at each end. It is inequilateral. The surface of the shell is smooth except for concentric lines which are darker in colour than the general surface of the shell and are spaced at regular intervals.

The foot and the edge of the mantle lobes normally extend beyond the shell in life, but they can be completely withdrawn and the shell valves closed. No siphons are visible from the exterior. The free edges of the mantle have short rounded protuberances; they are blunter than the papillae of *M. ferruginosa* and are not contractile. Each has a small dark spot which gives the appearance of a row of pallial eyes.

As in both species of *Montacuta*, there are only two pallial openings and little fusion between the mantle lobes. There is no inhalent, and only a very short exhalent siphon.

The foot is large and wedge-shaped (Figs. 16, 17, *f*). It has a blunt tip and a flat ventral surface which is used as a creeping sole. *Mysella* is active and progresses by a series of violent rocking movements similar to those of *Montacuta substriata* (Fig. 15).

A byssal gland is present, but no byssus has so far been observed in life. No threads were produced when several specimens were kept under observation in a dish, and it is probable that none is produced under normal conditions as the animal lives in soft sandy mud.

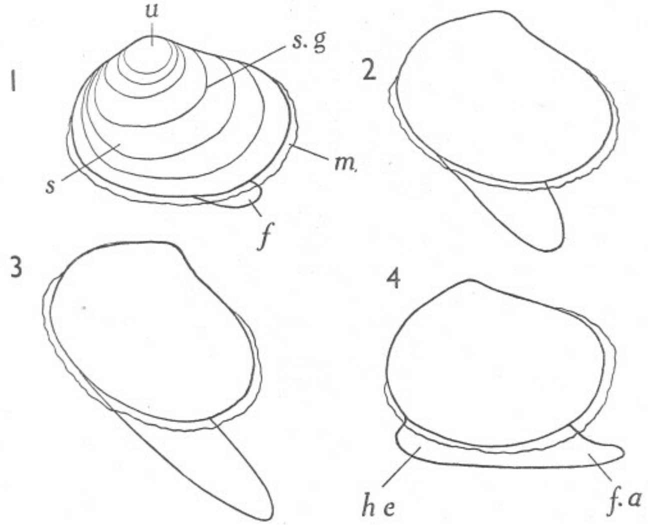


Fig. 15. *M. bidentata*. Four stages in movement of the living *Mysella*. ×4·5. *f*, foot; *f.a*, anterior portion of foot; *he*, heel; *m*, mantle; *s*, shell; *s.g*, striations showing growth stages; *u*, umbo.

Mantle cavity and ciliary currents

There is a single complete inner demibranch, similar in position to that of *Montacuta substriata*, but the lamellae are deeper, i.e. the distance from the axis to the free edge is greater (Fig. 16, *c*).

The adductor muscles are well developed and normal in position. They are approximately equal in size, but the anterior is rounder in shape than the posterior (Figs. 16, 17, 18, *a.a*, *p.a*).

Gills. The ciliation of the ctenidia is normal and similar to that of *Montacuta* (Fig. 16, *c*).

Palps. The labial palps are small (Figs. 16, 17, *l.p*) and the details of the ciliary currents over the surface were difficult to follow. They were observed to function in the normal manner passing large particles off the tips into the main rejection current and fine particles only into the mouth.

Visceral mass and foot. There is an active ciliation on the surface of the visceral mass (Fig. 17). The movement of particles is most active in the region below the umbo. Strong ciliation causes a rapidly moving "whirlpool" from which particles move along two definite tracks. A strong current passes down the posterior border of the visceral mass in a straight line from below the umbo to the heel of the foot. There are contributory currents on either side of the main stream and large masses of waste material are passed out of the mantle

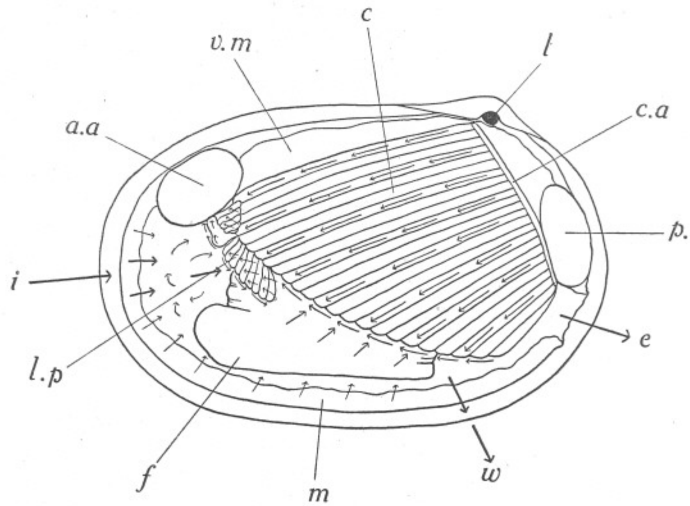


Fig. 16. *Mysella bidentata* with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. × 10. *a.a*, anterior adductor; *c*, ctenidium; *c.a*, axis of ctenidium; *e*, exhalent current; *f*, foot; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *v.m* visceral mass; *w*, waste.

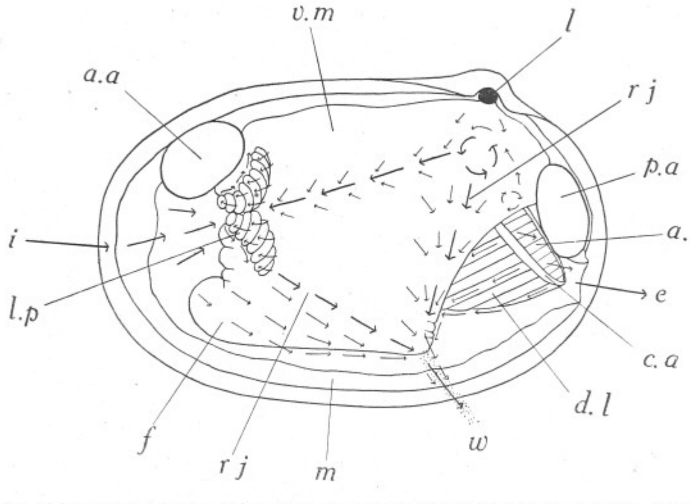


Fig. 17. *M. bidentata* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 10. *a.a*, anterior adductor; *a.l*, ascending lamella; *c.a*, axis of ctenidium; *d.l*, descending lamella; *e*, exhalent current; *f*, foot; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *rj*, rejection current; *v.m*, visceral mass; *w*, waste.

cavity immediately behind the heel of the foot. This is the rejection area (Fig. 17, *w*). A strong current also passes forwards from the "whirlpool" below the umbo to the labial palps. It appears to be chiefly finer particles which are passed along this track. They are sorted further by the labial palps, only the very fine particles being passed to the mouth, while the larger particles are passed into the rejection current passing along the foot. There are again contributory currents on either side of the main stream. There is also a slight movement of particles up the posterior end of the visceral mass, along the line of the axis of the ctenidium towards the umbo. These pass into one of the currents already mentioned.

There is an active ciliation on the sides of the foot. Large particles are passed off from the tips of the labial palps, diagonally backwards towards the heel of the foot, where they join the stream moving down the posterior side of the visceral mass, pass out over the border of the mantle and are left behind in long strings of mucus (Figs. 17, 18, *w*). The whole of the sides of the foot are ciliated and particles move in the same direction as the main stream, i.e. towards the heel of the foot.

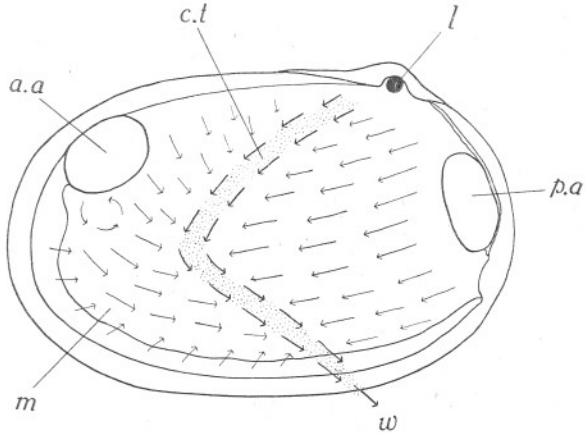


Fig. 18. *M. bidentata.* Ciliary currents on the mantle. × 10. *a.a*, anterior adductor; *c.t*, ciliated tract; *l*, ligament; *m*, mantle; *p.a*, posterior adductor; *w*, waste.

There are therefore three main currents: two of them, that along the posterior side of the visceral mass, and the current along the foot, are concerned entirely with rejection of waste material. The third current, that along the central part of the visceral mass, must also assist feeding, as the particles passed along it will be sorted by the labial palps, and any particles sufficiently fine will be passed into the mouth. This current is absent in *Montacuta* as is the ciliation at the posterior end of the visceral mass. The relatively larger size of the palps in *Mysella* may be correlated with this current supplying additional material for sorting.

Mantle. The mantle is also ciliated over practically the whole of its surface (Fig. 18), but there is a definite strongly ciliated track from a point below and slightly anterior to the umbo, which passes downwards and forwards. It then bends sharply back, and passes diagonally backwards, reaching the ventral border of the mantle at the main rejection point exactly below the umbo. This track is even more definite than that in *Montacuta substriata*. It is supplied by contributory currents on either side, which collect material from the whole of the mantle surface. The free border of the mantle is also ciliated and particles falling on to it are passed into the mantle cavity. This ciliation of the mantle is concerned entirely with rejection and is the most effective mechanism of this type found in any member of the group.

This strong ciliation of the surface of the visceral mass and mantle is probably connected with the muddy environment in which the animal normally lives. Removal of waste material is not brought about by contraction of the adductor muscles and mantle as it is in *M. ferruginosa*, but the ciliary mechanism is more active and efficient in *Mysella* than it is in *Montacuta*.

Devonia perrieri (Malard)

D. perrieri is commensal with *Leptosynapta inhaerens*. It lives attached to the body about one-third of the distance from the anterior end of the *Leptosynapta*. Only one specimen was found on each, and it was attached by the foot which is flat and probably acts as a sucker when spread out over the surface. The attachment is probably assisted by the spicules in the body wall of the *Leptosynapta*. *Devonia* also crawls over the surface of the *Leptosynapta* using its foot as a creeping sole, but the movements were not extensive and it was never found free in the mud. No byssal threads were observed, although *Devonia* possesses a byssal gland.

D. perrieri is not common. It was collected on the shore below the Marine Hotel, Salcombe, and could only be found at low water during spring tides.

D. perrieri is small. The specimens collected were all about the same size, and the shell measured about 7 × 5 mm., but when fully expanded the same specimens measured as much as 11 × 7 mm. The shell is white and fragile. It appears to be darker in colour in the region of the umbo owing to the colour of the visceral mass being visible through the shell. The shell is rectangular in shape and inequilateral (Fig. 19). The umbo is situated near the posterior end (*u*). There are faint concentric striations on the surface of the shell, but no definite markings. The edge of the shell is entire.

There is a permanent ventral gape between the shell valves, and the foot and mantle normally extend beyond them (Fig. 19, *f*, *m*). The mantle extends in life for a considerable distance beyond the shell in all directions except above the hinge. It is also reflected over the outer surface of the shell for a short distance on all sides except in the region of the hinge (*m.s*).

There are two pallial openings as in *Montacuta* and *Mysella*, but there is fusion between the two mantle lobes to a greater extent. The mantle extends for a considerable distance beyond the shell anteriorly and forms a "hood" over the inhalent opening (Fig. 19, *ho*). There is no permanent siphon, but a temporary siphon is formed by the edges of the mantle coming together above the foot and separating the inhalent from the pedal opening. The free edges of the mantle are turned back round this opening. The portion of the antero-ventral opening corresponding to the pedal opening is small, as the mantle lobes are fused for the posterior two-thirds of the ventral side. This must restrict the movement of the foot to some extent. The exhalent opening is very small. It is situated at the postero-ventral extremity of the mantle. Its position varies with the amount of extension of the mantle, but it is normally some distance beyond the shell. It is a small circular opening which can be closed by contraction of the mantle (Fig. 19, *e*). The mantle lobes are fused dorsally and for the whole of the posterior side except for the exhalent opening.

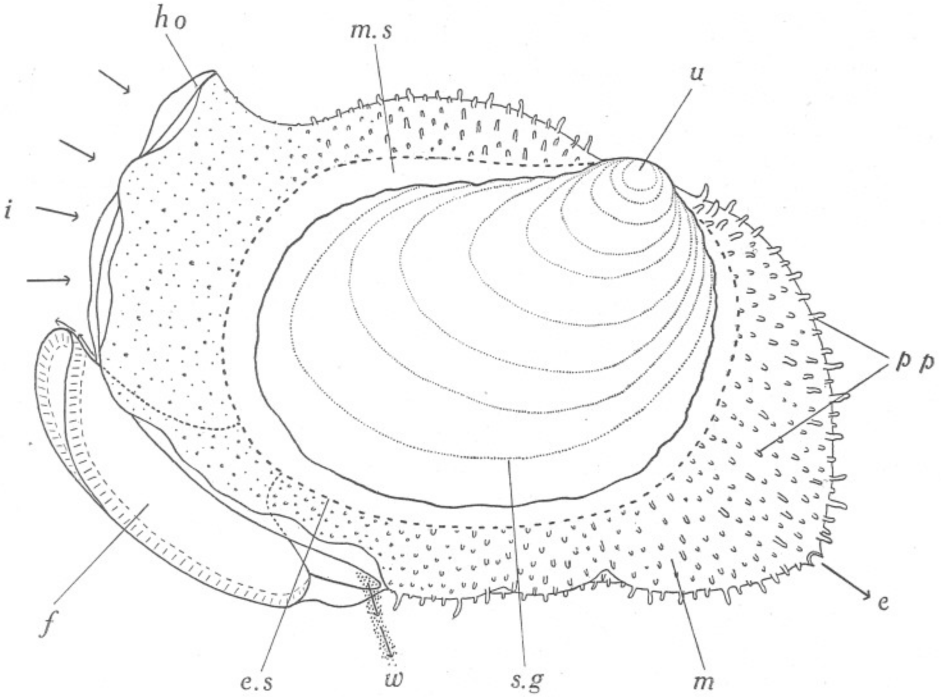


Fig. 19. *Devonia perrieri*. External appearance. × 10. *e*, exhalent current; *e.s*, edge of shell; *f*, foot; *ho*, hood; *i*, inhalent current; *m*, mantle; *m.s*, mantle covering shell; *pp*, papillae; *s.g*, striations showing growth stages; *u*, umbo; *w*, waste.

The surface of the whole of the mantle lobes which extends beyond the shell is covered with papillae (Fig. 19, *pp*). These are irregularly arranged and vary in size. They are largest on the posterior and ventral portions of the shell, and small on the lobes which form the inhalent siphon. There are none on the narrow band of mantle which is reflected over the outer surface of the shell.

The foot is cylindrical in shape near the visceral mass, but it is flattened out into a broad triangular disk anteriorly (Figs. 19, 20, *f*). The shape and movement of the foot are characteristic of this species. The foot is very large and can be greatly extended; the flattened triangular part is spread out over the body surface of the *Leptosynapta* and probably acts as a sucker. When fully extended this flattened part of the foot exceeds the size of the whole animal. The central part of the foot is thick and the gonad extends into it. The edges of the foot are thinner and indented. The indentations fit into the irregularities of the body wall of the *Leptosynapta*. The foot can be turned about in all directions when the animal is moving. It was never seen in life with the foot completely withdrawn between the lobes of the mantle.

A byssal gland is situated in the posterior portion of the foot and opens by a pore on the ventral surface of the anterior portion of the foot, but no byssus was observed in life. The sucker-like action of the foot is probably sufficient for attachment, assisted by the spicules of the *Leptosynapta*. According to Anthony (1916), however, *Devonia* is attached to *Synapta* by byssal threads which leave a scar on the body wall, but none of the *Devonia* personally collected was attached in this way, and did not produce any byssal threads while under observation.

Mantle cavity and ciliary currents

There is a single complete inner demibranch on each side. The ascending lamella is larger than the descending and extends dorsally in a supra-axial extension (Figs. 20, 21, *c*). The axis of the ctenidium is vertical (Fig. 20, *c.a*).

The adductor muscles are small (Figs. 20, 21, *a.a*, *p.a*). The anterior adductor is not only small but is situated at the antero-dorsal edge of the shell, almost on a level with the hinge and cannot be very effective.

Gills. The ciliation of the demibranch is normal (Fig. 20, *c*).

Palps. The labial palps are very small, but the ciliation appeared to be quite normal (Fig. 21, *l.p*).

Visceral mass and foot. There is some ciliation on the surface of the visceral mass, and particles pass from below the umbo in two streams (Fig. 21). One is forwards along the dorsal side towards the palps, where the particles are sorted, most being passed into a rejection current down the anterior border of the visceral mass, only the very finest being passed from the palps into the mouth. Particles also pass in a stream down the posterior border of the visceral mass and forwards along the ventral border to the foot. The ciliation is slight and neither of these currents is strong. They are concerned chiefly with rejection, although there may be some additional feeding from the current passing to the palps.

The ciliation of the foot is active (Figs. 20, 21, *f*). Waste material is passed along the cylindrical part of the foot from the visceral mass towards the tip and out along two definite tracks. One is up the dorsal side of the proximal end of the anterior part of the foot and out below the inhalent stream over the

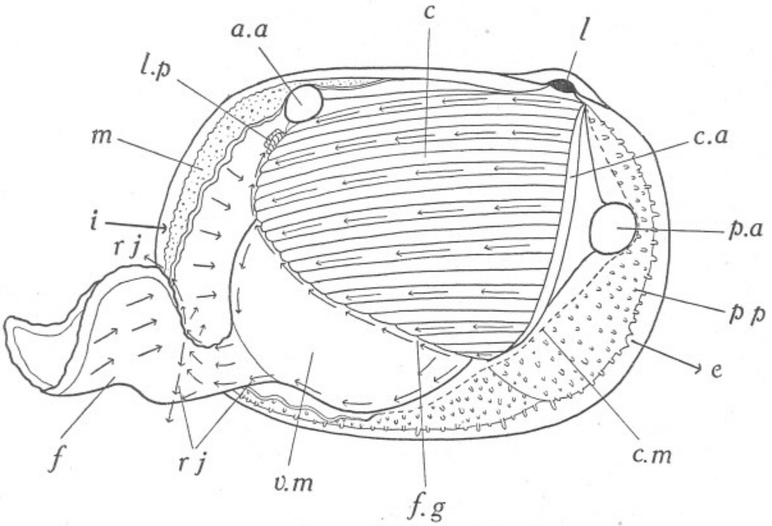


Fig. 20. *D. perrieri* with the left valve and mantle lobe removed to show the ciliary currents in the mantle cavity. × 10. *a.a*, anterior adductor; *c*, ctenidium; *c.a*, axis of ctenidium; *c.m*, cut edge of mantle; *e*, exhalent current; *f*, foot; *f.g*, food groove; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *pp*, papillae; *rj*, rejection current; *v.m*, visceral mass.

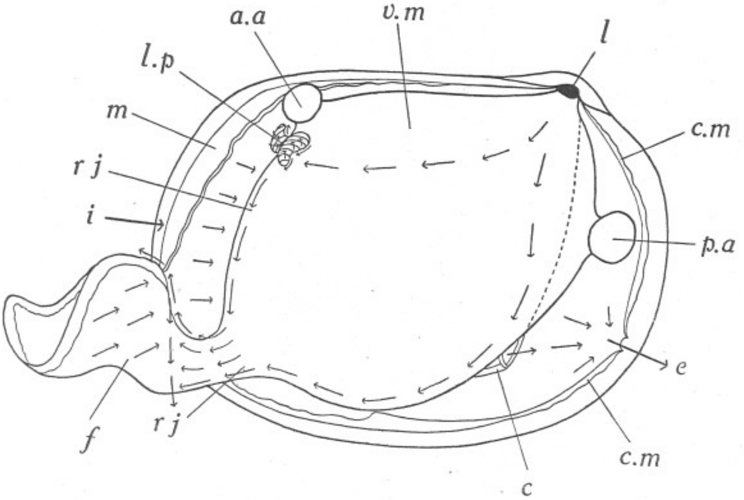


Fig. 21. *D. perrieri* with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 10. *a.a*, anterior adductor; *c*, ctenidium; *c.m*, cut edge of mantle; *e*, exhalent current; *f*, foot; *i*, inhalent current; *l*, ligament; *l.p*, labial palp; *m*, mantle; *p.a*, posterior adductor; *rj*, rejection current; *v.m*, visceral mass.

raised central part of the foot. It is separated from the inhalent current by the mantle edges, which come together and form a temporary siphon above it. The other is a ventrally directed stream in which waste material is passed out behind the foot at the posterior end of the pedal opening (Fig. 19, *w*). The whole of the ventral surface of the anterior portion of the foot is ciliated. Particles are passed from the anterior end back into one of the main streams. The edges of the triangular anterior part of the foot may be turned up so that waste particles are passed on to the dorsal surface of the foot and out in the dorsally directed current, or they may pass along the ventral surface and into the ventral current. Waste material is passed out entangled in mucus.

Mantle. The currents on the mantle were not examined thoroughly as the animals were too much damaged during dissection for complete observations of the ciliary currents, but there appeared to be some ciliation of the mantle surface which assisted in the removal of waste material in the two streams mentioned above. Most of the waste material is probably removed by the mantle currents, as the visceral mass is only slightly ciliated.

Galeomma turtoni Sowerby

G. turtoni is free living. It was collected by dredging in Stoke Bay, east of the Mewstone, Plymouth. Several specimens were found crawling on the surface, in the crevices of the red rock, in a position similar to that of *Kellia suborbicularis*, or in the holes bored in it by Pholadidae, *Saxicava*, etc. It is

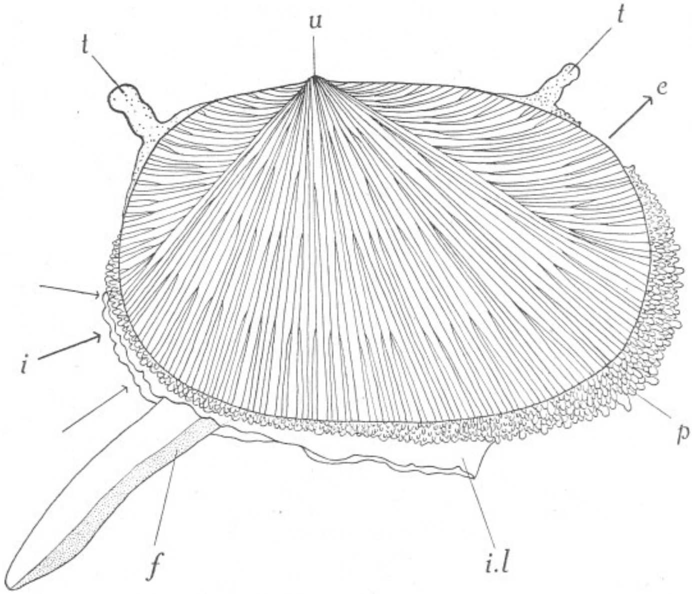


Fig. 22. *Galeomma turtoni*. External appearance, lateral view. × 10. *e*, exhalent current; *f*, foot; *i*, inhalent current; *i.l*, inner mantle lobe; *pp*, papillae; *t*, "tentacle"; *u*, umbo.

capable of active movement, crawling about on its foot, but it is often found attached to the rock by several fine byssus threads. In this case the animal is usually found suspended by the byssus, with the hinge hanging ventrally and the valves spread wide apart. When moving about, however, the hinge line is in the normal position, that is dorsal, with the foot extended ventrally.

The size of the shell of the specimens collected varied from 6·5 × 3·25 to 12 × 5 mm., and the whole animal was slightly larger when the mantle was fully expanded. The shell is pure silvery white in colour and fragile. It is never pigmented, and the whole animal is pure white except for the dark greenish mass of the digestive diverticula. The shell is rectangular in shape (Fig. 22). The surface of the shell is covered with fine raised lines which radiate from the umbo and branch towards the periphery. These raised ridges give a "lattice-work" effect as the shell is practically transparent between them. There are also two lines on either side of the umbo more prominent than the rest, which give the appearance of two lateral wings. The whole shell valve is almost flat, and when seen from the exterior the valves are only slightly convex. The umbo is raised slightly above the hinge line. The hinge is simple, practically straight, with no hinge teeth (Fig. 24, *h*).

There are two pallial openings. The inhalent-pedal opening is larger than it is in *Devonia* and extends for two-thirds of the ventral side (Fig. 22). The exhalent opening is also larger than in *Devonia*, it is situated postero-dorsally, and is in the form of a distinct siphon (Fig. 24, *e*).

The free borders of the mantle are greatly enlarged. The inner mantle fold (Yonge, 1936) is produced laterally and is fused with the corresponding lobe from the opposite side behind the pedal opening (Fig. 23, *f.m*). The fusion of the mantle is complete for the posterior third of the ventral side and for the whole of the posterior end except in the region of the exhalent opening (Fig. 22). Anteriorly there is fusion between the mantle lobes only for a short distance above the inhalent opening. The middle mantle fold has a thickened band round the edge of the shell valves and this bears numerous regularly arranged papillae. There are no papillae on the inner mantle fold which is produced laterally, it is smooth and very contractile. The free edges of the fold which form the borders of the inhalent and pedal openings are "frilled" (Fig. 23); they can be closed down on to the sides of the foot and thus close the inhalent opening temporarily although the foot can never be withdrawn completely within the mantle cavity. There are also two very large papillae, or "tentacles" on the dorsal part of the mantle at either side of the hinge (Figs. 22, 24, *t*). They are capable of considerable extension and are probably sensory in function, as they contract when touched. The outer mantle fold produces the shell. It is normal in function and in position, lying close under the shell.

The foot is large. It is divided into an anterior and posterior part by a deep transverse groove (Figs. 23, 24, *f*). The anterior portion is cylindrical in shape, capable of great extension, and even in the contracted condition it comprises the greater part of the foot. The posterior portion is short and rounded and contains a large byssal gland (Fig. 24, *b.g*).

The anterior tip of the foot is pushed out in a ventral direction when the animal starts to move and it can be twisted and turned about in all directions. It becomes temporarily fixed to the substratum, the posterior part of the foot then appears and the animal moves forwards on the flattened ventral surface of the whole foot, which forms a creeping sole. The posterior part forms the heel; it is compact and does not trail behind. The byssus is produced at the extreme posterior end of the foot, this region being dense white in colour owing to the presence of a large byssal gland. Only two or three threads are produced, these are white in colour and fine, but very strong. The animals were often found suspended from the rock by the byssus with the hinge line downwards, and when kept under observation in a finger bowl the animals were seen to climb up the sides of the bowl moving on the flat ventral surface formed by the foot and the fused mantle folds (Fig. 23). (When in this position

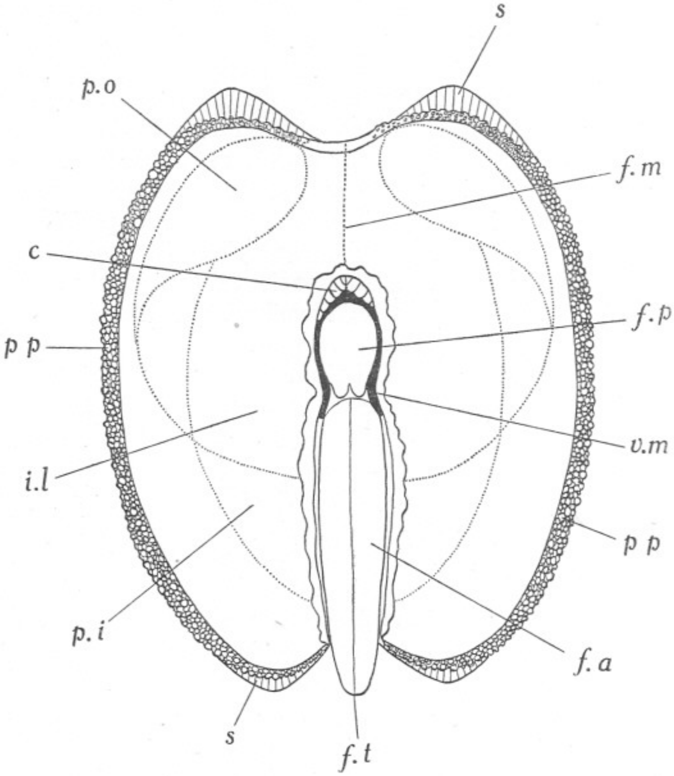


Fig. 23. *G. turtoni*. External appearance, ventral view. × 10. *c*, ctenidium; *f.a*, anterior portion of foot; *f.m*, fusion of mantle; *f.p*, posterior portion of foot; *f.t*, tip of foot; *i.l*, inner mantle lobe; *p.i*, position of inner demibranch; *p.o*, position of outer demibranch; *pp*, papillae; *s*, shell; *v.m*, visceral mass.

there is a wide ventral gape between the shell valves, and the mantle is fully extended.) Two or three byssal threads were then produced from the posterior end of the foot, by which the animal attached itself to the side of the bowl. The animal then hung suspended by these threads with the foot contracted and the flat ventral surface uppermost. The shell valves are drawn together when in this position, but there is always a considerable gape between them. The free edges of the mantle surrounding the inhalent and pedal openings closed down on to the sides of the foot, and the whole mantle contracted.

Mantle cavity and ciliary currents

There are two complete demibranchs on each side; the outer is smaller than the inner and does not extend so far ventrally (Fig. 24). The axis of the ctenidium runs diagonally backwards from below the umbo (Fig. 26, *c.a*).

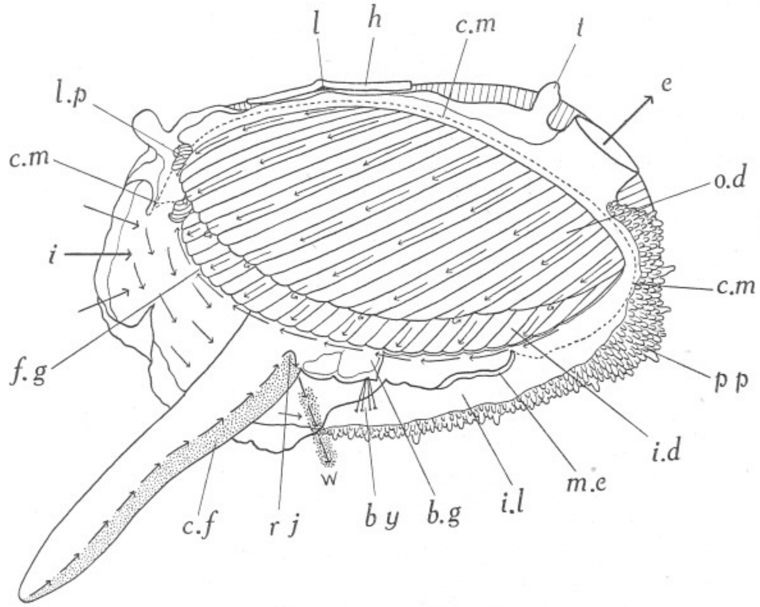


Fig. 24. *G. turtoni*, with the left valve and mantle lobe removed to show the ciliary currents on the visceral mass. × 10. *b.g*, byssal gland; *by*, byssus; *c.f*, ciliated portion of foot; *c.m*, cut edge of mantle; *e*, exhalent current; *f.g*, food groove; *h*, hinge; *i*, inhalent current; *i.d*, inner demibranch; *i.l*, inner mantle lobe; *l*, ligament; *l.p*, labial palp; *m.e*, mantle edge; *o.d*, outer demibranch; *pp*, papillae; *rj*, rejection current; *t*, "tentacle"; *w*, waste.

The adductor muscles are small (Fig. 26, *a.a*, *p.a*). The posterior adductor is larger than the anterior. Both are situated near the dorsal side of the shell and they probably have little function as there is only slight movement of the shell valves.

Gills. The ciliation of the gills is similar to that in *Kellia suborbicularis*. The outer demibranch is normal; particles are passed down both the descending and ascending lamellae and along the food groove at the distal edge towards the labial palps and the mouth. On the outer demibranch, however, particles pass down from the proximal to the distal edge on the outer or ascending lamella, in under the free edge and up the descending lamella towards the axis. There is, therefore, no food groove at the distal edge of the outer demibranch (Fig. 24). There is an orally directed axial current between the demibranchs.

Palps. The labial palps are relatively small, but as *G. turtoni* was the largest species to be examined the ciliary currents on the labial palps were examined in detail (Fig. 25). The ciliation is similar to that of *Kellia* and is quite normal. There appeared to be more movement of particles on the actual lips of the mouth than in *Kellia* (Fig. 25, *li*). Only very fine particles are passed into the mouth, these are revolved slowly and mixed with mucus before being taken in. Large particles are passed off the tips of the palps forming long strings of waste material entangled in mucus.

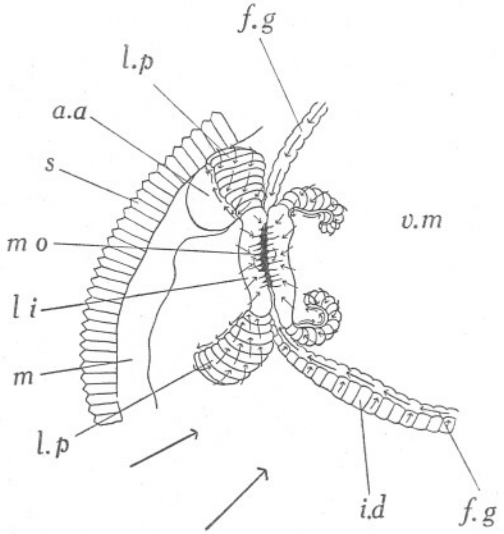


Fig. 25. *G. turtoni*. Ciliary currents on the labial palps. ×25. *a.a*, anterior adductor; *f.g*, food groove; *i.d*, inner demibranch; *li*, lip; *l.p*, labial palp; *m*, mantle; *mo*, mouth; *s*, shell; *v.m*, visceral mass. Large arrows indicate direction of part of main inhalent current.

Visceral mass and foot. The surface of the visceral mass is ciliated. Particles are passed slowly forwards over the whole surface from the posterior border towards the labial palps (Fig. 26). The strongest current is along the line of the axis, where the ascending lamella of the inner demibranch is fused with the visceral mass (*c.a*).

There is also an active ciliation on both the lateral and ventral surfaces of the foot (Fig. 26, *c.f*). Particles are passed up from the tip towards the base and are passed off the foot in a ventral direction at the level of the groove dividing the anterior part of the foot from the posterior (*w*). The chief rejection of waste material occurs here. Strings of mucus with waste material are passed out of the mantle cavity at the posterior end of the pedal opening (Figs. 24, 26, *w*) and left behind in a sticky mass. There is a band of strong cilia up either side of the foot, forming a definite lateral line. The whole of the ventral surface of the foot is also ciliated, but there is no ciliation on the dorsal surface (Figs. 24, 26).

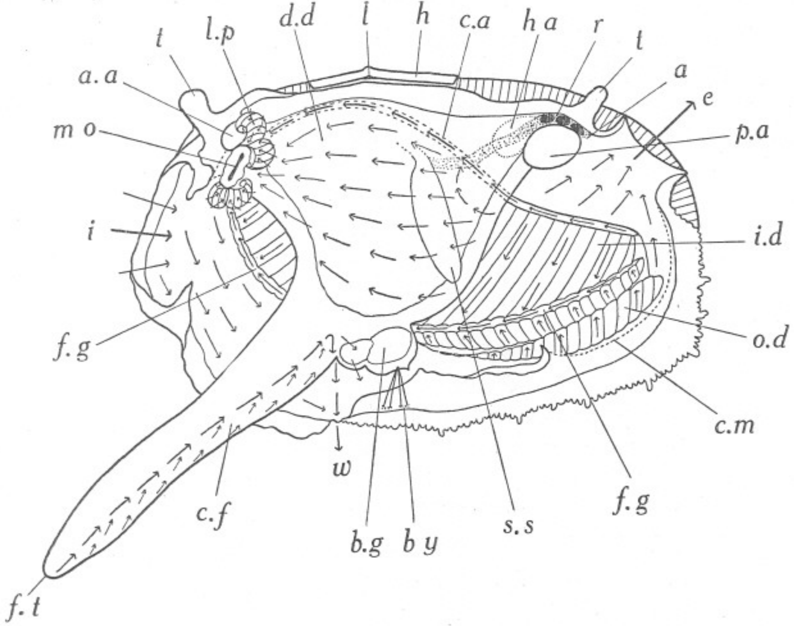


Fig. 26. *G. turtoni*, with the left valve, mantle lobe and gill removed to show the ciliary currents on the visceral mass. × 10. *a*, anus; *a.a*, anterior adductor; *b.g*, byssal gland; *by*, byssus; *c.a*, axis of ctenidium; *c.f*, ciliated portion of foot; *c.m*, cut edge of mantle; *d.d*, digestive diverticula; *e*, exhalent current; *f.g*, food groove; *f.t*, tip of foot; *h*, hinge; *ha*, heart; *i*, inhalent current; *i.d*, inner demibranch; *l*, ligament; *l.p*, labial palp; *mo*, mouth; *o.d*, outer demibranch; *p.a*, posterior adductor; *r*, rectum; *s.s*, style sac; *t*, "tentacle"; *w*, waste.

Mantle. There was apparently little ciliation on the actual surface of the mantle, but it was difficult to see because the mantle contracts at once when touched, and remains contracted when the visceral mass is removed. Also, the inner fold of the mantle obscures the rest of the inner surface of the mantle lobe, so that it cannot be seen even when partially dissected. The only currents observed were caused by ciliary action on the ctenidia and not by cilia on the mantle. No definite bands of cilia could be seen by transmitted light as in *Montacuta substriata* and *Mysella bidentata*, but the removal of waste is helped by sudden and irregular contractions of the adductors and mantle, by which water carrying waste material is shot out through the pedal and inhalent openings. In this it resembles *Kellia suborbicularis*, but in this case the majority of waste material passes out through the pedal, and not the inhalent opening, although some passes out of the anterior end of the opening which corresponds to the inhalent opening. The lack of ciliation of the mantle is probably correlated with the sudden violent movements which remove waste material, instead of the steady stream caused by ciliary action as seen in *Mysella bidentata*.

DISCUSSION

The British fauna contains representatives of the families Erycinidae, Montacutidae and Galeommatidae, which are of especial interest because they exhibit various stages in the progressive adaptation from the free-living condition (e.g. *Kellia*) to extreme modification for a commensal mode of life (e.g. *Devonia*) which is characteristic of the order Leptonacea. These modifications involve (1) reduction in the shell, (2) modification of the foot as a means of creeping, (3) change in direction of the flow of water through the mantle cavity, (4) change in the site and manner of expulsion of waste material from the mantle cavity. With all of these this paper is concerned, though especially with the last two. They also involve (5) incubation of the larvae to a relatively advanced state of development within the mantle cavity.

Kellia, *Lasaea*, *Montacuta*, and *Mysella* all have external shells and well-developed adductor muscles, and although the siphon, foot and mantle border may normally extend beyond the shell valves they can be withdrawn and the shell valves closed. There is, however, a reduction of the shell in *Galeomma* with an accompanying loss of hinge teeth and poor development of adductor muscles and also a permanent gape between the shell valves; the mantle and foot extend beyond them and cannot be withdrawn. Of the British species, the greatest reduction of the shell occurs in *Devonia*, in which not only is the shell reduced in size, but it is partly covered by the mantle. There is a ventral gape and the foot, siphons and mantle permanently extend for a considerable distance beyond the shell valves. The adductors are relatively smaller than in *Galeomma* and can have little function. The shells of *Galeomma* and *Devonia* are fragile as well as reduced in size. An extreme case is found in *Phlyctaenachlamys lysiosquillina*, an Australian species of the Galeommatidae, in which the shell is even more reduced in size and completely enclosed in the mantle (Leyborne Popham, 1939).

All members of this order have developed a creeping habit and the foot is modified to form an efficient creeping organ. *Lasaea* and *Mysella* especially are capable of rapid movement on the flattened ventral surface of the foot. The foot is also used as a means of attachment. Byssal glands are present in all the species examined, and byssus threads were observed in *Kellia*, *Lasaea*, *Montacuta substriata*, *Galeomma*, and in young specimens of *M. ferruginosa*. None was seen in *Mysella* which is not attached to its "host", nor in *Devonia*, but in this case the flattened foot probably acts as a sucker and serves as a means of attachment, as well as acting as a creeping organ.

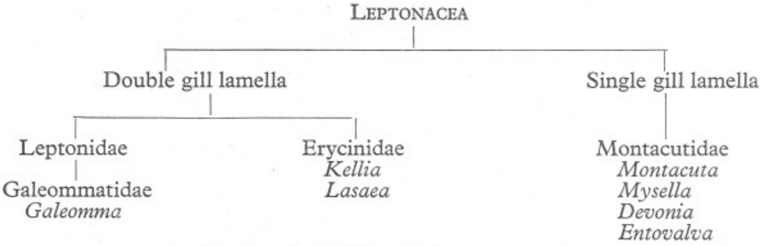
Throughout this group the respiratory and feeding current passes through the mantle cavity from anterior to posterior, i.e. the inhalent opening is *not* posterior as it is in the remainder of the Eulamellibranchia. This represents a reversion to the primitive molluscan condition which is still retained in the Loricata (Yonge, 1939 *a*) and in the families Nuculidae and Solenomyidae of the Protobranchia though not in the Nuculanidae (Yonge, 1939 *b*). This reversion may reasonably be associated with the loss of the burrowing habit in this order and with modification of the foot which has also re-acquired the properties of that of the primitive Mollusca.

With the exception of *Kellia*, the least specialized of the genera, where it is expelled by way of the inhalent siphon as in the great majority of the other Eulamellibranchia, waste material is removed ventrally from the mantle cavity. In *Devonia* it is passed out both ventrally and also below the inhalent current at the anterior end. This is probably due to the fact that *Devonia* normally lives attached to *Leptosynapta* and, when the foot is contracted, the free portion of the pedal opening behind the foot through which the waste matter is normally removed is very small, or closed completely when the mantle edges are in contact with the body-wall of the "host".

As has already been observed, the method of removal of waste through the ventral opening varies. This is correlated with the reduction of the shell and the development of a considerable amount of muscle in the mantle. It is seen in an advanced stage in *Phlyctaenachlamys lysiosquillina*, in which not only is waste matter removed but movement is assisted by forcing water out from the mantle cavity by sudden violent contractions of the mantle (Leyborne Popham, 1939). In *Lasaea* waste material is removed by ciliary action on the mantle aided by muscular contractions of the mantle border. In *Montacuta substriata* it is due partly to ciliary action of the foot, visceral mass and mantle, but chiefly to sudden contractions of the adductor muscles which are well developed in this species. In *M. ferruginosa* there is no ciliation on the visceral mass and only slightly on the foot. The surface of the mantle, however, is strongly ciliated, and waste material is removed both by this ciliary action and by sudden violent contractions of the adductors and the whole of the free part of the mantle lobes. This muscular activity is absent in *Mysella*, in which the mantle cavity is cleansed entirely by ciliary action. The visceral mass, foot and mantle are all strongly ciliated and the mechanism is efficient. In *Devonia* the cilia on the mantle appear to be the chief means of cleansing the mantle cavity, but *Galeomma* relies chiefly on muscular activity, assisted by ciliary action on the foot and visceral mass. As is stated above, this variation in the cleansing mechanism of the mantle cavity is also correlated with the differences in environment. Some species, notably *Mysella bidentata* which lives in conditions where there is a considerable amount of sediment in the water, have particularly strong ciliary action on the surface of the visceral mass, and these cilia, assisted by the comparatively large palps, can sort out large quantities of material quickly and efficiently. In *Montacuta substriata* which occurs in comparatively clear water, the ciliary action is weaker and the removal of waste material is assisted by muscular contractions which occur at irregular intervals depending on the amount of sediment present. These contractions probably occur infrequently in life except when there is an abnormal amount of sediment in the water.

In some members of this order the larvae are incubated in the mantle cavity to a relatively advanced state of development. Of the species examined *Lasaea* was found to have larvae with complete bivalve shells, resembling the adult but about one-tenth the size, in the mantle cavity. The larvae of *Kellia* are liberated at an earlier stage (Lebour, 1938), and although they possess bivalve shells they are not so similar to the adult form as those of *Lasaea*. The larvae of *Galeomma* are much less advanced than those of *Kellia* and have no shells when liberated. The period of incubation must therefore be comparatively short. *Montacuta ferruginosa* was found with shelled larvae in the mantle cavity and their development was observed up to a relatively late stage. The larvae were, however, removed from the mantle cavity for observation and the stage at which they are normally liberated was therefore not observed. No larvae were found in the mantle cavities in *M. substriata*, *Mysella* or *Devonia*, although they are reported to be hermaphrodite with incubation of the larvae in the mantle cavity (Pelseneer, 1911).

A detailed account of the structure and function of the ctenidia has been given by Ridewood (1903) and Atkins (1937), and it has been pointed out by Pelseneer (1911) that, although all the species examined are included in the order Leptonacea (the Lucinacea according to his classification), *Kellia* and *Galeomma* have ctenidia composed of two complete demibranchs while *Montacuta*, *Mysella* and *Devonia* have only one demibranch to each ctenidium. Pelseneer therefore divides the order into two groups, the Leptonidae, Galeommatidae and Erycinidae with two demibranchs and the Montacutidae with a single demibranch. This arrangement is shown in the following table.



(Table adapted from Pelseneer, 1911)

In every case the single demibranch is the inner, the outer having completely disappeared (Atkins, 1937; Purchon, 1939).

Lasaea is an interesting intermediate stage. The inner demibranch is normal and complete, but the outer demibranch is represented by a short descending lamella only. This is about one-third the length of the inner demibranch.

Taking *Kellia* as an example of the primitive condition, this order shows progressive loss of the outer demibranch, *Lasaea* being the "half-way stage". The loss of one demibranch is the specialized condition found only in the Lucinidae, Montacutidae and Teredinidae (Atkins, 1937). In the Lucinidae, a related order included in the sub-class Teleodesmacea (Dall, 1895) and the Teredinidae, however, it is the outer demibranch which remains (Purchon, 1939).

The systematic position of the species included in the Leptonacea and the reasons for their inclusion have already been reviewed (Leyborne Popham, 1939).

The members of the Leptonacea investigated form part of a series showing the development of commensalism in this order, which has already been described. The descriptions of the habits and of the general anatomy of the mantle cavity included in this paper reveal the modifications which have occurred in relation to the specialized mode of life of those which are commensals.

SUMMARY

The habitat, external appearance and habits of members of the Erycinidae, Montacutidae and Galeommatidae, three families included in the order Leptonacea, have been investigated and are described.

The ciliary currents of the gills, palps, visceral mass, foot and mantle are described in detail.

There is some reduction in the shell in this order. In *Kellia*, *Lasaea*, *Montacuta* and *Mysella* the shell is external and the adductor muscles are well developed. In *Galeomma* the shell and adductors are reduced, and in *Devonia* the shell is also partially covered by the mantle.

The foot is modified, and all members of this order progress on the flattened ventral surface of the foot which forms a creeping sole. The burrowing habit is lost.

In all species the inhalent current enters the mantle cavity at the anterior end and the exhalent current leaves it posteriorly. There is therefore a direct current through the mantle cavity.

In all except *Kellia* waste material is removed ventrally through the pedal opening. In *Kellia* it is shot out through the inhalent opening. Some waste material is also removed anteriorly, but below the inhalent current, in *Devonia*.

Waste material is removed from the mantle cavity either by ciliary or muscular activity and usually by the combined action of both. In *Kellia*, *Montacuta substriata* and *Galeomma* it is chiefly by muscular action, in *Lasaea* and *Devonia* it is chiefly ciliary action, assisted by some muscular contractions, while in *Mysella* it is entirely due to ciliary action, and in *Montacuta ferruginosa* muscular and ciliary action appear to play an equal part.

The efficiency of the cleansing mechanism and the speed at which the mantle cavity can be cleared varies with the environment, depending on the amount of sediment normally in the water.

Mysella, which occurs in a muddy environment, has a strongly ciliated visceral mass and mantle and a current, in addition to the normal rejection currents, which passes material forwards along the dorsal region of the visceral mass to the labial palps. These are comparatively larger than in the other species investigated. This is an additional sorting mechanism, and large quantities of material can be dealt with.

The ctenidia of *Kellia* and *Galeomma* are complete, each consisting of two demibranchs, but in *Montacuta*, *Mysella* and *Devonia* the outer demibranch is absent. *Lasaea* represents an intermediate stage with a complete inner demibranch and a short descending lamella of the outer demibranch only.

The degree of specialization varies with the degree of commensalism. *Kellia*, which is free-living, is the least specialized member of the group, and *Devonia*, the most advanced commensal, is the most specialized.

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SAND AND MUD COMMUNITIES IN THE DOVEY ESTUARY

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(Text-figs. 1–3)

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INTRODUCTION

This paper presents results of an ecological study towards high-tide level near the mouth of the Dovey estuary, carried out in 1925–6. The area was treated as an extension of the sea floor, the only comparable work at that time being submarine. Petersen (1918) showed that on the bed of shallow seas the fauna could be grouped into "animal communities", whose constitution was determined by depth, distance from shore, shelter and salinity. Analysed with regard to distance from high-water mark, and degree of shelter, the fauna of this part of the estuary shows Petersen's *Macoma* community over most of the area, with a *Corophium* community at high tide in the more sheltered part. Davis (1925), in the North Sea, substituted "soil associations" as an alternative ecological unit, a certain grade of soil carrying its typical fauna wherever it might be found. The two groupings already found in the Dovey estuary clearly emerged as soil associations, after adoption of a reliable method for analysis of fine-grade soils. Up to the present, oceanographers have used sieves or elutriation for soil analysis. These methods are unsatisfactory for examinations of estuarine soils, with their large proportion of fine material.

Not only do they fail to subdivide the finer grades of soil, but they are inaccurate in measuring the lower range they do register. Variety in methods of soil analysis, and lack of uniformity in fixing soil grades, make present data on estuarine soils of little value for comparative purposes. Investigation of the current agricultural method of soil analysis, devised by Robinson, proved it eminently suitable, in that it offers infinite possibilities for accurate subdivision of fine grade soils, and a simple and practically foolproof technique. The minimum particle diameter measured was 0·002 mm. It is suggested the method might profitably be employed for estuarine work in general.

Some suggestions are put forward regarding possible factors affecting the distribution of *Corophium volutator* and of *Macoma balthica*.

The fauna have been named in accordance with the Plymouth Fauna List (Marine Biological Association, 1931) with the exception of *Corophium arenarium* n.sp. Crawford, 1937, *Journ. Mar. Biol. Assoc.*, Vol. XXI, p. 598.

I wish to express my gratitude to Professor R. D. Laurie, M.A. for helpful advice and criticism during the course of this investigation; and to Dr E. E. Watkin for his kindness in helping me to bring the work up to date for publication. I should also like to thank Miss Blodwen Williams for her unfailingly cheerful help in obtaining the samples.

Description of the Area Investigated

Fig. 1 shows a map of the mouth of the sandy Dovey estuary, narrowed to a "bottle-neck" by sand dunes and Aberdovey Bar. Comparative shelter from west winds and tide is afforded by the dunes, and the tide does not rise in the estuary till it has been running at least an hour outside the bar. The area investigated, lying within the effective shelter of the dunes, is indicated by diagonal lines on the map. Its landward limit is a dyke, protecting the reclaimed land behind. On its western side it ends on the bank of the River Leri, flowing seawards from an artificial channel through Borth Bog.

Fig. 2 shows greater detail of this area and the locations of samples. It was made from field data obtained by paced measurements and a pocket compass. Over soft or difficult ground an overestimate of distance may be expected, and the experimental error will be variable. With one exception (sample 26) investigation was limited westward by the top of the Leri bank, but this line must not be read as low-water mark. Two major gullies traverse the area, and at low tide the streamlet is some distance away from the discernible edge of the gully. Samples were in some cases taken within this edge, as shown on the map.

The slope of the ground is imperceptible except at the gullies, becoming greater at the cockle bed at the northern limit of the area mapped in Fig. 2. Except over this region the water movement is normally gentle, lines of footmarks remaining obvious for over a week. In November 1925 the northern

Macoma-Bathyporeia patch was on a bank of coarser, very loose sand, above the level of samples to the east. By the following February this bank had disappeared, indicating considerable water movement.

The lower-lying gullies make comparative distances from high-water mark not directly comparable with comparative periods of emersion. High water of spring tides is well up the dyke, but high water of neap tides merely swells gully I, leaving dry soil on each side. In spite of this, however, the exposed soil does not, except in the south-west corner, become very dry in the interval. Its continual wetness is probably due to land drainage along the slope of the clay beneath, finally collecting up into the gullies, so that, unlike high-water levels in many estuaries, this part may be expected to show considerable salinity variation with the state of the tide. The sand to the north, however, is dry compared with that nearer high-water mark to the east. Other points of possible importance are the introduction of bog water by the Leri, and of sewage from Aberdovey, which, according to Durlacher (1914) ponds within the estuary as a result of the presence of the sand dunes.

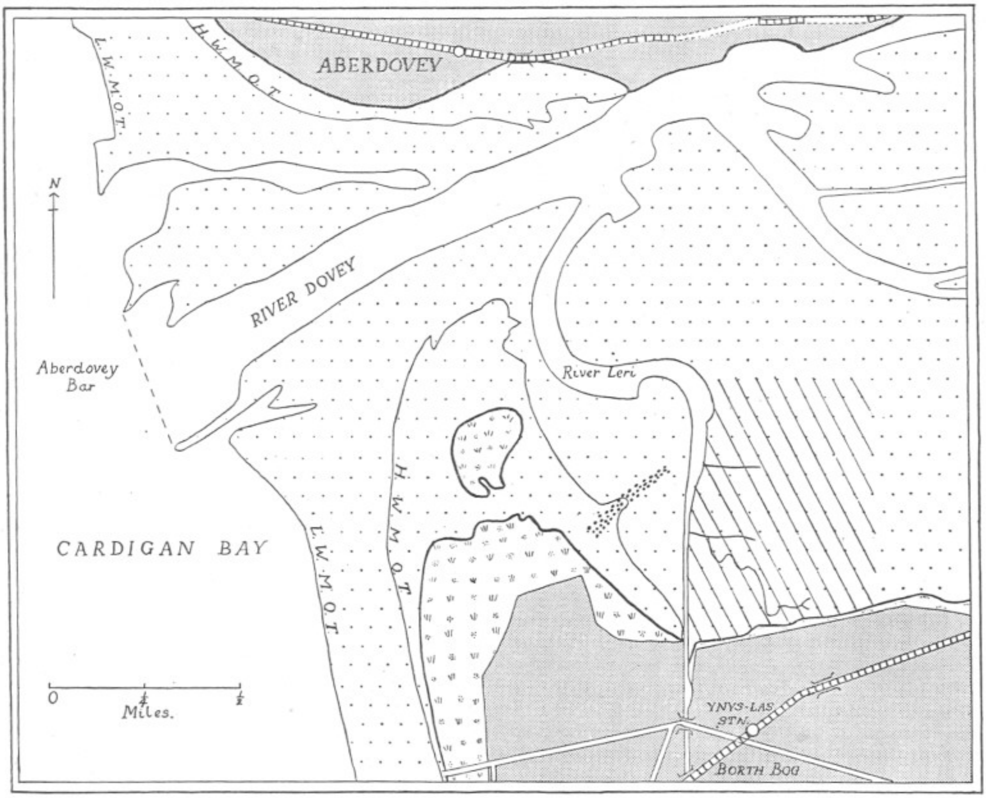

Fig. 1. Map of the mouth of the Dovey estuary. The area investigated (*ca.* $\frac{3}{4} \times \frac{1}{2}$ miles) is indicated by diagonal lines.

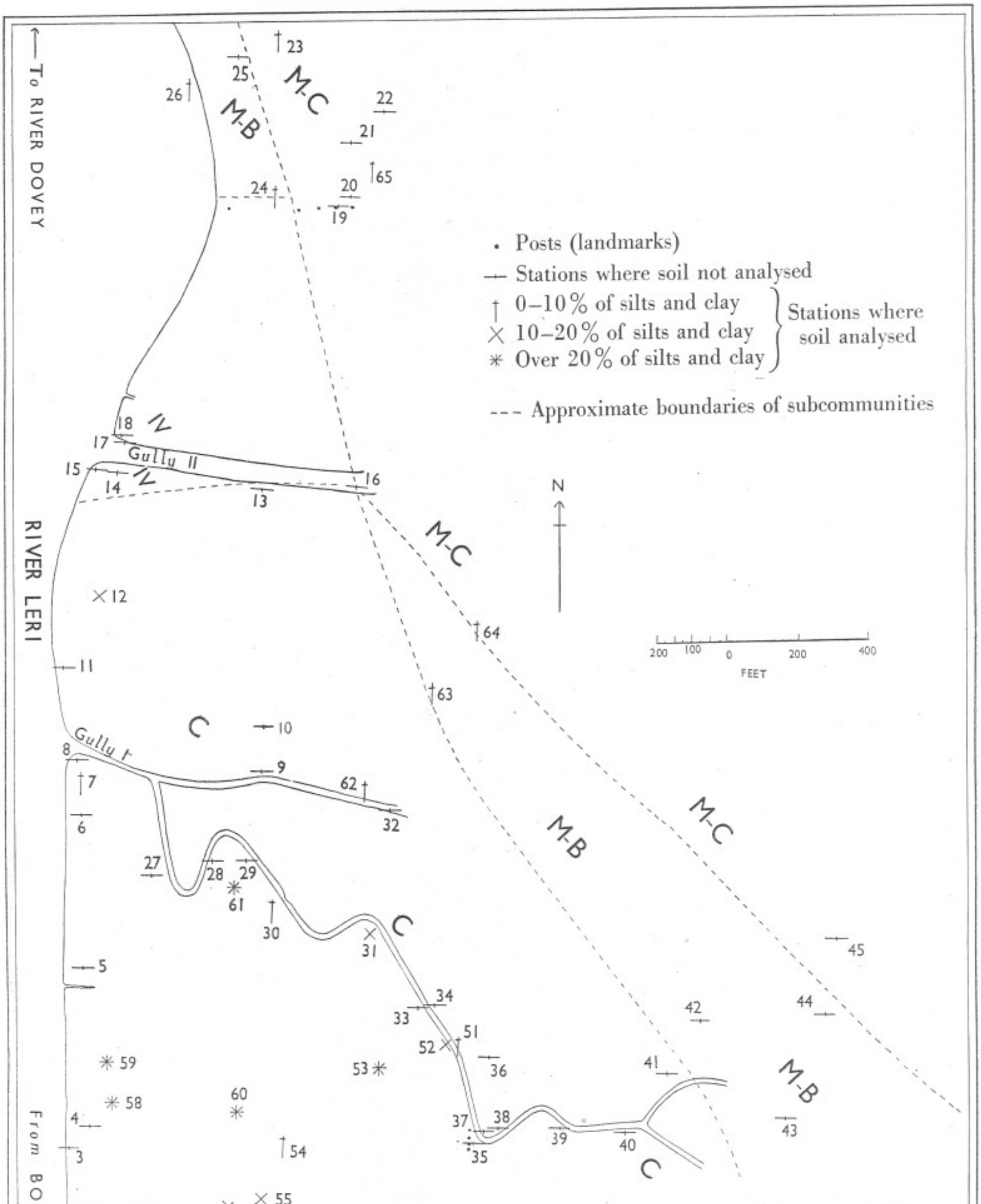

Fig. 2. Map of the eastern bank of the Leri in 1925. The Leri and the gullies are outlined as the top of the bank or, where this gives place to a gradual slope, to a delimiting line of soil along it. *C* = *Corophium* community; *M-B* = *Macoma-Bathyporeia* subcommunity; *M-C* = *Macoma-Cardium* subcommunity. Location of sample lies on intersection of lines.

The samples cover three easily distinguished types of soil. The south-west corner forms a patch of firm, sticky, grey mud with a bad skid surface. In an arc around this is softer, darker mud, finally giving way to the sand covering most of the estuary.

Within this general division into harder and softer mud, and sand, there is much local variation, both in nature of soil and degree of wetness, and the fauna appear to show a variation with both these factors.

Over most of the area the ground is bare. Scattered plants of *Salicornea Europea* were present in the south-west corner of sticky mud, but *Enteromorpha* formed a more obvious feature, and reappeared patchily on the northern cockle bed. *Fucus serratus* also occurred at the base of the posts in this region.

APPARATUS AND METHOD

Collection of Samples

For faunal counts a layer of soil 1 ft. sq. × 1 in. deep was cut out with a Beach Sampler, described below; and washed through a sieve of 1 mm. mesh, separating macrofauna and large fragments from microfauna and soil particles, which were neglected. Previous work in the area seemed to indicate that the surface inch contained a representative infauna. Samples for soil analysis were removed from the surface inch just outside the square, and bear the same reference number as the corresponding faunal sample.

To cut out the layer, two superimposed metal rings, each 1 in. deep and fitting over each other by pin and socket, were rammed into the soil, cutting edge downwards, until flush with the surface. A square metal frame of side 1 ft. and with 1 in. height marked was forced inside this ring to the depth of 1 in. The top ring was next removed and, after sufficient space had been gained by shovelling away sand from outside the square, a metal plate, also with a cutting edge, was forced horizontally between the square and the top of the second ring, an accurate square foot sample of the surface soil being thus obtained.

Over most of the area this method gave perfectly satisfactory sampling. Samples 20–23 inclusive, however, give a lower estimate of cockles than is representative for the area. Here the cockles were numerous enough to give the impression of ground closely and finely cobbled, with a thin overlay of sand. It was impossible to make any impression on this with a spade in most parts, and samples had therefore to be taken from patches relatively free of cockles. Even here, however, there was a maximum sampling of 149 per sq. ft. (= *ca.* 1580 per $m.^2$) as compared with 100–200 per $m.^2$ given as typical of a good ground by Spooner & Moore (1940, p. 317).

Mechanical Analysis of Soil

Four possible means of measuring soil particle size are: (1) by graduated sieves (Allen, 1899), (2) by elutriation, (3) by fractional sedimentation; (4) by rate of subsidence through a standing column of dispersion.

(i) *Analysis by sieving* is not suitable for fine soils. A mesh of diameter less than 0·2 mm. soon becomes inaccurate through wear; while if the sample is sieved dry, clay tends to fly off, and if wet, tends to "puddle" and clog the mesh.

(ii) *Analysis by elutriation.* Borley (1923) devised a three-chambered elutriator, once recognized as the standard apparatus for marine soils, which separated two grades of size—0·5 to 0·1 mm. diameter and 0·1 to 0·05 mm. diameter, finer soil being swept out and estimated by loss. Fraser (1932) used a four-chambered elutriator measuring a minimum particle diameter of 0·02 mm. Pirrie *et al.* (1932) varied the rate of current through a single tube elutriator, sweeping out successively coarser particles with increasing current, and recognizing a minimum diameter of 0·1 mm. only. These methods, again, do not allow for subdivision of the finer fraction of a soil, possibly of vast importance to an estuarine fauna. Borley's apparatus, at least, was also found to give inaccurate results when the sample contained a large percentage of fine material. An initial rate of flow appropriate for supporting the various grades in their respective chambers was found to increase to the point of serious error, with decreasing resistance of the sample as a growing fraction was removed by the current. An actual example may make this clear:

(1) Initial rate of flow = 187 c.c. per 100 sec.
(2) Immediately after introduction of sample: rate = 110 c.c. per 100 sec.
(3) Just before removal of sample: rate = 150 c.c. per 100 sec.
(4) After removal of sample: rate = 190 c.c. per 100 sec.

Thus it would be necessary, *for each sample*, to find by experiment the initial flow giving 110 c.c. per 100 sec. on introduction of sample; and then to adjust the flow during sampling to maintain this rate. Accuracy of analysis would be uncertain under these conditions.

(iii) *Fractional sedimentation.* Rees (1940) has tried this method, and, like myself, found it unsatisfactory. Soil grades are not cleanly separated.

(iv) *Rate of subsidence through a standing column.* The only method found suitable and reliable for analysis of fine-grade soils was that of Robinson for agricultural soils (1922). The soil analyses given in this paper were obtained by the use of Robinson's 1922 method in which the following soil grades were recognized:

(1) Separated by sieving through sieves of standard mesh:

Fine gravel	2·5 to 1·5 mm. and any coarser grades.

(2) Separated by sieving after treatment by hydrochloric acid:

Very coarse sand	1·5 to 1·0 mm.
Coarse sand	1·0 to 0·5 mm.
Medium sand	0·5 to 0·2 mm.

(3) Separated by subsidence in an ammoniacal dispersion after thorough shaking:

Fine sand	0·2 to 0·04 mm.
Silt	0·04 to 0·01 mm.
Fine silt	0·01 to 0·002 mm.
Clay	Less than 0·002 mm.

Hygroscopic moisture was calculated in a sample of the air-dried soil and "organic matter" by loss on ignition in a muffle furnace.

Since 1922 the details of Robinson's method have been somewhat revised by the International Society of Soil Science and the Chemistry Committee of the Agricultural Educational Association. Full details of the method, as at present used for the analysis of agricultural soils, are given in an appendix to Vol. V (1928) of *Agricultural Progress*, and a further discussion of the method in its application to the many varying types of soil throughout the world is given in "The dispersion of soils in mechanical analysis", *Technical Communication* No. 26 of the Imperial Bureau of Soil Science, London, 1933.

The modifications introduced have resulted in the recognition of somewhat different soil grades which may be summarized as follows:

(1) Separated by sieving through a standard round-hole 2 mm. mesh sieve:

Stones and fine gravel, particles greater than 2 mm.

(2) Separated by sieving through a standard square aperture 0·2 mm. mesh sieve after treatment with hydrogen peroxide to remove the organic matter and hydrochloric acid to remove the carbonates:

Coarse sand, 2·0 to 0·2 mm.

(3) Separated by sedimentation and by subsidence in an ammoniacal dispersion after thorough shaking:

Fine sand by sedimentation, 0·2 to 0·02 mm.
Silt by subsidence (pipette sampling), 0·02 to 0·002 mm.
Clay by subsidence (pipette sampling), less than 0·002 mm.

In addition, (*a*) the moisture content of the air-dried soil, (*b*) the carbonates expressed as calcium carbonate, (*c*) the loss by solution in the hydrogen peroxide, hydrochloric acid treatment (mainly the sesquioxides of aluminium and iron and the silica), (*d*) and the loss on ignition, which includes the organic matter and the combined water in the soil colloids, are estimated. These, together with the particles, are expressed as percentages of the air-dry soil.

I am of the opinion that the adoption of Robinson's method to marine and estuarine soils, with possibly slight modifications due to the "salt content" of such soils, and the lack of importance of the hygroscopic moisture of truly submarine soils, will prove of value to the marine biologist.

In considering the refinements of the agricultural method for application to marine soils, however, it is well to bear in mind the different object of the agriculturist. He is concerned with improving his soil to support a more profitable flora, and seeks to know its ultimate constitution. Improvement of the soil—except by cutting *Zostera*, for example—is outside the scope of the marine biologist. He is only concerned with untouched soil in its effect on a fauna. For example, we may imagine an estuarine soil of apparent silt. The agriculturist, after 24 hr. shaking and chemical treatment, might record much of this as finer grades. If it never appeared in this guise in the area concerned, the marine biologist might be wiser to neglect this drastic treatment and record it as silt, for correlation with its effective result in supporting a fauna adapted to conditions associated with soil particles of this average size. Hence additions to the agricultural methods since 1922 should be adopted only after investigation.

DETAILED RESULTS

The location of samples (1 ft. sq. × 1 in. deep) is shown in Fig. 2, and the results are given in three series, viz.:

(1) Table I and samples 1–26, Fig. 2, show faunal change with distance from high-tide mark.

(2) Table II and samples 27–48, Fig. 2, show faunal change with decreasing shelter.

(3) Table VI and samples 49–65 (with some of the previous ones) show faunal change with increasing fineness of soil.

In addition, weights of certain species are shown in Table III; Table IV gives detailed results of soil analysis; Table VII and Chart I demonstrate more clearly the presence of two soil associations.

Faunal Change with Distance from High-Tide Mark

Twenty-six samples were taken from high tide three-quarters of a mile towards low tide, not in a straight line, roughly along the banks of the Leri. Other variable factors in this series will be increased immersion, not progressive for every station, and some decrease in shelter.

The infauna falls into two well-defined groups, samples 1–13 lying across a *Corophium* ground, of which the typical animals are grouped together in section I, Table I; and 19–23 entering a *Macoma* belt, with *Cardium edule* as the subdominant form, together with *Corophium arenarium*, and whose typical animals are grouped in section II, Table I. This section is considered to be an intertidal phase of Petersen's "*Macoma* community", including as it does *Macoma balthica*, *Cardium edule*, *Arenicola marina* (small forms only were obtained in the surface inch examined, but surface casts were numerous) and, as epifauna on the posts, three other species which occur "practically speaking only within the area of the *Macoma* community" (Petersen, 1918), viz. *Mytilus edulis* and dense clusters of *Littorina littorea* at the base, and *Balanus balanoides* higher up. During the investigation no distinction was made between the two species of *Corophium*, as *C. arenarium* had not then been described. The two species, typical of mud and of sand respectively, do not commonly occur together in one sample, and on this basis, on the authority

TABLE I. FAUNAL CHANGE WITH DISTANCE FROM HIGH-TIDE MARK

Period of sampling—September and October (samples 9, 10, 13 and 16 taken in December)

Sample no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Section I																										
Corophium volutator (Pallas)	—	445	24	191	44	2	844	455	82	*21	20	29	*1193	1	5	*24	?2	?1	—	—	—	—	—	—	—	—
Nereis diversicolor Müller	—	9	—	3	2	3	4	1	1	—	—	—	4	—	—	3	—	—	—	—	3	3	—	—	—	—
Oligochaeta (pitted)	—	15	—	1	24	1	16	—	1	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—
Oligochaeta (smooth)	—	136	20	4	25	85	130	36	14	17	19	25	308	1	—	11	—	—	1	—	—	2	—	1	14	—
Nematoda	—	1062	—	35	98	114	479	97	48	168	57	35	649	—	—	4	—	—	67	292	9	113	2	—	14	—
Leptidae larva (Diptera)	—	—	8	6	6	6	—	2	11	2	8	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Heterocerus obsoletus (Coleoptera)	—	—	44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hydrobia ulvae Pennant	—	15	—	10	1141	403	11	407	×	×	206	180	×	15	2	×	2	3	38	45	905	1383	1038	29	5	6
Section II																										
Macoma balthica (Linnaeus)	—	1	—	1	11	2	6	2	1	2	1	—	16	11	7	15	19	8	401	195	369	416	657	58	4	—
Cardium edule Linnaeus	—	—	—	—	—	—	—	—	4	7	3	3	12	—	—	21	—	—	15	36	79	149	38	52	4	—
Arenicola marina Linnaeus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	1	—	1	—
Corophium arenarium Crawford	—	—	—	—	—	—	—	—	—	*—	—	*—	—	—	—	*—	?—	?—	21	62	3	10	6	3	—	—
Pygospio elegans Claparède	—	—	—	—	—	52	4	5	2	7	53	125	6	3	—	4	7	—	67	43	2	86	—	—	6	—
Eulalia sp.	—	—	—	—	—	4	1	—	6	—	—	—	7	—	—	—	—	—	1	2	2	33	9	—	6	—
Scoloplos armiger (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	2	2	1	80	32	3	15	9	—	—	—
Retusa alba (Kenmacher)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	5	7	4	2	—	—	—
Scrobicularia plana (da Costa)	—	—	—	—	—	—	—	—	—	—	—	1	2	—	1	—	—	—	—	3	39	66	—	—	—	—
Tellina tenuis da Costa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Praunus flexuosus (Müller)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Crangon vulgaris Linnaeus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Carcinus maenas (Pennant)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	4	2	—	—	—
Section III																										
Bathyporeia pilosa Lindström	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	42	18	14
Ophelia limacina (Rathke)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Nerine sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
Eurydice pulchra Leach	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	5	2	—	—	—	—	—	4	17
Section IV																										
Glycera convoluta Keferstein	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	—	7	—	—	1	—	—	—	—	—	—
Spio filicornis Fabricius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	—	30	—	—	—	—	—	—	—	—	—
Nephthys sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
Sphaeroma serratum (Fabricius)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—

* Probably a mixture of *C. volutator* and *C. arenarium*.
? Possibly *C. arenarium* instead, or in part (see Table III and text).

TABLE II. FAUNAL CHANGE WITH DECREASING SHELTER

Period of sampling—November and December

Sample no. ...	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Corophium volutator	5	81	142	14	28	39	855	316	84	409	287	2	31	34	127	1	—	—	—	—	—	—
Nereis diversicolor	2	—	—	3	—	—	1	—	—	—	—	—	—	2	—	—	2	—	—	—	—	—
Oligochaeta (pitted)	5	—	—	7	—	—	1	—	—	—	—	—	—	8	—	—	1	—	—	—	—	—
Oligochaeta (smooth)	13	24	8	15	19	5	13	1	1	13	1	—	5	6	2	—	10	—	1	4	3	1
Nematoda	44	91	121	238	73	85	266	—	3	116	1	—	47	113	32	1	93	32	25	47	103	4
Leptidae larva	19	13	17	1	12	8	6	7	9	9	5	—	16	4	14	1	—	—	—	5	4	3
Paragnathia formica ♂	—	—	1	—	37	—	—	2	98	—	—	—	2 Dead	—	—	—	—	—	—	—	—	—
Paragnathia formica ♀	—	—	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Paragnathia formica larval ♀	—	—	—	—	5	—	—	1	3	—	—	—	1	—	—	—	—	—	—	—	—	—
Hydrobia ulvae	26	292	×	×	×	×	4173	317	×	3360	1021	×	×	1734	×	1043	×	×	×	4169	×	51
Macoma balthica (*a*)	—	—	—	—	—	1	—	—	—	—	—	—	—	9	—	—	53	117	87	—	—	—
Macoma balthica (*b*)	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	47	27	—	19	—	—	—
Macoma balthica (*c*)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	19	—	—	—
Cardium edule (1)	2	—	4	4	2	5	16	1	—	24	1	1	—	7	—	17	2	18	17	—	—	—
Cardium edule (2)	—	—	—	2	1	—	2	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—
Cardium edule (3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Cardium edule (4)	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
Corophium arenarium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	1	2	40	401	66
Pygospio elegans	—	4	1	—	—	7	7	—	—	4	—	—	—	5	1	—	15	—	—	—	1	—
Eulalia sp.	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	5	—	—	—	—
Retusa alba	—	—	—	—	—	1	—	—	—	1	—	2	—	2	—	7	1	5	3	1	—	—
Carcinus maenas	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	1
Bathyporeia pilosa	—	—	—	—	—	2	—	—	—	—	—	2	—	—	—	—	37	6	5	64	9	3

of Dr Watkin, a separation of the two species has here been made. In August, 1938, the neighbourhood of sample 16 was found to contain a mixed population of the two, and as *C. volutator* is found to make a seasonal migration away from the gullies, it cannot now be determined which species constituted the *Corophium* noted in samples 9, 10, 13 and 62. Movement over the area is further indicated by the fact that in September 1925 *Corophium* was found swimming in the pools at the base of the posts, shown on the cockle bed, although it was absent from the neighbouring soil.

Two other sections are tabulated, section III, samples 24, 25 and 26, in more barren sand between the *Macoma-Cardium* ground and the Leri, in which *Bathyporeia pilosa* appears in numbers, may represent a *Macoma-Bathyporeia* subcommunity. In the transitional area between mud and sand (samples 14, 15, 17 and 18) a few species, chiefly polychaetes, make their sole appearance, and are grouped together in section IV.

Sections I and II are rendered more sharply distinct than they appear in the table by the fact that any section II animals found in samples 1–13 are all of smaller size than in the area considered typical for them, with the possible exception of *Scrobicularia*. This suggests that their presence nearer high-tide mark is limited to only a short time after spat fall or metamorphosis, and that the area is intrinsically unsuitable. The only obvious trespasser from section I is the nematode, which may actually include more than one species.

Hydrobia ulvae has not been taken into consideration in this grouping of the infauna, as it is largely a surface dweller. In view of Spooner & Moore's statement (1940, p. 327) that it is especially susceptible to disturbance of the ground by currents, it may be interesting to notice the increase in their numbers in the lee of a bank (samples 21, 22, 23) compared with their relative scarcity somewhat nearer high-water mark. Samples 22 and 23 show especially high figures, and are the only two samples where the presence of *Enteromorpha* was noted, possibly affording additional effective substrate as suggested by Spooner & Moore for *Zostera* (1940, p. 311).

Faunal Change with Decreasing Shelter

By taking a series of samples along gulley I, working away from the sheltering dune bank, it was possible to investigate the effect of shelter, with that of distance from high-tide line (and therefore period left uncovered) practically eliminated. Twenty-two samples (27–48 on Fig. 2) were made to cover this investigation, and Table II shows that the "*Corophium* community" is restricted to a very small part of the high-tide area, again giving place to the "*Macoma* community" about sample 42. Dr Watkin informs me that *Corophium volutator* does not recur higher in the estuary until the next freshwater streamlet emerges on to the flood plain. In April 1925 I found a few at Glandyfi, five miles up, at the head of the estuary. Again, the distribution of *C. arenarium* differs from that of *C. volutator*, following more closely that of *Bathyporeia pilosa*, and occurring with it in the drier patches in the wet *Arenicola* ground covered by samples 43–46. The order of dryness of these is

46 (driest), 43, 44, 45 (wettest) and the numbers of the two species mentioned decrease in that order of samples. *Corophium arenarium*, however, has its maximum density of population on a strip parallel to the dyke, in which sample 47 is included, and which does not appear so favourable to *Bathyporeia*.

In this series *Hydrobia ulvae* was not counted in each sample, but only in the samples containing the maximum and minimum number for each journey, thus saving a good deal of time. The total is recorded as × in the uncounted samples. The area covered by samples 36–46 inclusive seems to include the optimum for the species, having an average of about 1898 per sq. ft.—about 20,000 per m.^{2}, while the maximum is 4169 per sq. ft.—about 44,200 per m.^{2} Spooner & Moore (1940) point out that the maximum density for this species is usually high up on the beach, and give their own maximum at about 35,000 per m.^{2}

Weight as a Test of Suitable Environment

It has already been suggested, in considering Table I, that the "trespassers" from one community to another attain only a relatively small size. This suggestion was checked by recording the average "dry" live weight per species per sample for certain species, calculated from $\frac{\text{total weight}}{\text{number of individuals}}$ shown in Table III. Animals comparatively few in number, e.g. *Nereis*, *Pygospio*, were not weighed; nor were nematodes and oligochaetes, for those retained by the 1 mm. mesh are much of a size.

Only *Corophium volutator*, *C. arenarium*, *Bathyporeia pilosa*, *Macoma balthica* and *Cardium edule* were therefore weighed. *Corophium* and *Bathyporeia* were allowed to scramble, roll or wriggle across sheets of blotting paper till they left no further trail and appeared to be dry, and the molluscs were divided into groups and left to dry until surface water had evaporated. *Macoma* was divided up into three grades, which were determined after inspection of a large number of individuals. The three grades were:

(*a*) 1 to 3 mm. across broadest part; colourless or very pale.
(*b*) 3 to 8 mm. across broadest part; typically shiny pink or yellow.
(*c*) 8 mm. to largest sizes; generally a ringed, calcareous appearance.

Support for this grading is afforded by Horsman (unpublished) who finds *Macoma* grows from March to July at a rate of about 1 mm. per month. In its first season it attains a breadth of 3 mm.; in its second, 7 mm.; after which the generation becomes indistinguishable.

Cardium edule was easily divided by counting the number of annual rings, this number (1–4) being indicated in brackets in Table II and again in Table III.

In samples 34 and 37 many *Corophium volutator* were dead when examined, so could not be dried by the method adopted. Hence the average weight in sample 34 was calculated from some only of the total number, while no attempt was made to weigh those in sample 37.

Table III shows the position most favourable to the species investigated. Considering first *Cardium*—four year groups are present together only in

TABLE III. AVERAGE WEIGHT (MG.) OF SELECTED SPECIES IN DIFFERENT SAMPLES

Sample no.	*Corophium volutator*	*Corophium arenarium*	*Bathyporeia pilosa*	*Macoma balthica*			*Cardium edule*			
				a	*b*	*c*	1	2	3	4
29	1·211	—	—	—	—	—	0·025	—	—	—
30	1·42	—	—	—	—	—	0·00	18·5	—	—
31	1·46	—	—	—	—	—	1	57	—	—
32	0·65	—	0·2	0·00	—	—	6·48	—	—	—
33	5·33	—	—	—	—	—	2·35	19·65	—	2574·5
34	7·02	—	—	—	—	—	35·4	—	—	—
35	3·27	—	—	—	—	—	—	—	—	—
36	2·04	—	—	—	—	—	5·85	—	—	—
37	?	—	—	—	—	—	33·4	4230·2	—	—
38	0·2	—	0·3	—	16·68	—	10·4	—	—	—
39	1·84	—	—	—	—	—	—	—	—	—
40	1·03	—	—	0·01	—	—	3·71	—	—	—
41	3·3	—	—	—	—	—	—	—	—	—
42	—	—	—	—	109·36	—	7·62	—	—	—
43	—	0·09	0·96	0·38	1·89	200·2	0·1	—	—	—
44	—	0·00	?	—	17·82	—	30·9	—	—	—
45	—	0·2	0·12	0·41	34·89	218·89	15·9	37·4	3150·6	5192·9
46	—	2·5	1·26	—	—	—	—	—	—	—
47	—	2·61	0·16	—	—	—	—	—	—	—
48	—	0·45	0·13	—	—	—	—	—	—	—
	Corophium spp.									
9	1·22	—	—	0·00	—	—	9·6	—	—	—
10	1·54	—	—	0·00	—	—	1·49	—	—	—
13	1·18	—	—	1·02	84·78	75·7	295·04	—	7043·4	—
16	0·9	—	—	2·65	106·39	240·1	120	2717·3	5285·7	7955·5
62	0·9	—	—	—	—	—	5	—	—	—
63	—	—	0·2	—	—	—	29·3	—	—	—
64	—	—	0·68	0·67	179·5	240·2	46·1	1256·3	4078·2	3346·5

samples 16, 64, 45; and there is a rim of heavy first year *Cardium* round this in samples 13, 63, 44 (37 having heavy forms too). The remaining *Cardium* collected lie within the *Corophium* zone. Samples 9, 62, 32—close to the edge of the gully—have fairly well-grown forms; and some second-year *Cardium* were also found in samples along gully I. The remaining *Cardium* samples (10, 43—places uncovered slightly longer) contain only the first-year group and the average weight is very low. From this it appears that a line through samples 16, 64 and 45 represents the edge of the *Cardium*-bed proper, with a bordering zone of well-grown first-year forms. *Cardium* invading the *Corophium* zone does not live very long, doing best on the edges of the gully-bed (where the tidal effect lasts longest) but growing little, or perishing, in the areas subjected to still longer drying.

The edge of the established *Macoma* ground coincides fairly well with that of *Cardium*, but also extends to samples 13 and 43. South of this the smallest group occurs alone in samples 9, 10, 32 and 40—again by the gully—but the average weight of these is considerably less than that of first-year forms in the *Macoma* ground proper.

The average weights of *Corophium volutator* show that the heaviest average (7·02 mg.) was found in sample 34, the weight getting steadily less downstream towards the Leri, decreasing less steadily in the opposite direction. Such a gradation might be due, among other things, to difference in growth rate, or in breeding rate and proportion of young. *C. arenarium* does not attain so large a size as *C. volutator*, the heaviest average found being only 2·61 mg. The observed fall in average weight through samples 10, 13, 16, might be due to an increased proportion of *C. arenarium* in a mixed population, but this cannot now be determined.

The figures for *Bathyporeia pilosa* show its association with *Corophium arenarium*, and like this species it seems to "prefer" drier patches. For instance, in the series 46, 43, 45, passing from fairly dry to wet sand, the average weight steadily decreases, with a drop in the numbers of *C. arenarium*. Sample 47 was drier than 48 and had more numerous, heavier individuals of both species. Sample 63 was an exception in having large numbers of *Bathyporeia* (298) although it was very wet, but the individuals were all small.

FAUNA AND SOIL TEXTURE

Table IV shows the complete analysis for twenty-three samples, included in full for reference. In calculating Representative Numbers (Borley 1923, p. 30) the division of sand into medium and fine was ignored, being considered to stress unduly one of the less important ecological factors. Throughout, 100 × R.N. has been used to get a whole number. The R.N. was calculated from the following grades of size:

Sand ...	...	0·04 mm. minimum diameter.
Silt ...	...	0·01 mm. minimum diameter.
Fine silt	...	0·002 mm. minimum diameter.

TABLE IV. COMPLETE SOIL ANALYSIS FOR 23 SAMPLES SHOWN IN FIG. 2.

Proportions by weight of different grades given in percentages

(For accompanying fauna see Table VI)

Soil type II. 100 R.N. = 4·0 to 3·9

Sample no.	100 R.N.	"Moisture"	"Organic content"	Medium sand 0·5 to 0·2 mm.	Fine sand 0·2 to 0·04 mm.	Silt 0·04 to 0·01 mm.	Fine silt 0·01 to 0·002 mm.	Clay < 0·002 mm.
26	4·0	—	—	17·7	81·7	0·0	0·5	0·1
49	4·0	0·1	1·1	61·4	36·4	0·4	0·1	0·4
24	4·0	—	—	39·3	59·8	0·2	0·1	0·7
54	4·0	0·1	1·6	55·5	41·3	0·8	0·4	0·3
65	3·9	0·1	3·8	39·3	54·8	0·9	1·0	0·1
19	3·9	—	—	18·0	79·5	1·5	1·0	0·0
23	3·9	—	—	4·1	92·6	1·7	1·4	1·2
Soil type I. 100 R.N. = 3·8 to 2·0								
51	3·8	0·1	3·8	11·0	79·4	4·7	1·0	1·0
7	3·7	—	—	3·1	90·3	1·7	2·9	2·1
30	3·7	—	—	7·7	82·9	4·6	3·4	1·4
12	3·6	—	—	7·3	82·1	5·3	4·5	0·9
56	3·6	0·2	2·3	58·7	28·7	4·0	4·5	1·8
55	3·6	0·2	2·1	40·2	45·4	4·3	6·4	1·6
31	3·5	—	—	19·9	65·8	7·5	5·5	1·3
52	3·4	0·2	5·9	3·9	72·0	8·8	7·5	1·8
60	3·3	0·4	3·7	33·7	42·1	8·7	8·4	3·2
53	3·3	0·2	4·2	28·5	46·5	10·1	8·4	2·3
61	3·2	0·1	5·5	13·5	57·7	10·4	9·4	3·4
1	3·0	—	—	25·4	46·8	11·0	11·3	5·6
59	2·9	0·1	4·5	12·5	53·4	12·4	13·1	3·7
2	2·9	—	—	10·8	56·9	18·2	11·0	3·2
57	2·7	0·6	4·4	24·3	34·1	14·9	14·7	7·1
58	2·0	1·1	7·5	0·5	26·2	27·7	30·3	6·8

A statement of the moisture content has been given in some samples, as being of obvious importance in an intertidal area. The samples in which this is not noted had been oven-dried after collection, prior to analysis by Borley's method. The organic content of the soil has not, to my knowledge, received much attention from oceanographers, yet this must also be of importance to the infauna as a whole, and that not only in quantity, but also very probably in quality. Thus, presumably, an animal provided with jaws will tend to use them in comminition of coarse, recognizably organic matter which, to a current feeder, such as *Cardium edule*, or a "mud browser", such as *Arenicola*, would probably be of little or no value. Beside the physical state of the debris the chemical composition will also be important, but as it is not known exactly what chemical elements, and in what amount and combination, the various animals require, attention has been directed only to the first, i.e. to an estimate of the total organic matter present, and a separation of that recently deposited and still recognizable as such, from that now intimately connected with the soil particles themselves. This separation was most conveniently effected by means of the 0·2 mm. sieve.

In the fourteen samples investigated the amount of coarse organic matter is everywhere low, being highest at the base of the dyke (sample 50), and the percentage organic content does not appear to follow the R.N. very closely. Table V has been compiled by collecting together soil with the same percentage of recognizable, coarse, organic matter; and averaging for each grade so obtained the fine organic matter, total organic matter, summation percentage of silts and clay, and R.N. × 100.

TABLE V

Percentage coarse organic matter	Samples	Average percentage fine organic matter	Average percentage total organic matter	Average summation percentage silt and clay	Average R.N. × 100
2·6	50	4·9	7·5	20·4	2·9
0·3	54, 55, 60, 56, 49	1·86	2·6	9·1	3·7
0·2	51, 52, 53, 57, 61, 65	4·4	4·43	17·9	3·4
0·1	58, 59	5·9	6·0	47·0	2·4

Considered on this average basis, the R.N. and summation percentage of silts and clay show a relation with the fine organic content, and a slighter one with the total organic content, owing to the addition in sample 50 of a relatively large amount of coarse organic matter which was not deposited with the soil. The above figures, excluding sample 50, also indicate that the amount of coarse organic matter falls as the fine rises, so that the presence of the two divisions appears to be not entirely due to identical factors. Further, there is less coarse and more fine organic matter as the soil grows finer.

Table VI has been arranged without regard to topography, the samples being tabulated in ascending order of value of the summation percentage content of silts and clay, and it will be seen that the presence of the same

Table VI. Soil Associations. Period of Sampling: early September to mid-February

	Soil type II									Soil type I																	
Summation % of silts and clay	0	0	0·6	0·9	1·0	1·5	2·0	2·5	4·3	6·7	6·7	9·4	10·0	10·3	10·7	12·3	14·3	18·1	20·3	20·4	20·8	23·2	27·9	29·2	32·4	36·7	64·8
100 R.N.	4·0	4·0	4·0	4·0	4·0	4·0	3·9	3·9	3·9	3·8	3·7	3·7	3·6	3·6	3·6	3·6	3·5	3·4	3·3	3·3	3·3	3·2	3·0	2·9	2·9	2·7	2·0
Organic content %	—	—	—	1·1	—	1·6	3·8	—	—	3·8	—	—	—	2·3	—	2·1	—	5·9	3·7	7·45	4·2	5·5	—	4·5	—	4·4	7·5
Moisture content %	—	—	—	0·1	—	0·1	0·1	—	—	0·1	—	—	—	0·2	—	0·2	—	0·2	0·4	0·4	0·2	0·1	—	0·1	—	0·6	1·1
Number of sample	63	64	26	49	24	54	65	19	23	51	7	30	62	56	12	55	31	52	60	50	53	61	1	59	2	57	58
Association I:																											
Corophium volutator	—	—	—	—	—	—	—	—	—	41	844	14	*6	—	29	373	28	441	—	—	—	27	—	217	445	—	—
Nereis diversicolor	—	—	—	—	—	—	—	—	—	—	4	3	—	—	—	4	—	21	—	—	—	—	—	—	9	—	—
Oligochaeta (pitted)	—	—	—	—	—	—	—	1	—	—	16	7	—	—	—	—	—	—	—	—	—	—	—	—	15	—	—
Oligochaeta (smooth)	—	6	—	—	1	—	—	1	—	—	130	15	2	7	25	39	19	9	12	—	—	11	—	29	136	5	—
Nematoda	2	6	—	9	—	—	3	67	2	45	479	238	30	7	35	20	73	269	67	3	8	15	—	5	1062	—	—
Leptidae larva	—	—	—	—	—	—	—	—	—	—	—	1	8	27	2	—	12	—	3	11	—	21	—	13	—	—	11
Paragnathia formica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	—	—	—	—	—	—	—	—	—	—
Association II:																											
Macoma balthica	4	143	—	9	58	13	27	401	657	11	6	—	—	—	—	—	—	—	3	—	—	—	—	—	1	—	—
Cardium edule	10	15	—	—	52	—	45	15	38	—	—	6	1	—	3	—	3	4	3	—	—	—	—	—	—	—	—
Corophium arenarium	—	—	—	9	3	—	—	21	6	—	—	—	*—	—	—	—	—	—	—	3	—	—	—	—	—	—	—
Pygospio elegans	—	9	—	11	—	5	—	67	—	—	4	—	2	—	125	—	—	3	16	—	—	—	—	—	—	—	—
Eulalia sp.	—	—	—	—	—	—	—	1	9	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scoloplos armiger	—	—	—	—	—	—	—	80	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scrobicularia plana	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	3	—	—	—	—	—	—	—	—
Retusa alba	—	—	—	—	—	—	—	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bathyporeia pilosa	298	43	14	476	42	12	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* Possibly a mixture of *C. volutator* and *C. arenarium*.

groups of species is indicated, the *Macoma* community occurring in samples with a percentage lower than 6·7, and the *Corophium* community in the rest of the samples. *Bathyporeia pilosa* appears to be practically confined to soils with a summation percentage of 1 or less.

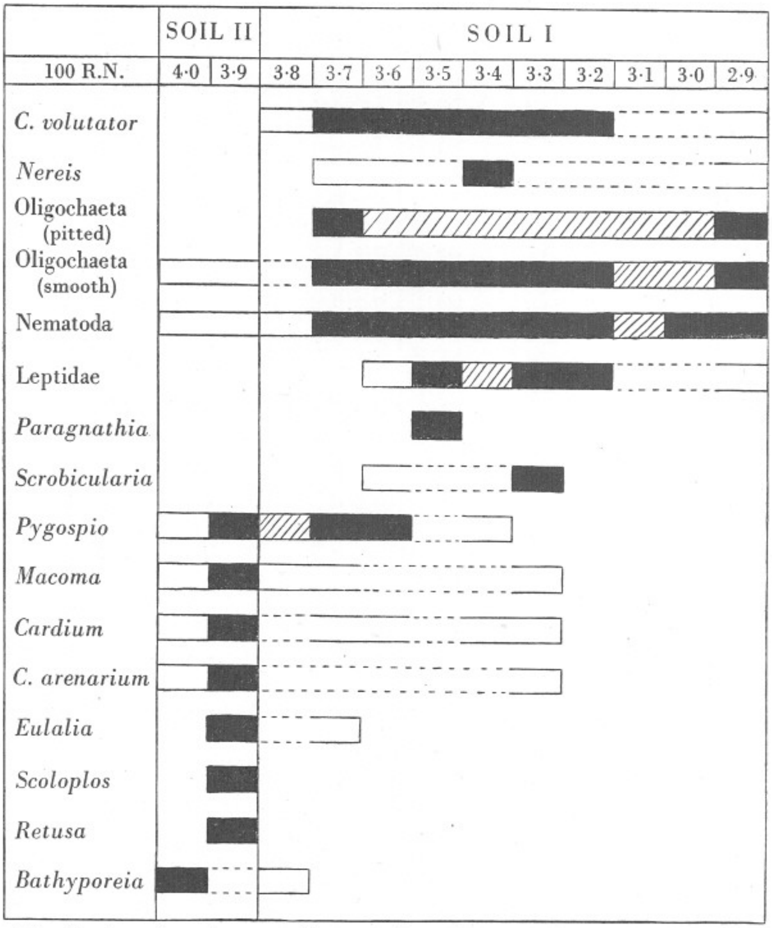

Fig. 3. Distribution of species according to soil grade. 50% zone, actual in black, assumed hatched; casual occurrences, actual outlined with continuous line, assumed outlined with broken line.

The smallness of the area sampled made it impossible to fix definite "class intervals" for the soil grades, but an attempt to trace a soil association in the area, following Davis, gave the following striking similarity with the "community" divisions (Table VII) in which the figures (number of individuals per sample per soil) are given correct to the first decimal place. Class A species have their "50% zone" (Davis, 1925, p. 13) confined to one soil; class B in both, and class C includes casual occurrences.

TABLE VII

	Soil type I (16* samples) 100 R.N. = 2·9 to 3·8	Soil type II (9 samples) 100 R.N. = 3·9 to 4·0
Class A	*Corophium volutator* (154)	*Macoma balthica* (146·0)
	Oligochaeta (29·5)	*Cardium edule* (19·4)
	Nematoda (147·8)	*Bathyporeia pilosa* (98·4)
	Nereis diversicolor (2·6)	*Corophium arenarium* (4·8)
	Leptid larvae (6·1)	*Eulalia* sp. (1·0)
	Paragnathia (3·0)	*Scoloplos armiger* (9·9)
		Retusa alba (0·7)
Class B	*Pygospio elegans* (8·7)	*Pygospio elegans* (10·1)
Class C	*Macoma balthica* (1·3)	Oligochaeta (1·0)
	Cardium edule (1·3)	Nematoda (9·9)
	Corophium arenarium (0·2)	

* Samples 57 and 58 are omitted from the calculations since they were from a barren mud area.

This table clearly shows that the soil association is identical with the Petersen community division previously advanced. *Pygospio elegans* is the only species in class B, and it will be remembered that the species was formerly relegated to the *Macoma* community by recognition of a size distinction which would not be obvious on consideration of numbers alone. The casual occurrences also agree with the former division.

The zoning of the species from the point of view of soil associations is shown in more detail in Fig. 3, which includes the full range of each species. Samples in which the 50% zone was actually found are shown in black, samples in which it is assumed are indicated by diagonal shading. Casual occurrences found are shown in white with a firm outline; and where these are merely assumed the outline is dotted.

DISCUSSION

Macoma balthica

It will be useful here to review the position with regard to the *Macoma* community. Petersen (1918, p. 17) states: "One community, the *Macoma* community, seems to be altogether independent of the composition of the level bottom, living equally well on pure sand and on pure mud." Davis (1925, p. 16) appears to suggest that the *Macoma* community is the only one that may be considered as a soil association, that is, it is *limited* as regards soil range. The above results, as far as they go, may appear to confirm Davis' statement, but further consideration points to the truth of the opposite view. Davis' soil I is, as far as I can judge, roughly comparable to the coarse part of my soil II, and as *M. balthica* occurs in the North Sea in soil IV only, it is listed as a class A species. Correlation with estuarine data, however, would give this species a much wider range of soils and support Petersen's remark concerning the catholicity of the species.

Remembering Davis' conclusion (p. 14) that, on the whole, the number of individuals increases with increasing fineness of soil, it is interesting to note that, as compared with 0·11 individuals of *M. balthica* per sq. m. in soil IV (Davis), I have an average of 146 individuals per sq. ft. (=about 1550 per sq. m.), while Fraser (1932, p. 82) found 3071 per sq. m. in "thick mud" (apparently finer than mine) and as many as 1030 per sq. m. in the muddy sand of his *Corophium* area. Thus Fraser finds *Macoma* in great abundance in two neighbouring soils of different texture (but with abundant microflora), in this case with the sand lying landward of the mud. That soil grade in itself is not a determining factor is further suggested by comparing the results of Bassindale (1938) and Rees (1940). The former finds it intolerant of both soft and clayey muds in the Mersey estuary, the latter finds it common in both on the Bristol channel. Thus the "50% Zone" of *Macoma* is not an *absolute* reality, but differs with the locality. The abundance of *Macoma* in estuaries possibly depends on two factors: (*a*) quality and quantity of available food supply, correlated with type of soil; and (*b*) available feeding time, correlated with distance below high-tide mark.

Corophium volutator

Hart (1930, p. 768) concludes that the distribution of *C. volutator* is limited by the type of soil, the most suitable being fairly soft grey mud. This description applies to the *Corophium* ground in the Dovey estuary, but I cannot with any confidence identify any of his soil analyses with any of mine. Nicol (1935, p. 220) thinks the importance of the soil second to that of salinity, finding *Corophium* as only a temporary inhabitant of the Aberlady salt marsh pools with a salinity of 5 ‰ or less, but that in the salter pools it is dependent on the type of bottom. I find it can live about six days in a salinity of 3 ‰, but cannot agree with Hart as to its length of survival in fresh water. While agreeing that *Corophium* is found in most abundance within a certain fairly recognizable type of soil, and that it has a wide range of salinity toleration (though with a definite lower limit), I am inclined to think that the distribution of this form is dependent rather on the primary factors determining the soil and salinity than on these secondary factors themselves, i.e. on slow current, and the meeting in the immediate neighbourhood of fresh and salt water.

In studying the ecology of *C. volutator* it may be most important to distinguish between areas where it is found over a period of months only and such a one as the Dovey estuary where it has been known over a period of thirteen years. Quatrefages (quoted in Bate & Westwood, 1863, p. 495) states: "about the end of April they come from the sea in myriads...and disappear in a single night about the end of October, to return again the following year." Ehrenbaum had a similar idea: "Uebrigens sind auch diese Corophien keine permanenten Bewohner der hochgelegenen Wattflaechen, sondern sie erscheinen dort zu Beginn der warmen Jahreszeit und verschwinden im Herbst wieder." Thus both Quatrefages and Ehrenbaum knew *Corophium* as a *summer visitor*, though when present the latter recorded as many as 50,000 per sq. m. Unless these writers are proved mistaken, this aspect of *Corophium volutator* must be included in any complete account of, and explanation of, its ecology. No indication of this possibility is found in this part of the Dovey estuary, and comparison of various localities from which *C. volutator* has been recorded suggests a possible reason for this difference in permanence.

In the summer of 1900 Allen & Todd recorded the species as very abundant in the Salcombe estuary, between Ditchend and Southpool Lake, in the typical type of mud. I examined this spot in March 1927, and after careful search found only two individuals. In April 1929, Hart (1930, p. 776) found a population in this part of less than one per sq. m. In the summer of the following year, 1901, Allen & Todd found it abundant in one part of the Exmouth estuary, near high tide and north of Salt House Lake, together with many species recorded in this investigation. I visited this spot in March 1927 and this time found neither *Corophium* nor *Corophium* mud. The mouths of the rivers Exe and Dovey are very strikingly similar, the one being the "mirror image" of the other, reading Exmouth for Aberdovey, Dawlish Warren for Borth Dunes, and Salt House Lake for the River Leri, with *Corophium* grounds in equivalent spots of each. I learnt that cartage of sand had recently resulted in the sea breaking through the Warren at Dawlish, with an obvious decrease in the shelter provided. This suggested the idea that in some way Borth Dunes might be a factor in the persistence of *Corophium* in the estuary of the Dovey. The only two places where I found abundant *Corophium* at Plymouth in 1927 were behind sluice gates in Landulph marsh, but not on the banks of the Tamar outside; and similarly behind sluice gates in Chelson meadows, though absent from the neighbouring banks of the Plym. Hart (p. 768) records large numbers also behind a sluice gate connecting a small river with "Stukey Freshes", a tidal creek in Norfolk. In the first two localities *Corophium* was present without its typical soil, but with very adequate shelter from any current until the sluice gate should be open. Thus, although the typical soil was absent, it was in still water that would have deposited any clay precipitated by a mixing of fresh and salt water, and thus favour production of such a soil.

Other records have been examined with a view to determining whether the *Corophium* ground was especially sheltered in any way, choosing those in which the population was fairly dense. Most of Hart's figures record relatively small populations and may possibly be found to be transitory occurrences; however, in August 1929 he found 1000 per sq. m. in a creek in a Salicornetum at Blakeney Point, Norfolk (p. 768), where presumably the current is slow. Fraser (1932, p. 70) found it abundantly on Dingle Beach, River Mersey, near the mouth of a small sewer, adequately protected by a revetment. Bassindale (1938, p. 85) found it higher up the River Mersey than Fraser, and on the opposite bank, in mud and muddy sand watered by two freshwater streams, namely Holpool Gutter and the River Gowy and its tributary, where the supernatant current is very slow. In the outer Mersey Area Bassindale (p. 87) records it in an area sheltered by the East Hoyle Bank and their reef of rocks, with *Macoma balthica* and *Arenicola marina* replacing *Corophium* some distance away from the shelter of the reef, as in the Dovey estuary. Bassindale's records refer to the period between May and October 1933. Percival (1929, p. 93) records it on the banks of the Tamar, where the slowness of the current is specially noted. Nicol (1935, p. 214–18) records it as abundant in certain salt marsh pools in Aberlady Bay and also on the shores of the Peffer Burn in the neighbourhood of some hulks which possibly offer a degree of shelter and where a freshwater stream is shown running across the mud. Elmhirst (1932, p. 59) records a population of 2000–10,000 per sq. m., together with 24,000–32,000 nematodes and 20,000–48,000 oligochaetes in samples to a depth of 15 cm. on Fairlie sands, coast of Ayrshire; I do not know what degree of shelter there was in this area. Rees (1940, p. 191) records it in large numbers (2400 per $m.^2$) beside a sewage outfall at low-water mark near Cardiff, but thinks it is probably transitory.

It seems, then, that in many places where *Corophium* has been noted in abundance there is a special factor for shelter in the neighbourhood, and often a freshwater stream. From these considerations, together with some experimental work not yet published, I am led to suggest the following explanation of the occurrence, both transitory and permanent, of *Corophium volutator*. I have a certain amount of reason to believe that under certain combinations of light and salinity *C. volutator* may leave the soil and "swim" until stranded by the falling tide. Where the water movements are very gentle, such as near a high-tide line in a sheltered area, it will be redeposited not very far from its original position and, if still over the appropriate proportions of silt and clay, will burrow. A clayey soil of 100 R.N. = 2 will be too stiff to allow easy penetrability, and a more sandy one of 100 R.N. = 4 will be associated with too strong a supernatant current to deposit *Corophium*. Any individuals which succeed in burrowing, in spite of the current, will lack the safeguard from desiccation provided by the normal clay burrow. On the other hand, if the community emerges from the soil into a stronger current, in a region without suitable shelter, it may well "disappear in a single night", being carried out to sea.

I make this as yet unproven suggestion as one means of testing its truth. It would be interesting if further records of *Corophium volutator* could include (*a*) the length of time it has persisted in the area, (*b*) any factor for shelter, (*c*) the presence or absence of freshwater streams over or near the bed, decreasing the salinity but also favouring the deposition of the necessary clay for burrowing, (*d*) evidence of sewage pollution, which is possibly a nutritive factor.

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REARING ANIMALS IN CAPTIVITY FOR THE STUDY OF TREMATODE LIFE HISTORIES. II.

By Miriam Rothschild

INTRODUCTION

The advantage of using laboratory-reared animals in the elucidation of trematode life histories is now generally recognized (Palombi, 1938; Stunkard, 1938, etc.). Further researches seem to emphasize this point. No matter how carefully controls are examined and no matter how precise is the morphological comparison between cercaria, metacercaria and adult fluke, the fact that the intermediate and final hosts have been exposed to previous infection in the wild—particularly by closely related species of worms—immediately detracts from the value of the experiments.

The successful efforts at hatching the black-headed gull in an incubator (Rothschild, 1936) led to the entirely erroneous assumption that the herring gull would prove an equally simple proposition. It is thought worth while publishing these practically negative results in case other workers should feel tempted to try a similar experiment.

The stoats, which were required for a dual purpose, were more easily reared than was anticipated. The repeated failure of infection experiments with white rats and various farmyard birds seemed to indicate that better results are obtainable with wild than domesticated animals; ferrets would otherwise have been selected as easier to rear and handle. The stoats proved most attractive and interesting animals to keep and served to illustrate the fact that the helminthologist must guard against the rival attraction of host over parasite.

Larus argentatus Pontopp.

Observations were begun on a colony of nesting herring gulls before laying commenced. It was thus easy to collect fresh eggs. Two dozen were taken soon after laying and transported by car, the journey lasting 12 hours. The eggs were then treated in precisely the same manner as those of the black-headed gull (Rothschild, 1936). All failed to develop, the contents remaining in a liquid state.

The shell of the herring gull's eggs appeared less fragile than that of the black-headed and it was thought that these might be incubated successfully by a hen. The following season, therefore, a further collection was made and a score of eggs equally divided between two hens. The majority of these were smashed by the hens, and the rest again failed to develop.

During the autumn, special "cross-bred" bantams were reared, which although retaining the staid sitting qualities of the larger breeds of domestic fowl, were of much lighter build. It was also considered possible that eggs of the herring gull sustained internal injury more easily than those of the black-headed and that a car journey involved too much shaking. The next batch of eggs was consequently conveyed by train and the box containing them held by an obliging passenger, thus avoiding any sudden jars or jolts. On this occasion there had been no opportunity for observing the colony of gulls before laying began, and it seems probable, in the light of subsequent events, that some of these eggs were not fresh. They were separated into three lots, two dozen of which were placed in an incubator, and twenty-four more divided between two cross-bred bantams. Each day, while the hen was feeding, one of the latter groups was heavily sprayed with water. Once again, all the eggs in the incubator failed to develop. Nineteen of the eggs under the bantams were smashed. Chicks developed in the remaining five eggs. Four died immediately before hatching between the 12th and 15th day, and the fifth hatched on the 14th day.

These experiments seem to suggest that there is a slightly better chance of hatching herring gull's eggs if they are collected some while after laying. It appears that a more practical method, provided a gullery is situated conveniently, is to allow the birds to incubate their own eggs and collect them immediately before hatching. Although there has been no opportunity to test this method personally, yet two experienced aviculturists have assured me that it has proved satisfactory. Six eggs of the common gull (*Larus canus* L.) and the arctic tern (*Sterna paradisaea* Brünn.) also failed to develop.

Larus ridibundus L.

Since 1936 four dozen of these birds have been reared every season and the number of chicks hatching successfully has increased by 50%. This is probably due to the fact that the eggs have been thoroughly soused with warm water twice a day. In the original experiments the chamber and the eggs themselves were undoubtedly kept too dry. It has since been learned that when attempting to hatch grebe's eggs in captivity, certain aviculturists actually float the eggs continuously in warm water within the incubator. In nature, even when nesting well away from the water, the black-headed gull probably settles down on her eggs with drops of moisture on the breast feathers.

Some difficulty was experienced in feeding infected fish and crabs to those birds which had previously been accustomed to cooked, hashed-up food only. It has proved useful to familiarize them with solid hard pieces of food, particularly the size and shape of small fish, before feeding experiments begin. When only a few cysts are available it is best, whenever possible, to use young birds which can still be fed easily from the hand and are at the stage when they swallow wholesale anything that is offered to them. Older birds may become fussy and particular, and also show a regrettable tendency to scatter their food.

After hours of labour expended in isolating some rare species of cercaria, and collecting and examining the cysts, it is trying in the extreme to see them flying to the four corners of the room with one shake of the bird's head. It is often difficult to induce certain individuals to eat alone if they are used to feeding in a flock, and it is a great saving of time and temper to accustom them to both solitary confinement and solitary meals if an experiment is in view. To sit by while the bird darts fretfully to and fro, ignoring its food and the progressively less viable cysts, imposes a strain on the most patient experimentalist. Recourse to forcible feeding is often unsuccessful as the birds are apt to regurgitate their food if frightened or excited.

Mustela erminea L.

Keeping stoats in captivity has generally been regarded by zoologists (Krumbiegel, 1935) as an exceedingly difficult proposition, but a perusal of the advertisement columns of the *Gamekeeper* and similar periodicals shows that this is frequently accomplished in less scientific circles.

It was found that the chief difficulties lie in locating the nest and subsequently capturing the litter at the right age for the purpose, namely before the young are old enough to take any nourishment apart from milk. As the breeding season for stoats seems to vary by several weeks or even months with individual pairs, this necessitates a constant watch being kept on the parents. This in turn frequently results in the stoats growing suspicious and moving the nest, or the young if they are born. In a nest situated in an old rabbit warren the parents have succeeded in moving them even while digging operations were in progress.

After capture, the baby stoats were kept at room temperature (60° F.) in a box filled with hay, the centre cavity of which was lined with flannel. It is essential to arrange the artificial nest in such a way that the animals cannot crawl out of it. This they frequently attempt to do, death from chill invariably resulting if they are successful. On one occasion five young were found dead, lying between the hay and the wooden side of the box.

The stoats were fed every 3 hr. during the day from 7 a.m. to 10 p.m. with warm cow's milk from a pipette. Even before their eyes are open at about 3 weeks old they begin to chew small pieces of raw rabbit flesh. The amount of meat given was gradually increased until at the age of 4–5 weeks their diet consisted entirely of young rabbit (raw) and one small saucer of milk. At first artificial vitamins were added to this diet, but these were later found to be superfluous. Chilled water was also provided. The stoats rarely bathed, although keepers who have also kept these animals in captivity reported the contrary.

At the age of one month the animals were provided with larger cages, about 4 by 2 ft., fronted with wire netting. One end was separated off as a sleeping chamber and filled with hay. The cages were placed on trestles in a small open shed in the garden.

After a few initial errors with regard to treatment in the early stages, the mortality rate was reduced to about 12%. Two of the stoats are now over 4 years old. As the animals thrive so well on rabbit, it is a simple matter to provide them with raw food which is known to be free from helminths (laboratory reared).

Although it seems improbable that these baby stoats could have become infected with trematodes during the first days of their life, yet the probability cannot be entirely excluded and breeding from these captive specimens is now being attempted. A successful brother and sister mating resulted in the birth of a litter, but the female unfortunately devoured her young.

Hydrobia jenkinsi (Smith) and Littorina rudis (Maton)

These gastropods are both viviparous, and rearing them in the laboratory has so far presented no difficulty. Mature examples of both species were collected in late summer. *Hydrobia jenkinsi* was kept in finger bowls in fresh water obtained from a hot tap (therefore considered free from viable helminth ova or miracidia) and fed with a variety of food, from boiled *Zostera* and lettuce to newspaper and bread. *Littorina rudis* was kept in a mixture of half sea and half fresh water and fed on *Ulva*, a substitute for which might be found with advantage, as even with repeated washings in hot water it cannot be regarded with absolute certainty as free from viable helminth ova.

The young of both species were born in the autumn and immediately removed to separate dishes. By the following spring they could be used for infection experiments. The mortality was low, but in *Littorina rudis* the growth was very uneven and numbers of specimens did not appear to develop at all. The maximum length attained in 12 months was 9 mm.

Peringia ulvae (Pennant)

This species was kept under the same conditions as described above for *Littorina rudis*. Collections were made from various habitats both in England and Scotland. It proved exceedingly difficult to get the species to breed in the laboratory. *Peringia ulvae* is not viviparous, but lays eggs which give rise to a free-swimming veliger. The nature of the difficulties involved are not properly understood, as at the first attempt large numbers of these veligers were successfully reared to maturity—the snails subsequently surviving 5 years! It has never been possible to repeat these experiments although the laboratory conditions were apparently identical.

The chief period of egg production in the laboratory is in the spring, but a certain number are also laid in the autumn. Hatching takes place about 10 days later. Except for the initial experiment referred to above, the veligers have invariably died after a few days of free-swimming life. It is possible that the exceedingly minute organisms which serve as food for these tiny veligers were only present in the water on the one occasion when they were reared successfully.

Carcinus maenas L.

This crab, which has been experimentally infected by me with "Ubiquita" cercariae from *Peringia ulvae* is almost always parasitized in the wild. In working out these trematode life histories it was therefore considered essential to rear the second intermediate host in the laboratory. The crabs were collected from the plankton in the megalopa stage. Each larva was placed in a separate finger bowl, the water of which was changed daily. Food consisted of small pieces of the mantle of mussels (*Mytilus edulis* L.). The bowls were kept scrupulously clean, all debris such as moults or uneaten food being removed instantly. The crabs attained a maximum size of 3 cm. across the carapace in 12 months. Until they had reached the adult stage they were kept in sea water, but subsequently were gradually accustomed to a mixture of half sea and half fresh water. Penetration with the Ubiquita Group of cercariae from *Peringia ulvae* was effected more satisfactorily in this medium.

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THE FECUNDITY OF THE HERRING OF THE SOUTHERN NORTH SEA

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(Text-figs. 1–4)

During the great East Anglian herring fishery of the autumn of 1933, material was collected for an investigation into the number of eggs produced by the herring. Hodgson (1925) has shown that most of the females of these herrings are in the penultimate stage of maturity (the Stage V of Hjort), that is, the contained eggs are large and yolky, but not yet glass-clear and ready to be spawned.

Hickling & Rutenberg (1936) have shown that, in the herring, the eggs destined to be spawned in the current season are ripened simultaneously, for there is, in an ovary in an advanced stage of ripeness, a very sharp separation in point of size between the active yolky eggs and the small yolkless ones. Farran (1938) likewise found that all the ripening eggs in a herring ovary are of approximately equal size, and that the number of eggs destined to ripen is fixed from the time that the storage of yolk has begun. In the herring, therefore, the large yolky eggs are the whole of the season's crop of eggs, and a count of them will give the absolute fecundity of the fish.

It is a simple matter to separate these yolky eggs from the ovary. The method used was modified from that of Raitt (1933). The ovaries, preserved and hardened in formalin, were cut into pieces, and shaken vigorously with water in a stoppered jar. The yolky eggs dropped out of their follicles and fell to the bottom of the jar. By removing the connective tissue of the ovary a complete separation of the yolky eggs was made without difficulty.

The eggs were counted by the method used by Nuttall (1913) in counting the eggs of ticks. On an ordinary sheet of glass three strips of glass are cemented in the form of a right-angled U, between the arms of which a fourth strip of glass slides readily backwards and forwards whilst closely applied to the arms of the U like a piston in a cylinder. Within the rectangle so formed the eggs to be counted are spread so as to form a uniform layer one egg deep. The product of the number of eggs lying against two adjacent sides of the rectangle is the number of eggs in the whole rectangle, and this first estimate may be checked by a count of the number of eggs against the remaining two sides of the rectangle.

Besides these observations on the fecundity of the herring, observations on the weight of the fish and of its gonads were made on some 475 herrings of known sex, length, and age.

THE FECUNDITY OF THE HERRING

In Table I are given the mean number of eggs produced by herrings at each centimetre of length, and at each age.

TABLE I. THE FECUNDITY OF THE HERRING

Mid-length cm.	Frequency	Mean no. of eggs	Calculated no. of eggs
		A. By length	
21·5	2	12,570	12,223
22·5	3	12,250	14,315
23·5	17	17,225	16,645
24·5	30	21,611	19,230
25·5	30	22,322	22,074
26·5	29	24,904	25,223
27·5	17	28,475	28,679
28·5	7	33,223	32,434
29·5	1	34,450	36,599
		B. By age	
age			
3	2	12,570	14,620
4	39	18,814	17,679
5	21	23,208	20,482
6	40	23,200	23,102
7	16	27,102	25,580
8	5	24,690	27,931
9	8	30,924	30,189
10	5	33,464	34,458

Table I A shows that the number of eggs produced increased rapidly with increase of length. By the method of least squares it can be calculated that the formula which best expresses the relation between length and fecundity is

$$F=0{\cdot}2954\,L^{3{\cdot}465}.$$

Fecundity, therefore, increases with length at a rate substantially greater than the third power of length. Farran (1938) found that in the Irish herrings the rate of increase was of the order of the 4·5 power of length.

The data given in the table above are shown in Fig. 1, where the line shows the calculated mean fecundity at each centimetre. They are in excellent agreement with the data published by Fulton (1891). The herrings he investigated were also winter-spawning fish, and mostly greater than 11 in. in length. If the number of eggs found in the fourteen herrings greater than 11 in. in length dealt with by Fulton is compared with that found among the twenty-five herrings greater than 27 cm. in length in the present work, it is found that the mean number of eggs produced is 32,470 according to Fulton, and 30,043 according to the present work. But on applying the statistical test of the Significance of the Difference between Means to the two arrays, it is found that there is no significant difference between them. The calculated value of "t" is 1·04471, corresponding to a value of P of 0·3 (Fisher, 1938). Therefore a difference between the means as great as, or greater than, that found, would occur by chance in homogeneous material in three trials out of ten. Fulton's results, and those here presented, are therefore in agreement.

Very different results were obtained by Mitchell (1913). She found values for the fecundity of the herring nearly three times as great as those found by Fulton. But Fulton noted that summer herring were said to be more fecund than winter herring, and the specimens examined by Mitchell were summer spawners.

Farran (1938) found that, in fish of the same length, the spring spawners produced about half as many eggs as the autumn spawners, though the eggs were 25 % larger. It is interesting to note that the fecundity of the winter spawners dealt with by Fulton and in the present paper lies between those for the autumn and spring spawners, as shown by Farran's figures. It may be that the fecundity of the herring is adapted in some way to the seasons, for the order of fecundity seems to be as follows: least fecund in spring spawners, more fecund in winter spawners, still more fecund in autumn spawners, and most fecund in summer spawners. One is tempted to relate this with the plankton cycle; and in any case the fecundity should be, as Farran shows, a valuable means of distinguishing between herrings of different "seasonal races".

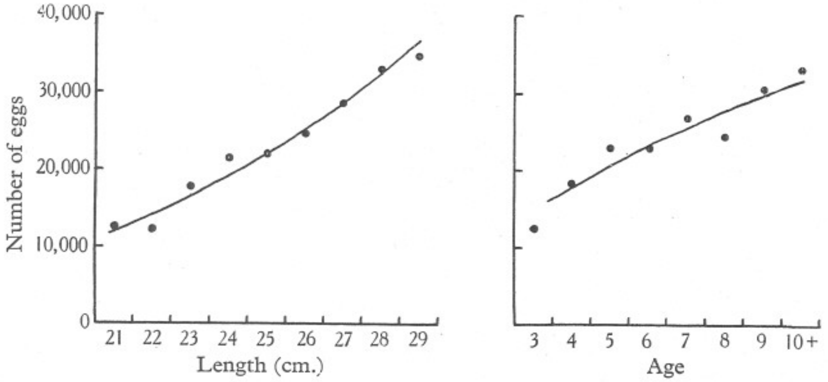

Fig. 1. Rate of increase in the fecundity of the herring with length and age.

The relation between age and fecundity is shown in Table I B. The formula which best expresses the relation between age and fecundity is

$$F = 7080 \text{ Age}^{0.66}.$$

The calculated regression is shown in Fig. 1 as a curve, and it would indicate a gradual falling off in the rate of increase of fecundity with increase of age. Farran also found indications of a decline in fecundity among the larger herrings in his samples.

THE WEIGHT OF THE GONADS

In Table II are given the average weights of the gonads of the herring at each centimetre of length, and at each age.

TABLE II. MEAN WEIGHT OF THE GONADS OF THE HERRING

A. By length

Mid-length cm.	Frequency ♂	Frequency ♀	Mean wt. (g.) ♂	Mean wt. (g.) ♀	Calculated mean wt. (g.) ♂	Calculated mean wt. (g.) ♀
21·5		1				
22·5	4	1	12·0	13·0	12·9	12·8
23·5	21	11	15·6	17·4	15·5	16·6
24·5	50	50	19·5	18·5	18·5	19·6
25·5	88	77	24·0	22·0	22·0	23·0
26·5	68	61	26·7	27·9	25·8	26·8
27·5	23	16	27·3	29·2	30·2	31·1
28·5	3	1	35·0	38·0	35·2	35·8

B. By age

Age	Frequency ♂	Frequency ♀	Mean wt. (g.) ♂	Mean wt. (g.) ♀	Calculated mean wt. (g.) ♂	Calculated mean wt. (g.) ♀
3	18	9	15·6	11·9	15·5	13·2
4	32	37	19·3	19·2	18·9	17·1
5	106	98	22·2	21·6	22·0	20·9
6	18	11	26·1	25·5	24·9	24·6
7	34	15	25·3	27·3	27·7	28·3
8	43	46	28·8	29·1	30·3	31·9
9	5	2	31·2	37·0	32·9	35·5
11	1		42·0		37·7	

The data are shown graphically in Fig. 2. It would seem that the ovary is heavier than the testis at any given length, but that, while the mean weight of the testis is greater than that of the ovary among the younger fish (Table II B) among the older fish the reverse is found.

The formulae which best express the relation between the length of the fish and the weight of its gonad are

$$\text{for the males}\quad W=0{\cdot}0000241\,L^{4{\cdot}2371},$$

and

$$\text{for the females}\quad W=0{\cdot}0000594\,L^{3{\cdot}973}.$$

The weight of the testis therefore increases with length at a slightly greater rate than the ovary, but both increase at a rate about proportional to the fourth power of the length. Farran (1938) found that the ovary of the herrings he investigated increased with length at a somewhat greater rate, namely, as the 4·5 power of length.

Comparing the increase in weight of the ovaries, with increase of length, with the increase in the number of eggs produced, it will be noted that the former increases at a slightly greater rate, namely, as $L^{3{\cdot}97}$ is to $L^{3{\cdot}47}$. The discrepancy is due to the simultaneous increase in weight of the permanent tissue of the ovary. Nevertheless, since the production of eggs is the dominant function of the ovary, a close correlation should be expected between the mean weight of the ovary and the mean number of eggs produced. This is so; the correlation coefficient is 0·9692 ($P < 0\cdot01$), and one gramme of ovary is equivalent to 965 eggs.

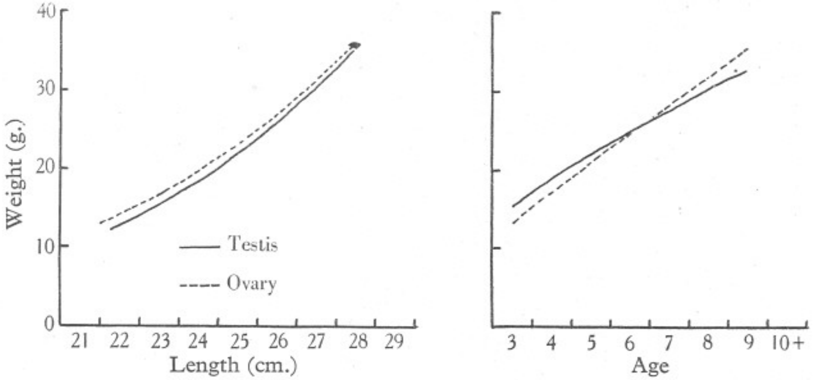

Fig. 2. Rate of increase in the weight of the gonads of the herring with length and age.

In Fig. 2 is also shown the relation between the age of the fish and the mean weight of the gonads. The ovary increases in weight, with increase of age, at a faster rate than the testis. This may be seen in the formulae below, which express the relation between the age of the fish and the mean weight of the gonads.

For the males $W = 7\cdot307\ \mathrm{Age}^{0\cdot684}$.

For the females $W = 4\cdot873\ \mathrm{Age}^{0\cdot904}$.

Comparing the rate of increase in the mean weight of the ovary, with age, with that of the mean number of eggs produced, it will be seen that the former increases at a substantially greater rate than the latter, namely, as $\mathrm{Age}^{0\cdot90}$ is to $\mathrm{Age}^{0\cdot66}$. But the production of a crop of eggs is an annual event, and it is attended by enormous changes in the volume of the ovary. It would therefore be expected that the permanent tissue of the ovary would show a considerable increase of thickness as a result of these successive expansions and contractions, and that the weight of the permanent tissue would increase more rapidly with age than with length, and more rapidly than the number of eggs produced.

THE WEIGHT OF THE FISH

In Table III are given the mean weights of the gutted herring of both sexes at each centimetre of length, and of the gutted herring together with their gonads.

The weight of the gutted fish alone increases, with length, according to the following formula,

$$W = 0\cdot1212\ L^{2\cdot132}.$$

That is, it increases at a rate nearer the square than the cube of the length.

TABLE III

Mid-length cm.	Frequency	Mean weight g.	Calculated mean weight g.
A. Mean weight of the gutted fish			
21·5	1	80	84
22·5	5	98	93
23·5	32	102	102
24·5	100	111	111
25·5	165	121	121
26·5	129	132	131
27·5	39	140	142
28·5	4	153	153
B. Mean weight of the gutted fish plus the gonads			
21·5	1	94	96
22·5	5	110	107
23·5	32	118	118
24·5	100	130	131
25·5	165	144	144
26·5	129	159	157
27·5	39	168	172
28·5	4	189	187

Other series of weights of herrings are available in the literature, but these are in every case the weights of the entire fish. To make the results here given comparable with these other series, it would be necessary to add to the weight of the gutted fish the weight of the gonad and gut. But, in the East Anglian herring shoals, the fish are not feeding, and the gut is a small organ weighing only a small percentage of the weight of the fish. It is proposed to neglect the weight of the gut, and to calculate only the relation between the length of the fish and the combined weights of the fish and its gonad. These data are given in Table III B, and from them the best-fitting equation of length and weight has been calculated. It is

$$W = 0{\cdot}06618\ L^{2{\cdot}372}.$$

Bjerkan (1917) gives data as to the weights of herrings taken at North Shields. From these it would appear that the best-fitting equation is

$$W = 0{\cdot}0421\ L^{2{\cdot}520}.$$

These herrings were mainly in Stage V of maturity, thus in much the same stage as those of East Anglia.

Orton (1916) gives a very complete series of data as to the length and weight (among a great number of other observations) of herrings taken in some hauls in the English Channel in December and January 1914–15. From his Table 3 the weights of some 20 fish at each half-centimetre of length were taken, and the mean weight at each half-centimetre calculated. The formula which best expresses the relation between length and weight is as follows

$$W = 0{\cdot}005838\ L^{3{\cdot}0875}.$$

These fish were taken in December, and had an average maturity, on Hjort's scale, of 4·5. In Orton's Table 4 are given the corresponding data for herrings taken in a haul in January. These herrings were in an average state of maturity of 5·2, and had a different relation between length and weight. This relation may be expressed by the formula

$$W = 0{\cdot}04108\ L^{2{\cdot}5006}.$$

Keys (1928) and Fraser (as quoted by Marshall *et al.* 1939) also used Orton's data to calculate the relation between weight and length in the herring. Their formulae are

$$\text{Keys,}\quad W = 0{\cdot}00268\ L^{3{\cdot}50}.$$

$$\text{Fraser,}\ W = 0{\cdot}00000337\ L^{3{\cdot}149}.$$

Neither formula fits the data extracted for the present paper, but, no doubt, much would depend on which of Orton's tables were used, and how the data were taken from them.

But the present writer's calculations show that, at least in herrings in an advanced state of maturity, the weight of the entire fish increases, with length, at a rate much less than the cube of the length, and therefore the fish alone, without the gonads and gut, must increase, with length, at an even slower rate, nearer the square than the cube of the length.

Among the small and immature herrings a different rate is found. Marshall *et al.* (1939) give data as to the weight of young herrings taken in the Firth of Clyde. From the data of fish caught in November and February, the relation between the wet weight of the fish, and length, is

$$W = 0{\cdot}004224\ L^{3{\cdot}120}.$$

In these immature herrings, of a length from 9·8 to 14·9 cm., the weight increased with length at a rate greater than the cube of the length.

Bjerkan (1917) gives a series of weights of "small fat herrings" from northern Norway, of a length from 16·0 to 24·5 cm. The relation between length and weight in these herrings, which were still immature, or, in the case of the largest fish, about to mature for the first time, is as follows,

$$W = 0{\cdot}006247\ L^{3{\cdot}0009}.$$

As a third comparison between the length-weight relation in young and small, and old and large herrings, the data published by Lea (1910) may be used. His Collection 6 gives the weight and length of a sample of herrings caught with the seine in northern Norway. The fish were all either immature, or, in the case of the largest fish, about to mature for the first time; their range in length was from 15·9 to 27·7 cm. The formula which best expresses the relation between length and weight in these herrings is

$$W = 0{\cdot}001772\ L^{3{\cdot}422}.$$

Thus the weight increased at a rate much greater than as the cube of the length. On the other hand, a sample of small herrings, of 13 to 19 cm., caught in the southern North Sea in August 1939, showed the following relation between length and the weight of the gutted fish

$$W = 0{\cdot}0270\ L^{2{\cdot}561}.$$

This rate of increase of weight is less than as the cube of the length, but is nevertheless substantially greater than the rate shown by the gutted mature herring of the southern North Sea which, as has been shown above, is as the 2·1 power of length.

In Table IV below, the herring material from the southern North Sea studied by me has been drawn up so as to show for each sex at each centimetre length and also at each age the mean weight of the gutted fish.

TABLE IV. MEAN WEIGHT OF THE GUTTED HERRING

Mid-length cm.	Frequency ♂	Frequency ♀	Mean wt. (g.) ♂	Mean wt. (g.) ♀	Calculated mean wt. (g.) ♂	Calculated mean wt. (g.) ♀
			A. By length			
21·5		1				
22·5	4	1	86	112	88	103
23·5	21	11	98	111	98	114
24·5	50	50	110	113	108	120
25·5	88	77	120	122	118	128
26·5	68	61	131	133	129	135
27·5	23	16	140	139	141	143
28·5	3	1	149	165	153	150
			B. By age			
3	18	9	105	112	102	112
4	32	37	110	119	111	118
5	106	98	117	120	119	122
6	18	11	130	126	126	126
7	34	15	126	131	132	130
8	43	46	133	133	138	131
9	5	2	136	136	143	136
11	1		165		152	

It would appear that the female has a greater mean weight than the male at lengths below 27 cm. but, as the differences are small, it is advisable to apply the test of the Significance of the Difference between Means to the data. There are too few observations at 21 cm. and 22 cm. to apply this test, but the mean weight of the female is much greater than that of the male among these small fish. Below are given the values for "t", and the corresponding values of P from Fisher's table, for each comparison.

TABLE V. SIGNIFICANCE OF THE DIFFERENCES BETWEEN THE MEAN WEIGHTS OF MALE AND FEMALE HERRINGS OF THE SAME LENGTH

Length cm.	Mean weight male g.	Mean weight female g.	t	p
23	98	111	2·8147	<0·01
24	110	113	1·2788	0·20
25	120	122	1·2752	0·20
26	131	133	0·9595	0·35
27	140	139	0·1714	0·85

The table shows that the values for "t" grow smaller with each centimetre increase in the length of the fish. At 23 cm. the means may be regarded as significantly different, but not among the larger fish. The smaller females are therefore definitely heavier than the males of the same length, but the difference grows less with increase of length, until there ceases to be any significant difference.

This finding means that the males must have a different relation between weight and length from the females. The females start at a higher mean weight, but are overtaken by the males with increasing length. They therefore increase in weight, with length, less rapidly than the males. This is confirmed by the calculated formulae to express the relation between weight and length in the two sexes. They are as follows:

For the males $W = 0{\cdot}0661\ L^{2{\cdot}312}$.

For the females $W = 1{\cdot}1471\ L^{1{\cdot}456}$.

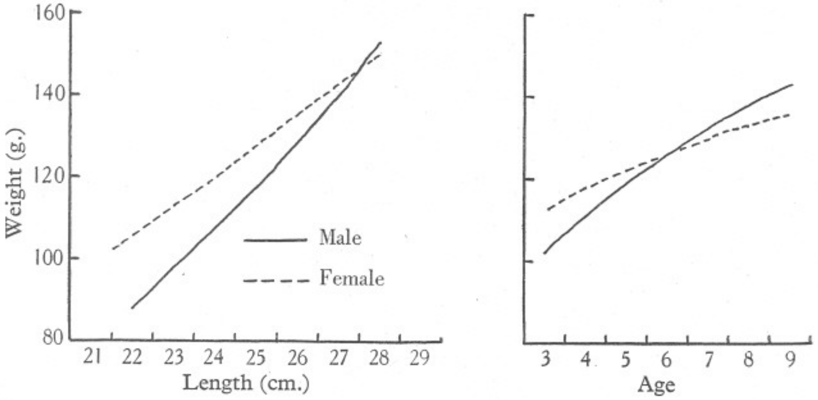

Fig. 3. Rate of increase in the weight of the gutted herring with length and age.

In Fig. 3 the mean weights of the male and female herrings at each centimetre are plotted, together with the regression lines based on the calculated mean weights (Table IV, mean weight).

In Table IV B are shown the average weights of the gutted fish at each age. Here the tendency is the same as was found in comparing length and weight, namely, the male starts at a lower mean weight, but catches up the female among the older fish.

The formulae to express the relation between age and weight are:

For the males $W = 72{\cdot}5\ \text{Age}^{0{\cdot}308}$.

For the females $W = 92{\cdot}1\ \text{Age}^{0{\cdot}177}$.

The regression lines of weight on age, together with the mean weights, are shown in Fig. 3.

THE FISH AND ITS GONAD

Wynne-Edwards (1929) studied the relation between the weight of the fish and the weight of its gonad in herrings from the Isle of Man, and reached the conclusion that "spawning does not draw on the resources of the fish to a greater extent than can be replaced with interest, each year....The growth of the gonads is in harmony with that of the other organs....Death cannot be due to the increasing tax of spawning ultimately exceeding the animal's powers of recovery."

This finding cannot be said to apply to the herrings of the southern North Sea. It has been shown that, in both sexes, the weight of the gonad increases, with increase of length, at a greater rate than the weight of the body which bears it. It has been shown (p. 622) that the gonads increase in weight, with increase of length, as the 4·2 power of the length in the males, and as the 4·0 power of length in the females, whereas, it was shown (p. 627) that the weight of the fish increases, with length, as the 2·3 power of length in the males, and as the 1·5 power of length in the females. The weight of the gonad therefore becomes an increasingly greater burden on the fish, and the ratio $\frac{\text{weight of gonad}}{\text{weight of fish}}$ is positively correlated both with length and with age.

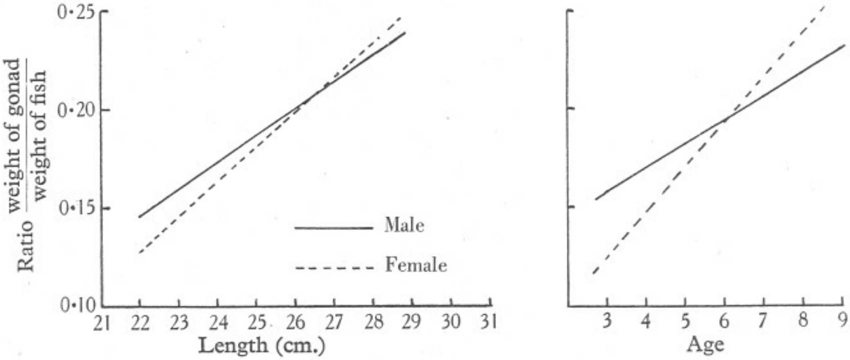

Fig. 4. Increase in the ratio $\frac{\text{weight of gonad}}{\text{weight of gutted fish}}$ with increase of length and of age in the herring.

In Fig. 4 the values of this ratio in both males and females are plotted against length and against weight. The correlation coefficients and the values for probability P are as follows:

Correlation	Coefficient	P
Between length and ratio, males	0·9432	$<0·01$
Between length and ratio, females	0·9763	$<0·01$
Between age and ratio, males	0·9845	$<0·01$
Between age and ratio, females	0·9589	$<0·01$

The regression coefficients and formulae have been calculated from these correlation coefficients, and the regression lines are plotted in Fig. 4. The gonad represents about 11% of the weight of the fish among females of three years of age, and about 15% among males, but the rate of increase is much greater among the females than among the males, so that at nine years of age the gonad represents some 27 % of the weight of the fish in the female, but only some 23 % in the male. If that rate of increase were maintained, the gonad would represent the absurd figure of half the weight of the fish at about twenty years of age in the female, though in the male it would then represent only some 36 %; and in both sexes the gonad would equal nearly half the weight of the fish at a length of about 40 cm.

In these herrings there is a disharmony between the growth of the fish and its gonad, such that an increasing strain must be put upon the fish with increase of length and age. This strain is shown by the decrease in the condition of the fish with increase of length and age, as shown by the relation between length and weight. But the strain is obviously less in the males than in the females, and this is probably the reason why the male maintains a better rate of increase of weight, both with length and with age, than the female.

The lighter burden laid on the male must have an important effect on the rate of growth and the rate of survival. It is a common experience to find that among fishes the males grow more slowly than the females, and also die out at an earlier age and at a smaller size. This is not so with the herring. That the male does not grow at a rate different from that of the female is sufficiently shown by the fact that no worker on this fish separates the sexes when calculating the growth rate. In the matter of the better survival of the male, the herring may be contrasted with the hake. In the latter fish, as the writer has shown (Hickling, 1933), the males outnumber the females among the younger fish, but the proportion of males to females progressively declines, until all fish older than twelve years are females, and only 25 % of the fish from ten to twelve years of age are males. But in the hake the male becomes mature much earlier in its life than the female, and the metabolic strain is a much heavier one in the male than in the female.

In the herring there is a tendency for the proportion of males to decline, with increase of age, as was pointed out long ago by Dahl (1907), but even in his samples of Norwegian spring herrings there was still an average of some 45 % of males among the fish of an age greater than twelve years. Similarly, in Collection 9 of Lea (1910), there were 56 % of males among the ten, and 41 % among the eleven-year old fish.

In Table IV of the present paper there are more males than females among the larger and older fish, and Dr Hodgson has very kindly put at my disposal the vast mass of data on the herring of East Anglia he has gathered. Selecting at random the years 1926 and 1927, and from each of these eight samples, taken both early and late in the season, the following is the average percentage of males both with regard to length and age.

Length and percentage of males

cm.	21	22	23	24	25	26	27	28
% males	65	51	46	46	47	48	40	45

Age and percentage of males

Age	3	4	5	6	7	8	9
% males	49	45	46	47	46	48	53

It is clear that there is no tendency for males to become rarer among the larger and older herrings in the southern North Sea.

The Comparative Spawning Powers of the Herring Shoals

Jensen (1927) found a very good relation between the anomalies from the "normal catch" from year to year in the herring fishery at Bornholm in the Baltic, and a sine curve with a period of 3·7 years. This periodicity can be explained by the fact that the three and four-year-old fish greatly predominate in the spawning shoals, and therefore as a rule produce the largest quantity of fry. The survivors of these fry again produce large quantities of fry when they mature at three and four years of age, and so a good year class, or pair of year classes, perpetuates its abundance, and produces abundant catches at intervals of three to four years.

Dr Hodgson has given me the results of his analyses of the age composition of the East Anglian herring shoals for the years 1923 to 1938 inclusive, of which the results for the years 1923 to 1928 have already been published (Hodgson, 1929). These take the form of a percentage of fish of each age in each season. Table V gives the mean percentage of fish at each age for the whole series of years, together with the calculated mean number of eggs produced by the females of each age, from Table I B. Thence, by calculation, is given the comparative spawning power of each age group in the series, and finally, the percentage of the total spawning power contributed by each age group.

Table V. Mean Age Composition of the East Anglian Herring Shoals, 1923–38, and Spawning Power at each Age Group

Age	3	4	5	6	7	8	9
Mean % of fish	12·1	28·5	23·3	15·3	10·3	6·0	3·0
Mean fecundity	14,600	17,700	20,500	23,100	25,600	27,900	30,200
Spawning power	176,660	504,450	477,650	353,430	263,680	167,400	90,600
Percentage	8·7	24·8	23·5	17·4	13·0	8·2	4·5

The table shows that at least three age groups contribute in a very important degree to the supply of eggs, and this would militate against the establishment of a periodicity in the abundance of eggs spawned, for a rich year class can contribute for three years in succession a supply of eggs sufficiently important to make good the deficiency due to poor year classes which precede or succeed it. It is, in fact, found that the "comparative spawning power" of these East Anglian herring shoals varies little from year to year. The ratio of the poorest to the best seasons in this series was 193 : 222, and there is no correlation between the "spawning power" of the herring shoals in any year and the percentage of three-year-old herrings which appear in the shoals three years later.

SUMMARY

The number of eggs produced by the herrings of the East Anglian shoals increases with the length of the fish at a rate equal to the 3·465 power of the length, and with the age of the fish to the 0·66 power of the age. This fecundity is compared with that found in other races of herrings.

The number of eggs produced is closely correlated with the mean weight of the ovary, and it is found that the weight of the ovary increases with length at a rate equal to the fourth power of the length, and that a slightly higher rate applies to the testis.

The weight of the gutted fish, however, increases in relation to the length at a much slower rate, namely, as the 2·3 power of the length in the males, and the 1·5 power of the length in the females.

The gonad, therefore, represents an increasing burden on the fish with increase of length, and the same is true with regard to age. Moreover, the strain of reproduction increases more rapidly with both length and with age in the female than in the male. This fact may explain the equal growth rate of male and female herrings, and also the survival of the male herrings to reach a large size and an advanced age, both of which phenomena are contrary to those found among many species of fishes.

The mature herrings show a sharp decline in the rate of growth in weight with length, as compared with immature herrings.

The data on the fecundity of the herring are applied to the age-distribution of the herrings of the southern North Sea, and it is concluded that the known changes in the age distribution from season to season do not cause a sufficiently great variation in the "spawning power" of the shoals to account for the variations in strength of the year-classes.

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AN ACCOUNT OF *MARINOGAMMARUS* (SCHELLENBERG) GEN.NOV. [AMPHIPODA], WITH A DESCRIPTION OF A NEW SPECIES, *M. PIRLOTI*

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From the Plymouth Laboratory

(Plate IV, Text-figs. 1–11)

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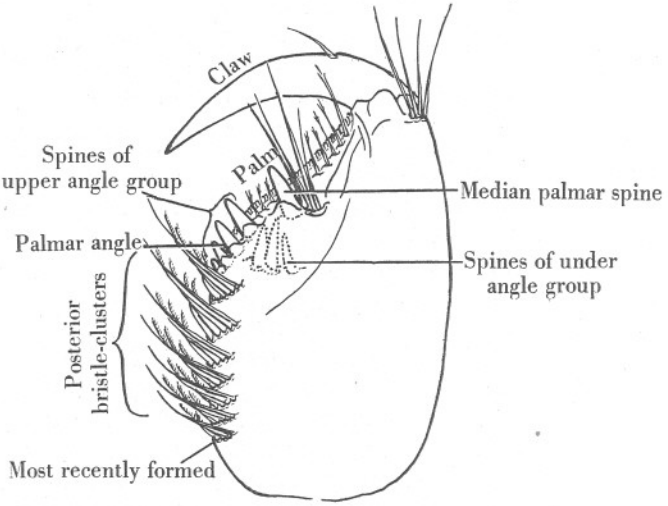
INTRODUCTION

The genus *Gammarus*, instituted by Fabricius in 1775, has come to include a large number of species—so many and so varied, in fact, that the necessity for a revision of the genus is well recognized. An extensive examination of the taxonomic literature has inevitably led to the conclusion that several more or less well-defined groups of species can be recognized among the total assemblage, and that some of these at least should be separated off as distinct genera.

In this present contribution we do not propose to discuss the dismemberment of *Gammarus* as a whole, but as a first step to treat one of the natural groups hitherto included within it. This group, here raised to generic status under the name of *Marinogammarus*, has been in special need of revision. It appears to have its headquarters in north-western Europe, and includes nearly half the British species of *Gammarus sens. lat.* Thus, from the point of view of our proposed aim of thoroughly revising the British species of this assemblage, an important part of the ground is here covered.

Karaman (1931) started the division of the genus, followed later by Schellenberg (1937*a*). The latter outlined and named several subgenera; but in the opinion of such well-known writers on Amphipoda as Prof. Jean-M. Pirlot and Prof. Louis Fage, these groups should be given full generic status, provided of course that they can be shown to possess distinct and constant characters. With this view we are in complete agreement. We have therefore taken one of the most clearly marked divisions, *Marinogammarus* (Schellenberg), giving its generic diagnosis, with descriptions and figures of all the six species which can be clearly recognized as belonging to it. It seems doubtful whether any other described species of palaearctic "*Gammarus*" not examined by us will prove to belong to this genus. Five of the six species are so far known to occur in Britain.

Our special thanks are due to Dr Isabella Gordon for her kind help in enabling us to have access to the collections preserved in the British Museum; to Prof. Louis Fage for having forwarded to us type specimens preserved in the Muséum National, Paris; to Prof. Jean-M. Pirlot, of the University of Liége, for having placed at our disposal various material, including specimens, microscope mounts, and drawings; and to Mr G. I. Crawford for having sent us material (collected by himself) from wide-spread localities for the purpose of this work.



The whole work has also greatly benefited from the opportunities we have had for examining material sent to us for determination. From having seen samples from a number of different localities, we have been able to confirm the constancy of specific characters, to make a first step in defining the distribution of the different species, and to reduce considerably the probabilities that still other overlooked species occur in Britain. Our grateful acknowledgements are due to the following zoologists: Mr R. Bassindale, Mr L. C. Beadle, Prof. A. D. Hobson, Mr R. MacDonald, Mr D. M. Reid, Hon. Miriam Rothschild, Dr K. Stephensen and Prof. C. M. Yonge. Records of material examined are listed under the separate species.

The terminology adopted throughout the paper is based on that of Stebbing (1906). The gnathopod armature, which has been found to show many interesting features, has been studied in greater detail than is perhaps customary: a diagram of a gnathopod hand is appended (p. 634) to make clear the designation of the structures referred to in the descriptions. The lateral plates of the first three pleon-segments are termed "epimera 1–3". The names used in describing certain types of setae are defined in a separate section at the end of the paper (pp. 676–81).

Measurements of length refer to the distance between the apex of the rostrum and the base of the telson, when the specimen is straightened out along a stage-micrometer. In the study of details of structure, specimens were dissected and their parts mounted for examination under the microscope. All drawings were made with the aid of a camera lucida. A set of permanent preparations, mounted in gum chloral solution, has been made for each species.

HISTORICAL

In north and west Europe, as well as in eastern North America, the species of the assemblage *Gammarus* comprise two very distinct types, recognized as long ago as 1815 by Leach. In his *Arrangement of the Crustacea* (1815, p. 359) Leach divided the species of *Gammarus* F. into two groups, according to the degree of development of the rami of uropod 3, characterized thus: "*cauda stylis geminatis superioribus stylo supero brevissimo*", with *G. aquaticus* (= *pulex*) and *G. marinus*; and "*cauda stylis geminatis superioribus stylis subaequalibus*", with *G. locusta* and *G. campylops*.

It must be noticed in passing that Leach's grouping contains an anomaly, which, as Walker (1911) has clearly shown, can only have been due to an unintentional error on the part of the author. Both *G. aquaticus* and *G. campylops* (see p. 673) had been placed in the wrong groups, and had doubtless been accidentally transposed. The necessity for this emendation must be accepted.

Of Leach's two divisions the second one should retain the generic name of *Gammarus*, with *locusta* (L.) as the type. The questions as to what other species are to be included in this segregate genus, and whether *pulex* and the freshwater forms which are grouped with it are to be given generic status, fall beyond the scope of the present work. It is only necessary to point out that *locusta* (L.), and the related species *duebenii* Liljeborg, *zaddachi* Sexton, and *chevreuxi* Sexton, are recognized as undisputed representatives of *Gammarus* in the restricted sense. These are relatively active free-swimming forms, seeking the cover of weeds and vegetable debris rather than of stones, and with their optimum environment in permanent waters. Their most noticeable structural character is to be found in the long and well-developed inner ramus of uropod 3, both rami being fringed with long setae.

Leach's first division, for the inclusion of *marinus*, is the group which, as already stated, is here treated as a separate genus. It includes the genotype *marinus* (Leach) and five related species, of which four have only been recognized quite recently. The name *Marinogammarus* has to be used, as Schellenberg (1937*a*) has already formed a subgenus of this designation, with *marinus* as the only certain representative known to him. The species are essentially bottom-living forms, inhabiting the intertidal zone, and living amongst stones and shingle. The most distinctive character which separates them from *Gammarus sens. str.* is the short inner ramus of uropod 3—almost scale-like in most species; but this character is also shared by diverse groups of species, inhabiting south-eastern Europe and western Asia, which clearly cannot be placed in *Marinogammarus*. For an adequate diagnosis of the latter a combination of characters has to be taken into consideration. The best brief description that can be devised is "*Gammarus*-like species, with short inner ramus, almost or completely lacking setae on hind peraeopods and on the urosome dorsally, with elongate eyes, and adapted for life in stony intertidal habitats."

GENUS Marinogammarus (Schell.)

Gammarus in part Leach, 1815, p. 359; Sars, 1894, p. 496; Stebbing, 1906, p. 460.
Gammarus subg. *Marinogammarus* Schellenberg, 1937*a*, p. 270.

Body smooth and rounded. Pleon-segments 4–6 (or urosome) at most with slight dorsal elevations, never strongly produced; with four groups of spines, median and lateral, the two median groups remaining more or less separated in the mid-dorsal line; no setae present among these spines. Sideplates 1–4 not very deep, margins rounded and almost glabrous; 4 about as broad as deep, smoothly rounded on distal margin. Epimera of pleon-segments 2 and 3 never greatly produced posteriorly, the postero-distal angle from slightly acute to strongly obtuse.

Head without conspicuous rostrum; lateral lobes rounded. Eyes large, elongate, sometimes notably long and narrow, usually in adult slightly constricted in middle. Antenna 1 longer than antenna 2; basal joint of peduncle always long; accessory flagellum of medium length, with from 4 to 9 joints. Antenna 2 with flagellum usually slightly shorter than peduncle, occasionally equal to it in length, sometimes bearing calceoli.

Oral parts. Upper lip a little wider than deep, slightly emarginate at apex; lower lip without inner lobes. Mandible normal, with strongly dentate cutting-edge, accessory plate, spine-row, molar, and 3-jointed palp; the right mandible bearing a long stiff feathered bristle behind the molar. Maxilla 1 with inner plate bearing long feathered setae, and outer provided with stout serrate spines; palp of the right maxilla with spine-teeth on the apex, that of the left with setiform spines. Maxilla 2 with rows of long serrated bristles on both inner and outer plates. Maxillipeds with inner plate armed distally with large spine-teeth; outer plate with long curved serrated spines and spine-teeth; palp well developed.

Gnathopods 1 and 2 subchelate, stronger in male than in female; hands in male usually not markedly different in size, occasionally 1 larger than 2; palmar median spine rounded, never truncate.

Peraeopods 1 and 2 sometimes more densely setose in female than in male. Peraeopods 3–5 armed with clusters of strong spines, setae rarely present; basal joint expanded, postero-distal corner of peraeopod 3 always free; claw strongly recurved.

Uropod 3 with outer ramus long and broad; inner ramus small, typically almost scale-like. Telson cleft to the base, each lobe at least twice as long as broad, with one lateral and one apical cluster of spines.

Male sensory setae usually with more or less abruptly narrowed apices; not developed on peraeopod 1.

Habitat essentially littoral, intertidal, sometimes further restricted to places subjected to freshwater influence. Structure and habits of species adapted for living under cover of stones.

Distribution: North Atlantic, temperate and boreal, coasts of west and north Europe and north-east America, range extending into adjoining seas.

Genotype: Gammarus marinus Leach, 1815.

Six species belonging to this genus are described below: *marinus* (Leach, 1815), *olivii* (Milne-Edwards, 1830), *obtusatus* (Dahl, 1938), *finmarchicus* (Dahl, 1938), *stoerensis* (Reid, 1938), and a new species, which we have called *pirloti* in honour of Prof. Pirlot of Liége.

A species of hitherto doubtful status, *Gammarus locustoides* Brandt 1851, has sometimes been provisionally grouped as a close relative of *marinus*, to which it bears a superficial resemblance. This species inhabits the coasts of the North Pacific, where the other marine *Gammarus* forms belong to *Anisogammarus*, a genus separated on the possession of thin processes attached to the gills. A re-examination of *G. locustoides* has shown it to possess this character; hence it is to be placed in that genus, and is not a *Marinogammarus*.

Marinogammarus marinus (Leach)

Text-figs. 1 *a–i*, 2 *a–j*, 11 *k*, *l*.

The principal references to the species are:

1815 *Gammarus marinus* Leach, *Trans. Linn. Soc.*, Vol. XI, p. 359.
1894 *Gammarus marinus* Sars, *Crust. Norway*, Vol. I, p. 497, Pl. 175.
1906 *Gammarus marinus* Stebbing, *Das Tierreich*, Vol. XXI, p. 472.
1925 *Gammarus marinus* Chevreux & Fage, *Faune de France*, Vol. IX, pp. 250–1, fig. 260.

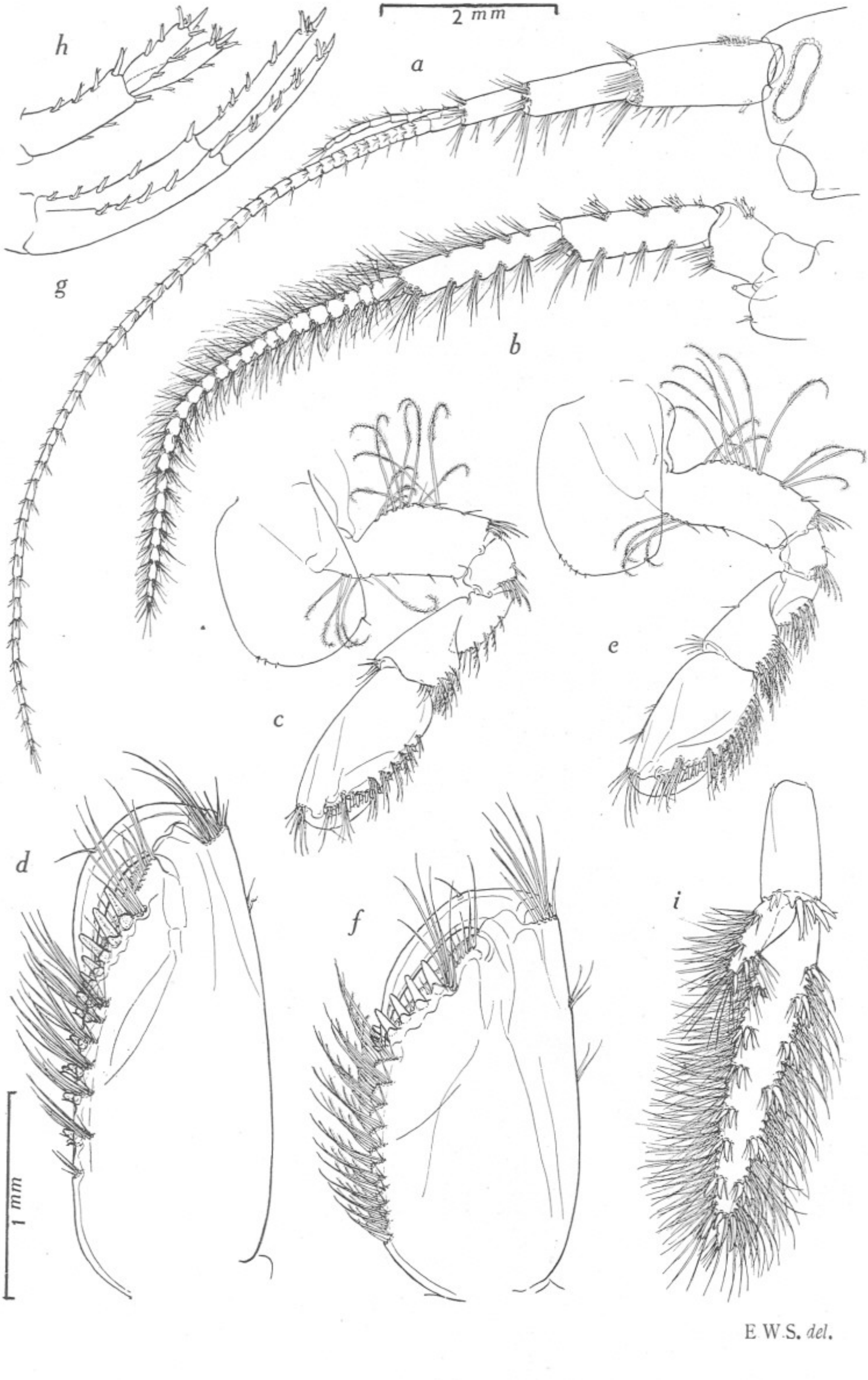
This species was instituted by Leach in 1815, but since then many other and quite distinct species have been frequently recorded as *marinus*, so that a great deal of confusion has been caused in the records of its distribution. For example, collections of "*marinus*" from the British coasts, Shetland, and the East Murmansk coast, have proved to be *obtusatus* Dahl; from Naples, *olivii* M.-Edw.; from Durham, *stoerensis* Reid, and so on. Many of the earlier writers classed *marinus* Leach as a variety of *locusta*. Spence Bate (1862, p. 215) recognized it as distinct, but included in its synonymy Milne-Edwards' *G. olivii* and *G. affinis*, as well as Rathke's *G. gracilis*, *G. poecilurus* and *G. kröyeri*. Stebbing (1906) follows him in this with the addition of *G. locustoides* Brandt. *Gammarus olivii*, however, has been proved a distinct species by Chevreux & Fage (1925), who examined and redescribed Milne-Edwards' types (see p. 645). The other species mentioned were not sufficiently defined or figured to be identified with any certainty.

Sars (1894) was the first to give a good definition and figures of *marinus*. We have refigured it here in order to draw attention to various details, particularly those which have diagnostic value in separating the species from others of the genus. These characters include the presence of a row of short spines (curvate in male, acute in female) on the posterior margin of the hand of gnathopod 1 (Text-fig. 1 *d*), and the form and arrangement of setae on uropod 3 (Text-fig. 1 *i*).

ADULT MALE.

Body slender and compressed. Pleon-segments 4–6 with dorsal spines more numerous than in the other species, the number increasing with age; each segment carrying two upward converging rows of 6–9 spines on each side, these four groups tending to merge into a continuous curved row. Sideplates 1–4 not very deep; 4 (Text-figs. 2 *b* and 2 *c*) about as broad as deep, distal expansion rather shallow, posterior expansion obliquely rounded. Epimera 2 and 3 (Text-fig. 2 *g*), postero-distal corner of 2 subquadrate, of

Text-fig. 1. *Marinogammarus marinus* (Leach), male. Figures drawn from an adult male, captured Plymouth district (Tamar Estuary, Thorn Point, 10. xii. 37), compared with specimens from other localities, Great Britain, Northern Ireland, Denmark and Norway. Magnification × 13, except *d* and *f* × 28. *a*, head and antenna 1, outer surface left side; *b*, antenna 2, outer surface left side; *c*, gnathopod 1, left side; *d*, gnathopod 1, left side, hand enlarged; *e*, gnathopod 2, left side; *f*, gnathopod 2, left side, hand enlarged; *g*, uropod 1, left side; *h*, uropod 2, left side; *i*, uropod 3, showing the inner ramus.



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3 somewhat acute and more produced than in the other species; posterior margins inset with numerous upward-pointing setules.

Head (Text-fig. 1 *a*) not quite as long as peraeon-segments 1 and 2 combined; with lateral lobes vertically truncate, distal margin rounded, sinus rather deep. Eyes notably long and narrow, slightly constricted in the middle, the elongation evident from a very early age; pigment black. Antenna 1 (Text-fig. 1 *a*) with joint 1 of peduncle clearly longer than joint 2, but somewhat shorter than 2 and 3 combined, joint 2 approaching twice length of joint 3; flagellum about $2\frac{1}{2}$ times as long as the peduncle, the number of joints reaching at least 47; accessory flagellum about half the length of the peduncle, 8-jointed in large specimens. Antenna 2 (Text-fig. 1 *b*) considerably shorter than antenna 1; flagellum about as long as peduncle, 26–29-jointed in large specimens; dense tufts of male sensory hairs (p. 680 and Text-fig. 11 *d*) developed on joints 4 and 5 of the peduncle, and on the flagellum; calceoli lacking. An occasional seta on peduncle of antenna 1 with bifurcate apex.

Gnathopods (Text-figs. 1 *c*–*f*). Hand of gnathopod 1 (Text-fig. 1 *d*) appreciably longer than that of gnathopod 2; elongate; palm oblique; median palmar spine not separated from the angle spines; the most distal of posterior bristle-clusters situated at the level of the palmar angle: this hand showing an important diagnostic character—the posterior margin being provided with a series of short curvate spines arising in connexion with the bristle-clusters, all the bristle-clusters, except the most proximal (i.e. the most recently formed), having 1 or 2 of these spines inset closely beside it on the extreme edge of the margin. Hand of gnathopod 2 (Text-fig. 1 *f*) with the palm nearly transverse, and palmar angle well-defined; median spine, as in gnathopod 1, not separated from angle spines; normal with respect to position of the most distal posterior bristle-cluster and to absence of curvate spines along posterior margin. Joint 5 subequal in length to that of gnathopod 1. Bifurcate setae on both gnathopods, except hand of gnathopod 1.

Peraeopods 1 and 2 (Text-fig. 2 *a*, *b*) sparsely setose, lacking both male sensory and bifurcate setae. Basal joint of peraeopod 3 (Text-fig. 2 *d*), with posterior distal angle free, subangulate; those of peraeopods 4 and 5 (Text-fig. 2 *e*, *f*) narrowed distally, with the angle "closed", inset with a group of 2 or 3 spines; posterior expansions in all three with numerous marginal setules. Peraeopod 4 with joint 4 over twice as long as distal width; peraeopods 4 and 5 with joint 5 rather longer than joint 6.

Uropod 1 (Text-fig. 1 *g*, *h*) reaching beyond uropod 2. Uropod 3 (Text-fig. 1 *i*) with outer ramus long, bearing dense clusters of spines and setae around both margins, the setae mainly of the male sensory type, and none plumose; second joint short, spiniform, with a tuft of setae at tip (in the newly hatched young this joint more than half the length of joint 1; Text-fig. 2 *i*); inner ramus very narrow, about one-quarter length of outer, nearly surrounded by a dense fringe of hairs and spines. Telson (Text-fig. 2 *j*) rather small, lobes distally divergent, each with a lateral cluster of spines near base, and a cluster of 3 on the truncate apex.

ADULT FEMALE.

Differences from adult male as follows.

Both antennae with bifurcate setae well distributed.

Gnathopods. Joint 5 longer in gnathopod 2 than in gnathopod 1. Hand of gnathopod 1 much smaller and very different in form from that of male, the palm not at all oblique; spines present, as in male, between the more distal of the posterior seta-clusters, these spines acute and not curvate. Hand of gnathopod 2 smaller than in male, elongate. Bifurcate setae well distributed on both gnathopods.

Peraeopods 1 and 2 (Text-fig. 2*c*) much more setose. Brood-plates comparatively large, anterior pair (attached to gnathopod 2) with hairs of anterior margin forming a continuous dense row.

Uropod 3 (Text-fig. 2*h*) with outer ramus bearing plumose hairs amongst the setal fringe on the inner margin; spines on inner margin long and slender; inner ramus very sparsely setose.

Eggs dark brownish when newly laid, changing to dull yellow as embryos develop; produced in batches of between 30 and 50; size rather smaller than in some of related species (average dimensions of one batch of 11 recently laid: 0·49 × 0·59 mm.). *Young* 2–2$\frac{1}{4}$ mm. at extrusion.

SIZE AND COLOUR.

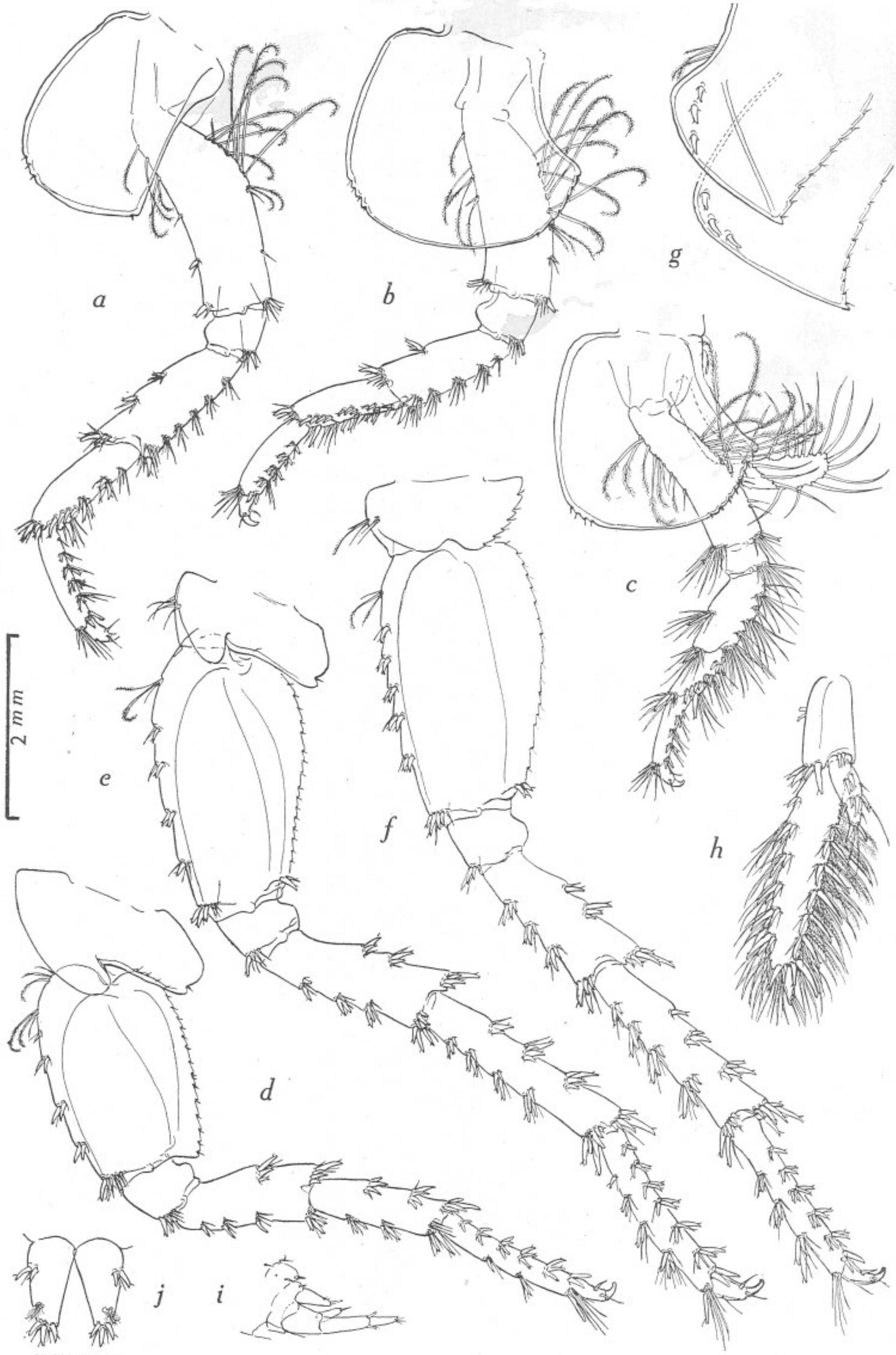
Length of male 15–25 mm.; female on average smaller, to about 20 mm. Colour dark green, sometimes suffused with reddish or yellowish brown, body pigment of adult typically denser than in related species; pleon-segments at most with diffuse patches of pink, never with clearly defined orange patches.

HABITAT.

A littoral species, distributed along the sea-coast, and penetrating estuaries for some distance; strictly intertidal, its optimum being between high-water neaps and about mid-tide level; seeking cover of stones, clusters of fucoids, and other objects lying on the ground; on gravels, mixed grounds, and even soft mud, but scarce or absent on cleaner sands or shingle.

MATERIAL EXAMINED.

England. SOUTH DEVON AND EAST CORNWALL: many samples, both from the coast near Plymouth and from the shores of estuaries from the River Lynher to the River Axe, including among others, the following: Plymouth Sound, shore of Sutton Pool, Rum Bay, Drake's Island, etc., less numerous in general than *M. obtusatus*; Plymouth district, seventy-five specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. Rivers Tamar, Lynher, and Tavy estuaries, in many samples from various points of the estuarine area, mainly in upper half of tidal zone under weeds and stones, reaching to



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North Hooe, Maristow Quay, Sconner Creek, head of Tamerton Lake, etc. (see Hartley & Spooner, 1938, Pl. XVIII), material recorded by Crawford (1937, p. 650) confirmed; the only species of *Marinogammarus* known from this area. River Plym estuary in fifteen samples, ranging up to Marsh Mills Railway Bridge; River Yealm estuary, in samples from near mouth and middle reaches; River Erme estuary, in four samples from near seaward end; River Avon estuary, plentiful intertidally under weeds and stones up to half a mile below Aveton Gifford; Kingsbridge estuary, under weeds, upper part of tidal zone in Blank's Mill Creek; River Exe estuary, intertidally opposite Woodbury Road Station and at Topsham; River Axe estuary, intertidally in two stations above Axmouth.

NORTH DEVON: River Taw estuary, Caen River, in two samples recorded by Crawford (1937, pp. 653–4), identity confirmed. NORTH SOMERSET AND WEST GLOUCESTER: Severn estuary: plentiful in many samples, mainly from upper tidal levels and about mid-tide, from Kilve to Sheperdine, March to August 1939; also one ♀ Sharpness, 16. iv. 39 (identified for Mr R. Bassindale).

LINCS: River Welland near Holbeach, pool on banks near sea-wall, 30. vii. 39 (Miriam Rothschild), 2 imm. NORTH-EAST YORKS AND DURHAM: River Tees: among specimens in tube labelled "*G. marinus* Leach", Tees Survey Investigations (material deposited at the Plymouth Laboratory), confirming that the species is at least included in the records given under this name by Alexander *et al.* (1935, p. 55). NORTHUMBERLAND coast: Howick, 2. vi. 39, sample containing many adults, but sizes small, showing evident signs of stunted growth (identified for Mr L. C. Beadle); Blyth, ditch from salt pans, 4. vii. 34, 7 large ♂♂, 8 large ♀♀, 1 imm. (identified for Prof. A. D. Hobson). ISLE OF MAN: Castletown, 7. ix. 38, 11 adults (coll. G. I. Crawford).

Scotland. EAST LOTHIAN: near Reed Point, under stones just below high-water mark, 1. v. 32, 1 ♂ and 1 ♀; Port Seton, under stones near high-water mark, 7. iii. 32, 1 ♂ and 2 ♀♀ (identified for Prof. A. D. Hobson). FIRTH OF TAY: samples from Tees Survey Investigations preserved in the Plymouth Laboratory as follows: Section XI of river, high-tide level, 3 examples, mid-tide level, numerous, low-tide level, many; Section X, low-tide level, a number; Section IX, high-tide level, one example, low-tide level, a number; Section VIII, tidal zone, 2 ♂♂ and 1 ♀: thus confirming the distribution of *G. marinus* given by Alexander *et al.* (1935, p. 55) (note, however, that a few *M. finmarchicus* were mixed with this species, see p. 661).

Text-fig. 2. *Marinogammarus marinus* (Leach), male and female. Figures drawn from same adult male as in Text-fig. 1, and a large female from same sample which hatched 49 young. Magnification × 13, except *i* × 45. *a*, peraeopod 1 of ♂, left side; *b*, peraeopod 2 of ♂, left side; *c*, peraeopod 2 of ♀, with brood-plate shown, left side; *d*, *e* and *f*, peraeopods 3, 4 and 5 respectively, of ♂, left side; *g*, epimera of pleon-segments 2 and 3 of ♂, left side; *h*, uropod 3 of ♀, left side; *i*, uropod 3 of one of this female's newly hatched young, taken from the incubatory pouch, showing the different proportions of the joints of outer ramus at birth, left side, × 45; *j*, telson of ♂.

ARGYLLSHIRE: Clachan Strand, 2. vi. 35, "under weed", 5 ♂♂, 9 ♀♀, 2 imm. (identified for Prof. A. D. Hobson). INNER HEBRIDES: Isle of Muck, August 1938 and 1939, in three samples, 1 ♂ and 6 imm.; Raasay, August 1937, in three samples, 4 ♂♂, 6 ♀♀, and 15 imm.; South Rona, August 1937, in thirteen samples, 50 ♂♂, 39 ♀♀, 73 imm. (identified for Prof. A. D. Hobson). WEST SUTHERLAND: Bay of Stoer, 14. iv. 39 (D. M. Reid), large ♂ and ♀ (confirmed by Dr K. Stephensen). ORKNEYS: Hoy, Quoyness, rocky shore near high water, 20 ♂♂, 5 ♀♀ and 8 imm. (coll. K. M. G. Fleming).

Ireland. ANTRIM: Whitehouse, 11. i. 36 (coll. R. MacDonald). WEST CORK: Glengarriff, shore, in *Fucus spiralis* and *Pelvetia canaliculata*, 23. vii. 38, five examples. SOUTH KERRY: Kenmare, shore, among *Ascophyllum*, etc., 23. vii. 39, twenty-five examples, adults and well-grown imm.; Kenmare, small brackish stream (with *G. zaddachi*), 23. vii. 38, 1 imm. (coll. G. I. Crawford).

Continental. DENMARK: ♂ and ♀ ovigerous, determined and dissected by Prof. J. Pirlot, "conforme aux figures de Sars". NORTH NORWAY: Svolvaer, Lofoten Islands, marine, sheltered, mid-tide, 26. vi. 39, 11 ♂♂ and 9 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

In view of the fact that any of the species of *Marinogammarus* may in the past have been recorded as "*marinus*" (and several notable instances of this have actually been found), the data on the distribution of this species will have to be reviewed afresh. At present it can be said that the species is widely distributed in the British Isles, and is probably the most abundant of the genus owing to its tolerance of estuarine as well as of marine conditions. Its presence along the western and northern coast of Scandinavia is also established.

This may be accepted as at least the main species referred to by Chevreux & Fage (1925, p. 251) as occurring along the Channel and Atlantic coasts. It may be noted that these authors give no instances of its occurrence on the Mediterranean coast of France, where it seems to be entirely replaced by *M. olivii*, and in the writings of Schäferna and Karaman no records for south-east Europe are given. In view of this, and in view, furthermore, of the fact that Stebbing's specimens of "*marinus*" from Naples were found to be *olivii* (see p. 649) extreme doubt may be expressed as to whether the species ranges into the Mediterranean Sea at all. Older records from this area, such as those quoted by Sars (1894, p. 498) must be taken to refer to *olivii* or some other species.

Marinogammarus olivii (Milne-Edwards)

Text-figs. 3*a*–*l*, 4*a*–*o* and 11*f*.

1830. *Gammarus olivii* Milne-Edwards, *Ann. Sci. Nat.*, Vol. xx, pp. 367, 372, Pl. X, figs. 9, 10.
1862. *Gammarus marinus in part*. Spence Bate, *Cat. Amphip. Brit. Mus.*, p. 215, Pl. XXXVIII, fig. 4.
1894. *Gammarus marinus in part*. Sars, *Crust. Norway*, Vol. I, p. 498.
1906. *Gammarus marinus in part*. Stebbing, *Das Tierreich*, Vol. XXI, p. 472.
1925. *Gammarus olivii* Chevreux & Fage, *Faune de France*, Vol. IX, pp. 251–2, fig. 262.

This is the only species of *Marinogammarus* as here defined which has not yet been recorded from Britain, but as it has been found in Morbihan, Brittany (Chevreux & Fage, p. 252), it may well occur also on this side of the Channel.

G. olivii was first described by Milne-Edwards from specimens taken at Naples. He considered it to resemble *G. locusta* except for several characters, such as the shape of the eyes, gnathopod hands, unequal rami of third uropods, etc. In 1862 Spence Bate included the species under *G. marinus* Leach, and was followed in this by Sars and Stebbing. Later Chevreux & Fage re-examined Milne-Edwards' type specimens preserved in the Paris Museum, and were thus enabled to give the excellent description and figures which placed the distinction of the species beyond question.

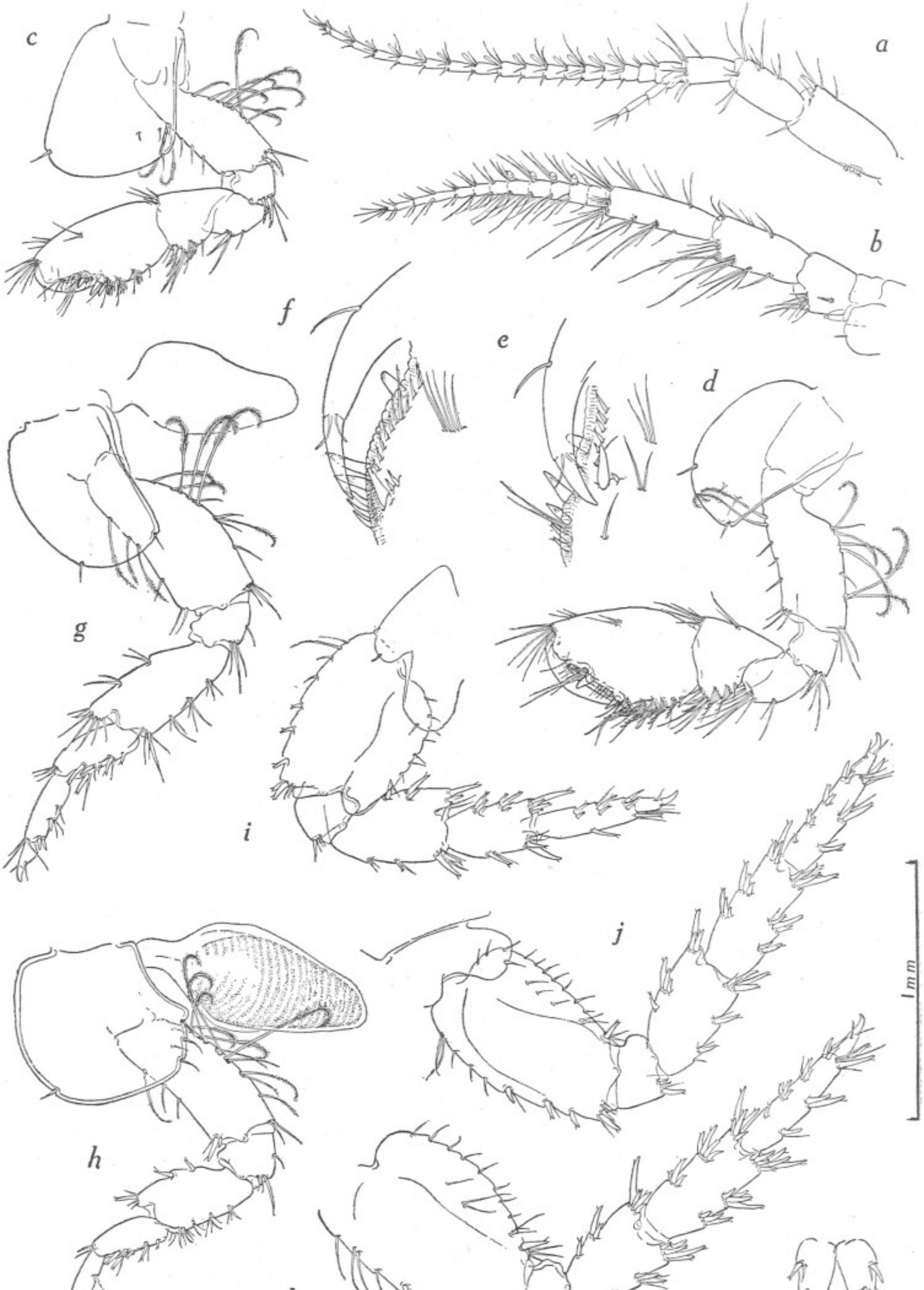
Through the courtesy of Professor Louis Fage we have had the opportunity of examining Milne-Edwards' types. We have also seen specimens, kindly forwarded by Dr Isabella Gordon, which are preserved in the British Museum. The latter include examples in Stebbing's collection, labelled "*Gammarus marinus*", from Naples: from one of these, a young male, most of the figures given here have been drawn.

It will be seen that *olivii* is clearly related to *marinus*, and not, as some recent authors have suggested, to *Gammarus pungens* Milne-Edwards.

ADULT MALE.

Pleon-segments 4–6 produced in rounded humps, spines short, armature very sparse and different from *marinus*; formula in specimens examined being 2 : 1 : 1 : 2 on each of the three segments. Sideplates 1–4 deeper than corresponding segments; 4 about as wide as deep, with 3–4 setae inset on the posterior expansion. Epimeron 2 (Text-fig. 4*a*) with posterior margin somewhat rounded, and distal angle subobtuse; epimeron 3 (Text-fig. 4*b*) with margin straight, and angle rectangular; margins with several small setae inset. Setose armature on body and limbs in general longer than in other species of genus.

Head (Text-fig. 4*k*) with lateral lobes truncate, and lightly concave, lower angle obtuse, sinus rather deep. Eyes relatively large, broader and more reniform in shape than in *marinus*; somewhat constricted in middle; described



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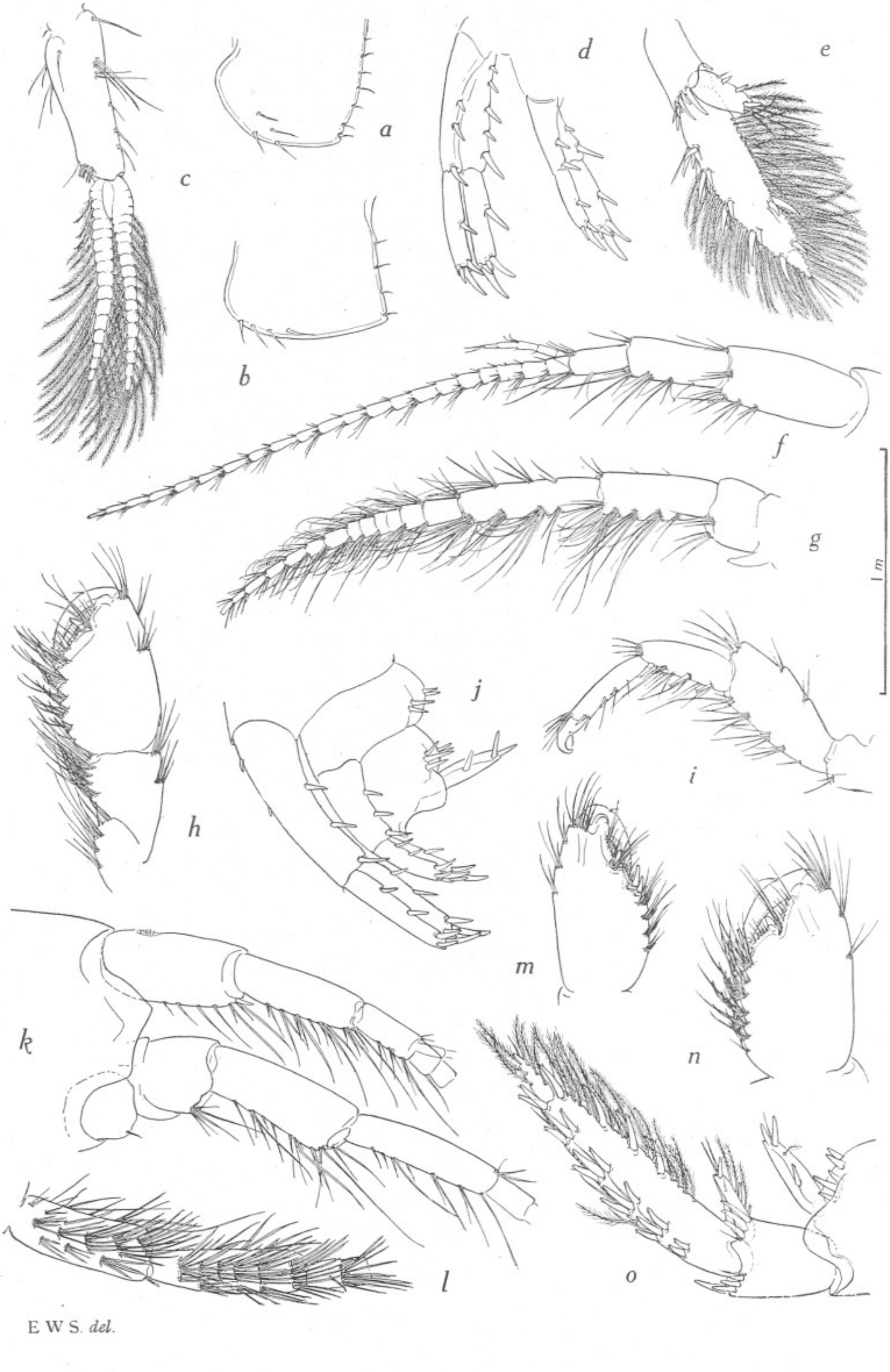
by Milne-Edwards as "plus lunulés que chez la Crevette locuste"; pigment brown, apparently soluble in alcohol. Antennae with setae relatively longer than in the other species of the genus. Antenna 1 (Text-figs. 3*a*, 4*f*, 4*k*), peduncle with joint 1 large and stout, longer than joint 2 but not as long as 2 and 3 combined; flagellum rather less than twice the length of the peduncle, possessing 22 joints in the largest specimen examined; accessory flagellum with about 5 joints. Antenna 2 (Text-figs 3*b*, 4*g*, 4*k*, 4*l*) not much shorter than antenna 1; flagellum shorter than peduncle, possessing about 14 joints in larger specimens, bearing calceoli on four proximal joints, and provided with rows of male sensory hairs (p. 680 and Text-fig. 11*f*) on under surface. Bifurcate setae apparently absent on both antennae.

Gnathopods (Text-figs. 3*c*–*f*, 4*h*, 4*m*, 4*n*). Hand of gnathopod 1 of distinctive shape, narrowed distally, palm very oblique, concave, irregularly undulate; palmar angle roundly produced; median spine separated from palmar angle-row by a wide gap; claw much curved, closing down over the under surface just behind the median spine (Text-fig. 3*e*). Hand of gnathopod 2 larger than that of gnathopod 1, palm rather oblique, slightly concave; median spine separated as in gnathopod 1; palmar angle rounded, well defined; tip of claw fitting into a tuberculated groove on under surface of palmar angle; posterior margin somewhat longer than palm. Both gnathopods bearing scattered bifurcate setae on the hands and some of the proximal joints, these setae less conspicuous than usual owing to their shorter apices.

Peraeopods (Text-figs. 3*g*–*k*, 4*i*) short and strongly built, especially the 3 hinder ones, joint 4 exceptionally broad in all. Peraeopods 1 and 2 sparsely setose, lacking both male sensory and bifurcate setae, joint 4 produced forward at anterior angle. Peraeopods 3–5 with numerous spine-clusters. Basal joint in peraeopod 3 with posterior distal angle free and well rounded; in peraeopods 4 and 5 basal joint abruptly narrowed behind, the angle "closed" and bearing one large spine; posterior expansions crenulate, with long and slender setules inset in the indentations.

Uropod 1 extending slightly further than uropod 2 (Text-figs. 4*d* and *j*). Uropod 3 (Text-figs. 4*e* and *o*), outer ramus long and broad, 2-jointed, carrying groups of spines, and densely fringed on both margins with long plumose setae: inner ramus very small and narrow, bearing feathered setae apically. Telson (Text-figs. 3*l* and 4*j*) extending to the length of peduncle of uropod 3;

Text-fig. 3. *Marinogammarus olivii* (Milne-Edwards), male. Figures drawn from a young male captured at Naples (Stebbing coll., in coll. Brit. Mus.); compared in detail with Milne-Edwards' type specimens, also from Naples (in coll. Mus. National, Paris), and with a specimen from Cap d'Antibes (in coll. Brit. Mus.). Magnification × 36, except *e* × 112. *a*, antenna 1, inner surface, right side, showing aesthetascs; *b*, antenna 2, outer surface, left side; *c*, gnathopod 1, left side; *d*, gnathopod 2, left side; *e*, gnathopod 1, under surface, right side, showing the palmar margin of hand, with the spine-clusters at the palmar angle, and the position of the claw when closed, × 112; *f*, gnathopod 2, under surface, as above; *g*, peraeopod 1, left side, with gill in outline; *h*, peraeopod 2, left side, with gill attached; *i*, *j*, *k*, peraeopods 3, 4, and 5 respectively, left side; *l*, telson.



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each lobe with lateral group of 1–2 spines, an apical group of 2 spines and 2 setae, and a pair of sensory plumose hairs inset in sockets below the apex.

Size: rather small, about 7–10 mm. in length, apparently of same range as *pirloti*. *Colour:* green (Milne-Edwards): translucent yellowish grey; eggs olive-green (Chevreux & Fage).

Habitat: Marine littoral, under stones (Chevreux & Fage).

MATERIAL EXAMINED.

Continental. ITALY: Naples, 2 ♂♂, Milne-Edwards' types of *Gammarus olivii* preserved in the Paris National Museum (sent by Prof. L. Fage) (Text-figs. 4*f–j*): Naples, three examples, including one young ♂ figured (Text-figs. 3*a–l*, 4*a–e*), Stebbing coll., preserved in coll. Brit. Mus. [1928–12–1], labelled "*Gammarus marinus*" (presumably original identification). SOUTHERN FRANCE: Cap d'Antibes, 1 ♂, A. O. Walker coll., in coll. Brit. Mus. [1925–9–8, 1167–76], det. Schellenberg as "*Gammarus* (*Echinogammarus*) *olivi* M. Edw." (Text-figs. 4*k–o*.)

DISTRIBUTION.

The records for this species are summarized by Chevreux & Fage (1925, p. 252). It is evident that the species has its headquarters in the western Mediterranean, seven localities along the Riviera coast of France and one in Corsica being given, and the species recorded as very common. Naples (the type locality), Tunisia, and Algeria are also quoted. Along the Atlantic seaboard localities include the Canary Islands and the Brittany coast at Etel, Morbihan. The species does not figure in lists of amphipod records from south-east Europe given by Schäferna and Karaman, and would thus appear not to extend into the eastern Mediterranean.

Text-fig. 4. *Marinogammarus olivii* (Milne-Edwards), male. Figs. *a–e* drawn from the same young male as in Text-fig. 3; Figs. *f–j* drawn *in situ* from older males, Milne-Edwards' type specimens (in coll. Mus. National, Paris); and Figs. *k–o* drawn *in situ* from another older male, captured at Cap d'Antibes (in coll. Brit. Mus.). Magnification × 36.

a, epimeron 2, left side; *b*, epimeron 3, left side; *c*, pleopod, showing coupling-spines on peduncle, and cleft spines of inner ramus; *d*, uropods 1 and 2, left side; *e*, uropod 3; *f*, antenna 1 (flagellum broken at tip), left side; *g*, antenna 2 (flagellum broken at tip), left side; *h*, gnathopod 2, terminal joints, left side; *i*, peraeopod 1, joints 4 to 7, left side; *j*, pleon-segments 5 and 6, with uropods 1 and 2 and telson; *k*, head and peduncle joints of antennae; *l*, antenna 2, peduncle joints 4 and 5, showing the sensory male hairs on under surface; *m*, hand of gnathopod 1, right side; *n*, hand of gnathopod 2, left side; *o*, uropod 3 (the plumose hairs of the outer margin have been broken off, but their sockets can be plainly seen between the spine clusters).

Marinogammarus obtusatus (Dahl)

Text-figs. 5*a–n*, 11*c*, *o*.

1938. *Gammarus obtusatus* Dahl, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. X, no. 34, pp. 125–8, figs. 11–21.

This species was found many years ago in Plymouth Sound by one of the authors (E. W. S.) and used in breeding experiments in the Laboratory. It is the "littoral species not yet named" referred to in the paper on "Moulting and Growth-Stages, etc." (Sexton, 1924, pp. 342–4); but although it was recognized as new to science and its characters noted for the work, no diagnosis was published. A brief recapitulation of its breeding habits, as then studied, is given on pp. 655–6.

More recently it was discovered in Belgium by Prof. J.-M. Pirlot, to whose courtesy we are indebted for material and information. Prof. Pirlot had a full description and series of drawings prepared when Dahl's publication appeared in 1938. Dahl's description was taken from material collected by the *Gunnerus* Expedition to Finmark under Mr Carl Dons in 1937.

In the meantime it had been ascertained that the species was plentiful at Plymouth and was actually being collected in greater number than *marinus*. In 1938 Reid pointed out the occurrence of Dahl's *obtusatus* in Britain, giving some widely separated localities, and indicating, as has since been amply confirmed, that the species is widespread and common. In collections examined we have found it quite as frequently as *marinus*, from which it differs in several conspicuous characters, yet under which name it has repeatedly passed. That it should have been so confused seems remarkable.

The only published description, that of Dahl, requires amplification in many particulars, and a more complete and detailed set of illustrations has been considered necessary. The species is readily recognized by the elongated peduncle joint 2 of antenna 1, by the long graduated outstanding setae of both antennae, by the small male gnathopod 2 contrasting with the large gnathopod 1, by the obtusely rounded posterior angles of the epimera (a character which is only shared by *stoerensis*), and by the prominence of the spines amongst the sparse setae of uropod 3.

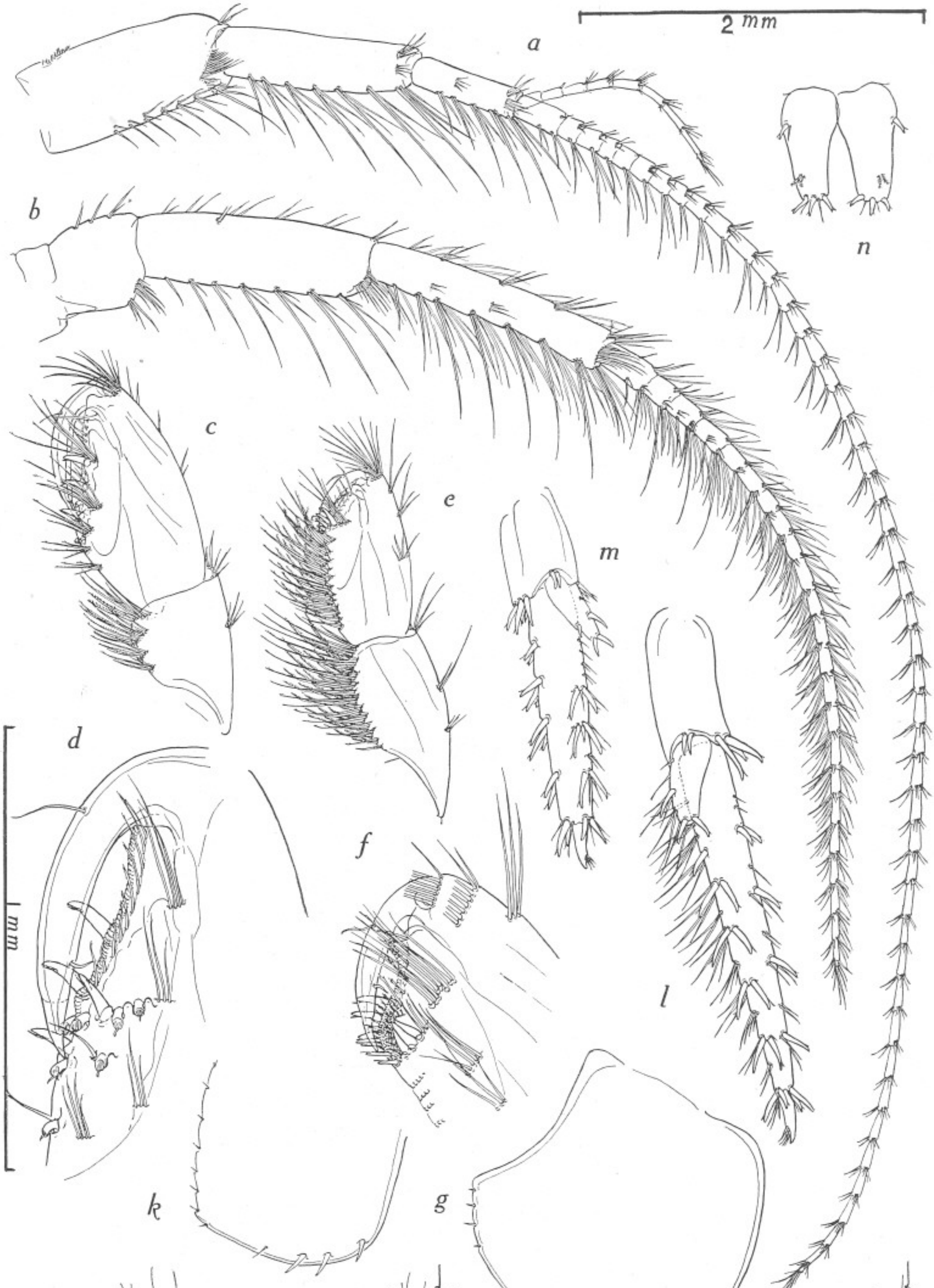
ADULT MALE.

Body compressed and slender, as in *marinus*. Pleon-segments 4–6 a little produced dorsally; spinose armature rather like that of *marinus* in the largest specimens; spines long, becoming numerous, each lateral group forming an upward curve, with the spines outstanding and divergent; the median groups set in a straight line across the distal margins; the lateral groups seen dorsally forming a series embracing also the outstanding spine-group on the peduncle of uropod 3; spine formula in large males: 5 : 3 : 3 : 5—4 or 5 : 2 : 2 : 4 or 5—4 : 1 : 1 : 4. Sideplate 4 (Text-fig. 5 *g*) about as broad as deep, of distinctive form, distal expansion very shallow thus bringing the posterior point of its greatest width unusually low, and giving the point an almost triangulate outline. Epimera 2 and 3 (Text-fig. 5*k*) resembling *stoerensis*; distal and posterior margins rounded, angle obtuse (hence the name of *obtusatus*); setules inset on posterior margin.

Head lateral lobes rounded; sinus not deep. Eye shorter than in *marinus* in early stages, but becoming increasingly elongate with age; in adults often clearly constricted in middle, sometimes sinuous in shape; pigment purplish black. Antennae (Text-fig. 5*a*, *b*) long; 1 longer than 2; peduncles longer in proportion than those of other species. In both antennae joints of peduncles and flagella showing a diagnostic feature—viz. each seta-cluster containing one long stiff outstanding seta, these outstanding setae forming a graded series on each joint (almost as in *Gammarus zaddachi* Sexton); flagella with the fourth outstanding seta the longest, the others decreasing in length towards the apex. Antenna 1 peduncle with joint 1 long and stout, joint 2 slender, fully equalling 1 in length. Primary flagellum with about 46 joints in large specimens; accessory flagellum with 7–9. Antenna 2 with flagellum of about 23–24 joints, subequal in length to the peduncle; male sensory hairs (p. 680 and Text-fig. 11*c*) rather sparse; calceoli lacking. Both antennae bearing numerous well-formed bifurcate setae (Text-fig. 11*o*).

Gnathopods (Text-fig. 5*c*–*f*). Hand of gnathopod 1 much larger than that of gnathopod 2; of distinctive structure, though on the same lines as that of *marinus*, differing in the greater obliquity of the palm, in the smaller number and the wider spacing of the angle-spines, and in the smaller number of the posterior bristle-clusters; palm undulate, very oblique, merging into the posterior margin of the hand without a defined angle; its margin bearing at equal intervals 3 long stout spines, the median and two of the angle-group, with the peculiar male curvate spines, as in *marinus*, on both sides of the angle, a single pair below it (Text-fig. 5*d*); posterior bristle-clusters few in number, the most distal arising, as in *marinus*, at the level of the angle-group. Gnathopod 2 with joint 5 subequal in length to 6, longer in proportion than in gnathopod 1. Hand of gnathopod 2 much smaller, and of very different structure from that of gnathopod 1; narrow, elongate, the posterior margin about twice length of palm; palm nearly transverse, concave, with palmar angle rounded, and spines not separated as in gnathopod 1; median spine adjacent to angle-group, but situated slightly in front of it, and almost as far down the palm as in *stoerensis*; posterior bristle-clusters numerous. Both gnathopods bearing numerous well-developed bifurcate setae.

Peraeopods 1 and 2 with setae and spines sparse. Peraeopod 3 (Text-fig. 5*h*) basal joint with postero-lateral angle free and rounded. This angle in peraeopods 4 and 5 (Text-fig. 5*i*, *j*) bearing spines inset on the under surface, but not completely "closed" and representing an interesting intermediate condition between *marinus* (closed) and *finmarchicus* (free). Peraeopods 4 and 5 relatively elongate, joint 4 about three times as long as broad, joints 5 and 6 subequal in length.



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Uropod 1 extending a little beyond uropod 2, bearing a long curved spine on peduncle. Uropod 3 (Text-fig. 5*l*) outer ramus 2-jointed; with clusters of long spines and of fine setae bordering the inner margin, and with spines and some small setae on outer side; much more sparsely setose than in *marinus*; plumose setae lacking: inner ramus very small, about 20% length of outer, bearing spines and setae on inner margin. Telson (Text-fig. 5*n*) as long as peduncle of uropod 3; lobes about twice as long as broad, each with one spine in lateral group, three spines with one stout seta in apical group, and a pair of plumose sensory hairs below the apex.

ADULT FEMALE.

Differences from adult male as follows.

Antenna 1 not longer than twice length of peduncle. Antenna 2 with gland-cone long and narrow.

Gnathopods: hands of somewhat similar size, very setose. Hand of gnathopod 1 much smaller than in ♂; posterior margin, as in ♂, developing a single pair of spines situated between the two most distal of the posterior bristle-clusters—these spines pointed, not curvate. Hand of gnathopod 2 narrow and elongate.

Peraeopods 1 and 2 sparsely setose, but setae on average longer and somewhat more numerous in each cluster than in male.

Brood-plates. Anterior brood-plate with setae along anterior margin numerous, but not so dense as in *marinus*.

Uropod 3 (Text-fig. 5*m*) with outer ramus relatively shorter and inner ramus longer than in ♂; rami with clusters of elongate spines along margins, but setae very few and short, giving the limb an almost glabrous appearance.

Eggs deep purple when newly laid; size relatively large, 0·60 × 0·70 mm.; and number in a brood relatively small (for further data see below). *Young* about 2½ mm. long at extrusion, larger than in *marinus*.

SIZE AND COLOUR.

Size range of adults a little less than that of *M. marinus*. Colour, pale brown to olive green, often with a distinct purple or pinkish tinge, occasionally individuals quite rich pink; no orange patches on pleon-segments 1–3.

Text-fig. 5. *Marinogammarus obtusatus* (Dahl). All figures except *f* and *m*, drawn from a large male, captured Steepholm Island, Bristol Channel; fig. *f* drawn from a male, 13 mm. long, and *m* from a large female, 12 mm. long (11 young in pouch), both captured Plymouth Sound, shore adjoining bathing-place, Feb. 1940. Magnification × 22·4, except *d* and *f* × 62. *a*, antenna 1 of ♂, outer surface, right side; *b*, antenna 2 of ♂, outer surface, right side; *c*, gnathopod 1 of ♂, terminal joints 5–7, left side; *d*, gnathopod 1 of ♂, under surface of distal portion of hand, right side, showing the spine-clusters at the palmar angle; *e*, gnathopod 2 of ♂, terminal joints 5–7, left side; *f*, gnathopod 2 of ♂, under surface of distal portion of hand, showing the spine-clusters and tuberculate surface of the palmar angle; *g*, sideplate 4, right side; *h*, peraeopod 3, left side, postero-distal angle of basal joint; *i*, peraeopod 4, left side, postero-distal angle of basal joint; *j*, peraeopod 5, left side, postero-distal angle of basal joint; *k*, epimeron 3, right side; *l*, uropod 3 of ♂; *m*, uropod 3 of ♀; *n*, telson.

HABITAT.

A littoral species, distributed along sea coast, but penetrating only a short distance into estuaries; essentially intertidal, but with optimum zone lower down the shore than *marinus*—about mid-tide level to low-water neaps. Like *marinus*, seeking cover of stones and seaweed, but typically associated with the less muddy and more stony grounds, and capable of existing amongst comparatively clean pebbles.

MATERIAL EXAMINED.

England. SOUTH DEVON: Plymouth Sound, various collections from shore below the Marine Biological Laboratory, Drake's Island, and Rum Bay: including preserved specimens of original material collected in 1913, and fresh collections in 1938 and 1939: abundant, taken in greater numbers than related species. Plymouth Breakwater, 2. viii. 89, one in the Laboratory museum, labelled "*Gammarus marinus*". Plymouth district: 473 specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles; by far the most numerous species. Wembury, under stones at mid-tide level, 17. iii. 39. NORTH SOMERSET: Severn Estuary: Steepholm Island, 2 ♂♂ and 1 ♀ (identified for Prof. C. M. Yonge): Kilve, mid-tide level, May and August 1939, considerable samples; Weston-super-Mare, Birnbeck Island, April and August 1939, considerable samples, but none in samples from higher up estuary (identified for Mr R. Bassindale). ISLE OF MAN: Port Erin, 30. viii. 38, 5 ♂♂, 3 ♀♀, 10 imm. and young; Port St Mary, rock crevices near high water, 12. ix. 38, 5 ♂♂, 4 ♀♀, 1 imm.; Bay na Carrickey, 9. ix. 38, 6 ♂♂ and 2 ♀♀ (all above sent by Mr G. I. Crawford). NORTHUMBERLAND: Cullercoats, 22. iii. 32, 3 ♂♂ and 1 (?) ♀ (sent by Mr G. I. Crawford); from north and south side of Bay, 14. x. 39, considerable samples of rather small average size (identified for Mr L. C. Beadle).

Scotland. BERWICKS: Burnmouth, under stones near high water, 8. v. 32, 6 ♂♂, 5 ♀♀, 2 imm.; EAST LOTHIAN, Port Seton, under stones near high water, 6 ♂♂, 6 ♀♀, 1 imm. (identified for Prof. A. D. Hobson). INNER HEBRIDES: Isle of Muck, Camas Mor, 23. viii. 38, 5 ♂♂, 9 ♀♀, 5 imm.; Raasay, August 1937, samples from four localities, including 18 ♂♂, 11 ♀♀ and 3 imm.; South Rona, August, 1937, samples from two stations, including 8 ♂♂, 7 ♀♀ and 4 imm. (identified for Prof. A. D. Hobson). ORKNEYS: Hoy, Quoyness, rocky shore, 7 ♂♂, 5 ♀♀, 2 imm. (coll. K. M. G. Fleming). SHETLANDS: large ♂ and two smaller, in Norman coll., Brit. Mus. [1911-11-8], labelled *Gammarus marinus*.

Ireland. COUNTY DOWN: Garrahan Isle, near Groomsport, 20. ix. 39, 3 ♂♂ from a number collected under stones (determined and sent by Mr R. MacDonald, confirmed E. W. S.).

Continental. BELGIUM: Blankenberghe, March 1935 and 1936, and April 1938 (various specimens, slides and drawings lent by Prof. J.-M. Pirlot).

NORTH NORWAY: Porsanger Fjord, Suogalina, 6. vii. 39, between mid-tide and low-water neaps, 17 ♂♂, 6 ♀♀, 10 imm.; Rimabukt, 10. vii. 39, between mid-tide and low water, under stones, 26 ♂♂, 19 ♀♀, 2 imm.; Rørwik, near Trondhjem, 24. vi. 39, mid-tide, ♂ and ♀ (coll. G. I. Crawford). EAST MURMANSK: shore of Barents Sea (det. *Gammarus marinus* Leach by Mme E. Gurjanova), 2 large ♂♂, in coll. Brit. Mus. [1936. 3. 8].

DISTRIBUTION.

Dahl (1938) described the species from specimens collected in localities in West Finmark (Type locality: Hasvik, Sørøy), and East Finmark. Further localities for the north and west coast of Norway are given above. Reid (1939) records *obtusatus* as plentiful in the Scilly Islands, at Plymouth, and on the north and west coasts of Sutherland. From the additional records given, it is evident that the species is distributed along the whole west coast of Great Britain, including outlying islands, and down the east coast at least as far south as Newcastle. From its discovery by Prof. Pirlot in Belgium, it may be expected to occur all round the shores of the North Sea in suitable localities, though probably more localized owing to the character of the shore. The species is often numerous where it occurs, and may entirely replace *marinus*, under which name it has often been recorded in the past.

BREEDING HABITS.

Numbers of the species were kept in the Laboratory for some years to study their life history particularly in regard to the growth-stages from birth to maturity. The results given here were obtained in laboratory conditions, it being impossible to make any observations in their natural habitat. The moulting and oviposition of the female were watched on several occasions, and were practically the same as observed and described for *G. chevreuxi* (Sexton, 1924, p. 344). The gonads show very clearly in life as dark purplish bands against the translucent greenish colour of the animal's body, and the eggs could be seen during oviposition passing down the oviducts as a continuous bright coloured line. The eggs when laid into the pouch are a rich reddish purple shade, large, and few in number, usually from 8 to 12 in a batch. In summer they take from 12 to 14 days to hatch, but the time of the young leaving the pouch varies considerably. Sometimes the female lets them all out in about 4–5 days, sometimes she keeps them until they all have had their first moults and then extrudes them and the cast skins together, or she may let them out 1 or 2 at a time over a period of several days. In one case observed the female kept some for 13 days, and, in another, one young was retained for 17 days and then was only let free by keeping the female on a slide until she opened her pouch. It is thus very difficult to know how many days to count as a moulting period as two or more moults may take place before extrusion. One young, extruded at 5 days, moulted afterwards at intervals of 8, 8, 9, 8, 10 and 12 days; and another of the same brood at 8, 9, 10, 9, 9 and 9 days. None reached maturity, partly owing to the difficulty of finding suitable food, and partly to the impossibility of providing surroundings sufficiently like their natural habitat to keep them healthy. They live normally under fucoids and small stones on the beach between tide-marks, but seaweed could not be used in the culture-pots because of its rotting and fouling the water.

The moulting period of the female is from 24 to 28 days in summer. In the experiments mentioned the females of the other species, viz. *Gammarus locusta*, *chevreuxi* and *pulex* extruded the young soon after hatching and moulted within a very short time; in *obtusatus*, twice the length of time appeared to be taken, an "incubatory" period of about 12–14 days till the eggs hatched, and a second period of the same length of time during which the young remained in the pouch for one or more growth stages.

Recent measurements of the eggs are as follows: average of batch of 8, newly laid, 0·60 × 0·69 mm.; and of another of 7 with embryos formed, 0·61 × 0·73 mm.

Marinogammarus finmarchicus (Dahl)

Text-figs. 6*a–h*, 7*a–f*, 11*b*, *j*, *p*.

1938. *Gammarus finmarchicus* Dahl, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. x, no. 34, pp. 125–8, figs. 1–10.

1938. *Gammarus* (*Marinogammarus*) *greenfieldi* Shoemaker, *Journ. Washington Acad. Sci.*, Vol. XXVIII, no. 7, pp. 329–32, fig. 2.

In 1937, one of the authors (G. M. S.), when revising amphipod material originally collected during the Tees Survey Investigations (see Alexander *et al.* 1935) and deposited in the Museum of the Plymouth Laboratory, discovered some specimens which clearly belonged to an undescribed species of *Gammarus*. They came from the estuary of the River Tay, East Scotland. Not long afterwards they were identified with a species which had just been independently described by Dahl (Jan. 1938) and Shoemaker (July 1938). In the meantime the presence of the species in the Plymouth district was discovered and living material examined. Dahl's name, *finmarchicus*, holds priority. Shoemaker's description is the more complete and his illustrations the more detailed. These descriptions are recapitulated below, with some details and figures added, for the sake of full comparison with the other species of the genus described here.

Three characters peculiar to *finmarchicus* distinguish it at a glance from the others, viz. in all the basal joints of the three hinder peraeopods the posterior distal angle is clearly free; the second joint of the outer ramus of uropod 3 is completely lacking; and the inner ramus of the same uropod is of appreciable length, attaining in the adult about 40% of that of the outer ramus. The somewhat fan-shaped arrangement of the tufts of setae on uropod 3 provides another character readily noticed in sorting specimens from mixed samples.

ADULT MALE.

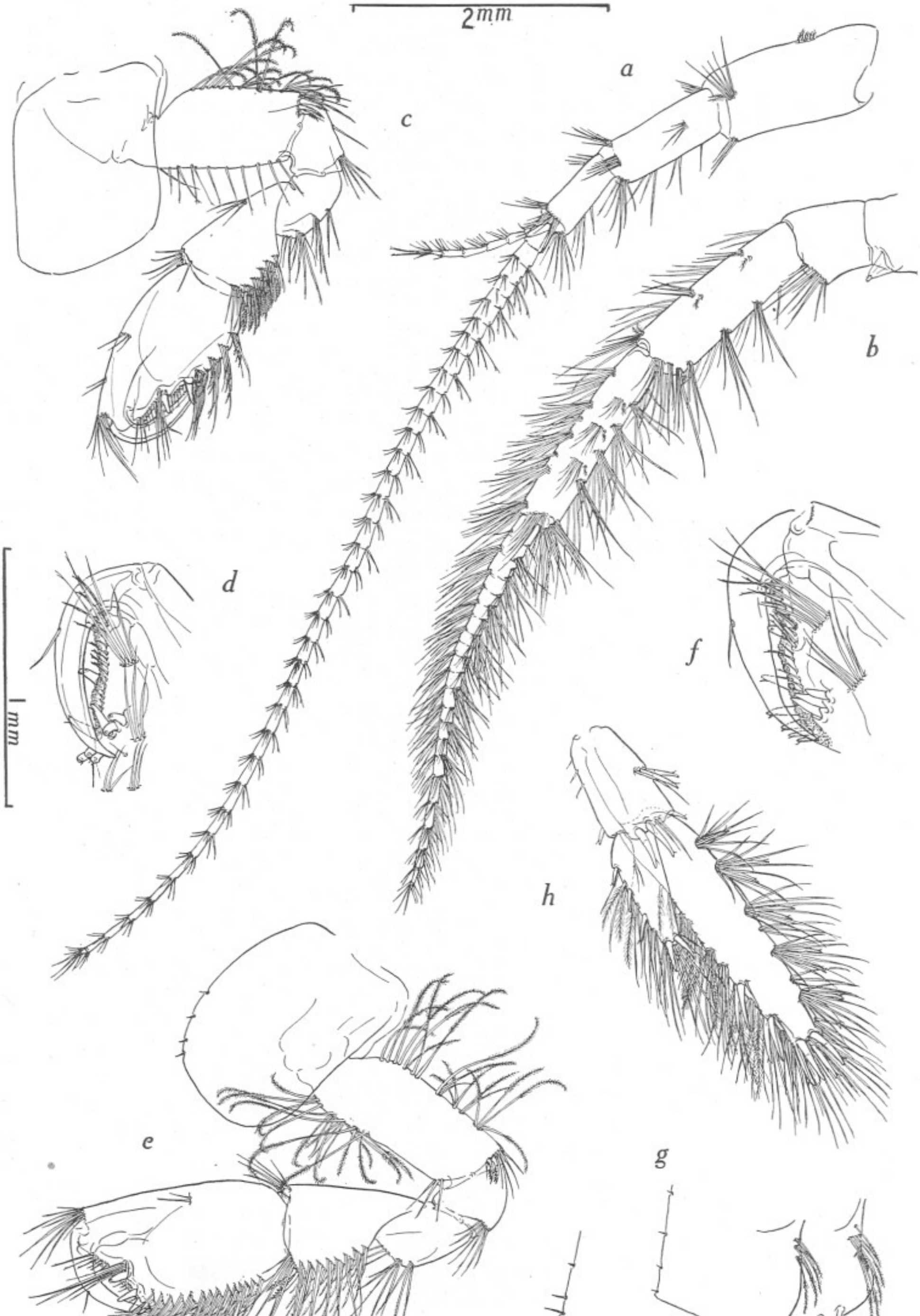
Body resembling *marinus*, a little less elongate than in *obtusatus*. Pleon-segments 4 and 5 very slightly raised dorsally, the spines in segments 4–6 arranged in four groups, the usual formula being 3 : 2 : 2 : 3—3 : 2 : 2 : 3—2 : 1 : 1 : 2. Sideplates 1–4 a little deeper than the corresponding segments, with distal margins rounded; sideplate 4 (Text-fig. 7*b*) as broad as deep, distal expansion shallow, with about 5 setules inset on the posterior expansion. Epimera 2 and 3 (Text-fig. 6*g*) with posterior margin straight, inset with a few setules, anterior margin carrying clusters of feathered setae; distal margin somewhat rounded, bearing 2–3 strong spines anteriorly; postero-distal angle subrectangular, not produced.

Head with lateral lobes broadly rounded; sinus rather deep. Eye subreniform in younger stages, elongate and narrow in larger animals; black. Antenna 1 (Text-fig. 6*a*) longer than antenna 2; joint 1 of peduncle stout and about a fourth as long again as joint 2; flagellum considerably more than twice the length of the peduncle, possessing about 40 joints in large specimens; accessory flagellum with 6–7 joints. Antenna 2 (Text-fig. 6*b*) peduncle with joint 4 stouter and slightly shorter than 5; flagellum possessing about 22 joints, somewhat shorter then peduncle; both peduncle and flagellum joints furnished with fan-shaped clusters of outstanding setae, a few small plumose sensory hairs, and numerous clusters of male sensory hairs (p. 680 and Text-fig. 11*b*); calceoli lacking. Bifurcate setae sparsely distributed on antenna 1. Mouth parts normal, agreeing with generic diagnosis; described and figured by Shoemaker (1938, p. 330).

Gnathopod 1 (Text-fig. 6*c*, *d*) with hand decidedly smaller than that of gnathopod 2, a little shorter and much narrower; palm very oblique, undulate, merging into the posterior margin, palmar angle, however, defined on each side by a long spine and groups of the small curvate male spines; tip of claw closing down between the latter on under surface of palm. Median spine in both gnathopod hands separated from spines of angle-group by a wide gap. Gnathopod 2 (Text-fig. 6*e*, *f*) with hand widest distally; palm nearly transverse, its angle well defined and marked by four graduated spines; posterior margin distinctly longer than palm, bearing numerous bristle-clusters.

Peraeopods (Text-fig. 7*a*–*e*) 1 and 2 with clusters of setae on posterior margin of joint 4, and of setae and spines on that margin of joints 5 and 6. Peraeopods 3–5 stout and armed with clusters of long spines and setae; basal joints more expanded than in other species of genus, with posterior expansion not narrowed distally, thus leaving the postero-distal angle almost as clearly free in peraeopods 4 and 5 as in peraeopod 3; this angle rounded in peraeopod 3, less so in peraeopod 4, and subangulate in peraeopod 5, each with a seta inset. Peraeopod 4 with joint 4 two and a half times as long as wide at apex; joints 5 and 6 subequal.

Uropod 1 extending a little beyond uropod 2; its peduncle with a prominent spine on lower margin. Uropod 3 (Text-fig. 6*h*) with outer ramus long and broad ending in a cluster of four long spines at apex, joint 2 completely



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lacking; outstanding fan-shaped groups of long slender spines and setae situated on both margins and apex, but spines lacking on proximal two-thirds of inner margin: inner ramus attaining about 40% the length of the outer, bearing spines and setae only on the inner margin and at the apex: long plumose setae distributed along inner margins of both rami. Telson (Text-fig. 7*f*) with each lobe about twice as long as broad, bearing three long spines and some setae in lateral cluster, three spines and several setae in apical cluster, and two short plumose sensory hairs in sockets below the apex.

ADULT FEMALE.

Differences from adult male as follows.

Antenna 1 with flagellum about twice length of peduncle. Bifurcate setae well distributed on antennae, especially on antenna 2.

Gnathopods. Hands smaller than in male, nearly equal in size; gnathopod 1 with palm of hand less oblique; gnathopod 2 with hand more elongate, the posterior margin fully twice as long as palm. (Peraeopods 1 and 2 with armature as in male.)

Brood-plates much as in *marinus*, but row of setae on anterior margin of first brood-plate only moderately dense.

Uropod 3 with armature of spines and setae much as in male, but setae sparser.

Eggs large (average size 0·55 × 0·65 mm. when newly extruded), and relatively few in number (10 to 30 in a batch).

Young extruded at comparatively large size, $2\frac{1}{2}$ mm. in length; eyes black; at once distinguished by the long spiniform setae on uropod 3, and by the absence of joint 2 of that limb.

SIZE AND COLOUR.

Size range comparable with that of *obtusatus*, only somewhat less than in *marinus*; male 15–20 mm., female on average smaller. Colour uniformly pale brown or yellowish, with at most slight infuscation on the posterior borders of some segments, often suffused with a brighter yellow, sometimes very deeply; no orange-red patches on sides of pleon.

HABITAT.

A marine littoral species, occurring intertidally along the sea coast, and for a short distance up estuaries. Frequenting stony ground, often in company with *obtusatus*, but generally scarcer and more local than that species.

Text-fig. 6. *Marinogammarus finmarchicus* (Dahl), male. Figures drawn from a male, taken on shore of River Tay estuary, East Scotland (Tees Survey collections). Magnification × 18, except *d* and *f* × 36. *a*, antenna 1, left side; *b*, antenna 2, left side; *c*, gnathopod 1, left side; *d*, gnathopod 1, right side, distal portion of hand from under surface, showing armature of palm and palmar angle; *e*, gnathopod 2, left side; *f*, gnathopod 2, right side as in *d*; *g*, epimera 2 and 3, right side; *h*, uropod.

Text-fig. 7. *Marinogammarus finmarchicus* (Dahl), male (*cont.*). Drawings from same male as in Text-fig. 6, × 18. *a*, peraeopod 1; *b*, peraeopod 2; *c*, peraeopod 3; *d*, peraeopod 4; *e*, peraeopod 5; *f*, telson.

MATERIAL EXAMINED.

England. SOUTH DEVON. Plymouth Sound, shore adjoining the bathing place below the Marine Biological Laboratory, 10. viii. 38, plentiful, both sexes and young stages under stones on concrete, in company with *M. obtusatus*. Plymouth district: 57 specimens out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. Revelstoke beach, under pebbles, 4. v. 40; both sexes.

NORTHUMBERLAND: Cullercoats, north of bay, 4. x. 39, 4 ♂♂ and 1 ♀ (mixed with a number of *M. obtusatus*) (identified for Mr L. C. Beadle): Cullercoats, south side of bay, 26. iii. 35, 1 ♂ and 1 ♀; Blyth, ditch from Salt Pans, 4. vii. 34, 1 imm. with other *Marinogammarus* specimens (identified for Prof. A. D. Hobson).

Scotland. EAST LOTHIAN: Port Seton, 7. iii. 32, under stones near high water, 1 ♂, 2 ♀♀ (identified for Prof. A. D. Hobson). FIRTH OF TAY: Section XI (see Alexander *et al.* 1935), high-tide level, 1 ♀, mid-tide level, 1 ♂, low-tide level, 2 ♂♂ and 2 ♀♀, all mixed with numerous *M. marinus* (Tees Survey collections, deposited in Plymouth Laboratory museum). INNER HEBRIDES: Raasay, in samples from two stations, August 1937, including 2 ♂♂, 3 ♀♀, 12 imm. South Rona, August 1937, in samples from two stations, including 1 ♂ and 2 imm. (identified for Prof. A. D. Hobson).

Ireland. COUNTY DOWN: south side, Great Copeland Island, 13. v. 39, "slightly brackish pool", large ♀ (sent and determined by Mr R. MacDonald, confirmed E. W. S.).

Continental. NORTH NORWAY: Porsanger Fjord, Honningsvåg, 5. vii. 39, just above mid-tide, 2 ♀♀, 1 imm.; Suogalina, 6. vii. 39, in brackish splash pools near high water, 9 ♂♂, 5 ♀♀, large size, lower half of tidal zone, 1 ♂; Rimabukt, 10. vii. 39, between mid-tide and low water, under stones, 3 ♂♂ and 1 ♀: Tromsö, Telegraph bugd, 30. vi. 39, swimming at half-tide, 4 ♂♂, 5 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

The species was previously known from West and East Finmark (type locality: Hasvik, Sørøy) (Dahl, 1938), and the Atlantic coasts of North America (Shoemaker, 1938). Additional localities for north Norway are given above. This is the first occasion on which *M. finmarchicus* has been recorded from Britain, and the records given above show that it is present on the south-west and north-east coasts of England, east and west coasts of Scotland, and north-west coast of Ireland. The species is evidently much scarcer and more localized than *obtusatus*, but our present knowledge of its range is insufficient to indicate whether it is as widely distributed.

Marinogammarus stoerensis (Reid)

Text-figs. 8*a*–*o*, 11*a*.

1938. *Gammarus marinus* Leach, var. *stoerensis* Reid, *Ann. Mag. Nat. Hist.*, ser. 11, Vol. 1, pp. 287–9, figs. *a*–*e*; ♀.

1938. *Gammarus* (*Marinogammarus*) *stoerensis* Stephensen, *Kong. Norske Vidensk. Selsk. Forhandl.*, Vol. XI, no. 36, pp. 143–6 (with figs.); ♂, ♀.

In 1932 females of a small species of *Gammarus*, recognized as undescribed, were collected by one of the authors (G. M. S.) near the mouth of the River Avon, South Devon. They were kept for some time in the Laboratory, attention being mainly given to the retarded development of the dark pigment in the eyes of the young. A few specimens of an unknown species, collected by Mr G. I. Crawford near the mouth of the River Yealm, South Devon, in 1936, were later discovered to be the same. These, furthermore, appeared to correspond with a form briefly described by Reid in 1938 as a variety of *marinus*, from females collected in Stoer Bay, West Sutherland, Scotland. This identification was confirmed by the examination of an immature female specimen kindly forwarded to us by Mr Reid, and was placed beyond doubt when a fuller description and figures by Dr Stephensen (1938) appeared shortly afterwards. Dr Stephensen established *stoerensis* as a distinct species, pointing out the differences from *marinus*. The species was collected about this time in additional localities in the Plymouth district.

Marinogammarus stoerensis differs from other species of the genus in several respects. The size is small, not exceeding 7 or 8 mm., the contrast being particularly evident in the males which are apparently of even smaller average size than the females; the brood-plates of the female, especially the two anterior pairs are abnormally broad, and at the same time relatively long, so that in life the full brood-pouch protrudes well below the level of the distal margins of the sideplates; the hands of the two gnathopods in the male are more alike than in related species; the 6th joints of peraeopods 4 and 5 are distinctly longer than the 5th joints; the eyes of the young at extrusion are red, gradually darkening during the earlier growth stages; and, finally, the cuticle is microscopically striate. Another striking character is the position of the median palmar spine on the hands of the male gnathopods. This spine, as in *marinus* (Text-fig. 1*d*, *f*) and *obtusatus* (Text-fig. 5*f*), appears to form one of a continuous row with the spines of the angle-group, but in this species is set unusually far back, and produces the appearance of a "quite naked palm" in the words of Stephensen (1938, p. 145).

The following amplified description is given for convenience of comparison with the other species described here.

ADULT MALE.

Body elongate, laterally compressed. Pleon-segments 4–6 not produced dorsally; the dorsal spines in four groups, with the spines short and few in number, the formula in the adult being: 1 : 1 : 1 : 1—2 : 1 : 1 : 2—1 : 0 : 0 : 1.

Sideplate 1 (Text-fig. 8*c*) parallel-sided; sideplate 4 (Text-fig. 8*h*) a little longer than greatest width; distal expansion rather deep and evenly rounded, with 2 setules inset posteriorly. Epimera 2 and 3 (Text-fig. 8*l*) with distal margins rounded, bearing 3 spines anteriorly; posterior distal angles obtuse, or obtusely quadrate.

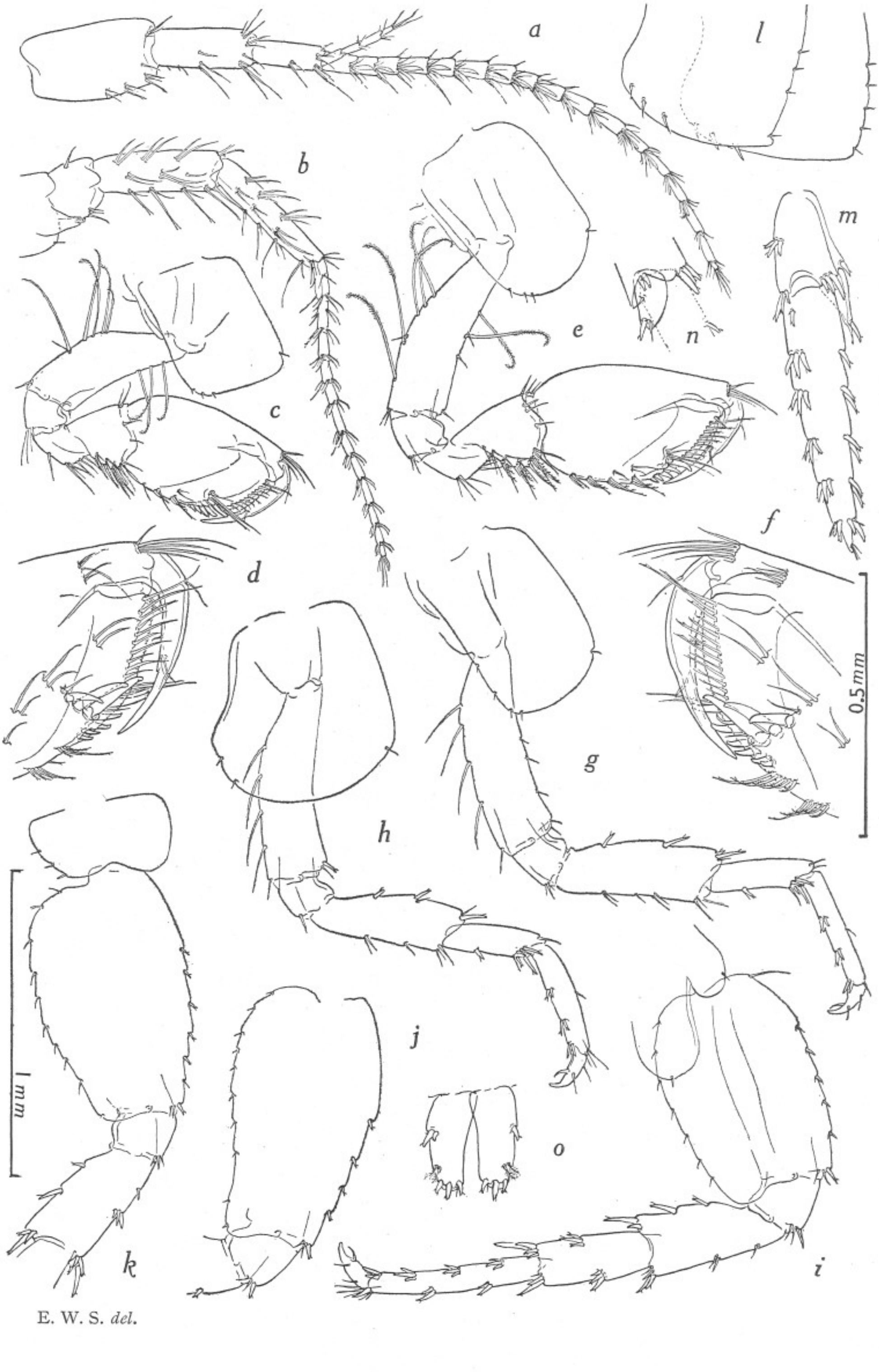
Head with lateral lobes rounded. Eye relatively large, often slightly constricted in middle. Antennae short with few joints, 1 rather longer than 2. Antenna 1 (Text-fig. 8*a*) peduncle with joint 2 long, but distinctly shorter than joint 1; flagellum less than twice length of peduncle, possessing about 17 joints; aesthetascs unusually long; accessory flagellum with about 4 joints. Antenna 2 (Text-fig. 8*b*) with joint 4 of peduncle broad, and about equal to joint 5 in length; flagellum about 13-jointed, slightly shorter than peduncle; setae sparse, the male sensory hairs (p. 680 and Text-fig. 11*a*) very few in number; calceoli lacking. Bifurcate setae only on basal joints of antennae 2.

Gnathopods (Text-fig. 8*c–f*) relatively large and more strongly-built than in the other species here described. Hand of gnathopod 1 shorter than that of gnathopod 2 but more similar in structure than in related species; palm less oblique than in related species, but still forming a continuous curve with posterior margin. Hand of gnathopod 2 with palm nearly transverse, palmar angle rounded, posterior margin a little longer than palm. Both gnathopod hands with median spine separated from base of claw by an unusually wide gap, this spine with its accompanying seta-cluster set close up against the angle spine row (Text-fig. 8*c*, *e*); spines of lower angle-group unusually long (Text-fig. 8*d*, *f*); claw with tip unusually long and slender.

Peraeopods 1 and 2 (Text-fig. 8*g*, *h*) very sparsely setose, lacking both bifurcate and male sensory setae. Peraeopods 3–5 (Text-fig. 8*i–k*) relatively elongate, furnished with short spines; basal joint in peraeopod 3 moderately expanded, with posterior distal angle free and well rounded; those of peraeopods 4 and 5 with posterior expansion much narrower distally but with the angles distinctly free and devoid of spines (condition intermediate between *obtusatus* and *finmarchicus*): joint 6 considerably longer than joint 5. Peraeopod 4 with joint 4 about twice length of apical width.

Uropod 1 scarcely extending beyond uropod 2, the apices of the rami of both, and of the telson, in line with the distal margin of peduncle of uropod 3. Uropod 3 (Text-fig. 8*m*) with outer ramus 2-jointed, broad and stout, bearing clusters of short spines, completely devoid of setae; inner ramus small and scale-like, with 1 small seta on inner margin, and 1 spine and 1 small seta apically. Telson (Text-fig. 8*o*) lobes about twice as long as wide; each with 1–2 spines in lateral cluster, a pair of plumose sensory hairs below the apex, and three spines in apical cluster.

Cuticle microscopically striated over almost the whole of the body, the striated effect being due to minute plications producing patterns resembling human finger-prints; the plications, under high magnification, apparently longitudinally serrate.



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ADULT FEMALE.

Differences from adult male as follows.

Antennae bearing numerous well-formed bifurcate setae.

Gnathopod hands smaller than in male. Peraeopods 1 and 2 not more setose than in male, but bearing some bifurcate setae, situated on joints 2 and 3 of peraeopod 1 and joint 2 of peraeopod 2.

Brood-plates, especially the two anterior pairs, attached to gnathopod 2 and peraeopod 1, abnormally large, being long and exceptionally broad; the two posterior, attached to peraeopods 2 and 3, clavate and broader than in other species; in life full brood-pouch visible well below the level of the margins of the sideplates and even protruding below the basal joints of the limbs.

Telson with 4 spines in each apical cluster.

Eggs relatively large for size of animal; number in one brood also relatively large, typically between 20 and 30; colour dark green when newly laid, the embryos becoming bright orange.

IMMATURE.

Eyes of young at extrusion containing very little dark pigment, appearing more or less bright red, the dark pigment accumulating during first few weeks of life, until eye-colour more or less black.

Uropod 3 outer ramus: stoutness, and shortness of spines, apparent at early age.

Cuticle not evidently microscopically striate in younger stages.

SIZE AND COLOUR.

Length of adult male abnormally small, $4\frac{1}{2}$–7 mm.; that of female on average somewhat larger, 5–8 mm.; young on average 1·3 mm. at extrusion. Colour translucent, pale slate-blue to greenish grey; at most, obscure diffuse patches of pink on hinder pleon-segments, well-defined orange patches not developed; bright orange of embryos very conspicuous in females with incubating brood.

HABITAT.

A marine littoral species, strictly intertidal, inhabiting the zone between high- and low-water neaps, characteristically where freshwater streams or

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Text-fig. 8. *Marinogammarus stoerensis* (Reid), male. Figures (except *n*) drawn from a male, 6 mm. long, taken at Kilve, shore of Bristol Channel, 7. v. 39 (R. Bassindale); compared with specimens from Plymouth district. Magnification × 45, except *d* and *f* × 77·5. *a*, antenna 1, left side, inner surface, showing the large aesthetascs; *b*, antenna 2, left side, inner surface, showing the male sensory hairs on the peduncle; *c*, gnathopod 1, right side; *d*, gnathopod 1, left side, distal portion of hand, from under surface, showing spine-cluster at palmar angle; *e*, gnathopod 2, right side; *f*, gnathopod 2, right side, as in *d*; *g*, *h*, peraeopods 1 and 2 respectively, right side; *i*, peraeopod 3, right side; *j*, peraeopod 4, right side, basal joint; *k*, peraeopod 5, right side, proximal joints 1–4; *l*, epimera 2 and 3, left side; *m*, uropod 3; *n*, uropod 3 of a female, inner ramus; *o*, telson.

seepage flow over the tidal zone; under flat stones with *Procerodes ulvae*, *Melita palmata*, etc.; penetrating for only a short distance into estuaries.

MATERIAL EXAMINED.

England. SOUTH DEVON AND EAST CORNWALL: Plymouth Sound: between Cawsand and Penlee Point, 5. viii. 38, numerous under stones in a small freshwater stream flowing over rocks of tidal zone, ♀♀ and immature; Bovisand Bay, 10. viii. 38, intertidally under stones, ground influenced by freshwater seepage, one ♀ ovigerous, 5 young ♂♂ and many young ♀♀, immature numerous, collected with *Procerodes ulvae*, etc.; Crownhill Bay, Bovisand, 11. x. 38, under stones about mid-tide level, in freshwater seepage 20 immature amongst numerous *M. pirloti*, with *Procerodes ulvae*. Plymouth district: Drake's Island, tidal zone, 24. i. 39, 1 ♂, 13. ii. 39, 1 ♀ and 1 imm. Three specimens (♀♀) out of 700 *Marinogammarus* preserved in the Laboratory stock bottles. South Devon coast: Wembury, Church beach, 12. viii. 38, under flat stones, etc., about mid-tide level, where freshwater stream flows over shore, young of both sexes and immature plentiful, no breeding adults; River Yealm estuary, near mouth, 18. iii. 34, under stones and *Fucus serratus* on sandy ground, 1 ♂ and 4 ♀♀ (G. I. Crawford); Revelstoke beach, 4. v. 40, very numerous in freshwater stream flowing over tidal zone, sheltering under pebbles and eating a green alga, ♀♀ with broods and immature plentiful, but no ♂♂; River Erme estuary, near mouth, 5. iii. 39, 1 ♂; River Avon estuary, near mouth, 22. iv. 32, one ♂ and several ♀♀, young reared in laboratory; Thurlestone, 15. x. 38, plentifully under stones at outflow of freshwater drain over reef of rocks, 3 young ♂♂, several young ♀♀, numerous imm.

NORTH SOMERSET: Severn estuary: Kilve, 7. v. 39, stream flowing over tidal zone, 4 ♂♂, 3 ♀♀, 1 imm. (identified for Mr R. Bassindale). DURHAM: 1 ♀ and another, in coll. Brit. Mus. [1911. 11. 8], labelled "*Gammarus marinus*" Leach.

Scotland. EAST LOTHIAN: Port Seton, under stones near high water, 7. iii. 32, one advanced imm., amongst other *Marinogammarus* spp. (identified for Prof. A. D. Hobson). WEST SUTHERLAND: Bay of Stoer (type locality), 1 maturing ♀ (sent by Mr D. M. Reid). INNER HEBRIDES: Isle of Muck, 3. viii. 38, in two stations, 4 ♀♀ and 2 imm. (identified for Prof. A. D. Hobson).

Continental. NORTH NORWAY: Hammerfest, Skaervoy, 2. vii. 39, mid-tide level, streamlet, 1 ♂ and 3 ♀♀ (coll. G. I. Crawford).

DISTRIBUTION.

So far *M. stoerensis* has only been recognized from Scotland, England and Norway. The localities for the latter country given by Stephensen (1938) with the additional one given above show that the species is well distributed along the west and north Norwegian coast. To the single previously known British locality of Stoer Bay (Reid, 1938), others are recorded above, and these, though few in number, indicate that the species is well distributed. If specially looked for the species will probably be found plentiful in many places, as it has proved to be in the Plymouth district. In ordinary collecting it is apt to escape notice owing to its small size and its localization to confined areas where there is freshwater influence.

Marinogammarus pirloti sp. nov.

Plate IV, figs. 1–17; text-figs. 9*a–f*, 10*a–e* and 11*e*, *g–i*, *m*, *n*.

The species here described was first noted from the Plymouth district in 1913, when it was recognized as new to science. It was kept at the Laboratory and used in the hybridizing experiments of 1913–14 (referred to as "another brackish water species at Cawsand within the tidal zone" Sexton, 1928, p. 52).

The first specimens, taken in August and September 1913, were from Cawsand Bay on the west side of Plymouth Sound, where a freshwater trickle falls into a tidal pool on the beach. The animals were present in numbers amongst the shingle, clinging to the under surface of flat stones. Later in the same year, the species was found at Wembury beach, in a similar habitat.

A fresh search in 1938 and 1939 revealed that the species was present in several localities in Plymouth Sound, e.g. Drake's Island, Bovisand Bay, Crownhill Bay near Bovisand, Wembury Point, as well as at Wembury Church beach, and Revelstoke, particularly abundant where there are freshwater trickles over the tidal zone. It is especially numerous at Wembury Point, from which the type specimens have been taken, under pebbles and flat stones in the upper part of the beach where the stony area borders on the reefs of rock, and where there is a good deal of infiltration of drainage water from the land. Here and in other places, it is often collected in company with *Procerodes* (*Gunda*) *ulvae*.

Specimens have also been taken from the following localities: Isle of Man, Niarbyl Bay, 18. ix. 38, collected by Mr G. I. Crawford, from a freshwater stream flowing over the beach; West Sutherland, Stoer Bay, 16. iv. 39, collected by Mr D. M. Reid from under stones, about half-tide mark, and noted as common. It thus seems probable that the species is widely distributed on rocky shores in the west of the British Isles, favouring stony beaches where there is freshwater influence. It is not, however, as yet known to penetrate into estuaries.

DESCRIPTION

ADULT MALE.

Body decidedly stout in appearance, with all its parts rounded. Pleon-segments 4–6 produced dorsally in rounded humps each carrying the four spine groups usual in the genus, the spine formula as follows: 2 : 1 : 1 : 2—3 : 1 : 1 : 3—2 : 1 : 1 : 2. Sideplates 1–4 rather deeper than the corresponding segments, convex, with the anterior distal angles much rounded; 3 and 4 of the same length, 3 narrow, 4 distally expanded, its length equal to the width across the expansion. Epimera of pleon-segments 1–3 (Pl. IV, fig. 13) with anterior margins rounded; posterior margin of 1 rounded, of 2 and 3 straight with two or three setae inset; postero-distal angle of 2 subobtuse, of 3 rectangular, both angles with a small acute projection.

Head measured along the dorsal line much longer than the 1st peraeon-segment, about five-sixths the length of the 1st and 2nd combined; rostrum not much produced; lateral lobes obliquely truncate, upper angle rounded and sloping gradually up to the insertion of antenna 1, lower angle obtuse, sinus below rather deep, with the post-antennal corner produced to a subacute angle.

Eye large and long, wide at both ends, somewhat narrowed towards the middle; retinal pigment black, occasionally rather dilute, the ommatidia separated by a reticulation of white pigment. Antenna 1 (Pl. IV, fig. 1) only a little longer than antenna 2; joint 1 of peduncle unusually large and stout, equal to combined length of joints 2 and 3, bearing 4 plumose hairs in the sensory groove; joint 2 barely one and a half times length of joint 3; primary flagellum about twice as long as the peduncle (with about 23 joints in larger specimens); accessory flagellum about 5-jointed. Whole antenna sparsely setose, the setae mainly of the bifurcate type; aesthetascs (Text-fig. 11*g*) present on all joints of primary flagellum except the first, inset on the under surface. Antenna 2 (Pl. IV, fig. 2) peduncle with joints 4 and 5 subequal in length, 4 stouter than 5; flagellum stout, subequal to the last three joints of peduncle, about 14-jointed, bearing calceoli (Pl. IV, fig. 3) on joints 2–7; dense fan-shaped clusters of male sensory setae developed all along inner surface from distal end of peduncle joint 4, the dense hair fringe so formed being conspicuous when animal viewed from above, the sensory setae themselves hyaline, flattened, and abruptly narrowed towards the apex (p. 680 and Text-fig. 11*e*); some of the setae on peduncle joints, usually the longest of each cluster, of bifurcate type (p. 677 and Text-fig. 11*n*.).

Mouth-parts normal (see Text-fig. 9 for details).

Gnathopods 1 and 2 of heavy build, not greatly dissimilar in size, hand of 2 broader but not longer than that of 1; basal joints unusually broad; median palmar spines rounded, not truncate; claw impinging on under surface owing to slight torsion of palm at the angle. Hand of gnathopod 1 (Pl. IV, figs. 4, 5) about the length of basal joint, elongate oval; palm very oblique, almost continuous with posterior margin; median palmar spine rounded and ridged on the tip, separate from spines of angle-group; claw closing between the two spine groups at the palmar angle, each group containing 1 spine like the median spine, and 2 of the small curvate type. Hand of gnathopod 2 (Pl. IV, figs. 6, 7) with palm not nearly so oblique as that of 1; palmar margin as in gnathopod 1, coarsely crenulate, with small deeply bifurcated setae along its inner edge, and longer ones on its outer side; ending, with a slight torsion on the under surface at the palmar angle in a groove or indentation minutely tuberculate; tip of claw fitting into groove between the angle-spine groups (Pl. IV, fig. 7); posterior margin slightly longer than palm. Bifurcate setae distributed on both gnathopods except hand of gnathopod 1.

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Text-fig. 9. *Marinogammarus pirloti*, sp.n. Mouth-parts of the adult male figured in Pl. IV, × 77·5; *a*, upper lip; *b*, lower lip; *c*, maxilla 1; *d*, maxilla 2; *e*, mandibles; *f*, maxilliped.

Peraeopods all with unusually broad 4th joints, and strongly recurved claws. Peraeopods 1 and 2 (Pl. IV, figs. 8, 9) sparsely setose, joints 5 and 6 armed with strong sensory spines of a special type; a few bifurcate setae present on joint 2 distally. Peraeopods 3–5 (Pl. IV, figs. 10–12) armed with clusters of short stout spines, setae present only in terminal clusters of joint 6. Basal joint of peraeopod 3 nearly as wide as long; its posterior distal angle produced to a rounded lobe; those of peraeopods 4 and 5 with this angle not free, the posterior expansion narrowing distally and ending in a group of 2 or 3 spines. Joint 4 of peraeopods 4 and 5 scarcely more than $1\frac{1}{2}$ times as long as wide distally; joints 5 and 6 subequal.

Gills well developed, ovate, stalked; carried on peraeon segments 2–7 (see Pl. IV, fig. 6); the second (attached to peraeopod 1) the longest, extending to about the distal end of 2nd (= basal) joint of the limb.

Pleopods comparatively short. Peduncles carrying a row of coupling spines, and strong setiform spines near the inner distal angle; coupling spines long, curved, with five hooks on the upper side, and two larger hooks underneath near apex; three coupling spines and two setiform on pleopod 1; two and two respectively on pleopod 2, and two and three on pleopod 3. Rami subequal, about $1\frac{1}{2}$ times length of peduncle, each with a large basal joint, and 16 to 18 small joints. Feathered swimming setae on all the joints; and cleft spines present on basal joints of inner rami, three on the first, two on the second, and two on the third; each spine with a strong feathered shaft, and a deeply cleft apex.

Uropod 1 (Pl. IV, fig. 14) extending beyond uropod 2 (Pl. IV, fig. 15), their peduncles reaching the level of the distal margin of pleon-segment 6. Uropod 3 (Pl. IV, fig. 16) outer ramus 2-jointed, joint 2 minute and bearing long setae, joint 1 long and broad, carrying groups of spines and a dense setal fringe on each margin, setal fringe of inner margin longer, composed mainly of plumose setae, that of outer margin composed of slender hyaline setae, none plumose. Telson (Pl. IV, fig. 17) cleft to the base; each lobe with an apical group of three spines, a lateral group of two spines, and a pair of short plumose sensory hairs inset in sockets on the upper surface between the two spine-groups.

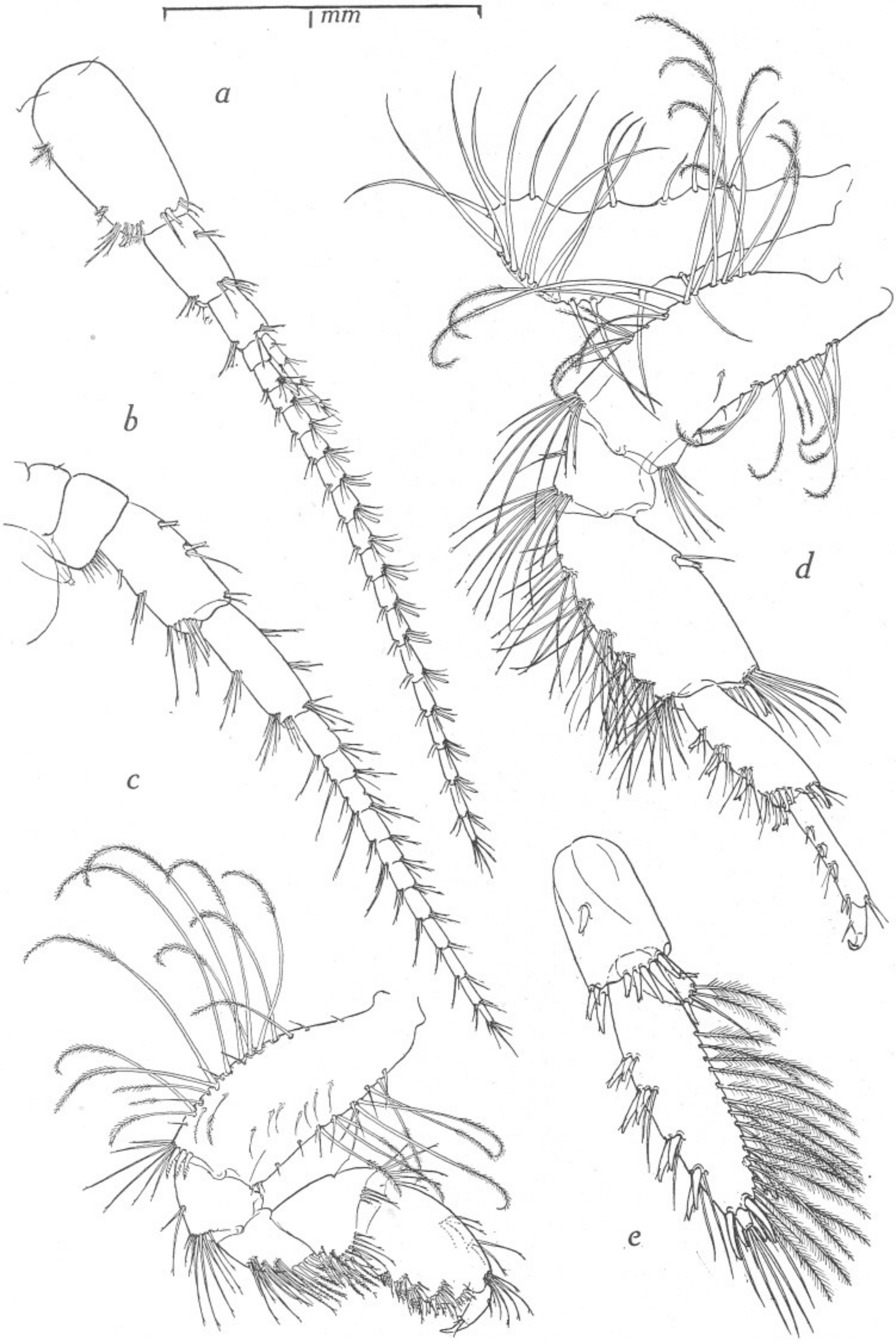
ADULT FEMALE (Text-fig. 10).

Differences from adult male as follows.

Antenna 1 (Text-fig. 10*a*) joint 1 of peduncle even more robust than in male, longer than combined length of joints 2 and 3. Antenna 2 (Text-fig. 10*b*) sparsely setose, but with more numerous bifurcate setae.

Gnathopods (Text-fig. 10*c*) with smaller hands, bifurcate setae well distributed and present on hand of gnathopod 1.

Peraeopods 1 and 2 (Text-fig. 10*d*) much more setose than in the male; joint 4 bearing clusters of long setae posteriorly, and a dense tuft at the anterior distal angle.



Text-fig. 10. *Marinogammarus pirloti* sp.n., adult female. Figures drawn from a female taken in the same sample as the male figured in Pl. IV (Wembury Point, south Devon), × 36. *a*, antenna 1, left side, under surface; *b*, antenna 2, right side; *c*, gnathopod 1; *d*, peraeopod 1; *e*, uropod 3.

Brood-plates, situated on gnathopod 2 and peraeopods 1–3, narrow; that on gnathopod 2 clavate; those on peraeopods 2 and 3 linear. The fringing hairs numbering successively on the right side 36, 18, 11 and 7; on the left side 34, 16, 10 and 7.

Uropod 3 (Text-fig. 10*e*) outer ramus with outer margin bearing groups of spines but very few setae, inner margin bearing only two distal groups of spines and a fringing row of long plumose setae.

Eggs very dark grey, almost black, when newly laid, changing to dull yellow as embryos develop; laid in rather small batches (17 in pouch of the female figured); relatively large (average size of one batch measured 0·54 × 0·69 mm.).

IMMATURE.

Eye black from time of extrusion. The characteristic large first joint of peduncle of antenna 1 distinguishable at an early age. Orange pigment patches present (see below).

SIZE AND COLOUR.

Size moderately small, male length to 14 mm., female to 11 mm.

Colour, pale green, often suffused with tinges of brown, pink or blue; irregular bright orange patches (clusters of "oil-globules") on sides of all pleon-segments, and small orange spots at the base of peraeopods 3–5.

DISTINGUISHING CHARACTERS.

The main diagnostic character of *M. pirloti* is the excessive disproportion in size between the large 1st joint and the short 2nd and 3rd joints of antenna 1, the former being fully equal in length to the two latter combined. Though a larger species than *stoerensis*, it is considerably smaller than *marinus*, *obtusatus*, or *finmarchicus*. Unlike any of these four species, it develops clearly defined patches of orange pigment on the sides of the pleon-segments.

The chief differences from *M. marinus* (p. 638) are as follows. In antenna 1, joint 1 equals 2 + 3 in length instead of being somewhat shorter, and joint 2 is not nearly twice the length of joint 3; the male sensory setae of antenna 2 are arranged in denser tufts and form a conspicuous fringe along the inner margin of the limb; calceoli are present on antenna 2; sideplate 4 has an appreciably deeper distal expansion; the joints of the peraeopods are in general broader, especially joints 4 and 5 of the three hinder; uropod 3 in the male has a dense fringe of plumose setae along the inner margin (this fringe in *marinus* consisting of slender straight setae with modified apices), and in both sexes the spines are stouter; the eye is never strikingly narrow relative to its length; orange pigment spots are developed; the size is smaller; and the body considerably stouter.

The diagnostic characters of *obtusatus* (p. 650), *finmarchicus* (p. 656) and *stoerensis* (p. 662) at once distinguish those species, and it only remains to refer to *olivii* (p. 645). To this latter species *pirloti* is evidently related. The size, form and general proportion of the limbs are very similar in the two species, except that *olivii* is rather more slender in build. In both species calceoli are present on the male antenna 2, and uropod 3 on its inner margin possesses a dense setal fringe of plumose hairs. There are, however, important differences, which may be summarized as follows. In *olivii* the setae and setules are in general notably longer than in other species of the genus, whereas, if anything, the reverse tendency is shown in *pirloti*; in *olivii* the relative lengths of the peduncle joints of antenna 1 are not abnormal, joint 1 being shorter than 2 and 3 combined, and the peduncles of both antennae are more setose; the male gnathopod 1 differs in the two species, that of *olivii* having somewhat more specialized features (see pp. 647 and 668 and compare Text-fig. 3*c*, *e* with Pl. IV, figs. 4, 5); the setal fringe of male uropod 3 contains plumose hairs on both margins in *olivii*, on the inner only in *pirloti*; in the male *olivii* there are only a few scattered bifurcate setae on the gnathopods, whereas in male *pirloti* they are distributed on both antennae and joint 2 of peraeopods 1 and 2; and in peraeopod 1 of *olivii* the antero-distal angle of joint 4 is more produced.

INDETERMINATE SPECIES.

Gammarus cam[p]ylops Leach.

1814 *Gammarus camylops* Leach, *Edinburgh Encycl.*, 1813–14, Vol. VII, p. 403 (written "*camylosps*" in Appendix).
1815 *Gammarus campylops* Leach, *Trans. Linn. Soc.*, Vol. XI, p. 360.
1830 *Gammarus camphylops* Milne-Edwards, *Ann. Sci. Nat.*, Vol. XX, p. 367.
1862 *Gammarus camptolops* Spence Bate, *Amph. Crust. Brit. Mus.*, p. 209, Pl. XXXVII, fig. 3.
1863 *Gammarus campylops* Spence Bate & Westwood, *Brit. Sessile-eyed Crust.* Vol. I, pp. 375–7.
non 1894 *Gammarus campylops* Sars, *Crust. Norway*, Vol. L, pp. 500–2, Pl. CLXXVI, fig. 2.
non 1906 *Gammarus camylops* Stebbing, *Das Tierreich*, Vol. XXI, pp. 476–7.
1911 *Gammarus marinus* var. Walker, *Ann. Mag. Nat. Hist.*, ser. 8, Vol. VII, pp. 397–9.
non 1922 *Gammarus locusta* var. *campylops* Schlienz, *Zool. Anz.*, Vol. LIV, pp. 215–17.

The status of this species, introduced by Leach (1814, 1815), has been the source of much confusion and controversy. Leach's descriptions were extremely meagre, the possession of a sinuous eye ("*oculis flexuosis*") being the only really diagnostic character given. However, his two type specimens—from Loch Ranza, Isle of Arran—were preserved in the British Museum, where they have been re-examined on two occasions. Spence Bate (1862, 1863) figured and drew up a short description of the species on the strength of the characters he found in these types, and in additional material which he assigned to the same species. He figures (1862, Pl. XXXVII) the inner ramus of uropod 3 as about 30% of the outer ramus. Other characters to which he calls attention include the produced infero-posterior angle of epimeron 3 (a character here shown to distinguish *marinus* from other related species), the "disc-shaped" basal segments of the hind peraeopods, the subequal gnathopods, etc. As to the shape of the eye, he figures it (1862) as elongate and constricted in the middle, but in his description he says it is "occasionally shaped like the letter S." He adds that the shape of the eye is not to be depended on as a specific character, as among a considerable number of specimens in his material he found as many, if not more, had eyes of a linear form. In the second description (1863, p. 375) his figure shows the eye definitely sigmoid. Unfortunately Spence Bate's descriptions are inadequate for critical purposes, and there is furthermore some doubt how far the few details he gives can be relied on.

More recently, however, Walker (1911) made a special re-examination of the types, with the help of Dr Calman; their report has to be considered the final word on the subject, as we have been informed that the specimens are no longer in existence. Mr Walker and Dr Calman found the specimens in a good state of preservation: they confirmed that the length of the inner ramus was correctly figured by Spence Bate, and in their opinion the specimens showed no definite character to separate them from *marinus* apart from the sigmoid eye. But they agreed that this character has no certain taxonomic value, and concluded that the types of *G. campylops* Leach could only be variants of *G. marinus*.

The significant point confirmed by Walker was that Leach's *campylops* had a short inner ramus and closely resembled *marinus*—or, as we should now put it, the species at least belonged to genus *Marinogammarus*. Further important points were made by Walker. Thus he points out the anomaly in Leach (1815), referred to on p. 635, and gives valid reasons for supposing that *aquaticus* (with long inner ramus) and *campylops* (with short inner ramus) had been unintentionally transposed in the original grouping of the four species of *Gammarus* known at that time. Walker was also in a position to call attention to the fact that *Gammarus campylops* Sars 1894 could not possibly be the same as Leach's species, and recognized, as can be readily confirmed from Sars's descriptions and drawings, that this species is an ally of *G. locusta* (L.), and may in fact only represent young forms of that species. This conclusion applies also to the *Gammarus camylops* of Stebbing (1906), whose description is simply a repetition of that of the species described and figured by Sars.

One further use of the name *campylops* remains to be mentioned. Schlienz (1922), accepting Walker's verdict that Sars's *campylops* was nothing to do with Leach's species, went further and attempted to identify Sars's species with *Gammarus zaddachi* Sexton 1912. Disregarding the question whether the name *campylops* could justifiably be used at all, and holding the erroneous view that *zaddachi* Sexton was only a variety of *G. locusta*, he was led to give *zaddachi* the name of *G. locusta* var. *campylops*! More recent German writers, however, have apparently discarded the view that *campylops* is synonymous with *zaddachi*.

In arriving at their own conclusions the present writers have to take consideration of the facts that distinct species allied to *marinus* are now known to exist, and that determinations of "*marinus*" made in the past may refer to any of these species. The conclusions are as follows. (i) The short original descriptions by Leach are inadequate to indicate with any certainty even to what group of species his *campylops* belonged. (ii) The supplementary descriptions by Spence Bate cannot be relied on for correctness of detail, and it is only through Walker's re-examination that the fact can be accepted that Leach's specimens possessed *marinus*-like characters. (iii) Walker's verdict to the effect that the types probably belonged to *marinus* has to be emended, in the light of our present knowledge, to the effect that they belonged to *marinus* or one of the other species of *Marinogammarus*. (iv) Since the types are no longer available for examination, the species remains indeterminate, and the name *camylops* or *campylops* Leach has to be relegated as a doubtful synonym of one of the species of *Marinogammarus*.

We may add that we entirely agree that Sars's *campylops* is not Leach's species. If this form proves indeed to be a valid species, it will require a new name (International Rules of Nomenclature, Article 35). While it may perhaps represent only a young stage (as Walker suggested), or a stunted population of *G. locusta*, the possibility that it is a form of *G. zaddachi* seems out of the question.

MATERIAL EXAMINED. A tube of seven specimens of queried *Gammarus campylops* from A. O. Walker's collection, preserved in the British Museum [1925. 9. 8: 1160–66] has been examined. The original label, in Walker's hand-writing, reads: "Argo: Killiebegs, 9. viii. 90, W.A.H.: *Gammarus campylops* Leach (or *locusta* juv.?)." The specimens have been re-determined as young stages of *G. locusta* (L.), the largest being a female which had just reached maturity.

KEY TO SPECIES OF *MARINOGAMMARUS*

a. Posterior angle of epimera 2 and 3 obtusely rounded; uropod 3 devoid of setae, or else antenna 1 with joints 1 and 2 equal in length.
(Body relatively elongate; never dense fringe of setae on uropod 3; peraeopods 1 and 2 only sparsely setose, even in adult female.)

b. Size relatively large (adults above 10 mm.); antenna 1 with joint 2 of peduncle as long as joint 1; hand of male gnathopod 1 considerably larger than that of gnathopod 2, brood-plates of female normal; spines on urosome and uropods acute and prominent; uropod 3 of normal shape, bearing setae in adult male; cuticle microscopically smooth ... ... *obtusatus* (Dahl)

bb. Size exceptionally small (adults below 8 mm.); antenna 1 with joint 2 of peduncle shorter than joint 1; hand of male gnathopod 1 not larger, actually rather smaller, than that of gnathopod 2; brood-plates of female abnormally large, especially in respect to breadth; spines on urosome dorsally few and short; uropod 3 more robust, completely lacking setae, and with short inconspicuous spines; cuticle microscopically striate ... ... *stoerensis* (Reid)

aa. Posterior angles of epimera 2 and 3 subrectangular or acute; uropod 3 bearing setae; antenna 1 with joint 2 of peduncle clearly shorter than joint 1.

b. Inner ramus of uropod 3 of one-third to two-fifths length of outer ramus; outer ramus of uropod 3 with joint 2 completely lacking; basal joints of peraeopods 4 and 5 with posterior distal angle clearly free and lacking group of spines. (Setae on uropod 3 arranged in rather conspicuous spreading tufts; epimera 2 and 3 subrectangular posteriorly; telson lobes with three spines in lateral group ... ... *finmarchicus* (Dahl)

bb. Inner ramus of uropod 3 less than one-third length of outer ramus; outer ramus with joint 2 present; basal joints of peraeopods 4 and 5 with posterior distal angle not free and bearing a group of spines. (Peraeopods 1 and 2 more densely setose in female.)

c. Larger species; epimeron 3 with posterior distal angle distinctly produced, acute; urosome spines numerous, the groups tending to coalesce into a single curved row; hand of male gnathopod 1 somewhat larger than that of gnathopod 2; median palmar spine of both male gnathopods adjacent to spines of palmar angle; peraeopods 4 and 5 rather more elongate, joint 4 three times as long as broad distally; uropod 3 lacking plumose setae; side-plate 4 with shallower distal expansion; male antenna 2 lacking calceoli *marinus* (Leach)

cc. Smaller species; angle of epimeron 3 subrectangular; urosome spines few in number, the groups remaining separated; hand of male gnathopod 1 smaller than that of gnathopod 2; median palmar spine of both male gnathopods separated from spines of palmar angle by a distinct gap; uropod 3 bearing a fringe of plumose setae (dense in male) at least on inner margin; peraeopods 4 and 5 stouter, joint 4 only twice as long as broad; sideplate 4 with rather deep distal expansion; calceoli present.

d. Antenna 1 with joint 1 robust, at least as long as 2 + 3 combined; peduncles of antennae less setose; hand of male gnathopod 1 of normal type; uropod 3 with setal fringe composed of plumose setae on inner margin only; setae in general shorter, setules normal. (Bifurcate setae present on both antennae and basal joints of peraeopods 1 and 2 in either sex) ... ... *pirloti* n.sp.

dd. Antenna 1 with joint 1 longer than 2, but clearly shorter than 2 + 3; peduncles of antennae more setose; hand of male gnathopod 1 with palmar angle roundly produced; uropod 3 with setal fringe composed of plumose setae on both outer and inner margins; setae and setules, in most places where they occur, relatively longer than in other species of genus. (Bifurcate setae absent on antennae and peraeopods of male; male sensory setae lacking on uropod 3) ... ... *olivii* (Milne-Edwards)

ON TYPES OF SETAE FOUND IN *MARINOGAMMARUS*

Species of this genus are relatively glabrous compared with other *Gammarus*-forms, and on the whole not richly supplied with setae. In some, however, antenna 2, the gnathopods distally, and uropod 3 may have dense fringes, and a moderate or sparse number of setae regularly occur along antenna 1 and peraeopods 1 and 2. The setae themselves are usually of more or less specialized types, possessing modified apices. Some marked specific distinctions have been discovered in the structure of certain of these types, as well as in their distribution or relative abundance. In this section it is proposed to give an outline of the main types of setae which occur, and to indicate the features which are usefully studied in their taxonomic bearing.

Examinations of setae have been made on parts mounted in gum chloral solution, under the magnification of a $\frac{1}{12}$ objective (oil immersion).

SIMPLE FORMS OF SETAE. Simple, unspecialized, setae taper gradually throughout their length towards the apex, are circular in cross section, and are devoid of any processes arising from their shaft. They possess the general feature common to all setae: the existence of a minute pore at the extreme apex, connecting with the hollow interior. This pore is clearly visible under high magnification; and when a seta from a fresh animal is examined, minute drops of fluid can be seen emerging from it when light pressure is exerted on the cover-slip. The distribution of simple forms of setae calls for no special discussion.

SETAE WITH FLANGED OR GROOVED APICES. In species of *Marinogammarus* the majority of the setae are not simple. Those which are not specialized in other respects usually possess modified apices. The modification consists either in the development of a flange or flattened groove at the apical end of the main shaft, or a subsidiary process arises near the apex so that this appears to be cleft, or both. Unbranched setae with flanged or grooved apices are perhaps the most generally distributed in all species. The setae thus modified may be short or long. The structure of the apex is most readily observed in short, relatively broad, setae, such as may be observed on antenna 1 of *M. marinus* female (Text-fig. 11*e*). The illustration shows how part of the shaft is compressed to form a thin flange, the thickened part being much narrowed. There appears to be a groove between the flange and the main portion of the shaft, at least at its base. The course of the central cavity passing upwards to the apical pore is clearly visible. Numerous setae in both sexes of *marinus* have essentially this type of apex. Text-fig. 11*k* illustrates the apex of a long seta from antenna 2 of the male.

Corresponding setae in other species have a similar general form, but show specific variations in pattern. Thus the flanged apices in *pirloti* (Text-fig. 11*m*) are often broad, show clearer indications of a groove, and can almost be termed narrowly spatulate. Minute striations can sometimes be seen on the flange, as in the seta illustrated. The most readily distinguished specific type is that found in *finmarchicus*, in which the apices have the appearance of one shown in Text-fig. 11*j*.

SETAE WITH BIFURCATE APICES. Sometimes the shaft of the seta is divided near its apex into two branches, producing an effect which is here termed "bifurcate" (Text-fig. 11*g*, *n*, *o*). The two branches are not symmetrical. In all types which have been studied the internal cavity passes up through only one of the branches, which carries the apical pore at its extremity, and which is here referred to here as the main branch. The second branch appears to be devoid of an internal cavity and apical pore. It is almost invariably shorter, sometimes considerably, and often narrower than the main branch: it is also typically sharper and less flexible. The main branch may be narrowly flanged just like the apex of an unbranched seta. The bifurcate setae of *pirloti* (Text-fig. 11*n*) are typically so flanged.

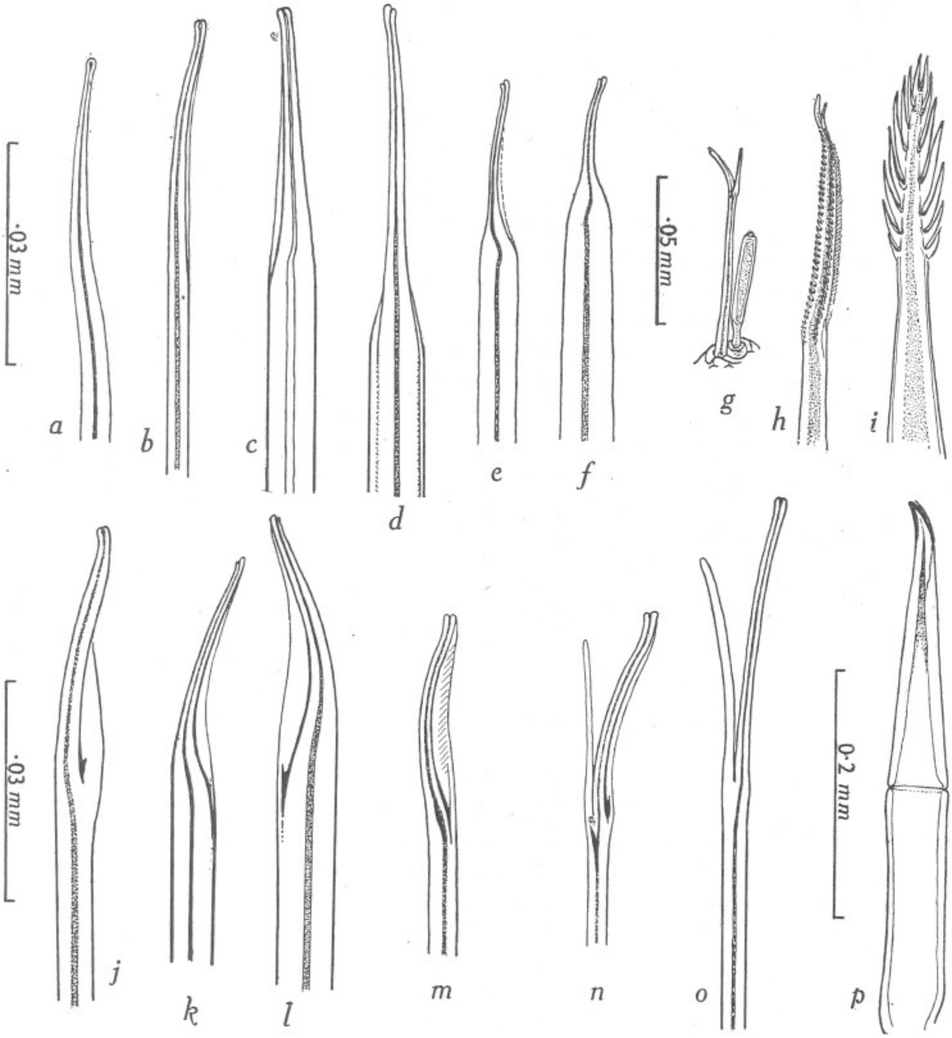
Specific differences in the form and dimensions of bifurcate setae occur. Thus in *obtusatus* (Text-fig. 11*o*) both branches are long and slender, the main branch being apparently without a flange. The few bifurcate setae present in male *olivii* have very short apices.

The frequency and distribution of bifurcate setae vary considerably in different forms. In the first place they are in general less abundant and more restricted in their distribution in the male sex than in the female of the same species. This difference is sometimes very marked, and is at least apparent in all species investigated. Two contrasting examples may be given. The females of both *pirloti* and *stoerensis* possess conspicuous bifurcate setae distributed on the following limbs: antenna 1 and 2, gnathopod 1 and 2, peraeopod 1, joints 2 and 3, peraeopod 2, joint 2. In the male *pirloti* the distribution is very similar, except that there are none on the hand of gnathopod 1 or on peraeopod 2, joint 2, and they are much sparser on antenna 2. In the male *stoerensis* they are almost entirely confined to the two gnathopods. When bifurcate setae are sparse, it is usually found that setae showing this condition are restricted to the longest one in a cluster.

Secondly there are specific differences. These are more apparent in the male. In *obtusatus* and *pirloti* the setae are well distributed on the anterior limbs, whereas in *marinus*, *olivii* and *stoerensis* they are confined to certain joints of the gnathopods, or almost so. In *olivii* they are particularly sparse, and provide an interesting contrast with the related *pirloti*. Usually there are none on the hand of male gnathopod 1; but some are present on the posterior margin in *stoerensis*. In the female, *marinus* completely, and *finmarchicus* almost, lacks these setae on peraeopods 1 and 2.

Apparently no bifurcate setae ever occur on uropod 3. It may also be noted that the specialized serrated setae (Text-fig. 11*h*) which are characteristic of the clusters on the posterior margins of gnathopod 1, joint 5 and gnathopod 2, joints 5 and 6, are typically bifurcate at the apex.

MALE SENSORY SETAE. The setae which fall in this category are developed in the male at sexual maturity as secondary sexual structures. Among Gammarids in general they may assume various forms: thus in *G. chevreuxi* they are slender, soft and curled. In *Marinogammarus* they are always straight, though typically more flexible and less strongly chitinized than other setae. Usually in this genus they are appreciably narrowed at the apex, sometimes very abruptly. Another characteristic feature is that these hairs occur in relatively few positions. It is in fact only on antenna 2 that they are always fully developed. They may also occur sparsely on the hand of gnathopod 2, and among the hair fringes of uropod 3, though in these positions they are less differentiated and should perhaps not be classed with the antennal setae at all. No special male setae of any sort are developed on any of the peraeopods.



G. M. S. *del.*

Text-fig 11. *Marinogammarus*, dermal armature. Figures drawn under $\frac{1}{12}$ objective. Magnification: *a–f* and *j–o* × 967, *g–i* × 384, *p* × 163. *a*, apex of male sensory seta from antenna 2 of *M. stoerensis* ♂; *b*, apex of male sensory seta from antenna 2 of *M. finmarchicus*; *c*, apex of male sensory seta from antenna 2 of *M. obtusatus*; *d*, apex of male sensory seta from antenna 2 of *M. marinus*; *e*, apex of male sensory seta from antenna 2 of *M. pirloti*; *f*, apex of male sensory seta from antenna 2 of *M. olivii*; *g*, *M. pirloti* ♂, aesthetasc and small bifurcate seta from antenna 1, under surface of flagellum joint 1; *h*, *M. pirloti* ♂, serrated falciform bristle from proximal bristle-cluster on gnathopod 2 hand; *i*, *M. pirloti* ♂, flat dentate spine from gnathopod 2, joint 5 (second spine in group of three on posterior margin distally); *j*, *M. finmarchicus* ♂, apex of long seta from uropod 3; *k*, *M. marinus* ♂, apex of long seta from peduncle of antenna 2; *l*, *M. marinus* ♀, apex of short seta from cluster on distal end of peduncle joint 2 of antenna 1; *m*, *M. pirloti* ♂, apex of long seta from palmar margin of gnathopod 2 hand (similar form on uropod 3, etc.); *n*, *M. pirloti* ♂, apex of long bifurcate seta from antenna 2 flagellum; *o*, *M. obtusatus* ♂, apex of long bifurcate seta from antenna 2 flagellum; *p*, *M. finmarchicus* ♂, spine from peraeopod 5, joint 4 apex.

The brief account and illustrations (Text-fig. 11 *a–f*) here given refer specifically to the setae developed in clusters along the inner border of antenna 2. These have a constant form in each species. The differences between the species are more apparent than may be suggested by the outline drawings.

In *stoerensis* (Text-fig. 11 *a*) they are relatively short, being somewhat broad at the base and tapering gradually towards the apex. The apical pore is conspicuous and the extremity is distinctly minutely bulbous. More flexible than the other setae on the limb, they often assume a curved or sinuous shape in microscope mounts. Their form is thus simple, and proves to be the least specialized of the six species. They are also developed in fewer numbers than in the other species. A few apparently similar setae occur on the gnathopod hands, but none on uropod 3 (which is glabrous).

The male sensory seta of *finmarchicus* (Text-fig. 11 *b*) is elongate and narrow, relatively simple in form, except that the apex, which tapers gradually, possesses a distinct, but very narrow, flange. These hairs are not so obviously distinguishable from certain other setae of antenna 2, but they are distinctly more flexible. They are developed in quite dense clusters. Setae which resemble them occur among the fringes of uropod 3.

In *obtusatus* (Text-fig. 11 *c*) the setae are not so greatly differentiated from other types, possessing a distinct flange on their gradually tapering apex. They are long, with stout shafts, and are developed in moderate numbers. Some similar setae occur on the relatively sparsely haired uropod 3.

The setae in *marinus* (Text-fig. 11 *d*) show a more distinctly narrowed apex, though the narrowing is not very abrupt. The shafts are rather broad, but not flattened. The setae are long, and arise in fairly dense clusters. Setae of a very similar type form a dense fringe along the inner border of uropod 3.

A still greater contrast between the male sensory setae and other types is found in *pirloti*. The former (Text-fig. 11 *e*), besides being less strongly chitinized and more flexible, have flattened shafts and are appreciably broader (compare Text-fig. 11 *e*, *n*). At the apex the seta narrows abruptly, and a fine narrow flange is visible at the base of the attenuated apical portion. These setae arise in dense clusters. Similar setae, but narrower and less differentiated, occur in a few clusters on the hand of gnathopod 2, and plentifully on uropod 3, especially along the outer margin.

In *olivii* (Text-fig. 11 *f*) these setae have a form resembling the above, except that the shafts are even broader, and the apices shorter. The similarity of the male sensory setae in *pirloti* and *olivii* provides striking confirmation of the view that these two species are nearly related. In *olivii*, too, they are developed in dense tufts; but setae which in any way resemble them are lacking on uropod 3.

PLUMOSE SETAE. Long setae with feather-like processes are often developed on uropod 3, where they may (as in other *Gammarus*-forms) form the main elements of the setal fringes. The extent to which they are developed in the different species is as follows.

In *marinus* none occur in the male, the relatively dense hair fringes being composed of setae of other types, but a few occur along the inner margin of the outer ramus in the female. In *obtusatus* (fringes sparse) and *stoerensis* (fringes altogether absent) they are lacking in both sexes. In *finmarchicus* a sparse row of plumose setae occurs along the inner margin of the outer ramus, each seta being associated with a separate cluster of non-plumose setae. In the two remaining species, *pirloti* and *olivii*, plumose setae form dense fringes, and occur on the short inner ramus as well as on the outer. In the former species, however, the fringe of plumose setae is situated only along the inner margin, whereas in the latter it extends around both margins.

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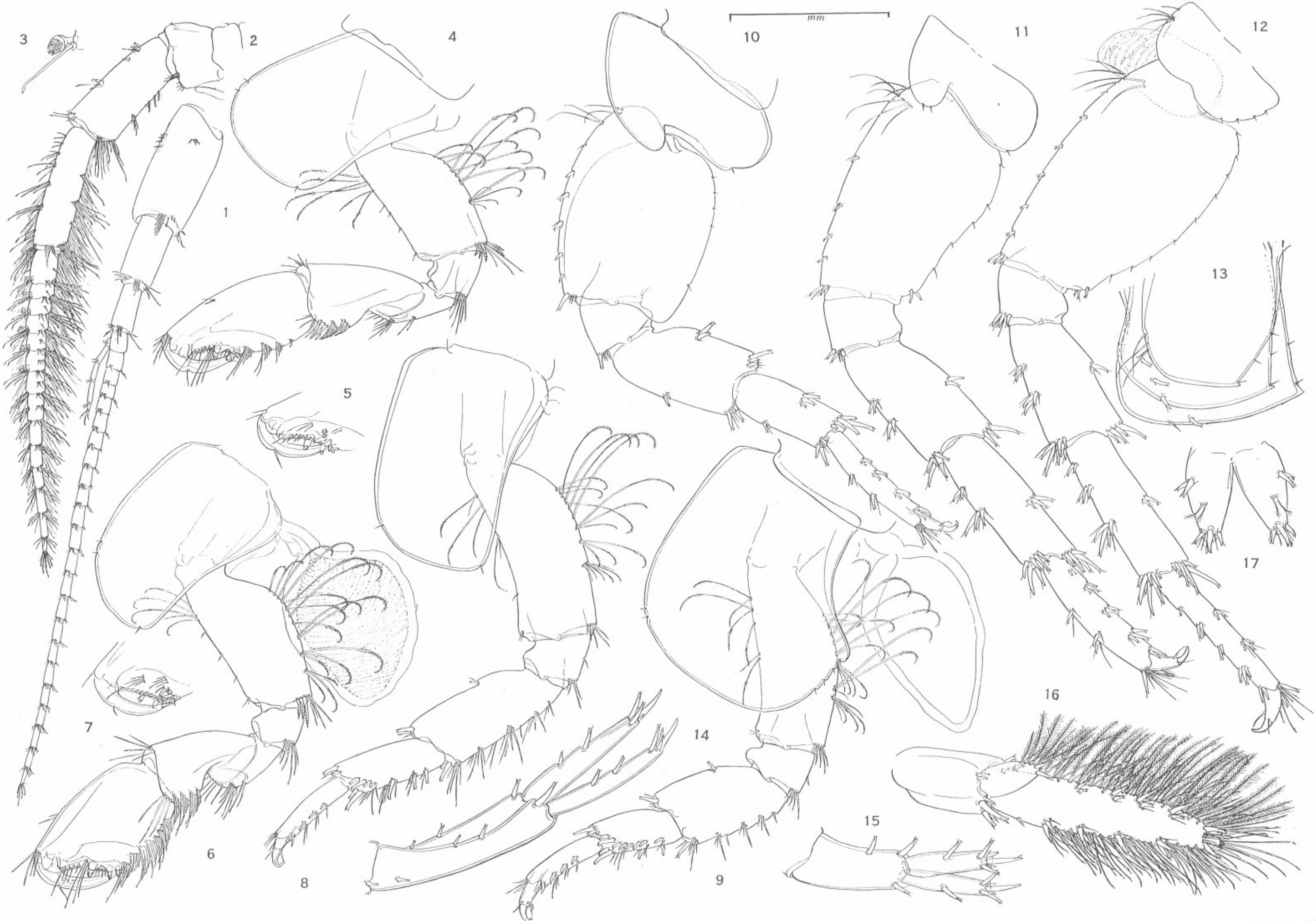
EXPLANATION OF PLATE IV.

Marinogammarus pirloti sp.n., adult male. Figures drawn from an adult male captured at Wembury Point, near Plymouth, 18. iii. 39. All figures, except fig. 3, reproduced at the same magnification of × 36.

Fig. 1, antenna 1; fig. 2, antenna 2; fig. 3, calceolus and bifurcate seta from joint 3 of antenna 2 flagellum, × 62; fig. 4, gnathopod 1; fig. 5, gnathopod 1, under surface of hand, showing the palmar margin and angle spines; fig. 6, gnathopod 2, with gill attached; fig. 7, gnathopod 2, under surface, showing the palmar margin and angle spines; fig. 8, peraeopod 1; fig. 9, peraeopod 2, with gill outlined; fig. 10, peraeopod 3; fig. 11, peraeopod 4; fig. 12, peraeopod 5; fig. 13, epimera of pleon-segments 1–3; fig. 14, uropod 1; fig. 15, uropod 2; fig. 16, uropod 3; fig. 17, telson, dorsal view.

POSTSCRIPT. For observations on the powers of osmotic regulation in *Marinogammarus obtusatus*, see Beadle and Cragg (1940). The same authors are publishing in the *Journal of Animal Ecology* further observations relating to some of their collections which we have determined and recorded under "material examined". Prof. A. D. Hobson is in possession of additional data on the habitats of examined material, some of which was collected by Dr E. A. T. Nicol.

PLATE IV



E. W. S. *del.*

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1939–40

The Council and the Officers.

Dr George Parker Bidder was elected President of the Association in June in place of Lord Moyne who had served for the preceding nine years.

Four ordinary meetings of the Council were held during the year in the Rooms of the Royal Society, London, at which the average attendance was fifteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used.

A subcommittee of the Development Commission's Advisory Committee on Fishery Research met at Plymouth in June under the chairmanship of Sir John Graham Kerr, M.P. A memorandum prepared by the Council was received by the Committee and members of the scientific staff were interviewed in turn.

The War.

At a meeting of a subcommittee of the Development Commission's Committee on Fishery Research held in London on September 12, it was recommended that during the war the Plymouth Laboratory should continue its work as normally as possible, and that the members of the staff should be retained in their present posts until such time as they are requisitioned for National Service. A number of the staff have been ear-marked as "key workers" who should, if possible, remain at the Laboratory throughout the war as a skeleton staff.

Dr W. R. G. Atkins has been in close touch with the scientific work of the Air Ministry at their Balloon Development Establishment. Although not in the direct employment of the Air Ministry, he has been working at Plymouth on the development of instruments required in balloon technique.

Four members of the technical staff of the Laboratory are already serving in H.M. Forces, and the mate of the Association's steam-drifter *Salpa* has been released for commercial fishing at his home port of Brixham.

Precautionary measures against air-raids have been taken, including the conversion into an air-raid shelter of the lower half of the tunnel leading from the Laboratory to the foreshore.

The Plymouth Laboratory.

The scheme for the renovation and extension of the main laboratory building, to which reference was made in last year's Report, has now been carried out. The success of the undertaking is a source of great satisfaction to the Council. A full statement of the costs of the work will be issued in due course and a list of the generous donations to the Building Fund will be found on p. 699.

During the course of the work on the extension of the Laboratory it was found that the fresh-water main was in bad condition, and a new pipe of asbestos cement has been laid. The Preparation Room and the Chief Laboratory Assistant's room have been renovated. Renovations have also been carried out in the engine-room, where they were urgently needed. The walls have been cleared of all disused pipes and cemented throughout, and the plant for circulating sea-water and air has been overhauled and reassembled in a compact lay-out. The other rooms in the basement have been cleared to provide much-needed general laboratory and journal storage. The road leading from the main entrance to the Director's house in front of the main building has been widened on the seaward side to provide better parking accommodation for cars. The exterior of the North building and Library has been painted where necessary, and the area between the North building and the Citadel wall has been cleared and laid with gravel.

The Aquarium.

The building work in connexion with the Laboratory extension necessitated closing the Aquarium to the public for some weeks during the early part of the year. The stock of exhibits was well maintained, however, and the usual steady flow of visitors throughout the summer ceased only at the outbreak of war.

The Ship and Motor Boat.

The steam-drifter *Salpa* and motor-boat *Gammarus* had both given continuous and satisfactory service until the war began. The *Salpa* was then laid up and her equipment stored, and on December 6 she was requisitioned by the Admiralty. The *Gammarus* is permitted to work in Plymouth Sound and Cawsand Bay, but in much restricted areas.

The Staff.

Dr S. Kemp and Mr F. S. Russell attended the thirty-second meeting of the International Council for the Exploration of the Sea, which was held in Berlin in May.

Dr M. V. Lebour resumed work at the Laboratory at the beginning of July after one year's leave in Bermuda where she continued her studies of molluscan and crustacean development. She has received a medal from

H.M. the King of the Belgians in appreciation of her help in classifying the natural history collections made during his voyage in the East in 1928–29.

Mr D. P. Wilson has been elected a Fellow of the Royal Photographic Society.

Dr L. H. N. Cooper left for America at the end of August on leave of absence to work in Prof. Harned's Laboratory at Yale. His expenses are being borne by a grant from the E. T. Browne fund of the Royal Society.

Mr P. R. Crimp, Student Probationer, left the service of the Association to take up a post under the Ministry of Agriculture and Fisheries as Whaling Inspector for the 1939–40 Antarctic whaling season.

It is with deep regret that the Council have to report the death of Miss A. R. Clark (Librarian) on August 12, after an operation. Miss Clark had been a valued and trusted servant of the Association for thirty-four years, and an acknowledgment of her services is to be published in the Journal of the Association. The post of Librarian has been filled by the promotion of Miss M. Sexton, and Miss D. R. Dibben has been appointed Director's Clerk and Assistant Librarian.

Mr A. J. Smith, Chief Laboratory Assistant, retired from the service of the Association on December 31, 1939. He had been a member of the staff since 1895. All who have worked at Plymouth will have appreciated Mr Smith's comprehensive knowledge of the Plymouth fauna, his deep enthusiasm for marine biology and the unstinted help that he gave to their needs, and they will have realized also that in his position as chief of the technical staff he has contributed very largely to the steady growth and prosperity of the Laboratory.

Since there was a general desire to make a gift to Mr Smith on the occasion of his retirement a letter was circulated to the members of the Association, and the sum of money so raised was sent to him in March with a letter from the President.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr G. P. Baerends, Holland (Chemical estimations. Nutrient salts).
H. Barnes, Plymouth (Hydroxylamine and nitrate degeneration in sea water).
F. H. Bennett, Oxford (General Zoology).
Dr A. M. Bidder, Cambridge (Library).
Dr G. P. Bidder, Cambridge (Library).
Prof. Alan A. Boyden, Rutgers University, N.J. (Proteins of crustacean blood).
Prof. M. A. & Mrs Brannon, University of Wisconsin, U.S.A. (Algae).
Miss E. H. Brown, Cambridge (Morphology of periostracum of *Mytilus*).
Miss M. J. Brown, University of Wyoming, U.S.A. (General collecting).
H. G. Callan, Oxford (Parasitic castration of *Leander serratus*).

J. S. Colman, Sheffield (Faunas inhabiting intertidal seaweeds).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
Dr van Dam, Netherlands (Oceanographical problems and methods).
Dr G. E. R. Deacon, "Discovery" Committee (*p*H standards).
Miss M. J. Dibb, London (Gregarines of polychaetes).
J. E. Forrest, London (Nudibranch molluscs).
Dr V. Fretter, London (Genital ducts of prosobranch molluscs).
A. Graham, London (Stomachs of prosobranchs).
Dr R. Gurney, Oxford (Decapod larvae).
R. J. Harrison, Kent (Biology of caprellids. Chemical analysis of *Sagitta*).
Dr T. J. Hart, "Discovery" Committee (Phytoplankton).
Miss O. Hartmann, California (General collecting).
C. F. Hickling, Lowestoft (Experimental marking of fish by tattooing).
A. L. Hodgkin, Cambridge (Electrical studies of the giant axon of the squid).
Prof. L. Hogben, Aberdeen (Chromatic response of selachians).
W. Holmes, Oxford (Myelinated nerves of *Leander serratus*).
A. F. Huxley, Cambridge (with Mr A. L. Hodgkin).
Miss P. M. Jenkin, Bristol (Oxygen deficit in lakes).
Dr M. W. Jepps, Glasgow (*Polystomella*).
R. R. M. Jones, Anglesea (Marine chironomids; museum).
Dr B. Katz, London (Crustacean nerves).
Dr H. W. Lissmann, Cambridge (Locomotory mechanism in the dogfish).
Dr O. & Mrs Löwenstein, Glasgow (Elasmobranch labyrinth: nervous system of *Ciona*).
A. G. Lowndes, lately Marlborough College (Density of living aquatic organisms).
Miss A. M. Lysaght, London (Zonation and life history of *Littorina neritoides*).
Miss M. F. Mare, Cambridge (Micro-fauna and -flora of mud deposits: phytoplankton).
Dr H. B. Moore, Bermuda (Plankton).
Dr E. H. & Mrs Myers, La Jolla, California (Foraminifera).
Dr A. G. Nicholls, Millport (Library).
Dr N. K. Panikkar, London (Osmo-regulation in marine animals).
Dr C. F. A. Pantin, Cambridge (Nerve-net in actinians).
Miss M. L. Popham, Bristol (*Galeomma* and Leptonidae).
R. J. Pumphrey, Cambridge (Myelinated nerves in Crustacea).
G. W. Robertson, Cambridge (Absorption of fats in actinians).
The Hon. Miriam Rothschild, London (Trematode parasites in *Hydrobia*).
F. K. Sanders, Oxford (Nervous system in elasmobranchs).
J. E. Smith, Cambridge (Nervous system of asteroids).
Miss N. G. Sproston, London (Metazoan parasites of fishes).
Miss F. A. Stanbury, Plymouth (Silica uptake by diatoms).
Dr H. Waring, Aberdeen (with Prof. L. Hogben).
T. H. Waterman, Harvard College, U.S.A. (Neuro-muscular transmission in *Maia*).
J. Z. Young, Oxford (Visual learning in *Sepia*).

The usual Easter Vacation Courses in Marine Biology were conducted by Mr D. P. Wilson and Mr G. A. Steven. They were attended by forty students from the Universities of Oxford, Cambridge, London, St Andrew's, Edinburgh, Southampton, Leeds, Wales (Bangor), Birmingham, Sheffield and Reading, and Middlesex Hospital.

A course in Marine Biology had also been arranged for the Summer Vacation, to be conducted by Prof. J. H. Orton, but this had to be cancelled on account of the war.

During the Easter Vacation, Mr J. M. Branfoot brought five students from Oundle School, Mr I. Hamilton four from Dauntsey's School, Dr W. L. Francis two from Repton School, Mr A. Gardiner two from Radley College, Mr A. H. Lewis three from Wellington College, Mr A. H. Wood three from Bradfield College, Mr H. C. W. Wilson four from Malvern College, Mr G. C. M. Harris four from Monckton Combe School, Mr R. H. Pott and Mr B. A. Barr six from Stowe School.

On Whit-Monday, May 29, a visit to the Laboratory was paid by about seventy-five delegates who were attending the annual conference of the South-Western Naturalists' Union in Plymouth. Demonstrations of work were given by members of the scientific staff and the party subsequently inspected the new laboratories.

Four boys from Cheltenham College worked in the Laboratory during January under the supervision of Mr A. G. Lowndes.

A conference of the Society for Experimental Biology was held in the Laboratory from July 13 to 15. Some sixty attended meetings in the Common Room and saw demonstrations by members of the Staff.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment

Further measurements of under-water illumination were made by Dr H. H. Poole and Dr W. R. G. Atkins using the cube photometer. It was found necessary completely to re-standardize the six specially sensitive large rectifier selenium cells. Such cells, even if their sensitivity as regards light of low intensity remains constant, may show serious changes in the curvature of the current-illumination relation. If undetected, this would result in bright light being under-estimated. It was found by Dr Poole that this curvature is most marked in the case of red light. The angular distribution of the light was studied at sea with the help of the cube photometer. Earlier results, which indicated that this did not vary appreciably with depth, were confirmed. The average obliquity of light penetrating water was 36°–40° with the vertical. No significant difference was detectable between that for a smooth sea with overcast sky and rough sea with either high or low sun. The percentage of light scattered upwards varied from about 5 per cent inside Plymouth breakwater to 2 per cent five miles and farther out to sea.

The vacuum sodium and selenium rectifier cells used by Prof. Ball in Ceylon were taken to the Jungfrau region of Switzerland by the Hon. Miriam Rothschild for measurements at high altitudes. Tests by Dr Atkins showed that the sodium cell remained quite constant; the selenium cell altered somewhat after several years' use. Another similar sodium cell was, however, completely ruined by the great heat of the Sudan at Wad Medani when continuously exposed for two years. In Plymouth such a cell is used for the recorder and remains constant.

Owing to the approach of war the submarine measurements were prepared for publication without more extended observations. Dr Atkins has been able to make use of the instruments purchased with various grants from the Royal Society in work for the R.A.F. either here or at a service station. To this work the instrumental equipment of the general physiology department has also contributed.

Dr L. H. N. Cooper has continued his routine observations on phosphate values in the Channel and has published in the Journal of the Association a paper on the inorganic constituents of certain marine organisms. In collaboration with Mr A. Milne he has studied submarine illumination in the silt-laden waters of the Tamar estuary. Extinction coefficients are naturally much higher than in the Channel, but in marked contrast with the open sea, red light in the estuary penetrates as well or better than any other. Dr Cooper has made progress with his work on the iron cycle in the sea and shortly before the war he went to America with the assistance of a grant from the Royal Society to continue his studies on this subject in Prof. Harned's Laboratory at Yale University.

Plankton

Dr H. W. Harvey has continued experimental work on the growth of phytoplankton. A method was found by which a mixed community similar in constitution to that occurring in the sea but many hundred times more dense, could be induced to grow in crude sea water *in vitro*. This led to determining various forms in which the organisms could be supplied with their nitrogen and phosphorus requirements; experiment showed that nitrogen in the form of ammonium was utilized in preference to nitrate and gave evidence that urea and uric acid could be utilized as such.

The growth of phytoplankton in crude sea water collected at intervals during the summer was usually marked by the small number of species which developed in it; no evidence was found that it was well seeded with resting spores of species which had been abundant earlier in the year. It was found that in waters collected during the summer the growth rate was increased by the addition of cystine and of sulphide, although the latter is soon oxidized. The minimum quantity of sulphide-sulphur required to give a distinct increase in rate was some 0·1 milligram per litre. Addition of these accessary nutrients, which increased the rate of growth, did not influence the composition of the community or its final density, which was dependent, in these experiments, upon the quantity of available nitrogen or phosphorus compounds added to the water.

Further experiments have been made on the effect of adding traces of manganese on the growth of *Dytilum Brightwelli* in sea water collected during the winter. These indicated that an increased growth rate is only brought about when the intensity of illumination is low or the period of illumination is reduced to a few hours daily. Experiments with a mixed culture indicated that *Thalassiosira gravida* responded in the same way to manganese while *Sceletonema costatum* was unaffected.

Mr D. P. Wilson has been studying the tri-radiate form of *Nitzschia closterium*. This is the diatom which has been kept in constant culture since Dr Allen started to grow it many years ago. The diatom is roughly spindle-shaped, but mixed with it there is a three-rayed form which has been known for a long time but not described. This tri-radiate organism was for long present in small numbers only, but recently it has dominated the cultures almost to the exclusion of the spindle type. It is not known whether the one type gives rise to the other or whether they are distinct organisms. Mr Wilson has isolated single cells of both kinds and from them has produced cultures of the two forms which have remained pure for some weeks and through several stages of subculturing. It will be interesting to discover whether they will do so indefinitely or whether in course of time tri-radiates will arise from the normal form and *vice versa*. It is of some importance to re-establish cultures of the normal form, as the tri-radiate shape seems less suitable as food for diatom-eating larvae.

Dr M. V. Lebour, who has been in Bermuda for a year, returned in July. Since then she has been spending most of her time finishing off the work done there, much of which fits in very well with her previous work at Plymouth on larval decapods and molluscs. She has made a résumé of the larval Pandalidae in which all the British forms are included, and has given a description of the hitherto unknown larvae of *Pandalus bonnieri*: these have been compared with *Parapandalus richardi* from Bermuda whose life-history she has followed from the first larva to the young form. This paper is now in the press and will be published in the Journal of the Association. A joint paper with Dr R. Gurney on larval Sergestidae is to be published in the *Discovery Reports*. This includes a description of the early larval stages of nearly all the Atlantic forms, many of which have been for the first time connected by moulting in the Bermuda Laboratory. A further paper with Dr Gurney on various decapod larvae is nearly ready for publication. This includes Hoplophorids, Stenopids and others. The prosobranch larvae, which have proved extremely interesting, are well in hand and a paper on these is nearly finished, as is one on larval crabs hatched out in the Laboratory.

Dr S. Kemp, when opportunity has permitted, has been working on the collections of pelagic Decapoda obtained by the *Discovery II* and the *Dana*. A preliminary note on *Acanthephyra purpurea* and its allies has been published in the *Annals and Magazine of Natural History*.

Mr F. S. Russell has continued to observe the changes in the plankton off Plymouth by means of weekly ring trawl collections. The results for the year 1938 have been published, and those for 1939 up to the outbreak of war are now in the press. The conditions in 1939, as shown by the composition of the *Sagitta* population, were very similar to those of 1938, although the numbers of *Sagitta* were on the whole even lower than in that year. There were indications of a slight incursion of *elegans* water in January and February. No unusual plankton animals were seen. A review of the researches on plankton indicator species over the whole of the North Sea area was published in the Journal of the Council for the Exploration of the Sea.

Mr Russell has made a further study of the nematocysts of medusae and a second paper on the subject has been published. Much time has been spent on the monograph of British medusae which is now nearing completion. Over seventy species have been described and many drawings made.

Mr W. J. Rees has continued his observations on hydroids and medusae. A revision of the hydroid genus *Campanulina* van Beneden, 1847, has resulted in the almost complete dismemberment of the genus and has necessitated the devotion of considerable time to literature. *Campanulina tenuis* van Beneden has been shown to be the sole species in the genus. The medusa-bearing species have been referred to the four genera, *Aequorea*, *Campomma*, *Phialella* and *Eirene*, while the species with fixed gonophores have been placed in *Opercularella*. A paper on this subject has been published during the year in the *Annals and Magazine of Natural History*. Observations on the hydroid of the medusa *Dipurena halterata* have now been published in the Journal.

The collections of hydromedusae made at Herdla and Valentia in 1937 and 1938 respectively have been examined and a list of the species found is now ready for publication. The hydroid of the medusa *Coryne tubulosa* was found growing in a bell jar at Herdla and its polyps showed an unusual form of budding. Free hydranths with medusa buds developed on the body of the parent hydranths and these buds became free. A similar method of budding has been observed by Miss M. J. Delap at Valentia in the related *Tricyclusa singularis*, and she has kindly allowed Mr Rees to publish her sketches of this rare hydroid.

Fauna of the Sea Floor

Three further papers on the ecology of the Tamar Estuary have been published during the year. These include papers on submarine illumination and the tucknet fishery, and a study of the intertidal macrofauna of the mudflats prepared by Mr G. M. Spooner and based on work carried out by himself and Dr H. B. Moore. Some of the results of this investigation were noted in the Report of Council for 1937. The population densities in the tidal zone and degree of penetration up-river are discussed for the whole macrofauna, special attention being given to the dominant species (four polychaetes, two crustaceans, seven molluscs). It is curious to find that all five of the strictly estuarine species dealt with, which reach their maximum in the middle reaches of the estuary, have a marked optimum somewhere in the upper half of the tidal zone, and tend to disappear towards low-water. The reason is that these species, because they occupy permanent burrows, or live on the surface of the mud, are all susceptible to the effects of current action. This is greatest on the edge of the main river channel, i.e. towards low-water, and appears to be the main cause of a marked decline of the total fauna (even to complete absence) in many places at this level.

Mr Spooner has continued investigations on the fauna which shelters in clumps of weeds, etc., in estuaries, particularly in connexion with the distribution of species of *Gammarus* which constitute the main element of this fauna. The succession of different species at different levels of the estuary has been followed up in rivers other than the Tamar, and the results are being prepared for press. Data are accumulating for other animals which are taken in company with *Gammarus* in the sievings.

The problems connected with the local variations of *Gammarus zaddachi* are being followed up. The special variety which occupies the middle reaches in estuaries has been traced in west country rivers other than the Tamar, but it is absent where the estuarine gradient is steep. Rearing in the laboratory has proved that both this variety and the normal type breed true in varying salinities.

In connexion with the work being carried out in collaboration with Mrs E. W. Sexton on the revision of the British species of *Gammarus*, various collections have been examined from different parts of the British Isles. A large collection was also examined from the Bassin de Chasse, Ostend, on behalf of a survey being conducted by the Brussels Museum.

During the year Mrs Sexton has published detailed drawings and a description of *G. tigrinus* referred to in the last report. This species, new to science, is of interest in being the only one yet recorded which has a special association with inland mineral waters. It occurs in large numbers, for example, in the Droitwich Spa district, in streams connected with the alkaline brine springs and possessing a peculiar mineral content. A quantitative analysis of the waters in which collections were made was carried out by Dr L. H. N. Cooper. He reported that the chloride, although not proportionately as high as in sea-water, was remarkable for inland waters. Calcium and magnesium were not very much greater than they would be in diluted sea water of the same chlorinity, whilst bicarbonate and sulphate were high.

A forthcoming publication, by Mrs Sexton and Mr Spooner, deals with another species which abounds on the shore under stones where fresh water trickles flow over the tidal zone. This is one of a group of five species of which until recently only *G. marinus* has been recognized. Three others, which prove to have a wide distribution in Britain, have recently been described by different authors, but a good deal of useful additional information on them has already been collected. The need for revision of the systematics and distribution of British *Gammarus* is enhanced by the increasing use of species of the genus in physiological experiments.

Mrs Sexton's work on the genetics of *Gammarus* suffered a great loss in August by the death of Miss Clark, who so ably assisted in it for many years. A large mass of data has still to be analysed and it is hoped that progress will be made in this during the coming months.

Mr P. R. Crimp continued his work on the microfauna of bottom deposits and it had reached an advanced stage when war broke out. He then accepted a temporary appointment under the Ministry of Agriculture and Fisheries as a Whaling Inspector, but hopes that it will be possible for him to prepare his results for the press during 1940.

Mr Wilson has again turned his attention to polychaete larvae, and to the larvae of the Magelonidae in particular. This work promises to be unusually interesting from both embryological and systematic points of view. He has found two species previously unrecognized in the Plymouth fauna: one of these appears to be new, the other is almost certainly *Magelona cincta* Ehlers which was first described from Algoa Bay, South Africa, and has subsequently been reported off the coast of Morocco. At Plymouth *M. cincta* is abundant in the Rame Mud and probably occurs elsewhere. A third species at Plymouth is the well-known *M. papillicornis* F. Müller, the only member of the Magelonidae previously recorded from the area.

The larvae of all three species have been obtained by artificial fertilization and reared for some time, but not as yet through to metamorphosis. Late stages have been obtained from the plankton and some specimens have metamorphosed in the laboratory. Those of *M. cincta* have been especially numerous and as devourers of larval lamellibranchs are of interest economically.

Early stages of *Magelona* have never been described although there have been several accounts of older larvae—descriptions, however, that are not without error. The early development is remarkable in that the prototroch grows out into two long palp-like organs and it is the basal portions of these organs which form the adult "palps" after the distal larval (prototrochal) portions have broken off. The problems raised must await interpretation until sections have been cut and studied. An additional puzzling feature is that in *M. papillicornis* all the larvae obtained by artificial fertilization have developed the prototrochal palp-like organ only on the right side. Such asymmetrical larvae have not been seen in fertilizations of the other species.

The early stages of *Glycera convoluta* have also been obtained and *Chaetopterus variopedatus* has been reared almost completely through its pelagic life. Material has been collected for detailed work on the histology of the development at some future date. Several attempts were again made to rear *Nephthys hombergi*, but this year, as so often previously, the cultures failed.

Fish and Fisheries

Continuing his work on the sense organs of fishes Dr A. Sand spent the first three months of the year at University College, London, where, by kind permission of Prof. A. V. Hill, he was engaged in the construction of a cathode ray oscillograph and amplifier, availing himself of the facilities and technical assistance of Prof. Hill's laboratory. The apparatus is now installed at the Plymouth Laboratory. During the summer, in collaboration with Dr Löwenstein of Glasgow, Dr Sand carried out an investigation on the quantitative aspects of the responses of the semicircular canals of the elasmobranch labyrinth. The problem arose out of their earlier work, and the experiments were made possible by the technique of obtaining single-fibre records from the isolated labyrinth preparation, which was described last year. This technique promises to lead to a complete analysis of the function of all the organs of the labyrinth, and this year's study of the horizontal canal is only the beginning of that programme.

As opportunity has permitted, Mr E. Ford has persevered with his studies of vertebral variation in fishes, and some interesting observations have been made concerning the relation between the number of rib-bearing vertebrae in the herring and the number of keeled scales along the ventral edge of the body between the throat and anus. This fresh information has an important bearing upon the significance of "keeled scale" counts as used in herring "race" investigations.

The winter drift-net fishery for herrings at Plymouth during the season of 1938–39 was again a complete failure and no samples were obtainable for examination. The virtual extinction of this fishery, though it may only be temporary, is much to be regretted. Apart from the loss of a valuable supply of fresh fish of excellent quality, the steam-drifter fleet from Lowestoft and the motor-drifter fleet from Cornwall have been deprived of a profitable source of income, while the Port of Plymouth has lost the business and revenue arising from the landing and marketing of the catches, and the maintenance requirements of the fishing fleets.

During recent years an increasing number of enquiries for forecasts of probable yield have come from fishing interests in Lowestoft and the West

Country, and it can at least be said that the forewarning of unfavourable prospects has spared a number of owners and crews the financial burden of a wasted visit to Plymouth. Attention is now being directed to the possibility of being able to detect at the earliest opportunity any change for the better in the fishing prospects.

The seasonal observations on the abundance of young fish in the plankton were continued by Mr Russell until the outbreak of war. The year 1939 has been the worst as regards production of young fish since these continuous observations were started. Almost all species were less than one-tenth as numerous as they were during the good years. The results of these observations are now in the press.

Mr G. A. Steven and Mr P. G. Corbin have continued their researches into the biology of the mackerel of western waters. Biometrical observations upon samples of mackerel from the large spring fishery based on Newlyn, Cornwall, over three consecutive seasons (1937–39) have now been collected and the data partially worked up. Age determinations derived from otolith readings (*vide* Report of Council for 1938, p. 13) have revealed the age compositions of the landings during those seasons. In 1937 fish in their fourth year of life (i.e. the 1934 year class) formed the main support of the fishery. Fish in their third year were caught in only negligible numbers. In 1938 fish in their fourth year (the 1935 year class) also made the chief contribution to that year's fishery, while fish in their third year were again very sparsely represented. In 1939, however, fish in their fourth year of life appeared in much smaller numbers than in the two previous years and the 1935 year class (now aged 4+ years) again made the major contribution to the fishery, followed closely by the 1934 year class (now aged 5+ years).

Newlyn Mackerel Fishery

Percentage Age-composition of Landing*

	2+	3+	4+	5+	6+	7 years and over
1937	7·4	45·7	22·7	17·0	5·7	1·6
1938	9·7	42·1	32·6	10·1	3·5	1·9
1939	6·5	20·1	31·4	22·1	11·6	8·3

* Some slight correction to these figures will need to be applied when more data are available as the proportion of unreadable otoliths is greatest in oldest year-classes thus affecting the percentages.

It becomes evident that the data directly obtainable from the Newlyn fishery are likely to prove inadequate for forecasting fluctuations in the yield, as the fishery can derive its main support from fish in their fourth year of life which are not sufficiently well represented in the catches at younger stages to act as a reliable index of their probable strength of recruitment to the stock at this age. Young fish are caught in larger numbers in shallow inshore waters later in the year, but the available statistics of landings relating to them are not adequate for forecasting purposes. To achieve this end some special means of obtaining reliable samples of the two- and three-year-old fish will have to be devised.

Three cruises have again been made this year for the collection of mackerel eggs, larvae, and post-larval stages, in addition to general plankton samples from the mackerel spawning and fishing grounds. The 1937 and 1938 mid-April cruises revealed that great spawning activity was already taking place at that time. This year, therefore, an earlier survey was carried out during a week's cruise which began on March 15, in order to ascertain, if possible, the approximate time of commencement of spawning. A few mackerel eggs were taken, 200 being the highest number at any station, and no larval stages were found. This very small maximum number of eggs and entire absence of larvae indicates that at the time of this survey spawning had only just begun.

Data obtained during the April cruise of 1937 suggested that probably two main centres of spawning activity exist on those grounds at this time of the year—one in a region south of Ireland and well to the westward of Land's End and another about 90 miles west of Ushant. A more extensive survey in 1938, made in conjunction with the fisheries branch of the Ministry of Agriculture of Eire, enabled a more precise delimitation of these two areas to be made. A strikingly similar distribution has again been found this year. The presence of these two centres of high spawning intensity in April would appear, therefore, to be a marked and constant feature of the spawning behaviour of the mackerel in this area. Their positions had changed only slightly from year to year. They become less well marked later in the season when the intensity of spawning is decreasing.

The third cruise this year was made at the end of June, and the material collected has not yet been fully worked up. On all cruises phytoplankton samples were collected and hydrographical data were obtained in April and June.

During the year many queries in connexion with the preservation of nets have been received by Dr Atkins. Advice has also been given as to the preservation of sand-bags. The methods found good in previous work were compared with new or modified treatments in several series of exposures of nets, trawl-twines and ropes immersed in the tidal basin at Pier Cellars, Cawsand. Though not quite complete, the work is being prepared for publication, as the last results were published four years ago, and the basin has been requisitioned by the Admiralty. The preservatives selected as most beneficial differ according to the use to which they are put; the materials vary from fine strand nets, for which good adherence is more important than good penetration, to thick ropes, for which good penetration is of the greatest importance.

The Library.

The thanks of the Association are again due to numerous Foreign Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent copies of their books or papers, which are much appreciated.

Published Memoirs.

Vol. xxiii, No. 2 of the Journal of the Association was issued in May, and Vol. xxiv, No. 1 in January.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association.

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Cooper, L. H. N. and Wilson, D. P., 1939. Formation of Native Lead under Laboratory Conditions. *Nature*, Vol. cxliii, p. 207.

Danielli, J. F., 1939. The Resistance of Nerve in Relation to Interpolar Length. *Journ. Physiol.*, Vol. xcvi, pp. 65–73.

Davson, H. and Danielli, J. F., 1938. Studies of the Permeability of Erythrocytes. V. Factors in Cation Permeability. *Biochem. Journ.*, Vol. xxxii, pp. 991–1001.

Fretter, V., 1939. The Structure and Function of the Alimentary Canal of some Tectibranch Molluscs, with a Note on Excretion. *Trans. Roy. Soc. Edin.*, Vol. lix, pp. 599–646.

Gurney, R. and Lebour, M. V., 1939. The Larvae of the Decapod Genus *Naushonia*. *Ann. Mag. Nat. Hist.* (11). Vol. iii, pp. 609–614.

Harvey, H. W., 1939. Biological Oceanography. *Recent Marine Sediments*: Amer. Assoc. Petroleum Geologists, pp. 142–152.

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Lebour, M. V., 1939. Decapod Crustacea associated with the Ascidian *Herdmania*. *Proc. Zool. Soc. Lond.*, Vol. cviii, B, pp. 649–653.

Moore, H. B., 1939. The Colonization of a New Rocky Shore at Plymouth. *Journ. Animal Ecol.*, Vol. viii, pp. 29–38.

Panikkar, N. Kesava, 1939. Osmotic Behaviour of *Palaemonetes varians* Leach. *Nature*, Vol. cxliv, pp. 866–867.

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Rothschild, Miriam, 1938. Further Observations on the Effect of Trematode Parasites on *Peringia ulvae* (Pennant) 1777. *Novitates Zoolog.*, Vol. xli, pp. 84–102.

Rothschild, Miriam, 1938. The Excretory System of *Cercaria coronanda* n.sp. together with Notes on its Life-history and the Classification of Cercariae in the Superfamily Opisthorchioidea Vogel 1934 (Trematoda). *Novitates Zoolog.*, Vol. XLI, pp. 148–163.

Rothschild, Miriam, 1938. A Note on the Fin-folds of Cercariae of the Superfamily Opisthorchioidea Vogel 1934 (Trematoda). *Novitates Zoolog.*, Vol. XLI, pp. 170–173.

Rothschild, Miriam, 1939. A Note on the Life Cycle of *Cryptocotyle lingua* (Creplin) 1825 (Trematoda). *Novitates Zoolog.*, Vol. XLI, pp. 178–180.

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Young, J. Z., 1939. Fused Neurons and Synaptic Contacts in the Giant Nerve Fibres of Cephalopods. *Phil. Trans. Roy. Soc. Lond.*, Vol. 229, B, pp. 465–503.

Membership of the Association.

Vice-Presidents. Lord Mildmay of Flete, P.C., and The Right Hon. Sir Reginald Dorman-Smith, M.P., were unanimously elected Vice-Presidents at the Annual General Meeting held in June. Upon his retirement from the office of President of the Association, Lord Moyne was also unanimously elected a Vice-President.

R. Olaf Hambro, Esq., has taken the place of Lord Hollenden, C.M.G., as Prime Warden of the Fishmongers' Company.

Annual Members. The total number of annual members on December 1, 1939, was 322 of whom 66 were elected in response to a special appeal.

Associate Members. The number of Associate Members has been increased to seven by the election of Dr A. Bowman, Mr W. L. Sclater and Mr A. J. Smith.

Finance.

Grant from Development Fund. The Council have again to express their thanks to the Development Commissioners for their continued support of the general work of the Laboratory.

Private Income. On October 17, 1938, certain members appointed by Council met representatives of the Development Commission to discuss how the private income of the Association could be increased. As results of this meeting a notice was circulated with the object of adding to the membership of the Association, and efforts were made to obtain further subscriptions as rental of tables at the Plymouth Laboratory. In the autumn of 1938 the University of London decided to rent an additional table, and during the present year tables have also been rented by the Royal College of Surgeons and the Royal College of Physicians. In addition a special donation has been received from Magdalen College, Oxford. During the year 66 new members have been elected, a figure which may be compared with 15, which is the average for the previous three years.

The Council gratefully acknowledges the following generous grants for the year:—

From the Fishmongers' Company (£600), the Royal Society (£50), the Ray Lankester Trustees (£20), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10).

A Special Grant of £50 from the E. T. Browne fund of the Royal Society for the purchase of embedding and drying ovens and section-cutting equipment.

The following sums have also been received as rentals of tables in the Laboratory: The Universities of Cambridge (£105), London (£105) and Oxford (£52. 10*s*.), the Royal College of Surgeons (£52. 10*s*.), the Royal College of Physicians (£52. 10*s*.), the British Association (£50), the Physiological Society (£30), the Universities of Bristol (£25), Birmingham (£15. 15*s*.), Manchester (£10. 10*s*.), Leeds (£10. 10*s*.), the Imperial College of Science and Technology (£10) and the University of Sheffield (£5).

Building Scheme.

The private donations made towards the cost of the Laboratory extension, now completed, amount to £4,174. 9*s.* 0*d.*

	£	*s.*	*d.*
Grant from the Rockefeller Foundation ...	2000	0	0
Legacy from the late Mr E. T. Browne ...	1000	0	0
Dr G. P. Bidder	500	0	0
The Fishmongers' Company	250	0	0
The Lord Moyne	150	0	0
Col. E. T. Peel	100	0	0
The Duke of Bedford	50	0	0
Viscount Astor	50	0	0
Anonymous	50	0	0
The Earl of Iveagh	10	0	0
Major Dorrien Smith	5	0	0
The Hon. J. H. Parker	3	3	0
Messrs E. Hardman & Co.	2	2	0
The Earl of Stradbroke	2	2	0
Miss O. S. Munday	2	2	0
	£4174	9	0

The Council is glad to report that, thanks to these generous gifts and a special grant of £3000 from the Development Fund, it has been possible to carry out the building scheme in full, including the reconstruction, renovation and furnishing of the first floor of the main laboratory, and the provision of a new heating installation.

President, Vice-Presidents, Officers and Council.

The following is the list of those proposed by the Council for election for the year 1940–41.

President

G. P. Bidder, Sc.D.

Vice-Presidents

The Duke of Bedford, K.G.
The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Lord St Levan, C.B., C.V.O.
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S.
Sir Nicholas Waterhouse, K.B.E.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. Peel, D.S.O., M.C.
Lord Mildmay of Flete, P.C.
The Right Hon. Sir Reginald Dorman-Smith, M.P.
The Lord Moyne, P.C., D.S.O.
Prof. J. Stanley Gardiner, F.R.S.
Sir Joseph Barcroft, C.B.E., F.R.S.
Prof. Walter Garstang, D.Sc.

COUNCIL

To retire in 1941

Prof. H. Graham Cannon, Sc.D., F.R.S.
R. S. Clark, D.Sc.
A. C. Gardiner
Prof. A. C. Hardy, D.Sc., F.R.S.
Prof. A. V. Hill, O.B.E., Sc.D., Sec. R.S., M.P.
Prof. D. L. Mackinnon, D.Sc.

To retire in 1942

H. G. Maurice, C.B.
Lord Rothschild, Ph.D.
J. R. Norman
Morley Neale

To retire in 1943

Prof. D. Keilin, Sc.D., F.R.S.
E. S. Russell, O.B.E., D.Sc.
Prof. E. J. Salisbury, D.Sc., F.R.S.
L. A. Harvey
H. Cary Gilson

Chairman of Council

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer

Guy Wood, M.B., M.R.C.P., 97 High Street, Hungerford, Berks.

Secretary

Stanley Kemp, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Sc.D.
The Lord Moyne, P.C., D.S.O.
A. T. A. Dobson, C.B., C.V.O., C.B.E. (Ministry of Agriculture and Fisheries)
R. Olaf Hambro (Prime Warden of the Fishmongers' Company)
Guy Wood, M.B., M.R.C.P. (Fishmongers' Company)
Admiral Sir Aubrey C. H. Smith, K.B.E., C.B., M.V.O. (Fishmongers' Company)
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
Prof. J. Gray, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society)
Sir Sidney Harmer, K.B.E., Sc.D., F.R.S. (Royal Society)
E. J. Allen, C.B.E., D.Sc., F.R.S. (*Honorary*)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH, 1940

	£	s.	d.	£	s.	d.
To SALARIES, including Association's Contributions to Superannuation				8394	16	4
,, LABORATORY WAGES, including National Insurance and Association's Contributions to Superannuation				2435	12	9
,, DEPRECIATION OF LIBRARY				395	14	2
,, SCIENTIFIC PUBLICATIONS, *Less* SALES ...				718	8	9
,, UPKEEP OF LABORATORIES AND TANK ROOMS:						
Buildings and Machinery	445	14	3			
Electricity, Gas, Coal, Oil and Water ...	345	14	1			
Chemicals and Apparatus	407	11	9			
Rates, Taxes and Insurance	104	13	9			
Travelling Expenses	122	0	5			
Stationery, Postages, Telephone, Carriage and Sundries	300	4	8			
Specimens	154	8	0			
				1880	6	11
,, MAINTENANCE AND HIRE OF BOATS:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1486	8	4			
Coal, Water, Oil, Petrol, etc.	197	8	10			
Maintenance and Repairs, with Nets, Gear and Apparatus	192	12	5			
Purchase of Material for Nets for Sale, excluding Labour	101	0	5			
Boat Hire and Collecting Expenses ...	13	13	6			
Insurance	184	4	0			
				2175	7	6
,, TRANSFER TO "SALPA" DEPRECIATION FUND				297	11	3
,, TRANSFER TO REPAIRS AND RENOVATIONS FUND				300	0	0
,, BALANCE, BEING SURPLUS FOR THE YEAR ...				7	3	9
				£16,605	1	5

	£	s.	d.	£	s.	d.
By GRANTS:						
Ministry of Agriculture and Fisheries Grant from Development Fund	13,401	10	8			
Fishmongers' Company	600	0	0			
Royal Society	50	0	0			
British Association	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee ...	10	0	0			
				14,141	10	8
,, SUBSCRIPTIONS (excluding Subscriptions received in advance)				302	9	9
,, DONATIONS				28	5	10
,, SALES:						
Specimens	681	3	11			
Fish (*less* Expenses)	41	13	8			
Nets, Gear and Hydrographical Apparatus	172	8	11			
				895	6	6
,, TABLE RENTS (including Universities of Cambridge £105; London £105; Oxford £52 10*s*.; Bristol £25; Birmingham £15 15*s*.; Leeds £10 10*s*.; Manchester £10 10*s*.; Sheffield £5; Royal College of Physicians £52 10*s*.; Royal College of Surgeons £52 10*s*.; Imperial College £10; Trustees of Ray Lankester Fund £20) ...				603	10	6
,, TANK ROOM RECEIPTS				473	8	0
,, INTEREST ON INVESTMENTS, *Less* TAX:						
General Fund	9	11	4			
Salpa Depreciation Fund	47	11	3			
				57	2	7
,, INTEREST ON BANK DEPOSITS *Less* BANK CHARGES				6	8	5
,, INCOME TAX RECOVERABLE				90	2	2
,, SALE OF DR M. V. LEBOUR'S BOOK					15	6
,, SALE OF "MARINE FAUNA OF PLYMOUTH" ...				6	1	6
				£16,605	1	5

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH, 1940

	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:						
On Open Account				816	15	0
PROPORTION OF SUBSCRIPTIONS RECEIVED IN ADVANCE	177	9	0			
GRANT RECEIVED IN ADVANCE	150	0	0			
				327	9	0
AQUARIUM GUIDE PRINTING FUND:						
As at 31st March, 1939	33	1	0			
Sale of Aquarium Guides	8	1	6			
	41	2	6			
Less: Expenditure	20	2	6			
				21	0	0
J. MARTIN, DECEASED, PENSION FUND:						
As at 31st March, 1939	82	15	0			
Add: Interest on Deposit Account		18	2			
	83	13	2			
Less: Payments made to J. Martin and to his legal representatives	83	13	2			
				–	–	–
SPECIAL APPARATUS FUND:						
As at 31st March, 1939	73	12	7			
Grant Received from the Royal Society	50	0	0			
	123	12	7			
Less: Expenditure	114	15	8			
				8	16	11
MACKEREL RESEARCH FUND:						
As at 31st March, 1939		16	11			
Grant Received	932	17	10			
	933	14	9			
Less: Expenditure	839	17	9			
				93	17	0

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at 31st March, 1931						
S.S. *Salpa*	2000	0	0			
Motor Boat *Gammarus*	150	0	0			
Nets, Gear and General Equipment	27	0	0			
				2177	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS:						
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at Cost						
As at 31st March, 1939	1309	16	2			
Additions during the year	138	14	10			
				1448	11	0
LIBRARY:						
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at Cost *less* Depreciation						
As at 31st March, 1939	2352	16	10			
Additions during the year	320	16	11			
	2673	13	9			
Less: Depreciation	395	14	2			
				2277	19	7
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS:						
As estimated by the Director				450	0	0
SUNDRY DEBTORS:						
Sale of Specimens and Journals				62	4	2
INCOME TAX RECOVERABLE				109	6	7
PREPAYMENTS				73	17	8
GENERAL FUND INVESTMENT at Market Value as at 31st March, 1931:						
£352 2*s.* 3*d.* Local Loans 3%				232	7	10
(Market Value at date £297 10*s.* 9*d.*)						
"SALPA" DEPRECIATION FUND INVESTMENTS at Cost:						
£590 6*s.* Local Loans 3%	506	10	9			
£2124 6*s.* 9*d.* Conversion Loan 3%	2148	18	0			
(Market Value at date £2633 15*s.* 2*d.*)				2655	8	9

BUILDINGS EXTENSION FUND:			
As at 31st March, 1939		1551 19 0	
Donations Received		3618 16 10	
	£ s. d.	5170 15 10	
Less: Expenditure	4926 17 6		
Loss on Sale of Investment	11 13 6	4938 11 0	
			232 4 10
E. T. BROWNE BEQUESTS FUND:			
As at 31st March, 1939		5456 0 4	
Interest on Investment, *less* Tax		109 13 3	
		5565 13 7	
Less: Expenditure		4 5 6	
			5561 8 1
"SALPA" DEPRECIATION FUND:			
Balance transferred from Reserve for Depreciation of Boats and Machinery as at 31st March, 1939		2357 17 6	
Transfer from Income and Expenditure Account		297 11 3	
			2655 8 9
COMPOSITION FEE FUND:			
As at 31st March, 1939		126 0 0	
Fees Received		31 10 0	
			157 10 0
REPAIRS AND RENOVATIONS FUND:			
As at 31st March, 1939		50 16 9	
Transfer from Income and Expenditure Account		300 0 0	
Interest on Investment		1 0 0	
		351 16 9	
Less: Expenditure		146 11 1	
			205 5 8
CONSTANT TEMPERATURE ROOMS FUND:			
As at 31st March, 1939		41 10 8	
Less: Expenditure		37 9 6	
			4 1 2
SURPLUS:			
As at 31st March, 1939		7088 15 7	
Add: Surplus for the year, as per Income and Expenditure Account		7 3 9	
The above surplus will be supplemented by receipt of compensation for the use of the *Salpa* by H.M. Government, the amount of which has not yet been ascertained.			7095 19 4
			£17,179 15 9

REPAIRS AND RENOVATIONS FUND INVESTMENT at Cost:		
£101 4*s*. Conversion Loan 3%		101 0 0
(Market Value at date £101 14*s*. 2*d*.)		
COMPOSITION FEE FUND INVESTMENTS at Cost:		
£18 8*s*. 6*d*. Local Loans 3%	15 15 0	
£139 2*s*. 11*d*. Conversion Loan 3%	141 15 0	
(Market Value at date £155 7*s*. 7*d*.)		157 10 0
BUILDINGS EXTENSION FUND INVESTMENT at Cost:		
£19 0*s*. 11*d*. Conversion Loan 3%		18 8 6
(Market Value at date £19 2*s*. 10*d*.)		
BROWNE BEQUESTS INVESTMENT at Cost:		
£5712 7*s*. 5*d*. Conversion Loan 3%		5609 13 3
(Market Value at date £5740 18*s*. 8*d*.)		
CASH AT BANK AND IN HAND:		
Coutts & Company—Current Account	1743 0 3	
Lloyds Bank Limited—Current Account	35 15 11	
	1778 16 2	
Cash in Hand	27 12 3	
		1806 8 5
		£17,179 15 9

D. L. MACKINNON } *Members of Council.*
E. J. ALLEN }

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Association and have obtained all the information and explanations we have required. Capital expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs according to the best of our information and the explanations given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. 9*th May*, 1940.

PRICE, WATERHOUSE & CO.

LIST OF GOVERNORS, FOUNDERS, MEMBERS AND ASSOCIATE MEMBERS

July 1940

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 41 *Mincing Lane, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
  The Prime Warden. (**Council,** 1886→)
  Smith, Admiral Sir Aubrey C. H., K.B.E., C.B., M.V.O., *Hay's Wharf and Dock, Southwark, S.E.* 1. (**Council,** 1938→)
  Wood, Guy, M.B., M.R.C.P., 99 *Sydenham Hill, S.E.* 26. (**Council,** 1932→; **Hon. Treasurer,** 1934→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, 10 *Whitehall Place, S.W.* 1
Bayly, Robert (the late). (**Council,** 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council,** 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council,** 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Cambridge.* (**Council,** 1899→; **President,** 1939→)
The Lord Moyne, P.C., D.S.O., 10 *Grosvenor Place, S.W.* 1. (**Vice-President,** 1929; 1939→; **President,** 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S., *Reservoir House, North Hill, Plymouth.* (Honorary). (**Council,** 1895→; **Secretary,** 1895–1936; **Hon. Governor,** 1937→)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall,* 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council,** 1884–92; **Hon. Treasurer,** 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary,** 1884–90; **President,** 1891–1929)
1884 Lord Masham (the late)
1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council,** 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President,** 1884–1913)

1884 Poulton, Prof. Sir Edward B., F.R.S., *Wykeham House*, *Oxford*. (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road*, *Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall*, *E.C.* 2
1889 The Worshipful Company of Grocers, *Poultry*, *E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., 42 *George Street*, *Plymouth*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square*, *S.W.* 1. (**Vice-President**, 1929 →)
1902 Gurney, Robert, D.Sc., *Bayworth Corner*, *Boars Hill*, *Oxford*. (**Council**, 1932–35)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S., *Anatomy School*, *Cambridge*
1913 Heron-Allen, E., F.R.S., *Large Acres*, *Selsey Bill*, *Sussex*
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens*, *W.* 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R., *The Court*, *St Fagan's*, *Glamorgan*
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., 125 *Lower Thames Street*, *E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street*, *Westminster*, *S.W.* 1
1925 Discovery Committee, *Colonial Office*, *Downing Street*, *S.W.* 1
1927 Bidder, Miss Anna, Ph.D., *Cavendish Corner*, *Cambridge*
1933 Peel, Col. E. T., D.S.O., M.C., c/o *Messrs Peel and Co., Ltd.*, *P.O. Box* 331, *Alexandria*, *Egypt*. (**Vice-President**, 1936 →)
1938 Buchanan, Dr Florence (the late)

MEMBERS

* Life Members

1939 Abercrombie, M., *Queen's College*, *Oxford*
1940 Adrian, Prof. E. D., M.D., D.Sc., LL.D., F.R.S., *Trinity College*, *Cambridge*
1895 Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S., *Reservoir House*, *North Hill*, *Plymouth*. (**Council**, 1895 →; **Secretary**, 1895–1936)
*1927 Amirthalingam, C., Ph.D., *Rahula Vidyalaya*, *Matara*, *Ceylon*
1932 Aquario Vasco da Gama, *Dafundo*, *Lisbon*, *Portugal*

*1911 Viscount Astor, 4 *St James's Square, London, S.W.* 1. (**Vice-President**, 1911→)
1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.I.C., F. Inst. P., F.R.S., *The Old Vicarage, Antony, East Cornwall*
*1910 Atkinson, G. T., 9 *Battery Green Road, Lowestoft, Suffolk*

1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow*
*1920 Baker, J. R., Ph.D., *New College, Oxford*
1936 Baldwin, E., Ph.D., *Biochemical Laboratory, Tennis Court Road, Cambridge*
1939 Barnes, H., 74 *Beaumont Road, Plymouth*
1934 Barnes, Miss M. G., *Painswick, Christchurch Road, Newport, Mon.*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, E. J. W., *Department of Zoology, University College, Nottingham*
1939 Bassindale, R., *Zoology Department, The University, Bristol*
1932 Bateman, J. B., Ph.D., *Johnson Foundation for Medical Physics, School of Medicine, University of Pennsylvania, Philadelphia, Pa., U.S.A.*
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, The University, Teviot Place, Edinburgh*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne*, 1
*1885 Beck, Conrad, C.B.E., 34 *Upper Addison Gardens, London, W.* 14
*1907 The Duke of Bedford, K.G., K.B.E., F.R.S., *Endsleigh, Tavistock*. (**Vice-President**, 1907→)
1928 Beer, G. R. de, D.Sc., F.R.S., *University College, Gower Street, London, W.C.* 1
1936 Begg, Miss C. R., *Nashdom, Novar Crescent, Kirkcaldy, Fife*
1926 Bělehrádek, Prof. J., M.D., *Albertov* 4, *Prague II, Czechoslovakia*
1939 Bennett, F., 8 *Holland Park, London, W.* 11
1925 Berrill, Prof. N. J., D.Sc., *McGill University, Montreal, Canada*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., *Department of Fisheries, P.O. Box* 744, *Singapore*
1930 Blaschko, Dr H., *Physiological Department, Downing Street, Cambridge*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1921 Blundell, H. S. Moss, C.B.E., *Herring Industry Board*, 8 *Buckingham Gate, London, S.W.* 1
1930 Bogorov, Dr B. G., *State Oceanographical Institute*, 17 *Werchnia Krasnoselskaja, Moscow, U.S.S.R.*
1936 Bogue, Prof. J. Yule, D.Sc., *Royal Veterinary College, Camden Town, London, N.W.* 1
1932 Bolitho, Capt. R. J. B., *Ponsandane, Penzance*
1928 Borowik, Dr J., *San Marino*, 71 *Kosciuszki Torun, Poland*
1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge*. (**Council**, 1918–24)
1935 Bosanquet, S. J. A., *Dingestow Court, Monmouth*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8
1898 Bowles, Col. Sir Henry, Bart., *Forty Hall, Enfield, Middlesex*. (**Council**, 1927–29)
1940 Brambell, Prof. F. W. Rogers, D.Sc., *University College of North Wales, Bangor, Caernarvonshire*

1926 Branfoot, J. M., *Oundle School, Oundle, Peterborough, Northants*
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1937 Bristol Grammar School, *Bristol*
1933 Bristol University, *Department of Zoology, Bristol*
1939 British Ropes, Ltd., *Western Avenue, Cardiff*
*1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*
1928 Brown, Miss E. M., 53 *Pepys Road, Wimbledon, London, S.W.* 20
1936 Brown, Herbert H., Ph.D., c/o *Colonial Secretary, Nassau, Bahamas*
1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., 3 *Stafford Terrace, London, W.* 8
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)

1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester*. (**Council**, 1927–30, 1932–34, 1937→)
1927 Carruthers, J. N., D.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1923 Carter, G. S., Ph.D., *Zoological Laboratory, Cambridge*
*1931 Cattell, Dr McKeen, *Cornell University Medical College*, 477 *First Avenue, New York City, U.S.A.*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1934 Church, R. G., *Northridge, Heene Road, Worthing*
1924 Clark, R. S., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen*. (**Council**, 1938→)
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., "*Discovery*" *Staff, British Museum (Natural History), Cromwell Road, London, S.W.* 7
*1886 Coates and Co., *Southside Street, Plymouth*
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *The Royal South Hants and Southampton Hospital, Centenary Appeal Office*, 105 *Graham Road, Southampton*
1933 Cole, H. A., *Fisheries Experiment Station, Castle Bank, Conway.*
*1885 Collier Bros., *Plymouth*
1930 Colman, J. S., *Department of Zoology, The University, Sheffield*, 10
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter*
*1933 Cooper, L. H. N., D.Sc., F.I.C., *The Laboratory, Citadel Hill, Plymouth*
1937 Corbin, P. G., 37A *Lansdowne Road, London, W.* 11
1937 Corbin, Mrs P. G., *Hunstrete House, Pensford, Somerset*
1937 Cosway, C. A., 20 *Maurice Road, Kings Heath, Birmingham*, 14
1933 Cotton, Col. R. Stapleton, *Rookwood, Clyro, Hereford*
1936 Crawford, G. I., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1909 Crawshay, L. R., *The Laboratory, Citadel Hill, Plymouth*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Animal Breeding Research Department, The University, Edinburgh*
1936 Crimp, P. R., 329 *Brincliffe Edge Road, Sheffield*, 11
1929 Crofts, Miss D. R., *King's College for Household and Social Science, Campden Hill, London, W.* 8
1930 Cuthbertson, N., *Edelweiss Cottage, Smith's Parish, Bermuda*

1922 Dale, Sir Henry H., G.C.M.G., C.B.E., M.D., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3. (**Council**, 1922–28)

*1919 Damant, Capt. G. C. C., R.N., C.B.E., *Thursford, Cambridge Road, East Cowes, Isle of Wight*. (**Council**, 1928–31, 1937–40)
1939 Danielli, J. F., *Biochemical Laboratory, Cambridge*
1929 Darby, Dr H. H., 155 *Lockwood Avenue, New Rochelle, New York, U.S.A.*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay*
1937 Davie, S. B., 1 *Cheltenham Place, Plymouth*
1925 Davis, F. M., *Fisheries Laboratory, Lowestoft, Suffolk*
1931 Dawes, B., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2
1938 Deacon, G. E. R., D.Sc., "*Discovery*" *Staff, British Museum (Natural History), Cromwell Road, London, S.W.* 7
1939 Dennell, Ralph, *Department of Zoology, Imperial College of Science and Technology, South Kensington, London, S.W.* 7
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, South Africa*
1910 Dobell, C. C., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3
1939 Dobson, A. T. A., C.B., C.V.O., C.B.E., *Ministry of Agriculture and Fisheries,* 7 *Whitehall Place, London, S.W.* 1. (**Council**, representing Ministry of Fisheries, 1938→)
1939 Dorman-Smith, Col. the Rt. Hon. Reginald H., M.P., *Stodham Park, Liss, Hants*. (**Vice-President**, 1939→)
1939 Dundee University College Library, *Dundee*
1937 Dyke, Frederick Montague, *Lever Bros., Ltd., Port Sunlight, Cheshire*

1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield*
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, Devon.*
1937 Evans, H. Muir, M.D., *Greenbank, St Mary's Road, Beccles*. (**Council**, 1937–40)
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*

1929 Faouzi, Dr Hussein, *Fisheries Research Laboratory, Kayed Bay, Alexandria, Egypt*
1922 Farran, G. P., *Department of Fisheries,* 2 *Kildare Place, Dublin*. (**Council**, 1922–26)
1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1928 Fisher, Prof. R. A., Sc.D., F.R.S., *Galton Laboratory, University College, London*. (**Council**, 1932–35)
1934 Fleming, Miss K. M. G., *The Rossan, Auchencairn, Castle Douglas, Kirkcudbrightshire*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth*
1935 Ford, E. B., *University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1939 Fowell, R. R., *Municipal Technical College, Mount Pleasant, Swansea*
1885 Fowler, G. Herbert, C.B.E., Ph.D., *The Old House, Aspley Guise, Bedfordshire*. (**Council**, 1891–1911; **Hon. Secretary**, 1891–95)
1933 Fox, Cuthbert L., *Wodehouse Place, Falmouth*

1912 Fox, Prof. H. M., F.R.S., *Zoological Department, The University, Edgbaston, Birmingham.* (**Council**, 1928–30, 1931–34)
1934 France: Office Scientifique et Technique des Pêches Maritimes, *Laboratoire de Lorient, Port de Lorient-Keroman, France*
1934 France: Office Scientifique et Technique des Pêches Maritimes, *Laboratoire de la Rochelle, France*
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
*1935 Fraser, James H., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1939 Fretter, Miss Vera, Ph.D., *Zoology Department, Birkbeck College, Fetter Lane, London, E.C.* 4
1930 Fritsch, Prof. F. E., D.Sc., F.R.S., *Botanical Laboratory, Queen Mary College, Mile End Road, London, E.* 1. (**Council**, 1931–34, 1937–40)

1938 Gardiner, A. C., *Metropolitan Water Board,* 177 *Rosebery Avenue, London, E.C.* 1. (**Council**, 1938→)
1935 Gardner, Adrian, *Roach River Fishery Co., Ltd., Burnham-on-Crouch, Essex*
1936 Gardner, Major Austin, M.C., *Seasalter and Ham Oyster Fishery Co., Ltd., Whitstable, Kent*
*1907 Garstang, Prof. W., D.Sc., *Five Elms, Apsley Road, Oxford.* (**Council**, 1907–10, 1923–28; **Vice-President**, 1940→)
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Department of Botany, King's College, Strand, London, W.C.* 2
1932 Ghardaqa Marine Laboratory of the Egyptian University, *Ghardaqa, Red Sea District, Egypt*
1935 Gilson, H. Cary, *Trinity College, Cambridge.* (**Council**, 1940→)
1910 Goodrich, Prof. E. S., D.Sc., LL.D., F.R.S., 12 *Park Town, Oxford.* (**Council**, 1915–20, 1924–28, 1930–33, representing Oxford University, 1934→)
1939 Goodrich, Dr Helen, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1931 Graham, Alastair, *Zoology Department, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Graham, Michael, *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36)
1930 Grant, R., c/o *International House, Chicago University, Illinois, U.S.A.*
1930 Gray, Dr A. M. H., 69 *Harley Street, London, W.* 1
1912 Gray, Prof. J., M.C., Sc.D., F.R.S., *King's College, Cambridge.* (**Council**, 1920–24, representing Cambridge University, 1928→)
1924 Guernsey: States Committee for Fisheries, *States Office, Guernsey*

1932 Hamilton, Ian I., *Dauntsey's School, West Lavington, near Devizes, Wilts.*
*1924 Harding, Ambrose, *The Hall, Madingley, Cambs.*
*1928 Harding, Mrs J. P., Sc.D., *Zoological Laboratory, Downing Street, Cambridge*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Oceanography, University College, Hull.* (**Council**, 1938→)
1929 Harington, Prof. C. R., Ph.D., F.R.S., 67 *Corringham Road, London, N.W.* 11. (**Council**, 1931–34)
*1885 Harmer, Sir Sidney F., K.B.E., D.Sc., F.R.S., *The Old Manor House, Melbourn, near Royston, Herts.* (**Council**, 1895–1912, 1918–23; representing Royal Society, 1925→; **Vice-President**, 1934→)
1932 Harris, J. E., Ph.D., *Christ's College, Cambridge*

1939 Harrison, R. J., *Gonville and Caius College, Cambridge*
1929 Hart, T. J., D.Sc., "*Discovery*" *Staff, British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
1934 Hartley, P. H. T., *Bulbeck Mill House, Barrington, Cambridge*
1924 Harvey, H. W., Sc.D., *The Laboratory, Citadel Hill, Plymouth*
1933 Harvey, L. A., *Department of Zoology, University College of the South West, Exeter*. (**Council**, 1940→)
1939 Hastings, Anna B., Ph.D., *British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S.*
1931 Henderson, G. T. D., Ph.D., *Department of Oceanography, University College, Hull*
1939 Henry, Dr Herbert G. M., *City Bacteriological Laboratories*, 150 *Great Charles Street, Birmingham*
1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1
1939 Herklots, G. A. C., Ph.D., *The University, Hong Kong*
1939 Hewer, H. R., *Department of Zoology and Applied Entomology, Imperial College of Science, London, S.W.* 7
1926 Hickling, C. F., *Fisheries Laboratory, Lowestoft, Suffolk*
1926 Hill, Prof. A. V., O.B.E., Sc.D., Sec.R.S., M.P., *Physiological Laboratory, University College, Gower Street, London, W.C.* 1. (**Council**, 1925–29, 1930–33, 1934–37, 1938→)
1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*
1919 Hillier, W. T., M.R.C.S., 73 *Francis Road, Edgbaston, Birmingham*
*1921 Hindle, Prof. E., Sc.D., *Department of Zoology, The University, Glasgow*
1937 Hinton, M. A. C., F.R.S., *British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
1926 Hirasaka, Prof. K., *Zoology Department, Imperial University, Formosa, Japan*
1926 Hobson, Prof. A. D., *King's College, Newcastle-on-Tyne*
1939 Hodgkin, A. L., *Trinity College, Cambridge*
1925 Hogben, Prof. Lancelot T., D.Sc., F.R.S., *Natural History Department, Marischal College, Aberdeen*. (**Council**, 1924–25)
1939 Holmes, W., *Magdalen College, Oxford*
1933 Horne, F. R., *Seale Hayne Agricultural College, Newton Abbot, Devon.*
1939 Hosker, Dr Anne, *University College, Leicester*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1936 Hudson, A., c/o *Overseas Farmers Cooperative Federation, Ltd.*, 4 *Fenchurch Avenue, London, E.C.* 3
1929 Hull University College, *Hull, Yorks.*
1928 Hunt, O. D., *Corrofell, Newton Ferrers, South Devon.*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1920–25)

1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
*1921 Jenkins, Mrs W., *Westhide, Hereford*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*

1934 John, D. Dilwyn, *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*
1923 Judge, J. J., 38 *Looe Street, Plymouth*

1940 Keilin, D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940)
1928 Kemp, Stanley, Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth.* (**Council**, 1929–30, 1932–34, 1935→; **Secretary**, 1936→)
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The Association was founded in 1884 at a meeting held in the rooms of the Royal Society of London with Professor T. H. Huxley in the chair. Amongst distinguished scientific men present on that occasion were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester, who was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £16,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv, p. 735 of this *Journal*.

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All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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